A review of *Silvanerpeton miripedes*, a stem amniote from the Lower Carboniferous of East Kirkton, West Lothian, Scotland

Marcello Ruta and Jennifer A. Clack

ABSTRACT: Previously described and new specimens of the anthracosaur *Silvanerpeton miripedes* from the Scottish Viséan of East Kirkton yield important new data which allow us to provide a more complete reconstruction of the skull roof, palate, braincase and lower jaw. A stout sacral rib and an incompletely ossified tarsus with a subquadrangular intermedium are also recorded for the first time. A remarkably well preserved humerus in extensor view shows similarities with humeri of immature specimens of the embolomere *Proterogyrinus*. A new cladistic analysis, built from combining characters used in two recent matrices, places *Silvanerpeton* in a basal position relative to embolomeres and more derived stem amniotes. Data from *Silvanerpeton* inform character polarity near the base of the amniote total group. We discuss some morphofunctional implications of character changes at the root of total group amniotes, acquisition of terrestrial habits, and patterns of early disparity in this clade.

KEY WORDS: anthracosaurs, basal stem amniotes, phylogeny, postcranium, skull.

The fossil record of early tetrapods continues to be enriched by remarkable discoveries and detailed reinterpretation of existing material. The wealth of new data is changing radically long-standing hypotheses of pattern and process near the root of limbed vertebrates' diversification, and has led to a re-assessment of the sequence of character changes and evolutionary scenarios of the fish-tetrapod transition. Despite much progress in integrating all available data sources for different Palaeozoic groups, additional work is needed to address persistent conflict in numerous domains of tetrapod phylogeny. Some of the causal factors responsible for this conflict have been examined (Ruta *et al.* 2003; Clack & Finney 2005), but a more thorough evaluation of the impact of novel data combinations on phylogeny requires fresh scrutiny.

Fossil vertebrates from the Lower Carboniferous (Viséan) East Kirkton Quarry near Bathgate in Scotland (West Lothian) have played a considerable role in reshaping our understanding of early tetrapod interrelationships and diversity. They add significantly to the notoriously sparse record of Lower Carboniferous tetrapods, and open a window on one of the earliest known terrestrial vertebrate communities (Clack 2002a; Ruta & Coates 2003; Clack & Finney 2005). This paper presents new data on one of the two East Kirkton 'reptiliomorphs' (*sensu* Säve-Söderbergh 1934), *Silvanerpeton miripedes* Clack, 1994. Our goals are: (1) to redescribe this taxon in detail; (2) to examine its phylogenetic position; and (3) to reanalyse character distribution near the base of the amniote total group. A second 'reptiliomorph' from East Kirkton, *Eldeceeon rolfei* Smithson, 1994, is now known from additional specimens, and will be redescribed in detail in a separate paper.

Silvanerpeton has been regarded as a basal anthracosaur. Anthracosaurs are short-limbed, long-bodied tetrapods exhibiting aquatic or semiaquatic habits, and found mostly in Carboniferous and Permian sediments of both North America and Europe. They include some of the best known tetrapods from Coal Measure deposits, and have long been thought to represent a discrete radiation of basal stem amniotes (e.g. Panchen 1970, 1980; Smithson 1985; Gauthier *et al.* 1988; Panchen & Smithson 1988). Their affinities have been debated

for nearly 140 years, since Huxley's (1863) description of *Anthracosaurus russelli* (for historical accounts and systematic synopses see: Watson 1926, 1929; Panchen 1970; Holmes 1984, 1989; Smithson 1985). Early reviews include works by Panchen (1975, 1980, 1985), Heaton (1980), Holmes (1984, 1989), Smithson (1985, 1994), Clack (1987, 1994), Clack & Holmes (1988), and Panchen & Smithson (1988). Recent compendia are those of Smithson (2000) and Clack (2002a). In the present paper, the term 'anthracosaurs' is used only informally. It is mostly co-extensive with Anthracosauroideae *sensu* Smithson (1985), and conforms to Watson's (1926, 1929) original concept of the group. Anthracosaurs include the monotypic family Eoherpetontidae and the Embolomeri. The latter consist of the following families: Anthracosauridae, Archeriidae, Eogyrinidae, and Proterogyrinidae. Some workers (Carroll 1969, 1970, 1991; Carroll *et al.* 1972; Boy & Bandel 1973; Heaton 1980) have placed gephyrostegids within anthracosaurs, but this is not universally accepted. The anthracosaur-like affinities of the armoured chroniosuchians from the Upper Permian to the Middle Triassic of Russia (Carroll *et al.* 1972; Golubev 1998a, b; Novikov *et al.* 2000) also need reassessing, and will not be considered here.

The interrelationships among anthracosaur families are debated (e.g. Holmes 1984, 1989; Smithson 1985; Clack 1987, 2001; Ahlberg & Clack 1998; Paton *et al.* 1999; Ruta & Coates 2003; Ruta *et al.* 2003; Klembara & Ruta 2004a; Clack & Finney 2005), but the monophyly of each is generally accepted. Recent cladistic analyses have not provided a consensus on the broad affinities of these vertebrates. Some studies have placed them among stem tetrapods (e.g. Anderson 2001; Vallin & Laurin 2004; Clack & Finney 2005), whereas others have relocated them to the base of the amniote total group (Paton *et al.* 1999; Clack 2001; Ruta *et al.* 2003; Klembara & Ruta 2004a, b, 2005a, b).

The anthracosaur species discussed here, *Silvanerpeton miripedes*, first described by Clack (1994), co-occurs at East Kirkton with another anthracosaur, *Eldeceeon rolfei* (Smithson 1994), the putative basal amniote *Westlothiana lizziae* (Smithson *et al.* 1994), the aïstopod *Ophiderpeton*

kirktonense (Milner 1994), the baphetid *Eucritta melanolim-netes* (Clack 2001), the temnospondyl *Balanerpeton woodi* (Milner & Sequeira 1994), and an undescribed microsaur (J.A.C., work in progress). All these taxa are represented in 'Unit 82' (Rolfe *et al.* 1994), a 300 mm-thick black shale bed close to the base of the exposure in the East Kirkton quarry, and many of them also occur through the lower half of the rest of the sequence. The East Kirkton site also includes isolated remains attributed to large temnospondyls (Milner & Sequeira 1994, 1998) or other taxa. The preponderance of tetrapod specimens in Unit 82 could be the result of collector bias, and the fact that the lithologies found in other parts of the sequence make the layers more difficult to split (S. P. Wood, pers. comm. 2006). Investigation of the taphonomic, strati-graphic and sedimentological relations of tetrapod taxa through the sequence is the subject of a planned future study by the present authors and colleagues.

Considerable new anatomical information is now available for *Silvanerpeton*, following discovery of several additional specimens, as well as re-examination and further partial prep-aration of the type material. Negative preparation and latex casting of a remarkable and previously unfigured specimen have exposed most of the skull roof bones, a large part of the palate, most of the basiparasphenoid complex in dorsal view, the lateral aspect of the lower jaw, the extensor surface of the right humerus, and assorted postcranial remains. A second, previously unfigured specimen shows a sacral rib and four ossified tarsal elements.

1. Material and methods

Specimen repositories are at the University Museum of Zoology, Cambridge (UMZC) and the National Museums of Scotland, Edinburgh (NMS G). Specimens were collected from the East Kirkton Limestone, Bathgate Hills Volcanic Formation, Strathclyde Group. Geological and stratigraphic settings of East Kirkton were discussed by Rolfe *et al.* (1994) and Smith *et al.* (1994), whereas its palaeoecology and palaeo-environment were analysed by Clarkson *et al.* (1994) and McGill *et al.* (1994).

Specimens were consolidated with dilute paraloid B72. Sarah M. Finney (J.A.C.'s former UMZC technician, now at Cambridge University Department of Earth Sciences) performed partial mechanical preparation of several of them. Elizabeth M. P. Pringle (J.A.C.'s former Ph.D. student in Cambridge) undertook negative preparation of UMZC T.1351, from which high-fidelity latex peels were obtained. Bone surface details were enhanced by coating latex with ammonium chloride sublimate.

The majority of specimens were drawn with a Wild M3 dissecting microscope equipped with camera lucida. Photo-graphs were taken using a Nikon D1 digital camera and processed using Adobe Photoshop 6 on a Macintosh G3. The cranial and postcranial reconstructions of *Silvanerpeton* are based mostly upon UMZC T.1351, and upon UMZC T.1317 and NMS G.1994.16.1, respectively.

2. Systematic palaeontology

Tetrapoda Goodrich, 1930
Amniota Goodrich, 1916
(Stem group of Amniota herewith)
Family undesignated
Genus *Silvanerpeton* Clack, 1994

Silvanerpeton miripedes Clack, 1994
(Figs 1–10)

Holotype. UMZC T.1317* part (a) and counterpart (b): almost complete skull and postcranial skeleton with both hind limbs well preserved.

Referred material. UMZC T.1251 part (a) and counterpart (b): a skull with associated pectoral girdle and forelimb elements (collected from a farm wall).

UMZC T.1252: a partial skeleton largely as natural mould with disrupted skull in lateral view (collected from a farm wall) (Figured Clack 1994).

UMZC T.1351*: a disrupted skull largely as natural mould, also a humerus, and part of the maxilla and premaxilla in the round.

NMS G.1994.16.1* part (a) and counterpart (b): a good postcranial skeleton with all the limbs and tail represented, as well as gastralia, a partial cheek and a lower jaw.

NMS G.1998.51.1 part (a) and counterpart (b): a large partial skeleton and disrupted skull, gastralia, ribs, a few limb bones, and a ball of stomach contents (collected from a quarry spoil heap).

NMS G.1998.51.2: a skull and lower jaws in dorsal view with disrupted palate (collected from a quarry spoil heap).

NMS G.2004.24.1*: a laterally compressed skull with good lower jaw and maxilla, and a disrupted postcranial skeleton.

NMS G.2004.24.2* part (a) and counterpart (b): very disrupted postcranial skeleton and a partial skull.

Locality. East Kirkton Quarry, Bathgate, near Edinburgh, West Lothian, Scotland.

Age and horizon. Viséan, Early Carboniferous; East Kirkton Limestone, Bathgate Hills Volcanic Formation, Strathclyde Group. Asterisked specimens derive from the Black Shale Unit 82.

Diagnosis (expanded and amended from Clack 1994: p. 372 ["Tetrapod with anthracosauroid skull structure and bone relationships; long slender tabular horn; large orbit bordered verntrally by narrow processes of jugal and lacrimal; maxilla with about 42 teeth and lower jaw with surangular crest. More than 30 preseacral vertebrae; gastrocentrous with pleurocentra almost complete hoops, and wedge-shaped intercentra; inter-clavicle kite-shaped with broad separation between the clavicles; pes with phalangeal count 23455; pelvic girdle with long postiliac process and stout iliac blade; femur about 37% of skull length; long postsacral ribs"] and based upon distri-bution of character-states in the cladistic analysis; optimised missing entries are not included).

Apomorphies: postorbital width at least one quarter of skull table width at same transverse level; jugal contributing to skull roof ventral margin; tabular lateral margin not emarginated; upper marginal teeth number smaller than lower marginal teeth; parasternal process neither elongate nor parallel-sided for most of its length; entepicondyle width smaller than half humeral length; absence of olecranon pro-cess; ilium posterior process slender, subhorizontal, rod-like, with parallel dorsal and ventral margins, and more than five times longer than deep.

Synapomorphies with more derived stem amniotes: pre-maxillae less than two-thirds as wide as skull; parietal-tabular suture present; intertemporal not interdigitating with cheek; supratemoral-squamosal contact smooth; subdermal, blade-like postero-lateral tabular horn present; rounded, subdermal, button-like posterior process of tabular absent; tabular-squamosal contact smooth; interorbital distance subequal to half skull table width; maxilla tooth number between 30 and 40; dermal skull ornament mostly irregular and shallow; ventral, exposed surface of vomers narrow, elongate, strip-like, without extensions anterolateral or posterolateral to choana and two and a half to three times longer than wide; vomers

separated by pterygoids for more than half length; length of portion of humeral shaft proximal to entepicondyle greater than humeral head width; radius shorter than ulna; five manus digits; scutes ovoid, no more than three times longer than broad.

Plesiomorphies in relation to more crownward stem amniotes: lacrimal length less than two and a half times its maximum preorbital depth; maxilla extending behind level of posterior orbit margin; posterior coronoid without postero-dorsal process; parasphenoid shagreen field present; humerus length greater than length of two and a half mid-trunk vertebrae; L-shaped proximal tarsal element absent.

3. Description

3.1. Skull roof

General aspect.   Based mostly upon UMZC T.1351, the skull outline is semielliptical in dorsal aspect, with no traces of sensory canals. The distance from the snout tip to a line connecting the posterior extremities of the quadratojugals is about 33 percent greater than the maximum skull width (measured between the posterior jugal rami). The broad, parabolic snout is slightly longer than the skull table (pre-orbital length:total skull length ≈ 0.31; skull table length:total skull length ≈ 0.27). The suspensorium is short, with shallow concave posterior margin oriented at about 60 degrees relative to the horizontal plane. The subelliptical, large orbits show poorly pronounced posteroventral and posterodorsal corners (minimum interorbital distance:orbit length ≈ 0.53; orbit length:total skull length ≈ 0.33).

Sculpture.   Sculpture varies in different skull regions. While the central parts of many large bones (e.g. nasals; frontals; parietals; lacrimals; squamosals) show a 'starburst' pattern of small, subcircular nutrient foramina and weak ridges, the peripheral portions (e.g. on both squamosals and quadratojugals) display elongate, subparallel foramina, irregular striations, and deep grooves. In smaller bones, the foramina appear uniformly distributed (e.g. lateral temporal series; postparietal) and reduced in number (prefrontal; postfrontal; postorbital). On the jugal and maxilla, the sculpture changes to a considerable degree. Elongate, widely spaced foramina and sulci are widespread on the ventral half of the maxilla lateral surface.

Sutures.   Sutural seams (Kathe 1999) and bone overlap surfaces (underlying lamellae of Kathe 1999; Klembara 1994, 1997; Kathe 1995; Clack 2002b) are described where visible.

Premaxilla.   The premaxillae (in particular, the left) are best observed in UMZC T.1351 (Figs 1, 2). In NMS G.1998.51.2 (Fig. 4), they are articulated and visible near the anterior margins of the right nasal and maxilla. In UMZC T.1252 and T.1317, they are incomplete and disrupted. Three portions can be distinguished. The tall, triangular nasal ramus narrows slowly dorsally and merges rather indistinctly into the ventral ramus. Its spatulate dorsal extremity carries vertical striations, and, together with its antimere, it would be wedged in life between the anteriormost tract of the nasal medial margins (NMS G.1998.51.2). The short and robust ventral ramus contacts the anterior extremity of the maxilla along a small, oblique suture. In NMS G.1998.51.2, the inter-premaxillary suture has a slightly indented aspect in its ventralmost part.

Nasal.   The flat and subrectangular nasals are slightly shorter and wider than the frontals (however, the nasal is broader than the frontal in UMZC T.1317) (Figs 1, 2, 3A), with a slightly sinuous common suture. The nasals of UMZC T.1351 differ slightly in size. The bone anterior margin is invariably disrupted (UMZC T.1351 and T.1317) or preserved only as a faint impression (e.g. NMS G.1998.51.2). In UMZC T.1317 (Fig. 5), the right nasal is deeply wedged between frontal and prefrontal.

Frontal.   The frontals are about three times as long as wide, subequal (except in UMZC T.1351), and shorter than the maximum orbit diameter. They narrow slightly posteriorly, and their maximum width lies just anterior to the level of the prefrontal-postfrontal suture. Behind this point, their lateral margins converge slightly posteromedially; anterior to it, they are subparallel. The interfrontal suture is sinuous (UMZC T.1351) (Figs 1, 2, 3A) or interdigitating (NMS G.1998.51.2) (Fig. 4). Sutures with surrounding bones are either weakly indented or smoothly curved. The frontal anterior margins are almost aligned with the orbit anterior margin.

Parietal.   The parietals (best seen in UMZC T.1351) (Figs 1, 2, 3A) are about twice as long as wide, and slightly longer than the nasals. Their prepineal region is irregularly triangular in outline, and widens rapidly rearward. Posterior to the pineal foramen, their surface is almost flat, and sends a small, sub-rectangular posterolateral extension contacting the tabular along a straight and short suture. The ossification centre lies just posterolateral to the pineal foramen. Sutural patterns vary. Both the interparietal and the parietal-supratemporal sutures are slightly sinuous, whereas the parietal-postfrontal and parietal–postparietal sutures are irregular.

The subelliptical pineal foramen bears a slightly raised rim, and lies immediately anterior to the interparietal suture mid length. In UMZC T.1351, the lateral underlying lamellae of both parietals are almost completely exposed (Fig. 3A). As in *Discosauriscus* (Klembara 1997, fig. 5), but unlike in some temnospondyls (Kathe 1999, figs 3–5), the lamellae are trans-versely striated near the lateral parts of their free margins. They are overlapped by the frontals anteriorly, the post-frontals anterolaterally, the intertemporal and supratemporal laterally. Anteriorly and anterolaterally, the striations are replaced by short and irregular crenellations.

Postparietal.   The postparietals (dorsal view in UMZC T.1351 (Figs 1, 2, 3A); left postparietal visible in NMS G.1998.51.2 (Fig. 4)) are quadrangular. Their lateral margins form slightly indented sutures with the tabulars. Their median suture is irregularly sinuous. Behind their posterior margins, they produce a small occipital flange, protruding slightly medially but reduced to a narrow strip laterally (UMZC T.1351). Flange extension and orientation are difficult to reconstruct, although the flange is unlikely to have protruded much behind the bone ornamented surface.

