

A new stereospondyl from the German Middle Triassic, and the origin of the Metoposauridae

RAINER R. SCHOCH*

Staatliches Museum für Naturkunde, Rosenstein 1, D-70191 Stuttgart, Germany

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Recent finds of well-preserved temnospondyl skeletons from the Lower Keuper (Ladinian, Middle Triassic) in southern Germany are assigned to a new genus and species, *Callistomordax kugleri*. This taxon is characterized by the following autapomorphies: (1) wide unpaired frontal; (2) vomerine fangs greatly enlarged to occupy entire width of element; (3) intercentra elongated and massive, anterior face being convex; (4) humerus semilunar with enlarged deltopectoral crest; (5) cleithrum strongly curved and bow-shaped; (6) trunk extremely elongated to reach three times the length of the skull. *Callistomordax* shares with the Metoposauridae the pattern of dermal ornamentation, the proportion of both posterior skull table and snout, the position of the lacrimal, the morphology of the basicranial region, and the structure of the clavicle and interclavicle. Phylogenetic analysis suggests *Callistomordax* to be the sister taxon of the Metoposauridae, nested within a grade formed by various trematosaurian taxa. In this assemblage, *Lyrocephaliscus* and a clade formed by *Almasaurus*, *Rileymillerus*, *Callistomordax*, and the Metoposauridae are sister taxa. In all variants of the cladistic analysis, *Callistomordax* and the Metoposauridae form immediate sister groups. According to the present findings, neither plagiosaurids nor brachyopoids and rhytidosteids are closely related to this ‘trematosaurian’ monophylum, although these taxa share a range of homoplasies. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, 152, 79–113.

ADDITIONAL KEYWORDS: *Callistomordax* – Keuper – Ladinian – phylogeny – Temnospondyli.

INTRODUCTION

Metoposaurids were large, 2–5-m long, stereospondyls exclusively known from the Upper Triassic (Hunt, 1993; Schoch & Milner, 2000). They were heavily ossified, salamander-like animals with flat skulls having small orbits located anterolaterally. The trunk was also mostly flattened and wide, with large, down-curved ribs and massive disc-shaped vertebral intercentra. In the Upper Triassic of North America and India, metoposaurids formed the only group of large temnospondyls, whereas in Europe they shared ecosystems with coeval cyclosteosaurids that were of similar size. Metoposaurids are so abundant in the North American Triassic that they have been proposed as biochronologically informative (Hunt, 1989). Recently, the group has again attracted attention, after new material emerged from the Middle Keuper facies in both Central and Eastern Europe (Sulej, 2002; Milner & Schoch, 2004).

The origin and phylogenetic relationships of metoposaurids have been debated for several decades, and their last revisor, Hunt (1993), discussed two widely diverging hypotheses of their relationships to other stereospondyls. One problem with this group is their evolutionary conservative, distinctive morphology that shows almost no plesiomorphic traits in any member of the clade. Another problem is the absence of any known stem-group representatives. Trimerorhachids and trematosaurians, two widely differing and distantly related temnospondyl clades, have been proposed as metoposaurid relatives (Hunt, 1993; Milner, 1990), but the actual evidence is rather poor, highlighting mostly superficial features such as the position of orbits or the elongated posterior skull table. Metoposaurids seemed to be a classic example of a clade in which the phylogeny can only be resolved by the discovery of new material.

In 1985, the experienced collector Werner Kugler of Crailsheim, southern Germany, recovered a temnospondyl skull from the Middle Triassic mudstones of the Lower Keuper (Erfurt Formation). As no

*E-mail: schoch.smns@naturkundemuseum-bw.de

other temnospondyls were known from that formation, except for the very different plagiosaurids (Hellrung, 2003), Kugler expected to have found a juvenile of a mastodonsaur, and indeed we know today that mastodonsaurid specimens of that size do occur. However, preparation revealed that the morphology differs from that of *Mastodonsaurus*, with the orbits set well anterior, the ornament involving high reticulate polygons, and the palate housing large laterally compressed fangs with strongly keeled anterior and posterior edges. The specimen was then given to the State Museum of Natural History at Stuttgart (SMNS), and in the course of a subsequent excavation at the same quarry in the year 2000, two other private collectors, Hans Michael Salomon and Traugott Haubold, collected two almost complete skeletons of the new animal lying in close proximity to one another. These specimens now form an excellent basis for the description of the new taxon.

Abbreviations used in the text: a, angular; ad-wi, adductor window; ap, anterior palatal window; ar, articular; at, atlas; at-na, atlantal neural arch; c1, anterior coronoid; c2, middle coronoid; c3, posterior coronoid; ch, choana; cl, clavicle; ct, cleithrum; d, dentary; dpc, deltopectoral crest; ec, ectopterygoid; eo, exoccipital; f, frontal; ha, haemal arch; hu, humerus; hy, hyobranchial element; ic, intercentrum; icg, intercondylar groove; icl, interclavicle; il, ilium; ju, jugal; la, lacrimal; m, maxilla; man, manus; me-wi, meckelian window; n, nasal; na, neural arch; oc-fl, occipital flange; p, parietal; par, prearticular; pc, processus cultriformis; pga, postglenoid area; pgp, preglenoid process; pl, palatine; pm, premaxilla; po, postorbital; pof, postfrontal; posp, postsplenic; pp, postparietal; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; ra, radius; sa, surangular; sc, scapulocoracoid; sp, splenic; sq, squamosal; st, supratemporal; ta, tabular; ul, ulna; vc, ventral crest; vo, vomer.

GEOLOGICAL SETTING

The type locality is a large limestone quarry near Vellberg in the Hohenlohe region of northern Baden-Württemberg (Brunner, 1973). Its richness in vertebrate fossils was first broadly acknowledged by private collectors in the early 1980s. The Lower Keuper is mostly exposed along the upper rim of the quarry, and, because only the limestones of the underlying Muschelkalk are economically significant, Lower Keuper sediments are usually destroyed by explosives, and the remaining debris is quickly removed. Therefore, articulated skeletons have been found mostly in focused excavations enabled and supported by the quarry owners.

In the type locality the fossil-bearing horizon forms part of a 1.5-m thick sequence of dark grey mudstones (Untere Graue Mergel sequence) wedged in between two hard carbonate layers, each 0.8–1.2-m thick. The fossiliferous bed is located near the top of the mudstone sequence, formed by a 50–150-mm-thick grey, decalcified clay rich in temnospondyl bones, skeletons of a tiny aquatic diapsid and scutes, and vertebrae of a small archosaur (Schoch, 2002a). The most frequent temnospondyls are *Mastodonsaurus giganteus* represented by various size classes, *Trematolestes hagdorni* (Schoch, 2006), and especially the new temnospondyl taxon to be described herein. In early 2000 an excavation yielded two articulated skeletons of the new taxon, in close proximity and aligned in parallel.

The mudstone sequence of the Untere Graue Mergel is generally believed to have formed under estuarine conditions, representing the brackish swamps and marshes that dominated much of southwestern Germany. The bivalve and ostracod faunas suggest a fluctuating salinity within that section, with the most fossiliferous beds having formed under oligohaline conditions. Although many vertebrate fossils in these beds are reworked, the remains of the new taxon are not: they constitute the most frequent finds of articulated material in the Vellberg quarry.

SYSTEMATIC PALAEOONTOLOGY

TEMNOSPONDYLI ZITTEL, 1888

STEREOSPONDYLI ZITTEL, 1888

TREMATOSAUROIDEA SÄVE-SÖDERBERGH, 1935

CALLISTOMORDAX GEN. NOV.

Etymology: *Callistos* (Greek: most beautiful), *mordax* (Latin: biting), in reference to the extraordinarily large fangs in the palate.

Type species: *Callistomordax kugleri* sp. nov. (by monotypy).

Diagnosis: As for the type and only species, given below.

CALLISTOMORDAX KUGLERI SP. NOV.

- | | | |
|------|---------------------------------|---------------------------------------|
| 1985 | 'Metoposaurier-Vorfahr' | Kugler & Bartholomä (1985: 16). |
| 1988 | 'oldest undoubted metoposaurid' | Morales (1988: 23a). |
| 1993 | 'probably a laticopid' | Hunt (1993: 90). |
| 1998 | Almasauridae gen. nov. sp. nov. | Schoch & Werneburg (1998: 637). |
| 2000 | Almasauridae gen. nov. sp. nov. | Schoch & Milner (2000: 120, fig. 85). |

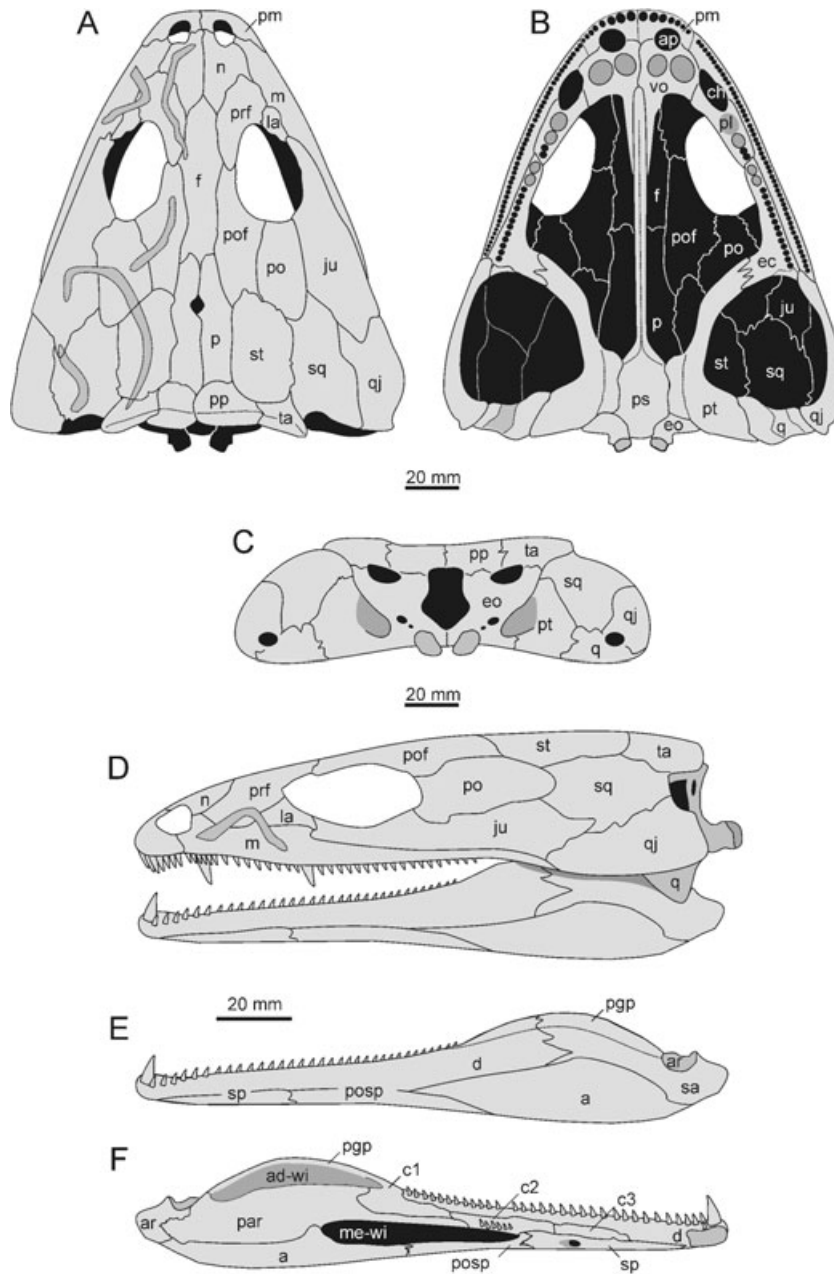


Figure 1. Skull reconstruction of *Callistomordax hugleri*. A, Skull roof (dorsal view); B, palate (ventral view); C, occiput (posterior view); D, skull and mandible (lateral view); E, mandible (lateral view); F, mandible (medial view). (Please refer to the list at the end of the Introduction for a definition of the abbreviations.)

Holotype: SMNS 82035, a nearly complete skeleton. The skull, exposed in dorsal view, has a length of 137 mm (from tip of premaxilla to back rim of post-parietal), and the length of the preserved skeleton is 1.23 m.

Type horizon: Top of Untere Graue Mergel (Bed 6 of Schoch, 2002a), Lower Keuper (Erfurt Formation), Longobardian (Upper Ladinian), Middle Triassic.

Type locality: Vellberg (Schumann quarry), northern Baden-Württemberg, southern Germany.

Referred material: From type locality: SMNS 90516, anterior two-thirds of skeleton with complete skull in dorsal view (153 mm); SMNS 55385, isolated, complete skull (148 mm; Figs 2A, 5); SMNS 90519, isolated left humerus (Fig. 7 D–F); SMNS 90520, parts of skeleton including well-preserved pectoral and

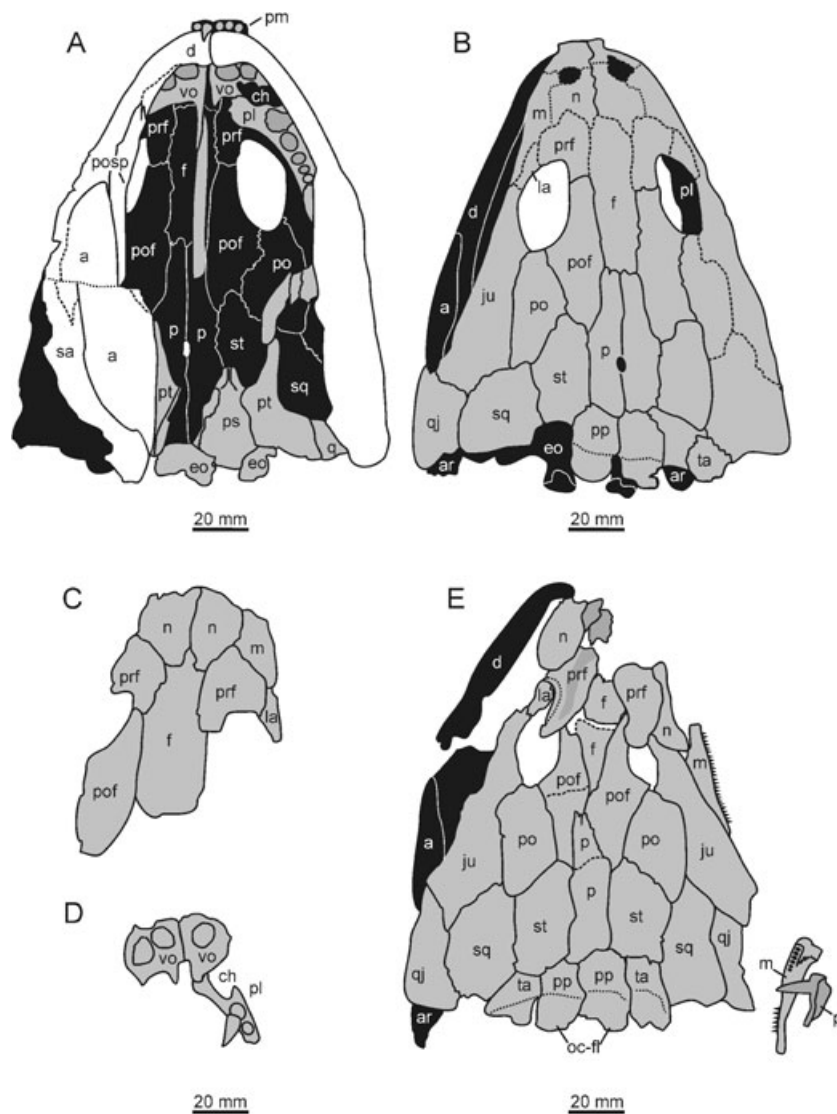


Figure 2. Skull material of *Callistomordax kugleri*. A, SMNS 55385 (ventral view); B, SMNS 55385 (dorsal view); C, SMNS 90520 (dorsal view); D, SMNS 90520 (ventral view); E, SMNS 82035 (type specimen, dorsal view). Dotted lines show poorly preserved sutures and/or fractures. (Please refer to the list at the end of the Introduction for a definition of the abbreviations.)

pelvic girdle (Fig. 7A, B, H, I) and crushed skull (145 mm); SMNS 90700, articulated skeleton lacking posterior half of tail, but including well-preserved girdles, appendages, and skull (125 mm) in ventral view (Fig. 7C); MHI-K1, a nearly complete postcranial skeleton including one humerus and both hind limbs; MHI-K2, fairly complete, small postcranial skeleton with pectoral girdle; MHI-K3, disarticulated large postcranial skeleton with scapulocoracoid (Fig. 7G), interclavicle, humerus, radius, and ilium; MHI-K4, small skull (95 mm); MHI-K5, slightly disarticulated skull with good snout region (160 mm). From Ummenhofen quarry: SMNS 90506, posterior part of trunk, pelvic elements, and hind limb (Fig. 9). From

Kupferzell locality: SMNS 81713, isolated articular; SMNS 84115–84118, 90521, isolated intercentra (Fig. 8C–L); SMNS 84119, atlas (Fig. 8A, B).

Stratigraphic range: Albertibank through Untere Graue Mergel, Lower Keuper (Erfurt Formation), Langobardian, Middle Triassic.

Etymology: In honour of Werner Kugler, private collector of Crailsheim, who found and prepared the first specimen. His general contributions to our understanding of Lower Keuper vertebrates have been outstanding.

