

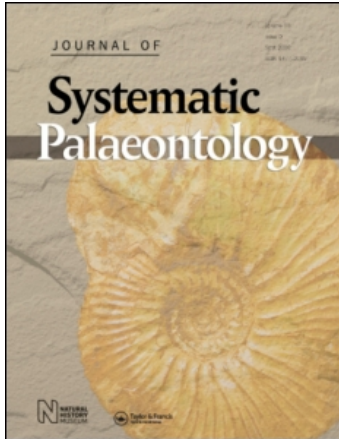
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Journal of Systematic Palaeontology

Publication details, including instructions for authors and subscription information:

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First published on: 06 December 2010

To cite this Article Dias-da-Silva, Sérgio and Marsicano, Claudia(2011) 'Phylogenetic reappraisal of Rhytidosteidae (Stereospondyli: Trematosauria), temnospondyl amphibians from the Permian and Triassic', Journal of Systematic Palaeontology, 9: 2, 305 – 325, First published on: 06 December 2010 (iFirst)

To link to this Article: DOI: 10.1080/14772019.2010.492664

URL: <http://dx.doi.org/10.1080/14772019.2010.492664>

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Phylogenetic reappraisal of Rhytidosteidae (Stereospondyli: Trematosauria), temnospondyl amphibians from the Permian and Triassic

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(Received 1 July 2009; accepted 7 May 2010; printed 31 May 2011)

All stereospondyl taxa previously placed within Rhytidosteidae are reviewed in a phylogenetic context. A parsimony analysis shows that *Pneumatostega*, *Trucheosaurus*, *Rhytidosteus* and *Nanolania* are placed outside Rhytidosteidae. If an implied weighting method is introduced in order to downweight homoplastic characters, then these taxa are placed within rhytidosteids (with the exception of *Rhytidosteus*), thus forming a resolved monophyletic group. This group is supported by four synapomorphies, including a twisted pterygoid quadrate ramus and sculpture consisting of a reticulate pattern with pustules or nodules at the junction between adjacent crests and ridges. Based on the topology of a majority rule consensus tree, we postulate a close relationship among all eastern Gondwanan rhytidosteids (Australian and Indian taxa) and among western Gondwanan taxa (South America, South Africa and Madagascar). Laurasian *Boreopelta* and *Peltostega* are successive paraphyletic taxa of both eastern and western groups. The Australian family 'Derwentiidae' is nested within Rhytidosteidae and is redefined as a subfamily (Derwentiinae nov.) which also includes *Indobrachyops*. Peltosteginae and Indobrachyopidae as currently defined in the literature are not supported. Rhytidosteinae is also not supported because *Laidleria*, *Pneumatostega* and *Rhytidosteus* do not emerge as a clade. The presence of the rhytidosteid *Trucheosaurus major* in the Late Permian of Australia suggests that rhytidosteids were already diversified at that time. Increasing efforts to collect Upper Permian and Lower Triassic rhytidosteids should help to improve stratigraphical, palaeogeographical and phylogenetic information regarding this widespread group of temnospondyls.

Keywords: Temnospondyli; Late Permian; Early Triassic; Pangaea; phylogeny; palaeobiogeography

Introduction

Rhytidosteidae are temnospondyls restricted to the Early Triassic of Pangaea, with a single record from the latest Permian of Australia (Marsicano & Warren 1998). This family was erected in 1920 by von Huene to include *Rhytidosteus capensis* from the Lower Triassic of South Africa (Owen 1884). Subsequently, the diagnosis of the family was emended by Cosgriff (1965) to include *Peltostega* (Wiman 1916; Nilsson 1946), from the Lower Triassic of Spitsbergen, and the new taxon *Deltasaurus*, from the Lower Triassic of Western Australia (Cosgriff 1965). In the same contribution, Cosgriff (1965) created the new superfamily Rhytidosteoidea to include both Rhytidosteidae and the monotypic family Laidleriidae (Kitching 1957). In their comprehensive review of Rhytidosteoidea, Cosgriff & Zawiskie (1979) removed Laidleriidae and erected a new family, Indobrachyopidae, to include 'short-faced' taxa such as *Indobrachyops* from India (von Huene & Sahni 1958), *Mahavisaurus* from Madagascar (Lehman 1966), *Rewana* from Australia (Howie 1972), and *Derwentia* from

Tasmania (Cosgriff 1974). In the same work, Cosgriff & Zawiskie (1979) restricted Rhytidosteidae to those taxa with a 'triangular' skull outline, such as *Rhytidosteus*, *Peltostega*, *Deltasaurus* and their new taxon *Pneumatostega*, also from the Lower Triassic of South Africa. Warren & Black (1985) argued that it was difficult to distinguish Indobrachyopidae from Rhytidosteidae using characters other than the skull outline; therefore, they assigned 'indobrachyopids' to Rhytidosteidae. Subsequently, Shishkin (1994) re-introduced Rhytidosteoidea to include Rhytidosteidae and Peltostegidae, the former including *Arcadia*, *Deltasaurus*, *Mahavisaurus*, *Rhytidosteus*, *Pneumatostega*, *Peltostega*, *Rewana* and *Derwentia*; the latter including *Boreopelta* and *Indobrachyops*. More recently, the superfamily was limited to Rhytidosteidae and Laidleriidae by Warren (1998).

Marsicano & Warren (1998) performed the first phylogenetic analysis using parsimony of all taxa assigned to rhytidosteids. Their cladogram recovered a monophyletic Rhytidosteidae, although the internal relationships of most included taxa were poorly resolved (Marsicano & Warren 1998). Schoch & Milner (2000) regarded rhytidosteids as

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basal stereospondyls and created Rhytidostea to include the families Lydekkerinidae, Rhytidosteidae (separated into two subfamilies, Rhytidosteininae and Peltosteginae), their new family Derwentidae (including the Australian genera *Acerastea*, *Derwentia* and *Rewana*, formerly placed within Rhytidosteidae) and Chigutisauridae. In their supertree of temnospondyls, Ruta *et al.* (2007) placed rhytidosteids as a paraphyletic assemblage relative to Brachyopoidea.

The main aim of the present paper is to reassess the phylogeny of rhytidosteids and related taxa, including newly described material from the latest Permian–Early Triassic of southern South America and the Early Triassic of Australia (Yates 2000; Dias-da-Silva *et al.* 2006; Piñeiro *et al.* 2007).

Institutional abbreviations

AMF: Australian Museum, New South Wales, Australia; **AMG:** Albany Museum, Grahamstown, South Africa; **AMNH:** American Museum of Natural History, New York, USA; **BMNH:** Natural History Museum, London, UK; **BMR:** Bureau of Mineral Resources, Canberra, Australia; **BPI:** Bernard Price Institute, Johannesburg, South Africa; **GSI:** Geological Survey of India; **MCN:** Museu de Ciências Naturais da Fundação Zoobotânica do RS, Porto Alegre, Brazil; **MMF:** Geological Survey of New South Wales, Sydney, Australia; **MNHN:** Muséum National d'Histoire Naturelle, Paris, France; **NMQR:** National Museum, Bloemfontein, South Africa; **PIN:** Paleontological Institute, Academy of Sciences, Moscow, Russia; **PIU:** Palaeontological Institute of the University of Uppsala, Sweden; **QM:** Queensland Museum, Brisbane, Australia; **SAM:** South African Museum, Cape Town, South Africa; **UCMP:** Museum of Paleontology, University of California, Berkeley, USA; **UMZC:** University Museum of Zoology, Cambridge, UK; **UMVT:** Museu de História da Vida e da Terra da Universidade do Vale do Rio dos Sinos, São Leopoldo, Brazil; **UTGD:** Department of Geology, University of Tasmania, Australia; **WAM:** Western Australian Museum, Perth, Australia.

Review of ingroup taxa

In this review, we summarize rhytidosteid taxonomy *sensu* Marsicano & Warren (1998) and material pertaining to each species. We discuss presumably related taxa based on previous phylogenetic analyses of stereospondyls, such as the 'lydekkerinids' (Milner 1990, 1991; Marsicano & Warren 1998; Yates & Warren 2000; Warren & Marsicano 2000; Schoch & Milner 2000; Piñeiro *et al.* 2007). Every taxon that has been referred to Rhytidosteidae is also included. In cases of synonymy, the senior synonym appears first. Figure 1 summarizes skull reconstructions of representative species.

Arcadia myriadens Warren & Black, 1985
(Fig. 1A)

Holotype. QM F10121, a partial skull, mandible, and some postcranial material (Fig. 1A).

Referred specimen. QM F12293, a juvenile skull.

Type locality and horizon. Duckworth Creek, Arcadia Formation, Australia. Induan, Early Triassic.

Remarks. This taxon was examined by the second author.
Boreopelta vavilovi Shishkin & Vavilov, 1985
(Fig. 1B)

Holotype. PIN 4115/1, a skull fragment (Fig. 1B).

Referred specimen. PIN 4113/5, a partial lower jaw.

Type locality and horizon. Karya-khos-Teryutekh River, Bulun District, Yakutsk Region, Teryutekhsкая Formation, Central Siberia, Russia. Olenekian, Early Triassic.

Remarks. Data from this taxon were taken from the literature. Shishkin & Vavilov (1985) included it in Rhytidosteidae. Later, Shishkin (1994) re-erected the family Peltostegidae to include *Boreopelta*, *Peltostega* and *Indobrachyops* due to the lack of a median axial trough in the skull roof, the almost complete absence of palatal shagreen, and the presence of a strongly flattened palatal arch (Shishkin 1994).

Chomatobatrachus halei Cosgriff, 1974

Holotype. UTGD 80738, a complete skull.

Paratypes. UTGD 58995, UTGD 85709, UTGD 85730, UTGD 87786 and TUZD 2104 (skull fragments); UTGD 85704 (a complete left mandibular ramus); UTGD 58986, UTGD 85705, UTGD 85706, UTGD 85783, UTGD 87803, UTGD 87804, UTGD 87521, UTGD 8722 and TUZD 1962 (mandibular fragments); UTGD 87789, UTGD 87790, UTGD 87791, UTGD 87792, UTGD 87793, UTGD 87794 and UTGD 87795 (incomplete skull fragments); UTGD 87796 (a nearly complete right mandibular ramus); UTGD 87797 (right incomplete clavicle).

Type locality and horizon. Meadowbank Dam, South-eastern Tasmania, Knocklofty Formation. Induan–Olenekian, Early Triassic.

Remarks. This taxon was examined by the second author.

Deltasaurus kimberleyensis Cosgriff, 1965

Holotype. WAM 62.1.44, a partial skull.

Paratypes. UCMP 61062-64 (skull remains); UCMP 61061, UCMP 61135, UCMP 61142, UCMP 61232, UCMP 61277, UCMP 61306, UCMP 61308-10, UCMP 61313, UCMP 61314, UCMP 61380, UCMP 61381, UCMP 61383-87, UCMP 61390 and UCMP 62156 (skull fragments); UCMP 61098 (incomplete articulated lower jaw); WAM 60.9.16, WAM 64.7.17, UCMP 61068, UCMP 61071, UCMP 61072, UCMP 61073, UCMP 61099-108, UCMP 61110-112, UCMP 61114, UCMP 61116-123, UCMP 61126, UCMP 61127, UCMP 62158, UCMP 64972, BMR F21794, BMR F21805, BMR F21807, BMR F 21817 (mandibular fragments); UCMP 61080, UCMP 61082, UCMP 61083, UCMP 61084, UCMP 61085, UCMP 61087, UCMP 61137 and UCMP 61307 (clavicles and clavicular

fragments); UCMP 61092 and UCMP 61237 (clavicular fragments); UCMP 61124, UCMP 61130, UCMP 61131, UCMP 61139, UCMP 61319, UCMP 61322, UCMP 61325, UCMP 61326 and UCMP 61327 (interclavicular fragments).

Type locality and horizon. West Kimberley, Western Australia, upper portion of Blina Formation. Olenekian, Early Triassic.

Remarks. This taxon was examined by the second author.

