The palatal dentition of tetrapods and its functional significance

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Abstract

The presence of a palatal dentition is generally considered to be the primitive condition in amniotes, with each major lineage showing a tendency toward reduction. This study highlights the variation in palatal tooth arrangements and reveals clear trends within the evolutionary history of tetrapods. Major changes occurred in the transition between early tetrapods and amphibians on the one hand, and stem amniotes on the other. These changes reflect the function of the palatal dentition, which can play an important role in holding and, manipulating food during feeding. Differences in the arrangement of palatal teeth, and in their pattern of loss, likely reflect differences in feeding strategy but also changes in the arrangement of cranial soft tissues, as the palatal dentition works best with a well-developed mobile tongue. It is difficult to explain the loss of palatal teeth in terms of any single factor, but palatal tooth patterns have the potential to provide new information on diet and feeding strategy in extinct taxa.

Keywords: Palatal dentition; Function; Feeding behavior; Cranial soft anatomy; Tetrapoda; Amniota; Evolution.

Introduction

Any consideration of feeding in vertebrates will include detailed discussion of the marginal dentition. Far less attention has been paid to the palatal dentition, although characters of the palatal dentition are used in phylogenetic analysis (early tetrapods, Sigurdsen & Bolt, 2010; Diapsida, Benton, 1985; Evans, 1988; Archosauria, e.g. Sereno, 1991; Lepidosauromorpha, e.g. Evans, 1991; Parareptilia, Tsuji, 2006; Rhynchosauria, Dilkes, 1998; Synapsida, Sidor, 2003; Abdala et al. 2008; Campione & Reisz, 2010; and Choristodera (Evans, 1990; Matsumoto, 2011). There is a general acceptance that an extensive palatal dentition is plesiomorphic for amniotes. However, the evolutionary history of this dentition is poorly understood, and detailed studies of its structure and function in either extant or extinct tetrapods are rare (e.g. Regal, 1966; Kordikova, 2002; Mahler & Kearney, 2006; Diedrich, 2010). During feeding, the jaws, tongue, and palate cooperate in food prehension, intra-oral transport, and swallowing, thus changes in the palatal dentition should reflect changes in feeding behaviour and/or changes in the anatomy of the oral soft tissues. Potentially, therefore, a better understanding of the functional morphology of the palatal dentition may provide an additional source of information on the biology of extinct tetrapods. Here we review the main trends in the evolutionary history of the tetrapod palatal dentition and then discuss them in relation to changes in the anatomy of the skull and oral soft tissues.

Material and Methods

Palatal tooth arrangements were mapped onto phylogenetic trees for the tetrapodomorph *Eusthenopteron,* early tetrapods, and basal Amniota (Ruta et al. 2003; Ruta & Coates, 2007; Snitting, 2008); Synapsida (Sidor, 2001); Parareptilia (Tsuji & Müller, 2009; Tsuji et al. 2012); and Diapsida (DeBraga & Rieppel, 1997; Rieppel & Reisz, 1999; Brusatte et al. 2010; Borsuk –Białynicka & Evans, 2009a; Dilkes & Sues, 2009). The data on palatal tooth arrangement patterns for each taxon were collected from descriptions in the literature or data matrices for phylogenetic analysis. For some synapsids and early diapsids, the palatal tooth arrangement has not been described, and specimens were examined first hand (see Appendix 1-7).

Evolutionary patterns in the palatal dentition of early tetrapods and amphibians

Early tetrapods (e.g. *Acanthostega*, Clack, 1994; *Ichthyostega*, Clack, 2012; *Pederpes*, Clack & Finney, 2005; *Crassigyrinus*, Clack, 2012; *Greererpeton*, Smithson, 1982; *Megalocephalus*, Beaumont, 1977) inherited the basic pattern of the palatal dentition (vomer, palatine, and ectopterygoid) from that of ancestral sarcopterygians (e.g. *Eusthenopteron*, Clack, 2012). There was a single lateral palatal tooth row on each side, running parallel to the jaw margin and with teeth of similar size (and/or larger) to those of the marginal dentition. In *Eusthenopteron,* the parasphenoid intervened between the vomers and the pterygoids in the midline, with the latter element expanded posterior to the marginal tooth row. Small teeth were randomly and widely distributed across the parasphenoid and pterygoid, forming a shagreen dentition. Early tetrapods retained shagreen teeth on the pterygoid (e.g. *Ichthyostega*, *Acanthostega*; Fig. 1), with parasphenoid teeth in a more limited area (e.g. *Acanthostega*, Clack, 1994; *Pederpes*, Clack & Finney, 2005*; Greererpeton*, Smithson, 1982; Fig. 1). This primitive arrangement was conserved in many Temnospondyli (e.g. *Phonerpeton*, Dilkes, 1990; *Doleserpeton*, Sigurdsen & Bolt, 2010), Anthracosauria (*Silvanerpeton*, Ruta & Clack, 2006; *Proterogyrinus*, Holmes, 1984; *Pholiderpeton*, Clack, 1987) and Seymouriamorpha (*Seymouria*, Klembara et al., 2005; *Discosauriscus*, Klembara, 1997; *Utegenia*, Laurin, 1996), with a tooth shagreen on all palatal elements but a reduction in the number of large lateral palatal teeth (Fig. 1). However, in temnospondyls enlargement of the interpterygoid vacuity separated the pterygoids with loss of their anterior midline contact (Fig. 1). As a result, the shagreen teeth on the pterygoid became more laterally restricted. In addition, the ventral surface of the interpterygoid vacuity was sometimes covered by a bony plate bearing patches of loosely set denticles (Schoch & Milner, 2000).

Many lepospondyls retained the primitive arrangement with a lateral palatal tooth row parallel to the jaw margin, but there is more variation in the presence and/or arrangement of the shagreen teeth on the palate and the parasphenoid (Fig. 1: e.g. *Odonterpeton*; *Tambachia,* Sumida et al. 1998). *Pantylus* (Romer, 1969) had teeth scattered across the palate (various sizes distributed randomly), *Brachydectes* (Wellstead, 1991) possessed longitudinally aligned midline vomerine tooth rows, and some derived taxa (e.g.

Cardiocephalus, Ptyonius, Carroll et al. 1998) had reduced or lost the shagreen teeth completely (Fig. 1). Further variations are listed in Appendix 1.

Living lissamphibians (Gymnophiona, Caudata, and Anura) have reduced shagreen teeth, and palatal teeth are usually restricted to the vomer and parasphenoid, although some species also bear teeth on a palatine/pterygopalatine (e.g. the caudates *Siren* and *Necturus*) or maxillopalatine (e.g. the gymnophionan *Dermophis*, Trueb, 1993). Gymnophiona generally have a single lateral vomerine tooth row parallel to the jaw margin (e.g. *Epicrionops,* Nussbaum, 1977) whereas in frogs (Anura) there is more often a transverse tooth row lying parallel, or nearly parallel, to the anterior part of the marginal tooth row (e.g. *Pelobates*, Roček, 1981; the hylid *Triprion*, Trueb, 1993) (see Appendix 1). The pattern in caudates is much more variable and ranges from a transverse anterior vomerine row (e.g. *Ambystoma;* the plethodontid *Desmognathus*, Trueb, 1993), a medial longitudinal row (e.g. the salamandrids *Notophthalmus* and *Taricha*, Trueb, 1993, Duellman & Trueb, 1994), a roughly "T" shaped combination row (e.g. the plethodontids *Pseudotriton* and *Stereochilus*, Regal, 1966, Wake, 1966), an anterior row parallel to the marginal tooth row (e.g. *Necturus*, Trueb, 1993; *Cryptobranchus*, Elwood & Cundall, 1994)(Fig. 2A), or a tooth platform in either the anterior (*Siren*, Trueb, 1993) or posterior part of the mouth in combination with a transverse anterior vomerine row (e.g. the plethodontids *Bolitoglossa* and *Plethodon*, Wake, 1966).

Evolutionary patterns in the palatal dentition of amniotes

A dramatic change occurred in the palatal dentition of Diadectomorpha, the sister taxon of the Amniota (e.g. Ruta et al. 2003; Ruta & Coates, 2007). They lost the early tetrapod pattern (a lateral palatal row and median tooth shagreen) and replaced it with an arrangement of longitudinally oriented rows of conical teeth on the anterior palatal elements (e.g. *Diadectes*, Olson, 1947; Berman et al. 1998; *Orobates*, Berman et al. 2004) and/or a transverse posterior row on the pterygoid flange (*Limnoscelis,* Williston, 1911, Berman et al. 2010; *Tseajaia*, Moss, 1972). This palatal morphology would have been inherited by early members of both Synapsida (mammals and stem-mammals) and Reptilia (Parareptilia+Eureptilia) when these two major clades diverged in the Late Carboniferous.

Synapsida

Recent phylogenetic analyses place either Caseidae or Ophiacodontidae + Varanopidae as the basal synapsid clade (Benson, 2012). In members of the Caseidae (e.g. *Cotylorhynchus*, Reisz & Sues, 2000; *Ennatosaurus*, Maddin et al. 2008) and Varanopidae (*Mesenosaurus*, Reisz & Berman, 2001, detailed information shown in Appendix 2), there were palatal teeth on the vomer, palatine, pterygoid, and, in some cases, the parasphenoid (Caseidae) and ectopterygoid (e.g. *Edaphosaurus*, Modesto, 1995). However, there was a general trend towards simplification and reduction of the longitudinal palatal tooth rows, while retaining the transverse pterygoid flange tooth row, which was usually located posterior to the marginal tooth row (Fig. 3). The vomerine tooth row tended to become narrower as the choanae elongated anteroposteriorly, and it was lost in Sphenacodontidae (e.g. *Dimetrodon*, Case, 1904; *Secodontosaurus*, Reisz et al. 1992; *Tetraceratops*, Laurin & Reisz, 1996). The posterior elongation of the choanae also had the effect of restricting the longitudinal palatine and pterygoid tooth rows to the back of the mouth (Fig. 3). In these non-therapsid synapsids, particularly in the carnivorous *Haptodus* (Laurin, 1993), *Dimetrodon* (Case, 1904)(Fig. 2B), and *Tetraceratops* (Laurin & Reisz, 1996), the pterygoid flange teeth were often larger than those of the longitudinal tooth rows (vomer, palatine, pterygoid). By contrast, the herbivorous *Edaphosaurus* lacked pterygoid flange teeth but developed a large plate of closely packed palatine and pterygoid teeth level with the posterior teeth of the marginal row (Fig. 3).

Further reductions occurred within the clade Therapsida (including Biarmosuchia, Dinocephalia, Anomodontia, and Theriodontia). Although some Biarmosuchia and Dinocephalia retained the transverse pterygoid flange tooth row, they lost vomerine teeth (the dinocephalian *Estemmenosuchus* is an exception, King, 1988) (Fig. 3). The longitudinal tooth rows were rearranged into either circular patches (e.g. the biarmosuchian *Lycaenodon*, Sigogneau-Russell,1989 and the dinocephalian *Syodon*, King, 1988), or a predominantly transverse, M-shaped anterior tooth row (e.g. *Biarmosuchus*, Ivakhnenko, 1999, and the dinocephalian *Titanophoneus*, King, 1988).

Loss of the palatal dentition occurred independently within Anomodontia (except the basal *Biseridens*, Liu et al. 2009) and Theriodontia (Modesto et al. 1999). In the latter group, a palatal dentition was retained in Gorgonopsidae and some Therocephalia (Fig. 4). The palatal dentition of gorgonopsids was similar to that in non-therapsids (e.g. Biarmosuchia), with posteriorly located circular tooth patches on the palatine and pterygoids (Fig. 4). The presence of a pterygoid flange row varied, even between species (e.g. *Cyonosaurus*, see Appendix 2). In Therocephalia, the medial palatal teeth were further restricted to a small area well posterior to the marginal tooth row (e.g. *Regisaurus*, Mendrez, 1972; Fourier & Rubidge, 2007; *Theriognathus*, Brink, 1956; *Viatkosuchus*, Tatarinov, 1995), or were lost completely (e.g. *Bauria*, Kemp, 1982; *Moschorhinus*, Battail & Surkov, 2000). Palatal teeth were absent in Cynodontia (the lineage leading to mammals).

Reptilia (Parareptilia+Eureptilia)

In contrast to Synapsida, many basal members of both Parareptilia and Eureptilia retained longitudinal palatal tooth rows, in conjunction with those on the pterygoid flange (Fig. 5–7; Appendix 3–4).

Parareptilia. Most parareptiles had the same palatal tooth arrangement as diadectidomorphs and basal amniotes, but shagreen teeth were generally absent (the Permian *Macroleter* was an exception, Tsuji, 2006). Several early parareptiles had teeth on the parasphenoid and/or ectopteryoid (e.g. *Millerosaurus,* Carroll, 1988 and *Lanthanosuchus,* Efremov, 1946; *Nyctiphruretus,* Tsuji et al. 2012), but whether as a retention of the primitive condition or a redevelopment is unclear. Most parareptiles retained a tooth row on the pterygoid flange (e.g. *Lanthanosuchus*, Efremov, 1946; *Nycteroleter*, Tverdokhlebova & Ivakhnenko, 1984), although this is absent in Procolophoniodea (including *Procolophon*, Carroll & Lindsay, 1985; Cisneros, 2008; *Barasaurus*, Piveteau, 1955; *Owenetta,* Reisz & Scott, 2002) and *Mesosaurus* (Modesto, 2006). Where present, the orientation of the flange row also varies from clearly transverse (most taxa) to more oblique (~ 45° to the transverse axis in *Scutosaurus* [Tsuji et al. 2012] and *Pareiasuchus* [Lee et al. 1997]) (Fig. 5). The longitudinal tooth rows are generally straight, but there was some variation within procolophonids. In *Procolophon*, the palatine and pterygoid tooth rows form a “w” shape (Carroll and Lindsay, 1985; Cisneros, 2008); *Owenetta* shows a triangular arrangement composed of vomer, palatine and pterygoid rows (Fig. 5); and *Bashkyroleter mesensis* had an additional row running parallel to the marginal dentition (Ivakhnenko, 1997).

Members of the Permian Bolosauridae (e.g. *Bolosaurus*, *Eudibamus*) generally lacked palatal teeth (Watson, 1954; Berman et al. 2000). This includes *Belebey maximi* and *B. chengi* (Ivakhnenko & Tverdochlebova, 1987; Müller et al. 2008), but pterygoid flange rows were present in *B. vegrandis* (Müller et al. 2008).

Eureptilia and stem Diapsida. Eureptilia also inherited the primitive amniote pattern of longitudinal and transverse palatal tooth rows, as shown by *Captorhinus* which had teeth on the palatine, pterygoid, and, variably, the parasphenoid (Warren, 1961; Modesto, 1998), but not the ectopterygoid. Warren (1961) recorded sporadic vomerine teeth in *Captorhinus* sp., but other authors recorded them as absent (Fox & Bowman, 1966). Perhaps they were variable like those of the parasphenoid, although *Labidosaurus* had lost both sets (Modesto et al. 2007). Parasphenoid teeth were present in several-other stem eureptilian taxa and stem diapsids (e.g. *Paleothyris*, Carroll, 1969; *Petrolacosaurus*, Reisz, 1981; *Orovenator*, Reisz et al. 2011), but ectopterygoid teeth were rare (e.g. *Araeoscelis*, Vaughn, 1955)(Fig. 6). *Claudiosaurus* appears to have been exceptional in replacing the discrete tooth rows with a shagreen of small teeth across all but the ectopterygoid bones (Carroll, 1981)(Fig. 6).

