

RHYTIDOSTEID TEMNOSPONDYLS IN GONDWANA: A NEW TAXON FROM THE LOWER TRIASSIC OF BRAZIL

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Abstract: A new South American Early Triassic stereospondyl is described and considered to represent a new taxon, *Cabralia lavinae* gen. et sp. nov. The material consists of two well-preserved skull fragments. According to recent phylogenetic analyses of rhytidosteids and related taxa, the new taxon is referred to the Rhytidosteidae based on the presence of orbits that are located close to the skull margins, an otic notch that is reduced to an embayment, tabular horns that are reduced and broad based, a straight posterior margin of the palate, skull sculpture with nodules and pustules, and a 'twisted' quadrate ramus of the pterygoid. The presence of a prominent lacrimal bone suggests a basal position within

Rhytidosteidae for *C. lavinae*, and possibly a close relationship with the Indian *Indobrachyops*, because all other known rhytidosteids exhibit the derived condition of an absence of the lacrimal. The presence of a basal rhytidosteid in the Paraná Basin of South America strongly supports previous hypotheses of a Gondwanan origin and radiation of stereospondyl temnospondyls during the Early Triassic, but leaves unresolved the question of where exactly they arose within that region.

Key words: Temnospondyli, Rhytidosteidae, Gondwana, palaeobiogeography, Early Triassic, Brazil.

At the beginning of the Triassic, temnospondyl stereospondyls were already widespread in Pangaea and are among the most frequently encountered tetrapods in Triassic continental deposits, predominating in both fluvial and lacustrine facies (Cosgriff 1984; Milner 1990; Schoch and Milner 2000; Warren 2000). Among them, rhytidosteids were already present in many different areas of Gondwana (Antarctica, South Africa, Madagascar, Australia, India) and Laurasia (Greenland, northern Europe) during the Early Triassic (Wiman 1916; Cosgriff 1974, 1984; Cosgriff and Zawiskie 1979; Shishkin 1980, 1994; Shishkin and Vavilov 1987; Marsicano and Warren 1998; Schoch and Milner 2000; Warren *et al.* 2000). Moreover, their short temporal distribution, from the latest Permian to the earliest Triassic (Marsicano and Warren 1998; Warren 2000), has led several authors to claim rhytidosteids as useful biostratigraphic markers (Cosgriff 1969, 1984; Anderson and Cruickshank 1978; Kitching 1978; Shishkin 1994; Groenewald and Kitching 1995).

In South America, the rhytidosteid record used to be doubtful and limited to scattered dermal skull fragments

that were tentatively referred to this group based on their pustular sculpture (Lavina and Barberena 1985; Dias-da-Silva *et al.* 2005). All these specimens were collected from the Lower Triassic Sanga do Cabral Formation in southern Brazil (Lavina and Barberena 1985). Recently, a new stereospondyl was found in the same horizon and was considered to represent a new rhytidosteid taxon (Dias-da-Silva and Schulz 1999). It consists of a fairly complete left half of the dermal skull roof with part of the occiput (U 4302), and a right palatal fragment (U 4303), which includes the corpus of the parasphenoid and the pterygoid. Both specimens were found close to each other but not in direct association.

The present contribution is a full description of the new rhytidosteid specimen. This record constitutes the first undoubted rhytidosteid temnospondyl from South America. The affinities of the taxon are discussed in a phylogenetic context by reference to recent analyses of rhytidosteids and related taxa (Milner 1990, 1991; Marsicano and Warren 1998; Yates and Warren 2000; Damiani 2001). Comparisons have been made with all known

rhytidosteids and some brachyopoids and 'lydekkerinids' (*sensu* Milner 1990, 1991). Nearly all rhytidosteid, 'lydekkerinid' and brachyopoid taxa mentioned in our discussion were observed directly by either Dias-da-Silva or Marsicano.

GEOLOGICAL SETTING

The Paraná Basin constitutes a large Ordovician–Cretaceous intracratonic depocentre filled with both marine and continental rocks. This basin extends over an area of about 1.4 million km², distributed over Brazil, Paraguay, Uruguay and Argentina (Barberena *et al.* 1985; Zalan *et al.* 1991). During the Triassic in the southern part of Brazil, the infilling was entirely non-marine, and the sequence is lithostratigraphically subdivided, from the base to the top, into the Sanga do Cabral Formation, the Santa Maria Formation and the Caturrita Formation (Andreis *et al.* 1980; Scherer *et al.* 2000). The Sanga do Cabral Formation (Text-fig. 1), which represents the Lower Triassic, also occurs in Uruguay, where the deposits are locally included in the Buena Vista Formation (Andreis *et al.* 1996). The Sanga do Cabral Formation (50–100 m thick) overlies the Upper Permian Rio do Rasto and Pirambóia formations. It is composed of massive to trough cross-bedded intraformational conglomerates and horizontally bedded sandstones that were interpreted as being deposited by braided river systems with poorly confined channels developed on a low-gradient alluvial plain. Towards the top, interbedded laminated mudstone lenses are present and have been related to deposition in small ponds and lakes (Scherer *et al.* 2000; Zeffass *et al.* 2003). Palaeocurrent data suggest a north-east trend for the fluvial transport, with the uplifted sedimentary terrane source areas located to the south and south-west (Zeffass *et al.* 2000). The bone-bearing beds correspond to the intraformational conglomerates, where vertebrate remains are generally found disarticulated and fragmented.

