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The Permotriassic branchiosaurid *Tungussogyrinus* Efremov, 1939 (Temnospondyli, Dissorophoidea) from Siberia restudied

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Abstract

Key Words

The enigmatic temnospondyl amphibian *Tungussogyrinus bergi* Efremov, 1939 shares clear synapomorphies with other branchiosaurids indicated by an anteriorly elongated infratemporal fossa and small branchial denticles. Therefore *Tungussogyrinus* clearly belongs to the dissorophoid family Branchiosauridae. This species is characterized by a number of derived features among temnospondyls: (1) an unusually elongated anterodorsal process of the ilium; (2) the character complex concerning the tricuspid dentition. *Tungussogyrinus* differs from all other branchiosaurids in these two autapomorphic characters. Herein, *Tungussogyrinus* is thought to represent the closest relative of a clade including all other branchiosaurids with its placement outside of this clade associated with a new feeding strategy to scrape algae with the tricuspid anterior dentition and the gracile built snout region. The subfamily Tungussogyrininae Kuhn, 1962 is newly defined here by the two derived characters of *Tungussogyrinus bergi*. All other branchiosaurid genera and species are included in a second subfamily Branchiosaurinae Fritsch, 1879.

Introduction

The newt-like branchiosaurids mostly lived in Permocarboniferous lakes of Laurussia. Thousands of specimens are known from the Saar-Nahe Basin and the Thuringian Forest Basin in Germany. Nearly all branchiosaurid species are characterised by neotenic characters. They kept larval features in mature stages, e.g. external gills and branchial denticles. The family Branchiosauridae consists of five genera and about 20 species plus subspecies.

The oldest species is *Branchiosaurus salamandroides* Fritsch, 1876 from the Westphalian D (Late Pennsylvanian, Moscovian) of Nýřany in the Czech Republic as opposed to *Tungussogyrinus bergi* Efremov, 1939 from the Permotriassic of Siberia as the last survivor of the dissorophoid family Branchiosauridae.

Tungussogyrinus bergi was found in the lower part of the Bugarikta Formation together with fishes, conchostracans, ostracods, charophyte algae, and other plant remains. Shishkin (1998) pointed out that the ostracod and conchostracan composition, as well as the data on charophytes and the presence of *Eoperleidus* Sytchevskaya, 1999, a member of the Triassic fish family Perleididae, are indicative for an Early Triassic age (and that is most probable), while the spore-pollen assemblage supports a Late Permian age of the basal Bugarikta Formation.

Efremov (1939) described the holotype specimen and in the same year, Bystrow (1939) figured this specimen again. The taxonomic assignment of *Tungussogyrinus* Efremov, 1939 remained controversial and the specimen has been identified as a branchiosaurid (Efremov 1939; Olson 1962; Shishkin 1998), a lepospondyl amphibian (Efremov 1953), a brachyopid member (Efremov 1939; Romer 1947, 1966; Shishkin 1964; Cosgriff 1969; Kuhn 1965), an indeterminable larva of a rhachitomous labyrinthodont (Shishkin 1973; Boy 1974), and a dissorophoid temnospondyl without clear branchiosaurid synapomorphy (Schoch & Milner 2008).

In 1989, I had the opportunity to study newly collected material of *Tungussogyrinus* in the Paleontological Institute of the Russian Academy of Sciences (PIN) in Moscow. Except for a dentition with tricuspid teeth, I was not able to find any significant differences to other branchiosaurids. Shishkin (1998) described selected specimens of the new material and pointed out that *Tungussogyrinus* is no brachyopid but a true branchiosaurid amphibian.

In 2002, I restudied all available specimens of *Tungussogyrinus*, which allowed for a detailed redescription of this Siberian branchiosaurid with many new, important features, which will be presented in the following.

Institutional Abbreviations. NHMM, Naturhistorisches Museum Mainz; PIN, Paleontological Institute of the Russian Academy of Sciences Moscow.

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Systematic palaeontology

Order **Temnospondyli** Zittel, 1888
Superfamily **Dissorophoidea** Bolt, 1969
Family **Branchiosauridae** Fritsch, 1879
Subfamily **Tungussogyrininae** Kuhn, 1962

Tungussogyrinus Efremov, 1939

Type species. Tungussogyrinus bergi Efremov, 1939

Tungussogyrinus bergi Efremov, 1939

Figures 1−6, 9A−B, 10A−C, 11A−B, 12A−B, 13A−B

Holotype. Specimen PIN 206/1a, b; PIN 206/1a was figured by Efremov (1939), Bystrow (1939), and reproduced in Shishkin (1998), but it is missing now. The counterpart PIN 206/1b was first figured in Shishkin (1998) and is shown here in Figure 2.

Type locality. Between the mouths of Upper and Lower Lyulyukta Creeks along the Lower Tunguska River, Central Siberia.

Type horizon. Dvuroginsk Horizon of the volcanogenic Tunguska strata, lower part of the Bugarikta Formation, Konvunchanian Group, Late Permian to Early Triassic (Shishkin 1998).

Additional material. The same horizon as stratum typicum, 1 km downstream of the mouth of the Upper Lyulyukta River (PIN 4262/1a, b; Fig. 3) and the Anakit River (all other specimens from PIN 4262/…; Figs 4−6).

The counterpart of the holotype PIN 206/1b and additional material collected in 1966 and a PIN-expedition headed by S. N. Getmanov in 1986, both under the number PIN 4262/…. Fourteen specimens are figured here (Figs 2−6), eight of which are figured for the first time (Figs 4, 5A−E, 6C−D, G−H).

Diagnosis. Characters comparable to lissamphibians, but derived relative to other branchiosaurids: (1) an unusually elongated anterodorsal process of the ilium as autapomorphic feature; (2) tricuspid teeth, homoplastic in respect to the microsaur *Batropetes*, but an autapomorphy with respect to branchiosaurids: in *Tungussogyrinus bergi* the tri-cuspid teeth are labiolingually compressed with mesiodistally aligned and slightly lingually curved cuspules; teeth with wide bases and a decreasing number of the teeth to six in the premaxilla; the tooth bearing portion of the premaxilla is low and the nasal and median intranasal fenestra in the snout region are large.

Character of uncertain polarity, but unique within temnospondyls: the second and third fingers of the manus are of equal length.

Synapomorphies shared by all branchiosaurids including *Tungussogyrinus bergi*: (1) the anterior expansion of the infratemporal fossae on the palate up to the anterior y-shaped palatine resulting in a gap between ectopterygoid and maxilla; (2) the branchial denticles have a small rounded base and one (? or possibly more) tooth like processes.

Characters shared with only some other branchiosaurids: Elongated preorbital region with long nasal and vomer as known from *Melanerpeton* Fritsch, 1878; expanded intraorbital region as comparable with *Apateon* v. Meyer, 1844; foreshortened postorbital region with short postorbital and supratemporal as known from *Melanerpeton gracile* (Credner, 1881) (as *Apateon gracilis* in Schoch & Fröbisch 2006) and *Branchiosaurus salamandroides*; frontals very short, do not extend beyond the anterior margin of the orbit; orbit elongated as known from *Melanerpeton*; pre- and postfrontal in contact as known from *Apateon dracyiensis* (Boy, 1972) and *Branchiosaurus salamandroides*; very short maxilla and a gap between maxilla and jugal as partly known from *Apateon, Melanerpeton* and *Schoenfelderpeton* Boy, 1986; jugal with short anterior process in contrast to *Branchiosaurus salamandroides*; robust shape of parasphenoid as known from *Melanerpeton gracile, Apateon dracyiensis* and *Branchiosaurus salamandroides*; palatine and ectopterygoid short as known from *Apateon*; elongated humerus as known from *Apateon dracyiensis*; second metacarpal and the proximal phalanx are more elongated as in the third digit as known from *Apateon dracyiensis* and *A. kontheri* Werneburg, 1988a; large transverse process completely on the neural arch as known from *Apateon dracyiensis*.

Description

All known specimens can be assigned to one species, *Tungussogyrinus bergi*. A reconstruction of the skull roof is shown in Figures 1A−B. The characteristic
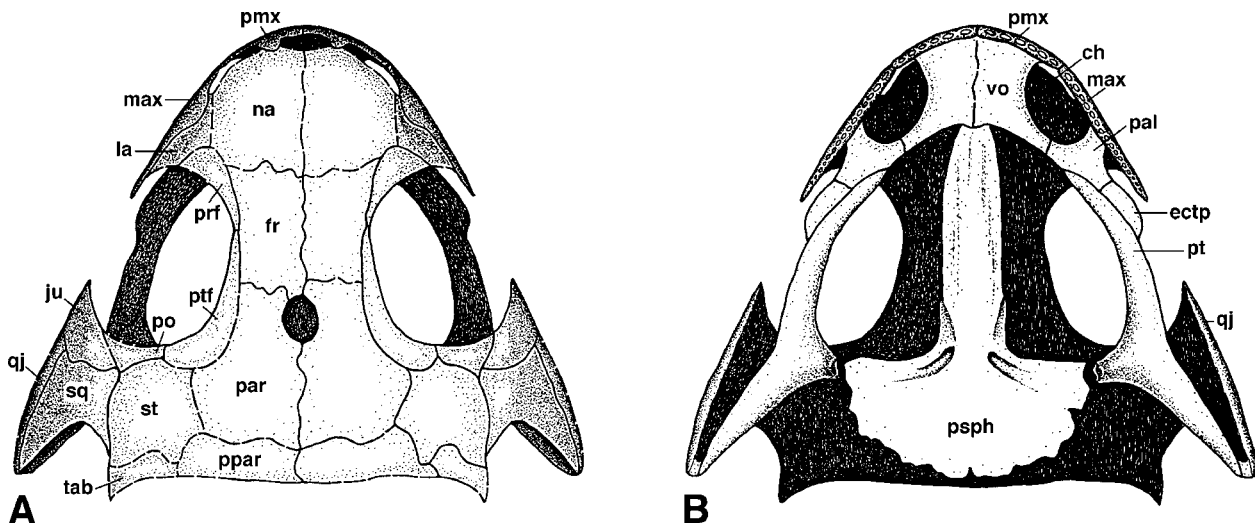

Figure 1. *Tungussogyrinus bergi* Efremov, 1939, reconstruction of skull, using a composite of several specimens (PIN 4262/1a, 6a, b, 7a, b, 9a, b). **A.** Dorsal view; **B.** Palatal view; skull length 9.2 mm. Abbreviations: **ch** − choana; **ectp** − ectopterygoid; **fr** − frontal; **ju** − jugal; **la** − lacrimal; **max** − maxilla; **na** − nasal; **pal** − palatine; **par** − parietal; **pmx** − premaxilla; **po** − postorbital; **ppar** − postparietal; **prf** − prefrontal; **psph** − parasphenoid; **pt** − pterygoid; **ptf** − postfrontal; **qj** − quadratojugal; **sq** − squamosal; **st** − supratemporal; **tab** − tabular; **vo** − vomer.
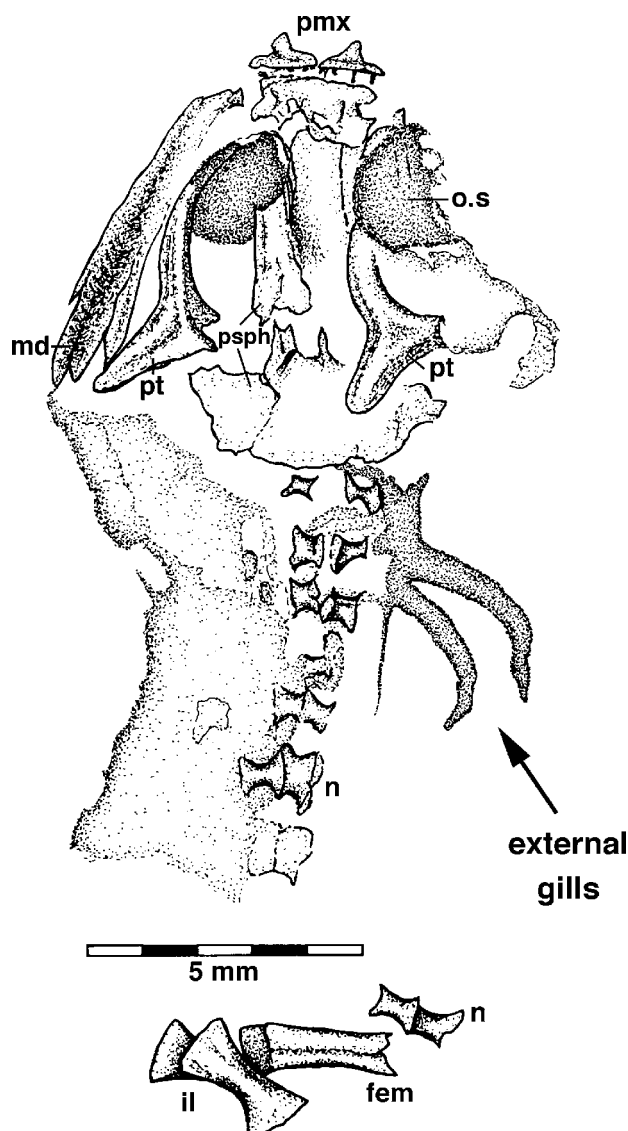
Figure 2. *Tungussogyrinus bergi*, holotype–counterpart PIN 206/1b; skull length $S_l = 7.5$ mm. Abbreviations: **fem** – femur; **il** – ilium; **md** – mandible; **n** – neural arch; **o.s** – orbital sac; **pmx** – premaxilla; **psph** – parasphenoid; **pt** – pterygoid.

shape of the premaxilla, parasphenoid, neural arch, and ilium of the holotype (Fig. 2) is represented in all of the referred specimens. Shishkin (1998) discussed the anatomy of the missing holotype specimen in detail as well as its affinity to the counter plate.