Derwentia warreni Cosgriff, 1974
(Fig. 1D)

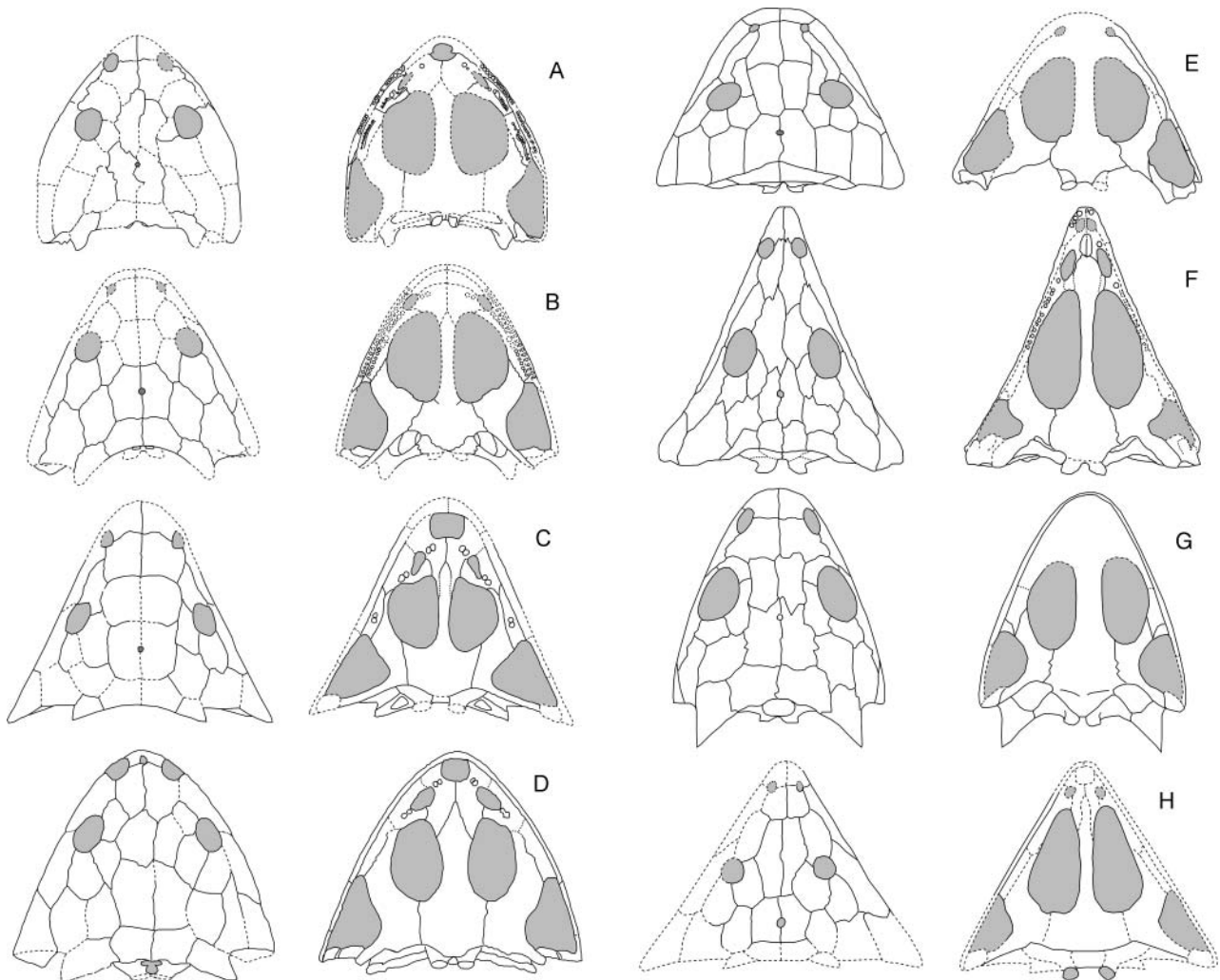


Figure 1. Line drawings of representative rhytidosteid taxa. On the left, dorsal view; on the right, ventral view, except for *Sangaia* and *Trucheosaurus* (J and K), both represented only by dorsal views. **A**, *Arcadia myriadens* (redrawn from Warren & Black 1985); **B**, *Boreopelta vavilovi* (redrawn from Shishkin & Vavilov 1985); **C**, *Deltasaurus kimberleyensis* (redrawn from Cosgriff 1965); **D**, *Derwentia warreni* (redrawn from Cosgriff 1974); **E**, *Indobrachyops panchetensis* (redrawn from von Huene & Sahni 1958); **F**, *Laidleria gracilis* (redrawn from Warren 1998); **G**, *Nanolania anatopretia* (redrawn from Yates 2000); **H**, *Pneumatostega potamia* (redrawn from Cosgriff & Zawiskie 1979); **I**, *Rhytidosteus capensis* (redrawn from Cosgriff & Zawiskie, 1979); **J**, *Sangaia lavinai* (redrawn from Dias-da-Silva *et al.* 2006); **K**, *Trucheosaurus major* (redrawn from Marsicano & Warren 1998). Not to scale.

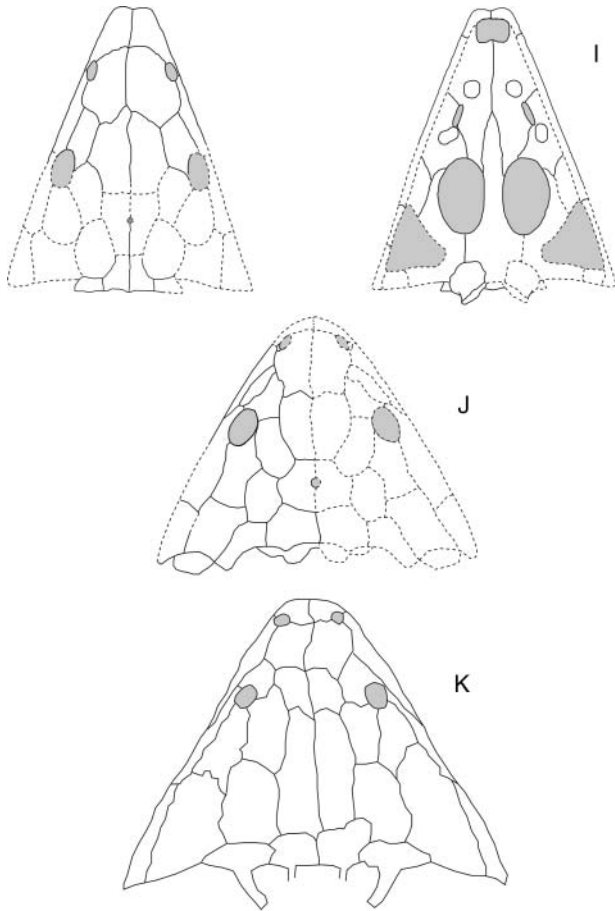


Figure 1. (Continued)

Holotype. UTGD 87784, a nearly complete skull (Fig. 1D).

Paratype. UTGD 87783, anterior portion of the palatal surface of the skull, including part of both vomers.

Referred material. UTGD 88066, basal portion of the cultriform process of the parasphenoid.

Type locality and horizon. Old Beach, south-eastern Tasmania, Knocklofty Formation. Induan-Olenekian, Early Triassic.

Remarks. This taxon was examined by the second author. Cosgriff (1974) placed *Derwentia* within Rhytidosteidae. Later, Cosgriff & Zawiskie (1979) included it in Indobrachyopidae. Subsequently, Milner (1990) argued that all Australian rhytidosteoid taxa (*Derwentia*, *Arcadia*, *Acerastea* and *Rewana*) should be placed within a new family, without formal nomination at that time. Finally, Schoch & Milner (2000) placed *Derwentia* and the other Australian taxa within the new family Derwentiidae.

Indobrachyops pachetensis von Huene & Sahni, 1958
(Fig. 1E)

Holotype. GSI 17754, a nearly complete skull (Fig. 1E).

Type locality and horizon. Dhenua, Raniganj Coalfield, Bengal, India, Upper portion of Panchet Formation. Induan, Early Triassic.

Remarks. Data from this species were taken from the literature. von Huene & Sahni (1958) initially described it as a member of Brachyopidae. Welles & Estes (1969) and Cosgriff (1969) removed it from this group and referred it to Temnospondyli *incertae sedis* because of the presence of a lacrimal bone, narial openings too close to each other, and the sculpturing pattern of the skull roof. Subsequently, Cosgriff & Zawiskie (1979) considered *Indobrachyops pachetensis* as the type species of the new family Indobrachyopidae. Warren & Black (1985) argued that the reconstruction of the skull made by von Huene & Sahni (1958) was 'too broad', the postorbital sutures very unique, and the lacrimal was actually absent, thus placing *Indobrachyops* within Rhytidosteidae. Marsicano & Warren (1998) interpreted *Indobrachyops* as a basal rhytidosteoid due to the presence in the specimen of lacrimal bone. Finally, Schoch & Milner (2000) considered *Indobrachyops* as a problematic taxon, and referred it to Rhytidostea *incertae sedis*.

Laidleria gracilis Kitching, 1957
(Fig. 1F)

Holotype. AMG 4313, a complete skull and most of the skeleton (Fig. 1F).

Type locality and horizon. Engcobo District, Eastern Cape Province, *Cynognathus* Assemblage Zone, Beaufort Series. Early Triassic.

Remarks. This species was examined by both authors. Kitching (1957) described it as possessing a mix of trematosauroid and capitosauroid characters and suggested the erection of a new family; nevertheless, he finally described it as a trematosaurid (Kitching 1957). Subsequently, *Laidleria* was placed within Laidleriidae in the Rhytidosteoidea (Cosgriff 1965). Later, Cosgriff & Zawiskie (1979) kept the family status and modified their opinion concerning the superfamily (*incertae sedis*). Warren & Black (1985) placed Laidleriidae within Rhytidosteoidea, and Carroll (1988) and Milner (1990) returned *Laidleria* to Rhytidosteidae. Later, Warren (1998) revalidated the Laidleriidae although Schoch & Milner (2000) returned *Laidleria* to Rhytidosteidae because the holotype possessed all the characters of Rhytidosteidae. Recently, Piñeiro *et al.* (2007) described a new temnospondyl from

Uruguay, *Uruiella liminea*; in their phylogenetic analysis they found that *Uruiella* and *Laidleria* were sister taxa and revived the family Laidleridae Kitching, 1957. In other phylogenies *Laidleria* was placed within Stereospondyli (e.g. Yates & Warren 2000). However, Piñeiro *et al.* (2007) considered both *Laidleria* and *Uruiella* to lie outside Stereospondyli.

Luzocephalus blomi Shishkin, 1980

Holotype. PIN 3784/1, a partial well-preserved skull.

Type locality and horizon. Luza, Kirov Province, Russia, Lower part of the Vetluga series, Krasnyye Baki horizon. Induan, Early Triassic.

Remarks. Data for this taxon were taken from the literature.

Lydekkerina huxleyi (Lydekker, 1889) Broom, 1915

1889 *Bothriceps huxleyi* Lydekker: 476.

1930a *Broomulus dutoiti* Broom: 9.

1930b *Putterillia platyceps* Broom: 8.

1948 *Limnoiketes paludinatans* Parrington: 434.

Holotype. BMNH R507, a complete skull.

Referred specimens. AMNH 9799, BMNH R6850, BPI 3223, BPI 4249, BPI 4319, BPI 4336, BPI 4683, NMQR 1428, NMQR 1431, NMQR 1432, NMQR 1435, NMQR 3182, SAM 3604, SAM K1121, SAM K1421, SAM TM 183, UMZC T214 (skulls).

Type locality and horizon. Edenberg, Orange Free State, South Africa, Beaufort Series, Katberg Formation, *Lystrosaurus* Assemblage Zone. Early Triassic.

Remarks. This taxon was examined by both authors. According to Jeannot *et al.* (2006), the cranial anatomy of the South African *Eolydekkerina magna* is, in many respects, similar to *L. huxleyi* and therefore its taxonomic validity is questionable. However, these authors did not synonymize this species with *L. huxleyi*.

Mahavisaurus dentatus Lehman, 1966

Holotype. MNHN MAE 3037, a nearly complete skull.

Type locality and horizon. Iraro, Madagascar, Middle Sakamena Formation. Induan, Early Triassic.

Remarks. Data for this taxon were taken from the literature. Lehman (1966) described a palatal fragment as belonging to an undetermined brachyopoid; Schoch & Milner (2000) placed this fragment in *M. dentatus*.

Nanolania anatopretia Yates, 2000

(Fig. 1G)

Holotype. QMF 12293, a postorbital fragment associated with lower jaw fragments (Fig. 1G).

Paratype. QMF 14480, a laterally complete skull with mandibles; QMF 35247, a poorly preserved skull with right mandibular ramus; QMF 35393, a badly preserved partial skull; QMF 39666, a posterior orbital and mandibular fragment.

