THÈSE DE DOCTORAT

DISSERTATION

COTUTELLE:

Université Pierre et Marie Curie
École doctorale
« Diversité du Vivant »

Universität Wien

Sujet de la thèse :

Titel der Dissertation:

Phylogeny of the limbed vertebrates with special consideration of the origin of the modern amphibians

présentée par

verfasst von
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UFR 927
Sciences de la Vie

A 091443
Doktoratsstudium Naturwissenschaften: Paläobiologie

pour obtenir le grade de

Docteur de l'Université Pierre et Marie Curie

angestrebter akademischer Grad:

Doktor der Naturwissenschaften
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Vienne (Autriche), août 2010

Wien, im August 2010

La composition précise du jury et la date de soutenance (prévue pour la première moitié de septembre 2010) ne pourront être fixées qu'après que la thèse sera jugée par les rapporteurs.

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Abstract

Despite decades of intensive research, the origins of the frogs incl. toads (Salientia), of the salamanders incl. newts (Caudata), and of the caecilians (Gymnophiona), together with that of the extinct Albanerpetontidae, remain controversial. Three groups of hypotheses persist in the literature: First, the aforementioned taxa could form a clade (Lissamphibia, a crown-group of which Albanerpetontidae may be a member or the sister-group), which could be nested among the Paleozoic temnospondyls, making the coeval lepospondyls stem-amniotes (temnospondyl hypothesis/TH). Second, Lissamphibia could belong among the lepospondyls; in this case, the temnospondyls would be stem-tetrapods (lepospondyl hypothesis/LH). Alternatively, the frogs and the salamanders may be temnospondyls while the caecilians may be lepospondyls (polyphyly hypothesis/PH). I have tried to discriminate between these alternatives both directly (by phylogenetic analysis) and indirectly (the PH predicts a much older divergence date between the modern amphibians than the age implied by the TH as well as the LH). Three partly novel dating methods support a Permian date, compatible with the TH and the LH but not the PH. These methods are: a time-calibrated supertree compiled and analyzed with new software; molecular divergence dating with several calibration points that have maximum age constraints; and calculation of confidence intervals on the time of origin of a clade – this latter method is independent of the phylogeny and uses stratigraphic data only. All three hypotheses have been supported by recently published phylogenetic analyses. Having made changes to three data matrices that supported the TH or the PH to make them congruent with the descriptive literature and personal observations, ordered potentially continuous characters, merged correlated characters, and scored ontogeny-affected characters as unknown in morphologically immature specimens, I find that these matrices (including the largest one published to date, which had bolstered the TH) support the LH upon reanalysis. This agrees with previous findings that small changes to a data matrix can cause large differences between the resulting trees. The TH is only a little less parsimonious than the LH in two of them, but the PH is much less parsimonious in all three. The phylogenetic position of Albanerpetontidae remains unstable.

Résumé

Malgré des décennies de recherche intensive, les origines des grenouilles, crapauds et rainettes (anoures et proches parents éteints : Salientia), des salamandres et tritons (urodèles et proches parents éteints : Caudata), des gymnophiones, et des albanerpétontidés (éteints) restent débattues. Trois groupes d'hypothèses persistent dans la littérature : Premièrement, les taxons mentionnés pourraient faire les parties d'un clade (Lissamphibia, un groupe apical dont les albanerpétontidés pourraient faire partie ou être le groupe-frère), qui pourrait se trouver parmi les temnospondyles paléozoïques, faisant des lépospondyles du même âge des amniotes-souche (hypothèse temnospondyle/HT). Deuxièmement, la position phylogénétique des lissamphibiens pourrait être parmi les lépospondyles ; dans ce cas-là, les temnospondyles seraient des tétrapodes-souche (hypothèse lépospondyle/HL). Comme alternative, les anoures et les urodèles pourraient être des temnospondyles tandis que les gymnophiones seraient des lépospondyles (hypothèse de polyphylie/HP). J'ai essayé de discriminer entre ces alternatives de façon directe (par analyse phylogénétique) et indirecte (la HP suggère une date de divergence bien plus ancienne entre les grands clades d'amphibiens modernes que la HT et aussi la HL). Trois méthodes de datation, en partie nouvelles, soutiennent une date permienne, compatible avec la HT et la HL mais non avec la HP. Ces méthodes sont : un arbre de synthèse calibré dans le temps, compilé et analysé à l'aide de nouveaux logiciels ; une datation moléculaire de divergences avec plusieurs points de calibration ayants des âges maximaux contraints ; et un calcul d’intervalles de confiance sur la date d’origine d’un clade – cette dernière méthode est indépendante de la phylogénie et utilise uniquement des données stratigraphiques. Les trois hypothèses ont toutes été soutenues récemment par des analyses phylogénétiques. Ayant effectué des changements à trois matrices de données qui soutenaient la HT ou la HP pour les rendre congruentes avec la littérature descriptive et des observations personnelles, ordonné des caractères potentiellement continus, fusionné des caractères correlés, et codé des caractères influencés par l’ontogenèse comme inconnus chez des spécimens morphologiquement immatures, je trouve que ces matrices (incluant la plus grande publiée, qui avait soutenu la HT) soutiennent la HL lors d’une réanalyse. Ceci correspond à des résultats antérieurs indiquants que de petits changements à un jeu de données peuvent causer des différences majeures entre les arbres résultants. La HT n’est qu’un peu moins parcimonieuse que la HL dans deux d’entre elles, mais la HP est beaucoup moins parcimonieuse selon les trois matrices. La position phylogénétique des albanerpétontidés reste instable.

Zusammenfassung

Trotz Jahrzehnten intensiver Forschung bleiben die Ursprünge der Frösche einschließlich Kröten und Unken (Salientia), Salamander einschließlich Molche (Caudata) und Blindwühlen (Gymnophiona), zusammen mit dem der ausgestorbenen Albanerpetontidae, kontrovers. Drei Gruppen von Hypothesen halten sich in der Literatur: Erstens könnten die erwähnten Taxa ein Monophylum bilden (Lissamphibia, eine Kronengruppe, von der Albanerpetontidae ein Mitglied oder die Schwestergruppe sein könnte), das in den paläozoischen Temnospondylen verschachtelt sein könnte, was aus den Lepospondylen des gleichen Zeitalters Stammgruppenamnioten machen würde (Temnospondylenhypothese/TH). Zweitens könnte Lissamphibia zu den Lepospondylen gehören; in diesem Fall wären die Temnospondylen Stammgruppentetrapoden (Lepospondylenhypothese/LH). Alternativ dazu könnten die Frösche und die Salamander Temnospondylen sein, während die Blindwühlen Lepospondylen wären (Polyphyliehypothese /PH). Ich habe versucht, zwischen diesen Alternativen sowohl direkt (durch phylogenetische Analyse) als auch indirekt zu unterscheiden (die PH sagt ein viel älteres Divergenzdatum zwischen den modernen Amphibien voraus als das Alter, das sowohl die TH als auch die LH implizieren). Drei zum Teil neuartige Datierungsmethoden stützen ein permisches Alter; das ist mit der TH und der LH vereinbar, aber nicht mit der PH. Diese Methoden sind: ein mit neuer Software erstellter und analysierter sowie an der Zeit kalibrierter Supertree; molekulare Divergenzdatierung mit mehreren Kalibrierungspunkten, deren maximales Alter beschränkt ist; und Berechnung von Konfidenzintervallen auf das Ursprungsdatum eines Monophylums – letztere Methode ist unabhängig von der Phylogenie und verwendet ausschließlich stratigraphische Daten. Alle drei Hypothesen werden von vor kurzem veröffentlichten phylogenetischen Analysen unterstützt. Ich habe Änderungen an drei Datenmatrizen vorgenommen, die die TH oder die PH gestützt hatten, um sie in Übereinstimmung mit der beschreibenden Literatur und eigenen Beobachtungen zu bringen, potentiell kontinuierliche Merkmale geordnet, korrelierte Merkmale zusammengelegt, und von der Ontogenie beeinflusste Merkmale in morphologisch nicht ausgewachsenen Exemplaren als unbekannt codiert; wenn ich sie neu analysiere, stützen diese Matrizen (einschließlich der größten bisher veröffentlichten, die die TH aufrecht erhalten hatte) die LH. Das stimmt mit früheren Ergebnissen überein, wonach kleine Änderungen an einer Datenmatrix große Unterschiede in den resultierenden Bäumen hervorrufen können. In zwei von diesen Matrizen ist die TH nur ein bisschen weniger sparsam als die LH, aber die PH entspricht in allen dreien deutlich weniger dem Parsimonieprinzip. Die phylogenetische Position der Albanerpetontiden bleibt instabil.

Résumé étendu français

« Rien en biologie n'a de sens qu'à la lumière de l'évolution »
– Theodosius Dobzhansky (1973)
« Rien en évolution n'a de sens sans une phylogénie »
– Gina C. Gould & Bruce J. MacFadden (2002, 2004)

Comptant près de 6700 espèces actuelles nommées (http://amphibiaweb.org au 12 août 2010), les amphibiens actuels représentent une partie non négligeable de la diversité actuelle des vertébrés. Il y a de grandes lacunes morphologiques entre les trois plus grands clades bien distincts : les grenouilles, crapauds et rainettes (groupe apical : Anura ; groupe total : Salientia), les salamandres et tritons (groupe apical : Urodela ; groupe total : Caudata) et les gymnophiones (groupe apical : Gymnophiona ; groupe total : Gymnophionomorpha, voir chapitre 3). Pour cette raison et d'autres, comme le nombre très petit de fossiles datant du début de l'histoire des amphibiens modernes (voir chapitre 6 pour une liste détaillée), l'origine des amphibiens actuels est controversée. Ceci a été aggravé plutôt que résolu par la découverte des albanerpétontidés (Estes & Hoffstetter 1976) mi-jurassiques à pliocènes (Gardner et al. 2003 ; Delfino & Salas 2007), qui constituent un clade d'animaux allongés en forme de salamandre (mais portants des écailles), et leur reconnaissance comme quatrième groupe d'amphibiens modernes (Fox & Naylor 1982). En général, les hypothèses sur la phylogénie des tétrapodes (voir les commentaires sur la nomenclature ci-dessous) ont largement atteint un consensus comme démontré dans figure 1, mais la position des amphibiens modernes dans cet arbre est très débattue. Avec des changements plutôt négligeables, trois groupes d'hypothèses persistent dans la littérature depuis le 19ème siècle :

- les amphibiens actuels pourraient constituer un clade, **Lissamphibia**,
    - dont la position phylogénétique pourrait se trouver parmi les temnospondyles dissorophoïdes, ce qui voudrait dire que les lépospondyles seraient des amniotes-souche (**hypothèse temnospondyle**) ;
    - comme alternative, les lissamphibiens pourraient être des lépospondyles (au plus probablement comme groupe-frère des lysorophiens) – dans ce cas-là les temnospondyles seraient des tétrapodes-souche (**hypothèse lépospondyle**) ;
- finalement, les amphibiens modernes pourraient être polyphylétiques – les anoures et (depuis la deuxième moitié des années 1980) les urodèles seraient des temnospondyles, les gymnophiones seraient des microsaures et donc des lépospondyles (**hypothèse de polyphylie**).

Avec l'origine des tortues (Lyson et al. 2010), l'origine des amphibiens modernes est l'une des deux grandes questions non résolues dans la phylogénie des tétrapodes.

Il n'est pas surprenant qu'on a déjà essayé d'utiliser de différents types de données pour résoudre ce problème – voir Schoch & Milner (2004), Anderson (2008), et les introductions aux chapitres 1 et 3 aussi bien que le chapitre 6 pour, tous pris ensemble, une liste probablement complète.

Le plus souvent, on a comparé des complexes de caractères chez des amphibiens actuels et des vertébrés paléozoïques pour que l'on puisse en tirer des conclusions phylogénétiques. Je ne mentionnerai que quelques exemples historiques : Cope (1888) s'est engagé pour l'hypothèse temnospondyle à base de son essai d'interpréter les centres vertébraux des amphibiens actuels comme homologues aux intercentres des temnospondyles. Watson (1940) a essayé de connecter les anoures à « *Miobatrachus* » (un synonyme plus jeune du temnospondyle *Amphibamus*) qu'il a décrit dans le même article. Parsons & Williams (1962, 1963) ont discuté une liste de traits du squelette et de l'anatomie molle, ce qui inclut les dents pédicellées (voir chapitre 3) de la plupart des amphibiens actuels ; en conclusion, ils ont soutenu la monophylie des lissamphibiens, bien que leurs essais (Parsons & Williams 1963) de chercher un ancêtre direct convenable pour les lissamphibiens parmi les fossiles connus étaient sans résultat. Bolt (1969, 1977, 1979, 1991) a brièvement décrit le temnospondyle amphibamidé *Doleserpeton* comme un « protolissamphibien » à cause de traits comme ses dents pédicellées (Bolt a considéré la monophylie des lissamphibiens probable mais pas certaine). Carroll & Currie (1975) et Carroll & Holmes (1980) ont plus ou moins fondé la version moderne de l'hypothèse de polyphylie en comparant les gymnophiones et les urodèles aux « microsaures » (parmi les lépospondyles), espécialement à *Rhynchonkos*, notant des similarités, et concluant que les gymnophiones et les urodèles sont dérivés des lépospondyle tout en acceptant un origine temnospondyle des anoures. L'origine temnospondyle des anoures, voir de tout les amphibiens modernes, a été reconstaté par Lombard & Bolt (1979) et Bolt & Lombard (1985), qui ont comparé l'oreille moderne des anoures à ce qu'ils ont interprété comme l'oreille moyenne de *Doleserpeton*. Anderson et al. (2008) ont soutenu une version similaire de l'hypothèse de polyphylie par leur analyse phylogénétique qui a inclus l'amphibamidé *Gerobatrachus*, décrit comme nouveau dans la même publication. Encore plus récemment, Sigurdsen & Bolt (2009) se sont prononcés pour l'hypothèse temnospondyle, se fondants sur leur réinterprétation de l'anatomie du coude des vertébrés non amniotes.

On a aussi utilisé la biologie du développement, à partir de ce que Bolt (1977, 1979) a noté des similarités entre les lissamphibiens et des temnospondyles amphibamidés juvéniles (si je ne prends pas en considération le fait que l'« école suédoise » éteinte a envoqué la polyphylie des tétrapodes à base de, parmi des autres raisons, leur ontogénie dès les années 1930). Les exemples les mieux connus sont fournis par Carroll et des coauteurs divers qui ont longtemps mis d'attention à des similarités au squelette viscéral et au développement du crâne et des extremités chez les temnospondyles branchiosauridés et les urodèles et qui en ont tiré la conclusion d'une relation ancêtre-déscendant ; ceci a trouvé son sommet dans les publications par Schoch & Carroll (2003), Carroll (2007) et Fröbisch et al. (2007). Cependant, Schoch (2006) a trouvé que beaucoup de ces similarités sont plésiomorphiques ; et Germain & Laurin (2009) ont reconstruit la séquence ancestrale du développement du crâne des urodèles (en utilisant une méthode nouvelle aussi bien qu'une autre qui avait été utilisé avant) et ont trouvé que cette séquence était bien distincte de la seule connue d'un temnospondyle.

Finalement, on a jusqu'à maintenant fait plusieurs analyses phylogénétiques, utilisant des données morphologiques (donc du squelette) aussi bien que moléculaires, voir ci-dessous (et dans chapitre 6).

Malgré tout ce travail, tous les trois hypothèses ont été soutenues par des analyses phylogénétiques publiées dans les années dernières. L'hypothèse temnospondyle a été soutenue le plus récemment par Ruta & Coates (2007), l'analyse de la phylogénie des tétrapodes appuyée par la plus grande matrice de données publiée jusqu'à maintenant, et (selon Sigurdsen 2009) par la thèse doctorale de Sigurdsen ; l'hypothèse lépospondyle est conforme aux résultats de l'analyse par Vallin & Laurin (2004) et à ceux des thèses doctorales de Pawley (2006 : app. 16) et Germain (2008) ; l'hypothèse de polyphylie a été soutenue le plus récemment par Anderson et al. (2008) dans sa forme plus ou moins classique, tandis que que McGowan (2002) et Carroll (2007) ont trouvé une version plus surprenante.

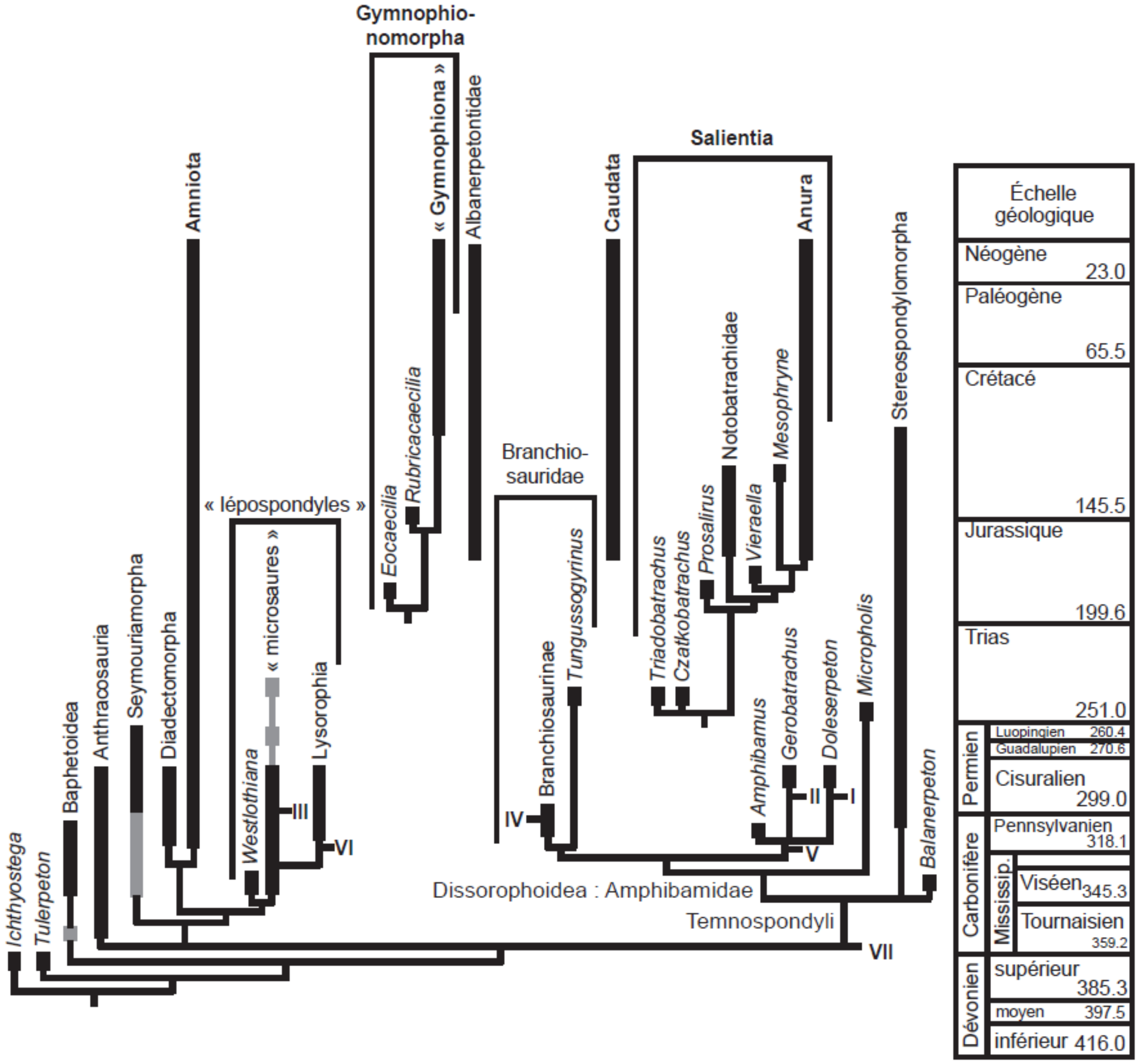

Figure 1 : Arbre de consensus fortement simplifié des tétrapodes, calibré dans le temps, montrant les positions possibles des amphibiens modernes ; modifié à partir de figure 2A du chapitre 6. Les noms de taxons actuels sont en gras. L'échelle stratigraphique, proportionnelle à l'exception du Tournaisien (gonflé), suit Gradstein et al. (2004) ; l'étage non étiquettée est le Serpoukhovien, qui a commencé il y a 324,4 ± 1,6 Ma. Les portions des lignées représentées dans le registre fossile sont représentées par des lignes noires gras ; ces lignes représentent généralement l'intervalle stratigraphique maximal qui peut être représenté par le registre fossile de chaque taxon, sauf que les seymouriamorphes d'Asie pourraient avoir des âges carbonifères (extension possible montrée en gris) ou permiens. L'anthracosaure le plus ancien et le baphétoïde possible qui a le même âge (en gris) sont pris d'Anderson et al. (2009) ; l'extension grise des « microsaures » au Guadalupien ou même le Trias inférieur est discutée au chapitre 6, ainsi que la position phylogénétique de *Tungussogyrinus*. Branchiosauridae fait partie d'Amphibamidae, mais ceci n'a été découvert qu'en 2009 (Fröbisch & Schoch 2009) ; jusque là, on pensait que ces clades étaient mutuellement exclusifs. La trichotomie contenant *Amphibamus*, *Gerobatrachus* et *Doleserpeton* suit les chapitres 3, 4 et 6. Normalement, mais pas toujours (Pawley 2006 ; Germain 2008), on trouve les « microsaures » comme un ensemble paraphylétique par rapport à Lysorophia et parfois des autres « lépospondyles » (non montrés). « Gymnophiona » contient Gymnophiona (actuel) et tous les fossiles qui pourraient être des membres de ce taxon ou ses plus proches parents – il n'y a pas de taxons éteints que l'on peut classifier sans ambigüité comme Gymnophiona (voir fig. 3 du chapitre 1, ou Gymnophiona est appelé « Apoda »). **Chiffres romaines :** Origines possibles de Lissamphibia ou de parties de ce taxon, placé aussi haut dans la stratigraphie que possible : **I**, Lissamphibia (HT), Batrachia (HP) ou Salientia (HP) ; **II**, Batrachia (HP) ; **III**, Gymnophionomorpha ou ce

taxon et Caudata (HP) ; **IV**, Lissamphibia (HT) ou Caudata (HP) ; **V**, Lissamphibia (HT), Batrachia (HP) ou Salientia (HP) ; **VI**, Lissamphibia (HL) ; **VII**, divergence entre les clades d'amphibiens actuels (HP). Selon la HL, la divergence entre Lissamphibia et ses plus proches parents connus dans le registre fossile s'est passée à **V** (sauf que quelques-uns des arbres les plus parcimonieux des deux analyses non contraintes du chapitre 5 ont trouvé les lissamphibiens comme plus proches d'autres clades de « lépospondyles » non montrés ici). Selon la HT, cette divergence pourrait avoir eu place à **I**, **IV** ou **V**. Selon la HP, la cladogenèse ayant séparé les clades d'amphibiens actuels est **VII**, et Gymnophionomorpha a eu son origine à **III** ; Caudata pourrait venir de **IV** selon les études récentes (**III** selon des études plus anciennes – Carroll & Holmes [1980] et des références qui y sont citées) et Salientia de **I** ou **V**, ou les deux ensemble (Batrachia) pourraient venir de **I**, **II** ou **V**. Noter la différence entre les âges de **I**, **IV**, **V** et **VI** d'une part (monophylie des lissamphibiens ; Mississippien terminal ou Pennsylvanien à Cisuralien) et **VII** d'autre part (HP ; Mississippien précoce ou plus tôt) ; cette différence d'âges est discutée en plus de détail au chapitre 6. **Abbréviations** : **HL**, hypothèse lépospondyle ; **Mississip.**, Mississippien ; **HP**, hypothèse de polyphylie ; **HT**, hypothèse temnospondyle.

Les analyses phylogénétiques mentionnées ci-dessus se fondent toutes sur des données morphologiques. Les données moléculaires ne permettent pas de distinguer entre les deux hypothèses de monophylie, parce que trop de taxons pertinents sont éteints – si les amphibiens actuels sont trouvés comme un clade excluant les amniotes, on ne peut pas dire si ce clade fait partie des temno- ou des lépospondyles. Cependant, des analyses moléculaires peuvent bien discriminer les deux hypothèses de monophylie de l'hypothèse de polyphylie (fig. 2) : toutes les analyses basées sur des données morphologiques publiées pendant les derniers onze ans, et presque toutes d'une période encore plus longue, ont eu comme résultat que les lépospondyles sont plus proches des amniotes que des temnospondyles. Ceci veut dire que l'hypothèse de polyphylie demanderait que les amphibiens actuels soient paraphylétiques par rapport aux amniotes – et un tel résultat (fig. 2b) n'a jamais été obtenu par une analyse moléculaire, à ma connaissance. (Comme liste probablement complète des analyses moléculaires pertinentes sauf San Mauro [2010], voir tableau 2 d'Anderson [2008].) Donc, les analyses moléculaires doivent toutes être interprétées comme réfutant l'hypothèse de polyphylie, malgré la grande diversité de gènes et taxons qui ont été utilisés (voir l'introduction au chapitre 1 et des grandes parties du chapitre 6).

Figure 2 : Interactions entre des hypothèses phylogénétiques appuyées par des données morphologiques et moléculaires. **a :** Simplification de figure 1. **b :** Résultat dérivé de données moléculaires attendu selon **a** si la HP est correcte. À ma connaissance, aucun arbre de telle topologie n'a jamais été publié. **c :** Résultat dérivé de données moléculaires compatible avec la HT et la HL, mais pas avec la HP. Abbréviations : **Liss.**, Lissamphibia ; **HL**, hypothèse lépospondyle ; **HP**, hypothèse de polyphylie ; **HT**, hypothèse temnospondyle.

On a récemment essayé d'utiliser des données non phylogénétiques pour distinguer entre les trois hypothèses. Zhang et al. (2005), par exemple, n'ont pas seulement conduit une analyse phylogénétique des amphibiens actuels fondée sur des données moléculaires (avec des résultats que l'on peut, comme toujours, simplifier comme fig. 2c mais non 2b) ; ils ont aussi daté les nœuds de l'arbre résultant, comparé ces dates de divergence à ce qu'ils ont cru savoir (en partie à tort, comme expliqué en détail au chapitre 1) sur la distribution stratigraphique des fossiles des temno- et lépospondyles, et conclu que ces dates ajoutent du soutien à l'hypothèse temnospondyle.

J'ai abordé la question de l'origine des amphibiens actuels de façon directe et indirecte. L'approche indirecte est celle de Zhang et al. (2005), à savoir de dater la divergence basale entre les amphibiens actuels et de comparer la date aux prédictions faites par les trois hypothèses – comme montré dans la figure 1, l'hypothèse de polyphylie prédit un âge maximum nettement plus ancien pour cette cladogenèse (première moitié du Carbonifère inférieur) que les deux hypothèses de monophylie (Carbonifère supérieur ou Permien inférieur). Or, je ne me suis pas limité à la datation moléculaire de divergences (faite au chapitre 1, avec des résultats not conformes avec l'hypothèse de polyphylie) ; j'ai aussi utilisé deux méthodes additionnelles, en partie nouvelles.

La première, expliquée et utilisée au chapitre 1 et commenté au chapitre 6, consiste à construire un arbre de synthèse, calibré dans le temps, du taxon en question, et à y insérer autant de fossiles que possible (dans leurs positions phylogénétiques et stratigraphiques) – 223 espèces dans ce cas-là –, ce qui permet de lire les âges des clades d'intérêt. Bien entendu, ceci dépend des suppositions sur les longueurs des branches internes et terminales, mais des tests de sensitivité divers, expliqués dans les appendices du chapitre 1, montrent que les effets de ces suppositions sont petits dans ces parties de l'arbre qui sont bien documentés par des fossiles. En plus, ces tests montrent que toutes les sources potentielles de biais dans l'arbre de synthèse ont une tendance de gonfler les dates de divergence. Il est un peu surprenant que cette méthode n'ait jamais été proposée ou utilisée avant, sauf le strict minimum qui est de lire des dates (de façon plus qualitative que quantitative) d'un arbre calibré dans la stratigraphie ; le fait qu'elle demande beaucoup de temps pourrait expliquer cela en partie.

La deuxième méthode, présentée au chapitre 2 et (elle aussi) commentée au chapitre 6, n'utilise pas de phylogénie. Elle calcule plutôt des intervalles de confiance sur la première apparition d'un clade à base de la distribution stratigraphique de ses fossiles. Elle se fonde sur la méthode publiée par Marshall (1997), mais j'ai ajouté une série de modèles de croissance exponentielle de la diversité des lissamphibiens pour tenir compte de la forte probabilité que la diversité lissamphibienne n'était pas constante pendant les derniers 250 (voir même 400) millions d'années ; comme démontré au chapitre 2, cette modification est nécessaire.

Tout comme l'a mentionné Anderson (2008), notre application de la première méthode suppose que l'hypothèse de polyphylie est fausse. C'est vrai aussi pour notre application de la deuxième méthode. Il pourrait donc sembler paradoxal que je présente les résultats dérivés de ces méthodes comme argument contre l'hypothèse de polyphylie, mais le chapitre 6 explique pourquoi je crois que c'est justifié : les deux méthodes pourraient facilement donner des dates pour l'origine des lissamphibiens qui seraient compatibles avec la prédiction de l'hypothèse de polyphylie (première moitié du Carbonifère inférieur), mais elles ne le font pas ; elles donnent plutôt des dates au Carbonifère supérieur ou Permien (pour la plupart Permien moyen et supérieur), ce qui est cohérent avec les deux hypothèses de monophylie.

On mentionne souvent dans la littérature qu'il semble y avoir un conflit fondamental entre les dates de divergence dérivées de données moléculaires et celles lues de la distribution stratigraphique des fossiles, ces dernières étant toujours plus jeunes que les autres. Rodríguez-Trelles et al. (2002) ont attribué ceci à l'usage rare d'âges maximaux pour des points de calibration en datation moléculaire : si la plupart ou tous les points de calibration dans une analyse ont des âges minimaux mais pas d'âges maximaux, tous les nœuds seront poussés vers des âges plus anciens, aussi loin que nécessaire pour éviter un conflit avec les âges minimaux. Brochu (2004a, b, 2006) a trouvé en plus qu'un équilibre de points de calibration et jeunes et anciens qui se trouvent à l'intérieur et à l'extérieur du clade d'intérêt est nécessaire pour obtenir des résultats réalistes. Au chapitre 1 je propose de nouveaux points de calibration à l'intérieur de Lissamphibia. Tous ont des âges maximaux ; j'ai utilisé ces points de calibration (à l'exception des âges maximaux de quelques-uns) dans la datation moléculaire au chapitre 1, avec des résultats qui sont très proches de ceux des deux méthodes fondées sur les fossiles. J'en conclus qu'il n'y a pas de conflit fondamental entre les données paléontologiques et moléculaires ; la datation moléculaire requiert une utilisation judicieuse des données fossiles, un problème qui n'est pas trivial mais pas insurmontable non plus.

L'approche directe est, naturellement, l'analyse phylogénétique. À cette fin, je n'ai pas construit mon propre jeu de données, mais j'ai recodé les matrices publiées par McGowan (2002) (chapitre 3), Anderson et al. (2008) (information supplémentaire au chapitre 4), et Ruta & Coates (2007) (chapitre 5) pour déterminer pourquoi elles donnent des résultats si différents. J'ai trouvé que les trois matrices contiennent beaucoup de différences par rapport à la littérature descriptive (quelques-unes des différences, je pense, représentent des fautes de frappe et de phénomènes similaires – ce qui n'est pas surprenant dans une matrice contenant des centaines, ou bien des dizaines de milliers, de cellules) ; ces codages problématiques ont beaucoup d'influence sur les résultats, comme le montrent mes modifications de ces matrices et les réanalyses suivantes. En outre, dans deux de ces matrices, aucun des caractères n'était ordonné. L'exception est celle de McGowan – McGowan a fait deux analyses, une où aucun des caractères n'était ordonné, une autre où tous les caractères à plusieurs états étaient ordonnés et deux d'entre eux n'avaient pas leurs états en bon ordre pour être ordonnés. Wiens (2001) a présenté un argument convaincant pour ordonner des caractères potentiellement continus. De façon similaire, aucun des auteurs des matrices citées n'a suivi la recommandation de Wiens et al. (2005) de coder les caractères influencés par l'ontogenèse comme inconnus chez des individus morphologiquement immatures (juvéniles ou pédomorphiques). Des caractères corrélés étaient présents aussi, particulièrement dans la matrice de Ruta & Coates (2007) qui contenait au moins 42 caractères qui étaient corrélés à au moins un autre. J'ai donc modifié les trois matrices, appliqué la méthode laborieuse de pondération de lacunes par une matrice de pas (Wiens 2001) à deux caractères au chapitre 3, et documenté tous mes recodages. Mes réanalyses montrent que les trois matrices modifiées soutiennent l'hypothèse lépospondyle, sauf celle de McGowan, qui soutient faiblement l'hypothèse temnospondyle si les lysorophiens (fig. 1) restent exclus et si le temnospondyle *Doleserpeton* est interprété comme morphologiquement mature. (Si on change l'une condition ou l'autre, on obtient l'hypothèse lépospondyle comme résultat.)

Je n'ai pas étudié la matrice de Vallin & Laurin (2004), qui soutient déjà l'hypothèse lépospondyle. C'est parce qu'on pourrait soupçonner l'originalité de mon travail si ma réévaluation trouvait toujours l'hypothèse lépospondyle ; il serait plus approprié que quelqu'un sans rapport avec notre laboratoire réévalue cette matrice. Un coup d'œil montre qu'elle contient bien des caractères vraisemblablement corrélés et que quelques effets de l'ontogenèse n'ont pas été pris en compte (ce qui ne surprend pas, comme Wiens et al. n'ont publié leur travail qu'un an plus tard).

La partie du chapitre 4 qui a été publiée directement dans la revue est une réponse très brève à l'article de synthèse d'Anderson (2008) qui a exprimé des doutes sur des méthodes et des résultats du chapitre 1. La partie du « matériel supplémentaire électronique » qui contient la réévaluation (mentionnée ci-dessus) de la matrice de données d'Anderson et al. (2008) a été requise par un referee. Le reste de ce supplément examine brièvement l'argument, souvent répété (Schoch & Milner 2004 ; Anderson et al. 2008) mais jamais quantifié, que l'hypothèse lépospondyle serait largement soutenue par des « caractères de perte » qui pourraient être corrélés à la petite taille corporelle des animaux en question et/ou à la pédomorphose (et donc les uns aux autres – Wiens et al. 2005). À la lumière des résultats, cet argument semble peu convaincant.

Le chapitre 5 n'est pas encore prêt pour soumission à un périodique (il est en partie formaté pour Geodiversitas). Il documente mon travail sur la matrice de Ruta & Coates (2007), se basant sur le chapitre V de la thèse doctorale de Damien Germain (2008) ; Damien co-signera la publication future.

Le chapitre 6 est un article de synthèse qui élabore des grandes parties du présent résumé et répond à quelques points souvent mentionnés, en partie par Anderson (2008). Le manuscrit a été évalué par un comité de lecture et sera bientôt retourné à l'éditeur dans sa version actuelle.

L'appendice est un manuscrit sur un sujet assez différent du reste de la thèse que j'ai décidé de ne pas en faire un chapitre. Il a été récemment accepté par le Journal of Vertebrate Paleontology pour le fascicule 30(5) ; la version que je présente, ce sont les épreuves non corrigées suivies par mes corrections proposées. Il contient une petite analyse de la phylogénie des amniotes (sans tortues). Ma contribution est similaire au reste de mon travail phylogénétique : j'ai fusionné des caractères (venant de deux matrices), codé des taxons pour ces caractères selon la littérature descriptive, ajouté des taxons, ordonné quelques caractères, ajouté des états à quelques caractères, fait les analyses phylogénétiques, et préparé l'illustration qui les présente.

Remarques sur la nomenclature

Comme l'expliquent en détail les chapitres 1 (en particulier le glossaire et l'appendice 6) et 3, j'ai essayé d'utiliser la nomenclature phylogénétique (Cantino & de Queiroz 2010, et des références là-dedans) où c'était possible, ce qui veut dire que j'ai appliqué des noms à des clades selon leur définitions phylogénétiques publiés s'ils en ont. Le plus important, c'est que Lissamphibia est un groupe apical, ce qui veut dire qu'il a une définition basée sur un nœud ; l'origine des lissamphibiens est donc l'évènement cladogénétique qui a séparé les ancêtres des gymnophiones de ceux des anoures – au cas où les gymnophiones et les anoures sont plus proches les uns des autres que chacun des deux ne l'est des amniotes. S'ils ne le sont pas (si, autrement dit, l'hypothèse de polyphylie est correcte), aucun clade ne peut être appelé Lissamphibia.

Quand ce n'était pas possible, j'ai appliqué la nomenclature des « animaux » basée sur les rangs (International Commission on Zoological Nomenclature 1999) autant que possible.

Beaucoup de noms, même des noms souvent utilisés, ne conviennent ni sous l'un ni sous l'autre système de nomenclature ; j'ai essayé de les utiliser de façon cohérente avec la littérature, sauf que la littérature est parfois incohérente et/ou vague.

Dans le titre, les introductions aux chapitres, et le chapitre 5 j'ai délibérément évité le nom Tetrapoda parce qu'il est le sujet d'une grande controverse (Laurin & Anderson 2004) : faut-il lui donner une définition fondée sur une apomorphie (comme par exemple « le premier organisme qui a possédé des doigts homologues à ceux d'*Homo sapiens*, et tous ses descendants », ou l'appliquer au groupe apical ou même au groupe total (Ruta et al. 2003 ; Ruta & Coates 2007 ; Coates et al. 2008) qui est normalement appelé Tetrapodomorpha ? Parfois je mentionne des « tétrapodes-souche » (*stem-tetrapods*), ce qui veut dire « tétrapodomorphes hors du groupe apical ». – Par contre, dans ce résumé, j'utilise la définition du nom Tetrapoda qui se fonde sur l'apomorphie mentionnée ; c'est la définition la plus largement utilisée par des paléontologues jusqu'à maintenant, et celle qui me permet d'être le plus concis.

Conclusion

Les amphibiens actuels forment un clade (Lissamphibia) qui a probablement eu son origine au Permien (il y a moins de 300 millions d'années) et dont les plus proches parents connus sont assez sûrement des « lépospondyles » permocarbonifères, ce qui veut dire que les temnospondyles, les anthracosaures, et même les seymouriamorphes sont des clades de tétrapodes-souche (fig. 1). Malgré tout, beaucoup de recherches restent à faire : il faudra redécrire certains fossiles, réétudier certains caractères chez beaucoup de spécimens dans le monde entier, chercher des nouveaux caractères, étudier l'ontogenèse et ses effets sur la phylogénétique en plus de détail chez quelques taxons, et des fossiles que l'on va découvrir apporteront, sans aucun doute, des nouvelles surprises.

Comme le montre l'appendice, l'amniote *Apsisaurus* du Permien inférieur n'est pas un sauropside diapside comme lequel il a été décrit à l'origine ; il s'agit plutôt d'un membre du groupe-frère de Sauropsida, d'un théropside, plus précisément d'un varanopidé, plus proche aux mammifères qu'aux oiseaux.

Remerciements

Avant tout je remercie mes directeurs de thèse : Michel Laurin pour conseil, discussion, soutien bureaucratique, et accès à énormément de littérature, ainsi que Gerhard Steiner également pour conseil et soutien bureaucratique – j'ai projeté un chapitre sur une analyse phylogénétique de gènes nucléaires sous sa direction, mais il ne sera réalisé que plus tard. Pour leur soutien financier, je suis reconnaissant à mes parents et grands-parents et au bureau autrichien de bourses. En outre je remercie mes collègues, surtout Jason Anderson, Marcello Ruta, Angela et Andrew Milner, Rainer Schoch, Adam Huttenlocker, Jason Pardo, et Per Ahlberg, pour des discussions intéressantes et utiles. Bernard Battail et Ronan Allain m'ont donné accès à des moulages de *Triadobatrachus* et *Karaurus* au Muséum national d'Histoire naturelle, ce qui était très utile.

Littérature citée dans ce résumé

Voir l'« introduction générale » (version anglaise de ce résumé) ci-dessous.

General Introduction

“Nothing in biology makes sense except in the light of evolution”
– Theodosius Dobzhansky (1973)
“Nothing makes sense in evolution without a phylogeny”
– Gina C. Gould & Bruce J. MacFadden (2002, 2004)

Counting close to 6700 named extant species (http://amphibiaweb.org as of August 12, 2010), the extant amphibians form a significant part of extant vertebrate diversity. There are large morphological gaps between the three largest uncontroversial clades: the frogs incl. toads (crown group: Anura; total group: Salientia), the salamanders incl. newts (crown group: Urodela; total group: Caudata), and the caecilians (crown group: Gymnophiona; total group: Gymnophionomorpha, see Chapter 3). For this and other reasons, such as a poor early fossil record (see Chapter 6 for a detailed list), the origin of the extant amphibians is controversial. This was compounded rather than resolved by the discovery of the Middle Jurassic to Pliocene (Gardner et al. 2003; Delfino & Salas 2007) albanerpetontids (Estes & Hoffstetter 1976), which form a clade of salamander-shaped, somewhat elongate, scaly animals (McGowan 2002), and their recognition as a fourth distinct group of modern amphibians (Fox & Naylor 1982). In general, the hypotheses on the phylogeny of the limbed vertebrates have largely reached a consensus as shown in Figure 3, but it remains unclear where to insert the modern amphibians into that tree. With rather slight changes, three groups of hypotheses have persisted in the literature ever since the late 19th century:

- the modern amphibians could form a clade, **Lissamphibia**,
    - which could be nested among the dissorophoid temnospondyls, in which case the lepospondyls are stem-amniotes (**temnospondyl hypothesis**);
    - alternatively, Lissamphibia could be the nested among the lepospondyls (most likely as the sister-group to Lysorophia), in which case the temnospondyls are stem-tetrapods (**lepospondyl hypothesis**);
- finally, the modern amphibians could be polyphyletic, with the frogs and (since the late 1980s) the salamanders being dissorophoid temnospondyls and the caecilians being microsaurian lepospondyls (**polyphyly hypothesis**).

Together with the origin of the turtles (Lyson et al. 2010), the origin of the modern amphibians is one of the two great unresolved questions in the phylogeny of the limbed vertebrates.

Unsurprisingly, many different lines of evidence have already been applied to this problem – see Schoch & Milner (2004), Anderson (2008), and the introductions to Chapters 1 and 3 as well as Chapter 6 for, in sum, a probably exhaustive list.

Most commonly, character complexes have been compared between extant amphibians and Paleozoic vertebrates for the purpose of drawing phylogenetic conclusions. I will only mention a few historical examples: Cope (1888) argued for the temnospondyl hypothesis based on his attempt to homologize the vertebral centra of extant amphibians to the intercentra of temnospondyls. Watson (1940) tried to link the frogs to “*Miobatrachus*” (a junior synonym of the temnospondyl *Amphibamus*) which was described in the same paper. Parsons & Williams (1962, 1963) discussed a list of features of the skeleton and the soft anatomy, including the pedicellate teeth (see Chapter 3) of most extant amphibians, and in conclusion supported lissamphibian monophyly, though their attempts (Parsons & Williams 1963) to search the fossil record for a suitable direct ancestor for Lissamphibia were fruitless. Bolt (1969, 1977, 1979, 1991) cursorily described the amphibamid temnospondyl *Doleserpeton* as a "protolissamphibian" based on features such as its pedicellate teeth (Bolt considered lissamphibian monophyly probable but not certain). Carroll & Currie (1975) and Carroll & Holmes (1980) more or less founded the modern version of the polyphyly hypothesis by comparing caecilians and salamanders to "microsaurian" lepospondyls (especially *Rhynchonkos*), noting similarities, and concluding that caecilians and salamanders are derived from lepospondyls while accepting a temnospondyl origin of frogs. The temnospondyl origin of frogs, if not all modern amphibians, was reaffirmed by Lombard & Bolt (1979) and Bolt & Lombard (1985), who compared the middle ears of frogs to what they interpreted as the middle ear of *Doleserpeton*. Anderson et al. (2008) bolstered a similar version of the polyphyly hypothesis based on their phylogenetic analysis which included the amphibamid *Gerobatrachus*, newly described in the same paper. Most recently, Sigurdsen & Bolt (2009) argued for the temnospondyl hypothesis based on their reinterpretation of non-amniote elbow anatomy.

Development biology has been employed as well, starting with Bolt (1977, 1979) noticing similarities between lissamphibians and juvenile amphibamid temnospondyls (if I ignore the fact that the extinct "Swedish school" argued for polyphyly of the limbed vertebrates based on, among other things, ontogeny from the 1930s onwards). Most prominently, Carroll and various coauthors have long pointed out similarities in the visceral skeleton and the skull and limb development of branchiosaurid temnospondyls and salamanders and drawing the conclusion of an ancestor-descendant relationship, culminating in the publications by Schoch & Carroll (2003), Carroll (2007), and Fröbisch et al. (2007). However, Schoch (2006) found many of these similarities to be plesiomorphic; and Germain & Laurin (2009) reconstructed the ancestral urodelan sequence of skull development (using a novel method as well as a previously used one) and found it rather different from the only known one of a temnospondyl.

Finally, several phylogenetic analyses have now been conducted, both of morphological (i.e. skeletal) and of molecular data, see below (and in Chapter 6).

In spite of all this work, all three hypotheses have been upheld by phylogenetic analyses published in the last few years. The temnospondyl hypothesis was most recently found by Ruta & Coates (2007), the analysis of limbed-vertebrate phylogeny based on the largest published data matrix so far, and reportedly (Sigurdsen 2009) by Sigurdsen's doctoral thesis; the lepospondyl hypothesis conforms to the results of the analysis by Vallin & Laurin (2004) as well as the doctoral theses of Pawley (2006: app. 16) and Germain (2008); the polyphyly hypothesis was most recently supported by Anderson et al. (2008) in its more or less classical form, while McGowan (2002) and Carroll (2007) found a surprising variant.

The abovementioned phylogenetic analyses are all based on morphological data. Molecular data cannot discriminate between the two monophyly hypotheses, because too many relevant taxa are extinct – when the extant amphibians are found to form a clade that excludes the amniotes, there is no way to tell whether that clade is nested among the temno- or the lepospondyls. However, molecular analyses can distinguish the two monophyly hypotheses from the polyphyly hypothesis (Fig. 4): almost all morphology-based analyses of the last 11 years, and most of an even longer period, have found the lepospondyls to be more closely related to the amniotes than to the temnospondyls. This means that the polyphyly hypothesis would require the extant amphibians to be paraphyletic with respect to Amniota – and such a result (Fig. 4b) has never been found by a molecular analysis as far as I know. (For a probably complete list of relevant molecular analyses except San Mauro [2010], see table 2 of Anderson [2008]). Consistently, thus, molecular analyses argue against the polyphyly hypothesis, despite the rather wide variety of genes and taxa employed (see the introduction to Chapter 1 and large parts of Chapter 6).

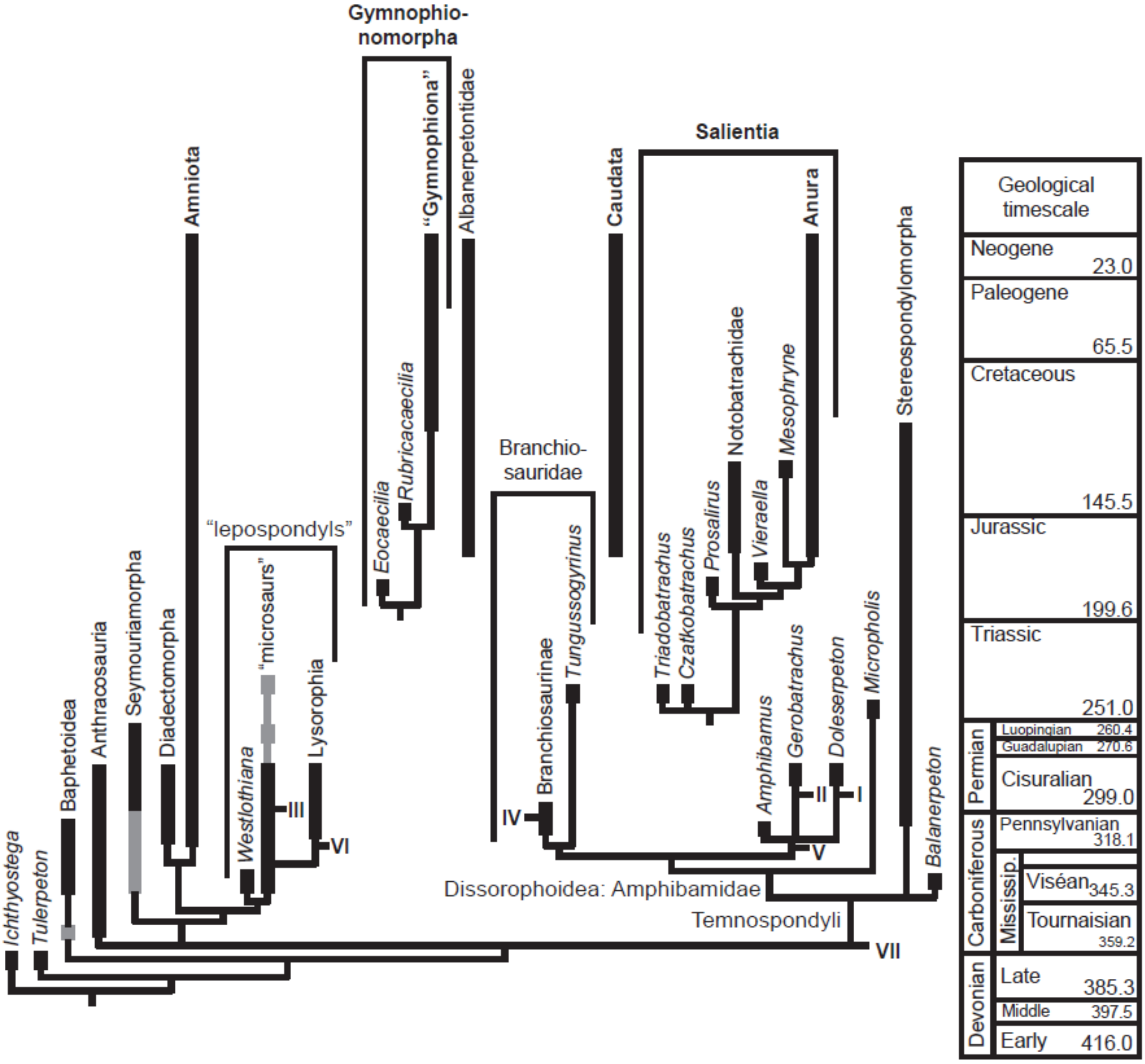

Figure 3: Strongly simplified, time-calibrated consensus tree of the limbed vertebrates, showing the possible positions of the modern amphibians; modified from figure 2A of Chapter 6. The names of extant taxa are in bold. The timescale follows Gradstein et al. (2004) and is proportional, except for the Tournaisian which is inflated; the unlabeled stage is the Serpukhovian, which began 324.4 ± 1.6 Ma ago. Known stratigraphic ranges are shown as thick black lines; this includes uncertainties, except for the Asian seymouriamorphs which may be Carboniferous (shown as a gray extension) or Permian in age. The oldest anthracosaur, and the possible baphetoid of the same age (in gray), are from Anderson et al. (2009); the gray extension of the "microsaurs" into the Guadalupian or even the Early Triassic is discussed in Chapter 6, as is the phylogenetic position of *Tungussogyrinus*. Branchiosauridae is shown nested within Amphibamidae, but this was only discovered by Fröbisch & Schoch (2009); until then, these clades were usually thought to be mutually exclusive. The trichotomy containing *Amphibamus*, *Gerobatrachus* and *Doleserpeton* follows Chapters 3, 4 and 6. The "microsaurs" are usually, but not always (Pawley 2006; Germain 2008), found to form a paraphyletic assemblage with respect to Lysorophia and sometimes other "lepospondyls" (not shown). "Gymnophiona" contains the extant Gymnophiona and all fossils that could be its members or its close relatives – no extinct taxa can be unambiguously assigned to Gymnophiona (see fig. 3 of Chapter 1, where Gymnophiona is called "Apoda"). **Roman numerals:** Possible origins of Lissamphibia or parts thereof, placed as high in the stratigraphy as possible: **I**, Lissamphibia (TH), Batrachia (PH) or Salientia (PH); **II**, Batrachia (PH); **III**, Gymnophionomorpha or that taxon and Caudata (PH); **IV**, Lissamphibia (TH) or Caudata (PH); **V**, Lissamphibia (TH), Batrachia (PH), or Salientia (PH); **VI**, Lissamphibia (LH); **VII**, split between the extant amphibian clades (PH). In other words, according to the LH, the split between Lissamphibia

and its closest known relatives happened at **VI** (except that some of the most parsimonious trees of the two unconstrained analyses in Chapter 5 have found Lissamphibia closer to other "lepospondyl" clades that are not shown). According to the TH, that split may have happened at **I**, **IV**, or **V**. According to the PH, the cladogenesis that separated the extant amphibian clades is **VII**, with Gymnophionomorpha originating at **III**; Caudata may have originated at **IV** according to the more recent studies (**III** according to older ones – Carroll & Holmes [1980] and references therein) and Salientia at **I** or **V**, or both together (Batrachia) may stem from **I**, **II** or **V**. Note the age difference between **I**, **IV**, **V** and **VI** on the one hand (lissamphibian monophyly; latest Mississippian or Pennsylvanian to Cisuralian) and **VII** on the other (PH; earliest Mississippian or earlier); this age gap is discussed further in Chapter 6. **Abbreviations: LH**, lepospondyl hypothesis; **Mississip.**, Mississippian; **PH**, polyphyly hypothesis; **TH**, temnospondyl hypothesis.

Attempts have lately been made to use nonphylogenetic evidence to discriminate between the three hypotheses. Zhang et al. (2005), for instance, not only performed a phylogenetic analysis of extant amphibians based on molecular data (with results that can be simplified, as always, to Fig. 4c but not 4b); they also dated the nodes on the resulting tree, compared these divergence dates to their partly erroneous knowledge of the fossil record of temno- and lepospondyls (this is explained at length in Chapter 1), and concluded that the dates lent new support to the temnospondyl hypothesis.

Figure 4: Interactions between phylogenetic hypotheses based on morphological and molecular data. **a:** Simplification of Figure 3. **b:** Result from molecular data expected based on **a** if the PH is correct. No such tree has, to the best of my knowledge, ever been published. **c:** Expected result from molecular data if the PH is incorrect. **Abbreviations: Liss.**, Lissamphibia; **PH**, polyphyly hypothesis.

I have approached the question of the origin of the extant amphibians both directly and indirectly. The indirect approach is that by Zhang et al. (2005): to date the basal divergence between the extant amphibians and compare it to the different predictions by the three hypotheses – as shown in Figure 3, the polyphyly hypothesis predicts a considerably larger maximum age for that cladogenesis (first half of the Early Carboniferous) than the two monophyly hypotheses do (Late Carboniferous or Early Permian). However, I have not limited myself to molecular divergence dating (done in Chapter 1, with results that contradict the polyphyly hypothesis); I have also used two more, partly novel, methods.

The first, explained and used in Chapter 1 and further commented on in Chapter 6, consists of building a time-calibrated supertree of the taxon in question, inserting as many extinct taxa as possible (into their phylogenetic and stratigraphic positions) – 223 species in this case –, and reading the ages of the nodes of interest from the tree. Of course this depends on the assumed lengths of internal and terminal branches and on the topology, but various sensitivity tests explained in the appendices to Chapter 1 show that the effects of those assumptions are small in those areas of the tree that have a good fossil record. Furthermore, these tests show that all potential sources of bias in the supertree tend to inflate the divergence dates. It is somewhat surprising that this method has never been proposed or used before, except for the bare minimum of (more qualitatively than quantitatively) reading dates from a time-calibrated tree; the fact that it is somewhat time-intensive may explain this in part.

The second method, presented in Chapter 2 and again commented on in Chapter 6, does not use a phylogeny. Instead, it calculates confidence intervals on the first appearance of a clade based on the stratigraphic distribution of its fossil record. It is based on the method published by Marshall (1997), but I have added a range of models of exponential growth of lissamphibian diversity to account for the strong likelihood that lissamphibian diversity was not constant throughout the last 250 (if not 400) million years; as demonstrated in Chapter 2, this modification is necessary.

As Anderson (2008) has correctly pointed out, our implementation of the first method requires the assumption that the polyphyly hypothesis is wrong. So does our implementation of the second method. It may therefore seem paradoxical that I present the results from these methods as evidence against the polyphyly hypothesis, but Chapter 6 explains why I think this is justified: both methods could easily give dates for the origin of Lissamphibia that would be compatible with the prediction by the polyphyly hypothesis (first half of the Early Carboniferous), but they do not; instead, they give Late Carboniferous to Permian dates (Middle and Late Permian ones for the most part), coherent with the two monophyly hypotheses.

It is often pointed out in the literature that there appears to be a fundamental conflict between divergence dates derived from molecular data and those read from the fossil record, with the latter consistently being younger than the former. Rodríguez-Trelles et al. (2002) attributed this to the rare use of maximum ages for calibration points in molecular dating: when most or all calibration points in an analysis have minimum but not maximum ages, all nodes will be pushed to higher ages however far is necessary to prevent conflict with any of the minimum ages. Brochu (2004a, b, 2006) further found that a balance of both young and old calibration points that lie both inside and outside the clade of interest is required for realistic results. In Chapter 1 I suggest new calibration points within Lissamphibia. All of them have maximum ages; these calibration points (except for the maximum ages of some) are used in molecular dating in Chapter 1, with results that are very close to those of the two fossil-based methods. I conclude that there is no fundamental conflict between paleontological and molecular data; molecular dating merely requires judicious use of the fossil evidence, a problem which is not trivial but not insurmountable either.

The direct approach is, of course, phylogenetic analysis. For this purpose I did not construct my own data matrix; rather, I investigated the published ones by McGowan (2002) (Chapter 3), Anderson et al. (2008) (supplementary information to Chapter 4), and Ruta & Coates (2007) (Chapter 5) to find out why they give such different results. All three turn out to contain large numbers of discrepancies with the descriptive literature (some of them, I suspect, typographic and similar errors – not surprising in a matrix of hundreds, or tens of thousands, of cells); these questionable scores have a large influence on the results, as my modifications of the matrices and subsequent reanalyses show. Furthermore, in two of them, all characters were unordered. The exception is McGowan’s matrix – McGowan performed two analyses, one with all characters unordered, one where all multistate characters were ordered and two of them had their states in the wrong order for ordering. Wiens (2001) has made a convincing argument for ordering potentially continuous characters. Similarly, the recommendation by Wiens et al. (2005) to deal with ontogeny-dependent characters by scoring them as unknown for morphologically immature (juvenile or paedomorphic) individuals was not heeded in any of the cited matrices. Correlated characters also occurred, especially in the matrix by Ruta & Coates (2007) which contained at least 42 characters that were correlated to at least one other character. I have modified all three matrices accordingly, applying Wiens’ (2001) time-consuming stepmatrix gap-weighting method to two characters in Chapter 3, and documenting all of my decisions in detail. Upon reanalysis, all three matrices support the lepospondyl hypothesis, except for McGowan’s matrix, which weakly upholds the temnospondyl hypothesis if the lysorophians (Fig. 3) remain excluded and if the temnospondyl *Doleserpeton* is taken at face value as morphologically mature. (Changing either condition results in the lepospondyl hypothesis.)

I have not examined the matrix by Vallin & Laurin (2004), which already supported the lepospondyl hypothesis. This is because it could raise suspicions about the originality of my work if my reappraisal still found the lepospondyl hypothesis to fit the data best; it would be more proper for someone without connections to our laboratory to reinvestigate that matrix. A cursory glance shows that it does contain likely correlated characters and that (unsurprisingly, as Wiens et al. published their relevant paper a year later) some effects of ontogeny were not taken into account.

The part of Chapter 4 that was published on paper is a very brief response to the review article by Anderson (2008) which had questioned methods and results of Chapter 1. The part of the Electronic Supplementary Material which contains the abovementioned revision of the data matrix by Anderson et al. (2008) was requested by a reviewer. The remainder of that supplement briefly examines the often repeated (Schoch & Milner 2004; Anderson et al. 2008) but never quantified argument that the lepospondyl hypothesis is to a large extent supported by "loss characters" which could be correlated to small body size and/or paedomorphosis (and thus to each other – Wiens et al. 2005). Judging from the results, that argument is unconvincing.

Chapter 5 is not yet ready for submission to a journal (it is partly formatted for Geodiversitas). It documents my work on the matrix by Ruta & Coates (2007), building on chapter V of Damien Germain's (2008) doctoral thesis; Damien will be a coauthor of the future publication.

Chapter 6 is a review article that expands on the present introduction and responds to a few commonly raised points, especially some brought up by Anderson (2008). It has undergone peer review and will soon be sent back to the editor in its present version.

The Appendix is a manuscript on a topic sufficiently different from the rest of the thesis that I decided not to make it a chapter. It was recently accepted by the Journal of Vertebrate Paleontology for issue 30(5); its present form are the uncorrected page proofs followed by my suggested corrections. It contains a small analysis of amniote phylogeny (without turtles). My contribution is similar to the rest of my phylogenetic work: I merged characters (from two matrices), scored taxa for them according to the descriptive literature, added taxa, ordered some characters, added states to some, performed the phylogenetic analyses, and prepared the illustration that presents them.

Nomenclatural remarks

As detailed in Chapters 1 (especially the glossary and appendix 6) and 3, I have tried to use phylogenetic nomenclature (Cantino & de Queiroz 2010, and references therein) wherever possible, which means I have applied names to clades according to their published phylogenetic definitions if they have any. Most importantly, Lissamphibia is a crown-group, meaning that it has a node-based definition; the origin of Lissamphibia is therefore the cladogenetic event that separated the ancestors of the caecilians from those of the frogs – provided that caecilians and frogs are more closely related to each other than either is to the amniotes. If they are not (if, in other words, the polyphyly hypothesis is correct), no clade can be called Lissamphibia.

Where that has not been possible, I have applied the rank-based nomenclature for "animals" (International Commission on Zoological Nomenclature 1999) as far as it is applicable.

Many names, even widely used ones, are not governed by either system of nomenclature; I have tried to use them in a way that is consistent with the literature, except that the literature is sometimes inconsistent and/or vague.

In the title, this introduction, the introductions to the chapters, and Chapter 5 I have tried to make a point of avoiding the name Tetrapoda because it is a matter of great controversy (Laurin & Anderson 2004) whether it should be given an apomorphy-based definition (along the lines of "the first organism that possessed digits homologous with those in *Homo sapiens*, and all its descendants") or applied to the crown group or even to the total group (Ruta et al. 2003; Ruta & Coates 2007; Coates et al. 2008) which is usually called Tetrapodomorpha. Occasionally I mention "stem-tetrapods"; this means "tetrapodomorphs that lie outside the crown group".

Conclusion

The extant amphibians form a clade (Lissamphibia) which probably originated in the Permian (less than 300 million years ago) and is most likely nested among the Permocarboniferous "lepospondyls", meaning that Temnospondyli, Anthracosauria, and even Seymouriamorpha are clades of stem-tetrapods (Fig. 3). However, much research remains to be done: certain fossils should be redescribed, certain characters should be restudied in many specimens around the world, new characters should be sought, ontogeny and its effects on phylogenetics should be studied in more detail in some taxa, and newly discovered fossils will, no doubt, bring new surprises.

As the Appendix shows, the Early Permian amniote *Apsisaurus* is not a diapsid sauropsid as originally described, but a member of the sister-group of Sauropsida, thus a theropsid, more precisely a varanopid, more closely related to the mammals than to the birds.

Acknowledgments

First of all I thank my supervisors: Michel Laurin for advice, discussion, bureaucratic support, and access to large amounts of literature; Gerhard Steiner likewise for advice and bureaucratic support – I had planned a chapter on phylogenetic analysis of nuclear genes under his supervision, but it will have to wait for later. For financial support I am grateful to my parents and grandparents and to the Austrian subsidy office for university students. I further thank several colleagues, including but not limited to Jason Anderson, Marcello Ruta, Angela and Andrew Milner, Rainer Schoch, Adam Huttenlocker, Jason Pardo, and Per Ahlberg, for interesting and helpful discussions. Bernard Battail and Ronan Allain provided very useful access to casts of *Triadobatrachus* and *Karaurus* at the Muséum national d'Histoire naturelle in Paris.

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Part 1

Dating the origin of Lissamphibia

Chapter 1

Molecular phylogeny and phylogeny-dependent paleontological and molecular dating of the origin of Lissamphibia

Molecular phylogenetics and molecular divergence dating have come a long way since Zuckerkandl & Pauling (1962) first presented the molecular-clock hypothesis. The models have become more and more complex to account for more and more realistic assumptions, and the methods have become more and more powerful – the methods of data generation, which nowadays means DNA isolation and sequencing, as well as the methods of phylogenetics and divergence dating –, so that cladogeneses are nowadays reconstructed and dated based on molecular data practically whenever these are available. Molecular dating in particular has the advantage that it does not require a good fossil record. Traditionally, the closest attainable approximation to the age of a clade was the age of the oldest fossil of that clade or its sister-group. The accuracy of this approach obviously depends strongly on the vagaries of preservation and discovery; molecular dating only requires a few calibration points to reconstruct – with confidence intervals – the ages of all nodes in a tree.

Calibration points, however, are necessary. One reason is that molecular divergence dating is, even in the ideal case, an equation with two variables: even if the mutation rate is constant throughout the tree, the branch lengths of the tree that is to be dated result from that mutation rate and from the ages of the nodes – either the rate or the age of at least one node need to be known so the other variable can be calculated. In practice (e.g. Shaul & Graur 2002; Graur & Martin 2004; Kolaczkowski & Thornton 2004; and references therein), every branch and every gene or rather every base pair has its own mutation rate, complicating the problem and necessitating several calibration points to avoid meaninglessly large confidence intervals on the node ages.

Divergence dating is not only an end in itself; it has applications in the understanding of evolutionary radiations and paleobiogeography, in questions like whether a radiation happened before or after a mass extinction event (which, in turn, has implications about the causes of the radiation) or in whether a disjunct distribution is due to vicariance or dispersal (if the cladogenesis in question happened after the habitats stopped being contiguous, dispersal must be invoked). A recent idea (Zhang et al. 2005) is to use molecular dating to distinguish between phylogenetic hypotheses which make different predictions about the dates of certain cladogeneses.

This paper began as a reply to Zhang et al. (2005), a study that reconstructed the phylogeny of extant sarcopterygians (with emphasis on Lissamphibia, which was found to be monophyletic) based on molecular data. Zhang et al. calculated the origin of Lissamphibia as having taken place 337 Ma ago, with a 95% confidence interval from 321 to 353 Ma ago (spanning the Mississippian epoch of the Carboniferous). They then went on to compare this date to their very scanty information on the fossil record of dissorophoid temnospondyls and lysorophian lepospondyls, and concluded that the temnospondyl hypothesis matched their results better than the lepospondyl hypothesis. As Lee & Anderson (2006) pointed out while we were working on the present study, Zhang et al. (2005) had used faulty information – the oldest known dissorophoids and lysorophians have approximately the same early Pennsylvanian age, and the divergence date in fact favors the polyphyly hypothesis.

However, as mentioned, Zhang et al. (2005) found Lissamphibia to be monophyletic with respect to Amniota, contradicting the polyphyly hypothesis (as explained in figure 4 of the General Introduction). The results by Zhang et al. thus contradict each other: the topology of the tree is only compatible with the two monophyly hypotheses, but the ages of the divergences on the tree favor the polyphyly hypothesis instead.

Expanding beyond a simple response to Zhang et al. (2005), the present paper attempts to resolve this contradiction. First, using the program Mesquite (Maddison & Maddison 2005), I compiled a supertree of lissamphibian phylogeny from the literature and added all extinct lissamphibian species, as far as possible, into their phylogenetic and stratigraphic positions. The supertree was not made by matrix-representation parsimony as commonly done, but by hand, which made it easier to weight sources against each other and to use written statements as sources (see Appendix 1 of this Chapter for details and sources; hereinafter, all mentioned Appendices, Tables and Figures belong to this Chapter). It is time-calibrated (using the Mesquite module Stratigraphic Tools; Josse et al. 2006), which means that the branch lengths are approximately proportional to absolute time. (They are, in other words, not meaningless as they usually are.) I did not use Pliocene and younger fossils (and subfossils) which have been referred to extant species and would therefore introduce so many internodes into the stratigraphically highest parts of the supertree that the ages of young nodes would be disproportionately increased. This leaves 223 extinct species of lissamphibians (Figures 3 through 7).

The ages of nodes on a time-calibrated tree depend on the assumed lengths of its branches (internodes). The fossil record does not directly provide constraints on any of them, except for minimum lengths for some terminal branches (a clade cannot be younger than the oldest fossil of its sister-group). We have therefore experimented with different sets of assumptions on the minimal lengths of terminal and internal branches, namely 0.1 to 5 Ma for both plus “stratigraphic fit” for terminal branches (meaning that each terminal branch occupies at least an entire geological stage) and 0.1 to 5 Ma for internal ones. Each of these sets, of which each hopefully encompasses all plausible values, results in different age estimates, but for nodes surrounded by many fossils the spread of these ages is much smaller than for poorly constrained divergences, as demonstrated in Appendix 4.

If the topology of a time-calibrated tree is trusted to be reasonably accurate, it can be used to test the quality of the fossil record of the clade in question, and vice versa; the worse the fossil record or the tree, the closer the congruence between stratigraphy and phylogeny should be to random. Several methods for measuring the stratigraphic fit of a tree have been published (most notably: Stratigraphic Consistency Index: Huelsenbeck 1994; Relative Completeness Index: Benton 1994; Gap Excess Ratio: Wills 1999). They measure the congruence between, on the one hand, the order of the ages of nested nodes predicted from the topology, and, on the other hand, the observed sequence of appearance based on the ages of their oldest fossils. This involves quantifying the amount of ghost lineages in the tree. The three cited methods are implemented in the program Ghost (Wills 1999). According to Ghost, the stratigraphic fit of the supertree presented in this paper is very high (p ~ 0.0001). It follows from these and other tests (empirical investigation of the effect of polytomies: Appendix 5) that the ages of most nodes in the tree cannot be severe underestimates.

(In addition, the AIG [actual implied gap] is new; we inserted it into the manuscript to satisfy a reviewer who wanted us to quantify the obvious fact that the supertree must have better stratigraphic fit than the molecular tree by Zhang et al. [2005] or indeed any molecular tree.)

Because of this high congruence, new calibration points for molecular dating can be derived from the supertree, and some of them can be assigned not only minimum but only maximum ages (the minimum age being the age of the oldest known member of the clade in question). This is possible when at least two taxa that lie close to but outside the node of interest (the more, the better) are present in the tree and are known from older fossils than the clade of interest. The new maximum age constraints are useful because very few calibration points within Lissamphibia had previously been known, while a balance of internal and external calibration points must be used – at least when using quartet dating – to derive realistic age estimates for cladogeneses within the clade in question (Brochu 2004a; meanwhile confirmed by Brochu 2004b, 2006).

We suspected that this imbalance, together with the lack of maximum ages for all calibration points (except the root) used by Zhang et al. (2005), could be the cause for the wide discrepancy between divergence dates based on molecular data (Zhang et al. 2005) and fossils (our supertree). The new calibration points we propose (Table 1) have enabled us to test this hypothesis by conducting our own divergence date estimation based on the same dataset as Zhang et al. (2005). The wide variety of results, based on analyses that differ in a large selection of parameters including the use of internal or external calibration points and of maximum ages, is presented in Appendix 10 (and in abbreviated form in Table 2); the most realistic sets of parameters result in date estimates that are close to those derived from the supertree (Guadalupian or Luopingian) and much younger than those found by Zhang et al. (2005). This resolves the conundrum: both the topology and the divergence dates of phylogenetic trees based on molecular data are compatible with the two monophyly hypotheses and contradict the polyphyly hypothesis.

For the molecular dating, we were unable to use the program Zhang et al. (2005) had used (Multidivtime; Thorne & Kishino 2002). We therefore tried three others. Only one, r8s (Sanderson 2002, 2003, 2006), turned out to be useful; the results it produced are presented in Table 2 and Appendix 10. The others, QDate (Rambaut & Bromham 1998) and PATHd8 (Anderson 2006), are mostly relegated to Appendices 8 & 9 and 11, respectively, for reasons explained in the text of this chapter.

Molecular phylogenetics by maximum likelihood and dating by penalized likelihood require a model of evolution. This model was chosen using the very widely used program ModelTest (Posada & Crandall 1998). However, as pointed out by Debruyne & Tassy (2004), ModelTest works by constructing a neighbor-joining “guide tree” from the data using the simplest possible model (the Jukes-Cantor model, in which all substitutions are equally probable) and then selecting those model parameters that fit the guide tree best. Neighbor-joining is a phenetic method, not a phylogenetic one, and indeed, the guide tree constructed by the unmodified version – Figure 8a – has polyphyletic frogs, a highly unrealistic result. Therefore, I modified ModelTest (which is a macro for the widely used phylogenetics program PAUP*; Swofford 2003) to use the most parsimonious tree as the guide tree. (In that tree, Figure 8b, the frogs are monophyletic.) The resulting model is presented in Appendix 7; the resulting most likely tree is shown in Figure 8d and differs from that produced by the unmodified version (Fig. 8c) in supporting the Procera hypothesis (salamanders and caecilians as sister-groups) instead of the more commonly found Batrachia hypothesis (salamanders and frogs as sister-groups).

I further tested the influence of tree topology on divergence dates, in other words, the question of what influence it has on divergence dates throughout a tree when that tree contains events that never happened. The opportunity arose because the tree by Zhang et al. (2005), as well as our attempt to replicate it, contains “Archaeobatrachia”, a grouping that is paraphyletic according to more focused analyses with better taxon sampling (both molecular and morphological), as a clade. To our surprise, the effect of “Archaeobatrachia” is very weak, as tested by repeating the analyses with a tree that was constrained to have “Archaeobatrachia” paraphyletic.

Both dating methods are further discussed on pp. 424–426 of Chapter 2 and in Chapter 6.

Appendix 6 explains our disagreements on nomenclature with Zhang et al. (2005) and Frost et al. (2006). Zhang et al. (2005) regularly used well-known clade names to refer to clades other than the ones to which the names belong, for instance Gymnophiona to designate its subgroup Stegokrotaphia or Anura when they meant the more restricted clade Bombinanura. (Non-stegokrotaphian gymnophionans were lacking from their dataset, so there simply is no clade in their tree that can be called Gymnophiona, for example.) Frost et al. (2006) coined a plethora of new names, but almost all of them lack definitions that would be specific enough to point at a single node or internode; it is often impossible to determine whether an extinct taxon of a given phylogenetic position should be considered part of a taxon with such a name or not.

Following a request by the editor of Systematic Biology, who was understandably concerned about the length of the paper, we removed the third dating method from the manuscript and expanded it into a publication of its own, Chapter 2 of this thesis.

Errata

The source (Roček 2000) I used to insert *Baurubatrachus* into the supertree (Fig. 7) claimed it to be Campanian in age and based this claim on the primary literature on *Baurubatrachus*. More likely, however (Fernandes & Coimbra 2000; Gradstein et al. 2004), the Marília Formation is Maastrichtian. As now mentioned in Chapter 5, this reduces the minimum age of the *Hyla*-*Bufo* divergence and thus falsifies our claim (p. 385 of the paper) that that split, unlike all others, has the same age according to fossil data as the one found by Zhang et al. (2005).

The phylogenetic positions of some species, especially North American Miocene species assigned to *Bufo* in the traditional (very wide) sense, may be far more precise than justifiable; the article by Bever (2005), which I discovered only after the manuscript was submitted, finds much of that material to be undiagnostic. Most of it consists of isolated right ilia.

Parts of hyloid and ranoid phylogeny within the supertree are now out of date, and the exact position of Xenoanura is somewhat controversial (I have, unfortunately not had the time necessary to compile a list of relevant publications), though large effects on divergence dates are unlikely, because only nodes not surrounded by many fossils are affected. As one test of this, see Appendices 2 and 3, where the supertree presented in the paper itself is compared to one based mostly on that by Frost et al. (2006). – Note that the figure of Appendix 2 is not legible when printed. It can be downloaded as a separate file from the website of Systematic Biology; alternatively, I can of course send the pdf file of the Appendices, which can be enlarged at will, to interested parties.

The paper may not make sufficiently clear that our implementations of both dating methods assume lissamphibian monophyly and that the dates they suggest are nonetheless evidence against the polyphyly hypothesis. (Anderson [2008] in particular seems to have misunderstood this point.) This is elaborated upon in Chapter 6 and in the General Introduction.

I cited Kolaczkowski & Thornton (2004), who found in their simulation studies that simple parsimony outperforms maximum likelihood and Bayesian analysis under a wide range of realistic conditions, even though (as they confirmed) it is more susceptible to long-branch attraction. That paper was, I did not know, only the beginning of a literature battle of which I know practically nothing else, especially not its current state. Clearly, I will need to familiarize myself with that literature should I decide to publish an update one day.

Zhang et al. (2005) claimed that the last known "microsaurs" are Early Triassic in age. We dismissed this as wrong based on the literature. It is, however, possible that Zhang et al. had access to unpublished information – as part of a faunal list in a conference abstract, Gao et al. (2008) report unspecified "lepospondyls" from the Early Triassic of China. Whether these are "microsaurs" (or even "lepospondyls" in the first place) remains to be seen.

More trivially, *Pliobatrachus* is spelled in lowercase in the legend of Figure 5.

Finally, Chapter 3 improves the nomenclature used here: *Apoda* Haworth, 1809, is the name of a moth genus, so it is preferable not to use Apoda Oppel, 1810, for the caecilian crown-group (or indeed at all), even though this matter is not governed by the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999) because Apoda Oppel, 1810, does not have a family-, genus- or species-group rank.

Author contributions

M. L. provided many ideas (such as the tests for the impact of branch length assumptions or polytomies using Stratigraphic Tools), access to the literature, funding from his research unit for publication of the color figure (Fig. 3), and contributed to the manuscript (especially Appendix 10), wrote the (technically unpublished) introduction to the appendices so they could be sent to colleagues as a single pdf file, and supervised me; I gathered the data, contributed the methods of molecular phylogenetics and divergence dating based on a course taught by Gerhard Steiner and on Debruyne & Tassy (2004), performed most of the analyses, wrote most of the manuscript (including all of the appendices other than most of Appendix 10), made the illustrations and tables, and handled most of our side of the submission and review process. The clade names and their definitions used in this Chapter (explained in the glossary that follows the references) are a compromise of our preferences.

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ISSN: 1063-5157 print / 1076-836X online
DOI: 10.1080/10635150701397635

Fossils, Molecules, Divergence Times, and the Origin of Lissamphibians

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Abstract.—A review of the paleontological literature shows that the early dates of appearance of Lissamphibia recently inferred from molecular data do not favor an origin of extant amphibians from temnospondyls, contrary to recent claims. A supertree is assembled using new Mesquite modules that allow extinct taxa to be incorporated into a time-calibrated phylogeny with a user-defined geological time scale. The supertree incorporates 223 extinct species of lissamphibians and has a highly significant stratigraphic fit. Some divergences can even be dated with sufficient precision to serve as calibration points in molecular divergence date analyses. Fourteen combinations of minimal branch length settings and 10 random resolutions for each polytomy give much more recent minimal origination times of lissamphibian taxa than recent studies based on a phylogenetic analyses of molecular sequences. Attempts to replicate recent molecular date estimates show that these estimates depend strongly on the choice of calibration points, on the dating method, and on the chosen model of evolution; for instance, the estimate for the date of the origin of Lissamphibia can lie between 351 and 266 Mya. This range of values is generally compatible with our time-calibrated supertree and indicates that there is no unbridgeable gap between dates obtained using the fossil record and those using molecular evidence, contrary to previous suggestions. [Calibration point; fossil record; Lissamphibia; molecular dating; phylogenetics; stratigraphic fit; supertree.]

The origin of lissamphibians has been hotly debated in the last few years, and the number of hypotheses about their origin has not decreased (Carroll, 2001; Schoch and Carroll, 2003; Schoch and Milner, 2004; Lee and Anderson, 2006), despite several detailed phylogenetic analyses (Laurin, 1998; Anderson, 2001; Ruta et al., 2003; Vallin and Laurin, 2004). The currently competing hypotheses can be divided into three main categories. First, some investigations suggest that Lissamphibia is monophyletic and derived from the temnospondyls (Fig. 1a, b), in which case its sister-group may be *Doleserpeton* (Bolt, 1969), (*Doleserpeton* + *Amphibamus*; Ruta et al., 2003), Branchiosauridae (Milner, 1990, 1993b), or a subgroup of Branchiosauridae (Trueb and Cloutier, 1991). Second, in other hypotheses (Fig. 1c), Lissamphibia is monophyletic but derived from the "lepospondyls" (Laurin, 1998; Vallin and Laurin, 2004). Third, several studies have suggested diphyly or triphyly of extant amphibians (Fig. 1d), with an origin of anurans and sometimes urodeles within temnospondyls (sometimes different temnospondyls), and an origin of apodans and sometimes urodeles within "lepospondyls" (Carroll and Currie, 1975; Carroll and Holmes, 1980; Carroll et al., 1999; Anderson, 2001; Carroll, 2001; Schoch and Carroll, 2003; Lee and Anderson, 2006).

Zhang et al. (2005) recently assessed the relative merits of these various paleontological hypotheses about the origin of lissamphibians by estimating the dates of the main cladogeneses (splits) within Lissamphibia and comparing the minimal age of Lissamphibia with the time of origin of its presumed sister-groups. Their test rests on the plausible hypothesis that the lissamphibians (here taken as a crown-group; see Glossary) should have started differentiating around the time when their presumed extinct sister-group first appeared in the fossil record. However, the large number of autapomorphies of Lissamphibia (e.g., Trueb and Cloutier, 1991:285; Milner, 1993b:17; Laurin, 1998:6; Ruta et al., 2003:272) suggests that the lissamphibian stem must have persisted a fairly long time before the crown-group started differentiating. A literal interpretation of the fossil record suggests that lissamphibians started differentiating well after the origin of any of their suggested Paleozoic relatives (Ruta and Coates, 2003). However, a literal interpretation of the fossil record always underestimates the date of appearance of taxa because it can only give a latest possible date of appearance, not an earliest possible date of appearance; therefore, Zhang et al. (2005) tried to determine when the first lissamphibians actually appeared by dating a few relevant cladogeneses within that clade. They concluded that Lissamphibia arose about 337 million years ago (Mya), with a 95% confidence interval extending from 321 to 353 Mya. This means that the divergence between the last common ancestors of apodans and batrachians occurred between the Tournaisian and the Serpukhovian (thus spanning the Early Carboniferous), probably in the Viséan. Zhang et al. (2005) argued that this date suggests that a temnospondyl origin of lissamphibians is more credible than a lepospondyl origin. This is based on the time overlap between the prospective sister- or stem-groups and the inferred time of origin of Lissamphibia. Zhang et al. (2005) believed that Dissorophoidea had appeared in the Viséan and that Lysorophia had appeared in the Late Carboniferous. Because this date of appearance of the first lysorophians is close to the upper (most recent) end of the 95% confidence interval of the origin of lissamphibians, Zhang et al. (2005) concluded that this hypothesis was less credible than an origin of lissamphibians from dissorophoids.

The reasoning of Zhang et al. (2005) relies on the implicit assumption that the observed time of appearance of dissorophoids and lysorophians in the fossil record is not misleading. We make similar assumptions below because one of our aims is to show that the methods used by Zhang et al. (2005), when used with correct stratigraphic data, suggest that all recent hypotheses about a monophyletic lissamphibian origin are consistent with the timing of lissamphibian diversification. A time-calibrated supertree of lissamphibians suggests a much later time of diversification of this clade than

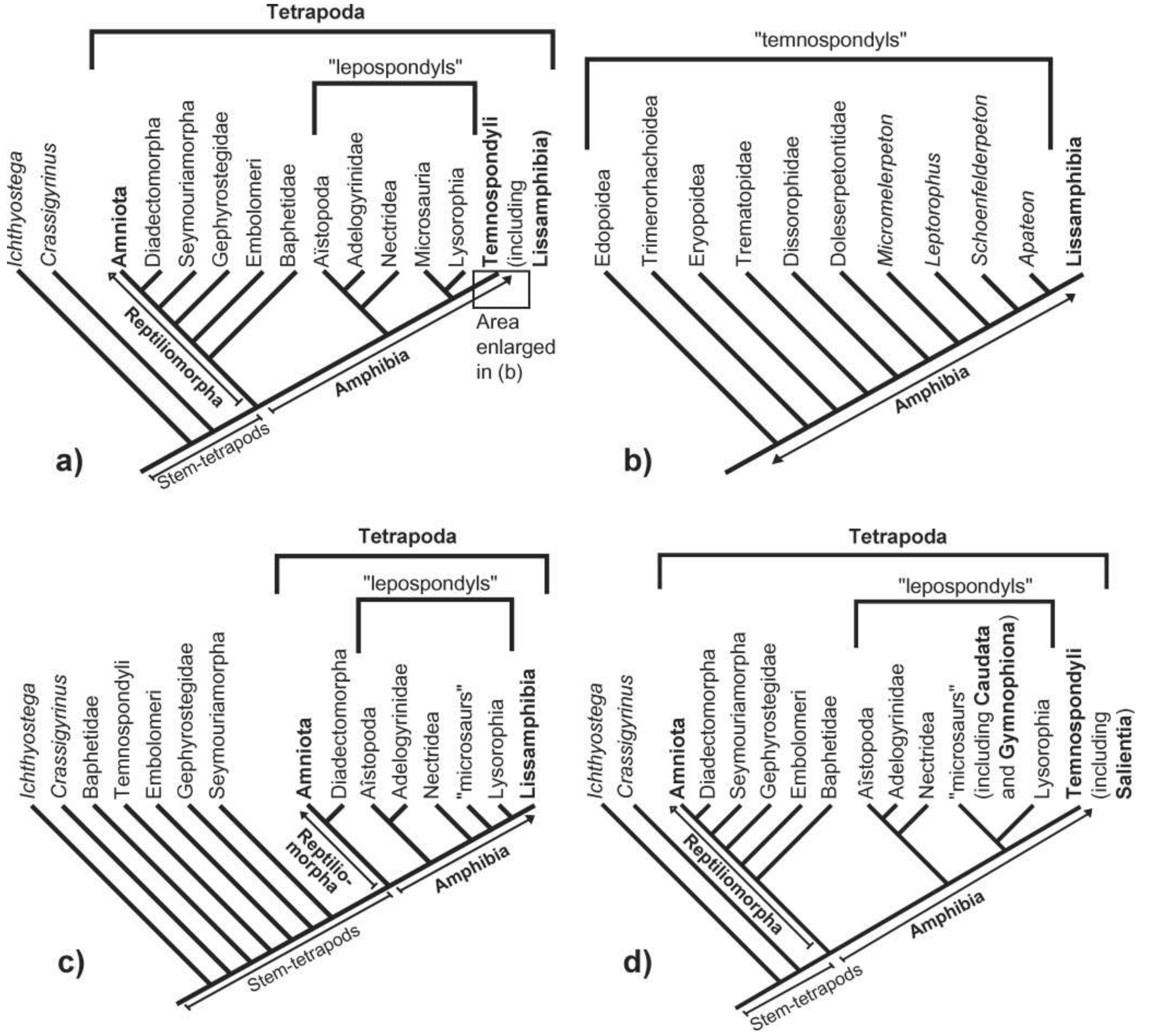

FIGURE 1. Competing phylogenetic hypotheses about the origin of extant amphibians showing (a and b) an origin of Lissamphibia within "temnospondyls"; (c) an origin of Lissamphibia within "lepospondyls"; (d) a polyphyletic origin of extant amphibians (the exact topology was not specified in most studies advocating this hypothesis; in some cases Caudata is placed among the temnospondyls). Names of extant taxa in bold.

argued by Zhang et al. (2005). Further, we date lissamphibian diversification by various methods, branch lengths obtained from several evolutionary models, and diverse combinations of calibration points, using the molecular data presented by Zhang et al. (2005). As such, our study attempts to be a fairly thorough analysis of both the fossil and molecular evidence about the timing of lissamphibian diversification.

MATERIALS AND METHODS

Stratigraphic Range of Paleozoic Stegocephalians

We assessed the stratigraphic range of potential relatives of Lissamphibia in the Paleozoic using the literature (Fig. 2). This survey was undertaken because the ranges used by Zhang et al. (2005) are clearly mistaken (see below).

Compilation of the Time-Calibrated Supertree

We suspected that the divergence dates within Lissamphibia inferred by Zhang et al. (2005) were too old when compared to the presumed sister-groups of Lissamphibia and to the lissamphibian fossil record. To test this idea, we have compiled a fairly extensive supertree of Lissamphibia and performed several sensitivity and statistical analyses.

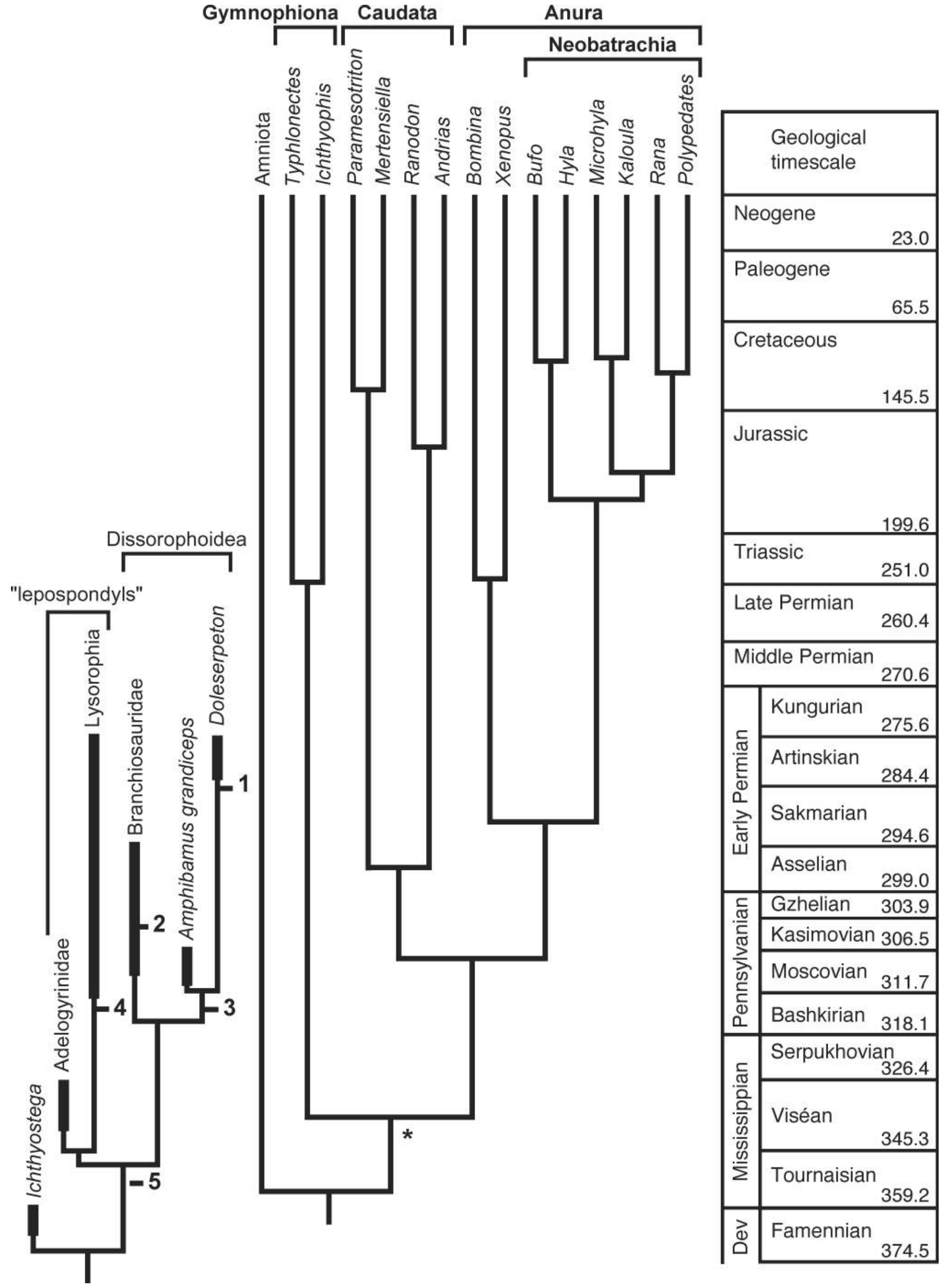

FIGURE 2. Stratigraphic range of proposed close relatives of Lissamphibia, possible positions of the lissamphibian stem, and main divergence dates within extant amphibians inferred by Zhang et al. (2005). Possible position of the lissamphibian stem (in all cases the placement of the stem has been put as high up into the geological section as seems plausible under the various phylogenetic hypotheses): 1, sister-group of *Doleserpeton* (Fig. 1a; Bolt, 1969); 2, within branchiosaurids (Fig. 1a, b; Trueb and Cloutier, 1991); 3, sister-group of a clade that includes *Doleserpeton* and *Amphibamus* (Fig. 1a; Ruta et al., 2003); 4, sister-group of lysorophians, within "lepospondyls" (Fig. 1c; Laurin, 1998); 5, polyphyletic origin in which some extant amphibians (gymnophiones, or gymnophiones and caudates) are nested within "lepospondyls" and the others are nested within temnospondyls (Fig. 1d; Carroll and Currie, 1975; Carroll and Holmes, 1980; Carroll et al., 1999). Known stratigraphic ranges (including uncertainties): thick lines; ghost ranges: thin lines. The latest possible time of divergence between the lissamphibian stem and its possible Paleozoic sister-group according to the dating of Zhang et al. (2005) is indicated by an asterisk (*). Note that this date is incompatible with the latest possible divergence date between the lissamphibian stem and its possible Paleozoic sister-groups (earliest possible divergence dates cannot be determined directly from the fossil record) but that it is compatible with the hypothesis that extant amphibians are polyphyletic with respect to Paleozoic stegocephalians (5). The geological time scale used is from Gradstein et al. (2004).

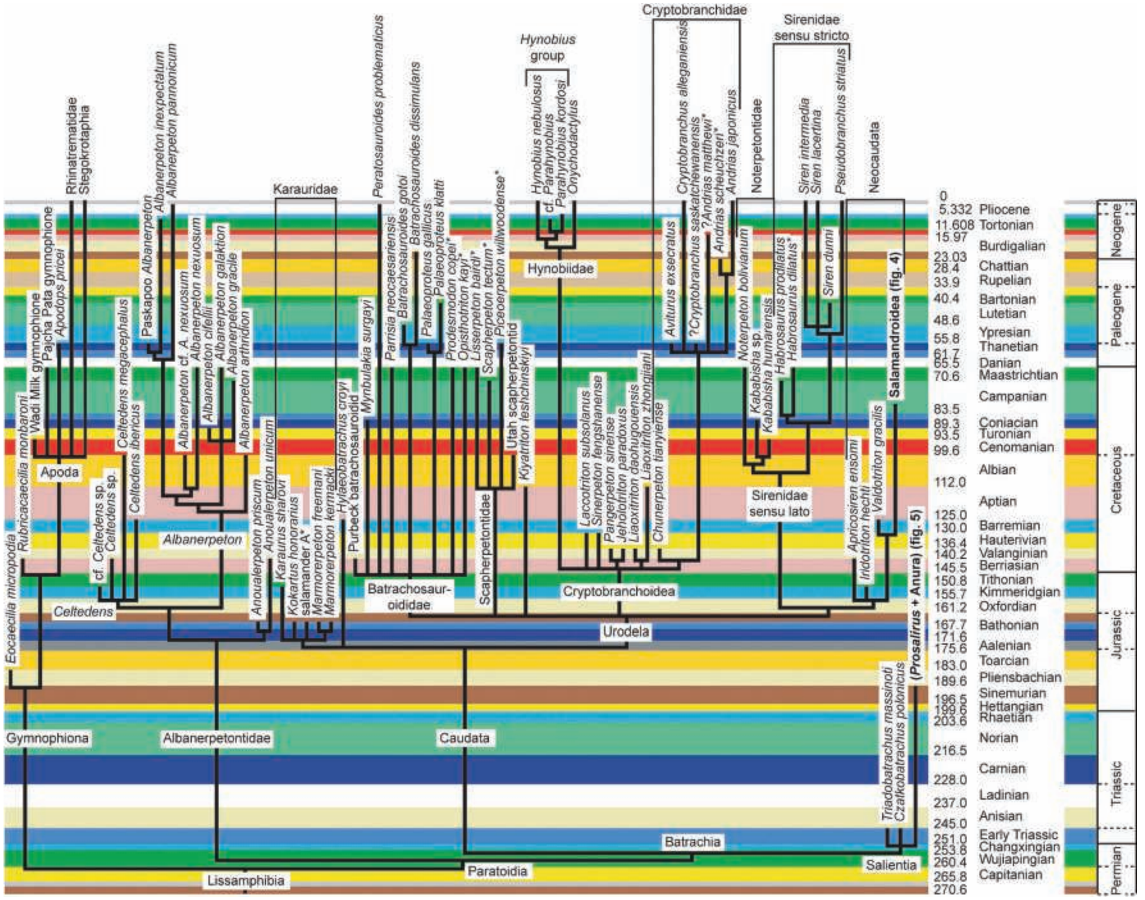

FIGURE 3. Time-calibrated supertree of extant and extinct lissamphibians, fitted to a geological timescale (Gradstein et al., 2004) in Mesquite (Maddison and Maddison, 2005). All extinct taxa that could be dated and placed with reasonable precision in the phylogeny are included; clades without a fossil record are collapsed or reduced to one representative species to save space. Taxa marked with an asterisk are known to extend at least into the following geological stage. All polytomies represent uncertainty (they are soft polytomies). The position of clade labels with respect to nodes, internodes, or terminal taxon labels is purely due to reasons of aesthetics and legibility, not, e.g., to the different types of phylogenetic definitions. See the text for more information. The sources are cited in Appendix 1. Continues in Figures 4 to 7. *Unlabeled stages from top to bottom:* "Quarternary" (Holocene + Pleistocene; beginning 1.806 Mya), Messinian (beginning 7.246), Serravallian (beginning 13.65), Langhian, Aquitanian (end 20.43), Priabonian (beginning 37.2), Selandian (end 58.7), Santonian (beginning 85.8), Callovian (beginning 164.7), Bajocian, Hettangian, Wordian (beginning 268.0), Roadian. The standard subdivisions of the periods are indicated by dashed lines. These are (*bottom to top*) "Guadalupian" and "Luopingian" for the Permian; "Early," "Middle," and "Late" for the Triassic and Jurassic; "Early" and "Late" for the Cretaceous; "Paleocene," "Eocene," and "Oligocene" for the Paleogene; and "Miocene" and "Pliocene" for the Neogene. The Early Triassic has now been divided into two stages (Gradstein et al., 2004), but we have not been able to apply this recent development to our data.

Taxa were selected and entered into a time-calibrated supertree (Figs. 3 to 7) in Mesquite (Maddison and Maddison, 2005) using the Stratigraphic Tools for Mesquite recently developed by our team (Josse et al., 2006). The terminal taxa were placed in the phylogeny and the stratigraphy according to several objective criteria (Appendix 1; all appendices of this paper can be downloaded from the Systematic Biology website at www.systematicbiology.org). In the absence of evidence to the contrary, all taxa (at all Linnaean ranks) were interpreted as clades. In some cases, like the Middle Jurassic to Early Cretaceous *Eodiscoglossus*, this might bias our conclusions towards earlier divergence dates, because paleoherpetologists have often attributed fragmentary fossils with few (if any) diagnostic characters to known (especially extant) taxa, sometimes based on unpolarized similarities. This practice may have resulted in the erroneous interpretation of paraphyletic taxa as clades. Thus, our approach could bias our results by yielding earlier diversification dates of several crown-groups, thereby decreasing the incongruence between our results and those of Zhang et al. (2005).

An effort was made to find the oldest known member of every clade, even if its phylogenetic position within that clade is unknown. We have expressed such uncertainties as polytomies (all polytomies in the supertree should be interpreted as soft polytomies). Again, this should generally bias our conclusions towards older divergence estimates because most possible resolutions of these polytomies would result in more recent appearances of crown-groups than shown here. As an extreme example, the divergence between the living *Bombina* and *Discoglossus* is Middle Jurassic in our tree (Fig. 5) because of the uncertain position of the Middle

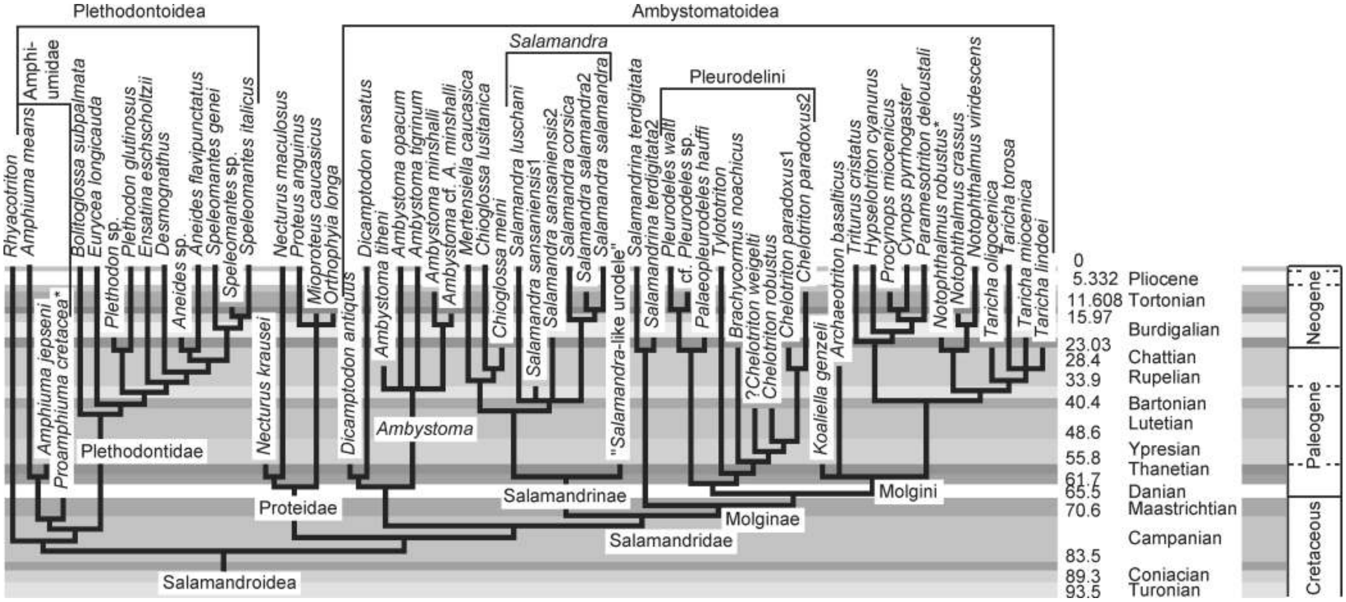

FIGURE 4. Time-calibrated supertree of extant and extinct Salamandroidea. See legend of Figure 3 for more information.

Jurassic *Eodiscoglossus oxoniensis* (Evans et al., 1990). Some resolutions of the polytomy (Discoglossoidea in Fig. 5, Discoglossoidea or Discoglossidae of most authors, Costata of Frost et al., 2006) in which these three taxa, the Early Cretaceous *Callobatrachus*, the Eocene and Oligocene *Opisthocoelellus*, and the Eocene (or Oligocene) to Pliocene *Latonia* lie, would yield much younger divergence date estimates for the living discoglossoids, as young as Oligocene in some cases. To study the impact of the polytomies on the age of appearance of various taxa, we have produced 10 random resolutions of all important polytomies in MacClade 4.06 (Maddison and Maddison, 2003) using the "equiprobable trees" algorithm, reproduced them manually into copies of our supertree, and redone the age adjustment of the tree using the Stratigraphic Tools (Josse et al., 2006), with the usual assumption that each species occupies at least an entire geological stage and that each internal branch is at least 3 My long. Ten random resolutions may seem low, but this procedure was time consuming because these topologies had to be manually entered into Mesquite and the stratigraphic adjustment had to be redone for each resolution of each polytomy; furthermore, many of the polytomies are trichotomies, for which every possible resolution occurs more often than once.

The huge phylogenetic analysis of Lissamphibia by Frost et al. (2006) appeared too late to be used as a source for the construction of our tree (with the exception of bufonid phylogeny). This opened the interesting possibility of testing if our analyses give different results for the tree by Frost et al. (2006) and our supertree (Appendices 2, 3). Therefore, we made a second supertree (Appendix 2) by rearranging our supertree to conform to the topology found by Frost et al. (2006).

A minimal internal branch length of 3 My was used when compiling the tree; this pushes speciose clades back in time, even when their fossil record is poor. A value greater than about 1 My is required to make the supertree legible (otherwise, many resolved clades would appear in the figures as if they were polytomies). The value of 3 My is, of course, arbitrary. If we had used 2 or 4 My, this would have modified the age of most clades only marginally; however, Laurin (2004) found that 3 My was a plausible minimal internal branch length in his study of early stegocephalian body size evolution. To test the impact of our branch length assumptions on the estimated age of the taxa, we have compiled the ages of 16 of the most relevant taxa yielded by 14 distinct assumptions (Appendix 4). Five of these assumptions differ only by the assumed minimal internal branch lengths (we tested values ranging from 0.1 to 5 My) and assumed, as shown in the supertree (Figs. 3 to 7), that each species occupied at least a whole geological stage. The value used to produce the supertree (3 My) was, for comparison, among those that we included. Another method that we used consists in assuming that each terminal branch (here represented by the included species) lasted at least a minimal amount of time (we tested values ranging from 0.1 to 5 My) and that each branch ends at the top of each geological stage; of course, minimal internal branch lengths must also be specified here (we tested values ranging from 0.1 to 5 My). Using three values each of internal and terminal branch lengths, nine cases were examined (Appendix 4). The 14 tested assumptions probably encompass all plausible values because it seems unlikely that the interval between most cladogenetic events included in our supertree was less than 0.1 My or more than 5 My. Using Stratigraphic Tools (Josse et al., 2006), these assumptions can be changed and the branch lengths of the supertree readjusted in seconds. However, the precision of the age is no better than about ±2 My if it is read by using the scale in Mesquite (as we did). Alternatively, accurate ages

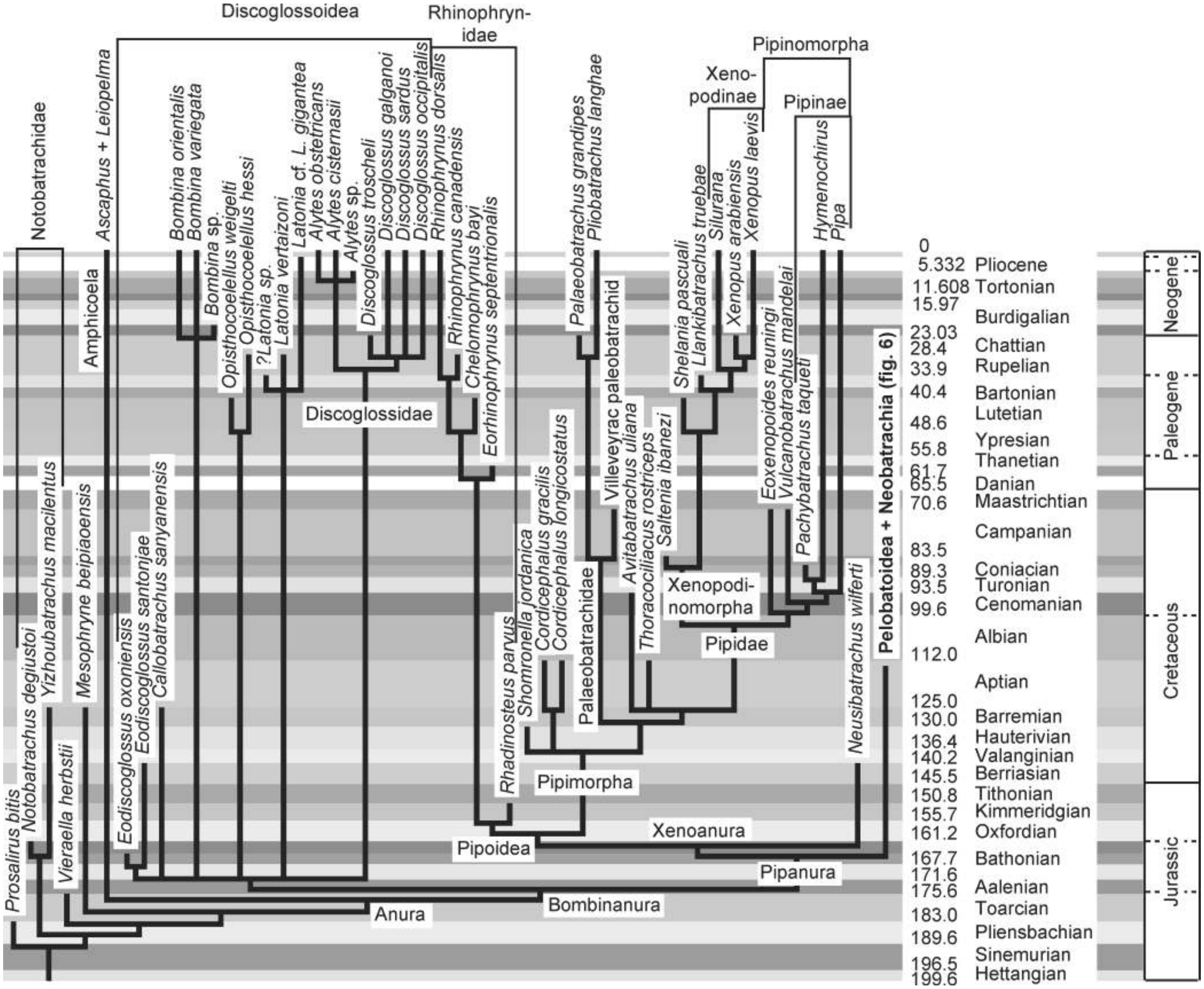

FIGURE 5. Time-calibrated supertree of extant and extinct Salientia (part). Continues in Figures 6 and 7. See legend of Figure 3 for more information. Note that *pliobatrachus*, the last palaeobatrachid, died out in the early Pleistocene.

could be computed by adding all the branches leading from the top of the tree to the various nodes, but given the several other imprecisions that affect the values obtained (real age of the various geological stage boundaries—up to ±4 My—location of the fossils compared to the stage boundaries, uncertainties about phylogenetic positions), the gain in precision would probably be more apparent than real. We have also tested the sensitivity of node ages to phylogenetic uncertainties by randomly resolving polytomies (Appendix 5).

Our supertrees include 223 extinct lissamphibian species, as well as several extant taxa that serve as a scaffold to ease the interpretation of the tree. Some of the extant species belong to large clades without a known fossil record.

More information about the supertree construction can be found in Appendix 1.

Because Frost et al. (2006) have produced the most comprehensive phylogeny of lissamphibians and proposed a detailed classification, we initially wished to use their nomenclature. However, several considerations led us to depart from this approach for most names (Appendix 6).

Fossils with uncertain stratigraphic positions (possible ranges spanning two or three stages) were interpreted as coming from the end of the lowest possible stage. In many cases, this results in a stratigraphic range that ends in the middle of the uncertainty interval; if this practice has introduced bias, it is towards older divergence estimates that should be more congruent with those of Zhang et al. (2005), especially because all terminal branches span at least an entire stage.

Test of the Stratigraphic Fit of the Supertree

To test if the lissamphibian fossil record is good enough for our subsequent calculations, we calculated the

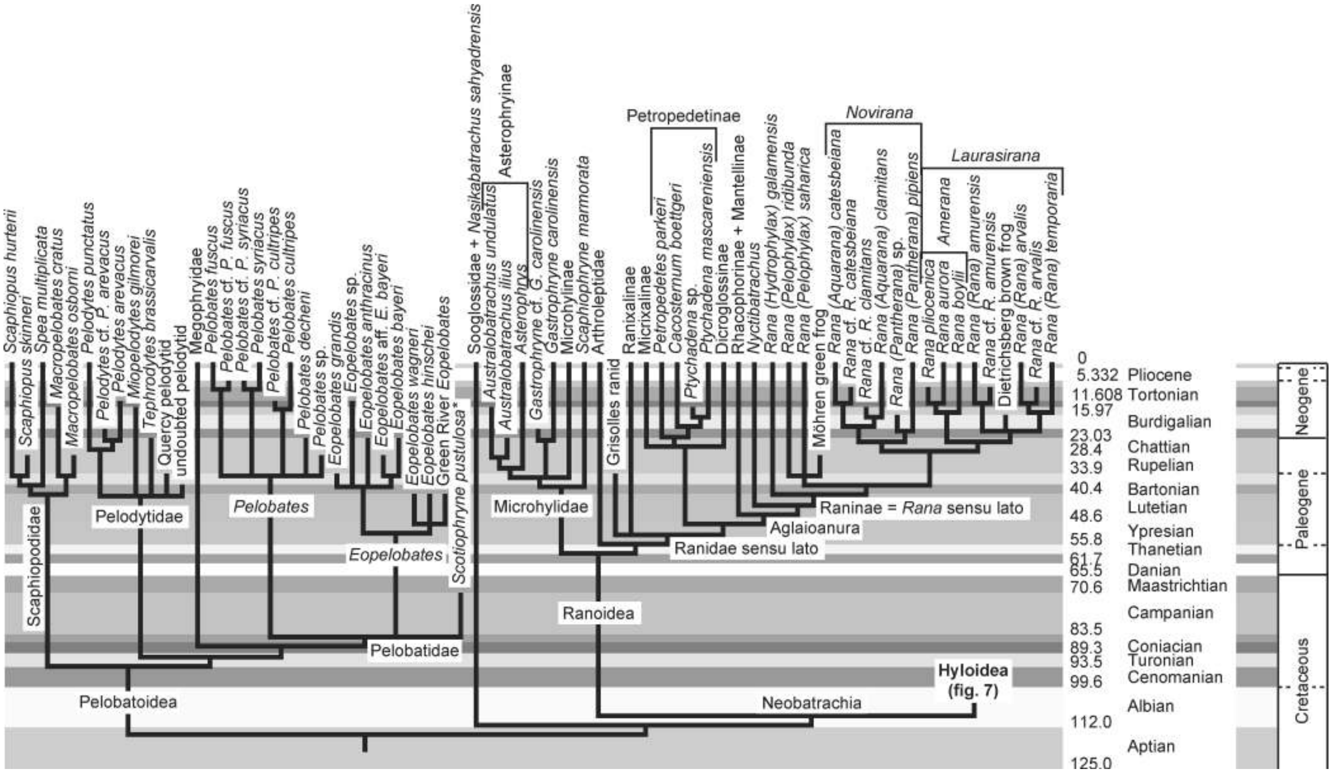

FIGURE 6. Time-calibrated supertree of extant and extinct Pelobatoidea and Neobatrachia (plus Sooglossidae & *Nasikabatrachus*). Continues in Figure 7. The name Aglaioanura comes from Frost et al. (2006). See legend of Figure 3 for more information.

stratigraphic fit of our trees. A low stratigraphic fit would mean that either the fossil record or the trees or both are of low quality; but given the quality and general congruence of the references used to construct the supertrees, we assume here that the trees are correct enough that they can be used to test the quality of the fossil record.

The stratigraphic fit of our supertrees was tested using Ghost (Wills, 1999), which computes three of the main stratigraphic fit indices, the Stratigraphic Consistency Index (SCI; Huelsenbeck, 1994), the Relative Completeness Index (RCI; Benton, 1994), and the Gap Excess Ratio (GER; Wills, 1999), and performs randomization of the

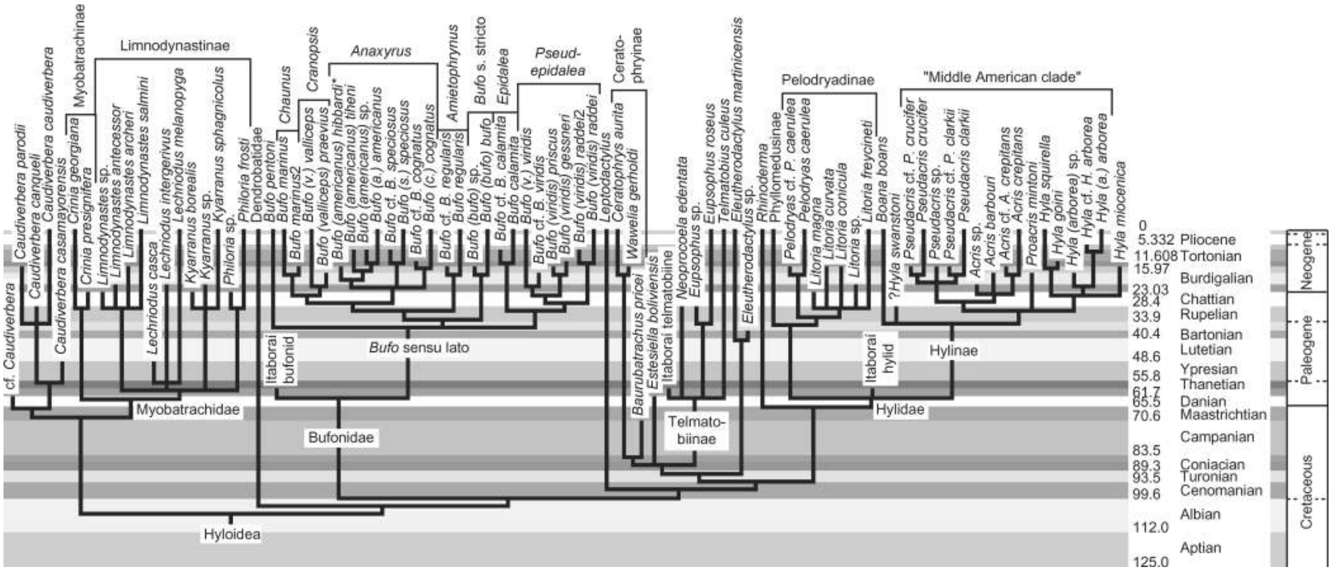

FIGURE 7. Time-calibrated supertree of extant and extinct Hyloidea. The resolution of *Bufo* sensu lato comes from Frost et al. (2006). See legend of Figure 3 for more information.

stratigraphic ranges to determine if the stratigraphic fit observed is better than random. We performed 9999 randomization replicates for each tree.

This test can assess both the fit of a tree to the fossil record, if the latter is considered sufficiently complete to be reliable, or (more importantly for our purpose) it can assess the completeness of the fossil record if the phylogeny is considered sufficiently reliable. This latter test is possible because if the fossil record of a group were very poor, we would expect a congruence between the order of cladogenesis and the order of appearance in the fossil record no better than random. Indeed, this method was used by Norell and Novacek (1992a, 1992b), Benton (1994, 1998, 2001), Benton and Storrs (1994), Benton and Simms (1995), Benton and Hitchin (1996), Benton et al. (1999, 2000), and Fara and Benton (2000), among others, to assess the quality of the known fossil record of various metazoans and its improvement in historical times.

The use of the SCI, RCI, and GER has been criticized because these indices are affected by the number of taxa in a tree, the number of stratigraphic ages of included taxa, and tree balance (Siddall, 1996, 1997; Pol et al., 2004). Thus, these indices cannot be used to compare the stratigraphic fit of trees that differ in any of these three factors. This is not a problem for our study because we only assess the stratigraphic fit of our trees by comparing these indices on our reference tree using the original (observed) stratigraphic ranges of taxa to the same indices on the same tree on which the stratigraphic ranges have been permuted. In this context, the use of these indices to assess the statistical significance of a stratigraphic fit should be unproblematic (Wills, 1999:567; Pol et al., 2004:70).

We have also tested the stratigraphic fit of the tree by Zhang et al. (2005) compared to that of our tree. As explained above, this is only meaningful if the trees are very similar; therefore, we pruned all taxa except for those used by Zhang et al. (2005) from our tree. Counting the branch lengths (in My) that lie between the first fossil of a clade and its estimated origin as ghost lineages, we calculated the total length of all ghost lineages (here termed the Actual Implied Gap, or AIG) for each tree. As the estimated date of origin, we used its molecular divergence date estimate without confidence intervals calculated by Zhang et al. (2005) and its divergence date based on a literal reading of our tree (with every terminal branch occupying at least an entire stage and minimal internal branch length set to 3 My). We interpreted the terminal branches as total clades and resolved polytomies in the way that gives the smallest gap; thus, we, e.g., counted the Wadi Milk Formation gymnophione as either Rhinatrematidae or Stegokrotaphia, which means that one of these two taxa is interpreted as having a continuous fossil record over the last 99.6 My.

Reanalysis of the Data Set of Zhang et al. (2005)

We calculated the most likely tree for the data set of Zhang et al. (2005: supplementary information) in PAUP* 4.0b10 (Swofford, 2003; 10 addition-sequence replicates, TBR swapping) using three different likelihood settings (evolutionary models) chosen by ModelTest 3.7 (see Posada and Crandall, 1998, for the first version) using the Akaike information criterion (following Posada and Buckley, 2004). We cannot replicate the model parameters Zhang et al. used (personal communication from P. Zhang), presumably because we used version 3.7 rather than 3.06.

Choice of models of evolution.—We would like to draw attention to some procedures followed by ModelTest that were not presented by the programmers (Posada and Crandall, 1998; Posada and Buckley, 2004). ModelTest begins by having PAUP* construct a tree from the data and then tests which parameters fit this tree best. That tree is a neighbor-joining tree calculated using the Jukes-Cantor model and is by default not displayed (Debruyne and Tassy, 2004). For the data of Zhang et al. (2005) this tree differs widely from all phylogenetic hypotheses proposed so far (Fig. 8a). We strongly disagree with this combination of approaches because it chooses the model parameters, which are subsequently used for the calculation of a phylogenetic tree, to fit a similarity diagram that is a poor representation of lissamphibian phylogeny. In this case, this is shown by the fact that Bombinanura (and by implication Anura) is polyphyletic, which is distressing because the monophyly of this taxon (in the context of this analysis: an anuran clade that excludes apodans and urodeles) is universally accepted and is supported by numerous apomorphies (Laurin, 1998; Frost et al., 2006). Accordingly, we modified the script of ModelTest 3.7 (which is a macro for PAUP*, that is, a NEXUS file) to calculate the most parsimonious tree (that is, a phylogenetic tree) and to display it. (This modified script is available from us upon request.) The tree (Fig. 8b) and model (Appendix 7) that result from this procedure are markedly different.

Still, the most parsimonious tree contains a monophyletic "Archaeobatrachia." Because we, like Zhang et al. (2005), consider this to be unlikely (see above), we inserted a constraint into the modified ModelTest script, requiring the topology (*Bombina* + (*Xenopus* + Neobatrachia)), which has so far been found by all studies that find "Archaeobatrachia" to be paraphyletic, except for that of Frost et al. (2006). The model calculated using this tree (see below) is very similar to the model chosen based on the unconstrained most parsimonious tree, presumably reflecting the fact that these two trees are much more similar to each other than to the neighbor-joining tree.

Divergence date estimates.—Zhang et al. (2005) used Multidivtime (Thorne and Kishino, 2002) to estimate the dates of the cladogeneses in their tree. For various reasons, including our unfamiliarity with UNIX commands, we found ourselves unable to use it. We had to resort to more user-friendly programs that use different dating algorithms, namely quartet dating as implemented in QDate 1.11 (Rambaut and Bromham, 1998), penalized likelihood (Sanderson, 2002) as implemented in r8s 1.71 (Sanderson, 2003, 2006), and a method recently presented by Anderson (2006), as implemented in PATHd8.

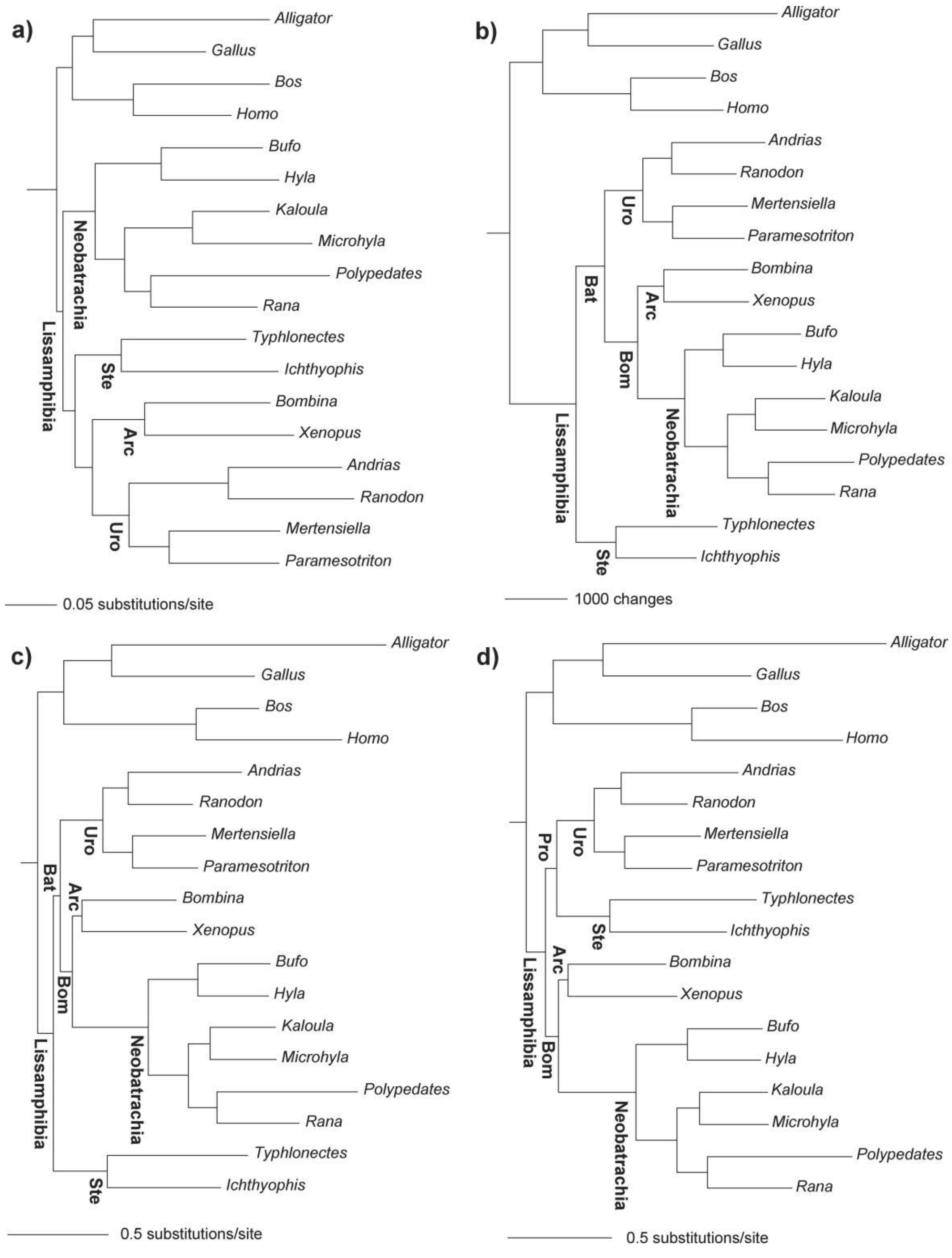

FIGURE 8. Trees produced from various analyses of the data set of Zhang et al. (2005). Dogfish (*Scyliorhinus canicula*), carp (*Cyprinus carpio*), and lungfish (*Protopterus dolloi*) not shown. (a) Neighbor-joining (phenetic) tree calculated using the Jukes-Cantor model, which is used by the stock version of ModelTest to choose the evolutionary model. Note the diphyly of Bombinanura. (b) Most parsimonious (phylogenetic) tree used by our modified ModelTest script to choose the model of evolution; the lungfish had to be constrained to be closer to the tetrapods than the carp. (c) Most likely (phylogenetic) tree calculated using a model chosen by the stock version of ModelTest 3.7 (Posada and Crandall, 1998) to fit the neighbor-joining (phenetic) tree from (a). Note the close similarity to the tree that Zhang et al. (2005: fig. 1) found; also note the difference in scale—0.5 substitutions per site on our tree are equal to 0.1 on theirs. (d) Most likely (phylogenetic) tree calculated using a model chosen by a slightly modified version of ModelTest 3.7 to fit the most parsimonious (phylogenetic) tree shown in (b). Note the similarity in branch lengths and the difference in topology to (c). Arc, Archaeobatrachia; Bat, Batrachia; Bom, Bombinanura; Pro, Procera; Ste, Stegokrotaphia; Uro, Urodela.

TABLE 1. Calibration points used in this study, or recommended (*), based on our supertree. The origin of Amniota had to be used because of the requirements of QDate; because of its poorly constrained upper bound, its use is likely to result in overly large confidence intervals in molecular divergence date estimation.

Taxon	Main taxonomic content	Minimal divergence age (Mya)	Maximal divergence age (Mya)
Tetrapoda*	Amphibia, Amniota	332	360
Amniota	Theropsida, Sauropsida	310	345
Anura*	Amphicoela, Bombinanura	170	185
Batrachia*	Salientia, Caudata	250	275
Bombinanura*	Discoglossoidea, Pipanura	170	185
Pipoidea*	Rhinophrynidae, Pipimorpha	155	175
Urodela*	Cryptobranchoidea, (Sirenidae sensu lato + Neocaudata)	155	170

However, unlike Zhang et al. (2005), we tested various combinations of internal and external calibration dates.

QDate can only use symmetric trees with four terminal taxa. Given the topology and point dates for the two most recent divergences, it calculates the age of the root node (with a confidence interval), assuming one constant rate of evolution for each half of the tree. Because few calibration points are available (Table 1), we were only able to date two divergences with QDate, namely the origin of Tetrapoda and the origin of Batrachia. Because QDate requires point estimates, we did the datings twice, using the upper and the lower bounds of the calibration points as point estimates. To avoid influence from the widely differing terminal branch lengths on the divergence date estimates (the molecular tree is far from ultrametric), we repeated each run of QDate 12 or 16 times with different combinations of terminal taxa. The exact quartets used are listed in Appendix 8.

The program r8s is more suitable for our purpose. Like Multidivtime, it can accept ranges as calibration points, multiple calibration points, and a complex phylogeny. Using the penalized-likelihood method and a range of smoothing parameters, we estimated a range of divergence dates (unfortunately, without confidence intervals). We were able to take two phylogenetic hypotheses into account, namely the monophyly of "Archaeobatrachia" as found by Zhang et al. (2005), and its paraphyly as (*Bombina* + (*Xenopus* + Neobatrachia)). The value of the smoothing parameter was selected using two selection procedures: one that minimizes the standardized squared difference between the predicted and the observed number of substitutions on each branch, as suggested by Sanderson (2002), and another that minimizes the relative error between the upper and the lower bounds of calibration dates on the one hand and the inferred dates on the other hand, as suggested by Near and Sanderson (2004).

Calibration points.—Zhang et al. (2005) used two external calibration points: the Dipnomorpha-Tetrapodomorpha (lungfish-tetrapod) split, assumed to have taken place 400 ± 10 Mya, and the Theropsida (Synapsida)-Sauropsida (mammal-bird/crocodile/lizard/turtle) split, supposedly 310 ± 10 Mya. The lower bounds on these ranges are almost certainly too young. The earliest known dipnomorph is late Lochkovian or early Pragian in age (Müller and Reisz, 2005); the Pragian (middle Early Devonian) ended 407.0 ± 2.8 Mya (Gradstein et al., 2004), so a lower bound of 410 rather than 390 Mya seems realistic for the uncertainty range of the dipnomorph-tetrapodomorph divergence. The presence and diversity of the earliest and basalmost known sarcopterygians and actinopterygians around the Silurian-Devonian boundary (Zhu et al., 1999, 2001, 2006) probably indicate that the split between dipnomorphs and tetrapodomorphs happened around this time at most (perhaps up to 420 Mya), but the very poor fossil record of gnathostomes (Cappetta et al., 1993; Gardiner, 1993a, 1993b), if not vertebrates in general (Blieck, 1984), in the Silurian precludes a more definitive statement on this.

The oldest known amniote, *Hylonomus lyelli*, apparently comes from the late Bashkirian (Calder, 1994), which ended 311.7 ± 1.1 Mya (Gradstein et al., 2004), so that the age of 310 My should be the lower (younger) bound rather than the midpoint of the date estimate of the theropsid-sauropsid divergence; an upper bound, on the other hand, is very difficult to estimate. In addition to the detailed argument provided by Reisz and Müller (2004), we wish to emphasize that the fossil record of stem-amniotes is not good enough to tell whether the apparent absence of amniotes before about 312 Mya is real. All undisputed stem-amniotes (*Solenodonsaurus* and Diadectomorpha; Vallin and Laurin, 2004, and references therein) are younger than *Hylonomus*. Tetrapods are very rare in the preceding stage (the Serpukhovian). The yet older Viséan stage has yielded the controversial *Westlothiana lizziae* which was originally interpreted as an amniote or close amniote relative but may not even be a tetrapod (Vallin and Laurin, 2004), the intriguing but poorly preserved *Casineria kiddi* for which similar suggestions have been made in the literature (Paton et al., 1999), and a few amphibians. The Tournaisian fossil record is so poor that the absence of tetrapods can again not be determined. Only in the Famennian (Upper Devonian) does the presence of several stem-tetrapods and the absence of any tetrapods enable us to conclude with reasonable confidence that the divergence between the lissamphibian and the amniote stems did not occur more than about 360 Mya, and that this divergence must significantly predate the origin of theropsids (synapsids) and sauropsids. In our QDate analyses we assumed an upper limit of 345 Mya (Appendix 9) based on the Viséan fossil record that has yielded several basal amphibians ("lepospondyls") and no amniotes, even though close relatives of the latter must have been present. As emphasized by Müller and Reisz (2005), this calibration is poorly constrained (in an interval that spans at least 35 My). Because of this, we expect the interval of inferred divergence dates based on molecular data to be correspondingly broad, but there is no reason to believe that they will be less reliable.

Zhang et al. (2005) did not use any internal calibration points. However, Brochu (2004) has found that, to get plausible divergence dates using quartet-dating, it is necessary to use both old and young calibration points. When only old divergence dates were used to calibrate the tree, the age estimates of other taxa were too old. This effect, if it extends beyond quartet-dating, may have overcompensated for the contrary effect produced by the underestimated age of the calibration points used by Zhang et al. (2005). Below, we suggest some calibration points within Lissamphibia for future molecular divergence time studies (Table 1); we have also used them to estimate divergence dates through penalized maximum likelihood in r8s (Sanderson, 2006).

RESULTS

Stratigraphic Range of Paleozoic Stegocephalians

The stratigraphic range of the dissorophoids reported by Zhang et al. (2005) is erroneous, and this invalidates their main conclusion about the origin of lissamphibians. Contrary to their statement, there is no evidence that Dissorophoidea appeared in the Viséan. The oldest known dissorophoids date from the Moscovian, in the Late Carboniferous (Milner, 1990, 1993a:672). Lysorophians and dissorophoids are abundant in the Moscovian locality of Linton, Ohio (Hook and Baird, 1986; Milner, 1993a:672). The oldest known dissorophoid (*Amphibamus grandiceps*) is only slightly older (Upper Westphalian C to Lower Westphalian D, both equivalent to Moscovian) and occurs in Mazon Creek, Illinois (Gregory, 1950; Milner, 1993a), where lysorophians (*Brachydectes*) are also present (Baird, 1964:14; Wellstead, 1991). Mazon Creek is a well-studied locality whose geological age is supported by several lines of evidence, including detailed studies of pollen and spores (Peppers, 1996, and references cited therein). The oldest undisputed lysorophian specimens come from Newsham (Boyd, 1980; Wellstead, 1991), date from the Westphalian B (equivalent to the late Bashkirian, the oldest stage of the Late Carboniferous), and are only slightly older than the oldest known dissorophoids. This locality is not as well known as Mazon Creek, but it is universally considered to be older (Wellstead, 1991; Turner et al., 2005; Jeffery, 2006). Lysorophians have even been reported from localities older than Newsham, such as Jarrow, that date from lower in the Westphalian B, but the specimens are poorly preserved and only tentatively attributed to Lysorophia (Boyd, 1980; Wellstead, 1991:71), so we will ignore them for the purposes of this study. To conclude, the latest possible date of appearance of Lysorophia is slightly earlier than that of Dissorophoidea, rather than much later as mistakenly reported by Zhang et al. (2005). Thus, the early divergence date inferred from the molecular date does not suggest an origin of lissamphibians among dissorophoids.

The preceding discussion simplifies the presentation of the hypothesis that lissamphibians are nested within temnospondyls to make it comparable to the argument presented by Zhang et al. (2005). However, to our knowledge, no paleontologist has suggested that Dissorophoidea as a whole were the sister-group to Lissamphibia. Rather, subclades of Dissorophoidea have been proposed as the sister-group (*Doleserpeton,* or a clade composed of the latter and *Amphibamus*) or stem-group (Branchiosauridae) of the lissamphibians (Bolt, 1969; Trueb and Cloutier, 1991; Ruta et al., 2003). This distinction is important because these subclades appeared later than Dissorophoidea as a whole. The first branchiosaurids appeared only slightly later than the first dissorophoids, in the Westphalian D (equivalent to Moscovian; Milner, 1993a), but *Doleserpeton* is much more recent (Artinskian; Fig. 2). Thus, two of the three proposed alternative positions of the lissamphibian stem suggest a later date for the origin of Lissamphibia than if Dissorophoidea were the sister-group of Lissamphibia (Fig. 2).

Time-Calibrated Supertrees

A literal interpretation of our tree (Figs. 3 to 7) confirms that the diversification of lissamphibians is much more recent than hypothesized by Zhang et al. (2005). Furthermore, there is a very good congruence between geological age and phylogenetic position. The four oldest salientian species (Triassic to Early Jurassic) all belong to the stem rather than to the crown-group Anura. These are *Triadobatrachus massinoti* (Rage and Roček, 1989) and *Czatkobatrachus polonicus* (Borsuk-Białynicka and Evans, 2002) from the Early Triassic, and *Prosalirus bitis* (Shubin and Jenkins, 1995) and *Vieraella herbstii* (Reig, 1961) from the Early Jurassic. Similarly, at least the two oldest gymnophiones belong to the stem; these are the Early Jurassic *Eocaecilia micropodia* (Jenkins and Walsh, 1993) and the Early Cretaceous *Rubricacaecilia monbaroni* (Evans and Sigogneau-Russell, 2001). Likewise, several stem-caudates are older than the oldest crown-caudates; these include *Kokartus honorarius* (Nessov, 1988), *Marmorerpeton kermacki* and *M. freemani* (Evans et al., 1988), and "Salamanders A and B" (Evans and Milner, 1991), all from the Middle Jurassic. The oldest known crown-salientian (anuran) is *Eodiscoglossus oxoniensis* from the Middle Jurassic (Evans et al., 1990). The oldest known possible crown-gymnophione (apodan) is an unnamed form from the Wadi Milk Formation in Sudan, which dates from the beginning of the Late Cretaceous (Cenomanian; Evans et al., 1996); however, the phylogenetic position of this gymnophione, and that of the terminal Cretaceous fossil from Pajcha Pata in Bolivia (Maastrichtian; Gayet et al., 2001), are poorly established; they could be stem-gymnophiones. The oldest gymnophione that was proposed to be related to an extant subgroup of apodans (i.e., to be within the crown-group) is the Paleocene *Apodops pricei* (Estes and Wake, 1972) that was argued to be a caeciliid; but at the time of its description Caeciliidae was thought to include all apodans except Ichthyophiidae, Scolecomorphidae, and Typhlonectidae. Even Rhinatrematidae was included, so in effect the place of *Apodops* could be anywhere within the crown-group or even just outside it. The oldest crown-caudate (urodele) is *Iridotriton hechti* from the Late Jurassic (Evans et al., 2005). Albanerpetontids, which may be the sister-group of Batrachia (Gardner, 2001; McGowan, 2002), first appear in the Middle Jurassic (Gardner et al., 2003), at the same time as the oldest crown-salientian (anuran), and before any crown-gymnophione (apodan) or crown-caudate (urodele). Thus, there do not seem to be any major anomalies in the stratigraphic distribution of lissamphibian fossils, and this suggests that our time-calibrated trees can be used to assess the approximate time of origin of at least some lissamphibian clades.