The stem diapsid pattern was inherited by members of some descendant clades (e.g. *Youngina*, Gow, 1975) but parasphenoid and ectopterygoid teeth were generally absent. Subsequently, members of the two major crown diapsid clades, Archosauromorpha and Lepidosauromorpha, showed parallel patterns of reduction from the primitive palatal pattern (Fig. 6–7).

Basal archosauromophs, like *Protorosaurus* (Late Permian, Seeley, 1887) and *Czatkowiella* (Early Triassic, Borsuk-Białynicka & Evans, 2009a), retained longitudinal tooth rows on the vomer, palatine and pterygoid, but lacked teeth on either the pterygoid flange or parasphenoid (ectopterygoid teeth unknown; Fig. 7). In contrast, Choristodera (if these are archosauromorphs, e.g. Evans, 1988, 1990; Gauthier et al. 1988) generally retained the pterygoid flange row and expanded the longitudinal pterygoid row into a broad tooth battery. Most choristoderes, including the earliest (Middle - Late Jurassic *Cteniogenys*; Evans, 1990), lacked parasphenoid teeth, so their presence in the Early Cretaceous neochoristodere *Ikechosaurus* (Brinkman & Dong, 1993) was probably a reacquisition (Fig. 2C). The broad-snouted Paleocene choristodere *Simoedosaurus* (e.g. Sigogneau-Russell & Russell, 1978) is characterized by shagreen teeth covering the palate, and there may be a relationship between snout width and palatal tooth row width in this group (Matsumoto & Evans, 2015).

Members of some early archosauromorph clades (e.g. Rhynchosauridae, Langer & Schultz, 2000; Trilophosauria, Spielmann et al. 2008) independently lost the palatal dentition, possibly in association with the evolution of a specialized marginal dentition, but the primitive arrangement was retained in archosauriform stem taxa (*Tanystropheus* being unusual in having vomerine teeth running parallel to the marginal tooth row [Wild, 1973])(Fig. 7).

Most crown-group archosaurs lacked palatal teeth (Dilkes & Sues, 2009), but a longitudinal row persisted on the palatal ramus of the pterygoid in a few taxa, including the early pterosaur *Eudimorphodon* (Wild, 1978), the basal non-avian dinosaur, *Eodromaeus,* and the basal sauropodmorph *Eoraptor* (Martinez et al. 2011; Sereno et al. 2012).

Marginal and palatal teeth were both present in the oldest recorded chelonian, the late Triassic aquatic *Odontochelys* (Li et al. 2008), which had longitudinal tooth rows on the vomer, palatine and pterygoid, but not the pterygoid flange. A similar palatal tooth arrangement was present in the terrestrial *Proganochelys* (Gaffney, 1990; Kordikova, 2002)(Fig. 7), but teeth were absent in all known later testudine taxa.

Within the aquatic Sauropterygia, Placodontia is exceptional in the possession of plate-like crushing palatal teeth that were larger than those of the marginal dentition (Neenan et al., 2013)(Fig. 6). However, the palatal dentition was lost at an early stage in the Eosauropterygia (e.g. *Nothosaurus*, Albers & Rieppel, 2003; *Simosaurus*, Rieppel, 1994) and Ichthyopterygia (Motani, 1999). A single individual of the basal ichthyosaur *Utatsusaurus hataii* reportedly had teeth on the pterygoid, but some re-examination is needed (Motani, 1999, and personal communication to RM, 2007).

In Lepidosauromorpha, the longitudinal rows remained extensive in stem lepidosaurs like the kuehneosaurs and in early rhynchocephalians (e.g. *Gephyrosaurus*, Evans, 1980), but the pterygoid flange row was lost in most taxa (Fig. 6). The palate of early squamates remains unknown but was probably like that of stem-lepidosaurs. Crown rhynchocephalians lost the pterygoid teeth but preserved and enlarged the lateral palatine row (e.g. *Palaeopleurosaurus*, Carroll & Wild, 1994; *Priosphenodon*, Apesteguia & Novas, 2003; *Sphenodon*, Jones et al. 2012), which was realigned so as to lie parallel to the maxillary tooth row. This arrangement allows the specialized shearing mechanism that characterizes Rhynchocephalia (Jones et al. 2012), whereby the teeth of the dentary bite between the maxillary and palatine tooth rows. Squamates only rarely have palatine teeth (e.g. polychrotines, *Lanthanotus*, *Heloderma*) but pterygoid teeth are more common (Mahler & Kearney, 2006; Evans, 2008), usually along the margins of the interpterygoid vacuity (Fig. 6). Without well-preserved early members of major lineages, it is difficult to determine whether palatine teeth were lost multiple times, or have occasionally been regained as has been suggested for the vomerine teeth of the anguid *Ophisaurus apodus* (Evans, 2008)(Fig. 6). In snakes, the small-mouthed scolecophidians, anomochilids, and uropeltids lack any palatal teeth (Cundall & Irish, 2008), but this is likely to be a specialization rather than the primitive condition. ‘Primitive’ alethinophidian snakes (e.g. cylindrophiids, aniliids, xenopeltids) have a row of teeth on both the palatine and pterygoid, and this arrangement is retained in macrostomatan snakes, where enlarged palatal teeth play an important role in gripping prey as it is drawn into the mouth (Mahler & Kearney, 2006; Cundall & Irish, 2008). Again, the palatine teeth, at least, may have been regained (Cundall & Greene, 2000). The palate is incompletely known in basal fossil snakes like the Cretaceous *Najash* (Zaher et al. 2009) and *Dinilysia* (Zaher & Scanferla, 2012), but the marine simoliophids (e.g. *Haasiophis*, Tchernov et al. 2000) already show the macrostomatan configuration.

Discussion

The review presented above highlights the variation in palatal tooth morphology that exists across tetrapods, but also show some clear trends, summarized in Figure 8. The first is a major difference between early tetrapods and Temnospondyli ('amphibians'), on the one hand, and early amniotes on the other. Early amniotes are characterized by a rearrangement of the palatal dentition to produce a series of distinct longitudinal and/or transverse tooth rows. This arrangement was retained in early representatives of both Synapsida and Reptilia, but there followed a similar, but independent, pattern of reduction in both lineages, starting with the teeth on the parasphenoid and ectopterygoid, and then the vomer and/or pterygoid flange. Within synapsids, all remaining palatal teeth were lost in the ancestors of cynodonts, concomitant with the evolution of the secondary palate. However, as most Reptilia have only a primary palate, palatal teeth persisted somewhat longer, especially in parareptiles and early members of both Archosauromorpha and Lepidosauromorpha. Palatal teeth were lost completely in the ancestors of crown-group crocodiles and turtles, and in early non-avian dinosaurs. In contrast, lepidosaurs tended to retain (or regain) at least some palatal teeth, most often on the posterior part of the pterygoid plate. Regain would also help to explain the presence of parasphenoid teeth in some derived members of Choristodera and *Kuehneosaurus*, despite their absence in more primitive members of the same lineages. It seems likely the developmental mechanism for generating palatal teeth was suppressed rather than lost in some lineages, a phenomenon that has been reported for the marginal dentition in, for example, birds and frogs (Harris et al. 2006; Wiens, 2011).

These trends in the arrangement and subsequent reduction of the palatal dentition raise questions about the role of palatal teeth generally and of different patterns (e.g. tooth shagreen versus distinct rows) or groups (e.g. transverse pterygoid flange teeth versus longitudinal rows) of palatal teeth. Like the marginal dentition, the palatal dentition would be expected to reflect diet and feeding strategy to some degree, but diet alone is less likely to explain major trends. Palate morphology should also be correlated with structures in the floor of the mouth, notably the tongue, the hyobranchial apparatus, and the pharynx, as well as jaw muscles like the pterygoideus that have palatal attachments, and with other aspects of feeding strategy including skull kinesis and jaw movements.

Based on studies of living taxa (as referenced below), Figure 9 presents a summary of some major changes that are thought to have occurred in the soft tissues and/or feeding mechanics of major tetrapod groups. Some of these changes may be correlated with changes in the palatal dentition. However, developing functional hypotheses to explain palatal tooth distribution in extinct taxa is complicated by the fact that, with the exception of snakes (which are highly specialized), most living amniotes have either significantly reduced the palatal dentition (lizards, rhynchocephalians) or lost it completely (chelonians, archosaurs, mammals). Moreover, examination of the palatal surface in a bony skull provides an incomplete understanding of its original structure, much of which relies on the presence of overlying soft tissues. Thus, for example, an apparently smooth bone surface may have been covered in life by keratinized oral epithelium that was itself ridged or papillate (Fig. 10).

One of the major challenges faced by early land animals was food acquisition (e.g. Lauder & Gillis, 1997). Although aquatic animals often rely on suction feeding to ingest prey and transport it through the mouth toward the pharynx (e.g. Lauder & Shaffer, 1993; Deban & Wake, 2000; Iwasaki, 2002), terrestrial animals must move food physically into the mouth, pass it towards the back of the oral cavity (intra-oral transport, e.g. Smith, 1993; Schwenk, 2000a), and finally push into the pharynx prior to swallowing. The palatal dentition, lying between the teeth of the upper jaws, is positioned to assist the tongue and jaws primarily in intra-oral transport. Very small or thin prey may be moved by the tongue alone (due to surface adhesion) but the development of a palatal gripping surface would have made it easier to manipulate (and perhaps subjugate) larger, potentially resistant, food items. The longitudinal palatal rows of adult terrestrial salamanders have also been correlated with the possession of a mobile tongue (Regal, 1966; Wake & Deban, 2000), the two working together to hold and transport food. However, the absence of intrinsic muscles in most amphibian tongues (Schwenk, 2000a) may limit their mobility and power within the oral cavity.

A muscular tongue with both extrinsic and intrinsic muscles is found in many amniotes and probably evolved in stem members of that group, followed by keratinization of the epithelial surface (Iwasaki, 2002). This type of tongue is well adapted to work against the roof of the mouth during intra-oral transport and also to help to roll the food into a bolus at the back of the oral cavity (Schwenk, 2000a). It may therefore be significant that the inferred evolution of this type of tongue (stem-amniotes) was coincident with the change in the pattern of palatal teeth into an ordered arrangement of distinct longitudinal rows. In the absence of a muscular pharynx, a muscular tongue is also used to push the food bolus into the entrance of the pharynx, a process known as pharyngeal packing (Schwenk, 2000a). Teeth on the posterior part of the palate (parasphenoid and pterygoid flanges) may originally have been important in holding the food bolus in place at the entrance to the pharynx, but perhaps became less so as food positioning and swallowing became more efficient (e.g. by expansion of posterior lobes on the tongue, or by kinetic movements of the jaws and palate, Schwenk 2000a).

Reacquisition of parasphenoid teeth (as in the Late Triassic kuehneosaurs and the neochoristodere *Ikechosaurus*) may therefore indicate a change in skull biomechanics or feeding strategy whereby an extra gripping surface at the entrance to the pharynx was beneficial. In kuehneosaurs, at least, this may have been correlated with a potential for the quadrates (and attached pterygoids) to splay out laterally to increase pharyngeal width (SE unpublished). Moreover, a subsequent increase in size of the pterygoideus muscle in later lineages, parts of which attach to the pterygoid flange, may have resulted in loss of the pterygoid flange tooth row (e.g. King et al. 1989; Maier et al. 1996).

The dichotomy in the fate of the palatal dentition between archosauromorphs and lepidosauromorphs may, in part, reflect changes in the archosaurian tongue. Both crocodiles and birds, and thus potentially their common archosaurian ancestor, have lost much of the intrinsic tongue musculature (Schwenk, 2000a). Instead of using the tongue for prehension and transport, they mainly use jaw prehension, inertial feeding, and gravity (Schwenk, 2000a). Loss of the palatal dentition would be consistent with this, as would the development of a secondary palate in derived crocodiles. However, some extant archosaurs (birds, crocodiles) and chelonians (e.g. the sea turtles *Dermochelys coriacea, Chelonia mydas*) have keratinized epithelium forming corny papillae and/or rugae on the palate and/or on the tongue (e.g. Shimada et al. 1990; Kobayashi et al. 1998; Iwasaki, 2002) (Fig. 10). These may have a role analogous to that of the original palatal dentition, especially in turtles where a muscular tongue is retained. In some birds, palatal papillae run transversally across the back of the oral cavity, an arrangement similar to that of a pterygoid flange tooth row. Harrison (1964) suggested that this arrangement, which can also occur across the back of the tongue, facilitates positioning of prey prior to swallowing, a role that we also infer for the pterygoid flange and parasphenoid teeth of more primitive amniote taxa.

Most lepidosaurs have a mobile muscular tongue with a papillose surface (Schwenk, 2000b). Although many non-iguanian lizards used jaw prehension to bring food into the mouth, aided by varying levels of kinesis, most lizards still use the tongue for intraoral transport and pharyngeal packing, with the latter aided in most taxa by enlarged posterior lobes on the tongue (chameleons, varanids and some teiids lack these). The retention of clusters or lines of teeth on the posterior part of the pterygoid plate, close to the opening of the pharynx (Mahler & Kearney, 2006) may help in positioning/restraining the food bolus during packing. Pharyngeal packing is followed by pharyngeal compression, in which external neck muscles (constrictor colli) contract to squeeze the bolus into the muscular esophagus for swallowing (Schwenk, 2000a). However, the bolus needs to be pushed posterior to the main body of the hyoid before compression begins, to ensure it does not move back up into the mouth instead. In derived anguimorphs and snakes, together or independently depending on the phylogenetic hypothesis, the anterior part of the tongue is bifid and slender, with a purely chemosensory role. In *Varanus*, this change in tongue function is compensated for by the adoption of inertial feeding whereby food items are effectively thrown to the back of the mouth (Schwenk, 2000b). Snakes employ a different strategy, using kinetic jaws and, especially in macrostomatans, enlarged palatine and pterygoid teeth, to draw prey to the back of the mouth for swallowing. As noted above, these may be a secondary development, given that both tongue action and inertial feeding are precluded in snakes.

The fossil record of synapsids is generally good, permitting many stages in the evolution of the mammalian feeding apparatus, such as heterodonty, reduction of the accessory jaw bones, and formation of a bony secondary palate, to be followed. Coincident changes in oral soft anatomy must also have occurred (Fig. 9), although these are more difficult to pinpoint in time. They include formation of a soft tissue secondary palate prior to the bony one (choanal folds), extension of the bony secondary palate by a muscular soft palate to improve the separation of food and air streams, and muscularization of the pharynx so that the food bolus can be formed within the oropharynx rather than in the mouth, and then swallowed rapidly (e.g. Maier et al. 1996; Schwenk, 2000a). This would have reduced the need for parasphenoid or pterygoid flange teeth. The mammalian tongue remained large and muscular, and reduction of the hyoid apparatus gave it greater mobility for intraoral transport, aided by the development of muscular cheeks. Although palatal teeth were lost, many terrestrial mammals (like birds and turtles) have developed transverse palatal rugae to help to grip food. These rugae are generally reduced in aquatic mammals that feed under water (e.g. suction feeders) where a gripping palatal surface is less useful (Werth, 2000), although Beaked Whales are an exception to this, in developing papillose rugosities to hold their slippery prey (Heyning & Mead, 1996).

