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A reassessment of the temnospondyl amphibian *Perryella olsoni* from the Lower Permian of Oklahoma

Marcello Ruta and John R. Bolt

ABSTRACT: Additional mechanical preparation of the type material of the temnospondyl amphibian *Perryella olsoni* (Lower Permian, Wellington Formation, Oklahoma) highlights new cranial and postcranial features and provides additional data on previously known structures. Important new information is available for the quadrate, palatal bones and their associated dentition, parasphenoid, and appendicular skeleton. The revised diagnosis and redescription of *Perryella* provide the basis for a re-evaluation of its systematic affinities. A cladistic analysis of (mostly) Carboniferous and Permian temnospondyls, together with several Devonian and Carboniferous stem tetrapod outgroups, supports a single origin for temnospondyls. The sequence of branching events within temnospondyls consists of: (1) a paraphyletic Edopoidea; (2) a clade of Zatracheidae, Eryopidae, and basal Archegosauriformes; (3) a monophyletic Dvinosauria; and (4) a monophyletic Dissorophoidea. *Perryella* is nested within Dvinosauria in an intermediate position between Trimerorhachidae and Dvinosauroidea.

KEY WORDS: Carboniferous, characters, Dissorophoidea, Dvinosauroidea, phylogeny, Temnospondyli, Triassic, Trimerorhachidae

Temnospondyls (ranging from the Lower Carboniferous to the upper Lower Cretaceous) are the most species-rich group of early tetrapods, as well as one of the most widely distributed, with records from all continents including Antarctica. From the middle Pennsylvanian onward, they become increasingly abundant in the fossil record (e.g. Milner 1990; Holmes 2000). The group as a whole is of considerable phylogenetic and zoological interest, due to the possible close relationship of some of its Palaeozoic and earliest Triassic representatives with extant amphibians. Indeed, several authors consider temnospondyls as a whole to be a paraphyletic assemblage relative to some, or all, of the three modern amphibian orders (Bolt 1969, 1977, 1979, 1991; Milner 1988, 1990, 1993, 2000; Trueb & Cloutier 1991; Ruta *et al.* 2003; Carroll 2004; see Schoch & Milner 2004 for a comprehensive review). However, this evolutionary hypothesis has not generated consensus (e.g. Laurin 1998; Laurin & Reisz 1999; Anderson 2001; Vallin & Laurin 2004), and is still debated. Much of the interest in the phylogeny of temnospondyls as a whole is due to the fact that numerous Palaeozoic species, in particular, appear to be quite generalised, primitive tetrapods (e.g. Milner & Sequeira 1994; Holmes *et al.* 1998). For this reason, the group represents an important component of large-scale studies of the anatomy, diversity, and interrelationships of early limbed vertebrates. In view of this, and given the considerable amount of fossil material available, it appears remarkable that very few studies have addressed the interrelationships of temnospondyls as a group, using both a large number of taxa and an extensive sampling of characters from the whole skeleton. However, the very large number of species (many of which require revision) implies that any comprehensive cladistic treatment of temnospondyls appears to be unfeasible at present.

Published large-scale phylogenies have focused mostly on Stereospondyli, a diverse clade of temnospondyls ranging from the Lower Permian to the upper Lower Cretaceous, and with a peak in diversity in the Lower Triassic (e.g. Milner 1990; Schoch & Milner 2000; Yates & Warren 2000; Warren 2000; Warren *et al.* 2001). In contrast, no papers have tackled in detail the interrelationships of Palaeozoic taxa. In this context, all the available studies have usually targeted the phylogenetic position of one or a few key species using small exemplars (*sensu* Prendini 2001) outside the groups of interest (e.g. Milner & Sequeira 1994, 1998; Holmes *et al.* 1998; Laurin & Soler-Gijón 2001, 2006; Sequeira 2004; Sidor *et al.* 2005; Damiani *et al.* 2006; Steyer *et al.* 2006). In other papers (e.g. Bolt 1991; Trueb & Cloutier 1991; Gardner 2001; Ruta *et al.* 2003), emphasis on the temnospondyl theory of amphibian origins implies that both the Carboniferous and the Permian exemplars are dominated almost exclusively by members of the Dissorophoidea (e.g. Bolt 1969, 1974a–c, 1977, 1979, 1991; Milner 1988, 1990, 1993; Schoch & Rubidge 2005), because these have been placed in close phylogenetic proximity to at least some of the crown amphibians (Schoch & Milner 2004). Finally, we note that even the most comprehensive recent cladistic analyses of early tetrapod interrelationships include only a limited number of Palaeozoic species (e.g. seven in Vallin & Laurin 2004; 21 in Ruta *et al.* 2003, of which 12 are represented by dissorophoids). A novel cladistic analysis of early tetrapods, based upon an increased sampling of postcranial data and including numerous species from all major temnospondyl groups, is currently being prepared by Dr Kat Pawley (pers. comm. 2006), formerly at the Department of Zoology of La Trobe University in Melbourne, Australia.

Despite much recent progress in our understanding of both comparative morphology and family-level interrelationships of temnospondyls (e.g. Milner 1990; Holmes 2000), numerous phylogenetic problems persist. In this connection, new and better information is of paramount importance. In particular, taxa that show either unusual features or combinations of characters observed in different groups are of remarkable interest, because they may provide additional data on the polarity of several anatomical traits and thus potentially elucidate the pattern of relationships even within well-established clades.

Recently, the present authors initiated a series of investigations into the anatomy and affinities of some poorly understood Carboniferous and Permian temnospondyls, as part of a research project that aims to develop a character data base for use in future cladistic analyses. One of the least well known taxa, and the subject of the present work, is *Perryella olsoni* (Lower Permian, Wellington Formation, Noble County, Oklahoma), first described by Carlson (1987; for the stratigraphic and geological settings of the collecting site, see Carlson 1968). Carlson's (1987) original work was based mostly on the skull and associated fragmentary postcranial material of the holotype, with additional information from several other specimens, not all of which were adequately prepared and/or figured at that time. Carlson (1987) described a puzzling combination of features in *Perryella*. In some of these features, *Perryella* resembles members of the superfamilies Dissorophoidea and Trimerorhachoidea (the latter taxonomic term is now considered to be obsolete and is formally replaced by Dvinosauria; Yates & Warren 2000). Carlson (1987) accordingly suggested that *Perryella* should be regarded as an *incertae sedis* taxon, pending a better knowledge of the morphology and interrelationships of several other Palaeozoic taxa. In 1990, Milner placed *Perryella* among the Dissorophoidea, but likewise treated it as *incertae sedis*. More recently, based upon additional observations of the type specimens, Milner & Sequeira (1997) suggested that *Perryella* represents an aberrant member of the Amphibamidae, one of the more derived families of dissorophoids (Bolt 1991; Milner 1990, 1993; Schoch & Rubidge 2005). Understanding of the taxonomic composition and intrinsic relationships of dissorophoids, dvinosaurs, and other temnospondyls has changed significantly since Carlson's (1987) paper. As new comparative data have become available, it is appropriate to reconsider both the affinities of *Perryella* and their bearing on the interrelationships of major clades of non-stereospondyl temnospondyls. Additional mechanical preparation of the type material of *Perryella* has yielded a considerable amount of important new information, which has allowed us to amend the original description and diagnosis.

The descriptive part of this paper focuses mostly on the cranial anatomy of *Perryella*, as data on its postcranium are still limited. We also present the first computer-assisted cladistic analysis of several of the best known Permian and Carboniferous (and some Lower Triassic) temnospondyls. The major conclusion from the present investigation is that *Perryella* is a member of the Dvinosauria, although many of its cranial features appear to be autapomorphic within this clade. These results augment our knowledge of both stratigraphic and geographical distribution of dvinosaurs, and add to the spectrum of morphological variation in this group.

1. Methods

Consolidation of specimens through the application of cyanoacrylate superglue, followed by mechanical preparation using a pin vice, revealed small and often delicate anatomical details of several structures (including the quadrate, palatal bones, morphology and distribution of the palatal dentition, choana, basicranial articulation, dorsal surface of the parasphenoid, limb and girdle elements), and resulted in further exposure of elements that had been only partially prepared at the time of the original description. In several cases, it was necessary to remove layers of plaster and a thin coating of glue that had been used to reinforce brittle or fragmented specimens at the time of the original preparation.

Various specimens were drawn using a camera lucida. Four enlarged projections of the skull (dorsal, ventral, right lateral, and right half of occipital) were drawn.

2. Taxonomic terminology

In this paper, the vernacular term 'dvinosaurs' implies a reference to Dvinosauria *sensu* Yates & Warren (2000), including the families Trimerorhachidae, Eobrachyopidae, Dvinosauridae, and Tupilakosauridae. The Eobrachyopidae, Dvinosauridae, and Tupilakosauridae are grouped together in the clade Dvinosauroidea *sensu* Yates & Warren (2000), informally referred to as 'dvinosauroids' hereafter. The vernacular term 'dvinosaurids' applies exclusively to the family Dvinosauridae. Finally, we opted for the term Zatracheidae (vernacular: zatracheids) instead of Zatrachydidae (vernacular : zatrachydids) (Welles & Peachy 1953; F. Witzmann, pers. comm. 2006) for a small clade of temnospondyls characterised by the possession of tubercles and horn-like bony outgrowths of the cheek and mandible.

3. Systematic palaeontology

Amphibia Linnaeus, 1758
Temnospondyli Zittel, 1888
Dvinosauria Yates & Warren, 2000
Dvinosauroidea Watson, 1919
Family unassigned
Genus *Perryella* Carlson, 1987
Perryella olsoni Carlson, 1987
Figs 1–24

Repository. Science Museum of Minnesota (SMM), St. Paul, USA. Catalogue numbers of all referred specimens are preceded by the same institutional acronym, hereafter omitted for brevity.

Holotype. P82.10.1, nearly complete skull, shoulder girdle, remnants of limbs.

Referred material. The following list is from Carlson (1987, p. 135–136): 'P82.10.2, vertebrae, limb; P82.10.3, partial skull; P82.10.4, vertebrae; P82.10.5, partial skull; P82.10.6, skull, vertebrae, limb; P82.10.7, partial skull; P82.10.8, partial skull; P82.10.9, parasphenoid, vertebrae; P82.10.10, skull; P82.10.11, partial skull; P82.10.12, vertebrae; P82.10.13, partial skull; P82.10.14, partial skull; P82.10.15, skull fragments; P82.10.16, partial skull; P82.10.17, partial skull; P82.10.18, vertebrae.'

Age, horizon, and locality. Lower Permian, Wellington Formation, Noble County, Oklahoma. See Olson 1967 and Carlson (1968, 1987) for details.

Emended diagnosis (based on list of autapomorphies from cladistic analysis). Frontal and parietal of approximately equal length; frontal contributing to orbit margin; squamosal-tabular suture not extending onto skull table dorsal surface; anteroventral ramus of postorbital deeply wedged into dorsal ramus of jugal; maximum jugal depth ventral to orbit greater than/subequal to half length of anteroposterior orbit diameter; minimum interorbital distance smaller than anteroposterior orbit diameter; length of anteroposterior orbit diameter approximately equal to distance between posterior margin of orbit and anterodorsal margin of squamosal; orbit centre approximately at midlength between anterior extremity of premaxillae and posterior margin of skull roof; orbit centre

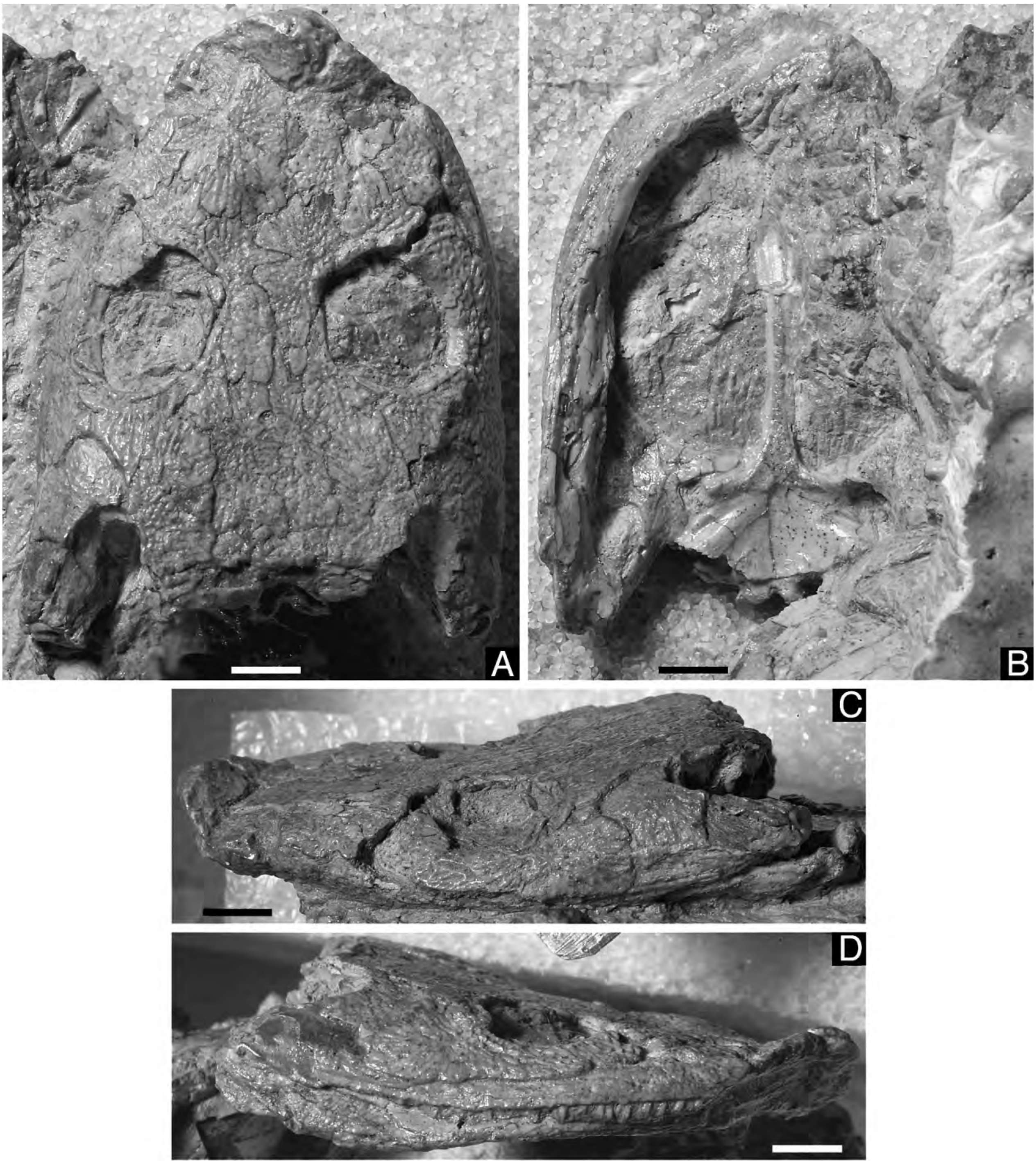

Figure 1 *Perryella olsoni* Carlson, 1987: Holotype skull (P82.10.1) in (A) dorsal, (B) ventral, (C) left lateral, and (D) right lateral views. Note general proportions and morphology of constituent bones. All scale bars = 5 mm.

closer to posterodorsal margin of squamosal than to anterior extremity of premaxillae; absence of lateral line system on skull roof; vomer with denticles; palatine with denticles; internal process of pterygoid for basipterygoid articulation with broadly triangular outline in ventral aspect; maximum combined width of interpterygoid vacuities greater than half width of skull table; parasphenoid denticles distributed exclusively anterior to the level of basipterygoid processes; absence of distinctly raised ectepicondylar ridge; internal trochanter of femur forming poorly raised rugose area; in anterior view, internal trochanter and shaft of femur not separated by deeply incised, notch-like web of bone.

4. Description

4.1. Generalities of skull table

4.1.1. Dermal ornament. The external sculpture of the skull is a well developed example of the pit-and-ridge type observed in the majority of temnospondyls (Figs 1–4, 8E, 17A, B, 19A–C). Its intensity varies considerably in different parts of the skull. The largest skull bones generally show a distinct pattern of ridges, usually radiating out from the ossification centre of the bone (e.g. parietal, frontal, supratemporal, jugal; see Bystrow 1935). However, the squamosal ornament radiates from a point situated near the posterodorsal extremity of the bone lateral surface, immediately anterior to the squamosal embayment (Figs 1A, C, D, 4, 6A, B, 8E, 17B, 19A, C, D). The ornament on smaller bones generally shows a less well developed radiating pattern (e.g. the laterally exposed portion of the palatine, or LEP; Figs 2, 3), or none at all.

4.1.2. Lateral line. The identification of any traces of a lateral line system in *Perryella* is problematic. The present authors can say confidently that there is no evidence for a system of canals running within the bones, because the communicating foramina expected in such a system are absent. Any indication of a lateral line system associated with dermal elements must therefore be in the form of open sulci. However, there is little evidence for these. Carlson (1987) identified a lateral line sulcus on the lower jaw, but as noted below, this is probably incorrect. Both in the holotype and in a few other specimens, a poorly defined and shallow groove runs parallel to the orbital margin of each of the circumorbital bones, except the jugal (Figs 1A, 3A, B, 19A). However, such a groove does not resemble closely the indisputable lateral line sulci observed in other Palaeozoic species (notably, the circumorbital pattern of eobrachyopid dvinosauroids, such as *Acroplous* and *Isodectes*; e.g. Foreman 1990; Sequeira 1998), and represents merely a shallow depression of the sculptured external surface. In the absence of clear evidence for the presence of lateral line sulci elsewhere in the skull, it is concluded that they are absent.

4.1.3. Skull sutures. Sutures are irregularly interdigitating and strongly interlocking in places (e.g. snout and most of the skull roof). At the junction between the cheek and the skull roof, they are generally smoother. Where disarticulation occurs, it is possible to observe the pattern of bone overlap in the form of underlying lamellae and/or smooth bevels (*sensu* Kathe 1999). Notably, an extensive lamella covered in weak longitudinal ridges projects from the dorsal margin of the squamosal and underlaps the postorbital (Fig. 8E). Deep to its orbital exposure, the palatine carries a series of irregular lamellae, presumably overlapped in life by prefrontal, maxilla, jugal, and lacrimal (Figs 2, 3; Carlson 1987). The anteroventral lamella of the prefrontal, partly visible in some specimens, accommodates most of the lateral half of the lacrimal (Figs 2, 3). A strongly interlocking suture occurs around the triple junction formed by squamosal, jugal, and quadratojugal (Figs 1C, D, 17B, 19C).

4.1.4. Osteological description of the skull table. General proportions of the cranial bones and morphology of the sutures are visible in the illustrations, and therefore will not be described in detail in the text.

Based upon the results of cladistic analysis (see below), *Perryella* is placed within the clade Dvinosauria. Therefore, the following descriptive account emphasises almost exclusively those features of *Perryella* that are observed in other dvinosaurs, as well as those distinctive traits that differentiate it from other members of this clade. For brevity, references to primary literature on dvinosaur taxa discussed here will not be repeated hereafter. They are as follows: Case (1935; pers. obs.) on *Trimerorhachis*; Chase (1965; pers. obs.) on *Neldasaurus*; Hotton (1959), Coldiron (1978), and Foreman (1990; pers. obs.) on *Acroplous*; Sequeira (1998; pers. obs.) on *Isodectes*; Shishkin (1973) on both *Dvinosaurus* and *Tupilakosaurus*; Warren (1999) on *Thabanchuia*; Milner & Sequeira (2004 and pers. obs.) on *Slaugenhopia*; Milner (1980) on *Eugyrinus*.

The snout is invariably disrupted or missing in most specimens, so that the identification of the premaxilla is problematic. A lightly sculptured bone fragment, visible anterior to the common suture between the nasals in the holotype (Fig. 1A), is interpreted as the remnant of a presumably left premaxilla, but no distinctive features can be discerned. A small, abraded fragment on the right side of the snout in P82.10.10 (not shown here) is likewise interpreted as a right, incomplete premaxilla. No septomaxilla could be identified in the available material.

The very broad nasals occupy the central part of the preorbital skull region, and are best seen in the holotype (Figs 1A, 19A). However, their anteriormost portions are either missing or heavily disrupted in other specimens. On both sides of the holotype skull, just anterior to the small anterior margins of the lacrimals, are two areas of matrix partially covered in plaster that may represent remnants of the external nostrils, but the outline and size of these cannot be determined. The maximum combined width of the nasals is distinctly greater than that of the frontals, as in most other dvinosaurs. However, they appear to be much larger (compared with other median paired bones of the skull table) than in other dvinosaurs, including the long-snouted *Neldasaurus*.

Uniquely among dvinosaurs, the frontals contribute to the anteromesial quarter of the orbit margin (as shown clearly by the holotype), and possess slightly raised, thickened orbital rims. As in *Trimerorhachis* and especially *Neldasaurus*, they extend well anterior to the orbits. The strong interlocking suture between the frontals, best observed in the holotype (Figs 1A, 19A), develops in various degrees in different specimens. A slightly indented suture is observed in *Neldasaurus* and, to a lesser degree, in *Acroplous* and *Isodectes*, whereas in *Thabanchuia* and *Tupilakosaurus*, this suture is strongly interdigitating. In particular, *Thabanchuia* resembles most closely *Perryella* in the interlocking pattern of the frontal bones.

The parietals are slightly narrower than the supratemporals (a common and, to the best of the present authors' knowledge, previously undiscussed feature observed in the majority of dvinosaurs) and about as long (Figs 1A, 19A). In dorsal view, they extend from a point immediately posterior to the dorsalmost part of the temporal embayment to a point slightly anterior to the posterior margin of the orbit. The small, circular parietal foramen occupies the anterior one-fourth of the interparietal suture, unlike in other dvinosaurs (except *Thabanchuia*) in which the foramen is placed slightly more posteriorly. Both degree of elongation and relative proportions of the parietals resemble those of the majority of dvinosaurs, and are accounted for by the overall lengthening of the skull roof during ontogeny (a conspicuous feature observed, in particular, in *Trimerorhachis*, *Neldasaurus*, *Acroplous*, and *Isodectes*, but developed to a smaller degree in dvinosaurids and tupilakosaurids as well).

The irregularly quadrangular prefrontals contribute both to the anterior and to a small part of the anteromesial margin of the orbit (Figs 2, 3A, B, 19A, C). The short and stout posterior process of the prefrontal has no equivalent in the majority of other dvinosaur taxa, with the sole exception of *Trimerorhachis sandovalensis* (Berman & Reisz 1980). The mesial margin of the prefrontal is strongly concave, and accommodates the laterally protruding, preorbital part of the frontal lateral margin. It also shows a slightly raised rim which is less pronounced than the orbital rim on the frontal. The shape of the prefrontal-frontal suture, best observed in the holotype (Fig. 1A), occurs in other specimens as well, and is seemingly a unique feature of *Perryella*.

The postfrontals contribute to the mesial and part of the posteromesial orbit margin, along which they carry a slightly raised rim. Each postfrontal forms a 'stepped' suture with the parietal, resulting in a sudden decrease in the parietal width at the level of, and immediately anterior to, the parietal foramen. Unlike in other dvinosaurs (except for *Dvinosaurus* itself), the postfrontal and prefrontal have similar length and width (Figs 1A, 19A).

The broadly rectangular supratemporals are about twice as long as wide, and dominate the lateral part of the skull roof

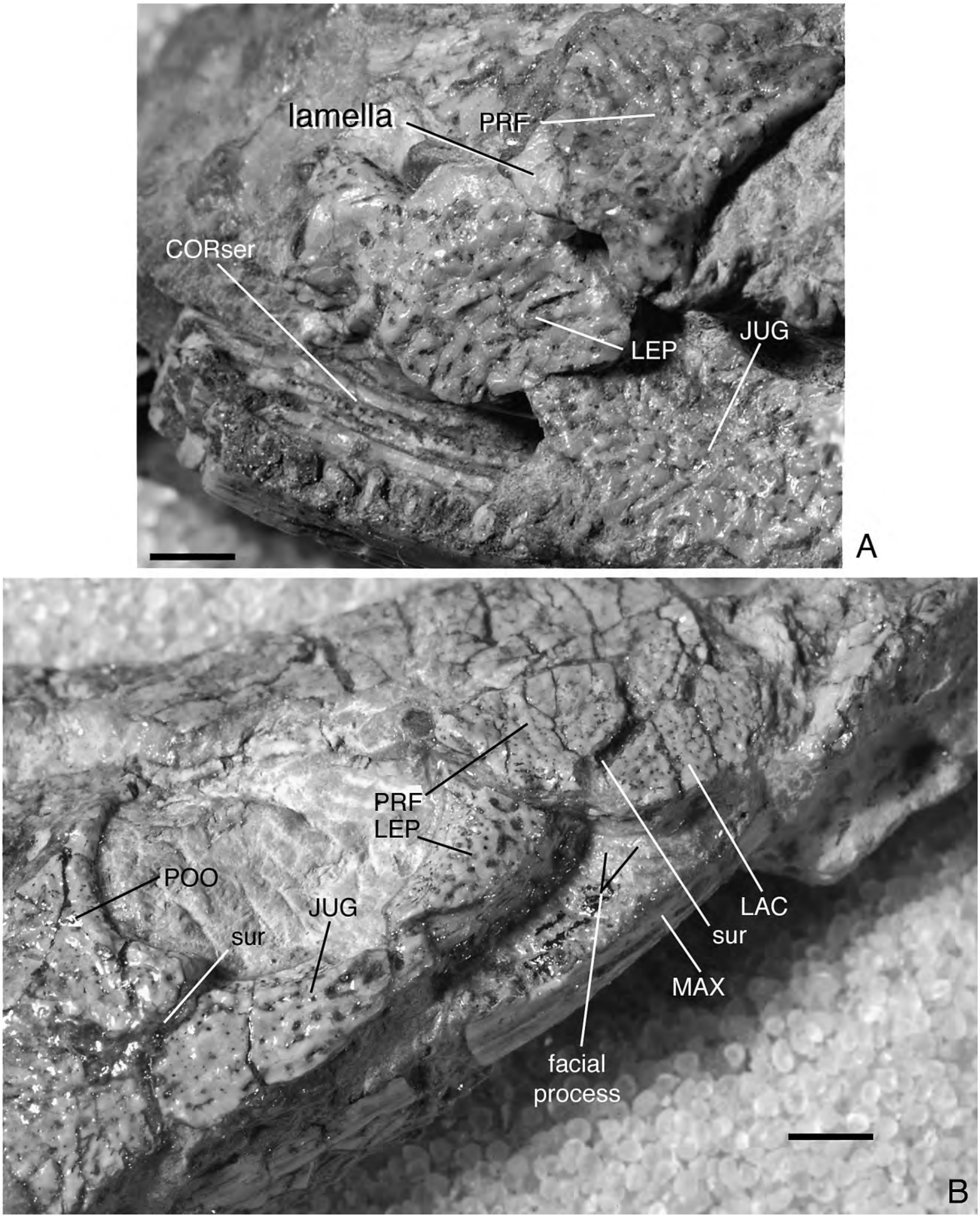

Figure 2 *Perryella olsoni* Carlson, 1987: (A) P82.10.11, anterior part of disrupted skull in left dorsolateral view; (B) P82.10.10, anterior part of disrupted skull in right dorsolateral view. Note ornamented surface of lateral exposure of palatine. All scale bars = 2 mm. Abbreviations: (CORser) series of coronoids; (JUG) jugal; (LAC) lacrimal; (LEP) lateral exposure of palatine; (MAX) maxilla; (POO) postorbital; (PRF) prefrontal; (sur) suture.

(Figs 1A, 19A). They are almost as long as the squamosals with which they form a very short suture. Posterior to this suture, the rearmost portion of the supratemporal lateral margin shows a small, shallow but distinct notch in dorsal aspect. The supratemporal-squamosal suture intersects the temporal embayment just medial to the anteriormost point of this notch.

Data on the tabulars are based almost exclusively on the holotype. In this specimen, the ornamented surface of the tabulars is reduced both in length and in width (this character is common to all dvinosaurs), and contributes to less than 25% of the skull roof width along the posterior margin of the latter (Figs 1A, 19A). Loss of the posterolateral corner of the right tabular of P82.10.1 (Fig. 1A) occurred subsequent to Carlson's

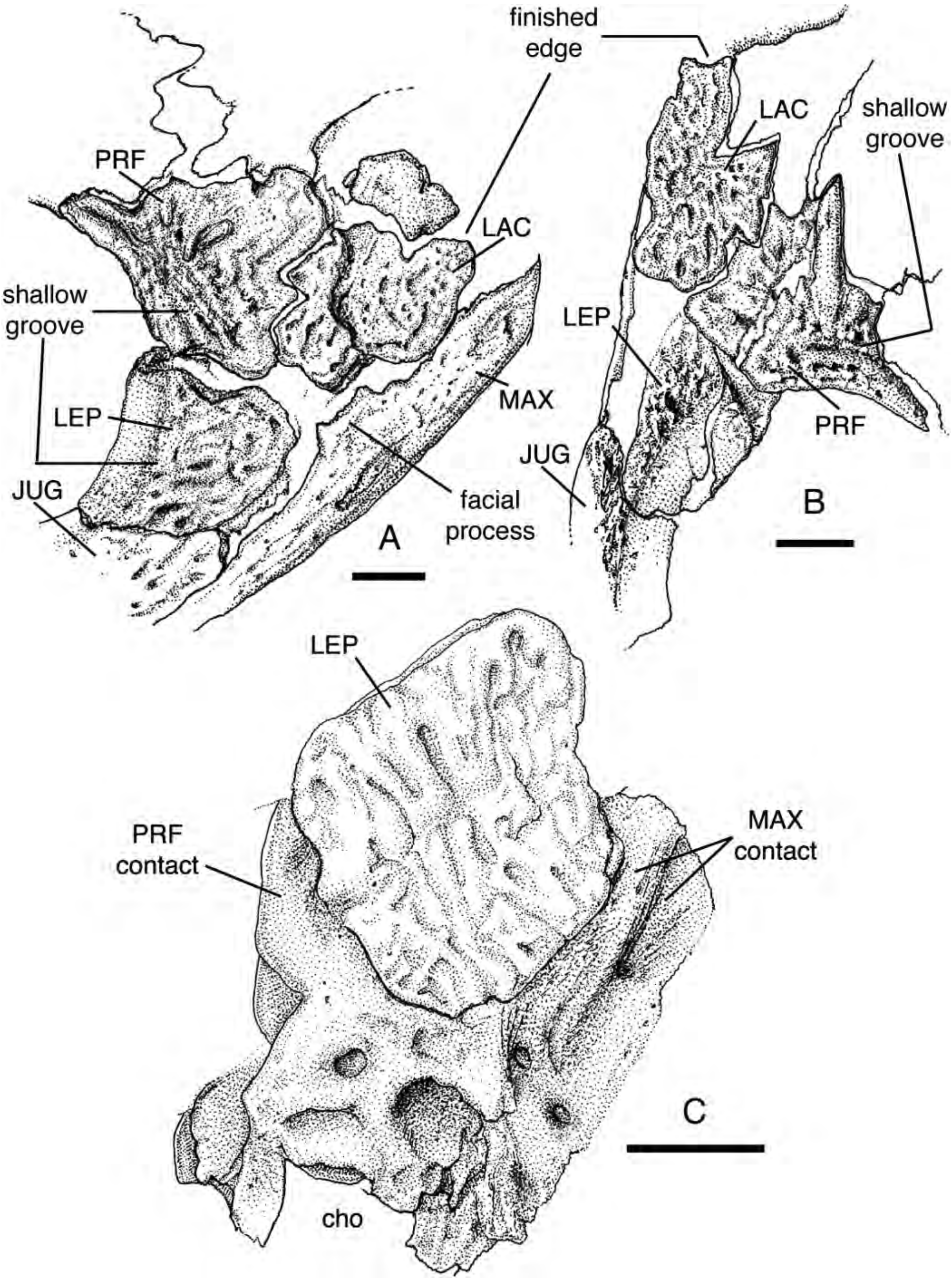

Figure 3 *Perryella olsoni* Carlson, 1987: (A) P82.10.1, camera lucida drawing of anterior part of skull and part of circumorbital bones of right side in dorsolateral view; (B) P82.10.1, camera lucida drawing of anterior part of skull and part of circumorbital bones of left side in dorsal view; (C) P82.10.11, camera lucida drawing of ornamented surface of lateral exposure of left palatine with areas of overlap for adjacent bones. All scale bars=2 mm. Abbreviations: (cho) choana; (JUG) jugal; (LAC) lacrimal; (LEP) lateral exposure of palatine; (MAX) maxilla; (PRF) prefrontal.

(1987) description. A small triangular occipital flange continues mesially into a similar, more strongly developed flange from the postparietal (Fig. 5A, B). The small tabular 'horn' illustrated by Carlson (1987) lies entirely ventral to the ornamented bone surface (data from P82.10.17, which was figured by Carlson, are informative in this respect) and appears as a thickening on the lateral portion of the dorsal surface of the occipital flange, rather than a 'horn' proper. Figure 19C illustrates a ventrally directed flange (interpreted by Carlson as providing support for the distal extremity of the stapes), based upon information from the left tabular of P82.10.17 (not figured). The connection of this flange with the stapes cannot be ascertained, due to damage.

The external, ornamented surfaces of the small, subrectangular postparietals are separated from their occipital flanges by a narrow transverse sulcus, as in the tabulars (Figs 1A, 19A). As in some (but not all) dvinosaurs (*Acroplous*, *Isodectes*, and *Tupilakosaurus*), a distinctive character of the postparietal of *Perryella* is the fact that its ornamented surface decreases in length abruptly in a mediolateral direction, and forms an L-shaped ('stepped'; Sequeira 1998) suture with the supratemporal. The postparietal–supratemporal suture can be followed in part on the right and left side of the skull table of the holotype, immediately anteromesial to the postparietal-tabular sutures.

The maxilla extends posteriorly to a point situated slightly behind the quadratojugal mid length, and overlaps extensively the ventral underlying lamella of the latter, as clearly seen in P82.10.11 (Fig. 17B). More anteriorly, the depth of the maxilla is slightly smaller than that of the suborbital ramus of the jugal, and increases slowly from the level of the anterior margin of the orbit forward (Figs 1C, D, 17A, B). Anteriorly, it forms a low dorsal (facial) process (Figs 2B, 3A). The maxilla resembles those of *Trimerorhachis* and *Neldasaurus* in proportions, but differs from the foreshortened maxillae of eobrachyopids and other dvinosauroids.

The lacrimal is separated from the margin of the orbit by the prefrontal-palatine contact, and is sutured with the maxilla immediately anterior to the maxillary dorsal process (Figs 1A, C, D, 2, 3). In the holotype, both lacrimals display a small finished edge along their anterior margins, which presumably bordered the nostrils. Outline and proportions of the lacrimals of *Perryella* are unique. Thus, they differ from the long, narrow, and almost strap-like lacrimals of *Neldasaurus*, from the vaguely ‘cleaver’-shaped lacrimals of *Trimerorhachis*, and from the subtrapezoidal lacrimals of *Acroplous* and *Isodectes*. They are nearly equidimensional and approximately square in outline, and form strongly interdigitating sutures with prefrontals and nasals.

The jugal contributes to most of the ventral and posteroventral parts of the orbit margin (Figs 1C, D, 17B). It is unique among the circumorbital bones, in that it does not possess a raised orbital rim. However, it shows a smooth, conspicuous orbital wall oriented at a slightly obtuse angle with its external surface. The overall aspect of the bone is massive and, unlike the jugal of other dvinosaurs (except for *Neldasaurus*), its depth does not decrease substantially anteriorly.

The postorbital is triangular. Its posterior corner is deeply wedged between supratemporal and squamosal (Figs 1A, 19A), and nearly reaches the level of the anteriormost portion of the temporal embayment. The bone contributes to most of the posterior margin of the orbit, and bears a slightly raised rim. Its lateral corner is accommodated by a notch situated on the dorsal margin of the jugal. The postorbital of *Perryella* resembles those of *Acroplous* and *Isodectes*, differing from those only in its more triangular outline (greater width : length ratio) and in the fact that its lateral process extends lateral to the orbit’s lateralmost margin (in dorsal aspect).

The squamosal (best seen in Figure 17B) has a deep embayment (temporal notch). From the posterior margin of its ornamented surface, a smooth flange (also known as descending lamina of squamosal) projects internally and is exposed in occipital view (Figs 1A, C, D, 4, 6A, B, 8E, 19C). The flange is trough-shaped, unsculptured, covered in foramina and faint furrows, and is delimited from the rest of the external surface of the bone by a slightly raised rim. In its posterior part, the surface of the squamosal flange carries a small anteroposterior ridge. This ridge (Fig. 8E) emerges indistinctly from the surface of the flange, becomes stronger posteriorly (where it carries a sharper dorsal edge), and runs slightly closer to the medial than to the lateral margin of the flange. In its most posterior tract, the ridge produces a small but distinctive swelling. At this level, the ridge turns slightly ventralward and merges into the rearmost portion of the squamosal, which is nearly vertical and vaguely crescent-like. This crescent-like area continues smoothly into the lateral surface of the bone. Just anterodorsal to the region where the crescent-like area joins the lateral surface is a shallow longitudinal trough (Fig. 8E). The ventral edge of the crescent-like area is deeply concave, and produces a blunt process medially, which was presumably in contact with the dorsal surface of the quadrate (as in *Trimerorhachis*). The lateral portion of the crescent-like area is flat.

