

A NEW TEMNOSPONDYL FROM THE PERMO-TRIASSIC BUENA VISTA FORMATION OF URUGUAY

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Abstract: A partial skull recovered from conglomerates of the Permo-Triassic Buena Vista Formation in Uruguay belongs to a new species, *Uruiella liminea* gen. et sp. nov. This species is characterized by a broadly triangular skull with laterally projecting posterior corners, rhytidosteid-like dermal sculpturing, and orbits positioned close to the skull margin. *Uruiella liminea* is distinguished from other temnospondyls by a combination of primitive and derived character states, such as the anterior extent of the palatine ramus of the pterygoid, which excludes the ectopterygoid and most of the palatine from the lateral border of the interpterygoid vacuity, and the absence of both tabular horns and otic notches. A phylogenetic analysis places *Uruiella* and the enigmatic Early Triassic *Laidleria* in a clade to which we attach

the family name Laidleriidae. The Plagiosauridae and the Laidleriidae form a clade at the base of Dvinosauria, which is the sister group of a clade that includes Stereospondyli and Archegosauroida. This result is unexpected because *Laidleria* and Plagiosauridae are nested deeply within Stereospondyli in most phylogenies. The sister-group relationship of *Uruiella* and *Laidleria* suggests that a ghost lineage for the latter genus extends down into the earliest Triassic and perhaps even into the Late Permian, which in turn would suggest survivorship of the Laidleriidae through the Permo-Triassic extinction event.

Key words: Dvinosauria, Laidleriidae, Permo-Triassic, Uruguay.

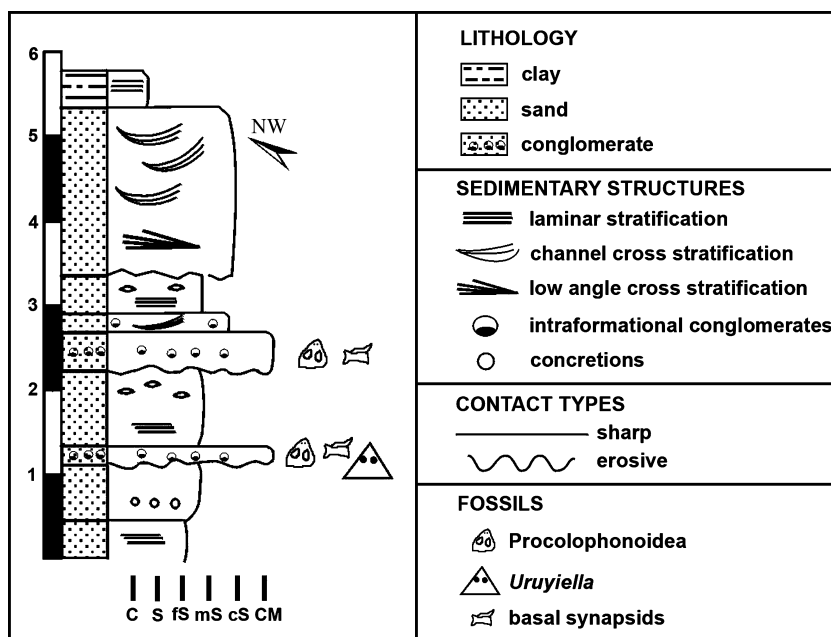
UNTIL recently, almost all known South American Late Permian and Early Triassic temnospondyls were from the Paraná Basin of southern Brazil. Short- and long-snouted rhinesuchoid basal stereospondyls (Barberena 1998; Barberena and Dias 1998) and probable archegosauroids (Price 1948; Dias and Barberena 2001; Dias and Schultz 2003) come from the Brazilian Late Permian Rio do Rasto Formation, whereas rhytidosteids (Lavina and Barberena 1985; Dias-da-Silva *et al.* 2006) and probable lydekkerinids (Barberena *et al.* 1981, 1985) were recovered from the Early Triassic Sanga do Cabral Formation.

Road-cut exposures in Cerro Largo County, Uruguay, have yielded mostly disarticulated postcranial elements and partial skulls of continental tetrapods that together form the Colonia Orozco fauna (Piñeiro and Ubilla 2003). This assemblage may represent part of a Permo-Triassic continental community in South America, because it includes varanopids (Piñeiro *et al.* 2003) and the small reptile *Pintosaurus magnidentis*, a taxon whose closest relatives are procolophonoids from the lowermost Triassic of South Africa and Russia (Piñeiro *et al.* 2004).

Temnospondyls are represented by a fragmentary skull of a dvinosauroid (Marsicano *et al.* 2000) and some mastodonsauroid mandibles (Piñeiro *et al.* 2003; Piñeiro 2004).

In general the record of Late Permian temnospondyls in Gondwana is sparse. Currently, it includes basal stereospondyls such as the terrestrial *Peltobatrachus pustulatus* (Panchen 1959), some rhinesuchids from Africa and the Indian subcontinent (Kitching 1978; Rubidge *et al.* 1995; Werneburg and Schneider 1996), as well as the rhinesuchoids and archegosauroids from South America. Recently, new material has been described from western Africa, which includes more basal forms, including edopoid temnospondyls (Sidor *et al.* 2005). Finally, an advanced Palaeozoic stereospondyl, the putative rhytidosteid *Trucheosaurus major*, has been recovered from the uppermost Permian of Australia (Marsicano and Warren 1998).

The Dvinosauria (*sensu* Yates and Warren 2000) are also represented in Late Permian (Milner and Sequeira 2004) to Early Triassic temnospondyl faunas. In recent phylogenies, Dvinosauria has been regarded as close to either the Stereospondylomorpha within the clade



TEXT-FIG. 1. Stratigraphic section of the Buena Vista Formation, showing the level that yielded *Uruyiella liminea* gen. et sp. nov. Abbreviations: C, clay; S, silt; fs, fine sand; mS, medium sand; cS, coarse sand; CM, conglomerate.

Limnarchia (Yates and Warren 2000) or the Brachyopidea and thus positioned outside of the Stereospondyli (Damiani and Kitching 2003). Until recently, the Dvinosauria were restricted to the Laurasian area of Pangaea (Shishkin 1973), but the discovery of both the Early Triassic tupilakosaurid *Thabanchuia oomie* in South Africa (Warren 1999) and a fragmentary skull related to the *Dvinosaurus*-Tupilakosauridae clade in the Late Permian–Early Triassic Buena Vista Formation of Uruguay (Marsicano *et al.* 2000) extended the geographical distribution of Dvinosauria to the Southern Hemisphere.

Here we describe a new temnospondyl from the Permian–Triassic of southern South America. The specimen consists of a well-preserved partial skull from the basalmost conglomerate levels of the Buena Vista Formation in Uruguay (Text-fig. 1). The phylogenetic relationships of the new taxon are analysed and the palaeobiogeographical implications of the resulting hypothesis are discussed.