Changing the assumptions about minimal branch lengths (Appendix 4) does not significantly alter our conclusions because for most clades the range of values of minimal computed age using our paleontological database encompasses less than 30 My. The age of the oldest nodes is especially stable, which is not surprising considering that this value is constrained by fossils separated from these nodes by only a few branches. For instance, the age of Salientia varies between 246 and 252 My (Appendix 4). Conversely, the age of relatively speciose clades with a poor fossil record is poorly constrained by our method. This is best exemplified by Ranoidea, whose minimal age varies between 34 and 74 My, depending on the chosen minimal branch length assumptions (Appendix 4). In all cases, even taking into account that they are estimates of minimal rather than actual divergence dates, our dates remain much younger than those suggested by Zhang et al. (2005). For instance, the age of Lissamphibia varies between 246 and 267 My (260 My in our reference supertree), and that of Bombinanura varies between 166 and 187 My (174 My in our reference tree). By comparison, Zhang et al. (2005) inferred ages of 337 and 290 My for these taxa, and the confidence intervals of these ages (321 to 353 and 268 to 313 My, respectively) exclude our range of paleontological ages. The paleontological age of nearly all clades of lissamphibians represented in the data of Zhang et al. (2005) is excluded from the 95% credibility interval computed by Zhang et al. (2005; Fig. 9). The only exception is the smallest clade that includes *Hyla* and *Bufo*, for which our age estimate is compatible with that of Zhang et al. (2005); the (*Kaloula* + *Microhyla*) clade does not have a known fossil record, so we are not able to infer a divergence date for it. Finally, the set of assumptions that we have used to build the supertree (Figs. 3 to 7) yields dates that are often among the oldest or at least average among the fourteen sets of assumptions that we have tested (Appendix 4).

Similarly, our use of polytomies generally biases our results towards congruence with the greater ages of taxa obtained by Zhang et al. (2005). This is shown by our random resolution test of polytomies that affect the age of 15 polytomies containing 23 taxa (Appendix 5). As our tests show, the average age on randomly resolved trees for the taxa surveyed is 77 My, whereas the average age of the same taxa on our reference tree (with polytomies) is 80 My (Appendix 5). Thus, the presence of polytomies in our supertree tends to slightly overevaluate the age of the taxa, making them more similar to the ages proposed by Zhang et al. (2005) than most random resolutions would.

Adopting the rather different topology presented by Frost et al. (2006) does not alter the age of most taxa significantly, to the extent that they can be compared (Appendix 3). The two trees are mostly congruent, but in the case of Pipidae we had to create a large polytomy because we are unable to fit most fossil pipoids into the unorthodox topology found by Frost et al. (2006). The whole tree is available in the online supplementary data (Appendix 2); here, we only compare the geological age of 16 taxa on our tree and that by Frost et al. (2006). This comparison shows that the average age for these 16 taxa differs only by 1 My (less than 1% of the absolute age). Thus, our results appear to be reasonably robust to changes in topology.

The stratigraphic fit for our lissamphibian tree is surprisingly good, with a RCI of −2.5161, a SCI of 0.4583, and a GER of 0. 8146. The probability that such values are generated by a random association between phylogeny and fossil record is about 0.0001. By implying that the fossil record is fairly complete, this suggests that the minimal divergence dates of our tree are not severely underestimated.

The tree based on that by Frost et al. (2006) has similar values, except for the RCI: RCI =−187.7249, SCI = 0.4861, GER = 0.8057. The probability for this being a random result is identical.

Inevitably, our tree (reduced to the taxa used by Zhang et al., 2005) has much better stratigraphic fit than the molecular tree of Zhang et al. (2005). Our tree has an Actual Implied Gap (AIG) of 857.1 My, the one by Zhang et al. (2005) has an AIG of 1906.7 My.

Calibration Points for Molecular Analyses

Raaum et al. (2005: fig. 2) have proposed criteria for identifying calibration points for molecular dating: “It is best to have fossils [...] attributed to one or the other, or both, of the extant lineages, as well as other fossil specimens from around the time of the split” which lie outside the crown-group in question (Raaum et al., 2005: fig. 2); the more there are, and the better the tree fits their ages, the more probable it is that the fossil record is well enough sampled around the divergence to allow a reliably accurate estimate of the latter’s date. This is arguably the case for a few divergences in our supertree, but the fossil record of lissamphibians is not ideal in this respect. We suggest the use of the dates discussed below (Table 1) as possible internal calibration points for determining a molecular timescale within Lissamphibia (to be used together with at least one external calibration point), but only the minimal divergence dates are well-constrained; maximal ages are much more difficult to determine.

Origin of Bombinanura.—The divergence between Discoglossoidea and Pipanura (or, according to Frost et al., 2006, that between Xenoanura and Sokolanura), and the preceding one between Bombinanura and Amphicoela, seem to have taken place between the middle Middle Jurassic and the middle Early Jurassic (Fig. 5), some 170 Mya (Gradstein et al., 2004) at the latest and probably not much more than 185 Mya. The lower bound for both divergences in both trees is provided by the oldest known discoglossoid, *Eodiscoglossus oxoniensis*,

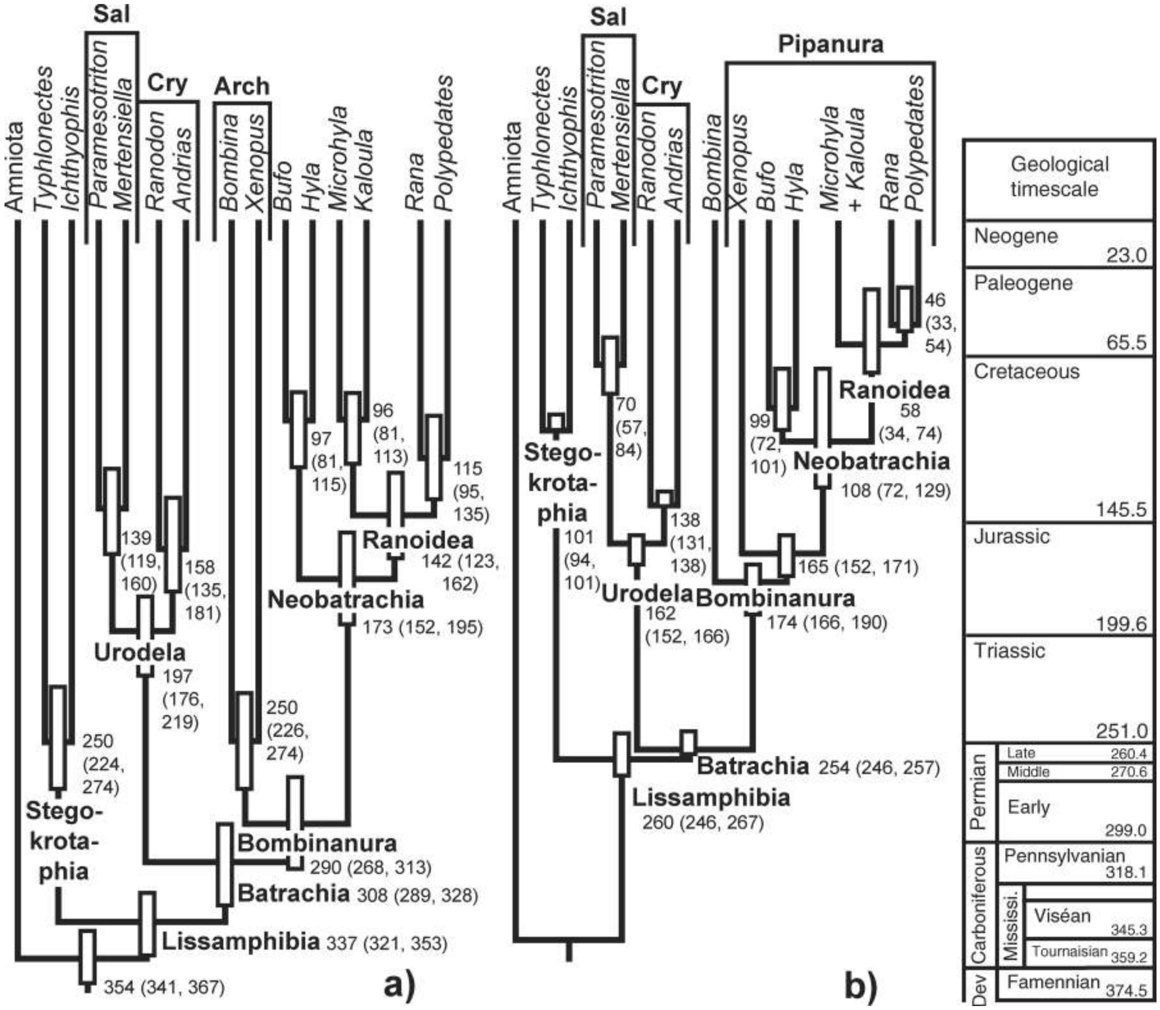

FIGURE 9. Comparison between lissamphibian divergence dates implied by (a) the analysis of molecular data by Zhang et al. (2005) and (b) paleontological data (from Figs. 3 to 7). In (a), credibility intervals (95%) are represented by boxes; the best estimates and lower and upper boundaries of the 95% credibility intervals (in My) are also indicated in parentheses. In (b), we are unable to date the origin of the smallest clade that contains *Microhyla* and *Kaloula* because it does not have a fossil record. The numbers given next to the nodes represent the estimated age given the assumptions used to build the supertree (each species occupies at least an entire geological stage, and the minimal internal branch length is set at 3 My), followed, in parentheses, by the minimal and maximal latest possible age obtained by using the various minimal branch length assumptions listed in Appendix 4. Thus, these numbers are not really confidence intervals but represent ranges of values of the minimal (rather than actual) divergence dates; still, they give an idea of the plausible range in the paleontological age of each taxon (also shown as boxes around each node). Paleontological ages are not given for the basal node (Tetrapoda) because it is not included in our supertree. Note that the paleontological estimates of minimal divergence dates (b) lie in most cases outside the 95% credibility interval of the molecular dates (a) by Zhang et al. (2005), with only the smallest clade, which includes *Bufo* and *Hyla*, being an obvious exception. Arch, Archaeobatrachia; Cry, Cryptobranchoidea; Mississi., Mississippian; Sal, Salamandridae.

which is Bathonian in age. An upper bound may be estimated from *Vieraella* and *Prosalirus*, two successive sister-groups of Anura, the ages of which are thought to be Toarcian or Aalenian (Roček, 2000) and Pliensbachian (Shubin and Jenkins, 1995), respectively. However, the much later appearance date of *Mesophryne* (creating a ghost lineage of at least 55 My), which is the sister-group to Anura, as well as the complete lack of known fossil amphicoelans, raises the possibility that Bombinanura and Anura are older than our supertree suggests, as may the wholesale absence of known salientians between the middle Early Jurassic and the Early Triassic. Accordingly, we have repeated those runs of r8s where the origin of Bombinanura was used as a calibration point, assuming that the distance between the minimal and the maximal age was twice or three times as large as proposed here (that is, a maximal age of 200 or 215 My). The divergence between Discoglossoidea and Pipanura (or Xenoanura and Sokolanura) obviously must have happened after the basal divergence of Anura, but the fossil record does not tell how much later. A great separation seems to be unlikely given the small number of synapomorphies that have been proposed for Discoglossoidea, Pipanura, and Sokolanura.

Origin of Pipoidea.—Rhinophrynids and pipimorphs may have diverged in the Middle or early Late Jurassic, between about 155 and 175 My. The earliest known rhinophrynid, *Rhadinosteus*, is Kimmeridgian or Tithonian in age (Henrici, 1998); an upper bound is only provided by the divergence between Discoglossoidea and Pipanura or Xenoanura and Sokolanura (see above). The only known stem-xenoanuran, *Neusibatrachus*, is from the Berriasian or younger (Roček, 2000; Chiappe and Lacasa-Ruiz, 2002; Padian, 2004) and thus younger than the xenoanuran crown-group (Pipoidea). Pelobatoidea and Neobatrachia, together the sister-group of Xenoanura in our main tree, do not appear in the fossil record before the Campanian (some 75 Mya).

Origin of Urodela.—A Middle or early Late Jurassic (∼155 to ∼170 Mya) origin seems plausible for Urodela (that is, Caudata of Frost et al., 2006). The earliest known urodelan is the basal neocaudate *Iridotriton* (Kimmeridgian or Tithonian: Evans et al., 2005; see also He et al., 2004, and Wang and Rose, 2005). Urodeles are so far not known from the Bathonian deposits in western Europe and central Asia, which have yielded relatively abundant karaurids, the only currently undisputed nonurodelan caudates. The complete absence of known older caudates is, however, not encouraging, given the size of the gap implied by the oldest known salientians. Accordingly, as with Bombinanura, we have repeated those runs of r8s where we used the origin of Urodela as a calibration point, under the assumption that the distance between the minimal and the maximal age was twice or three times as large as proposed here (that is, a maximal age of 185 or 200 My).

Some recent studies (San Mauro et al., 2005; Mueller, 2006; Bossuyt et al., 2006) have used the age of the oldest known cryptobranchid, *Chunerpeton tianyiense*, as the minimum age of the split between Cryptobranchidae and Hynobiidae. Originally (Gao and Shubin, 2003) this age was reported as 161 My (equivalent to the Middle-Late Jurassic boundary; Gradstein et al., 2004), but this rests on the idea that the Daohugou Beds, which have yielded *Chunerpeton*, belong to the Jiulongshan Formation, on top of which lies the ignimbrite that has yielded the radiometric date. Reportedly, however, they overlie rather than underlie the even higher Tuchengzi Formation (He et al., 2004). A radiometric date from somewhere in the upper part of this formation is 139.4 ± 0.2 My (Swisher et al., 2002), equivalent to the Berriasian-Valanginian boundary (Gradstein et al., 2004) in the early part of the Early Cretaceous. If this stratigraphic relationship is correct, the Daohugou Beds cannot be older than Valanginian, and Zhang et al. (2005) are mistaken in interpreting *Chunerpeton* as supporting their molecular divergence date estimate of Cryptobranchoidea (181 to 135 Mya, best estimate of 158 Mya). Based on the Barremian-Aptian boundary age of the Yixian Formation and on crude biostratigraphy, the Daohugou Beds could be as young as Barremian (and were assumed to be so by Wang and Rose, 2005). However, they underlie the Yixian Formation (He et al., 2005), so this is their youngest possible age. In keeping with our treatment of stratigraphic uncertainty explained above, we have assumed a Valanginian age in the construction of our tree and the calculation of its stratigraphic fit.

A Middle Jurassic age of the Daohugou Beds is defended by Gao and Ren (2006), who maintain that the beds underlie the ignimbrite (and the Tuchengzi Formation) and highlight several problems in the paper by He et al. (2004), but He et al. (2005) provide evidence, not addressed by Gao and Ren (2006), that the Daohugou Beds overlie the ignimbrite. A resolution to this debate does not appear to be in sight; to us, it seems that the correlation of the many outcrops assigned to the Daohugou Beds and other formations over a vast area of hilly terrain in Liaoning, Hebei, and Inner Mongolia might benefit from a review.

In any case, this problem only affects the ages of Cryptobranchoidea and Urodela, which is not a problem for our molecular dating. We only assume a minimal divergence date for Cryptobranchoidea (140 My). The age bracket of Urodela (minimum 155 My, maximum 170, 185, or 200 My) is also irrelevant because we never found a younger age than 170 My (older than any of the proposed ages of the Daohugou Beds) for that clade; whenever a constraint was active, it was the upper (older) one.

On a related note, He et al. (2006) date the Dabeigou Formation, which has yielded *Sinerpeton* and *Laccotriton*, as around 130 Mya (Hauterivian-Barremian boundary; Gradstein et al., 2004). Originally (Gao and Shubin, 2001), this layer was reported as Tithonian (late Late Jurassic) simply because it overlies the Zhangjiakou Formation, which is 151 My old (Kimmeridgian-Tithonian boundary).

Origin of Batrachia.—The oldest known batrachians are *Triadobatrachus* and *Czatkobatrachus*, both from the Early Triassic. Because their precise age within the Early Triassic is unknown, we think that the minimal age of Batrachia should be assumed around 250 My; that is, the Induan-Olenekian boundary (249.7 ± 0.7 Mya; Gradstein et al., 2004), which lies very close to the Permian-Triassic (Changxingian-Induan) boundary itself (251.0 ± 0.4 Mya). The maximal age is in principle as poorly constrained as that of Lissamphibia itself; however, we choose the rich Artinskian fossil record (284.4 ± 0.7 to 275.6 ± 0.7 Mya), which has yielded many basal amphibians but no lissamphibians, to establish the upper bound at 275 Mya, based on the consideration that it is more probable that two lineages of stem-lissamphibians are "hiding" in it than that four lissamphibian lineages (Gymnophiona, Albanerpetontidae, Salientia, and Caudata) await discovery in Artinskian sediments (Table 1).

Origin of Tetrapoda.—There is much confusion in the literature about the age of Tetrapoda because this taxon has been used as if it were defined by an apomorphy (the origin of the limb) in most paleontological studies, but as if it were a crown-group in most neontological studies that have used it in any precise sense (Laurin and Anderson, 2004). Thus, a brief discussion of the minimal and maximal age of Tetrapoda (the crown-group) may be useful, even though our supertree only includes lissamphibians. The oldest undoubted tetrapod, the amphibian *Lethiscus stocki*, comes from the Wardie shales of

Scotland. These lie in the Lower Oil Shale Group and are mid-Viséan (Holkerian) in age (Wellstead, 1982; Carroll, 2000). The Holkerian dates from about 332 to 339 Mya (Gradstein et al., 2004), so Tetrapoda cannot have originated less than 332 Mya. This is the minimal age of Tetrapoda under any recent phylogeny (Ruta and Coates, 2003). The upper bound is as always less secure, but the presence of several species of stem-tetrapods in the Famennian (375 to 359 Mya) suggests that an upper bound of 360 Mya is realistic. This bound is plausible because most Famennian stegocephalians come from fairly high up in that stage (Blom et al., 2005) and because of the large number of apomorphies shared by tetrapods but not by Devonian stegocephalians (Laurin, 1998).

Molecular Phylogenetic Analysis

Because the neighbor-joining tree (Fig. 8a) is a phenogram rather than a cladogram, we do not discuss its peculiarities in detail even though this is the tree to which the stock version of ModelTest tries to fit the model.

The most likely tree calculated using this model (Fig. 8c) is much more congruent with published phylogenetic hypotheses than the neighbor-joining tree. The topology is identical to that found by Zhang et al. (2005: fig. 1), and the branch lengths are quite similar, despite the major differences in the models (Appendix 7). The especially short internal branches, which we also note in Zhang et al. (2005: fig. 1) appear implausible by comparison with morphological and paleontological data.

The unconstrained most parsimonious tree (Fig. 8b) contains the same topology, but the internal branch lengths appear more plausible; the branch subtending Lissamphibia is the longest of all internal branch lengths (consistent with morphological and paleontological data), and the other nodes are almost evenly spaced, with internal branch lengths almost half as long (on average) as the terminal ones.

Surprisingly, when the unconstrained most parsimonious tree is used as the guide tree for ModelTest and the resulting model used for a maximum-likelihood analysis, the most likely tree (Fig. 8d) shows Gymnophiona and Caudata, rather than Salientia and Caudata, as sister-groups (rendering Batrachia redundant with Lissamphibia), coherent with the so-called "Procera hypothesis" (but the branch lengths are very similar to those in Fig. 8c). Zhang et al. (2005) have summarized the history of both phylogenetic hypotheses. In both maximum likelihood trees the branches in this region of the tree are very short (not, however, in the most parsimonious tree), much shorter than the terminal branches. Indeed, Zhang et al. (2005: fig. 1) have found a low bootstrap value for Batrachia (as well as for Lissamphibia, "Archaeobatrachia", and Bombinanura). Alternatively, this lack of robustness in the position of anurans, urodeles, and apodans may reflect the low density of the taxon sampling (Hedtke et al., 2006).

According to the simulation study by Kolaczkowski and Thornton (2004), maximum parsimony fares better than maximum likelihood (and Bayesian analysis) under a wide range of realistic conditions, in spite of its undeniably greater susceptiveness to long-branch attraction (which is confirmed by Kolaczkowski and Thornton, 2004). This is because parsimony does not need an assumption on how many rate categories there are; in many real cases more or less each nucleotide position evolves at its own speed, causing potential problems for approaches that include evolution models (maximum likelihood and Bayesian analysis) but not for maximum parsimony. Thus, we do not think that the most parsimonious tree, which finds Bombinanura and Urodela as sister-groups (Fig. 8b), is necessarily less probable or a worse explanation for the data of Zhang et al. (2005) than the most likely tree (Fig. 8d). Furthermore, the branch lengths of the most parsimonious tree fit morphological data better than the most likely trees, in which many internal branches are disquietingly short.

Finally, we note that the "Procera hypothesis" would remove a large stratigraphic gap from our tree (the entire basal ghost lineage of Gymnophiona, about 70 My; Fig. 3). However, the position of Albanerpetontidae, which has its own long ghost lineage on our tree, is unclear under that topology.

All trees show *Bombina* and *Xenopus* as sister-groups. The consistency of this result still cannot rule out long-branch attraction, however.

Molecular Divergence Date Estimates

Quartet dating using QDate.—The age of the calibration points has more influence on the inferred divergence dates than the model of evolution (Appendix 9). The age of Tetrapoda estimated by Zhang et al. (2005) is contained within the range of our estimates regardless of which model is used, except when the upper (younger) bounds of the calibration points are used under the model that fits the neighbor-joining tree best. The age estimates for Batrachia, on the contrary, are always much younger than the entire confidence interval found by Zhang et al. (2005)—in fact, they are all younger than the oldest batrachian fossils, the Early Triassic (245 to 251 Mya) salientians *Triadobatrachus* and *Czatkobatrachus*. Because the morphology of the fairly well-preserved *Triadobatrachus* leaves little doubt about its salientian affinities (Rage and Roček, 1989), the age of Batrachia as estimated by QDate is clearly erroneous.

Penalized-likelihood dating using r8s.—Contrary to our expectations, the topology has very little influence on the divergence dates (Table 2, Appendix 10), possibly because the branch lengths are so similar. Thus, long-branch attraction, if it explains the archaeobatrachian monophyly recovered in our analyses, has little impact on the molecular dates using model 1 (Table 2, Appendix 10). Similarly, the smoothing parameter, which was selected using two cross-validation procedures (see above), only moderately influences the results (Table 2). In contrast, the choice of calibration points has by far the most impact. Using only external calibration points yields

TABLE 2. Summary of the divergence dates obtained from penalized likelihood as implemented in r8s (full data and calculations in Appendix 10). Rows 1 and 2 are included for comparison purposes. Row 1 consists of the point estimates and 95% confidence intervals found by Zhang et al. (2005). Row 2 shows the results from our supertree where the "point estimate" was derived from setting all internal branches to 3 My or longer and having all terminal branches occupy minimally an entire geological stage, and the range represents values obtained from other combinations of branch lengths (listed in Appendix 4). The values in rows 3 to 7 are based on the dates obtained using several combinations of calibration dates, evolutionary models, topologies, penalty functions, and smoothing factors (selected by cross-validation out of 92 analyses in rows 3 to 6). Other settings of smoothing factors examined to assess the impact of this parameter on dates and found in Appendix 10 are not considered here, except in row 7. Row 3 shows the total range of values achievable when the smoothing factor is selected by cross-validation (when the two cross-validation procedures selected different values, both were used); each line in rows 4 to 7 holds one of these factors constant and shows the results from analyses varying all other factors. In each cell of rows 3 to 7, the first number represents the average age of several tests; the minimal and maximal values given by various analyses are shown in parentheses. Bat, Batrachia; Bom, Bombinanura; Cry, Cryptobranchoidea; Liss, Lissamphibia; Neo, Neobatrachia; Pro, Procera; sm, smoothing factor; Uro, Urodela.

		Liss	Bat or Pro	Bom	Neo	Uro	Cry
1:	Zhang et al. (2005)	337 (321–353)	308 (289–328)	290 (268–313)	173 (152–195)	197 (176–219)	158 (135–181)
2:	Our time-calibrated supertree	260 (246–267)	254 (246–257)	175 (166–185)	108 (72–124)	162 (152–166)	143 (138–150)
3:	All analyses with optimal smoothing factors ($n = 38$)	282 (250–356)	263 (227–347)	223 (185–338)	167 (106–296)	195 (170–273)	146 (140–184)
4.1:	External calibration dates only or external and internal without upper bound ($n = 8$)	340 (321–356)	325 (300–347)	317 (288–338)	237 (173–296)	250 (224–273)	165 (150–184)
4.2:	Internal calibration points with upper bounds (with or without external calibration points) ($n = 30$)	267 (250–291)	246 (227–263)	198 (185–215)	149 (106–192)	180 (170–200)	141 (140–150)
5.1:	Based on model 1 ($n = 19$)	291 (255–356)	270 (250–347)	226 (185–338)	200 (163–296)	201 (170–273)	143 (140–154)
5.2:	Based on model 3 ($n = 19$)	273 (250–342)	255 (227–320)	220 (185–316)	134 (106–196)	189 (170–239)	149 (140–184)
6.1:	With monophyletic Archaeobatrachia ($n = 20$)	281 (250–356)	262 (232–347)	223 (185–338)	168 (110–296)	194 (170–272)	145 (140–184)
6.2:	With topology (*Bombina*, (*Xenopus*, Neobatrachia)) ($n = 18$)	284 (250–356)	264 (227–347)	224 (185–338)	166 (106–294)	196 (170–273)	146 (140–179)
7.1:	sm = 1 ($n = 21$)	292 (250–345)	266 (227–335)	228 (185–326)	170 (97–284)	197 (170–259)	142 (129–179)
7.2:	sm = 3000–10000 (lowest value available) ($n = 21$)	289 (250–356)	272 (234–347)	231 (185–358)	187 (120–320)	202 (170–273)	146 (140–183)

very old divergence date estimates (Table 2); using only internal ones yields some that are younger than the fossil record allows (Appendix 10). Both must be used to obtain realistic estimates for most clades, as Brochu (2004) found for quartet-dating using a crocodilian data set. By using internal and external calibration points together, we find divergence dates (Table 2) much more recent than those estimated by Zhang et al. (2005) and more compatible with paleontological evidence for all considered clades (within and outside Lissamphibia). Doubling or even tripling the distance between the minimal and maximal ages of Bombinanura and Urodela when they were used as calibration dates had rather little effect; the dates of divergences within Lissamphibia became older, those outside became younger (Appendix 10).

The choice of the penalty function altered the results only moderately. A new log penalty function penalizes differences in the logarithm of rates on neighboring branches; the older, additive function penalizes the squared differences in rates across neighboring branches in the tree. Most analyses were performed with the log penalty function, which is supposed to yield more realistic deep divergence time estimates from shallow calibration points, but an analysis using the additive (older) function yielded only slightly to moderately older ages for Tetrapoda, Lissamphibia, and Neobatrachia (Appendix 10, setting 2.6b).

Dating using PATHd8.—This method, presented by Anderson (2006), did not yield plausible results (Appendix 11). These results will not be discussed further.

DISCUSSION

Time of Origin of Lissamphibia, Topology, and the Previously Suggested Amphibian Stem-Groups

Of all the main paleontological hypotheses on lissamphibian origins, the one most compatible with the early lissamphibian appearance date inferred by Zhang et al. (2005) is the hypothesis of a polyphyletic origin (Figs. 1d, 2; Lee and Anderson, 2006). However, because all recent phylogenetic analyses of early stegocephalians have found that the "lepospondyls" are more closely related to the amniotes than to any temnospondyls (Carroll, 1995; Laurin, 1998; Anderson, 2001; Ruta et al., 2003; Vallin and Laurin, 2004), this would result in Lissamphibia being paraphyletic with respect to Amniota, but all molecular phylogenies of Tetrapoda have found a monophyletic Lissamphibia (Hedges et al., 1990; Hedges and Maxson, 1993; Hay et al., 1995; Feller and Hedges, 1998; Zardoya and Meyer, 2001; Zhang et al., 2005). Thus, despite the good match in timing, a polyphyletic origin of lissamphibians is incompatible with the topology recovered by all recent molecular phylogenetic studies of amphibians and can be rejected on that basis (Laurin, 2002). The stratigraphic range of Paleozoic stegocephalians does not help to identify the presumed sister-group of the lissamphibians because dissorophoids and lysorophians first appeared at approximately the same time.

Diversification of Lissamphibia According to the Fossil Record

Our time-calibrated supertree of lissamphibians (Figs. 3 to 7) suggests much more recent dates of lissamphibian diversification (Fig. 9). Instead of a basal lissamphibian divergence in the Viséan (337 Mya), the absence of any lissamphibian fossil before the Early Triassic (251 to 245 Mya) suggests that this crown-group arose in the Permian, probably less than 300 Mya. This impression is reinforced by the excellent and highly significant stratigraphic fit of our tree (tested using three indices in conjunction with randomization tests), which indicates that the fossils occur in an order coherent with the topology. Thus, the fossil record of Lissamphibia is probably not too incomplete to be suitable for our purpose. This record implies dates of lissamphibian diversification that are consistently more recent than those inferred by Zhang et al. (2005) using molecular data (Fig. 9); this applies to all lissamphibian divergences dated by Zhang et al. (2005) and present in our tree except one (*Bufo*/*Hyla*).

Molecular Data on the Origin and Diversification of Lissamphibia

Zhang et al. (2005:391) wrote: "The amphibian species were carefully selected so that every major amphibian group contained at least two species (in an effort to reduce long-branch attraction artefacts)." Yet they only selected two "archaeobatrachians" (*Xenopus* and *Bombina*), even though they explicitly consider "Archaeobatrachia" to be paraphyletic (Zhang et al., 2005:394, and the footnote to their table 2). In their tree (our Fig. 9a), the two "archaeobatrachians" are sister-groups that have a very early divergence date. San Mauro et al. (2004) find the same topology and attribute it to long-branch attraction; Vences et al. (2003), San Mauro et al. (2005), Roelants and Bossuyt (2005), and Frost et al. (2006) find "Archaeobatrachia" to be paraphyletic, as does the morphological analysis of Gao and Wang (2001); Hoegg et al. (2004), who likewise find "Archaeobatrachia" as paraphyletic, find high numbers of unique substitutions in two genes (although none used by Zhang et al., 2005) in *Bombina*, *Pipa*, and *Xenopus*. Consequently, we suspect that the monophyletic Archaeobatrachia that both Zhang et al. (2005) and we have found is a good example of long-branch attraction. However, we have shown that the impact of this potential artefact on the dates of all divergences ancestral to (*Xenopus* + *Bombina*) is minimal (Table 2; Appendices 9 to 11).

Molecular divergence date estimates are highly sensitive to the choice of calibration points, as well as to the assumed model of evolution (and general method of estimating the dates) and the branch lengths of the tree used. As Brochu (2004) found for quartet-dating, using only ancient external calibration points yields very old divergence date estimates under a penalized-likelihood method, whereas using only internal calibration points yields divergence dates that are sometimes younger than the fossil record allows. Both must be included to obtain realistic estimates. Zhang et al. (2005) used only external calibration points; this may be the reason for their generally very old divergence date estimates, overcompensating for the effects of the unrealistically young dates they assumed for their calibration points. Another possible factor is the tendency of Bayesian methods to overestimate divergence dates reported by Anderson (2006). Regardless of the explanation, it is clear that the molecular data used by Zhang et al. (2005) are compatible with the paleontological dates derived from our time-calibrated supertree. Thus, contrary to previous suggestions, there is no strong opposition between molecular and paleontological dates, at least in this case. We suggest that discrepancies between these types of dates may often arise from an inadequate choice of calibration points.

ACKNOWLEDGMENTS

We thank Zhang Peng and Qu Lianghu for sending us their tree (Zhang et al., 2005) with its outgroups, branch lengths, and their model parameters, Wang Yuan for a digital picture of *Mesophryne*, Roger Smith and Linda Trueb for digital pictures of *Vulcanobatrachus*, and Farish Jenkins for pictures of the holotype of *Eocaecilia*. Jeffrey Thorne kindly sent us compiled versions of Multidivtime and associated programs for Mac OS X and tried in vain to help us use them; Sudhir Kumar confirmed that a more user-friendly version will not be forthcoming soon. Andrew Rambaut successfully explained the use of QDate; Christopher A. Brochu suggested the use of r8s; Michael Sanderson managed to explain enough basic UNIX to enable us to use r8s; Andreas Rossoll kindly suggested that we reinstall r8s when it did not work (and indeed turned out to be corrupted), ending a period of 4 idle days. Cajsa Anderson answered questions about PATHd8. The draft was improved by comments from Susan Evans, Norman MacLeod, Roderic Page, Jean-Claude Rage, Armand de Ricqlès, Jorge Cubo, and an anonymous referee. We thank Wayne Maddison and Peter Midford for their help with the development of the Stratigraphic Tools for Mesquite, and René Zaragüeta i Bagils and Hervé Lelièvre for discussions on the relationships between phylogenies and geological age even though we have fundamental disagreements on this subject. Wayne Maddison also updated the Stratigraphic Tools and StratAdd modules to make them compatible with Mesquite 1.1. D.M. was supported by a subsidy for university students from the Federal Government of Austria; M.L. received financial assistance from the CNRS and French Ministry of Research through grants to the FRE 2696.

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First submitted 26 February 2006; reviews returned 12 April 2006;
final acceptance 27 November 2006
Associate Editor: Norman MacLeod

GLOSSARY

The definitions below are not to be understood as formally proposed definitions. They are only intended to make our present use of taxon names explicit.

Amniota: the smallest clade that includes birds and mammals (a crown-group).

Amphibia: the largest clade that includes Lissamphibia but not Amniota.

Anura: the smallest clade that includes all extant frogs (a crown-group).

Apoda: the smallest clade that includes all extant caecilians (a crown-group).

Batrachia: the smallest clade that contains Salientia and Caudata (a crown-group).

Caudata: the largest clade that includes Urodela but neither Anura nor Apoda.

Dipnomorpha: the largest clade that includes lungfish but not tetrapods.

Gymnophiona: the largest clade that includes Apoda but neither Anura nor Urodela.

Lissamphibia: the smallest clade that includes Apoda, Anura and Urodela, but not Amniota (a crown-group).

Salientia: the largest clade that includes Anura but neither Urodela nor Apoda.

Sauropsida: the largest clade that includes birds but not mammals.

Stegocephali: the smallest clade that includes all limbed vertebrates. Often called Tetrapoda in the literature.

Tetrapoda: the smallest clade that contains Lissamphibia and Amniota (a crown-group).

Tetrapodomorpha: the largest clade that includes tetrapods but not lungfish.

Theropsida: the largest clade that includes mammals but not birds. Often called Synapsida in the literature.

Urodela: the smallest clade that includes all extant salamanders (sensu lato; cryptobranchoids, sirenids, and salamandroids).

NOTE ADDED IN PROOF

Using many color photographs, Wang et al. (2005) have shown that the Daohugou Beds and the overlying and underlying strata are complexly folded, and that the Daohugou Beds overlie the 159 to 164 My old ignimbrite of the Tiaojishan Formation. Reports of the Tuchengzi Formation underlying the Daohugou Beds, however, were due to misidentifications; the position of the Tuchengzi Formation relative to the Daohugou Beds remains unknown. Therefore the age of the Daohugou Beds may be Oxfordian to Barremian. "We propose that the Daohugou fossil assemblage probably represents the earliest evolutionary stage of the Jehol Biota based on both vertebrate biostratigraphy and the sedimentological and volcanic features which suggest the Daohugou deposit belongs to the same cycle of volcanism and sedimentation as the [end-Barremian and early Aptian] Yixian Formation of the Jehol Group." (Wang et al. 2005:2369). Thus, *Pangerpeton, Jeholotriton, Liaoxitriton daohugouensis* and *Chunerpeton* could conceivably be somewhat older, but more probably younger, than indicated in Figure 3.

Wang, X., Z. Zhou, H. He, F. Jin, Y. Wang, J. Zhang, Y. Wang, X. Xu, and F. Zhang. 2005. Stratigraphy and age of the Daohugou Bed in Ningcheng, Inner Mongolia. Chin. Sci. Bull. (English edition) 50:2369–2376.

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Appendices

Please note that for your convenience, we have downloaded the 11 appendices from the Systematic Biology web site, corrected a small typographic mistake in an author name, and added the tree of Appendix 2, which was not put onto the web site, for reasons unclear to us. We single-spaced everything to make these appendices less bulky, and justified the text to make it look nicer, but these are otherwise identical to the versions that you will find on-line. We have then produced a single pdf file for electronic distribution and printing. Please note that the tree of Figure 2 will not be legible at that size. If you really want to see it, please look at it on-screen, at a higher magnification level. There was no easy way to print this tree (it would require several pages).

Please note that to keep this document to a manageable size, we did not include the intermediate calculations of Appendix 10 in this pdf version; if you want it, please download it from the *Systematic Biology* web site, or contact us.

If you wish to receive more information, do not hesitate to contact us.

David Marjanovic

Michel Laurin

APPENDIX 1. Methods and sources used to compile the main phylogeny (Figs. 3–7) and to determine the stratigraphic distribution of various lissamphibian species, and of the fossiliferous localities.

We have not used the Matrix Representation Parsimony (MRP) method (Baum, 1992) that has been used in several recent studies (such as Bininda-Emonds et al., 1999), because this method would not take qualitative differences between the original phylogenies into consideration (i.e. whether or not they were based on a data matrix, how the matrix was analyzed, how many characters and taxa were included, how they were coded, etc.). Furthermore, the position of several extinct lissamphibians was expressed in the text of our sources without presenting an explicit phylogenetic tree or cladogram; such information could not have been easily incorporated into a supertree produced by MPR. However, there were few competing phylogenies for most taxa, with the notable exception of high-level anuran and urodele phylogeny. To resolve incompatibilities between these, we followed the most recent studies because they were usually the most comprehensive in terms of number of included taxa and characters and used the most sophisticated methods of analysis. More details on our supertree construction method can be found in Laurin (2004).

The main tree assumes that internal branches are at least 3 Ma long. There are two advantages to the use of nonzero minimal internal branch lengths: firstly, it compensates somewhat for the fact that paleontological dates necessarily underestimate the real time of appearance of the clades; secondly, it minimizes the discrepancies in inferred divergence times that might arise because of uneven preservation potential. Of course, this procedure could in some cases push back the origin of clades to a ridiculously ancient date, but this was not a problem in our tree. For instance, this method yields an approximate age of origin of Hyloidea in the Albian (99.6 to 112 Ma ago). This very speciose clade (more than 2700 extant species; Pough et al., 2004) has a very poor fossil record (33 species from the Mesozoic and Paleogene); therefore, we expect that the oldest fossil from that clade probably postdates the actual origin of this taxon considerably. The fact that this fossil, the Campanian (70.6 to 83.5 Ma ago) *Baurubatrachus pricei,* is deeply nested within Hyloidea confirms this suspicion. However, our inferred date of appearance of Hyloidea is only about 30 Ma older than the age of this oldest known hyloid. The age of the next larger clade that contains Hyloidea and that has an equally poor fossil record (Neobatrachia) is probably also underestimated because this clade has a long inferred ghost lineage (about 50 Ma) that extends from about 115 Ma to about 165 Ma ago (Figs 5, 6). On the other hand, the yet again much greater antiquity of the enclosing clade (Pipanura) is probably not an artefact of our method because the absolute minimal age of that clade is constrained by the pipoid *Rhadinosteus parvus* (Fig. 5) which dates from the Kimmeridgian or Tithonian (155.7 ± 4.0 to 145.5 ± 4.0 Ma ago). An alternative to our procedure would have been to specify negligible minimal internal branch lengths, but this approach increases the discrepancy between our paleontological age estimates (Appendix 4) and the molecular age estimates provided by Zhang et al. (2005). More complex approaches could be imagined because the recovery potential of species is presumably not constant with time (it presumably decreases with increasing antiquity of the species) and because the proportion of extinct species in a clade probably increases with the antiquity of the clade. However, the recovery potential and extinction probability are not known; therefore, such approaches were not attempted here. Any bias that our procedure introduces (compared to using negligible minimal internal branch lengths) makes our supertree more congruent with the results of Zhang et al. (2005), so this approach is conservative. Most importantly, our assumptions on minimal branch lengths influence only the graphic representation of the supertree and our estimates of the age of the various nodes. They have no impact on our calculations of the confidence interval of the age of origin of Lissamphibia performed below because the actual age of the oldest known fossil in every clade was used in those analyses.

Some extinct taxa were not included in our tree at all because their positions were too uncertain; this includes, for example, the Gobiatidae from the Late Cretaceous of Mongolia and Uzbekistan, which are mainly known from maxilla fragments and whose monophyly and position within Salientia are enigmatic – they have been said to be "morphologically intermediate between the Leiopelmatidae [probably Amphicoela of our usage, thus equal to Leiopelmatidae as used by Frost et al. (2006) but not, for example, by Roelants and Bossuyt (2005)] and Discoglossidae [Discoglossoidea of our usage, Costata in Frost et al. (2006)]" (Rocek, 2000). We have, however, included the Batrachosauroididae and Scapherpetontidae, two possible clades whose positions within Urodela are unknown, but which have left several well-preserved fossils (Estes, 1981; Milner, 2000). These serve mainly to illustrate the quality of the lissamphibian fossil record. In agreement with Milner (2000) and in the absence of phylogenetic studies on those taxa, we have placed them in the basal polytomy of Urodela (following the convention outlined above). Both taxa consist only of paedomorphic species, and paedomorphosis has been shown to be a serious obstacle to morphological salamander phylogenetics (Wiens et al., 2005). The presence of primitive similarities between the scapherpetontids and the salamandroids (Milner, 2000) means that our divergence date estimate for Salamandroidea and some clade(s) therein could be too young; the age of Urodela, however, is not affected by this.

Conversely, we have excluded most palaeobatrachids (Anura: Pipoidea) because the phylogeny of Palaeobatrachidae has to our knowledge never been investigated and because many of the named species could be synonyms. However, we have included the oldest and the youngest known palaeobatrachids, as well as a species known from good material. We have followed the same approach with *Latonia* (Anura: Discoglossoidea). (See Rage and Rocek [2003] for both.)

In the supertree we have ignored the Pliocene and Pleistocene record on the grounds that most of it belongs to extant species (Sanchíz, 1998; Delfino, 2004) or to extant genera (such as *Rana* and *Bufo* as used by most authors) which contain many species whose phylogenetic positions are unknown (Sanchíz, 1998). Exceptions were made only for the last representatives of larger clades, such as the last palaeobatrachid (early Pleistocene). Furthermore, the evolutionary radiation of many extant genera probably predates the Pliocene, as shown by our compilation (Figs. 3–7). An effort was made to include at least one close living relative of every extinct taxon.

We used the geological timescale presented by Gradstein et al. (2004); some of the information about the equivalence between local and global scales is from Harland et al. (1990). A few dating problems arose because variable geological timescales were used in the past. When no more precise stratigraphic information was given, "early", "middle" and "late" Eocene were interpreted as Ypresian, Lutetian and Bartonian (= Bartonian + Priabonian, see above) because of the lengths of those stages. Likewise, "early", "middle" and "late" Miocene were considered to be Aquitanian, Langhian and Tortonian. The "early" and "late" Oligocene were equated with the Rupelian and Chattian. The rare occurrences of "middle Paleocene" were considered to be Selandian; because this stage was rarely recognized before 2004, we may have misassigned Selandian fossils to the Thanetian ("late Paleocene").

SOURCES

Amphibian phylogeny and first appearance dates follow Estes (1981), Ensom et al. (1991), Milner (1993), Rocek (1994, 1996, 2000), Böhme (1998), Gubin (1991), Henrici (1998), Sanchíz (1998), Veith et al. (1998), Venczel (1999, 2004), Báez (2000), Báez et al. (2000), Bossuyt and Milinkovitch (2000, 2001), Hossini (2000), Liu et al. (2000), Rocek and

Rage (2000), Vences et al. (2000), Chan et al. (2001), Gao and Shubin (2001), Gao and Wang (2001), Kosuch et al. (2001), Pramuk et al. (2001), Weisrock et al. (2001), Chiappe and Lacasa-Ruiz (2002), Evans and McGowan (2002), Meegaskumbura et al. (2002), Rage and Rocek (2003), Sumida et al. (2003), Veith et al. (2003), Gao and Chen (2004), He et al. (2004, 2006), Martínez-Solano et al. (2004), San Mauro et al. (2004), Dubois (2005), Evans et al. (2005), Roelants and Bossuyt (2005), Venczel and Sanchíz (2005), Wiens et al. (2005), Wang and Rose (2005), Mueller (2006), Wang and Evans (2006), as well as the appropriate Tree of Life pages (Larson, 1996a, b).

Albanerpetontid ages and phylogeny are taken from Gardner (2001, 2002) and Venczel and Gardner (2003, 2005).

Pelobatoid phylogeny is an educated guess based on Roelants and Bossuyt (2005), Rocek and Rage (2000) (position of *Eopelobates*), Henrici (2002) (phylogeny and composition of *Eopelobates*), and Rage & Rocek (2003) (position of *Scotiophryne* as pelobatid, although their use of this term is sufficiently vague that it could simply be a pelobatoid incertae sedis). This may overestimate the age of the pelobatoid diversification.

Bufonid phylogeny follows Frost et al. (2006).

Some highly incomplete or briefly described fossils would have required us to make very large polytomies. For example, the three extinct taxa included in Apoda in Fig. 3 could lie almost anywhere within Apoda or outside it (as long as they are closer to Apoda than *Rubricacaecilia* is). Rather than collapse all of Apoda into a huge polytomy, we have only expanded the basal divergence of Apoda into a polytomy that includes the three extinct species. (Our polytomies are thus more similar to an Adams consensus than to a strict consensus of all possible resolutions.) This way we can display the monophyly and interior topology of Stegokrotaphia. Similar cases are Urodela (Figs. 3, 4; see text), Discoglossoidea (Fig. 5), where *Eodiscoglossus*, *Callobatrachus*, *Opisthocoelellus*, and/or *Latonia* might be part of Alytidae or Bombinidae (whose only certain member in our tree is *Bombina*), Hylidae (Fig. 7), where "*Hyla*" *swanstoni* may lie anywhere within the "Middle American clade", *Bufo* sensu lato, where the phylogenetic positions of the extant species "*B.*" *pentoni* is unknown (Frost et al., 2006), Ranidae sensu lato, where the "Grisolles ranid" could lie anywhere within that clade (although in this case the uncertainty could be increased by the fact that we were not able to determine the exact concept of Ranidae used in the description of that fragmentary fossil, or in later compilations like that by Rage and Rocek [2003]), and the salamanders *Hylaeobatrachus*, *Kiyatriton*, and (to a lesser degree) *Apricosiren*, as well as possibly Batrachosauroididae and Scapherpetontidae (Fig. 3). Thus, a literal reading of our tree may underestimate the divergence times of some clades.

We found out about several fossil salamanders too late to include them into our locality database: the probably Valanginian to Barremian (He et al., 2004; Wang and Rose, 2005) *Pangerpeton sinensis* (Wang and Evans, 2006), the unnamed scapherpetontid from the Albian of Utah (Evans and McGowan, 2002), the unnamed middle Miocene species of the plethodontid *Speleomantes* (Venczel and Sanchíz, 2005), and the Tortonian and later hynobiid *Parahynobius* (Venczel, 1999). The latter three may, however, have been found in localities that are already in our database.

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APPENDIX 2. Supertree based on the tree by Frost et al. (2006).

The lissamphibian fossils are inserted according to the references of Appendix 1; the nomenclature by Frost et al. (2006) is used. In cases where it is unclear how Frost et al. (2006) use a name, we have labeled all possibilities with that name followed by a question mark. Names that are not used by Frost et al. but could be added to their classification without disrupting it, such as Albanerpetontidae, are marked by parentheses to facilitate comparison to our main tree (Figs. 3–7).

Batrachia occurs only once in our tree, but nevertheless bears a question mark. This is because Frost et al. discuss the name Paratoidia but do not decide whether it should be used (they do not use it in their classification, but this may simply be because all albanerpetontids are extinct); it remains unclear if they intend Batrachia to be a crown-group, excluding Albanerpetontidae, or a total group, including Albanerpetontidae. (In the latter case Paratoidia would be a junior synonym of Batrachia according to the rationale used elsewhere by Frost et al. [2006].)

The position of name labels with respect to nodes or internodes is purely due to reasons of aesthetics and legibility, not, for example, the different types of phylogenetic definitions.

Because our sampling of extant taxa is much smaller than that of Frost et al. (2006), and because Frost et al. (2006) have named every clade that is not identical in known extant content to any other (in their tree), several of the names they use are synonyms on our tree. In such cases, these names are put in the same place on the tree, separated by slashes, and arranged from most to least inclusive (left to right). For example, in "Cladophrynia/Tinctanura/Athespatanura", Athespatanura includes Hylidae and Leptodactyliformes (as well as an unclear number of their last few common ancestors), Tinctanura includes Athespatanura and Amphignathodontidae (not shown), and Cladophrynia includes Tinctanura and Cryptobatrachidae (not shown).

Frost et al. (2006) split the traditionally huge genera *Rana* and *Bufo* into many smaller genera. The names of these genera (and those of the two subgenera of the revised *Rana*) are written on the tree as clade names, but to facilitate comparison with the literature (especially Sanchíz, 1998) and with our main tree (Figs. 3–7), we have kept the traditional subgenera of *Rana* and species groups of *Bufo* in the names of the terminal taxa. As an example, the traditional *Rana (Pelophylax) ridibunda* is called *Pelophylax ridibundus* by Frost et al. (2006).

Species names followed by "1" or "2" mark first and last occurrences of certain long-lived species, often the first occurrence of an extant species. Species names marked with an asterisk indicate that the range of the species is known to extend into at least the following geological stage (sometimes more).

Polytomies and stratigraphic uncertainties are treated as in the main tree.

NOTE

The figure was produced before we got a hold of the article by Evans and McGowan (2002). Therefore, *Apricosiren* and the "Utah scapherpetontid" are missing; they should have the same (range of possible) phylogenetic positions in this tree as in our main tree (Figs. 3–7). Also note that the "Purbeck batrachosauroidid" is Berriasian rather than Tithonian in age, that an unmentioned species of *Marmorerpeton* occurs in the Oxfordian of an unmentioned locality in Portugal together with "salamander A" , and that the age of *Hylaeobatrachus* is given as Barremian rather than Hauterivian by Evans and McGowan (2002).

The Permian is treated according to a timescale older than that by Gradstein et al. (2004); this is irrelevant because no Permian lissamphibians are known. The "Kazanian" comprises the Wordian and the earlier half of the Capitanian, the “Tatarian” consists of the later half of the Capitanian, the Wujiapingian, and the Changxingian.

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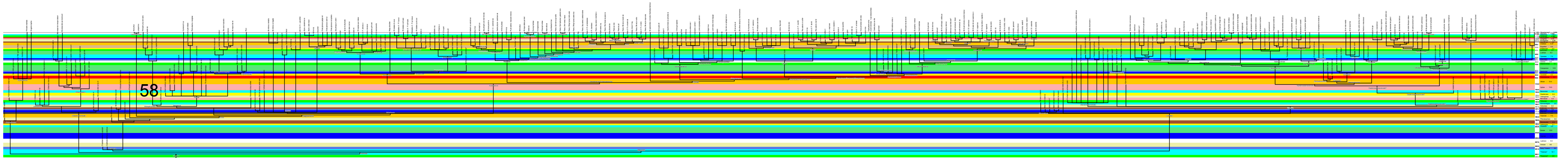
All are cited in the article itself.



APPENDIX 3. Comparison between the estimated minimal age of various taxa under our supertree and under the phylogeny of Frost et al. (2006). In both cases, the trees assume the same minimal branch length settings (stratigraphic fit and a minimal internal branch length of 3 Ma). For those taxa whose names have branch-based definitions, the dates reported represent the beginning of the differentiation of the taxon (the first divergence within it), not the appearance of its branch (or stem). "Clade (*Hyla, Bufo*)" refers to the smallest clade that includes *Hyla* and *Bufo*, nameless on our tree. When clade composition is not directly comparable because of topological differences, the name preferred by Frost et al. (2006) is marked with an asterisk. The average age is rounded off to the nearest Ma.

Taxa	Age on our supertree	Age on the tree of Frost et al. (2006)
Lissamphibia	260	260
Gymnophiona	190	190 (Parabatrachia)
Apoda	100	100 (Gymnophiona)
Batrachia	254	254
Caudata	174	174 (possibly Urodela)
Urodela	162	160 (Caudata)
Cryptobranchoidea	143	143
Salamandridae	70	70
Salientia	252	252
Anura	178	180
Pipanura	165	178 (Lalagobatrachia*)
Neobatrachia	111	108
Hyloidea	105	105 (Hyloides)
Clade (*Hyla, Bufo*)	99	97 (Athespatanura*)
Ranoidea	58	61 (Ranoides)
Microhylidae	38	38
Ranidae	52	56 (Natatanura)
Average age	140	141

APPENDIX 4. Estimated date of appearance of selected taxa in the supertree under various assumptions of branch lengths. The dates, in Ma ago, have a precision of ~ 2 Ma, resulting from the resolution of the scale displayed in Mesquite. When only one number is given, stratigraphic fit was used (a given species is assumed to have been present throughout at least one geological stage). When two numbers are given, the first one is the minimal internal branch length (as under stratigraphic fit) and the second is the minimal terminal branch length (the species are not assumed to have existed throughout at least a given geological stage, but to have lasted at least a given number of years before the end of the geological stage in which they have been preserved). The smallest clade that includes *Kaloula* and *Microhyla* (represented in the data of Zhang et al. [2005]) is a small part of Microhylinae which does not have a fossil record; the next larger clade for which fossils are known is Microhylidae, which is included here. For the taxa that have a branch-based definition, the dates reported represent the beginning of the radiation of the taxon, not the appearance of its branch (or stem). All calculations were performed using Stratigraphic Tools (Josse et al., 2005). * Branch length assumptions used to produce the supertree (Figs. 3–7).

	Branch length assumptions													
Taxa	0.1 Ma	1 Ma	2 Ma	3 Ma*	5 Ma	0.1 Ma/0.1 Ma	0.1 Ma/1 Ma	0.1 Ma/5 Ma	1 Ma/0.1 Ma	1 Ma/1 Ma	1 Ma/5 Ma	5 Ma/0.1 Ma	5 Ma/1 Ma	5 Ma/5 Ma
Lissamphibia	252	254	258	260	267	246	248	250	248	249	253	261	262	266
Gymnophiona	190	190	190	190	190	183	183	188	183	184	189	183	184	189
Apoda	100	100	100	100	100	94	94	99	94	95	100	94	95	100
Batrachia	252	253	254	254	257	246	247	250	247	248	251	250	251	256
Urodela	157	159	160	162	166	152	153	156	153	154	158	161	162	166
Cryptobranchoidea	140	141	142	143	146	138	139	144	138	140	147	141	144	150
Salamandridae	60	62	66	70	84	57	58	62	60	61	65	76	77	81
Salientia	252	252	252	252	252	246	247	250	246	247	250	246	247	250
Anura	169	171	174	178	183	166	168	174	168	170	188	180	183	190
Bombinanura	169	170	172	175	178	166	168	174	167	169	187	175	178	185
Pipanura	158	160	162	165	171	152	153	156	153	156	159	166	168	171
Neobatrachia	85	91	99	108	124	72	73	77	78	79	83	111	112	116
Hyloidea	85	91	99	105	119	72	73	77	78	79	83	106	107	111
(*Hyla*, *Bufo*)	85	89	94	99	109	72	73	77	77	78	82	96	97	101
Ranoidea (*Microhyla*, *Rana*)	38	42	50	58	74	34	36	40	37	38	42	69	70	74
Microhylidae	29	31	34	38	44	23	24	28	26	27	31	39	40	44
Ranidae	38	40	47	52	65	35	36	40	35	36	40	59	60	64
Aglaioanura	38	38	43	46	55	35	36	40	33	34	38	49	50	54

APPENDIX 5. Estimated date of appearance of selected taxa under various random resolutions of the polytomies in the supertree. The results are based on ten random resolutions of the polytomies produced by the equiprobable model of MacClade 4.06 (Maddison and Maddison, 2003). All dates are in Ma ago and rounded to 1 Ma. The "undoubted pelodytid" is mentioned as such by Rage and Rocek (2003); it comes from the Bartonian of somewhere in France. For the taxa that have a branch-based definition, the dates reported represent the beginning of the differentiation of the taxon, not the appearance its branch (or stem).

Designation of polytomy	Taxa included in the polytomy	Age (right) of relevant taxa (below) on reference tree	Average age on random trees	Minimal age on random tree	Maximal age on random trees	Age on reference tree
Apoda	Wadi Milk gymnophione, Pajcha Pata gymnophione, *Apodops,* Rhinatrematidae, Stegokrotaphia	Apoda	70	11	109	100
Salientia	*Triadobatrachus,* *Czatkobatrachus*, other Salientia	Batrachia	257	257	257	254
		Lissamphibia	263	263	263	260
Discoglossoidea	*Eodiscoglossus,* *Callobatrachus,* *Bombina,* *Opisthocoelellus,* *Latonia,* Discoglossidae	Discoglossoidea (crown)	146	34	180	171
		Anura	183	177	186	177
Bombina	*Bombina* spp.	*Bombina* (crown)	19	2	26	23
Discoglossus	*Discoglossus* spp.	*Discoglossus* (crown)	21	5	34	28
	Discoglossus, *Alytes*	Discoglossidae (crown)	33	31	37	31
Pelobatidae	*Pelobates*, *Eopelobates*, *Scotiophryne*	(*Pelobates* + *Eopelobates*)	81	55	87	84
	Pelobatidae, Megophryidae, Pelodytidae, Scaphiopodidae	Pelobatoidea	95	93	96	93
Pelodytidae	*Pelodytes*, *Miopelodytes*, *Tephrodytes*, Quercy pelodytid, "undoubted pelodytid"	Pelodytidae	46	43	49	40
Pelobates	*Pelobates* spp.	*Pelobates* (crown)	33	17	43	34

Pelophylax	*Rana (Pelophylax) ridibunda*, *R. (P.) saharica*, Möhren green frog	*Pelophylax* (crown)	27	2	37	34
		Ranoidea	60	58	61	58
Telmatobiinae	*Telmatobius*, *Eupsophus*, *Neoprocoela*, Itaboraí telmatobiine	Telmatobiinae (crown)	67	65	68	62
Hylidae	Hylinae, Itaboraí hylid, (Pelodryadinae + Phyllomedusinae)	Hylidae (crown)	54	37	65	62
		(Hylidae + *Rhinoderma*)	67	65	68	65
Cryptobranchidae (crown)	Cryptobranchidae except *Chunerpeton*	Cryptobranchidae (crown)	55	31	68	59
Siren	*Siren* spp.	*Siren* (crown)	37	2	52	49
		Sirenidae (crown)	54	52	55	52
Ambystoma	*Ambystoma* spp.	*Ambystoma* (crown)	28	2	40	34
Salamandra	*Salamandra* spp.	*Salamandra* (crown)	36	18	43	37
		Salamandrinae (crown)	43	40	46	40
Average			77	59	86	80

APPENDIX 6. Biological nomenclature. Here we present arguments for why we decided not to follow the nomenclature of Frost et al. (2006) and why we believe that we cannot in fact follow all of it. We also explain why some clades seem to bear different names in our paper and in that of Zhang et al. (2005).

Frost et al. (2006) explicitely state that the names they use apply to clades. They do not, however, use phylogenetic definitions. Above the "superfamily level" a "concept" is given, but only in very few cases does this concept include a statement that a name is meant to apply to a crown-group (such as Anura, which we use in a very similar way, or Amphibia, which they use as a senior synonym of Lissamphibia). For all other names it is impossible to determine where exactly the names given by Frost et al. (2006) fit on our tree because the extinct species included in our tree are not present on theirs. In several cases this is as a genuine problem; e.g., we cannot determine if Frost et al. (2006) intended *Valdotriton* and *Iridotriton* to be part of Diadectosalamandroidei. This falsifies the claim by Frost et al. (2006:147) that "fossil taxa [...] can be placed within this framework with relatively little effort" and highlights the limitations of an approach that does not use explicit phylogenetic definitions.

Frost et al. (2006) seem to follow an approach akin to the "phylogenetic system of reference" advocated by Härlin (1998), even though they do not cite him: a taxon is considered a set of smaller taxa, and if its membership or its diagnostic characters change, so may its name. Thus, Frost et al. (2006) coin the new name Diadectosalamandroidei instead of using the existing name Salamandroidea for the sole reason (Frost et al., 2006:357) that, unlike previous studies (e.g. Wiens et al., 2005), they find Sirenidae to be a member of Salamandroidea. While stability of content and of diagnostic characters is without question a laudable goal, tying taxon names to contents plus diagnostic characters as rigidly as advocated by Frost et al. (2006) results in a proliferation of names that we find undesirable.

Furthermore, Frost et al. (2006) name every non-redundant clade in their phylogeny above what they consider to be the "family level". Together with their emphasis on stability of content and diagnosis, this results in many of these names becoming inapplicable under alternative phylogenies, thus exacerbating taxonomic instability. This approach has been used in the nomenclature of Placentalia (e.g., Waddell et al., 1999a, b), sometimes to the point that names are explicitely applied to hypotheses rather than to clades (Waddell et al., 1999a:32) and that the word "clade" is used instead of "hypothesis" (Nishihara et al., 2006:9929). We do not follow this approach because it requires changes in names every time a phylogenetic hypothesis changes. Instead, we use the principles of phylogenetic nomenclature as outlined in the PhyloCode (Cantino and de Queiroz, 2006), which has the advantage of not resulting in a proliferation of new names.

We have tried to use the nomenclature by Frost et al. (2006) on the tree that is based on theirs (Appendix 2). When a name could apply to several nested clades that have different known contents, we have indicated all of these.

On our main tree, we have followed published phylogenetic definitions for names that have one (or more). In cases where more than one definition of a name has been published, we have made choices based on our personal preferences because the PhyloCode is not yet implemented. For example, we use Apoda for a crown-group and Gymnophiona for its total group rather than the other way around (advocated by Cannatella and Hillis, 1993) because *Eocaecilia* is not, as the name Apoda implies, "footless". These choices have been influenced by the recent literature (e.g. we use Caudata for a total group and Urodela for its crown-group, like e.g. Wang and Rose [2005] and Evans et al. [2005]).

Zhang et al. (2005) have followed a "fuzzy tree-thinking" approach to nomenclature (O'Hara, 1997; Laurin and Anderson, 2004) that has, unfortunately, repeatedly occurred in publications on molecular phylogenetics (e.g. Jaillon et al., 2004): for each clade, they have chosen the best-known name that belongs to a clade of roughly similar content. Thus, they use the name Anura to describe the smallest clade that includes all frogs (anurans) which are represented in their data matrix – but because neither *Ascaphus* nor *Leiopelma* are in that matrix, that clade is not Anura. Two names are available for it, Bombinanura and Discoglossanura (Ford and Cannatella, 1993), yet Zhang et al. (2005) mention neither of them. Because of their phylogenetic definitions, these two names are synonyms if *Bombina* and *Discoglossus* are more closely related to each other than to Neobatrachia; this is the case on our tree and on that of Frost et al. (2006). Zhang et al. (2005) have included *Bombina* but not *Discoglossus* in their analysis; to ensure comparability of our tree to theirs, we have decided to use Bombinanura on our tree, too. Similarly, Zhang et al. (2005) use Gymnophiona instead of the much less inclusive Stegokrotaphia, Salamandroidea instead of the much smaller Salamandridae (perhaps to enhance the similarity to Cryptobranchoidea, which is its sister-group on their tree because of the low number of taxa in that tree), Ranoidea for a considerably smaller clade that had no name before Frost et al. (2006) called it Aglaioanura (assuming that Aglaioanura is meant to be a crown-group), Microhyloidea for a small subset of Microhylinae, and Bufonoidea (usually considered a junior synonym of Hyloidea) for another unnamed clade that excludes many hyloids (Athespatanura of Frost et al. [2006], if that is a crown-group). Zhang et al. (2005:298) use Salientia both for Bombinanura and for the total group to which it actually refers (including Bombinanura, *Ascaphus*, and *Leiopelma*, as well as the Early Triassic *Triadobatrachus* and *Czatkobatrachus* which are mentioned on the same page as belonging to Salientia). We discuss this issue to enable readers to compare the same taxa in our study and in Zhang et al. (2005). For instance, the age of “Anura” in Zhang et al. (2005) should be compared with the age of Bombinanura in our study (Appendices 3–5; Fig. 9) or in the paleontological literature in general (where this clade is usually unnamed), rather than with the age of Anura.

A last important nomenclatural clarification concerns the statement by Zhang et al. (2005:392) that “[t]he ray-finned fishes (carp, *Cyprinus carpio*; dogfish, *Scyliorhinus canicula*) were used as outgroup species.” While the carp is indeed a ray-finned fish (Actinopterygii), the dogfish is a ground shark (Chondrichthyes: Carchariniformes); the carp is more closely related to the ingroup than (to) the dogfish. The GenBank entry for accession number NC_001950, used by Zhang et al. (2005:table 2), correctly reflects this phylogenetic position in the classification given there. However, this does not have any effects on the tree published by Zhang et al. (2005:fig. 1) because it is rooted in a polytomy, in other words, the outgroup is not assumed to form a clade (Zhang P. and Qu L., pers. comm.).

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APPENDIX 7. Model parameters chosen by Modeltest 3.7 using a neighbor-joining (NJ) and the most parsimonious (MP) guide trees, compared to the model used by Zhang et al. (2005; pers. comm.) which was selected by Modeltest 3.06. Only four rate categories and the Akaike Information Criterion (AIC) were used for all three. The G-T substitution rate is always 1.0000; the other substitution rates are expressed as fractions of it. The constrained guide tree, unlike the others, contains the topology (*Bombina* + (*Xenopus* + *Neobatrachia*)).

	Zhang et al. (2005)	NJ guide tree (Model 1)	MP guide tree (Model 2)	Constrained MP guide tree (Model 3)
Model	GTR+I+Γ	TIM+I+Γ	GTR+I+Γ	GTR+I+Γ
-ln likelihood	68906.7891	3084.1284	150448.6875	150457.3281
K	unknown	8	10	10
AIC	137833.5781	6184.2568	300917.3750	300934.6562
Base frequencies				
A	0.2653	0.4478	0.3768	0.3768
C	0.2783	0.0004	0.2943	0.2943
G	0.1726	0.4510	0.0824	0.0825
T	0.2838	0.1008	0.2464	0.2465
Substitution rates				
A-C	1.7889	1.0000	0.2962	0.2968
A-G	4.0193	0.6821	3.5295	3.4192
A-T	1.7584	1.3913	0.5150	0.5129
C-G	0.6678	1.3913	0.5526	0.5504
C-T	5.7568	0.0000[a]	3.7833	3.7863
Proportion of invariable sites (I)	0.3644	0.0156	0.1011	0.1013
α shape parameter (Γ)	0.6970	0.4837	0.2733	0.2772

[a] PAUP* refused to accept this peculiar value, so we set it to 0.00001.

APPENDIX 8. Quartets used for quartet-dating in QDate 1.11 (see Table 2).

The 56 quartets (2 x 12 for Tetrapoda, 2 x 16 for Batrachia/Lissamphibia) are in the format required by QDate: "*Gallus Bos* 310 *Hyla Ranodon* 250" means that the ancestors of *Gallus* and *Bos* diverged 310 Ma ago while those of *Hyla* and *Ranodon* diverged 250 Ma ago; QDate will then calculate the divergence date between these two clades. The many repetitions serve to average out the effects of long branches (especially those of *Alligator* and *Polypedates*), which drastically increase the divergence date estimates, and to allow for a range of calibration dates (compare the first quartet, copied above, with the thirteenth, "*Gallus Bos* 345 *Hyla Ranodon* 275").

Gallus Bos 310 *Hyla Ranodon* 250
Alligator Homo 310 *Hyla Ranodon* 250
Gallus Homo 310 *Hyla Ranodon* 250
Alligator Bos 310 *Hyla Ranodon* 250
Gallus Bos 310 *Bufo Paramesotriton* 250
Alligator Homo 310 *Bufo Paramesotriton* 250
Gallus Homo 310 *Bufo Paramesotriton* 250
Alligator Bos 310 *Bufo Paramesotriton* 250
Gallus Bos 310 *Polypedates Andrias* 250
Alligator Homo 310 *Polypedates Andrias* 250
Gallus Homo 310 *Polypedates Andrias* 250
Alligator Bos 310 *Polypedates Andrias* 250
Gallus Bos 345 *Hyla Ranodon* 275
Alligator Homo 345 *Hyla Ranodon* 275
Gallus Homo 345 *Hyla Ranodon* 275
Alligator Bos 345 *Hyla Ranodon* 275
Gallus Bos 345 *Bufo Paramesotriton* 275
Alligator Homo 345 *Bufo Paramesotriton* 275
Gallus Homo 345 *Bufo Paramesotriton* 275
Alligator Bos 345 *Bufo Paramesotriton* 275
Gallus Bos 345 *Polypedates Andrias* 275
Alligator Homo 345 *Polypedates Andrias* 275
Gallus Homo 345 *Polypedates Andrias* 275
Alligator Bos 345 *Polypedates Andrias* 275
Bombina Hyla 170 *Ranodon Mertensiella* 150
Xenopus Polypedates 170 *Ranodon Mertensiella* 150
Bombina Polypedates 170 *Ranodon Mertensiella* 150
Xenopus Hyla 170 *Ranodon Mertensiella* 150
Bombina Rana 170 *Ranodon Mertensiella* 150
Xenopus Kaloula 170 *Ranodon Mertensiella* 150
Bombina Kaloula 170 *Ranodon Mertensiella* 150
Xenopus Rana 170 *Ranodon Mertensiella* 150
Bombina Hyla 170 *Andrias Paramesotriton* 150
Xenopus Polypedates 170 *Andrias Paramesotriton* 150
Bombina Polypedates 170 *Andrias Paramesotriton* 150
Xenopus Hyla 170 *Andrias Paramesotriton* 150
Bombina Rana 170 *Andrias Paramesotriton* 150
Xenopus Kaloula 170 *Andrias Paramesotriton* 150
Bombina Kaloula 170 *Andrias Paramesotriton* 150
Xenopus Rana 170 *Andrias Paramesotriton* 150

Bombina Hyla 185 *Ranodon Mertensiella* 170
Xenopus Polypedates 185 *Ranodon Mertensiella* 170
Bombina Polypedates 185 *Ranodon Mertensiella* 170
Xenopus Hyla 185 *Ranodon Mertensiella* 170
Bombina Rana 185 *Ranodon Mertensiella* 170
Xenopus Kaloula 185 *Ranodon Mertensiella* 170
Bombina Kaloula 185 *Ranodon Mertensiella* 170
Xenopus Rana 185 *Ranodon Mertensiella* 170
Bombina Hyla 185 *Andrias Paramesotriton* 170
Xenopus Polypedates 185 *Andrias Paramesotriton* 170
Bombina Polypedates 185 *Andrias Paramesotriton* 170
Xenopus Hyla 185 *Andrias Paramesotriton* 170
Bombina Rana 185 *Andrias Paramesotriton* 170
Xenopus Kaloula 185 *Andrias Paramesotriton* 170
Bombina Kaloula 185 *Andrias Paramesotriton* 170
Xenopus Rana 185 *Andrias Paramesotriton* 170

APPENDIX 9. Molecular divergence dates (rounded to Ma ago) calculated by quartet dating using QDate 1.11 using the evolution models from the three right columns of Appendix 7, compared to those reported (with confidence intervals) by Zhang et al. (2005) and to those from our supertree (Figs. 3–7). “Model 1” was chosen by the stock version of Modeltest 3.7, “Model 2” was chosen by our modification of Modeltest 3.7 using the most parsimonious tree instead of a neighbor-joining tree, and “Model 3” was chosen by our modification of Modeltest 3.7 using the most parsimonious tree obtained under the constraint of (*Bombina* (*Xenopus* + Neobatrachia)). Because of the limitations of this program, each divergence date was calculated using 12 or 16 quartets (“n”, right column). The exact quartets used are listed in Appendix 8. In each cell, the lower and upper bounds of the confidence interval are given for the whole set of quartets. Values in parentheses represent the range of lower and upper bounds yielded by the various quartets. Note that all QDate estimates for Batrachia are too young because they do not reach the age of *Triadobatrachus* and *Czatkobatrachus* (Early Triassic, 245–251 Ma ago). Also note that some estimates for Tetrapoda are likewise too young (see Table 1 and the text).

Basal divergence of:		Tetrapoda		Batrachia	
Zhang et al. (2005)		354 (341–367)		308 (289–328); 337 (321–353)[a]	
Our time-calibrated supertree (paleontological dates; Appendix 4)		– [before 332; see Table 1 and text]		254 (246–257)	
This study		Minimal age of calibration dates	Maximal age of calibration dates	Minimal age of calibration dates	Maximal age of calibration dates
	Calibration points	Amniota (310), Batrachia (250)	Amniota (345), Batrachia (275)	Bombinanura (170), Urodela (150)	Bombinanura (185), Urodela (170)
	n	12	12	16	16
Model 1	Lower bound	314 (310–321)	346 (345–355)	178 (174–181)	197 (193–201)
	Average	326	360	185	206
	Upper bound	343 (335–350)	379 (370–387)	193 (190–197)	215 (210–219)
Model 2	Lower bound	316 (310–331)	350 (345–367)	180 (173–188)	200 (192–208)
	Average	329	364	193	213
	Upper bound	350 (335–366)	387 (371–405)	203 (195–212)	225 (216–234)
Model 3	Lower bound	316 (310–331)	350 (345–366)	181 (174–188)	200 (192–208)
	Average	329	364	193	214
	Upper bound	350 (335–366)	387 (371–405)	203 (195–211)	225 (216–234)

[a] According to the most likely tree using “Model 2”, Lissamphibia and Batrachia are synonyms (“Procera hypothesis”); 308 Ma ago is the divergence date Zhang et al. (2005) find for Batrachia, 337 Ma ago the one for Lissamphibia.

Appendix 10. Divergence dates calculated by penalized maximum likelihood using r8s 1.71 (TN algorithm) under different assumptions. All dates rounded to 1 Ma. When two ages separated by a dash are given for a calibration point, they represent its minimal and maximal age; a single date represents the minimal age alone unless marked as "fixed". The dates estimated by Zhang et al. (2005) and those given by a literal reading of our supertree (Figs. 3–7) are shown for comparison. The higher the value of the smoothing parameter, the closer the assumed rates of evolution to a molecular clock. See Appendices 9 and 11 for "Model 1–3". Trees derived from Model 1 contain Batrachia (Salientia and Caudata are sister-groups to the exclusion of Gymnophiona; Fig. 8c), while trees derived from Models 2 and 3 contain Procera (Caudata and Gymnophiona are sister-groups to the exclusion of Salientia; Fig. 8d). In both cases, an alternative containing the topology (*Bombina* + (*Xenopus* + Neobatrachia)) is also considered.

Abbreviations: D-T, the Dipnomorpha-Tetrapodomorpha divergence. Each setting number designates a unique combination of evolutionary model, topology, and calibration points (or bounds thereof), but ignores the smoothing parameter. **Symbols:** * smoothing parameter value selected by the substitution-based cross-validation procedure of r8s minimizing normalized, __-like error; † value selected by the fossil-based cross-validation procedure using constrained nodes and minimizing fractional error (both cross-validation procedures are based on the lowest score of 25 tests that varied the log of the smoothing factor from 0 to 6 by increments of 0.25 [only tests that did not fail were considered], and only dates obtained using smoothing parameters yielded by these cross-validation analyses are incorporated into Table 5, except for the last two rows of Table 5 that evaluate the impact of the smoothing factor).

Footnotes: a Multidivtime is capable of using dates with standard deviations, in these cases 10 Ma, as calibration points, but r8s requires precise borders for the age ranges of calibration points; b Fossil-based cross-validation is possible and informative when at least one node is fixed and two nodes are constrained with both upper and lower bounds; c these dates are younger than the fossil record allows; d these dates are not necessarily too young because the oldest known cryptobranchoids may be only 130 or even 125 Ma old, depending on the correlation of the Daohugou Beds (see article) and the resolution of the basal cryptobranchoid polytomy; e when the value selected by the cross-validation procedure yielded errors in r8s, slightly different values were used (shown); f setting used to assess the impact of the smoothing factor (last two lines of Table 5).

			Calibration points	**Smoothing parameter**	**D-T**	**Tetrapoda**	**Amniota**	**Lissamphibia**	**Batrachia or Procera**	**Bombinanura**	**Neobatrachia**	**Urodela**	**Cryptobranchoidea**
	Zhang et al. (2005)		**D-T 400 ± 10; Amniota 310 ± 10 a**	**–**	**–**	**354 (341–367)**	**–**	**337 (321– 353)**	**308 (289–328)**	**290 (268–313)**	**173 (152–195)**	**197 (176–219)**	**158 (135–181)**
Setting number	**Our time-calibrated supertree (paleontological dates; Appendix 4)**		**–**	**–**	**–**	**–**	**–**	**260 (246– 267)**	**254 (246-257)**	**175 (166-185)**	**108 (72-124)**	**162 (152-166)**	**143 (138-150)**
1.1	Monophyletic Archaeobatrachia (Model 1)	Attempts to replicate the results by Zhang et al. (2005)	D-T 390–410; Amniota 300–320	1 f	392 c	339	309c	327	319	310	270	243	129 d
				5623* bf	390 c	350	320	342	334	326	286	264	150
				100000	390 c	358	320	351	346	339	303	280	165
1.2		Internal and external calibration points: minimal ages only	D-T fixed 410; Amniota 310; Batrachia 250; Cryptobranchoidea 140; Archaeobatrachia 170; Urodela 155; Bombinanura 170	1 f	–	356	325	345	335	326	284	258	140
				50	–	356	325	345	336	327	285	258	140
				3162* bf	–	364	334	356	347	338	296	272	153
				100000	–	377	341	371	365	358	320	295	174
1.3		Internal and external calibration points: minimal and maximal ages	D-T fixed 410; Amniota 310; Batrachia 250; Cryptobranchoidea 140; Archaeobatrachia 170; Urodela 155–170; Bombinanura 170–185	1 f	–	334	310	301	250	185	139	170	140
				50	–	333	310	289	250	185	153	170	140
				3162* f	–	329 c	310	280	250	185	165	170	140
				10000†	–	328 c	310	281	250	185	168	170	140
				100000	–	328 c	310	284	250	185	173	170	140
1.4		Internal and external calibration points: increased maximal ages	D-T fixed 410; Amniota 310; Batrachia 250; Cryptobranchoidea 140; Archaeobatrachia 170; Urodela 155–185; Bombinanura 170–200	1 f	–	333	310	298	250	200	153	185	140
				50	–	332	310	286	250	200	167	185	140
				3162* f	–	329	310	282	250	200	178	185	140
				10000†	–	328	310	283	250	200	181	185	140
1.5		Internal calibration points only	Batrachia 250; Cryptobranchoidea 140; Archaeobatrachia 170; Urodela 155–170; Bombinanura 170–185	1 f	335 c	282 c	256 c	269	250	185	139	170	140
				50	314 c	270 c	246 c	260	250	185	154	170	140
				10000* bf	286 c	260 c	236 c	255	250	185	167	170	140
1.6		Internal calibration points only: increased maximal ages	Batrachia 250; Cryptobranchoidea 140; Archaeobatrachia 170; Urodela 155–185; Bombinanura 170–200	1 f	328 c	278 c	252 c	266	250	200	154	185	140
				50	312 c	269 c	245 c	259	250	200	168	185	140
				5623* bf	290 c	261 c	238 c	255	250	200	178	185	140
1.7		Internal and external calibration points with Tetrapoda: maximal ages further increased	D-T fixed 410; Tetrapoda 332-360; Amniota 310; Batrachia 250; Cryptobranchoidea 140; Archaeobatrachia 170; Urodela 155–200; Bombinanura 170–215	1 f	–	332	310	292	250	215	169	198	140
				1778*	–	332	310	288	258	215	189	200	140
				5623† f	–	332	310	291	260	215	192	200	140
2.1	(*Bombina* + (*Xenopus* + Neobatrachia)) (Model 1)	Attempt to replicate the results by Zhang et al. (2005)	D-T 390–410; Amniota 300–320	1 f	394 c	342	312	331	321	312	271	246	130 d
				5623* bf	390 c	351	320	342	334	326	284	265	151
2.2		Internal and external calibration points: minimal ages only	D-T fixed 410; Amniota 310; Batrachia 250; Cryptobranchoidea 140; Pipanura 155; Urodela 155; Bombinanura 170	1 f	–	357	326	345	335	326	283	259	140
				3162* bf	–	366	335	356	347	338	294	273	154
2.3		Internal and external calibration points: minimal and maximal ages	D-T fixed 410; Amniota 310; Batrachia 250; Cryptobranchoidea 140; Pipanura 155; Urodela 155–170; Bombinanura 170–185	1 f	–	335	310	302	250	185	152	170	140
				3162*† f	–	329	310	280	250	185	163	170	140
2.4		Internal calibration points only	Batrachia 250; Cryptobranchoidea 140; Pipanura 155; Urodela 155–170; Bombinanura 170–185	1 f	336 c	284 c	258 c	270	250	185	152	170	140
				5000* bef	290 c	262 c	239 c	255	250	185	163	170	140
2.5		Internal calibration points only: increased maximal ages	Batrachia 250; Cryptobranchoidea 140; Pipanura 155; Urodela 155–185; Bombinanura 170–200	1 f	329 c	279 c	254 c	267	250	200	166	185	140
				5000* bef	291 c	262 c	239 c	256	250	200	176	185	140
2.6		Internal and external calibration points: increased maximal ages	D-T fixed 410; Amniota 310; Batrachia 250; Cryptobranchoidea 140; Pipanura 155; Urodela 155–185; Bombinanura 170–200	1 f	–	334	310	298	250	200	165	185	140
				50	–	333	310	289	250	200	170	185	140
				500	–	330 c	310	282	250	200	173	185	140
				5000, 5623†* f	–	329 c	310	282	250	200	177	185	140
				50000	–	328 c	310	284	250	200	184	185	140
				500000	–	328 c	310	286	253	200	185	185	140
2.6b		Same, but penalty parameter set to additive instead of logarithmic-additive	Same as above	1	–	339	310	317	250	200	172	185	140
				32*	–	329	310	280	250	200	176	185	140
				100†	–	329	310	282	250	200	179	185	140
2.7		Internal and external calibration points with Tetrapoda: maximal ages further increased	D-T fixed 410; Tetrapoda 332-360; Amniota 310; Batrachia 250; Cryptobranchoidea 140; Pipanura 155; Urodela 155–200; Bombinanura 170–215	1 f	–	333	310	295	254	215	179	200	140
				3162*† f	–	332	310	289	258	215	189	200	140

3.1	Monophyletic Archaeobatrachia (Model 3)	Attempt to replicate the results by Zhang et al. (2005)	D-T 390–410; Amniota 300–320	1* b, 50	390 c	360	320	325	305	301	186	228	175
3.2		Internal and external calibration points: minimal ages only	D-T fixed 410; Amniota 310; Lissamphibia 250; Cryptobranchoidea 140; Archaeobatrachia 170; Urodela 155: Bombinanura 170	1* b	–	378	337	342	320	316	196	239	184
				50	–	378	337	342	320	317	196	239	184
3.3		Internal and external calibration points: minimal and maximal ages	D-T fixed 410; Amniota 310; Lissamphibia 250; Cryptobranchoidea 140; Archaeobatrachia 170; Urodela 155–170; Bombinanura 170–185	1 f	–	354	310	250	227	185	97	170	140
				1000†	–	348	310	250	232	185	112	170	140
				3162† f	–	347	312	250	234	185	120	170	140
3.4		Internal and external calibration points: increased maximal ages	D-T fixed 410; Amniota 310; Lissamphibia 250; Cryptobranchoidea 140; Archaeobatrachia 170; Urodela 155–185; Bombinanura 170–200	1 f	–	353	310	250	228	200	108	176	140
				50	–	353	310	251	231	200	111	176	140
				1000*	–	349	310	256	239	200	122	179	140
				5623† f	–	354	320	262	246	200	133	182	141
3.5		Internal calibration points only	Lissamphibia 250; Cryptobranchoidea 140; Archaeobatrachia 170; Urodela 155–170; Bombinanura 170–185	1	333 c	300 c	264 c	250	230	185	97	170	140
				50	323 c	293 c	259 c	250	231	185	100	170	140
				562*	307 c	282 c	251 c	250	233	185	110	170	140
3.6		Internal calibration points only: increased maximal ages	Lissamphibia 250; Cryptobranchoidea 140; Archaeobatrachia 170; Urodela 155–185; Bombinanura 170–200	1	322 c	292 c	258 c	250	233	200	109	178	140
				50	316 c	288 c	255 c	250	233	200	112	178	140
				316* b	307 c	282 c	251 c	250	234	200	118	178	140
3.7		Internal and external calibration points with Tetrapoda: maximal ages further increased	D-T fixed 410; Tetrapoda 332-360; Amniota 310; Batrachia 250; Cryptobranchoidea 140; Archaeobatrachia 170; Urodela 155–200; Bombinanura 170–215	1	–	353	310	259	237	215	119	178	140
				562*	–	360	310	262	244	215	129	181	140
				1778†	–	350	312	265	248	215	135	184	142
4.1	(*Bombina* + (*Xenopus* + Neobatrachia)) (Model 3)	Attempt to replicate the results by Zhang et al. (2005)	D-T 390–410; Amniota 300–320	1* bf	391 c	360	320	321	300	288	173	224	171
				50	390	359	319	320	299	287	173	223	171
				5000 f	390	359	320	321	301	289	188	222	172
				500000	390	360	320	320	298	293	212	209	161
4.2		Internal and external calibration points: minimal ages only	D-T fixed 410; Amniota 310; Lissamphibia 250; Cryptobranchoidea 140; Pipanura 155; Urodela 155; Bombinanura 170	1* bf	-	378	335	336	315	302	181	234	179
				50	-	377	335	336	315	302	182	234	179
				5000 f	-	381	344	341	320	307	199	236	183
4.3		Internal and external calibration points: minimal and maximal ages	D-T fixed 410; Amniota 310; Lissamphibia 250; Cryptobranchoidea 140; Pipanura 155; Urodela 155–170; Bombinanura 170–185	1† f	-	353	310	250	227	185	106	170	140
				50	-	353	310	250	228	185	107	170	140
				500	-	351	310	251	232	185	110	170	140
				1000*	-	349	310	252	234	185	112	170	140
				5000 f	-	355	320	256	239	185	121	170	140
				50000	-	369	339	261	244	185	137	170	140
4.4		Internal calibration points only	Lissamphibia 250; Cryptobranchoidea 140; Pipanura 155; Urodela 155–170; Bombinanura 170–185	1 f	329 c	298 c	263 c	250	231	185	106	170	140
				50	323 c	293 c	259 c	250	231	185	107	170	140
				1000* b	307 c	282 c	252 c	250	233	185	113	170	140
				10000 f	297 c	279 c	253 c	250	234	185	125	170	140
4.5		Internal calibration points only: increased maximal ages	Lissamphibia 250; Cryptobranchoidea 140; Pipanura 155; Urodela 155–185; Bombinanura 170–200	1	319 c	291 c	257 c	250	233	200	116	178	140
				100	313 c	286 c	254 c	250	234	200	118	178	140
				316* b	309 c	284 c	252 c	250	234	200	119	178	140
4.6		Internal and external calibration points: increased maximal ages	D-T fixed 410; Amniota 310; Lissamphibia 250; Cryptobranchoidea 140; Pipanura 155; Urodela 155–185; Bombinanura 170–200	1 f	–	354	310	260	237	200	115	179	140
				100	–	354	310	263	241	200	116	180	140
				1000*†	–	353	313	268	249	200	122	184	141
				10000 f	–	356	320	271	254	200	136	185	144
4.7		Internal and external calibration points with Tetrapoda: maximal ages further increased	D-T fixed 410; Tetrapoda 332-360; Amniota 310; Batrachia 250; Cryptobranchoidea 140; Pipanura 155; Urodela 155–200; Bombinanura 170–215	1	–	355	310	269	246	215	125	181	140
				562†	–	354	313	275	255	215	129	187	143
				1778*	–	358	320	282	263	215	134	195	150

APPENDIX 11. Molecular divergence dates calculated using PATHd8 1.0, rounded to the nearest Ma. The following constraints were used in all trials: Dipnomorpha-Tetrapodomorpha divergence fixed to 410 Ma ago (PATHd8 requires one fixed age); Tetrapoda minimal age 335 Ma (if this constraint was not used, the age of Tetrapoda was calculated as 310 Ma under Model 1 – younger than the oldest fossils), Batrachia minimal age 250 Ma, Urodela minimal age 155 Ma and maximal age either 170 or 185 Ma, Cryptobranchoidea minimal age 140 Ma, Archaeobatrachia (where present) minimal age 170 Ma, Bombinanura minimal age 170 Ma (omitted when Archaeobatrachia was present) and maximal age 185 or 200 Ma (see below). The data found by Zhang et al. (2005) and those read from our supertree (Figs. 3–7; Appendix 4) are included for comparison. "Model 1" and "Model 3" have the same meaning as in Appendix 9. Because of the zero-length branches (e.g. Tetrapoda, Lissamphibia, and Batrachia are all inferred to be 335.000 Ma old in some analyses), and because almost all constraints are hit in every trial, we do not consider these results reliable. In PATHd8 it is not possible to vary any settings comparable to the smoothing parameter of r8s; this might be the reason for the obvious artefacts. As with r8s we have not calculated divergence dates for Model 2 because it is almost identical to Model 3.

	Zhang et al. (2005)	Our time-calibrated supertree	Model 1				Model 3			
			Monophyletic Archaeobatrachia		(*Bombina* + (*Xenopus* + Neobatrachia))		Monophyletic Archaeobatrachia		(*Bombina* + (*Xenopus* + Neobatrachia))	
			Maximal ages: Urodela 170, Bombinanura 185	Maximal ages: Urodela 185, Bombinanura 200	Maximal ages: Urodela 170, Bombinanura 185	Maximal ages: Urodela 185, Bombinanura 200	Maximal ages: Urodela 170, Bombinanura 185	Maximal ages: Urodela 185, Bombinanura 200	Maximal ages: Urodela 170, Bombinanura 185	Maximal ages: Urodela 185, Bombinanura 200
Tetrapoda	354 (341–367)	–	335	335	335	335	371	372	371	372
Amniota	–	–	310	310	310	310	371	372	371	372
Lissamphibia	337 (321–353)	260 (246–267)	335	335	335	335	250	255	250	255
Batrachia	308	254	335	335	335	335	215	255	213	255

(Model 1) or Procera (Model 3)	(289–328)	(246–257)								
Bombinanura	290 (268–313)	175 (166–185)	185	200	185	200	185	200	185	200
Neobatrachia	173 (152–195)	108 (72–124)	163	176	162	175	141	153	140	152
Urodela	197 (176–219)	162 (152–166)	170	185	170	185	170	185	170	185
Cryptobranchoidea	158 (135–181)	143 (138–150)	140	140	140	140	142	155	142	155

Chapter 2

Phylogeny-free paleontological dating of the origin of Lissamphibia

As elaborated upon in the preceding Chapter, the dating of cladogeneses is a thriving field with interesting applications. Most divergence dating is currently done using molecular data, with contributions from the fossil record limited to providing calibration points. As the preceding Chapter shows, these calibration points need to be chosen with great care, or the method risks producing unrealistic results. If not enough calibration points are available, molecular dating becomes a risky enterprise. Furthermore, molecular dating of course requires that enough members of the clade in question are still extant or have died out recently enough that molecular data are available of them. This precludes application to mostly or entirely extinct clades. Smaller problems (as explained in the preceding Chapter) include the fact that molecular dating needs a phylogeny, and molecular phylogenetics is not a set of trivial problems; the difficulties of alignment, for example, deserve mention (Morrison 2009), even though they are not considered in Chapter 1.

Chapter 1 presents another method that uses the fossil record more extensively and does not use molecular data. That method still requires a reasonably well resolved phylogenetic hypothesis, which is not available for many taxa, and it requires a certain number of fossils that can be placed in that phylogeny with some precision.

A third method was developed, in three stages, by Marshall (1990, 1994, 1997); it, too, does not use molecular data, and unlike both of the other methods it does not use a phylogenetic tree at all. Instead, it calculates confidence intervals on the origin of a clade, using only a recovery potential function for fossils through time (see below) and the number and temporal distribution of the horizons that have yielded the fossils of that clade. (That the taxon in question is a clade is the only assumption about phylogeny that the method requires.) In other words, it asks how long before its first appearance in the fossil record a clade originated, and assigns a probability for this to every point in time before the first appearance.

This paper grew out of a part of the preceding Chapter that we took out and published separately as requested by the editor (chiefly because of length constraints). It builds on the method by Marshall (1997), which allows the temporal distribution of the fossiliferous horizons to be nonrandom.

From the literature I compiled a list of 1207 localities that have yielded lissamphibian fossils, ordered by stratigraphic position as precisely as possible. The relative ages of many localities could not be resolved, so I spaced all localities of “the same age” evenly within the amount of time they could lie in, under the realistic assumption that no two localities have the exact same age. The sites show a strong “pull of the Recent” in that they are more or less exponentially more closely spaced the younger they are; this necessitated the use of the method by Marshall (1997) as opposed to Marshall (1994) or Marshall (1990). Marshall himself reviewed the manuscript very favorably.

Some localities are known to have yielded lissamphibian fossils at several horizons. Because this is very sparsely documented in the literature, we have equated every locality with one horizon; this underestimates the number of fossil-bearing horizons and should thus inflate the width of the confidence intervals, making our approach conservative.

The method requires, as mentioned, a recovery potential function for fossils through geologic time. This function must not be based on the observed stratigraphic distribution of the fossils (because that would create a logical circle and would prevent the calculation of confidence intervals – fossil-recovery probabilities would quickly fall to 0 outside the known stratigraphic range of the clade). Instead, I digitized the geological map of the world (Bouysse et al. 2000) to calculate the relative area of exposed sediments from each of the relevant periods (by counting the pixels in Photoshop® and adjusting for the distorting projection of the map); the amount of exposed sediments should be roughly proportional to the number of known fossiliferous sites.

However, a Kolmogorov-Smirnov goodness-of-fit test (p. 420 of this paper) shows that this recovery potential function based only on the exposed area of fossiliferous rocks is inadequate. Indeed, when using this function alone, Marshall's (1997) method leads to unrealistically small confidence intervals of less than 0.5 Ma beyond the age of the oldest known lissamphibians (about 250 Ma; Table 4, Fig. 4C6). This seems to be the case because Lissamphibia is a long-lived clade known from hundreds of fossil-bearing horizons that document a timespan during which lissamphibian diversity did not stay constant (one way or another, it must have increased from two species to the present number of well over 6000), contrary to an assumption of the method by Marshall (1997). We therefore expanded the method by adding eleven models of exponential growth of lissamphibian diversity. These models differ in their assumptions on how much this diversity decreased during the Permian-Triassic, Triassic-Jurassic, and Cretaceous-Paleogene boundary mass extinction events, and in their starting dates (which are the null hypotheses we tried to reject). Due to lack of data, the extinction rates at each event had to be estimated from the literature on other taxa (though see below); we made five sets of them, of which one has all values at 0. As starting dates of lissamphibian diversification, we used the age of Lissamphibia (without confidence intervals) as calculated by Zhang et al. (2005; 337 Ma ago, Mississippian) and Roelants et al. (2007; 368.8 Ma ago, Late Devonian) in order to avoid biasing our results away from the high ages found by molecular divergence-dating analyses. These ten functions yield an estimate of standing lissamphibian biodiversity which we then multiplied by the recovery potential function derived from the exposed area of fossiliferous rocks. The resulting confidence intervals (Table 4, Fig. 4C1–5) stay mostly within the Permian, for the most part even within the Guadalupian or Luopingian. The exception is the set that (unrealistically) assumes that lissamphibians are immune to mass extinction events; it results in a Cisuralian age for the older bound of the 50% confidence interval and a Late Devonian age for the older bound of the 75% confidence interval.

The mode of diversification of Lissamphibia is not known. In addition to exponential models, argued for by Benton (2001), we therefore also considered linear and sigmoid (logistic) ones. However, linear ones would give extremely high ages, while sigmoid ones would require estimating several parameters that are difficult or impossible to derive from the known data – and would give small, perhaps too small, confidence intervals.

In order to remedy the abovementioned lack of knowledge of changes in lissamphibian biodiversity in general and around mass extinctions in particular, I used the supertree of Chapter 1 and the module Stratigraphic Adds (Faure et al. 2006) for Mesquite (Maddison & Maddison 2005) to calculate three indices of lissamphibian biodiversity through time (Fig. 2): the number of observed species in each stage, the number of observed species in each stage divided by stage duration in Ma, and the number of lineages (observed species plus ghost lineages). The third index was calculated under the assumption of stratigraphic fit for terminal branches and a minimum duration of 3 Ma for internal branches; see the introduction to Chapter 1. However, most of the signal in the change of the first two indices over time seems to be taphonomic; I even described the first one as "nearly useless" (p. 421). The third index is dominated by ghost lineages that lead to extant species. Comparison of all three suggests a modest decrease in lissamphibian diversity at or around the Cretaceous-Paleogene boundary; various other declines in the Cenozoic and possibly Mesozoic could be artefacts.

The discussion section compares molecular and phylogeny-dependent paleontological dating to the method used here (pp. 424–426; see also Ch. 5) and argues once again for a Permian age of Lissamphibia as being the hypothesis that is globally the most compatible with the data.

Errata

New localities have of course been discovered since this paper was published, but the number of Chinese "Early Cretaceous" localities was already too small, and some of them are apparently Late (Hu et al. [2009] and references therein) or maybe even Middle Jurassic in age – stratigraphic correlation is very difficult in the huge, vegetated, hilly terrain (pers. obs.) of northeastern China where some strata are folded into hairpin shapes, different biostratigraphic indicator fossils sometimes point at different ages, and radiometric dating is often possible, but not often enough.

The paper may not make sufficiently clear that our implementation of this dating method assumes lissamphibian monophyly and that the dates it suggests are nonetheless evidence against the polyphyly hypothesis. (Anderson [2008] in particular seems to have misunderstood this point.) This is elaborated upon in Chapter 6 and in the General Introduction.

Author contributions

M. L. provided the ideas and access to the literature, performed most of the calculations, contributed to the manuscript, and supervised me; I gathered the data (which soon proved to be the most time-consuming task for this paper), performed the rest of the calculations, wrote most of the manuscript including all appendices, made the illustrations and tables, and handled most of our side of the submission and review process.

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Assessing confidence intervals for stratigraphic ranges of higher taxa: The case of Lissamphibia

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Marjanović, D. and Laurin, M. 2008. Assessing confidence intervals for stratigraphic ranges of higher taxa: The case of Lissamphibia. *Acta Palaeontologica Polonica* 53 (3): 413–432.

To evaluate stratigraphic evidence for the time of origin of the clade of extant amphibians (Lissamphibia), we attempt to establish a confidence interval on the lower bound of the stratigraphic range of this clade. This is based on the stratigraphic distribution of 1207 fossiliferous localities that have yielded lissamphibians, the relative area of sedimentary rocks from various periods (upper Paleozoic to present) exposed on the continents, and ten exponential-growth models of lissamphibian diversity that differ by the assumed effects of three major biological crises and the assumed starting times of lissamphibian diversification. The results suggest a more recent origin of Lissamphibia than advocated in most recent molecular studies. They are also more compatible with monophyly than with polyphyly of the extant amphibians, but heavily depend on poorly constrained assumptions about lissamphibian extinction rates during biological crises. Counts of lissamphibian diversity through time that consider ghost lineages and stage durations show moderate declines across the Cretaceous–Paleogene and Oligocene–Miocene boundaries.

Key words: Lissamphibia, origination time, evolution of biodiversity, stratigraphic range, fossil record, mass extinction.

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Introduction

The possible origins of the extant amphibians (Lissamphibia) from temnospondyls (e.g., Ruta et al. 2003; Schoch and Milner 2004; Ruta and Coates 2007), lepospondyls (e.g., Laurin 1998; Vallin and Laurin 2004), or polyphyletically from both (e.g., Carroll et al. 2004; Anderson 2007) have been debated for a long time, but no consensus has emerged (Fig. 1). Recently, Zhang et al. (2005) compared their molecular divergence date estimates with appearance dates of presumed relatives of Lissamphibia in the fossil record in order to determine which hypothesis about lissamphibian origins best fits the molecular estimates. They found that their molecular estimate for the origin of Lissamphibia had the most overlap with what they thought to be the age of the first dissorophoid temnospondyls, and therefore considered the hypothesis that lissamphibians are temnospondyls to be the one best supported by this line of evidence. However, several errors in the paleontological data used by Zhang et al. (2005), and in their interpretation of these data, invalidate this result (Marjanović and Laurin 2007).

The study by Zhang et al. (2005) is but one of several recent attempts made by molecular biologists to date the appearance of lissamphibians (San Mauro et al. 2005; Roelants et al. 2007). All these studies suggest that lissamphibians appeared in the Late Devonian or Early Carboniferous (between about 370 and 335 Ma ago). As pointed out by Lee and Anderson (2006), such an early origin of Lissamphibia would favor a polyphyletic origin for this group, which is incompatible with nearly all recently published phylogenies supported by data matrices (Laurin 2002). Conversely, an age of origin of Lissamphibia which clearly postdates the latest possible divergence date for temnospondyls and "lepospondyls" would refute all hypotheses of a polyphyletic origin of Lissamphibia from both of these groups (Marjanović and Laurin 2007). The oldest known lissamphibian dates from the Early Triassic (less than 251 Ma ago), and our time-calibrated supertree of lissamphibians (which includes 223 extinct species), as well as our own molecular dating of the basal divergence of this taxon, suggest a Permian origin (Marjanović and Laurin 2007), less than 300 Ma ago, which in turns implies lissamphibian monophyly. This is not the first time that a major discrepancy is found between the times of origin advocated by molecular phylogeneticists and paleontologists; similar controversies revolve around the timing of the diversification of crown-group birds (Padian and Chiappe 1998; Bleiweiss 1999; Marshall 1999; Chiappe and Dyke 2002; Dyke and van Tuinen 2004; Clarke et al. 2005), placental mammals (Hedges et al. 1996; Kumar and Hedges 1998; Waddell et al. 1999, 2001; van Tuinen and Hadley 2004; Wible et al. 2007), vertebrates (Janvier 1996; Delgado et al. 2001), and other taxa. However, this debate should not be construed as a straightforward disagreement between molecular phylogeneticists and paleontologists because specialists of both fields have sometimes worked together and found that the molecular data were compatible with the relatively recent diversification times indicated by fossil evidence (e.g., Ericson et al. 2006; see also Waddell et al. 2001). Nev-

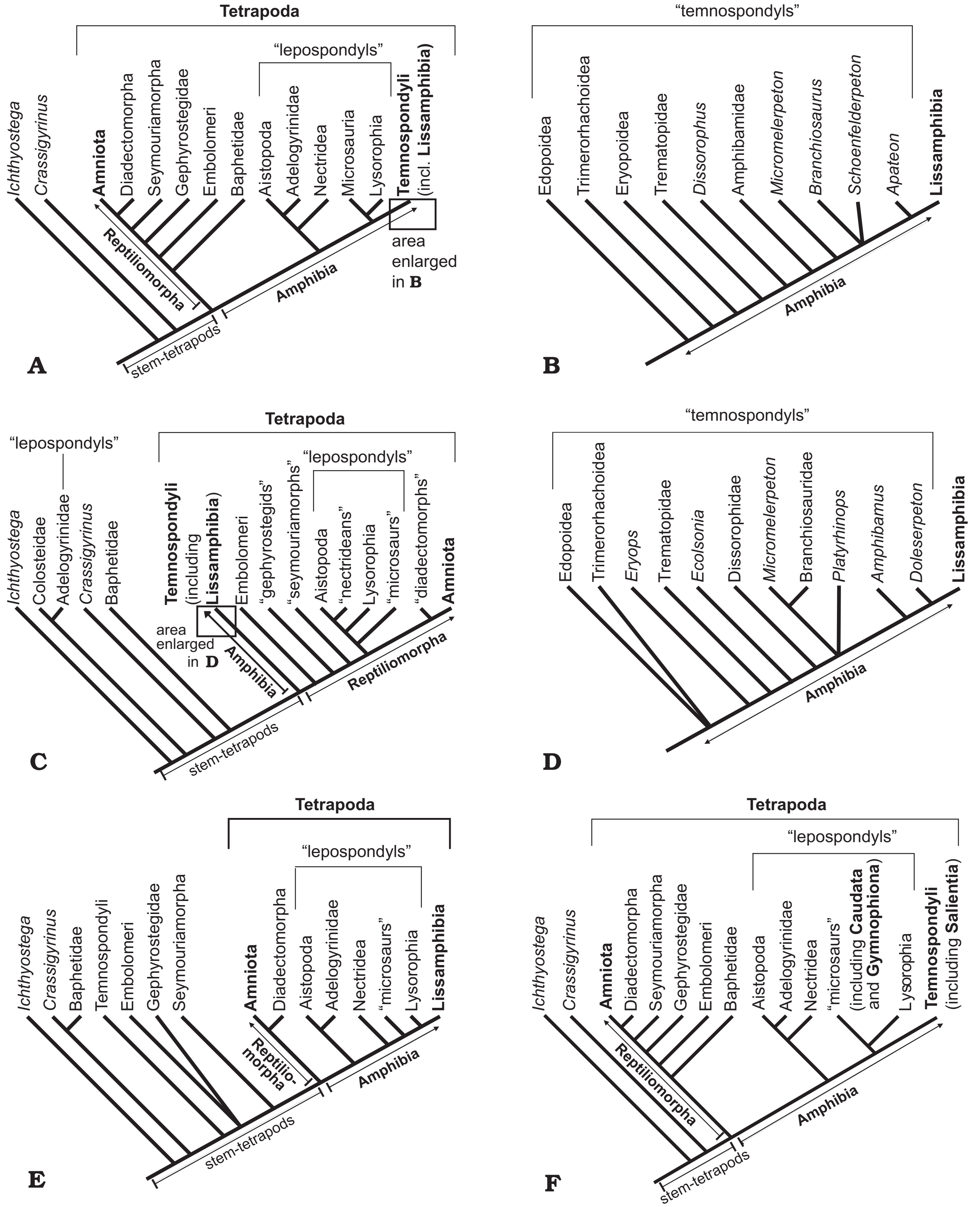

Fig. 1. Current hypotheses on the origin of the extant amphibians. Extant taxa in bold, paraphyletic taxa in quotation marks. **A**, **B**. Monophyletic origin from within the temnospondyls, with lepospondyls at the basalmost part of the amphibian stem (Panchen and Smithson 1988; Trueb and Cloutier 1991; Lombard and Sumida 1992; Ahlberg and Milner 1994). **C**, **D**. Monophyletic origin from within the temnospondyls, with the lepospondyls as reptiliomorphs (Ruta and Coates 2007; see also Ruta et al. 2003). **E**. Monophyletic origin from within the lepospondyls (Vallin and Laurin 2004; see also Laurin and Reisz 1997, 1999). **F**. Diphyletic origin with the anurans as temnospondyls, caecilians as lepospondyls, and urodeles as either temnospondyls or lepospondyls (Carroll and Currie 1975; Carroll and Holmes 1980; Carroll et al. 2004).

ertheless, most recent diversification dates of lissamphibians based on molecular data (San Mauro et al. 2005; Zhang et al. 2005; Roelants et al. 2007) are much older than what a literal interpretation of the fossil record suggests, and this suggests that a critical appraisal of the fossil record of lissamphibians would be useful.

Here we calculate confidence intervals on the date of origin of Lissamphibia based on data from the fossil record, using methods proposed by Marshall (1990, 1994, 1997). We propose modifications of these methods required or warranted when the taxon of interest is known from a large number (hundreds) of fossil-bearing horizons and when its diversification presumably impacted significantly on its fossil-recovery potential. Recently Marjanović and Laurin (2007) dated the appearance of this taxon using two methods: a time-calibrated paleontological supertree and molecular dating. The present study takes a third approach which, contrary to the two other methods used by Marjanović and Laurin (2007), does not use phylogenetic information (other than the assignment of a fossil to Lissamphibia) to date the appearance of Lissamphibia. This study was undertaken to determine if all these techniques give consistent results, and to determine which of them is the most precise.

Material and methods

Stratigraphic distribution of fossiliferous localities and analytical methods.—Confidence intervals on the stratigraphic range of taxa can be computed using information about the temporal distribution of the fossil occurrences of a taxon (Marshall 1990, 1994, 1997). Thus, we have compiled a database on the age of 1207 fossiliferous localities that range from the Early Triassic to the Recent. Most of these localities are listed by Sanchíz (1998), but a few more were taken from Estes (1981) and the primary literature (Appendix 1). We then sorted these localities by age. Most of the Mesozoic localities cannot be dated more precisely than the stage level (average duration about 5 Ma); many of the Cenozoic localities (those located in Europe) are dated more precisely using Land Mammal Ages (average duration of about 1.4 Ma). These localities were then assumed to be uniformly distributed throughout the stages or mammal ages to calculate the mean gap size within each stage or biozone. This procedure yields uniform gap sizes within each stage or biozone (Appendix 2, http://app.pan.pl/SOM/app53-Marjanowic_Laurin_SOM.pdf), but considering the large number of time divisions (51) used in our analysis, this should not alter the results substantially. We have assumed that no two localities are exactly of the same age. This assumption may have been occasionally violated, but this effect (probably rare considering the vastness of geological time) is probably more than compensated by our simplifying assumption that each locality has yielded lissamphibian fossils at a single horizon. Thus, the number of localities that we have used is much more likely to underestimate than to overestimate the number of horizons that have yielded lissamphibian fossils. Consequently, the confidence intervals based on these numbers are likely to be too large, rather than too narrow, and this should minimize the difference between our estimate of the maximum age of Lissamphibia and the deep ages reported by recent molecular studies (San Mauro et al. 2005; Zhang et al. 2005; Roelants et al. 2007). We cannot provide a count of horizons that yielded fossil lissamphibians at each locality because this information is usually not reported (a notable exception is Venczel and Gardner [2005] reporting *Albanerpeton pannonicum* from 25 successive horizons of a single locality). At best, the thickness of sediments that have yielded such fossils is occasionally provided. For instance, fossils of the basal pipimorph frog *Shomronella jordanica* have been found throughout a thickness of 1.5 m (Estes et al. 1978), and the basal pipinomorph frog *Eoxenopoides reuningi* was found over 33 m of sediment (Estes 1977). The amount of time that these layers represent was not reported (and is usually difficult or impossible to determine), but it clearly cannot be very short, at least in the second case.

Unlike many studies that perform molecular divergence date estimates, we used the compilation by Milner (1993) only to check that we had not overlooked relevant data, because Milner (1993) focuses only on first and last occurences of families, while our study requires data of all relevant fossiliferous localities (not only the oldest and youngest for each taxon). Furthermore, the two other approaches used in our previous study (Marjanović and Laurin 2007) focused on species rather than families or taxa of another particular supraspecific rank because the supraspecific Linnaean categories are entirely artificial and subjective. Comparative studies should focus on evolutionary lineages rather than arbitrary and, in our opinion, meaningless taxonomic levels (Laurin 2005, 2008; Bertrand et al. 2006).

Marshall (1990, 1994, 1997) described a series of methods to infer the confidence interval of the true stratigraphic range of a taxon. These methods are difficult to use in this case because not all their assumptions are met. The first method assumes that “fossil horizons are distributed randomly and that collecting intensity has been uniform over the stratigraphic range” (Marshall 1990:1). The second method offers a partial relaxation of this assumption, but still as-

Table 1. Correlation (as shown by R^2) between gap size and geological age in various subsamples of 1207 localities with lissamphibian fossils.

Cumulative number of localities	End of the interval (in Ma)*	R^2	Probability
1207	0 (Holocene)	0.201	< 0.0001
425	5.33 (Miocene)	0.203	< 0.0001
215	23.03 (Oligocene)	0.203	< 0.0001
78	65.5 (Maastrichtian)	0.212	< 0.0001
43	99.6 (Albian)	0.276	0.0003
20	145.5 (Tithonian)	0.426	0.0018

* End of the time interval represented by the sampling; the interval always starts at the oldest locality (Early Triassic, 251 Ma ago); only the age (stage name and absolute minimum age in Ma) of the youngest locality of each subsample is given.

sumes "no correlation between stratigraphic position and the sizes of gaps between adjacent fossil horizons" (Marshall 1994: 460). When such a correlation is present, this method should only be used as a first-order approximation. Thus, we have tested for such a correlation by performing simple linear regressions between gap size and geological age (Table 1), and by performing a Kolmogorov-Smirnov goodness-of-fit test in Statview® (Caldarola et al. 1998). Because both tests indicated the presence of a correlation between gap size and geological age (see below), neither of these two methods (Marshall 1990, 1994) can provide a reliable confidence interval of the stratigraphic range of Lissamphibia.

The fossil-recovery potential function.—The remaining method (Marshall 1997) requires a recovery potential function; it was suggested that it be based on the exposure surface of fossiliferous rocks or on water depth (for marine organisms whose depth preference is known). The second criterion is obviously inapplicable because many lissamphibians are terrestrial whereas others are aquatic (hence their recovery potential does not vary uniformly with water depth), and there is no convenient way to determine water depth or any comparable parameter in 1207 continental localities. However, Marshall (1997: 169) further indicated that the recovery function should not be based on the empirical distribution of finds (because this would lead to a recovery potential of 0 beyond the known stratigraphic range and thus preclude calculation of a confidence interval). Thus, the data on the evolution of lissamphibian diversity (Fig. 2) cannot be used to determine the recovery potential function.

To determine the exposure surface of fossiliferous rocks, we have digitized the geological world map by Bouysse et al. (2000) which is a flat projection of the globe onto three surfaces: the two poles (in polar views) and the rest of the world (in Mercator projection). Both of these projections cause distortion: in Mercator projection the equatorial areas appear smaller than they should, whereas the high-latitude areas appear too large. The distortion is caused by the 10°-wide longitudinal zones appearing equally wide from 0 to 80° rather than narrower as they should with increasing latitude, and by the height of the 10°-high longitudinal zones being proportional to their latitude rather than constant. To compensate for these distortions, we scaled each band of 5° height to its real area assuming that the Earth is spherical. The polar projections, which covered only 20° (from 70 to 90° in latitude) in the Arctic and 30° in the Antarctic, were considered flat in our calculations; the resulting error must be negligible because the exposure area around the poles is very small. Submarine outcrops were ignored, as they are never prospected for lissamphibian fossils. We used Photoshop® 7 to count the pixels representing the various periods in order to estimate the relative surface covered by sediments of these periods (Table 2).

The geological map by Bouysse et al. (2000) uses a coarse geological scale (i.e., "upper Paleozoic" or "Jurassic and Cretaceous"). To maximize the power of our statistical tests for verifying that the assumptions of Marshall's (1997) method were met, we considered it preferable to estimate the area covered by sediments from shorter periods. Thus, we assumed that the amount of sediment deposited during any period was proportional to the duration of the period. This does not require that sedimentation be steady: the assumption is only that sedimentation over long periods of time (at least a few Ma) did not change significantly on a worldwide scale. However, even if this assumption is not met, this is not a serious problem because it only decreases the power of the extra tests that we performed to verify that the assumptions were met; heterogeneities in sedimentation rates would not alter the results of our confidence interval on the stratigraphic range of lissamphibians. For instance, the Paleocene lasted 9.7 Ma and the "Tertiary" lasted 63.7 Ma, so we inferred that the area of Paleocene sediments equaled 0.152 times the area covered by the "Tertiary" (9.7 Ma/63.7 Ma = 0.152). The only exception is for the "Quaternary": instead of giving the Holocene a minute proportion of the "Quaternary" (0.0115 Ma/1.806 Ma = 0.0064), we arbitrarily assigned it 0.1 of the "Quaternary" record to compensate for the much greater sampling effort that results from the archaeozoological research on historic, protohistoric and late prehistoric sites. This procedure cannot have reduced the power of the test because the Kolmogorov-Smirnov goodness-of-fit test uses the observed maximum difference between predicted and observed values (the observed values being the cumulated number of fossiliferous localities at various periods, starting in the Triassic), and our method does not affect this difference for any of the times for which it can be unambiguously established using the geological map (at the end of the Triassic, at the end of the Cretaceous, and at the end of the Pliocene). The only partial exception is for the end of the Pliocene because part of the Cenozoic sediments is only identified as undifferentiated Cenozoic, so we had to assume that a part of this was from the Pleistocene and Holocene. Thus, our interpolation of the area covered by sediments for shorter periods can only increase the power of the Kolmogorov-Smirnov test; it cannot have adverse effects on any other calculations. This procedure also enables us to better assess the quality of the fit of our recovery potential function using linear regressions.

Preliminary analyses using the Kolmogorov-Smirnov test indicated that the area of exposure of rocks of various ages was a poor predictor of the number of fossiliferous sites yielding lissamphibians ($D_{max} = 0.38$; $P \leq 0.001$). Results using this function are reported below (CI 6 in Fig. 3 and Tables 3, 4) for comparison purposes, to demonstrate that another

Table 2. Relative area of sedimentary rocks in continental areas.

Period	Relative area
"Quaternary"	0.264
"Tertiary" (including indeterminate Cenozoic)	0.297
Jurassic and Cretaceous	0.264
Triassic	0.034
Upper Paleozoic (Carboniferous and Permian)	0.141

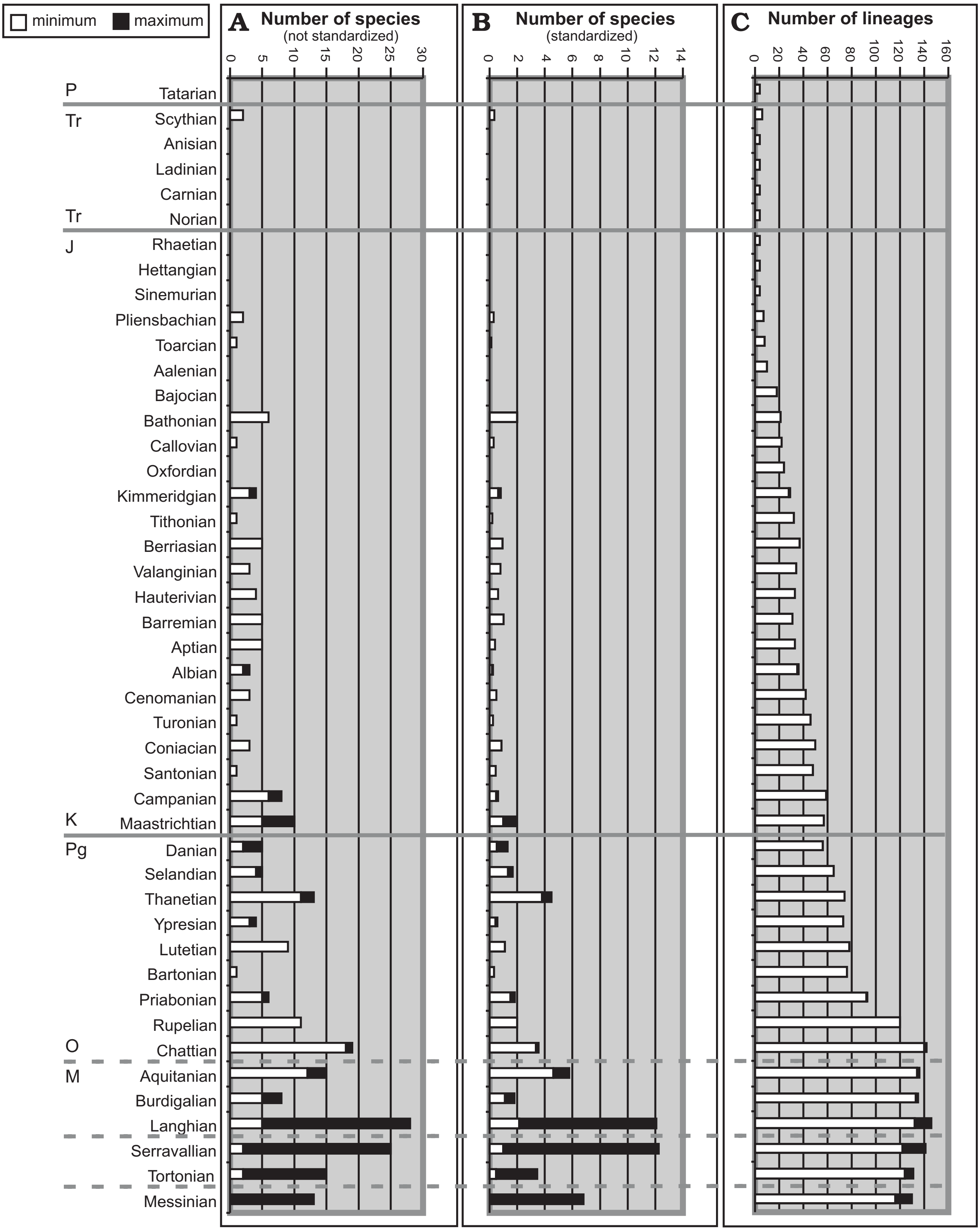

Fig. 2. Lissamphibian biodiversity through time. **A**. Number of species found in each geologic stage. **B**. Standardized species numbers, calculated to account for uneven stage durations. **C**. Number of lineages, obtained by adding the number of recorded species and the number of ghost lineages for each geologic stage. Major biological crises identified in other taxa are shown as continuous gray lines. Minor crises that may have affected lissamphibians are shown as dashed gray lines. Since most post-Miocene species are excluded, this figure ends with the terminal Miocene. Minimum (white) and maximum (black) values have been calculated under various assumptions about the age of several middle Miocene species and the status of specimens with questionable affinities. The geologic timescale follows Gradstein et al. (2004) in all figures. Abbreviations: J, Jurassic; K, Cretaceous; M, Miocene; O, Oligocene; P, Permian; Pg, Paleogene; Tr, Triassic.

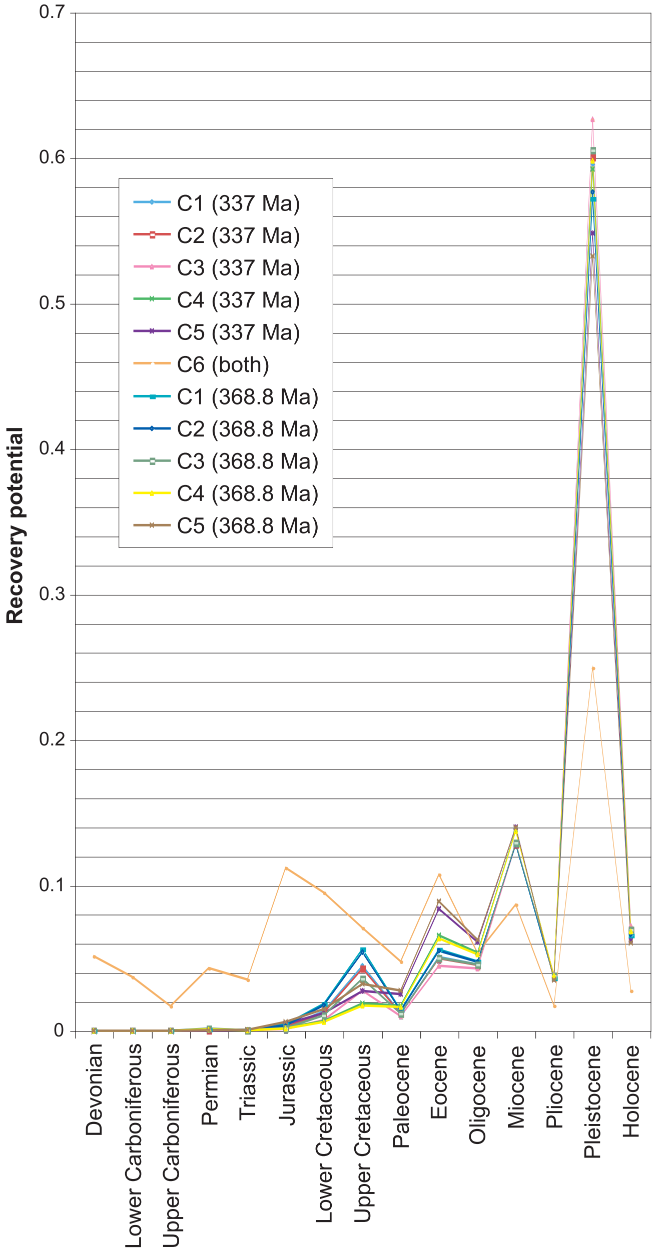

Fig. 3. A histogram of the curves (C) representing the recovery potential functions showing each period's or epoch's fraction of the total recovery potential calculated under eleven different assumptions (Table 4: CI 1–CI 6, which assume six different rates across extinction events and two different ages of origin for each except CI 6 which is independent of the age of origin). A bar chart of these data would be more appropriate than a dot-and-line graph, but much more difficult to read. The total recovery potential under each assumption (i.e., the area under each "curve") is 1. Note the wide divergence between CI 6, which is based only on the exposure area of sedimentary rocks (Table 1), and all others, which include an exponential model of diversification. The much lower recovery potential of CI 1–Cl 5 in the Paleozoic generates correspondingly wider CIs.

approach was required. Thus, we developed a second approach which we combined with the first. This second approach models the increasing lissamphibian diversity through time. During lissamphibian diversification, the number of species present in this clade increased from one to several thousand, and this diversification must have been accompanied by a great expansion of the geographic range and the diversity of habitats used by lissamphibians. All these changes must have had major effects on the fossil recovery potential of this group. Several plausible models could be used, including a simple exponential function to model the evolution of biodiversity of lissamphibians through time:

$$B = 2^{t/d} \qquad (1)$$

where B is the biodiversity (number of species) at a given time, t is the time (Ma), and d is the time necessary for doubling the number of lineages.

To simplify, we will call the ratio t/d "g" (for generations). Thus, the equation becomes:

$$B = 2^{g} \qquad (2)$$

This approach is consistent with Benton's (2001: 227) recent argument that an exponential pattern describes the evolution of terrestrial vertebrate biodiversity since their origin well, but it may greatly overestimate the rate of lissamphibian diversification (see below). Therefore it is significant that equation (2) cannot be adjusted using the lissamphibian fossil record because the quality of the latter is precisely what we are trying to assess. However, the exponential function can be adjusted by inserting today's biodiversity (6157 species; Anonymous 2007) and that of the time at which the diversification started. That time is not known (and it is precisely what we want to infer), but the null hypothesis that we wish to test is the hypothesis suggested by recent molecular studies (San Mauro et al. 2005; Zhang et al. 2005; Roelants et al. 2007) that Lissamphibia started diversifying in the Late Devonian to Early Carboniferous, between 368.8 and 337 Ma ago. The oldest (Table 4, rows 5–8) and most recent (Table 4, rows 1–4) times proposed in these studies were used as the beginning of lissamphibian diversification. The fossil recovery potential (R) between the clade origin (368.8 or 337 Ma ago) and any given time can be obtained by integrating function (2), which gives:

$$R = 2^{g}/(\ln 2) + C \qquad (3)$$

where ln designates the natural logarithm, and C is a constant common to all indefinite integrals. To obtain the recovery potential between two arbitrary points in time (e.g., the beginning and end of a geological stage), the definite integral of the intervening period must be calculated by simple subtraction. Note that what we call "clade origin" here (368.8 or 337 Ma ago) is the time at which the first cladogenesis occurred within Lissamphibia (this is what molecular studies can date). Thus, our method can yield confidence intervals up to a full generation (g) older. The value of g varies depending on the assumed extinction rates in biological crises, but it is on the order of 20–25 Ma. Thus, our method cannot yield upper bounds older than about 390 or 370 Ma, depending on which of the two ages of clade origin (368.8 or 337 Ma) is used.

The recovery potential values obtained from the exponential growth model can also be divided by the duration of a given geological period as a proxy of average standing

Table 3. Correlation (as shown by R^2) and discrepancy (D) between the predicted number of fossiliferous lissamphibian localities according to various models and the recorded number of localities. CI 1–CI 6 are confidence intervals as distinguished (in the row below) by the extinction percentages at the K/Pg (Cretaceous/Paleogene), P/Tr (Permian/Triassic), and Tr/J (Triassic/Jurassic) boundaries; in parentheses follows the time (in Ma) necessary for doubling the number of species. All numbers were calculated using 337 Ma as the beginning of lissamphibian diversification; using 368.8 Ma instead yields very similar results (not shown).

Period/ epoch	Predicted number of localities						Recorded number of localities
	CI 1	CI 2	CI 3	CI 4	CI 5	CI 6	
	P/Tr 0.9; Tr/J 0.5; K/Pg 0.8 (18.53)	P/Tr 0.9; Tr/J 0.6; K/Pg 0.8 (18.21)	P/Tr 0.95; Tr/J 0.8; K/Pg 0.76 (16.65)	P/Tr 0.8; Tr/J 0.5; K/Pg 0.2 (25.20)	Exponential growth (no extinctions) (29.08)	Surface of exposures only	
Holocene	82.70	83.36	87.29	81.73	75.11	37.07	220
Pleistocene	719.62	724.96	756.78	715.19	661.66	333.67	466
Pliocene	45.16	45.42	46.96	45.62	43.05	23.12	96
Miocene	154.96	154.84	154.72	166.24	168.98	116.07	210
Oligocene	55.08	54.49	51.62	64.75	73.50	71.29	66
Eocene	61.30	60.04	53.87	79.23	101.07	143.63	56
Paleocene	14.68	14.22	12.00	21.06	30.44	63.62	15
Late Cretaceous	54.04	51.53	33.46	22.63	33.81	94.44	35
Early Cretaceous	16.15	15.07	8.70	8.20	14.58	127.12	23
Jurassic	3.05	2.76	1.34	2.08	5.32	149.83	18
Triassic	0.26	0.29	0.23	0.25	0.47	47.15	2
$R^2_{\text{(log-transformed)}}$	0.892	0.894	0.898	0.882	0.865	0.058	
$P_{\text{(log-transformed)}}$	0.0001	0.0001	0.0001	0.0001	0.0001	0.4746	
D	0.1138	0.1133	0.1304	0.1146	0.1201	0.3994	
$P_{(D)}$*	5.17 E-14	7.00 E-14	3.06 E-18	3.36 E-14	1.48 E-15	1.18 E-167	

* Computed using equation (5) (see text).

Table 4. Lower (oldest) bounds (Ma ago) of the confidence intervals (CI) for the fossil record-based assessments of the stratigraphic range of Lissamphibia according to various models. CI 1–CI 6 are confidence intervals as distinguished (in the row below) by the extinction percentages at the K/Pg (Cretaceous/Paleogene), P/Tr (Permian/Triassic), and Tr/J (Triassic/Jurassic) boundaries (see also text).

Molecular divergence date estimate (Ma ago)	Confidence level	CI 1	CI 2	CI 3	CI 4	CI 5	CI 6*
		P/Tr 0.9; Tr/J 0.5; K/Pg 0.8	P/Tr 0.9; Tr/J 0.6; K/Pg 0.8	P/Tr 0.95; Tr/J 0.8; K/Pg 0.76	P/Tr 0.8; Tr/J 0.5; K/Pg 0.2	No extinction event	No model of diversity
337 (Zhang et al. 2005)	50%	260 (Capitanian–Wujiapingian boundary)	260 (Capitanian–Wujiapingian boundary)	257 (Wujiapingian)	270 (Roadian)	319 (Serpukhovian)	251 (uppermost Changxingian)
	75%	277 (Artinskian)	274 (Kungurian)	264 (Capitanian)	324 (Serpukhovian)	–	251 (uppermost Changxingian)
	80%	285 (Sakmarian)	281 (Artinskian)	267 (Wordian)	–	–	251 (uppermost Changxingian)
	95%	–	–	304 (Kasimovian-Gzhelian boundary)	–	–	251 (uppermost Changxingian)
368.8 (Roelants et al. 2007)	50%	255 (Wujiapingian)	255 (Wujiapingian)	253 (Changxingian)	260 (Wujiapingian)	280 (Artinskian)	251 (uppermost Changxingian)
	75%	261 (Capitanian)	260 (Capitanian–Wujiapingian boundary)	256 (Wujiapingian)	272 (Kungurian)	378 (Frasnian)	251 (uppermost Changxingian)
	80%	263 (Capitanian)	261 (Capitanian)	257 (Wujiapingian)	277 (Artinskian)	–	251 (uppermost Changxingian)
	95%	279 (Artinskian)	275 (Artinskian– Kungurian boundary)	263 (Capitanian)	381 (Frasnian)	–	251 (uppermost Changxingian)

* CI 6 is based only on the surface of exposed rocks, hence its size is independent of the assumed age of the basal node of Lissamphibia.

lissamphibian biodiversity. This approach seems more appropriate than directly using the fossil recovery potential calculated for a period based on the exponential diversification model because the latter would result in a high potential if a period were very long. In fact, the length of the period is irrelevant; what matters is the abundance of lissamphibians in the former biological communities, and the area of exposed fossiliferous rocks. Whether these rocks represent e.g., 1 Ma or 10 Ma should have no impact on the recovery potential.

The estimated average biodiversity in each period can be multiplied by the area of exposures of rocks of various periods on the continents to yield the recovery potential curve; this is the method that was adopted here (Table 3). With this model, we should be able to determine if the fossil record of lissamphibians is consistent with our starting assumption of lissamphibian origins, i.e., the timings suggested by Zhang et al. (2005) and Roelants et al. (2007), and diversification. We have found that our recovery potential function is adequate using a Kolmogorov-Smirnov test of goodness of fit for continuous distributions. The exact probability for the values of D at our high sample size ($n = 1207$) is not reported in Zar (1984), but it can be computed by isolating α (the probability threshold) in the formula used when n is large:

$$D_{\alpha\, n} = ([-\ln(\alpha/2)]/2n)^{1/2} \qquad (4)$$

From this equation α can be extracted:

$$\alpha = 2e^{-2nD^2} \qquad (5)$$

In this case, what is computed is a probability ($\alpha = p$).

We have also tested the correlation between the observed number of localities and the predicted number of localities using our recovery potential functions using a simple linear regression in Statview® (Caldarola et al. 1998) and using a regression with 9999 permutations in Permute! (Casgrain 2005). We tested normality using Progiciel R (Casgrain et al. 2004). Since the distribution of the localities in the various periods was lognormal rather than normal, the values were log-transformed (Table 3).

Lissamphibians in mass extinction events.—The simple exponential diversification model is probably unrealistic because most taxa that originated in the Paleozoic have suffered mass extinction at least a few times in their history (Nitecki 1984; Hallam and Wignall 1997). The simple exponential function predicts that the number of lissamphibian species will double in the next 15 to 25 Ma, but this seems unlikely because many of these species are currently becoming extinct through habitat loss and introduced diseases in combination with climate change and other causes (Pounds et al. 2006). The models that seem most appropriate include three major crises: the Permian–Triassic boundary (P/Tr), the Triassic–Jurassic boundary (Tr/J), and the Cretaceous–Paleogene boundary (K/Pg) mass extinction events. We have used plausible ratios of species extinction (Tables 3–4: CI 1–CI 3), although they are poorly constrained because nearly nothing is known about how these extinctions affected lissamphibians, with the partial exception of the K/Pg crisis (Cretaceous/Paleogene, often called K/T for Cretaceous/Tertiary in older literature) which may not have affected lissamphibians as strongly as many other terrestrial vertebrate taxa (Archibald and Bryant 1990; Sheehan and Fastovsky 1992). The end-Permian event is generally considered the most severe (Erwin 1993; Benton 2003), and in one of our analyses we consider that it probably eliminated 90% of the lissamphibian species of that time. A similar percentage of extinction has been calculated for marine metazoans by Hallam and Wignall (1997: table 1.1). Lower extinction levels have been assumed for the end-Triassic and end-Cretaceous events, as suggested by various studies, most of which focused on marine metazoans (Nitecki 1984; Erwin 1993: table 1; Hallam and Wignall 1997: table 1.1). It might be objected that the extinction levels of lissamphibians may not have been comparable to those of marine metazoans; therefore we also assess the implications of lower extinction levels in lissamphibians (Tables 3, 4: CI 4–CI 5).

The K/Pg and Eocene/Oligocene mass extinction events apparently eliminated species of medium to large body size in foraminifera (Norris 1991), and the P/Tr crisis had a similar effect on gastropods (Payne 2005). Thus, given the small size of lissamphibians relative to other tetrapods, it might be suggested that they must have suffered comparatively low extinction levels (for tetrapods) during biological crises. This is congruent with the results presented by Fara (2000), who found that all lissamphibian families survived the K/Pg event. However, vertebrates may be an exception to this rule: an analysis of body size evolution using 93 species of stegocephalians that date from the latest Middle Permian to the Early Triassic has failed to find a statistically significant size decrease across the P/Tr boundary (Laville 2007). (Throughout this paper, Stegocephali refers to the clade composed of the first animal with digits homologous to those of *Homo sapiens* and all descendants of that ancestor; see Laurin, 1998.)

Since the extinction levels are poorly constrained and influence the inferred limits of the confidence intervals on the time of origin of Lissamphibia, four combinations of values were used. We consider the first two the most plausible, while the third one uses values reported by Hallam and Wignall (1997: table 1.1). The fourth set of values assumes that lissamphibians were much less affected by the great biological crises than most other taxa. To calculate the value of the recovery potential, this potential has to be calculated separately in each time interval bounded by two successive mass extinctions. A fifth set of values assumes that lissamphibians were unaffected by biological crises. These five extinction level settings were used to compute confidence intervals under the assumption that the basal split in Lissamphibia occurred 337 or 368.8 Ma ago. The combination of all these settings yields ten models (Tables 3, 4: CI 1–5; Fig. 3). An eleventh model (Tables 3, 4: CI 6; Fig. 3), based only on the surface of exposures, is provided only to illustrate the need for a model of lissamphibian diversification.

Little is known about the evolution of lissamphibian biodiversity through time, but, as mentioned above, our recovery potential function requires information about lissamphibian biodiversity evolution. Therefore, our study would benefit from any improvement in our understanding of lissamphibian biodiversity through time. Thus, we have used the new StratAdd module (Faure et al. 2006) for Mesquite (Maddison and Maddison 2005) to compile three indices of lissamphibian biodiversity through time in order to assess the fate of Lissamphibia around the K/Pg boundary (Fig. 2) using the supertree by Marjanović and Laurin (2007). These indices are: (i) a simple count of observed species in each stage; (ii) a standardized count of observed species in each stage (obtained by dividing the first index by the stage duration in Ma); (iii) a count of all observed species plus all inferred ghost lineages in each stage. The last index incorporates phylogenetic information and is based on our supertree, incorporating the corresponding minimum branch length assumptions (each species occupies at least a whole geological stage, and the minimum internal branch length is 3 Ma). Thus, ghost ranges are longer here than in other studies because they have usually been computed under the assumption that internal branches can have zero length (Wills 1999). Ghost ranges are potentially important in species-level studies on biological crises (as opposed to studies using more inclusive taxa) because species have a relatively short duration (at least among vertebrates), on the order of a single geological stage. Therefore, studies neglecting ghost ranges would be very sensitive to taphonomic artefacts such as the fluctuating quality of the fossil record; in a worst-case scenario, a group with a good fossil record in one stage and no fossil record in the next would appear to have undergone complete extinction. However, if many of the species present in the first (oldest) stage had descendants in later stages and if the phylogeny were reasonably well known, methods that take ghost lineages into consideration would infer much lower extinction rates. Simulations are required to more precisely assess the merits of various approaches to study mass extinctions, but they are beyond the scope of this paper. Most previous studies on extinction patterns in early vertebrates did not incorporate ghost range estimates (Erwin 1993; Hallam and Wignall 1997). Our first two indices do not use any phylogenetic information, but still differ from most previous studies in this field by being done at the species (rather than genus, family or order) level (see Ward et al. 2006 for a partial exception).

Early studies on the evolution of biodiversity did not standardize for stage duration "because of considerable uncertainty in the durations of stages" (Raup and Sepkoski 1984: 801). Over the last twenty years, this uncertainty has greatly diminished for the Cenozoic, so we have calculated these durations from the ages given by Gradstein et al. (2004). In the Mesozoic there are still stages whose beginning and end is associated with uncertainty on the scale of the duration of the stage itself (e.g., the Kimmeridgian, whose duration we consider to be 4.9 Ma, while both its beginning and its end have confidence intervals of ± 4.0 Ma; Gradstein et al. 2004), but we do not try to test for mass extinctions within the Mesozoic. Recent studies have generally standardized for time in various ways (e.g., Alroy 1999, 2000; Ward et al. 2006); our second biodiversity index is also time-standardized.

We did not calculate either background or total extinction rates because the lifetime of most species is highly uncertain; in most cases, species are known from a single stage, but the actual duration of their lineages (including ghost ranges) may be far greater. Thus, it is very difficult to measure extinction rates; but the minimum biodiversity at any given time can be measured more objectively. Our analysis might indicate whether or not it is appropriate to include extinction events in the model of lissamphibian biodiversity, although, given the paucity of Triassic and Jurassic lissamphibian fossils, only the K/Pg boundary event and less important crises that occurred in the Cenozoic can be studied in this taxon.

Uncertainties about the assignment of fossils to geological stages of the Miocene complicated the analysis because many lissamphibian fossils are only dated to middle Miocene in the literature, whereas our scale divides this interval into Langhian and Serravallian. Therefore, we computed all biodiversity indices using two versions of our supertree, one in which all species of uncertain age were put in the Langhian and another in which these species were placed in the Serravallian. There are also several records of fossils whose taxonomic assignment is questionable and that could represent distinct species or (often) the oldest records of their respective species. Again, we calculated the three biodiversity indices while either considering these specimens of questionable affinities to be distinct species, or excluding them. The latter approach would be justified if these specimens were ancestral to at least some of the other species in our tree, if they belonged to known species not included in our tree, or if they were—as argued by Bever (2005) for many fossils attributed to *Bufo* sensu lato (i.e., not sensu Frost et al. 2006)—based on non-diagnostic material. We then computed the maximum and minimum biodiversity according to the three indices and two versions of the supertree (differing in stage assignment of middle Miocene lissamphibians), and these are the values reported in the Results section.