The Early Triassic age of the Sanga do Cabral Formation is based on its correlation with the 'impoverished zone' (*Procolophon* Subzone *sensu* Neveling *et al.* 1999) of the Karoo Basin in South Africa (Abdala *et al.* 2002; Cisneros and Schultz 2002). This was based on the presence of *Procolophon pricei* and *P. brasiliensis* and putative non-mammalian cynodonts of ?thrinaxodontid affinities in both southern Brazil and South Africa (Abdala *et al.* 2002; Cisneros and Schultz 2002).

Institutional abbreviations. U, Universidade Vale do Rio dos Sinos, Rio Grande do Sul (Brazil).

Anatomical abbreviations. apj, alar process of the jugal; ar, ascending ramus of the pterygoid; ex, exoccipital; f, frontal; ios,

infraorbital sulcus; j, jugal; l, lacrimal; mx, maxilla; p, parietal; paf, parietal foramen; pf, prefrontal; po, postorbital; pof, postfrontal; pp, postparietal; pqf, paraquadrate foramen; pr, palatine ramus of the pterygoid; psp, parasphenoid; pt, pterygoid; ptf, posttemporal fenestra; q, quadrate; qj, quadratojugal; qr, quadrate ramus of the pterygoid; sh, palatal shagreen; smx, septomaxilla; sos, supraorbital sulcus; sq, squamosal; st, supratemporal; t, tabular; X, vagus foramen.

SYSTEMATIC PALAEOLOGY

TEMNOSPONDYLI Zittel, 1888

STEREOSPONDYLI Zittel, 1888

TREMATOSAURIA Romer, 1947 (*sensu* Yates and Warren, 2000)

RHYTIDOSTEIDAE von Huene, 1920

Revised diagnosis. Temnospondyl stereospondyls with triangular or subtriangular skulls that are shallow in occipital view; orbits and external nares close to the margins of the skull; lacrimal bone and lacrimal flexure usually absent; sculpture of the dermal bones with a 'spider's web' pattern with prominent nodes or pustules at the points of junction and bifurcation of sculpture ridges; tabular horns reduced or absent and otic embayment poorly incised or absent; quadrate ramus of the pterygoid narrow and 'twisted' (*sensu* Marsicano and Warren 1998); presence of a distinctive triangular quadrate condyle; pterygoid-parasphenoid plate broad and the cultriform process of the parasphenoid also broad and not ventrally keeled; ascending ramus of the pterygoid usually does not reach the skull roof, producing a dorsal palatoquadrate fissure; ventral surface of the palatal bones is uniformly covered by a shagreen of small denticles.

CABRALIA gen. nov.

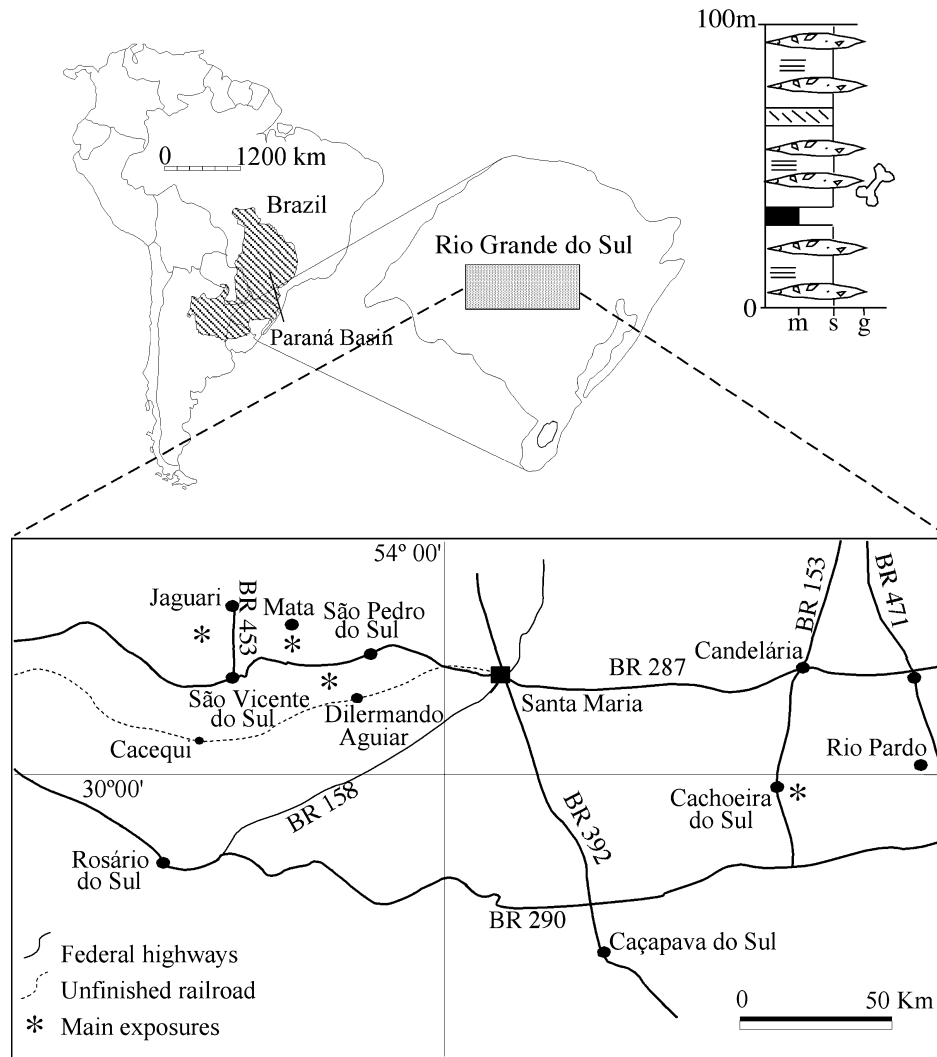
Derivation of name. From the lithostratigraphic unit, Sanga do Cabral Formation, from which the new specimens were recovered.

