# The seymouriamorph tetrapod *Ariekanerpeton sigalovi* from the Lower Permian of Tadzhikistan. Part II: Postcranial anatomy and relationships

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ABSTRACT: The postcranial skeleton of *Ariekanerpeton sigalovi* (Seymouriamorpha: Discosauriscidae; Lower Permian, Tadzhikistan) differs from that of like-sized *Discosauriscus* specimens in showing: wider interclavicle anterior plate with smaller, rhomboidal sculptured field on its ventral surface not reaching plate posteromedial margins; broader interclavicle plate-stem junction; slightly narrower interclavicle posterior stem; anteroposteriorly narrower clavicle ventral plate with convex posterior margin; shorter, more robust humerus; four phalanges on fourth manus digit (five phalanges in *Discosauriscus*); ilium more elongate dorsoventrally with anteroposteriorly narrower neck; posterior process of iliac blade oriented distinctly posterodorsally rather than horizontally; more gracile atlantal rib; broadened distal end of second presacral rib. A revised cladistic analysis of the best known seymouriamorph species retrieves *Ariekanerpeton* either as sister group to both species of *Discosauriscus*, or to *D. austriacus* only.

KEY WORDS: *Discosauriscus*, ontogeny, phylogeny, postcranial skeleton, *Utegenia*.

The origin, diversification and interrelationships of amniotes – from their separation from lissamphibians to the origin of their modern (crown group) radiation – are much debated. Despite recent new information from palaeontological and molecular work, our understanding of these events still lags substantially behind that of comparable episodes in vertebrate evolution, e.g. the origins of birds and mammals. In addition, much controversy revolves around the basic anatomy, taxon membership, and intrinsic/extrinsic relationships of the diverse array of pre-amniote (stem amniote) Permo-Carboniferous groups. One of these – the seymouriamorphs – is of particular interest because of its diversity, peculiar geographical and stratigraphic distributions, and amount of ontogenetic data (Milner 1993). There is no agreement on the composition, status and broad phylogenetic position of seymouriamorphs (see Bulanov 2003 for a recent review), and many of its putative members are still poorly understood, despite recent reassessments (for an overview of seymouriamorph anatomy and classification see: Watson 1917, 1954; White 1939; Bystrow 1944; Romer 1966; Carroll 1970; Heaton 1980; Smithson 1985; Panchen & Smithson 1988; Sumida & Lombard 1991; Lombard & Sumida 1992; Sumida *et al.* 1992; Sumida 1997; Laurin 2000; Berman *et al.* 2000).

Seymouriamorphs from Eurasia are usually thought to be represented by immature and/or paedomorphic stages, but this is intensely debated (Ivakhnenko 1981, 1987; Kuznetsov & Ivakhnenko 1981; Laurin 1995, 1996a, b, c, 2000; Klembara 1997; Bulanov 2000, 2002, 2003; Klembara & Bartík 2000; Malakhov 2000; Malakhov & Dujsebayeva 2001; Klembara & Ruta 2004a, b, 2005). Several species are represented by numerous and exceptionally well-preserved specimens that occupy a wide size range. Thus, they provide a unique opportunity to examine ontogenetic modifications (especially in the skull) and to assess the impact of size-related features on the phylogeny of assorted pre-amniote groups. As in the case of other Palaeozoic tetrapods, the broad affinities of

seymouriamorphs are not agreed upon (e.g. Laurin & Reisz 1999; Clack 2002; Ruta *et al.* 2003). Following their previous papers (Klembara & Ruta 2004a, b, 2005), the present authors consider them to be more closely related to amniotes than they are to lissamphibians (Gauthier *et al.* 1988; Panchen & Smithson 1988; Lee & Spencer 1997; Ruta *et al.* 2003).

This paper completes recent reassessments (Klembara & Ruta 2004a, b, 2005) of the anatomy, ontogeny and relationships of the Asiatic seymouriamorphs *Utegenia shpinari* from Kazakhstan and *Ariekanerpeton sigalovi* from Tadzhikistan (see Tatarinov 1968, Ivakhnenko 1981, 1987, Kuznetsov & Ivakhnenko 1981, Laurin 1996a, b, Klembara 1997, and Klembara & Bartík 2000). Revision of the type material and information from numerous additional specimens of both taxa has resulted in the discovery of many new cranial and postcranial characters. These data made it possible to correct inaccuracies of former descriptions, to amend to a considerable degree previous cranial reconstructions, to expand and revise current diagnoses, and to explore the impact of ontogenetic data on discriminating between phylogenetic and size-linked features.

The present work examines the postcranial anatomy of *Ariekanerpeton* and compares it with that of *Discosauriscus austriacus* (Klembara 1997; Klembara & Bartík 2000), the best known of all seymouriamorphs. Klembara & Ruta (2005) redescribed in detail the skull anatomy of *Ariekanerpeton*, provided a revised cranial diagnosis, and examined skull changes during ontogeny.

The present paper focuses mainly on postcranial anatomical features. Characters that have received cursory treatment or have been inadequately illustrated in previous works are dealt with in greater detail, in particular those with diagnostic value among the best known seymouriamorphs, and those for which ontogenetic information is available (for additional information, see Ivakhnenko 1981, 1987 and Laurin 1996b).
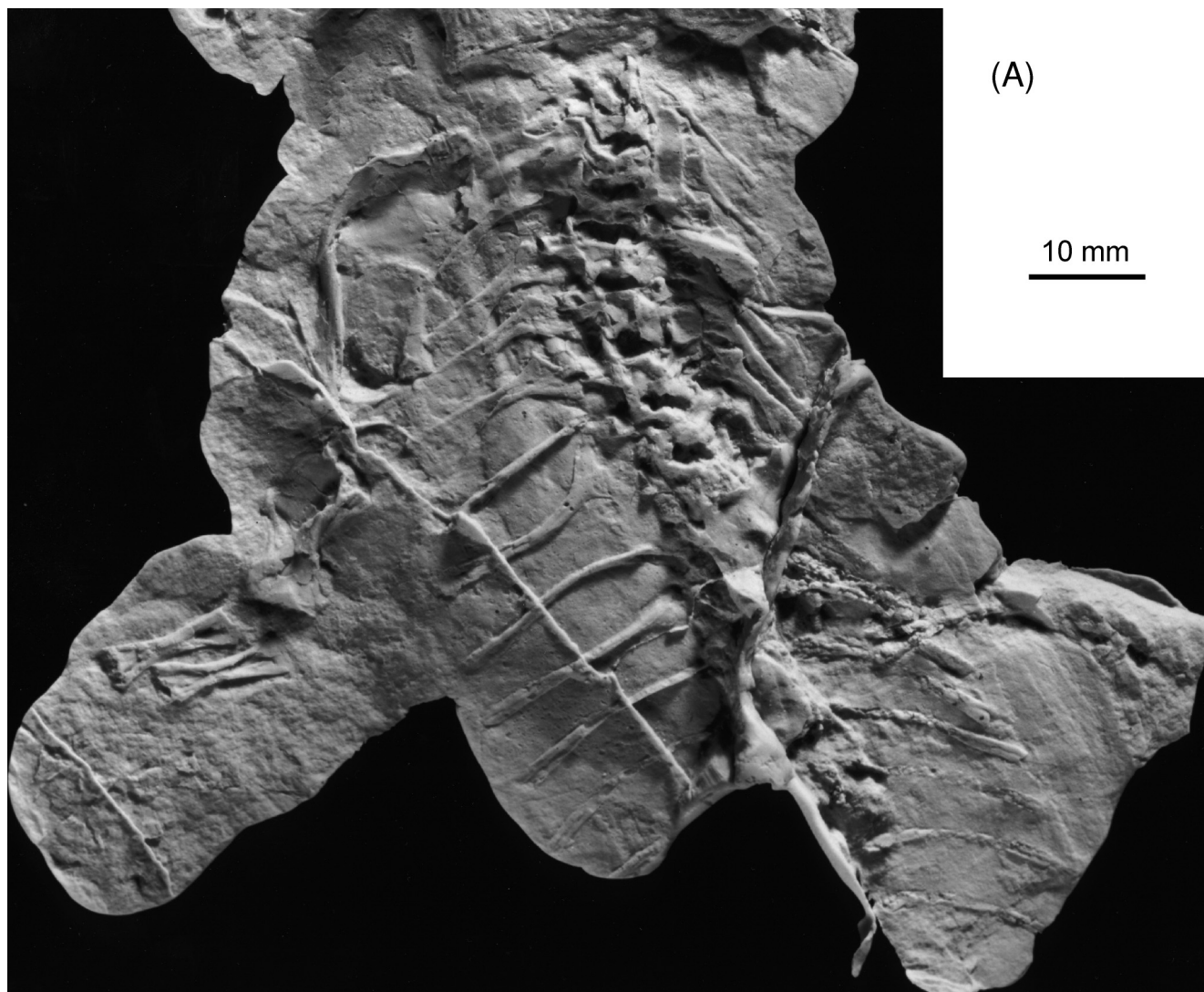
**Figure 1** (A).

## 1. Material and methods

High-fidelity latex casts of acid-etched specimens were photographed under raking light to enhance details of bone surface and texture. Several casts were drawn with a Zeiss dissecting microscope equipped with a camera lucida.

Details of the geological and stratigraphic settings were given by Klembara & Ruta (2005; see also Tatarinov 1968 and Ivakhnenko 1981, 1987).

## 2. Systematic palaeontology

Seymouriamorpha Watson, 1917
Discosauriscidae Romer, 1947
(see revised diagnosis of family by Klembara 2005)
Genus *Ariekanerpeton* Ivakhnenko, 1981
*Ariekanerpeton sigalovi* (Tatarinov, 1968)
Figs 1–9

**Repository.** Palaeontological Institute of the Russian Academy of Sciences in Moscow (PIN). All latex casts used in this study are deposited in the Department of Ecology of Comenius University in Bratislava, and bear the same registration numbers as the original specimens.

**Holotype**. PIN 2079/1, skull and postcranial skeleton in dorsal aspect, both slightly disrupted but almost complete.

**Referred specimens preserving postcranial material**. PIN 2079/262a, b, 509a, 747, 777. PIN 2079/262a, b, the largest specimen available (skull length = 48 mm; Klembara & Ruta 2005), provides additional information on anterior trunk vertebrae and ribs, dermal and endochondral pectoral girdle and humerus.

**Age, type horizon and locality**. Lower Permian of the Sarytaypan locality; Leninabad province, Kuramin Ridge, Adrasman district, Tadzhikistan.

The age of the deposits is assumed to be coeval with the Lower Rotliegend of central Europe, although correlations are uncertain (Laurin 1996b; Ivakhnenko 1981; Berman *et al.* 1997; Klembara & Ruta 2005). We note that classical Lower Rotliegend strata from France and Germany have been redated by Königer *et al.* (2002), who considered them to be latest Carboniferous.

**Revised postcranial diagnosis** (amended and expanded from Ivakhnenko 1981 and Laurin 1996b; see also Klembara & Ruta 2005 for diagnostic cranial characters of *Ariekanerpeton*). A discosauriscid seymouriamorph distinguished from like-sized *Discosauriscus* specimens by the following combination of features: interclavicle anterior plate broader for its length and with comparatively narrower lateral angles; subrhomboidal sculptured field on ventral surface of interclavicle anterior plate smaller, not reaching plate posteromedial margins; interclavicle posterior stem slightly narrower for its length; clavicle
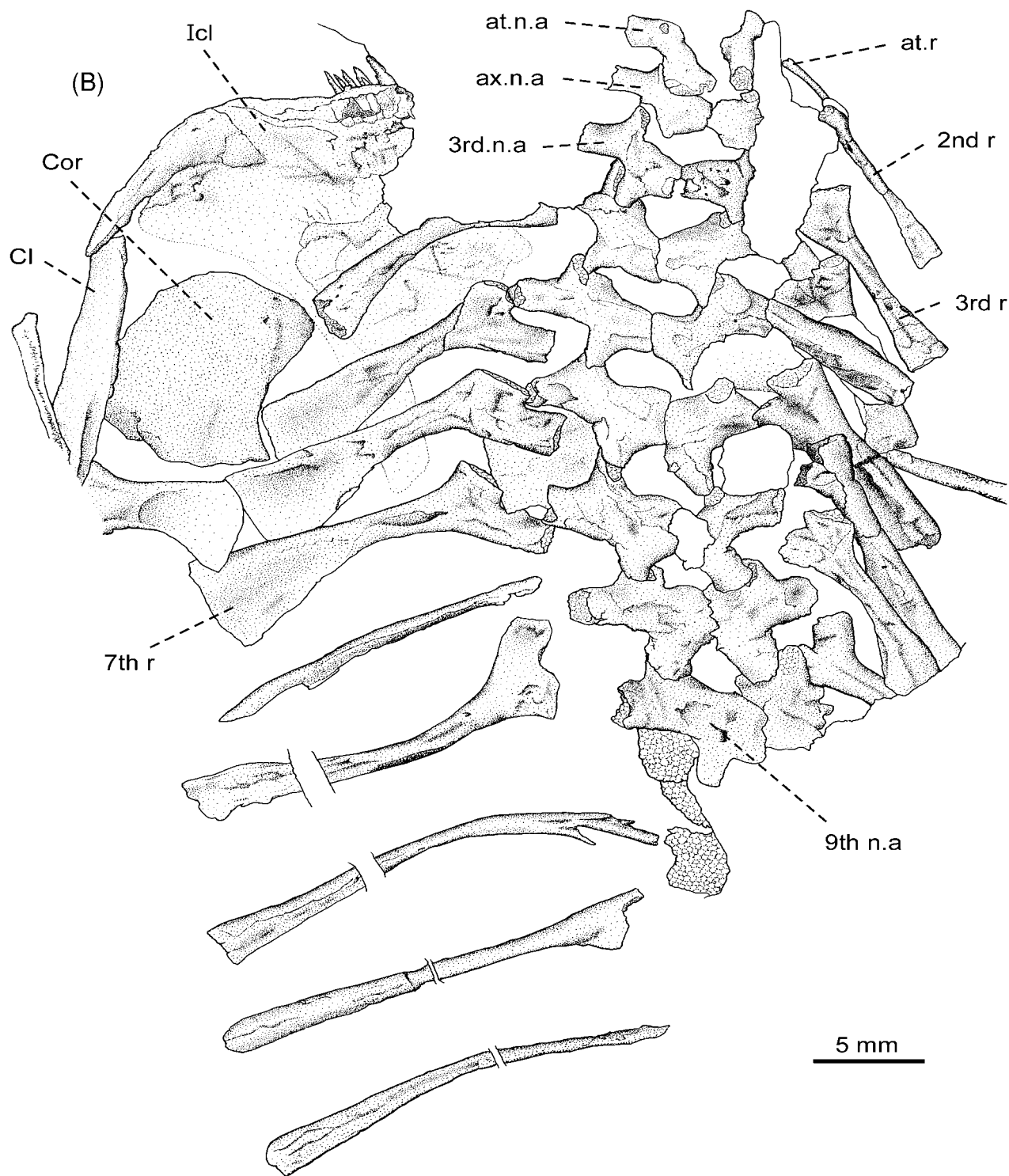
**Figure 1** (B).

**Figure 1** *Ariekanerpeton sigalovi*: (A) PIN 2079/262b, latex cast of anterior half of postcranial skeleton in dorsal view; (B) drawing of the same specimen (left forelimb and posteriormost right ribs have not been figured).

ventral plate anteroposteriorly narrower and with smoothly convex posterior margin; humerus shorter and stouter; four phalanges on fourth manus digit (five phalanges in *Discosauriscus*); ilium more elongate dorsoventrally with neck slightly narrower anteroposteriorly; ilium posterior process oriented distinctly posterodorsally; atlantal rib more gracile and splinter-like; distal extremity of second presacral rib slightly expanded.

