

# THE POSTCRANIUM OF *ARCHEGOSAURUS DECHENI*, AND A PHYLOGENETIC ANALYSIS OF TEMNOSPONDYL POSTCRANIA

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**Abstract:** The gharial-like *Archegosaurus decheni* from the Permian/Carboniferous boundary of south-west Germany is one of the best known temnospondyls. Based largely on new material, we restudied the postcranial anatomy of this species, including ontogenetic aspects. *A. decheni* has 24 presacral vertebrae, and the length of the deep tail exceeds the length of the rest of the body. Neural spines are moderately high and slowly become differentiated during ontogeny. The intercentra start to ossify very late. Distal uncinatate processes are developed on the anterior ribs in adult specimens. Only the ventral portion of the scapula is ossified. The slender ilium and the ischium are not co-ossified, and the pubis remained cartilaginous. Among stereospondylomorph temnospondyls, the very short and rudimentarily developed humerus exhibits a unique morphology. Carpals and tarsals start to ossify only in the largest specimens. The poorly ossified postcranium indicates that *A. decheni* was primarily an

aquatic temnospondyl. We undertook a phylogenetic study of *A. decheni* and 16 other temnospondyls, based exclusively on postcranial characters. We analysed 52 characters, obtaining a single most parsimonious tree that agrees in many aspects with cranium-based analyses: *Trimerorhachis* and *Dvinosaurus* form a basal clade (Dvinosauria), followed by monophyletic euskelians (dissorophoids plus eryopids) and finally the stereospondylomorphs, within which *A. decheni* is nested above *Scleurocephalus*. Among stereospondyls, trematosaurids and metoposaurids form a clade, whereas the chigutisaurid *Siderops* is nested with capitosaurids. The primitive condition of Temnospondyli is still not adequately understood, especially the degree of terrestriality of the earliest temnospondyls.

**Key words:** Temnospondyli, *Archegosaurus*, postcranium, ontogeny, phylogenetic analysis, palaeobiology.

TEMNOSPONDYL phylogeny is very much focused on the skull, with most of the significant character states stemming from the cranial and mandibular regions (Boy 1990, 1996; Milner 1990a, b, 1993; Holmes *et al.* 1998; Schoch 2000; Yates and Warren 2000; Damiani 2001; Schoch and Milner 2004). Indeed, there are only a handful of postcranial skeletons that are complete enough to form the basis of a reasonable phylogenetic study. This is particularly true for stereospondyls, the largest clade of temnospondyls, which existed mainly in the early Mesozoic and are known mostly from their huge and massive skulls because temnospondyl skeletons were prone to disassociation prior to burial, and thus are frequently neglected by collectors. In particular, Triassic stereospondyls are abundant in bonebeds and channel-fill deposits in which articulated skeletons are an exception (Schoch and Milner 2000).

One of the most completely preserved temnospondyls, indeed outstanding among all lower tetrapods, is the gharial-like *Archegosaurus decheni* from the Permian/Car-

boniferous boundary of south-west Germany, which reached a total length of nearly 2 m. It was described in considerable detail by von Meyer (1854, 1858), whose contributions made temnospondyls well known at that time in vertebrate palaeontology. Today *Archegosaurus* is represented by a large number of skeletons of various sizes that preserve a wide range of developmental stages as well as individual variation. At the same time, *Archegosaurus* is a highly relevant taxon from both stratigraphic and phylogenetic points of view. Its relatively old stratigraphic age is consonant with its prospective phylogenetic position at the base of the Stereospondylomorpha (Yates and Warren 2000), and in many respects of cranial anatomy *Archegosaurus* sheds light on the plesiomorphic condition of stereospondyls.

In the present study, we describe all hitherto unknown or poorly documented aspects of the postcranium in *Archegosaurus decheni*. Since the pioneering works of von Meyer (1854, 1858), numerous new specimens of

*A. decheni* have been collected and prepared. In addition to a re-examination of previously described material, we consider so far undescribed and exceptionally well-preserved specimens. These new data give insights into the life history of *Archegosaurus*. Finally, we perform a cladistic analysis of the best known temnospondyls, for the first time based on postcranial anatomy alone. This may shed some light on both the problems of temnospondyl phylogeny reconstruction and previously unconsidered aspects of their evolution.

## PREVIOUS WORK

Although the postcranial skeleton of *A. decheni* had already been studied to some extent by Goldfuss (1847), Jordan (1849) and Burmeister (1850), it was von Meyer (1854, 1858) who first presented an authoritative assessment of the whole skeleton. He was the first to recognize the vertebrae of *A. decheni* as consisting of the neural arch and a multipartite centrum, composed of a crescent-shaped intercentrum and paired smaller pleurocentra. This vertebral construction became known later as the rhachitinous vertebral type. Von Meyer also provided evidence for a persistent notochord in the vertebral column. However, he was mistaken in attributing *A. decheni* to reptiles rather than amphibians, although the concepts defining these groups were far from clear-cut at that time (Schoch 1999). Vogt (1854) contradicted von Meyer's view in showing that no postembryonic amniote possesses an undivided notochord. He thus concluded that *A. decheni* cannot be classified as 'saurian', but represents a 'special family of amphibians' (Vogt 1854, p. 677). Owen (1861, p. 202) supported Vogt's point of view and regarded *A. decheni* as a 'transitional form between the batrachians and the ganoids'. By the end of the nineteenth century, the amphibian nature of temnospondyls and *A. decheni* was generally accepted (Lydekker 1890; Zittel 1890).

Subsequent to von Meyer, little was published on the postcranial anatomy of *A. decheni*. Quenstedt (1861) described and illustrated a temnospondyl pes which probably belongs to a large individual of *A. decheni*, the only one in which ossified tarsals were known at that time. This tarsus, then housed in the collection of the Institut und Museum für Geologie und Paläontologie in Tübingen, was studied by Baur (1886), Emery (1897), Zwick (1898), Jaekel (1909a, see below), and Schaeffer (1941). Each author arrived at different conclusions about the origin of the tarsal elements.

Further work on *A. decheni* was carried out by Otto Jaekel at the turn of the twentieth century. He published a thorough reconstruction of selected vertebrae of adult *A. decheni* and was the first to demonstrate distal uncinate processes on the thoracic ribs (Jaekel 1896a, b). He

reported the proportional length of the tail (Jaekel 1896b) as well as aspects of limb morphology (Jaekel 1909a). Since then, no detailed description of the postcranial anatomy of *A. decheni* has been published.

*Institutional abbreviations.* BSM, Bayerische Staatssammlung für Paläontologie und Historische Geologie, München, Germany; GPIT, Institut und Museum für Geologie und Paläontologie Tübingen, Germany; IGS, Institut de Géologie Strasbourg, Université Louis Pasteur, France; MB, Museum für Naturkunde, Humboldt-Universität zu Berlin, Germany; NNM, Naturalis Museum, Leiden, Holland; PIMUZ, Paläontologisches Institut und Museum der Universität Zürich, Switzerland; SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany; SMNK, Staatliches Museum für Naturkunde, Karlsruhe, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TM, Teylers Museum, Haarlem, Holland.

*Abbreviations used in the text-figures.* bd, branchial denticles; c, centrale; caf, crista aspera femoris; cla, clavicle; clei, cleithrum; dc, distal carpal; dia, diapophysis; dt, distal tarsal; eo, exoccipital; fem, femur; fi, fibula; fib, fibulare; fna, facet for neural arch; fpc, facet for pleurocentrum; fs, fibular sulcus; haem, haemal arch; hum, humerus; i, intermedium; ic, intercentrum; icl, interclavicle; il, ilium; mc, metacarpals; mt, metatarsals; na, neural arch; pc, pleurocentrum; phal, phalanges; po, popliteal fossa; poc, posterior crest; ppo, parapophysis; pro, proatlas; przyg, prezygapophysis; ps, parasphenoid; pzyg, postzygapophysis; ra, radius; rad, radiale; sc, scapulocoracoid; sgb, supraglenoidal buttress; sgf, supraglenoidal foramen; sta, stapes; ti, tibia; tib, tibiale; tr, trochanter; ul, ulna; uln, ulnare.

## SYSTEMATIC PALAEOLOGY

TETRAPODA Goodrich, 1930

TEMNOSPONDYLI Zittel, 1890

STEREOSPONDYLOMORPHA Yates and Warren, 2000

ARCHEGOSAURUS Goldfuss, 1847

*Type species.* *Archegosaurus decheni* Goldfuss, 1847, from the Autunian of Lebach, Germany.

*Archegosaurus decheni* Goldfuss, 1847

Text-figures 1–10

*Material.* Complete larval skeletons: MB.Am.124, 134, 227, 229, 252, 1368, PIMUZ A/II 0021; complete juvenile skeletons: MB.Am.117, 127; complete adult skeleton: MB.Am.953, with dorsal side (a) and ventral side (b, counterpart); larval skulls plus pectoral girdle and presacral vertebral column: BSM (1869) III 6, IGS U II 1/2, U III 5/3, MB.Am.179, 218, 222, 230, 236, 272, 289, 323, SMNK 39/13, TM 1154, GPIT/Am/233, SMNS 81850; isolated larval skull: IPB R 432; juvenile skulls plus

anterior vertebral column and pectoral girdle: MB.Am.275, NNM 39083, SMF A14; adult skulls plus anterior parts of the trunk: MB.Am.329, 160, SMF A35; adult presacral vertebrae: MB.Am.263, 271, 1366; pelvis with tail of adult specimen: MB.Am.273; anterior part of tail of adult specimen: MB.Am.268; manus of adult specimen: MB.Am.255.

In *A. decheni*, specimens up to 150 mm skull length can be referred to as larvae because they bear dentigerous branchial plates that were attached to the cartilaginous ceratobranchials (Witzmann 2004a). They indicate the presence of open gill slits and the possibility of external gills. The largest specimens with branchial plates are IGS U III 5/3, IPB R 432 (both with a skull length of c. 140 mm), and SMNS 81850 (skull length c. 150 mm). The subsequent juvenile and adult phase can only be distinguished arbitrarily for descriptive purpose. Specimens with skull lengths between 150 and 200 mm are defined here as juveniles, whereas the adult phase starts with the formation of distal uncinat processes on the ribs (skull length > 200 mm). Gubin (1997) reported a skull length of 118 mm after which allometric growth of the skull proportions in *A. decheni* stopped, implying that the adult phase started with this size. However, an extensive size series of 96 skulls ranging from less than 20 to almost 280 mm in length shows that allometric growth did not cease in the largest known specimens (Witzmann 2004b).

In addition to unambiguous material of *A. decheni*, our description of vertebral morphology is partially based on well-preserved material lacking the skull (MB.Am.1366, 263, 268, 271). Their assignment to *A. decheni* is justified by the height and morphology of the neural spines, as well as the proportions and direction of their transverse processes. This also applies to MB.Am.273 from which the tail is described; though the skull is not preserved in this specimen, it can be assigned to *A. decheni* because the morphology of the pelvic girdle, hindlimbs and vertebrae is identical to MB.Am.953, a complete specimen of approximately the same size. The only other temnospondyl known from the Lebach locality and horizons, *Cheliderpeton latirostre*, is only rarely preserved in the Black Shale Horizon. The latter is usually poorly preserved, indicating its allochthonous state, whereas the skeletal remains of *Archegosaurus decheni* are mostly preserved in articulation, which suggests an autochthonous burial (Boy 1977).

**Diagnosis.** *Archegosaurus decheni* is characterized by two autapomorphic cranial characters (from Witzmann 2006a): choanae extremely elongate and narrow, laterally concave, reaching more than one-fifth of skull length and three times naris length; four symphyseal fang loci on the dentary medial to the marginal tooth row on each mandibular ramus; and a single autapomorphic postcranial character: humerus very short with stout shaft, unossified ends, and without processes, even in adults.

### Description

#### Vertebrae

Jaekel (1896a, 1909b) restored two selected vertebrae of the trunk, one of the pelvic region, and two of the tail, and pub-

lished a restoration of a trunk vertebra in anterior and posterior view (Jaekel 1896a, figs 2–9), but did not describe the proatlas-atlas-axis complex. In the following, we add new data on the vertebral morphology of adult specimens, before we go into the details of vertebral ontogeny. *A. decheni* shares the classic rhachitinous vertebrae with *Cheliderpeton*, *Sclerocephalus* and *Eryops* (von Meyer 1858; Jaekel 1896a, 1909b; Moulton 1974; Boy 1988, 1993).

Each segment consists of a well-ossified neural arch, an anteroventral, crescent-shaped intercentrum, and paired posterolateral pleurocentra of lozenge-shaped outline in lateral view. Unlike in most stereospondyls, the lateral exposure of the pleurocentrum is quite substantial and extends well ventrally to about the mid-level of the intercentrum. However, the pleurocentra of the anterior and mid-trunk regions never run as far ventral as the intercentra, a condition reported in the trimerorhachid *Neldasaurus* (Chase 1965) and the amphibamid dissorophoids (Daly 1994; Schoch and Rubidge 2005).

**Proatlas-atlas-axis complex in adults.** The atlas-axis complex is exposed only in a few large specimens: MB.Am.953a (Text-fig. 1A), NNM39083 (Text-fig. 1B), SMF A14, SMF A35 and MB.Am.160. The proatlas is preserved anterior to the atlas in SMF A14, NNM39083, and probably in MB.Am.275. This element is poorly preserved, revealing only a short neural spine that is directed posterodorsally (SMF A14).