Type locality and horizon. Headwaters of Duckworth Creek, south-west of Bluff, south central Queensland (Queensland Museum locality L215), Arcadia Formation (Rewan Group). Early Triassic (Induan).

Remarks. This taxon was examined by the second author. Warren & Hutchinson (1990) described the holotype of *Nanolania* as belonging to a juvenile *Arcadia myriadens*.

Peltostega erici Wiman, 1916

1946 *Peltostega wimani* Nilsson: 33.

Holotype. PIU U 24, posterior portion of a well-preserved skull, broken close to the orbital openings.

Referred specimen. PIU U 39, posterior part of the skull fractured behind the orbits.

Type locality and horizon. Mt Andersson, Sassen Valley, Spitsbergen, Svalbard, Kongressfjellet Formation, Sticky Keep Member. Olenekian, Early Triassic.

Remarks. Data from this taxon were taken from the literature. Säve-Söderbergh (1935) created the family Peltostegidae for *Peltostega erici* and *P. wimani* (PIU U 39) which Nilsson (1946) included in the new superfamily Peltostegoidea. Romer (1947) included both species within Trematosauridae and later Cosgriff (1965) created the superfamily Rhytidosteoidea for *Deltasaurus*, *Peltostega* and *Rhytidosteus* (Rhytidosteidae von Huene, 1920). Schoch & Milner (2000) considered the superfamily as a valid taxon.

Pneumatostega potamia Cosgriff & Zawiskie, 1979

Holotype. BPI F981, a dorsal mould of a skull roof (Fig. 1H).

Referred specimen. SAM 11188, partial skull fragments (palatal fragments and a partial lower jaw) and postcranial remains (vertebral elements, a left clavicle and an interclavicle).

Type locality and horizon. Middelburg, Cape Province of South Africa. *Lystrosaurus* Assemblage Zone, Beaufort Series. Early Triassic.

Remarks. This taxon was examined by the second author.

Rewana quadricuneata Howie, 1972

Holotype. QM F6471, a partial skull and skeleton.

Referred specimen. AMF 54126, isolated skull and postcranial fragments.

Type locality and horizon. Southern Queensland, Australia, Rewan Group, Arcadia Formation, Induan, Early Triassic.

Remarks. This taxon was examined by the second author.

Rhytidosteus capensis Owen, 1884
(Fig. 1I)

1994 *Rhytidosteus uralensis* Shishkin: 128.

Holotype. BMNH R. 455, partial skull and associated mandibular fragments (Fig. 1I).

Referred specimens. BMNH R.503, four skull fragments and clavicle; PIN 2394/17 (*R. uralensis*), a partial lower jaw.

Type locality and horizon. Beersheba, Orange Free State, South Africa, Katberg Formation, *Lystrosaurus* Assemblage Zone. Early Triassic.

Remarks. This taxon was examined by both authors.

Sangaia lavinai Dias-da-Silva & Marsicano, 2006
(Fig. 1J)

2006 *Cabralia lavinai* Dias-da-Silva *et al.*: 382.

Holotype. UMVT 4302, the left half of a partial skull, a partial palate (Fig. 1J).

Paratype. UMVT 4303, a partial right palatal fragment, including part of the parasphenoid and the pterygoid.

Referred specimens. PV 0497 T, MCN PV 2606 (skull fragments).

Type locality and horizon. Municipality of Cachoeira do Sul, Rio Grande do Sul, Brazil, Rosário do Sul Group, Sanga do Cabral Formation. Early Triassic.

Remarks. This taxon was examined by both authors. Dias-da-Silva & Marsicano (2006) changed the generic name *Cabralia* to *Sangaia*, as this name was preoccupied by a Brazilian butterfly (see Moore 1882).

Trucheosaurus major (Woodward, 1909)
(Fig. 1K)

1909 *Bothriceps major* Woodward: 319.

1956 *Trucheosaurus major* Watson: 327.

Holotype. MMF 12697a, a partially complete skull, AMF 50977, an articulated postcranial skeleton, and BMNH R3728, the counterpart of both skull and postcranial skeleton (Fig. 1K).

Type locality and horizon. Airly, Sydney Basin, New South Wales, Australia, Glen Davis Formation. Late Permian.

Remarks. This taxon was examined by the second author. It was originally described as a brachyopid taxon (*Bothriceps major*). Later, Watson (1956) referred the specimen to a new genus, *Trucheosaurus major*, keeping its brachyopid identity. Welles & Estes (1969) returned it to *Bothriceps*, arguing that the new taxonomic status could not be justified. Finally, Marsicano & Warren (1998) re-evaluated the holotype, returned it to *Trucheosaurus*, and placed it within Rhytidosteidae.

Phylogenetic analysis

Data matrix and computational analysis

The data matrix (Appendix 1) was constructed based on 87 morphological characters (skull and mandible) and 28 terminal taxa. When a character state could not be coded because the anatomical feature was either not preserved or could not be determined, it is indicated by a question mark (?) in the data matrix. Those characters that are methodologically inapplicable are indicated by a dash (–). Multistate characters were treated as unordered in the analysis in order to avoid personal interpretations on how a particular multistate character evolved. If, after the analysis, a particular multistate character is found as a transformational series, the analysis itself should provide the evidence of sequential character evolution. Character states are indicated by the numbers 0, 1, 2, 3 and 4. As plesiomorphy should not be assumed a priori, in several cases character states other than 0 represent the plesiomorphic condition.

The phylogenetic analysis was performed using PAUP 4.0 for Macintosh (Swofford 2004). The data matrix was processed using heuristic search, further addition sequence, with stepwise addition. The search was rooted on the outgroup, consisting of five taxa. The analysis recovered 103 most parsimonious trees (MPTs) of 305 steps each. The consistency index was 0.3770 (see the strict and majority rule consensus trees in Fig. 2). Bremer support values for each internal node were calculated as a measure of clade strength. In order to diminish the influence of highly homoplastic characters in the overall topology of the MPTs,

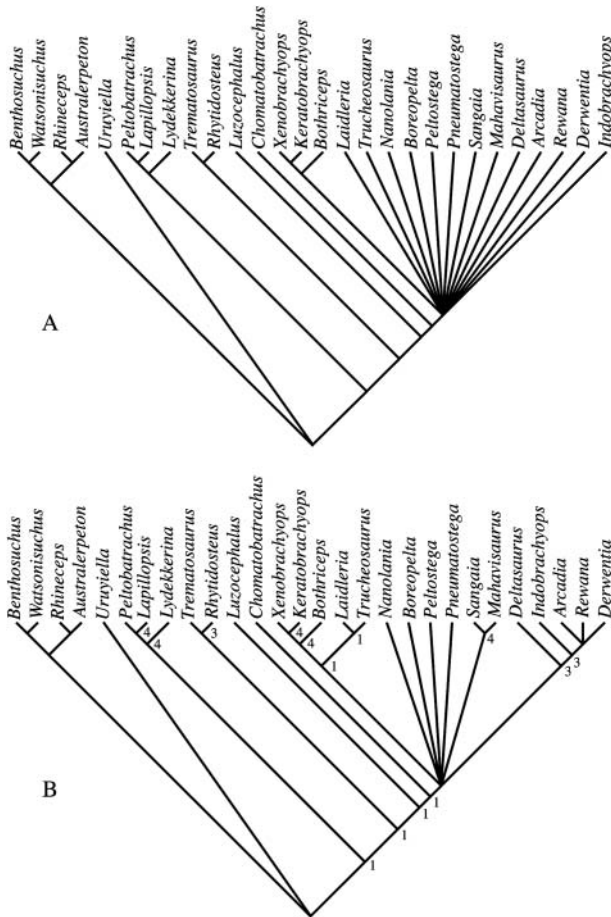


Figure 2. **A**, strict consensus of 103 most parsimonious trees of 305 steps each; mandibular data included (consistency index = 0.3770; retention index = 0.5366); **B**, majority rule (50%) consensus tree; the numbers represent the decay index (Bremer Support) for each node.

the characters were weighted using the implied weighting method of Goloboff (Goloboff 1993, 1995), which does not require independent estimations of weighting. He suggests that the weight of a character is a function of its fit to a cladogram. So, the best cladogram maximizes fit, giving a measure of 'total fit'. The function of fit to a cladogram requires consideration of fit in terms of homoplasy. Accordingly, the best ('fittest') tree is not necessarily the shortest solution. In his implied weighting method, Goloboff (1993, 1995) followed Farris (1969) who stated that homoplastic characters should be strongly downweighted, so their influence in the overall topology for a given character set is minimized. In the present contribution, after the first analysis (where 103 MPTs were recovered) the data matrix was rerun and, with this alternative approach, 20 'fittest' trees were found (consistency index of 0.3758, retention index of 0.5341, 'Goloboff fit with $k = 2$ ' of -50.24881). Strict and majority rule consensus trees are depicted in Fig. 4. They were rooted using the outgroup method, characters were optimized using the Acctran algorithm, and character

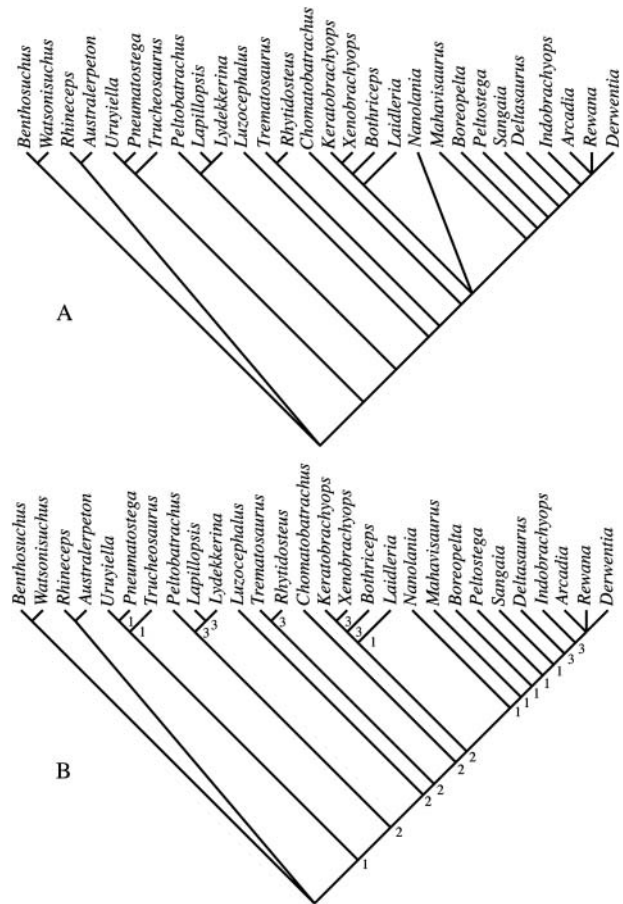


Figure 3. **A**, strict consensus of the seven most parsimonious trees of 277 steps each; mandibular data excluded (consistency index = 0.3646; retention index = 0.5429); **B**, majority rule (50%) consensus tree; the numbers represent the decay index (Bremer Support) for each node.

evolution was determined with the use of MacClade 3.0 (Maddison & Maddison 1992).