Conclusions

Palatal teeth clearly had an important role in holding and manipulating food within the mouth (although they may occasionally have contributed to food reduction), and it is reasonable to conclude that an extensive palatal dentition was correlated with a well-developed mobile tongue (although the obverse is not necessarily true). The more anterior palatal teeth (vomer, palatine, anterior pterygoid) were probably used mainly during intraoral transport, whereas posterior palatal teeth, notably those on the pterygoid flange and parasphenoid, may have had a greater role in positioning and stabilizing the food bolus at the entrance to the pharynx. Subsequent loss/reduction of the palatal dentition in derived members of most major tetrapod lineages was probably linked to anatomical and functional changes that rendered a palatal gripping surface less important or effective. These include

1. reduction of the tongue (e.g. archosaurs, varanid lizards).
2. functional replacement of the palatal dentition with palatal or lingual rugosities (e.g. some turtles, mammals), or with keratinized papillae (e.g. birds).
3. skull or jaw adaptations that improved food holding (e.g. cranial kinesis)
4. changes in feeding strategy (e.g. the adoption of inertial feeding, *Varanus*, crocodiles)
5. invasion of the ventral palatal surface by pterygoid musculature
6. development of an extensive hard and soft palate (e.g. mammals).

No single factor can be invoked to explain the loss (or reacquisition) of palatal teeth in any one taxon, and many aspects remain poorly understood (e.g. the relationship between skeletal and soft tissue anatomy in the palate; the developmental biology of the palatal dentition). Nonetheless, palatal tooth patterns have the potential to provide additional information on diet and feeding strategy in extinct taxa and would benefit from further more detailed study.

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Figure captions

Fig. 1 Phylogenetic tree for early tetrapods and amphibians showing arrangement of palatal dentition. Colour coding of the palatal figures is consistent in all figures (tree modified from Ruta & Coates, 2007). Palatal figures as follows: 1, *Eusthenopteron*; 2, *Acanthostega*; 3, *Pederpes*; 4, *Crassigyrinus*; 5, *Greerepeton*; 6, *Edops*; 7, *Balanerpeton* (original image reflected); 8, *Phonerpeton*; 9, *Doleserpeton*; 10, *Dermophis mexicanus*, Gymnophiona; 11, *Stereochilus marginatum,* Caudata; 12, *Gastrotheca walker*, Anura; 13, *Silvanerpeton*; 14, *Proterogyrinus*; 15, *Seymouria*; 16, *Odonterpeton*; 17, *Rhynchonkos*; 18, *Cardiocephalus* (original image reflected); 19, *Pantylus*; 20, *Brachydectes*; 21, *Batrachiderpeton*; 22, *Ptyonius*; 23, *Diadectes*. Image sources: 1,2,4, Clack, 2012; 3, Clack & Finney, 2005; 5, Smithson, 1982; 6, Romer & Witter, 1942; 7, Holmes 2000; 8, Dilkes, 1990; 9, Sigurdsen & Bolt, 2010; 10-12, Duellman & Trueb, 1994; 13, Ruta & Clack, 2006; 14, Holmes, 1984; 15, Klembara et al. 2005; 16-22, Carroll et al. 1998; 23, Reisz & Sues, 2000；1, 10-13, 20 original without scale. Abbreviations: ANTH, Anthracosauria; LISS, Lissamphibia; SEY, Seymouriamorpha.

Fig. 2 Photographs of the palatal tooth arrangement in various lineages: A, *Andrias japonicas* (Lisamphibia; NSM-PO-H-447); B, *Dimetrodon limbatus* (Synapsida; AMNH FR 4001); C, *Ikechosaurus sunailinae* (Choristodera, Diapsida; IVPP V9611-3), grey coloured area marks nasopalatal trough and blue coloured area marks the distribution of the palatal dentition. Institutional abbreviations: American Museum Natural History (AMNH); IVPP Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China (IVPP); National Museum of Nature and Science, Tokyo (NSM). Anatomical abbreviations: d, dentary; ept, ectopterygoid; hy, hyoid; pal, palatine; psh, parasphenoid; pt, pterygoid; pt fl, pterygoid flange; v, vomer.

Fig. 3 Skulls of synapsids in palatal view (phylogeny based on Sidor, 2001): 1 *Cotylorhynchus*; 2, *Ennatosaurus*; 3, *Mesenosaurus*; 4, *Varanosaurus*; 5, *Edaphosaurus*; 6, *Haptodus*; 7, *Secodontosaurus*; 8, *Tetraceratops*; 9, *Biarmosuchus*; 10, *Lycaenodon*; 11, *Herpetoskylax*; 12, *Titanophoneus*; 13, *Syodon*; 14, *Styracocephalus* (original without scale); 15, *Estemmenosuchu*s; 16, *Struthiocephalus*. Image sources: 1, Reisz & Sues, 2000; 2, Maddin et al. 2008; 3, Reisz & Berman, 2001; 4, Berman et al. 1995; 5, Modesto, 1995; 6, Laurin, 1993; 7, Reisz et al. 1992; 8, Laurin & Reisz, 1996; 9, Ivakhnenko, 1999; 10-11, Sigogneau-Russell, 1989; 12-13, 15, King 1988; 14, Rubidge & van den Heever, 1997; 16, Rubidge, 1991. Abbreviations: BIAR, Biarmosuchia; CASE, Caseasauria; DINO, Dinocephalia; OPHI, Ophiacodontidae; SPHE, Sphenacodontidae; VARA, Varanopidae.

Fig. 4 Skulls of synapsids in palatal view (phylogeny based on Sidor, 2001), continued from Figure 4: 1, *Aelurosaurus*; 2, *Arctognathus*; 3, *Leontocephalus*; 4, *Scylacops*; 5, *Aloposaurus*; 6, *Gorgonops*; 7, *Arctops*; 8, *Prorubidgea*; 9, *Dinogorgon*; 10, *Rubidgea* (original without scale); 11, *Theriognathus*; 12 *Viatkosuchus* (original without scale); 13 *Regisaurus*. Image sources: 1-10, Sigogneau-Russell, 1989; 11,13, Kemp, 1982; 12, Tatarinov, 1995.

Fig. 5 Skulls of parareptiles in palatal view (phylogeny based on Tsuji et al., 2012). 1, *Mesosaurus*; 2, *Millerosaurus*; 3, *Acleistorhinus*; 4, *Nyctiphruretus*; 5, *Procolophon* (original without scale); 6, *Owenetta*; 7, *Scutosaurus*; 8, *Pareiasuchus*; 9, *Macroleter*; 10, *Nycteroleter*; 11, *Bashkyroleter mesensis*. Image sources: 1, Modesto, 2006; 2, 4,7, Carroll, 1988; 3, DeBraga & Reisz, 1996; 5, Carroll & Lindsay, 1985; 6, Reisz & Scott, 2002; 8, Lee et al. 1997; 9, Tsuji, 2006; 10, Tverdokhlebov & Ivakhnenko, 1984; 11, Ivakhnenko, 1997. Abbreviations: LANT, Lanthanosuchidae; BOL, Bolosauridae; PROCOL, Procolophonoidea; PAREIA, Pareiasauria.

Fig. 6 Skulls of Eureptilia and Diapsida, Sauropterygia, Ichthyopterygia, and Lepidosauromorpha in palatal view (phylogeny based on DeBraga & Rieppel, 1997; Pyron et al. 2013; Rieppel & Reisz, 1999; Wiens et al. 2010) 1, *Captorhinus*; *2, Paleothyris*; 3, *Petrolacosaurus*; 4, *Araeoscelis*; 5, *Claudiosaurus*; 6,*Youngina*; 7, *Placodus*; 8, *Kuehneosaurus*; 9, *Marmoretta*; 10, *Gephyrosaurus*; 11, *Clevosaurus*; 12, *Sphenodon*; 13, *Lacerta*; 14, *Ctenosaura* (original without scale); 15, *Ophisaurus*; 16 *Heloderma*; 17, *Shinisaurus*; 18, *Platecarpus* (original without scale); 19, *Anilius*. Image sources: 1, Reisz & Sues, 2000; 2, Benton, 2000; 3, Reisz, 1981; 4, Vaughn, 1955; 5-7, Carroll, 1988; 8, Robinson, 1962; 9, Evans, 1991; 10-11, Jones, 2006; 12,18, Romer, 1956; 13-17, Evans, 2008; 19, Cundall & Irish, 2008. Abbreviation: Rhyncho, Rhynchocephalia.

Fig. 7 Skulls of Archosauromorph in palatal view (phylogeny based on Brusatte et al. 2010; Borsuk−Białynicka & Evans, 2009a; Dilkes & Sues, 2009): 1, *Czatkowiella*; 2, *Cteniogenys*; 3, *Proganochelys*; 4, *Mesosuchus*; 5, *Tanystropheus*; 6, *Proterosuchus*; 7, *Osmolskina*; 8, *Euparkeria*; 9, *Doswellia*; 10, *Proterochampsa*. Image sources: 1, Borsuk−Białynicka & Evans, 2009a; 2, Evans, 1990; 3,6, Carroll, 1988; 4, Dilkes, 1998; 5, Wild, 1987; 7, Borsuk−Białynicka & Evans, 2009b; 8, Ewer, 1965; 9, Weems, 1980; 10, Sill, 1967.

Fig. 8 Summary of evolutionary patterns in the palatal dentition of tetrapods.

Fig. 9 Summary of evolutionary history of soft tissues related to feeding through tetrapod evolution (see text for detail and references).

Fig. 10 Keratinized oral epithelium in extant taxa; A, *Anas platyrhynchos* (Mallard; KPM-NF 2002622, floor of mouth (left) and palate (right); B, *Spheniscus demersus* (African Penguin; KPM-NF 2002403), dissection photographs and CT image of a sagittal section; C, *Osteolaemus tetraspis* (Dwarf Crocodile; Ueno Zoo, Tokyo Japan, no number), palatal surface; D, *Chelonia agassizii* (Galápagos Green Turtle; KPM-NFR 389), palatal surface with keratinized keels and serrations. Institutional abbreviation: Kanegawa Prefectural Museum of Natural History (KPM-NF).

Appendices 1–4

1. Early tetrapods and amphibians, arrangement of the palatal dentition
2. Synapsida, arrangement of the palatal dentition
3. Parareptilia, arrangement of the palatal dentition
4. Diapsida, arrangement of the palatal dentition

Supplementary information

Sup-Fig. 1. Skulls of early tetrapods in palatal view. A, *Eusthenopteron* (original without scale); B, *Acanthostega*; C, *Pederpes*; D, *Crassigyrius*; E, *Greerepeton*; F, *Edops*; G, *Balanerpeton*; H, *Phonerpeton*; I, *Doleserpeton*; J, *Silvanerpeton*; K, *Proterogyrinus*; L, *Pholiderpeton*; M, *Seymouria*; N, *Odonterpeton*; O, *Microbrachis*; P, *Hapsidopareion*; Q, *Rhynchonkos*; R, *Cardiocephalus* (original image reflected); S, *Pantylus*; T, *Brachydectes* (original without scale); U, *Batrachiderpeton*; V, *Ptyonius*; W, *Diadectes*; X, *Dermophis mexicanus* (Gymnophiona); Y, *Stereochilus marginatum* (Caudata); Z, *Gastrotheca walker* (Anura), original without scale. Image sources: A, B,D, Clack, 2012; C, Clack & Finney, 2005; E, Smithson, 1982; F, Romer & Witter, 1942; G, Holmes, 2000 (original image reflected); H, Dilkes, 1990; I, Sigurdsen & Bolt, 2010; J, Ruta & Clack, 2006; K, Holmes, 1984; L, Clack, 1987; M, Klembara et al. 2005; N, P-T, Carroll et al. 1998; O, Vallian & Laurin, 2004; U-V, Carroll et al. 1998; W, Reisz & Sues, 2000; X-Z, Duellman & Trueb, 1994 . Colour coding on the palate same as text Figures 1–7.

Sup-Fig. 2 Skulls of synapsids in palatal view, Part 1: A, *Cotylorhynchus* (Caseasauria); B, *Ennatosaurus* (Caseasauria); C, *Mesenosaurus* (Varanopidae); D, *Varanosaurus* (Ophiacodontidae); E, *Edaphosaurus*; F, *Haptodus*; G, *Secodontosaurus* (Sphenacodontidae); H, *Tetraceratops*; I, *Biarmosuchus*; J, *Lycaenodon* (Biarmosuchia); K, *Titanophoneus* (Dinocephalia); L, *Syodon* (Dinocephalia); M, *Styracocephalus* (Dinocephalia, original without scale bar); N, *Estemmenosuchus* (Dinocephalia); O, *Struthiocephalus* (Dinocephalia); P, *Ulemosaurus* (Dinocephalia). Image sources: A, Reisz & Sues, 2000; B, Maddin et al. 2008; C, Reisz & Berman, 2001; D, Berman et al. 1995; E, Modesto, 1995; F, Laurin, 1993; G, Reisz et al. 1992; H, Laurin & Reisz, 1996; I, Ivakhnenko, 1999; J, Sigogneau-Russell,1989; K-L, N-P, King, 1988; M, Rubidge & van den Heever, 1997.

Sup-Fig. 3 Skulls of synapsids in palatal view, Part 2: A, *Otsheria* (Anomodontia, original without scale); B, *Aelurosaurus* (Gorgonopsidae); C, *Arctognathus* (Gorgonopsidae); D, *Leontocephalus* (Gorgonopsidae); E, *Scylacops* (Gorgonopsidae) ; F, *Arctops* (Gorgonopsidae); G, *Prorubidgea* (Gorgonopsidae) ; H, *Dinogorgon* (Gorgonopsidae) ; I, *Rubidgea* (Gorgonopsidae); J, *Moschorhinus* (Therocephalia); K, *Theriognathus* (Therocephalia); L, *Viatkosuchus* (Therocephalia, original without scale bar); M, *Regisaurus* (Therocephalia); N, *Bauria* (Therocephalia, original without scale); O, *Dvinia* (Cynodontia, original without scale). Image sources: A, K, M-N, Kemp, 1982; B-I, Sigogneau-Russell, 1989; J, Mendrez, 1974a; L, Tatarinov, 1995; O, Tatarinov, 1968.