GEOLOGICAL AND STRATIGRAPHICAL SETTING

The holotype comes from intraformational conglomerates of the Buena Vista Formation that crop out in Cerro Largo County near Colonia Orozco, c. 10 km north-east of Melo City, Uruguay. The Buena Vista Formation is part of the Paraná Basin infilling, which extends over Uruguay, Argentina, Brazil and Paraguay, and with the underlying Yaguarí Formation constitutes the Yaguarí–Buena Vista Subgroup (Bossi and Navarro 1991), which overlies conformably the Early Permian Melo Formation. The

depositional environment suggested by the Yaguarí–Buena Vista succession is related to the establishment of continental conditions in the basin (Goso *et al.* 2001; Piñeiro 2002). In particular, the Buena Vista Formation is related to alternating high- and low-energy deposition in a flood plain covered by ephemeral braided streams and laterally associated lakes. Semi-arid and dry periods, punctuated by strong, seasonal rains, are the most probable climatic conditions for the deposition of this unit (Goso *et al.* 2001).

The Buena Vista Formation consists of interdigitated fine- to medium-grained red fluvial sandstones, which contain thin intercalated layers of intraformational stream-flood-dominated mudstone conglomerates and red mudstone levels of variable thickness (Bossi and Navarro 1991; Goso *et al.* 2001; Piñeiro and Ubilla 2003). The size of the mud clasts in the conglomerates decreases from bottom to top in the succession, and carbonate nodules are more common in the uppermost levels (Text-fig. 1).

The formation was previously assigned to the Lower Triassic, based mainly on lithological correlation with the Sanga do Cabral Formation in the Brazilian part of the Paraná Basin (Azevedo *et al.* 1985; Ferrando and Andreis 1986; Bossi and Navarro 1991). The Early Triassic age of the Brazilian unit is supported by the presence of *Procolophon* (Barberena *et al.* 1985; Cisneros and Schultz 2002), a temnospondyl of rhytidosteid affinities (Dias-da-Silva *et al.* 2006), and putative non-mammalian cynodonts of thrinaxodontid affinities (Abdala *et al.* 2002), taxa that are components of the Early Triassic *Lystrosaurus* Assemblage Zone of South Africa (Groenewald and Kitching 1995). However, these taxa are conspicuously absent from the Buena Vista Formation, thereby precluding a good

biocorrelation between these units. The formation has yielded vertebrae of the basal synapsid family Varanopidae (Piñeiro *et al.* 2003), a group for which there is no evidence elsewhere of a record younger than the late Middle Permian (according to the standard global chronostratigraphic scale, e.g. Jin *et al.* 1997); a procolophonoid, *Pintosaurus magnidentis*, which appears to have a transitional morphology, particularly in the dentition (Piñeiro and Ubilla 2003; Piñeiro 2004; Piñeiro *et al.* 2004); and mastodontosauroid material that retains several primitive characters that are not present in Triassic representatives of the group (Piñeiro and Ubilla 2003; Piñeiro 2004; Piñeiro *et al.* submitted). Basal synapsids come from the lowermost conglomerate levels that yielded the temnospondyl described in this paper, whereas the mastodontosauroid material and the procolophonoid were recovered from levels that are approximately 10 m higher (Piñeiro 2004). On the basis of the current composition of the Colonia Orozco fauna, it is hard to decide whether the age of the formation is Late Permian or Early Triassic. Recent radiometric data indicate that the underlying Yaguari Formation is 269.8 ± 4.7 Ma or Middle Permian in age (de Santa Ana *et al.* 2006). Thus, it is slightly older than the Late Permian age assigned by Bossi and Navarro (1991). A Middle Permian age was also recently suggested for the correlative Rio do Rasto Formation in Brazil (Cisneros *et al.* 2005) on the basis of palaeontological data. Because the contact between the Yaguari and Buena Vista formations is gradational, a Late Permian age could be inferred for the latter (de Santa Ana *et al.* 2006), at least for the lower part of the unit with the conglomerates that produced the varanopid vertebrae. Accordingly, it is possible that the Buena Vista Formation preserves the Permo/Triassic boundary (PTB) in South America. However, the exact position of the PTB elsewhere has been debated in the recent literature. For example, its position in the Karoo Basin of South Africa has been the subject of several recent papers, which place it either at the bottom of the Palingkloof Member of the Balfour Formation (Ward *et al.* 2000, 2005; Smith and Ward 2001) or at the top of this unit, where it is coincident with a fungal proliferation event that apparently indicates widespread devastation of arboreal vegetation (Steiner *et al.* 2003).

Institutional abbreviations. FC-DPV, Departamento de Palaeontología de Vertebrados, Facultad de Ciencias, Montevideo, Uruguay.

Abbreviations used in the text-figures. ap, alar process of the jugal; aqf, accessory quadrate foramen; ar, ascending ramus of the pterygoid; ec, ectopterygoid; eo, exoccipital; ep, epipterygoid; j, jugal; m, maxilla; p, parietal; pal, palatine; pf, postfrontal; po, postorbital; pp, postparietal; pr, palatal ramus of pterygoid; pt, pterygoid; ptc, pterygoid corpus; q, quadrate; qj, quadratojugal;

qr, quadrate ramus of the pterygoid; sq, squamosal; st, supra-temporal; t, tabular.

SYSTEMATIC PALAEOLOGY

Order TEMNOSPONDYLI Zittel, 1888

Family LAIDLERIIDAE Cosgriff, 1965

Genus URUYIELLA gen. nov.

Derivation of name. After Uruguay, the country in which the specimen was found.

Type species. *Uruiella liminea* sp. nov.

Species included. The type and only known species.

Diagnosis. As for species, because the genus is monotypic.

Uruiella liminea sp. nov.

Text-figures 2–3

Derivation of name. Latin, *limine*, boundary, with reference to the stratigraphic position of the specimen close to the Permo/Triassic boundary.

Holotype. FC-DPV 1598, a partial skull.

Type locality and horizon. Colonia Orozco Town, Cerro Largo County, Uruguay. Lowermost intraformational conglomerates of the Permo-Triassic Buena Vista Formation, Paraná Basin (Text-fig. 1). See Piñeiro *et al.* (2003, fig. 1) for geographical location.

Diagnosis. *Uruiella* is distinguished from all other temnospondyls by the following combination of characters: ornamentation consisting of ridges enclosing small depressions with a small tubercle at the junctions of the ridges; orbits located close to the skull margin; anteroposteriorly elongate bones of the skull roof posterior to the orbits; absence of tabular horns and otic notch; palatine ramus of the pterygoid extended well forward to the most posterior palatine tooth; quadrate ramus of the pterygoid bearing a moderately developed oblique ridge; a trough on the ventral surface of the quadratojugal, forming an ‘overhang’ in occipital view; paraquadrate foramen absent from the posterolateral surface of the quadratojugal; and accessory quadrate foramen present and positioned in the middle part of the ventral quadratojugal trough.

Description

FC-DPV 1598 (Text-figs 2–3) consists of the left, posterior half of a skull, including parts of the skull roof, the palate, and the

occiput. The general shape of the preserved fragment suggests a subtriangular skull, with nearly straight lateral margins, and a pointed snout. The orbits were located close to the lateral margin of the skull table, presumably in the anterior half of the skull roof. The posterior margin of the skull table is gently concave with the posterolateral corners projected beyond this margin. Although somewhat distorted, the skull is markedly shallow. In occipital view (Text-fig. 2E–F) it is very shallow with the quadrate condyle slightly beneath the level of the pterygoid corpus. In the central region, only a fragment of the paroccipital process, preserved partially as an internal mould, and the vertical process of the left exoccipital are preserved. The paroccipital process is medially directed and delimits, along with the vertical process, a relatively small, dorsoventrally flattened post-temporal fenestra.

