The skull of the Early Triassic archosauromorph reptile *Prolacerta broomi* and its phylogenetic significance

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Description of new and re-examination of previously described cranial remains of *Prolacerta broomi* Parrington allows reappraisal of the structure of the skull in this basal archosauromorph reptile. The ventral margin of the premaxilla is slightly deflected, and there is a relatively large lateral foramen in the maxilla that is bounded anteriorly by the premaxilla; both features are shared with the basal rhynchosaur *Mesosuchus* and the basal archosauriform *Proterosuchus*. Implantation of the marginal dentition is ankylothecodont: the teeth are rooted relatively deeply, bounded lingually by a deep wall of the jaw, and anchored to the jaw by bone of attachment. The pineal foramen varies in size from little more than a scar in the interparietal suture to a suboval opening several millimetres in diameter. Contrary to previous claims, the skull roof in *Prolacerta* was akinetic and quadrate mobility (streptostyly) was absent. Phylogenetic analysis of a previously published data matrix, modified by the addition of new anatomical data and reinterpretation of some characters, corroborates the hypotheses of the polyphyly of Prolacertiformes (Protorosauria) and of a close relationship between *Prolacerta* and Archosauriformes. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, **140**, 335–351.

ADDITIONAL KEYWORDS: anatomy – Archosauromorpha – phylogeny – Reptilia – Triassic.

INTRODUCTION

Problems of the origins and early diversification of crown-group Diapsida are highlighted by the taxonomic history of *Prolacerta broomi*, a small reptile from the Early Triassic of South Africa and Antarctica. Parrington (1935) erected *Prolacerta broomi* for a skull from the Lower Triassic *Lystrosaurus* Assemblage Zone of South Africa. He regarded the new reptile as intermediate between more basal diapsids (such as *Youngina*) and lizards, primarily because of the incomplete lower temporal bar. Despite its supposed squamate affinities, Parrington assigned *Prolacerta* to Thecodontia, a grouping now recognized as paraphyletic but at the time regarded as a 'stem' group for all more derived taxa of archosaurian reptiles. The discovery of a second specimen of *Prolacerta* allowed a more complete description of the skull by Camp

(1945a), who concluded that *Prolacerta* was the closest relative of the Late Permian reptile *Protorosaurus*, then thought to be an early lepidosaur. Camp (1945b) concurred with Parrington (1935) that *Prolacerta* was closer to the ancestry of lizards than any other taxon known at the time. Materials of *Prolacerta* continued to be collected from the Lower Triassic *Lystrosaurus* Assemblage Zone in South Africa (Kitching, 1977) and correlative strata of the Fremouw Formation in Antarctica (Colbert, 1987).

The view that *Prolacerta* was an ideal precursor of lizards was widely accepted (e.g. Robinson, 1967, 1973; see also Wild, 1980) until Gow (1975) described the first reasonably complete skeleton. Gow (1975) made detailed comparisons with *Proterosuchus* and concluded that *Prolacerta* was close to the ancestry of archosaurian reptiles (now equivalent to Archosauriformes, Gauthier, Kluge & Rowe, 1988), but concluded that the latter genus and taxa he considered its closest relatives (*Macrocnemus* and *Tanystropheus*) belonged in a new order, Parathecodontia, which was subsequently recognized only by Kitching (1977) and Bartholomai (1979). Brinkman (1981) accepted the

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hypothesis that *Prolacerta* and its presumed allies (as Prolacertiformes) were basal archosauromorphs, whereas others preferred to regard *Prolacerta* more vaguely as an 'eosuchian' (e.g. Currie, 1980; Evans, 1980); at the time, Eosuchia was conceived as the diapsid ancestral 'stock' that had given rise to both archosaurs and lepidosaurs. Wild (1980) rejected Gow's views and instead interpreted *Prolacerta*, along with *Macrocnemus* and the Tanystropheidae, as an early lineage of Squamata. Subsequently, various cladistic studies placed *Prolacerta* with *Protorosaurus*, *Macrocnemus* and *Tanystropheus* in a monophyletic Prolacertiformes (equivalent to Protorosauria of some authors) at the base of Archosauromorpha (Benton, 1985; Chatterjee, 1986; Evans, 1988; Gauthier, 1994). The validity of Prolacertiformes, however, was seriously questioned by Dilkes (1998), who provided compelling evidence that it was a polyphyletic assemblage, and identified *Prolacerta* as the sister taxon of Archosauriformes (see also Sues, 2003).

New cranial material of *Prolacerta* has become available since the publication of the study by Gow (1975), providing a basis for a re-evaluation of both the skull structure of this early archosauromorph and its phylogenetic relationships. Advances in mechanical preparation of vertebrate fossils also permit reassessment of previously described material. The cranial structure of *Prolacerta* is redescribed here in detail in order to provide an anatomical basis for comparisons of this historically and phylogenetically important taxon, and to test the hypothesis that it is more closely related to archosauriforms (exemplified by such taxa as *Proterosuchus*) than to the other basal archosauromorphs with which it was grouped by most previous authors.

Institutional abbreviations: BP, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; CM, Carnegie Museum of Natural History, Pittsburgh; UMZC, Museum of Zoology, Cambridge University, Cambridge; UCMP, Museum of Paleontology, University of California, Berkeley.

Anatomical abbreviations used in Figures 1–8: a m f – anterior maxillary foramen; a s f – anterior surangular foramen; an – angular; ar – articular; ax – axis; bo – basioccipital; co – coronoid; d – dentary; ec – ectopterygoid; eo – exoccipital; ep – epipterygoid; f – frontal; j – jugal; la – lacrimal; n – nasal; mr – mandibular ramus; mx – maxilla; op – opisthotic; p – parietal; pbs – parabasisphenoid; pal – palatine; pf – postfrontal; pra – prearticular; prf – prefrontal; prm – premaxilla; pro – prootic; p s f – posterior surangular foramen; pt – pterygoid; q – quadrate; qj – quadratojugal; s – stapes; sa – surangular; scl – scleral ossicle(s); sm – septomaxilla; so – supraoccipital; sp – splenial; sq – squamosal; st – supratemporal.

MATERIAL AND METHODS

Prior to this study, most specimens were prepared by mechanical means with the use of needles mounted in pin-vices, airscribe tools and, for some specimens, by use of a disc rotary tool. Only BP/1/2675 was prepared using acetic acid by Gow (1975). However, acid preparation made the disarticulated bones friable. For this reason we have not relied upon BP/1/2675 for this study, and readers are referred to Gow (1975) and Evans (1986) for descriptions of this specimen. The remaining materials were prepared further primarily with the use of pin-vices tipped with tungsten carbide bits, accompanied by occasional use of a Murray Micro-Jack 5 airscribe. In the case of BP/1/5375, intractable, overlying matrix combined with the absence of supporting rock under the delicate mandibular elements precluded preparation by mechanical means. For this reason, the left mandibular ramus of BP/1/5375 was only partially exposed from the encasing matrix.

Skeletal materials of the following squamates were used for comparative purposes: *Cnemidophorus tigris* (CM 43514), *Crotaphytus collaris* (CM 118967), *Ctenosaura* sp. (CM 35155), *Cyclura cyclura* (CM 144934), *Eumeces laticeps* (CM 32056), *Heloderma suspectum* (CM 37481), *Iguana iguana* (CM 92303), *Lacerta* sp. (CM 67296), *Laudakia stellio* (CM 39116), *Phrynosoma asio* (CM 92308), *Sceloporus clarkii* (CM 48668), *Tupinambis teguixin* (CM 35162), *Uromastyx* sp. (CM S-9115) and *Varanus niloticus* (CM 67294).

SYSTEMATIC PALAEONTOLOGY

DIAPSIDA OSBORN, 1903
ARCHOSAUROMORPHA HUENE,
1946 *SENSU* BENTON, 1985
PROLACERTA BROOMI PARRINGTON, 1935

Diagnosis. Distinguished by the presence of septomaxillae, conspicuous posterolateral exposure of the lacrimal duct openings (condition unknown in some other possibly related taxa, e.g. *Protorosaurus*), absence of postparietals, and by extensive contact between the surangular and the prearticular in the articular region of the mandibular ramus.

Holotype. UMZC 2003.40, a partial skull and mandible.

Material examined. BP/1/471 (holotype of subjective junior synonym *Pricea longiceps* Broom & Robinson, 1948), a complete skull with attached mandible; BP/1/2675, a nearly complete skull, now mostly disarticulated, with postcranial skeleton; BP/1/4504a, a skull of a small individual; BP/1/5066, a partial, flattened skull; BP/1/5375, a skull, complete from mid-snout to

occiput with accompanying portions of the mandible; UCMP 37151, a complete skull with articulated cervical vertebrae.

Horizon and geographical provenance. *Prolacerta* is currently known only from the Lower Triassic *Lystrosaurus* Assemblage Zone (Beaufort Group) of South Africa (Groenewald & Kitching, 1995) and correlative strata of the Fremouw Formation in the Transantarctic Mountains of Antarctica (Colbert, 1987). The holotype of *P. broomi* came from Harrismith Commonage, Harrismith District, Free State, South Africa. The specimens used in this study were collected from the following South African localities: BP/1/471, Honingkrans (Hueningkrans), Burgersdorp District; BP/1/2675, Harrismith Commonage; BP/1/4504a, Fairydale, Bethulie District; BP/1/5066, Queen's Hill, Harrismith District; BP/1/5375, Rietport, Dewetsdorp District; UCMP 37151, Big Bank, Harrismith District (UCMP locality V36115).

DESCRIPTION

Many specimens of *Prolacerta* are preserved in hard mudstone and were prepared using grinding tools, which unfortunately resulted in the destruction of sculpturing and other fine features in some specimens. BP/1/5066 and UCMP 37151 were preserved in softer, easily prepared matrix, and both reveal that the skull of *Prolacerta* is virtually devoid of the shallow pits and other forms of dermal sculpturing found in stem diapsids such as *Youngina*. BP/1/5066 shows that the frontal bears a shallow longitudinal furrow that continues posteriorly on to the parietal, whereas UCMP 37151 preserves numerous labial foramina and several short longitudinal flutes on the surfaces of the major tooth-bearing elements.