**Comments**. A pes-related character, namely presence of four phalanges on fifth digit, has not been included in the diagnosis, because of uncertainty as to its validity (but see comments in

Klembara & Bartík 2000). This is due to conflict between the data reported by Ivakhnenko (1981) and those from one of the specimens figured by Laurin (1996b, fig. 5), namely PIN 2079/509a. The latter is the single most complete (albeit disrupted) specimen showing the full complement of presacral vertebrae, in addition to pectoral and pelvic girdles and limbs. Unfortunately, little more than the backbone and remains of the pectoral and pelvic girdles were available to the present authors. Attempts to retrieve a better cast from PIN or to locate the original specimen proved to be unsuccessful.
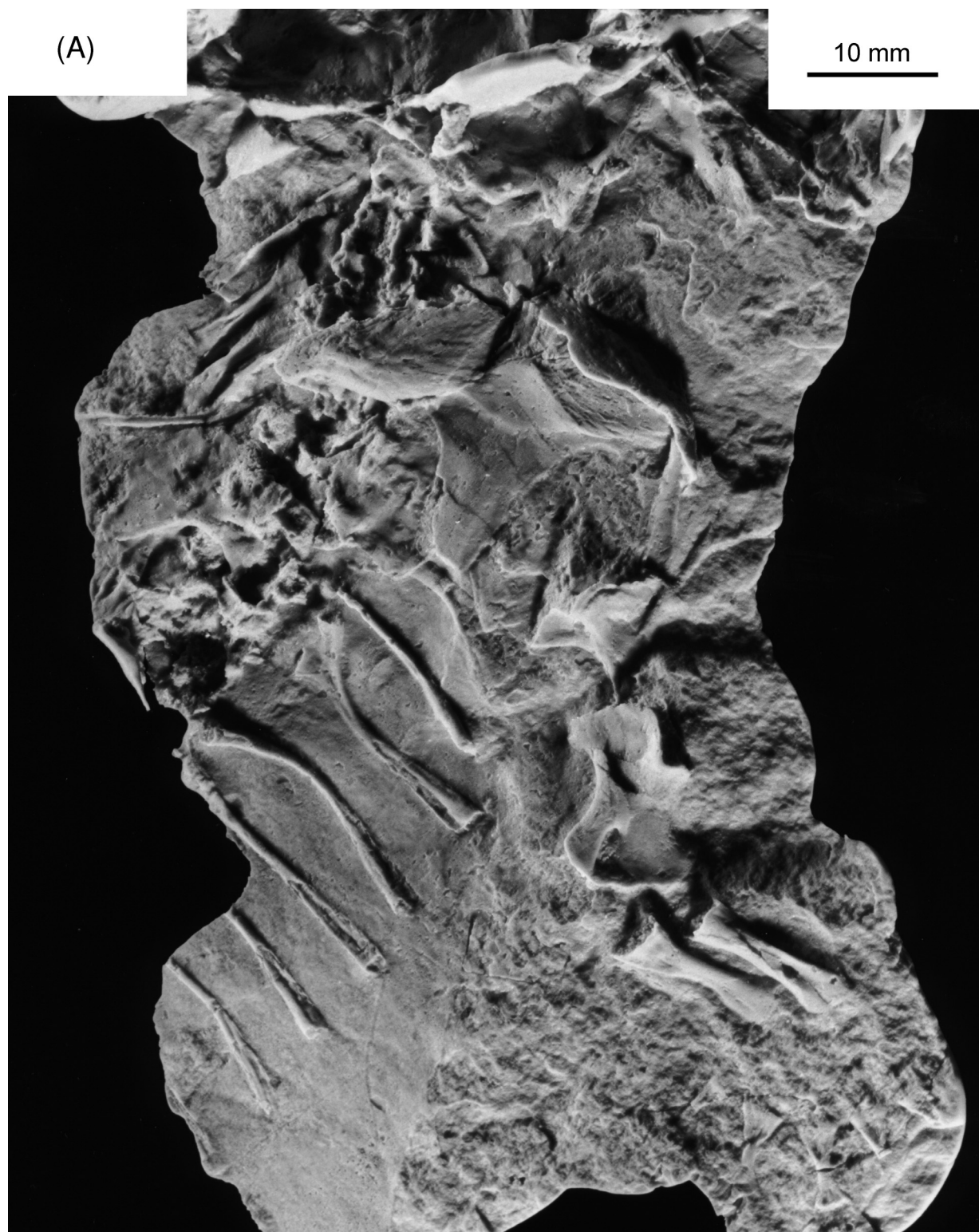
(A)                                                          10 mm



**Figure 2**  (A).

# 3. Description

## 3.1. Pectoral girdle and limb

**3.1.1. Interclavicle**. The interclavicle shape conforms to the pattern of most stem amniote groups (Figs 1–4, 5D), particularly in the presence of a long posterior stem. A long stem also characterises other tetrapods, including *Ichthyostega* (Jarvik 1996), whatcheeriids (Lombard & Bolt 1995; Clack 2002), and microsaurs (Carroll & Gaskill 1978; the latter were regarded as a stem amniote radiation by Ruta *et al.* 2003), although its proportions (e.g. width:length ratio; lateral margins profile and orientation) vary.

In *Ariekanerpeton*, the somewhat arbitrary boundary between plate and stem is marked by a broad flexure along the interclavicle lateral margins. Anterolateral and posterior to this flexure, the margins are straight or gently concave. The plate is wider than long and vaguely subelliptical, with a high width:length ratio. It resembles closely the interclavicles of *Seymouria* and *Discosauriscus*, but differs from the sub-rhomboidal plate of *Utegenia*. Differences are also observed in
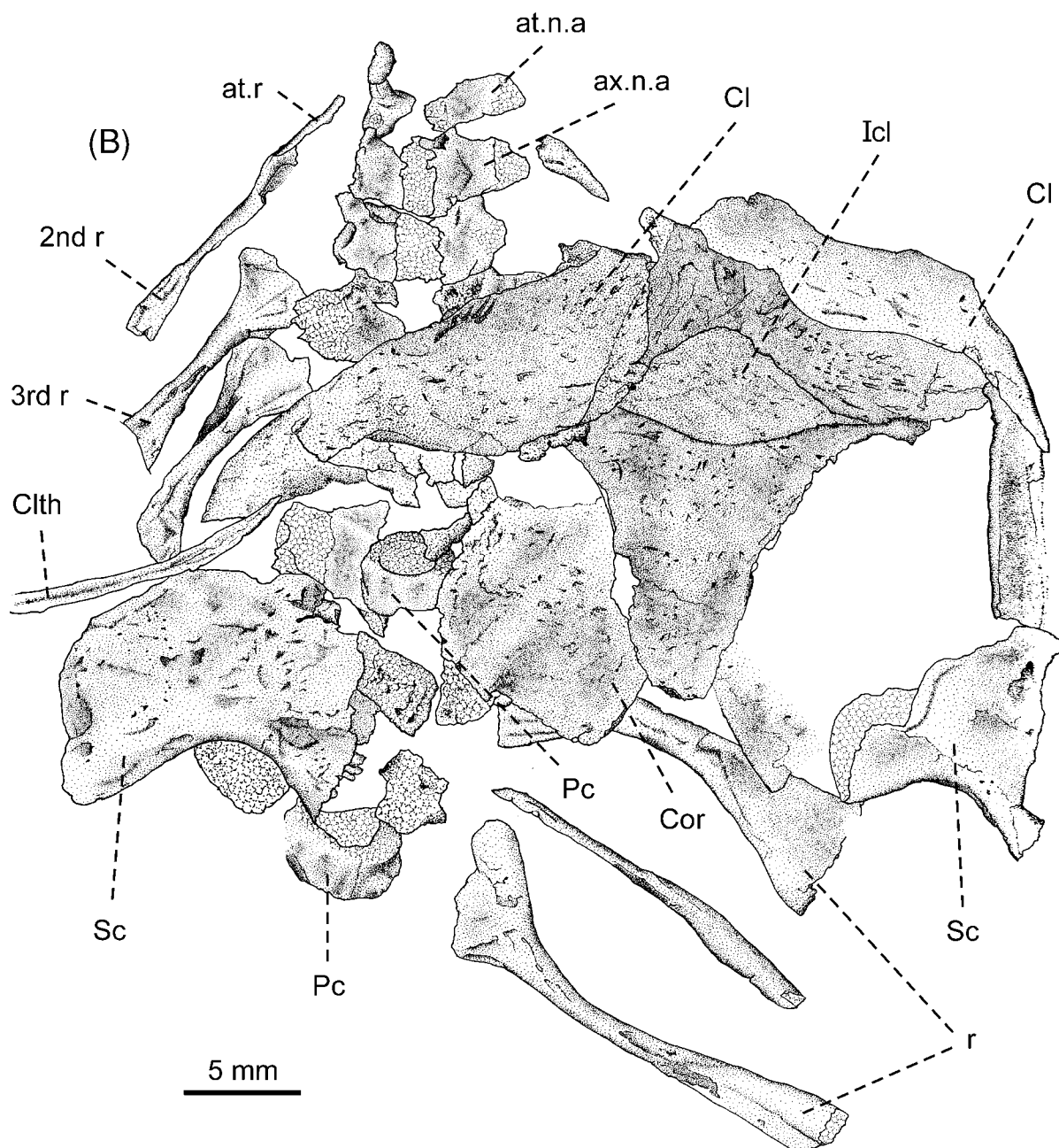
**Figure 2** (B).

**Figure 2** *Ariekanerpeton sigalovi*: (A) PIN 2079/262a, photograph of anterior half of postcranial skeleton in ventral view; (B) drawing of the same specimen (left forelimb and posteriormost right ribs have not been figured).

the orientation of its anterior and anterolateral margins and in the extension of its anterior fringe. It is anterorposteriorly narrower and wider than that of like-sized *D. austriacus* (Fig. 3C, D). Its lateral angles are more acutely triangular rather than bluntly semielliptical, and the curvature of its anterior margin is more gentle (concavity index $\approx 14.3$ per cent as opposed to $27.7$ per cent in *D. austriacus*; such values are calculated using the distance $D$ between the lateral angles of the plate, and the distance $d$ between a line connecting these two angles and the anteriormost point of the plate anterior margin; the $d/D$ ratio, expressed as a percentage, is the concavity index).

The dorsal surface is mostly flat or only slightly depressed in its anterior half. It bulges inconspicuously anterolaterally, but becomes shallower near its lateral angles. The central part of the posterior half of its dorsal surface is gently convex.

Peripherally, this surface bears widely spaced shallow grooves, weak striations, pits, and small foramina. Near the junction with the stem, weak rugosities and scalloped depressions are visible. Some of the peripheral grooves deepen progressively towards the plate anterior margin, where they are intercalated with thin, strip-like ridges. These confer a fringe-like aspect to the anterior margin. The ventral surface is divided into two areas with different ornamentation separated by a broadly reversed V-shaped ridge. The V arms delimit the posterior boundaries of two depressions which accommodate the clavicular plates. Posterior to the V-shaped ridge is a central, subrhomboidal and slightly thickened area covered in pits, shallow rugosities and depressions. The lateralmost portions of the posterior margins of the subrhomboidal area are sub-parallel to the posteromedial margins of the interclavicle plate, and delimit two shallow, oblique, smooth depressions in the

posteromedial areas of the latter. The subrhomboidal area thus appears much smaller than in similar-sized *D. austriacus* specimens (Figs 3C, D, 5D).

The interclavicle stem is narrower for its length and less robust than in *D. austriacus* (Fig. 3C, D). As in *D. austriacus*, its lateral margins carry small but distinct anterior and posterior constrictions which delimit a small bulge. The anterior part of the stem ventral surface shows a broad and low ridge, almost indistinct near the anterior constriction, but stronger posteriorly and flanked by shallow, elongate lateral depressions. The posterior part of the ventral surface has an elongate median furrow. The stem posterior end bears digitiform processes and narrow longitudinal striations. In a corresponding position, its dorsal surface carries a blunt crest narrowing posteriorly and delimited by weak grooves.

**3.1.2. Clavicle**. The clavicle resembles closely that of *Discosauriscus*, except for its narrower ascending process and spoon-shaped plate (Figs 2, 3A, B, 4A, B). A small emargination along the plate posterolateral angle marks the separation between process and plate. The plate dorsal surface is flat or gently concave centrally, and slightly raised peripherally, with few small foramina and weak striations (Fig. 3B). In PIN 2079/262b, a large elliptical foramen is visible near the posteromedial corner of the dorsal surface of the left plate. The plate ventral surface is gently convex and carries a blunt torus (Fig. 4A; see Klembara 1997). Low tubercles and ridges radiate out from the torus running mostly medially. The plate posterior margin is markedly convex, unlike the distinctly angular margin of *Discosauriscus* (Klembara & Bartík 2000; Klembara 1996, fig. 3). Its anteromedial corner is truncated. Its convex to irregularly sinuous anterior margin carries shallow sulci intercalated with irregular tuberosities and ridges, developed mostly in its central part, and conferring to it a vaguely serrated aspect. As in *Discosauriscus*, the clavicles meet loosely along an interdigitating suture.

The broadly triangular clavicular process has slightly convex (in lateral view) anterior and posterior margins. Its anterior margin is somewhat thickened. Most of the process external surface is unremarkable and carries some striations and fine pits (Figs 3A, B, 4A, B). The dorsal part of its internal surface is trough-like and accommodates the ventral third of the cleithrum (Fig. 4).

**3.1.3. Cleithrum**. The narrow and elongate cleithrum (Figs 2, 4A, B, 5A) is hollowed along its whole length, with a smooth or weakly striated external surface, and resembles its homologue in *Discosauriscus* (Klembara & Bartík 2000).

**3.1.4. Scapula**. The semilunate scapula (Figs 1, 2, 4A, 5A-C) is similar to that of *Discosauriscus* (Klembara & Bartík 2000, fig. 20a-b, e-g). Its posterodorsal apex projects backward, but less strongly so than in *Discosauriscus*. Its posterior margin is less concave in its dorsal two-thirds (especially in mid-sized and large specimens), despite variation (e.g. Fig. 5A). The dorsal third of its thick posterior margin bears a robust ridge that continues anteriorly and ventrally as a posteriorly concave crest. The crest widens rapidly ventrally before merging into the unfinished ventral surface of the bone. Anterior to the ridge, the bone external surface is flat to shallowly concave. A small, striated, lightly pitted, depressed area lies just anterior to the anteroventral tract of the flared ventral end of the ridge. Elongate foramina and shallow parallel grooves are observed in the dorsal half of the external surface, and near its posterodorsal apex.

Posterior to the ridge, the scapula shows a narrow, tall triangular area that is deeply excavated in its middle part by the supraglenoid fossa. The fossa is heavily buttressed posteriorly by the thickened posteroventral margin of the bone, and deepens ventrally immediately posterior to the

ventral most part of the ridge, where the supraglenoid foramen is visible. In mid-sized specimens, the foramen is narrow and dorsoventrally elongate, whereas in larger specimens it is subcircular. In the smallest specimens, the foramen resembles a dorsoventrally elongate and deep furrow. It opens in the upper part of the ventral half of the supraglenoid triangular space, immediately posterior and medial to the middle third of the ridge (see Coates 1996 for a discussion of the position of the supraglenoid foramen in different groups of early tetrapods).

**3.1.5. Coracoid**. The coracoid, best observed in PIN 2079/777 and PIN 2079/509a (Figs 1–2, 4A, 5D), is an irregular, subquadrangular plate with unfinished margins, as in like-sized specimens of *Discosauriscus*. Its articular portion is thick. Its subscapular fossa is shallow. No other remarkable features can be observed.