Dorsal surface of the skull. The bones of the skull roof (Text-fig. 2A–B) are covered with a fine ornament that consists of pitting with small pustules or nodules on the junctions of the crests. The ridges and pits are slightly elongated, particularly over the quadratojugal and the squamosal. Poorly developed sensory canals are partially visible over the postorbital. Even though some of the elements of the skull roof are damaged, the sutures are clear in many places, thus allowing an accurate reconstruction of the bone patterns.

The posterior margin of the left orbit is preserved, suggesting that the orbits were relatively small and oval. All the postorbital bones are remarkably large and anteroposteriorly elongated. In fact, the postorbital, squamosal, quadratojugal, and supra-temporal are each almost twice as long as they are wide. The postfrontal is a relatively large bone that forms the posteromedial border of the orbit (Text-fig. 2A–B). The shape and the relative size of the bones behind the orbit are comparable with that described in the Permian rhytidosteid *Trucheosaurus major* from Australia (Marsicano and Warren 1998). Although the bones of the posterior margin of the table are incomplete, what is preserved strongly suggests that an otic embayment and a tabular horn were absent. Moreover, the absence of the tabular horns can be inferred using the position of the paraoccipital process in relation to the ventral surface of the tabular bone. Dorsally, the tabular has a long oblique suture with the squamosal owing to its posterolateral elongation. This condition was only previously described by Warren (1998) for the South African taxon *Laidleria gracilis* and by Marsicano and Warren (1998) for *T. major*.

Although the posterolateral corner of the skull is slightly damaged, the quadratojugal clearly projects posterolaterally. The gently concave shape of the posterior skull table margin is comparable with the condition observed in both *T. major* (Marsicano and Warren 1998) and *L. gracilis* (Warren 1998). The quadratojugal bears a longitudinal, ventral trough close to its contact with the quadrate, thus forming the lateral overhang described by Yates and Warren (2000, fig. 10) for *Laidleria* and plagiosaurs. Within this trough, there is a foramen (Text-fig. 2C) in the same position as the accessory paraquadrate foramen present in the basal trematosauroid *Benthosuchus sushkini* (Bystrow and Efremov 1940; Damiani and Yates 2003) and the Permian taxon *Peltobatrachus pustulatus* (Panchen 1959). Although the end of the quadratojugal is damaged, it appears

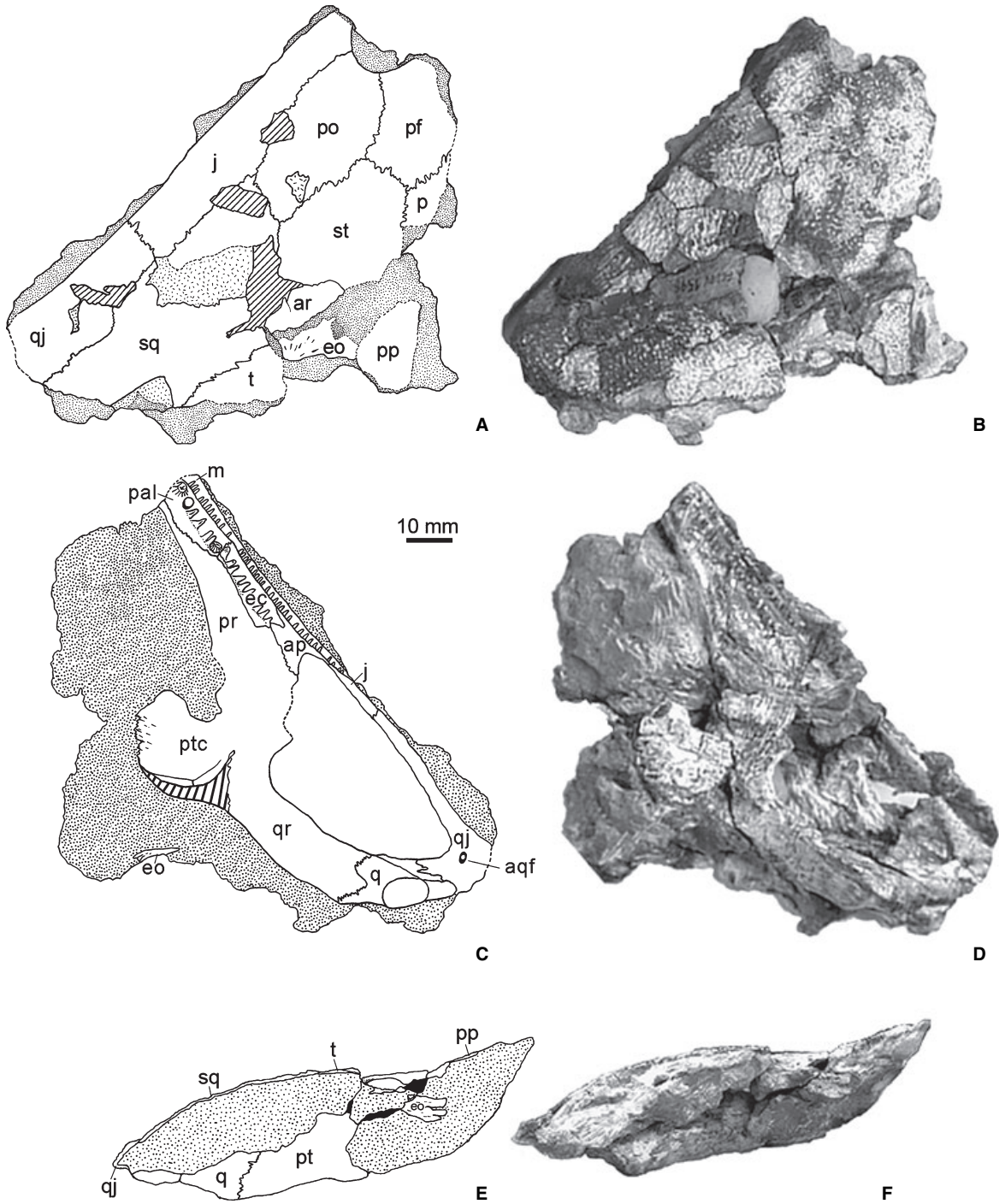
that the paraquadrate foramen is absent from the occipital surface (Text-fig. 2C–D).

