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Osteology of *Leptopleuron lacertinum* Owen, a procolophonid parareptile from the Upper Triassic of Scotland, with remarks on ontogeny, ecology and affinities

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**ABSTRACT:** The Late Triassic reptile *Leptopleuron lacertinum* Owen, 1851 is described for the first time in full anatomical detail, based on newly produced silicone and plastic casts of the numerous specimens preserved as natural moulds. Previously, only the braincase has been described from these detailed casts. *Leptopleuron* is reconstructed as a 270-mm-long reptile with a long tail, although it is possible that even the largest known specimens were still sub-adults. Within Procolophonoidea, *Leptopleuron* is distinguished by the following non-braincase autapomorphies: two flattened, triangular spines of equal size on the quadrate-jugal; V-shaped groove on the jugal; the anterior tip of the jugal in contact with the posterolateral extension of the nasal; minimal contact between the jugal and the postorbital; frontals narrow anterior to the orbitotemporal openings; the vomerine dentition consisting of a tall and a short pair of fangs; broad medial ridge of pleurocentra of the dorsal vertebrae divided into three separate ridges by two deep grooves on each pleurocentrum; distinct three-fold depression pattern on the ventral side of ischium; and the first phalanx on the fifth pedal digit being long and slim. *Leptopleuron* shares some features with living sand lizards and might have lived a burrowing lifestyle. The dentition and body shape of *Leptopleuron* imply it ate a diet of fibrous plant material or hard-shelled invertebrates.

**KEY WORDS:** Carnian, Leptopleuroniinae, mode of life, morphology, Procolophonoidea

The Procolophonoidea is an important group of small- to medium-sized parareptiles that emerged in the Late Permian, had a global distribution during the Triassic and disappeared by the end of the Triassic period (Modesto *et al.* 2001, 2003; Reisz & Scott 2002; Cisneros 2008a; Säilä 2009). Recent phylogenetic studies (Modesto *et al.* 2001, 2003; Ketchum & Barrett 2004) suggest a high survivorship of up to 84% for procolophonoids through the Permian-Triassic (P/Tr) mass extinction event. This is in contrast to rank-based studies estimating that the extinction event killed up to 80% of all terrestrial tetrapods (Maxwell 1992). Additionally, procolophonoids have been central to broader investigations of reptile phylogeny since procolophonids were identified as the possible sister group of turtles by Reisz & Laurin (1991) and Laurin & Reisz (1995).

The Lossiemouth Sandstone Formation (late Carnian; Late Triassic) near Elgin, northeast Scotland, preserves a diverse biota including at least four genera of basal archosaurs, a rhynchosaurs, a phenodontid, a possible coelurosaur dinosaur and the procolophonid *Leptopleuron* (Benton & Walker 1985). The leptonpleuronine procolophonid *Leptopleuron lacertinum* is represented by numerous specimens collected since the species was first described (Owen 1851). Nevertheless, apart from a recent description of the braincase (Spencer 2000), a detailed osteological description has not been forthcoming. This is mostly because specimens are preserved as natural moulds in fine-grained, cemented sandstone and casting them with plaster and gutta percha in the nineteenth century did not reveal the finer details of the skull and skeleton of *Leptopleuron* (Owen 1851; Mantell 1852; Huxley 1866; Boulenger 1904; Huene 1912, 1920). The moulds, however, preserve considerable detail when modern methods, employing PVC and silicone rubber as casting materials, are used, as in this present study. Additionally, several specimens are included that have not been previously described in the literature. The high number of specimens and the quality of the preservation means that *Leptopleuron* can rival the best-known procolophonoid genus *Procolophon*, found in South Africa, Antarctica and South America (Cisneros 2008b), in the amount of information preserved and discovered. Furthermore, the anatomical description of the postcranial skeleton of *Procolophon* (deBraga 2003) was somewhat compromised by the inclusion of a specimen, used to illustrate many details of the skeleton, that was later given the status of Procolophonidae *incertae sedis* (Modesto & Damiani 2007; Cisneros 2008b). Thus, this present study of the cranial and postcranial anatomy of *Leptopleuron* makes it the only procolophonid with an accurate description of its detailed, full morphology to be published to date.

1. **The history of the name *Leptopleuron***

The story of the naming of *Leptopleuron* is intriguing and forms a part of the famous rivalries between Sir Richard Owen...
and Dr Gideon Mantell during the 19th Century. This has led to some debate about the correct name for the reptile now recognised as *Leptopleuron lacertinum*. The first published paper to discuss and name the holotype of *Leptopleuron lacertinum* was by Owen (1851). His brief description was published on the 20th December 1851, but a more detailed description of the same specimen by Mantell was announced on the 17th December 1851, and read out at the meeting the Geological Society of London on 7th January 1852 (Benton 1980). Even before this occasion, Owen and Mantell had been involved in a series of rivalries, and Owen was generally considered to have acted unethically by rushing his short paper out before Mantell’s (Benton 1980). Mantell named the reptile *Telerpeton elginense*, and because of his more detailed account of the animal and Owen’s assumed unscrupulous behaviour, the name *Telerpeton elginense* was used when further description of additional specimens were published by Huxley (1866), Boule (1904) and Huene (1912, 1920). However, some previously unpublished letters between Charles Lyell and Dr Gideon Mantell, brought to light by Benton (1983), indicate that Mantell was well aware of Owen’s intention to publish on the specimen and that Lyell was urging Mantell to speed up his description to beat Owen to the post. Thus it might have been Mantell instead of Owen who was acting unethically. Furthermore, because Owen’s publication made it to press first, the name *Leptopleuron lacertinum* Owen must be accepted as the official name for the reptile discussed in this present paper.

2. Geological settings

The reptile-bearing rocks near Elgin, Scotland, preserve evidence of both Permian and Triassic faunas. The Upper Triassic Lossiemouth Sandstone Formation is exposed in several small fault-bounded blocks at the locations of Lossiemouth, Spynie and Findrassie (Fig. 1). The deposition of the sandstone is aeolian, with the colour being buff, yellow or pink (Peacock et al. 1968; Benton & Walker 1985). The grain size is between 0.2 mm and 0.5 mm, and the rock is composed of quartz, feldspar and, less often, brownish chert and quartzite (Peacock et al. 1968). The reptiles, including *Leptopleuron*, were discovered within this sandstone in several quarries around Lossiemouth, Spynie and Findrassie, but a good quality specimen of *Leptopleuron* was also found on a glacially-transported block of Lossiemouth Sandstone bed near Urququhart (Benton & Walker 1985). More information on the sedimentology, biota and taphonomy of the Lossiemouth Sandstone can be found in Benton & Walker (1985).

