Skeletal development of the temnospondyl *Acanthostomatops vorax* from the Lower Permian Döhlen Basin of Saxony

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ABSTRACT: The development of the skeleton of the small temnospondyl *Acanthostomatops vorax* is described, based on 32 specimens from the Lower Rotliegend of Niederhäslich in Saxony. Both individually and ontogenetically, the skull table, length of gape, and dentition of the parasphenoid are broadly variable. The stapes has a short and straight shaft and a well-defined two-headed proximal region. Small specimens have three or four pairs of ossified ceratobranchials in the gill region, while the adult hyobranchium is composed of four pairs of hypobranchials and probably some additional elements. The postcranium is characterised by a stout and well-ossified humerus that is already large in small larvae, a minute rectangular interclavicle, a robust but short femur, a relatively short trunk with 21–22 presacrals and a moderate tail with 28 vertebrae. In adults, the trunk skeleton became proportionally shorter and the femur smaller with respect to skull length. Metamorphosis is best indicated by the disappearance of the larval gill skeleton, which was probably resorbed, while the structure of the limbs and axial skeleton as well as the absence of lateral line sulci suggest a terrestrial existence for adults.

KEY WORDS: Hyobranchium, metamorphosis, ontogeny, postcranium, Rotliegend, skull, variability, Zatracheidae.

The zatracheids form a small and still enigmatic clade of possibly terrestrial temnospondyls, which are well-defined by flat and wide, spine-bearing skulls, but whose postcrania are largely unknown. They fall within a larger group of temnospondyls with obvious terrestrial features, such as short bodies, strong limbs, and well-ossified girdles. This group includes the eryopids, dissorophoids and zatracheids, and since it was found monophyletic by Yates & Warren (2000) it has been referred to as the Euskelia. There are two major unsettled questions regarding this assemblage: (1) its potential status as a monophylum and (2) its relationship to the modern amphibians or Lissamphibia, as hypothesised by some authors (see Schoch & Milner 2004 for a recent overview). Both problems need much further work on poorly known members and a description of inadequately understood anatomical regions, with the zatracheids forming a small yet significant cornerstone in this field.

Zatracheids are known from only a few localities on two continents (North America and Europe), with two assemblages having yielded the bulk of the material: the Lower Permian Abo Formation in northern New Mexico, which has produced almost exclusively cranial material of *Zatrachys serratus*, and the Permo-Carboniferous Niederhäslich Formation of Dresden in Germany, which gave the partially articulated skeletons of *Acanthostomatops vorax*. After the initial descriptions provided by Geinitz & Deichmüller (1882), Credner (1883) and Case (1911), Langston (1953), Boy (1989) and Schoch (1997) have revised some aspects of this material, focusing mostly or exclusively on the skull. On the basis of these studies, recent analyses have concluded that zatracheids form a clade somehow related to dissorophoids (Holmes *et al.* 1998), eryopids (Boy 1990), or both (Schoch 1997; Yates & Warren 2000).

Despite the previous descriptions of *Acanthostomatops*, there remain numerous uncertainties regarding the postcranial skeleton, as well as the ontogeny of the entire skeleton. This study seeks to address these problems by reexamining Geinitz & Deichmüller's (1882) and Credner's (1883) original material, which since the end of the Cold War has become more freely accessible.

1. Material

All of the material comes from a thin layer of hard limestone from the same mine at Niederhäslich. It probably formed under lacustrine conditions (Schneider 1994). The skeletons are usually preserved as well-defined imprints, as the rather soft bone weathered easily to leave only a natural mould. In most cases, silicon casting of these moulds gives good results. The data presented here are based on examination of both silicon casts and original moulds.

Throughout the present paper, skull length is used as a measure of size, herein defined as the distance from the tip of the snout to the posterior margin of the postparietals. A total of 31 specimens of *Acanthostomatops* were investigated for this study, with individuals ranging from 13·5 mm to 75 mm in skull length (Fig. 1A). These specimens are housed in the following four institutions:

1. Landesamt für Umwelt und Geologie, Freiberg, Germany. When last described by Boy (1989), these specimens were still located in Dresden. (This material had different numbers before the 1990s, labelled 'S'). In the present study, we refer throughout to the new numbering. (LFUG): 13070 (ventral, 22 mm), 13214 (lectotype, ventral, 33 mm; Credner 1883, pl. 11, fig. 2), 13215 (ventral, 25 mm; Boy 1989, fig. 2a), 13221 (dorsal, circa 17 mm, with postcranium; Credner 1883, pl. 12, fig. 8), 13225 (dorsal, 32 mm), 13227 (ventral, 20 mm, with anterior trunk), 13229 (dorsal, 15 mm, with almost complete postcranium; Steen 1937, fig. 4/3), 13230 (ventral side of 13562, 58 mm), 13231 (ventral, 50 mm), 13232 (dorsal, 55 mm), 13235 (dorsal, 17 mm; Boy 1989, fig. 1a), 13236 (dorsal and ventral, 16 mm), 13237 (ventral, 38 mm), 13240 (dorsal, 17 mm), 13241 (ventral, 13·5 mm),

13244+13245 (ventral and dorsal, 75 mm, with postcranium; Steen 1937, figs 2/5, 4/5, pl. 1, figs 1, 2, pl. 2, fig. 1; Boy 1989, figs 1d, 2b, 3, 4f, g), 13417 (dorsal, 15 mm, with complete postcranium), 13522+13523 (dorsal and ventral, 23 mm, with anterior trunk), 13555 (dorsal, 45 mm, with anterior trunk), 13556 (lectotype counter-slab, dorsal, 33 mm; Credner 1883, pl. 11, fig. 1), 13561 (dorsal, 20 mm), 13562 (dorsal, 58 mm), 13563 (dorsal, 30 mm), 13566+13567 (ventral and dorsal, postcranium with complete tail, fragmentary skull estimated 32 mm on the basis of comparison of the parasphenoid size with that of LFUG-13215 and 13523), 13582+13583 (dorsal and ventral, very slender skull, 32 mm).

2. Naturhistorisches Museum Chemnitz, Germany. (NHMC-F): 9887 (ventral, 26 mm).
3. Staatliches Museum für Naturkunde, Dresden, Germany. (MMG-SaP): 129 (dorsal, 37 mm), 130 (dorsal, 36 mm, with postcranial elements; Geinitz & Deichmüller 1882, pl. 7, fig. 9), 131 (dorsal, 26 mm, with postcranial elements), 132 (dorsal, 34 mm), 743 (dorsal, 38 mm, with postcranial elements). Uncatalogued: disarticulated skull with good parasphenoid (circa 30 mm).
4. Museum für Naturkunde Berlin, Germany. (MB): Am.411 (dorsal, 19 mm, with anterior trunk).

The small skeleton figured by Steen (1937, pl. 2, figs 2, 3, skull length about 15 mm) was the only previously described specimen not available to us; it is not present in any of the above-listed collections.

2. Systematic palaeontology

Temnospondyli Zittel, 1888
Zatracheidae Cope, 1882
Acanthostomatops Kuhn, 1961
Acanthostomatops vorax (Credner, 1883)

1882 *Melanerpeton spiniceps* Geinitz & Deichmüller, pp. 27–30, pl. 8, figs 8–11 partim!
1883 *Acanthostoma vorax* Credner, pp. 277–288, pl. 11, figs 1–6, pl. 12, figs 1–2.
1937 *Acanthostoma vorax* Steen, pp. 491–499, figs 1–4, pl. 1, 2.
1961 *Acanthostomatops vorax* Kuhn, p. 79.
1989 *Acanthostomatops vorax* Boy, pp. 133–151, figs 1–5.

Lectotype. LFUG-13556, skull roof, and LFUG-13214, palate (=S-285+286) (Credner 1883, pl. 11, figs 1, 2). This skull measures 33 mm.

Type horizon. Niederhäslich-Schweinsdorf Formation, Lower Rotliegend, Autunian, ? Asselian (lowermost Permian).

Type locality. Niederhäslich at Freital near Dresden, Saxony, Germany.

Referred material. In addition to the lectotype, 30 specimens have been identified as *A. vorax* and these were all examined for the present study (for complete list see Material section).

Diagnosis. Autapomorphic character-states are: (1) lacrimal and prefrontal project into orbit, (2) quadratojugal with two large lateral spikes and angular with five ventral spikes, (3) interclavicle transversely rectangular and very small, reaching less than half the area of the parasphenoid plate, (4) humerus large and solid from small size on, longer than femur in larger specimens. Characters shared with other temnospondyls: (1) postorbital skull table abbreviated with supratemporals, parietals, and postparietals being especially short; (2) choana laterally constricted by fang bases; (3) pronounced muscular pockets at posterolateral rim of parasphenpoid plate; (4)

deltoid denticle field on base of parasphenoid process and plate; (5) 21–22 presacral vertebrae; (6) humerus with supinator; (7) trunk only 1.6 times longer than skull in adults.

***Non* Acanthostomatops**. The specimen Werneburg (1998, p. 50, figs 1–3) described as a larval specimen of *A. vorax* is actually a medium-sized individual of the micromelerpetontid dissorophoid *Branchierpeton amblystomum* (Credner 1881). In addition to lacking all autapomorphies of *A. vorax*, this small specimen (17 mm skull length) has a different snout morphology and an elongated posterior skull table, the latter being a synapomorphy of micromelerpetontids. Examination of the counterpart of Werneburg's (1998, fig. 1) specimen revealed that there is no internasal fontanelle and that the preorbital region is substantially shorter than in *Acanthostomatops*. Apparently, Werneburg interpreted a fracture in the nasal as the rim of the internasal fontanelle. Likewise, the interclavicle and cleithrum are quite different from those of *Acanthostomatops*, and in the latter the presence of ossified vertebral centra is not observed in specimens smaller than 75 mm skull length. The present authors further agree with Credner (1883, p. 278) in that the isolated postcrania described and figured by Geinitz & Deichmüller (1882, pl. 7, figs 6, 7) as *A. vorax* (*Melanerpeton spiniceps*) are to be referred to *Onchiodon labyrinthicus*.

3. Description

3.1. General outline of the skull

Geinitz & Deichmüller (1882), Credner (1883), Steen (1937) and most notably Boy (1989) have described many aspects of the skeleton in *Acanthostomatops vorax*. Throughout these studies, the adult skull formed the focus of interest, although Boy (1989) listed various ontogenetic changes and reconstructed skulls of different size. He was the first to notice and characterise distinct morphs, coined by him 'narrow skull' and 'wide skull', respectively. The interorbital width, measuring the shortest distance between the orbits, varies particularly in *Acanthostomatops*. The present authors' measurements do not unequivocally reveal such a dimorphic distribution, as the sample of 12 analysed specimens is simply too small (Fig. 1B, C). In our view, the analyzed distribution of morphometric parameters does not confirm a simple dimorphism – to name just the most obvious: jugal width, snout width, snout length, interorbital width, squamosal length, and the shape and size of the internasal fontanelle are all very variable even across this small sample. Boy (1989, p. 139) already highlighted the limited use of the concept of dimorphism by referring to some inconsistent character distributions.

In the case of the ratio of interorbital width against skull length (Fig. 1B), the small specimens (15–38 mm skull length) appear the least variable, plotting within a narrow zone around the 0·2 level. In larger specimens greater than 38 mm, values between 0·18 and 0·3 are reached. Apparently, there was no allometric trend of this parameter at all, although some dimorphism in large specimens cannot be ruled out. The length of the snout (preorbital region) as measured against skull length is also subject to variation (Fig. 1C), but generally increased slightly with age.