Results

Evolution of biodiversity in Lissamphibia.—The raw (unstandardized) observed number of species per epoch varies widely and, to a large extent, randomly (Fig. 2A). This index obviously reflects mostly taphonomic artefact and is nearly useless to assess the fate of lissamphibians across the K/Pg boundary. However, this graph shows the stratigraphic distribution of the lissamphibian species that are included in the supertree (which includes most known extinct lissamphibian species, except for those dating from the Pliocene or Pleistocene), and, as such, nicely summarizes this aspect of our data.

The standardized observed number of species (Fig. 2B) also varies widely, but perhaps a little less than the raw number of species (Fig. 2A). The differences between both indices are enlightening. For instance, the raw number of species sug-

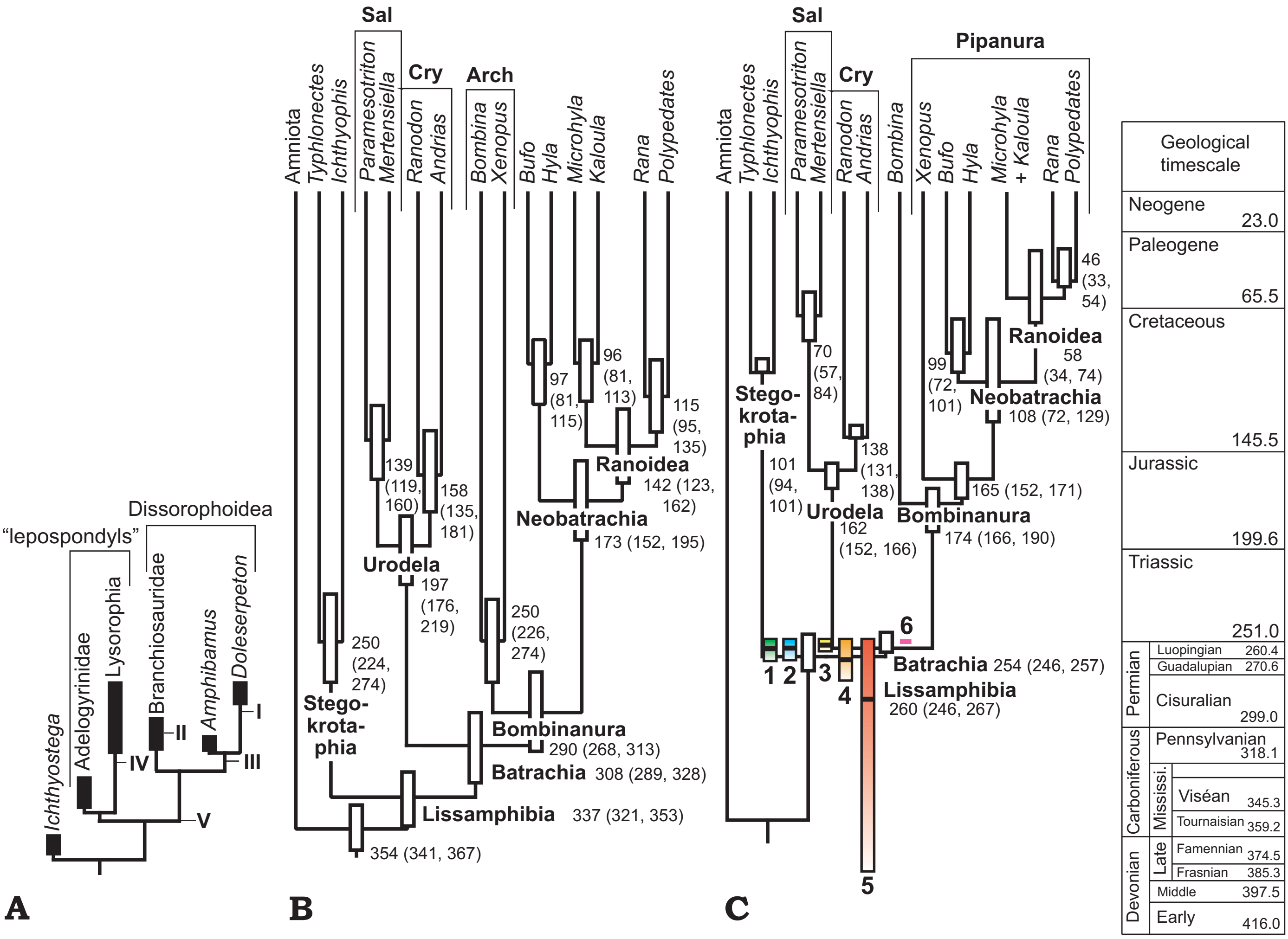

Fig. 4. A comparison of the origination (**A**–**C**) and diversification (**B**, **C**) times of Lissamphibia according to time-calibrated phylogenetic trees of (**A**) Stegocephali, (**B**) Lissamphibia based on the molecular analysis by Zhang et al. (2005), and (**C**) Lissamphibia based on the fossil record (Marjanović and Laurin 2007). In **A**, the stem of Lissamphibia is placed as high in the geological section as plausible under the various phylogenetic hypotheses: (I) as the sister-group of *Doleserpeton*; (II) within Branchiosauridae; (III) as the sister-group of the *Doleserpeton* + *Amphibamus* clade; (IV) as the sister-group of Lysorophia; (V) polyphyletic from within "lepospondyls" (caecilians, or caecilians and caudates) and "temnospondyls". Known stratigraphic ranges are shown as thick lines, ghost ranges as thin lines. In **B**, the 95% credibility intervals of molecular dates are represented by blank boxes; the best estimates and lower and upper boundaries of the credibility intervals are also indicated in parentheses. In **C**, the numbers given next to the nodes represent the age estimates (Ma) based on the assumptions used for the supertree by Marjanović and Laurin (2007: fig. 9b). In parentheses follow the ranges of minimum (rather than actual) divergence dates as obtained using various minimum branch length assumptions (Marjanović and Laurin 2007: appendix 4); these ranges, also represented as blank boxes, are not true confidence intervals. The colored boxes represent the confidence intervals on the lower bound of the stratigraphic range of Lissamphibia calculated in the present paper (1–6 correspond to the lower half of Table 4: CI 1–Cl 6), where the bottom of the rectangle shows the lower limit of the 75% confidence interval and the black bar in each colored box corresponds to the lower limit of the 50% confidence interval. Abbreviations: Arch, Archaeobatrachia; Cry, Cryptobranchoidea; Mississi., Mississippian; Sal, Salamandridae.

gests a 50% diversity drop at the K/Pg boundary, but the standardized values suggest a more moderate reduction. Similarly, the raw values suggest moderate drops in lissamphibian diversity in three Cenozoic time intervals (Chattian/Aquitanian, Langhian/Serravallian, and Tortonian/Messinian), but the standardized values show moderate increases in diversity, which suggests that these variations in raw values mostly represent taphonomic artefacts. However, even the standardized observed numbers of species are probably affected by taphonomic factors, as shown by comparisons with the observed number of lineages (see below).

The count of lineages appears to be much less affected by taphonomic artefacts, judging by the smooth shape of the diversity curve (Fig. 2C). However, the signal in this index is probably overwhelmed to a large extent by the numerous ghost ranges that lead to extant species. This is illustrated by the number of observed species (5 to 10) and high number of lineages (57) in the Maastrichtian; there are about 50 ghost lineages in that stage, and most of them lead to extant species. Thus, this index should have a low power to detect extinction events. Nevertheless, four drops in diversity are visible. The first occurs between the Campanian (59 lineages) and the

Danian (56 lineages). The second drop (from about 140 to about 135 lineages) is across the Chattian/Aquitanian (Oligocene/Miocene) boundary that is not considered a time of major biological crisis (Hallam and Wignall 1997), although many species of corals became extinct at that time (Edinger and Risk 1995). Another slight reduction in number of lineages (from about 140 to about 130) is across the Langhian/Serravallian boundary, in the middle Miocene. An extinction event at that time was recognized by Raup and Sepkoski (1984). The fourth slight drop (from about 127 to about 123 lineages), between the Tortonian and the Messinian (late Miocene), may result partly from our deliberate omission of the Pliocene and Quaternary (sub)fossils, but it may also reflect a genuine reduction in lissamphibian biodiversity because an extinction event in North American mammals has long been recognized at that time (Webb and Barnoski 1989). The three possible Tertiary crises identified on the basis of the number of lineages, and the K/Pg event, also appear as times of elevated extinction level according to the first index, i.e., the raw number of observed species (Fig. 2A).

Comparison of the three indices suggests that there was a slight reduction in lissamphibian diversity across the K/Pg boundary, but the other reductions we detected in the Cenozoic could be artefacts.

Confidence interval of the stratigraphic range of Lissamphibia.—The confidence interval of the stratigraphic range of Lissamphibia had to be computed using a method that can cope with nonrandom distribution of fossil horizons (Marshall 1997) because the correlation between gap size and geological age in our data is highly significant, as shown by simple linear regressions (Table 1). A Kolmogorov-Smirnov goodness-of-fit test on the 78 Mesozoic localities also indicates a strong deviation from an even temporal distribution of localities ($p < 0.001$). A method that assumes there is no such correlation (Marshall 1994) suggests that there is a 99% probability that the 80% confidence interval of the stratigraphic range of Lissamphibia extends no more than 425,000 years beyond the first appearance of fossils, i.e., beyond the beginning of the Triassic (into the very latest Permian). In this method, the limits of confidence intervals have confidence probabilities.

More plausible results were obtained by the fossil recovery potential curve using the method advocated by Marshall (1997). The fossil recovery potential functions based on an exponential diversification model and on the area of exposed rock (Table 3) show moderate discrepancies between predicted and observed number of localities ($D_{max} = 0.11$ or 0.12). These deviations are highly significant ($P < 0.001$), but this largely reflects the high number of localities (1207) used to compute this statistic. Marshall's (1997) method seems to have been designed for cases where far fewer localities are known, and accordingly, his test maximizes the power to find deviations between the predicted and the observed number of localities; with several hundred localities, obtaining a recovery potential function without significant deviations from the observed number of localities and obtained independently from the distribution of localities seems extremely unlikely. Our linear regression using Permute! (Casgrain 2005) shows that most of our recovery potential functions explain at least 85% of the observed variance in the observed number of localities; the associated probability for this being a random pattern is less than 0.0001 (Table 3). Thus, we conclude that the recovery potential functions are adequate, and we report the results of these calculations, with the caveat that one of the recommendations by Marshall (1997) cannot be followed exactly as he suggested.

The functions that assume that lissamphibians were affected by biological crises to about the same extent as most metazoans (Table 4: CI 1–CI 3; Fig. 4) yield a 50% confidence limit of lissamphibian origins extending down to the Late Permian (Wujiapingian or Changxingian; 253 to 260 Ma ago, depending on model and molecular estimate adopted). The 75% confidence limit still also implies much younger dates of lissamphibian origin than suggested by most recent molecular studies (San Mauro et al. 2005; Zhang et al. 2005; Roelants et al. 2007), with an earliest possible time of appearance between 256 and 277 Ma ago (Wujiapingian to Artinskian). Three other functions, including one that does not predict the number of localities well (Table 3: CI 6), have highly variable lower bounds to their confidence intervals and give highly variable results (Table 4: CI 4–CI 6; Fig. 4). Assuming that the great biological crises had minor or no effects on lissamphibians (CI 4–Cl 5) gives a 50% confidence limit ranging from the Wujiapingian (260 Ma ago) to the Serpukhovian (319 Ma ago; late Mississippian). The 75% confidence limit under the same assumptions (CI 4–Cl 5) ranges from 272 Ma ago (Kungurian) to 378 Ma ago (Frasnian, Upper Devonian). Since digits may not have appeared before the Famennian (Laurin et al. 2000) and the earliest known crown-tetrapods date from the Viséan (Laurin 2004), and because the fossil record of the Upper Devonian is quite good (Janvier 1996), an origin of lissamphibians in the Frasnian is highly unlikely. The model incorporating only the exposure area of sediments has a poor fit (Table 3: CI 6) and gives a ridiculously recent confidence interval (terminal Changxingian). This result is provided only to illustrate the need to have an adequate recovery potential function.

Discussion

Evolution of biodiversity and the fate of Lissamphibia across mass extinction events.—We have found large differences in the reconstructed pattern of lissamphibian biodiversity shown by raw and standardized observed number of species. Earlier studies of biodiversity through time (e.g., Smith 1994 and references therein) did not standardize for stage duration; the need for standardization was recognized by Alroy (1998, 1999, 2000) and Alroy et al. (2001), who used absolute ages instead of stage assignments and also standardized for sampling intensity (Alroy 1999, 2000; Alroy et al. 2001). Unfortunately, we know too little about the sampling of the lissamphibian fossil record in collections and in the literature to standardize for this.

Incorporation of extinction events into the models is supported to an extent by the literature and by our new analyses. Among taxa that have been interpreted as stem-amphibians (= stem-lissamphibians), the temnospondyls suffered a great reduction in biodiversity towards the end of the Permian, although their record is not good enough to determine if this was a slow decline or a result of the end-Permian crisis (Milner 1990, 1991). The "lepospondyls" also declined steadily in diversity in the Permian, but in their case, complete extinction (except for the lineage which probably led to the lissamphibians) seems to have occurred well before the end of the Permian (contra Zhang et al. 2005: figs. 2, 3) because only a few species persist into the Middle to Late Permian (Carroll 2000). Less is known about how lissamphibians fared in times of biological crises. Aquatic vertebrates, especially those living in freshwater, may have been little affected by the K/Pg boundary event (Clemens 1982; Fara 2000); however, this conclusion is based mostly on turtles and crocodilians, which have a much better fossil record.

Our data suggest that lissamphibian biodiversity dropped (but only moderately) at least twice (biological crises before the K/Pg boundary cannot be studied because critical data are lacking): between the Maastrichtian (or possibly the Campanian) and the Danian, and across the Oligocene/Miocene boundary (Fig. 2). Thus, lissamphibians may have been moderately affected by the K/Pg event, and a literal reading of lineages (Fig. 2C) suggests a gradual decline rather than a catastrophic extinction event, although the two other indices suggest a more rapid reduction in diversity consistent with a catastrophic K/Pg event (Fig. 2A, B). The apparently gradual decline in lissamphibian diversity suggested by the lineage count in that interval (Fig. 2C) may also be due to the Signor-Lipps effect (Signor and Lipps 1982), reflecting the relatively scanty fossil record of lissamphibians in the Mesozoic. This interpretation is consistent with the stratigraphic range extension of *Albanerpeton galaktion* from the Campanian to the Maastrichtian (Gardner 2000).

These results give moderate support to our incorporation of major biological crises into the recovery potential function because our data suggest that lissamphibian diversity did not undergo unchecked exponential diversification through time; some periods seem to show at least moderate decline. Our study did not focus on biological crises and we do not want to emphasize our results on how extinction events affected lissamphibians because our database was not primarily compiled for this purpose. We have found limited evidence that, contrary to previous suggestions (Clemens 1982; Archibald and Bryant 1990; Fara 2000), lissamphibians were affected by biological crises, at least by the K/Pg boundary event; however, the effect of this crisis appears to have been modest in this clade, at least by comparison with dinosaurs.

The difference between our results and those of Fara (2000) reflect the taxonomic level at which the studies were performed. Fara (2000) found that all lissamphibian families survived the K/Pg boundary, and we too have found the extinction of only one clade that is sometimes considered a family (Noterpetontidae, not documented in Fara's source: Milner 1993). However, at the species level, the extinction event was more noticeable, with five or six species becoming extinct at or near that boundary. Archibald and Bryant (1990) found few extinctions in lissamphibian species from northeastern Montana at the K/Pg boundary, but a new species from the Maastrichtian of Bolivia (*Noterpeton bolivianum*) was subsequently described (Rage et al. 1993), and the stratigraphic range of *Albanerpeton galaktion* extended (Gardner 2000).

Comparisons with molecular dating of the origin of Lissamphibia.—Those recovery potential functions that best predict the observed number of localities and assume plausible extinction levels of lissamphibians in biological crises (Table 4, CI 1–Cl 4) yield moderately different lower (older) limits on the stratigraphic range of Lissamphibia (Fig. 4), most of which are significantly younger than the results of Zhang et al. (2005). None of the 80% confidence intervals are compatible with the Late Devonian age of Lissamphibia which was the point estimate by San Mauro et al. (2005) and Roelants et al. (2007), or even with the Mississippian age calculated by Zhang et al. (2005). However, the credibility intervals on these molecular dates span the interval from 417 to 328 Ma ago, thus including the entire Devonian and most of the Mississippian (San Mauro et al. 2005). They are even wider if the penalized-likelihood dating by Roelants et al. (2007: online supplementary dataset) is considered; in that analysis, the age of Lissamphibia is estimated at 352 Ma, with a credibility interval which ranges from 370 to 304 Ma ago (a timespan that includes most of the Carboniferous as well as the end of the Devonian). Still, of all confidence intervals, only the 95% confidence interval of CI 4 overlaps these molecular dates (entirely so in the case of Zhang et al. 2005).

All these ancient molecular dates of lissamphibian diversification, which are difficult to reconcile with the fossil record, can be explained by the choice of calibration dates. Zhang et al. (2005) used only two external, ancient calibration points, namely the divergence between dipnomorphs and tetrapodomorphs and the origin of Amniota, which they placed at 400 Ma ago and 300–320 Ma ago, respectively (see Marjanović and Laurin [2007] for a discussion of these dates). Roelants et al. (2007) used 24 calibration dates, including 22 within Lissamphibia, but only two, the origins of crown Tetrapoda (sensu Laurin and Anderson 2004) and Amniota, had estimated upper bounds. All other calibration points, i.e., all those within Lissamphibia, had only minimum (lower) bounds. Such a choice of calibration dates has been found to yield unrealistically ancient dates (Brochu 2004a, b, 2006; Marjanović and Laurin 2007). Furthermore, the upper bound used for Tetrapoda (385 Ma ago) is probably too old; this is the beginning of the Late Devonian (385–359 Ma ago), from which several stem-tetrapods, but no tetrapods, are known (Laurin et al. 2000). A few more stem-tetrapods, some of them closer to the crown-group than all known Devonian ones, have also been found in Tournaisian strata (359–345 Ma old), where tetrapods are so far still unknown, and this suggests that 360 Ma is a more appropriate upper bound for Tetrapoda (Marjanović and Laurin 2007). San Mauro et al. (2005) used Amniota (set at 338–288 Ma ago), Batrachia (at least 230 Ma ago), Cryptobranchoidea (at least 161 Ma ago, but see Wang et al. [2005]), Anura (at least 140 Ma ago), and several more; however, only a single external (Amniota) and a single internal calibration date (the divergence between *Mantidactylus wittei* and *Mantidactylus* sp. from the Comoro islands, not more than 15 Ma ago) had an upper bound. All these factors probably explain the very ancient dates obtained by Zhang et al. (2005) and Roelants et al. (2007), and to a lesser extent those of San Mauro et al. (2005) (since those authors used one internal calibration date with an upper bound). In contrast, the most recent molecular divergence date estimates (Hugall et al. 2007: fig. 5, table 3) approach or include the Permian–Carboniferous boundary (nucleotides: 322 ± 19 Ma ago; amino acids: 292 ± 28 Ma ago) even though its calibration points are all external to Lissamphibia. This may, as Hugall et al. (2007: 552) point out, be due to the fact that nuclear genes were used because "mtDNA divergences typically saturate at these timescales" so that the basal branches of mitochondrial-DNA trees are too short and the other branches too long. However, Hugall et al. (2007) chose no less than five calibration points and used all of them as fixed ages (i.e., they had an upper bound); this probably contributed to yielding reasonable ages.

There is no irreconcilable difference between paleontological and molecular dates. Our own molecular dating which incorporates internal and external calibration dates with lower and (in a few cases) upper bounds yields results compatible with evidence from the fossil record (Marjanović and Laurin 2007). These dates result from a reanalysis of the data of Zhang et al. (2005) using penalized likelihood (Sanderson 2003) and several combinations of calibration dates, of topologies (with mono- or paraphyletic "Archaeobatrachia"), of evolutionary models, and of smoothing factors (the smoothing factor in penalized likelihood determines how much the rates of evolution are allowed to differ between sister-groups). Our results were presented briefly, but because of the complexity and number of the analyses involved (Marjanović and Laurin 2007: table 2 and appendix 10), a summary highlighting our most relevant findings may be useful. The set of calibration dates which yielded the most plausible results included both external (Dipnomorpha–Tetrapodomorpha divergence, fixed at 410 Ma ago, and Amniota, at least 310 Ma ago) and internal calibration dates. The latter included only minimum (lower) bounds in most cases, such as Cryptobranchoidea (at least 140 Ma ago), and, depending on topology, Pipanura (at least 155 Ma ago) or "Archaeobatrachia" (at least 170 Ma ago) and Batrachia or Lissamphibia (both set to at least 250 Ma ago). When the upper bound was reasonably well constrained, we used both upper and and lower bounds, but varied the upper bound to test its impact on the molecular dates. Thus, the age of Urodela was constrained between 155 Ma ago (lower bound) and 170, 185 or 200 Ma ago (upper bound), and the age of Bombinanura was set between 170 Ma ago (lower bound) and 185, 200, or 215 Ma ago (upper bound). These 22 analyses yielded ages of Lissamphibia ranging from 250 to 291 Ma ago, with an average of 272 Ma ago, which suggest a Permian origin for Lissamphibia (Gradstein et al. 2004).

Confidence interval on the origination time of Lissamphibia using the fossil record.—We have tried to compute confidence intervals on the stratigraphic range of Lissamphibia to determine its probable earliest time of appearance based on its fossil record. Because of the numerous assumptions made in these calculations, we do not wish to put too much confidence into these results, although these assumptions are perhaps not more unreasonable than those used for molecular divergence dating (Lee 1999; Shaul and Graur 2002; Brochu 2004a, b; Graur and Martin 2004; Britton 2005). The requirements about the distribution of fossiliferous localities that enable application of the methods proposed by Marshall (1990, 1994, 1997) are severely limiting; none of the proposed methods was entirely suitable for our purpose, although the latest one (Marshall 1997) is adequate when modified as suggested above. The recommendation to use a Kolmogorov-Smirnov goodness-of-fit test for continuous distributions in order to detect deviations between observed and predicted number of localities (Marshall 1997) was proposed for situations in which relatively few localities were known. In Marshall's (1997) example, the species are represented in 10 horizons. Thus, a Kolmogorov-Smirnov test may be too stringent when many localities exist, because significant deviations will almost always be found. For example, the deviations between our various functions and the observed number of localities were always highly significant ($D = 0.11$ to 0.13; $p < 0.0001$) because Lissamphibia is represented by 1207 localities. However, the same value of the D statistic yields non-significant results ($p > 0.05$) with a lower sample of 120 localities, which is still much higher than the cases envisioned by Marshall (1997). When a taxon is present in a large number of horizons, we suggest using regressions (with permutations, if the distribution of observed number of localities is not normal) to verify that the recovery potential function predicts the actual number of localities well. In this case, we suggest that the coefficient of determination (R^2) be examined; even if the relationship is significant ($p < 0.05$), we do not recommend using this method if the R^2 is less than about 0.8 (admittedly an arbitrary threshold). In our case, this method suggests that our recovery potential functions incorporating geological age, an exponential model, and the surface of exposure of sedimentary rocks, are adequate. The other model that uses only the exposure surface is clearly inadequate, as shown by its much lower coefficient of determination in the linear regression. Establishing confidence intervals of stratigraphic ranges of taxa remains an open problem, but this is hardly surprising because much relevant information is usually missing, such as the sampling effort in the field, the exact age of the fossiliferous localities, and the abundance of the relevant taxa in their former biological communities.

The confidence intervals CI 5 and to a lesser extent CI 4 extend deep into the past because our exponential function yields a very low lissamphibian biodiversity in the Paleozoic, ranging from two species in the Viséan (337 Ma ago) or Famennian (368.8 Ma ago) to a maximum of 72 species at the end of the Permian. Thus, despite the fairly extensive Permian exposures, the lissamphibian recovery potential for that period is much smaller than for the Cenozoic, in which lissamphibian diversity has grown (according to our preferred model) from 400 to 6157 species. Other biodiversity models, such as logistic or steady-state models, would have yielded greater biodiversity in the Paleozoic and, hence, much smaller confidence intervals. A steady-state model that can be exemplified by taking only the exposure area of sedimentary rocks into consideration gives ridiculously short confidence intervals (Table 4: CI 6; Fig. 4) and is inconsistent with the evolution of estimated lissamphibian biodiversity using any of the three indices used here (Fig. 2) or with the observed number of localities (Table 3). The model that assumes that lissamphibians were unaffected by all biological crises and diversified exponentially gives an excessively long 75% confidence interval that extends into the Late Devonian in one case and is not calculable in the other (Table 4: CI 5; Fig. 3), yet it fits the observed number of localities almost as well as the other exponential models that incorporate the effect of biological crises, which yield drastically smaller confidence intervals (Table 4: CI 1–CI 4; Fig. 3). Thus, this method is less conclusive (in this case) than obtaining minimum paleontological ages from a time-calibrated supertree (Marjanović and Laurin 2007), but the results obtained by both of these methods, and by our molecular dating (Marjanović and Laurin 2007), are all compatible. Furthermore, we should point out that recent divergence date estimates from molecular data (Zhang et al. 2005; Roelants et al. 2007; Marjanović and Laurin 2007) encompass a similarly large range of dates, ranging from 368.8 to 255 Ma ago.

Other methods could have been used to compute confidence intervals on the origin of Lissamphibia. For instance, Foote et al. (1999) assessed various scenarios on the timing of placental mammal diversification by using a model of diversification which assumes a constant probability of cladogenesis and extinction, and uses only biodiversity at present and at the first time of appearance in the fossil record as input. It might be interesting to test this method using our data, but we preferred using Marshall's (1997) method because it uses all the data on the stratigraphic distribution of the relevant fossils. By contrast, since only two Triassic localites have yielded lissamphibian fossils, the method of Foote et al. (1999) would use only about 0.17% of the available data (2/1207) presented in Appendix 2 (SOM). We expect that discarding over 99.8% of our data would result in wider confidence intervals, although this would have to be verified by applying the method. Furthermore, the assumption of constant diversification and extinction rates required by the method of Foote et al. (1999) may not be realistic over the studied geological timespan, because several mass extinction events may have affected lissamphibians.

The method we use here does not distinguish node-, apomorphy- and branch-based taxa, and hence, the confidence intervals calculated here do not necessarily apply to Lissamphibia (the amphibian crown-group). Marshall (1999) stated that the time of origin that he obtained (for some bird taxa) were "actually the origination time of the first diagnosable synapomorphy". In the case of Lissamphibia, the situation is a little different because the name of this taxon has had a clear phylogenetic meaning for at least a few decades (the amphibian crown-group). However, contrary to molecular divergence dating that clearly dates a cladogenesis, the confidence interval based on stratigraphy could also be conceived of as dating the branch-based taxon that includes Lissamphibia and all unknown extinct taxa that are more closely related to Lissamphibia than to its closest known relatives (lysorophians and/or dissorophoids). In that case, the basal dichotomy in Lissamphibia may be younger than our calculations suggest. Globally, our calculations of the confidence interval on the stratigraphic range of Lissamphibia suggest that this taxon is younger than advocated by San Mauro et al. (2005) and Roelants et al. (2007). However, our calculations give less precise results than a time-calibrated supertree (Marjanović and Laurin 2007) and, under some assumptions on the impact of mass extinction events (Table 4: CI 4–Cl 5), cannot exclude the divergence times inferred by Zhang et al. (2005). Globally, the molecular and the paleontological evidence are most compatible with an origin of Lissamphibia sometime in the Permian, between about 290 and 255 Ma ago.

Acknowledgments

We thank Nathalie Le Roy (CNRS, UMR 7179, Paris, France) and Christopher A. Brochu (University of Iowa, Iowa City, USA) for their helpful comments, as well as Andrzej Elżanowski (Uniwersytet Wrocławski, Wrocław, Poland) and Michael S.Y. Lee (South Australian Museum, Adelaide, Australia) for a fruitful discussion of stylistic issues. An earlier draft of this article was improved by suggestions from Susan Evans (University College London, London, UK), Norman MacLeod (Natural History Museum, London, UK), Roderic Page (University of Glasgow, Glasgow, UK), Jean-Claude Rage (CNRS, UMR 5143, Paris, France), Armand de Ricqlès and Jorge Cubo (both CNRS, UMR 7179, Paris, France), and three anonymous referees. In a later draft, Charles Marshall (University of California, Los Angeles, USA) pointed out errors in some of our initial calculations; as Dave Barry reportedly said, "psychology is really biology, biology is really chemistry, chemistry is really physics, physics is really math, and math is really hard". We are furthermore indebted to Wayne Maddison (University of British Columbia, Vancouver, Canada) and Peter Midford (University of British Columbia, Vancouver, Canada) for their help with the development of the Stratigraphic Tools for Mesquite. Wayne Maddison also updated the Stratigraphic Tools and StratAdd modules to make them compatible with Mesquite 1.1. D. M. benefited from the support granted to university students by the Federal Republic of Austria; M. L. received financial assistance from the CNRS and French Ministry of Research through grants to the UMR (Unité Mixte de Recherche) 7179.

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Appendix 1

List of localities that have yielded lissamphibian fossils

Localities represented by a number instead of a name bear the same number in Sanchíz (1998: 146–180), and this citation is not repeated for them. Correlation of terrestrial deposits across continents is usually difficult. We have kept the original stratigraphic designation of each site (that is, mostly those used by Sanchíz 1998). For the correlation of these, apart from the primary literature, we have relied on Sanchíz (1998: 3) and simplified it. For example, in Sanchíz (1998) the Casamayoran, a South American Land Mammal Age, begins and ends a bit earlier than the Ypresian, an official (Gradstein et al. 2004) stage, does; because we lack evidence to the contrary, we have considered all Casamayoran sites to be Ypresian in age and therefore show them in the same cell. Abbreviations: Fm, Formation.

Geological stage	Number of localities	Duration of stage(s) (Ma)	Name of localities and reference, or locality number in Sanchíz (1998)
Lower Triassic	2	6	108, Czatkowice (Evans and Borsuk-Białynicka 1998)
Pliensbachian or Toarcian	1	14	561
Pliensbachian	1	6.6	367
Toarcian	1	7.4	?896
Bajocian	1	3.9	Upper Bajocian: 348
Bathonian	at least 5	3	Qýzýlsu (Nessov 1988); Upper Bathonian: 543, 1027, 1154

Geological stage	Number of localities	Duration of stage(s) (Ma)	Name of localities and reference, or locality number in Sanchíz (1998)
Upper Bathonian to Callovian, or possibly lower Oxfordian	1	~6.5	70
Callovian to Oxfordian	3	9	585, 653, 1079
Kimmeridgian	3	4.9	Karabastau suite (Milner 2000), Guimarota and Porto Dinheiro (Estes 1981)
Kimmeridgian or Tithonian	1	10.2	846
Tithonian	1	5.3	Lower Purbeck (Ensom et al. 1991)
Lower Cretaceous indet.	4	45.9	157, 380, 465, 788
Berriasian	1	5.3	Anoual (Gardner et al. 2003)
Upper Berriasian or lower Valanginian	1	< 9.1	939
Hauterivian or Barremian	1	11.4	960
Hauterivian	2	6.4	1095, Bernissart (Estes 1981) Not counted: Fengshan (Dabeigou Fm, Hauterivian rather than Barremian according to He et al. 2006)
Barremian	> 6	5	461, 627, Calizas de la Huérguina Fm (McGowan 2002) Lower B.: 347; Barremian-Aptian boundary: all localities of the Yixian Fm
Aptian	>3	13	?327, ?710, all localities of the Jiufotang Fm
Aptian or Albian	3	25.4	34, 536, ?779
Albian	3	12.4	183, Pietraroia (McGowan 2002); Upper Albian: 537
Late Cretaceous indet.	1	34.1	646
Cenomanian	4	6.1	1145, 886 (assuming this is *Avitabatrachus* – Báez et al. 2000); Lower Cenomanian: 538, 953
Turonian	1	< 4.2	Upper Turonian: 289
"Late Turonian to Santonian"	1	<10	547
Coniacian	4	3.5	285, 287, 288; Upper Coniacian: 286
Coniacian to Santonian	1	5.8	472
Santonian	1	< 2.3	Lower Santonian: 516
Santonian to Campanian	1	15.2	534
Campanian or Maastrichtian	3	18	15, 23, 797
Campanian	6	12.9	18, 346, 501, 1135; Upper Campanian: 337, 338
Upper Campanian or lower Maastrichtian	1	< 18	664
Maastrichtian	11	5.1	46, 203, 335, 359, 433, 591, 718, 816, 940, Pajcha Pata (Gayet et al. 2001); Upper Maastrichtian: 588
Maastrichtian and Danian hopelessly mixed	1	8.9	147
"undetermined Tertiary"	1	63.694	447
Paleocene indet.	1	9.7	586
Danian/"Lower Paleocene"	5	3.8	?410, 845, 1055; Puercan: 1087; Torrejonian: 1063
Selandian/"Middle Paleocene"	3	3	323; Riochican: 485; Tiffanian: 328
Thanetian/"Upper Paleocene"	5	2.9	584, 708, Naran-Bulak Suite (Gubin 1991), Ravenscrag Fm (Estes 1981); MP6: 185
Eocene or Oligocene	2	32.77	184, 798
Eocene indet.	4	21.9	11, ?349, 630, 686
Ypresian/"Lower Eocene"	9	7.2	?130, 952, 1176, 1182; Casamayoran: 170, 808; MP7: 273, 971; MP10: 1222
Lutetian	13	8.2	Mustersan: 780; Bridgerian: 1028; "Middle Eocene": 80, 372; MP11: 667; MP11–13: 351; MP13: 53; Uintan: 320, 353, 424, 833, 863, 996
Upper Eocene or Oligocene	1	14.87	73
Upper Eocene or lower Oligocene	1	12	763
Upper Eocene indet.	4	6.5	98, 223, 1099, 1181
Bartonian	6	3.2	Duchesnean: ?242; "Duchesnean or Chadronian": 1056; MP16: 137, 383, 595, 893
Priabonian	22	3.3/4	MP17: 51, 128, 427, ?428, ?429, 430, 451, 598, 635, 803, 834, 905, ?1073, Hordle Cliff (Holman and Harrison 2003); MP18: 373, 915; MP19: 213, 311, 431, 904, 975; MP20: 1168

Geological stage	Number of localities	Duration of stage(s) (Ma)	Name of localities and reference, or locality number in Sanchíz (1998)
Oligocene or Miocene	3	28.568	633, 755, 768
Oligocene indet.	5	10.87	60, 324, 821, 826, 1059
Chadronian	1	6	?473
Rupelian	24	5.5	78, 165, 306, 463, 490, 575, 691, ?965, ?1105, 1109, 1121; MP21: 444, 449, 862, 902, 999; MP22: 647, 681; MP23: 191, 486, 791; Orellan: 319; Whitneyan: 344
“Middle Oligocene”	3	10.87	151, 416, 579
Chattian	19	5.37	95, 397, 399, 774, 1040, 1199; MP27: 129; MP28: 303, 343, 790; MP29: 682; Deseadan: 881, 921; MP30: 214, 764, 906, 1010; “uppermost Oligocene”: 642; Arikareean: 811
“Neogene indet.” = Miocene or Pliocene	13	21.224	507, 616, 632, 758, 819, 857, 868, 869, 887, 934, 1083, 1093, 1108
“late Oligocene or early Miocene”	4	< 12.43	400, 435, 890, 1163
“Oligocene-Miocene boundary”	11	very little	153, ?511, 557, 573, 619, 674; MN0: 442, 748, 1022, 1118, 1207
Miocene indet.	8	17.698	8, 123, 180, ?364, 527, 572, 706, 1074
“Lower or middle Miocene”	1	11.422	1191
Lower Miocene indet.	15	7.06	14, 145, 300, 321, 497, 590; Arikareean: 161, 162, 644, 655, 1184; Agenian or Orléanian: 411, 483, 509, 767
Agenian	14	maybe 3	24, ?88, 375; MN1: 786, 1157, 1158; MN1–2: 759, 877, 1062; MN2: 422, 594, 1094; MN2a: 916; MN2b: 721
Burdigalian	30	4.46 or more	?626; MN3: 462, 663, 719, 987, 1014, 1066; MN4: 20, 271, 861, 900, 908, 1104; MN4a: 44, 149; MN4b: 227, 1020; MN4–5: 1125; MN5: 97, 333, ?393, 818, 856, 1002; Shanwangian: 951; Hemingfordian: 1052; Colhuehuapian: 187, 216; Santacrucian: 883, 884
Burdigalian or middle Miocene (“late Orléanian or early Astaracian”)	2	< 8.822	MN5–6: 702; MN5–7: 22
Middle Miocene	53	4.362	168; Barstovian: 29, 116, 215, 295, 361, 363, 458, 550, 736, 740, 852, 898, 1078; Friasian: 392, 476, 583, 1113; Tunggurian: ?1188; Astaracian: MN6: 265, 282, 334, 637, 933, 936, 1071; MN6-8: 7, 50, ?107, 109, Hasznos, Szentendre, Sámsonháza 3,; Mátraszőlős 1, M. 2, Felsőtárkány 1, F. 3/2 (Venczel 2004); MN7: 100, 386; MN7–8: 186, 312, 624, 750, 761, 840, 937, 1007, ?1129; MN8: 217, 385, 549; “Upper Astaracian”: 994
Middle or upper Miocene	22	?4	891; Friasian or Chasicoan: 77; Barstovian or Clarendonian: 301; Clarendonian: 113, 374, 615, 679, 1137, 1149; Vallesian: ?605; MN9: 28, 55, 169, 384, 1070, 1107; MN9–10: 159, 576; MN10: 27, 600, 652, 1018
Upper Miocene	60	6.276	503, 1186; “Vallesian-Turolian”:787; “Upper Vallesian or middle Turolian”: MN 10-12: 1069; Turolian: MN11: 10, 47, 243, 267, 567, 744, 800, 909, 1103, 1140; MN11-13: 206, 247, 326, 684; MN12: 21, 221, 222, 240, 249, 639, 650, 742, 810, 938, 1034, 1080; MN12–13: 194, 976; MN13: 30, ?40, 140, 241, 299, 339, 640, 651, 683, 825, 922, 1102, 1114; Hemphillian: 264, 278, 294, ?318, 408, 603, 613, 625, 832, 859, 874, 899, 941, 1178, 1193
Upper Miocene and/or Pliocene	5	9.802	195, 398, 753; “Upper Miocene or lower Pliocene”: 230, 310
Pliocene indet.	14	3.562	112, ?518, 544, 1160; Ruscinian or Villanyian: MN14–16: 1172; Blancan: 89, 102, 114, 331, 404, 452, 873, 930, 1167
“Lower Pliocene”	31	2.744	Montehermosan: 229, 481, 688, 848; Ruscinian: MN14: 17, 629, 769, 799, 820, 841; MN14–15: 174, 520, 570, 1126; MN15: 41, 167, 228, 245, 315, 369, 489, ?510, 562, 596, 749, 842, 942, 948, 949, 1000, 1165
“Middle or upper Pliocene”	1	1.794	648
“Upper Pliocene”	37	0.782	556, 589, 814, 1225, 1227, 1229, 1230; Youhean: 150; Chapadmalalan: 844; Villanyian: 545, ?1092; MN16: 39, 67, 68, 103, 105, 201, 313, 345, ?370, 395, 412, 657, 738, 864, 879, 1075, 1077, 1166, 1198; MN16–17: 1110; MN17: 504, 610, 694, 712, 1130, 1132
“Upper Pliocene or Pleistocene”	2	2.5765	989, 1015
“Pliocene-Pleistocene boundary”/”Upper Pliocene or Lower Pleistocene”	7	1.807	71, 136, 322, 519, 568, 796, 1133
Pleistocene and/or Holocene	9	1.806	261, 263, 620, 666, 737, 782, 885, 978; “Lower Pleistocene to Holocene”: 355

Geological stage	Number of localities	Duration of stage(s) (Ma)	Name of localities and reference, or locality number in Sanchíz (1998)
Pleistocene indet.	62	1.7945	19, 38, 117, 199, 220, 248, 259, 293, 389, 443, 502, 505, 513, 517, 521, 529, 530, 531, 532, 533, 553, 554, ?559, 566, 569, 582, 629, 634, 654, 660, 662, 678, 680, 689, 701, 709, 730, 751, 802, 809, 815, 827, 912, 927, 944, 957, 959, 964, 966, 973, 977, 1004, 1049, 1050, 1058, 1106, 1123, 1156, 1164, 1185, 1205, 1211, 1213
Lower and/or middle Pleistocene	4	1.68	467, 614, 1086, 1203
Lower Pleistocene	62	1.025	57, 84, 91, 104, 106, 118, 181, 188, 202, 234, 246, ?283, 358, 366, 418, 445, 446, 478, 482, 496, 512, 539, 541, 558, 560, 563, 581, 602, 612, 649, 713, 714, 746, 754, 764, 871, 925, 946, 979, 984, 993, 1013, 1017, 1041, 1084, 1085, 1098, 1115, 1131, 1134, 1142, 1155, 1171, 1189, 1194, 1197, 1200, 1206, 1214, 1215, 1226, 1228
Middle and/or upper Pleistocene	9	0.7695	42, 276, 407, 450, 687, 995, 1036, 1047, 1170
Middle Pleistocene to Holocene	1	0.781	597
Middle Pleistocene	81	0.655	1, 9, 16, 25, 37, 43, 63, ?66, 76, 90, 127, 132, 152, 158, 198, 219, 250, 251, 253, 268, 271, 280, 281, 291, 302, 307, 329, 341, 365, 376, 379, 396, 413, 419, 421, 440, 455, 460, 479, 515, 526, 593, 606, 618, 685, 690, 693, 700, 717, 725, 747, 757, 762, 801, 828, 829, 851, 865, 876, 931, 982, 988, 997, 1001, 1005, 1006, 1019, 1021, 1024, 1044, 1064, 1076, 1096, 1117, 1128, 1141, 1161, 1162, 1175, 1192, 1221
Upper Pleistocene	206	0.1145	2, 12, 35, 56, 59, 61, 64, 65, 72, 75, 81, 82, 87, 96, 115, 120, 121, 122, 125, 126, 135, 139, 146, 154, 156, 164, 172, 176, 178, 182, 193, 204, 205, 207, 208, 210, 211, 218, 231, 232, 235, 238, 239, 252, 254, 257, 258, 270, 277, 279, 290, 292, 297, 305, 308, 317, 330, 332, 336, 342, 352, 354, 360, 368, 382, 387, 390, 394, 401, 402, 409, 415, 426, 434, 437, 439, 464, 469, 470, 477, 480, 484, 487, 488, 491, 492, 494, 495, 498, 499, 522, 523, 525, 542, 551, 555, 578, 580, 587, 601, 604, 607, 617, 621, 631, 641, 659, 661, 665, 671, 672, 673, 675, 677, 696, 697, 704, 716, 720, 724, 728, 729, 731, 732, 734, 735, 739, 743, 745, 756, 776, 777, 871, 789, 793, 794, 795, 805, 824, 830, 831, 835, 836, 838, 839, 855, 866, 867, 882, 894, 897, 901, 910, 911, 923, 926, 928, 929, 932, 947, 955, 956, 961, 962, 972, 974, 980, 981, 983, 985, 990, 998, 1003, 1008, 1009, 1011, 1012, 1025, 1026, 1029, 1035, 1038, 1046, 1048, 1053, 1057, 1068, 1088, 1091, 1097, 1100, 1112, 1124, 1127, 1139, 1153, 1173, 1177, 1183, 1195, 1196, 1202, 1204, 1208, 1210, 1217
Upper Pleistocene and/or Holocene	61	0.126	36, 45, 58, 69, 99, 141, 148, 155, 177, 196, 200, 224, 226, 275, 340, 350, 423, 438, 448, 459, 528, 540, 622, 623, 636, 656, 668, 676, 705, 722, 766, 773, 804, 806, 813, 817, 853, 854, 858, 870, 880, 945, 969, 991, 1039, 1042, 1045, 1090, 1116, 1120, 1122, 1147, 1179, 1180, 1187, 1190, 1201, 1212, 1216, 1224; “Pleistocene-Holocene boundary”: 1089
Holocene	189	0.0115	3, 4, 5, 6, 26, 31, 32, 33, 52, 54, 57, 62, 74, 79, 83, 85, 86, 92, 94, 101, 110, 111, 124, 131, 134, 138, 143, 144, 160, 163, 166, 171, 173, 175, 179, 189, 190, 192, 209, 225, 236, 237, 244, 255, 256, 260, 262, 266, 269, 274, 284, 298, 304, 309, 314, 316, 325, 356, 357, 362, 377, 378, 381, 388, 391, 403, 405, 406, 414, 417, 420, 425, 432, 436, 441, 453, 454, 456, 457, 466, 468, 471, 474, 475, 493, 500, 506, 524, 535, 546, 548, 552, 565, 571, 574, 592, 599, 611, 638, 643, 645, 658, 669, 670, 692, 695, 698, 699, 707, 711, 715, 723, 726, 727, 733, 741, 752, 760, 770, 771, 772, 775, 778, 783, 784, 785, 807, 812, 822, 823, 837, 843, 847, 849, 850, 860, 872, 875, 878, 888, 892, 895, 903, 907, 913, 914, 917, 919, 920, 954, 958, 967, 968, 970, 986, 992, 1016, 1023, 1030, 1031, 1032, 1033, 1037, 1051, 1054, 1061, 1065, 1067, 1072, 1081, 1101, 1111, 1119, 1136, 1138, 1143, 1144, 1146, 1148, 1150, 1151, 1152, 1159, 1169, 1174, 1218, 1219, 1220, 1223

Appendix 2

Localities ordered in geological time, along with inferred stratigraphic gap between localities. Superscript numbers indicate the first locality in each geological stage.

Locality number (1–1207)	Geological age (Ma)	Gap between localities (between localities n and n+1)
1[1]	251	3
2	248	51.5
3[2]	196.5	6.9
4	189.6	7
5	182.6	7
6	175.6	4
7	171.6	3.9
8	167.7	0.6
9	167.1	0.6
10	166.5	0.6
11	165.9	0.6
12	165.3	0.6
13	164.7	3
14	161.7	3
15	158.7	3
16	155.7	1.633
17	154.067	1.633
18	152.434	1.634
19	150.8	0.2
20	150.6	5.1
21[3]	145.5	2.65
22	142.85	2.65
23	140.2	6.175
24	134.025	0.825
25	133.2	3.2
26	130	0.625
27	129.375	0.625
28	128.75	0.625
29	128.125	0.625
30	127.5	0.625
31	126.875	0.625
32	126.25	0.625
33	125.625	0.625
34	125	2.166
35	122.834	2.166
36	120.668	2.167
37	118.501	2.167
38	116.334	2.167
39	114.167	2.167
40	112	3.1
41	108.9	3.1
42	105.8	3.1
43	102.7	3.1
44	99.6	1.525[4]
45	98.075	1.525
46	96.55	1.525
47	95.025	1.525
48	93.5	2.1
49	91.4	2.1
50	89.3	0.7
51	88.6	0.7
52	87.9	0.7
53	87.2	0.7
54	86.5	0.7
55	85.8	1.15
56	84.65	1.15
57	83.5	1.29
58	82.21	1.29
59	80.92	1.29
60	79.63	1.29
61	78.34	1.29
62	77.05	1.29
63	75.76	1.29
64	74.47	1.29
65	73.18	1.29
66	71.89	1.29
67	70.6	0.425
68	70.175	0.425
69	69.75	0.425
70	69.325	0.425
71	68.9	0.425
72	68.475	0.425
73	68.05	0.425
74	67.625	0.425
75	67.2	0.425
76	66.775	0.425
77	66.35	0.425
78	65.925	0.425
79[5]	65.5	0.633333333
80	64.86666667	0.633333333
81	64.23333333	0.633333333
82	63.6	0.633333333
83	62.96666667	0.633333333
84	62.33333333	0.633333333
85	61.7	0.75
86	60.95	0.75
87	60.2	0.75
88	59.45	0.75
89	58.7	0.58
90	58.12	0.58
91	57.54	0.58
92	56.96	0.58
93	56.38	1.3
94[6]	55.08	0.72
95	54.36	0.72
96	53.64	0.72
97	52.92	0.72
98	52.2	0.72
99	51.48	0.72
100	50.76	0.72
101	50.04	0.72
102	49.32	0.72
103	48.6	0.546666667
104	48.05333333	0.546666667
105	47.50666667	0.546666667
106	46.96	0.546666667
107	46.41333333	0.546666667
108	45.86666667	0.546666667

Locality number (1–1207)	Geological age (Ma)	Gap between localities (between localities n and n+1)
109	45.32	0.546666667
110	44.77333333	0.546666667
111	44.22666667	0.546666667
112	43.68	0.546666667
113	43.13333333	0.546666667
114	42.58666667	0.546666667
115	42.04	0.546666667
116	41.49333333	0.546666667
117	40.94666667	0.546666667
118	40.4	0.4
119	40	0.4
120	39.6	0.4
121	39.2	0.4
122	38.8	0.4
123	38.4	0.4
124	38	0.4
125	37.6	0.4
126	37.2	0.058928571
127	37.14107143	0.058928571
128	37.08214286	0.058928571
129	37.02321429	0.058928571
130	36.96428571	0.058928571
131	36.90535714	0.058928571
132	36.84642857	0.058928571
133	36.7875	0.058928571
134	36.72857143	0.058928571
135	36.66964286	0.058928571
136	36.61071429	0.058928571
137	36.55178571	0.058928571
138	36.49285714	0.058928571
139	36.43392857	0.058928571
140	36.375	0.275
141	36.1	0.275
142	35.825	0.275
143	35.55	0.165
144	35.385	0.165
145	35.22	0.165
146	35.055	0.165
147	34.89	0.165
148	34.725	0.4125
149	34.3125	0.4125
150[7]	33.9	0.171875
151	33.728125	0.171875
152	33.55625	0.171875
153	33.384375	0.171875
154	33.2125	0.171875
155	33.040625	0.171875
156	32.86875	0.171875
157	32.696875	0.171875
158	32.525	0.171875
159	32.353125	0.171875
160	32.18125	0.171875
161	32.009375	0.171875
162	31.8375	0.171875
163	31.665625	0.171875
164	31.49375	0.171875
165	31.321875	0.171875
166	31.15	0.171875
167	30.978125	0.171875
168	30.80625	0.171875
169	30.634375	0.171875
170	30.4625	0.171875
171	30.290625	0.171875
172	30.11875	0.171875
173	29.946875	0.171875
174	29.775	0.171875
175	29.603125	0.171875
176	29.43125	0.171875
177	29.259375	0.171875
178	29.0875	0.171875
179	28.915625	0.171875
180	28.74375	0.171875
181	28.571875	0.171875
182	28.4	0.157941176
183	28.24205882	0.157941176
184	28.08411765	0.157941176
185	27.92617647	0.157941176
186	27.76823529	0.157941176
187	27.61029412	0.157941176
188	27.45235294	0.157941176
189	27.29441176	0.157941176
190	27.13647059	0.157941176
191	26.97852941	0.157941176
192	26.82058824	0.157941176
193	26.66264706	0.157941176
194	26.50470588	0.157941176
195	26.34676471	0.157941176
196	26.18882353	0.157941176
197	26.03088235	0.157941176
198	25.87294118	0.157941176
199	25.715	0.157941176
200	25.55705882	0.157941176
201	25.39911765	0.157941176
202	25.24117647	0.157941176
203	25.08323529	0.157941176
204	24.92529412	0.157941176
205	24.76735294	0.157941176
206	24.60941176	0.157941176
207	24.45147059	0.157941176
208	24.29352941	0.157941176
209	24.13558824	0.157941176
210	23.97764706	0.157941176
211	23.81970588	0.157941176
212	23.66176471	0.157941176
213	23.50382353	0.157941176
214	23.34588235	0.157941176
215	23.18794118	0.157941176
216[8]	23.03	0.072222222
217	22.95777778	0.072222222
218	22.88555556	0.072222222
219	22.81333333	0.072222222
220	22.74111111	0.072222222
221	22.66888889	0.072222222
222	22.59666667	0.072222222
223	22.52444444	0.072222222
224	22.45222222	0.072222222
225	22.38	0.072222222
226	22.30777778	0.072222222

Locality number (1–1207)	Geological age (Ma)	Gap between localities (between localities n and n+1)
227	22.23555556	0.072222222
228	22.16333333	0.072222222
229	22.09111111	0.072222222
230	22.01888889	0.072222222
231	21.94666667	0.072222222
232	21.87444444	0.072222222
233	21.80222222	0.072222222
234	21.73	0.072222222
235	21.65777778	0.072222222
236	21.58555556	0.072222222
237	21.51333333	0.072222222
238	21.44111111	0.072222222
239	21.36888889	0.072222222
240	21.29666667	0.072222222
241	21.22444444	0.072222222
242	21.15222222	0.072222222
243	21.08	0.072222222
244	21.00777778	0.072222222
245	20.93555556	0.072222222
246	20.86333333	0.072222222
247	20.79111111	0.072222222
248	20.71888889	0.072222222
249	20.64666667	0.072222222
250	20.57444444	0.072222222
251	20.50222222	0.072222222
252	20.43	0.10372093
253	20.32627907	0.10372093
254	20.22255814	0.10372093
255	20.11883721	0.10372093
256	20.01511628	0.10372093
257	19.91139535	0.10372093
258	19.80767442	0.10372093
259	19.70395349	0.10372093
260	19.60023256	0.10372093
261	19.49651163	0.10372093
262	19.3927907	0.10372093
263	19.28906977	0.10372093
264	19.18534884	0.10372093
265	19.08162791	0.10372093
266	18.97790698	0.10372093
267	18.87418605	0.10372093
268	18.77046512	0.10372093
269	18.66674419	0.10372093
270	18.56302326	0.10372093
271	18.45930233	0.10372093
272	18.3555814	0.10372093
273	18.25186047	0.10372093
274	18.14813953	0.10372093
275	18.0444186	0.10372093
276	17.94069767	0.10372093
277	17.83697674	0.10372093
278	17.73325581	0.10372093
279	17.62953488	0.10372093
280	17.52581395	0.10372093
281	17.42209302	0.10372093
282	17.31837209	0.10372093
283	17.21465116	0.10372093
284	17.11093023	0.10372093
285	17.0072093	0.10372093
286	16.90348837	0.10372093
287	16.79976744	0.10372093
288	16.69604651	0.10372093
289	16.59232558	0.10372093
290	16.48860465	0.10372093
291	16.38488372	0.10372093
292	16.28116279	0.10372093
293	16.17744186	0.10372093
294	16.07372093	0.10372093
295	15.97	0.071508197
296	15.8984918	0.071508197
297	15.82698361	0.071508197
298	15.75547541	0.071508197
299	15.68396721	0.071508197
300	15.61245902	0.071508197
301	15.54095082	0.071508197
302	15.46944262	0.071508197
303	15.39793443	0.071508197
304	15.32642623	0.071508197
305	15.25491803	0.071508197
306	15.18340984	0.071508197
307	15.11190164	0.071508197
308	15.04039344	0.071508197
309	14.96888525	0.071508197
310	14.89737705	0.071508197
311	14.82586885	0.071508197
312	14.75436066	0.071508197
313	14.68285246	0.071508197
314	14.61134426	0.071508197
315	14.53983607	0.071508197
316	14.46832787	0.071508197
317	14.39681967	0.071508197
318	14.32531148	0.071508197
319	14.25380328	0.071508197
320	14.18229508	0.071508197
321	14.11078689	0.071508197
322	14.03927869	0.071508197
323	13.96777049	0.071508197
324	13.8962623	0.071508197
325	13.8247541	0.071508197
326	13.7532459	0.071508197
327	13.6817377	0.071508197
328	13.61022951	0.071508197
329	13.53872131	0.071508197
330	13.46721311	0.071508197
331	13.39570492	0.071508197
332	13.32419672	0.071508197
333	13.25268852	0.071508197
334	13.18118033	0.071508197
335	13.10967213	0.071508197
336	13.03816393	0.071508197
337	12.96665574	0.071508197
338	12.89514754	0.071508197
339	12.82363934	0.071508197
340	12.75213115	0.071508197
341	12.68062295	0.071508197
342	12.60911475	0.071508197
343	12.53760656	0.071508197
344	12.46609836	0.071508197

Locality number (1–1207)	Geological age (Ma)	Gap between localities (between localities n and n+1)
345	12.39459016	0.071508197
346	12.32308197	0.071508197
347	12.25157377	0.071508197
348	12.18006557	0.071508197
349	12.10855738	0.071508197
350	12.03704918	0.071508197
351	11.96554098	0.071508197
352	11.89403279	0.071508197
353	11.82252459	0.071508197
354	11.75101639	0.071508197
355	11.6795082	0.071508197
356	11.608	0.089657143
357	11.51834286	0.089657143
358	11.42868571	0.089657143
359	11.33902857	0.089657143
360	11.24937143	0.089657143
361	11.15971429	0.089657143
362	11.07005714	0.089657143
363	10.9804	0.089657143
364	10.89074286	0.089657143
365	10.80108571	0.089657143
366	10.71142857	0.089657143
367	10.62177143	0.089657143
368	10.53211429	0.089657143
369	10.44245714	0.089657143
370	10.3528	0.089657143
371	10.26314286	0.089657143
372	10.17348571	0.089657143
373	10.08382857	0.089657143
374	9.994171429	0.089657143
375	9.904514286	0.089657143
376	9.814857143	0.089657143
377	9.7252	0.089657143
378	9.635542857	0.089657143
379	9.545885714	0.089657143
380	9.456228571	0.089657143
381	9.366571429	0.089657143
382	9.276914286	0.089657143
383	9.187257143	0.089657143
384	9.0976	0.089657143
385	9.007942857	0.089657143
386	8.918285714	0.089657143
387	8.828628571	0.089657143
388	8.738971429	0.089657143
389	8.649314286	0.089657143
390	8.559657143	0.089657143
391	8.47	0.089657143
392	8.380342857	0.089657143
393	8.290685714	0.089657143
394	8.201028571	0.089657143
395	8.111371429	0.089657143
396	8.021714286	0.089657143
397	7.932057143	0.089657143
398	7.8424	0.089657143
399	7.752742857	0.089657143
400	7.663085714	0.089657143
401	7.573428571	0.089657143
402	7.483771429	0.089657143
403	7.394114286	0.089657143
404	7.304457143	0.089657143
405	7.2148	0.089657143
406	7.125142857	0.089657143
407	7.035485714	0.089657143
408	6.945828571	0.089657143
409	6.856171429	0.089657143
410	6.766514286	0.089657143
411	6.676857143	0.089657143
412	6.5872	0.089657143
413	6.497542857	0.089657143
414	6.407885714	0.089657143
415	6.318228571	0.089657143
416	6.228571429	0.089657143
417	6.138914286	0.089657143
418	6.049257143	0.089657143
419	5.9596	0.089657143
420	5.869942857	0.089657143
421	5.780285714	0.089657143
422	5.690628571	0.089657143
423	5.600971429	0.089657143
424	5.511314286	0.089657143
425	5.421657143	0.089657143
426[9]	5.332	0.05488
427	5.27712	0.05488
428	5.22224	0.05488
429	5.16736	0.05488
430	5.11248	0.05488
431	5.0576	0.05488
432	5.00272	0.05488
433	4.94784	0.05488
434	4.89296	0.05488
435	4.83808	0.05488
436	4.7832	0.05488
437	4.72832	0.05488
438	4.67344	0.05488
439	4.61856	0.05488
440	4.56368	0.05488
441	4.5088	0.05488
442	4.45392	0.05488
443	4.39904	0.05488
444	4.34416	0.05488
445	4.28928	0.05488
446	4.2344	0.05488
447	4.17952	0.05488
448	4.12464	0.05488
449	4.06976	0.05488
450	4.01488	0.05488
451	3.96	0.05488
452	3.90512	0.05488
453	3.85024	0.05488
454	3.79536	0.05488
455	3.74048	0.05488
456	3.6856	0.05488
457	3.63072	0.05488
458	3.57584	0.05488
459	3.52096	0.05488
460	3.46608	0.05488
461	3.4112	0.05488
462	3.35632	0.05488

Locality number (1–1207)	Geological age (Ma)	Gap between localities (between localities n and n+1)
463	3.30144	0.05488
464	3.24656	0.05488
465	3.19168	0.05488
466	3.1368	0.05488
467	3.08192	0.05488
468	3.02704	0.05488
469	2.97216	0.05488
470	2.91728	0.05488
471	2.8624	0.05488
472	2.80752	0.05488
473	2.75264	0.05488
474	2.69776	0.05488
475	2.64288	0.05488
476	2.588	0.017
477	2.571	0.017
478	2.554	0.017
479	2.537	0.017
480	2.52	0.017
481	2.503	0.017
482	2.486	0.017
483	2.469	0.017
484	2.452	0.017
485	2.435	0.017
486	2.418	0.017
487	2.401	0.017
488	2.384	0.017
489	2.367	0.017
490	2.35	0.017
491	2.333	0.017
492	2.316	0.017
493	2.299	0.017
494	2.282	0.017
495	2.265	0.017
496	2.248	0.017
497	2.231	0.017
498	2.214	0.017
499	2.197	0.017
500	2.18	0.017
501	2.163	0.017
502	2.146	0.017
503	2.129	0.017
504	2.112	0.017
505	2.095	0.017
506	2.078	0.017
507	2.061	0.017
508	2.044	0.017
509	2.027	0.017
510	2.01	0.017
511	1.993	0.017
512	1.976	0.017
513	1.959	0.017
514	1.942	0.017
515	1.925	0.017
516	1.908	0.017
517	1.891	0.017
518	1.874	0.017
519	1.857	0.017
520	1.84	0.017
521	1.823	0.017
522[10]	1.806	0.011141304
523	1.794858696	0.011141304
524	1.783717391	0.011141304
525	1.772576087	0.011141304
526	1.761434783	0.011141304
527	1.750293478	0.011141304
528	1.739152174	0.011141304
529	1.72801087	0.011141304
530	1.716869565	0.011141304
531	1.705728261	0.011141304
532	1.694586957	0.011141304
533	1.683445652	0.011141304
534	1.672304348	0.011141304
535	1.661163043	0.011141304
536	1.650021739	0.011141304
537	1.638880435	0.011141304
538	1.62773913	0.011141304
539	1.616597826	0.011141304
540	1.605456522	0.011141304
541	1.594315217	0.011141304
542	1.583173913	0.011141304
543	1.572032609	0.011141304
544	1.560891304	0.011141304
545	1.54975	0.011141304
546	1.538608696	0.011141304
547	1.527467391	0.011141304
548	1.516326087	0.011141304
549	1.505184783	0.011141304
550	1.494043478	0.011141304
551	1.482902174	0.011141304
552	1.47176087	0.011141304
553	1.460619565	0.011141304
554	1.449478261	0.011141304
555	1.438336957	0.011141304
556	1.427195652	0.011141304
557	1.416054348	0.011141304
558	1.404913043	0.011141304
559	1.393771739	0.011141304
560	1.382630435	0.011141304
561	1.37148913	0.011141304
562	1.360347826	0.011141304
563	1.349206522	0.011141304
564	1.338065217	0.011141304
565	1.326923913	0.011141304
566	1.315782609	0.011141304
567	1.304641304	0.011141304
568	1.2935	0.011141304
569	1.282358696	0.011141304
570	1.271217391	0.011141304
571	1.260076087	0.011141304
572	1.248934783	0.011141304
573	1.237793478	0.011141304
574	1.226652174	0.011141304
575	1.21551087	0.011141304
576	1.204369565	0.011141304
577	1.193228261	0.011141304
578	1.182086957	0.011141304
579	1.170945652	0.011141304
580	1.159804348	0.011141304

Locality number (1–1207)	Geological age (Ma)	Gap between localities (between localities n and n+1)
581	1.148663043	0.011141304
582	1.137521739	0.011141304
583	1.126380435	0.011141304
584	1.11523913	0.011141304
585	1.104097826	0.011141304
586	1.092956522	0.011141304
587	1.081815217	0.011141304
588	1.070673913	0.011141304
589	1.059532609	0.011141304
590	1.048391304	0.011141304
591	1.03725	0.011141304
592	1.026108696	0.011141304
593	1.014967391	0.011141304
594	1.003826087	0.011141304
595	0.992684783	0.011141304
596	0.981543478	0.011141304
597	0.970402174	0.011141304
598	0.95926087	0.011141304
599	0.948119565	0.011141304
600	0.936978261	0.011141304
601	0.925836957	0.011141304
602	0.914695652	0.011141304
603	0.903554348	0.011141304
604	0.892413043	0.011141304
605	0.881271739	0.011141304
606	0.870130435	0.011141304
607	0.85898913	0.011141304
608	0.847847826	0.011141304
609	0.836706522	0.011141304
610	0.825565217	0.011141304
611	0.814423913	0.011141304
612	0.803282609	0.011141304
613	0.792141304	0.011141304
614	0.781	0.005954545
615	0.775045455	0.005954545
616	0.769090909	0.005954545
617	0.763136364	0.005954545
618	0.757181818	0.005954545
619	0.751227273	0.005954545
620	0.745272727	0.005954545
621	0.739318182	0.005954545
622	0.733363636	0.005954545
623	0.727409091	0.005954545
624	0.721454545	0.005954545
625	0.7155	0.005954545
626	0.709545455	0.005954545
627	0.703590909	0.005954545
628	0.697636364	0.005954545
629	0.691681818	0.005954545
630	0.685727273	0.005954545
631	0.679772727	0.005954545
632	0.673818182	0.005954545
633	0.667863636	0.005954545
634	0.661909091	0.005954545
635	0.655954545	0.005954545
636	0.65	0.005954545
637	0.644045455	0.005954545
638	0.638090909	0.005954545
639	0.632136364	0.005954545
640	0.626181818	0.005954545
641	0.620227273	0.005954545
642	0.614272727	0.005954545
643	0.608318182	0.005954545
644	0.602363636	0.005954545
645	0.596409091	0.005954545
646	0.590454545	0.005954545
647	0.5845	0.005954545
648	0.578545455	0.005954545
649	0.572590909	0.005954545
650	0.566636364	0.005954545
651	0.560681818	0.005954545
652	0.554727273	0.005954545
653	0.548772727	0.005954545
654	0.542818182	0.005954545
655	0.536863636	0.005954545
656	0.530909091	0.005954545
alpha657	0.524954545	0.005954545
658	0.519	0.005954545
659	0.513045455	0.005954545
660	0.507090909	0.005954545
661	0.501136364	0.005954545
662	0.495181818	0.005954545
663	0.489227273	0.005954545
664	0.483272727	0.005954545
665	0.477318182	0.005954545
666	0.471363636	0.005954545
667	0.465409091	0.005954545
668	0.459454545	0.005954545
669	0.4535	0.005954545
670	0.447545455	0.005954545
671	0.441590909	0.005954545
672	0.435636364	0.005954545
673	0.429681818	0.005954545
674	0.423727273	0.005954545
675	0.417772727	0.005954545
676	0.411818182	0.005954545
677	0.405863636	0.005954545
678	0.399909091	0.005954545
679	0.393954545	0.005954545
680	0.388	0.005954545
681	0.382045455	0.005954545
682	0.376090909	0.005954545
683	0.370136364	0.005954545
684	0.364181818	0.005954545
685	0.358227273	0.005954545
686	0.352272727	0.005954545
687	0.346318182	0.005954545
688	0.340363636	0.005954545
689	0.334409091	0.005954545
690	0.328454545	0.005954545
691	0.3225	0.005954545
692	0.316545455	0.005954545
693	0.310590909	0.005954545
694	0.304636364	0.005954545
695	0.298681818	0.005954545
696	0.292727273	0.005954545
697	0.286772727	0.005954545
698	0.280818182	0.005954545

Locality number (1–1207)	Geological age (Ma)	Gap between localities (between localities n and n+1)
699	0.274863636	0.005954545
700	0.268909091	0.005954545
701	0.262954545	0.005954545
702	0.257	0.005954545
703	0.251045455	0.005954545
704	0.245090909	0.005954545
705	0.239136364	0.005954545
706	0.233181818	0.005954545
707	0.227227273	0.005954545
708	0.221272727	0.005954545
709	0.215318182	0.005954545
710	0.209363636	0.005954545
711	0.203409091	0.005954545
712	0.197454545	0.005954545
713	0.1915	0.005954545
714	0.185545455	0.005954545
715	0.179590909	0.005954545
716	0.173636364	0.005954545
717	0.167681818	0.005954545
718	0.161727273	0.005954545
719	0.155772727	0.005954545
720	0.149818182	0.005954545
721	0.143863636	0.005954545
722	0.137909091	0.005954545
723	0.131954545	0.005954545
724	0.126	0.000433712
725	0.125566288	0.000433712
726	0.125132576	0.000433712
727	0.124698864	0.000433712
728	0.124265152	0.000433712
729	0.123831439	0.000433712
730	0.123397727	0.000433712
731	0.122964015	0.000433712
732	0.122530303	0.000433712
733	0.122096591	0.000433712
734	0.121662879	0.000433712
735	0.121229167	0.000433712
736	0.120795455	0.000433712
737	0.120361742	0.000433712
738	0.11992803	0.000433712
739	0.119494318	0.000433712
740	0.119060606	0.000433712
741	0.118626894	0.000433712
742	0.118193182	0.000433712
743	0.11775947	0.000433712
744	0.117325758	0.000433712
745	0.116892045	0.000433712
746	0.116458333	0.000433712
747	0.116024621	0.000433712
748	0.115590909	0.000433712
749	0.115157197	0.000433712
750	0.114723485	0.000433712
751	0.114289773	0.000433712
752	0.113856061	0.000433712
753	0.113422348	0.000433712
754	0.112988636	0.000433712
755	0.112554924	0.000433712
756	0.112121212	0.000433712
757	0.1116875	0.000433712
758	0.111253788	0.000433712
759	0.110820076	0.000433712
760	0.110386364	0.000433712
761	0.109952652	0.000433712
762	0.109518939	0.000433712
763	0.109085227	0.000433712
764	0.108651515	0.000433712
765	0.108217803	0.000433712
766	0.107784091	0.000433712
767	0.107350379	0.000433712
768	0.106916667	0.000433712
769	0.106482955	0.000433712
770	0.106049242	0.000433712
771	0.10561553	0.000433712
772	0.105181818	0.000433712
773	0.104748106	0.000433712
774	0.104314394	0.000433712
775	0.103880682	0.000433712
776	0.10344697	0.000433712
777	0.103013258	0.000433712
778	0.102579545	0.000433712
779	0.102145833	0.000433712
780	0.101712121	0.000433712
781	0.101278409	0.000433712
782	0.100844697	0.000433712
783	0.100410985	0.000433712
784	0.099977273	0.000433712
785	0.099543561	0.000433712
786	0.099109848	0.000433712
787	0.098676136	0.000433712
788	0.098242424	0.000433712
789	0.097808712	0.000433712
790	0.097375	0.000433712
791	0.096941288	0.000433712
792	0.096507576	0.000433712
793	0.096073864	0.000433712
794	0.095640152	0.000433712
795	0.095206439	0.000433712
796	0.094772727	0.000433712
797	0.094339015	0.000433712
798	0.093905303	0.000433712
799	0.093471591	0.000433712
800	0.093037879	0.000433712
801	0.092604167	0.000433712
802	0.092170455	0.000433712
803	0.091736742	0.000433712
804	0.09130303	0.000433712
805	0.090869318	0.000433712
806	0.090435606	0.000433712
807	0.090001894	0.000433712
808	0.089568182	0.000433712
809	0.08913447	0.000433712
810	0.088700758	0.000433712
811	0.088267045	0.000433712
812	0.087833333	0.000433712
813	0.087399621	0.000433712
814	0.086965909	0.000433712
815	0.086532197	0.000433712
816	0.086098485	0.000433712

Locality number (1–1207)	Geological age (Ma)	Gap between localities (between localities n and n+1)
817	0.085664773	0.000433712
818	0.085231061	0.000433712
819	0.084797348	0.000433712
820	0.084363636	0.000433712
821	0.083929924	0.000433712
822	0.083496212	0.000433712
823	0.0830625	0.000433712
824	0.082628788	0.000433712
825	0.082195076	0.000433712
826	0.081761364	0.000433712
827	0.081327652	0.000433712
828	0.080893939	0.000433712
829	0.080460227	0.000433712
830	0.080026515	0.000433712
831	0.079592803	0.000433712
832	0.079159091	0.000433712
833	0.078725379	0.000433712
834	0.078291667	0.000433712
835	0.077857955	0.000433712
836	0.077424242	0.000433712
837	0.07699053	0.000433712
838	0.076556818	0.000433712
839	0.076123106	0.000433712
840	0.075689394	0.000433712
841	0.075255682	0.000433712
842	0.07482197	0.000433712
843	0.074388258	0.000433712
844	0.073954545	0.000433712
845	0.073520833	0.000433712
846	0.073087121	0.000433712
847	0.072653409	0.000433712
848	0.072219697	0.000433712
849	0.071785985	0.000433712
850	0.071352273	0.000433712
851	0.070918561	0.000433712
852	0.070484848	0.000433712
853	0.070051136	0.000433712
854	0.069617424	0.000433712
855	0.069183712	0.000433712
856	0.06875	0.000433712
857	0.068316288	0.000433712
858	0.067882576	0.000433712
859	0.067448864	0.000433712
860	0.067015152	0.000433712
861	0.066581439	0.000433712
862	0.066147727	0.000433712
863	0.065714015	0.000433712
864	0.065280303	0.000433712
t865	0.064846591	0.000433712
866	0.064412879	0.000433712
867	0.063979167	0.000433712
868	0.063545455	0.000433712
869	0.063111742	0.000433712
870	0.06267803	0.000433712
871	0.062244318	0.000433712
872	0.061810606	0.000433712
873	0.061376894	0.000433712
874	0.060943182	0.000433712
875	0.06050947	0.000433712
876	0.060075758	0.000433712
877	0.059642045	0.000433712
878	0.059208333	0.000433712
879	0.058774621	0.000433712
880	0.058340909	0.000433712
881	0.057907197	0.000433712
882	0.057473485	0.000433712
883	0.057039773	0.000433712
884	0.056606061	0.000433712
885	0.056172348	0.000433712
886	0.055738636	0.000433712
887	0.055304924	0.000433712
888	0.054871212	0.000433712
889	0.0544375	0.000433712
890	0.054003788	0.000433712
891	0.053570076	0.000433712
892	0.053136364	0.000433712
893	0.052702652	0.000433712
894	0.052268939	0.000433712
895	0.051835227	0.000433712
896	0.051401515	0.000433712
897	0.050967803	0.000433712
898	0.050534091	0.000433712
899	0.050100379	0.000433712
900	0.049666667	0.000433712
901	0.049232955	0.000433712
902	0.048799242	0.000433712
903	0.04836553	0.000433712
904	0.047931818	0.000433712
905	0.047498106	0.000433712
906	0.047064394	0.000433712
907	0.046630682	0.000433712
908	0.04619697	0.000433712
909	0.045763258	0.000433712
910	0.045329545	0.000433712
911	0.044895833	0.000433712
912	0.044462121	0.000433712
913	0.044028409	0.000433712
914	0.043594697	0.000433712
915	0.043160985	0.000433712
916	0.042727273	0.000433712
917	0.042293561	0.000433712
918	0.041859848	0.000433712
919	0.041426136	0.000433712
920	0.040992424	0.000433712
921	0.040558712	0.000433712
922	0.040125	0.000433712
923	0.039691288	0.000433712
924	0.039257576	0.000433712
925	0.038823864	0.000433712
926	0.038390152	0.000433712
927	0.037956439	0.000433712
928	0.037522727	0.000433712
929	0.037089015	0.000433712
930	0.036655303	0.000433712
931	0.036221591	0.000433712
932	0.035787879	0.000433712
933	0.035354167	0.000433712
934	0.034920455	0.000433712

Locality number (1–1207)	Geological age (Ma)	Gap between localities (between localities n and n+1)
935	0.034486742	0.000433712
936	0.03405303	0.000433712
937	0.033619318	0.000433712
in0 938	0.033185606	0.000433712
939	0.032751894	0.000433712
940	0.032318182	0.000433712
941	0.03188447	0.000433712
942	0.031450758	0.000433712
943	0.031017045	0.000433712
944	0.030583333	0.000433712
945	0.030149621	0.000433712
946	0.029715909	0.000433712
947	0.029282197	0.000433712
948	0.028848485	0.000433712
949	0.028414773	0.000433712
950	0.027981061	0.000433712
951	0.027547348	0.000433712
952	0.027113636	0.000433712
953	0.026679924	0.000433712
954	0.026246212	0.000433712
955	0.0258125	0.000433712
956	0.025378788	0.000433712
957	0.024945076	0.000433712
958	0.024511364	0.000433712
959	0.024077652	0.000433712
960	0.023643939	0.000433712
961	0.023210227	0.000433712
962	0.022776515	0.000433712
963	0.022342803	0.000433712
964	0.021909091	0.000433712
965	0.021475379	0.000433712
966	0.021041667	0.000433712
967	0.020607955	0.000433712
968	0.020174242	0.000433712
969	0.01974053	0.000433712
970	0.019306818	0.000433712
971	0.018873106	0.000433712
972	0.018439394	0.000433712
973	0.018005682	0.000433712
974	0.01757197	0.000433712
975	0.017138258	0.000433712
976	0.016704545	0.000433712
977	0.016270833	0.000433712
978	0.015837121	0.000433712
979	0.015403409	0.000433712
980	0.014969697	0.000433712
981	0.014535985	0.000433712
982	0.014102273	0.000433712
983	0.013668561	0.000433712
984	0.013234848	0.000433712
985	0.012801136	0.000433712
986	0.012367424	0.000433712
987	0.011933712	0.000433712
988[11]	0.0115	5.25114E-05
989	0.011447489	5.25114E-05
990	0.011394977	5.25114E-05
991	0.011342466	5.25114E-05
992	0.011289954	5.25114E-05
993	0.011237443	5.25114E-05
994	0.011184932	5.25114E-05
995	0.01113242	5.25114E-05
996	0.011079909	5.25114E-05
997	0.011027397	5.25114E-05
998	0.010974886	5.25114E-05

Notes:

[1] first locality of 2 in the Triassic.
[2] first locality of 8 in the Jurassic.
[3] first locality of 23 in the Early Cretaceous.
[4] first locality of 35 in the Late Cretaceous.
[5] first locality of 15 in the Paleocene.
[6] first locality of 56 in the Eocene.
[7] first locality of 66 in the Oligocene.
[8] first locality of 210 in the Miocene.
[9] first locality of 96 in the Pliocene.
[10] first locality of 466 in the Pleistocene.
[11] first locality of 220 in the Holocene.

Part 2

Phylogenetic analyses of lissamphibian inter- and intrarelationships

Chapter 3

Reevaluation of the data matrix by McGowan (2002)

Phylogenetic analysis was introduced into vertebrate paleontology in the mid-late 1980s (e.g. Gauthier 1984, 1986; Sereno 1984). Originally, perhaps owing to the lack of fast computers and powerful software and to difficulties in using the software that was available, many considered it too time-consuming for regular application. This led to the publication of trees that were apparently built by hand but, a fact which seems to have been inspired by the explicitness of phylogenetic analyses, came with a list of character state changes that supported each internode. Still, however, no data matrix was published, and the publications do not mention whether there was a systematic attempt to determine if the presented tree was the globally most parsimonious explanation for the distribution of even just the character states listed as support for the internal branches. An early instance is the tree of Benton (1985); two younger examples (Milner 1988, 1993) are historical milestones in amphibian phylogenetics.

Computer-assisted phylogenetic analyses of lissamphibian inter- and intrarelationships, with published data matrices and explicit methods, began with publications like Trueb & Cloutier (1991) and Cannatella & Hillis (1993). Most of the earliest analyses of lissamphibian interrelationships assumed the temnospondyl hypothesis *a priori* and only tested which temnospondyls were the closest relatives of Lissamphibia; this changed with Laurin (1994) and Laurin & Reisz (1997), analyses which resurrected the lepospondyl hypothesis based on, for their time, large data matrices with taxon samples diverse enough to test the inter- and intrarelationships of the extant amphibians adequately. The temnospondyl hypothesis was recovered by phylogenetic analysis no sooner than by Ruta et al. (2003), who had compiled a larger data matrix than all their predecessors. (For more on the history of phylogenetic analysis of Paleozoic limbed vertebrates and modern amphibians, see Chapter 6.)

According to what they both told me in person, Michel Laurin (the most prominent proponent of the lepospondyl hypothesis) once mentioned to Jason Anderson (one of the two most prominent proponents of the polyphyly hypothesis) that no phylogenetic analysis had ever supported the polyphyly hypothesis (PH). J. A. quipped that the little-known analysis by McGowan (2002) had supported it. He did not mean this very seriously (pers. comm. to me), but M. L. took it seriously, because McGowan (2002) had indeed performed a cladistic analysis that can reasonably be said to have found the PH, albeit a peculiar version of it (Figure 2 of this Chapter; incompatible with all other versions of the PH except the one found by the analysis by Carroll [2007]). M. L. suspected there could be mistakes in the data matrix and asked me to have a look. Indeed, the matrix contained – as documented in Appendix 1 of this Chapter – a duplicated character, two characters that needed to be split because they conflated two independent characters each, characters the scoring of which was impossible to replicate because the limits of the states were not defined (and no morphological gap that would line up with the scoring is apparent in the data), characters that had too few states to describe the morphological variation among the taxa in the matrix, a large number of cells the scoring of which was at odds with the descriptive literature, and an artificial all-zero outgroup that was, as McGowan (2002) made clear, modeled after basal temnospondyls, so it is in fact part of the ingroup (which contains temno- and lepospondyls in addition to lissamphibians). Finally, McGowan performed two analyses, one with all characters unordered, one with all multistate characters ordered; in the latter, the states of the multistate characters were ordered according to the numbers McGowan had given to those states, even in cases where state 0 lies in the middle of a transformation series. (McGowan took care to always assign the number 0 to the most plesiomorphic state; I think he did this to ensure that the all-zero ancestor could indeed be scored 0 for every character. Phylogenetics software, after all, does not require that the most plesiomorphic state be numbered 0.)

I merged the duplicated characters, split the conflated ones apart, defined the limits of states wherever necessary, applied stepmatrix gap-weighting (Wiens 2001) to the two most continuous characters rather than dividing their apparently unbroken variation into states arbitrarily, added states where necessary, checked every single cell for accuracy against the descriptive literature (supported by personal observations of specimens of *Triadobatrachus*, *Micromelerpeton*, *Apateon*, and *Microbrachis*; they all agreed with the literature), replaced the all-zero ancestor by two real outgroups (*Whatcheeria* and *Crassigyrinus*), and decided for each character separately whether it should be ordered or unordered or be treated according to a more complicated, tailored stepmatrix (for criteria, see Wiens 2001). The new outgroups are both very distant to the ingroup, but this was necessary to make sure they really lie outside the ingroup; the relationships of all possible close relatives of the latter (colosteids, baphetids, *Eucritta*, anthracosaurs in a wide sense, *Caerorhachis*) are controversial. I further tried to make sure that taxa known only from immature or paedomorphic specimens were scored as unknown for ontogeny-related characters if they had not reached the adult phenotype of close relatives, an approach that I derived from the one recommended by Wiens et al. (2005).

Analysis of the revised matrix results in the temnospondyl hypothesis (Fig. 6a), though the highest bootstrap value supporting this arrangement is only 37% (Fig. 6b).

It is noteworthy that the matrix contains all temnospondyls that had been considered close to the ancestry of some or all extant amphibians in recent publications, as well as a large sample of “microsaurian” lepospondyls, but lacked lysorophians, even though Lissamphibia and Lysorophia had been found to be sister-groups in a series of papers (Laurin & Reisz 1997, 1999; Laurin 1998). I therefore added the only well-known lysorophian, *Brachydectes*, to the matrix after reinterpreting the homology of some of its skull roof bones. Even though *Brachydectes* comes out of this reinterpretation (Fig. 4) as slightly less similar to the lissamphibians than previously thought, analysis of this augmented matrix results in the lepospondyl hypothesis (Fig. 6c), with *Brachydectes* supported as the sister-group of Lissamphibia + Albanerpetontidae by a bootstrap value of 50% (Fig. 6d).

Based on some features of *Doleserpeton* and various statements in the literature (see p. 157), I wondered if *Doleserpeton* should be scored as morphologically immature. I therefore prepared a third analysis, which meant nothing more than changing three cells of the matrix to unknown. *Brachydectes* was not included, because the above analysis already shows that adding *Brachydectes* results in the lepospondyl hypothesis – still, this analysis recovers the lepospondyl hypothesis, though with weak support (Fig. 6e, f; a bootstrap value of 39% keeps the lissamphibians together with the “lepospondyls”, one of 41% keeps them outside the temnospondyls).

Shortly after we submitted the first version of the manuscript, *Gerobatrachus* was described (Anderson et al. 2008) as a key fossil that supported the polyphyly hypothesis. Clearly, *Gerobatrachus* is as relevant as *Brachydectes*, so we added it to the matrices for two last two abovementioned analyses. For the last matrix, I scored it as morphologically immature, treating it like *Doleserpeton*. When these matrices are analyzed, *Gerobatrachus* comes out as a temnospondyl (the sister-group to *Doleserpeton* or its close relative *Amphibamus*); there are no other changes to the trees, which continue to support the lepospondyl hypothesis, and even the bootstrap values stay almost identical; I did not bother making illustrations to show these results (especially considering how long the manuscript already was).

In sum, then, a data matrix with (as far as possible) the original taxon and character sample of McGowan (2002) supports the lepospondyl hypothesis, and is more easily compatible with the temnospondyl hypothesis than with the polyphyly hypothesis.

In some ways, the present Chapter should be regarded as a proof-of-concept paper which shows how careful modification of a matrix can change the resulting trees. It would be easy to simply dismiss McGowan's tiny matrix (20 taxa, 41 characters) as already superseded by more recent, much larger matrices like those of Vallin & Laurin (2004), Ruta & Coates (2007), or Anderson et al. (2008), not to mention Chapters 4 and 5, all of which have more taxa, more characters, and a larger ratio of characters to taxa. However, McGowan's matrix, while small, is nicely balanced. There are characters that support the temnospondyl hypothesis, characters that support the lepospondyl hypothesis, and characters that support the polyphyly hypothesis; judging from my subjective impression, none of these groups seems to be over- or underrepresented. Except for the omission of *Brachydectes* (*Gerobatrachus* had not yet been described), the taxon sample contains all of the most important taxa for the question. The size of the matrix made it possible not only to scrutinize every single cell, but also to apply time-consuming approaches like stepmatrix gap-weighting, something I have not been able to do in Chapters 4 and 5.

It appears that McGowan relied too much on general statements in the literature and did not check carefully enough whether they were true for every member of a given taxon. The tree resulting from the reanalysis without addition of *Brachydectes* or interpretation of *Doleserpeton* as morphologically immature is almost 64% longer than McGowan's; in other words, McGowan overlooked large amounts of character conflict.

One unfortunate fact is that I have not been able to ask McGowan any questions. He does not currently have an academic affiliation, his former supervisor (Susan Evans) does not know how to reach him, and my half-day-long attempt to find contact information in Google has failed.

In Chapter 1 we had, like maybe half of the recent literature, used Gymnophiona for the total group of caecilians and Apoda for their crown-group. Apoda Oppel, 1810, is a junior homonym of the moth genus *Apoda* Haworth, 1809; it is therefore better not to use it. Accordingly, we now follow the other common usage of the name Gymnophiona (i.e., as the name for the crown-group), and I came up with the names Gymnophionomorpha for a branch-based clade approximating the total group and Gymnophioniformes for a node-based clade that includes the Early Cretaceous *Rubricacaecilia* and the crown-group but not *Eocaecilia*. These names and their phylogenetic definitions are formed in analogy to many names and definitions in amniote nomenclature.

Errata and similar comments

I claim on p. 163 of the paper that the atlas of *Doleserpeton* has not been described or illustrated in lateral view in any publication. This is incorrect (Bolt 1991: fig. 5). However, my scoring of *Doleserpeton* as unknown for presence or absence of the interglenoid tubercle of the atlas (the only character affected by the incorrect claim) is nonetheless defensible, because this character is inapplicable – the place where such a tubercle could be is occupied by a very large notochordal canal. (Actually, I should probably have given three states to this character – presence of an interglenoid tubercle, a flat surface, or a large notochordal canal –, though the last of these states occurs rarely and may be unique to *Doleserpeton* in this matrix; if so, it would be as uninformative as a score of "unknown".)

All that has so far been published on *Gerobatrachus* is the very short Nature article by Anderson et al. (2008). The text of that paper says the teeth of *Gerobatrachus* are pedicellate (they have, in other words, a poorly mineralized hinge in the crown), a feature found in lissamphibians, some teleosts, and a handful of dissorophoid temnospondyls like *Doleserpeton* (Bolt 1991: fig. 4) and *Amphibamus*. *Gerobatrachus* is a close relative of the latter two, so pedicellate teeth would not be surprising; yet, the resolution of the photograph provided by Anderson et al. (2008: fig. 3a) is very low, hampering comparison. Lack of pedicely is strongly suggested by the mode of preservation: complete teeth and empty alveoli are preserved, but not a single lone pedicel, even though, in fossils of animals with pedicellate teeth, all crown tips have usually fallen off while most or all pedicels are preserved in place (e.g. *Doleserpeton*: Bolt 1991: fig. 4; *Eocaecilia*: Jenkins et al. 2007: 327). Neither of us has seen the specimen, and pedicely is often restricted to an ontogenetic stage that the single known specimen may not record, so we scored *Gerobatrachus* as unknown for pedicely. Anderson (pers. comm.) insists the teeth are pedicellate; we hope his upcoming monographic description will clarify this issue.

One character claimed by Anderson et al. (2008) to support the polyphyly hypothesis is the basale commune, a single bone that represents distal tarsals 1 and 2 in salamanders and, according to the interpretation by Anderson et al., *Gerobatrachus*. Although this is not a character in McGowan's matrix, I compared the tarsi of *Gerobatrachus* and other temnospondyls (pp. 168–169) to evaluate the hypothesis that one of the two preserved tarsals of *Gerobatrachus* is a basale commune. I find several other possibilities to be more parsimonious. Among the very few temnospondyls with ossified and illustrated tarsi, I rather shamefully overlooked *Eoscopus*, illustrated by Daly (1994: fig. 11) as mentioned in Chapter 6; however, the tarsus of this close relative of *Gerobatrachus*, *Doleserpeton*, and *Amphibamus* does not change my conclusions.

An anonymous reviewer pointed out that Ivachnenko (1978) was wrong when he claimed that the Late Jurassic stem-salamander *Karaurus* had 15 presacral vertebrae; according to that reviewer, as well as to Ivachnenko's own plate IX and to photos of the holotype that M. L. took in 2006, there are only 12 or 13. We documented this on page 180. Meanwhile, we have studied a cast of the holotype that is housed at the Muséum national d'Histoire naturelle in Paris and can now confirm that *Karaurus* has 13 presacral vertebrae.

Finally, concerning the way of coding ontogeny-affected characters that was recommended by Wiens et al. (2005: 96), I mistakenly attributed my modification of their approach to them. I had not actually read their paper in three years and had misremembered it. See Chapter 6 for a detailed explanation; as I write there, I think my modified approach is a better choice for coding extinct taxa than the original one is.

Author contributions

As described above, M. L. provided the basic idea, access to the literature, and access to specimens of *Micromelerpeton*, *Apateon*, and *Microbrachis*, made mostly stylistic contributions to the manuscript, and supervised me, notably helping with some decisions on how to score certain taxa for certain characters; I did the rest.

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Contributions to Zoology, 77 (3) 149-199 (2008)

A reevaluation of the evidence supporting an unorthodox hypothesis on the origin of extant amphibians

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Key words: Albanerpetontidae, *Brachydectes,* coding, continuous characters, data matrix, *Gerobatrachus*, Gymnophioniformes, Gymnophionomorpha, Lissamphibia, Lysorophia, morphology, ontogeny, paleontology, phylogeny, scoring, stepmatrix gap-weighting

Abstract

The origin of frogs, salamanders and caecilians is controversial. McGowan published an original hypothesis on lissamphibian origins in 2002 (McGowan, 2002, *Zoological Journal of the Linnean Society,* 135: 1-32), stating that Gymnophiona was nested inside the 'microsaurian' lepospondyls, this clade was the sister-group of a caudate-salientian-albanerpetontid clade, and both were nested inside the dissorophoid temnospondyls. We have investigated McGowan's data matrix and disagree with the scoring of 35% of the cells. All taxa and all but two characters are affected. In some cases, we have a different interpretation about correspondence between morphology and character states, or we delimit states differently (or use information that was unknown in 2002). In others, we report probable typographic errors. When these cells and characters are revised, the most parsimonious trees – now longer by almost 64% – support one of the three commonly advocated hypotheses, namely a monophyletic Lissamphibia nested, together with its sister-group Albanerpetontidae, within the temnospondyls (next to *Doleserpeton*) – even though we did not add any characters or taxa to the very small data matrix. This exemplifies the impact of errors in data matrices on the results of phylogenetic analyses. Adding the lysorophian *Brachydectes*, however, results in the Lissamphibia-Albanerpetontidae clade becoming the sister-group of *Brachydectes* and settling within the lepospondyls rather than the temnospondyls, thus supporting another of the previously published three hypotheses. This latter finding does not change if the recently described *Gerobatrachus* is also added. Finally, when *Doleserpeton* is interpreted as morphologically immature (which means scoring three characters as unknown instead of known), Lissamphibia and Albanerpetontidae are again nested within the 'microsaurian' lepospondyls, even though *Brachydectes* is not included in this analysis. This, too, does not change if *Gerobatrachus* is added and likewise treated as morphologically immature. Bootstrap supports are rather low under all assumptions. Such lability was to be expected from the small size of the data matrix.

Contents

Introduction

The origin of lissamphibians remains highly contentious, despite decades of intensive research (Vallin and Laurin, 2004; Pawley, 2006: appendix 16; Anderson, 2007; Ruta and Coates, 2007; Marjanović and Laurin, 2007; Anderson *et al.*, 2008a). Our hypotheses about the relationships between the relevant extinct taxa (from the late Paleozoic and early Mesozoic) have been fairly stable in phylogenetic analyses over the last two decades (the various groups of 'lepospondyls' are the obvious exception), while widely divergent opinions persist on where to insert the anurans, urodeles and gymnophionans into this tree. Part of the problem is a stratigraphic gap between the oldest known representatives of the lissamphibians on the one hand and the first appearance of most or all of their proposed sister-groups on the other, as noted by Schoch and Milner (2004).

Early phylogenetic analyses of paleontological data divided most early limbed vertebrates into an amphibian clade composed of temnospondyls and lepospondyls, and a reptiliomorph clade composed of embolomeres, seymouriamorphs, diadectomorphs and amniotes (Gauthier *et al.*, 1988; Trueb and Cloutier, 1991; Lombard and Sumida, 1992; Ahlberg and Milner, 1994; Fig. 1a, b). However, nearly all recent paleontological studies indicate that the lepospondyls are closer to the amniotes than the temnospondyls and the seymouriamorphs are, and this topology is now nearly consensual (Carroll, 1995, 2007: fig. 77; Laurin and Reisz, 1997, 1999; Laurin, 1998a, b; Anderson, 2001, 2007; Ruta *et al.*, 2003; Vallin and Laurin, 2004; Pawley, 2006; Ruta and Coates, 2007; Anderson *et al.*, 2008a; see Fig. 1c-e, g-h) – only the position of the extant amphibians within this tree is not. This latter question has not yet been resolved, even though it has been assessed using anatomical data on extant (Carroll and Currie, 1975; Carroll and Holmes, 1980) and extinct (Milner, 1988, 1993; Laurin and Reisz, 1997, 1999; Laurin, 1998a, b; Anderson, 2001, 2007; Ruta *et al.*, 2003; Carroll *et al.*, 2004; Schoch and Milner, 2004; Vallin and Laurin, 2004; Pawley, 2006; Ruta and Coates, 2007; Anderson *et al.*, 2008a) forms, as well as developmentary (Schoch and Carroll, 2003; Schoch, 2006; Anderson, 2007) and molecular data (Laurin, 2002; Zhang *et al.*, 2005; Lee and Anderson, 2006; Marjanović and Laurin, 2007). All molecular analyses (including those which did not have an investigation of lissamphibian origins as their main purpose: *e.g.*, San Mauro *et al.*, 2005; Frost *et al.*, 2006; Roelants *et al.*, 2007) suggest that the extant amphibians are more closely related to each other than to Amniota, as do all morphological analyses based on extant taxa, but paleontological analyses suggest several incompatible hypotheses about lissamphibian origins.

Currently, three main hypotheses (all with variants) on lissamphibian origins are discussed based on morphological data. The first hypothesis (Fig. 1a-d) advocates a single origin within dissorophoid temnospondyls (Bolt, 1969 [with reservations], 1977; Milner, 1988, 1993; Panchen and Smithson, 1988; Trueb and Cloutier, 1991; Lombard and Sumida, 1992; Ahlberg and Milner, 1994; Ruta *et al.*, 2003; Ruta and Coates, 2007; Jenkins and Walsh in Jenkins *et al.*, 2007). The second hypothesis (Fig. 1e) advocates a single origin within lepospondyls (Laurin and Reisz, 1997, 1999; Laurin, 1998a, b; Vallin and Laurin, 2004; see also Pawley, 2006: 239 and appendix 16). In the third hypothesis (Fig. 1f, g), the extant amphibians are deemed to have originated from at least two, but usually three groups of Paleozoic stegocephalians (Carroll and Currie, 1975; Carroll and Holmes, 1980; Schoch and Carroll, 2003; Carroll *et al.*, 2004; Carroll, 2007; Carroll in Jenkins *et al.*, 2007; Anderson, 2007; Anderson *et al.*, 2008a), once or twice within lepospondyls (gymnophionans and sometimes urodeles), and once or twice within dissorophoid temnospondyls (anurans and sometimes urodeles). Unlike the two monophyly hypotheses, it is not compatible with the results of the molecular analyses cited above, and has so far only been supported by two very similar published data matrices (Anderson, 2007; Anderson *et al.*, 2008a) (Fig. 1g).

The phylogenetic analysis by McGowan (2002) supports a fourth hypothesis (Fig. 2): the extant amphibians are diphyletic, the ('microsaurian') lepospondyls are stem gymnophionans, and the lepospondyls including the extant amphibians are nested within the (dissorophoid) temnospondyls, contradicting the consensus that Temnospondyli and Lepospondyli form mutually exclusive clades (Carroll, 1995; Vallin and Laurin, 2004; Pawley, 2006; Ruta and Coates, 2007; Anderson, 2007; Anderson *et al.*, 2008a). This highly unorthodox hypothesis is relevant because another, more recent and more comprehensive, study has obtained similar results (Carroll, 2007: fig. 77; see Fig. 1h). The present study was undertaken solely to determine whether or not the suggestions that the lepospondyls are nested within the temnospondyls, and whether or not the extant amphibians are diphyletic, are supported by

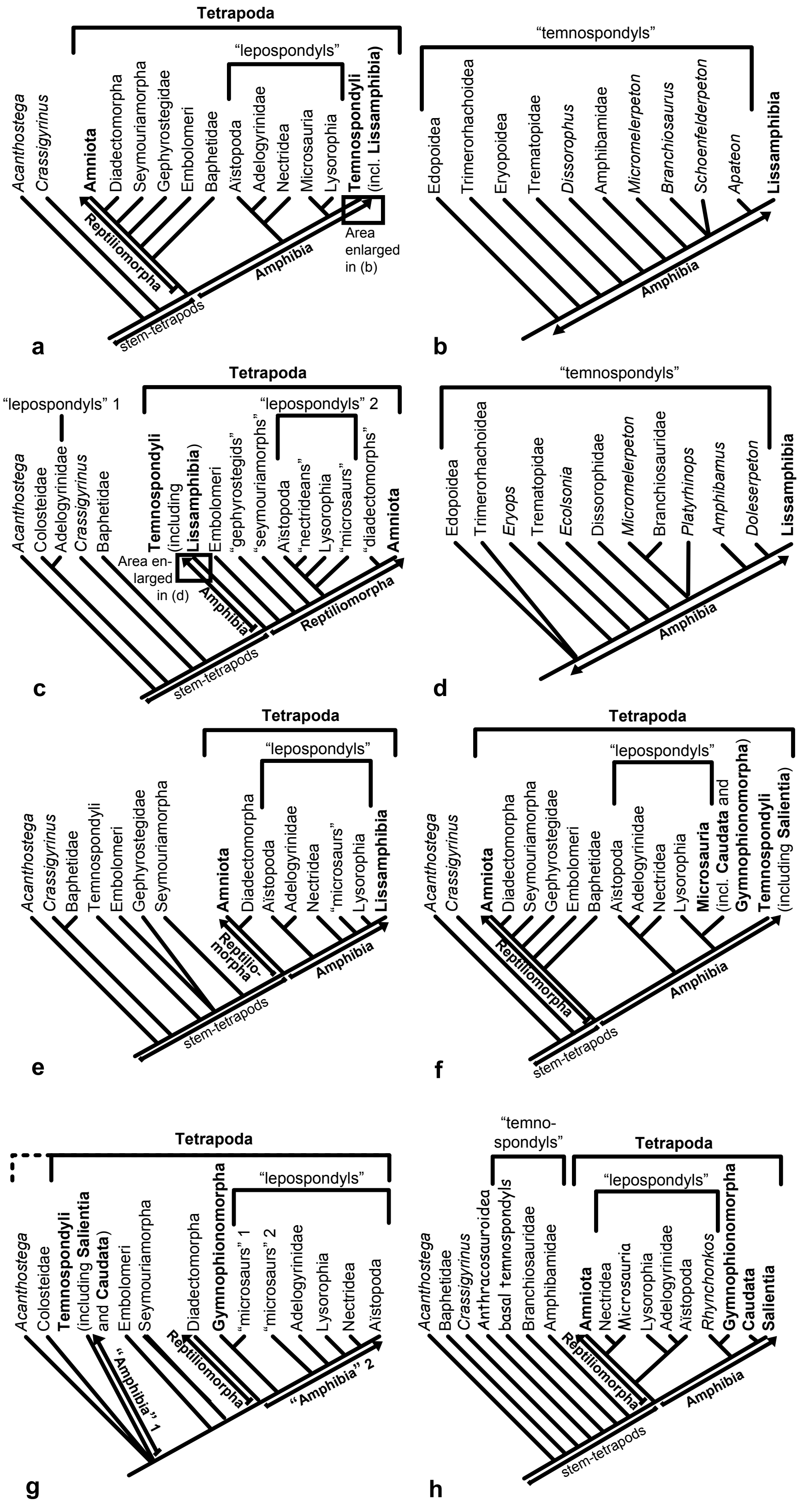


Fig. 1. The currently discussed hypotheses on the origin of the extant amphibians. Extant taxa in bold, paraphyletic taxa in quotation marks. (a, b) Monophyletic origin within the temnospondyls as suggested by Panchen and Smithson (1988), Trueb and Cloutier (1991), Lombard and Sumida (1992), and Ahlberg and Milner (1994); lepospondyls form the basalmost part of the amphibian stem. ((b) is simplified from Trueb and Cloutier, 1991; Amphibamidae contains the topology ('*Tersomius*' (*Doleserpeton*, *Amphibamus*)).) (c, d) Monophyletic origin within the temnospondyls, most lepospondyls are reptiliomorphs; simplified from Ruta and Coates (2007; see also Ruta *et al.*, 2003). (e) Monophyletic origin within the lepospondyls, simplified from Vallin and Laurin (2004; see also Laurin and Reisz, 1997, 1999; Pawley, 2006: 239 and appendix 16). (f) Diphyletic origin in which frogs are temnospondyls, caecilians are lepospondyls, and salamanders may be one or the other (Carroll and Currie, 1975; Carroll and Holmes, 1980; Carroll *et al.*, 2004). (g) Diphyletic origin in which frogs and salamanders are temnospondyls and caecilians are lepospondyls – note that the name Amphibia ceases to apply to any clade; the solid line shows the minimum content of Tetrapoda, the stippled line the maximum content; simplified from Anderson (2007; see also Anderson *et al.*, 2008a). (h) Monophyletic origin in which *Rhynchonkos* is a lissamphibian, amniotes are lepospondyls, and all of these together are temnospondyls; simplified from the result of Carroll's (2007) analysis (fig. 77), not from his preferred tree (fig. 78) which is 36 steps longer. In (h), 'Anthracosauroidea' is an OTU that includes Embolomeri, Gephyrostegidae and Seymouriamorpha; 'basal temnospondyls' is an OTU composed of *Dendrerpeton* and *Balanerpeton*; the 'Microsauria' OTU consists of all 'microsaurs' except *Rhynchonkos* – Carroll did not test the monophyly of any of these assemblages and in fact believes (Carroll and Currie, 1975, through Carroll, 2007) that the 'Microsauria' OTU is paraphyletic with respect to *Rhynchonkos* (and Gymnophionomorpha).

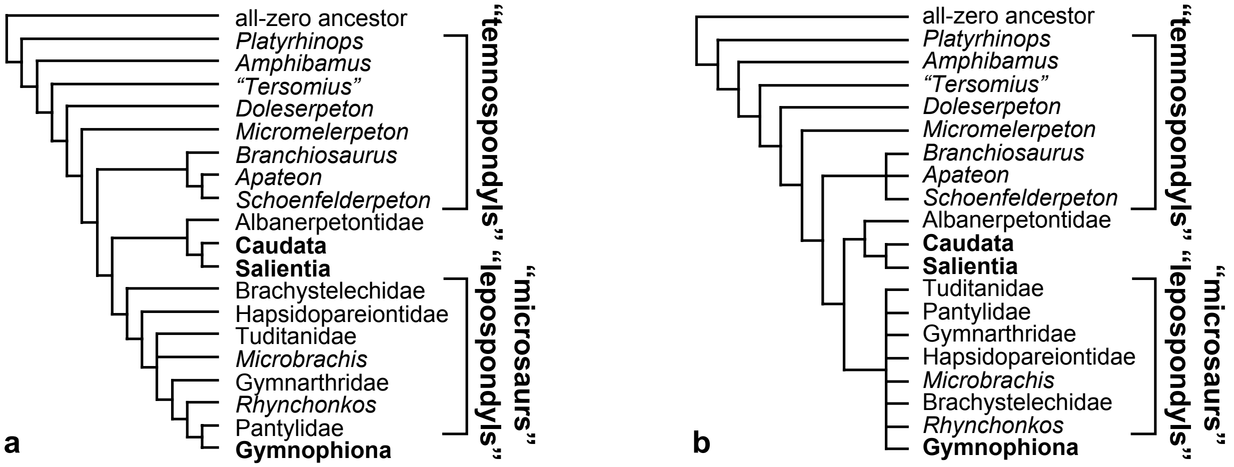


Fig. 2. The impact of ordering characters in McGowan's (2002) matrix. (a) McGowan's (2002: fig. 15) result (strict consensus of the two most parsimonious trees; length = 95 steps, CI = 0.4947, RI = 0.7513, RC = 0.3717) obtained by leaving all characters unordered: the microsaurian lepospondyls are closer to Gymnophionomorpha than Batrachia is, and Lissamphibia including the microsaurs is monophyletic within the dissorophoid temnospondyls. (b) Strict and majority-rule consensus (identical) of the 8 most parsimonious trees (length = 97 steps, CI = 0.4845, RI = 0.7608, RC = 0.3686) which result when all multistate characters in McGowan's (2002) matrix are ordered according to their state numbers (0 > 1 > 2 > 3). This consensus tree was described but not illustrated by McGowan (2002: 20). Note that, in the present case, ordering the multistate characters reveals additional character conflict and therefore decreases the resolution. Extant taxa are in boldface.

the data which were originally used to advocate them (McGowan, 2002) when these data are subjected to a detailed revision; Carroll's (2007) work will be addressed elsewhere, as will be that of Ruta and Coates (2007), Anderson (2007), and Anderson *et al.* (2008a).

Nomenclatural remarks

Phylogenetic nomenclature

Phylogenetic nomenclature is used throughout this work, in a way that would be compatible with the ICPN (International Code for Phylogenetic Nomenclature: Cantino and de Queiroz, 2007; earlier drafts were called PhyloCode) if the ICPN were already implemented.

We discontinue our previous usage (Marjanović and Laurin, 2007) and instead follow Cannatella and Hillis (1993), Frost *et al.* (2006), Wilkinson and Nussbaum (2006) and Jenkins *et al.* (2007: 358) in using the name Gymnophiona for the caecilian crown group. The name Apoda Oppel 1810 has often (*e.g.*, Trueb and Cloutier, 1991; Ruta and Coates, 2007) been used for the crown group (and Gymnophiona for the total group) in paleontological literature, but it is a junior homonym of the moth genus *Apoda* Haworth 1809 (Dundee, 1989; Wilkinson and Nussbaum, 2006; Naish, 2008) and should therefore not be used for an amphibian clade.

To facilitate discussion of gymnophionans and their relatives, we introduce the new clade names Gymnophioniformes and Gymnophionomorpha. (Because the ICPN will not be retroactive, and because these names are not registered, they are not hereby established and will need to be published anew once the ICPN is in effect.) Fig. 3 serves as the reference phylogeny (required by the ICPN in Article 9.6) for both, but note that both names can be applied to any phylogeny, not only to the reference phylogeny; the reference phylogeny merely serves to clarify our intent (ICPN Note 9.6.1). Gymnophioniformes has a node-based definition with *Caecilia tentaculata* L. 1758 and *Rubricacaecilia monbaroni* Evans and Sigogneau-Russell 2001 as internal specifiers. Gymnophionomorpha has a branch-based definition with *Caecilia tentaculata* L. 1758 as the internal specifier and *Rana temporaria* L. 1758, *Salamandra salamandra* (L. 1758), *Albanerpeton inexpectatum* Estes and Hoffstetter 1976, *Brachydectes newberryi* Cope 1868, *Rhynchonkos stovalli* (Olson 1970), *Batropetes fritschi*

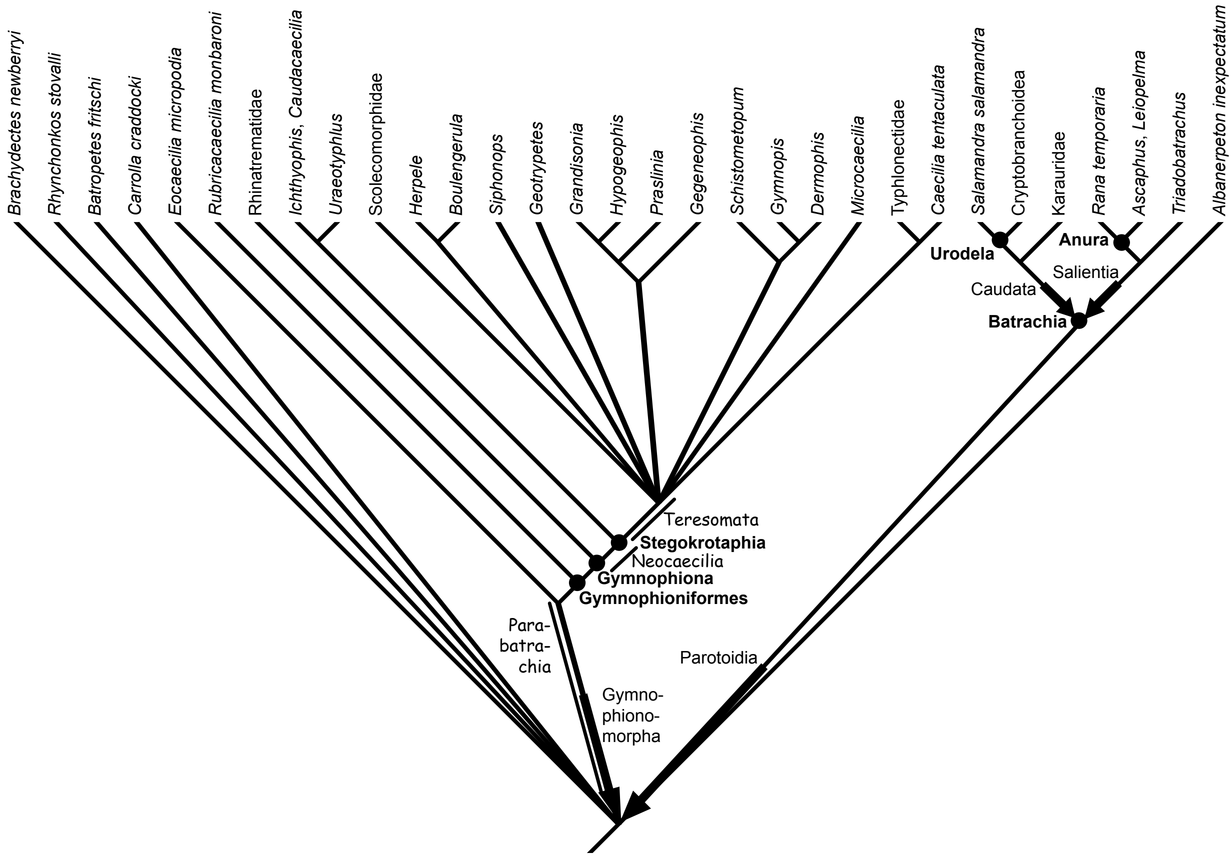


Fig. 3. Reference phylogeny for Gymnophioniformes and Gymnophionomorpha (new clade names) which additionally shows our usage of several other taxon names. Of these, those with node-based definitions are in boldface, those with branch-based definitions in regular typeface, and those without definitions in the font Comic Sans MS. The topology is a strict consensus of the opinions and results of Anderson (2001, 2007 except for Batrachia), Anderson *et al.* (2008a) except for the position of Albanerpetontidae, Evans and Sigogneau-Russell (2001), Vallin and Laurin (2004), Wilkinson and Nussbaum (2006), Jenkins *et al.* (2007), Ruta and Coates (2007) and Carroll (2007 and references therein) and fully compatible with McGowan's (2002; see Fig. 2) and our own results (Fig. 6), as well as with those of the molecular analysis by Frost *et al.* (2006) (except for the position of *Siphonops*), and even with Moodie's (1909) and Eaton's (1959) opinion that *Brachydectes* is a close relative of Gymnophiona. Dots mark the first member of clades whose names have node-based definitions, arrows point to the first member of clades whose names have branch-based definitions (the first member lying at the tip of the arrow, not beyond). Teresomata, Neocaecilia and Parabatrachia lack phylogenetic definitions; their first members could lie anywhere in the indicated ranges and still be compatible with the usage by Wilkinson and Nussbaum (2006) respectively Frost *et al.* (2006).

(Geinitz and Deichmüller 1882), and *Carrolla craddocki* Langston and Olson 1986 as external specifiers. The first three external specifiers serve to prevent Gymnophionomorpha from including any of the other three large lissamphibian (or possibly lissamphibian) clades, taking account of the conflicting hypotheses that exist on their interrelationships. The other four prevent it from including all or many 'lepospondyls' in the event of extant amphibian polyphyly: *Brachydectes* was considered a close relative of Gymnophiona as used here by Moodie (1909) and Eaton (1959); *Rhynchonkos* has been hypothesized to be the sister-group of Gymnophionomorpha by Carroll (Carroll and Currie, 1975, through Carroll, 2007, and Carroll in Jenkins *et al.*, 2007); and *Eocaecilia*, the only lissamphibian in the data matrix of Anderson (2001), is the sister-group of *Batropetes* + (*Carrolla* + *Quasicaecilia*) in his most parsimonious tree (Anderson, 2001: fig. 6), while it forms a polytomy with *Rhynchonkos*, (*Batropetes* + *Quasicaecilia*), and *Carrolla* in the Adams consensus of all trees that are one step less parsimonious (Anderson, 2001: fig. 7) as well as in the strict consensus of the most parsimonious trees found by Vallin and Laurin (2004: fig. 7) in their reanalysis of Anderson's (2001) matrix. Anderson (2007) and Anderson *et al.* (2008a) are congruent with Anderson (2001) in the position of *Eocaecilia* (the other lissamphibians being found as temnospondyls, i.e., in remote branches of the tree). We deliberately do not use *Quasicaecilia* as an external specifier because it is known from a single, highly incomplete and immature specimen and because its name implies that it should not be automatically excluded from Gymnophionomorpha by definition.

Ruta and Coates (2007) have found Gymnophionomorpha (represented by *Eocaecilia*) and Albanerpetontidae as sister-groups; the undefined name Parabatrachia Frost *et al.* 2006 ("the taxon composed of living caecilians + *Eocaecilia*"; Frost *et al.*, 2006: 356) might be used for such a clade.

Within Gymnophiona, Wilkinson and Nussbaum (2006: 44) have suggested "the anatomically neutral Neocaecilia" as a replacement for the anatomically misleading name Stegokrotaphia Cannatella and Hillis 1993 (not all stegokrotaphians have a stegokrotaphic [= unfenestrated and unembayed] skull, nor is the stegokrotaphic condition necessarily an apomorphy of any clade within Gymnophionomorpha or even Lissamphibia). We nonetheless retain Stegokrotaphia for "the most recent common ancestor of Caeciliaidae [sic], Ichthyophiidae, Scolecomorphidae, and Uraeotyphlidae, and all of its descendants" (Cannatella and Hillis, 1993: 2) because this name is older and because, unlike Neocaecilia, it has a phylogenetic definition (although none of the specifiers of that definition are 'species, specimens or apomorphies', which is required by the ICPN in Article 11.1). Perhaps Neocaecilia could be used for a slightly more inclusive clade in the future, if extinct taxa closer to Stegokrotaphia than to Rhinatrematidae will be identified, in analogy to the successful resolution of former synonyms such as Salientia and Anura, Caudata and Urodela, Eutheria and Placentalia, Metatheria and Marsupialia, Rhynchocephalia and Sphenodonti(d)a, Ophidia and Serpentes, or Testudinata and Testudines. (Wilkinson and Nussbaum [2006: 45] specify that Neocaecilia is a clade and mention an autapomorphy, but they do not provide information which indicates whether that clade has a node-based, branch-based, or apomorphy-based definition.)

Rank-based nomenclature

We would like to provide a few comments about the status and correct spelling of a few relevant taxon names (discussed in other sections of this paper) in the context of rank-based ('Linnaean') nomenclature. Contrary to common usage, *Boulengerul**a*** is feminine (by virtue of not being 'Boulengerul**us**'), so that *B. taitan**us*** Loveridge 1935 is an incorrect original spelling and automatically corrected to *B. taitan**a*** by ICZN Articles 31.2 and 34.2 (International Commission on Zoological Nomenclature, 1999). According to the same articles, no formal emendation is necessary, and the correct spelling must be attributed to Loveridge 1935. All this also holds if the likewise feminine *Afrocaecilia* (of which *B. taitana* is the type species) is recognized.

Likewise, *Albanerpeton* is neuter, which makes the original spelling of the type species, *A. inexpectat**um***, correct and those of *A. nexuos**us***, *A. gracil**is*** and *A. pannonic**us*** incorrect; the correct spellings (which again must be attributed to the original authors) are *A. nexuos**um***, *A. gracil**e*** and *A. pannoni**cum***. *Anoualerpeton*, *Chunerpeton*, *Pangerpeton* and *Sinerpeton*, too, are neuter, so that *A. unic**us***, *A. prisc**us***, *C. tianyiens**is***, *P. sinens**is*** and *S. fengshanens**is*** are correctly spelled *A. unic**um***, *A. prisc**um***, *C. tianyiens**e***, *P. sinens**e*** and *S. fengshanens**e***.

Finally, Heyler (1994) appears to be wrong in claiming that only the International Commission on Zoological Nomenclature has the authority to designate neotypes and that therefore the designation of a neotype for *Apateon pedestris* by Boy (1986) is invalid: whenever "no name-bearing type specimen (i.e. holotype, lectotype, syntype or prior neotype) is believed extant and an author considers that a name-bearing type is necessary to define the nominal taxon objectively", that author has the right to designate a neotype (ICZN Article 75.1). Boy's (1986) designation of a neotype for *A. pedestris* fulfills all requirements of Article 75 and is therefore, to the best of our knowledge, valid.

Abbreviations

CI, RI, RC:	consistency index, retention index, rescaled consistency index (see Swofford and Begle, 1993: 54).
MPT:	most parsimonious tree.
OTU:	Operational Taxonomic Unit.

Methods

Addition of Brachydectes *and homology of its dermal skull bones*

In trying to test whether McGowan's (2002) matrix supports his phylogenetic hypothesis, we are logically bound to McGowan's choices of characters and taxa. However, we have decided to deviate from this principle in one respect: McGowan included in his matrix all temnospondyls that have been considered (at one time or another, alone or together with others in the list) particularly close relatives of some or all of the lissamphibian OTUs: *Doleserpeton*, *Amphibamus*, *Platyrhinops*, '*Tersomius*', *Schoenfelderpeton*, *Apateon*, and *Branchiosaurus*. On the lepospondyl side, however, McGowan restricted himself to *Rhynchonkos*, the likely sister-group of the caecilians according to Carroll and Currie (1975) and Carroll (2000, 2007), and (in hindsight) the brachystelechids, which occupy more or less the same position according to Anderson (2001, 2007) and Anderson *et al.* (2008a). He did not include any lysorophians, even though Lysorophia has been identified as the sister-group of Lissamphibia in all published phylogenetic analyses that support the lepospondyl hypothesis (Laurin and Reisz, 1997, 1999; Laurin, 1998a; Vallin and Laurin, 2004; see also Pawley, 2006: appendix 16). To examine the effects of McGowan's decision not to include any lysorophian, we have coded *Brachydectes* as an OTU (as a composite of its two species, *B. newberryi* and *B. elongatus*) and performed analyses with and without *Brachydectes* (see below).

The skull roof and cheek region of *Brachydectes* (the only sufficiently well known lysorophian) have proven difficult to interpret in that the identities of their component bones are unclear. This makes it difficult to score *Brachydectes* for those characters in the present matrix that deal with the presence/absence of the tabular, postorbital, postfrontal and supratemporal. In lateral view, there is a large T- or 7-shaped bone that overlies the squamosal laterally and extends ventrally almost to the jaw articulation. On the occiput and the caudal part of the skull roof, a narrow dumbbell-shaped median bone forms the dorsal margin of the foramen magnum and contacts the parietal as well as the exoccipital.

Traditionally (Sollas, 1920; Romer, 1966; Bolt and Wassersug, 1975), the T-shaped bone was considered the supratemporal, and the median bone the suproccipital (Fig. 4). It follows that the square bone that lies on each side between the 'suproccipital', parietal, 'supratemporal' and exoccipital and participates in skull roof and occiput represents the tabular, and that the postparietals are absent (at least as separate bones), as are the postorbitals and postfrontals. However, among the microsaurs, generally considered the closest known relatives (mono- or paraphyletic) of Lysorophia, a supratemporal is never present (see Appendix I, character 13), and wherever a supratemporal is present in other lepospondyls, it is always a long, narrow strip of bone that lies on the skull roof between the tabular and the squamosal, unlike the 'T bone' of *Brachydectes*.

In his review of the Lysorophia, Wellstead (1991) agrees with the identification of the 'suproccipital' and the absence of postorbital and postfrontal, but he considers the 'T bone' the tabular and the square bone between it and the 'suproccipital' the postparietal. It follows that the supratemporal is absent. The latter fact agrees with the situation in the microsaurs, but under this interpretation the tabular has a strange shape and extends lateroventrally much farther than in any other taxon, and the postparietals are separated from each other by the suproccipital, an autapomorphic configuration.

We suggest a third interpretation that is possibly more parsimonious. In the brachystelechid 'microsaur' *Batropetes* (Carroll, 1991: fig. 5), the postorbital (plus the caudal half of the postfrontal) has a shape and position very similar to those of the 'T bone' in *Brachydectes* (Wellstead, 1991: figs 2, 3). Thus, we propose that the 'T bone' is the postorbital, an interpretation consistent with the ventral extent of this bone. The 'square bone' would then be the tabular, as suggested by its position in the caudolateral corner of the skull table and as in the traditional interpretation. The postparietal is a small, median bone in the 'microsaur' *Odonterpeton* (Carroll and Gaskill, 1978) and absent in the brachystelechid 'microsaurs'. Our interpretation is coherent with our view that the lysorophians and at least some 'microsaurs' form a clade (Vallin and Laurin, 2004), since there is no discrete postparietal in *Brachydectes* (according to our interpretation). This absence, together with the plesiomorphically small size of the parietals, explains why the suproccipital participates in the skull roof, which it does not do in any other lepospondyl.

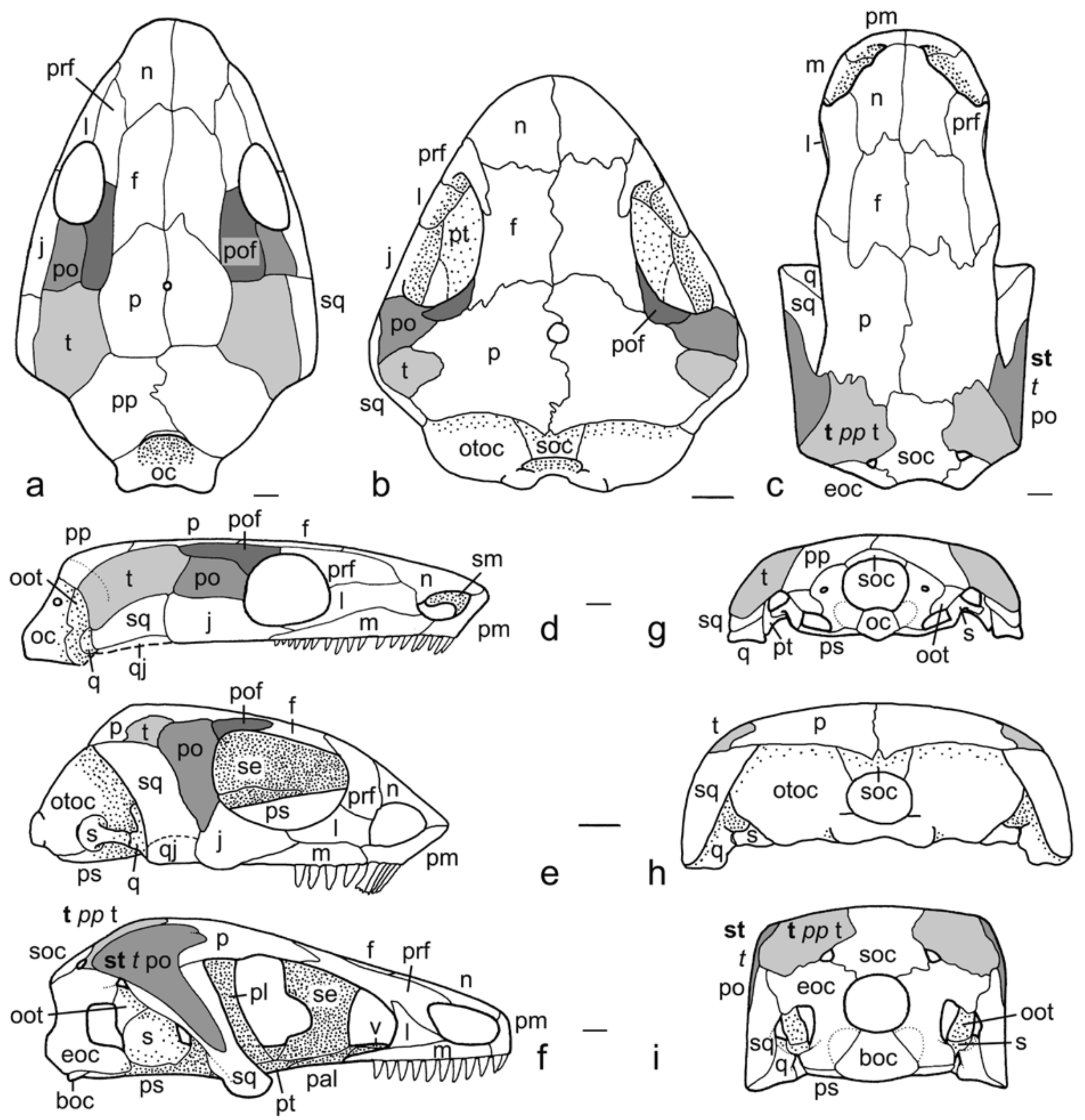


Fig. 4. Our interpretation of the homologies between the dermal skull bones of three 'lepospondyls': (a, d, g) *Rhynchonkos* (reproduced from Laurin and Reisz, 1997, and Laurin, 1998a), (b, e, h) *Batropetes* (redrawn from Carroll, 1991), and (c, f, i) *Brachydectes* (reproduced from Laurin and Reisz, 1997, and Laurin, 1998a). (a, b, c) Dorsal view; (d, e, f) right lateral view; (g, h, i) occipital view. Abbreviations: boc, basioccipital; eoc, exoccipital; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; oc, fusion of exoccipital and basioccipital; oot, opisthotic; otoc, fusion of prootic, opisthotic, exoccipital, and basioccipital; p, parietal; pal, palatine; pl, pleurosphenoid; pm, premaxilla; po, postorbital; pof, postfrontal; pp, postparietal; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; s, stapes; se, sphenethmoid; sm, septomaxilla; soc, suproccipital; sq, squamosal; st, supratemporal; t, tabular; v, vomer. Where interpretations of *Brachydectes* differ, those by Sollas (1920), Romer (1966) and Bolt and Wassersug (1975) are in bold, those by Wellstead (1991) are in italics, and ours are in regular typeface; they are always given in this order. The shaded bones are the tabular (light), the postorbital (intermediate), and the postfrontal (dark) according to our interpretation. Bones at the bottom of fenestrae or of skull roof emarginations are stippled.

We have scored the tabular as present, because all three interpretations agree on its presence, even though only two of them agree on which bone is the tabular. We have also scored the supratemporal as absent, because two of the three interpretations agree on its absence. We have furthermore scored the postfrontal as absent, because the two published interpretations agree on its absence and because there is no evidence of its presence. However, unlike all analyses which have found Lysorophia and Lissamphibia as sister-groups (Laurin and Reisz, 1997, 1999; Laurin, 1998a; Vallin and Laurin, 2004; Pawley, 2006), we have scored the postorbital as present, because of the similarity of the 'T bone' to the postorbital of brachystelechids in general and *Batropetes* in particular. Both the postorbital and the postfrontal are absent in all known lissamphibians, except for the probable presence of the postfrontal ancestrally in Gymnophionomorpha (discussed below), and present in all other taxa in our data matrix.

Ontogeny and phylogenetic position of Doleserpeton

Ever since its preliminary description (Bolt, 1969), *Doleserpeton* has commonly been considered the sister-group of Salientia, Batrachia, or Lissamphibia as a whole (*e.g.*, Bolt 1977, 1979; Milner, 1993 [with reservations]; Roček and Rage, 2000; Ruta and Coates, 2007). However, Bolt (1979: 554, 557; see also Bolt, 1969, 1977) considered the specimens postmetamorphic but juvenile, like all known postmetamorphic specimens of *Amphibamus* (except YPM 794, which is more mature: Daly, 1994: 27). Some of the character states that *Doleserpeton* shares with the extant amphibians and which have been argued in the literature as indicating a close relationship between the latter and *Doleserpeton* are also found in juveniles but not adults of *Amphibamus*, *Platyrhinops* and '*Tersomius*' (Milner, 1982; Clack and Milner, 1993; Daly, 1994; Schoch, 2001, 2002). This opens up the possibility that some or all of the supposed synapomorphies of *Doleserpeton* and extant amphibians that are not found in adults of amphibamids other than *Doleserpeton* are juvenile features of unknown phylogenetic distribution that may occur widely among (at least) dissorophoids – for most of which growth series are unknown – rather than indicating a close relationship between extant amphibians and specifically *Doleserpeton*. This holds regardless of whether some or all of the extant amphibians are themselves paedomorphic dissorophoids (an opinion shared by all of the references cited above in this paragraph). To evaluate the impact of the general assumption that *Doleserpeton* is morphologically adult, we have run one of our analyses (see below) twice, once with all characters scored as if the described material of *Doleserpeton* were adult, and once with the potentially juvenile features (characters 7, 35, and 40; see Appendices 1 and 2) scored as unknown, as recommended by Wiens *et al.* (2005) for the phylogenetic analysis of juvenile or paedomorphic OTUs (in order to avoid the confounding effects of correlated characters and those of the absence of character states that appear late in non-truncated ontogenies).

Unfortunately, the plentiful and well-preserved but often disarticulated material of *Doleserpeton* (M. L., pers. obs. January 1996) has never been thoroughly described in a publication.

Ontogeny and phylogenetic position of Brachydectes

On a similar note, it has been suggested that the apparently obligatorily aquatic lysorophians (of which only *Brachydectes* is adequately known) are "heavily paedomorphic" (Schoch, 2002: 294), and that this is manifested not only in their well-developed hyobranchial apparatus and (most spectacularly) in the persistent suture between their left and right neural arches, but also in character states like the lack of postfrontal and jugal – which are included in the present matrix and are potential synapomorphies of (at least) Caudata, Salientia, and *Brachydectes*. However, in the continued absence of any knowledge on ossification sequences of *Brachydectes* and its closest relatives (Wellstead, 1991: 67), and in view of the fact that other certainly (adelogyrinids, *Microbrachis*, diplocaulid nectrideans) and probably (some aïstopods) obligatorily aquatic and possibly paedomorphic lepospondyls show no such bone losses, we have not scored such characters as unknown in *Brachydectes* in any analysis, because we would have had to interpret *Brachydectes* according to the ontogeny of the phylogenetically far distant dissorophoid temnospondyls. Coding it according to the ontogeny of extant amphibians would mean to assume a close relationship *a priori*, and it would raise new questions – for example, the arrangement of the vomerine teeth of *Brachydectes* is identical to that of larval and paedomorphic salamanders, but never seen in anuran or gymnophionan ontogeny. We hope that lysorophian or at least 'microsaurian' ossification sequences will one day come to light.

A partial ossification sequence of the deeply nested aïstopod *Phlegethontia*, consisting of three stages, has been described by Anderson (2002, 2007). However, the second stage shows a complete jugal as well as the rostrodorsal corner of the postfrontal, while the squamosal is still incomplete and (an autapomorphy of Phlegethontiidae) the parietal never appears at all, as it is unnecessary because of the uniquely hyperossified braincase. These features, along with the full ossification of the prefrontal and the maxilla at the second stage, and that of the entire caudal half of the braincase (except the sagittal and nuchal crests) at the first stage (when cleithra, gastralia, teeth and even ribs are lacking), show that the highly derived ossification sequence of *Phlegethontia* was not only very different from all known lissamphibian and temnospondyl ossification sequences, but also never led through a stage comparable to the adult condition of *Brachydectes*. It is therefore unfortunately irrelevant for determining paedomorphosis in the latter.

Comparison of the palate of *Brachydectes* (especially the width of the cultriform process, the caudal extent of the maxilla relative to that of the palatine, the orientation of the pterygoid, and the lack of interpterygoid vacuities; Fig. 4) to those of larval and paedomorphic lissamphibians (Reiss, 2002) does suggest paedomorphosis in *Brachydectes* and a close relationship between these taxa, but this latter assumption is one of the very questions the present analysis is meant to test. We have therefore refrained from using this assumption in our coding.

Addition of Gerobatrachus *and its ontogeny and phylogenetic position*

Gerobatrachus hottoni was recently (Anderson *et al.*, 2008a) described as a temnospondyl that shares apomorphies with batrachians (salientians and caudates) but not with gymnophionomorphs and thus bolsters the polyphyly hypothesis; this hypothesis is indeed supported by the phylogenetic analysis conducted by Anderson *et al.* (2008a). Therefore, even though it was unknown to McGowan in 2002, this animal is as relevant to the present work as *Brachydectes*; we have included it in two of our five analyses.

Gerobatrachus was described as juvenile, based on the very large relative size of its pineal foramen (Anderson *et al.*, 2008a: 515) and presumably on the tiny size of the only known specimen (11 cm total length, less than 2 cm skull length). Further features compatible with a young ontogenetic age are the poor ossification of the tail, the extremely short ribs, the absence of pubis, scapulocoracoid, and most of the braincase in the specimen, the very large orbits and nares, and the lack of vomerine fangs (whether palatine fangs were present is, as far as we can tell, unknown, and not mentioned in the description). The shapes and relative sizes of lacrimal and prefrontal, as far as they can be seen in ventral view, are most similar to those of late larval and metamorphosing specimens of *Apateon gracilis* (Schoch and Fröbisch, 2006: fig. 1B, C).

However, other features conflict with such an assessment and suggest an age much closer to morphological maturity: Anderson *et al.* (2008a: 516) mention that "[t]he olecranon process is surprisingly well-ossified [sic] for the inferred young ontogenetic stage of the specimen". All dermal skull bones are ossified, and the contact between maxilla and quadratojugal is established. At least two tarsals are ossified (more may have been present and lost *post mortem* – the tibiae and fibulae are missing on both sides). The quadrates and the articulars are completely ossified; this generally happened late in temnospondyls, for example no sooner than metamorphosis in *Apateon* (Schoch and Fröbisch, 2006). The same holds for other endochondral skull bones: the otic capsule is partially ossified, as is the sphenethmoid, and at least the left epipterygoid has likewise been identified in the specimen (Anderson *et al.*, 2008a: 515 and fig. 2). In relation to the intercentra, the pleurocentra are even larger than in the most mature *Doleserpeton* specimens (see above).

Most of the features that are compatible with immaturity are also compatible with alternative explanations. Disregarding phylogenetic effects, the relative size of the pineal foramen, the orbits and the nares is inversely correlated not directly to ontogeny, but to absolute body size. Of the shoulder girdle, only the cleithra and a part of the right clavicle are present; perhaps the scapulocoracoids were separated from the body together with the interclavicle (of which no trace remains). The missing parts of the braincase may likewise have drifted away prior to fossilization. Finally, the poorly ossified tail, the short ribs, and the absence of the pubis (where applicable) are also found in many or all adult lissamphibians, an observation that has (for the tail at least) not escaped the attention of Anderson *et al.*

(2008a); vomerine (and palatine) fangs are absent not only in lissamphibians, but also in all known specimens of *Doleserpeton* (but see above).

We have therefore treated *Gerobatrachus* the same way as *Doleserpeton* (see above), running one analysis with all characters scored as if the described material of *Gerobatrachus* and *Doleserpeton* were adult, and one with the potentially juvenile features of both taxa (characters 1, 10, 21, 35, 40, and 41 for *Gerobatrachus*, characters 7, 35, and 40 for *Doleserpeton*; see Appendices 1 and 2) scored as unknown.

We do not consider it most likely that the known specimen of *Gerobatrachus* was fully adult, but treating it as such is the only objective way to assess the potential impact of its ontogenetic stage on its inferred phylogenetic affinities. Coding it as adult means taking several character states at face value that *Gerobatrachus* shares with lissamphibians in general and batrachians (caudates and salientians) in particular and may thus bias our results toward those of Anderson *et al.* (2008a).

Phylogenetic analysis

All analyses were performed in PAUP* 4.0b10 (Swofford, 2003) on a Macintosh G5. The data matrix was originally created in MacClade 4.06 (Maddison and Maddison 2003) by copying McGowan's (2002) data matrix by hand, but all modifications of the resulting NEXUS file were carried out in PAUP*. These modifications are based on the literature and personal observations of specimens cited in Appendix-Table 1 and discussed in detail in Appendix 1. Because of the small number of taxa in the data matrix, we were able to use the branch-and-bound algorithm for all analyses. We treated polymorphism differently from uncertainty (PAUP* command: "pset mstaxa = variable"). Inapplicable characters were scored as unknown ('?') because PAUP* (like, as far as we know, all currently available phylogenetics programs) is not capable of treating inapplicable characters in any other way, but are marked with hyphens in Appendix 2 to make our decisions more transparent.

Five analyses were performed: three where *Doleserpeton* was interpreted as morphologically adult, one of them without *Brachydectes* and *Gerobatrachus*, one with *Brachydectes* and without *Gerobatrachus*, and one with both; and two where *Doleserpeton* was interpreted as juvenile or paedomorphic (see above) and *Brachydectes* was excluded, one with *Gerobatrachus* and one without it. Since the latter two analyses recovered the lissamphibians within the 'lepospondyls' as we expected (the possibly paedomorphic characters of *Doleserpeton* are among the few synapomorphies between this animal and lissamphibians), we did not do additional analyses with *Doleserpeton* interpreted as juvenile or paedomorphic and with *Brachydectes* included (addition of *Brachydectes* is expected to attract lissamphibians into 'lepospondyls').

Bootstrap analyses under the same five settings were conducted using heuristic searches (1000 bootstrap replicates, 20 addition-sequence replicates within each, random addition sequence, 10 trees held at each step, TBR swapping) because branch-and-bound analyses soon proved to be too time-consuming, presumably because of the high amount of character conflict in the matrix.