A further development was the exclusion of mandibular characters from data matrix. In most rhytidosteids character states for mandibular elements are either scarce or unknown. In other words, mandibular characters in the present data matrix largely comprise missing entries. This situation generates instability and therefore multiplies the quantity of most parsimonious trees. Following the exclusion of mandibular features (characters 76–87), the data matrix was rerun and the number of MPTs dramatically dropped. With this secondary approach, ingroup relationships became better supported and more resolved. In the parsimony analysis, the number of MPTs dropped from 103 to 7 (see Fig. 3A, B) (consistency index of 0.3646; retention index of 0.5429; 277 steps). The same approach was performed with the implied weighting method. As a result, the number of 'fittest' trees dropped from 20 to 5 (see Fig. 5A, B). The results are discussed with respect to all applied methods (e. g. parsimony analysis with and

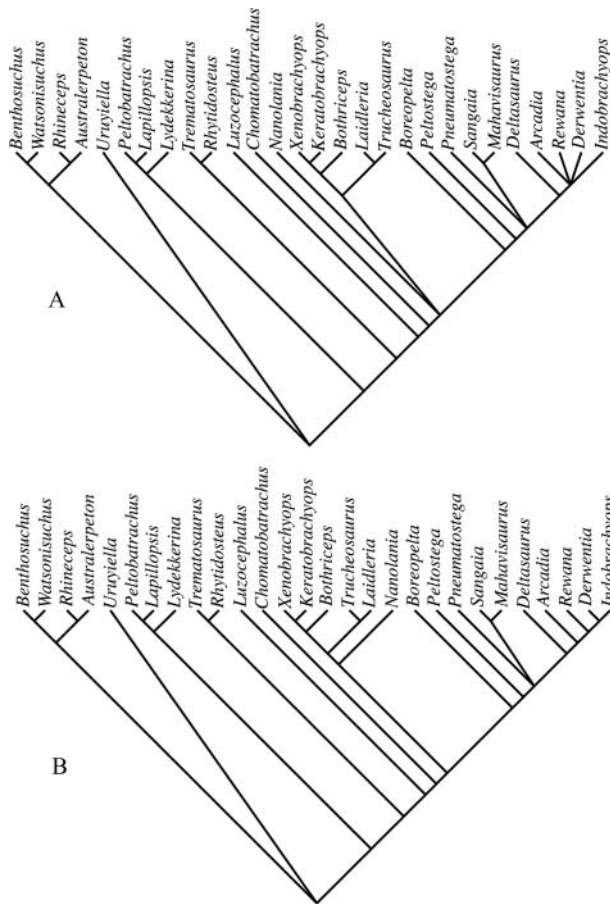


Figure 4. Implied weighting analysis. **A**, strict consensus of 20 'fittest' trees; mandibular data included (Goloboff fit = -50.24881 ; consistency index = 0.3758 ; retention index = 0.5341); **B**, majority rule (50%) consensus tree of 20 'fittest' trees.

without mandibular characters; implied weighting method, with and without mandibular characters). However, we provide a deeper discussion for the 'fittest' tree presented in Fig. 5B, because with the exclusion of mandibular characters and the use of implied weighting analysis it shows more robust and resolved results. Also, character supporting nodes (see below) were based on the same cladogram.

Outgroup. The rhinesuchids *Rhineceps* and *Australerpeton*, the mastodonsauroids *Watsonisuchus* and *Benthosuchus* and the non-stereospondyl temnospondyl *Uruyiella* were selected as outgroup taxa based on more inclusive previous hypotheses (Milner 1990; Yates & Warren 2000; Piñeiro *et al.* 2007).

Ingroup. The selection of the ingroup taxa was based on recent phylogenetic analyses of temnospondyls producing slightly different topologies (Milner 1990, 1991; Marsicano 1999; Schoch & Milner 2000; Warren & Marsicano 2000; Yates & Warren 2000; Damiani 2001; Pawley &

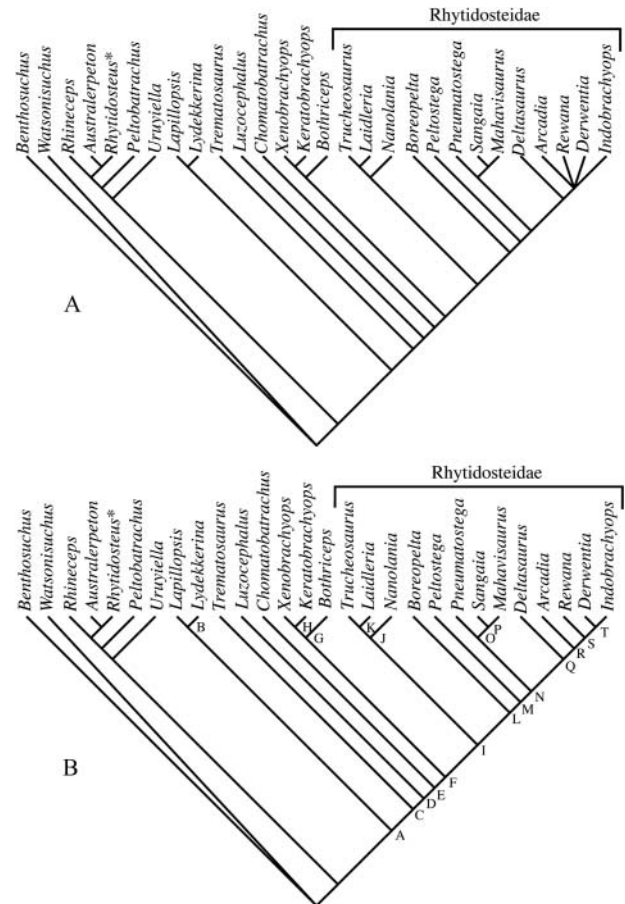


Figure 5. Rhytidosteid phylogeny resulting from the implied weighting analysis; mandibular data excluded. **A**, strict consensus of the five 'fittest' trees (Goloboff fit = -43.82125 ; consistency index = 0.3594 ; retention index = 0.5325); **B**, majority rule (50%) consensus tree of the five 'fittest' trees. Asterisks in **A** and **B** indicate the unexpected position of *Rhytidosteus* outside Rhytidosteidae.

Warren 2005; Piñeiro *et al.* 2007). Thus, all taxa previously allied to rhytidosteids have been included in order to resolve ingroup relationships. Only the type species of each genus was used in the present data matrix (see Appendix 2). In spite of the incompleteness of several rhytidosteids (e.g. *Boreopelta*, *Peltostega*, *Pneumatostega*, *Rewana*, *Rhytidosteus* and *Trucheosaurus*), none was excluded from the analysis. The sole exception is *Acerastea* since the holotype of the type species comprises several highly fragmentary pieces. Brachiopoids were included in the analysis since they were regarded in previous contributions as the sister-group of rhytidosteids (Warren and Marsicano 2000; Yates and Warren 2000). All brachiopoids used in the present contribution were examined personally by the second author.

Characters supporting nodes. In order to facilitate the identification of characters supporting specific nodes of the 'fittest' tree presented in Fig. 5B, each listed character

number is placed between brackets and its corresponding state in parenthesis.

Synapomorphies that are 'reversed' or homoplastic deeply in the cladogram are herein considered unequivocal. In the present section, only the nodes that comprise the Rhytidosteidae (I, J, K, L, M, N, O, P, Q, R, S, T) are discussed (see Fig. 5B). Nonetheless, relevant aspects regarding more inclusive external nodes are provided and commented in the discussion.

Node I. Rhytidosteidae von Huene, 1920

Included taxa. *Nanolania*, *Trucheosaurus*, *Laidleria*, *Boreopelta*, *Peltostega*, *Pneumatostega*, *Sangaia*, *Mahavisaurus*, *Deltasaurus*, *Arcadia*, *Rewana*, *Derwentia* and *Indobrachyops*.

Ambiguous synapomorphies. Orbits located about halfway along the skull length [1(0)]; interorbital distance greater than 50% of the width of the skull at midorbital level [2(1)]; sculpture of spider-web pattern with pustules or nodules on the junctions of crests and ridges [4(1)].

Unambiguous synapomorphy. Pterygoid quadrate ramus horizontally oriented proximally and vertically oriented distally so it appears twisted [47(1)].

Remarks. The monophyly of Rhytidosteidae is fully supported in this analysis and most character distributions for this clade are highly congruent. Yates & Warren (2000) considered that interorbital space greater than 50% of the width of the skull at midorbital level [2(1)] to be a derived condition of Trematosauria. However, in the present analysis this is a synapomorphy of Rhytidosteidae independently shared with *Trematosaurus* and *Xenobrachyops*. In *Laidleria*, this character exhibits the plesiomorphic condition (interorbital distance less than 50% of the width of the skull at midorbital level) [2(0)]. The type of sculpturing (character 4) on the dermal bones with nodules and pustules on the junctions of crests and ridges has long been regarded as a diagnostic character state of Rhytidosteidae (see Cosgriff & Zawiskie 1979; Marsicano & Warren 1998). This is fully corroborated in the present analysis, as most rhytidosteids present this condition, which is unknown only in *Derwentia* and *Nanolania*. In addition, the overall distribution of this character is highly congruent among the remaining ingroup taxa. The condition found in Rhytidosteidae is independently shared with *Luzocephalus*, *Lapillopsis* and *Uruiella*. *Peltobatrachus* exhibits exclusively pustulate ornamentation, while in *Nanolania* and *Derwentia* the condition is unknown. The 'twisting' of the palatal ramus (character 47, state 1) was for the first time defined by Marsicano & Warren (1998) and listed as a synapomorphy of Rhytidosteidae. This is undoubtedly a distinctive condition for this clade and only *Derwentia* shows the plesiomorphic state (pterygoid quadrate ramus evenly curved from

the horizontal to the vertical plane throughout its length) [47(0)]. In *Trucheosaurus*, *Pneumatostega*, *Mahavisaurus* and *Rhytidosteus* the quadrate ramus is not preserved

Node J

Included taxa. *Nanolania*, *Trucheosaurus* and *Laidleria*.

Unambiguous synapomorphy. Posttemporal fenestrae reduced to small foramina or entirely closed [46(2)].

Remarks. Character 46 is unknown in *Trucheosaurus*, but the overall distribution of state character [46(2)] is highly congruent in the analysis, as it only occurs in node J. However, the sister group relationship between these three taxa should be interpreted with caution due to the incompleteness of the Permian taxon.

Node K

Included taxa. *Trucheosaurus* and *Laidleria*.

Ambiguous synapomorphies. Tabulars reduced to thin slivers lying against the posterior margin of the skull roof [24(1)]; otic notch absent [29(2)]; post quadratojugal process of the skull roof present [31(1)].

Remarks. The highly fragmentary *Trucheosaurus* has 62 missing entries in the data matrix. It is quite reasonable to assume that the close relationship between this taxon and *Laidleria* is a product of an artefact caused by global parsimony. It is important to remark that, as previously stated by Piñeiro *et al.* (2007), *Laidleria* shows a mosaic of derived and plesiomorphic character states. In the present analysis, *Laidleria* is returned to Rhytidosteidae and, in contrast to the Piñeiro *et al.* (2007), it is positioned away from *Uruiella* (considered a sister taxon of *Laidleria* in that analysis). *Uruiella* occupies the most basal position together with *Peltobatrachus* and the rhinesuchids *Australerpeton* and *Rhineceps*. An alternative phylogenetic placement for *Laidleria* is provided by Yates & Warren (2000) who considered it to be a derived taxon closely related to Plagiosauridae.

Node L

Included taxa. *Boreopelta*, *Peltostega*, *Pneumatostega*, *Sangaia*, *Mahavisaurus*, *Deltasaurus*, *Arcadia*, *Rewana*, *Derwentia* and *Indobrachyops*.

Ambiguous synapomorphies. Postorbital elongated [20(0)]; quadrate ramus of the pterygoid slightly downturned [48(1)]; parasphenoid plate expanded transversely creating lateral 'wings' [73(1)].

Remarks. The shape of the postorbital bone (character 20) is unknown in *Rhytidosteus*, *Arcadia* and *Rewana*. *Uruiella*, *Trematosaurus*, *Xenobrachyops* and *Trucheosaurus* are

convergent with the derived condition found in this node. In node R, this character is reversed to the condition found in outgroup and basal ingroup taxa. The quadrate ramus of the pterygoid is slightly downturned [48(1)] and this condition is also present *Peltobatrachus* and *Lapillopsis*. This character is unknown in *Trucheosaurus*, *Rhytidosteus*, *Pneumatostega*, *Mahavisaurus* and *Rewana*. In brachyopoids (Node G), the quadrate ramus of the pterygoid is strongly downturned ('U' shaped). The presence or absence of lateral 'wings' on the parasphenoid plate (character 73) is unknown in *Uruiella*, *Trucheosaurus*, *Rhytidosteus*, *Pneumatostega*, *Mahavisaurus* and *Rewana*. *Laidleria* and *Nanolania* show the plesiomorphic condition (parasphenoid plate subrectangular without lateral 'wings').

Node M

Included taxa. *Peltostega*, *Pneumatostega*, *Sangaia*, *Mahavisaurus*, *Deltasaurus*, *Arcadia*, *Rewana*, *Derwentia* and *Indobrachyops*.

Ambiguous synapomorphy. Pterygoids without ornament [74(0)].

Remarks. This node is poorly supported as in many of the included taxa the condition is unknown (*Trucheosaurus*, *Rhytidosteus*, *Pneumatostega*, *Mahavisaurus*, *Rewana* and *Indobrachyops*). Thus, it could characterize a less inclusive group within Rhytidosteidae. The lack of ornament on the pterygoids [74(0)] is shared with *Trematosaurus* and *Xenobrachyops*.