3.2. Skull roof

In the present study, we focus on the cranial morphology of the smallest specimens and the developmental changes in *Acanthostomatops vorax*. The most conspicuous feature is the large preorbital region and the poor degree of allometry of most cranial traits (Fig. 2). In small specimens, the preorbital region roughly matches the length of orbits and postorbital skull table combined. The ratio of preorbital length to skull
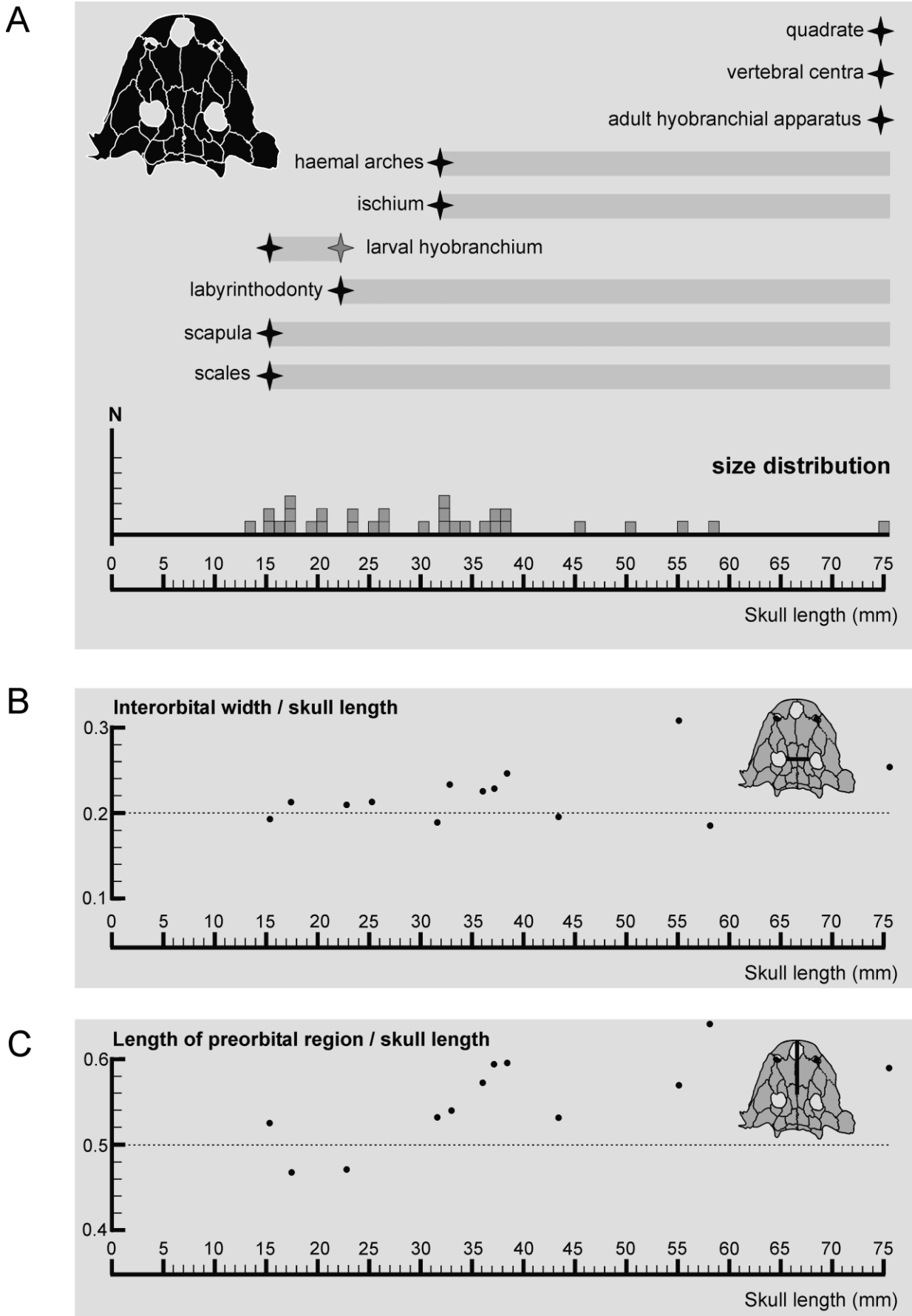
Figure 1 *Acanthostomatops vorax*. (A) size frequency distribution: number of investigated specimens (y axis) mapped against skull length (x axis) and chronology of developmental events (a black asterisk represents first appearance of an ossified element in ontogeny, whereas a grey asterisk marks its last appearance, due to resorption); (B) ratio of interorbital width against skull length (y axis) plotted against skull length (x-axis); (C) ratio of preorbital length against skull length (y axis) plotted against skull length (x-axis).
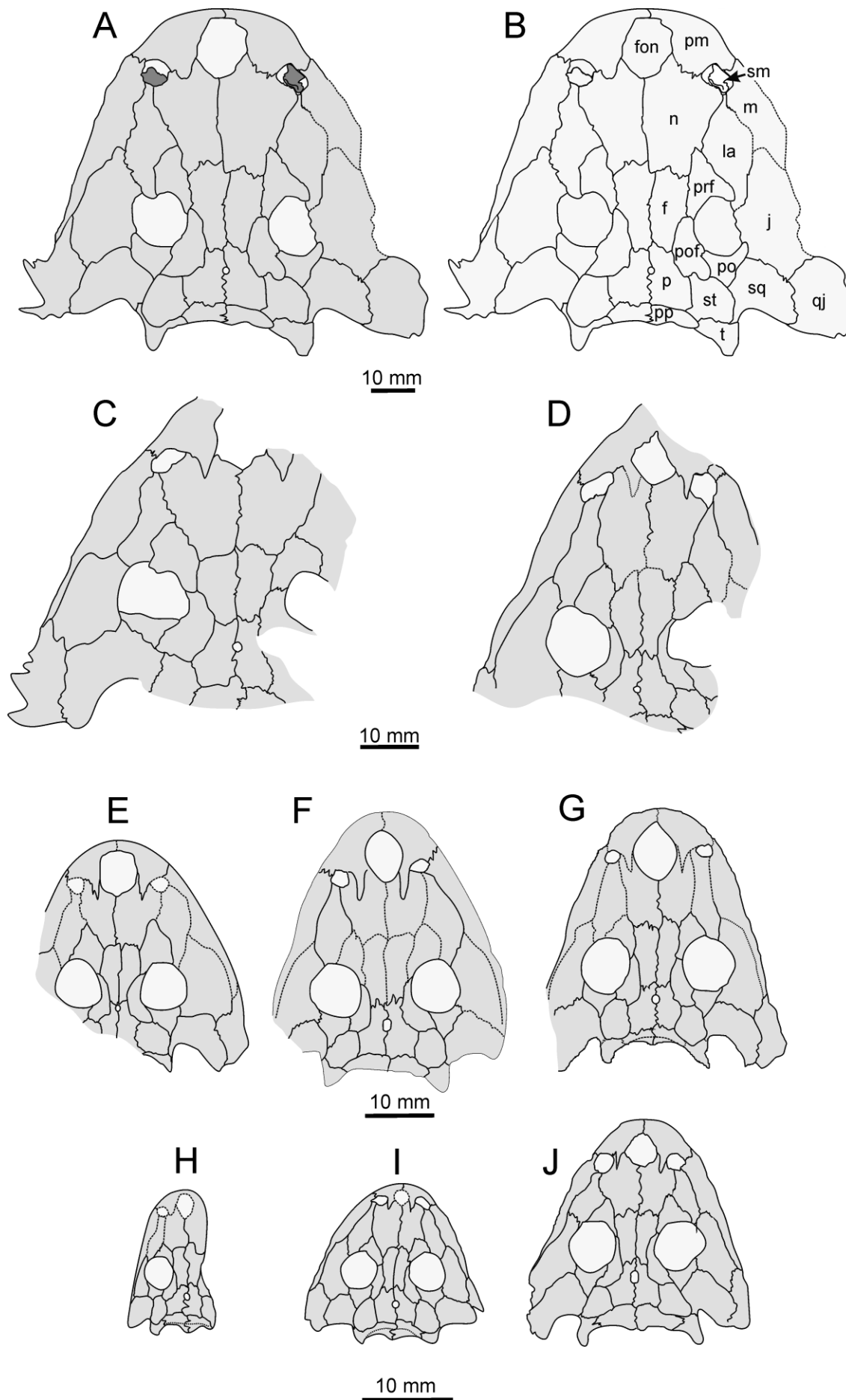
Figure 2 *Acanthostomatops vorax*. Dermal skull roofs of differently sized specimens in dorsal view: (A), (B) LFUG-13245, 75 mm; (C) LFUG-13232, 55 mm; (D) LFUG-13562, 58 mm; (E) LFUG-13556, 33 mm; (F) MMG-SaP-129, 37 mm; (G) MMG-SaP-130, 36 mm; (H) LFUG-13417, 15 mm; (I) LFUG-13235, 17 mm; (J) LFUG-13522, 23 mm.

length ranges from 0·47 in the smallest specimens to 0·64 in large individuals (Fig. 1C). The best-preserved small specimen (LFUG-13417) has a snout-to-skull ratio of 0·52. In this, larvae of *Acanthostomatops* are clearly unique among temnospondyls in having a long snout region from a small size upwards.

3.2.1. Preorbital region. In the smallest larval specimens, the preorbital region already reaches 1·6 to 1·8 times the length of the posterior skull table. This is much higher than in similar-sized larvae of other temnospondyls (*Sclerocephalus*: 0·8–1·3, *Onchiodon*: 1·0–1·2, observation by the present authors). Likewise, the nasal and lacrimal of small *Acanthostomatops* have nearly adult proportions, while the premaxilla experienced a substantial positive allometry within the 23–35 mm range. The same applies to the dorsal internasal fontanelle, which is proportionally largest in slender-skulled specimens.

3.2.2. Skull table and cheek. In general, small skulls already have strongly asymmetrical sutures. For instance, the medial suture between the parietals is strongly serrated. The supratemporal is narrow in 15–20 mm specimens, having an elongated rectangular outline (Fig. 3A, B). In slightly larger skulls (from 23 mm on), the posteromedial part has become wider, constricting the parietal posterolaterally (Fig. 3C). In the large adults, the supratemporal covers an almost quadrangular area, having an irregular outline (Fig. 3D). The parietal is proportionally narrower in the 15–17 mm skulls, with its posterior half being narrower than the anterior one. The postorbital is pointed, forming a near-perfect triangle; in larger specimens, it has more rounded margins and only a faintly pointed end. The prefrontal does not clearly reach the postfrontal in the tiny specimen (LFUG-13417; Fig. 3A), but does so in all larger specimens. Likewise, the anterior portion of the jugal forms only a slender process in 13–17 mm skulls. LFUG-13417 further differs from all others in having a squamosal that does not reach the tabular on the dorsal side; this feature develops slowly with larger size, being most clearly established in adults.

3.2.3. Length of gape. The length and posterior extension of the squamosal and quadratojugal varies in small larvae. While in the 15 mm skull LFUG-13417 the supposedly more mature condition is established with the squamosal at least at the same level as the postparietal (Fig. 3A), the 17 mm LFUG-13235 and the 23 mm LFUG-13522 (Figs 2I, J, 3B, C) have abbreviated squamosals ending level with the parietal-postparietal suture. This may indicate differences in feeding, as the former specimen has a proportionally longer gape. However, this is far from clear as long as a concomittant dimorphism in dentition has not been proven. Variation in gape length persists in large specimens (55 and 58 mm skull length), whilst the 75 mm LFUG-13244+45 has a remarkably short gape (Figs 3D, 4). A proportionally longer gape is mostly found in specimens with narrower preorbital regions, more slender jugals, and narrower interorbital regions and may be correlated. Yet the specimen with the widest skull (LFUG-13232; Fig. 2C) has a quadrate with the most posterior position of the entire sample.

3.2.4. Occipital flange. The smallest specimens have a single and medial, well-developed occipital flange (Fig. 3A–C) that is proportionally larger than in adults – in the small larvae it is even larger than the ornamented part of the bone. In large specimens, the flange descends ventrally, often only visible in ventrally exposed skulls.

3.2.5. Otic notch. A tabular horn is developed from a small size on, in larger specimens forming the bulk of the element (Figs 2, 3). Although it does not reach the length it attains in *Zatrachys* (Schoch 1997), the horn is still larger than

in many other temnospondyls. It is peculiar in being ornamented not only on top, but also along the entire lateral flank, suggesting that skin reached well down into the otic notch region. This implies that the tympanum – assuming that it was present – must have attached to the frame of the otic notch in a different fashion than was supposedly the case in other temnospondyls (Bolt & Lombard 1985), with two alternatives emerging: either (i) the tympanum was embedded more deeply within the notch, much below the level of the skull table, or (ii) it was slit-like, restricted to the squamosal margin, and not reaching the tabular attached to some unknown and unpreserved structure. The latter possibility is suggested by the fact that the squamosal does not have a downcurved ornamented area, as would be expected if the tympanum was located at a much deeper level. The present authors thank Andrew Milner for drawing our attention to this feature. Ventrally, the tabular bears a deep socket for the attachment of the parotic process (Fig. 4), which remained unossified throughout all samples.

3.2.6. Sclerotic ring. Ossified platelets of the sclerotic ring are present even in the smallest complete specimen, there being at least ten elements (LFUG-13417; Fig. 3A); there are no palpebral ossicles as in some dissorophoids of similar size. The medial plates at the postfrontal–prefrontal margin are large and rectangular, whereas the lateral and anterior plates are tiny and quadrangular. In the 58 mm skull LFUG-13562, two lateral plates of the sclerotic ring are exposed in the left orbit, revealing the presence of such a ring also in large *Acanthostomatops*. In most specimens larger than 20 mm skull length sclerotic plates are not observed, but it is possible that they are obscured by sediment.

3.3. Palate

3.3.1. Palatal ossicles. The lectotype preserves numerous tiny, tooth-bearing palatal ossicles similar to those known from many temnospondyls, e.g. *Adamanterpeton* (Milner & Sequeira 1998), *Platyrhinops* (Carroll 1964; Clack & Milner 1994), *Uranocentrodon* (van Hoepen 1915), and trematosaurids (Schoch 2006). In another specimen (LFUG-13523) palatal ossicles are especially numerous and quite large, obviously having covered the interpterygoid vacuities. The tiny teeth attached to them are similar in morphology to those of the pterygoid and vomer. In the 38 mm skull MMG-Sap-743, large palatal ossicles are present at the periphery of the anterior palatal fontanelle, whilst in the 75 mm LFUG-13245 most of the dentigerous palatal ossicles are unusually tiny (Fig. 4).