SKULL ROOF

The premaxillae of UCMP 37151 are slightly disarticulated from the rest of the snout (Figs 1, 2), but the right element of BP/1/471 is preserved in full articulation and, contrary to the statement by Dilkes (1998: 524) that the premaxilla is not downturned as in *Proterosuchus*, shows that its ventral margin slopes anteroventrally (Fig. 3B). The left premaxilla of UCMP 37151 is slightly more complete than the right, and, if properly articulated with the maxilla, would show an inclination similar to that seen on the right side of BP/1/471. The dorsal process of the premaxilla is a small, transversely compressed blade (Fig. 2), but its length is unknown because the tip is not present in any of the available specimens. The posterodorsal process arises from the posterolateral corner of the pre-
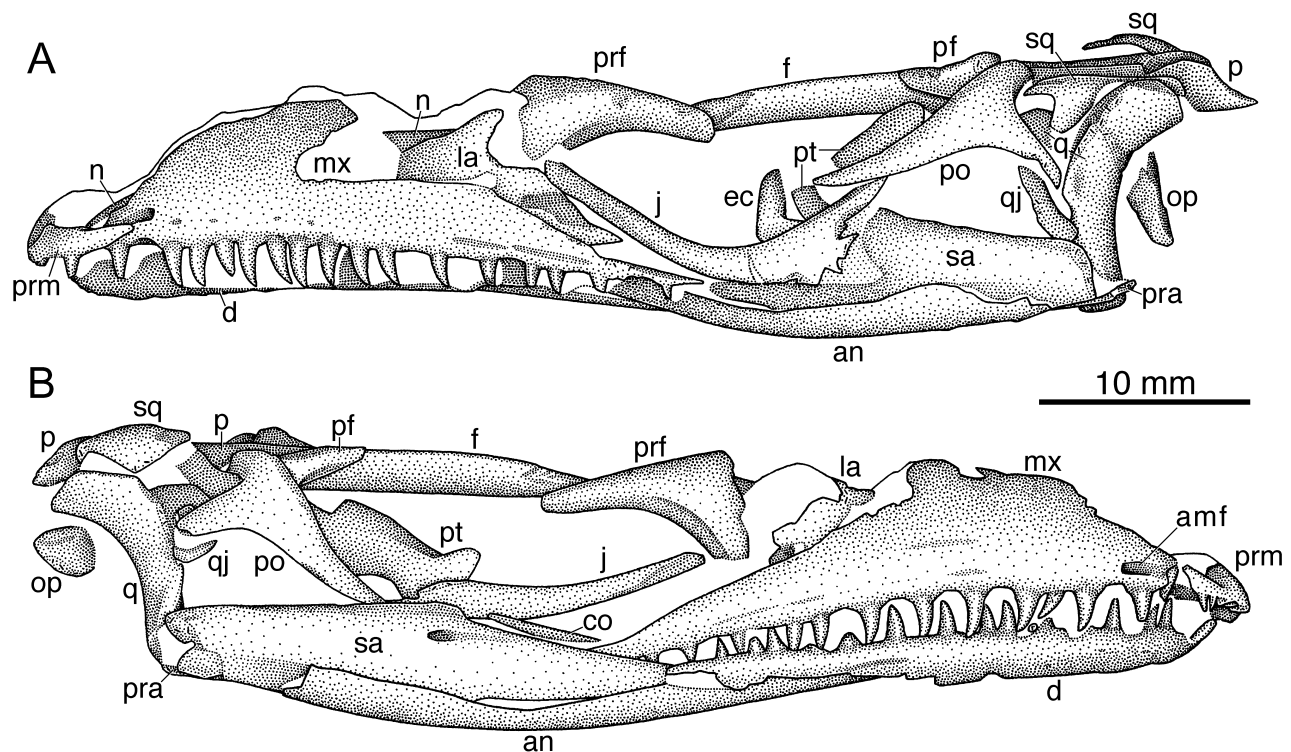

Figure 1. *Prolacerta broomi*, UCMP 37151. Skull in left (A) and right (B) lateral views.
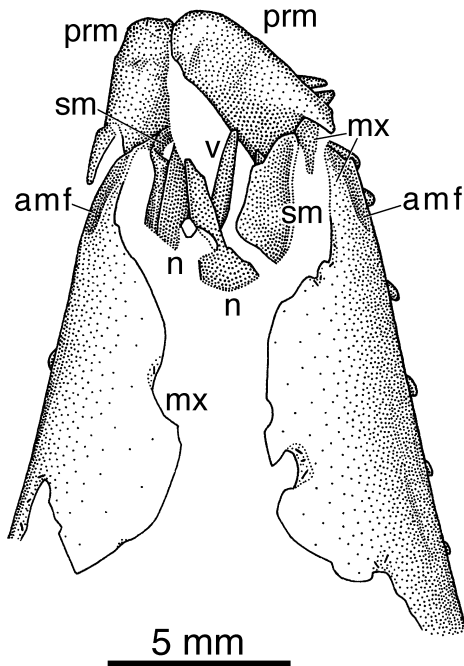
Figure 2. *Prolacerta broomi*, UCMP 37151. Rostral region in dorsal view.

maxilla and extends along the posterior margin of the external naris and contacts the lateral margin of the nasal, thereby excluding the maxilla from the narial margin. The alveolar margin accommodates five teeth, which change in shape from conical to slightly recurved from the first to the fifth. Most premaxillary teeth project from the ventral margin at a right angle, but a few parallel those in the maxilla. Given the thickness of the alveolar region of the premaxilla, it is doubtful that these teeth are implanted deeply, which may account for why the largest premaxillary teeth are never seen to exceed the size of posterior maxillary teeth. The premaxillary teeth are ankylosed to the alveolar bone.

Septomaxillae are preserved only in UCMP 37151 (Fig. 2). The right element is better exposed then the left, and reveals that the septomaxilla is a flat, quadrangular structure with a prominent lateral lip. The septomaxilla is hidden by the posterodorsal process of the premaxilla in lateral aspect, but it would have been fully exposed within the posterior region of external naris in dorsal aspect.

The maxilla is an elongate, blade-like structure (Figs 1–4, 7, 8). As correctly recognized by Gow (1975), the maxilla is surmounted by a thin, dorsal lamella that forms most of the snout in lateral aspect. A conspicuous foramen punctures the lateral surface of maxilla anteriorly at the base of the lamella, and opens into a short, deep channel that is truncated anteriorly at the suture with the premaxilla. A similar

arrangement of foramen and groove is present also in *Proterosuchus* (Welman, 1998) and *Protorosaurus* (H.-D. Sues pers. observ. on skull in the Ottoneum in Kassel, Germany), and a pair of topographically similar openings are seen in *Mesosuchus* (Dilkes, 1998: figs 5 and 7). Juul (1994) has referred to the opening in both *Proterosuchus* and *Mesosuchus* as the subnarial foramen, a term taken from the literature on saurischian dinosaurs (e.g. Madsen, 1976). However, the foramen present in *Prolacerta* differs from the saurischian subnarial foramen in that it does not open medially into the choana. For this reason (and for others outlined in the discussion), we do not believe that the maxillary foramen in *Prolacerta* (and, by extension, that of *Proterosuchus*, *Protorosaurus* and *Mesosuchus*) is homologous with the saurischian subnarial foramen. Accordingly, the opening seen in *Prolacerta*, *Proterosuchus* and *Mesosuschus* is termed here the 'anterior maxillary foramen'. Many squamates have enlarged supralabial foramina, and some taxa (e.g. *Chamops*: Gao & Fox, 1996; *Eolacerta*: Müller, 2001) feature enlarged foramina in the same approximate position as the anterior maxillary foramen of *Prolacerta*, which suggests that the opening in *Prolacerta*, *Proterosuchus*, *Protorosaurus* and *Mesosuchus* may be an enlarged supralabial foramen, one that might be homologous with the openings seen in squamates.

The maxillae of the largest complete skull (BP/1/471; Figs 3, 4) have room for 24 or 25 tooth positions. The teeth are homodont, with slightly to moderately recurved crowns that are slightly compressed labiolingually. Cutting edges are present on the anterior and posterior (or mesial and distal) margins. The anteriormost teeth are slightly smaller than the more posterior teeth, which are subequal in the region ventral to the dorsal lamella. Posteriorly, the maxillary teeth display a progressive decrease in size to the posterior end of the dentition. As illustrated by the damaged right maxilla of BP/1/471 (Fig. 3B), the largest teeth are implanted deeply into the bone. The teeth are ankylosed to the jaw by bone of attachment. BP/1/2675 demonstrates that the lingual wall of the maxillary alveolar margin extended as far ventrally as the labial wall, the absence of resorption pits in the lingual wall and the preservation of replacing teeth in several alveoli (Gow, 1975: figs 13, 13A and 32; pers. observ.), conditions that together indicate ankylothecodont implantation (*sensu* Chatterjee, 1974).