**3.1.6. Humerus**. The well preserved left humerus of PIN 2079/262a, b (Figs 1, 2, 6) permits detailed comparisons with the *Discosauriscus* humeri figured by Klembara & Bartík (2000). The humeri of specimens other than PIN 2079/262a, b are slightly to heavily disrupted and/or incomplete (Fig. 4A) and do not provide additional information. Based on cranial evidence and on comparisons with *Discosauriscus*, Klembara & Ruta (2005) considered PIN 2079/262a, b to be late metamorphic or early juvenile. Despite its robust aspect, the humerus of PIN 2079/262a, b reveals features found in humeri of immature *Discosauriscus*. Its outline is approximately L-shaped, as in several early tetrapods. Its unfinished proximal and distal ends are of similar size, and oriented at about 38 degrees, as in *Discosauriscus*. The shaft anterior edge is semicircular. The slightly longer and shallower posterior edge runs along an almost straight line and merges into a posterior dorsal process of the humeral head. This process is interpreted as the insertion for the m. subcoracoscapularis (Klembara *et al*. 2001, fig. 4k, *contra* Klembara & Bartík 2000, fig. 21d). The proximal articular surface, visible mostly in flexor view, follows the curvature of the humeral head, running along its anterior part (where it is narrow and strap-shaped), and widening proximal to the deltopectoral crest. The latter is strongly buttressed distally, proximodistally elongate in extensor view, and similar to that of large *Discosauriscus* (Klembara & Bartík 2000, fig. 21g). The humerus distal end is incompletely preserved anteriorly (flexor view) and posteriorly (extensor view), with no clear separation between radial and ulnar facets. It flares anteriorly, but forms a narrow strip posteriorly. Its anterior part turns sharply around the anterior angle of the humerus distal end, and is visible in anterior view.

The distal part of the shaft anterior edge bears a weak supinator process (Klembara *et al*. 2001, fig. 4b, c, e, h, i, k). The part of the periosteal margin from which the ectepicondyle projects proximally is slightly emarginated in extensor view, as in immature *Discosauriscus* (Klembara & Bartík 2000, fig. 20e, f). The ectepicondyle is broad and runs obliquely from the distal articular surface to the bone proximal third. In cross section, it is slightly convex and decreases in height proximally.

The entepicondyle bears a semicircular posterior apex, differing from the sharply angular apex of some of the largest *Discosauriscus* (Klembara & Bartík 2000, fig. 21d). An elliptical entepicondylar foramen pierces the anterior half of its surface, close to the bone distal periosteal margin. The distance of the foramen from the entepicondyle posterior margin corresponds approximately to two foramen widths in flexor view. Such proportions recall those of immature *Discosauriscus* (Klembara & Bartík 2000, fig. 20e-g). In flexor view, the foramen smooth, finished rim appears to be sunk between two oblique, pillar-like strips of periosteal surface. The posterior
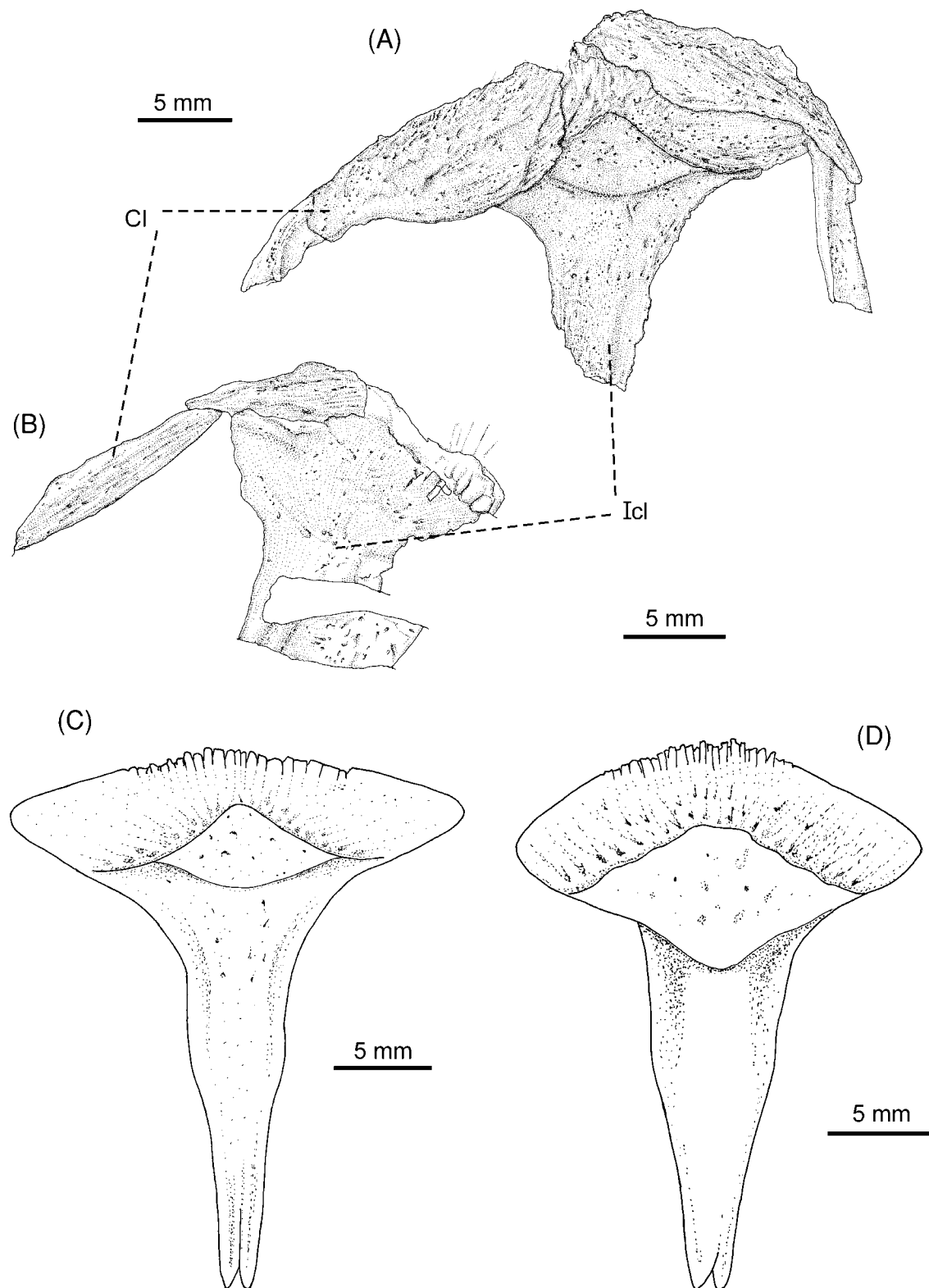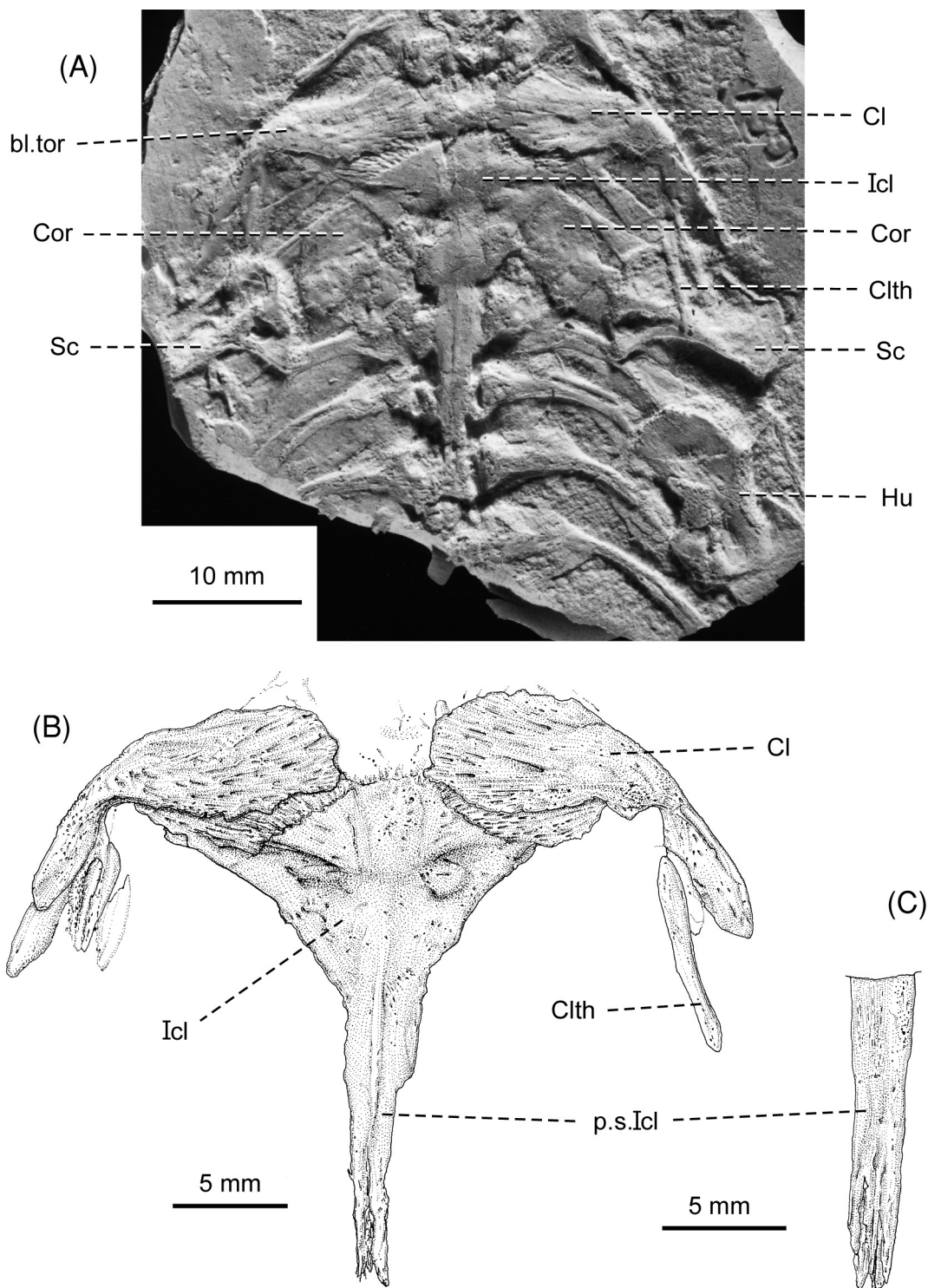
**Figure 3** (A–C) *Ariekanerpeton sigalovi*: (A) PIN 2079/262a, drawing of dermal pectoral bones in ventral view; (B) drawing of the same bones in dorsal view; (C) restoration of interclavicle in ventral view. (D) *Discosauriscus austriacus*: restoration of interclavicle in ventral view based on specimen KO 80.

strip overhangs the rim posterodistal part, and merges smoothly into the surrounding surface. The anterior strip borders the rim anteroproximal part.

In flexor view, small foramina and striations occupy a semicrescentic area along the deltopectoral crest and the shaft anterior edge. In a corresponding position, the extensor surface is irregularly perforated. Large foramina are present on the shaft central part, on the ectepicondyle distal half, and the

humeral head distal part. An m. scapulohumeralis insertion could not be detected. In both *Discosauriscus* and *Seymouria sanjuanensis*, this insertion is marked by a scar lying proximal and posterior to the deltopectoral crest on the humeral head extensor surface. The m. latissimus dorsi insertion is perhaps represented by a small pitted scar aligned with the ectepicondyle, close to the periosteal margin of the proximal articular surface (Klembara *et al*. 2001, fig. 4k).
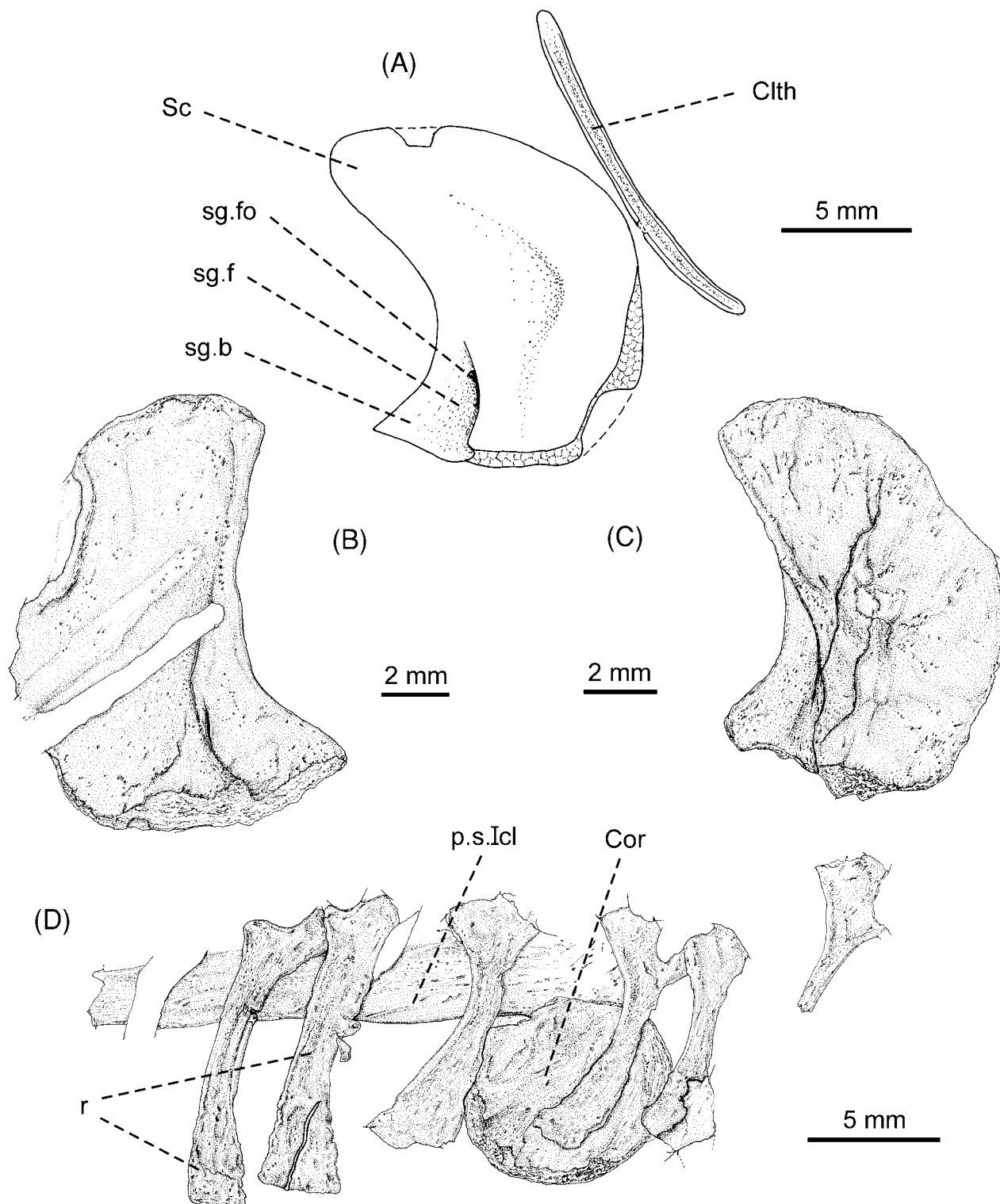
**Figure 4** *Ariekanerpeton sigalovi*: (A) PIN 2079/777, photograph of pectoral region of postcranial skeleton in ventral view; (B) drawing of dermal pectoral bones of the same specimen in ventral view; (C) PIN 2079/747, drawing of posterior portion of interclavicle stem.