3.3.2. Parasphenoid. This bone underwent an interesting ontogeny and shows extensive individual variation (Fig. 5B–G). In a 20 mm skull (LFUG-13227; Fig. 5E) the parasphenoid is dominated by a large deltoid denticle field that occupies the entire centre of the parasphenoid plate and continues far onto the cultriform process. The posterolateral corners of that field are pointed and merge into small posterolateral wings, recalling the situation in *Lydekkerina* (Shishkin *et al.* 1996), and the posterior margin of the tooth patch is markedly concave. The parasphenoid plate still lacks the prominent muscular pockets of those from larger size classes, although the small posterolateral wings may well form the lateral margins of such muscle attachments. The basipterygoid processes are simple yet prominent, attaching by means of an overlapping suture to the medial rami of the pterygoids. The denticle field is clearly set off from the basipterygoid processes by grooves parallel to the margin of the field. In LFUG-13215 (25 mm skull length; Fig. 5F) and a similar-sized, disarticulated specimen (MMG-SaP uncatalogued), the denticle field is smaller and more restricted to the anterior part of the parasphenoid plate. In these and larger specimens, the outline of the denticle field varies from broad deltoid with pointed lateral ends to narrow with
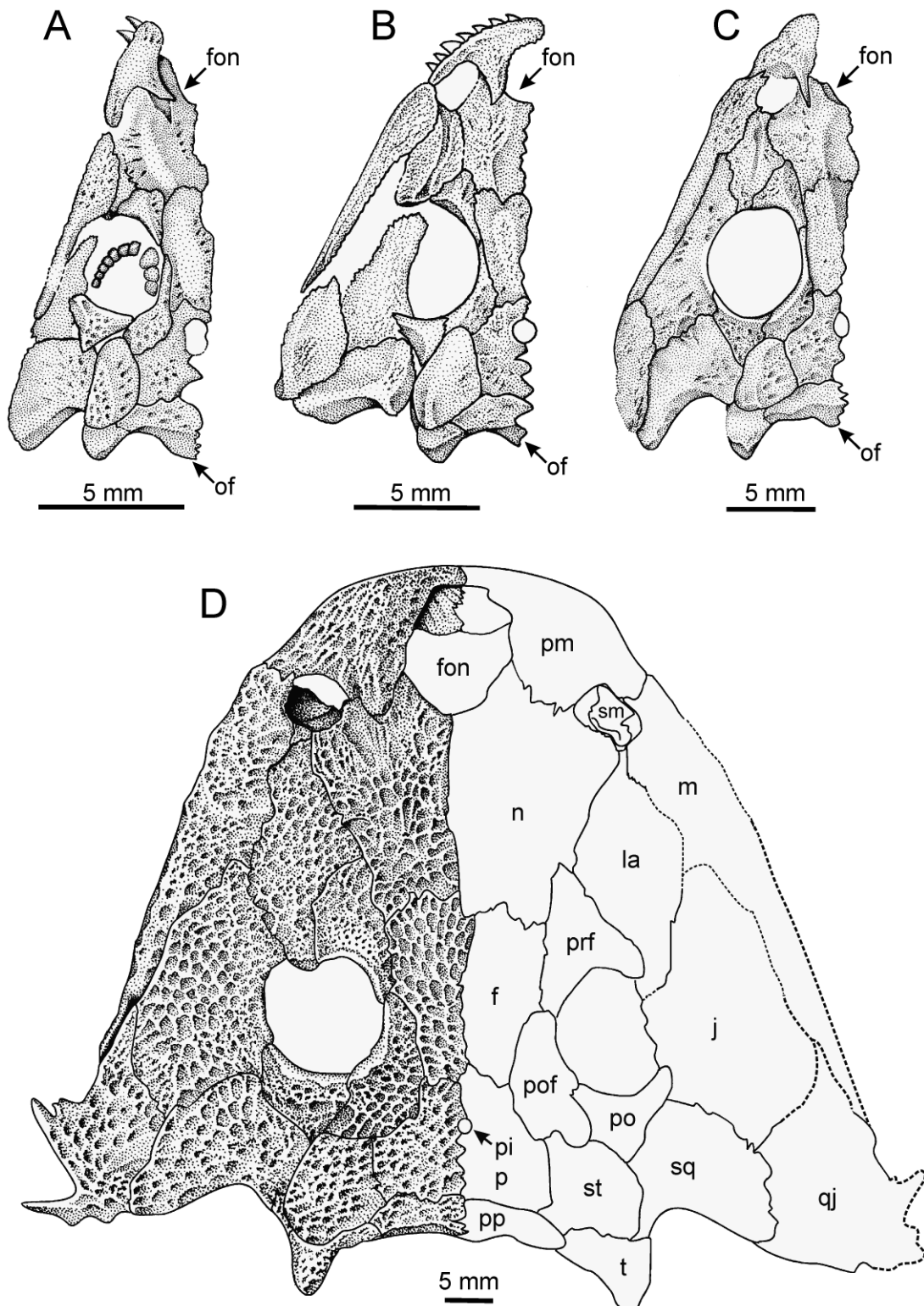
Figure 3 *Acanthostomatops vorax*. Sculptural development of the dermal skull roof: (A) LFUG-13417, 15 mm; (B) LFUG-13235, 17 mm; (C) LFUG-13522, 23 mm; (D) LFUG-13245, 75 mm.

rounded posterior margin and not set off from the anterior part emplaced on the cultriform process. The best-preserved parasphenoid is that of LFUG-13566+13567, where the element is completely exposed from both ventral and dorsal sides (Fig. 5C, D). The denticle field is laterally framed by shallow grooves, and in LFUG-13566 there is a small opening on both sides, not far from the anterior margin of the parasphenoid plate. These openings appear to be exit foramina for the internal carotid artery, as described by Boy (1989). It is striking that this configuration is unequivocally present in only

two specimens (LFUG-13214, 13566), while many others appear to lack openings altogether. Entrance foramina, as postulated by Boy (1989), are not preserved, but may have been located in the posterolateral corners of the parasphenoid plate, probably on the dorsal side. In large specimens (e.g. LFUG-13244), the muscular attachments in the posterolateral corners have become very pronounced, with the anterior margin clear-cut and forming true pockets (Figs 4, 5B). In the antero-medial portion of the dorsal side of the parasphenoid plate of LFUG-13567, a small rectangular area is preserved which is
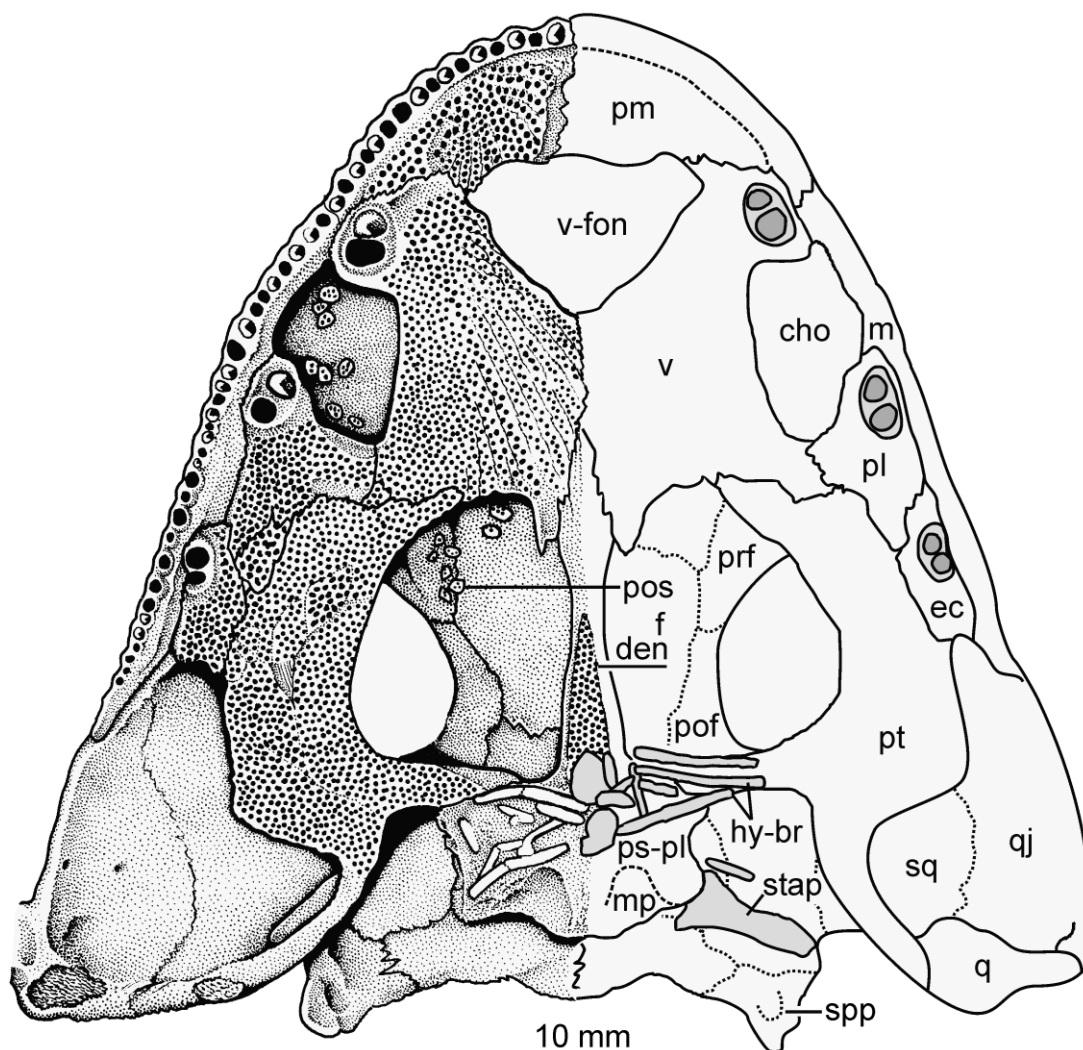
Figure 4 *Acanthostomatops vorax*. Palate of the largest specimen LFUG-13244 (75 mm) with ossified hypobranchials and stapes.

slightly raised and has a rugose surface (Fig. 5D). Similar structures are known from *Dvinosaurus* (Shishkin 1973) and *Apateon* (Boy 1972), where they have been termed *crista sellaris* and interpreted as a facet for an articulation with the basisphenoid cartilage formed by the parasphenoid. From this elevated area, the parapterygoid crest (*crista parapterygoidea* of Bystrow & Efremov 1940) runs posterolaterally. It was found to have served as site of attachment for the ventral process of the stapes (see below) in several temnospondyls, such as *Aphaneramma* (Säve-Söderbergh 1936), *Lyrocephaliscus* (Mazin & Janvier 1983), and *Mastodonsaurus* (Schoch 2000). The crest is separated from the shallower, almost anteroposteriorly-oriented paroccipital crest (*crista paroccipitalis*) by a broad furrow, the *sulcus intercristatus* of Bystrow & Efremov (1940). The shallow basioccipital fossa (fossa basioccipitalis) is situated between the left and right part of the paroccipital crest.

3.3.3. Pterygoid, ectopterygoid, palatine, vomer. The marginal series of palatal elements is characterised by large, dentigerous areas (Fig. 4). The teeth are uniform, tiny, and closely set. On the vomer, which houses the most extensive of these tooth-patches, teeth are arranged in radial rows converging towards a point near the vomerine fang pair. These rows are separated by grooves. On the palatine and ectopterygoid, the rows are less clear but exist, while on the pterygoid the arrangement of groups of denticles follows a more reticulate

pattern. The fangs are labyrinthodont with marked infolding at their bases, and are markedly curved with the crowns pointing both buccally and posteriorly. Labyrinthodonty is first apparent in skulls of 22 mm size (LFUG-13070).