Palate. The left pterygoid is the only remnant of the central part of the palate (Text-fig. 2C–D). Ornamentation covers the corpus and the palatine ramus. The corpus appears to be wider than long, but it is broken close to its presumed suture with the parasphenoid. The palatine ramus is anteriorly elongated, and excludes the ectopterygoid and the preserved part of the palatine from the border of the interpterygoid vacuity. The ventral surface of the palatine ramus is ornamented close to the corpus. Anterior to this, the surface of the ramus is covered by a large, raised shagreen of denticles that extends to the level of the ectopterygoid-palatine suture. Anterior and medial to the denticles, the remaining surface of the ramus is smooth. Although the lateral border of the palatine ramus is partially broken, its shape suggests that it might have projected posterolaterally within the subtemporal vacuity as a posterolateral flange ('pterygoid flange' of Watson 1962). This vacuity is anteroposteriorly elongated and medially limited by a long, narrow quadrate ramus of the pterygoid, which contacts posterolaterally the medial surface of the quadrate. The quadrate ramus of the pterygoid is shallow and smoothly upturned to form the ascending ramus of the pterygoid. The proximal portion of the quadrate ramus and the ascending ramus of the pterygoid appear to contact the skull roof, such that there is no palatoquadrate fissure. Ventral to the ascending lamina, the medial surface of the quadrate ramus bears a shallow crest, the oblique ridge ('crista obliqua' of Bystrow and Efremov 1940), which extends posteriorly to the level of the suture with the quadrate. The distal portion of this crest forms the ventral limit of a horizontal groove that extends to the base of the posterior end of the ascending ramus. The occiput is broken into three pieces, making it possible to see the internal structure of the ascending ramus of the pterygoid (Text-fig. 3). In dorsal view, the proximal half of the ramus is smoothly concave. It curves dorsally and backwards to contact the ventral surface of the skull roof (Text-fig. 3C–D). The end of the ascending ramus above the pterygoid corpus has a dorsoventral thickening similar to, although less developed than, the dorsal column that was described as a derived chigutisaurid character by Warren and Hutchinson (1983), but also appears to be present in several other stereospondyl groups (Yates and Warren 2000).

The ectopterygoid is a narrow, elongated bone bearing a row of nine laterally compressed teeth that continues onto the palatine, where six teeth are preserved. The ectopterygoid and palatine teeth are slightly larger than the maxillary teeth. Tusks are absent from both series.

The subtemporal vacuity is bounded anteriorly by the alar process of the jugal and laterally by the maxilla, jugal and quadratojugal, which also forms the lateroposterior corner of the vacuity. The ectopterygoid and the preserved part of the palatine do not contribute to the lateral border of the interpterygoid vacuity because of the anterior elongation of the palatine ramus of the pterygoid.

Part of the left epipterygoid is attached to the anterior border of the ascending ramus and, although not complete, is clearly expanded both proximally and distally (Text-fig. 3A–B). It is



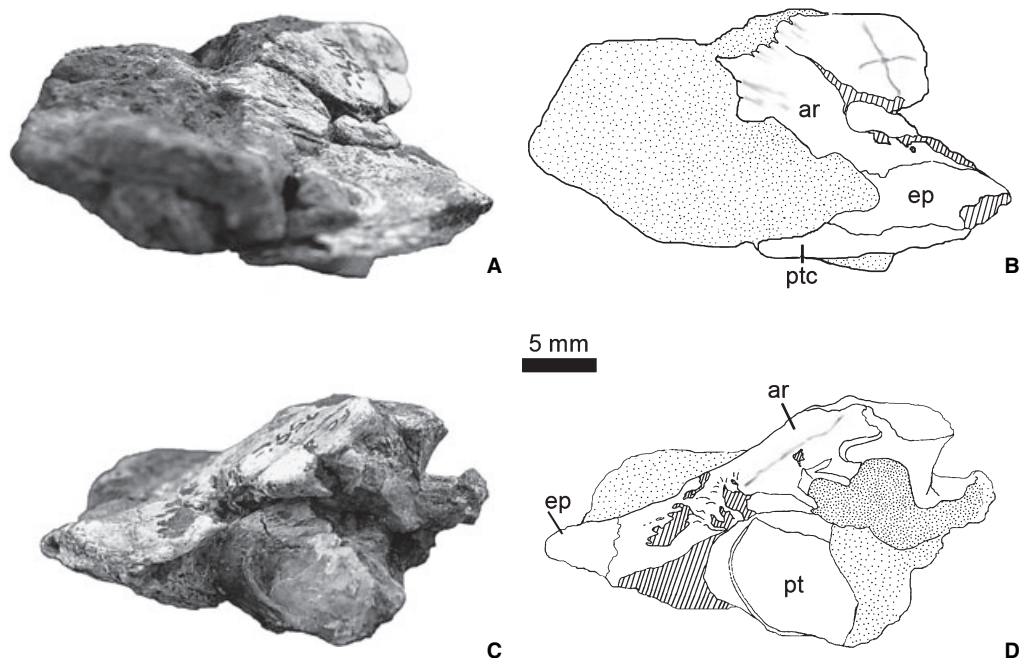
TEXT-FIG. 2. *Uruyiella liminea* gen. et sp. nov., FC-DPV 1598, from the Upper Permian–Lower Triassic of Uruguay. Skull in A–B, dorsal, C–D, ventral, and E–F, occipital views; interpretive drawings and photographs.

horizontally orientated and follows the marked curvature of the ascending ramus of the pterygoid.

The left quadrate is a stout bone that is partially visible ventrally and medially on the occipital surface of the cheek. The quadrate condyle is smoothly ‘screw-shaped’, with an antero-posteriorly orientated portion and a smaller one nearly perpendicular to the other.

PHYLOGENETIC ANALYSIS

In order to determine the affinities of *Uruyiella* to other temnospondyls in a phylogenetic context, we constructed a taxon-character matrix of 59 osteological characters (47 cranial, eight mandibular and four postcranial) and 13



TEXT-FIG. 3. *Uruyiella liminea* gen. et sp. nov., FC-DPV 1598, from the Upper Permian–Lower Triassic of Uruguay. Ascending ramus in A–B, anterior, and C–D, posterior views; photographs and interpretive drawings.

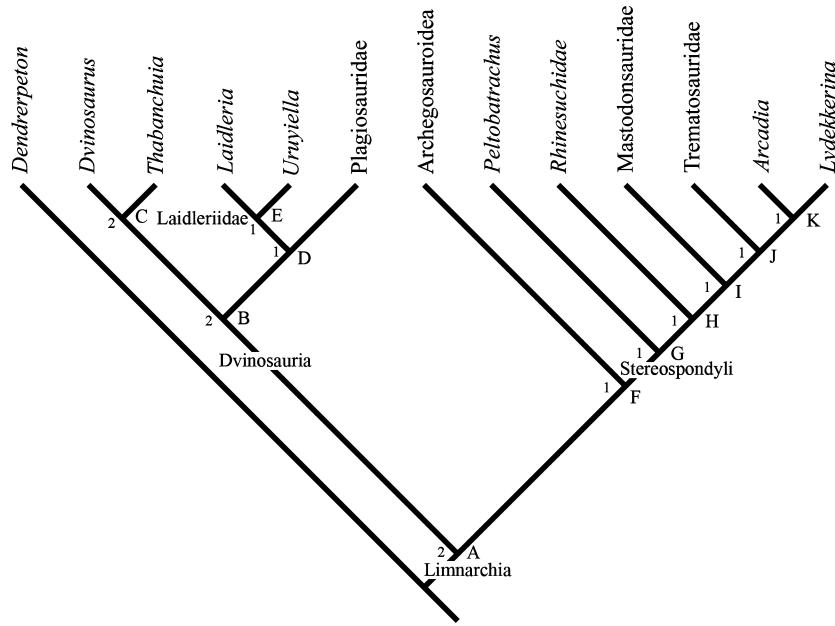
terminal taxa (see Appendix). Most characters were modified from those used by previous authors (Yates 1999; Warren and Marsicano 2000; Yates and Warren 2000; Damiani 2001). Character 47 is new. Several previously used characters in other phylogenies were not considered in our analysis because they could not be coded with confidence from the literature or their coding could be influenced by ambiguous interpretations. The excluded characters are mainly those related to the shape and proportions of the skull, conditions that in temnospondyls are extremely variable during ontogeny.