The paired atlantal neural arch is not fused in the midline. In lateral view, the neural spine is slender and tapering. It is directed posterodorsally and abuts against the neural arch of the axis. The dorsal ends of the paired atlantal neural spines do not meet in the midline, but are directed dorsolaterally as in *Eryops* (Moulton 1974, fig. 9A). In the specimens studied, the articular surface for the exoccipitals is not exposed on the atlas. The atlantal intercentrum is preserved in only three specimens: fragmentarily in NNM39083, MB.Am.160 and in MB.Am.953a. In the latter, it shows the typical crescent shape but seems to be less high than the intercentra of the following trunk vertebrae. It possesses a roughened surface on its dorsal (inner), anterior and posterior sides, both suggesting a significant continuation in cartilage.

The robust neural arch of the axis is elongate anteroposteriorly compared with the adjacent vertebrae (Text-fig. 1A), though it is shorter than that of the third vertebra. The morphology of the axis neural arch is quite similar to that of *Sclerocephalus* (Boy 1988). According to Berman and Reisz (1980), the axial neural arch also forms a massive structure in *Trimerorhachis sandovalensis*. This condition is also found in *Acanthostega* (Coates 1996). The axis is the first rib-bearing vertebra in *A. decheni* (contra Jaekel 1896a).

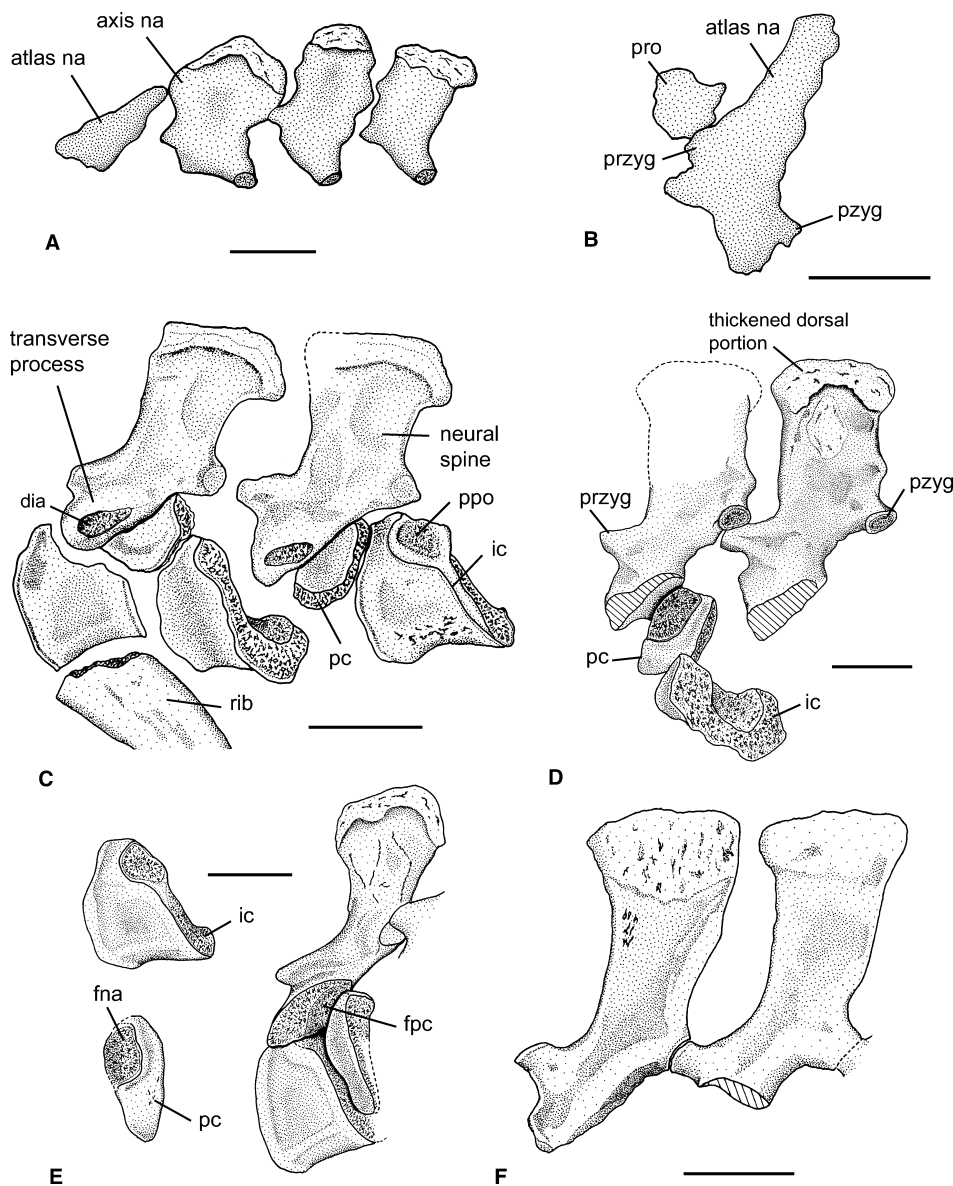
**Third and fourth vertebra in adults.** In *Eryops*, the neural arch of the fourth vertebra is distinctly lower than the third and fifth vertebrae (Moulton 1974). This was also reported in *Sclerocephalus* (Boy 1988), *Australerpeton* (Dias and Schultz 2003), and is the case in *Trimerorhachis sandovalensis* (Berman and Reisz 1980, fig. 7A). A similar differentiation of neural arch morphology is also present in *A. decheni*, but less marked. In both MB.Am.953a and SMF A14, the neural arch of the fourth

vertebra is slightly reduced in height compared with the adjacent vertebrae.

*Trunk vertebrae in adults.* The neural arches of the trunk vertebrae (Text-fig. 1C–F) have tall neural spines. MB.Am.1366 and 263 (Text-fig. 1C–D) suggest that their dorsal portion is more thickened than described by Jaekel (1896a, figs 8–9). The dorsal surface of the neural arches is rugose, and the lateral sides bear tuberosities. Some neural spines on the anterior half of the trunk show a low, lateral ridge that is orientated vertically, similar to *Australerpeton* (Dias and Schultz 2003). The neural spines

become gradually higher and more slender caudally (Text-fig. 1F; Jaekel 1896a). The highest neural spines are located in the posteriormost trunk and the sacral regions.

The articulation facets of the postzygapophyses face ventrolaterally and slightly posteriorly (Text-fig. 1C–F). Accordingly, the facets of the prezygapophyses are aligned dorsomedially and slightly anteriorly, having a slightly convex surface. The articulation surfaces are proportionally smaller than in *Eryops* (Moulton 1974), *Onchiodon* (Geinitz and Deichmüller 1882), *Balanerpeton* (Milner and Sequeira 1993) and *Dendrerpeton* (Holmes *et al.* 1998). The neural canal measures less than 5 mm in diameter



**TEXT-FIG. 1.** *Archegosaurus decheni*, vertebrae of adult specimens. A, MB.Am.953a, the four anteriormost vertebrae in lateral view. B, NNM39083, proatlas and atlas in lateral view. C, MB.Am.1366, vertebrae of the anterior trunk region in lateral view. D, MB.Am.263, vertebrae of the middle part of the trunk in lateral view. E, MB.Am.1366, vertebrae of the anterior trunk region; intercentrum and pleurocentrum (left) in lateral view, vertebra (right) in posterolateral view. F, MB.Am.271, vertebrae of the posterior trunk region in lateral view. Scale bars represent 10 mm.

and is not closed ventrally. The ossification of the floor of the neural canal is a reflection of either age or size (Moulton 1974). For example, Dias and Schultz (2003) described the neural canal of an adult specimen of *Australerpeton* as ventrally closed by bone, whereas it is still not ossified ventrally in an early adult specimen. The vertebra of a very large and probably adult specimen of the archegosaurid *Platyoposaurus stuckenbergi* (Gubin 1991, fig. 28) does have an ossified neural canal floor.

The transverse processes bear posteriorly slightly concave facets for the pleurocentra (Text-fig. 1E). These facets were probably covered by cartilage because they possess a roughened surface. A smaller area of unfinished bone is present on the anterior part of the transverse process that articulated with the pleurocentrum of the anterior vertebra. This contrasts with the reconstruction of Jaekel (1896a, fig. 9), who placed the pleurocentra posteroventral to the intercentrum. The width of the neural arches, as measured between the lateral ends of the transverse processes in MB.Am.953a (skull length 226 mm), increases gradually from the axis (width of 27.5 mm) to posterior vertebrae and reaches its maximum width at the fourteenth and fifteenth vertebra (c. 40 mm). Subsequently, it decreases gradually to about 28 or 29 mm in the posterior trunk region ('lumbar' region). The transverse process terminates in the posterolaterally facing, anteroposteriorly slightly elongate diapophysis (Text-fig. 1C) for articulation with the rib.

The intercentra are crescent-shaped in transverse view and provide a large space for the notochord. All surfaces of the intercentra are unfinished except the outer surface. Two longitudinal rugose ridges are present on the ventrolateral surface (Text-fig. 1E). Similar ridges are present in the rhinesuchid stereospondyl *Uranocentron* (van Hoepen 1915). As described by Jaekel (1896a), the posterior part of the dorsolateral side of the intercentrum is expanded and slightly elevated. It forms the concave articulation facet for the rib (the parapophysis), which is more conspicuous than the condition in *Eryops* (Moulton 1974). The facet is unfinished. In the posterior trunk region, the intercentra become slightly lower (e.g. MB.Am.263, MB.Am.271).

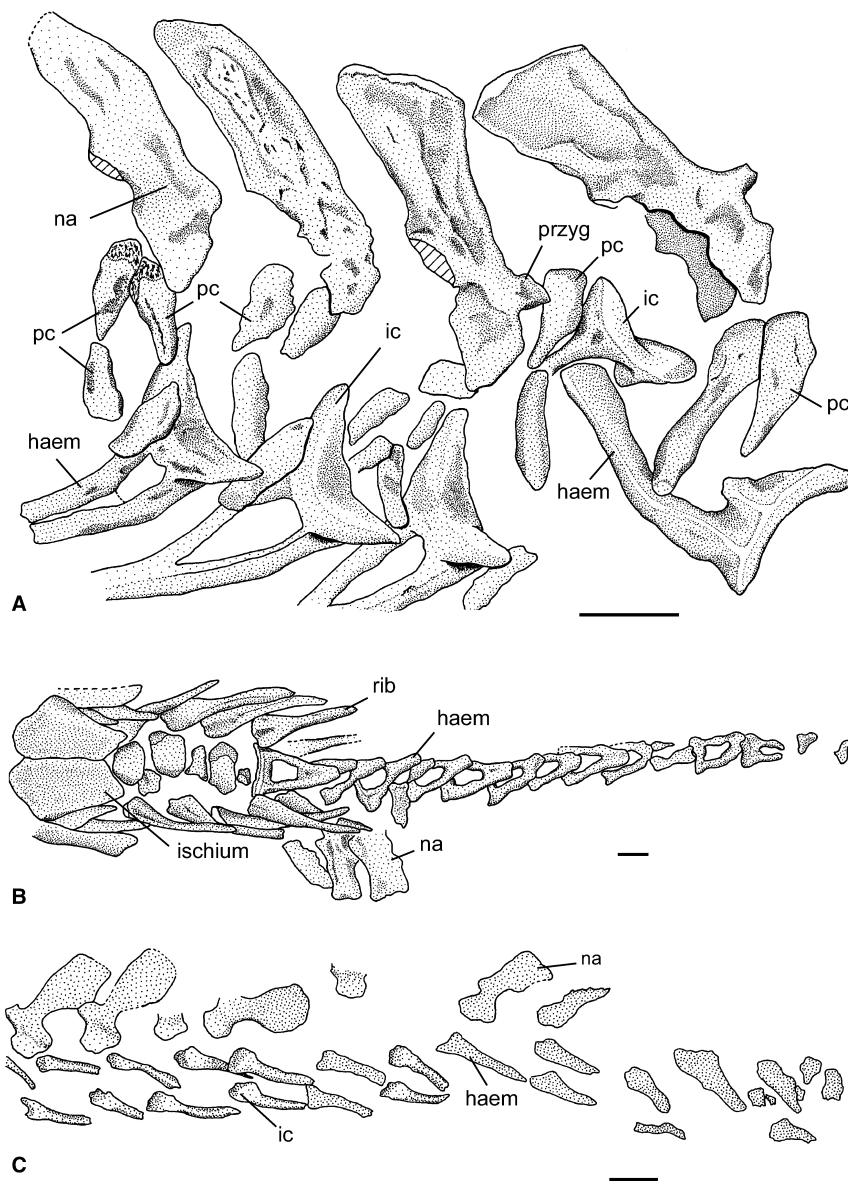
The trunk pleurocentra are lozenge-shaped and bent slightly in sagittal view to embrace the chorda partially. The dorsal part of the pleurocentrum is thicker and more massive than the narrower, flattened ventral part (Text-fig. 1E). Except for its lateral (outer) surface, the pleurocentrum is unfinished. The lateral surface is smooth and concave, so that the margins curve outwards and unfinished bone is visible anterolaterally and posterolaterally. A similar morphology is present in *Eryops* (Moulton 1974). The pleurocentrum bears an elevation with a concave and unfinished surface on the anterior edge of its dorsal part (Text-fig. 1D–E). This is the facet for articulation with the ventral surface of the neural arch, as also described in *Eryops* (Moulton 1974) and the colosteid *Greererpeton* (Godfrey 1989). Text-figure 1E shows the appropriate facet on the neural arch, and in Text-figure 1C, the pleurocentrum is in articulation with the neural arch. As also described by von Meyer (1858) and Jaekel (1896a), the pleurocentra extend increasingly ventrally from anterior to posterior in the trunk. This contrasts with the situation in the presumably more terrestrial basal temnospondyl *Balanerpeton*, in which the intercentra become succeedingly

longer in the posterior trunk and supersede the ventral extension of the pleurocentra (Milner and Sequeira 1993).