**3.1.7. Radius and ulna**. Radius and ulna (once again best observed in PIN 2079/262a, b) are almost as long as the humerus (Fig. 6A, B). The radius is slightly shorter than the ulna, with slightly expanded proximal (smaller) and distal (larger) ends, and is narrowest at the level of its proximal third. Its anterior edge is less concave than its posterior edge. A weak ridge runs along the distal part of the posterior edge in extensor view. The extensor surface is covered in irregular foramina, densely arranged in the middle of the shaft and along its posterior edge. In flexor view, small foramina are visible on a strip-like area along the posterior edge and on the distal end.

The ulna differs from the radius mainly in its larger proximal end and narrower mid shaft portion. The olecranon is poorly defined. The anterior margin of its distal end is gently convex. The narrowest point of its shaft is subcentral. Its posterior edge is shallower than its anterior edge. There is no evidence of a subcentral longitudinal groove on the bone flexor surface, unlike in *Discosauriscus* (Klembara & Bartík 2000, fig. 21d). In flexor view, a weak ridge runs parallel to the

**Figure 5** *Ariekanerpeton sigalovi*: (A) PIN 2079/262a, drawings of right scapula in external view and right cleithrum in internal view; (B) PIN 2079/777, drawing of left scapula in lateral view; (C) PIN 2079/747, drawing of right scapula in lateral view; (D) PIN 2079/509a, partial anterior postcranial skeleton in ventral view.

proximal third of the flat posterior edge, the distal third of which carries a low crest (visible mostly in extensor view). The shaft anterior edge is bluntly convex in cross section. In extensor view, the proximal end of the ulna, the central part of its distal end, and the shaft edges, carry foramina and rugosities. The flexor surface displays small and widely spaced foramina in its distal half.

**3.1.8. Manus**. Both the right manus of the holotype and the left manus of PIN 2079/262a, b show five metacarpals (Figs 1, 2, 6C), of which III and IV are the largest. Based on

comparisons between their proximal ends, I and II were probably slightly shorter than III. The preserved portion of the proximal end of V is slender. No other bones are preserved in our casts. Ivakhnenko (1981) reported a phalangeal formula is 2–3–4–4–3 (but see comments in Laurin 1996b).

### 3.2. Pelvic girdle and limb

**3.2.1. Ilium**. The best preserved ilium, accessible in lateral view, belongs to PIN 2079/509a (Fig. 7). The acetabular portion is connected with the iliac blade by a stout, subvertical

neck. The ilac blade bears a massive, posterodorsally oriented posterior process with a bluntly truncated, squared-off, unfinished termination. The iliac blade anterodorsal part is heavily disrupted. However, its preserved portion suggests that no strongly developed anterodorsal process was present. Its dorsal margin is slightly concave in lateral view. The subelliptical, preserved portion of the acetabulum shows an approximately straight ventral margin. Below this margin, a small portion of the unfinished articular surface is visible. The acetabulum is not buttressed prominently dorsally and has a sharp, thin, semicircular dorsal rim.

The robust iliac neck bears concave anterior and posterior margins and widens rapidly posterodorsally. A distinct arcuate crest runs close and almost parallel to its anterior margin, starting from a point situated immediately dorsal to the anterodorsal acetabular rim. Its ventral and dorsal extremities merge indistinctly into the ilium external surface. The crest delimits the posterior margin of a dorsoventrally elongate, anterior depression of the neck. A shallower, dorsoventrally elongate depression occurs near the neck posterior margin, where it is delimited anteriorly by a weak, poorly defined ridge. The neck region comprised between these two depressions forms a slightly raised broad ridge.

The ilium resembles that of similar-sized specimens of *Discosauriscus* (Klembara & Bartík 2000, figs 5, 6a, 24). However, the following differences are noted: (1) higher height:length ratio; (2) anteroposteriorly narrower neck; and (3) iliac blade posterior process oriented distinctly posterodorsally rather than horizontally, and subtrapezoidal rather than rectangular in lateral aspect. In *Discosauriscus*, the anterior half of the posterior process ventral surface (immediately posterodorsal to the iliac neck) shows a slight depression, marked dorsally by a narrow ridge that '. . . runs along the anterior section of the ventral margin of the posterior iliac process anteriorwards, and fades out above [and slightly behind] the supraacetabular buttress' (Klembara & Bartík 2000, p. 307). Such depression and ridge show the same spatial relationships relative to the iliac neck, acetabulum, and posterodorsal process as the shallow posterior depression described in *Ariekanerpeton*. The latter bears a shallow dorsal depression, homologous to a similarly placed iliac shelf in *Discosauriscus*, but poorly delimited laterally.

**3.2.2. Ischium and pubis**. We have nothing to add to former descriptions (Laurin 1996b).

**3.2.3. Hind limb**. Femur, tibia and fibula are observed in the holotype. However, their preservation is poor. Their epiphyses are unfinished. According to Ivakhnenko (1981), the pes phalangeal formula is 2–3–4–5–4 (see also Laurin 1996b, and remarks following the diagnosis above).

## 3.3. Axial skeleton

**3.3.1. Vertebrae**. Several specimens show the complete array of 24 presacral vertebrae, but only the first nine presacrals of PIN 2079/262a, b (Figs 1, 2, 8A) are preserved in any significant detail. In the same specimen, three incompletely preserved pleurocentra (associated with the sixth, seventh and ninth vertebra) are also visible. The ossified portions of the paired atlas neural arch (Fig. 1) are subrectangular in lateral aspect, project markedly posterodorsally, and lie entirely behind the level of the transverse process. The arch posterior margin is almost straight and subvertical in lateral view. Its anterior margin is slightly arcuate and oriented posterodorsally to anteroventrally. Its unfinished subelliptical apex suggests the presence of a small cartilaginous spine. The poorly pronounced, bluntly terminated prezygapophysis projects slightly laterally and anteroventrally. Its dorsal surface bears a small, subcircular area with a coarse texture

for the proatlas articulation. Immediately anteromedial to the prezygapophysis is a small, lateral transverse process with a seemingly flattened lateral extremity which was presumably oriented anteroventrally and merged almost indistinctly with the pedicel. With its counterpart, the transverse process forms part of the dorsal wall of the neural canal. The postzygapophysis is small but distinct, and its posterior extremity is aligned almost vertically with the neural arch. The subquadrangular atlas pedicel is low in lateral view. The overall morphology of the atlas neural arch resembles that of *D. austriacus* (Klembara & Bartík 2000, fig. 2), although in the latter the neural arch is more robust and with a less inclined anterior margin, and has a stouter transverse process.

The robust axial neural arch is twice as large as, and slightly taller than, the atlas arch. Left and right arches were presumably connected by cartilage, a condition observed also in KO 80, a specimen of *D. austriacus* similar in size to PIN 2079/262a, b (Klembara & Bartík 2000). Its outline is somewhat intermediate between that of the atlas and those of subsequent vertebrae, which are subtrapezoidal to subquadrangular. The axis anterior and posterior zygapophyses are well developed and lie approximately on a horizontal plane. The laterally unfinished quadrangular pedicel is slightly larger than the atlas pedicel.

The third to fifth neural arches are not coossified dorsally, and abut against each other along a smooth, straight middorsal line. The neural arches of the sixth to ninth vertebra, however, are coossified and form in places a strongly interdigitating suture. The third to ninth neural arches are quadrangular in lateral aspect, and increase gradually in length. Their robust, rod-like pedicels become progressively longer anteroposteriorly. Their transverse processes are mediolaterally short and robust. Their anteroposterior width appears to be reduced relative to the length of the neural arches. Their unfinished lateral extremities are progressively enlarged, and terminate ventrolaterally or laterally. Both anterior and posterior zygapophyses are strongly developed and buttressed. In lateral aspect, they are separated from the anterolateral and posterolateral margins of the neural arches by distinct arcuate bony bridges. The prezygapophyses elongate articular facets are oriented distinctly dorsomedially, whereas those of the postzygapophyses face ventrolaterally. The dorsal portions of the seventh to ninth neural arches are transversely swollen (see Sumida 1997 and Sumida & Modesto 2001 for a discussion of this character in stem and basal crown amniotes), i.e. the lateral surfaces of the arch are smoothly convex, although comparatively less so than in *Seymouria* (White 1939). In specimen KO 80 of *D. austriacus*, the swelling of the neural arches begins at the level of the sixth vertebra. No noteworthy features distinguish the anterior presacrals of *Ariekanerpeton* from those of *Discosauriscus*.

Although the preserved portions of the known pleurocentra suggest that they are ring-shaped, a faint longitudinal suture on the dorsal surface of the ninth pleurocentrum indicates that the ring is not completely fused dorsally.

**3.3.2. Ribs**. Combined information from different specimens (Figs 1, 2, 4A, 5D, 8B, 9) permits a full restoration of all 24 presacral ribs. These are well preserved and only slightly crushed along their shafts. Changes in their length, curvature, profile and degree of expansion of their distal extremities are similar to those of like-sized *D. austriacus* (Klembara & Bartík 2000, fig. 13), although there are minor differences.

The well preserved atlas rib of PIN 2079/262a, b is a simple, slender, rod-like bone slightly expanded proximally (albeit incompletely preserved; Laurin 1996b) but slightly damaged
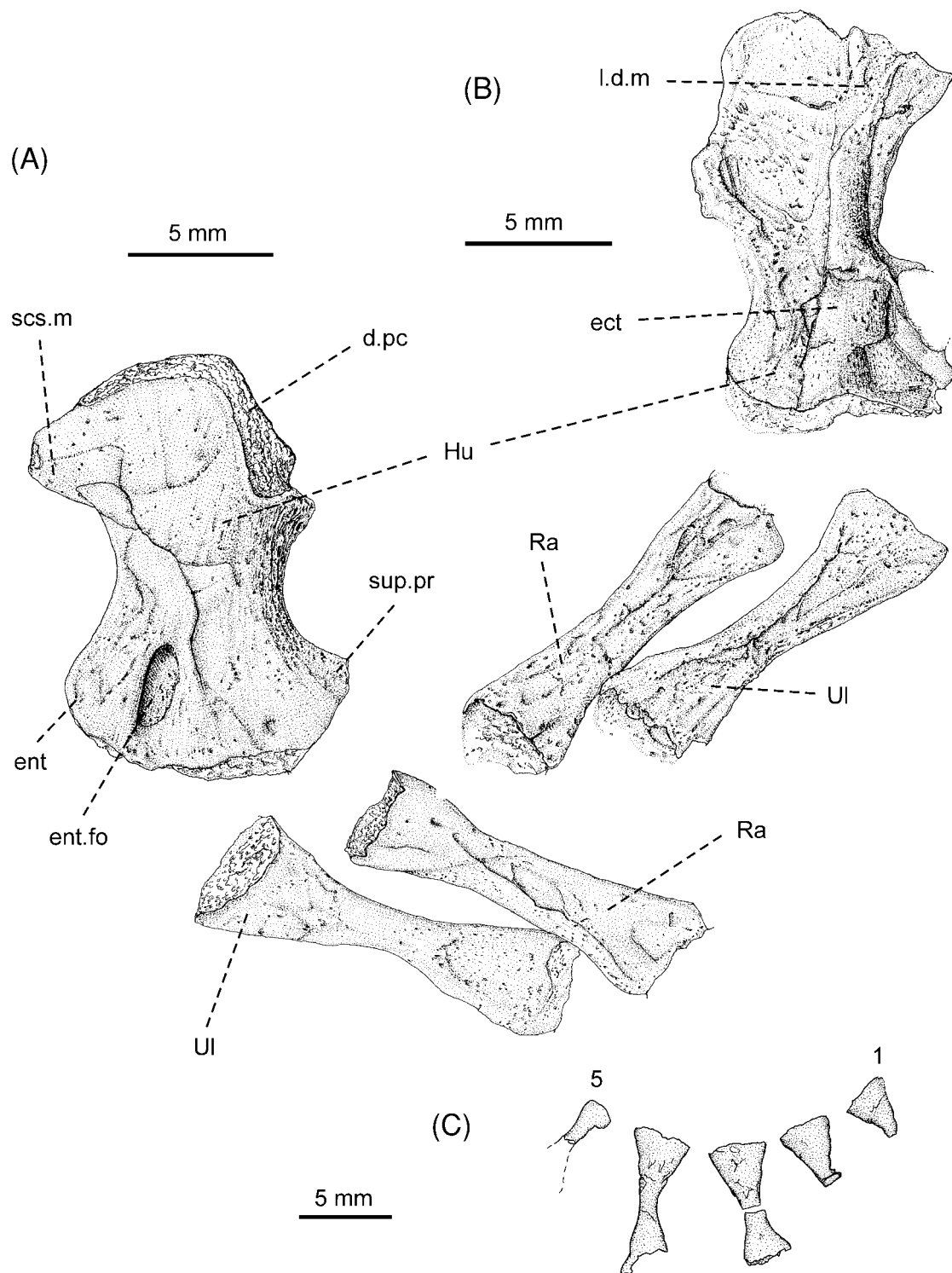
**Figure 6** *Ariekanerpeton sigalovi*: (A) PIN 2079/262a, drawing of left forelimb in flexor (ventral) view; the humerus lies parallel to the plane of the distal part of its ventral surface; (B) drawing of the same specimen in extensor (dorsal) view; the humerus lies parallel to the plane of the distal part of its dorsal surface; (C) PIN 2079/262a, drawing of metacarpals in flexor view.

distally. As in *D. austriacus*, neither the capitulum nor the tuberculum are developed. Its length is about one-third of the length of the axis rib.

The axis rib is unfinished at both ends. Although partially damaged proximally, both tuberculum and capitulum are recognisable. It is slightly compressed dorsoventrally, with an almost straight posterior margin and a gently concave anterior margin. Unlike its homologue in *D. austriacus*, its distal extremity is slightly expanded and about twice as wide as the mid-shaft portion.

The third presacral rib has a narrow shaft with more strongly concave anterior and posterior margins and a slightly more expanded distal extremity than the axis rib. Its articular end is anteroposteriorly broad, and about twice as large as that of the axis rib.

The transition from the third to the fourth presacral rib is marked by an accentuated increase in the concavity of the anterior margin and a slightly sinuous posterior margin. The distal extremity of the fourth rib is a little wider than that of the third rib, but it is unlike the wide, flat, triangular extremity
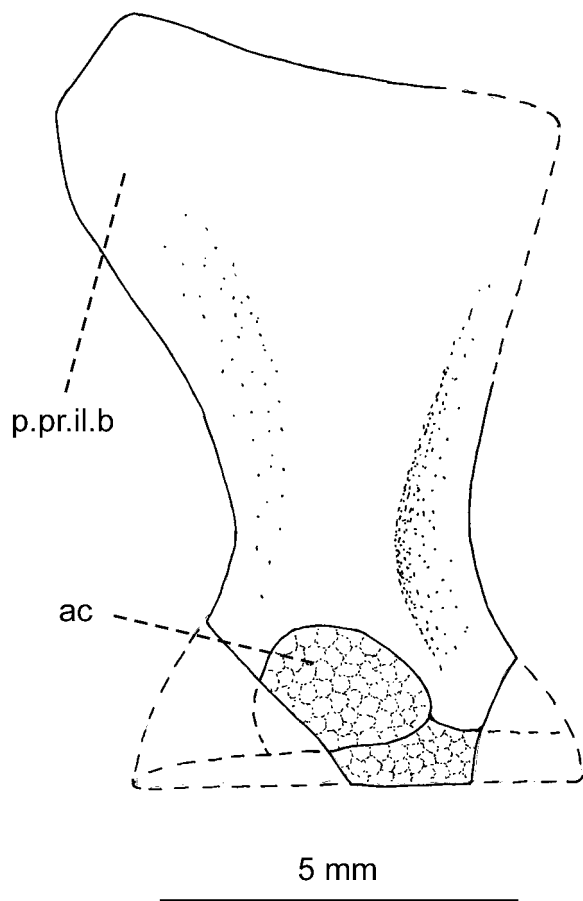
**Figure 7** *Ariekanerpeton sigalovi*: reconstruction of right ilium in lateral view based on PIN 2079/509a.

of the fifth to ninth ribs. There is a shallow notch between capitulum and tuberculum. Both distal and proximal ends of the third to twenty-fourth ribs are unfinished. Their proximal bicipital extremities are slightly flattened, with a stout subcylindrical capitulum and a short tuberculum.