Node N

Included taxa. *Pneumatostega*, *Sangaia*, *Mahavisaurus*, *Deltasaurus*, *Arcadia*, *Rewana*, *Derwentia* and *Indobrachyops*.

Ambiguous synapomorphies. Exoccipital condyles not projected beyond the posterior margin of the skull table [33(0)]; pterygoids with denticles [75(1)].

Remarks. The exoccipital condyles projected beyond the posterior margin of the skull table is a reversal to the condition found in the outgroup and basal ingroup taxa. This character is unknown in *Rhytidosteus*, *Trucheosaurus*, *Boreopelta*, *Pneumatostega*, *Mahavisaurus* and *Rewana*. The presence of denticles on the pterygoids [75(1)] is a reversal to the plesiomorphic condition found in outgroup and basal ingroup taxa. This character is unknown in *Rhytidosteus*, *Trucheosaurus*, and *Mahavisaurus*.

Node O

Included taxa. *Pneumatostega*, *Sangaia* and *Mahavisaurus*.

Ambiguous synapomorphy. Parietal-frontal contact behind the posterior orbital margin [17(2)].

Unambiguous synapomorphies. Jugal extends anterior to orbital margin [14(0)].

Remarks. This node is weakly supported, due to the presence of one highly homoplastic ambiguous condition (character 17 state 2), and a single unambiguous synapomorphy (character 14 state 0), that presents an isolated reversal to the condition found outside node F. However, character 14 is unknown in *Uruiella*, *Peltobatrachus*, *Boreopelta*, *Peltostega*, *Mahavisaurus*, *Rewana*, *Derwentia* and *Indobrachyops*.

Node P

Included taxa. *Sangaia* and *Mahavisaurus*.

Ambiguous synapomorphy. Skull margins slightly convex [3(1)].

Unambiguous synapomorphy. Contribution of the squamosal to the tabular horns [27(1)].

Remarks. The slightly convex outline of the skull margins [3(1)] is shared with *Peltobatrachus*, nodes A, G and R. This character is unknown in *Boreopelta* and *Peltostega*. The contribution of the squamosal to the tabular horns (character 27), was first reported by Dias-da-Silva *et al.* (2006) for *Sangaia lavinae*, who suggested that this could be a synapomorphy that would relate *Sangaia* to *Mahavisaurus*, a relationship which is corroborated in the present analysis. However, the sister group relationship between these two taxa should be considered with caution, due to the fragile support for this node.

Node Q: Derwentiinae nov

Included taxa. *Deltasaurus*, *Arcadia*, *Rewana*, *Derwentia* and *Indobrachyops*.

Ambiguous synapomorphies. Postorbital quadrangular or rounded but not anteroposteriorly elongated [20(1)]; posterior margin of palate almost straight [52(1)]; posterior edge of the ectopterygoid contributes to the anterior margin of the subtemporal fossa [58(0)].

Unambiguous synapomorphy. Parasphenoid and cultriform process with denticle field [72(3)].

Remarks. We erect a new subfamily for this node which is almost equivalent to the Derwentiidae of Schoch & Milner (2000) (see Discussion). The shape of the postorbital bone (character 20) is a reversal to the condition found in most taxa outside node L. The shape of the posterior

margin of palate (character 52) is unknown in *Rhytidosteus*, *Trucheosaurus*, *Pneumatostega*, *Arcadia* and *Rewana*. The character state for this node [52(1)] is also present in *Lapillopsis*, *Trematosaurus*, and Node G (with the exception of *Xenobrachyops*). The presence or not of an alar process of the jugal (character 58) is unknown in *Peltobatrachus*, *Rhytidosteus*, *Luzocephalus*, *Keratobrachyops*, *Bothriceps*, *Laidleria*, *Trucheosaurus*, *Peltostega*, *Pneumatostega*, *Mahavisaurus*, *Rewana* and *Indobrachyops*. *Chomatobatrachus* exhibits the same condition (alar process absent) as the present node. The existence of a denticle field over the parasphenoid and cultriform process [72(3)] is only shared with *Peltobatrachus*; therefore, this character state is considered an unambiguous synapomorphy.

Node R

Included taxa. *Arcadia*, *Rewana*, *Derwentia* and *Indobrachyops*.

Ambiguous synapomorphies. Skull margins slightly convex [3(1)]; supraorbital sensory sulcus widely separated from infraorbital sulcus [11(0)]; medial margin of the choana with a row of teeth [67(1)].

Remarks. The relative position of the supraorbital sensory sulcus in relation to the infraorbital sulcus (character 11) is inapplicable to *Peltobatrachus* and *Lapillopsis*. It is unknown in *Uruiella*, *Lydekkerina*, *Bothriceps*, *Trucheosaurus*, *Nanolania*, *Boreopelta*, *Peltostega*, *Mahavisaurus* and *Rewana*. The condition found in this node is shared with *Luzocephalus*, *Keratobrachyops* and *Pneumatostega*. The presence of a row of teeth in the medial margin of the choana [67(1)] represents a reversal to the condition found outside node A and also in *Trematosaurus*, *Luzocephalus* and *Chomatobatrachus*. This character is unknown in *Uruiella*, *Peltobatrachus*, *Rhytidosteus*, *Bothriceps*, *Trucheosaurus*, *Nanolania*, *Boreopelta*, *Peltostega*, *Pneumatostega*, *Sangaia*, *Mahavisaurus*, *Deltasaurus* and *Indobrachyops*.

Node S

Included taxa. *Rewana*, *Derwentia* and *Indobrachyops*.

Ambiguous synapomorphy. A straight tooth row running transversely between the vomerine fangs [68(1)].

Remarks. The presence of a straight tooth row running transversely between the vomerine fangs [68(1)] is shared with *Luzocephalus* and *Lydekkerina*. However, the distribution of this condition is highly homoplastic and in most analyzed taxa this character is unknown. The sister group relationship of this node should be considered with caution due to its fragile support.

Node T

Included taxa. *Derwentia* and *Indobrachyops*.

Ambiguous synapomorphies. Prefrontal and jugal not in contact [16(0)].

Remarks. This node is supported by a single synapomorphy that is also present in *Rhytidosteus* and *Xenobrachyops*. The distribution of this character is unknown in *Uruiella*, *Peltobatrachus*, *Boreopelta*, *Peltostega*, *Mahavisaurus* and *Rewana*.

Discussion

Parsimony analysis shows that the MPTs found here are weakly supported. In fact, most of the internal nodes show decay indexes (DI) of 1 and just a few of either 2 or 3. In rare cases DIs of 4 are present (see Figs 2B and 3B). Indeed, most of the internal nodes collapse with the addition of a single step during the heuristic search. Two main points might help to understand why this is a recurrent issue when dealing with temnospondyl phylogeny:

1. The high degree of ecological convergence which plays a significant role shaping the skeleton of temnospondyls, especially in aquatic stereospondyls (see the ecomorphic discussion by Defauw 1989), thus increasing the number of homoplastic characters. We attempted to overcome this high degree of homoplasy in our analysis by using implied weighting (Goloboff 1993, 1995).
2. Many taxa used in the present analysis comprise a single specimen which is frequently highly fragmentary, thus decreasing the number of informative characters. These taxa can behave as 'wild cards' in computational analysis using parsimony, occupying different positions in different MPTs (Huelsenbeck 1991; Nixon & Wheeler 1992; Novacek 1992). Again, the use of the methodological approach of implied weighting was used as an attempt to reduce the influence of 'wild card taxa' in our analysis. However, no taxa were discarded a priori as they could possess significant congruent characters that might improve the resolution of the MPTs (see Kearney 1998, 1992; Anderson 2002). Also we explored the effect of removing mandibular characters from the data matrix as these are responsible for many missing entries.

Thus, both the large number of convergent characters and missing data seem to have played a significant role in reducing the stability of the MPTs found in the present analysis. However, these obstacles should not prevent attempts to understand the phylogenetic relationships of long

established fossil groups that are fragmentary and/or highly homoplastic.

Parsimony analysis

The strict consensus tree generated using a complete dataset of characters (e.g. skulls and mandibles) shows a generalized polytomy with just a few nodes resolved (Fig. 2A). Brachyopoidea is a robust clade present in all cladograms (Figs 2–5). An unexpected result found in the parsimony analysis is the placement of *Rhytidosteus* outside the ingroup, in a basal position as a sister taxon of *Trematosaurus*, with or without the inclusion of mandibular elements in the analysis (Figs 2 and 3). In fact, the holotype of *Rhytidosteus* comprises an anterior pre-orbital fragment, with the rostrum and mandible preserved. Both its ‘longirostrine’ condition among rhytidosteids and its large amount of missing entries could explain this position. *Laidleria*, *Trucheosaurs* and *Nanolania* occupy different positions in the cladograms according to the methodology used. *Laidleria* and *Nanolania* exhibit a mosaic of plesiomorphic and derived characters. This could explain their variable position when a different approach is used. The same occurs with *Trucheosaurus* which is a highly fragmentary taxon, so the number of missing entries for this taxon could explain its different placements according to the methodology used. The Australian family Derwentiidae Schoch & Milner (2000) is not supported, unless we redefine it to include also the Indian taxon *Indobrachyops*, and the taxon is here considered as a subfamily (Derwentiinae). In fact, the present analysis clearly demonstrates that *Deltasaurus*, *Arcadia*, *Rewana*, *Derwentia* and *Indobrachyops* form a well-supported group. In the present study, Derwentiinae is always recovered, regardless of the methodology used (e.g. parsimony and implied weighting, with and without the inclusion of mandibular characters; see Figs 2B, 3–5). Therefore, we erect the new taxon, Derwentiinae, to include the Australian and Indian rhytidosteid taxa.

South African and South American taxa rhytidosteid are not closely related according to the results found using Goloboff’s methodology. Again, this might be related to the problems discussed at the beginning of the present section. In the original description of the South American rhytidosteid *Sangaia lavinai* (Dias-da-Silva *et al.* 2006) it was stated that this taxon was a basal rhytidosteid probably closely related to the Indian *Indobrachyops*. The present results do not support this statement. Moreover, the position of *Sangaia* is significantly different in each phylogenetic approach. In the parsimony analysis (when mandibles are excluded from the data matrix), *Sangaia* is the sister taxon of Derwentiinae, which includes *Indobrachyops* as the sister taxon of *Arcadia*, *Derwentia* and *Rewana* (Fig. 3A, B), and its position changes with the implied weighting approach (see next section). This Indian genus is a poorly described taxon which certainly needs further preparation and redescription. The same situation

holds for *Mahavisaurus*. Therefore, it is quite probable that some features in both taxa are misinterpreted and thus new morphological data for both *Mahavisaurus* and *Indobrachyops* might result in an alternative hypothesis of relationships.

The Laurasian *Boreopelta* and *Peltostega* are successive paraphyletic taxa with respect to Western Gondwanan (node O) and Eastern Gondwanan taxa (node Q) when mandibles are removed from the analysis. Nevertheless, when implied weighting is used, they change to a different position in the cladogram (see below).

Implied weighting analysis

Through the use of this methodology, most rhytidosteids form a natural clade (Figs 4, 5). Only those problematic taxa already discussed are placed outside Rhytidosteidae, namely *Laidleria* and *Nanolania* (both presenting a *mélange* of basal and derived characters) and *Trucheosaurus* and *Rhytidosteus* (both highly fragmentary). With mandibular characters removed from the data matrix, *Laidleria*, *Nanolania* and *Trucheosaurus* constitute a clade (node I) within Rhytidosteidae. *Rhytidosteus* moves to a basal position as the sister taxon of *Australerpeton*, an unexpected result. Again, the ‘longirostrine’ outline of the type specimen and its fragmentary nature could explain this unpredicted position. However, we suggest that *Rhytidosteus* possesses four state characters that justify its inclusion within Rhytidosteidae: interorbital distance greater than 50% of the width of the skull at midorbital level [2(1)]; spider-web pattern of sculpturing with pustules or nodules on the junctions of crests and ridges [4(1)]; lacrimal bone absent [12(1)]; and anterior end of jugal about level with or posterior to anterior orbital margin [14(1)]. Unfortunately, due to the incompleteness of this taxon, the present analysis failed to support this assumption. We believe that this dilemma may be solved after collecting more complete material attributable to *Rhytidosteus*.