Type species. *Cabralia lavinai* sp. nov.

Holotype. U 4302, a nearly complete left half of a dermal skull roof and occiput.

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

Diagnosis. A rhytidosteid temnospondyl distinguished from all other rhytidosteids by the following combination of characters: presence of a well-developed lacrimal with no lacrimal flexure on the infraorbital sensory sulcus of the



TEXT-FIG. 1. Location map of the main outcrops of the Sanga do Cabral Formation in Rio Grande do Sul, and generalized stratigraphic section of the unit modified from Zeffass *et al.* (2003); the bone indicates the tetrapod-bearing level.

lateral line system; tabular horns composed of both the tabular and the squamosal; presence of horn-like projections on the posterior margin of the postparietal; ornamented septomaxilla located behind the posterior border of the nares; the jugal extends beyond the anterior orbital margin; compared with other rhytidosteid taxa, the ascending ramus of the pterygoid is relatively tall and arises from dorsal surface of the pterygoid as a smooth concave lamina.

Cabralia lavinae sp. nov.

Text-figures 2–6

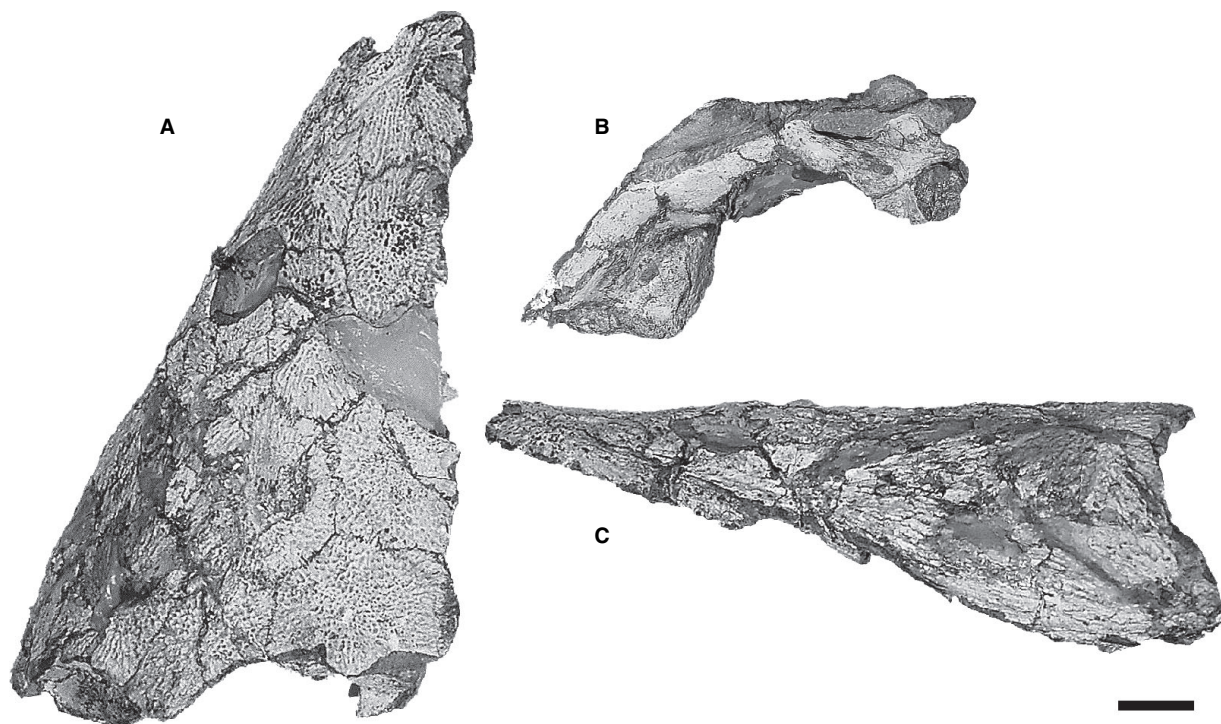
Derivation of name. In honour of Dr Ernesto Luiz Lavina, a Brazilian geologist who collected the specimens.

Diagnosis. As for the genus by monotypy.