The nasal is a long, slightly curved sheet of bone (Figs 1–4, 7). It is narrow anteriorly but becomes transversely expanded posteriorly to almost double the anteriormost breadth of the bone. Interestingly, Camp's (1945a: pl. 1) drawing of UCMP 37151 is accurate, but he misinterpreted the dorsal lamella of the maxilla as broken portions of the nasals (Camp, 1945a: figs 1, 2); both nasals are actually completely
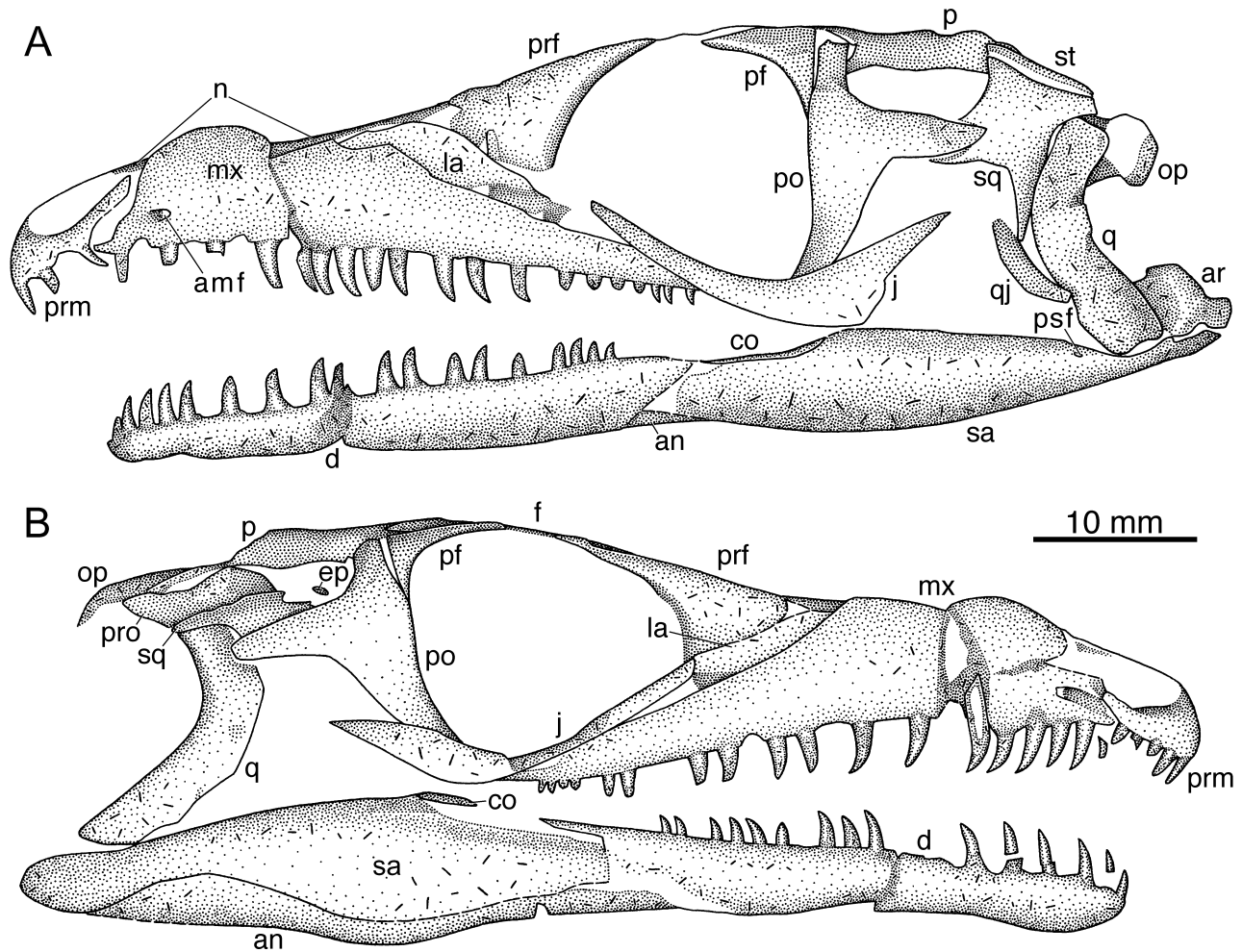
Figure 3. *Prolacerta broomi*, BP/1/471. Skull in left (A) and right (B) lateral views.

preserved, as in BP/1/471, because their anterior tips can be seen in dorsal view (Fig. 2) in the same orientation as the posterior, better exposed portions (Camp, 1945a: pl. 1). Judging from UCMP 37151, the nasal appears to form the posterior half of the dorsal margin of the external naris. There is no basis for the anteriorly notched nasal as depicted in Gow's (1975: fig. 11) reconstruction.

Laterally exposed posterior openings for the lacrimal duct are the most conspicuous features of the lacrimal of *Prolacerta* (Figs 1, 3, 7, 8). Apparently confused by these structures, Camp (1945a) restored the prominent openings in UCMP 37151 as rather loose-fitting sutural surfaces for the reception of the anterior tip of the jugal (Camp, 1945a: fig. 1). Gow (1975) described and illustrated the openings of the lacrimal duct correctly. Both authors surmised that the lacrimal had some degree of contact with the nasal, and their suspicions are borne out by BP/1/471 and BP/1/5375, both of which preserve a short but

unequivocal suture between these two bones. The lacrimal has a slightly greater dorsoventral height than shown in the reconstruction by Gow (1975: fig. 12).

The prefrontal is a triangular element with an attenuated posterodorsal process in lateral aspect (Figs 1, 3). The suture with the nasal is shorter than illustrated by Gow (1975: fig. 11). The edge forming the orbital margin is also slightly concave in dorsal aspect, rather than slightly convex as restored by that author.

The frontal is elongate and only slightly shorter than the nasal (Fig. 4). It somewhat underlies the nasal. In large skulls, the frontal reaches its greatest transverse width both anterior and posterior to the interorbital region. In BP/1/5066, however, the frontal reaches its greatest breadth only at its anterior end; the posterior end is no wider than the narrowest part of the bone (Fig. 6). The orbital margin is conspicuously raised above the remainder of the bone, and there is a slight lipping of the medial edge of the bone,
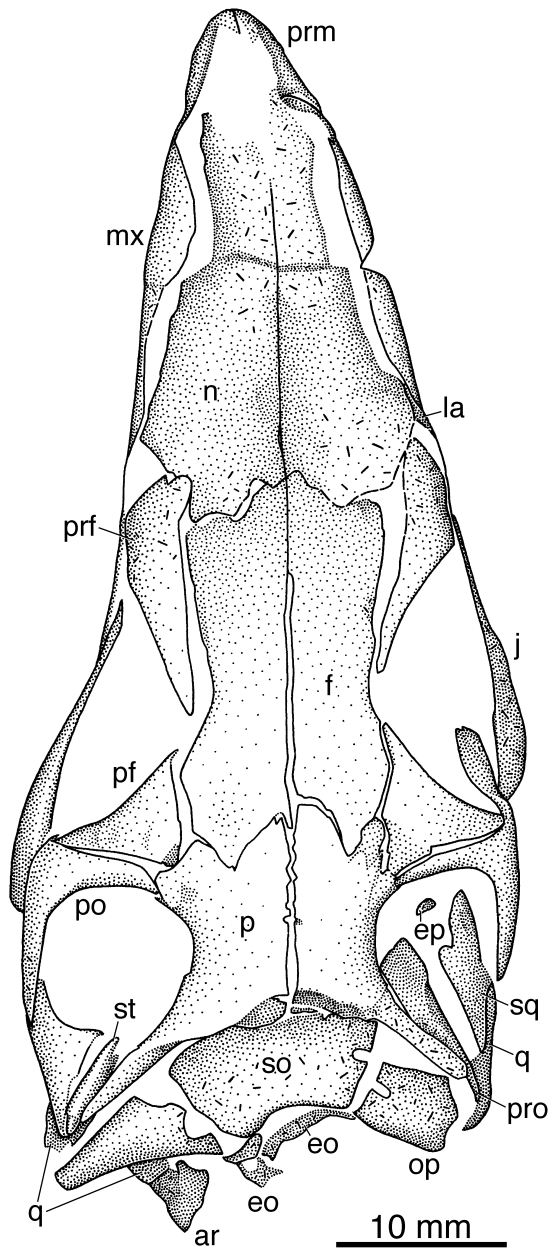
Figure 4. *Prolacerta broomi*, BP/1/471. Skull in dorsal view.

Figure 5. *Prolacerta broomi*, BP/1/471. Skull in occipital view.

The structure of the parietal is well known from the work of Camp (1945a) and Gow (1975), obviating the need for a detailed description here. It is noteworthy that the size of the pineal foramen is quite variable in *Prolacerta*. In BP/1/5375 (Fig. 7) and in BP/1/2675 [the principal specimen used by Gow (1975) for his description] this opening is relatively large, whereas in both BP/1/471 and BP/1/5066 it has been reduced to a tiny slit (orientated transversely and anteroposteriorly, respectively), and in UCMP 37151 the pineal foramen is entirely absent. The variance in the form of the pineal foramen does not appear to be size-related: the individual represented by BP/1/5375, which has a relatively large pineal foramen, is approximately the same size (judging from the parietals and the frontals) as the individual represented by BP/1/5066, which features a small, sagittally aligned scar in the position of the parietal foramen. The dorsal extent of the surface for the external origin of the adductor musculature ('ventromedial flange' of Benton, 1985; Laurin, 1991; 'ventrolateral flange' of Dilkes, 1998) is also variable. The ridge marking the most medial extent of the musculature falls a couple of millimetres short of the midline in UCMP 37151 (Camp, 1945a: pl. 1), whereas it extends almost to the midline, resulting in a narrow sagittal furrow posterior to the pineal foramen and between the paired parietals in BP/1/5066. (The ridges that mark the dorsal extent of the surfaces for the adductor muscles have been ground away during preparation in BP/1/471.) The occipital wing of the parietal twists as it extends posterolaterally, so that its posterior surface becomes visible in dorsal aspect posterior to the supratemporal opening.