Sup-Fig. 4 Skulls of Parareptilia in palatal view. A, *Mesosaurus*; B, *Millerosaurus*; C, *Lanthanosuchus*; D, *Acleistorhinus* (Lanthanosuchidae); E, *Belebey* (Bolosauridae); F, *Nyctiphruretus*; G, *Procolophon* (Procolophonoidea, original without scale); H, *Owenetta* (Procolophonoidea); I, *Scutosaurus* (Pareiasauria); J, *Pareiasuchus* (Pareiasauria); K, *Macroleter* ('nycteroleter'); L, *Nycteroleter*; M, *Bashkyroleter mesensis* ('nycteroleter', original without scale). Image sources: A, Modesto, 2006; B,F,I, Carroll, 1988; C,D, DeBraga &

Reisz, 1996; E, Ivakhnenko & Tverdochlebova, 1987; G, Carroll & Lindsay, 1985; H, Reisz & Scott, 2002; J, Lee et al. 1997; K, Tsuji, 2006; L, Tverdokhlebov & Ivakhnenko, 1984; M, Ivakhnenko, 1997.

Sup-Fig. 5 Skulls of eureptiles and basal diapsids (A-F), Sauropterygia (G–H), Ichthyopterygia (I), and Lepidosauromorpha (J–Z) in palatal view: A, *Captorhinus*; *B, Paleothyris*; C, *Petrolacosaurus*; D, *Araeoscelis*; E, *Claudiosaurus*; F, *Youngina*; G, *Placodus*; H, *Simosaurus*; I, *Ichthyosaurus* (original without scale); J, *Kuehneosaurus*; K, *Marmoretta*; L, *Gephyrosaurus* (Rhynchocephalia); M, *Clevosaurus* (Rhynchocephalia) ; N, *Sphenodon* (Rhynchocephalia); O, *Hemitheconyx* (Squamata, Gekkota); P, *Tropidophorus* (Squamata, Scincoidea); Q, *Lacerta* (Squamata, Lacertoidea); R, *Uromastyx* (Squamata, Iguania); S, *Ctenosaura* (Squamata, Iguania: original without scale); T, *Xenosaurus* (Squamata, Anguimorpha); U, *Ophisaurus* (Squamata, Anguimorpha); V, *Heloderma* (Squamata, Anguimorpha); W, *Shinisaurus* (Squamata, Anguimorpha) ; X, *Varanus* (Squamata, Anguimorpha) ; Y, *Platecarpus* (Squamata, Mosasauria: original without scale); Z, *Anilius,* Squamata, Serpentes). Image sources: A, Reisz & Sues, 2000; B, Benton, 2000; C, Reisz, 1981; D, Vaughn, 1955; E-G, Carroll, 1988; H, Rieppel, 1994; I,N,Y, Romer, 1956; J, Robinson, 1962; K, Evans, 1991; L-M, Jones, 2006; O-X, Evans, 2008; Z, Cundall & Irish, 2008.

Sup-Fig. 6 Skulls of Archosauromorpha in palatal views: A, *Czatkowiella*; B, *Cteniogenys* (Choristodera); C, *Proganochelys* (Testudines); D, *Mesosuchus* (Rhynchosauria); E, *Trilophosaurus;* F, *Paradapedon* (Rhynchosauria); G, *Tanystropheus*; H, *Proterosuchus*; I, *Euparkeria*; J, *Doswellia*; K, *Proterochampsa*; L, *Rutiodon* (Phytosauria); M, *Stagonolepis* (Aetosauria); N, *Sphenosuchus* (Crocodylomorpha); O, *Ornithosuchus*. Image sources: A, Borsuk−Białynicka & Evans, 2009a; B, Evans, 1990; C, E, F, H, Carroll, 1988; D, Dilkes, 1998; G, Wild, 1987; I, Ewer, 1965; J, Weems, 1980; K, Sill, 1967; L-M, O, Kuhn, 1976; N, Walker, 1990.

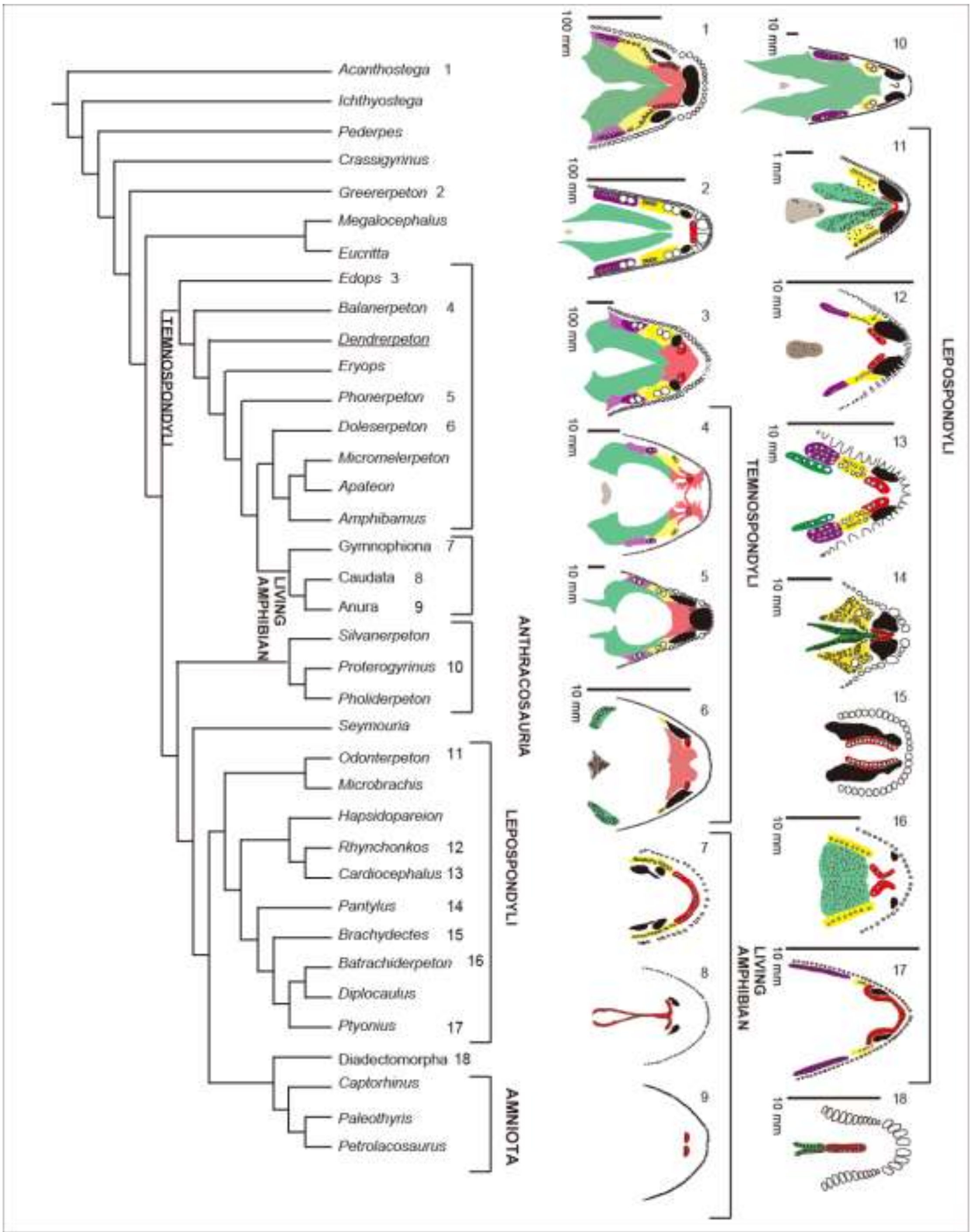

Acanthostega 1
Ichthyostega
Pederpes
Crassigyrinus
Greererpeton 2
Megalocephalus
Eucritta
Edops 3
Balanerpeton 4
Dendrerpeton
Eryops
Phonerpeton 5
Doleserpeton 6
Micromelerpeton
Apateon
Amphibamus
Gymnophiona 7
Caudata 8
Anura 9
Silvanerpeton
Proterogyrinus 10
Pholiderpeton
Seymouria
Odonterpeton 11
Microbrachis
Hapsidopareion
Rhynchonkos 12
Cardiocephalus 13
Pantylus 14
Brachydectes 15
Batrachiderpeton 16
Diplocaulus
Ptyonius 17
Diadectomorpha 18
Captorhinus
Paleothyris
Petrolacosaurus
TEMNOSPONDYLI
LIVING AMPHIBIAN
ANTHRACOSAURIA
LEPOSPONDYLI
AMNIOTA
TEMNOSPONDYLI
LIVING AMPHIBIAN
LEPOSPONDYLI
100 mm
10 mm
1 mm

Fig.1

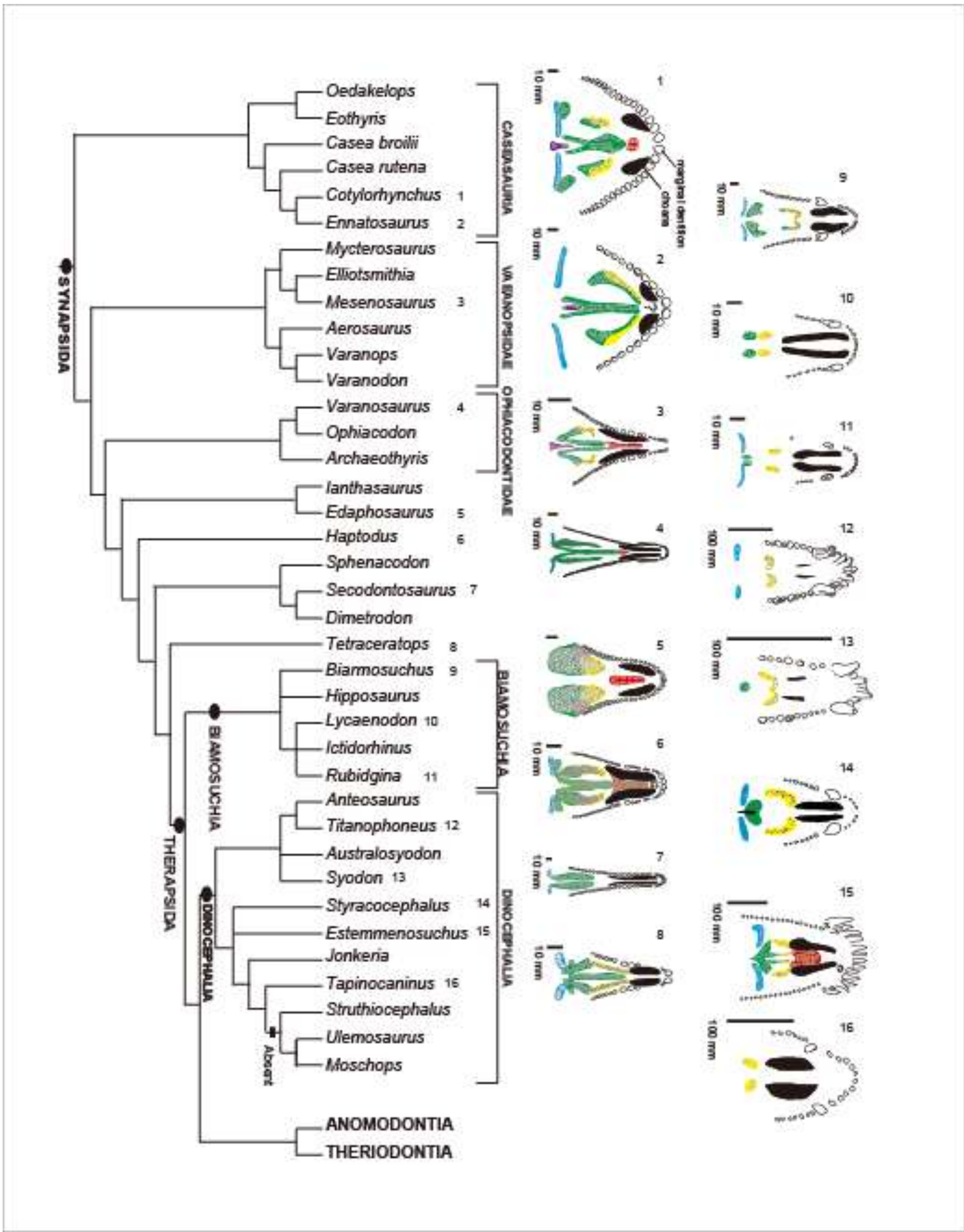

Oedakelops
Eothyris
Casea broilii
Casea rutena
Cotylorhynchus 1
Ennatosaurus 2
Mycterosaurus
Elliotsmithia
Mesenosaurus 3
Aerosaurus
Varanops
Varanodon
Varanosaurus 4
Ophiacodon
Archaeothyris
Ianthasaurus
Edaphosaurus 5
Haptodus 6
Sphenacodon
Secodontosaurus 7
Dimetrodon
Tetraceratops 8
Biarmosuchus 9
Hipposaurus
Lycaenodon 10
Ictidorhinus
Rubidgina 11
Anteosaurus
Titanophoneus 12
Australosyodon
Syodon 13
Styracocephalus 14
Estemmenosuchus 15
Jonkeria
Tapinocaninus 16
Struthiocephalus
Ulemosaurus
Moschops
ANOMODONTIA
THERIODONTIA
SYNAPSIDA
THERAPSIDA
BIARMOSUCHIA
DINOCEPHALIA
Absent
CASEASAURIA
VARANOPIDAE
OPHIACODONTIDAE
marginal dentition
choana
10 mm
100 mm