The fifth to ninth ribs are flared distally and their free extremities do not differ remarkably in size, although the ribs themselves increase steadily in length. Rib expansion begins at mid-shaft length or at the junction between proximal third and distal two-thirds of rib length in the fifth to eighth ribs. In the ninth to twelfth ribs, the expansion occupies the distal third or fourth of the rib length and decreases gradually. The proximal margins of the fifth to ninth ribs show a markedly asymmetrical concavity, their curvature being more accentuated proximally than distally. Their posterior margins are mostly straight.

The ninth to twelfth ribs are more slender and smoothly curved than preceding ribs, carry subparallel anterior and posterior margins with nearly symmetrical proximodistal profile, and a deeply incised asymmetrical notch (in plan view) between capitulum and tuberculum. The distal extremities of the tenth to twelfth ribs are only slightly wider than the mid-shaft portion. The twelfth rib is a slender rod, resembling the following two or three ribs in width and curvature. It is comparable in size with the thirteenth rib, which is the longest of the presacral series.

In the thirteenth to twenty-fourth ribs, the notch between capitulum and tuberculum becomes progressively shallower anteroposteriorly, so that the tuberculum is reduced to little more than an articular facet confluent with the rib shaft. In the most posterior three or four ribs, the capitulum is a slender and gracile. The sixteenth to twenty-first ribs are straight, rod-like,

with a circular cross-section and decrease uniformly in length. The twenty-second to twenty-fourth ribs taper to a point distally and are shaped like robust spurs (Figs 8B, 9).

A partially preserved sacral rib is observed in the holotype (reconstruction in Figure 8B). Although incomplete, it is estimated to have been only slightly longer than the last presacral rib, and similar in proportions to the sacral rib of like-sized specimens of *Discosauriscus austriacus*. Its preservation makes it difficult to ascertain the shape of the capitular and tubercular heads (no apparent groove between these is visible, unlike in *D. austriacus*; Klembara & Bartík 2000, figs 11d, 13). Distally, its profile in plan view is spatulate (however, we note the incomplete preservation of its posterodistal portion) but there is apparently no expansion immediately distal to the capitular and tubercular heads, unlike in *D. austriacus*. In addition, the angular notch along the proximal half or third of its posterior margin is shallower than a semicircular, deeply incised and similarly positioned notch of the *D. austriacus* sacral rib.

### 3.4. Integument
No scales have been recorded in the available material (but see Ivakhnenko 1981, 1987 and Bulanov 2003).

## 4. Ontogeny

Analysis of ontogenetic changes in the postcranial skeleton is necessarily limited, given the paucity of material. However, it is noted that the scapula of small specimens is sickle-shaped or semicrescentic. In large specimens, its posterodorsal apex is less pronounced and its posterior margin is shallower. The triangular supraglenoidal area is deeper and sharply delimited by the anterior scapular ridge and the posterior supraglenoid buttress. The most remarkable changes in the dermal pectoral girdle are increase in length:width ratio of the clavicular plate, and enlargement of the anterior bulge of the interclavicle stem. The proximal ventral curvature of the cervical and anterior trunk ribs is more accentuated in large specimens, and their flared distal ends are comparatively wider than in mid-sized specimens. Overall, the degree of ossification of the postcranium is comparable with that of *D. austriacus* (Klembara & Bartík 2000).

## 5. Comparisons

Given the strong similarities between *Ariekanerpeton* and *Discosauriscus* (especially *D. austriacus*), comparisons will focus mainly on these two genera. For a discussion of *Utegenia* and additional differences among seymouriamorphs, see Laurin (1996a, b), Klembara (1997), Klembara & Bartík (2000), Bulanov (2003) and Klembara & Ruta (2004a, b, 2005). Differences between the postcranial skeletons of *Ariekanerpeton* and *D. austriacus* (based mostly on comparisons between specimens of similar size, in particular PIN 2079/262a, b and KO 80) are as follows:

(1) Anterior plate of interclavicle broader and shorter. **Remarks:** The interclavicles of *Ariekanerpeton* specimen PIN 2079/262a, b and *D. austriacus* specimen KO 80 are of comparable size, and have been reconstructed to the same length in Figure 3C, D. Their length is measured from the stem posterior end to the center of the plate anterior margin. The *Ariekanerpeton* plate is shorter and wider than that of *D. austriacus*, both in absolute size and in relative proportions. Its anterior margin is less strongly convex. Its lateral angles are more narrowly acute and pointed. Despite some intraspecific and ontogenetic
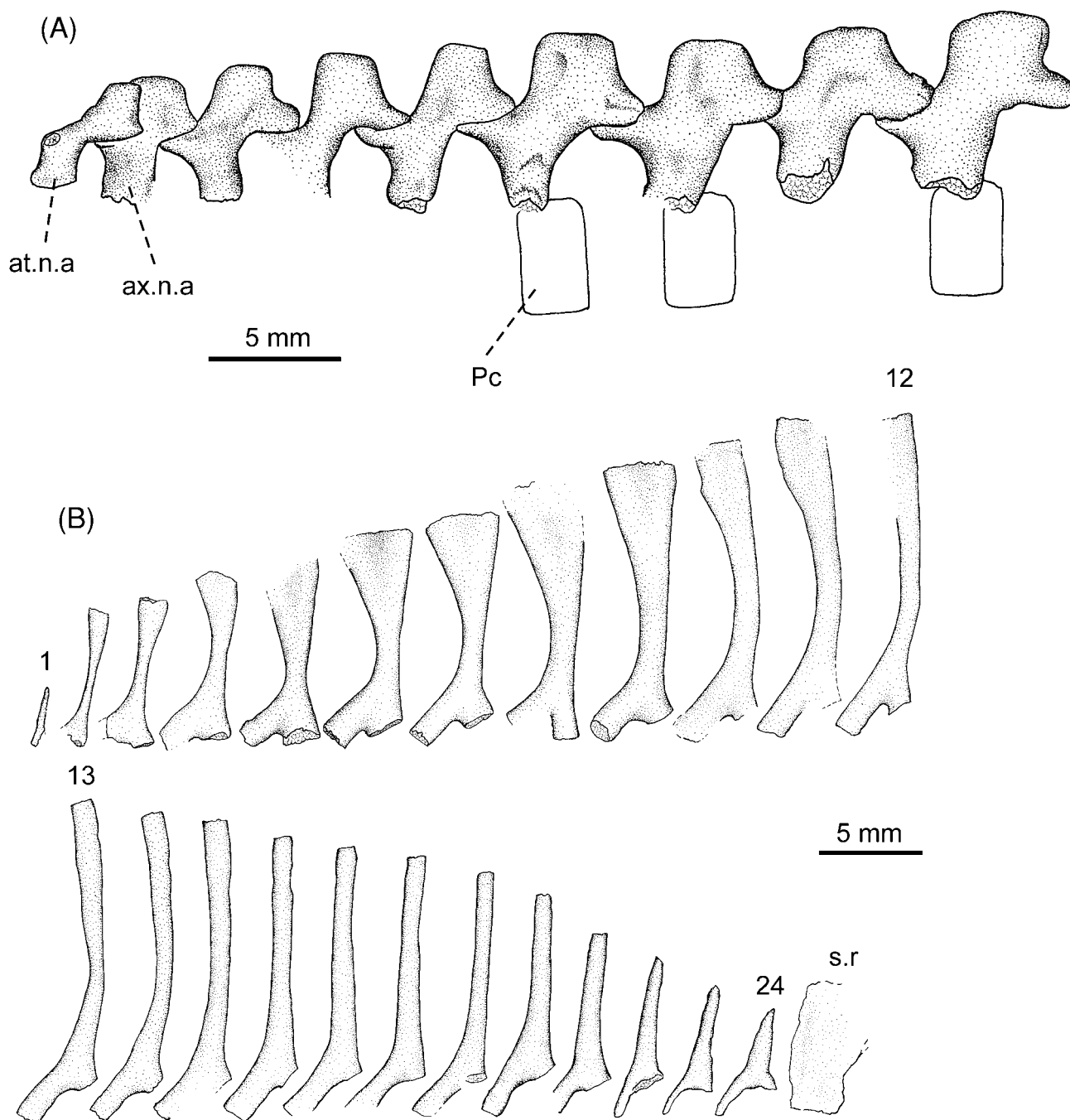
**Figure 8**  *Ariekanerpeton sigalovi*: (A) restoration of first nine presacral vertebrae based on PIN 2079/262a, b (see Figures 1 and 2); (B) restoration of presacral ribs and sacral rib of the right side in dorsal view based on PIN 2079/262a, b and PIN 2079/747.

variation (e.g. see Špinar 1952, figs 18, 24, 36, 37), in none of the specimens of *D. austriacus* does the interclavicle plate resembles that of *Ariekanerpeton*. Unfortunately, *Ariekanerpeton* interclavicles do not cover comparable size ranges, making it difficult to ascertain whether small specimens resemble larger ones.

(2) Subrhomboidal sculptured field on ventral surface of interclavicle plate smaller. **Remarks**: In both *Ariekanerpeton* and *D. austriacus*, the subcentral area of the interclavicle ventral surface bears a bilaterally symmetrical, subrhomboidal thickening with small foramina. This area is highly variable in size in small specimens of *D. austriacus*, and therefore comparisons with *Ariekanerpeton* are necessarily restricted to large individuals.

In *D. austriacus* KO 80, the subrhomboidal field is more than half as large as the whole interclavicle plate,

and occupies mostly its posterior half, extending well behind the transitional region between plate and stem. Its irregular anterolateral margins converge at a bluntly truncated, broadly obtuse anterior end, which lies slightly anterior to the transverse level of the interclavicle plate lateral angles. Its posterolateral margins converge posteriorly into a smoothly convex posterior end. Its lateral extremities merge into the plate posterolateral margins, immediately anterolateral to the plate-stem transitional region.

In *Ariekanerpeton*, the size of the subrhomboidal field is less than one third of that of the interclavicle plate. Its lateral extremities taper narrowly and lie medial to the plate posterolateral margins. As a result, a large part of the posterior and posterolateral areas of the ventral surface of the interclavicle plate are exposed (Fig. 3C, D;
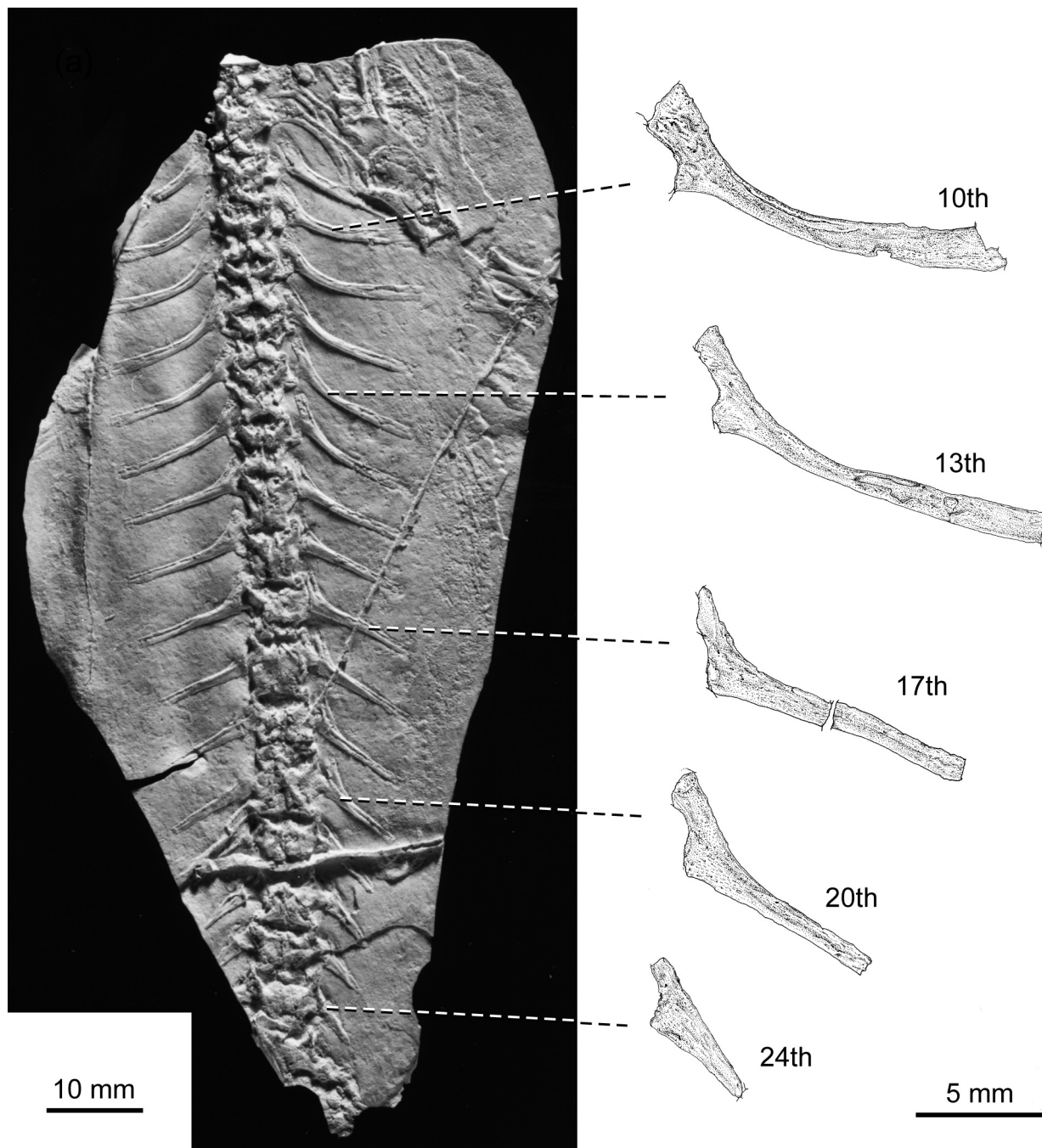
**Figure 9**  *Ariekanerpeton sigalovi*: PIN 2079/747, complete sequence of posterior half of backbone, showing presacral vertebrae and ribs in dorsal view (left), and enlarged drawings of selected ribs (right).

Klembara 1996, figs 2, 4A), and broader than corresponding regions in *D. austriacus*. The subrhomboidal field posterior margin is slightly convex. Its anterolateral, concave margins terminate into a lappet-like anterior end. The field is divided into an anterior and posterior portions of unequal size, unlike in *D. austriacus*.

(3) Posterior stem of interclavicle slightly narrower. **Remarks:** Klembara & Janiga (1993) and Klembara & Bartík (2000) showed that relative size and width of the interclavicle stem vary considerably in *D. austriacus*. Several specimens figured by Špinar (1952) illustrate the slender proportions of its posterior half and the progressive enlargement and differentiation of its anterior bulge (resulting from deepening of paired constrictions along the stem lateral margins; see Klembara & Bartík 2000 for illustrations of additional specimens). Stouter stem proportions characterise some of the specimens

figured by Klembara & Bartík (2000, fig. 18), in particular KO 80 (Fig. 3D). In the latter, the stem anterior half is broad and massive, with barely any suggestion of an anterior bulge, and with lateral margins diverging slightly anterolaterally. Its posterior half narrows abruptly posteriorly, but is similarly stout.