*Sacral vertebra and postsacral vertebral column of large specimens.* The width (as measured above) of the sacral neural arch (twenty-fifth vertebra) is slightly larger than in the adjacent anterior vertebrae (c. 30 mm in MB.Am.953a), and the transverse process with the diapophysis is slightly elongated anteroposteriorly. The size of the transverse processes decreases from anterior to posterior in the postsacral vertebral column. Thus, a distinct transverse process is no longer developed in about the sixth or seventh postsacral neural arch (Text-fig. 2A). The neural spines are more slender, less massive, and their dorsal margins are less thickened than in the trunk vertebrae, and diminish gradually in size in the tail. The neural spines are inclined posteriorly, and the angle of inclination increases towards the tip of the tail. Compared with the trunk vertebrae, the zygapophyses of the caudal neural arches are proportionally smaller. In the posterior part of the tail, the neural arches are only rudimentarily developed (Text-fig. 2C).

Eighteen intercentra are visible posterior to the ischium in MB.Am.953b (Text-fig. 2B). At least 21 caudal vertebrae are preserved in this specimen, taking into consideration the vertebrae obscured by the ischium. Seven caudal ribs are visible in the same specimen. The intercentra bear haemapophyses from the sixth caudal vertebra distally. These are flattened mediolaterally and expanded distally (Text-fig. 2A). Compared with those of the trunk, the intercentra of the tail itself are distinctly lower. As described by Jaekel (1896a), their degree of ossification decreases gradually towards the tip of the tail. In the middle and posterior part of the tail, the intercentra are paired. In the posterior region of the tail, the ossified, paired portion of the intercentrum is restricted to the ventralmost part of the notochord. Thus, there is a large unossified gap between neural arch and intercentrum (Text-fig. 2C). The haemapophyses are short and not fused distally in the posterior region of the tail.

The pleurocentra extend far ventrally in the anterior caudal vertebrae. The dorsal part of each is proportionally less massive than that of the presacral pleurocentra, and the ventral part is flattened mediolaterally (Text-fig. 2A). Facets for articulation with the neural arch are present in the seven or eight anterior-most postsacral pleurocentra. Compared with the trunk pleurocentra, the facets of the caudal pleurocentra are proportionally distinctly smaller. Paired pleurocentra appear to approach one another at the ventral midline. Pleurocentra of one vertebra are preserved in transverse view in MB.Am.287, forming a ring that opens dorsally. The ring is very thin in its ventral region, and the two halves are only weakly fused ventrally. It is slightly constricted in the middle part of one side. The ring belongs approximately to the ninth postsacral vertebra. The other caudal vertebrae in this specimen are visible in lateral view; it cannot be determined if their pleurocentra are fused ventrally or not. The caudal pleurocentra in *A. decheni* become slender and less massive posteriorly, and are increasingly constricted in their lateral part. From the tenth postsacral vertebra onwards, they are divided into dorsal and ventral portions on either side (Text-fig. 2A), a condition illustrated by von Meyer (1858, pl. 21, fig. 5) and reported by Jaekel (1896a). Van Hoepen (1915) also described this phenomenon in the eighth and ninth postsacral

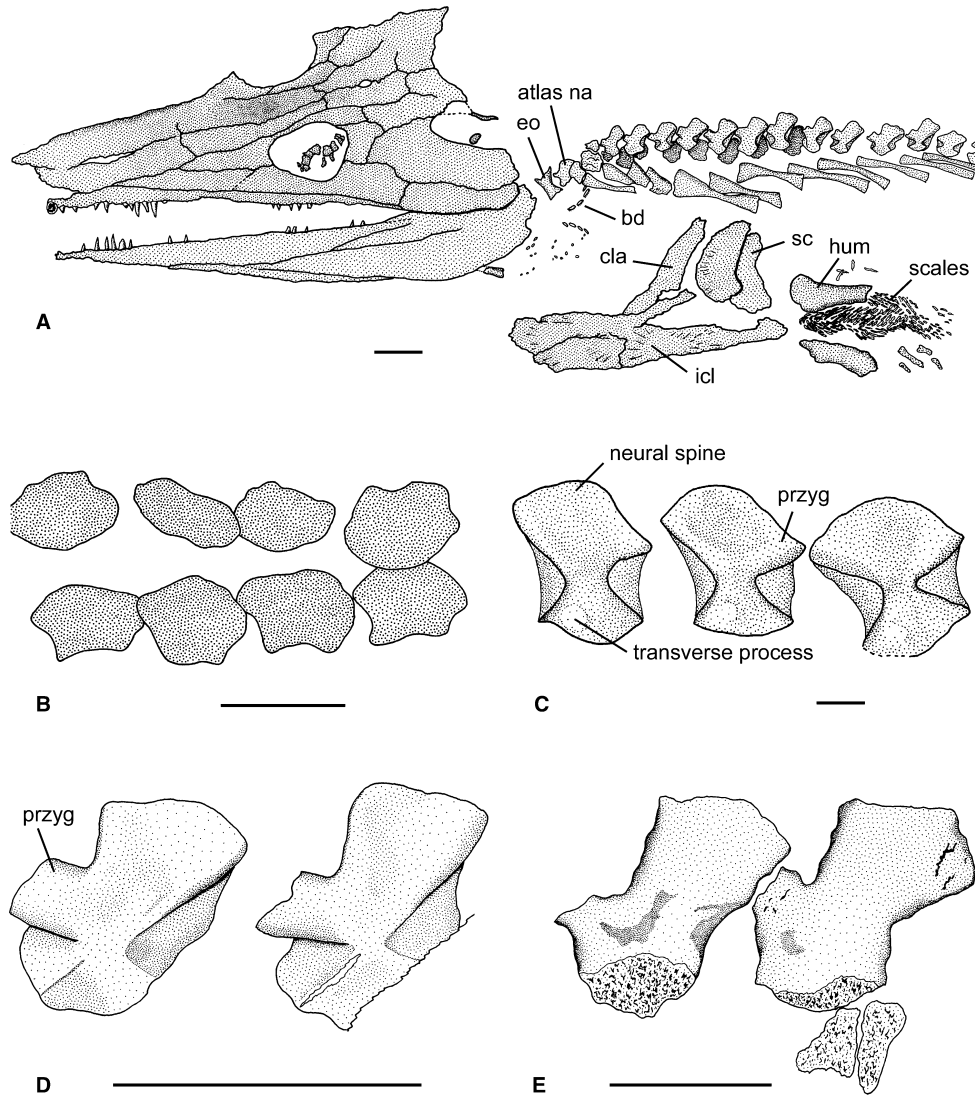


**TEXT-FIG. 2.** *Archegosaurus decheni*. Caudal vertebrae of adult specimens. A, MB.Am.268, lateral view of vertebrae with haemal arches. B, MB.Am.953b, ischia and anterior tail region in ventral view. C, MB.Am.273, middle part of the tail in lateral view; the anteriormost vertebra in this figure is approximately caudal 18. Scale bars represent 10 mm.

vertebrae of *Uranocentron*. The pleurocentra become gradually smaller and less ossified further posteriorly. They are present as four ill-defined, small oval pieces of bone per vertebra in the posterior part of the tail in MB.Am.273. This region of the tail consisted to a large degree of cartilage. In *Eryops*, the pleurocentra of the anterior caudal vertebrae extend ventrally also, and may fuse in the largest specimens (Moulton 1974). In contrast to *A. decheni*, pleurocentrum and intercentrum can co-ossify in the pelvic region of *Eryops*. Pleurocentra also extend far ventrally in the anterior tail region of the dissorophoid *Phonerpeton*, unlike the presacral pleurocentra (Dilkes 1990, fig. 10).

*Length of the caudal series.* It is not possible to ascertain the exact number of caudals because the posterior and less ossified

part of the tail is missing in almost all specimens. The tail is best visible in MB.Am.273. About 27 or 28 postsacral vertebrae are present from the sacral vertebra to the posterior end of the concretion, measuring *c.* 370 mm. The posterior region of the tail is preserved lateral to this anterior portion because the tail is curved and its posterior part directed into the concretion again. The length of the missing portion between these two parts of the tail can be estimated as 150–200 mm, according to the size of the neural arches in the anterior and posterior portion. The preserved posterior part measures 90 mm in length and consists of six vertebrae. One can extrapolate that the tail terminated after at least another 50 mm, so that we estimate a total tail length of 650–700 mm. The complete specimen MB.Am.953, which is of similar size to MB.Am.273, has a snout-vent length



**TEXT-FIG. 3.** *Archegosaurus decheni*. Early to late larval specimens. A, IGS U II 1/2 (skull length more than 90 mm), skull and anterior trunk in lateral view. B, trunk neural arches of the smallest specimen MB.Am.134 (skull length 18 mm) in ventral view. C, trunk neural arches of MB.Am.230 (skull length c. 60 mm) in lateral view. D, neural arches of IGS U II 1/2 (skull length more than 90 mm) in lateral view. E, neural arches of presumed presacral vertebrae 9 and 10 with remnants of centra in MB.Am.275 (skull length 148 mm) in lateral view. Scale bars represent 1 mm in B–C and 10 mm in A, D–E.

of slightly more than 600 mm. According to these data, the tail is longer than the length of the skull and the trunk in adults. Jaekel (1896b) briefly mentioned the tail of an individual (probably MB.Am.273) that he estimated as having a skull length of 270 mm, but this figure is too large for that specimen.

*Ontogeny of vertebrae.* In larvae of *A. decheni* the anteriormost vertebrae are rarely preserved. They are generally obscured by the elements of the large pectoral girdle. In IGS U II 1/2 (skull length more than 90 mm; Text-fig. 3A) the anterior part of the vertebral column is visible and reveals that the atlas is comparatively small, with an anterior process that possibly represents a part of the articulating facet with the exoccipital. Its neural spine is low and slender. The axis is preserved in articulation with the

first rib. Its neural spine is larger and broader than that of the atlas, but the axis is nevertheless distinctly smaller than the vertebrae of the thoracic region. Nothing can be said about the third vertebra, because it is too poorly preserved. The fourth vertebra seems to possess a slightly narrower neural spine than the posteriorly following vertebrae, as in adult specimens.

The neural arches are the first vertebral elements that ossify during ontogeny of *A. decheni* (Witzmann 2006b). In the smallest available specimen (MB.Am.134; Text-figs 3B, 4A), the neural arches lack neural spines and transverse processes. Zygapophyses are rudimentarily developed, and only the two or three anteriormost neural arches are ossified in the postsacral vertebral column (Witzmann 2006b). In specimens exhibiting a skull length of c. 30 mm, the zygapophyses are more distinctly developed and

become more robust during ontogeny. The neural spines are still not developed in specimens of a skull length of c. 50 mm.

In MB.Am.252 (skull length c. 65 mm), approximately the anteriormost 15 neural arches of the caudal vertebral column are ossified. They are more weakly ossified than in the trunk, and they become increasingly smaller and more ill-defined posteriorly. In specimens of this size, the neural spines are developed as low outgrowths, and small transverse processes are present in the neural arches of the trunk (Text-fig. 3C).

In MB.Am.227 (Text-fig. 5A; skull length c. 84 mm), the halves of the neural arches are still not fused and no centra are ossified. The neural spines are still low. IGS U II 1/2 has a skull length of more than 90 mm. Its neural arches possess proportionally higher neural spines, and distinct prezygapophyses are now visible in specimens of this size (Text-fig. 3D). The transverse processes are still small. In MB.Am.275 (skull length 148 mm; Text-fig. 3E), the neural spines are already moderately high.

The vertebral centra are still cartilaginous in PIMUZ A/II 0021, which has a skull length of 95 mm. At a skull length of slightly more than 100 mm, however, the intercentra start initial ossification. Von Meyer (1858, pl. 13, figs 4, 6) illustrated ill-defined bony elements in the anterior trunk region of two specimens with skull lengths of c. 110–120 mm (estimated from the lengths of the interclavicles) that can be interpreted as intercentra. In the material investigated here, intercentra are first visible at a skull length of c. 120 mm, e.g. MB.Am.272.

In *Onchiodon*, the transverse processes, neural spines and zygapophyses develop earlier in ontogeny than in *A. decheni*. The zygapophyses are comparatively well developed in specimens with a skull length of around 20 mm, and transverse processes are already visible at slightly more than 30 mm skull length. Neural spines are moderately high at a skull length of c. 60 mm (Witzmann 2005).

#### Rib morphology

The short, straight ribs of the smallest specimen (MB.Am.134, skull length 18 mm; Text-fig. 4A) are restricted to the anterior half of the trunk. At a skull length of c. 50 mm, all ribs of the trunk are ossified.

In larval specimens beyond 30 mm skull length, the rib of the axis (= first rib) and of the third vertebra are short, straight and hardly expanded distally (e.g. BSM 1869 III 6). In the thoracic region, the ribs increase in length and curvature, and their distal portion broadens increasingly (Text-figs 3A, 4B–C; see also the reconstruction in Text-fig. 10A). The ribs become shorter and more slender distally again from vertebrae 8–11, and the posterior presacral ribs are much abbreviated. The proximal rib heads are not differentiated into capitulum and tuberculum.