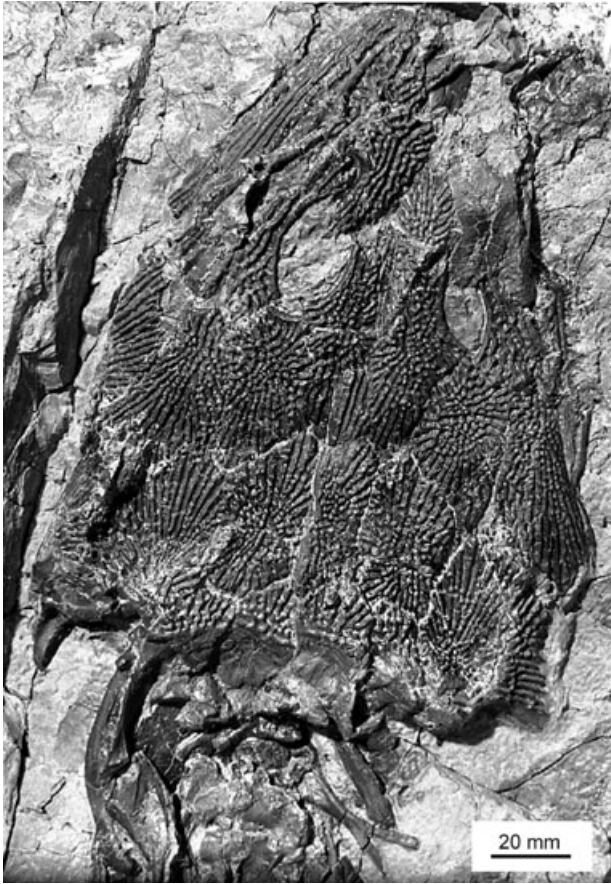


Figure 3. *Callistomordax kugleri*, skull of the type specimen SMNS 82035 (dorsal view).

Diagnosis: Autapomorphic character states are as follows: (1) frontals co-ossified, with single medial anterior tip and blunt posterior end (Figs 1A, 4B); (2) pterygoid distinct by very broad and flat quadrate ramus combined with a particularly slender and narrow palatine ramus (Figs 1B, 5); (3) subtemporal windows nearly round and wider than the basicranial region (Fig. 1B); (4) anterior palate very short, with vomers and palatines dominated by huge fangs the sockets of which occupy most of the bone surfaces, and minute, obliquely orientated choanae (Figs 1B, 5); (5) palatal and symphyseal fangs laterally compressed and keeled; (6) intercentra forming open crescents with high flanks (except when fused to pleurocentra, then giving a disc-shaped compound bone, see Fig. 8C, D) with pointed upper ends and a massive, anteroposteriorly elongated ventral portion that has a quadrangular outline (Fig. 8C–J); (7) shaft of cleithrum curved in semilunar fashion (Fig. 7H, I).

Derived characters shared with other taxa:

1. *Callistomordax* and the Metoposauridae: clavicle extending well posteriorly on interclavicle, with

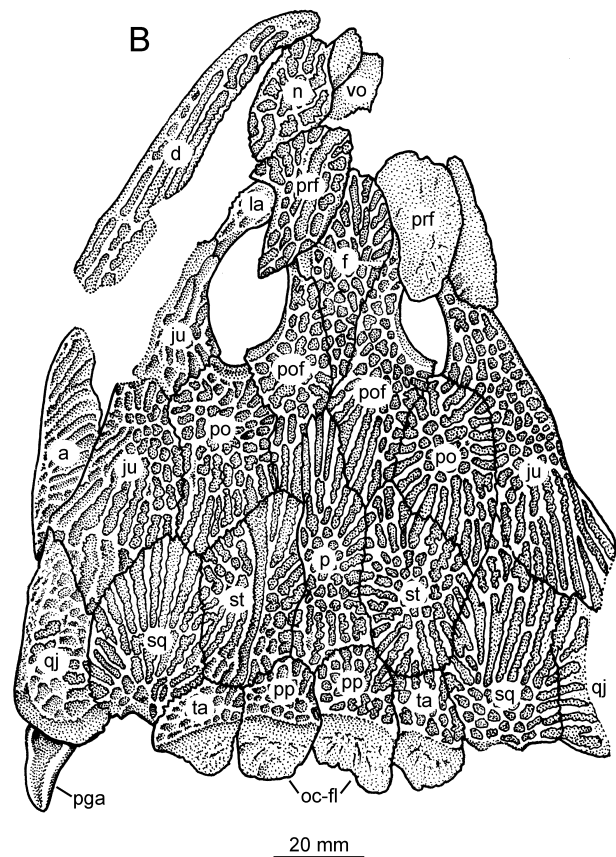
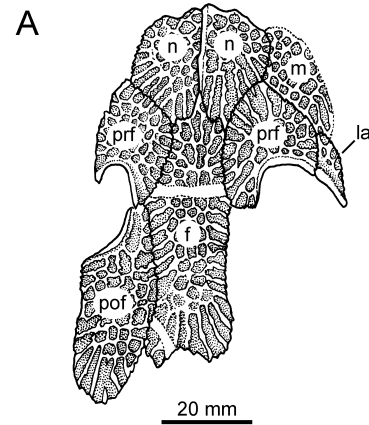


Figure 4. Skull material of *Callistomordax kugleri*. A, SMNS 90520 (dorsal view); B, SMNS 82035 (dorsal view). (Please refer to the list at the end of the Introduction for a definition of the abbreviations.)

the radial arrangement of the ornament pointing posteromedially.

2. *Callistomordax*, *Rileymillerus*, and the Metoposauridae: lacrimal forms small element confined to the anterolateral margin of the orbit [Bolt & Chatter-

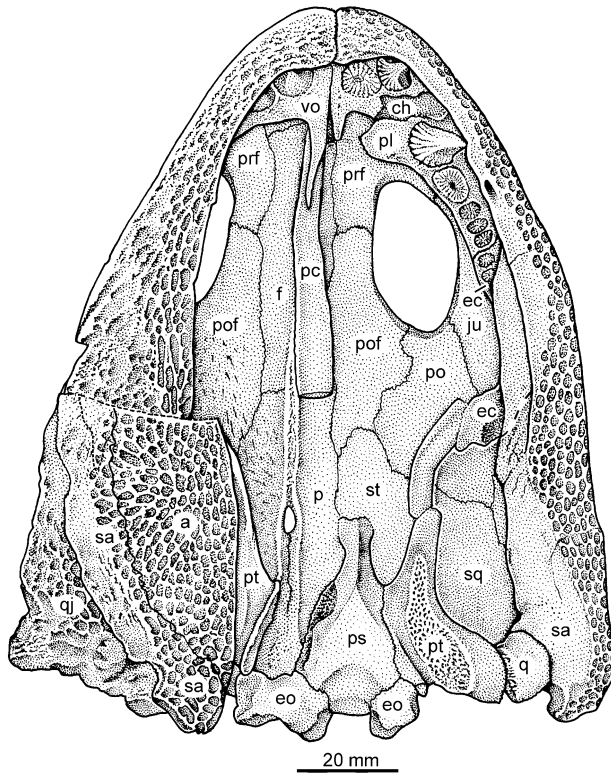


Figure 5. *Callistomordax kugleri*, structure of palate and mandible exemplified by SMNS 55385 (ventral view). (Please refer to the list at the end of the Introduction for a definition of the abbreviations.)

jee, 2000 regarded this as a lateral exposure of the palatine (LEP), in analogy with dissorophoids].

3. *Callistomordax* and *Almasaurus*: cultriform process forms a prominent ventral keel, which rises from a ridge on the anterior portion of the basal plate, and terminates shortly posterior to the point where the parasphenoid is framed by posteromedial processes of the vomers; snout narrow, with the nares in the terminal position and located in close proximity.

Trigonosternum latum: Schmidt (1931) described and named a partial interclavicle from the Lower Keuper of Kölleda in Thuringia (Germany) as a new genus and species, *T. latum*, which he referred to the Metoposauridae. Colbert & Imbrie (1956) have argued that the assignment of this fragment to metoposaurids is based on a misinterpretation caused by a wrong orientation of the interclavicle, which is followed here. The type and only specimen is not only indeterminate, but differs from the interclavicle of *C. kugleri* in ornamentation and overall shape (Werneburg, 1990; Schoch & Milner, 2000).

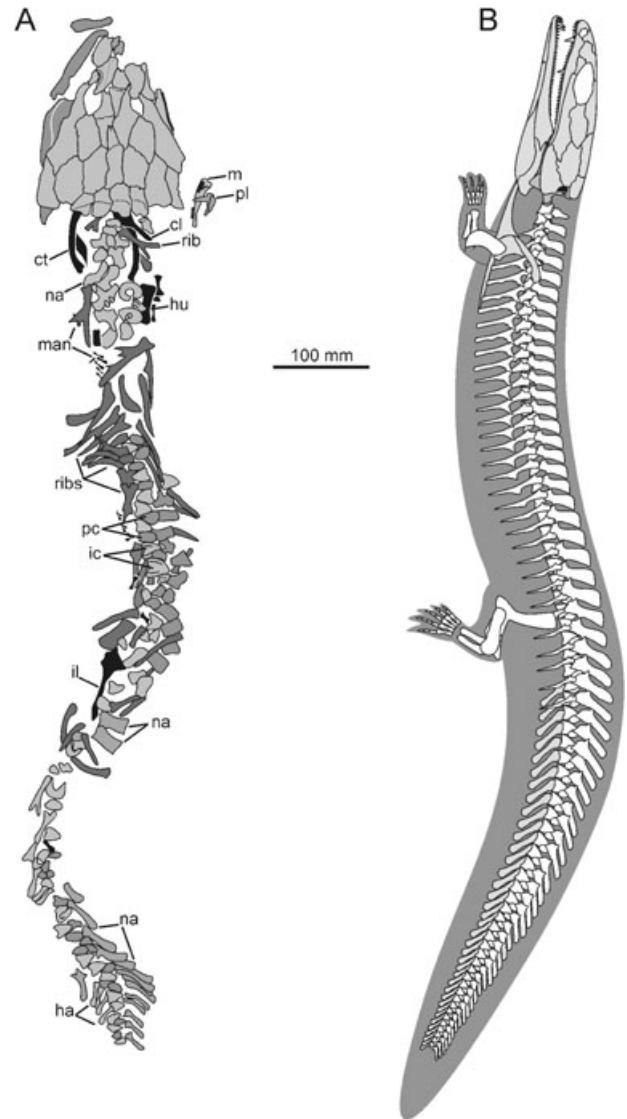


Figure 6. Complete skeleton of *Callistomordax kugleri*. A, SMNS 82035 (dorsal view), with bones from different regions marked in shades of grey (limbs and girdles, black; pleurocentra, neural arches, and ribs, dark grey; intercentra and haemal arches, light grey); B, restoration based on A and SMNS 90516, SMNS 90700, and MHI-K3. (Please refer to the list at the end of the Introduction for a definition of the abbreviations.)

DESCRIPTION

GENERAL

The entire skeleton is preserved apart from the tip of the tail and part of the braincase. The holotype preserves the skull roof and most of the postcranium, although in places disarticulation of the limbs and girdles obscures a few elements (Fig. 6A). This information is complemented by five additional articulated specimens. In SMNS 90516 the anterior two thirds of

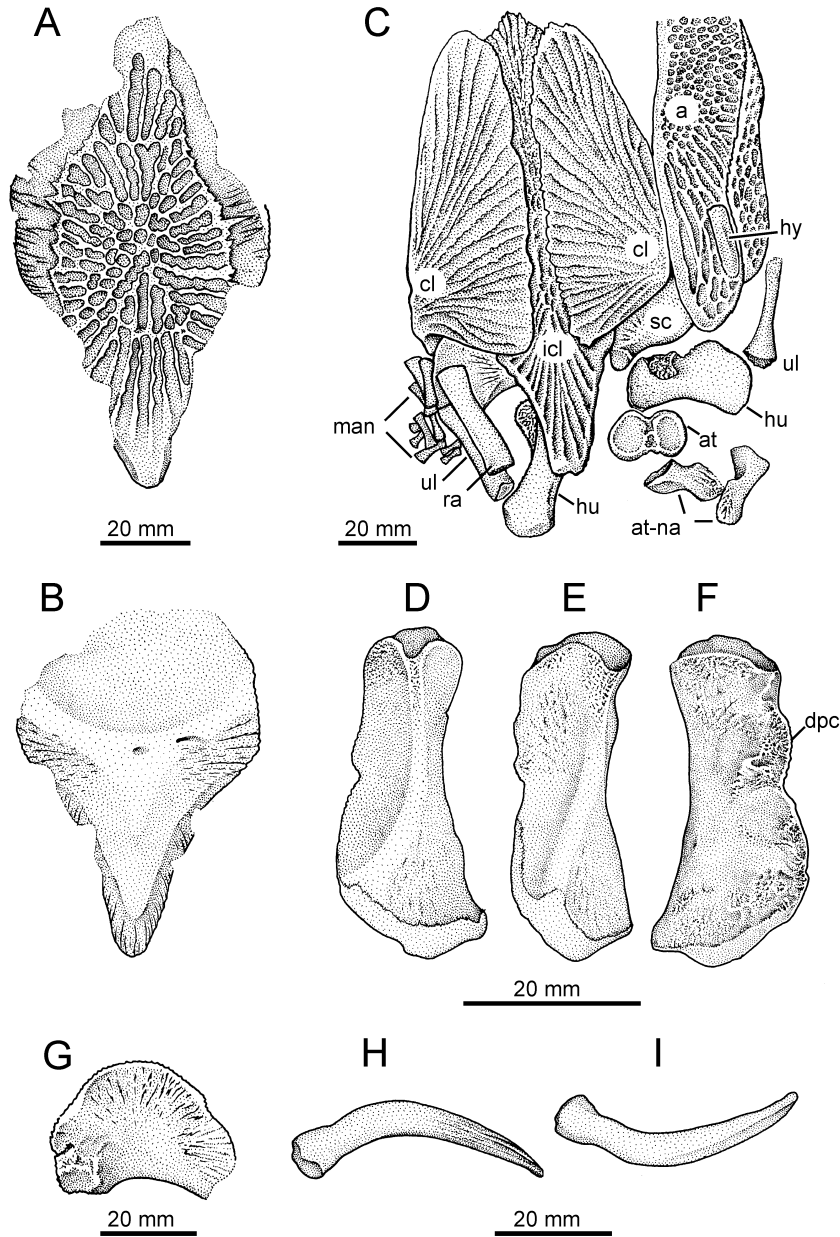


Figure 7. Pectoral girdle of *Callistomordax hugleri*. A, interclavicle, SMNS 90520 (ventral view); B, interclavicle, SMNS 90520 (dorsal view); C, pectoral girdle, right mandible, and atlas in loose articulation, SMNS 90700 (ventral view); D–F, left humerus, SMNS 90519 – D, dorsal view, E, anterior view, F, ventral view; G, scapulocoracoid, MHI-K3 (lateral view); H, I, cleithrum, SMNS 90520 – H, medial view, I, lateral view. (Please refer to the list at the end of the Introduction for a definition of the abbreviations.)

the skull and postcranium are present, preserved in a very similar mode as in the holotype. SMNS 90520 adds further details to the structure of single elements, particularly the internal structure of the skull, the pectoral girdle, and vertebrae. SMNS 90506 preserves important parts of the pelvis and hind limbs, and SMNS 90700 gives information on the pectoral girdle, forelimb, atlas, and the hyobranchial region

(Fig. 7C). A juvenile skull is preserved in MHI-K4, reaching only half the length of the type specimen and having a proportionately shorter postorbital skull table.

SKULL

The skulls of *Callistomordax* are crushed throughout and considerably flattened by compaction, which in

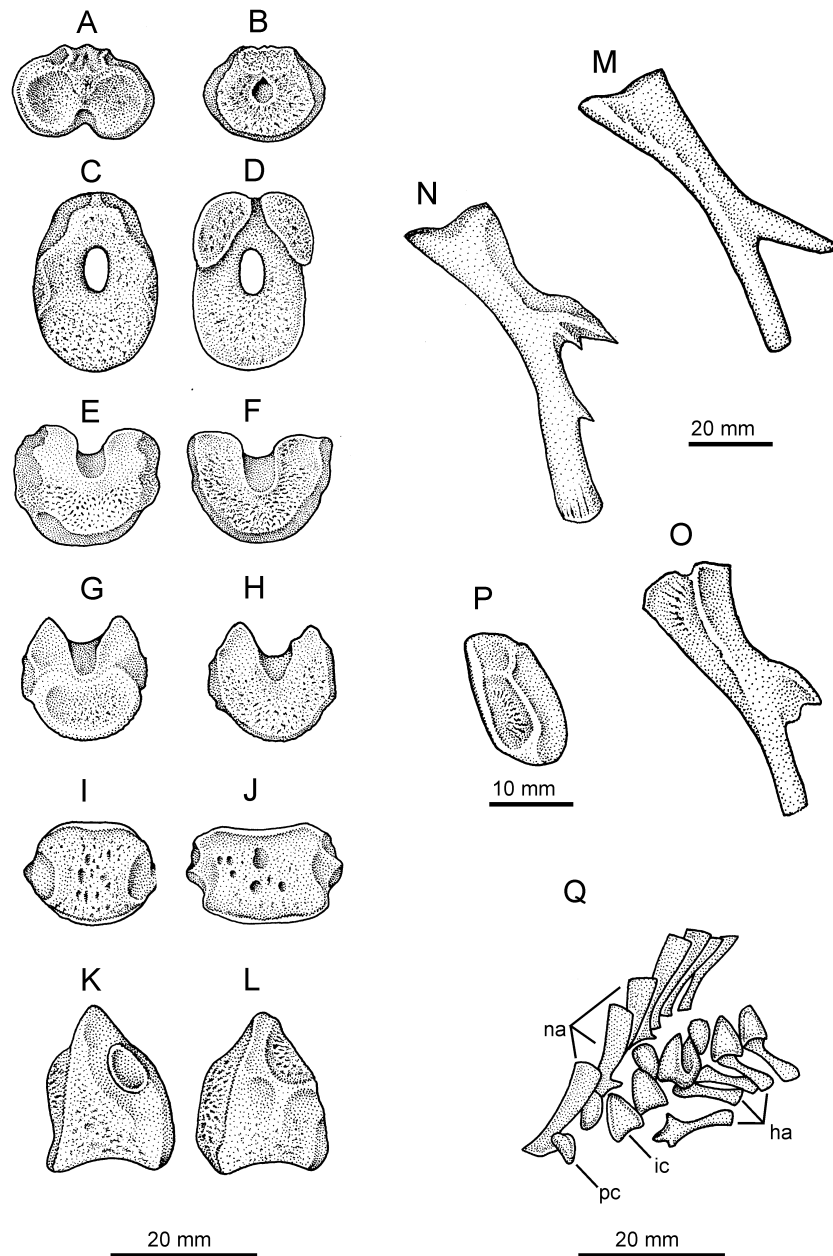


Figure 8. Axial skeleton of *Callistomordax hugleri*. A, atlas, SMNS 84119 (anterior view); B, SMNS 84119 (posterior view); C, 'stereospondylous' anterior trunk intercentrum with pleurocentra firmly attached to intercentrum, SMNS 84115 (anterior view); D, same as C (posterior view); E, anterior trunk intercentrum, SMNS 84116 (anterior view); F, same as E (posterior view); G, posterior trunk intercentrum, SMNS 84117 (anterior view); H, same as G (posterior view); I, same as G (ventral view); J, same as E (ventral view); K, same as E (lateral view); L, same as G (lateral view); M, axis rib, SMNS 82035; N, trunk rib, SMNS 82035; O, caudal rib, SMNS 90700; P, trunk pleurocentrum, SMNS 90520; Q, anterior tail section, SMNS 82035. (Please refer to the list at the end of the Introduction for a definition of the abbreviations.)

some places makes identification of sutures in the snout and anterior palate difficult. In the occipital region, crushing and displacement are most severe. However, the six specimens complement one another fairly well, so that only a few regions remain poorly preserved.