In *Ariekanerpeton* PIN 2079/262a, b, the robust stem resembles that of some of the largest *D. austriacus*, other than KO 80. It differs from the latter mostly in the presence of a distinct bulge and in the more strongly concave anterior half of its lateral margins.

(4) Clavicle plate anteroposteriorly narrower. **Remarks**: In several mid-sized and large *D. austriacus* specimens, the broad, spatulate or spoon-shaped clavicle plates are only slightly wider (mediolaterally) than long (anteroposteriorly). In *Ariekanerpeton*, the subelliptical clavicle plates are much wider than long.

(5) Clavicle plate with convex posterior margin. **Remarks:** In *Ariekanerpeton*, the clavicle plate bears a sinuous posterior margin (gently convex along its central and medial parts). In *D. austriacus*, such margin often forms a distinct protruding angle (e.g. Klembara & Bartík 2000, fig. 17). This contacts the medial end of the posterolateral margin of the interclavicle plate (see Klembara 1996, figs 2–4).

(6) Humerus shorter and stouter. **Remarks:** Major differences between the humerus of PIN 2079/262a, b and those of assorted *D. austriacus* specimens have been discussed above. In summary, despite the overall size of PIN 2079/262a, b, its humerus is more 'immature-looking' than the largest *Discosauriscus* humeri, as shown by: absence of well developed muscular processes; broadly concave profile of its anterior margin; robust, poorly differentiated shaft; weakly protruding, triangular entepicondyle; large, distally placed entepicondylar foramen; weak, low ectepicondylar ridge. Comparisons with the humerus of KO 80 (not figured) confirms such differences. More complete limb material from larger *Ariekanerpeton* is necessary to assess rate and extent of changes in later growth stages, and whether such changes match those in *Discosauriscus*.

(7) Four phalanges on fourth manus digit. **Remarks:** Four phalanges appear in Laurin's (1996b, fig. 5) illustration of PIN 2079/509. A 2–3–4–4–3 manus phalangeal formula is shared with *Utegenia* (Kuznetsov & Ivakhnenko 1981; Laurin 1996a; Klembara & Ruta 2004b) and *Seymouria sanjuanensis* (Klembara & Bartík 2000). All these taxa differ from *D. austriacus* in which the fourth manus digit shows five phalanges.

Although Laurin (1996b, p. 663) quoted Ivakhnenko (1981) incorrectly as having reported a phalangeal formula of 2–3–4–5–3 for the *Ariekanerpeton* pes (in fact, Ivakhnenko reported a formula of 2–3–4–5–4; see Klembara & Bartík 2000), his illustration of PIN 2079/509 seems to suggest that the fourth pes digit included only three phalanges (the most distal of these appears to taper to a point and resembles the distal phalanges of the first to third digits). To complicate matters further, Ivakhnenko (1987, fig. 4) reconstructed the pes of *Ariekanerpeton* with a 2–3–4–5–3 formula, which contradicts the statement in his text about the presence of a fourth phalanx. The present authors suspect that Laurin (1996b) was correct in evaluating the phalangeal formula, and that the formula reported by Ivakhnenko (1981) was printed incorrectly. If this is the case, then the pes phalangeal formula of *Ariekanerpeton* matches that of *D. austriacus*, *S. sanjuanensis* and *Utegenia*.

(8) Ilium more expanded dorsoventrally. **Remarks:** In like-sized *D. austriacus* specimens, the ilium is more robust and dorsoventrally shorther (Klembara & Bartík 2000, fig. 24) than in *Ariekanerpeton*.

(9) Ilium neck slightly narrower anteroposteriorly. **Remarks:** In *D. austriacus*, the ilium neck is anteroposteriorly broader and stouter than in *Ariekanerpeton*.

(10) Posterior process of iliac blade oriented distinctly posterodorsally. **Remarks:** In *D. austriacus*, the posterior process of the iliac blade is oriented almost horizontally.

(11) Atlas rib more gracile. **Remarks:** In *Ariekanerpeton*, the preserved part of the slender shaft of the atlas rib is about 30 per cent as long as the axis rib. Regardless of its actual length, it differs from its homologue in *D. austriacus*, in which it is wider for its length and about half as long as the axis rib (Klembara & Bartík 2000, fig. 13).

(12) Expanded distal extremity of axis rib. **Remarks:** In PIN 2079/262a, b, the distal extremities of both left and right axis ribs are slightly compressed dorsoventrally, whereas their shafts are rod-like. In *D. austriacus*, the shaft of the axis rib is round in cross section and of uniform thickness throughout its length (Klembara & Bartík 2000, fig. 13).

(13) Round scales with smooth external surface. **Remarks:** Ivakhnenko (1981, 1987) reported smooth scales in 'larval' (our quotes) individuals of *Ariekanerpeton*. He postulated that the absence of concentring rings indicates that metamorphosis occurred immediately after their first year. In larger individuals, considered by Ivakhnenko (1981) to be postmetamorphic, scales are absent. We could not observe scales in our material, and can therefore neither confirm nor dismiss Ivakhnenko's (1981, 1987) finds. Bulanov (2003, fig. 51) illustrated a 'juvenile' (PIN 2079/465) with traces of body squamation. He stated that the largest specimen retaining scales has a skull length of 30 mm (PIN 2079/252), from which he concluded that '. . . *Ariekanerpeton* either passed through metamorphosis at the same size as *Discosauriscus* from Moravia or retained *squamation* [Bulanov's italics] at postlarval stages' (Bulanov 2003, p. 94). Regrettably, none of the individuals preserving body scales was available to the present authors.

As regards attribution of various specimens to 'larvae' or 'juveniles', Klembara & Ruta (2005) examined Ivakhnenko's (1981, 1987) and Laurin's (1996b) arguments and showed that identification of various growth stages is not as easy as they hypothesised. Klembara & Ruta (2005) showed that gill impressions, degree of dermal and endochondral skull ossification, and modifications of individual skull bones (including relative proportions) are very similar in *Ariekanerpeton* and *D. austriacus* (see also Klembara 1995, 1997), and concluded that these taxa show comparable ontogenetic trajectories. Based upon available evidence, the largest *Ariekanerpeton* individuals compare well with like-sized *D. austriacus*, which were attributed by Klembara (1995, fig. 6A) to late metamorphic stages (e.g. KO 80).

## 6. Phylogenetic analysis

Klembara & Ruta (2004b) built a data set for early tetrapods, including the best known genera of seymouriamorphs (*Utegenia*, *Ariekanerpeton*, *Discosauriscus* and *Seymouria*), as part of an ongoing project aiming to investigate pattern and process at the base of early amniote phylogeny. Their analysis was much more limited in scope than other recent studies of Palaeozoic tetrapod interrelationships (Anderson 2001; Laurin & Reisz 1999; Clack 2002; Ruta *et al.* 2003), and aimed to reassess the intrinsic relationships of seymouriamorphs in the light of new anatomical data on *Ariekanerpeton*, *Utegenia* and *Discosauriscus*. We are in the process of constructing a more comprehensive data base for stem amniotes using a revised and expanded version of Ruta *et al.*'s (2003) matrix. However, Klembara (2005) has recently revised the matrix of Klembara & Ruta (2004b) in conjunction with the description of a new genus and species of discosauriscid seymouriamorph, *Makowskia laticephala*, from the Lower Permian of the Czech Republic. The character list and revised data matrix are reported in Appendixes 1 and 2, respectively. The matrix yields six most parsimonious trees at 525 steps, with a Consistency Index of 0·3996 (excluding uninformative characters), a Retention Index of 0·6948, and a Rescaled Consistency Index of 0·2793. In three of six trees *D. austriacus* and *D. pulcherrimus* are sister taxa to *Ariekanerpeton* (one of them, see
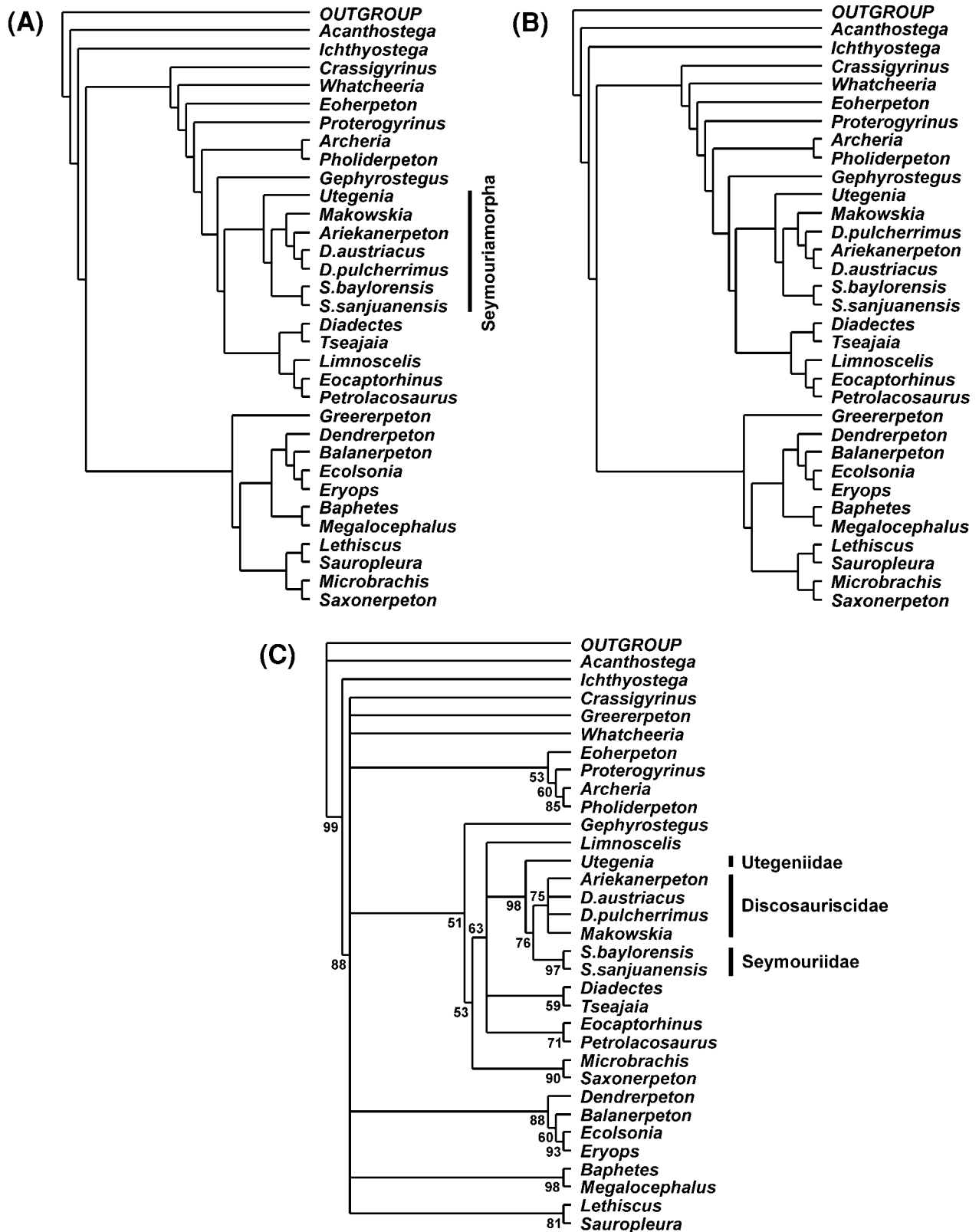
**Figure 10** (A, B) Two of six most parsimonious trees obtained from a cladistic analysis of the revised version of Klembara & Ruta's (2004b) data set (see text for details); trees were printed using TREE VIEW (Page 1996). (C) a 50 per cent majority-rule bootstrap consensus tree.

Fig. 10A), and in three remaining trees *Ariekanerpeton* and *D. austriacus* are sister taxa to *D. pulcherrimus* (one of them, see Fig. 10B). The bootstrap analysis is shown in Figure 10C. A strict consensus of the six shortest trees reveals considerable loss of resolution among post-Devonian tetrapods. However, it is here noted that this is due exclusively to the different placements of five taxa, namely the aïstopod *Lethiscus*, the

nectridean *Sauropleura*, the microsaurs *Microbrachis* and *Saxonerpeton*, and the discosauriscid *Discosauriscus pulcherrimus*. The positions of these taxa in some of the trees appears compatible with the results from Ruta *et al.*'s (2003) recent analysis, in particular as regards the stem group amniote affinities of lepospondyls (*Lethiscus, Sauropleura, Microbrachis, Saxonerpeton*). In all trees, seymouriamorphs form a

clade, but note that *Utegenia* has switched to a basal position, as in Laurin's (1996b) trees. The weakly supported position of this taxon as sister group to discosauriscids only was discussed by Klembara & Ruta (2004b). Furthermore, note that removal of *Makowskia* from the data set results in a poor resolution for seymouriamorphs. Characters supporting the placement of *Ariekanerpeton* were detailed by Klembara & Ruta (2005). Here, the character-state changes supporting seymouriamorph monophyly are listed, as follows: 1 (c.i. $=0.182$; 2 $\Rightarrow$ 1): position of mid point of maximum anteroposterior orbit diameter in the middle of skull length; 14 (c.i. $=1$; 0 $\Rightarrow$ 2): postorbital with elongate dorsomedial ramus for postfrontal; 15 (c.i. $=0.8$; 0 $\rightarrow$ 2): presence of elongate and recurved blade-like process projecting from posterolateral ventral surface of tabular; 53 (c.i. $=0.222$; 0 $\rightarrow$ 2): presence of median paired posterior process of parasphenoid; 58 (c.i. $=0.25$; 1 $\Rightarrow$ 0): presence of fangs on vomer; 73 (c.i. $=0.5$; 0 $\rightarrow$ 1): presence of row(s) of denticles lining the exochoanal margin; 76 (c.i. $=1$; 0 $\Rightarrow$ 1): presence of anterior, triangular, wedge-like, more or less distinct process immediately anterior to basipterygoid processes; 82 (c.i. $=1$; 0 $\Rightarrow$ 1): presence of otic tubes; 88 (c.i. $=0.333$; 0 $\Rightarrow$ 1): separate scapular and coracoid; 112 (c.i. $=0.25$; 0 $\rightarrow$ 1): presence of relatively small posterior Meckelian fenestra between prearticular and angular; 113 (c.i. $=0.5$; 0 $\rightarrow$ 1): presence of relatively small anterior Meckelian fenestra between splenial, postsplenial and prearticular; 114 (c.i. $=0.2$; 1 $\rightarrow$ 0): absence of single, large elongate Meckelian fenestra leaving narrow mesial exposure of splenial; 134 (c.i. $=1$; 0 $\rightarrow$ 1): presence of L-shaped deltopectoral crest; 143 (c.i. $=0.333$; 1 $\rightarrow$ 0): tarsus without L-shaped (i.e. proximally notched) proximal element; 145 (c.i. $=1$; 0 $\rightarrow$ 1): absence of stapedial foramen.