Perryella differs from other dvinosaurs in having a deeply incised squamosal embayment and a convoluted squamosal-quadratojugal suture. The embayment is similar in proportions to those of dissorophoids, but it is less deep dorsoventrally (in lateral view), and less concave anteroposteriorly. However, we point out that it compares well, in shape and size, with the embayment of some of the largest *Trimerorhachis* skulls (pers. obs.), although its outline is more deeply concave than in the latter.

The quadratojugal (Figs 1C, D, 6A-d, 17B, 18B, C, 19C) consists of an elongate body exposed on the ventrolateral surface of the skull and a small occipital surface (Figs 6A, B, 8D, E). Ventrally, the body shows an extensive lamella underlapped by the maxilla; dorsally, the quadratojugal underlaps the squamosal along a flat bevel (only partially visible) (Fig. 17B). The boundary between the lateral and occipital surfaces is marked by an abrupt termination of the bone’s dermal sculpture.

The occipital surface is divided into a lateral and a mesial area by a low oblique ridge. The lateral area is shallowly concave and slightly tilted dorsally, where it joins the posteriormost extremity of the squamosal (see above). The mesial area carries a mesially-open notch which may appear dorsoventrally narrow or deformed to various degrees, and is delimited by dorsal and ventral blunt processes (Fig. 8D). These are irregularly triangular to digitiform and often broken mesially. In P82.10.6 (right side), they nearly contact each other. Comparisons with other temnospondyls suggest that the notch is homologous to the paraquadrate foramen. The latter occupies more than 50% of the quadratojugal occipital surface in dvinosaurs and some stereospondyls. Thus, *Perryella* is unique in showing an incomplete foramen, the medial portion of which would be delimited by the rearmost part of the lateral surface of the quadrate. In P82.10.1, the occipital surface of the left quadratojugal carries a small, subcircular foramen (?accessory paraquadrate foramen; Shishkin 1973) situated lateral and slightly ventral to the dorsal and ventral processes of the quadratojugal occipital surface (Figs 4A, 8D). The foramen opens at the bottom of a shallow recess, where the two processes meet. Immediately lateral to this recess, a web of bone extends between the two processes (Fig. 8D, E).

Ventrally and posteriorly, the quadratojugal shows a cup-like bony structure (Figs 6B–D, 18B, C, 19B). In ventral aspect, a narrow neck delimits the ‘cup’ from the lateral part of the occipital surface of the bone. The medial portion of the ‘cup’ is occupied by the posterolateral surface of the quadrate. The ossified portion of the quadrate does not extend to the lateralmost extremity of the cup, and the rugose morphology of the latter indicates that it was probably filled with a cartilaginous pad in life. Carlson (1987) argued that in P82.10.6, the quadratojugal forms part of the jaw joint (specifically, the ‘cup’ would clasp a swelling on the lateral surface of the articular). Close examination of this specimen, however, reveals that some displacement has taken place, and that part of the swelling is in fact formed by matrix.

Poorly preserved sclerotic plates are observed in the holotype (Fig. 1A), but their outline and number cannot be reconstructed.

4.2. Palate

Preparation has revealed a substantial amount of new morphology on the palate (Figs 10–16). Nearly complete and fully exposed right vomers occur in P82.10.5 and P82.10.10. The vomer is longer than wide, and bears a robust and slightly curved fang, only slightly compressed mediolaterally in its distal half, as well as a replacement pit (neither the fang nor the pit are visible in the holotype; Figs 10A, 11, 12A, C, 19B). The fangs are situated in close proximity and anterior to the choana. The vomer palatal surface extends for an uncertain

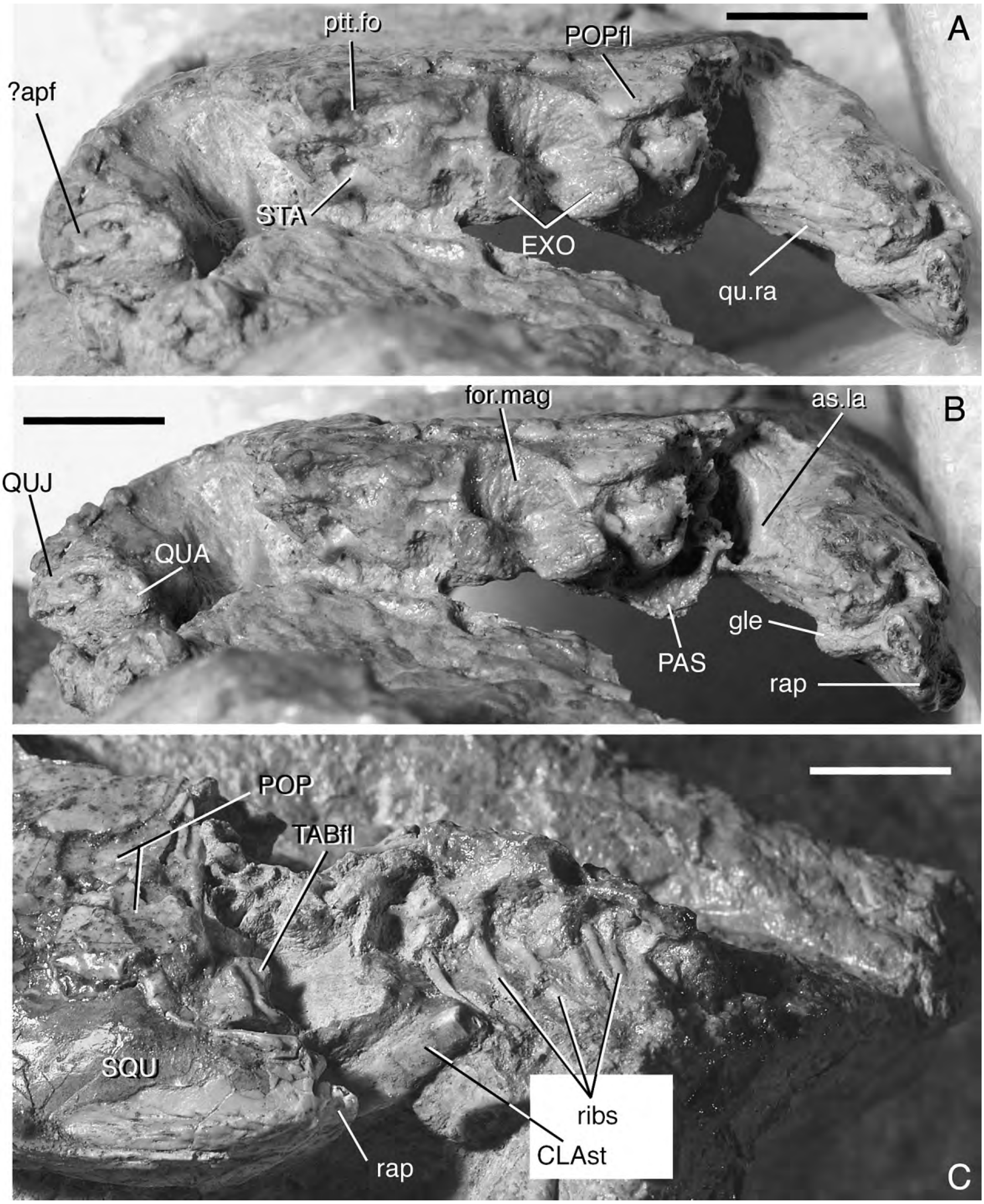

Figure 4 *Perryella olsoni* Carlson, 1987: (A, B) P82.10.1, two slightly different views of skull in occipital view; (C) P82.10.6, left dorsolateral view of incomplete skull plus associated anterior portion of postcranial skeleton. Note occipital flanges. All scale bars = 5 mm. Abbreviations: (apf) accessory paraquadrate foramen; (as.la) ascending lamina of pterygoid; (CLAst) clavicle stem; (EXO) exoccipital; (for.mag) foramen magnum; (gle) glenoid surface of articular; (PAS) parasphenoid; (POP) postparietal; (POPfl) postparietal flange; (ptt.fo) posttemporal fossa; (QUA) quadrate; (QUJ) quadratojugal; (qu.ra) quadrate ramus of pterygoid; (rap) retroarticular process of lower jaw; (SQU) squamosal; (STA) stapes; (TABfl) tabular flange.

distance anterior to the fang and pit. Neither transverse nor perichoanal tooth rows are present. Most of the palatal surface is covered in a shagreen of tiny denticles, of which only the bases are visible. In some places, the denticles form irregular longitudinal rows. The interchoanal region shows one or two weakly developed ridges, but most of this area is heavily fractured. A conspicuous palatine process articulates with, and overlaps in part, the palatine just mesial to the posterior margin of the choana. The body of the vomer extends slightly posterior to the level of the posterior margin of the choana and flanks the anterior extremity of the cultriform process. As a result, the latter is narrowly wedged between the vomers, and perhaps slightly overlapped by them. Just mesial to the palatine process, the smoothly sinuous posterior margin of the vomer contributes to the anterior margin of the interpterygoid vacuity.

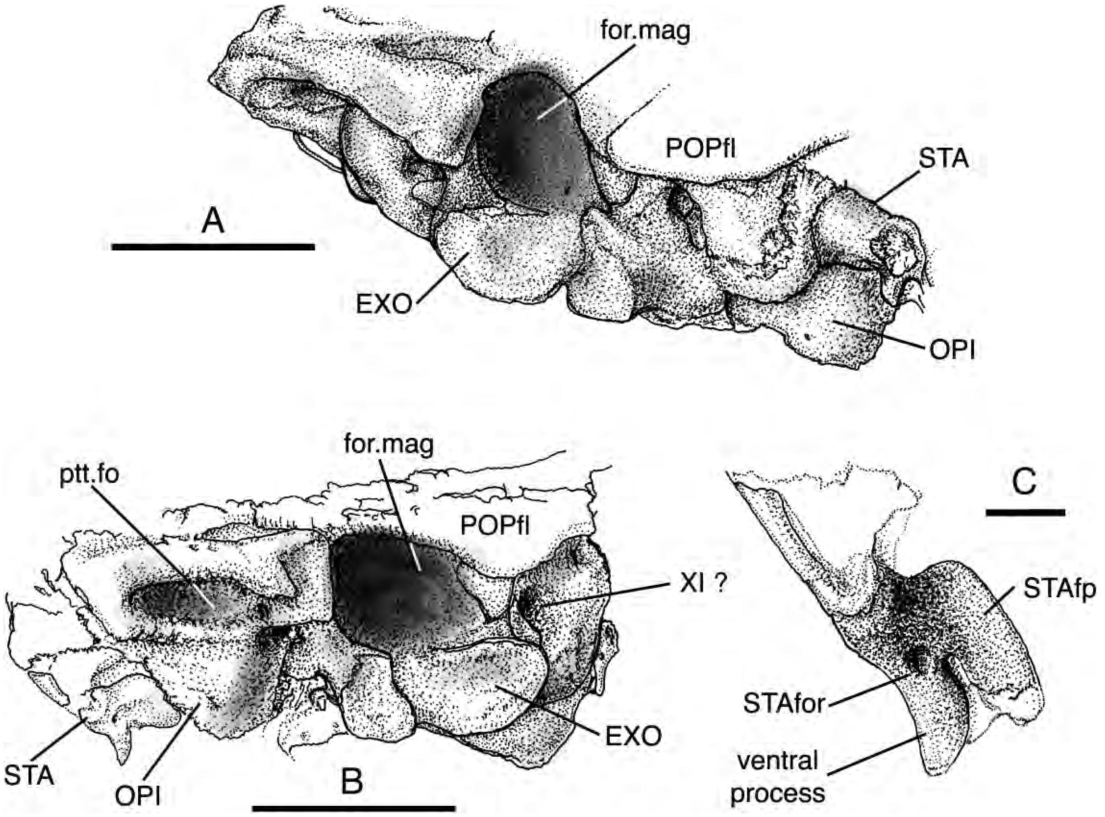

Figure 5 *Perryella olsoni* Carlson, 1987. P82.10.1: Camera lucida drawings of (A, B) right posterolateral and left posterolateral views, respectively, of occipital surface of skull, and (C) left stapes. Note elliptical posttemporal fossa, swollen opisthotic with possible opening for XI cranial nerve, and stapedial foramen. Scale bars in A, B = 5 mm; scale bar in C = 1 mm. Abbreviations: (EXO) exoccipital; (for.mag) foramen magnum; (OPI) opisthotic; (POPfl) postparietal flange; (ptt.fo) posttemporal fossa; (STA) stapes; (STAfor) stapedial foramen; (STAfp) stapedial footplate; (XI) opening for 11th cranial nerve.

The palatine (Figs 10A, 11, 12A, B, D, 19B) shows a massive fang and a replacement pit (only slightly smaller than those on the vomer) in the central part of its palatal surface, on a slightly raised area with irregularly ornamented texture and scattered foramina. The lateralmost part of the palatal surface is not visible in any specimen. Anterior to the fang and pit, robust ridges and excavations run almost longitudinally. Anteriorly, the choanal margin of the bone is delimited by an anterolateral and an anteromesial process. The former is poorly preserved, but appears to have been shorter than the latter. The anteromesial process is smooth. Its choanal margin thins slightly anteriorly. Medially, it abuts against, and apparently overlaps in part the palatine process of the vomer. Denticles are sparsely distributed on the palatine. Behind the fang and pit, the palatal surface of the bone is very irregular. A short, crest-like, and eroded tooth row extends for a short distance posterior to the fang. The articulation of the palatine with surrounding bones was discussed by Carlson (1987). The lateral exposure of the palatine (LEP) widens slightly anteriorly. It consists of an irregularly sculptured lateral surface and a smooth, mesial shelf lying within the orbit. This shelf continues posteriorly onto the jugal and anteriorly onto the prefrontal (Figs 2, 3).

A slender, incompletely preserved sliver of bone on the right side of the palate of P82.10.5, is interpreted as the remnant of an ectopterygoid (Fig. 12A). The present authors rule out the possibility that the element in question represents an extension of the palatine, given its position, its general proportions relative to those of the surrounding bones, and the fact that it carries two eroded replacement pits. Immediately posterior to these pits, the surface of the bone is irregular and without distinctive features. A small, acuminate, triangular fragment with finished margins lies mesial to the posteriormost part of the ectopterygoid, as preserved. It probably represents the anterior end of the palatal ramus of the right pterygoid. In a second specimen, P82.10.10, the anterior extremity of the palatal ramus of the right pterygoid abuts against the posterior part of the mesial margin of the ectopterygoid. This spatial configuration of palatal bones is reminiscent of the condition in eobrachyopids and tupilakosaurids, but occurs in several other temnospondyls as well (chiefly among stereospondyls).

The pterygoid (Figs 1B, 10B, 13, 19B) is distinctly triradiate, but remains incompletely known because the lateralmost portion of the palatal ramus is usually covered by the lower jaw rami. In its general proportions, the pterygoid of *Perryella* resembles most closely that of *Trimerorhachis*. If the pterygoids are oriented anatomically, then it is possible to deduce that the anterior extremity of the palatal ramus extended approximately to the level of the orbit mid length. Both the posterior margin of the vomer and the preserved part of the medial margin of the palatine contribute to the broad palatal vacuities. These observations suggest that the palatal ramus of the pterygoid either reached as far anteriorly as the posteriormost part of the medial margin of the palatine, or formed only a point contact with the posterior extremity of this margin (which is the configuration shown by *Acroplous* and *Isodectes*). It is also possible that the palatal ramus of the pterygoid did not extend beyond the ectopterygoid (the situation observed in *Tupilakosaurus* and, possibly, *Thabanchuia*). The medial margin of the palatal ramus is more strongly concave than that of any other dvinosaur. The preserved portion of its ventral surface is flat and covered by an extensive shagreen of denticles, represented only by their bases in the available

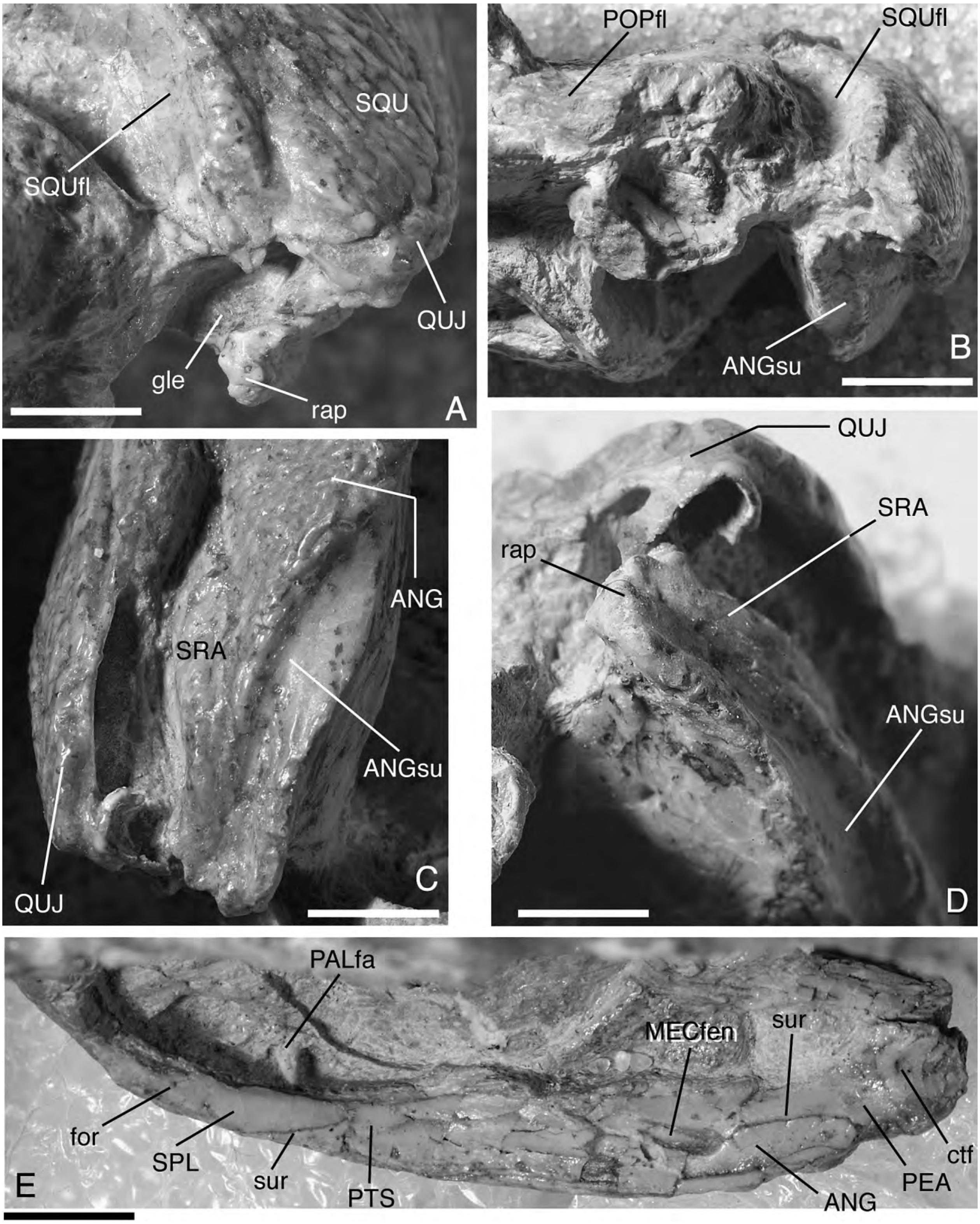

Figure 6 *Perryella olsoni* Carlson, 1987: (A–D) P82.10.11, posterior part of suspensorium and lower jaw (including lower jaw articulation) of right side in (A) dorsolateral, (B) occipital, (C) ventrolateral, and (D) posteroventrolateral views; (E) P82.10.1, right lower jaw ramus in ventromesial view. Note cup-like structure on ventral surface of quadratojugal, extension of squamosal flange, and elongate sulcus on angular. All scale bars=5 mm. Abbreviations: (ANG) angular; (ANGsu) angular sulcus; (ctf) chorda tympani foramen; (for) foramen; (gle) glenoid surface of articular; (MECfen) Meckelian fenestra; (PALfa) palatine fang; (PEA) prearticular; (POPfl) postparietal flange; (PTS) postsplenial; (QUJ) quadratojugal; (rap) retroarticular process of lower jaw; (SPL) splenial; (SQU) squamosal; (SQUfl) squamosal flange; (SRA) surangular; (sur) suture.

specimens. The denticulated area follows closely the curvature of the palatal vacuities, but stops short of the mesial margin of the palatal rami, thus delimiting the internal edge of a smooth, narrow flange with a gentle dorsal slope. The denticulated area extends to the proximal third of the ventral surface of the internal process (for basipterygoid articulation), as well as to the lateral and central parts of the anterior region of the quadrate ramus (see below; Fig. 13).

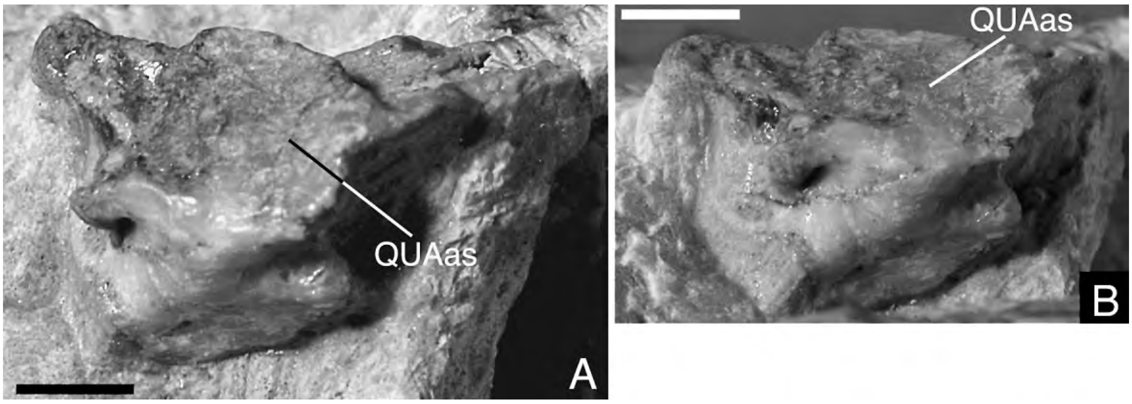

Figure 7 *Perryella olsoni* Carlson, 1987: (A, B) P82.10.11, two slightly different views of articulation surface of quadrate; identification of the latter as a left or right element proved to be impossible. Note processes and depressions on the bone. All scale bars = 2 mm. Abbreviations: (QUAas) articulation surface of quadrate.

The robust internal process for the basipterygoid articulation has a slightly concave (in ventral view) anterior profile, and merges smoothly into the palatal ramus. In a parasagittal section, its anterior surface is strongly convex. Its articulation facet is elongate mediolaterally. No further details are available (Fig. 13).

In ventral aspect, the quadrate ramus is divided into a broad, subquadrangular anterior part and a posteriorly tapering, subrectangular posterior part (Fig. 13). The anterior part is flat in its mesial half, but slopes slightly ventrolaterally in its lateral half. The posterior part is nearly straight and oriented slightly posterolaterally. It is flat or only slightly concave medially, and curves ventralward laterally. Its flat rearmost portion terminates bluntly, and rests against the mesial wall of the quadrate (Figs 8C, 9B–D, 17C; see below). In occipital view (Figs 4A, B, 19D), the quadrate ramus confers a 'vaulted' profile to the palate, as in several dvinosauroids (see description of this condition in Warren & Hutchinson 1983 and Warren & Marsicano 1998, and comments in Bolt & Chatterjee 2000). In ventral aspect, the lateral margin of the quadrate ramus turns abruptly laterally and continues into the pterygoid basicranial region (or corpus) along a slightly sinuous course. A thin, posteromesially concave ascending lamina raises from the dorsal surface of the quadrate ramus (Figs 4B, 19D). The lamina is markedly separate from the squamosal by a narrow space.

A peculiar feature of the pterygoids is the presence of a notch on the posterolateral margin of the corpus, aligned nearly transverse to the basipterygoid process (Fig. 13). The corresponding area of both pterygoids in the holotype is not clearly visible, and therefore comparisons with other specimens are limited. The notches are lined by smooth, finished periosteal bone and extend anteromesially for a short distance, terminating abruptly. They do not merely form excavations along the posterolateral margin of the corpus. In addition, a thin bony sheet extends across their dorsal portion, so that they form ventrally open recesses within the thickness of the corpus. These notches are not considered to be homologous with the so-called pterygoid incisures of tupilakosaurid dvinosaurs (Shishkin 1973; Warren 1999; Milner & Sequeira 2004). The tupilakosaurid incisures occupy a narrow space between the stout quadrate ramus and the robust and abbreviated basipterygoid process. In contrast, the pterygoid notches of *Perryella* are lateral to the quadrate ramus. To the best of our knowledge, no other temnospondyl possesses such notches.

4.3. Quadrate and epipterygoid

The quadrate has a complex morphology, although is it is not exposed in the round in any of the specimens (Figs 7, 8A–D, 9). Its dorsal surface, so far as it can be determined, is smooth, flat, and nearly featureless except for a conspicuous crest, broadly convex in lateral profile, that widens slightly from posterior to anterior. In its posterior part, the crest merges with the quadrate's posterior surface. Mesially, it continues smoothly with the bone's mesial surface. Laterally, it arises abruptly from its dorsal surface (Fig. 9C, D). The quadrate's mesial and lateral surfaces are occupied by large, shallow depressions intercalated with broad, low ridges (Fig. 9A). These surfaces pass almost indistinctly into the posterior surface, which appears featureless except for the presence of a shallow ventral depression. The subelliptical ventral surface is divided into a lateral (smaller) and a medial (slightly larger) facet (Fig. 9B). Together, these facets form the articular portion of the quadrate. This is slightly smaller than the glenoid area of the articular bone proper, but whether the lateral part of the glenoid area articulated with the ventral surface of the quadratojugal is dubious (cf. Williston 1915 and Case 1935; see also below). In occipital view, the quadratojugal foramen would be bounded laterally by the finger-like processes of the quadratojugal occipital exposure, and mesially by the quadrate lateral surface. In addition, the squamosal would rest on the lateral portion of the dorsal surface of the quadrate, immediately lateral to the dorsal crest of the latter (see above) (Figs 8C–E, 9).

A small bone visible near the anterior extremity of the skull of P82.10.10 is interpreted as an epipterygoid (Fig. 14), based upon comparisons with other temnospondyls (e.g. Yates & Warren 2000, fig. 8; Robinson *et al.* 2005, fig. 7). As the present authors interpret it, it possesses a broad basal portion and an elongate ascending process, and resembles a much more lightly built version of the epipterygoid of *Edops* (Romer & Witter 1942). However, there appears to be no distinct, broad laminar otic process for the articulation with the crista parotica of the opisthotic, unlike in *Edops*, in which the process in question occurs immediately posterior to the ascending process. The presumed homologue of the otic process is represented only by a modest swelling. More laterally and posteriorly, the *Perryella* epipterygoid carries a rather irregular expansion in the form of a flat lamina. The articulation socket for the basipterygoid forms a slightly thickened, elongate rim.

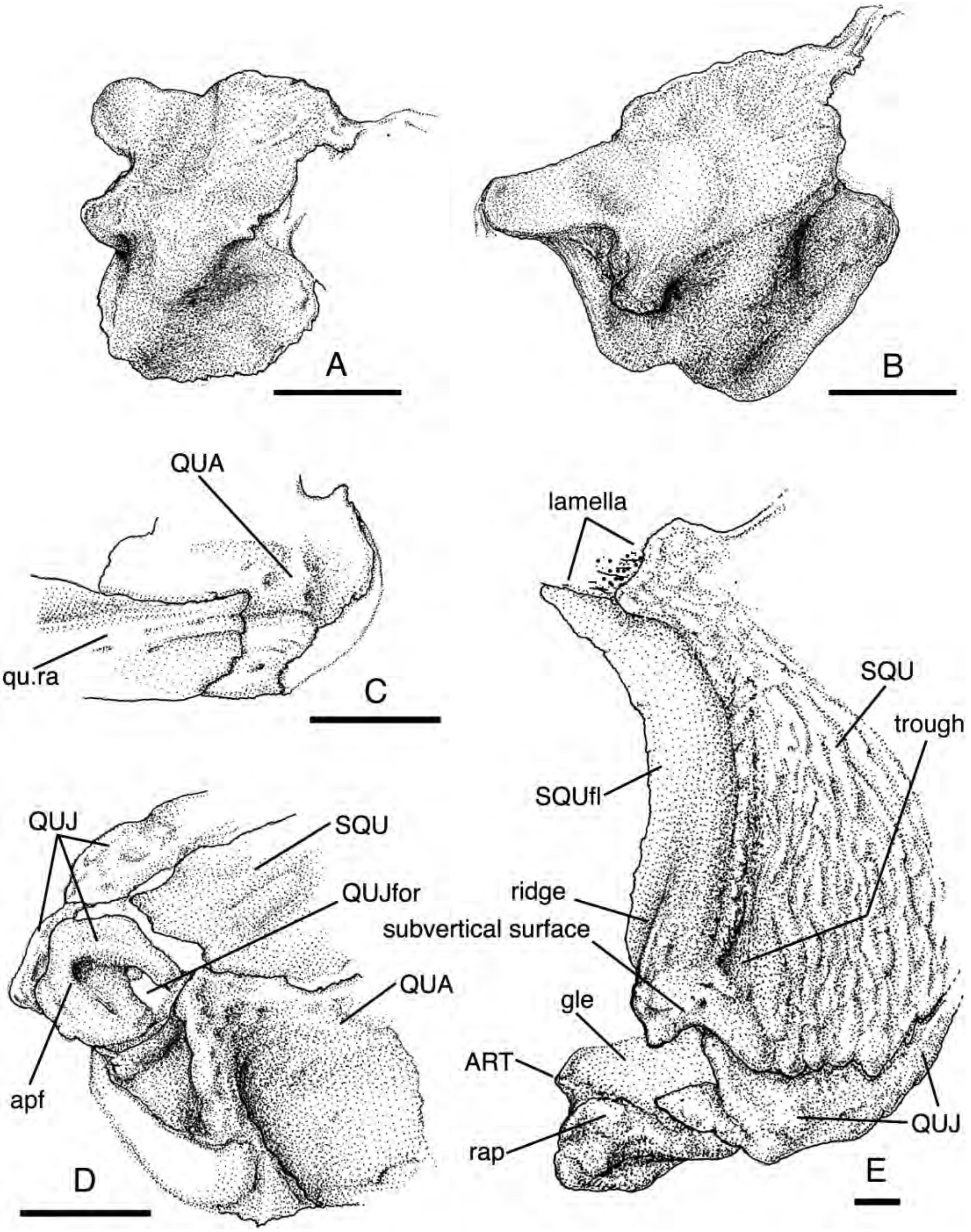

Figure 8 *Perryella olsoni* Carlson, 1987: (A, B) P82.10.5, camera lucida drawings of two slightly different views of articulation surface of quadrate (see also Figure 7); (C) P82.10.1, camera lucida drawing of mesial view of posterior extremity of pterygoid quadrate ramus from right side, abutting against mesial surface of partially preserved right quadrate; (D) P82.10.1, camera lucida drawing of posterodorsal view of posterior part of suspensorium and mesial view of partially preserved quadrate of left side; note quadratojugal foramen encircled in part by digitiform projections on posterior surface of quadratojugal; (E) P82.10.11, camera lucida drawing of posterior part of suspensorium and lower jaw (including lower jaw articulation) of right side in dorsolateral view. All scale bars = 2 mm. Abbreviations: (apf) accessory paraquadrate foramen; (ART) articular; (gle) glenoid surface of articular; (QUA) quadrate; (QUJ) quadratojugal; (QUJfor) quadratojugal foramen; (qu.ra) quadrate ramus of pterygoid; (rap) retroarticular process of lower jaw; (SQU) squamosal; (SQUfl) squamosal flange.

4.4. Parasphenoid, neural endocranium and stapes

The parasphenoid is well preserved both dorsally and ventrally (Figs 1B, 15, 16, 19B). Its subpentagonal basal plate resembles those of *Neldasaurus*, *Trimerorhachis*, and *Dvinosaurus*. It is wider than long in P82.10.1 and P82.10.9, but its posterior and posterolateral margins are slightly eroded. The preserved portion of the plate in P82.10.5 is more equidimensional in outline. Its posterior margin is either straight or gently concave. Its posterolateral margins are not as strongly embayed and elongate as those of *Neldasaurus*, and resemble more closely those of *Trimerorhachis* in general proportions and orientation. Along each lateral margin, immediately posterior to the articular processes for the pterygoid, the basal plate bears a small, shallow excavation (Fig. 16A). This marks the lateralmost boundary of a weak, shallow depression that runs anteromesially on the ventral surface (Fig. 16A, B). This depression becomes gradually less distinct from posterolateral to anteromesial, before disappearing just posterior to the posterolateral margin of the denticulated field (see below). The depression varies slightly in depth and extensions in different

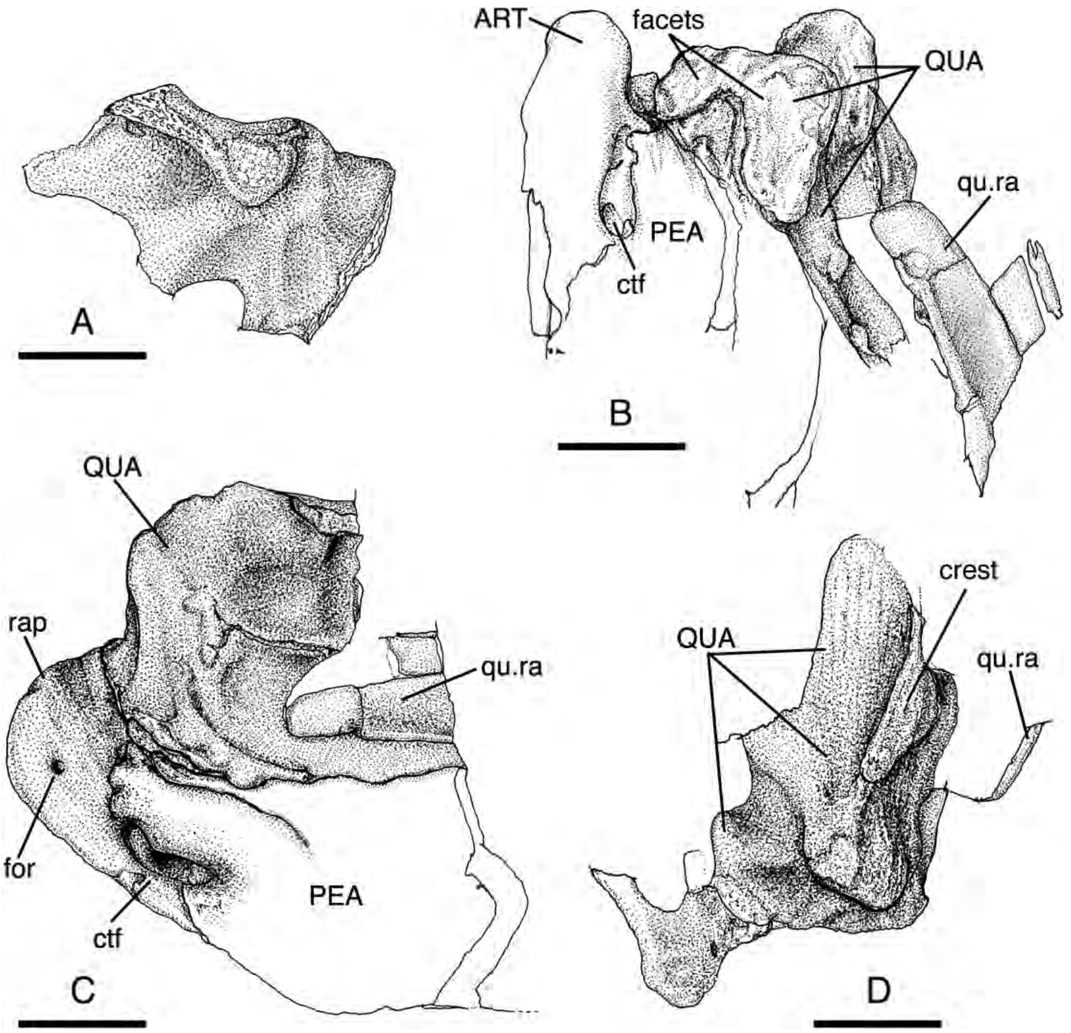

Figure 9 *Perryella olsoni* Carlson, 1987: (A–D) P82.10.5, camera lucida drawings of quadrate and posterior extremity of lower jaw of left side in articulation; (A) posterodorsolateral, (B) posteroventromesial, (C) mesial, and (D) dorsal views. Note posterior extremity of quadrate ramus of left pterygoid in mesial view. All scale bars = 2 mm. Abbreviations: (ART) articular; (ctf) chorda tympani foramen; (for) foramen; (PEA) prearticular; (QUA) quadrate; (qu.ra) quadrate ramus of pterygoid; (rap) retroarticular process of lower jaw.

specimens. A second deeper depression, or groove (Fig. 16A, B), is situated posterior to the first, runs posterolaterally to anteromesially on the lateralmost portions of the basal plate, and is delimited anterolaterally by a sharp ridge (Fig. 16A). This second depression ends in a small notch along the lateral margins of the plate, anterior to its posterolateral corners. Anteromesially, it becomes shallower before merging smoothly into the ventral surface of the plate. Similar grooves delimited by anterolateral ridges occur in *Neldasaurus* and *Trimerorhachis*, but in these taxa the ridges are less well developed and more poorly delimited from the articular processes than in *Perryella*. Grooves and ridges are not present in *Dvinosaurus*, although the latter possesses well developed notches on the lateral margins of the plate.