The skull has a parabolic outline, with slightly convex lateral margins and a narrow but blunt snout tip. The pineal foramen is in a relatively far posterior position within the skull table, a feature shared with metoposaurids, trematosaurids, trimerorhachids, and colosteids. As in most of these taxa the orbits have a

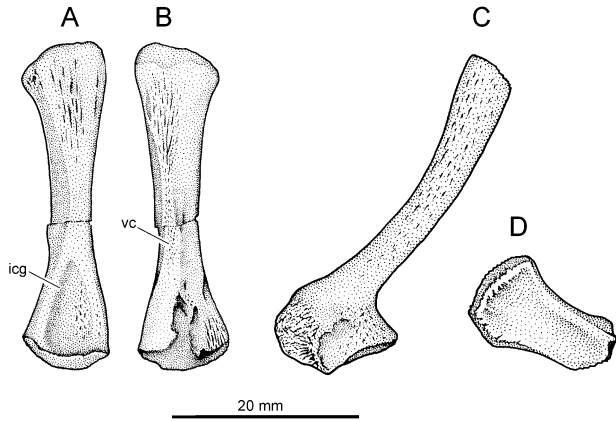


Figure 9. Pelvic girdle of *Callistomordax kugleri*. A, femur, SMNS 90506 (dorsal view); B, femur, SMNS 90506 (ventral view); C, ilium, SMNS 90506 (lateral view); D, ischium, MHI-K2 (lateral view). (Please refer to the list at the end of the Introduction for a definition of the abbreviations.)

lateral position, although they are relatively large. They are oval with narrowed anterior and posterior ends, and thickened rims. The interorbital region is relatively slender compared with metoposaurids, housing an unpaired, probably medially fused frontal bone, and an equal area on both sides formed by a prefrontal–postfrontal contact (Figs 1–4). The snout is short and narrows anteriorly, with large, medially expanded nares.

The palate is dominated by large interpterygoid vacuities bordered by extremely slender, obliquely orientated pterygoids, and a parasphenoid with a thin, crest-bearing cultriform process and a sagittally rectangular, smooth basal plate (Fig. 1B). The vomer is short and bears proportionately very long fangs, the sockets of which are arranged more medially than in most other temnospondyls. The teeth are of different sizes and shapes, with relatively long, laterally compressed tusks or fangs, as contrasted by numerous tiny marginal and palatine–ectopterygoid teeth. All marginal teeth are keeled on their anterior and posterior sides. The parasphenoid and pterygoids are edentulous in most specimens, but bear well-defined, pitted areas in those regions that housed denticle patches in many other temnospondyls. The subtemporal fenestrae are large and unusually long, reaching nearly half the length of the skull. This gives a reduced length for the tooth arcade, a feature also occurring in brachyopoids and plagiosaurids (Damiani & Warren, 1996; Hellrung, 2003).

Skull roof

The skull roof is well-preserved throughout and the sutures are mostly visible, although they may be

overprinted by intense ornamentation in places. Most sutures are rather straight, although locally prominent polygonal ridges may suggest serrated suture lines. The ornamentation is much more pronounced than in other temnospondyls occurring in the same horizons and localities as *Callistomordax*, which makes even small fragments readily identifiable (Figs 3, 4). Most dermal skull bones are thick. Dermal ornamentation consists of short, massive ridges, with sharp dorsal edges that generally fall into one of two major types. Small, even-sided polygons dominate most of the central areas of elements, whereas elongated, closely spaced and strictly parallel ridge systems cover most of the peripheral areas of longer elements. The latter type is especially present in zones of intensive growth, such as in the posterior skull table and cheek, whereas the snout is uniformly covered by polygonal ornament. However, the polygonal type is much more dominant in SMNS 55385 and 90520, whereas in SMNS 82035 and 90516 the long radial grooves are much more abundant. In a few regions (e.g. parietal, supratemporal), when the preservation is excellent, small foramina are located in the centre of each polygonal pit. The general appearance of the polygons in *Callistomordax* is most similar to that of metoposaurids and *Almasaurus*, although the zones of intensive growth are much less elongated in *Callistomordax*. Another typical feature is the arrangement of tiny polygons in a single row, replacing and at first sight resembling elongate grooves. The ornament is most pronounced at the corners of the polygons, which may form small tubercles exceeding the average height of the ridges.

The lateral line canals are faintly expressed in a few regions, but are otherwise ‘submerged’ in the intense ornamentation (Fig. 4B). Definitive sulci are found in the postglenoid area of the mandible, the nasals, prefrontals, the central region of the jugal, the squamosal, postorbital, and supratemporal (Fig. 1A). The canals are relatively narrow, only slightly wider than the average sculpturing polygons, and differ from the polygons in their length, which usually exceeds that of the polygons. The sulci are only continuous and well expressed in the interorbital and cheek regions of MHI-K5.

The premaxilla is well preserved in MHI-K5, where it reveals the morphology and position of the naris. It forms a large dorsal opening, being medially expanded, much as in metoposaurids (Colbert & Imbrie, 1956), and located very close to the blunt tip of the snout. Its outline is sagittally oval, and it is framed by the premaxilla, nasal, and maxilla; there is no trace of an ossified septomaxilla. The premaxilla forms a long palatal shelf that is dorsally exposed by the naris. The posterior halves of the nares are

located above the paired anterior palatal openings, whereas the anterior parts are floored by the palatal shelves of the premaxillae, which rise continuously towards the narrow anterior rim of the snout. This rim is thickened and covered by numerous tiny pits rather than ridges.

On the left side of SMNS 55385, the premaxilla has at least three larger teeth near the symphysis, whereas posterolaterally the teeth become smaller, to finally attain the features of the maxillary dentition (Figs 1A, 2A). Ventrally, the premaxilla forms the anterior margin of the paired anterior openings, the presence of which is indicated by the vomer in SMNS 90520. The premaxillary teeth have round sockets, are at best weakly compressed anteroposteriorly, and are faintly keeled.

In SMNS 90520, both nasals are well-preserved and remain in articulation (Fig. 4A). The anterior margin of the nasal has a medial concavity forming the posterior rim of the naris. Laterally, the nasals have only a poorly defined margin. The nasal is almost twice as long as wide, and is small compared with that of most other temnospondyls. It is clearly smaller by area than the prefrontal, and reaches only half the length of the frontal. The anterolateral portion of the nasal is covered by a substantial lateral line sulcus, which widens and deepens anteriorly. Although the snout may appear generally similar, the internarial width of *Callistomordax* exceeds that of *Almasaurus*, giving the tip of the snout a distinctly wider and more blunt outline than in the latter. The maxilla is well preserved, although ornamentation is so irregular that definitive sutures are difficult to trace. In the type specimen, the right maxilla is displaced to a point lateral of the cheek. It has minute, closely set teeth that become ever smaller posteriorly. The total tooth count may well exceed 80, with the anteriormost ones having sockets three times larger than those at the posterior rim. Throughout, the teeth form a continuous arcade rather than alternating with empty sockets as commonly seen in eryopids and stereospondylomorph temnospondyls. The maxilla ends well anterior to the anterior margin of the subtemporal fenestra. The crowns of the teeth are laterally compressed and at least the anterior teeth are faintly keeled.

The only ornamented region is the alary process of the maxilla that sutures broadly to the prefrontal, and has only very narrow contact with the nasal and premaxilla. It bears a prominent lateral line sulcus (infraorbital line) that is moderately curved. The maxilla is unusually short, ending anterior to the posterior end of the ectopterygoid. Hence, it neither forms a part of the rim of the subtemporal window nor contacts the quadratojugal. The maxillary denti-

tion is remarkable in consisting of numerous minute teeth that become ever smaller posteriorly.

The lacrimal is medially sutured to an extensive prefrontal, which has a pronounced lateral wing framing the anterior end orbit on both sides (Fig. 4A). It forms by far the smallest element in the skull roof, closely resembling that of *Metoposaurus diagnosticus* (Sulej, 2002; Milner & Schoch, 2004), *Buettneria perfecta* (Sawin, 1945; Colbert & Imbrie, 1956), and the small element in *Rileymillerus* that is described as a laterally exposed palatine by Bolt & Chatterjee (2000). It forms only part of the anterolateral rim of the orbit. The margin of the skull is very slender in that region because of the extreme anterolateral position of the orbits. The lacrimal contacts the jugal posteriorly in a short suture, but has broad contact with the prefrontal. The lacrimal is further peculiar in forming a continuous descending flange that firmly attaches to the dorsal side of the palatine. Although there is no suture visible between the palatine and lacrimal in SMNS 55385, in the holotype and in SMNS 90520 the palatine and lacrimal are clearly separated by crushing. This suggests they were at least not completely co-ossified, although very tight suturing is evident.

The frontal is only well preserved in SMNS 90520, where most of its dorsal and ventral surfaces have been prepared. Neither side preserves any trace of a midline suture, although the bone is clearly bilaterally symmetrical (Figs 1A, 2B, C, 4A). The dorsal exposure of the anterior portion narrows continuously and wedges deeply between the nasals to end in a pointed tip. The ventral side is substantially wider and has a blunt end. Posteriorly, the frontal shares a transversely aligned suture with the equally slender but clearly paired parietals. The ventral side of the frontal is smooth with a faint sagittal crest along the midline that heightens posteriorly. This crest may indicate fusion of initially separate frontal primordia, but there is no trace of a suture.

The anterior end of the parietal is about the same width as the frontal, but widens posteriorly as it makes contact with the supratemporal in an elongated and straight suture. Its general outline is rectangular, with the pineal foramen situated in the anterior third. The foramen is elongated and narrow, but very small, and situated in a depression of similar shape. Sculpturing is particularly well-defined and elongated: parallel polygons radiate towards the lateral and anterior margins.

The heavily ossified and posteriorly thickened post-parietal is only about one fourth of the length of the parietal. Its deeply sculptured dorsal surface is roughly quadrangular, but the outline of the sutures forms a pentagon. The occipital flange is largely smooth and must have sloped posteroventrally prior

to crushing (Fig. 1C). It bears a well-defined depression that runs parallel to the posterior margin of the dorsal face, but widens medially.

The prefrontal is the largest element of the preorbital region. Its outline forms an irregular hexagon, having a widened anterior portion with a triangular tip, and forming both the medial and lateral part of the anteriorly narrowing orbit. The anterodorsal rim of the orbit is markedly thickened, with the prefrontal part forming a pronounced ridge that, in contrast to other parts of the orbit rim, extends onto the dorsal surface to form an unornamented area. Pre- and postfrontal meet in a broad suture, thereby excluding the frontal from the border of the orbit both dorsally and ventrally. Laterally the prefrontal has an extensive suture with the lacrimal, whereas the concave, anterolateral margin has a similarly long contact with the alary flange of the maxilla. In the right prefrontal of the type specimen the ventral surface is exposed, revealing a centrally rugose area, which possibly served in muscle attachment, as has been suggested for capitosauroids (Schoch, 1997).

The postfrontal is long, having the same length as either the parietal or frontal. As in some trematosaurids, the posteromedial portion is much wider than the adjacent parietals and frontal. On the lateral side the relatively long suture with the postorbital slopes anterolaterally, but does not form a lateral wing as in trematosaurids. The posterior tip may be pointed or rounded, but is clearly narrower than the bulk of the posterior portion. The postorbital contribution to the orbit is minor, being restricted by large contributions of the postfrontal and jugal.

The supratemporal forms an elongated polygon, with five or six edges. It is shorter than the parietal, the anterior part of which extends well beyond the anterior end of the supratemporal, but is almost twice as wide. The anterior third of the element has a lateral suture converging medially to the mostly sagittal medial suture. Some specimens have deep temporal sulci crossing the suture with the tabular.

The tabular is smaller than the postparietal, but shares with it the thickened posterior rim and the proportionately large, deep-reaching occipital flange. The tabular horn is simple and is not set off from the main body of the element. Its blunt posterolateral end never extends posteriorly. The squamosal embayment is rather wide but very shallow. It is more similar to that of metoposaurids than *Almasaurus*, and does not have a sunken unsculptured rim as described by Yates & Warren (2000) for the latter.

The squamosal resembles the supratemporal in shape and size, having a straight sagittal medial and an anteromedially directed lateral margin. Both anterior and posterior ends are narrower than is the element at mid level. The squamosal embayment

forms a semicircular concavity. The suture with the jugal is about as long as that with the quadratojugal. The falciform crest, a posteromedial outgrowth of the squamosal embayment, is poorly developed and almost entirely formed by the quadratojugal.

The postorbital varies in both width and shape of the posterior end, which may be either pointed (SMNS 82035) or transversely straight (SMNS 55385). The lateral margin is mostly straight and the suture not serrated, but it may curve medially near the anterior end.

The jugal is the longest element in the skull roof, becoming continuously wider posteriorly (Figs 1A, 4B). It differs from all other bones in the mode of sculpturing, which consists of unusually small and numerous polygons in the central region, markedly larger polygons anteriorly, and elongated ridges posteriorly. The rim of the orbit is thickened, but the unornamented part does not extend onto the dorsal surface as in the prefrontal. The infraorbital sulcus is deeply developed in the anteriormost region, becoming shallower near the transverse curvature. The lateral margin is heavily ornamented except for the posterior fourth of the element, which is smooth. Ventrally, the jugal participates in the integration of pterygoid, ectopterygoid, and maxilla by means of a process pointing posteromedially (Fig. 1B). This condition differs from the typical stereospondyl situation in which a simple ventral column forms a trochlea-shaped anterior rim of the subtemporal window. The ventromedial process in *Callistomordax* is not only much longer and bends into a horizontal plane, but also bears two pointed outgrowths that firmly set into the palatine ramus of the pterygoid, which are only seen from the dorsal side. In addition, the anterior portion of the jugal forms a robust ventral ridge along its lateral rim. This ridge is completely attached to the dorsal face of the ectopterygoid, as the lacrimal is to the palatine.

The roughly triangular quadratojugal is about as long as the squamosal. The suture with the jugal is short, whereas it has a long concave contact with the squamosal. Polygons dominate over parallel ridges of ornament, and the posterior rim is characterized by a wide, largely unornamented area similar to the occipital flange of the posterior skull table. There is a pronounced ventral process, which together with the broad quadrate ramus of the pterygoid supports the massive quadrate.

Palate

The palate is known from three specimens that complement each other, SMNS 55385, SMNS 90520 (Figs 2A, D, 5), and SMNS 90700. The interpterygoid vacuities have a characteristic outline, being twice as

wide anteriorly than posteriorly. They are bordered by an extremely slender palatine ramus of the pterygoid, elongated thin ectopterygoid and palatine, a vomer with long and slender posteromedial processes, and a thin cultriform process of the parasphenoid (Figs 1B, 5). The subtemporal fenestrae are wide and subcircular in shape, exceeding the width of the basicranial region. The oval choana is relatively small. Anteriorly, the vomer and premaxilla formed the margins of paired and circular palatal openings, apparently for accommodation of large fangs projecting from the symphyseal region of the mandible. The vomer is short and largely occupied by four extraordinarily large, round-based fangs arranged in a transverse row.