Tungussogyrinus bergi apparently was a small growing species with specimens ranging in skull length from 5 up to 11 mm. The skull bones, especially the palatal elements, are well ossified; the nasal is elongated but the sculpture of the dorsal skull roof is not well preserved. The following description of individual bones is given in relation to the most comparable branchiosaurids.

Skull roof. Most elements of the skull roof are only incompletely preserved and can be seen in ventral view. The general skull shape is triangular with a rounded snout. The postorbital region is distinctly shortened (ra-

tio of the postorbital skull length to the midline skull length $H_l/S_l = 0.30$ in Fig. 1), and the orbit is elongated, reaching posteriorly to the level of the pineal foramen. Jugal and maxilla do not make contact ventral to the orbit, leaving a gap along the ventral orbital rim as known from *Apateon dracyiensis* (Boy 1986; Werneburg 2001) and *Schoenfelderpeton prescheri* (Boy 1986). The otic notch of the squamosal is medium in depth as compared to the deep shape in amphibamids (Anderson et al. 2008a).

The circumorbital elements of the skull roof include the postfrontal, which is posteriorly narrow in ventral aspect as often seen in branchiosaurids. It is wider in the largest specimen in dorsal view (Fig. 6A). The anteriorly elongated postfrontal is in contact with the posteriorly elongated prefrontal (Figs 1A, 3B, 4, 5D). The postorbital is visible in Figure 3B and has a triangular shape. The jugal ossifies early and is present in specimens with a skull length of 7–9 mm (Figs 3A, 5A, 5D–E). It is triangular in shape with a relatively wide posterior and a short anterior part which is in contrast to the anteriorly extended jugal in *Branchiosaurus salamandroides* (Schoch & Milner 2008). An element that likely represents the lacrimal is preserved (Figs 3A, 5D), but its exact shape cannot be determined.

The description of the bones from the median and postorbital skull roof starts with the nasal, which is not completely preserved (Figs 3A–B, 5D), but seems to be an elongate element similar to the nasal of *Melanerpeton*. This can be concluded when comparing its preserved length to the combined length of the skull and the parasphenoid, vomers and premaxillae (Figs 1A–B, 3A–B). A proportional elongation of the nasals and snout region takes place through the ontogenetic development of the species *Tungussogyrinus bergi*, whereas the full extent of the elongation is seen in a stage with a skull length of 9 mm. The intraorbital region is generally wide (ratio of width of the intraorbital region to the midline skull length $IO_w/S_l = 0.30–0.36$; Figs 3B, 6A, 6D) as known from most species in *Apateon*. In some specimens the distance between the orbits seems to be narrower (Figs 4, 5A, 5D), but this region is not well preserved and likely distorted in this region. Sclerotic elements are not recorded in any of the available specimens. The frontals are wide in accordance with the broad intraorbital region, but very short and do not extend beyond the anterior margin of the orbit (Figs 1A, 3B, 6A, 6D). As a variant, one frontal in specimen PIN 4262/1a contacts the pineal foramen (Fig. 3B). The parietals are large, posteriorly wide, and anteriorly constricted by the posterior widening of the postfrontals (Figs 1A, 3B) which is in contrast to the narrow parietals in *Apateon dracyiensis* (Werneburg 2001). The ventral aspect of the parietal shows an anterolaterally directed crest with a double bifurcation in posteromedial direction (Fig. 3B). This crest, named "Parietalleiste" (Pfannenstiel 1932) or crista orbitotemporalis (Shishkin 1973), is marking the margin of the orbitotemporal region of the endocranium known in
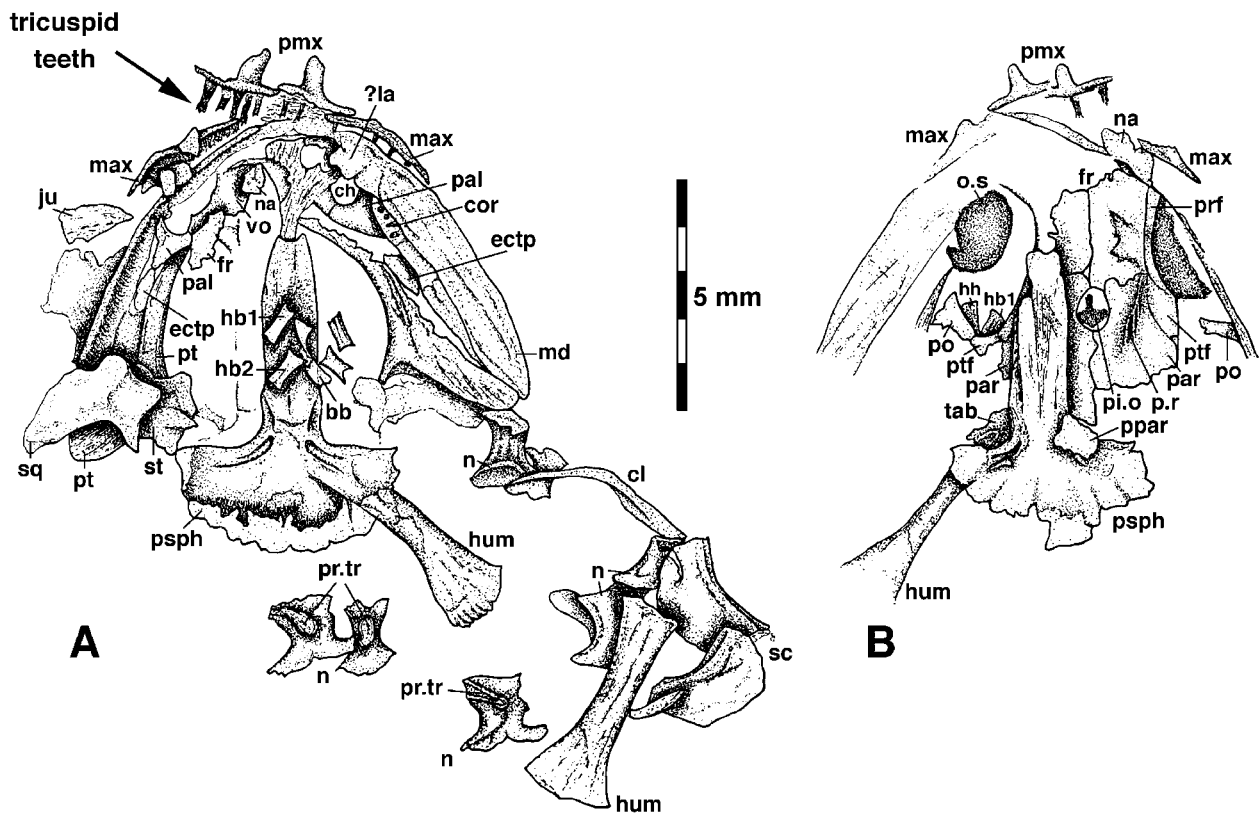
Figure 3. *Tungussogyrinus bergi*, the most complete specimen, $S_l = 9.2$ mm. **A.** PIN 4262/1b, dorsal view with ventral imprint of the parasphenoid; **B.** PIN 4262/1a, ventral view. Abbreviations: **bb** – basibranchial; **ch** – choana; **cl** – clavicle; **cor** – coronoid; **ectp** – ectopterygoid; **fr** – frontal; **hb1, 2** – hypobranchial 1 and 2; **hh** – hypohyal; **hum** – humerus; **ju** – jugal; **la** – lacrimal; **max** – maxilla; **md** – mandible; **n** – neural arch; **na** – nasal; **o.s** – orbital sac; **pal** – palatine; **par** – parietal; **pi.o** – pineal organ sac; **pmx** – premaxilla; **po** – postorbital; **ppar** – postparietal; **p.r** – parietal ridge; **prf** – prefrontal; **pr.tr** – transverse process of neural arch; **psph** – parasphenoid; **pt** – pterygoid; **ptf** – postfrontal; **sc** – scapulocoracoid; **sq** – squamosal; **st** – supratemporal; **tab** – tabular; **vo** – vomer.

many branchiosaurids (e.g. *Apateon dracyiensis* in Werneburg 2001; *Melanerpeton eisfeldi* Werneburg, 1988a and *Apateon kontheri* in Werneburg et al. 2007) and other temnospondyls. The pineal foramen is large, and in one specimen (PIN 4262/1a) the sac of the pineal organ is preserved as well as the orbital sac (both in Fig. 3B), as first reported in *Apateon dracyiensis* (Werneburg 2001: fig. 5). The postparietal is moderately elongate (Figs 3B, 5D) as known from *Apateon dracyiensis*. A portion of the tabular with the paroccipital process is preserved in ventral view (Fig. 3B), but its exact shape remains unclear. The supratemporal is relatively short, in accordance with the foreshortened postorbital skull (Figs 1A, 3A) as known from *Melanerpeton gracile* (Werneburg 1991) and *Branchiosaurus salamandroides* (Schoch & Milner 2008). The postorbital skull roof is moderate in width (ratio of width of the postorbital skull to the midline skull length $H_w/S_l = 0.83$), as compared to other branchiosaurid species (Werneburg 1989).

The cheek region shows a well represented squamosal (Figs 3A, 5B, 5D–E, 6C–D, 6F), although differing preservation shows deeper or flatter incisures for the otic notch (Fig. 1A), as known from most other bran-

chiosaurids (Werneburg 1989). The quadratojugal cannot be demonstrated with certainty in any of the specimens investigated.