Occurrence and stratigraphical range. Municipality of Cachoeira do Sul, Rio Grande do Sul (Brazil); Sanga do Cabral Formation of the Rosário do Sul Group (Paraná Basin), Lower Triassic (equivalent to the *Procolophon* Subzone *sensu* Neveling *et al.* 1999).

Description

Preservation. U 4302 consists of most of the left half of a skull, with the skull table bones well preserved; only the tip of the snout and the ventral border of the cheek are missing. In palatal view, only a fragment of the alar process of the jugal and part of the ventral border of the maxilla are present. The maxilla preserves the broken bases of teeth along its ventral margin. The ornamentation and sutures of the skull table bones are clear, although in the temporal region the sutures become less distinguishable because of the presence of several cracks. In occipital



TEXT-FIG. 2. *Cabralia lavinai* gen. et sp. nov., holotype U 4302. Photographs of partial skull in A, dorsal, B, occipital, and C, lateral views. Scale bar represents 20 mm.

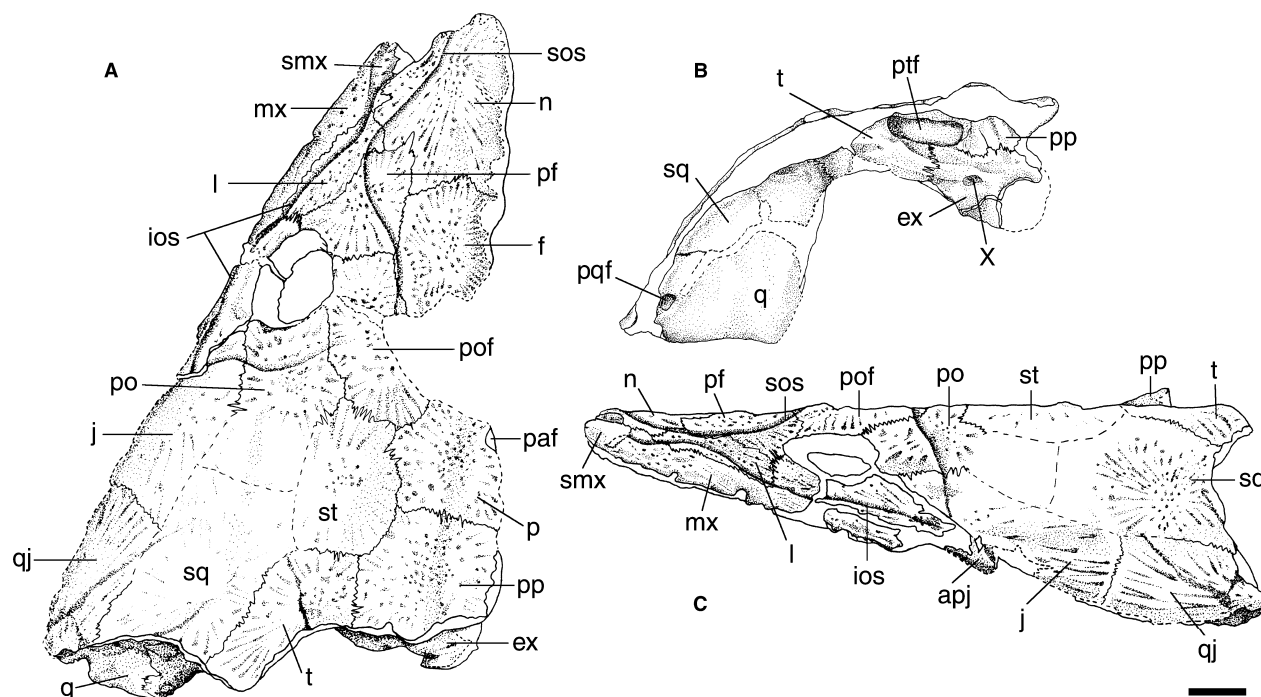
view, the skull outline appears to be deeply vaulted. However, there is a post-mortem fracture between the tabular and squamosal bones, so the likely overall occipital shape is shallower than it appears. The paratype specimen U 4303 includes a right palatal fragment, which is partially preserved.

Skull. The skull is dorsoventrally flattened and gently subtriangular, with the occiput very broad and the lateral margins nearly straight (Text-figs 2–3). The nostrils were evidently close to the anterior margin of the skull table and are anteroposteriorly elongated with a slightly raised medial-posterior border. The orbits are located in the anterior half of the skull; they are relatively small, anteroposteriorly oval and close to the lateral border of the skull roof. The left half of a rounded pineal (parietal) foramen is visible in the left parietal. The occipital border of the skull roof is slightly concave between the tabular horns, which are unsupported, broadly based triangles, and limit medially a shallow otic notch. A short projection extends posteriorly from the postparietal. In dorsal view, the occipital and the quadrate condyles are nearly in the same transverse line. The skull table seems to have a depressed midline particularly over the postparietals and the parietals.