In all *Perryella* specimens in which the parasphenoid is exposed, the portion of the lateral margin of the basal plate immediately behind the marginal notch is damaged. Therefore, the presence of a pointed *processus parafenestralis* (see Shishkin 1973), such as is observed in *Dvinosaurus*, *Neldasaurus* and *Trimerorhachis*, cannot be ascertained. Posterior to the groove lies a robust, oblique crest (Fig. 16A, B) with a smoothly convex external surface. The central, subtriangular area delimited by the left and right crests is overall very shallow (Fig. 17A), but deepens slightly along the central part of the posterior margin of the basal plate. No foramina for the internal carotid arteries have been observed. A small, irregular opening visible in the holotype, immediately to the right of the midline and behind the denticulated area (Fig. 16A) might represent one such foramen; its identification is uncertain.

The basal plate passes anteriorly, almost indistinctly, into the cultriform process, which narrows rapidly immediately in front of the basicranial articulation, and continues anteriorly as a nearly parallel-sided structure until it meets the vomers. Here, the cultriform process widens slightly (Fig. 16B). More than half of the ventral surface of the process is covered with a denticle field that narrows to a point anteriorly (the extension of the denticle field is shown in Figures 16A and 19B). The anterior part of the process forms a shallow, median longitudinal depression, and terminates in a slightly spatulate extremity, similar to that of *Acroplous*, but less pronounced than that of other dvinosaurs. The anterior extremity of the process lies dorsal to the vomers and is partly visible between their posteromedial ends.

A denticulated field forms a slightly raised, broad triangular area on the parasphenoid plate (Figs 16A, B, 19B). The cores of tiny denticles are visible as small dark spots and as a result, the whole surface reveals a coarsely granular, shagreen texture. In lateral aspect, this surface slopes rearward and dorsalward (in anatomical orientation). It narrows rapidly anteriorly and continues as a narrow strip on the posterior half of the cultriform process, before terminating abruptly in a point.

Most of the central part of the basal plate's dorsal surface (Figs 15, 16C), well posterior to the level of the articular processes, is smooth and gently convex, except for two shallow, but clearly defined, posterior areas next to the basal plate midline. As in *Trimerorhachis*, a pair of prominent ridges run across the dorsal surface, from a point situated posterolateral to the base of the cultriform process to the basal plate's posterolateral corner (in a position that mirrors that of the ventral oblique grooves). Each ridge is blunt-topped in its anterior half, becomes sharper further posteriorly, terminates in a small process overhanging the plate margin, and separates a narrow, posteromesial, trough-like surface from a wide, anterolateral, gently concave surface. The latter rises steeply along the anterolateral corners of the basal plate, forming the lateral part of the dorsal edge of the articular (or basipterygoid) process. More mesially, the dorsal surface of the plate slopes slightly ventrally and is gently arcuate.

Just lateral to the base of the cultriform process, the mesial half of the articular process has a convex anterior margin. More laterally, this margin continues as a transversely elongate, slightly depressed facet for the articulation with the pterygoid (Figs 15, 16D). A diminutive and rather indistinct foramen is present at the base of the cultriform process. It corresponds to the arteria palatina foramen, such as was described by Shishkin (1973) in *Dvinosaurus*. There is, however, no sulcus associated with the course of this artery.

The dorsal surface of the basisphenoid is not preserved. Anterior to a transverse crack filled with matrix in P82.10.9 (Fig. 16C), the parasphenoid surface slopes slightly anteroventrally and shows a central, stout, elongate prominence flanked by two small sulci. This prominence (Fig. 16C) merges anteriorly into a subhorizontal triangular area of bone. This carries a slight central depression flanked by two deep grooves, presumably marking the course of the internal carotid arteries. The grooves deepen backward. Their posterior boundary is marked by two foramina. More anteriorly, they are separated for a short distance, then widen slightly and become confluent with a wide middle longitudinal sulcus on the cultriform process (Fig. 16C). The sulcus is delimited by two lateral ridges, which are broader posteriorly, but thinner and sharper anteriorly.

No additional information on the exoccipital, basioccipital, opisthotic, and stapes resulted from the present study (Figs 4A, B, 5; see also Carlson 1987). The large posterior articulation facets of the exoccipitals are noted, similar to the condition in dvinosaurids and perhaps also *Isodectes*, but unlike that of *Acroplous*, *Tupilakosaurus*, and trimerorhachids, in all of which an ossified basioccipital also participates in the occipital condyle (Shishkin 1973). In *Perryella*, there is no evidence of a recessed basioccipital. The peculiar shape of the stapes (Figs 4A, 5) appears to be autapomorphic for *Perryella*. Carlson (1987) identified two structures on the proximal extremity of the stapes, namely a footplate and a 'ventral process'. The latter, as implied by Carlson (1987), may be homologous to part of the 'ventral proximal head' (*sensu* Lombard & Bolt 1988), known in several temnospondyls, including *Trimerorhachis*. In other respects, however, it is difficult to compare the stapes of *Trimerorhachis* with that of *Perryella*. For instance, the stapes of *Trimerorhachis* contacts the skull only proximally, while the stapes of *Perryella* is thought to have contacted the underside of the tabular (Carlson 1987; however, this conclusion cannot be corroborated by available material). Shishkin (1975) reconstructed a stapes in *Dvinosaurus primus* in which the distal end, at least, resembles that of *Perryella* in having a similar hypothesised connection to the tabular. Appealing though this comparison may appear, it should be pointed out that Shishkin's (1975) reconstruction is also largely hypothetical: the ossified portion of the *Dvinosaurus* stapes does not preserve all the processes shown in his reconstruction, including the 'processus extrastapedialis' that forms the contact with the tabular. In this regard, the stapes of *Perryella* remains *sui generis* among temnospondyls.

4.5. Lower jaw

Information on the lower jaw is scanty. The most conspicuous details of its lateral aspect are known in several specimens (Figs 1B–D, 2A, 6, 10, 11, 17, 18), but an accurate reconstruction could not be provided. The lateral profile of its posterior extremity resembles closely those of *Trimerorhachis* and *Neldasaurus*, and is unlike the flat and nearly horizontal posteroventral profile of the *Tupilakosaurus* and *Dvinosaurus* jaws. The long, slender dentary is exposed in lateral and dorsal views only. Its maximum depth is slightly less than that of the maxilla. The bone is divided into a posterior, edentulous postdental process and an anterior, tooth-bearing portion. The postdental process narrows rapidly in its rearmost part before it ends at a bluntly truncated point. Its course suggests that the dentary abutted against the lateral surface of the anterior third of the surangular, as in *Trimerorhachis*. Most of its external surface is smooth or shows very low, irregular flat ridges and shallow pits, and resembles a weak version of the sculpture on the infradentary bones (see below). A denser pitting is observed on the tooth-bearing portion. The lateral surface of the dentary bears a shallow but distinct and very linear groove (e.g. Fig. 17A). This groove is present in approximately the anterior one-third of the dentary. However, it is noted that no specimen displays the symphysial region; therefore, the full anteroposterior extent of this sulcus remains uncertain. Carlson (1987) considered it to be a lateral line sulcus, in which case it would presumably be homologous to the oral sulcus, but this is not certain. Its posterior connection with the mandibular sulcus cannot be seen, and its narrowness and constant dimension over its observable course, in conjunction with its extreme linearity, are problematic. We suggest that this groove may not be associated with the lateral line system at all, and may in fact represent a groove for the external mandibular artery.

In ventral aspect, the splenial occupies less than one-third of the lower jaw length. Its ornamented surface is slightly less extensive than that of the postsplenial. It is very broadly convex along its dorsal margin, and abuts against a shallow depression on the ventrolateral surface of the dentary. This depression is delimited externally by a sharp, thin ridge (Fig. 18A). The anteriormost part of a longitudinal sulcus is observed immediately dorsal to the boundary between the ornamented surface and the smooth, mesial lamina of the splenial (this lamina wraps around the ventral surface of the jaw and contributes to a substantial part of the lingual surface of the jaw's anterior third). Identification of this sulcus as part of the lateral line system is uncertain. The spatial relationships of the mesial lamina to the symphysis, prearticular, and coronoids are unclear. Ventrolateral aspects of various jaw rami show that the splenial stops a little short of the anteriormost fourth of the lower jaw, underlapping the dentary before the latter turns sharply medially to meet its antimere, but it is unclear whether the splenial contributed to the jaw symphysis. In its posterior part, just ventral to the rear end of its ornamented surface, the splenial overlaps the postsplenial.

The postsplenial resembles a slightly enlarged version of the splenial. It is wider than the splenial ventrally, slightly deeper in lateral aspect, with a more sharply delimited longitudinal

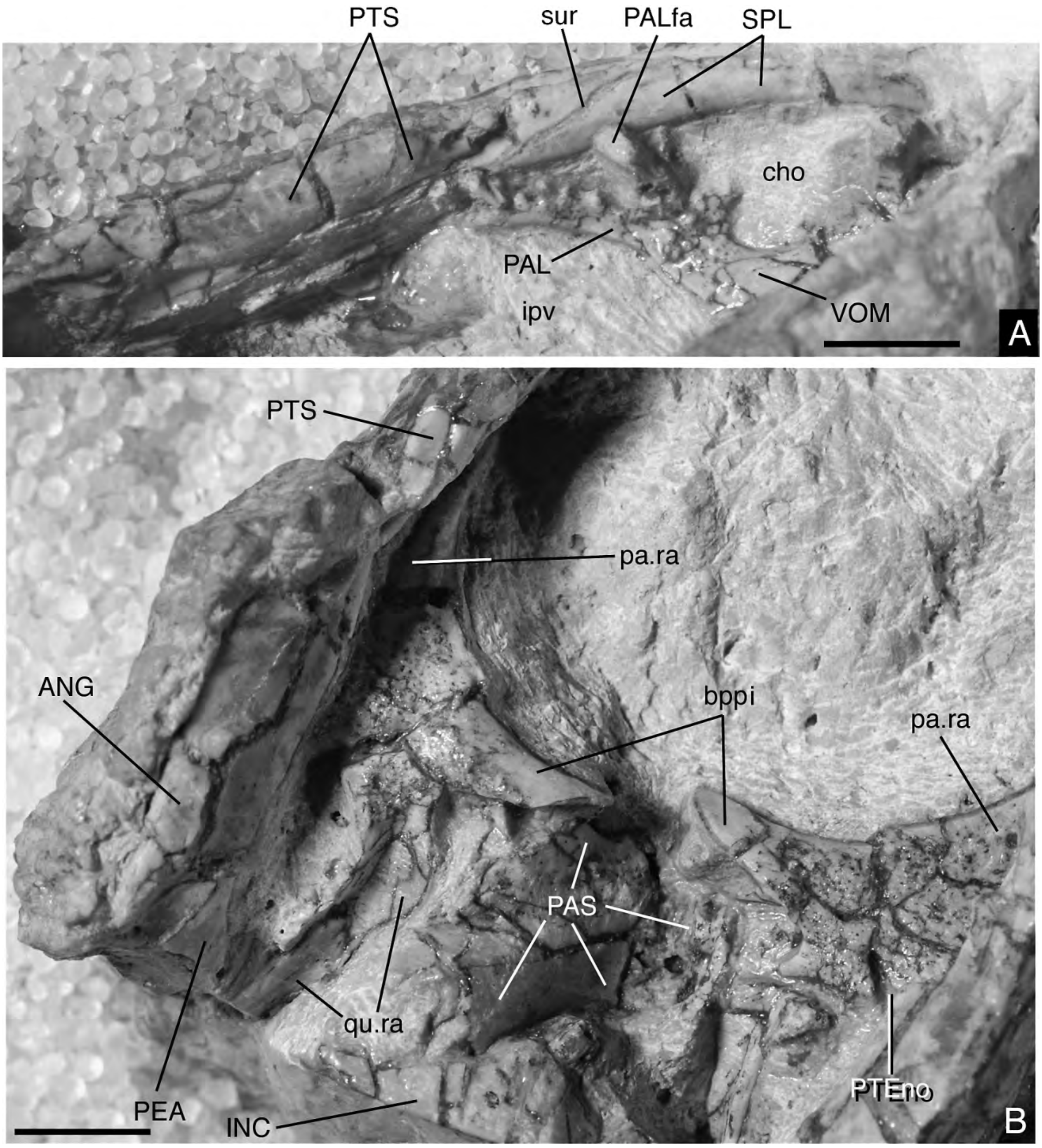

Figure 10 *Perryella olsoni* Carlson, 1987, P82.10.10: (A) ventromesial view of anterior part of right lower jaw ramus and anterior portion of right half of palate; (B) partially preserved pterygoids and parasphenoid plate. Note articulation between vomer and palatine, palatine fang, and shape of basipterygoid process. All scale bars = 5 mm. Abbreviations: (ANG) angular; (bppi) internal process for basipterygoid articulation; (cho) choana; (INC) interclavicle; (ipv) interpterygoid vacuity; (PAL) palatine; (PALfa) palatine fang; (pa.ra) palatal ramus of pterygoid; (PAS) parasphenoid; (PEA) prearticular; (PTEno) pterygoid notch; (PTS) postsplenial; (qu.ra) quadrate ramus of pterygoid; (SPL) splenial; (sur) suture; (VOM) vomer.

sulcus on its ventrolateral surface, and with a coarser external sculpture. Its contribution to the jaw's mesial surface is extensive, but its full dorsal extent on this surface is not visible. In mesial aspect, close to its ventral margin, the postsplenial bears a small subcircular to elliptical foramen (Fig 11A). Posteriorly, the ventral surface of the postsplenial overlaps the angular (the degree of such an overlap is comparable to that between splenial and postsplenial). The rearmost part of the postsplenial delimits most of the ventral margin of the posterior Meckelian foramen (Fig. 18A), together with a smaller contribution from the anterior portion of the mesial lamina of the angular.

The angular dominates the posterior half of the lower jaw lateral surface (Fig. 17B). It is shaped broadly like a quarter of a circle, with an irregularly convex dorsal margin sloping steeply anteroventrally, unlike in *Trimerorhachis*, where it slopes more gently. Its lateral surface displays a radiating pattern of shallow and weak ridges, narrow sulci, and diminutive pits. The centre of ossification is likely to correspond to the point of maximum curvature on the bone ventral margin, where pitting is more intense and more coarsely tuberculated. Posteriorly, the angular shows a deep, broad, and trough-like sulcus with a smooth surface (Figs 6B-d, 17B, 18D, E). At first we assumed that this sulcus might be homologous to the

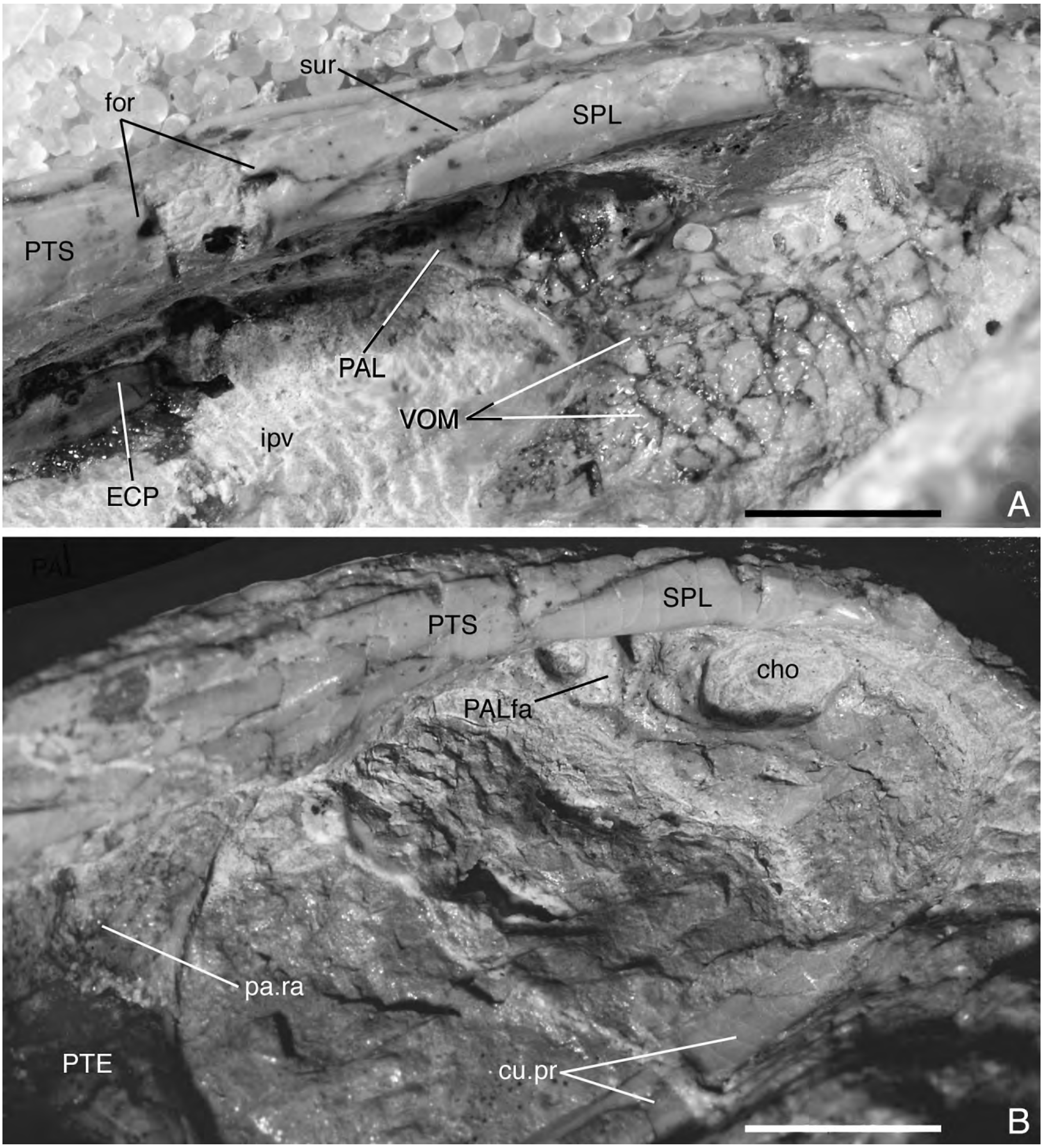

Figure 11 *Perryella olsoni* Carlson, 1987: (A) P82.10.5, ventromesial view of anterior part of right lower jaw ramus and anterior portion of right half of palate. (B) P82.10.1, almost complete right side of palate and anterior part of right lower jaw ramus in ventromesial view. Note choana and palatine fang. All scale bars = 5 mm. Abbreviations: (cho) choana; (cu.pr) cultriform process of parasphenoid; (ECP) ectopterygoid; (for) foramen; (ipv) interpterygoid vacuity; (PAL) palatine; (PALfa) palatine fang; (pa.ra) palatal ramus of pterygoid; (PTE) pterygoid; (PTS) postsplenial; (SPL) splenial; (sur) suture; (VOM) vomer.

rearmost tract of the mandibular sulcus, as a comparison with *Trimerorhachis* suggests, but its size and depth are most unusual; also, none of the foramina that usually dot the depth of the mandibular sulcus in *Trimerorhachis* are visible in *Perryella*. An alternative function (e.g. muscle attachment) is possible, but remains untestable. The sulcus is shallower in its ventral part (where it merges with the ventral margin of the bone, giving rise to a flange) and is visible in posterior view. Along its course, the sulcus is separated from the angular ornamented surface by a pronounced rim, less conspicuous along its dorsalmost part. It then continues for a short distance onto the surangular. The angular wraps around the posterior margin of the jaw forming a narrow lamina on the jaw's mesial surface; the lamina contacts the prearticular along an interdigitated suture of variable shape. The course of the suture is interrupted by a small foramen (?angular foramen of Bolt & Lombard 2001; Fig. 19E). Its position is indicated by a small semielliptical indentation oriented posteroventrally. A more conspicuous foramen on the mesial surface of the left lower jaw ramus of P82.10.5 (Fig. 9C) is 'sunken' in the middle of a subelliptical depression slightly disrupted by breakage. Slightly anterior to the posteroventral corner of the angular, the bone's mesial lamina expands abruptly dorsally into a subelliptical flange. In its anteriormost part, the mesial lamina contributes

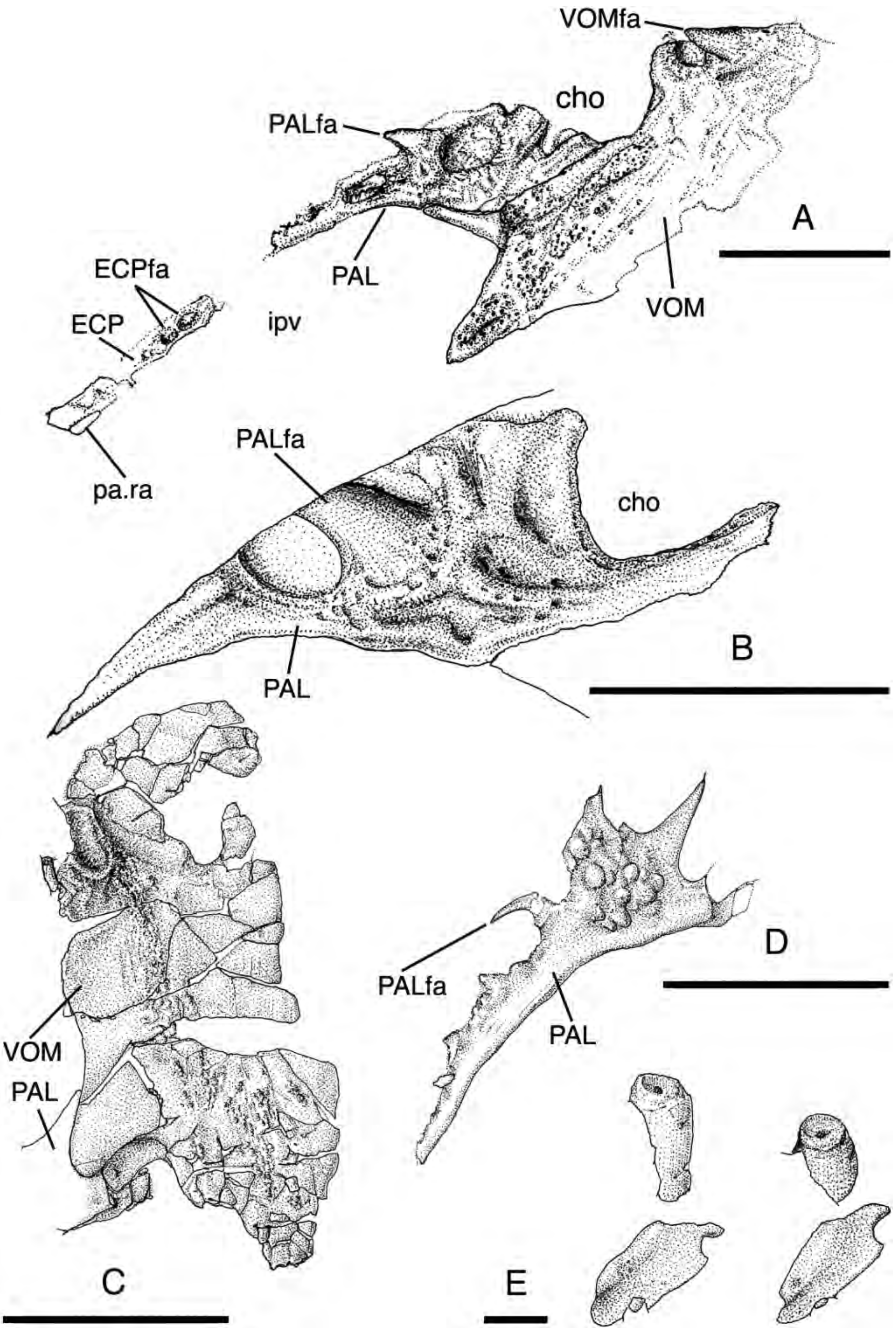

Figure 12 *Perryella olsoni* Carlson, 1987: (A) P82.10.5, camera lucida drawing of bones of palatal series of right side; (B) P82.10.1, camera lucida drawing of palatine of right side; (C, D) P82.10.10, camera lucida drawings of vomer and palatine of right side, respectively; (E) P82.10.11, camera lucida drawings of two slightly different views of isolated palatal fang of uncertain attribution, possibly vomerine. Note articulation between vomer and palatine, palatine and vomerine fangs, and shape of choanal margin. Scale bars in A–D = 5 mm; scale bar in E = 1 mm. Abbreviations: (cho) choana; (ECP) ectopterygoid; (ECPfa) ectopterygoid fang; (ipv) interpterygoid vacuity; (PAL) palatine; (PALfa) palatine fang; (pa.ra) palatal ramus of pterygoid; (VOM) vomer; (VOMfa) vomer fang.

to the posterior and ventral borders of the posterior Meckelian foramen. Finally, the angular is overlapped anteriorly by a stout rectangular process of the postsplenial. The shape of the angular mesial lamina differs from that of other dvinosaurs (where known), in which a subelliptical and flange-like dorsal projection is absent. However, a common feature of such a lamina in all dvinosaurs is the fact that its depth measures a third or less of the depth of the adjacent part of the prearticular (Coldiron 1978; see also Warren & Hutchinson 1983).

The surangular resembles that of *Trimerorhachis*, but it is not fully exposed in any specimen. There is evidence that its anteriormost part is overlapped by the postdental process of the dentary. In lateral aspect, the preserved portion of its dorsal margin is slightly concave. Immediately ventral to this margin, the external surface of the bone is slightly depressed. Further ventrally, it forms a longitudinal thickening (Fig. 18D). Near its posterior end, the bone's lateral surface is slightly tuberculated. The angular–surangular suture can be followed for a short distance at the level of the posterodorsal part of the angular sulcus (see above). It becomes indistinct and disappears before reaching the posterior edge of the bone. The suture's course can be followed on the mesial surface, where it is irregularly sinuous, before it becomes indistinct more dorsally. One or possibly two small foramina are visible just dorsal to the posterior edge of the surangular, on the mesial surface of the jaw. Another small subcircular foramen may be present in a slightly more dorsal position relative to these two foramina (Fig. 18D).

The smooth prearticular is well preserved in its posterior portion, but its relationships to infradentaries and coronoids cannot be reconstructed. It can be divided into a broad, vaguely spatulate posterior part, a 'neck', and an anterior part (Figs 17C, 18E). The 'neck' is situated dorsal to the angular mesial lamina. Its dorsal margin delimits the mesial edge of the adductor fossa. No mesially protruding ridge is present along this margin, unlike the situation in some other tetrapods. Its anterior part can be followed only for a short distance anterior and dorsal to the posterior Meckelian foramen, which it borders. Its posterior part is pierced by a subcentral chorda tympani foramen (Fig. 18E). More posteriorly, it forms a strongly interdigitating suture with the surangular. The prearticular-angular suture has been described above. In P82.10.5, a conspicuous angular foramen is visible.

Information on the coronoids is limited to an incompletely exposed coronoid surface in the left lower jaw ramus of P82.10.11 (Fig. 2A). It may belong to part of the middle and posterior coronoids, but no obvious sutures are visible. The surface is elongate, with nearly straight lateral and mesial margins. Its central part carries a slightly raised ridge which bears a row of small tooth sockets.

No specimen shows a fully exposed articular. In P82.10.5, a diminutive part of its dorsal (glenoid) area is visible on the left side but no distinctive features can be detected. However, the presence of a shallow transverse groove is noted, immediately posterior to the posterior margin of the glenoid, followed by a rather inconspicuous retroarticular process. A deeper transverse groove, or trough, is present in dvinosauroids (see also Yates & Warren 2000).

4.6. Marginal teeth

The marginal dentition is poorly preserved. There is room for about 35+ maxillary tooth positions (32 according to Carlson 1987), but only 21 teeth (nearly all of which are broken) are visible in the best preserved specimen. There is no caniniform region in the anterior part of the maxilla, as preserved (Fig. 1C, D). Decrease in tooth size appears to have been uniform and gradual from anterior to posterior. Some of the best preserved tooth crowns are conical and their tips are oriented posteromesially. No labyrinthine structure can be seen and although preservation and small size make it difficult to ascertain the shape of the crowns, there is no evidence of pedicely. In a handful of specimens, broken dentary teeth and/or tooth sockets exhibit a slight degree of anteroposterior compression. The dentary tooth count cannot be established.

The palatal fangs (Figs 10A, 11, 12, 19B, C) are about 30% larger than the adjacent marginal teeth, and show pointed crowns directed slightly posteromesially. They do not display any labyrinthine infolding. The vomerine fangs are slightly longer and more robust than the palatine fangs. The ectopterygoid tooth sockets suggest that their corresponding teeth (?fangs) are slightly more gracile than the palatine fangs. As in numerous other temnospondyls, including dvinosaurs, the palatal fangs would project slightly below the level of the upper marginal dentition in lateral view.

4.8. Postcranial skeleton

4.8.1. Shoulder girdle. Carlson's (1987) description of the clavicles and interclavicles (Figs 4C, 20A) is supplemented by a few additional data. In the course of this project, additional dermal bones of the shoulder girdle have been exposed through preparation. The shape of the clavicular stem and the transition between the clavicle stem and the clavicle plate are shown in Figure 20A. An incomplete interclavicle attributed by the present authors to *Perryella* (P82.10.2; Fig. 21A) possesses a subrhomboidal outline, but it is broken posterior to the anterior fringe-like sculpture, such as is seen in P82.10.1 (Fig. 20A). The dorsal surface of this interclavicle is smooth with scattered foramina and shallow sulci. A small portion of the ventral surface of the bone is preserved as an external mould. The latter carries a series of irregularly distributed, subelliptical tubercles and faint ridges radiating out from the centre of the plate, as preserved. Such structures correspond to foramina and grooves on the anatomically ventral (external) surface of the interclavicle. No additional data on the clavicles emerged from this study.

An element tentatively interpreted as an incomplete right scapula preserved in mesial view and with eroded margins is also known (Fig. 21B). Its identification is only provisional, and no traces of a scapular foramen could be found. It resembles the *Trimerorhachis* scapula figured by Case (1935, figs 15, 16). An association of bones, including an incomplete clavicle, cleithrum, and endochondral shoulder girdle (presumably from the left side) is preserved in P82.10.3 (Fig. 24D). The scapula possesses a prominent supraglenoid foramen but no other significant features. The cleithrum is a simple, rod-like bone with a slightly expanded and flattened dorsal extremity.

4.8.2. Forelimb. P82.10.21 exhibits the best preserved and most complete humerus, from the right side and mostly in extensor view (Fig. 21C–F). Its aspect and general proportions are consistent with those of other dvinosaur humeri. The proximal and distal ends of the humerus are separated by a slender and relatively short shaft, and lie on two planes forming an angle of approximately 90 degrees. A sharp periosteal margin surrounds the proximal articulation surface. A small and poorly pronounced deltopectoral crest oriented anteroventrally is visible at the distalmost portion of the caput humeri. The crest is slightly buttressed in its lateralmost part, best seen in extensor view. The extensor surface of the caput humeri reveals scars and irregular, faint striations oriented subparallel to the main axis of the humeus. A slightly raised tubercle, immediately distal to the point of maximum curvature of the proximal articulation surface, occupies a similar position to the insertion for the *latissimus dorsi* muscle in other tetrapods (Moulton 1974), although part of its surface is damaged by cracks. The remaining part of the extensor surface of the caput humeri is almost featureless.

The ectepicondylar ridge is broad and poorly distinct. It originates, proximally, as an indistinct thickening from a point immediately distal to the shaft mid length. More distally, it increases in thickness only slightly, where it approaches the periosteal margin of the distal articular surface. Posterior to the ridge, the surface of the bone is slightly depressed. The entepicondyle is subtriangular, and merges smoothly into the shaft. A narrow groove, ventral to the ectepicondylar ridge, separates the latter from a distally eroded supinator process. The latter merges almost indistinctly into the anterior surface of the distal half of the shaft. A well-preserved right humerus exposed in flexor aspect (P82.10.3) provides additional data

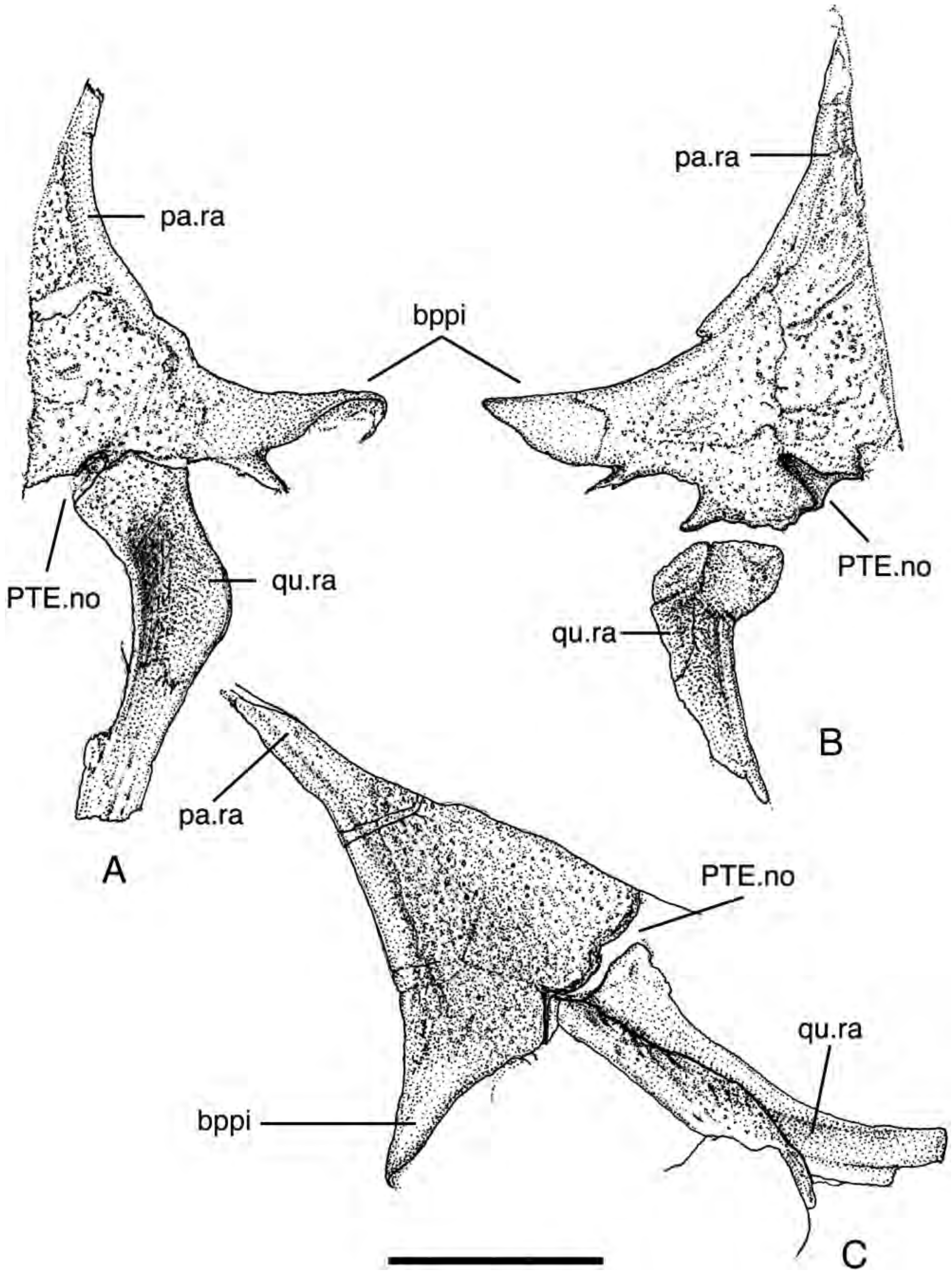

Figure 13 *Perryella olsoni* Carlson, 1987: (A, B) P82.10.10, camera lucida drawings of right and left pterygoids, respectively; (C) P82.10.5, camera lucida drawing of pterygoid of left side. Note distribution of shagreen and notches. All scale bars = 5 mm. Abbreviations: (bppi) internal process for basipterygoid articulation; (pa.ra) palatal ramus of pterygoid; (PTEno) pterygoid notch; (qu.ra) quadrate ramus of pterygoid.

(Fig. 24C). It shows a pronounced supinator process and a flange-like entepicondyle that is slightly wider than that of P82.10.21.

A slender radius visible in extensor view, preserved in close proximity to the humerus of P82.10.21 and apparently in articulation with the latter, has no distinctive features. The ulna is likewise poorly preserved, although a small olecranon process is present.

4.8.3. Pelvic girdle. An incomplete right iliac blade and ischium are illustrated in Figure 24E. The iliac blade has an eroded dorsal margin. Neither the iliac neck nor the acetabulum are preserved. The ischium is nearly complete. It is distinctly longer than tall, with a slightly thickened dorsal edge and a smooth, finely pitted lateral surface.