The effects of relaxing seymouriamorph monophyly were explored using reverse constraints. A search for the shortest trees in which seymouriamorphs do not form a monophyletic group yields six trees (not figured here) which are just one step longer than the most parsimonious trees and do not differ significantly from the latter (under Kishino-Hasegawa, Templeton and Winning-sites tests). In these suboptimal trees, *Utegenia* appears removed from other seymouriamorphs. A search was then made for the minimal trees in which discosauriscids plus seymouriids do not appear as a clade. In two trees at one extra step that are not compatible with a discosauriscid-seymouriid clade, *Utegenia* is sister taxon to discosauriscids, although seymouriamorphs still appear as a monophyletic group.

A consequence of the relocation of *Utegenia* to a more basal stem amniote position is that several of its 'anthracosaur'-like cranial features appear to be transitional between those of more derived seymouriamorphs (as well as diadectomorphs and various basal crown group amniotes) and those of embolomeres and gephyrostegids (Gauthier *et al.* 1988; Carroll 1991; Smithson 2000; Ruta *et al.* 2003; Klembara & Ruta 2004a). As Laurin (1996b, p. 664) suggested in his reassessment of *Ariekanerpeton*, '... the vertebral anatomy ... documents a morphocline starting with embolomeres and culminating with lepospondyls and modern amniotes in which the pleurocentrum becomes progressively larger, and the intercentrum dwindles and eventually disappears' (see Romer 1947 and Panchen 1967 for discussions of vertebral centra homologies and their evolution among early tetrapods, and Sumida 1997 and Sumida & Modesto 2001 for recent syntheses). However, vertebral characters are only one aspect of the 'transitional' nature of many skeletal features of basal seymouriamorphs. More numerous and striking similarities were noted by Klembara & Ruta (2004a) in the skull morphology of *Utegenia*, including the proportions of cheek and circumorbital bones.

Given the available evidence, monophyly of seymouriids plus discosauriscids, with utegeniids as the immediate outgroup to the other two families, best accounts for the distribution of several skull roof, palate, braincase (Klembara & Ruta 2004a, b, 2005; Bulanov 2003) and postcranium (Klembara & Ruta in 2004b; present study) characters. However, reassessment of other putative seymouriamorphs from Eurasia (Bulanov 2003) is of paramount importance to provide a stringent test of seymouriamorph status and broader affinities, and recent discoveries (e.g. Klembara 2005) illustrate a higher diversity for the group than previously suspected.

## 7. Acknowledgements

## 8. Explanation of figure lettering

(ac) acetabulum; (at.n.a) atlas neural arch; (at.r) atlantal rib; (ax.n.a) axis neural arch; (bl.tor) blunt torus; (Cl) clavicle; (Clth) cleithrum; (Cor) coracoid; (dp.c) deltopectoral crest; (ect) ectepicondyle; (ent) entepicondyle; (ent.fo) entepicondyle foramen; (Hu) humerus; (Icl) interclavicle; (l.d.m) process for insertion of latissimus dorsi muscle; (n.a) neural arch; (Pc) pleurocentrum; (p.pr.il.b) iliac blade posterior process; (p.s.Icl) posterior stem of interclavicle; (r) rib; (Ra) radius; (Sc) scapula; (scs.m) process for insertion of subcoracoscapularis muscle; (sg.b) supraglenoid buttress; (sg.f) supraglenoid fossa; (sg.fo) supraglenoid foramen; (s.r) sacral rib; (sup.pr) supinator process; (Ul) ulna.

## 9. Appendix 1. Character list

Bibliographic sources for each taxon can be found in Klembara & Ruta (2004b).

1. Position of mid point of maximum anteroposterior orbit diameter: closer to tip of snout than to posterior end of skull (0); in the middle of skull length (1); closer to posterior end of skull than to tip of snout (2).
2. Absence (0) or presence (1) of antorbital vacuities.
3. Skull longer than broad (0) as broad as long (1) or broader than long (2).
4. Preorbital region of skull less than twice as wide as long (0) or at least twice as wide as long (1).
5. Absence (0) or presence (1) of condition: nasals much shorter than frontals (less than one-third as long as frontals).
6. Total width of premaxillae more (0) or less (1) than two-thirds of the width of the skull table.
7. Absence (0) or presence (1) of distinct, triangular or digitiform, dorsal alary processes of premaxillae, widely separated by intervening nasals.

8. Presence (0) or absence (1) of prefrontal-postfrontal suture.

9. Position of prefrontal-postfrontal suture relative to the mid-length of the frontal: posterior (0); at the same level (1); anterior (2).

10. Broad (0) or point-like (1) prefrontal-postfrontal contact.

11. Postorbital medial margin straight for most of its length or very gently curved (1), irregularly sinuous (0).

12. Postorbital not broader than long (0) or broader than long (1).

13. Postorbital without distinct ventrolateral (jugal) ramus (0), with incipient ramus (1), with well developed and elongate ramus (2).

14. Postorbital without distinct dorsomedial ramus for postfrontal (0), with incipient ramus (1), with elongate ramus (2).

15. Absence of outgrowth from posterolateral ventral surface of tabular (0), presence of outgrowth in the form of spike-like unornamented component (1), elongate and recurved blade (2), rectangular, plate-like process (3), presence of conical extension of unornamented portion of posterolateral corner of tabular (4).

16. Absence (0) or presence (1) of tabular buttons.

17. Absence (0) or presence (1) of prolonged posterolateral ornamented surface of tabular.

18. Septomaxilla absent (0) or present (1).

19. Septomaxilla forming part of skull roof (0) or not (1).

20. Septomaxilla touching nasal (0) or not (1).

21. Nostrils slit-like (0), round (1), elliptical and wide (2), elliptical and elongate (3), keyhole-shaped and longer than premaxilla (4).

22. Maximum diameter of nostril less wide than (0) or almost as wide as premaxilla (1).

23. Intertemporal present (0) or absent (1).

24. Intertemporal smaller than supratemporal (0) or larger than/comparable in size with supratemporal (1).

25. Parietal-tabular contact absent (0) or present (1).

26. In lateral view, quadratojugal underlies jugal (0), jugal–quadratojugal suture is oriented approximately dorso-ventrally (1), jugal underlies quadratojugal (2).

27. Jugal not interposed between maxilla and quadratojugal (0) or interposed (1).

28. Absence (0) or presence (1) of flange-like, ventrolateral sheet of bone formed by tabular and supratemporal.

29. Prefrontal–jugal suture absent (0) or present (1) (lacrimal not entering orbit).

30. Dorsalmost part of quadratojugal above (0) or below (1) highest point of maxilla.

31. Absence (0) or presence (1) of posteromedial extensions of unornamented portions of postparietals projecting posteroventrally (presence of a rearward process).

32. Suborbital ramus of lacrimal present and long (0) (more than one third of ventral half of orbit rim), present and short (1) (less than one third of ventral half of orbit rim), absent (2).

33. Postorbital region of jugal longer (0) or shorter (1) than suborbital region.

34. Depth of suborbital region of jugal more (0) or less (1) than half of the length of anteroposterior orbit diameter.

35. Length of postorbital region of jugal more (0) or less (1) than one third of the length of the postorbital cheek region.

36. Postorbital process of jugal rectangular, with bluntly terminated posterior end (1) or not (0).

37. Broad (0) or narrow (1) postorbital–jugal contact (length of suture less than three times the distance between dorsalmost and ventralmost point of orbital edge of postorbital).

38. Posterior apex of postorbital lying posterior to (0) or anterior to/at same level as rearmost part of postfrontal (1).

39. Together, parietals not (0) broader than long or broader (1).

40. Lateral margins of skull table irregular (0), straight or gently concave (1), convex at level of supratemporals (2).

41. Squamosal embayment absent (0), shallow (squamosal straight) (1), deep and dorsoventrally broad (squamosal semicircular) (2), deep and dorsoventrally narrow (3).

42. Unornamented otic flange of squamosal absent (0), narrow (1), broad ventrally (2), narrow ventrally and broad dorsally (3).

43. Squamosal-tabular suture present (0) or absent (1).

44. Maxilla highest point in anterior third of its length (0) or in the middle (1).

45. Palatal vacuities absent (0), present narrow (1), present broad (2).

46. Shape of cultriform process biconvex (0), narrow triangular (1), parallel-sided (2), with proximal constriction followed by swelling (3).

47. Ventral surface of pterygoid palatal ramus covered with shagreen (0), with radiating, densely spaced low ridges with denticle rows (1), with radiating sharp ridges with denticles (2), with densely spaced denticle rows radiating from posterior mid-length of palatal ramus (3), with tooth row(s) along medial margin (4), with multiple rows running mostly parallel to mesial and lateral margins of palatal ramus (5), smooth (6).

48. Transverse pterygoid flange absent (0), present as an incipient downturning [torus transiliens] (1), present as a distinct ridge (2).

49. Absence (0) or presence (1) of teeth on transverse pterygoid flange.

50. Pterygoids not visible in lateral aspect below ventral margin of jugal and quadratojugal (0) or visible (1).

51. Absence (0) or presence (1) of posterior plate of parasphenoid.

52. Absence (0) or presence (1) of ventrolateral crests of parasphenoid.

53. Median posterior process of parasphenoid absent (0), present and unpaired (1), present and paired (2).

54. Parasphenoid posterolateral processes absent (0), present and short (1), present, elongate and wing-like (2).

55. Parasphenoid cultriform process with shagreen (0), with patch of denticles (1), with radiating ridges and denticle rows (2), smooth (3).

56. Posterior plate of parasphenoid behind cultriform process with shagreen (0), with denticulated field (1), sculptured with or without denticles (2), with light striations (3), smooth (4), smooth with denticles arranged in rows or scattered (5).

57. Ventral, exposed surface of vomers narrow, elongate and strip-like (1) or not (0).

58. Presence (0) or absence (1) of fangs on vomer.

59. Absence (0) or presence (1) of shagreen on vomer.

60. Presence (0) or absence (1) of subcentral tooth row (teeth comparable in size to marginal series, often aligned with fangs) on vomer, or presence of row along medial margin (2).

61. Presence (0) or absence (1) of denticle row (line of small teeth between tooth row and lateral margin of the bone) on vomer.

62. Presence (0) or absence (1) of fangs on palatine.

63. Absence (0) or presence (1) of shagreen on palatine.
64. Presence (0) or absence (1) of tooth row on palatine.
65. Presence (0) or absence (1) of denticle row on palatine.
66. Presence (0) or absence (1) of fangs on ectopterygoid.
67. Absence (0) or presence (1) of shagreen on ectopterygoid.
68. Presence (0) or absence (1) of tooth row on ecto-pterygoid.
69. Presence (0) or absence (1) of denticle row on ecto-pterygoid.
70. Denticle rows on vomer (continuation of rows on pterygoid) absent (0) or present (1).
71. Denticle rows on palatine (continuation of rows on pterygoid) absent (0) or present (1).
72. Denticle rows on ectopterygoid (continuation of rows on pterygoid) absent (0) or present (1).
73. Row(s) of denticles lining the exochoanal margin absent (0) or present (1).
74. Ectopterygoid partly separated from cheek (1) or not (0).
75. Ectopterygoid longer than (0), as long as (1), shorter than (2) palatine.
76. Anterior, triangular, wedge-like, more or less distinct process immediately anterior to basipterygoid processes absent (0) or present (1).
77. Lateral margins of posterior plate of parasphenoid not sharp (0) or sharp (1).
78. Lateral margins of posterior plate of parasphenoid raised all around (1) or not (0).
79. Lateral margins of posterior plate of parasphenoid confluent with anterior wedge-like process (1) or not (0).
80. Jagged margins of posterior plate of parasphenoid behind basipterygoid processes present (1) or absent (0).
81. Posterolateral angles of posterior plate of parasphenoid extending laterally on medioventral part of posterolateral processes (0) or not (1) (forming acute angles with horizontal plane).
82. Absence (0) or presence (1) of otic tubes.
83. Absence (0) or presence (1) of suborbital fenestra.
84. Posttemporal fossae large (0) (dorsal surface of fossa occupying more than half of maximum width of tabular ornamented surface), small (1), absent (2).
85. Interclavicular stem absent (0), elongate and subtriangular with blunt posterior end (1), elongate and rod-like but without expansion along its shaft (2), elongate and rod-like and with broadened posterior portion (3), elongate and rod-like and with middle expansion along its shaft (4).
86. Anterior margin of ventral plate of clavicle without (0) or with (1) fimbriate indentations.
87. Clavicle ventral plate with anterior expansion (0) or anteroposteriorly narrowed (1).
88. Scapular and coracoid not separate (0) or separate (1).
89. Cleithrum with (0) or without dorsal expansion (1).
90. Cleithrum with (0) or without (1) branchial lamina.
91. Atlantal rib present (0) or absent (1).
92. Chevron-like rectangular gastralia present (0), round gastralia present (1), absence of gastralia (2).
93. Angular reaches rear end of jaw (1) or not (0) in lateral aspect.
94. Adductor ('surangular') crest absent (0), formed only by surangular (1), formed by third coronoid and surangular (2), formed by dentary (3).
95. Three (0) or one (1) coronoids.
96. Posterior coronoid not exposed in lateral view (0) or exposed (1).
97. Contact between anterior coronoid and mesial lamina of splenial absent (0) or present (1).

98. Contact between middle coronoid and mesial lamina of splenial absent (0) or present (1).
99. Mesial lamina of angular absent (0) or present (1).
100. Rearmost part of mesial lamina of splenial closer to adductor fossa (1) than to anterior margin of lower jaw (0).
101. Posterior coronoid without (0) or with (1) posterodorsal process.
102. Suture between prearticular and surangular absent (0) or present (1).
103. Suture between prearticular and splenial present (0) or absent (1).
104. Postsplenial present (0) or absent (1).
105. Mesial lamina of postsplenial absent (0) or present (1).
106. Denticles on prearticular absent (1) or present (0).
107. Adductor fossa faces dorsally (0) or mesially (1).
108. Fangs on anterior coronoid present (0) or absent (1).
109. Fangs on middle coronoid present (0) or absent (1).
110. Fangs on posterior coronoid present (0) or absent (1).
111. Mesially projecting flange on dorsal edge of prearticular absent (0) or present (1).
112. Relatively small posterior Meckelian fenestra between prearticular and angular absent (0), present and small (1), present and large (2) (depth comparable with size of adductor fossa; occasionally shifted slightly anteriorly to involve postsplenial).
113. Relatively small anterior Meckelian fenestra between splenial, postsplenial and prearticular absent (0), present and small (1), present and large (2) (depth comparable with size of adductor fossa; occasionally shifted slightly anteriorly to involve postsplenial).
114. Single, large elongate Meckelian fenestra leaving narrow mesial exposure of splenial (diadectid pattern) absent (0) or present (1).
115. Anterior elongate fenestra between ventromedial anterior lamina of dentary and splenial absent (0) or present (1).
116. Parasymphysial plate present (0) or absent (1).
117. Tooth row of parasymphysial plate absent (0) or present (1).
118. Fang pair of parasymphysial plate absent (0) or present (1).
119. Denticle field on anterior coronoid absent (0) or present (1).
120. Denticle field on middle coronoid absent (0) or present (1).
121. Denticle field on posterior coronoid absent (0) or present (1).
122. Anterior fang pair on dentary present (0) or absent (1).
123. Number of presacral vertebrae: 30 (0), 30–38 (1), more than 38 (2), 30–28 (3), fewer than 28 (4).
124. Pleurocentra paired (0), fused ventrally but forming incomplete rings dorsally (1), forming complete rings (2), fused dorsally but not ventrally (3), with dorsal extremities in contact but not fused (4).
125. Intercentra low (0), crescent (1), disc-like (2), with dorsal extremities in contact but not fused (3).
126. Swollen neural arches absent (0) or present (1).
127. Absence (0) or presence (1) of laterally compressed, rectangular to fan-shaped neural arches.
128. Absence (0) or presence (1) of condition: dorsalmost extremity of ossified part of neural spine aligned vertically with posterior level of pleurocentrum of the same vertebral segment.
129. Absence (0) or presence (1) of condition: height of ossified portion of neural spine plus arch reduced (less than the distance between pre- and postzygapophysis).
130. One (0) or two (1) sacral ribs.