Sculpturing and lateral line system. The bones of the skull roof display a reticulate pattern of ornamentation ('spider's web' pattern, *sensu* Cosgriff and Zawiskie 1979) in that it consists of pitting at the bone ossification centres, which becomes a ridge-grooved pattern peripherally. Small, rounded nodes occur at the points of junction of the radiating and concentric ridges, and no zones of intensive growth are visible. The lateral line system con-

sists of narrow grooves that are better preserved in the bones of the anterior half of the skull. The infraorbital sulcus runs along the maxilla, close to the suture with the lacrimal, continues over it and extends posteriorly onto the jugal, lateral and posterior to the orbit. There is no lacrimal flexure of the infraorbital sulcus on the lacrimal bone. The supraorbital sulcus extends anteroposteriorly medial to the external naris, crossing the nasal, prefrontal, frontal and postfrontal.

Skull roof. The ventral rim of the skull roof is formed, anteriorly, by the maxilla (the anteriormost part of which is not preserved) and, posteriorly, by the jugal and quadratojugal. A small, sculptured septomaxilla is present on the posterolateral border of the external naris. It is quite rounded and bordered laterally by the maxilla and medially by the nasal. The jugal extends slightly anterior to the orbit to form its ventrolateral rim, whereas the posterior limits of the jugal are not clear. On the posterolateral corner of the skull the quadratojugal projects slightly backwards as a short knob. The lacrimal is well developed and anteroposteriorly elongated, but it does not contact either the nostril or the orbit. The prefrontal is L-shaped and forms the anterior border of the orbit, where it contacts the jugal to exclude the lacrimal from the orbital margin. The postfrontal, which is part of the circumorbital series, is narrowly rectangular and forms the posteromedial border of the orbit. The postorbital forms the posterior border of the orbit, but its sutures are not clear posteriorly. The nasal is a quadrangular, relatively large bone which contacts, behind the septomaxilla, the maxilla and the lacrimal. Posteriorly the nasal has a broad contact with the frontal and the prefrontal. When compared with the marginal and circumorbital series, the



TEXT-FIG. 3. *Cabralia lavinae* gen. et sp. nov., holotype U 4302. Interpretive drawings of partial skull in A, dorsal, B, occipital, and C, lateral views. Scale bar represents 20 mm. For explanation of abbreviations, see text.

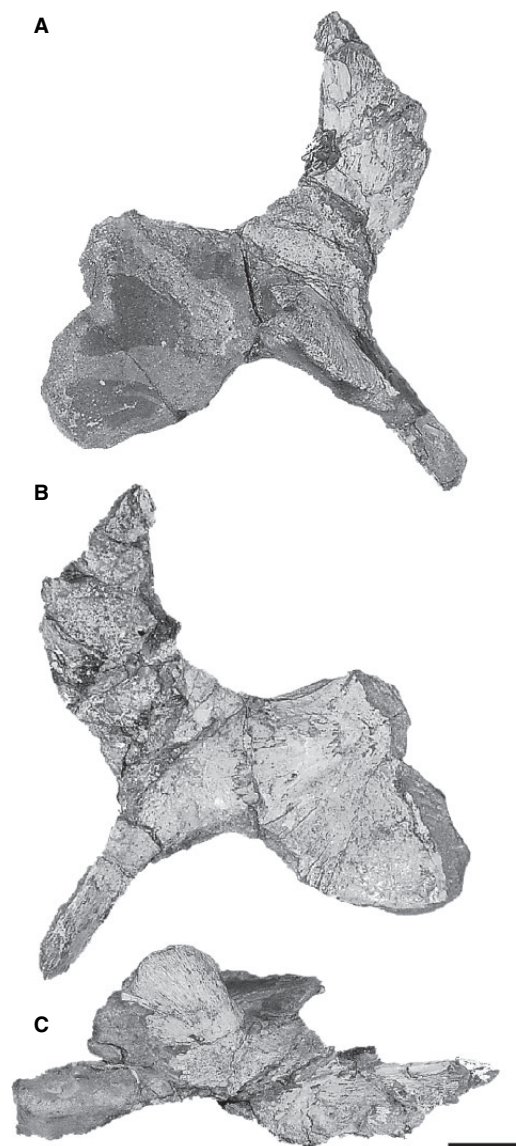
remaining bones of the midline series, namely the frontal, the parietal and the postparietal, are polygonal and relatively wide. The short, 'horn-like' occipital process of the postparietal is broader than it is long. Posterior to the postfrontal, the large, polygonal supratemporal is bordered by the postfrontal, the parietal, the postparietal and the tabular, although the contact with the squamosal is not preserved. The tabular has a long suture with the squamosal, half-way along the otic embayment, and the tabular projection (tabular horn) is formed partially by the squamosal. The broad-based, triangular tabular horn is unsupported distally. Finally, the squamosal is a large bone and its posterior border forms the outline of the central portion of a shallow otic embayment.