Intertemporal.   The pyriform intertemporals, about as large as the postorbitals, contribute to nearly half of the skull table lateral margins. In UMZC T.1351 (Figs 1, 2, 3A), both intertemporals have smoothly curved margins. In NMS G.1998.51.2 (Fig. 4), the irregular left intertemporal is dis-rupted. The bone lateral margin fits into a small anterior concavity along the postorbital medial margin. Along the posterior half of its lateral margin, the intertemporal ornamented surface turns sharply ventrally, and forms a small, narrow, strip-like flange in contact with the postorbital posteromedial margin. This flange deepens slightly rearward, and is continuous with a similar, larger ventral flange of the supratemporal. A shallow notch is visible along the inter-temporal anterior margin in dorsal aspect. Lateral to this notch, the bluntly convex anterior margin is accommodated by the postfrontal.
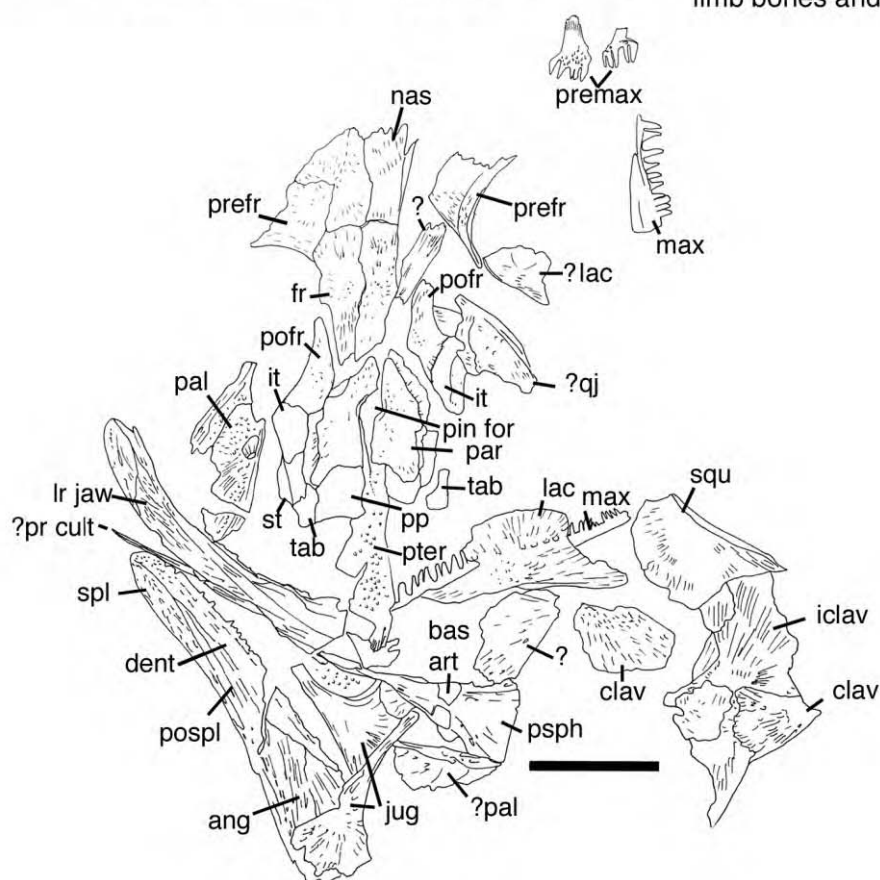
Supratemporal.   The supratemporal is widest in its anterior half, and narrows abruptly posteriorly. Its lateral margin is straight and directed slightly posteromedially. A
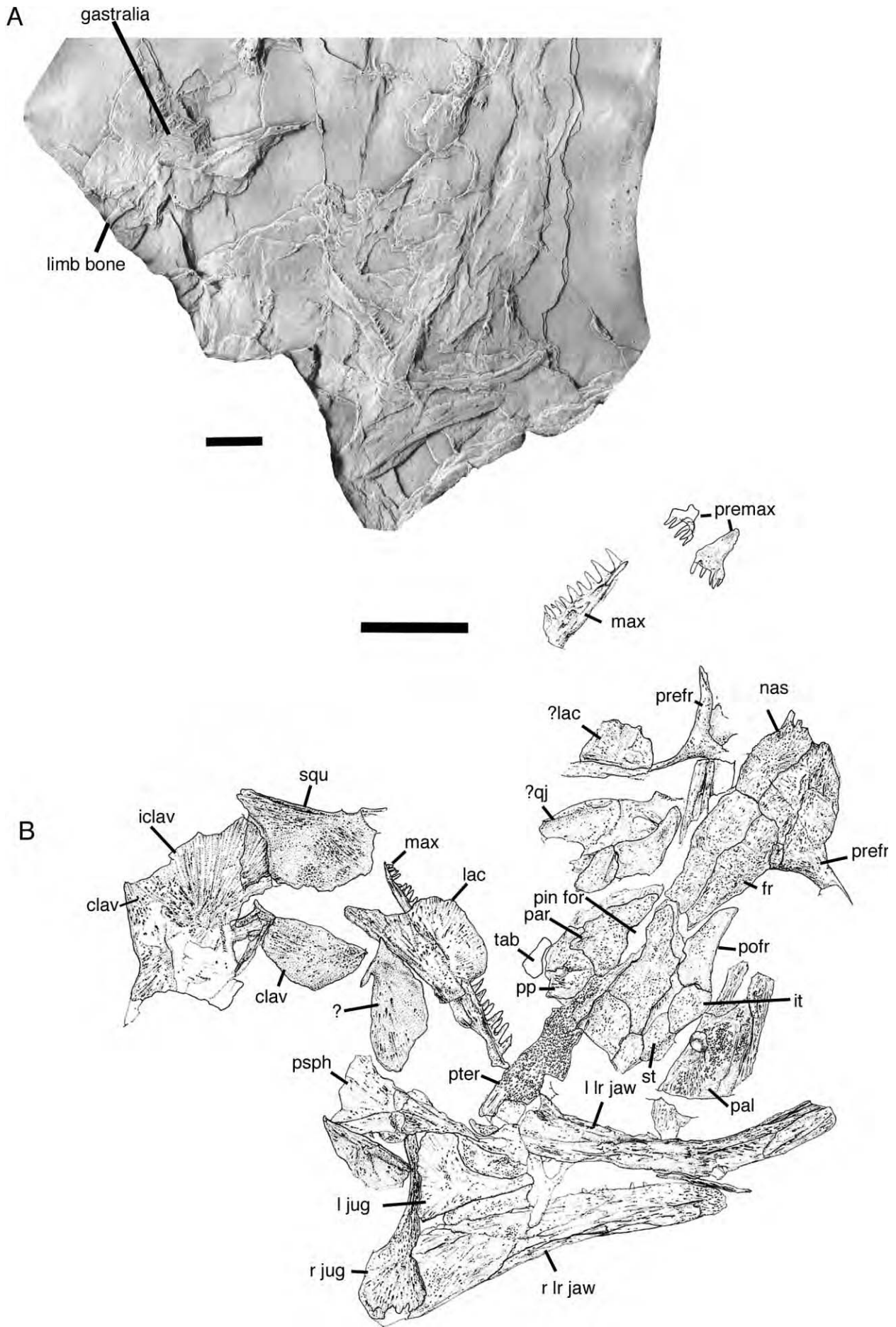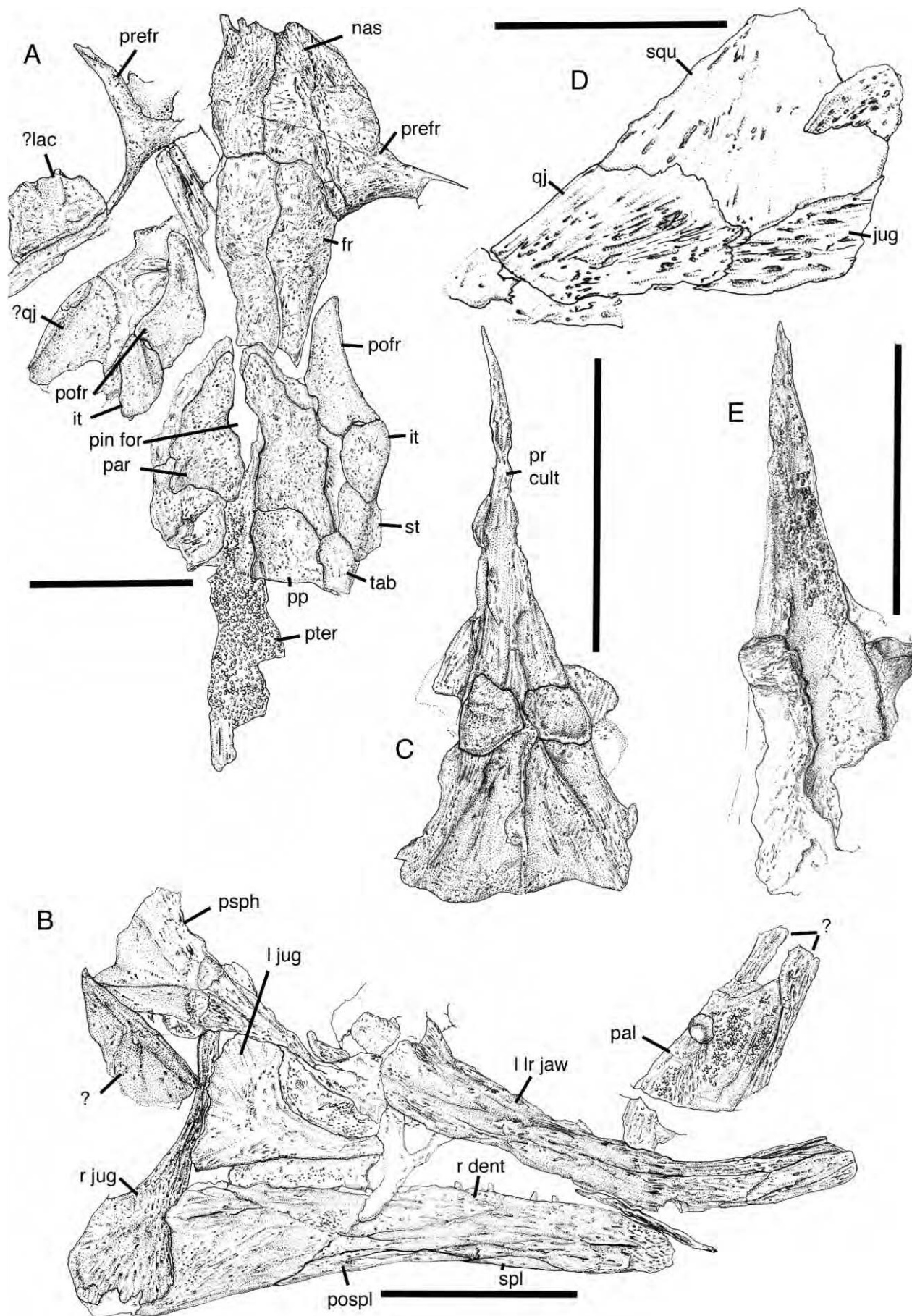
Figure 1 *Silvanerpeton miripedes* UMZC T.1351: (A) Photograph of the specimen, mainly as natural mould, with humerus, part of the left maxilla, and left tabular prepared to reveal bone surface; (B) Map of the specimen, excluding the humerus, limb bones and gastralia indicated on the photograph. Note that the specimen and map are left-right reversed relative to the intact animal. Scale bars = 10 mm.

Figure 2 *Silvanerpeton miripedes* UMZC T.1351: (A) Photograph of the latex peel (made before surface preparation of the tabular and the humerus); (B) Detailed drawing of the complete specimen, excluding the humerus, gastralia and limb bones. Scale bars=10 mm.

Figure 3 *Silvanerpeton miripedes* UMZC T.1351 and UMZC T.1252: (A)–(C) UMZC T. 1351: (A) Close-up drawing showing skull table, snout, and other bones including part of the pterygoid; (B) Close-up drawing showing both lower jaws, both jugals, braincase in dorsal view and palatine; (C) Close-up drawing of braincase in dorsal view; (D)–(E) UMZC T.1252: (D) Cheek region with quadratojugal, squamosal and part of jugal; (E) Braincase in ventral view. Scale bars = 10 mm.
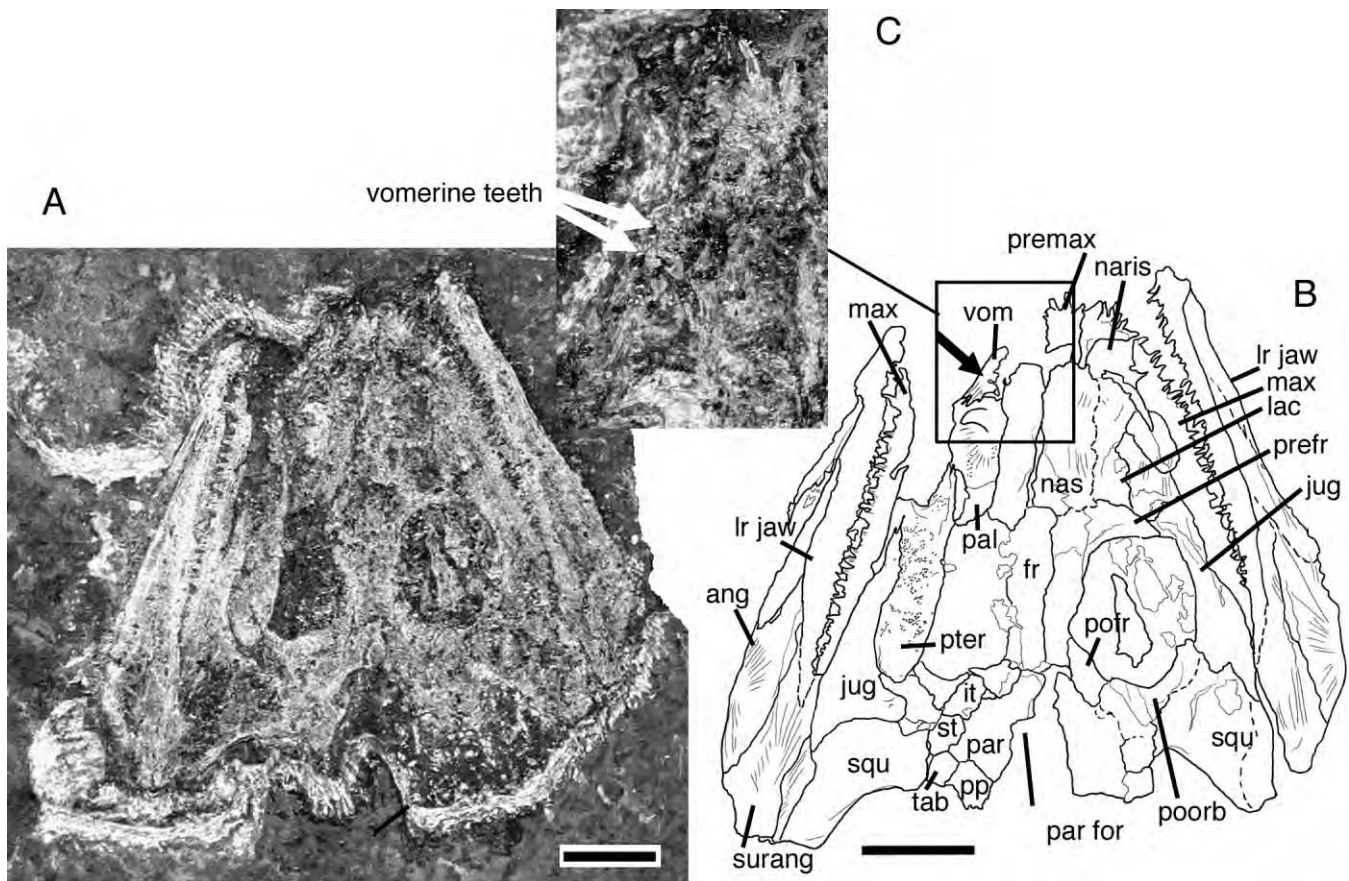
Figure 4 *Silvanerpeton miripedes* NMS G.1998.51.2: (A) Photograph of the specimen; (B) Map of the specimen, with inset to show position of C; (C) Close-up of region bearing vomerine teeth. Scale bars=10 mm.

narrow ventrolateral flange overlaps the squamosal dorsal margin (left side of skull table in NMS G.1998.51.2 (Fig. 4), right side in UMZC T.1351 (Fig. 3A)). The anterior portion of the flange contacts the postorbital posterior apex, and as a result, the intertemporal is narrowly separated from the squamosal.

Tabular. The tabulars are longer than wide. Their posterior margins are oriented slightly posterolaterally. Their straight lateral margins are aligned with the supratemporal lateral margins. The right tabular of UMZC T.1351 (Fig. 3A) and the left tabular of NMS G.1998.51.2 (Fig. 4) carry small and incompletely preserved ventrolateral flanges, probably contacting the squamosal near their anterior extremity. The right tabular of UMZC T.1317 is eroded, but a small and splinter-like portion of its tabular horn has been further exposed through mechanical preparation since Clack's (1994) original description (Fig. 5C). As preserved, the horn is one-third as long as the ornamented surface of the tabular, and oriented slightly posterolaterally. No such horn has been found on any other specimen, presumably because the appropriate surface is not preserved. In UMZC T.1351, a narrow occipital flange extends posteriorly from the right tabular. As in the case of the postparietal, the flange is narrow and strip-like.

Prefrontal. The prefrontals are clearly visible in UMZC T.1351 (Figs 1, 2, 3A). Their slender and elongate posterior ramus contributes to the anterior third of the orbit dorsal margin. In UMZC T.1351, the lateral surface of the right prefrontal is longitudinally striated and inclined smoothly ventrolaterally, indicating a low orbital shelf. In UMZC T.1351 and NMS G.1998.51.2 (Fig. 4), the anterior two-thirds of the prefrontal expands rapidly, and is sharply separated from its posterior, rod-like ramus. Anteriorly, the bone is

broad and fan-shaped, and its external surface is oriented markedly mediolaterally. This surface ends in a small ventrolateral apex, and contributes to the dorsal half of the orbit anterior margin. A large area of the prefrontal underlaps the broad, anterior part of the lacrimal (see also Klembara 1997, figs 5, 8). The prefrontal abuts against both the posterior third of the nasal lateral margin and the anterior half of the frontal lateral margin.

Postfrontal. The semicrescentic postfrontals bear a slightly concave ventrolateral margin contributing to about two-thirds of the orbit dorsal margin. Their width increases behind the level at which they meet frontal and parietal. Anterior to this level, the anterior ramus of the postfrontal tapers gently. The notch that appears along the bone posterior margin separates a stout, triangular posterolateral process (in contact with the postorbital) from a blunt posteromedial process (wedged between intertemporal and parietal). The suture with the postorbital (visible on the left side of NMS G.1998.51.2) is small and irregular. The tips of the anterior rami of the left and right postfrontals of UMZC T.1351 carry small, straight sutural margins, suggesting a point-like contact with the prefrontal. In the same specimen, a small lamella projects from the anterior ramus of the left postfrontal, and was almost certainly overlapped by the prefrontal posterior end and by a short tract along the posterior half of the frontal lateral margin (cf. *Discosauriscus*; Klembara 1997, fig. 5). Further posteriorly, the postfrontal-frontal suture forms a butt-joint (Kathe 1999, fig. 3).

Postorbital. The postorbitals (best preserved in NMS G.1998.51.2) (Fig. 4) are approximately chevron-shaped, with a stout, triangular posterior ramus, a robust, sub-rectangular ventral ramus, and a slender dorsal ramus. The latter makes a point contact with the posterolateral process of
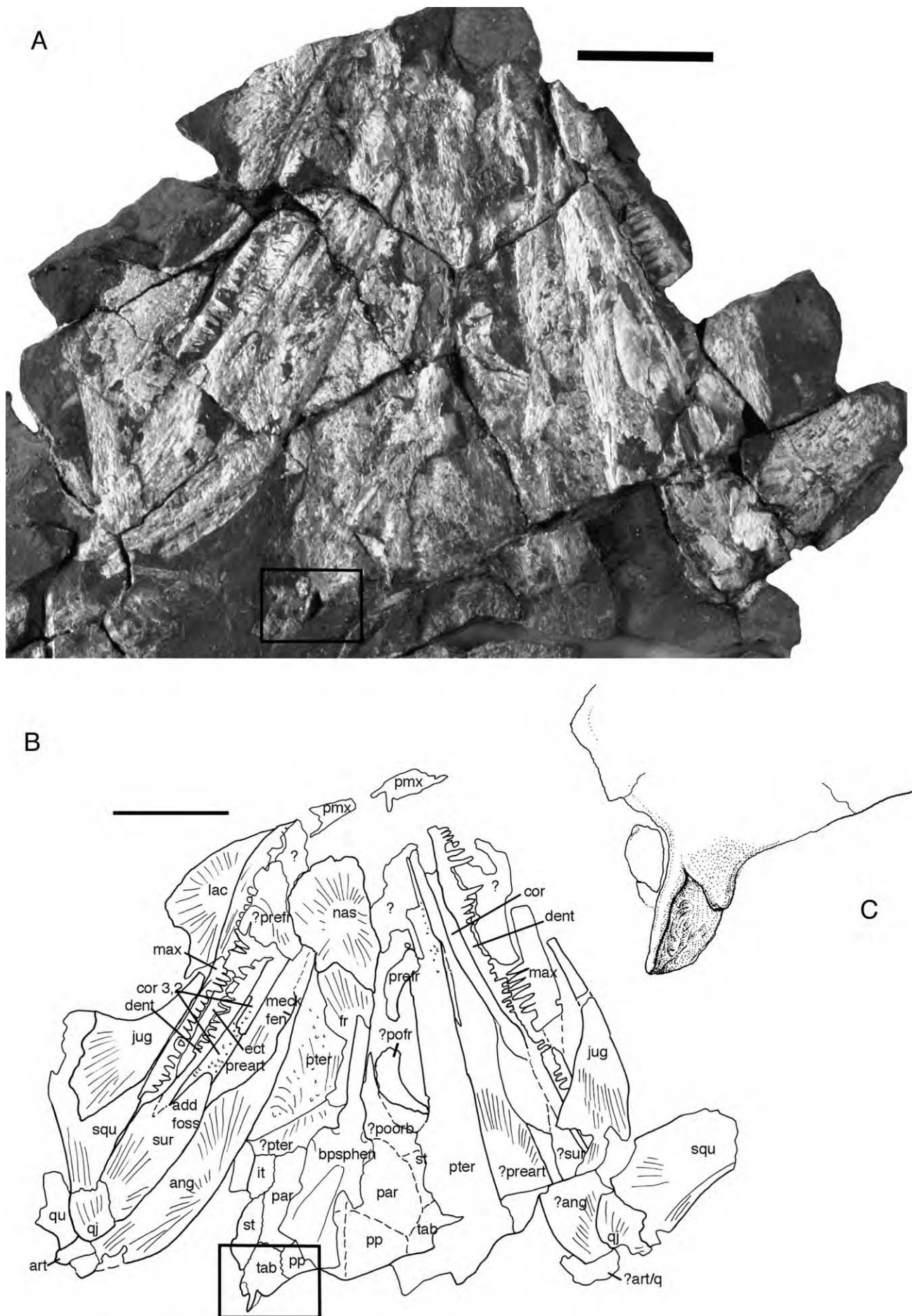
Figure 5 *Silvanerpeton miripedes* UMZC T.1317, holotype skull: (A) Close-up photograph of the skull, from the counterpart (UMZC T.1317b); (B) Map of the skull drawn from part and counterpart, with inset to show position of C; (C) Drawing of tabular horn after preparation. Scale bars=10 mm.

the postfrontal. Extension and orientation of the jugal-postorbital suture are reconstructed only tentatively, although the postorbital presumably overlapped a small dorsal lamella of the jugal dorsal ramus in life (see Klembara 1997).