The silicone casting process started with cleaning the natural moulds of any residue with compressed air. They were then coated with two thin layers of paraloid in acetone (mild solution) 30 minutes apart, to cement any loose sand particles, and coated with silicone releaser after a further 30 minutes. A silicone mixture (95% Tiranti T20 silicone rubber and 5% solvent) was then created in an air cabinet, and was coloured reddish brown/other dark colour to make the casts easier to study and photograph. A thin layer of the silicone mixture was spread onto the natural moulds with a brush, and this was left to set for four or more hours. After this, a thicker layer of silicone was poured into the natural mould, and immediately after pouring it was shaken for some minutes to remove air bubbles from the silicone. This was left to set for two or more, and then finished either by creating a solid silicone support or by creating a supporting plaster cast that was separated from the silicone by a layer of cling film. All natural moulds and the casts were photographed and studied under a light microscope. The specimens and their components were also measured and illustrated with stipple drawings (Figs 4–19).

Institutional abbreviations: AMNH, American Museum of Natural History, New York; BGS(GSM), The British Geological Survey Museum, Keyworth, Nottingham; BMNH, The Natural History Museum, London; CGP, Council for Geoscience, Pretoria; ELGNM, Elgin Museum, Elgin; GPIT, Institut für Geowissenschaften der Universität Tübingen; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow; RSM, National Museum of Scotland, Edinburgh; UTM, University of Toronto at Mississauga.
4. Systematic palaeontology

Superfamily Procolophonoidea Romer, 1956
Family Procolophonidae Cope, 1889
Subfamily Leptopleuroninae Ivakhnenko, 1979
Genus Leptopleuron Owen, 1851

Type and only species. Leptopleuron lacertinum Owen, 1851.

Leptopleuron lacertinum Owen, 1851; p. 2.

v.1852 Telerpeton elginense Mantell, pp. 100–105, pl. 4, figs 1–6, 8–9.
v.1852 Telerpeton elginense Mantell; Lyell, p. 10, fig. 522.
v.1866 Telerpeton elginense Mantell; Huxley, pp. 77–84, figs A–E.
v.1904 Telerpeton elginense Mantell; Boulenger, pp. 470–480, text fig. 99, pl. 30–32.
v.1912 Telerpeton elginense Mantell; Huene, pp. 82–93, pl. 6–9.
v.1920 Telerpeton elginense Mantell; Huene, pp. 189–192, figs 1–3.
v.1928 Telerpeton; Gilmore, p. 5.
v.1946 Leptopleuron lacertinum Owen; Colbert, pp. 238–258, figs 4, 18.
v.1980 Leptopleuron lacertinum Owen; Benton, pp. 41–44, fig. 3.
v.1983 Leptopleuron lacertinum Owen; Benton, pp. 123–136, fig. 1.
v.1985 Leptopleuron lacertinum Owen; Benton & Walker, pp. 210, 226, text figs 3E, 6B–C, 8.
v.2000 Leptopleuron lacertinum Owen; Spencer, pp. 21–29, figs 1–7.

Holotype. RSM 1891.92.528, part and counterpart sandstone slabs, preserving the natural mould of a partial skull and most of the postcrania of a small, juvenile individual (Figs 2, 11).

Referred material. RSM 1966.43.7 (poorly-preserved ventral postcrania); RSM 1984.20.34 (skull with excellent braincase); ELGNM 1920.5 (well-preserved skull and postcrania); ELGNM 1978.718 (well-preserved postcrania with partial skull); BGS(GSM) 91087 (poorly-preserved dorsal postcrania); BGS(GSM) 91093 (postcrania with good hind limb preservation in ventral view); BMNH R3136 (well-preserved skull and postcrania); BMNH R3145, (skull and postcrania in ventral view); BMNH R3362 (partial skull and postcrania); BMNH R3558 (right mandibular ramus); BMNH R3917 (partial skull and postcrania); BMNH R3918 (postcrania with long tail); BMNH R3919 (skull and anterior postcrania); BMNH R3927 (palatal view of skull); BMNH R3928 (left posterior edge of skull); BMNH R3930 (partial maxilla and jugal); BMNH R3931 (left mandibular ramus); BMNH R4779 (well-preserved skull and postcrania); BMNH R5487 (partial skull); GPIT/AM/00682 (moderately-preserved skull and postcrania).

Type locality and horizon. Spynie, near Elgin, northeast Scotland, Lossiemouth Sandstone Formation.

Geographical and temporal distribution. Limited to the Upper Triassic (late Carnian) Lossiemouth Sandstone Formation of Scotland, locations around Lossiemouth, Spynie, and Urquhart.

Diagnosis. Small procolophonid reptile, reaching 270 mm in snout-tail length in (sub)adults. Within Procolophonoidae, Leptopleuron is characterised by the following unique autapomorphies: vomerine dentition consisting of a tall and a short pair of fangs; frontals narrow anterior to the orbitotemporal openings; V-shaped groove on the jugal; anterior tip of the
jugal in contact with the posterolateral extension of the nasal; minimal contact between the jugal and the postorbital; two flattened, triangular spines of equal size on the quadratojugal; occipital condyle strongly tripartite; metotic foramen not surrounded by bone; ascending process of basiphenoid foreshortened, forming a robust flat ended expansion, and with lateral lamella; processus infrastapedialis columella aligned with long axis of footplate; loss of foramen for nerve IX on ventral ramus of the opisthotic; posterior opening of vidian canal behind the basipterygoid process; facial nerve foramen not enclosed by the prootic; transverse process of prootic rests on the dorsal surface of the opisthotic paraoccipital process; basal tubera of basioccipital covered ventrally by basal tubera of basiphenoid; broad medial ridge of pleurocentra of the dorsal vertebrae divided into three separate ridges by two deep grooves on each pleurocentrum; distinct three-fold depression pattern on the ventral side of ischium; fifth pedal digit has only two phalanges, with proximal phalanx equal in length to two proximal phalanges of digit four.