and together the two raised areas form a long, shallow furrow passing down the length of the dorsal surface of the bone. Laterally, the frontal contacts the prefrontal anteriorly and the postfrontal posteriorly along simple butting sutures. The posterior end of the frontal slightly overlaps the parietal, with which it shares a serrated suture. The serrated nature of this suture is clear in large specimens (e.g. BP/1/471: Fig. 4), whereas the contact between the frontal and the parietal in BP/1/5066 is a simple diagonal suture for the most part (Fig. 6).
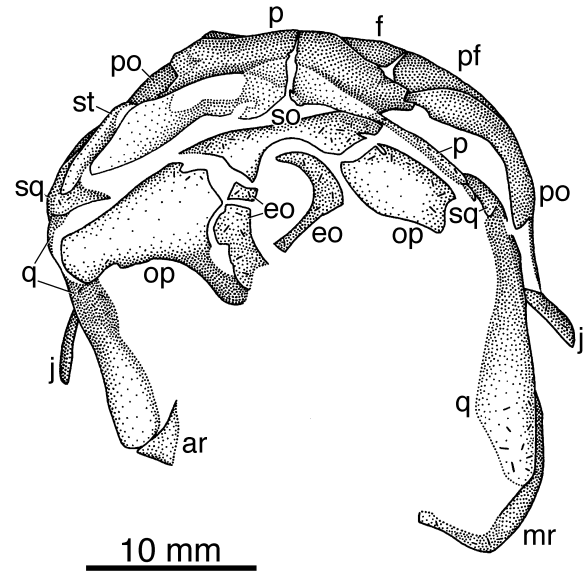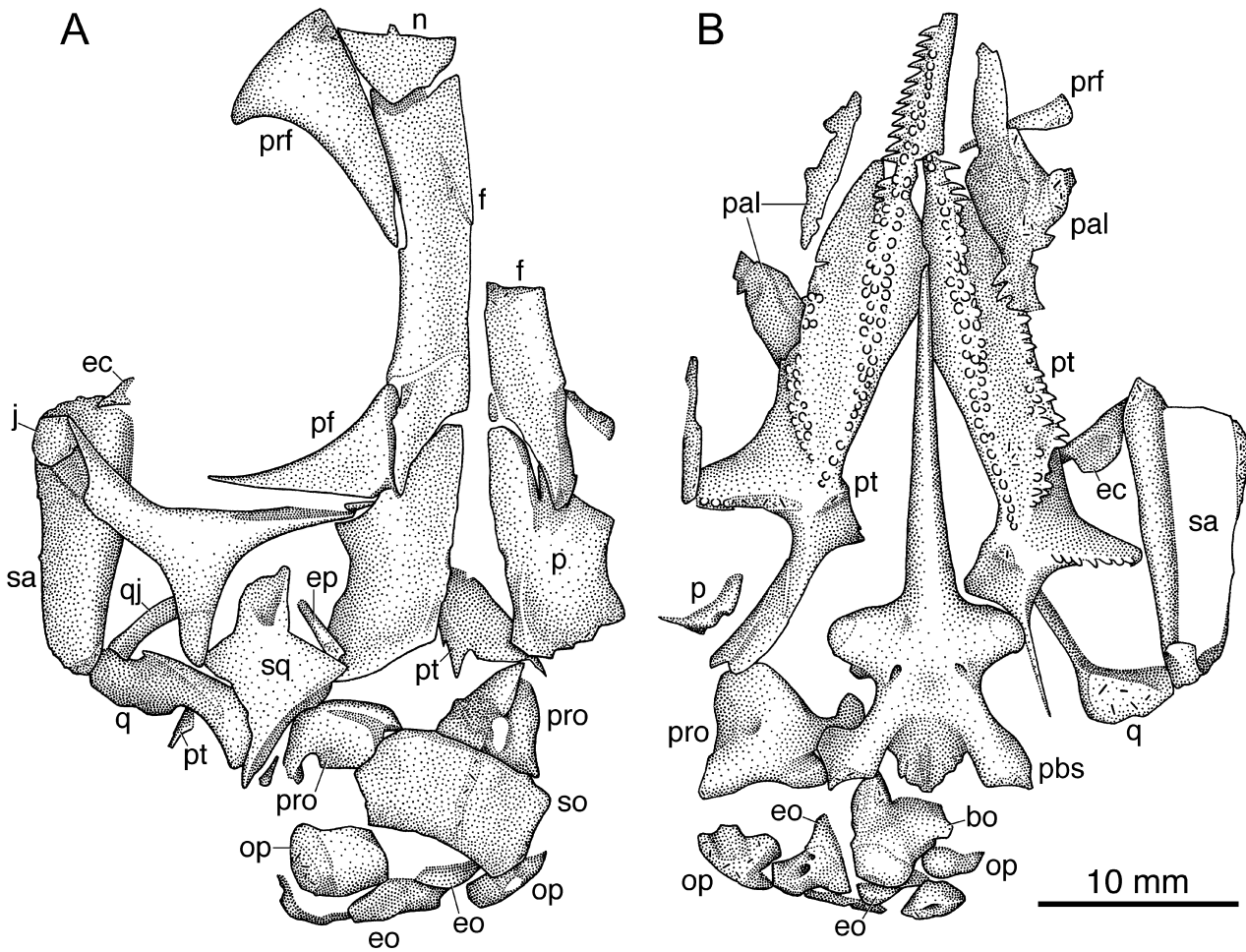
Figure 6. *Prolacerta broomi*, BP/1/5066. Skull in dorsal (A) and ventral (B) views.

The shape of the postfrontal is another feature in *Prolacerta*. This bone approaches the outline of an equilateral triangle in BP/1/471 (Fig. 4) and UCMP 37151 (Camp, 1945a) but it is conspicuously attenuated laterally in BP/1/5066. It forms abutting contacts with the frontal and the postorbital, but the posteromedian corner of the postfrontal is overlapped by the parietal. The postfrontal is excluded from the supratemporal opening by the dorsomedial process of the postorbital; there is not even the small posterior dorsal excavation suggestive of expansion on to the postfrontal of the dorsal origin of the jaw adductor musculature, as in *Youngina* (Reisz, Modesto & Scott, 2000).

The triradiate postorbital (Figs 1, 3, 4, 6–8) differs little from that in most basal diapsids. The dorsomedian process is anteroposteriorly compressed and contacts almost the entire posterior margin of the postfrontal; its distal tip has a small but definite contact with the parietal. The posterior process is the shortest ramus of the postorbital; its distal tip fits firmly into an excavation on the lateral surface of the anterior process of the squamosal. The anteroventral process of the postorbital is slightly curved and extends far ventrally along the anterior margin of the dorsal process of the jugal; as in *Mesosuchus* (Dilkes, 1998), its extends ventrally to, but does not reach, the dorsal surface of the palate.

Of all the bones of the skull roof, the jugal appears to be the most susceptible to post-mortem damage. The posterior or subtemporal ramus is missing from both jugals in BP/1/471 (Fig. 3), and UCMP 37151 has suffered damage to the subtemporal ramus of the left jugal (Fig. 1A) since Camp's (1945a) description. The preservation of the skull roof on the left side of BP/1/5375 is comparably pristine, and shows that the posterior process of the jugal is a posteriorly attenuating sliver of bone that nearly reaches the suspensorium (Fig. 8A). The dorsal or postorbital process of the jugal is the shortest of the three rami. The anterior process is long and slender. It extends forwards to contact the lacrimal along the orbital margin; the distal end of the
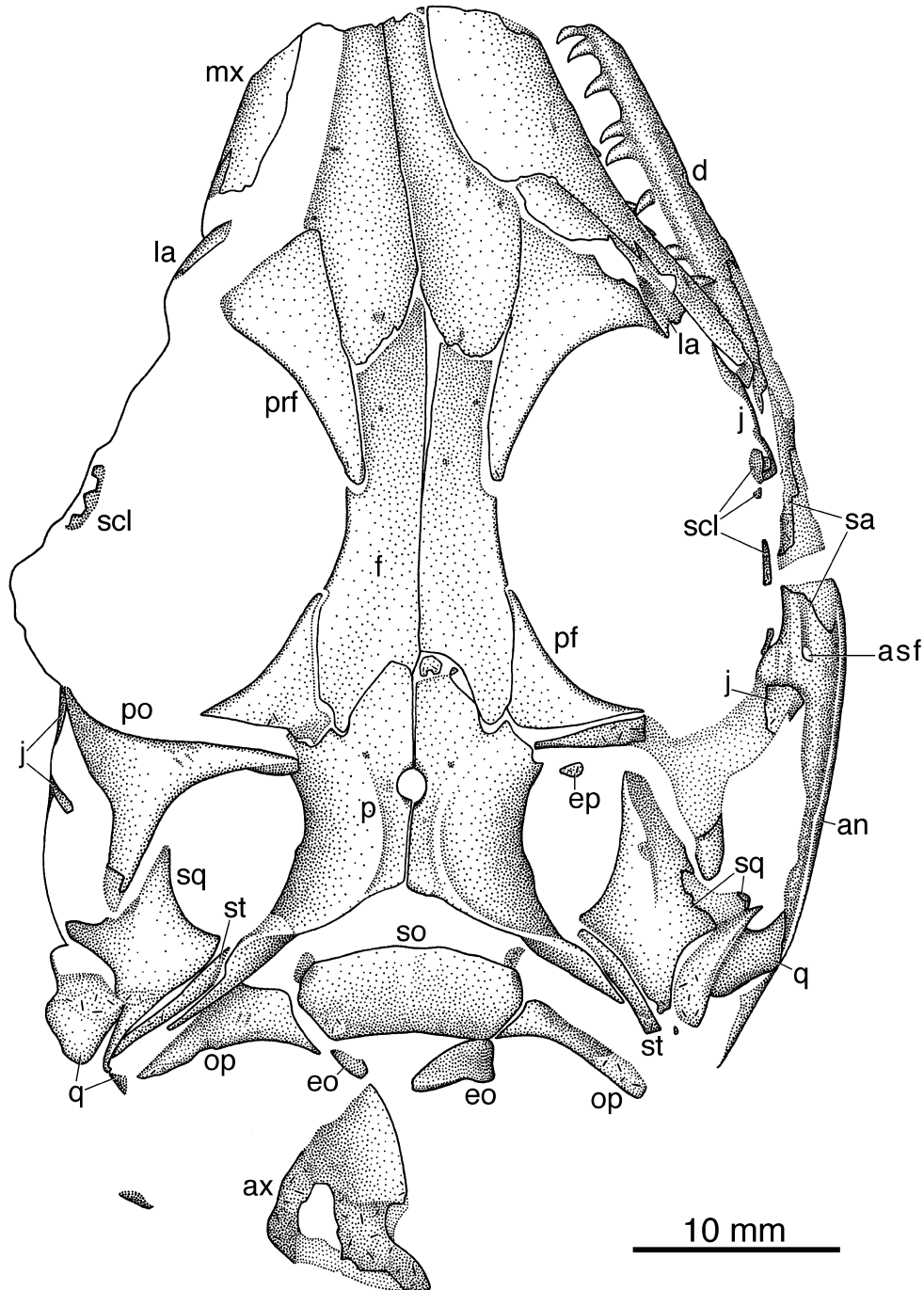
Figure 7. *Prolacerta broomi*, BP/1/3575. Skull and axis in dorsal view.

anterior process is overlain laterally by the maxilla, such that anteriorly the jugal is very narrowly exposed in lateral aspect near its contact with the lacrimal.