Jugal.   In UMZC T.1351 (Figs 1, 2, 3B), left and right jugals are exposed, respectively, in internal and external view. NMS G.1998.51.2 (Fig. 4) shows anterior, posterior, and part of the dorsal process of the left jugal, as well as the anterior process of the incompletely preserved right jugal. The jugal is distinctly triradiate, and thus differs from its homologue in other anthracosaurs. The slender, elongate anterior process is nearly constant in depth in its anterior two-thirds, and contributes to most of the orbit ventral margin. It increases rapidly and uniformly in depth posteriorly, and merges into the subtrapezoidal dorsal process. The dorsally truncated dorsal process contributes to the ventral half of the orbit posterior margin. In UMZC T.1317 (Fig. 5) and T.1351, this margin is gently concave. The posterior margin of the dorsal process is much shallower than its anterior margin, and continues smoothly into the posterior process. The latter is poorly developed in UMZC T.1351, but conspicuous in NMS G.1998.51.2 (Fig. 4), UMZC T.1317 (Fig. 5) and NMS G.1994.16.1 (left jugal) (Fig. 6). Its ventral margin is straight (UMZC T.1317 and T.1351) or gently convex, and forms an obtuse angle with the anterior process. In NMS G.1998.51.2, this margin lies below the level of the maxilla (Fig. 4).

The jugal of UMZC T.1317 (Fig. 5) shows a poorly preserved lamella with weak longitudinal striations. It projects from the entire posterior margin, and was presumably overlapped by squamosal and quadratojugal in life (cf. *Discosauriscus*; Klembara 1997, fig. 5). In UMZC T.1351, modifications of the surface texture on the internal surface of the left jugal suggest that the lamella probably extends to the dorsal margin of the dorsal process (Fig. 3B). In this specimen, the jugal internal surface carries fine peripheral striations and weak ridges, commonly observed on the internal side of lamellae in other tetrapods (e.g. see Kathe 1995, 1999; Klembara 1997; Klembara & Ruta 2004a). Nutrient foramina and shallow grooves are visible in the central part of the bone internal surface.

Lacrimal.   In UMZC T.1351, left and right lacrimals are exposed in external and internal views, respectively (Fig. 2). In addition, UMZC T.1317 shows a well-preserved right lacrimal (Fig. 5). In NMS G.1998.51.2, both lacrimals are disrupted and only their outlines are discernible. In lateral view, the lacrimal dominates the skull preorbital region. It is divided into a short, stout posterior process and a tall, subrectangular anterior lamina (squamous part). It differs from its homologue in other anthracosaurs, in which it shows an irregular outline, and is reminiscent of that of some seymouriamorphs, in particular discosauriscids (Ivakhnenko 1987; Laurin 1996a, b; Klembara 1997). The posterior process is about one-third as long as the lamina, decreases slowly in depth rearward, contributing to less than one-third of the orbit ventral margin. In UMZC T.1317, the posterior tip of the process lies dorsal to, and is slightly separated from, the anterior part of the jugal anterior process, in what appears to be a natural spatial arrangement. The anterior lamina is mostly flat, thicker in its ventral third but thinning progressively towards its dorsal margin. The latter is divided into a posterior third, which interdigitates with the prefrontal anteroventral margin, and an anterior two-thirds, which abuts against the nasal lateral margin. The orbital margin of the anterior lamina does not show any opening for the nasolacrimal canal (e.g. Klembara 1997, figs 11, 23, 33), although this may be due to preservation.

The probable right lacrimal of UMZC T.1351 (Fig. 3A), exposed in internal view, shows a robust, oblique ridge running

from the anteroventral corner of the orbital margin to a point situated immediately behind the anteroventral corner of the lamina. Ventral to the ridge, irregular foramina, shallow pits, and low crests dot the internal surface of the lacrimal posterior process. Along its ventral edge, this surface protrudes into a small irregular lamella, probably interposed between the maxilla and palatine in life (cf. Klembara 1997, figs 10, 11). More anteriorly, the suture between lacrimal and maxilla may have formed a butt-joint, but the nature of the sutural contact is not clearly discernible. Dorsal to the internal ridge, the bone internal surface is featureless, except for the presence of some small nutrient foramina and of an anteroventrally convex, low crest which divides the surface into two shallow, unequal surfaces. The functional significance of this crest is unknown (?flange for orbitonasal membrane; Klembara 1997).

Squamosal.   The squamosals are best observed in UMZC T.1351 (Figs 1, 2), NMS G.1998.51.2 (Fig. 4) and, in part, UMZC T.1252 (Fig. 3D). The bone is approximately crescent-like, with a steeply sloping, straight to gently concave posterior margin. In its dorsalmost part, this margin is slightly embayed. A thin, weak ridge runs parallel to the posterior margin for most of its length, and separates the ornamented surface from a narrow, smooth flange. In UMZC T.1351 (Fig. 2), the dorsal part of the right squamosal sends a thin underlying lamella with a jagged margin (cf. Klembara 1997, fig. 5).

Quadratojugal.   In UMZC T.1317 (Fig. 5), both quadratojugals appear as incomplete bony lumps near the postero-ventral corners of the squamosals. The outline of the ornamented surface of the right quadratojugal is observed in UMZC T.1252 (Fig. 3D) (Clack 1994). It is subtrapezoidal, with indented anterior and dorsal margins, posteroventrally inclined and straight posterior margin, and gently convex ventral margin (also visible in UMZC T.1317). The bone terminates posteriorly in a broad triangular apex. Anteriorly, it forms a small, oblique, and interdigitating suture with the jugal posterior process. It resembles its homologue in other anthracosaurs (except for its relatively smaller size), especially in its irregular outline and dorsoventral depth, but differs from the elongate and nearly strap-shaped quadratojugal of various seymouriamorphs (White 1939; Laurin 1995, 1996a–c; Klembara & Ruta 2004a) and *Gephyrostegus* (Carroll 1970).

Maxilla.   UMZC T.1351 (Figs 1, 2), NMS G.1998.51.2 (Fig. 4), NMS G.1994.16.1 (Fig. 6), and NMS G.2004.24.1 show almost complete maxillae in lateral view. Part of the right maxilla appears to be exposed in mesial view in UMZC T.1351 (Figs 1, 2). The bone reaches its maximum depth in its anterior quarter. From this point, it narrows uniformly up to the anterior level of its posterior quarter. Behind this level, it tapers rapidly to its point-like, free posterior extremity. The latter does not contact the quadratojugal, as hypothesised by Clack (1994), but lies either at the level of the orbit posterior margin (NMS G.1998.51.2) (Fig. 4) or just posterior to it (UMZC T.1317) (Fig. 5). The maxilla contributes to most of the ventral margin of the nostril (e.g. NMS G.1998.51.2) (Fig. 4). In mesial view, grooves and elongate foramina occur dorsal to the narrow maxillary shelf.

3.2. Palate

Pterygoid.   Although none of the specimens shows a complete palate, available data suggest that it was closed, as in other anthracosaurs (Clack 1994). The shape of the pterygoid (e.g. in NMS G.1998.51.1) (Fig. 7A, B, right arrow), recalls that of embolomeres (Holmes 1984, 1989). Its broad quadrate ramus merges indistinctly into the basicranial region, but compaction makes it difficult to infer its orientation relative to the palatal ramus (Holmes 1984, 1989; Clack 1987). NMS G.1998.51.1 shows a slightly protruding dorsomesial margin of
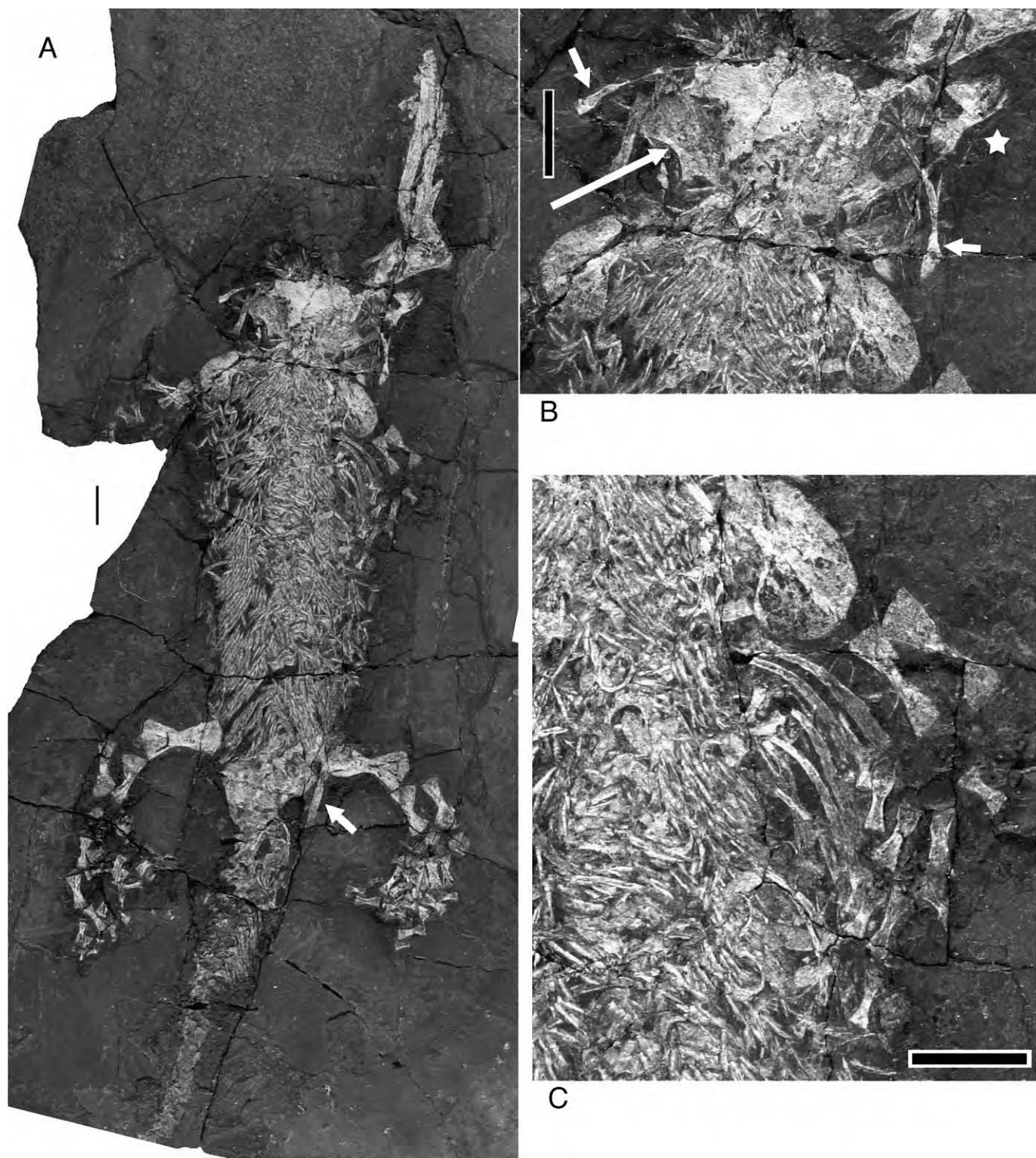
Figure 6 *Silvanerpeton miripedes* NMS G.1994.16.1: (A) Photograph of complete specimen. Postiliac process indicated by a white arrow; (B) Close-up of shoulder girdle region showing cleithra (short white arrows), scapulocoracoid (long white arrow) humeri, and interclavicle. White star indicates a displaced ilium; (C) Close-up of right manus showing five metacarpals. Scale bars = 10 mm.

the quadrate ramus. There is no evidence of the strongly downturned, toothless flange that characterises *Archeria* and *Proterogyrinus*, although this may be due to the high degree of diagenetic compaction.

In the lateralmost part of the basicranial region, where palatal and quadrate rami meet, the pterygoid of NMS G.1998.51.1 (Fig. 7B, left arrow) sends a small, blunt trapezoidal process, which recalls a similarly positioned process in *Proterogyrinus* (Holmes 1984), *Archeria* (Holmes 1989), and *Pholiderpeton scutigerum* (Clack 1987). In these taxa, the

process contacts a medial extension of the jugal. The resulting bridge of bone, or 'insula jugalis', delimits the anterior margin of the subtemporal fenestra. However, the presence of a mesially directed jugal process in *Silvanerpeton* is uncertain. In UMZC T.1351, the ventral edge of the mesial surface of the left jugal is irregularly thickened, although no obvious process is visible.

The palatal ramus is a broad triangular lamina that tapers anteriorly. Its ventral surface is poorly preserved and incomplete. However, the holotype bears striations and a
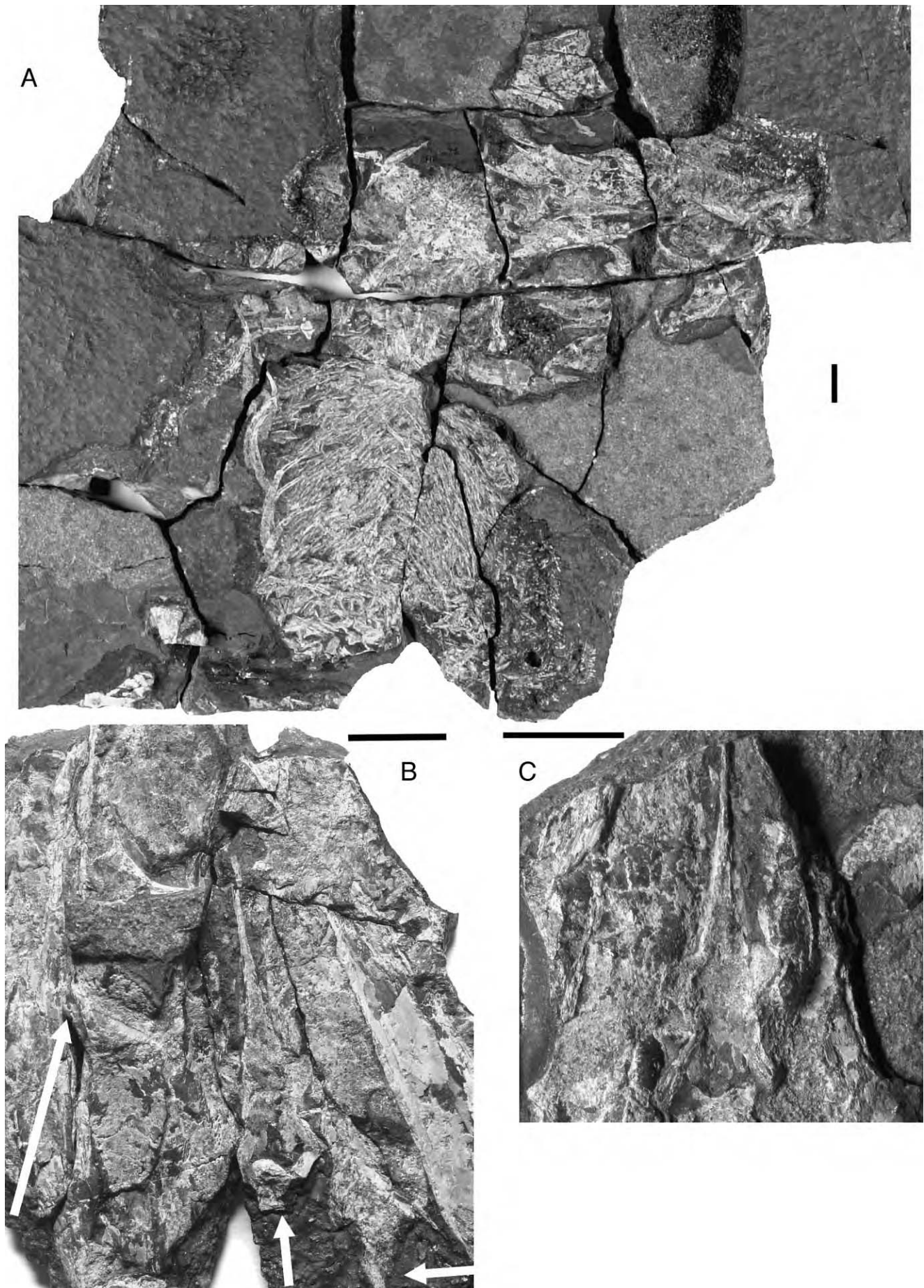
Figure 7 *Silvanerpeton miripedes* NMS G.1998.51.1: (A) Photograph of main specimen; (B) Close-up photograph of counterpart of skull showing ptergyoid process contacting the jugal (left white arrow), quadrate ramus of the pterygoid (right white arrow) and the basioccipital (central white arrow); (C) Close-up of the skull of the main specimen showing braincase with basipterygoid processes. Scale bars = 10 mm.

scatter of denticle patches separated by irregular, weathered areas. A uniform shagreen occupies irregular areas of the palatal ramus of UMZC T.1252 (Clack 1994, fig. 3). The basicranial recess, best observed in NMS G.1998.51.1 (Fig. 7B, C) and UMZC T.1252 (Clack 1994, fig. 3)), is strongly flattened, presumably as a result of compaction, although it probably formed a shallow subpyramidal excavation in life (cf. *Caerorhachis*; Ruta *et al*. 2001). Its rim is slightly thickened (Clack 1994, fig. 3), and divided into a longer posterior, and a much shorter anterior part, together forming a broadly V-shaped pattern in plan view. The anterior arm of the 'V' continues anteriorly into the free edge of a slightly oblique facet for articulation with the basipterygoid process.

Vomer. The only undoubted vomer is an incomplete right element observed in ventral view in NMS G.1998.51.2 (Fig. 4). Preservation is poor, and its shape cannot be made out. However, there are at least two teeth preserved (Fig. 4C), and the surface shows a few denticles. These have been incorporated into the reconstruction, with the caveat that there may have been additional teeth in the row.

Palatine In UMZC T1351, an almost complete but disrupted right palatine is visible in ventral aspect (Fig. 3B). A second is preserved on NMS G.1998.51.2 (Fig. 4). In UMZC T.1351, a crack runs across its posterior half, and its posterior extremity is covered in part by the left lower jaw ramus. Behind the crack, the bone probably tapers to some degree. The preserved portion of its rearmost surface (immediately behind the fracture) is slightly narrower than its anteromedial process (see below), but its irregular medial edge suggests that the posteromedial area is incomplete. The overall outline is subrectangular, with almost straight lateral and medial margins diverging slightly anteroposteriorly. The palatine contributes to the posteromedial and posterior parts of the choanal margin. The robust, subtriangular anteromedial palatine process contacts the vomer. The broken base of a stout fang bearing faint traces of dentine infolding is visible near the palatine medial margin, a short distance away from the choanal margin. A weak depression, perhaps a replacement pit, is visible posterolateral to the fang. Faint oblique striations occur slightly medial and posterior to the fang and pit. The ventral surface of the palatine is covered in a denticle shagreen. Irregular and denticle-less patches of bone surface (e.g. in the lateral part of its central third) represent eroded areas. Small clusters of tiny denticles occur on the rearmost part of the bone, posterior to the fang and pit and in the central part of the anteromedial process. Slightly larger denticles occur in the anterior central third and along a longitudinal lateral strip of its ventral surface.

Ectopterygoid. An ectopterygoid cannot be identified with certainty in UMZC T.1351, but a sliver of bone, possibly representing a remnant of an ectopterygoid, is visible in UMZC T.1317 (Fig. 5).

3.3. Braincase

The basiparasphenoid is preserved in dorsal view in UMZC T.1351 (Figs 1, 2, 3C), and in ventral view in UMZC T.1252 (Fig. 3E) and NMS G.1998.51.1 (Fig. 7). The elongate, triangular cultriform process, or parasphenoid stem, is delimited by straight lateral margins, and narrows rapidly to a point anteriorly. Its dorsal surface is smoothly convex in its anterior half, but slightly depressed more posteriorly. At the same transverse level as the basipterygoid processes, the central portion of the basiparasphenoid dorsal surface bears an elongate, stout, low ridge slightly sunk between two poorly defined lateral depressions. The ridge anterior end is bluntly truncated. Its posterior portion widens to a small degree and is partly concealed under the anteromedial corners of the sellar

processes (anterolateral margins of dorsum sellae; Clack & Holmes 1988). This region corresponds, at least topographically, to the retractor pit recess observed in several stem amniotes and basal crown amniotes (White 1939; Heaton 1979; Clack & Holmes 1988).