The tooth bearing bones are especially interesting as they show many apomorphic features that provide insight into the ecology of *Tungussogyrinus*. The maxilla is very short (Figs 3A–B, 5F) and, with the short jugal and elongated orbit, indicate a large gap at the margin of the skull roof. There are about 15 maxillary teeth, which is also the number of teeth present in the preserved part of the dentary (Fig. 5). The four anterior-most maxillary teeth have a wide base and a tricuspid tooth crown (Fig. 6C). The same tooth structure was found by the author in several premaxillary bones in 1989 (Figs 3A–B, 4A, 5C, 6H). The number of premaxillary teeth lies between six and seven. Each individual tooth is very long, the base is mesiodistally wide, but narrows in the mid part, while the tip is broadened and supports three mesiodistally aligned, conspicuous cuspules (Figs 10A–B). The median cusp is a little bit larger than the two lateral ones. These teeth are labiolingually compressed and mesiodistally expanded, and the head of the tooth is slightly curved lingually. There is no indication of pedicely between the head and the body of the tooth. However, an
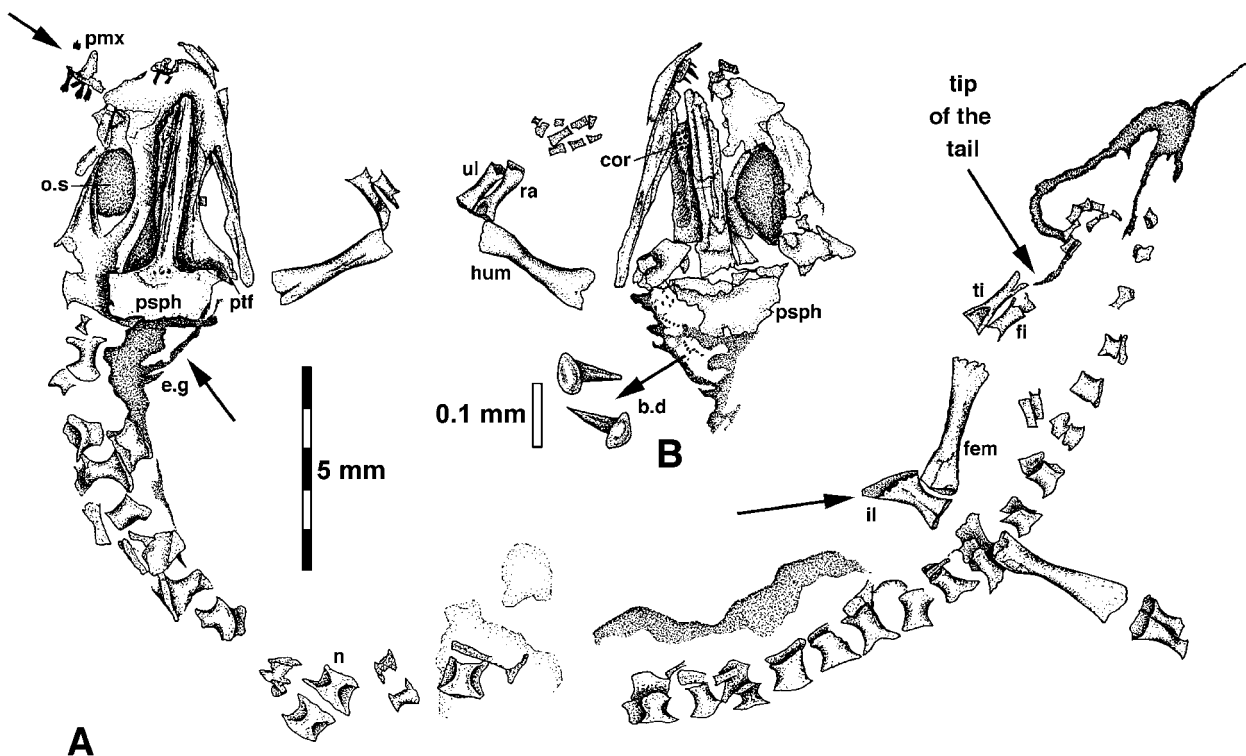
Figure 4. *Tungussogyrinus bergi*. **A.** PIN 4262/4a, the complete skeleton from the snout to the tip of the tail. Note the tricuspid teeth, the external gills and the anterodorsally directed process of the ilium; **B.** PIN 4262/4b, note the presence of branchial denticles; S_l about 8 mm. Abbreviations: **b.d** – branchial denticles; **cor** – coronoid; **e.g** – external gills; **fem** – femur; **fi** – fibula; **hum** – humerus; **il** – ilium; **n** – neural arch; **o.s** – orbital sac; **pmx** – premaxilla; **psph** – parasphenoid; **ptf** – postfrontal; **ra** – radius; **ti** – tibia; **ul** – ulna.
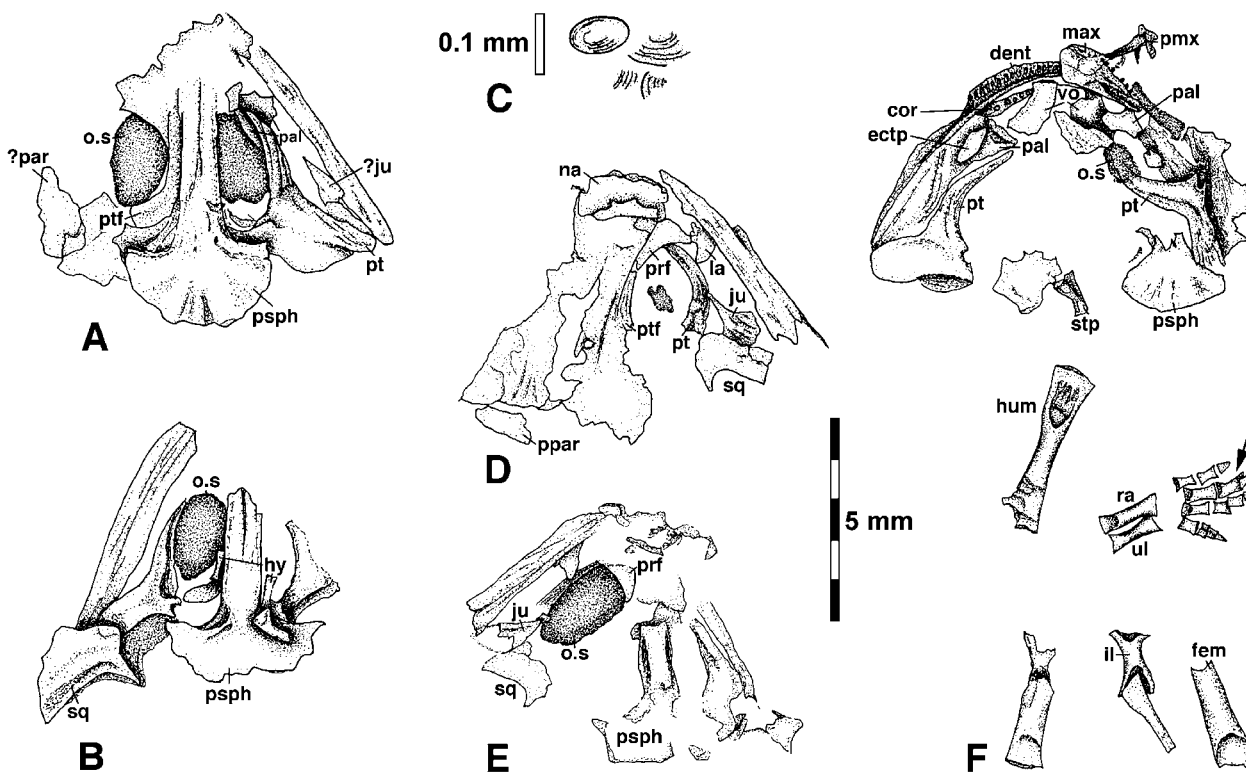

Figure 5. *Tungussogyrinus bergi*. **A–B.** PIN 4262/9a, b, S_l about 7,5 mm, in dorsal (**A**) and ventral view (**B**); **C.** Scales from the middle trunk region, PIN 4262/12b; **D–E.** PIN 4262/6a, b, S_l about 7 mm, in dorsal (**D**) and ventral (**E**) view; **F.** PIN 4262/5, S_l about 7 mm, in dorsal view. Abbreviations: **cor** – coronoid; **dent** – dentary; **ectp** – ectopterygoid; **fem** – femur; **hy** – hyobranchial bone; **hum** – humerus; **il** – ilium; **ju** – jugal; **la** – lacrimal; **max** – maxilla; **na** – nasal; **o.s** – orbital sac; **pal** – palatine; **par** – parietal; **pmx** – premaxilla; **ppar** – postparietal; **prf** – prefrontal; **psph** – parasphenoid; **pt** – pterygoid; **ptf** – postfrontal; **ra** – radius; **sq** – squamosal; **stp** – stapes; **ul** – ulna; **vo** – vomer.
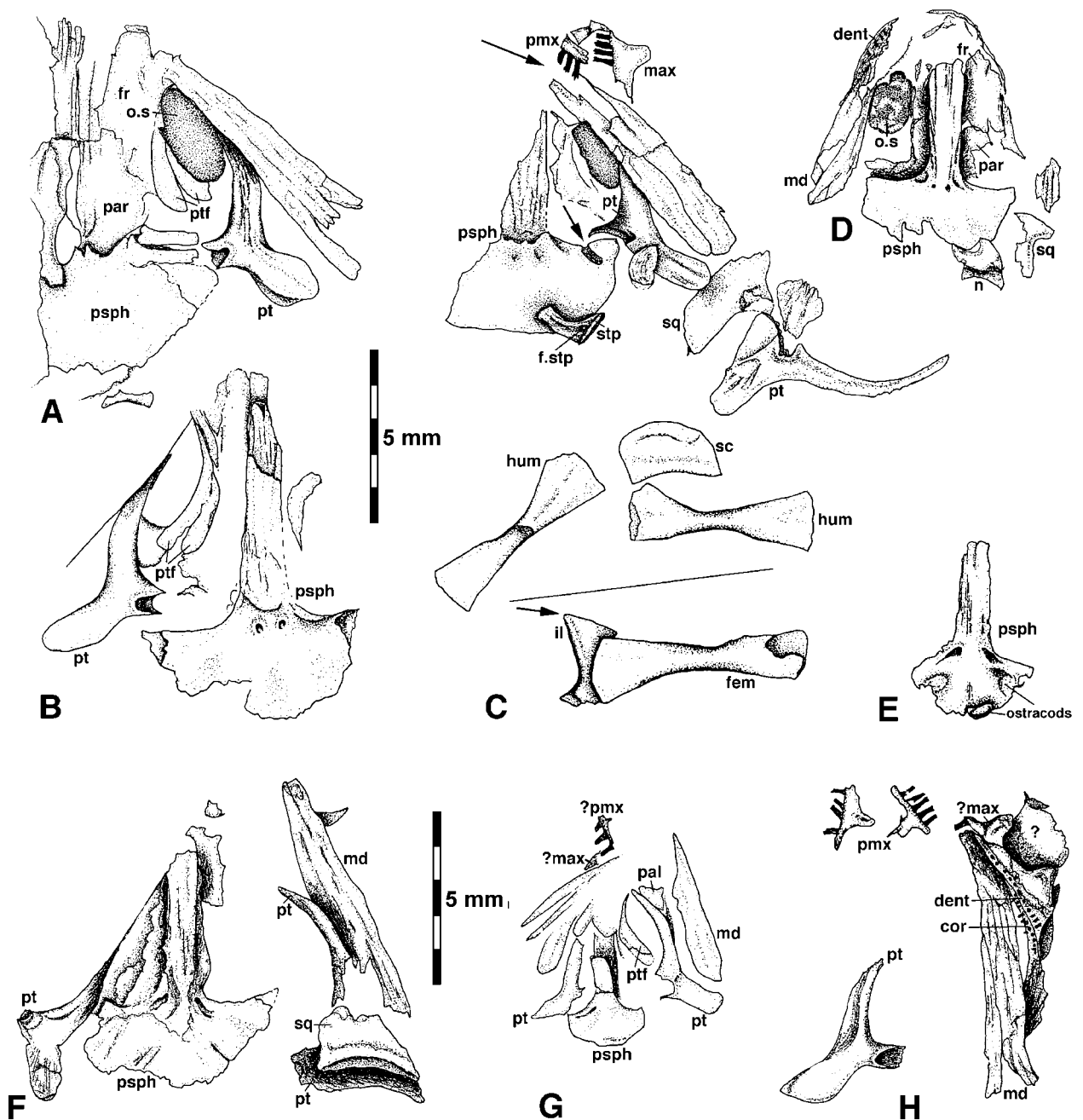
Figure 6. *Tungussogyrinus bergi*. **A–B.** PIN 4262/7a, b, S$_l$ about 11 mm, in dorsal (**A**) and ventral (**B**) views. Note the divided postfrontal; **C.** PIN 4262/2, S$_l$ about 10 mm, in dorsal view, note the tricuspid teeth, the furrow on the dorsal parasphenoid plate, the stapes and the anterodorsal processus of the ilium; **D.** PIN 4262/8, S$_l$ about 7.5 mm, in ventral view; **E.** PIN 4262/20, ventral parasphenoid, S$_l$ about 7 mm; **F.** PIN 4262/11, ventral view, S$_l$ about 9 mm; **G.** PIN 4262/3, dorsal view, smallest specimen, S$_l$ about 5 mm; **H.** PIN 4262/without number, but with blue arrow, S$_l$ about 8–9 mm. Abbreviations: **cor** – coronoid; **dent** – dentary; **fem** – femur; **fr** –frontal; **f.stp** – stapedial foramen; **hum** – humerus; **il** – ilium; **max** – maxilla; **md** – mandible; **n** – neural arch; **o.s** – orbital sac; **pal** – palatine; **par** – parietal; **pmx** – premaxilla; **psph** – parasphenoid; **pt** – pterygoid; **ptf** – postfrontal; **sc** – scapulocoracoid; **sq** – squamosal; **stp** – stapes.

isolated tricuspid tooth crown preserved close to a premaxilla (Figs 4A, 10A) indicates the possibility of pedicely. One premaxillary tooth shows a large replacement pit at the base (Fig. 10A). The premaxilla is a slender element and the tooth bearing ventral plate is very low. The ascending process is very long and narrows (Figs 10A–B). The median intranasal fenestra enclosed by premaxillae and nasals as well as the narial openings are slightly larger than in most other branchiosaurids.