The pterygoid has a well-ossified and large ascending lamella (LFUG-13567), which must have formed a completely or largely closed occipital surface in the cheek region. In the pterygoid, the entire surface of the ventrally exposed parts is covered with teeth. The basipterygoid ramus becomes only slightly proportionally longer in large specimens, adding little to the greater width of adult skulls. In contrast to almost all other temnospondyl larvae, this ramus is well ossified from the smallest sizes, eventually forming a complete facet for the basipterygoid articulation. Likewise, the palatine ramus is broad and firmly sutured with both the palatine and vomer, completely separating the interpterygoid vacuities from the palatine and ectopterygoid. In large specimens, the palatine ramus is proportionally nearly twice as wide as in small ones. Similarly, palatine and ectopterygoid experienced little changes during ontogeny, becoming somewhat wider, as in *Onchiodon* (Boy 1990) and unlike *Sclerocephalus* (Boy 1988; Schoch 2003). The medial process of the palatine, which is broadly sutured with the vomer, is twice as wide in adults compared to small larvae. Unlike in many other temnospondyls, the morphology of the vomer, anterior palatal fontanelle, and the choana is remarkably constant through ontogeny.
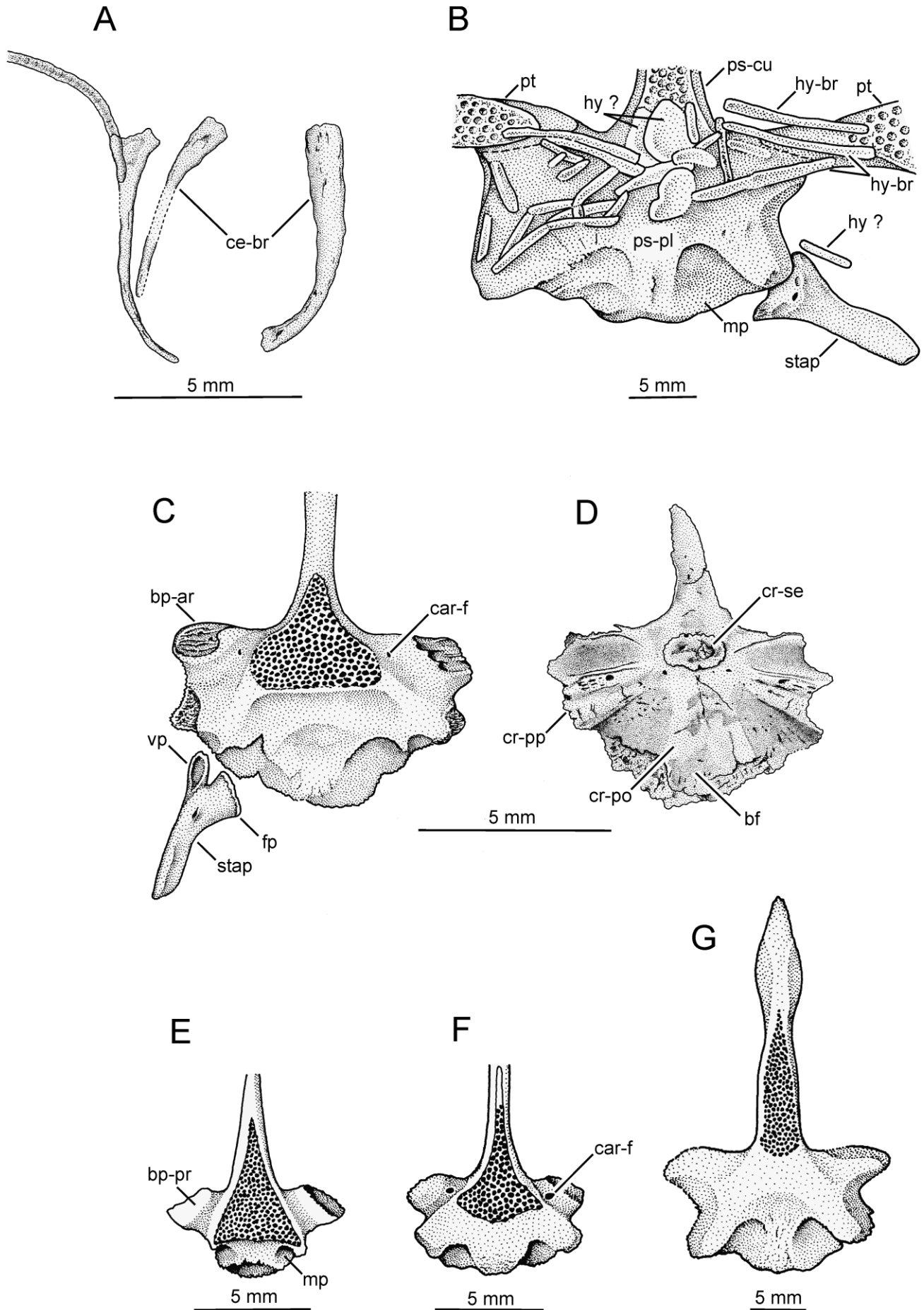
Figure 5 *Acanthostomatops vorax*. (A), (B) hyobranchial elements: (A) ossified ceratobranchials of the larval specimen LFUG-13070, 22 mm; (B) ossified hypobranchials on the ventral side of the parasphenoid plate in LFUG-13244 (75 mm). (C)–(G) parasphenoids of differently sized specimens: (C) LFUG-13566, circa 32 mm, ventral, with stapes; (D) LFUG-13567, dorsal; (E) LFUG-13227, 20 mm, ventral; (F) LFUG-13215, 25 mm, ventral; (G) LFUG-13244, partially restored, 75 mm, ventral.

3.4. Endocranium

The braincase and palatoquadrate regions remained to a large extent unossified throughout the size classes studied. There is no trace of a bony sphenethmoid, basisphenoid, basioccipital, exoccipital or epipterygoid at any stage. The only element that can be unequivocally confirmed is the quadrate, which is present as a distinct ossification only in the largest specimen (LFUG-13244, Fig. 4). This corresponds well with the presence of an articular bone in the mandible of the same specimen. The absence of an ossified exoccipital is particularly remarkable, as this element was the first to appear in the sequence of braincase elements in many temnospondyls (Bystrow & Efremov 1940; Boy 1995; Witzmann 2005), and is even present in large specimens of more aquatic taxa such as *Sclerocephalus* (personal observation by present authors) or *Trimerorhachis* (Case 1935). The posterolateral margins of the parasphenoid plate have two prominent rugose areas with upcurved margins that probably attached to the exoccipital region, which remained cartilaginous. In contrast, the basioccipital region (basioccipital fossa) is smooth and probably did not house a large basioccipital cartilage; this is weak evidence for the existence of a two-headed, medially separate occipital articulation. Except for the facet for the basisphenoid cartilage formed by the parasphenoid, no ossified part of the basisphenoid itself is visible.

3.5. Visceral apparatus

3.5.1. Hyobranchial skeleton.

In *Acanthostomatops vorax*, various ossified elements of the hyobranchial apparatus are preserved in small specimens as well as in the largest known skull. As the small and large specimens differ conspicuously in the structure and composition of the hyobranchium, we describe them in separate sections.

Small specimens. Steen (1937) described three pairs of ossified branchial arches in the smallest specimen studied ('specimen A', skull length about 15 mm). Morphology and position of these structures indicate that they represent ceratobranchials. According to Steen's (1937) photographs (pl. 2, figs 2, 3), there might also be a fourth arch present on the left side. The present authors also found three bony bars on the left side posterior to the 22 mm long skull of LFUG 13070 (Fig. 5A). The medial end is greatly expanded and flattened, whereas the curved shaft is slender and rounded in cross section. Posterolateral to the left orbit, a fourth bar is present which is curved and of similar length to the posterior bars, but is much more robust. It is possible that this bar represents the first ceratobranchial, and the succeeding arches become increasingly more slender posteriorly, resembling the situation in *Dvinosaurus* (Bystrow 1938) and *Trimerorhachis* (Olson 1979). Alternatively, the broader arch could represent a ceratohyal. With the exception of the narrow posteriormost element that has a rugose bony structure, the ceratobranchials have a largely smooth surface and are better ossified in *Acanthostomatops* than in larval *Onchiodon* (Witzmann 2005). As Steen (1937) and Boy (1989) noted, the hyobranchial apparatus of *Acanthostomatops* lacks branchial dentition, and there is no ossified basibranchial.

Largest specimen. In the palate of LFUG-13244 (75 mm skull length), the ventral surface of the parasphenoid plate is covered by six elongate bony rods and several smaller, less clearly defined elements (Fig. 5B). Most of these bones have a spongy structure. The largest elements are relatively long and thin, being only very gently curved. On either side, at least three rods of similar size are present, arranged in an antero-posterior sequence. The arrangement of these numerous bones resembles most closely the hyobranchium of lysorophians (Wellstead 1991). On the right side of the parasphenoid plate

(ventral view), three slender, simple bars are preserved, each of them being longer than half the width of the parasphenoid plate. The anterior two are parallel and directed anteromedially, whereas the third is aligned posteromedially; this is obviously the result of disarticulation. On the left side, at least three similar elements are present, albeit more fragmentary and disarticulated.

Apart from the long bars, several short bones are present that are largely anteroposteriorly aligned. In addition to the bony rods described, at least four plate-like bones are preserved in the centre of the parasphenoid plate and at the base of the cultriform process. It is not clear if these structures also belong to the hyobranchial apparatus.

3.5.2. Stapes.

In LFUG-13566, the complete right stapes is preserved near the posterolateral margin of the parasphenoid plate, very close to its probable articulation at the parapterygoid crest (Fig. 5C). The stapes of this specimen is about as long as the parasphenoid plate, having a straight shaft and a differentiated proximal head. The latter is clearly bipartite, with a long ventral process and a wide footplate. The general morphology of the stapes matches that of *Eryops* (Sushkin 1927; Sawin 1941), *Trimerorhachis* (Bolt & Lombard 1985) and *Mastodonsaurus* (Schoch 2000). The ventral process bears a notch suggesting some kind of articulation with the parapterygoid crest of the parasphenoid. At some distance from the bifurcation, the shaft bears a slit-like opening supposedly for the stapedial artery. The short and straight shaft has a uniform width throughout the distal half and bears a ridge along the antero-medial side, paralleling the long axis of the shaft. The stapes is shorter than in most stereospondyls and the larger eryopoid-grade temnospondyls, but is clearly longer and more differentiated than in the dissorophoids *Doleserpeton* (Bolt & Lombard 1985), *Amphibamus* (Daly 1994), and *Micromelerpeton* (Boy 1995).

In addition, the ventral side of the adult skull LFUG-13244 preserves the stapes on the right side in ventral view (Figs 4, 5B). The head region is partly obscured by the underplating parasphenoid plate, but it is consistent with that of LFUG-13566 in becoming wider towards the proximal end. The existence of a separate ventral process is indicated by a groove between the ventral (posterior) part of the proximal region and the footplate proper. A stapedial foramen is also present close to the bifurcation, being somewhat larger than in LFUG-13566.

Boy (1989, p. 143, fig. 4a) described and figured a stapes-like element in a 58 mm skull (LFUG-13562) located in isolation within the right orbit. Although more ambiguous than LFUG-13566, this bonelet may well form part of a stapes, preserving only the proximal head region and a small portion of the medial shaft. A large pit or opening near the 'head' of that element resembles the stapedial foramen in location and shape, although its exact size is obscured by sediment. The main difference between this fragmentary element and the complete stapes in LFUG-13566 is the undivided, simple 'head' region, which with the now available evidence may now be interpreted as incomplete.

3.6. Mandible

The mandible was described in detail by Boy (1989), who also provided a reconstruction of the adult condition. The present authors add only a short note on one point where they came to a different conclusion, namely the existence of a Meckelian window. They found some evidence for such a window in the outline on the angular in LFUG-13245, which has a pronounced concave recess along its anterodorsal margin. The height of this window is unclear due to the disarticulation of the angular, but its posterior and ventral margins are well

preserved. The minimal length of the Meckelian window can therefore be assessed, and reaches about one sixth of the total length of the mandible. In addition, the articular makes its appearance only in the largest specimen (LFUG-13245) as a coarse-grained bone of roughly quadrangular shape; the articular facet is well-established, and the bone extends ventrally and anteriorly along the internal surface of the angular and surangular, respectively.

3.7. Postcranial skeleton

Only a few specimens include parts of the postcranium, although it appears that most material was originally deposited in articulated state. However, as the postcranial elements of *Acanthostomatops* are mostly feebly ossified, it is obvious that the focus of collecting at Niederhäslich was on skulls. A similar collection bias was reported by Boy (1990). In addition to Steen's (1937) and Boy's (1989) observations on the postcranium, which were both rather cursory, the present authors have examined all available material with particular emphasis on the tail skeleton, girdles, and limbs. Boy (1989) in particular based most of his description on the largest individual (LFUG-13244+45), whereas the present authors have recognised a full range of fragmentary specimens that add information both on the ontogeny and the anatomy of various postcranial elements, permitting a quite complete skeletal restoration of *Acanthostomatops*.

3.7.1. Axial skeleton. *Acanthostomatops* has a rather short trunk composed of 21–22 presacral vertebrae. In combination with the abbreviated tail, this small-growing zatracheid was short-built with a disproportionally large skull. In the small larva LFUG-13229, the ratio trunk to skull length is 1·9, whereas in the largest specimen (LFUG 13244+45), it is 1·6.

Neural arches of the trunk. As is common among larval temnospondyls (e.g. Boy 1974), specimens smaller than 20 mm skull length have still separate and poorly ossified neural arches (LFUG-13417, 13221, 13229, MB.Am.411). The neural spines are very low and form a slightly convex dorsal margin above the rudimentarily developed zygapophyses (Fig. 6A, B). The ventral portion of the neural arches is slender and lacks transverse processes. In specimens of 20–35 mm range, neural arches are still poorly ossified but the neural spines are proportionally slightly higher (LFUG-13522, 13523, 13566, MMG-SaP-131). Three-dimensionally preserved neural arches have inwardly curved anterior and posterior margins wrapping around the medial surface but failing to meet each other medially (Figs 6C, D, 7). They probably represent primordia of perichondral bone formation enclosing a cartilaginous core.

In LFUG-13244+45, most parts of the presacral vertebral column are exposed (Figs 8, 9A, B). The neural spines are robust and relatively low, although markedly higher than figured by Boy (1989, fig. 4b). Their dorsal portion is thickened with a rugose surface on top, a feature present at least in the posterior half of the column. Whereas the postzygapophyses form ill-defined depressions at the posterior base of the neural spine, the prezygapophyses are large and well developed. Their unfinished articulation surfaces face dorsomedially and anteriorly. The neural canal is not exposed in any of the neural arches and it cannot be determined if it was open or closed ventrally. With respect to the width of the neural arch, the neural spine is broad in anterior view. In the mid-trunk region, the angle between the transverse process and the neural spine is slightly higher than 100°, if seen in anterior view. When viewed dorsally, the transverse process is aligned at approximately right angles to the central portion of the neural arch, so that the anteroposteriorly elongated diapophysis faces laterally and slightly ventrally. However, these measurements cannot be

taken in other regions of the vertebral column because of crushing of the neural spines and the transverse processes.