The preserved parts of the robust sellar processes are irregularly quadrangular, with a distinct peripheral rim, and are situated immediately above the posterodorsal insertion of the basipterygoid processes. The overall proportions of this area of the basisphenoid are similar to those of *Archeria* (Clack & Holmes 1988). However, the bases of the two sellar processes are broader and more closely appressed than in *Archeria*.

Posterior to the sellar processes, the basiparasphenoid dorsal surface expands rapidly. A noteworthy feature is the presence of two shallow subtriangular areas delimited by two low, straight posterolateral ridges and by a poorly preserved, central longitudinal crest. The anteriormost ends of the two ridges and the crest are situated behind the medialmost points of the sellar processes. The ridges are sharp anteriorly, but merge smoothly with the surrounding bone surface posteriorly. Striations and pits are visible in places between ridges and crest. Clusters of small foramina are present lateral and posterior to the ridges, and along the posterior margin of the basiparasphenoid dorsal surface.

The ventral surface of the parasphenoid is covered in a dense, uniform denticle shagreen. Denticles are best observed on the gently arcuate ventral surface of the parasphenoid stem, and extend for most of its length. Near the stem anterior extremity, no denticles have been observed, and the bone surface appears to be only lightly striated (UMZC T.1351; Fig. 3C), although this may be an artefact of preservation. In NMS G.1998.51.1 (Fig. 7), the denticle-covered area is more extensive. By analogy with other anthracosaurs, it is reasonable to assume that denticles occupied most of the parasphenoid plate ventral surface.

The parasphenoid plate is about 25 percent shorter than the stem, slightly longer than wide, and with gently concave lateral margins. It bears a shallow, elongate depression, such as is observed in other anthracosaurs and several primitive amniotes (Heaton 1979; Reisz 1981; Holmes 1984, 1989; Smithson 1985; Clack & Holmes 1988; Clack 2002a). However, unlike in embolomeres (Clack & Holmes 1988), this depression is not delimited by robust, posteriorly diverging ventrolateral ridges. The slightly sinuous posterior margin of the plate is seemingly finished, and its lateral corners (?basal tubera) protrude slightly.

The robust, subhemispherical basipterygoid processes, best observed in ventral aspect in UMZC T.1252 (Fig. 3E) and NMS G.1998.51.2 (Fig. 7C), are coarsely tubercular and lightly striated ventrally. Their transverse, narrow articular facets are oriented anteroventrally, and indicate a mobile, anthracosaur-like type of articulation with the pterygoids (Clack & Holmes 1988). They are gently concave, with a sharply delimited margin, and inclined slightly mediolaterally.

The basioccipital is visible in ventral view in NMS G.1998.51.1. Its surface is featureless, except for two shallow ventrolateral depressions and a low median ventral ridge, and resembles the basioccipital of embolomeres (see Holmes 1984, 1989).

Skull reconstructions in dorsal, lateral, and palatal views (Fig. 8) summarise for the most part information gleaned from UMZC T.1351, with additional data from UMZC T.1317 and NMS G.1998.51.2. The nasals of UMZC T.1351 appear to be shorter (relative to the frontals) than in NMS G.1998.51.2, although this is due to disruption and incomplete preservation of their anterior parts. When compared to NMS G.1998.51.2

(Fig. 4), UMZC T.1351 shows comparatively larger orbits. However, if a certain amount of anteroventral curvature of the snout is accounted for, then the proportions of the preorbital region of the skull in NMS G.1998.51.2 resemble those of UMZC T.1351.

3.4. Lower jaw

The outer face of the lower jaw is preserved in several specimens, although the course of the sutures is often difficult to make out. The inner face is represented only in UMZC T.1317 (Fig. 5). Reconstructions are provided in Figure 8. The lower jaw shows some advanced features relative to those of other anthracosaurs. Its depth was calculated from the reconstructed mesial aspect employing the method outlined by Clack (1987), and expressed as percentage of total jaw length. Its value (19·86) is lower than those attributed to most other anthracosaurs, except for *Proterogyrinus* (19·2; data in Clack 1987), and is closer to those of *Discosauriscus* (20; based upon Klembara 1997) and *Caerorhachis* (20·85; Ruta *et al.* 2001). In its general proportions, the lower jaw ramus of *Silvanerpeton* resembles those of *Discosauriscus* and *Eoherpeton*. Unlike *Discosauriscus*, however, *Silvanerpeton* has a less deep and shorter surangular crest represented by a small anteroventral slope or 'step' at the anterior end of the surangular dorsal margin. This slope is similar to that of *Eoherpeton*, but less pronounced than that of *Pholiderpeton scutigerum* and *Archeria*. The jaw outline differs remarkably from that of embolomeres, in all of which the posterior half of the jaw ramus is deep and robust.

Preservation makes it difficult to ascertain whether the posterior coronoid contributes to the surangular crest, as in some seymouriamorphs (*Kotlassia*; *Discosauriscus*; *Utegenia*; Bystrow 1944; Klembara 1997; Klembara & Ruta 2004a), temnospondyls (*Eryops*; Sawin 1941), gephyrostegids (*Gephyrostegus*; Carroll 1970), and embolomeres (*Pholiderpeton scutigerum*; *Archeria*; Clack 1987; Holmes 1989; Ahlberg & Clack 1998; Ruta *et al.* 2001).

Dentary. UMZC T.1351 preserves one of the best examples of the dentary outer surface (Figs 1, 2, 3C). The bone is robust and about 30 percent deeper than the maxilla. Its maximum depth is at the level of the angular anterior extremity. From this point, the dentary narrows rapidly backward, forming a short, robust process appressed against the anteroventral part of the surangular crest. The posterior end of this process is poorly preserved.

Splenial and postsplenial. These bones are of approximately equal length. The splenial is spindle-shaped in ventral aspect, and tapers rapidly posteriorly. Anteriorly, it terminates short of the ventrally oriented, anterior extremity of the dentary, to which it is appressed. The postsplenial extends well behind the level of the tooth-bearing portion of the dentary in lateral view, reaching as far back as the anterior margin of the surangular crest. A narrow strip of bone visible along the lower margin of the right lower jaw of UMZC T.1317 (Fig. 5) bears a shallow, semielliptical, and elongate notch. The latter might correspond to the ventral margin of the anterior Meckelian foramen in embolomeres. The strip of bone is tentatively interpreted as a disrupted mesial lamina of the postsplenial.

Angular. The angular is lanceolate in lateral view, and overlaps a narrow, ventral strip-like area of the external surface of the surangular. In UMZC T.1317 (Fig. 5), angular and surangular are visible in lingual aspect and meet along a subhorizontal suture. The narrow and slender anterior process of the angular forms a short suture with the dentary, and is tightly wedged between surangular and postsplenial.

Prearticular. The prearticular is poorly preserved, and only a splinter-like portion of its medial surface is visible in T.1317 (Fig. 5) on both rami. Its broadly concave posterodorsal margin delimits the adductor fossa medial edge, and probably overlaps to some degree the posteromedial corner of the posterior coronoid.

Coronoids. These are incompletely preserved and best observed in UMZC T.1317 (Fig. 5). The posterior coronoid is narrow and elongate. Its acuminate posterior process covers in part the ventromedial margin of the posterior dentary process, and delimits the anterior edge of the adductor fossa. Scattered denticles occur on its dorsal surface. The posterior coronoid forms an irregularly indented suture with the middle coronoid. The lateral extremity of this suture lies distinctly anterior to its medial extremity. As a result, the anteriormost portion of the posterior coronoid appears as a narrow splinter wedged between the mesial shelf of the dentary and the incomplete middle coronoid. The anterior coronoid is not preserved.

3.5. Dentition

The premaxilla has seven slender, subcylindrical to subconical teeth (Fig. 1, 2, 8). Either the second or the third most anterior tooth is slightly larger than remaining teeth. The premaxillary tooth count is higher than in *Anthracosaurus* (two), *Archeria*, *Neopteroplax*, and *Pholiderpeton attheyi* (three), *P. scutigerum* (four), *Proterogyrinus* and *Eoherpeton* (five; *Eoherpeton* data are based upon the present authors' observations; however, Smithson's 1985 reconstruction shows six teeth).

About 35–40 tooth positions are estimated to have been present in the maxilla (Fig. 8). The more anterior teeth are subcylindrical and taper abruptly near their tip. The more posterior teeth are conical. All teeth are slightly compressed labiolingually, especially in their dorsal half, and most point slightly backward. Weak striations marking dentine infoldings extend for more than half of tooth crown height.

Combined information from UMZC T.1317, UMZC T.1351, NMS G.1998.51.2 and NMS G.2004.24.1 suggests the presence of approximately 37+ dentary tooth positions (Fig. 8). Teeth 17 to 24 (anteroposterior count) are the largest. Other teeth become progressively smaller anteriorly and posteriorly. All teeth are subcylindrical, with a rapidly narrowing, rearward-pointing crown tip, and are appressed against a vertical shelf of the dentary dorsolateral margin. Fang pairs are present on the palatine and at least two teeth on the vomer seen best on UMZC T.1351 (Figs 1–3) and NMS G.1998.51.2 (Fig. 4, inset) respectively. None is well preserved and crown shape cannot be described in detail. There appears to be no dentition on the coronoids apart from a denticle field.

Palatal and coronoid dentitions do not show noteworthy features. The denticles are small and conical, but details of their external surface are difficult to observe. In several places, they appear as eroded, blunt-topped structures.

3.6. Axial skeleton

There are only a few observations to be added to Clack (1994). One is the presence of the sacral ribs, visible in the holotype (T.1317a). They are preserved in close proximity to the ilia, and appear as short, stout elements with flared ends (Fig. 10F). Another is the better preserved tail of NMS G.1994.16.1, which shows 7 or 8 well-ossified haemal arches following the elongate postsacral ribs (Fig. 9C). The tail centra are all apparently almost complete rings or deep crescents, though none is fully embolomerous. The same specimen shows what may be an atlas arch close to the morphologically right scapulocoracoid. This is very similar to the atlas arch of *Pholiderpeton* (Clack 1987) (Fig. 10E; left element). Another possible atlas arch is preserved in UMZC T.1317 (Fig. 10E, right element).
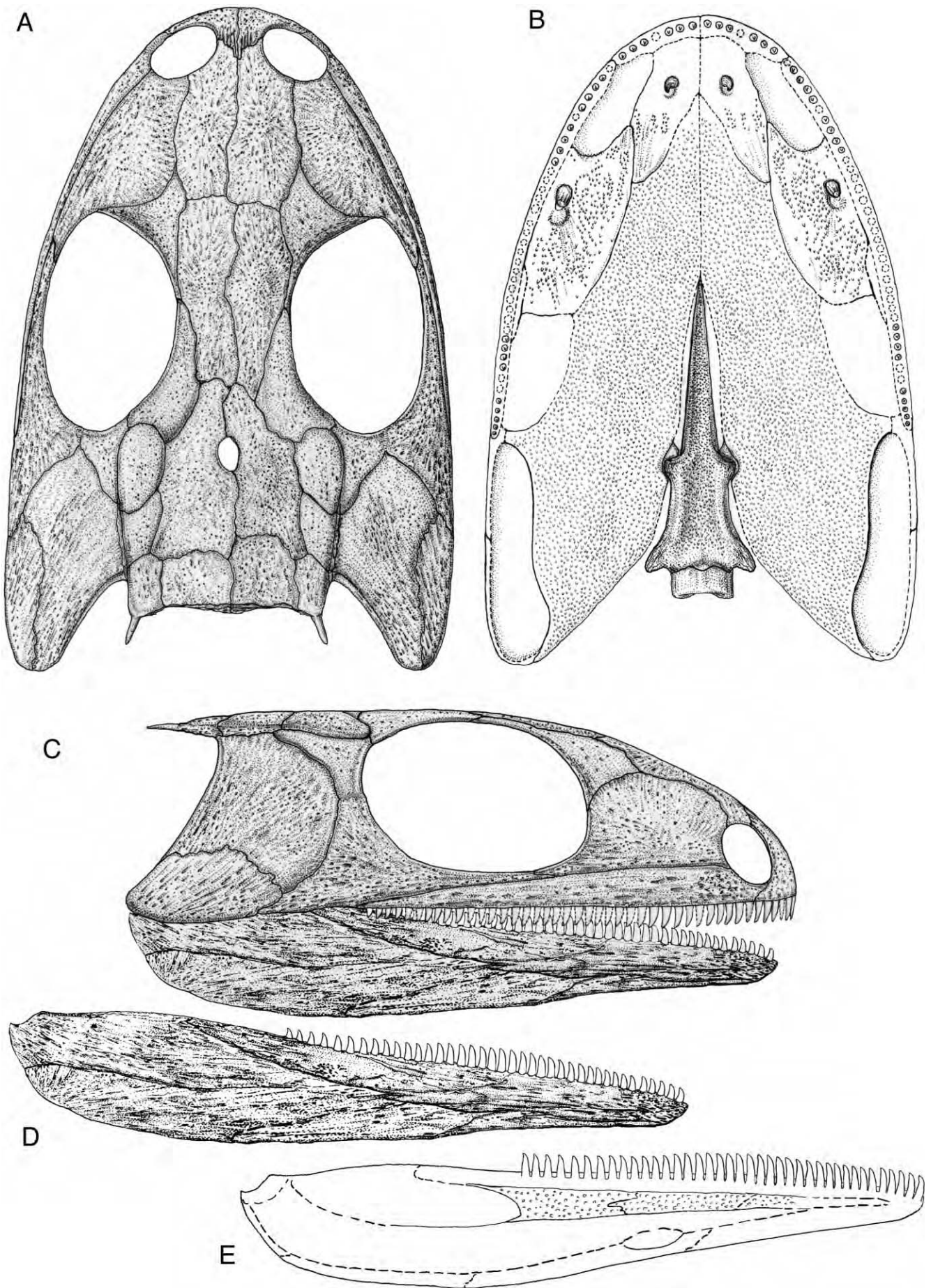
Figure 8 *Silvanerpeton miripedes* Skull reconstruction: (A) Dorsal view; (B) Ventral view; (C) Right lateral view; (D) Lateral view of lower jaw; (E) Medial view of lower jaw. These reconstructions are based mostly upon UMZC T.1351, with additional data from UMZC T.1317, NMS G.1998.51.2 and NMS. G. 1998.51.1 (see text for details). Maximum snout-quadrate length of skull (in NMS G. 1998.51.1) is about 80 mm.
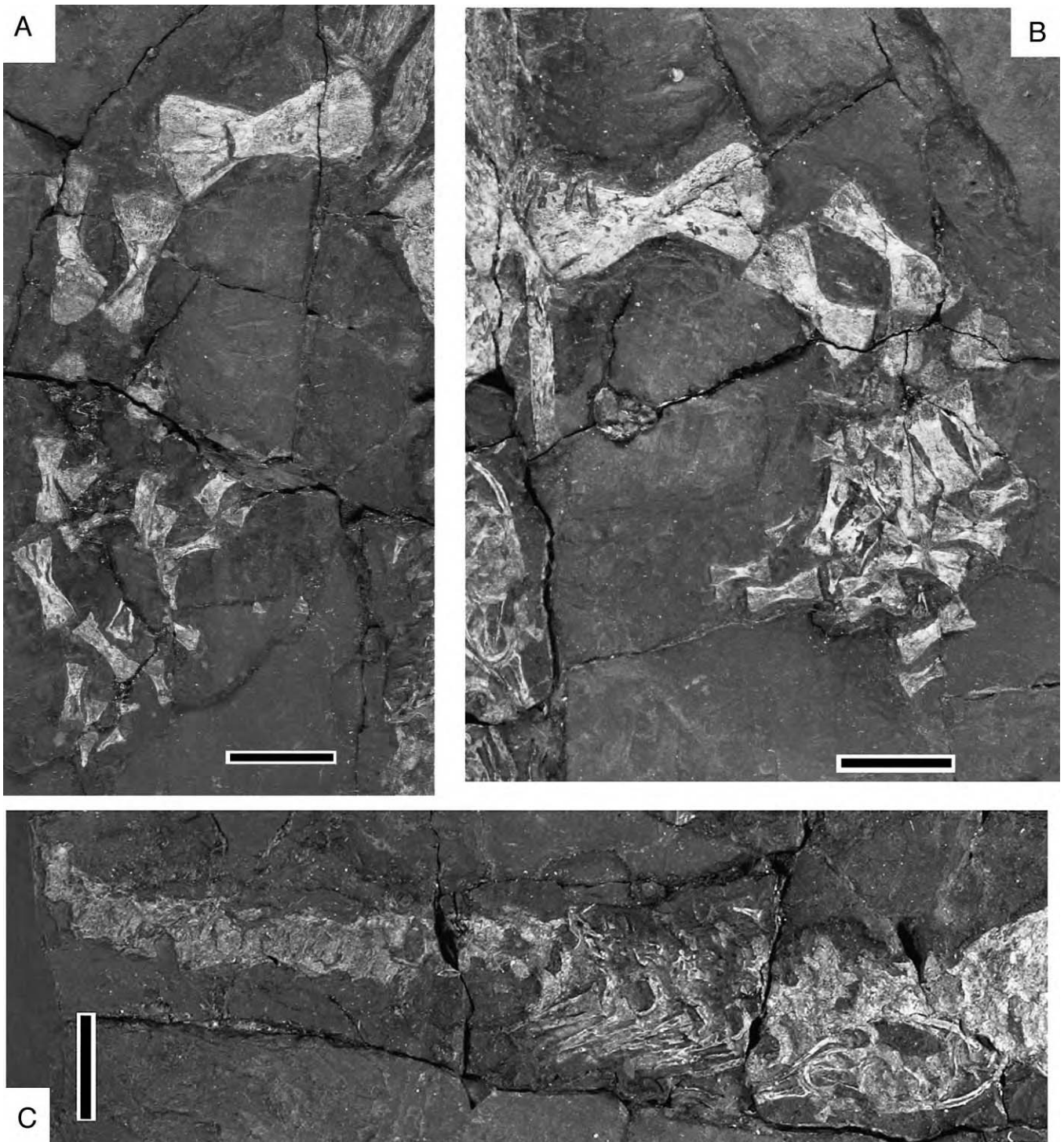
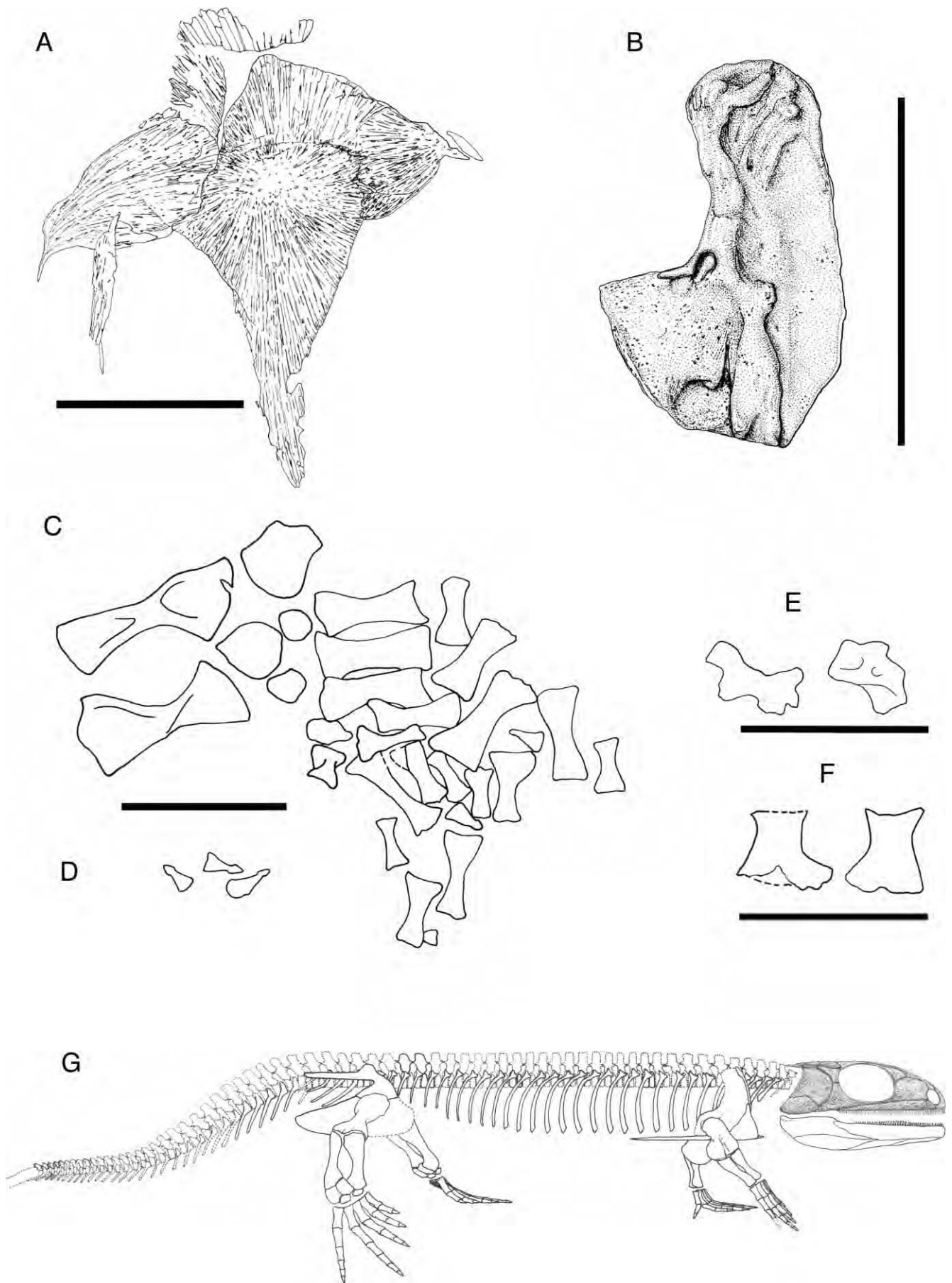**Figure 9** *Silvanerpeton miripedes* NMS G.1994.16.1: (A) Close-up photograph of left pes; (B) Close-up photograph of right pes. Also note postiliac process to the left; (C) Close-up photograph of the tail region showing haemal arches. Scale bars=10 mm.