Figure 2

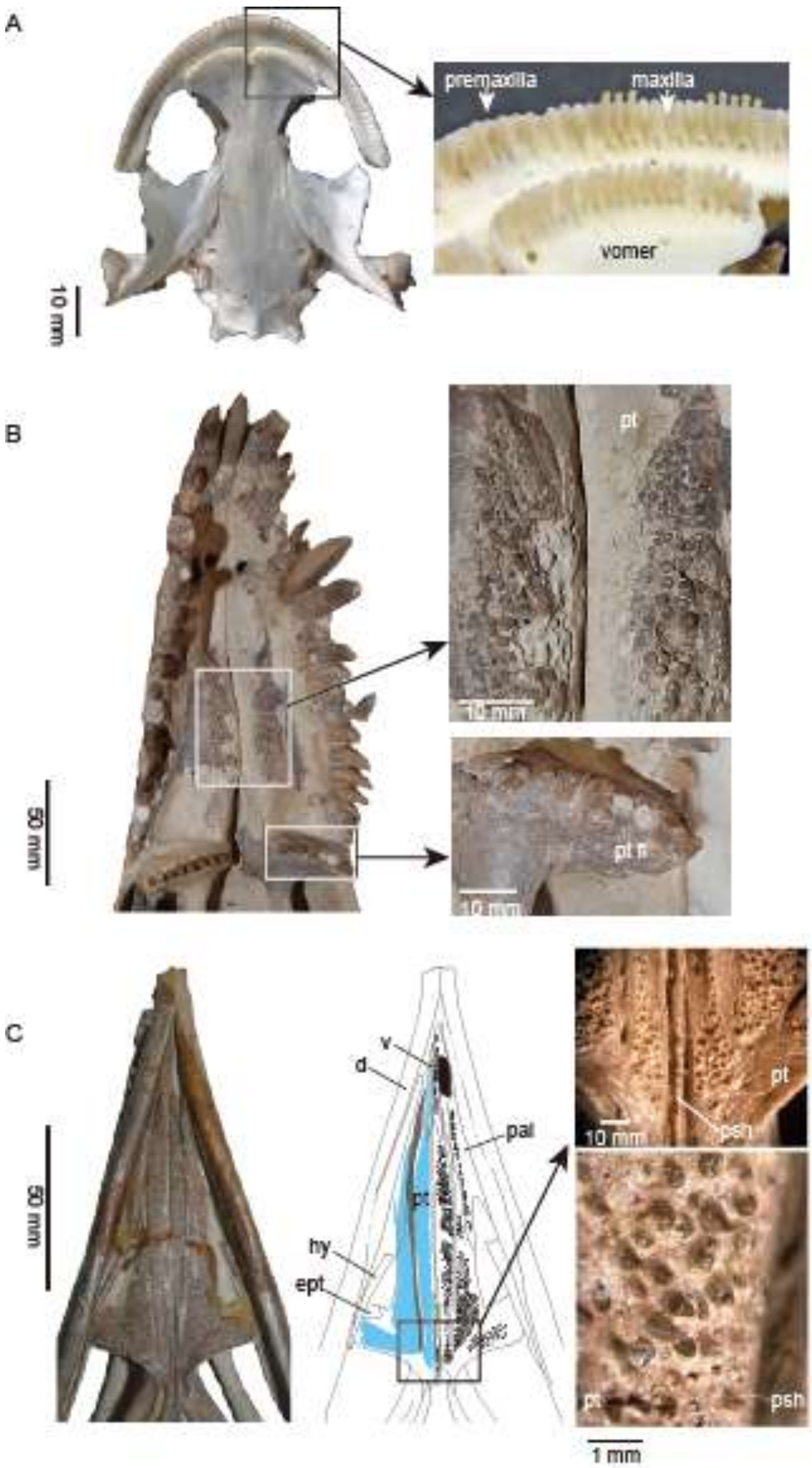

A
premaxilla
maxilla
vomer
10 mm
B
pt
10 mm
50 mm
10 mm
C
v
d
pal
pt
hy
ept
50 mm
pt
psh
10 mm
pt
psh
1 mm

Figure 3

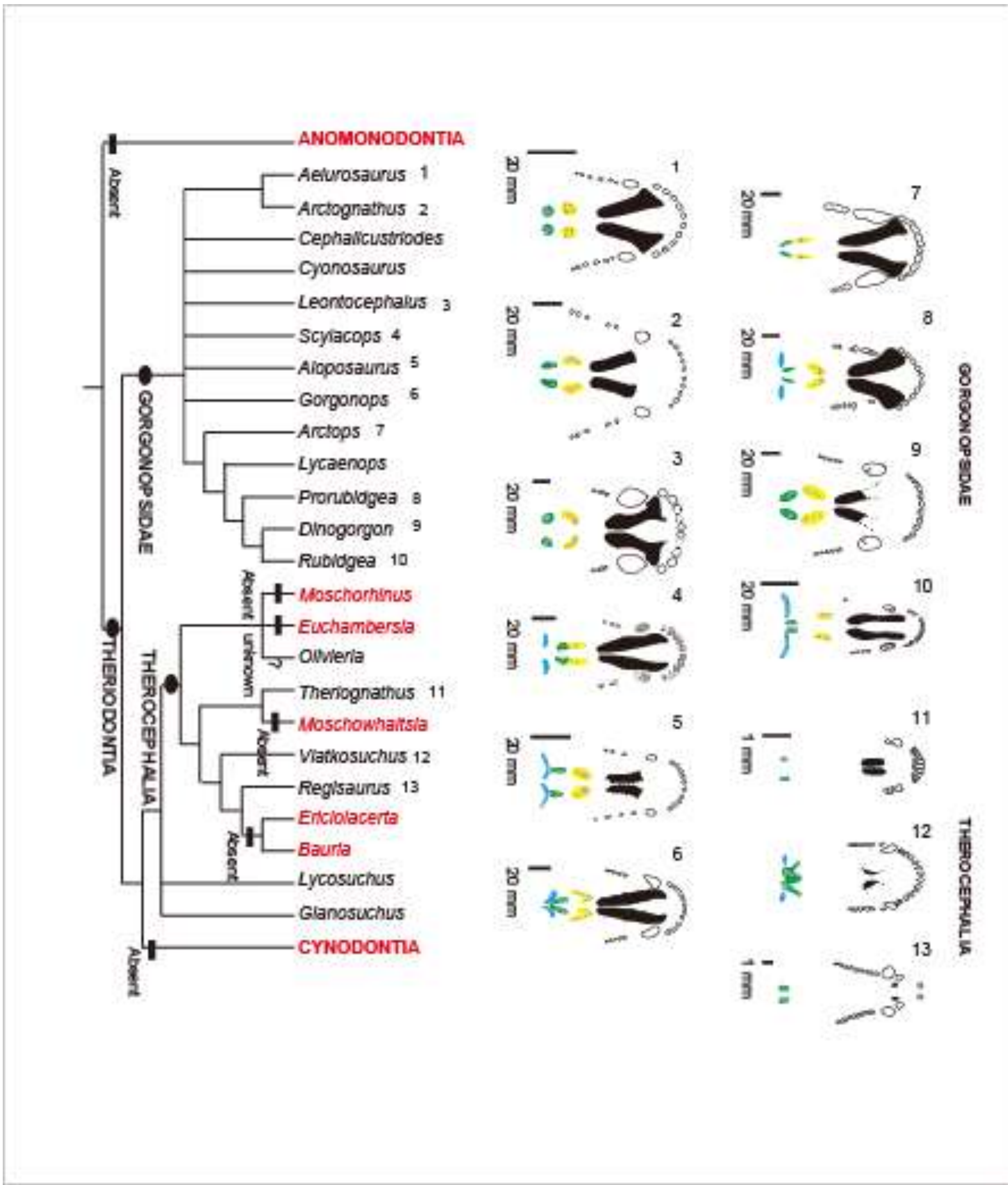
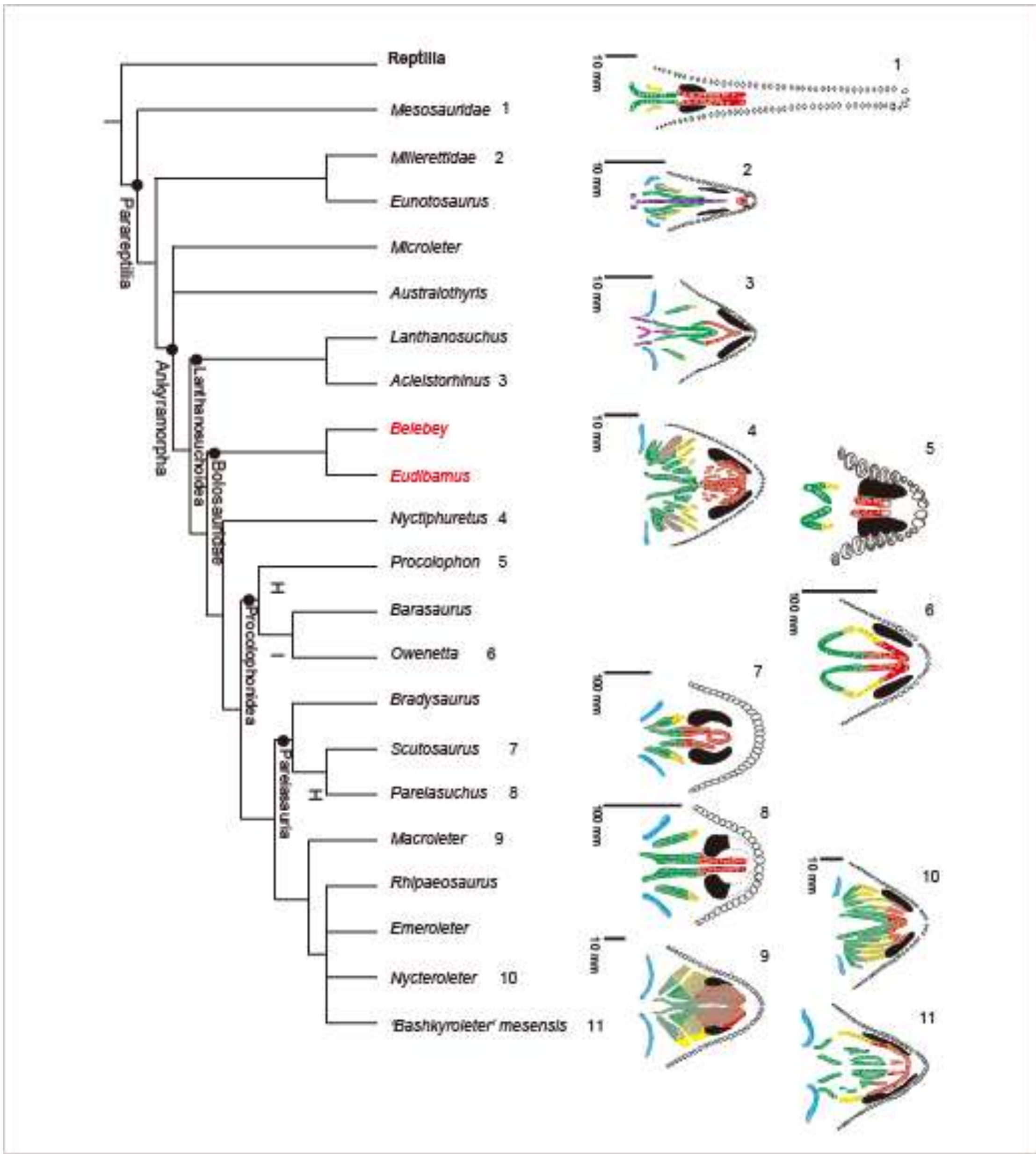
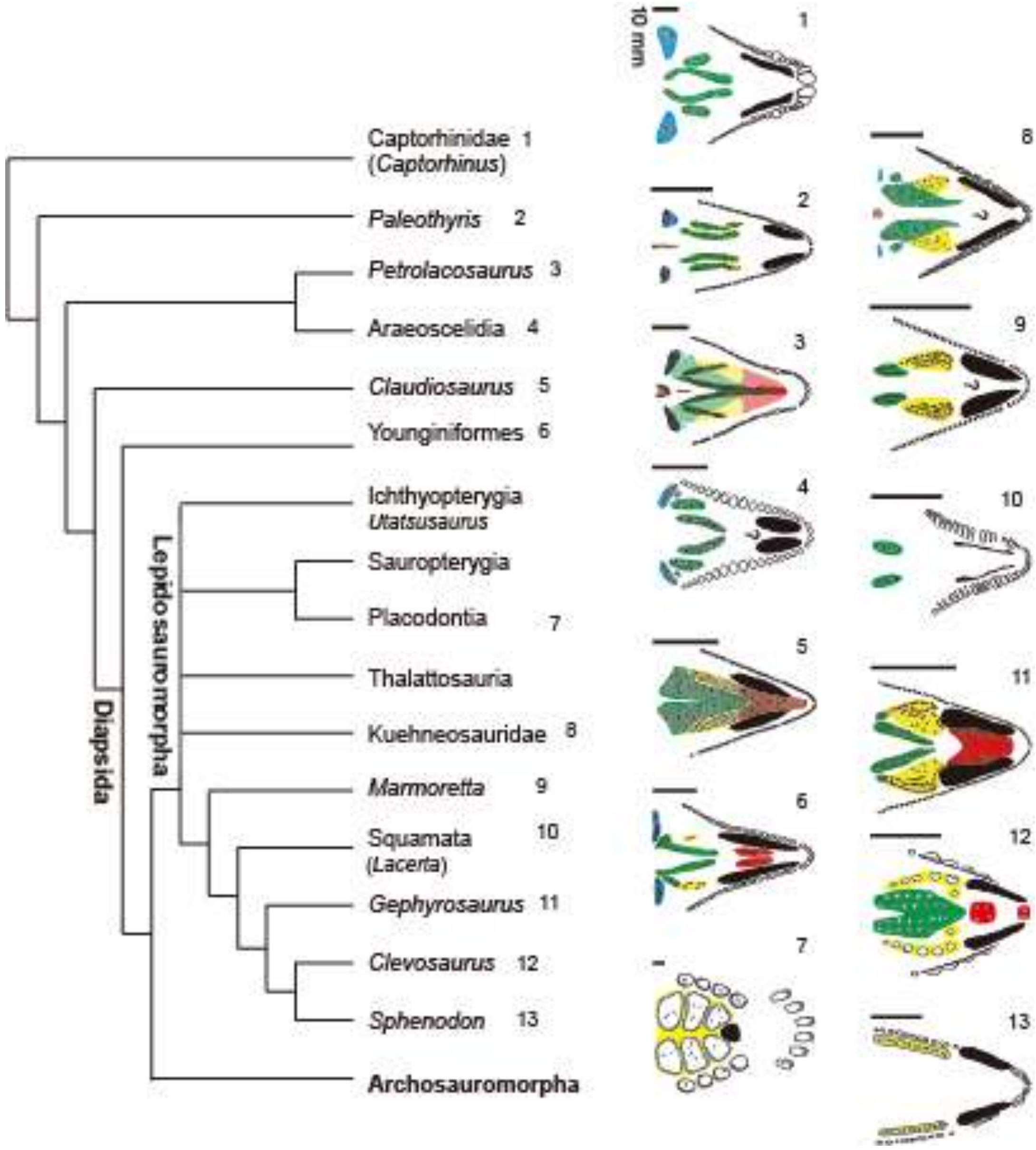

ANOMONODONTIA
Aelurosaurus 1
Arctognathus 2
Cephalicustriodes
Cyonosaurus
Leontocephalus 3
Scylacops 4
Aloposaurus 5
Gorgonops 6
Arctops 7
Lycaenops
Prorubidgea 8
Dinogorgon 9
Rubidgea 10
Moschorhinus
Euchambersia
Olivieria
Theriognathus 11
Moschowhaitsia
Viatkosuchus 12
Regisaurus 13
Ericiolacerta
Bauria
Lycosuchus
Glanosuchus
CYNODONTIA
Absent
unknown
?
GORGONOPSIDAE
THERIODONTIA
THEROCEPHALIA
20 mm
1 mm
1
2
3
4
5
6
7
8
9
10
11
12
13