In order to reduce *a priori* assumptions of presumed monophyly of certain groups, generic terminal taxa were employed in the analysis. However, some higher level stereospondyl taxa were used according to previous analyses of temnospondyls (e.g. Yates and Warren 2000). The ingroup includes Permian stereospondyls such as *Peltobatrachus* (Panchen 1959) and the Rhinesuchidae (Broom 1908; Watson 1962), the stereospondylomorph Archegosauroida (Gubin 1991; Yates and Warren 2000), the basal trematosaurid *Benthosuchus* (Bystrow and Efremov 1940; Damiani 2001; Damiani and Yates 2003), the lydekkerinid *Lydekkerina* (Broom 1930; Shishkin *et al.* 1996), the rhytidosteid *Arcadia myriadens* (Warren and Black 1985; Marsicano and Warren 1998), the Mastodontosauridae (Damiani 2001), the Plagiosauridae excluding *Laidleria* (Panchen 1959; Warren 1985, 1995), *Laidleria* (Warren 1998), the tupilakosauroid *Thabanchuia* (Warren 1999), the new Uruguayan taxon *Uruyiella* and the dvinosaurid

Dvinosaurus (Bystrow 1938). Based on more inclusive temnospondyl phylogenies, the basal temnospondyl *Dendrerpeton* (Carroll 1967; Holmes *et al.* 1998) was used as the outgroup.

The analysis was performed using the branch-and-bound search algorithm of PAUP 3.1.1. (Swofford 1993). The characters were polarized by the outgroup method and optimized using the DELTRAN algorithm. All characters were treated as unweighted and characters 15, 24, 29, 45, 52, 53 and 55 were ordered. The strength of the branches was determined by calculating the decay index for each node, and these values are indicated in Text-Figure 4. One most parsimonious tree (Text-fig. 4) was obtained in the analysis, with a length of 131 steps, a consistency index of 0.51, a retention index of 0.55 and a rescaled consistency index of 0.28.

As in the recent phylogeny of Yates and Warren (2000), our analysis identified two monophyletic groups, the Dvinosauria and the Stereospondylomorpha, united in the node-based Limnarchia. However, the composition of these clades is substantially different. Whereas Yates and Warren (2000) discovered that both *Laidleria* and the Plagiosauridae nested deeply within the Stereospondyli, in our analysis these taxa were closely related to members of the Dvinosauroida (*sensu* Yates and Warren 2000), i.e. they fall outside of Stereospondyli. Moreover, in our hypothesis, the rhytidosteid *Arcadia* is the sister taxon of the Lydekkerinidae, a relationship that is consistent with certain previous analyses that placed the rhytidosteids



TEXT-FIG. 4. Most parsimonious tree obtained in the phylogenetic analysis, with Bremer support values for each clade. Nodes are supported by the following characters (numbers correspond to characters listed in the Appendix; a negative sign indicates a reversal; an asterisk denotes ambiguous optimization of the character state): A (= Limnarchia), 3 (1), 5 (1), 23 (1), 27 (1), 46 (2)*; B (= Dvinosauria), 2 (1), 15 (2), 17 (1), 21 (1)*, 29 (1)*, 36 (1)*, 42 (1)*, 43 (1), 44 (1)*, 53 (2)*, 52 (2)*; C, 7 (1), 22 (2)*, 25 (1)*, -32, 37 (1)*, 39 (1)*, 51 (1); D, 4 (1)*, 9 (1)*, 19 (1), 20 (1)*, 24 (2)*, 35 (1)*, 55 (2)*; E, 1 (1)*, 41 (1)*; F (= Laidleriidae), 4 (1)*, 10 (1), -12, -14, 24 (1)*, 45 (1), G (= Stereospondyli), -8, 22 (1)*, 50 (1), H, 2 (1), 11 (1), 20 (1), -26, 29 (1)*, 30 (1), 40 (1)*, 44 (1)*, 47 (1), 54 (1), I, 13 (1), 16 (1)*, 24 (2), 25 (1), 35 (1), 42 (1)*, 51 (1), J, 17 (1), 31 (1), 34 (1), 36 (1)*, 56 (1), K, 1 (1)*, 14 (1), -44.

close to related lydekkerinids (Marsicano 1999; Schoch and Milner 2000), but not with others (Yates and Warren 2000), where the rhytidosteids were found to occupy a more derived position.

The sister-group relationship between the clade consisting of the dvinosauroids *Dvinosaurus* and *Thabanchuia* and the Plagiosauridae plus Laidleriidae (node B) is supported by the following synapomorphies (numbers are characters listed in the Appendix, with states enclosed in parentheses; an asterisk denotes ambiguous optimization): otic notch absent, 15 (2); sensory sulci present on the skull roof, 2 (1); a squamosal-tabular suture present dorsally on the skull roof, 17 (1); palatine ramus of the pterygoid lacking a posterolateral flange, 36 (1)*: reversed in *Uruyiella*; pterygoid denticles absent, 43 (1): reversed in *Uruyiella*; palatine and ectopterygoid denticles absent, 44 (1)*; the quadrate condyles positioned at level, or in front, of the occipital condyles, 21 (1)*: unknown in *Uruyiella*; a straight vomerine tooth row present between the vomerine fangs, 29 (1)*: unknown in *Laidleria* and *Uruyiella*; vomer denticles absent, 42 (1)*: unknown in *Uruyiella*; all three coronoids without denticles, 52 (2)*: unknown in *Uruyiella* and *Laidleria*; and a continuous tooth row present in all three coronoids, 53 (2)*: unknown in

Thabanchuia, *Uruyiella* and *Laidleria*. Characters 2 and 36 were found by Yates and Warren (2000) to be unambiguous synapomorphies that support Dvinosauria in their analysis, whereas the absence of an otic notch diagnoses their more inclusive Dvinosauroidae.

The sister-group relationship of the Plagiosauridae and the Laidleriidae (node D) is not well supported, as indicated by its low Bremer value (see Text-fig. 4). The following synapomorphies support node D: a sulcus present on the ventral surface of the quadratojugal, lateral to the quadrate condyles, so that the quadratojugal forms an overhang in occipital view, 19 (1); tabular and exoccipital contacting at the paroccipital process, 20 (1)*; the maxilla forms a suture with the nasal, 4 (1)*: unknown in *Uruyiella*; the pre- and postfrontal are not in contact, so that the frontal contributes to the orbital margin, 9 (1)*: unknown in *Uruyiella*; the presence of double exoccipital condyles with no basioccipital contribution to the articular surface, 24 (2)*: unknown in *Uruyiella*; the palatine ramus of the pterygoid is retracted, so the palatines contribute to the margin of the interpterygoid vacuities, 35 (1)*: indeterminate in *Uruyiella*; and the height of neural spines is less than or equal to the length between the pre- and postzygapophyses, 55 (2)*: unknown in *Uruyiella*.