The two NEXUS files (with *Doleserpeton* and *Gerobatrachus* interpreted as morphologically adult, and with both interpreted as morphologically immature) are included as an online appendix.

Rooting the tree

McGowan (2002) rooted his trees on a hypothetical ancestor, requiring him to decide a priori which state of each character was plesiomorphic. (This state he always labeled 0, even when it was in the middle of a series that should be ordered as in character 37; see Appendix 1. This makes the hypothetical ancestor an all-zero ancestor.) Because of the following reasons, it seems to us that McGowan assumed that 'microsaurs' and lissamphibians are temnospondyls (which is also his result: Fig. 2) and therefore modeled his all-zero ancestor on basal temnospondyls:

- various references to "early" or "basal temnospondyls" (*e.g.,* p. 26) or "early primitive tetrapods, e.g. *Eryops*" (p. 27) to explain the polarization of most characters (it should be noted that *Eryops* lived in the Permian, later than several of the taxa in the present matrix, and has many apomorphies even if only compared to other temnospondyls);
- the explanation of character 40 in its entirety (p. 29: "Primitively, the orbit of temnospondyls was large; the derived condition of small orbits is seen in gymnophionans and microsaurs".);
- wordings like "*Trematops* and descendents [sic]" (p. 28) or "*Amphibamus* upwards" (p. 27) that (if we interpret 'descendants' as 'sister-group'

and 'upwards' as 'and its sister-group') make sense on the tree by Milner (1988) – which McGowan (2002) cites, and where the lissamphibians are temnospondyls (although the 'microsaurs' are not) – but not in the context of most other phylogenetic hypotheses; in this context, we should mention that Milner (1988) did not conduct a cladistic analysis, but only presents a phylogenetic tree (containing only lissamphibians and 'other' temnospondyls) and a list of apomorphies which support each node, without evaluating if other arrangements of the taxa discussed in the paper (various temno- and lepospondyls) would be more parsimonious;

- and the fact that the supposedly plesiomorphic state of character 31 (explained as being present in "e.g., early temnospondyls"; p. 28) is shared only by *Platyrhinops* and the all-zero ancestor in his matrix – fittingly, McGowan finds *Platyrhinops* to be the sister-group of the rest of the ingroup.

We prefer to avoid this approach because the assumptions used in the construction of all-zero ancestors are less explicit and testable than the scoring of real outgroups, which can usually be done in more objective ways. Furthermore, if the all-zero ancestor was based on temnospondyls, this is problematic because the latter are part of the ingroup; including temnospondyls in both the ingroup and the outgroup is tantamount to assuming before the analysis is conducted that the temnospondyls are paraphyletic with respect to the rest of the ingroup – even though this is part of what the analysis is supposed to test. Thus, in order to avoid assumptions on whether 'microsaurs' or lissamphibians are temnospondyls, we replaced the all-zero outgroup by *Whatcheeria* and *Crassigyrinus*, which clearly (*e.g.*, Ruta and Coates, 2007; Carroll, 2007; Warren, 2007) lie outside the smallest clade that contains all members of the ingroup of McGowan's study, and rooted the tree on *Whatcheeria*. (Not surprisingly, *Crassigyrinus* was always found to be the sister-group of the rest of the ingroup.) Both of them show, for a few characters, a state that McGowan (2002) considered derived, highlighting one of the problems that can result from the use of an all-zero outgroup.

Interpretation of the OTUs

We did not test the monophyly of the supraspecific OTUs, taking the monophyly of the taxa used as OTUs by McGowan and described by Carroll (1998) at face value (with one or two exceptions, see below). We note, however, that the monophyly of a few of these taxa is poorly supported. Nevertheless, we did not break them down into smaller, clearly monophyletic OTUs because this would have required adding many more characters and would thus have made our analyses difficult to compare with McGowan's.

When characters are not constant in a supraspecific OTU, we scored that OTU as polymorphic, with the exception of Salientia, Caudata and Gymnophionomorpha (whose internal relationships are to a large extent agreed upon), for which we reconstructed the plesiomorphic state using parsimony as shown in Fig. 5. The exception to this exception are the quantitative characters 20 and 40 (see Appendix 1), where such a reconstruction would require a squared-change parsimony analysis, detailed branch-length data, and various tests to ensure that there are no statistical artefacts (Laurin, 2004); to avoid these problems, we scored Salientia, Caudata and Gymnophionomorpha as polymorphic for character 20 and used the representatives with the most plesiomorphic values to code them for character 40.

In this paper, the term 'amphibamids' refers to the OTUs *Platyrhinops*, '*Tersomius*', *Amphibamus*, and *Doleserpeton*; 'branchiosaurids' refers to *Branchiosaurus*, *Apateon*, and *Schoenfelderpeton*; and 'microsaurs' include Tuditanidae, Pantylidae, Gymnarthridae, Hapsidopareiontidae, *Microbrachis*, Brachystelechidae, and *Rhynchonkos*. These do not imply an a priori opinion on the monophyly of any of these assemblages (depending on the phylogeny, our use of 'amphibamids' may or may not agree with the phylogenetic definition of Amphibamidae by Anderson *et al.*, 2008b). McGowan (2002) found the amphibamids and the microsaurs to be paraphyletic but the branchiosaurids to be monophyletic.

Trivially, we have changed the OTU name 'Microbrachidae' to '*Microbrachis*' because *M. pelikani* is the only species referred to Microbrachidae by Carroll and Gaskill (1978) and Carroll (1998) and because McGowan (2002) used the name *Rhynchonkos* instead of the monotypic Rhynchonkidae.

Microsaurs. – Milner (1988: 85) felt that *Carrolla* was "a juvenile ostodolep[id]id" rather than a brachystelechid as assumed elsewhere in the literature and here. However, Milner (1993) and Carroll (1998) did not mention this suggestion, and Anderson (2001,

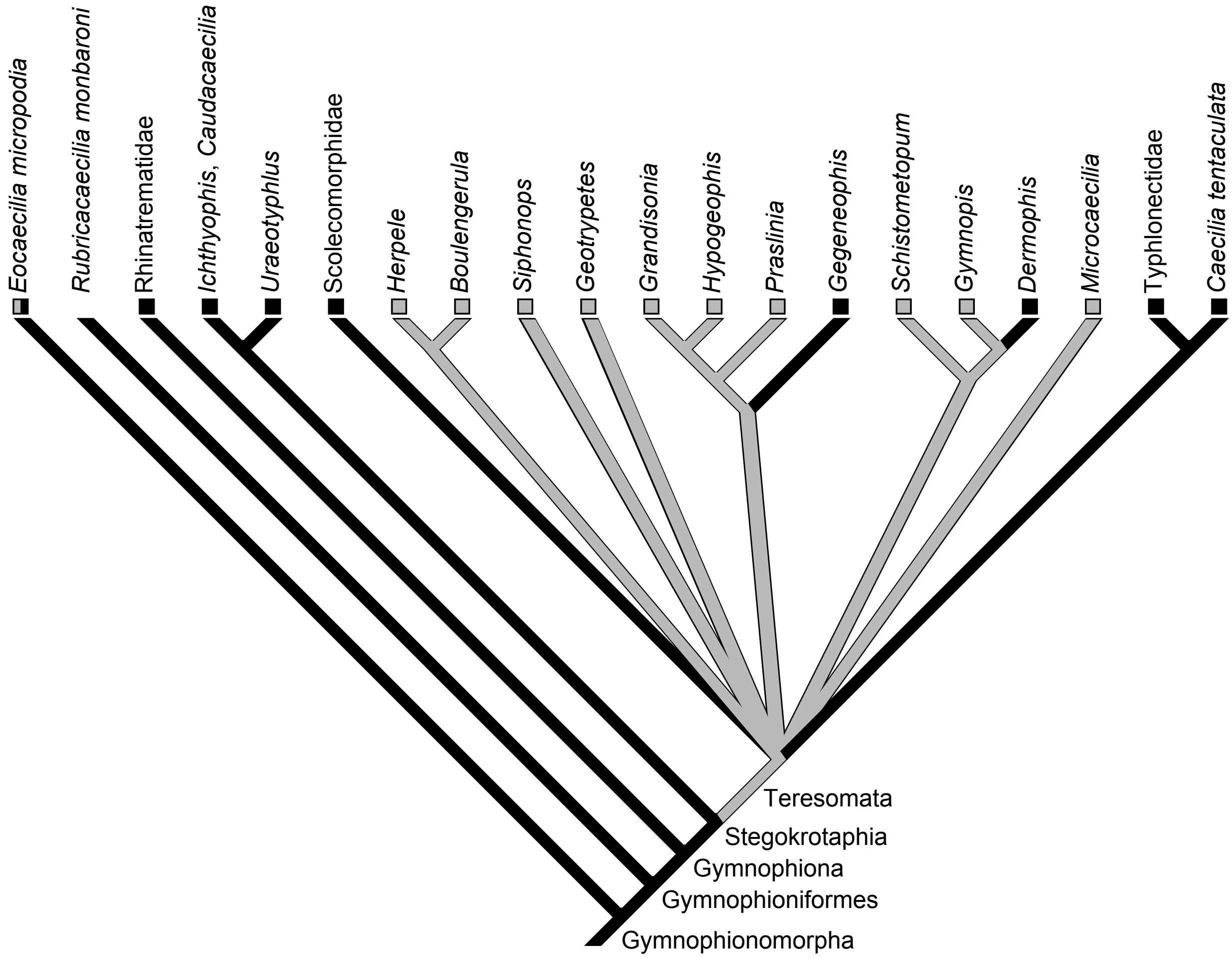


Fig. 5. A demonstration of the method used to score supraspecific OTUs: character 8 (ectopterygoid at least about half as long as the palatine [0], about a third as long or shorter [1], or absent [2]) optimized onto a supertree of Gymnophionomorpha compiled from Evans and Sigogneau-Russell (2001), Jenkins *et al.* (2007), and Wilkinson and Nussbaum (2006). No gymnophionomorph is known to have state 0; state 1 is shown as gray, state 2 as black; *Rubricacaecilia* is scored as unknown and *Eocaecilia* as partial uncertainty (state 1 or 2). Even though teresomatans known to lack an ectopterygoid are underrepresented in this tree, the basal node of Gymnophionomorpha is most parsimoniously optimized as possessing state 2. This does not change under any resolution of the teresomatan polytomy (not shown); we have tested this for each character.

2007) found *Carrolla* nested within Brachystelechidae (although the changes to Anderson's [2001] matrix by Vallin and Laurin [2004: fig. 7] introduce *Rhynchonkos* and *Eocaecilia* into the same clade, forming a five-branched polytomy), so we have, like McGowan (2002), used *Carrolla* (along with other genera, see Table 1) to code Brachystelechidae.

Carroll and Gaskill (1978) reluctantly included *Saxonerpeton* in Hapsidopareiontidae. Subsequently, Schultze and Foreman (1981) found *Saxonerpeton* as the sister-group of the (other) gymnarthrids, far away from the hapsidopareiontids. The publication by Carroll (1998), which was McGowan's (2002: table 2) only source for the coding of all microsaurs except *Rhynchonkos*, did not follow this suggestion and, as far as we have been able to find, neither mentions it nor cites Schultze and Foreman (1981). Subsequently, however, Anderson (2001, 2007) and Anderson *et al.* (2008a) confirmed Carroll and Gaskill's (1978) opinion (see also Vallin and Laurin, 2004: fig. 7) that *Saxonerpeton* was more closely related to *Hapsidopareion* than to the gymnarthrids. Because Anderson's analyses are the most comprehensive analyses of lepospondyl intrarelationships published so far, we have followed them and have, like McGowan (2002), used *Saxonerpeton* to code the Hapsidopareiontidae OTU in spite of the widely divergent findings by Ruta and Coates (2007); however, Anderson (2001, 2007) and Anderson *et al.* (2008a) did not order any of their many multistate characters, not even ones like the number of sacral vertebrae or the number of caudal rib pairs, which casts doubt on the reliability of their results (and the results of the modified version of the 2001 matrix by Vallin and Laurin, 2004: fig. 7).

Stegotretus was described as a pantylid (Berman *et al.*, 1988). Without comment, Carroll (1998) lists it among the gymnarthrids, mentioning a difference from *Pantylus* in the diagnosis, but none from any 'other' gymnarthrid. We presume an inadvertent error on Carroll's part; this is congruent with the fact that Ruta and Coates (2007) and Anderson (2007) find *Pantylus* and *Stegotretus* or *Pantylus* and (*Stegotretus* + *Sparodus*) as sister-groups. Thus, we have, presumably unlike McGowan (2002), used *Stegotretus* to code Pantylidae.

Sparodus was considered a gymnarthrid by Carroll and Gaskill (1978) and Carroll (1988, 1998), but it shares similarities, including derived ones (like the single very large coronoid tooth) with Pantylidae, and indeed Anderson (2001, 2007) found it to be a pantylid. However, the published analyses of microsaurian intrarelationships contradict each other in many ways – for example, Anderson (2001, 2007) found Gymnarthridae and Pantylidae to be close relatives, while Ruta and Coates (2007) found them far apart, and at least Anderson's (2001) results are not very well supported (Anderson, 2001: fig. 7; Vallin and Laurin, 2004: fig. 7); we have therefore decided to ignore *Sparodus* and not to use it for the coding of any OTU. This is probably not a deviation from McGowan's coding: *Sparodus* was very poorly known in 1978, Carroll (1998) devotes only a single short paragraph to it (apart from an illustration of the disarticulated skeleton), and McGowan (2002) does not cite the description of that skeleton (Carroll, 1988), so McGowan probably did not use *Sparodus* to code Gymnarthridae.

Lastly, Ruta and Coates (2007) found Tuditanidae sensu Carroll (1998) to be paraphyletic. Because they only used two of the four species included in Tuditanidae by Carroll (1998) and Carroll and Gaskill (1978), and because they also find many other groups that are commonly considered clades to be paraphyletic (such as Diadectomorpha and even Diadectidae with respect to Amniota), we here assume the monophyly of Tuditanidae sensu Carroll (1998) in order to avoid unnecessary deviations from McGowan's (2002) coding, although this is clearly a matter that deserves more attention.

Branchiosaurids. – Many nominal species have been shuffled around several times between *Branchiosaurus, Apateon, Leptorophus,* and *Melanerpeton* (Appendix 3); *Branchiosaurus* and *Apateon* are OTUs in McGowan's (2002) matrix.

In his table 2, McGowan (2002) explains that he coded *Branchiosaurus* after "*Branchiosaurus* cf. *B. petrolei*" and cites Boy (1972, 1978, 1987) as his sources (as well as personal observations of many specimens). Boy (1972, 1978) did treat "*B.* cf. *B. petrolei*", but Boy (1987) only kept the type species *B. salamandroides* (and the then poorly known *B. fayoli*) in *Branchiosaurus*. Furthermore, McGowan cites Boy (1986, 1987) as his sources for *Apateon*, but *Apateon pedestris* sensu Boy (1986, 1987), the type species of *Apateon* (which is, for most workers, about the same as the subgenus *Branchiosaurus (Protriton)* sensu Boy [1972]), contains the same specimens as "*Branchiosaurus* cf. *B. petrolei*" sensu Boy (1972, 1978). It follows that, unless he confused his references, McGowan (2002) inadvertently scored the same species twice, once as *Branchiosaurus* and once as *Apateon*. We have scored *Branchiosaurus* only after *B. salamandroides* and *B. fayoli.*

Neither a phylogenetic analysis of the many species and subspecies (!) of Branchiosauridae nor a review of the many opinions on synonymy between its species and subspecies currently exist (see Appendix 3 for a partial compilation of these opinions); in other words, it is not clear whether or not our *Apateon* OTU forms a clade which excludes our *Branchiosaurus* and *Schoenfelderpeton* OTUs. But in any case, *Branchiosaurus* and *Apateon* score identically in our matrix, except for the retention of ventral scales in the former (Schoch, pers. comm. October 5th, 2007), the greater number of uncertainties in the former, and the greater number of polymorphisms in the latter, and so do *Schoenfelderpeton* and *Apateon*, to the extent that *Branchiosaurus* and *Schoenfelderpeton* have only three unambiguous differences; thus, the unclear monophyly of our *Apateon* OTU does not seem to matter for the purposes of our analysis.

Yet another problem has recently surfaced with *Branchiosaurus salamandroides*: Milner (2007) reports that many specimens that were previously referred to it are actually larvae of a quite different dissorophoid, the trematopid *Mordex laticeps*. Furthermore, Clack and Milner (2007) find that another specimen is a larva of *Platyrhinops lyelli*. Most likely, thus, our *Branchiosaurus* OTU is chimeric and should be scored as unknown for more characters. However, as noted above, this does not seem to be a problem for the present analysis, because our *Branchiosaurus* and *Apateon* OTUs differ only in a single score and in completeness.

Amphibamids. – McGowan (2002: table 2) cited only Boy (1980), the description of *Tersomius graumanni,* as his source for the scoring of *Tersomius,* even though he scored several characters as known which are unknown in *T. graumanni.* However, *T. graumanni* is now referred to its own genus *Eimerisaurus,* which is closely related to *Micromelerpeton* (Boy, 2002) rather than being an amphibamid. Furthermore, most specimens previously referred to the type species *T. texensis* are (following Schoch and Rubidge, 2005) cautiously mentioned as "*Tersomius'* sp." by Huttenlocker et al. (2007), who found this probably monophyletic assemblage – the descriptions of which we have used to code the *'Tersomius'* OTU – to be more closely related to *Plemmyradytes* and *Micropholis* than to *'Tersomius' mosesi.* The fragmentary type specimen of *T. texensis* was not included in the analysis by Huttenlocker *et al.* (2007) or in ours. To make comparison with the literature easier, we use the designations *Eimerisaurus, 'Tersomius',* and *'Tersomius texensis',* although we do not thereby endorse the validity of the latter two designations.

Revision of the matrix

McGowan (2002) did not define the limits between the states of (potentially) continuous characters. In some, like character 32 (frontals "wide" or "narrow" without further explanation), we were forced to make far-reaching interpretations that may or may not be congruent with the original intent (we have not been able to contact McGowan), but we have tried to use state delimitations which maximize congruence with the original coding, except if the distribution of phenotypes suggested that another delimitation was more appropriate. All these are discussed in Appendix 1.

Unlike McGowan, we have not run blanket analyses where all multistate characters are ordered or unordered. Instead, following *e.g.* Wiens (2001), multistate characters that form a clear morphocline (such as 'large/small/absent' or 'many/intermediate/few') have been ordered, because the similarity between adjacent states is of the same kind as the similarity between values which are considered the same state. Thus, to reject ordering such characters would be logically equal to rejecting the lumping of different values into states. Multistate characters whose states can plausibly all be derived from each other with equal ease have not been ordered. We have not ordered cases of doubt. In Appendix 1 we state after the name of each multistate character whether it was ordered or unordered in our analyses, and justify this decision in the discussion of that character. Two characters (20 and 40) are ordered using Wiens' (2001) stepmatrix gap-weighting method, and one character (3) is partially ordered, following its own stepmatrix.

Appendix 1 constitutes the list of our changes to McGowan's data matrix, including the changes to character definitions and state delimitations as well as our detailed justifications for these modifications. (Our changes affect all characters except two and all OTUs.) The revised data matrix itself is Appendix 2.

Results

Analyzing the unaltered matrix with all characters unordered replicates the strict consensus tree (of two most parsimonious trees) shown by McGowan (2002) in his fig. 15, except that either Microbrachidae or Tuditanidae may be the sister-group of the Gymnarthridae-Gymnophiona clade (Fig. 2a); McGowan's idiosyncratic representation of that part of the tree may indicate the same trichotomy, but this is not explained in his article.

Analyzing the unaltered matrix with all multistate characters (6, 9, 37, 39, 41) ordered according to their state numbers (0 > 1 > 2 > 3) replicates the results mentioned by McGowan (2002: 20); the topology of the consensus tree (not illustrated by McGowan) is much less resolved (Fig. 2b) than the tree that results from the unordered analysis.

Having made all the changes discussed in Appendix 1, and treating the multistate characters as ordered or unordered (or neither, requiring a stepmatrix) as mentioned in their names in that appendix, we performed five parsimony analyses as explained in the Methods section, as well as five bootstrap analyses under the same conditions. The strict consensus trees, and the corresponding bootstrap trees, differ strongly (Fig. 6) from the ones that result from McGowan's original matrix (Fig. 2).

In the most parsimonious trees of all five analyses, the lepospondyls (monophyletic microsaurs, or "paraphyletic 'microsaurs + Albanerpetontidae +" Lissamphibia, or the latter three + *Brachydectes*) are the sister-group of Temnospondyli. The extant amphibians always form a monophyletic Lissamphibia which is the sister-group of Albanerpetontidae. The position of the clade which includes albanerpetontids and lissamphibians – within Lepospondyli or within Temnospondyli – varies between analyses. *Micromelerpeton* is always the sister-group of all other temnospondyls, and the tuditanids are always the sister-group of the remaining lepospondyls.

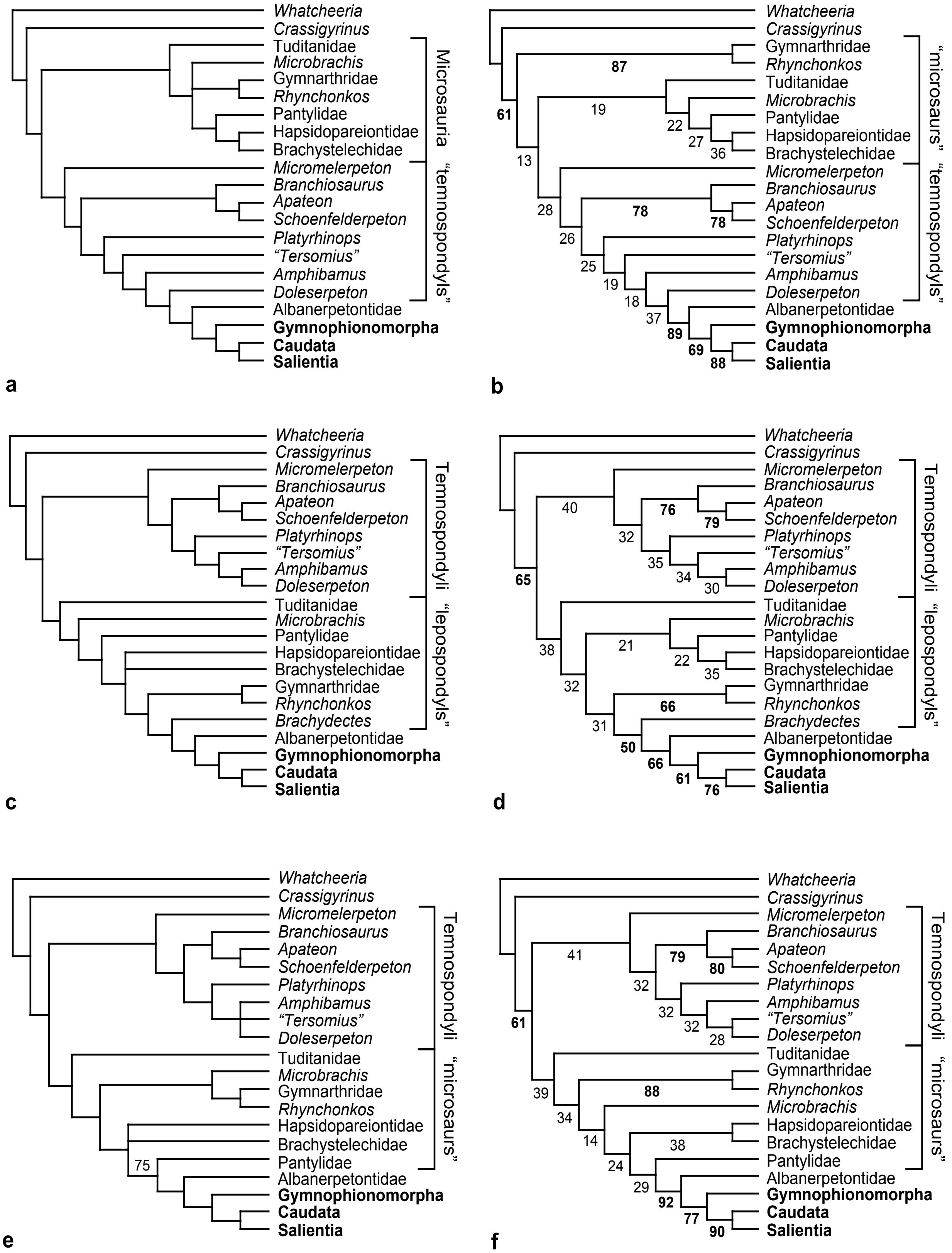
When *Brachydectes* and *Gerobatrachus* are excluded and *Doleserpeton* is coded as morphologically adult (as done by McGowan), PAUP* finds 3 MPTs (length = 152.606 steps, CI without parsimony-uninformative characters = 0.5118, RI = 0.6949, RC = 0.3756), in all of which Lissamphibia and Albanerpetontidae are nested within the 'amphibamids' as the sister-group of *Doleserpeton* (Fig. 6a). This clade is the sister-group of Branchiosauridae, and both together form a temnospondyl clade with *Micromelerpeton*.

A bootstrap analysis conducted under the same assumptions, however, reveals glaring weaknesses (Fig. 6b). The grouping of *Doleserpeton* with a clade which includes Albanerpetontidae and Lissamphibia has negligible support (bootstrap value of 37%). Temnospondyl monophyly (including Lissamphibia) only appears in 28% of the trees retained by the bootstrap analysis, and the 'microsaurs' are paraphyletic to the rest of the ingroup. Even the ingroup as a whole (minus *Crassigyrinus*) is not robust (bootstrap value of 61%). Support values above 75% are only found for Batrachia, Lissamphibia + Albanerpetontidae, Branchiosauridae, *Apateon* + *Schoenfelderpeton*, and Gymnarthridae + *Rhynchonkos*.

When *Brachydectes* is included, *Gerobatrachus* is excluded, and *Doleserpeton* coded as morphologically adult (Fig. 6c), 2 MPTs are found (length = 162.392 steps, CI without parsimony-uninformative characters = 0.4825, RI = 0.6776, RC = 0.3442), in which the Lissamphibia-Albanerpetontidae clade is the sister-group of *Brachydectes* and nested within the 'microsaurs'. The arrangement of the 'microsaur' OTUs is compatible with that proposed by Milner (1993: fig. 4), even though our matrix lacks ostodolepidids, Milner's tree (no matrix was published) lacks *Microbrachis*, Brachystelechidae, *Brachydectes*, Albanerpetontidae and Lissamphibia, and only four of the 12 characters mentioned by Milner are present in our matrix. (Milner counts 13 characters, but his C3 and C11 are different states of the same character, our character 38.)

The corresponding bootstrap analysis (Fig. 6d) does not support this 'microsaur' topology, however. The clade composed of *Brachydectes*, Albanerpetontidae and Lissamphibia has a bootstrap value of 50%, but in spite of this, temnospondyl monophyly is very poorly supported (at a value of 40%), as is lepospondyl-lissamphibian monophyly (38).

Fig. 6. Phylogenetic hypotheses resulting from our modifications of McGowan's (2002) matrix, multistate characters ordered or unordered as indicated in our Methods section. Extant taxa in bold. Numbers above internodes are percentages of MPTs (omitted if 100%), numbers below internodes are bootstrap percentages (in bold if 50 or higher). (a) Strict and majority-rule consensus (identical) of the 3 MPTs from the analysis run without *Brachydectes* or *Gerobatrachus* and with *Doleserpeton* interpreted as morphologically adult (length of each MPT = 152.606 steps, CI without parsimony-informative characters = 0.5118, RI = 0.6949, RC = 0.3756). (b) Bootstrap tree corresponding to (a). (c) Strict consensus of the 2 MPTs from the analysis run with *Brachydectes* included and *Doleserpeton* coded as morphologically adult (length = 162.392 steps, CI without uninformative characters = 0.4825, RI = 0.6776, RC = 0.3442); when *Gerobatrachus* is added and coded as morphologically adult, the same 2 MPTs (not shown) are found with *Gerobatrachus* as the sister-group of *Doleserpeton* (length = 166.478 steps, CI without parsimony-uninformative characters = 0.4701, RI = 0.6676, RC = 0.3308). (d) Bootstrap tree corresponding to (c); when *Gerobatrachus* is added and coded as morphologically adult, it is found as the sister-group of *Amphibamus*, and most bootstrap values decrease slightly, but otherwise the tree is identical (not shown). (e) Majority-rule consensus of the 8 MPTs from the analysis run without *Brachydectes* or *Gerobatrachus* and with *Doleserpeton* interpreted as immature or paedomorphic (length = 151.599 steps, CI without parsimony-uninformative characters = 0.5154, RI = 0.6969, RC = 0.3792); when *Gerobatrachus* is added and coded as morphologically immature, the same 8 MPTs result (length = 152.599 steps, CI without parsimony-uninformative characters = 0.5118, RI = 0.6965, RC = 0.3765), with *Gerobatrachus* as the sister-group of *Amphibamus* (not shown). (f) Bootstrap tree corresponding to (e); when *Gerobatrachus* is added and coded as morphologically immature, it is found as the sister-group of *Amphibamus*, and many bootstrap values decrease slightly, but otherwise the tree is identical (not shown). See text for more information. ▶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Crassigyrinus
Tuditanidae
Microbrachis
Gymnarthridae
Rhynchonkos
Pantylidae
Hapsidopareiontidae
Brachystelechidae
Micromelerpeton
Branchiosaurus
Apateon
Schoenfelderpeton
Platyrhinops
"Tersomius"
Amphibamus
Doleserpeton
Albanerpetontidae
Gymnophionomorpha
Caudata
Salientia
Microsauria
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Whatcheeria
Crassigyrinus
Gymnarthridae
Rhynchonkos
Tuditanidae
Microbrachis
Pantylidae
Hapsidopareiontidae
Brachystelechidae
Micromelerpeton
Branchiosaurus
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Schoenfelderpeton
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Micromelerpeton
Branchiosaurus
Apateon
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Platyrhinops
"Tersomius"
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Doleserpeton
Tuditanidae
Microbrachis
Pantylidae
Hapsidopareiontidae
Brachystelechidae
Gymnarthridae
Rhynchonkos
Brachydectes
Albanerpetontidae
Gymnophionomorpha
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Micromelerpeton
Branchiosaurus
Apateon
Schoenfelderpeton
Platyrhinops
"Tersomius"
Amphibamus
Doleserpeton
Tuditanidae
Microbrachis
Pantylidae
Hapsidopareiontidae
Brachystelechidae
Gymnarthridae
Rhynchonkos
Brachydectes
Albanerpetontidae
Gymnophionomorpha
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Temnospondyli
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Apateon
Schoenfelderpeton
Platyrhinops
Amphibamus
"Tersomius"
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Tuditanidae
Microbrachis
Gymnarthridae
Rhynchonkos
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Brachystelechidae
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The values for Batrachia, Lissamphibia, and (Albanerpetontidae + Lissamphibia) are consistently lower than when *Brachydectes* is excluded; the only values in the entire tree that remain above 75% are those for Batrachia, Branchiosauridae, and *Apateon* + *Schoenfelderpeton*.

When *Gerobatrachus* is included and coded as morphologically adult, the otherwise same two trees (length = 166.478 steps, CI without parsimony-uninformative characters = 0.4701, RI = 0.6676, RC = 0.3308) as those summarized in Fig. 6c result (not shown); *Gerobatrachus* is found as the sister-group of *Doleserpeton*.

The corresponding bootstrap tree (not shown) likewise has the same topology as Fig. 6d, with *Gerobatrachus* as the sister-group of *Amphibamus* at a bootstrap value of 26%. Most support values all over the tree decrease by 1 to 4%. The most notable exception is Temnospondyli, which drops from 40 to 29%; other nodes within Temnospondyli show similar behavior. Support for Lissamphibia only decreases from 61 to 57%, for (Albanerpetontidae + Lissamphibia) from 66 to 62%, for (*Brachydectes* + (Albanerpetontidae + Lissamphibia)) merely from 50 to 49%, and for the lepospondyl-lissamphibian clade from 38 to 33%. The only increase in support is found for the Hapsidopareiontidae-Brachystelechidae clade (from 35 to 37%).

The analysis where *Doleserpeton* is coded as immature or paedomorphic (i.e. characters 7 and 35 are scored as unknown and 40 as mostly unknown) and *Brachydectes* and *Gerobatrachus* are excluded finds 8 MPTs (length = 151.599 steps, CI without parsimony-uninformative characters = 0.5154, RI = 0.6969, RC = 0.3792). The majority-rule consensus tree (Fig. 6e), as well as the strict consensus, shows the Albanerpetontidae-Lissamphibia clade nested within the 'microsaurs'. *Doleserpeton* forms a trichotomy with *Amphibamus* and '*Tersomius*' within Temnospondyli.

The bootstrap analysis conducted under the same assumptions yields a very similar tree (Fig. 6f). At a bootstrap value of 39% for the 'microsaur'-lissamphibian clade and 41% for the temnospondyl clade, however, the exclusion of Lissamphibia from Temnospondyli cannot be considered significantly corroborated. Values above 75% are found for Batrachia, Lissamphibia, Albanerpetontidae + Lissamphibia, Gymnarthridae + *Rhynchonkos*, Branchiosauridae, and *Apateon* + *Schoenfelderpeton*.

Adding *Gerobatrachus* and treating it as morphologically immature does not change the topology shown in Fig. 6e or the number of MPTs (length = 152.599 steps, CI without parsimony-uninformative characters = 0.5118, RI = 0.6965, RC = 0.3765); *Gerobatrachus* is found as the sister-group of *Amphibamus* (not shown).

The corresponding bootstrap tree (not shown) is identical in topology to the one shown in Fig. 6f, except for a grouping of *Gerobatrachus* with *Amphibamus* that has a support value of 50%. The bootstrap values in the rest of the tree are identical to those in Fig. 6f or lower by up to 3%, except for the smallest clade that contains Hapsidopareiontidae and Salientia, which rises from 24% to 28%, and for two nodes within Temnospondyli that drop from 32% to 25% and 27%. The support for Lissamphibia is 74% instead of 77%; the value for Lissamphibia + Albanerpetontidae does not change.

Discussion

Implications of the size of the matrix

Because of its small size (19, 20 or 21 ingroup and 2 outgroup taxa, 38 or 39 parsimony-informative characters – less than twice as many parsimony-informative characters as taxa), the present revised matrix still provides a limited test of the interrelationships between frogs, salamanders, caecilians, temnospondyls, and 'lepospondyls', as shown by the generally low bootstrap values, most of which lie consistently below 50%. Among the most important limitations of the matrix are the following:

The number of characters in relation to the number of taxa is low, compared to recent phylogenetic analyses like those of Müller (2004), Vallin and Laurin (2004), Hill (2005), Wiens *et al.* (2005), Ruta and Coates (2007), Wible *et al.* (2007), Turner *et al.* (2007), or Luo *et al.* (2007).

By comparison with the same publications, all of which concern phylogenetic questions of comparable size to that of our analysis (or even the very same question), the number of taxa itself is very low. Only a few representatives of the dissorophoid temnospondyls are included, presumably explaining why we (and Anderson *et al.*, 2008a) fail to replicate the topology found by Huttenlocker *et al.* (2007) or that found by Anderson *et al.* (2008b), while all other temnospondyls are missing, exaggerating the convergent similarities between dissorophoid temnospondyls and 'microsaurs' and/or lissamphibians; for example, the basalmost temnospondyls retain the intertemporal bone in the skull roof, showing that separate losses of this bone occurred in temnospondyls and the ancestry of 'microsaurs', while in our tree the absence of the intertemporal (character 17, state 1) appears as an autapomorphy of the ingroup (excluding *Crassigyrinus*) as a whole. Most larger 'microsaur' taxa ('families' as classified by Carroll, 1998) are present, but neither the well-known ostodolepidids nor *Odonterpeton* (which retains small postparietals that are fused to each other, but has lost the tabulars) nor *Utaherpeton* are. The latter is the oldest known 'microsaur', and it may be one of the basalmost ones (Vallin and Laurin, 2004), although Anderson (2007) suggests a very different topology. Likewise absent are all other lepospondyls, except for our addition of the only well-known lysorophian (*Brachydectes*). Representatives of the reptiliomorph clade (which includes Amniota, Diadectomorpha and *Solenodonsaurus*), which is more closely related to the lepospondyls than the temnospondyls are (Carroll, 1995, 2007; Vallin and Laurin, 2004; Pawley, 2006; Ruta and Coates, 2007; Anderson, 2007; Anderson *et al.*, 2008a), are missing, as is the probable (Laurin and Reisz, 1999; Vallin and Laurin, 2004; Pawley, 2006; Ruta and Coates, 2007) basal lepospondyl *Westlothiana*.

Last but not least, the often polymorphic compound OTUs produce problems of their own; some of them may not even be monophyletic, as mentioned above.

Together, these problems may explain why the topology we find changes so drastically (Fig. 6) with the addition of a single taxon (*Brachydectes*) or even a change to the scores of three cells (the interpretation of *Doleserpeton* as immature or paedomorphic), even though the addition of *Gerobatrachus* hardly has any effect.

Implications of the quality of the matrix

Not only the quantity of the data contributes to the quality of a phylogenetic analysis; so does the quality of the data. Wrong scores guarantee wrong results. This may range from slightly inaccurate branch lengths or support values to outright randomized topology – and, importantly, there does not seem to be an easy way of predicting what kinds or amounts of error in the data matrix will lead to which mistakes in the tree(s). The results by Warren (2007: fig. 10A, B) may serve as an extreme example: when the score of a single cell was changed in a matrix of 27 taxa and 195 characters, the topology changed radically. We therefore consider it justified to publish articles (like Jenner, 2001) that scrutinize the data matrices of earlier publications and would like to encourage the production of more such work, unoriginal though it arguably is. Such reanalyses are extremely important to resolve the current controversy about the origin of extant amphibians. Without such studies, we risk seeing a proliferation of different phylogenies by different authors, without these ever converging. Although it may be difficult to approach, there is only a single reality, and scrutinizing data matrices to improve their accuracy (i.e. agreement with reality) is the most direct strategy to achieve a consensus. We chose to start working towards this goal with the smallest of the current matrices on lissamphibian origins, namely, McGowan's (2002) matrix. The small size of that matrix has enabled us to carefully scrutinize all characters in all taxa in a reasonable amount of time, and to use fairly sophisticated methods to deal with continuous characters (Wiens, 2001); the same will presumably not be possible with much larger matrices such as those by Ruta and Coates (2007) and Anderson (2007).

Our work shows that, when the clearly erroneous and the debatable scores are changed, the data matrix supports lissamphibian monophyly. Thus, only three published cladistic analyses which have found lissamphibian diphyly remain (Carroll, 2007: fig. 77 'arguably'; Anderson, 2007; Anderson *et al.*, 2008a); they will be reassessed elsewhere.

One reason for this drastic difference in the topologies found by McGowan (2002) and us seems to be that McGowan's matrix contains far less character conflict than our revision: the MPTs of which the strict consensus is shown in Fig. 2b (original matrix, all multistate characters ordered) have 97 steps, while the MPTs of which the strict consensus is shown in Fig. 6a (revised matrix, original taxon sampling) have 152.606 steps – about 63.56% more. Judging from his matrix and his character descriptions, it seems to us that McGowan has frequently attributed the same character state to all temnospondyls, all amphibamids, or all 'microsaurs' without carefully checking for exceptions. Similarly, none of the cells in McGowan's matrix contain a polymorphism, while 29 cells in ours do, contributing to the increase in tree length.

Analyses without Gerobatrachus

Without our addition of *Brachydectes* and *Gerobatrachus*, and when *Doleserpeton* is interpreted as morphologically adult, this lissamphibian clade – together with its sister-group, Albanerpetontidae – is nested within the amphibamid temnospondyls, as the sister-group of *Doleserpeton* (Fig. 6a), as suggested previously (Bolt, 1969; Ruta and Coates, 2007; see also Fig. 1d). This contrasts sharply with the topology supported by McGowan's (2002) original coding, in which the 'microsaurs' were part of the smallest clade which included all extant amphibians, and in which the 'temnospondyls' were paraphyletic with respect to that clade.

When *Brachydectes* is included, however, a clade composed of Lissamphibia, Albanerpetontidae, and *Brachydectes* is nested within the 'microsaurs' rather than within the temnospondyls, which form a clade that is the sister-group of the rest of the ingroup (Fig. 6c; compare Fig. 1e).

When *Doleserpeton* is interpreted as immature or paedomorphic and *Brachydectes* is excluded, the analysis behaves as if *Brachydectes* were included (except for poorer resolution among the 'microsaurs'): the clade which includes Albanerpetontidae and Lissamphibia is nested within the 'microsaurs' and not within the temnospondyls (where *Doleserpeton* is found as usual) (Fig. 6e).

Together with the low bootstrap percentages, this lability that results from the presence or absence of a single OTU (*Brachydectes*) or three changes to the coding of another (*Doleserpeton*) highlights the importance of taxonomic sampling and the impact of heterochronic characters. Excluding one of the closest proposed proposed Paleozoic relatives of Lissamphibia (*Brachydectes*) can change the position of extant amphibians. Heterochronic characters may be present in *Doleserpeton*, in other dissorophoids, and perhaps also in *Brachydectes*, and these may influence phylogenetic reconstruction, as recently emphasized by Wiens *et al.* (2005). Lissamphibian origins remain to be assessed by a study of the causes of the incompatibilities between more comprehensive studies such as Vallin and Laurin (2004), Ruta and Coates (2007) and Anderson (2007).

It is, however, interesting that the bootstrap values of Batrachia, Lissamphibia, and Lissamphibia + Albanerpetontidae are noticeably lower when *Brachydectes* is present than otherwise. This suggests that *Brachydectes* is morphologically intermediate between 'microsaurs' and lissamphibians + albanerpetontids, rather than just happening to be marginally more similar to the latter clade than the closest 'microsaurs' are.

Interpretation of Gerobatrachus *and effects of its addition to our analyses*

Gerobatrachus was described as a stem-batrachian, and the phylogenetic analysis accompanying its description (Anderson *et al.*, 2008a) found lissamphibian diphyly. In stark contrast to this finding, adding *Gerobatrachus* to either our analysis where *Brachydectes* is included (with *Gerobatrachus* coded as adult) or to the analysis where *Doleserpeton* is coded as morphologically immature (with *Gerobatrachus* treated the same way as *Doleserpeton*) does not change the results; *Gerobatrachus* is found as the sister-group of either *Doleserpeton* or *Amphibamus*, the monophyletic Lissamphibia stays in the lepospondyl clade, and the bootstrap values within this clade decrease imperceptibly. Further study of the only known specimen of *Gerobatrachus* is clearly needed, as is its inclusion in larger data matrices.

One character, the *os basale commune* (fusion of distal tarsals 1 and 2), deserves special attention, even though it is not considered in McGowan's (2002) and therefore our matrix. This compound bone, which is otherwise only known in caudates, was described as present in *Gerobatrachus* (Anderson *et al.*, 2008a). However, we see no reason to interpret the bone in question, which is one of only two preserved tarsal bones, as a *basale commune*. Comparison with the tarsi of salamanders (Shubin and Wake, 2003: figs 1B, 4, 8, 11, 12, 13B&C) and temnospondyls (Boy, 1988: fig. 10B; Milner and Sequeira, 1994: fig. 15; Shubin and Wake, 2003: fig. 3B) or even other stem-tetrapods (embolomeres: Holmes, 1984: fig. 36; colosteids: Godfrey 1989: fig. 26) shows greater resemblance of the bone in question, in shape and relative size, to other tarsals, most often the centralia 1 (traditionally called 'y' in salamanders) and 2 (traditionally called 'centrale' in salamanders), the intermedium, and distal tarsal 4. Based on its preserved position and its size, we consider an identification as the centrale 2 most likely, but this should be considered tentative as long as no reasonably complete tarsus is known for *Gerobatrachus* or in fact, as far as we know, any temnospondyl other than *Acheloma* (of which *Trematops*, figured by Shubin and Wake [2003], is a junior synonym:

Dilkes and Reisz, 1987), *Sclerocephalus* (Boy, 1988), and *Balanerpeton* (Milner and Sequeira, 1994), not counting the incompletely preserved tarsi of *Ecolsonia* (Berman *et al.*, 1985: fig. 12G) and *Eryops* (Pawley and Warren, 2006: 562) and the incompletely ossified one of *Micropholis* (Schoch and Rubidge, 2005: fig. 7A).

Moreover, we doubt the interpretation by Anderson *et al.* (2008a) of the teeth as pedicellate, a derived condition shared by Lissamphibia, *'Tersomius'*, *Amphibamus* and *Doleserpeton* in the present matrix (Clack and Milner, 1993), and have scored them as unknown; see Appendix 1, character 5.

'Microsaur' phylogeny

The interrelationships of the 'microsaurs' are relatively stable (but not robust; Fig. 6b, d, f) in our analyses, though the presence or absence of *Brachydectes* has an effect on the topology. Consistently, the partitioning of Microsauria into Tuditanomorpha and Microbrachomorpha by Carroll and Gaskill (1978) is contradicted by our MPTs and bootstrap trees; this is not surprising, because this hypothesis has never been supported by a phylogenetic analysis – indeed, the monophyly of Microbrachomorpha (*Microbrachis*, *Hyloplesion*, *Odonterpeton*, Brachystelechidae, and later *Utaherpeton*) was already doubted by Carroll and Gaskill (1978: 11, 113) themselves. However, the few characters on which the distinction between Tuditanomorpha and Microbrachomorpha is based (see Carroll, 1998) are not included in our matrix, and the bootstrap values never surpass 38% in this part of the tree. Thus, this result must be taken with considerable caution, for the reasons explained above.

The phylogenetic position of Albanerpetontidae

All of our analyses find Lissamphibia and Albanerpetontidae as sister-groups, a position so far only suggested by Pawley (2006: appendix 16), except that McGowan and Evans (1995: 145) mentioned that "a tree that reverses the positions of gymnophionans and albanerpetontids is only slightly longer" (than a tree where Albanerpetontidae and Batrachia are sister-groups, the arrangement also found by McGowan [2002], see Fig. 2) and that at least one of the 64 MPTs found by Ruta *et al.* (2003) contains the same topology. However, the bootstrap supports for Lissamphibia without Albanerpetontidae are always lower than those for Lissamphibia + Albanerpetontidae, even though they lie at or above 57% in all five analyses: the grouping of Albanerpetontidae with Lissamphibia is better supported than the exclusion of Albanerpetontidae from Lissamphibia (although not by much when *Brachydectes* is present).

By assuming the monophyly of Karauridae + Urodela (together our Caudata OTU) to the exclusion of Albanerpetontidae, our analyses are incapable of reproducing the result by Trueb and Cloutier (1991), who found *Albanerpeton* in two equally parsimonious positions as the sister-group of either *Karaurus* or Urodela (called Caudata by them). However, even though Anderson (2007) and Anderson *et al.* (2008a) have replicated this finding (as far as possible with their taxon sampling, which, like our matrix, had a single Caudata OTU), we consider this position unlikely because McGowan and Evans (1995) and McGowan (2002), among others, have conclusively argued against it (partly based on evidence that was unknown in 1991), and because our analyses never find the Albanerpetontidae and the Caudata OTUs as sister-groups, instead recovering a robust Batrachia clade which excludes Albanerpetontidae and is among the three best-supported clades of each tree. Thus, we think that the albanerpetontids are either basal parotoidians (the sister-group of Batrachia), or the sister-group of Gymnophionomorpha as found by Ruta and Coates (2007), or stem-amphibians (the sister-group of Lissamphibia).

This uncertainty makes it all the more frustrating that we have 'missed' the last living albanerpetontids by fewer than two million years: Delfino and Sala (2007) report a late Pliocene cooccurrence of *Albanerpeton pannonicum* and the extant plethodontid salamander *Speleomantes*. We hope that perhaps it will one day be possible to gain molecular data from the youngest albanerpetontid material.

Acknowledgments

We thank Jason Anderson for several electronic reprints and for alerting us to the fact that Clack and Milner (1993) had moved '*Amphibamus*' *lyelli* into its own genus *Platyrhinops*, an anonymous referee for useful comments on an earlier draft, Rainer Schoch and Florian Witzmann for comments that likewise improved this paper, Hendrik Müller for an electronic reprint and for discussion, Darren Naish for a nomenclatural discussion (see Naish, 2008), Mark Wilkinson for a constructive review of an earlier draft, and two anonymous referees for exceptionally thorough and useful reviews; finally, we are grateful to one of these two referees, who pointed out that *Karaurus* has fewer than the 15 presacral vertebrae that the text of its original description, but not the plate, credits it with.

D. M. benefited from a subsidy to university students by the Federal Republic of Austria.

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Received: 28 May 2008
Accepted: 14 August 2008

Online supplementary information is accessible through:
http://www.ctoz.nl and
http://www.repository.naturalis.nl

Appendix-Table 1. The sources for our data matrix (Appendix 2). The listed specimens of *Apateon*, *Microbrachis* and *Micromelerpeton* were examined, but did not contradict the literature or reveal additional information.

OTU	Species used to code OTU (type species first, the others in alphabetical order)
Whatcheeria	*W. deltae*
Crassigyrinus	*C. scoticus*
Branchiosaurus	*B. salamandroides*, *B. fayoli*
Apateon	*A. pedestris* (including '*Branchiosaurus* cf. *B. petrolei*'), *A. caducus*, *A. dracyi* (including *A.* '*dracyiformis*'), *A. flagrifer*, *A. gracilis*, *A. intermedius*, *A. kontheri*, *Branchiosaurus petrolei sensu* Heyler (1994); see Appendix 3 for a synonymy list
Schoenfelderpeton	*S. prescheri*
Albanerpetontidae	*Albanerpeton inexpectatum*, *A. arthridion*, *A. galaktion*, *A. nexuosum*, *A. pannonicum*, *Celtedens megacephalus, C. ibericus*
Tuditanidae	*Tuditanus punctulatus*, *Asaphestera intermedia*, *Boii crassidens*, *Crinodon limnophyes*
Hapsidopareiontidae	*Hapsidopareion lepton*, *Llistrofus pricei*, *Saxonerpeton geinitzi*
Pantylidae	*Pantylus cordatus*, *Stegotretus agyrus*
Gymnarthridae	*Cardiocephalus sternbergi* (of which *Gymnarthrus* is a junior synonym), *C. peabodyi*, *Bolterpeton carrolli, Euryodus primus*, *E. dalyae*, *E.* sp., *Hylerpeton dawsoni*, *Leiocephalikon problematicum*
Microbrachis	*M. pelikani*
Brachystelechidae	*Batropetes fritschi* (replacement name for *Brachystelechus fritschi*), *Carrolla craddocki, Quasicaecilia texana*
Rhynchonkos	*R. stovalli* (replacement name for *Goniorhynchus stovalli*)
Gymnophionomorpha	*Eocaecilia micropodia*, *Rubricacaecilia monbaroni*, various gymnophionans
Caudata	Karauridae: *Karaurus sharovi*, *Kokartus honorarius*, *Marmorerpeton* sp.; various extant and Mesozoic members of Urodela (the crown-group of Caudata); possible urodeles: all members of Batrachosauroididae, *Hylaeobatrachus croyi*, *Jeholotriton paradoxus*, *Laccotriton subsolanus*, *Liaoxitriton zhongjiani*, *L. daohugouensis*, *Pangerpeton sinense*, *Prosiren elinorae*, *Ramonellus longispinus*, all 'scapherpetontids', *Sinerpeton fengshanense*
Salientia	*Triadobatrachus massinoti*, *Prosalirus bitis*, *Vieraella herbstii*, *Notobatrachus degiustoi*, *Yizhoubatrachus macilentus*, various extant and extinct members of Anura (the crown-group of Salientia)
Platyrhinops	*P. lyelli* (formerly often called *Amphibamus lyelli*)
Amphibamus	*A. grandiceps*
'*Tersomius*'	'*T. texensis*' (but see Huttenlocker *et al.*, 2007)
Doleserpeton	*D. annectens*
Micromelerpeton	*M. credneri*
Brachydectes	*B. newberryi*, *B. elongatus*
Gerobatrachus	*G. hottoni*

coded after
Lombard and Bolt (1995), Bolt and Lombard (2000)
Panchen (1985), Panchen and Smithson (1990), Clack (1996, 1998)
Milner (1986), Boy (1987), Werneburg (1987), Heyler (1994)
Boy (1978, 1986, 1987), Werneburg (1986, 1988a, b, c, 1991, 1996, 2001, 2002), Schoch (1992, 2002), Heyler (1994), Ronchi and Tintori (1997), Boy and Sues (2000), Holmes (2000), Schoch and Fröbisch (2006); MB.Am.1080, MB. Am.1165, MB.Am.1169 (all three *A. pedestris*)
Boy (1986, 1987)
Fox and Naylor (1982), McGowan and Evans (1995), McGowan (2002), Venczel and Gardner (2005)
Carroll and Baird (1968), Carroll and Gaskill (1978)
Carroll and Gaskill (1978)
Romer (1969), Carroll and Gaskill (1978), Berman *et al.* (1988)
Carroll and Gaskill (1978), Anderson and Reisz (2003)
Carroll and Gaskill (1978), Vallin and Laurin (2004); MB.Am.808, MB.Am.815.1, MB.Am.815.2 (counterplate of MB.Am.815.1), MB.Am.815.3 (plaster mold of MB. Am.815.1), MB.Am.815.5 (plaster mold of MB.Am.815.2), MB.Am.822.2 (plaster cast), MB.Am.825.1 (plaster cast), MB.Am.830.1 (plaster cast), MB.Am.831, MB.Am.836, MB.Am.837, MB.Am.838.2 (guttapercha cast), MB.Am.839
Carroll and Gaskill (1978), Langston and Olson (1986), Carroll (1990, 1991, 1998)
Carroll and Gaskill (1978), Carroll (1998, 2000)
Duellman and Trueb (1986), Jenkins and Walsh (1993), Carroll (2000, 2007), Evans and Sigogneau-Russell (2001), Wake (2003), Müller *et al.* (2005), Müller (2006), Jenkins *et al.* (2007)
Thorn (1968), Nevo and Estes (1969), Estes (1969, 1981), Ivachnenko (1979), Carroll and Holmes (1980), Duellman and Trueb (1986), Evans *et al.* (1988, 2005), Evans and Milner (1996), Milner (2000), Gao and Shubin (2001), Rose (2003), Wang (2004), Wang and Rose (2005), Wang and Evans (2006), Carroll (2007), Averianov *et al.* (2008)
Reig (1961), Carroll and Holmes (1980), Duellman and Trueb (1986), Sanchíz (1998), Roček and Rage (2000), Púgener *et al*. (2003), Gao and Chen (2004), Carroll (2007); MNHN MAE 126a, b (part and counterpart of the holotype and only known specimen [a negative – a natural mold of the dissolved bones] of *Triadobatrachus massinoti*, along with a silicon rubber mold [a positive] and a cast [a negative])
Carroll (1964), Bolt (1979), Milner (1982, 1993), Clack and Milner (1993), Daly (1994), Schoch (2002)
Carroll (1964), Bolt (1979), Milner (1982, 1986, 1993, 2000), Clack and Milner (1993), Daly (1994), Schoch (2001)
Carroll (1964, 2000), Bolt (1977), Clack and Milner (1993)
Bolt (1969, 1977)
Boy (1972, 1995), Boy and Sues (2000), Holmes (2000), Lillich and Schoch (2007); MB.Am.1180
Wellstead (1991)
Anderson *et al.* (2008a)

Appendix 1

Institutional abbreviations

MB:	Museum für Naturkunde der Humboldt-Universität zu Berlin.
MNHN:	Muséum National d'Histoire Naturelle (Paris).
YPM:	Yale Peabody Museum (New Haven).

Modified scores, character definitions and state delimitations

Character 1: ribs longer (0) or shorter (1) than three successive articulated vertebrae in adults.

McGowan did not quantify this character; he called the states "short straight ribs" and "long straight ribs", explaining only that "[l]ong straight ribs around the body are found in early temnospondyls and Palaeozoic amphibians; short straight ribs first appear in *Balanerpeton*" (McGowan, 2002: 26). We also note that not all ribs are straight; in the present data matrix, straight ribs with expanded ends seem to be limited to the dissorophoids and Salientia, while the ribs of all other OTUs are curved and pointed.

Setting the boundary between the states at the length of three successive articulated vertebrae keeps the condition of the most mature known branchiosaurids and (marginally) the most mature *Micromelerpeton* specimens published so far as 1, as scored by McGowan (who assigned state 1 to all temnospondyls and lissamphibians in his matrix, and state 0 to all microsaurs and the all-zero ancestor), and thus congruent with the state in lissamphibians. Rib length increases in the ontogeny of *Apateon dracyi*: a larva with ribs only as long as one vertebra is pictured by Werneburg (2001, 2002), but in the ontogenetically older holotype, the longest ribs reach 3 times vertebral length (Werneburg, 2002). However, the ribs stopped growing at this stage in *Apateon gracilis* (Schoch, pers. comm. November 20th, 2007), the only species of which metamorphosed individuals are known. We have therefore scored *Apateon* as showing state 1 and *Branchiosaurus* and *Schoenfelderpeton* as unknown.

Our definition also necessitates scoring *Rhynchonkos* and even *Cardiocephalus* (and thus, because rib length is unknown in other gymnarthrids, Gymnarthridae as a whole) as 1 (Carroll and Gaskill, 1978). McGowan had scored all microsaurs as retaining long ribs.

It is possible that this character is, in temnospondyls, size-related rather than directly ontogeny-related, with small individuals (whether larval or adult) having short straight ribs and large adults having long curved ribs. Indeed, adult dissorophids have the long curved ribs that are normal for temnospondyls, while the small *Dendrerpeton* (Holmes *et al.*, 1998) and *Balanerpeton* (Milner and Sequeira, 1994) have short straight ribs despite being phylogenetically far distant from Dissorophoidea. The transformation between these two states is well documented in growth series of *Archegosaurus* and *Sclerocephalus* (Witzmann and Schoch, 2006). However, such a relation between rib length, rib curvature and body size does not exist in microsaurs (see illustrations in Carroll and Gaskill, 1978, and Carroll *et al.*, 2004: fig. 5) or lissamphibians (see illustrations in Estes, 1981, and Jenkins and Walsh, 1993). Furthermore, the temnospondyl *Acheloma* including *Trematops*, which is larger than all temnospondyls in the present matrix, has ribs shorter than those of published specimens of *Micromelerpeton* (Case, 1911: fig. 46; Boy and Sues, 2000; Holmes, 2000).

In the recently announced (Lillich and Schoch, 2007) metamorphosed specimens of *Micromelerpeton*, the ribs are unmistakably longer than three successive articulated vertebrae (Schoch, pers. comm. November 20th, 2007), so we have scored *Micromelerpeton* as showing state 0.

The only known specimen of *Gerobatrachus* exhibits state 1. For the analysis where we consider it juvenile, however, we have scored it as unknown because the ribs become relatively longer in dissorophoid ontogeny (see above).

By coding variation in rib length compared to vertebra length, we imply that the length of vertebrae depends only on absolute body size. This might be expected to be an issue in elongate animals with reduced or absent limbs, namely Gymnarthridae, *Brachydectes*, and Gymnophionomorpha; however, comparison of figs 9 (showing the plesiomorphic microsaur *Asaphestera*, considered a tuditanid) and 35 (showing the gymnarthrid *Cardiocephalus peabodyi*) of Carroll and Gaskill (1978) to each other and to fig. 1 of Wellstead (1991) (showing both species of *Brachydectes*) argues against such an interpretation for the taxa in the present matrix: they all show similar proportions except for the number of vertebrae and the length of the ribs. Additionally, neither taxa with drastically long nor taxa with drastically short vertebrae compared to the height of the vertebrae occur in this matrix; compare sauropod dinosaur necks or the difference between the aïstopods *Phlegethontia longissima* and *P. linearis* (Anderson, 2002: fig. 10).

Character 2: Caudodorsal triangular (alary) process of the premaxilla with a broad base flanked on both sides by a straight, transverse premaxilla-nasal suture (0); narrow median caudodorsal process of the premaxilla (1); broad dorsal process with straight, transverse premaxilla-nasal contact (2) (unordered).
McGowan only distinguished 'broad' (0) and 'narrow' (1) premaxilla-nasal contacts and did not explain how he defined these states; his explanation of the 'narrow' condition (which he calls 'alary process') did not enable us to understand it. In McGowan's matrix, a narrow contact (his state 1) was a potential synapomorphy of temnospondyls and lissamphibians.

No sequence is obvious for the three states, theoretically or empirically, so we have kept this character unordered.

The distribution of the three redefined states is more complex than the initial coding. Generally, state 0, the 'alary process' proper, is characteristic of temnospondyls, state 1 is standard in amniotes, and state 2 is common in lepospondyls, but there are exceptions.

Pantylus and *Stegotretus* show a condition intermediate between states 1 and 2; accordingly, Pantylidae has been scored as having one or the other.

We have scored Caudata as possessing state 0, because this state is observed in *Karaurus*, *Kokartus*, *Cryptobranchus*, *Batrachuperus*, *Salamandrella*, *Valdotriton*, *Necturus*, *Salamandra*, and *Pleurodeles*, despite the fact that *Amphiuma*, *Opisthotriton*, and arguably *Ambystoma* have state 1 (Milner, 2000); clearly, state 0 is plesiomorphic for Caudata.

Salientia shows state 1 (unknown in *Triadobatrachus*).

We have scored Gymnophionomorpha as polymorphic (states 0 and 1) because Gymnophiona possesses state 1, the condition in *Rubricacaecilia* is unknown, and *Eocaecilia* shows state 0 (Jenkins *et al.*, 2007).

The condition seen in *Gerobatrachus* (Anderson *et al.* 2008a: fig. 2a) does not fit any of the three states here, but this is not surprising given the tiny size of the specimen: the skull is less than 2 cm long, so that the relatively enormous external nares do not leave much space for an alary process (state 0). Furthermore, the skull is only visible in ventral view and the premaxilla appears to be damaged on both sides. Lastly, in the analysis where we consider the specimen to be juvenile, we have to take into account that the shape of the premaxilla-nasal contact can change in dissorophoid ontogeny. In sum, we have scored *Gerobatrachus* as unknown for the purposes of both analyses that include it.

Character 3: Teeth with one cusp throughout ontogeny (0), a labiolingual ridge at any point in ontogeny (1), two cusps arranged labiolingually at any point in ontogeny (2), or two or three cusps arranged mesiodistally at any point in ontogeny (3) (stepmatrix).
State 1 is among the most conspicuous characters shared by most lissamphibians (with the albanerpetontids as the most notable exception – assuming that they are lissamphibians; see Discussion) and all of the amphibamids in the present matrix. The sequence 0 > 1 > 2 is obvious (Bolt, 1977; Anderson and Reisz, 2003), suggesting ordering, but state 3 does not necessarily fit into this straight sequence: a lineage evolving from state 2 to state 3 or the reverse might pass through states 1 and 0, through a state (not present in this matrix) where at least three cusps are arranged in a triangle or another two-dimensional shape (compare the molariform teeth of mammalomorphs), or possibly even rotate the teeth. We have therefore applied the stepmatrix shown in Appendix-Table 2 to this character. For more information on stepmatrices see Swofford and Begle (1993: 15-18).

Appendix-Table 2. The stepmatrix for character 3.

From	To			
	State 0	State 1	State 2	State 3
State 0	0	1	2	1
State 1	1	0	1	2
State 2	2	1	0	2
State 3	1	2	2	0

McGowan (2002) only distinguished monocuspid (0) and bicuspid (1) teeth (and did not expressedly state which ontogenetic stage was coded); to account for the tricuspid teeth of albanerpetontids and *Batropetes* (McGowan explicitly mentioned this condition and coded it as monocuspid), we have added state 3. The three cusps of these teeth are arranged mesiodistally, rather than linguolabially as in the bicuspid teeth of most lissamphibians and amphibamids. The two cusps of the teeth of *Carrolla* are also arranged in a mesiodistal line, and the teeth of *Quasicaecilia* are unknown, so we have scored Brachystelechidae as only possessing state 3.

Anderson and Reisz (2003) and Anderson (2007) argue for recognizing the teeth of *Bolterpeton* and *Cardiocephalus* sp., which possess a short edge instead of a sharp point, as "weakly bicuspid", citing Bolt (1977, 1980). This is our state 1, which therefore occurs only as part of the polymorphism of Gymnarthridae. (The dissorophoid temnospondyl cf. *Broiliellus*, which shares this state according to Bolt [1977], is not part of the present matrix.) McGowan's state 1 thus becomes our state 2.

Juvenile '*Tersomius texensis*' have bicuspid teeth, at least sometimes (Bolt, 1977); this is how McGowan scored *Tersomius*, but as his source for *Tersomius* he only cited Boy (1980) who states the opposite for the "postmetamorphic" (but juvenile: Boy, 2002: 428) specimen of *Eimerisaurus* (his *Tersomius graumanni*). Because *Eimerisaurus* is closely related to *Micromelerpeton* rather than a species of *Tersomius*, we have, like McGowan has apparently done, coded '*Tersomius*' after '*T. texensis*' as showing state 2.

Character 4: Ventral scales (gastralia) well ossified (0), poorly ossified (1), or absent (2) (ordered).

McGowan did not distinguish ventral and dorsal scales; however, even outside of amniotes and diadectomorphs, the presence of one does not necessarily imply the presence of the other (Witzmann, 2007), so we treat these two characters separately; the dorsal scales are treated in our character 42. Furthermore, McGowan coded only two states, presence (0) and absence (1) of scales; we have separated states 1 (poorly ossified) and 2 (absent) for the ventral scales to account for the difference between *Platyrhinops* and Gymnophionomorpha on the one hand and Caudata, Salientia, and *Whatcheeria* on the other.

A sequence is apparent: a lineage evolving from state 0 to state 2 or the reverse would more likely than not pass through state 1. We have therefore ordered the character.

McGowan coded all microsaurs as retaining scales. However, there is no evidence for ventral scales in *Tuditanus*, and, given the preservation of some specimens (*e.g.*, Carroll and Baird, 1968), we take this as evidence of absence. Still, ventral scales are present in *Asaphestera* and *Crinodon* (Carroll and Gaskill, 1978: 183). Thus, we have scored Tuditanidae as polymorphic (states 0 and 2).

Scales are furthermore completely absent in all articulated gymnarthrid specimens, and the associations of disarticulated gymnarthrids with scales are all questionable (Carroll and Gaskill, 1978: 183), so we score Gymnarthridae as lacking ventral scales (as well as dorsal ones, see character 42).

Likewise, "[s]cales are not known among the several articulated specimens of" *Rhynchonkos* (Carroll and Gaskill, 1978: 185), and McGowan did not cite evidence to the contrary, so we have corrected McGowan's scoring of state 0 to state 2.

Scales are plesiomorphic for Gymnophiona. They are unknown in *Eocaecilia* and *Rubricacaecilia*, but the poorly ossified state of gymnophionan scales makes it unlikely that such scales would have been preserved in *Eocaecilia*; preservation of any scales in the fragmentary *Rubricacaecilia* would be unexpected. We have therefore scored Gymnophionomorpha as possessing state 1. The homology of gymnophionan scales with those that are plesiomorphically present in bony vertebrates is uncertain (Zylberberg and Wake, 1990), but to avoid unnecessary deviations from the original coding, we assume their homology, as McGowan did.

In *Platyrhinops*, coded as having lost the scales by McGowan, "[g]astralia are only present in the largest [American] specimen and then poorly ossified in relation to size compared to *A*[*mphibamus*] *grandiceps* and most Palaeozoic temnospondyls"; "poorly developed gastralia" are also present in one Czech specimen (Clack and Milner, 1993: 186-187). This is recoded as our state 1 (poorly ossified).

The condition in '*Tersomius*' and *Doleserpeton* is unknown, *contra* McGowan (Clack and Milner, 1993).

Character 5: Teeth never pedicellate (0) or pedicellate at some point in ontogeny (1).

State 1 is among the most conspicuous characters shared by most lissamphibians (but not the albanerpetontids) and certain amphibamids.

Juvenile '*Tersomius texensis*' have pedicellate teeth, at least sometimes (Bolt, 1977); this is how McGowan (who did not expressedly consider ontogenetic variation) scored *Tersomius*, but as his source for *Tersomius* he only cited Boy (1980) who states the opposite for the "postmetamorphic" (but juvenile: Boy, 2002: 428) specimen of *Eimerisaurus* (his *Tersomius graumanni*). Because *Eimerisaurus* is closely related to *Micromelerpeton* rather than a species of *Tersomius*, we have scored '*Tersomius*' after '*T. texensis*' as showing state 1.

Gerobatrachus was described as having pedicellate teeth. However, even though such teeth are not unexpected in an amphibamid (especially a possibly juvenile one), we doubt their occurrence in *Gerobatrachus*. The only available illustration is fig. 3a of Anderson *et al.* (2008a), a photo whose relatively low resolution leaves considerable room for interpretation. Of the three teeth shown in that figure, all of which were interpreted as being pedicellate, the left and the right one only show a constriction so far as we can see; the middle one may have an obliquely oriented break that may be continuous with what appears to be a break in the matrix between the middle tooth and the right one. Furthermore, even articulated fossils with pedicellate teeth most often preserve the pedicels, but not the crowns, which have fallen off, as indicated by Jenkins *et al.* (2007: 327) for *Eocaecilia*: "Although tooth crowns are rarely preserved in situ on the pedicels, disarticulated tooth crowns were recovered […]". Judging from fig. 2 (two drawings with fairly high resolution), the specimen preserves a large number of empty alveoli and a few complete teeth, but no lone pedicels. Because we have not seen the specimen and because the ontogeny of *Gerobatrachus* is unknown, we have scored the pedicely of *Gerobatrachus* as unknown for both analyses that include it.

Character 6: Number of presacral vertebrae: over 24 (0), 18 to 24 (1), 17 or less (2) (ordered).

Except for certain derived salamanders, lissamphibians other than gymnophionans share short presacral vertebral columns (state 1 or 2) with the branchiosaurids, *Amphibamus*, *Gerobatrachus*, the pantylids, and the brachystelechids. Neomorphic presacral vertebrae do not, as far as we know, ever appear *en masse*, nor do presacral vertebrae disappear *en masse*, and large saltational changes in the location of the pelvis and the caudal extent of the internal organs are likewise improbable, so we think that changes in this character are normally gradual, justifying our decision to order this character, a decision that is already implied in not coding each number of vertebrae as a separate state (Wiens, 2001).

McGowan distinguished two states within our state 2. One, however (his state 2: "16 or fewer" presacral vertebrae), was limited to Caudata, and the other (McGowan's state 3: "5-8 presacral vertebrae" – which should be 5 to 9 or 10, including the atlas [*Vieraella* (9 or 10) and *Ascaphus* (9): Púgener *et al.*, 2003; *Leiopelma* (9) and *Notobatrachus* (9): Carroll, 2007: fig. 62]) is restricted to Salientia other than *Triadobatrachus*. *Triadobatrachus* – mentioned as possessing less than 16 presacrals, but apparently not considered in the coding of 'Salientia', by McGowan – shows an intermediate state in McGowan's coding, namely 14 presacral vertebrae (Roček and Rage, 2000). Furthermore, some basal caudates have less than 16 presacral vertebrae: *Karaurus* has 12 or 13 (Ivachnenko, 1979: plate IX; pers. obs. on photos taken by M. L. in 2006; *contra* the text of Ivachnenko, 1979), *Pangerpeton* has 14 (Wang and Evans, 2006), *Liaoxitriton zhongjiani* has 15 (Wang and Rose, 2005), and *Liaoxitriton daohugouensis* has 15 or 16 (Wang, 2004), as do *Jeholotriton* and an unnamed Early Cretaceous caudate from Spain (Wang and Rose, 2005). Rather than retaining these two states, one of which occurs only as an autapomorphy of part of one OTU, we have merged them.

Extant salamanders have 10 to 60 presacral vertebrae (Duellman and Trueb, 1986), but this wide range (most of which is confined to Plethodontidae) is clearly a recent phenomenon: in addition to the examples mentioned above, *Valdotriton* has 17 presacrals (Milner, 2000), *Iridotriton* is estimated at the same number (Evans *et al.*, 2005), *Hylaeobatrachus* and *Laccotriton* have 16 (Wang and Rose, 2005), and *Chunerpeton*, described as the oldest (most likely Early Cretaceous; Wang *et al.*, 2005) cryptobranchid, has 15 (Gao and Shubin, 2003). Hence, the most parsimonious hypothesis is that Caudata primitively had no more than 17 presacrals (state 2). For early urodele phylogeny see Evans *et al.* (2005).

Character 7: Palatine fangs present (0) or absent (1) in adults.
In McGowan's matrix, state 1 united most of the ingroup – branchiosaurids, microsaurs, and *Doleserpeton*; he did not mention ontogeny.

To ensure that this character is independent of character 35 (which refers to vomerine fangs), we have reworded the definition of this character from the original which referred to "palatal" fangs. *Pantylus*, which has palatine but not vomerine fangs (see below and character 35), shows that these two characters are indeed independent. The embolomeres, which are not included in this analysis, have fangs on the palatine and the ectopterygoid, but not on the vomer; this further demonstrates that these two characters are reasonably independent.

The difference between "teeth" and "fangs", not explained by McGowan (2002: 26) except by means of a few examples, is somewhat difficult to judge in branchiosaurids. We have coded all as possessing 'fangs' because, except for clearly larval specimens, they all have two sizes of teeth on both the vomer and the palatine, and the bigger teeth occur singly or in the familiar pairs, while the smaller ones qualify as denticles (Boy, 1972, 1978, 1986, 1987). Possibly 'tusk' would be a better term than 'fang'.

The replacement pit which often accompanies the fang in a pair has, to our knowledge, not been described or illustrated in any microsaur. However, this could be related to the small size of the specimens, which makes observation of such pits difficult, or to the speed of tooth replacement, so we do not consider it as a criterion for distinguishing 'teeth' and 'fangs'; instead, we rely on size, fangs being larger than marginal teeth.

McGowan (2002: 26) stated that the tuditanid *Asaphestera* lacks fangs, presumably because the large teeth on its palatine (larger than the marginal teeth, as mentioned by McGowan) are arranged in a row parallel to the marginal dentition (Carroll and Gaskill, 1978), rather than alone or in pairs. Based on their size, however, we consider them fangs. The relevant region of the palate is unknown in *Tuditanus* and *Boii* (Carroll and Gaskill, 1978), but *Crinodon*, not mentioned by McGowan, has several fangs in an irregular (and asymmetric) distribution (Carroll and Gaskill, 1978), so we have scored Tuditanidae as possessing palatine fangs based on *Asaphestera* and *Crinodon*.

Pantylus has one large fang on each palatine (Carroll and Gaskill, 1978). McGowan did not consider these "large crushing teeth on the palatal bones" (McGowan, 2002: 26) 'fangs', perhaps because they are rather blunt, but we see no reason to doubt their primary homology to palatine fangs. On the other hand, *Stegotretus* (Berman *et al.*, 1988) lacks this tooth and instead has a hole in the palatine that accommodated the coronoid 'tusk' (which is also present in *Pantylus*). We have therefore scored Pantylidae as polymorphic.

Brachystelechidae is scored as lacking palatine fangs because *Carrolla*, the only brachystelechid which can be scored, has "[p]robably no palatal dentition" (Carroll, 1998: 63).

As far as known, *Doleserpeton* lacks palatine fangs; however, this condition is also found in juveniles of *Amphibamus* but not in the single adult specimen (Daly, 1994), so we have scored this character as unknown in *Doleserpeton* in the analysis where we treat the described material of *Doleserpeton* as morphologically immature.

Character 8: Ectopterygoid at least about half as long as palatine (0), about a third as long as the palatine or shorter (1), or absent (2) (ordered).
McGowan distinguished only two states which he called "large" and "small or absent". In his matrix, the resulting state 1 is shared by most of the ingroup – all dissorophoids other than *Platyrhinops*, all lissamphibians, and almost half of the microsaurs.

As usual with quantitative characters, McGowan did not explain how he defined the states. However, a morphological gap between 'large' and 'small' is readily apparent in the distribution. Still, this is a potentially continuous character and should therefore be ordered (Wiens, 2001).

McGowan coded '*Tersomius*', *Micromelerpeton*, *Branchiosaurus*, and *Apateon* as possessing state 1, but their ectopterygoid is at least as long compared to the palatine as that of *Platyrhinops* ('*Tersomius*': Bolt, 1977; *Micromelerpeton*: Boy, 1995; *Branchiosaurus*: Boy, 1987; *Apateon*: Boy, 1978, 1986, 1987; *Platyrhinops*: Clack and Milner, 1993), which he scored '0', and are very different from the other taxa McGowan scored as showing state 1. In '*Tersomius*' as reconstructed by Bolt (1977: fig. 2), the ectopterygoid is even longer than the palatine. Accordingly, we have scored all these OTUs as possessing state 0.

Unlike the other branchiosaurids, *Schoenfelderpeton*, scored by McGowan as having a small or absent ectopterygoid, indeed has an extremely small, toothless ectopterygoid (Boy, 1986). It is apparently never that small in the ontogeny of *Apateon* (Schoch, 1992, and pers. comm. November 20th, 2007). Thus, we have scored *Schoenfelderpeton* as having state 1.

The presence or absence of ectopterygoids is unknown in *Eocaecilia* (although state 0 can be ruled out: Jenkins *et al.*, 2007) and *Rubricacaecilia*. In gymnophionans, the ectopterygoid is usually absent, but state 1 has been reported in *Grandisonia* (Carroll and Currie, 1975), *Geotrypetes*, *Schistometopum*, *Herpele*, *Siphonops*, *Gymnopis* (Duellman and Trueb, 1986: 309, but not the fig. 13-10 cited there; for *Gymnopis*, see also Jenkins *et al.*, 2007: fig. 6C), *Microcaecilia* (Renous, 1990), *Praslinia* (Wake, 2003), and *Hypogeophis* (Müller, 2006). Less unambiguously, Wake (2003: fig. 7H) illustrates a skull of *Boulengerula taitana* (a close relative of *Herpele*; Wilkinson and Nussbaum, 2006) in ventral view, where a peculiar flange of bone of comparable size and position to the ectopterygoids of the aforementioned gymnophionans is continuous with the palatine but not the maxillary portion of the maxillopalatine, separated from the maxillary portion by a suture on the right side and a notch on the left side of the skull. However, all of these gymnophionans are teresomatans (Wilkinson and Nussbaum 2006), so that Gymnophiona, and Gymnophionomorpha as a whole, is still most parsimoniously scored as ancestrally lacking ectopterygoids (state 2), as shown in Fig. 4. (See also Swofford and Begle, 1993: 24.) The ectopterygoid seen in the abovementioned teresomatans must be considered a reversal (or a neomorph not homologous with the ectopterygoid), at least at the present state of knowledge of the fossil record.

(In the rhinatrematid *Epicriniops*, the vomerine/palatine toothrow, and the ridge to which it is attached, continues onto the pterygoid in adults [Nussbaum, 1977: fig. 1], suggesting the possibility that the ectopterygoid is present and fused to the pterygoid. However, as far as we know, this possibility is currently untested, so we take the adult condition – absence of a separate ectopterygoid – at face value.)

This leaves state 1 to *Schoenfelderpeton* and the hapsidopareiontid and brachystelechid microsaurs, and state 2 to the albanerpetontids, salamanders, frogs, pantylids, and *Doleserpeton*, as well as *Brachydectes* and Gymnophionomorpha.

Character 9: Intercentra at least as large as pleurocentra (0), markedly smaller (1), or absent (2) (ordered).
In McGowan's matrix, state 2 occurred in Caudata, Salientia, Albanerpetontidae, and most microsaurs, while state 1 was ascribed to Gymnophionomorpha, the remaining microsaurs, *Doleserpeton*, and *Micromelerpeton*; the rest of the ingroup was given state 0.

McGowan omitted the "at least" part from state 0, but most of the taxa he scored as such have more or less classical rhachitomous vertebrae, where the intercentra are larger than the pleurocentra.

Crassigyrinus has large crescentic intercentra and lacks ossified pleurocentra altogether; this almost certainly corresponds to small and cartilaginous pleurocentra and therefore to state 0.

Pleurocentra are likewise unknown from branchiosaurids; intercentra are preserved in a single specimen, the most mature one known of *Apateon gracilis* (Schoch and Fröbisch, 2006). In the absence of illustrations or descriptions, we interpret the presence of intercentra and absence of pleurocentra in that specimen, together with the fact that the intercentra ossify before the pleurocentra (Schoch and Fröbisch, 2006; Witzmann, 2006) in temnospondyls that are known to be rhachitomous (state 0), as indications that *Apateon gracilis* was rhachitomous, too. Thus, we have coded *Apateon* as 0 and *Branchiosaurus* and *Schoenfelderpeton* as unknown.

In some extant frogs, the intervertebral discs mineralize and then sometimes fuse to adjacent (pleuro)centra (Duellman and Trueb, 1986: 332). Carroll (2007: 43) therefore compares these discs to intercentra. However, such ossifications have not been reported from *Ascaphus*, *Leiopelma* (Carroll, 2007: 43), or any Mesozoic anuran as far as we know (except for atlas and probably axis intercentra, which are present in *Triadobatrachus*: Roček and Rage, 2000), so we consider these cases to be reversals and have kept McGowan's scoring of Salientia as (plesiomorphically) lacking intercentra (state 2).

While small intercentra (state 1) are present in *Eocaecilia* (Jenkins *et al.*, 2007), they are absent in Gymnophiona (Duellman and Trueb, 1986), if not Gymnophioniformes as a whole (judging from the basapophyses of *Rubricacaecilia*: Evans and Sigogneau-Russell, 2001; see also character 11). Given the mineralized intervertebral discs of some frogs mentioned above, as well as the rather chaotic distribution of intercentra in microsaurs, we cannot simply assume that state 1 is plesiomorphic for Gymnophionomorpha and have therefore scored this OTU as polymorphic (states 1 and 2).

As shown by Boy (1972, 1995), *Micromelerpeton* is rhachitomous, having much larger intercentra than pleurocentra (0), rather than gastrocentrous (1) as scored by McGowan.

Character 10: Dermatocranium and neurocranium can disarticulate from each other *post mortem* (0) or not (1) in adults.
McGowan (2002: 27) called this character absence (0)/presence (1) of "fusion of the neurocranium and dermatocranium" and did not mention ontogenetic considerations. In his original coding, state 1 ("fusion") was a potential synapomorphy of microsaurs and lissamphibians. However, obliteration of the sutures (actual fusion; Irmis, 2007) is limited to a single OTU, Gymnophionomorpha (where the large parasphenoid and the entire caudal half of the neurocranium fuse to form the so-called os basale), necessitating our present reinterpretation to avoid making the character parsimony-uninformative.

Branchiosaurids are almost always found as complete articulated skeletons, so the skull had little opportunity to disarticulate, but, like McGowan, we have scored them as 0 because their exoccipitals ossify very late (and most of the rest of the braincase may not ossify at all, even after metamorphosis; Schoch, 2002).

All codable microsaurs (Carroll and Gaskill, 1978; Carroll, 1990) except the pantylids (Romer, 1969; Carroll and Gaskill, 1978; Berman *et al.*, 1988) and possibly *Carrolla* (Langston and Olson, 1986) show state 0. To avoid problems with the interpretation of ontogeny (*Quasicaecilia*, which, taken at face value, has state 0, is only known from a very juvenile specimen), we have scored Brachystelechidae as unknown.

Also *contra* McGowan, however, we have scored *Doleserpeton* as 1 because of its high degree of neurocranium ossification, unusual for a temnospondyl, but common in lissamphibians: “Prootic and opisthotic bones are well ossified, although rarely fused. […] There is no supraoccipital bone, and indeed no room for one, as the opisthotics cover the tops of the exoccipitals and, in maturer specimens, fuse above the foramen magnum.” (Bolt, 1969: 889)

We have scored ‘*Tersomius*’ as unknown because Carroll (1964) does not make the condition clear; he does, however, explain that the braincase is less well ossified than in *Doleserpeton*.

In *Gerobatrachus*, the braincase is slightly disarticulated and highly incomplete, but the latter may reflect lack of ossification of some elements, if the specimen represents a juvenile. We have interpreted this condition as disarticulation (state 0) in the analysis where we treat *Gerobatrachus* as adult, but scored this character as unknown in the analysis where we treat it as immature or paedomorphic.

Character 11: Basapophyses absent (0) or present (1).

The so-called basapophyses of salamanders and albanerpetontids are thickenings on the cranioventral edges of the centra that usually bear articular processes. McGowan scored the condition in Gymnophionomorpha as unknown because “[i]t is not known whether the parapophyses of gymnophionans are homologous [to the basapophyses of salamanders]” (McGowan, 2002: 27). Indeed the misnamed ‘parapophyses’ of gymnophionans are closely associated with the parapophyses, unlike the basapophyses of salamanders (Duellman and Trueb, 1986: figs 13-23, 13-25; Evans and Sigogneau-Russell, 2001: fig. 6), but, judging from the condition in *Rubricacaecilia* where, unlike in at least some extant caecilians, the basapophyses are associated with the ventral edge of the centrum (Evans and Sigogneau-Russell, 2001: fig. 6), this seems to have more to do with the position of the parapophysis on the centrum (in the middle in salamanders, near the cranial edge in caecilians) than with the homology of the basapophyses of each group, so, in the absence of contradictory developmentary or fossil evidence, they should be considered primary homologues.

Basapophyses are thus present in Gymnophioniformes (Duellman and Trueb, 1986; Evans and Sigogneau-Russell, 2001), although the basapophyses of *Rubricacaecilia* lack processes (Evans and Sigogneau-Russell, 2001). In *Eocaecilia*, however, basapophyses are entirely absent (Carroll, 2000; Evans and Sigogneau-Russell, 2001; Jenkins *et al.*, 2007), so we have coded Gymnophionomorpha as polymorphic.

In Caudata, basapophyses are likewise widespread but not universal. Most importantly, they are lacking in the two karaurids that can be scored for this character (*Marmorerpeton*: Evans *et al.*, 1988: fig. 8f, h; *Kokartus*: Averianov *et al.*, 2008). They are furthermore absent in 1) all ‘scapherpetontids’ (Estes, 1981), an enigmatic, possibly polyphyletic (Evans *et al.*, 1988) caudate assemblage of unknown (and almost uninvestigated), therefore possibly basal, phylogenetic position(s) within Caudata; 2) in *Jeholotriton* (Wang and Rose, 2005) and 3) *Pangerpeton* (Wang and Evans, 2006) which are known to share a single synapomorphy (single-headed ribs on all vertebrae) with Cryptobranchoidea, ‘salamander B’ from the Middle Jurassic of England, and the Late Jurassic neocaudate *Iridotriton* (Evans *et al.*, 2005) and may therefore be assumed to lie somewhere around the origin of Urodela, and apparently 4) in the mysterious caudate *Ramonellus* (judging from the figures in Nevo and Estes, 1969). (Note that the assignment of *Jeholotriton* and *Pangerpeton*, together with all other Mesozoic East Asian caudates, to Cryptobranchoidea by Marjanović and Laurin [2007] was based only on the single-headed ribs, a number of plesiomorphies, and geography.) With basapophyses being present in most of Urodela but absent in the only two scorable certain non-urodeles (*Marmorerpeton* and *Kokartus*) as well as in most possible non-urodeles (Batrachosauroididae and *Prosiren* possess basapophyses: Estes 1969, 1981), we have scored Caudata as polymorphic because both states are observed within the group and both states can equally parsimoniously be reconstructed for the first caudate.

Like McGowan, we consider taxa in which the pleurocentra do not reach the ventral margin of the vertebral column to lack basapophyses, because they invariably lack comparable thickenings or processes on the pleuro- as well as intercentra. Carroll (2000), on the other hand, implies that basapophyses and intercentra are mutually exclusive and functionally analogous (or even homologous, though this appears doubtful to us). Therefore we cannot exclude the possibility that coding the basapophyses as unknown (= inapplicable) rather than absent in taxa that retain intercentra might have been more appropriate.

In either case, however, basapophyses are present in Albanerpetontidae but absent or unknown in all other OTUs except for the polymorphisms of Gymnophionomorpha and Caudata. This distribution makes this character parsimony-uninformative – a consequence of the usage of supraspecific OTUs.

Character 12: Radial condyle of humerus not much larger (0) or substantially larger (1) than ulnar condyle.

A gap in the distribution of this potentially continuous character is evident. According to McGowan’s coding, state 1 is present in lissamphibians and in most microsaurs.

This condyle often does not ossify in salamanders, so our (and McGowan’s) coding of all temnospondyls as 0 rather than unknown is tentative. McGowan added hemispherical shape to size, but that shape is not present in gymnarthrids and *Pantylus* (Carroll and Gaskill, 1978: figs 33G, 41B, 122A, B) and is more strongly dependent on ossification than size is.

Tuditanidae has state 0 (Carroll and Gaskill, 1978: figs 5D and 8E), *contra* McGowan (2002). In *Tuditanus* the radial condyle is even smaller than the ulnar one.

Saxonerpeton, the only scorable hapsidopareiontid, has a radial condyle that is only marginally larger than the ulnar condyle and lacks a ball in distal view (Carroll and Gaskill, 1978: figs 24, 123C). Therefore, we have changed the score of Hapsidopareiontidae from uncertain to 0.

Rhynchonkos likewise shows state 0 (Carroll and Gaskill, 1978: fig. 69B).

McGowan cited Jenkins and Walsh (1993) for his statement that *Eocaecilia* shows state 1. Neither that publication nor those by Carroll (2000, 2007) contain any description or illustration of the distal end of the humerus, but Jenkins *et al.* (2007: 344) confirm the presence of “a bulbous, hemispheroidal capitulum for the proximal radius" on the distal end of the humerus, so we have retained McGowan's score for Gymnophionomorpha (state 1).

Character 13: Tabular present (0) or absent (1).
McGowan followed Carroll's interpretation (Carroll and Gaskill, 1978; Carroll, 1998) that the large bone in the caudolateral corner of the microsaur skull roof should be considered the tabular. Carroll (1998) acknowledges that, based on its position and its large size, it could be a fusion of tabular and supratemporal; but in other lepospondyls, whenever a separate supratemporal is present, it is a long, narrow strip of bone that lies between the large tabular and the squamosal (see illustrations in Wellstead, 1982, and Bossy and Milner, 1998), so it may have genuinely vanished in the microsaurs or alternatively makes up a small part of the 'tabular' or the squamosal, while the tabular itself is present. Therefore we have retained McGowan's coding of all microsaur OTUs as possessing a tabular and lacking a supratemporal (see character 37).

Eocaecilia likewise possesses a bone that could be a supratemporal or a tabular (Jenkins *et al.*, 2007). It is absent in Gymnophiona (and the skull is unknown in *Rubricacaecilia*), but because we do not see a reason to assume that it could be a neomorph (for example, *Eocaecilia* lacks osteoderms that could have participated in the formation of the skull roof and be identified as supernumerary skull bones like in some ankylosaurian dinosaurs), we regard it as primary homologous to the supratemporal or the tabular. Unfortunately, without making an a priori assumption about whether gymnophionomorphs are temno- or lepospondyls, we cannot decide between these two options. We therefore choose to score this bone as a tabular to avoid the possibility of a counterintuitive reversal: temnospondyls have both a supratemporal and a tabular, so the condition of *Eocaecilia* can be derived from the temnospondyl condition by the loss of a bone in either case; microsaurs have only the tabular, so that, if *Eocaecilia* is coded as possessing a supratemporal instead, the reappearance of a long-lost bone would be required if Gymnophionomorpha were nested among the microsaurs. With the tabular thus being present in *Eocaecilia*, unknown in *Rubricacaecilia* and absent in Gymnophiona, we have coded Gymnophionomorpha as polymorphic.

The tabular is thus absent only in Albanerpetontidae, Caudata, Salientia, and part of Gymnophionomorpha (see the Methods section for our coding of *Brachydectes* as retaining the tabular).

Character 14: Interglenoid tubercle of atlas absent (0), present (1).
State 1 was a synapomorphy of lissamphibians and microsaurs (reversed in Salientia) in McGowan's matrix.

The atlantal centrum is unknown in all branchiosaurids, in which only the neural arches ossify (except for the most mature specimen of *Apateon gracilis*, which has ossified intercentra, but still no pleurocentra; Schoch and Fröbisch, 2006). Therefore, we have changed their scores from 0 to unknown.

Given the fact that McGowan neither mentioned *Rubricacaecilia* nor cited its description (Evans and Sigogneau-Russell, 2001), we do not know why he scored Gymnophionomorpha as ancestrally possessing the interglenoid tubercle; however, this score is the most parsimonious one, because both *Eocaecilia* and *Rubricacaecilia* (Evans and Sigogneau-Russell, 2001; Jenkins *et al.*, 2007) show this feature in spite of its absence throughout Gymnophiona (Duellman and Trueb, 1986).

McGowan likewise coded the interglenoid tubercle as absent in all amphibamids. It is, however, unknown in all of them except *Gerobatrachus,* which possesses state 1 (Anderson *et al.*, 2008a). In *Doleserpeton*, the presence or absence of the tubercle has never been described or illustrated, even though the atlas was already mentioned as known by Bolt (1969); Carroll (2007: fig. 65C) does illustrate the atlas, but the drawing in cranial view is not sufficiently three-dimensional for us to judge if a tubercle like that seen in *Gerobatrachus* (or smaller) was present (although, in that case, it would have to have been much flatter dorsoventrally than in the lissamphibians that possess it – whether this was also the case in *Gerobatrachus*, which is currently only accessible in ventral view, is unknown), and the text does not mention the condition of *Doleserpeton*. We have accordingly scored *Doleserpeton*, *Amphibamus*, *'Tersomius'* and *Platyrhinops* as unknown.

In sum, the condition of all temnospondyls in the matrix except *Gerobatrachus* (and that of *Whatcheeria*) is unknown, and state 0 is restricted to Salientia and *Crassigyrinus*; all other OTUs have state 1.

Character 15: Interclavicle large in relation to the clavicles (0), small (1), or absent (2) (ordered).
McGowan combined size and shape in this character, but the shape varies very widely in ontogeny wherever ontogenetic series are known (*Branchiosaurus*: Werneburg, 1987; *Apateon*: Werneburg, 1986, 1988a; Boy, 1987; Schoch, 1992; *Micromelerpeton*: Boy, 1995). He also did not distinguish between 'small' and 'absent'; the latter condition is likely an autapomorphy of Lissamphibia or a slightly larger clade and therefore of interest to the present study. Small interclavicles (state 1) are known from the three branchiosaurids, Gymnarthridae, *Platyrhinops*, *Amphibamus*, *Micromelerpeton*, and *Brachydectes*.

Morphological gaps in this potentially continuous character are readily apparent. Since it is potentially continuous, however, it should be ordered (Wiens, 2001).

Contra McGowan, the interclavicle of *Rhynchonkos* is unknown (Carroll, 1998: 22).

Despite its comparable anatomical position, the omosternum of some frogs does not seem to be homologous to the interclavicle because it is always at least partially cartilaginous and apparently an autapomorphy of a clade within the crown-group Anura (Duellman and Trueb, 1986). The monotreme interclavicle does have an endochondral part (which forms part of the sternum in therians), but this element has so far not been found in any other vertebrates (Vickaryous and Hall, 2006). Therefore we retain McGowan's scoring of Salientia as lacking an interclavicle.

Character 16: Number of coronoids in adults: 0 or 1 (0), 2 (1), 3 (2) (ordered).
McGowan's character 16 stated the presence (0) or absence (1) of the supratemporal. This character duplicated character 37 (supratemporal small [0]/large [1]/absent [2]) with less precision, so we have removed it (including the erroneous 'unknown' scoring of character 16 for *Branchiosaurus*).

The rostralmost coronoid is always lost first. We have therefore ordered this character.

To preserve the original numbering of the other characters, we have given the number 16 to one of the derivatives of the original character 39; McGowan's character 39 concerned the number and the dentition of the coronoids at once (in only three states), yet these two characters do not always correlate. For example, '*Tersomius*' has three toothless coronoids (Carroll, 1964), combining the most plesiomorphic state of the number with the most derived state of the dentition. We have also added the ontogenetic specification in the name of the present character to account for losses and fusions that are not visible in the fossils of adults.

Contra McGowan (2002), the lower jaws of *Platyrhinops* and *Amphibamus* have not been described or illustrated anywhere in the literature he cites, nor in the additional literature we have been able to find. Accordingly, both had to be scored as unknown.

Generally, lissamphibians lack coronoids as adults. Most salamanders possess at least one coronoid as larvae, but only neotenic species retain at most one into adulthood (Rose, 2003), so we have coded Caudata as lacking coronoids as adults (state 0), ignoring the neotenic species following Wiens *et al.* (2005). No coronoid has, to the best of our knowledge, ever been reported in Salientia or Albanerpetontidae (although lingual views of clearly articulated lower jaws of albanerpetontids are rarely available). In the few known gymnophionan ontogenies, a single coronoid fuses to the dentary and an ossification of Meckel's cartilage to form the 'pseudodentary' and bears the second, lingual toothrow (Müller *et al.*, 2005; Müller, 2006) which is also found on the 'pseudodentary' of *Eocaecilia*. Thus, adult anurans lack discernible coronoids because no such centers of ossification ever appear in ontogeny; metamorphosed urodeles lack discernible coronoids because they are resorbed in ontogeny; and adult caecilians lack discernible coronoids because they are fused to the dentaries. These three conditions may not be homologous. However, coding them as different states would lead to problems: except for ontogenetic data, the only evidence for the existence of a coronoid in adult gymnophionomorphs is the lingual toothrow. In taxa without a coronoid toothrow and without a well-studied ontogeny (such as Albanerpetontidae and *Brachydectes*), it is thus impossible to determine the presence of toothless coronoids that might have fused to the dentary. Therefore we have decided to score the adult condition at face value. However, because – ignoring gymnophionan ontogeny as mentioned – none of the OTUs in our matrix happen to show a single coronoid, we have coded the presence of a single coronoid as the same state as the complete lack of coronoids. The loss of two of the three coronoids in the adult appears homologous between Gymnophiona, Urodela, Anura, Albanerpetontidae and *Brachydectes*, even if the loss of the third coronoid may not be.

Thus, we have coded Albanerpetontidae, Gymnophionomorpha, Caudata, Salientia and *Brachydectes* as having 0 or 1 coronoids (state 0).

Where the lingual side of the lower jaw is known, at least one coronoid is present in all other OTUs, although, because the number of coronoids cannot be determined with any more precision, *Apateon*, *Schoenfelderpeton*, Tuditanidae and Pantylidae had to be coded as unknown. Two coronoids (state 1) are counted in *Rhynchonkos*, two or three (state 1 or 2) in *Micromelerpeton*, and three (state 2) in *Whatcheeria*, *Crassigyrinus*, Gymnarthridae, *Microbrachis* and '*Tersomius*'.

Character 17: Intertemporal present (0) or absent (1).
Contra McGowan, there is no sign of an intertemporal in *Platyrhinops* (Clack and Milner, 1993), *Amphibamus* (Milner, 1982), '*Tersomius*' (Carroll, 2000), or for that matter *Eimerisaurus* (Boy, 1980, 2002). It is of course imaginable that the intertemporal is actually present and fused to the supratemporal, perhaps explaining the size of the 'supratemporal' (and possibly also some of the pathologic states reported by Boy [1972] in a few *Micromelerpeton* specimens), but the same holds for all other temnospondyls in the matrix (and would make the microsaurs very difficult to score, requiring detailed and hardly testable assumptions about the fate of the intertemporal in their ancestors). We suspect a typographic error on McGowan's part.

Thus, the presence of an intertemporal (unknown in *Gerobatrachus*) is limited to the outgroups (*Whatcheeria* and *Crassigyrinus*) in our matrix, so that its absence serves as an autapomorphy of the ingroup. This is an obvious artefact of the taxon sampling (Vallin and Laurin, 2004; Pawley, 2006; Ruta and Coates, 2007; Anderson, 2007).

Character 18: Lacrimal at least about as large (in area) as the prefrontal (0), much smaller than the prefrontal (1), or absent (2) (ordered).
We have coded 'small' and 'absent' as separate states to increase the amount of signal that can be extracted from the character. McGowan only distinguished "large" (0) and "absent or very small" (1), with state 1 being limited to Gymnophiona, Caudata, and Salientia.

Morphological gaps in this potentially continuous character are readily apparent between morphologically adult specimens. Still, being potentially continuous, it should be ordered (Wiens, 2001).

McGowan (2002: 27) described the branchiosaurids as having a small lacrimal, but scored them as having a large one. The latter is correct at least for *Apateon*: the lacrimal reaches normal temnospondyl proportions (lacrimal about twice as large as prefrontal) in adults of *Apateon gracilis* (Schoch and Fröbisch, 2006). The known (immature or neotenic) specimens of *Branchiosaurus* and *Schoenfelderpeton* show a condition intermediate between our states 0 and 1, as do immature *Apateon* specimens (Boy, 1987; Heyler, 1994); rather than scoring this condition (where the lacrimal is almost as large as the prefrontal) as state 0 and potentially biasing our results against McGowan's, we have scored *Branchiosaurus* and *Schoenfelderpeton* as having state 0 or 1 (Wiens *et al.*, 2005).

Eocaecilia has a corner in the orbit where a small lacrimal could have been, although none has been found in any specimen (Jenkins *et al.*, 2007). In Gymnophiona, a small lacrimal that later fuses to the maxillopalatine has been reported in the ontogeny of *Gegeneophis* (Müller *et al.*, 2005) and *Hypogeophis* (Müller, 2006), but this bone does not lie in the position where a lacrimal would be expected; after research on caecilians that have separate septomaxillae and prefrontals as adults, Müller now considers it the prefrontal (H. Müller, pers. comm. March 30th, 2008). With the condition in *Rubri-*

cacaecilia unknown, we have scored Gymnophionomorpha as lacking a lacrimal (state 2).

Plesiomorphically, salamanders possess a small lacrimal (Thorn, 1968; Ivachnenko, 1979; Duellman and Trueb, 1986; Gao and Shubin, 2001). This corresponds to our state 1.

Frogs lack any trace of a lacrimal where determinable (Duellman and Trueb, 1986; Sanchíz, 1998), so we have coded Salientia as 2, even though the condition in *Triadobatrachus* is unknown (Roček and Rage, 2000; pers. obs. May 30th, 2008).

In sum, apart from uncertainties, we assign state 1 only to Caudata and *Brachydectes* (though in the latter the small relative size of the lacrimal could be a result of the short snout and the very large prefrontal) and state 2 to Gymnophionomorpha and Salientia.

Character 19: Scapulocoracoid a single bone (0) or two bones (1) in adults.

McGowan assigned state 1 to Albanerpetontidae, Salientia, and the temnospondyl OTUs (except for *Micromelerpeton*, which he coded as unknown).

However, we have not been able to find a mention of separate scapulae and coracoids in any temnospondyl in the literature, with the notable exception of *Mastodonsaurus* (Schoch, 1999). Instead (*e.g.*, *Onchiodon*: Boy, 1990; *Archegosaurus*: Witzmann and Schoch, 2006; *Sclerocephalus*: Meckert, 1993), there is a single ossification center in the dorsal part of the scapular portion, as is apparently the case in microsaurs (Carroll and Gaskill, 1978; Carroll, 1991).

On the other hand, it is not obvious where the phylogenetic signal in this character lies and thus how it should be coded. Separate scapular and coracoid ossifications occur not only in amniotes, diadectomorphs, and *Mastodonsaurus*, but also in frogs, in the paedomorphic salamanders *Amphiuma* and *Siren* (Goodrich, 1930), a "presumably […] younger individual" of the likely paedomorphic stem-salamander *Kokartus* (Averianov *et al.*, 2008: 480, fig. 7B), and in the distantly related (Laurin and Reisz, 1999; Vallin and Laurin, 2004; Ruta and Coates, 2007; Anderson, 2007) seymouriamorphs. Even a specimen of *Whatcheeria* shows state 1; two others have, despite the absence of a suture, a notch in the place where the scapula and the coracoid would be expected to have fused (Lombard and Bolt, 1995). It is thus possible that at least two bones or cartilages are primitively present in limbed vertebrates and may (or may not) fuse during ontogeny, as they observably do in many amniotes (*e.g.*, Vickaryous and Hall, 2006), *Mastodonsaurus* (Schoch, 1999), and apparently *Kokartus* (Averianov *et al.*, 2008: fig. 7A). If so, the phylogenetic signal of this character probably lies in the point in ontogeny at which (if ever) the bones or perhaps cartilages fuse. By only scoring the adult condition, we have hopefully extracted part of this phylogenetic signal without having to make assumptions about the ontogeny of the OTUs. (Due to the absence of independent ontogenetic data, we have coded *Whatcheeria* as polymorphic.)

As mentioned, McGowan coded all three branchiosaurid OTUs as possessing state 1. However, the endochondral shoulder girdle is to the best of our knowledge entirely unknown in *Branchiosaurus* and *Schoenfelderpeton*.

In larval, metamorphosing, and neotenic *Apateon*, the endochondral shoulder girdle consists only of a part of the dorsal part of the scapular portion (Boy and Sues, 2000); however, the coracoid portion is ossified in the most adult known specimen of *Apateon gracilis* (Werneburg, 1991; Schoch and Fröbisch, 2006) and is continuous with the scapular portion (illustrated by Werneburg, 1991; confirmed by Schoch, pers. comm. October 5th, 2007); thus, we have assigned state 0 to *Apateon*.

"Only in the largest specimens of *Microbrachis* is there any ossification of the primary shoulder girdle. At most there is only a small triangular bone, apparently restricted to the area of the scapular blade adjacent to the glenoid." (Carroll and Gaskill, 1978: 174; see also fig. 119) We regard this condition as related to the paedomorphosis of this perennibranchiate microsaur and therefore (Wiens *et al.*, 2005) score it as unknown.

"The suture between the scapula and [the] coracoid is preserved as a faint lineation that passes from the incisure across the glenoid" in *Eocaecilia* (Jenkins *et al.*, 2007: 343). Shoulder girdles are not known elsewhere in Gymnophionomorpha. Therefore we have changed the score of Gymnophionomorpha to state 1.

We have not been able to find any mention of the endochondral shoulder girdle of any of the amphibamid OTUs in the literature, except for a short statement in Carroll (1964), which implies that there was a single bone in *Platyrhinops*, and Bolt's (1969: 890) mention of the existence of a "scapulocoracoid" in *Doleserpeton*, which we take to mean that a single bone is present. Accordingly, we have scored *Platyrhinops* and *Doleserpeton* as 0 and *Amphibamus* and '*Tersomius*' as unknown. It is not evident to us why McGowan assigned state 1 to all of them; we suspect a typographic error.

We interpret Boy's (1995: 444; translated by D.M.) remark that '[t]he scapulocoracoid is almost completely ossified' in the most metamorphic specimens of *Micromelerpeton* as state 0; McGowan had scored it as unknown.

This leaves state 1 to Albanerpetontidae, Gymnophionomorpha, Salientia, and part of the polymorphic *Whatcheeria*.

Character 20: Ratio of width of cultriform process of parasphenoid to length of skull base (see state definitions in Appendix-Table 3) (ordered).

McGowan did not quantify this character or explain how he divided this continuous character into states, only distinguishing "slender cultriform process" (0) and "wide anteriorly projecting parasphenoid" (1) and noting that state 0 occurred in "temnospondyls" (McGowan, 2002: 27); state 1 united Gymnophiona, Caudata and Salientia in his matrix. We have measured (Appendix-Table 3, Appendix-Fig. 1) the length of the skull base as the rostrocaudal distance between the rostral margin of the basipterygoid processes and the caudal margin of the skull in the sagittal plane in ventral view, and the width of the cultriform process rostral to the bulk of the constriction (or anywhere along the length, if a constriction is absent). To divide this continuous character into discrete states, we have used stepmatrix gap-weighting (Wiens, 2001): each observed value is a separate state, the weight of each transition is directly proportional to the difference between the values that the states represent, and the character is ordered. As the factor that converts the mentioned differences into the weights of the transitions, we

Appendix-Table 3. Ratio of the width of the cultriform process of the parasphenoid to the length of the skull base in ventral view (character 20), ordered by ratio. All values are rounded (the unrounded values are plotted in Appendix-Fig. 1). OTUs in parentheses mean that we consider the species in question an outlier and have not used it for the coding of the OTU, as explained in the text. Within Caudata and Salientia, all Mesozoic species, as well as the extant *Ascaphus*, *Leiopelma*, Cryptobranchidae and Hynobiidae, are marked in boldface because they – except *Chunerpeton tianyiense* – were preferred for determining the coding of the Caudata and Salientia OTUs. The weight of each transition is the difference in the absolute value of the ratio (5th column) divided by the total difference in this ratio between state 0 (as shown by *Celtedens megacephalus*) and state V (as shown by *Salamandra atra*), i.e., (~0.667 – ~0.054 =) ~0.613, and multiplied by the average maximum weight of the characters (except characters 20 and 40) in the present matrix, i.e., 1.375. States beyond that of *Salamandra atra* are not considered because PAUP* does not allow more than 32 states per character (0 to 9 and A to V). See text for more information. *, rounded up from 0.00548246 to prevent rounding error in the sum: the unrounded values add up to 1.375, but the rounded values would only add up to 1.374.

OTU	Measured species	Source	Ratio	Difference to following OTU	State of character 20	Weight of transition to next state
Albanerpetontidae	*Celtedens megacephalus*	McGowan, 2002: fig. 13	0.1	0.054	0	0.123
Microbrachis	*M. pelikani*	Vallin and Laurin, 2004	0.154	0.013	1	0.064
(Salientia)	*Rhinophrynus dorsalis*	Duellman and Trueb, 1986: fig. 13-17	0.166	0.015	–	
Platyrhinops	*P. lyelli*	Clack and Milner, 1993	0.182	0.010	2	0.024
Pantylidae	*Pantylus cordatus*	Carroll and Gaskill, 1978	0.192	0.007	3	0.018
Brachystelechidae	*Quasicaecilia texana*	Carroll, 1998	0.2	0.017	4	0.040
Gymnarthridae	*Euryodus primus*	Carroll and Gaskill, 1978	0.217	0.022	5	0.050
Crassigyrinus	*C. scoticus*	Clack, 1996	0.239	0.011	6	0.025
Tuditanidae	*Tuditanus punctulatus*	Carroll and Gaskill, 1978	0.25	0.023	7	0.052
Schoenfelderpeton	*S. prescheri*	Boy, 1986	0.273	0.013	8	0.030
Apateon	*A. caducus*	Boy and Sues, 2000	0.286	0.014	9	0.033
Salientia	***Triadobatrachus massinoti***	Roček and Rage, 2000	0.3	0.013	A	0.029
Gymnarthridae	*Cardiocephalus sternbergi*	Carroll and Gaskill, 1978	0.313	0.003	B	0.008
Brachystelechidae	*Carrolla craddocki*	Carroll, 1998	0.316	0.002	C	0.006*
Doleserpeton	*D. annectens*	Bolt, 1969	0.318	0.015	D	0.035
Amphibamus	*A. grandiceps*	Milner, 2000	0.333	0	E	
Branchiosaurus	*B. salamandroides*	Boy, 1987	0.333	0	E	
Tuditanidae	*Crinodon limnophyes*	Carroll and Gaskill, 1978	0.333	0.030	E	0.069
Rhynchonkos	*R. stovalli*	Carroll and Gaskill, 1978	0.364	0.011	F	0.026
Micromelerpeton	*M. credneri*	Boy, 1995	0.375	0	G	
Brachystelechidae	*Batropetes fritschi*	Carroll and Gaskill, 1978	0.375	0.014	G	0.032
Hapsidopareiontidae	*Saxonerpeton geinitzi*	Carroll and Gaskill, 1978	0.389	0.040	H	0.105
(Salientia)	*Leptodactylus bolivianus*	Duellman and Trueb, 1986: fig. 13-17	0.429	0.006	–	
'*Tersomius*'	'*T. texensis*'	Bolt, 1977	0.435	0.020	I	0.045
Hapsidopareiontidae	*Hapsidopareion lepton*	Carroll and Gaskill, 1978	0.455	0.024	J	0.054
Brachydectes	*B. elongatus*	Wellstead, 1991	0.478	0.021	K	0.154
(Caudata)	***Chunerpeton tianyiense***	Carroll, 2007: fig. 47	0.5	0	–	
(Salientia)	*Calyptocephalella gayi* ('*Caudiverbera caudiverbera*')	Duellman and Trueb, 1986: fig. 13-17	0.5	0.045	–	
Salientia	***Leiopelma auroraensis***	Sanchíz, 1998: fig. 17	0.545	0.010	L	0.023

Salientia	***Ascaphus* sp.**	Carroll and Holmes, 1980	0.556	0	M	
Caudata	*Dicamptodon* sp.	Milner, 2000	0.556	0	M	
Caudata	*Stereochilus marginatus*	Duellman and Trueb, 1986: fig. 13-4	0.556	0.021	M	0.049
Caudata	***Batrachuperus sinensis***	Carroll and Holmes, 1980	0.577	0.011	N	0.026
Gymnophionomorpha	*Eocaecilia micropodia*	Carroll, 2000	0.588	0.012	O	0.027
Salientia	*Notaden nichollsi*	Duellman and Trueb, 1986: fig. 13-17	0.6	0.015	P	0.035
Salientia	***Notobatrachus degiustoi***	Sanchíz, 1998: fig. 20	0.615	0	Q	
Caudata	***Hynobius naevius***	Carroll and Holmes, 1980	0.615	0.016	Q	0.037
Caudata	*Siren* sp.	Carroll and Holmes, 1980	0.632	0.008	R	0.019
Gymnophionomorpha	*Ichthyophis glutinosus*	Carroll, 2000	0.64	0.007	S	0.016
Caudata	*Hynobius tsuensis*	Carroll and Holmes, 1980	0.647	0.020	T	0.045
Caudata	*Taricha granulosa*	Duellman and Trueb, 1986: fig. 13-3	0.667	0	U	
Caudata	***Opisthotriton* sp.**	Carroll and Holmes, 1980	0.667	0	U	
Salientia	***Yizhoubatrachus macilentus***	Gao and Chen, 2004	0.667	0	U	
Salientia	*Phyllomedusa venusta*	Duellman and Trueb, 1986: fig. 13-18	0.667	0	U	
Salientia	*Triprion petasatus*	Duellman and Trueb, 1986: fig. 13-18	0.667	0.033	U	0.076
Caudata	*Salamandra atra*	Carroll and Holmes, 1980	0.7	0.014	V	
Salientia	*Brachycephalus ephippium*	Duellman and Trueb, 1986: fig. 13-17	0.714	0	(V)	
Salientia	*Rhamphophryne festae*	Duellman and Trueb, 1986: fig. 13-17	0.714	0.013	(V)	
Caudata	***Salamandrella keyserlingii***	Duellman and Trueb, 1986: fig. 13-3	0.727	0.023	(V)	
Caudata	***Andrias davidianus***		0.75	0	(V)	
Salientia	*Pelobates fuscus*	Duellman and Trueb, 1986: fig. 13-17	0.75	0	(V)	
Caudata	*Phaeognathus hubrichti*	Carroll and Holmes, 1980	0.75	0.015	(V)	
Caudata	***Cryptobranchus alleganiensis***	Carroll and Holmes, 1980	0.765	0.005	(V)	
Caudata	***Kokartus honorarius***	Milner, 2000	0.769	0.009	(V)	
Caudata	*Rhyacotriton olympicus*	Duellman and Trueb, 1986: fig. 13-3	0.778	0	(V)	
Caudata	*Plethodon jordani*	Duellman and Trueb, 1986: fig. 13-4	0.778	0.222	(V)	
Caudata	*Pseudobranchus striatus*	Duellman and Trueb, 1986: fig. 13-3	0.8	0.018	(V)	
Caudata	*Erycea neotenes*	Duellman and Trueb, 1986: fig. 13-4	0.818	0.015	(V)	
Caudata	***Liaoxitriton daohugouensis***	Wang, 2004	0.833	0	(V)	
Salientia	*Osteocephalus leprieurii*	Duellman and Trueb, 1986: fig. 13-18	0.833	0.833	(V)	
Caudata	*Ambystoma maculatum*	Carroll and Holmes, 1980	0.917	0.017	(V)	
Caudata	*Valdotriton gracilis*	Milner, 2000	0.933	0.067	(V)	
Caudata	*Amphiuma means*	Duellman and Trueb, 1986: fig. 13-3	1	0	(V)	
Caudata	***Pangerpeton sinense***	Wang and Evans, 2006	1	0	(V)	
Salientia	*Gastrotheca walkeri*	Duellman and Trueb, 1986: fig. 13-15	1	0	(V)	
Salientia	*Hemiphractus proboscideus*	Duellman and Trueb, 1986: fig. 13-18	1	0	(V)	
Salientia	*Smilisca baudinii*	Duellman and Trueb, 1986: fig. 13-18	1	0	(V)	
Salientia	*Phrynohyas venulosa*	Duellman and Trueb, 1986: fig. 13-18	1	0.133	(V)	
Caudata	***Karaurus sharovi***	Ivachnenko, 1979	1.133	0.117	(V)	
Caudata	*Necturus* sp.	Carroll and Holmes, 1980	1.25	0	(V)	
Salientia	*Barbourula busuquanensis*	Duellman and Trueb, 1986: fig. 13-17	1.25	0	(V)	
Salientia	*Gastrotheca ovifera*	Duellman and Trueb, 1986: fig. 13-18	1.25	0	(V)	
Salientia	*Pseudacris clarkii*	Duellman and Trueb, 1986: fig. 13-18	1.25	0.135	(V)	
Caudata	***Habrosaurus dilatus***	Milner, 2000	1.385		(V)	

have not chosen 1 as suggested by Wiens (2001), but 1.375, which is the average maximum possible weight of each character in the present matrix (i.e. their number of states minus one) if we disregard characters 20 and 40. These weights are used to construct a symmetric stepmatrix (see supplementary information) that produces an ordered character the states of which are not equidistant.

PAUP* can only deal with multistate characters up to 32 states. Because of polymorphism, we found more than 32 states in the terminal taxa. We have recognized 32 states, starting from the lowest values. The states which could not be recognized by PAUP* all represent variation within OTUs (Salientia and Caudata) whose plausible ancestral morphotype is encompassed in our 32 states, so this should not be a problem.

By using "cultriform process" vs. "parasphenoid" in the names of his character states, McGowan implied using the distinctness of the cultriform process as a criterion for character delimitation. However, whether the cultriform process is distinct from the basal plate of the parasphenoid depends less on the breadth of the cultriform process than on the presence of lateral processes on the parasphenoid that cover the basipterygoid processes of the basisphenoid, as shown by the very similar values for *Siren* and *Hynobius* (0.61-0.65, measured in the illustrations by Carroll and Holmes, 1980) where the cultriform process is unambiguously distinct from the basal plate in *Hynobius* but continuous with it in *Siren*, as well as by the value of 1 found in *Pangerpeton* (Wang and Evans, 2006) in which the cultriform process is very distinct, so we have not used this additional criterion.

The following codings are not immediately obvious from Table 3 and deserve comment:

Tuditanidae is polymorphic, with *Tuditanus* possessing state 7 and *Crinodon* showing state E.

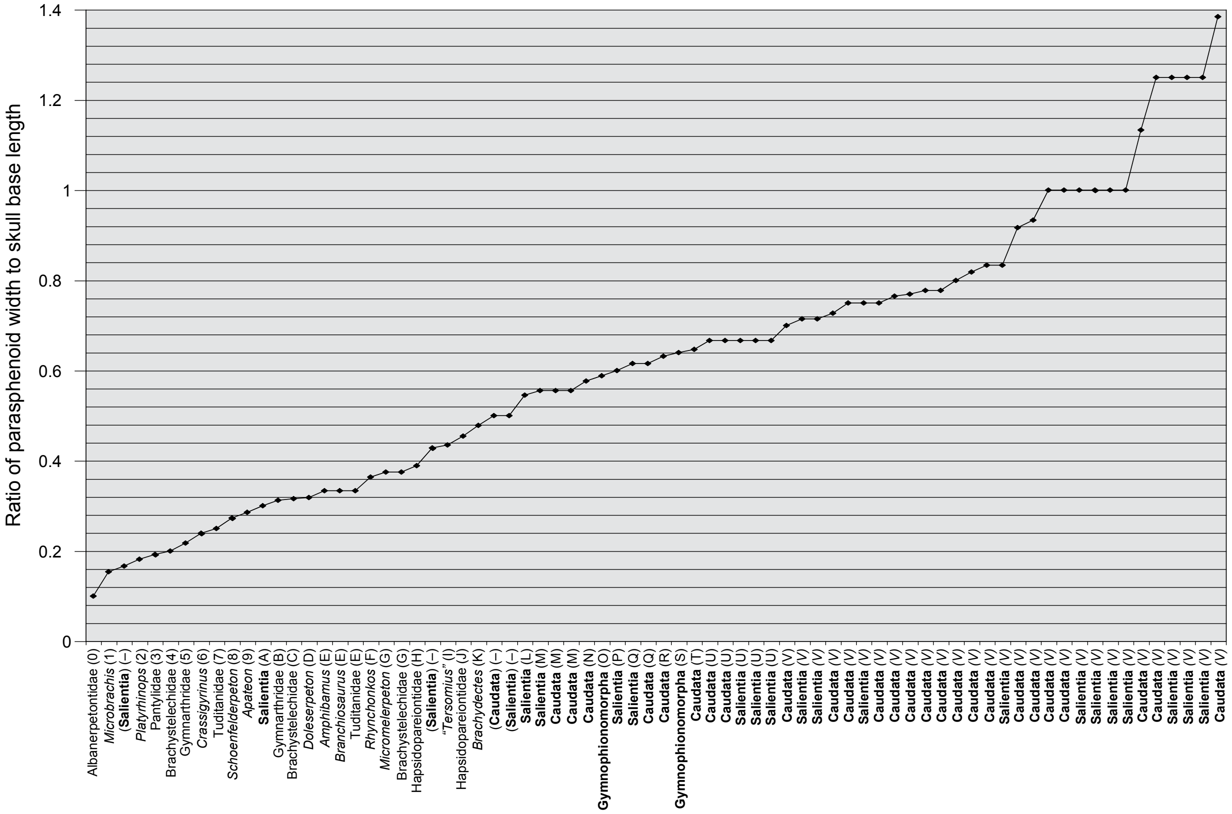
Hapsidopareiontidae is polymorphic, with *Saxonerpeton* showing state H and *Hapsidopareion* possessing state J.

Brachystelechidae is likewise polymorphic, with *Quasicaecilia* having state 4, *Carrolla* state C and *Batropetes* state G.

So is Gymnarthridae, with state 5 in *Euryodus primus* and state B in *Cardiocephalus sternbergi*.

Eocaecilia shows state O, and the gymnophionan *Ichthyophis* shows state S, making Gymnophionomorpha polymorphic.

The only measured caudate with a state lower than M is *Chunerpeton* (between states K and L). Because it is thought to be nested several nodes within the crown-group (as a cryptobranchid), and because the measured karaurids (*Karaurus* and *Kokartus*) as well as the extant cryptobranchids (*Andrias*



Appendix-Fig. 1. Ratio of cultriform process width to skull base length in dorsal view (character 20). The line drawn between the data points is meant to visualize the sizes of the morphological gaps by its varying steepness. The state of each OTU is indicated after its name. Extant taxa in bold. Data shown in Appendix-Table 3.

and *Cryptobranchus*) have very high ratios, we regard the condition in *Chunerpeton* as autapomorphic and have scored Caudata as possessing states M, N, Q, R, T, U, and V.

Triadobatrachus has a very narrow cultriform process (state A) (Roček and Rage, 2000: fig. 3). Otherwise, Salientia shows states L and higher, with the lone and clearly derived exceptions of *Rhinophrynus* (between 1 and 2), *Leptodactylus* (between H and I), and *Calyptocephalella* ('*Caudiverbera*') (between K and L) (Appendix-Table 3; Appendix-Fig. 1). We have therefore scored Salientia as possessing states A, L, M, P, Q, U and V.

Character 21: Pubis ossified (0) or not (1).
The pubis does not ossify in *Crassigyrinus*, branchiosaurids, caudates, and salientians (with the exception of Pipidae: Goodrich, 1930; Cannatella and Trueb, 1988); the situation is unknown in *Eocaecilia* (Jenkins *et al*., 2007) and inapplicable in Gymnophioniformes (except possibly *Rubricacaecilia*, in which the presence of limbs and limb girdles is unknown).

Because we have not been able to find descriptions or illustrations of the pubes of *Amphibamus* and *Platyrhinops*, nor statements on whether they are known at all, we have scored both OTUs as unknown.

McGowan scored '*Tersomius*' as having an ossified pubis, but the referral of any pelvis to *Tersomius* is too uncertain (Huttenlocker *et al*., 2007), so we have coded '*Tersomius*' as unknown.

On the other hand, McGowan scored *Micromelerpeton* as unknown, but the recently discovered largest and most mature specimens have an ossified pubis (Lillich and Schoch, 2007), so we have assigned it state 0.

Contradictory statements exist in the literature about *Brachydectes*. Wellstead (1991) states on p. 25 that "[t]he ilium, ischium, and pubis form a simple, triangular plate with a modest iliac blade at the apex, but do not co-ossify", yet explains that, of all lysorophians, remains of the pelvic girdle are only known from one specimen each of *B. newberryi* (both ilia and ischia: p. 33, fig. 8C) and *B. elongatus* (the left ilium: p. 45, fig. 20C). Schoch and Milner (2004: 360) cite Wellstead (1998) for stating that *Brachydectes* lacks an ossified pubis, but we have not been able to find such a claim in Wellstead (1998) who simply repeats (on p. 142) the sentence cited above *verbatim*. Because of the disarticulated condition of the *B. newberryi* specimen that preserves the ilia and ischia, we have scored the pubis of *Brachydectes* as unknown.

In the only known specimen of *Gerobatrachus*, the pubes are missing; given the good preservation of the articulated ischia and the caudalmost presacral vertebrae, this suggests a lack of ossification. We have accordingly scored *Gerobatrachus* as possessing state 1 for the analysis where we treat it as adult, but as unknown for the analysis where we treat it as immature or paedomorphic.

Character 22: Opercular absent (0) or present (1).
This refers to the ear ossicle found in most extant salamanders and frogs (*os operculare auris*), not to the largest bone in the gill lid of more plesiomorphic bony vertebrates (*os operculare*), which is not homologous to any ear ossicle. In McGowan's matrix, presence of the opercular (state 1) is a synapomorphy of Caudata and Salientia, with the situation unknown in Albanerpetontidae.

Usually the opercular is thought to be restricted to salamanders and frogs (and now *Eocaecilia*; Jenkins *et al*., 2007). However, in the explanation of the present character, McGowan (2002: 27) notes: "It is not known whether the accessory ossicle (AO) seen in some microsaurs *e.g.,* gymnarthrids, ostodolep[id]ids and *Rhynchonkos*) is homologous or analogous with the opercular (Carroll […], 1998). Therefore, it is treated as unknown in those microsaurs that are known to possess an AO." However, Carroll and Gaskill (1978: all quotes 163-164) show that the matter is more complicated:

"Except in *Pantylus*, the otic capsule is open ventrally [in microsaurs], posterior or medial to the footplate of the stapes. In *Pantylus*, this area is filled in with a small but distinct ossification not known in other early tetrapods. An ossification in this position brings to mind the opercular bone in salamanders […]. It appears much too fully integrated with the skull, in this genus at least, to function as a movable ear ossicle."

"In *Goniorhynchus* [= *Rhynchonkos*], gymnarthrids, and ostodolep[id]ids, a further ear ossicle [= other than the stapes] has been consistently observed. It is referred to simply as an accessory ossicle. Typically, it is a small, vertically oriented plate of bone, suspended above the stem of the stapes. It must have been fairly strongly set in connective tissue to have survived the decomposition of the skulls without significant displacement. It may be significant that it occurs in all the tuditanomorph microsaurs in which the occiput is behind the level of the quadrate, and in no other forms."

"Without implying any significant relationship, the closest analogy with the ear structure of microsaurs may be provided by the modern salamanders. […] Although there is no supporting evidence from physiological experimentation, it is assumed that two methods of sound conduction are practiced by urodeles: from the jaws via the stapes in aquatic forms; and through the forelimbs and shoulder girdle via the 'opercularis' muscles and the operculum in terrestrial forms […]. There is, of course, no possibility of verifying the presence of any opercularis muscle in microsaurs, but the possibility of there being more than a single sound-conducting system is suggested by the configuration of the stapes and its relation to surrounding structures."

"Ostodolep[id]ids, gymnarthrids, and goniorhynchids [= rhynchonkids = *Rhynchonkos*] all have an unossified area adjacent to the footplate of the stapes that might be attributed to the presence of a salamanderlike operculum. In *Pantylus* there is, however, a separate but quite immovable ossification in this area. There is also the possibility that the accessory ossicle acted in some way like an operculum, to detect airborne vibrations, while the massive stapes transmitted groundborne, low[-] frequency oscillations." (This would, however, be unlike terrestrial frogs, where – whenever both are present – the operculum detects low-frequency vibrations, whether air- or groundborne, and the stapes high-frequency airborne ones; unlike terrestrial salamanders, where the operculum is the only bone that functions in hearing and again detects low-frequency vibrations; and unlike aquatic frogs and salamanders, in which the operculum is absent and the stapes transmits water-borne oscillations; see below and Lombard and Bolt, 1979.)

However, Jenkins *et al*. (2007: 359) add: "The accessory ear ossicle described by Carroll and Gaskill (1978: 163, fig. 113) in *Rhynchonkos* and other microsaurs is consistently suspended above the stem of the stapes; in shape and position this ossicle appears to differ from the operculum of *Eocaecilia*, which [like in batrachians] is oval and, in one specimen at least, is preserved in close association with the fenestra ovalis."

In sum, the opercular of frogs and salamanders, the 'accessory ossicle' of gymnarthrids and *Rhynchonkos*, and possibly the unique bone of *Pantylus* might be analogous in function, but while primary homology to the opercular cannot be ruled out for the extra ossicle of *Pantylus*, it is ruled out between lissamphibians on one hand, and gymnarthrids and *Rhynchonkos* on the other, by Jenkins *et al.* (2007). Because no additional research seems to have been done on this question, we have changed the scores of Gymnarthridae and *Rhynchonkos* to state 0, but that of Pantylidae to unknown.

Furthermore (Lombard and Bolt, 1979: 46), "[t]he otic opercular bone fails to develop in those frogs and salamanders which are totally aquatic in adult life", and in amphibious and terrestrial salamanders it develops only at metamorphosis. The reason seems to be that the opercular system can pick up groundborne and low-frequency airborne vibrations, but not waterborne ones. Therefore we have scored all OTUs that are only known from unambiguously obligatorily aquatic individuals – *Whatcheeria*, *Crassigyrinus*, *Micromelerpeton*, *Branchiosaurus*, *Schoenfelderpeton*, *Microbrachis*, and *Brachydectes* – as inapplicable (i.e. unknown). We have also scored *Apateon* as unknown (rather than absent) because most of its braincase apparently does not ossify even after metamorphosis.

The condition in Gymnophiona should be interpreted as inapplicable rather than absent, because the opercular system not only includes the bone, but also the opercular muscle, which connects the bone to the shoulder girdle; no trace of a shoulder girdle is present in extant caecilians, which means that the opercular system cannot be present (Milner, 1988; Jenkins *et al.*, 2007). Because both the braincase and the presence or absence of the shoulder girdle are unknown in *Rubricacaecilia*, we have had to rely entirely on *Eocaecilia* to code Gymnophionomorpha; in *Eocaecilia*, as mentioned above, the opercular is present (Jenkins *et al.*, 2007). We have accordingly changed the score of Gymnophionomorpha to state 1.

In sum, state 0 unites the amphibamids, Brachystelechidae, Hapsidopareiontidae, Tuditanidae, Gymnarthridae and *Rhynchonkos* in our matrix, while state 1 is found in Gymnophionomorpha, Caudata and Salientia. All other OTUs are scored as unknown (or inapplicable).

Character 23: Postorbital present (0) or absent (1).
State 1 occurs in Albanerpetontidae, Caudata, and Salientia.

Jenkins *et al.* (2007) reconstruct a postfrontal, but no postorbital, for *Eocaecilia*. Within Gymnophiona, a 'circumorbital bone' that may be homologous with the postfrontal or possibly the postorbital is present in *Ichthyophis* and *Uraeotyphlus* (Duellman and Trueb, 1986; Carroll, 2000; Wake, 2003); rhinatrematid ontogeny is poorly known (in adult rhinatrematids the orbit is entirely surrounded by the maxillopalatine, which may or may not include the fused pre- and postfrontal). Following Jenkins *et al.* (2007), we have scored the postorbital as absent in Gymnophionomorpha (*contra* McGowan) and retained McGowan's scoring of the postfrontal (character 24) as present.

See above for our scoring of *Brachydectes* as possessing a postorbital (and not possessing a postfrontal).

Character 25: Jugal present (0) or absent (1).
Salientia and Caudata lack jugals, as does *Brachydectes*.

A jugal is present in *Eocaecilia* (Jenkins and Walsh, 1993; Jenkins *et al.*, 2007), which is probably why McGowan scored Gymnophionomorpha as possessing a jugal. A jugal is, however, apparently absent throughout gymnophionan ontogeny (Wake, 2003; Müller *et al.*, 2005; Müller, 2006), so we have scored Gymnophionomorpha as polymorphic.

It has not escaped our attention that the 'squamosal' of Gymnophiona occupies the same area as the squamosal and the jugal of *Eocaecilia* throughout gymnophionan ontogeny (compare Wake, 2003; Müller, 2006; Jenkins *et al.*, 2007). As far as we can tell, interpretation of this bone as either the squamosal or the jugal is more or less equally parsimonious, with both interpretations leading to similar numbers of problems, so possibly Gymnophionomorpha should rather be scored as always possessing a jugal. However, given this ambiguity and the fact that in *Gegeneophis* this bone appears in a decidedly dorsal position (Müller *et al.*, 2005: fig. 2a), we have opted to stay conservative. Fossil evidence could be very helpful, but has not been discovered so far – the skull of *Rubricacaecilia* is unknown (with the probable exception of the palatine).

Character 26: Hyobranchial skeleton not ossified (0) or ossified (1) in adults.
Absence of hyobranchial bones is difficult to distinguish from *post-mortem* disarticulation in all but the best-preserved articulated specimens, and ontogenetic variation is also widespread at least in temnospondyls and salamanders; surprisingly, this variation can go in both directions, with ossified hyobranchial elements being present in larvae and disappearing during metamorphosis in some taxa, changing shape but staying present in the adults of others, and absent in larvae and ossifying during metamorphosis in yet others (Wake, 1989; Schoch, 2001; Witzmann and Schoch, 2006). McGowan assigned state 0 to the amphibamids, Salientia, Caudata, Gymnophiona, and the all-zero ancestor, while the branchiosaurids, *Micromelerpeton*, Pantylidae, and Hapsidopareiontidae shared state 1 in his matrix.

Due to the lack of known adults for *Branchiosaurus* and *Schoenfelderpeton*, we have scored both as unknown.

Hyobranchial elements are not preserved in the metamorphic specimens of *Apateon gracilis* (Schoch and Fröbisch, 2006: 1470), but *post-mortem* disarticulation cannot be ruled out, so we have scored *Apateon* as unknown.

McGowan states that hyobranchial bones are present in the albanerpetontid *Celtedens megacephalus* and illustrates them (McGowan, 2002: fig. 13), but scores them as unknown in albanerpetontids; we go with the text and figure rather than the matrix.

None of the many articulated specimens of *Microbrachis* preserves a hyobranchus (Carroll and Gaskill, 1978; Vallin and Laurin, 2004). However, the paedomorphic condition of all known specimens makes this unreliable. Therefore (Wiens *et al.*, 2005) we have kept McGowan's scoring of *Microbrachis* as unknown.

McGowan scored Caudata as possessing state 0. However, the hyobranchial skeleton is partly ossified in cryptobranchoids, sirenids, and *Karaurus* (Ivachnenko, 1979), making it plausible that this is the plesiomorphic state for Caudata – unless paedomorphosis (in cryptobranchoids and sirenids) and the presumed juvenile age of the only known *Karaurus* specimen (Ivachnenko, 1979) explain this ossification. Accordingly, we have scored Caudata as unknown.

The hyobranchial skeleton disappears in *Amphibamus* during metamorphosis (Schoch, 2001), so we have kept McGowan's score (state 0).

Character 27: Acrodont or subthecodont (0) or pleurodont (1) tooth implantation.

McGowan coded all lissamphibians and branchiosaurids as pleurodont (and did not mention subthecodont implantation, lumping it with acrodonty, which probably does not occur in this data matrix at all).

The distinction between the states of this character is often a matter of degree; for example, some microsaurs like *Microbrachis* apparently have somewhat pleurodont lower jaws (Carroll and Gaskill, 1978), as occurs in some temnospondyls outside the present data matrix, where the labial wall of the dentary is slightly higher than the lingual wall, and the teeth are attached to it as well as to the alveolar floor (D. M., pers. obs. of a not yet catalogued specimen likely belonging to *Metoposaurus diagnosticus krasiejowensis*, July 2007). We have kept McGowan's coding of 0 for such intermediate cases.

However, *Carrolla* is "possibly pleurodont" (Langston and Olson, 1986: 11; see also fig. 4). Because teeth and tooth-bearing bones are entirely unknown in *Quasicaecilia*, and because the tooth attachment of *Batropetes* has never been commented upon and cannot be determined from the available figures, we have scored Brachystelechidae as unknown.

Character 28: Ectopterygoid contacting maxilla (0) or separated from maxilla by rostral expansion of subtemporal fenestra (1).

McGowan scored this character as unknown only in Albanerpetontidae and Brachystelechidae, even though it is inapplicable in the absence of an ectopterygoid (character 8). State 1 appears in his matrix for the branchiosaurids and Pantylidae.

However, like the albanerpetontids, salamanders and frogs, *Pantylus* and *Stegotretus* lack a separate ectopterygoid (*e.g.*, Carroll and Gaskill, 1978; Berman *et al.*, 1988), so we have scored Pantylidae as unknown (inapplicable).

Carrolla has state 0; we have generalized this to Brachystelechidae because the condition in *Batropetes* and *Quasicaecilia* is unknown.

Whenever a distinct ectopterygoid is present in gymnophionans (see character 8), it contacts the maxillary portion of the maxillopalatine, so we have retained McGowan's score of Gymnophiona as showing state 0.

Salamanders and frogs (like *Brachydectes*) lack an ectopterygoid, so we have scored them as unknown (inapplicable) rather than as sharing the branchiosaurid condition.

Character 29: Prefrontal-postfrontal suture (0); frontal participates in margin of orbit (1).

Unlike McGowan, we have scored this character as inapplicable (i.e. unknown) when the postfrontal is absent (in Albanerpetontidae, Caudata, Salientia, and *Brachydectes* – see above). McGowan had assigned state 1 to these taxa as well as to '*Tersomius*', *Doleserpeton*, *Micromelerpeton*, Brachystelechidae, Hapsidopareiontidae, and the branchiosaurids.

However, *Branchiosaurus* shows state 0 (Milner, 1986; Werneburg, 1987; Heyler, 1994).

Apateon is polymorphic: independently of ontogenetic stage, *A. caducus*, *A. pedestris*, *A. flagrifer* (Werneburg, 1986, 1988b), *A. kontheri* (Werneburg, 1988a), and *A. gracilis* (Schoch and Fröbisch, 2006) show state 1, while *A. intermedius* and *A. dracyi* possess state 0 (Werneburg, 1988c, 1996, 2001).

The only gymnophionomorph where this character is unambiguously applicable is *Eocaecilia*, which has state 0. In those gymnophionans in which a 'circumorbital' is present, its contact with the prefrontal is variable – sometimes the squamosal and the maxillopalatine share a suture instead, because the orbit is so small (Carroll, 2000: fig. 2E, right side) – but the frontal (and even the prefrontal) never participates in the orbit margin; instead, the entire dorsal margin of the orbit is formed by the 'circumorbital' which we here interpret as the postfrontal (see above). This condition could either be scored as state 0 or as inapplicable, neither of which contradicts McGowan's scoring of Gymnophionomorpha as having only state 0. We have therefore retained this score.

Character 30: Intervomerine fenestra absent (0) or present (1).

This feature is often called the 'intervomerine pit' despite lacking a bony 'floor'. McGowan scored it as present in Caudata, Salientia, '*Tersomius*', and *Micromelerpeton*, and as unknown in Hapsidopareiontidae, *Microbrachis*, Brachystelechidae, and *Rhynchonkos*.

Microbrachis, however, possesses state 0 (Vallin and Laurin, 2004).

Character 31: More (0) or less (1) than 60 teeth per upper jaw ramus.

Among the taxa in the present matrix, only *Platyrhinops* is known to possess state 0, so the character is parsimony-uninformative. It was not uninformative in the original, where McGowan had also given state 0 to the all-zero ancestor because "e.g. early temnospondyls" share it (McGowan, 2002: 28).

McGowan scored the branchiosaurids as unknown, and indeed most illustrations of branchiosaurid skulls ignore the usually badly crushed marginal toothrows, but *Branchiosaurus salamandroides* (Werneburg, 1987), *Apateon* spp. (Boy, 1972, 1978; Werneburg, 1986, 1988a, b, c, 2001), and *Schoenfelderpeton* (Boy, 1986) are all known to have state 1.