Atlas and axis. The anteriormost vertebrae are scarcely preserved, and atlas and axis cannot be determined with certainty because of the poor state of preservation. The first three neural arches seem to be more slender than the posterior ones (LFUG-13417; Fig. 6A). In LFUG-13522 (Fig. 6C), the first three or four neural arches are smaller than the succeeding arches; small, paired bony elements posteroventral to the occipital flange of the postparietals might represent components of the proatlas in this specimen.

Intercentra. The slender, wedge-shaped structures in LFUG-13229 described as intercentra by Steen (1937, fig. 3) are actually parts of the pectoral girdle. According to the present authors' findings, only the largest specimen (LFUG-13244+45) preserves unequivocal ossified inter- and pleurocentra (Figs 8, 9A). They are well-ossified throughout. As centra were still unossified in a 45 mm skull (LFUG-13555), their formation must have started in specimens within the 45–75 mm range. As described by Boy (1989), the unpaired intercentra are large and have a mostly smooth outer surface without parapophyses. In lateral view, each of the trunk intercentra is anteroposteriorly elongated with a blunt-ending flank (ascending process). The cross-section of an intercentrum shows that it is strikingly thin, leaving a large space for the unrestricted notochord, similar to the thin-walled intercentra of the basal temnospondyl *Dendrerpeton acadianum* (Holmes *et al.* 1998). The dorso-medial side of the intercentra is coarsely rugose.

Pleurocentra. As in *Dendrerpeton* (Holmes *et al.* 1998) and *Zatrachys* (Langston 1953), the paired pleurocentra are more massive than the intercentra. They also form wedge-shaped elements with the dorsal portion being broader than the tapering ventral part. As described by Steen (1937) and Boy (1989), both lateral and medial surfaces are roughened (Figs 8, 9A). The pleurocentra extend far ventrally almost towards the ventral midline, similar to dissorophoids (Boy 1985, 1995), as well as trimerorhachids and saurerpetontids (Chase 1965; Hotton 1959). In the available material, the pleurocentra seem to become more slender and shorter caudally in the trunk. A similar condition, in which the pleurocentra become more restricted in the posterior part of the trunk, is found in *Dendrerpeton* (Holmes *et al.*1998).

Caudal vertebral column. The almost complete tail of *Acanthostomatops* is preserved in LFUG-13566+67, on which the following description is based (Fig. 7). The tail is proportionally short and consists of only 28 vertebrae. In that region, the neural arches bear very low spines that are more slender than in the trunk. The size of the neural arches decreases rapidly towards the end, with the posteriormost arches subquadrangular in outline. Haemal arches are stout and distally not fused, and are therefore difficult to distinguish from the caudal rib series. The fifth caudal vertebra is the last one with ribs and the first one with haemal arches in the vertebral column. All succeeding vertebrae have haemal arches but lack centra. LFUG-13566+67 reveals that the haemal arches started to ossify prior to the centra, a pattern also present in *Micromelerpeton credneri* (personal observation by the present authors).

Ribs. Ribs are rarely preserved, and there is no specimen with a complete series of ribs. It is unclear whether the atlas or axis bore the first rib. The first two ribs are short and slender whereas the following ones are distinctly broadened at both ends, a consistent feature of both small and large specimens (Figs 6A, C, 9C, D). During ontogeny, the ribs of the trunk become proportionally longer. The proximal end is single-headed, as Langston (1953, fig. 16d) described for *Zatrachys*
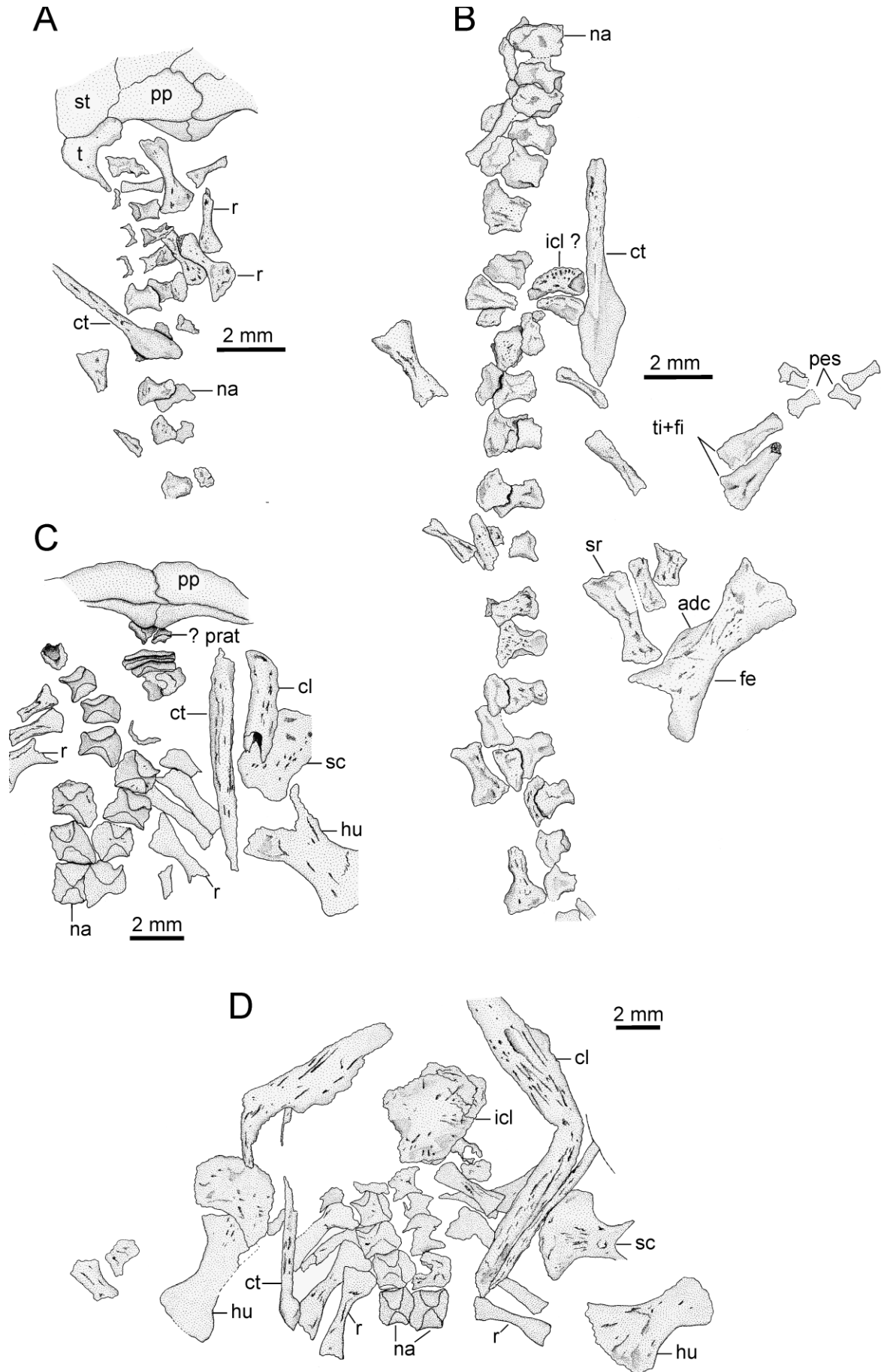
Figure 6 *Acanthostomatops vorax*. Postcranial larval skeletons: (A) LFUG-13417, 15 mm, dorsal; (B) LFUG-13229, 15 mm, dorsal; (C) LFUG-13522, 23 mm, dorsal; (D) LFUG-13523, 23 mm, ventral.
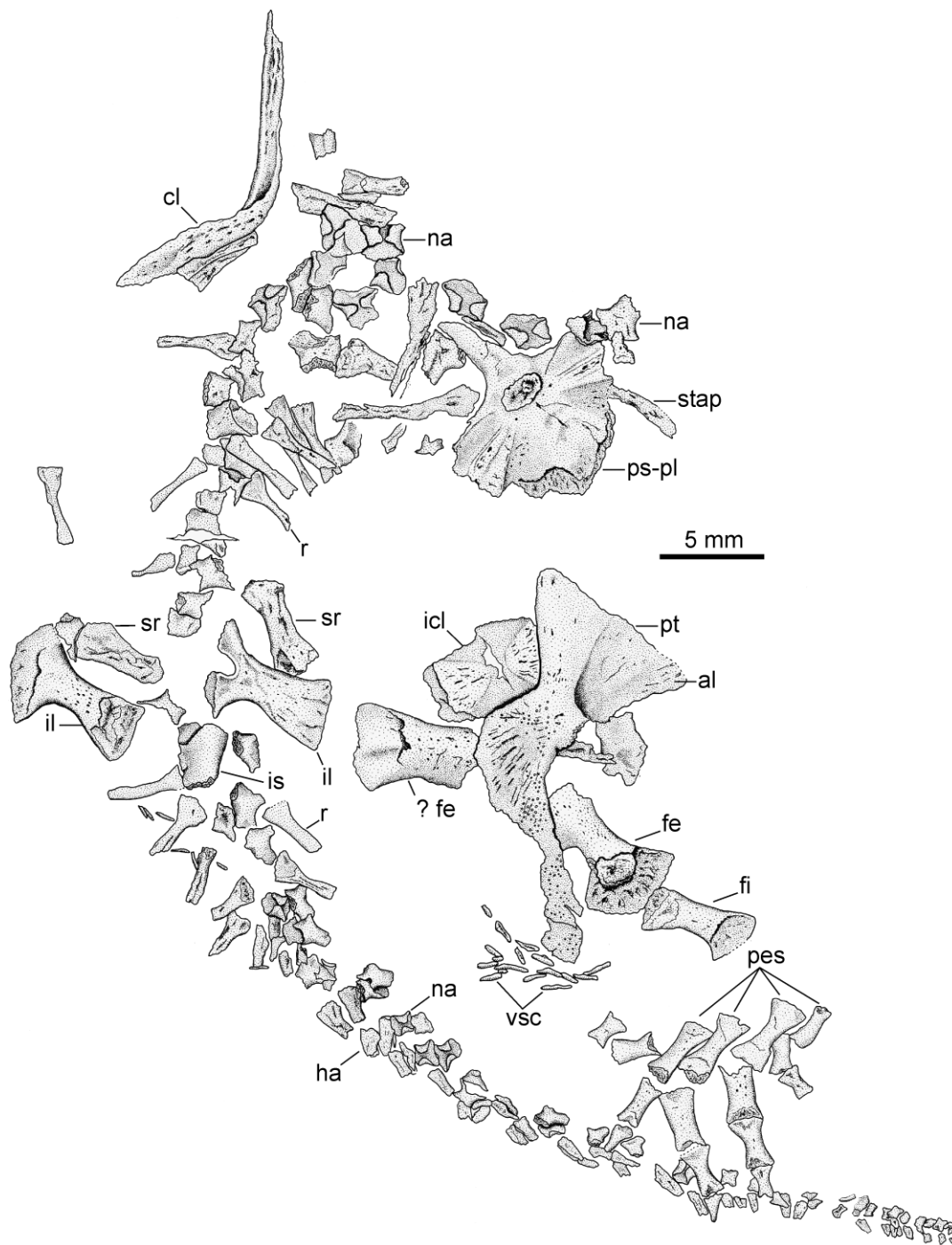
Figure 7 *Acanthostomatops vorax*. LFUG-13567, circa 32 mm, dorsal, postcranial skeleton with complete tail and fragments of pectoral and pelvic girdle, hindlimb, and palate.

serratus. As in the latter taxon, there are no uncinate processes. The ribs of the posterior trunk are slender and become shorter caudally (Fig. 9E). In one of the smallest specimens (LFUG-13229), the sacral rib is already differentiated with a stout proximal head and a considerably expanded distal end (Fig. 6B). In LFUG-13566+67 it is more robust with a proportionally broader shaft (Fig. 7), and in LFUG-13245 the expanded distal end has almost three times the width of the shaft (Fig. 9F), reaching proportions comparable to the massive sacral rib of *Eoscopus lockardi* (Daly 1994, fig. 10). As reported, the first five caudal vertebrae have short ribs with a broadened head and a slender shaft (Fig. 7).

3.7.2. Pectoral girdle. In its general outline, the pectoral girdle of *Acanthostomatops* is very slender. It includes the

standard complement of bones: interclavicle, clavicles, cleithra, and incompletely ossified scapulocoracoids.