Remarks. The early descriptive work on Leptopleuron by Owen (1851), Mantell (1852), Huxley (1866), Boulenger (1904), and Huene (1912, 1920) did not offer a diagnosis for Leptopleuron lacertinum, even though its similarities with, and differences from, other procolophonids, especially Procolophon, were noticed early on (Boulenger 1904; Huene 1912). Many bones of Leptopleuron were discussed, and also illustrated, in the early papers but because of the limited casting methods available at the time, many details were not obvious and some were incorrectly interpreted. Examples include the number of sacral ribs, which was reported as two (Boulenger 1904; Huene 1912) when in reality the number is three, and the very sizeable intercentra that were never identified as such before this present paper. Spencer (2000) provided a detailed description of the braincase and autapomorphies for Leptopleuron found in this region. All of his autapomorphies are considered valid, with the exception of the reduced length of the cultriform process of the parasphenoid because this condition is also found in Hypsognathus (Sues et al. 2000) within Procolophonoidae.

5. Anatomical description

5.1. Skull

The skull of Leptopleuron is reconstructed as 55 mm long (Fig. 3), based on the deduced size for the skull of the largest postcrania, BGS(GSM) 91093 (Table 1). The dimensions of the skull are based on the well-preserved cranium of BMNH R4779 (Fig. 4), as it has not been flattened in the same manner as some of the otherwise well-preserved specimens and appears to retain its original dimensions. Additionally, the preservation of the natural mould of BMNH R4779 in several perfectly interlocking blocks allowed the production of three-dimensional casts of the whole skull, along with details of the inner structures and dentition. The width of the skull, excluding the quadratojugal horns, is approximately equal to the length of the skull in the larger, more mature specimens, and the height (including the mandible) is approximately 32 mm. Many suture lines can be seen in BMNH R4779, but information from several other specimens (Figs 5–8) has also been used for the reconstruction. The braincase of Leptopleuron is only discussed here in its relation to the other bones of the skull, because a detailed description of this structure is provided by Spencer (2000).

5.1.1. Premaxilla. The premaxilla of Leptopleuron excludes the maxilla from the external narial opening, meeting the nasal bone both on the anterior and posterior sides of the opening (Fig. 5B). No septomaxilla appears to be present in
lingual side, making the labial cusp reach lower than the lingual. There are two supralabial foramina on the maxilla, the first one larger than the second. They are located above the gap between the first and second tooth, or above the second tooth, and above the gap between the third and fourth tooth (Fig. 4C–F). Laterally, the maxilla makes contact only with the nasal and the jugal that meet above the maxilla, excluding it from contacting the lacrimal (Fig. 4D–F).

5.1.3. Nasal. The nasal forms the dorsal margin of the external naris, with slim lateral extensions around it that terminate about midway down the margin of the naris on both its anterior and posterior side (Figs 4D–E, 5). The dorsal portion of the nasal extends both between the prefrontals to meet the frontal and around the lacrimal making contact with the jugal (Figs 4A, D–E, 6A). This dorsomedial extension of the nasal is an autapomorphy of Leptopleuron, as it prevents the lacrimal–maxillae contact that is present in all other procolophonoids. Only the anterior portion of the nasal, around and above the external naris, and the extension between the lacrimal and the maxilla can be seen in lateral view, because of the flattening of the skull in the dorsoventral plane.

5.1.4. Prefrontal. The prefrontal of Leptopleuron has dorsal exposure between the frontal and the lacrimal, with the nasals surrounding the anterior tip of this exposure (Figs 4A, 6A). This bone is similar to that of Procolophon (Carroll & Lindsay 1985), and differs markedly from the prefrontal of Hypsognathus, which is restricted to the anterior bony wall of the orbitotemporal opening (Sues et al. 2000). Leptopleuron was mistakenly scored having a similar prefrontal to Hypsognathus in the analysis of Modesto et al. (2002) based on a cast of GPIT/AM/00682 (Figs 6B, 18), and this mistaken scoring has been replicated in many following analyses (Modesto & Damiani 2003; Piñeiro et al. 2004; Cisneros 2008a, c). The prefrontal continues inside the orbitotemporal opening, forming the antorbital wall together with the lacrimal. The medial region of the prefrontal inside the orbit has not been well preserved in most specimens, with GPIT/AM/00682 showing the best preservation (Fig. 6B). No medial extension of the

Figure 4 Leptopleuron lacertinum Owen, 1851, BMNH R4779. Skull and mandible in (A) dorsal view, (B) palatal view, (C) occipital view (slightly ventral angle), (D) anterior view, and (E) right lateral view; (F) snout in left lateral view. Scale bar=10 mm. Anatomical abbreviations: a=angular; ar=articular; bo=basioccipital; bs=basisphenoid; d=dentary; ect=ectopterygoid; eo=exoccipital; ept=epipterygoid; f=frontal; j= jugal; l=lacrimal; m=maxilla; n=nasal; pal=palatine; pm=premaxilla; po=postorbital; prf=prefrontal; pt=pterygoid; q=quadratid; qj=quadratojugal; sa=surangular; sof=suborbital foramen; sp=splenial; sq=squamosal; st=supratemporal; v=vomer.
prefrontal, present in most other procophodonts, can be observed, but this area is poorly preserved in the majority of specimens. The prefrontal is excluded from contacting the suborbital foramen (Fig. 6B).

5.1.5. Lacrimal. The lacrimals extend on the skull roof between the nasal and the jugal on the lateral side and the prefrontal on the medial side. Almost the whole orbital part of the lacrimal is highly concave, forming a deep depression towards the inside of the snout (Figs 4A, 6B). This depression is interpreted as the posterior entrance of the orbitonasal canal or lateral orbitonasal foramen sensu Heaton (1979), although the actual foramen cannot be seen in any specimen. In Hypsognathus this groove is more extensive, formed by the lacrimal, the palatine and the prefrontal together, whereas in Procolophon there is no groove associated with the orbitonasal foramen (Carroll & Lindsay 1985; Sues et al. 2000). Below the depression, the lacrimal terminates at the dorsal opening of the suborbital foramen where it meets the palatine, the ectopterygoid and the jugal (Figs 4A, 6B).

5.1.6. Frontal. The frontals of Leptopleuron form the medial margins of the orbitotemporal openings as in other procophodonts. However, unlike other taxa, where the anterior portion of the frontals is the same width as the width between the orbits (Carroll & Lindsay 1985; Reisz & Scott 2002) or much broader (Sues et al. 2000), in Leptopleuron the anterior portion is much narrower before joining the border of the orbitotemporal openings (Fig. 6A). This is an autapomorphy of Leptopleuron.