4.8.4. Hindlimb. The best preserved femur (P82.10.18; Fig. 22A–E) is a slender bone from the right side exposed in extensor, flexor, and anterior aspects. In extensor view, its anterior margin is broadly concave and deepest slightly distal to the bone midlength. The proximal end is slightly expanded and gently convex in cross section, but becomes flatter along its anterior margin, at the level of the proximal portion of the adductor ridge. A poorly developed ridge rises almost indistinctly from a point just proximal to the bone midlength and runs obliquely towards the robust tibial condyle, into which it merges smoothly. The tibial condyle appears strongly convex in cross section along its anterior margin. The semielliptical intercondylar fossa deepens slightly distally. A slightly fragmented fibular condyle, represented by a displaced triangular fragment, covers the posterior part of the intercondylar fossa.

The central area of the flexor surface is dominated by an oblique adductor crest. In its proximal fifth, the crest is broad and with an irregularly convex profile. More distally, it thins abruptly and carries a sharp and slightly concave (in lateral view) edge. The depth of the adductor crest is nearly constant,

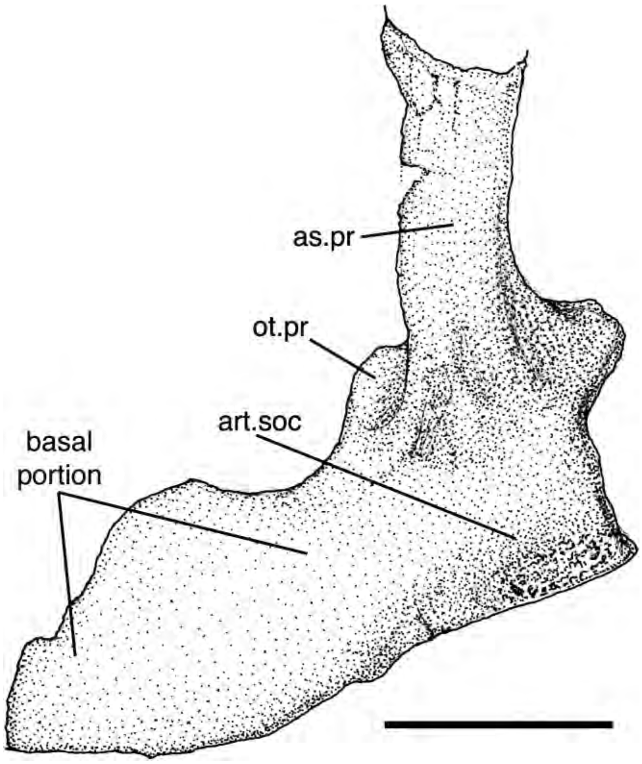

Figure 14 *Perryella olsoni* Carlson, 1987: P82.10.10, epipterygoid, presumably belonging to left side, in posteromesial view. Note robust ascending process and slight thickening around edge of articulation socket for basipterygoid. Scale bar = 1 mm. Abbreviations: (art.soc) socket of epipterygoid for articulation with basipterygoid; (as.pr) ascending process of epipterygoid; (ot.pr) otic process of epipterygoid.

except distally, where it rises slightly to form a small, flat, triangular protuberance. The distal portion of this protuberance decreases rapidly in height, and terminates abruptly at the edge of the popliteal excavation, in the distal part of the flexor surface. The preserved part of the popliteal excavation is semicircular and is surrounded by a slightly raised rim. Posterior to the proximal fifth of the adductor ridge, the flexor surface of the bone is broadly concave and corresponds, at least in part, to the intertrochanteric fossa seen in other tetrapods, although it has no clear posterior boundary. Both the extensor and the flexor surfaces are extensively pitted by foramina and shallow sulci. In places (e.g. central proximal part of extensor surface; flexor surface immediately anterior to popliteal excavation; margins of periosteal surface around proximal and distal extremities), the surface of the bone is lightly scarred or weakly striated.

A second femur (P82.10.2; Fig. 23F–I), found in association with a heavily eroded tibia and fibula, has a slightly different morphology from that of P82.10.18. It has a more robust shape than the femur of P82.10.18, and bears a thinner and shorter adductor ridge, a larger popliteal excavation, and a more clearly delimited intertrochanteric fossa. At present, it is not known whether such differences represent individual/ontogenetic variation for *Perryella*, or whether they imply a separate taxonomic attribution.

The fibula (Fig. 20B, C) is incompletely known. It has a slighty expanded and flattened proximal extremity, much as in other tetrapods, but shows no other noteworthy features. The better preserved tibia (Fig. 23) is known only in extensor and anterior views. Its proximal end is slightly flared, with a low central ridge that separates a flat anterior portion from a convex posterior portion. The ridge terminates approximately at the level of the shaft mid length where it merges seamlessly into the bone surface. The distal extremity of the bone is expanded, but less so than the proximal extremity, and its articulation surface is oriented obliquely to the main axis of the bone.

An autopod (tentatively labelled as a left manus by Carlson 1987, fig. 11) is visible in P82.10.6 (Fig. 24F) The presence of five digits and the overall size suggests that it might represent a posterior rather than an anterior autopod, but available information does not allow the confident arbitration between these alternative interpretations. In this respect, it is noted that a five-digited manus, although rare, has been documented in some temnospondyls, e.g. certain specimens of the dissorophoid *Micromelerpeton credneri* (Boy 1971, Witzmann & Pfretzschner 2003).

4.8.5. Axial skeleton. Further preparation of a string of vertebrae and associated ribs in P82.10.2 (Fig. 24A) and P82.10.18 (Fig. 24B) yielded additional data. A pleurocentrum intervening between adjacent intercentra shows the characteristic wedge-like lateral aspect observed in several other temnospondyls. The intercentra are larger and structurally bipartite, in a manner similar to that recorded by Milner & Sequeira (1994) in *Balanerpeton*. A straight suture runs along the ventral midline of the conjoined contralateral intercentral elements. The intercentra are shaped like broad wedges in lateral view and would form a crescent-like structure with their antimeres. Temnospondyl intercentra develop from paired anlagen that fuse later in ontogeny (e.g. Boy 1974, 1995; Witzmann 2006a). The occurrence of unfused intercentra in some *Perryella* specimens suggests that they may represent juveniles. No clear indication of the area of attachment for the ribs could be observed on the centra. The ribs (Figs 4C, 24B) are straight or very gently curved, cylindrical, and with no obvious distinctive features (Carlson 1987) (Figs 4C, 24B).

5. Phylogenetic relationships

5.1. Choice of taxa

The interrelationships and taxonomic boundaries of each of the major temnospondyl clades have a long and complicated history. Milner (1990), followed by Holmes (2000), identified five major groups. At the base of the temnospondyl radiation, he placed the Edopoidea, which represent a small group of species superficially resembling alligators or gharials (e.g. Milner & Sequeira 1998; Sequeira 2004; Sidor *et al.* 2005). The basal position of this group is generally accepted. Edopoids included in this analysis encompass all species discussed by Milner & Sequeira (1998), but the present authors have not considered two recently described representatives of this group, *Nigerpeton* and *Saharastega* (Sidor *et al.* 2005; Damiani *et al.* 2006; Steyer *et al.* 2006). More detailed surveys of the anatomy and affinities of both taxa were published whilst this present paper was undergoing review. *Nigerpeton* is certainly a suitable candidate for inclusion in future cladistic analyses, but there are reservations as far as the interpretation of *Saharastega* as an edopoid is concerned.

The content and the intrinsic/extrinsic relationships of remaining groups of temnospondyls are debated. For the purposes of the present work, the most significant areas of phylogenetic disagreement concern Milner's (1990) 'Trimerorhachoidea [= Dvinosauria]-Brachyopoidea' and 'crown Stereospondyli' clades (see also Schoch & Milner 2000, Warren 2000, and Yates & Warren 2000).

Character-state distribution and taxonomic composition of Dvinosauria were reviewed by Warren (1999), Yates & Warren (2000), Holmes (2000), and Milner & Sequeira (2004). The phylogenetic proximity of trimerorhachids, eobrachyopids, dvinosaurids, and tupilakosaurids is generally accepted (see

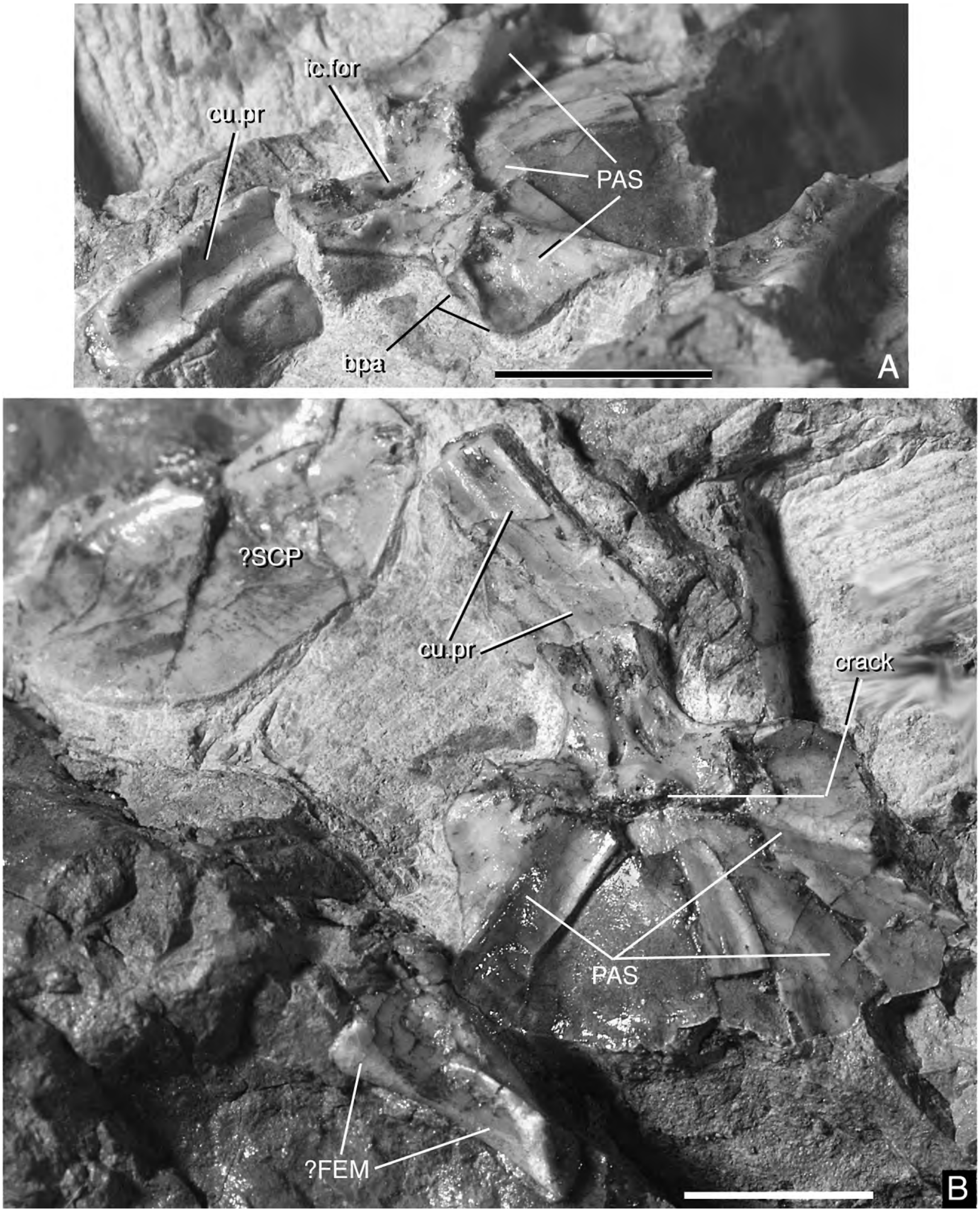

Figure 15 *Perryella olsoni* Carlson, 1987: (A, B) P82.10.9, right anterodorsolateral and dorsal views, respectively, of parasphenoid complex. Note central longitudinal depression on dorsal surface of cultriform process, foramina for internal carotid arteries, and system of ridges and depressions on parasphenoid plate. All scale bars = 5 mm. Abbreviations: (bpa) articulation facet of basipterygoid process; (cu.pr) cultriform process of parasphenoid; (FEM) femur; (ic.for) foramen for internal carotid artery; (PAS) parasphenoid; (SCP) scapula.

Coldiron 1978). However, a major discrepancy between Milner's (1990) and Yates & Warren's (2000) preferred phylogenetic hypotheses concerns the position of Brachyopidae (see Warren 2000 for a review), a family of predominantly Triassic species with broad skulls and abbreviated snouts, and including some of the largest amphibians ever discovered (Steyer & Damiani 2005). This family has been assigned either to dvinosaurs (Milner 1990) or to stereospondyls (e.g. Yates & Warren 2000). Warren (2000) and Yates & Warren (2000) have questioned the affinities of Brachyopoidea (consisting of the two families Brachyopidae and Chigutisauridae; Watson 1956; Warren & Hutchinson 1983; Warren & Marsicano 1998; Damiani & Kitching 2003) with dvinosaurs, and have placed the former among derived stereospondyls, at the apical end of

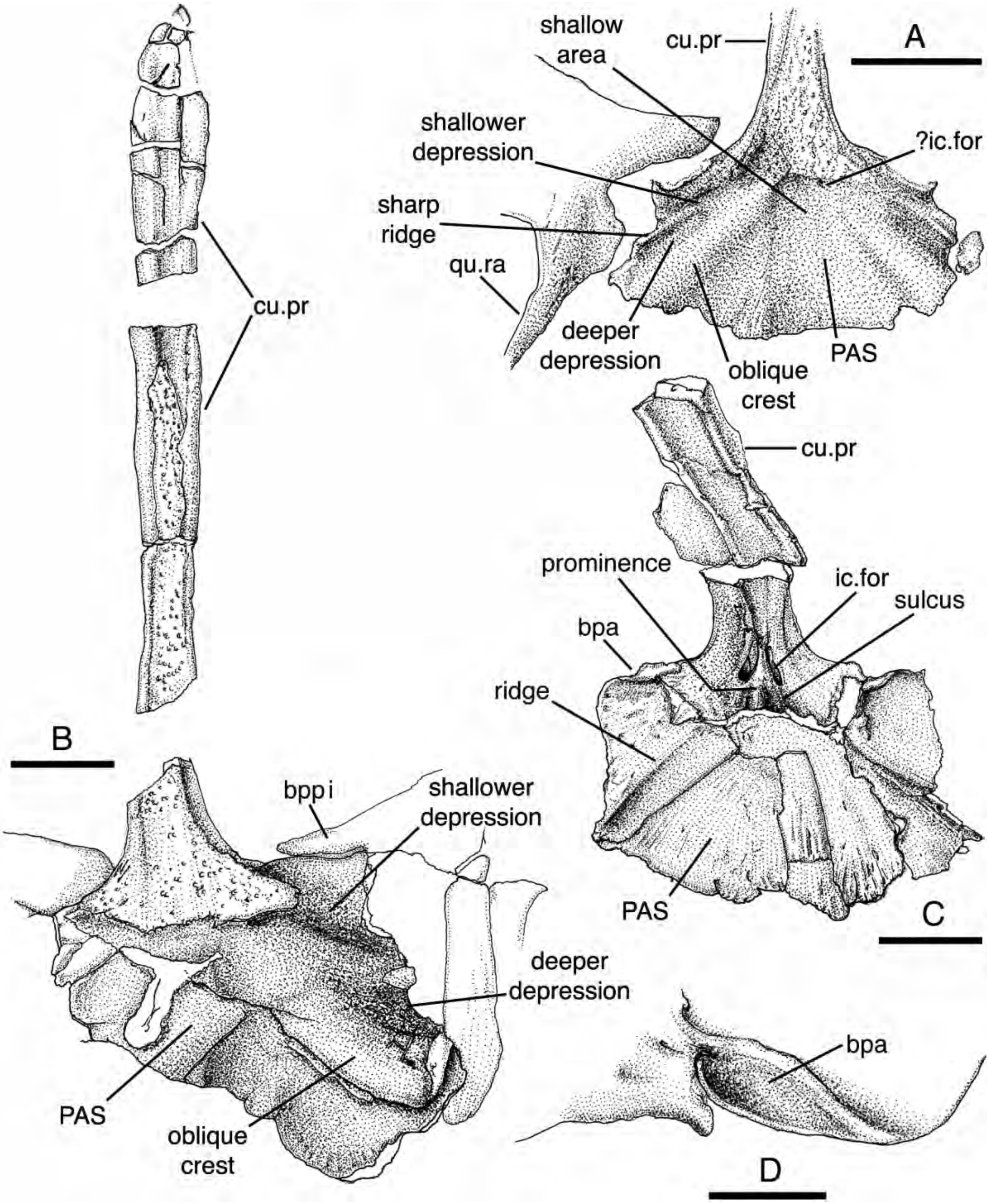

Figure 16 *Perryella olsoni* Carlson, 1987: (A) P82.10.1, camera lucida drawing of posterior ventral plate of parasphenoid and rearmost portion of cultriform process; (B) P82.10.5, camera lucida drawing of parasphenoid; (C, D) P82.10.9, dorsal view of parasphenoid complex and close-up view of basicranial region in anterodorso-lateral view, respectively. Note central longitudinal depression on dorsal surface of cultriform process, foramina for internal carotid arteries, system of ridges and depressions on parasphenoid plate, and distribution of denticles. Scale bar in A=5 mm; scale bars in B, C=2 mm; scale bar in D=1 mm. Abbreviations: (bpa) articulation facet of basipterygoid process; (bppi) internal process for basipterygoid articulation; (cu.pr) cultriform process of parasphenoid; (ic.for) foramen for internal carotid artery; (PAS) parasphenoid; (qu.ra) quadrate ramus of pterygoid.

a clade Trematosauria that includes, in proximodistal sequence, the groups Trematosauroidea, Metoposauroidea, Plagiosauroidea, Rhytidosteidae, and Brachyopoidea.

Schoch & Milner (2000) retained chigutisaurids within stereospondyls, but excluded brachyopids from the latter. Therefore, the vexing question of the taxonomic membership of dvinosaurs revolves, ultimately, around the placement of brachyopids in such a clade (e.g. Milner 2000) or its exclusion from it (e.g. Yates & Warren 2000). Recently, Damiani & Kitching (2003) retrieved a sister group relationship between brachyopoids and dvinosaurs. The present analysis is primarily concerned with Permo-Carboniferous temnospondyl groups and their interrelationships. In our matrix, the base of the stereospondyl radiation is represented by such genera as *Cheliderpeton* and *Sclerocephalus* (basal archegosauriforms *sensu* Schoch & Milner 2000). If brachyopids were a clade within stereospondyls, then resolution of their affinities would fall outside the aims of this present paper, as it would require

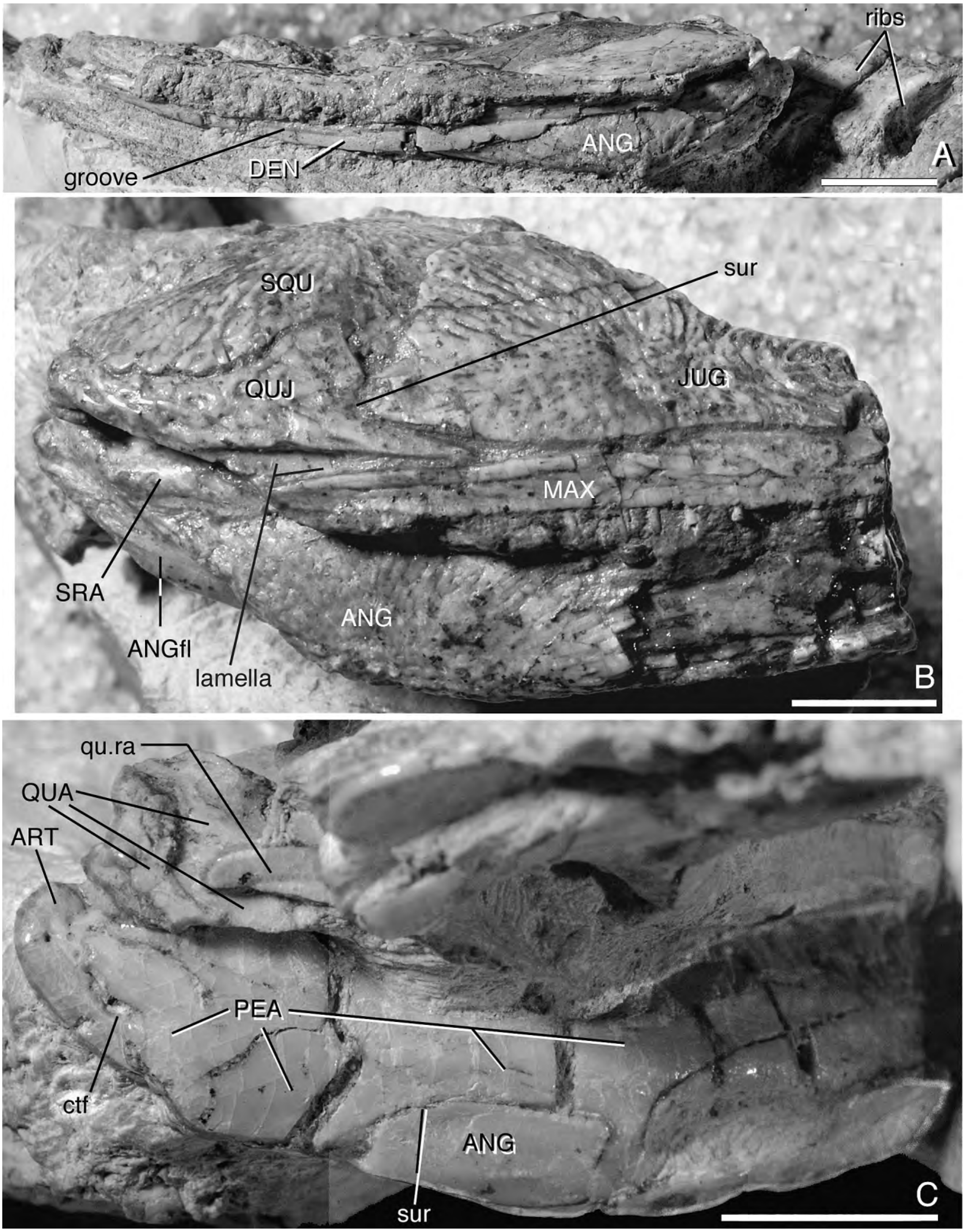

Figure 17 *Perryella olsoni* Carlson, 1987: (A) P82.10.6, dorsoventrally compressed skull in left lateral view plus anteriormost portion of associated postcranium; (B) P82.10.11, suspensorium and posterior part of maxilla and lower jaw in right lateral view; note broad flange along posterior margin of angular and complex sutural pattern between squamosal, quadratojugal and jugal; note also underlying lamella of quadratojugal exposed as a result of slight ventral displacement of maxilla; (C) P82.10.5, quadrate and posterior part of lower jaw of left side in mesial view. Note pterygoid quadrate ramus of left side in proximity to quadrate mesial surface. All scale bars = 5 mm. Abbreviations: (ANG) angular; (ANGfl) angular flange; (ART) articular; (ctf) chorda tympani foramen; (DEN) dentary; (JUG) jugal; (MAX) maxilla; (PEA) prearticular; (QUA) quadrate; (QUJ) quadratojugal; (qu.ra) quadrate ramus of pterygoid; (SQU) squamosal; (SRA) surangular; (sur) suture.

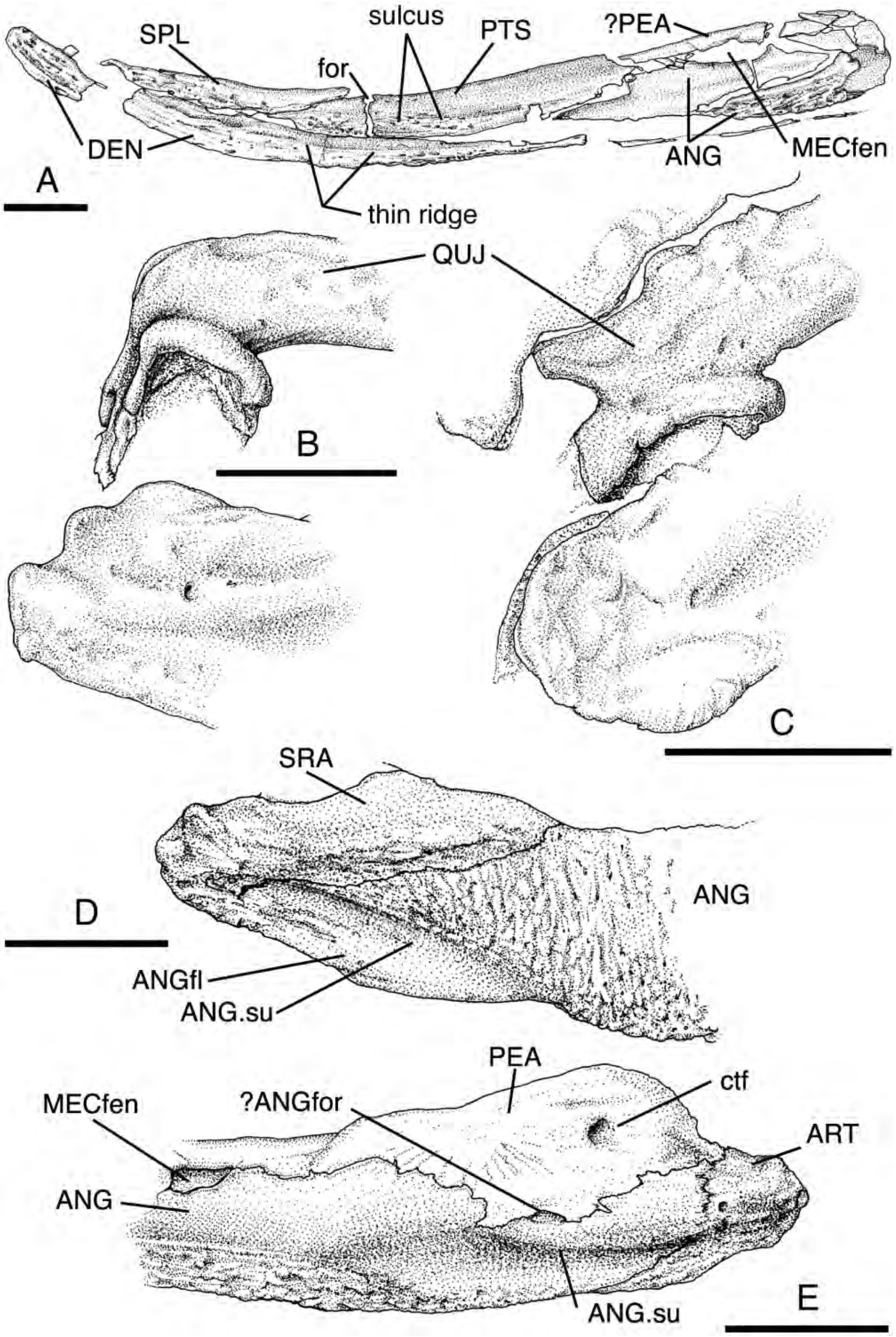

Figure 18 *Perryella olsoni* Carlson, 1987: (A) P82.10.3, camera lucida drawing of slightly disrupted but essentially complete lower jaw ramus of right side in ventromesial view; (B, C) P82.10.11, camera lucida drawings of posteroventrolateral and (mostly) lateral views, respectively, of posterior part of quadratojugal and lower jaw of right side; note cup-like structure on ventral surface of quadratojugal; (D, E) P82.10.11, camera lucida drawings of posterior part of lower jaw. Note broad flange along posterior margin of angular. Scale bars in A, D, E=5 mm; scale bars in B, C=3 mm. Abbreviations: (ANG) angular; (ANGfl) angular flange; (ANGfor) angular foramen; (ANGsu) angular sulcus; (ART) articular; (ctf) chorda tympani foramen; (DEN) dentary; (for) foramen; (MECfen) Meckelian fenestra; (PEA) prearticular; (PTS) postsplenial; (QUJ) quadratojugal; (SPL) splenial; (SRA) surangular.

inclusion of a wider range of stereospondyl groups (e.g. in order to test for their phylogenetic placement close to such derived clades as trematosaurs, metoposaurs, and plagiosaurs; Yates & Warren 2000).

In addition, the specialised cranial morphology of brachyopids reveals that they do not share any derived feature with *Perryella*. If brachyopids did in fact belong in the dvinosaurs, then presumably they were more derived than trimerorhachids and *Perryella*. Based on their skull proportions, position of the orbits, and morphology of the palate, they would be allied most closely to the eobrachyopid-dvinosaurid-tupilakosaurid group (see Hotton 1959 and Milner 1990, and discussion in Damiani & Kitching 2003). The range of temnospondyls in the present data is thus appropriate for elucidating alternative hypotheses of relationships of *Perryella* (see also discussion in Carlson 1987).

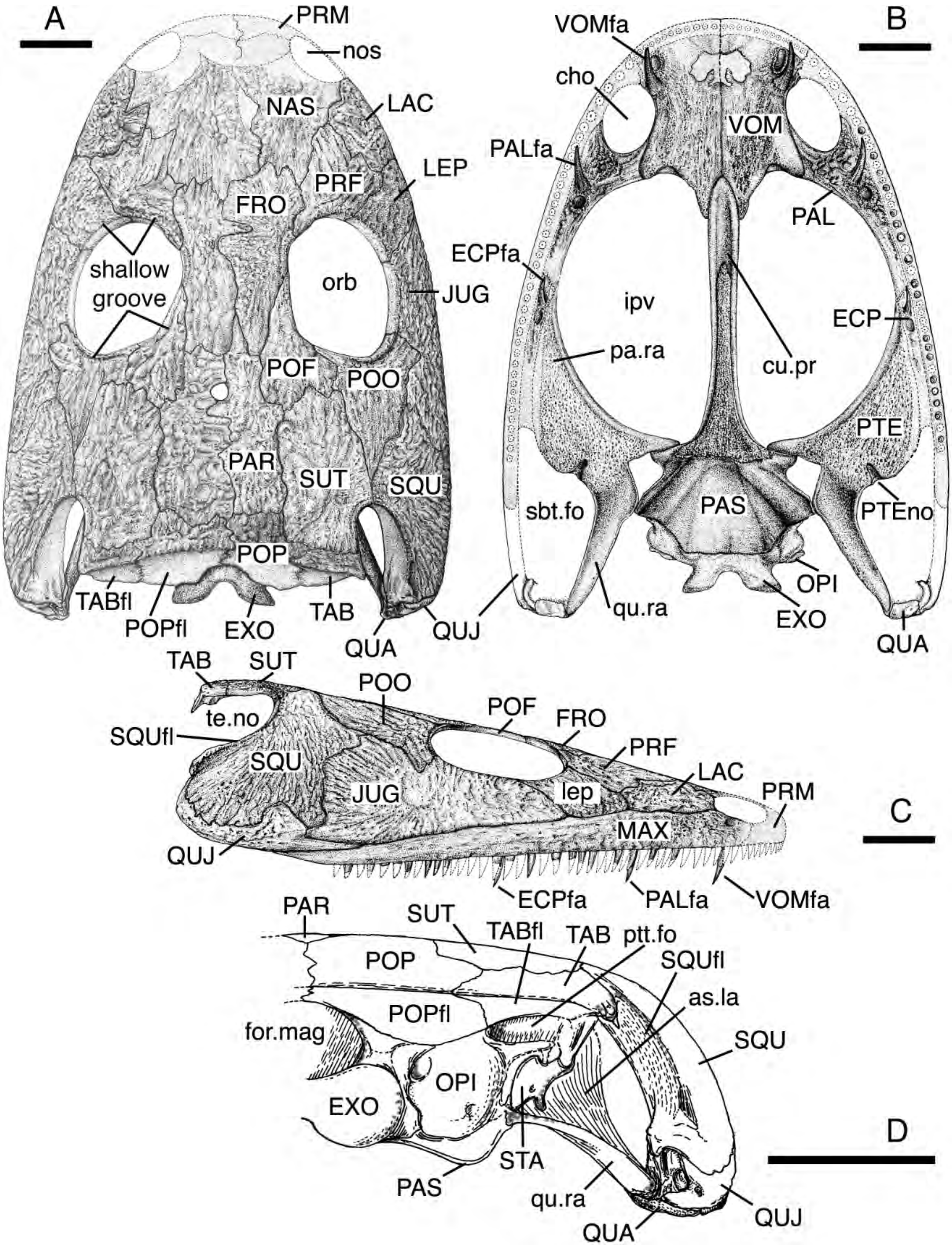

Figure 19 *Perryella olsoni* Carlson, 1987: labelled reconstruction of the skull in (A) dorsal, (B) ventral, (C) right lateral, and (D) occipital views. Small portions of both exoccipitals and opisthotic, as well as the dorsal process of the stapes, although partly visible in lateral view, have been removed for the purpose of including labels. The occipital aspect of the skull is schematic and slightly enlarged relative to other skull views, and only its right side is shown. All scale bars = 5 mm. Abbreviations: (as.la) ascending lamina of pterygoid; (cho) choana; (cu.pr) cultriform process of parasphenoid; (ECP) ectopterygoid; (ECPfa) ectopterygoid fang; (EXO) exoccipital; (for.mag) foramen magnum; (FRO) frontal; (ipv) interpterygoid vacuity; (JUG) jugal; (LAC) lacrimal; (LEP) lateral exposure of palatine; (MAX) maxilla; (nos) nostril; (OPI) opisthotic; (orb) orbit; (PAR) parietal; (pa.ra) palatal ramus of pterygoid; (PAL) palatine; (PALfa) palatine fang; (PAS) parasphenoid; (POF) postfrontal; (POO) postorbital; (POP) postparietal; (POPfl) postparietal flange; (PRF) prefrontal; (PRM) premaxilla; (PTE) pterygoid; (PTEno) pterygoid notch; (ptt.fo) posttemporal fossa; (qu.ra) quadrate ramus of pterygoid; (QUA) quadrate; (QUJ) quadratojugal; (sbt.fo) subtemporal fossa; (SQU) squamosal; (SQUfl) squamosal flange; (STA) stapes; (SUT) supratemporal; (TAB) tabular; (TABfl) tabular flange; (te.no) temporal (or squamosal) notch; (VOM) vomer; (VOMfa) vomer fang.

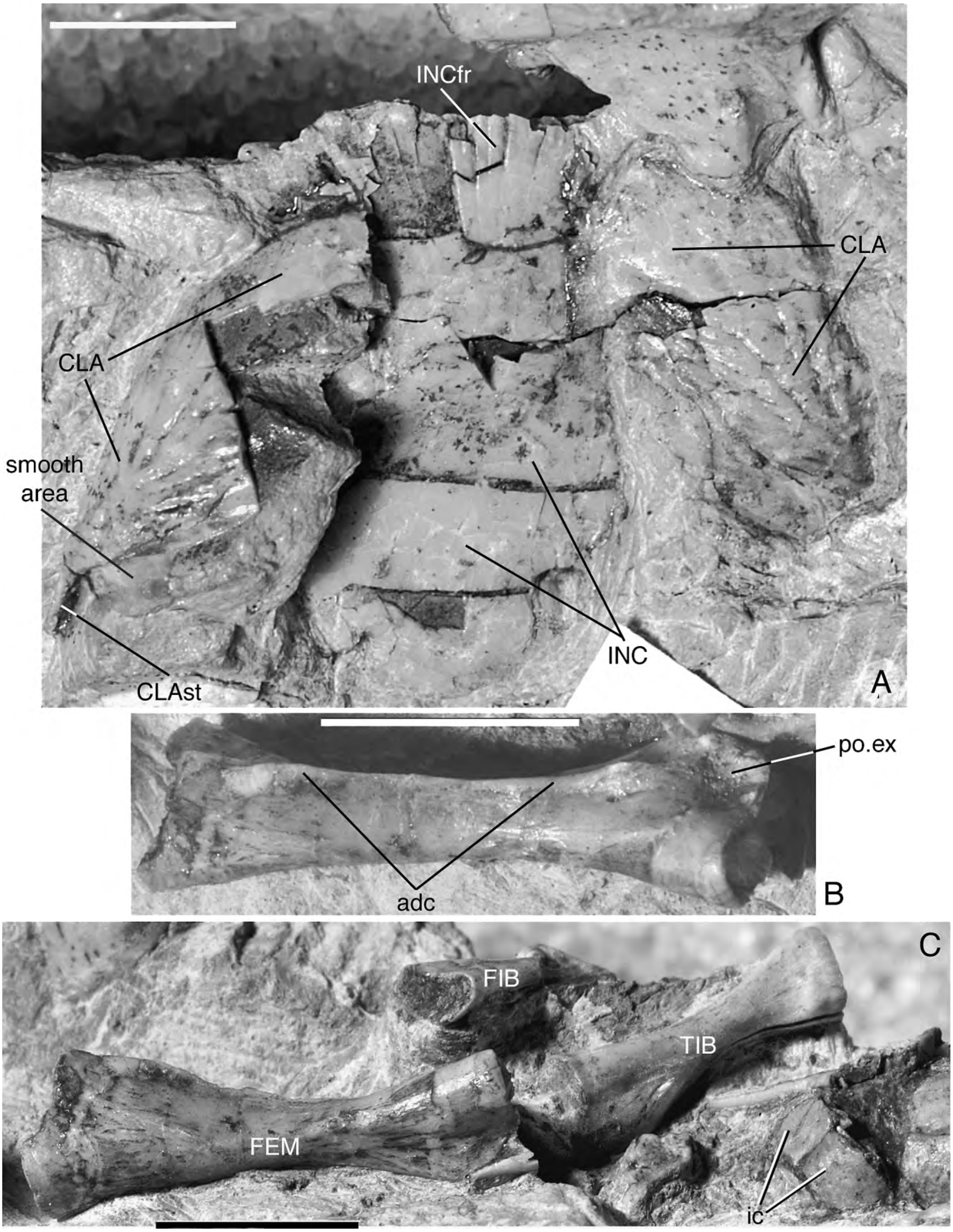

Figure 20 *Perryella olsoni* Carlson, 1987: (A) P82.10.1, dermal pectoral girdle in ventral (i.e. external) view; note anterior fringe on interclavicle and smooth transitional area between stem and plate of clavicle; (B, C) P82.10.18, well-preserved femur of right side in flexor and extensor views, respectively (complete tibia and incomplete fibula are in close proximity to the femur). Note adductor ridge on femur. All scale bars = 5 mm. Abbreviations: (adc) adductor crest of femur; (CLA) clavicle; (CLAst) clavicle stem; (FEM) femur; (FIB) fibula; (ic) intercentrum; (INC) interclavicle; (INCfr) interclavicle fringe; (po.ex) popliteal excavation of femur; (TIB) tibia.