3.7. Appendicular skeleton

3.7.1. Pectoral girdle. The interclavicle is similar to those of other anthracosaurs in its smooth transition between anterior plate and irregularly tapering stem (T.1317, Fig. 10A). The clavicle plate is narrower than in other anthracosaurs, with a smaller length:width ratio (i.e. less expanded along its medial margin; Romer 1957; Holmes 1984; Clack 1987; Smithson 2000) (UMZC T.1351, Fig. 2; UMZC T.1317, Fig. 10A). NMS G.1994.16.1 shows well-preserved, slender elongate cleithra with slightly expanded dorsal blades (Fig. 6B, short white arrows). It also shows relatively well-preserved scapulocoracoids. These are single units with no obvious division into scapular and coracoid regions (Fig. 6B, long white arrow).

3.7.2. Fore limb. Clack (1994) described the humeri of specimens UMZC T.1317 and UMZC T.1252 in which, however, surface details cannot be observed. UMZC T.1351 yields considerable new data, based upon a right humerus that has been almost completely exposed in extensor aspect (Figs 1, 10B). This is rather small relative to skull and femur, and almost as long as the frontals (i.e. about 31·43 percent of the distance from the snout tip to the skull table posterior margin). Its overall proportions resemble those of immature *Proterogyrinus* specimens (Holmes 1980, fig. 7o–t).

Figure 10 *Silvanerpeton miripedes*: (A) UMZC T.1317. Close-up drawing of interclavicle and clavicles; (B) UMZC T.1351. Close-up drawing of humerus after preparation; (C)–(D) NMS G.1994.16.1 (same scale bar for each); (C) Map of the right pes showing tarsal bones; (D) Map of the unguals from the left pes; (E) Possible atlantal arches. Left element NMS G.1994.16.1, right element, UMZC T.1317. (F) UMZC T.1317. Probable sacral ribs; (G) Complete skeletal reconstruction of *Silvanerpeton miripedes* in right lateral view. Scale bars=10 mm.

The humerus is L-shaped, with an elongate proximal half. The broadly concave posterior margin of the latter merges smoothly with the entepicondyle proximal margin, thus forming a slightly obtuse angle. Anterior to this angle, the keyhole-shaped entepicondylar foramen is oriented at about 45 degrees relative to the bone proximodistal axis. Unlike in other tetrapods (*Acanthostega*, Coates 1996; *Whatcheeria*, Lombard & Bolt 1995; *Greererpeton*, Godfrey 1989a; *Archeria*, Romer 1957; *Proterogyrinus*, Holmes 1980, 1984), the major axis of the foramen is not parallel to the anterior tract of the entepicondyle proximal margin. In addition, the foramen is placed more anteriorly, much as in *Eoherpeton* (Smithson 1985).

A poorly pronounced, elongate swelling lying immediately proximal to the mid point of the shaft posterior margin is probably homologous to 'process 2' (Coates 1996), also seen in *Acanthostega* (Coates 1996), *Ichthyostega* (Jarvik 1996), *Tulerpeton* (Lebedev & Coates 1995), *Eoherpeton* (Smithson 1985), *Proterogyrinus* (Holmes 1980, 1984), and *Archeria* (Romer 1957; in which it is represented by a weak protrusion). The posterior surface of the humerus shaft bears a thick, irregular ridge which runs from a point immediately distal to the posterior apex of the caput humeri to the entepicondylar foramen. This ridge joins the anterior region of the humerus extensor surface along a concave slope. Posterior to the entepicondylar foramen, it runs for a very short distance along the entepicondyle proximal margin. Anterior to the foramen, it turns anterodistally, narrows slightly, and then expands again giving rise to a blunt tubercle near the proximal extremity of the ectepicondyle.

The ectepicondyle resembles those of *Archeria* and, in particular, *Proterogyrinus*. It is vaguely bottle-shaped in outline. The 'bottle' neck appears as a small constriction distal to the blunt tubercle. The ectepicondyle is mostly straight, running approximately parallel to the humerus proximodistal axis. It widens more distally, where it approaches the finished, dorsal margin of the radial articular surface. The distalmost part of its dorsal surface carries an elongate, shallow depression (cf. *Proterogyrinus*; Holmes 1980, 1984).

Anterior to the ectepicondyle, the humerus extensor surface is flat or gently convex, and carries scattered nutrient foramina. More proximally, it shows rugosities, striations, and a weak oblique crest anterodistal to which the surface becomes shallower. This shallow area may correspond to the concavity for the *m. scapulohumeralis*, such as was described by Holmes (1980) in *Proterogyrinus* (see also Romer 1957). Unlike in *Proterogyrinus*, however, the concavity does not '. . . deepen distally to form a proximally facing pocket with an overhanging shelf' (Holmes 1980, p. 361). Instead, it merges smoothly into the central anterior region of the extensor surface. Near the posterior apex of the caput humeri and in the central part of the humerus proximal half (just anterior to its thickened posterior margin), the bone surface is irregular. Posterior tubercles and striations correspond in position to the tuberosities which Holmes (1980) described as giving insertions to the *m. subcoracoscapularis* in *Proterogyrinus*. An anteroposteriorly oriented and subrectangular tuberosity might correspond, in part, to the insertion for the *m. latissimus dorsi*, which is aligned with the ectepicondyle (discussion in Coates 1996). A subspherical bump is observed more anterodistally. Both *Discosauriscus* and *Seymouria sanjuanensis* show an irregular depression in a similar position (Klembara & Bartík 2000 and Klembara *et al.* 2001). This was interpreted by Klembara *et al.* (2001) as the insertion area for the *m. scapulohumeralis* (but see also Klembara & Bartík 2000).

A broad obtuse projection in the distal quarter of the humerus anterior margin marks the position of the supinator process. The entepicondyle is an elongate, subtrapezoidal sheet of bone with an acuminate, proximal posterior angle. Its surface is perforated by foramina, and bears a weakly striated, shallow depression immediately posterior to the ectepicondyle proximal half. The entepicondyle of *Silvanerpeton* differs from its homologue in immature *Proterogyrinus* (Holmes 1980), in which it is subsemicircular in outline, and recalls more closely that of juvenile *Discosauriscus* (Klembara & Bartík 2000, figs 20g, 21). It differs also from the subrectangular and proximodistally elongate entepicondyle of anthracosaurs, *Tulerpeton*, and *Whatcheeria*, and from the stout entepicondyle of *Pederpes* (Lebedev & Coates 1995; Lombard & Bolt 1995; Clack & Finney 2005).

The presence of five digits is confirmed by NMS G.1994.16.1 in which the metacarpals are preserved (Fig. 6C). Combined with data from the left and right manus of UMZC T.1252 (Clack 1994, fig. 3), the phalangeal counts for digits I–IV can be restored as 2–3–4–5 with a reasonable degree of confidence. However, manual unguals are not preserved in all cases. As discussed by Clack (1994, p. 374), '. . . digit five appears to have had more than the three phalanges as restored in *Gephyrostegus* by Carroll (1970)'. Together with the amniote-like tetrapod *Casineria* (Paton *et al.* 1999) from the mid Viséan of Scotland, *Silvanerpeton* is one of the earliest Lower Carboniferous tetrapods in which the manus phalangeal count can be reconstructed in significant detail.

The visible manus unguals are not preserved well enough in any specimen to allow comparison with those of the pes (see below).

3.7.3. Pelvic girdle. The most distinctive feature of the pelvic girdle is the posteriorly directed, straight postiliac process. The outline of the dorsal blade is incomplete, and best observed in UMZC T.1317 (Clack 1994) and NMS G.1994.16.1 (Fig. 6A, white arrow). It is stout and subtrapezoidal in outline, perhaps with a bluntly truncated dorsal edge. Its posterior edge merges with the anteriormost tract of the dorsal margin of the postiliac process along a gently concave line. The dorsal blade lies more posteriorly, relative to the puboischiadic plate, than in other anthracosaurs, as suggested also by the strongly backturned and elongate iliac neck. The length:depth ratio of the postiliac process is about 7. This value is greater than in most other anthracosaurs (see also Clack 1994), but compares well with the lowermost ratio reported by Godfrey *et al.* (1991) in the smallest specimen of the embolomere *Calligenethlon* (7·9), and is lower than the ratios in the gephyrostegid *Diplovertebron* (8·8), in the largest *Calligenethlon* specimen (8·5), and in Godfrey *et al.*'s (1991) unnamed Nova Scotia embolomere (9·3). The postiliac process is also similar to that of the amniote-like *Casineria*, although its outline in the latter is gently sigmoidal, with a length:width ratio of about 8·1 (Paton *et al.* 1999).

3.7.4. Hind limb. The femur, tibia, and fibula do not require redescription (Clack 1994). Newly recorded features are the four or five tarsal elements preserved in NMS G.1994.16.1 (Figs 9A, B, 10C). The right pes of this specimen is somewhat disrupted, although metatarsals and phalanges lie in close proximity to each other. Between the distal extremities of the tibia and fibula and the proximal extremities of metatarsals III–V are five bones. Four of these are visible as polygonal areas with well delimited margins, and although only their cross-sectional surfaces are preserved, no considerable displacement has taken place. The fifth bone is a diminutive square element visible immediately proximal to metatarsal V. A smaller trapezoidal bone (or possibly two small bones superimposed) lies at a short distance from the proximal articulation between metatarsals III and IV. One or both of these latter two may represent a centrale or a distale, but their

identification is conjectural. The two largest tarsal elements might represent a fibulare and an intermedium. The intermedium is approximately rectangular. Its longer tibial and shorter fibular margins converge proximally into a short, stout process. Thus, unlike in *Tulerpeton* (Lebedev & Coates 1995), *Caerorhachis* (Ruta *et al*. 2001), embolomeres (Romer 1957; Holmes 1984), *Westlothiana* (Smithson *et al*. 1994), some diadectomorphs (Berman & Henrici 2003), and certain primitive crown amniotes (Romer 1946; Heaton 1979; Reisz 1981), the proximal margin of the intermedium of *Silvanerpeton* does not show a notch (for a discussion of this character see Coates 1996 and Ruta *et al*. 2001) (Figs 9A, B, 10C). Overall shape and proportions of the intermedium resemble those of some temnospondyls (Milner & Sequeira 1994) and *Greererpeton* (Godfrey 1989a), and are presumably primitive for stem amniotes. The elliptical fibulare is the largest tarsal bone. It is disrupted, but resembles that of other tetrapods.

As regards the pes, NMS G.1994.16.1 shows unguals with distinct triangular expansions at their tips (Fig. 10D). Re-examination of the holotype, an animal about 15 percent smaller, confirms that it too bears similar expansions, though they are correspondingly smaller and more difficult to spot. Note also the incorrect phalanageal reconstruction of the pedal digits of *Silvanerpeton* illustrated by Clack (2002c, fig. 4 – *fide* R. L. Carroll). A reconstruction of the complete skeleton is provided in Figure 10G.

3.8. Body armour
No additional observations are added to Clack (1994). The shape and arrangement of gastralia are shown in Figure 6.

3.9. Comparisons
3.9.1. Anthracosaurs. The spike-like tabular horn (Panchen 1972; Holmes 1984, 1989; Smithson 1985; Clack 1987) is probably the most distinctive trait shared by *Silvanerpeton* and anthracosaurs. However, preservation makes it difficult to ascertain whether such horn resembles closely that of embolomeres, in which it consists of a lower (smooth) and an upper (mostly ornamented) component separated by a notch or pit (Clack 1987). The slender posterolateral projection of the tabular in UMZC T.1317 may be homologised to the lower component of the embolomere horn, although it is comparatively shorter. Furthermore, the outline of the tabular ornamented surface is considerably narrower (for its length) than in other anthracosaurs, and with a less strongly arcuate posterior margin. In *Silvanerpeton*, the shallow embayment in the dorsal tract of the squamosal posterior margin resembles vaguely that of *Pholiderpeton scutigerum* (Clack 1987), but differs from the narrow, elongate excavation (in lateral projection) observed in other anthracosaurs. The squamosal is relatively less elongate than in most embolomeres, and more similar to that of *Eoherpeton* (Smithson 1985) and *P. scutigerum*. Its posterior margin is smoothly concave, and unlike the gently convex margin of *P. scutigerum*, the straight margin of *Archeria*, and the slightly sigmoid margin of *Proterogyrinus* (Holmes 1984, 1989). As in the majority of other anthracosaurs, the deep quadratojugals form a large part of the suspensorium. Characters distinguishing *Silvanerpeton* from other anthracosaurs are the large orbits and the posteromedially converging, straight lateral margins of the skull table. In anthracosaurs, these margins are invariably smoothly convex along most of their length. The *Silvanerpeton* skull table is widest at the level of the intertemporal anterior one-third. In other anthracosaurs, its maximum width occurs at various levels, e.g. at the supratemporal–tabular suture (*Archeria*; *Neopteroplax*; *Pholiderpeton scutigerum*); coinciding

with supratemporal mid-length (*Proterogyrinus*; *Anthracosaurus*; *Eoherpeton*); close to the supratemporal anterior half (*Palaeoherpeton*); or near the intertemporal-supratemporal suture (*Pholiderpeton attheyi*) (Romer 1963; Panchen 1964, 1970, 1972, 1977; Holmes 1984, 1989; Smithson 1985; Clack 1987). The supratemporals are similar to those of *P. attheyi* and *Neopteroplax*, but smaller and narrower relative to skull table width. As in *Archeria* and *Proterogyrinus*, the parietals of *Silvanerpeton* narrow anteriorly. In particular, they differ from those of *Archeria* in that they are not tightly wedged between the posterior margins of the frontals. Furthermore, they send subrectangular posterolateral projections squeezed between postparietals and supratemporals, a condition observed also in *Proterogyrinus*, *Neopteroplax*, and *P. attheyi*. *Silvanerpeton* resembles embolomeres in possessing elongate and narrow frontals and nasals. The frontals taper rapidly rearward, as in *Palaeoherpeton* and *Proterogyrinus*. The nasal:frontal length ratio compares well with those of *Eoherpeton*, *Palaeoherpeton*, and *Proterogyrinus*, but is smaller than those of *P. attheyi* and *Archeria*. The braincase of *Silvanerpeton* differs from that of other anthracosaurs (where known), in that the cultriform process is elongate triangular and comparatively broader, relative to the parasphenoid plate. Finally, the lower jaw is less deep than that of embolomeres in its rear third, but its overall outline is similar to that of *Eoherpeton*.

3.9.2. Gephyrostegids. Some cranial features of *Silvanerpeton* appear to be surprisingly derived for a Lower Carboniferous 'reptiliomorph', and foreshadow conditions observed in some Late Carboniferous and Permian stem amniotes (gephyrostegids; seymouriamorphs). Gephyrostegids have been hypothesised to occupy an intermediate phylogenetic position between anthracosaurs and more derived stem amniotes (Carroll 1970, 1991; Lee & Spencer 1997; Ruta *et al*. 2003), based on a suite of cranial and postcranial characters (see Vallin & Laurin 2004 for alternative phylogenetic hypotheses). Similarities between *Gephyrostegus* and *Silvanerpeton* include the parabolic skull outline and the straight lateral margins of the skull roof. With regards to the latter feature, Carroll's (1970, fig. 6) cranial reconstruction of *Gephyrostegus* shows that the lateral margins of the tabulars are not aligned with those of the supratemporals (the situation observed in *Silvanerpeton*), but lie slightly medial to them. Furthermore, the intertemporal and supratemporal of *Gephyrostegus* are aligned with the ventrolateral ramus of the postfrontal, and the supratemporals are distinctly larger than the intertemporals. Finally, *Silvanerpeton* differs from *Gephyrostegus* in having anteriorly tapering parietals, broader postparietals, and slightly larger orbits. Despite differences in details of sutural seams and proportions of various circumorbital and snout bones, *Silvanerpeton* and *Gephyrostegus* show many features in common. Thus, their jugals bear a slender suborbital ramus and a broad, subtriangular posterior ramus. In both, the lacrimal sends a short suborbital ramus (slightly longer in *Silvanerpeton*), and its squamous anterior part contributes to a large proportion of the lateral surface of the snout. The latter condition resembles that of one of the two skull morphotypes of *Gephyrostegus* figured by Carroll (1970, fig. 6b). The morphotype in question differs from *Silvanerpeton* in showing slender postfrontals and subtriangular, posteriorly tapering postorbitals. Both *Gephyrostegus* and *Silvanerpeton* have broad, relatively short squamosals with a shallow, concave posterior margin. Carroll (1970) reconstructed a small, toothless transverse flange on the pterygoids of *Gephyrostegus*, but no such flange occurs in *Silvanerpeton* (diagenetic flattening is unlikely to have obliterated it completely without breakage). Similarities in the palate construction of both taxa are also evident in the estimated proportions of vomer and palatine and

in the position of their fangs, though it should be noted that Carroll's (1970) two reconstructions of the *Gephyrostegus* palate differ significantly from each other in a number of features, and the genus is in need of review.

3.9.3. Seymouriamorphs. Except for a few gradistic characters (e.g. snout elongation), *Silvanerpeton* bears little resemblance to seymouriids, but superficial similarities with discosauriscids are more numerous (White 1939; Kuznetsov & Ivakhnenko 1981; Ivakhnenko 1987; Laurin 1995, 1996a–c, 2000; Klembara 1997; Berman *et al.* 2000; Bulanov 2003; Klembara & Ruta 2004a), and include: triradiate jugals; slender suborbital ramus of jugal; large contribution of squamous part of lacrimal to snout lateral surface; short, distinct suborbital ramus of lacrimal; large orbits; triradiate postorbital bearing well developed posteroventral ramus (in most discosauriscids). The posterior extension of the post-orbital of *Silvanerpeton* recalls the condition of *Utegenia* and some other seymouriamorphs (eg. Klembara & Ruta 2004a; Klembara 2005). The phylogenetic analysis suggests however that these similarities are likely to be homoplasies. Differences between *Silvanerpeton* and the majority of other seymouriamorphs include the presence, in the former, of a shallow posterior margin of the squamosal (also in *Utegenia*) and a comparatively narrower skull roof. The basiparasphenoid of *Silvanerpeton* resembles more closely that of embolomeres and gephyrostegids, in which it is elongate and subrectangular, than that of seymouriamorphs, in which it is transversely expanded and bears wing-like posterolateral processes. As in seymouriamorphs, however, the cultriform process is elongate and triangular (Klembara & Ruta 2004a; Klembara 2005).

4. Phylogenetic analysis

4.1. General remarks

We undertook a cladistic analysis of selected Palaeozoic tetrapods (see Appendixes 1 and 2) to infer the position of *Silvanerpeton*. Our study is not intended as an exhaustive investigation of early tetrapod relationships, and only provides a framework for exploring character distribution among basal 'reptiliomorphs'. To this end, we built a new matrix by combining characters from Clack (2002c) and Ruta *et al.* (2003), based upon the following protocol (for details, see Clack & Finney 2005): Ruta *et al.*'s (2003) data set was first reduced to match the taxonomic content of Clack's (2002c); characters not employed by Ruta *et al.* (2003) but used by Clack (2002c) were included in the new matrix. Character scores were checked for all taxa and modifications were introduced to account for new data.