Interclavicle. Fragments of the interclavicle are probably visible in LFUG-13229 (Fig. 6 B), and this unusually small element is well preserved in only three specimens (LFUG-13227, 13523, 13566+67; Figs 6D, 7, 10A–C). Nothing is known of the later ontogeny of the interclavicle in specimens beyond 32 mm skull length. The area it covers is even smaller than half the parasphenoid plate (LFUG-13566+67). It is transversely rectangular, with unclear margins. In contrast to Boy (1989, fig. 5a), the present authors consider the convex margin to be the posterior one, and the almost straight edge being anterior (Fig. 10A, B). This is based on LFUG-13523 and 13227 in which the orientation of the interclavicle can be
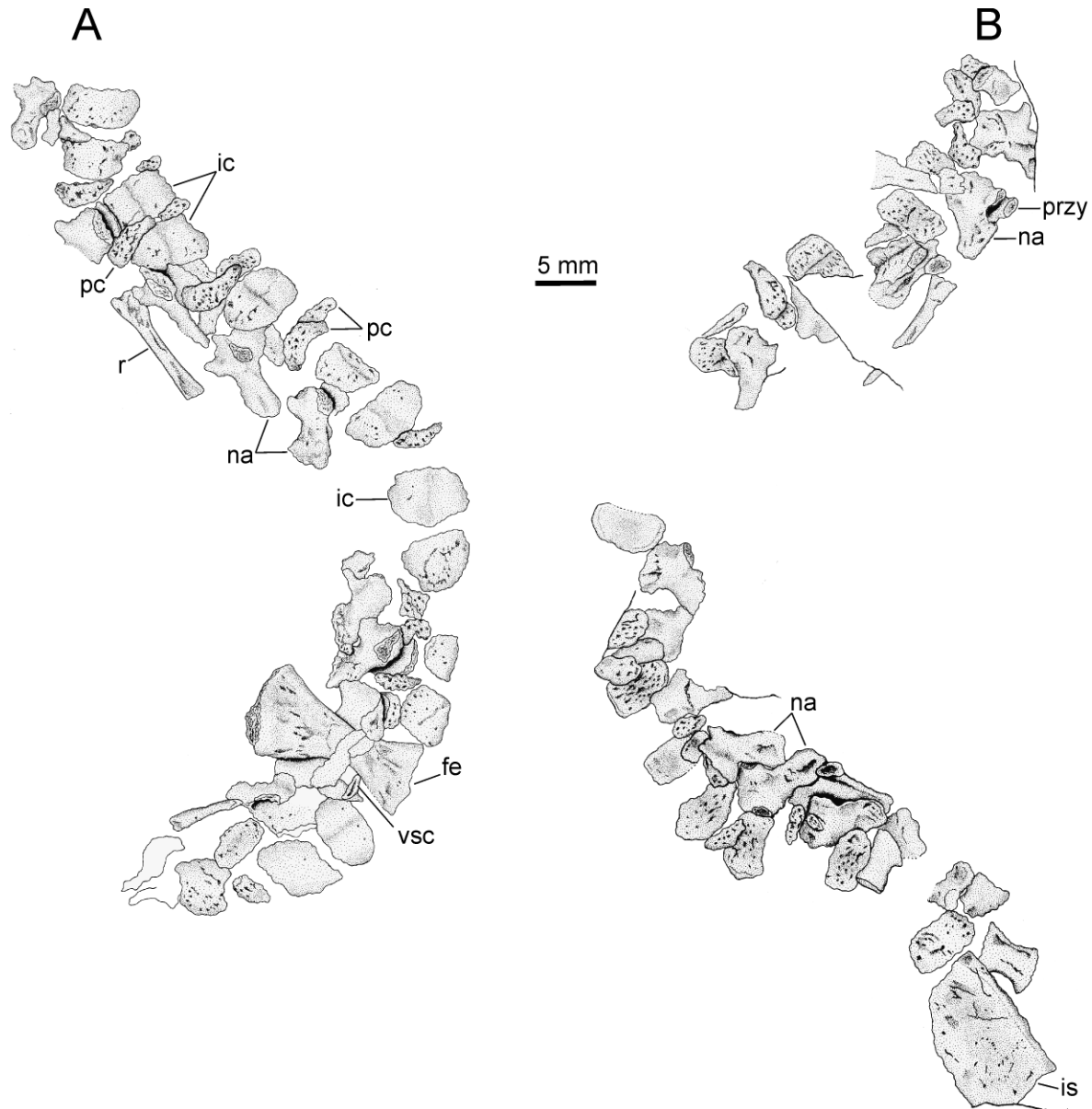
Figure 8 *Acanthostomatops vorax*. Vertebral column of the largest specimen LFUG-13244+45 (75 mm): (A) LFUG-13244, ventral, with femur; (B) LFUG-13245, dorsal, with ischium.

determined (Figs 6D, 10C). The present new orientation gives the roughly triangular ornamented field a more familiar outline, with the pointed end facing anteriorly, a condition established in many dissorophoids. A posterior process is not developed, and the anterior margin is not serrated. As indicated by the overlap facets, the clavicular blades overlapped the interclavicle far medially but did not meet in the ventral midline. In branchiosaurids, where the interclavicle is similarly small, there is only a short overlap of the clavicles (Boy 1972). The dorsal surface is slightly convex and largely smooth, except for the parts dorsal to the clavicular facets which are raised and bear radially aligned striations. A semilunar ridge, which is so typical of many temnospondyls, is not established on the dorsal side.

Clavicles.   The clavicles are also known only in small specimens. Again as in dissorophoids, the clavicular blades are very slender (LFUG-13227, 13523, 13566) and their ventral surface is ornamented by ridges and furrows (Figs 6D, 7, 10C). However, the shaft (prescapular process) is peculiar in being very slender and much longer than in larval *Sclerocephalus* (Schoch 2003), *Archegosaurus* (Witzmann & Schoch in press) and *Onchiodon* (Witzmann 2005). Its medial side bears a broad

groove bordered anteriorly by a bulge, where the slender shaft of the cleithrum was set in. Obviously, only the dorsal head of the cleithrum extended above the clavicle, which is a rather unusual situation among temnospondyls.

Cleithra.   The cleithra are adequately preserved only in very small specimens (LFUG-13417, 13229; Fig. 6A, B) and in the largest individual (LFUG-13244+45; Fig. 10D, E). The slender element bears an asymmetrical dorsal head with the posterior portion being longer than the anterior part. In LFUG-13229, the head ends in a pronounced dorsal outgrowth. Throughout ontogeny, the head of the cleithrum is proportionally smaller and much more slender than in *Onchiodon* (Witzmann 2005), *Sclerocephalus* (Schoch 2003; Meckert 1993) and dissorophids (Berman *et al.* 1985). In LFUG-13244, almost the complete cleithrum is preserved in medial view and the cleithral head in lateral view on the counterslab LFUG-13245. Compared with the taxa cited above, the head lacks posterior extension dorsal to the scapulocoracoid. The lateral side of the head is convex and bears radially aligned grooves anterolaterally. On the medial side, it is divided by a crest that continues onto the dorsal half of the shaft. This forms the articulation facet for the scapulocoracoid.
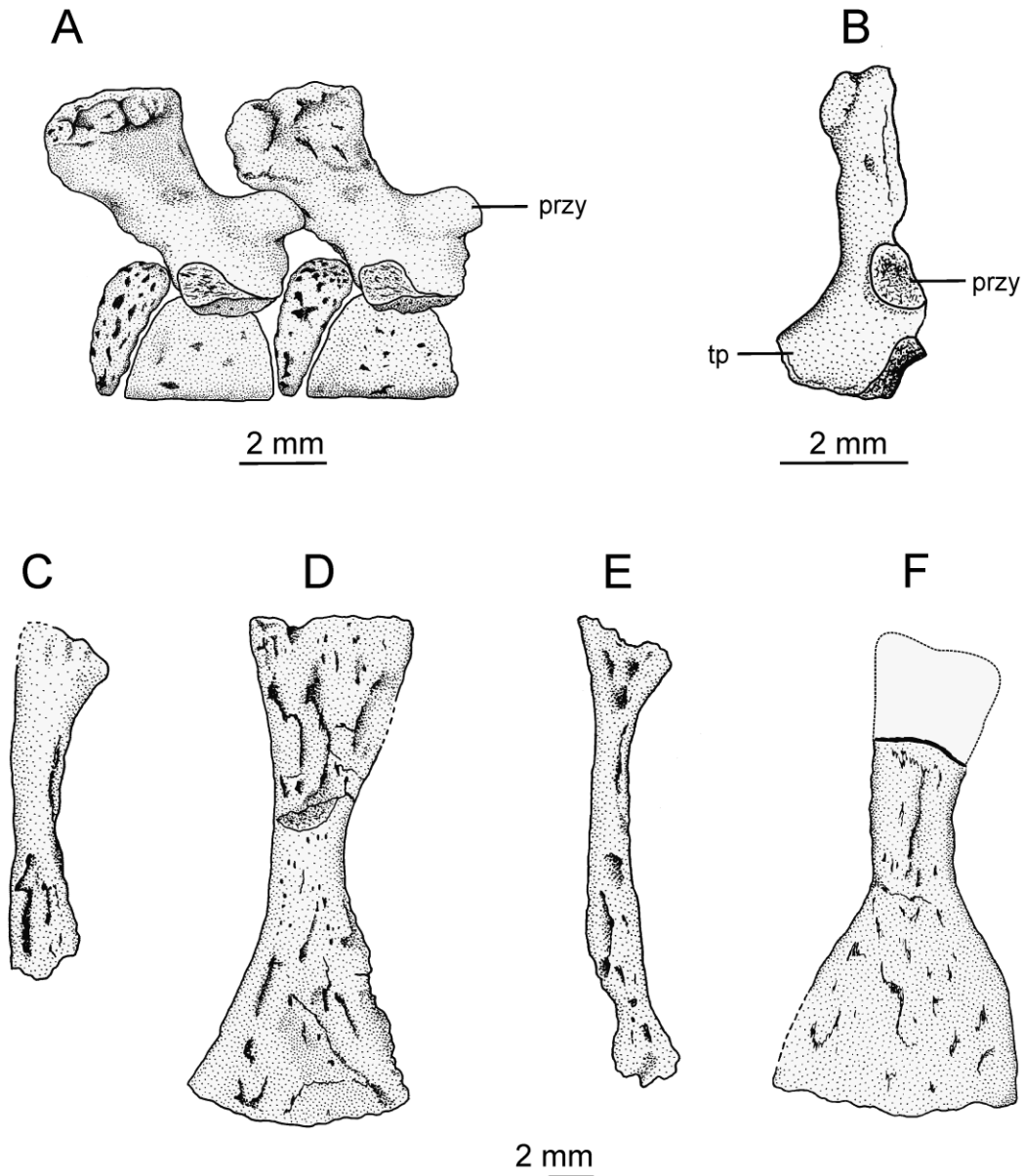
Figure 9 *Acanthostomatops vorax*. (A) reconstruction of vertebrae based on LFUG-13244+45 in lateral view; (B) LFUG-13244, right portion of neural arch in anterior view; (C)–(F) ribs of LFUG-13244+45: (C) first rib; (D) thoracal rib; (E) rib from the posterior half of the trunk; (F) sacral rib.

Scapulocoracoid.   The smallest specimen with ossified parts of the scapulocoracoid is 19 mm long MB.Am.411. However, Steen's (1937, pl. 2, figs 2–3) 'specimen A' (15 mm) preserved the clear-cut outlines of the scapulocoracoid. Further specimens are LFUG-13522+23 (Fig. 6C, D), MMG-SaP-130, and 131. Throughout the sample, the element forms a rather short, semilunar plate with ill-defined margins that is substantially shorter than the humerus.

3.7.3. Forelimb. ***Humerus***.   Again, this bone is preserved only in specimens of small and intermediate size (LFUG-13229, 13523, MMG-SaP-130, 131, 743). As compared to the short, very rudimentary humeri of larval *Sclerocephalus* (Boy 1972; Schoch 2003), *Archegosaurus* (Witzmann & Schoch in press), and *Onchiodon* (Witzmann 2005), that of *Acanthostomatops* is much more complete and robust at comparable stages. By 15 mm skull length, it is already well differentiated (Fig. 11A), with fairly complete ends (LFUG-13229 and Steen's 'specimen A'). The humerus is clearly waisted, with the shaft being proportionally more slender and longer than in the above-listed temnospondyls. The proximal head is more expanded and massive than the distal end. In 36 mm MMG-SaP-130 the humerus has a deltopectoral crest and a tiny supinator process (Fig. 11C), while 38 mm MMG-SaP-743 (Fig. 11B) preserves the humerus in its three-dimensional shape, suggesting a near-perfect tetrahedral structure with proximal and distal ends being aligned at an angle of nearly 90°. Interestingly, the humerus is longer than the femur in specimens beyond about 30 mm skull length, a unique feature amongst temnospondyls. In smaller specimens, however, the femur is longer than the humerus (see below).

Radius and ulna.   These bones are adequately preserved only in LFUG 13566 (Fig. 11D) and MMG-SaP-130 (Fig. 11C). They reach somewhat more than half the length of the humerus. The ulna is slightly longer than the radius, but an olecranon process is not present. The element is more expanded proximally than distally. The radius is distally broader than the ulna.