In the cladogram depicted in Fig. 5B, some of the outgroups form a clade which includes *Uruiella*, *Peltobatrachus*, *Rhineceps*, *Australerpeton* and *Rhytidosteus* and is the sister-group of node A. The Uruguayan taxon is therefore a basal stereospondyl in contrast with the results of Piñeiro *et al.* (2007) who considered it a non-stereospondyl and the sister taxon to *Laidleria*. In the present analysis, *Laidleria* occupied a more derived position (Node K) within Rhytidosteidae. Node A is a well supported clade due to the presence of three unambiguous and two ambiguous synapomorphies.

Three ‘lydekkerinids’ were included in this analysis (*Lydekkerina*, *Luzocephalus* and *Chomatobatrachus*). *Lydekkerina* is nested within Node B as the sister taxon of *Lapillopsis*, whereas *Luzocephalus* and *Chomatobatrachus* are successive sister taxa of (Brachyopoidea + Rhytidosteidae) in agreement with a previous hypothesis that considered ‘Lydekkerinidae’ as a paraphyletic group

(Milner 1990, 1991; Yates & Warren 2000). Damiani (2001) suggested that 'lydekkerinids' might be monophyletic, although a detailed parsimony analysis of all 'lydekkerinid' taxa was required in order to evaluate the alleged monophyly of the group.

According to previous analyses, such as those of Yates & Warren (2000), Warren & Marsicano (2000) and Schoch & Milner (2000), Chigutisauridae is the sister group of Rhytidosteidae. This is confirmed herein by eight ambiguous and two unambiguous synapomorphies that support Node F [(*Xenobrachyops*, *Keratobrachyops*) + (*Bothriceps*)] + (Rhytidosteidae)].

The clade Rhytidosteidae was only previously analysed in a phylogenetic context by Marsicano & Warren (1998) who considered it as a monophyletic group, though the internal relationships of most included taxa remained unresolved in their hypothesis. More recently, Ruta *et al.* (2007) performed a phylogenetic analysis of Temnospondyli and included several rhytidosteids which were found to be paraphyletic regarding Brachyopoidea. In the present reassessment, the monophyletic status of this group (Node I) is reinforced (by four synapomorphies) and the internal relationships are more resolved (Fig. 5).

Node J (*Nanolania*, *Trucheosaurus* and *Laidleria*) is weakly supported by a single synapomorphy (posttemporal fenestrae reduced to small foramina or entirely closed [46(2)]) and its internal relationship should be viewed with caution. The South African *Pneumatostega*, the South American *Sangaia* and the Madagascan *Mahavisaurus* form a clade (Node O). This node is supported by two synapomorphies, one ambiguous and one unambiguous (parietal-frontal contact behind the posterior orbital margin [17(2)]; jugal extends anterior to orbital margin [14(0)]). Again, the internal relationships are weakly resolved. In its original description, *Sangaia* was considered a basal rhytidosteid, more closely related to the Indian *Indobrachyops* than to any other rhytidosteid due to the presence in both taxa of a prominent lacrimal bone, a feature lost in more advanced rhytidosteids (Dias-da-Silva *et al.* 2006). However, the present analysis suggests that *Indobrachyops* is a derived taxon deeply nested within Derwentiinae, whereas *Sangaia* falls outside this groups and is the sister-taxon of *Mahavisaurus* (node P) from Madagascar. At this point, it is interesting to remark that within Rhytidosteidae (node I) the eastern Gondwanan rhytidosteids (Australian and Indian taxa, node Q Derwentiinae) are more closely related to the western Gondwanan taxa (South Africa, South America and Madagascar, node O). As stated in the previous section, the Australian family 'Derwentiidae' of Schoch & Milner (2000) is redefined as a subfamily and amended to include *Indobrachyops*. The Subfamily Peltosteginae Säve-Söderberg, 1935 (see Schoch & Milner 2000) is not supported as the taxa originally included (*Boreopelta*, *Deltasaurus*, *Mahavisaurus* and *Peltostega*) occupy

different positions in the topology presented herein (*Boreopelta* and *Peltostega* are successive sister taxa with respect to node N, *Mahavisaurus* is the sister taxon of *Sangaia*, and *Deltasaurus* is nested within Derwentiidae). For the same reason, the subfamily Rhytidosteinae von Huene, 1920 (see Schoch & Milner 2000), is not supported in our analysis as the taxa included do not form a natural group (*Laidleria*, *Pneumatostega* and *Rhytidosteus*). The family Indobrachyopidae Cosgriff & Zawiskie (1979) is also not supported in this study, since *Mahavisaurus* does not form a clade with *Indobrachyops*.

Palaeogeographical implications

According to the resulting phylogeny and considering the stratigraphic distributions of the taxa included, the radiation of Rhytidosteidae probably took place long before the end of the Permian (Fig. 6). The presence of the rhytidosteid *Trucheosaurus major* in Upper Permian strata from Australia (Glen Davis Formation) and its position within Rhytidosteidae suggest that the basal diversification of the group occurred during the Late Palaeozoic, as was originally proposed by Marsicano & Warren (1998). Consistent with the richness of Australian rhytidosteids and the putative sister-group relationship between *Trucheosaurus* and *Nanolania* (node J), an Australian origin for the group is supported by the present analysis, as previously suggested by Warren *et al.* (2000). According to Marsicano & Warren (1998), the apparent abruptness of the Permo-Triassic turnover in the temnospondyl record could be both due to the lack of recent and comprehensive phylogenetic reviews of the known temnospondyl taxa and/or a taphonomic artefact. In general, recent phylogenetic

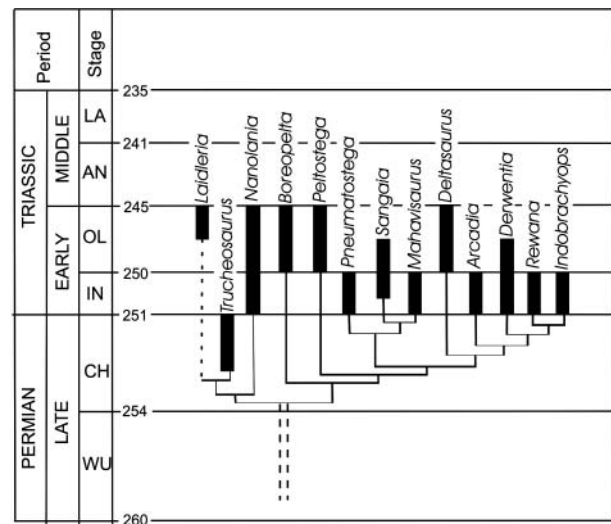


Figure 6. Calibrated tree, using the rhytidosteid phylogeny from Figure 5B. Solid bars indicate approximate temporal distributions of the taxa based on published ages of rhytidosteid-bearing units; dashed bars represent ghost lineages and ghost taxa.

analyses of advanced stereospondyl groups (e.g. Schoch & Milner 2000; Warren & Marsicano 2000; Yates & Warren 2000), provide evidence that stereospondyls already had a widespread distribution in the Early Triassic, both in Laurasian and Gondwanan areas, with some ghost lineages extending from the Late Permian.

Some authors have proposed that stereospondyls radiated from a group of Permian forms that survived to the Permo-Triassic event in a 'safe haven' in eastern Gondwana, probably Antarctica (Warren *et al.* 2000; Yates & Warren 2000). Stereospondyls rapidly diversified after that, spreading to the rest of Gondwana and Laurasia at the beginning of the Triassic. However, the present analysis suggests a slightly different scenario for the evolution of advanced Mesozoic stereospondyls. The presence of the basal stereospondyl *Uruiella liminea* and mastodontosaurids in Permo-Triassic strata in Uruguay (Piñeiro *et al.* 2007) might be evidence that stereospondyls were more widely distributed in Gondwana before the Permian extinction. However, it is important to remark that *Uruiella liminea* was firstly described as a non-stereospondyl (Piñeiro *et al.* 2007). Nevertheless, the structure of its basicranium closely relates it to Stereospondyli (see Yates & Warren 2000), as also found in the present analysis. Therefore, its presence in putative Permian beds reinforces the hypothesis that stereospondyls were probably an important and fairly diverse component of tetrapod faunas at least in western Gondwana at the end of the Palaeozoic. The increasing information provided by Permian and Early Triassic South American temnospondyls is changing former ideas regarding the evolution of this most species-rich group of basal tetrapods. It is also pointing researchers in new directions on the question of how Pangaea was re-occupied by stereospondyls during the Triassic.

Rhytidosteids are an interesting group of trematosaurian stereospondyls which probably constitute one of the earliest diversifications of this group. Despite the highly fragmentary nature of most of the specimens included in this family, they are critical in any discussion about the origin and early diversification of stereospondyls and the impact of the Permian-Triassic event on the group. Therefore, increasing efforts in prospecting and collecting in Upper Permian and Lower Triassic rhytidosteid-bearing deposits should help to improve our knowledge of this interesting and widespread group of temnospondyls.

Acknowledgements

The authors are grateful to the following individuals and institutions for allowing us to study the temnospondyl material under their care: Jennifer Clack (Museum of Zoology, Cambridge), Eugene Gaffney (American Museum of Natural History, New York), Farish Jenkins (Museum of Comparative Zoology, Harvard), Robert Jones (Australian

Museum, Sydney), Tania Lindner Dutra (Universidade Vale do Rio dos Sinos, Brazil), Angela Milner (Natural History Museum, London), Ian Percival (Geological Survey of New South Wales, Sydney), Bruce Rubidge (Bernard Price Institute, Johannesburg), Roger Smith (South African Museum, Cape Town), Kathi Stait (Geology Department, University of Tasmania) and Anne Warren (La Trobe University, Melbourne). Anne Warren also reviewed an earlier version of this article. We also thank Juan Carlos Cisneros for his suggestions regarding the phylogenetic methodology used in this work. Afnan Khalil A. Suleiman and Ana Luiza Ramos Ilha prepared the line drawings in Fig. 1. We are grateful to Andrew Milner and Marcello Ruta for reviewing the manuscript and providing pertinent comments. This work was funded by CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil; project numbers 304068/2003-9 and 500919/2009-7) to SDS, and UBACyT X133, PICT 07-1902 and PIP CONICET 5120 (Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina) to CM.

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Appendix 1: character list

The following list of characters is based on personal observations of the original material and taken and/or redefined from previous analyses such as those of Marsicano & Warren (1998), Warren & Marsicano (2000), Yates & Warren (2000), Schoch & Milner (2000), Damiani (2001) and Pawley & Warren (2005). All characters are treated as unordered in the analysis.

Skull table

- Orbits located about halfway along the skull length (0); orbits located in front of the midlength of the skull (1); orbits located behind midlength of the skull (2).
- Interorbital distance less than 50% of the width of the skull at midorbital level (0); interorbital distance greater than 50% of the width of the skull at midorbital level (1).
- Skull margins straight, or slightly concave (0); slightly convex (1).
- Sculpture of the dorsal skull roof forms a ‘normal’ ridge-grooved pattern without pustules or nodules on the junctions (0); spider-web pattern with pustules or nodules on the junctions of crests and ridges (Cosgriff & Zawiskie 1979) (1); only pustules are present (2).
- Nares not close to skull midline (distance between nares twice width of one naris; or greater) (0); nares close to skull midline (distance between nares approximates width of one naris) (1).
- Nares rounded (0); narrow and elongated (1).
- Presence of snout formed by an anterior expansion of the premaxilla; present (0); absent (1).
- Snout margins continually converging towards the tip (0); tip of snout expanded so that the snout margins run parallel, or are concave before the tip (1).
- Sensory sulci well developed (e.g. deeply incised) (0); present but poorly developed (e.g. shallow) (1); deeply incised between orbit and nostril only (2); sensory sulci absent (3). We consider that sensory sulci development is a sequential transformation. Therefore, this character was treated as ordered in this analysis.
- Infraorbital sulcus straight or gently curved (0); infra-orbital sulcus with a step-like flexure between the orbit and the naris (1); flexure ‘Z’ shaped (2).
- Supraorbital sensory sulcus widely separated from infraorbital sulcus (0); runs closely parallel to infraorbital sulcus between naris and orbit (1).
- Lacrimal bone present (0); absent (1).
- Contact between premaxilla and nasal anterior to the nares (0); at level of the nares (1); posterior to the nares (2).
- Jugal extends anterior to orbital margin (0); anterior end of jugal about level with or posterior to anterior orbital margin (1).
- Maxilla in the orbital margin (0); maxilla not in the orbital margin (1).
- Prefrontal and jugal not in contact (0); prefrontal and jugal form a suture (1).
- Parietal–frontal contact anterior to the posterior orbital margin (0); at the level of the posterior orbital margin (1); behind the posterior orbital margin (2).
- Pre- and post-frontals form a suture (0); pre- and post-frontals fail to contact so that the frontal contributes to the orbital margin (1).
- Postparietal pair less than four times wider, transversely than anteroposteriorly long (0); greater than four times wider than long (1).
- Postorbital elongated (0); postorbital quadrangular or rounded but not anteroposteriorly elongated (1).
- Straight or concave posterior squamosal margin in dorsal view (0); convex and overhanging squamosal margin (falciform crest) (1).
- Maxilla and nasal not in contact (0); maxilla and nasal forming a suture (1).
- Maxilla and quadratojugal form a suture (0); maxilla and quadratojugal do not contact at all (1).
- Tabulars are well developed rectangular to triangular bones (0); tabulars reduced to thin slivers lying against the posterior margin of the skull roof (1).
- Tabular horn not supported from underneath (0); tabular horn supported (1).
- Tabular horns end in the same level or anterior to the posterolateral corners of the skull roof (0); tabular horns extend posteriorly to the posterolateral corners of the skull roof (1).
- Tabular horns composed exclusively of the tabular (0); squamosal participates on the tabular horns (1).
- Tabular horn without a thin ventrally projecting crest of bone (0); ventrally projected crest of bone present in tabular horn (1).
- Otic notch deep (0); otic notch is a wide shallow embayment (1); otic notch absent (2).