5.1.7. Parietal. The postfrontal is absent and the parietal has taken up the space occupied by it in Procolophon (Carroll & Lindsay 1985), forming a small wedge between the postero-lateral margin of the frontal and the orbitotemporal opening (Fig. 6A, C). This condition is also present in some other procolophonids, including Hypsognathus (Sues et al. 2000). However, the parietals do not extend as far anteriorly between the orbits as in Hypsognathus (Sues et al. 2000) and the large pinnae foramen is situated nearer to the border of the parietals and the frontals. Nevertheless, it is positioned well anterior to the posterior margin of the orbitotemporal openings (Fig. 6A). However, the shape and size of the orbitotemporal openings, resemble those of Procolophon (Carroll & Lindsay 1985) rather than Hypsognathus, which has extremely elongated ones (Sues et al. 2000). Behind the orbitotemporal openings, the parietals make up the posterior margin of the skull, together with the supratemporals. In dorsal view, the parietals form a slight wedge-shaped projection at their junction before turning steeply downwards to create a ledge overhanging the occiput (Fig. 6A, C). The occipital ledge most likely reflects the anterior extent of the epaxial neck musculature (Carroll & Lindsay 1985). On the ventral surface, far anterior to the posterior margin of the skull, there is a small, slightly raised facet that articulates with the dorsal process of the supra-occipital (Spencer 2000). Postparietals do not appear to be present.

5.1.8. Postorbital. The postorbitals make up the postero-lateral margin of the orbitotemporal openings, extending approximately half way along the opening. Only the anterior-most tip of the postorbital makes contact with the jugal, whereas contact with the quadratojugal is extensive (Fig. 4A, E). Contact between postorbital and quadratojugal is present in many derived procophodonts, but in these taxa there is also extensive contact between the postorbital and the jugal (Carroll & Lindsay 1985; Novikov & Sues 2004; Csíros 2008a, pers. obs. SAM-PK-10192 for Teraophon). Thus, the condition of reduced contact between the postorbital and the jugal is an autapomorphy of Leptopleuron.

5.1.9. Jugal. The jugal of Leptopleuron resembles that of Hypsognathus (Sues et al. 2000) in being deep, and having a convex, anteroventrally-facing ventral margin. However, the convex margin in Leptopleuron has a far gentler downwards curvature, and the ventral margin terminates at the level of the tooth-bearing margin of the maxilla (Figs 4D–F, 5A, 11C). The jugal forms the anterolateral margin of the orbitotemporal opening, and below this, above the temporal margin of the cheek, there is a narrow, V-shaped groove on the lateral surface (Fig. 4D–F) that is unique to Leptopleuron. Anterior to this, a medial process of the jugal makes contact with the postero-lateral extension of the nasal (Fig. 4A, E).

5.1.10. Quadratojugal. The quadratojugal of Leptopleuron bears two spines of approximately equal size. Both are dorso-ventrally flattened. The anterior one, attached slightly more ventrally, points laterally, whereas the posterior one points in a postero-lateral direction (Figs 4, 5B). The spines bear grooves, which in most specimens are very faint (Figs 4, 5B, 6A, 11C), but in RSM 1984.20.34 are extremely deep on all preserved spines (Fig. 6D). Because RSM 1984.20.34 shows exceptionally good preservation of fine details (including of the brain case, Spencer 2000), this is considered to reflect the real condition of the bony spines. In Procolophon and Hypsognathus faint grooves have been considered indicative of a keratinous covering in life (Carroll & Lindsay 1985; Sues et al. 2000). The quadratojugal also bears a network of grooves on the lateral surface around the spines (Figs 4A–E, 5A, 11C), possibly reflecting the vascular supply to the specialised epidermal tissue covering the spines (Sues et al. 2000). The quadratojugal does not extend as far ventrally as that of Hypsognathus (Sues et al. 2000) but the postero-lateral expansion is very similar in both taxa. The middle ear cavity, containing the otic notch, is totally excluded from lateral view because the quadratojugal is expanded posteriorly to form the lateral wall of the cavity (Fig. 4C, E).

5.1.11. Quadrate. The central portion of the quadrates, which features the articular facet on its ventral side, is transversely expanded. It is broadly overlapped by the ventral expansion of the squamosal to which the dorsal extension of the quadrates articulate (Figs 4C, 8A). The posteroventral tip of the quadratojugal contacts the lateral side of the quadrates only slightly, as the squamosal extends between them (Figs 4C, 8A). No quadratojugal can be seen in any
specimen. Anteriorly the quadrate articulates with the quadrate flange of the pterygoid (Figs 4C, 8A).

5.1.12. Squamosal. In lateral and dorsal views the squamosal has only a small exposure between the quadratojugal, the postorbital and the supratemporal (Figs 4A, E, 6A). The large ventral expansion of the squamosal, hidden in lateral view by the quadratojugal, makes up the medial wall and the roof of the middle ear cavity (Figs 4B–C, 8A). The medial edge of this expansion contacts the posterodorsal expansion of the pterygoid, and curves around their contact surface, forming a pilaster-like structure above the quadrate (Figs 4B–C, 8A).

5.1.13. Supratemporal. The supratemporals of Leptopleuron occupy a much smaller space on the skull table than those of Procolophon (Carroll & Lindsay 1985). Together with the parietals, they form the steep ledge that overhangs the occiput (Figs 4, 6A, C). The opisthotic attaches ventrally to the
anteromedial edge of supratemporal (Spencer 2000). The sharp posterolateral corners of the supratemporals were considered as a (fourth) pair of horns by Huene (1920), but they are not analogous in structure to the quadratojugal horns, as these 'true' horns show traces of keratinous coverage and blood supply to the horn (see section 5.1.10). The sharp corners of the supratemporal are more similar to the anterolateral corners of the jugals that were considered as the first pair of horns by Huene (1920) but neither is considered a 'true' horn here. Thus the number of horns, or spines, is only two, both located on the quadratojugal.

5.1.14. Vomer. In palatal view, the vomers form the inter-narial bar, together with the ventral portion of the premaxilla. A pair of tall vomerine fangs is situated at the anterior end of the vomer (Fig. 7D), at the same level as the third maxillary tooth. These fangs are followed by a row of denticles in Procolophon (Carroll & Lindsay 1985), but in Leptopleuron there is only another, shorter pair of fangs in a more posterior position (Fig. 7A–B) and the rest of the vomer is devoid of teeth or denticles. This arrangement of vomerine dentition has not been reported for any other procolophonoid.