Character 32: Frontals no more than 50% longer than broad (0) or at least 50% longer than broad (1).

McGowan did not quantify this character ("wide paired frontals" (0), "narrow paired frontals" (1); McGowan, 2002: 28). He assigned state 1 to *Doleserpeton* and *Micromelerpeton* and state 0 to all other OTUs.

There is a large morphological gap between the states in most OTUs; the frontal of taxa displaying state 0 is about as long as broad, whereas it is usually at least twice as long as broad in state 1. In the present matrix only adult specimens of *Platyrhinops* and some brachystelechids, some gymnophionans, and some caudates are known to have state 0, as detailed below; therefore the character is parsimony-uninformative. We also do not understand why McGowan made explicit that in both states the frontals are "paired" – the frontals are fused in albanerpetontids and some salientians, yet McGowan neither distinguished this condition as a separate state nor scored the mentioned taxa as inapplicable/unknown.

Branchiosaurus has state 1 (Werneburg, 1987; Boy, 1987).

In *Apateon gracilis* the frontals are very long and narrow and grow in length throughout its ontogeny (Werneburg, 1988c, 1991; Schoch and Fröbisch, 2006). The same holds for *A. flagrifer* (the youngest specimens approach state 0: Werneburg, 1986, 1988b; Boy, 1987). This is also seen in *A. intermedius* (Werneburg, 1996), *A. dracyi* (where the youngest specimens approach state 0; Boy, 1986, 1987; Werneburg, 1988c, 2001), *A. pedestris* (Boy, 1978, 1986, 1987; the youngest specimens approach state 0: Heyler, 1994), *A. kontheri* (Werneburg, 1988a), *A. caducus* (Boy, 1978, 1987; Schoch, 2002; Schoch and Fröbisch, 2006), and *A. pusillus* (Boy, 1987). Interestingly, the ontogeny of *Platyrhinops* runs in the other direction (Schoch, 2002).

Schoenfelderpeton has state 1 (Boy, 1986, 1987).

Albanerpetontidae has state 1 (*Albanerpeton*: Fox and Naylor, 1982; *Celtedens*: McGowan, 2002).

We have scored Tuditanidae as state 1, though this is only unambiguous in *Crinodon* and *Boii* (Carroll and Gaskill, 1978: Figs 10, 11, 12).

Hapsidopareiontidae is scored 1, primarily after *Llistrofus* (Carroll and Gaskill, 1978: figs 15, 16).

Pantylidae shares state 1 (Carroll and Gaskill, 1978: fig. 25; Berman *et al.*, 1988: figs 9A, 10B).

Rhynchonkos, too, has state 1, though only marginally so in the apparently less crushed specimen (Carroll and Gaskill 1978: fig. 63).

Microbrachis has state 1 (not quite clear in the reconstruction by Vallin and Laurin [2004], but unambiguous in the specimen drawings by Carroll and Gaskill [1978: figs 74, 75, 77A, 78A]).

Batropetes, too, possesses state 1 (Carroll and Gaskill, 1978), but *Carrolla* and *Quasicaecilia* are closer to 0 (Carroll, 1998). Although the conditions of *Carrolla* and *Quasicaecilia* could be related to their short snouts and the possibly juvenile condition of the specimens (especially in *Quasicaecilia*), we score Brachystelechidae as polymorphic.

Eocaecilia seems to possess state 1 (although this is not straightforward to measure due to the unique shape of the frontal; Jenkins *et al.*, 2007), but all or almost all gymnophionans figured by Duellman and Trueb (1986) have 0, as do some of those figured by Carroll (2000). We have thus scored Gymnophionomorpha as polymorphic.

According to the literature, the frontals are fused to the parietals in all salientians. In the skull roof of *Triadobatrachus*, where the strong sculpture and the fact that the only known specimen is a natural mold make it extremely difficult, if not impossible, to distinguish sutures from cracks or even from meaningless patterns in the sculpture – in our opinion, even the presence, let alone the position, of the pineal foramen proposed by Roček and Rage (2000) cannot be ascertained (pers. obs. May 30th, 2008) – one of the possible frontal-parietal sutures would put *Triadobatrachus* at the boundary between state 0 and state 1. In short, we have scored Salientia as unknown.

With the exception of *Jeholotriton* (Wang and Rose, 2005), urodeles and possible urodeles show state 1 (extant: Duellman and Trueb, 1986; *Sinerpeton*: Gao and Shubin, 2001; *Valdotriton*: Evans and Milner, 1996; apparently also *Iridotriton*: Evans *et al.*, 2005), but its sister-group, the Karauridae, possesses state 0 (*Karaurus* and *Kokartus*: Milner, 2000). Accordingly we have scored Caudata as polymorphic.

'*Tersomius texensis*' (Carroll, 2000) shows state 1, as incidentally does *Eimerisaurus* (Boy, 1980, 2002), so we have scored '*Tersomius*' accordingly.

Character 33: Contact between maxilla and jugal and/or quadratojugal present (0) or absent (1).
In McGowan's matrix, state 1 unites *Apateon*, *Schoenfelderpeton*, and Caudata.

Because *Apateon gracilis* has state 0 from metamorphosis onwards (Schoch and Fröbisch, 2006), and even without metamorphosis such a contact is established in late larval stages of *A. pedestris* and *A. caducus* (see character 8; Schoch, 1992), we score *Apateon* as 0 and *Schoenfelderpeton* as unknown (Wiens *et al.*, 2005).

This restricts state 1 to Caudata and *Brachydectes*, so that, when *Brachydectes* is excluded from the analysis, the character becomes parsimony-uninformative.

Character 34: Pterygoid-vomer suture excluding palatine from interpterygoid vacuity (0); palatine participates in margin of interpterygoid vacuity (1); palatine absent (2) (unordered).
McGowan assigned state 0 to all microsaurs (except Brachystelechidae, scored as unknown) and the all-zero ancestor, and state 1 to all other OTUs (except Albanerpetontidae, scored as unknown).

Carrolla and *Batropetes* have state 0 (Carroll, 1998), however, so we have scored Brachystelechidae as 0.

Brachydectes lacks interpterygoid vacuities (the parasphenoid and the pterygoids are in contact throughout), but because the pterygoids are sutured to the vomers, so that the palatines do not contact the parasphenoid, we have assigned state 0 to *Brachydectes*.

Of all caudates only sirenids have a (separate) palatine as adults. The lack of a palatine is a third state (state 2). The sirenids are not the sister-group of the rest of Caudata, therefore their condition is most parsimoniously interpreted as a reversal (perhaps related to their paedomorphosis); we have accordingly assigned state 2 to the Caudata OTU.

Character 35: Vomerine fangs present (0) or absent (1) in adults.
See character 7 for more information. McGowan deemed vomerine fangs present only in the amphibamids, *Micromelerpeton*, and the all-zero ancestor, scoring Albanerpetontidae as unknown; he also did not mention ontogeny.

Following Carroll and Gaskill (1978), we judge *Crinodon* to possess vomerine fangs. Because the vomer is unknown in *Asaphestera*, *Tuditanus*, and *Boii* (Carroll and Gaskill, 1978), we score Tuditanidae as showing state 0.

Brachystelechidae is scored as lacking vomerine fangs because *Carrolla*, the only scoreable brachystelechid, has "[p]robably no palatal dentition" (Carroll, 1998: 63).

Doleserpeton is famous for lacking vomerine fangs and possessing a tooth row instead (Bolt, 1969, 1977). We suspect that McGowan's scoring of *Doleserpeton* as possessing vomerine fangs is a typographic error and have assigned it state 1. However, the condition seen in *Doleserpeton* is also found in juveniles of *Amphibamus* but not in the single adult specimen (Daly, 1994), so we have scored this character as unknown in *Doleserpeton* in the analysis where we treat the described material of *Doleserpeton* as immature.

Character 36: Teeth on cultriform process of parasphenoid present (0) or absent (1) in adults.
McGowan scored the branchiosaurids, Albanerpetontidae, Caudata, Salientia, '*Tersomius*', and *Doleserpeton* as possessing state 1, and Pantylidae as unknown; he also did not mention ontogeny.

The pantylid *Stegotretus* has teeth on the cultriform process (Berman *et al.*, 1988), so we have assigned state 0 to Pantylidae.

Cardiocephalus lacks parasphenoid teeth (Carroll and Gaskill, 1978: 56), while *Euryodus* has teeth on the cultriform process and elsewhere on the parasphenoid (Carroll and Gaskill, 1978: fig. 38B, p. 64, figs 42 and 43, and p. 69). In the other gymnarthrids the parasphenoid is unknown. Accordingly, we have scored Gymnarthridae as polymorphic.

Carrolla, as mentioned above, lacks a palatal dentition altogether, while *Batropetes* has "a few small denticles at the base of the cultriform process of the parasphenoid" (Carroll, 1991). Carroll (1990) never mentions the presence or absence of any palatal dentition in *Quasicaecilia*. Thus, we have scored Brachystelechidae as polymorphic.

We have also scored Gymnophionomorpha as polymorphic because *Eocaecilia* is unique among known caecilians in retaining denticles on the cultriform process (Carroll, 2000; Jenkins *et al.*, 2007).

Platyrhinops (Schoch, 2002) and *Amphibamus* (Daly, 1994, Schoch, 2001) lack denticles on the cultriform process (state 1) after metamorphosis, so we have scored both accordingly (Wiens *et al.*, 2005); McGowan had scored both as retaining them (state 0), which is the case in *Platyrhinops* before metamorphosis is completed (Schoch, 2002).

Character 37: Supratemporal at least about twice as long as broad (0), about as long as broad (1), or absent (2) (ordered).
The ordering sequence, changed from the original (which had "supratemporal [as] long as broad" as state 0 and "supratemporal longer than broad" as state 1), follows from the fact that supratemporals in state 0 are about twice as large as supratemporals in state 1 (relative to total skull size) because the supratemporal in state 1 is shorter but not broader than in state 0. Since we have replaced the all-zero ancestor by real taxa, the fact that state 1, rather than 0, is most likely plesiomorphic does not matter anymore because the tree is rooted by the outgroup, not by the character states that we happen to call '0'; what matters is that in order to change from state 0 to state 2 (as now coded) or vice versa a lineage would most likely have to pass through state 1, supporting the present ordering sequence instead of McGowan's.

Thus, McGowan gave our state 1 to the all-zero ancestor, *Branchiosaurus*, *Apateon*, and the amphibamids, and our state 0 to *Schoenfelderpeton* and *Micromelerpeton*.

Apateon flagrifer (Werneburg, 1986, 1988b), *A. pedestris* (Boy, 1978; Heyler, 1994), and *A. kontheri* (Werneburg, 1988a) have state 0, but *A. intermedius* shows state 1 (Werneburg, 1996), as does the adult and metamorphosed *A. gracilis* (Schoch and Fröbisch, 2006). *A. dracyi* (Werneburg, 2001) and *A. caducus* (Schoch and Fröbisch, 2006), however, change from 1 to 0 in ontogeny. (Incidentally, the same change happens in *Seymouria sanjuanensis* and in *Discosauriscus*: Klembara *et al.*, 2007.) To cope with this diversity, we have scored *Apateon* as possessing both state 0 and state 1.

We did not change McGowan's scoring of all microsaurs as lacking a supratemporal (state 2), but see character 13.

As explained above, we have scored *Brachydectes* as sharing state 2.

For Gymnophionomorpha, see character 13.

Character 38: Caudal edge of skull roof straight or concave (0) or convex (1) in dorsal view.
McGowan's matrix shows state 1 for all microsaurs and Gymnophiona.

McGowan (2002: 29) defined this character as "0, posterior skull shape straight; 1, posterior skull shape convex", but even if a smooth (straight or hyperbolic) line is drawn between the caudolateral edges of the tabulars and the caudal tips of the exoccipitals, most microsaurs still have straight or even concave caudal skull margins, despite being scored as having convex ones. Because the braincase never makes a large difference and is often not preserved in temnospondyls, we omit it from the character definition.

Tuditanids have straight or concave caudal skull edges (Carroll and Gaskill, 1978), corresponding to state 0.

Hapsidopareiontids have straight edges (Carroll and Gaskill, 1978).

Pantylus has a very slightly convex edge (Romer, 1969; Carroll and Gaskill, 1978) that we consider to be within the definition of 'straight' because of uncertainty in the reconstruction resulting from distortion of the specimen and probable individual variation. Furthermore, it is very far from the condition seen in caecilians or *Cardiocephalus*. The condition in *Stegotretus* is likewise almost straight, though marginally concave (Berman *et al.*, 1988). We have accordingly scored Pantylidae as having state 0.

Microbrachis has either a straight (Carroll and Gaskill, 1978) or a slightly concave edge (Vallin and Laurin, 2004), but not a convex one as coded by McGowan.

Gymnarthridae is scored as polymorphic because *Cardiocephalus* has a convex and *Euryodus* (especially *E. dalyae*) a straight caudal skull roof edge; the condition in the other gymnarthrids is unknown (Carroll and Gaskill, 1978, despite the reconstructions in fig. 104).

McGowan also scored Brachystelechidae as having a convex caudal skull edge, but *Batropetes* and *Carrolla* have straight ones (Carroll and Gaskill, 1978; Carroll, 1998), while the one of *Quasicaecilia* is (perhaps ironically) strongly concave (Carroll, 1998).

This leaves state 1 for Gymnophionomorpha, *Rhynchon-*

kos, and *Brachydectes*, and 0 for all other OTUs, except for the polymorphisms mentioned above.

Character 39: Coronoid region with fangs and shagreen (0), shagreen only (1), a single toothrow parallel to that of the dentary (2), toothless (3) (unordered).
See character 16 for the number of coronoids, treated as the same character by McGowan. We have not ordered this character because a gradual reduction of the coronoid dentition might be a reduction in size (0 > 2 > 1 > 3 or 2 > 0 > 1 > 3), number of rows (1 > 0 > 2 > 3), or both (0 > 1 > 2 > 3); each of these possibilities implies a different ordering sequence, and we lack data to decide between these possibilities or even to test the underlying assumption that any reduction of the coronoid dentition has to be gradual at all.

The situation in *Branchiosaurus* is unknown (*contra* McGowan).

Schoenfelderpeton (states 0, 1 or 2) and *Apateon* (entirely unknown) are scored after Boy (1986).

Tuditanidae is scored after *Crinodon*, which has "a number of large coronoid fangs" that are slightly bigger than the marginal teeth (Carroll and Gaskill, 1978: 25, fig. 10).

Pantylidae is scored as possessing state 0 because the teeth are irregulary arranged and have irregular sizes, even though a classical 'shagreen' is not present.

The polymorphism for Gymnarthridae (states 1 and 2) follows from the conditions of *Hylerpeton* (which has a second toothrow consisting of two teeth on coronoid III; still state 2) on the one hand and *Leiocephalikon* (which has three toothrows on coronoid III; state 1) (Carroll and Gaskill, 1978), *Bolterpeton* (which has a shagreen at least on coronoids I and II; state 1) and *Cardiocephalus* sp. (two parallel rows of small teeth spanning all three coronoids; most similar to state 1) (Anderson and Reisz, 2003) on the other hand. For *Cardiocephalus sternbergi*, Carroll and Gaskill (1978) reconstruct what looks like a shagreen (state 1 or 0), but "[t]he coronoids cannot be exposed, and only the anterior portion of the dentary can be seen" (Carroll and Gaskill, 1978: 57), so we did not take that species into account.

McGowan scored Hapsidopareiontidae as having "three coronoids with irregular teeth" (his state 0), but the situation is unknown in all hapsidopareiontids (Carroll and Gaskill, 1978).

Gymnophionomorpha shows state 2 (the portion of the 'pseudodentary' that bears the lingual toothrow in gymnophionans is indeed homologous to a coronoid; Müller *et al.*, 2005; Müller, 2006).

As stated above, '*Tersomius*' has three toothless coronoids (state 3) (Carroll, 1964).

The lower jaws of *Platyrhinops* and *Amphibamus* have not been described or illustrated anywhere in the literature McGowan (2002) cites, nor in the additional literature we have been able to find. Accordingly, both had to be scored as unknown.

The score of *Micromelerpeton* (state 1) follows Boy (1995).

Character 40: Ratio of orbit length to skull-roof length (see state definitions in Appendix-Table 4) (ordered).
McGowan did not quantify this character or explain how he measured orbit size to divide this continuous character into two states; he assigned state 1 ("reduced orbits") to Gymnarthridae, *Microbrachis*, *Rhynchonkos* and Gymnophiona, and state 0 ("large orbits") to all other OTUs.

We have measured the ratio of rostrocaudal orbit length (independent of orbit orientation) to skull-roof length along the midline in dorsal view (Appendix-Table 4, Appendix-Fig. 2). Using this metric, it turns out McGowan placed the boundary between the two states into one of the smallest available gaps in the distribution (between *Microbrachis*, state 1, and *Micromelerpeton*, state 0). We see no reason for this decision. Instead, we have used stepmatrix gap-weighting (Wiens, 2001) as explained above for character 20.

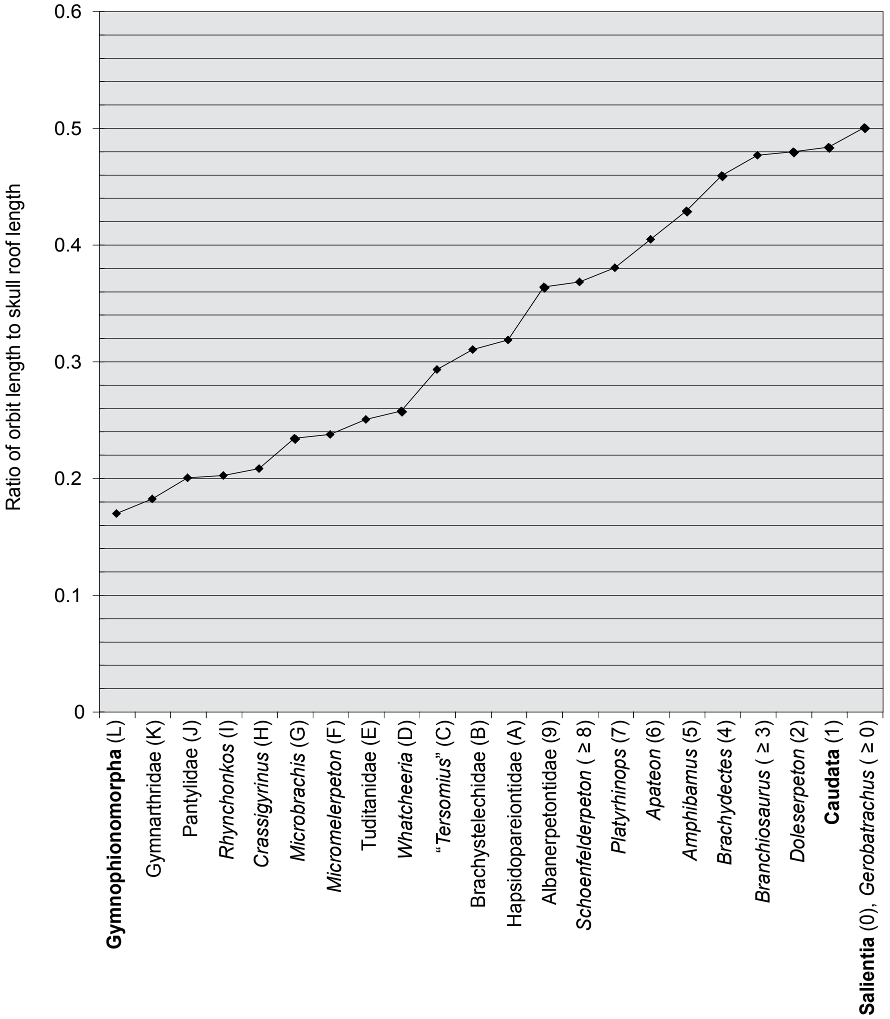
We have scored *Branchiosaurus* and *Schoenfelderpeton* as possessing their measured character state or any higher-numbered one (see Appendix-Table 4), because none of the known specimens are adult and because, unsurprisingly, relative orbit size decreases in the ontogeny of *Apateon gracilis* (Schoch and Fröbisch, 2006).

We have not measured any salientians, but, with very few and clearly derived exceptions, such as *Calyptocephalella* ('*Caudiverbera*': Duellman and Trueb, 1986: figs 13-17F), the orbit makes up at least half of skull length (Reig, 1961; Duellman and Trueb, 1986; Sanchíz, 1998; Gao and Chen, 2004; Carroll, 2007). Although most of its snout is not preserved, so that the skull roof length is unknown, the same seems to hold for *Triadobatrachus* judging from the curvature of its jaws (Roček and Rage, 2000; pers. obs. May 30th, 2008). Thus, we have treated Salientia as having a ratio of 0.5 and thus possessing state 0.

The skull roof of *Gerobatrachus* is slightly disarticulated, so precise measurements cannot be made. However, the orbits were clearly about half as long as the skull roof (Anderson *et al.*, 2008a: fig. 2). We have therefore scored this taxon as possessing state 0 in the analysis where we treat it as adult, and as unknown (i.e., state 0 or higher) in the analysis where we treat it as immature or paedomorphic.

The other scores are explained in Appendix-Table 4. To further avoid the effect of ontogeny, we have only used the smallest ratio we could find for each OTU, except for Gymnophionomorpha, where we have only used *Eocaecilia* which was, in what is most parsimoniously interpreted as a plesiomorphic condition, less strongly adapted to burrowing (Jenkins *et al.*, 2007) and thus has relatively larger orbits than the extant caecilians (including the aquatic ones, which retain small eyes).

We have not tried to correct for the well-known ontogeny-independent correlation between relative eye size and absolute body size. Firstly, we are not aware of any other ontogeny-independently size-dependent characters in our matrix – size itself has a strong phylogenetic signal (Laurin, 2004) and can therefore do no harm if only one character correlated to it is present in a data matrix. Secondly, most of the animals studied here have similar sizes. Thirdly, the orbits of (at least) salientians, caudates, and presumably albanerpetontids and *Brachydectes* accommodate not only the eyes, but also jaw muscles, the relative size of which does not have a simple relationship with body size; in fact, all else being equal, the expected relation between orbit size and body size could even be negative, because muscle force scales with muscle cross-sectional area and thus the 2nd



Appendix-Fig. 2. Ratio of rostrocaudal orbit length to skull roof length in dorsal view (character 40). The line drawn between the data points is meant to visualize the sizes of the morphological gaps by its varying steepness. The state of each OTU is indicated after its name. Extant taxa in bold. Data shown in Appendix-Table 4.

power of body length, while body mass scales with the 3rd power, so that, if bite forces are to be proportional to body mass, a larger body requires disproportionately large jaw muscles and thus disproportionately large orbits (or 'orbitotemporal fenestrae' as they are sometimes called in salientians and caudates). Last but not least, not much of a size trend is apparent in the data – most conspicuously, the largest animal in the data matrix, *Crassigyrinus*, has a relative orbit size similar to those of small microsaurs; the next largest animal, *Whatcheeria*, has a much larger relative orbit size than *Crassigyrinus*; and *Whatcheeria* has considerably larger orbits than *Micromelerpeton*, the temnospondyl with the most plesiomorphic skull shape in the matrix, which in turn has only marginally larger orbits than the paedomorphic microsaur *Microbrachis*. Furthermore, while eye size is correlated to lifestyle in extant amphibians (larvae and aquatic adults having markedly smaller eyes than terrestrial adults; Witzmann and Pfretzschner, 2003), this does apparently not hold for other taxa in the present matrix, at least not for *Micromelerpeton*, which has "strikingly large [orbits] for a water-dwelling amphibian" (compared to extant amphibians) (Witzmann and Pfretzschner, 2003: 761), yet considerably smaller ones than the equally aquatic and much larger *Whatcheeria*, as mentioned above. Also, like *Micromelerpeton*, *Whatcheeria* does not have a disproportionately small skull.

Character 41: jaw joints well caudal of the exoccipitals (0), at the same level (within 5% of skull length in the sagittal plane) (1), or well rostral to it (2) (ordered).

McGowan had exchanged states 1 and 2 to fit his scenario of evolution, even though it has to be assumed that the evolutionary change between these two states of this continuous character must have happened gradually, passing through the third, which is why we have ordered this character (Wiens, 2001). Thus, McGowan assigned our state 1 to Pantylidae and Salientia, and state 0 to the amphibamids, *Micromelerpeton*, and the all-zero ancestor.

We have added the quantification of the states of this potentially continuous character (although few if any borderline cases exist where presumably adult specimens cannot be assigned to one of two adjacent states by eye), and the speci-

Appendix-Table 4. Ratio of rostrocaudal orbit length to skull roof length in dorsal view (character 40). All values are rounded (the unrounded values are plotted in Appendix-Fig. 2); the largest differences between two successive OTUs are highlighted in bold and were used to define the state boundaries. The weight of each transition is the difference in the absolute value of the ratio (5th column) divided by the total difference in this ratio between state K (as shown by *Eocaecilia micropodia*) and state 0 (as shown by Salientia), i.e., (~0.169 – ~0.5 =) ~0.331, and multiplied by the average maximum weight of the characters (except characters 20 and 40) in the present matrix, i.e., 1.375. See text for more information.

OTU	Measured species	Source	Ratio	Difference to following OTU	State of character 20	Weight of transition to next state
Gymnophionomorpha	*Eocaecilia micropodia*	Carroll, 2000	0.169	0.012	L	
Gymnarthridae	*Euryodus primus*	Carroll and Gaskill, 1978	0.182	0.018	K	0.051
Pantylidae	*Pantylus cordatus*	Carroll and Gaskill, 1978	0.2	0.002	J	0.076
Rhynchonkos	*R. stovalli*	Carroll and Gaskill, 1978	0.202	0.006	I	0.008
Crassigyrinus	*C. scoticus*	Clack, 1998	0.208	0.026	H	0.025
Microbrachis	*M. pelikani*	Vallin and Laurin, 2004	0.234	0.004	G	0.108
Micromelerpeton	*M. credneri*	Boy, 1995	0.237	0.013	F	0.015
Tuditanidae	*Tuditanus punctulatus*	Carroll and Gaskill, 1978	0.25	0.007	E	0.053
Whatcheeria	*W. deltae*	Bolt and Lombard, 2000	0.257	0.036	D	0.030
'*Tersomius*'	'*T. texensis*'	Carroll, 2000	0.293	0.017	C	0.148
Brachystelechidae	*Batropetes fritschi*	Carroll, 1991	0.310	0.008	B	0.071
Hapsidopareiontidae	*Hapsidopareion lepton*	Carroll and Gaskill, 1978	0.318	0.046	A	0.035
Albanerpetontidae	*Celtedens ibericus*	McGowan, 2002: fig. 5	0.364	0.004	9	0.189
Schoenfelderpeton	*S. prescheri*	Boy 1987	0.368	0.012	8 or higher	0.017
Platyrhinops	*P. lyelli*	Schoch, 2002	0.38	0.024	7	0.051
Apateon	*A. gracilis*	Schoch and Fröbisch, 2006	0.404	0.024	6	0.101
Amphibamus	*A. grandiceps*	Schoch, 2001	0.429	0.030	5	0.101
Brachydectes	*B. elongatus*	Wellstead, 1991	0.459	0.017	4	0.127
Branchiosaurus	*B. salamandroides*	Boy 1987	0.476	0.003	3 or higher	0.071
Doleserpeton	*D. annectens*	Bolt, 1969	0.479	0.004	2	0.012
Caudata	*Karaurus sharovi*	Ivachnenko, 1979	0.483	0.017	1	0.017
Salientia	see text	see text	0.5		0	0.069
Gerobatrachus	see text	see text	~ 0.5		0 or higher	

fication of what 'occiput' should mean – if the caudal margin of the skull roof were chosen, too much correlation with character 38 would likely result.

McGowan scored all branchiosaurids as showing our state 2, but this character changes from 2 to 1 and then to 0 in ontogeny, reaching 1 in neotenic adults of *Apateon caducus* and late larvae of *A. gracilis*, and continuing to 0 in adults of *A. gracilis* (Schoch and Fröbisch, 2006). (In *Leptorophus tener*, too, state 0 is known to occur: Boy, 1986.) Accordingly, we have scored *Apateon* as 0 and the other two branchiosaurids as unknown (Wiens *et al*., 2005) because metamorphic adults are only known from *A. gracilis*. In the case of *Branchiosaurus*, however, we have been able to restrict the uncertainty to 'state 0 or 1', because *B. salamandroides* is known to have reached at least state 1 (Boy, 1987).

The tuditanids *Asaphestera*, *Crinodon*, and most likely *Boii* have state 1, but *Tuditanus* itself exhibits state 0 (Carroll and Gaskill, 1978), so we have scored Tuditanidae as possessing both states.

The hapsidopareiontids *Hapsidopareion*, *Llistrofus*, and *Saxonerpeton* (Carroll and Gaskill, 1978) and *Microbrachis* (Carroll and Gaskill, 1978; Vallin and Laurin, 2004) show state 1.

The karaurid *Kokartus* (Milner, 2000) seems to be the only caudate with state 1; all others have state 2 (Duellman and Trueb, 1986; Milner, 2000), so we have kept McGowan's scoring of Caudata as possessing state 2.

Triadobatrachus has state 0 (Roček and Rage, 2000), while all other salientians (Sanchíz, 1998) seem to have state 1 as scored by McGowan (with a few clearly derived exceptions), so we have scored Salientia as showing both states.

Gerobatrachus exhibits state 1, which we have taken at face value for the analysis in which we treat *Gerobatrachus* as adult. Further growth could, however, have resulted in state 0 because the suspensorium normally moves caudally in temnospondyl and lissamphibian ontogeny (Schoch and Fröbisch, 2006, and references therein), so we have scored it as possessing state 1 or 0 for the analysis where we treat it as immature or paedomorphic.

Character 42: Dorsal scales well ossified (0), poorly ossified (1), or absent (2) (ordered).

McGowan treated dorsal and ventral scales as the same character, but they are independent (Witzmann, 2007), so we have have split McGowan's character 4; see our character 4 for more information. Furthermore, McGowan coded only two states, presence (0) and absence (1) of scales; we have separated states 1 (poorly ossified) and 2 (absent) for the dorsal scales to account for the difference between *Tuditanus* and Gymnophionomorpha on the one hand and most other OTUs on the other, and ordered it for the same reason as character 4.

Dorsal scales are absent (state 2) in *Whatcheeria*, *Crassigyrinus*, *Rhynchonkos* (see also character 4), Caudata, Salientia, and *Brachydectes*. Elsewhere, dorsal scales are generally present (states 0 and 1). Their absence in both outgroups happens to make their presence an autapomorphy of the ingroup, illustrating once again the dangers of low outgroup sampling in particular and low taxon sampling in general.

Although they are reduced in *Tuditanus* (Carroll and Baird, 1968; Carroll and Gaskill, 1978: 17, 183), dorsal scales are well ossified in the other tuditanids, so we have assigned states 0 and 1 to Tuditanidae.

Most specimens of *Pantylus* lack scales, and the single exception only shows "fragments" (Carroll and Gaskill, 1978: 183); however, this is likely due to disarticulation and/or preparation. "[E]xtensive scalation" (Carroll and Gaskill, 1978: 183) is present in *Trachystegos*, which may or may not be a pantylid or gymnarthrid, among other possibilities (Carroll and Gaskill, 1978; Schultze and Foreman, 1981; Berman *et al*., 1988; Carroll, 1998). No specimen of *Stegotretus* is well enough preserved that the absence of scales could be taken at face value. Based on the 'fragments' in the mentioned *Pantylus* specimen, we have scored dorsal scales as well ossified in Pantylidae.

Scales are absent in all articulated gymnarthrid specimens, and the associations of disarticulated gymnarthrids with scales are all questionable (Carroll and Gaskill, 1978: 183), so we have scored Gymnarthridae as lacking dorsal scales (as well as ventral ones, see character 4) under the assumption that *Trachystegos* is not a gymnarthrid.

Among brachystelechids, only *Batropetes* is known from more than an isolated skull, and *Batropetes* has not been prepared in dorsal view (Carroll, 1991). We have therefore scored Brachystelechidae as unknown.

Scales are not known in *Eocaecilia*, but given the poor preservation potential of the scales of extant caecilians and the state of preservation of all specimens of *Eocaecilia* shown or described by Jenkins *et al.* (2007), we have relied on Gymnophiona alone (*Rubricacaecilia* being much too fragmentary for us to expect preserved scales) in assigning state 1 to Gymnophionomorpha.

Among amphibamids, dorsal scales are known only from *Eoscopus* (Daly 1994), which is not in the present matrix. However, as in character 4, we have only taken this at face value (state 2) for *Platyrhinops* and *Amphibamus*, for which specimens are known that are well enough preserved to distinguish nonpreservation from absence.

Appendix 2

The revised data matrix

Parentheses indicate polymorphism, curly brackets uncertainty (treated differently in our analyses). Inapplicable scores are marked with hyphens here, but were treated as unknown. The numbers followed by an asterisk in the line for *Doleserpeton* were replaced by '?' (characters 7 and 35) or '{23456789ABCDEFGHIJKL}' (character 40) in the analyses in which we treated the described material of *Doleserpeton* as immature, and those in the line for *Gerobatrachus* by '?' (characters 1, 10, 21, 35, and 40) or '{01}' (character 41) in the analysis in which we treated the only known specimen of *Gerobatrachus* as immature.

	5	10	15	20	25	30	35	40	42
Whatcheeria	02020	0??00	000?0	200(01)?	0-000	00?0?	110??	?100D	02
Crassigyrinus	01000	00000	00000	200?6	1-000	00000	11000	0100H	02
Branchiosaurus	?0000	100?0	000?1	?1{01}?E	1-000	?1100	11010	110?{3 through L}	{01}0
Apateon	10020	10000	000?1	?1009	1?000	?11(01)0	11010	1(01)0?6	00
Schoenfelderpeton	??020	101?0	000?1	?1{01}?8	1-000	?1110	11?10	100{012}{8 through L}	?0
Albanerpetontidae	11300	1?221	11112	01010	0?110	11--0	110??	12039	20
Tuditanidae	0(12)0(02)0	00020	00010	?100(7E)	00000	?0000	11000	0200E	(01)(01)
Pantylidae	0{12}000	1(01)221	01010	?1003	0?000	10-00	11001	0200J	10
Gymnarthridae	12(01)20	01010	01011	2100(5B)	00000	?0000	11001	(01)2(01)(12)K	22
Hapsidopareiontidae	01000	01120	00010	?100(HJ)	00000	1001?	11001	020?A	10
Microbrachis	02000	01020	00010	210?1	0-000	?0000	11001	0201G	10
Brachystelechidae	02300	1112?	00010	?100(4CG)	00000	??01?	1(01)001	(01)20?B	2?
Rhynchonkos	12020	01010	0001?	110?F	00000	?000?	11001	0212I	22
Gymnophionomorpha	1(01)211	012(12)1	(01)1(01)12	0121(OS)	?110(01)	01000	1(01)011	(01)212L	21
Caudata	10221	21221	(01)1112	0110(MNQRTUV)	11111	?1--1	1(01)121	12021	22
Salientia	11221	21221	01102	0121(ALMPQUV)	11111	01--1	1?011	12030	(01)2
Platyrhinops	10210	00000	000?1	?1002	?0000	00000	00010	110?7	01
Amphibamus	10201	10010	000?1	?10?E	?0000	00000	11010	110?5	02
'*Tersomius*'	102?1	?000?	000??	210?I	?0000	00011	11010	1103C	0?
Doleserpeton	102?1	01*211	000??	?100D	00000	00010	11011*	110?2*	0?
Micromelerpeton	00000	00000	000?1	{12}100G	0-000	10011	11010	0001F	00
Brachydectes	01020	01221	00011	0110K	?-011	10--0	11101	121?4	22
Gerobatrachus	1*???	2?010*	0?01?	?????	1*?000	?00??	?1011*	1{01}0?0*	1*?

Appendix 3

Branchiosaurid synonymy

This table is an attempt to trace the history of the systematics of the branchiosaurids relevant to our study through selected parts of the literature. For the purposes of this paper, we have followed the latest reviews, i.e., Schoch (2004) and Schoch and Fröbisch (2006) where possible, and Werneburg (1996) elsewhere. Empty cells indicate that a species was not yet known, dashes indicate that it was known but not mentioned by the publication in question. 'Sic' indicates consistent misspellings, 'sic!' marks gender mismatches between genus and species name (= violations of ICZN Articles 31.2 and 34.2, which are automatically corrected, and have been used in the correct form, *e.g.*, by Werneburg *et al.* [2007] who retain the classification by Werneburg [1996]) as well as the unjustified emendation of '*dracyi*' to '*dracyiensis*'. Abbreviations: par., partim; pos., possibly; sub., subgenus; *A.*, *Apateon*; *B.*, *Branchiosaurus*; *L.*, *Leptorophus*; *M.*, *Melanerpeton*; *P.*, *Protriton*; *S.*, *Schoenfelderpeton*; *a.*, *amblystomus*; *b.*, *brachyrhynchus*; *f.*, *fayoli*; *ped.*, *pedestris*; *pet.*, *petrolei*; *pr.*, *prescheri*; *s.*, *salamandroides*.

Before Boy (1972)	Boy (1972)	Boy (1978)	Boy (1986), Werneburg (1986)	Boy (1987)	Werneburg (1988a, c)	Werneburg (1996)	Heyler (1994)	Schoch (2004), Schoch and Fröbisch (2006)
B. s.[1]	*B. (B.) s.*	*B. s.* (pos. sub. *B. (B.)*)	*B. s.*		*B. s.*		*B. s.*	–
B. f.	*B. (B.) s.* or pos. *B. (B.) f.*	*B. f.* or pos. *B. s.* – or pos. sub. *B. (?M.)*	*?B. f.*		–	*B. f.*	*B. f.*	–
holotype of *A. ped.*[2]	undiagnostic	–	*A. ped. ped.*		*A. ped.*		undiagnostic	*A. ped.*
B. a. par., *B. credneri* par., *B.* cf. *B. pet.*[3]	*B. (P.)* cf. *B. pet.*	*B.* cf. *B. pet.* (pos. sub. *B. (?M.)*)					*B. ped.* (species name invalid!)	
P. pet.[4], *Pleuronura pellati*; later *B. pet.*	*B. (P.) pet.*	*B. pet.* (pos. sub. *B. (?M.)*)	pos. *A. ped. ped.*	*A. ped. ?pet.*	*A. ?pet.*	–	*B. pet.*	–
	B. (?P.) dracyi	*B. dracyi* (pos. sub. *B. (B.)*)	*A. dracyi*		*A. dracyiensis* [sic!]		*B. dracyensis* [sic]	*A. dracyi*
B. tener, later *L. tener*[5]	–	–	*A. dracyiformis*					
	–	–	*S. pr.*		*S. pr.*		apparently *B. pr.*	–
	L. tener	*B. tener* (pos. its own sub. *B. (L.)*)	*L. tener*		*M. tenerum*		(by implication *L. tenerum* [sic!])	–
B. pet. par., *B. flagrifer*	*B. (P.) flagrifer* or *B. (P.) pet.*	*B. flagrifer* or *B. pet.* (pos. sub. *B. (?M.)*)	*A. flagrifer*		*A. flagrifera* [sic!]		*B. flagrifera* [sic!], *B. flagrifer* *B. b.*	*A. flagrifer*
B. b.	–	pos. *B. b.*; ??sub. *B. (?M.)*)	*A. ped. b.*	*A. ped. ?b.* (pos. *A. flagrifer*)				–
M. pusillum[6]	*B. (P.) pusillus*	*B. pusillus* (pos. sub. *B. (M.)*)	*A. pusillus*		*M. pusillum*		(recommends against the use of *M.*)	(by implication *M. pusillum*)
B. caducus	*B. (P.) caducus*	*B. caducus* (pos. sub. *B. (?M.)*)	*A. caducus*		*A. caduca* [sic!]		*B. caduca* [sic!]	*A. caducus*
B. gracilis; later *B. a.* par.; *B. pet.* par.	*B. (P.) gracilis*	*B. gracilis* (pos. sub. *B. (?M.)*)	*A. gracilis*		*M. gracile*		*B. gracilis*	*A. gracilis*
					A. kontheri		*B. kontheri*	–
						A. intermedius		–
	B. sp. vom Humberg	*B. humbergensis* (pos. sub. *B. (L.)*)	*L. humbergensis*		*M. humbergense*		*B. humbergense* [sic!]	*M. humbergense*

[1] Type species of *B.* – [2] Type species of *A.* – [3] Includes the neotype of *A. ped.* – [4] Type species of *P.*, which was regarded as a *nomen oblitum* by Boy (1972). – [5] Type species of *L.* – [6] Type species of *M.*

Chapter 4

Reevaluation of the data matrix by Anderson et al. (2008) and partial reply to Anderson (2008)

Anderson (2008) wrote a long, detailed review article on the origins of the extant amphibians. In it, he defended the polyphyly hypothesis (see the General Introduction and the introduction to Chapter 3) and replied to a few points raised by Chapter 1. We think he misinterpreted parts of that publication and wrote a reply, using the opportunity to present a summary of Chapters 2 and 3 as well. This reply was under tight space constraints because it is a "Brief Commentary"; I have therefore tried to keep the present introduction very short in order to avoid simply repeating the paper.

A fairly common claim in the present debate is that the lepospondyl hypothesis relies on "loss characters" which could result from paedomorphosis and/or miniaturization and could thus be correlated to each other, so that counting them separately would artificially inflate their weight. The article by Anderson (2008) is the latest publication to repeat this idea. We find this argument rather inconsistent; for instance, in the matrix by Anderson et al. (2008), more than one out of every five characters is a "loss character" according to our definition (the first definition that has, to the best of our knowledge, ever been proposed; Supplementary Table 1 of this paper). A statistical test (Huelsenbeck 1991) shows (Suppl. Table 3) that the "loss characters" in the matrices of Vallin & Laurin (2004 – the last published phylogenetic analysis before Chapter 3 to support the lepospondyl hypothesis; Suppl. Table 2) and Anderson et al. (2008) are not strongly correlated to each other and appear to contain phylogenetic signal. Furthermore, not all "loss characters" support the lepospondyl hypothesis; at least one favors the temnospondyl hypothesis (footnote 4 to Suppl. Table 2).

Both reviewers requested that we give, as supplementary information, the same treatment to the data matrix by Anderson et al. (2008) than we had to the matrix by McGowan (2002) in Chapter 3. The matrix by Anderson et al. (2008) is considerably larger, so we were not able to check every cell, but still we found discrepancies to the primary literature in 39 characters; I also ordered 38 characters (an overlapping set). Analysis of the resulting modified matrix supports the lepospondyl hypothesis by some of the highest bootstrap and Bremer values in the tree (Suppl. Figure). Remarkably, in the complete results of the bootstrap analysis, there is almost no support for the temnospondyl hypothesis and very little for the polyphyly hypothesis, and the support for the latter is comparable to that for a hypothesis that has never been proposed in the literature and would have the frogs and salamanders as lepo- and the caecilians as temnospondyls, the inverse of the polyphyly hypothesis (Suppl. Tables 4, 5).

Errata and updates

We mention my continuation of a chapter of Damien Germain's (2008) doctoral thesis; this is Chapter 5 of this thesis.

Having noticed that Milner (1980: 392) called the teeth of the "nectridean" lepospondyl *Scincosaurus* "pedicellate […] without a line of abscission", I cited this self-contradictory description as possible evidence of pedicellate teeth in a lepospondyl. The teeth of *Scincosau-*

rus are not pedicellate; the word had only been used to describe the shape of the tooth crowns with their expanded tips on cylindrical shafts – these shafts could be called “pedicels” according to the general meaning of that word (Angela Milner, pers. comm. September 2009; Milner & Ruta 2009).

I found the literature to contradict itself on the number of fingers per hand (four or five) in the “nectridean” lepospondyls *Keraterpeton* and *Diceratosaurus* (Electronic Supplementary Material 1: 12). In July 2009, I had an opportunity to observe the specimen of *Diceratosaurus* that Jaekel (1902) had figured; it unambiguously has five fingers per hand. This surprised Angela Milner, who has found *Keraterpeton* to possess only four (pers. comm. September 2009). The Appendix to Chapter 5 presents this issue in detail.

In order to make as few changes to the matrix as necessary, we did not apply my reinterpretation of the homology of some skull roof bones of *Brachydectes* (Chapter 3). This may not be defensible, but is unlikely to have had a large impact.

As mentioned in the introduction to Chapter 3, Anderson (pers. comm.) insists that *Gerobatrachus* has pedicellate teeth and a basale commune. Scoring the former as present and repeating the analysis changes nothing (*Gerobatrachus* was already optimized as having pedicellate teeth because *Doleserpeton* and *Amphibamus* do); scoring the latter as present adds one step to the most parsimonious trees, but changes neither the topology nor even the support values. This is now mentioned in Chapter 6.

Author contributions

M. L. played an important role in shortening the manuscript (again and again) so it would fit into the allotted space, and supervised my work; I performed the analyses, wrote Electronic Supplementary Material 1, and made the illustration (Suppl. Figure/Electronic Supplementary Material 2); the manuscript itself is a collaborative effort that would be difficult to tease apart, and so are the modifications to the data matrix except that I decided which characters to order.

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Evol Biol
DOI 10.1007/s11692-009-9065-8

COMMENTARY

The Origin(s) of Modern Amphibians: A Commentary

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Received: 20 January 2009 / Accepted: 24 June 2009

Anderson (2008) recently reviewed the controversial topic of extant amphibian origins, on which three (groups of) hypotheses exist at the moment. Anderson favors the "polyphyly hypothesis" (PH), which considers the extant amphibians to be polyphyletic with respect to many Paleozoic limbed vertebrates and was most recently supported by the analysis of Anderson et al. (2008). Another is the "temnospondyl hypothesis" (TH—lissamphibians nested within temnospondyls), most recently supported by Ruta and Coates (2007). We prefer the "lepospondyl hypothesis" (LH—lissamphibians nested within "lepospondyls"; most recently supported by Vallin and Laurin 2004 and Marjanović and Laurin 2008a). We would like to clarify important points that were not discussed in Anderson's review, or for which crucial arguments were left out.

Anderson (2008) argues that most molecular dates favor the PH because they suggest a Devonian or Early Carboniferous diversification of Lissamphibia. This is inaccurate, since the confidence intervals of the dates obtained by Hugall et al. (2007) range from Early Carboniferous to Middle Permian, and our own molecular dating suggests a Permian origin. Indeed, three methods (molecular dating, a paleontological supertree and a confidence interval on the stratigraphic range of Lissamphibia) all hint at a Permian or (less likely) a Late Carboniferous origin of Lissamphibia (Marjanović and Laurin 2007, 2008b).

Citing Schoch and Milner (2004), Anderson (2008, p. 234) argues that the LH is mainly supported by loss characters, and that this is problematic "given the relative ease that these losses can arise via paedomorphosis, which appears to evolve repeatedly." This is especially surprising because we count (Supplementary Table 1) about fifty loss characters in the matrix by Anderson et al. (2008)—more than one out of five characters—, including several that describe the loss of bones that ossified late in the ontogeny of branchiosaurids (Schoch 1992) and/or the aïstopod *Phlegethontia* (Anderson 2002) and are absent in lissamphibians.

Furthermore, Anderson's remark amounts to criticizing the use of loss characters simply because they *could* be homoplastic. Yet, Anderson (2008) emphasizes development characters such as digit development and skull ossification order, which are *known* to be homoplastic. For instance, under Anderson's version of the PH, the similarity between the digit development orders of the branchiosaurid temnospondyl *Apateon* and the urodeles is either convergent, or homologous between these two taxa but reversed in anurans; indeed, Johanson et al. (2007) suggest that the digits of tetrapods are homologous to the "radials" of other sarcopterygians and find the "radials" of the Australian lungfish to develop independently of the rest of the forelimb (pectoral fin), like in urodeles and *Apateon* (and unlike in anurans and amniotes, where the limb chondrifies in a strict proximal-to-distal sequence), strongly suggesting that the urodele-*Apateon* pattern is plesiomorphic—regardless of whether the PH, the TH, or the LH is (closest to) correct. Anderson (2008, p. 242) furthermore mentions that "the pattern of cranial ossification […] has compared very closely with the sequence of cranial ossification seen in salamanders" (making explicit on the next page that these

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Electronic supplementary material The online version of this article (doi:10.1007/s11692-009-9065-8) contains supplementary material, which is available to authorized users.

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similarities are plesiomorphic); more recently, however, Germain and Laurin (2009) have shown that the ancestral urodele sequence, even though poorly constrained, differed in several respects from that of *Apateon*.

Nonetheless, the suggestion that loss characters are likely to be strongly correlated to each other and homoplastic is serious; and indeed the matrix by Vallin and Laurin (2004) contains a greater proportion of loss characters (Supplementary Table 2) than that by Anderson et al. (2008). Unfortunately, no rigorous test of this possibility exists. The closest workable approximation we are aware of is the skewness test proposed by Huelsenbeck (1991), which measures how well a set of characters is compatible with different numbers of phylogenetic hypotheses: the smaller the g_1 statistic, the fewer trees are compatible with the character set, and the stronger is therefore the coherent phylogenetic signal in that character set. The g_1 of the loss characters is much lower (and thus their phylogenetic signal higher) than that of the others in the matrix of Vallin and Laurin (2004), but higher in that of Anderson et al. (2008), and highly significant in all four partitions (Supplementary Table 3), showing that loss characters are not necessarily strongly correlated to each other, and that they appear to contain a phylogenetic signal.

Matrices of various sizes support the various hypotheses on lissamphibian origins. Anderson (2008, p. 234), citing Schoch and Milner (2004), criticizes the "limited number of taxa analyzed" by LH proponents. There is a trade-off between quantity and quality in a data matrix for a given time investment, and quality is as important as quantity for reaching accurate phylogenetic results. Even small matrices are sometimes not coded carefully enough. We recently showed that 35% of the cells of the first matrix that supported the PH, that by McGowan (2002), were problematic (Marjanović and Laurin 2008a); with only the original taxa included, our modified version supports the TH, while adding *Gerobatrachus* and the "lepospondyl" *Brachydectes* results in the LH.

Until recently, few studies supported the LH, but two recent dissertations which contain large phylogenetic analyses bolster it (Pawley 2006, p. 239 and appendix 16; Germain 2008a). Pawley (2006) built upon the data matrix by Ruta et al. (2003), which originally supported the TH; Germain (2008a) merely took the matrix by Ruta and Coates (2007), which likewise originally supported the TH, did not change its taxon or character sampling (except for fusing four correlated characters), and improved the accuracy of the scoring. Although Germain (2008a) found the LH to be only one step more parsimonious than the TH, continuation of his work by David Marjanović (supplemented by the fusion of further correlated characters and the addition of information published in or after 2007) has so far increased the difference to eight steps. Incidentally, the LH is no longer supported only by Michel Laurin and his students; neither of us knew of Pawley's dissertation till 2 years after the defense.

As with that by McGowan (2002), we find much to disagree with in the matrix of Anderson et al. (2008). Our rescoring and/or recoding of 39 characters and all but five taxa (and ordering of 38 of the multistate characters for reasons explained by Marjanović and Laurin 2008a, p. 163, partially overlapping with the set of rescored characters) supports the LH, with the lysorophian *Brachydectes* as the sister-group of Lissamphibia; the bootstrap and Bremer values for a "lepospondyl"-lissamphibian clade (Amphibia) which excludes all temnospondyls are high. Again as with the matrix by McGowan (2002), our changes range from the correction of probable typographic errors (like the alleged lack of a cleithrum in *Triadobatrachus* and "frogs" in character 193, or the alleged absence of a caudolateral flange or corner on the pterygoid that constricts the subtemporal fenestra in *Seymouria* and *Limnoscelis* in character 120) to disagreements of interpretation; for example, having compared all described temnospondyl tarsi, we are not convinced that an *os basale commune* (character 207) is present in *Gerobatrachus* (Marjanović and Laurin 2008a, pp. 168–169), and although strong cases for tooth pedicely (character 99) in closely related temnospondyls have been made, we do not think the published evidence establishes whether *Gerobatrachus* shares this feature (Marjanović and Laurin 2008a, p. 179), so we had to score these two characters as unknown in *Gerobatrachus*. See the Electronic Supplementary Material for more information about the cells that were rescored, the supporting references, the methods, the resulting topology, the support values, and the modified matrix.

Furthermore, possibly pedicellate teeth have now been described in an aïstopod (Germain 2008b) and may be present in another (Carroll 1998, Fig. 4B). In addition, Milner (1980, p. 392) calls the teeth of the nectridean *Scincosaurus* "pedicellate […] without a line of abscission"; to the best of our knowledge, the teeth of *Scincosaurus* have never been mentioned in the literature before or since (most notably not by Bossy and Milner 1998). Further research will be necessary to determine if pedicely is much more widespread than previously thought.

For all these reasons, we conclude that the polyphyly hypothesis is less likely than suggested by Anderson (2008), and that the lepospondyl hypothesis seems to be at least as well supported as the temnospondyl hypothesis.

Acknowledgments J.-C. Rage, D. Wake, and two anonymous referees commented on previous drafts of this paper; we are especially grateful to D. Wake for several constructive suggestions.

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Electronic Supplementary Material 1 to

The origin(s) of modern amphibians: a commentary

by

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This supplement contains the methods, materials and results of our reanalysis of the data matrix by Anderson *et al*. (2008) and of our application of the skewness test by Huelsenbeck (1991) to the matrices by Anderson *et al*. (2008) and Vallin and Laurin (2004), including supplementary references and the Supplementary Tables. The Supplementary Figure (ESM2), the data matrix (ESM3), and the trees used to find the ancestral states of the "frogs" (ESM4) and "salamanders" OTUs (ESM5) are separate files.

Legend to the Supplementary Figure (ESM2): Strict consensus of the four most parsimonious trees (see Results section). Numbers below internodes are bootstrap percentages (in bold if 50 or higher; "–" indicates clades contradicted by the bootstrap tree, always by clades with bootstrap percentages of 40 or less), numbers above internodes are Bremer values. Some or all of the Bremer values shown as "≥ 5" might actually be 5, because we were unable to find all trees that were up to 5 steps longer than the most parsimonious trees, although the fact that an earlier iteration of this analysis, with a dataset that differed only in two cells, found the same results makes this possibility unlikely.

All amphibians that are not lissamphibians are "lepospondyls" (alternatively, a case could be made that Lepospondyli is – under the present phylogenetic hypothesis – a junior synonym of Amphibia). Strictly speaking, Amphibia is defined with respect to Amniota and therefore cannot be applied to this tree, which lacks amniotes, but the close relationship of *Limnoscelis* and Amniota has never been doubted. The temnospondyl *Gerobatrachus* is marked with an arrow.

Methods

The matrix was manipulated in Mesquite 2.6+ (Maddison and Maddison, 2009) on an Intel Macintosh; the analyses were conducted in PAUP* 4.0b10 (Swofford, 2003) on a G5 Macintosh.

We treated polymorphism differently from uncertainty (PAUP* command: "pset mstaxa=variable"). For the reasons explained below, characters 103, 146, 163 and 217 were excluded from all analyses (but kept in the matrix to retain the original numbering for all characters); furthermore, characters 137, 161, 188, and (now) 207 are parsimony-uninformative.

The main analysis was a heuristic search with 10,000 addition-sequence replicates (random addition sequence, 10 trees held at each step, TBR swapping, no limit on rearrangements). Five additional analyses were performed to find all trees that are up to one to five steps longer (the search for those up to five steps longer than the minimum length had to be terminated after 370,000 trees due to lack of memory), in order to find Bremer support values; these analyses had otherwise identical settings to the main analysis, except for consisting of only 200 addition-sequence replicates. We also conducted a bootstrap analysis with 200 bootstrap replicates (100 addition-sequence replicates within each, 10 trees held at each step, TBR swapping).

The term "loss character" seems never to have been defined. We opt for a strict definition: the wholesale loss (on the most parsimonious trees of the publication in question) of entire bones or structures between bones (like fontanelles or the parietal foramen) or on them (canals for the lateral-line system, dermal sculpturing). We have not counted the loss of processes of bones, even conspicuous ones like the tabular "horns", or other potentially continuous characters; we have also not counted meristic characters (like the number of vertebrae in certain parts of the column). The lists of loss characters in the matrices of Anderson *et al.* (2008) and Vallin and Laurin (2004) are presented in Supplementary Tables 1 and 2, respectively.

We calculated the g_1 statistic for the loss characters and the remaining characters of both matrices (using PAUP*; Swofford, 2003). Unfortunately, Huelsenbeck (1991: table 1; reproduced in Supplementary Table 3, left side) only lists the 5% and 1% significance thresholds for 6, 7 and 8 taxa; the matrices by Vallin and Laurin (2004) and Anderson *et al.* (2008) are both much larger. However, from 6 to 8 taxa, the thresholds decrease with increasing taxon number. We conclude that all values (Supplementary Table 3, right side) are most likely highly significant, so that all four partitions contain a phylogenetic signal of comparable and high strength.

Modified scores, character definitions and state delimitations

All characters were left unordered by Anderson *et al.* (2008). However, potentially continuous multistate characters should always be ordered, because the assumption that any character state can more easily change into a similar state than into a very different one was already used for subdividing the potential continuum into discrete states (Wiens, 2001; see Marjanović and Laurin, 2008, for a previous application of this principle). Altogether, we ordered characters 1, 2, 16, 29, 32, 34, 39, 74, 75, 82, 87, 103, 115, 126, 128, 130, 134, 136, 138, 144, 145, 149, 155, 159, 170, 172, 179, 181, 183, 195, 197, 198, 200, 201, 204, 208, 209, and 211. In four cases, the state numbers were not in the appropriate order for this. We exchanged states 0 and 1 of characters 16 and 115. The former state 3 of character 34 was put at the other end, so that the new states 0, 1, 2 and 3 correspond to the old states 3, 0, 1 and 2. The states of character 145 had to be rearranged more extensively: the new states 0, 1, 2 and 3 correspond to the old states 2, 0, 1 and 3, respectively.

More trivially, Anderson *et al.* (2008) used "?" for missing data and "-" to indicate inapplicable codings, a distinction that no currently existing phylogenetics program can deal with. The hyphen is interpreted as a gap (in a DNA or protein sequence, implying a mixed dataset) by PAUP*; fortunately, the default setting is to interpret gaps as missing data. To avoid problems with the other setting (which is to interpret gaps as a 5th base/21st amino acid), we have replaced every hyphen by a question mark in the NEXUS file (ESM3).

Yet more trivially, we have corrected the spelling "*Hapsidoparion*" to *Hapsidopareion*.

Because of the size of this matrix and various time constraints, we have not checked the accuracy of every cell; we have revised mostly those characters whose distribution of states across taxa seemed anomalous and those where we redelimited the states. Indeed, we only noticed the errors in character 193 (see below) after the first submission and had to repeat all analyses; it is therefore possible that the matrix still contains errors.

Despite this, only changes are listed below (as in Marjanović and Laurin, 2008); listing the cells we found to be accurate would require too much space and time.

Character 16: lacrimal possesses both dorsal (prefrontal/frontal) and ventral (jugal/maxillary) processes (0), ventral process only (1), or neither (2) (ordered). In *Acanthostega*, as correctly coded by character 15, the lacrimal does not participate in the orbit margin (being excluded by prefrontal-jugal contact), so we have scored it as inapplicable (= unknown).

At least some specimens of *Micropholis* possess the caudal process (Schoch and Rubidge, 2005: figs. 3B, E), giving it states 1 and 2 (a polymorphism).

We have also changed Branchiosauridae from state 2 to state 1, because the morphologically most mature known specimens possess the ventral process (Schoch and Fröbisch, 2006: figs. 1C, D).

The ventral process is likewise present in Albanerpetontidae (McGowan, 2002: fig. 5B).

This also seems to be the ancestral state for those salamanders (that is, the hynobiids) which possess a lacrimal which participates in the orbit margin, for example *Hynobius* (Carroll and Holmes, 1980: fig. 4A, C).

Limnoscelis appears to lack both processes (Fracasso, 1983: fig. 3A), although this could be a matter of definition.

Character 22: Prefrontal-postfrontal suture (0); frontal participates in margin of orbit (1). Anderson *et al*. (2008) defined state 0 only as the opposite of state 1, without mentioning the fact that it contains several different states (for example, *Brachydectes* lacks postfrontals and has a prefrontal-parietal contact which excludes the frontal from the orbit margin). Furthermore, redefining state 0 as we have done makes explicit that many animals that, at face value, show state 1 should actually be scored as inapplicable.

This includes all lissamphibians in the present matrix except *Eocaecilia* (which was correctly scored as possessing state 0), because they all lack postfrontals and therefore cannot help lacking a prefrontal-postfrontal contact.

Character 26: Dorsal process of premaxilla: broad, low, indistinct (0); alary process (broad, vaguely triangular) (1); moderately high, vaguely rectangular, or acutely triangular linked directly to base (2); narrow and long, along the sagittal plane or parasagittal (3) (unordered). This coding differs from that by Anderson *et al*. (2008) so as to better fit the morphological diversity seen especially in extant amphibians. It is congruent with the findings of Good and Wake (1992), but it recognizes two states within the condition that Good and Wake (1992) considered primitive.

Greererpeton shows state 1 (Smithson, 1982).

Seymouria baylorensis is borderline between states 0 and 2 (see Laurin, 1996); we have decided on state 2.

Limnoscelis possesses state 2 (Fracasso, 1983).

All states except 0 occur in salamanders: *Karaurus* has state 1 (Ivachnenko, 1978: fig. 1); Hynobiidae shows states 3 (*Hynobius tsuensis*), 1 (*Batrachuperus sinensis*), and indeterminate (*Hynobius naevius*) (Carroll and Holmes, 1980: fig. 4). According to figure 5 of the same paper, state 2 occurs in Cryptobranchidae. *Ambystoma* (*ibid*., fig. 6) and plethodontids (*ibid*., fig. 7) possess state 3. Salamandrids can have state 3 (*ibid*., fig. 8A) or be indeterminate (*ibid*., fig. 8B). Proteidae exhibits state 3 (*ibid*., fig. 9), as do Amphiumidae (*ibid*., fig. 10) and Sirenidae (ibid., fig. 11). To code the single OTU "salamanders", we have used the same approach as in Marjanović and Laurin (2008): optimizing this diversity onto the phylogenetic hypothesis shown in fig. 8 of Wiens *et al*. (2005) when *Karaurus* is added as the sister-group of Urodela, states 1 and 3 emerge as most parsimoniously plesiomorphic for Caudata as a whole, so we have assigned it state 1 or 3 (partial uncertainty).

Most anurans have state 3 (Duellman and Trueb, 1986: figs. 13-17 and 13-18).

Most "microsaurs" also had to be rescored according to Carroll and Gaskill (1978).

Character 34: Caudal margin of the skull roof: undulating (0); concave (1); straight (2); convex (3) (ordered). The place of state 0 in this sequence is certainly debatable; an alternative would have been to consider the median caudal projection of the skull roof a separate character, as Ruta and Coates (2007: 96) did (twice: characters POSPAR 4 and POSPAR 8), defensible by the fact that most but not all taxa with an undulating margin would otherwise count as concave.

The margin is straight in *Brachydectes* (Wellstead, 1991: figs. 2, 3, 8) and undulating in *Sauropleura* (Bossy and Milner, 1998: fig. 53B), arguably *Ptyonius* (ibid., fig. 53G), and *Eocaecilia* (Jenkins *et al*., 2007: figs. 1, 2).

Character 39: Large otic notch approaching orbit: absent (0); intermediate (1); close (2) (ordered). Because the albanerpetontids lack an otic or other temporal notch or other embayment, we consider this character (which appears to describe the distance between the rostral margin of the "otic notch" and the caudal margin of the orbit) inapplicable to them.

Character 51: Parietal-squamosal contact: absent (0), present (1). This character is only applicable when the supratemporal is absent. (When present, the supratemporal extends from the tabular and/or the caudal margin of the skull roof to the postorbital, unless a temporal fenestra intervenes as it does in many amniotes and aïstopods; in the latter the fenestra separates the parietal from the squamosal, making the present character likewise inapplicable.) The presence of the supratemporal is already coded as state 0 of character 5; keeping state 51(0) for taxa with 5(0) would therefore correlate these two characters.

Both states occur in *Microbrachis* (Carroll and Gaskill 1978: figs. 77, 78).

Character 59: Tabular: present (0); absent (1). Having examined the only known (and very confusing) specimen of *Triadobatrachus* (see Marjanović and Laurin, 2008: appendix-table 1), we provisionally disagree with J. Anderson's otherwise unpublished reinterpretation of its skull roof and agree with the literature (*e.g.*, Rage and Roček, 1989) that tabulars are absent in this animal.

Character 74: Number of premaxillary teeth ≥ 10 (0); 5–9 (1); < 5 (2) (ordered). All three states occur in salamanders: *Karaurus* has about 25 premaxillary teeth (Ivachnenko, 1978: 364, fig. 1a); *Batrachuperus sinensis* (Hynobiidae) possesses 9; *Cryptobranchus* and *Ambystoma* both possess more than 10; *Phaeognathus hubrichti* (Plethodontidae) shows about 8; *Salamandra atra* exhibits only about 4; more than 10 are present in *Notophthalmus viridescens* (Salamandridae) and *Necturus* (Proteidae); only about 5 occur in *Amphiuma* and in *Habrosaurus* (Sirenidae). Using the same approach and the same references as for character 26, states 0 and 1 emerge as candidates for the plesiomorphic state, so we have coded the salamander OTU as possessing state 0 or 1.

Using the same approach, only state 0 (rather than 0 or 1) emerges as plesiomorphic for frogs: *Yizhoubatrachus* (10 on the right, 11 on the left premaxilla: Gao and Chen, 2004), *Notobatrachus* (reconstructed with 14 to 15: Sanchíz, 1998: fig. 20B), *Mesophryne* (16 teeth are preserved on an incomplete premaxilla: Gao and Wang, 2001: 461), *Eodiscoglossus* (at least 15 tooth positions: Evans *et al*., 1990: 302), and *Ascaphus* (Carroll and Holmes, 1980: fig. 3A) all show well over 10 teeth; the variation in *Leiopelma* even includes 15 to 25 teeth (Sanchíz, 1998: 16, fig. 19G).

Both *Albanerpeton* (McGowan, 2000: 367; Venczel and Gardner, 2005: 1282) and *Celtedens* (McGowan, 2002: 5) possess both state 0 and state 1. The only known premaxilla of *Anoualerpeton* with a complete toothrow preserves 10 teeth (Gardner *et al*., 2003: 308). Taken at face value, this would make state 0 more parsimonious as the plesiomorphic condition of Albanerpetontidae, but because of the limited sample size we have preferred to score Albanerpetontidae as polymorphic.

Character 75: Number of maxillary teeth: ≥ 30 (0); 20–29 (1); < 20 (2) (ordered). *Albanerpeton* possesses states 1 and 2 (Gardner, 1999: 536; 2000: 367; Venczel and Gardner, 2005: 1282), while the composite maximum estimate for *Anoualerpeton* (Gardner *et al.*, 2003: 308) is 25 teeth, thus staying in state 1. In the absence of evidence to the contrary from *Celtedens*, and due to the small sample size of *Anoualerpeton*, we have extrapolated the polymorphism of *Albanerpeton* to Albanerpetontidae as a whole.

Character 84: Occipital condyle: concave (0); convex (1). State 1 was ascribed to *Gerobatrachus*, but the occipital condyle is not preserved (Anderson et al., 2008: figs. 1, 2). We have therefore scored *Gerobatrachus* as unknown.

Character 85: Occipital condyle: single (0); double (1). We have changed the score of *Gerobatrachus* from state 1 to unknown for the reasons mentioned under character 84.

Ecolsonia, on the other hand, possesses a "distinctly double occipital condyle" (Berman *et al*., 1985: 16).

State 1 is shared by *Asaphestera* (Carroll and Gaskill, 1978: fig. 6E), *Hapsidopareion* (*ibid*., fig. 13B), *Pelodosotis* (*ibid*., fig. 48A), *Micraroter* (*ibid*., fig. 53), *Pantylus* (*ibid*., fig. 25), *Cardiocephalus sternbergi* (*ibid*., figs. 30B, C), *Cardiocephalus peabodyi* (judging from the articular surfaces on the atlas: *ibid*., fig. 31), *Euryodus primus* (for the same reason: *ibid*., figs. 37, 38, 41), *Euryodus dalyae* (ibid., figs. 42–44), *Rhynchonkos* (*ibid*., figs. 63–65), *Microbrachis* (*ibid*., figs. 77–79; Vallin and Laurin, 2004: 62), *Stegotretus* (Berman *et al*., 1988: 310), *Sauropleura scalaris* (Bossy, 1976: 96 and fig. 25b), *Ptyonius* (Bossy, 1976: 145), and *Brachydectes* (Wellstead, 1991: figs. 2, 15C).

"The surfaces that formed part of the occipital condyle cannot be seen" in *Tuditanus* (Carroll and Baird, 1968: 12), suggesting that the reconstruction in ventral view by Carroll and Gaskill (1978: fig. 4) is just that – a reconstruction. We have therefore changed its score to unknown.

Much the same holds for *Batropetes* (Carroll and Gaskill, 1971: 454) and *Saxonerpeton* (Carroll and Gaskill, 1978: 34).

Bossy (1976: 209) describes the occipital condyle of *Urocordylus* as "semidouble", suggesting an intermediate morphology which we have coded as unknown for the sake of simplicity.

Character 86: Jugular foramen: between opisthotic and exoccipital (0); through exoccipital (1). This character has not been described in *Doleserpeton*, so we have changed its score to unknown.

In frogs, the exoccipital is almost always fused to other braincase bones (Duellman and Trueb, 1986: table 13-1), making it impossible to evaluate the position of the jugular foramen relative to the opisthotic and forcing us to score the frogs as unknown.

Character 87: Jaw articulation: caudal to occiput (0); even with occiput (1); rostral to occiput (2); far rostral to occiput (over 20% of basal skull length) (3) (ordered). The frogs were scored as 0 (a state that really occurs in the separate OTU *Triadobatrachus*, which was scored correctly; Rage and Roček, 1989), but *Notobatrachus* (Sanchíz, 1998), *Vieraella* (Carroll and Holmes, 1980: fig. 3), *Ascaphus* (same figure, and Noble, 1931: fig. 81A), and others like *Pelobates* possess state 2. *Mesophryne* appears to show state 1, but is incompletely preserved and somewhat disarticulated (Gao and Wang, 2001: fig. 4). We have scored it as unknown (though we should have restricted this somewhat).

Character 89: Palatine fangs: present (0); absent (1). This character originally referred to “palatal teeth” in general, but this would correlate to several others like 94 (presence and arrangement of vomerine teeth) and especially 90, which treated fangs and toothrows as states of the same character, even though both can occur together (like in *Acanthostega*: Clack, 1994: fig. 11C).

Asaphestera is restored by Carroll and Gaskill (1978: fig. 7) as possessing a row of very large teeth on the palatine and ectopterygoid. We count this as state 0 (see Marjanović and Laurin, 2008: 180), even though we also count it as state 1 of the next character (as originally scored).

The palate of *Diceratosaurus* is illustrated in Jaekel (1902: plate III); it shows state 1.

The palatine of *Adelogyrinus* is unknown (Andrews and Carroll, 1991).

Character 90: Palatine teeth (marginal-sized): absent (0); multiple in rows (1); multiple random (2) (unordered). See character 89.

Greererpeton possesses a row of palatine teeth (Smithson, 1982).

Limnoscelis lacks palatine teeth (Fracasso, 1983: fig. 2).

Micropholis possesses a palatine toothrow (Schoch and Rubidge, 2005: fig. 1D).

The only known adult specimen of *Amphibamus* possesses fangs instead of a toothrow (Daly, 1994).

The palatine teeth of *Gerobatrachus* are small enough to count as denticles, and are not arranged in rows (Anderson *et al*., 2008: fig. 2a).

All teeth on the palatine of *Microbrachis* are small enough to count as denticles (Carroll and Gaskill, 1978); this means state 0.

The palate of *Diceratosaurus* is illustrated in Jaekel (1902: plate III); it shows state 1.

The palatine of *Adelogyrinus* is unknown (Andrews and Carroll, 1991).

The palatine of *Brachydectes* is toothless (Wellstead, 1991).

Triadobatrachus has a preserved and apparently toothless palatine, so we have given it state 1 (Rage and Roček, 1989).

Palatine teeth are likewise always absent in the “frogs” OTU (Duellman and Trueb, 1986: 318).

Character 94: Vomerine teeth: absent (0); forming a single row (1); forming a field (2) (unordered). This definition is new. “Teeth” are about the size of the marginal teeth, markedly larger than denticles and smaller than fangs; state 2 is what is exhibited by the sirenids.

Doleserpeton possesses states 1 and 2; there is both a row (near the choana) and a field (Bolt 1969). This might, however, be an artefact of the fact that the marginal teeth are tiny – no teeth of *Doleserpeton* are sufficiently smaller to count as denticles.

Amphibamus, Gerobatrachus, and *Limnoscelis* show state 0.

Character 99: Tooth pedicely: absent (0); present (1). We have scored *Gerobatrachus* as unknown for the reasons explained in Marjanović and Laurin (2008: 179) and done the same with *Oestocephalus*, *Phlegethontia*, and *Scincosaurus* for the reasons explained in the main text of the present paper.

Character 100: Denticles on vomers: present (0); absent (1). *Gerobatrachus* was scored 0, but, judging from the illustrations rather than the text of Anderson *et al*. (2008), its vomerine teeth are unambiguously small enough to count as denticles, giving it state 0.

Character 102: Denticles on parasphenoid: present (0), absent (1). *Triadobatrachus,* frogs, salamanders and albanerpetontids (*Celtedens*: McGowan, 2002: fig. 13; denticles are also not mentioned for the incomplete parasphenoid part of the os basale of *Albanerpeton inexpectatum* by Estes and Hoffstetter, 1976: 314) possess state 1, while *Eocaecilia* shows state 0 (Jenkins *et al*., 2007).

Character 103: Palatal teeth: larger than marginals (0), equal to marginals (1). This character is correlated to several others (such as 89, 90, 93 and 94); we have therefore excluded it from our analyses.

Character 105: Parasphenoid basal plate: roughly quadrangular, basipterygoid articulations narrowly spaced (0); about as broad as long, articulations moderately distant (1); rectangular laterally, anteroposteriorly narrow, basipterygoid articulations distant (2) (ordered). State 1 was added because the condition in the following OTUs fits neither state 0 nor state 2 (the former state 1):

Tuditanus (Carroll and Gaskill, 1978: fig. 4); *Hapsidopareion* (*ibid*., fig. 13); *Saxonerpeton* (*ibid*., fig. 22); *Cardiocephalus sternbergi* (*ibid*., fig. 30); *Euryodus primus* (*ibid*., figs. 36–38); *Euryodus dalyae* (*ibid*., figs. 42, 43); *Pelodosotis* (*ibid*., fig. 48); *Micraroter* (*ibid*., fig. 53); *Rhynchonkos* (*ibid*., figs. 63–65); *Microbrachis* (ibid., fig. 77; Vallin and Laurin, 2004: fig. 5B); *Stegotretus* (Berman *et al*., 1988: fig. 8); *Ptyonius* (Bossy, 1976: fig. 49; Bossy and Milner, 1998: fig. 55B); *Diploceraspis* (Beerbower, 1963: fig. 4); *Scincosaurus* (Bossy and Milner, 1998: fig. 57D); *Oestocephalus* (Carroll, 1998: fig. 3); *Brachydectes* (Wellstead, 1991: fig. 2); *Eocaecilia* (Jenkins et al., 2007); salamanders (Carroll and Holmes, 1980).

Furthermore, the condition is unknown in the following OTUs: *Gerobatrachus* (where the caudal part of the palate is very fragmentary and somewhat disarticulated, so that the statement in the text about the shape of the parasphenoid may not be warranted; Anderson *et al*., 2008); *Urocordylus* (Bossy and Milner, 1998: fig. 55A); *Batrachiderpeton* (where the parasphenoid has a unique shape and is incompletely preserved; Bossy and Milner, 1998: fig. 57B); *Adelogyrinus* (Andrews and Carroll, 1991: fig. 6).

The condition in *Phlegethontia* counts as state 0 (Anderson, 2002: fig. 4:2).

Character 109: Stapes orientation: lateral, towards quadrate (0); dorsal, towards squamosal embayment, elongate columella (1). Salamanders possess state 0.

Character 120: Pterygoid extending into subtemporal fenestra, constricting it: no (0); yes (1). The pterygoid sometimes extends a corner (especially when a transverse flange is present on the pterygoid, like in *Seymouria* [Laurin, 1996] or *Limnoscelis* [Fracasso, 1983]; incidentally, both were erroneously scored as 0, which we can only explain as a typographic error; but also in the absence of a flange, such corners occur, like in the correctly scored *Eryops*: Sawin, 1941: plate 2) or a rounded flange (like in the correctly scored *Balanerpeton*: Milner and Sequeira, 1994) into the subtemporal fenestra, which was erroneously called “posttemp fen” in the supplementary information of Anderson *et al*. (2008), the posttemporal fenestra being on the occiput.

State 1 is further present in *Dendrerpeton* (Milner, 1996: fig. 6), *Asaphestera*, *Hapsidopareion*, *Saxonerpeton* (all Carroll and Gaskill, 1978: fig. 108), *Euryodus primus* and *E. dalyae* (both Carroll and Gaskill, 1978: fig. 109), *Microbrachis* (Vallin and Laurin, 2004), and *Eocaecilia* (Jenkins *et al*., 2007).

Branchiosauridae is polymorphic (Boy, 1978, 1986, 1987).

The condition in *Tuditanus* is unknown because the lower jaws are in place (Carroll and Baird, 1968).

In *Cardiocephalus sternbergi*, the condition is so intermediate (Carroll and Gaskill, 1978: fig. 30) that we score it as unknown.

The palate of *Batropetes* is too incomplete to tell (Carroll, 1991: fig. 5B).

The only illustration of the palate of *Sauropleura scalaris* that we know about is fig. 55C of Bossy and Milner (1998). It shows a juvenile. This may be interesting because the adult of *S. pectinata*, illustrated in fig. 55D, exhibits state 1. Therefore we do not take fig. 55C at face value and score *S. scalaris* as unknown rather than 0.

The only illustration of the palate of *Ptyonius* known to us is fig. 55C of Bossy and Milner (1998). It shows state 0 on the left side and state 1 on the right. Taking into account that this line drawing is a somewhat schematic reconstruction, we have scored *Ptyonius* as unknown.

The palate is entirely unknown in *Adelogyrinus*. The only adelogyrinid palate illustrated by Andrews and Carroll (1991: fig. 13C) is that of *Adelospondylus* (which, incidentally, appears to possess state 1, even though the reconstruction in fig. 13D omits it almost entirely); *Adelospondylus* is not *Adelogyrinus*.

State 0 is present in all salamanders (except *Hynobius*, *Ambystoma*, and the salamandrid *Tylototriton*: Ivachnenko, 1978; Carroll and Holmes, 1980), as well as in *Triadobatrachus* (Rage and Roček, 1989: fig. 2B).

In crown-group frogs, state 0 is present (Duellman and Trueb, 1986: figs. 13-3, 13-4), except, under a generous interpretation, in *Ascaphus* (Carroll and Holmes, 1980: fig. 3A). State 0 is also found in *Vieraella* (Carroll and Holmes, 1980: fig. 3B) and *Yizhoubatrachus* (Gao and Chen, 2004), while *Notobatrachus* (Sanchíz, 1998: fig. 20B) and *Mesophryne* (Gao and Wang, 2001) possess state 1. In the continued absence of data from animals like *Prosalirus* (Shubin and Jenkins, 1995), whether the optimization for the “frogs” OTU is state 0 or ambiguous depends on how generous we are with *Ascaphus*; because there is no flange or other process in *Ascaphus* – instead, the rod-shaped pterygoid is bent as a whole to make the medial margin of the subtemporal fenestra concave instead of straight or convex –, we have decided to count *Ascaphus* and thus the “frogs” as a whole as having state 0 (which happens to be shared by *Triadobatrachus* and the salamanders, see above).

Character 121: Ectopterygoid: present, with fang-pit pair (0); present, without fang-pit pair (1); absent (2) (unordered). Although this character could be ordered on the grounds that the present sequence of states could be interpreted as a gradual shrinking of the ectopterygoid, we have not ordered it because we have not tested the assumption that there is a strong correlation between the size of the ectopterygoid and the presence of fangs.

State 2 is new (Anderson *et al.* did not distinguish it from state 1). It occurs in *Doleserpeton* (Bolt, 1969), both pantylids (*Pantylus*: Carroll and Gaskill, 1978: fig. 25; *Stegotretus*: Berman *et al.*, 1988: 308), *Brachydectes* (Wellstead, 1991: fig. 2), salamanders (Carroll and Holmes, 1980), *Triadobatrachus* (Rage and Roček, 1989) and the other frogs (Duellman and Trueb, 1986: figs. 13-17 and 13-18).

While the presence of a very small ectopterygoid (too small to bear fangs; known, if indeed homologous to the ectopterygoid, in several extant teresomatan caecilians – see Marjanović and Laurin, 2008: 181, for a list and some discussion) cannot be excluded in *Eocaecilia* (Jenkins *et al.*, 2007: 304), it is at least as probable that this bone was entirely absent (as reconstructed in Jenkins *et al.*, 2007: fig. 1). We have therefore changed its score to state 1 or 2.

Character 146: Vertebral development: arches, then centra (0); arches and centra simultaneously (1). In the absence of a very detailed growth series, it is impossible to distinguish state 1 from a simple lack of temporal resolution. There is widespread agreement about this among development biologists (*e.g.*, Bininda-Emonds *et al.*, 2003: 341). Such detailed growth series that show the stages of the ossification of the vertebral column are probably not available in any fossil limbed vertebrates other than the “branchiosaurs”, where the development of most endochondral bones was delayed (Schoch and Fröbisch, 2006). We have therefore excluded this character, which was already coded for only nine taxa (including two extant ones, one of which is polymorphic), from our analyses.

Perhaps not surprisingly, however, state 0 is known to occur in *Utaherpeton* (Carroll and Chorn, 1995: fig. 4b).

Character 163: Neural arches of the trunk: paired (0), fused (1). Except (presumably) in *Acanthostega* (which is polymorphic), this character is correlated to ontogenetic age and paedomorphosis. Therefore, all occurrences of state 0 except (presumably) *Acanthostega* should be scored as unknown (Wiens et al., 2005); this would make the character parsimony-uninformative. We have excluded this character from all analyses.

Character 168: Cranial surface of atlas centrum: same size as caudal surface (0); laterally expanded (1). The cranial surface is slightly expanded in *Sauropleura scalaris* (Bossy, 1976: 102 and fig. 25b), giving it state 1.

The same holds for *Ptyonius* (*ibid*., fig. 51a) and *Urocordylus* (*ibid*., 215).

The only preserved atlas centrum of *Keraterpeton* we know of (Huxley and Wright, 1867; Jaekel, 1902) is in dorsal view, hiding the cranial and the caudal surface and forcing us to score *Keraterpeton* as unknown.

The condition seems to be likewise unknown in *Diceratosaurus* and *Scincosaurus*.

Brachydectes possesses state 1 (Wellstead, 1991: figs. 11C, 18).

Character 179: Ribs: at least as long as three successive articulated vertebrae and curved in adults (0); like state 0, but straight (1); shorter than three successive articulated vertebrae in adults (2) (unordered). Anderson *et al*. (2008) called the states "elongated and sometimes curved", "straight", and "short, simple rod", but rib length and curvature are continua, so quantification was necessary to make reproducible coding possible. We have imported the quantification we used in Marjanović and Laurin (2008: 177); all the cautionary notes mentioned there apply here.

While close to the limit (like, *e.g.*, those of *Micraroter*: Carroll and Gaskill, 1978: fig. 57), the longest ribs of *Greererpeton* are longer than three successive vertebrae and are curved ventrally and (slightly) caudally (Godfrey, 1989: figs. 1, 3, 4); they are not outside the range of other OTUs with state 0, unlike the case of *Diplocaulus* with its long, very straight ribs.

Both the cervical (Berman *et al*., 1985: fig. 13) and the proximal caudal (*ibid*., fig. 10C, D) ribs of *Ecolsonia* – others are not preserved – are longer than three successive vertebrae and "moderately curved" (*ibid*.: 20).

The ribs of *Eocaecilia* are slightly curved, but curvature is not mentioned in either the original or our wording of state 2, and the ribs are only about as long as one vertebra (Jenkins *et al*., 2007); we have accordingly scored *Eocaecilia* as possessing state 2 (like, incidentally, all other lissamphibians).

As explained in Marjanović and Laurin (2008: 177–178), we have also scored *Balanerpeton*, *Dendrerpeton*, *Acheloma*, *Cardiocephalus peabodyi*, and *Rhynchonkos* as having state 1.

In *Euryodus primus*, no complete ribs seem to be known (Carroll and Gaskill, 1978: 64), and the rib fragments illustrated by Carroll and Gaskill (1978: fig. 39) are much shorter than three vertebrae. We have therefore scored *E. primus* as unknown.

We are not aware of a description or illustration of the ribs of *Stegotretus*; Berman *et al*. (1988: 312) state that "[a]lthough ribs are ubiquitous, none are sufficiently preserved or exposed to warrant description." Accordingly, we have scored *Stegotretus* as unknown.

The ribs of *Adelogyrinus* (Andrews and Carroll, 1991: fig. 6) are very similar to those of Greererpeton, but shorter (and somewhat straighter), fitting the definition of state 2.

Even though *Lethiscus* just reaches state 0 (Wellstead, 1982: figs. 1, 9A), the two aïstopods in the present matrix, *Ophiderpeton* and *Phlegethontia*, have clear cases of state 2 (Baird, 1964: fig. 1; Anderson, 2002, figs. 9, 10).

With both *Greererpeton* and *Ecolsonia* corrected to state 0, state 1 turns out to be unique to *Diplocaulus*. A case could be made for merging it into state 0 (ribs in state 2 are not necessarily straight), but we deem such a change unnecessary.

Character 181: Number of sacrals: one (0), two (1), three (2) (ordered). Several "microsaurs" were scored as possessing two sacral vertebrae. We cannot replicate this:

Carroll and Baird (1968: 14) argue that *Tuditanus* has two sacral vertebrae: "[…] two vertebrae with atypical ribs. The rib of the first, best seen in the type specimen, is thickened at the base and is evidently a sacral [rib]; the rib of the second vertebra is obscure. From the narrowness of the iliac blade it is doubtful that more than a single sacral rib could have articulated directly. Aside from its specialized rib, the principal [= first; Carroll and Gaskill, 1978: 16] sacral vertebra does not appear to differ significantly from its neighbors. The second appears to have a considerably larger transverse process." There are only two specimens. In the type (Carroll and Baird, 1968: figs. 4, 5B) the sacral region (with the pelvis, the proximal part of the left femur, and the entire right hindlimb and the tail) is missing – except for the mentioned rib, which is clearly disarticulated and may therefore belong to a vertebra that is not preserved. The referred specimen (ibid., figs. 6, 7) is preserved in ventral view, so that the pelvis obsures the sacral region more or less completely. We find ourselves unable to judge how many sacrals *Tuditanus* has (even the number 3 cannot be excluded) and therefore have to score it as unknown.

Carroll and Gaskill (1978: 57; see also fig. 31) state that, in the only articulated specimen of *Cardiocephalus peabodyi*, "[t]here are thirty-seven presacral vertebrae and two sacrals. The block is truncated in the middle of the second sacral, and there is not a trace of caudals." The second sentence means that state 2 (three sacrals) cannot be excluded.

Two sacral ribs are known from *Pelodosotis*, but it is apparently not known if they are from the same vertebra, and then the specimen ends (Carroll and Gaskill, 1978: 85; see also fig. 58A). It must therefore be scored as unknown.

The sacral region of *Rhynchonkos* is apparently known only in the specimen FM-UR 2414, which is stated by Carroll and Gaskill (1978: 109) to possess two sacrals, but illustrated in a way that shows it is much too fragmentary to tell (*ibid*., fig. 70). We conclude that *Rhynchonkos* must be scored as unknown.

In *Utaherpeton*, "[t]wo vertebrae lie adjacent to the central portion of the pelvic girdle. The more anterior is associated with a structure that can be identified as a sacral rib. The second is crushed below the level of the rest of the column and partially covered by the head of the femur. It is uncertain whether it was a second sacral or a first caudal. The ilium is so narrow that it is unlikely to have accommodated more than a single sacral rib." (Carroll *et al*., 1991: 318) Evidently, *Utaherpeton* must be scored as possessing one or two sacrals (and, of course, the latter possibility is clearly less probable than the former).

Character 183: Number of caudal rib pairs: 5 or more (0), 4 (1), 3 (2), 2 or fewer (3) (ordered). *Triadobatrachus* was given states 0 or 3; we have changed this to unknown because we cannot see a reason to exclude all other states (Rage and Roček, 1989: 11).

Character 191: Cleithrum head: aligned along cranial rim of scapula (0); caudodorsally enlarged head wrapping around dorsal scapula (1). *Sauropleura scalaris* (Bossy, 1976: fig. 33) and *Brachydectes* (Wellstead, 1991: fig. 19D) show state 1.

Character 192: Cleithrum head: dorsally greatly expanded, much wider than shaft (0); simple rod without or with slight dorsal expansion (1). *Sauropleura scalaris* and *Brachydectes* again possess state 1 (same references as above). So does *Ptyonius* (Bossy, 1976: fig. 57a).

Character 193: Cleithrum: ossified (0); unossified (1). *Triadobatrachus* and frogs possess state 0 (Rage and Roček, 1989; Duellman and Trueb, 1986), leaving state 1 only to Albanerpetontidae and salamanders.

Character 201: Deltopectoral crest: weak (0), intermediate (1), prominent (2) (ordered). State 2 occurs in *Acanthostega* (Coates, 1996: fig. 16), *Proterogyrinus* (Holmes, 1984: fig. 26) and *Greererpeton* (Godfrey, 1989: fig. 18), while *Eocaecilia* possesses state 0 (Jenkins *et al*., 2007: fig. 41).

The plesiomorphic condition for salamanders appears to be state 0, judging from *Chunerpeton* (assigned to Cryptobranchidae; Gao and Shubin, 2003: figs. 1, 2), *Ranodon* (Hynobiidae; Averianov, 1995: fig. 4), *Palaeoamphiuma* (Amphiumidae; Rieppel and Grande, 1998: fig. 5), and *Necturus* (Proteidae; Wischnitzer, 1979: fig. 2-8), even though *Parahynobius betfianus* (Hynobiidae; Venczel, 1999: fig. 2E).

Character 203: Humerus length: long, > 4 trunk centra (0); short (1). Where known (*Celtedens*: McGowan, 2002: fig. 3), albanerpetontids possess state 1.

Character 206: Carpals: fully or partly ossified (0); unossified (1). Where known (*Celtedens*: McGowan, 2002: 11), albanerpetontids possess state 0.

Character 207: Basale commune: absent (0); present (1). For the reasons explained in Marjanović and Laurin (2008) – such as comparisons to all other known temnospondyl tarsi and the fact that the tarsus of *Gerobatrachus* is highly incomplete and disarticulated from the lower leg on both sides –, we have changed the score of *Gerobatrachus* to unknown. This makes the character parsimony-uninformative.

Character 208: Number of digits in manus: 5 or more (0), 4 (1), 3 (2) (ordered). Apparently like Anderson *et al*. (2008), we have not counted the prepollex as a digit, and we have counted the metacarpal as part of the digit (so that *Scincosaurus*, which possesses what “may represent a very reduced fifth” metacarpal, retains state 0; Bossy and Milner, 1998: 99, fig. 66G).

We have furthermore accepted the decision by Anderson *et al*. (2008) to score *Eocaecilia* as having three digits per hand (and foot: character 219), something that Jenkins *et al*. (2007) consider highly likely but not certain.

Greererpeton was long interpreted as having four fingers per hand, and was scored accordingly. However, Coates (1996: 415) mentions and illustrates a fairly well preserved specimen with five fingers and mentions another that preserves four, one of which is the (distinctively small) fifth. Consequently, there is no evidence for four fingers (state 1) in any specimen of *G.* in the literature, and we code *G.* as pentadactyl (state 0).

Dendrerpeton preserves four distal carpals (Holmes *et al*., 1998), which means that four or more fingers were present (state 0 or 1).

We infer that *Acheloma* had four or more fingers (state 0 or 1) because it appears to have had five distal carpals (Olson, 1941), of which the tiny cranialmost one could belong to a prepollex. As in *Dendrerpeton*, no metacarpals or fingers are preserved.

Micropholis possessed four fingers per hand (Schoch and Rubidge, 2005: 512), giving it state 1.

Tambachia was scored as unknown, but state 2 can be excluded (Sumida *et al*., 1998), so we have scored it as showing state 0 or 1.

Saxonerpeton, on the other hand, is so incompletely preserved that none of the states can be ruled out (Carroll and Gaskill, 1978: 38).

Rhynchonkos was scored as 1, but while four metacarpals are preserved, a higher number cannot be excluded based on the preservation (Carroll and Gaskill, 1978: 111).

Urocordylus has state 0 (Bossy and Milner, 1998: 98–99, fig. 66A).

Bossy and Milner (1998) say *Keraterpeton* has state 1 as originally scored. However, Jaekel (1902) provides a line drawing of *Keraterpeton* (fig. 2) that shows articulated but incomplete hands which may well have had five fingers. Huxley and Wright (1867) claim five metacarpals and fingers to be present, but their plate XIX (or at least our bad photocopy of it) appears to show only four; Bossy (1976:304), contradicting Bossy and Milner (1998), writes "My own investigations corroborate the existence of the five-digit manus in this genus." Awaiting a reply from Milner, we have scored *Keraterpeton* as possessing state 0 or 1.

Jaekel (1902) says three times explicitly that *Diceratosaurus* had pentadactyl hands, and illustrates a convincing pentadactyl hand in the specimen drawing (plate IV-6), even though Bossy & Milner (1998) explicitly disagree, stating the animal to be tetradactyl as originally coded. This is all the more surprising because Bossy earlier (1976: 304) wrote "Diceratosaurus definitely has five forefingers (pers. obs.)". Because we have not been able to find the reason for this discrepancy, we have scored *Diceratosaurus* as possessing state 0 or 1.

Character 217: Number of distal tarsals: 6 (0), 5 or fewer (1). Three OTUs were scored as possessing six distal tarsals: *Acanthostega*, *Tuditanus*, and part of the salamanders (the "salamanders" OTU is scored as having state 0 or 1, but polymorphism was clearly intended). Regardless of which condition is plesiomorphic for salamanders, we think the extra distal tarsal is not homologous between any of these taxa. In *Acanthostega*, the caudalmost "distal tarsal", to which three "metatarsals" attach directly, is better interpreted as the fibulare (*e.g.*, Coates, 1996: fig. 24; Johanson *et al*., 2007: fig. 1); in the fully articulated referred specimen of *Tuditanus*, the distal tarsal that does not correspond to a metatarsal lies on the caudal side (Carroll and Baird, 1968: figs. 6, 7) and could therefore represent a postminimus (or, of course, something entirely different like a sesamoid), but neither the fibulare nor a prehallux; in the salamanders with an extra distal tarsal, this is the prehallux (as the first digital ray in the foot of *Acanthostega*, including the "first" distal tarsal rather than the "sixth", might be) or the centrale 1 (the so-called "prehallux" in Duellman and Trueb, 1986: fig. 13-33B; the "centrale" in that figure is the centrale 4). We have therefore excluded this character from our analyses.

Results and conclusion

Four most parsimonious trees were found (length = 1264 steps, consistency index excluding parsimony-uninformative characters = 0.2659, retention index = 0.6003, rescaled consistency index = 0.1610). Their only differences lie in whether *Ecolsonia* (in two trees) or *Tambachia* (in the two others) is the sister-group of *Acheloma*, and in whether Pantylidae (= *Pantylus* + *Stegotretus*) is the sister-group of Ostodolepididae (= *Pelodosotis* + *Micraroter*) (in two trees) or of *Batropetes* + (*Rhynchonkos* + Gymnarthridae [= *Cardiocephalus* + *Euryodus*]) (in the two others). The strict consensus is shown in the Supplementary Figure.

All most parsimonious trees support the lepospondyl hypothesis, with a monophyletic Lissamphibia as the sister-group of *Brachydectes* and nested inside the "microsaurs", even though the positions of the paraphyletic "nectrideans" and the aïstopods (*Oestocephalus*, *Phlegethontia*) as well as the topology of the "microsaurs" differ from those found by Vallin and Laurin (2004).

The bootstrap values (see the Supplementary Figure) are generally low – indeed, several clades are contradicted by the bootstrap tree, which for example finds Nectridea to be monophyletic (if only in 39% of the replicates) and arranges the "microsaurs" in a rather different way. The monophyly of Lissamphibia is found in only 23% of the bootstrap replicates, and the *Brachydectes*-Lissamphibia clade in only 22.

Nonetheless, Amphibia (= everything more closely related to Lissamphibia than to Amniota, here including Lissamphibia and the "lepospondyls") has a bootstrap percentage of 68. A clade composed of all temnospondyls and all lissamphibians but no "lepospondyls" does not occur in the list put out by PAUP* that shows all clades found in 5% or more of the bootstrap replicates (reproduced below as Supplementary Table 4), arguing strongly against the temnospondyl hypothesis.

No clade that includes *Gerobatrachus* and some or all lissamphibians but no "lepospondyls" has a bootstrap percentage greater than 14 (Supplementary Tables 4 and 5), and no clade that includes all temnospondyls and some lissamphibians, but no "lepospondyls", has a bootstrap value greater than 7. We think that the support for a special relationship between *Gerobatrachus* and some lissamphibians is not significant, because it is not only small in absolute terms and much smaller than the support for the clade composed of all "lepospondyls" and lissamphibians (68, see above), but also smaller than the support for clades which contain frogs, salamanders and lepospondyls but neither any temnospondyls nor *Eocaecilia*, contradicting both the monophyly of extant amphibians and all existing versions of the polyphyly hypothesis (18 and smaller); see Supplementary Table 5 for a more detailed comparison. At 22, the highest bootstrap percentage for any clade compatible with the polyphyly and not the lepospondyl hypothesis is not significantly higher either (the clade in question consists of *Eocaecilia* and the "microsaur" *Rhynchonkos*, and is the only clade with a bootstrap value above 14% that is compatible with the polyphyly hypothesis).

127 trees have the minimum length or are one step longer. Their strict consensus is poorly resolved (all nodes marked "1" in the supplementary figure collapse), *e.g.*, *Eocaecilia* is no longer guaranteed to be the sister-group of the clade composed by the other "lissamphibians", but it still contains a "nectridean"-aïstopod-"lissamphibian"-*Brachydectes* clade nested inside two more clades of amphibians, from which all of the "temnospondyl" clades (Temnospondyli having collapsed) are excluded. The majority-rule consensus is practically identical in topology to the strict consensus of the most parsimonious trees.

1635 trees are up to two steps longer than the minimum length. In the strict consensus, Amphibia survives and still excludes all "temnospondyls" while still including the fully resolved Albanerpetontidae + (salamanders + (*Triadobatrachus* + frogs)) clade. The topology of the majority-rule consensus has not changed.

13,396 trees are up to three steps longer than the minimum length. The only noteworthy change in the strict consensus is that Albanerpetontidae is no longer guaranteed to be the sister-group of the salamanders + (*Triadobatrachus* + frogs)); Amphibia survives. The topology of the majority-rule consensus has changed imperceptibly.

The same holds for the 81,754 trees that are up to four steps longer than the minimum.

Because the computer had run out of memory, the search for trees up to five steps longer than the minimum length was terminated after 367,200 trees had been found. Their strict consensus does not contain Amphibia anymore (Amphibia thus has a Bremer value of 5); even salamanders and (*Triadobatrachus* + frogs) take part in the basal polytomy. The majority-rule consensus has changed imperceptibly in topology and is still almost completely resolved; Amphibia, for example, still occurs in all but four of the 367,200 trees.

The lepospondyl hypothesis is thus strongly supported by the present matrix, even though no characters or taxa were added to the matrix by Anderson *et al*. (2008), and even though the taxon sampling outside of Amphibamidae and Amphibia is poor. For further conclusions regarding errors in data matrices see Marjanović and Laurin (2008).

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Supplementary Table 1: List of loss characters in the matrix by Anderson *et al.* (2008). All of them are retained in our version of the matrix (ESM3), although 137 is parsimony-uninformative.

4 Intertemporal: present (0), absent (1)
5 Supratemporal: present (0), absent (1)
10 Squamosal-tabular [contact]: absent (0), present (1), fused (2)[1]
13 Lacrimal: present (0), absent (1)
18 Quadratojugal: present (0), absent (1)
24 Nasals: present (0), absent (1)
27 Internarial fontanelle: absent (0), present (1)
28 Septomaxilla: ossified (0), unossified (1)[2]
38 Otic notch: present (0), absent (1)
45 Postorbital: present (0), absent (1)
53 Postparietals: paired (0), fused (1), absent (2)
54 Parietal foramen: present (0), absent (1)
59 Tabular: present (0), absent (1)
64 Lateral line canal grooves: present (0), absent (1)
65 Dermal sculpturing: circular pits (0), shallow ridges and grooves (1), little to none (2)
81 Labyrinthine in-folding [sic]: present (0), absent (1)
83 Supraoccipital: absent (0), present (1)
89 Palatal teeth: present (0), absent (1)
92 Anterior [part of] palatine: short anteromedial process articulating with vomer at choana (0), long anteromedial process, more medial than lateral (1), palatine absent (2)
93 Vomerine teeth: present (0), absent (1)
96 Intervomerine rostral fenestration: absent (0), present (1)
97 Denticles on pterygoid: present (0), absent (1)
98 Teeth on pterygoid: absent (0), present (1)
100 Denticles on vomers: present (0), absent (1)
101 Denticles on palatines: present (0), absent (1)
102 Denticles on parasphenoid: present (0), absent (1)
107 Basicranial articulation: loose (0), sutured or fused (1)
108 Stapes: perforated stem (0), imperforate stem (1), no stem (2)[3]
114 Sphenethmoid: ossified (0), unossified (1)
115 Interpterygoid vaccuities [sic]: narrow (“closed”) (0), wide (1), fused at midline (2)[4]
121 Ectopterygoid: present with fang-pit pair (0), present[,] lacking fang-pit pair (1), absent (2)[5]
126 Surangular: normal (0), reduced (1), absent (2)
128 Number of splenials: 2 (0), 1 (1), 0 (2)[6]
130 Meckelian fossae [sic – actually fenestrae, lacking a bony floor]: 2 or more (0), 1 (1), 0 (2)
136 Number of coronoids: 3 (0), 2 (1), 1 (2), 0 (3)[7]
137 Coronoid teeth: present (0), absent (1)
140 Jaw sculpture: present (0), absent (1)
141 Ossified hyoids: present (0), absent (1)
148 Trunk intercentra: present (0), absent (1)
156 Haemal arches: present (0), absent (1)
167 Atlas-axis intercentra: present (0), absent (1)
169 Atlas centrum: multipartite (0), single notochordal (1), single odontoid (2)[8]
174 Proatlantes: present (0), absent (1)
176 Atlas ribs: one pair (0), two pairs (1), absent (2)[9]

190 Interclavicle sculpture: present (0), absent (1)
193 Cleithrum: ossified (0), unossified (2)[2]
196 Supraglenoid foramen: present (0), absent (1)
208 Number digits – manus: 5 or more (0), 4 (1), 3 (2)[10]
219 Number of digits, pes: 5 or more (0), 4 or less (1)[11]

[1] State 2, the presence of a single bone in the area normally occupied by the squamosal and the tabular, can at least as easily be interpreted as the loss of the tabular with replacement by the squamosal (or imaginably the other way around).

[2] These are dermal bones, so “unossified” equals “absent”.

[3] State 1 refers to the loss of the stapedial foramen.

[4] This obviously refers to the pterygoids touching each other and/or the parasphenoid throughout the length of their medial margins, in other words, the loss of the interpterygoid vacuities as seen for example in *Seymouria* and *Batrachiderpeton*.

[5] This character refers to the loss of the fangs and the loss of the bone that carries them and therefore counts as two loss characters.

[6] This character refers to the sequential loss of two bones and therefore counts as two loss characters. We have opted not to treat character 53 the same way, because there is evidence for the fusion of the two postparietals (left and right), but none for the fusion of the two splenials (“presplenial” and “postsplenial” in each hemimandible).

[7] Referring to the sequential loss of three bones, this character counts as three loss characters.

[8] States 1 and 2 both refer to the absence of the atlas intercentrum, so this character counts as a single loss character.

[9] State 1 refers to the fusion of atlas and axis, so this character counts as a single loss character.

[10] Counted as two loss characters.

[11] Counted as one loss character.

Supplementary Table 2: List of loss characters in the matrix by Vallin and Laurin (2004). Except for character 3, taken from the NEXUS file of Vallin and Laurin (2004), the spellings of the names of the characters and their states are taken from Laurin (1998); the six characters added later are not loss characters.

1 Lateral-line location in adults: in channels below the surface of the dermal bones (0), in grooves at the surface of the dermal bones (1), in soft tissues or absent (2)
2 Lateral-line grooves in ontogeny: present at least in the adults (may also be present in larvae) (0), present only in the larvae (1), never present (2)
3 Dermal sculpturing: ‘honeycomb’ pattern of ridges and pits (0), cosmine (1), shallow pits widely spaced from each other on an otherwise smooth surface (2), narrowly separated protuberances (3), smooth (4), broadly separated low tubera (5)[1]
4 Rostrum: absent, mouth terminal (0), short, high rostrum protruding anterior to the premaxillary teeth (1), long, low (2)
5 Orbit shape: ovoid (0), confluent with a large antorbital fenestra (1), open posteriorly (2)[2]
10 Anterior tectal: present (0), absent (1)
15 Pineal foramen: present (0), absent (1)
16 Intertemporal: present (0), absent (1)
17 Supratemporal: present (0), absent (1)
18 Tabular: present (0), absent (1)
22 Postparietal number: two (paired) (0), single, median (1), none (2)
25 Prefrontal: present (0) absent (1)
27 Postfrontal: present (0), absent (1)

28 Postorbital: reaches orbit (0), excluded from orbit (1), absent (2)
29 Lacrimal: reaches orbit (0), excluded from orbit (1), absent (2)
30 Jugal: borders orbit (0), excluded from orbit (1), absent (2)
31 Temporal emargination: absent, area covered by opercular bones (0), present, bordered by squamosal, tabular, and (sometimes) supratemporal (1), absent, area covered by squamosal, supratemporal, and tabular (2), present, bordered by quadrate (3), present, bordered by squamosal (4)[3]
35 Quadratojugal: present (0), absent (1)
37 Lateral palatal tooth row: present, complete (0), incomplete (1), absent (2)
39 Palatal recess: median (0), divided medially (1), absent (2)
40 Vomerine fangs: present (0), absent (1)
41 Vomerine shagreen of denticles: absent (0), present (1)
42 Palatine: discrete (0), fused or absent (1)
44 Palatine fangs: present (0), absent (1)
45 Palatine shagreen of denticles: absent (0), present (1)
46 Ectopterygoid: present (0), absent (1)
47 Ectopterygoid fangs: present (0), absent (1)
48 Ectopterygoid shagreen of denticles: absent (0), present (1)
51 Pterygoid shagreen of denticles: present (0), absent (1)
54 Interpterygoid vacuity: narrow (0), broad (1), absent (2)
58 Parasphenoid denticles: present (0), absent (1)
60 Ventral cranial fissure: present (0), absent (1)
65 Braincase endochondral roof: ossified as a unit (0), unossified (1), composed of exoccipital (2), composed of a discrete supraoccipital (3)[4]
67 Basioccipital and exoccipital: indistinguishably fused in adults (0), suturally distinct throughout ontogeny (1), basioccipital never distinct (2)[5]
70 Preopercular: present (0), absent (1)
71 Subopercular: present (0), absent (1)
72 Epipterygoid ossification: present (0), absent (1)
74 Basicranial articulation: not fused, potentially mobile (0); sutured, immobile (1)
78 Stapedial foramen: present (0), absent (1)
79 Mandibular fenestrae: absent (0), small fenestrae present in splenial, postsplenial, and angular (1), large fenestra(e) present between angular, postsplenial, splenial, and prearticular (2)
80 Anterior coronoid: present (0), fused or absent (1)
81 Middle coronoid: resent (0), fused or absent (1)
82 Posterior coronoid: present (0), fused or absent (1)
83 Anterior splenial: present (0), fused or absent (1)
84 Postsplenial: present (0), fused or absent (1)
85 Angular: present (0), fused or absent (1)
86 Surangular: present (0), fused or absent (1)
88 Coronoid fangs: present (0), absent (1)
89 Coronoid denticles: absent (0), present (1)
90 Dentary: dentigerous (0), edentulous
92 Medial mandibular tooth row: on coronoids (0), absent (1), on pseudodentary (2)
96 Labyrinthine infolding: present (0), absent (1)
98 Presacral centra (excluding atlas-axis complex): large, crescentic intercentra and small, paired, dorsal pleurocentra (0); cylindrical intercentra only (1); crescentic intercentra only (2); crescentic intercentra and cylindrical pleurocentra (3); circular intercentra and pleurocentra (4); cylindrical pleurocentra only (5)[6]
109 Atlantal intercentrum: present (0), absent (1)

115 Number of sacral vertebrae: none (0), one (1), two or more (2)
117 Discrete dorsal fin: present (0), absent (1)
118 Radials in caudal fin: present (0), absent (1)
120 Interclavicle: without a parasternal process (0), with a parasternal process (1), absent (2)
121 Clavicle: present (0), absent (1)
123 Cleithrum: with a dorsal expansion (0), slender, without a discrete dorsal expansion (1), with a ventral expansion (2), absent (3)
125 Anocleithrum: present (0), absent (1)
126 Lateral extrascapular: present (0), absent (1)[7]
127 Median extrascapular: present (0), absent (1)[7]
130 Humerus: present (0), absent (1)
141 Number of digits in manus: none (0), eight (1), five (2), four (3)[8]
142 Number of pelvic ossifications: one (0), three (1), two (2)[9]
150 Number of pedal digits: none (0), seven (1), five (2), four (3)[10]
151 Number of phalanges in second pedal digit: two (0), three (1)
152 Number of phalanges in third pedal digit: three (0), four (1)
153 Number of phalanges in fourth pedal digit: four (0), five (1), three (2)
154 Number of phalanges in fifth pedal digit: four (0), five (1), three (2), two (3)
155 Lepidotrichia in caudal fin: present (0), absent (1)

[1] State 4 refers to the loss of sculpturing.

[2] State 2 refers to the loss of bones such as the postorbital.

[3] State 2 refers to loss of the emargination.

[4] Under the lepospondyl hypothesis, loss of the suproccipital (from state 3 to state 1) is a lissamphibian autapomorphy; this disappears under the temnospondyl hypothesis, however. This character could thus be said to be a loss character that supports the temnospondyl hypothesis.

[5] State 2 refers to the loss of the basioccipital: “The basioccipital of lissamphibians is never distinct and there does not appear to be a discrete ossification centre for this element (2).” (Laurin, 1998)

[6] States 1 and 2 refer to the loss of pleurocentra, and state 5 to the loss of intercentra. Therefore this character is counted as two loss characters.

[7] Counted as a single loss character because a functional correlation is hypothesized and no taxon is known to possess either lateral extrascapulars or the median one but not both.

[8] Counted as three loss characters: no taxon with seven manual digits is known, but one with six (*Tulerpeton*) is, even though it is not present in the matrix.

[9] State 2 refers to loss of ossification of the pubis.

[10] Counted as three loss characters (even though the only known taxon with six pedal digits, *Tulerpeton*, is not present in the matrix).

Supplementary Table 3: Left: Significance thresholds for the g_1 statistic for different numbers of taxa (from Huelsenbeck, 1991: table 1); right: rounded values of the g_1 statistic for the loss characters and the remaining characters of the matrices of Anderson *et al*. (2008) and Vallin and Laurin (2004). Note that these are actually two separate tables that should be compared to each other and are put side-by-side here for this purpose.

"g_1 values less than the values in the table are outside of the 95% or 99% confidence limits for tree-length distributions from random data." (Huelsenbeck, 1991: legend of table 1)

Abbreviations: "Loss", loss characters as defined in the text and listed in Supplementary Tables 1 and 2; "Others", all other characters of the same matrix.

Significance thresholds from Huelsenbeck (1991: table 1)				Character type	Anderson *et al*. (2008)	Vallin and Laurin (2004)
P value	6 taxa	7 taxa	8 taxa		54 taxa	48 taxa
0.05	–0.51	–0.45	–0.34	Loss	–0.31	–0.55
0.01	–0.67	–0.60	–0.47	Others	–0.35	–0.37

Supplementary Table 4: Table of results of the bootstrap analysis, put out by PAUP* (Swofford, 2003). Temnospondyls marked in green, lissamphibians in red; the taxa between these two blocks are the "lepospondyls". Clades that are compatible with the polyphyly hypothesis (by containing some or all temnospondyls, frogs, and salamanders, but not *Eocaecilia* or any "lepospondyls", or by containing *Eocaecilia* and some or all "lepospondyls" but no temnospondyls, frogs or salamanders) are underlined; clades that contradict both the monophyly of extant amphibians and the polyphyly hypothesis (by containing frogs, salamanders and lepospondyls but neither any temnospondyls nor *Eocaecilia*) are marked in ***bold and italics***. See Supplementary Table 5 for more explanation.

```
Bipartitions found in one or more trees and frequency of occurrence (bootstrap
support values):

         1         2         3         4         5   5
123456789012345678901234567890123456789012345678901234      Freq      %
-----------------------------------------------------------------------
..........................................**..........    199.27  99.6%
....................................................**    194.20  97.1%
..............................................**......    191.54  95.8%
....................................***...............    185.08  92.5%
........**............................................    182.37  91.2%
.......................................**.............    175.80  87.9%
...................................................***    175.33  87.7%
.......................................*****..........    166.14  83.1%
...........**...*.....................................    165.15  82.6%
.............................**.......................    154.56  77.3%
.....**...............................................    152.97  76.5%
.....................................**...............    150.99  75.5%
..................................................****    139.58  69.8%
.........................................***..........    137.91  69.0%
.........................**...........................    135.68  67.8%
....................**********************************    135.01  67.5%
...........................**.........................    134.38  67.2%
...........**.........................................    122.21  61.1%
.........................****.........................    104.44  52.2%
........................*..........*..................    104.21  52.1%
........***..***.***..................................    103.06  51.5%
.............*.....*..................................    100.40  50.2%
....................................********..........    100.23  50.1%
......................**..............................     94.83  47.4%
.*.*****************************************************     91.23  45.6%
....................*************************.********     87.15  43.6%
.............*...***..................................     82.27  41.1%
....................**................................     79.27  39.6%
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....................................*********.........     78.56   39.3%
...**.................................................     77.15   38.6%
.....***************..................................     73.01   36.5%
....*...............**********************************     71.65   35.8%
.............*.*.***..................................     70.02   35.0%
.................**...................................     69.70   34.9%
............*...*.....................................     67.41   33.7%
.*.**...............**********************************     60.55   30.3%
..........*...*.......................................     60.19   30.1%
....................************.************.********     57.17   28.6%
...**...............**********************************     55.51   27.8%
.......................................******.........     55.29   27.6%
.....**.***..***.***..................................     51.79   25.9%
..........*..***.***..................................     50.69   25.3%
.............*....**..................................     48.15   24.1%
..........................***.........................     48.04   24.0%
.......*...**...*.....................................     47.39   23.7%
........************..................................     46.21   23.1%
.................................................*****     45.39   22.7%
.....*************************************************     44.91   22.5%
...............................*.................*....     44.81   22.4%
................................................******     44.24   22.1%
........................*....**.......................     40.50   20.3%
..........*..*.*.***..................................     40.20   20.1%
.*.**.................................................     39.81   19.9%
....................................*********.********     38.59   19.3%
.........................****..*......................     38.55   19.3%
........................*******....*..................     38.37   19.2%
.*.*..................................................     37.35   18.7%
...***************************************************     36.94   18.5%
....................................*********.**..****     36.29   18.1%
.....**.************..................................     36.23   18.1%
..............................................********     34.55   17.3%
....................................*********.***.****     33.98   17.0%
........***..***.*************************************     33.13   16.6%
................................*............*........     33.05   16.5%
..............................................**..****     31.88   15.9%
........**...*.*.***..................................     30.42   15.2%
....................................*********.**......     30.37   15.2%
..........*....*......................................     29.52   14.8%
..****************************************************     28.82   14.4%
....................************.*.**********.********     28.78   14.4%
....................................**................     28.24   14.1%
........................********.*.**********.********     28.16   14.1%
...................*...............................***     27.88   13.9%
........**********************************************     27.79   13.9%
.......................................***............     27.64   13.8%
....................................********..********     24.39   12.2%
.........................***..........................     24.39   12.2%
....................**************.**********.********     24.39   12.2%
........................********.*.*..................     24.28   12.1%
........**....*.......................................     24.15   12.1%
.............*...*.*..................................     23.86   11.9%
....................**************.*******************     22.20   11.1%
.......*************..................................     22.08   11.0%
..............................................***.....     21.73   10.9%
..*..***************..................................     21.69   10.8%
........***..*.*.***..................................     20.51   10.3%
........................*....**....*..................     20.32   10.2%
.........................******.......................     20.03   10.0%
...............................*.*..*********.********     19.14    9.6%
.................................*..*********.********     18.89    9.4%
......................*.........................*.....     18.80    9.4%
.........................****..*.................*....     18.70    9.3%
.....**.**********************************************     18.69    9.3%
..............................................***.****     18.49    9.2%
........**........*...................................     18.24    9.1%
....................*******************************...     18.04    9.0%
.....**.***..***.*************************************     18.04    9.0%
.................***..................................     17.94    9.0%
```

```
...............................*.*....................     17.78   8.9%
......................**********.*.**********.********     17.58   8.8%
.................................................*.***     17.31   8.7%
....................****..............................     17.20   8.6%
..*..*************************************************     17.12   8.6%
..................................*.*********.********     16.83   8.4%
........................********.*.*.............*....     16.64   8.3%
......................**********.************.********     16.17   8.1%
..................................................**..     15.88   7.9%
.........................****......*..................     15.77   7.9%
....................................*.*...............     15.57   7.8%
.............*....*...................................     15.29   7.6%
....................................*****.............     15.18   7.6%
....................................********..**......     15.06   7.5%
..........*..*.....*..................................     15.06   7.5%
........***...........................................     15.04   7.5%
....................*.............*...................     14.89   7.4%
.................................**.*********.********     14.85   7.4%
.............*...***...............................***     14.79   7.4%
................................................**....     14.60   7.3%
.....***************...............................***     14.57   7.3%
.......................................**.**..........     14.39   7.2%
........................*****......*..................     14.34   7.2%
....................*************************.*****...     14.20   7.1%
........***..***.***...............................***     14.20   7.1%
........**...*....**..................................     14.13   7.1%
.............*.....*...............................***     14.00   7.0%
........**...*...***..................................     13.67   6.8%
.........................****..*.*....................     13.41   6.7%
........................*******.......................     13.27   6.6%
....................************...*..................     13.22   6.6%
..................................*...........**......     13.19   6.6%
..........................**..........................     13.13   6.6%
........................********...*..................     13.12   6.6%
.......................................*.***..........     13.11   6.6%
.................................*...............*....     12.77   6.4%
..................................*.********..........     12.66   6.3%
...................*..............................****     12.58   6.3%
.....*..***..***.***..................................     12.26   6.1%
................................................*.****     12.25   6.1%
...............................*.*...............*....     12.21   6.1%
......................**........*.....................     12.05   6.0%
...............................*....*********.********     11.93   6.0%
........................*****..*.*.*.............*....     11.76   5.9%
..............................................**.*****     11.71   5.9%
.........................****..*.*..*********.********     11.39   5.7%
........***..*******..................................     11.02   5.5%
.......***********************************************     10.76   5.4%
......................**********.*.*..................     10.72   5.4%
....................************.*.*..................     10.69   5.3%
..............*.....**********************************     10.58   5.3%
..................................*.*********.**......     10.54   5.3%
....................************.************.*****...     10.48   5.2%
....................************.*.*.............*....     10.36   5.2%
.........................**....*......................     10.28   5.1%
....*...............*******************************...     10.15   5.1%
.........................****..*...*..................     10.02   5.0%

2102 groups at (relative) frequency less than 5% not shown
```

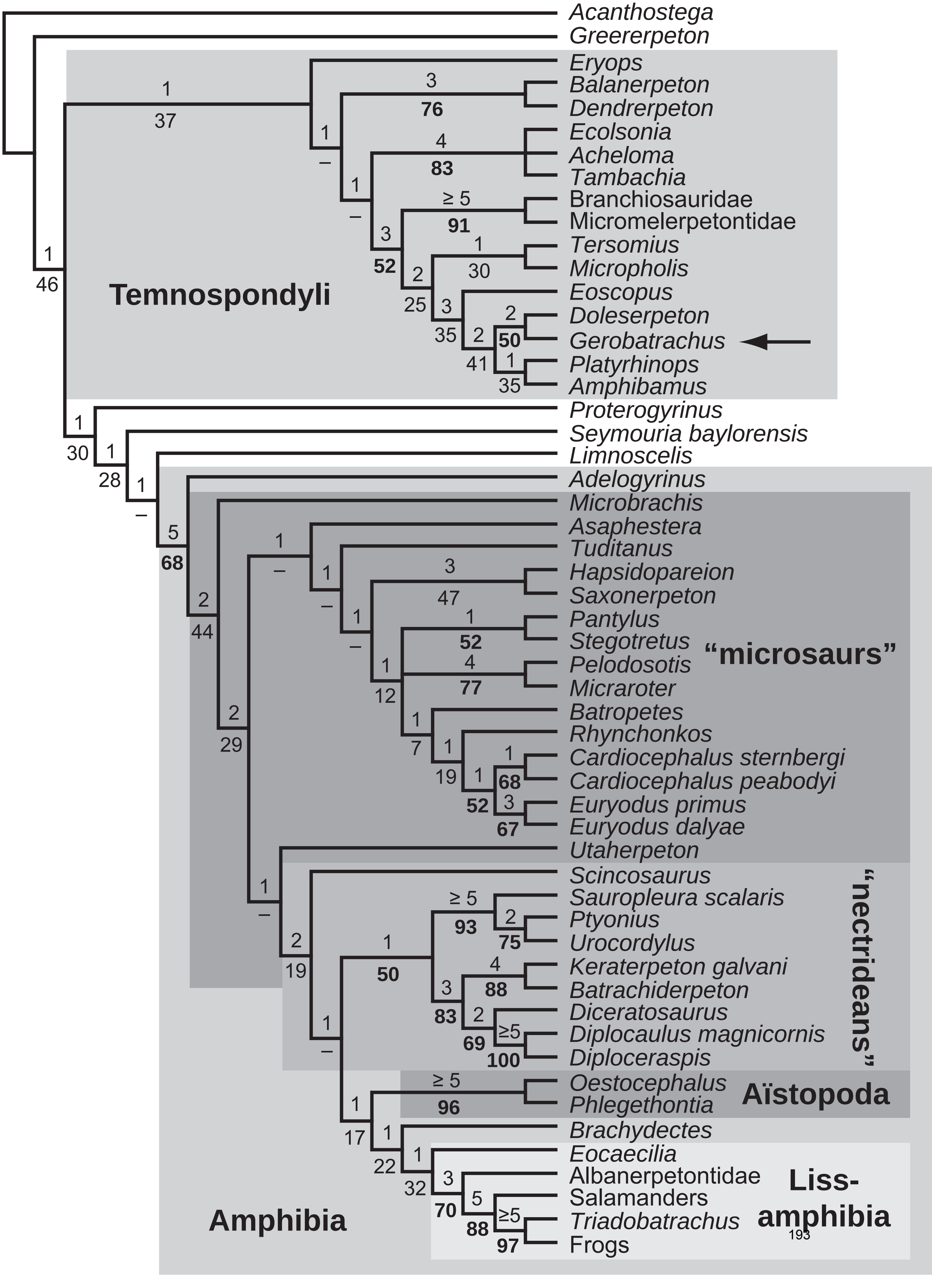
Supplementary Table 5: List of the clades found in the bootstrap analysis which are compatible with the polyphyly hypothesis (Supplementary Table 4, underlined) and of those that are incompatible with both the monophyly of extant amphibians and the polyphyly hypothesis (Supplementary Table 4, bold and italics), with others added for comparison. Clades that contradict the lepospondyl hypothesis but not the polyphyly hypothesis are marked in bold.

Abbreviations: LH, lepospondyl hypothesis; PH, polyphyly hypothesis; TH, temnospondyl hypothesis; Salientia: *Triadobatrachus* and the “frogs” OTU.

Contents of the clade	Clade contradicts:			Bootstrap percentage
	LH	PH	TH	
all “lepospondyls”, Lissamphibia	no	yes	yes	67.5
all “lepospondyls” except *Adelogyrinus*, Lissamphibia	no	yes	yes	43.6
Temnospondyli	no	yes	yes	36.5
all “lepospondyls”, Lissamphibia, *Limnoscelis*	no	yes	yes	35.8
all “lepospondyls”, Lissamphibia, *Limnoscelis*, *Seymouria*, *Proterogyrinus*	no	yes	yes	30.3
all “lepospondyls” except *Adelogyrinus* and *Microbrachis*, Lissamphibia	no	yes	yes	28.6
all “lepospondyls”, Lissamphibia, *Limnoscelis*, *Seymouria*	no	yes	yes	27.8
all temnospondyls except *Eryops*, *Ecolsonia*, *Acheloma* and *Tambachia*	no	yes	yes	25.9
Tersomius, *Doleserpeton*, *Micropholis*, *Eoscopus*, *Platyrhinops*, *Amphibamus*, *Gerobatrachus* (thus same as above except *Balanerpeton*, *Dendrerpeton*, Branchiosauridae and Micromelerpetontidae)	no	rather yes	rather yes	25.3
Doleserpeton, *Amphibamus*, *Gerobatrachus*	no	rather no	rather no	24.1
all temnospondyls except *Balanerpeton*, *Dendrerpeton* and *Eryops*	no	yes	yes	23.1
Lissamphibia	no	yes	no	22.7
Rhynchonkos, Eocaecilia	**yes**	**no**	**yes**	**22.4**
Brachydectes, Lissamphibia	no	yes	yes	22.1
Tersomius, *Doleserpeton*, *Eoscopus*, *Platyrhinops*, *Amphibamus*, *Gerobatrachus*	no	rather yes	rather yes	20.1
all “nectrideans”, Aïstopoda, *Brachydectes*, Lissamphibia	no	yes	yes	19.3
all “nectrideans”, Aïstopoda, Albanerpetontidae, salamanders, Salientia	yes	yes	yes	18.1
Aïstopoda, *Brachydectes*, Lissamphibia	no	yes	yes	17.3
all “nectrideans”, Aïstopoda, *Brachydectes*, Albanerpetontidae, salamanders, Salientia	yes	yes	yes	17.0
all temnospondyls except *Balanerpeton*, *Dendrerpeton*, *Eryops*, *Ecolsonia*, *Acheloma* and *Tambachia*, all “lepospondyls”, Lissamphibia	no	no[1]	rather yes	16.6
Aïstopoda, Albanerpetontidae, salamanders, Salientia	yes	yes	yes	15.9
all “lepospondyls” except *Microbrachis*, *Utaherpeton* and *Adelogyrinus*, Lissamphibia	no	yes	yes	14.4
same as above except *Tuditanus*, *Asaphestera*, *Hapsidopareion* and *Saxonerpeton*	no	yes	yes	14.1
***Gerobatrachus*, salamanders, Salientia**	**yes**	**no**	**no**	**13.9**
all temnospondyls except *Balanerpeton*, *Dendrerpeton* and *Eryops*, all “lepospondyls”, Lissamphibia	no	no[1]	rather yes	13.9
all “nectrideans” except *Scincosaurus*, Aïstopoda, Brachydectes, Lissamphibia	no	yes	yes	12.2
all “lepospondyls” except *Utaherpeton* and	no	yes	yes	12.2

Adelogyrinus, Lissamphibia				
Doleserpeton, *Platyrhinops*, *Gerobatrachus*	no	rather no	rather no	11.9
all “lepospondyls” except *Utaherpeton*, Lissamphibia	no	yes	yes	11.1
Greererpeton, Temnospondyli	no	yes	yes	10.8
Rhynchonkos, *Batropetes*, all “nectrideans”, Aïstopoda, *Brachydectes*, Lissamphibia	no	yes	yes	9.6
same as above except *Rhynchonkos*	no	yes	yes	9.4
Hapsidopareion, *Brachydectes*	no	no	no	9.4
Gymnarthridae, ***Rhynchonkos*, *Eocaecilia***	**yes**	**no**	**yes**	**9.3**
all temnospondyls except *Eryops*, all “lepospondyls”, Lissamphibia	no	no[1]	rather no	9.3
Aïstopoda, *Brachydectes*, Lissamphibia except *Eocaecilia*	yes	yes	yes	9.2
all “lepospondyls”, ***Eocaecilia*,** **Albanerpetontidae**	**yes**	**no**	**yes**	**9.0**
all temnospondyls except *Eryops*, *Ecolsonia*, *Acheloma* and *Tambachia*, all “lepospondyls”, Lissamphibia	no	no[1]	rather no	9.0
Platyrhinops, *Amphibamus*, *Gerobatrachus*	no	rather no	rather no	9.0
Lissamphibia without Albanerpetontidae	no	yes	no	8.7
Utaherpeton, all “nectrideans”, Aïstopoda, *Brachydectes*, Lissamphibia	no	yes	yes	8.4
Pantylidae, Gymnarthridae, Ostodolepididae, ***Rhynchonkos*, *Batropetes*, *Eocaecilia***	**yes**	**no**	**yes**	**8.3**
all “lepospondyls” except *Tuditanus*, *Asaphestera*, *Microbrachis* and *Adelogyrinus*, Lissamphibia	no	yes	yes	8.1
Albanerpetontidae, salamanders	no	no	no	7.9
Batropetes, *Utaherpeton*, all “nectrideans”, Aïstopoda, *Brachydectes*, Lissamphibia	no	yes	yes	7.4
***Doleserpeton*, *Platyrhinops*, *Amphibamus*, *Gerobatrachus*,** **salamanders, Salientia**	**yes**	**no**	**yes**	**7.4**
Brachydectes*, *Eocaecilia	**yes**	**no**	**yes**	**7.3**
Temnospondyli, salamanders, Salientia	**yes**	**no**	**yes**	**7.3**
all “lepospondyls” except ***Adelogyrinus*, *Eocaecilia*,** **Albanerpetontidae**	**yes**	**no**	**yes**	**7.1**
***Doleserpeton*, *Gerobatrachus*,** **salamanders, Salientia**	**yes**	**no**	**yes**	**7.0**
Batropetes*, *Eocaecilia	**yes**	**no**	**yes**	**6.4**
Gerobatrachus*,** **Lissamphibia except** ***Eocaecilia	**yes**	**no**	**yes**	**6.3**
Brachydectes, Lissamphibia except *Eocaecilia*	yes	yes	yes	6.1
Rhynchonkos*, *Batropetes*, *Eocaecilia	**yes**	**no**	**yes**	**6.1**
Pantylidae, Gymnarthridae, ***Rhynchonkos*, *Batropetes*, *Eocaecilia***	**yes**	**no**	**yes**	**5.9**
all “lepospondyls” except ***Utaherpeton*** **and** ***Adelogyrinus*, *Eocaecilia*,** **Albanerpetontidae**	**yes**	**no**	**yes**	**5.2**
same as above except Albanerpetontidae and all “nectrideans” other than ***Ptyonius*** **(!)**	**yes**	**no**	**yes**	**5.1**

[1] This only holds if highly unconventional arrangements like those found by McGowan (2002), where “lepospondyls” and lissamphibians are found inside Temnospondyli, are counted as acceptable within the polyphyly hypothesis.


Acanthostega
Greererpeton
Eryops
Balanerpeton
Dendrerpeton
Ecolsonia
Acheloma
Tambachia
Branchiosauridae
Micromelerpetontidae
Tersomius
Micropholis
Eoscopus
Doleserpeton
Gerobatrachus
Platyrhinops
Amphibamus
Temnospondyli
Proterogyrinus
Seymouria baylorensis
Limnoscelis
Adelogyrinus
Microbrachis
Asaphestera
Tuditanus
Hapsidopareion
Saxonerpeton
Pantylus
Stegotretus
Pelodosotis
Micraroter
Batropetes
Rhynchonkos
Cardiocephalus sternbergi
Cardiocephalus peabodyi
Euryodus primus
Euryodus dalyae
"microsaurs"
Utaherpeton
Scincosaurus
Sauropleura scalaris
Ptyonius
Urocordylus
Keraterpeton galvani
Batrachiderpeton
Diceratosaurus
Diplocaulus magnicornis
Diploceraspis
"nectrideans"
Oestocephalus
Phlegethontia
Aïstopoda
Brachydectes
Eocaecilia
Albanerpetontidae
Salamanders
Triadobatrachus
Frogs
Liss-amphibia
Amphibia

Chapter 5

Reevaluation of the data matrix by Ruta & Coates (2007)

The analysis by Ruta & Coates (2007) of the phylogeny of the limbed vertebrates is based on the largest published data matrix on this subject (so far) and should therefore, all else being equal (but see Chapters 3 and 6), have yielded the most reliable results. It found the temnospondyl hypothesis to be nine steps more parsimonious than the lepospondyl hypothesis.

I have not directly worked on the matrix by Ruta & Coates (2007); rather, this chapter is a continuation of chapter V of Damien Germain's (2008) dissertation. Based on comparisons to the descriptive literature, D. G. changed hundreds of cells. Having also merged the perhaps most extreme case of correlated characters (DIG 1 through DIG 4; see Appendix 1 of this Chapter), he found the lepospondyl hypothesis to be one step more parsimonious than the temnospondyl hypothesis.

I made a large number of additional changes to the matrix (based on the descriptive literature and my observations of casts of *Triadobatrachus* and *Karaurus*), ordered many characters, gave some a stepmatrix, scored OTUs that are only known from morphologically clearly immature specimens as unknown for ontogeny-affected characters unless they displayed the expected adult condition (a modification of the approach recommended by Wiens et al. [2005: 96]; see Chapters 3 and 5), and merged large numbers of correlated characters; the total number of parsimony-informative characters has decreased from 331 to 289 (and may have to shrink a bit further still). At the same time, the number of steps in the most parsimonious trees has increased by several hundred because my changes have introduced character conflict (and polymorphism). Anyway, the lepospondyl hypothesis is now eight steps more parsimonious than the temnospondyl one, as shown by a constrained search that required *Brachydectes* (the only lysorophian lepospondyl in the matrix) to lie outside of a clade that contained the dissorophoid temnospondyl *Doleserpeton* and the three salientians (*Triadobatrachus*, *Notobatrachus*, *Vieraella*). The polyphyly hypothesis, which would not contradict this constraint, is much less parsimonious than both (judging from manual manipulation of the tree, followed by rearrangement by subtree pruning and regrafting, in Mesquite [Maddison & Maddison 2009]).

Gerobatrachus was published (Anderson et al. 2008) after the article by Ruta & Coates (2007), so I had to add it to the matrix to better test the polyphyly hypothesis (as I did to the matrix of Chapter 3). I took this opportunity to add eight other interesting taxa: the presumably basal temnospondyls *Nigerpeton*, *Saharastega* and *Iberospondylus*, the branchiosaurid temnospondyl *Tungussogyrinus* which had occasionally been thought to lie close to the origin of salamanders and/or frogs, the presumed "microsaur" *Utaherpeton* and the unnamed "Goreville microsaur", the theropsid amniote *Eothyris* (the other three amniotes in the matrix are sauropsids, which had made it impossible to test the old idea that the diadectomorphs are theropsids rather than non-amniotes), and the recently redescribed chroniosuchian *Chroniosaurus* (to the best of my knowledge, this is the second time ever that a chroniosuchian is included in a phylogenetic analysis). Analysis of this enlarged matrix increases rather than decreases the difference between the lepo- and the temnospondyl hypothesis; it lies at ten steps (as opposed to eight for the original taxon sample, see above), as shown by a search that used the same constraint as above. Interestingly, this constrained search finds *Gerobatrachus* as the sister-group of a clade composed of Lissamphibia and *Doleserpeton*, rather than directly as the sister-group of Lissamphibia.

French dissertations are limited to three years; adding a fourth year is difficult and strongly discouraged. Consequently, I have not yet been able to write a proper manuscript about the work presented in this Chapter or even to conduct all analyses that would be interesting to do. Notably, analyses of robustness (bootstrap and Bremer analyses) are missing entirely and will have to be added before publication; so are analyses where the weight of characters with many states is reduced (see characters 20 and 40 of Chapter 3 as examples) and constrained analyses that measure how many steps less parsimonious certain arrangements are than the most parsimonious ones – for instance, a test of "lepospondyl" polyphyly (suggested by Andrew Milner, pers. comm.; compare also Clack & Klembara 2009: fig. 10), with the "nectrideans" constrained to be closer to the adelospondyls and colosteids than to the "microsaurs", would be interesting. – The absence of an abstract and an introduction in this manuscript is not a great problem in the context of this thesis, because the future introduction will undoubtedly be very similar to those of the other chapters of this thesis, especially Chapter 6, and to the General Introduction. Similarly, the somewhat laconic discussion section will be elaborated (see Chapters 3 and 6; for stratigraphic implications of the results, see Chapter 6), but the essentials, I think, are there. Finally, the complete lack of figures other than the ASCII-art consensus trees is rather painful from a didactic point of view. Many of the characters, especially, should be illustrated, and will be for publication. At least the trees are legible.

For the same reason, there is no discussion of which autapomorphies support which clades, something that will sorely need to be rectified before submission. I have kept the complete change and apomorphy lists of all four analyses and can send them to readers upon request; at about 190 pages in 8-point font size, they would be too expensive to print. (The change lists note at which internode each character changes states; the apomorphy lists document the ambiguous and unambiguous autapomorphies that support each internode.) Naturally, I can also send the NEXUS file, which contains the data matrix and instructions to PAUP* (Swofford 2003) and Mesquite (Maddison & Maddison 2009). For publication, I will mold it into a legible, useful table format (something not done, incidentally, by e.g. Ruta & Coates [2007] or Clack & Klembara [2009]), but this is very time-consuming for such a large matrix.

My coding of the albanerpetontids reflects my reinterpretation of their unique atlas-axis complex, which I wanted to present in Chapter 6 but which had to be taken out of that manuscript for lack of space. As in mammals, this complex accommodates dorsoventral and lateral movements of the head at separate joints. Traditionally (e.g. Fox & Naylor 1982), this complex is considered to consist of the atlas (a complete vertebra consisting of a centrum and fused, fully formed, full-size neural arch), the axis (a centrum that lacks any trace of a neural arch), and the third vertebra (again a complete vertebra consisting of a centrum and fused, fully formed, full-size neural arch). The "axis" is commonly sutured to the "third vertebra". Dorsoventral movements of the head occurred between the skull and the atlas, lateral ones between the atlas and the "axis". By comparison to amniotes and "microsaurs", I think it is more parsimonious to interpret the "axis" as only the intercentrum of the axis, even though intercentra are otherwise unknown in albanerpetontids, while the "third vertebra" would be the pleurocentrum and neural arch of the axis. This will be illustrated and discussed at some length in the publication of the present Chapter; due to lack of time, I have not been able to do this yet.

The Appendix-Tables, which show the stepmatrices for those characters that are neither ordered nor unordered, are placed within the Appendix directly after the characters in question for ease of reading. Of course, this will have to be changed for publication.

Author contributions

M. L. supervised me, helping with some decisions on how to treat certain characters and how to score certain taxa for certain characters; I did the rest. I only started my work when D. G. submitted his thesis, so he has not contributed to the work presented here, although the three of us intend to publish together (chapter V of D. G.'s dissertation has not yet been published); the manuscript will be submitted to Geodiversitas, though it is not yet fully formatted according to its requirements.

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A preliminary reevaluation of the largest published data matrix of limbed-vertebrate phylogeny supports the lepospondyl, not the temnospondyl, hypothesis

David Marjanović, Michel Laurin

Abbreviations

CG78: Carroll & Gaskill (1978).
DG: Damien Germain.
ESM: electronic supplementary material.
MNHN: Muséum national d'Histoire naturelle, Paris.
MPT: most parsimonious tree.
OTU: operational taxonomic unit.
RC07: Ruta & Coates (2007).