Palate. The only palatal structures preserved with the left half of the skull roof U 4302 are part of the alar process of the jugal and a small section of the maxilla. Palatal fragment U 4303 consists of a right pterygoid with part of the corpus of the parasphenoid attached (Text-figs 4–5). The parasphenoid preserves only the right half of the corpus, which is broken anteriorly very close to the base of the cultriform process, with which it has a broad suture. The ventral surface of the parasphenoid is smooth and flat with no ornamentation and/or shagreen of denticles. Similarly, the pterygoid corpus is devoid of shagreen. Conversely, a dense shagreen is preserved on the palatine ramus of the pterygoid, which is broken away anteriorly close to its suture with the palatine. The quadrate ramus of the pterygoid is posterolaterally directed, with its proximal portion being orientated horizontally and its posterior portion being orientated vertically such that the whole ramus appears 'twisted' (*sensu* Marsicano and Warren 1998). Distally, it is broken off, so its contact with the

quadrate is not preserved. The ascending ramus of the pterygoid arises along the dorsal surface of the pterygoid corpus and continues over the dorsal surface of the proximal half of the quadrate ramus. The ascending ramus is relatively tall and probably reached the skull table. It curves smoothly inward proximally, above the pterygoid corpus, and is slightly recurved posteriorly in occipital view.

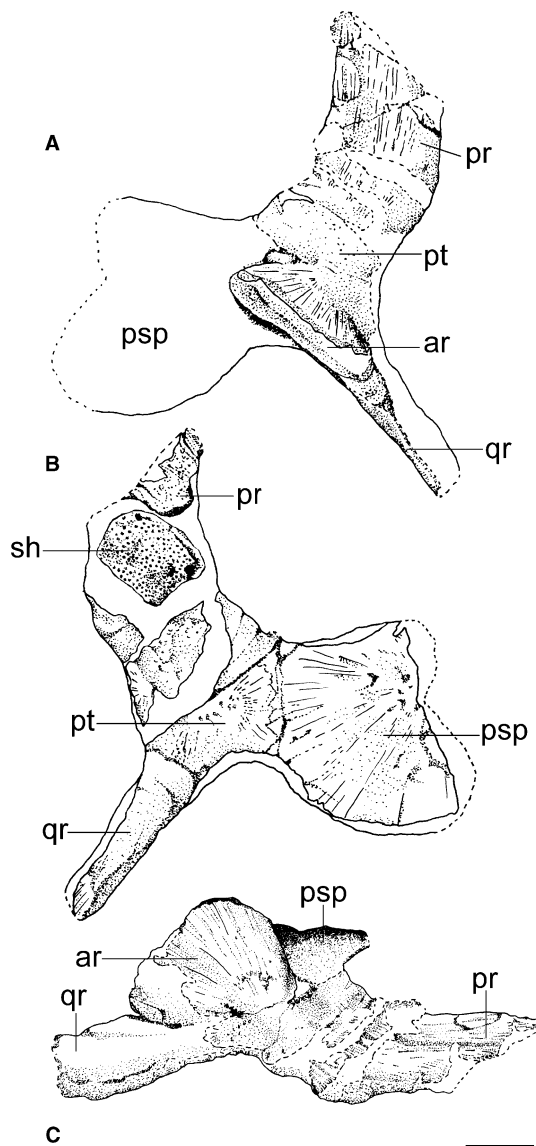
Occiput. In posterior view, the general shape of the palate in U 4302 is slightly vaulted. The exoccipital condyle is elliptical in cross-section and short. The paroccipital process is a short, anteroposteriorly flattened blade that contacts a ventromedially directed occipital process of the tabular. A large foramen, probably for the vagus nerve (CN X), occurs close to the base of the paroccipital process just lateral to the exoccipital condyle. The vertical process of the exoccipital is short and broad, producing a subrounded posttemporal fenestra. The occipital surface of the cheek is composed of the descending lamina of the squamosal, the quadratojugal and the quadrate. Both the squamosal and the quadratojugal surfaces are partially broken so that the quadrate is completely exposed in occipital view. A large paraquadrate foramen is present on the ventrolateral corner of the quadratojugal. The occipital surface of the cheek forms a vertically orientated trough (squamosal–quadratojugal trough), which is bordered dorsolaterally by a smooth, occipital flange of the squamosal and the quadratojugal.

Comparison. The possession by *Cabralia* of a subtriangular, nearly straight-sided skull, with a wide occiput and the orbits close to the lateral skull margins (see reconstruction



TEXT-FIG. 4. *Cabralia lavinai* gen. et sp. nov., paratype U 4303. Photographs of a partial palate in A, dorsal, B, ventral, and C, dorsolateral views. Scale bar represents 20 mm.