5.1.15. Palatine. The suture lines between the palatine, the pterygoid and the ectopterygoid have not been preserved in any specimen in palatal view, but the outline of the palate can be seen in dorsal view in BMHN R4779 (Fig. 4A), and this was used as the basis of the palatal outline in the reconstruction.
(Fig. 3C). As in Hypsognathus (Sues et al. 2000), the palatine is short and ventral.

5.1.16. Ectopterygoid, pterygoid and epipterygoid. The interpterygoid vacuity of Leptopleuron is short and more circular than in Procolophon (Carroll & Lindsay 1985), but both taxa have small denticles on the pterygoid around the anterior part of the vacuity (Figs 4A–B, 7A). The basisphenoid attaches to the pterygoid, forming the posterior edge of the vacuity (Fig. 4A–B). The transverse flange of the pterygoid, to which the ectopterygoid also contributes, is extremely flat, vertically oriented, and reaches the midline of the mandible ventrally (Figs 4C, 8A–B). The structure of the transverse flange is similar in Kapes (Novikov & Sues 2004) and Hypsognathus (Sues et al. 2000). Behind the flange, the pterygoid has a short quadrangle process that contacts the anterior extension of the quadrate, and a sheet-like posterodorsal expansion of the pterygoid makes broad contact with the occipital flange of the squamosal (Figs 4A–C, 8A). The rod-like epipterygoid is directed posterodorsally (Fig. 4A), and contacts the prootic (Spencer 2000).

5.2. Mandible

The mandible is preserved in occlusion with several skulls (Figs 4, 8A, B), but in the case of BMNH R4779, it has been possible to create a separate cast of a part of the left mandibular ramus (Fig. 8G, H). In addition, several partial mandibles were discovered separately. BMNH R3548 shows the lateral surface of a partial left mandibular ramus with clear sutures, R3931 the medial surface of another partial left mandibular ramus and R3558 shows some additional features in medial view (Fig. 8C–F). The mandible is somewhat shorter than the skull (Spencer 2000). The mandible with clear sutures, R3558 shows some additional features in medial view (Fig. 4A), but in the case of BMNH R4779, it has been possible to create a separate cast of a part of the left mandibular ramus (Fig. 8G, H). The structure of the transverse flange is similar in Kapes (Novikov & Sues 2004) and Hypsognathus (Sues et al. 2000). Behind the flange, the pterygoid has a short quadrangle process that contacts the anterior extension of the quadrate, and a sheet-like posterodorsal expansion of the pterygoid makes broad contact with the occipital flange of the squamosal (Figs 4A–C, 8A). The rod-like epipterygoid is directed posterodorsally (Fig. 4A), and contacts the prootic (Spencer 2000).

5.3. Axial skeleton

The vertebral column of Leptopleuron is preserved to some degree in many of the specimens, but the best preservation of the dorsal side of the presacral and sacral regions can be seen in the articulated skeleton ELGNM 1978.718 (Fig. 9). The presacral number in this specimen is 26, although only the right posterolateral end of the atlas–axial complex is preserved. The proatlas is not present in any specimen but most of the atlas–axis complex is preserved to some degree in BMNH R4779 (Fig. 10A).

5.3.1. Atlas–axis complex. The atlantal neural spine is short and appears to have a notch on the dorsal margin (Fig. 10A). However, the tip of the spine is not well preserved and might have been taller. Because only the right side can be seen, it is also not clear if the atlantal neural arch was composed of two loosely attached halves, as is the case in Procolophon (deBraga 2003) and other procolophonids, with the dorsal surface being concave posterior to the jaw joint (Figs 4C, 8A). There is also a short process on the medial side of the articular. This is best preserved in RSM GY1984.20.34, where it has concave surfaces on both medial and dorsal sides (Fig. 8A).

5.3.2. Presacral vertebrae. The succeeding vertebrae are not well preserved in BMNH R4779, but their structure can be seen quite well in ELGNM 1978.718. Presacras 3 to 5 are quite small. The neural spines are pillar-like, the cross-section...
Figure 9 *Leptopleuron lacertinum* Owen, 1851. ELGNM 1978.718, skull and postcrania in (A) dorsal and (B) ventral views. Scale bar=10 mm. Anatomical abbreviations: ast=astralocalcaneum; ch=chevron; cl=clavicle; fe=femur; hu=humerus; icl=interclavicle; il=ilium; int=intercentrum; is=ischium; ob. for=obturator foramen; p. cor=posterior coracoid; pu=pubis; s1, s2, s3=sacral ribs; sc=scapula; ti=tibia; ul=ulna; V=digit number.
being almost round in 3 and 4, and more oval anteroposteriorly in 5 (Fig. 9A). There is no buttressing of the zygapophyseal regions in these vertebrae. From presacral 6 posteriorly, there is a gradual change in the shape and size of the vertebrae; they become larger and extend more transversely. The postzygapophyseal buttressing of the neural arch reaches its full extent in presacral 13 but the change in the vertebrae is gradual with no certain marker for the end of the cervical region and the beginning of the dorsal. However, associated ribs indicate that at least from vertebra 8 onwards, the vertebrae are dorsal because they have true dorsal ribs attached. The buttressing of the prezygapophyseal region of the neural arch is not as clearly visible, as the postzygapophysis of the previous vertebra naturally overlaps it (Fig. 9A). However, the buttress is much narrower on the prezygapophysis and it is directed anterolaterally, as opposed to the postzygapophyseal buttresses that are laterally directed. Both the pre- and postzygapophyseal ends of the neural arch are somewhat flared out, but they are not, however, as strongly pinched in and separated by a groove as they are in Procolophon (pers. obs. CGP/1/122) and in SAM-PK-7711, a specimen that was assigned to Procolophon by deBraga (2003), but is now regarded as an indeterminate procolophonid (Modesto & Damiani 2007) or possibly referable to the taxon Teratophon spinigenis (Cisneros 2008b). After vertebra 13, the buttressing and flaring of the arches remains fairly constant in the dorsal region (Fig. 9A). The shape of the neural spine also changes quite dramatically through the presacral region, growing taller and leaning backwards until the tip of the spine lies above the prezygapophyseal region of the following vertebrae. The spine terminates in a fairly circular bony process. However, the spine also has a pronounced anterior ridge, starting as two separate ridges on the inner edges of the prezygapophysis that meet in the middle and continue as one along the anterior edge of the spine (Fig. 10B–D). The structure of the spine and all other aspects of the dorsal vertebrae can be seen in specimens BMNH R4779, RSM 166.43.7 and BGS(GSM) 91087 (Fig. 10B–F).