The squamosal is a roughly cruciform element (Figs 1, 3, 4, 6–8). It has an anterior process that underlies the postorbital, a ventral process that overlies much of the quadrate and the dorsal end of the quadratojugal, and dorsal and posterior processes that extend towards and contact the supratemporal. The ventral process is very slender in all specimens, and it appears to be particularly elongate in BP/1/5375 (Fig. 8A). The ventral (or anteroventral) process does not contribute to the quadrate foramen, being separated from it by the underlying quadratojugal. The
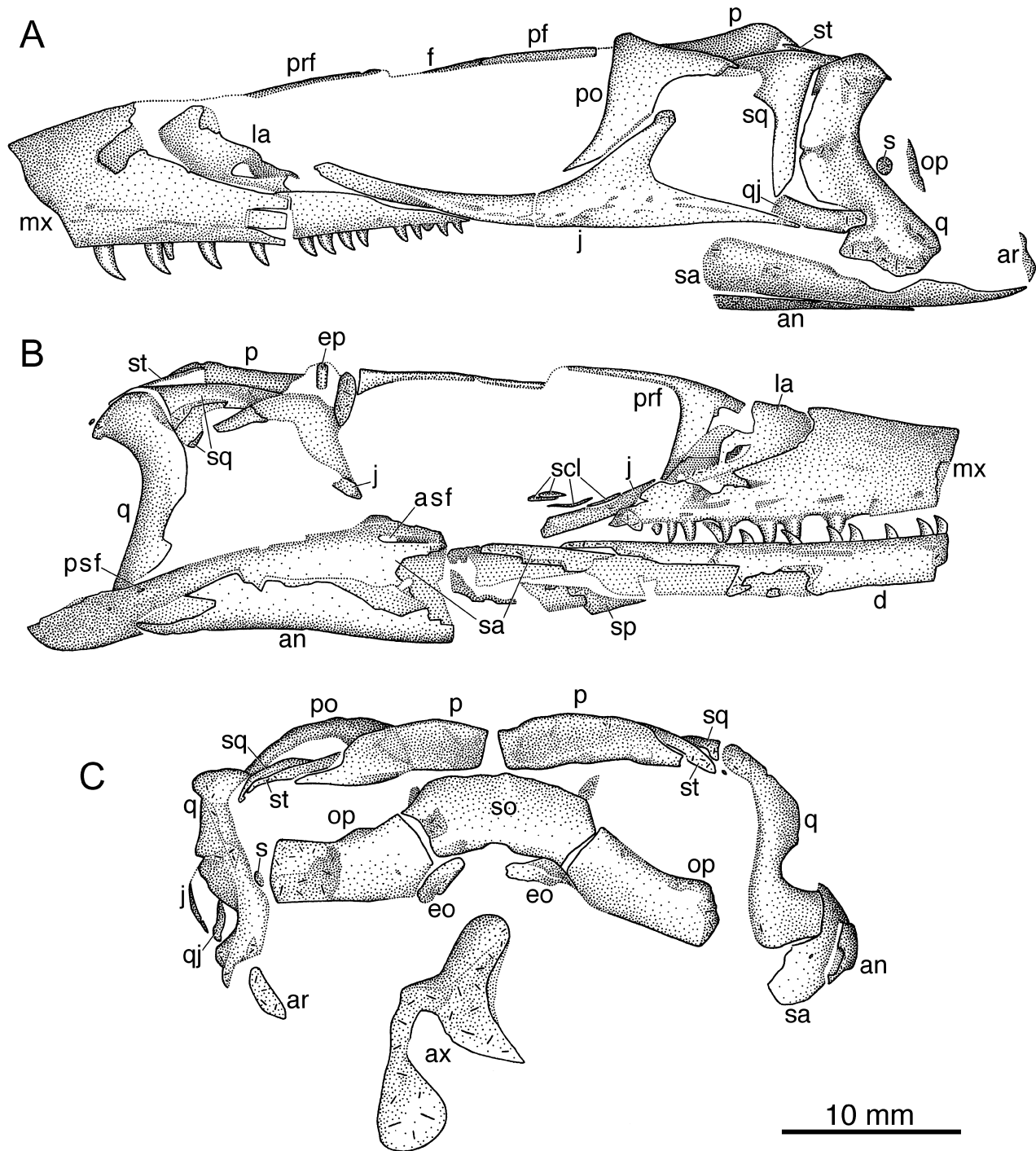
Figure 8. *Prolacerta broomi*, BP/1/3575. Skull in left lateral (A), right lateral (B) and occipital (C) views.

posterior margin of the squamosal is embayed for the reception of the quadrate, the dorsal end of which is completely roofed over by the posterior process of the squamosal. The posteromedian margin of the squamosal has a shallow shelf for the reception of the supratemporal.

Evans (1980) was unable to confirm the presence of the supratemporal in the specimens of *Prolacerta* available to her, but both BP/1/471 and BP/1/5375 establish the presence of this element (Figs 3A, 4, 5, 7, 8). It is a small, splint-like bone nestled between the squamosal and the occipital wing of the parietal. The

supratemporal seems to have been easily lost post mortem, as it is missing in BP/1/5066 and UCMP 37151, each of which have a slightly disarticulated skull roof.

The quadratojugal is a slightly crescentic, strapshaped and vertically orientated bone (Figs 1, 3A, 7). It sheathes the lateral crest of the quadrate and forms the lateral margin of the quadrate foramen. The dorsal end of the quadratojugal underlies the ventral tip of the squamosal.

PALATE

The ectopterygoid, palatine and vomer are poorly represented in our study material. Camp (1945a) and Gow (1975) illustrated and described the vomer as an attenuated triangular element, with long rows of small teeth of denticles that extend anteroposteriorly across the ventral surface. Neither the palatine nor the ectopterygoid of BP/1/5066 (Fig. 6B) add to the accounts by Camp (1945a) and Gow (1975).

Both pterygoids of BP/1/5066 (Fig. 6B) are well preserved and reveal that Camp (1945a) was closer than Gow (1975) in illustrating the exact arrangement of the three palatal tooth clusters. The pattern of the pterygoid dentition suggests that the anterolateral tooth cluster continued smoothly on to the palatine. BP/1/5066 also indicates that the pterygoid has a dorsal lamella of moderate height. There is no scarring evident on the medial surface of the lamella, which corroborates the interpretation that the pterygoids were fully separated at the midline in life. The quadrate flange of the right pterygoid of BP/1/5066 is almost completely exposed in dorsal and ventral views, and it is seen to support a well-developed tympanic (or arcuate) flange. This last feature was illustrated but not described either by Camp (1945a) or Gow (1975).

The epipterygoid is poorly exposed in all our material, and nothing more than the distal tip of the columella can be seen to poke through the matrix investing the supratemporal fenestrae of BP/1/471, BP/1/5066 and BP/1/5375 (Figs 3B, 4, 6, 7, 8B).

All specimens preserve at least one quadrate, permitting a thorough description of this element (Figs 1, 3, 5–8). The quadrates of BP/1/471 are poorly prepared but still show the primary features of this relatively tall bone and its strongly concave posterior margin (Figs 3, 4). The quadrate comprises a main stem (*sensu* Robinson, 1973), which is seen mainly as the posterior crest in lateral view; an anteromedially directed lamella, which is sutured to the quadrate ramus of the pterygoid along its medial surface; a ventral condylar region; and a tympanic crest, which underlies the quadratojugal and the anteroventral process of the squamosal and is notched by a relatively large quadrate foramen. The tympanic crest resembles that of lepidosauromorphs except for the absence of a conch. The dorsal head of the quadrate, where the main stem, tympanic crest and pterygoid lamella converge, fits snugly into an embayment in the posteroventral part of the squamosal. The structure of the condyles is not well exposed in any of the articulated skulls under study by us, and those of the single well-exposed quadrate of BP/1/5066 were damaged by weathering.

BRAINCASE

The account by Evans (1986) obviates a detailed description of the elements of the braincase. In can be noted that the available material confirms several variable features of the braincase of *Prolacerta*. The braincase of BP/1/2675, described and illustrated by Gow (1975), differs in two major respects from those of BP/1/5066 and UCMP 37151. In ventral view, there is a shallow furrow formed between the cristae ventrolaterales of the parabasisphenoid of BP/1/2675, whereas a deep, parabolic depression lies between these cristae in both BP/1/5066 (Fig. 6B) and UCMP 37151 (Camp, 1945a: pl. 1). The cristae ventrolaterales of BP/1/2675 form thin ridges anteriorly that conceal the foramina for the carotid foramina in ventral aspect, whereas these cristae in the other two specimens are low and rounded, and the ventral openings for the internal carotid arteries are clearly visible at the bases of the basipterygoid processes. In BP/1/2675, the exoccipitals and basioccipital are indistinguishably fused to each other, as are the supraoccipital and the opisthotics, whereas in BP/1/5066 (Fig. 6) they remain distinct elements. This is not a simple ontogenetic difference because, as estimated from the width of the parasphenoid across the basipterygoid processes, the braincase of BP/1/5066 is approximately 5% larger than that of BP/1/2675. Only in BP/1/2675 do the exoccipitals meet dorsally and exclude the supraoccipital from the dorsal margin of the foramen magnum, as in the archosauriform *Proterosuchus*; there is no evidence of such contact in BP/1/5066 or in BP/1/5375.

MANDIBLE

In most of our material the mandible is exposed only in lateral aspect. The primarily medial elements are seen only where their edges extend slightly beyond those of the lateral elements. In the case of the splenial, it is seen as an attenuated triangle lying ventral to the contact between the dentary and the angular. The coronoid appears as a narrow splint atop the coronoid eminence in lateral aspect. The prearticular is visible only posteriorly where it, along with the caudal

end of the surangular, sheaths the ventral face of the articular.

Gow (1975) counted 27 tooth positions in the disarticulated dentary of BP/1/2675. There are at least 25 and 26 positions, respectively, in the left and right dentaries of BP/1/471 (Fig. 3), and approximately the same number in the right dentary of UCMP 37151 (Fig. 1B). In the latter specimen, the lateral surface of the dentary is preserved well enough to show the infralabial foramina and even short longitudinal channels, similar to those on the maxillae. Neither Gow (1975: fig. 20) nor Camp (1945a: fig. 1) restored the relationships of the dentary with the postdentary bones correctly; Gow exaggerated the length of the contact with the surangular and at the expense of that with the angular, whereas Camp showed the exact opposite. The preservation of the mandible in BP/1/471 (Fig. 3B) suggests that the dentary had a narrow labial exposure extending backwards almost to, if not actually reaching, the coronoid.

In lateral view, the surangular and the angular meet along a broadly meandering suture (Figs 1, 3). The dorsal edge of the former element forms a shallow coronoid eminence that decreases in height posteriorly and merges with the main body of the bone just anterior to the jaw joint. The posterior end of the surangular sheaths the lateral surface of the articular almost to the posterior tip of the retroarticular process. In UCMP 37151, the posterior end of the right angular is missing and shows that the surangular extends ventrally to make a firm contact with the prearticular. Unlike the dentary the labial surface of the surangular is devoid of sculpturing, but there is a conspicuous, anteriorly opening foramen immediately ventral and posterior to the contact with the coronoid bone (Figs 1, 7, 8; not seen in BP/1/471 because its presence is obscured by polishing as a result of preparation). This opening appears to be the anterior surangular foramen of *Proterosuchus* (Welman, 1998: fig. 4) and other crown-group diapsids (e.g. Oelrich, 1956; Madsen, 1976). The surangular of *Prolacerta* also shares with *Proterosuchus* and other crown-group diapsids the presence of a posterior surangular foramen. In *Prolacerta*, this is a relatively small lateral opening that lies close to the dorsal margin bordering the articulating facet (Figs 3A, 8B).