The basiptyergoid region is disarticulated in both specimens in which the palate is exposed. In SMNS 55385 the right pterygoid remains in natural position, but the parasphenoid and left pterygoid have been displaced towards the left side. Both basiptyergoid sutures are crushed, although the left is still in loose articulation. The cultriform process is broken slightly anterior to its base, and further anterior it continues in an oblique orientation. The crest faces laterally instead of ventrally, at first sight suggesting a broad and flat cultriform process, as is typical of metoposaurids, instead of a narrow and keeled process. However, the proper orientation of the cultriform process becomes clearer by the morphology of its base, which is well preserved and undistorted. The base of the cultriform process and the anteriormost portion of the basal plate bear a ridge that rises and sharpens anteriorly. In the vomerine region the parasphenoid wedges between elongate posteromedial processes of the vomer, there again forming a largely flat process with a slightly broadened anterior end. Hence, the parasphenoid is a slender element, with a delicate cultriform process and an elongated basicranial region. The ventral surface of the base of the cultriform process becomes somewhat wider as it merges into the basal plate. There, the prominent vertical crest merges into a ridge that rapidly broadens posteriorly to frame a deltoid, heavily pitted area on the anterior basal plate. This area resembles the area aspera of other stereospondyls (Bystrow & Efremov, 1940), but is edentulous. The outline of the basal plate is roughly pentagonal, becoming continuously wider posteriorly.

The basicranial suture is substantially longer than in *Almasaurus* and most other stereospondyls, resembling most closely the situation in trematosaurids, metoposaurids, and mastodontosaurids. The whole basicranial region has the outline of a long rectangle, of which only the posterior fourth is framed by the smallish exoccipitals, whereas the remaining portion is sutured to the pterygoids (Fig. 5). The central and

posterior portions of the basal plate are largely smooth, with a central depression and a weak groove running in the posterolateral direction. The basiptyergoid suture is serrated and deep, forming an alternating overlap-underlap-overlap situation with the pterygoid. The posterior rim of the basal plate is not set off from the rest of the element, but is smooth and lacks any grooves, shelves, or 'pockets'. The exoccipitals have a long suture with the basal plate, excluding it broadly from the posterior margin of the palate, with the exception of the unossified basioccipital region, where a small posteromedial exposure of the parasphenoid exists.

The unusually slender and thin palatine ramus of the pterygoid has a convex anteromedial margin that constricts the interptyergoid vacuities markedly (Figs 1B, 5). Its orientation is anterolateral, roughly at an angle of 45° to the parasagittal. Although the ventral surface is flat and smooth, the dorsal side has a prominent central ridge. The anterolateral end is firmly sutured with the posteromedial projection of the ectopterygoid. The latter has a particularly long suture bearing numerous parallel ridges and grooves. The central basiptyergoid region of the pterygoid is well separated from the basiptyergoid suture by a wide groove running along the entire basicranial region. The quadrate ramus of the pterygoid is relatively short, but remarkably broad and flat, forming a stark contrast to the delicate palatine ramus. This correlates with an unusual shape of the quadrate trochlea, with which the pterygoid is firmly sutured. The exoccipital has a short suture with the basiptyergoid ramus, formed by a large lateral projection of the former.

The palatine is peculiar in having a broad dorsal process by which it is firmly attached to the lacrimal. Dorsolaterally, it forms a tight suture with the lacrimal by means of an ascending ridge: the concave, smooth dorsal surface of the palatine is pierced by a large foramen in the anterior part of the bone. The palatine bears two large teeth posterior to the tusk pair. The ventral surface of the bone is mostly covered by tooth sockets, except for the thickened posterior rim of the choana. The tooth arcade starts anteriorly with a pair of large tusks, followed immediately by two or three teeth that are much larger than the neighbouring teeth of the maxilla (Fig. 1B). The palatine has a slender anteromedial process that forms a rather narrow suture with the vomer.

The ectopterygoid is longer than the palatine. In SMNS 90520 it bears a pair of small tusks, succeeded posteriorly by a row of 12 much smaller teeth. Although the tusks occupy the whole width of the slender element, the following teeth are confined to the lateral margin of the bone. As with the palatine, the ectopterygoid teeth are at least twice as long as

the minute maxillary teeth, and are not as closely set. The posterior third of the ectopterygoid is broadened to form a large and robust medial projection that is firmly sutured with the pterygoid. Although the length of this projection is unparalleled among temnospondyls, similar conditions have been reported in some brachyopoids (Warren & Hutchinson, 1983), metoposaurids (Colbert & Imbrie, 1956), and *Almasaurus* (Dutuit, 1976).

The plate-like portion of the vomer is quadrangular and largely occupied by a pair of transversely aligned fangs (Figs 1B, 5). Their sockets have peculiar and highly variable outlines, ranging from quadrangular to triangular. There are no other teeth preserved on the medial vomerine plate, although this portion is very badly crushed in both specimens in which the vomer is exposed.

The choana is narrow and curved, paralleling the labial margins of the palatine and vomer. Its lateral extension is unclear, but the preserved part is different from both *Almasaurus* (where it is a straight and elongate oval) and metoposaurids (where it forms a short oval); a superficially similar situation is only present in saurerpetontids (Sequeira, 1998).

Occiput

The crushed occiput is partially preserved in SMNS 55385 and SMNS 90520. The exoccipitals are present and well ossified, with smallish and widely separated occipital condyles, and high dorsal projections attaching to the postparietals (as vertical columns) and tabulars (as paroccipital processes). The condyles have medially curved articulation facets (Figs 1C, 5). The condyles reach a level well posterior to the occipital rim of the dermal skull and behind the quadrate condyles. Post-temporal openings are preserved in SMNS 90520; they were probably smaller than in most other stereospondyls. The base of the condylar process is pierced by a large anterior and a tiny posterior foramen.

Endocranial and hyobranchial regions

Both SMNS 55385 and SMNS 90520 preserve parts of the neurocranium and the associated parts of the dermatocranium. Although the sphenethmoid, exoccipital, and quadrate are well ossified, all other regions appear not to have been ossified. The sphenethmoid forms a rather short and slender element with smooth and convex lateral walls pierced by a large foramen (? *nervus opticus*) near its anterior end. Ventrally it bears a sagittally aligned groove and scars suggesting attachment of musculature. The sphenethmoid is narrow, similar to that of trematosaurids, and exceeds only slightly the width of the cultriform process (Fig. 5). In cross section, the cultriform process must have had a V-shaped dorsal slot

to receive the braincase, and a deep-reaching and sharp ventral keel quite similar to that of *Thoosuchus* (Getmanov, 1989). Despite the rather extensive ossification of most skeletal elements in *Callistomordax*, the otic and epipterygoid regions remained unossified. The stapes was either not preserved or is not exposed.

Of the hyobranchial apparatus at least one short rod, which seems to have belonged to the ceratobranchials, is preserved (SMNS 90700). The tubiform space between the clavicle and mandible preserves several plate-like bones to which denticles are attached. These are probably branchial ossicles similar to those known from other temnospondyls (Boy, 1988; Schoch, 2002b). Interestingly they are rather broad, but poor preservation does not allow a more definitive assessment of tooth implantation on these ossicles.

Mandible

The mandible is well preserved in SMNS 55385, SMNS 90520, and MHI-K6, in combination revealing all of its external and ventral and most of the internal surface (Figs 1E, F, 5). The mandible is low except for the region anterior to the glenoid, where a prominent elevated labial wall of the adductor chamber – referred to here as the preglenoid process – is located. In the living animal, when the mouth was closed, this process must have reached well dorsal into the subtemporal window of the skull, and served for the attachment of powerful adductor musculature. Dermal ornament is intense on the surangular, angular, and the splenials. The dentary has a pitted external side at least in the anterior half. Otherwise bone surfaces are smooth with fine striations at best, such as along the entire dorsal portion of the preglenoid process.

The symphysis is sagittally expanded to accommodate at least one large tusk, which is keeled on both anteromedial and posterolateral sides, followed by marginal teeth four times smaller than the tusk, and posteriorly accompanied by at least one extra tooth, similar in position to the postsymphyseal dentition of other temnospondyls (Bystrow & Efremov, 1940; Bolt & Chatterjee, 2000). The symphyseal tusk is not an extra tooth medial to the dentary arcade, but comprises the anteriormost tooth in that series (Fig. 1E, F). Posteriorly, the teeth increase in size to reach about one third of the length of the tusk, but then gradually become smaller again. The dentary teeth are throughout intermediate in size, between the tiny maxillary teeth and the larger, and more robust, palatine and ectopterygoid dentition.

The adductor chamber is poorly preserved on the internal side, and the morphology of the adductor fenestra remains unclear. The labial side of the chamber is well-preserved in SMNS 55385 and

SMNS 90520, framed by the elevated labial wall of the adductor chamber. This is formed by the surangular and dentary, which are tightly sutured both labially and lingually. Among temnospondyls, only the enigmatic 'trematosaurian'-grade taxon *Infectosaurus* (Shishkin, 1960) has a preglenoid process of similar height. Some specimens of *Metoposaurus* also have such a process, although much shorter and lower than in the latter cases (Dutuit, 1976: fig. 30).

The coronoid series is poorly preserved, but MHI-K6 and SMNS 55385 provide evidence of all three coronoids. As usual, the posterior coronoid forms the anterior margin of the adductor fenestra, and indeed this is the only safe evidence for the existence of such a fenestra in *Callistomordax*. Teeth are not preserved on this rather short element, which expands for some distance along the internal margin ventral to the dentary arcade, but does not reach the Meckelian fenestra ventrally. The middle coronoid is located ventral to the dentary tooth row, and contributes about one fourth of the dorsal margin of the Meckelian window. Its anterior portion is thickened and bears a series of mostly ill-defined, relatively large teeth. The two posteriormost sockets are well-preserved and closely set. They seem to form a sagittal row, accompanied by a range of smaller, irregularly placed teeth dorsal to it. The anterior, edentulous coronoid is entirely smooth and short, ending shortly posterior to the symphyseal region.

The ventral series of dermal elements is very slender and tightly sutured, with bone contacts difficult to trace. The angular is only slightly longer than the anteriorly following postsplenic, whereas the splenic is only about two thirds of the length of the postsplenic. Angular and postsplenic form the ventral margin of the Meckelian fenestra in about equal parts. The window is extremely elongated, measuring one third of the length of the whole lower jaw; according to MHI-K6 it was probably rather slender.

The postglenoid region (PGA) is robust and houses a completely ossified articular (Figs 1E, 5). Although the external side is dominated by the surangular, the posterior and posteromedial portions expose a relatively large part of the articular, continuing onto the glenoid facet. Anteriorly, the articular is sutured to the angular and prearticular. There is no hamate process as in lydekkerinids or capitosauroids; instead, all margins of the glenoid facet are about equally high.

POSTCRANIUM

Axial skeleton

The vertebral column is well exposed in SMNS 82035, SMNS 90516, SMNS 90520, and SMNS 90700, and a range of isolated intercentra add further information

on the three-dimensional structure of the central elements. The presacral count is 26–28, and there is evidence of at least 28–30 caudal vertebrae (SMNS 82035, SMNS 90700), although the number of tail vertebrae is likely to have exceeded 40 (Fig. 6).

The atlas is known from an isolated specimen (SMNS 84119), which must have been substantially smaller than the articulated specimens (Fig. 8A, B). SMNS 84119 is from the Kupferzell locality, and was considerably worn by transport prior to deposition. Assignment of this atlas to *Callistomordax* was possible because a very similar atlas is present in SMNS 90700 (Fig. 7C). The anterior face of the atlas is perfectly bilobed, with round left and right condylar facets, and a strongly concave posterior face bearing a central hollow that housed the anteriormost portion of the notochord. The neural arches of the atlas, preserved in the type specimen, are lower and less differentiated than the following neural arches. In cross section, the posterior side of the atlas is transversely oval.

Neither the axis nor an identifiable third vertebra are exposed as a whole. However, their intercentra are clearly preserved in the type specimen. They are of similar size and do not differ from the subsequent intercentra. In general, anterior and mid-trunk intercentra are massive, anteroposteriorly elongated bones that differ quite substantially from the stereotyped crescents of rhachitinous intercentra (Romer, 1947; Moulton, 1974). In *Callistomordax*, the ventral aspect of a trunk intercentrum is quadrangular in outline, with clearly rounded edges and a saddle-shaped surface (Fig. 8I, J). The latter bears large grooves and foramina aligned mostly in sagittal fashion. The pleurocentra are always well ossified and paired, sometimes approaching one another closely (Fig. 8). In addition, they reach much further ventrally than they do in capitosauroids, and their tight attachment to the anterior and posterior sides of the intercalated intercentrum causes the latter to have triangular flanks with pointed dorsal ends. In one isolated specimen the pleurocentra are still attached to the intercentrum, and may even be partially fused to it. This segment probably represents an anterior trunk vertebra, as concluded from the parapophyses. The most peculiar and unique feature is that the intercentrum reaches as far dorsal as the tip of the pleurocentra, thus almost attaining a stereospondylous condition. It is equally possible that this may be either an old individual or a hyperossified specimen (Fig. 8C, D).

Throughout the anterior and mid-trunk region, the intercentra are of similar height and the pleurocentra are large and robust. Towards the sacrum, the intercentra become somewhat lower and the anterior bulge is less pronounced. Furthermore, the parapophyses migrate ever more ventrally as the tail is approached.

In this region, the pleurocentra are smaller and not as heavily ossified; in general, the quantity of cartilage appears to have been greater than further anterior.

The neural arches of the anterior trunk region are low with a rugose dorsal tip. They have long transverse processes, resembling those of *Mastodonsaurus* (Schoch, 1999), but towards the mid level of the trunk they become successively shorter. The prezygapophyses are well developed throughout the trunk, forming oval and well-separated facets. The postzygapophyses form only faint projections at the posterior base of the neural spine. From the posterior third of the trunk backwards, the neural spines become successively higher. They have flat and smooth lateral flanks, and their outline is rectangular with straight vertical anterior and posterior margins. The spines are relatively broad and nearly rectangular in outline, although their poor preservation indicates that they were rather feebly ossified and thin.

The ribs of the trunk are elongate, have thin rod-like shafts bearing diverse uncinat processes, and have broadened distal ends that, according to their concave and rugose end, must have been cartilage capped (Fig. 8M, N). The shafts are slightly curved at about mid level. The anteriormost rib, probably that of the axis, is markedly shorter than the following ones, and has a narrow distal end. It bears a single spine-like uncinat process at about mid level (Fig. 8N). The subsequent ribs are about one third longer and have broadened distal ends. Their uncinat processes are more differentiated, often having several pointed ends and being covered by various ridges or crests ending in the spines. Further posterior, at about the mid level of the trunk, the ribs have a single, very long uncinat spine reaching or even exceeding the length of the distal (postuncinat portion) of the shaft. The sacral rib is not exposed. Judged by the general similarity of the rib cage to that of trematosaurids (Schoch, 2006), the sacral rib was probably longer and more solid than the preceding ones. Unlike in capitosauroids and metoposauroids, the trunk of *Callistomordax* must have had a vertically oval cross section along most of its length, although it was probably still somewhat wider than in *Trematolestes* (Schoch, 2006).

Caudal skeleton

The tail was probably longer than the trunk, thus reaching more than three times the length of the skull (Fig. 6). In the anterior tail skeleton, the neural spines are approximately the same height as in the sacral region, but much more slender, becoming ever more gracile posteriorly. At the same time, their posterior inclination becomes accentuated. Haemal arches are present from the fourth caudal vertebra

backwards, whereas ribs are last preserved at the level of the sixth caudal vertebra. The haemal arches, attached to the intercentra, bear spines of about the same length as the neural spines in each vertebral segment. Pleurocentra are also present throughout. They are of reduced size and have a proportionally much smaller lateral face than in the trunk. The tail was obviously high and powerful, with a roundish-oval cross section at the base, where simple and short caudal ribs are present, but posteriorly was more laterally compressed, with a vertically oval cross section.

Appendicular skeleton

Pectoral girdle and forelimb: This region is well preserved and almost completely exposed. However, only a combination of data from different specimens permits a comprehensive restoration of this region. The most important specimens are SMNS 90520 and SMNS 90700, in which all constituting elements except for the scapulocoracoid are preserved.

The flat dermal elements are rather small, with a thinly ossified long rhomboidal interclavicle, with rather short clavicles attaching to it only along its anterolateral rim (Fig. 7A–C). The curved cleithrum is almost as long as the dorsal process of the clavicle. It is almost as large as many trunk ribs, and its outline cannot be confused with any other element. The head develops continuously from the curved shaft, with the anterior margin forming a faint projection, whereas the posterior facet, to which the scapulocoracoid must have been attached, is posterodorsally widened to form a rugose surface (Fig. 7H, I). In the ventral third of the element the facet is orientated anteriorly, changing into a medial orientation further dorsally. At the dorsal end, the facet ends in a slim slit demarcated by a posterior process. The scapulocoracoid is preserved in MHI-K3, a large specimen, where this bone is smallish and poorly ossified. It is semilunar in outline, with a rugose glenoid region and marked radial striations on the lateral surface (Fig. 7G).

The humerus is known from the holotype, three further articulated skeletons (SMNS 90700, MHI-K1, MHI-K3), and an isolated specimen from the same horizon and locality (SMNS 90519). It differs markedly from the humeri of all other temnospondyls in having a deltopectoral crest expanding along the entire anterior face to form a convex anterior margin (Fig. 7C–F). Distally, the crest merges into a supinator region, but no separate supinator process is developed. This extended anterior crest gives the humerus a totally different outline compared with other temnospondyls. It recalls the situation in early tetrapods, particularly *Proterogyrinus* and *Greererpeton* (Holmes, 1984; Godfrey, 1989), where a defined shaft does not exist. However, contrary to early tetrapods,

the shaft in *Callistomordax* still has an oval cross section, whereas the expanded crest forms a continuous outgrowth of the anterior margin of the shaft. Also in contrast to the humerus of early tetrapods, epicondylar foramina are absent. The deltopectoral region proper forms a ventral boss reaching from about the mid level of the shaft almost to the proximal head region. Similar, distally reaching deltopectoral bosses are reported from metoposaurids (Sawin, 1945; Dutuit, 1976), *Eryops* (Miner, 1925), or *Dvinosaurus* (Nikitin, 1995). Unlike many stereospondyl humeri, the humerus of *Callistomordax* has proximal and distal ends aligned at almost a right angle, and the tetrahedral shape is highlighted by the continuous anterior crest. Dorsally, the shaft is well set off from the much thinner crest, whereas on the ventral side, the shaft, flat distal end, and crest form a single plain. The whole crest region is ventrally covered by dense pitting, whereas the dorsal side bears mostly grooves on an otherwise smooth surface.