Palatal view. The relationship between the dorsal portion of the palatal elements and the cartilaginous structures of the skull were discussed in detail by Shishkin (1998) and will not be further discussed here. The
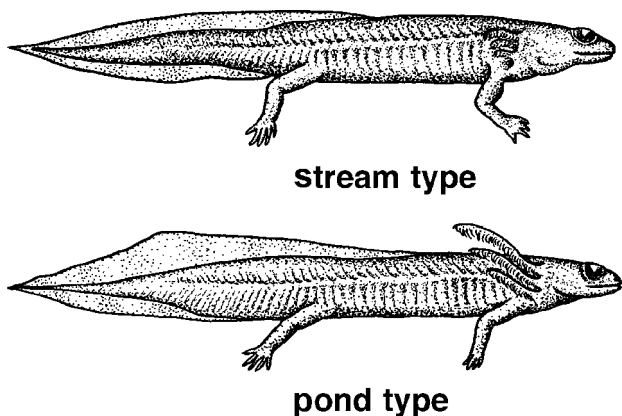
Figure 7. The ecomorphotypes of branchiosaurids with stream type (above) and pond type (after Werneburg 2002). The known specimens of *Tungussogyrinus* belong to the stream type.

shape of the parasphenoid is diagnostic for this species. It has a very large and elongate basal plate. The cultriform process is widened throughout most of its length and only slightly constricted at its anterior end and posterior base (Fig. 3A). This robust shape of the parasphenoid is only known in branchiosaurids of the *Apateon*

kontheri-group, especially from *A. dracyiensis*, *A. intermedius,* and *A. kontheri* (Werneburg 1988a, 1996, 2001). However, there seems to be some variation in the width of the cultriform process, which may in part be due to small differences between the ventral and dorsal aspect of the process (Figs 3A–B, 4A–B, 5E), but a slight dimorphism is also reported from *Apateon dracyiensis* (Werneburg 2001: tab. 2, figs 10b–c, 13).

The foramina and transverse grooves for the internal carotid arteries are placed anteromedially on the base of the parasphenoid in ventral view. Surprisingly, a second transverse groove is preserved on the anterolateral edge of the dorsal parasphenoid base (Fig. 6C), which was thus far unknown for branchiosaurids. Shishkin (1973) reported on a similar structure in *Dvinosaurus primus* Amalitzky, 1921 as an imprint of the vena palatina, which is located at the anterolateral edge of the ventral parasphenoid base. The latter structure has been recorded for one Sardinian branchiosaurid, a specimen of *Melanerpeton eisfeldi* in ventral view too (Werneburg et al. 2007: fig. 4A). Apparently, the imprint of the vena palatina on the parasphenoid is present only in some branchiosaurid specimens.
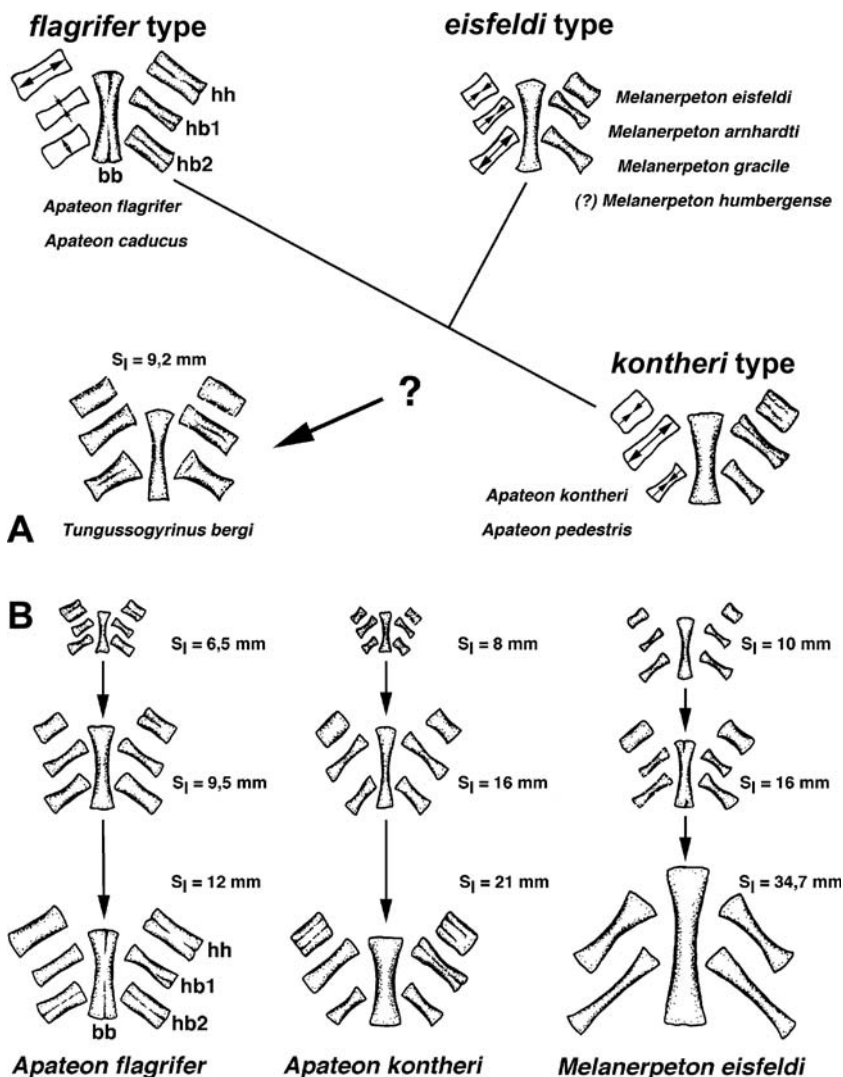

Figure 8. A. The three variants of the ossified parts of the hyobranchial skeleton in branchiosaurids (after Werneburg 1986, 1988a) and the reconstructed hyobranchium of *Tungussogyrinus bergi*. The reconstruction of the hyobranchial apparatus of *T. bergi* is based on PIN 4262/1a, b; **B.** The ontogenetic development of the three variants of the branchiosaurid hyobranchial skeleton. Abbreviations: **bb** – basibranchial; **hb1,2** – hypobranchial 1 and 2; **hh** – hypohyal.
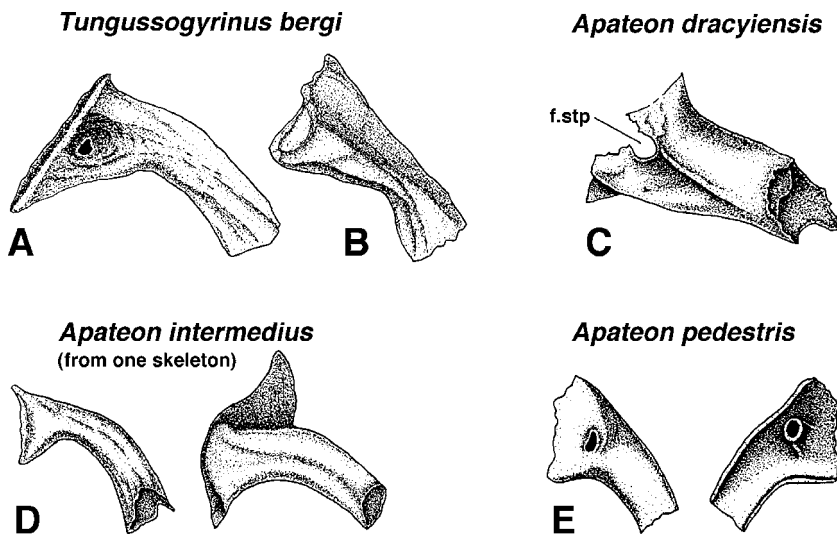
Tungussogyrinus bergi

Apateon dracyiensis

Apateon intermedius
(from one skeleton)

Apateon pedestris

Figure 9. The branchiosaurid stapes with the stapedial foramen. **A−B.** *Tungussogyrinus bergi*; **A.** PIN 4262/2. **B.** PIN 4262/5; **C.** *Apateon dracyiensis* (after Werneburg 2001); **D.** *Apateon intermedius* (after Werneburg 1996); **E.** *Apateon pedestris* (after Boy 1972). Abbreviation: **f.stp** – stapedial foramen.

The pterygoid has a slender and elongated palatal ramus (Figs 2, 3A, 5F, 6C, 6G). Shishkin (1998) assumed that the pterygoid reaches the vomer and completely separates the palatine from the interpterygoidal fenestra, but the reconstruction of the best preserved specimen (Figs 1B, 3) clearly shows that the palatine is intercalated between the pterygoid and vomer at the margin of the interpterygoidal fenestra. The lamina ascendens between the quadratic and basipterygoidal ramus is preserved in some specimens (Figs 5F, 6C, 6F). The basipterygoidal ramus is narrow and not well ossified in almost all specimens, but in one specimen (PIN 4262/without number) it is medially expanded (Fig. 6H). Such exceptions are known from other branchiosaurids, too.

The palatine is y-shaped, which is a synapomorphy for all branchiosaurids (Boy 1972; Schoch & Milner 2008). It is anteriorly expanded to contact the vomer and maxilla. The posterior part is narrower and without

contact to the maxilla (Figs 1B, 3A, 5A, 5F, 6G). The palatine and ectopterygoid of *Tungussogyrinus* are short, like in the branchiosaurid genus *Apateon*. The ectopterygoid has the same breadth as the posterior portion of the palatine (Figs 1B, 3A, 5F) and has no contact with the maxilla. This gap between the maxilla, palatine, and ectopterygoid indicates that the infratemporal fossa is extended far anteriorly along the lateral edge of the ectopterygoid. Palatine, ectopterygoid, and vomer are mostly preserved in dorsal view; therefore no palatal dentition is visible. The vomer is narrow and very elongated (Figs 1, 3A, 5F) compared to *Melanerpeton tenerum/Leptorophus tener* (Boy 1986), and the choana is wide and elongated (Fig. 1) like in *Melanerpeton humbergense* (Boy 1978).

Visceral ossifications and gills. The shape of the stapes can be determined in PIN 4262/5 (Fig. 5F), PIN 4262/2 (Fig. 6C) and possibly in 4262/9b (Fig. 5B). The wide ba-
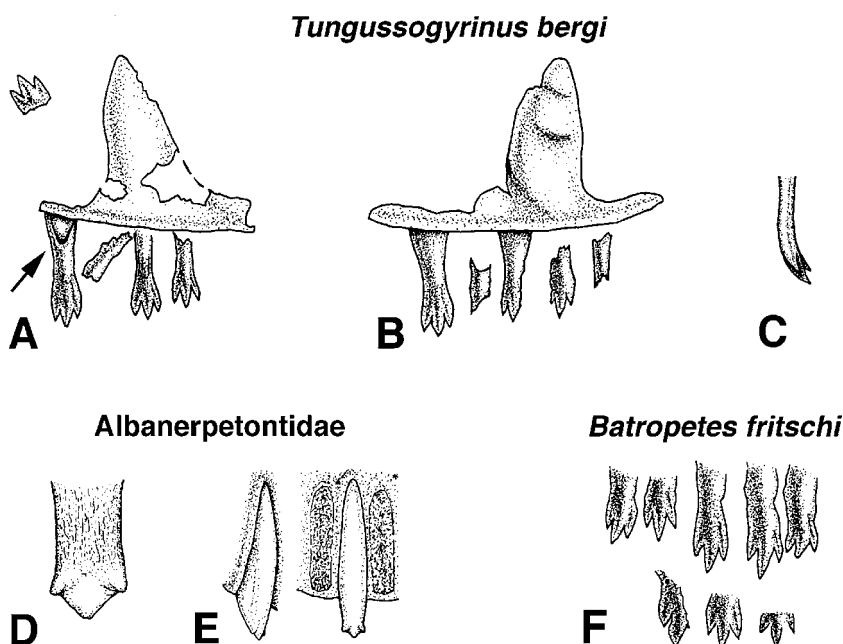
Tungussogyrinus bergi

Albanerpetontidae

Batropetes fritschi

Figure 10. Dentition of branchiosaurids (**A−C**), albanerpetontids (**D−E**) and microsaurs (**F**). **A−C.** Tricuspid teeth in *Tungussogyrinus bergi*; **A.** Premaxilla, PIN 4262/4a, note the isolated tricuspid crown, perhaps a hint of pedicelly; **B.** Premaxilla PIN 4262/1b; **C.** Premaxillary tooth in distal and slightly lingual views; **D.** One tooth of the dentary of *Anoualerpeton priscus* Gardner et al., 2003. (drawn after a photograph in Gardner et al. 2003); **E.** Premaxillary tooth (inverted) in lingual and distal plus slightly lingual views of *Albanerpeton inexpectatum* Estes and Hoffstetter, 1976 (drawn after Gardner 2001); **F.** Tricuspid teeth of the dentary (above) and premaxilla in *Batropetes fritschi* (Geinitz & Deichmüller, 1882), NHMM-PW 2001/309-LS (drawn after a photograph from K. Krätschmer).
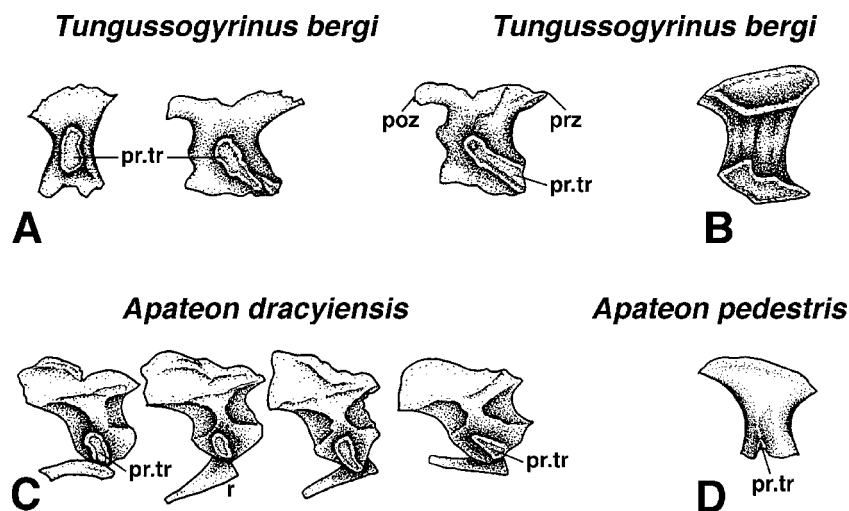
Tungussogyrinus bergi   **Tungussogyrinus bergi**

Apateon dracyiensis   **Apateon pedestris**

Figure 11. The branchiosaurid neural arch in lateral (**A, C, D**) and medial view (**B**), note the shape of the transverse process (diapophysis). **A–B.** *Tungussogyrinus bergi*, PIN 4262/1b (Fig. 1A); **C.** *Apateon dracyiensis* (after Werneburg 2001); **D.** *Apateon pedestris* (after Boy 1972). Abbreviations: **poz** – postzygapophysis of neural arch; **pr.tr** – transverse process of neural arch; **prz** – praezygapophysis;

sal plate supports a columella with a large stapedial foramen on its base and extends into a much narrower branch (Figs 9A–B). The questionable stapes as described by Shishkin (1998: fig. 5) can clearly be identified as a humerus that is located near the parasphenoid (Figs 3A–B). The general morphology of the branchiosaurid stapes can be compared with related taxa (Fig. 9).