The following taxa were added to Clack's (2002c) data matrix: *Anthracosaurus russelli*; *Archeria crassidisca*; *Ariekanerpeton sigalovi*; *Bruktererpeton fiebigi*; *Casineria kiddi*; *Discosauriscus austriacus*; *Paleothyris acadiana*; *Utegenia shpinari*. We note that Ruta *et al.* (2003) did not consider *Casineria* or *Silvanerpeton* in their study. The new matrix (33 taxa; 314 characters), built in MacClade version 4.0.8 (Maddison & Maddison 2005), was subjected to a parsimony analysis with PAUP* version 4.0b10 (Swofford 2003). Heuristic search protocols followed Ruta *et al.* (2003), and yielded three most parsimonious trees (MPTs) at 912 steps (Fig. 11), with *Eusthenopteron* as outgroup. Basic tree statistics are as follows: C.I. = 0·3502 (255 parsimony-informative characters); R.I. = 0·5683; R.C. = 0·2237. The MPTs differ only in the relative positions of *Casineria*, *Westlothiana*, and microsaurs.

4.2. Branch support and tree topology

Node support was assessed via bootstrap (Felsenstein 1985; based on 50 per cent majority-rule consensus from 10,000

replicates), and decay index (Bremer 1988) values (Fig. 11). A T-PTP test was employed to compare the length of the MPTs with those of the shortest tree(s) obtained after permuting and randomly reassigning character-states to taxa (and maintaining proportions of each state). We randomised our matrix 100 times. The test found that the MPTs are significantly shorter than trees from the permuted data ($P = 0·01$).

The branching sequence of post-Devonian stem tetrapods includes *Crassigyrinus*, whatcheeriids (*Pederpes*, *Whatcheeria*), and baphetids (with *Eucritta* as sister taxon to all other baphetids; Clack 2001). Remaining tetrapods form two monophyletic groups. The first consists of *Caerorhachis* and temnospondyls (*Balanerpeton*, *Dendrerpeton*) as successive sister taxa to a nectridean (*Ptyonius*)-adelospondyl (*Adelogyrinus*)-colosteid (*Greererpeton*) clade. In the second group, *Silvanerpeton* is the most basal stem amniote. Crownward of it is an anthracosaur clade consisting of eoherpetontids (*Eoherpeton*) plus embolomeres, with *Anthracosaurus* and *Proterogyrinus* as successive sister taxa to *Archeria* plus *Pholiderpeton*. More distally, *Gephyrostegus* and *Bruktererpeton* are successive sister taxa to other 'reptiliomorphs'. Seymouriamorphs (*Seymouria*, *Utegenia*, *Ariekanerpeton*, and *Discosauriscus*) are adjacent to a group including crown amniotes (*Paleothyris*; Laurin & Reisz 1995) as sister taxon to a *Westlothiana*-*Casineria*-microsaur (*Microbrachis*, *Saxonerpeton*) clade.

The relative positions of *Crassigyrinus* and whatcheeriids agree with the results of Ruta *et al.* (2003), but conflict with those of Clack (2002c), who considered whatcheeriids to be the most basal tetrapods after those of the Devonian. While these results can be intuitively related to a greater 'influence' of Ruta *et al.*'s (2003) characters, it is not obvious which of these (or combinations thereof) favour such an arrangement, considering that several of Clack's (2002c) characters are also included here (Clack & Finney 2005). However, if the branching sequence from *Eusthenopteron* to *Crassigyrinus* is left unchanged and all taxa more derived than *Crassigyrinus* are collapsed in a polytomy, then the six shortest trees that are not compatible with this constrained topology place *Crassigyrinus* in a more derived position than whatcheeriids (such trees do not differ significantly from the MPTs). These finds corroborate Clack's (2002c) conclusions that whatcheeriids and *Crassigyrinus* compete strongly for their placement as the basalmost Carboniferous stem tetrapods.

Finally, although our data fail to retrieve *Caerorhachis* as a basal stem amniote (Ruta *et al.* 2001, 2003), regrafting *Caerorhachis* as sister group to 'reptiliomorphs' does not entail a significantly different redistribution of characters ($P \geqslant 0·05$). Although the senior author favours a stem amniote placement for *Caerorhachis*, lack of adequate skull material implies that the phylogenetic position of this taxon is likely to shift around the basal node of the tetrapod crown group, depending upon character and taxon selection (Ruta & Coates in press).

5. Discussion

5.1. The problem of scaling and ontogeny

A vexing issue concerns the validity of characters that distinguish *Silvanerpeton* from anthracosaurs. Are the characters in question size- or ontogeny-related? Despite the fact that *Silvanerpeton* is much smaller than the Permo-Carboniferous anthracosaurs, its pattern of ossification suggests to us that available specimens were close to maturity when they died, and this taxon might have been characterised by precocious ossification at a relatively small body size (see below). These conclusions are based mostly upon postcranial characters. However, comparisons among different specimens are difficult,
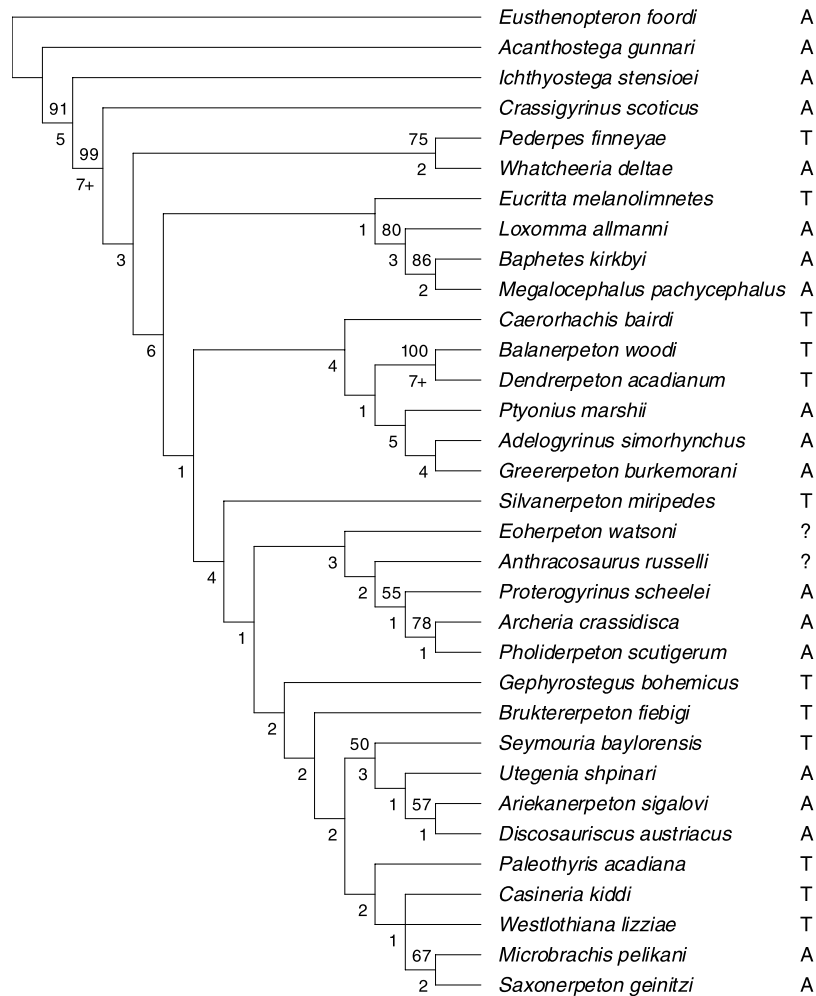
Figure 11 Strict consensus of the three most parsimonious trees derived from the analysis (see text for details). Numbers below branches are Bremer support values. Those above branches are bootstrap percentage values. The letters A and T, next to each taxon name, denote aquatic and terrestrial habit.

due to incomplete preservation of relevant features. In the absence of complete ontogenetic series, we can only speculate that some of the features listed below may only partly be related to age and/or size.

Clack (1994) demonstrated that *Silvanerpeton* is clearly distinguished from *Eldeceeon* by body proportions and degree of postcranial ossification at similar presacral length, and there is no doubt that *Silvanerpeton* is also distinct from all other known stem amniotes, including anthracosaurs. Some of the distinguishing features include, amongst others: shape and proportions of the skull table, in particular the morphology of the intertemporals and the straight, posteromesially oriented lateral margins of the table; shape of the lacrimal, which is deep and contributes to most of the lateral aspect of the preorbital skull region; posterior margin of the suspensorium, which exhibits a shallow curvature; triradiate jugals, in particular the presence of a well-developed posterior and dorsal ramus; morphology and proportions of the para-sphenoid stem; and morphology of the tarsal intermedium (absence of a proximal notch). The depth and forward extent of the anterior ramus of the jugal might be affected during growth as it is known to be in *Greererpeton* (Godfrey 1989b). It is associated with the reduction of relative orbit size seen during the growth of many vertebrates.

Assuming that preorbital skull elongation and relative reduction of orbit size occurred during later ontogenetic stages, we speculate that the final product of associated skull roof transformations would result in a more mature

Silvanerpeton stage resembling *Proterogyrinus*. There is no reason to assume that the pattern of preorbital skull bones would change dramatically. For example, elongate nasals occur in *Silvanerpeton* as well as in the much larger eoherpe-tontids and embolomeres. Even after imposing a pattern of snout elongation resembling the more extreme versions among embolomere skulls, *Silvanerpeton* might still retain large lacrimals, as opposed to the slender, much more elongate lacrimals of anthracosaurs. Data from Eurasiatic seymouria-morphs (Klembara & Ruta 2004a, 2005a) indicate that, apart from minor modifications in its dorsalmost part, the free margin of the suspensorium maintains almost isometric proportions during ontogeny, except at the transition between very early larval stages. This might well be the case among less derived stem amniotes, including *Silvanerpeton* and anthracosaurs, although evidence is circumstantial.

5.2. Inferred life habits

NMS G.1994.16.1 shows relatively well ossified tarsal elements and seemingly robust limbs, the latter feature being also present in the holotype. The humerus of UMZC T.1351 has well developed processes and ridges, although its overall shape (in particular, relative proportions and size of the entepicondyle) resemble those of immature *Proterogyrinus*. The dermal elements of the shoulder girdle are also well developed and exhibit clearly demarcated edges (e.g. UMZC T.1351). In contrast, the orbits are large relative to skull length, especially in UMZC T.1351, but comparatively slightly

smaller in UMZC T.1317 and NMS G.1998.51.2. *Proterogyrinus* is the only anthracosaur in which the orbits are also relatively large compared to the skull (about 0·22 orbit length: skull length), but they do not reach the proportions of the *Silvanerpeton* orbits (0·33). The absence of strongly interdigitated sutures on the skull table, coupled with presence of large orbits and weakly developed dermal sculpture, appear to be consistent with the interpretation of *Silvanerpeton* as either an immature or a paedomorphic taxon. The denticle-covered parasphenoid stem is also consistent with immaturity or heterochrony, by analogy with the situation in some temnospondyls (e.g. Boy & Sues 2000), where denticles disappear progressively from the parasphenoid stem in an antero-posterior direction during later ontogenetic stages.

Certain postcranial features (e.g. strongly ossified and robust limbs; ossified tarsus in at least one specimen; presence of robust interclavicle and clavicles with well defined edges) suggest at least partial precocious ossification in a relatively small, terrestrially adapted animal, although its centra do not form complete rings and resemble a primitive gastrocentrous type. The relatively large feet indicate that *Silvanerpeton* was capable of sustained 'rear-wheel drive' modality of locomotion; although broad, the feet are not paddle-like and/or elongate, and thus do not seem to be well-adapted for aquatic propulsion. This is also indicated by the presence of relatively large, well-ossified ankle bones seemingly abutting tightly against each other (a clear demarcation of their boundaries is often obscured by preservation and patterns of cleavage on the slab surface). In addition, although the fore limb is small, the well-developed processes of the humerus show that *Silvanerpeton* necessitated support on land, although perhaps without involving powerful forward and backward fore limb strokes (relatively small subtriangular entepicondyle; absent or poorly developed olecranon process). The preserved part of the tail allows us to deduce that it was not flattened or deep, and therefore not suitable for an aquatic medium. Rather, it is relatively robust at least anteriorly, which may indicate a balancing action during locomotion. In its overall body proportions, *Silvanerpeton* resembles some extant teiid lizards.

Given available evidence (see also next section), we hypothesise that the early history of the amniote stem featured small, precociously ossified, presumably terrestrial tetrapods. However, Laurin (2004) has shown that at the base of his 'batrachomorph' radiation (basalmost stem amniotes here) were tetrapods with an average skull length of about 60 mm. This value is slightly greater than the average for *Silvanerpeton* (between 40 and 50 mm), and suggests that on average, basal amniotes were smaller than basal lissamphibians (edopoids). Interestingly, following their phylogenetic separation from basal stem lissamphibians, amniotes already showed a remarkable diversification and acquisition of different morphotypes (e.g. contrast body proportions among East Kirkton 'reptiliomorphs', as well as between those and other Lower Carboniferous amniote-like taxa, e.g. *Casineria* and *Caerorhachis*). Most of these animals probably occupied the niche of small predators feeding on invertebrates or small vertebrates, and might have been partially nocturnal in habits (one of the possible biological explanations for large orbit size in *Silvanerpeton*). The more derived, larger counterparts of these 'protoanthracosaurs', namely eoherpetontids and embolomeres, invaded aquatic environments and developed adaptations similar to those of modern crocodiles, a widespread habitus among Palaeozoic tetrapods including basal temnospondyls (Milner & Sequeira 1998). At a post-anthracosaurlevel of evolution, stem amniotes exhibited a range of habits, from semiaquatic to fully terrestrial, and indeed, the pattern of character acquisition among them reflects progressive adaptation to life on land (e.g. Sumida 1997). Exceptions, e.g. some seymouriamorphs (Klembara 1997; Klembara & Ruta 2004a, b, 2005a, b), are likely to represent preservation bias towards aquatic ontogenetic stages, unless these taxa are neotenous.

Janis and Keller (2001) documented relative head: body length proportions in extinct and extant amniotes and non-amniotes. They showed that in general, in amniotes, the head was relatively shorter than in non-amniotes, a feature that they associated with breathing mechanisms: buccal pumping in non-amniotes versus costal aspiration in amniotes. They found that all non-anthracosaurian non-amniotes had head lengths at least 30% of their snout-vent lengths, but that in amniotes generally this proportion is below 27%. Further taxa can now be added to their list and considered in this context: *Silvanerpeton*, 28%; *Eldeceeon*, 30%; *Eucritta*, 36·5%; *Caerorhachis*, 35%; *Pederpes*, 37%; *Westlothiana*, 17%; *Discosauriscus*, 27%; *Utegenia*, 24%; and *Ariekanerepton*, 37%. *Silvanerpeton* and *Eldeceeon* therefore fall between amniotes and non-anthracosaurian non-amniotes, approximating to Janis and Keller's (2001) published figure of 28·5% for *Gephyrostegus*. *Eucritta*, *Caeorhachis* and *Pederpes* cluster with non-anthracosaurian non-amniotes. *Ariekanerepton*, a discosauriscid, has an anomalously large head, but the closely related *Utegenia* clusters with amniotes. The latter taxon is smaller than the other discosauriscids, and has a relatively longer body. These studies take no account of presacral length, but that factor will obviously affect the results, as in the case of *Westlothiana* with its elongate body. It is also interesting to note that, since there is no head preserved for *Casineria*, we cannot assume that its proportions were amniote-like, despite the phylogenetic analysis which places it close to basal amniotes (Paton *et al.* 1999). The postcranial skeleton of *Casineria* is similar in size and in several morphological features to that of *Caerorhachis*, whose head is relatively large. Simple head: snout-vent ratios can only provide a rough guide to the physiology of any particular tetrapod taxon, and must be seen in the context of other factors.

5.3. Life-styles at the base of the tetrapod crown

Our inferences do not, of course, rule out the possibility that *Silvanerpeton* went through an aquatic larval stage during its development, and we suspect that this condition might have characterised the vast majority of, if not all, early tetrapods including the more fully terrestrial ones. In the Viséan, when they are first documented, various stem amniotes showed terrestrial or semiterrestrial life-styles. A subsequent radiation, typified by embolomeres, reverted to more fully aquatic habits. It is also interesting to note that several taxa that lie close to the base of the tetrapod crown (e.g. *Caerorhachis* and *Eucritta*) also show terrestrial habits. In recent cladistic analyses, the position of these taxa has been discussed extensively (Ruta *et al.* 2003). Regardless of their position in relation to the lissamphibian-amniote separation, current data seem to favour a subaerial, presumably terrestrial environment for the origin of the modern tetrapod radiation. Such palaeoecological inference, however, is tentative, as it relies upon several other factors, including optimisation of character-states that relate to presumed life habits under accelerated and delayed transformations, placement of key taxa near the base of crown tetrapods, and tree topology. Vallin & Laurin (2004) have recently discussed the habitats and life-styles of various groups of early tetrapods, and concluded, based upon their preferred tree topology, that the origin of crown tetrapods can be traced to an amphibious ancestor.

The present authors have not categorised life-styles as terrestrial, aquatic, or amphibious, as Vallin & Laurin (2004) did. Instead, we have coded taxa based upon presumed
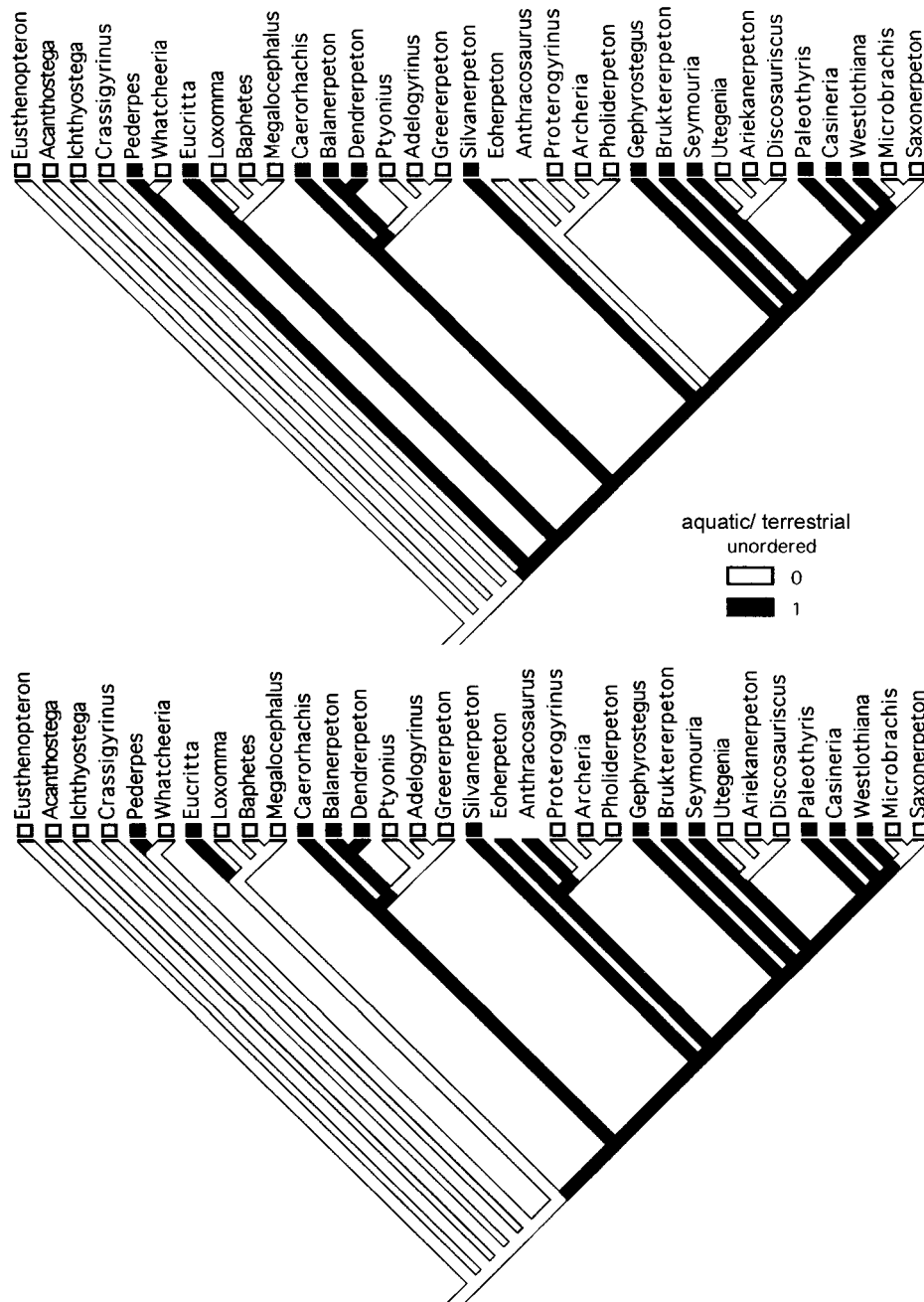
Figure 12 ACCTRAN (above) and DELTRAN (below) optimisation of aquatic (white branches) and terrestrial (black branches).

terrestrial or aquatic habits of adults only (life cycles can be inferred with confidence in a handful of tetrapods only, and identification of the life stage represented by any particular specimen is often speculative, especially in the absence of complete growth series). We were interested in 'bracketing' the habit of the last common ancestor of crown tetrapods, given hypothesised habits of putative adult members of basalmost lissamphibian and amniote plesions. Habits were optimised on the MPTs under ACCTRAN and DELTRAN, and treated as binary (Figs 11, 12). An aquatic state was assigned to Devonian taxa, *Crassigyrinus*, *Whatcheeria*, adelospondyls, colosteids, microsaurs, nectrideans, and embolomeres (data from Clack 2002a and Vallin & Laurin 2004). Both ACCTRAN and DELTRAN favour a terrestrial state at the base of the crown. Under ACCTRAN, an aquatic to terrestrial change is placed at the *Crassigyrinus*-whatcheeriids internode (Bolt & Lombard 2000; Clack & Finney 2005).