The radius and ulna are poorly exposed in the type, but are well preserved in SMNS 90700 and the MHI material (Fig. 7C). Both elements are substantially thinner than the humerus, but are nearly the same length as the humerus (radius, 0.92 humerus length; ulna, 0.77 humerus length). The radius is flat, has a very faintly curved long axis, and has a proximal end that is slightly wider than the distal end. The ulna is more like a narrow rod with only poorly broadened ends, the proximal one forming a socket for the articulation with the humerus and having raised margins; there is no sign of an olecr.

The manus has apparently four digits, as suggested by four almost similar-sized elongated metacarpals (Fig. 7C). No ossified carpal elements are preserved in any specimen. The metacarpals and phalanges are throughout long and slender bones, suggesting a gracile but moderately elongate hand skeleton that reached the length of the forearm.

Pelvic girdle and hindlimb: This region is partially preserved in a fragmentary specimen, SMNS 90506, where there is substantial evidence of the ilium, femur, tibia, fibula, and several metatarsals. In a second specimen (MHI-K4), the ischium, ilium, femur, and fibula are present. In SMNS 90700, the ilium, femur, lower leg, and pes is completely preserved and almost in full articulation.

The ilium has an elongated and slender shaft that is slightly concave anteriorly (Fig. 9C). The base of the shaft is markedly bent dorsal to the level where it merges into the acetabular region. In anterior view, the shaft is markedly curved laterally and then bends into a more vertical plain at about the mid level. The bending point bears a ridge and various muscle scars. The acetabulum is relatively small, confined to the

anterior half of the base, and is set off from the posterior half of the base by a deep depression. The shaft is proportionately longer than in almost all other temnospondyls, especially stereospondyls. Although the ilium of *Callistomordax* resembles that of *Trematolestes*, the latter has a different acetabular region in that the actual facet is smaller (Schoch, 2006). In addition, the anterodorsal rim of the acetabulum differs in being thinner and forming a simple ridge rather than a boss as in *Callistomordax*. The ischium of *Callistomordax* is small but well ossified, with clearly defined and completely formed bony margins (Fig. 9D). It is rectangular and does not differ from the ischium of metoposaurids, as described by Dutuit (1976).

The femur is longer than the humerus, with a humerus-to-femur ratio of 0.74, whereas the ilium is slightly longer than the femur (femur-to-ilium ratio: 0.833). In SMNS 90506, the femur has been entirely cleaned from matrix and is excellently preserved. It is more robust than in the coeval *Trematolestes* (Schoch, 2006), and has more differentiated condyles (Fig. 9A, B). In anterior view, the femur has a clearly convex dorsal surface and a faintly concave ventral surface. Proximally, the dorsal portion is smooth and simply rounded, forming a continuous rod up to the distal fourth of the element, which bears a weakly developed intercondylar groove. The intercondylar groove is triangular in outline, separating the equally sized condyles. The distal tip is poorly ossified, consisting of granular bone. On the ventral side, the ventral crest is restricted to the distal third, distally merging into an irregular, roughened area. The shaft is ventrally nearly straight, and is mostly smooth with poorly defined pitting. Finally, the proximal portion is occupied by a ventrally convex, markedly grooved region of triangular shape similar to the trochanter scars of metoposaurids (Dutuit, 1976: fig. 67).

The tibia and fibula are markedly shorter than the femur (tibia, 0.71 femoral length; fibula, 0.6 femoral length). The tibia has a slender shaft with a rather flat oval cross-section, and almost similar broadened proximal and distal ends, which are both somewhat incompletely preserved. The ventral side has a prominent ridge aligned along the main axis of the element. The fibula has broadened ends that are both medially expanded, the proximal one being less prominent.

In SMNS 90700, a good portion of the pes is in articulation, including digits 3 and 4, whereas the others are slightly disarticulated, in combination suggesting a phalangeal formula of 2-3-3-3-3. No ossified tarsal elements are present.

Dermal scales

Six articulated, well-preserved skeletons show no indication of gastralia or other dermal ossifications,

suggesting that they were absent in *Callistomordax*. This is in accordance with recent observations on trematosaurid postcrania (Steyer, 2002; Schoch, 2006) and those of metoposaurids (Dutuit, 1976), although Janvier (1992) reported dermal scales in a restricted region near the otic notch in the trematosaurid *Tertremoides*.

CALLISTOMORDAX AND THE METOPOSAURIDAE

PREVIOUS CONCEPTS OF METOPOSAURID RELATIONSHIPS

The origin of the metoposaurids has puzzled workers for more than one and a half centuries, beginning with Hermann von Meyer (in Meyer & Plieninger, 1844; Meyer, 1857) who first described them. After their subsequent discovery in North America, India, and Morocco, metoposaurids turned out to be one of the most clear-cut and well-defined, yet at the same time one of the most isolated, temnospondyl groups.

As knowledge of Mesozoic temnospondyls has grown enormously during the 20th century, any phylogenetic study of metoposaurid origins must include potentially related taxa. In the last nine decades, as many as ten different hypotheses have been proposed as to the origin and evolution of the Metoposauridae.

1. Watson (1919) proposed the first large-scale, highly influential evolutionary scheme of temnospondyls (he referred to them as a subgroup of his Labyrinthodontia), in which he tied metoposaurids in his 'grade' Stereospondyli, separate from trimerorhachids and other 'Rhachitomi-grade' temnospondyls. However, he was not explicit about specific relationships to other stereospondyl groups. Watson's (1919) concept was opposed by Säve-Söderbergh (1935), who classified metoposaurids with other temnospondyls with long postorbital skull tables, notably trimerorhachids.
2. Romer (1947) moved one step ahead in not only classifying metoposaurids among the Labyrinthodontia, as Watson had done three decades before, but also by further specifying that metoposaurids were closely related to brachyopids and plagiosaurids; he used the superfamily name Brachypoidea to include all three families. In this concept, both trematosaurids and capitosaurids were excluded from that superfamily. Romer's (1947) concept was followed by Dutuit (1976), who was hesitant whether to rank the almasaurids with Romer's Brachypoidea.
3. Shishkin (1973) followed Säve-Söderbergh (1935) in seeking the metoposaurid origin among more primitive temnospondyls, notably trimer-

orhachids, saurerpetontids, and dvinosaurids. He further considered brachyopids and (nontemnospondyl) colosteids, but not plagiosaurids, as close relatives of metoposaurids.

4. Warren & Black (1985) performed the first phylogenetic analysis 'by hand', in which they envisioned a Stereospondyli divided into a trematosaurian and a capitosaurian group. This is the first time that a major dichotomy was explicitly proposed in stereospondyl phylogeny, indeed one with a deep-reaching split: rhinesuchids, lydekkerinids, capitosauroids, almasaurids, and metoposaurids were ranked among the capitosaurian group, contrasted by trematosaurids, rhytidosteids, brachyopids, and chigutisaurids, which together formed their trematosaurian group. Most subsequent studies are variants of this concept, with various permutations in sister-groups relationships in particular.
5. Milner (1990) suggested the most radical alternative to Warren & Black's (1985) hypothesis. His phylogenetic study was the first to include all major groups of temnospondyls based on Hennigian principles. In Milner's (1990) cladogram, metoposaurids originated from a particular clade of short-snouted trematosaurians, with 'laticopids' (almasaurids) forming their sister group and indicating the plesiomorphic condition for many metoposaurid traits. In this concept, chigutisaurids and rhytidosteids were derived from lydekkerinids, thus being not immediately related to metoposaurids or even the larger trematosaurian clade. As a further stark contrast to Warren & Black (1985), Milner (1990) ranked brachyopids and plagiosaurids not among the stereospondyls, but sought their ancestry among more 'primitive' Permian temnospondyls.
6. Hunt (1993), in revising the family Metoposauridae, discussed two alternative scenarios for deriving the group from other temnospondyls: (1) an origin from 'primitive' (trimerorhachid) temnospondyls, and (2) a stereospondyl ancestry for the group. In his trimerorhachid hypothesis, Hunt (1993) placed metoposaurids as a sister group to brachyopids, arguing for both to be nested with the Lower Permian Trimerorhachidae. In his alternative stereospondyl hypothesis, he envisioned the Laticopidae (Almasauridae) as a sister group of the metoposaurids, together nested with *Mastodonsaurus*, *Eocyclotosaurus*, and finally the Capitosauridae.
7. Yates & Warren (2000) performed the first computer-assisted cladistic analysis of stereospondyls, including many taxa relevant to the present study. Their findings were clearly different from the aforementioned in several points: (1)

they suggested plagiosaurids to be nested with other short-skulled stereospondyls (brachyopids, chigutisaurids, and rhytidosteids in particular), and within that assemblage they envisioned the small, carapace-bearing *Laidleria* as an immediate sister group to the plagiosaurids; (2) they suggested that the latter clade was nested deeply within a group that included trematosaurids, *Almasaurus*, and metoposaurids, referring to the whole assemblage as the Trematosauria; and (3) they found *Lydekkerina* to form a clade with *Mastodonsaurus* and capitosauroids (a group they termed Capitosauria). By that, Yates & Warren (2000) confirmed the trematosaurian concept of metoposaurid ancestry proposed by Milner (1990), albeit with a large clade of short-skulled stereospondyls also having arisen from a vast clade they termed Trematosauria.

8. Schoch & Milner (2000) attempted to form a phylogenetic frame for a higher-ranking taxonomy of stereospondyls, ranking the metoposaurids with *Almasaurus*, the Platystegidae, and Lyrocephaliscidae in a clade of broad-skulled trematosaurians. They referred to the whole clade of slender-skulled and broad-skulled trematosaurians as Trematosauroida, which would necessarily include the Metoposauridae, but explicitly excluded from that group all short-skulled temnospondyls such as brachyopids, chigutisaurids, rhytidosteids, and plagiosaurids.
9. Steyer (2002) was the first to restrict a numerical cladistic analysis to trematosaurian in-group relationships, considering the metoposaurids, *Almasaurus*, and *Inflectosaurus* to be not intimately related to the trematosaurids proper. He found that these three formed a monophylum nested below a dichotomy of capitosauroids ('mastodonsauroids') and trematosaurians s.s., with only the latter referred to as the Trematosauridae by him. In this hypothesis, *Lyrocephaliscus* and *Platystega* are nested together with *Tertrema* within a monophyletic Trematosaurinae, contrasted by a long-snouted sister group Lonchorhynchinae.
10. Most recently, Damiani & Yates (2003) published a more inclusive computer-assisted analysis of trematosaurid phylogeny, again changing the picture in various points. Although not considering brachyopids or plagiosaurids, they found rhytidosteids to nest with the 'primitive' stereospondyl *Lydekkerina* to form a clade distinct from all trematosaurians, which in their cladogram formed a grade towards *Almasaurus* and the Metoposauridae. This most closely resembles the hypotheses of Milner (1990) and Schoch & Milner (2000). In particular, their analysis agreed with

the latter authors in nesting *Lyrocephaliscus* with the almasaurid-metoposaurid clade, whereas they found evidence for a separate position of *Platystega* with *Tertrema* and the lonchorhynchines.

To summarize, the origin of metoposaurids is still highly controversial, and has been sought among at least three different major nodes or grades within temnospondyl phylogeny: (1) an early origin from *Trimerorhachis*-like taxa (Säve-Söderbergh, 1935; Shishkin, 1973; Hunt, 1993, hypothesis A) – this would require an extraordinarily long ghost lineage and would leave most of the character evolution towards metoposaurids entirely hypothetical; (2) a separate origin in a basal stereospondyl grade before the capitosaurian–trematosaurian dichotomy (Watson, 1919; Romer, 1947; Steyer, 2002), with *Almasaurus* forming their sister taxon and potentially indicating plesiomorphic states for various metoposaurid autapomorphies; and finally (3) an origin within a large trematosaurian clade, with *Lyrocephaliscus* and *Almasaurus* forming successive sister taxa of the Metoposauridae (Milner, 1990; Schoch & Milner, 2000; Yates & Warren, 2000; Damiani & Yates, 2003).

The last general hypothesis presents the most detailed account of character evolution, as some character states would have evolved prior to *Lyrocephaliscus*, others with the almasaurid grade, and yet others in the immediate stem of the metoposaurids. On the other hand, the evolution of many features is still unclear in the several variants of that concept, in particular the postcranium for which little articulated material is known. *Callistomordax* forms a good opportunity to tackle both problems, and by doing so review the case of metoposaurid phylogeny within stereospondyls, especially after the Upper Triassic *Rileymillerus*, a new, *Almasaurus*-like taxon, was recently described by Bolt & Chatterjee (2000).

PHYLOGENETIC ANALYSIS

The present analysis is based on 19 taxa and 100 characters from all parts of the skeleton (Fig. 10; Appendix). Most character states were taken from the recent literature (all authors are cited in the character list), but some states expressed in *Callistomordax* were added. Multistate characters were treated as unordered throughout. All variants of the present analysis were performed in the branch-and-bound mode of PAUP 3.1 (Swofford, 1991), and characters were traced by making use of MacClade 2.0 (Maddison & Maddison, 1992). The analysis was run in the ACCTRAN mode.

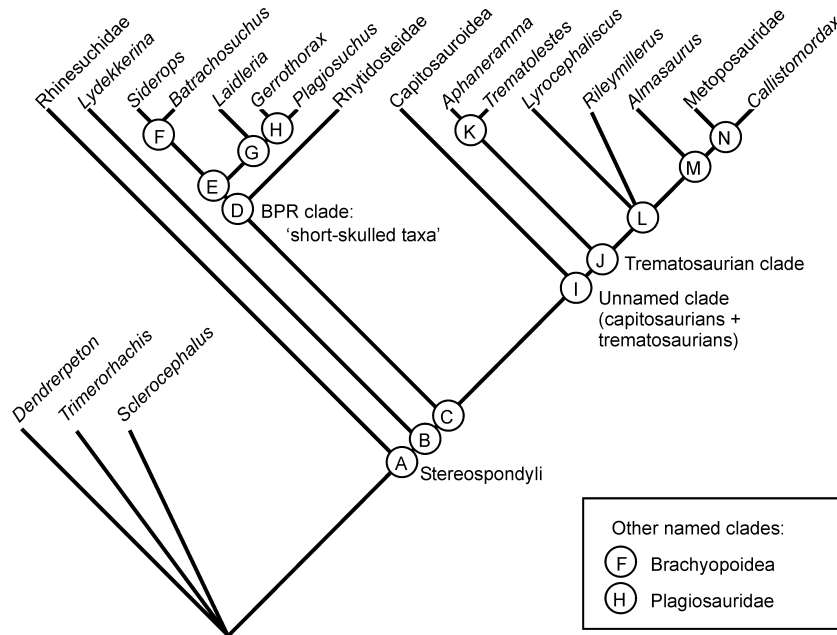


Figure 10. Cladogram, depicting results of the preferred phylogeny (pretrematosaurian hypothesis). Nodes are defined and discussed in the text. See the Phylogenetic analysis for details.

Taxa

Three successively more derived outgroups were included to root the ingroups.

1. *Dendroperpeton acadianum* (Holmes, Carroll & Reisz, 1998) is one of the known plesiomorphic temnospondyls.
2. *Trimerorhachis insignis* (Case, 1935) was included because the last revising author of the metoposaurids, Hunt (1993), made explicit reference to trimrorhachids, after Shishkin (1973) had suggested all temnospondyls with short faces and long posterior skull tables may have formed a clade.
3. *Sclerocephalus haeuseri* (Boy, 1988; Meckert, 1993; Schoch, 2003; R. R. Schoch, pers. observ.) is considered a stereospondylomorph (stem stereospondyl) by all recent authors (Boy, 1990; Schoch & Milner, 2000; Yates & Warren, 2000).

Ingroups:

4. the Rhinesuchidae, here represented by *Rhineceps nyasaensis* (Watson, 1962) and *Uranocentron senekalensis* (van Hoepen, 1915; R. R. Schoch, pers. observ.);
5. *Lydekkerina huxleyi* (Broili & Schröder, 1937; Shishkin, Rubidge & Kitching, 1996; Pawley & Warren, 2005);
6. the chigutisaurid *Siderops kehli* (Warren & Hutchinson, 1983);
7. the brachyopid *Batrachosuchus* spp. (Watson, 1919, 1956; Welles & Estes, 1969);
8. *Laidleria gracilis* (Kitching, 1957; Warren, 1998);
9. the Rhytidosteidae, as a terminal taxon (based on *Rhytidosteus capensis* of Cosgriff, 1965; *Deltasaurus kimberleyensis* of Cosgriff, 1974; *Peltostega erici* of Säve-Söderbergh, 1936 and Janvier, 1983; *Trucheosaurus major* of Marsicano & Warren, 1998);
10. the plagiosaurine *Gerrothorax pustuloglomeratus* (Hellrung, 2003);
11. the plagiosuchine *Plagiosuchus pustuliferus* (Hellrung, 2003; R. R. Schoch, pers. observ.);
12. the capitosauroid *M. giganteus* (Schoch, 1999), as representative of the capitosauroids (single exception: character 43, the derived state of which occurs in *Mastodonsaurus*, whereas other capitosauroids retain the plesiomorphic state, see Schoch, 2000 and Damiani, 2001),
13. the long-snouted trematosaurid *Aphaneramma rostratum* (Wiman, 1917; Säve-Söderbergh, 1936);
14. *Trematolestes hagdorni* (Schoch, 2006);
15. *Lyrocephaliscus euri* (Säve-Söderbergh, 1936; Mazin & Janvier, 1983);
16. *Rileymillerus cosgriffi* (Bolt & Chatterjee, 2000);
17. *Almasaurus habbazi* (Dutuit, 1972, 1976);
18. the Metoposauridae, as represented by *Dutuitosaurus ouazzoui* (Dutuit, 1976), *Buettneria perfecta* (Sawin, 1945; Colbert & Imbrie, 1956; Hunt, 1993), and *M. diagnosticus* (Meyer & Plieninger, 1844; Meyer, 1857; Hunt, 1993; Sulej, 2002; Milner & Schoch, 2004);
19. *C. kugleri*, as based on the present findings.