A complete hyobranchial skeleton is preserved in the specimen PIN 4262/1 (Figs 3A, B), and some isolated elements are recorded (Fig. 5B). The reconstructed ossified hyobranchial skeleton for the skull length of 9 mm is illustrated in comparison with that of other branchiosaurids (Fig. 8A). The basibranchial is a curved element and preserved in situ in PIN 4262/1. It is here interpreted that curvature occurred likely due to deformation and the basibranchial was therefore reconstructed as a straight element. However, it is possible that the curved shape is natural. Hypobranchial 1 is a little bit longer than hypobranchial 2 (Fig. 8A), whereas the latter element is more robust. The hypohyal is shorter and thicker than the hypobranchials (PIN 4262/1; Fig. 3B).

The branchial denticles of *Tungussogyrinus* are described here for the first time and are preserved in one specimen (PIN 4262/4b; Fig. 4B). The branchial denticles have an oval base with one tooth-like process. It is possible that more than one tooth-like process were present in *Tungussogyrinus*, because it is known from *Apateon dracyiensis* and other branchiosaurids that one or more processes may be visible depending on the preservation. Two specimens show relatively short external gills in soft tissue preservation (Figs 2, 4).

Lower jaw. The posterior part of the mandible is not well preserved. The dentary bears almost 20 teeth (Figs 5F, 6H). The bases of the posterior teeth are mesiodistally compressed and labiolingually aligned, meaning that the posterior teeth of the dentary are probably more conical and differ from the tricuspid teeth with a mesiodistally expanded base known from the premaxilla and anterior maxilla. The bases of the anterior dentary teeth are more mesiodistally widened and represent probably the tricuspid teeth, although the

tips themselves are not preserved (Fig. 6H). A slender, elongate tooth bearing bone located in some specimens (Figs 3A, 4B, 5F, 6H) is a coronoid of the lower jaw (a precoronoid after Shishkin 1998). Such a robust, ossified coronoid with relatively large teeth and denticles in one to two rows is rarely preserved in branchiosaurids (e.g. in *Apateon dracyiensis*; Boy 1986: fig. 16a).

Postcranial skeleton. Only the paired neural arches are ossified in the vertebral column. In medial view (Figs 3A, 11B), it resembles *Apateon pedestris* v. Meyer, 1844 (Boy 1972: fig. 43a). Their post- and praezygapophyses are extended and the transverse processes (diapophyses) are expanded ventrodorsally and laterally. They reach the dorsal half of the neural arch, and are mostly oblique or rarely straight in shape (Figs 3A, 11A), similar to *Apateon dracyiensis* (Fig. 11C). There are approximately 20 presacral (Fig. 4), and at least eight postsacral vertebrae. Soft tissue preservation is visible in the anterior trunk region with external gills of the holotype specimen PIN 206/1b (Fig. 2) and in specimen PIN 4262/4 with external gills and the posterior end of the tail (Fig. 4). Only few ribs are preserved and correspond in their shape with the short, straight ribs with expanded ends with those of all other branchiosaurids.

The humerus is elongated, but is not longer than the femur. The ratio of the humerus length to the skull length is 0.52–0.60 (Figs 3, 5F, 6C) but only 0.40 in one specimen (Fig. 4). The elongated humerus is also known in *Apateon dracyiensis* (Werneburg 2001; see paragraph "General comparisons"), but in exceptional cases, the humerus is longer than the femur in this species. The forelimbs may show a possible size dimorphism (Figs 12A–B); in PIN 4262/5 it is larger than in PIN 4262/4b, especially the humerus and manus, although the skull length is only 7 mm as opposed to 8 mm. The forelimb of PIN 4262/4b is smaller and only the radius and ulna are of the same length and shape as in the previous specimen. Metacarpal 2 and especially the next proximal phalanx of digit 2 are more elongated than metacarpal 3 and the following proximal phalanx of digit 3 (Figs 12A–B). The phalangeal formula of the
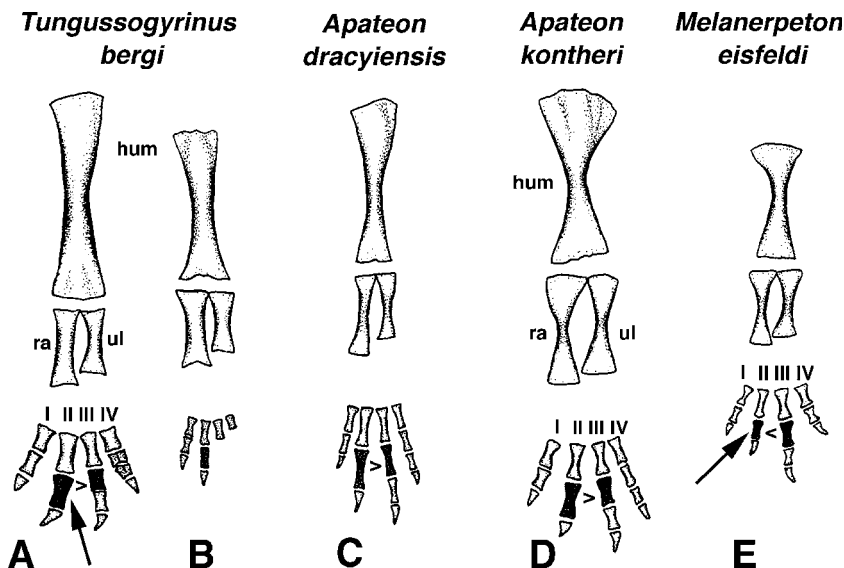
Figure 12. Branchiosaurid forelimb, note the large first phalangal bone of the second digit. **A – B.** *Tungussogyrinus bergi*, **A.** PIN 4262/5, S_l about 7 mm; **B.** PIN 4262/4b, S_l about 8 mm; **C.** *Apateon dracyiensis* (after Werneburg 1988b); **D.** *Apateon kontheri* (after Werneburg 1988a); **E.** *Melanerpeton eisfeldi* (after Werneburg 1988a). Abbreviations: **hum** – humerus; **ra** – radius; **ul** – ulna.

manus is 2 – 2 – 3 – 3, and the second and third digits are of equal length.

Only two elements of the shoulder girdle are preserved, the clavicle and the scapulocoracoid. The clavicle is lightly built and it probably has a short ventral plate (Fig. 3A) as known for most branchiosaurids. The scapulocoracoid is crescent shaped (Figs 3A, 6C). The tibia is more elongated than the fibula (Fig. 4A).

The ilium is the only element of the pelvic girdle preserved (Figs 2, 4A, 5F, 6C). The ventral part is relatively small. The base of the dorsal iliac shaft is wider (Fig. 13), and the dorsomedial part of the ilium is much expanded. The anterodorsal process is unusually long. This feature is visible in two specimens (PIN 4262/4a: Figs 4A, 13A; PIN 4262/2: Figs 6C, 13B) and is not known from other branchiosaurids (Fig. 13). Two further ilia are preserved, albeit not showing as much detail (Figs 2, 5F), but one of them (specimen PIN 4262/5) shows the acetabulum in lateral view (Fig. 5F).

Thin scales are preserved in a few instances (Fig. 5C). They are relatively large with a width of nearly 1 mm. They have 4–5 concentric growth rings comparable to the ventral scales of *Apateon flagrifer* Whittard, 1930 (Werneburg 1986b: fig. 7). In contrast only one to three rings are visible on the scales of *Apateon dracyiensis* and *Apateon kontheri* (Werneburg 1988a, 1988b).

General comparisons

Heterodont dentition. The anterior dentition of *Tungussogyrinus bergi* is labiolingually compressed and mesiodistally tricuspid, but the teeth of the posterior parts of dentary and maxilla are monocuspid. Notably though, bicuspid teeth (as reported by Shishkin 1998) are not present in the Siberian species.

The heterodont dentition in *Tungussogyrinus bergi* is distributed as follows:

(1) Premaxilla with 6 (or 7) tricuspid teeth;

(2) Maxilla with at least 4 (or 5) tricuspid teeth and about 10 posterior teeth probably monocuspid;

(3) Dentary with anterior 10 (or 11) probably tricuspid and about 10 posterior teeth probably monocuspid.

The nature of tooth attachment is not clear in *Tungussogyrinus bergi* (Fig. 5F). The related branchiosaurid species *Apateon dracyiensis* has pleurodont dentition in the lower jaw (Werneburg 2001). Pleurodont implantation is also known from *Doleserpeton* Bolt, 1969 (Bolt 1991) and branchiosaurids of Sardinia (Werneburg et al. 2007). On the other hand acrodont dentition is observed in *Apateon pedestris* (Boy 1978: fig. 5). It should be noted that the posterior dentary tooth bases are anteroposteriorly compressed in *Tungussogyrinus* (Fig. 5F) as are the tooth sockets in the dentary of *Apateon pedestris*.

Tungussogyrinus bergi is the first branchiosaurid known to have multicuspid teeth. However, they are not bicuspid as in most lissamphibians, the microsaur *Carrolla* Langston & Olson, 1986 and some amphibamids (e.g. *Doleserpeton* and possibly *Tersomius* Case, 1910; Bolt 1977, 1979). Rather, the anterior dentition of *Tungussogyrinus* is tricuspid, like that of the microsaur *Batropetes fritschi* (Geinitz & Deichmüller, 1882; Carroll 1991) as well as albanerpetontid amphibians (Gardner 2001; Gardner et al. 2003). The three individual cuspules are larger than in *Batropetes* and in albanerpetontids, and the teeth are more labiolingually compressed and lingually curved in *Tungussogyrinus*. However, such differences are also seen in extant amphibians. A higher variability in the crown morphology of teeth is known from some ambystomatid salamanders showing club-shaped or tricuspid teeth (Beneski & Larsen 1989). Moreover, the anuran tadpoles of *Bufo americanus* Holbrook, 1836 (Tubbs et al. 1993: fig. 2c) and *Rana chensinensis* David, 1875 (Herrmann & Kabisch 1992) also possess tricuspid teeth-like structures in the keratinous mouthparts in certain stages of their ontogenetic development. The fetal teeth of the
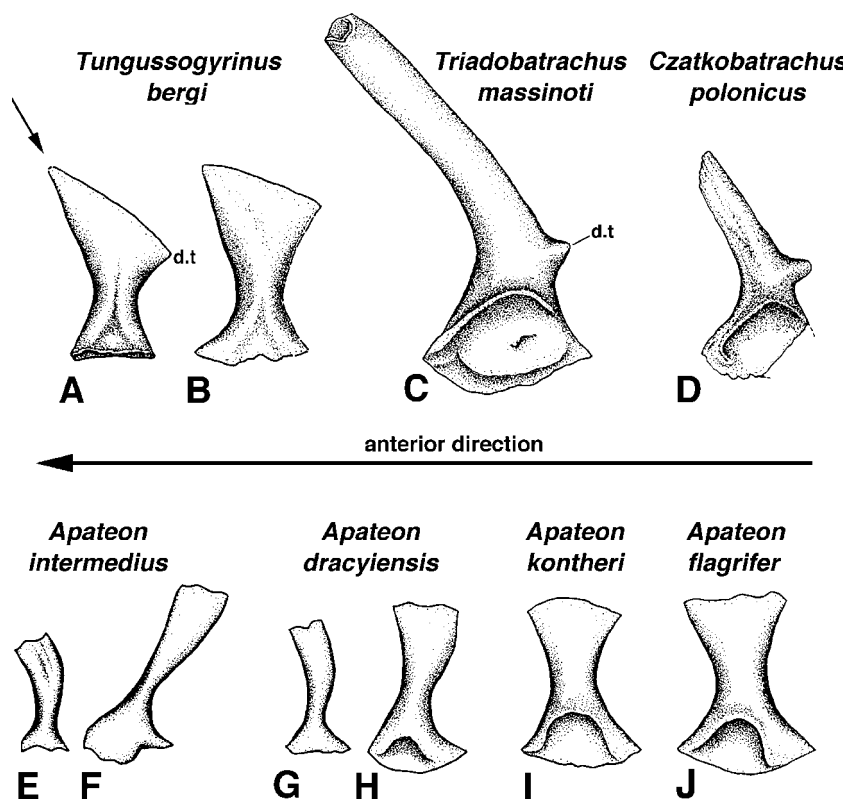
Figure 13. The ilium of branchiosaurids (**A–B, E–J**) in comparison with that of Triassic proanuran stages (**C–D**). **A–B.** *Tungussogyrinus bergi*, note the anterodorsal process; **A.** PIN 4262/4a; **B.** PIN 4262/2; **C.** *Triadobatrachus massinoti* (Piveteau, 1936) (after Rage and Roček 1989), with a long anterodorsal process and a small dorsal tubercle; **D.** *Czatkobatrachus polonicus* (after Evans and Borsuk-Białynicka 1998); **E–F.** *Apateon intermedius* (after Werneburg 1996); **G, H.** *Apateon dracyiensis* (after Werneburg 1988a); **I.** *Apateon kontheri* (after Werneburg 1988b); **J.** *Apateon flagrifer* (after Werneburg 1986b). Abbreviation: **d.t** – dorsal tubercle of ilium.