Capetus and *Dendrerpeton confusum* appear to be generalised temnospondyls. However, their morphology departs from that of *Balanerpeton* and *Dendrerpeton acadianum* (Milner 1980; Milner & Sequeira 1994; Holmes *et al.* 1998), which have been thought to occupy a basal position in temnospondyl phylogeny (Milner 1990; but see also discussion in Ruta *et al.*

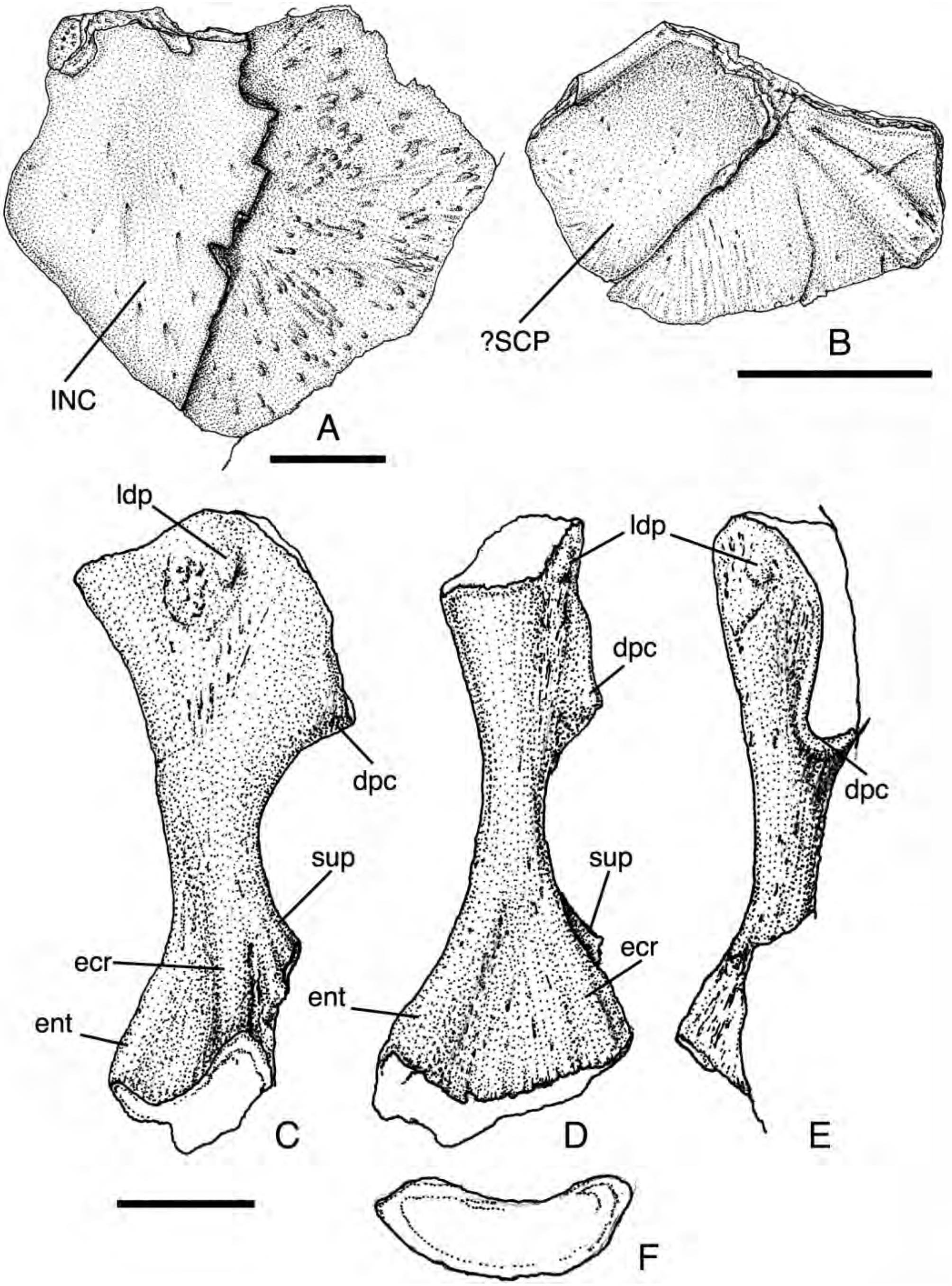

Figure 21 *Perryella olsoni* Carlson, 1987: (A) P82.10.2, camera lucida drawing of incomplete interclavicle in dorsal (i.e. internal or visceral) view; external mould of right half of bone ventral (i.e. external) surface visible on the right; (B) P82.10.9, camera lucida drawing of putative right scapula in mesial view; (C–F) P82.10.21, camera lucida drawings of humerus of right side in (C) extensor, (D) posterior, (E) anterior views, respectively, with (F) outline of articulation surface of distal extremity. Note development and morphology of ridges and processes on humerus. Scale bars in A, C–F = 2 mm; scale bar in B = 5 mm. Abbreviations: (dpc) deltopectoral crest of humerus; (ecr) ectepicondyle ridge; (ent) entepicondyle; (INC) interclavicle; (ldp) latissimus dorsi process of humerus; (SCP) scapula; (sup) supinator process of humerus.

2003). For this reason, and in light of conflicting hypotheses of relationships for *Balanerpeton* and *Dendrerpeton acadianum*, both of these taxa have been included in the present data set. Eryopids (*Eryops* and *Onchiodon*) and zatracheids (*Acanthostomatops* and *Zatrachys*) have also been considered. Finally, the sampling of dissorophoids is the same as in Ruta *et al.* (2003), with the addition of the trematopid *Anconastes*. Whilst this present work was in review, Schoch & Rubidge (2005) published a revision of the amphibamid *Micropholis stowi*, which will be considered in expanded analyses of temnospondyl interrelationships.

5.2. Data processing

To investigate the affinities of *Perryella*, the present authors built a character-taxon data matrix in MacClade version 3.0.1 (Maddison & Maddison 1992). Fourteen Permo-Carboniferous and Devonian tetrapod outgroups and 40 temnospondyl species have been considered (Appendix 1). Taxa were coded for 197 cranial and 48 postcranial characters (Appendix 2), all of which were left unweighted and unordered. The data matrix (Appendix 3) was processed under maximum parsimony settings in PAUP* version 4.0b10 (Swofford 2003), and rooted on the fish-like stem-group

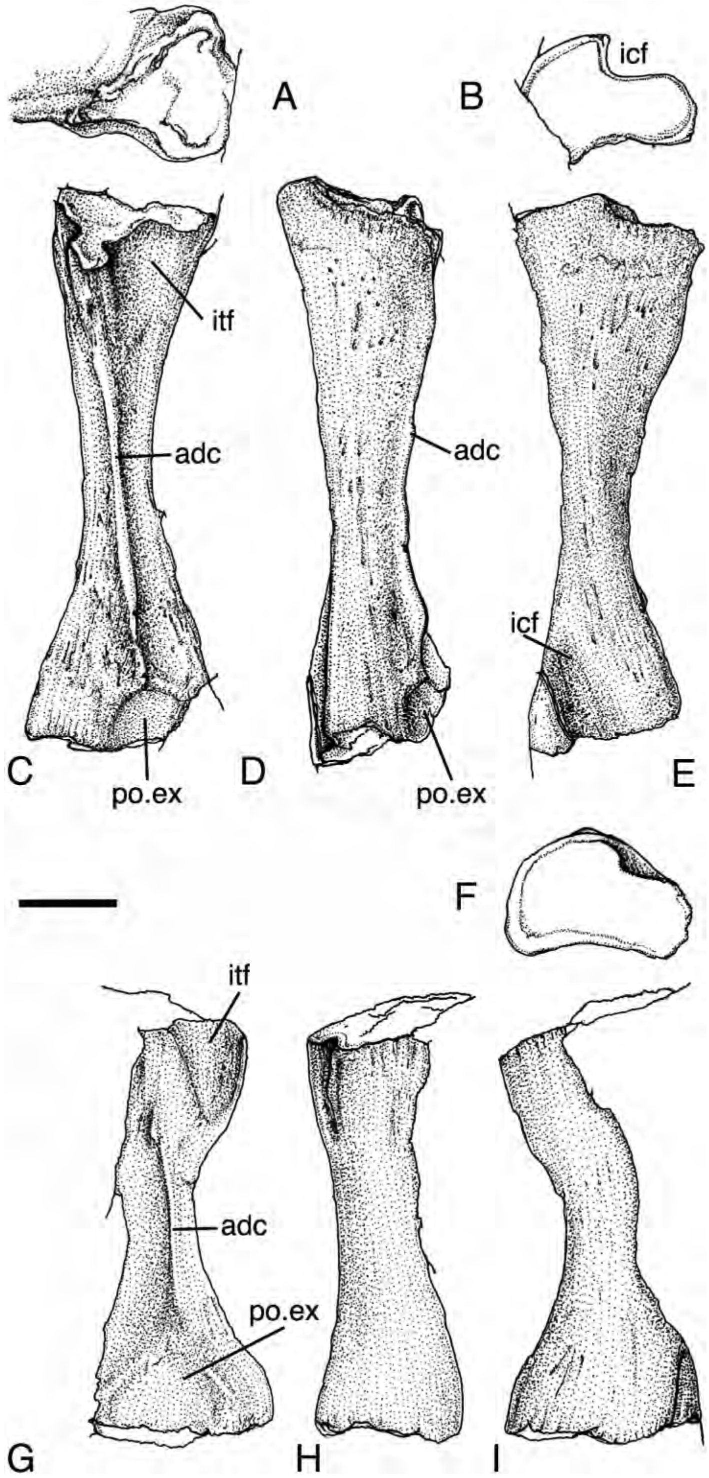

Figure 22 *Perryella olsoni* Carlson, 1987: (A–E) P82.10.18, camera lucida drawings of femur of right side in (A) proximal, (B) distal, (C) flexor, (D) anterior, and (E) extensor views, respectively; (F–I) P82.10.2, camera lucida drawings of femur of right side tentatively assigned to *Perryella* in (F) distal, (G) flexor, (H) posterior, and (I) extensor views, respectively. Note development and morphology of ridges and processes on femur. All scale bars=2 mm. Abbreviations: (adc) adductor crest of femur; (icf) intercondylar fossa of femur; (itf) intertrochanteric fossa of femur; (po.ex) popliteal excavation of femur.

tetrapod *Panderichthys*. A heuristic search was used, based upon the following settings: 1000 random stepwise addition sequences; tree bisection-reconnection (TBR) branch swapping, keeping one tree in memory at any one time, and subsequently saving multiple trees by swapping on all the trees retained from the 1000 sequences.

5.3. Results

PAUP* yielded two shortest trees at 902 steps (C.I.≈0·31 excluding two uninformative characters; R.I.≈0·63; R.C.≈0·2), the strict consensus of which is shown in Figure 25. *Edops* appears as the most basal temnospondyl in the present study. All other edopoids form a trichotomy with one branch leading to *Adamanterpeton*, one branch leading to the two *Chenoprosopus* species, and one branch leading to *Procochleosaurus* as sister taxon to the two *Cochleosaurus* species.

Capetus occupies a basal position relative to an archegosauriform-eryopid-zatracheid clade. The latter clade consists of three groups: (1) zatracheids,

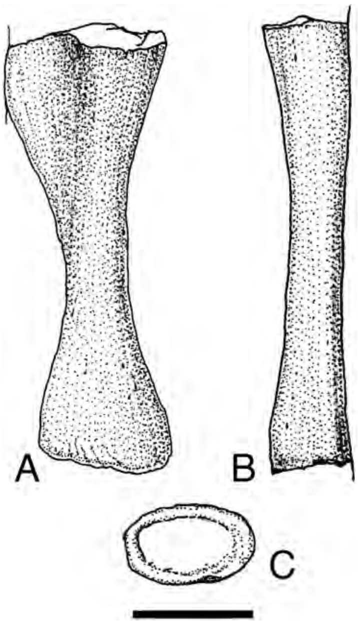

Figure 23 *Perryella olsoni* Carlson, 1987: P82.10.18, camera lucida drawings of tibia of right side in (A) extensor and (B) anterior views, with (C) outline of articulation surface of distal extremity. All scale bars=2 mm.

(*Zatrachys*+*Acanthostomatops*); (2) *Eryops*; (3) basal archegosauriforms, (*Onchiodon*+(*Cheliderpeton*+*Sclerocephalus*)).

Dendrerpeton acadianum and *Balanerpeton* are successive sister taxa to Dvinosauria.

Dendrerpeton confusum is sister taxon to Dissorophoidea. The latter are divided into two groups. The first group consists of dissorophids plus trematopids, (*Broiliellus*+(*Ecolsonia*+(*Acheloma*+(*Anconastes*+*Phonerpeton*)))). The second group consists of amphibamids as a series of sister taxa to a micromelerpetontid-branchiosaurid clade. In particular, *Platyrhinops*, *Eoscopus*, and (*Amphibamus*+*Doleserpeton*) form successive sister groups, in that order, to a (*Micromelerpeton* + (*Apateon* + (*Leptorophus* + *Schoenfelderpeton*))) clade.

At the base of Dvinosauria, *Eugyrinus*, Trimerorhachidae (*Neldasaurus*+*Trimerorhachis*), and *Perryella* form successive sister taxa, in that order, to Dvinosauroidea. The latter include Eobrachyopidae (*Acroplous*+*Isodectes*), Dvinosauridae (*Dvinosaurus*), and Tupilakosauridae (*Slaugenhopia*+(*Thabanchuia*+*Tupilakosaurus*)). The topology of dvinosaurs matches that retrieved by Yates & Warren (2000). The present study confirms Milner's (1980) suggestion that *Eugyrinus* is a basal dvinosaur (see also Milner *et al*. 2002).

The branching sequence of post-*Panderichthys* outgroups includes, in order of increasing distance from the root of the tree, *Acanthostega*, *Ichthyostega*, a (*Tulerpeton*+(*Ossinodus*+(*Pederpes*+*Whatcheeria*))) clade, *Crassigyrinus*, a (*Colosteus*+*Greererpeton*) clade, and a (*Eucritta*+(*Loxomma*+(*Baphetes*+*Megalocephalus*))) clade.

When all characters are reweighted by the maximum values of their rescaled consistency indexes, PAUP* finds one tree (C.I.=0·56; R.I.=0·82; R.C.=0·47). The sequence of outgroups is the same as that of the most parsimonious trees from the unweighted search. Resolution is added to the edopoid node. *Procochleosaurus* is basal to remaining edopoids (except *Edops*). The two *Chenoprosopus* species form the sister taxon to an (*Adamanterpeton* + (*Cochleosaurus bohemicus* + *Cochleosaurus florensis*)) clade. *Capetus* appears as the sister taxon to all post-edopoid temnospondyls.

5.4. Node support

The data set was bootstrapped with the fast heuristic search option in PAUP*, based upon 10,000 replicates. Several ingroup taxa and the majority of outgroups appear to be collapsed in a 50% majority-rule consensus. There is no support for basal dvinosaurs, and four genera, *Eugyrinus*, *Trimerorhachis*, *Neldasaurus*, and *Perryella*, are not resolved in the consensus. Dvinosauroids receive 74% bootstrap support. The three constituent families of this clade are joined in a trichotomy. Eobrachyopids, tupilakosaurids, and the *Thabanchuia-Tupilakosaurus* clade have 72, 74, and 70% support, respectively. Bootstrap support for other nodes is shown in Figure 26.

Computation of decay index values (Bremer support values) proved to be time-consuming. For this reason, we report only the results from the first three rounds of computations (i.e. those based upon strict consensus topologies of trees at one, two, and three extra steps; Fig. 25). The notation 3+indicates those nodes for which the decay index value is 4 or higher. The nodes subtending dvinosaurs, dvinosauroids, and tupilakosaurids have a rather high support (3+). Moderate support (2) is assigned to the *Perryella*-dvinosauroid clade, to eobrachyopids, and to the dvinosaurid-tupilakosaurid clade. Low support (1) is given to the nodes subtending trimerorhachids, derived tupilakosaurids, and dvinosaurs other than *Eugyrinus*. For a list of character-state changes supporting dvinosaurs and those supporting *Perryella* as sister taxon to dvinosauroids, see Appendix 4.

5.5. Matrix manipulation

A series of experiments were devised to evaluate the statistical significance of the differences in alternative tree topologies, with particular reference to dvinosaurs and to the placement of *Perryella* inside or outside this clade. Significance levels of different tree shapes were based on the Kishino-Hasegawa, Templeton, and Winning-sites tests, all performed in PAUP*. For brevity, tree shapes relevant to each of the following experiments are not illustrated, but are available upon request from the authors.

In the first experiment, *Perryella* was constrained to appear in a basal position relative to all other dvinosaurs, which were collapsed in a polytomy. PAUP* retrieved 19 trees at 902 steps (C.I.≈0·31; R.I.≈0·625; R.C.≈0·2). Their strict consensus is well resolved. *Perryella* is basal to a fully resolved Dvinosauria. *Neldasaurus*, *Trimerorhachis*, and *Eugyrinus* appear in order of increasing proximity to Dvinosauroidea, with *Dvinosaurus* as sister taxon to an eobrachyopid-tupilakosaurid clade. The 19 suboptimal trees do not differ significantly ($P \gg 0{\cdot}05$) from the two most parsimonious trees.

In the second experiment, we searched for tree topologies which are not compatible with the monophyly of dvinosaurs. PAUP* retrieved one tree at 905 steps (C.I.≈0·31, R.I.≈0·62, and R.C.≈0·19), not differing significantly from the shortest trees ($P \gg 8 > 0{\cdot}05$). In this tree, the (*Balanerpeton*+*Dendrerpeton acadianum*) clade is sister taxon to all dvinosaurs other than *Eugyrinus*. The relationships of dvinosaurs other than *Eugyrinus* are the same as those in the most parsimonious trees.

In the third experiment, we searched for tree topologies which are not compatible with the placement of *Perryella* as sister taxon to dvinosauroids. There are 19 such topologies, identical to those from the first experiment (see above).

In the fourth experiment, deletion of *Perryella* from the data destabilises the position of a few temnospondyls, and yields ten trees at 876 steps (C.I.≈0·32; R.I.≈0·63; R.C. ≈0·20). Dvinosauria emerge as a clade, and their topology in the strict consensus is fully resolved, with *Neldasaurus*, *Trimerorhachis*,

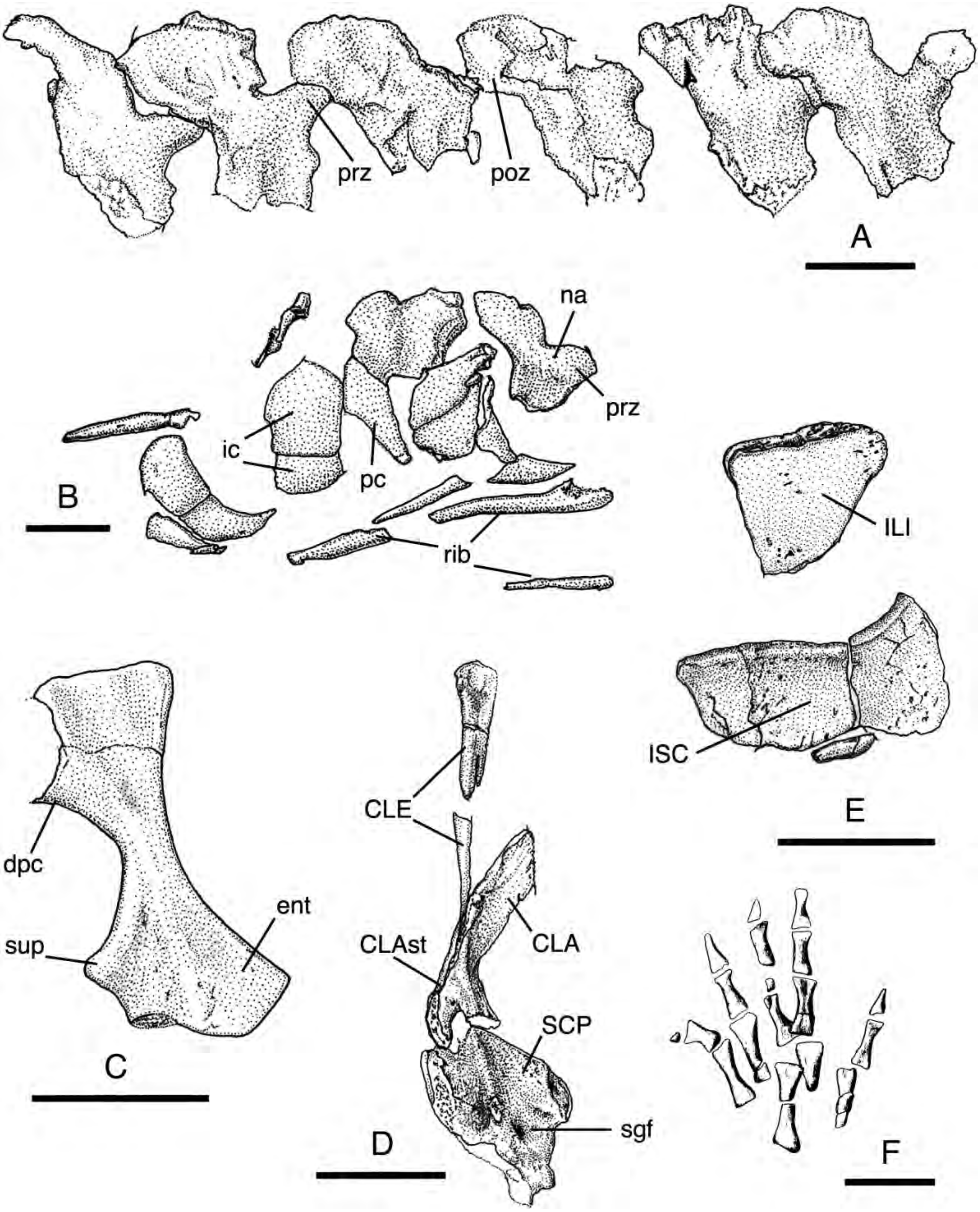

Figure 24 *Perryella olsoni* Carlson, 1987: (A) P82.10.18, camera lucida drawing of string of neural arches in right lateral view; centra and ribs associated with such arches have been omitted; (B) P82.10.2, camera lucida drawing of centra in right ventrolateral view; some incomplete neural arches associated with such centra have been omitted; (C) P82.10.3, camera lucida drawing of well preserved humerus of right side in flexor view; note prominent entepicondyle and spur-like supinator process; (D) P82.10.3, camera lucida drawing of incomplete shoulder girdle of (presumably) left side; note clavicular blade and scapular foramen; (E) P82.10.18, camera lucida drawing of ilium and ischium of right side; (F) P82.10.6, autopod, possibly a pes in ventral aspect (from Carlson 1987, fig. 11). Scale bars in A, B = 2 mm; scale bars in C–E = 5 mm; scale bar in F = 10 mm. Abbreviations: (CLA) clavicle; (CLAst) clavicle stem; (CLE) cleithrum; (dpc) deltopectoral crest of humerus; (ent) entepicondyle; (ic) intercentrum; (ILI) ilium; (ISC) ischium; (na) neural arch; (pc) pleurocentrum; (poz) postzygapophysis; (prz) prezygapophysis; (SCP) scapula; (sgf) supraglenoid foramen; (sup) supinator process of humerus.

Eugyrinus, and *Dvinosaurus* as successive sister taxa, in that order, to a clade of eobrachyopids plus tupilakosaurids. As in the most parsimonious trees, dissorophoids and dvinosaurs emerge as sister groups.

In the fifth experiment, *Perryella* was constrained to cluster with amphibamids (e.g. see Milner & Sequeira 1997). There are 20 trees at 911 steps compatible with this arrangement (C.I. ≈ 0·31; R.I. ≈ 0·62; R.C. ≈ 0·19), in all of which *Perryella* appears as sister taxon to a monophyletic Amphibamidae. These trees are, however, not significantly different (P ≫ 0·05) from the two most parsimonious topologies, and do not require a significant reshuffling of taxa. This result is not totally unexpected, because *Perryella* shows similarities with some dissorophoids.

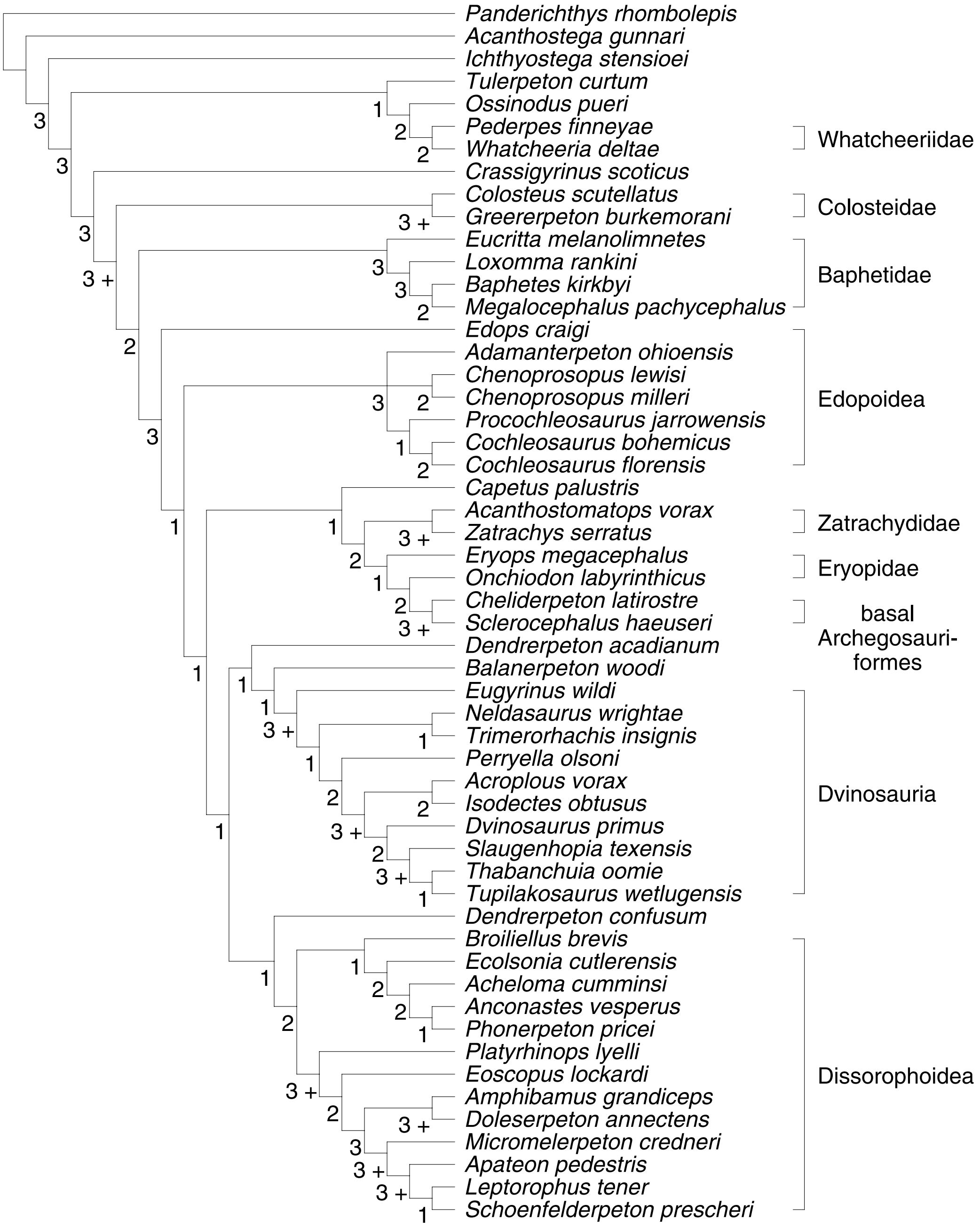

Figure 25 Phylogenetic analysis of representative Permo-Carboniferous and Lower Triassic temnospondyls (see text for details); strict consensus of two most parsimonious trees; numbers at cladogram nodes represent decay index values; the 3+notation refers to those nodes for which decay index values are 4 or higher.

Finally, a sixth experiment was devised to assess the significance of different phylogenetic topologies for temnospondyls as a whole. In particular, our most parsimonious trees differ from the widely cited hypothesis of large-scale temnospondyl relationships put forward by Milner (1990) and slightly modified by Holmes (2000). We built a topological constraint in which the branching sequence of families and superfamilies reflects Milner's (1990) preferred topology. In addition, we imposed minimum constraints on the interrelationships of taxa belonging to each family or superfamily, as follows:

1. Edopoids were placed as a monophyletic group at the base of the temnospondyls, but their intrinsic relationships were left unresolved.
2. *Balanerpeton* and *Dendrerpeton acadianum* were placed as successive sister taxa to all remaining temnospondyls, based on Milner & Sequeira (1994); however, we did not specify any topological constraint for *D. confusum*.
3. The next clade consisted of dvinosaurs; within the latter, an unresolved clade consisting of trimerorhachids plus *Eugyrinus* was placed as sister group to dvinosaurids; also, we placed eobrachyopids (saurerpetontids of Milner 1990) in a polytomy with an unresolved clade of tupilakosaurids, to account for the possibility that eobrachyopids might represent a grade group (Milner 1990); finally, no constraint was specified for *Perryella*, to account for the possibility that it might fall outside the dvinosaur clade.
4. *Capetus* was placed as sister taxon to the two basal archegosauriforms, *Cheliderpeton* and *Sclerocephalus*, following Schoch & Milner (2000).
5. Monophyletic zatracheids and eryopids were placed as successive sister groups, in that order, to dissorophoids; constituent families within dissorophoids (trematopids; dissorophids; micromelerpetontids; branchiosaurids; amphibamids) were treated as monophyletic, but the intrinsic

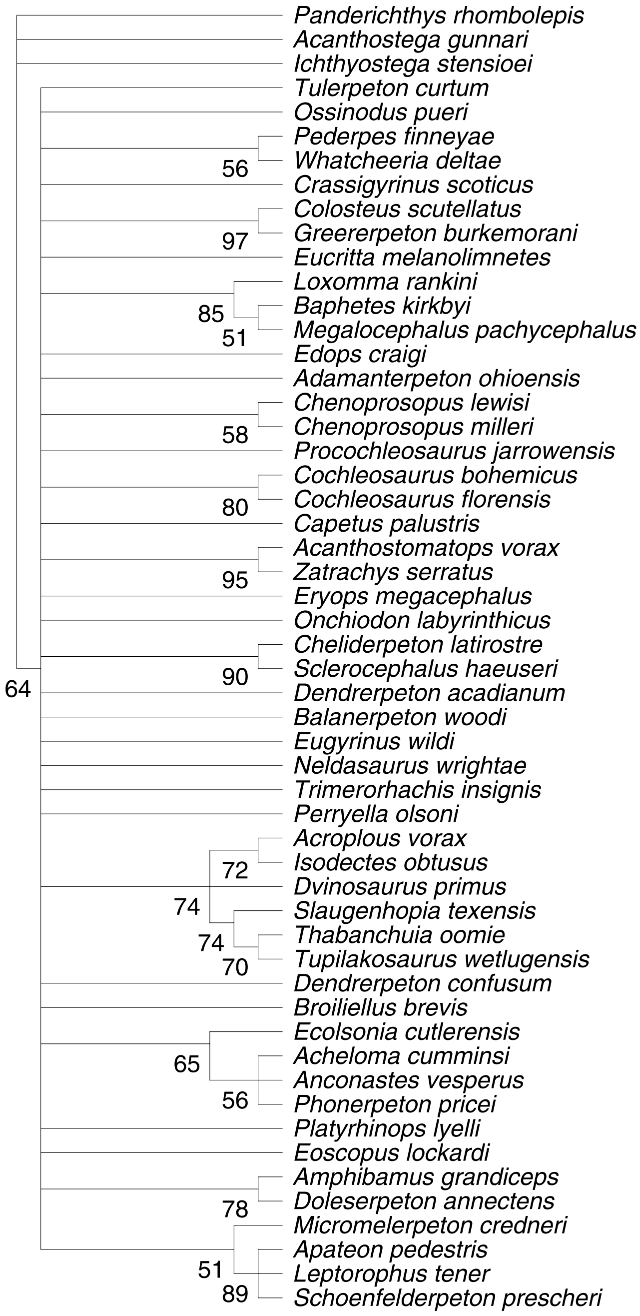

Figure 26 Bootstrap 50% majority-rule consensus; only nodes with values of 50% or more are represented.

relationships of each of these families were left unresolved, although their branching sequence reflected Milner's (1990) preferred arrangement.

6. A PAUP* search of all minimal trees compatible with Milner's (1990) topology yields three shortest trees at 960 steps (C.I.$\approx$0·29; R.I.$\approx$0·6; R.C.$\approx$0·17). These trees (Fig. 27; strict consensus) entail a significantly different rearrangement of character-states than the two shortest trees from the original analysis (P$<$0·0001). Noteworthy is the fact that *Perryella* and *Dendrerpeton confusum* form a clade that occupies a basal position relative to all other temnospondyls.

6. Discussion

Available evidence suggests that, anatomically, *Perryella* represents a level of organisation of dvinosaurs intermediate between that of trimerorhachids and that of dvinosauroids. As in all dvinosaurs, it shows a slight degree of elongation of the skull table, in particular at the level of its parietals, supratemporals, and postorbitals. A previously unrecorded apomorphy of all dvinosaurs is represented by the relative proportions and size of the supratemporals, which are wider than the parietals and dominate the lateral portions of the skull table, a feature also recorded in *Perryella*. The orbits occupy a central position on the skull table. They are larger, relative to the overall skull size, and less widely spaced than in other dvinosaurs. Subcentral orbits are also documented in *Trimerorhachis mesops* (Olson 1955), *Neldasaurus* (Chase 1965), and *Eugyrinus* (Milner 1980). The supratemporal-postparietal suture appears to be deeply incised in its lateralmost part, and thus confers an L-shaped ('stepped') aspect to the postparietal ornamented surface. This feature has also been reported in eobrachyopids and tupilakosaurids, but not in dvinosaurids (Milner & Sequeira 2004; but see also comments in Sequeira 1998, p. 254). The slender, diminutive, abbreviated tabulars of *Perryella* resemble those of dvinosauroids (in which they are wider than long), although reduction of these bones is also documented in derived dissorophoids. The squamosal embayment is more pronounced than that of trimerorhachids, but it resembles those of large *Trimerorhachis* skulls with regard to its dorsoventral slope and anteroposterior depth (an embayment is absent in dvinosauroids; see also Milner *et al*. 2002). The occurrence of a foramen on the quadratojugal occipital surface is consistent with a dvinosaur placement for *Perryella*, although this character is more widely distributed in temnospondyls (e.g. Yates & Warren 2000). The orbital exposure of the palatine (also a feature of many dissorophoids) is shared with both eobrachyopids and tupilakosaurids (e.g. Warren 1999; Milner & Sequeira 2004), but the exceptional development as well as intense sculpturing of the palatine exposure in *Perryella* is noted. The broadly subpentagonal shape of the parasphenoid plate and the presence, on such a plate, of deep, posterolaterally directed grooves delimited anteriorly by ridges and terminating in notches along the plate posterolateral margins, are all features observed in dvinosaurids and trimerorhachids. The preserved portion of the scythe-like, foreshortened palatal ramus of the pterygoid is nearly identical to that of trimerorhachids. *Perryella* lacks all of the diagnostic characters of tupilakosaurids, including: 'kidney'-shaped postorbital with remarkably convex posterior margin; postorbital-parietal suture; small postfrontals which are less than half as extensive as prefrontals, and contribute to less than one third of orbit dorsal margin; long, narrowly crescent-like prefrontals; broad, flat cultriform process, the maximum width of which is greater than half of the width of the parasphenoid plate; and pterygoid incisures between corpus and quadrate ramus of pterygoid (Warren 1999; Milner & Sequeira 2004). The presence of denticle shagreen on the cultriform process is also observed in some dissorophoids (e.g. *Micropholis*; Schoch & Rubidge 2005). Its occurrence in *Perryella* may reflect either immaturity or retention of a juvenile feature (see Boy 1988, 1990), e.g. via neoteny, which is consistent with other, presumably heterochronic traits in this taxon, such as the large orbits. Parasphenoid denticles are recorded in *Eugyrinus* as well.