A terrestrial origin scenario is also supported in part by data from temnospondyls, the most species-rich group of early tetrapods. If placed on the lissamphibian stem – a hypothesis that has generated substantial and heated debate (Ruta *et al.* 2003; Vallin & Laurin 2004, Laurin & Soler-Gijon 2006) – temnospondyls inform plesiomorphic life-style conditions for the amphibian total group. Current phylogenetic hypotheses place a Permo-Carboniferous radiation of alligator- and gharial-like species – the Edopoidea – as the most basal temnospondyls (e.g. Milner 1990, 1993; Milner & Sequeira 1998; Holmes 2000; Ruta *et al.* 2003). Within this radiation, the basal genera *Edops* and *Adamanterpeton* have been hypoth-esised to be terrestrial (Milner & Sequeira 1998; Holmes 2000), and Milner & Sequeira (1998) argued in favour of terrestrial habits in at least one derived edopoid (*Cochleosaurus florensis*).

These conclusions are not affected by the taxonomic sam-pling used in this work. Thus, if states related to putative

terrestrial and aquatic habits are optimised on the phylogeny proposed by Ruta *et al.* (2003), then a terrestrial origin for the tetrapod crown is also supported. This is easily inferred from the observation that in their cladogram, both the lissamphibian and the amniote total groups include land-dwelling plesiomorphic members. Regrafting problematic taxa such as *Eucritta* and *Caerorhachis* does not alter this scenario. Furthermore, the latter is not necessarily in conflict with the hypothesis put forward by Vallin & Laurin (2004), if the most primitive members of stem lissamphibians and stem amniotes in their preferred tree were terrestrial as adults. Comparisons between the various tree topologies are limited, as Vallin & Laurin (2004) used supraspecific groups as terminal units. However, optimisations may differ if groups are subdivided more finely (e.g. if species are used), and if terminal taxa exhibit a variety of states near the base of the crown group. Ultimately, palaeobiological inference will have to rely upon a more complete picture of the origin and interrelationships of groups that gravitate about the base of the tetrapod crown.

6. Acknowledgements

7. Abbreviations used in figures

(add foss) adductor fossa; (ang) angular; (art) articular; (art/q) articular or quadrate; (bas art) basal articulation; (bpsphen) basiparasphenoid; (clav) clavicle; (cor 1, 2, 3), anterior (first), middle (second) and posterior (third) coronoid; (dent) dentary; (ect) ectopterygoid; (fr) frontal; (iclav) interclavicle; (it) intertemporal; (jug) jugal; (lac) lacrimal; (max) maxilla; (meck fen) meckelian fenestra; (nas) nasal; (pal) palatine; (par) parietal; (par for) parietal foramen; (pin for) pineal foramen; (pmx) premaxilla; (pofr) postfrontal; (poorb) postorbital; (pospl) postsplenial; (pp) postparietal; (preart) prearticular; (pr cult) cultriform process; (prefr) prefrontal; (psph) parasphenoid; (pter) pterygoid; (qj) quadratojugal; (qu) quadrate; (spl) splenial; (squ) squamosal; (st) supratemporal; (sur) surangular; (tab) tabular; (vom) vomer.

8. Appendix 1: Character list (See discussion in Clack 2002a, Ruta *et al.* 2003, and Clack & Finney 2005).

1. PREMAX 1. Absence (0) or presence (1) of alary process.
2. PREMAX 3. Alary process less than (0) or at least one-third as wide as premaxillae (1).
3. PREMAX 7. Premaxillae more (0) or less than (1) two-thirds as wide as skull.
4. PREMAX 9. Absence (0) or presence (1) of shelf-like premaxilla-maxilla contact mesial to tooth row on palate.
5. TEC 1. Presence (0) or absence (1) of anterior tectal.
6. LAT ROS 1. Presence (0) or absence (1) of lateral rostral.
7. SPTMAX 1. Absence (0) or presence (1) of septomaxilla.
8. SPTMAX 2. Septomaxilla not a detached ossification inside nostril (0); detached (1).
9. NAS 1. Absence (0) or presence (1) of paired dorsal nasals.
10. NAS 2. Nasals more (0) or less than (1) one-third as long as frontals.
11. NAS 5. Absence (0) or presence (1) of condition: nasals broad plates delimiting most of nostril posterodorsal and mesial margins, with lateral margins diverging abruptly anteriorly.
12. NAS 6. Parietal/nasal length ratio less than (0) or greater than 1.45 (1).
13. PREFRO 2. Prefrontal less than (0) or more than (1) three times longer than wide.
14. PREFRO 6. Prefrontal not sutured with premaxilla (0) or sutured (1).
15. PREFRO 7. Prefrontal without (0) or with (1) stout, lateral outgrowth.
16. PREFRO 8. Absence (0) or presence (1) of condition: prefrontal entering nostril margin.
17. PREFRO 9. Prefrontal not sutured with maxilla (0) or sutured (1).
18. LAC 2. Lacrimal not allowing (0) or allowing (1) contact between prefrontal and jugal.
19. LAC 4. Lacrimal without (0) or with (1) dorsomesial digitiform process.
20. LAC 5. Lacrimal without (0) or with (1) V-shaped emargination along posterior margin.
21. LAC 6. Absence (0) or presence (1) of condition: portion of lacrimal lying anteroventral to orbit abbreviated.
22. LAC 7 (new). Total length of lacrimal less than (0) or more than (1) two and a quarter times its maximum preorbital depth.
23. MAX 3. Maxilla extending behind level of posterior margin of orbit (0); terminating anterior to it (1).
24. MAX 5. Maxilla not entering (0) or entering (1) orbit margin.
25. FRO 1. Frontal unpaired (0) or paired (1).
26. FRO 2. Frontal shorter than (0), longer than (1), or subequal to (2) parietals.
27. FRO 6. Absence (0) or presence (1) of condition: anterior margin of frontals deeply wedged between posterolateral margins of nasals.
28. PAR 1. Absence (0) or presence (1) of parietal/tabular suture.
29. PAR 2. Absence (0) or presence (1) of parietal/postorbital suture.
30. PAR 4. Anterior margin of parietal lying in front of (0), level with (1), or behind (2) orbit midlength.
31. PAR 5. Anteriormost third of parietals not wider than frontals (0); at least marginally wider (1).
32. PAR 6. Parietals more than two and a half times as long as wide (0) or less (1).
33. PAR 8. Parietal–frontal suture not strongly interdigitating (0); strongly interdigitating (1).
34. PAR 9. Parietal–postparietal suture not strongly interdigitating (0); strongly interdigitating (1).
35. POSPAR 2. Postparietals paired (0) or unpaired (1).
36. POSPAR 3. Postparietal less than (0) or more than (1) four times wider than long.
37. POSPAR 4. Postparietals without (0) or with (1) median lappets.
38. POSPAR 5. Absence (0) or presence (1) of postparietal/exoccipital suture.
39. POSPAR 10. Nasals not smaller than postparietals (0) or smaller (1).
40. POSFRO 3. Postfrontal not contacting tabular (0) or contacting it (1).
41. POSFRO 4. Absence (0) or presence (1) of condition: posterior margin of postfrontal lying flush with posterior jugal margin.
42. INTEMP 1. Intertemporal present (0) or absent (1) as a separate ossification.
43. INTEMP 2. Intertemporal not interdigitating with cheek (0) or interdigitating (1).

44. INTEMP 3. Intertemporal not contacting squamosal (0) or contacting it (1).

45. INTEMP 4 (new). Absence (0) or presence (1) of condition: intertemporal shaped like a small, subquadrangular bone, less than half as broad as the supratemporal.

46. SUTEMP 1. Presence (0) or absence (1) of supratemporal.

47. SUTEMP 2. Absence (0) or presence (1) of condition: supratemoral forming anterior edge of temporal notch.

48. SUTEMP 3. Absence (0) or presence (1) of condition: supratemoral narrow and strap-like, at least three times as long as wide.

49. SUTEMP 4. Supratemporal contact with squamosal smooth (0) or interdigitating (1).

50. TAB 1. Tabular present (0) or absent (1) as separate ossification.

51. TAB 2. Absence (0) or presence (1) of subdermal, blade-like postero-lateral tabular horn.

52. TAB 3. Absence (0) or presence (1) of rounded, subdermal, button-like posterior process of tabular.

53. TAB 4. Tabular contacts squamosal on dorsal surface of skull table (0) or not (1).

54. TAB 5. Tabular contact with squamosal smooth (0) or interdigitating (1).

55. TAB 7. Parietal–parietal width smaller than (0) or greater than (1) distance between posterior margin of skull table and posterior margin of orbits measured along the skull midline.

56. POSORB 2. Postorbital without (0) or with (1) ventrolateral digitiform process fitting into deep vertical jugal groove.

57. POSORB 3. Postorbital contributing to (0) or excluded from (1) margin of orbit.

58. POSORB 4. Postorbital irregularly polygonal (0) or broadly crescentic and narrowing to a posterior point (1).

59. POSORB 5. Postorbital not contacting tabular (0) or contacting it (1).

60. POSORB 6. Postorbital not wider than orbit (0) or wider (1).

61. POSORB 7. Absence (0) or presence (1) of condition: postorbital at least one quarter the width of the skull table at the same transverse level.

62. POSORB 8. Anteriormost part of dorsal margin of postorbital with sigmoid profile absent (0) or present.

63. SQU 1. Anterior part of squamosal lying behind (0) or in front (1) of parietal midlength.

64. SQU 3. Squamosal without (0) or with (1) broad, concave semicircular embayment.

65. SQU 4. Absence (0) or presence (1) of 'squamosotabular' in place of squamosal and tabular.

66. JUG 2. Jugal not contributing (0) or contributing (1) to ventral margin of skull roof.

67. JUG 3. Jugal not contacting (0) or contacting (1) pterygoid.

68. JUG 4. Jugal depth below orbit greater (0) or smaller (1) than half orbit diameter.

69. JUG 7. Jugal without (0) or with (1) V-shaped indentation of dorsal margin.

70. JUG 8. Jugal not extending (0) or extending (1) anterior to anterior orbit margin.

71. QUAJUG 2. Absence (0) or presence (1) of condition: quadratojugal much smaller than squamosal.

72. QUAJUG 3. Absence (0) or presence (1) of condition: quadratojugal an anteroposteriorly elongate and dorsoventrally narrow splinter of bone.

73. QUA 1. Quadrate without (0) or with (1) dorsal process.

74. PREOPE 1. Absence (1) or presence (0) of preopercular.

75. INT FEN 1. Absence (0) or presence (1) of internarial fenestra.

76. ORB 1. Interorbital distance greater than (0), smaller than (1), or subequal to (2) half skull table width.

77. ORB 2. Interorbital distance greater than (0), smaller than (1) or subequal to (2) maximum orbit diameter.

78. ORB 3. Absence (0) or presence (1) of angle at anteroventral orbit corner.

79. ORB 4 (new). Absence (0) or presence (1) of condition: in lateral view, orbit deeper than long.

80. PIN FOR 2. Position of pineal foramen behind (0), at the level of (1) or anterior to (2) interparietal suture mid length.

81. PTF 1. Fossa at dorsolateral corner of occiput, not bordered laterally, roofed over by skull table and floored by dorsolateral extension of opisthotic (0); fossa near dorsolateral corner of occiput, roofed over by occipital flanges of tabular and postparietal and bordered laterally and ventrally by dorsolateral extension of opisthotic meeting ventromedial flange of tabular (1); small fossa near ventrolateral corner of occiput bordered laterally by ventromedial flange of tabular, roofed over by dorsal portion of lateral margin of supraoccipital-opisthotic complex and floored by lateral extension of opisthotic (2); absence of fossa (3).

82. SKU TAB 1. Absence (0) or presence (1) of abbreviated skull roof postorbital region.

83. SC 1. Lateral line system on skull roof totally enclosed (0); mostly enclosed with short sections in grooves (1); mostly in grooves with short sections enclosed (2); entirely in grooves (3); absent (4).

84. SC 2. Mandibular canal totally enclosed (0); mostly enclosed, short sections in grooves (1); mostly in grooves, short sections enclosed (2); entirely in grooves (3); absent (4).

85. VOM 1. Absence (0) or presence (1) of condition: ventral, exposed surface of vomers (i.e. excluding areas of overlap with surrounding bones) narrow, elongate, and strip-like, without extensions anterolateral or posterolateral to choana and two and a half to three times longer than wide.

86. VOM 4. Vomer without (0) or with (1) denticles.

87. VOM 5. Vomer excluded from (0) or contributing to (1) interpterygoid vacuities.

88. VOM 7. Vomer not forming (0) or forming (1) suture with maxilla anterior to choana.

89. VOM 8. Vomer with (0) or without (1) toothed lateral crest.

90. VOM 9. Vomer with (0) or without (1) anterior crest.

91. PAL 1. Palatine with (0) or without (1) fangs.

92. PAL 2. Palatine without (0) or with (1) denticles.

93. PAL 4. Palatine with (0) or without (1) tooth row (3+).

94. ECT 2. Ectopterygoid with (0) or without (1) fangs.

95. ECT 3. Ectopterygoid without (0) or with (1) denticles.

96. ECT 4. Ectopterygoid longer than/as long as palatines (0) or not (1).

97. ECT 5. Ectopterygoid with (0) or without (1) tooth row (3+).

98. PTE 3. Absence (0) or presence (1) of pterygoid flange oriented transversely.

99. PTE 9. Pterygoid without (0) or with (1) posterolateral flange.

100. PTE 10. Pterygoids not sutured with each other (0) or sutured (1).

101. PTE 13. Pterygoid without (0) or with (1) distinct, mesially directed process for the basipterygoid recess.

102. PTE 16. Palatal ramus of pterygoid without (0) or with (1) distinct, anterior, unornamented digitiform process.

103. INT VAC 1. Presence (0) or absence (1) of interpterygoid vacuities.

104. INT VAC 2. Absence (0) or presence (1) of condition: interpterygoid vacuities occupying at least half of palatal width.

105. INT VAC 3. Absence (0) or presence (1) of condition: interpterygoid vacuities concave along their whole margins.

106. INT VAC 4. Absence (0) or presence (1) of condition: interpterygoid vacuities together broader than long.

107. ANT VAC 1. Presence (0) or absence (1) of anterior palatal vacuity.

108. ANT VAC 2. Anterior palatal vacuity single (0) or double (1).

109. SUPOCC 1. Supraoccipital absent (0) or present (1) as separate ossification.

110. EXOCC 3. Absence (0) or presence (1) of condition: exoccipitals enlarged, about as broad as high and forming stout, double occipital condyles.

111. EXOCC 4. Absence (0) or presence (1) of condition: exoccipitals forming continuous, concave, strap-shaped articular surfaces with basioccipital.

112. BASOCC 1. Basioccipital notochordal (0) or not (1).

113. BASOCC 6. Absence (0) or presence (1) of condition: basioccipital circular and recessed.

114. OPI 2. Absence (0) or presence (1) of condition: opisthotic forming thick plate with supraoccipital, separating exoccipitals from skull table.

115. PASPHE 1. Parasphenoid without (0) or with (1) elongate, strut-like cultriform process.

116. PASPHE 3. Parasphenoid without (0) or with (1) posterolaterally directed, ventral thickenings (ridges ending in basal tubera).

117. PASPHE 6. Parasphenoid without (0) or with (1) single median depression.

118. PASPHE 7. Parasphenoid without (0) or with (1) paired lateral depressions.

119. PASPHE 9. Ventral cranial fissure not sutured (0); sutured but traceable (1); absent (2).

120. PASPHE 12. Parasphenoid without (0) or with (1) triangular denticle patch with raised margins at base of cultriform process.

121. JAW ART 1. Jaw articulation lying behind (0), level with (1) or anterior to (2) occiput.

122. PSYM 1. Presence (0) or absence (1) of parasymphysial plate.

123. PSYM 2. Parasymphysial plate without (0) or with (1) paired fangs.

124. PSYM 3. Parasymphysial plate without (0) or with (1) tooth row.

125. PSYM 4. Parasymphysial plate with (0) or without (1) denticles.

126. DEN 2. Dentary with (0) or without (1) anterior fang pair.

127. DEN 3. Dentary with (1) or without (0) chamfered ventral margin.

128. DEN 4. Dentary without (0) or with (1) U-shaped notch for premaxillary tusks.

129. SPL 2. Absence (0) or presence (1) of condition: rearmost extension of mesial lamina of splenial closer to anterior margin of adductor fossa than to anterior end of jaw.

130. SPL 3. Absence (0) or presence (1) of suture between splenial and anterior coronoid.

131. SPL 4. Absence (0) or presence (1) of suture between splenial and middle coronoid.

132. POSPL 2. Postsplenial without (0) or with (1) mesial lamina.

133. POSPL 3. Postsplenial with (0) or without (1) pit line.

134. ANG 2. Angular without (0) or with (1) mesial lamina.

135. ANG 3. Angular contacting prearticular (0) or not (1).

136. ANG 4. Angular not reaching (0) or reaching (1) posterior end of lower jaw.

137. SURANG 3. Surangular with (0) or without (1) pit line.

138. PREART 5. Prearticular sutured with splenial (0) or not (1).

139. ANT COR 2. Anterior coronoid with (0) or without (1) fangs.

140. ANT COR 3. Anterior coronoid with (0) or without (1) denticles.

141. ANT COR 4. Anterior coronoid with (0) or without (1) tooth row.

142. MID COR 1. Middle coronoid present (0) or absent (1).

143. MID COR 2. Middle coronoid with (0) or without (1) fangs.

144. MID COR 3. Middle coronoid with (0) or without (1) denticles.

145. MID COR 4. Middle coronoid with (0) or without (1) marginal tooth row.

146. POST COR 2. Posterior coronoid with (0) or without (1) fangs.

147. POST COR 3. Posterior coronoid with (0) or without (1) denticles.

148. POST COR 4. Posterior coronoid with (0) or without (1) tooth row.

149. POST COR 5. Posterior coronoid without (0) or with (1) posterodorsal process.

150. POST COR 6. Posterior coronoid not exposed (0) or exposed (1) in lateral view.

151. POST COR 7. Posterodorsal process of posterior coronoid not contributing (0) or contributing (1) to tallest point of lateral margin of adductor fossa ('surangular' crest).

152. ADD FOS 1. Adductor fossa facing dorsally (0) or mesially (1).

153. TEETH 5. Dentary teeth not larger (0) or larger (1) than maxillary teeth.

154. TEETH 6. Marginal tooth crowns not chisel-tipped (0) or chisel-tipped (1).

155. TEETH 7. Marginal tooth crowns without (0) or with (1) dimple.

156. CLE 2. Cleithrum with (0) or without (1) postbranchial lamina.

157. CLE 3. Cleithrum co-ossified with (0) or separate from (1) scapulocoracoid.

158. CLA 3. Clavicles meet anteriorly (0) or not (1).

159. INTCLA 1. Absence (0) or presence (1) of condition: posterior margin of interclavicle drawn out into parasternal process.

160. INTCLA 2. Absence (0) or presence (1) of condition: parasternal process elongate and parallel-sided for most of its length.