Figure 4



1082 Figure 5



1083

1084 Figure 6

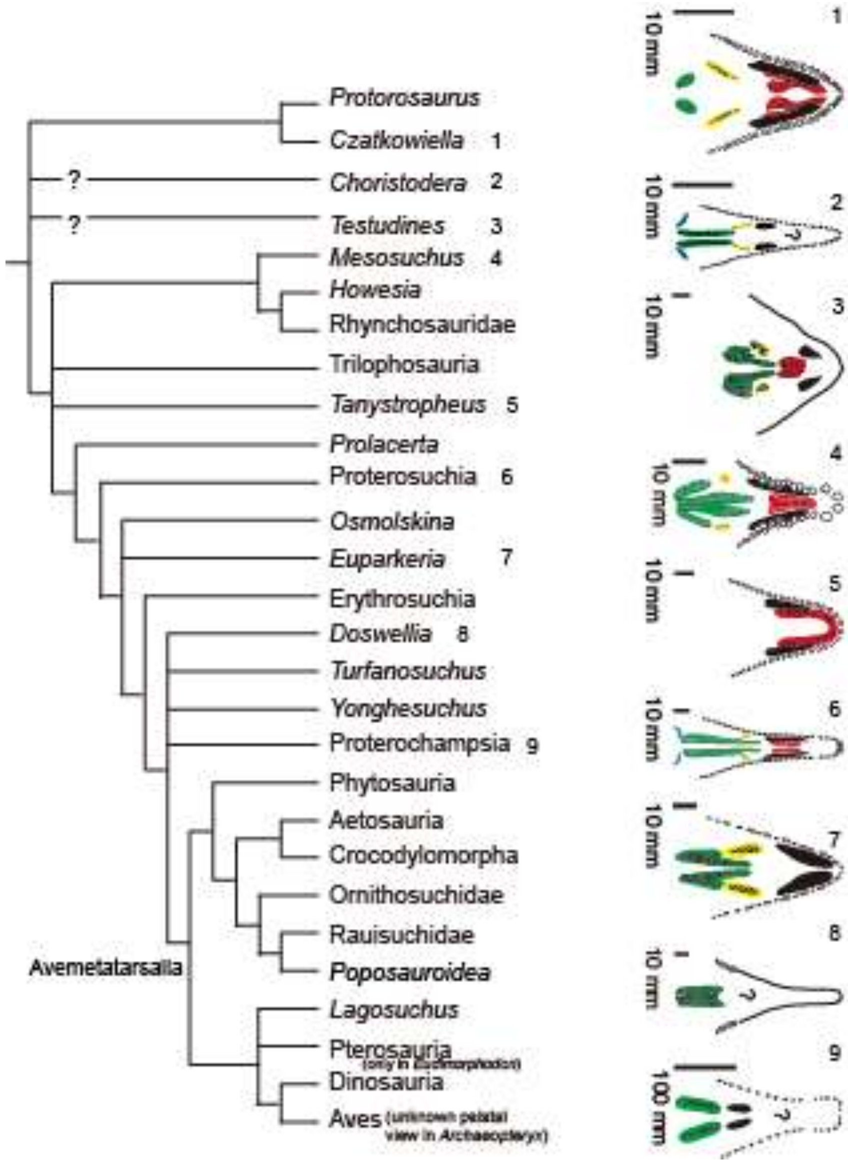
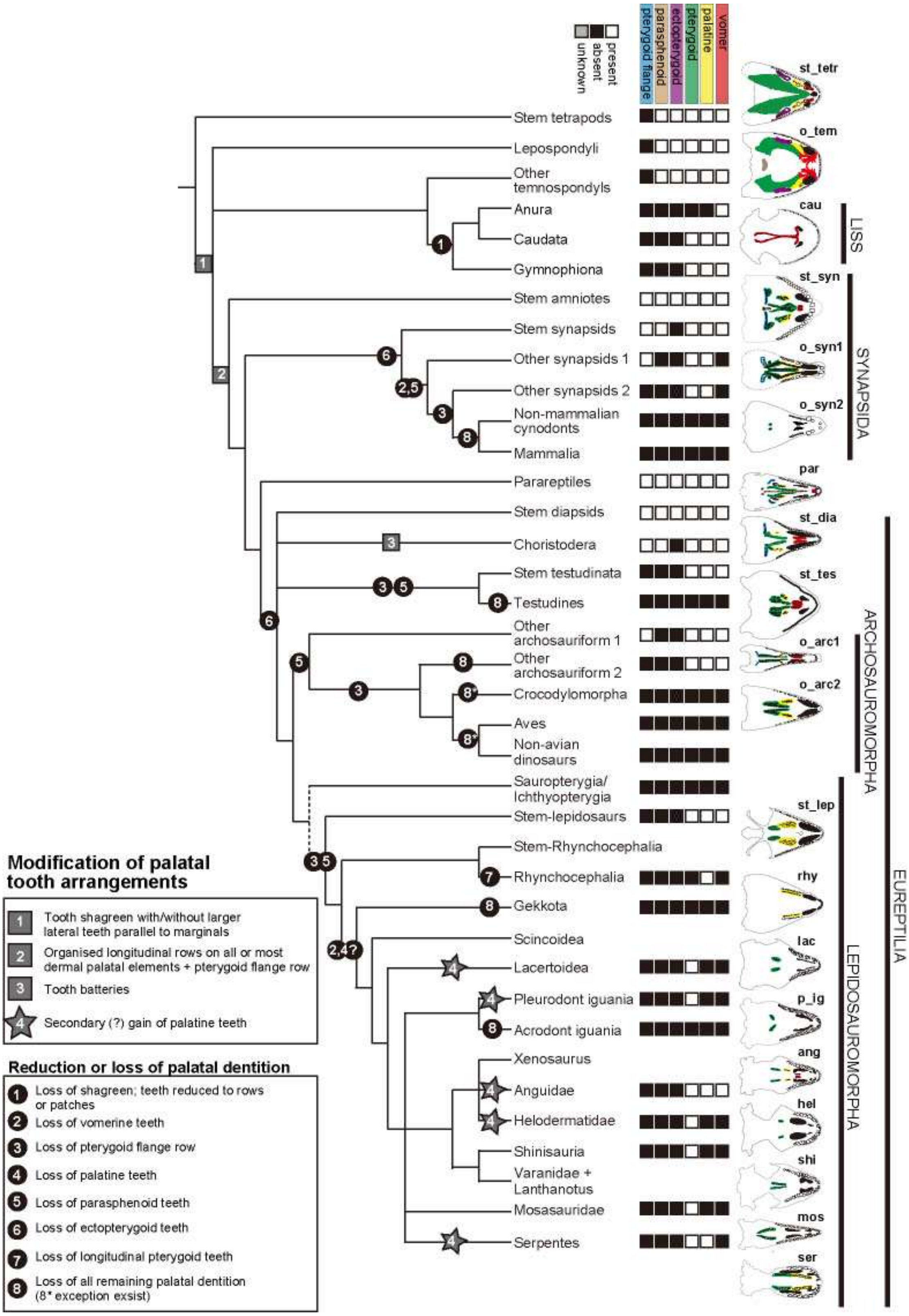

Protorosaurus
Czatkowiella 1
?
Choristodera 2
?
Testudines 3
Mesosuchus 4
Howesia
Rhynchosauridae
Trilophosauria
Tanystropheus 5
Prolacerta
Proterosuchia 6
Osmolskina
Euparkeria 7
Erythrosuchia
Doswellia 8
Turfanosuchus
Yonghesuchus
Proterochampsia 9
Phytosauria
Aetosauria
Crocodylomorpha
Ornithosuchidae
Rauisuchidae
Poposauroidea
Avemetatarsalia
Lagosuchus
Pterosauria
Dinosauria
Aves (unknown palatal view in Archaeopteryx)
10 mm
10 mm
10 mm
10 mm
10 mm
10 mm
10 mm
10 mm
100 mm
1
2
3
4
5
6
7
8
9

Figure 7



vomer
palatine
pterygoid
ectopterygoid
parasphenoid
pterygoid flange
present
absent
unknown
Stem tetrapods
Lepospondyli
Other temnospondyls
Anura
Caudata
Gymnophiona
Stem amniotes
Stem synapsids
Other synapsids 1
Other synapsids 2
Non-mammalian cynodonts
Mammalia
Parareptiles
Stem diapsids
Choristodera
Stem testudinata
Testudines
Other archosauriform 1
Other archosauriform 2
Crocodylomorpha
Aves
Non-avian dinosaurs
Sauropterygia/ Ichthyopterygia
Stem-lepidosaurs
Stem-Rhynchocephalia
Rhynchocephalia
Gekkota
Scincoidea
Lacertoidea
Pleurodont iguania
Acrodont iguania
Xenosaurus
Anguidae
Helodermatidae
Shinisauria
Varanidae + Lanthanotus
Mosasauridae
Serpentes
st_tetr
o_tem
cau
st_syn
o_syn1
o_syn2
par
st_dia
st_tes
o_arc1
o_arc2
st_lep
rhy
lac
p_ig
ang
hel
shi
mos
ser
LISS
SYNAPSIDA
ARCHOSAUROMORPHA
LEPIDOSAUROMORPHA
EUREPTILIA
Modification of palatal tooth arrangements
1 Tooth shagreen with/without larger lateral teeth parallel to marginals
2 Organised longitudinal rows on all or most dermal palatal elements + pterygoid flange row
3 Tooth batteries
4 Secondary (?) gain of palatine teeth
Reduction or loss of palatal dentition
1 Loss of shagreen; teeth reduced to rows or patches
2 Loss of vomerine teeth
3 Loss of pterygoid flange row
4 Loss of palatine teeth
5 Loss of parasphenoid teeth
6 Loss of ectopterygoid teeth
7 Loss of longitudinal pterygoid teeth
8 Loss of all remaining palatal dentition (8* exception exsist)

Figure 8

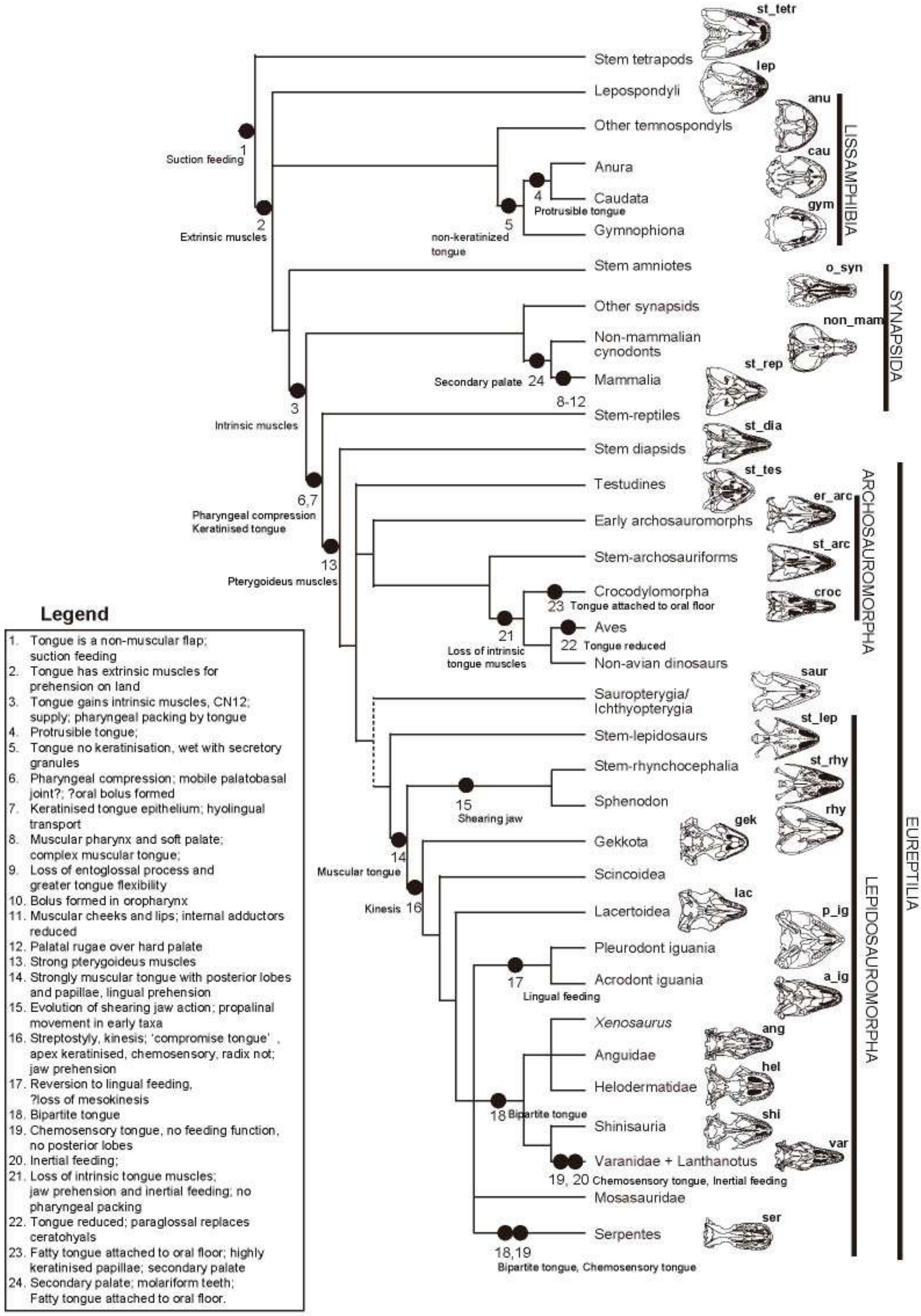

Stem tetrapods
Lepospondyli
Other temnospondyls
Anura
Caudata
Gymnophiona
Stem amniotes
Other synapsids
Non-mammalian cynodonts
Mammalia
Stem-reptiles
Stem diapsids
Testudines
Early archosauromorphs
Stem-archosauriforms
Crocodylomorpha
Aves
Non-avian dinosaurs
Sauropterygia/ Ichthyopterygia
Stem-lepidosaurs
Stem-rhynchocephalia
Sphenodon
Gekkota
Scincoidea
Lacertoidea
Pleurodont iguania
Acrodont iguania
Xenosaurus
Anguidae
Helodermatidae
Shinisauria
Varanidae + Lanthanotus
Mosasauridae
Serpentes
1 Suction feeding
2 Extrinsic muscles
3 Intrinsic muscles
4 Protrusible tongue
5 non-keratinized tongue
6,7 Pharyngeal compression Keratinised tongue
13 Pterygoideus muscles
Secondary palate 24
8-12
14 Muscular tongue
Kinesis 16
15 Shearing jaw
17 Lingual feeding
18 Bipartite tongue
19, 20 Chemosensory tongue, Inertial feeding
18,19 Bipartite tongue, Chemosensory tongue
21 Loss of intrinsic tongue muscles
22 Tongue reduced
23 Tongue attached to oral floor
st_tetr
lep
anu
cau
gym
o_syn
non_mam
st_rep
st_dia
st_tes
er_arc
st_arc
croc
saur
st_lep
st_rhy
rhy
gek
lac
p_ig
a_ig
ang
hel
shi
var
ser
LISSAMPHIBIA
SYNAPSIDA
ARCHOSAUROMORPHA
LEPIDOSAUROMORPHA
EUREPTILIA
Legend
1. Tongue is a non-muscular flap; suction feeding
2. Tongue has extrinsic muscles for prehension on land
3. Tongue gains intrinsic muscles, CN12; supply; pharyngeal packing by tongue
4. Protrusible tongue;
5. Tongue no keratinisation, wet with secretory granules
6. Pharyngeal compression; mobile palatobasal joint?; ?oral bolus formed
7. Keratinised tongue epithelium; hyolingual transport
8. Muscular pharynx and soft palate; complex muscular tongue;
9. Loss of entoglossal process and greater tongue flexibility
10. Bolus formed in oropharynx
11. Muscular cheeks and lips; internal adductors reduced
12. Palatal rugae over hard palate
13. Strong pterygoideus muscles
14. Strongly muscular tongue with posterior lobes and papillae, lingual prehension
15. Evolution of shearing jaw action; propalinal movement in early taxa
16. Streptostyly, kinesis; 'compromise tongue', apex keratinised, chemosensory, radix not; jaw prehension
17. Reversion to lingual feeding, ?loss of mesokinesis
18. Bipartite tongue
19. Chemosensory tongue, no feeding function, no posterior lobes
20. Inertial feeding;
21. Loss of intrinsic tongue muscles; jaw prehension and inertial feeding; no pharyngeal packing
22. Tongue reduced; paraglossal replaces ceratohyals
23. Fatty tongue attached to oral floor; highly keratinised papillae; secondary palate
24. Secondary palate; molariform teeth; Fatty tongue attached to oral floor.