Juvenile and adult specimens (e.g. MB.Am.117, 127, 953) have proportionally distinctly longer thoracic ribs which exhibit greater curvature, although the ribs of the axis and vertebra 3 remain short and are only slightly curved (Text-fig. 5B). The thoracic ribs bear posterodistal expansions (distal uncinat processes *sensu* Schoch 1999) in specimens beyond c. 200 mm skull length. The expansions are medially (internally) concave, giving them a spatulate appearance. Ribs of vertebrae 12–19 are curved and hardly expanded distally, whereas the posteriormost presacral ribs have a rather rudimentary appearance as in larvae (see

also the reconstruction in Text-fig. 10B). The flattened proximal rib heads consist of fused capitulum and tuberculum without a distinct incision between them also in adults. Distal uncinat processes have been described in a variety of adult temnospondyls that achieve large body sizes. In contrast to *A. decheni*, the distal uncinat processes in the archegosaurid *Platyposaurus* are longer, spine-like, and situated about half-way along each rib (Konzhukova 1955; Gubin 1991). In both *Mastodonsaurus* (Schoch 1999) and *Eryops* (Miner 1925; Moulton 1974), the distal uncinat processes are expanded in a blade-like fashion and proportionally much larger than in *A. decheni*. Most similar to *A. decheni* in size and shape are the distal uncinat processes in the stereospondylomorph *Australerpeton* (Dias and Schultz 2003).

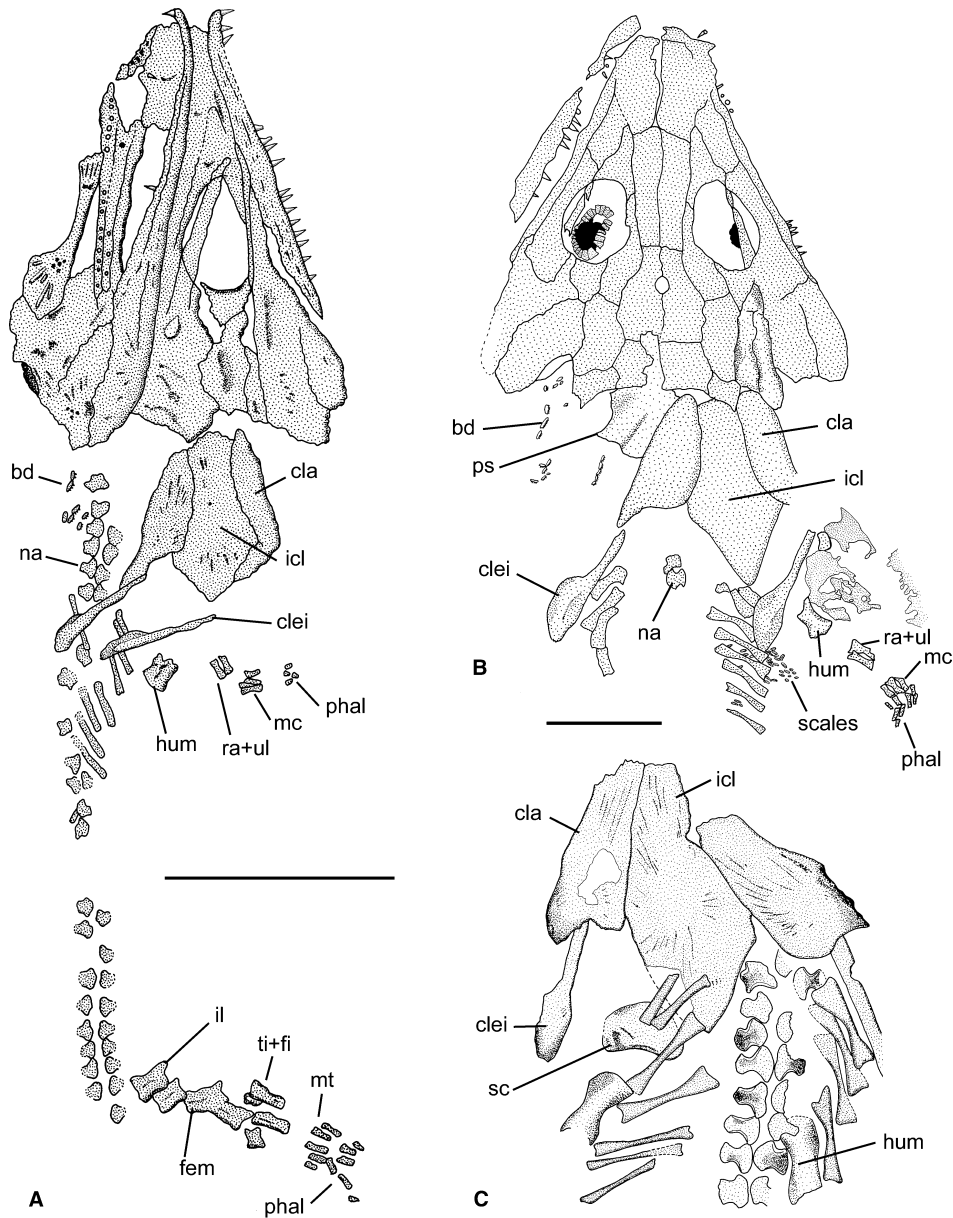
The sacral rib (of vertebra 25) is undifferentiated in the smallest specimen in which it is ossified (skull length c. 65 mm). In larger specimens, it has a stout proximal head, a short shaft, and a flattened, broadened distal end for articulation with the ilium (Text-figs 5, 6A–B). It is, however, proportionally distinctly more slender than in *Eryops* (Moulton 1974) and the amphibioid *Eoscopus* (Daly 1994).

At least seven caudal ribs are present in MB.Am.953a (Text-fig. 5B). They are longer than the posteriormost four trunk ribs and decrease gradually in length. Their proximal ends are flattened and broadened (Text-figs 5B, 7D).

#### Pectoral girdle

As is common in temnospondyls, the pectoral girdle of *A. decheni* consists of five dermal elements, the unpaired, median interclavicle and the paired clavicles and cleithra, as well as the enchondral scapulocoracoid. The dermal bones are already ossified in the smallest available specimen with a skull length of 18 mm. In contrast, the scapulocoracoid starts to ossify much later during increase in skull length (Witzmann 2006b).

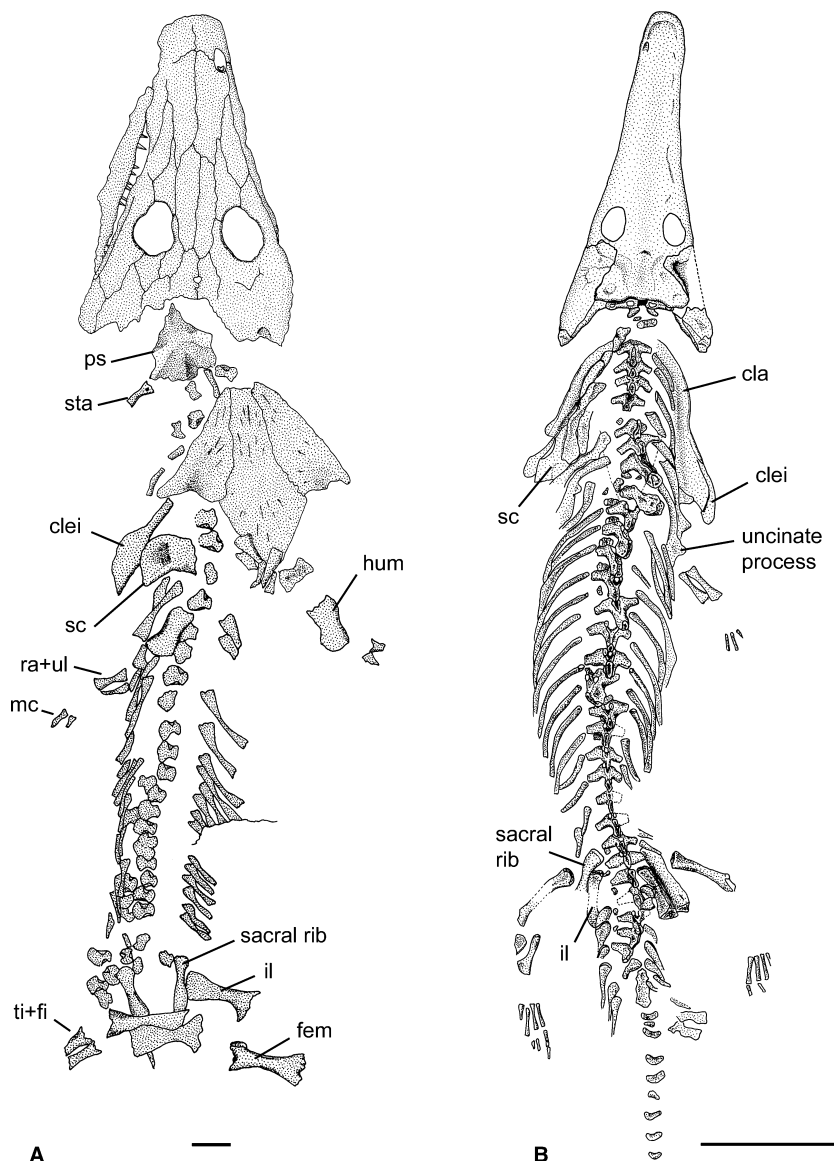
*Interclavicle.* The interclavicle is of an elongated rhomboidal shape. In the smallest specimen, it is longer than wide (Text-fig. 4A). Its length increases with strong positive allometry; the ratio of length to width varies from 1.4 in small specimens to 2.8 in large ones. The interclavicle of *A. decheni* resembles that of *Scleerocephalus* (Boy 1988; Meckert 1993) and *Cheliderpeton*, although in *Cheliderpeton* it is more slender (Boy 1993). The anterior margin of the interclavicle is convex and serrated (Text-fig. 6F). The ventral surface displays the characteristic temnospondyl dermal sculpture pattern. The centre of ossification is indicated by dermal pits and is situated medial to the posterior margin of the ventral clavicular blades. The dermal pits grade into furrows and ridges that radiate outwards. Furrows and ridges are most distinct in the anterior part of the interclavicle. The articulation facets overlapped by the clavicles possess fine ridges. These surfaces are proportionally slender (e.g. GPI-T/Am/233) as compared with *Scleerocephalus*. The posterolateral margin of the interclavicle lacks dermal sculpture; this region is covered by long-oval dermal scales. The dorsal surface of the interclavicle is almost smooth, but the original surface is rarely preserved. There are fine striations on the dorsal surface both on the left and on the right side of the posterolateral part of the interclavicle in MB.Am.289b that may be interpreted as an attachment area of hypaxial musculature.



**TEXT-FIG. 4.** *Archegosaurus decheni*. Larval specimens in ventral view. A, MB.Am.134 (skull length 18 mm), complete skeleton of smallest known larva. Redrawn after Witzmann (2006b). B, MB.Am.222a (skull length 32 mm), skull plus pectoral girdle and anterior trunk. C, MB.Am.179 (skull length 53 mm), pectoral girdle plus anterior trunk. Scale bars represent 10 mm.

*Clavicle.* The clavicle consists of a narrow ventral triangular blade with a posterodorsally orientated shaft (Text-figs 3A, 4–5, 6C–D, F). The shaft arises posterodorsally at an angle of c. 135 degrees (e.g. IGS U II 1/2). The ossification centre with dermal pits is located in the region of the curvature from the ventral blade into the shaft. The dermal sculpture does not extend onto the shaft. The clavicles do not meet ventrally in the midline. Compared with dissorophoids (Boy 1972), *Acanthostomatops* (Boy 1989) and *Eryops* (Miner 1925), the ventral blade is proportionally much more elongated in an anteroposterior direction.