It is important to note that *Uruiella* could not be coded for five of these characters. Its position as the sister taxon of *Laidleria* is not an unexpected result, because of similarities mentioned in the description. These include a triangular skull, orbits located close to the lateral margin, and the general arrangement and shape of most dermal roofing bones. The long oblique suture present between the tabular and the squamosal, in particular, was otherwise described only for *Laidleria* and *Trucheosaurus* as a condition that is rarely present in temnospondyls that lack otic notches (Warren 1998). According to our analysis, *Uruiella* also shares with *Laidleria* the ornamentation of the dorsal skull roof that consists of uniformly small pits enclosed by a network of ridges, with small pustules sometimes present at the junction of the ridges, 1 (1); and the presence of ornamentation on the ventral surface of the pterygoid, 41 (1). Nevertheless, whereas the first character is shared with rhytidosteids, the second appears in several stereospondyl taxa, including *Peltobatrachus*, *Benthosuchus* and *Lydekkerina*.

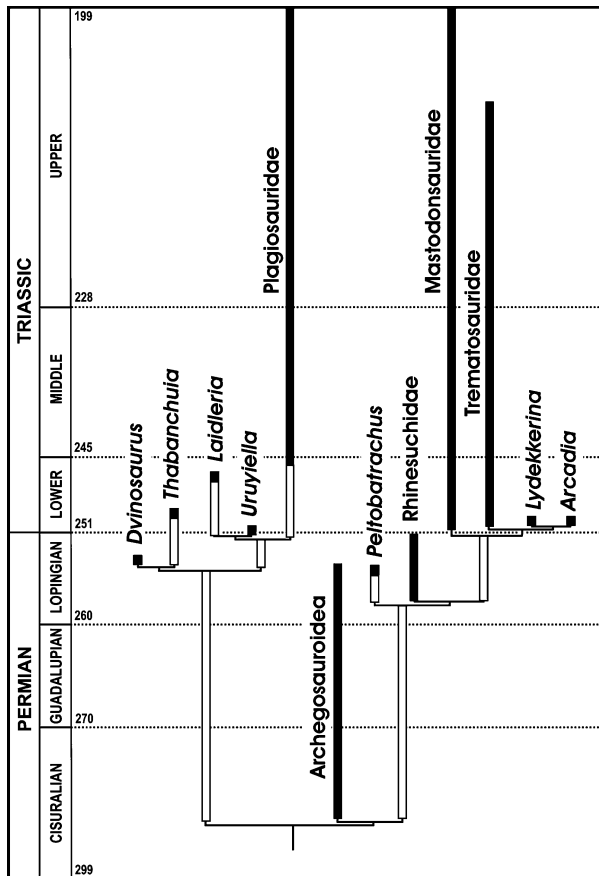
DISCUSSION

Our analysis places *Uruiella* outside the Stereospondyli, in a clade with *Laidleria* that, in turn, is the sister group of Plagiosauridae. A similar close relationship between *Laidleria* and the plagiosaurids was found by Yates and Warren (2000), but their phylogeny nests these taxa deeply within the Stereospondyli. The relationships of both *Laidleria* and the plagiosaurids have been contradictory. *Laidleria* was first allied with the trematosaurids (Kitching 1957) and subsequently it was placed in the family Laidleriidae, both as a taxon within the superfamily Rhytidosteioidea (Cosgriff 1965, 1974) or as superfamily *incertae sedis* in Temnospondyli (Cosgriff and Zawiski 1979). Recently, *Laidleria* was placed within the Rhytidosteidae by both Warren (1998) and Marsicano and Warren (1998), or nested deeply within the Stereospondyli as the sister taxon of the Plagiosauridae by Yates and Warren (2000). Similarly, the relationships of the plagiosaurids have been controversial since they were considered as stem Lissamphibia close to *Peltobatrachus* (Milner 1990), or derived trematosaurian stereospondyls (e.g. Warren 2000; Yates and Warren 2000).

The disagreements over the position of *Laidleria* within Temnospondyli could be attributable to a mosaic of derived and primitive character states. A similar condition can be seen in *Uruiella* despite its much more fragmentary nature. For instance, the anterior extension of the palatine ramus of the pterygoid in *Uruiella* (Text-fig. 2C–D), which excludes the ectopterygoid and at least the posterior part of the palatine from the interpterygoid vacuity, is only comparable with the condition present in Palaeozoic

temnospondyls (e.g. Watson 1962; Gubin 1991; Schoch and Milner 2000). Moreover, the presence of a posterolateral flange of the pterygoid in *Uruiella* is a structure absent in most Mesozoic stereospondyls (Capitosauria + Trematosauria *sensu* Yates and Warren 2000). Nevertheless, the structure of the quadrate ramus of the pterygoid in *Uruiella* (smoothly upturned to form the distal part of the ascending ramus of the pterygoid and ventrally bearing a shallow oblique ridge) is more similar to that present in Triassic stereospondyls such as *Lydekkerina* (pers. obs.), *Lapillopsis* (Yates 1999), *Luzocephalus* (Shishkin 1980), and *Thoosuchus* and the trematosaurids (Yates and Warren 2000; Damiani and Yates 2003). On the other hand, the shape of the quadratojugal in *Uruiella* was described and figured by Yates and Warren (2000, fig. 10) only for *Laidleria* and the plagiosaurids. It should be noted, however, that the trough is deeper and more ventrally orientated in *Uruiella* (Text-fig. 2E–F). In addition, there is an accessory paraquadrate foramen on the ventral surface of the quadratojugal in *Uruiella* (Text-fig. 2C–D), a condition found in Palaeozoic taxa such as *Dvinosaurus* (Bystrow (1938), *Peltobatrachus* (Panchen 1959) and some archegosaurids (Gubin 1991), but present also in some basal Mesozoic temnospondyls, such as the trematosauroid *Benthosuchus sushkini* (Bystrow and Efremov 1940; Damiani and Yates 2003) and the mastodontosauroid *Parotosuchus haughtoni* (Damiani 2002). This foramen is absent in both *Laidleria* and the plagiosaurids.

The retention of primitive characters in *Uruiella* is a feature common to most of the specimens from the Buena Vista Formation (Piñeiro and Ubilla 2003; Piñeiro 2004). The procolophonoid *Pintosaurus magnidentis* (Piñeiro *et al.* 2004) and several mastodontosauroids (Piñeiro and Ubilla 2003; Piñeiro 2004; Piñeiro *et al.* submitted) are examples. This could imply that they represent early stages in the evolution of taxa that are present in younger continental communities. This feature, along with the absence of Triassic indicator fossils, strongly suggests a transitional age for the fossiliferous conglomerates of the Buena Vista Formation, close to the Permo/Triassic boundary. On the other hand, the presence of one unequivocal Palaeozoic group, the 'pelycosaurian' Varanopidae, remains puzzling. These specimens could have been reworked from older deposits (Piñeiro *et al.* 2003), as suggested by the conglomeratic nature of the levels that yielded the fossils. However, the fossil record of varanopids is characterized by several long ghost lineages among taxa, which are frequently represented by a single specimen from a restricted geographical area (Reisz *et al.* 1998). Thus, the eventual discovery of more complete varanopid material in the Buena Vista Formation could indicate that this group of basal synapsids survived in Gondwana at least until the end of the Permian Period.