caecilian *Typhlonectes compressicauda* (Duméril & Bibron, 1841) (Wake 2003) are similar too.

Visceral ossifications. Tungussogyrinus bergi is a short-gilled branchiosaurid with small, triangular branchial teeth. The ossified hyobranchial apparatus is characteristic for the neotenic condition frequently recorded in branchiosaurids (Boy & Sues 2000). Three variants of the ossified parts of the hyobranchial skeleton are known (Boy 1978; Werneburg 1989). All three types are preserved in three branchiosaurid species, *Apateon flagrifer*, *A. kontheri* and *Melanerpeton eisfeldi*, from one lake-complex in the Lower Rotliegend of the Thuringian-Forest-Basin (Werneburg 1986b, 1988b) (Fig. 8B). The *flagrifer* type is presented in *Apateon caducus* and *A. flagrifer*, the *kontheri* type in *A. pedestris* and *A. kontheri*, and the *eisfeldi* type in *Melanerpeton eisfeldi*, *M. arnhardti*, *M.* (? or *Apateon) gracile* and probably in *M. humbergense*. The differences between the types of hyobranchial skeleton lie in the proportional differences in length and width of their ossified parts (Fig. 8A).

The reconstruction of the ossified hyobranchial apparatus of *Tungussogyrinus bergi* (Fig. 8A) is in the general configuration very close to the *kontheri* type known from *Apateon dracyiensis* and *A. pedestris*, but in individuals with a skull length of 9 mm, it is also similar to the *flagrifer* type. A definitive assignment to one type is not possible at this point, because an early ontogenetic stage is only recorded by a single specimen.

Postcranial skeleton. Only the neural arches are ossified in the vertebral column, which is characteristic of

branchiosaurids and other temnospondyls larvae, and in contrast to lepospondyls, where the centrum usually ossifies early in ontogeny as well (Shishkin 1998). The transverse processes are very rarely preserved in branchiosaurids, and when known they are small and only slightly extended (e.g. *Apateon pedestris*; Fig. 11D). The transverse processes are visible in one specimen of *Tungussogyrinus bergi* (Fig. 11A), where they are larger than in *Apateon dracyiensis* (Fig. 11C). However, in the latter the processes belong to the 16th to 19th presacral vertebrae as opposed to the anterior third or fourth rib bearing vertebrae in specimen PIN 4262 of *Tungussogyrinus*, which usually bear the largest ribs in branchiosaurids (Fig. 3A). Nonetheless, in both species the transverse process is large, prominent and entirely located on the neural arch. This is very similar to the condition in *Triadobatrachus* Kuhn, 1962 (Rage & Roček 1989: figs 1a, 2a) and with a slightly smaller size in *Doleserpeton* (Bolt 1969: fig. 4).

The forelimb of *Tungussogyrinus bergi* shows a slender, elongated humerus and some interesting characters in the manus. In most other branchiosaurids the third finger is the most elongated, but in *Tungussogyrinus* the second and third digit are equal in length (Fig. 12). The second metacarpal and the proximal phalanx are more elongated than in the third digit. These proportions of the metacarpal and the proximal phalanx are also present in the manus of *Apateon dracyiensis* (Werneburg 1988a, 2001), *A. kontheri* (Werneburg 1988b), and sometimes in *A. pedestris* (Boy 1972: fig. 51). In all other branchiosaurid species the third finger of the manus is the largest digit, and the second metacarpal

and proximal phalanx are shorter than in the third digit (Fig. 12E).

The short ventral part of the ilium is similar in *Tungussogyrinus*, *Apateon intermedius*, and *A. dracyiensis* (Fig. 13) from the Lower Rotliegend (Gzhelian/Asselian). The shaft and dorsal part of the ilium in *Tungussogyrinus* are more expanded than in these other branchiosaurids, also seen in *Apateon kontheri*, *A. flagrifer*, and most other branchiosaurids, which are known from a more recent part of the Rotliegend (Asselian/Sakmarian). Surprisingly, the dorsal process is unusually extended anteriorly. This character is not known from any other branchiosaurid.

Possible dimorphism. One anatomical feature displaying dimorphism is presented in *Tungussogyrinus*. The forelimb is larger and more robustly developed in a specimen with a slightly smaller skull length (PIN 4262/5: Figs 5F, 12A) than in another one with a 1 mm larger skull (PIN 4262/4b: Figs 4B, 12B). The humerus of PIN 4262/5 is more elongated and the digits are larger, but the ulna and radius have equal length in both specimens.

Differences in the length of the humerus are also known in *Apateon dracyiensis* (Werneburg 1988b, 2001). In *A. dracyiensis*, probably intraspecific variability, and differential preservation are suspected causes for the large interval of the ratio of the length of the humerus to the skull length: $HUM_l/S_l = 0.38-0.58$. But the humerus is relatively shorter in the late ontogenetic stage of *A. dracyiensis* ($HUM_l/S_l = 0.31-0.33$; ontogenetic shift!). However, variation between the robust and the very slender manus within the same ontogenetic stage is as also known in *A. dracyiensis* from different localities (Werneburg 2001: fig. 3b, the holotype from Dracy St Loup/France, and e.g. fig. 9b, a specimen from Tabarz/Germany). But there is only one example from hundreds of investigated specimens in *A. dracyiensis*. Differences in proportion of the limbs are sometimes indicative for sexual dimorphism in modern amphibians, but the fossil record in *Tungussogyrinus bergi* is too limited and the experiences from the related species *Apateon dracyiensis* point towards fossil preservation as the cause for this dimorphism.

Discussion

Systematic and phylogenetic position

The presence of the otic notch and the shorter presacral region of the vertebral column are features of dissorophoids and not of brachyopoid amphibians (Shishkin 1998). Moreover, *Tungussogyrinus* possesses a clear synapomorphy of the Branchiosauridae – the anterior expansion of the infratemporal fossae on the palate up to the anterior palatine resulting in a gap between ectopterygoid and maxilla (Fig. 1B). The branchial denticles have a small rounded base and one tooth-like process. The foramina as well as the grooves of the

internal carotid arteries are clearly visible on the basal plate of the parasphenoid and it lacks a distinct, coarsely sculptured area. All these features clearly characterise *Tungussogyrinus* as belonging to the clade Branchiosauridae.

The genus and species *Tungussogyrinus bergi* is characterised by three derived characters. The first is interpreted as an autapomorphy: the elongated anterodorsal process of the ilium. This character is similar in tendency, but not identical, with that of the proanurans *Czatkobatrachus* Evans & Borsuk-Białynicka, 1998 (Fig. 13D) and *Triadobatrachus* (Fig. 13C; Rage & Roček 1989), and it is not known from other branchiosaurids or other non-anuran temnospondyls. The second character is homoplastic with respect to microsaurs, but it is an autapomorphy for *Tungussogyrinus* with respect to other branchiosaurids: the tricuspid teeth with wide bases and a decrease in tooth number to probably six in the premaxilla; the tooth bearing bone of the premaxilla is low, the premaxilla is lightly built, and large median intranasal and nasal fenestrae were possibly present in the gracile snout region. This suggests a new feeding strategy. The third feature is of uncertain polarity and unique within temnospondyls: the second and third finger is of the same length. In all other branchiosaurids and other temnospondyls the third finger is the most elongated one of the manus.

The genus *Tungussogyrinus* shows a mosaic of characters present in both most closely related branchiosaurid genera. Characters shared with *Apateon* are: (1) the short palatine and ectopterygoid; and (2) an expanded intraorbital region. Characters shared with *Melanerpeton* are: (1) an elongated orbita; and (2) an elongation of the preorbital region with a long nasal and vomer.

Tungussogyrinus bergi shares the most characters with *Apateon dracyiensis* (compare Werneburg 2001): (1) pre- and postfrontal in contact; (2) expanded intraorbital region; (3) very short maxilla; (4) jugal with short anterior process; (5) gap between maxilla and jugal; (6) robust shape of parasphenoid; (7) palatine and ectopterygoid short; (8) elongated humerus; (9) metacarpal 2 and proximal phalanx II more elongated as metacarpal 3 and proximal phalanx III; and (10) transverse process is large, prominent and completely located on the neural arch.

Two additional features complete the definition of the species *Tungussogyrinus bergi*: (11) foreshortened postorbital region with short postorbital and supratemporal, shared with *Melanerpeton gracile* (Werneburg 1988c, 1991, 2003; or *Apateon gracilis* in the sense of Schoch & Fröbisch 2006) and *Branchiosaurus salamandroides* (Boy 1987; Werneburg 1987); and (12) very short frontal reaching up to the anterior orbital margin.

The phylogenetic relationships of *Tungussogyrinus* within the family Branchiosauridae is very important for the understanding of the evolution of the branchiosaurids. Many features are the same in *Tungussogyrinus* and *Apateon, A. dracyiensis* as well as *Melanerpeton*, but these characters are plesiomorphic or of uncertain

polarity. Herein, *Tungussogyrinus* is thought to represent the closest relative of a clade including all other branchiosaurids with its placement outside the latter clade associated with a new feeding strategy to scrape algae with the tricuspid anterior dentition and the gracile snout region.

Shishkin (1998) re-established again the subfamily Tungussogyrininae Kuhn, 1962. This subfamily is newly defined here by the two unique features of *Tungussogyrinus bergi*: (1) Elongated anterodorsal process of the ilium; (2) Tricuspid anterior dentition, slightly built premaxillae, and large median intranasal and nasal fenestrae in the gracile snout region.

Consequently, all other branchiosaurid genera and species are included in the second subfamily Branchiosaurinae Fritsch, 1879 and are characterized by: (1) Ilium with short, equally long antero- and posterodorsal processes (without an elongated anterodorsal process); (2) Monocuspid dentition and a more robust snout region.

Palaeoecology and palaeobiogeography of *Tungussogyrinus*

Tungussogyrinus bergi was most probably a neotenic form. It shows the characteristic combination of external gills, branchial denticles and the ossified hyobranchial apparatus as known from almost all branchiosaurids (Boy & Sues 2000). However, the branchiosaurid species *Melanerpeton gracile* from the Rotliegend (Lower Permian) of the Döhlen-Basin is known from a unique metamorphosed population (Werneburg 1991). All other branchiosaurid species demonstrate neoteny.

The tricuspid teeth of the anterior dentition may have been useful to scrape algae in water as known from fishes (e.g. for extant cyprinodontiforms, personal communication with B. Reichenbacher, Munich). The premaxilla is consistently gracile and the intranarial fossa is large. Therefore this premaxilla is not robust enough for carnivorous feeding with hard shells. A comparable feeding strategy is known from extant larval lissamphibians using multicuspid tooth like structures. The tadpoles of *Bufo americanus* probably scrape algae too (Tubbs et al. 1993).