30. Squamosal and tabular separated by the supratemporal (0); squamosal-tabular suture present on the dorsal skull roof (1).
31. Post quadratojugal process of the skull roof; absent (0); present (1).
32. Post postparietal process of the skull roof; absent (0); present (1).

Occiput

33. Exoccipital condyles not projected beyond the posterior margin of the skull table (0); exoccipital condyles projected well beyond the posterior margin of the skull table (1).
34. Quadrate condyles behind the occipital condyles (0); in the same transverse line as the occipital condyles (1); anterior to the occipital condyles (2).
35. Bilobed occipital condyle with reduced basioccipital contribution (0); double occipital condyles with no basioccipital contribution (1).
36. Exoccipital condyles elliptical, facing posteromedially (0); more rounded, facing posteriorly, held on short stalk (1).
37. Squamosal-quadratojugal trough absent (0); present (1).
38. Quadratojugal forms a simple corner with the quadrate in occipital view (0); a sulcus present on the quadratojugal; lateral to the quadrate condyles; so that the quadratojugal forms an overhang in occipital view (1) (*sensu* Yates & Warren 2000).
39. Ascending ramus of the pterygoid contacts the squamosal (0); ascending ramus does not contact the squamosal; creating an upper palatoquadrate fissure (1).
40. Ascending ramus of the pterygoid thickened by an ascending column positioned towards its medial edge (1); column absent (0).
41. Ascending ramus of the pterygoid forms a continuous curve with the posterior edge of the quadrate ramus (0); ascending ramus of the pterygoid arises from the dorsal surface as a shallow; uncurved lamina (1); ascending ramus of the pterygoid arises from the dorsal surface as a gently concave lamina which is also curved posteriorly in vertical section (2); ascending ramus of the pterygoid arises from the dorsal surface as a gently concave lamina (3).
42. Foramen passing through the stapes (0); stapedia foramen absent (1).
43. Posterior face of quadrate ramus of the pterygoid without an oblique ridge (0); a low rounded oblique ridge present (1); oblique ridge is a large sharp edged crest (2).
44. Occipital face of the quadrate without a dorsal process (0); quadrate with a dorsal process (1).
45. Paraquadrate foramen present on occipital portion of quadratojugal (0); present on posteroventrolateral ornamented portion of quadratojugal (1); absent (2).
46. Post temporal fenestra markedly wider than deep (0); about as wide as deep as or deeper than wide (1); post temporal fenestrae reduced to small foramina or entirely closed (2).
47. Pterygoid quadrate ramus evenly curved from the horizontal to the vertical plane throughout its length (0); horizontally oriented proximally and vertically oriented distally so it appears twisted (1).
48. Quadrate ramus of the pterygoid level with palate (0); quadrate ramus slightly downturned (1); quadrate ramus strongly downturned (2).

Palate

49. Choana round or oval (0); slit-like (1).
50. Anterior palatal fossa not perforated (0); anterior palatal fossa perforated to form an anterior palatal vacuity (1).
51. Single anterior palatal fossa (0); anterior palatal fossae paired divided by a median ridge (1).
52. Posterior margin of palate curved (0); almost straight (1).
53. Quadrate condyles double and markedly screw-shaped with the medial condyle extended anteriorly (0); quadrate condyle double and triangular, the apex of the triangle lateral (1); quadrate condyle double with two parts subequal in size (2).
54. Maxilla forming most of the lateral border of choanae (0); lateral processes of vomer and palatine approach one another so as to reduce the maxillary contribution (1); vomer-palatine suture lateral to the choanae excludes maxilla entirely (2).
55. Palatine ramus of the pterygoid meets palatine on the lateral margin of interpterygoid vacuity (0); pterygoid retracted so ectopterygoid is exposed in the interpterygoid vacuity and contributes to strut between interpterygoid and subtemporal vacuities (1); pterygoid markedly retracted so ectopterygoid makes a large contribution to strut between interpterygoid and subtemporal vacuities (2).
56. Palatine ramus of the pterygoid bears a posterolateral flange (0); flange absent (1).
57. Lateral margin of the pterygoid; bordering the subtemporal vacuity concave (0); lateral margin of the pterygoid straight in ventral view (1).
58. Posterior edge of the ectopterygoid contributes to the anterior margin of the subtemporal fossa (0); posterior end of the ectopterygoid separated from the subtemporal fossa by an alar process of the jugal (1).

59. Width of interpterygoid vacuity pair less than 90% of the length (0); width of pair greater than 90% of the length (1).
60. Width of the cultriform process of the parasphenoid at its midpoint less than 10% of the length of the process (using the anterior and posterior ends of the interpterygoid vacuities as the length of the cultriform process) (0); width of cultriform process more than 10% of its length (1).
61. Ventral surface of the cultriform process narrow and rounded (0); gently convex (1); flat ventral surface and unexpanded anteriorly (2); flat and expanded anteriorly between the vomers (3); ventral surface of the cultriform process flat with a median keel (4).
62. Vomerine depression or foramen just anterior to cultriform process of the parasphenoid absent (0); present (1); present as a vacuity (2).
63. Posteromedial corner of the palatine simple; not extending posterior to the most anterior ectopterygoid tooth (0); elongate posteromedial process of the palatine extending posterior to the most anterior ectopterygoid tooth (1).
64. Ectopterygoid with enlarged tusks at its anterior end (0); ectopterygoid tusks absent (1).
65. Ectopterygoid with only one or two teeth (0); ectopterygoid with a tooth row of more than three teeth (1).
66. Absence of a tooth row behind the palatine tusks (0); four to six palatine teeth (1); more than seven palatine teeth (2).
67. Medial margin of the choana without teeth (0); medial margin of the choana with a row of teeth (1).
68. Vomers without a row of teeth between the vomerine fangs (0); a straight tooth row running transversely between the vomerine fangs (1); transverse vomerine tooth row 'V' shaped (2).
69. Vomers with a field of denticles (0); vomers without a field of denticles (1).
70. Posterior end of the ventral surface of the parasphenoid plate without sharp rimmed depressions (0); rounded widely separated depressions ('pockets') at the posterior end of the ventral surface of the parasphenoid plate with sharp anterior rims (muscular crests) (1); depressions transversely widened so that the muscular crests approach each other forming transverse ridges (2).
71. Exoccipital and pterygoid not in contact or contact not visible ventrally (0); exoccipital-ptyerygoid suture visible in ventral view (1).
72. Round patch of denticles on the parasphenoid at the base of the cultriform process (0); parasphenoid denticle field enlarged to a transverse 'belt' extending between the pterygoid-parasphenoid articulations (1); parasphenoid denticles absent (2); paras-

phenoid and cultriform process with denticle field (3).

73. Parasphenoid plate subrectangular without lateral 'wings' (0); parasphenoid plate expanded transversely creating lateral 'wings' (1).
74. Pterygoids without ornament (0); ventral surface of the pterygoids with ornament (1).
75. Pterygoids without denticles (0); pterygoids with denticles (1).

Mandible

76. No extension of the mandible behind the glenoid fossa (0); postglenoid area (PGA) on the mandible (1).
77. No arcadian groove at the posterior end of the mandible (0); arcadian groove present (1).
78. Prearticular extending anteriorly, at least as far as the level of the midpoint of the middle coronoid (0); prearticular not extending anterior to the level of the suture of the middle and posterior coronoids (1).
79. Posterior meckelian foramen bordered by the prearticular, postsplenial and the angular (0); posterior meckelian foramen bordered by the prearticular and postsplenial exclusively (1).
80. Parasymphysial teeth (includes parasymphysial tusks) behind the marginal tooth row (0); parasymphysial teeth absent (1).
81. All three coronoids with field of small denticles (0); field of denticles restricted to the posterior coronoid (1); coronoids without any denticle fields (2).
82. Prearticular not extending posterior to the level of the glenoid (0); prearticular extending posterior to the glenoid, covering the medial face of the articular (1).
83. Mandibular sulcus shallow or absent at its posterior end (0); mandibular sulcus deeply incised at its posterior end (1).
84. Postglenoid process (if present) on the posterior end of the mandible no longer than the arcadian process (0); postglenoid process much longer than the arcadian process (1).
85. Chordatympanic foramen located on the suture between the articular and the prearticular (0); chordatympanic foramen located on the prearticular alone (1); chordatympanic foramen absent (2).
86. Mandible without a hamate process (0); tall hamate process projecting dorsally immediately in front of the anteromedial corner of the glenoid of the mandible (1).
87. Coronoid bones without teeth other than denticles (0); posterior coronoid with a row of teeth (1); all coronoids with a continuous tooth row (2).