*Cleithrum.* The cleithrum forms a rod-like bone with an expanded dorsal blade (Text-figs 4–5, 6C–D, F) that does not, however, expand as much posteriorly as in *Eryops* or dissorophoids. The shaft is slender, and the blade-like dorsal head is continuous with the shaft and lacks curvature in small specimens. The width of the head varies individually. The head is usually more expanded anteriorly than posteriorly and continues as a posterodorsally directed process. With increasing size, the shaft becomes proportionally stouter and mediolaterally flattened. The dorsal head bends posteriorly in specimens with skull lengths greater



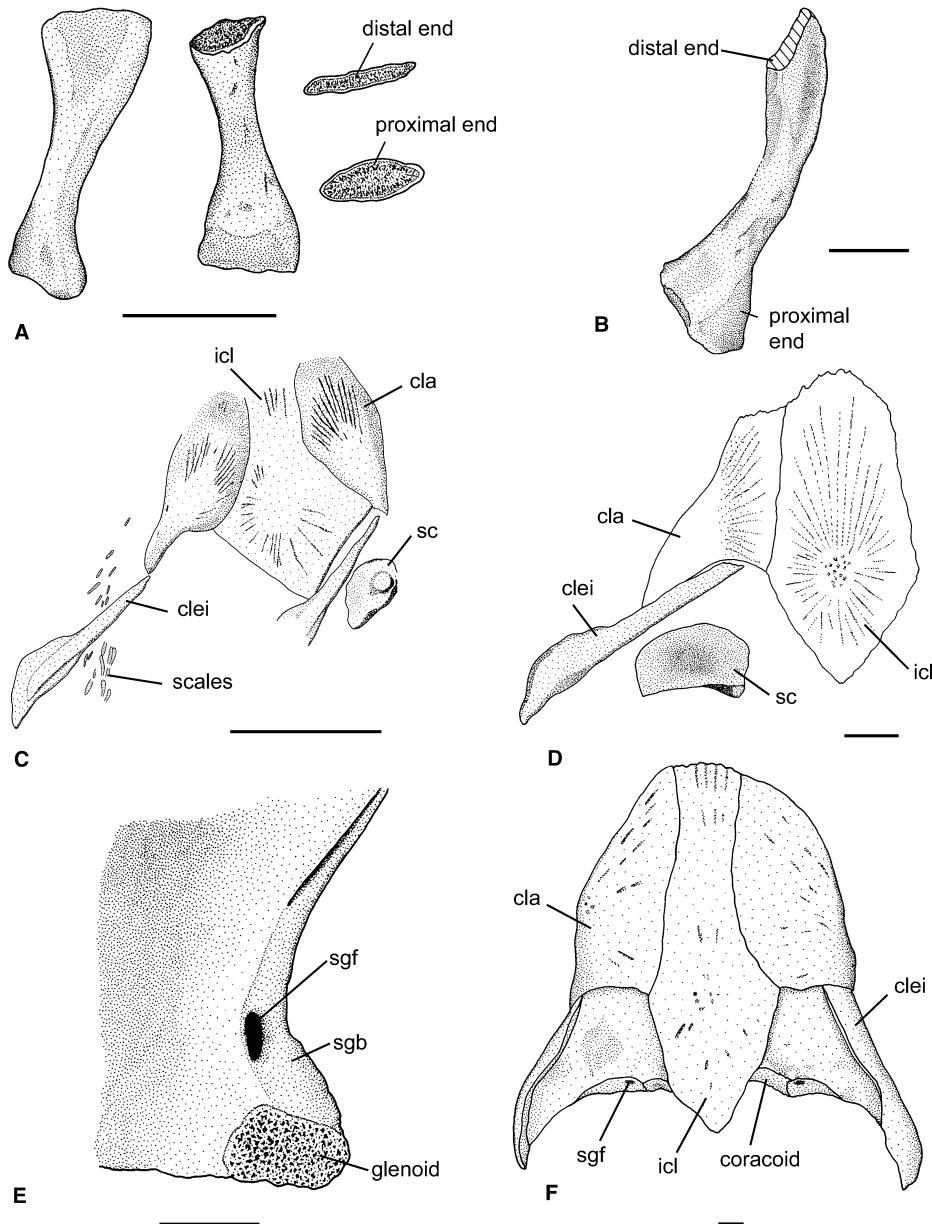
**TEXT-FIG. 5.** *Archegosaurus decheni*. Complete skeletons, redrawn after Witzmann (2006b). A, MB.Am.227 (skull length c. 84 mm), larval specimen in ventral view; the skull is a natural mould and shows the sutures on the dorsal surface. B, MB.Am.953a (skull length 226 mm), adult specimen in dorsal view. Scale bars represent 10 mm in A and 100 mm in B.

than c. 80 mm. It is clearly more posteriorly directed in MB.Am.953b (skull length 226 mm; Text-fig. 6F). The head still tapers distally into a spine. The lateral part of the cleithrum is convex as exposed in MB.Am.953b. No dermal sculpture is present on the shaft or on the dorsal blade. In contrast to *Sclerocephalus haeuseri* (Meckert 1993), the head does not enlarge significantly as size increases. The cleithrum of *A. decheni* resembles most closely that of *Australerpeton* (Dias and Schultz 2003).

**Scapulocoracoid.** The posteroventral portion of the ossified scapula is first preserved in a specimen with a skull length of c. 38 mm (Text-fig. 6C), and exhibits an ill-defined outline. In larger larvae (50–150 mm skull length), the ossified portion is reniform with a convex anterior and a concave posterior margin (Text-figs 3A, 4C, 5A, 6D). The posteroventral part is thickened, including the supraglenoidal buttress that tapers dorsally. The ossified scapular portion is distinctly thinner anteriorly and dorsally. In MB.Am.289 (skull length c. 110 mm), the supraglenoidal

foramen is visible on the posterolateral side of the buttress. This foramen has an elongated oval shape with the long axis directed dorsoventrally. The unfinished margins of the scapular blade indicate that it continued anteriorly and dorsally in cartilage. The coracoid portion with the glenoid region remained cartilaginous in specimens of this size range and is thus not preserved.

Parts of the coracoid portion are ossified in the large specimen MB.Am.953b (skull length 226 mm; Text-fig. 6F), although there is no suture detectable between the scapular and coracoid components. The scapular portion is directed posterodorsally and thickens ventrally in this specimen. The supraglenoidal foramen is preserved. Ventral to the supraglenoidal buttress, the coracoid element is visible, but its ventral part is obscured by the interclavicle. The glenoid region ventral to the supraglenoidal buttress is poorly defined and probably consisted to a large degree of cartilage. The dorsal part of the scapulocoracoid is bent slightly medially. Imperfect preservation precludes recognition of glenoidal and supracoracoid foramina.



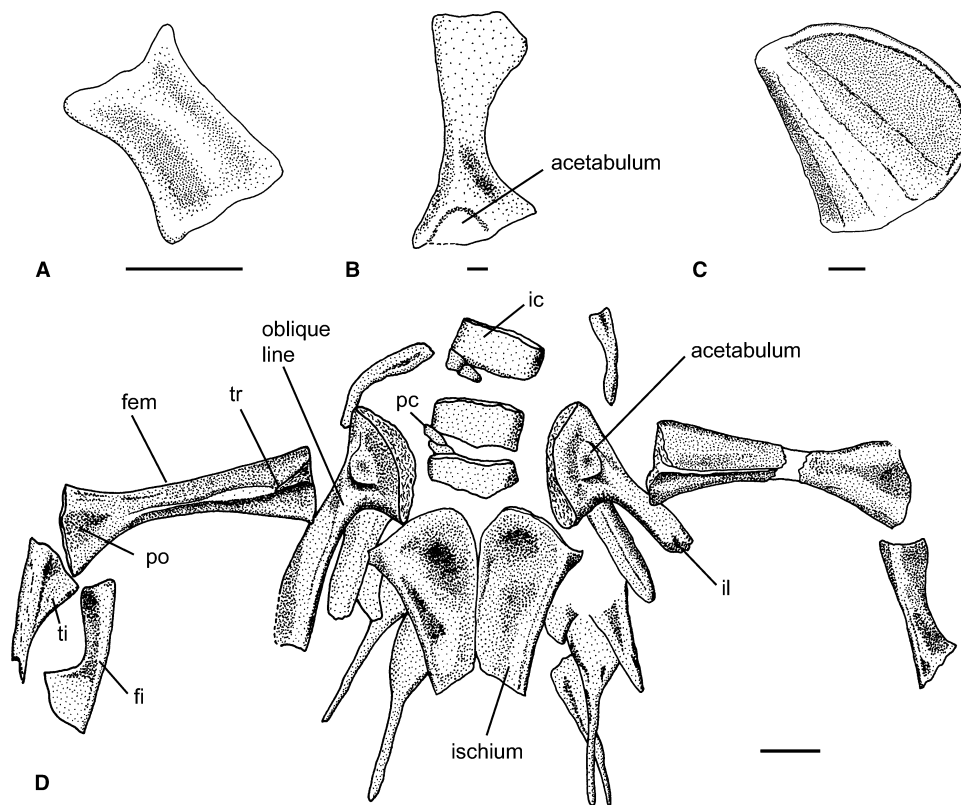
**TEXT-FIG. 6.** *Archegosaurus decheni*. A–B, sacral ribs. A, MB.Am.1368 (skull length c. 130 mm), late larval specimen, left sacral rib in anterior (left) and posterior view (middle), as well as in distal and proximal view (right). B, MB.Am.284 (skull length 171 mm), juvenile specimen, left sacral rib in dorsal view. C–F, pectoral girdle. C, MB.Am.218 (skull length 38 mm), dermal pectoral girdle and initial ossification of the scapula in ventral view. D, SMNK 39/13 (skull length 129 mm), dermal pectoral girdle with scapula in dorsal view. E, MB.Am.329 (skull length c. 200 mm), posterior part of the scapulocoracoid in lateral view. F, MB.Am.953b (skull length 226 mm), pectoral girdle in ventral view. Scale bars represent 10 mm.

The posterior part of the scapulocoracoid, with parts of the glenoid, is preserved in MB.Am.329b (skull length c. 200 mm; Text-fig. 6E). It possesses a roughened surface and was probably covered by cartilage. In general, the scapulocoracoid, and particularly its coracoid portion in *A. decheni*, is much less massive than in *Sclerocephalus* (Meckert 1993), *Onchiodon* (Boy 1990) and *Eryops* (Miner 1925). The coracoid blade of *A. decheni* is even less developed than in the proportionally small scapuloc-

oracoid of the aquatic stereospondylomorph *Australerpeton* (Dias and Schultz 2003).

#### *Pelvic girdle*

*Ilium*. The ilium is already partly ossified in the smallest known larva (MB.Am.134), which has a skull length of 18 mm (Witzmann 2006b). It is not clearly differentiated and is almost



**TEXT-FIG. 7.** *Archegosaurus decheni*. Ontogeny of the pelvic region. A, MB.Am.134 (skull length 18 mm), ilium. B, MB.Am.236 (skull length 82 mm), ilium in lateral aspect with ossified acetabulum. C, MB.Am.229 (skull length 79 mm), ischium. D, MB.Am.298 (skull length c. 200 mm), pelvic region in ventral view. Scale bars represent 1 mm in A–C and 10 mm in D.

rectangular in lateral view (Text-figs 4A, 7A). In larger individuals, the ilium consists of a triangular base and a posterodorsally sloping slender shaft, which is expanded dorsally (Text-figs 5A, 7B). As ontogeny progresses, the iliac shaft becomes proportionally more slender (Text-fig. 7D). The ossified dorsal border of the round acetabulum is visible for the first time on the lateral side of the base in MB.Am.236 (skull length c. 80 mm; Text-fig. 7B). It is framed by a dorsal buttress. The oblique line (*linea obliqua sensu* Bystrow and Efremov 1940) is present in large specimens (Text-fig. 7D), running from the anterior part of the triangular base in a posterodorsal direction along the shaft. The triangular base of the ilium enlarges proportionally with growth. The outer surface of the ilium is largely smooth. The surface for articulation with the sacral rib is slightly concave and bears some dorsoventrally directed striae. There was probably only a ligamentous connection between ilium and sacral rib in the living animal.

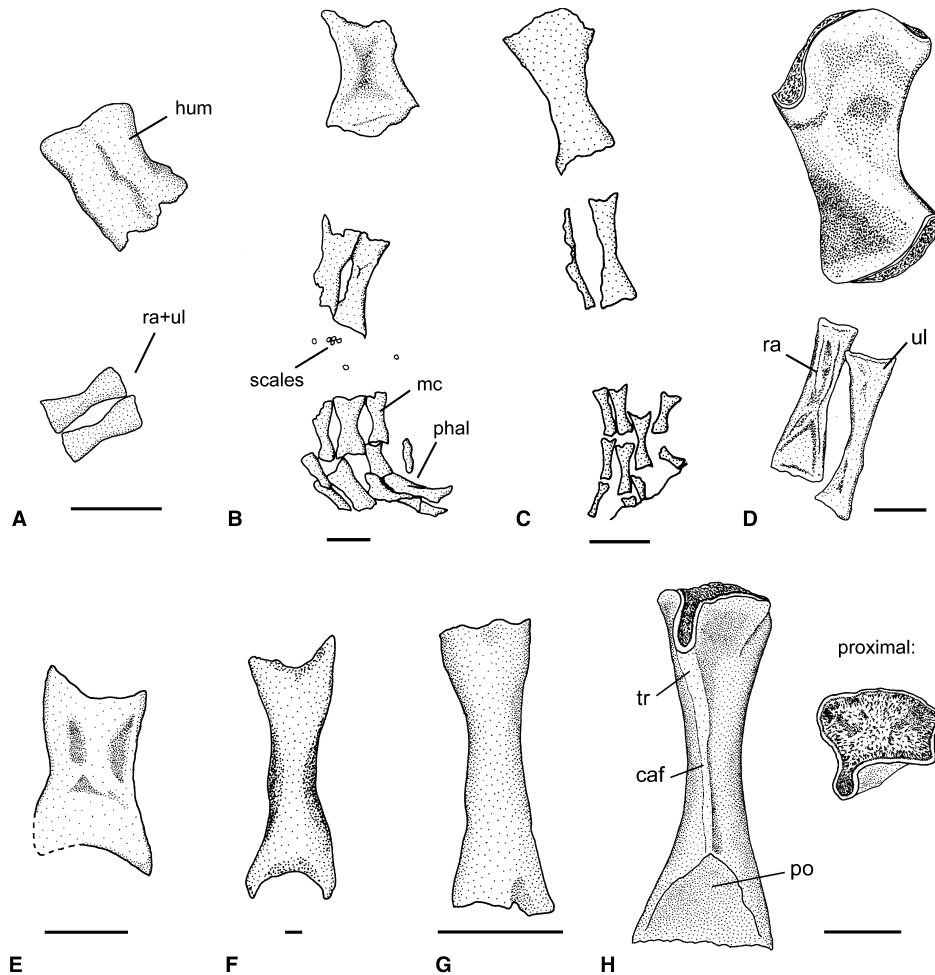
**Ischium.** The ischium clearly ossifies later than the ilium (Witzmann 2006b). It is visible for the first time in a specimen with a skull length of c. 65 mm and is figured in one of 79 mm (Text-fig. 7C) as a small crescentic bone. The ischium is convex medially and thickened along its straight lateral margin. The ischium is smaller than the triangular iliac base in small, larval specimens. It attains a trapezoidal shape (Text-figs 2B, 7D) and becomes distinctly larger than the iliac base in the

largest specimens. Both ischia are only weakly fused along the midline in MB.Am.953b (skull length 226 mm).