Relatively short external gills are recorded in *Tungussogyrinus bergi*. This feature is an important character of the ecomorphotype stream type (Duellman & Trueb 1986). The shape of the caudal fin, the second character of this ecotype, is not preserved in the Siberian material. However, it is very likely that the known population of *Tungussogyrinus bergi* belongs to the stream type (compare with Werneburg 2002), and inhabited water with a high content of oxygen as indicated by the short external gills (Duellman & Trueb 1986). It is known from extant larvae of salamanders that the stream type forms often crawl on the substratum (Duellman & Trueb 1986) which is compatible with the proposed feeding strategy of algae grazer in *Tungussogyrinus bergi*. Ponds, small lakes or parts of larger lakes, as well as flood plains and river channels, are environments usually inhabited by the stream type larvae, whereas the high content of oxygen is decisive.

Lakes of small size and high content of oxygen were likely part of the environment inhabited by the branchiosaurid *Tungussogyrinus bergi*, which may have especially occupied the benthic zone of the water. The sediments of localities that yielded specimens of *Tungussogyrinus* are mostly laminated siltstone with grey (from water with higher content of oxygen) and brown beds (with higher organic content and more anaerobic conditions). Many ostracods and conchostracans co-occur with the amphibian skeletons on the same bedding plane (Fig. 6E), which indicates good living conditions in the benthic zone of the lake.

Branchiosaurids are r-strategists using neoteny, a small size and a high reproductive rate (Boy & Sues 2000) and can be regarded as an evolutionary successful clade. *Tungussogyrinus* represents a relict of this earlier Late Pennsylvanian/Early Permian radiation, surviving nearly 30–40 million years and having colonized the Siberian area about eight thousand kilometres away from the probable area of branchiosaurid origination in the Central Pangean Mountains according to its oldest fossil record (*Branchiosaurus salamandroides* from the Westphalian D of the West Bohemian Basin; Werneburg 1987, 1988d). The palaeoposition of Siberia was close to the North Pole at the time of the Permo-Triassic boundary (after C. R. Scotese: Paleomap web site: www.scotese.com), but according to recorded plant fossils the climatic conditions were similar to the climate of the Central Pangean Mountains close to the palaeoequator. The occurrence of *Tungussogyrinus bergi* in Siberia is the northern-most and eastern-most of branchiosaurids. The western-most and southern-most occurrences of branchiosaurids are documented by the branchiosaurid *"Milnererpeton"* Hunt et al., 2002 from Late Pennsylvanian strata of New Mexico (Hunt et al. 1996; Werneburg & Lucas 2007). The branchiosaurid occurrences in Europe reach from Sardinia in the south (Werneburg et al. 2007) to Central Germany in the north (Werneburg 1996), and from the French basins (Werneburg 2003) in the west up to the Czech basins in the east (Werneburg 1986a).

Summary

The Late Permian or Early Triassic *Tungussogyrinus bergi* of Siberia may belong, together with *Micropholis* Huxley, 1860 from the Early Triassic of South Africa, to the stratigraphically youngest dissorophoid amphibians. Therefore its taxonomic status as well as the relationship of the mostly Permocarboniferous branchiosaurids to the lissamphibians are of special interest.

This study provides new information, complementing Shishkin's (1998) study, including the description and illustration of eight additional specimens. A reconstruction of the dorsal and palatal view of the skull, as well as the

hyobranchial skeleton, is presented (Figs 1, 8). Tricuspid teeth and their distribution in the jaws of *Tungussogyrinus* are reinvestigated, clearly demonstrating their tricuspid condition rather than bicuspid, as presumed by Shishkin (1998). The shape of branchial denticles, stapes, and pineal organ sac is described for the first time, as is the postcranial anatomy showing the unique shape of the ilium, the forelimb (with questionable dimorphism) and scales. Comparisons of *Tungussogyrinus* concerning the ecomorphic type of branchiosaurids, the ontogenetic and morphogenetic development of the hyobranchial skeleton, the stapes, the dentition, the neural arch, the forelimb, and the ilium facilitated deeper understanding of its morphology (Figs 7–13).

Tungussogyrinus bergi is a valid species and genus and clearly belongs to the family Branchiosauridae. The Siberian species is characterised by an elongated anterodorsal process of the ilium. The tricuspid teeth are a unique character within dissorophoids. *Tungussogyrinus* displays characters of the closely related taxa and shares a number of characters with *Melanerpeton*, *Apateon* and especially *Apateon dracyiensis* from the Permo-Carboniferous, but these characters are plesiomorphic or of uncertain polarity. *Tungussogyrinus* is the closest relative of a clade including all other branchiosaurids. Therefore, the concept of the subfamilies Tungussogyrininae Kuhn, 1962 and Branchiosaurinae Fritsch, 1879 is established.

The amphibamids and branchiosaurids may both be closely related to the Lissamphibia (Anderson et al. 2008a, 2008b; Carroll 2004, 2007a, 2007b; Schoch & Milner 2008). They share many different characters of anurans as well as urodelans and albanerpetontids. *Tungussogyrinus bergi* exposed an additional derived feature, which is similar to proanurans: the elongated anterodorsal process of the ilium (Fig. 13).

Tungussogyrinus bergi was probably a neotenic form with external gills, branchial denticles and ossified hyobranchial apparatus, as were most other branchiosaurids. The Siberian species developed a new unique feeding strategy among branchiosaurids and other temnospondyls. The specimens may have scraped algae with the tricuspid anterior dentition. The premaxilla is lightly built and the anterior opening is large, in agreement with this feeding strategy. These branchiosaurids may have lived in small lakes with a high content of oxygen in the benthic zone. The Tunguska Basin in Central Siberia contains the most northern and most eastern occurrence of branchiosaurid amphibians.

Acknowledgements

References

Amalitzky, W. P. 1921. Dvinosauridae: North Dvina Excavations of Prof. Amalitzky. Russian Akademii Nauk, Petrograd.

Ammon, L. 1889. Die permischen Amphibien der Rheinpfalz. Straub, München.

Anderson, J. S. 2007. Incorporating ontogeny into the matrix: a phylogenetic evaluation of developmental evidence for the origins of modern amphibians. *In* Anderson, J. S. & Sues, H.-D. (eds). Major Transitions in Vertebrate Evolution. Indiana University Press, Bloomington: pp. 182–227.

Anderson, J. S., Henrici, A. C., Sumida, S. S., Martens, T. & Berman D. S. 2008a. *Georgenthalia clavinasica*, a new genus and species of dissorophoid temnospondyl from the Early Permian of Germany, and the relationships of the family Amphibamidae. – Journal of Vertebrate Paleontology 28 (1): 61–75.

Anderson, J. S., Reisz, R. R., Scott, D., Fröbisch, N. B. & Sumida, S. S. 2008b. A stem batrachian from the Early Permian of Texas and the origin of frogs and salamanders. – Nature 453: 515–518.

Beneski, J. T. Jr. & Larsen, J. H. Jr. 1989. Interspecific, ontogenetic, and life history variation in the tooth morphology of mole salamanders (Amphibia, Urodela, and Ambystomatidae). – Journal of Morphology 199: 53–69.

Bolt, J. R. 1969. Lissamphibian origins: possible protolissamphibian from the Lower Permian of Oklahoma. – Science 166: 888–891.

Bolt, J. R. 1977. Dissorophoid relationships and ontogeny, and the origin of the Lissamphibia. – Journal of Paleontology 51: 235–249.

Bolt, J. R. 1979. *Amphibamus grandiceps* as a juvenile dissorophid: evidence and implications. *In* Nitecki, M. H. (ed.). Mazon Creek Fossils. Academic Press, New York: pp. 529–563.

Bolt, J. R. 1991. Lissamphibian Origins. *In* Schultze, H.-P. & Trueb, L. (eds). Origins of the higher groups of tetrapods: controversy and consensus. Cornell University Press, New York: pp. 194–222.

Boy, J. A. 1972. Die Branchiosaurier (Amphibia) des saarpfälzischen Rotliegenden (Perm, SW-Deutschland). – Hessisches Landesamt für Bodenforschung 65: 1–137.

Boy, J. A. 1974. Die Larven der rhachitomen Amphibien (Amphibia, Temnospondyli, Karbon-Trias). – Paläontologische Zeitschrift 48: 236–268.

Boy, J. A. 1978. Die Tetrapodenfauna (Amphibia, Reptilia) des Saarpfälzischen Rotliegend (Unterperm, SW-Deutschland) 1. *Branchiosaurus*. – Mainzer Geowissenschaftliche Mitteilungen 7: 27–76.

Boy, J. A. 1986. Studien über die Branchiosauridae (Amphibia: Temnospondyli). 1. Neue und wenig bekannte Arten aus dem mitteleuropäischen Rotliegenden. – Paläontologische Zeitschrift 60: 131–166.

Boy, J. A. 1987. Studien über die Branchiosauridae (Amphibia: Temnospondyli, Ober-Karbon – Unter-Perm). 2. Systematische Übersicht. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 174 (1): 75–104.

Boy, J. A. 1993. Evolution bei Amphibien. – Veröffentlichungen Übersee-Museum Bremen, Naturwissenschaften 11: 27–40.

Boy, J. A. & Sues, H.-D. 2000. Branchiosaurs: Larvae, Metamorphosis and Heterochrony in Temnospondyls and Seymouriamorphs. *In* Heatwole, H. & Carroll, R. L. (eds). Amphibian Biology, vol. 4, Palaeontology. Surrey Beatty & Sons, Chipping Norton: pp. 1150–1197.

Bystrow, A. P. 1939. Blutgefäßsystem der Labyrinthodonten (Gefäße des Kopfes). – Acta Zoologica 20: 125–155.

Carroll, R. L. 1991. *Batropetes* from the Lower Permian of Europe – a microsaur, not a Reptile. – Journal of Vertebrate Paleontology 11: 229–242.

Carroll, R. L. 2001. The origin and early radiation of terrestrial vertebrates. – Journal of Paleontology 75: 1202–1213.

Carroll, R. L. 2004. The importance of branchiosaurs in determining the ancestry of the modern amphibian orders. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 232: 157–180.

Carroll, R. L. 2007a. The Palaeozoic ancestry of salamanders, frogs, and caecilians. – Zoological Journal of the Linnean Society 150 (Suppl. 1): 1–140.

Carroll, R. L. 2007b. Dissorophoids as a uniquely informative model for the study of patterns, processes, and rates of vertebrate evolution. – Journal of Vertebrate Paleontology 27 (suppl. to 3): 56A.

Carroll, R. L., Bossy, K. A., Milner, A. C., Andrews, S. M. & Wellstead, C. F. 1998. Lepospondyli. *In* Wellnhofer, P. (ed.). Encyclopedia of Palaeoherpetology, part 1. Verlag Dr. Friedrich Pfeil, München: pp. 1–220.

Carroll, R. L. & Gaskill, P. 1978. The order Microsauria. – American Philosophical Society 126: 1–211.

Carroll, R. L., Kuntz, A. & Albright, K. 1999. Vertebral development and amphibian evolution. – Evolution & Development 1: 36–48.

Case, E. C. 1910. New or little known reptiles and amphibians from the Permian (?) of Texas. – Bulletin of the American Museum of Natural History 28: 163–181.

Cosgriff, J. W. 1969. *Blinasaurus*, a brachyopid genus from Western Australia and New South Wales. – Journal of the Royal Society of Western Australia 52 (3): 65–88.

Credner, H. 1881. Die Stegocephalen (Labyrinthodonten) aus dem Rothliegenden des Plauen'schen Grundes. 1. Theil. – Zeitschrift der Deutschen geologischen Gesellschaft 33: 298–333.

David, A. 1875. Journal de mon troisieme voyage d'exploration dans l'Empire Chinois. Librairie Hachette, Paris.

Duellmann, W. E. & Trueb, L. 1986. Biology of Amphibians. Mc Graw-Hill, New York.

Dumeril, A. M. C. & Bibron, G. 1841. Erpétologie générale ou histoire naturelle complètes des reptiles. Vol. 8. Librairie encyclopédique de Roret, Paris.

Efremov, J. A. 1939. First Representative of Siberian Early Tetrapoda. – Comptes Rendus de l'Academie des Sciences de l'URSS 23: 106–110.

Efremov, J. A. 1953. The second find of a Permian amphibian in the Tunguska Basin of Siberia. – Doklady Akademy Nauk SSSR, Novy Serii 91 (4): 943–946.

Estes, R. & Hoffstetter, R. 1976. Les Urodèles du Miocène de La Grive-Saint-Alban (Isère, France). – Bulletin du Museum National d'Histoire Naturelle, 3e Serie 398: 297–343.

Evans, S. E. & Borsuk-Białynicka, M. 1998. A stemgroup frog from the Early Triassic of Poland. – Acta Palaeontologica Polonica 43: 573–580.