Milner & Sequeira's (1997) suggestion that *Perryella* may be an advanced dissorophoid (more specifically, an amphibamid) requires additional scrutiny. Milner & Sequeira (1997) cited the following characters as being characteristic of advanced dissorophoids: (1) a prominent pterygoid flange; and (2) lack of a supinator process. However, the posterolateral margin of the pterygoid does not show a flange in a position comparable to that of the flange of derived dissorophoids, although part of the palatal ramus is obscured in most specimens. There appears to be no abrupt change in the curvature of the

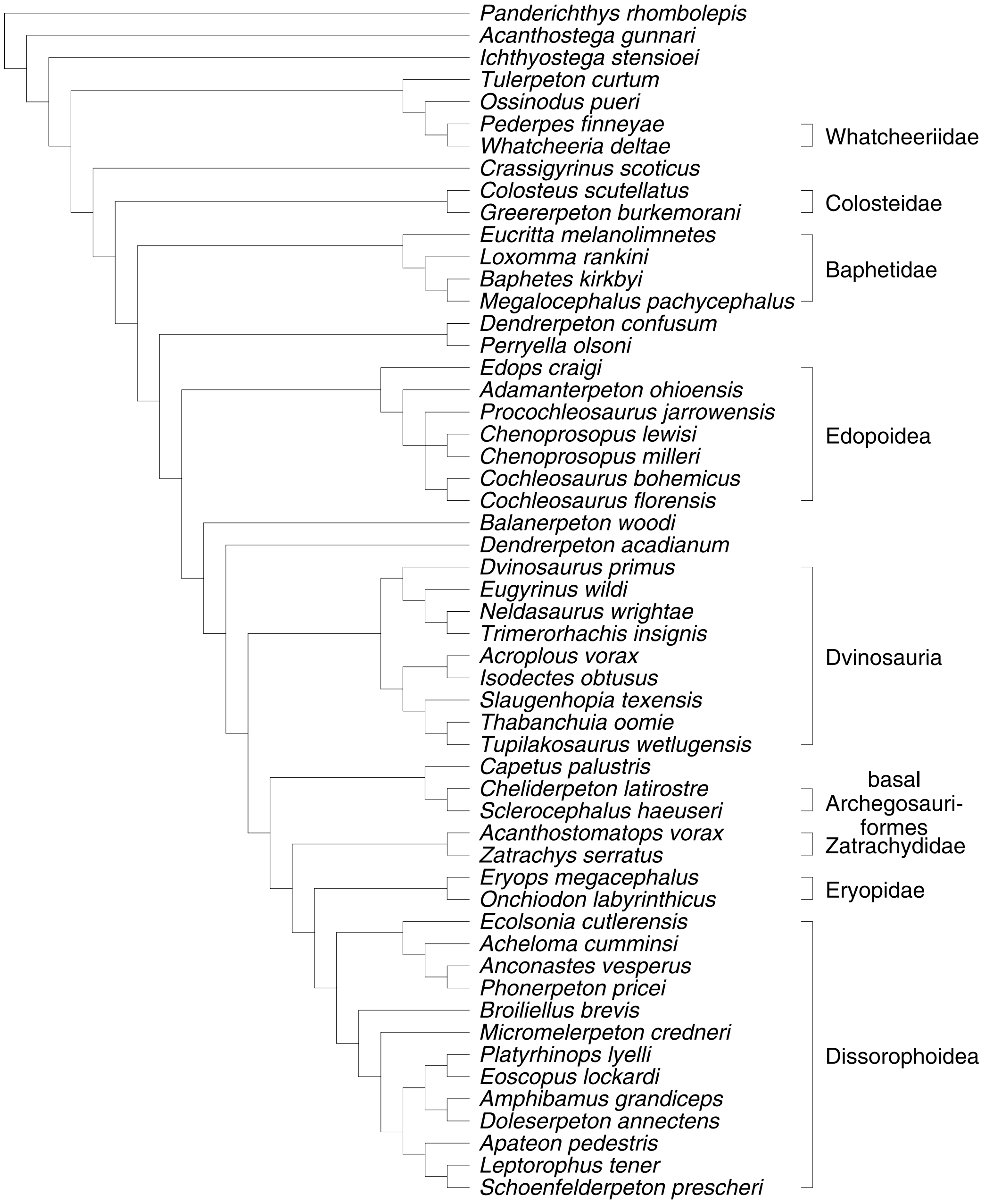

Figure 27 Strict consensus of all suboptimal trees compatible with Milner's (1990) preferred topology for higher-level temnospondyl phylogeny (see text for details).

pterygoid posterolateral margin, as far as we can tell, and further preparation of the holotype skull has revealed that the connection between the lateral margin of the quadrate ramus and the rearmost part of the lateral margin of the palatal ramus is smoother than shown by Carlson (1997). *Perryella* shows a distinct supinator process, unlike most advanced dissorophoids. A supinator process has also been documented in the amphibamid *Tersomius mosesi* by Daly (1994), in which the process in question is shaped like a broad, stout, triangular flange confluent with the distal articulation surface of the humerus. However, attribution of the limb material illustrated by Daly (1994) to *T. mosesi* is uncertain (Schoch & Rubidge 2005).

Among the putative amphibamid characters of *Perryella*, such as were highlighted by Milner & Sequeira (1997), the following require comment: (1) an abbreviated skull table is not a feature of *Perryella*, as the degree of shortening of postparietals and tabulars is not comparable with that of amphibamids, in which the ornamented surfaces of both bones resemble slender strips; (2) the cultriform process of the parasphenoid does show denticles, however these are not arranged in rows, but rather form a continuous shagreen; (3) the wide parasphenoid plate is more similar to that of basal dvinosaurs than to that of amphibamids, in showing posterolaterally directed ridges and grooves and two broad posterolateral excavations; (4) finally, the present authors' observations could not confirm Milner & Sequeira's (1997) statement that the pleurocentra meet along the ventral mid line; in fact, the wide crescent-shaped bones that intervene between neural arches are clearly intercentra (antimeres tightly sutured along the ventral midline), and unequivocal, ventrally incomplete, narrowly triangular pleurocentra have been found in association with such intercentra. Finally, the frontal contribution to the orbit is the most puzzling feature of *Perryella*, as it is not observed in other dvinosaurs, although it is present in several dissorophoids. However, we note that the frontal is excluded from the orbit margin in some dissorophoids (e.g. *Amphibamus grandiceps*; *Platyrhinops lyelli*; *Tersomius texensis*; Carroll 1964; Bolt 1979; Milner 2000; Schoch & Milner 2004).

The Lower Permian age of *Perryella* is seemingly at odds with the Pennsylvanian record of some dvinosauroids, notably *Erpetosaurus*, *Dawsonerpeton*, *Lafonius*, and *Isodectes* (the range of the latter extends into the Lower Permian; Sequeira 1998; Milner *et al*. 2002; *Erpetosaurus*, *Lafonius*, and *Dawsonerpeton* need reassessment; see Berman 1973 and Hook 1983). This suggests, assuming the correctness of the phylogenetic hypothesis presented in the present paper, that the evolutionary diversification of post-trimerorhachid dvinosaurs began, minimally, during the late part of the Pennsylvanian. Recent revisions (Milner & Sequeira 2004) indicate an earlier stage of clade diversification for derived dvinosaur families than that suggested by their fossil record.

Finally, it is hoped that new data on *Perryella* will inform to some degree current issues of basal temnospondyl phylogeny and biogeography.

7. Acknowledgements

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8. Appendix 1. Ingroup and outgroup taxa

Bibliographic sources for each taxon are reported below; asterisks indicate those taxa that have been examined directly by one or both authors (using either casts or original specimens).

Temnospondyli:
Acanthostomatops vorax (Boy 1989); *Acheloma cumminsi** (Olson 1941; Dilkes & Reisz 1987); *Acroplous vorax** (Hotton 1959; Coldiron 1978; Foreman 1990); *Adamanterpeton ohioensis* (Milner & Sequeira 1998); *Amphibamus grandiceps** (Watson 1940; Gregory 1950; Carroll 1964; Bolt 1979; Milner 1993); *Anconastes vesperus* (Berman *et al*. 1987); *Apateon pedestris* (Schoch 1992, 2004; Schoch & Carroll 2003); *Balanerpeton woodi** (Milner & Sequeira 1994); *Broiliellus brevis** (Carroll 1964); *Capetus palustris** (Sequeira & Milner 1993); *Cheliderpeton latirostre* (Boy 1993; Schoch & Milner 2000); *Chenoprosopus lewisi* (Langston 1953; Milner & Sequeira 1998); *Chenoprosopus milleri* (Mehl 1913; Hook 1993; Milner & Sequeira 1998); *Cochleosaurus bohemicus** (Milner & Sequeira 1998; Sequeira 2004); *Cochleosaurus florensis* (Rieppel 1980; Godfrey & Holmes 1995); *Dendrerpeton acadianum** (Carroll 1967; Milner 1980, 1996; Godfrey *et al*. 1987; Holmes *et al*. 1998); *Doleserpeton annectens** (Bolt 1969); *Dvinosaurus primus* and *D. egregius* (Bystrow 1938; Shishkin 1973); *Ecolsonia cutlerensis* (Berman *et al*. 1985); *Edops craigi** (Romer & Witter 1942); *Eoscopus lockardi** (Daly 1994); *Eryops megacephalus** (Miner 1925; Sawin 1941; Romer 1947; Moulton 1974); *Eugyrinus wildi* (Watson 1940, Milner 1980); *Isodectes obtusus** (Watson 1956; Sequeira 1998); *Leptorophus tener* (Boy 1986; Boy & Sues 2000); *Micromelerpeton credneri* (Boy 1995; Boy & Sues 2000); *Neldasaurus wrightae** (Chase 1965); *Onchiodon labyrinthicus* (Boy 1990); *Perryella olsoni** (Carlson 1987; present work); *Phonerpeton pricei** (Dilkes 1990); *Platyrhinops lyelli* * (Carroll 1964; Clack & Milner 1994; Milner 2000; Schoch & Milner 2004); *Procochleosaurus jarrowensis* (Sequeira 1996); *Thabanchuia oomie* (Warren 1999; Milner & Sequeira 2004); *Schoenfelderpeton prescheri* (Boy 1986; Boy & Sues 2000); *Sclerocephalus haeuseri* (Boy 1988; Meckert 1993; Schoch & Milner 2000; Schoch 2003); *Slaugenhopia texensis** (Milner & Sequeira 2004); *Trimerorhachis insignis** (Williston 1915, 1916; Case 1935); *Tupilakosaurus wetlugensis* (Shishkin 1973); *Zatrachys serratus** (Langston 1953; Paton 1975; Schoch 1997);

Outgroups:
*Acanthostega gunnari** (Clack 1994a, b, 1998b, 2002b; Coates 1996); *Baphetes kirkbyi** (Beaumont 1977; Milner & Lindsay 1998); *Colosteus scutellatus** (Hook 1983); *Crassigyrinus scoticus** (Panchen 1973; Panchen & Smithson 1990; Clack 1996, 1998c); *Eucritta melanolimnetes** (Clack 1998a, 2001); *Greererpeton burkemorani** (Smithson 1982; Godfrey 1989; Bolt & Lombard 2001); *Ichthyostega stensioei** (Jarvik 1996; Clack *et al*. 2003); *Loxomma rankini* (Beaumont 1977); *Megalocephalus pachycephalus** (Beaumont 1977); *Ossinodus pueri** (Warren & Turner 2004); *Panderichthys rhombolepis* (Vorobyeva & Schultze 1991; Ahlberg & Clack 1998); *Pederpes finneyae** (Clack 2002a; Clack & Finney 2005); *Tulerpeton curtum* (Lebedev & Clack 1993; Lebedev & Coates 1995); *Whatcheeria deltae** (Lombard & Bolt 1995).

9. Appendix 2. Character list

Each character is accompanied by a bold number that identifies exclusively its position in the present data matrix, and by an italicised acronym that identifies the same character in Ruta *et al*.'s (2003) data matrix. This convention is adopted because the same character may occupy different places in different versions of the data matrix, due to the addition or removal of other characters. Acronyms are slightly simplified relative to Ruta *et al*. (2003). The number which follows each acronym serves to distinguish different characters that pertain to the same bone. As an example: *PRM 1* is the acronym that always identifies the character 'Absence (0) or presence (1) of alary process of the premaxilla', in all versions of the data set. *PRM 2* and *PRM 3* of Ruta *et al*. (2003) have not been used here, but *PRM 4* is included. Formulations of characters are followed by concise descriptions. New characters added to Ruta *et al*. (2003) are denoted by an asterisk.

Premaxilla (PRM)

1. *PRM 1*. Absence (0) or presence (1) of alary process of the premaxilla. *Remarks*: The alary process is a subtriangular bony lappet that arises from the posterolateral margin of the dorsal ramus of the premaxilla, and extends posteriorly overlapping the nasal along or near the margin of the external nostril.
2. *PRM 4*. Absence (0) or presence (1) of condition: premaxilla with no distinct nasal and maxillary processes, and with its medial margin only slightly shorter than its lateral margin. *Remarks*: In edopoids, the premaxilla shows a conspicuous elongation along its lateral margin, from its lateralmost extremity, in contact with the maxilla, to its anterior point (anterior extremity of interpremaxillary suture). The bone increases uniformly in width anteromedially, but the interpremaxillary suture is less than half as long as its lateral margin.
3. *PRM 9*. Absence (0) or presence (1) of a shelf-like premaxilla-maxilla contact occurring mesial to the marginal tooth row on the palate, and extending mesially for at least twice the width of such row. *Remarks*: In some taxa, both the premaxilla and the maxilla produce a ventral bony 'shelf' which projects mesial to the marginal dentition.

Tectal (TEC)

4. *TEC 1*. Presence (0) or absence (1) of an anterior tectal. *Remarks*: This character refers to a small bone bordering the external nostril dorsally, and found in basal tetrapods, such as the Devonian *Acanthostega* and *Ichthyostega*, as well as in the piscine ancestors of tetrapods.

Septomaxilla (SEP)

5. *SEP 2*. Septomaxilla sutured (0) or not sutured (1) to dermal circumnarial bones. *Remarks*: Unlike in Ruta *et al.* (2003), the present authors have eliminated two characters, one related to the presence of a lateral rostral and one related to the presence of a septomaxilla. Homology between these two bones has been generally accepted, although we opted to treat them as separate bones in our former review. However, the occurrence of a septomaxilla cannot always be shown in the available material of several taxa, and we are not confident that it could be treated as a simple presence/absence character. Therefore, we have scored as unknown those instances in which a septomaxilla is not observed, and have coded exclusively for its position relative to the margin of the external naris (i.e. as part of the skull roof or as a detached ossification).

Nasal (NAS)

6. *NAS 2*. Nasals more (0) or less than (1) one-third as long as the frontals. *Remarks*: Metric cut-off points used to discriminate states were selected following ratio measurements in different groups. The length of each bone was measured along the greatest distance between its anterior and posterior extremities. Paired bones often appear to be comparable in size. However, in those cases in which a bone differs slightly from its antimere, the largest of the two antimeres is chosen for measurements.

*7. *NAS 3*. Absence (0) or presence (1) of a nasal-maxilla contact. *Remarks*: A nasal-maxilla contact is observed in some edopoids, some basal archegosauriforms, as well as some dvinosaurs.

8. *NAS 5*. Absence (0) or presence (1) of condition: nasals broad plates contributing to more than 50% of the posterodorsal and mesial borders of the external naris, and with lateral margins diverging abruptly in their anterior parts. *Remarks*: The derived condition characterises, among others, several dissorophoids. In the derived state, the anterior tracts of the lateral margins of the nasals diverge markedly anterolaterally, so that these binnes crease abruptly in width anteriorly. This condition is not linked to the size of the external nostril.

9. *NAS 6*. Parietal/nasal maximum length ratio less than (0) or more than 1.45 (1). *Remarks*: The length of the bones is measured parallel to the skull midline. Metric cut-off points used to discriminate states were selected following ratio measurements in different groups, and the condition expressed by state 1 is best exemplified by colosteids.

Prefrontal (PRF)

10. *PRF 2*. Prefrontal less than (0) or more than (1) three times longer than wide. *Remarks*: The length of the bone is measured parallel to the skull midline, between the rearmost and anteriormost points of its dorsomesial surface.

*11. *PRF 5*. In dorsal aspect, lateralmost point of the suture between the prefrontal and the postfrontal situated at the level of the anterior half of the orbit length (measured parallel to the skull midline) (0) or at the level of the middle/posterior half of such length (1). *Remarks*: State 1 occurs sporadically among both ingroup and outgroup taxa, e.g. in some dvinosaurs and dissorophoids.

12. *PRF 6*. Absence (0) or presence (1) of a prefrontal-premaxilla contact. *Remarks*: A prefrontal-premaxilla contact is observed in colosteids.

13. *PRF 7*. Prefrontal without (0) or with (1) a stout lateral protuberance, forming a constriction between the outline of the orbit and that of the antorbital vacuity. *Remarks*: In most baphetids, the keyhole-shaped orbits reveal a constriction between the orbit proper and the antorbital vacuity. The constriction is delimited laterally by a stout process on the lateral margin of the prefrontal. However, the baphetids *Spathicephalus* and *Kyrinion* (not included in the present data), do not show a constriction; instead, their orbits possess an elongate, subelliptical, and smooth outline (Beaumont & Smithson 1998; Clack 2003).

14. *PRF 8*. Absence (0) or presence (1) of condition: prefrontal contributing to the margin of the external naris. *Remarks*: State 1 is observed in some trematopids and in some dvinosaurs within the ingroup.

15. *PRF 9*. Absence (0) or presence (1) of a prefrontal-maxilla contact (1). *Remarks*: A prefrontal-maxilla contact is observed in some dvinosaurs within the ingroup.

16. *PRF 10*. Prefrontal contributes to more (0) or less than (1) half of the anteromesial margin of the orbit. *Remarks*: In dorsal view, and imagining the division of the orbit outline into four quadrants, the derived state refers to the contribution of the orbital margin of the prefrontal to the anteromesial quadrant (quadrants are delimited by lines running through the mesialmost, lateralmost, anterior, and posterior points of the orbit).

*17. *PRF 11*. Absence (0) or presence (1) of a prefrontal-jugal contact. *Remarks*: A prefrontal-jugal contact is seen in edopoids, eryopoids, and basal archegosauriforms.

Lacrimal (LAC)

18. *LAC 1*. Presence (0) or absence (1) of lacrimal as separate ossification. *Remarks*: Separately ossified lacrimals are absent in dvinosaurids and tupilakosaurids (see discussion in Warren 1999 and Milner & Sequeira 2004).

19. *LAC 5*. Lacrimal without (0) or with (1) an anteriorly directed, V-shaped emargination along its posterior margin. *Remarks*: The antorbital vacuity of *Baphetes* and *Megalocephalus* has an acute, triangular anterior apex excavated in the posterior margin of the lacrimal.

Maxilla (MAX)

*20. *MAX 1*. External maxilla-premaxilla contact: narrow contact point (0), in lateral aspect measuring less than one-third of the projected maximum height of the maxilla, or broad contact (1), in lateral aspect measuring more than one-third of the projected maximum height of the maxilla. *Remarks*: State 0 is widespread in outgroup taxa.

*21. *MAX 2*. Posterior extremity of the maxilla ends posterior (0) or anterior to (1) the anterior border of the subtemporal fossa. *Remarks*: State 1 is seen in certain edopoids and dvinosaurs.

22. *MAX 3*. Maxilla extending posterior to the level of the posterior margin of the orbit (0) or terminating at the level of such margin or anterior to it (1). *Remarks*: In a lateral view of the skull, the derived state occurs among assorted ingroup taxa, including edopoids, zatracheids, eryopoids, and some dvinosaurs.

*23. *MAX 4*. Absence (0) or presence (1) of inward inflection of skull outline in dorsal view at the level of the maxilla-premaxilla suture. *Remarks*: In dorsal aspect, the skull of such taxa as *Edops*, *Eryops*, and *Sclerocephalus* shows a shallow concave profile along the anterolateral margins of the snout.

24. *MAX 5*. Maxilla not contributing (0) or contributing (1) to the margin of the orbit. *Remarks*: In some dissorophoids, the dorsal margin of the maxilla enters the orbit.

25. *MAX 8*. Absence (0) or presence (1) of a subrectangular, flange-like facial process of the maxilla along the anterior half of the dorsal margin of the bone. *Remarks*: State 1 is observed found in certain dissorophoids.

*26. *MAX 10*. Maxilla contacts palatine along the whole lateral margin of the latter (0) or only at the anterior extremity of such margin (1). *Remarks*: In branchiosaurid dissorophoids, the maxilla is sutured with the palatine along a short tract of the anterior portion of the palatine lateral margin.

*27. *MAX 11*. Absence (0) or presence (1) of a maxilla-vomer contact anterior to the choana. *Remarks*: In some edopoids, dissorophoids, zatracheids, as well as certain dvinosaurs, the vomer forms a suture with the maxilla, visible anterior to the choana in ventral aspect. The derived state is also found in some basal archegosauriforms, e.g. *Archegosaurus decheni* (Witzmann 2006b).

*28. *MAX 12*. Presence (0) or absence (1) of a maxilla-quadratojugal contact. *Remarks*: The maxilla does not contact the quadratojugal in some edopoids, dissorophoids, and dvinosaurs.

Frontal (FRO)

29. *FRO 2*. Frontal shorter than (0), longer than (1), or subequal to (2) the parietal. *Remarks*: The length of each bone was measured along the greatest distance between its anterior and posterior extremities. Paired bones appear to be often comparable in size. However, in those cases in which a bone differs slightly from its antimere, the larger of these is selected for measurements. The distribution of states is not congruent either between or within different groups of temnospondyls.

30. *FRO 4*. Frontal excluded from (0) or contributing to (1) the margin of the orbit. *Remarks*: In some dissorophoids and dvinosaurs, the lateral margin of the frontal contributes to the orbit.

31. *FRO 6*. Absence (0) or presence (1) of condition: anterior margins of the frontals wedged between the posterolateral margins of the nasals for at least one-third of the maximum length of the latter. *Remarks*: Bone length is measured parallel to the skull midline. State 1 occurs in some outgroups only.

Parietal (PAR)

32. *PAR 2*. Absence (0) or presence (1) of a suture between the parietal and the postorbital. *Remarks*: Aside from its presence in some outgroups, a suture between the parietal and the postorbital characterises some dvinosaurids and all tupilakosaurids.

33. *PAR 4*. Anterior margin of parietal lying anterior to (0), approximately level with (1), or posterior to (2) the midlength of the orbit. *Remarks*: The midlength of the orbit is measured along its greatest anteroposterior diameter, in dorsal aspect. State 2 is observed in all ingroup taxa.

34. *PAR 6*. Parietals more (0) or less (1) than two and a half times as long as wide. *Remarks*: Among ingroup taxa, state 0 occurs in basal archegosauriforms, as well as in most dvinosaurs and some edopoids.

35. *PAR 8*. Absence (0) or presence (1) of condition: suture between the parietal and the frontal strongly interdigitating. *Remarks*: Strong interdigitations of the sutural seam are shaped like a series of interlocking, finger-like projections, resulting in a wavy, irregularly sinuous profile of the seam.

*36. *PAR 10*. Combined width of both parietals subequal to (0), smaller than (1), or larger than (2) the interorbital width. *Remarks*: The greatest width of the articulated parietals is measured between the most lateral projections of their lateral margins. The interorbital width is the smallest distance between the medial margins of the orbits. This condition is not linked to the orbit size or contributions of the frontals to the orbit margin.

*37. *PAR 11*. Combined width of both parietals smaller than (0), subequal to (1), or larger than (2) the maximum length of these bones. *Remarks*: The maximum length of the parietals is measured parallel to the skull midline.

*38. *PAR 12*. Parietal–supratemporal suture less than half as long as the supratemporal (0) or at least half as long as the supratemporal (1). *Remarks*: In taxa showing state 0, the supratemporal-parietal suture is situated in the posterolateral region of the external surface of the parietal. This configuration is seen sporadically in the ingroup, but is more widespread among outgroup taxa.

*39. *PAR 13*. Maximum width of parietal more than (0), subequal to (1), or less than (2) that of the supratemporal. *Remarks*: State 2 (sometimes in a polymorphic combination with state 1) is seen in dvinosaurs, as well as certain other temnospondyls.

Postparietal (POP)

40. *POP 3*. Postparietal less than (0) or more than (1) four times wider than long. *Remarks*: State 1 accounts for the anteroposteriorly abbreviated ornamented area of the postparietals in dissorophoids.

41. *POP 4*. Postparietals without (0) or with (1) median lappets. *Remarks*: Some outgroups have a pronounced process of the posteromesial corner of the postparietal external surface that adjoins its antimere forming a posteriorly directed lappet.

42. *POP 10*. Total exposed area of the external surface of the postparietal not larger (0) or larger (1) than the external surface of the nasal. *Remarks*: In colosteids, the external surface of the nasals is less extensive than that of the postparietals. This character is not associated with characters 8 and 9 above.

*43. *POP 11*. Postparietals not tapering (0) or tapering abruptly laterally (1). *Remarks*: In *Perryella* and most dvinosauroids, the anteroposterior length of the external surface of the postparietal decreases in a mediolateral direction.

*44. *POP 12*. Postparietals without (0) or with (1) lateral lappets. *Remarks*: The postparietal of some edopoids and some zatracheids carries a flat, spatulate process projecting backward from the posterior margin of the ornamented surface of the bone.

*45. *POP 13*. Postparietals not forming (0) or forming (1) an L-shaped ('stepped') suture with the supratemporals. *Remarks*: In some dvinosauroids, the postparietal–pratemporal suture has an angular profile, resulting in an L-shaped external surface of the postparietal (but see also Sequeira 1998; the present authors found slightly L-shaped postparietals in one specimen of *Acroplous* in the collections of the Natural History Museum of the University of Kansas, KUVP 49533).

Postfrontal (POF)

*46. *POF 5*. Absence (0) or presence (1) of condition: external surface of the postfrontal less than one third of the external surface of the postorbital. *Remarks*: State 1 is found in tupilakosaurids, in which the postfrontal is a small polygonal bone, the external surface of which makes up less than 30% of that of the postorbital.

Intertemporal (INT)

47. *INT 1*. Intertemporal present (0) or absent (1) as a separate ossification. *Remarks*: No separately ossified intertemporal is found in the majority of temnospondyl clades. It occurs in edopoids and basal dvinosaurs, as well as in a number of primitive genera such as *Capetus*, *Balanerpeton*, and *Dendrerpeton*.

48. *INT 3*. Absence (0) or presence (1) of intertemporal-squamosal contact. *Remarks*: An intertemporal-squamosal contact is found in whatcheeriids.

*49. *INT 4*. Absence (0) or presence (1) of condition: intertemporal less than half as broad as the supratemporal. *Remarks*: State 1 occurs in some baphetids and in some basal dvinosaurs, as well as in the temnospondyls *Balanerpeton* and *Procochleosaurus*.

*50. *INT 5*. Absence (0) or presence (1) of condition: intertemporal a subquadrangular bone approximately as long as wide. *Remarks*: The distribution of this character is nearly coextensive with that of the previous character, but describes an independent morphological condition.

Supratemporal (SUT)

51. *SUT 2*. Absence (0) or presence (1) of condition: supratemporal bordering the anterior edge of the squamosal embayment. *Remarks*: In baphetids and in the whatcheeriid *Pederpes*, the supratemporal posterior margin is excavated by the anterior part (dorsal view of the skull) of the squamosal embayment (i.e. the free posterior margin of the suspensorium in lateral aspect).

52. *SUT 4*. Supratemporal contact with squamosal smooth (0) or interdigitating (1). *Remarks*: A strongly interlocking suture between the lateral margin of the supratemporal and the dorsal margin of the squamosal is observed in taxa from very different groups.

Tabular (TAB)

53. *TAB 3*. Absence (0) or presence (1) of a conical posterior process of the tabular projecting backward from the bone ventral to the level of the skull table. *Remarks*: In baphetids as well as colosteids, the process in question is a small conical extension of the occipital surface of the tabular, separated from the ornamented portion of the skull table.

54. *TAB 4*. Suture between the squamosal and the tabular present in part on the dorsal surface of the skull table (0) or not (1). *Remarks*: In some outgroups and in some dvinosaurs, part of the squamosal-tabular suture runs onto the dorsal surface of the skull table.

*55. *TAB 11*. Absence (0) or presence (1) of condition: tabulars more than three times wider than long. *Remarks*: In some dvinosaurs, the width of the sculptured surface of the tabular exceeds its maximum length, measured parallel to the midline of the skull.

*56. *TAB 12*. Maximum length of the tabular ornamented surface not less (0) or less than (1) one-third of the maximum length of the postparietal external surface. *Remarks*: The length of both bones is measured parallel to the midline of the skull. The derived state is found in some dvinosaurs, and appears sporadically in some dissorophoids and edopoids.

Postorbital (POO)

57. *POO 4*. Postorbital not narrowing (0) or narrowing (1) to an acute posterior point. *Remarks*: The shape of the postorbital ornamented surface may appear extremely irregular, especially among stem tetrapods. The derived state refers to the presence of a tapering, subtriangular posterior process of the postorbital, a morphology recorded in most ingroup taxa. However, some dvinosaurs, among others, are notable exceptions.

58. *POO 6*. Postorbital not wider (0) or wider (1) than the orbit. *Remarks*: The width of the postorbital is measured, in external view, as the distance between the anteroventral (lateral) and anterodorsal (mesial) processes. The width of the orbit is measured between its lateralmost and mesialmost points of its outline, perpendicular to the midline of the skull.

*59. *POO 9*. Length of the suture between the postorbital and the jugal less (0) or more (1) than half of the maximum length of the former. *Remarks*: The maximum length of both the postorbital and its sutural contact with the jugal are measured parallel to the skull midline.

*60. *POO 10*. Absence (0) or presence (1) of a ventrolateral extension of the postorbital extending into the jugal. *Remarks*: In some temnospondyls, including *Perryella*, the anteroventral ramus of the postorbital (in lateral aspect) is deeply inserted into, and accommodated by, a notch in the dorsal ramus of the jugal. In dorsal aspect, the extremity of the anteroventral ramus of the postorbital is wedged into the jugal.

Squamosal (SQU)

61. *SQU 1*. Anteriormost extension of the external surface of the squamosal lying posterior to (0), in front of (1), or approximately level with (2) the parietal midlength. *Remarks*: In dorsal view, the position of the anteriormost point of the external surface of the squamosal is related to the midlength of the parietal external surface. State 1 is widely distributed among ingroup taxa, whereas state 2 occurs only in a handful of these, including some dvinosaurs.

62. *SQU 3*. Squamosal without (0) or with (1) a concave embayment along its posterior margin. *Remarks*: The present authors have not discriminated among different degrees of curvature of the embayment (see next character). The present character refers exclusively to the presence of a concavity along the posterior margin of the bone. Notably, some dvinosaurs lack such concavity.

63. *SQU 6*. Absence (0) or presence (1) of condition: squamosal embayment approximately semicircular. *Remarks*: In some dissorophoids (notably, amphibamids), zatracheids, and a handful of other forms, the posterior margin of the squamosal has a semicircular outline in lateral aspect.

*64. *SQU 7*. Supratympanic flange of the squamosal (a ventrally convex, downward projection of the lateral ventral margin of the bone) absent (0), present but not in contact with the tabular immediately ventral to the supratemporal (1), or in contact with the tabular immediately ventral to the supratemporal (2). *Remarks*: A definition of the supratympanic flange was provided by Bolt (1974b). When the skull is oriented in lateral aspect, the flange shows different types of configuration as regards its relationships with the lateral temporal bones. In some taxa, it has a sutural contact with the tabular just ventral to a ventral extension of the supratemporal.

*65. *SQU 8*. Supratemporal shorter than the squamosal (0) or comparable in length to it (1). *Remarks*: The length of both bones is measured parallel to the midline of the skull. In the case of the squamosal, it is the distance between the anteriormost point of its external surface and the rearmost point of its posterior margin (in lateral or dorsal views).

Jugal (JUG)

66. *JUG 3*. Jugal not contacting (0) or contacting (1) pterygoid. *Remarks*: In some outgroup and ingroup taxa (notably some dvinosaurs and some edopoids), a jugal-pterygoid contact is established via a bridge of bone in the form of a stout process or flange with contribution from one or both bones; this bridge of bone delimits the anterior margin of the subtemporal fossa in ventral view, thus preventing the ectopterygoid from entering the fossa.

67. *JUG 4*. Jugal depth below the orbit greater than/subequal to (0) or smaller than (1) half of the anteroposterior orbit diameter. *Remarks*: In the majority of the ingroup taxa, the maximum dorsoventral extension of the jugal (from the margin of the orbit to its ventral edge) is smaller than 50% of the maximum diameter of the orbit, measured parallel to the midline of the skull.

68. *JUG 8*. Jugal not extending (0) or extending (1) anterior to the anterior margin of the orbit. *Remarks*: State 1 refers to the position of the anterior point of the jugal anterior ramus relative to the anterior margin of the orbit, when the skull is observed in lateral view.

Quadratojugal (QUJ)

*69. *QUJ 4*. Absence (0) or presence (1) of lateral bony protuberances and/or spines on the quadratojugal. *Remarks*: In zatracheids, the external surface of the quadratojugal is intensely sculptured and consists of spiny processes and a coarsely irregular texture.

*70. *QUJ 5*. Quadratojugal foramen absent (0), present on the occipital surface of the bone but occupying less than one-third of the width of this surface (1), or present and occupying at least one-third of the width of this surface (2). *Remarks*: The foramen in question is particularly evident in dvinosaurs and in basal archegosauriforms, in which it occupies the central part of the posterior surface of the bone, and is clearly observed in occipital view.

Quadrate (QUA)

71. *QUA 1*. Quadrate without (0) or with (1) a dorsal process. *Remarks*: In several dissorophoids, the posterior dorsal surface of the quadrate carries a process directed dorsally.

Preopercular (PRO)

72. *PRO 1*. Presence (0) or absence (1) of a preopercular. *Remarks*: A preopercular occupies the posterior surface of the suspensorium (in lateral aspect) in some stem tetrapods.

External naris (NOS)

73. *NOS 1*. Absence (0) or presence (1) of condition: external naris posterolaterally expanded. *Remarks*: The derived state is a feature of branchiosaurid dissorophoids, in which the outline of the external naris widens in its posterolateral portion (in dorsal aspect), so that its width, measured perpendicular to the skull midline, increases anteroposteriorly.

74. *NOS 3*. Absence (0) or presence (1) of condition: external naris key-hole shaped in lateral view. *Remarks*: In trematopid dissorophoids, the nostril is expanded anteroposteriorly, and shows substantial contributions from the nasal and the maxilla (or lacrimal), and smaller contributions from the prefrontal and the premaxilla. In dorsal and lateral aspect, its outline consists of a subrounded, shorter anterior part and a semielliptical, longer posterior part.

75. *NOS 4*. Absence (0) or presence (1) of condition: external naris greater axis at least 70% of the length of the internasal suture. *Remarks*: In several dissorophoids, the maximum anteroposterior length of the external naris, measured parallel to the skull midline, occupies a considerable proportion of the snout length. We arbitrarily chose, as a metric cut-off point for the derived state, the length of its greater axis relative to the suture between the two nasals.

*76. *NOS 5*. External naris orientation: facing primarily ventrolaterally (0) or facing primarily dorsolaterally (1). *Remarks*: State 0, shown for instance by *Acanthostega* and *Ichthyostega*, is that of an external naris lying in close proximity to the upper jaw margin and the border of which delimits a plane oriented mostly ventrolaterally.

77. *NOS 6*. Upper margin of external naris smoothly curved (0) or irregularly fimbriated (1). *Remarks*: An irregularly fimbriated, upper margin of the external naris occurs in both whatcheeriids and *Crassigyrinus*.

Orbit (ORB)

78. *ORB 1*. Minimum interorbital distance greater than (0), smaller than (1), or subequal to (2) half skull table width. *Remarks*: The minimum interorbital distance is the shortest distance between the mesial margins of the borders of the two orbits. The width of the skull table is the distance between the lateralmost points of the supratemporals. This character is independent of characters 30 and 36 above.

79. *ORB 2*. Minimum interorbital distance greater than (0), smaller than (1), or subequal to (2) the maximum diameter of the orbit. *Remarks*: The maximum diameter of the orbit is the maximum distance between the anterior and posterior points of its outline, measured parallel to the skull midline.

80. *ORB 3*. Anteroventral corner of the orbit smoothly curved (0) or angular (1). *Remarks*: State 1 refers to the condition of certain outgroups, in which the anteroventral (in lateral aspect) portion of the orbit outline is acutely triangular.

*81. *ORB 4*. Absence (0) or presence (1) of condition: orbit higher than long. *Remarks*: In lateral view, state 1 refers to the ratio between the maximum distance that intervenes between the supraorbital and the infraorbital bones, and the anteroposterior orbit diameter (i.e. the distance between the anterior and posterior points of its outline measured parallel to the skull midline).

*82. *ORB 5*. Anteroposterior orbit diameter shorter than (0), longer than (1), or subequal to (2) the distance between the posterior margin of the orbit and the anterodorsal margin of the squamosal. *Remarks*: In lateral aspect, the distance between the posterior margin of the orbit and the anterodorsal margin of the external surface of the squamosal is measured parallel to the skull midline.