5.3.3. Details of dorsal vertebrae. The neural spine is tall and slim, and the ridge on the anterior edge is very prominent (Fig. 10B–D). As the tip of the neural spine leans behind the postzygapophyseal region, there is also a thin posterior ridge on the spine that continues all the way down, and protrudes between the postzygapophyseal buttresses (Fig. 10E–F). Because of the delicate nature of the ridge, it has not been preserved on all dorsal vertebrae but, in addition to RSM 166.43.7, it can also be seen in dorsals 24, 25 and 26 of BMNH R4779 (Fig. 13A). This ridge has not been reported on any other procolophonoid, but it appears to be present in Procolophon (pers. obs. CGP/1/122) and possibly on SAM-PK-7711 (deBraga 2003). The slightly swollen, anterolaterally-directed prezygapophysis can be seen to flare distinctively, with circular articulating facets (for the postzygapophysis of the preceding vertebra) on the dorsal surface. The transverse processes are situated just below and behind the prezygapophyseal buttresses, forming double flanges with the prezygapophysis in dorsal view (Fig. 10B–D). The diaphysis of the transverse process is extensive and roughly triangular, facing anterolaterally (Fig. 10B–C). The anterior end of the pleurocentrum is more or less circular (Fig. 10C). Most specimens seem to retain the pleurocentra in natural position, but excellent preservation of a solitary neural arch in RSM 116.43.7, one of the largest specimens (Fig. 10E–F), and the ventral exposure of some
neural arches in BMNH R3136 (Fig. 12C), implies that they were not fused together. The general appearance of the vertebrae is more like that of *Soturnia* (Cisneros & Schultz 2003) and *Hypsognathus* (Colbert 1946; pers. obs. on AMNH 1676) than *Procolophon* or SAM-PK-7711 (deBraga 2003). However, relatively large intercentra are present between the pleurometa in the presacral vertebral series (Figs 9B, 11B), a feature that has not been reported in leptopleuronine procolophonids before. They are at least as massive as in *Procolophon* (deBraga 2003). The pleurocentra have very deeply concave ends and were most likely amphicoelous (Fig. 10C). This can also be seen in the holotype where some of the pleurocentra are preserved without the intercentra between them. The size of the pleurocentra stays fairly constant throughout the presacular series. Each pleurocentrum has a pair of ventrolateral concavities, separated by a rounded median ridge, a condition similar to that in most early tetrapods and *Procolophon* (deBraga 2003). However, the broad median ridge is divided into three separate ridges by two deep grooves on each pleurocentrum (Figs 11D, 13B), which is different from the single, median

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**Figure 11**  *Leptopleuron lacertinum* Owen, 1851. RSM 1891.92.528 (holotype): Skull and postcranial in (A) dorsal and (B) ventral views; (C) skull in right lateral view; (D) close-up of two well-preserved pleuro- and intercentra of the dorsal vertebral series. Scale bar (A–B)=10 mm; (C–D)=5 mm. Anatomical abbreviations: d=dentary; fe=femur; fi=fibula; hu=humerus; icf=intercondylar fossa; int=intercentrum; is=ischium; j=jugal; ob. for=obturator foramen; pl=pleurocentrum; pu=pubis; qj=quadratojugal; s1, s2, s3=sacral ribs; ti=tibia.
groove in *Procolophon* (deBraga 2003), and has not been reported in any other procolophonoid.

### 5.3.4. Sacral vertebrae

The three sacral vertebrae in ELGNM 1978.718 are preserved to some degree and show a sharp decrease in the swelling of the zygapophysis, along with a dorsoventrally orientated groove along the sides of the neural spine in sacrals two and three. The first and second sacral vertebrae are fairly similar in size to the dorsals, but their transverse processes protrude farther laterally than in any dorsal vertebra (Fig. 9A). There is a thin posterior ridge, similar to the dorsal series, on the neural spine of at least the first sacral vertebra (Fig. 13A). The sacral ribs were not fused to the vertebrae, and are disarticulated in some specimens (Figs 9A, 11A), and where the ribs articulate with vertebrae there is a distinctive suture line (Figs 12A, 13A). The sacral pleurocentra are preserved in one specimen, BMNH R3145, although the third one very poorly (Fig. 17B). The ventrolateral concavities are relatively deep and as a result the median ridge is much narrower. It is also less rounded, lower and the deep grooves seen in the presacral pleurocentra are not present. The overall appearance is flat, and although the sacral ribs are not connected to the vertebrae as preserved, it appears the transverse processes extended all the way to the ventral edge of the pleurocentra, making the ribs level with the

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**Figure 12** *Leptopleuron lacertinum* Owen, 1851. BMNH R3136: (A) partial skull and postcrania in dorsal view; (B) anterior and (C) posterior portion of postcrania in ventral view. Scale bar=10 mm. Anatomical abbreviations: a. cor=anterior coracoid; ad=adductor ridge; ast=astralocalcaneum; ce=centrale; dpc=deltoplep-
Figure 13  Leptopleuron lacertinum Owen, 1851. BMNH R4779, postcrania, in (A) dorsal and (B) ventral views. Scale bar=10 mm. Anatomical abbreviations: ast=astralocalcaneum; ce=centrale; dpc=deltoplectoral crest; fe=femur; hu=humerus; int=intercentrum; intf=intratrochanteric fossa; pl=pleurocentrum; ra=radius; s1, s2, s3=sacral ribs; ti=tibia; ul=ulna; I–V=digit numbers.
pleurocentra. Sacral intercentra are not present in any specimen (Fig. 17B).