Material and methods

Quality of the matrix by RC07

The matrix by RC07 is an update of that by Ruta et al. (2003). The changes consist in the addition of taxa (RC07: app. 1), the addition of characters (interspersed in RC07: app. 2), and the fusion of correlated characters. Such fusion was sometimes done by simply removing one character from a correlated pair instead of going through the cells pair by pair and merging the scores. VOM 10 and PAL 3 are an example we have looked at in detail. VOM 10 concerned the presence (0) or absence (1) of a contact between vomer and pterygoid, PAL 3 described the absence (0) or presence (1) of a contribution by the palatine to the margin of the interpterygoid vacuities. These are correlated in that the palatine cannot contribute to the interpterygoid vacuity margin when the vomer and the pterygoid contact each other medial to the palatine, while the vomer and the pterygoid cannot contact each other when the palatine spans the entire distance between the maxilla and the interpterygoid vacuity. It is in principle imaginable that a taxon could possess VOM 10(0) and PAL 3(1) simultaneously, but this would require a median contact between the palatines, a condition never observed in a primary palate (as far as we know) and absent from the present matrix (if Carroll's [1970] unusual reconstruction of one, but not the other, specimen of *Gephyrostegus* is discounted). Thus, the scores for these characters can only differ in taxa where the palatine is absent, and that condition is part of a separate character (PAL 8); also, the palatine is never absent when the vomer and the pterygoid reach each other. RC07 kept VOM 10 without making any changes to it (other than scoring it for the added taxa) and summarily deleted PAL 3. This way they missed the following contradictions between the ways these characters were scored:

- *Eusthenopteron* was scored PAL 3(1), but VOM 10(0). It has PAL 3(0) (Panchen & Smithson 1987: fig. 9a).
- *Crassigyrinus* had PAL 3(?) but VOM 10(0). It has PAL 10(0), too (Clack 1998: fig. 4B).
- *Whatcheeria* had VOM 10(?) but PAL 3(0). Lombard & Bolt (1995) do not state the condition of VOM 10 explicitly, but it must be VOM 10(0) because they would surely have mentioned a palatine-palatine contact in the midline…
- Lacking palatines, *Karaurus*, *Valdotriton* and *Notobatrachus* should be scored VOM 10(?) rather than VOM 10(1). Unsurprisingly, they were all already scored as having PAL 3(?).
- Contradicting its original score, *Limnoscelis* has VOM 10(0) (Fracasso 1983: fig. 2) to go with its original score of PAL 3(0).

- The same holds for *Westlothiana* (Smithson et al. 1994: figs. 2, 5A, 6B).
- A contact between the palatines is very hard to imagine in *Tuditanus* given CG78: fig. 4; thus, it should have been scored VOM 10(0) to equal its PAL 3(0).
- Contrary to its original score, *Euryodus* has PAL 3(0) (CG78: figs. 36–38, 42, 43), fitting its original score of VOM 10(0).
- *Adelospondylus* was scored PAL 3(0), but should be scored as unknown because the rostral part of the palate is just missing (Andrews & Carroll 1991), even though 0 looks like a safe bet (fig. 13C, D), especially judging from its score of VOM 10(0).
- *Scincosaurus* was scored VOM 10(1). Bossy & Milner (1998: fig. 57D) and Milner & Ruta (2009: identical fig. 3) appear to be certain of state 0, fitting its VOM 10(0).
- Contradicting its original score, *Urocordylus* apparently cannot be reconstructed without VOM 10(0) (Bossy & Milner 1998: fig. 55A). This fits its original score of PAL 3(0).
- Contrary to its original score, Jaekel (1902: 129) explicitly mentions that *Diceratosaurus* has VOM 10(0), as predicted from its score of PAL 3(0).

Comparison between PAL 3 and VOM 10 would have eliminated the lapses from the scoring of VOM 10, yet they were all kept in the matrix when PAL 3 was deleted.

Modifications to the matrix

The present work has two historical layers. Starting from the matrix by RC07, DG compared many characters to the literature and made hundreds of changes documented in chapter V of his doctoral thesis (Germain 2008a) supervised by ML. These changes are not listed in the present manuscript. Because French theses have a limited duration, DG was unable to continue this enormous work, so DM added the modifications documented in the Appendix to this manuscript: ordering many characters (especially potentially continuous ones, as recommended by Wiens [2001]), giving others a stepmatrix, scoring OTUs known only from clearly imma-ture or paedomorphic specimens as unknown for clearly ontogeny-affected characters (a modification of the approach recommended by Wiens et al. [2005: 96]; used by Marjanović & Laurin [2008, 2009]), and, like DG, changing scores that contradict the descriptive literature or the observations of specimens by DM and ML.

For the following taxa DM compared most or all cells to the literature:

- *Ventastega* (Ahlberg et al. 1994, 2008 – previously missing data only)
- *Crassigyrinus* (Panchen 1985; Panchen & Smithson 1990; Clack 1998)
- *Whatcheeria* (Lombard & Bolt 2006 – lower jaw and teeth only)
- *Baphetes* (Milner & Lindsay 1998, Milner et al. 2009 – only previously missing data and explicitly stated contradictions to older literature)
- *Eucritta* (Clack 2001)
- Albanerpetontidae (Estes & Hoffstetter 1976; Fox & Naylor 1982; McGowan 2002; Gardner et al. 2003; Venczel & Gardner 2005)
- *Eocaecilia* (Jenkins et al. 2007)
- *Bruktererpeton* (Boy in Boy & Bandel 1973)
- *Eoherpeton* (Panchen 1975; Smithson 1985)
- *Kotlassia* (Bulanov 2003 – skull only)
- *Diadectes* (Case 1910, 1911; Case & Williston 1912; Olson 1947; Moss 1972; Berman et al. 1992, 1998, 2004)
- *Westlothiana* (Smithson et al. 1994)
- *Scincosaurus* (Milner & Ruta 2009)
- *Ossinodus* (Warren & Turner 2004; Warren 2007)

- *Pederpes* (Clack & Finney 2005)
- *Orobates* (Berman et al. 2004)
- *Leptoropha* (Bulanov 2003)
- *Tseajaia* (Moss 1972; Berman et al. 1992)

For a few of these, especially *Ventastega*, not all changes that concern previously missing data are documented in the Appendix.

Parts of the above list have puzzling implications. For instance, RC07 and Ruta et al. (2003) did not cite Ahlberg et al. (1994) and clearly did not use that publication; Ahlberg et al. (1994) described large parts of the skull, e.g. almost the entire palate, which were scored as entirely unknown by RC07. It is hard to imagine that Ruta and his coauthors did not have access to the work of Ahlberg et al. (1994), which was published appreciably earlier than 2003 in the relatively widely available Philosophical Transactions of the Royal Society of London, Series B.

On the other hand, Ruta et al. (2003) did cite Boy in Boy & Bandel (1973) as their source for the scoring of *Brukterersepton*. This publication is, however, written in German, which may explain the differences between that description and the scoring by RC07 (though some of the figures contradict the matrix of RC07, too). Fortunately, German is DM's native language.

Despite the overlap in authors, many discrepancies exist between the matrix by RC07 and the redescriptions of *Caerorhachis* (Ruta et al. 2002), *Silvanerpeton* (Ruta & Clack 2006), *Ariekanerpeton* (Klembara & Ruta 2004a, b), and *Utegenia* (Klembara & Ruta 2005a, b).

Ruta et al. (2003) scored *Kotlassia* after the description by Bystrow (1944); RC07 did not change this. Bystrow explicitly synonymized *Kotlassia* and *Karpinskiosaurus* and did not document which parts of his description were based on which specimen(s). Bulanov (2003) disagreed with Bystrow and separated the two taxa again, considering them rather distant relatives, but he merely mentioned the existence of postcrania of *Kotlassia* (the entire monograph describes only the cranial anatomy of a wide range of seymouriamorphs). A useful description of the postcrania of specifically *Kotlassia* does therefore not exist as far as we know; we have accepted the scores by RC07 at face value for the time being.

One OTU of RC07 is a composite of *Paleothyris acadiana* and *Protorothyris archeri*. These two species are morphologically similar, so we have not made a special effort to weed out scorings based on *Protorothyris*, but our changes to this OTU are exclusively based on the description of *Paleothyris* by Carroll (1969). This is because *Protorothyris* is, according to the only phylogenetic analysis that has included it so far, more closely related to *Petrolacosaurus* (another OTU in this matrix) than to *Paleothyris*; *Paleothyris* could even be more closely related to *Captorhinus* (also represented in this matrix) than to either *Protorothyris* or *Petrolacosaurus* (Müller & Reisz 2006).

Added taxa

We have tacitly interpreted the OTUs as genera rather than species (Albanerpetontidae is of course not affected). This has allowed us to fill in some missing data and to approach more plesiomorphic morphotypes. We do not think the polymorphisms this has occasionally introduced are a problem. With the exception of *Dendrerpeton* (Ruta 2009) and of course *Pholiderpeton* (which was already coded as two separate OTUs by RC07 and indeed Ruta et al. [2003]), the monophyly of all the few genera in this matrix that are not monospecific is fairly obvious, at least with respect to the other OTUs of this matrix, and has not been disputed in the literature. We have not used information from *“Dendrerpeton” confusum*.

Pawley (2006: 207) added the headless skeleton known as *Casineria kiddi* to the matrix by Ruta et al. (2003) and found that it scored identically (except for the distribution of missing data) to *Caerorhachis bairdi* which comes from a similar but not identical age and locality, going so far as to call them "indistinguishable based on the available evidence" (Pawley 2006: 195, 239). This is a considerable surprise, because *Casineria* has been suggested to be a close relative or even member of Amniota (Paton et al. 1999), while *Caerorhachis* is variously considered to be close to the origin of temnospondyls and/or anthracosaurs (Ruta et al. 2002, and references therein). Yet, in our matrix, *Casineria* and *Caerorhachis* again differ only in their distribution of missing data; indeed, based on the descriptive literature, we confirm Pawley's (2006: 239; see also 195) remark that, "[a]s in *Caerorhachis bairdi*, none of the postcranial characteristics claimed to be 'reptiliomorph' in *Casineria kiddi* are truly apomorphic for the amniote lineage. All are present in temnospondyls […], or potentially may be present in basal temnospondyls (including the five[-]digit manus), because they are plesiomorphic for early tetrapods." We have therefore gone ahead and used *Casineria* to fill in missing data of *Caerorhachis* (documented for each character in App. 1). For the time being, however, we refrain from synonymizing the two taxa formally, because we have not looked for differences between them in characters that are not represented in our matrix, and because we have not seen the specimens.

On the same page, Pawley reports to have found the "microsaurs" *Tuditanus* and *Asaphestera* (both included by Ruta et al. [2003] and RC07) to likewise score identically except for missing data. They do differ in our matrix, so we have kept them separate instead of merging them into a Tuditanidae (which would follow the classification by CG78).

Analogously to that of Marjanović & Laurin (2008b), the main goal of the present work is to find out which hypothesis on the origin of the modern amphibians the matrix by RC07 supports if we keep, as far as possible, its taxon and character sample. However, *Gerobatrachus* was described too late (Anderson et al. 2008) to be included in the matrix of RC07, yet it is highly relevant because the phylogenetic analysis included in its description supported the polyphyly hypothesis. We have therefore added *Gerobatrachus* to the present matrix in order to find out if it changes the results. At this opportunity we also added the following taxa:

- *Chroniosaurus* is the most thoroughly described representative (Clack & Klembara 2009) of the enigmatic Chroniosuchia, with most of the skeleton being preserved. These animals have, at least recently (e.g. Laurin 2000), been considered embolomeres (anthracosaurs) mainly because of their embolomerous centra, but their confusing mosaic of character states is compatible with a number of other phylogenetic positions as well. If related to the embolomeres, these apparently terrestrial animals (Laurin et al. 2004; Clack & Klembara 2009) also have a potential to influence the positions of the embolomeres themselves, *Gephyrostegus, Bruktererpeton, Silvanerpeton,* perhaps *Caerorhachis,* and possibly *Solenodonsaurus* in our tree.
- *Nigerpeton* was described (Steyer et al. 2006) as a cochleosaurid edopoid temnospondyl. The edopoids are thought to be close to the base of Temnospondyli, so we expected an influence on the position of Temnospondyli and on the interrelationships of its largest constituent groups. The skull and lower jaw is known.
- *Saharastega*, of which likewise the entire skull is known (Damiani et al. 2006), has had an unstable phylogenetic position within Temnospondyli, though it has always stayed close to the base. Based on a few character states that are rather odd for a temnospondyl, it has even been suggested to be a seymouriamorph, though not in the peer-reviewed literature (Yates 2007). It almost certainly is a temnospondyl, but, as for *Nigerpeton*, we expected an influence on the inter- and large-scale intrarelationships of the temnospondyls. In addition, this is of course an opportunity to clarify the position of *Saharastega* itself.

- *Iberospondylus* is a rather early temnospondyl known from most of the skull and various postcranial remains. The three phylogenetic analyses that have included it so far (Laurin & Soler-Gijón 2001, 2006; Pawley 2006: fig. 44) have given three different results, and two of them were based on very small matrices. The present matrix, large as it is, is an opportunity to clarify the position of *Iberospondylus*; as it does not seem to belong to any of the large recognized temnospondyl clades, the interrelationships of the latter could also be influenced, though we caution that the sampling of Temnospondyli is somewhat poor (compare the analyses by Pawley [2006] or Ruta [2009]).
- *Tungussogyrinus* has occasionally been considered a caudate, which would be highly interesting considering its Early Triassic age. Werneburg (2009) redescribed it as the sister-group to all other branchiosaurids, but noted similarities to lissamphibians, especially one apomorphy shared with Salientia. It might thus bolster the temnospondyl hypothesis or certain versions of the polyphyly hypothesis.
- *Utaherpeton* was a surprising omission by RC07, given the facts that it is among the oldest known "microsaurs" and has been considered a basal microsaur (Carroll et al. 1991; Carroll & Chorn 1995; Anderson 2001; Anderson et al. 2008), the sister-group of *Microbrachis* and thus a basal member of the "microsaur"-lysorophian-lissamphibian clade (Vallin & Laurin 2004), or close to a "nectridean"-aïstopod-lysorophian-lissamphibian clade (Marjanović & Laurin 2009: ESM 2). Similarities to the "nectrideans" were already noted in the original description (Carroll et al. 1991). A variety of interesting effects on lepospondyl intra- and perhaps even interrelationships could expected from its addition to the present matrix.
- The diadectomorphs (in the present matrix: *Diadectes*, *Orobates*, *Tseajaia*, *Limnoscelis*) are usually thought to be stem-amniotes. It has, however, been proposed (e.g. Berman et al. 1992) to consider them the closest known relatives of Synapsida, together forming Theropsida, the sister-group of Sauropsida. Surprisingly, all certain amniotes in the matrix by RC07 (*Petrolacosaurus*, *Paleothyris*, *Captorhinus*) are sauropsids; the lack of unambiguous theropsids means that the matrix was unable to test the mentioned hypotheses, even though its large amount of non-amniote OTUs would have made it very well suited for such a purpose. *Eothyris* is the basalmost synapsid of which the skull has been described in detail (Reisz et al. 2009). Adding *Eothyris* makes it possible to test the different hypotheses of diadectomorph interrelationships, and might further influence diadectomorph monophyly (not found by Ruta & Coates [2003], RC07, or even Germain [2008a]). – The characters PREMAX 1-2-3, L SC SKU 1, SC 1 and SC 2 were scored after *Oedalops*, its closely related sister-group, based on the same publication (Reisz et al. 2009).
- The "Goreville microsaur" is among the oldest known "microsaurs". Although it was deliberately not named by Lombard & Bolt (1999), it differs from all other OTUs in this matrix, so we do not see a reason not to include it; its somewhat unusual combination of plesio- and apomorphic character states (noted in its detailed description) could change the topology of the tree. Eight badly preserved specimens, amounting to most of the skeleton, are known.

Another logical candidate for addition would have been *Eldeceeon*, but it is being redescribed according to Ruta & Clack (2006).

Phylogenetic analysis

The modified matrix was analyzed in PAUP* 4.0b10 (Swofford 2003) on a computer with an Intel® i5™ 750™ processor (2.67 GHz) and 2.99 GB of usable RAM. Four analyses were conducted: with and without the added taxa, with and without a constraint against the lepospondyl hypothesis. Each heuristic search used 1000 addition-sequence replicates (with random addition sequence), each of which was restricted to a hundred million rearrangements by tree bisection and reconnection. Total calculation time was about 34½ hours. The constraint forced the dissorophoid temnospondyl *Doleserpeton* to be closer to the three salientians (*Triadobatrachus, Notobatrachus, Vieraella*) than the lysorophian lepospondyl *Brachydectes;* this allows both the temnospondyl and the polyphyly hypothesis.

Results

The unconstrained analysis without added taxa supports the lepospondyl hypothesis, even though both temno- and lepospondyls are poorly resolved in the strict consensus. In the majority-rule consensus ("Fig." 1; the differences to the strict consensus are marked in gray in all "Figures"), Holospondyli (the paraphyletic "nectrideans" and Aïstopoda) is the sister-group of Lissamphibia, unlike most previous analyses where Lysorophia (*Brachydectes*) occupies that position. The 5,339 MPTs (majority-rule consensus shown in "Fig." 1) have a length of 1850 steps (a drastic increase over the 1584 steps found by RC07 or even the 1667 found by Germain [2008a]), a consistency index of 0.2114, a retention index of 0.6568, and a rescaled consistency index of 0.1388.

When constrained against the lepospondyl hypothesis, analysis of the matrix without added taxa supports the temnospondyl hypothesis, with Lissamphibia as the sister-group to *Doleserpeton*. Most of the strict consensus (the black parts of "Fig." 2) of the MPTs is well resolved; in particular, resolution of the lepospondyl clade is perfect except for the trichotomy formed by the urocordylid "nectrideans", and Dissorophoidea (including Lissamphibia) is likewise fully resolved. The 635 resulting MPTs have a length of 1858 steps, a consistency index of 0.2104, a retention index of 0.6549, and a rescaled consistency index of 0.1378.

The unconstrained analysis with the added taxa ("Fig." 3) finds the lepospondyl hypothesis, even though *Gerobatrachus* is among the added taxa. In the very well resolved strict consensus, *Brachydectes*, *Utaherpeton* (thus arguably not a "microsaur"), Lissamphibia, and Holospondyli form a polytomy. (*Brachydectes* and Lissamphibia are sister-groups in the majority-rule consensus tree.) *Gerobatrachus* is found as the sister-group of *Doleserpeton* in an otherwise unchanged dissorophoid temnospondyl clade. *Tungussogyrinus* is the sister-group of *Leptorophus* within Branchiosauridae, similar but not identical to the position supported by Werneburg (2009); *Nigerpeton* is a cochleosaurid as described by Steyer et al. (2006) and found again by Pawley (2006), though, surprisingly, *Chenoprosopus* no longer is one, instead forming the sister-group to *Edops* + *Eryops*; *Iberospondylus*, *Capetus*, and *Saharastega* together form the sister-group to all other temnospondyls, which, for *Saharastega* at least, is a result similar to that by Damiani et al. (2006) but differs strongly from the findings of Pawley (2006); *Kotlassia* and *Seymouria* are sister-groups, which is rather astounding given that none of the added taxa nest close to them (the closest are *Chroniosaurus* and *Eothyris*); *Eothyris* turns the basal amniote node into a trichotomy and confirms the current majority opinion that the diadectomorphs are not amniotes; the same two "microsaur" clades are found as in the constrained analysis without added taxa, and the Goreville microsaur nests in the very poorly resolved more basal one. *Chroniosaurus* is one node farther removed from the crown than Temnospondyli is; it is not an anthracosaur (interestingly, Anthracosauria lies no less than four more nodes away). Unsurprisingly, the added OTUs have introduced additional character conflict: the 210 resulting MPTs have a length of 2008 steps, a consistency index of 0.1947, a retention index of 0.6447, and a rescaled consistency index of 0.1255.

The constrained analysis with added taxa ("Fig." 4) has a very poorly resolved strict consensus. The lissamphibians (fully resolved in the same pattern as always) form the sister-group of *Doleserpeton*, followed (not preceded) by *Gerobatrachus*, then *Micromelerpeton* with the branchiosaurids, then *Eoscopus*, and only then *Amphibamus* + *Platyrhinops*; the fully resolved amphibian ("temnospondyls" and lissamphibians) clade lies within a huge polytomy (the tetrapod crown group) which also contains *Chroniosaurus*, *Solenodonsaurus*, Seymouriamorpha (again with *Kotlassia* and *Seymouria* as sister-groups), Diadectomorpha + Amniota, and no less than fourteen "lepospondyl" clades. The largest among these is Holospondyli; another contains *Brachydectes* and *Utaherpeton*. Outside the polytomy, resolution is rather good. The 1,012 MPTs are 2018 steps long and have a consistency index of 0.1938, a retention index of 0.6425, and a rescaled consistency index of 0.1245.

Consistent differences of all four analyses to the analysis by RC07 include seymouriamorph monophyly; diadectomorph monophyly; whatcheeriids at the base of the post-Devonian clade and colosteids + adelospondyls closer to the crown-group; *Silvanerpeton*, Anthracosauria, and *Caerorhachis* less closely related to the crown-group than Temnospondyli (already found by Pawley [2006] and Germain [2008a], except that Pawley [2006] found *Caerorhachis* to be a temnospondyl); and *Eryops* being closer to Edopoidea than to Dissorophoidea among the temnospondyls.

The monophyly of "whatcheeriids" (*Whatcheeria*, *Pederpes*, *Ossinodus*; possibly the Devonian *Tulerpeton* – "Fig." 2; Clack & Klembara 2009: fig. 10) and "gephyrostegids" (*Gephyrostegus*, *Bruktererpeton*) remains a set of open questions, as does the exact position of the "gephyrostegids". "Microsaur" relationships are remarkably stable; the "microsaurs" seem to fall into two clades that form successively less close relatives to a lysorophian-lissamphibian-holospondyl-*Utaherpeton* clade, although *Asaphestera* and the Goreville microsaur act as wildcards to varying degrees depending on the taxon sample and the constraint against the lepospondyl hypothesis.

The perhaps surprising finding by RC07 that *Acherontiscus* and Adelogyrinidae form the sister-group of Colosteidae, far away from their traditional position among the lepospondyls (see also Clack & Klembara 2009: fig. 10), is upheld in all trees by a large number of synapomorphies, even though Germain (2008a) had found (*Acherontiscus* + Adelogyrinidae) as the sister-group of Aïstopoda. Likewise upheld is the finding by RC07 that Aïstopoda is nested within the "nectrideans" as the sister-group of Urocordylidae. Among the "microsaurs", *Saxonerpeton* is almost always found as the sister-group of *Hapsidopareion*, consistent with the tentative classification by CG78, although little of the rest of their "microsaur" classification is upheld, especially not the dichotomy into "tuditanomorphs" and "microbrachomorphs".

Caerorhachis (including *Casineria*) consistently occupies a position similar to those found by Ruta et al. (2002) and RC07; it is neither a temnospondyl as suggested by Godfrey et al. (1987) and found – for *Caerorhachis* and *Casineria* separately – by Pawley (2006), though it comes close in some analyses, nor is it anywhere near Amniota, in spite of the position proposed for *Casineria* by Smithson et al. (1999) and references therein. Consistently, it is one node closer to the crown group of limbed vertebrates than Anthracosauria is.

RC07 found *Westlothiana* to be the basalmost "lepospondyl", and so do we, even though we have changed many of its scores.

Discussion

When the changes described above are made, especially bringing the scoring into closer congruence with the descriptive literature and merging correlated characters, the matrix by RC07 supports the lepospondyl hypothesis, which is found to be eight steps more parsimonious than the temnospondyl hypothesis, which in turn is much more parsimonious than the polyphyly hypothesis. This is particularly important because the matrix by RC07 is the largest one that has to date been published on the subject of the phylogeny of limbed vertebrates and the origins of the modern amphibians.

Adding OTUs, including *Gerobatrachus*, to the matrix increases this difference to ten steps – rather than decreasing it as the description of *Gerobatrachus* by Anderson et al. (2008) suggested.

This addition of taxa to the analysis also has other unexpected effects, like affecting the internal relationships of Seymouriamorpha even though none of the added taxa is a seymouriamorph or a particularly close relative of that clade. As previously demonstrated (Mortimer 2006; Butler & Upchurch 2007), every OTU in a data matrix can influence the position of every other OTU in the resulting cladogram.

Unstable areas of the tree and other phenomena highlight promising areas for future research. These include redescription of *Solenodonsaurus* (currently being undertaken; Witzmann pers. comm.), *Westlothiana* (currently being undertaken; Anderson pers. comm.), *Eldeceeon* (see above), *Asaphestera* (a "microsaur" of surprisingly unstable relationships), *Sauravus* (the presumed sister-group of *Scincosaurus*; not included in the present matrix), *Casineria* (especially in order to determine whether it is distinguishable from *Caerorhachis*), *Gephyrostegus*, perhaps *Utaherpeton* (see below), and others. The fact that the number of characters in this matrix is less than three times the (original) number of OTUs suggests that the matrix may not contain enough characters to yield reliable results for all parts of the tree; this is bolstered by the fact that the matrices of McGowan (2002), Vallin & Laurin (2004), RC07, and Anderson et al. (2008) all contain characters that the three others lack. Other potentially informative characters, for instance the shape and ornamentation of the bony scales, have never been used in any phylogenetic analysis of limbed vertebrates, to the best of our knowledge. That postcranial characters in particular are underused is implied by the craniocentrism of the present matrix – 197 of the 289 characters, a bit more than two thirds, describe the skull, lower jaw, or teeth; Pawley (2006), who added many postcranial characters to the matrix of Ruta et al. (2003) and found different results, appears to confirm this suspicion.

Utaherpeton was described as one of the oldest "microsaurs" (Carroll et al. 1991, Carroll & Chorn 1995). Our results ("Fig." 3, 4) indicate instead that it could occupy a crucial position close to the origins of Lysorophia, Lissamphibia, and Holospondyli.

Like RC07 and Germain (2008a), we find that the anthracosaurs *Pholiderpeton scutigerum* and *Ph. attheyi* are not sister-groups. A logical consequence (if para- or polyphyletic genera are to be avoided) would be to reinstate the genus name *Eogyrinus* for *Ph. attheyi*. However, we refrain from performing a nomenclatural act, because neither the matrix of RC07 nor the changes to it by Germain (2008) or us are focused on embolomere phylogeny, and because Pawley (2006) did find these two species as sister-groups. Despite the perfect resolution of Anthracosauria in all four of our analyses, more characters and probably more taxa will be necessary to test the phylogenetic position of *Ph. attheyi*. (Several anthracosaurs – *Palaeogyrinus*, *Pteroplax*, *Neopteroplax*, *Calligenethlon*, *Carbonoherpeton*, *Aversor* – are not included in the present matrix.)

Surprising reversals

It is not surprising that homoplasy is rampant (as shown by the tree indices) in a matrix with 102 or 111 taxa that span two hundred million years. Some reversals, though, are unexpected even within this context. We hope that they will instigate future research.

One example is the fact that one of the apomorphies which support the robust sister-group relationship of Urocordylidae and Aïstopoda, and thus "nectridean" paraphyly, is the reappearance of the supratemporal bone in the skull; this bone is lost in all other "lepospondyls" except the basalmost one, *Westlothiana*. Yet more surprising is the fact that the supratemporal is long and unusually narrow in urocordylids, aïstopods, and probably *Westlothiana* (see character SUTEMP 3 in App. 1); this character state adds support to the hypothesis that the supratemporal of urocordylids and aïstopods is indeed a supratemporal rather than a neomorph.

The "nectrideans" *Urocordylus* and *Diceratosaurus* have five fingers per hand (see character DIG 1-2-3-4 in App. 1), even though many more basal "lepospondyls", not to mention other "nectrideans" like *Sauropleura* and *Keraterpeton*, are known to have four or three. Yet, in spite of this and the abovementioned supratemporal, moving some or all "nectrideans" close to the "lepospondyl" base in Mesquite (Maddison & Maddison 2009) requires a substantial number of additional steps. Furthermore, *Urocordylus* and *Diceratosaurus* are not particularly close relatives; *Urocordylus* is a urocordylid like *Sauropleura*, while *Dicerat-osaurus* is a diplocaulid like *Keraterpeton*.

Thus, according to our results, the supratemporal reappeared once after having been lost, and pentadactyly even did so twice.

Even tetradactyly may have been lost and regained. The only taxa in this matrix that are known to have only three fingers per hand (see character DIG 1-2-3-4 in App. 1) are *Microbrachis*, *Hyloplesion*, and *Odonterpeton*. They never form a clade in our analyses – but in some of them they form a paraphyletic series from which four-fingered "microsaurs", if not other "lepospondyls" (including the abovementioned five-fingered "nectrideans"!) and the lissamphibians, descend.

Acknowledgments

We are indebted to Ronan Allain for prolonged access to casts of *Triadobatrachus* and *Karaurus* at the MNHN. D. M. further thanks Jason Anderson, Andrew Milner, Angela Milner, Marcello Ruta, and Florian Witzmann for discussions.

For part of the work period, D. M. was supported by the Austrian subsidy office for university students.

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```
  ,----------------------------------------------------------------------------------------------------------------------------- Eusthenopteron
  |    ,------------------------------------------------------------------------------------------------------------------------ Panderichthys
--+    |    ,------------------------------------------------------------------------------------------------------------------- Ventastega
  `--100    +------------------------------------------------------------------------------------------------------------------- Acanthostega
       |    |    ,-------------------------------------------------------------------------------------------------------------- Ichthyostega
       `--100    |    ,--------------------------------------------------------------------------------------------------------- Tulerpeton
          . `--100    |                                                                                                   ,----- Whatcheeria
          .      |    |   ,------------------------------------------Whatcheeriidae-------------------------------------100----- Pederpes
          .      `--100   +----------------------------------------------------------------------------------------------------- Ossinodus
          .           |   |    ,------------------------------------------------------------------------------------------------ Crassigyrinus
          .           |   |    |                                                                           Colosteidae    ,----- Colosteus
          .           `--54    |                                                                                ,-------100----- Greererpeton
          .             . |    |   ,--------------------------------------------------------------------------100    ,---------- Acherontiscus
     Tetrapoda          . `--100   |                                                                            `--100    ,----- Adelospondylus
 (apomorphy-based)      .      |   |                                                                                 `--100----- Adelogyrinus
                        .      |   |                                                                      Adelogyrinidae  `----- Dolichopareias
                        .      `--91                                                                                      ,----- Baphetes
                        .          |    ,-------------------------------Baphetidae--------------------------------------100----- Megalocephalus
                        .          |    |   ,----------------------------------------------------------------------------------- Eucritta
                        .          |    |   |                                                              ,-------------------- Eoherpeton
                        .          `--100   |                                                  Embolomeri  |    ,--------------- Proterogyrinus
                        .          .    |   |                                                         ,--100    |         ,----- Archeria
                        .          .    |   |                                                         |    `--100    ,--100----- Ph. scutigerum
                        .          .    `--75    ,-----------Anthracosauria--------------------------75         `--100    ,----- Ph. attheyi
                        .          .        |    |                                                    |              `--100----- Anthracosaurus
                        .          .        |    |                                                    `------------------------- Silvanerpeton
                    maximum and minimum     |    |    ,------------------------------------------------------------------------- Caerorhachis
                    of pentadactyl clade    |    |    |                                                   Edopoidea   ,--------- Edops
                                            |    |    |                                                          ,--100   ,----- Chenoprosopus
                                            `--100    |                                                    ,--100    `--100----- Cochleosaurus
                                                 |    |                                    ,-------------100   `---------------- Eryops
                                                 |    |                                    |               `-------------------- Capetus
                                                 |    |                                    |                              ,----- Acheloma
                                                 |    |                                ,--59    ,--Trematopidae---------100----- Phonerpeton
                                                 |    |                                |   |    |     ,------------------------- Ecolsonia
                                                 `--100..Terrapoda Pawley              |   `--100     |   ,----Dissorophidae---- Broiliellus
                                                      |  unpublished (2006)            |     .  `--100    |   Amphi-      ,----- Amphibamus
                                                      |                                |     .        |   |   bamidae ,--80----- Platyrhinops
                                                      |                                |     .        `--100  ,------64--------- Doleserpeton
                                                      |                            ,--75     .            |   |       `--------- Eoscopus
                                                      |                            |   |     .            `--93    ,------------ Micromelerpeton
                                                      |                            |   |  Dissorophoidea      `--100    ,------- Apateon
                                                      |                            |   |                           `--100    ,-- Leptorophus
                                                      |    ,----Temnospondyli----100   |             Branchiosauridae   `--100-- Schoenfelderpeton
                                                      |    |                       |   `---------------------------------------- Dendrerpeton
                                                      |    |                       |                                      ,----- Isodectes
                                                      `--100                       |                Trimerorhachoidea ,--75----- Neldasaurus
                                                           |                       |                             ,--100--------- Trimerorhachis
                                                           |                       `----------------------------75-------------- Balanerpeton
                                                           |                                                              ,----- Bruktererpeton
                                                           `--75-----------------Gephyrostegidae-------------------------87----- Gephyrostegus
                                                               `----Neospondyli Pawley unpublished (2006): next page
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                                                                                            ,------------------------------------- Albanerpetontidae
                                                                                            |                               ,------- Karaurus
                                                                                       ,--100               ,---Caudata---100------- Valdotriton
                                                                                       |    `--Batrachia--100               ,------- Triadobatrachus
                                                                    ,--Lissamphibia--100                    `--Salientia--100    ,-- Notobatrachus
                                                                    |                  |                                    `--100-- Vieraella
                                                                    |                  `-------Gymnophionomorpha-------------------- Eocaecilia
                                                                ,--74                  ,----------Scincosauridae-------------------- Scincosaurus
                                                                |   |                  |                        ,------------------- Keraterpeton
                                                                |   |                  |    ,--Diplocaulidae--100    ,------------- Batrachiderpeton
                                                  Pannectridea  |   `--Holospondyli--100    |                   `--100    ,--------- Diceratosaurus
                                                Germain (2008a) |                      |    |                        `--100    ,---- Diplocaulus
                                                  unpublished   |                      |    |                             `--100---- Diploceraspis
                                                            ,--74                      `--100                             ,--------- Ptyonius
                                                            |   |                           |        ,--Urocordylidae---100   ,----- Sauropleura
                                                            |   |                           |        |                    `--51----- Urocordylus
                                                            |   |                           `------100                   ,---------- Lethiscus
                                                            |   |                                    `--Aïstopoda------100    ,----- Oestocephalus
                                                        ,--51   |                                                        `--100----- Phlegethontia
                                                        |   |   `-----------------------------Lysorophia---------------------------- Brachydectes
                                                        |   +-----------------“microsaur” 3----------------------------------------- Batropetes
                                                        |   |                                                ,---------------------- Tuditanus
                                                        |   `-----------------“microsaurs” 2---------------100                ,----- Pantylus
                                                        |                                                    `--Pantylidae--100----- Stegotretus
                                                        |                                       ,----------------------------------- Asaphestera
                                                        |                                       |                             ,----- Micraroter
                                                   ,--100                                   ,--51    ,---Ostodolepididae----100----- Pelodosotis
                                                   |    |                                   |   `--100    ,------------------------- Rhynchonkos
                                                   |    |                                   |        `--100                   ,----- Cardiocephalus
                                                   |    |                               ,--51             `--Gymnarthridae--100----- Euryodus
                                                   |    |                               |   |                                 ,----- Saxonerpeton
                                    ,--Amphibia--100    |                           ,--51   `------Hapsidopareiontidae------100----- Hapsidopareion
                                    |              |    |                       ,--51   `------------------------------------------- Odonterpeton
                                    |              |    `----“microsaurs” 1----51   `----------------------------------------------- Hyloplesion
                                    |              |                            `--------------------------------------------------- Microbrachis
                                    |              `-------------------------------------------------------------------------------- Westlothiana
                    ,--Tetrapoda--100                                                                                         ,----- Diadectes
                    | (crown-group) |                                                                       ,--Diadectidae--100----- Orobates
                    |               |                                                                  ,--100----------------------- Tseajaia
                    |               |                                             ,--Diadectomorpha--100---------------------------- Limnoscelis
                    |               `-------------------------------------------100                                      ,---------- Captorhinus
               ,--100                                                             `--Sauropsida (Amniota?)-------------100    ,----- Paleothyris
               |    |                                                                                                    `--100----- Petrolacosaurus
               |    |                                                                  ,------------------------------------------- Kotlassia
               |    |                                                                  |                                ,---------- Discosauriscus
               |    |                                                                  |                           ,--100    ,----- Leptoropha
Neospondyli--100    `---------------Seymouriamorpha-----------------------------------100                           |    `--100----- Microphon
Pawley (2006)  |                                                                        |    ,--Discosauriscidae--100         ,----- Ariekanerpeton
 unpublished   |                                                                        `--100                      `-------100----- Utegenia
               |                                                                             `-------------------------------------- Seymouria
               `-------------------------------------------------------------------------------------------------------------------- Solenodonsaurus
```

“Figure” 1 (preceding two pages): 50% majority-rule consensus of the MPTs resulting from the unconstrained analysis with the original taxon sample of RC07; numbers are percentages of MPTs that contain the node in question. Nodes and internodes that do not occur in the strict consensus are additionally marked in gray. The names Terrapoda Pawley 2006, Neospondyli Pawley 2006, and Pannectridea Germain 2008a are unpublished, so we deliberately do not use them in the text, but they are too useful not to use at all, even though Pannectridea is not defined. Albanerpetontidae is a single OTU; *Caerorhachis* includes *Casineria* (see text). Abbreviation: *Ph.*, *Pholiderpeton*.

```
  ,------------------------------------------------------------------------------------------------------------------------------------ Eusthenopteron
--+    ,------------------------------------------------------------------------------------------------------------------------------ Panderichthys
  `--100    ,------------------------------------------------------------------------------------------------------------------------- Ventastega
       |    +------------------------------------------------------------------------------------------------------------------------- Acanthostega
       `--100    ,-------------------------------------------------------------------------------------------------------------------- Ichthyostega
          . |    |    ,--------------------------------------------------------------------------------------------------------------- Tulerpeton
          . `--100    +--------------------------------------------------------------------------------------------------------------- Ossinodus
          .      `--100   ,--Whatcheeriidae
          .         . |   |    ,------------------------------------------------------------------------------------------------------ Crassigyrinus
      Tetrapoda     . `--55    |                                                                                       ,--Colosteidae
  (apomorphy-based) .     `--100   ,---------------------------------------------------------------------------------100    ,--------- Acherontiscus
                    .          |   |                                                                                   `--100--Adelogyrinidae
                    .          `--96    ,--Baphetidae
                    .              |    |   ,----------------------------------------------------------------------------------------- Eucritta
                    .              `--100   |                                                                                   ,--Embolomeri
                    .              .    |   |    ,---------------------------Anthracosauria------------------------------------90----- Silvanerpeton
                    .              .    `--90    |    ,------------------------------------------------------------------------------- Caerorhachis
                    .              .        |    |    |                                                                     ,--100--Edopoidea
                    .              .        |    |    |                                                                ,--100    `----- Eryops
                    .              .        `--100    |                                  ,----------------------------60    `---------- Capetus
                    .              .             |    |                                  |                             `--------------- Dendrerpeton
                    .              .             |    |                              ,--90    ,--Trematopidae
                  maximum and minimum            |    |                              |   |    |    ,----------------------------------- Ecolsonia
                  of pentadactyl clade           |    |                              |   `--100    |    ,------------------------------ Broiliellus
                                                 `--100                              |     .  `--100    | Amphiba-          ,---------- Amphibamus
                                            Terrapoda |                              |     .       |    |  midae       ,--100    ,----- Doleserpeton
                                                      |                              |     .       `--100  .      ,--100    `--100--Lissamphibia
                                                      |               ,--Amphibia--100     .            |  . ,--100    `--------------- Platyrhinops
                                                      |               |              |  Dissorophoidea  `--100    `-------------------- Eoscopus
                                                      |               |              |                       |                ,----- Micromelerpeton
                                                      |               |              |                       `--------------100--Branchiosauridae
                                                      |               |              |                                         ,----- Isodectes
                                                      `--Tetrapoda--100              |                   Trimerorhachoidea ,--90----- Neldasaurus
                                                       (crown-group)  |              |                                ,--100--------- Trimerorhachis
                                                                      |              `-------------------------------90-------------- Balanerpeton
                                                                      |                                                        ,----- Bruktererpeton
                                                                      |   ,------------------Gephyrostegidae------------------95----- Gephyrostegus
                                                                      `--90    ,---------------------------------------------------- Solenodonsaurus
                                                                          `--100    ,--Seymouriamorpha
                                                                  Neospondyli  |    |         ,--Diadectomorpha
                                                                               `--100    ,--100--Sauropsida (Amniota?)
                                                                                    |    |    ,---------------------------------------- Westlothiana
                                                                                    `--100    |              ,--“microsaur” 3
                                                                                         |    |         ,--100--“microsaurs” 2
                                                                                         `--100    ,--100    ,-------Lysorophia-------- Brachydectes
                                                                               Lepospondyli   |    |    `--100    ,---Scincosauridae--- Scincosaurus
                                                                                 (without     |    |      .  `--100    ,--Diplocaulidae
                                                                              Acherontiscus   |    |  Pannec-   . `--100             ,-- Ptyonius
                                                                                   and        `--100  tridea?   .      |         ,--57-- Urocordylus
                                                                              Adelogyrinidae)      |     Holospondyli  |    ,--100------ Sauropleura
                                                                                                   |                   `--100--Aïstopoda
                                                                                                   `--“microsaurs” 1: next page
```

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```
                                     ,-------------- Asaphestera
                                ,--100   ,--Ostodolepididae
                                |    `--100   ,----- Rhynchonkos
                           ,--100        `--100--Gymnarthridae
                       ,-100    `--Hapsidopareiontidae
                  ,--100   `------------------------ Odonterpeton
“microsaurs” 1--100    `---------------------------- Hyloplesion
                  `--------------------------------- Microbrachis
```

“Figure” 2: 50% majority-rule consensus of the MPTs resulting from the constrained analysis with the original taxon sample of RC07. The constraint forced the dissorophoid temnospondyl *Doleserpeton* to be closer to the three salientians (*Triadobatrachus*, *Notobatrachus*, *Vieraella*) than the lysorophian lepospondyl *Brachydectes*; this allows both the temnospondyl and the polyphyly hypothesis. Named clades that occur in the strict consensus and are identical to their counterparts in “Fig.” 1, such as Lissamphibia, are collapsed. See legend of “Fig.” 1 for more information.

```
  ,---------------------------------------------------------------------------------------------------------------------------------- Eusthenopteron
  |    ,----------------------------------------------------------------------------------------------------------------------------- Panderichthys
--+    |               ,------------------------------------------------------------------------------------------------------------- Ventastega
  `--100               +------------------------------------------------------------------------------------------------------------- Acanthostega
       |               |    ,-------------------------------------------------------------------------------------------------------- Ichthyostega
       `--Tetrapoda--100    |    ,--------------------------------------------------------------------------------------------------- Tulerpeton
         (apomorphy-   `--100    |                                                                                              ,---- Whatcheeria
            based)          `--100                                                                                         ,--100---- Pederpes
                                 |    ,------------------------------Whatcheeriidae--------------------------------------100--------- Ossinodus
                                 |    |    ,----------------------------------------------------------------------------------------- Crassigyrinus
                                 `--100    |                                                                             ,------Colosteidae
                                   .  `--100   ,-----------------------------------------------------------------------100    ,------ Acherontiscus
                                   .       |   |                                                                         `--100--Adelogyrinidae
                                   .       `--60                                                                           ,--Baphetidae
                                   .           |    ,-----------------------------Baphetoidea----------------------------100--------- Eucritta
                                   .           `--100    ,--------------------------------------------------------------------------- Silvanerpeton
                                   .           .    `--100    ,--(Anthracosauria =) Embolomeri
                                   .           .         `--100               ,------------------------------------------------------ Caerorhachis
                                maximum and minimum           `--Terrapoda--100    ,------------------------------------------------- Gephyrostegus
                                of pentadactyl clade                          `--100    ,-------------------------------------------- Bruktererpeton
                                                                                   `--100    ,--------------Chroniosuchia------------ Chroniosaurus
                                                                                        `--100--Temno- + Neospondyli: below

                                                                                                                         ,----- Edops
                                                                                                                    ,--100----- Eryops
                                                                                                               ,--100---------- Chenoprosopus
                                                                                       ,---------------------100         ,----- Cochleosaurus
                                                                                       |                       `-------100----- Nigerpeton
                                                                                       |                                 ,----- Isodectes
                                         ,-------------------------------------------100                            ,--100----- Trimerorhachis
                                         |                                             |    ,--Trimerorhachoidea--100---------- Neldasaurus
                                         |                                             `--100                            ,----- Balanerpeton
                                    ,--100                                                  `--------------------------100----- Dendrerpeton
                                    |    |                    ,--Trematopidae
                                    |    |                    |    ,----------------------------------------------------------- Ecolsonia
                                    |    `--Dissorophoidea--100    |    ,-------------------Dissorophidae---------------------- Broiliellus
                                    |                         `--100    |                                                ,----- Amphibamus
                                    |                              |    |                  ,---------------------------100----- Platyrhinops
                                    |                              `--100                  |                             ,----- Doleserpeton
                                    |                                   |                  |         ,-----------------100----- Gerobatrachus
                ,--Temnospondyli--100                                   `--Amphibamidae--100         |    ,-------------------- Micromelerpeton
                |                   |                                                      |    ,--100    |    ,--------------- Apateon
                |                   |                                                      |    |    `--100 Br.|         ,----- Leptorophus
                |                   |                                                      `--100         `--100    ,--100----- Tungussogyrinus
                |                   |                                                           |              `--100---------- Schoenfelderpeton
   see above--100                   |                                                           `------------------------------ Eoscopus
                |                   |                                                                                    ,----- Capetus
                |                   |                                                                               ,--100----- Saharastega
                |                   `-----------------------------------------------------------------------------100---------- Iberospondylus
                |
                `--Neospondyli: next page
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```
                                                                                                        ,--69--Lissamphibia
                                                                    ,----------------------------------69   `----Lysorophia---- Brachydectes
                                                      Pannectridea  |                                   `---------------------- Utaherpeton
                                                               ,--100                  ,-------Scincosauridae------------------ Scincosaurus
                                                               |    |                  |    ,--Diplocaulidae
                                                               |    `--Holospondyli--100    |                            ,----- Ptyonius
                                                               |                       `--100                        ,--65----- Urocordylus
                                                          ,--100                            |    ,--Urocordylidae--100--------- Sauropleura
                                                          |    |                            `--100--Aïstopoda
                                                          |    |    ,--“microsaur” 3
                                                          |    `--100--“microsaurs” 2
                                                          |                                                    ,--------------- Asaphestera
                                                     ,--100                                                ,--51    ,--Ostodolepididae
                                                     |    |                                                |   `--100    ,----- Rhynchonkos
                                                     |    |                                            ,--51        `--100--Gymnarthridae
                                                     |    |                                        ,--51   `--Hapsidopareiontidae
                                      ,--Amphibia--100    |                                    ,--51   `----------------------- Odonterpeton
                                      |              |    |                                    |   `--------------------------- Hyloplesion
                                      |              |    `----------“microsaurs” 1----------100                         ,----- Microbrachis
                      ,--Tetrapoda--100              |                                         `------------------------51----- Goreville microsaur
                      | (crown-group) |              `------------------------------------------------------------------------- Westlothiana
                      |               |                                                            ,--Diadectomorpha
                      |               |                                                            |             ,------------- Captorhinus
                      |               `----------------------------------------------------------100             |        ,---- Paleothyris
                 ,--100                                                                            `--Amniota--100   ,--100---- Petrolacosaurus
                 |    |                                                                                          `--50--------- Eothyris
                 |    |                                                                                                  ,----- Kotlassia
                 |    |                                                                                     ,----------100----- Seymouria
--Neospondyli--100    `-----------------------------Seymouriamorpha---------------------------------------100    ,--Discosauriscidae
                 |                                                                                          `--100       ,----- Ariekanerpeton
                 |                                                                                               `-----100----- Utegenia
                 `------------------------------------------------------------------------------------------------------------- Solenodonsaurus
```

“Figure” 3: 50% majority-rule consensus of the MPTs resulting from the unconstrained analysis with the augmented taxon sample. Named clades that occur in the strict consensus and are identical to their counterparts in “Fig.” 1 are collapsed. Abbreviation: **Br.**, Branchiosauridae. See legend of “Fig.” 1 and 2 for more information.

```
  ,----------------------------------------------------------------------------------------------------------------------------------- Eusthenopteron
--+   ,------------------------------------------------------------------------------------------------------------------------------- Panderichthys
  `--100              ,--------------------------------------------------------------------------------------------------------------- Ventastega
      |               +--------------------------------------------------------------------------------------------------------------- Acanthostega
      `--Tetrapoda--100    ,---------------------------------------------------------------------------------------------------------- Ichthyostega
        (apomorphy-   |    |    ,----------------------------------------------------------------------------------------------------- Tulerpeton
           based)     `--100    |                                                                                                ,---- Whatcheeria
                           |    |                                                                                           ,--100---- Pederpes
                           `--100    ,---------------------------------------Whatcheeriidae-------------------------------100--------- Ossinodus
                                |    |    ,------------------------------------------------------------------------------------------- Crassigyrinus
                                `--100    |                                                                                 ,--Colosteidae
                                  .  `--100   ,---------------------------------------------------------------------------100    ,---- Acherontiscus
                                  .       |   |                                                                             `--100--Adelogyrinidae
                                  .       `--62                                                                                  ,--Baphetidae
                                  .           |    ,---------------------------------Baphetoidea-------------------------------100---- Eucritta
                                  .           `--100    ,----------------------------------------------------------------------------- Silvanerpeton
                                  .           .    `--100    ,--(Anthracosauria =) Embolomeri
                                  .           .         `--100               ,-------------------------------------------------------- Caerorhachis
                               maximum and minimum           `--Terrapoda--100    ,--------------------------------------------------- Gephyrostegus
                               of pentadactyl clade                          `--100    ,---------------------------------------------- Bruktererpeton
                                                                                  `--100    ,--------------Chroniosuchia-------------- Chroniosaurus
                                                                                       `--100--Tetrapoda (crown-group): below

                                                                                                                              ,---- Edops
                                                                                                                         ,--100---- Eryops
                                                                                                                    ,--100--------- Chenoprosopus
                                                                                            ,---------------------100         ,---- Cochleosaurus
                                                                                            |                       `-------100---- Nigerpeton
                                                                                            |                                 ,---- Isodectes
                                    ,-----------------------------------------------------100                            ,--100---- Trimerorhachis
                                    |                                                       |    ,--Trimerorhachoidea--100--------- Neldasaurus
                                    |                                                       `--100                            ,---- Balanerpeton
                               ,--100                                                            `--------------------------100---- Dendrerpeton
                               |    |                    ,--Trematopidae
                               |    |                    |    ,-------------------------------------------------------------------- Ecolsonia
                               |    `--Dissorophoidea--100    |    ,--------------------------Dissorophidae------------------------ Broiliellus
                               |                         `--100    |                                                          ,---- Amphibamus
                               |                              `--100                  ,-------------------------------------100---- Platyrhinops
                               |                                   |                  |                                       ,--Lissamphibia
                               |                                   |                  |                                  ,--100---- Doleserpeton
                ,--Amphibia--100                                   `--Amphibamidae--100         ,----------------------100--------- Gerobatrachus
                |              |                                                      |    ,--100    ,----------------------------- Micromelerpeton
                |              |                                                      |    |    |    |              ,-------------- Apateon
                |              |                                                      |    |    `--100  Branchio-   |         ,---- Leptorophus
                |              |                                                      `--100         `--sauridae--100    ,--100---- Tungussogyrinus
                |              |                                                           |                        `--100--------- Schoenfelderpeton
                |              |                                                           `--------------------------------------- Eoscopus
  --Tetrapoda--93              |                                                                                              ,---- Capetus
  (crown-group) |              |                                                                                         ,--100---- Saharastega
                |              `---------------------------------------------------------------------------------------100--------- Iberospondylus
                `--Neospondyli: next page
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```
                ,--------------------------------------------------------------------------------------------------- Solenodonsaurus
                |                                                                                              ,---- Kotlassia
                |                                                                                         ,--100---- Seymouria
                |   ,----------------------------------Seymouriamorpha----------------------------------100--Discosauriscidae
--Neospondyli--93   |                                                                       ,--Diadectomorpha
                |   |                                                                       |                  ,---- Captorhinus
                |   |   ,-----------------------------------------------------------------100             ,---51---- Eothyris
                `--93   |                                                                   `--Amniota--100    ,---- Paleothyris
                    |   |                                                                                 `--100---- Petrolacosaurus
                    |   |                 ,------------------------------------------------------------------------- Westlothiana
                    `--93                 |                                                                    ,---- Batropetes
                        |                 |   ,---------------------------“microsaurs” 3----------------------68---- Asaphestera
                        |                 |   |                                                                ,---- Tuditanus
                        |                 |   +---------------------------“microsaurs” 2----------------------53--Pantylidae
                        |                 |   |                                                                ,---- Saxonerpeton
                        |                 |   |                                       ,--Hapsidopareiontidae--93---- Hapsidopareion
                        `--Lepospondyli--93   +--------------------------------------53----------------------------- Odonterpeton
                             (without     |   |                                                           ,--Ostodolepididae
                           Acherontiscus  |   +---------------------------------------------------------100    ,---- Rhynchonkos
                                and       |   |                                                           `--100--Gymnarthridae
                          Adelogyrinidae) |   |   ,----------------------------------------------------------------- Microbrachis
                                          |   |   |   ,------------------------------------------------------------- Hyloplesion
                                          `--93--53   |                                                        ,---- Brachydectes
                                              |   `--53   ,------------------Lysorophia----------------------100---- Utaherpeton
                                              |       |   |                  ,----Scincosauridae-------------------- Scincosaurus
                                              |       `--93                  |    ,--Diplocaulidae
                                              |  Pannec-  `--Holospondyli--100    |                        ,-------- Ptyonius
                                              |  tridea?                     `--100    ,--Urocordylidae--100   ,---- Sauropleura
                                              |                                   `--100                   `--50---- Urocordylus
                                              |                                        `--Aïstopoda
                                              `--------------------------------------------------------------------- Goreville microsaur
```

“Figure” 4: 50% majority-rule consensus of the MPTs resulting from the constrained analysis with the augmented taxon sample. The same constraint as for “Fig.” 2 was used. Named clades that occur in the strict consensus and are identical to their counterparts in “Fig.” 1 are collapsed. See legend of “Fig.” 1 and 2 for more information.

Appendix: List of characters and modifications to the data matrix of Germain (2008a).

The names of all characters and their states are unchanged from RC07 unless a change is explained; unnumbered characters were used by RC07 but have been deleted by us. We did not add any characters, except for splitting state 0 of TEETH 3 into the new state 0 of TEETH 3 (character 190) and the entire new character TEETH 10 (character 197), and for replacing SUTEMP 2 by the new character SUTEMP 5 (character 55) which may be another, more explicit way to describe the same morphological difference.

All multistate characters mention in their names whether they are ordered, unordered, or treated according to a stepmatrix.

In the interest of making our scoring decisions transparent, the taxa we have added are mentioned in cases where their scores could be controversial.

1. PREMAX 1-2-3: **Caudodorsal process of premaxilla: broad, low, indistinct (0); alary process (broad, vaguely triangular) (1); moderately tall, vaguely rectangular, or acutely triangular but occupying the entire mediolateral width at its base (2); narrow and long, along the sagittal plane or parasagittal (3) (unordered).** Within state 3, the mediolateral position of the process is not considered, because it probably depends on the width of the premaxilla.

This character changes states from 0 to 1 in the ontogeny of *Apateon gracilis* (Schoch & Fröbisch 2006); we have tried to take this into account when scoring OTUs known only from immature or paedomorphic individuals (Wiens et al. 2005; Marjanović & Laurin 2008).

RC07 treated this character complex as three separate characters: PREMAX 1, “Premaxillary alary process: absent (0); present (1)”; PREMAX 2, “Premaxilla alary process shorter than wide (0) or as long as/ longer than wide (1)”; and PREMAX 3, “Premaxilla alary process less than (0) or at least one-third as wide as premaxilla (1)”. Not only are PREMAX 2 and PREMAX 3 inapplicable when PREMAX 1 has state 0; they do not (even together) cover the diversity of shapes of the contact between premaxilla and nasal seen in the taxon sample. Accordingly, we have replaced all three characters by character 26 of Marjanović & Laurin (2009), itself based on character 2 of Marjanović & Laurin (2008) and the work of Good & Wake (1992).

Crassigyrinus and *Microbrachis* were scored for PREMAX 2 and PREMAX 3 in spite of being also scored PREMAX 1(0), which, as mentioned, made PREMAX 2 and PREMAX 3 inapplicable. Some OTUs were scored for the latter two characters in spite of being also scored PREMAX 1(?), which had the same effect.

The state of *Colosteus* and *Greererpeton* is here called 1; this is probably arguable.

State 0 occurs in *Eusthenopteron* (Jarvik 1967; Brazeau & Ahlberg 2006), *Panderichthys* (Vorobyeva & Schultze 1991), *Acanthostega* and *Ventastega* (Ahlberg et al. 2008), *Whatcheeria* (Lombard & Bolt 1995), *Baphetes* and *Megalocephalus* (Beaumont 1977), *Eucritta* (Clack 2001 – it looks like 2 in the reconstruction, but the photo strongly suggests the pieces of bone in question are median rostrals rather than processes of the premaxilla), *Chenoprosopus* (Langston 1953), *Trimerorhachis*, *Neldasaurus* (Chase 1965), *Caerorhachis* (Ruta et al. 2002 – though 1 and 2 would also be more or less defensible scores), *Eoherpeton* (Smithson 1985, though this is somewhat arguable), *Proterogyrinus* (Holmes 1984), *Archeria* (Holmes 1989), *Discosauriscus* (Klembara & Ruta 2005a), *Sauropleura*, *Ptyonius*, *Keraterpeton*, and *Batrachiderpeton* (Bossy & Milner 1998), *Ariekanerpeton* (Laurin 1996a; Klembara & Ruta 2005a), and *Utegenia* (Laurin 1996b; Klembara & Ruta 2004a).

State 1: *Ichthyostega* (Ahlberg et al. 2008), *Colosteus* (Hook 1983), *Greererpeton* (Smithson 1982), *Isodectes* (Sequeira 1998), *Karaurus* (Ivachnenko 1978: fig. 1; pers. obs. of cast in MNHN), *Balanerpeton*, *Dendrerpeton*, *Eryops*, *Apateon* (Schoch & Fröbisch 2006), *Micromelerpeton*, *Ecolsonia*, *Doleserpeton*, *Eoscopus*, *Platyrhinops*, *Amphibamus*, *Dolichopareias* (Andrews & Carroll 1991), *Capetus* (Sequeira & Milner 1993), and, perhaps surprisingly, *Utaherpeton* (Carroll et al. 1991: fig. 6.1, 7).

State 2: *Tulerpeton* (as far as can be told from the isolated premaxilla + vomer; Lebedev & Clack 1993), *Crassigyrinus* (Clack 1998), *Pholiderpeton attheyi* (Panchen 1972), *Anthracosaurus* (Clack 1987a), *Pholiderpeton scutigerum* (Clack 1987b), *Bruktererpeton* (Boy in Boy & Bandel 1973), *Gephyrostegus* (Carroll 1970), *Seymouria* (Laurin 1996c; see Marjanović & Laurin [2009: ESM 1] for discussion), *Limnoscelis* (Fracasso 1983), *Captorhinus* (Fox & Bowman 1966; Heaton 1979), *Petrolacosaurus* (Reisz 1981), *Westlothiana* (Smithson et al. 1994), *Batropetes* (Carroll 1991), *Tuditanus*, *Asaphestera*, *Hapsidopareion*, *Saxonerpeton*, *Pantylus*, *Cardiocephalus*, *Pelodosotis*, *Micraroter*, *Rhynchonkos*, *Microbrachis*, *Stegotretus*, *Diceratosaurus*, *Diplocaulus*, *Diploceraspis*, *Scincosaurus*, *Adelogyrinus*, *Oestocephalus*, *Phlegethontia*, *Eocaecilia* (Jenkins et al. 2007), Albanerpetontidae, *Notobatrachus* (Estes & Reig 1973), *Silvanerpeton* (Ruta & Clack 2006), *Tseajaia* (Moss 1972).

State 3: *Phonerpeton* (Dilkes 1990: fig. 3), *Valdotriton* (Evans & Milner 1996), *Diadectes* (Berman et al. 1998), *Orobates* (Berman et al. 2004).

Unknown (and not scored as such by RC07): *Cochleosaurus* (Godfrey & Holmes 1995), *Kotlassia* (Bulanov 2003), *Urocordylus*, *Acheloma* (Dilkes & Reisz 1987 – in spite of this, it was scored for PREMAX 2 and 3), *Triadobatrachus*, *Leptorophus* & *Schoenfelderpeton* (Boy 1986, 1987), *Solenodonsaurus* (Laurin & Reisz 1999), *Paleothyris* (Carroll 1969), *Adelospondylus* (Andrews & Carroll 1991), *Lethiscus* (Wellstead 1982; Anderson et al. 2003), *Leptoropha* & *Microphon* (Bulanov 2003 – known to be 0 in juvenile skulls, but this could be ontogenetic), *Vieraella* (Estes & Reig 1973), *Ossinodus* (Warren 2007), *Pederpes* (Clack & Finney 2005), *Gerobatrachus* (Marjanović & Laurin 2009: ESM 1).

Edops has states 0, 2, or 3 (Romer & Witter 1942). *Euryodus* is polymorphic, possessing states 0 and 2 (CG78). *Brachydectes* has states 1 or 2 (we cannot decide based on Wellstead 1991).

2. PREMAX 4: **Premaxilla with flat, expanded anteromedial dorsal surface and elongated along its lateral margin but not along its medial margin, when observed in dorsal aspect: absent (0); present (1).**

3. PREMAX 7: **Premaxillae more (0) or less than (1) two-thirds as wide as skull.** RC07 have "skull table" instead of "skull", but go on to explain: "The total width of the conjoined premaxillae is measured as the distance between their lateralmost extremities; the total skull table width is between the lateral extremities of the suspensoria." It follows that this is merely an instance of their exchange of the terms "skull table" and "skull roof".

State 1 is present in *Ventastega* (Ahlberg et al. 1994) and Albanerpetontidae (McGowan 2002, Venczel & Gardner 2005).

4. PREMAX 8: **Anteriormost surface of premaxilla oriented obliquely, so that mouth opens subterminally: absent (0); present (1).**

Lethiscus has state 0 (Anderson et al. 2003).

5. PREMAX 9: **Shelf-like contact between premaxilla and maxilla occurring medial to marginal tooth row on palate and extending medially for at least twice the width of such a row: absent (0); present (1).** From here on, RC07 consistently wrote "mesial" (toward the jaw symphysis, along the curvature of the jaw) when they clearly meant "medial" (toward the sagittal plane, much more similar to "lingual" than to "mesial" for most of the length of most jaws).

Albanerpetontidae has state 0 (McGowan 2002, Venczel & Gardner 2005), as does *Lethiscus* (Anderson et al. 2003).

6. TEC 1: **Anterior tectal: present (0); absent (1).** We follow Panchen (1967), Clack (1998), and RC07 in considering the septomaxilla homologous to the lateral rostral rather than the anterior tectal, though we would like to point out that this question has received disquietingly little attention in the literature.

The condition of *Lethiscus* is unknown (Wellstead 1982; Anderson et al. 2003).

7. SPTMAX 2: **Septomaxilla with exposure on skull surface (0), wholly inside nostril (1), absent (2) (unordered).** RC07 did not distinguish states 0 and 2, calling the character "Septomaxilla a detached ossification inside nostril: no (0); yes (1)".

Eocaecilia shows state 0 (Jenkins et al. 2007).

State 2 is only used for taxa of which many articulated skulls are known; otherwise we interpret absence as possible post-mortem loss or incomplete preparation (as cautioned by RC07) and code it as unknown. Nonetheless, state 2 is thus already present in the Devonian *Acanthostega* (Ahlberg et al. 1994; Clack 1994, 2002a, 2003), the Mississippian *Greererpeton* (Smithson 1982), in *Colosteus* (Hook 1983), *Baphetes* (Milner et al. 2009), and *Trimerorhachis insignis* (Case 1935). *Trimerorhachis sandovalensis*, however, has state 0 (Berman & Reisz 1980); *Trimerorhachis* is therefore scored as polymorphic.

Acheloma shows state 1 (Dilkes & Reisz 1987). The same seems to hold for *Phonerpeton* (Dilkes 1990), but the presence of a lateral exposure (known in a close relative of both, *Tambachia*: Sumida et al. 1998) cannot be excluded, so we have scored *Phonerpeton* as possessing states 0 or 1.

8. NAS 1: **Paired nasals: absent (0); present (1).**

Ventastega has state 1 (Ahlberg et al. 2008).

9. NAS 2: **Nasals more (0) or less than (1) one-third as long as frontals.**

State 0 is plesiomorphic for Albanerpetontidae, as far as can be reconstructed from the fact that it occurs in both species of *Celtedens* (McGowan 2002) as well as in *Albanerpeton pannonicum* (Venczel & Gardner 2005); only *A. inexpectatum* shows state 1 (Estes & Hoffstetter 1976; Venczel & Gardner 2005), the state RC07 ascribed to Albanerpetontidae as a whole. Unfortunately, no other albanerpetontids preserve nasals.

The state of *Leptoropha* is unknown (Bulanov 2003).

10. NAS 5: **Parts of medial margins of external nares formed by nasals parallel (0), at an angle (1).** The original wording, “Nasals broad plates delimiting most of the posterodorsal and me[d]ial margins of nostrils and with lateral margins diverging abruptly in their anterior portions: absent (0), present (1)”, describes a combination of three characters: the length/width ratio of the nasals (possibly correlated to the length-width ratio of the snout and thus probably to the nasal/frontal length ratio, NAS 2, as well as the nasal/parietal length ratio, NAS 6), the relative position of nasals and external nares (plausibly correlated to the position and shape of the nasal-premaxilla suture, PREMAX 1-2-3), and the character described here.

This character is inapplicable when the nasal does not participate in the narial margin. This is the case in *Acanthostega* and *Ichthyostega*, where the anterior tectal intervenes, in *Proterogyrinus* (Holmes 1984) and apparently *Solenodonsaurus* (Laurin & Reisz 1999), which have a premaxilla-lacrimal suture instead, and likewise in *Greererpeton* (Smithson 1982) and *Colosteus* (Hook 1983), in which the premaxilla and the prefrontal meet instead of the nasal and the naris (see PREFRO 6 below). The state of this character is furthermore unknown in *Westlothiana* (Smithson et al. 1994), *Tuditanus* (CG78) and *Lethiscus* (Wellstead 1982; Anderson et al. 2003).

State 0 is found contrary to RC07 in *Ptyonius* (Bossy & Milner 1998) and *Phlegethontia* (Anderson 2002), though the latter fact may be due to the extremely small nasals of that animal.

State 1 is almost ubiquitous, being found in *Crassigyrinus* (Clack 1998), *Whatcheeria* (Bolt & Lombard 2000), *Baphetes* and *Megalocephalus* (Beaumont 1977), *Eucritta* (Clack 2001), *Chenoprosopus* (Langston 1953), *Isodectes* (Sequeira 1998), *Trimerorhachis* (Berman & Reisz 1980), *Dendrerpeton* (Holmes et al. 1998), *Eryops* (Sawin 1941), *Micromelerpeton* (though the least paedomorphic morphotype is somewhat borderline: Boy 1995), *Phonerpeton* (Dilkes 1990), *Broiliellus* (Williston 1916; Langston 1953), *Eoscopus* (Daly 1994), Albanerpetontidae (Venczel & Gardner 2005), *Eocaecilia* (Jenkins et al. 2007), *Caerorhachis* (Ruta et al. 2002), *Eoherpeton* (though this is not entirely clear; Panchen 1975, Smithson 1985), *Archeria* (Holmes 1989), *Pholiderpeton attheyi* (Panchen 1972), *Anthracosaurus* (Clack 1987a), *Pholiderpeton scutigerum* (Clack 1987b), *Bruktererpeton* (Boy in Boy & Bandel 1973: pl. 8), *Gephyrostegus* (Carroll 1970), *Microphon* (though juvenile), apparently *Kotlassia*, *Discosauriscus*, *Ariekanerpeton*, and *Utegenia* (Bulanov 2003; Klembara & Ruta 2005a), *Limnoscelis* (Fracasso 1983), *Diadectes* (Berman et al. 1992, 1998), *Captorhinus* (Fox & Bowman 1966; Heaton 1979), *Paleothyris* (perhaps a bit borderline; Carroll 1969), *Petrolacosaurus* (Reisz 1981), *Microbrachis* (Vallin & Laurin 2004), *Asaphestera*, *Hapsidopareion*, *Saxonerpeton*, *Pantylus*, *Cardiocephalus*, *Euryodus*, *Pelodosotis*, *Micraroter*, *Rhynchonkos*, *Hyloplesion*, and *Odonterpeton* (CG78), *Batropetes* (Carroll 1991), *Stegotretus* (Berman et al. 1988), *Brachydectes* (Wellstead 1991), *Acherontiscus* (Carroll et al. 1998), *Adelogyrinus* and *Dolichopareias* (Andrews & Carroll 1991), *Ptyonius* and *Batrachiderpeton* (Bossy & Milner 1998), *Diceratosaurus* (Jaekel 1902; Milner 1980; Bossy & Milner 1998), *Oestocephalus* (Carroll 1998), *Phlegethontia* (Anderson 2002), *Capetus* (Sequeira & Milner 1993), apparently *Orobates* (Berman et al. 2004), *Pederpes* (Clack & Finney 2005), *Silvanerpeton* (Ruta & Clack 2006), and *Tseajaia* (Moss 1972; Berman et al. 1992).

11. NAS 6: **Parietal/nasal length ratio less than (0) or greater than 1.45 (1).**

State 0 is known to occur in *Dendrerpeton* (Holmes et al. 1998) and *Pholiderpeton scutigerum* (Clack 1987b: fig. 38).

Sauropleura is polymorphic (Bossy & Milner 1998).

12. PREFRO 1: **Separately ossified prefrontal: present (0); absent (1).**

13. PREFRO 2: **Prefrontal less than (0) or more than (1) three times longer than wide […] in dorsal aspect.**

State 1 is found in *Eocaecilia* (Jenkins et al. 2007).

Albanerpetontidae is polymorphic (McGowan 2002, Venczel & Gardner 2005).

14. PREFRO 3: **Antorbital portion of prefrontal forming near-equilateral triangular lamina: absent (0); present (1).**

Albanerpetontidae shows state 0 (Venczel & Gardner 2005). The condition is unknown in *Westlothiana* (Smithson et al. 1994) and *Tseajaia* (Moss 1972; Berman et al. 1992).

15. PREFRO 6: **Prefrontal/premaxilla suture: absent (0); present (1).**

State 1 is apparently present in *Albanerpeton inexpectatum*, but absent in *A. pannonicum* and in *Celtedens* (Venczel & Gardner 2005). According to Gardner et al. (2003), *Albanerpeton* and *Celtedens* are sister-groups; the condition in the sister-group to the clade formed by both, *Anoualerpeton*, is unknown. We consequently infer that state 0 is the plesiomorphy for Albanerpetontidae and have scored Albanerpetontidae as possessing state 0.

16. PREFRO 7: **Prefrontal without (0) or with (1) stout, lateral outgrowth.**

State 1 is not limited to baphetids – *Karaurus* possesses a very clear case of it (Ivachnenko 1978; pers. obs. of a cast of the only known specimen in the MNHN).

17. PREFRO 8: **Prefrontal entering nostril margin: no (0); yes (1).**

Colosteus shows state 1 (Hook 1983).

Incidentally, as for a few other characters (see below), RC07: 94 claim that this character “shows no clear phylogenetic pattern”. Yet, the distribution of its states is far from chaotic. State 1 is a synapomorphy of Colosteidae, Adelospondyli, and possibly *Crassigyrinus*; of *Acheloma*, *Phonerpeton*, and possibly *Ecolsonia*; and, remarkably, of *Brachydectes*, Lissamphibia (represented by *Karaurus*), all “nectrideans” except *Batrachiderpeton* and *Diplocaulus*, and two out of three aïstopods (the exception being *Lethiscus*). Clearly isolated occurrences of state 1 are limited to *Isodectes* and *Batropetes*. In total, this character has only 10 steps for 102 taxa.

18. PREFRO 9: **Lacrimal reaches naris or septomaxilla (0); prefrontal-maxilla suture rostral to lacrimal (1).** The original wording, “Prefrontal/maxilla suture: absent (0); present (1)”, did not distinguish a suture rostral to the lacrimal from a suture caudal to it; the latter condition is covered by LAC 2, see below.

This character is inapplicable when the lacrimal is absent or unknown; this is the case in *Eocaecilia* (Jenkins et al. 2007) and *Valdotriton* (Evans & Milner 1996).

The redefinition further confers state 0 on *Karaurus* (Ivachnenko 1978) and *Diplocaulus* (Bossy & Milner 1998).

The condition in *Dolichopareias* is unknown (Andrews & Carroll 1991).

19. PREFRO 10: **Prefrontal contributes to more (0) or less than (1) half of orbit anterome[d]ial margin.**

State 1 is found in Albanerpetontidae (Venczel & Gardner 2005).

20. LAC 1: **Separately ossified lacrimal: present (0); absent (1).**

Eocaecilia has state 1 (Jenkins et al. 2007); the condition in *Westlothiana* is unknown (Smithson et al. 1994).

21. LAC 2-5: **Contact between lacrimal and orbit: unremarkable (0); absent, prefrontal contacts jugal or maxilla at its orbital margin (1); V-shaped emargination (2) (unordered).** Unordered because state 2 could arise from state 1 without proceeding through state 0.

This is a merger of two characters (LAC 2 and LAC 5 of RC07) the states 1 of which cannot occur together. There is, at best, no point in keeping them separate. We have added a mention of the maxilla to state 1 so that *Karaurus*, which lacks jugals, can be scored (as having state 1).

This character is inapplicable when the lacrimal is missing; this applies to *Eocaecilia* (see LAC 1 above). It is unknown in *Proterogyrinus* (Holmes 1984).

Adelogyrinus, *Adelospondylus* and *Dolichopareias* possess state 0 or 1 (Andrews & Carroll 1991). State 0 is found in Albanerpetontidae (Venczel & Gardner 2005).

22. LAC 4: **Lacrimal without (0) or with (1) dorsome[d]ial digitiform process.**

We have scored *Tseajaia* as unknown (Moss 1972; Berman et al. 1992).

Micraroter is polymorphic (CG78).

LAC 6: **Portion of lacrimal lying anteroventral to orbit abbreviated: absent (0); present (1).** RC07 go on to explain this character as follows: “In several lepospondyls (as well as in some temnospondyls), the antorbital part of the lacrimal is considerably foreshortened, regardless of relative snout proportions[,] and barely extends for one fourth of its total length anteroventral to the orbit.”

Despite this statement, and a similar one by Ruta et al. (2003: 307) which names several lepospondyls as having state 1, state 0 is instead present in all “lepospondyls”, including *Acherontiscus* and the adelogyrinids. Usually the entire lacrimal lies rostral to the orbit; even in small, large-eyed animals like *Doleserpeton* (Bolt 1969), *Batropetes* (Carroll 1991), *Microbrachis* (Vallin & Laurin 2004) and the urocordylids (Bossy 1976), more than half of it does. With state 0 occurring even in *Acheloma* (Bolt 1974; Dilkes & Reisz 1987; arguably Olson 1941) and *Phonerpeton* (Dilkes 1990, 1993), state 1 does not occur in this matrix at all; this makes the character parsimony-uninformative, so we have deleted it.

In the future, this character could be made informative by redefining it to describe how much of the ventral margin of the orbit the lacrimal forms, that is, how far the lacrimal extends caudally rather than rostrally to the rostral margin of the orbit. This is because, in this matrix, the lacrimal always extends as far rostrally as the naris, the septomaxilla, or the prefrontal and the maxilla let it (the latter applies to taxa with state PREFRO 9(1), where the prefrontal-maxilla suture is always very short) – derived amniotes, in which the lacrimal is excluded from a contact with the naris or the septomaxilla by a rostrocaudally long maxilla-nasal contact (making PREFRO 9 inapplicable), have not been included. How far rostrally the lacrimal can extend thus depends only on the length of the snout; it is the part caudal to the rostral margin of the orbit that can vary in length freely.

If redefined in such a way, however, this character would have to be merged with MAX 5/PAL 5 (see below).

23. MAX 3-9: **Caudal end of maxilla lying caudal to caudal margin of orbit (0), between caudal margin of orbit and caudal margin of vomer (1), or at most at the same level as the caudal end of the vomer (2) (ordered).** This character is ordered because potentially continuous characters should be ordered (Wiens 2001).

RC07 used two separate characters, MAX 3 having the caudal margin of the orbit and MAX 9 the caudal margin of the vomer as the threshold. We have merged them because half of the states of these characters predicted each other – the vomer never extends caudal to the orbit, which means that MAX 3(0) predicted MAX 9(0), while MAX 9(1) required MAX 3(1).

State 0 occurs in *Eocaecilia* (Jenkins et al. 2007) and *Bruktererpeton* (Boy in Boy & Bandel 1973).

Westlothiana has states 0 or 1 (Smithson et al. 1994).

24. MAX 5/PAL 5: **Ventral margin of the orbit formed by: lacrimal-jugal or prefrontal-jugal suture (0); maxilla (1); lateral exposure of the palatine (2) (unordered).** This is another merger of two characters that partly predicted each other.

When the jugal is absent (see JUG 1 below), this character is inapplicable.

Apateon, *Leptorophus* and *Schoenfelderpeton* were scored as showing state 1, but *Apateon* acquires state 2 after metamorphosis, judging from the one known adult specimen of *A. gracilis* (Schoch & Fröbisch 2006). This suggests that this character is ontogenetically variable in branchiosaurids as a whole; accordingly, we have scored *Apateon* as possessing state 2 only, *Leptorophus* (of which metamorphic individuals are unknown) as having state 1 or 2, and *Schoenfelderpeton* (and also *Tungussogyrinus*) as unknown because the jugal does not (yet) extend to the region ventral to the orbit in the first place.

We have scored Albanerpetontidae as polymorphic (0&1) because *Celtedens ibericus* and *Albanerpeton inexpectatum* are reconstructed as having state 1 while *A. pannonicum*, the species where this region is best preserved, shows state 0 (Venczel & Gardner 2005).

State 0 further occurs in *Ossinodus* (Warren 2007).

25. MAX 6: **Maxillary arcade closed (0) or open (1) posteriorly.**

Schoenfelderpeton is now scored as unknown (like *Tungussogyrinus*), because the observed condition (state 1) is likely due to paedomorphosis, if not indeed larval age of the known individuals. This is based on the ontogeny of its close relative *Apateon*.

Brachydectes, in contrast, is scored as possessing state 1; the ontogeny of this “lepospondyl” is unknown, and there is no evidence it would ever have reached state 0. The jugal and the quadratojugal bones are lacking entirely (see JUG 1 and QUAJUG 1 below).

26. MAX 7: **Dorsal margin of maxilla forming distinct dorsal ‘step’: no (0); yes (1).**

27. MAX 8: **Dorsal margin of maxilla: low compared to naris and/or septomaxilla (0); tall and rounded (1); distinct process (2) (unordered).** The original wording mentions an “approximately rectangular flange”, which is called “subrectangular” in the next sentence; such a condition does not occur in the taxon sample, the dorsal process (if present) is always rounded and/or triangular to varying degrees. Furthermore, there were mistakes in the scoring – *Triadobatrachus* was scored as possessing the (sub)rectangular process even though the whole region is unknown; *Doleserpeton* was scored the same way despite lacking any trace of a process except a gentle, very low rounding (Carroll & Holmes 1980: fig. 26). We have therefore coded the states that we see in the surveyed taxa.. The character is unordered because intermediates between 1 and 2 as well as directly between 0 and 2 exist, see below.

State 0: *Eusthenopteron*, *Panderichthys* and *Acanthostega* (Long & Gordon 2004), *Ventastega* (Ahlberg et al. 1994), *Ichthyostega* (Ahlberg et al. 2005), *Colosteus* (Hook 1983), *Greererpeton* (Smithson 1982), *Crassigyrinus* (Clack 1998), *Whatcheeria* (Lombard & Bolt 1995), *Baphetes* and *Megalocephalus* (Beaumont 1977), *Edops* (Romer & Witter 1942), *Chenoprosopus* (Hook 1993), *Cochleosaurus* (Godfrey & Holmes 1995; Milner & Sequeira 1998: fig. 12C), *Isodectes* (Sequeira 1998), *Trimerorhachis* (Case 1935; Berman & Reisz 1980), *Balanerpeton* (Milner & Sequeira 1994), *Dendrerpeton* (Milner 1980, 1996; Godfrey et al. 1987; Holmes et al. 1998), *Eryops* (Sawin 1941), *Acheloma* (Bolt 1974), *Ecolsonia* (Berman et al. 1985), *Broiliellus* (Williston 1916: fig. 44), *Doleserpeton* (Carroll & Holmes 1980: fig. 26), *Eoscopus* (Daly 1994; Huttenlocker et al. 2007), *Platyrhinops* (Schoch 2002: fig. 4), *Micromelerpeton* (Boy 1995), *Eocaecilia* (Jenkins et al. 2007), *Caerorhachis* (Ruta et al. 2002), *Eoherpeton* (Panchen 1975, Smithson 1985), *Proterogyrinus* (Holmes 1984), *Archeria* (Holmes 1989), *Pholiderpeton attheyi* (Panchen 1972), *Anthracosaurus* (Panchen 1977), *Pholiderpeton scutigerum* (Clack 1987b), *Bruktererpeton* (Boy in Boy & Bandel 1973), *Gephyrostegus* (Brough & Brough 1967), *Solenodonsaurus* (Laurin & Reisz 1999), *Kotlassia* (Bulanov 2003), *Discosauriscus* (Klembara 1993; Klembara et al. 2006, 2007), *Seymouria* (Laurin 2000), *Diadectes* (Berman et al. 1992, 1998), *Limnoscelis* (Romer 1946), *Captorhinus* (Heaton 1979), *Paleothyris* (Carroll 1969), *Petrolacosaurus* (Reisz 1981), *Westlothiana* (Smithson et al. 1994), all “microsaurs” (CG78; Berman et al. 1988; Caroll 1991) except *Pantylus* (which has state 2: CG78), *Brachydectes* (Wellstead 1991), *Acherontiscus* (Carroll et al. 1998), *Dolichopareias* (Andrews & Carroll 1991), all “nectrideans” (Jaekel 1902: table II; Moodie 1912; Bossy & Milner 1998; Milner & Ruta 2009) except *Batrachiderpeton* and *Diploceraspis* (for which we cannot find illustrations of the skull in lateral view), *Oestocephalus* (Carroll 1998), *Phlegethontia* (Anderson 2002), *Ariekanerpeton* (Laurin 1996a; Klembara & Ruta 2005a), *Leptoropha* and *Microphon* (Bulanov 2003), *Capetus* (Sequeira & Milner 1993), *Orobates* (Berman et al. 2004), *Pederpes* (Clack & Finney 2005), *Silvanerpeton* (Ruta & Clack 2006), *Tseajaia* (Moss 1972) and *Utegenia* (Laurin 1996b; Klembara & Ruta 2004a).

State 1: *Phonerpeton* (Dilkes 1990), *Karaurus* (Ivachnenko 1978), *Lethiscus* (Wellstead 1982), and *Ossinodus* (Warren 2007).

State 2: *Apateon* (Werneburg 1991: fig. 2, 5), *Leptorophus* (somewhat uncertain: Boy 1986), *Schoenfelderpeton* (Boy 1986), Albanerpetontidae where codable, though close to state 0 (unknown in *Celtedens*: McGowan 2002; unique condition in *Anoualerpeton priscum*: Gardner et al. 2003: fig. 3D$_1$), *Pantylus* (CG78), *Notobatrachus* (like Albanerpetontidae: Estes & Reig 1973).

Unknown: *Eucritta* (Clack 2001 – the fossils are so crushed that the photo, the specimen drawing, the reconstruction, and the text do not really cooperate), *Adelospondylus* and *Adelogyrinus* (Andrews & Carroll 1991), *Batrachiderpeton* and *Diploceraspis*.

Neldasaurus is scored as possessing state 0 or 1 because of its intermediate condition (Chase 1965). *Amphibamus* is scored the same way based on Schoch (2001: fig. 4), because illustrations of its skull in lateral view do not seem to exist. *Vieraella* is likewise partially uncertain (Estes & Reig 1973).

Valdotriton has state 1 or 2 (“The maxillae bear facial processes of uncertain size”: Evans & Milner 1996: 632).

28. FRO 1: **Frontal unpaired (0) or paired (1).**

State 0 is a very rare condition in this matrix. It is called 0 instead of 1 because RC07 assigned it to the outgroup (*Eusthenopteron*), but the large unpaired bone in the “snout mosaic” is just one of several possibilities for homologues of the frontals. Judging from the fontanelle of *Ventastega* (Ahlberg et al. 2008) and *Acanthostega* (Clack 2003), it is at least as probable that the large median bone disappeared and lacks a homologue in limbed vertebrates, while one of the bone pairs lateral to it is homologous to the frontals. We have accordingly scored *Eusthenopteron* as unknown.

29. FRO 2: **Frontals shorter than parietals (0), approximately equal in length (1), or longer than parietals (2) (ordered).** We have exchanged states 1 and 2 to make it possible to order this continuous character.

The frontals become longer in the ontogeny of *Apateon*; adults have state 2 (Schoch & Fröbisch 2006). For the same reason, *Schoenfelderpeton* is scored as unknown.

Kotlassia shows state 0 (Bulanov 2003: S53).

State 1 is found in Albanerpetontidae (Venczel & Gardner 2005), *Ariekanerpeton* and *Leptoropha* (Bulanov 2003).

Orobates (Berman et al. 2004) and *Tseajaia* (Moss 1972, Berman et al. 1992) show state 2.

The condition of *Ossinodus* is unknown (Warren 2007).

30. FRO 4: **Prefrontal-postfrontal suture (0); frontal contributes to orbit margin (1).** State 0 was originally called “Frontal excluded from […] orbit margin”; we have defined it more precisely and scored the character as inapplicable when the pre- and/or the postfrontal is absent, which is the case in Albanerpetontidae, *Karaurus*, *Valdotriton*, *Triadobatrachus*, *Notobatrachus*, *Vieraella*, *Brachydectes* and *Phlegethontia* (see PREFRO 1 and POSTFRO 1 below).

Westlothiana shows state 0 (Smithson et al. 1994).

Odonterpeton is scored as unknown because CG78 reconstruct state 0 on the left but state 1 on the right side, mention in the text that the right postfrontal is not preserved, and include a specimen drawing that does not clarify this situation.

31. FRO 5: **Co-ossified frontal and parietal (frontoparietal bone): absent (0); present (1).**

RC07 claim that “[i]n the most primitive salientian, *Triadobatrachus*, a suture between the antimeres of the frontoparietal complex is still traceable”, but, according to our repeated personal observations of a latex mold of the only known specimen (MNHN MAE 126), this applies only to the caudal part of the suture between the left and the right frontoparietal; we cannot find a suture between the frontals and the parietals, and none has ever been reported in the literature. We have therefore scored state 1 for *Triadobatrachus*.

32. FRO 6: **Frontal anterior margin deeply wedged between nasal posterolateral margins: absent (0); present (1).**

State 1 is found in Albanerpetontidae (Venczel & Gardner 2005).

33. PAR 1: **Supratemporal-postparietal suture (0); parietal-tabular suture (1).** This character is inapplicable when any of these bones is missing. RC07 did not specify state 0 (calling the character “Parietal/tabular suture: absent (0); present (1)”), leading them to score many cells in ways predictable from other cells.

The supratemporal is missing in all “lepospondyls” except *Westlothiana* (state 1 – Smithson et al. 1994), *Ptyonius* (1) and *Sauropleura* (1 – Bossy & Milner 1998), *Lethiscus* (unknown – Wellstead 1982: fig. 1; compare Anderson 2003: fig. 3C for why state 1 cannot be excluded) and *Oestocephalus* (1 – Anderson 2003: fig. 3C; contra Carroll 1998), and in *Eocaecilia* (Jenkins et al. 2007; see below), so we have scored them all as unknown.

Micromelerpeton was scored as unknown, but is polymorphic, sometimes between the left and the right sides of the same individual (Boy 1995).

34. PAR 2/POSFRO 3/INTEMP 1/SUTEMP 1: **Intertemporal present (0); supratemporal-postfrontal contact (1); parietal-postorbital contact, supratemporal present (2); parietal-postorbital contact, supratemporal absent (3); tabular-postfrontal contact, supratemporal absent (4) (stepmatrix).** Four correlated characters had been fused: no known limbed vertebrate has a supratemporal (SUTEMP 1(0) in the original) but not an intertemporal (INTEMP 1(1)); states 1 through 3 or 4 track gradual shrinking of the supratemporal (its rostral end reaches the postfrontal in state 1, but not in state 2, and in states 3 and 4 the bone is entirely absent); all states other than 0 are impossible when the intertemporal is present; and a parietal-postorbital contact (states 2 and 3, originally PAR 2(1)) is impossible when the supratemporal is too large (states 0 and 1) as well as when the tabular contacts the postfrontal (state 4, originally POSFRO 3).

Whenever there is an intertemporal, it contacts the postfrontal and the supratemporal, separating the parietal and the postorbital. The only possible exception is the right side of one specimen of *Greererpeton* (Smithson 1982): it has a tiny extra bone that could be an atavistic reappearance of the intertemporal (even though a long parietal-postorbital contact is present) or a pathological neomorph; see various “branchiosaurs” for alleged occurrences of such phenomena (Boy 1972). We have therefore scored *Greererpeton* as possessing state 2.

Taxa that lack not only the supratemporal but also the tabular and/or postfrontal (*Acherontiscus*, Adelogyrinidae, *Odonterpeton*, *Brachydectes*, Lissamphibia other than *Eocaecilia*, and *Phlegethontia*) are scored as having state 3 or 4.

Bruktererpeton was scored as unknown for INTEMP 1, but the entire left skull table is nicely preserved (Boy in Boy & Bandel 1973: 50 and fig. 5) and demonstrates state 0. State 0 is further present in *Panderichthys* and in *Ventastega* (Lukševičs et al. 2003; Ahlberg et al. 2008).

Appendix-Table 1: Stepmatrix for character PAR 2/POSFRO 3/INTEMP 1/SUTEMP 1.

from ↓ to →	0	1	2	3	4
0	0	1	1	2	3
1	1	0	1	1	2
2	1	1	0	1	2
3	2	1	1	0	1
4	3	2	2	1	0

35. PAR 4: **Anterior margin of parietal lying in front of (0), level with (1), or behind (2) orbit midlength (ordered).** We have ordered this continuous character.

State 2 is recorded in *Kotlassia* (Bulanov 2003) and *Ossinodus* (Warren 2007).

36. PAR 5: **Anteriormost third of parietals not wider (0) or at least marginally wider (1) than frontals.**

State 0 is present in *Acanthostega*, *Ichthyostega*, *Ecolsonia* (Berman et al. 1985), *Broiliellus* (Williston 1916: fig. 44), *Amphibamus* (Schoch 2001), *Micromelerpeton* (Boy 1995: fig. 8), *Apateon* (throughout its ontogeny: Schoch & Fröbisch 2006), *Karaurus* (Ivachnenko 1978), *Tuditanus*, *Hapsidopareion* and *Saxonerpeton* (CG78).

Rhynchonkos is polymorphic (CG78).

A (separate) parietal is absent in *Triadobatrachus* (see FRO 5 above), *Notobatrachus*, *Vieraella*, and *Phlegethontia*; we have accordingly scored them as unknown.

37. PAR 6: **Parietals more (0) or less (1) than two and a half times as long as wide.**

Brachydectes has state 1 (even though *B. newberryi* almost reaches state 0; Wellstead 1991); *Triadobatrachus* lacks separate parietals (see FRO 5 above) and is therefore scored as unknown.

38. PAR 7: **Squamosal participates in dorsal surface of skull roof: no (0); yes (1).** The original wording, “Parietal/squamosal suture extending in part onto the dorsal surface of the skull table: no (0); yes (1)”, is not applicable to the vast majority of the taxon sample, because the parietal and the squamosal are separated by other

bones; yet, all those OTUs were scored as possessing state 0. We therefore speculate that our wording, which can be applied to all taxa in this matrix, was intended.

Triadobatrachus is somewhat disarticulated and crushed, making it difficult to judge whether the parietal-squamosal suture is on the dorsal or the lateral side of the skull roof; we have scored it as unknown.

Captorhinus is borderline in that the parietal-squamosal suture forms the boundary between the skull table and the cheek (Heaton 1979); we have chosen to count this as state 0. State 0 is further present in *Batropetes* (Carroll 1991), *Paleothyris* (Carroll 1969), and *Tseajaia* (Moss 1972).

We count *Petrolacosaurus* (Reisz 1981) as possessing state 1 because we consider the dorsally-facing supratemporal fenestrae to form part of the dorsal surface of the skull.

Under our reinterpretation of this character, state 0 is found in Albanerpetontidae (McGowan 2002; Venczel & Gardner 2005) and *Notobatrachus* (Estes & Reig 1973).

39. PAR 8: **Parietal/frontal suture strongly interdigitating: no (0); yes (1).**

Although "strongly" is not defined, we have scored *Kotlassia* as possessing state 0 (Bulanov 2003: fig. 30).

Apateon has state 1 based on the largest metamorphic individual (Werneburg 1991: fig. 5b). State 1 is further found in *Baphetes* (Milner et al. 2009) and *Diadectes* (Berman et al. 1992, 1998).

Phlegethontia lacks parietals, so we have scored it as unknown.

40. PAR 9: **Parietal/postparietal suture strongly interdigitating: no (0); yes (1).** RC07 state that "[t]here appears to be no clear phylogenetic signal associated with this character". Indeed, most occurrences of state 1 are limited to single OTUs; still, state 1 holds the colosteids and the adelogyrinids together (unknown in *Acherontiscus*) as well as the aïstopods, the urocordylids, and ambiguously the diplocaulids (of which only the basalmost member, *Keraterpeton*, has state 1).

Kotlassia has state 0 (Bulanov 2003: fig. 30); *Eoscopus* is somewhat borderline (Daly 1994), but we prefer scoring it as sharing state 0.

State 1 occurs in *Baphetes* (Milner et al. 2009) and *Diadectes* (Berman et al. 1992, 1998).

We interpret *Brachydectes* as lacking separate postparietals (Marjanović & Laurin 2008), making this character inapplicable to it.

41. POSPAR 1-2: **Postparietal(s) paired (0), single (1), or absent (2).** The two original characters, presence/absence of postparietals and absence/presence of median fusion of the postparietals, make each other inapplicable, so we have fused them.

There is no evidence for postparietals in any albanerpetontid, so we have scored Albanerpetontidae as having state 2.

We have also scored *Brachydectes* as sharing state 2 because of our reinterpretation of the homologies of certain bones of its skull roof (Marjanović & Laurin 2008). This makes all other POSPAR characters inapplicable to *Brachydectes*.

As we have not seen the specimen, we have trouble understanding the condition of *Tseajaia*: Moss (1972: 10) reports state 1, and his photos (pl. 1 and 3) are compatible with this – if it shows a suture, then that suture is much thinner than the others in that skull. Berman et al. (1992: 490) say explicitly that Moss was wrong and present another photo of the same skull (the holotype, UCMP 59012) which is much brighter, shows drastically narrower sutures, and lacks a strong contrast between the suture between the postparietals and the other sutures. It looks like all sutures in that photo are enhanced in black ink, though. We accept the more recent interpretation (Berman et al. 1992) and have scored *Tseajaia* as possessing state 0, unusual though this is for a diadectomorph.

Brukterpeton has state 0 or 1 (Boy in Boy & Bandel 1973). We have scored *Gerobatrachus* the same way because it is not evident whether the sutured fragment close to the caudal end of the skull table belongs to the parietals or the postparietals.

42. POSPAR 3-6: **Dorsally exposed part of postparietal less (0) or more than four times as wide as long (1) or absent, postparietals entirely on occipital surface of skull (2) (ordered).** We have fused two characters (POSPAR 3: size of dorsal exposure; POSPAR 6: presence of dorsal exposure) that we consider parts of a single continuous character.

Diadectes possesses both state 0 (North American species: Berman et al. 1992) and state 1 (*D. absitus*: Berman et al. 1998).

State 1 is further present in *Hapsidopareion* and *Saxonerpeton* (CG78).

Hyloplesion has state 2 (CG78).

Pelodosotis was scored POSPAR 3(0) and POSPAR 6(?). Of these contradictory scores, the former is correct (CG78); *Pelodosotis* thus possesses state 0 of the present character.

Ariekanerpeton, *Leptoropha* and *Microphon* have state 0 (Bulanov 2003).

Because the skull roof of *Gerobatrachus* is exposed in ventral view only, we have scored it as unknown.

43. POSPAR 4-8: **Edge between the dorsal and the caudal surfaces of the skull lacking (0) or possessing (1) a caudal process in the midline.** This is a fusion of two characters we deem not merely correlated but identical, with POSPAR 4 ("Postparietals without (0) or with (1) median lappets") meaning the combination of a caudal process with a vertical occipital surface and POSPAR 8 ("Postparietals without (0) or with (1) sinuous posterior ridge") the combination of a caudal process with an inclined occipital surface. (The difference between a vertical and an inclined surface is character POSPAR 7, see below.) Fitting this interpretation, POSPAR 8(1) was only scored for *Micraroter* and *Pelodosotis*, while POSPAR 4(1) was limited to *Crassigyrinus*, *Whatcheeria*, embolomeres other than *Eoherpeton*, and *Ptyonius*. – Our wording makes the character applicable to taxa that lack postparietals.

Crassigyrinus in fact has a very clear case of state 0 (Panchen 1985; Clack 1998). We have also kept state 0 for *Micromelerpeton* and *Apateon* because this condition is seen in the most mature known specimens

State 1 is present in *Ventastega* (Ahlberg et al. 2008), *Kotlassia* (Bulanov 2003), *Tseajaia* (Moss 1972; Berman et al. 1992), *Diadectes* (Berman et al. 1992; very weakly expressed in *D. absitus*, but present throughout [Berman et al. 1998]; see also Case 1910), *Orobates* (Berman et al. 2004), *Asaphestera* (where the caudal process comprises the entire caudal edge of the postparietal; CG78) and *Eocaecilia* (Jenkins et al. 2007).

Solenodonsaurus was scored POSPAR 4(?) but POSPAR 8(0). We have kept the former of these apparently contradictory scores because it is not clear where the sagittal suture lies in the skull of *Solenodonsaurus* (Laurin & Reisz 1999; Pawley 2006: 205).

Ossinodus was scored in the same ways. Here, too, we have kept the question mark, because precisely that part of the postparietals is not preserved (Warren 2007).

44. POSPAR 5: **Postparietal-exoccipital suture: absent (0); present (1).** This character may have to be merged with OPI 2, see below.

The state of this character is unknown in *Eusthenopteron*, where the entire braincase is fused, so that exoccipitals cannot be discerned (Carroll & Chorn 1995).

We have, however, assigned state 1 to *Eocaecilia* (Jenkins et al. 2007) because the part of the os basale (fusion product of the entire braincase and the parasphenoid) that is contacted by the postparietals cannot realistically be anything else.

45. POSPAR 7: **Postparietals without (0) or with (1) posteroventrally sloping occipital exposure.**

State 1 occurs in *Orobates* (Berman et al. 2004).

Diadectes is polymorphic (Berman et al. 1998: 57).

The condition is unknown in *Westlothiana* (Smithson et al. 1994).

46. POSPAR 9: **Postparietals without (0) or with (1) broad, concave posterior emargination.**

According to RC07, state 1 is limited to "some" diplocaulids (i.e. all except *Keraterpeton*), but it is also found in *Tseajaia* (Berman et al. 1992; contra Moss 1972) and *Ossinodus* (Warren 2007).

47. POSPAR 10: **Nasals not smaller (0) or smaller (1) than postparietals.**

48. POSFRO 1: **Separately ossified postfrontal: present (0); absent (1).**

Bruktererpeton has state 0 (Boy in Boy & Bandel 1973).

49. POSFRO 4: **Postfrontal posterior margin lying flush with jugal posterior margin: no (0); yes (1).**

Westlothiana has state 0 (Smithson et al. 1994).

Orobates shows state 1 (Berman et al. 2004), as does *Microphon* (Bulanov 2003).

50. INTEMP 2: **Intertemporal not interdigitating (0) or interdigitating (1) with cheek.** "There appears to be no signal associated with the derived state of this character" according to RC07. Yet, in the trees of which the strict consensus is shown in "Fig." 1, this character has only eight steps. State 1 is an autapomorphy of Whatcheeriidae, Baphetoidea, (*Pholiderpeton attheyi* + *Anthracosaurus*), and a clade that contains Seymouriamorpha, Temnospondyli, and (ambiguously) *Caerorhachis*; reversals are limited to *Trimerorhachis, Capetus,* and Discosauriscidae. Thus, even though the present character is unknown or inapplicable in most OTUs, it clearly displays phylogenetic signal.

We have scored *Ossinodus* as having state 1 because the suture between skull table and cheek is not smooth and because a separate intertemporal is fairly likely to be present (Warren 2007). For character 35 of this matrix (PAR 2/POSFRO 3/INTEMP 1/SUTEMP 1), we have assigned state 0 (intertemporal present) or 2 (parietal-postorbital contact, supratemporal present) to it.

51. INTEMP 3: **Intertemporal/squamosal suture: absent (0); present (1).**

The condition is of course unknown (inapplicable) for *Diadectes*, which was correctly (Berman et al. 1992, 1998) scored as lacking an intertemporal.

As for the preceding character, we have scored *Ossinodus* as showing state 1 in case there is a suture separating the possible intertemporal from the postorbital (Warren 2007).

52. INTEMP 4: **Intertemporal shaped like a small, subquadrangular bone, less than half as broad as the supratemporal: absent (0); present (1).**

As for the preceding two characters, we have scored *Ossinodus* as showing state 1 in case there is a suture separating the possible intertemporal from the postorbital (Warren 2007).

SUTEMP 2: **Supratemporal forming entire edge of dorsalmost part (in lateral aspect) of temporal notch: no (0); yes (1).** We cannot replicate the coding of this character, because we do not know where to draw the line between the "notch" and the rest of the "embayment" that RC07 mention in the explanation of this character. Furthermore, some OTUs which lack any trace of an embayment or notch were scored 0 instead of unknown (only those lacking a supratemporal were scored as unknown). Therefore, we have replaced this character by the new, though similar, SUTEMP 5, the scores of which have almost the same distribution as that done by RC07 for the present character.

53. SUTEMP 3: **Supratemporal narrow and strap-like, at least three times as long as wide: absent (0); present (1).**

The text and the skull reconstruction by Smithson et al. (1994) ascribe state 0 to *Westlothiana* (making it similar to diadectomorphs and basal amniotes), and RC07 accepted this. However, based on the specimen drawing (Smithson et al. 1994: fig. 5B), we strongly suspect that the occipital bone plate in question belongs to the squamosal rather than to the supratemporal. If this is correct, the supratemporal is within the range of state 1 (which is otherwise limited to urocordylids, aïstopods, and the diadectomorph *Orobates*). We have therefore changed the score of *Westlothiana* to 1, and hope that the ongoing redescription(s) of *Westlothiana* will clarify the issue. It is highly unfortunate that the published specimens were split through the bone, so that one slab contains the dorsal side of the skull roof in ventral view and the other side holds the ventral side of the skull roof in dorsal view.

54. SUTEMP 4: **Supratemporal-squamosal suture: smooth (0); interdigitating (1).** According to RC07, "no clear signal is associated with the distribution of the derived state". At 14 steps, the state distribution of this character is indeed not very tidy, and optimization is ambiguous at several nodes; nonetheless, state 1 is synapomorphic of Temnospondyli, *Solenodonsaurus*, and Seymouriamorpha, while state 0 is autapomorphic of Discosauriscidae and of the amniote-diadectomorph-amphibian clade.

55. SUTEMP 5: **Rostral border of temporal embayment formed only by squamosal (0) or at least in part by supratemporal (1).** This character is new and replaces SUTEMP 2, see above; the scores are identical, except that this character is inapplicable when there is no embayment (SQU 3(0), see below), and except for the following list. We use "otic/temporal/spiracular notch/embayment" as synonyms.

This character is not applicable to *Acanthostega*, because the entire edge of its temporal embayment is formed by the tabular, or to *Ichthyostega*, where the embayment is too short (rostrocaudally) to come anywhere near the supratemporal.

Crassigyrinus and *Whatcheeria* possess state 1, not 0.

Diadectes is polymorphic (North American species: 0 [Berman et al. 1992]; *D. absitus*: 1 [Berman et al. 1998]).

56. TAB 1/SQU 4: **Separately ossified tabular: present (0); absent (1).** RC07 distinguished TAB 1, which had the present name, from SQU 4, which described the absence (0) or presence (1) of a single bone in the places normally occupied by the squamosal, the tabular, and the supratemporal. SQU 4(1) was limited to the adelogyrinids. Based on which bones are lost in other taxa in this matrix (and elsewhere among amniotes), we interpret the "squamosotabular bone" (Andrews & Carroll 1991) as simply the squamosal, so that the adelogyrinids lack tabulars and SQU 4 turns out to be a duplicate of TAB 1.

State 1 is present in Albanerpetontidae (McGowan 2002).

57. TAB 2: **Blade-like, posterolateral horn of tabular lying ventral to tabular ornamented surface: absent (0); present (1).**

58. TAB 3: **Rounded, button-like posterior process of tabular lying ventral to tabular ornamented surface: absent (0); present (1).**

TAB 4: **Tabular/squamosal suture extending onto skull table dorsal surface: present (0); absent (1).** This character is scored for almost all taxa, yet almost none possess a tabular-squamosal suture. It could be reinterpreted as the presence or absence of participation of the squamosal in the dorsal surface of the skull roof, but that is already PAR 7. Because it is further influenced by presence and position of the supratemporal and the temporal embayment, it would be inapplicable to most of the taxon sample if taken literally. We have therefore deleted this character. As it was scored by RC07, it required the same number of steps under the temnospondyl and the lepospondyl hypothesis.

59. TAB 5: **Tabular/squamosal suture: smooth (0); interdigitating (1).** This character is inapplicable in the absence of contact between the tabular and the squamosal.

60. TAB 6: **Tabular (including its ornamented surface) elongate posterolaterally or posteriorly in the form of a massive, horn-like process, conferring a boomerang-like shape to [the] skull outline in plan view: absent (0); present (1).** Evidently "plan" means dorsal and ventral.

61. TAB 7: **Parietal-parietal width smaller than (0) or greater than (1) distance between skull roof posterior margin and orbit posterior margin, measured along skull midline.** RC07 used "skull table" instead of "skull roof". We interpreted the width to mean the maximum width between the lateral margins of the parietals.

State 0 is found in *Kotlassia* (just barely; Bulanov 2003: fig. 30), state 1 occurs in *Scincosaurus* (Milner & Ruta 2009).

Saharastega is scored 1 because it has state 1 for the left orbit and exact equality between the distances for the right orbit.

62. TAB 8: **Tabular without (0) or with (1) posteroventrally sloping occipital exposure.**

State 1 occurs in *Orobates* (Berman et al. 2004) and *Tseajaia* (Moss 1972, Berman et al. 1992).

Diadectes is polymorphic (Berman et al. 1992, 1998).

Unknown for *Eocaecilia* (where it is not clear if the tabular had any occipital exposure; Jenkins et al. 2007) and *Westlothiana* (Smithson et al. 1994).

63. TAB 9: **Dorsoventrally flattened, posteriorly directed, subhorizontal outgrowth from posterolateral ventral surface of tabular: absent (0); present (1).**

We have scored this character as unknown (inapplicable) in *Eocaecilia* because the tabular probably lacks an exposed ventral surface (Jenkins et al. 2007).

The condition is unknown in *Scincosaurus* (Milner & Ruta 2009).

64. TAB 10: **Tabulars entirely on occipital surface: no (0); yes (1).**

65. POSORB 1: **Separately ossified postorbital: present (0); absent (1).**

We now interpret *Brachydectes* as having state 0 (Marjanović & Laurin 2008).

66. POSORB 2: **Postorbital without (0) or with (1) ventrolateral digitiform process fitting into deep, vertical groove along jugal lateral surface.**

State 1 is found in *Eryops* (Sawin 1941).

Unknown in *Westlothiana* (Smithson et al. 1994).

67. POSORB 3: **Postorbital contributing to (0) or excluded from (1) orbit margin.**

Due to our reinterpretation (see POSORB 1), state 0 is scored for *Brachydectes*.

68. POSORB 4: **Postorbital irregularly polygonal (0) or broadly crescentic and narrowing to a posterior point (1).** We have adopted a very broad interpretation of "broadly crescentic" and concentrated on absence and presence of the pointed caudal end. Very likely, however, many more states should be distinguished to represent the diversity of postorbital shapes found in this matrix.

Kotlassia was scored 1, but its caudal point is far ventral (Bulanov 2003: fig. 30), instead of dorsal as usual; we prefer to treat this unique condition as state 0.

Seymouria was scored 1, but the caudal end of its postorbital is a straight vertical suture (Laurin 2000: fig. 1).

Due to our reinterpretation (see POSORB 1), state 1 is scored for *Brachydectes*. It is further present in *Paleothyris* (Carroll 1969), *Petrolacosaurus* (though this may be due to the temporal fenestrae; Reisz 1981), and *Westlothiana* (at least on the right side, and at least in the specimen drawings as opposed to the reconstruction; Smithson et al. 1994).

69. POSORB 5: **Postorbital/tabular suture: absent (0); present (1).**

We have scored this character as unknown (inapplicable) when the supratemporal is present.

Due to our reinterpretation (see POSORB 1), state 1 is scored for *Brachydectes*.

Microbrachis is apparently polymorphic (CG78; Vallin & Laurin 2004).

70. POSORB 6: **Postorbital not wider (0) or wider (1) than orbit.** Judging from the original scoring, this is meant to be measured in strict dorsal view.

Due to our reinterpretation (see POSORB 1), state 0 is scored for *Brachydectes*.

The condition is so borderline in the reconstruction of *Nigerpeton* (Steyer et al. 2006) that we have scored it as unknown.

71. POSORB 7: **Postorbital at least one-fourth of the width of the skull table at the same transverse level: absent (0); present (1).** RC07 used "skull roof" instead of "skull table".

Due to our reinterpretation (see POSORB 1), state 0 is scored for *Brachydectes*. It further occurs in *Colosteus* (Hook 1983) and *Silvanerpeton* (Ruta & Clack 2006).

State 1 occurs in *Ichthyostega* (Ahlberg et al. 2008), *Baphetes* and *Megalocephalus* (Beaumont 1977), *Eucritta* (Clack 2001), *Edops* (Romer & Witter 1942), *Eryops* (Sawin 1941), *Neldasaurus* (Chase 1965), *Kotlassia* (Bulanov 2003: fig. 30), *Scincosaurus* (Milner & Ruta 2009), all diplocaulids (Milner 1980), and *Chroniosaurus* (Clack & Klembara 2009).

Unknown in *Adelogyrinus* (Andrews & Carroll 1991).

Microphon is polymorphic (Bulanov 2003: fig. 16, 22), though we caution that this difference between *M. exiguus* (state 1) and *M. gracilis* (state 0) could be ontogenetic, with the known skull of *M. gracilis* being closer to maturity than that of *M. exiguus*.

72. POSORB 8: **Anteriormost part of postorbital me[d]ial margin with sigmoid profile in dorsal or lateral aspect: absent (0); present (1).**

Due to our reinterpretation (see POSORB 1), state 0 is scored for *Brachydectes*.

73. SQU 1: **Anterior part of squamosal lying posterior to (0) or anterior to (1) parietal midlength.**

Westlothiana shows state 0 (Smithson et al. 1994).

Adelospondylus and *Adelogyrinus* have state 1 (Andrews & Carroll 1991).

SQU 2 is merged with JAW ART 1, see below.

74. SQU 3: **Caudolateral edge of skull: straight or convex (0); dorsoventrally tall embayment (1); dorsal notch (2) (unordered).** The original name and description of this character contradict each other: "*Squamosal without (0) or with (1) broad, concave embayment.* An embayment is widespread among early tetrapods, a deeply incised squamosal notch is seen only in some stem amniotes and, conspicuously, in temnospondyls and salientians." [italics in the original] Judging from its name, the "deeply incised squamosal notch" (found, incidentally, in few temnospondyls and no salientians!) was lumped with the complete absence of an embayment into the same state – and indeed this was reflected in the matrix. We have not ordered this character because the temporal embayment could disappear by rostrocaudal shortening (which might pass from state 2 over 1 to 0 or directly from 2 to 0) or by dorsoventral narrowing (from 1 over 2 to 0).

Within state 2, a difference between a short triangular notch (as in *Eoherpeton*: Smithson 1985) and a narrow, deep one which has almost parallel edges for much of its length (e.g. *Seymouria*: Laurin 1996c, 2000; *Phonerpeton*: Dilkes 1990) could be recognized, but this is already included in other characters (TAB 7, ORB 5).

Capetus appears to pass from state 1 to state 2 in its ontogeny (Sequeira & Milner 1993). The difference between these states is not, however, size-dependent, as demonstrated by the occurrence of state 2 in the tiny *Gerobatrachus* (Anderson et al. 2008), as well as by the fact that *Phonerpeton* has state 2 (Dilkes 1990) while *Dendrerpeton*, at the same skull size, has state 1 (Holmes et al. 1998).

State 1 further seems to occur in *Gephyrostegus*, though this might even differ between the known specimens (Carroll 1970). It is present in *Adelogyrinus* (Andrews & Carroll 1991), *Ecolsonia* (Berman et al. 1985; that the tabular and the quadratojugal meet caudal to the embayment does not matter), *Solenodonsaurus* (Laurin & Reisz 1999), *Diadectes* (Berman et al. 1992, 1998), *Ariekanerpeton* and *Utegenia* (Klembara & Ruta 2004a, 2005a), *Leptoropha* (Bulanov 2003), *Orobates* (Berman et al. 2004), *Silvanerpeton* (Ruta & Clack 2006), and *Tseajaia* (Moss 1972, Berman et al. 1992).

State 2, the plesiomorphy, is seen in *Ventastega* (Ahlberg et al. 2008), *Chenoprosopus* (Langston 1953: fig. 8), *Eryops* (DM pers. obs. of a cast on exhibit in the MNHN; very difficult to tell from publications like Sawin 1941), *Caerorhachis* (Ruta et al. 2002), all anthracosaurs, and *Microphon* (Bulanov 2003).

From the available illustrations, we cannot tell if *Edops* (Romer & Witter 1942) and *Kotlassia* (Bulanov 2003: fig. 30) have state 1 or 2.

75. SQU 5: **Squamosal without (0) or with (1) internal shelf bracing quadrate from behind.** We have not counted the caudal exposure of the squamosal found in amniotes as state 1.

Unknown in *Bruktererpeton* (Boy in Boy & Bandel 1973).

76. JUG 1: **Separately ossified jugal: present (0); absent (1).**

77. JUG 2-6: **Maxilla-quadratojugal contact (0); jugal contributes to ventral edge of skull between maxilla and quadratojugal, but does not project ventrally beyond toothrow (1); jugal laterally overlaps toothrow (2) (ordered).** We have merged two correlated characters that we interpret as parts of a continuous character.

Schoenfelderpeton is scored as unknown due to its paedomorphosis.

Eocaecilia has state 0; the quadratojugal is not preserved, but the ventral does not reach as far ventral as the maxilla and does not contact the caudal end of the maxilla (Jenkins et al. 2007).

Unknown in *Leptoropha* (Bulanov 2003: fig. 12); inapplicable in *Hapsidopareion* and *Pelodosotis* due to CHE EMA 1(1) (see below).

78. JUG 3: **Jugal/pterygoid contact: absent (0); present (1).**

Eocaecilia has state 0 (Jenkins et al. 2007). So does *Ossinodus*, in spite of the palatal exposure of the jugal (Warren 2007) that gives state 1 to *Saharastega* (Damiani et al. 2006).

79. JUG 4: **Depth of jugal ventral to orbit greater (0) or smaller (1) than half of anteroposterior eye diameter.**

Ichthyostega has state 1 (Jarvik 1996). So does Albanerpetontidae (McGowan 2002, Venczel & Gardner 2005).

We have scored *Eucritta* as unknown because only juvenile specimens are known and relative eye size decreases in the ontogeny of most animals.

80. JUG 7: **Jugal without (0) or with (1) V-shaped indentation of its orbital margin.**

Unknown in *Westlothiana* (Smithson et al. 1994).

81. JUG 8: **Jugal not extending (0) or extending (1) anterior to orbit anterior margin.** This character is only applicable to OTUs with MAX 5/PAL5(0).

Unknown in *Westlothiana* (Smithson et al. 1994).

82. QUAJUG 1: **Separately ossified quadratojugal: present (0); absent (1).**

83. QUAJUG 2: **Quadratojugal depth less than one-fourth of squamosal depth: absent (0); present (1).**

Unknown in *Scincosaurus* (Milner & Ruta 2009).

84. QUAJUG 3: **Quadratojugal anteroposteriorly elongate and bar-like: no (0); yes (1).**

State 1 is reconstructed for *Eocaecilia* (Jenkins et al. 2007).

85. QUA 1: **Quadrate without (0) or with (1) dorsal process.**

Unknown in *Scincosaurus* (Milner & Ruta 2009).

86. PREOPE 1: **Preopercular: present (0); absent (1).** RC07 had exchanged the states in the text but not in the matrix.

Ventastega has state 0 (Ahlberg et al. 1994).

So does *Whatcheeria* (Lombard & Bolt 1995; Bolt & Lombard 2000). Ruta et al. (2003), the preceding version of RC07, cited Clack (1998, 2001) for the absence of the preopercular (1) in all post-Devonian tetrapods, but Clack (1998) confirmed the presence of the preopercular in *Whatcheeria* (as part of the argument for the absence of this bone in *Crassigyrinus*), and Clack (2001) mentioned neither the preopercular nor *Whatcheeria*.

State 0 further occurs in *Ossinodus* (Warren 2007).

87. NOS 1: **Nostrils posterolaterally expanded: absent (0); present (1).**

Unknown in *Westlothiana* (Smithson et al. 1994).

88. NOS 3: **Nostrils keyhole-shaped: absent (0); present (1).** This character can almost certainly be merged with NOS 1, but we have not looked into this yet; both characters are irrelevant to lissamphibian origins.

89. NOS 4: **Nostrils elliptical, with greater axis orientated obliquely in anteromedial to posterolateral direction: absent (0); present (1).** RC07 added a further restriction on the length of the external nares in relation to the suture between the nasals, but this would make the character correlated to the length of the snout

(for instance, it would require *Saharastega* to have 10-cm-long nares to qualify for state 1, which it otherwise does) and inapplicable in taxa without a suture between the nasals or without nasals.

State 1 is present in albanerpetontids where known (McGowan 2002; Venczel & Gardner 2005).

Unknown in *Westlothiana* (Smithson et al. 1994).

90. INT FEN 1: **Internarial fenestra: absent (0); present (1).** Interestingly, RC07 count the presence of "median rostrals" as state 1, regardless of whether there is a fenestra present additional to them or not. With *Ventastega* and *Acanthostega* possessing both a fenestra (or fontanelle) and a pair of "median rostrals", and baphetids possessing a pair of "median rostrals" but no fenestra, the "median rostrals" should most likely be considered a separate character.

Apateon is polymorphic, with *A. gracilis* having state 0 throughout its ontogeny (Schoch & Fröbisch 2006).

91. ORB 1: **Interorbital distance greater than (0), subequal to (1), or smaller than half of skull […] width (ordered).** We have exchanged states 1 and 2 to make ordering of this continuous character possible.

Brukterpeton has state 2 (Boy in Boy & Bandel 1973), as does *Tseajaia* (Moss 1972, Berman et al. 1992).

Diadectes is polymorphic (Berman et al. 1992, 1998).

92. ORB 2: **Interorbital distance greater than (0), subequal to (1), or smaller than maximum orbit diameter (2) (ordered).** We have exchanged states 1 and 2 to make ordering of this continuous character possible.

Tseajaia shows state 1 or arguably 2 (Moss 1972, Berman et al. 1992); we have decided on state 1.

Eucritta is scored as unknown for having juvenile eye size.

We have scored Albanerpetontidae, *Karaurus*, *Valdotriton*, *Notobatrachus* and *Vieraella* as unknown, because it is unknown how much of the orbitotemporal fenestra is homologous to the orbit. (RC07 had already scored *Brachydectes* as unknown, presumably for the same reason.) Only the interorbital width of *Triadobatrachus* is so small that even the smallest realistic estimates for eyeball size result in state 2, which was already scored.

93. ORB 3: **Angle at orbit anteroventral corner: absent (0); present (1).**

State 1 is observed in *Eocaecilia* (Jenkins et al. 2007).

The condition in *Westlothiana* is unknown (Smithson et al. 1994).

94. ORB 4: **Orbit deeper than long: no (0); yes (1).**

Eocaecilia has state 0 (Jenkins et al. 2007). All other lissamphibians are scored as unknown because it is unknown how much of the orbitotemporal fenestra is homologous to the orbit. (RC07 had already scored *Brachydectes* as unknown, presumably for the same reason.)

95. ORB 5: **Orbit anteroposterior diameter shorter than (0), subequal to (1), or longer than (2) distance between orbit posterior margin and suspensorium anterodorsal margin (ordered).** We have exchanged states 1 and 2 to make ordering of this continuous character possible, and interpret the rostral end of the temporal embayment (if present) as "suspensorium anterodorsal margin".

Acanthostega has state 2 (Clack 2003).

We have scored *Brachydectes* (Wellstead 1991: fig. 2E) and all lissamphibians other than *Eocaecilia* as unknown because it is unknown how much of the orbitotemporal fenestra is homologous to the orbit.

96. PIN FOR 2: **Pineal foramen occurring posterior to (0), at the level of (1), or anterior to (2) interparietal suture midlength, or absent (3) (stepmatrix).** States 0 to 2 are ordered due to forming a continuous character, but state 3 is only one step away from all others.

Appendix-Table 2: Stepmatrix for characters PIN FOR 2 and HUM 7-9.

from ↓ to →	0	1	2	3
0	0	1	2	1
1	1	0	1	1
2	2	1	0	1
3	1	1	1	0

97. L SC SKU 1: **Lightly sculptured area (subdued ornament) adjacent to skull roof midline: absent (0); present (1).**

98. PTF 1: **Posttemporal fossa occurring at occiput dorsolateral corner, delimited dorsally by skull table, not bordered laterally and floored by dorsolateral extension of opisthotic (0); fossa present near occiput dorsolateral corner, delimited dorsally by occipital flanges of tabular and postparietal and bordered laterally as well as ventrally by dorsolateral extension of opisthotic meeting tabular ventromedial flange (1); small fossa present near occiput ventrolateral corner, bordered laterally by tabular ventromedial flange, delimited dorsally by dorsal portion of the lateral margin of the suproccipital–opisthotic complex and floored by lateral extension of opisthotic (2); absence of fossa (3) (unordered).** It is possible that this character should be ordered or be treated according to a more complex stepmatrix, but we are not sure about this and cannot find a suggestive pattern in the data, so we leave it unordered by default.

Doleserpeton shows state 1 (Sigurdsen 2008).

Eocaecilia (Jenkins et al. 2007) and *Orobates* (Berman et al. 2004) have state 3.

99. SKU TAB 1: **Postorbital region of skull roof abbreviated and at least one-third wider than long: absent (0); present (1).**

State 1 is found in *Eocaecilia* (Jenkins et al. 2007) and *Vieraella* (Estes & Reig 1973).

100. FONT 1: **Dorsal exposure of frontoparietal fontanelle: absent (0); present (1).**

101. TEM FEN 1: **Broad opening in skull postorbital region: absent (0); present (1).** RC07 had added "(aïstopod pattern)" in front of the colon, but potential primary homologues of the aïstopod temporal fenestra can be found elsewhere.

Most obviously, the diapsid *Petrolacosaurus* has two temporal fenestrae. In principle, they could have arisen from a single fenestra that was subdivided by a contact between processes of the postorbital and the squamosal; there is no evidence that this actually happened, but, firstly, to take this into account would mean to insert assumptions about secondary homology into the determination of primary homology; secondly, the lateral temporal fenestra has subdivided itself in just such a fashion (by a contact between processes of the jugal and the squamosal) in several dinosaurs, e.g. *Cryolophosaurus* (Hammer & Hickerson 1994). We have therefore scored *Petrolacosaurus* as possessing state 1.

On the other hand, fenestrae can become confluent with other openings. Both temporal fenestrae and the orbit of Cenozoic and many Mesozoic birds represent such a case; so might, at least in principle, the "orbitotemporal fenestra" of all lissamphibians other than *Eocaecilia*. We have therefore scored them all as sharing state 1. This does not, however, apply to the "orbitotemporal fenestra" of *Brachydectes*, because we now interpret the bone that forms its caudal margin as the postorbital (see POSORB 1); there is no fenestra between the postorbital and the squamosal, so *Brachydectes* keeps its score of 0.

102. CHE EMA 1: **Ventral emargination of cheek (pattern of certain tuditanomorph microsaurs): absent (0); present (1).** This pattern really does not seem to occur in this matrix elsewhere than in *Hapsidopareion*, *Micraroter* and *Pelodosotis*, though we fail to find a clade with the composition ascribed to Tuditanomorpha by CG78.

The "tuditanomorph" *Cardiocephalus* was scored and mentioned by RC07 as sharing state 1. We disagree; instead of the cheek being emarginated, the jaw joint is displaced ventrally in *Cardiocephalus* (like in ophiacodontid amniotes: Romer & Price 1940), making the ventral margin of the cheek concave even though no part of it lies dorsal to the toothrow.

The cheek (jugal, quadratojugal) is absent in *Brachydectes*, *Karaurus* and *Valdotriton*; we have accordingly scored them as unknown.

IFN 1: **Interfrontonasal: absent (0); present (1).** As RC07 explicitly mention, this character is parsimony-uninformative because state 1 is limited to *Eryops*. We have therefore deleted it. We do not see the point of already inserting this character now in case other taxa which possess state 1 (e.g. the "microsaur" *Crinodon*: CG78) will some day be added to a future version; at present, all it does is to make the matrix look larger than it is.

103. SUS 1: **Anteroposteriorly narrow, bar-like squamosal: absent (0); present (1).**

State 1 is found in all lissamphibians except *Eocaecilia* (0 as already scored) and *Vieraella* (unknown).

104. SC 1: **Lateral line system on skull roof totally enclosed (0), mostly enclosed with short sections in grooves (1), mostly in grooves with short sections enclosed (2), entirely in grooves (3), absent (4) (ordered).** RC07 had "skull table" instead of "skull roof". We have ordered this and the following character because the present sequence of states represents a gradual movement of the lateral-line organ from inside the bones to their surface and beyond (the organ is present in extant aquatic lissamphibians, but never leaves traces on bones).

States 0 and 4 can be difficult to distinguish from the outside. Indeed, Warren (2007) reports that *Edops*, *Chenoprosopus*, and *Eryops*, previously thought to have state 4, have state 0. It has to be expected that other taxa in this matrix that are scored 4 will turn out to share state 0 if reinvestigated. Most notably, *Dendrerpeton* has "pits and perforations" for the postcranial lateral line in the ventralmost row of dorsal scales (Pawley 2006: 188), so the absence of traces of cranial lateral lines in this taxon is unexpected and may turn out to be spurious.

Albanerpetontidae has state 4 according to all literature about this taxon.

Discosauriscus reaches state 4 when adult (Klembara 2009). This is interpreted as part of a transition to a fully terrestrial life. Accordingly, we have added state 4 as an option (partial uncertainty) to all seymouriamorphs for this and the following character, except of course *Seymouria* (which already had state 4 for both) and *Kotlassia* (which is unknown for both).

Scincosaurus is polymorphic, with most specimens having state 4 but some showing state 2 instead (Milner & Ruta 2009).

Ossinodus has state 1 or 2 (Warren 2007).

We have scored *Chroniosaurus* as possessing state 0 or 4; state 4 occurs in the specimens described by Clack & Klembara (2009), state 0 in quadratojugals attributed to "*Jugosuchus*", some of which could be referable to *Chroniosaurus* (Clack & Klembara 2009: 17).

Nigerpeton is scored at face value, i.e. as having state 3; however, Warren (2007) emphasizes that the actual surface of the two known skulls is eroded away and may have covered the canals, so that states 0 through 2 stay within the realm of possibility.

105. SC 2: **Mandibular canal totally enclosed (0), mostly enclosed with short sections in grooves (1), mostly in grooves with short sections enclosed (2), entirely in grooves (3), absent (4) (ordered).**

Baphetes has state 1, 2, or 3 (Milner et al. 2009).

Albanerpetontidae has state 4 according to all literature about this taxon.

Unknown in *Scincosaurus* (Milner & Ruta 2009).

Nigerpeton is scored at face value, i.e. as having state 3; however, Warren (2007) emphasizes that the actual surface of the two known skulls is eroded away and may have covered the canals, so that states 0 through 2 stay within the realm of possibility.

106. VOM 1-13: **Vomer approximately as wide as long or wider (0), intermediate (1), at least 2½ times longer than wide (2) (ordered).** This is a merger of two correlated characters that described parts of a continuous character.

State 0 is found in *Colosteus* (Hook 1983: fig. 1), *Eoscopus* (Daly 1994), and *Ariekanerpeton* (Klembara & Ruta 2005a: fig. 13).

State 1: *Caerorhachis* (Ruta et al. 2002: fig. 5c), *Bruktererpeton* (though almost state 2; Boy in Boy & Bandel 1973: fig. 7), *Asaphestera* (most likely; CG78: fig. 7), apparently *Micraroter* (CG78: fig. 53, 56), *Rhynchonkos* (CG78: fig. 63, 64), *Lethiscus* (Anderson et al. 2003), *Capetus* (Sequeira & Milner 1993: fig. 9), *Pederpes* (as reconstructed by Clack & Finney 2005: fig. 17), *Silvanerpeton* (Ruta & Clack 2006: fig. 8), and *Utegenia* (Klembara & Ruta 2004a: fig. 14) unless this is ontogenetic.

State 2 is present in *Hapsidopareion* (CG78: fig. 13, 14). Furthermore, the snout of *Archeria* is so long and narrow that state 2 must have been present, so we have scored *Archeria* accordingly, even though its vomer is unknown (Holmes 1989: fig. 1B). State 2 is similarly inevitable in *Orobates* (Berman et al. 2004: fig. 3).

In *Eoherpeton* (Smithson 1985: fig. 8) and *Proterogyrinus* (Holmes 1984: fig. 3), the vomer is entirely unknown, but the skull is too narrow for state 0, so we have ascribed state 1 or 2 to both.

As reconstructed (Panchen 1972: fig. 7), *Pholiderpeton attheyi* has state 1 on the left and 2 on the right side. We have scored it as polymorphic.

Gephyrostegus has state 1 or 2 (Carroll 1970).

The condition in *Kotlassia* is unknown (Bulanov 2003).

State 1 or 2 is present in *Cardiocephalus* (CG78: fig. 30) and *Euryodus* (CG78: fig. 37, 38).

The vomers of *Microbrachis* are so inclined (rostromedially to caudolaterally) that we cannot decide between states 0 and 1 (Vallin & Laurin 2004: fig. 5).

Ossinodus, too, has state 0 or 1 (Warren 2007: fig. 6).

107. VOM 3: **Vomer with (0) or without (1) fangs comparable in size to, or larger than, marginal teeth (premaxillary or maxillary).**

Jarvik (1996) reconstructed *Ichthyostega* with state 1. Ahlberg et al. (1994) demonstrate that it had state 0 instead.

The most mature known individual of *Amphibamus* has state 0 (Daly 1994: 27). We regard this as the adult condition (see also Marjanović & Laurin 2008: 193).

The vomer is completely toothless (state 1) in *Anthracosaurus* (Panchen 1977) and *Pholiderpeton scutigerum* (Clack 1987b).

State 1 is further found in *Lethiscus* (Anderson et al. 2003).

108. VOM 4: **Vomer without (0) or with (1) small teeth (denticles), the basal diameter and/or height of which is less than 30% of that of adjacent marginal teeth (premaxillary or maxillary) and remaining vomer teeth (if present).** RC07 further specified that the denticles "form[…] [a] continuous shagreen or discrete, [sic] patches", but denticles occur in other arrangements as well.

The vomer of *Bruktererpeton* has two rows of denticles in its caudal corner (Boy in Boy & Bandel 1973). We count this as state 1.

Scincosaurus (Milner & Ruta 2009) and *Tseajaia* (Moss 1972) show state 0.

109. VOM 5-10/PAL 8/PTE 10-12-18/INT VAC 1: **Interpterygoid vacuities absent, pterygoids sutured to each other plus contacting parasphenoid along entire length (0); interpterygoid vacuities present, pterygoids still sutured rostrally (1); contact between pterygoids absent, pterygoid-vomer suture still present (2); palatine participates in interpterygoid vacuity margin, pterygoid overlaps it medially (3); pterygoid entirely caudal to palatine, but not the salamander condition (4); palatine absent, but not the salamander condition (5); the salamander condition (6) (ordered).** This is a fusion of eight correlated characters that represent parts of a single continuous character, the gradual size increase of the interpterygoid vacuities. "The salamander condition" is PTE 18(1): "Pterygoid palatal ramus a robust, abbreviated, flange-like to digitiform structure, as long as or barely longer than combined length of quadrate ramus plus basicranial articulation". We have not directly represented VOM 5, "Vomer excluded from (0) or contributing to (1) interpterygoid vacuities", because it depends at least in part on the width of the skull or the interpterygoid vacuities (if *Scincosaurus* or *Bruktererpeton* had wider skulls or interpterygoid vacuities, their vomers would end up forming the rostral margins of the interpterygoid vacuities, unless a neomorphic medial process appeared on the pterygoids), though this distinction could be added to the present character as a split of state 2. The width of the interpterygoid vacuities is coded here as INT VAC 2-3-4.

Ventastega has state 0 (Ahlberg et al. 1994).

We ascribe state 0 or 1 to *Ichthyostega* because Jarvik's (1996) reconstruction is not fully clear and because Jarvik's written description is too much unlike other descriptions of pterygoids of limbed vertebrates (in terms of which features are described) to be helpful.

Carroll's (1970) specimen drawings of *Gephyrostegus* contradict both of his reconstructions. All we can say is that the palatine is probably present (because palatine fangs are preserved), ruling out states 5 and 6, and that the preserved bony palate is so broad as to make state 4 highly unlikely. We have scored it as having state 0, 1, 2, or 3.

McGowan (2002: 9) limits the possibilities for Albanerpetontidae to state 1, 2, or 3.

Brachydectes has a unique condition with an extremely broad parasphenoid that makes interpterygoid vacuities impossible. We follow our previous practice (Marjanović & Laurin 2008: 192) in ascribing state 2 to *Brachydectes* because there is a pterygoid-vomer rather than a palatine-parasphenoid contact and because the pterygoids do not come anywhere near each other (being separated by the parasphenoid).

It seems a safe assumption that *Westlothiana* possessed palatines (Smithson et al. 1994). We have scored it as having state 1 or 2, though whether 0 and 3 can really be excluded might be arguable.

Batropetes may have state 1, 2, 3, or 4 (Carroll 1991), though whether 4 is really possible might be arguable.

The reconstruction and the specimen drawing of *Adelospondylus* (Andrews & Carroll 1991) are not very similar. We assign state 0, 1, 2, or 3 to it.

Diadectes shows state 0 in some American species (Olson 1947), state 1 or 2 in others (Case & Williston 1912), and state 1 in *D. absitus* (Berman et al. 1998). We have scored it as possessing states 0 and 1 because making partial uncertainty part of a polymorphism is not possible.

Limnoscelis has state 2 (Fracasso 1983: 126).

In seymouriamorphs the palate closes during ontogeny. Therefore we have assigned state 0 to *Discosauriscus* (Klembara 1997: fig. 28, not fig. 24 or fig. 34), state 0, 1, or 2 to *Kotlassia* (instead of just the observed state 2: Bulanov 2003), and state 0 or 1 to *Leptoropha* (the pterygoid of which is known: Bulanov 2003: S33), *Microphon, Ariekanerpeton*, and *Utegenia*.

Lethiscus possesses state 2 (Anderson et al. 2003: 1074).

110. VOM 7: **Vomer/maxilla suture anterior to the choana: absent (0); present (1).**

Lethiscus has state 0 (Anderson et al. 2003).

111. VOM 8: **Vomer with (0) or without (1) toothed lateral crest.**

Eoscopus (Daly 1994), *Bruktererpeton* (Boy in Boy & Bandel 1973), almost certainly *Lethiscus* (Anderson et al. 2003), and *Microphon* (Bulanov 2003) have state 1.

112. VOM 9: **Vomer with (0) or without (1) transversely orientated, anterior crest.**

Eoscopus (Daly 1994), *Bruktererpeton* (Boy in Boy & Bandel 1973), almost certainly *Lethiscus* (Anderson et al. 2003), and *Microphon* (Bulanov 2003) have state 1.

113. VOM 11: **Vomer without (0) or with (1) nearly transverse patch of small teeth (denticles) lying posterome[d]ial to choana.**

Bruktererpeton has state 0 (Boy in Boy & Bandel 1973).

114. VOM 12: **Distinct posterolateral process of vomer bordering more than half of choana posterior margin: absent (0); present (1).**

Bruktererpeton has state 0 (Boy in Boy & Bandel 1973), as does *Lethiscus* (Anderson et al. 2003).

Unknown in *Scincosaurus* (Milner & Ruta 2009).

115. PAL 1: **Palatine with (0) or without (1) fangs comparable in size to or larger than marginal teeth (premaxillary or maxillary).**

Jarvik (1996) reconstructed *Ichthyostega* with state 1. Ahlberg et al. (1994) demonstrate that it had state 0 instead.

The most mature known individual of *Amphibamus* has state 0 (Daly 1994: 27). We regard this as the adult condition (see also Marjanović & Laurin 2008: 180).

Lethiscus has state 1 (Anderson et al. 2003).

All PAL characters are inapplicable to *Oestocephalus,* which lacks (separate) palatines (VOM 5-10/PAL 8/PTE 10-12-18/INT VAC 1(5)).

Tseajaia has state 1 (Moss 1972: 12).

116. PAL 2: **Palatine without (0) or with (1) small teeth (denticles), the basal diameter and/or height of which is less than 30% of that of adjacent marginal teeth (maxillary) and remaining palatine teeth (if present).** See VOM 4; RC07 even had “remaining vomer teeth” instead of “remaining palatine teeth”.

Limnoscelis possesses state 1 (Fracasso 1983: 121).

Orobates (Berman et al. 2004) and *Tseajaia* (Moss 1972: 12) have state 0.

117. PAL 4: **Palatine with (0) or without (1) row of teeth (3+) comparable in size to, or greater than marginal teeth (maxillary) and parallel to these.**

Bruktererpeton shows state 1 (Boy in Boy & Bandel 1973: 51).

Lethiscus has state 0 (Anderson et al. 2003).

Unknown in *Orobates* (Berman et al. 2004).

118. PAL 6: **Palatine articulates with maxilla only at anterior extremity of the former: absent (0); present (1).**

Bruktererpeton shows state 0 (Boy in Boy & Bandel 1973: 51), as does *Lethiscus* (Anderson et al. 2003).

Unknown in *Orobates* (Berman et al. 2004).

119. PAL 7: **Palatine shaped like a slender, strut-like bone: absent (0); present (1).** RC07 did not quantify this character.

Amphibamus was given state 1 by RC07, which is supported by Schoch (2001), but the individual drawn by Schoch is not adult, because it lacks the palatine fangs noted by Daly (1994: 27) in the most mature known specimen (see PAL 1). Considering Schoch’s (2002) reconstruction of the palate of *Platyrhinops*, the shape of the palatine may depend on the presence of fangs; Daly (1994) does not illustrate it, so we have scored *Amphibamus* as unknown.

Lethiscus has state 0 (Anderson et al. 2003).

120. ECT 1: **Separately ossified ectopterygoid: present (0); absent (1).**

The condition is unknown in *Eocaecilia* (Jenkins et al. 2007; see Marjanović & Laurin 2008: 181 for discussion of ectopterygoids in gymnophionomorphs).

Diplocaulus possesses state 1 (Bossy & Milner 1998), as do *Oestocephalus* (Carroll 1998) and *Phlegethontia* (Anderson 2002).

Tseajaia has state 0 (Moss 1972: 12).

121. ECT 2: **Ectopterygoid with (0) or without (1) fangs comparable in size to or larger than marginal teeth (premaxillary or maxillary) and remaining ectopterygoid teeth (if present).**

Tseajaia has state 1 (Moss 1972: 12).

Unknown in *Bruktererpeton* (Boy in Boy & Bandel 1973: 51) and *Orobates* (Berman et al. 2004).

122. ECT 3: **Ectopterygoid without (0) or with (1) small teeth (denticles), the basal diameter and/or height of which is less than 30% of that of adjacent marginal teeth (maxillary) and remaining ectopterygoid teeth (if present).** See VOM 4.

Tseajaia shows state 0 (Moss 1972: 12).

123. ECT 4: **Ectopterygoid longer than/as long as (0) or shorter than (1) palatine.**

Unknown in *Bruktererpeton* (Boy in Boy & Bandel 1973: 51).

Tseajaia shows state 0 (Moss 1972: 12).

124. ECT 5: **Ectopterygoid with (0) or without (1) row of teeth (3+) comparable in size to, or greater than marginal teeth (maxillary) and parallel to these.**

Tseajaia shows state 0 (Moss 1972: 12).