**General outline.** The pelvic girdle of *A. decheni* consisted to a large degree of cartilage. The ventral margin of the iliac base and the dorsolateral margin of the ischium are unfinished regions and continued in cartilage. In the largest specimens, the ossified parts of ilium and ischium are still separated. Ossified remains of the pubis have never been found. The pelvic girdle of *A. decheni* is fragile and slender. It is incompletely ossified compared with the massive pelvic girdle of *Eryops*, which has a broad iliac blade and a large puboischiadic plate (Miner 1925), and the fully ossified pelvic girdle of *Sclerocephalus haeuseri*, in which the elements are fused (Boy 1988). In contrast to *A. decheni*, a sub-adult specimen of *Australerpeton* possesses an ossified pubis (Dias and Schultz 2003).

#### Limbs

**Forelimb.** The ontogeny of the forelimb is shown in Text-figure 8A–D. The humerus is a short bone without any differentiation in small specimens. In the smallest known larva, the ossified middle part of the humerus is a roughly rectangular mid-part of the shaft. Large specimens possess a short, slender



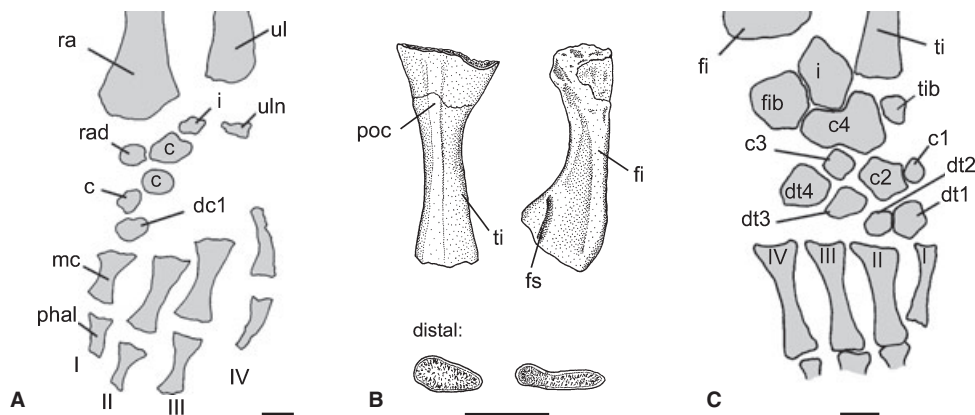
**TEXT-FIG. 8.** *Archegosaurus decheni*. A–D, ontogeny of the forelimb. A, MB.Am.134 (skull length 18 mm), larval specimen. B, MB.Am.222 (skull length 30 mm), larval specimen. C, MB.Am.124 (skull length 140 mm), late larval specimen. D, MB.Am.953b (skull length 226 mm), early adult specimen. E–H, ontogeny of the femur. E, MB.Am.134, larval specimen. F, MB.Am.229 (skull length 79 mm), larval specimen. G, MB.Am.1368 (skull length c. 130 mm), late larval specimen. H, MB.Am.1370 (skull length more than 150 mm), juvenile specimen, in ventral (left) and proximal view. Scale bars represent 1 mm in A–B, E–F and 10 mm in C–D, G–H.

humerus that is almost straight, with unfinished distal and proximal ends that are rotated in relation to one another at an angle of 45–50 degrees. A deltopectoral crest that diminishes in height towards the distal end is visible proximally. No supinator process is developed, the ect- and entepicondyles are of moderate size, and no entepicondylar foramen pierces the bone. The length of the humerus amounts to c. 75 per cent of the femur length. The humerus is c. 1.7 times longer than the radius in large specimens.

The humerus of large specimens of *A. decheni* is rudimentarily developed compared with large specimens of *Eryops* (Miner 1925) and *Sclerocephalus* (Meckert 1993). In these more terrestrial temnospondyls, the humerus is much more robust, has a distinct supinator process, and the proximal and distal condyles are set against each other at an angle of c. 90 degrees. The presumed aquatic stereospondylomorph *Australerpeton* has a more strongly developed humerus than *A. decheni*, with a distinct supinator process and a large proximal deltoid process (Dias and Schultz 2003).

The radius and ulna are almost indistinguishable and poorly differentiated in small specimens (Text-fig. 8A–C). In adults, the ulna is slightly larger than the radius (Text-fig. 8D), and the olecranon process is very small. The lateral margins of the shafts of the radius and the ulna are almost straight, whereas the medial edges of the shafts are concave. The radius is more symmetrical than the ulna, being more flattened in its distal third, which is medially concave.

The carpals remained cartilaginous in almost all specimens. However, von Meyer (1858, pl. 15, fig. 12) and Jaekel (1909a) illustrated an extraordinary large manus (the radius of this specimen having a length of more than 60 mm) with six ossified carpals (MB.Am.255; Text-fig. 9A). It cannot be said with certainty if this manus belongs to *A. decheni* because that specimen is an isolated find. Alternatively, it might stem from a large adult *Cheliderpeton latirostre*. It may still be tentatively assigned to *A. decheni* because *Cheliderpeton latirostre* was found only rarely in the siderite concretions of Lebach (Boy 1987). The fact that



**TEXT-FIG. 9.** *Arcehosaurus decheni*. Extremities. A, a large manus that is tentatively assigned to *A. decheni*; after Witzmann (2006b). B, juvenile specimen, tibia and fibula in medial and distal view. C, pes; new interpretation of the lost specimen from the Tübingen collection, redrawn from Quenstedt (1861). Scale bars represent 10 mm.

the carpals are poorly ossified supports assignment to *A. decheni* because these elements are cartilaginous in early adult specimens (e.g. MB.Am.953), and start to ossify only in large adults. Gubin (1991, fig. 34B) illustrated a manus of *Platyoposaurus stuckenbergi* that, despite being smaller than MB.Am.255, included more bones that are also more heavily ossified. The manus of *A. decheni* consists of four digits having the phalangeal formula 2.2.3.2, as in *Eryops* (Miner 1925) and *Sclerocephalus* (Boy 1988). The unguals are long and tapering, forming comparatively large 'claws'. The second and third digits are longer than the first and fourth, and the third is the longest.

**Hindlimb.** The femur is the longest bone of either limb (Text-figs 4A, 5, 7D), reaching about twice the length of the humerus. The ontogeny of the femur is shown in Text-figure 8E–H. Its distal and proximal ends are also unfinished in large specimens. An internal trochanter is present below the proximal head, grading into the adductor crest that runs distally on the ventral side of the femur to the popliteal fossa. In its general outline, the femur of *A. decheni* resembles that of *Platyoposaurus stuckenbergi* (Gubin 1991) and *Australerpeton cosgriffi* (Dias and Schultz 2003), with the difference that the internal trochanter is more pronounced in the last two species.

The tibia is the same length as the fibula (Text-fig. 9B). Its proximal head is clearly expanded compared with the distal end. A distinct posterior crest (crista posterior *sensu* Bystrow and Efremov 1940) runs ventrally from the expanded proximal head to the distal end. The fibula has a broad and flattened distal end, a concave medial margin, and a fibular sulcus that crosses the medial edge of the ventral surface of the flattened distal part. The distal end is angled for articulation with the intermedium medially. The fibula attains 0.6–0.7 times the length of the femur.

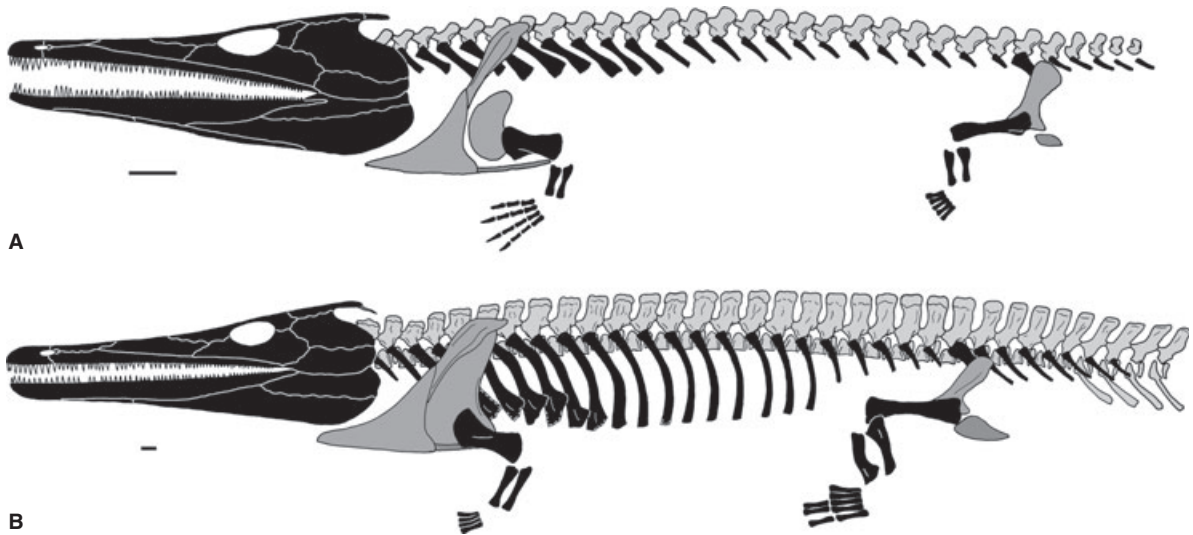
Tarsal elements ossify only in the largest individuals. Quenstedt (1861, pl. 3, fig. 6) illustrated parts of the hindlimb of a very large specimen, now missing from the Institut für Geologie und Paläontologie in Tübingen (M. Maisch, pers. comm. 2003). It is not clear, however, if this specimen belongs to *A. decheni* or *Cheliderpeton*. Its tibia was longer than 70 mm and at least 11 ossified tarsals and four metatarsals were present. Baur (1886), Emery (1897), Jaekel (1909a) and Schaeffer (1941) interpreted

the tarsus in Quenstedt's specimen, but no consensus was reached concerning the designation of the component elements. When compared with the tarsal morphology of other temnospondyls (e.g. Schaeffer 1941; Boy 1988; Werneburg and Steyer 2002), it is most likely that the tarsus of Quenstedt's specimen consisted of the following elements (Text-fig. 9C): fibulare, intermedium and a small tibiale; a large centrale 4, a small centrale 1, a medium-sized centrale 2, and a small centrale 3; five distal tarsals must have been present in the living animal, but tarsal 5 was not preserved. The tibiale was a strikingly small element in Quenstedt's specimen, comparable with that of *Sclerocephalus hauseri* (Boy 1988, fig. 10B), but distinctly smaller than in *Cheliderpeton vranayi* (Werneburg and Steyer 2002, fig. 3A).

Metatarsals and phalanges are preserved in MB.Am.1370. Five metatarsals are present, indicating the existence of five toes, as suggested by Baur (1886) and Jaekel (1896a). The phalanges are disarticulated in MB.Am.1370 and, therefore, the phalangeal formula cannot be determined. It can be seen, however, that the terminal phalanges are long and tapering 'claws', as in the manus.

## PALAEOBIOLOGY OF ARCHEGOSAURUS

Most extant aquatic urodeles are anguilliform swimmers (D'Août and Aerts 1997), i.e. thrust is generated by lateral undulations of both trunk and tail. This is the most likely type of aquatic locomotion performed by larvae and juveniles of *A. decheni*. Distal uncinat processes, which may have strengthened the comparatively weak rhachitinous vertebral column of temnospondyls and early tetrapods (Panchen 1967), were still not developed at these growth stages in *A. decheni* (Text-fig. 10A). However, the trunk is relatively short compared with aquatic temnospondyls like *Micromelerpeton credneri* (Boy 1972, 2003), *Trimerorhachis* (Case 1935) and *Neldasaurus* (Chase 1965). The length of the tail is unknown in larval and juvenile specimens of *A. decheni*.



**TEXT-FIG. 10.** Reconstructions of the skeleton of *Archegosaurus decheni*. A, larval specimen, based mostly on IGS U II 1/2, MB.Am.227, 323, and TM 1154. B, early adult specimen, based mostly on MB.Am.953. Scale bars represent 10 mm.

Adult *A. decheni* had a deep tail that was longer than the rest of the body. The distal uncinat e processes in the anterior half of the trunk probably reduced the flexibility of the thoracic region. The major propulsive thrust was thus produced by lateral undulations of the long tail and, to a certain degree, also by undulations of the posterior-most trunk. In the posterior trunk region, ribs form simple, short rods (Text-fig. 10B). In this region and the base of the tail, pleurocentra extend more ventrally, approaching the midline as they do in amphibamids (Daly 1994). This may have served a higher flexibility in that region. We suggest that adult *A. decheni* may have been 'sub-carangiform' swimmers, following the terminology of Breder (1926) in Bond (1996). Reduced flexibility in the anterior trunk might be advantageous in avoiding yawing movements and in achieving a more efficient mode of swimming (Bond 1996). In an analogous fashion, osteoderms and gastralia along with the hypaxial musculature account for a stiffened trunk in extant crocodiles (comparable with a 'torpedo'; von Wettstein 1937), and the laterally flexible tail forms a powerful propulsive organ (Seebacher *et al.* 2003). According to Wermuth (1964), a proportionally long tail may be expected in crocodiles that live in spacious lakes or in the sea and are able to swim long distances. For example, the Australian Saltwater Crocodile (*Crocodylus porosus*) has the proportionally longest tail among crocodiles, and swims frequently many nautical miles from shore in the open sea (Wermuth 1964).