5.3.5. Caudal vertebrae. There are at least 31 caudal vertebrae in BMNH R3918 (Fig. 15A), although very few details have been preserved. In comparison to the dorsal and sacral vertebrae, they are smaller in size. Some details of the caudals can be seen in BMNH R3362, where the vertebrae lean towards the left (Fig. 14), and in ELGNM 1978.718 (Fig. 9A). The preserved neural spines are tall and more gracile than in the other regions and no buttressing of the zygapophyseal regions appears to be present. The best-preserved caudals in the middle of the region in BMNH R3362 appear somewhat larger than in the same region of BMNH R3918 (Figs 14, 15A), being around the size of the first cervical vertebrae. However, despite the poor preservation, it is clear that they become smaller towards the end of the series (Fig. 14). The first caudal pleurocentrum has a broader medial ridge than the sacral pleurocentra but it is not as broad or high as in the presacral series (Figs 13B, 17B). However, the grooves that divide the median ridge into three parts in the presacral are here situated on the ventrolateral edges of the medial ridge, with the result that there is only one elevated ridge, situated in the centre of the median ridge (Figs 13B, 17B). The following pleurocentra appear fairly similar (Figs 13B, 15B, 17B), but again many details are not apparent because of poor preservation. Large intercentra are present at least at the beginning of the caudal series (Figs 13B, 15B). The haemal arches and spines, also called chevrons, which would have attached to the pleurocentra, have the same wishbone outline as in SAM-PK-7711 (deBraga 2003). Several are preserved on the ventral side of ELGNM 1978.718, stacked together underneath the caudal vertebrae (Fig. 9B).

5.3.6. Presacral ribs. The atlantal and axial ribs have not been preserved in any specimen. The axial neural arch has an articulation point for a rib, but it cannot be determined whether this rib also articulated with the following intercentrum. Of the other cervical ribs, only one disarticulated, straight rib has been preserved in ELGNM 1920.5 (Fig. 16A). The eighth vertebra in ELGNM 1978.718 has a long, recurved rib that can be considered as a true dorsal associated with the vertebrae (Fig. 9A), but because the more anterior ribs are not preserved, it is unclear whether this is the first dorsal rib. Because of poor preservation, it is uncertain whether the ribs were dichocephalic or holoccephalic. However, at least in the dorsal series, the ribs had dorsoventrally elongated heads that appear to have been divided into two articulating surfaces (Fig. 13B, next to well-preserved pleurocentrum 13?). The longest preserved rib is rib 13 in ELGNM 1978.718, being 6.5 times the length of a dorsal vertebra (Fig. 9), and it is possible that some of the following ribs would have been even longer.

5.3.7. Sacral ribs. The sacral ribs of *Procolophon* are very similar to those of *Procolophon* (deBraga 2003). The ribs of sacrals 1 and 2 are strongly expanded dorsoventrally at their distal end, whereas those of sacral 3 have quite a distinct appearance with only modest flaring at the ends (Figs 9A, 11A, 14, 16A, 17B). Sacral ribs 1 and 2 also appear to be strongly concave on their posterior side. This is clearly evident on ELGNM 1978.718 and BMNH R4779 (Figs 9A, 13A). All the sacral ribs are disarticulated in ELGNM 1920.5, but they are still located in the pelvic region and their anterior side is exposed on the dorsal slab, exposing also the articulating surface with the iliac blade of sacral ribs 2 and 3 (Fig. 16A).

5.3.8. Caudal ribs. The first seven caudal ribs have been preserved on BMNH R3136 (Fig. 12A, C) and they manifest the same primitive L-shaped configuration when viewed above, as in *Procolophon* and *Procolophon* (deBraga 2003). There is evidence of ribs being present throughout at least two thirds of the caudal series (Fig. 14), but the preservation is extremely poor. In SAM-PK-7711, the ribs become gradually smaller posteriorly, with the last one only a laterally directed nubbin (deBraga 2003), and it is possible the same is true of *Leptoleuron*.

5.4. Pectoral girdle

The pectoral girdle of *Leptoleuron* consists of a tall scapular blade, anterior and posterior coracoids, interclavicle and clavicle; no cleithrum appears to be present. The scapula and coracoids are not fused together and remain separate elements while forming the glenoid cavity for the articulation of the proximal end of the humerus.

5.4.1. Scapula. The scapula is extremely well preserved in BMNH R3136, and the details of the ventral end, the glenoid, the posterior side and the lateral side of the blade can be seen in ventral view, as the blade has fallen down (Fig. 12B). The medial side of the blade is exposed on the dorsal view of BMNH R3136 (Fig. 12A). The scapula is similar in shape to that of other primitive reptiles, *Procolophon* and SAM-PK-7711 (deBraga 2003), but it is not very robust and the blade is fairly slim, expanding only slightly towards the end (Figs 9A, 12A). The lateral side of the blade is concave, and in ELGNM 1920.5 there are bony ridges on both sides of this concavity.
running along the edges of the blade (Fig. 16A). Above the oval glenoid facet, there is a supraglenoid buttress, which is accentuated by a deep sulcus on the lateral surface of the blade and a depression around the supraglenoid foramen, which is situated on the supraglenoid buttress (Fig. 12B), a primitive position. Next to the glenoid facet, there are rugosities on the ventral end of the scapula, which must have been associated with the dorsal side of the anterior coracoid (Fig. 12B). The medial side of the blade is somewhat convex and the posterior edge of the blade is thickened (Fig. 12A). The blade finishes with a fairly straight, slightly rugose margin to which a possible cartilaginous suprascapula might have attached (Fig. 12A–B).

5.4.2. Coracoids. The overall structure of the anterior and posterior coracoids of *Leptopleuron* is similar to those of *Procolophon*, but their shape and size are slightly different. The anterior coracoid is transversely elongated instead of circular and the posterior coracoid is at least equal in size to the anterior coracoid. The anterior coracoid is perforated by a coracoid foramen, positioned at the lateral margin (Fig. 16B). The posterior coracoid is conspicuously waisted. There is also a prominent bony ridge running along its anterolateral edge, separating the ventral surface and the anterolateral corner that associates with the anterior coracoid and the scapula to form the glenoid (Fig. 9B).

5.4.3. Interclavicle and clavicle. The interclavicle has an anchor-like outline with a long median process and paired lateral processes at the cranial end (Figs 9B, 16B). It is indistinguishable from the interclavicle of *Procolophon* (deBraga 2003). Unfortunately, the slim, paired clavicles of *Leptopleuron* are not well preserved or well exposed in any specimen, but these too appear very similar to those of

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Figure 15  *Leptopleuron lacertinum* Owen, 1851. BMNH R3918, postcrania, in (A) dorsal and (B) ventral views. Scale bar=10 mm. Anatomical abbreviations: a. cor=anterior coracoid; entep. for=enterpicondylar foramen; fe=femur; fi=fibula; hu=humerus; icl=interclavicle; il=ilium; int=intercentrum; is=ischium; p. cor=posterior coracoid; pl=pleurocentrum; pop=popliteal fossa; pu=pubis; s2=sacral rib; ti=tibia.
Procolophon (Fig. 16B). As in all known specimens of Procolophon (deBraga 2003), it is not possible to determine how far the dorsal process of the clavicle extends along the edge of the scapular blade because of the fragmentary nature of these elements in all specimens.