The angular is the longest mandibular element, extending from the base of the retroarticular process to the approximate midpoint of the dentary (Figs 1, 3, 8). Posteriorly, the angular has a deeply overlapping suture with the surangular. Judging from the sutural pattern on the right mandibular ramus of UCMP 37151, the latter element probably excludes the former from more than half of the floor of the adductor fossa. Gow (1975) remarked that there is an incipient 'angular process', but the well-preserved angulars of the available specimens have gently curved ventral margins in lateral aspect.

The articular is not well exposed in any of the available specimens. Even the articulars of UCMP 37151, which was illustrated as preserving complete elements by Camp (1945a: pl. 1), are now missing. In BP/1/471, only the left articular is visible (Fig. 3A) and what is exposed resembles that illustrated by Gow (1975: fig. 20) in having an abbreviated, laterally aligned retroarticular process.

CRANIAL KINESIS IN *PROLACERTA*: A RECONSIDERATION

Gow (1975) postulated that, although not as kinetic as the skulls of squamate reptiles, the skull of *Prolacerta* approached a lizard-like structure in the absence of a lower temporal bar and could have had a limited degree of kinesis. His discussion focused on the mobility of the quadrate (streptostyly), with minor consideration of kinesis among the neighbouring dermal bones. According to Gow (1975), the articular region of the quadrate could move slightly anteriorly with respect to the dorsal end, which articulated in the concave posteroventral emargination of the squamosal. Although not as extensive as streptostyly in squamates, the movement of the quadrate in *Prolacerta* postulated by Gow (1975) would have facilitated a slightly more posteriorly directed bite force for the lower marginal dentition. In support of this idea, Gow (1975: 113) noted that the arcs he ascribed to the tip of the mandible during 'normal' and 'streptostylic' jaw closure together described the shape of generalized marginal tooth of a carnivorous 'thecodont'.

Although this hypothesis is intriguing, Evans (1980: 244) argued that the ventral ramus of the squamosal of *Prolacerta* 'hugged the quadrate and held it firmly to the skull'. The new, better preserved specimens that were unavailable to Gow (1975) support Evans's (1980) contention that streptostyly was highly unlikely in *Prolacerta*. The squamosals of the specimens available to Gow (1975) are damaged and do not demonstrate the full range in the size of the ventral process. BP/1/5375 indicates that the ventral process of the squamosal could extend as far ventrally as the dorsal margin of the quadrate foramen. As the former feature is closely coupled with the quadrate tympanic process, any protrusion of the quadrate would result in the ventral tip of the squamosal entering the region presumably occupied by the periphery of the tympanum, an action that hardly seems possible. Indeed, the nature of the contact between the squamosal and the quadrate, where the latter fitted into a moderately deep embayment between the posterodorsal and ventral processes of the squamosal, would have effectively

limited any possible pivoting by the quadrate upon its proximal end.

Gow (1975) argued that the entire temporal region in *Prolacerta* was lightly built and would have permitted compensatory movements in association with motion of the quadrate. For instance, he described the contact between the postorbital and the squamosal as 'loose', permitting both anteroposterior and dorsoventral movement. Gow also proposed that the contact between the postorbital and the postfrontal would have allowed the former to move lateral to the latter. He further argued that the curved nature of the contacts between the postorbital and the jugal and between the latter bone and the maxilla would have allowed sliding actions. However, the contact between the postorbital and the squamosal is well developed, because the posterior ramus of the former lies in a moderately deep and long lateral furrow on the anterior process of the squamosal. The suture between the postorbital and the postfrontal is a relatively deep, butt-like contact, which would seem poorly suited to facilitate even 'slight' sliding. If Gow (1975) was correct in identifying sliding contacts among the circumorbital elements, we would expect that postorbitals and jugals would be rarely preserved in the otherwise complete skulls of *Prolacerta*. The observation that these elements are invariably preserved in their expected positions, and frequently in normal contact with neighbouring bones in even slightly disarticulated skulls (e.g. BP/1/5375), indicates that the circumorbital bones of *Prolacerta* were firmly sutured to each other.

Finally, Gow (1975) proposed that slight flexure of the long snout would have been made possible by the thinness of the nasals. This hypothesis is just as unlikely as the one proposing streptostyly and kinesis for the posterior bones of the skull roof. The nasal does not appear to be so thin that it would have been subject to slight bending during biting. Furthermore, it shares an extensive overlapping suture with the dorsal lamella of the maxilla (as noted by Gow), and, in combination with the thickness of the nasal, this contact would have precluded flexure of the roof of the snout. We conclude that the skull of *Prolacerta* shows no clear evidence of potential cranial kinesis.

PHYLOGENETIC ANALYSIS

Dilkes (1998) hypothesized that *Prolacerta* was the closest relative of *Proterosuchus* and *Euparkeria*, which together represented Archosauriformes in his study. This was an unexpected result of his analysis because, until then, *Prolacerta* was invariably classified by most authors with a number of other Permo-Triassic diapsids in a group called Prolacertiformes (or Protorosauria). The sister-group relationship between

Prolacerta and Archosauriformes was one of the better supported groupings in Dilkes's (1998) analysis, requiring six additional steps to collapse in a Bremer analysis.

Our reappraisal of the skull of *Prolacerta* has necessitated recoding of several of Dilkes's (1998) characters for this genus, and has also generated two additional characters for phylogenetic consideration (see below). These changes have the potential to alter the position of *Prolacerta* with respect to Archosauriformes. For example, Benton (1985) cited the presence of a downturned premaxilla and distally expanded haemal spines in support of a sister-group relationship between *Prolacerta* and *Proterosuchus*. Dilkes (1998) accepted the latter character but dismissed the former, remarking that the premaxilla of *Prolacerta* was not turned downwards as in *Proterosuchus*. However, our present study confirms Benton's (1985) claim that the premaxilla is indeed downturned in *Prolacerta*, although not to the degree seen in *Proterosuchus*.

We reappraised the characters used by Dilkes (1998) in order to incorporate the new anatomical information as a result of our reappraisal of the skull of *Prolacerta*. We reinterpreted some of Dilkes's characters, and we included brief descriptions of two new characters. Because we are interested primarily in the relationships of *Prolacerta*, we deleted the more derived rhynchosaurian taxa (*Rhynchosaurus*, *Hyperodapedon*, *Stenaulorhynchus* and *Scaphonyx*), retaining only *Mesosuchus* and *Howesia* as representatives of Rhynchosauria; the deletion of the four taxa renders 16 of Dilkes's (1998) characters uninformative (nos. 1, 9, 13, 16, 33, 41, 54, 60, 62, 63, 70, 71, 72, 111, 112 and 118). We reran this modified version of Dilkes's (1998) original data matrix, with all characters unweighted and unordered, using PAUP 4.0b10 (Swofford, 2002). The following paragraphs outline our modifications to the data matrix of Dilkes (1998).

FORM OF SUTURE BETWEEN PREMAXILLA AND MAXILLA ABOVE DENTIGEROUS MARGIN (17)

This character is equivalent to Juul's (1994) character 37, which equated the small opening interrupting the suture between the premaxilla and the maxilla in *Proterosuchus* and Erythrosuchidae with the subnarial foramen of saurischian dinosaurs. Juul (1994) also identified subnarial foramina in Prestosuchidae and *Postosuchus* among the taxa that he included in his analysis. Dilkes's (1998) definition of this character suggests that he does not agree with Juul's (1994) broad homologization of 'subnarial foramina' among archosauromorphs, and we concur. The opening in *Prolacerta* issues from a longitudinal channel in the maxilla, and exits only laterally at the suture with the premaxilla. Welman's (1998) illustrations suggest that

the same condition is present in *Proterosuchus*, and we have identified this foramen in *Protorosaurus* (pers. observ. on cast). By contrast, the subnarial foramen of saurischians is present in the suture between the maxilla and the premaxilla, and it clearly does not originate from a channel in the maxilla (Madsen, 1976; Brochu, 2003). The openings in basal archosauromorphs and in saurischians are not comparable. Indeed, optimization of 'subnarial fenestra or foramen' on to Juul's (1994: fig. 1) cladogram indicates that this feature in saurischians was acquired independently from that in more basal archosauromorphs.

Some fossil and extant squamates (e.g. *Chamops*: Gao & Fox, 1996; *Eolacerta*: Müller, 2001; *Ctenosaura* sp., *Cyclura cyclura*, *Iguana iguana*, *Lacerta* sp., *Phrynosoma asio*, *Sceloporus clarkii*, *Tupinambis teguixin*, *Uromastyx* sp.) feature enlarged supralabial foramina that may be homologous with the anterior maxillary foramen of *Prolacerta*, whereas others do not (e.g. *Cnemidophorus tigris*, *Crotaphytus collaris*, *Eumeces laticeps*, *Heloderma suspectum*, *Laudakia stellio, Varanus niloticus*). Accordingly, we have recoded Squamata as polymorphic with respect to this character.

POST-TEMPORAL FENESTRA (53)

Dilkes (1998) regarded large post-temporal fenestrae as the plesiomorphic character-state and small fenestrae as the apomorphic state. We appreciate the difficulties of defining such a subjective character in discrete terms, but we disagree that the fenestrae of both *Mesosuchus* and *Howesia* can be interpreted as 'large' when compared with other taxa included in his analysis. For example, the post-temporal fenestra for these two genera as restored by Dilkes (1995, 1998) are closely comparable in relative size to those restored for *Prolacerta* by Gow (1975: fig. 12). In all three taxa, the post-temporal fenestra is approximately the same size as the foramen magnum, whereas those in the taxa coded by Dilkes (1998) as large (e.g. *Hyperodapedon*; Chatterjee, 1974) have post-temporal fenestrae that are several times larger than the foramen magnum. Accordingly, we have recoded *Mesosuchus* and *Howesia* as '1' for this character.

ANTEROVENTRAL PROCESS OF SQUAMOSAL (34)

Dilkes (1998) distinguished three states for this character: (1) broad ventrally, with distal width approximately equal to dorsoventral height; (2) narrow ventrally, with distal width less than dorsoventral height; and (3) absent. *Prolacerta* and other derived diapsids were coded as having the last character. It is unclear, however, what Dilkes (1998) actually meant

by 'anteroventral process of squamosal' because of the terminology used by some authors and variation in this feature among the taxa under consideration. For example, Evans (1980: fig. 16) labelled an 'anteroventral process' on the squamosal of *Gephyrosaurus* but mentioned only a 'ventral process' in her description of that element. Furthermore, our examination of a specimen of *Youngina* (BP/1/3859) revealed that the ventral portion of the squamosal in this diapsid is like that of *Prolacerta* in being a ventrally narrowing flange, except that it is relatively broader anteroposteriorly in the former; it is difficult to determine if the distal width of the ventral process is less than the dorsoventral height in *Youngina* because there is no clear demarcation between the anterior margin of the ventral process and the ventral margin of the anterior process that contacts the postorbital. We reinterpret this character as referring to the form of the ventral process of the squamosal, rather than to an 'anteroventral process', and we see no need to code the condition in *Youngina* as different from those in related taxa, and those coded as '2' by Dilkes (1998) are recoded here as '1'. As no terminal taxon in Dilkes's (1998) analysis entirely lacks a ventral process of the squamosal, his derived state 2 for this character ('anteroventral process absent') is deleted.