161. INTCLA 3. Absence (0) or presence (1) of condition: interclavicle wider than long.

162. INTCLA 4. Interclavicle rhomboidal with posterior half longer (0) or shorter (1) than anterior half.

163. SCACOR 1. Absence (0) or presence (1) of separate scapular ossifications.

164. SCACOR 2. Glenoid subterminal (0) or not (1) (scapulocoracoid extending ventral to posteroventral margin of glenoid).

165. SCACOR 3. Presence (0) or absence (1) of enlarged glenoid foramen.

166. SCACOR 4. Absence (0) or presence (1) of ventromesially extended infraglenoid buttress.

167. ANOCLE 1. Presence (0) or absence (1) of anocleithrum.

168. HUM 1. Latissimus dorsi process offset anteriorly (0) or aligned with ectepicondyle (1).

169. HUM 2. Absence (0) or presence (1) of distinct supinator process projecting anteriorly.

170. HUM 3.   Presence (0) or absence (1) of ventral humeral ridge.

171. HUM 4.   Latissimus dorsi process confluent with (0) or distinct from (1) deltopectoral crest.

172. HUM 5.   Presence (0) or absence (1) of entepicondylar foramen.

173. HUM 6.   Presence (0) or absence (1) of ectepicondylar foramen.

174. HUM 7.   Presence (0) or absence (1) of distinct ectepicondyle.

175. HUM 8.   Absence (0) or presence (1) of condition: ectepicondylar ridge extending distally to reach distal humeral end.

176. HUM 9.   Distal extremity of ectepicondylar ridge aligned with ulnar condyle (0), between ulnar and radial condyles (1), or aligned with radial condyle (2).

177. HUM 10.   Humerus without (0) or with (1) expanded extremities (waisted).

178. HUM 11.   Radial condyle terminal (0) or ventral (1).

179. HUM 13.   Posterolateral margin of entepicondyle lying distal with respect to plane of radial-ulnar facets (0) or not (1).

180. HUM 14.   Posterolateral margin of entepicondyle markedly concave (0) or not (1).

181. HUM 15.   Width of entepicondyle greater (0) or smaller (1) than half humeral length.

182. HUM 16.   Portion of humeral shaft length proximal to entepicondyle smaller (0) or greater (1) than humeral head width.

183. HUM 17.   Presence (0) or absence (1) of accessory foramina on humerus.

184. HUM 18.   Humerus length greater (0) or smaller (1) than the length of two and a half mid-trunk vertebrae.

185. RAD 1.   Radius longer (0) or shorter (1) than humerus.

186. RAD 2.   Radius longer than (0), as long as (1), or shorter than (2) ulna.

187. ULNA 1.   Absence (0) or presence (1) of olecranon process.

188. ILI 3.   Absence (0) or presence (1) of dorsal iliac process.

189 ILI 6.   Supraacetabular iliac buttress less (0) or more (1) prominent than postacetabular buttress.

190. ILI 7.   Absence (0) or presence (1) of transverse pelvic ridge.

191. ILI 10.   Acetabulum directed posteriorly (0) or laterally (1).

192. ISC 1.   Ischium not contributing (0) or contributing (1) to pelvic symphysis.

193. FEM 1.   Absence (0) or presence (1) of distinct process on internal trochanter.

194. FEM 2.   Absence (0) or presence (1) of condition: internal trochanter separated from femur by distinct trough-like space.

195. FEM 3.   Absence (0) or presence (1) of distinct rugose area on fourth trochanter.

196. FEM 4.   Proximal end of adductor crest of femur not reaching (0) or reaching (1) midshaft length.

197. FEM 5.   Femur shorter than (0), as long as (1), or longer than humerus (2).

198. TIB 7.   Without (0) or with (1) flange on posterior edge.

199. FIB 1.   Fibula not waisted (0) or waisted (1).

200. FIB 3.   Absence (0) or presence (1) of ridge near posterior edge of fibula flexor surface.

201. FIB 4.   Absence (0) or presence (1) of rows of tubercles near posterior edge of flexor surface of fibula.

202. TAR 1.   Absence (0) or presence (1) of ossified tarsus.

203. TAR 2.   Absence (0) or presence (1) of one proximal tarsal ossification, or presence of more than two ossifications (2).

204. TAR 3.   Tarsus without (0) or with (1) L-shaped proximal tarsal element.

205. TAR 4.   Absence (0) or presence (1) of distal tarsals between fibulare and digits.

206. TAR 5.   Absence (0) or presence (1) of distal tarsals between tibiale and digits.

207. RIB 2.   Cervical ribs with (0) or without (1) flattened distal ends.

208. RIB 3.   Ribs mostly straight (0) or ventrally curved (1) in at least part of the trunk.

209. RIB 5.   Absence (0) or presence (1) of triangular spur-like posterodorsal process in at least some trunk ribs.

210. RIB 6.   Absence (0) or presence (1) of condition: elongate posterodorsal flange in midtrunk ribs.

211. CER VER 3.   Axial arch not fused (0) or fused (1) to axial (pleuro)centrum.

212. TRU VER 1.   Absence (0) or presence (1) of extra articulations above zygapophyses in at least some trunk and caudal vertebrae.

213. TRU VER 2.   Absence (0) or presence (1) of condition: neural and haemal spines rectangular to fan-shaped in lateral view.

214. TRU VER 3.   Absence (0) or presence (1) of condition: neural and haemal spines facing each other dorsoventrally.

215. TRU VER 4.   Haemal spines not fused (0) or fused (1) to caudal centra.

216. TRU VER 5.   Absence (0) or presence (1) of extra articulations on haemal spines.

217. TRU VER 7.   Absence (0) or presence (1) of ossified pleurocentra.

218. TRU VER 8.   Trunk pleurocentra not fused midventrally (0) or fused (1).

219. TRU VER 9.   Trunk pleurocentra not fused middorsally (0) or fused (1).

220. TRU VER 10.   Neural spines without (0) or with (1) distinct convex lateral surfaces.

221. TRU VER 11.   Neural spines of trunk vertebrae not fused to centra (0) or fused (1).

222. TRU VER 13.   Presence (0) or absence (1) of trunk intercentra.

223. TRU VER 14.   Trunk intercentra not fused middorsally (0) or fused (1).

224. TRU VER 15.   Absence (0) or presence (1) of lateral and ventral carinae on trunk centra.

225. TRU VER 19.   Absence (0) or presence (1) of condition: tallest ossified part of neural arch of posterior trunk vertebrae lying above posterior half of vertebral centrum.

226. TRU VER 20.   Absence (0) or presence (1) of prezygapophyses on trunk vertebrae.

227. TRU VER 21.   Absence (0) or presence (1) of postzygapophyses on trunk vertebrae.

228. TRU VER 22.   Absence (0) or presence (1) of prezygapophyses on proximal tail vertebrae.

229. TRU VER 23.   Absence (0) or presence (1) of postzygapophyses on proximal tail vertebrae.

230. TRU VER 24.   Absence (0) or presence (1) of prezygapophyses on distal tail vertebrae.

231. TRU VER 25.   Absence (0) or presence (1) of postzygapophyses on distal tail vertebrae.

232. TRU VER 26.   Absence (0) or presence (1) of capitular facets on posterior rim of vertebral midtrunk centra.

233. TRU VER 27.   Height of neural arch in midtrunk vertebrae greater (0) or smaller (1) than distance between pre- and postzygapophyses.

234. DIG 1.   Absence (0) or presence (1) of digits.

235. DIG 2.   Absence (0) or presence (1) of no more than four digits in manus.

236. DIG 3.   Absence (0) or presence (1) of no more than five digits in manus.

237. DIG 4. Absence (0) or presence (1) of no more than three digits in manus.

238. DOR FIN 1. Presence (0) or absence (1) of dorsal fin.

239. CAU FIN 1. Presence (0) or absence (1) of caudal fin.

240. BAS SCU 1. Presence (0) or absence (1) of basal scutes.

241. Anterior tectal: narial opening ventral to it (0); narial opening anterior to it (1).

242. Basioccipital: indistinguishable from exoccipitals (0); separated by suture (1).

243. Basioccipital: ventrally exposed portion longer than wide (0); shorter than wide (1).

244. Lacrimal contributes to narial margin: no, excluded by anterior tectal (0); yes (1); no, excluded by nasal/maxillary or prefrontal/maxillary suture (2).

245. Maxilla external contact with premaxilla: narrow contact point not interdigitated (0); interdigitating suture (1).

246. Median rostral (=internasal): mosaic (0); paired (1); single (2); absent (3).

247. Nasals contribute to narial margin: no (0); yes (1).

248. Opisthotic paroccipital process ossified and contacts tabular below post-temporal fossa: no (0); yes (1); post-temporal fossa absent (2).

249. Postparietal occipital flange exposure: absent (0); present (1).

250. Prefrontal/postfrontal suture: anterior half of orbit (0); middle or posterior half of orbit (1); absent (2).

251. Premaxilla forms part of choanal margin: broadly (0); point (1); excluded by vomer (2).

252. Squamosal suture with supratemporal position: at apex of temporal embayment (0); dorsal to apex (1); ventral to apex (2).

253. Tabular emarginated lateral margin: no (0); yes (1).

254. Tabular facets/buttresses for braincase ventrally: no (0); single (1); double (2).

255. Tabular occipital flange exposure: absent (0); extends as far ventrally as does postparietal (1); extends further ventrally than does postparietal (2).

256. Ectopterygoid reaches adductor fossa: no (0); yes (1).

257. Palatine/ectopterygoid exposure: more or less confined to tooth row (0); broad mesial exposure additional to tooth row (1).

258. Pterygoids flank parasphenoid: for most of length of cultriform process (0); not so (1).

259. Pterygoid junction with squamosal along cheek margin: unsutured (0); half and half (1); sutured entirely (2).

260. Parasphenoid wings: separate (0); joined by web of bone (1).

261. Parasphenoid sutures to vomers: yes (0); no (1).

262. Parasphenoid carotid grooves: curve round basipterygoid process (0); lie posteromedial to basipterygoid process (1).

263. Vomers separated by parasphenoid for more than half length: yes (0); no (1).

264. Vomers separated by pterygoids: for more than half length (0); for less than half length (1); not separated (2).

265. Ectopterygoid denticle row: present (0); absent (1).

266. Maxilla tooth number: more than 40 (0); 30–40 (1); less than 30 (2).

267. Maxillary caniniform teeth (about twice the size of neighbouring teeth): absent (0); present (1).

268. Palatine row of smaller teeth: present (0); absent (1).

269. Palatine denticle row: present (0); absent (1).

270. Parasphenoid shagreen field: present (0); absent (1).

271. Parasphenoid shagreen field location: anterior and posterior to basal articulation (0); posterior to basal articulation only (1); anterior to basal articulation only (2).

272. Pterygoid shagreen: dense (0); a few discontinuous patches or absent (1).

273. Prearticular denticulated field: defined edges (0); scattered patches (1); absent (2).

274. Premaxillary teeth with conspicuous peak: absent (0); present (1).

275. Vomer fang pairs: present (0); absent (1).

276. Vomerine fang pairs noticeably smaller than other palatal fang pairs: no (0); yes (1).

277. Vomerine row of small teeth: present (0); absent (1).

278. Vomerine shagreen field: absent (0); present (1).

279. Vomerine denticle row lateral to tooth row: present (0); absent (1).

280. Upper marginal teeth number: greater than lower (0); same (1); smaller than lower (2).

281. Oral sulcus of mandibular canal: absent (0); present (1).

282. Meckelian bone visible between prearticular and infradentaries: present (0); absent (1).

283. Naris position: ventral rim closer to jaw margin than height of naris (0); distance to jaw margin similar to or greater than height of naris (1).

284. Naris shape: slit-like (0); round or oval (1); upper margin ragged (2).

285. Naris orientation: ventrally facing (0); dorsolaterally facing (1).

286. Naris size relative to choana: less than 50 per cent (0); same or larger (1).

287. Suspensorium proportions: distance from quadrate to temporal embayment anterior margin about equal to maximum orbit width (discounting any anterior extensions) (0); distance less than maximum orbit width (1); distance more than maximum orbit width (2).

288. Ornament character: fairly regular pit and ridge with star-burst pattern at regions of growth (0); irregular but deep (1); irregular but shallow (2); absent or almost absent (3).

289. Centra: rhachitomous (0); gastrocentrous (1); holospondylous (2).

290. Centrum (sacral): distinguishable by size and shape from pre- and postsacrals (1); not so distinguishable (0).

291. Cleithrum dorsal end: smoothly broadening to spatulate dorsal end (0); distal expansion marked from narrow stem by notch or process or decrease in thickness (1); tapering (2).

292. Cleithrum stem cross section at mid section: flattened oval (0); complex (1); single concave face (2).

293. Femur adductor blade: distinguished distally from shaft by angle or notch (0); fades into shaft distally (1).

294. Humerus shape: ends more or less untorted (0); ends offset by more than 60 degrees (1).

295. Humerus latissimus dorsi process: part of ridge (0); distinct but low process (1); spike (2).

296. Humerus anterior margin: smooth finished bone convex margin (0); anterior keel with finished margin (1); cartilage-finished (2); smooth concave margin (3).

297. Humerus radial and ulnar facets: confluent (0); separated by perichondral strip (1).
298. Neural arch ossification: paired in adult (0); single in adult (1).
299. Neural arch (sacral): distinguishable by spine morphology (1); not so distinguishable (0).
300. Pelvis: single ossification (0); at least two ossifications per side (1).
301. Pelvis obturator foramina: multiple (0); single or absent (1).
302. Ribs (trunk): no longer than height of neural arch plus centrum (0); less than two and a half times this height (1); more than two and a half times this height (2).
303. Ribs (trunk): tapered distally or parallel-sided (0); expanded distally into overlapping posterior flanges (1).
304. Ribs (trunk) bear proximodorsal (uncinate) processes: absent (0); present (1).
305. Ribs (trunk) differ strongly in morphology in 'thoracic' region: absent (0); present (1).
306. Rib (sacral) distinguishable by size: shorter than trunk ribs, longer than presacrals (1); same length as presacrals (0).
307. Rib (sacral) distinguishable by shape: broader than immediate presacrals but not broader than mid-trunk proximal shafts (0); broader than mid-trunk proximal shafts (1).
308. Scapulocoracoid dorsal blade: absent (0); present (1).
309. Scutes: tapered and elongate, four times or greater than four times longer than broad (0); ovoid, no more than three times longer than broad (1).
310. Tibia and fibula width at narrowest point: 50 per cent of length (0); less than 30 per cent of length (1).
311. Tibia and fibula meeting along their length (0); separated by interepipodial space (1).
312. Number of pes digits: more than five (0); five (1); fewer than five (2).
313. Posterior process of ilum a slender, subhorizontal rod, with parallel dorsal and ventral margins, more than five times longer than deep: absent (0); present (1).
314. Process '2' of humerus: absent (0); present (1).

9. Appendix 2: Data matrix

Characters are subdivided into groups of 10, and numbered from left to right; '?' denotes unknown or inapplicable characters; alternative states within ( ) brackets imply polymorphism, those within { } imply uncertainty.

Acanthostega gunnari
```
0?00010?10   0000000100   0000120011   1100000000   01???00010   1000000001   1000000001
0000111000   0011000000   0001000001   0000000100   0000000010   0011001000   0010101011
0011011000   ?000000110   0000100000   0000100011   0001100100   1111101001   0100000000
0000001000   0000011110   0001000101   0000010000   100001000?   1010000001   ?001000002
010000200?   0000101000   0000010000   0001
```

Adelogyrinus simorhynchus
```
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0001?12000   ?0?3??????   ??????????   ?????????0   011???????   1????100??   ?01??11???
??????????   ??01111?0?   01????1???   ??????????   ??????????   ??????????   ???????111
?0????111?   01?1?11???   ?10????1??   ????2?31?11   ?????11001   1???110011?   ?0??1?0??1
0?????1120   ??????10?   ?0010??0?   ????
```

Anthracosaurus russelli
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??????????   ??????????   ??????????   ?111131210   0112210012   1?1?120?1?   ?1201?1010
0?0211222?   ??????????   ??????????   ????
```

Archeria crassidisca
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1010110111   0101011111   0000011100   1010120011   0111121111   1110112011   0121110100
0000001110   0010011111   1001010111   ?111031210   ?11?2000?1   ?0??100?11   ?021?????1
11021?0(01)11   1210110101   1200011?1   1101
```

Ariekanerpeton sigalovi
```
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1010110110   1100011011   101?0???01   1010121011   0011110??1   11????2?1?   ?????0100
?0000011(01)1   0000011???   ?001010111   ?111131{01}11   0101211021   10?0120111   ?020001112
?101101(12)1?   22?11300?1   1100011111   1100
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Balanerpeton woodi
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0001011002   ?144011011   0110101010   0001111??0   010?100020   01???00001   0111001110
11???101??   ?110011110?   000???1?01   ?011??1011   0011111010   1111?02010   0120110000
0000001000   000011111?   ?001100111   ??211?31?01   1010011112?   0112100110   10200?1110
0111111000   1?01?3?101   ?000010111   1100
```

Baphetes kirkbyi
```
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?00000????   ?00???????   ?????????1   1?11011100   1211211021   1012110110   0020001110
010111200?   11?1220??1   ??1?????01   1??0
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??111??{23}1?   {12}21010?00?   ?2000??111   11??

Caerorhachis bairdi
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0000001100   0000011111   1001???111   ????031??1   ?01?0????   1?11100110   100?011111
01?111201?   ??0????1??   ?1000???01   110?

Casineria kiddi
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??????????   ??????????   ??????????   ??????????   ??????????   ??????????   ??????????
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Crassigyrinus scoticus
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01121121??   11101200?1   ?2000???01   1?00

Dendrerpeton acadianum
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Discosauriscus austriacus
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1010110111   1100011011   1010010001   1010121011   00111101?1   1110002010   0?????0000
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2020001112   ?101100010   22111300?1   1100011111   1100

Eoherpeton watsoni
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01?111121?   ??101101?0   1200???1?1   1?01

Eucritta melanolimnetes
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Eusthenopteron foordi
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0000000002   0000000000   0000000000   0000000000   0000000000   1000000000   0000000001
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?00?0??0?   0??0?0?0?0   ?0?????0??   ??00

Gephyrostegus bohemicus
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Greererpeton burkemorani
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0101111000   1100110101   1101001111   1100

Ichthyostega stensioei
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000000000?   00000?11?0   02101??000   0000

Loxomma allmanni
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Megalocephalus pachycephalus
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??????????	??????????	??????????	1112?11100	121?211021	1012110110	0020001110
01011120??	??????????	??????????	????			

Microbrachis pelikani
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1000001110	01?0111111	1111001111	?110?31211	0?0?111101	1010120111	?0201?1110
010110?120	2?11?3?101	?200011??1	1100			

Paleothyris acadiana
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0101101(23)21	??11?30101	1200011101	1100			

Pederpes finneyae
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0000??10?0	0000011???	?001???111	???10?1?10	?21?10?000	??????1010	001?0000??
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Pholiderpeton scutigerum
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1010110111	0101011?1?	??00010??0	?0?01{12}??11	111?121???	??????????	??????0100
?000001110	0010011???	??01?????1	?112031210	?012200010	1011100111	?0201?1011
1102112211	11101?0111	?200011111?	????			

Proterogyrinus scheelei
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010?112210	1?11120101	0200011111	1101			

Ptyonius marshii
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??????????	??0001110?	010??11?0?	?11???0111	1110111070	11????201?	???????100
111111???0	1??0011111	1001100111	???1?311?1	0?0???01?1	1?10120001?	??201?0011
0?1111?320	0??1?3?101	110000??01	1200			

Saxonerpeton geinitzi
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??????????	??00011111	1001??1?01	?011??1111	1111121010	111001(12)010	0120110100
?00?????0	???0111???	?111001?1	?111?31211	0?0?111101	1?10110111	?0?01?1111
??0110?320	2??1?3?101	?200011?1	1100			

Seymouria baylorensis
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0000001111	1000111111	1001010111	?111131111	01??211021	10?0121111	?020001112
0111112011	1?01131111	1100011?1	1100			

Silvanerpeton miripedes
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?0???10100	?1000?1110	000?????0?	?0101?0011	1110120122	11?????2?1?	?120??0100
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??011?1(012)1?	1??0?????1	{12}00011111	1110			

Utegenia shpinari
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?0000001(01)0	0000011111?	?001010111	?111131{01}11	0001111021	10?0120010	
0020001112	?10110121?	22??{12}300?1	11000??110	1100		

Westlothiana lizziae

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Whatcheeria deltae

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MARCELLO RUTA, Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, UK.
e-mail: m.ruta@bristol.ac.uk

JENNIFER A. CLACK, University Museum of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK.
email:j.a.clack@zoo.cam.ac.uk