Appendix 2: data matrix

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Benthosuchus</i>	2	0	0	0	0	1	0	1	0	2	1	0	1	0	1	1	1	0	0	1
<i>Watsonisuchus</i>	2	0	0	0	0	?	1	–	1	?	?	0	?	0	1	1	0	1	0	1
<i>Rhineceps</i>	2	0	0	0	0	1	1	–	2	0	0	0	1	0	1	1	1	0	0	1
<i>Australerpeton</i>	2	0	0	0	1	1	0	1	1	0	?	0	0	0	1	1	1	0	0	1
<i>Peltobatrachus</i>	0	0	1	2	?	?	?	?	3	–	–	?	?	?	?	?	1	0	0	1
<i>Xenobrachyops</i>	1	1	1	0	1	0	1	–	0	1	1	1	?	1	0	0	2	0	1	0
<i>Bothriceps</i>	1	0	1	0	0	0	1	–	?	?	?	1	0	1	1	1	0	0	0	1
<i>Keratobrachyops</i>	1	0	1	0	1	0	1	–	0	0	0	1	1	1	1	1	2	0	1	1
<i>Lapilopsis</i>	0	0	1	1	0	1	1	–	3	–	–	0	1	0	1	1	0	1	0	1
<i>Trematosaurus</i>	2	1	0	0	1	1	0	1	0	0	1	0	1	0	1	1	2	0	1	0
<i>Lydekkerina</i>	0	0	1	0	0	0	1	–	1	1	?	0	1	0	1	1	0	0	0	1
<i>Luzocephalus</i>	2	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1
<i>Chomatobatrachus</i>	0	0	0	0	0	0	0	0	1	1	1	0	2	0	1	1	0	0	1	1
<i>Laidleria</i>	2	0	0	1	1	0	0	0	0	0	1	1	1	1	1	1	0	1	0	1
<i>Uruyiella</i>	1	?	0	1	?	?	?	?	1	?	?	?	?	?	?	?	2	?	?	0
<i>Rhytidosteus</i>	2	1	0	1	0	1	0	1	?	0	1	1	0	1	0	0	?	0	?	?
<i>Boreopelta</i>	?	1	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0
<i>Deltasaurus</i>	?	1	0	1	0	0	1	–	0	0	1	1	1	1	1	1	1	0	0	1
<i>Arcadia</i>	1	1	1	1	0	?	1	–	0	0	0	1	1	1	1	1	2	0	0	1
<i>Peltostega</i>	0	1	?	1	0	?	?	?	?	?	?	?	?	?	?	?	1	?	0	0
<i>Pneumatostega</i>	?	1	0	1	?	?	1	–	1	0	0	1	?	0	1	1	2	0	?	0
<i>Derwentia</i>	1	1	1	?	0	0	1	–	1	0	0	1	1	?	?	0	2	0	0	1
<i>Nanolania</i>	0	1	0	?	0	1	1	–	1	?	?	1	1	1	1	1	0	0	0	1
<i>Sangaia</i>	0	1	1	1	0	?	1	–	2	0	1	0	?	0	1	1	2	0	0	0
<i>Mahavisaurus</i>	0	1	1	1	0	?	1	–	0	0	?	1	?	?	?	?	0	0	0	1
<i>Indobrachyops</i>	0	1	1	1	0	?	1	–	0	0	0	0	?	?	1	0	1	0	?	1
<i>Trucheosaurus</i>	1	1	0	1	0	0	1	–	?	?	?	1	1	1	1	1	1	0	1	0
<i>Rewana</i>	1	1	1	1	?	?	1	–	?	?	?	?	?	?	?	?	?	?	?	?
Taxon	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
<i>Benthosuchus</i>	1	1	1	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	–
<i>Watsonisuchus</i>	1	1	?	0	?	?	0	0	0	1	0	0	0	0	1	0	0	0	0	–
<i>Rhineceps</i>	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	–
<i>Australerpeton</i>	1	1	?	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	–
<i>Peltobatrachus</i>	0	?	?	0	?	0	0	0	1	0	1	0	0	0	0	0	1	0	0	–
<i>Xenobrachyops</i>	0	1	?	1	–	0	–	–	2	1	0	0	1	1	1	1	1	0	0	1
<i>Bothriceps</i>	0	1	?	0	0	0	0	0	1	1	0	0	1	1	1	1	1	0	1	?
<i>Keratobrachyops</i>	0	1	0	0	0	1	0	0	1	1	0	0	1	2	1	1	1	0	0	1
<i>Lapilopsis</i>	0	1	0	0	0	1	0	0	0	1	0	1	0	1	1	1	1	0	1	0
<i>Trematosaurus</i>	0	1	1	0	0	1	0	0	0	1	0	0	1	1	1	1	1	0	0	0
<i>Lydekkerina</i>	0	–	0	0	0	1	0	0	0	1	0	1	0	1	0	1	0	1	0	–
<i>Luzocephalus</i>	0	1	1	0	?	0	0	0	0	1	0	0	0	0	1	0	1	0	1	–
<i>Chomatobatrachus</i>	0	0	1	0	?	0	0	0	0	1	0	0	1	1	1	0	1	0	1	–
<i>Laidleria</i>	0	1	1	1	–	0	–	–	2	1	1	0	1	1	1	1	1	1	1	1
<i>Uruyiella</i>	0	?	1	1	–	–	–	–	2	1	0	?	0	0	?	?	0	1	?	0
<i>Rhytidosteus</i>	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?
<i>Boreopelta</i>	0	?	?	?	0	?	?	?	1	1	?	0	?	1	1	?	1	?	1	1
<i>Deltasaurus</i>	0	1	1	0	0	0	0	0	1	1	?	0	0	1	1	?	1	0	1	0
<i>Arcadia</i>	0	1	1	0	0	0	0	0	1	1	0	1	0	0	1	0	1	0	1	0
<i>Peltostega</i>	0	?	?	0	0	0	0	0	1	1	0	0	1	1	1	1	1	?	1	0
<i>Pneumatostega</i>	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Derwentia</i>	0	1	1	0	0	0	0	0	1	1	0	0	1	1	1	0	1	0	1	0
<i>Nanolania</i>	0	1	?	0	0	1	0	0	1	1	0	1	1	2	1	1	1	0	1	0
<i>Sangaia</i>	0	1	1	0	0	0	1	0	1	1	1	1	0	1	1	1	1	0	0	1
<i>Mahavisaurus</i>	0	?	?	0	0	0	1	0	1	1	?	0	?	?	?	?	?	?	?	?
<i>Indobrachyops</i>	0	0	?	0	?	?	?	?	1	1	0	0	0	1	1	?	1	?	?	?
<i>Trucheosaurus</i>	0	1	?	1	–	–	–	–	2	1	1	0	?	?	?	?	?	?	?	?
<i>Rewana</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Taxon	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
<i>Benthosuchus</i>	0	0	2	0	0	0	0	1	0	1	0	1	1	0	0	1	0	1	0	0
<i>Watsonisuchus</i>	0	0	2	1	0	0	0	1	0	1	?	1	0	0	0	1	0	1	0	0

Appendix 2: data matrix

<i>Rhineceps</i>	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
<i>Australerpeton</i>	0	?	2	0	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	
<i>Peltobatrachus</i>	0	?	1	0	0	0	0	1	?	?	?	0	0	?	?	0	0	?	1	
<i>Xenobrachyops</i>	3	?	0	1	0	1	0	2	0	1	0	0	2	1	2	1	?	1	1	
<i>Bothriceps</i>	?	?	0	?	2	1	0	2	0	1	0	1	2	?	1	1	1	?	1	
<i>Keratobrachyops</i>	2	?	0	1	0	0	0	2	0	1	0	1	2	1	1	1	1	?	1	
<i>Lapillopsis</i>	?	0	1	0	0	1	0	1	0	1	0	1	0	0	1	0	0	1	1	
<i>Trematosaurus</i>	1	1	1	0	0	0	0	0	0	1	1	1	1	0	1	1	0	1	0	
<i>Lydekkerina</i>	0	0	1	1	?	0	0	0	0	1	1	0	1	0	0	1	0	1	1	
<i>Luzocephalus</i>	0	?	1	1	0	0	0	0	0	1	0	0	0	1	?	1	0	?	0	
<i>Chomatobatrachus</i>	1	?	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0	
<i>Laidleria</i>	0	1	0	1	0	2	1	0	0	?	?	0	2	1	?	0	0	?	1	
<i>Uruyiella</i>	0	?	1	?	?	?	?	0	?	?	?	?	?	?	0	0	0	1	?	
<i>Rhytidosteus</i>	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	
<i>Boreopelta</i>	0	?	0	?	?	0	1	1	?	?	?	0	?	?	1	1	0	1	?	
<i>Deltasaurus</i>	1	?	0	?	?	1	1	1	0	1	0	1	?	2	0	1	0	0	1	
<i>Arcadia</i>	1	?	0	?	0	0	1	1	?	?	?	?	1	1	?	?	0	0	1	
<i>Peltostega</i>	1	?	0	?	1	0	1	1	?	?	?	0	1	?	?	1	0	?	?	
<i>Pneumatostega</i>	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Derwentia</i>	0	?	0	0	2	0	0	0	0	1	0	1	0	1	?	1	0	0	1	
<i>Nanolania</i>	1	?	0	0	2	2	1	0	?	?	?	0	?	?	1	1	0	1	1	
<i>Sangaia</i>	3	?	0	?	0	0	1	0	?	?	?	0	1	?	?	?	0	1	?	
<i>Mahavisaurus</i>	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Indobrachyops</i>	?	?	0	?	?	?	1	1	?	?	?	1	1	?	?	1	0	?	1	
<i>Trucheosaurus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Rewana</i>	1	?	0	?	?	?	1	?	?	1	0	?	1	1	1	1	0	?	1	
Taxon	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
<i>Benthosuchus</i>	0	0	1	1	1	2	1	2	1	2	0	1	0	1	1	1	1	1	0	0
<i>Watsonisuchus</i>	0	0	1	1	1	2	1	2	1	2	0	2	0	0	1	1	?	1	0	0
<i>Rhineceps</i>	2	0	0	0	1	2	1	1	0	1	0	1	0	0	1	0	—	0	0	0
<i>Australerpeton</i>	1	0	1	1	1	2	1	0	1	1	0	2	0	0	1	0	—	?	?	0
<i>Peltobatrachus</i>	0	?	?	?	?	?	?	?	?	1	0	3	0	1	1	1	?	?	?	?
<i>Xenobrachyops</i>	2	1	0	0	0	0	0	0	1	0	0	2	0	0	0	1	0	1	?	0
<i>Bothriceps</i>	2	0	?	?	?	?	?	?	?	0	0	2	0	1	0	1	0	?	?	?
<i>Keratobrachyops</i>	2	1	0	0	1	0	0	0	1	0	0	2	0	1	0	1	0	1	1	0
<i>Lapillopsis</i>	0	0	0	1	0	0	0	0	1	1	0	2	0	1	1	1	1	?	1	1
<i>Trematosaurus</i>	1	0	1	1	1	1	1	0	1	0	0	1	0	0	1	1	0	1	0	?
<i>Lydekkerina</i>	0	0	0	1	1	1	0	1	0	1	0	1	0	1	1	1	1	1	0	0
<i>Luzocephalus</i>	0	0	?	?	?	1	1	1	1	0	0	0	0	1	1	?	?	?	?	?
<i>Chomatobatrachus</i>	0	0	0	0	1	2	1	2	1	2	0	2	0	1	0	?	?	?	?	?
<i>Laidleria</i>	3	0	?	?	1	2	0	0	0	0	?	?	0	1	0	1	?	?	?	?
<i>Uruyiella</i>	?	?	0	1	1	2	?	?	?	?	?	?	?	1	1	?	?	?	?	?
<i>Rhytidosteus</i>	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	1	1	?	?	?
<i>Boreopelta</i>	?	?	?	0	1	?	?	?	?	0	0	?	1	1	0	?	?	?	?	?
<i>Deltasaurus</i>	2	?	0	1	0	0	0	0	0	0	0	3	1	0	1	1	?	0	0	?
<i>Arcadia</i>	2	?	0	1	1	2	1	?	?	?	?	?	1	0	1	1	1	1	0	0
<i>Peltostega</i>	?	?	?	?	1	?	?	?	?	0	0	2	1	0	0	?	?	?	?	?
<i>Pneumatostega</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	1	0	?
<i>Derwentia</i>	2	0	?	?	?	?	1	1	?	0	0	3	1	0	1	?	?	?	?	?
<i>Nanolania</i>	?	?	?	?	?	?	?	?	?	2	0	2	0	1	0	?	?	?	?	?
<i>Sangaia</i>	?	?	?	?	?	?	?	?	?	0	0	2	1	0	1	?	?	?	?	?
<i>Mahavisaurus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	1	0
<i>Indobrachyops</i>	?	?	?	?	?	?	?	?	?	?	?	3	1	?	1	?	?	?	?	?
<i>Trucheosaurus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Rewana</i>	2	2	0	1	1	2	1	1	0	?	?	?	?	?	1	?	?	?	?	?
Character Taxon	81	82	83	84	85	86	87													
<i>Benthosuchus</i>	2	0	1	—	0	0	1													
<i>Watsonisuchus</i>	2	0	1	—	0	1	1													
<i>Rhineceps</i>	0	0	1	—	0	0	0													
<i>Australerpeton</i>	2	0	1	—	0	1	2													
<i>Peltobatrachus</i>	?	0	0	0	0	0	?													
<i>Xenobrachyops</i>	2	1	0	—	2	0	1													

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Appendix 2: data matrix

<i>Bothriceps</i>	?	1	0	–	1	0	?
<i>Keratobrachyops</i>	1	0	0	–	?	0	0
<i>Lapilopsis</i>	2	0	0	1	1	0	2
<i>Trematosaurus</i>	?	0	?	–	?	0	2
<i>Lydekkerina</i>	0	0	1	0	0	1	2
<i>Luzocephalus</i>	?	?	?	?	?	?	?
<i>Chomatobatrachus</i>	?	?	?	?	?	?	?
<i>Laidleria</i>	?	0	0	–	?	?	?
<i>Uruyiella</i>	?	?	?	?	?	?	?
<i>Rhytidosteus</i>	?	0	1	?	?	?	?
<i>Boreopelta</i>	?	?	?	?	?	?	?
<i>Deltasaurus</i>	0	0	0	?	0	1	0
<i>Arcadia</i>	0	0	1	0	0	1	0
<i>Peltostega</i>	?	?	?	?	?	?	?
<i>Pneumatostega</i>	0	?	?	?	?	?	0
<i>Derwentia</i>	?	?	?	?	?	?	?
<i>Nanolania</i>	?	?	?	?	?	?	?
<i>Sangaia</i>	?	?	?	?	?	?	?
<i>Mahavisaurus</i>	0	0	1	0	?	1	0
<i>Indobrachyops</i>	?	?	?	?	?	?	?
<i>Trucheosaurus</i>	?	?	?	?	?	?	?
<i>Rewana</i>	?	?	?	?	?	?	?