Fritsch, A. 1876. Über die Fauna der Gaskohle des Pilsener und Rakonitzer Beckens. – Sitzungsberichte der königlich-böhmischen Akademie der Wissenschaften 1875: 70–79.

Fritsch, A. 1878. O novém ještěrů z permských vápenců u Broumovo. – Vesmír 7: 249.

Fritsch, A. 1879. Neue Übersicht der in der Gaskohle und den Kalksteinen der Permformation in Böhmen vorgefundenen Tierreste. – Sitzungsberichte der königlichen böhmischen Gesellschaft der Wissenschaften 1879: 184–195.

Fröbisch, N. B. & Reisz, R. R. 2007. A new Lower Permian amphibamid (Dissorophoidea, Temnospondyli) from the Fissure Fill deposits near Richards Spur, Oklahoma. – Journal of Vertebrate Paleontology 27 (suppl. to 3): 78A.

Gardner, J. D. 2001. Monophyly and affinities of albanerpetontid amphibians (Temnospondyli; Lissamphibia). – Zoological Journal of the Linnean Society 131: 309–352.

Gardner, J. D., Evans, S. E. & Sigogneau-Russell, D. 2003. New albanerpetontid amphibians from the Early Cretaceous of Morocco and Middle Jurassic of England. – Acta Palaeontologica Polonica 48 (2): 301–319.

Geinitz, H. B. & Deichmüller, J. V. 1882. Nachträge zur Dyas II. Mitteilungen aus dem königlichen mineralogisch-geologischen und praehistorischen Museum in Dresden, 5. Heft, VIII: Die Saurier der unteren Dyas von Sachsen. – Palaeontographica, Neue Folge 9, VIII: 1–46.

Herrmann, H.-J. & Kabisch, K. 1992. Investigations on ranid larvae in Southern Sakhalin Island, Russia. – Asiatic Herpetological Research 4: 68–75.

Holbrook, J. E. 1836. North American herpetology, vol. 1. Dobson, Philadelphia.

Hunt, A., Lucas, S. G. & Berman, D. S. 1996. A new amphibamid (Amphibia Temnospondyli) from the Late Pennsylvanian of central New Mexico, USA. – Paläontologische Zeitschrift 70: 555–565.

Hunt, A., Lucas, S. G. & Berman, D. S. 2002. *Milnererpeton*, a replacement name fort he temnospondyl genus *Milneria*. – Paläontologische Zeitschrift 76: 125–126.

Huttenlocker, A. K., Small, B. J. & Pardo, J. D. 2007. *Plemmyradytes shintoni*, gen. et sp. nov., an Early Permian amphibamid (Temnospondyli: Dissorophoidea) from the Eskridge Formation, Nebraska. – Journal of Vertebrate Paleontology 27: 316–328.

Huxley, T. H. 1860. On some Amphibian and Reptilian Remains from South Africa and Australia. – Quarterly Journal of the Geological Society London XV: 642–658.

Kuhn, O. 1962. Die vorzeitlichen Frösche und Salamander, ihre Gattungen und Familien. – Jahrbuch des Vereins Vaterländischer Naturkunde Württemberg 117: 327–372.

Kuhn, O. 1965. Die Amphibien. System und Stammesgeschichte. Oeben, Krailling bei München.

Langston, W. Jr. & Olson, E. C. 1986. *Carrolla craddocki*, a new genus and species of microsaur from the Lower Permian of Texas. – Pearce-Sellards-Series 43: 1–20.

Meyer, H. v. 1844. [Briefliche Mitteilung an Professor Bronn]. – Neues Jahrbuch für Mineralogie 1844: 336–337.

Milner, A. R. 1988. The relationships and origin of living amphibians. *In* Benton, M. J. (ed.). The Phylogeny and Classification of the Tetrapods Vol. 1: Amphibians, Reptiles, Birds. Systematic Associations Special Volume 35A, London: pp. 59–102.

Olson, E. C. 1962. Late Permian terrestrial vertebrates, USA and USSR. – American Philosophical Society, Transactions, new Series 52: 1–224.

Pfannenstiel, M. 1932. Gehirnkapsel und Gehirn fossiler Amphibien. – Monographien zur Geologie und Paläontologie 2 (6): 1–85.

Piveteau, J. 1936a. Une forme ancestrale des Amphibiens Anoures dans le Trias inférieur de Madagascar. – Comptes rendus hebdomadaires des séances de l'Académie des Sciences 19: 1607–1608.

Rage, J. G. & Roček, Z. 1989. Redescription of *Triadobatrachus massinoti* (Piveteau, 1936), an anuran amphibian from the early Triassic. – Palaeontographica A 206: 1–16.

Roček, Z. & Rage, J. G. 2000. Proanuran stages (*Triadobatrachus, Czatkobatrachus*). *In* Heatwole, H. & Carroll, R. L. (eds). Amphibian Biology, vol. 4, Palaeontology. Surrey Beatty & Sons, Chipping Norton: pp. 1283–1294.

Romer, A. S. 1947. Review of the Labyrinthodontia. – Bulletin of the Museum of Comparative Zoology, Harvard 99 (1): 1–368.

Romer, A. S. 1966. Vertebrate paleontology. University of Chicago Press, Chicago.

Ruta, M. & Coates, M. I. 2007. Dates, nodes and character conflict: addressing the lissamphibian origin problem. – Journal of Systematic Palaeontology 5: 69–122.

Ruta, M., Coates, M. I. & Quicke, D. L. 2003. Early tetrapod relationships revisited. – Biological Reviews 78: 251–345.

Schoch, R. R. & Carroll, R. L. 2003. Ontogenetic evidence for the Paleozoic ancestry of salamanders. – Evolution & Development 5 (3): 314–324.

Schoch, R. R. 2006. Skull ontogeny: developmental patterns of fishes conserved across major tetrapod clades. – Evolution & Development 8: 524–536.

Schoch, R. R. & Fröbisch, N. B. 2006. Metamorphosis and neoteny: alternative pathways in an extinct amphibian clade. – Evolution 60 (7): 1467–1475.

Schoch, R. R. & Milner, A. R. 2008. The intrarelationships and evolutionary history of the temnospondyl family Branchiosauridae. – Journal of Systematic Palaeontology 2008: 1–23.

Schoch, R. R. & Rubidge, B. S. 2005. The amphibamid *Micropholis* from the *Lystrosaurus* Assemblage Zone of South Africa. – Journal of Vertebrate Paleontology 25: 502–522.

Shishkin, M. A. 1964. Stereospondyli. *In* Orlov, J. A. (ed.). [Fundamentals of Paleontology: Amphibians, Reptiles and Birds]. Nauka, Moscow: pp. 83–122. [In Russian]

Shishkin, M. A. 1973. (Morphology of Early Amphibians and the Evolutionary Problems in the Lower Tetrapods). – Trudy Paleontologisheski Institut Akademiya Nauk SSSR 137: 1–260. [In Russian]

Shishkin, M. A. 1998. *Tungussogyrinus* – A relict neotenic dissorophoid (Amphibia, Temnospondyli) from the Permo-Triassic of Siberia. – Paleontological Journal 32 (5): 521–531.

Sytchevskaya, E. K. 1999. Freshwater fish fauna from the Triassic of Northern Asia. *In* Arratia, G. & Schultze, H.-P. (eds). Mesozoic Fishes 2: Systematics and the fossil record. Verlag Dr. Friedrich Pfeil, München: pp. 445–468.

Trueb, L. O. E. & Cloutier, R. 1991. A Phylogenetic Investigation of the Inter- and Intra-relationships of the Lissamphibia (Amphibia: Temnospondyli). *In* Schultze, H.-P. & Trueb, L. (eds). Origins of the Higher Groups of Tetrapods: Controversy and Consensus. Cornell University Press, New York: pp. 223–313.

Tubbs, L. O. E., Stevens, R., Wells, M. & Altig, R. 1993. Ontogeny of the oral apparatus of the tadpole of *Bufo americanus*. – Amphibia-Reptilia 14: 333–340.

Wake, M. H. 2003. The osteology of caecilians. *In* Heatwole, H. & Davis, M. (eds). Amphibian Biology, vol. 5: Osteology. Surrey Beatty & Sons, Chipping Norton: pp. 1809–1876.

Werneburg, R. 1986a. Branchiosaurier aus dem Rotliegenden (Unterperm) der ČSSR. – Zeitschrift für geologische Wissenschaften 14 (6): 673–686.

Werneburg, R. 1986b. Die Stegocephalen (Amphibia) der Goldlauterer Schichten (Unterrotliegendes, Perm) des Thüringer Waldes, Teil I: *Apateon flagrifer* (Whitt.). – Freiberger Forschungshefte C 410: 87–100.

Werneburg, R. 1987. Dissorophoiden (Amphibia, Rhachitomi) aus dem Westfal D (Oberkarbon) der ČSSR. *Branchiosaurus salamandroides* Fritsch 1876. – Zeitschrift für geologische Wissenschaften 15 (6): 681–690.

Werneburg, R. 1988a. Die Stegocephalen der Goldlauterer Schichten (Unterrotliegendes, Unterperm) des Thüringer Waldes, Teil II: *Apa-*

teon kontheri n. sp., *Melanerpeton eidfeldi* n. sp. und andere. – Freiberger Forschungshefte C 427: 7–29.

Werneburg, R. 1988b. Die Stegocephalen (Amphibia) der Goldlauterer Schichten (Unterrotliegendes, Unterperm) des Thüringer Waldes, Teil III: *Apateon dracyiensis* (Boy), *Branchierpeton reinholdi* n. sp. und andere. – Veröffentlichungen Naturkundemuseum Erfurt 7: 80–96.

Werneburg, R. 1988c. Die Amphibienfauna der Oberhöfer Schichten (Unterrotliegendes, Unterperm) des Thüringer Waldes. – Veröffentlichungen Naturhistorisches Museum Schleusingen 3: 2–27.

Werneburg, R. 1988d. Paläobiogeographie der labyrinthodonten Amphibien im Oberkarbon und Rotliegenden Mitteleuropas. – Zeitschrift für geologische Wissenschaften 16 (9): 929–932.

Werneburg, R. 1989. Labyrinthodontier (Amphibia) aus dem Oberkarbon und Unterperm Mitteleuropas – Systematik, Phylogenie und Biostratigraphie. – Freiberger Forschungshefte C 436: 7–57.

Werneburg, R. 1991. Die Branchiosaurier aus dem Unterrotliegend des Döhlener Beckens bei Dresden. – Veröffentlichungen Naturhistorisches Museum Schleusingen 6: 75–99.

Werneburg, R. 1996. Temnospondyle Amphibien aus dem Karbon Mitteldeutschlands. – Veröffentlichungen Naturhistorisches Museum Schleusingen 11: 23–64.

Werneburg, R. 2001. *Apateon dracyiensis* – eine frühe Pionierform der Branchiosaurier aus dem Europäischen Rotliegend, Teil 1: Morphologie. – Veröffentlichungen Naturhistorisches Museums Schleusingen 16: 17–36.

Werneburg, R. 2002. *Apateon dracyiensis* – eine frühe Pionierform der Branchiosaurier aus dem Europäischen Rotliegend, Teil 2: Paläoökologie. – Veröffentlichungen Naturhistorisches Museum Schleusingen 17: 17–32.

Werneburg, R. 2003. The branchiosaurid amphibians from the Lower Permian of Buxières-les-Mines, Bourbon ĺArchambault Basin (Allier, France) and their biostratigraphic significance. – Bulletin Société Géologique de France 174 (4): 343–349.

Werneburg, R. & Lucas, S. 2007. "*Milnererpeton*" from the Late Pennsylvanian of New Mexico is the first truly "European branchiosaurid" from North America. – Journal of Vertebrate Paleontology 27 (suppl. to 3): 164A.

Werneburg, R., Ronchi, A. & Schneider, J. W. 2007. The lower Permian branchiosaurids (Amphibia) of Sardinia (Italy): systematic palaeontology, palecology, biostratigraphy and palaeobiogeographic problems. – Palaeogeography, Palaeoclimatology, Palaeoecology 252 (2007): 383–404.

Werneburg, R. & Schneider, J. W. 2006. Amphibian biostratigraphy of the European Permocarboniferous. *In* Lucas, S. G., Schneider, J. W. & Cassinis, G. (eds). Nonmarine Permian Chronology and Correlation. Geological Society of London: pp. 201–215.

Whittard, W. F. 1930: The structure of *Branchiosaurus flagrifer* sp. n., and further notes on *Branchiosaurus amblystomus* Credner. – Annual Magazine Natural History London 10 (5): 500–513.

Zittel, K. von. 1888. Handbuch der Paläontologie. I. Abt. Paläozoologie. 3. Teil: Vertebrata (Pisces, Amphibia, Reptilia). R. Oldenbourg, München, Leipzig.