Results

I shall first report the consensus obtained by all variants of the phylogenetic analysis, then list the differences among variants, and finally discuss the two alternative phylogenetic hypotheses. These alternatives differ in the position where the short-faced stereospondyls (plagiosaurids, *Laidleria*, chigutisaurids, and brachyopids) nest: a basal split is called the pretrematosaurian hypothesis, a position of the short-faced clade within the trematosaurians of the trematosaurian hypothesis.

Consensus: (1) Metoposaurids and *Callistomordax* are always sister groups; (2) metoposaurids and *Callistomordax* are nested within a larger trematosaurian clade that includes trematosaurids, lyrocephaliscids, and *Almasaurus*; (3) within that trematosaurian clade, *Aphaneramma* and *Trematolestes* form a monophylum; (4) *Mastodonsaurus* (as representing capitosauroids) is not nested with *Lydekkerina*, but forms its own branch; (5) the short-skulled stereospondyls form a monophylum, falling into two distinct clades; (6) a brachyopoid clade including brachyopids (*Batrachosuchus*) and chigutisaurids (*Siderops*); and (7) a clade formed by *Laidleria* and the plagiosaurids (*Gerrothorax* plus *Plagiosuchus*). The position of the Rhytidosteidae is suggested to be ambiguous by a bootstrap value below 50, and proved to be critical to the whole analysis.

Variants of analysis: The analysis gave two strikingly divergent results, depending on the inclusion or exclusion of the Rhytidosteidae (Fig. 11). Other variants (exclusion of *Trimerorhachis*, exclusion of *Batrachosuchus*, exclusion of one or both plagiosaurids, and exclusion of *Laidleria* with or without the retention of plagiosaurids) had only a minor effect on the topology. The following sections summarize all those points in which these two alternatives (and all their variants) disagree.

Pretrematosaurian hypothesis (Fig. 11A): This is based on a matrix including Rhytidosteidae. The main feature of this topology is that the short-skulled stereospondyls branch off before the capitosaurian–trematosaurian dichotomy. The resulting three most parsimonious trees comprise all possible variants of the three-taxon statement *Rileymillerus*, *Almasaurus*, and (*Callistomordax* plus Metoposauridae). Each of the three topologies requires 222 steps and has a consistency index of 0.536, a retention index of 0.719, and a rescaled consistency index of 0.386.

Trematosaurian hypothesis (Fig. 11B): A matrix that excludes the Rhytidosteidae gives a quite different result. The topology of the trematosaurian clade is

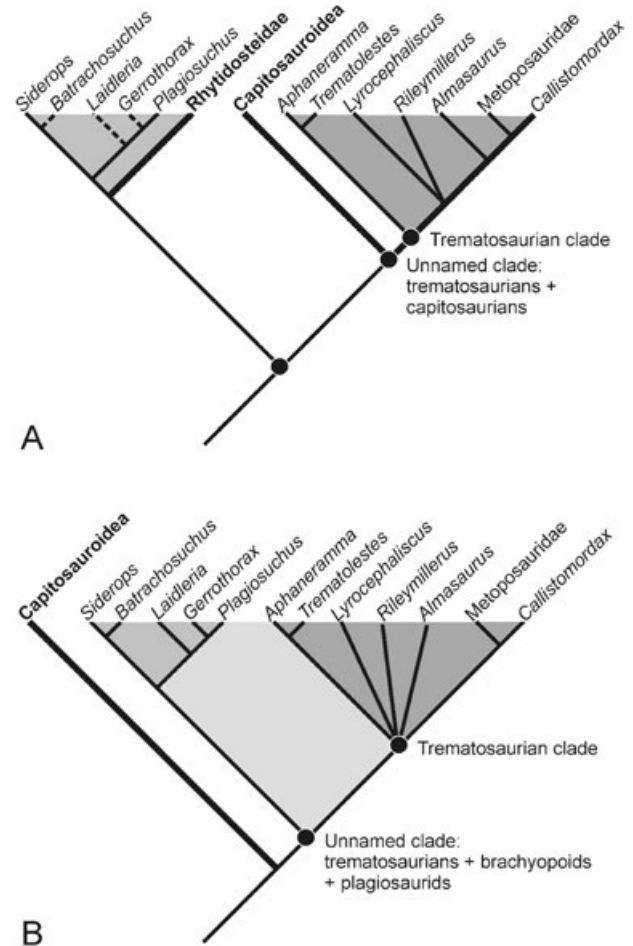


Figure 11. Comparison of alternative hypotheses (consensus trees) derived from variant cladistic analyses. A, pretrematosaurian hypothesis (including Rhytidosteidae); B, trematosaurian hypothesis (excluding Rhytidosteidae).

very poorly resolved, with a basal polytomy that gives six alternative most parsimonious trees. The differences to the pretrematosaurian hypothesis are as follows: the short-skulled stereospondyls – brachyopids, chigutisaurids, *Laidleria*, and the two plagiosaurids – are nested with the trematosaurian clade, forming its sister taxon. The trematosaurian clade proper forms a polytomy with the following constituents: (1) a clade including *Aphaneramma* plus *Trematolestes*; (2) *Lyrocephaliscus*; (3) *Almasaurus*; (4) *Rileymillerus*; and finally (5) a clade encompassing the Metoposauridae plus *Callistomordax*. (In the strict Adams consensus tree variant, *Lyrocephaliscus*, *Almasaurus*, the Metoposauridae, and *Callistomordax* form successive sister groups, whereas *Rileymillerus* falls outside and is nested with the basal trematosaurian polytomy). In all variants of this analysis, the capitosauroids thus form the sister group of trematosaurians plus the short-skulled stereospondyls. Each

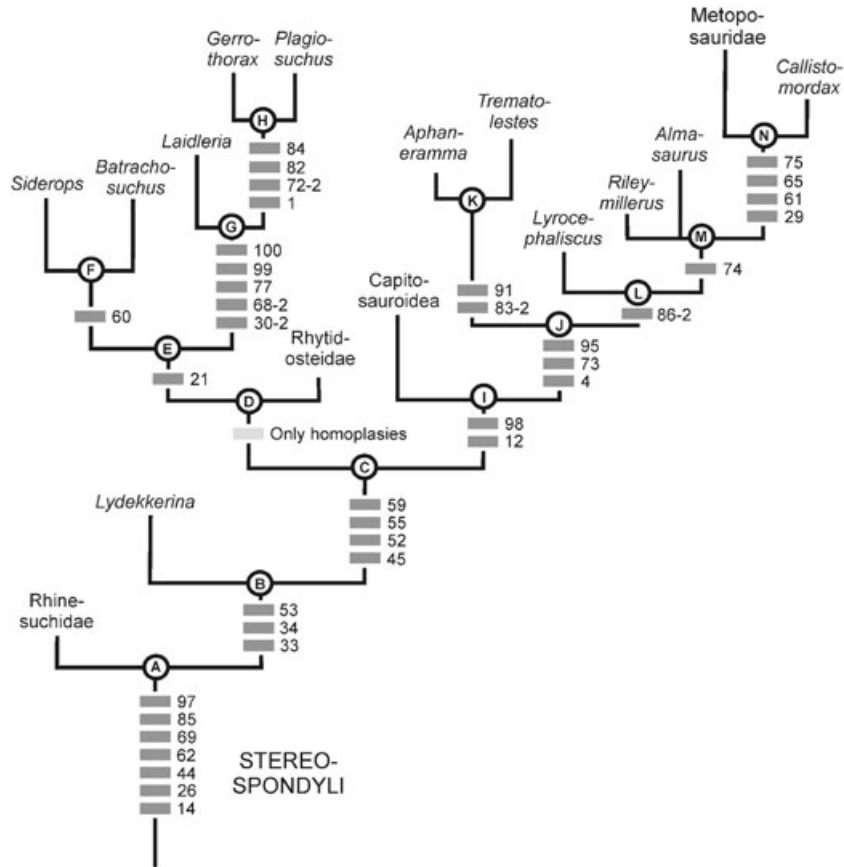


Figure 12. Supporting synapomorphies, mapped onto a cladogram of the preferred phylogeny. Only unequivocal character distribution is counted here as synapomorphy.

of the six topologies requires 219 steps and has a consistency index of 0.543, a retention index of 0.721, and a rescaled consistency index of 0.392.

Preferred phylogeny (Figs 10, 11A, 12): The hypothesis found to be more plausible here is the pretrematosaurian hypothesis. The reasons for the preference are threefold: (1) it does not exclude ‘problematic’ taxa such as the rhytidosteids; (2) some of the characters supporting the trematosaurian hypothesis are either multiply homoplastic (i.e. they occur even outside stereospondyls), or are inadequately understood at present; and (3) a calibration of the two hypotheses with the fossil record reveals that the pretrematosaurian hypothesis requires markedly shorter ghost lineages than the trematosaurian hypothesis (Fig. 13).

In the following section I discuss all nodes on Figure 10 with regard to their former appearance in the literature, their support from characters, and their relative robustness, as assessed by the decay-testing procedures Bootstrap and Bremer, both of which were performed in PAUP 3.1. To make the results easier to read, I use the operational abbreviation

‘BPR clade’ for the possibly monophyletic assemblage of brachyopids, chigutisaurids, *Laidleria*, the plagiosaurids, and the rhytidosteids. The name ‘trematosaurian clade’ will be used for the probable monophylum formed by trematosaurids, *Lyrocephaliscus*, *Almasaurus*, *Rileymillerus*, the metoposaurids, and *Callistomordax*.

Node A: The present analysis supports a monophyletic Stereospondyli. This includes rhinesuchids, *Lydekkerina*, the BPR clade, the capitosauroids, and the trematosaurian clade. Stereospondyls as such have been proposed by Yates & Warren (2000) and Yates (1999), whereas Schoch & Milner (2000) excluded both the plagiosaurids and brachyopids from the Stereospondyli proper. The present analysis supports this clade robustly, with seven synapomorphies (characters 14, 26, 44, 62, 69, 85, and 97), six steps of Bremer support, and a 96% Bootstrap.

Node B: All postrhinesuchid stereospondyls. Most of the recent phylogenetic studies place *Lydekkerina* in a slightly advanced position with respect to rhine-

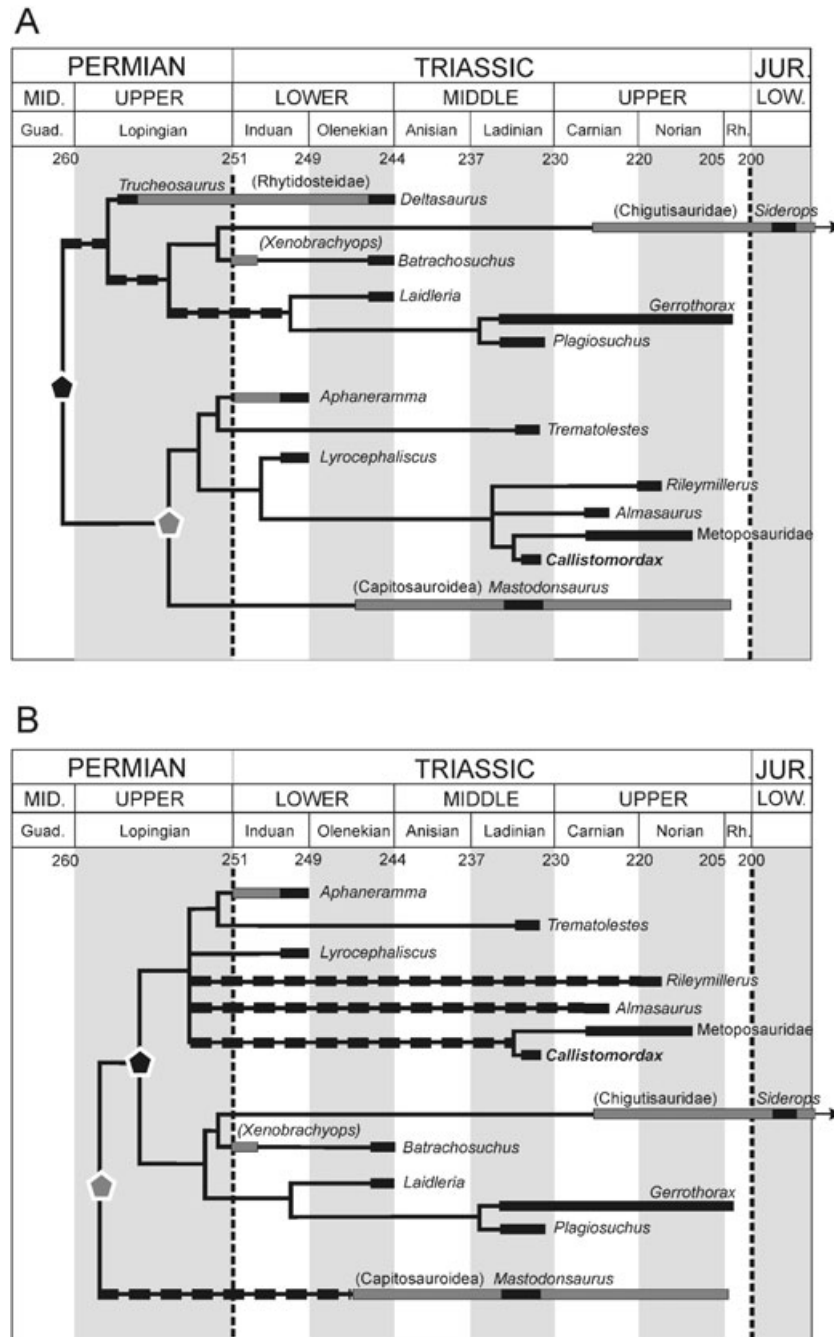


Figure 13. Stratigraphical calibration of the two phylogenies discussed in the text. A, pretrematosaurian hypothesis (preferred phylogeny); B, trematosaurian hypothesis. Bold dashed lines mark ghost lineages that are substantially longer than in the alternative scenario, pentagons mark origin of major clades.

suchids, regardless of whether the latter form a clade or a grade. Here, this hypothesis is supported by three synapomorphies (33, 34, and 53), one step of Bremer support, and a 74% Bootstrap.

Node C: Stereospondyls higher than rhinesuchids and lydekkerinids. This is in accordance with Yates &

Warren (2000), but contradicts the concept of Schoch & Milner (2000) and Damiani & Yates (2003), who both found (at least) the rhytidosteids to be nested with the Lydekkerinidae. The present hypothesis is firmly supported by four synapomorphies (45, 52, 55, and 59), five steps of Bremer support, and a 99% Bootstrap.

Node D: BPR clade (all short-skulled stereospondyls: Chigutisauridae, Brachyopidae, *Laidleria*, Plagiosauridae, and Rhytidosteidae). First suggested by Warren & Black (1985) and underscored with a cladistic analysis by Yates & Warren (2000), the monophyly had been doubted by Milner (1990) and Schoch & Milner (2000). In the present analysis the hypothesis of a monophyletic BPR assemblage is suggested, although it lacks support from unequivocal synapomorphies, and relies on two steps of Bremer support and a Bootstrap of below 50%.

Node E: Brachyopoidea plus (Plagiosauridae plus *Laidleria*). This clade has not been found by previous authors; Yates & Warren (2000) suggested a similar grouping but included rhytidosteids, which they conceived more derived than plagiosaurids and *Laidleria*, forming the sister taxon of the brachyopoids. The group proposed here is supported by one synapomorphy (character 21), two steps of Bremer support, and a 80% Bootstrap.

Node F: Brachyopoidea (Chigutisauridae plus Brachyopidae). This clade was proposed by Warren & Hutchinson (1983), and found by Warren & Black (1985) and Yates & Warren (2000) to be monophyletic. In the present hypothesis it is supported by one synapomorphy (60), three steps of Bremer support, and a 70% Bootstrap.

Node G: Plagiosauridae plus *Laidleria*. This clade was first found by Yates & Warren (2000). Here it is supported by five synapomorphies (characters 30-2, 68-2, 77, 99, and 100), three steps of Bremer support, and an 82% Bootstrap.

Node H: Plagiosauridae (*Gerrothorax* plus *Plagiosuchus*). Plagiosaurids have mostly been considered a robust monophylum (Watson, 1919; Romer, 1947; Panchen, 1959; Yates & Warren, 2000). In the present hypothesis, plagiosaurid monophyly is firmly supported by four synapomorphies (characters 1, 72-2, 82, 84), seven steps of Bremer support, and a 100% Bootstrap.

Node I: Capitosauroida plus trematosaurian clade. This clade was recognized by Milner (1990) and Schoch & Milner (2000) but not by Warren & Black (1985) and Yates & Warren (2000), who found the BPR clade nested within their Trematosauria. The case for a capitosaurian-trematosaurian 'superclade' is not particularly strong, being supported by only two synapomorphies (characters 12 and 98), one step of Bremer support, and a Bootstrap of below 50%.