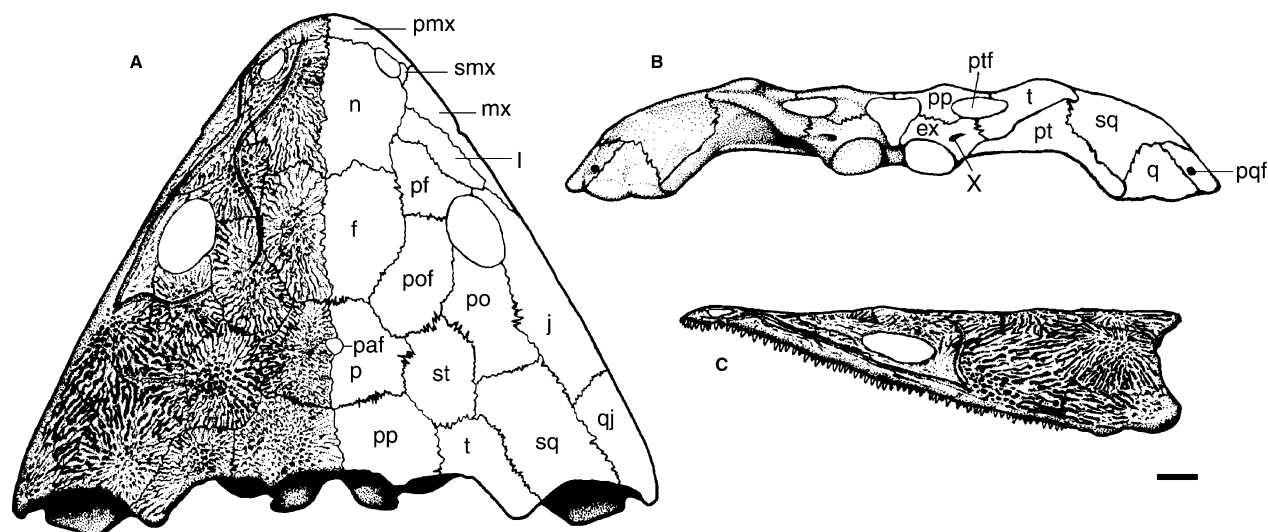
in Text-fig. 6) is shared with several rhytidosteids such as *Deltasaurus kimberleyensis* Cosgriff, 1965, *Laidleria gracilis* Kitching, 1957 (redescribed by Warren 1998), *Mahavisaurus dentatus* Lehman, 1966, *Pneumatostega potamia* Cosgriff and Zawiskie, 1979 and *Trucheosaurus major* Woodward, 1909 (redescribed by Marsicano and Warren 1998). The Brazilian taxon also shares with the Australian taxa *Arcadia myriadens* Warren and Black, 1985, *Derwentia warreni* Cosgriff, 1974, *Nanolania anapretia* Warren and Hutchinson, 1990 (reinterpreted by Yates 2000), *Rewana quadricuneata* Howie, 1972 and *Trucheosaurus* the anterior position of the orbits. As mentioned above, the sculpturing of the dermal bones in *Cabralia* follows the so-called



TEXT-FIG. 5. *Cabralia lavinai* gen. et sp. nov., paratype U 4303. Interpretive drawings of partial palate in A, dorsal, B, ventral, and C, dorsolateral views. Scale bar represents 20 mm. For explanation of abbreviations, see text.

‘spider’s web’ rhytidosteid pattern (*sensu* Cosgriff and Zawiskie 1979), where nodules or pustules are developed on the points of junctions and bifurcation of the crests and ridges. This condition is present in nearly all rhytidosteids (Marsicano and Warren 1998), including *Indobrachyops panchetensis* von Huene and Sahni, 1958 and the ‘lydekkerinid’ *Luzocephalus blomi* Shishkin, 1980.

Cabralia shares with ‘lydekkerinids’ some characters that are plesiomorphic for rhytidosteids (see Yates and Warren 2000), such as the presence of an ornamented septomaxilla, a well-developed lacrimal bone and the absence of a palatoquadrate fissure. A lacrimal is also pre-



TEXT-FIG. 6. *Cabralia lavinae* gen. et. sp. nov., reconstruction of the skull in A, dorsal, B, occipital and C, lateral views. Scale bar represents 20 mm. For explanation of abbreviations, see text.

sent in the Indian rhytidosteid *Indobrachyops*. In the Brazilian taxon the tabular horn and otic embayment are reduced, as in all rhytidosteids except for *Trucheosaurus* and *Laidleria*, where both a tabular horn and an otic notch are absent. As previously mentioned, the tabular horn of *Cabralia* is unusual due to the small contribution from the squamosal, a condition previously observed only in the rhytidosteid *Mahavisaurus* from Madagascar (Lehman 1966; Cosgriff and Zawiskie 1979).

The ascending ramus of the pterygoid in *Cabralia* differs from all 'lydekkerinid' and rhytidosteid taxa in which the structure is relatively well known. This ramus in the Brazilian taxon arises from the dorsal surface of the pterygoid as a smoothly concave lamina and continues over the proximal half of the dorsal surface of the quadrate ramus. In 'lydekkerinids' the ascending ramus of the pterygoid forms a continuous curve with the posterior edge of the quadrate ramus, and does not extend across the dorsal surface of the ramus (see Warren and Black 1985). In rhytidosteids the ascending ramus of the pterygoid arises from the dorsal surface of the pterygoid corpus, as in *Cabralia*, but it is a relatively shallow, uncurved lamina that crosses obliquely the corpus of the pterygoid (Warren and Black 1985; Marsicano and Warren 1998). The morphology of the ascending process in *Cabralia* is comparable with that described in brachyopoids, particularly in chigutisaurids, where the process is relatively tall and contacts the skull table. The quadrate ramus of the pterygoid of *Cabralia* is slightly downturned in occipital view, such as in the rhytidosteids *Arcadia* and *Nanolania*, and is also horizontally orientated proximally and vertically orientated distally ('twisted' *sensu* Marsicano and Warren 1998). This condition is present in all rhytidosteids except the Australian *Derwentia*. In *Derwentia*, as in

'lydekkerinids', the quadrate ramus of the pterygoid is evenly curved from the horizontal plane of the corpus to the vertical plane throughout its length.