Manus.   The manus is not completely preserved in any specimen. It is exposed in LFUG 13566 (Fig. 11D), where the following phalangeal formula was derived: ?2–?2–3–?3. Provided this to be the correct count, it would be identical with that of *Onchiodon labyrinthicus* (Witzmann 2005). The
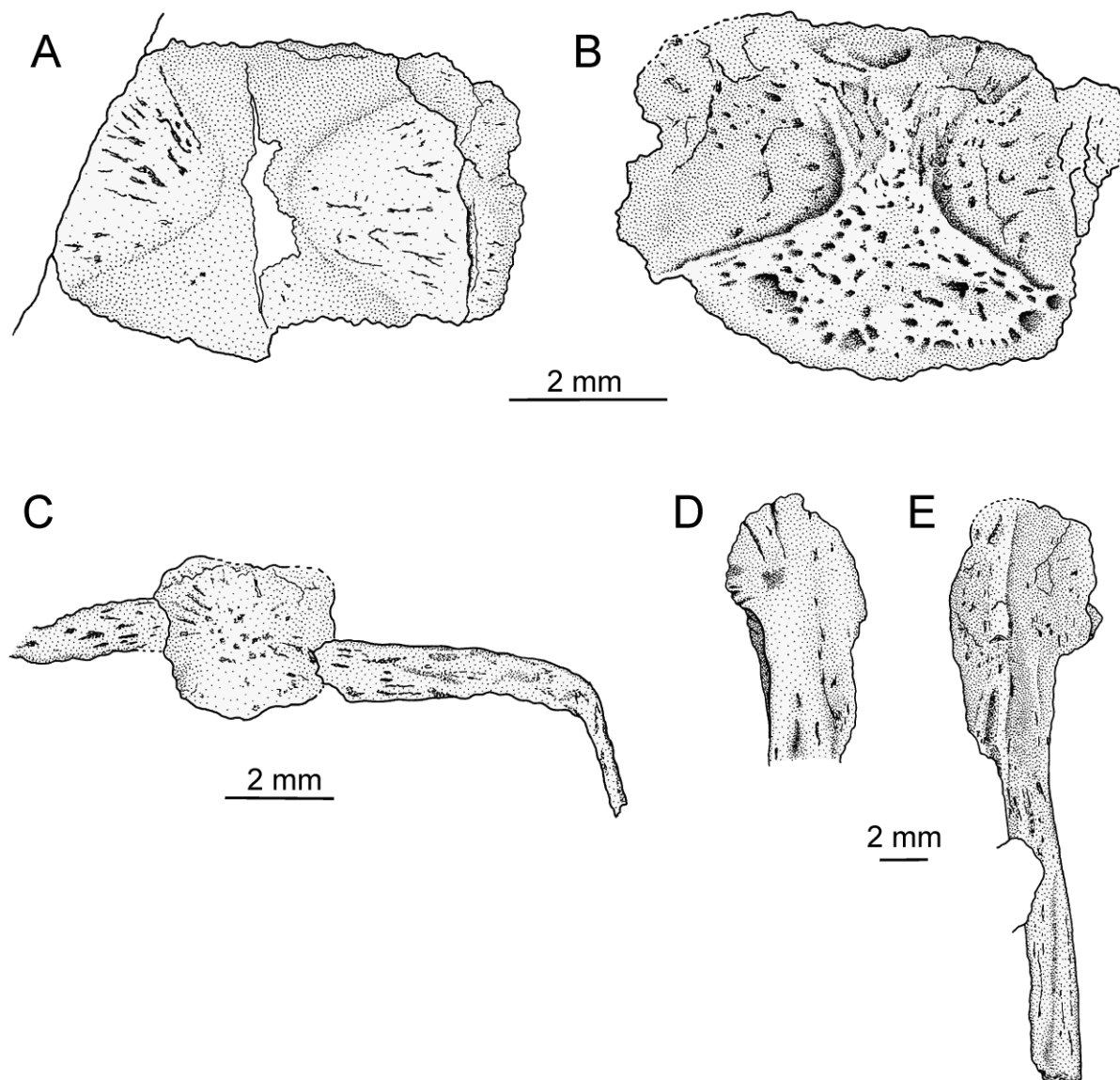
Figure 10 *Acanthostomatops vorax*. Elements of the dermal pectoral girdle: (A), (B) LFUG-13566+67, circa 32 mm, interclavicle: (A) dorsal; (B) ventral; (C) LFUG-13227, 20 mm, ventral, interclavicle and clavicles; (D), (E) LFUG-13244+45 (75 mm) cleithrum: (D) lateral; (E) medial.

terminal phalanges consist of short, blunt claws. There are no carpal bones.

3.7.4. Pelvic girdle. In the pelvic girdle, the ilium and ischium have been found in different size stages, whereas the pubis is not preserved. Ilium and ischium are not co-ossified in any specimen.

Ilium. By 17 mm skull length (LFUG-13221), the ilium is the only ossified element of the pelvic girdle (Fig. 12A). Dorsal to the small triangular base, the iliac blade is stout, low and almost rectangular in lateral view, being only slightly expanded dorsally. In LFUG-13566+67, it is more differentiated, having a well-established dorsal frame to the acetabulum and a shaft with an expanded dorsal portion (Fig. 7). In LFUG-13245, the ilium is rather robust with a large and rounded-triangular base (Fig. 12C). The dorsal rim of the acetabulum has an irregular outline and is expanded posterodorsally, and the bone surface of the acetabulum is markedly rugose. The broad, probably vertically aligned shaft resembles that of *Eryops* (Romer 1922) and *Onchiodon* (Romer 1925; Boy 1990), although in the latter it is even more expanded at the dorsal end. A ventral shelf that must have attached to the ischium is preserved; its greatest extension is at about mid-level of the acetabulum and

continues to a point well anterior to it. This indicates either a markedly anterior extension of the ischium, or alternatively the existence of a pubic ossification at this size stage.

Ischium. The ischium formed clearly after the ilium, by 32 mm skull length (LFUG-13566+67; Fig. 7). At this size, it is still shorter than the base of the ilium. The outline is trapezoidal with the anterior and posterior margins being almost straight. Its anterior portion is deeper and thicker than the posterior part. While the dorsal portion is laterally convex, the ventrolateral portion has a concave surface. In LFUG-13245, the crescent-shaped ischium is proportionally larger, and the anterior margin has a bulbous surface (Fig. 8B). In the posterior half, the lateral surface is concave, while the posterior end has a convex, thickened margin.

3.7.5. Hindlimb. *Femur*. LFUG-13229 preserves both the humerus (Fig. 11A) and the femur (Fig. 6B) permitting a size comparison between them. There, the femur is about 1·7 times longer than the humerus. (Confusingly, Steen 1937, fig. 3 referred to the femur as the humerus in this specimen). In LFUG-13229, the femur has a moderately long and slender shaft and a pronounced adductor crest, and it is about 1·8 times longer than the fibula in LFUG-13221 (Fig. 12A).
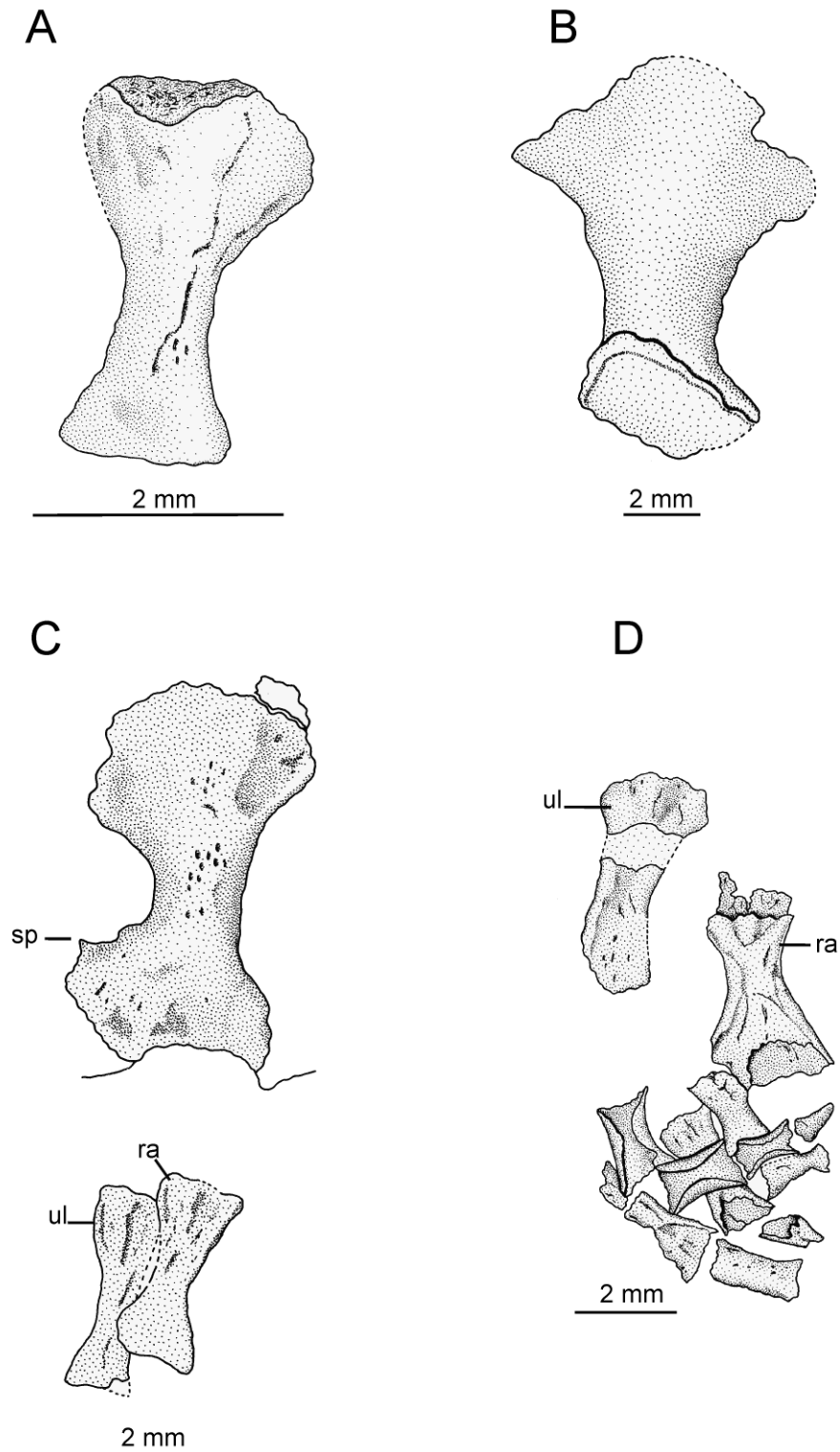
Figure 11 *Acanthostomatops vorax*. Forelimbs: (A) LFUG-13229, 15 mm, humerus; (B) MMG-SaP-743, 38 mm, humerus; (C) MMG-SaP-130, 36 mm, humerus, radius, and ulna; (D) LFUG-13566, circa 32 mm, radius, ulna, and manus.

During later ontogeny, the femur reveals a negative allometry with respect to skull length (LFUG-12566+67; Fig. 7), and in the largest specimen LFUG-13244 it is massive and strikingly short (Fig. 12B). The clearly two-headed distal end is 1.3 times wider than the proximal end. The shaft is narrowest in the proximal third of the bone. In the large specimen, the adductor crest is knife-edged but proportionally lower than in LFUG-13229.

Tibia and fibula.   These bones can already be distinguished in small specimens (e. g. LFUG-13221; Fig. 12A). The tibia is slightly shorter than the fibula and has a more expanded proximal head compared to the distal end. The fibula has a pronounced, enlarged distal end that is angled medially. Its lateral and medial margins are clearly concave. In a larger specimen (LFUG-13566; Fig. 7), the fibula is overall more slender and the lateral margin less concave.

Pes.   LFUG-13566+67 is the only specimen in which the foot is adequately preserved, and was figured by Boy (1989, fig. 5c). The present authors suggest that the phalangeal formula probably reads: ?2–**2**–3–4–?3 rather than ?2–**?3**–3–?4–3 as
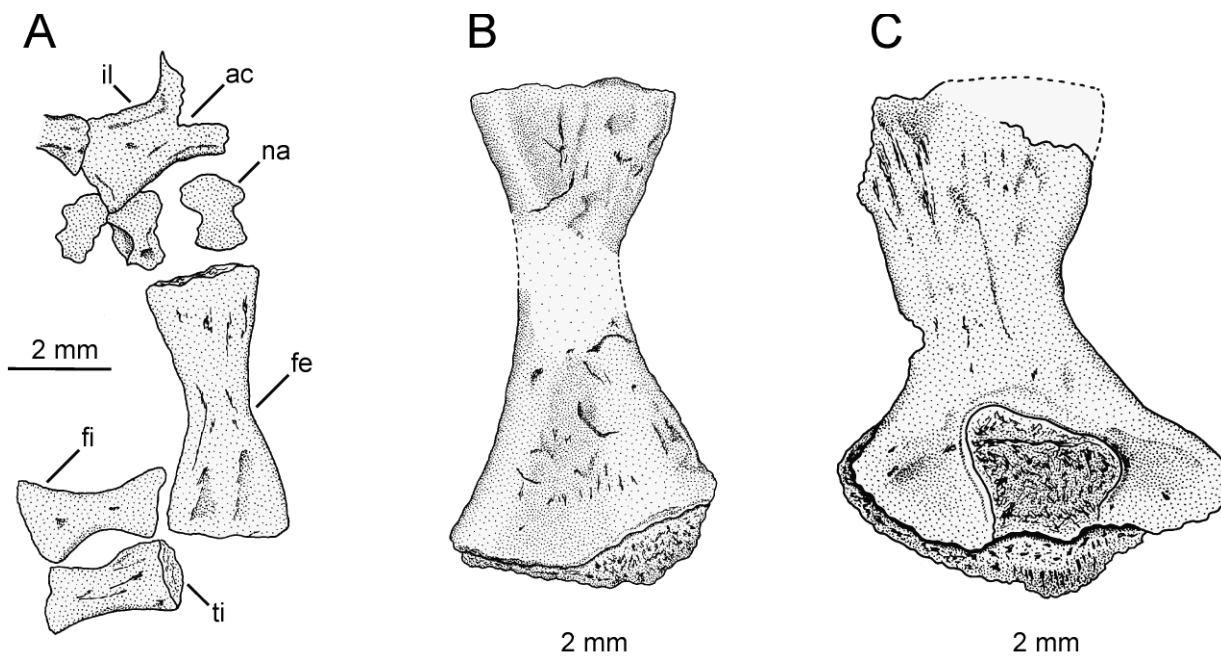
Figure 12 *Acanthostomatops vorax*. (A) LFUG-13221, 17 mm, ilium, femur, tibia and fibula; (B) LFUG-13244, 75 mm, femur; (C) LFUG-13245, 75 mm, ilium.

proposed by Boy (1989). The terminal phalanges are short and pointed (Fig. 7). There is no evidence of ossified tarsals.