TEXT-FIG. 5. Calibrated tree, using the cladogram in Text-figure 4. Solid, thick bars indicate approximate temporal distributions of the taxa (modified from Yates and Warren 2000); open thick bars represent ghost lineages and ghost taxa. Time scale from Gradstein *et al.* (2004).

The low support found in all of the nodes in the present analysis, including the traditional Stereospondyli, could be the result of a combination of different conditions, frequently found in temnospondyl phylogenies. Thus, as discussed above, a low Bremer support might arise from the poor preservation of several specimens and the resulting absence of informative characters, along with the high number of homoplastic characters used in the analyses.

The new composition of the Dvinosauria revealed by our analysis, along with a probable latest Permian or earliest Triassic age for the Buena Vista Formation, suggests the existence of two ghost lineages, one for the Laidleriidae and one for the Plagiosauridae, extending back into the Late Permian (Text-fig. 5). Moreover, a Late Permian age for the fossiliferous conglomerates of the formation could also indicate a potential survivorship for temnospondyls in the Gondwanan region of Pangaea, as previously suggested by Yates and Warren (2000).

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APPENDIX

List of characters used in the phylogenetic analysis

Most characters were taken from Marsicano and Warren (1998), Yates (1999), Warren and Marsicano (2000), Yates and Warren (2000), and Damiani (2001). No. 47 is new.

1. Ornamentation of the dorsal skull roof: consisting of ridges enclosing depressions, which become elongated in areas of skull elongation (0); consisting of uniform small pits enclosed by a network of ridges, adorned in places with small pustules at the junction of the ridges (1); consisting of regularly spaced pustules (2).
2. Sensory sulci: absent from the skull roof of adults (0); present (1).
3. Posterior dorsal margin of the premaxilla: with a triangular posterior process medial to the naris (0); forming a simple suture with the nasal (1).
4. Maxilla-nasal contact: absent (0); maxilla and nasal form a suture (1).
5. Maxilla and quadratojugal: form a suture (0); maxilla making point contact, at most, with the quadratojugal (1).
6. Lacrimals: present (0); absent (1).
7. Anterior dorsal process of the palatine: absent from the dorsal surface of the skull roof (0); dorsal process present and exposed on the dorsal skull roof (1).
8. Orbits: located close to the skull midline (0); close to the skull margin (1).
9. Pre- and postfrontal contact: present and forming a suture (0); pre- and postfrontal fail to contact, so that the frontal contributes to the orbital margin (1).
10. Prefrontal-jugal contact: absent (0); prefrontal and jugal form a suture (1).
11. Postorbital: anterolaterally unexpanded (0); anterolaterally expanded ('hooked' *sensu* Damiani 2001) (1).
12. Anterior end of the jugal: extends well anterior to the anterior margin of orbit (0); extends no further than the anterior margin of orbit (1).
13. Tabular horns: present and terminate anterior to, or at level of, the posterolateral corner of the skull roof (0); present and extend posteriorly to the posterolateral corner of the skull roof (1).
14. Tabular horns: present as well-developed and posteriorly projected structures (0); tabular horns reduced to a broadly based triangle or absent (1).
15. Otic notch: deep (0); shallow (1); absent (2).
16. Squamosal margin of the otic notch: straight or concave (0); convex (1).
17. Squamosal: separated from the tabular by the supratemporal (0); a squamosal-tabular suture present dorsally on the skull roof (1).
18. Postparietal: transverse width of paired bones less than four times their anteroposterior length (0); greater than four times their anteroposterior length (1).
19. Quadratojugal: in occipital view, forms a simple corner with the quadrate (0); a sulcus is present on the ventral surface of the quadratojugal, lateral to the quadrate condyles, so that the quadratojugal forms an overhang (1).
20. Tabular and exoccipital: not in contact (0); in contact on the paroccipital process (1).
21. Quadrate condyles location: positioned well behind the occipital condyles (0); positioned at level or in front of the occipital condyles (1).
22. Parasphenoid denticles: present as a round patch at the base of the cultriform process (0); present as a transverse 'belt' that extends between the pterygoid-parasphenoid articulations (1); absent (2).
23. Paraquadrate foramen of quadratojugal: absent (0); present (1).
24. Occipital condyles: single, with the basioccipital forming the largest contribution to the articulating surface (0); bilobed, with reduced basioccipital contribution to the articular surface (1); double and formed by exoccipitals only (2).
25. Anterior palatal fossa: absent (0); present (1).
26. Anterior palatal fossa: single (0); paired, divided by a median ridge (1).
27. Maxilla and vomer: not in contact or in point contact (0); forming a suture (1).
28. Vomer-palatine contact external to the choana: absent (0); present so the maxilla is excluded from the border of the choana (1).
29. Vomerine tooth row between the vomerine fangs: absent (0); a straight tooth row runs transversely between the vomerine fangs (1); a V-shaped tooth row runs between the vomerine fangs (2).
30. Vomerine teeth along the medial margin of the choanae: absent (0); present (1).
31. Posteromedial corner of the palatine: simple, not extending posterior to the most anterior ectopterygoid tooth (0); with a posteromedial process reaching or extending posterior to the most anterior ectopterygoid tooth (1).
32. Ectopterygoid tusks: present (0); absent (1).
33. Ectopterygoid: contributes to the anterior margin of the subtemporal fossa (0); separated from the subtemporal fenestra by the alar process of the jugal (1).
34. Palatine ramus of the pterygoid: extends anteriorly to the anteriormost ectopterygoid tooth (0); ramus retracted posterior to the first ectopterygoid tooth (1).
35. Palatine ramus of the pterygoid: extends anteriorly to contact the vomers, excluding the palatines from the margin of the interpterygoid vacuities (0); ramus retracted, so the palatines contribute to the margin of the interpterygoid vacuities (1).
36. Palatine ramus of the pterygoid: bearing a posterolateral flange (0); flange absent (1).
37. Ascending ramus of the pterygoid: contacts the squamosal (0); does not contact the squamosal, creating a palatoquadrate fissure (1).
38. Ascending ramus of the pterygoid: without a thickened ascending column on its posterior surface (0); ascending column present (1).
39. Lateral margin of the pterygoid bordering the subtemporal vacuity: concave in ventral view (0); lateral margin straight (1).
40. Oblique ridge of the pterygoid: absent (0); present (1).