125. ECT 6: **Ectopterygoid/maxilla contact: present (0); absent (1).** This character may seem correlated with PAL 6, and indeed state 1 of the latter does not occur without state 1 of the former in this matrix, but nonetheless the latter can exist without the former: it can mean that the subtemporal fenestra extends all the way to the middle of the palatine (as it does in branchiosaurids), or it can be due to the suborbital fenestra found in diapsids (such as *Petrolacosaurus*), which is separated from the subtemporal fenestra by an ectopterygoid-jugal (as in *Petrolacosaurus*) or ectopterygoid-maxilla contact (as in crocodyliforms and some dinosaurs); we therefore keep it separate.

Tseajaia shows state 0 (Moss 1972: 12).

ECT 7: **Ectopterygoid narrowly wedged between palatine and pterygoid: no (0); yes (1).** RC07 explicitly ascribe state 1 to *Odonterpeton* and *Hyloplesion*, but *Odonterpeton* has state 0 (CG78: fig. 99). This makes this character parsimony-uninformative, so we have deleted it.

126. PTE 3-9: **Flange on pterygoid: absent, pterygoid margin of subtemporal fenestra concave or straight throughout (0); rostrolateral-caudomedial orientation (1); mediolateral orientation (“transverse flange”), without row of large teeth (2); same with row of large teeth (3) (ordered).** RC07 treated the “posterolateral flange” (PTE 9) separately from the “transverse flange” (PTE 3), but we think the “transverse flange” is only an extreme of a continuum the rest of which is called “posterolateral flange”. Indeed, the two flanges never occur together.

Interestingly, PTE 3 is called “Transverse flange of pterygoid absent (0), present without transverse tooth row (1), or present and carrying transverse tooth row.” – the number “(2)” is omitted. This may be a simple typographic error, except for the fact that state 2 did not occur in the matrix except in the partial uncertainty (state 1 or 2) that was scored for *Leptoropha* and *Tseajaia*.

State 3 of the present character (= state “2” of PTE 3) is present in *Limnoscelis* (Fracasso 1983: fig. 2), *Paleothyris* (Carroll 1969), and *Petrolacosaurus* (Reisz 1981).

Tseajaia has state 2 (Moss 1972).

Vieraella shows state 1 (Estes & Reig 1973: fig. 1-2).

The condition is entirely unknown in *Colosteus* (Hook 1983: fig. 1B), *Whatcheeria* (the palate of which has not yet been described: Bolt & Lombard 2000), *Eucritta* (the reconstruction, Clack 2001: fig. 8, appears overly ambitious based on the accompanying text and specimen drawings), *Batropetes* (Carroll 1991), *Asaphestera* (CG78: fig. 6F), and apparently *Pederpes* (Clack & Finney 2005).

127. PTE 7: **Pterygoid quadrate ramus orientated mostly laterally in ventral aspect: absent (0); present (1).** It is possible that this is correlated to JAW ART1/SQU 2, but we have not tried to find out how fixed the spatial relations between the pterygoid and the occiput are.

This character is inapplicable to *Scincosaurus*, which lacks a distinct quadrate ramus (Milner et al. 2009).

128. PTE 11: **Pterygoid/maxilla contact: absent (0); present (1).** Because the ectopterygoid, if present, usually lies between the pterygoid and the maxilla, it would have been tempting to merge this character with ECT 1, but Clack (1998: fig. 4B) suggests that the maxilla and the pterygoid could meet caudal to the ectopterygoid in *Crassigyrinus*, so we have kept them separate.

Bruktererpeton (Boy in Boy & Bandel 1973) and *Lethiscus* (Anderson et al. 2003) have state 0.

129. PTE 13: **Pterygoid without (0) or with (1) distinct, me[d]ially directed process for basipterygoid articulation.** State 1 requires large interpterygoid vacuities, so we have scored it as inapplicable to OTUs scored VOM 5-10/PAL 8/PTE 10-12-18/INT VAC 1(0) or INT VAC 2-3-4(0).

State 1 is found in *Hyloplesion* (in the largest of the three specimens drawn in CG78: fig. 89), *Diplocaulus* (Bossy & Milner 1998: fig. 57C) where the process is very broad rostrocaudally but no less distinct than elsewhere, *Diploceraspis* (Beerbower 1963: fig. 4A) where the same situation prevails (partly obscured by the fact that the quadrate ramus is situated so far medially), *Ptyonius* (Bossy 1976: fig. 44, 49), and *Capetus* (Sequeira & Milner 1993).

130. PTE 14: **Quadrate process of pterygoid more than (0) or at most twice as long as maximally broad (1).** The original wording was more impressionistic: "Pterygoid quadrate ramus a robust structure, indistinctly merging into basal and palatal processes: absent (0); present (1)", explained in the next sentence as the quadrate ramus being "a stout structure, slightly longer than wide and without a neat separation from the rest of the bone". We have reduced this to the length/width ratio, which we have changed because the quadrate ramus is considerably longer than broad in most OTUs that were scored 1 (all lissamphibians, *Micromelerpeton*, and all branchiosaurids were scored 1, everything else was given state 0).

Remarkably, state 0 as defined by us occurs in *Micromelerpeton* (Boy 1995), all branchiosaurids (Boy 1986, 1987), and the lissamphibians *Eocaecilia* (Jenkins et al. 2007), *Triadobatrachus* (Roček & Rage 2000; DM and ML, pers. obs. of latex mold of MNHN MAE 126), and *Valdotriton* (Evans & Milner 1996).

We find state 1 in *Baphetes* (Beaumont 1977), *Eucritta* (Clack 2001), *Isodectes* (Sequeira 1998), *Caerorhachis* (Ruta et al. 2000), *Eoherpeton* (Smithson et al. 1985), *Pholiderpeton scutigerum* (Clack 1987b), *Ph. attheyi* (Panchen 1972), *Cardiocephalus*, *Asaphestera*, *Micraroter* (marginally), and *Rhynchonkos* (CG78), *Scincosaurus* (Milner & Ruta 2009), *Batrachiderpeton* (Bossy & Milner 1998), *Diceratosaurus* (Jaekel 1902), *Diplocaulus* (the pterygoids of which which look like those of the salamander *Karaurus*: Bossy & Milner 1998), *Diploceraspis* (Beerbower 1963), *Capetus* (Sequeira & Milner 1993) and *Silvanerpeton* (Ruta & Clack 2006).

Euryodus is polymorphic (CG78).

The condition is unknown in *Anthracosaurus* (Panchen 1977), *Batropetes* (Carroll 1991), *Odonterpeton* (CG78: fig. 99A), *Adelospondylus* (Andrews & Carroll 1991; it is too difficult to decide how to measure the reconstruction drawing and how to interpret it in relation to the specimen drawings), *Keraterpeton* (Huxley & Wright 1867; Jaekel 1902), and inapplicable in *Brachydectes* which lacks a quadrate process (Wellstead 1991) as well as in *Oestocephalus* (Carroll 1998) and *Phlegethontia* (Anderson 2002) which lack clear sutures between the pterygoid and other bones such as the epipterygoid and the quadrate.

PTE 15: **Pterygoid quadrate ramus straight, rod-like and gently tapering distally in ventral aspect: absent (0); present (1).** The ventral surface of the quadrate ramus further "is parallel-sided for most of its length and narrows smoothly in its rearmost part" in state 1, which is supposed to be present in "some dissorophoids and *Eocaecilia*". This unquantified description turns out to be difficult to apply to many (if not most) OTUs, or at least to the line drawings that fail to show that the quadrate ramus is a more or less vertical lamina. The visible tapering of the process further depends strongly on preservation. We fail to see a difference between the conditions of *Broiliellus* (scored 0 by RC07), *Platyrhinops* (0), *Eoscopus* (1), *Doleserpeton* (1), or probably even *Eocaecilia* (1). For the time being, we have therefore deleted this character.

131. PTE 16: **Pterygoid palatal ramus without (0) or with (1) distinct, anterior and unornamented digitiform process.** State 1 requires that the pterygoids meet rostrally to the parasphenoid; where this is not the case (VOM 5-10/PAL 8/PTE 10-12-18/INT VAC 1 having a state other than 0 or 1), this character is inapplicable.

State 0 is found in *Kotlassia* (Bulanov 2003: fig. 30b).

The condition of *Westlothiana* is unknown (Smithson et al. 1994).

132. PTE 17: **Basal region of pterygoid immediately anterior to quadrate ramus without (0) or with (1) sharply defined, elongate longitudinal groove.**

133. PTE 19: **Robust, strut-like, [sic] pterygoid–squamosal process providing support for quadrate: absent (0); present (1).**

134. INT VAC 2-3-4: **Interpterygoid vacuities not concave along their entire rostral, lateral and caudal margins (0); concave, but together at most as wide as half of the palate (1); together at least half as wide as palate, but at most as wide as long (2); together wider than long (3).** This is a merger of three correlated characters that represent parts of a continuous character.

135. CHO 1: **Choana wider in its anterior half than in its posterior half: no (0); yes (1).**

Bruktererpeton has state 0 (Boy in Boy & Bandel 1973: 51).

Unknown in *Scincosaurus* (Milner & Ruta 2009).

136. CHO 2: **Choana expanded transversely along its medial margin: absent (0); present (1).**

Bruktererpeton has state 0 (Boy in Boy & Bandel 1973: 51).

Unknown in *Scincosaurus* (Milner & Ruta 2009).

137. ANT VAC 2: **Anterior palatal vacuity present and single (0), present and double (1), or absent (2) (unordered).** RC07 created this character by merging ANT VAC 1 and ANT VAC 2 of Ruta et al. (2003). We have not ordered this character because no sequence is obvious.

Bruktererpeton has state 0 (Boy in Boy & Bandel 1973: 51), as does *Lethiscus* (Anderson et al. 2003).

The condition is unknown in *Scincosaurus* (Milner & Ruta 2009) and *Tseajaia* (Moss 1972: 12).

138. SUPOCC 1: **Separately ossified supr[…]occipital: absent (0); present (1).**

Unknown in *Eusthenopteron*, where the entire braincase is fused (Carroll & Chorn 1995).

Bolt (1969: 889) states explicitly that *Doleserpeton* clearly shows state 0: "There is no supraoccipital bone, and indeed no room for one, as the opisthotics cover the tops of the exoccipitals and, in maturer specimens, fuse above the foramen magnum." This is confirmed by Sigurdsen (2008).

Eocaecilia shares state 0, as demonstrated by the median dorsal suture in the braincase (Jenkins et al. 2007) – the suproccipital is a single median bone and would make such a suture impossible. The same holds for *Notobatrachus*, at least in the reconstruction by Estes & Reig (1973).

Euryodus was scored as unknown, but we cannot distinguish its condition from that of *Cardiocephalus* which was scored 0 (both according to CG78); we have assigned state 0 to both.

Unknown in *Megalocephalus* (due to fusion: Beaumont 1977: 65f.), *Phonerpeton* (Dilkes 1990), *Eoscopus*, where "[b]raincase bones […] were unossified in all specimens" (Daly 1994: 8), *Eoherpeton* (Holmes 1984: fig. 4), *Westlothiana*, where the bone interpreted as such by Smithson et al. (1994) could just as well be e.g. a part of the otic capsules, and *Phlegethontia*, where the braincase roof is thin but fused.

Olson (1941: 162) states that a suproccipital is present in *Acheloma*, even though it is not visible in caudal view. However, we wonder if the braincase roof (ventral to the postparietals) is instead formed by a fusion of the prootics; sutures are absent throughout the braincase according to fig. 8C, and the statement that the supposed suproccipital is "joining the otics laterally" can be interpreted either way. We have therefore scored *Acheloma* as unknown.

139. EXOCC 2-3-4-5/BASOCC 1-5-6: **Basioccipital notochordal (0), occipital cotyle formed by basioccipital alone (1), occipital cotyle formed by basioccipital and (dorsal third) exoccipitals (2), occipital condyle formed the same way (3), exoccipital articulating surfaces dorsolateral to basioccipital, basioccipital cotyle articulating with interglenoid tubercle (4), basioccipital not participating in articulation or absent, exoccipital condyles not touching each other (5), two condyles or flat surfaces touching each other, "exoccipital-basioccipital complex" (6) (stepmatrix).** We have merged seven correlated characters, each of which had only one of its two states described; state 1 of each of these characters made state 1 of all six others impossible. State 0 of the present character is BASOCC 1(0); state 6 is a modification of EXOCC 2(1) and EXOCC 5(1) and occurs in *Acheloma* (Olson 1941: 162), *Phonerpeton* (Dilkes 1990), *Ecolsonia* (Berman et al. 1985), and *Doleserpeton* (Sigurdsen 2008).

OTUs known to possess an intercotylar tubercle on the atlas (CER VER 4(1)) are scored as having state 4, 5, or 6 of the present character if it is in fact unknown, because only these three states can occur in that case. The only occurrences of this are *Saxonerpeton* (made explicit by CG78: 34), *Ptyonius*, and *Gerobatrachus* (Anderson et al. 2008).

Because three and not just one states can occur, we have not merged CER VER 4 with the present character. For convenience, however, we have ignored the fact that CER VER 4(0) apparently makes state 4 of the present character impossible (a partial uncertainty of six states is probably more trouble than it is worth).

State 1 makes a surprise appearance in *Kotlassia* (Bulanov 2003: S56).

State 2 is present in *Eryops* (Sawin 1941) and *Dendrerpeton*. (The occipital cotyle of *Eryops* is dorsoventrally compressed and bilobed rather than circular, but states 5 or 6 are not reached.) It also appears to occur in *Ariekanerpeton* (Klembara & Ruta 2005a) and probably *Utegenia* (Klembara & Ruta 2004a); the same seems to hold for *Discosauriscus*, where the poorly ossified basioccipital is a caudally flat plate, but the exoccipitals appear to participate in the cotyle.

The taphonomically crushed *Tseajaia* appears to possess state 3, as far as we can tell from Moss (1972).

We have also assigned state 3 to *Captorhinus* because it has a condyle, even though no sutures can be traced in its "exoccipital-basioccipital complex".

State 5 is found in *Batropetes* (assuming the reconstruction by Carroll (1991: fig. 5) can be trusted), *Asaphestera* (as far as we can interpret CG78: fig. 6E), *Hapsidopareion* (CG78: 27, 28), and *Rhynchonkos* (CG78: fig. 65E, F). Incidentally, the fact that it is not known to occur in any temnospondyls in this matrix is a sampling artefact; state 5 is widespread or universal in stereospondyls such as *Gerrothorax* (Jenkins et al. 2008).

Interestingly, *Greererpeton* has states 1 or 2: "The components of the occipital arch are co-ossified in *Greererpeton* and the sutures between the basioccipital and exoccipitals could not be traced in any specimen" (Smithson 1982: 57f.). "The outline of the deeply concave occipital condyle is variable. For example, in CMNH 11079 it is almost circular but in CMNH 11068 it is approximately pentagonal" (Smithson 1982: 58). It does not seem to have state 0: "In a number of specimens, for example CMNH 11068 and 11090, a median groove for the notochord lies above the centre of the concavity and extends a short distance into the body of the bone." This probably falls under "notochordal pit" and not under state 0.

Oestocephalus and *Phlegethontia* lack sutures in the braincase, making it impossible to determine which bones make up their circular occipital cotyle; they are therefore scored as possessing state 1 or 2.

Gephyrostegus (Carroll 1970: 274 and fig. 5) and *Silvanerpeton* (Ruta & Clack 2006) have state 0, 1, or 2.

Entirely unknown in *Baphetes* (Beaumont 1977), apparently *Amphibamus* (Watson 1940; Carroll 1964; Daly 1994), *Caerorhachis* (Ruta et al. 2002), *Hyloplesion* (CG78), and *Orobates* (Berman et al. 2004). We have scored *Sauropleura* and *Urocordylus* the same way, although state 6 can be excluded for unspecified urocordylids (Bossy & Milner 1998: 86).

Odonterpeton appears to have state 5 or 6 (CG78: fig. 116L; see also CER VER 4 below).

Utaherpeton, which has lateral facets for the exoccipitals on the basioccipital, is scored 2 or 4 because Carroll et al. (1991) do not explicitly argue against the condition seen in *Eryops*.

Appendix-Table 3: Stepmatrix for character EXOCC 2-3-4-5/BASOCC 1-5-6.

from ↓ to →	0	1	2	3	4	5	6
0	0	1	1	2	2	3	3
1	1	0	1	2	2	3	2
2	1	1	0	1	1	2	2
3	2	2	1	0	2	3	3
4	2	2	1	2	0	1	2
5	3	3	2	3	1	0	1
6	3	2	2	3	2	1	0

140. OPI 2: **Exoccipitals contact skull roof: yes (0); no (1); separate exoccipitals and/or opisthotics absent (2) (unordered).** No sequence for ordering suggests itself. The original wording was "Opisthotic[s] forming a thickened plate together with the supraoccipital, preventing the exoccipitals from contacting the skull table: absent (0); present (1)", but whether a "plate" is present depends on PTF 1, and the present wording removes the correlation to SUPOCC 1.

Merging the present character with SUPOCC 1 is not an option, because *Archeria* (which was correctly scored as having state 1) possesses huge opisthotics that separate the postparietals from the exoccipitals, but there is just a narrow unossified slit where a cartilaginous suproccipital may have been (Holmes 1989: fig. 10A), showing that SUPOCC 1(0) and the redefined OPI 2(1) can occur together. However, the present character may have to be merged with POSPAR 5, see above.

State 2 is new and accounts for *Eusthenopteron* (Carroll & Chorn 1995), Albanerpetontidae, *Eocaecilia*, *Valdotriton*, *Oestocephalus* and *Phlegethontia*; state 0 or 2 occurs in *Odonterpeton* (CG78: 145f.) and *Notobatrachus* (Estes & Reig 1973), state 1 or 2 in *Batropetes* (Carroll 1991).

Doleserpeton has state 1 (Bolt 1969: 889; Sigurdsen 2008). So do *Tseajaia* (Moss 1972) and *Asaphestera* (CG78: 19).

State 0 occurs in *Pelodosotis* (CG78: fig. 48), apparently *Hyloplesion* (CG78: 137), and *Ariekanerpeton* (made explicit by Klembara & Ruta 2005a).

Unknown in *Eoherpeton* (Smithson 1985: fig. 5C) and *Proterogyrinus* (Holmes 1984: fig. 4).

141. PASPHE 1: **Cultriform process gradually tapering to a rostral point(0) or parallel-sided along most of its length (1).** This is a rewording of the original name of this character and its explanation; the process cannot help being "elongate", because taxa where it does not reach the vomers are not included in this matrix.

Lethiscus has state 0 (Anderson et al. 2003).

State 1 is shown by the only known albanerpetontid parasphenoid (McGowan 2002).

142. PASPHE 2: **Anterior, triangular, wedge-like, more or less distinct process immediately anterior to level of basipterygoid processes: absent (0); present (1).**

Kotlassia seems to have state 0 (Bulanov 2003: S54, fig. 30).

143. PASPHE 3: **Parasphenoid without (0) or with (1) a pair of posterolaterally orientated, ventral thickenings (ridges ending in basal tubera).**

The only known albanerpetontid parasphenoid shows state 0 (McGowan 2002).

The drawings and even the photos by Moss (1972) are not three-dimensional enough to show which state *Tseajaia* has, and the text does not mention it; we have therefore scored *Tseajaia* as unknown.

144. PASPHE 4: **Parasphenoid without elongate, broad posterolateral processes (0), or with processes that are less than (1), or at least half as wide as (2) parasphenoid plate (ordered).** We have ordered this character because it is continuous.

The only known albanerpetontid parasphenoid shows state 0 (McGowan 2002). The same state is found in *Lethiscus* (Anderson et al. 2003).

145. PASPHE 6: **Parasphenoid without (0) or with (1) single median depression.**

The only known albanerpetontid parasphenoid shows state 0 (McGowan 2002).

146. PASPHE 7: **Parasphenoid without (0) or with (1) paired lateral depressions.**

The only known albanerpetontid parasphenoid shows state 0 (McGowan 2002).

147. PASPHE 9: **Ventral cranial fissure not sutured (0); suture visible in ventral view, caudal margin of parasphenoid lying rostral to or at it (1); or parasphenoid extending caudal to suture (2) (ordered).** We have reworded this character to make clear what state 2, originally "Ventral cranial fissure […] not traceable", means in practice – fusion of the basisphenoid and the basioccipital is rare, and when it occurs, it is hardly ever determinable in a fossil, let alone described or illustrated, but the caudal extent of the parasphenoid is fairly readily observable. Because the states of this character form a sequence of progressively firmer immobilization of the ventral cranial fissure (which forms part of a joint in *Eusthenopteron* and *Panderichthys*), we have ordered the character.

Ichthyostega has state 1 (Clack 2000).

Pederpes was scored 1, but may just as well have had state 0, because the basioccipital is not preserved (Clack & Finney 2005).

Diadectes is polymorphic, having states 1 and 2 (Moss 1972), with only state 1 being documented in *D. absitus* (Berman et al. 1998).

Tseajaia has state 1 (Moss 1972: fig. 2, 4A, 15B; pl. 4; and various allusions in the text).

148. PASPHE 11: **Basipterygoid processes of the basisphenoid shaped like anterolaterally directed stalks, subtriangular to rectangular in ventral view and projecting anterior to the insertion of the cultriform process: absent (0); present (1).** This is one of the more unnerving characters: state 1 is a carefully explained combination of states of two characters (shape and position of basipterygoid processes) which may or may not correlate – no demonstration of this is attempted by RC07 or Ruta et al. (2003) –, and state 0 comprises everything else, potentially a large number of distinguishable states. More attention will have to be paid to the present character (and to its conditions of applicability) in the future. We have not deleted it from our analyses because it requires no less than two more steps under the lepospondyl hypothesis than under the temnospondyl hypothesis.

Nonetheless, *Lethiscus* shows state 1 (Anderson et al. 2003).

In *Scincosaurus* the condition is unknown (Milner & Ruta 2009).

149. PASPHE 12: **Parasphenoid without (0) or with (1) patch of denticles sitting on raised triangular area near cultriform process posterior extremity.** State 0 contains both the complete absence of denticles and their presence everywhere from the rostral tip to caudal to the basipterygoid articulations. Furthermore, there are plenty of taxa with an oval, rather than "triangular", "raised […] area near cultriform process posterior extremity" that holds a patch of denticles. It is noteworthy that there is no other character in this matrix which describes the dentition of the parasphenoid. More attention will have to be paid to the present character in the future.

Lacking denticles on the parasphenoid altogether, Albanerpetontidae (McGowan 2002) and *Tseajaia* (Moss 1972) display state 0.

150. PASPHE 13: **Parasphenoid much wider than long immediately posterior to level of basal articulation: absent (0); present (1).**

State 0 is found in Albanerpetontidae (McGowan 2002) and *Lethiscus* (Anderson et al. 2003).

151. PASPHE 14: **Ventral plate of parasphenoid (caudal to basal articulations) more or less triradiate/triangular (0), rectangular (1), or rectangular with a caudal lobe (2) (unordered).** Dividing this character into states (RC07 distinguished only two: "subrectangular" and everything else) is difficult because such a wide continuum of shapes exists (notably, state 2 includes pentaradiate conditions that can look like part of an octogon and hexaradiate shapes, and state 0 encompasses bi-, tri-, and tetraradiate shapes); this diversity of shapes is also why we have not ordered this character.

We have ignored the relatively huge fenestrae ovales for the purposes of scoring this character. This allows state 1 in *Triadobatrachus*, *Notobatrachus*, and *Vieraella* (Estes & Reig 1973: fig. 1-2). Much smaller excavations of the parasphenoid plate for the fenestrae ovales occur in *Archeria* (Holmes 1989) and the temnospondyl *Tersomius* which is not included in this matrix (Carroll 1964).

State 0: *Greererpeton*, *Crassigyrinus*, *Baphetes*, *Megalocephalus*, *Eucritta* if the reconstruction by Clack (2001) can be trusted, *Cochleosaurus* (Godfrey & Holmes 1995), *Isodectes*, *Neldasaurus*, *Balanerpeton*, *Acheloma* (Olson 1941: fig. 8), *Anthracosaurus* (Panchen 1977), *Pholiderpeton scutigerum*, *Discosauriscus*, *Seymouria*, *Captorhinus*, *Paleothyris*, *Petrolacosaurus*, *Tuditanus*, *Pantylus*, *Saxonerpeton*, *Hapsidopareion*, *Pelodosotis*, *Cardiocephalus*, *Microbrachis* (Vallin & Laurin 2004), *Adelospondylus*, *Ariekanerpeton*, *Leptoropha, Microphon* (borderline; Bulanov 2003), *Pederpes*, *Tseajaia* (Moss 1972: fig. 2), *Utegenia*.

State 1: the four OTUs mentioned above, *Panderichthys* (though the plate is very short), *Edops* (Romer & Witter 1942), *Chenoprosopus* (Langston 1953), *Eryops* (Sawin 1941), *Phonerpeton* (Dilkes 1990: fig. 1B), *Ecolsonia*, *Amphibamus* (Daly 1994: fig. 21 right side), *Doleserpeton*, *Micromelerpeton*, *Apateon*, *Leptorophus* and *Schoenfelderpeton* (Boy 1987), Albanerpetontidae (McGowan 2002), *Eoherpeton*, *Proterogyrinus, Pholiderpeton attheyi*, *Gephyrostegus*, *Micraroter, Brachydectes*, *Scincosaurus*, *Sauropleura*.

State 2: *Platyrhinops* (Clack & Milner 1993), *Karaurus*, *Valdotriton*, *Batropetes*, *Rhynchonkos*, *Diploceraspis*, *Lethiscus* (Anderson et al. 2003), *Oestocephalus* (Carroll 1998).

Trimerorhachis is polymorphic, with *T. sandovalensis* showing state 2 (Berman & Reisz 1980) but *T. insignis* (Schoch 1999) and other species (Case 1935) showing state 0.

Euryodus is likewise polymorphic, with *E. dalyae* possessing state 2 and *E. primus* displaying state 0.

Unknown: *Eusthenopteron* (inapplicable because there only are two caudal processes that are together narrower than at the basal articulation: Ahlberg et al. 1996), *Acanthostega* (inapplicable because the parasphenoid barely extends caudally beyond the basal articulation), *Ichthyostega* (inapplicable because the parasphenoid does not extend caudally beyond the basal articulation at all), *Batrachiderpeton*, *Capetus* (Sequeira & Milner 1993).

152. JAW ART 1/SQU 2: **Jaw articulation lying caudal to (0), level with (1), or rostral to occiput but with rostrodorsally to caudoventrally inclined or vertical caudolateral edge of squamosal (2), or caudolateral edge of squamosal caudodorsally to rostroventrally inclined (3) (ordered).** State 2, the previous SQU 2(1), required JAW ART 1(2), so we have merged these characters. Because the present character is continuous, we have ordered it.

RC07 commented JAW ART 1 (their character 187) as follows: “There appears to be no clear signal associated with the distribution of different character-states, even within the same clade.” Indeed, this character is somewhat labile. Still, states other than 0 occur (in the original taxon sample) only in *Eusthenopteron*, (*Acherontiscus* + Adelogyrinidae), and the seymouriamorph-diadectomorph-amniote-amphibian clade; state 2 and 3 are limited to amphibians, and state 0, otherwise very rare in the seymouriamorph-diadectomorph-amniote-amphibian clade, is unusually common in the urocordylid-aïstopod clade.

State 0 is found in *Phonerpeton* (Dilkes 1990), *Eoscopus* (Daly 1994), *Eoherpeton* (Smithson 1985), *Bruktererpeton* (Boy in Boy & Bandel 1973: pl. 7), *Gephyrostegus* (Carroll 1970: fig. 6A), *Westlothiana* (Smithson et al. 1994: text and fig. 2), *Lethiscus* (Anderson et al. 2003; contra Wellstead 1982: fig. 5B), and *Oestocephalus* (Carroll 1998).

Tseajaia has state 1 (Moss 1972: fig. 2; Berman et al. 1992: fig. 9).

Keraterpeton (Bossy & Milner 1998: fig. 57A, 78) shows state 2. So does even the largest known skull of *Orobates* (Berman et al. 2004: fig. 8A).

State 3 occurs in Albanerpetontidae, *Karaurus*, *Valdotriton*, *Diceratosaurus*, and *Scincosaurus*.

Batrachiderpeton, Diplocaulus and *Diploceraspis* possess state 2 or 3.

Urocordylus has state 0, 1, or 2.

The condition is entirely unknown in *Dolichopareias* (Andrews & Carroll 1991) and *Phlegethontia*, where it cannot be determined due to the unique shape of the squamosal (Anderson 2002).

Many taxa go from a higher to a lower state in ontogeny. Accordingly, we have scored *Trimerorhachis* and *Isodectes* as having state 0 or 1 because the trimerorhachoids show evidence of paedomorphosis throughout the skeleton and *Schoenfelderpeton* as possessing state 0, 1, or 2 (instead of just the observed 2). *Micromelerpeton* (Boy 1995) and *Apateon* (Schoch & Fröbisch 2006) are scored 0 based on the most mature specimens. *Leptoropha* and *Microphon* are scored as unknown because the halfway complete skull roofs known of them do not come from adult individuals (Bulanov 2003).

Gerobatrachus has state 0 or 1 based on the different possibilities for where the occiput could have been in life.

Eothyris is scored as possessing state 2 based on fig. 2 of Reisz et al. (2009), contradicting their text.

153. PSYM 1: **Parasymphysial plate: present (0); absent (1).**

154. PSYM 2: **Parasymphysial plate without (0) or with (1) paired fangs, comparable in size with or greater than dentary teeth.**

RC07 cite Ahlberg & Clack (1998) as saying that *Megalocephalus* has state 1, but Milner & Lindsay (1998: 220) state that it has state 0 and cite a pers. comm. by Ahlberg & Clack. We have accordingly changed the score of *Megalocephalus* to 0.

155. PSYM 3: **Parasymphysial plate without (0) or with (1) anteroposterior tooth row oriented subparallel to marginal dentary teeth and the basal diameter and/or height of which [= of the teeth in the parasymphysial toothrow] is 30 % or greater than that of marginal teeth and twice or more that of denticles, if present.**

156. PSYM 4: **Parasymphysial plate with (0) or without (1) small teeth (denticles) forming continuous shagreen or discrete patches and the basal diameter and/or height of which is less than 30% of that of adjacent marginal dentary teeth.**

DEN 1: **Dentary with (0) or without (1) accessory tooth rows.** According to RC07, state 0 occurs in *Captorhinus* and *Pantylus*. In fact, *Pantylus* has a single toothrow on the dentary – the additional toothrows of the lower jaw all lie on a coronoid (Williston 1916: fig. 27; CG78: fig. 25 bottom middle, 25 bottom right, and 114C). This makes the character parsimony-uninformative, so we have deleted it. For the sake of completeness, we would further like to mention that state 0 is limited to one of the three species of *Captorhinus* and not plesiomorphic for the genus as a whole (Kissel et al. 2002).

157. DEN 2: **Dentary with (0) or without (1) anterior fangs generally comparable in size with, or greater than, other dentary teeth and lying close to symphysial region and usually lingual to marginal dentary teeth.** Instead of "lingual", RC07 had "mesial" (and probably meant "medial").

Baphetes has state 0 (Milner & Lindsay 1998; Milner et al. 2009).

Scincosaurus shows state 1 (Milner & Ruta 2009).

In *Leptoropha* the condition is unknown (Bulanov 2003).

158. DEN 3: **Dentary with (1) or without (0) 'chamfered' margin.**

State 0 is, unsurprisingly, documented in *Scincosaurus* (Milner & Ruta 2009).

159. DEN 4: **Dentary without (0) or with (1) U-shaped notch for premaxillary tusks.**

Karaurus has state 0 (DM, pers. obs. of cast housed in MNHN).

160. DEN 7: **Dentary toothed (0) or toothless (1).**

State 0 is documented in *Scincosaurus* (Milner & Ruta 2009).

DEN 8: **Dentary length greater (0) or smaller (1) than half of distance between snout and occiput.** According to RC07, state 1 is present in *Batropetes* and *Brachydectes*. However, the condition of *Batropetes* is in fact unknown (Carroll 1991). This makes the character parsimony-uninformative. Additionally, it probably requires JAW ART 1/SQU 2(3). We have deleted it.

161. SPL 2: **Posteriormost extension of splenial me[d]ial lamina closer to anterior margin of adductor fossa than to anterior extremity of jaw, when the lower jaw ramus is observed in me[d]ial aspect and in anatomical connection (i.e. symphysial region orientated towards the observer): absent (0); present (1).** We follow RC07 in homologizing the single splenial of amniotes with the presplenial and not the postsplenial, though we are not aware of any evidence for or against this. The only exception is the condition of *Petrolacosaurus*, which was reported to be the only amniote to possess a (uniquely small) postsplenial (Reisz 1981); following a pers. comm. by Reisz, we have kept POSPL 1(0) for *Petrolacosaurus*, but we still wonder if the supposed postsplenial might actually be a fragment of the angular instead.

Whatcheeria has state 1 (Lombard & Bolt 2006).

Unknown in all lissamphibians, because there is no evidence for a splenial in any of them. (The occasional reports from caecilian ontogeny in fact refer to a coronoid: Müller et al. 2005; Müller 2006.)

162. SPL 3: **Splenial/anterior coronoid suture: absent (0); present (1).**

Whatcheeria has state 1 (Lombard & Bolt 2006).

163. SPL 4: **Splenial/middle coronoid suture: absent (0); present (1).** According to RC07, there is "no clear phylogenetic pattern" in the distribution of the states of this character. This is, however, difficult to evalue given the fact that this character is scored as unknown for most OTUs. It has only seven steps in the most parsimonious trees for the original taxon sample; state 1 keeps the baphetoids (only known in *Megalocephalus*), the anthracosaurs, *Gephyrostegus*, the seymouriamorphs, and the crown group together, while one of the reversals to state 0 was inherited by a temnospondyl clade that contains *Ecolsonia* and Amphibamidae but not Trematopidae (or at least *Phonerpeton*).

Whatcheeria has state 0 (Lombard & Bolt 2006).

Tseajaia shows state 1 (Moss 1972: 19).

164. POSPL 1: **Separately ossified postsplenial: present (0); absent (1).**

165. POSPL 2: **Postsplenial without (0) or with (1) me[d]ial lamina.**
Whatcheeria has state 0 (Lombard & Bolt 2006).

166. POSPL 3: **Postsplenial with (0) or without (1) pit line.**

167. ANG 1: **Separately ossified angular: present (0); absent (1).**
State 0 is known in *Baphetes* (Milner et al. 2009) and *Lethiscus* (Anderson et al. 2003)
State 1 is found in Albanerpetontidae (Estes & Hoffstetter 1976; Venczel & Gardner 2005).

168. ANG 2: **Angular without (0) or with (1) me[d]ial lamina.**
Whatcheeria has state 0 (Lombard & Bolt 2006).
Inapplicable in Albanerpetontidae, see ANG 1.

ANG 3: **Angular/prearticular suture: present (0); absent (1).** As RC07 stated, state 1 is limited to *Acanthostega* in the present data matrix; the character is therefore parsimony-uninformative, and we have deleted it.

169. ANG 4: **Angular not reaching (0) or reaching (1) lower jaw posterior end.**
Baphetes has state 0 (Milner et al. 2009).
The condition of *Westlothiana* is probably not known, judging from the specimen drawings in Smithson et al. (1994).

170. SURANG 1: **Separately ossified surangular: present (0); absent (1).**
State 0 is documented in *Whatcheeria* (Lombard & Bolt 2006), *Baphetes* (Milner et al. 2009), and *Lethiscus* (Anderson et al. 2003).

171. SURANG 3: **Surangular with (0) or without (1) pit line.**
Whatcheeria has state 1 (Lombard & Bolt 2006), as does *Baphetes* (Milner et al. 2009).
Unknown in *Westlothiana* where the surface of the bone is unknown (Smithson et al. 1994).

172. SURANG 5: **Surangular lateral exposure much smaller than angular lateral exposure: no (0); yes (1).** We have not investigated a possible correlation with ANG 4.
Whatcheeria has state 0 (Lombard & Bolt 2006), as do *Baphetes* (Milner et al. 2009) and *Lethiscus* (Anderson et al. 2003).
Following the illustrations by Berman et al. (2004) against the text, we have also scored *Orobates* as possessing state 0.

173. PREART 5: **Prearticular/splenial suture: present (0); absent (1).**

174. ANT COR 1: **Separately ossified anterior coronoid: present (0); absent (1).**
Unknown in *Orobates* (Berman et al. 2004).

175. ANT COR 2: **Anterior coronoid with (0) or without (1) fangs comparable in size to or larger than marginal dentary teeth.**

176. ANT COR 3: **Anterior coronoid with (0) or without (1) small teeth (denticles) forming continuous shagreen or discrete patches and the basal diameter and/or height of which is less than 30% of that of adjacent marginal dentary teeth.**
Whatcheeria has state 1 (Lombard & Bolt 2006).

177. ANT COR 4: **Anterior coronoid with (0) or without (1) anteroposterior tooth row orientated subparallel to marginal dentary teeth and the basal diameter and/or height of which is 30% greater than that of marginal teeth and twice or more that of denticles, if present.**

178. MID COR 1: **Separately ossified middle coronoid: present (0); absent (1).**
Baphetes has state 0 (Milner et al. 2009).
Unknown in *Orobates* (Berman et al. 2004).

179. MID COR 2: **Middle coronoid with (0) or without (1) fangs comparable in size to or larger than marginal dentary teeth.**

180. MID COR 3: **Middle coronoid with (0) or without (1) small teeth (denticles) forming continuous shagreen or discrete patches and the basal diameter and/or height of which is less than 30% of that of adjacent marginal dentary teeth.**

Baphetes has state 0 (Milner et al. 2009).

181. MID COR 4: **Middle coronoid with (0) or without (1) anteroposterior tooth row orientated subparallel to marginal dentary teeth and the basal diameter and/or height of which is 30% greater than that of marginal teeth and twice or more that of denticles, if present.**

182. POST COR 1: **Separately ossified posterior coronoid: present (0); absent (1).**

Baphetes has state 0 (Milner et al. 2009).

It is not clear which coronoid(s) is/are preserved in the Goreville microsaur (Lombard & Bolt 1999), but the posterior one is probably the safest bet because it is the most common one.

183. POST COR 2: **Posterior coronoid with (0) or without (1) fangs comparable in size to or larger than marginal dentary teeth.**

Whatcheeria has state 1 (Lombard & Bolt 2006).

184. POST COR 3: **Posterior coronoid with (0) or without (1) small teeth (denticles) forming continuous shagreen or discrete patches and the basal diameter and/or height of which is less than 30% of that of adjacent marginal dentary teeth.**

Baphetes has state 0 (Milner et al. 2009).

Diadectes shows state 1 (Berman et al. 1998: fig. 11).

185. POST COR 4: **Posterior coronoid with (0) or without (1) anteroposterior tooth row orientated subparallel to marginal dentary teeth and the basal diameter and/or height of which is 30% or greater than that of marginal teeth and twice or more that of denticles, if present.**

186. POST COR 5-7: **Posterior coronoid without posterodorsal process (0); with a process that does not contribute to the tallest point of lateral margin of adductor fossa (1); or with a process that does (2) (ordered).** This is a continuous character (gradual enlargement of the posterodorsal process).

Whatcheeria has state 2 (Lombard & Bolt 2006).

187. POST COR 6: **Posterior coronoid exposed in lateral view: no (0); yes (1).**

Baphetes has state 0 (Milner et al. 2009).

188. ADD FOS 1: **Adductor fossa facing dorsally (0) or me[d]ially (1).**

Baphetes has state 1 (Milner et al. 2009).

State 1 is found in *Eocaecilia* (Jenkins et al. 2007).

189. TEETH 1: **Marginal tooth pedicely at any point in ontogeny: absent (0); present (1).** This character is usually difficult to score in small animals unless sections and electron micrographs are done – or unless the tooth crowns have fallen off post mortem, leaving the pedicels in place (a very common occurrence in lissamphibian fossils). Most OTUs that are potentially relevant to lissamphibian origins remain to be investigated.

We have added the specification about ontogeny because pedicely often appears or disappears in lissamphibian ontogeny.

Apateon and *Schoenfelderpeton* were scored as unknown, but the only published report of pedicely in any branchiosaurid specimen (*Apateon*: Schoch & Carroll 2003) looks very much like a preservational artefact to us. We have therefore scored both taxa as having state 0.

Carroll (1998: fig. 4B, 8A) illustrates a dentary and maxillae of *Oestocephalus* where many teeth appear to be broken at the same level, as if the crowns had fallen off of pedicels, and mentions this similarity on p. 158. We have scored *Oestocephalus* as unknown.

Germain (2008b) cautiously suggests on the basis of electron micrographs that the teeth of *Phlegethontia* could be pedicellate. We have therefore scored it as unknown.

Anderson et al. (2008) report pedicely in *Gerobatrachus*. However, as pointed out previously (Marjanović & Laurin 2008), the resolution of the photo (fig. 3a) is too low to tell, and not one of the teeth is preserved as a lone pedicel – there are only complete teeth and empty alveoli. Given that we have not seen the specimen (the forthcoming detailed description by Anderson et al. will doubtless provide additional information) and that the single known specimen of *Gerobatrachus* does not provide ontogenetic information, we have scored it as unknown, even though pedicellate teeth are expected in a derived amphibamid. (They are indeed present, as scored by RC07, in *Amphibamus* and *Doleserpeton*; for the latter, see Bolt [1991: fig. 4]).

190. TEETH 3: **Maximum number of labiolingually arranged cusps per tooth at any point in ontogeny: one cusp (0); a ridge (1); two or three separate cusps (2) (ordered).** We have ordered this partially meristic, partially continuous character.

The original wording was: "Marginal teeth without (0) or with (1) two cuspules labiolingually arranged." RC07 go on to state that the mesiodistally arranged cusps of *Batropetes* and Albanerpetontidae "cannot be treated as an alternative state, as they are not readily comparable". The two OTUs in question were scored 0. We do not understand why this condition was not treated as a third state of the same character (as done by Marjanović & Laurin 2008); however, given the diversity of cusp arrangements among the OTUs of this matrix (especially the OTUs we have added), we have instead split this character, treating the number of labiolingually (TEETH 3) and mesiodistally arranged cusps (the new character TEETH 10) separately. Taxa that have two or more cusps in both directions do not occur in this matrix, but exist – "HOMO *noſce Te ipsum*" ("human, learn to known yourself"; Linnaeus 1758, capitals and italics in the original).

Leptorophus has state 0 (Boy 1986, 1987).

State 1 occurs in *Broiliellus* according to Bolt (1977). We have accepted this, but it is possible that the specimen Bolt described is misattributed – Carroll (1964) reports state 0 for *Broiliellus*. State 1 is further found in *Cardiocephalus* (Anderson & Reisz 2003; Anderson 2007); as Anderson & Reisz (2003) point out, this state may be much more widespread but overlooked.

State 2 is found in *Platyrhinops* (Clack & Milner 1993), *Amphibamus* (Daly 1994), *Doleserpeton* (Bolt 1969, 1977, 1991), *Eocaecilia* (Jenkins et al. 2007), and *Notobatrachus* (Estes & Reig 1973), *Diadectes* (which has three cusps in a labiolingual row: Berman et al. 2004) and *Orobates* (Berman et al. 2004).

Unknown in *Karaurus* (DM, pers obs. of cast housed in MNHN) and *Pederpes* (Clack & Finney 2005: 322).

191. TEETH 4: **Conspicuous peak involving one or more anterior maxillary teeth: absent (0); present (1).**

Chenoprosopus has state 1 (Hook 1993); unlike *Cochleosaurus* (Godfrey & Holmes 1995), it has a caniniform region on the maxilla, not only on the premaxilla.

Acheloma shows state 1 (Dilkes & Reisz 1987: fig. 3), as does *Phonerpeton* (Dilkes 1990: fig. 1).

Germain (2008a) erroneously assigned state 1 to *Broiliellus* and *Leptorophus*. Both were scored 0 by RC07, and this is correct (Carroll 1964; Boy 1987).

Bruktererpeton has an admittedly weak version of state 1 (Boy in Boy & Bandel 1973).

Cardiocephalus has state 0 (CG78).

Euryodus is polymorphic; whether the caniniform tooth of one of the two species counts as "anterior" is debatable, but the number of maxillary teeth rostral to it is low.

Scincosaurus is unknown for this character (Milner & Ruta 2009).

Lethiscus has state 0 (Anderson et al. 2003).

We have assigned state 0 to *Nigerpeton* because its huge maxillary tusks are not part of the marginal toothrow and therefore likely not homologous to any part of it.

192. TEETH 5: **Dentary teeth larger than maxillary teeth: no (0); yes (1).**

We have scored *Crassigyrinus* as having state 1 because almost all dentary teeth are larger than all maxillary ones (Clack 1998).

Dendrerpeton is polymorphic, because *D. acadianum* has state 1 at least sometimes (compare Carroll 1967 to Godfrey et al. 1987).

In *Neldasaurus,* only 1/3 to ½ of its dentary teeth are larger than the maxillary teeth (Chase 1965: fig. 2, 6), but we count this as state 1 because the larger teeth do not form a specialized caniniform (or other) region.

Trimerorhachis has state 1 (Case 1935: fig. 13, pl. VII).

State 0 is mentioned for *Bruktererpeton* in table 7 of Boy in Boy & Bandel (1973).

We count *Caerorhachis* as having state 1, even though not all dentary teeth are larger than all maxillary teeth (Ruta et al. 2002).

State 0 is present in *Scincosaurus* (from comparing fig. 2A and fig. 4 of Milner & Ruta 2009).

Orobates was scored polymorphic, presumably due to its long incisiform dentary teeth that are longer than the maxillary teeth. We exclude incisiform teeth (a very rare specialization in this matrix) from consideration and therefore score *Orobates* as possessing only state 0.

193. TEETH 6: **Marginal tooth crowns chisel-tipped: no (0); yes (1).**

194. TEETH 7: **Marginal tooth crowns without (0) or with (1) 'dimple'.**

195. TEETH 8: **Marginal tooth crowns robust and conical: absent (0); present (1).**

Karaurus has state 0 (DM, pers. obs. of cast housed in MNHN).

196. TEETH 9: **Number of maxillary teeth greater than 40 (0), between 30 and 40 (1), smaller than 30 (2) (ordered).** As this is a meristic (practically continuous) character, we have ordered it. Indeed, changes between states 0 and 2 are much rarer in our results than changes between 0 and 1 or 1 and 2. Note also that RC07 ascribe "little phylogenetic signal" to this character, when in fact the distribution of the states is nowhere near random; 25 steps for 102 taxa (under both the lepospondyl and the temnospondyl hypothesis) is a relatively high number for characters in this matrix, but phylogenetic signal is clearly present: states 1 and 2 are rare in temnospondyls, while almost all members of the seymouriamorph-diadectomorph-amniote-amphibian clade have state 2.

Bruktererpeton has "ca. 40 teeth" in the maxilla, giving it state 0 or 1 (my translation of Boy in Boy & Bandel 1973: 50).

Similarly, *Lethiscus* has state 0 or 1 (Anderson et al. 2003).

State 2 is found in *Leptoropha* (Bulanov 2003).

197. TEETH 10: **Maximum number of mesiodistally arranged cusps per marginal tooth at any point in ontogeny: 1 (0), diamond-shaped crown with mesial and distal ridges that lead to the mesial and distal corners or very short cusps (1), 3 (2), more (3) (ordered).** This character is ordered for the same reasons as TEETH 3.

State 0 is the plesiomorphy, found in all OTUs that preserve tooth crowns except for the following:

State 1 is found in *Discosauriscus* (at least in the tooth in the third alveolus in fig. 10 of Klembara 1997) and *Scincosaurus* (Milner & Ruta 2009).

State 2 occurs in *Batropetes* (Carroll 1991) and *Tungussogyrinus* (Werneburg 2009).

State 3 is limited to *Leptoropha* and *Microphon* (Bulanov 2003) in the present matrix.

Albanerpetontidae is polymorphic, with *Anoualerpeton* possessing state 1 (Gardner et al. 2003) and its sister-group, composed of *Celtedens* and *Albanerpeton*, showing state 2 (e.g. Estes & Hoffstetter 1976; Fox & Naylor 1982; McGowan 2002).

We have assigned state 0 to *Saharastega*, where the tooth tips are unknown but there is no space for multiple cusps unless they were extremely narrow.

198. CLE 1: **T-shaped dorsal expansion of cleithrum: absent (0); present (1).**

State 0 is known in *Baphetes* (Milner & Lindsay 1998) and *Caerorhachis* (after *Casineria*; Paton et al. 1999).

199. CLE 2: **Cleithrum with (0) or without (1) postbranchial lamina.** Probably unlike RC07, we count everything that is primarily homologous to a postbranchial lamina as state 1; this includes laminae that may have the wrong size or shape to function as a postbranchial lamina, so we do not hypothesize on which of the taxa we have scored 0 actually possessed internal gills in life. What sizes and shapes are possible for a functional postbranchial lamina has not, to the best of our limited knowledge, ever been investigated. Indeed, cleithra of limbed vertebrates are almost never illustrated or described in cranial or caudal view (the postbranchial lamina is impossible to see in lateral view, and difficult or impossible to recognize in medial view); sometimes, like in the description of the postcranium of *Greerpeton* by Godfrey (1989), it has been illustrated but not recognized (as previously noticed by Coates 1996). We suspect therefore that state 0 is more widespread than we have been able to score.

Under our possibly expanded definition, state 0 is present in *Ventastega* (Ahlberg et al. 2008: fig. 2b, 3e – contradicting the text which probably uses a stricter definition), *Baphetes* (Milner & Lindsay 1998; Milner et al. 2009), and *Archeria* (Pawley 2006; compare the conditions of *Ichthyostega* [Jarvik 1996: pl. 45] and *Greererpeton* [Godfrey 1989: fig. 17b], which were already scored 0).

We have kept state 1 for *Ossinodus*, which has a candidate lamina, because Warren & Turner (2004) identify that lamina as the sutural surface for the clavicle. State 1 is also preserved in *Caerorhachis* or at least *Casineria* (Paton et al. 1999).

Unknown (or at least not sufficiently well illustrated and described) in *Proterogyrinus* (Holmes 1984), *Pholiderpeton scutigerum* (Clack 1987b), *Bruktererpeton* (Boy in Boy & Bandel 1973), *Gephyrostegus* (Carroll 1970), *Adelogyrinus* (Andrews & Carroll 1991: 252), and *Pederpes* – the cross-section shown in fig. 11A, B of Clack & Finney (2005) could be in dorsal or ventral view and is not identified as either. (The text does state a postbranchial lamina is absent, but this may refer to a stricter definition.)

200. CLE 3: **Cleithrum co-ossified with scapulocoracoid: yes (0); no (1).**

Baphetes has state 1 (Milner & Lindsay 1998; Milner et al. 2009), as does *Caerorhachis* (after *Casineria*; Paton et al. 1999).

Inapplicable to *Karaurus* which lacks cleithra entirely.

201. CLA 3: **Clavicles meet anteriorly: yes (0); no (1).**

State 0 occurs in *Diadectes* (Case 1911: 79, fig. 26) and *Orobates* (Berman et al. 2004: fig. 2B).

Baphetes has state 1 (Milner & Lindsay 1998).

202. INTCLA 1: **Interclavicle posterior margin not drawn out into parasternal process (0), with parasternal process that is not parallel-sided (1), or with elongate, slender process that is parallel-sided for most of its length (2) (unordered).** For the time being, we have not ordered this character because we have yet to compare the data on its changes in ontogeny and phylogeny.

Baphetes has state 1 (Clack 2001; Milner et al. 2009: 326).

Tseajaia shows state 2 (Moss 1972); the process has a unique club-shaped expansion at the caudal end, but is otherwise parallel-sided.

203. INTCLA 3: **Interclavicle wider than long (excluding parasternal process, if present): absent (0); present (1).**

Baphetes has state 0 (Milner et al. 2009: 326; Clack 2001).

We have scored *Schoenfelderpeton* as unknown due to its strong paedomorphosis.

Bruktererpeton has state 0 (Boy in Boy & Bandel 1973: fig. 10).

204. INTCLA 4: **Interclavicle rhomboidal with posterior part longer (0) or shorter (1) than anterior part.**

Baphetes has state 0 (Milner et al. 2009: 326; Clack 2001).

205. INTCLA 5: **Transversely elongate grooves and ridges on central part of interclavicle ventral surface: absent (0); present (1).**

206. SCACOR 1: **Separate scapular ossification: absent (0); present (1).** As previously pointed out (e.g. Marjanović & Laurin 2008: 185), ontogenetic fusion makes this character difficult to interpret. Also, the taxon sample is perhaps somewhat unfortunate – the two salamanders in this matrix, *Karaurus* and *Valdotriton*, both have state 0, but *Kokartus*, a close relative of *Karaurus*, shows state 1 in an apparently immature specimen (Averianov et al. 2008: 480, fig. 7B), as do adults of the extant paedomorphic salamanders *Amphiuma* and *Siren* (Goodrich 1930).

Nonetheless, we have scored *Platyrhinops* (implied by Carroll 1964) and *Micromelerpeton* (implied by Boy 1995: 444) as possessing state 0.

In contrast, we have not been able to find any mention of the endochondral shoulder girdle of *Amphibamus* in the literature (Carroll's [1964] "*Amphibamus lyelli*" is *Platyrhinops*) and have therefore scored it as unknown.

Eocaecilia shows state 1 (Jenkins et al. 2007).

Where known (*Celtedens*: McGowan 2002), albanerpetontids have state 1.

Caerorhachis likewise shows state 1 (after *Casineria*; Paton et al. 1999).

In *Bruktererpeton* the condition is unknown because the coracoid region is entirely unossified (Boy in Boy & Bandel 1973).

Captorhinus is well known to have state 1.

207. SCACOR 2: **Glenoid subterminal: yes (0); no (1).**

We have scored *Ossinodus* (Warren & Turner 2004: fig. 9I) and *Greererpeton* (Godfrey 1989) as unknown due to lack of ossification or preservation; indeed, *Ossinodus* preserves more bone ventral to the glenoid than the very well ossified *Pantylus* has.

State 1 is found in *Eocaecilia* (Jenkins et al. 2007), Albanerpetontidae (McGowan 2002), *Caerorhachis* (*Casineria*; Paton et al. 1999), and *Scincosaurus* (Milner et al. 2009).

208. SCACOR 3: **Enlarged [supra]glenoid foramen: absent (0); present (1).** "Loss of an enlarged glenoid foramen occurs sporadically and does not show any clear phylogenetic signal" (RC07) – this is because reversals to state 0 happened only once (lepospondyl hypothesis) or twice (temnospondyl hypothesis) in isolated OTUs, while state 1 is, in stark contrast, autapomorphic of a large clade of amphibians. On some topologies, this character has only four steps.

Unfortunately, RC07 did not define "enlarged"; we have therefore kept state 0 for the large-looking supraglenoid foramen of *Ossinodus* (Warren & Turner 2004).

Eocaecilia, however, clearly has state 0 (Jenkins et al. 2007).

209. SCACOR 4: **Ventrome[d]ially extended infraglenoid buttress: absent (0); present (1).**

State 1 occurs in *Eocaecilia* (Jenkins et al. 2007) and *Westlothiana* (Smithson et al. 1994: 392).

210. ANOCLE 1: **Anocleithrum: present (0); absent (1).**

Complete articulated skeletons of *Celtedens*, with the even scales in place, demonstrate state 1 for Albanerpetontidae (McGowan 2002).

Casineria, and thus *Caerorhachis*, likewise has state 1 (Paton et al. 1999).

The dorsal end of the cleithrum of *Tseajaia* is known and lacks a contact surface for an anocleithrum, so we have taken the absence of a preserved anocleithrum at face value and scored *Tseajaia* as possessing state 1.

211. HUM 1: **Latissimus dorsi process offset anteriorly relative to the ectepicondyle (0) or aligned with the latter (1).**

State 1 appears to occur in *Karaurus* (DM, pers. obs. of cast housed in MNHN).

212. HUM 2: **Distinct supinator process projecting anteriorly: absent (0); present (1).**

State 0 occurs in *Baphetes* (Milner & Lindsay 1998), *Doleserpeton* (Sigurdsen & Bolt 2009), and *Eocaecilia* (Jenkins et al. 2007).

213. HUM 3: **Sharp-edged, ventral humeral ridge: present (0); absent (1).**

State 0 is known from *Tulerpeton* and *Eoherpeton* (Milner & Lindsay 1998).

Doleserpeton (Sigurdsen & Bolt 2009), *Eocaecilia* (Jenkins et al. 2007), Albanerpetontidae (McGowan 2002), and *Tseajaia* (Moss 1972: fig. 9A) have state 1.

214. HUM 4: **Latissimus dorsi process confluent with (0) or distinct from (1) deltopectoral crest.**

215. HUM 5: **Entepicondyle foramen: present (0); absent (1).**

Caerorhachis has state 0 (after *Casineria*; Paton et al. 1999).

Unknown, or at least neither described nor illustrated, in *Orobates* (Berman et al. 2004).

216. HUM 6: **Ectepicondyle foramen: present (0); absent (1).**

Scincosaurus has state 1 (Milner & Ruta 2009), as does *Caerorhachis* (after *Casineria*; Paton et al. 1999).

Unknown, or at least neither described nor illustrated, in *Orobates* (Berman et al. 2004).

217. HUM 7-9: **Distal extremity of ectepicondyle ridge: aligned with ulnar articulation (0); between ulnar articulation and radial condyle (1); aligned with radial condyle (2); ectepicondyle ridge absent (1) (stepmatrix).** This character uses the same stepmatrix as PIN FOR 2, for the same reasons. We have merged HUM 7 (presence/absence of the ridge) and HUM 9 (position of its distal end) because HUM 9 was the only character left that required HUM 7(1) now that HUM 8 is deleted (see below). We use the term “ulnar articulation” instead of “ulnar condyle” because the articular surface for the ulna on the humerus is a trochlea rather than a condyle in most OTUs of this matrix (see Sigurdsen & Bolt 2009).

Eocaecilia has state 3 (Jenkins et al. 2007).

HUM 8: **Ectepicondyle ridge reaching distal humeral end: no (0); yes (1).** State 0 was scored for *Eusthenopteron*, *Notobatrachus*, and *Vieraella* – but the latter two lack the ectepicondyle ridge in the first place, so they have to be scored as unknown, which limits state 0 to *Eusthenopteron* and thus makes the character uninformative. We have accordingly deleted it.

218. HUM 10: **Humerus without (0) or with (1) waisted shaft.**

Caerorhachis has state 1 (after *Casineria*; Paton et al. 1999).

219. HUM 11: **Position of radial condyle: terminal (0); ventral (1).**

State 1 is now documented in *Doleserpeton* (Sigurdsen & Bolt 2009), *Eocaecilia* (Jenkins et al. 2007), *Westlothiana* (Smithson et al. 1994: fig. 12), and apparently *Orobates* (Berman et al. 2004).

220. HUM 12: **Humerus slender and elongate, its length being more than three times the maximum width of its distal end: absent (0); present (1).**

Caerorhachis has state 0 (after *Casineria*; Paton et al. 1999).

221. HUM 13: **Posterolateral margin of entepicondyle lying distal relative to plane of radial and ulnar facets: yes (0); no (1).**

State 1 is found in *Karaurus* (DM, pers. obs. of cast housed in MNHN).

222. HUM 14: **Posterolateral margin of the entepicondyle markedly concave: yes (0); no (1).**

Karaurus (DM, pers. obs. of cast housed in MNHN) and *Caerorhachis* (after *Casineria*; Paton et al. 1999) have state 1.

223. HUM 15: **Width of entepicondyle greater (0) or smaller (1) than half humerus length.**

Baphetes (Milner & Lindsay 1998), *Karaurus* (DM, pers. obs. of cast housed in MNHN), *Caerorhachis* (as *Casineria*; Paton et al. 1999), *Diadectes* (Case 1911: fig. 28), *Orobates* (Berman et al. 2004), and *Tseajaia* (Moss 1972: 32) have state 1.

224. HUM 16: **Portion of humerus shaft length proximal to entepicondyle smaller (0) or greater (1) than humerus head width.**

Baphetes shows state 1 (Milner & Lindsay 1998), as do *Karaurus* (DM, pers. obs. of cast housed in MNHN) and *Caerorhachis* (after *Casineria*; Paton et al. 1999).

Unknown in *Scincosaurus* (Milner & Ruta 2009).

225. HUM 17: **Accessory foramina on humerus: present (0); absent (1).**

226. HUM 18: **Humerus length smaller (0) or greater (1) than combined length of two and a half mid-trunk vertebrae.** RC07 had exchanged the states in the text but not in the matrix, except maybe for the taxa they added (all of the following except *Baphetes*, which was scored as unknown):

State 1 is found in *Baphetes* (Milner & Lindsay 1998 – the longest intercentrum is 22 mm long, the humerus somewhere around 85; this should ensure state 1 even if the vertebrae were very rhachitomous), *Caerorhachis* (after *Casineria*; Paton et al. 1999), *Notobatrachus* and *Vieraella* (Estes & Reig 1973), *Orobates* (Berman et al. 2004: fig. 1), *Pederpes* (Clack & Finney 2005), *Silvanerpeton* (Ruta & Clack 2006), and *Tseajaia* (Moss 1972: pl. 2).

Utaherpeton changes from state 1 to state 0 in ontogeny (Carroll & Chorn 1995: table 1). We have only considered the adult condition.

227. HUM 19: **Process ‘2’ on humerus: absent (0); present (1).**

Caerorhachis, or anyway *Casineria*, has state 0 (Paton et al. 1999).

228. RAD 1: **Radius longer (0) or shorter (1) than humerus.**

Baphetes has state 1 (Milner & Lindsay 1998), as do *Doleserpeton* (Sigurdsen & Bolt 2009) and *Caerorhachis* (after *Casineria*; Paton et al. 1999).

229. RAD 2: **Radius longer than (0), as long as (1), or shorter than (2) ulna (ordered).** This is a continuous character.

State 1 is found in *Eocaecilia* (Jenkins et al. 2007) and Albanerpetontidae (McGowan 2002).

Caerorhachis is given state 2 after *Casineria* (Paton et al. 1999).

230. RAD 3: **Compound radio-ulna: absent (0); present (1).**

Baphetes is known to have state 0 (Milner & Lindsay 1998).

231. ULNA 1: **Olecranon process: absent (0); present (1).**

Eocaecilia has state 1 (Jenkins et al. 2007).

Unknown in *Doleserpeton* (Sigurdsen & Bolt 2009).

232. ILI 3: **Dorsal iliac process: absent (0); present (1).**

233. ILI 4: **Posterior iliac process subhorizontal, stout, abbreviated posteriorly and tapering rearward in lateral aspect: absent (0); present (1).** It will have to be investigated how much diversity is hiding inside state 0. To define state 1, at least three of the four statements on size and shape will have to be quantified.

234. ILI 6: **Supr[…]acetabular iliac buttress less (0) or more (1) prominent than postacetabular buttress.**

235. ILI 7: **Transverse pelvic ridge: absent (0); present (1).**

236. ILI 9: **Ilium shaped like an elongate rod directed anteriorly/anterodorsally: absent (0); present (1).**

Tungussogyrinus has an intermediate condition that we count as state 1, following Werneburg (2009).

ILI 10: **Acetabulum directed posteriorly/posterolaterally (0) or laterally (1).** As RC07 point out, this character is parsimony-uninformative, so we have deleted it.

ISC 1: **Ischium contributing to pelvic symphysis: no (0); yes (1).** As RC07 point out, this character is parsimony-uninformative, so we have deleted it.

237. PUB 1: **Number of pubic obturator foramina: multiple (0), single (1), or absent (2) (ordered).** We have ordered this meristic character.

238. FEM 1: **Internal trochanter raised as a distinct protuberance: absent (0); present (1).**

239. FEM 2: **Internal trochanter separated from the general surface of the femur shaft by a distinct, trough-like space: absent (0); present (1).**

240. FEM 3: **Fourth trochanter of femur with distinct rugose area: no (0); yes (1).**

241. FEM 4: **Proximal end of femur adductor crest reaching midshaft length: no (0); yes (1).**

Diadectes has state 1 (Case 1911: fig. 30a; Berman et al. 1998: fig. 18A).

So does *Orobates* (Berman et al. 2004).

242. FEM 5: **Femur shorter than (0), as long as (1), or longer than humerus (2) (ordered).** This is a continuous character.

Caerorhachis is scored 2 after *Casineria* (Paton et al. 1999).

243. FEM 6: **Internal trochanter of femur shaped like a flat, triangular, acuminate process: absent (0); present (1).**

244. TIB 6: **Outline of tibia medial margin shaped like a distinct, subsemicircular embayment contributing to interepipodial space and the diameter of which is less than one-third of bone length: absent (0); present (1).**

Since almost any condition is by definition state 0, it is not surprising that state 0 is known to occur in Albanerpetontidae (McGowan 2002) and *Karaurus* (Ivachnenko 1978; pers. obs. of cast housed in MNHN).

245. TIB 7: **Tibia without (0) or with (1) flange along its posterior edge.**

Karaurus has state 0 (DM, pers. obs. of cast housed in MNHN).

246. FIB 1: **Fibula waisted: no (0); yes (1).**

247. FIB 3: **Ridge near posterior edge of fibula flexor surface: absent (0); present (1).**

Orobates has state 0 (Berman et al. 2004).

248. FIB 4: **Rows of tubercles near posterior edge of fibula flexor surface: absent (0); present (1).**

Orobates has state 0 (Berman et al. 2004).

249. TAR 2: **Separate tibiale, intermedium, and/or centrale 4 (0); astragalus (1).** The original wording counted the "[p]roximal tarsal ossifications: absent (0); presence of single ossification (1); presence of more than two ossifications (2)". This did not distinguish incomplete ossification of the tarsus from fusion of individual tarsals. The degree of ossification depends both on ontogeny and on lifestyle (with aquatic taxa ossifying the tarsus later and/or to a lesser degree than terrestrial ones). Furthermore, incomplete ossification and incomplete preservation can only be distinguished in articulated skeletons. Finally, the astragalus usually comes with a calcaneum (= fibulare), so there are two "[p]roximal tarsal ossifications" – yet no state is available between "single" and "more than two", so OTUs with an astragalus were scored as having state 1 or 2! We do not consider this tenable and have redefined the character to consider fusion only.

Eocaecilia has state 0 (Jenkins et al. 2007), as do Albanerpetontidae (McGowan 2002), *Triadobatrachus* (Roček & Rage 2000), *Microbrachis* (CG78: 124), and *Scincosaurus* (Milner & Ruta 2009).

We count *Gephyrostegus* as possessing state 1: the tibiale and the intermedium are (although incompletely) fused, and the lateralmost centrale in fig. 9 of Carroll (1970) should be the centrale 3, not 4.

In *Euryodus* the condition is unknown (CG78: 65).

250. TAR 3: **L-shaped proximal tarsal element: absent (0), present (1).**

Eocaecilia has state 0 (Jenkins et al. 2007), as do Albanerpetontidae (McGowan 2002) and *Tseajaia*, assuming that Moss (1972) has interpreted the tarsus correctly (the shapes of the tibiale and the intermedium are rather unusual).

Tuditanus shows state 1 (Carroll & Baird 1968: fig. 10B).

251. TAR 4: **Distal tarsal ossifications between fibulare and digits: absent (0); present (1).**

Albanerpetontidae has state 1 (McGowan 2002).

Remarkably, *Scincosaurus* shows state 0 (Milner & Ruta 2009).

252. TAR 5: **Distal tarsal ossifications between tibiale and digits: absent (0); present (1).**

Albanerpetontidae has state 1 (McGowan 2002).

Scincosaurus shows state 1 (Milner & Ruta 2009).

Orobates has state 0; of all distal tarsals only the fourth is ossified (Berman et al. 2004).

253. RIB 1: **Ribs K-shaped in at least some part of the trunk: absent (0); present (1).**

Lethiscus retains state 0 (Anderson et al. 2003).

254. RIB 2: **Cervical ribs with (0) or without (1) flattened distal ends.**

Unknown in *Ossinodus* (Warren & Turner 2004; Warren 2007).

255. RIB 3: **Ribs mostly straight (0) or ventrally curved (1) in at least part of the trunk.**

The "first dorsal rib" of *Tseajaia* has "cervical rib" morphology (Moss 1972); this may be why it (and it alone) was scored as polymorphic. The definition refers to "at least part of the trunk", however, meaning that *Tseajaia* has state 1.

256. RIB 4: **Broad rectangular flanges in at least some trunk ribs: absent (0); present (1).**

Lethiscus has state 0 (Anderson et al. 2003).

257. RIB 5: **Triangular spur-like posterodorsal process in at least some trunk ribs: absent (0); present (1).**

Baphetes shows state 1 (Milner & Lindsay 1998).

Lethiscus has state 0 (Anderson et al. 2003).

258. RIB 6: **Elongate posterodorsal triangular flange in the midtrunk ribs: absent (0); present (1).**

Lethiscus has state 0 (Anderson et al. 2003).

259. RIB 7: **Trunk ribs longer (0) or shorter (1) than three successive articulated vertebrae in adults.** The measured vertebrae should be from the same region of the trunk as the vertebrae.

RC07 added the unquantified terms "poorly ossified" and "slender" to the definition of state 1 and did not test if all three traits are correlated. We have reduced the character to length alone, making it identical to McGowan's (2002) character 1 as modified by Marjanović & Laurin (2008: 177f.). Thus, we have scored *Micromelerpeton* as possessing state 0 which, according to Schoch (pers. comm. to Marjanović & Laurin 2008: 178), is observed in the metamorphosed specimens announced by Lillich & Schoch (2007), and we have scored *Balanerpeton*, *Dendrerpeton*, *Acheloma* (Case 1911: fig. 46), *Rhynchonkos*, *Cardiocephalus*, *Oestocephalus* (Carroll 1998; Anderson 2003) and *Phlegethontia* (both species; Anderson 2002: fig. 10) as having state 1.

Importantly, *Acheloma* (Case 1911: fig. 46) demonstrates that this character is not correlated to absolute body size, even though *Utaherpeton* adds to the already known sample of taxa which change from state 0 to state 1 in their ontogeny (Carroll et al. 1991; Carroll & Chorn 1995).

State 0 is further found in *Baphetes* (Milner & Lindsay 1998).

Unknown in *Phonerpeton* (Dilkes 1990) and in *Westlothiana* where it is too borderline to tell (Smithson et al. 1994).

260. CER VER 1: **Halves of atlas neural arch unfused (0) or fused (1).**

Euryodus is polymorphic, with *E. dalyae* having state 0 as scored, but *E. primus* showing state 1 (CG78: fig. 115).

We have scored *Gerobatrachus* as possessing state 1, following the matrix by Anderson et al. (2008), surprising though this is (*Doleserpeton* has state 0, as was correctly scored; Bolt 1991: fig. 5).

261. CER VER 3: **Axis arch not fused (0) or fused (1) to axis (pleuro)centrum.**

Eocaecilia has state 1 (Jenkins et al. 2007).

We also ascribe state 1 to Albanerpetontidae because we strongly suspect that the entirely arch-less "axis" is in fact the axis intercentrum, and the "third cervical" is the axis pleurocentrum + neural arch.

262. CER VER 4: **Odontoid process, or tuberculum interglenoideum, on anterior surface of atlas body: absent (0); present (1).** It is a good question if this process – also called "intercotylar tubercle"; not homologous to the odontoid process of mammals, which consists of the entire atlas pleurocentra that are fused to the axis – should be considered homologous regardless of whether the "atlas body" consists of pleuro- or intercentra. Unfortunately, whether the atlantes of, say, lissamphibians consists of pleuro- or intercentra is itself a difficult question, so we have followed RC07 in considering all such processes primarily homologous.

We have scored this character as unknown for OTUs with any state of EXOCC 2-3-4-5/BASOCC 1-5-6 other than 5 or 6, because the process does not (as far as known) and probably cannot occur together with states

0 through 3 of EXOCC 2-3-4-5/BASOCC 1-5-6 and by definition occurs with state 4 (where the cotyle of the basioccipital articulates with it).

Furthermore, this character is inapplicable to *Doleserpeton*, where the area where a tubercle could be is occupied by the huge notochordal canal (Bolt 1991: fig. 5).

We cannot find a description or illustration of the atlantes of *Amphibamus* or *Eoscopus*; the most likely source, Daly (1994), does not describe any atlas centra, except for mentioning the very existence of one in *Platyrhinops* (which RC07 already scored as unknown). We have therefore scored both as unknown.

Based on our personal observations of a latex infilling of *Triadobatrachus* (MNHN MAE 126), we cannot completely exclude the possibility that a small tubercle was present. We have therefore scored *Triadobatrachus* as unknown.

The condition is further unknown in *Hyloplesion* (CG78: 131).

Odonterpeton was scored as unknown. CG78: 167 imply state 0, but this may refer to a large process as commonly found in "microsaurs"; the process can be very small in lissamphibians, and indeed CG78: fig. 116L shows state 1. We have scored state 1 as present in *Odonterpeton*.

Notobatrachus has a small tubercle and thus state 1 (Jenkins & Shubin [1998] and references therein).

263. TRU VER 1: **Extra articulations above zygapophyses in at least some trunk and caudal vertebrae: absent (0); present (1).**

264. TRU VER 2: **Neural and haemal spines rectangular to fan-shaped in lateral view: no (0); yes (1).**

265. TRU VER 3: **Neural and haemal spines aligned dorsoventrally: absent (0); present (1).**

The entire tail is unknown in *Colosteus* (Hook 1983), *Crassigyrinus* (Panchen 1985), apparently *Neldasaurus* (Chase 1965), apparently *Broiliellus* (Carroll 1964), de facto *Platyrhinops* (Carroll 1964: 235), *Eoherpeton* (Smithson 1985), *Pholiderpeton scutigerum* (Clack 1987b), *Solenodonsaurus* (Laurin & Reisz 1999), *Stegotretus* (Berman et al. 1988), and *Ariekanerpeton* (Klembara & Ruta 2005b), and it has (at least) never been described in *Doleserpeton*. Similarly, no haemal arches are preserved in *Triadobatrachus* (Roček & Rage 2000), and none were ossified in described specimens of *Apateon* or *Leptorophus*.

266. TRU VER 4: **Haemal spines not fused (0) or fused (1) to caudal centra.** According to RC07, state 1 is "observed almost exclusively in nectrideans", but this statement does not seem defensible to us.

Importantly, haemal arches are not homologous to intercentra or parts thereof (contra, e.g., Williston 1912: 466, or Carroll & Chorn 1995: 49). This is demonstrated by the separate haemal arches and intercentra of animals like the stereospondyl temnospondyl *Trematolestes* (Schoch 2006: fig. 6H). Therefore, this character cannot be interpreted as "haemal spines not/fused to caudal pleurocentra", and is not inapplicable to OTUs where the pleurocentra do not participate in the ventral margin of the vertebral column. It is also, unfortunately, not a cheap way of determining whether an animal has intercentra (see TRU VER 7, 8, 9, 13-14).

State 1 is thus present at a minimum in *Eusthenopteron* (Coates 1996), *Acanthostega* (Coates 1996), *Ichthyostega* (Jarvik 1996), *Greererpeton* (Godfrey 1989), *Dendrerpeton* (Holmes et al. 1998: fig. 1), *Eryops* (Moulton 1974: fig. 6–8), *Acheloma* (Case 1911: 135), *Phonerpeton* (Dilkes 1990: fig. 10), *Amphibamus* and *Eoscopus* (Daly 1994), *Ecolsonia* (Berman et al. 1985), *Karaurus* (Ivachnenko 1978: 366; DM, pers. obs. of cast housed in MNHN), *Caerorhachis* (Ruta et al. 2002), *Proterogyrinus* (Holmes 1984), *Archeria* (Holmes 1989), *Pholiderpeton attheyi* (Panchen 1972), *Bruktererpeton* (Boy in Boy & Bandel 1973: fig. 8), *Discosauriscus* (Klembara & Bartík 2000), *Seymouria* (White 1939: 356), *Limnoscelis* (Williston 1912: 466, fig. 25; Berman & Sumida 1990: 326), *Diadectes* (Berman et al. 1998: 78), *Captorhinus* (Dilkes & Reisz 1986: 1294), *Petrolacosaurus* (Reisz 1981: 36), *Westlothiana* (Smithson et al. 1994), *Micraroter* (CG78: 97, fig. 58), *Ossinodus* (Warren 2007), *Silvanerpeton* (Ruta & Clack 2006), and *Utegenia* (Klembara & Bartík 2000: fig. 30). It is also suggested for *Balanerpeton* by fig. 10C of Milner & Sequeira (1994); we have accepted this at face value.

A large number of taxa where the tail is poorly or not known were scored as having state 0 by RC07. This includes *Colosteus* (Hook 1983), *Crassigyrinus* (Panchen 1985), apparently *Neldasaurus* (Chase 1965), apparently *Broiliellus* (Carroll 1964), de facto *Platyrhinops* (Carroll 1964: 235), *Eoherpeton* (Smithson 1985), *Pholiderpeton scutigerum* (Clack 1987b), *Solenodonsaurus* (Laurin & Reisz 1999), *Stegotretus* (Berman et al. 1988), and *Ariekanerpeton* (Klembara & Ruta 2005b), where the entire tail is unknown, as well as *Doleserpeton*, where it has (at least) never been described. Other cases include *Baphetes*, *Platyrhinops* (Carroll 1964), and *Gephyrostegus* (Carroll 1970).

Unknown in Albanerpetontidae (McGowan 2002) and *Paleothyris* (Carroll 1969); inapplicable to *Triadobatrachus* which does not preserve any haemal arches (Roček & Rage 2000).

Unclear from the description and illustrations of *Pantylus* in CG78; scored as unknown.

We have further scored *Trimerorhachis* as unknown for this reinterpreted character because we have not been able to find any description or illustration of its (known) tail. The same holds for *Kotlassia*, where Bystrow (1944) did not distinguish *Karpinskiosaurus* from *Kotlassia* and Bulanov (2003) describes the skull only.

Batropetes is polymorphic (Carroll 1991).

267. TRU VER 5: **Extra articulations on haemal spines: absent (0); present (1).**

State 1 is found in *Scincosaurus* (Milner & Ruta 2009).

The entire tail is unknown in *Colosteus* (Hook 1983), *Crassigyrinus* (Panchen 1985), apparently *Neldasaurus* (Chase 1965), apparently *Broiliellus* (Carroll 1964), de facto *Platyrhinops* (Carroll 1964: 235), *Eoherpeton* (Smithson 1985), *Pholiderpeton scutigerum* (Clack 1987b), *Solenodonsaurus* (Laurin & Reisz 1999), *Stegotretus* (Berman et al. 1988), and *Ariekanerpeton* (Klembara & Ruta 2005b), and has (at least) never been described in *Doleserpeton*. Similarly, no haemal arches are preserved in *Triadobatrachus* (Roček & Rage 2000).

268. TRU VER 7: **Ossified pleurocentra: absent (0); present (1).**

We have scored this and the next two characters as unknown in all taxa where the vertebrae are monospondylous, because in them there is no way – other than phylogenetic reconstruction – whether the single centrum is the inter- or the pleurocentrum (or rather the fused pair of inter- or pleurocentra). This applies to *Karaurus*, *Valdotriton*, *Tuditanus* (CG78: 15), *Asaphestera* (CG78: fig. 8A), *Saxonerpeton* and *Hapsidopareion* (CG78: fig. 116A, B), probably *Cardiocephalus* (CG78: 58), *Hyloplesion* (CG78: fig. 88), *Odonterpeton* (CG78: fig. 98), *Brachydectes* (Wellstead 1991), and *Scincosaurus* (Bossy & Milner 1998; Milner & Ruta 2009). The only exception is *Utaherpeton*: the tail of the immature specimen of demonstrates that the only ossified centra are pleurocentra because the last few are broad dorsally but narrow to a point ventrally (Carroll & Chorn 1995).

State 1 is found in *Utegenia* (Klembara & Ruta 2004b).

Unknown in *Ichthyostega* (Ahlberg et al. 2005: 138).

269. TRU VER 8: **Trunk pleurocentra fused midventrally: no (0); yes (1).**

Unknown (like the pleurocentra in their entirety) in *Ichthyostega* (Ahlberg et al. 2005: 138) and *Schoenfelderpeton* (Boy 1987).

Orobates has state 1 (Berman et al. 2004: fig. 11).

270. TRU VER 9: **Trunk pleurocentra fused middorsally: no (0); yes (1).**

Unknown (like the pleurocentra in their entirety) in *Ichthyostega* (Ahlberg et al. 2005: 138).

Orobates has state 1 (Berman et al. 2004: fig. 10B).

State 0 is observed in the tail and possibly the last presacral vertebra of the immature specimen of *Utaherpeton*, but the condition is unknown in the other vertebrae (which should be more advanced ontogenetically) of that specimen and entirely unknown in the adult specimen (Carroll & Chorn 1995). We have therefore scored *Utaherpeton* as unknown for this character.

271. TRU VER 10: **Neural arches without (0) or with (1) distinct convex lateral surfaces.**

We have scored *Utegenia* as unknown because the observed state 0 is also found in larvae but not postmetamorphic individuals of *Discosauriscus*, in which the appearance of state 1 is interpreted as part of the transition to terrestrial life (Klembara 2009).

272. TRU VER 11: **Neural arches of trunk vertebrae fused to centra: no (0); yes (1).** According to RC07, this character "does not appear to be simply related to […] inferred degree of specimen maturity", yet there is evidence that *Batropetes* (see below) changes from state 0 to state 1 in ontogeny, and in amniotes this is a very widely used marker for skeletal maturity (Irmis 2007); among OTUs with holospondylous vertebrae, it seems to us that only paedomorphic ones keep state 0 throughout life.

Centra are altogether unknown in *Leptorophus* (Boy 1987); they probably only ossified during metamorphosis (if metamorphosis ever occurred in *Leptorophus*). We have accordingly scored it as unknown.

Saxonerpeton, *Hapsidopareion*, *Micraroter*, and *Cardiocephalus* have state 0 according to the data matrix by Anderson et al. (2008).

State 1 is documented in *Eocaecilia* (Jenkins et al. 2007) and Albanerpetontidae (Estes & Hoffstetter 1976; Fox & Naylor 1982; McGowan 1996) as well as in *Platyrhinops* and *Batrachiderpeton* (according to the data matrix by Anderson et al. 2008).

Following the most mature specimen (Carroll 1991), we have scored *Batropetes* as possessing state 1.

273. TRU VER 12: **Bicipital rib bearers on trunk centra: absent (0); present (1).**

274. TRU VER 13-14: **Trunk intercentra: fused middorsally (0), separate middorsally (1), absent (2) (ordered).** Intercentra in state 1 have a wide range of sizes; usually they are crescent-shaped, and their dorsal tips do not touch. Evidently, this is a single continuous character, with the degree of intercentrum ossification gradually decreasing from state 0 to state 2 (though something in the middle of state 1 is the plesiomorphy).

Solenodonsaurus is known (Carroll 1970: 294f.) to have very small intercentra that are very far from reaching the dorsal edge of the pleurocentra (or rather the notochord) and thus cannot possibly have been fused middorsally; this means state 1.

Orobates has state 2 (only the first four vertebrae, counted as "neck" rather than "trunk", have intercentra; Berman et al. 2004: fig. 11).

275. TRU VER 15: **Anteroposteriorly elongate, lateral and ventral carinae on trunk centra: absent (0); present (1).**

Orobates has state 0 (Berman et al. 2004: fig. 11).

276. TRU VER 16: **Strong proximal emargination along anterior and posterior margins of haemal spines: absent (0); present (1).** RC07 added "of tail vertebrae" at the end; this is redundant.

The entire tail is unknown in *Colosteus* (Hook 1983), *Crassigyrinus* (Panchen 1985), apparently *Neldasaurus* (Chase 1965), apparently *Broiliellus* (Carroll 1964), de facto *Platyrhinops* (Carroll 1964: 235), *Eoherpeton* (Smithson 1985), *Pholiderpeton scutigerum* (Clack 1987b), *Solenodonsaurus* (Laurin & Reisz 1999), *Stegotretus* (Berman et al. 1988), and *Ariekanerpeton* (Klembara & Ruta 2005b), as well as *Doleserpeton*, where it has (at least) never been described. Similarly, no haemal arches are preserved in *Triadobatrachus* (Roček & Rage 2000).

277. TRU VER 18: **Striated ornament on vertebral centra: absent (0); present (1).**

278. TRU VER 19: **Tallest ossified part of neural arch in posterior trunk vertebrae situated above (aligned vertically with) posterior half of vertebral centrum: no (0); yes (1).** State 1 is much more widespread than RC07 scored it, at least if we assume that the neural spine counts as part of the neural arch, and if "entirely behind the centrum" still counts as "above […] posterior half" as opposed to the middle or the anterior half.

For instance, it is found in *Acanthostega* and *Ichthyostega* (Ahlberg et al. 2005) and *Caerorhachis* (Ruta et al. 2002).

Unknown in Albanerpetontidae.

279. TRU VER 20: **Prezygapophyses on trunk vertebrae: absent (0); present (1).**

Albanerpetontidae has state 1.

280. TRU VER 21: **Postzygapophyses on trunk vertebrae: absent (0); present (1).** One should think (as Pawley [2006: 205] did) that pre- and postzygapophyses only occur together, yet this is not the case: *Crassigyrinus* and *Trimerorhachis* were correctly scored as having state 0 of this but state 1 of the preceding character. We therefore keep these characters separate.

Albanerpetontidae has state 1.

281. TRU VER 22-24: **Prezygapophyses absent throughout the tail (0), present only on proximal tail vertebrae (1), or present throughout the tail (2) (ordered).** As far as known, it does not occur, and would be unexpected from functional considerations, that prezygapophyses occur in the distal but not the proximal part of the tail, so we have fused the two characters in question into an ordered multistate character that tracks the gradual spread of prezygapophyses. The same holds for the postzygapophyses, treated in the next character.

At least in the present matrix, there is no OTU that is known to have zygapophyses in the trunk but not the proximal tail or vice versa. It is possible that more characters should be merged.

We have scored *Bruktererpeton* (Boy in Boy & Bandel 1973) as possessing state 1 or 2 for this and the next character because the distal tail is not described and only visible in one illustration, the plate, the resolution of which is insufficient to determine whether zygapophyses are present.

We have assigned the same score, again for both characters, to *Westlothiana*, the distal part of the tail of which is entirely unknown (Smithson et al. 1994).

Similar things hold for Albanerpetontidae (McGowan 2002), so we have scored it the same way.

282. TRU VER 23-25: **Postzygapophyses absent throughout the tail (0), present only on proximal tail vertebrae (1), or present throughout the tail (2) (ordered).**

283. TRU VER 26: **Capitular facets situated on posterior rim of vertebral midtrunk centra: absent (0); present (1).** State 0 will need to be divided; the capitular facet often sits on the intercentrum when inter- and pleurocentra are both present, or it can sit in the center of a pleurocentrum in gastrocentral vertebrae.

State 1 is found in *Scincosaurus* (Milner & Ruta 2009). We have also assigned it to *Eocaecilia*, where the facets commonly straddle two neighboring centra (Jenkins et al. 2007).

284. TRU VER 27: **Height of the ossified portion of the neural arch in midtrunk vertebrae greater (0) or smaller (1) than the distance between pre- and postzygapophyses.**

State 1 is found in *Eocaecilia* (Jenkins et al. 2007) and *Scincosaurus* (Milner et al. 2009).

Tseajaia is given state 0 because that state is found in the dorsoventrally longest neural spines.

285. TRU VER 28: **Crenulations or fimbriate sculpture along dorsal margin of ossified portion of neural spines: absent (0); present (1).**

286. TRU VER 29: **Intravertebral foramina for spinal nerves in at least some trunk vertebrae: absent (0); present (1).**

287. TRU VER 30: **Transverse processes stout and abbreviated, the length of which is less than 30% of neural arch height: absent (0); present (1).** State 0 probably hides some phylogenetically informative diversity. For instance, Carroll & Chorn (1995: 49f.) mention that adelogyrinids (scored as having state 1) "are unique among lepospondyls in having very *long* transverse processes […] as in primitive labyrinthodonts" (emphasis added), implying that their condition is intermediate (in terms of length) between those seen in other "lepospondyls" and elsewhere.

288. DIG 1-2-3-4: **"Independent radials" (0); polydactyly (1); pentadactyly (2); tetradactyl forelimb (3); tridactyl forelimb (4); limblessness (5) (stepmatrix).** RC07 treated the presence/absence of digits (DIG 1), the presence/absence of four or fewer fingers per hand (DIG 2), the presence/absence of five or fewer fingers per hand (DIG 3), and the presence/absence of three or fewer fingers per hand (DIG 4) as completely independent characters. It goes without saying that, if a taxon has three or fewer fingers per hand, it also has fewer than four and fewer than five, yet RC07 did not even provide for these cases by scoring inapplicability. We have therefore merged all these characters. The stepmatrix orders states 0 through 4 and makes loss of digits (attainment of state 5) cost only one step, while regaining limbs is forbidden (infinite cost).

The present character differs from DIG 5 of Germain (2008a) by having a stepmatrix, containing partial uncertainty, and defining states 0 and 5 morphologically where Germain (2008a) had called them "primary absence of digits" and "secondary absence of digits", which should be an inference from the analysis and not an assumption of coding. It differs from DIG 1 of Ruta & Bolt (2006) in not splitting polydactyly into two states (eight and six fingers per hand, each only present in a single OTU), in providing for OTUs with three fingers per hand or without limbs (both absent from the matrix of Ruta & Bolt [2006]), and again in having a stepmatrix instead of being unordered.

We have not counted the prepollex/-hallux, where identifiable as such, as a digit, because it is not homologous to an "independent radial" (Johanson et al. 2007) and because it is so common in otherwise four-fingered lissamphibians (if only, in most cases, as something like a distal carpal). The postminimus of *Tulerpeton* does count, but the possibly homologous pisiform bone does not, because its homology is unclear, because it is only a carpal without a digit, and because it is common in less-than-pentadactyl hands.

Greererpeton is often thought to have tetradactyl hands, but Coates (1996: 415) mentions and illustrates a well preserved hand with five fingers and mentions another that preserves four, one of which is the distinctively small fifth. Accordingly, we have scored *Greererpeton* as having state 2, even though the closely related *Colosteus* really does seem to have only four fingers per hand as scored by RC07 (the third is the longest, as common in tetradactyl limbs, not the fourth as would usually be expected in a pentadactyl one; Hook 1983).

Only states 0 and 5 can be ruled out for *Crassigyrinus* (Panchen 1985; Panchen & Smithson 1990), *Baphetes* (Milner & Lindsay 1998), *Ecolsonia* (Berman et al. 1985 – inferred from the hindlimb), *Doleserpeton* (Bolt 1969), *Eocaecilia* (Jenkins et al. 2007), *Pholiderpeton scutigerum* (Clack 1987b), *Kotlassia* (Bystrow 1944 – inferred from the hindlimb, and assuming the hindlimb does not belong to *Karpinskiosaurus* instead, see Bulanov [2003]), *Stegotretus* (Berman et al. 1988), *Saxonerpeton* (CG78: 38), *Asaphestera*, *Cardiocephalus*, *Euryodus*, *Pelodosotis* (CG78), *Ossinodus* (Warren 2007), and *Pederpes* (Clack & Finney 2005); we have thus scored them all as having state 1, 2, 3, or 4.

The same appears to hold for *Whatcheeria* (Lombard & Bolt 1995: 483; Bolt & Lombard 2000: 1049), even though the latter source makes state 4 appear unlikely.

In *Eucritta*, the same holds. The hindlimb does appear to be pentadactyl, which would strongly suggest five or fewer fingers in the forelimb, but we do not think polydactyly – especially a small postminimus like in the hand of *Tulerpeton* – can be ruled out.

Trimerorhachis has state 2 or 3 (Case 1935).

Dendrerpeton preserves four distal carpals (Holmes et al. 1998). That most likely means four or five fingers (state 2 or 3).

We have kept *Eryops* as tetradactyl, but it should be noted that this is a somewhat tenuous inference (Gregory et al. 1923; Miner 1925): the hand is preserved in a single specimen which is not quite articulated and not quite complete.

No metacarpals or fingers are preserved in *Acheloma*, but there appear to have been five distal carpals (Olson 1941), of which the tiny cranialmost one could belong to a prepollex; this means four or five fingers and thus state 2 or 3.

Doleserpeton has state 3 (Sigurdsen & Bolt 2009), as do *Platyrhinops* (Carroll 1964) and *Leptorophus* (judging from the drawings in Werneburg 2007).

Caerorhachis is given state 2 after *Casineria* (Paton et al. 1999).

Brukterpeton can safely be given state 2 (Boy in Boy & Bandel 1973: 63 and fig. 14).

Solenodonsaurus has at least four metacarpals (Carroll 1970), giving it state 1, 2, or 3. The same holds for *Rhynchonkos*, where four metacarpals are preserved but a higher number cannot be excluded based on the preservation (CG78: 111).

Westlothiana preserves parts of four fingers and may have had more, meaning state 1, 2, or 3.

As Ruta et al. (2003) point out, it is not actually known whether the lack of preserved limbs in *Acherontiscus* and all three adelogyrinids is genuine or merely taphonomic. Unlike RC07, we deliberately side with the former interpretation in order to bias our analysis towards the traditional hypothesis of a close relationship between adelogyrinids and aïstopods (e.g. Vallin & Laurin 2004; Germain 2008a) and against our results (and those of RC07) which find the adelogyrinids and *Acherontiscus* as the sister-group to the colosteids.

Keraterpeton has state 3 (A. C. Milner, pers. comm. to DM, September 2009) as scored by RC07. This agrees with Bossy & Milner (1998), contradicting Bossy (1976) and possibly Jaekel (1902: fig. 2), probably agreeing with pl. XIX of Huxley & Wright (1867), and contradicting the text of Huxley & Wright (1867) which mentions five metacarpals and fingers.

Diceratosaurus, however, has state 2 (DM, pers. obs. of “specimen II” = MB.I.102.16.1 = MB.Am.776.1, Humboldt-Museum für Naturkunde, Berlin, July 2009), agreeing with Jaekel (1902: three times explicitly, and pl. IV-6, which shows the same “specimen II”) and with Bossy (1976) but contradicting Bossy & Milner (1998).

We have not been able to find a mention of forelimb material of *Diplocaulus* in the literature, except that Williston (1909) mentions four “metapodials” that are apparently metatarsals. Accordingly we have scored *Diplocaulus* as possessing state 1, 2, 3, or 4.

Appendix-Table 4: Stepmatrix for character DIG 1-2-3-4.

from ↓ to →	0	1	2	3	4	5
0	0	1	2	3	4	1
1	1	0	1	2	3	1
2	2	1	0	1	2	1
3	3	2	1	0	1	1
4	4	3	2	1	0	1
5	infinite	infinite	infinite	infinite	infinite	0

DOR FIN 1: **Ossified lepidotrichia in dorsal fin: present (0); absent (1).** As RC07 point out, this character is parsimony-uninformative, so we have deleted it.

289. CAU FIN 1: **Ossified lepidotrichia in caudal fin: present (0); absent (1).**

Enough of the tail of *Brukterpeton* is known to justify scoring state 1 as present (Boy in Boy & Bandel 1973).

Complete tails of *Hyloplesion*, preserving state 1, are known (CG78).

We have scored both *Proterogyrinus* and *Archeria* as unknown, because at least the 20 distalmost tail vertebrae in the latter (Holmes 1989) and more in the former (Holmes 1984) are unknown. The neural and haemal spines of the last preserved vertebrae are rather pointed in both, so we are not sure that a tail fin can be excluded. This is especially relevant now that Clack (2002b) has reported supraneural radials (though lepidotrichia are not mentioned) in an unspecified anthracosaur.

Further unknown in *Acherontiscus* (the tail tip, and possibly the entire tail, is unknown; Carroll et al. 1998) and *Tseajaia* (almost the entire tail is unknown; Moss 1972).

BAS SCU 1: **Basal scutes: present (0); absent (1).** As RC07 point out, this character is parsimony-uninformative, so we have deleted it.

Chapter 6

Review article

Because the phylogeny of limbed vertebrates in general and the origin(s) of the extant amphibians in particular are such lively topics, review articles appear in, it seems to me, ever shorter intervals. Such papers have been written from the point of view of the temnospondyl hypothesis (Milner 1988, 1993; Trueb & Cloutier 1991; Ruta et al. 2003; Schoch & Milner 2004; Ruta & Coates 2007; Coates et al. 2008) and the polyphyly hypothesis (Carroll 1999, 2007; Carroll et al. 2004; Anderson 2008); the only one written from the point of view of the lepospondyl hypothesis, however, is that by Laurin (two parts: 1998a, b). (The publication by Parsons & Williams [1963] argued against the polyphyly hypothesis without deciding on an alternative.) For this reason, and because of the many recent developments in this subject, it seemed appropriate to write a new review article.

This manuscript was submitted to Zoologica Scripta in late May; I have not reformatted it since, except for removing the provisorial page numbers and for single-spacing it, setting the references to 10 pt, and moving the abstract onto the title page in order to save space. It has recently undergone peer review; the version presented here already takes the comments by the two anonymous reviewers and the editor into account and will be sent back to the editor as soon as I will finish writing the cover letter begun by M. L. The focus of the manuscript lies on developments that happened after the latest previous reviews (Anderson 2008; Coates et al. 2008) were written, including but not limited to Chapters 2 through 5, chapter V of Damien Germain's (2008) doctoral thesis, chapter 8 and appendix 16 of Kat Pawley's (2006) doctoral thesis, and the publication by Germain & Laurin (2009). We also used the opportunity to reply to a few points raised by Anderson (2008) that we were unable to address in Chapter 4.

Discussed topics include:

- "Carroll's Gap", as we call the almost complete lack of a Middle Permian to Early/Middle Jurassic fossil record of modern amphibians and all of their potentially closest relatives – regardless of which hypothesis is favored –, as a reason for why the origin of the modern amphibians is still controversial after more than a century of intensive research;
- character conflict – complex, if not confusing, distributions of character states among modern amphibians and their potentially closest relatives – as another such reason;
- incompatibility between the polyphyly hypothesis and any phylogenetic analysis of molecular data conducted so far (figure 4 of the General Introduction);
- nomenclature from Chapter 3;
- the fact (Pawley 2006) that, contrary to claims in the recent literature, the lepospondyl hypothesis is no longer supported only by M. L. and his students or coauthors;
- diversity within the lepospondyl and polyphyly hypotheses;
- the lack of consensus on the intrarelationships of the modern amphibians, i.e., the interrelationships of frogs, salamanders, caecilians, and albanerpetontids, and the interactions of the two main hypotheses on this question with the three main hypotheses on the interrela-

tionships of the modern-amphibians – due to the abovementioned character conflict, some combinations are more parsimonious than others;

- the implications and lack thereof of the size of data matrices on the results of phylogenetic analyses;
- the effects of correlated characters on phylogenetic analysis;
- the effects of questionable scores in data matrices, with Chapters 3, 4, and 5 (the last is cited as "D. M.'s ongoing work" and the like) as evidence that at least part of the conflict between the published phylogenetic analyses of morphological data is such an effect;
- a discussion of the matrix by Carroll (2007), which I have not scrutinized in detail the way I have done with those by McGowan (2002; Chapter 3) and Anderson et al. (2008; Chapter 4);
- the use of comparative development biology in phylogenetics, exemplified by the patterns of limb formation in salamanders vs. frogs and amniotes, the basale commune (Chapters 3, 4), and paedomorphosis, peramorphosis and miniaturization, and skull ossification sequences;
- in connection with skull ossification sequences, the fact that phylogenetics cannot be done by comparing only two taxa – more are needed to distinguish symplesiomorphies from synapomorphies (noted previously by, e.g., Ruta & Coates [2007]);
- still in connection with skull ossification sequences, the fact that it cannot be assumed a priori that any extant representative of a taxon (like *Ranodon sibiricus*) conserves the ancestral state of that taxon (like Urodela or Caudata) – instead, the ancestral state must be reconstructed, a task for which the method developed by Germain & Laurin (2009) works better than any other proposed so far (according to the simulations in that paper);
- my reinterpretation of the homologies of certain skull roof bones of the lysorophian lepospondyl *Brachydectes* (Chapter 3), responding to points raised by Anderson (pers. comm. September 2009) – the reinterpretation does not depend on *Brachydectes* being a close relative of any particular "microsaur" and is bolstered by additional anatomical evidence that was not yet mentioned in Chapter 3;
- the three methods of dating the origin of Lissamphibia (Chapters 1 and 2) and the implications of their consistent results on lissamphibian interrelationships, emphasizing the importance of maximum ages for internal calibration points (as predicted by Rodríguez-Trelles et al. [2002]) and addressing two misunderstandings by Anderson (2008) and San Mauro (2010) each;
- the ages of three calibration points chosen by Igawa et al. (2008) that are inflated because of misunderstandings of the paleontological literature and therefore biased their molecular divergence date analysis towards too old dates – two of them further exaggerated by Anderson (2008: table 2) due to another misunderstanding (he mistook the ages of the tetrapod crown-group and Lissamphibia as those of Lissamphibia and Batrachia, respectively; Batrachia is the smallest clade that contains the frogs and the salamanders);
- the conclusion of Chapters 1 through 5 – that the lepospondyl hypothesis is better supported than the temnospondyl and much better supported than the polyphyly hypothesis by several independent lines of evidence.

Author contributions

M. L. played a large role in breaking up my overly long sentences and in shortening the manuscript so it would fit the space restrictions; these restrictions are generous, but the topic is larger still. The text cut out of this chapter may end up in the publication of Chapter 5. Due to time constraints on my part, M. L. also handled our side of the submission process, while I dealt with the comments by editor and reviewers mostly on my own (though under supervision). I wrote the manuscript, made the illustrations, and came up with the term and concept of “Carroll’s Gap” (in analogy to Romer’s Gap, the near-complete lack of limbed vertebrates from the first half of the Mississippian, a term coined by Coates & Clack [1995]). Both of us studied a cast of *Triadobatrachus*.

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The origin(s) of extant amphibians: review and perspective

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Origin(s) of extant amphibians
David Marjanović, Michel Laurin

Marjanović, D. & Laurin, M. (2010). Early evolution of limbed vertebrates and the origins of extant amphibians: a review. *Zoologica Scripta*, *00*, 000–000.

The origins of the extant amphibians (frogs, salamanders, caecilians) remain controversial after over a century of debate. Three groups of hypotheses persist in the current literature, the "temnospondyl hypothesis" (TH) which roots Lissamphibia (the smallest clade composed of the extant amphibians) within the Paleozoic temnospondyls, the "lepospondyl hypothesis" (LH) which postulates a monophyletic Lissamphibia nested within the Paleozoic "lepospondyls", and the "polyphyly hypothesis" (PH), according to which the frogs and the salamanders are temnospondyls while the caecilians are lepospondyls. We present a review of our recent publications in this field, which show more support for the LH than for the TH, and considerably less for the PH than for either of the other two. Still, a consensus will not be reached soon, despite the increasing range of data and types of analysis that are used (morphological phylogenetics, molecular phylogenetics, development biology, molecular divergence dating, paleontological supertree dating, calculation of confidence intervals on first appearances in the fossil record).

Introduction

Much has been written since the late 19th century on the origins of the frogs, salamanders, and caecilians, a problem further complicated since the 1970s by the discovery of a fourth clade of unclear relationships, the Middle Jurassic to Pliocene albanerpetontids (salamander-shaped, somewhat elongate, scaly animals). Exciting advances have been made recently, such as the discovery of new fossils (cited below), the development of new methods (Marjanović & Laurin 2007, 2008a), the use of data from development biology (e.g. Hinchliffe & Vorobyeva 1999; Johanson et al. 2007), and progress in molecular (Zhang et al. 2005; Frost et al. 2006; Roelants et al. 2007; Hugall et al. 2007; Marjanović & Laurin 2007; Igawa et al. 2008; San Mauro 2010) as well as morphological phylogenetics (cited below). Despite this, three groups of hypotheses persist in the literature today (Fig. 1).

The most widespread one is surely the "temnospondyl hypothesis" (TH hereinafter; Fig. 1A–D). It posits that the frogs (crown-group: Anura, total group: Salientia), the salamanders (crown-group: Urodela, total group: Caudata), and the caecilians (crown-group: Gymnophiona, total group: Gymnophionomorpha – see below) form a clade, called Lissamphibia, which also either contains or is the sister-group of Albanerpetontidae and is nested within the amphibamid and/or branchiosaurid dissorophoid temnospondyls. The amphibamids, an intensively studied group (Huttenlocker et al. 2007; Anderson et al. 2008a, b; Fröbisch & Reisz 2008; Sigurdsen 2008, 2009; Sigurdsen & Bolt 2009), are known from the Late Carboniferous to the Early Triassic. They differ from other temnospondyls in their small body sizes and various traits that are in many cases shared by some or all lissamphibians (and in many cases lepospondyls); some of these traits are adaptations to a terrestrial lifestyle. The Late Carboniferous to Early Permian branchiosaurids, recently shown to be nested within Amphibamidae (Fröbisch & Schoch 2009), are mostly known from larvae and neotenic adults that resemble modern neotenic salamanders (Schoch 2009). The TH was most recently supported by the phylogenetic analysis of Ruta & Coates (2007) and the as yet unpublished one announced by Sigurdsen (2009).

Another is the "lepospondyl hypothesis" (LH). In its modern form (Fig. 1E; Vallin & Laurin 2004; Pawley 2006: app. 16, figs. 88, 89, 91, 92; Germain 2008; Marjanović & Laurin 2008b, 2009), it postulates a close relationship between Lissamphibia (again ignoring the exact position of the albanerpetontids) and certain "lepospondyls", especially the eel-like Late Carboniferous to Early Permian lysorophians and (recently) the coeval "nectrideans" (a possibly paraphyletic assemblage of mostly aquatic animals of small size and diverse shapes) and aïstopods (small, snake-like, probably terrestrial animals). More distant relationships are hypothesized to exist with the "microsaurs", a diverse, probably paraphyletic assemblage of mostly terrestrial to amphibious animals, some of them burrowing (Anderson et al. 2009). Temnospondyli is a clade of stem-tetrapods under the LH, and the tetrapod crown-group is smaller than according to the other hypotheses; it includes amniotes, diadectomorphs, and lepospondyls, but not seymouriamorphs or anthracosaurs.

The third is the "polyphyly hypothesis" (PH), most recently supported by Anderson et al. (2008b; Fig. 1G). Under this hypothesis, there is no Lissamphibia, because the frogs are considered to be amphibamid temnospondyls and the caecilians to be "microsaurian" "lepospondyls" (closely related to the elongate, possibly burrowing Early Permian *Rhynchonkos*). The salamanders were originally advocated to be "microsaurs" (Carroll & Holmes 1980; Fig. 1F), but are now thought to be branchiosaurid temnospondyls (Carroll 2007; Fig. 1H) or found, together with the albanerpetontids, to be the sister-group of the frogs (Anderson et al. 2008b). Less plausible variants of the PH (Fig. 1H) were found by McGowan (2002) and Carroll (2007: fig. 77).

Reviews of the current state of research on the phylogeny of limbed vertebrates in general and the origin of the extant amphibians in particular have recently been published by proponents of the PH (Carroll et al. 2004; Carroll 2007; Anderson 2008) and of the TH (Ruta et al. 2003; Schoch & Milner 2004; Ruta & Coates 2007; Coates et al. 2008). We would like to provide a complementary review and summarize information contained in recent publications.

Why is the origin of the lissamphibians so controversial?

Our inability to reach a phylogenetic consensus is often attributed to the notorious incompleteness of the fossil record. Indeed, our knowledge of the fossil record of lissamphibians and their potential closest relatives contains considerable gaps (Fig. 2A). The caecilians have almost no known fossil record; apart from isolated vertebrae from the Late Cretaceous and the Paleocene, which belong to the crown-group (Gymnophiona) or close relatives of it, there is disarticulated Early Cretaceous material from a stem-group representative (*Rubricacaecilia*) and a number of articulated partial skeletons of an Early Jurassic stem-caecilian (*Eocaecilia*). The fossil record of salamanders reaches down into the Middle Jurassic and then just stops, unless the badly preserved, superficially described, and tiny *Triassurus* from the Late Triassic of Kyrgyzstan (Ivachnenko 1979) is a caudate (Ruta & Coates [2007] mention one potential unique synapomorphy) rather than a temnospondyl larva (Schoch & Milner 2004). The albanerpetontids likewise have no known fossil record before the Middle Jurassic. Stem-salientians are known from the Early Jurassic and later, and from the Early Triassic forms *Triadobatrachus* and *Czatkobatrachus* (Evans & Borsuk-Białynicka 2010).

All potential sister-groups of Lissamphibia or of its main constituent clades are much older (Fig. 2). Under all hypotheses, a gap of at least 70 Ma must be inferred at the base of the group(s). Dissorophoid temnospondyls are not known after the Early Permian, with the sole exceptions of the Early Triassic amphibamids *Micropholis* and *Tungussogyrinus* (a branchiosaurid) and perhaps the undescribed “branchiosaurid-like temnospondyl” mentioned by Gao et al. (2004); *Micropholis* has never been considered particularly close to any extant amphibians, and while caudate affinities had been suggested for *Tungussogyrinus* (Schoch & Milner 2004), its latest redescription (Werneburg 2009) argues strongly against this. “Lepospondyls” are rare after the Early Permian; they are represented by an undescribed presumed “microsaur” from the Middle or Late Permian of Russia (Ivakhnenko et al. 1997: 14), by a diplocaulid “nectridean” from the Middle to Late Permian of Morocco (Dutuit 1988; Germain 2008), and by unspecified “lepospondyl amphibians” from the Early Triassic of China (Gao et al. [2008]; called “a microsaur-like lepospondyl” by Gao et al. [2004]). If lissamphibians and lysorophians are sister-groups, or if the lissamphibians are nested within the branchiosaurs (Trueb & Cloutier 1991), a stem-lissamphibian ghost lineage into the Late Carboniferous is required. A shorter but still sizable gap is required under the TH if *Doleserpeton* or *Gerobatrachus* (Anderson et al. 2008b) are closely related to some or all extant amphibans. Incidentally, contrary to a statement by San Mauro [2010: 554], Anderson et al. [2008b] described *Gerobatrachus* as an amphibamid. Because their phylogenetic analysis supported the PH, which means that there is no clade that can be called Lissamphibia, *Gerobatrachus* should not be called an “unequivocal lissamphibian”, even though Anderson et al. (2008) argue that it is closely related to a subset of extant amphibians. The PH requires two or three ghost lineages extending down to the Early Permian or earlier. Barring future surprises from the purported Middle/Late Permian and Triassic lepospondyls, wide gaps separate the oldest known lissamphibians from all of their potential closest relatives, and similarly wide gaps exist in our knowledge of the early history of Lissamphibia itself. However, the subsequent history of Lissamphibia, from the Early Cretaceous onwards, is documented by a reasonably rich fossil record (Marjanović & Laurin 2007, 2008a).

In analogy to "Romer's Gap" (Coates & Clack 1995), we would like to introduce the term "Carroll's Gap" for the time from the Middle Permian to the Early Jurassic which has so far yielded almost no fossils of lissamphibians or any of their potential close relatives (Laurin 1998; Carroll et al. 2004; Carroll 2007). Both gaps are illustrated in Figure 2.

On their own, such gaps need not be a problem. Phylogenetic analysis can be, and is almost always, done without taking stratigraphic data into account. In this case, however, fossils from the mentioned gaps would show whether all three main lissamphibian clades converge on a single ancestral morphotype, as predicted by the TH and the LH, or not, as suggested by the PH. In the former case, such fossils would also narrow down the diversity of possible character combinations for the ancestral lissamphibians, which would help discriminate between the TH and the LH. Two examples should suffice to illustrate this.

All extant amphibians as well as the albanerpetontids lack the paired postparietal and tabular bones at the caudal edge of the skull roof – yet *Eocaecilia*, the oldest and basalmost known caecilian, possesses well developed postparietals as well as a pair of extra bones which are most parsimoniously interpreted as tabulars (Jenkins et al. 2007). On the other hand, postparietals are missing in the brachystelechid "microsaurs" (Carroll 1991) and apparently in lysorophians (Marjanović & Laurin 2008b; Fig. 3). Anderson et al. (2008b) scored *Triadobatrachus* as possessing postparietals and tabulars, although our own inspections of the specimen have failed to replicate this observation.

Similarly, the jugal bone is absent in all extant amphibians and lysorophians, and appears late in the ontogeny of the branchiosaurid temnospondyls (Schoch 2002, and references therein), yet *Eocaecilia* (Jenkins et al. 2007) and albanerpetontids (McGowan 2002; Venczel & Gardner 2005) possess jugals.

An alternative way to assess the origin of extant amphibians might be to turn to evidence independent of morphology, that is, molecular data. However, so many of the relevant taxa are extinct that sequence-based analyses cannot distinguish between the TH and the LH – both predict lissamphibian monophyly with respect to Amniota. Still, molecular data can discriminate between monophyly (TH or LH) on one hand and the PH on the other.

Lissamphibian monophyly with respect to Amniota has indeed been found in every molecular analysis we are aware of (Laurin 2002; Anderson 2008; San Mauro 2010), despite the wide diversity of genes (nuclear and mitochondrial), techniques, and taxon samples that have been used. Lissamphibian monophyly with respect to Amniota is incompatible with the PH because all large phylogenetic analyses of early limbed vertebrates (Table 1) show that the "lepospondyls" are closer to the amniotes than to the temnospondyls. Thus, the PH predicts paraphyly of the extant amphibians in molecular trees.

Morphological phylogenetics so far leads to several mutually contradicting results. This could in part be due to differences in character and taxon sampling in the published data matrices, but also to different approaches to coding characters or to questionable scores. Recently, our lab (Germain 2008; Marjanović & Laurin 2008b, 2009) has started to explore the latter possibility. In the data matrices by McGowan (2002), Ruta & Coates (2007) and Anderson et al. (2008), we have found many scores we disagree with. These range from differences of interpretation over different state delimitations to, apparently, cases where entire clades were scored as having the same state but not every member was checked, momentary confusions of states 0 and 1, and probable typographic errors. Having at least partially rescored the abovementioned matrices to reflect the descriptive literature, we have found that they all support the LH (Table 1).

Detailed assessment of the reasons for topological incompatibilities was not undertaken until recently because it is a time-consuming task. For instance, our reappraisal of

McGowan’s (2002) small matrix fills 51 pages of mostly fine print (Marjanović & Laurin 2008b). That matrix is well suited as a test case: it is so small (21 taxa, 41 characters) that it was feasible to scrutinize every cell, to perform seven different analyses (including bootstrapping) based on different assumptions and thus five different matrices, and to use time-consuming methods, most notably stepmatrix gap-weighting (Wiens 2001), on some characters. We found and documented many cases where, e.g., all temnospondyls or all “microsaurs” had been given the same character state even though the character is not known in some of these OTUs or even though (occasionally) another state is known to be present; the matrix by McGowan (2002) contains many scores that differ from published descriptions, and this, it seems, had a large influence on the results.

Nomenclature

A few short comments on nomenclature are necessary because some taxon names mentioned below have multiple meanings and some taxa have more than one name in the recent literature.

The caecilian crown-group (e.g. Schoch & Milner 2004; Marjanović & Laurin 2007) and sometimes the total group (Cannatella & Hillis 1993) have been called Apoda. However, *Apoda* Haworth, 1809, is the name of a moth genus, so Apoda Oppel, 1810, should not be used for a clade of tetrapods. For this reason, we now (Marjanović & Laurin 2008b) follow the other common usage, i.e., calling the caecilian crown-group (rather than the total group) Gymnophiona. In the same paper we also proposed the new name Gymnophionomorpha that is intended to apply to the largest clade that includes the caecilians but excludes the frogs, salamanders, albanerpetontids, and “lepospondyls”.

Under the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999), family names remain valid if they are based on genus names that have been sunk into synonymy. The nomenclature of “lepospondyls” contains no less than three such cases: Gymnarthridae is named after a junior synonym of *Cardiocephalus*, Brachystelechidae after a junior synonym of the preoccupied name *Petrobates* Credner, 1890, that *Batropetes* replaces, and Cocytinidae after a junior synonym of *Brachydectes*. Perhaps by analogy, Ruta & Coates (2003), Carroll (2007 and earlier), and Anderson (2008) continued to use the name Goniorhynchidae for the monotypic family that contains *Rhynchonkos stovalli*. However, *Goniorhynchus* Olson, 1970, is not a junior synonym of *Rhynchonkos*; instead, *Rhynchonkos* Schultze & Foreman, 1981, is a replacement name for *Goniorhynchus* Olson, 1970, which was preoccupied by the beetle *Goniorhynchus* Hampson, 1896. If a taxon is to be named Goniorhynchidae, it must have the valid genus *Goniorhynchus*, not the invalid one, as its type; therefore, Goniorhynchidae Carroll & Gaskill, 1978, has always been invalid and should never have been erected. Accordingly, Zanon (1988) coined the replacement name Rhynchonkidae. This is the name that should be used if one is not content to refer to the only known genus and species directly by their own names.

The current states of the lepospondyl and the polyphyly hypotheses

Anderson (2008) and Sigurdsen & Bolt (2009), among others, suggested that the lepospondyl hypothesis on the origin of lissamphibians (LH) is only supported by M. L. and his collaborators. This is incorrect, even though the LH certainly lacks broad support at present. Working without our knowledge, Pawley (2006: figs. 88, 89, 91, 92) reworked the matrix of Ruta et al. (2003), which initially supported the TH, and performed a large number of analyses on it. In all analyses with the same taxon sampling as Ruta et al. (2003), presented in app. 16, she found support for the LH, except in the analysis without postcranial characters, which led to a large polytomy encompassing all temnospondyls, seymouriamorphs, “lepospondyls”, and amniotes (fig. 90). Even in that latter analysis, Amphibamidae is monophyletic with respect to Lissamphibia + Albanerpetontidae, a result that is compatible neither with any version of the temnospondyl hypothesis (TH) proposed in the last 15 years, where Lissamphibia is thought to be nested within Amphibamidae, nor with the polyphyly hypothesis (PH). In the analyses with her own preferred taxon sampling, which are presented in chapter 6 of the thesis, Pawley omitted all extant amphibians, but she did mention on p. 239 that the postcranial evidence favors the LH over the TH. Unfortunately, the reasons for many of Pawley’s coding decisions are not better documented than those of Ruta et al. (2003).

Unsurprisingly, some diversity now exists within the LH concerning which “lepospondyls” are the closest relatives of Lissamphibia and where Albanerpetontidae fits (Fig. 4). Vallin & Laurin (2004) found the lysorophians to be sister-group of Lissamphibia, followed by the brachystelechid “microsaurs” and then various other “microsaurs” (Fig. 4A). Other studies (Germain 2008; Marjanović & Laurin 2008b, 2009 – Figs. 4C, D, E) generally also have Lysorophia as the sister-group of Lissamphibia (or the latter plus Albanerpetontidae, when the latter is outside Lissamphibia), but the topology varies among more distant relatives of Lissamphibia. When she replaced the postcranial dataset of Ruta et al. (2003) by her own, but kept their taxon sample, Pawley (2006: figs. 91, 92 – Fig. 4B) found the closest relatives of Lissamphibia to be Albanerpetontidae, followed by lysorophians and a clade composed of aïstopods and adelogyrinids; all these are nested among the “nectrideans” (Pawley 2006: fig. 91) or form their sister-group (Pawley 2006: fig. 92). The latest preliminary result (Fig. 4F) of D. M.’s ongoing work based on a modified version of the matrix of Germain (2008), itself derived from Ruta and Coates (2007), shows Lissamphibia (including Albanerpetontidae) as the sister-group to a “nectridean”-aïstopod clade (Holospondyli), with the next closest relative being Lysorophia followed by the paraphyletic “microsaurs”. A monophyletic Microsauria was found by Pawley (2006: figs. 88, 89, 91, 92) and Germain (2008).

Similarly, there are considerable differences between the versions of the polyphyly hypothesis (PH) by Anderson (2007) and Anderson et al. (2008b) on the one hand and Carroll (2007 and earlier) on the other: while both agree on frogs and salamanders (exception: Carroll & Holmes 1980) being temnospondyls and caecilians being lepospondyls (Fig. 1H), Anderson (2007) and Anderson et al. (2008b) found Salientia and Caudata as more closely related to each other than to any Paleozoic taxon (Fig. 1G), while Carroll derived the frogs from amphibamids and the salamanders from branchiosaurids. Carroll (2007: fig. 78) also considered lepospondyl interrelationships to be quite different from those found by Anderson (2001, 2007) and Anderson et al. (2008b).

Phylogeny of Lissamphibia

As if the confusion about the origin(s) of the extant amphibians were not enough, there is no broad consensus in the current literature on whether the frogs or the caecilians are the extant sister-group of the salamanders. The first hypothesis recognizes Batrachia, a clade formed by anurans and urodeles; the second recognizes Procera, formed by urodeles and gymnophionans. The position of the albanerpetontids is even less clear, with all possible positions except a sister-group relationship to the frogs having been supported by phylogenetic analyses within the last ten or indeed four years. To some degree, as pointed out in the literature, these hypotheses interact with the abovementioned hypotheses on the origin of Lissamphibia, because several character states present in amphibamids (especially *Doleserpeton* or *Gerobatrachus*) or “lepospondyls” (especially lysorophians) are present in some but not all lissamphibians.

Batrachia or Procera?

Anderson (2008) portrays the Procera hypothesis as part of the LH. This is indeed the topology that best fits the results of Vallin & Laurin (2004; Fig. 4A) and earlier installments of the LH, but the Batrachia hypothesis is strongly supported by the bootstrap analyses of Marjanović & Laurin (2008b: fig. 6d, 2009: supplementary figure; see also Figs. 1D, E). Likewise, Germain (2008) found the Batrachia hypothesis (frogs and salamanders as sister-groups to the exclusion of caecilians) to be better supported (Fig. 4C), as does D. M.'s ongoing continuation of his work (Fig. 4G). Pawley (2006) found the same result in some (figs. 90, 91, 92 – Fig. 1B) but not others of her analyses (fig. 89 shows Procera; fig. 88 shows a polytomy between Salientia, the gymnophionomorph *Eocaecilia*, Caudata, and Albanerpetontidae). In fact, as pointed out by Bolt (1991), Ruta et al. (2003) and Schoch & Milner (2004), the Procera hypothesis is more compatible with the TH because certain character states are shared only by salientians and dissorophoid temnospondyls; a possible example is the tympanic middle ear, of which any trace is lacking in Caudata and Gymnophionomorpha (and, as far as can be determined, Albanerpetontidae), but which several authors believe to have been present in many or most temnospondyls, including all terrestrial and amphibious dissorophoids (e.g. Bolt & Lombard 1985). Under the Batrachia hypothesis combined with the TH, homology of the salientian and the putative dissorophoid tympanum would require two (or, depending on the position of the albanerpetontids, more likely three) independent losses that resulted each time in convergence with the stapedial morphology and spatial relationships seen in lepospondyls and early amniotes but not any temnospondyls. In any case, the presence of a tympanum in temnospondyls is debatable; Laurin and Soler-Gijón (2006) reviewed evidence that most temnospondyls lacked a tympanum.

The Batrachia hypothesis appears to be better supported than the Procera hypothesis by both morphological (Ruta & Coates 2007; Germain 2008; Marjanović & Laurin 2008b, 2009) and, to a lesser extent, molecular data (Marjanović & Laurin 2007; Anderson 2008: table 2; San Mauro 2010). No analysis which included albanerpetontids has ever found Procera; but of course all of these have been morphological.

The phylogenetic position of Albanerpetontidae

Unfortunately, the confusion summarized by Marjanović & Laurin (2008b: 169) still reigns: the albanerpetontids were long interpreted as stem-caudates (Trueb & Cloutier 1991) and were again found in such a position by Anderson (2007) and Anderson et al. (2008b); arguing against this hypothesis, McGowan & Evans (1995) and McGowan (2002), as well as Marjanović & Laurin (2009; Fig. 4F), found Albanerpetontidae and Batrachia as sister-groups; Ruta & Coates (2007) recovered Albanerpetontidae and Gymnophionomorpha as sister-groups; and Pawley (2006: app. 16; Fig. 4B) and Marjanović & Laurin (2008b; Figs. 4D, E) found Albanerpetontidae and Lissamphibia as sister-groups, an arrangement called "only slightly longer" than an albanerpetontid-batrachian clade by McGowan & Evans (1995: 145) and contained in at least one of the 64 most parsimonious trees found by Ruta et al. (2003).

Potential reasons for this lack of consensus are easy to find: despite their vast stratigraphic distribution, most albanerpetontids are known only from isolated frontal and jaw bones. Complete skeletons (with fully articulated scales, possible femoral glands, and a body outline) have only been found for the Early Cretaceous *Celtedens*, and these are preserved in two dimensions; worse yet, all specimens have been split through the bone, which hampers interpretation of certain features (such as most of the skull).

Quantity and quality of data in matrices

Quantity

Schoch & Milner (2004: 355) and Anderson (2008: 234) mentioned that the matrix of Vallin & Laurin (2004), which supports the LH, is considerably smaller than those which support the TH (Ruta et al. 2003; Ruta & Coates 2007) or than some that support the PH (Anderson 2007; Anderson et al. 2008b) and used this as an argument against the LH.

However (Table 1), the matrices by Pawley (2006: app. 16) that support the LH are much bigger than that of Vallin & Laurin (2004), ranking highest in numbers of characters among all phylogenetic analyses of the phylogeny of limbed vertebrates conducted so far. They also rank second in the number of taxa (together with the source of that taxon list, the matrix by Ruta et al. 2003). The first rank in taxon number, and the second in character number, goes to Germain (2008), supporting the LH, and Ruta & Coates (2007), supporting the TH. By quantity alone, thus, there are no significant differences in size between the largest matrices which support the LH and the TH.

Importantly, character counts can be inflated in ways that mean they should not be taken at face value. One example is the “atomization” of characters by coding correlated features separately. This has the same effect as weighting some characters higher than others and should therefore be strictly avoided. Of course, which characters are correlated is usually a difficult or at least time-consuming question to answer, but some cases in the literature appear obvious to us. The probably most extreme example consists of characters 313 through 316 of Ruta et al. (2003), which are quoted below and are identical to characters 333 through 336 of Ruta & Coates (2007):

“313. Absence (0) or presence (1) of digits.
314. Absence (0) or presence (1) of no more than four digits in manus.
315. Absence (0) or presence (1) of no more than five digits in manus.
316. Absence (0) or presence (1) of no more than three digits in manus.”

If an animal has no more than three fingers per hand, it also has no more than four and no more than five; this was not taken into account in the matrices. Accordingly, Germain (2008) merged these characters into a single multistate character, which follows (translated):

“333. Primitive absence of fingers (0), more than five fingers (1), five fingers (2), four fingers (3), three fingers (4), secondary absence of fingers (5).”

This can probably still be improved – most evidently, the wordings “primitive absence” and “secondary absence” should be modified so as to avoid assumptions of secondary homology in the coding of primary homology, and the character should be ordered. Some of these concerns were addressed by Ruta & Bolt (2006: 157), who used a single (but unordered) multistate character, although (as mentioned) Ruta & Coates (2007) did not.

Quality

It has been argued that data quality is at least as important as data quantity for testing phylogenetic hypotheses (Jenner 2001; Marjanović & Laurin 2008b: 167; Morrison 2009). In this perspective, several recent studies have focused on scrutinizing published data matrices to ensure that they were of comparable scoring quality.

To verify the data supporting the TH, Germain (2008) checked the accuracy of the scoring of part of the data matrix of Ruta & Coates (2007), found the scoring of many cells to be incompatible with the descriptive literature, and rescored them. Analysis of the resulting matrix suggests that the LH (Germain 2008: fig. 5.15) is more parsimonious than the temnospondyl hypothesis (TH), but only by one step. More recently, an extension of this work by D. M. has (so far) increased the gap to eight steps (ten steps if *Gerobatrachus* and 10 other OTUs are added).

Two matrices supporting the PH have recently been scrutinized in this way. The first (McGowan 2002) initially supported a version of the PH that was replicated only by Carroll (2007). Not only, however, was this matrix tiny (20 ingroup OTUs, 41 characters); it was also riddled with cells of codings that contradict the descriptive literature. We (Marjanović & Laurin 2008b) checked every cell against the literature and specimens of *Micromelerpeton*, *Apateon*, *Microbrachis* and *Triadobatrachus*, and changed the scoring of 35% of the cells (which includes redefining the state limits of some characters and splitting or fusing others). Every change to the matrix is documented and justified in appendix 1 of Marjanović & Laurin (2008b). The resulting version of McGowan's matrix supports either the TH or the LH, the latter if either the lysorophian *Brachydectes* is added or the described material of *Doleserpeton* is considered immature or paedomorphic (see below) – adding *Gerobatrachus* has no effect, though several of the apomorphies it shares with some or all lissamphibians are not in the matrix.

The second matrix supporting the PH to be reexamined recently, that of Anderson et al. (2008), was scrutinized in less detail because of its much larger size, but rescoring following the same methods resulted in a matrix that supports the LH (Marjanović & Laurin 2009; the changes to the matrix are documented in the electronic supplementary material).

The third matrix supporting the PH (Caroll 2007) has not been subjected to the same scrutiny. However, we find several problems to be readily apparent. For instance, many characters (Carroll 2007: app. 3) contain "inapplicable" *as a state*, so that the loss of limb bones and the pelvic girdle is coded several times for the same OTU, which amounts to arbitrarily weighting such characters higher than all others. The extreme is nine times each for the humerus (characters 69 through 77, which describe the humerus, all contain a state called "does not apply") and the rest of the forelimb (characters 78 through 86); furthermore, these losses are not independent, because the humerus is never lost when the lower forelimb is still present, so that a single loss of the forelimb counts as eighteen synapomorphies. As is otherwise universal practice, these cells should be scored as "inapplicable", that is, "unknown".

Many characters in Carroll's (2007) matrix have extremely high numbers of states. The extreme is twelve states each for characters 19 and 45; there are only 23 OTUs in the matrix, which means, for these characters, on average less than two OTUs for each state. "All characters are unordered" (Carroll 2007: 119), so these characters are almost parsimony-uninformative – an unordered character of which each state only occurred in one OTU would be uninformative.

The taxon list contains suprageneric OTUs that Carroll himself (2007) explicitly considers paraphyletic with respect to other OTUs, for example "Microsauria" with respect to "*Rhynchonkos*" or "Basal Temnospondyls" with respect to "Branchiosauridae" and "Amphibamidae".

Finally, we think that some (perhaps many) codings seem difficult, if not impossible, to justify. For example, characters 115 (ossification of whole dermal skull at once vs. two orders of sequential ossification) and 116 (ossification of neural arches before centra or not) are scored as known for most "lepospondyls". In fact, the only "lepospondyl" of which even a partial skull ossification sequence (three stages) is known is the highly apomorphic aïstopod *Phlegethontia* (Anderson 2002, 2007; see also Marjanović & Laurin 2008b: 158), and the only known "lepospondyl" of which even a small part of the vertebral ossification sequence is known is *Utaherpeton* (suggested to be a basal "microsaur": Carroll et al. 1991; Carroll & Chorn 1995). The fact that the smallest known specimens of a taxon already possess all skull bones does not mean that these bones all appeared, fully formed, at the same time; it simply means that we have not found even younger, smaller, and less well mineralized individuals yet.

This review shows that, contrary to the impression that could be gathered by counting the number of published matrices, papers, or paleontologists which support the PH or, to some extent, the TH, neither hypothesis is nearly as well supported as it might seem at first glance. Conversely, the LH, although so far supported by the smallest number of studies or scientists, appears to have fairly strong support from morphological data matrices.

Evo-Devo

Ontogeny evolves. This means that Haeckel's "Biogenetic Fundamental Law" ("ontogeny recapitulates phylogeny") is wrong, so phylogeny cannot be reconstructed by merely observing ontogeny. On the other hand, it also means we can use shared derived similarities in the ontogeny of different taxa as evidence in phylogenetics – as characters in a data matrix for phylogenetic analysis. Some morphologists (Carroll 2007; Anderson 2008; Werneburg & Sánchez-Villagra 2009; Olori 2009) have argued that this should be done more often than it is.

For instance, Anderson (2008: 242) reviewed the two main well-known patterns of distal limb formation in extant tetrapods (Schmalhausen 1915; Shubin & Alberch 1986; Johanson et al. 2007: 759, 765). The first occurs in frogs and amniotes. Their limbs chondrify in a predominantly proximal-to-distal sequence, with most of the mesopodium forming before the autopodium, which in turn develops in a mostly caudal-to-cranial sequence: digital ray IV forms first (and appears to grow from the ulnare/fibulare), followed by III and V, then II, and then I. The second occurs to varying degrees in salamanders (most strongly in *Triturus* among the forms investigated so far) and, as far as its ossification sequence suggests, the temnospondyl *Apateon* (Fröbisch et al. 2007). There, the digital rays appear in a cranial-to-caudal sequence, so that I and/or II appear first and seemingly without direct contact with more proximal elements, followed by III, then IV, and then (in the foot) V, and only afterwards is the chondrification of the carpus/tarsus completed (from both sides, proximal and distal). Thus, limb development includes two partly linked characters: the order in which digits appear (cranial to caudal or the reverse), and the proximo-distal development sequence (proceeding in a proximo-distal order or proceeding to an extent from the metapodials proximally).

Furthermore, "the salamander pattern" is not monolithic, and this complicates the discussion of these characters. In the salamandrid *Triturus* (Blanco & Alberch 1992), as well as in *Ambystoma* (Franssen et al. 2005), the basale commune (distal carpals/tarsals 1 + 2, see below) becomes a separate cartilaginous element before all other mesopodials, so that much of the mesopodium forms from distal to proximal, very much unlike in amniotes or frogs; and in *Salamandrella*, a hynobiid and thus a generally rather plesiomorphic salamander, as well as in the highly nested plethodontid *Desmognathus aeneus*, which has direct development rather than a free-swimming larva, the mesopodium forms mostly in a proximal-to-distal sequence (though the centralia form last) (Vorobyeva & Hinchliffe 1996; Hinchliffe & Vorobyeva 1999; Franssen et al. 2005). Finally, digit III, not IV, is the first to appear in the frog hand (IV is in the foot).

Craniocaudal condensation sequence of digits

It has been suggested that the cranial-to-caudal pattern of salamanders is due to natural selection on pond-dwelling larvae that use their forelimb buds for locomotion while the digits are developing (Schmalhausen 1915; Hinchliffe & Vorobyeva 1999; Franssen et al. 2005). The digits at the cranioventral corner of the limb – I and II – are thus predicted to form first because they are located most closely to the substrate and hence are the most solicited in larval locomotion. *Salamandrella* larvae have a long "fin" that is supported by the developing fingers I and II, while *Ambystoma* and *Triturus* larvae touch the substrate directly with the tips of those fingers; this could explain the differences among salamanders with pond-dwelling larvae. Amniotes and frogs lack selection pressure for precocious development of I and II and are free to emphasize those digits that are longest and strongest in the adult, namely III in the hand and IV in the foot (in frogs) or IV in both (in amniotes), from the beginning of development. In *Desmognathus aeneus*, a salamander that spends the entire "larval" stage in the egg and hatches fully metamorphosed, finger III acquires much of its cartilaginous skeleton before that of finger I starts forming (although II is still the first); in the adult, as in the soft anatomy of the embryo, II and III are equal in length and much longer than I and IV (Franssen et al. 2005). *D. aeneus* further resembles amniotes and frogs in that the digits form as a paddle that later subdivides by apoptosis; in other salamanders such as *Ambystoma*, every digit is a separate outgrowth from its limb bud (Franssen et al. 2005).

We suggest that the use of the developing forelimbs in locomotion is plesiomorphic for limbed tetrapods. While difficult to test, this hypothesis is supported by the antiquity of the "salamander pattern" of development (*Apateon* is Pennsylvanian in age; Fröbisch et al. 2007) and the fact that free-swimming, pond-dwelling larvae without the specializations of tadpoles are optimized as plesiomorphic for limbed vertebrates. Such larvae with a long median fin (representing the fused dorsal, caudal, and anal fins) and external gills are shared at least by lungfishes, temnospondyls, and seymouriamorphs. This morphotype, together with any use of developing forelimbs, was lost in frogs due to the evolution of the "gill lid" which covers the forelimb bud in tadpoles almost all the way to metamorphosis, and independently in amniotes and direct-developing salamanders because the entire larval stage was transferred into the egg (or into the mother).

There is no known outgroup that could be used to polarize this character. Under the TH, the LH, and Anderson's version of the PH, it therefore requires at least three steps (appearance of digits included), regardless of what the ancestral condition is. Under Carroll's version of the PH, where the caudates are branchiosaurids, the frog-amniote pattern is optimized as ancestral (two steps). Thus, in isolation, this character supports Carroll's version of the PH over all alternatives, as noted by Fröbisch et al. (2007, 2010) – unless arguments such as our suggestion above can support the salamander pattern as ancestral.

Circumstantial evidence for the salamander pattern being indeed plesiomorphic comes from Early Carboniferous stem-tetrapods like the colosteid *Greererpeton* (Godfrey 1989) and the anthracosaur *Proterogyrinus* (Holmes 1980, 1984). In the foot of *Greererpeton*, all proximal and central tarsals are ossified, while of the distal ones, only the first is present even in articulated specimens. In *Proterogyrinus*, the only carpals to ossify at all (even though all tarsals are ossified) are the first and the second distal ones. In contrast, in the Early Permian diadectomorphs *Tseajaia* and *Orobates* (close relatives of the amniotes), the only ossified distal tarsal is the fourth (Moss 1972; Berman & Henrici 2003; Berman et al. 2004), as expected for the frog-amniote pattern.

Proximodistal condensation sequence of appendages

Johanson et al. (2007) provided the novel suggestion that the metapodial-to-mesopodial condensation pattern is primitive. Based on their study of the development genetics of the

Australian lungfish (*Neoceratodus forsteri*), they suggested that the “independent radials” are homologous to digits. The radials form without connection to the rest of the fin skeleton and only later form joints with it, as in salamanders, in which the digits form independently of the rest of the limb skeleton and only later connect to it by the appearance of the missing carpals/tarsals (Johanson et al. 2007: 765). This suggests that it is plesiomorphic for the digital rays to form independently of the rest of the limb as observed in salamanders (Johanson et al. 2007: 765–766). This hypothesis is equally parsimonious under all current phylogenetic hypotheses.

As Johanson et al. (2007: 766) noted, the salamander pattern being primitive could explain why the chondrification and the ossification sequence do not match in frogs and amniotes. Like those of *Apateon* and salamanders, the anuran and amniote metapodials and digits ossify before the carpals/tarsals, while the chondrification sequence is different. The chondrification sequence, it seems, has undergone more evolution than the ossification sequence. This would further explain why the number of centralia in the carpus and tarsus of limbed vertebrates in general is so unstable (ranging from 0 to 4 even in cases where fusion events can be excluded) and why these bones do not line up with the distal carpals/tarsals – the more space there is between the digital rays and the unconnected rest of the limb, the more centralia can form (Johanson et al. 2007: 765–766).

The basale commune

The *os basale commune*, which represents distal carpals/tarsals 1 and 2 (they condense, chondrify, and ossify as a unit), is present in all salamanders. It was unknown elsewhere until Anderson et al. (2008b) reported the presence of a basale commune in the tarsus of the amphibamid temnospondyl *Gerobatrachus*. Its presence is a potential synapomorphy of *Gerobatrachus* and salamanders which could bolster the PH (though not Anderson’s particular version of it). As we have explained previously (Marjanović & Laurin 2008b: 168–169, 2009: electronic supplementary material 1: character 207), we are not convinced that either of the two preserved tarsals in the feet of *Gerobatrachus* is a basale commune: judging from comparisons of the drawings and photos of Anderson et al. (2008b) to the few known complete tarsi of other temnospondyls (among which we had overlooked *Eoscopus*: Daly 1994: fig. 11) and other stem-tetrapods – as opposed to salamanders –, the most likely identity of the supposed basale commune is the centrale 2, followed closely by several other possibilities, but not distal tarsals 1 or 2 or what their hypothetical fusion product (or for that matter a neomorphic bone that would occupy their spaces) would look like. (Comparing the very incompletely preserved tarsus of *Gerobatrachus* to the tarsi of salamanders and determining the homologies of the tarsals of *Gerobatrachus* on that basis would amount to assuming a close relationship between *Gerobatrachus* and salamanders *a priori*. Before all else, we think, *Gerobatrachus* should be compared to its fellow amphibamid *Eoscopus*, followed by their fellow dissorophoid *Ecolsonia*; all temnospondyl tarsi, all the way to the very early representative *Balanerpeton* which probably has a phylogenetic position somewhere close to the origin of temnospondyls, seem to be very similar.) Nonetheless, scoring *Gerobatrachus* as possessing a basale commune in the matrix of Marjanović & Laurin (2009) has no effect on the (LH-supporting) results except for adding a step to the four most parsimonious trees; even the Bremer value of Amphibia (i.e., the “lepospondyl”-lissamphibian clade) does not decrease.

Sigurdsen & Bolt (2009: fig. 3A) report the absence of a basale commune in the carpus of *Doleserpeton*, a close relative (perhaps the sister-group) of *Gerobatrachus*. This indicates that the basale commune, if present in *Gerobatrachus*, is not widespread among amphibamids.