TOOTH IMPLANTATION (55)

Camp (1945a) described the tooth implantation in *Prolacerta* as 'pleurothecodont', whereas Gow (1975: 100) described the implantation as thecodont. Some workers (e.g. Motani, 1997) equate 'pleurothecodonty' with subthecodonty, which was the condition coded for *Prolacerta* by Dilkes (1998). Camp's (1945a) assessment was based on UCMP 37151, in which only the premaxillary dentition can be observed in views other than strictly labial, but we feel this limited exposure of the lingual area of a dentigerous element is not sufficient for a thorough identification of tooth implantation in *Prolacerta*. We can eliminate the possibility of thecodont implantation in *Prolacerta* because, despite their relatively deep implantation, the teeth are clearly ankylosed into their sockets by bone of attachment (i.e. there is no clear demarcation between the teeth and the alveolar portion of the bone, as in living crocodilians). Gow's (1975) description of BP/1/2675 shows clearly that although the teeth of *Prolacerta* are ankylosed to the jaw, the teeth are set in relatively deep sockets. Chatterjee (1974: 230) called this type of tooth implantation 'ankylothecodont'. However, we use additional evidence in support of our identification of ankylothecodont implantation in *Prolacerta*. For instance, the manner of tooth replacement is intimately tied to implantation, and in tetrapods exhibiting subthecodont implantation, the replacement teeth

first appear in resorption pits, which manifest as excavations in the lingual wall of the alveolar portions of dentigerous elements (e.g. Modesto, 1996). In *Prolacerta*, the lingual walls of the tooth-bearing bones are not modified during tooth replacement; replacing teeth appear within the sockets of the teeth that have been shed (Gow, 1975: fig. 32) and thus the marginal teeth can be considered to be 'alveolarized' (Rieppel, 2001). This method of tooth replacement is shared with archosaurs, which are characterized by thecodont implantation. The marginal dentition of *Prolacerta* is essentially identical to that of archosaurs except for the manner in which the teeth are held in place.

RATIO OF LENGTHS OF METATARSALS I AND IV (123)

Dilkes (1998) distinguished three states: the plesiomorphic condition was defined as metatarsal I less than 0.4 the length of metatarsal IV, a first derived state with the former between 0.3 and 0.4 the length of the latter, and a second derived state with the former less than 0.3 the length of the latter. Our re-examination largely corroborates Dilkes's (1998) breakdown of character-states for this feature. Because we are not using *Hyperodapedon* and *Stenaulorhynchus*, Dilkes's state 2 does not apply in our analysis. We note, however, that *Trilophosaurus*, with a figure of 0.41 (Gregory, 1945), lies very close to the figure of 0.4 that Dilkes (1998) used to separate the primitive state from the first derived state. It would appear that the figure used by Dilkes (1998) was an arbitrary one. Alternatively, a figure ranging within 0.42–0.45 (*Petrolacosaurus* at 0.47 would represent the revised 'low end' of the range for the plesiomorphic condition) could have been used to separate these states 0 and 1, which would result in having to code *Trilophosaurus* as derived state 1 instead of state 0. The result of this alternative coded state for *Trilophosaurus* is discussed below. See Appendix for data on this character used in our analysis.

RATIO OF LENGTHS OF DIGITS III AND IV (124)

Dilkes (1998) recognized three states: the primitive condition – length of pedal digit III 0.8 or less than that of digit IV, and two derived conditions – length of digit III between 0.8 and 0.9 that of digit IV (derived state 1) and length of digit III over 0.9 that of digit IV (derived state 2). Our reanalysis of this character suggests that recognition of only two character states is supported by the data. The first has the length of digit III 0.64–0.81 the length of digit IV, and represents the primitive condition (the outgroup taxon *Petrolacosaurus* forms the low end of this range). The second condition has the length of digit III about 1.00–1.15 that

of digit IV. This condition is the derived state and it is found only in *Megalancosaurus*, *Langobardisaurus* and *Drepanosaurus* among the taxa used in our analysis. See Appendix for data on this character used in our analysis.

ANTERIOR SURANGULAR FORAMEN (145, NEW CHARACTER)

Prolacerta has a conspicuous, anteriorly opening foramen and groove on the lateral surface of the surangular, at the base of the coronoid eminence. It is strongly reminiscent of the anterior surangular foramen of *Allosaurus* (Madsen, 1976) and other archosaurs, and, in the absence of evidence to the contrary, we regard the opening in *Prolacerta* as homologous. Among the archosauromorph taxa included in our analysis, only *Proterosuchus* (Welman, 1998) and *Euparkeria* (Ewer, 1965) share the presence of an anterior surangular foramen. This opening is present in many squamates, such as *Ctenosaura* (Oelrich, 1956), but it appears to be absent in *Gephyrosaurus* (Evans, 1980).

Coding for the data matrix of Dilkes (1998) is as follows: taxa coded as primitive (0): *Petrolacosaurus*, *Youngina*, *Gephyrosaurus*, *Howesia*, *Mesosuchus* and *Champsosaurus*; taxa coded as having the derived state (1): Squamata, *Prolacerta*, *Proterosuchus*, *Euparkeria* and *Cteniogenys*. The remaining taxa are coded as '?'.

POSTERIOR SURANGULAR FORAMEN (146, NEW CHARACTER)

The surangular in *Prolacerta*, *Proterosuchus* and *Euparkeria* has a small foramen on the lateral surface at the level of the jaw joint. The foramen in these three taxa occupies the same position as the posterior surangular foramen of later archosauromorphs (Madsen, 1976), and, in the absence of evidence to the contrary, we regard these openings as homologous. Squamates (e.g. Oelrich, 1956) and *Gephyrosaurus* (Evans, 1980) also feature a posterior surangular foramen.

Coding for the data matrix of Dilkes (1998) is as follows: taxa coded as primitive (0): *Petrolacosaurus*, *Youngina*, *Howesia*, *Mesosuchus* and *Champsosaurus*; taxa coded as having the derived state (1): *Gephyrosaurus*, Squamata, *Prolacerta*, *Proterosuchus* and *Euparkeria*. The remaining taxa are coded as '?'.

ADDITIONAL CODING CHANGES

During the course of this study we found it necessary to make the following additional changes to codings in Dilkes's (1998) data matrix. *Prolacerta* has been recoded as '0' for characters 14, 73 and 79, and recoded
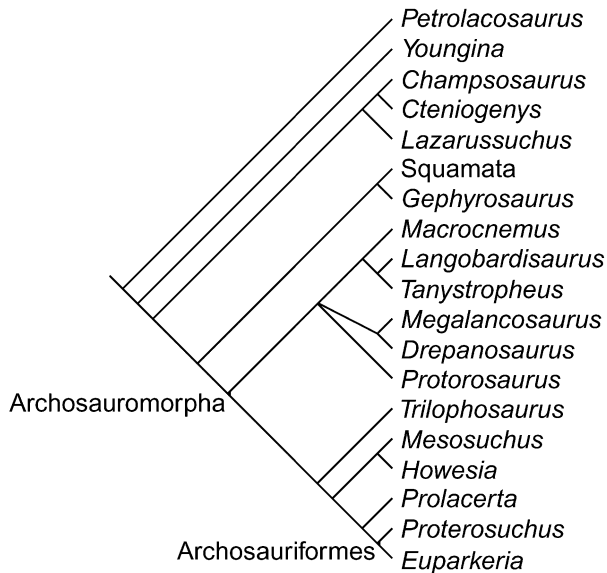
Figure 9. Strict consensus of the two shortest trees discovered in a PAUP analysis of a modified version of the data matrix published by Dilkes (1998). Both trees have a length of 310 steps, a consistency index (excluding uninformative characters) of 0.50 and a rescaled consistency index of 0.32.

as '1' for character 6. Based on new data provided by Reisz *et al.* (2000), *Youngina* is recoded as '0' and '1' for characters 22 and 24, respectively. *Champsosaurus* (Erickson, 1972) has been recoded as '1' for character 19. *Langobardisaurus* (Renesto & Dalla Vecchia, 2000) and *Trilophosaurus* (Sues, 2003) are recoded as '1' and '2', respectively, for character 4.

RESULTS AND DISCUSSION

Invoking the branch-and-bound search option of PAUP for analysing the modified version of the data matrix from Dilkes (1998), we recovered two most parsimonious trees, the consensus of which is shown in Figure 9. These trees do not differ significantly from the topologies of the two most parsimonious trees found by Dilkes (1998), except that tanystropheid interrelationships are now fully resolved, but the position of *Protorosaurus* is now unresolved with respect to tanystropheids and drepanosaurids. Coding *Trilophosaurus* as '1' for character 123 does not change tree topology; this additional modification adds one extra step to tree length and alters the other tree statistics very slightly.

The sister-group relationship between *Prolacerta* and Archosauriformes remains one of the most stable groupings among basal archosauromorph taxa. Collapsing this clade required six extra steps in the

Bremer analysis conducted by Dilkes (1998), whereas five extra steps are required in the present analysis. Most of the other neodiapsid clades are more poorly supported, requiring only 1–4 extra steps to collapse. The well-supported sister-group relationship between *Prolacerta* and Archosauriformes corroborates Dilkes's (1998) conclusion that Prolacertiformes (*s.l.*) is a paraphyletic group.

The clade *Prolacerta* + Archosauriformes will eventually require a name, and both Prolacertilia (Huene, 1940) and Prolacertiformes (Camp, 1945b) would appear to be available names. The former nomen has seen slightly less usage (e.g. Watson, 1957; Kuhn-Schnyder, 1962; Kitching, 1977; Tatarinov, 1978; Rieppel & Gronowski, 1981) compared with the latter (e.g. Romer, 1966; Benton, 1985; Evans, 1986; Benton & Allen, 1997; Jalil, 1997; Renesto & Dalla Vecchia, 2000). However, both have been used to denote a small group of basal diapsids, and we consider it problematical to reapply these terms elsewhere in the diapsid crown-group. Accordingly, we do not name the clade *Prolacerta* + Archosauriformes at this time. Similarly, Protorosauria, which has been used as an alternative name for taxa generally grouped under Prolacertiformes, might be used as the nomen for the clade comprising *Protorosaurus*, drepanosaurids and tanystropheids. However, several of these 'prolacertiform' or 'protorosaurian' taxa will soon be restudied (A. Gottmann, pers. comm.; O. Rieppel, pers. comm.), and these revisions would serve as better venues for defining and naming archosauromorph clades.