Figure 9

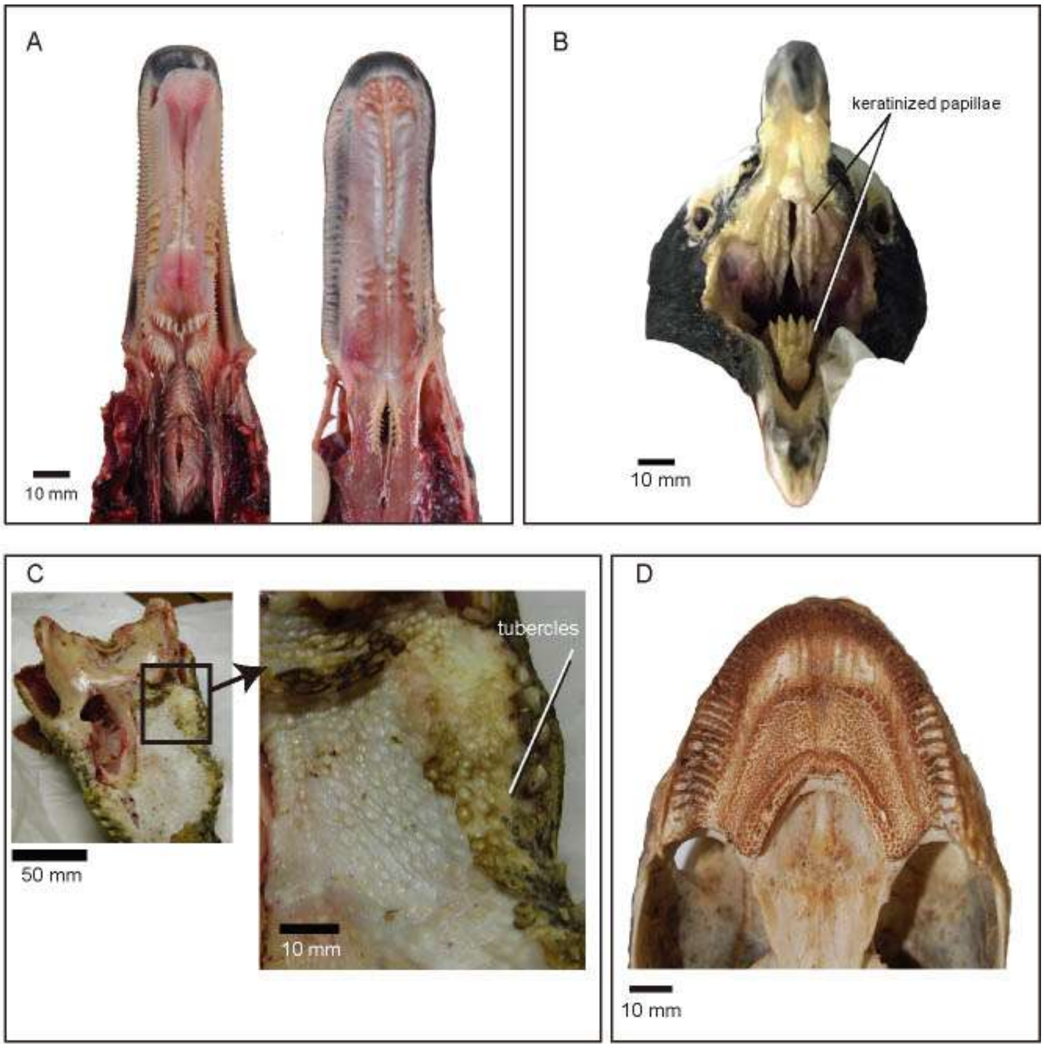
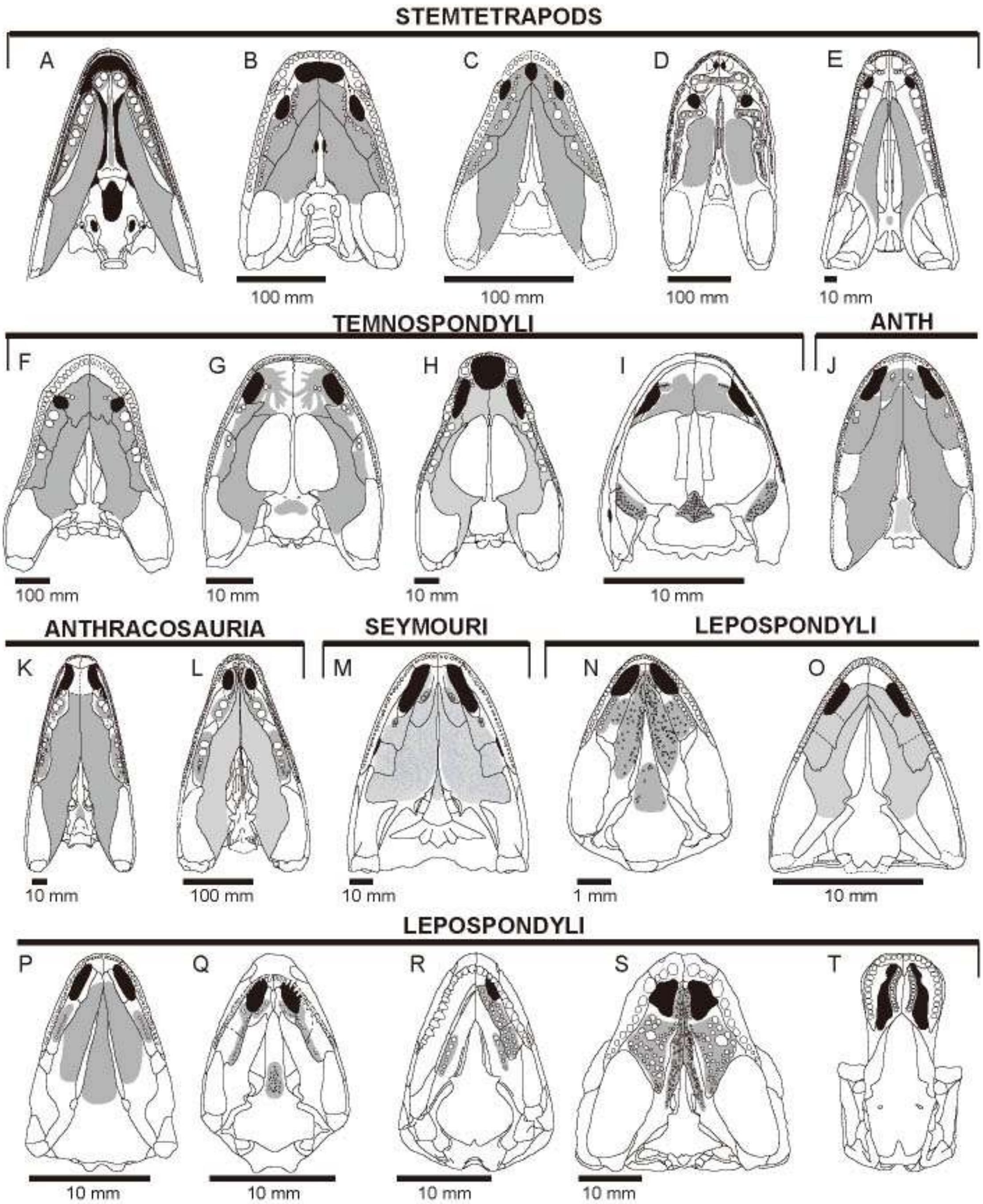
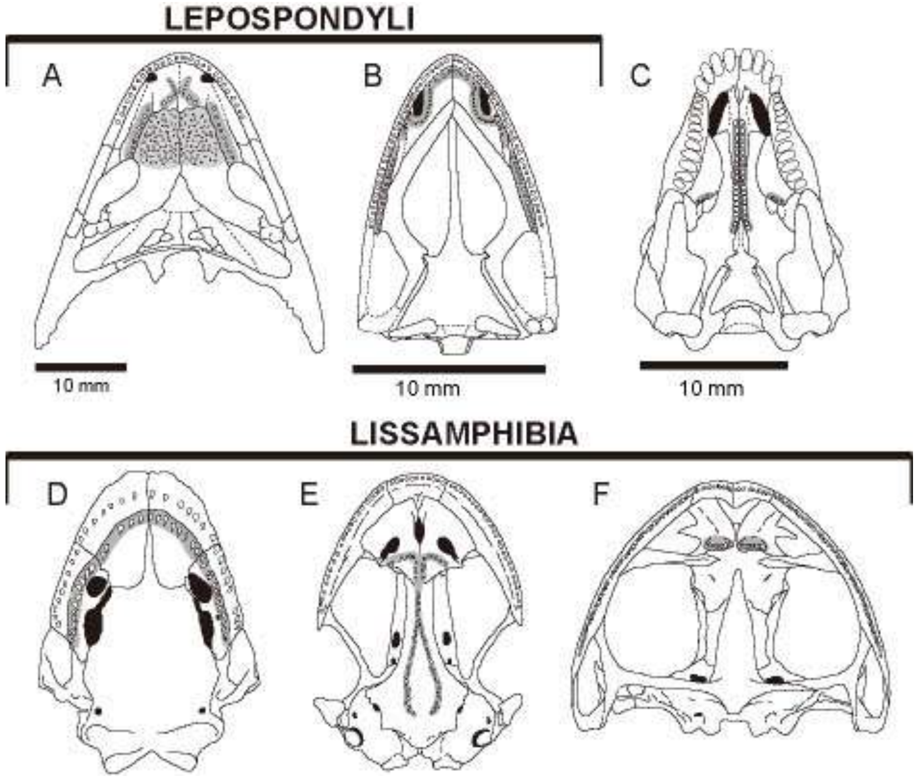