131. Dorsal process of iliac blade high (0), low rounded (1), absent (2), with dorsal notch dividing the blade into small anterior and posterior processes (3).
132. Posterodorsal process of iliac blade elongate and slender (0), stout and abbreviated posteriorly (1), stout and broad posterodorsally (2).
133. Transverse line of ilium absent (0), present (1), presence of iliac shelf (2).
134. Absence (0) or presence (1) of condition: deltopectoral crest L-shaped.
135. Deltopectoral crest in the middle of humerus length (0), more or less halfway between caput humeri and radial condyle, or more proximal (1).
136. Ectepicondyle offset relative to latissimus dorsi process (0) or aligned with the latter (1).
137. Distal extremity of ectepicondyle aligned with ulnar facet (0), between ulnar and radial facets (1), aligned with radial facet (2).
138. Presence (0) or absence (1) of ectepicondylar foramen.
139. Presence (0) or absence (1) of entepicondylar foramen.
140. Distance from most proximal point of articular surface of caput humeri to radial condyle smaller (0) or greater than twice the width of caput humeri (1) in extensor view.

141. Entepicondyle about half as long as humeral shaft (0) or less (1).
142. Olecranon process absent (0) or present (1).
143. Tarsus without (0) or with (1) L-shaped proximal element.
144. Manus with more than five (0), five (1), four (2), three (3) digits.
145. Stapedial foramen present (0) or absent (1).
146. Atlantal pleurocentrum paired (0) or fused (1) in mature individuals.
147. Absence (0) or presence (1) of anteriorly directed, mid-ventral process of axial intercentrum-atlantal pleurocentrum complex.
148. Axial neural arch and pleurocentrum unfused (0) or fused (1).
149. Axial intercentrum and atlantal pleurocentrum unfused (0) or articulated/fused (1).
150. Longest mid-trunk ribs shorter than (0) or at least as long as (1) four mid-trunk vertebrae.

## 10. Appendix 2. Data matrix

**OUTGROUP**

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 00000 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 |
| 00000 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 |
| 00000 | 00000 | 00000 | 00000 | 00000 | 00000 | | | | | | |

*Acanthostega*

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 20000 | 00000 | 00000 | 000?? | 00??? | 00010 | 0?000 | 00000 | 11001 | 000?0 | 00000 | ?0000 |
| 00000 | 10000 | 00000 | 00000 | ?0000 | 00000 | 00000 | 00000 | 00000 | 00111 | 00000 | 01100 |
| 00000 | 00000 | 00000 | 00000 | 00000 | ?0000 | | | | | | |

*Archeria*

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 20000 | 10000 | 10001 | 010?? | 21001 | 01010 | 1?101 | 00000 | 11101 | 301?1 | 11113 | 31??? |
| ????? | ??01? | 00?0? | 00000 | 00?21 | 00001 | 0?010 | 11111 | 11001 | 11111 | 12200 | 00111 |
| 11122 | 00000 | 00101 | 12101 | 0111? | 10001 | | | | | | |

*Ariekanerpeton*

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 00110 | 10011 | 11223 | 00101 | 21001 | 01101 | 01111 | 00011 | 22101 | 11201 | 11223 | 21001 |
| 10011 | 10111 | 11111 | 11110 | 01112 | 11111 | 01120 | 01111 | 1??01 | 11111 | ?1?01 | 1??11 |
| 11420 | 101?0 | 21?10 | 12100 | 0??1? | ????1 | | | | | | |

*Balanerpeton*

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 10000 | 01021 | 10000 | 00??? | 10000 | 00000 | 01111 | 00000 | 22102 | 200?0 | 10013 | 10011 |
| 10111 | 01110 | 00001 | 00000 | 000?0 | 00001 | ?1000 | 01010 | 00101 | 11111 | 00000 | 1??11 |
| 10401 | 00000 | 20001 | ?2101 | 01020 | ??000 | | | | | | |

*Baphetes*

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 21000 | 00000 | 00000 | 10100 | 10000 | 11000 | 01110 | 00000 | 03100 | 100?? | 11010 | 00011 |
| 10111 | 01110 | 00000 | 00000 | ?000? | 01?00 | ????? | ????? | ????? | ????? | ????? | ????? |
| ????0 | ?0??? | ??00 | 02100 | 0???? | ????? | | | | | | |

*Crassigyrinus*

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 10000 | 00001 | 10004 | 00101 | 00000 | 00010 | 1?000 | 00002 | 01101 | 100?0 | 11001 | 30000 |
| 10001 | 00010 | 00000 | 00000 | ?00?? | 00?01 | ?0000 | 00011 | 00000 | 00111 | ?0010 | 00111 |
| ?01?1 | 0?00? | 00000 | 11000 | 00??? | ?0??1 | | | | | | |

*Dendrerpeton*

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 10000 | 01000 | 10000 | 00100 | 10000 | 00100 | 02110 | 00000 | 12102 | 200?0 | 11203 | 00011 |
| 10111 | 01110 | 00000 | 00000 | ?00?0 | 00001 | ?100? | ??10 | ???01 | ?1??? | ?1000 | ????? |
| ??401 | 0000? | 20101 | ?2100 | 110?0 | ????0 | | | | | | |

*Diadectes*

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 20000 | 10000 | 10000 | 00100 | 001?1 | 01000 | 12111 | 00010 | 11100 | 14201 | 10123 | 31102 |
| 10111 | 01110 | 00012 | 00000 | 00?12 | 01001 | 02022 | 1??11 | 1001? | 11??1 | 00011 | 1???? |
| 01420 | 10111 | 11201 | 12100 | 01110 | 11111 | | | | | | |

*Discosauriscus austriacus*

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 00110 | 10010 | 11223 | 00101 | 21011 | 01101 | 11111 | 00011 | 22100 | 12201 | 11223 | 21001 |
| 10011 | 10110 | 11111 | 11110 | 01112 | 11111 | 01120 | 11111 | 10001 | 11111 | 11101 | 1??11 |
| 11420 | 10110 | 21210 | 12101 | 0??11 | 0?000 | | | | | | |

*Discosauriscus pulcherrimus*

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 00010 | 10020 | 11223 | 00101 | 21011 | 01101 | 11111 | 01011 | 22100 | 13201 | 11223 | 51001 |
| 10011 | 10110 | 11111 | 11110 | 01112 | 11111 | 01120 | 11111 | 10001 | 11111 | ????1 | 1??11 |
| 11420 | 10110 | ??10 | 12101 | 0??11 | ????? | | | | | | |

*Ecolsonia*
| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 10000 | 011?? | 10000 | 00111 | 401?0 | 00000 | 01010 | 00000 | 32002 | 200?0 | 10013 | 3001? |
| ?01?? | 01??0 | 00001 | 00000 | 000?0 | 01001 | ??020 | 11010 | 10101 | 11111 | 01000 | 1??11 |
| 11?03 | 0000? | 22001 | 1211? | 010?? | ????0 | | | | | | |

*Eocaptorhinus*
| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 10000 | 101?? | 0020? | ??11? | 111?? | 21?01 | 01110 | 00010 | 00?11 | 14211 | 11100 | 31100 |
| 11011 | ????0 | 1?0?? | 00000 | ?010? | ?10?? | 12121 | 1??11 | 1001? | 11??1 | 01?01 | 1???? |
| 01420 | 10111 | 2200? | ????1 | 11110 | 10111 | | | | | | |

*Eoherpeton*
| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 20000 | 10000 | 10004 | 01??? | 10001 | 00010 | 1?010 | 00012 | 1110? | ??0?? | 11??? | 31??? |
| ?0?0? | 0?0?0 | 00000 | 00000 | ????2? | 000?? | ??010 | 01111 | ??001 | 01111 | 1100? | ??11 |
| 1??11 | 0000? | 00100 | 11101 | 0???? | ????1 | | | | | | |

*Eryops*
| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 20000 | 01000 | 10000 | 00111 | 30000 | 00010 | 0?000 | 00000 | 13102 | 200?1 | 10013 | 30011 |
| 10111 | 01110 | 00001 | 00000 | 00000 | 01001 | 1?020 | 11010 | 10101 | 11111 | 01000 | 1???? |
| 10401 | 00000 | 22101 | 12110 | 01020 | ?0001 | | | | | | |

*Gephyrostegus*
| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 20000 | 101?? | 1?200 | 01??? | ?0001 | 00000 | 1111? | 00011 | 11101 | ?01?? | ????? | ?0111 |
| 00111 | 01110 | 00010 | ????? | ??0?2 | 01011 | 00020 | 11111 | 1?000 | 11001 | 10010 | 1??11 |
| 10410 | 0010? | 00100 | 12101 | 0111? | 10001 | | | | | | |

*Greererpeton*
| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 10001 | 00000 | 00000 | 100?? | 10??0 | 10000 | 01000 | 00000 | 00001 | 200?0 | 11103 | 10001 |
| 10001 | 00010 | 00000 | 00000 | 00000 | 00000 | ?0000 | 01010 | 00000 | 10011 | 00010 | 0010? |
| 10201 | 00000 | 20000 | 11100 | 01010 | 00000 | | | | | | |

*Ichthyostega*
| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 00000 | 00000 | 00000 | 000?? | 00??? | 00010 | 0?000 | 00000 | 00000 | 170?0 | 00003 | ?0100 |
| 11001 | 10010 | 00001 | 00000 | ?0021 | 00000 | ??000 | 01001 | 00000 | 00111 | 00000 | 00100 |
| 00401 | 00000 | 00000 | 10000 | 0100? | ????1 | | | | | | |

*Lethiscus*
| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 00001 | 10020 | 0000? | ?0??? | 101?? | ??00? | 00?11 | 00000 | 0000? | 1???? | ????? | ????? |
| ????? | ????? | ????? | ????? | ????? | ????? | ?0??? | ????? | ????? | ????? | ????? | ????? |
| ??22? | 01??? | ????? | ????? | ????? | 10100 | | | | | | |

*Limnoscelis*
| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 20000 | 10000 | 00200 | 00110 | 311?1 | 21001 | 01010 | 00010 | 00101 | 16210 | 11003 | 51101 |
| 11011 | 10110 | 00012 | 00000 | ?0?1? | 01011 | 021?? | ???11 | 1?01? | ?1??? | ?001? | ????? |
| ??420 | 10111 | 21201 | 12100 | 0111? | 11111 | | | | | | |

*Makowskia*
| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 00210 | 10010 | 11223 | 00101 | 21011 | 01101 | 11111 | 01111 | 22110 | 12201 | 11223 | 21001 |
| 10011 | 10110 | 00111 | 11111 | 01114 | 11111 | ?11?? | 1??1? | ???01 | ????? | ????? | ????? |
| ?1?20 | 10??? | ???10 | 1?10? | 0??1 | ????? | | | | | | |

*Megalocephalus*
| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 21000 | 00000 | 00000 | 10100 | 101?0 | ?0000 | 01110 | 00000 | 03100 | 100?? | 11010 | 00011 |
| 10111 | 01110 | 00000 | 00000 | ?000? | ????? | ??000 | 01111 | 01001 | 11111 | 00100 | 00100 |
| 00??? | ????? | ????? | ????? | ????? | ????? | | | | | | |

*Microbrachis*
| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 00000 | 10010 | 00200 | 00??? | 101?1 | 11?00 | 00010 | 00010 | 00001 | 110?0 | 10201 | 31111 |
| 11111 | 11111 | 11002 | 00000 | ?0002 | 01011 | 0?130 | 01011 | 10001 | 11111 | 01000 | 1??11 |
| 1012? | 00110 | 3000? | ??101 | 10?30 | 10001 | | | | | | |

*Petrolacosaurus*
| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 20000 | 101?? | 01210 | 001?? | 111?1 | 2100? | 01111 | 00010 | 00?01 | 1421? | 11001 | 01112 |
| 11111 | 10110 | 10012 | 00000 | ?0102 | 01001 | 02111 | 1??11 | 10001 | 11??1 | 00001 | 1???? |
| 01420 | 10111 | 20001 | 12101 | 11110 | 10111 | | | | | | |

*Pholiderpeton*
| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 20000 | 11??? | 10001 | 010?? | ??00? | 10010 | 1?100 | 000?2 | 11101 | 301?0 | 11??3 | 31101 |
| 1???? | 00010 | 00000 | 00000 | ?0021 | 00001 | ?0010 | 11111 | 11001 | 11111 | 12200 | 00011 |
| 10?22 | 0000? | ??01 | 1??0? | 01??0 | 10001 | | | | | | |

*Proterogyrinus*
| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 10000 | 10001 | 10001 | 010?? | 10001 | 01000 | 1?010 | 10002 | 11101 | 300?1 | 11113 | 01??? |
| ?0011 | 0001? | 00?00 | 00000 | 00021 | 00001 | ?0010 | 01?1? | 0??0? | 111?1 | 12200 | ???1? |
| 10141 | 00000 | 00101 | 11101 | 0111? | 00001 | | | | | | |

*Sauropleura*
| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 00001 | 00010 | 10000 | 000?? | 111?1 | 00000 | 00010 | 00000 | 00001 | 150?0 | 10003 | 31101 |
| 11001 | 10010 | 0000? | 00000 | ?00?0 | 00001 | ?0031 | 0??11 | 0001? | 01??1 | 00000 | 1???? |
| ?142? | 01000 | 20000 | ??110 | 01??? | 10100 | | | | | | |

*Saxonerpeton*
| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 20000 | 101?? | 00200 | 00??? | 111?1 | ?1?01 | 00010 | 00010 | 00001 | 1?0?0 | 10201 | 31111 |
| 11111 | ????0 | 0?0?? | 00000 | ?00?2 | 01011 | 0?13? | ????? | ????? | ????? | ????? | ????? |
| ??42? | ?0110 | 20001 | ??101 | 1102? | 10001 | | | | | | |

*Seymouria baylorensis*
| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 10000 | 10010 | 11223 | 00111 | 31011 | 00101 | 12111 | 00111 | 32100 | 10201 | 11123 | 31011 |
| 10111 | 11110 | 00011 | ?0010 | ?1?12 | 01111 | 12120 | 11111 | 10001 | 11111 | ?1101 | 1??11 |
| 11420 | 10111 | 01210 | 12100 | 0?011 | 10000 | | | | | | |

*Seymouria sanjuanensis*

```
10000  10010  11223  01???  31011  00101      11111  00011  32100  10201  11123  31011
10111  11110  000?1  11010  01?12  01111      121??  ?????  ?0?01  ?????  ?????  ?????
??420  10111  ???10  12100  0101?  ??000
```

*Tseajaia*

```
20000  10000  00000  00???  211?0  01000      10110  00010  12101  2421?  1?023  31102
10111  01110  00012  00000  00??3  01101      02?2?  ??111  1001?  11?11  0001?  1??11
11420  10111  11201  12100  01010  11111
```

*Utegenia*

```
10000  10000  10122  00101  21001  01001      11110  10012  11101  11201  11222  31001
10001  10011  11112  10000  01112  ?0111      00130  0??1?  10001  11111  1???1  1??11
11320  ?0??0  21???  ?????  ???1?  ????1
```

*Whatcheeria*

```
20000  00000  1120?  ?1???  10000  ??0?0      1?000  01000  0?10?  ?0???  1??13  3?0?0
?0?0?  0?0??  ?????  ?????  ????2  00101      ??000  ?????  0??00  ??111  0000?  01011
10131  00000  00000  01100  01???  ????1
```

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