41. Palatal ornamentation: absent from ventral surface of the corpus of parasphenoid and pterygoid (0); present on either or both of these bones (1).
42. Vomer denticles: present (0); absent (1).
43. Pterygoid denticles: present (0); absent (1).
44. Palatine and ectopterygoid denticles: present on one or both of these bones (0); absent from both (1).
45. Posterior end of parasphenoid: ventral surface without sharp-rimmed depressions (pockets) (0); with rounded, widely separated depressions with sharp anterior rims (muscular crests) (1); with transversely widened depressions, so that the muscular crests approach each other forming transverse ridges (2).
46. Parasphenoid-ptyergoid contact: parasphenoid articulates with a depression in the corpus of the pterygoid, behind a short triangular medial process of the pterygoid (0); an elongated cylindrical medial process of the pterygoid abuts the parasphenoid (1); corpus of the pterygoid forming a broad contact along the lateral margins of the parasphenoid plate (2).
47. Accessory quadrate foramen on quadratojugal: present (0); absent (1).
48. Arcadian groove at the posterior end of the mandible: absent (0); present (1).
49. Prearticular: extends anteriorly at least as far as the level of the mid-point of the middle coronoid (0); extends no further anteriorly than the level of the suture of the middle and posterior coronoids (1).
50. Chorda tympanic foramen of the mandible: present on the prearticular-articular suture (0); formed entirely by the prearticular (1); absent (2).
51. Post-glenoid area of mandible: slopes ventrally away from the glenoid socket in lateral view, or is flat-topped or with a gently upward curvature (0); with a transverse trough behind glenoid socket followed by a dorsally bulging tip (1).
52. Coronoid denticles: a field of small denticles on all three coronoids (0); a field of denticles restricted to the posterior coronoid (1); denticles absent (2).
53. Coronoid teeth: coronoid series without teeth other than denticles (0); posterior coronoid with a row of teeth (1); continuous tooth row on all three coronoids (2).
54. Hamate process of the mandible: absent (0); present (1).
55. Height of neural spines: greater than the length between the pre- and postzygapophyses (0); less than or equal to the length between the pre- and postzygapophyses (1); less than 40 per cent of the length between the pre- and postzygapophyses (2).
56. Clavicular facets on the ventral surface of the interclavicle: separated by an intervening strip of ornament (0); in contact anteriorly (1).
57. Intercondylar fossa on the dorsal surface of the distal femur: large, deep, and sharply defined (0); small, shallow, vaguely defined (1).
58. Supinator process of the humerus: part of a crest that is confluent with the deltopectoral crest (0); discrete projection of bone (1).

Character-data matrix used in this study

| | 5 | | | | | 10 | | | | | 15 | | | | | 20 | | | | | 25 | | | | | |
|-----------------------|---|---|---|---|---|----|---|---|---|---|----|---|---|---|---|----|---|---|---|---|----|---|---|---|---|---|
| <i>Dendrerpeton</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | |
| <i>Dvinosaurus</i> | 0 | 1 | 1 | 0 | ? | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | |
| <i>Thabanchuia</i> | 0 | 1 | 1 | 0 | ? | 1 | 1 | 1 | 0 | 0 | 0 | 1 | ? | 1 | 2 | ? | 1 | 0 | 0 | 1 | 1 | 2 | ? | 0 | 1 | |
| Archegosauroidae | 0 | 0 | 1 | 1 | ? | 0 | ? | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| <i>Peltobatrachus</i> | 2 | 0 | ? | ? | ? | ? | ? | 0 | 0 | ? | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | |
| Rhinesuchidae | 0 | 1 | 1 | 1 | 1 | 0 | ? | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 |
| <i>Lydekkerina</i> | 1 | 1 | 1 | 1 | 1 | 0 | ? | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 1 | |
| Trematosauria | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | |
| <i>Laidleria</i> | 1 | 1 | 1 | 1 | 1 | ? | ? | 1 | 1 | 1 | 0 | 1 | ? | 1 | 2 | ? | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 2 | ? | |
| Plagiosauridae | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | ? | 1 | 2 | ? | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | |
| Rhytidosteidae | 1 | 1 | 1 | 1 | ? | 1 | 0 | 1 | 0 | ? | ? | 1 | 1 | 1 | 0 | 0 | 1 | ? | 0 | 1 | 1 | 1 | 1 | 2 | 1 | |
| Mastodontosauridae | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 1 | |
| <i>Uruiella</i> | 1 | 1 | ? | ? | ? | ? | ? | 1 | ? | ? | 0 | ? | ? | 1 | 2 | ? | 1 | 0 | 1 | 1 | ? | ? | ? | 0 | ? | |

| | 30 | | | | | 35 | | | | | 40 | | | | | 45 | | | | | 50 | | | | |
|-----------------------|----|---|---|---|---|----|---|---|---|---|----|---|---|---|---|----|---|---|---|---|----|---|---|---|---|
| <i>Dendrerpeton</i> | ? | 0 | 0 | 0 | 0 | ? | ? | ? | 0 | 0 | 0 | ? | ? | 0 | ? | 0 | 0 | 0 | 0 | 0 | 1 | ? | 0 | ? | ? |
| <i>Dvinosaurus</i> | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Thabanchuia</i> | 1 | ? | 1 | 1 | 0 | 0 | 0 | ? | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | ? | 0 | ? | ? |
| Archegosauroidae | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | ? | 0 | ? |
| <i>Peltobatrachus</i> | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | 0 | ? | 0 | 0 | 1 | ? | 0 | ? | 1 | 2 | 0 | 1 | ? | 0 |
| Rhinesuchidae | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | ? | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 0 | 0 |
| <i>Lydekkerina</i> | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | ? | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | ? | 0 |
| Trematosauria | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 2 | 0 | 1 | 1 | 0 |

| | 30 | | | | 35 | | | | 40 | | | | 45 | | | | 50 | | | | | | | | | |
|--------------------|----|---|---|---|----|---|---|---|----|---|---|---|----|---|---|---|----|---|---|---|---|---|---|---|---|---|
| <i>Laidleria</i> | ? | 1 | 1 | ? | 0 | ? | ? | ? | 1 | 1 | 1 | 1 | ? | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | ? | ? | ? | ? |
| Plagiosauridae | ? | 1 | 0 | 1 | 1 | 0 | 1 | ? | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 1 |
| Rhytidosteidae | 0 | ? | 0 | 0 | ? | ? | ? | 0 | ? | ? | ? | 1 | ? | ? | 0 | 0 | 0 | 0 | 0 | 0 | ? | 2 | 1 | 1 | ? | 1 |
| Mastodontosauridae | 0 | ? | ? | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | ? | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 0 |
| <i>Uruiella</i> | ? | ? | ? | ? | ? | 0 | 1 | 1 | 0 | ? | 0 | 0 | 0 | 0 | 1 | 1 | ? | 0 | 1 | ? | 2 | 0 | ? | ? | ? | ? |

| | 55 | | | | 58 | | | |
|-----------------------|----|---|---|---|----|---|---|---|
| <i>Dendroperpeton</i> | 0 | ? | ? | ? | 1 | 0 | ? | 0 |
| <i>Dvinosaurus</i> | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 1 |
| <i>Thabanchuia</i> | 1 | ? | 2 | 0 | ? | 1 | ? | ? |
| Archegosauroidae | 0 | ? | ? | 0 | ? | ? | ? | ? |
| <i>Peltobatrachus</i> | 0 | ? | ? | 0 | 0 | ? | 1 | 1 |
| Rhinesuchidae | 0 | 0 | 0 | 1 | ? | ? | 0 | 1 |
| <i>Lydekkerina</i> | 0 | 1 | ? | 1 | ? | 1 | ? | ? |
| Trematosauria | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 0 |
| <i>Laidleria</i> | 0 | ? | ? | ? | 2 | ? | ? | ? |
| Plagiosauridae | 0 | 2 | 2 | 0 | 2 | 1 | ? | 0 |
| Rhytidosteidae | 0 | 0 | 0 | 1 | ? | ? | ? | ? |
| Mastodontosauridae | 1 | 0 | 0 | 1 | ? | 0 | ? | ? |
| <i>Uruiella</i> | ? | ? | ? | ? | ? | ? | ? | ? |