A
10 mm
B
keratinized papillae
10 mm
C
50 mm
tubercles
10 mm
D
10 mm

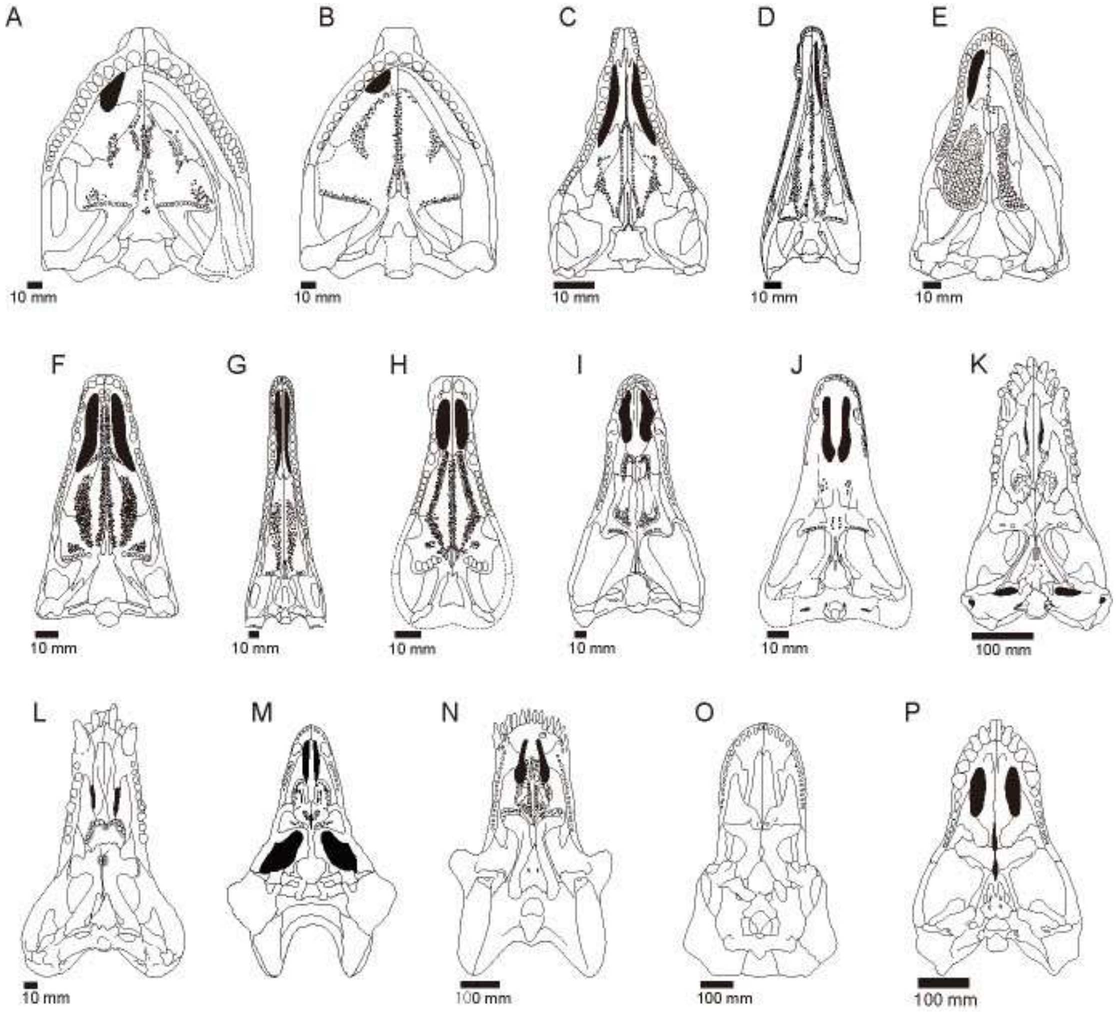
Figure 10

Supplementary figures

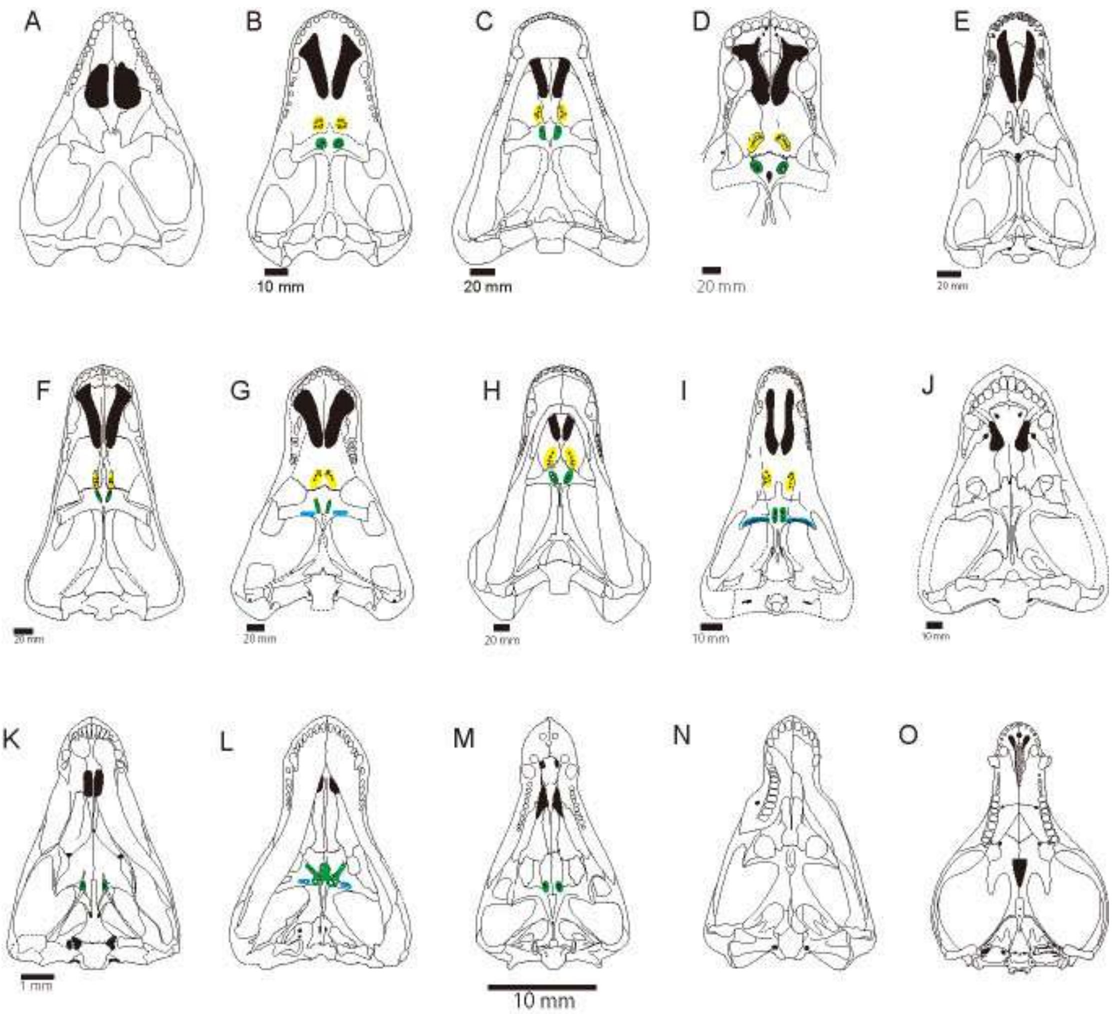




LEPOSPONDYLI
A
B
C
10 mm
10 mm
10 mm
LISSAMPHIBIA
D
E
F

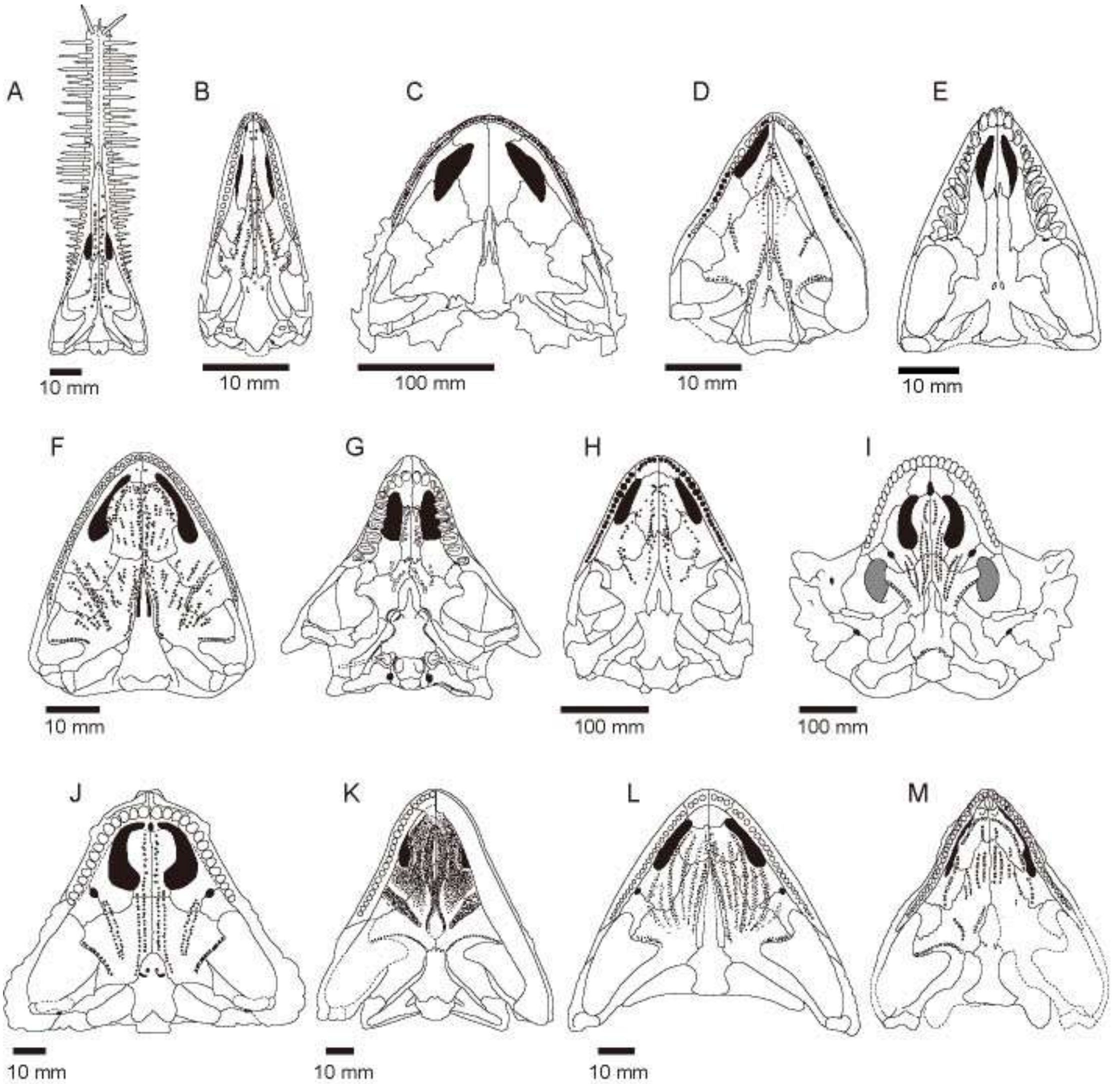


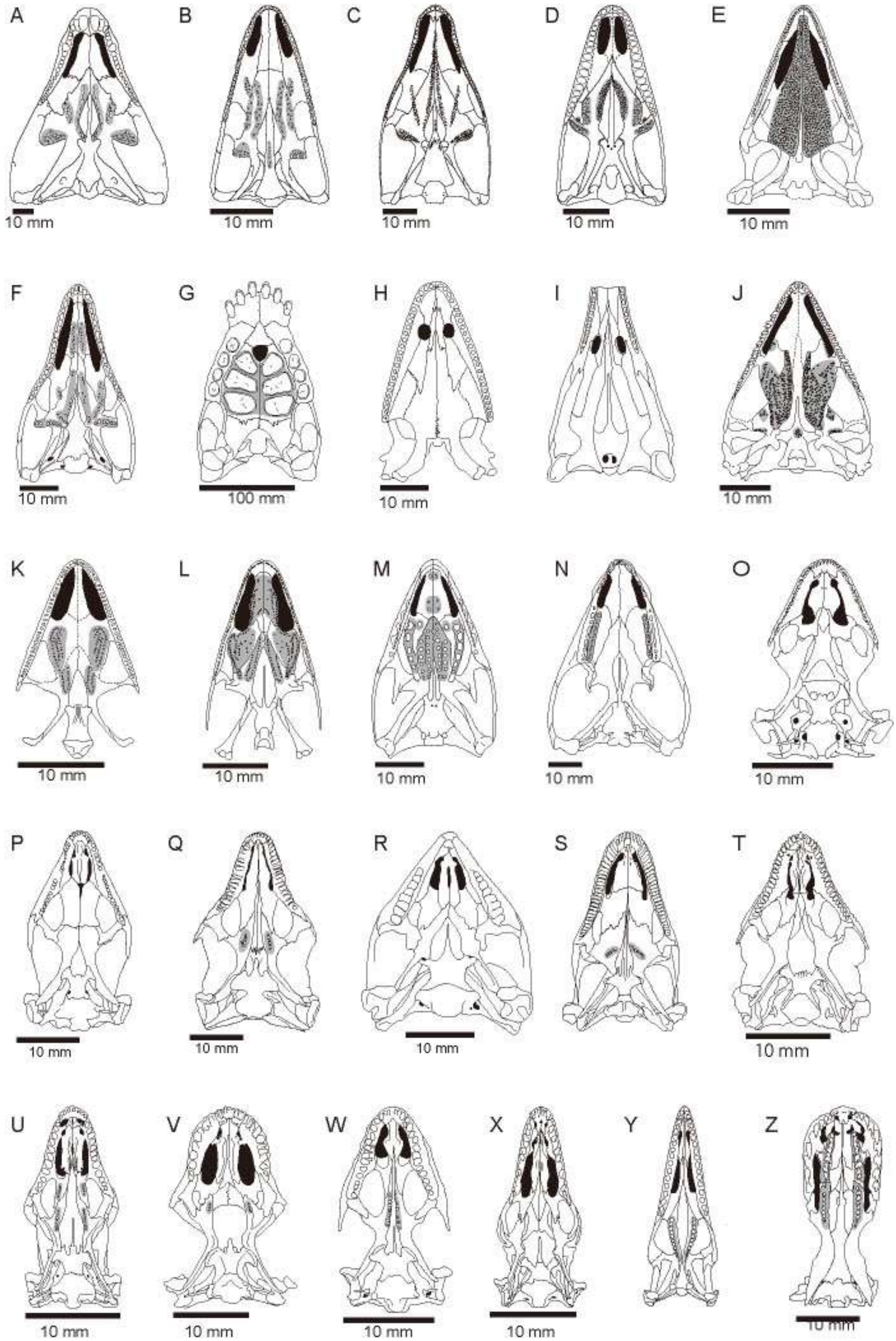
A
B
C
D
E
10 mm
10 mm
10 mm
10 mm
10 mm
F
G
H
I
J
K
10 mm
10 mm
10 mm
10 mm
10 mm
100 mm
L
M
N
O
P
10 mm
100 mm
100 mm
100 mm



A
B
C
D
E
10 mm
20 mm
20 mm
20 mm
F
G
H
I
J
20 mm
20 mm
20 mm
10 mm
10 mm
K
L
M
N
O
1 mm
10 mm

1098


A
B
C
D
E
10 mm
10 mm
100 mm
10 mm
10 mm
F
G
H
I
10 mm
100 mm
100 mm
J
K
L
M
10 mm
10 mm
10 mm


A
10 mm
B
10 mm
C
10 mm
D
10 mm
E
10 mm
F
10 mm
G
100 mm
H
10 mm
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J
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K
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P
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Q
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R
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S
T
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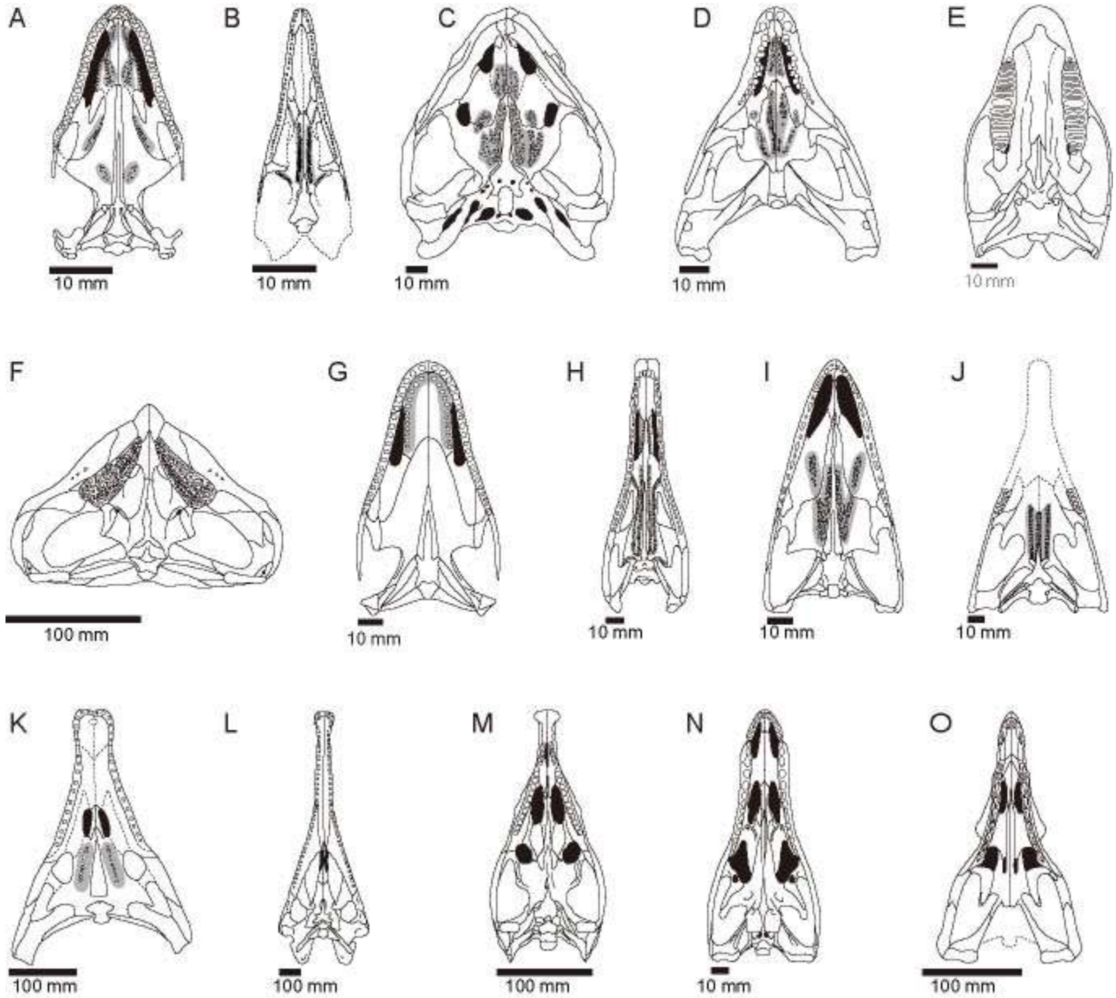
U
10 mm
V
10 mm
W
10 mm
X
10 mm
Y
Z
10 mm

1101 
A
B
C
D
E
10 mm
10 mm
10 mm
10 mm
10 mm
F
G
H
I
J
100 mm
10 mm
10 mm
10 mm
10 mm
K
L
M
N
O
100 mm
100 mm
100 mm
10 mm
100 mm