*83. *ORB 6*. Orbit centre closer to the anterior extremity of the premaxillae than to the posterior margin of the skull roof (0), occupying approximately the mid-length between the anterior extremity of the premaxillae and the posterior margin of the skull roof (1), or closer to the posterior margin of the skull roof than to anterior extremity of the premaxillae (2). *Remarks*: Landmarks chosen for this character refer to a dorsal projection of the skull. This character describes a different condition from the following character.

*84. *ORB 7*. Orbit centre closer to the anterior extremity of the premaxillae than to the posterodorsal margin of the squamosal (0), occupying mid-length between the anterior extremity of the premaxillae and the posterodorsal margin of the squamosal (1), or closer to the posterodorsal margin of the squamosal than to the anterior extremity of the premaxillae (2). *Remarks*: The present character overlaps in part with the preceding character, but the distributions of states for these characters are not entirely congruent. The posterodorsal portion of the squamosal is the rearmost point, either in lateral or in dorsal view, of its dorsal margin in contact with the bones of the lateral temporal series.

*85. *ORB 8*. Minimum interorbital distance smaller (0), subequal to (1), or greater (2) than the distance between the posterior margins of the orbits and the mid point of the posterior margin of the skull table. *Remarks*: Measurements are taken parallel to the skull midline. Landmarks refer to a dorsal projection of the skull.

*86. *ORB 9*. Minimum interorbital distance smaller (0), subequal to (1) or greater than (2) the distance between the anterior margins of the orbits and the anterior extremity of the premaxillae. *Remarks*: Measurements are taken parallel to the skull midline. Landmarks refer to a dorsal projection of the skull.

*87. *ORB 10*. Anteroposterior orbit diameter less than (0) or equal to/greater than (1) four times the distance of the posterior orbit margin from the squamosal posterodorsal margin. *Remarks*: State 1 is observed in amphibamid dissorophoids (see also character 82 above, from which, however, the present character differs).

Pineal foramen (PIF)

*88. *PIF 1*. Pineal foramen present (0) or absent (1). *Remarks*: Closure of the foramen during growth was discussed by Milner & Sequeira (1998) as a shared derived trait of some edopoids. In the absence of data on the fate of the foramen during the ontogeny of other taxa, it is assumed that the presence of a foramen in these typifies the condition of their species.

89. *PIF 2*. Position of the pineal foramen posterior to (0), approximately level with (1), or anterior to (2) the interparietal suture mid length. *Remarks*: The interparietal suture length is measured between its anterior and posterior extremities, parallel to the skull midline.

Skull features (SKU)

90. *SKU 1*. Zone of subdued ornament adjacent to the midline suture of the skull roof absent (0), present on premaxillaries, nasals, frontals, parietals and postparietals (1) or present only on premaxillaries, nasals, and frontals (2). *Remarks*: Sequeira (2004) is followed in assigning the various conditions of the skull sculpture to edopoids, in most of which an area of lightly sculptured and/or smooth bone is present along the skull midline. The area in question extends over different bones in different taxa.

91. *SKU 2*. Absence (0) or presence (1) of condition: postorbital region of the skull roof at least one-third wider than long. *Remarks*: In several dissorophoids, as well as in taxa from other temnospondyl groups, the area of the skull roof that lies posterior to the level of the orbits appears foreshortened. Its width is measured as the maximum distance between the lateral margins of the bones of the lateral temporal series.

Sensory canals (SC)

92. *SC 1*. Lateral line system on skull roof totally enclosed (0), mostly enclosed with short sections in sulci (1), almost entirely in sulci with short sections enclosed (2), entirely in sulci (3), or absent (4). *Remarks*: Ahlberg & Clack (1998) have been followed for the distribution of states of this character.

*93. *SC 3*. Absence (0) or presence (1) of a lateral line system confined almost entirely to circumorbital bones. *Remarks*: As discussed by Sequeira (1998), state 1 is shared by eobrachyopid dvinosauroids. In these, sensory canals are arranged almost exclusively around the orbits.

Vomer (VOM)

*94. *VOM 2*. Absence (0) or presence (1) of vomerine ridges radiating towards the margins of the snout from a centre near the anteromesial corner of the choanae. *Remarks*: A set of ridges radiating out towards the snout is observed in *Eryops* and in some edopoids.

95. *VOM 3*. Vomer with (0) or without (1) fangs. *Remarks*: The term fangs is employed here to identify teeth in which the basal diameter and/or height are 25% greater in maximum basal diameter and/or height than the average size of the adjacent marginal premaxillary or maxillary teeth (definition slightly modified from Bolt & Lombard 2001). Two (rarely one or more than two) appressed tooth positions on the ventral surface of the vomer, close to the choana or in a subcentral position, are usually larger than the rest of the vomerine teeth (e.g. denticles), if present.

96. *VOM 4*. Vomer without (0) or with (1) denticles. *Remarks*: Denticles form either discrete patches or a continuous shagreen, and their basal diameter is 20% or less of the average maximum basal diameter and/or height of the adjacent marginal teeth (definition slightly modified from Bolt & Lombard 2001).

97. *VOM 5*. Vomer excluded from (0) or contributing to (1) the interpterygoid vacuities. *Remarks*: Primitively in outgroups, as well as in edopoids, the vomers do not participate in the vacuities.

*98. *VOM 6*. Absence (0) or presence (1) of condition: vomer with posterolateral ramus that extends posteriorly along the medial margin of the palatine. *Remarks*: In some dissorophoids and dvinosaurs, the posterolateral part of the vomer sends an elongate process that flanks the palatine instead of abutting directly against the latter.

99. *VOM 8*. Vomer with (0) or without (1) a toothed, raised crest running anteroposteriorly and lying mesial to the choana. *Remarks*: Primitively, the crest in question is observed in certain outgroups.

100. *VOM 9*. Vomer with (0) or without (1) a transversely oriented, anterior crest. *Remarks*: A transverse thickening of the ventral

surface of the vomer is seen in some outgroups. This character overlaps almost completely with the previous character.

101. *VOM 12*. Absence (0) or presence (1) of condition: vomer forming more than half of the posteromesial margin of the choana. *Remarks*: This character occurs sporadically in some dissorophoids, in which the vomer borders a large portion of the posteromesial margin of the choana. In ventral view, and imagining the division of the choana outline into four quadrants, the derived state refers to the contribution of the vomer to the posteromesial quadrant.

*102. *VOM 14*. Vomerine fangs aligned subparallel to the marginal tooth row (0) or not parallel (1). *Remarks*: In some dvinosaurs and in outgroup taxa, the vomerine fangs are subparallel to the row of adjacent upper marginal teeth.

*103. *VOM 15*. Vomer prechoanal length less than (0) or greater than/equal to (1) interchoanal width. *Remarks*: The length of the prechoanal portion of the ventral surface of the vomer is measured between a transverse line passing through the anteriormost points of the choanal border and the anterior margin of the vomer, and parallel to the skull midline. The interchoanal width is the minimum transverse distance between the mesialmost portions of the choanal borders.

*104. *VOM 16*. Vomer without (0) or with (1) an interchoanal tooth row. *Remarks*: In certain dvinosaurs, a row of teeth runs transversely (or nearly so) on the ventral surface of the vomer, and occupies a position mesial to the choana.

*105. *VOM 17*. Vomer without (0) or with (1) a row of teeth (3+) bordering the mesial margin of the choana. *Remarks*: In some dvinosaurs, some basal archegosauriforms, as well as some dissorophoids, a number of teeth are aligned along the mesial margin of the choanal border.

*106. *VOM 18*. Vomer extending posteriorly along the lateral margins of the anterior extremity of the cultriform process (1) or not (0). *Remarks*: In some ingroups, e.g. some dvinosaurs, some basal archegosauriforms, and some edopoids (among others), the posteromesial corners of the vomers extend posteriorly and flank the lateral margins of the cultriform process, near the anterior extremity of the latter.

*107. *VOM 19*. Vomer with (1) or without (0) a lappet-like, median septum. *Remarks*: Both Bolt (1974c) and Dilkes (1990) described a dorsally reflected lappet arising from the posteromesial portion of the vomer in trematopids, and forming a septum with its antimere.

Palatine (PAL)

108. *PAL 1*. Palatine with (0) or without (1) fangs. *Remarks*: See above (character 95) for the definition of fangs.

109. *PAL 2*. Palatine without (0) or with (1) denticles. *Remarks*: See above (character 96) for the definition of denticles.

*110. *PAL 3*. Palatine excluded from (0) or contributing to (1) the interpterygoid vacuity. *Remarks*: The plesiomorphic state occurs in several ingroup taxa, including edopoids, some dissorophoids, basal archegosauriforms, and zatracheids, as well as in certain primitive forms such as *Balanerpeton*, *Capetus*, and *Dendrerpeton acadianum*. This character differs from character 98 above, although the present authors are aware of the fact that a vomer-palatine contact necessarily precludes a contribution of palatines to the interpterygoid vacuities.

111. *PAL 4*. Palatine with (0) or without (1) an anteroposterior tooth row consisting of three or more teeth subparallel to the marginal tooth row. *Remarks*: In some ingroup and outgroup taxa, the ventral surface of the palatine bears a row of teeth that are slightly smaller than fangs (if present) but larger than denticles (if present). The main distinctive feature is the alignment of a number of these teeth and their arrangement parallel to the upper marginal dentition. The tooth row in question is primitively present in most stem tetrapods, as well as in a number of primitive and derived temnospondyls.

112. *PAL 5*. Palatine without (0) or with (1) a laterodorsal exposure (LEP) in the anteroventral margin of the orbit. *Remarks*: A LEP contributes to the anteroventral angle of the orbit outline in some dvinosaurs and dissorophoids.

113. *PAL 7*. Absence (0) or presence (1) of condition: entire postchoanal part of palatine a slender and strut-like bone, comparable in width or less wide than the maxilla in ventral aspect and at least 30% as wide as the maximum width of the choana. *Remarks*: An elongate and narrow postchoanal region of the palatine is found in some dissorophoids. Length and width of this region are measured along and perpendicular to its axis of greater elongation, respectively, i.e. parallel to the marginal dentition.

Ectopterygoid (ECP)

114. *ECP 2*. Ectopterygoid with (0) or without (1) fangs. *Remarks*: See above (character 95) for the definition of fangs.

115. *ECP 3*. Ectopterygoid without (0) or with (1) denticles. *Remarks*: See above (character 96) for the definition of denticles.

116. *ECP 4*. Ectopterygoid longer than/as long as (0) or shorter than (1) the palatine. *Remarks*: The length of both palatal bones is measured along their axis of greater elongation, parallel to the adjacent ventral edge of the skull table.

117. *ECP 5*. Ectopterygoid with (0) or without (1) an anteroposterior tooth row consisting of three or more teeth subparallel to the marginal tooth row. *Remarks*: In state 0, the ventral surface of the ectopterygoid bears a row of teeth. The main distinctive feature of these is their arrangement parallel to the upper marginal dentition. Except for some dvinosaurs, some dissorophoids, and basal archegosauriforms, most ingroup taxa do not bear a tooth row.

118. *ECP 6*. Presence (0) or absence (1) of an ectopterygoid-maxilla contact. *Remarks*: In branchiosaurids, the lateral margin of the ectopterygoid fails to contact the mesial margin of the maxilla.

Pterygoid (PTE)

*119. *PTE 5*. Absence (0) or presence (1) of condition: palatal ramus and quadrate ramus of the pterygoid stout, poorly differentiated from one another at the level of the pterygoid corpus, together forming a continuous and subtriangular sheet of bone in ventral aspect. *Remarks*: In *Acroplous* and tupilakosaurids, the quadrate ramus appears as a robust and triangular lamina in ventral projection, wider than long, and merging seamlessly into the pterygoid corpus. Its anterolateral portion continues into the posterolateral region of the palatal ramus. The latter forms a subtrapezoidal to subrectangular lamina in ventral aspect.

*120. *PTE 8*. Absence (0) or presence (1) of a posterior pterygoid incisure. *Remarks*: The incisure is a shared derived feature of tupilakosaurid dvinosaurs. In these, a notch is visible immediately lateral to the pterygoid-parasphenoid suture, and just medial to the posterior margin of the quadrate ramus.

121. *PTE 9*. Pterygoid without (0) or with (1) a posterolateral flange, that is an inflection in the rearmost portion of the lateral margin of the palatal ramus. *Remarks*: In ventral aspect, the portion of the lateral margin of the pterygoid palatal ramus that lies immediately lateral to the corpus and just anterior to the anterior portion of the quadrate ramus forms a more or less distinct flange with a sinuous free margin in many temnospondyls (except several dvinosaurs and some dissorophoids).

122. *PTE 10*. Absence (0) or presence (1) of a suture between the two pterygoids. *Remarks*: In several outgroups and in *Edops*, the palatal rami of both pterygoids come in contact near their anterior extremities.

123. *PTE 12*. Absence (0) or presence (1) of condition: palatal ramus of the pterygoid forming a butt joint with the posterior margin of the palatine, thus producing a continuous sheet of bone with the latter. *Remarks*: In several taxa, the lateral margin of the palatal ramus of the pterygoid contacts the palatine along the mesial margin of the latter. In some amphibamids, the anterior extremity of the palatal ramus sutures with the posterior margin of the palatine, so that these two bones form a continuous and strip-like surface.

124. *PTE 13*. Conditions of the internal process for the basipterygoid articulation: absence of a distinct, mesially protruding internal process (0); process present, with a triangular outline in ventral aspect, (1); process present, its medial half forming an elongate, bar-like structure in ventral aspect (2). *Remarks*: In state 2, the tubular internal process is distinctly set off from the corpus of the pterygoid. In state 1, it protrudes mesially, but it is conical in shape.

*125. *PTE 20*. Absence (0) or presence (1) of condition: anterior part of the free lateral margin of the palatal ramus of the pterygoid shallowly concave or almost straight. *Remarks*: Dvinosauroids other than *Dvinosaurus* show a nearly straight (in ventral aspect) free portion of the lateral margin of the pterygoid palatal ramus, the anteriormost part of which borders the subtemporal fossa.

*126. *PTE 21*. Absence (0) or presence (1) of condition: anteriormost part of the palatal ramus of the pterygoid shaped like an anteriorly expanded, subrectangular plate extending only to the level of the ectopterygoid-palatine suture or slightly anterior to it. *Remarks*: State 1 describes the specialised condition of dvinosauroids other than *Dvinosaurus*, and refers to the squared-off outline of the anterior portion of the palatal ramus as well as to its spatial relationships with other bones of the lateral palatal series.

*127. *PTE 22*. Presence (0) or absence (1) of denticle shagreen on the pterygoid. *Remarks*: A uniform cover of small teeth on the ventral surface of (mostly) the pterygoid palatal ramus is found in the majority of taxa covered in this study, except for several dvinosauroids among the ingroup taxa, in which either shagreen is absent, or confined to small discrete patches.

*128. *PTE 23*. Absence (0) or presence (1) of condition: suture between pterygoid and parasphenoid extending for approximately the entire length of the parasphenoid basal plate. *Remarks*: In ventral aspect, the internal process of the pterygoid corpus and the basal plate of the parabasisphenoid complex form an elongate suture in tupilakosaurids, extending for almost the entire length of the plate, from its posterior margin to the transverse level of the basipterygoid processes.

*129. *PTE 24*. Absence (0) or presence (1) of condition: lateral margin of the quadrate ramus of the pterygoid downturned. *Remarks*: In dvinosauroids, the quadrate ramus of the pterygoid is ventrally curved in its lateralmost part, conferring a 'vaulted' aspect (in occipital view) to the palate. The downward curvature may extend in part anteriorly to the palatal ramus.

*130. *PTE 25*. Presence (0) or absence (1) of a suture between the vomer and the palatal ramus of the pterygoid. *Remarks*: The derived state, observed in many dissorophoids and dvinosaurs among others, is that in which the pterygoid palatal ramus does not contact the vomer.

Interpterygoid vacuities (IPV)

131. *IPV 1*. Presence (0) or absence (1) of interpterygoid vacuities. *Remarks*: In the majority of the taxa considered here, vacuities are present between the medial margins of the palatal bones (the pterygoids and/or one or more bones of the lateral palatal series) and the lateral margins of the parasphenoid (mostly, the cultriform process of the latter). In a number of ingroup taxa, such as baphetids, the palatal vacuities are absent, a condition known as 'closed' palate.

132. *IPV 2*. Absence (0) or presence (1) of condition: interpterygoid vacuities occupying at least half of the maximum palatal width. *Remarks*: In most temnospondyls (except for *Edops*), the maximum width of both interpterygoid vacuities (also including the width of the intervening cultriform process of the parasphenoid) is at least half as the width of the palate at the same transverse level.

133. *IPV 3*. Absence (0) or presence (1) of condition: margins of the palatal bones delimiting the interpterygoid vacuities concave along their whole length. *Remarks*: Except in the case of a few temnospondyls (*Edops*; *Capetus*; *Procochleosaurus*), the vacuities of the majority of temnospondyls are concave along their whole margins, although the degree of curvature of such margins varies.

134. *IPV 4*. Maximum combined width of interpterygoid vacuities less than their length (0), greater than their length (1), or vacuities approximately as long as wide (2). *Remarks*: The various conditions of this character relate the maximum combined width of the vacuities (including the width of the intervening cultriform process of the parasphenoid) to their length. The latter is measured parallel to the skull midline from the anteriormost point of their margin (delimited either by the vomer or by the palatal ramus of the pterygoid) to the anterior margin of the ventral plate of the parabasisphenoid complex). State 2 characterises only a handful of dvinosauroids, whereas the other two states are approximately equally distributed among the rest of the ingroup taxa.

*135. *IPV 5*. Maximum combined width of interpterygoid vacuities less (0) or more (1) than half skull table width. *Remarks*: The maximum width of the skull table is measured as the maximum distance between the lateral margins of the lateral temporal series.

*136. *IPV 6*. Maximum combined width of interpterygoid vacuities occurring posterior to their mid-length (0) or anterior to it (1). *Remarks*: In *Perryella* and dvinosauroids, each vacuity reaches its maximum width anterior to its midlength.

Choana (CHO)

137. *CHO 1*. Absence (0) or presence (1) of condition: choana with a subtriangular outline, wider anteriorly and approximately acuminate posteriorly. *Remarks*: The derived condition is a feature of some edopoids and *Dendrerpeton acadianum*.

*138. *CHO 3*. Maximum length of the choana greater (0) or smaller (1) than its maximum width. *Remarks*: In ventral aspect, length and width are measured as the distances, respectively, between anterior and posterior, and between lateral and mesial points of the choanal margin, parallel and perpendicular to the skull midline. The derived state occurs in assorted ingroup and outgroup taxa.

Anterior palatal fenestra (FEA)

139. *FEA 1*. Anterior palatal fenestra: present and single (median fenestra) (0), present and double (paired fenestrae) (1), or absent (2). *Remarks*: In several stem tetrapods and some temnospondyls, either a single or two anterior openings are visible on the anterior surface of the palate.

Anterior palatal fossa (FOA)

140. *FOA 3*. Anterior palatal fossa present and single (0), present and double (1), or absent (2). *Remarks*: Regardless of the presence or absence of an anterior opening(s), or fenestra(e) on the anterior surface of the palate (see previous character), some taxa show a depression (single or paired) in an identical position. It is noted that the distribution of the states for the present and the preceding character do not necessarily co-occur. A fenestra may or may not open at the bottom (anatomically dorsal) of a fossa, and the latter may or may not be pierced by fenestrae.

Exoccipital (EXO)

*141. *EXO 1*. Absence (0) or presence (1) of an exoccipital-tabular contact. *Remarks*: A sutural contact between a vertically oriented process rising from the body of the exoccipital and a facet or flange descending from the ventral surface of the tabular is found in some dvinosauroids.

*142. *EXO 6*. Absence (0) or presence (1) of an exoccipital-postparietal contact. *Remarks*: An exoccipital-postparietal contact is observed in some dissorophoids, edopoids, and dvinosaurs, among the groups selected for the present study, although the distribution of this character is more widespread. According to Smithson (1982), an exoccipital-postparietal contact is a general feature of temnospondyls, although not all taxa in this group are reconstructed with such a contact (e.g. *Dvinosaurus*; Shishkin 1973). For this reason, we have conservatively coded for the presence of the exoccipital-postparietal contact only in those taxa in which the relationships between these two bones are unequivocal.

Basioccipital (BAO)

143. *BAO 1*. Basioccipital notochordal (0) or not (1). *Remarks*: Primitively in some outgroups, the basioccipital forms a thin ring of bone surrounding the notochord, as in *Acanthostega*, *Ichthyostega*, and *Crassigyrinus*, in contrast to the more derived condition of an ossified, subcylindrical body with a distinct posterior surface, and articulated with the exoccipitals.

*144. *BAO 2*. Absence (0) or presence (1) of a basioccipital-pterygoid contact. *Remarks*: The basioccipital contacts the pterygoids in tupilakosaurids. In ventral aspect, two ventrolateral processes of the basioccipital extend anteriorly to form a suture with the posterior part of the internal process for the basipterygoid articulation.

*145. *BAO 3*. Ventrally exposed portion of basioccipital longer than wide (0) or shorter than wide (1). *Remarks*: In ventral aspect, the projected surface of the basioccipital is anteroposteriorly abbreviated in the majority of outgroups and all ingroup taxa.

*146. *BAO 4*. Absence (0) or presence (1) of condition: exoccipital posterior facets expanded and appressed to each other, so as to obliterate basioccipital posterior surface. *Remarks*: There are several degrees of expansions of the exoccipital posterior facets and reduction of the basioccipital posterior surface. In the derived condition exhibited by many dissorophoids, the basioccipital is completely concealed (or absent) and the exoccipital posterior facets make up the whole articular surface of the occiput.

Parasphenoid (PAS)

147. *PAS 9*. Cranial fissure on the ventral surface of the parabasisphenoid complex not sutured (0), sutured but traceable (1), or not traceable (2). *Remarks*: This character is left unordered, although state 1 represents an intermediate stage between states 0 and 2. The latter is seen in most taxa. State 1 does not identify a clade, and occurs only in a small number of stem tetrapods. In the primitive state, the two halves of the braincase are visibly separated and a conspicuous fissure intervenes between them. In the derived states, either a suture is observed, or the two braincase halves appear fused.

148. *PAS 11*. Basipterygoid processes of the basisphenoid not extending (0) or extending (1) anterior to the posterior extremity of the cultriform process, so that the latter appears to be 'sunken' between them in ventral aspect. *Remarks*: In some dissorophoids, the basipterygoid processes are wing-like and project distinctly anterolaterally, occurring slightly anterior to the proximal insertion of the cultriform process. Thus, the latter appears to be 'sunken' along the shallowly concave, anterior margin of the parabasisphenoid plate. The posterior extremity of the cultriform process is identified at the transverse level between the proximal portions of the basipterygoid processes.

*149. *PAS 15*. Absence (0) or presence (1) of elongate grooves flanked by distinct ridges running anteromedially to posterolaterally on the ventral surface of the parasphenoid plate from a point situated immediately behind the basipterygoid processes to a posterolateral notch visible along the lateral margin of such a plate. *Remarks*: The derived condition is observed in basal dvinosaurs, including *Perryella*.

*150. *PAS 16*. Absence (0) or presence (1) of an expansion at the base of the parasphenoid cultriform process. *Remarks*: In eryopoids and some basal archegosauriforms, the cultriform process widens near its rear end.

*151. *PAS 17*. Absence (0) or presence (1) of condition: outline of the parasphenoid plate waisted immediately posterior to the basipterygoid processes and narrowing rearward so that its posterior margin measures less than half of the width between such processes. *Remarks*: A 'waisted' parasphenoid plate tapering rapidly rearward is the condition seen in eobrachyopid dvinosaurs.

*152. *PAS 18*. Absence (0) or presence (1) of a broad embayment along the posterolateral margins of the parasphenoid plate, extending anteroposteriorly for at least one-third of the length of the parasphenoid plate. *Remarks*: The length of the parasphenoid plate is measured as the distance between its posterior margin and the posterior end of the cultriform process. In the majority of dvinosaurs, the lateral margins of the plate are concave, and the length of such concavity (measured parallel to the skull midline), forms 30% or more of the length of the plate.

*153. *PAS 19*. Parasphenoid denticle distribution: present anterior and posterior to the basal articulation (0); posterior to the basal articulation only (1); anterior to the basal articulation only (2); absent (3); on a triangular area between the basipterygoid processes (4). *Remarks*: These various conditions reflect differences in the distribution of the denticle shagreen on the parasphenoid ventral surface. The basal articulation landmark is a transverse line passing through the proximal (i.e. the posterior) insertions of the basipterygoid processes.

*154. *PAS 20*. Indicated course of the carotid arteries on the parasphenoid plate relative to the basipterygoid processes: grooves traversing the bases of the processes in ventral view (0); presence of a foramen opening medial to the processes (1); presence of a foramen opening posterior to the processes (2). *Remarks*: This is a simpler version of a character used by Yates & Warren (2000). It tries to capture the conditions in the present authors' study group, but it is by no means exhaustive of all conditions shown by other temnospondyls or other early tetrapod groups.

*155. *PAS 21*. Width of the cultriform process at mid point less than (0) or more than (1) 20% of the total length of the process. *Remarks*: The length of the process is measured between its anterior extremity and a transverse line passing through the proximal (i.e. the posterior) insertions of the basipterygoid processes. The derived state is observed in zatracheids, eryopoids, and some dvinosaurs.

*156. *PAS 22*. Absence (0) or presence (1) of condition: cultriform process visible between the posteromedial portions of the vomers for at least half of the vomer length. *Remarks*: In some dvinosauroids, the cultriform process appears wedged, in ventral aspect, between the vomers.

*157. *PAS 23*. Absence (0) or presence (1) of a raised triangular area which occupies the base of the cultriform process. *Remarks*: In some amphibamids and in *Dendrerpeton acadianum*, the area of the ventral surface of the parasphenoid where the cultriform process merges into the ventral plate is occupied by a raised area (usually covered in denticles), and with a thickened anterior edge. This character differs from character 153 (concerned with denticle distribution only) in that it describes the occurrence of a lappet-like structure arising from the ventral side of the base of the cultriform process.

*158. *PAS 24*. Absence (0) or presence (1) of condition: basipterygoid processes triangular, acutely pointed (in ventral aspect), and anterolaterally directed. *Remarks*: State 1 occurs in eobrachyopids, and confers a 'winged' aspect to the parasphenoid plate of members of this clade.

Jaw articulation (JAT)

159. *JAT 1*. Jaw articulation lying posterior to (0), level with (1), or anterior to (2) the posterior facets of the exoccipitals. *Remarks*: In ventral view, the position of the jaw articulation (corresponding to the posterior margin of the quadrate/suspensorium in dorsal aspect) relative to the posterior facets of the exoccipitals is described by state 0 in most ingroup taxa. Some edopoids, dissorophoids, dvinosaurs, and zatracheids show state 1. State 2 is observed only in a few dvinosaurs and dissorophoids. In the majority of cases, the posterior facets of the exoccipitals lie only slightly posterior to the posterior margin of the skull table, so the latter can be used as a landmark in those cases in which the occiput is not preserved. The position of the jaw articulation relative to the occiput varies with ontogeny and, therefore, the recorded states ought to refer to the last recorded growth stages (Boy 1990, 1995; F. Witzmann, pers. comm. 2006).

*160. *JAT 2*. Absence (0) or presence (1) of a retroarticular process, that is an extension of the dorsal surface of the lower jaw behind the posterior margin of the articular, and at least two-thirds as long as the anteroposterior length of the glenoid surface of the latter. *Remarks*: The length of the process and that of the articular glenoid area are measured parallel to the skull midline. In the case of the articular, its length is the minimum distance between its anterior and posterior margins. As defined, a retroarticular process is observed in dvinosaurs, basal archegosauriforms, and some dissorophoids.

*161. *JAT 3*. Absence (0) or presence (1) of a transversely elongate trough on the retroarticular process. *Remarks*: The area lying immediately behind the posterior margin of the articular has a mediolaterally oriented sulcus in dvinosauroids.

Adsymphysial (ADS)

162. *ADS 1*. Presence (0) or absence (1) of an adsymphysial bone. *Remarks*: This bone, visible anterior to the coronoid series on the mesial surface of the lower jaw, is absent in temnospondyls, but widespread in several other groups of early tetrapods. However, Anderson (2005, 2006) has reported an adsymphysial bone in a jaw ramus of the dissorophoid *Cacops*.

163. *ADS 2*. Adsymphysial bone without (0) or with (1) fangs. *Remarks*: As per Bolt & Lombard's (2001) definition (slightly

modified here), fangs are defined as being 25% greater in maximum basal diameter and/or height than the average size of adjacent marginal (dentary) teeth. They are present in some stem tetrapods, e.g. *Acanthostega*, *Greererpeton*, *Megalocephalus*, *Baphetes*, and *Crassigyrinus* (Ahlberg & Clack 1998).

164. *ADS 3*. Adsymphysial bone without (0) or with (1) a row of teeth oriented subparallel to the marginal teeth and the size of which is approximately equal to that of the latter. *Remarks*: A row of teeth of variable size characterises *Acanthostega* and *Whatcheeria*.

165. *ADS 4*. Adsymphysial bone with (0) or without (1) either a continuous shagreen or discrete patches of denticles. *Remarks*: Denticles (20% or less of the average maximum basal diameter and/or height of the adjacent marginal teeth; see Bolt & Lombard 2001) occur in *Panderichthys* and *Acanthostega* (Ahlberg & Clack 1998).

Dentary (DEN)

166. *DEN 2*. Dentary with (0) or without (1) parasymphysial fangs. *Remarks*: See above (character 95) for a definition of fangs. The fangs, where present, lie close to the symphysial region, and generally internal (mesial) to the marginal tooth row. Their absence in temnospondyls is patchy (e.g. in some edopoids, dissorophoids, and zatracheids).

167. *DEN 4*. Dentary without (0) or with (1) a lateral notch for reception of premaxillary fangs. *Remarks*: Uniquely among early tetrapods, colosteids carry an anterior U-shaped excavation on the anterolateral surface of the dentary.

Splenial (SPL)

168. *SPL 2*. Absence (0) or presence (1) of condition: rearmost extension of the mesial lamina of the splenial closer to the anterior margin of the adductor fossa than to the anterior end of the jaw. *Remarks*: When the lower jaw ramus is observed in mesial view, the rearmost point of the projected mesial area of the splenial may lie closer either to the anteriormost point of the dorsal edge of the adductor fossa or to the symphysial area. State 1 occurs sporadically among outgroups.

Postsplenial (PTS)

169. *PTS 2*. Postsplenial without (0) or with (1) a mesial lamina. *Remarks*: In some outgroups, the postsplenial does not wrap around the ventral margin of the lower jaw and bears no exposure on the mesial surface of the latter.

Angular (ANG)

170. *ANG 2*. Angular without (0) or with (1) a mesial lamina. *Remarks*: The distribution of this character is partly coextensive with that of the preceding character (see also data matrix for differences).

*171. *ANG 5*. Ventral margin of the angular smoothly curved in lateral aspect (0) or nearly flat for most of its length (1). *Remarks*: The lateral profile of the angular ventral margin varies. In dvinosauroids and zatracheids, the angular ventral margin is horizontal for most of its length in lateral aspect.

Prearticular (PEA)

*172. *PEA 1*. Centre of ossification on the mesial surface of the prearticular lying level with the posterior end of the posterior coronoid (0), with approximately the middle of the adductor fossa (1), or with the posterior end of the adductor fossa (2). *Remarks*: In most tetrapods, the mesial surface of the prearticular is nearly featureless. However, magnification of this surface may often reveal a series of faint striations, minute foramina, or weak sulci. The arrangement of these follows a 'starburst'-like pattern, and from this, it is possible to provide an estimate of the position of the centre of radiation, from which these structures fan out. States 0 and 1 appear in the outgroups, whereas state 2 is documented in a handful of ingroups, where observations are possible. The posterior end of the posterior coronoid marks the anterior edge of the adductor fossa. The posterior edge of such fossa coincides with the anterior margin (in dorsal aspect) of the articular.

*173. *PEA 2*. In medial view, prearticular extending anteriorly at least as far as the level of the mid point of the middle coronoid (0) or not extending/barely extending anterior to the level of the suture between the mid and the posterior coronoid (1). *Remarks*: The derived state occurs only sporadically in the ingroup (e.g. some dvinosaurs, dissorophoids, and zatracheids).

*174. *PEA 4*. Absence (0) or presence (1) of a prearticular-surangular contact. *Remarks*: The prearticular is known to contact the surangular in a handful of temnospondyls, but in the majority of taxa the relationships between the dermal bones at the back of the lower jaw are usually difficult to reconstruct, as sutures are not always traceable (see also Bolt & Lombard 2001).

175. *PEA 5*. Presence (0) or absence (1) of a prearticular-splenial contact. *Remarks*: State 1 is widespread among ingroup taxa, whereas state 0 is found mostly among outgroups.

*176. *PEA 6*. Field of denticles on the prearticular consisting of: continuous area (0), scattered patches (1), or absent (2). *Remarks*: Following Ahlberg & Clack (1998), state 2 is the general condition of most ingroups, whereas state 1 occurs sporadically in some outgroups. State 0 describes a condition in which the field of denticles is uniformly distributed; state 1 refers to the presence of isolated patches of denticles separated by smooth areas.

*177. *PEA 7*. Absence (0) or presence (1) of a strong medial inflection of the upper part of the mesial surface of the prearticular. *Remarks*: In trematopid dissorophoids, the mesial margin of the adductor fossa and the area of the prearticular mesial surface immediately ventral to it projects strongly medially. In dorsal aspect, this projection appears as a flange-like shelf.

Anterior coronoid (CO1)

178. *CO1 2*. Anterior coronoid with (0) or without (1) fangs. *Remarks*: See above (e.g. character 95) for a definition of fangs. Fangs are present in a few outgroups and in the tupilakosaurid *Thabanchuia*.

179. *CO1 3*. Anterior coronoid with (0) or without (1) denticles. *Remarks*: See above (e.g. character 96) for a definition of denticles. Denticles form either a continuous shagreen or discrete patches, and are recorded in most taxa. They are absent in many outgroups.

180. *CO1 4*. Anterior coronoid with (0) or without (1) an anteroposterior row of teeth oriented subparallel to the marginal (dentary) teeth and the size of which is 30% or more than that of the adjacent marginal dentary teeth and twice or more than that of the denticles, if present. *Remarks*: In some outgroups, and rarely within the ingroup, the anterior coronoid bears a row of small teeth.

*181. *CO1 5*. Presence (0) or absence (1) of an anterior coronoid-prearticular contact. *Remarks*: Only *Balanerpeton* and *Eryops* show the plesiomorphic condition that is seen in several outgroups.

*182. *CO1 6*. Absence (0) or presence (1) of an anterior coronoid-splenial contact. *Remarks*: The plesiomorphic state occurs in a few outgroups.

Middle coronoid (CO2)

183. *CO2 2*. Middle coronoid with (0) or without (1) fangs. *Remarks*: See character 95 for a definition of fangs *sensu* Bolt & Lombard (2001).

184. *CO2 3*. Middle coronoid with (0) or without (1) denticles. *Remarks*: See character 96 for a definition of denticles *sensu* Bolt & Lombard (2001). Denticles occur rarely within the ingroup.

185. *CO2 4*. Middle coronoid with (0) or without (1) an anteroposterior row of teeth oriented subparallel to the marginal dentary teeth and the size of which is 30% or more than that of the adjacent marginal dentary teeth and twice or more than that of the denticles, if present. *Remarks*: Primitively, a row of teeth is present in some outgroups only.

*186. *CO2 5*. Absence (0) or presence (1) of a middle coronoid-splenial contact. *Remarks*: The suture in question is observed in some ingroup taxa (*Phonerpeton*, *Trimerorhachis*, and *Cochleosaurus florensis*).

Posterior coronoid (CO3)

187. *CO3 3*. Posterior coronoid with (0) or without (1) denticles. *Remarks*: See character 96 for a definition of denticles *sensu* Bolt & Lombard (2001). Denticles are absent in basal archegosauriforms and *Dvinosaurus*.

187. *CO3 4*. Posterior coronoid with (0) or without (1) an anteroposterior row of teeth oriented subparallel to the marginal

dentary teeth and the size of which is 30% or more than that of the adjacent marginal teeth and twice or more than that of the denticles, if present. *Remarks*: *Dvinosaurus*, *Perryella*, and *Sclerocephalus* show the primitive condition exhibited by several outgroups. Boy (1988) illustrated a denticle patch on the posterior coronoid of a juvenile mandible of *Sclerocephalus*. The larval mandible figured by Schoch (2003) possesses a row of denticles (F. Witzmann, pers. comm. 2006). Accordingly, *Sclerocephalus* has been coded according to information in Boy (1988).

189. *CO3 5*. Posterior coronoid without (0) or with (1) a posterodorsal process. *Remarks*: In all ingroup and some outgroup taxa, a process projects backward from the posterolateral corner of the main corpus of the posterior coronoid, and builds part of the lateral wall of the adductor fossa.

190. *CO3 6*. Posterior coronoid not visible (0) or visible (1) in lateral view. *Remarks*: In some taxa, a sliver of bony surface from the posterior coronoid (usually, its posterior process) is visible in lateral aspect dorsal to the posterior extremity of the dentary. It is often appressed in part against the latter and/or against the surangular, and usually forms an interdigitating suture with the latter.