By analogy, we conclude that adults of *Archegosaurus decheni* were active swimmers. This is further supported by the fact that *A. decheni* is normally found in articulation (i.e. autochthonous) in the deeper parts of large

freshwater lakes (Boy 1977). The limbs remain rather weakly developed in large individuals and presumably reduced drag on the body during swimming.

Postcranial morphology indicates that *A. decheni* had a limited capability for terrestrial locomotion. The limbs are weakly ossified, even compared with the presumably mainly aquatic stereospondylomorph *Australerpeton* (Dias and Schultz 2003). Especially the rudimentary, very short humerus forms a striking contrast even to that of the closely related *Cheliderpeton*. Significant also is the small size of the scapular ossification and the poorly mineralized glenoid region. In *Eryops*, muscles crucial to land locomotion attach on the coracoid portion (Miner 1925), which is incompletely ossified in *A. decheni*. Miner also interpreted the cleithrum as the attachment site for muscles stabilizing the pectoral girdle while walking on land. The small size of the cleithral head in *A. decheni* might indicate that these muscles were more weakly developed than in *Sclerocephalus*, *Eryops* and *Cacops*. The slender ilium, as well as the large amount of cartilage in the pelvic girdle, suggest that the hindlimb musculature was poorly developed. Finally, the proportionally smaller zygapophyses and lower neural spines compared with terrestrial temnospondyls are suggestive of a less sturdy presacral column in *A. decheni*.

## PHYLOGENETIC ANALYSIS

Most basal temnospondyls attained relatively small adult body size and were not heavily ossified. This is especially obvious in the axial skeleton, where centra remained

rudimentary rhachitinous crescents and ribs were short rods lacking uncinata processes. Size-linkage of character states thus forms a real problem in temnospondyl phylogeny, for among early tetrapods, this vast group has the broadest reported size range, with body lengths spanning 50 mm to 5 m. Also, according to multiple cases of conflicting evidence, the degree of ossification must have been repeatedly reduced in temnospondyl phylogeny, with obvious problems for phylogeny reconstruction (Schoch 2000).

#### Previous work

Detailed descriptions of temnospondyl postcrania were given by Bystrow (1938) for *Dvinosaurus*, Case (1935) for *Trimerorhachis*, Miner (1925) and Moulton (1974) for *Eryops*, Williston (1910), DeMar (1968), Boy (1972) and Schoch and Rubidge (2005) for dissorophoids, Konzukova (1955), Gubin (1991) and Dias and Schultz (2003) for stereospondylomorphs, Watson (1958), Howie (1970) and Schoch (1999) for capitosauroids, Dutuit (1976) for metoposaurids, Warren and Hutchinson (1983) and Marsicano (1993) for brachyopoids, and Hellrung (2003) for the plagiosaurid *Gerrothorax*. Furthermore, Schoch and Milner (2000) reported a complete trematosaurid from the Lower Keuper of Germany, which will be referred to as the 'Ladinian trematosaurid' in the present analysis; the full description is provided by Schoch (2006). Steyer (2002) recently described the anterior trunk region of the trematosaurid *Wantzosaurus*.

Despite their useful compilation of comparative postcranial data, none of these studies commented on phylogenetic significance on a broader scale. DeFauw (1989) discussed ecological implications of postcranial data of different temnospondyls, but did not attempt an explicit analysis of relationships.

The first paper dealing with the postcranium of temnospondyls with an explicit phylogenetic focus was by Warren and Snell (1991). They compiled data on the postcrania of stereospondyls and discussed the phylogenetic significance of numerous character states. These authors found most of their postcranial characters to be rather problematic, often forming homoplasies not readily identified as such. It was therefore clear to us that the present study had to address this particular problem. Yates and Warren (2000) analysed temnospondyl relationships on a large scale, making use of 121 characters. Among these, 19 were postcranial, and all those relevant to the present study have been adopted here.

There is a widespread belief that in temnospondyls postcranial characters are inferior to cranial characters because of the supposedly larger impact ontogeny had on these character states. However, the same can be said

about various skull characters, many of which underwent significant ontogenetic changes (Boy 1988, 1989, 1990; Warren and Hutchinson 1988; Schoch 2002, 2003). Therefore, we view the present study as a test of postcranial characters and consequently have analysed them separately from cranial features.

#### Taxa

*Outgroup.* Colosteidae serves as the outgroup in our analysis, and we have used the large colosteid *Greererpeton burkemorani* (Godfrey 1989) as the primary source for polarity determination. Supplementary information is taken from *Colosteus scutellatus* (Hook 1983). We chose colosteids not because we rank them among the temnospondyls, but because of their great general similarity to temnospondyls. Milner (1990a) and subsequent authors have demonstrated that colosteids form a clade on their own, which need not be closely related to temnospondyls (Ruta *et al.* 2003).

*Ingroup.* (1) *Dendrerpeton acadianum*. We restricted this terminal taxon to the single specimen described by Holmes *et al.* (1998), whereas the *Dendrerpeton* material studied by Milner (1980, 1996) probably does not pertain to the same taxon (A. R. Milner, pers. comm. 2004). We considered the somewhat more derived, yet geologically much older temnospondyl *Balanerpeton woodi* (Milner and Sequeira 1993) and found it to code for the same character polarity throughout our set of postcranial characters as does *Dendrerpeton* (*sensu* Holmes *et al.* 1998). *Balanerpeton* was also useful in adding information about one character state unknown in *Dendrerpeton*, the morphology of the fourth neural spine (character 9, see character list in Appendix). (2) *Trimerorhachis insignis*. The main source for our character coding is Case (1935). In the single case of character 9, we have referred to *Trimerorhachis sandovalensis* (Berman and Reisz 1980). (3) *Dvinosaurus primus*. Sources are Bystrow (1938) for the whole postcranium and Shishkin (1987) for aspects of the vertebral segments. (4) Dissorophidae. Here represented by only two species, *Cacops aspidephorus* and *Dissorophus multicinctus*, complementing one another (Williston 1910; DeMar 1968). (5) Amphibamidae. We follow Daly (1994) and Schoch and Rubidge (2005) in the concept of that family, which includes all miniaturized dissorophoids other than branchiosaurids. The main taxon we refer to is *Amphibamus grandiceps* (Watson 1940; Milner 1982; Daly 1994), supplemented by *Micropholis stowi* (Broili and Schröder 1937; Schoch and Rubidge 2005). (6) Eryopidae. We refer to *Eryops megacephalus* (Miner 1925; Moulton 1974) and *Onchiodon labyrinthicus* (Boy 1990; Witzmann 2005). According to new data on Upper Pennsylvan-

nian *Eryops*, both taxa are very similar and probably closely related (A. R. Milner, pers. comm. 2004). We have coded most characters after *Eryops*, adding only data from *Onchiodon* where the state is unknown for *Eryops*. (7) *Sclerocephalus hauseri* (Broili 1926; Boy 1988; Meckert 1993). (8) *Archegosaurus decheni* (von Meyer 1858; present study). (9) *Australerpeton cosgriffi* (Barberena 1998; Dias and Schultz 2003). (10) *Uranocentron senegalensis* (van Hoepen 1915; observations by RRS). (11) *Gerrothorax pustuloglomeratus* (Hellrung 2003). (12) *Plagiosuchus pustuliferus* (von Huene 1920; observations by RRS). (13) *Siderops kehli* (Warren and Hutchinson 1983). (14) New Ladinian trematosaurid from the Lower Keuper of Germany (Schoch and Milner 2000; Schoch 2006). (15) *Metoposaurus ouazzoui* (Dutuit 1976). (16) *Paracyclotosaurus davidi* (Watson 1958). (17) *Mastodonsaurus giganteus* (Schoch 1999).

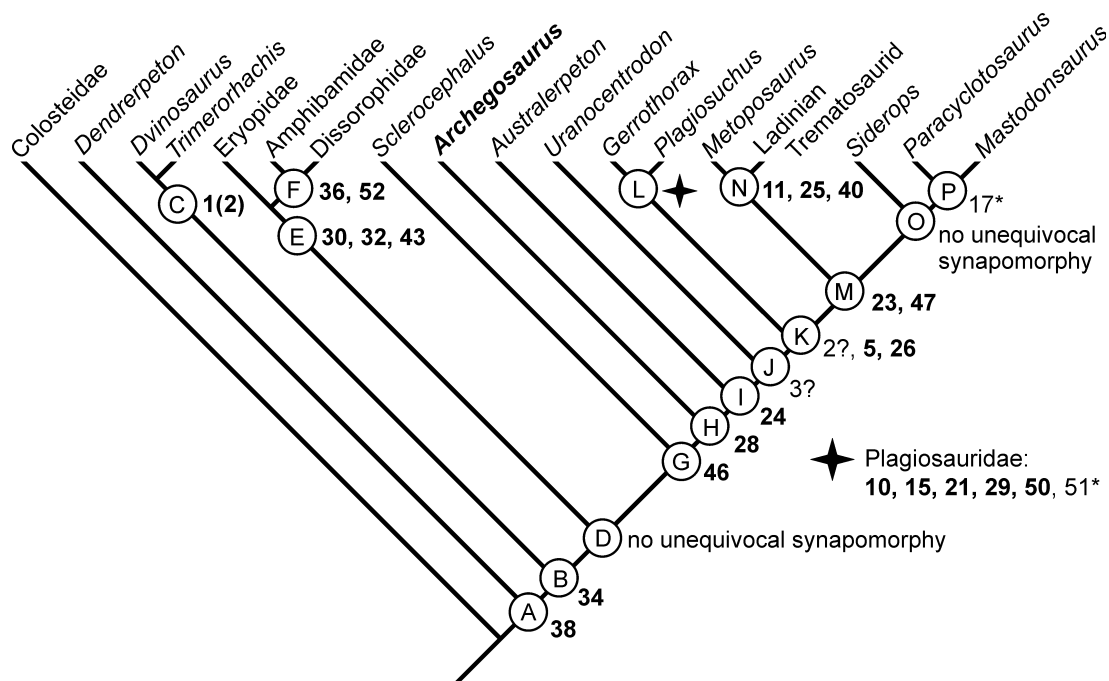
### Characters

All characters and character states are given and defined in the character list in the Appendix, and the distribution of character states is given in the character-taxon matrix, also in the Appendix. A range of these features was discussed by Warren and Snell (1991), and numerous characters were used by Yates and Warren (2000). Most of the others result from original research carried out by

RRS; otherwise their sources are indicated. As most of the taxa considered are not represented by juveniles or larvae, early ontogenetic stages (e.g. in *Sclerocephalus*; see Schoch 2003 or herein on *Archegosaurus*) have been ignored. In general, we have intentionally considered the largest known specimens of each taxon to be decisive for coding, rather than code an ontogenetically advanced character state as polymorphic variant.

### Analysis

The programmes PAUP 3.1 (Swofford 1991) and MacClade 2.0 (Maddison and Maddison 1992) were used to analyse the data set presented in the character-taxon matrix in the Appendix. The branch-and-bound search algorithm was used throughout. We preferred binary character codings, but in two cases (characters 1 and 17) multiple states had to be coded. All characters were run unordered. The analysis (52 characters, 17 ingroup taxa, Colosteidae as the outgroup) resulted in the discovery of one most parsimonious topology, which is fully resolved and requires 96 steps (Text-fig. 11). The consistency index of this tree is 0.62, the retention index is 0.80 and the rescaled consistency index is 0.50. We also conducted Bremer and bootstrap analyses to determine clade strengths; the resulting values for both analyses are listed below for the various clades.



**TEXT-FIG. 11.** Phylogenetic analysis of temnospondyls based exclusively on postcranial characters. See Appendix for definition and distribution of character states. Cladogram resulting from analysis; node-supporting characters mapped (bold, synapomorphies; standard font, homoplasies).

## RESULTS

*Clade A.* Temnospondyli. This group is diagnosed by one unequivocal synapomorphy (38).

*Clade B.* Unnamed clade. This comprises all temnospondyls higher than *Dendropeton* and is diagnosed by one unequivocal synapomorphy (34).

*Clade C.* *Dvinosaurus primus* plus *Trimerorhachis insignis*. This group forms part of a larger assemblage of short-snouted, primitive temnospondyls, the Dvinosauria, which was found to be monophyletic by Yates and Warren (2000) in their much more extensive, skull-based analysis. Clade C is diagnosed by one unequivocal synapomorphy (character 1, state 2), and has Bremer and bootstrap support values of 2 and 0.86, respectively.

*Clade D.* This unnamed clade includes all temnospondyls more closely related to *Eryops* and stereospondyls than to Dvinosauria, and forms an alternative to the Limnarchia suggested by Yates and Warren (2000) (see below). Here, this group is only supported by ambiguous synapomorphies (6, 7), but a similar clade was suggested by Milner (1990a, 1993) based in part on cranial synapomorphies.

*Clade E.* Eryopidae plus Dissorophoidea. A close relationship between eryopids and dissorophoids was suggested by Milner (1990a, b), who explicitly referred to postcranial features, and supported by Schoch (1997). Yates and Warren (2000) also found this grouping, albeit with *Eryops* being more closely related to zatracheids, calling the whole clade the Euskelia. Clade E is diagnosed by three unequivocal synapomorphies (30, 32, 43), one polymorphic character (20), and has a Bremer support value of 3 and a bootstrap value of 0.75.