Node J: Trematosaurian clade. A very similar group has been suggested by Milner's (1990) phylogenetic study, followed by Schoch & Milner (2000) and Damiani & Yates (2003). Steyer (2002) disagrees, excluding *Almasaurus* and the Metoposauridae from the trematosaurian clade, whereas Warren & Black (1985) and Yates & Warren (2000) added the entire BPR clade to their Trematosauria. The trematosaurian clade as defined here is supported by three synapomorphies (characters 4, 73, and 95), three steps of Bremer support, and a 62% Bootstrap.

Node K: *Aphaneramma* plus *Trematolestes*. The monophyly of these two well-preserved trematosaurians is supported by two synapomorphies (characters 83-2, 91), two steps of Bremer support, and a 60% Bootstrap.

Node L: *Lyrocephaliscus* plus (*Almasaurus*, *Rileymillerus*, Metoposauridae, and *Callistomordax*). This new grouping is supported by one synapomorphy (character 86-2), one step of Bremer support, and a Bootstrap below 50%.

Node M: *Almasaurus*, *Rileymillerus*, plus (Metoposauridae plus *Callistomordax*). This unresolved trichotomy is supported by one synapomorphy (character 74), three steps of Bremer support, and a Bootstrap of 56%.

Node N: Metoposauridae plus *Callistomordax*. This clade is supported by four synapomorphies (characters 29, 61, 65, and 75), two steps of Bremer support, and a 73% Bootstrap.

DISCUSSION

Before the two divergent hypotheses are discussed, it should be emphasized that the present analysis is necessarily constrained and incomplete. Limited by the need to keep the number of taxa at an operational level, various interesting taxa, such as the derwentids (see Schoch & Milner, 2000 for a definition), lonchorhynchine trematosaurids (Welles, 1993), and other trematosaurians (Damiani & Yates, 2003; Damiani, 2004), had to be left out. However, Steyer (2002), Damiani & Yates (2003), and Schoch (2006) have recently worked on a phylogeny of trematosaurians, where no clear consensus could be reached.

Likewise, the relationship of the dvinosaurians – a clade suggested by Yates & Warren (2000) to encompass trimerorhachids, saurerpetontids, *Dvinosaurus*, and tupilakosaurids – was not the focus of interest here. The present study accepts Yates & Warren's (2000) concept of dvinosaurians being relatively primitive temnospondyls, as opposed to brachyopoids

(brachyopids plus chigutisaurids), which here nested deeply within a monophyletic Stereospondyli. Among these, I included only the brachyopoids that were also found to be monophyletic here.

The stem of the Stereospondyli has been focused on by Boy (1990), Gubin (1997), Yates & Warren (2000), Schoch & Milner (2000), and Witzmann & Schoch (2006), who came to broadly similar conclusions. *S. haeuseri*, the best known among the most primitive stereospondylomorphs, is here considered the most closely related outgroup of the analysed set of taxa.

Pre-trematosaurian origin of brachyopoids and plagiosaurids

In the hypothesis preferred here, brachyopoids, *Laidleria*, and plagiosaurids originated before the trematosaurian–capitosaurian dichotomy. On a general scale, this was suggested by Milner (1990) and Schoch & Milner (2000), but these authors sought the origin of both brachyopids and plagiosaurids outside the stereospondyls, and linked chigutisaurids with lydekkerinids.

In the present scenario, brachyopids and chigutisaurids are sister taxa nested with *Laidleria* and the plagiosaurids. The rhytidosteids form the most primitive branch of that short-skulled clade, or equally likely a grade at their stem. Several clearly plesiomorphic character states of rhytidosteids highlight the plausibility of that concept, as do the primitive features shared by plagiosaurids and rhytidosteids.

Palatine ramus of pterygoid (character 53 and 58): In temnospondyls, the anterior ramus of the pterygoid was subject to manifold modifications, in most cases involving a thinning or foreshortening of the ramus (Milner, 1990). In capitosauroids and the large trematosaurian clade defined here, the pterygoid fails to reach both the vomer and the palatine. The only exceptions are taxa in which an apomorphic posteromedial projection of the palatine contacts the pterygoid. In brachyopoids, *Laidleria*, and plagiosaurids, a similar morphology is established, but always without a posteromedial process of the palatine. This potential synapomorphy of capitosauroids, trematosaurians, and short-faced stereospondyls is weakened by the rhytidosteid *Deltasaurus*, which possesses a well-established contact between the pterygoid and palatine. This character distribution suggests short-skulled stereospondyls evolved the reduced pterygoid in parallel with capitosauroids and trematosaurians. The frequent reduction of the pterygoid in taxa as far apart as dissorophoids, zatracheids, plagiosaurids, and capitosauroids makes a convergent acquisition of a reduced pterygoid plausible.

Shagreen of palatal denticles: The retention of additional tooth patches on the vomer, palatine, and ectopterygoid is a plesiomorphic character state retained by rhytidosteids. These palatal bones are covered by small teeth in rhinesuchids and the more primitive stereospondylomorphs (Schoch & Milner, 2000; Witzmann, 2006). In combination with other characters, this suggests the clade branched before the capitosaurian–trematosaurian dichotomy.

Anterior palatal vacuity (character 43): The palatal vacuity of lydekkerinids, capitosauroids, brachyopoids, rhytidosteids, and plagiosaurids is unpaired, and the very similar outline of the anterior palatal depression in rhinesuchids suggests this to be the primitive condition. (In rhinesuchids the anterior palate may be perforated, but then differs from all other cases in being tiny and deeply emplaced within a much larger unpaired depression, see Schoch, 2000.) Early in the evolution of the trematosaurian clade a wide medial bridge separated the anterior palatal opening in the midline, which is retained throughout the trematosaurian clade as defined here. In capitosauroids, such a medial subdivision evolved at least twice: once in mastodontosaurids and a second time within the cyclotosaurids (Schoch, 2000). The primitive condition for capitosauroids was a heart-shaped unpaired opening.

Knife-edged cultriform process (character 50): Trematosaurians are readily recognized by this derived feature, and even highly derived taxa such as *Almasaurus* and *Callistomordax* retain this. Metoposaurids lack this condition, instead having a greatly expanded and flattened parasphenoid that obviously evolved after *Callistomordax* separated from the metoposaurid stem line. None of the short-skulled stereospondyls has a knife-edged cultriform process.

Trematosaurian origin of brachyopoids, Laidleria, and plagiosaurids

This concept was outlined and developed by Warren & Black (1985) and Yates & Warren (2000). In the present analysis, it is only supported in those variants of the analysis in which rhytidosteids are excluded from the data matrix. The reason for this is that it prevents the plesiomorphic character states of rhytidosteids to outweigh the derived character states shared between some or all taxa of the trematosaurian clade and the short-skulled stereospondyls. *Laidleria*, which has previously been considered as a rhytidosteid relative (Schoch & Milner, 2000), was not found to be closely related with the ATM clade, and its exclusion does not affect the resulting topology. I have not dealt with the in-group phylogenies of brachyopids, chigutisaurids, or rhytidosteids. The various papers of Anne

Warren and coworkers have covered these questions in depth, and suggested that the relationship may be more complicated than a simple 'two families – two clades' solution (Warren & Hutchinson, 1983; Warren & Black, 1985; Damiani & Warren, 1996; Marsicano & Warren, 1998; Warren, 1998; Warren & Marsicano, 2000; Yates & Warren, 2000).

Location of orbit (character 5): In stereospondyls the lateral placement of the orbits is shared by all taxa of the BPR clade, and also by all representatives of the trematosaurian clade. However, this state evolved in parallel at least once outside the Stereospondyli, namely in the vast dvinosaurian clade (Milner, 1990; Warren, 1999).

Tusks keeled (character 35): Carinate fangs are present in brachyopoids (Warren & Davey, 1992), and in some taxa of the trematosaurian clade. Within the metoposaurids, keeled tusks and marginal teeth have been reported in *Metoposaurus* (Milner & Schoch, 2004), but poor preservation or inadequate preparation of other material precludes an assessment of this character in other metoposaurids at the moment. However, the occasional presence of carinate teeth in other temnospondyls (*Cyclotosaurus*, Kuhn, 1942; *Sclerocephalus*, R. R. Schoch, pers. observ.) suggests that this state must have arisen at various times in parallel.

Characters of unclear significance

Lacrimal presence (characters 7 and 8): This is a critical character to any phylogenetic study of stereospondyls. Brachyopoids, rhytidosteids, and *Laidleria* have no lacrimal, and in some trematosaurids, some metoposaurids, *Rileymillerus*, and in *Callistomordax* the element is in an unusual position and/or has a peculiar morphology. Bolt & Chatterjee (2000) suggested that in *Rileymillerus* the tiny element wedged in between the jugal and prefrontal is a laterally exposed palatine (LEP) rather than a lacrimal. If this be the case, such a structure would have formed convergently to the condition in dissorophids (Bolt, 1974), saurerpetontids (Sequeira, 1998), and tupilakosaurids (Marsicano & Warren, 1998). In an LEP, the palatine forms an ornamented dorsal projection set into the rim of the orbit. However, in *Callistomordax* the palatine and its supposed dorsal projection are separated by disruption along a horizontal plane, suggesting that they were attached by means of a suture rather than forming a unit. This does indeed indicate that the small element may be a lacrimal that failed to expand anteriorly, or alternatively – as is probably the case in *Trematolestes* (Schoch, 2006) – it was overplated by the prefrontal and maxilla, respectively. The absence of a lacrimal in

rhytidosteids, brachyopoids, and *Laidleria* represents a shared derived state, but the condition in plagiosaurids is uncertain. Despite having been figured as possessing a lacrimal in the plesiomorphic position, I found no unequivocal evidence of a lacrimal being present in any of the skulls I examined (contra Hellrung, 2003). This leaves the question unsettled, and poses an additional problem to the already difficult homology question just outlined. Hence, without any substantial new data on the plagiosaurids, or the sutural structure of the 'lacrimal' region in brachyopoids, rhytidosteids, and many trematosaurids, there will be no clarification of this point.

Ribs with uncinata spines (character 81): This feature is very interesting yet confined to the few taxa of which articulated finds are available, in particular *Trematolestes* and *Callistomordax*. As all other derived character states suggest that these two genera are not intimately related, the possession of such elongated spines must be a more widespread feature, probably characterizing a grade within the trematosaurian clade, similar to the possession of a knife-edged parasphenoid.

Narrow intercentra (character 73): This feature is again restricted to a few trematosaurian taxa, and, among the available material, it is best exemplified by the *Trematolestes* and *Callistomordax*.

Relationships of the Plagiosauridae

The plagiosaurids have not formed the focus of the present study, but their inclusion is believed to be critical to the analysis. The findings of the present analysis corroborate the data of Yates & Warren (2000), in which the small (yet unfortunately imperfectly known) *Laidleria* appears to form a plausible sister taxon. A critical synapomorphy, the carapace of dorsal osteoderms, is perhaps not as convincing, as dermal ossicles are known from several other, more distant temnospondyls: dissorophids (DeMar, 1966), trematopids (Berman, Reisz & Eberth, 1985), *Peltobatrachus* (Panchen, 1959), and *Sclerothorax* (Schoch *et al.*, 2007). On the other hand, none of these taxa has a laterally widened carapace and correlated rib cage (character 100), tiny postfenestral windows (character 30-2), or lacks pleurocentra, whereas the intercentra are greatly enlarged and tightly fitting (character 77). Thus, although the transformation of numerous characters remains unknown, *Laidleria* appears to be a rather good candidate in looking for the origin of plagiosaurids. Resolution of this question requires further study of plagiosaurids, particularly the rich material of *Plagiosuchus* and *Plagiosternum* from Germany, as well as a thorough reconsideration

of *Peltobatrachus pustulatus*, which Panchen (1959) suggested as a plagiosaurid relative.

The origin of metoposaurids

All analyses performed for the present study firmly place *Callistomordax* as the sister taxon of metoposaurids, nested above *Almasaurus* and *Rileymillerus*. This provides further evidence for a trematosaurian origin of metoposaurids, a concept first suggested by Milner (1990), expanded by Schoch & Milner (2000), and essentially confirmed by a cladistic analysis in Damiani & Yates (2003). The divergent topology proposed by Steyer (2002), placing the metoposaurids plus *Almasaurus* outside the Trematosauria proper, is based on a more restricted set of characters, most of which were included in the present analysis. Steyer's (2002) analysis did not consider short-skulled stereospondyls (thereby causing homoplasies shared between these and trematosaurians to be treated as synapomorphies), and included only two postcranial characters. Postcranial characters shared between the almost completely known *Trematolestes* (Schoch, 2006) and *Callistomordax* have turned out to be shared derived states. Along with other postcranial data also shared with *Aphaneramma* and *Lyrocephaliscus*, these postcranial data have a strong impact on the placement of *Callistomordax*, and consequently of the metoposaurids. Most of these postcranial features are not synapomorphic, because they are reversed or modified in metoposaurids, which evolved flattened trunks and stereospondylous intercentra in parallel to capitosauroids and brachyopoids.

The incompletely known *Microposaurus casei* may also be a close relative of *Almasaurus* and the metoposaurid stem. Unfortunately, its lack of sutures resulting from large-scale co-ossification prevents a more definitive assignment of the taxon, although Damiani (2004) has convincingly argued for a platystegid relationship of *Microposaurus*. Skull outline and general proportions of *Microposaurus* match those of *Almasaurus* almost as well as those of *Infectosaurus* and *Platystega*. It is quite possible that platystegids and almasaurids formed a grade within which *Microposaurus* and *Almasaurus* were slightly more advanced towards the metoposaurid condition. Many other features are derived character states shared with some trematosaurians and/or brachyopoids, such as the configuration of the posterior skull table, its ornamentation, the foreshortened preorbital region, and the apomorphic condition of the lacrimal region. *Almasaurus*, *Callistomordax*, and the metoposaurids share only one unequivocal synapomorphy, the quadrangular ventral surface of the intercentrum.

Unlike *Almasaurus* and *Rileymillerus*, *Callistomordax* had already acquired several important metoposaurid synapomorphies: among these, the more

massive medial trochlea of the quadrate (character 61), the occiput with its deep sloping postparietals and tabulars (character 29), and the anteriorly convex intercentrum (character 75-1), are the most outstanding.

On the other hand, the palate of *Callistomordax* retains numerous plesiomorphic features, such as the structure of the basicranium, mixed with autapomorphies like the dentition and many aspects of its postcranial anatomy. The elongation of the trunk, paralleling the situation in dvinosaurians, was accomplished in a unique way: the intercentra formed bulbous, ventrally elongated wedges that despite the rather conventional presacral count of 26–28 amounted to a trunk three times the length of the skull. (This feature may also characterize *Almasaurus*, but the existing postcranial data of that taxon are too poor to permit clarity).

The stereospondyl condition (character 72-1) probably evolved in parallel, once in capitosauroids (*Mastodonsaurus*), a second time in plagiosaurids where the intercentrum became cylindrical (character 72-2), and a third time in metoposaurids. The mid-trunk intercentra of *Mastodonsaurus* and the metoposaurids – which usually form the most fully ossified centra – differ in that those of *Mastodonsaurus* are higher, forming near-perfect circles in transverse outline, as contrasted by transverse ovals in metoposaurids (Dutuit, 1976: fig. 35; Schoch, 1999: figs 28, 31). The neural arches are also substantially higher in capitosauroids as compared with metoposaurids.

In *Dvinosaurus*, *Trimerorhachis*, and *Kourerpeton*, the elongation of the body was produced by an increase in the number of vertebrae (Bystrow, 1938; Olson & Lammers, 1976), and in tupilakosaurids this led to the evolution of diplospondylous, disc-shaped vertebrae (Shishkin, 1973; Warren, 1999), which effectively doubled the number of elements and thereby increased flexibility. This degree of flexibility was obviously not reached by *Callistomordax*.

PALAEOBIOLOGY OF *CALLISTOMORDAX*

Articulated skeletons of *C. kugleri* occur most frequently in mudstones that formed under estuarine conditions. The shallow Lower Keuper Basin, spanning most of Central Europe, was repeatedly flooded by the Tethys. Subsequent regression left a diversified landscape with brackish swamps, larger lakes, and saltwater marshes (Beutler, Hauschke & Nitsch, 1999). Under these conditions, some larger water bodies existed long enough to permit algae, conchostacans, fish, and aquatic tetrapods to invade and form small ecosystems. Such a body of water probably existed at Vellberg, where mudstones rich in organic matter bear a large fauna of fish (hybodontiform

Acrodus, the actinopterygians *Saurichthys*, *Gyrolepis*, *Dipteronotus*, and *Serrolepis*, and juveniles of the dipnoan *Ptychoceratodus*) as well as diverse tetrapods (R. Böttcher, pers. comm.). Marine forms (*Nothosaurus*, *Neusticosaurus*, and *Psephosaurus*) are absent, whereas both 'lacustrine' temnospondyls and chroniosuchians, as well as terrestrial archosaurs and small choristodere-like diapsids, are abundant (Schoch, 2002a; R. R. Schoch, unpubl. data). Furthermore, *Callistomordax* is found in various bonebeds with mixed lacustrine and marine faunas, but it is only represented there by isolated bones. At the type locality, and only in the type horizon, *Callistomordax* is much more abundant with numerous articulated finds, including complete ones such as the holotype, as well as specimens reaching only half the 'adult' skull length of 130–160 mm. Tiny single remains such as interclavicles and skull fragments suggest the taxon was present with small larvae reaching hardly 100 mm in total length. In the type horizon, a low degree of salinity (oligohaline state) is indicated by the presence of the ostracod *Darwinula* sp. and the bivalve *Unionites brevis* (Schoch, 2002a). None of the articulated specimens of *C. kugleri* has any gut or intestinal content. The available data on the fauna suggest that at least one actinopterygian, *Serrolepis* sp., was autochthonous and probably highly abundant in the lake in which the deposit formed. A second taxon, a ceratodontid lungfish, is represented by juvenile skeletons often found in a semiarticulated but highly distorted, condition.