3.7.6. Dermal scales. Steen (1937, p. 498) reported 'a patch of very delicate scaling' in the small 'specimen A' with a skull length of approximately 15 mm. Although it is not clear if these were rounded-oval dorsal or spindle-shaped ventral scales, this observation shows that the dermal scales started to ossify early in larval ontogeny. By 32 mm skull length (LFUG-13566; Fig. 7), spindle-shaped scales with a convex ventral and concave dorsal margin are preserved that were arranged in a V-pattern on the ventral side of the trunk in the living animal. An isolated scale of this type is also preserved in the largest specimen (LFUG 13245; Fig. 8A). Dorsal scales are not preserved.

4. Discussion

Boy (1989) split the 24 specimens of *Acanthostomatops vorax* investigated by him into four ontogenetic phases which he referred to as 'larval' (smaller than 20 mm skull length), 'metamorphosing' (20–30 mm), 'juvenile' (30–60 mm), and 'adult' (beyond 60 mm) respectively. Boy's concept of ontogenetic phases including the metamorphic phase is based exclusively on developmental changes in ornamentation, by analogy to his findings in *Sclerocephalus* (Boy 1988). However, such changes in ornamentation alone do not form sufficient evidence for a metamorphosis in most temnospondyls (Schoch 2001).

4.1. Hyobranchial remodelling
Boy & Sues (2000) and Schoch (2001) suggested that the resorption of branchial denticles may be an important criterion for metamorphosis in temnospondyls because it indicates the remodelling of ceratobranchials in analogy to extant salamanders. However, the lack of branchial dentition in *Acanthostomatops*, makes the recognition of any metamorphic phase difficult. One possibility is to consider the probable resorption of ossified ceratobranchials as a metamorphic event (Schoch 2002). In *Onchiodon*, this event occurred more or less simultaneously with the resorption of branchial denticles (Wit-

zmann 2005). In *Acanthostomatops*, there are no ossified ceratobranchials preserved in specimens larger than 22 mm skull length. This suggests their resorption between 20 and 30 mm, thus corroborating nicely the metamorphic phase in Boy's (1989) model.

The large specimen LFUG-13244+45 lacks any ceratobranchials. Instead, it preserves a full range of rather different, mostly straight and delicate elements in the anterior part of the parasphenoid plate, at about the level where an 'adult' hyobranchial skeleton is to be expected. Morphologically, the long bony rods match the hypobranchials most closely. If this interpretation is correct, then large *Acanthostomatops* had a total of four pairs of ossified hypobranchials, in contrast to trimerorhachoids, dissorophoids, and most extant salamanders, in which only two such pairs are or were ossified (Bystrow 1938; Boy & Sues 2000). More than two pairs occur also in lysorophians (four pairs, Wellstead 1991), adelogyrinids (three pairs, Andrews & Carroll 1991), and the tristichopterid sarcopterygian *Eusthenopteron* (Jarvik 1980), which may indicate the plesiomorphic state. The nature of the short rods and plate-like bones in the vicinity of the possible hypobranchials of LFUG-13244 is unclear; they could either form segments of the hyoid arch or alternatively represent medial ossifications in the basibranchial region.

In sum, the larval hyobranchial apparatus was probably reorganised in specimens beyond 22 mm skull length, starting with the resorption of ceratobranchials. In the adult hyobranchium, only the anteroventral portion of the skeleton was ossified. Thus, in *Acanthostomatops* a 'larval' gill-supporting skeleton apparently transformed into an 'adult' tongue-supporting apparatus. By analogy with extant salamanders, this 'adult' hyobranchial apparatus might have served a tongue-supporting function that assisted in prey capture. This fits into the concept that in zatracheids, an enlarged intermaxillary gland played a key role in terrestrial feeding (Schoch 1997).

4.2. Life history of *Acanthostomatops*
Biphasic life-cycles where there is a shift from an aquatic to a terrestrial mode of life are difficult to prove in the fossil record.
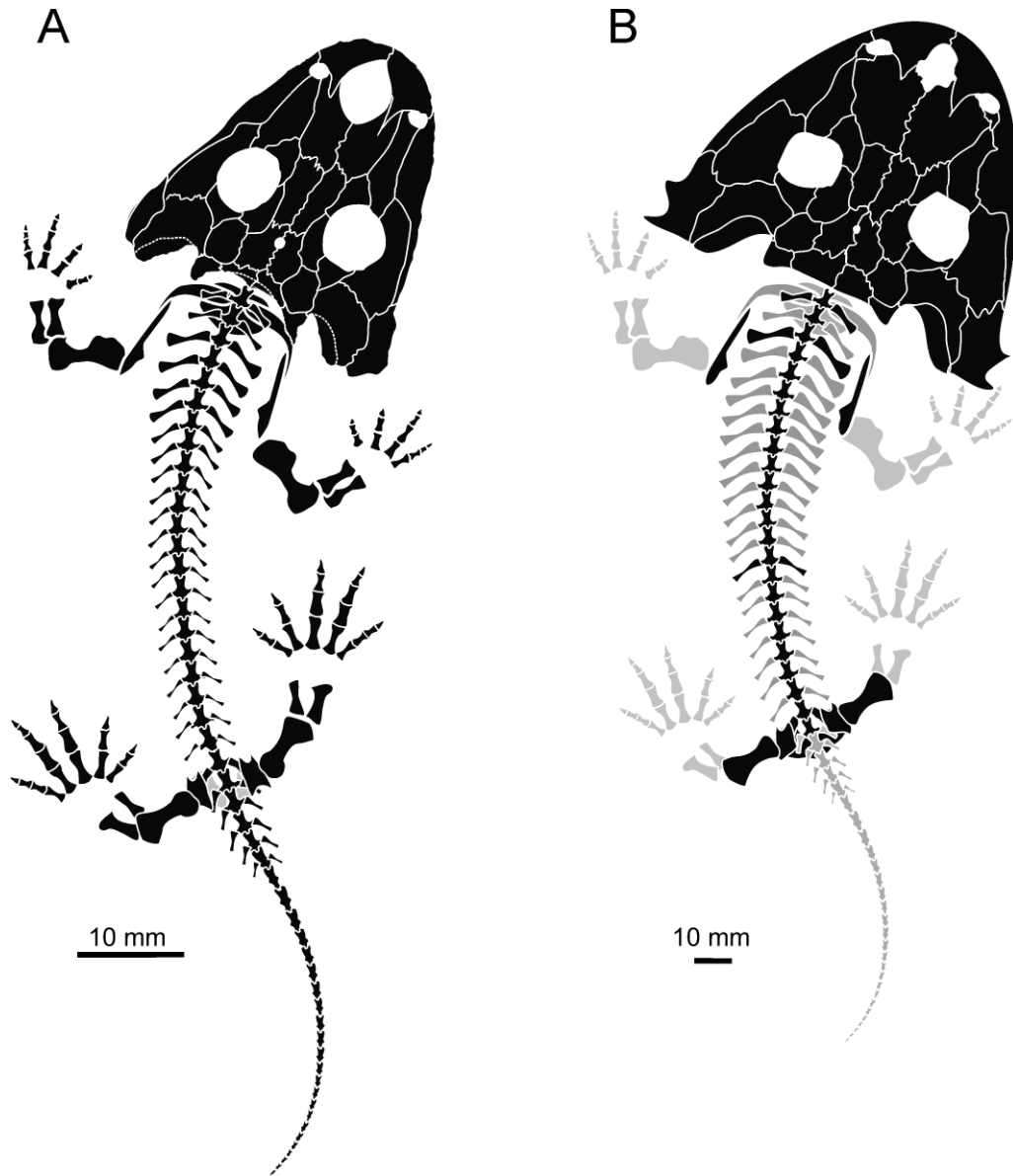
Figure 13 *Acanthostomatops vorax*. Reconstructions of complete skeletons in dorsal view: (A) early juvenile skeleton, based on several specimens; (B) adult specimen, based on LFUG-13244+45; unknown parts of the skeleton are shown in grey.

Boy (1989) and Schoch (2002) assumed such a transition during life history of *Acanthostomatops*, following Paton (1975) who regarded the adults of the zatracheids *Dasyceps* and *Zatrachys* as terrestrial forms.

4.2.1. Larvae. Specimens smaller than 25–30 mm skull length probably lived as aquatic larvae in the Niederhäslich lake. Their possession of ossified ceratobranchials is a larval adaptation. These ceratobranchials probably supported external gills and stiffened the gill clefts. (The lack of any external gills in the Niederhäslich material is in agreement with the lack of any skin preservation, except for ossified scales.) An aquatic mode of life is also supported by the poorly ossified postcranial skeleton. On the other hand, the smallest known specimens already have features that foreshadow a terrestrial mode of life realised in adult ontogeny. These include having a well-developed, differentiated humerus, a femur with a distinct adductor crest, the small dermal elements in the pectoral girdle, the nasolacrimal duct, and the proportionally short bony tail. The large intervomerine fontanelle is already well defined, which is believed to have housed an intermaxillary gland used in terrestrial feeding (Schoch 1997). In larvae, the proportionally larger size of the hindlimb and the longer trunk

suggest an active mode of swimming, probably by lateral undulation of the axial skeleton and a support in steering by the hindlimb.

4.2.2. Juveniles. Specimens in the 30–60 mm skull size range probably still lived in the water. This is suggested by the high frequency of specimens in that size range as indicated by the size distribution given in Figure 1A. The still feebly ossified postcranial skeletons, especially the unossified vertebral centra, still missing carpals and tarsals, and the low degree of ossification of scapulocoracoid and pelvis, suggest these animals were not capable of an entirely terrestrial existence. Boy (1989) supposed that the juveniles lived probably as semi-aquatic animals in the shallow littoral zone. The slow ossification of the postcranial skeleton in *Acanthostomatops* is shared with *Onchiodon* (Boy 1990; Witzmann 2005) and *Sclerocephalus* (Boy 1988; Schoch 2003), but stands in stark contrast to the rapid ossification in dissorophoids. A restoration of a juvenile skeleton is shown in Figure 13A.

4.2.3. Adults. The ossification of the vertebral centra, which must have occurred in specimens of between 45 mm and 75 mm skull length, marks an important change. With its huge skull and the short trunk and limbs, an adult

Acanthostomatops was rather stout, quite similar to the extant leptodactylid frog *Ceratophrys*. Like *Ceratophrys*, it may well have been a rather passive terrestrial predator that lurked for passing prey. In such a situation, a projectable tongue might have been an advantage; the peculiar adult tongue skeleton of *Acanthostomatops* may shed some light on this topic. Although the humerus, carpals and tarsals, and scapulocoracoid are not preserved in the adult specimen, there are some novel 'adult' features suggesting a terrestrial life. These are the proportionally large zygapophyses that probably strengthened the vertebral column in supporting the animal on land, the proportionally large ischium with its sutural connection to the ilium, the robust and vertical iliac blade, and the general absence of lateral lines. Furthermore, there is some admittedly weak evidence for the existence of a pubic ossification. The terrestrial life of adult *Acanthostomatops* is also supported by the size distribution of the material studied by the present authors: It shows that large juveniles and adults are very rare. Boy & Sues (2000) interpreted this as a result of departure from the aquatic habitat. A reconstructed adult skeleton is illustrated in Figure 13B.

5. Acknowledgements

6. Abbreviations used in figures

ac—acetabulum
adc—adductor crest
al—ascending lamella
bf—basioccipital fossa
bp-ar—facet for basipterygoid articulation
bp-pr—basipterygoid process
car-f—exit foramina for the internal carotid
ce-br—ceratobranchials
cho—choana
cl—clavicle
cr-po—paroccipital crest
cr-pp—parapterygoid crest
cr-se—crista sellaris
ct—cleithrum
den—denticle field
ec—ectopterygoid
f—frontal
fe—femur
fi—fibula
fon—internasal fontanelle
fp—footplate
ha—haemal arch
hu—humerus
hy—hyobranchial element
hy-br—hypobranchials
ic—intercentrum
icl—interclavicle
il—ilium
is—ischium
j—jugal
la—lacrimal
m—maxilla
mp—muscular pocket
n—nasal

na—neural arch
of—occipital flange
p—parietal
pc—pleurocentrum
pi—pineal foramen
pl—palatine
pm—premaxilla
po—postorbital
pof—postfrontal
pp—postparietal
prat—proatlas
prf—prefrontal
przy—prezygapophyses
ps-cu—cultriform process of parasphenoid
ps-pl—parasphenoid plate
pt—pterygoid
q—quadrate
qj—quadratojugal
r—rib
ra—radius
sc—scapulocoracoid
sm—septomaxilla
sp—supinator process
spp—socket for parotic process
sq—squamosal
sr—sacral rib
st—supratemporal
stap—stapes
t—tabular
ti—tibia
tp—transverse process
ul—ulna
v—vomer
v-fon—vomerine fontanelle
vp—ventral process
vsc—ventral scale

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