Paedomorphosis, peramorphosis, miniaturization: cases where "ontogeny discombobulates phylogeny"

Paedomorphosis is the presence of character states in the adult that were, in ancestors of the taxon in question, restricted to earlier ontogenetic stages; peramorphosis is the opposite, namely the exaggeration of adult features that fail to stop their development. Importantly, both can be restricted to parts of the body and therefore occur in the same animal. For instance, compared to the ancestral ape condition, the human head shape is paedomorphic while human hindlimb length relative to the rest of the body is peramorphic. However, paedomorphosis is commonly an organism-wide phenomenon caused by neoteny (slowed-down development of all of the body except the sexual organs) or progenesis (precocial development of the sexual organs truncating the development of the rest of the body). This is expected to result in the correlated appearance of many juvenile character states in the same adult, and convergent evolution of paedomorphosis should thus result in many convergent similarities between the adults of disparate taxa (such as, possibly, the "absence characters" of Schoch & Milner [2004] or "loss features" of Anderson [2008: 240]; on these specifically, see Marjanović & Laurin [2009]). If these character states are all taken at face value in a phylogenetic analysis, they will be counted as large numbers of correlated and therefore spurious synapomorphies between paedomorphic taxa. Wiens et al. (2005: 96) suggested three methods for dealing with paedomorphosis in phylogenetic analysis and found disadvantages to all of them, but recommended to score the adult morphology of paedomorphic OTUs as unknown.

We have tried (Marjanović & Laurin 2008b, 2009) to implement a modified version of this approach when scoring taxa that are known to exhibit paedomorphosis and taxa known only from immature and/or paedomorphic individuals (a common occurrence in the fossil record). The modification is to score only those characters as unknown that are known to be influenced by ontogeny, and even then only if the observed state is limited to immature stages in close relatives. This eliminates the main disadvantage of the method recommended by Wiens et al. (2005), which is that we would end up without any data for some OTUs. However, it combines the disadvantages of the other methods, even though we still think it combines the highest number of advantages.

Naturally, determining which individuals are immature or paedomorphic is not always trivial. Wiens et al. (2005) worked on extant taxa with known ontogenies and a clear-cut metamorphosis that makes it relatively easy to determine whether a species is paedomorphic and whether a character is affected by this (even though there are phenomena like the partial metamorphosis of cryptobranchids and *Amphiuma*, or the miniaturization of some fully metamorphosing plethodontids such as *Thorius* and *Oedipina*). Moreover, Urodela is a fairly closely-knit taxon of obvious monophyly, which means that inferences can easily be drawn from the ontogeny of one species to that of another; and the data matrix of Wiens et al. (2005) contains characters that specifically describe larval morphology; such characters are absent from the matrices that we have recoded. More generally, among Paleozoic limbed vertebrates, reasonably complete growth series are only known from a few temnospondyls (including, among the dissorophoids, several branchiosaurids and micromelerpetontids), and a clearly delimited metamorphosis has only been described in the branchiosaurid *Apateon* (Werneburg 1991; Schoch & Fröbisch 2006), while other temnospondyls developed in more gradual ways (Schoch 2001, 2009). Among "lepospondyls", the ontogeny of the postcranial skeleton is known in some detail from a few representatives such as the aquatic "microsaurs" *Hyloplesion* (Carroll & Gaskill 1978) and *Microbrachis* (Olori 2008), but a skull ossification sequence has only been discovered for the aïstopod *Phlegethontia*, and that sequence comprises only three known stages (Anderson 2002, 2007). The ontogeny of other taxa can at present only be inferred by phylogenetic bracketing, and this method quickly reaches its limits, as the following example will illustrate.

When discussing the LH, Schoch (2002: 294) suggested that lysorophian “lepospondyls” in general and *Brachydectes* (the only well-known lysorophian) in particular are “heavily paedomorphic”, and that this feature could be responsible for the position the lysorophians occupy in the LH by resulting in correlated derived states shared by lysorophians and some or all lissamphibians. As previously pointed out (Marjanović & Laurin 2008b: 157–158), *Brachydectes* indeed shows several features that indicate paedomorphosis in osteichthyans generally, such as the persistent suture between left and right neural arches (Wellstead 1991). Whether other features could be due to paedomorphosis is, however, difficult to ascertain.

One case is the absence of the jugal bones in lysorophian skulls (“leaving” a gap in the lateroventral margin of the skull). The jugal is likewise missing in frogs, salamanders, and extant caecilians (but not *Eocaecilia* or albanerpetontids), and appears late in temnospondyl ontogeny, staying small and apparently never reaching the (paedomorphically short) maxilla in the highly paedomorphic branchiosaurid *Schoenfelderpeton*. It is therefore tempting to attribute the lack of jugals in lysorophians (and perhaps their short maxillae) to their paedomorphosis. But such an inference would be based on an assumption of a close relationship to temnospondyls. To interpret the lysorophian skull from an evo-devo perspective, we need to examine the ontogeny of at least one (other) close relative of lysorophians, ideally another unquestioned “lepospondyl”, which can only be *Phlegethontia* at present (see above). In *Phlegethontia*, the jugal is present in the second of the three known stages, before even the premaxilla; as previously pointed out, the ontogeny of *Phlegethontia* does not lead through a stage that resembles the adult (and only known) condition of lysorophians (Marjanović & Laurin 2008b: 158).

We suspect that the absence of the jugal is not paedomorphic in lysorophians, but may be related to jaw mechanics instead – the “orbitotemporal fenestra” is drastically enlarged caudally, apparently to provide space for jaw-closing muscles caudal to the eye (Wellstead 1991: fig. 2E).

The jugal is of particular interest because its absence in frogs and salamanders (and, before the discovery of *Eocaecilia*, caecilians) has often been thought to be explicable by paedomorphosis from a dissorophoid temnospondyl ancestor which truncated its ontogeny before the jugal and several other dermal bones of the skull and shoulder girdle ossified (Schoch & Milner 2004; Carroll 2007). In turn, this paedomorphosis has itself been suggested to be part of miniaturization – peramorphosis of the endochondral skeleton leading to truncation of growth and paedomorphosis of the dermal skeleton, as observed in certain especially tiny extant plethodontid salamanders. But because “lepospondyl” skull ossification sequences are unknown apart from *Phlegethontia*, to accept this scenario would amount to assuming a close relationship between dissorophoids, frogs and salamanders (in other words, the TH or the PH). We have therefore continued to score the jugals in frogs and salamanders as absent (Marjanović & Laurin 2008b, 2009).

Another feature of lysorophians, the broad cultriform process and consequent lack of interpterygoid vacuities, can be interpreted as due to paedomorphosis if a lissamphibian-like ontogeny is assumed: in lissamphibians, the cultriform process becomes relatively narrower and the interpterygoid vacuities broader during ontogeny (Reiss 2002), so that *Brachydectes* resembles larval and neotenic lissamphibians (Marjanović & Laurin 2008b: app.-table 3) but neither adult lissamphibians nor temnospondyls of any ontogenetic stage (Schoch 2001, 2002). This may hint at a more lissamphibian-like ontogeny in lysorophians than in temnospondyls.

Other features might be compatible with this, but have a more complex distribution: “for example, the arrangement of the vomerine teeth of *Brachydectes* [Wellstead 1991: fig. 2B] is identical to that of larval and paedomorphic salamanders, but never seen in anuran or gymnophionan ontogeny” (Marjanović & Laurin 2008b: 157), let alone temnospondyl ontogeny. “Lepospondyl” ontogeny is too poorly known for comparisons.

Doleserpeton and Lissamphibia share the presence of regular-sized teeth instead of a tusk and its replacement pit on each vomer and palatine. This feature has been considered an important synapomorphy of these taxa in many publications (Bolt 1979, 1991; Schoch & Milner 2004). However, such teeth are also present in premetamorphic and juvenile postmetamorphic specimens of its close relative *Amphibamus*, except in the largest known specimen, which has a tusk instead (Daly 1994). The known material of *Doleserpeton* has been considered juvenile or progenetic (Bolt 1977; 1979: 553, 560), though “probably postmetamorphic” (Bolt, 1979: 554), and “miniaturized”, i.e., paedomorphic in the dermal skeleton (Sigurdsen 2008). We therefore think that *Doleserpeton* should be scored as unknown for this character in phylogenetic analyses (Marjanović & Laurin 2008b: 157, 180, 193). *Gerobatrachus* has even smaller teeth (arguably “denticles”) instead of tusks, but its ontogenetic age is unclear (Marjanović & Laurin 2008b: 158–159). Furthermore, with the exception of the “microsaur” *Crinodon* (Carroll & Gaskill 1978), “lepospondyls” uniformly lack vomerine fangs, like lissamphibians.

Finally, as their name suggests, many “microsaurs” are so small that miniaturization effects may be expected (e.g. Carroll 2007). Unfortunately, the ontogeny of large as well as small “microsaurs” – and “lepospondyls” in general – is (as mentioned) so poorly known that only vague suggestions have ever been made as to which characters could be affected by this. In our phylogenetic analyses, we have therefore taken “microsaur” anatomy at face value. We hope that this tacit assumption will become testable by new discoveries.

Skull ossification sequences – or: phylogenetics with two taxa

Carroll and various coauthors have pointed out the close similarities between the cranial ossification sequences of the extant hynobiid salamander *Ranodon* and the branchiosaurid dissorophoid temnospondyl *Apateon* and drawn the conclusion that the salamanders are branchiosaurids (Carroll et al. 1999; Schoch & Carroll 2003; Carroll et al. 2004; Carroll 2007; see also Schoch & Fröbisch 2006). However, this argument suffers from problems inherent in both its method and its data.

Firstly, this argument requires the assumption that the skull ossification sequences of salamanders are more similar to those of branchiosaurids than to those of other amphibamids, the “lepospondyls” *Rhynchonkos* and *Brachydectes*, and other potentially relevant taxa. This assumption cannot be tested at present, because the skull ossification sequences of all these animals are unknown (see above on *Phlegethontia*). This alone invalidates the entire argument (Ruta & Coates 2007).

Secondly, the similarities between *Ranodon* and *Apateon* may not be all that close (Anderson 2007: 191).

Furthermore, it appears that many of the character states that *Ranodon* shares with *Apateon* but not with frogs or caecilians are not synapomorphies, but symplesiomorphies: Schoch (2006) found them to be shared by the actinopterygians *Amia*, *Acipenser* and *Polypterus*, as well as the lungfish *Neoceratodus*. Indeed, his phylogenetic analysis of cranial ossification sequences (fig. 1) recovered *Apateon* as a stem-tetrapod; as Schoch (2006: 529) noted, this is predicted by the LH but not compatible with the TH or the PH.

Lastly, the mentioned argument requires the assumption that *Ranodon* has conserved the ancestral urodelan skull ossification sequence. While this animal is generally rich in plesiomorphies, it is not the ancestral urodele (crown-group salamander), let alone the ancestral caudate (total-group salamander).

Reconstruction of the ancestral urodelan skull ossification sequence using a novel method based on squared-change parsimony and phylogenetically independent contrasts shows that, for four bones, the 95% confidence interval excludes *Apateon* even though those intervals are for the most part very broad (Germain & Laurin 2009). According to simulations in the same publication, the new method outperforms the most sophisticated previously existing method, event-pair cracking using Parsimov (Jeffery et al. 2005), in both type I error rate and power; nonetheless, Parsimov yields similar results, except that even *Ranodon* is sometimes found to lie outside the range of most parsimonious ossification times for the ancestral urodele (confidence intervals cannot be calculated by that method). Thus, the similarities in the skull ossification sequences between *Apateon* and the ancestral urodele are smaller than implied in most studies. Incidentally, Germain & Laurin (2009: fig. 5) confirm Anderson's (2007: 191) statement that *Apateon* and *Ranodon* are not very similar to each other either – for many bones they lie on opposite sides of the midpoint of the confidence interval for the ancestral urodele.

New discoveries of fossils will most likely be necessary if cranial ossification sequences are to become a significant source of information in the phylogenetics of early limbed vertebrates. The lack of known cranial ossification sequences is not restricted to "lepospondyls" – even in the famous *Eusthenopteron*, which could otherwise serve as an appropriate outgroup for such studies, the smallest known specimens already have a full complement of fully ossified dermal skull bones, even though changes in proportions and the gradual ossification of the postcranial skeleton have been studied in detail in large collections of larger individuals (Schultze 1984; Cote et al. 2002).

Homologies in the lysorophian skull roof

With the publication of Laurin & Reisz (1997), the lysorophian "lepospondyls" regained a prominent position in the discussion on the origin of the extant amphibians. One of the characters that supported the finding of lysorophians and lissamphibians as sister-groups (Laurin 1994, 1998; Laurin & Reisz 1997, 1999; Vallin & Laurin 2004; Pawley 2006: figs. 91, 92; see also app. 14) was their shared lack of postorbital bones in the skull.
Recently (Marjanović & Laurin 2008b: 155–157), however, we offered a new interpretation of the identities of the bones that make up the caudal part of the skull roof in lysorophians; that is, we think the bones identified as the tabular and postparietal by Wellstead (1991) can be more parsimoniously considered the postorbital and tabular, respectively. In sum, this interpretation (Fig. 3) makes the lysorophians slightly less lissamphibian-like than Wellstead's (1991): although the postparietals are absent (like in all known lissamphibians except *Eocaecilia*), the postorbitals are present, unlike in all known lissamphibians, including *Eocaecilia* (Jenkins et al. 2007).

Importantly, this interpretation does not depend on the assumption of a close relationship between lysorophians and brachystelechid "microsaurs"; the latter (*Batropetes* in Fig. 3) should merely be considered an example of "lepospondyls" with large orbits and a rostrocaudally narrow cheek region, a condition which we expect to lead to dorsoventrally long and rostrocaudally narrow postorbitals and squamosals.

As an interesting byproduct, our interpretation allows more confident identification of the putative posttemporal foramen of *Brachydectes*. In our interpretation, the tabular borders this foramen as in most early limbed vertebrates. In Wellstead's (1991) interpretation, the postparietal contributes to its margin, which is unusual; this led Wellstead (1991: 18) to question the identification of the foramen in question as homologous to the posttemporal fenestra. Moreover, our interpretation restores the contact between tabular and exoccipital, another widespread plesiomorphy.

Dating the appearance of Lissamphibia

Assuming its monophyly, the age of Lissamphibia is highly contentious. Some authors (San Mauro et al. 2005; Roelants et al. 2007) proposed an origin of Lissamphibia in the Late Devonian (360–370 Ma ago). Hugall et al. (2007) found mid-Carboniferous (323 ± 19 Ma based on nucleotide data) or Late Carboniferous/Early Permian ages (292 ± 28 Ma based on amino acid data), about both of which they cautioned that, "[g]iven that all the lissamphibian nodes are outside the most basal calibration employed, they may be prone to being over- (rather than under-) estimated" (Hugall et al. 2007: 558). Using three methods for molecular dating and his preferred set of calibration points, San Mauro (2010: table 3) found Late Carboniferous point estimates surrounded by 95% confidence intervals that sometimes extend into the Early Carboniferous and/or the Early or even Middle Permian. Our results (Marjanović & Laurin 2007, 2008a) suggest a yet more recent, Permian age (300–255 Ma).

Molecular dating offers a way of answering the question of when a cladogenesis happened without having to rely entirely on the imperfect fossil record. Dates estimated this way for the origin of Lissamphibia have been advanced as support for the TH (Zhang et al. 2005) and the PH (Lee & Anderson 2006; Anderson 2008). While these particular arguments relied on a misunderstanding of the literature about the fossil record of temno- and lepospondyls in the first case and on questionable decisions about calibration points in both cases (Marjanović & Laurin 2007), divergence dates can be used to discriminate between phylogenetic hypotheses (as also noted by San Mauro [2010], who used his molecular date estimates for cautiously arguing against the PH).

Despite being imperfect, however, the fossil record itself can also provide estimates of divergence dates if used as the input for methods that take its sampling density into account. We have developed two such approaches (Marjanović & Laurin 2007, 2008a), which are summarized below along with recent work in molecular dating.

Contrary to what San Mauro (2010: 556) claims, we have never made an "assertion that the lissamphibian fossil record is complete enough to be read literally". It is not; this is why two such complex approaches are necessary.

Fossil-based supertree

Any taxon is at least as old as its oldest known fossil representative. How much older it is depends on how many internodes (branches) separate that fossil from the origin of the taxon, and on how long those internodes are. The first question can be approximately answered by a phylogenetic tree with the fossil in it; the answer to the second can be estimated by testing if different arbitrary but realistic values give similar results.

Therefore, we (Marjanović & Laurin 2007) used a set of 14 assumptions about minimal branch lengths (Table 2) on a hand-made supertree of Lissamphibia. The minimal length of terminal branches ranged from 0.1 Ma to 5 Ma or a whole geological stage, and the minimal length of terminal branches varied from 0.1 Ma to 5 Ma (a 50-fold range of values). Because of these wide ranges, the age of clades with a poor fossil record, such as Ranoidea (Table 2), depends strongly on the assumptions about minimal branch lengths. This is because in such cases the oldest fossil is usually deeply nested, and the method yields a minimal clade age equal to the age of the oldest fossil plus the sum of all internal branches connecting it to the root of the clade. Thus, the age of Ranoidea varied between 34 and 74 Ma (Table 2). Conversely, clades with a fairly good fossil record typically have fossils close to the base, and in such cases assumptions about minimal branch lengths have little impact. For Lissamphibia, this procedure yielded ages that varied from 246 to 267 Ma ago (Fig. 2C, Table 2). The variation of about 21 million years found for the origin of Lissamphibia yielded by this method is almost identical to the size of the 95% confidence interval of the date of origin of Lissamphibia found by the molecular dating study of Zhang et al. (2005), suggesting that it is not artificially narrow.

We also (Marjanović & Laurin 2007) assessed the impact of phylogenetic uncertainty (in the form of polytomies) by randomly resolving each polytomy in our supertree ten times and comparing the average age of several crown-clades under these random resolutions with the age under the preferred tree. The results show that the use of polytomies tends to slightly inflate the age of most clades (Table 3).

These results are significant with respect to the PH: the date of origin of Lissamphibia is incompatible with the PH, a fact that *does not automatically follow* from lissamphibian monophyly and therefore constitutes *additional* evidence against the PH.

Stratigraphy-based, phylogeny-free dating

Marjanović & Laurin (2008a) modified a method first proposed by Marshall (1997) and used it to date the appearance of Lissamphibia. This method calculates a confidence interval on the appearance of a taxon based on the stratigraphic distribution of the horizons or localities that have yielded fossils of this taxon (1207 localities in this case) and the following factors that determine how many fossils we should expect to be known from each geological stage: the relative area of exposed rocks from the relevant stages, exponential-growth models that differ by the assumed starting date of lissamphibian diversification, and the assumed effects of mass extinctions taken from the literature and based on observed extinction rates in various taxa (too little is currently known about the history of lissamphibian diversity to estimate this from their fossil record). The Devonian and Early Carboniferous starting dates were taken from Roelants et al. (2007) and Zhang et al. (2005) in the two different sets of calculations of stratigraphic confidence intervals in order to sample a broad range of biologically plausible models and assumptions. Realistic settings on the other variables result in 75% confidence intervals that stay within the Permian and 50% confidence intervals that begin no later than the Middle (Guadalupian) or even Late Permian (Luopingian) (Fig. 2B; Marjanović & Laurin 2008a: fig. 4C1–4).

In the future, this method could be improved by taking changes in the ratio of terrestrial to marine sediments over time into account (it was assumed to be constant in Marjanović & Laurin [2008a]), but we do not expect this to result in large changes to the results because our models explained from 85 to 90% of the variance in the temporal distribution of fossiliferous localities that have yielded lissamphibians.

Molecular dating, choice of calibration dates

Some molecular estimates of the time of origin of Lissamphibia suggest Early Carboniferous (Viséan or ealier) or even Devonian dates of origin of Lissamphibia (references in Anderson [2008] and San Mauro [2010]). The choice of characters (that is, genes: mitochondrial or nuclear, coding for a wide variety of proteins, tRNAs and/or rRNAs) does not seem to have a noticeable effect on the divergence date estimates. Brochu (2004a, b, 2006) and Marjanović & Laurin (2007) showed that the calibration points are most critical, and that it is necessary to use multiple calibrations, both shallow and deep, both within and outside the clade of interest. Indeed, several of the most recent studies (Roelants & Bossuyt 2005; San Mauro et al. 2005; Roelants et al. 2007; Marjanović & Laurin 2007; Vieites et al. 2007; Igawa et al. 2008; some of the analyses by San Mauro 2010) have used such a combination of calibration constraints. An important difference between the studies, however, lies in the use of maximum ages which most of the recent studies used only for external constraints. Rodríguez-Trelles et al. (2002) suspected this fact of artificially inflating molecular divergence date estimates and predicted that the use of maximum ages would bring these estimates into much closer accord with the fossil record. Marjanović & Laurin (2007) used maximum age constraints for two or three internal calibration points (the origins of Urodela, Bombinanura, and in some analyses the tetrapod crown-group) in all analyses that resulted in Permian dates of origin for Lissamphibia. (We also proposed [Marjanović & Laurin 2007: 381–382] maximum ages for the origins of Pipoidea and Batrachia, but did not use them in any analysis.) The prediction by Rodríguez-Trelles et al. (2002) was further confirmed by San Mauro (2010: table 3). San Mauro's preferred analyses had only external calibration points and found the abovementioned early Late Carboniferous dates for the origin of Lissamphibia, with confidence intervals of various sizes as mentioned. When he added internal calibration points with maximum ages from Marjanović & Laurin (2007), a narrow 95% confidence interval (320–292 Ma ago; latest Early Carboniferous to earliest Permian) resulted, with a midpoint of only 305 Ma ago (latest Carboniferous); adding internal calibration points without maximum ages instead resulted in older divergence date estimates than those found by the preferred analyses.

Use of the internal calibration constraints was validated by testing the overall quality of the lissamphibian fossil record using the time-calibrated supertree mentioned above. We chose those maximum ages based on the the presence of older sister-taxa of the clade of interest (Fig. 5), as suggested by Raaum et al. (2005). We furthermore selected only dates that did not strongly depend on assumptions about minimum branch lengths (Table 2). This method is based on the assumption that the fossilization potential of lineages within and outside the crown-groups should be comparable.

We seem to have failed to make sufficiently clear that we used these selection criteria to select upper bounds of calibration constraints (Marjanović & Laurin 2007: 380). For instance, Anderson (2008: 242) asked: "How can one be certain that *Eocaecilia* is placed in the fossil record close to the real time of divergence with no ghost lineage, when above it in the stratigraphic column there are two known ghost lineages totaling approximately 90 million years?" Similarly, San Mauro (2010: 556) has argued against using *Eocaecilia* to constrain a calibration point. It is not *possible* to use the Early Jurassic *Eocaecilia* to constrain a calibration point: *Eocaecilia* is practically alone on the long gymnophionomorph stem, making it useless for calibration points within Gymnophionomorpha, and Batrachia (*Triadobatrachus* and *Czatkobatrachus*) is known to be older than *Eocaecilia*, making *Eocaecilia* useless for calibration points within Batrachia or any clade that contains the latter. Therefore we deliberately did not use *Eocaecilia* as a calibration constraint.

San Mauro (2010: 556), however, gives an entirely different reason for why *Eocaecilia* should not be used to constrain a calibration point: its "phylogenetic affinities are still equivocal (Anderson, 2008; Jenkins et al., 2007)". In fact, in their monographic redescription of *Eocaecilia*, Jenkins et al. (2007) have shown that a large number of gymnophionomorph autapomorphies are present in *Eocaecilia* and confirmed the consensus that its phylogenetic position is as shown in Figure 2A. Anderson (2008) explicitly agreed that *Eocaecilia* is closely related to Gymnophiona, and mentioned two of those autapomorphies. The only skepticism we have encountered so far has come from a small number of neontologists such as a reviewer of Marjanović & Laurin (2008b) who emphasized the many differences between *Eocaecilia* and Gymnophionomorpha but neither addressed the synapomorphies of these two taxa (and the Early Cretaceous *Rubricacaecilia*, which is in some respects intermediate: Evans & Sigogneau-Russell [2001]; see Fig. 2A) nor suggested any alternative phylogenetic position for *Eocaecilia*. We are not aware of any publication that would substantiate this vague doubt. A fair amount of phenetic distance between *Eocaecilia* and Gymnophiona has to be expected from the former's Early Jurassic age. The only sense in which the phylogenetic position of *Eocaecilia* is unclear (at present) is that in which the position of Gymnophionomorpha as a whole is unclear: TH, LH, or PH.

The global test on the quality of the fossil record that we performed on our dataset consists of comparing the order of appearance of taxa expected on the basis of the topology of the reference tree to the observed stratigraphic order of appearance of the taxa. Similar comparisons are done for populations of trees in which the stratigraphic ranges of taxa have been randomly permuted. Significance is established by the proportion of randomized trees that have as good a match (or better) than the reference tree. This test was performed using Ghost (Wills 1999), and it yielded a highly significant correlation ($p \sim 0.0001$; Marjanović & Laurin 2007: 380).

The significance of this test seems not to have been fully appreciated. Anderson (2008: 242) doubted the relevance of the result, claiming that Huelsenbeck (1994) "demonstrated that a relatively low number of consistent nodes (four in his example) are necessary to find significant consistency of the tree with the fossil record, and this significant consistency remains present in all trees several steps from most parsimonious". However, Huelsenbeck (1994: 476) explained the results of his analyses of one particular dataset (fig. 2); he did not draw any generalizations from it – to the contrary, his table 1 lists two trees that are inconsistent with the stratigraphic record even at the $p \leq 0.1$ level despite having 7 and 25 nodes that are consistent with the stratigraphy (out of 10 and 37 possible nodes). Thus, the lissamphibian record – although highly incomplete in absolute terms! – is "probably not too incomplete" (Marjanović & Laurin 2007: 385) to supply maximum ages for a few carefully selected calibration points.

Igawa et al. (2008), who used minimum and maximum ages for two (out of five) internal and all external calibration points, nonetheless found Lissamphibia to be 335 (352–317) Ma old. This result is very similar to the one by Zhang et al. (2005), who used an earlier version of the same dataset (with fewer taxa) and the same programs, but only two calibration points, both of them external. At first sight, this might be taken to mean that the number and maximum ages of calibration points do not matter much. In contrast, we would like to point out that some of the calibration dates used by Igawa et al. (2008: table 2) are based on misunderstandings of the paleontological literature. An external and two internal calibration constraints shall serve as examples:

The origin of Archosauria (the divergence between the crocodile and bird lineages) is put at 252–257 Ma ago by Igawa et al. (2008), and Reisz & Müller (2004) are cited as the source. In fact, Reisz & Müller (2004) attribute this age to the crocodile-squamate (archosauromorph-lepidosauromorph) divergence, which preceded the crocodile-bird divergence. Reisz & Müller (2004) do not mention the latter much, but no member of Archosauria is known from earlier than the Middle or possibly latest Early Triassic ("rauisuchians" in Ivakhnenko et al. 1997), around 240 to 245 Ma ago; Müller & Reisz (2005) suggest maximum and minimum ages of 251 and 243 Ma for the crocodile-bird divergence based on the presence of numerous stem-archosauriforms but the absence of archosaurs in the Early Triassic record, and the presence of one stem-archosauriform but no archosaurs in the Permian sediments investigated so far (thus fulfilling the criteria by Raaum et al. 2005).

Igawa et al. (2008) further attribute a minimum age of 168 Ma to the divergence between Discoglossidae and Bombinatoridae, citing Milner (1993) who called *Eodiscoglossus oxoniensis* the earliest known discoglossid. This reflects the imprecise taxon delimitation in rank-based nomenclature (Laurin 2008): for much of the 20th century it was usual to use the name Discoglossidae for what is now more often called Discoglossoidea, a clade that includes both Discoglossidae in the current sense and Bombinatoridae (formerly Bombinatorinae). *Eodiscoglossus* is at present a discoglossoid incertae sedis, and there is no reason to assume it is a discoglossid. It is potentially useful to molecular dating as the oldest known crown-group frog (Fig. 5; Marjanović & Laurin 2007), but cannot presently be used to date cladogeneses within Discoglossoidea. In fact, the minimal divergence date between Discoglossidae and Bombinatoridae is poorly constrained by the fossil record because the affinities of most relevant fossils are uncertain (Marjanović & Laurin 2007: fig. 5) – it could be as recent as Lutetian (middle Eocene, less than 49 Ma ago).

Finally, both the minimum and the maximum dates given for the divergence between Rhacophoridae and Mantellidae by Igawa et al. (2008: table 2) are not directly based on the fossil or the geological record. Instead, they are *results* of the molecular dating analysis by Bossuyt & Milinkovitch (2001). To use such a date as a calibration point for molecular divergence dating is suboptimal (e.g. Graur & Martin 2004).

Incidentally, Anderson (2008: table 2) cites Igawa et al. (2008) as having found Lissamphibia to be 355 (370–340) and Batrachia to be 335 (352–317) Ma old, which would be more compatible with the PH than with the LH or the TH. In fact, the latter is the age of Lissamphibia found by Igawa et al. (2008); the former is the age of the tetrapod crown-group, in other words, the divergence between the ancestors of Lissamphibia and those of Amniota (Igawa et al. 2008: 123).

Altogether, keeping in mind the caveats discussed above, it appears that molecular dating refutes, rather than supports, the PH (as noted by San Mauro [2010]).

Conclusions

At present, the lepospondyl hypothesis on the origin of the extant amphibians (LH) appears to be somewhat better supported than the temnospondyl hypothesis (TH) and considerably more so than the polyphyly hypothesis (PH), based on several independent lines of evidence including phylogenetics and three methods of dating the divergence of the extant amphibians from each other. If correct, this implies that, while thousands of (mostly endangered) species of “lepospondyl” descendants are still with us, the temnospondyls are entirely extinct and lie outside the tetrapod crown-group.

Acknowledgments

We thank Bernard Battail and Ronan Allain for access to the only known specimen, a cast, and a mold of *Triadobatrachus*, as well as a cast of *Karaurus*. Jason Anderson provided helpful discussion; Nadia Fröbisch and Diego San Mauro kindly sent electronic reprints. Two anonymous reviewers made helpful comments.

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Table 1: Sizes of the latest few data matrices for tetrapod phylogenetics in “genealogical” and chronological order (matrices that are based on each other follow each other in chronological order and lie between the same horizontal lines). Matrices that do not contain any lissamphibians are omitted. Treatment as morphologically immature (= sexually immature or paedomorphic) means that presumably ontogeny-dependent characters are scored as unknown unless the state associated with morphological maturity is present (based on the approach recommended by Wiens et al. [2005]); note that this does not need to concern the entire skeleton (it is possible to be peramorphic in some characters and paedomorphic in others at the same time). Finding out the exact number of parsimony-informative characters in the analyses by Pawley (2006) is not easy, so we present the total number of characters, but Pawley (2006: 205) mentions that all characters were parsimony-informative, apparently in all analyses. For all other references, we either inspected the matrix by eye to find uninformative characters and subtract them from the total or used PAUP* 4.0b10 (Swofford 2003) to determine their number.

Publication	Supported hypothesis	Number of taxa (outgroups included)	Number of parsimony-informative characters	Comments
Laurin (1994)	LH	38	150	Lissamphibia sister to Lysorophia, nested among “microsaurs”; Batrachia with frogs nested inside paraphyletic salamanders
Laurin & Reisz (1997)	LH	38	154	Publication of the above with some characters added; caecilians and frogs form a polytomy with the three salamander OTUs
Laurin (1998)	LH	43	153	The above with *Doleserpeton*, *Apateon*, *Eryops*, *Westlothiana*, and *Karaurus* added, some characters corrected, some added, some deleted; Procera with caecilians nested inside paraphyletic salamanders
Laurin & Reisz (1999)	LH	45	154	The above with *Solenodonsaurus* and *Tulerpeton* added, one character added, many cells corrected (table 3)
Vallin & Laurin (2004: fig. 6)	LH	49	159	The above with *Microbrachis*, *Asaphestera*, *Cardiocephalus* and *Utaherpeton* added, some cells corrected (table 3), five characters added, several characters recoded
Anderson (2001)	PH or LH	48 or 49	181	Almost complete sample of lepospondyls, but no salientians or caudates and few other taxa in the matrix; *Eocaecilia* sister-group to brachystelechid “microsaurs”
Vallin & Laurin (2004: fig. 7)	PH or LH	48	181	The above with some changes (Vallin & Laurin 2004: 66–68); almost complete loss of resolution among “microsaurs”
Anderson (2007)	PH	62	196	Matrix from Anderson (2001) with extant amphibians, albanerpetontids, and

				dissorophoids added; see text
Anderson et al. (2008b)	PH	54	216	Taxa and characters from the above and Anderson et al. (2008a) with omission of the most poorly known lepospondyls
Marjanović & Laurin (2009)	LH	54	211	Taxa and characters from Anderson et al. (2008b), but many changes to individual cells, some states redefined, many multistate characters ordered, four characters deleted; supports the LH
McGowan (2002)	PH	20	41	Gymnophionomorpha nested among “microsaurs”, together forming sister-group of Batrachia + Albanerpetontidae; all together nested inside Dissorophoidea; all-zero ancestor modeled after basal temnospondyls; no other taxa in the matrix
Marjanović & Laurin (2008b: fig. 6a)	TH	21	38	Taxa and characters from the above, but all-zero ancestor replaced by two real taxa, characters split and fused, states redefined, and many changes to individual cells
Marjanović & Laurin (2008b: fig. 6c)	LH	22 or 23	39	As above, but addition of *Brachydectes* and optionally *Gerobatrachus* (not shown in the figure)
Marjanović & Laurin (2008b: fig. 6e)	LH	21 or 22	38	As above, but *Doleserpeton* and, when added, *Gerobatrachus* (not shown in the figure) interpreted as morphologically immature; *Brachydectes* not added
Ruta et al. (2003)	TH	90	308	Lissamphibia nested in Temnospondyli
Pawley (2006: app. 16)	LH	90	352	Main source is the above, but many additions of characters (including cranial characters that seem correlated to others), as well as removal of ontogeny-dependent and parsimony-uninformative ones and many changes to individual cells; Lissamphibia sister to *Phlegethontia*, whether characters are reweighted (fig. 89) or not (fig. 88)
Pawley (2006: app. 16)	LH	90	371 or 376	Same as above, but cranial characters unmodified from Ruta et al. (2003), only postcranial ones modified; Lissamphibia-Albanerpetontidae clade sister to *Brachydectes* (Lysorophia), nested in “nectridean”-aïstopod-*Acherontiscus*-adelospondyl clade (fig. 91); reweighting resolves basal polytomy of that clade to nectridean monophyly (fig. 92); the text of app. 16 (p. 389) says 376 characters, while tables 16 and 17 say 371
Ruta & Coates (2007)	TH	102	333	Addition of taxa and addition and removal of characters to/from Ruta et al. (2003), but almost no changes to any cells
Germain (2008: fig.	LH	102	330	Taxon and character list identical to Ruta & Coates (2007), except for fusion of

5.15)				five correlated characters; many changes to individual cells; Lissamphibia-Albanerpetontidae clade sister to *Brachydectes* (Lysorophia); TH is one step less parsimonious (fig. 5.16), though ongoing work by D. M. has increased the difference to currently 8 steps (and decreased the number of informative characters to currently 289); PH requires many more steps
Carroll (2007)	PH	23	113	Similar results to McGowan (2002); see text

Table 2 (from Marjanović & Laurin 2007: app. 4): Estimated date of appearance of selected taxa in the supertree of Marjanović & Laurin (2007) under various assumptions of branch lengths. The dates, in Ma ago, have a precision of ~ 2 Ma, resulting from the resolution of the scale displayed in Mesquite. When only one number is given, stratigraphic fit was used (a given species is assumed to have been present throughout at least one geological stage). When two numbers are given, the first one is the minimal internal branch length (as under stratigraphic fit) and the second is the minimal terminal branch length (the species are not assumed to have existed throughout at least a given geological stage, but to have lasted at least a given number of years before the end of the geological stage in which they have been preserved). For the taxa that have a branch-based definition, the dates reported represent the beginning of the differentiation of the taxon, not the appearance its branch (or stem). All calculations were performed using Stratigraphic Tools (Josse et al. 2005). * Branch length assumptions used to produce the supertree of Marjanović & Laurin 2007 (figs. 3–7).

Note that the *Hyla-Bufo* divergence may be too old, because the oldest fossil in this clade that was included in the supertree was *Baurubatrachus*, which is Maastrichtian (70.6 – 65.5 Ma) rather than Campanian (83.5 – 70.6 Ma) in age (Roček 2000; Fernandes & Coimbra 2000; Gradstein et al. 2004). Gymnophionomorpha and Gymnophiona were called “Gymnophiona” and “Apoda”, respectively, by Marjanović & Laurin (2007); see the “Nomenclature” section of the present paper.

	Branch length assumptions													
Taxa	0.1 Ma	1 Ma	2 Ma	3 Ma*	5 Ma	0.1 Ma/0.1 Ma	0.1 Ma/1 Ma	0.1 Ma/5 Ma	1 Ma/0.1 Ma	1 Ma/1 Ma	1 Ma/5 Ma	5 Ma/0.1 Ma	5 Ma/1 Ma	5 Ma/5 Ma
Lissamphibia	252	254	258	260	267	246	248	250	248	249	253	261	262	266
Gymnophionomorpha	190	190	190	190	190	183	183	188	183	184	189	183	184	189
Gymnophiona	100	100	100	100	100	94	94	99	94	95	100	94	95	100
Batrachia	252	253	254	254	257	246	247	250	247	248	251	250	251	256
Urodela	157	159	160	162	166	152	153	156	153	154	158	161	162	166
Cryptobranchoidea	140	141	142	143	146	138	139	144	138	140	147	141	144	150
Salamandridae	60	62	66	70	84	57	58	62	60	61	65	76	77	81
Salientia	252	252	252	252	252	246	247	250	246	247	250	246	247	250
Anura	169	171	174	178	183	166	168	174	168	170	188	180	183	190
Bombinanura	169	170	172	175	178	166	168	174	167	169	187	175	178	185
Pipanura	158	160	162	165	171	152	153	156	153	156	159	166	168	171
Neobatrachia	85	91	99	108	124	72	73	77	78	79	83	111	112	116
Hyloidea	85	91	99	105	119	72	73	77	78	79	83	106	107	111
(*Hyla*, *Bufo*)	85	89	94	99	109	72	73	77	77	78	82	96	97	101

Ranoidea (*Microhyla*, *Rana*)	38	42	50	58	74	34	36	40	37	38	42	69	70	74
Microhylidae	29	31	34	38	44	23	24	28	26	27	31	39	40	44
Ranidae	38	40	47	52	65	35	36	40	35	36	40	59	60	64
Aglaioanura	38	38	43	46	55	35	36	40	33	34	38	49	50	54

Table 3 (from Marjanović & Laurin 2007: app. 5): Estimated date of appearance of selected taxa under ten random resolutions of the polytomies in the supertree of Marjanović & Laurin (2007) produced by the equiprobable model of MacClade 4.06 (Maddison & Maddison 2003). All dates are in Ma ago and rounded to 1 Ma. The “undoubted pelodytid” is mentioned as such by Rage & Roček (2003); it comes from the Bartonian of France. For the taxa whose names have a branch-based definition, the dates reported represent the oldest known node in the taxon, not the appearance of the taxon as a whole.

Designation of polytomy	Taxa included in the polytomy	Age (right) of relevant taxa (below) on reference tree	Average age on random trees	Minimal age on random tree	Maximal age on random trees	Age on reference tree
Gymnophiona	Wadi Milk caecilian, Pajcha Pata caecilian, *Apodops*, Rhinatrematidae, Stegokrotaphia	Gymnophiona	70	11	109	100
Salientia	*Triadobatrachus*, *Czatkobatrachus*, other Salientia	Batrachia	257	257	257	254
		Lissamphibia	263	263	263	260
Discoglossoidea	*Eodiscoglossus*, *Callobatrachus*, *Bombina*, *Opisthocoelellus*, *Latonia*, Discoglossidae	Discoglossoidea (crown)	146	34	180	171
		Anura	183	177	186	177
Bombina	*Bombina* spp.	*Bombina* (crown)	19	2	26	23
Discoglossus	*Discoglossus* spp.	*Discoglossus* (crown)	21	5	34	28
	Discoglossus, *Alytes*	Discoglossidae (crown)	33	31	37	31
Pelobatidae	*Pelobates*, *Eopelobates*, *Scotiophryne*	(*Pelobates* + *Eopelobates*)	81	55	87	84
	Pelobatidae, Megophryidae, Pelodytidae, Scaphiopodidae	Pelobatoidea	95	93	96	93
Pelodytidae	*Pelodytes*, *Miopelodytes*, *Tephrodytes*, Quercy pelodytid, “undoubted pelodytid”	Pelodytidae	46	43	49	40
Pelobates	*Pelobates* spp.	*Pelobates* (crown)	33	17	43	34
Rana (Pelophylax)	*Rana (Pelophylax)*	*Rana (Pelophylax)* (crown)	27	2	37	34

	ridibunda, R. (P.) saharica, Möhren green frog					
		Ranoidea	60	58	61	58
Telmatobiinae	*Telmatobius*, *Eupsophus*, *Neoprocoela*, Itaboraí telmatobiine	Telmatobiinae (crown)	67	65	68	62
Hylidae	Hylinae, Itaboraí hylid, (Pelodryadinae + Phyllomedusinae)	Hylidae (crown)	54	37	65	62
		(Hylidae + *Rhinoderma*)	67	65	68	65
Cryptobranchidae (crown)	Cryptobranchidae except *Chunerpeton*	Cryptobranchidae (crown)	55	31	68	59
Siren	*Siren* spp.	*Siren* (crown)	37	2	52	49
		Sirenidae (crown)	54	52	55	52
Ambystoma	*Ambystoma* spp.	*Ambystoma* (crown)	28	2	40	34
Salamandra	*Salamandra* spp.	*Salamandra* (crown)	36	18	43	37
		Salamandrinae (crown)	43	40	46	40
Average			77	59	86	80

Figure legends

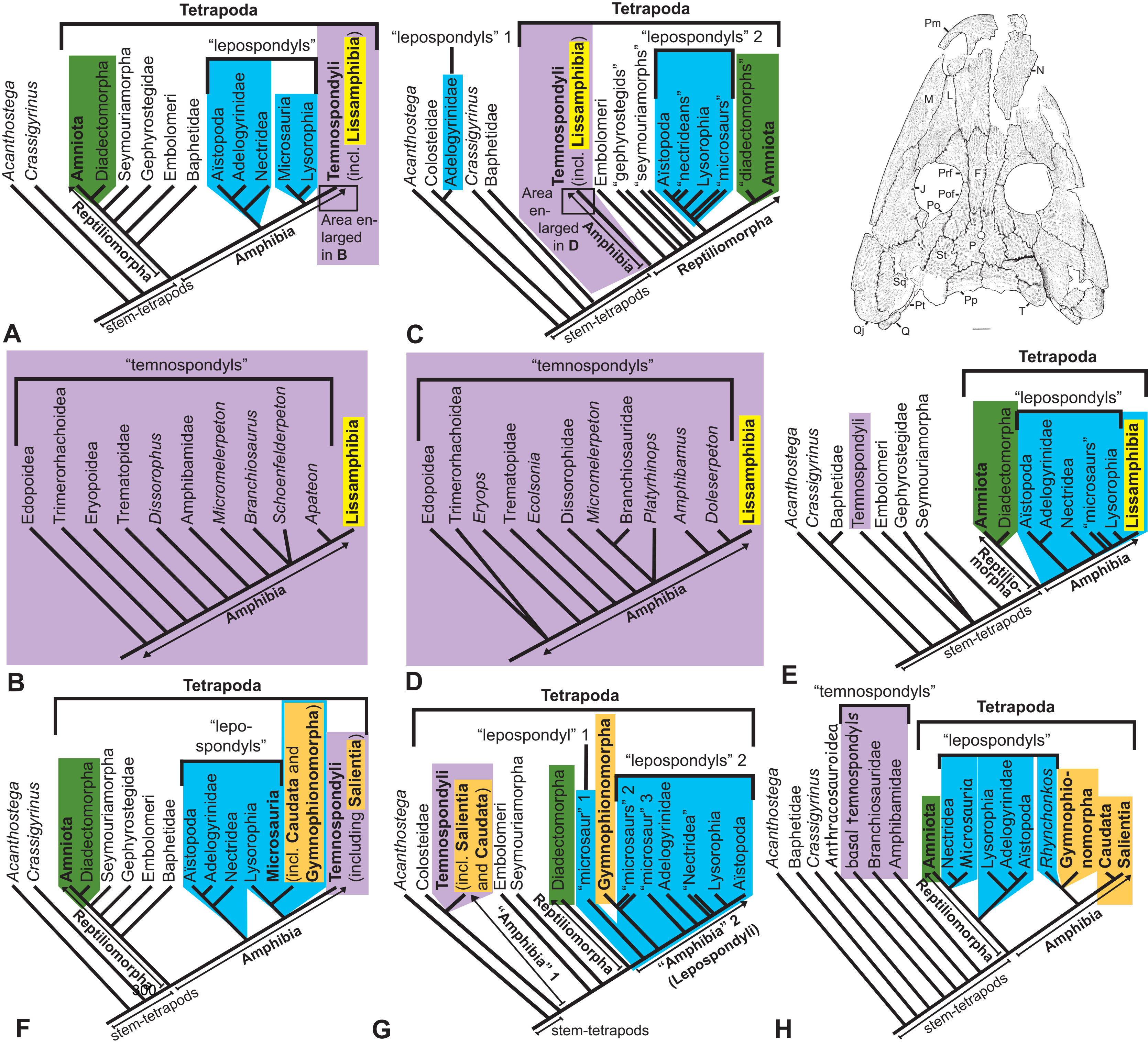
Figure 1 (modified from Marjanović & Laurin 2008b: fig. 1). Hypotheses on the origin of Lissamphibia in the recent literature. Extant taxa in bold; extant amphibians underlain in yellow (lightest gray) if monophyletic (Lissamphibia) or pastel orange (next darker gray) if polyphyletic, temnospondyls underlain in violet (middle gray), "lepospondyls" in cyan (next darker gray), the amniote-diadectomorph clade in green (darkest gray). A, B. Temnospondyl hypothesis (TH) as of the late 1980s and early 1990s; B is simplified from Trueb & Cloutier (1991). C, D. TH according to Ruta & Coates (2007). E. Lepospondyl hypothesis (LH); simplified from Vallin & Laurin (2004). F. Polyphyly hypothesis (PH), simplified from Carroll & Holmes (1980) through Carroll et al. (2004). G. PH simplified from Anderson et al. (2008b); the name Amphibia does not apply to any clade under this topology. H. A version of the PH, simplified from Carroll (2007: fig. 77), where extant amphibians and "lepospondyls" are nested inside the "temnospondyls". In H, "Anthracosauroidea" is an OTU that includes Embolomeri, Gephyrostegidae and Seymouriamorpha; "basal temnospondyls" is an OTU composed of *Dendrerpeton* and *Balanerpeton*; the "Microsauria" OTU consists of all "microsaurs" except *Rhynchonkos*. I, skull roof of the temnospondyl *Iberospondylus schultzei*, modified from Laurin & Soler-Gijón (2001); scale bar = 1 cm.

Figure 2. Time-calibrated trees showing Romer's and Carroll's Gaps. Names of extant taxa in bold. Known stratigraphic ranges, including uncertainties, are shown by thick lines. The timescale follows Gradstein et al. (2004); the unlabeled stage is the Serpukhovian, which began 326.4 ± 1.6 Ma ago; Mississi. = Mississippian. A. A phylogeny of early limbed vertebrates and extant amphibians. The "microsaurs" are likely paraphyletic with respect to Lysorophia; their gray extension consists of the undescribed possible representatives from the mid-late Permian of Russia and the late Early Triassic of China (see text). The undescribed possible branchiosaurid from the late Early Triassic of China (see text) is not shown, because *Tungussogyrinus* has about the same age. The position of *Gerobatrachus* in a trichotomy follows Marjanović & Laurin (2008b, 2009); that of *Tungussogyrinus* is taken from Werneburg (2009); the oldest known "microsaur" was announced by Clack (2009). Note how all "lepospondyls", amphibamids, or lissamphibians from Carroll's Gap are restricted to four or possibly five representatives from the Early Triassic, with the single exception of the purported Russian "microsaur"; their age range is shown as a bleached zone in Carroll's Gap. "Gymnophiona" includes Gymnophiona and all fossils that either belong to it or represent its closest known relatives – no fossils can be unambiguously assigned to Gymnophiona; see Marjanović & Laurin (2007: fig. 3, as "Apoda"). The Roman numerals represent possible origins of Lissamphibia or parts thereof, placed as high in the geological section as possible: (I) Lissamphibia (TH), Batrachia (PH), or Salientia (PH); (II) Batrachia (PH); (III) Gymnophionomorpha (PH); (IV) Lissamphibia (TH) or Caudata (PH); (V) Lissamphibia (TH), Batrachia (PH), or Salientia (PH); (VI) Lissamphibia (LH); (VII) basal split between the extant amphibians (PH). B (from Marjanović & Laurin 2007: fig. 9b and Marjanović & Laurin 2008a: fig. 4C). Time-calibrated phylogeny of Lissamphibia showing stratigraphic estimates of the age of that clade. The colored rectangles (1–4) represent the confidence intervals on the origin of Lissamphibia calculated under four different assumptions on the presumed severity of the impact of mass extinction events (Permian-Triassic, Triassic-Jurassic, and Cretaceous-Paleogene boundaries) on lissamphibian diversity. The bottom of each colored rectangle shows the older limit of the 75% confidence interval, the black bar the older limit of the 50% confidence interval. Note that none of the rectangles extends beyond the base of Carroll's Gap, while the PH predicts a date within Romer's Gap (VII in A) for the split between Gymnophionomorpha and Salientia.

Figure 3 (modified from Marjanović & Laurin [2008b: fig. 4]). Reinterpretation of the skull roof of the lysorophian “lepospondyl” *Brachydectes* (C, F, I) in comparison to the “microsaurian lepospondyls” *Rhynchonkos*, and *Batropetes*. A, B, C, dorsal view; D, E, F, right lateral view; G, H, I, caudal (occipital) view. Where interpretations of *Brachydectes* differ, those by Sollas (1920), Romer (1966) and Bolt & Wassersug (1975) are in bold, those by Wellstead (1991) are in italics, and ours (Marjanović & Laurin 2008b) are in regular typeface; they are always shown in this order. The colored bones are, in our interpretation, the tabular (yellow/light gray), the postorbital (cyan/middle gray), and the postfrontal (magenta/dark gray). Abbreviations: boc, basioccipital; eoc, exoccipital; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; oc, fusion of ex- and basioccipital; oot, opisthotic; otoc, fusion of pro- and opisthotic to ex- and basioccipital; p, parietal; pal, palatine; pl, pleurosphenoid; pm, premaxilla; po, postorbital; pof, postfrontal; pp, postparietal; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; s, stapes; se, sphenethmoid; sm, septomaxilla; soc, suproccipital; sq, squamosal; st, supratemporal; t, tabular; v, vomer. Scale bar: 1 cm.

Figure 4. Crown-group tetrapod phylogeny according to analyses that support the LH, showing diversity within the LH. All are simplified from their sources (by collapsing suprageneric taxa), and the names are made comparable. Internal topology of Microsauria in B and C not shown. Colored boxes: yellow (lightest gray), Lissamphibia; pastel green (next darker gray), Lysorophia; cyan (next darker gray), Amphibia; olive (next darker gray), “microsaurs”; violet (next darker gray), “nectrideans”; teal (next darker gray), Aïstopoda; dark green (darkest gray), amniotes and diadectomorphs. A. Vallin & Laurin (2004: fig. 6). B. Pawley (2006: fig. 92), with the taxon sample and cranial characters of Ruta et al. (2003) but Pawley’s own set of postcranial characters, and reweighting. C. Germain (2008: fig. 5.15). D. Marjanović & Laurin (2008b: fig. 6c). Tuditanidae and Hapsidopareiontidae are OTUs that may not be monophyletic; their composition was not tested, but carried over from McGowan (2002). E. Marjanović & Laurin (2009: supplementary figure). F. Current preliminary results of the ongoing work by D. M. on the data matrix of Germain (2008) without added taxa. The majority-rule consensus is shown; internodes absent from the strict consensus are gray.

Figure 5. Criteria for choosing calibration points and determining their minimum and maximum ages (after Raaum et al. 2005: fig. 2) exemplified by the origin of Bombinanura (i.e., the cladogenesis in which Discoglossoidea and Pipanura originated). Known stratigraphic ranges shown by thick lines. The minimum age is the age of the oldest known bombinanuran fossil, the discoglossoid *Eodiscoglossus oxoniensis* (circled). The maximum age is more difficult to constrain, but is probably close to the bottom of the interval marked by the double arrow, from which bombinanurans are not known, even though closely related and ecologically similar salientians (*Prosalirus* and *Vieraella*) were present. That fossils of the *Mesophryne* lineage older than *Eodiscoglossus* have not been discovered, and that Amphicoela (*Ascaphus* and *Leiopelma*) lacks a known pre-Pleistocene fossil record altogether, is unfortunate, but has little relevance for the above argument. The root of this tree extends down to the approximate age of the oldest known salientians, *Triadobatrachus* and *Czatkobatrachus*.


A
Tetrapoda
"lepospondyls"
Acanthostega
Crassigyrinus
Amniota
Diadectomorpha
Seymouriamorpha
Gephyrostegidae
Embolomeri
Baphetidae
Aïstopoda
Adelogyrinidae
Nectridea
Microsauria
Lysorophia
Temnospondyli
(incl. Lissamphibia)
Area enlarged in B
Reptiliomorpha
Amphibia
stem-tetrapods
B
"temnospondyls"
Edopoidea
Trimerorhachoidea
Eryopoidea
Trematopidae
Dissorophus
Amphibamidae
Micromelerpeton
Branchiosaurus
Schoenfelderpeton
Apateon
Lissamphibia
Amphibia
C
Tetrapoda
"lepospondyls" 1
"lepospondyls" 2
Acanthostega
Colosteidae
Adelogyrinidae
Crassigyrinus
Baphetidae
Temnospondyli
(incl. Lissamphibia)
Embolomeri
"gephyrostegids"
"seymouriamorphs"
Aïstopoda
"nectrideans"
Lysorophia
"microsaurs"
"diadectomorphs"
Amniota
Area enlarged in D
Amphibia
Reptiliomorpha
stem-tetrapods
Pm
N
M
L
Prf
F
J
Pof
Po
St
P
Sq
Pt
Pp
T
Qj
Q
D
"temnospondyls"
Edopoidea
Trimerorhachoidea
Eryops
Trematopidae
Ecolsonia
Dissorophidae
Micromelerpeton
Branchiosauridae
Platyrhinops
Amphibamus
Doleserpeton
Lissamphibia
Amphibia
E
Tetrapoda
"lepospondyls"
Acanthostega
Crassigyrinus
Baphetidae
Temnospondyli
Embolomeri
Gephyrostegidae
Seymouriamorpha
Amniota
Diadectomorpha
Aïstopoda
Adelogyrinidae
Nectridea
"microsaurs"
Lysorophia
Lissamphibia
Reptiliomorpha
Amphibia
stem-tetrapods
F
Tetrapoda
"lepospondyls"
Acanthostega
Crassigyrinus
Amniota
Diadectomorpha
Seymouriamorpha
Gephyrostegidae
Embolomeri
Baphetidae
Aïstopoda
Adelogyrinidae
Nectridea
Lysorophia
Microsauria
(incl. Caudata and Gymnophionomorpha)
Temnospondyli
(including Salientia)
Reptiliomorpha
Amphibia
stem-tetrapods
G
Tetrapoda
"lepospondyl" 1
"lepospondyls" 2
Acanthostega
Colosteidae
Temnospondyli
(incl. Salientia and Caudata)
Embolomeri
Seymouriamorpha
Diadectomorpha
"microsaur" 1
Gymnophionomorpha
"microsaurs" 2
"microsaur" 3
Adelogyrinidae
"Nectridea"
Lysorophia
Aïstopoda
"Amphibia" 1
Reptiliomorpha
"Amphibia" 2
(Lepospondyli)
stem-tetrapods
H
"temnospondyls"
Tetrapoda
"lepospondyls"
Acanthostega
Baphetidae
Crassigyrinus
Anthracosauroidea
basal temnospondyls
Branchiosauridae
Amphibamidae
Amniota
Nectridea
Microsauria
Lysorophia
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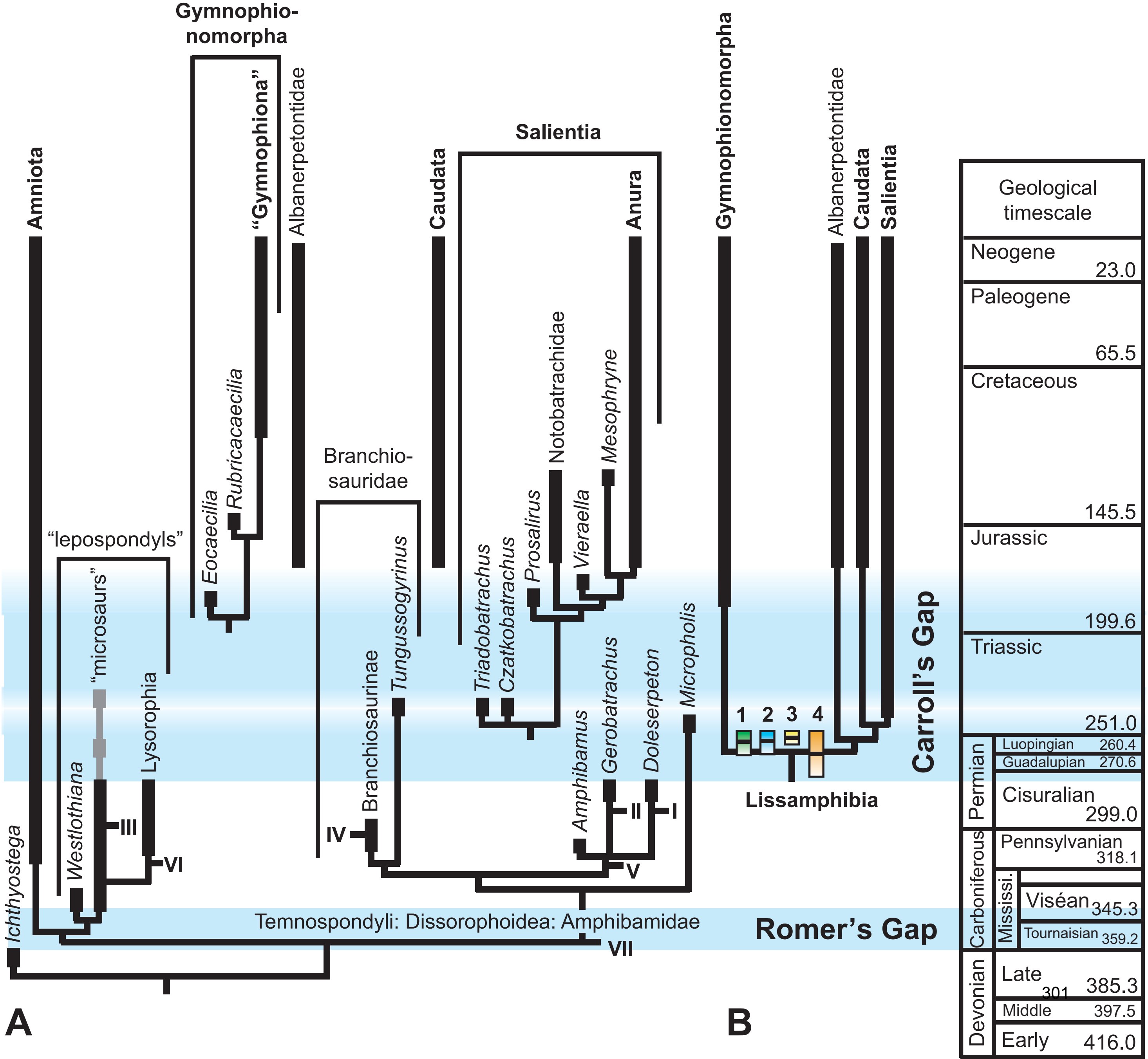
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Lissamphibia
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Paleogene
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Cretaceous
145.5
Jurassic
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Triassic
251.0
Permian
Luopingian
260.4
Guadalupian
270.6
Cisuralian
299.0
Carboniferous
Pennsylvanian
318.1
Mississi.
Viséan
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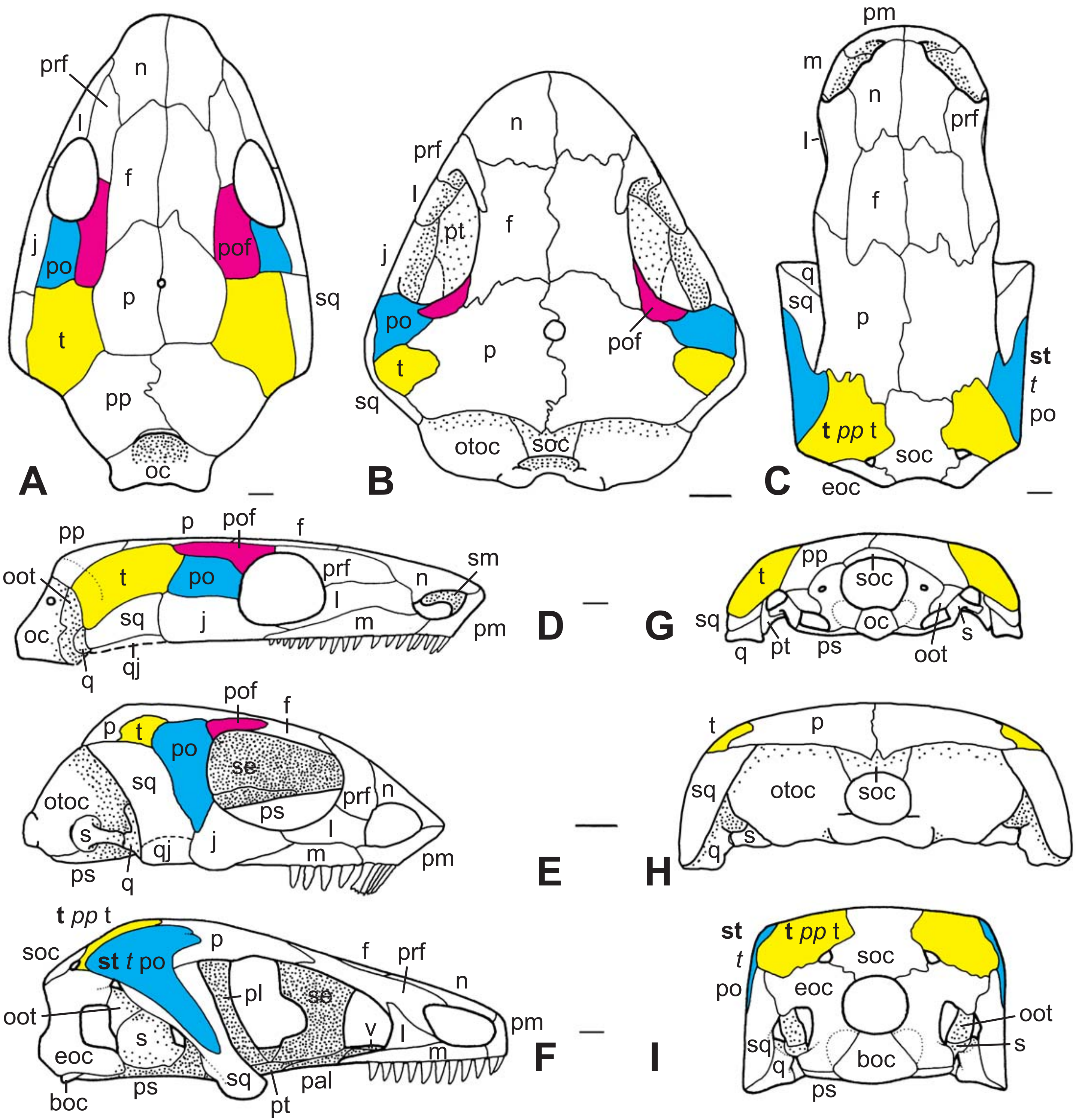
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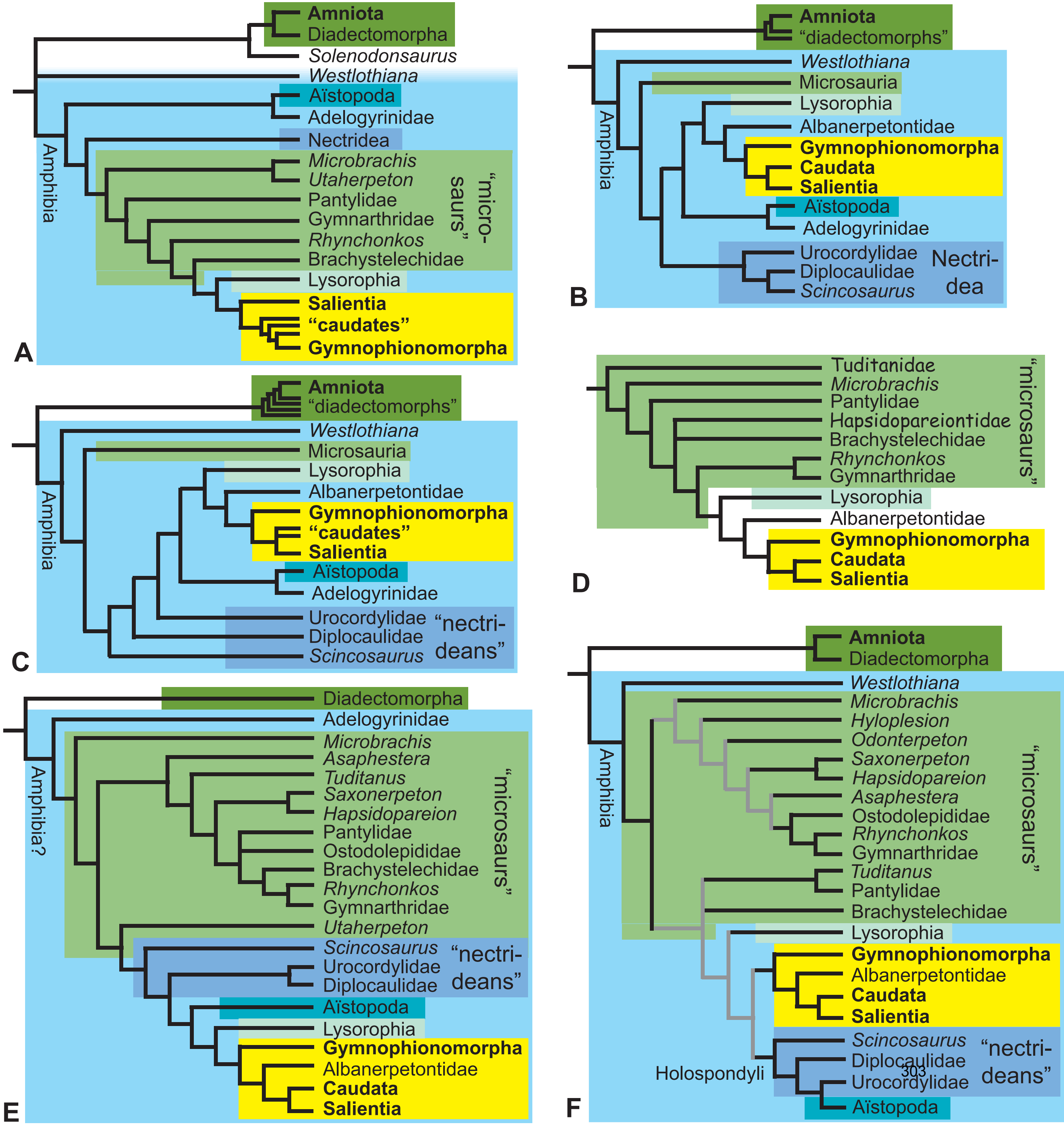
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Aïstopoda
Adelogyrinidae
Nectridea
Microbrachis
Utaherpeton
Pantylidae
Gymnarthridae
Rhynchonkos
Brachystelechidae
"micro-saurs"
Lysorophia
Salientia
"caudates"
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Amniota
"diadectomorphs"
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"caudates"
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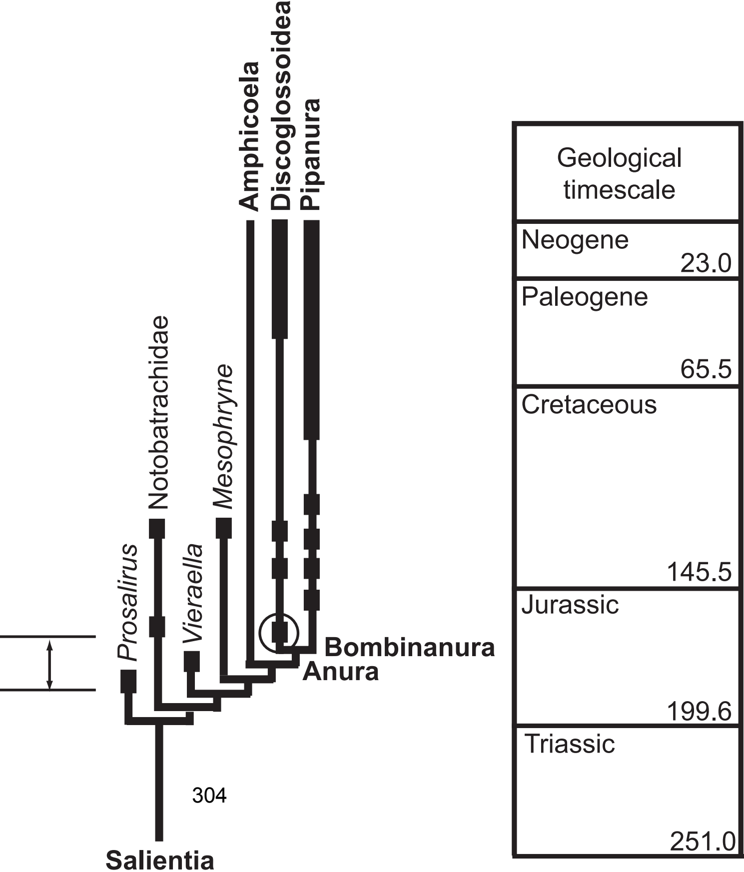
Amphicoela
Discoglossoidea
Pipanura
Notobatrachidae
Mesophryne
Prosalirus
Vieraella
Bombinanura
Anura
Salientia
Geological timescale
Neogene
23.0
Paleogene
65.5
Cretaceous
145.5
Jurassic
199.6
Triassic
251.0

Appendix

Reevaluation of the phylogenetic position of the Early Permian amniote *Apsisaurus*

Most extant limbed vertebrates are amniotes. Because the name-giving amniotic egg (which has a shell and contains extraembryonic membranes in addition to the yolk sac, unlike the eggs of other extant vertebrates) hardly ever fossilizes unless it has a thoroughly mineralized shell, the name Amniota has, in modern practice, a node-based definition as the smallest clade that contains all birds and mammals (a crown-group). Almost by definition, thus, the clade Amniota consists of two sister-groups, Theropsida and Sauropsida (Goodrich 1916), where Ther**o**psida is the mammalian side of the tree, which harbors the synapsid "reptiles" (and is therefore often called Synapsida in its entirety), such as the ther**a**psids; Sauropsida is the avian one, which also contains all extant "reptiles": turtles/tortoises/terrapins (Testudines), lizards/snakes/amphisbaenians (Squamata), tuatara (*Sphenodon*), crocodiles (Crocodylia) and birds (Neornithes). Except for Testudines (according to, most recently, Lyson et al. [2010]), all extant sauropsids belong to a clade called Diapsida.

Both theropsids and sauropsids, including diapsids, are already known from the latest stages of the Carboniferous. However, almost all Paleozoic amniotes are either theropsids or belong to a non-diapsid clade of sauropsids that has variously been called Anapsida (e.g. Benton 1997), Parareptilia (e.g. Müller & Tsuji 2007), Proganosauria (e.g. Vickaryous & Hall 2006), or Pan-Testudines (Joyce et al. 2004; Lyson et al. 2010), and most of the rest (fairly close relatives of Diapsida) are grouped as Captorhinidae; Permocarboniferous diapsids are remarkably rare – and about half of those form the clade Araeoscelidia which did not survive into the Mesozoic.

Among the basalmost theropsids, the clade Varanopidae is noteworthy. As the name suggests, these Pennsylvanian to Guadalupian (Late Carboniferous to Middle Permian) animals were fairly strongly convergent with Varanidae (the extant monitor lizards/goannas) in particular and Diapsida in general.

In 1991, Michel Laurin described the new taxon *Apsisaurus witteri*, based on a partial skeleton of Cisuralian (Early Permian) age, as a basal diapsid that was more closely related to the diapsid crown-group than to Araeoscelidia. Many anatomical and phylogenetic studies of the varanopid theropsids were published subsequently, and the supposed diapsids *Archaeovenator* (unnamed till then), *Mesenosaurus*, and *Heleosaurus* were redescribed as varanopids. Finally, in 2007, Robert Reisz restudied the only known specimen of *Apsisaurus*, found varanopid autapomorphies in it, and informed M. L., who agreed about their presence. To properly test the phylogenetic position of *Apsisaurus*, they started merging the varanopid-centered data matrix from the description of *Archaeovenator* (Reisz & Dilkes 2003) and the diapsid-centered data matrix from the description of *Apsisaurus* (Laurin 1991). Lacking time, R. R. and M. L. left the majority of this work to me. I found very high support for *Apsisaurus* being, as meanwhile expected, a varanopid and not a diapsid. This result further reduces our conception of diapsid diversity in the Permian and increases known varanopid diversity by providing, to some extent, an intermediate between the Carboniferous *Archaeovenator* and the other (Permian) varanopids.

The manuscript has been accepted by the Journal of Vertebrate Paleontology and will be published in issue 30(5) in September this year. I present the uncorrected page proofs followed by my suggested corrections; these have been approved by M. L., but it remains to be seen how R. R. (the first and corresponding author) will handle them.

Author contributions

I have not seen the specimen, which is kept in the Museum of Comparative Zoology at Harvard University.

The decisions to replace *Cotylorhynchus* (of the matrix by Reisz & Dilkes 2003) by *Casea*, which has fewer apomorphies, and to replace the unitary "Squamata" OTU (of the matrix by Laurin 1991) by the extant iguanian *Chalarodon madagascariensis* were made by M. L. and R. R.; R. R. also added characters 6, 18, and 60. I merged the many duplicated characters that (mostly) resulted from the merger, filled in almost all of the large amounts of missing data the merger generated, added the outgroup (*Tseajaia*, a diadectomorph that lacks the autapomorphies of the very large, probably semiaquatic *Limnoscelis* and those of the herbivorous Diadectidae; suggested by M. L.), and added the Early Cretaceous squamates *Huehuecuetzpalli* and *Dalinghosaurus* to help replace the previous "Squamata" OTU (*Huehuecuetzpalli* was described as a stem-squamate; Reynoso 1998). I further added characters 1, 86, 101, 105, 106 and 110 to improve resolution and restore squamate monophyly, (re)defined the limits of some characters, added states to some, ordered 27 characters, conducted the analyses, made Figure 3, and wrote the legend of Figure 3, both appendices, and a few sentences in the "Analysis and Discussion" section.

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UJVP #501441, VOL 30, ISS 5

APSISAURUS WITTERI FROM THE LOWER PERMIAN OF TEXAS: YET ANOTHER SMALL VARANOPID SYNAPSID, NOT A DIAPSID

Robert R. Reisz, Michel Laurin, and David Marjanović

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Robert R. Reisz, Michel Laurin, and David Marjanović

Journal of Vertebrate Paleontology 30(5):1–4, September 2010

SHORT COMMUNICATION

APSISAURUS WITTERI FROM THE LOWER PERMIAN OF TEXAS: YET ANOTHER SMALL VARANOPID SYNAPSID, NOT A DIAPSID

ROBERT R. REISZ,[*,1] MICHEL LAURIN,[2,†] and DAVID MARJANOVIĆ[2,†]; [1]Department of Biology University of Toronto Mississauga, 3359 Mississauga Road, Mississauga, Ontario L5L 1C6, Canada, robert.reisz@utoronto.ca; [2]UMR 7179, Equipe Squelette des Vertébrés, Université Paris 6, 4 Place Jussieu, case 19 75005, Paris, France

Paleozoic varanopid synapsids and diapsids, rare members of the terrestrial fossil assemblages, are not closely related to each other but appear to have acquired a number of interesting similarities that have resulted in their frequent misidentification. They have relatively gracile skeletons, especially when compared to their contemporary synapsid and reptilian relatives. In addition, most varanopids and diapsids of the Upper Carboniferous and Lower and Middle Permian are quite small, have slender limbs, and a lower temporal fenestra, often with a slender lower temporal bar. Consequently, assignment of these small predators to one of these two clades has often been difficult, especially if critical parts of the skull roof are missing in the preserved skeleton. For example, *Petrolacosaurus kansensis*, known from a single locality in the Upper Carboniferous of Kansas, was variously identified as a diapsid and a synapsid before a thorough restudy based on several articulated skeletons led to its identification as the oldest known diapsid (Reisz, 1977). *Archaeovenator*, based on a single small skeleton from the Upper Carboniferous of Kansas, was first identified as a diapsid reptile, but a restudy of the material clearly showed that it was a basal varanopid (Reisz and Dilkes, 2003). Perhaps the most striking examples are those of *Mesenosaurus* and *Heleosaurus*, two Middle Permian varanopid synapsids from Russia and South Africa that were previously misidentified as archosauromorph and eosuchian diapsids, respectively (Reisz and Berman, 2001; Reisz and Modesto, 2007). The gradual but steady increase of our knowledge of the anatomy and early history of these two important Middle Permian taxa explains partly why they have been re-identified as synapsids.

As part of a reexamination of all Permo-Carboniferous amniotes, the enigmatic small *Apsisaurus witteri* was restudied (Laurin, 1991). In the original description of this taxon, a phylogenetic analysis of early diapsids was also included, laying the groundwork for the present study. At that time *Apsisaurus* was identified as an eosuchian diapsid reptile, and its relationships to other diapsids was evaluated in the phylogenetic analysis that used *Paleothyris* and *Captorhinus* as outgroups. This approach, which excluded synapsids from the analysis, was reasonable at that time. The known anatomy of *Apsisaurus witteri* firmly placed it as the sister taxon of Neodiapsida (Laurin, 1991:fig. 11), even though much of the skull roof was not preserved. Thus, the region of the skull that would preserve the superior temporal fenestra was unknown. Subsequent work on little-known amniotes that turned out to be varanopid synapsids dramatically increased our understanding of their anatomy, alerting us to the possibility that *Apsisaurus* may be a varanopid. In fact, many of the features used to identify the partial skeleton of *Apsisaurus* as a diapsid are also present in the more completely known small varanopid synapsids, the Mycterosaurinae, especially in the postcranial region.

SYSTEMATIC PALEONTOLOGY

SYNAPSIDA Osborn, 1903
VARANOPIDAE Romer and Price, 1940
APSISAURUS WITTERI Laurin, 1991

Diagnosis—Small varanopid synapsid characterized by the presence of anteroposteriorly elongate, tall neural spines, very slender humerus with entepicondylar width being less than 30% of total length of the limb element. Differs from *Mesenosaurus*, *Mycterosaurus*, *Aerosaurus*, and *Varanodon* in the lack of strong recurvature of the marginal dentition.

Holotype—MCZ 1474, partial skeleton including an incomplete skull and mandibles, posterior cervical, dorsal, sacral, and anterior caudal vertebrae and ribs, proximal parts of forelimb and hindlimb.

Locality and Horizon—Archer City bonebed, approximately 2 km from Archer City, Texas; Archer City Formation, Wichita Group, Lower Permian (see Laurin, 1991).

ANALYSIS AND DISCUSSION

Our careful reexamination of the holotype and only known specimen of *Apsisaurus witteri* (Figs. 1, 2) has revealed that a surprising number of osteological features, previously viewed either as generic autapomorphies or as diapsid synapomorphies, are actually also present in varanopid synapsids. For example, some cranial features that were part of the original diagnosis of this taxon, namely the slender triradiate jugal with a relatively short subtemporal process (Fig. 1A–C) and the small quadratojugal that does not reach the lateral temporal fenestra, are also features that are clearly present in the basal mycterosaurine *Archaeovenator* (Reisz and Dilkes, 2003). Another interesting diagnostic feature of *Apsisaurus* listed in the original description is the dentition—relatively large, sharply pointed teeth. Although most varanopids have labiolingually compressed and recurved teeth (Evans et al., 2008), the teeth of the basal varanopid *Archaeovenator* show the primitive condition, lacking strong recurvature, and appear to be superficially indistinguishable from those of *Apsisaurus*. Other cranial features have turned out to be misinterpretations of the anatomy of *Apsisaurus*. Most significant among these cranial features is the probably mistaken identification of the presence of a suborbital fenestra. This feature is generally viewed as a diapsid synapomorphy, but comparisons with the palates of *Mesenosaurus* and *Archaeovenator*, where this area of the skull is particularly well preserved, revealed that the area mistakenly interpreted as a fenestra in *Apsisaurus* is a damaged area of the palatine (Reisz and Berman, 2001; Reisz and Dilkes, 2003). This opening, poorly preserved in the holotypic specimen, is more reasonably interpreted as either preservational or preparational damage of the dorsal surface of the palate. In particular, the peculiar position of this supposed opening in *Apsisaurus* is unlike that of any diapsid suborbital fenestra, being bordered medially by the pterygoid, and laterally by the palatine and ectopterygoid.

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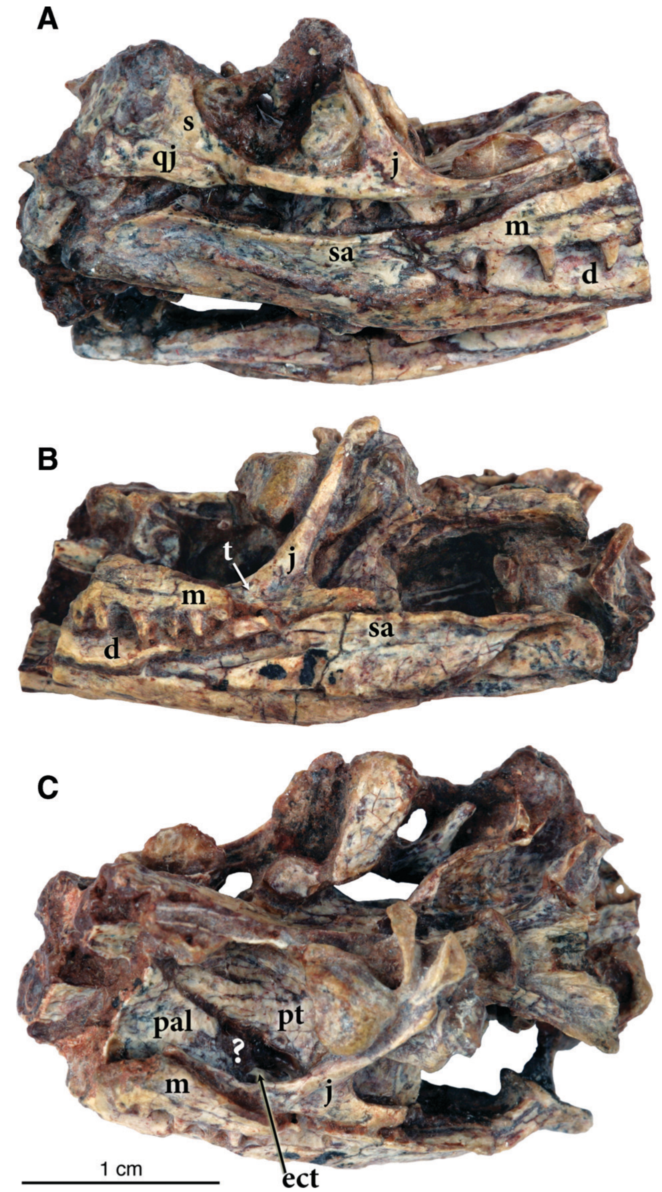

4C/Art

FIGURE 1. Skull of *Apsisaurus witteri* (Museum of Comparative Zoology, Harvard University, MCZ 1474) in (**A**) right lateral, (**B**) left lateral, and (**C**) partial dorsal views. Although the both mandibles are preserved, the skull has suffered transverse crushing, and the anterior part of the snout and most of the skull roof is missing. '?' identifies location of the originally proposed suborbital fenestra (see text for discussion). **Anatomical abbreviations**: **d**, dentary; **ect**, ectopterygoid; **j**, jugal; **m**, maxilla; **pal**, palatine; **pt**, pterygoid; **q**, quadrate; **s**, squmosal; **sa**, surangular; **t**, tubercle.

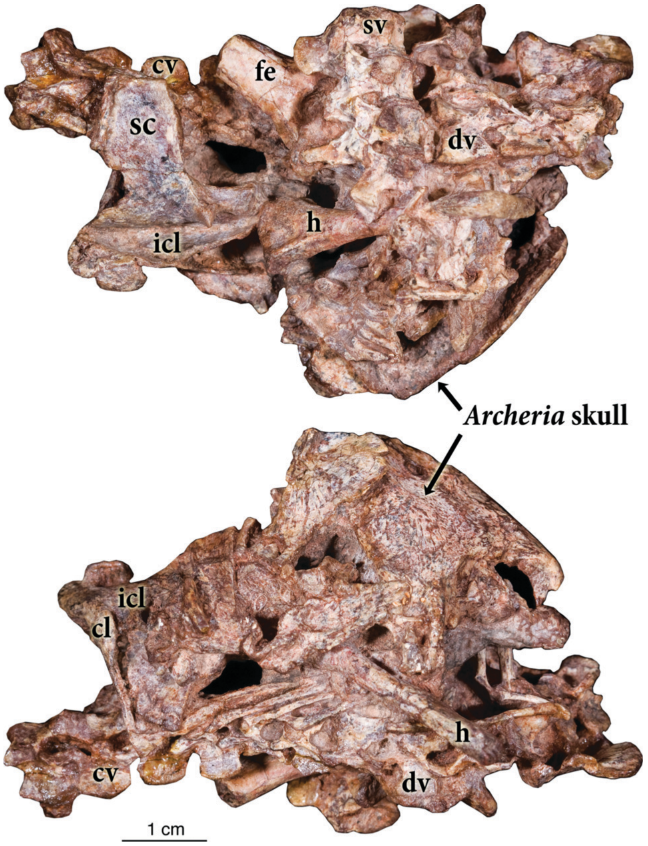

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FIGURE 2. **A**, dorsal and **B,** ventral views of block containing curled up partial postcranium of *Apsisaurus witteri* (MCZ 1474), together with skull roof of *Archeria.* **Anatomical abbreviations**: **cl**, clavicle; **cv**, cervical vertebra; **dv**, dorsal vertebra; **fe**, femur; **h**, humerus; **icl**, interclavicle; **sc**, scapula; **sv**, sacral vertebra.

In all early diapsids this opening is bordered laterally by the maxilla or the jugal (Reisz, 1981; deBraga and Reisz, 1995).

A few additional cranial features of *Apsisaurus witteri* interpreted as diapsid autapomorphies (Laurin, 1991) were based on poorly preserved parts of the skull and were probably misinterpreted. The posterior edge of the squamosal was interpreted as being sufficiently reduced to expose the quadrate, a derived condition present in *Youngina,* but reexamination of the specimen indicates that this region of the skull is very poorly preserved, and it is possible that the very thin, sheet-like posterior portion of the bone may have been lost prior to the original study of the specimen (Fig. 1C). This region of the squamosal is readily damaged in varanopid synapsids.

A striking feature of the skull of *Apsisaurus*, overlooked in the original description, is the presence of a small tubercle on the body of the left jugal (Fig. 1B), a distinctive varanopid feature (Reisz and Modesto, 2007). The body of the right jugal has been damaged, and little of the actual lateral surface remains. The small lateral projection on the body of the jugal, just at the level of the ventral edge of the orbit, is similarly present in mycterosaurine varanopids, and is not present in members of any other clade of currently known Early Permian amniotes. The slender mandible of *Apsisaurus* is virtually indistinguishable from that of *Archaeovenator*. Notable similarities are the slenderness of the ramus and the tall lateral exposure of the articular bone (Reisz and Dilkes, 2003:fig. 2A), and a modest posteriorly directed retroarticular process. As in *Varanops* and *Varanodon*, the surangular has a horizontal shelf along its dorsal edge (R. R. Reisz, pers. observ.).

Postcranially, the skeleton of *Apsisaurus* is surprisingly similar to that of *Archaeovenator.* In the vertebral column (Fig. 2), the anterior cervicals are slightly longer than the mid-dorsals, there are two subequal pairs of sacral ribs, and the cervical and dorsal vertebrae have well-developed median ventral ridges. Contrary to the condition in *Archaeovenator*, but similar to that in *Mycterosaurus*, the dorsal vertebrae of *Apsisaurus* have tall neural spines, and some neural arches show clear evidence of gentle lateral excavation of the neural arches.

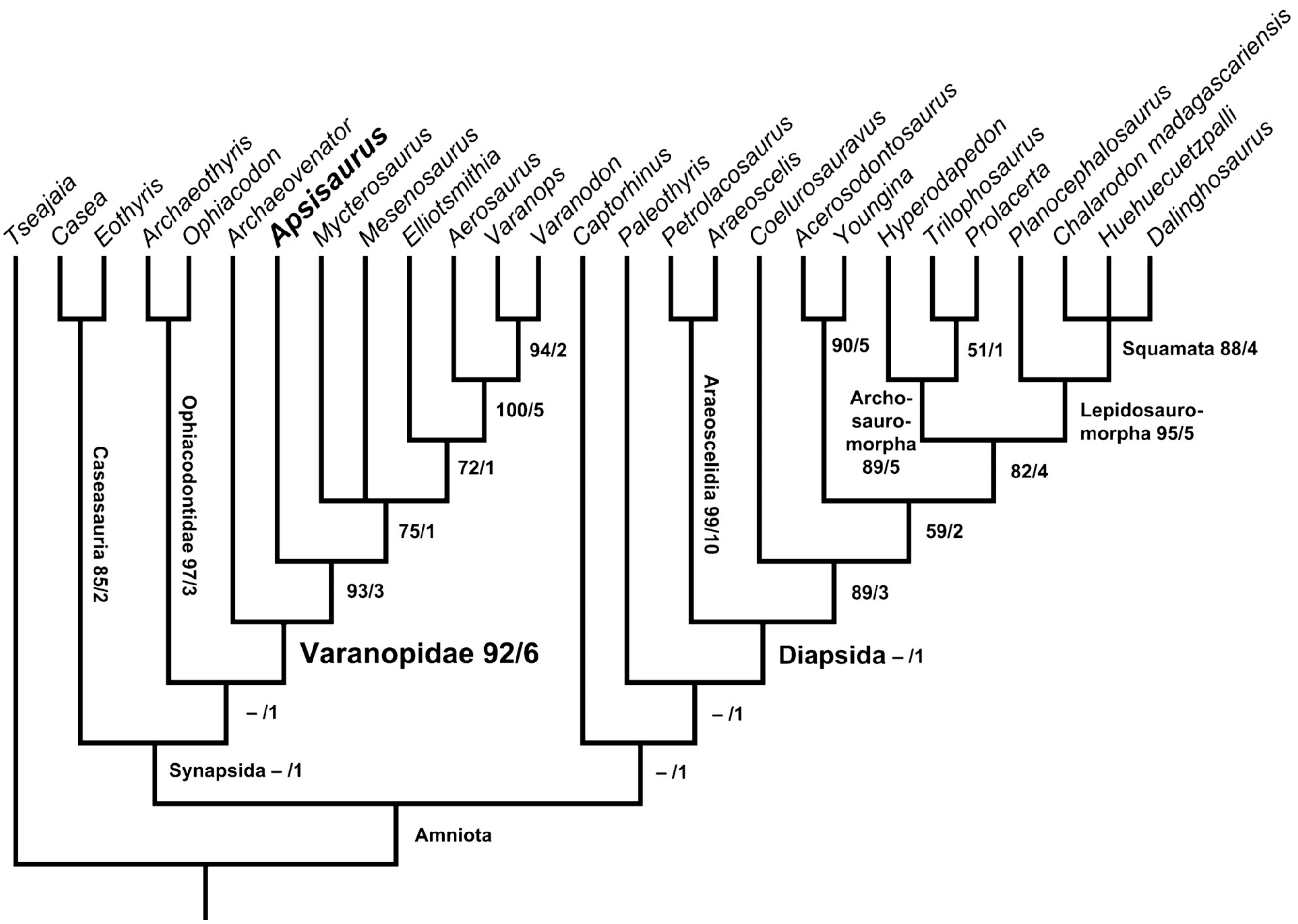

FIGURE 3. Strict consensus of the six most-parsimonious trees (length = 378 steps, consistency index = 0.4471, retention index = 0.7210, rescaled consistency index = 0.3223). Numbers to the left of a slash are bootstrap percentages ('–' for clades contradicted by the bootstrap tree), those to the right are decay indices. Unambiguous autapomorphies of two selected clades (numbering follows online supplementary data Appendices S1 and S2 and represents the character number followed by the state number in parentheses): Varanopidae: 11(1), premaxillary narial shelf rounded, transitions smoothly into ventral edge of skull; 21(1), posterodorsal expansion of external naris pinched between nasal and maxilla; 24(1), lacrimal does not reach external naris; 28(1), parietal extension over interorbital region more than marginal; 38(1), squamosal occipital shelf narrow, quadrate exposed in occipital view; 41(2), ventral temporal bar narrow, occupying less than 20% of postorbital skull height; 46(2), anterior extent of quadratojugal $\leq$ anterior extent of ventral portion of squamosal; 51(1), basipterygoid processes long, wing-like, with long articulating facets that face anteriorly; 53(1), tabular narrow and slender, without a ventral expansion; 67(1), hyoid long, directed posteriorly beyond skull; 101(1), hindlimb almost as long as trunk or longer. Smallest clade including *Apsisaurus* and *Varanodon*: 34(1), tuberous ornamentation on prefrontal and/or jugal present; 69(1), cervical centra longer than caudal dorsal centra; 70(1), ventral surface of cervical centra strongly keeled; 71(1), cervical neural arch excavation shallow but present.

The diagnostic appendicular features of *Apsisaurus*, such as a large head of the interclavicle and a pubic tubercle, are also present in the basal varanopid *Archaeovenator* (Reisz and Dilkes, 2003). Some similarities between the preserved portions of the appendicular skeleton of *Apsisaurus* and well-known mycterosaurine varanopids are also striking. Of particular importance are several anatomical features of the limb elements, and limb proportions. These features were used by Laurin (1991) in his phylogenetic analysis for resolving relationships within diapsids, and anatomical and proportional characters of the preserved parts of the limbs were major contributing factors in determining the identity and phylogenetic relationships of *Apsisaurus*. More recent work has allowed us to recognize that most of these features are also seen in mycterosaurine varanopids. For example, the femur is slender, significantly longer than the humerus, and is sigmoidal in outline, as in mycterosaurines. Proximally, the morphology of the internal trochanter, and the size and shape of the intertrochanteric fossa, is identical to that in *Mycterosaurus* (Reisz et al., 1997). Distally, the two condyles of the femur are nearly equal to each other, as in mycterosaurines. On the ulna, only a slight proximal convexity, as in mycterosaurines, rather than a fully formed process represents the olecranon.

These striking similarities between the mycterosaurine varanopids that have been recently discovered or restudied, and the considerably more fragmentarily known *Apsisaurus*, led us to reconsider its identity. All the available evidence points to *Apsisaurus* being a varanopid synapsid rather than a diapsid reptile. Of particular relevance is the discovery of the lateral tubercle on the body of the jugal, an unusual feature that is widely distributed among varanopids. We therefore decided to test this possibility in a phylogenetic analysis using an expanded basal amniote data set. We combined basal synapsid (Reisz and Dilkes, 2003) and diapsid (Laurin, 1991) data matrices in MacClade 4.08 (Maddison and Maddison, 2003), added a few characters and a diadectomorph outgroup (see online supplementary data Appendix S1), ordered those characters that form morphoclines (see online supplementary data Appendix S1), especially potentially continuous ones (following Wiens, 2001), and analyzed the resulting data set in PAUP* 4.0b10 (Swofford, 2003) using a heuristic search with 10,000 addition-sequence replicates, random addition sequence, and no constraints on the time or the number of rearrangements. (The same settings were used for the 10 decay-index analyses. A bootstrap analysis with 1000 replicates was also conducted, each replicate consisting of 100 unconstrained addition-sequence replicates with random addition sequence.) The purpose of this analysis is not to determine the phylogeny of Amniota, but rather to test whether *Apsisaurus* nests among diapsids or among varanopid synapsids, as the available evidence suggests. The resulting data matrix includes 27 taxa and 113 characters (online supplementary data Appendices S1 and S2).

The analysis yielded six most parsimonious trees, the strict consensus of which is given in Figure 3. The tree largely reflects the established consensus, with monophyletic Synapsida, Caseasauria, Ophiacodontidae, Varanopidae, and most other widely recognized taxa sampled in our matrix. *Apsisaurus* is nested within Varanopidae, and not even in the basal-most position, which is occupied by *Archaeovenator*. The position of *Apsisaurus* within Varanopidae is strongly supported in our analysis because the sister-group relationship between *Apsisaurus* and the clade formed by most other varanopids has a bootstrap value of 93% and a decay index (Bremer value) of 3; most importantly, the clade Varanopidae itself, including *Apsisaurus* and *Archaeovenator*, has a bootstrap value of 92% and a decay index of 6. The analysis thus provides strong evidence that *Apsisaurus witteri* is a varanopid synapsid, nested well within that clade. The purpose of this study was not to determine its exact phylogenetic relationships within the Varanopidae; for this reason, several recently reevaluated varanopid taxa known from fragmentary remains were not included in this analysis. A research program on the review of this interesting clade of basal synapsids is in progress, with planned revisions of all member taxa and description of new pivotal forms. A thorough analysis of varanopid phylogeny will be part of that study and is not included here.

CONCLUSIONS

The result of our study that *Apsisaurus witteri* is a varanopid synapsid, not an eosuchian diapsid, has significant implications to our understanding of both synapsid and diapsid evolution. First, this finding increases the known diversity of varanopid synapsids even further. Even though varanopids are relatively rare members of Lower and Middle Permian assemblages, their fossil record has been expanding steadily in the last three decades both taxonomically and temporally. Varanopids are now known from Carboniferous and Lower Permian rocks in North America and Europe, and from Middle Permian strata of Russia and South Africa. Varanopids range in size from 30 cm to over 200 cm in total body length (Reisz and Laurin, 2004), and they are distinct from other members of their terrestrial vertebrate assemblages in being relatively gracile predators.

Conversely, and more significantly, the taxonomic diversity of diapsid reptiles in the Paleozoic has suffered another loss, resulting in an extremely scant fossil record for these reptiles. This is a startling development when considering that diapsids came to dominate the Mesozoic era so completely and continue to be taxonomically more diverse than synapsids even today. Although diapsid reptiles first appear in the fossil record in the Pennsylvanian, less than 10 million years after the first appearance of the oldest known reptiles and synapsids, their fossil record is very poor throughout the remainder of the Paleozoic, when amniote evolution experienced its first massive diversification. With the recognition that *Apsisaurus* is not a diapsid reptile, the Middle Permian *Lanthanolania* (Modesto and Reisz 2002) from north-central Russia becomes the oldest known neodiapsid (oldest known eosuchian, sensu Laurin, 1991). All other, older diapsid reptiles are members of Araeoscelidia, a clade of small, gracile forms that represent the initial Carboniferous and Early Permian diversification of diapsids (deBraga and Reisz 1995). These diapsids are only known from a handful of localities in North America and Europe. Only in the Late Permian do we see the appearance of other diapsids, the younginiform eosuchians. Future discoveries may alter this perceived pattern of early diapsid evolution, but for now, the picture that emerges is that diapsids were rare during the initial stages of amniote diversification, or that they diversified in habitats that where the fossilization potential was low.

ACKNOWLEDGMENTS

This research was financed by NSERC Discovery Grant to R.R.R., the CNRS (operating grants of UMR 7179 and 7207), the French Ministry of Research, and by a subsidy to university students by the Federal Republic of Austria. We thank Diane Scott for the photographs of the specimens, Dr. Sean Modesto for useful discussions, and the staff of the Museum of Comparative Zoology, Harvard University, for permission to borrow and study this specimen.

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Received July 3, 2009; accepted April 17, 2010.

Q1: The journal is Palaeontology.
Q2: We refer to version 4.06 of the program, published by Sinauer Associates in Sunderland, Massachusetts.

Line 7: The first paragraph appears to begin with one empty space, neither a full tabulation nor the complete lack of one. This should be rectified. – At the end of the line, please remove "the".
Line 40: I'm not sure how much sense it makes to say that Apsisaurus was "identified" as an eosuchian. After all, the name Eosuchia was defined in that very paper to contain *Apsisaurus*; up to then, Eosuchia had been a "rhizome group" into which most or all early stem-diapsids were lumped, a mere bubble in a romerogram. Our phylogenetic analysis has found Eosuchia to be a junior synonym of Amniota. Therefore, I suggest to replace "an eosuchian" by "a" in line 40.
Line 47: Replace "preserve" by "contain".
Line 54: Remove "the Mycterosaurinae," (including the comma) without replacement. According to Fig. 3, there are no mycterosaurines except *Mycterosaurus* and possibly *Mesenosaurus*.
Line 82: Replace "mycterosaurine" by "varanopid". According to Fig. 3, *Archaeovenator* lies outside the clade formed by Mycterosaurinae and Varanopinae; to the best of my knowledge, this result has never been contradicted by a phylogenetic analysis or even just a published opinion – most importantly, Reisz and Dilkes (2003), who are cited in the same sentence (and thus could be misunderstood as a reference for assigning *Archaeovenator* to Mycterosaurinae), found *Archaeovenator* to be the basalmost varanopid in their phylogenetic analysis, exactly as Fig. 3 does.
Legend to Fig. 1: Remove "the" in the third line without replacement. Instead, insert "the" between "identifies" and "location" in the fifth line. In the last line, insert "**qj**, quadratojugal;" in front of "**s**".
Legend to Fig. 2: In the first two lines, replace "curled up" by "curled-up" (with a hyphen).
Line 190: Remove the comma without replacement.
Line 219: Replace "an eosuchian" by "a". (See comment to line 40.)
Line 245 and 246: Replace "neodiapsid (oldest known eosuchian, sensu Laurin, 1991)" by "non-araeoscelidian diapsid". It is not quite clear what the phylogenetic definition of Neodiapsida is; for Eosuchia, see the above comment to line 40.
Line 246: Remove "other," (comma included) without replacement.
Line 252: Replace "younginiform eosuchians" by "younginiforms".
Line 258: Insert "a" between "by" and "NSERC".
Line 268: "uppermost" should be in lowercase.
Line 272: Insert "Palaeontology" in front of the volume & page numbers. **(This answers Q1.)**
Lines 276 and 277: "Analysis", "Phylogeny", "Character" and "Evolution" should be in uppercase. At the end of line 277, add: "Version 4.06. Sinauer Associates, Sunderland, Massachusetts." **(This answers Q2.)**
Line 302: Insert a space between "D." and "W. Dilkes".

APPENDIX 1: Annotated list of characters. Numbers in citations, if preceded by a space, are character numbers, not page numbers.

The outgroup, *Tseajaia*, was chosen as the presumably most plesiomorphic member of Diadectomorpha, the sister group to Amniota.

Cotylorhynchus (from the matrix of Reisz and Dilkes, 2003) has been replaced by the more plesiomorphic *Casea*. The *Casea* OTU is coded after *Casea broilii* and "*Casea*" *rutena* which was recently (Maddin et al., 2008) found not to belong to *Casea*; however, because there are no other caseids in this matrix, this should not have caused any problems.

To avoid having to reconstruct the ancestral squamate morphotype based on assumptions on the currently controversial state of squamate phylogeny, Laurin's (1991) Squamata OTU has been replaced by three new OTUs: the extant iguanian *Chalarodon madagascariensis* (scored after Blanc, 1965), the Early Cretaceous possible anguimorph *Dalinghosaurus* (after Evans and Wang, 2005), and the Early Cretaceous possible stem-squamate *Huehuecuetzpalli* (after Reynoso, 1998).

1. Tooth attachment (unordered) (Dilkes, 1998: 55; modified from Laurin, 1991: G4): subthecodont (= protothecodont) (0); ankylothecodont (1); pleurodont (2); acrodont (teeth fused to jawbone in adults so that no root can be discerned; no tooth replacement) (3).

Captorhinus lacked tooth replacement in adults (Heaton, 1979:22), and Heaton (1979) shows fusion in several figures. We have therefore assigned state 3 to it.

Youngina has state 1 (Gow, 1975), and so does *Prolacerta* (Modesto and Sues, 2004).

2. Caudal curvature of marginal teeth (ordered) (modified from Reisz and Dilkes, 2003: 1): strong (0); slight (1); absent (2).

Originally, states 0 and 1 included circular cross-section versus mediolateral compression of the teeth in their description. This was already a separate character (34) in the same matrix; it is now character 4, because indeed it does not always covary with curvature.

3. Serrations on teeth (Reisz and Dilkes, 2003: 32): absent (0); present (1).

4. Lateral compression of marginal dentition (modified from Reisz and Dilkes, 2003: 1, 34): only distally or nowhere (0); over two-thirds of tooth (1).

5. Shape of antorbital region (Reisz and Dilkes, 2003: 12): broad, nasal largely dorsal element (0); narrow and tall, nasal has nearly vertical contribution to snout (1).

Prolacerta is scored 0 after Modesto and Sues (2004:fig. 3, 4).

In *Planocephalosaurus*, the nasal seems to have a vertical contribution, but the snout is so broad that we scored it as having state 0.

6. Antorbital-postorbital ratio (new): postorbital part (caudal margin of orbit to caudal tip of skull) longer than antorbital part (0); antorbital part of snout (tip to rostral margin of orbit) longer (1).

Trilophosaurus was scored as unknown because its ratio is precisely 1 (as far as can be determined from the literature).

7. Snout proportions (Reisz and Dilkes, 2003: 53): width > height (0); width < height (1).

This character might be thought to be correlated to snout length (see character 6), but *Trilophosaurus* has state 1 in spite of its short snout.

8. Number of premaxillary teeth (ordered) (modified from Laurin, 1991: G1, and Reisz and Dilkes, 2003: 41): ≥ 5 (0); 2 to 4 (1); 0 (2).

Specimens of *Captorhinus* with three or five teeth per premaxilla are known, but rare; the vast majority has four, so we scored *Captorhinus* as having state 1.

9. Premaxillary rostral process (Reisz and Dilkes, 2003: 51): absent (0); present (1).

10. Downturned premaxilla (ordered) (modified from Dilkes, 1998: 6): no (0); slightly (1); strongly (2).

Morphological gaps between the states are readily apparent.

Casea is scored as possessing states 0 and 1 because *C. broilii* shows state 0 while "*C.*" *rutena* possesses state 1.

11. Premaxillary narial shelf (reworded from Reisz and Dilkes, 2003: 2): more or less sharp edge between lateral (= sculptured, if sculpture is present) surface of skull and ventral wall of naris (0); rounded ventral narial shelf that transitions smoothly into ventral edge of skull (1).

12. Dorsolateral process of premaxilla (modified from Laurin, 1991: F1): absent (0); extends behind naris (1).

13. Maxilla dorsal process (unordered) (modified from Reisz and Dilkes, 2003: 5): absent (0); starts just behind external naris, extends to level of dorsal narial margin (1); spike-like, just in front of orbit, overlies lacrimal (2); massive, pillar-like, extends above narial margin (3).

14. Maxilla-prefrontal contact (Reisz and Dilkes, 2003: 6): absent (0); present (1).

15. Maxillary tooth number (modified from Reisz and Dilkes, 2003: 28): 25 or fewer (0); 26 or more (1).

16. Caniniform region (ordered) (modified from Laurin, 1991: B1, and Reisz and Dilkes, 2003: 39): region absent (0); region present (1); one or two caniniform teeth present (2).

Variation exists between the several species of *Ophiacodon*, with some being borderline between states 0 and 1 (Romer and Price, 1940: plate 1), but those that can be clearly assigned to a state have state 1, so we scored the *Ophiacodon* OTU accordingly.

Mesenosaurus is scored 1, but a score of 2 could also be defensible.

17. Maxilla dorsal of caniniform tooth or region (ordered) (modified from Reisz and Dilkes, 2003: 10): flat (0); swollen (1); well-defined buttress (2).

This character is scored as inapplicable in taxa that have state 16(0).

18. Septomaxilla shape (ordered) (new): pillar-like (0); curled sheet (1); flat sheet (2).

19. Septomaxilla lateral sheet-like exposure (Reisz and Dilkes, 2003: 42): absent (0); present (1).

20. External nares (ordered) (modified from Laurin, 1991: F2): marginal (minimal distance between nares ≥ 0.35 snout width at same level) (0); close to midline (1); confluent (2).

21. Naris posterodorsal expansion (ordered) (Reisz and Dilkes, 2003: 43): absent (0); pinched between nasal and maxilla (1); greatly enlarged, between nasal and lacrimal (2).

22. Nasal length (Reisz and Dilkes, 2003: 50): ≤ frontal (0); > frontal (1).

The length of either bone does not include narrow processes, which are often very long.

Youngina is scored as unknown because the two descriptions (Gow, 1975; Carroll, 1981) contradict each other.

23. External narial shelf on nasal (Reisz and Dilkes, 2003: 49): absent (0); present (1).

24. Lacrimal length (modified from Laurin, 1991: B2): participates in margin of external naris (0); does not reach external naris (1).

In *Dalinghosaurus*, the lacrimal and the prefrontal are fully fused, making it impossible to score this character for it, although the fusion product reaches the naris.

25. Lacrimal duct (ordered) (Reisz and Dilkes, 2003: 19): opens on posterior edge of lacrimal (0); opens laterally near posterior edge of lacrimal (1); opens laterally on concave surface of lacrimal (2).

Aerosaurus, *Varanops* and *Varanodon* possess state 2, *Prolacerta* shows state 1 (R. R. R., pers. obs.).

26. Frontal orbital border (Reisz and Dilkes, 2003: 13): absent or narrow (0); broad and forms most of dorsal edge (1).

27. Frontal posterolateral process (ordered) (modified from Reisz and Dilkes, 2003: 4): absent, fr-par suture forming right angle to parasagittal plane (0); absent or very short, fr-par suture forming obtuse angle to parasagittal plane (1); long, narrow, forming acute angle with parasagittal plane (2).

28. Parietal extension over interorbital region (modified from Reisz and Dilkes, 2003: 16): absent or marginal (0); present (1).

29. Parietal ventrolateral flange (Laurin, 1991: D1): absent (0); present (1).

Scored as applicable only in taxa where the parietal borders a temporal fenestra (i.e., in diapsids).

30. Sagittal crest on parietals (Laurin, 1991: G2): absent (0); present (1).

31. Size of pineal foramen (ordered) (modified from Laurin, 1991: G3): large, more than 25% of mid-parietal length (0); small, less than 25% of mid-parietal length (1); absent (2).

32. Position of pineal foramen in dorsal view (ordered) (modified from Reisz and Dilkes, 2003: 17): parietal-parietal suture rostral to foramen longer than caudal to it (foramen caudal) (0); equal (foramen in middle) (1); rostral shorter than caudal (foramen rostral) (2); foramen in frontal-parietal suture (3).

Scored as inapplicable in OTUs that have 31(2).

33. Prefrontal-nasal suture (Laurin, 1991: E1): parasagittal, at least in its caudal third (0); anterolateral (1).

34. Tuberous ornamentation on prefrontal and/or jugal (modified from Reisz and Dilkes, 2003: 14): absent (0); present (1).

35. Squamosal anterodorsal process (Reisz and Dilkes, 2003: 8): no or little underlap of posterior process of postorbital (0); extensive underlap of posterior process of postorbital (1).

Scored as inapplicable in the absence of a lateral temporal fenestra.

Planocephalosaurus has a unique condition that we have scored as state 1; coding it as a separate state would also be defensible.

36. Squamosal posterodorsal process (Reisz and Dilkes, 2003: 33): absent (0); present (1).

Scored as inapplicable in the absence of a lateral temporal fenestra.

37. Squamosal ventral process (ordered) (modified from Laurin, 1991: D2 and E4, and Reisz and Dilkes, 2003: 24): broad, contributes to posteroventral edge of lateral temporal fenestra (0); narrow, does not border lateral temporal fenestra ventrally (1); squamosal confined dorsally (2).

38. Squamosal occipital shelf (ordered) (reworded from Reisz and Dilkes, 2003: 15; contains Laurin, 1991: B5): broad, contributes to occipital surface of skull (0); narrow, quadrate exposed in occipital view (1); absent, posterior edge of quadrate exposed in lateral view (2).

39. Dorsal temporal fenestra (ordered) (Laurin, 1991: A1, B3): absent (0); present, postfrontal does not enter (1); present, postfrontal enters (2).

The postfrontal is absent in *Chalarodon*, so it is scored as having states 1 or 2.

40. Lateral temporal fenestra (unordered) (modified from Laurin, 1991: A2, and Reisz and Dilkes, 2003: 3, part of 9, 11): absent (0); present, quadratojugal excluded (1); present, quadratojugal enters or is absent (2).

Trilophosaurus is polymorphic: *T. buettneri* has state 0, while *T. jacobsi* displays state 2 instead.

41. Ventral temporal bar (zygomatic arch) (ordered) (modified from Laurin, 1991: B4 and J1, and Reisz and Dilkes, 2003: 18): absent (no fenestra) (0); tall, occupying more than 20% of skull height (1); narrow but complete, occupying less than 20% of postorbital skull height (2); incomplete (3); absent (with fenestra) (4).

42. Ventral margin of postorbital region (modified from Reisz and Dilkes, 2003: 52): straight or convex (0); concave, though nowhere dorsal to tooth row (1).

Scored as inapplicable in taxa where state 41(4) is present.

43. Dorsal and lateral surfaces of postorbital (modified from Reisz and Dilkes, 2003: 25): form smooth curve (or dorsal surface absent, postorbital not participating in skull roof) (0); sharply divided (meeting at edge) (1).

44. Postorbital lateral boss at orbital margin (Reisz and Dilkes, 2003: 37): absent (0); present (1).

45. Postorbital posterior process (modified from Laurin, 1991: I1, and Reisz and Dilkes, 2003: 23) shorter than in state 1 (0); if temporal fenestrae absent: reaches supratemporal, if at least one fenestra present: extends beyond caudal margin of fenestrae (1).
46. Anterior extent of quadratojugal (ordered) (modified from Reisz and Dilkes, 2003: 36): maxilla-quadratojugal suture (0); extending anterior to ventral portion of squamosal, but not contacting maxilla (1); ≤ anterior extent of ventral portion of squamosal (2); quadratojugal absent (3).
47. Quadratojugal superficial anterodorsal process (Reisz and Dilkes, 2003: 35): absent (0); present (1).
48. Suborbital fenestra (Laurin, 1991: A3): absent (0); present (1).
49. Teeth on transverse flange (unordered) (modified from Laurin, 1991: E5, and Reisz and Dilkes, 2003: 30): single row on edge (0); additional teeth anterior to single row (or no rows recognizable) (1); absent (2).
50. Parasphenoid dentition posterior to level of transverse flange (ordered) (Reisz and Dilkes, 2003: 45): absent (0); along edges (1); on edges and posterior body (2).
51. Basipterygoid processes (unordered) (modified from Reisz and Dilkes, 2003: 20): short, broad, with short articulating facets facing anterolaterally (0); long, wing-like, with long articulating facets facing anteriorly (1); long, with hemispherical articulating facets facing more or less anterolaterally (2).

Archaeovenator and *Apsisaurus* show state 1 (R. R. R., pers. obs.).

52. Supratemporal (ordered) (modified from Reisz and Dilkes, 2003: 22): broad element of skull table (0); slender, in parietal and squamosal trough (1); absent (2).
53. Tabular (ordered) (modified from Laurin, 1991: E3, and Reisz and Dilkes, 2003: 46): large, sheet-like (with ventral expansion) (0); narrow, slender (1); absent (2).
54. Postparietal size (ordered) (modified from Laurin, 1991: E2 and G5 = J2): sheet-like, both together not much smaller than suproccipital in state 59(1) (0); small, splint-like (1); absent (2).
55. Quadrate shape (ordered) (modified from Laurin 1991: E7, J3): straight posteriorly (0); shallowly emarginated (1); with conch (2).
56. Occipital margin of quadrate (ordered) (modified from Reisz and Dilkes, 2003: 27): anterior slope ≥ 80° (0); 80° > anterior slope > 50° (1); anterior slope ≤ 50° (2).
57. Paroccipital process shape (modified from Reisz and Dilkes, 2003: 26): vertical or nearly vertical sheet, height ≥ 0.5 transverse length (0); elliptical in cross-section, height < 0.5 transverse length (1).
58. Paroccipital process attachment (modified from Laurin, 1991: A4 and E6, and Reisz and Dilkes, 2003: 26) (ordered): ends freely (0); weak contact (1); strong contact (2).
59. Size of posttemporal fenestra (ordered) (modified from Dilkes, 1998: 53, 54): large compared to suproccipital (narrow dorsal process of suproccipital tapers dorsally) (0); small (because of broad, plate-like dorsal process of suproccipital) (1); more or less foramen (2); absent (3).

Morphological gaps between the states are readily apparent.

60. Number of coronoids (new): two (0); one (1).
61. Shape of posteroventral edge of angular (Reisz and Dilkes, 2003: 38): ridged or keeled (0); rounded (1).
62. Size of lateral exposure of angular (Laurin, 1991: J4): wide (0); narrow (1).

A morphological gap between the states is readily apparent.

63. Retroarticular process size (ordered) (modified from Laurin, 1991: B6, E10, J5): absent (0); small (1); large (2).
64. Retroarticular process composition (modified from Laurin, 1991: J5): composite (0); formed only by articular (1).

65. Stapes (modified from Laurin, 1991: E8): robust, with thick shaft (0); slender, rod-like shaft (1).
66. Stapedial foramen (Laurin, 1991: E9): present (0); absent (1).
67. Hyoid (Reisz and Dilkes, 2003: 40): short, directed to quadrate region (0); long, directed posteriorly beyond skull (1).
68. Notochordal canal (Laurin, 1991: F3): present throughout ontogeny (0); absent in adults (1).
69. Cervical centra length (modified from Laurin, 1991: H1): no longer than caudal dorsals (0); longer than caudal dorsals (1).
70. Ventral surface of cervical centra (modified from Laurin, 1991: H2): rounded (0); strongly keeled (1).
71. Cervical neural arch excavation (ordered) (modified from Reisz and Dilkes, 2003: 47): absent (0); shallow (1); deep (2).

The restriction to cervical vertebrae follows Reisz and Modesto (2007:737).

72. Neural spines (replacing Laurin, 1991: C1): triangular (0); rectangular (1).

The rounded neural spines of *Tseajaia* are scored 1 because they are not pointed.

73. Ratio of height of mid-dorsal neural spines from base of zygapophysis : maximum centrum height (modified from Reisz and Dilkes, 2003: 31): ≤ 1.5 (0); > 1.5 (1).
74. Midventral surface of dorsal centra (ordered) (modified from Laurin, 1991: H2, and Reisz and Dilkes, 2003: 44): rounded (0); ridged (with slightly swollen sides) (1); keeled (sharp edge) (2).
75. Transverse processes in trunk (Laurin, 1991: F5): short (0); moderately long (1).
76. Mammillary processes on caudal cervical and cranial dorsal neural spines (Laurin, 1991: H3): absent (0); present (1).
77. Accessory process on craniolateral surface of cranial cervical ribs (Laurin, 1991: H4): absent (0); present (1).
78. Cervical ribs (Laurin, 1991: F4): some or all holocephalous (0); all dichocephalous (1).
79. Trunk ribs (Laurin, 1991: D3): dichocephalous (0); holocephalous (1).
80. Sacral ribs (ordered) (Reisz and Dilkes, 2003: 48): two unequal (0); two equal (1); three (2).

The original state 3 (four sacral ribs) does not occur in this matrix.

81. Sternum (Laurin, 1991: A5): not mineralized (0); mineralized (bone or calcified cartilage) (1).

Scored as unknown for taxa not known from sufficiently articulated specimens.

82. Interclavicle shape (modified from Laurin, 1991: J6, and deBraga and Reisz, 1995: 26): +-shaped (cranial process present) (0); T-shaped (cranial process absent) (1).
83. Interclavicle webbed between processes (modified from Laurin, 1991: J6): yes (head triangular or diamond-shaped) (0); no (rather sharp angles between processes) (1).
84. Minimal interclavicle shaft width (modified from Laurin, 1991: J6): ≤ 0.105 tip-to-tip width (0); ≥ 0.137 tip-to-tip width (1).
85. Cleithrum (Laurin, 1991: E11): present (0); absent (1).
86. Cranial margin of scapula (modified from deBraga and Reisz 1995: 27): straight, at least dorsally (0); convex along entire length (1).
87. Supraglenoid foramen (Reisz and Dilkes, 2003: 29): absent (0); present (1).
88. Triceps process on coracoid (modified from Laurin, 1991: H5): small or absent (0); large (1).

A morphological gap between the states is readily apparent.

Varanops has state 1 (R. R. R., pers. obs.).

89. Ratio of width of distal head of humerus to shaft length (Laurin, 1991: D4): ≥ 0.3 (0); < 0.3 (1).

90. Entepicondyle (Laurin, 1991: I2): moderately large (0); strongly developed at maturity (1).
91. Entepicondylar foramen (Laurin, 1991: F6): present (0); absent (1).
92. Ectepicondylar region (ordered) (modified from Laurin, 1991: J7): foramen, process bridged (0); supinator process present, groove present (1); process, groove and foramen absent (2).
93. Radius-humerus length ratio (ordered) (modified from Laurin, 1991: A6, H7): < 0.68 (0); 0.68 to 0.82 (1); > 0.82 (2).
94. Radius shape (Laurin, 1991: I3): straight (0); twisted in lateral view (1).
95. Olecranon process (unordered) (modified from Laurin, 1991: C2): prominent, extension of ulna (0); absent or low (1); prominent, ossifies separately (2).
96. Medial centrale carpi (Laurin, 1991: F7): present (0); absent (1).
97. Lateral centrale carpi (Laurin, 1991: E12): large (0); small or absent (1).

Varanodon has state 0 (R. R. R., pers. obs.).

98. Pelvic girdle (Laurin, 1991: J8): solid (0); fenestrate (1).
99. Lateral and distal pubic tubercles (modified from Laurin, 1991: H6): small or absent (0); large (1).

A morphological gap between the states is readily apparent.

100. Acetabulum (Laurin, 1991: B7): elongate (0); circular (1).
101. Hindlimb-trunk length ratio (new): hindlimb much shorter than trunk (0); hindlimb almost as long as trunk or longer (1).

A morphological gap between the states is readily apparent.

Planocephalosaurus is scored 1 on the assumption that it had a similar vertebral count to that of *Sphenodon*.

102. Distal articular surface of femur (reworded from Laurin, 1991: B8): uneven, fibular condyle projecting distinctly beyond tibial condyle (0); approximately at same level (1).
103. Femur maximum length : distal width ratio (modified from Reisz and Dilkes, 2003: 21): < 4 (0); ≥ 4 (1).
104. Femur-humerus length ratio (ordered) (modified from Laurin, 1991: C3): > 1.2 (0); 1 to 1.2 (1); < 1 (2).

Youngina has state 1 (R. R. R., pers. obs.).

105. Femoral and humeral shaft diameters (modified from deBraga & Reisz 1995: 38): femur = 150% humerus (0); more or less equal (up to 120%) (1).
106. Lower leg : foot length ratio (modified from deBraga and Reisz, 1995: 33 and 42): articulated tibia + tibiale/astragalus longer than articulated 4th metatarsal + digit (0); shorter (1).
107. Astragalus-calcaneum articulation (unordered) (modified from Laurin, 1991: F8): flat (0); concave-convex (1); foramen on calcaneum, articulation expanded (2); sutured or fused (3).
108. Lepidosauriform ankle joint (Laurin, 1991: J9): absent (0); present (1).
109. Lateral tuber on calcaneum (Laurin, 1991: F9): absent (0); present (1).
110. Metapodials overlapping proximally (deBraga and Reisz, 1995: 43): no (0); yes (1).
111. Fourth metatarsal (Laurin, 1991: F10): short (0); long (at least 40% of digit IV) (1).
112. Fifth distal tarsal (Laurin, 1991: E13): present (0); absent (1).
113. Fifth metatarsal (Laurin, 1991: E14): straight (0); hooked (1).

APPENDIX 2: Data matrix. The analysis distinguished polymorphism (in parentheses) from partial uncertainty (in curly brackets), but not inapplicability (“-”) from missing data (“?”); we nonetheless make the latter distinction here to make our decisions more transparent.

	5	10	15	20	25	30	35	40	45	50	55
Tseajaia	01000	101?{01}	10000	21000	0000?	010-0	00?0-	1-100	00000	10010	00001
Casea	{01}1000	0011(01)	00100	0-000	00100	010-0	01000	10001	10001	00010	00010
Eothyris	{01}1000	00110	00000	21?00	00100	010-0	00000	10001	10001	0001?	00000
Archaeothyris	01001	11?0?	?0001	10??0	01000	120-0	00?00	?0??1	11101	10?0?	010{01}0
Ophiacodon	{01}1?11	11000	00001	10000	01000	110-0	00000	00001	11101	10000	01000
Mycterosaurus	{01}0111	11000	10310	10?00	10011	121-0	00010	10101	20111	200?1	11100
Mesenosaurus	{01}0111	11000	10310	11000	10011	121-0	00010	10201	20111	20011	11100
Elliotsmithia	0011?	11???	?0???	?????	?????	121-0	00?11	10101	20111	1000?	?1100
Aerosaurus	00011	11100	10200	12010	20012	121-0	00011	?1202	20110	11002	111?0
Varanops	{01}0011	11100	10201	12010	20012	121-0	00011	11202	20110	110?2	11110
Varanodon	{01}0011	01100	10201	12011	20012	121-0	00011	?1202	20110	11?0?	11110
Archaeovenator	{01}1001	11100	10001	0-010	20010	121-0	00000	10101	20101	20000	11100
Captorhinus	31000	00111	00000	10100	00000	010-0	0210-	0-000	00000	20010	01200
Paleothyris	{01}1000	10000	00001	20100	0000?	110-0	1000-	0-000	00000	20010	01100
Petrolacosaurus	01000	10000	00001	20100	00000	12100	11000	00112	10000	10111	01100
Araeoscelis	01000	1?000	00000	20??0	00000	12100	1200-	0-110	00000	20110	01100
Apsisaurus	{012}100?	?????	?????	?????	?????	?????	???1?	?02?1	20???	200{01}?	1???0
Coelurosauravus	(03)100?	110?0	00110	0-?0?	1101?	?1100	???00	0?222	4-010	20???	?0???
Acerosodontosaurus	0100?	1??0?	0?1?1	0-???	?0?10	121??	??0?0	01?22	20001	10???	?????
Youngina	11000	10100	00111	0-100	0?010	12110	10000	01222	20001	10100	01101
Trilophosaurus	11000	?1200	0???0	0-?00	0?010	02111	2-101	0221(02)	(04)000?	21120	0{12}2{12}1
Hyperodapedon	11000	00202	01110	0-?02	00010	11011	2-100	02212	20000	10120	02221
Prolacerta	10010	10001	01100	0-201	01011	12110	(12)0100	02212	30000	20100	012{12}1
Planocephalosaurus	31000	10100	00110	0-?01	0001?	11010	10101	02222	30000	20120	22222
Chalarodon m.	22000	00100	00110	0-101	00010	10010	13100	022{12}	4-000	3-120	21222
Huehuecuetzpalli	21001	10000	00110	0-??1	0001{01}	10010	13000	02212	4-000	3-1??	?1222
Dalinghosaurus	21000	?0100	00110	0-??1	000?1	10010	13100	?2212	4-000	3-12?	01222

	60	65	70	75	80	85	90	95	100	105	110	113
Tseajaia	10010	000-0	0?000	01000	00100	0?010	01001	01100	?00?0	0??10	00000	0?0
Casea	10120	000-0	00000	01001	00102	00000	00001	01000	00010	00021	10000	000
Eothyris	100{23}0	0?0-?	?????	?????	?????	?????	?????	?????	?????	?????	?????	???
Archaeothyris	??03?	0?0-0	??0?0	0111?	0??00	0111?	?0?01	01???	??01?	?001?	???0?	0??
Ophiacodon	10030	000-0	00000	01111	00100	00(01)10	00001	01100	00010	00010	00001	000
Mycterosaurus	10120	?0??0	01011	1111?	00?01	0????	110?0	01?01	0?010	?1100	?000?	000
Mesenosaurus	0?030	00100	01011	11010	00?01	0????	?10?0	01?01	000??	000??	?000?	0?0
Elliotsmithia	201{123}?	0010?	?1???	?????	?????	?????	?????	?????	?????	?????	?????	???
Aerosaurus	201?0	1010?	?1011	11110	00102	00000	00000	01101	00000	111??	12001	100
Varanops	201?0	10100	?10?1	11120	00102	00010	00100	01201	00000	11101	12001	100
Varanodon	201{23}0	1010?	?1011	11121	00102	0???0	00100	01101	00?00	??10?	????1	1??
Archaeovenator	0??{123}?	000-?	?1000	01010	00101	0000?	01???	?????	0?0??	1?1??	10001	000
Captorhinus	01011	10100	00000	00?00	00000	00010	01001	02000	00000	10011	10000	000
Paleothyris	1?011	000-0	00000	00020	00100	0?0?0	01010	01000	00000	00110	10000	000
Petrolacosaurus	01011	000-0	0?011	21110	11000	00010	11110	01200	00010	10010	00001	000
Araeoscelis	01111	000-0	0?011	20010	11000	10010	11110	00200	00010	10100	00001	000
Apsisaurus	{01}0???	00???	??011	11010	0??01	?000?	01010	01101	??00?	?1000	?????	???
Coelurosauravus	0????	1010?	???00	?0000	0000?	????0	???10	00100	0??01	11111	10001	000
Acerosodontosaurus	0???1	??10?	??000	11010	00?1?	????0	????1	01?11	00001	?1??1	?????	???
Youngina	01101	10100	00000	01000	0001{01}	?0000	0?001	0?11?	00101	?1111	?0?0?	?00
Trilophosaurus	0120?	1?201	1?100	11111	0111?	?0011	00000	11101	11001	11111	11011	111
Hyperodapedon	00201	10201	1?100	01011	00111	01101	00000	11001	11001	11011	1?001	111
Prolacerta	01211	1020?	??110	01011	01110	?0001	1?000	11?01	11000	11101	01011	111
Planocephalosaurus	0????	1121?	??000	000?0	00010	?1101	00110	00???	??101	11101	?3101	??1
Chalarodon m.	01201	11211	1110?	10110	00010	00101	10020	00102	01101	?1101	13100	011
Huehuecuetzpalli	012?1	11??1	?1?00	??000	0?01{01}	1???1	?0000	00102	??1??	11101	13101	011
Dalinghosaurus	0?{12}?1	112??	???0?	000?0	-0011	00111	?0010	?010?	??1??	11100	03101	011

Curriculum vitae

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Peer-reviewed publications:

The last known impact factor is given for Evolutionary Biology, the most recently published one for the other journals.

David Marjanović & Michel Laurin (submitted): **The origin(s) of extant amphibians: review and perspective**. *Zoologica Scripta*. (IF = 2.6)
Robert R. Reisz, Michel Laurin & David Marjanović (in press): ***Apsisaurus witteri* from the Early Permian of Texas: yet another small varanopid synapsid, not a diapsid**. *Journal of Vertebrate Paleontology* **30**(5) (will be published in September 2010). (IF = 1.5)
David Marjanović & Michel Laurin (2009): **The origin(s) of modern amphibians: a commentary**. *Evolutionary Biology* **36**: 336–338. (IF = 3.5)
David Marjanović & Michel Laurin (2008b): **A reevaluation of the evidence supporting an unorthodox hypothesis on the origin of extant amphibians**. *Contributions to Zoology* **77**(3): 149–199. (IF = 1.2)
David Marjanović & Michel Laurin (2008a): **Assessing confidence intervals for stratigraphic ranges of higher taxa: The case of Lissamphibia**. *Acta Palaeontologica Polonica* **53**(3): 413–432. (IF = 1.1)
David Marjanović & Michel Laurin (2007): **Fossils, molecules, divergence times, and the origin of lissamphibians**. *Systematic Biology* **56**(3): 369–388. (IF = 7.8)

Together, these publications have been cited 48 times so far; my H index is 3.

Semi-popular publication:

Michel Laurin & David Marjanović (2006). **Un congrès paléontologique gigantesque dans un pays gigantesque (IPC 2006)**. *Journal de l'Association Paléontologique Française* 50: 14–17.

Invited presentation at a conference:

Invited and partially financed by the International Society for Phylogenetic Nomenclature.

David Marjanović (2006): **The ivory tower. How can we win the necessary acceptance for the PhyloCode?** Oral presentation at the Second Meeting of the International Society for Phylogenetic Nomenclature (New Haven). 15th page of the unpaginated online-only abstract volume (http://www.phylonames.org/pdf/ISPN_Meeting_Program2006.pdf).

Regular presentations at conferences:

All were/will be oral, except for 2009c, which was a poster. I am the presenting author in all cases. Unadorned numbers are the page numbers of the abstract volumes.

David Marjanović (2010): **Age and relationships of the modern amphibians (Tetrapoda: Salientia, Caudata, Gymnophiona, Albanerpetontidae)**. Romer Prize session at the 70th Annual Meeting of the Society of Vertebrate Paleontology (Pittsburgh). Online-only supplement to *Journal of Vertebrate Paleontology* **30**(5): 129A.

David Marjanović & Michel Laurin (2010b): **Phylogénie des tétrapodes avec considération spéciale de l'origine des amphibiens modernes**. Perspectives on vertebrate evolution: topics and problems; conference to celebrate the retirement of Pr[of]. Armand de Ricqlès (Paris). No abstract volume.

David Marjanović & Michel Laurin (2010a): **Age and relationships of the modern amphibians (Tetrapoda: Salientia, Caudata, Gymnophiona, Albanerpetontidae)**. 8th Annual Meeting of the European Association of Vertebrate Palaeontologists (Aix-en-Provence). 55.

David Marjanović & Michel Laurin (2009c): **A closer look at published data matrices reveals support for the "lepospondyl hypothesis" on the origin of extant amphibians**. 69th Annual Meeting of the Society of Vertebrate Paleontology (Bristol). Online-only supplement to *Journal of Vertebrate Paleontology* **29**(3): 142A.

David Marjanović & Michel Laurin (2009b): **A closer look at published data matrices reveals support for the "lepospondyl hypothesis" on the origin of Lissamphibia**. 7th Annual Meeting of the European Association of Vertebrate Palaeontologists (Berlin). 45.

David Marjanović & Michel Laurin (2009a): **A reevaluation of the evidence supporting an unorthodox hypothesis on the origin of extant amphibians**. Tribute to Charles Darwin and [the] Bernissart Iguanodons: new perspectives on vertebrate evolution and Early Cretaceous ecosystems (Brussels). 64.

David Marjanović & Michel Laurin (2008c): **Dating the origin of Lissamphibia by three techniques suggests a Permian, monophyletic origin**. 68th Annual Meeting of the Society of Vertebrate Paleontology (Cleveland, Ohio). Supplement to *Journal of Vertebrate Paleontology* **28**(3): 112A.

Michel Laurin & David Marjanović (2008): **Near-consensus definitions of the names Amphibia and Lissamphibia. Which names, which definitions, which clades?** Third Meeting of the International Society for Phylogenetic Nomenclature (Halifax). No abstract volume.

David Marjanović & Michel Laurin (2008b): **Dating the origin of Lissamphibia by three techniques suggests a Permian, monophyletic origin**. 5th Symposium on Permo-Carboniferous Faunas (Hradec Králové, Czech Republic). 19–21.

David Marjanović & Michel Laurin (2008a): **Dating the origin of Lissamphibia by three techniques suggests a Permian, monophyletic origin**. 6th Annual Meeting of the European Association of Vertebrate Palaeontologists (Spišská Nová Ves, Slovakia). 63–64.

David Marjanović & Michel Laurin (2007): **Fossils, molecules, divergence times, and the origin of lissamphibians**. 5th Annual Meeting of the European Association of Vertebrate Palaeontologists (Carcassonne, France). 43.

David Marjanović & Michel Laurin (2006): **Fossils, molecules, divergence times, and the origin of lissamphibians**. Second International Palaeontological Congress (Běijīng). 153.

David Marjanović (2004b): **A proposal for the definition of Aves L. 1758 in accordance with Recommendations 11A and 11E**. First International Meeting on Phylogenetic Nomenclature (Paris). No abstract.

David Marjanović (2004a): **How to preserve historical usage in phylogenetic definitions? Self-destructive definitions for names of grades**. First International Meeting on

Phylogenetic Nomenclature (Paris). 5, online only (http://www.phylonames.org/pdf/ISPN_Meeting_Program2004.pdf).

Award:

I have won a Student Research Grant from The Paleontological Society (2010) for visiting museums in Switzerland to study placodonts and other animals possibly close to the origin of turtles (the originally intended topic of this thesis). Unfortunately, any work on the observations I will make there will have to wait for my first postdoc period.

Higher education:

2003 – 2006	Study of paleobiology (A 443) at the University of Vienna, ending in a **thesis** entitled “Body size evolution, the Cope-Depéret rule, and biological extinctions in dinosaurs” and an examination passed with the highest mark, and resulting in the degree of ***Mag. rer. nat.* (Master of Natural Sciences)**. Publication will have to wait for the acceptance of a manuscript by M. L. which will evaluate statistical methods that can be used to test for evolutionary trends.
2000 – 2003	Study of biology (A 437) at the University of Vienna (would amount to a bachelor if that title had already existed in Austria at that time; was continued as the above)
2001 – 2008	Study of molecular biology (A 490) at the University of Vienna, ending, after a reorganization of the curriculum, with what will be counted as a bachelor in biology (molecular biology is not a separate discipline anymore)
2000 – 2001	Study of chemistry (A 419) at the University of Vienna (discontinued)
May & June 2000	*AHS-Matura* at BG XII^3 (Erlgasse), Vienna (final exams of secondary school which confer the right to study at a university; equivalent to French *baccalauréat*)

Fieldwork:

Lasting two weeks per year in most cases, sometimes longer; always in July and/or August.

2007 – 2010	Annual excavations in the Late Triassic marls of **Krasiejów** (Poland) under the direct or indirect supervision of Prof. Jerzy Dzik (Polish Academy of Sciences, Warsaw) or Prof. Adam Bodzioch (University of Opole) – that is, supervised digging in the extended morning, largely unsupervised preparing of fossils in the afternoon
2004	Excavations in the Tithonian plated limestones of **Crayssac** (France) led by Prof. Jean-Michel Mazin (then Poitiers, now Lyon)
2003	Excavations in the Berriasian marls of **Cherves-de-Cognac** (France) led by Prof. Jean-Michel Mazin (then Poitiers, now Lyon)
1999	Introduction into the preparation of fossils in the Dinosaur Farm Museum (**Isle of Wight**, United Kingdom) supervised by Prof. Stephen Hutt
1997	Excavations in the Maastrichtian marls of **Aix-en-Provence** (France)

Memberships:

- **Society of Vertebrate Paleontology** (http://www.vertpaleo.org)
- **The Paleontological Society** (http://www.paleosoc.org)
- **International Society for Phylogenetic Nomenclature** (http://www.phylonames.org)

- Elected member of the **Committee on Phylogenetic Nomenclature** (suborganization of the above; term will end in 2011)
- **Dinosaur Mailing List** (http://www.dinosaurmailinglist.org, archives: http://dml.cmnh.org)
- **PhyloCode mailing list** (currently defunct) **and bulletin board** (currently at http://phylonom.wildprehistory.org/index.php due to problems with the original forum at phylonames.org)
- registered editor of the English-language **Wikipedia** (http://en.wikipedia.org), though no contributions in the last two years due to lack of time
- registered editor of **Palaeos.org** (http://www.palaeos.org), though I have contributed almost nothing so far

Languages:

German (native)
English (8 years in school; reading & writing every day; fluent)
French (somewhat limited higher vocabulary and higher grammar, otherwise fluent; I have spent most of the last five years in France)
Russian (4 years in school; limited vocabulary)
Chinese (Standard Mandarin [Pǔtōnghuà]; occasional courses during late secondary school and early university years; basics, very little literacy in Chinese characters)
Spanish (1 year; basics; also, ability to read scientific articles)
Italian (ability to read scientific articles)
Polish (4 x 2 weeks of round-the-clock exposure, see “Fieldwork” section above, greatly helped by considerable similarity to Russian and my interest in linguistics; uttermost basics, literacy, much of grammar, ability to largely understand conversations about scientific topics)

Latin (6 years in school)