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REFERENCES

Bartholomai A. 1979. New lizard-like reptiles from the Early Triassic of Queensland. *Alcheringa* **3:** 225–234.

Benton MJ. 1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society* **84:** 97–164.

Benton MJ, Allen JL. 1997. *Boreopricea* from the Lower Triassic of Russia and the relationships of the prolacertiform reptiles. *Palaeontology* **40:** 931–953.

Brinkman D. 1981. The origin of the crocodiloid tarsi and the interrelationships of thecodontian archosaurs. *Breviora* **464:** 1–23.

Brochu CA. 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Society of Vertebrate Paleontology Memoir* **7:** 1–138.

Broom R, Robinson JT. 1948. Some new fossil reptiles from the Karroo beds of South Africa. *Proceedings of the Zoological Society of London B* **118:** 392–407.

Camp CL. 1945a. *Prolacerta* and the protorosaurian reptiles. Part I. *American Journal of Science* **243:** 17–32.

Camp CL. 1945b. *Prolacerta* and the protorosaurian reptiles. Part II. *American Journal of Science* **243:** 84–101.

Chatterjee S. 1974. A rhynchosaur from the Upper Triassic Maleri Formation of India. *Philosophical Transactions of the Royal Society of London B* **267:** 209–261.

Chatterjee S. 1986. *Malerisaurus langstoni*, a new diapsid reptile from the Triassic of Texas. *Journal of Vertebrate Paleontology* **6:** 297–312.

Colbert EH. 1987. The Triassic reptile *Prolacerta* in Antarctica. *American Museum Novitates* **2882:** 1–19.

Currie PJ. 1980. A new younginid (Reptilia: Eosuchia) from the Upper Permian of Madagascar. *Canadian Journal of Earth Sciences* **17:** 500–511.

Dilkes DW. 1995. The rhynchosaur *Howesia browni* from the Lower Triassic of South Africa. *Palaeontology* **38:** 665–685.

Dilkes DW. 1998. The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. *Philosophical Transactions of the Royal Society of London B* **353:** 501–541.

Erickson BR. 1972. The lepidosaurian reptile *Champsosaurus* in North America. *Science Museum of Minnesota, Paleontology Monograph* **1:** 1–91.

Evans SE. 1980. The skull of a new eosuchian reptile from the Lower Jurassic of South Wales. *Zoological Journal of the Linnean Society* **70:** 203–264.

Evans SE. 1986. The braincase of *Prolacerta broomi* (Reptilia, Triassic). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **173:** 181–200.

Evans SE. 1988. The early history and relationships of the Diapsida. In: Benton MJ, ed. *Phylogeny and classification of the tetrapods, volume 1: amphibians, reptiles, birds*. Oxford: Clarendon Press, 221–260.

Ewer RF. 1965. The anatomy of the thecodont reptile *Euparkeria capensis* Broom. *Philosophical Transactions of the Royal Society of London B* **248:** 379–445.

Gao K, Fox RC. 1996. Taxonomy and evolution of Late Cretaceous lizards (Reptilia: Squamata) from western Canada. *Bulletin of the Carnegie Museum of Natural History* **33:** 1–107.

Gauthier JA. 1994. The diversification of the amniotes. In: Prothero DR, Schoch RM, conveners. *Major features of vertebrate evolution. Short Courses in Paleontology No. 7*. Knoxville: The University of Tennessee, 129–159.

Gauthier JA, Kluge AG, Rowe T. 1988. Amniote phylogeny and the importance of fossils. *Cladistics* **4:** 105–209.

Gow CE. 1975. The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. *Palaeontologia Africana* **18:** 89–131.

Gregory JT. 1945. Osteology and relationships of *Trilophosaurus*. *University of Texas Publication* **4401:** 273–359.

Groenewald GH, Kitching JW. 1995. Biostratigraphy of the *Lystrosaurus* Assemblage Zone. In: Rubidge BS, ed. *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*. Pretoria: South African Committee for Stratigraphy, Biostratigraphic Series 1: 35–39.

Huene Fv. 1940. Die Saurier der Karroo-, Gondwana- und verwandten Ablagerungen in faunistischer, biologischer, und phylogenetischer Hinsicht. *Neues Jahrbuch für Geologie und Paläontologie, Abteilung B* **83:** 246–347.

Huene Fv. 1946. Die grossen Stämme der Tetrapoden in den geologischen Zeiten. *Biologisches Zentralblatt* **65:** 268–275.

Jalil N-E. 1997. A new prolacertiform diapsid from the Triassic of North Africa and the interrelationships of the Prolacertiformes. *Journal of Vertebrate Paleontology* **17:** 506–525.

Juul L. 1994. The phylogeny of basal archosaurs. *Palaeontologia Africana* **31:** 1–38.

Kitching JW. 1977. The distribution of the Karroo vertebrate fauna. *Memoirs of the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand* **1:** 1–131.

Kuhn-Schnyder E. 1962. Ein weiterer Schädel von *Macrocnemus bassanii* Nopsca aus der anisischen Stufe der Trias des Monte San Giorgio (Kt. Tessin, Schweiz). *Paläontologische Zeitschrift (H. Schmidt-Festband)* 110–133.

Laurin M. 1991. The osteology of a Lower Permian eosuchian from Texas and a review of diapsid phylogeny. *Zoological Journal of the Linnean Society* **101:** 59–95.

Madsen JH Jr. 1976. *Allosaurus fragilis*: a revised osteology. *Utah Geological and Mineral Survey Bulletin* **109:** 1–163.

Modesto SP. 1996. A basal captorhinid reptile from the Fort Sill fissures, Lower Permian of Oklahoma. *Oklahoma Geology Notes* **56:** 4–14.

Motani R. 1997. Temporal and spatial distribution of tooth implantation in ichthyosaurs. In: Callaway JM, Nicholls EL, eds. *Ancient marine reptiles*. San Diego: Academic Press, 81–103.

Müller J. 2001. Osteology and relationships of *Eolacerta robusta*, a lizard from the Middle Eocene of Germany (Reptilia, Squamata). *Journal of Vertebrate Paleontology* **21:** 261–278.

Oelrich TM. 1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). *University of Michigan, Museum of Zoology, Miscellaneous Publications* **94:** 1–167.

Osborn HF. 1903. On the primary division of the Reptilia into

two sub-classes, Synapsida and Diapsida. *Science* **17:** 275–276.

Parrington FR. 1935. On *Prolacerta broomi*, gen. et sp. n. and the origin of lizards. *Annals and Magazine of Natural History* **16:** 197–205.

Reisz RR, Modesto SP, Scott D. 2000. *Acanthotoposaurus bremneri* and the origin of the Triassic archosauromorph reptile fauna of South Africa. *South African Journal of Science* **96:** 443–445.

Renesto S, Dalla Vecchia FM. 2000. The unusual dentition and feeding habits of the prolacertiform reptile *Langobardisaurus* (Late Triassic, Northern Italy). *Journal of Vertebrate Paleontology* **20:** 622–627.

Rieppel O. 2001. Tooth implantation and replacement in Sauropterygia. *Paläontologische Zeitschrift* **75:** 207–217.

Rieppel O, Gronowski RW. 1981. The loss of the lower temporal arcade in diapsid reptiles. *Zoological Journal of the Linnean Society* **72:** 203–217.

Robinson PL. 1967. The evolution of the Lacertilia. *Problèmes Actuels de Paléontologie (Évolution des Vertébrés), Colloques Internationaux du Centre National de la Recherche Scientifique* **163:** 395–407.

Robinson PL. 1973. A problematic reptile from the British Upper Trias. *Journal of the Geological Society* **129:** 457–479.

Romer AS. 1966. *Vertebrate paleontology*, 3rd edn. Chicago: University of Chicago Press.

Sues H-D. 2003. An unusual new archosauromorph reptile from the Upper Triassic Wolfville Formation of Nova Scotia. *Canadian Journal of Earth Sciences* **40:** 635–649.

Swofford DL. 2002. *PAUP*: phylogenetic analysis using parsimony (*and other methods)*, Version 4.0b10. Sunderland, MA: Sinauer Associates.

Tatarinov LP. 1978. Triassic prolacertilians of the USSR. *Paleontological Journal* **12:** 505–514.

Watson DMS. 1957. On *Millerosaurus* and the early history of the sauropsid reptiles. *Philosophical Transactions of the Royal Society of London* **240:** 325–400.

Welman J. 1998. The taxonomy of the South African proterosuchids (Reptilia, Archosauromorpha). *Journal of Vertebrate Paleontology* **18:** 340–347.

Wild R. 1980. Die Triasfauna der Tessiner Kalkalpen. XXIV. Neue Funde von *Tanystropheus* (Reptilia, Squamata). *Schweizerische Paläontologische Abhandlungen* **102:** 1–43.

APPENDIX

RATIO OF LENGTHS OF METATARSALS I AND IV (123)

Values for taxa ascribed to the primitive state: *Trilophosaurus*: 0.41; *Petrolacosaurus*: 0.47; *Protorosaurus*: 0.47; *Macrocnemus*: 0.49; *Uromastyx*: 0.55; *Prolacerta*: 0.57; *Champsosaurus*, 0.58; *Euparkeria*: 0.61; *Tanystropheus*: 0.73–0.79; *Langobardisaurus*: 0.80; *Megalancosaurus*: 0.88; *Drepanosaurus*: 1.03. Values for taxa ascribed to the derived state: *Mesosuchus*: 0.35; *Proterosuchus*: 0.33.

RATIO OF LENGTHS OF PEDAL DIGITS III AND IV (124)

Values for taxa ascribed to the primitive state: *Petrolacosaurus*: 0.64; *Protorosaurus*: 0.73; *Trilophosaurus*: 0.74; *Tanystropheus*: 0.78; *Macrocnemus*: 0.79 (est.); *Uromastyx*: 0.78; *Prolacerta*: 0.81; *Mesosuchus*: 0.82 (est.). Values for taxa ascribed to the derived state: *Megalancosaurus*: 1.03; *Langobardisaurus*: 1.09; *Drepanosaurus*: 1.14.