191. *CO3 7*. Posterodorsal process of posterior coronoid not contributing (0) or contributing (1) to the tallest point of the lateral margin of the adductor fossa ('surangular' crest). *Remarks*: In lateral or mesial view, the process in question may form the tallest point of the lateral margin of the adductor fossa. In some taxa, it is the surangular that contributes to such point.

Adductor fossa (ADF)

192. *ADF 1*. Lateral and mesial margins of the adductor fossa lying approximately at the same dorsoventral level (0), or mesial margin lying in a ventral position relative to the lateral margin (1). *Remarks*: State 0 characterises most outgroups, in which the plane delimited by the margins of the fossa is nearly horizontal.

Meckelian bone (MEC)

*193. *MEC 1*. Presence (0) or absence (1) of Meckelian ossification extending for most of the length of the jaw. *Remarks*: Primitively in some outgroups, a Meckelian ossification occupies a large proportion of the jaw length.

Teeth (TEE)

194. *TEE 1*. Absence (0) or presence (1) of pedicely on the marginal teeth. *Remarks*: Pedicely is a feature of some dissorophoids, and one of the most frequently discussed dissorophoid-lissamphibian synapomorphies (see Bolt 1991, Milner 1993, and Schoch & Milner 2004). In these taxa, the teeth bear a base, or pedicel, upon which the apical portion of the tooth crown sits. The region between these two portions is uncalcified or weakly calcified.

195. *TEE 3*. Marginal teeth without (0) or with (1) two labiolingually arranged cuspules. *Remarks*: Two labiolingual cusps characterise some dissorophoids (discussion of this feature can be found in Bolt 1991, Milner 1993, and Schoch & Milner 2004).

196. *TEE 4*. Absence (0) or presence (1) of a conspicuous caniniform region in maxillary dentition that involves one or more teeth. *Remarks*: A caniniform region is a widespread but irregularly distributed feature, and occurs in several unrelated taxa. It is most evident in *Ichthyostega* and whatcheeriids, as well as in certain temnospondyls (including basal archegosauriforms, eryopoids, some dissorophoids, and *Capetus*). Such peak is exhibited by one or more teeth which appear to be conspicuously larger (20% or more) than the average maximum basal diameter and/or height of the maxillary teeth.

197. *TEE 9*. Number of maxillary teeth greater than 40 (0), between 30 and 40 (1), or less than 30 (2). *Remarks*: There appears to be little phylogenetic signal associated with the distribution of the different states, all of which are represented among both ingroup and outgroup taxa.

Clavicle (CLA)

198. *CLA 3*. Presence (0) or absence (1) of a suture between the anteroventral plates of the clavicles. *Remarks*: In state 1, the anteroventral plates of the clavicles are not in contact with each other, and a strip of the ventral surface of the interclavicle is visible between them. On both sides of this strip, the impressions of the clavicular plates are discernible, and their morphology provides clues to the degree of separation between them. State 0 is rarely represented in the ingroup (e.g. *Neldasaurus*; *Thabanchuia*).

Interclavicle (INC)

199. *INC 1*. Absence (0) or presence (1) of condition: posterior margin of the interclavicle forming a parasternal process. *Remarks*: In certain dvinosauroids and several outgroups, the interclavicle is drawn out posteriorly to different degrees. In most taxa where a parasternal process is present, the latter is distinctly set off from the corpus of the interclavicle. In other taxa, the boundary between the corpus and the process is less distinct. In all cases, the length of the interclavicle corpus (i.e. to the exclusion of the process, if present) is measured from its anterior extremity to the point where its posterolateral margins are deflected (i.e. show a change in their curvature, e.g. they become sinuous) before continuing into the lateral margins of the process.

200. *INC 2*. Absence (0) or presence (1) of condition: parasternal process parallel-sided for most of its length. *Remarks*: State 1 is observed in whatcheeriids, *Ossinodus*, *Ichthyostega*, *Dvinosaurus*, and *Thabanchuia*.

201. *INC 3*. Absence (0) or presence (1) of condition: interclavicle wider than long (excluding parasternal process, if present). *Remarks*: In those taxa in which a parasternal process is present, the length of the interclavicle is measured from its anterior extremity to the transverse level of the points where its posterolateral margins are deflected rearward and continue into the lateral margins of the process. The present character is thus not redundant with character 199 above.

*202. *INC 5*. Absence (0) or presence (1) of condition: sculpture on the central part of the ventral surface of the interclavicle with predominantly transversely oriented grooves and ridges. *Remarks*: In *Pederpes* and *Ossinodus*, the ventral surface of the interclavicle shows a system of sharp-edged and often coalescent ridges separated by grooves, oriented chiefly transversely and subparallel to each other.

Scapulocoracoid (SCP)

203. *SCP 1*. Absence (0) or presence (1) of a separate scapular ossification. *Remarks*: In those taxa in which a scapulocoracoid complex is observed, it is often possible to distinguish the presence of either separate ossifications or a single ossification. Relating these conditions to ontogenetic stages is challenging, as comparative material is not always abundant, and there appears to be no direct link with overall size or degree of ossification in remaining portions of the skeleton. In *Whatcheeria*, *Trimerorhachis*, and *Dvinosaurus*, the scapula appears to have ossified separately from the coracoid.

204. *SCP 4*. Absence (0) or presence (1) of an infraglenoid buttress extended ventromesially. *Remarks*: An infraglenoid buttress, observed in tetrapods more derived than *Acanthostega*, is described as a thickening jutting out on the visceral (i.e. internal) side of the scapular blade, lying posterior to the subscapular fossa, and sweeping mesioventrally towards the floor of the coracoid region of the scapulocoracoid (M. I. Coates, pers. comm. 2005).

Humerus (HUM)

205. *HUM 1*. Latissimus dorsi process of the humerus offset anteriorly (0) or aligned with the ectepicondyle ridge proximodistally (1). *Remarks*: In state 1, the latissimus dorsi process is aligned with the ectepicondyle ridge when the greater axis of the latter is prolonged in a proximal direction. *Acanthostega*, *Baphetes*, and *Whatcheeria* show state 0.

206. *HUM 2*. Absence (0) or presence (1) of a distinct supinator process of the humerus projecting anteriorly from the distal portion of the anterior surface of the humerus shaft. *Remarks*: In some taxa, the attachment area for the supinator may be represented by faint rugosities. However, in others it bears a conspicuous, blunt digitiform process arising from the distal part of the anterior surface of the humerus shaft. Examples of this process are observed in dissorophoids (*Acheloma*; *Ecolsonia*; *Phonerpeton*), dvinosaurs (*Dvinosaurus*; *Perryella*), edopoids (*Edops*), eryopoids (*Eryops*), and a number of basal archegosauriforms (*Sclerocephalus*).

207. *HUM 3*. Presence (0) or absence (1) of a sharp-edged ridge on the ventral surface of the humerus. *Remarks*: In several outgroups, a sharp oblique ridge traverses the flexor surface of the humerus, as in several osteolepiform fishes.

208. *HUM 4*. Latissimus dorsi process and deltopectoral crest connected (0) or not connected (1) by a bony ridge. *Remarks*: In the primitive condition, best exemplified by *Acanthostega* (see Coates 1996), the latissimus dorsi process is in continuity with the deltopectoral crest, and these two structures are connected by a thin bony sheet. In other taxa, they are separated, although in *Pederpes* (Clack & Finney 2005) a thin ridge detaches from the latissimus dorsi process and runs anteriorly, stopping just short of the anterior margin of the humerus.

209. *HUM 5*. Presence (0) or absence (1) of an entepicondylar foramen. *Remarks*: Within the ingroup, an entepicondylar foramen is seen in *Balanerpeton* and *Dendrerpeton acadianum*.

210. *HUM 6*. Presence (0) or absence (1) of an ectepicondylar foramen. *Remarks*: The foramen in question occurs only in some outgroups.

211. *HUM 7*. Presence (0) or absence (1) of a distinctly raised ectepicondyle ridge. *Remarks*: From the ectepicondyle, a ridge runs in a proximal direction on the extensor surface of the humerus. It is usually robust and blunt-topped, but variation in shape and proportions are known, especially among stem tetrapods. It is absent in several dissorophoids.

212. *HUM 9*. Distal extremity of the ectepicondylar ridge aligned with ulnar condyle (0), placed between the ulnar and radial condyles (1), or aligned with radial condyle (2). *Remarks*: The states of this character are not ordered, but it is pointed out that the distribution of the three states shows a good congruence with the phylogenetic pattern, in that state 1 appears in several basal stem tetrapods from the Devonian and Carboniferous, whereas state 0 is seen in *Acanthostega* and *Ichthyostega*.

213. *HUM 10*. Humerus not waisted (0) or waisted (1). *Remarks*: The presence of a distinctly concave (anteroposteriorly and proximodistally) surface of the shaft characterises most taxa in the study group, although there are exceptions, e.g. among stem tetrapods.

214. *HUM 11*. Radial condyle terminal (0) or ventral (1). *Remarks*: In state 1, the radial condyle appears on the distal part of the flexor surface of the humerus. In the primitive state, it occupies the terminal surface of the distal extremity of the bone.

215. *HUM 12*. Humerus slender and elongate, its length being less (0) or more (1) than three times the maximum width of its distal end. *Remarks*: Metric cut-off points were chosen based upon a survey of humerus proportions in all taxa. The derived state characterises mostly some derived dissorophoids. In these, the humerus does not show the elaborate, tetrahedral shape of primitive tetrapods, and resembles a 'stretched' hourglass. The distal end width is measured in the plane of its dorsoventral flattening, perpendicular to the axis of greater elongation of the bone. The length of the humerus is measured as the distance between the point of maximum curvature (usually, the most proximal point in anatomical orientation) of the caput humeri and the plane of the distal articular surface (distalmost point of ulnar facet or rearmost point, in dorsal aspect, of the distal articular surface).

216. *HUM 13*. Posterodistal corner of the entepicondyle projecting distal to the ulnar facet (0) or not (1). *Remarks*: The derived condition refers to a distal extension of the entepicondyle relative to the distal articular surface. *Acheloma*, *Eryops*, and *Sclerocephalus* show the derived state.

217. *HUM 15*. Width of the entepicondyle greater (0) or smaller (1) than half of the length of the humerus. *Remarks*: The entepicondyle width, measured on the plane of flattening of the entepicondyle, is the distance between the rearmost extremity of the latter and a line drawn parallel to the bone greater axis and passing through the posterior edge of the ulnar facet. The derived state occurs mostly in some dissorophoids and some dvinosaurs.

218. *HUM 16*. Length of the part of the humerus shaft that lies proximal to the entepicondyle smaller (0) or greater (1) than the maximum width of the humerus head. *Remarks*: The maximum width of the humerus head is measured, on its plane of flattening, perpendicular to the greater axis of the bone. It is the maximum distance between its anterior and posterior margins. The length of the shaft is the distance between the point of attachment of the posterior margin of the entepicondyle to the general surface of the bone and a plane that passes immediately distal to the humerus deltopectoral crest. While in some taxa these points appear to be weakly defined, they are nonetheless identifiable. The derived state occurs mostly in some dissorophoids and some dvinosaurs.

219. *HUM 17*. Presence (0) or absence (1) of accessory foramina piercing the flexor surface of the humerus. *Remarks:* In osteolepiform fishes and certain stem tetrapods, the humerus is pierced by numerous foramina (particularly evident on its flexor surface), but the number of these decreases in more derived taxa, so that a few conspicuous foramina only remain.

220. *HUM 19*. Absence (0) or presence (1) of process '2' of humerus. *Remarks*: Based on Coates (1996) and Ruta *et al.* (2003), process '2' is situated along the posterior edge of the humerus head, proximal to the anterior end of the entepicondyle proximal margin; it is seen in some stem tetrapods (*Acanthostega*; *Whatcheeria*), although it occurs sporadically in some basal crown tetrapods as well.

*221. *HUM 20*. Absence (0) or presence (1) of a capitellum. *Remarks*: A subhemispherical radial condyle, or capitellum, is observed in taxa as diverse as *Ichthyostega*, *Sclerocephalus*, *Phonerpeton*, *Eryops*, and *Acheloma*.

*222. *HUM 21*. Absence (0) or presence (1) of a finished periosteal surface between the radial and the ulnar facets. *Remarks*: A strip of smooth periosteal bone intervenes between radial and ulnar facets in *Acanthostega* and *Ichthyostega* (Coates 1996).

Radius (RAD)

223. *RAD 2*. Radius longer than (0), as long as (1), or shorter than (2) the ulna. *Remarks*: Primitively, the radius is slightly longer than the ulna. Although there are no instances of a radius longer than an ulna showing an olecranon process (see next character), the present character has been kept separate from the next character, as future finds might document a wider range of variation in the proportions of these two bones.

Ulna (ULN)

224. *ULN 1*. Absence (0) or presence (1) of olecranon process of ulna. *Remarks*: A digitiform or hook-like process projecting from the proximal extremity of the ulna occurs in the majority of tetrapods more derived than *Acanthostega*, but its absence in some taxa might be due to immaturity or paedomorphism (e.g. in some small dissorophoids). For simplicity, a typological approach to the coding of this character has been adopted.

Ilium (ILI)

*225. *ILI 1*. Absence (0) or presence (1) of condition: iliac blade flared dorsally. *Remarks*: In some taxa (notably, *Eryops*, *Acanthostomatops*, *Dvinosaurus*, *Neldasaurus*, *Onchiodon*, and *Trimerorhachis*), the iliac blade increases in length abruptly towards its dorsal margin and has a fan-like shape. Its maximum length is at least 30% greater that of the iliac neck.

*226. *ILI 2*. Major axis of iliac blade inclined strongly posterodorsally (0) or nearly vertical (1). *Remarks*: In some eryopoids, dissorophoids, zatracheids, dvinosaurs, and basal archegosauriforms, the axis of greater elongation of the iliac blade is vertical or nearly so. The slightly posterodorsally inclined iliac blade of *Cheliderpeton* has been coded as 1; the markedly inclined blade of *Sclerocephalus* has been coded as 0 (see Boy 1988, 1993).

227. *ILI 3*. Absence (0) or presence (1) of dorsal iliac process. *Remarks*: A double-headed ilium, consisting of a dorsal blade and a posterodorsal process, is widespread among primitive tetrapods, but the dorsal blade is not developed in fish-like stem tetrapods.

228. *ILI 7*. Lateral surface of the ilium without (0) or with (1) an oblique ridge oriented anteroventrally to posterodorsally and running on the iliac neck and blade. *Remarks*: A ridge sweeping from a point just dorsal to the acetabulum and running posterodorsally along an oblique course is found in ingroup taxa as diverse as *Dvinosaurus*, *Eryops*, as well as *Dendrerpeton acadianum*.

Pubis (PUB)

229. *PUB 1*. Number of obturator foramina in pubic bone: multiple (0) or single (1). *Remarks*: This character (see also Coates 1996 and Clack 2002b) can be coded in very few taxa, as in several groups the pubic bones are not ossified. Multiple foramina characterise Devonian taxa and *Whatcheeria*.

Femur (FEM)

230. *FEM 1*. Internal trochanter of the femur shaped like a poorly raised rugose area (0) or a protruding process (1). *Remarks*: The internal trochanter may appear either as a weakly developed, indistinct rugosity, or as a conspicuous, blunt or digitiform process. *Perryella* and *Sclerocephalus* exemplify the plesiomorphic state. In most other taxa, the internal trochanter protrudes conspicuously.

231. *FEM 2*. Absence (0) or presence (1) of condition: internal trochanter separated from the shaft of the femur by a trough-like space in anterior view. *Remarks*: In some taxa, the internal trochanter and the part of the femur shaft from which it detaches are separated by a deeply notched web of bone.

232. *FEM 3*. Absence (0) or presence (1) of fourth trochanter of the femur. *Remarks*: The fourth trochanter carries a distinct rugose area in *Eryops*, but it is absent or weakly developed in other ingroup taxa.

233. *FEM 4*. Proximal extremity of the adductor crest of the femur not reaching (0) or reaching (1) midshaft length. *Remarks*: This character has been discussed at length by Coates (1996), and refers to the extension, in a proximal direction, of the proximal extremity of the adductor crest, on the flexor surface of the femur. The crest terminates proximally in a blade.

234. *FEM 5*. Length of the femur comparable to (0) or greater than (1) that of the humerus. *Remarks*: The femur length is the distance between the proximal articular surface and the distalmost point of its condyles. State 0 is seen in *Acanthostega*. The length of the humerus is measured as the distance between the point of maximum curvature (usually, the most proximal point in anatomical orientation) of the caput humeri and the plane of the distal articular surface (distalmost point of ulnar facet or rearmost point, in dorsal aspect, of the distal articular surface).

Tibia (TIB)

235. *TIB 6*. Outline of the medial margin of the tibia bordering interepipodial space not shaped (0) or shaped (1) like a subsemicircular embayment. *Remarks*: The derived state is observed in *Whatcheeria* (Lombard & Bolt 1995) and *Pederpes* (Clack 2002b; Clack & Finney 2005), both of which exhibit a massively built, stout tibia with flared proximal and distal ends. The length of the tibia is measured, in extensor or flexor aspect, along the greatest distance that intervenes between the ossified portions of the proximal and distal ends. In whatcheeriids, the length of the medial margin of the tibia bordering the interepipodial space is less than one-third of the length of the tibia.

Fibula (FIB)

236. *FIB 1*. Outline of the fibula not waisted (0) or waisted (1) in extensor view. *Remarks*: As in the case of other limb bones, a waisted morphology implies a shaft constriction.

237. *FIB 3*. Absence (0) or presence (1) of a proximodistally oriented ridge lying close to the posterior edge of the flexor surface of the fibula. *Remarks*: The ridge in question occurs in some outgroups (see Coates 1996 and Ruta *et al*. 2003).

238. *FIB 4*. Absence (0) or presence (1) of tubercle rows lying close to the posterior edge of the flexor surface of the fibula. *Remarks*: This character is kept separate from the preceding character, although such rows of tubercles might be homologous with the continuous ridge seen in an almost identical position on the fibula of certain taxa (see preceding character).

Cervical ribs (RCE)

239. *RCE 2*. Cervical ribs with (0) or without (1) anteroposteriorly expanded distal ends. *Remarks*: In some ingroup and outgroup taxa, the distal extremity of most or all cervical ribs is either dorsoventrally flat or carries a terminal triangular flange.

Trunk ribs (RTR)

240. *RTR 3*. Shaft of trunk ribs mostly straight (0) or strongly curved ventrally (1) in at least part of the trunk. *Remarks*: The rib shaft is often slightly curved ventrally in very large temnospondyls (Schoch & Milner 2000; Yates & Warren 2000; F. Witzmann, pers. comm. 2006). However, in several species the rib shaft is straight or nearly so. *Ichthyostega*, *Whatcheeria*, and *Crassigyrinus* possess strongly curved ribs, similar to those of amniotes.

241. *RTR 4*. Absence (0) or presence (1) of broad posterior flanges projecting from at least some trunk ribs. *Remarks*: This character describes broad (at least twice as wide as the rib proximal shaft), often overlapping, and laminar sheets of bone which occupy a considerable portion of the rib length in the mid portion of the trunk. Considerable variation occurs, as revealed by *Eryops* and *Pederpes* (overview in Clack & Finney 2005). However, F. Witzmann (pers. comm., 2006) has informed us that the ribs in the anterior half of the trunk of large *Sclerocephalus* possess broad posterior flanges often pierced by foramina, similar to the condition of *Pederpes* (Clack & Finney 2005).

242. *RTR 7*. Absence (0) or presence (1) of condition: longest trunk ribs shaped like slender rods, the length of which is less than the length of three midtrunk vertebrae. *Remarks*: As defined here, the character in question is found in branchiosaurids and amphibamids. The length of the vertebrae is measured between their pre- and postzygapophyses, in lateral aspect.

Trunk vertebrae (VTR)

243. *VTR 14*. Intercentra of trunk vertebrae open dorsally (0) or at least some intercentra closed dorsally (1). *Remarks*: The derived state of this character refers to the presence of a dorsally continuous intercentrum, often resembling a flat cylinder or spool. In our data set, state 1 is a shared derived feature of tupilakosaurids.

Digits (DIG)

244. *DIG 1*. Number of digits present in the anterior limb: none (0); eight (1); six (2); five (3); four (4). *Remarks*: Ruta *et al*. (2003) have discussed alternative treatments for this character, e.g. as a multistate character. The present authors have not coded for the posterior autopod, as the number of digits in the latter (except for some Devonian taxa) does not display the degree of variation that is observed in the anterior autopod, given the present taxonomic sample.

Caudal fin (FIC)

245. *FIC 1*. Presence (0) or absence (1) of a caudal fin supported at least in part by a dorsal and a ventral rows of lepidotrichia. *Remarks*: This character refers to the condition of a set of fully ossified lepidotrichia. Therefore, any integument fold of the tail that has no ossified lepidotrichia (e.g. the tail of the branchiosaurid *Apateon*) is discounted. As defined here, this character applies to osteolepiforms, *Acanthostega*, and *Ichthyostega*.

10. Appendix 3. Data matrix

Characters are numbered from left to right and divided into groups of ten. Question marks are used for both inapplicable and unknown states. The notations { } and ( ) imply, respectively, uncertainty and polymorphic coding. The following replacements have been made: a=(0,1); b=(1,2); c=(1,3); d={0,1}; e={1,2}; f={2,3}.

Acanthostomatops vorax

1101100000	0000000001	010000a010	0021002110	0000001???	0a?100a011	
1110000110	0100010200	022220002?	14?0011011	0000010010	1000111000	
1002000000	0111000000	??????2000	0001100000	?????10?11	1?10120???	
1????????1	111000110?	10????????	??????????	????1100??	?????1????	?????

Acheloma cumminsi

1001??0000	?001010001	000000?011	0021021111	0000001???	0001001000	
1102001000	1101110110	0122000020	14?00?1???	??000010?0	1000?1??00	
1002000000	0110000000	0110112000	00??000000	?????10???	0?????1???	
??????????	?1100a????	??0111?111	0211000110	10?10100?1	001?01???0	000??

Acroplous vorax

?001?00010	0000000001	1100001100	002a0001b0	0010101???	?00?011000	
10?0111002	0100010200	0000010000	0110001011	0000010001	1100011010	
0000111011	011201011?	0110102000	113?010121	1????00??1	1?????0???	
??????0?1?	011000110?	00???01?11	0?1?11?010	??1???????	?????????0	000??

Adamanterpeton ohioensis

0101000000	0000001001	100000?110	002101111?	?????00000	01????1000	
110001010?	?100010000	0022d00001	04?1010011	0100000010	1000111000	
1?01000000	0110001022	??????200?	?01?000?00	?1???10?11	0????20???	
??????????	??1000e???	??????????	??????????	??????????	??????????	?????

Amphibamus grandiceps

10?1?00100	0000010001	0001100?10	00210??111	0000001???	00????101?	
111000100?	1100010110	0122?11020	1???111011	1?00000111	0?10011000	
0002000001	0111100022	0?10112100	000?000000	??????0???	??????????	
??????????	?11110010?	0001?01?11	1?1?111110	?0??0000??	???10100?0	01041

Anconastes vesperus

10?1100000	?001010001	?0010??0?1	0021??1110	0000001???	01?1000000	
?10e0?1000	?101110??0	0122??0??0	14????????	??????1???	??????????	
??????????	01????????	??10?1200?	00?2??000?	??????0???	??????????	
??????????	???0012???	??????????	??????????	??????????	??????????	?????

Apateon pedestris

1001?00110	?000010001	0001110011	0021021111	0000001???	01?1001010	
1100001000	?110110110	0101010020	1??0001011	1?00000001	0011010100	
000100?001	0111100022	??????2100	003100001?	??????0???	?????20???	
??????????	?1??00?10?	1001?01???	1?1?111110	?0100000??	???101??00	01041

Balanerpeton woodi

1001?00100	1000000001	0000000010	0021121110	0000000011	01010010aa	
1110001000	0100010110	0201000020	14?0011011	0100010010	1000101000	
1000000000	0111100022	0?10102000	0011000000	?1???00011	0?10120101	
01101001??	?11000010?	000??01?00	1?10010010	00110000?1	1?01010000	00041

Broiliellus brevis

?0?1?00000	?000010001	0000000021	0021001120	0000001???	0001001010	
110e001000	?100010120	0122000020	14?0011011	0?00000011	1?0????00	
1002000001	0111100022	??????2000	00?1000000	??????0?11	0?????????	
??????????	?110000???	??0??0??11	1?1?010110	?0??00?011	0????????0	000?1

Capetus palustris

1001?00000	0000010001	000000?010	0021110a10	0000000000	0001001011	
1100000100	0100010000	0022100000	04?001?011	0??0000??0	?00????00	
1?00000000	0101000122	??????2000	00??000000	??????0??1	0?????????	
??????????	???001d?0?	00????????	??????????	??????????	??????????	?????

Cheliderpeton latirostre

0001001000	0000001001	0000000010	0020000110	0000001???	010100a010	
1100000101	?100010110	0022000010	04?0001011	0100010000	0001000000	
1001000000	0110000021	??????2000	0011000001	01???00011	0?0?1201?1	
?11?1?0111	111001110?	00????????	??????????	????01????	??????????	?????

Chenoprosopus lewisi

01?1001000	0000001001	?0000??120	0021020110	0000000000	00010a1010	
11001?1100	0100010200	0122000012	04?0010011	0?100000?0	?0?0???00	
1001000000	0110000022	0????0????	?????0???0	??????0?11	0?????????	
??????????	???0001???	?0????????	??????????	????0000?0	0?1???????	?????

Chenoprosopus milleri

0101001001	0000001001	1000000110	00211e0110	0000000000	0?01001010	
1100010100	0100010200	00220001?2	04?0010011	0110000010	1000101000	
1001000000	0110000022	0?10102000	003?000000	??????0?11	0?????????	
??????????	???0001???	??????????	??????????	??????????	??????????	?????

Cochleosaurus bohemicus

0101000000	0000001001	0100000110	0020010010	0001000000	0001001aa1	
1100010100	0100010200	01220001?1	04?1010011	0110010010	1000101000	
1001000000	0110001022	0?10102000	0011000010	?1???10011	020??20101	
??101?0110	0110001???	??????????	??????????	??????????	??????????	?????

Cochelosaurus florensis
0101000000 0000001001 1100001110 0021022110 0001000000 000100100a
1100010100 0100010100 01220001?1 04?1010011 0110010010 1000101000
1001000000 0111101022 ??????2000 001?000010 ?1???10011 0?0?020101
?11011011? 0110001??? ?????????? ?????????? ?????????? ?????????? ?????

Dendrerpeton acadianum
1001100000 1000000001 ?00000?000 0021121111 0000000000 0111001001
1100001a00 1100010200 0012000020 04?0011011 0100000010 1000101000
1001000000 0110101022 0?10102001 0011001000 ??????0?11 0?????0???
?????????? ?11000010? 0001?01?00 0210010010 0011000111 1?1101??00 00041

Dendrerpeton confusum
00?1?00000 000000000? ??0?0???20 0021001110 0000000000 00?10010??
?11?0????? ???0?1?00? 0112110020 04???????? ?????????1 ??0???????
?????????? 0????????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????

Doleserpeton annectens
1001?00100 ?000010001 0000100011 0021021101 0000001??? 00010110?0
111000100? 1100110110 0122001020 14?0111011 1?00000101 011????00
1012000001 0111100022 0?10112100 004100100? ?1???10?11 0?????????
?????????? ???1100??? ??0????11 1?1?111110 ?0?00000?1 1?1??????0 0104?

Dvinosaurus primus
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0000001010 0112010021 0?10102000 0131110021 1???????11 1201?20???
??????1011 1110002111 1011111111 0210011010 00111001?1 1011010010 0004?

Ecolsonia cutlerensis
10?1?00000 ?001010001 000000?021 0021122111 0000001??? 0101001010
110200100? 0101110120 0112000010 14?0011011 0?000??010 ?10011?000
1000000000 01110000?? 0110112000 003100000? ?1????0011 0?1?120101
11101001?? ?11000210? 1001111111 0211011?10 ?0?1010011 0?1??100?0 000??

Edops craigi
?101000000 0000001001 0010000010 0021010010 0000000000 0111001111
1100000100 0100010100 0022000000 04?1010011 0100000010 1000101000
1100000000 0000000122 0110102000 00?1000000 01???00011 0?0??20101
?1101?011? 0110002??? ?????11?11 0211010010 00???????? ?????????? ??0??

Eoscopus lockardi
1001?00000 ?000010001 0001001021 00210?1111 0000001??? 0101??10?0
1111001000 1100010110 0122001020 14?0011011 1100000011 1000?11000
1002000001 0111100020 0????12000 0041001000 ?1????0011 021??20101
1?101?011? ?11000010? 000??01?11 1?1?111110 00210000?1 1011010000 01041

Eryops megacephalus
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0110100111 111001010? 0001111111 0211000010 1021a101?1 0111011000 10041

Eugyrinus wildi
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110000100? 0100010000 0101120020 0f00?????? ??0????0?? ?0??????00
1??0??000? 011110???? ??10102010 011?0?0010 ?????????? ??????????
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????

Isodectes obtusus
1001000010 0001000001 1000000100 002000012a 0010100011 000001100a
10?011100? 0100010100 0000010010 0110001011 00000100?1 ?10?????0?
00?0110011 0110110012 0110102000 113?000121 1????00??? 1?????????
???????111 111000d?10 00???????? ?????????? ?????????? ?????????? ?????

Leptorophus tener
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Micromelerpeton credneri
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1100001000 ?100010110 01000a0020 1100001011 0100000001 0111010000
1001000001 0111100000 ??????2000 0001000011 01????0011 0?1?120???
111?10?111 11100??10? 00???0??11 1?1?0???10 ?0100000?? ???1?1??00 0104?

Neldasaurus wrightae
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1000000000 0110000012 0110102010 01??000001 0????00?11 0?????0???
?????????? ?11000000? 000?10?111 0210010110 00211100?1 0?1?????0 0004?

Onchiodon labyrinthicus
1001000000 0000001001 000000?010 002111a110 0000001??? ?a0100101a
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?1101?0111 111001110? 00?1?????? ?????????? ????1100?? ?????????? ????1

Perryella olsoni
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1100a?0002 01???1?110 0212000020 04?0011?11 0000010011 ?100????00
10010?0011 01111100?? 0110102010 012e000001 0?????0?11 02???201??
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Phonerpeton pricei
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1002000000 0110000022 0110112000 0031000000 ?1???00011 0?11121101
1110110111 111001d??? ???11111?1 02110????? 10?1?????? ?????????0 000??

Platyrhinops lyelli
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Procochleosaurus jarrowensis
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11000?010? ?100???120 0122000001 04???????? ?????????? ?00????00
1?0100?0?? 010?00???? ?????????? ????????1? ?????00??? 0?????????
??????01?? ?1?00?1?0? ?0???????? ?????????? ?????????? ?????????? ??0??

Schoenfeldereton prescheri
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????????11 111?000?0? 10???0??11 1?1?0???10 ?010?????? ?????????? ???4?

Sclerocephalus haeuseri
1001001000 0000001001 0010000020 0020a00110 0000001??? 0a0100101a
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1001000000 0110000021 ??????2001 00c2010001 01???00011 020?120110
?111100111 111001110? 000111?111 021?001010 10110000?0 001101??10 00041

Slaugenhopia texensis
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?????????? ???????0?? ?????????? ?e0??????? ?????????? ????????01
??????11?? 1????????? ??????2?00 00301?00?? ?????????1 1?????????
?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????

Thabanchuia oomie
?001?0??10 1?011001?? 010000??00 0120100120 0000011??? ?a0000010a
20?01?10?? ?100?1?200 0000020020 0300001011 00011100?1 1100????11
0000111111 01111101dd 1?11102000 003?110021 1????0001? a????200??
??0??????? ?????0?011 00???????? ?????????? ?????????? ????????10 001??

Trimerorhachis insignis
1001?00000 0000000001 0000001000 0020020120 0000000011 0100001a00
0100101002 0100010110 0000000000 0f00001111 0001100000 0001000000
0000000000 0110000112 0110102010 0131000011 01???00011 0211120101
1110110110 011000d10? 0011?01111 0210010110 00111000?1 1011010000 00041

Tupilakosaurus wetlugensis
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20?0101002 ?100010000 0000020020 0300001011 010??10001 1100000011
0000111111 01110101dd 1111102000 00311?00?1 1????00??? 1?????????
?????????? ?1?0002??? ?????????? ?????????? ?????????? ?????????? ??1??

Zatrachys serratus
1101100000 0000000001 0a0000a010 0021112110 0001001??? 0a?a0010a1
b110000a10 0100010000 022220002? 14?001a011 001001001a 1000111000
1002000001 0111000000 0????02000 000?100010 ?1???10?11 1????20101
??101?0111 1110002??? ?????????? ?????????? ?????????? ?????????? ??0??

Acanthostega gunnari						
0000?00000	0000001000	0000000020	0111021010	0000001???	0100000101	
00?0000100	0000000110	0022000000	0100000000	0000000000	0001000000	
0000000000	0000000010	0000001000	0030000000	?011000000	0000010110	
0011001000	?010000110	0000000000	0000010001	0100001001	1100001000	00010
Baphetes kirkbyi						
0001000000	0010000010	0000000110	0021021100	0000000011	1111000000	
10?0000001	0100010120	0122000000	0300010011	0000000010	1000101000	
0100000000	1?????0022	0010102000	0000000000	?0101?0???	0????20???	
??????????	???0001???	????000101	0200010010	00??0010??	????0110??	??0??
Colosteus scutellatus						
00?1?10011	01001?0000	000000??10	1120120120	0100001???	01?0000100	
10?0000000	?100010200	0022000000	0200??????	??0??000?0	0000??0000	
0100000000	0000000112	??????2???	000?000000	?????11???	0????20110	
??????0100	???000?00?	00????????	??????????	??????????	??????????	??04?
Crassigyrinus scoticus						
0011100000	1001001001	0000001010	0021?21a20	1000000???	00010000?0	
10?000000?	0100011111	0222000000	0100000000	0?00000000	0000000000	
0100000000	0000000110	??001?1000	0020000000	?010110101	01000d0101	
001010????	?010001???	00??100100	0e00010000	00000010?1	11110110?1	000??
Eucritta melanolimnetes						
00?1?00000	100000001?	0000000020	0021021000	0000000011	11?1001000	
0100001000	?1000??111	0122000000	0???010011	0????00010	1000??0000	
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Greererpeton burkemorani						
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Ichthyostega stensioei						
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Loxomma rankini						
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Megalocephalus pachycephalus						
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Ossinodus pueri						
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Panderichthys rhombolepis						
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Pederpes finneyae						
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Tulerpeton curtum						
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Whatcheeria deltae

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11. Appendix 4. Ingroup and outgroup taxa

11.1. Character-states supporting dvinosaurs

Twenty-three characters, none of which is uniquely derived, support Dvinosauria, as follows: 11 (c.i.=0.167; 1→0); 27 (c.i.=0.167; 0→1); 34 (c.i.=0.143; 1⇒0); 37 (c.i.=0.167; 1⇒0); 39 (c.i.=0.25; 1→2); 43 (c.i.=0.333; 0→1); 52 (c.i.=0.083; 1→0); 54 (c.i.=0.2; 1⇒0); 70 (c.i.=0.667; 0→2); 92 (c.i.=0.364; 4⇒3); 96 (c.i.=0.167; 1→0); 102 (c.i.=0.2; 1→0); 109 (c.i.=0.143; 1→0); 115 (c.i.=0.2; 1→0); 117 (c.i.=0.167; 1→0); 139 (c.i.=0.2; 2→1); 149 (c.i.=0.5; 0⇒1); 152 (c.i.=0.5; 0⇒1); 186 (c.i.=0.25; 0→1); 203 (c.i.=0.333; 0→1); 209 (c.i.=0.333; 0→1); 210 (c.i.=0.25; 0→1); 225 (c.i.=0.333; 0→1).

11.2. Character-states supporting *Perryella* as sister taxon to dvinosauroids

The position of *Perryella* as sister group to a monophyletic Dvinosauroidea is supported by 17 characters, of which two are uniquely derived: 45 (c.i.=0.333; 0⇒1); 47 (c.i.=0.143; 0⇒1); 56 (c.i.=0.333; 0⇒1); 66 (c.i.=0.25; 0→1); 110 (c.i.=0.25; 0⇒1); 112 (c.i.=0.25; 0⇒1); 126 (c.i.=0.5; 0→1); 129 (c.i.=1; 0⇒1); 130 (c.i.=0.2; 0⇒1); 136 (c.i.=1; 0⇒1); 173 (c.i.=0.333; 1→0); 188 (c.i.=0.25; 1→0); 197 (c.i.=0.154; 0⇒1); 206 (c.i.=0.2; 0→1); 217 (c.i.=0.25; 0⇒1); 228 (c.i.=0.25; 0→1); 239 (c.i.=0.2; 0→1). Characters 66, 173, 228, and 239 are scored as unknown in *Perryella*.

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M. RUTA* and J. R. BOLT, Department of Geology, The Field Museum of Natural History,
1400 South Lake Shore Drive, Chicago, Illinois 60605-2496, USA
E-mails: bolt@fieldmuseum.org; mruta@fieldmuseum.org
*Current address: Department of Earth Sciences, University of Bristol, Wills Memorial Building,
Queen's Road, Bristol BS8 1RJ, UK
E-mail: m.ruta@bristol.ac.uk

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