The ventral surface of the parasphenoid and pterygoid corpus is flat and smooth in *Cabralia* without any sign of ornamentation or denticles. In *Cabralia*, denticles are only present in the palatine ramus of the pterygoid. In 'lydekkerinids' they are clearly present on both the corpus of the parasphenoid and the corpus and palatal ramus of the pterygoid (e.g. *Chomatobatrachus halei* Cosgriff, 1974; *Eolydekkerina magna* Shishkin *et al.*, 1996; and *Lydekkerina* sp.). Conversely, and similarly to *Cabralia*, denticles appear to be restricted to some bones of the palatal series in rhytidosteids (e.g. *Derwentia*, *Laidleria* and *Nanolania*).

DISCUSSION

Yates and Warren (2000) carried out a phylogenetic analysis of Temnospondyli and, within that group, considered Stereospondyli as a monophyletic group diagnosed by several derived character states. Within Stereospondyli, the Brazilian *Cabralia* can be referred to Trematosauria (*sensu* Yates and Warren 2000), based on the presence of an interorbital space that is greater than 50 per cent of the skull width at the mid-orbital level and the absence of ventral depressions ('pockets' *sensu* Watson 1962) on the ventral surface of the parasphenoid plate. The presence of a reduced otic embayment in *Cabralia* places it in an unnamed clade that includes Rhytidosteidae, *Laidleria*, plagiosaurids and brachyopoids (see Yates and Warren 2000).

The first computerized phylogenetic analysis of the Rhytidosteidae was carried out by Marsicano and Warren

(1998), who considered it to be a monophyletic group diagnosed by several unequivocal synapomorphies. That analysis also supported the hypothesis that 'lydekkerinids' were paraphyletic with respect to rhytidosteids (Milner 1990, 1991). In contrast, a recent phylogenetic analysis of mastodonsauroid stereospondyls by Damiani (2001) suggested that 'lydekkerinids' might be monophyletic, although he pointed out that a detailed parsimony analysis of all 'lydekkerinid' taxa was required in order to solve this conflicting hypothesis.

In Marsicano and Warren's (1998) analysis the relationships within Rhytidosteidae are poorly resolved. Hence, a new phylogenetic analysis of the rhytidosteids and related groups will be considered fully elsewhere (Dias-da-Silva and Marsicano in prep.). Nevertheless, some considerations concerning the likely position of *Cabralia* within Rhytidosteidae can be discussed. Based on several synapomorphies listed in Marsicano and Warren (1998), *Cabralia* is considered here to be a rhytidosteid because of the position of orbits close to the skull margins, an otic notch that is reduced to a shallow embayment, tabular horns that are reduced and broadly based, a straight posterior margin of the palate, skull sculpturing with nodules and pustules, and a 'twisted' quadrate ramus of the pterygoid. *Cabralia* appears to occupy a more basal position within Rhytidosteidae, more closely related to *Indobrachyops* than to all other rhytidosteids, due to the presence of a well-developed lacrimal bone. The shape of the ascending process of the pterygoid in *Cabralia* is different from that in other rhytidosteids (see Warren and Black 1985; Marsicano and Warren 1998). Intriguingly, it resembles that in brachyopoids (see Warren and Marsicano 2000), a group that in a phylogenetic analysis of temnospondyls was considered to be the sister group of rhytidosteids (Yates and Warren 2000).

The apparent radiation of stereospondyls in the Early Triassic was suggested to be a continuation of a Late Permian event that probably took place in Gondwana, because the earliest and most diverse of the Triassic temnospondyl faunas occur in that area (Marsicano and Warren 1998; Warren 2000). Moreover, Warren *et al.* (2000) proposed that the stereospondyls arose in east Gondwana, survived the end-Permian extinction in a refugium in what is now Australia, and then radiated rapidly and spread throughout Gondwana and Laurasia by the earliest Triassic. This scenario is justified by the presence of the basal members of the Stereospondyli (e.g. *Lapillopsis*, *Peltobatrachus*, rhinesuchids) and the most diverse Early Triassic stereospondyl faunas, including basal members of Brachyopoidea, in east Gondwana (Warren 2000; Warren *et al.* 2000). It is interesting to note that two of the basal members of Stereospondyli considered above (*Peltobatrachus* and rhinesuchids) are known from a west Gondwanan area, what is now southern Africa, which was

relatively close to the Paraná Basin throughout its history (e.g. Zersass *et al.* 2003). Moreover, the Upper Permian levels of the Paraná Basin also include representatives of rhinesuchids, known from several specimens (Barberena 1998; Barberena and Dias 1998; Dias and Barberena 2001). Only the lapillopsids are still unknown from west Gondwana (Yates 1999; Yates and Sengupta 2002).

The presence of a putative basal rhytidosteid in southern South America strongly supports previous hypotheses for a Gondwanan origin of stereospondyls (Milner 1990; Marsicano and Warren 1998; Warren *et al.* 2000). However, it raises interesting questions with regard to their geographical origin within that landmass, because a west Gondwanan origin cannot be ruled out according to the evidence presented herein. New intensive prospecting for temnospondyl remains in Late Permian–Early Triassic sequences of the Paraná Basin might shed light on stereospondyl origin and diversification in Gondwana.

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