Callistomordax was obviously an able swimmer, as its elongated body proportions suggest, and there are no anatomical features in the vertebral column that would contradict that. The presence of disproportionately large, keeled fangs and the powerful adductor musculature, indicated by the shape of the subtemporal fenestrae, as well as the preglenoid process in the mandible, suggest it may have tackled larger prey items, perhaps rather active animals that struggled fiercely after initial capture. The presence of branchial denticles in the region between the pectoral girdle and mandible indicates the possibility of open gill slits, which would have played a role in underwater feeding. In combination with the lateral line sulci present throughout ontogeny, and the structure of the postcranial skeleton, *Callistomordax* is here concluded to have been a predominantly aquatic animal.

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- (2000), with ‘S & M’ are from Schoch & Milner (2000), with ‘S & R’ from Schoch & Rubidge (2005), and with ‘W & S’ from Witzmann & Schoch (2006), with ‘WA & SN’ from Warren & Snell (1991), and with ‘Y & W’ from Yates & Warren (2000).

Skull roof

- Ornament (elements). Reticulate ridges of various sizes (0), isolated pustules (1).
- Ornament (snout). Polygons or short grooves (0), or mostly radial, elongated grooves (1).
- Ornament (general). Shallow ridges of variable height (0), high ridges throughout (1).
- Ornament (intensive growth). Elongated ridges (‘zones of intensive growth’) confined to snout only (0), or prepineal growth zone established on extended anterior parietal and postorbital (1).
- Orbit location. Medial, framed by wide jugals laterally (0), or lateral emplacement, framed by very slender jugals (1).
- Orbit margins. Raised well above skull plain (0), or flush with roof (1). (D)
- Lacrimal. Present (0), or absent (1).
- Lacrimal position. Long element anterior to orbit (0), or small and confined to lateral orbit margin (1).
- Nasal width. Nasal longer than wide (0), or as wide as long (1).
- Naris position. At lateral margin of snout, opening laterally (0), or set well medially, opening anteriorly (1).
- Lateral line sulci in adults. Present (0), absent (1).
- Infraorbital sulcus. With simple curve on lacrimal (0), or with pronounced S-shaped lacrimal flexure (1). (D)
- Supraorbital sulcus. Passing medial to lacrimal (0), or entering lacrimal (1). (D, S)
- Maxilla, nasal. Maxilla separated from nasal (0), or sutured to nasal (1). (Y & W)
- Maxilla, prefrontal. Separated by lacrimal (0), or in wide contact (1).
- Prefrontal, postfrontal. Sutured (0), or separated by frontal (1). (D, S)
- Prefrontal, jugal. Separated by lacrimal (0), or in contact (1).
- Postorbital. Not wider than orbit (0), or with substantial lateral process projecting into jugal (1).
- Postorbital, postfrontal. Shorter than supratemporal and parietal (0), or as long, or longer than supratemporal and parietal (1).
- Otic notch. Semicircular embayment between squamosal and posterior skull table (0), or straight transverse posterior skull margin without embayment between cheek and table (1).

APPENDIX

CHARACTERS ANALYSED

Characters marked with ‘B & C’ are from Bolt & Chatterjee (2000), with ‘D’ are from Damiani (2001), with ‘D & Y’ are from Damiani & Yates (2003), with ‘M’ are from Milner (1990), with ‘S’ are from Schoch

21. Supratemporal. Longer than wide (0), or quadrangular, giving a foreshortened posterior skull table (1).
 22. Jugal (ventral process). No ventral outgrowth (0), or insula jugalis framing subtemporal window (1).
 23. Jugal (anterior extension). Jugal ending at or behind level of anterior orbit margin (0), or extending anteriorly (1).
 24. Intertemporal. Present (0), or absent (1).
 25. Squamosal, tabular. Separated by supratemporal (0), or sutured (1).
 26. Squamosal, falciform crest. Posterior rim of squamosal straight (0), or with convex projection, referred to as falciform crest (1).
 27. Tabular, horn. Tabular forming substantial posterior or posterolateral projection (0), or with blunt end (1).
 28. Posterior skull rim. Cheek posterior to tabular horns (0), or at one level (1).
- Occiput*
29. Occipital flange. Descending flange of occipital portion of postparietals forming a bulge (0), or long smooth blades as long as the dermal portion of the postparietal (1).
 30. Postfenestral window. Large opening, having at least double the width of the foramen magnum (0), much smaller than the foramen magnum (1), or reduced to a tiny foramen (2). (Y & W)
 31. Quadrate and occipital condyles. Quadrate condyles posterior to occipital ones (0), at same level (1), or well anterior (2). (Y & W)
 32. Paraquadrate foramen (quadratojugal). Absent (0), or present (1). (Y & W)
- Palate*
33. Dentition (marginal). Heterogeneous, varying sizes and distances (0), or homogeneous, small teeth, equidistant (1). (S, S & M)
 34. Dentition (marginal, tooth bases). Round or oval (0), or forming transversely broadened ovals (1). (S, S & M)
 35. Palatal tusks (cross section). Round or oval (0), or laterally compressed and keeled on at least one side (1). (B & C)
 36. Dentition (vomer). Tooth patches present at least in small specimens (0), or dentition entirely restricted to vomerine fangs (1).
 37. Dentition (vomerine tusks). Sockets aligned sagittally (0), or transversely (1).
 38. Transverse tooth row (transvomerine). Absent (0), or present (1). (S & M)
 39. Parasphenoid shagreen. Tooth patches present (0), or teeth entirely absent (1). (Y & W)
 40. Ectopterygoid, fangs. Present (0), or absent (1). (Y & W)
 41. Anterior palatal opening. Forming a continuous depression on the vomer (0), or perforated to accommodate symphyseal fangs (1).
 42. Anterior palatal depression. Posterior rim round (0), or straight transverse (1). (S, S & M)
 43. Anterior palatal opening(s). Unpaired (0), or paired (1). (D & Y)
 44. Basicranium, contact. Joint between basal plate and pterygoid (0), or sutural contact (1).
 45. Basicranium, suture. Suture much shorter than basal plate, reaching at best 40% of its length (0), or suture almost as long as basal plate (1).
 46. Parasphenoid. Suturing with exoccipitals (0), or underplating exoccipitals (1).
 47. Basicranium, carotids. Internal carotids entered basicranium ventrally near base of cultriform process (0), or at posterolateral corner of bone (1).
 48. Parasphenoid, plate. Basal plate quadrangular or wider than long (0), or sagittally rectangular (1).
 49. Cultriform process (width). Base not wider than rest, clearly set off from basal plate (0), or merging continuously into plate (1).
 50. Cultriform process (shape). Ventrally flat (0), knife-edged and keel-shaped (1), or with ridge emplaced on broader base (2).
 51. Parasphenoid (muscular pockets). Posterolateral corner with faint depressions or smooth (0), housing large pockets (1), or pockets entirely absent (2).
 52. Parasphenoid (posterolateral process). Posterolateral margin straight (0), or with lateral wing (1).
 53. Pterygoid, vomer. Pterygoid and vomer in contact (0), or separated by palatine (1).
 54. Pterygoid, ventral ornament. Palatine ramus of pterygoid smooth (0), or ornamented with reticulate ridges (1).
 55. Pterygoid, exoccipital. No contact (0), or sutured lateral to parasphenoid (1).
 56. Pterygoid width. Palatine and quadrate regions forming slender rami (0), or broad shelves (1).
 57. Pterygoid, ectopterygoid. Palatine ramus exclusively formed by pterygoid (0), or with posteromedial projection of ectopterygoid.
 58. Pterygoid, palatine, ectopterygoid. Pterygoid contacting both ectopterygoid and palatine (0), or pterygoid only in contact with ectopterygoid (1).
 59. Palatine, vomer. Suture aligned posterolaterally (0), or with medial wing framing the interpterygoid vacuity anteriorly (1).
 60. Palate structure. In occipital view, pterygoids either sloping continuously ventrolaterally or flat horizontal (0), or vertically downcurved at right angle with basicranium (1).
 61. Quadrate trochlea (medial bulge). Medial bulge only slightly larger than lateral one (0), or being at least two times longer and twice as wide (1).

62. Occipital condyle. Trilobed, with basioccipital forming ventral part of facet (0), or bilobed exoccipital condyle with reduced basioccipital contribution (1). (M)
63. Exoccipital condyles. Short and broad base, projecting only with their posterior half behind the rim of the skull table (0), or almost the complete element posterior to level of occipital flange (1).

Mandible

64. Retroarticular process. Absent or present as very faint outgrowth (0), or longer than glenoid facet (1).
65. Preglenoid process. Labial side of surangular with straight dorsal margin anterior to glenoid (0), or forming dorsal projection well above the level of the glenoid articulation (1).
66. Meckelian window. Small round or oval opening (0), or elongate window as long or longer than the adductor fossa (1).
67. Symphyseal teeth. No accessory teeth posterior to symphyseal tusks (0), or a transverse row of such teeth (1). (Y & W, D & Y)

Axial skeleton

68. Presacral count. 23–25 vertebrae (0), 27–28 (1), or 20–21 (2) (Character states not ordered). (W & S)
69. Transverse process (orientation). Short, directed posteriorly (0), or distally extended with diapophysis pointing laterally (1).
70. Transverse process (length). Shorter than dorsal spine is high (0), or markedly longer (1).
71. Neural spine (height). Low throughout vertebral column (0), or dorsally extended in posterior portion of trunk and tail (1). (W & S)
72. Intercentrum (shape). Presacral intercentra form simple wedges (0), dorsally closed discs (1), or dorsally closed and elongated cylinders (2). (Y & W)
73. Intercentrum (width). Chordal canal wider than intercentrum high (0), narrower (1). (W & S)
74. Intercentrum (ventral surface). Ventral surface shorter than wide in ventral view, giving transversely rectangular outline (0), or as long as wide, quadrangular (1).
75. Intercentrum anterior surface. Always concave (0), or convex at least in some presacral centra (1). (WA & SN)
76. Parapophysis. Segmental (0), or intersegmental (1). (WA & SN)
77. Pleurocentrum (presence). Ossified (0), unossified (1). (W & S)
78. Pleurocentrum (lateral surface). As large as that of intercentrum (0), or smaller (1). (W & S)
79. Ribs (morphology). Anterior trunk ribs simple rods (0), or with uncinat processes (1). (W & S)

80. Ribs (uncinate blades). If present, small and spine-like (0), or extensive and blade-like (1). (W & S)
81. Ribs (uncinate spines). Short (0), or elongated, as long as shaft (1).
82. Interclavicle (central ornamented area). Rhomboidal (0), or pentagonal and posteriorly widest (1).
83. Interclavicle (proportions). As long as wide (0), 1.3 times as long as wide (1), or more than twice as long as wide (2).
84. Interclavicle (posterior margin). With posterior process (0), or transversely straight (1).
85. Interclavicle (anterior margin). Serrated (0), or smooth (1).
86. Interclavicle, clavicles. Clavicles broadly separated by interclavicle ventrally (0), leaving only a narrow stripe of interclavicle in between (1), or in contact and excluding anterior part of interclavicle from ventral exposure (2).

Limb skeleton

87. Scapula (glenoid facet). Ossified (0), or unossified (1). (W & S)
88. Humerus (supinator). Present (0), or absent (1). (Y & W)
89. Humerus (condyles). Distal end narrow (0), or broadened to give extensive condyles (1). (S & R)
90. Humerus (torsion). Strong, 70–90° (0), or weak, well below 60° (1). (W & S)
91. Humerus (shape). Tetrahedral, with both ends wider than shaft (0), or only distal end wider than shaft because of rudimentary proximal head (1).
92. Ilium (dorsal portion). Anterior margin of shaft straight (0), or concave (1).
93. Ilium (dorsal end). Tip of dorsal end continuous (0), or much broadened (1).
94. Ilium (height). Shaft more than twice the length of the base (0), or shorter (1). (S & R)
95. Ilium (shaft). Shaft inclined posterodorsally (0), or vertical (1).
96. Pubis. Unossified (0), or ossified (1). (W & S)
97. Femur. Intercondylar fossa forming deep and elongated trough (0), or reduced to short depression (1). (Y & W)

Postcranium, general

98. Gastral squamation. Ossified dermal scutes (0), or dermis naked (1). (Y & W, W & S)
99. Dorsal squamation. Dorsal region naked (0), or covered by dermal ossicles (1). (W & S, S & R)
100. Rib cage. Trunk narrower than skull or as wide (0), or trunk substantially wider than lateral margin of cheeks at about mid level (1).

Table A1. Character–taxon matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
	<i>Den</i>	<i>Tri</i>	<i>Sec</i>	<i>Ura</i>	<i>Lyd</i>	<i>Sid</i>	<i>Bra</i>	<i>Lai</i>	<i>Rhy</i>	<i>Ger</i>	<i>Pla</i>	<i>Cap</i>	<i>Aph</i>	<i>Tre</i>	<i>Lyr</i>	<i>Ril</i>	<i>Alm</i>	<i>Met</i>	<i>Cal</i>
1. Ornament type	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
2. Ornament of snout	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0
3. Ornament, ridges	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1
4. Ornament zones	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
5. Orbit location	0	0	0	0	0	1	1	1	1	0	0	0	1	1	1	1	1	1	1
6. Orbit margin	0	0	0	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1
7. Lacrimal presence	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
8. Lacrimal position	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	?	1	1
9. Nasal width	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	?	0	1	1
10. Naris position	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	?	1	1	1
11. Lateral line sulci	1	0	1	0	0,1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
12. Infraorbital flexure	0	0	?	0	0,1	0	0	0	?	0	0	1	1	1	1	?	1	1	1
13. Supraorbital sulcus	0	0	?	0	0	?	?	?	?	0	0	1	0	0	1	?	1	1	0
14. Maxilla, nasal	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
15. Maxilla, prefrontal	0	0	0	0	0	1	1	1	1	0	0	0	?	1	?	1	1	1	1
16. Pre-, postfrontal	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0
17. Prefrontal, jugal	0	0	1	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	0
18. Postorbital	0	0	0	0	0	1	1	1	1	0	1	0	1	1	1	1	1	1	1
19. Postorbital length	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1	1	1	1
20. Otic notch	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	1	0	0	0
21. Supratemporal	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0
22. Jugal ventral proc.	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	?	0	0	1
23. Jugal anterior ext.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1
24. Intertemporal	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
25. Squamosal, tabular	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
26. Squamosal, crest	0	0	0	1	1	1	1	?	1	?	?	1	1	1	1	0	1	1	1
27. Tabular horn	0	1	0	0	0	0	1	1	0	1	1	1	0	0	0	1	0	0	0
28. Cheek, tabular horn	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
29. Occipital flange	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
30. Post-temporal wind.	0	0	0	0	0	1	1	2	0	2	2	0	0	0	0	0	0	1	1
31. Quadrate, occiput	0	1	0	0	1	2	1	2	1	2	2	1	1	1	1	2	2	2	2
32. Paraquadrates for.	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
33. Marginal teeth	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table A1. Continued

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
	Den	Tri	Sec	Ura	Lyd	Sid	Bra	Lai	Rhy	Ger	Pla	Cap	Aph	Tre	Lyr	Ril	Alm	Met	Cal
34.	Tooth bases	0	0	0,1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
35.	Fangs keeled	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1
36.	Vomer, teeth	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
37.	Vomer, tusks	0	0	0	0	1	1	1	1	1	1	0	0	0	1	1	1	1	0,1
38.	Transver. row vom.	0	1	0	1	1	1	1	1	1	1	1	0	0	1	?	0	0	1
39.	Parasph. shagreen	0	0	0	0	1	1	0	1	0,1	1	1	0	0	0	1	1	1	1
40.	Ectopter., tusks	0	0	0	0	1	1	1	0	1	1	1	0	0	0,1	1	1	0	1
41.	Ant. pal. opening	0	1	0	1	1	1	1	1	0	0	1	1	1	1	?	1	1	1
42.	Ant. pal. fossa	0	1	0	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1
43.	Ant. pal. op. paired	?	?	?	0	0	0	?	0	0	0	0	1	1	1	?	1	1	1
44.	Basiscranial joint	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
45.	Basiscranial contact	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
46.	Parasphen., exocc.	0	0	0	0	0	1	0	0	0	0	0	1	1	1	?	1	1	1
47.	Carotid foramina	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
48.	Parasphen. plate	0	0	0	0	0	1	1	0	0	0	1	1	1	1	1	1	1	1
49.	Cultrif. proc. base	0	0	0	0	0,1	1	1	1	1	1	0	0	0	0	1	0	1	0
50.	Cultrif. proc. ventr.	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1
51.	Muscular pockets	0	0	1	1	2	2	2	2	2	2	1	2	2	2	2	2	2	2
52.	Parasphenoid	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53.	Pterygoid, vomer	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
54.	Pter. vent. ornam.	0	0	1	1	0	1	1	0	0	0	0	0	0	1	0	0	1	0,1
55.	Pterygoid, exocc.	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
56.	Pterygoid stout	0	0	0	0	1	1	1	1	1	1	0	0	0	1	0	0	0	0
57.	Palatine ramus	0	0	0	0	1	1	1	0	1	1	0	0	0	0	?	1	1	1
58.	Palatine, ectopt.	0	0	0	0	1	1	1	0	1	1	0	1	1	1	1	1	1	1
59.	Palatine, vomer	0	0	0	0	1	1	1	1	1	1	1	1	1	1	?	1	1	1
60.	Palate downcurved	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
61.	Quadrate (medial)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
62.	Condyle	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
63.	Exoccipital	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
64.	Retroarticular proc.	0	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1
65.	Preglenoid proc.	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0
66.	Meckelian window	0	0	1	1	1	?	?	?	0	?	2	2	2	?	0	2	2	2