*Clade F.* Dissorophoidea (here restricted to Dissorophidae plus Amphibamidae). Dissorophoids were first recognized as a clade by Bolt (1969) and Boy (1972). Here, characters 36 and 52 support the monophyly of this grouping, which has a Bremer support value of 3, and a bootstrap value of 0.83.

*Clade G.* Stereospondylomorpha, including *Sclerocephalus hauseri* and all more derived taxa. A clade of similar composition has been suggested by Yates and Warren (2000), and (with the exception of plagiosaurids and *Siderops*) by Schoch and Milner (2000). This large clade is diagnosed by only one unequivocal synapomorphy (46), the replacement of the intercondylar trough by a shallow groove on the distal end of the femur, and one reversal (22, reversed in *Siderops*). As discovered here, Stereospondylomorpha has a Bremer value of 2, and a bootstrap value of 0.71. This clade is a classic example not only for Hennig's stem-group problem (i.e. the slow and step-by-step acquisition of synapomorphies; see Boy 1981), but also the frequent reversal of charac-

ters somewhere along the extraordinarily long stereospondyl branch (Schoch and Milner 2000).

*Clade H.* *Archegosaurus*, *Australerpeton*, and Stereospondyli. This clade has been identified by both Yates and Warren (2000) and Schoch and Milner (2000) on the basis of cranial characters. Character 28 diagnoses this clade, which has Bremer and bootstrap values of 1 and 0.7, respectively.

*Clade I.* *Australerpeton* and Stereospondyli. This grouping is supported by one unequivocal synapomorphy (24), a Bremer support value of 1, and a bootstrap value of 0.51.

*Clade J.* Stereospondyli. As found here, the clade comprises rhinesuchids (*Uranocentrodon*), plagiosaurids (*Gerrothorax* and *Plagiosuchus*), chigutisaurids (*Siderops*), capitosauroids (*Mastodonsaurus*, *Paracyclotosaurus*), trematosaurids, and metoposaurids. Stereospondyli is diagnosed here by only one equivocal synapomorphy (3?), and is supported by Bremer and bootstrap values of 1 and 0.73, respectively.

*Clade K.* Unnamed clade. This is a robust group including all stereospondyls higher than *Uranocentrodon*. It is diagnosed by two unequivocal synapomorphies (5, 26) and one equivocal character (2?), and has a Bremer support value of 4 and a bootstrap value of 0.93. A firm nesting of plagiosaurids within the stereospondyls, suggested by Yates and Warren (2000), is of particular interest, because this small clade has been linked with various, boldly different clades of lower tetrapods, among them microsaurids (Jaekel 1913), brachyopoids (Säve-Söderbergh 1935), *Peltobatrachus* (Panchen 1959), zatracheids (Shishkin 1987) and *Laidleria* (Yates and Warren 2000). Our results suggest that plagiosaurids nest higher than rhinesuchids but clearly below the more derived stereospondyls, which with capitosauroids, trematosaurids and metoposaurids, comprise the largest group of Mesozoic temnospondyls. This position implies that the Plagiosauridae had a long unrecorded history, after they had split from post-rhinesuchid stereospondyls not later than the beginning of the Late Permian. The relatively high number of autapomorphies of the clade (the postcranial characters alone provide strong support for their monophyly) is consonant with this interpretation of a long and unrecorded history.

*Clade L.* Plagiosauridae. This is the most robust clade in the present analysis. Following Hellrung (2003), *Plagiosuchus* and *Gerrothorax* have widely divergent cranial morphologies but share several derived character states in the postcranium. Among these, six characters (10, 15, 21, 29, 50, 51) are unequivocal synapomorphies, and the clade is supported by a Bremer value of 7 and a bootstrap value of 1.0. Plagiosauridae *sensu stricto* (i.e. excluding *Peltobatrachus*) has always been considered to be monophyletic.

*Clade M.* Capitosauroids, chigutisaurids, trematosaurids, metoposaurids. No such grouping has been suggested before. Here, it is diagnosed by two unequivocal characters (23, 47), and has a Bremer support value of 1 and bootstrap support under 0.5.

*Clade N.* Trematosaurids and metoposaurids. Schoch and Milner (2000) and more recently Damiani and Yates (2003) have suggested a close relationship between these two clades. Here, it is diagnosed by three unequivocal synapomorphies (11, 25, 40), and has Bremer and bootstrap values of 1 and 0.54, respectively.

*Clade O.* Capitosauroids and chigutisaurids. This grouping is most surprising because it contradicts the concepts put forward by both Yates and Warren (2000) and Schoch and Milner (2000). Whereas the results of the latter study cannot be strictly compared with ours (lydekkerinids as closest relatives of chigutisaurids), the former study found chigutisaurids nested with brachyopids, rhytidosteids, plagiosaurids, trematosaurids and metoposaurids. Only the last two clades could be considered herein, because the others have very incompletely known postcrania. Clade O is not diagnosed by any unequivocal characters and has a bootstrap support value of less than 0.5, yet has a Bremer support value of 1.

*Clade P.* The capitosauroids *Mastodonsaurus* and *Paracyclotosaurus*. These taxa are similar in most characters and in the present analysis their monophyly is diagnosed by one equivocal synapomorphy (17), and exhibits a Bremer support value of 1 and a bootstrap value of 0.68.

### Discussion

Our analysis is unorthodox in the choice of characters and in considering only taxa with reasonably preserved postcrania. Rather than hoping to present an *ultima ratio*, we wish to make a case for analysing postcranial data in temnospondyls. Therefore, it is certainly interesting that the result of our analysis of exclusively postcranial data is in general agreement with many recent skull-based analyses of temnospondyls, especially the large analysis performed by Yates and Warren (2000). The two major differences between our result and that of the cited paper are (1) the position of the Dvinosauria and (2) the position of the plagiosaurids outside the most advanced stereospondyls (= capitosauroids plus trematosauroids *sensu* Schoch and Milner 2000). This means that, despite various homoplasies in the structure of the limbs and girdles as well as the morphology of the ribs, the postcranium supports the major topological features shared by most of the recent temnospondyl phylogenies.

Pawley and Warren (2004) have recently warned not to use postcranial characters that may have been subject to major ontogenetic changes, following Steyer's (2000) clas-

sic demonstration of problems posed by development for character coding in temnospondyls. We entirely concur (see Schoch 1998 for a similar discussion), but wish to emphasize that there is no principal difference between postcranial and cranial characters in this respect at all. In a first step to overcome these difficulties, we have included only the most mature, which usually means the largest, specimens for each of the taxa analysed here. This problem is certainly not exclusively a matter of metamorphosis or neoteny, as non-transforming *Mastodonsaurus* exemplifies, which underwent substantial changes in the latest stages of its ontogeny, where additional elements ossified (Schoch 1999).

A serious problem in postcranium-based phylogenetic analyses is the assessment of phylogenetic polarity. In many ways, the colosteids are similar to temnospondyls, potentially highlighting plesiomorphic states shared with early temnospondyls (Milner 1990a). However, *Greererpeton* is not only much larger than *Dendrerpeton* and *Balanerpeton* but also differs by the incompleteness of ossification in the girdles (scapula, coracoid, pubis) and limbs. Colosteids were most probably aquatic as adults, an interpretation suggested by prominent lateral line sulci, the small and poorly ossified limbs, the low and poorly ossified neural arches, and the presence of branchial ossicles in the gill clefts of adults. Furthermore, the presence of a postbranchial lamina on the cleithrum is suggestive of internal gills (Lebedev and Coates 1995).

The most primitive temnospondyls show a broad range of morphologies. Adaptations to a terrestrial existence are obvious at least in *Dendrerpeton* and *Edops*, but are less clear in *Balanerpeton*. The cochleosaurids, on the other hand, were probably aquatic animals, retaining lateral line sulci (enclosed in bone) as recently found by Sidor *et al.* (2005) in Nigerian material. This leaves the question unsettled as to whether the first temnospondyls were terrestrial or aquatic. Differences among limbs and girdles of early terrestrial temnospondyls may indicate the convergent origins of terrestriality within the clade. At least in more advanced temnospondyls, the independent evolution of metamorphosis has been suggested by divergent modes of metamorphosis (Schoch 2002).

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## APPENDIX

### Character list

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1. Presacral count. 23–25 (0), 27–29 (1), 31–33 (2), or higher (3).
  2. Atlas width. Same size as axis (0) or distinctly wider (1).
  3. Atlas-exoccipital contact. Atlas articulates with exoccipital and basioccipital (0) or only with exoccipital (1).
  4. Parapophysis. Segmental (0) or intersegmental (1).
  5. \*Transverse process length. Shorter than dorsal spine is high (0) or markedly longer (1).
  6. \*Neural spine tip. Unossified, rugose (0) or completely ossified (1).
  7. \*Neural spine height. As high as distance between zygapophyses (0) or higher (1).
  8. \*Neural spine alignment. Vertical (0) or posterodorsally inclined (1).
  9. \*Neural spine reduction. Fourth neural spine as high as others (0) or height reduced (1).
  10. \*Neural spine lateral face. Lateral sides straight vertical (0) or with lateral projections (1).
  11. Intercentrum canal. Chordal canal wider than intercentrum is high (0) or narrower (1).
  12. Intercentrum flank. Flank reaching only half the height of the central portion (0) or higher (1).
  13. Intercentrum disk-shaped. Presacral intercentra crescent-shaped (0) or dorsally closed (1).
  14. Pleurocentrum flank. Flank as large as that of intercentrum (0) or smaller (1).
  15. Pleurocentrum presence. Ossified (0) or unossified (1).
  16. Pleurocentrum disc-shaped. Presacral pleurocentra disc-shaped (0) or ventrally open (1).
  17. Rib morphology. Simple rod (0), with short uncinat spikes (1), or wide uncinat blades (2).
  18. Rib length. Long and curved (0) or short and straight (1).
  19. Sacral rib. As long as ilium and slender (0) or much shorter and stout (1).
  20. Interclavicle shape. Longer than wide (0) or wider than long (1).
  21. Interclavicle posterior rim. Forming posterior process (0) or transversely straight (1).
  22. Interclavicle size. Shorter than postorbital skull (0) or longer (1).
  23. Interclavicle process. Anteriorly blunt (0) or with long anterior process (1).
  24. Interclavicle margin. Anterior margin serrated (0) or smooth (1).
  25. Interclavicle, clavicle. Overlapping suture with clavicle confined to anterior half (0) or extending posteriorly (1).
  26. Clavicles. Anteriorly well separated by interclavicle (0) or approach or in contact with one another (1).
  27. Clavicles. Narrow-based, rod-like dorsal shaft (0) or broad-based, with anteriorly expanded shelf and pronounced sigmoidal curvature (1).
  28. Cleithrum dorsal extension. Head bordering scapula dorsally (0) or only anteriorly (1).
  29. Cleithrum anterior rim. Head with slightly convex or straight anterior rim (0) or with pronounced anterior projection (1).
  30. Scapula. Dorsally not completely ossified (0) or dorsally complete (1).
  31. Coracoid. Fully ossified ventral to glenoid facet (0) or incomplete/unossified (1).
  32. Humerus condyles. Condyles cartilaginous (0) or fully ossified (1).
  33. Humerus torsion. Torsion strong, 70–90° (0) or weak, well below 60° (1).
  34. Humerus foramen. Entepicondylar foramen present (0) or absent (1).
  35. Humerus supinator. Supinator process present (0), or absent (1).
  36. Humerus shaft length. Shaft short, forming one-third the length of element (0) or much longer (1).
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	Col	Den	Tri	Dvi	Dis	Am	Ery	Scl	Arc	Aus	Ura	Ger	Pla	Sid	Mas	Par	Tre	Met
31	0	0	1	1	0	0	0	0	0	0	0	1	1	1	A	1	1	1
32	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1	1	1
34	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
35	0	0	1	0	1	1	0	0	1	0	1	0	1	1	A	1	1	A
36	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
37	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
38	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
39	1	1	1	1	1	1	1	1	1	1	?	1	1	1	?	0	1	1
40	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	1	1
41	0	0	0	0	1	1	1	0	0	?	0	1	0	1	1	1	0	0
42	0	0	0	0	1	0	0	0	0	?	0	1	0	0	0	0	0	0
43	0	0	0	0	1	1	1	0	0	?	0	0	0	0	0	0	0	0
44	1	0	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1
45	0	0	1	1	0	0	0	A	1	0	0	1	1	1	A	1	1	1
46	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
47	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
48	0	0	0	?	0	0	0	0	0	?	1	1	1	1	1	0	1	1
49	0	0	1	1	0	0	0	0	0	0	A	1	1	1	1	1	1	1
50	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
51	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0
52	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0

Abbreviations in character-taxon matrix: Am, Amphibamidae; Arc, *Archegosaurus decheni*; Aus, *Australerpeton cosgriffi*; Col, Colosteidae; Den, *Dendrerpeton acadianum*; Dis, Dissorophidae; Dvi, *Dvinosaurus primus*; Ery, Eryopidae; Ger, *Gerrothorax pustuloglomeratus*; Mas, *Mastodonsaurus giganteus*; Met, *Metoposaurus ouazzoui*; Par, *Paracyclotosaurus davidi*; Pla, *Plagiosuchus pustuliferus*; Scl, *Sclerocephalus haeuseri*; Sid, *Siderops kehli*; Tre, Ladinian trematosaurid; Tri, *Trimerorhachis insignis*; Ura, *Uranocentron senekalensis*.