5.5. Forelimbs

The forelimbs of Leptopleuron are less well preserved than many other parts of the skeleton, and although most of the features of the humerus can be seen, many details of the ulna, the radius, the manus and the carpus have not been preserved.

5.5.1. Humerus. The proximal end of the humerus is nearly identical to that of Procolophon and SAM-PK-7711 (deBraga 2003) in having a pronounced deltopectoral crest and large glenoid facet separated by a deep sulcus (Fig. 12B). However, the general appearance of the humerus of Leptopleuron is somewhat less robust, with a less pronounced entepicondyle region and a narrowed distal end. However, the distal end is not fully preserved in any specimen and might have been broader than it appears in BMNH R3136 and R3918 (Figs 12A, 15A). Nevertheless, the supinator process is also reduced in size, adding to the narrower appearance. An entepicondylar foramen is present, but no ectepicondylar foramen can be seen (Fig. 15A). A well-preserved humerus in anterodorsal view, minus the edge of the entepicondylar region and foramen, can be seen in BMNH R3362 (Fig. 14). Torsion between the proximal glenoid surface and distal humeral facets is 45 degrees or less, a huge reduction of torsion in comparison to Captorhinus and other Palaeozoic tetrapods. Similar reduction was reported in SAM-PK-7711 (deBraga 2003).

5.5.2. Ulna and radius. The ulna is larger than the radius, but the difference is not as pronounced as in SAM-PK-7711 (deBraga 2003). The proximal articulating facet for the humerus has not been preserved in any specimen, but the fairly small olecranon can be seen in ELGNM 1920.5 (Fig. 16A). A fairly deep sulcus runs in the middle of the lateral surface of the ulna (Fig. 16A). The distal end of the radius appears fairly broad (Fig. 16B) and it has a convex articular facet (Fig. 16A).

5.5.3. Carpus and manus. Only a few things can be said of the carpus and manus of Leptopleuron. A radiale is present in
Figure 17  *Leptopleuron lacertinum* Owen, 1851. (A) BMNH R3919, ventral view of left forelimb and coracoids. (B) BMNH R3145, ventral view of the pelvic area. (C) dorsal and (D) ventral views of the pelvic girdle and hind limbs of BMNH R3917. All to same scale. Scale bar=10 mm. Anatomical abbreviations: a. cor=anterior coracoid; c. for=coracoid foramen; fe=femur; fi=fibula; hu=humerus; il=ilium; is=ischium; ob. for=obturator foramen; p. cor=posterior coracoid; pl=pleurocentrum; pu=pubis; ra=radius; s1, s2, s3=sacral ribs; ti=tibia.
and medial sides. The caudal edge is also somewhat raised, making the overall appearance slightly concave. The obturator foramen is fairly round and the height of the pubic tubercle, situated in the craniolateral corner, is almost twice that of the bony ridge that runs along the edges. In ELGNM 1978.718 the pubis appears somewhat rounder in shape and slightly more concave, but otherwise similar to the holotype (Fig. 9B), whereas the left pubis of BMNH R3136 has a similar shape to the holotype (Fig. 12C).

5.6.3. Ischium. The shape of the ischium is like that of Procolophon (deBraga 2003), and many basal amniotes, but there are distinct depressions on the ventral surface. The depressions are best seen in BMNH R3136, where the ventral surface bears two large depressions posteriorly, along with smaller, banded, depressions on the anterior end (Fig. 12C). These depressions are considered an autapomorphy of Leptopleuron.

5.7. Hindlimbs

5.7.1. Femur. The femur of Leptopleuron is a fairly slender bone. It is very similar to the femur of Procolophon and SAM-PK-7711 (deBraga 2003) in overall shape and also has the same sigmoidal curvature that deflects its proximal head dorsally. The ventral and anterior surfaces, and part of the proximal head, of a left femur are exposed in BMNH R3136. The proximal articular surface is slightly concave, and the internal trochanter is damaged, but the adjoining high adductor ridge is present, forming the anterior border of the deep intertrochanteric fossa (Fig. 12C). The distal end is expanded and the deep circular popliteal fossa on the ventral side is well exposed in BMNH R3918 (Fig. 15A), whereas the tibial condyles and a deep, triangular intercondylar fossa that separates them on the dorsal side are fairly well preserved in the holotype (Fig. 11A).

5.7.2. Tibia and fibula. The tibia has features in common with both that of Captorhinus (Fox & Bowman 1966) and SAM-PK-7711 (deBraga 2003). In posterior view, exposed on the dorsal views of the holotype, BMNH R3362, and GPIT/AM/00682, the tibia is slightly curved medially (Figs 11A, 14, 18), as opposed to laterally in SAM-PK-7711. The mediolateral dimensions of the proximal head are more like those of SAM-PK-7711, making the head nearly square in proximal view, but the V-shaped groove that excavates the tibial shaft is deeper (Fig. 18), as in Captorhinus. This groove is bordered anteriorly by the cranial crest, which was the attachment site for the triceps femoralis, and posteriorly by a less prominent bony crest (Fig. 18). In lateral view, exposed on the ventral views of BMNH R3136 and BGSGSM 91093, the proximal end of the tibia is concave below the convex medial and lateral tibial facets (Figs 12C, 19). The distal end of the tibia is narrower than the proximal end, and can be seen articulating with the astragalus in BGSGSM 91093 and BMNH R4779 (Figs 13B, 19). As in the posterior view, the tibia is bowed medially in anteromedial view (Fig. 9B). Below the proximal articulating facet, there is a distinct groove along the lateral edge of the bone until the point where the bone bows medially. In SAM-PK-7711 (deBraga 2003), where the tibia bows laterally, there is a roughened area with large pits in this area. It is possible that these were present also in Leptopleuron, but all
that has been preserved is the groove along the bone (Fig. 9B). Not much can be said of the fibula, which is not well preserved in any specimen. The overall shape, in posterior view (Fig. 18), shows that both the proximal and distal ends were slightly flared, the distal end somewhat more so. The distal end itself is in a convex articulating surface for the astragalus.

5.7.3. Tarsus and pes. The tarsus is well preserved in several specimens (Figs 9, 12, 13, 19), although BMNH R4779 is the only specimen where both the ventral and dorsal views of the same tarsus are preserved (Fig. 13). The astragalus and the calcaneum are fused together, forming an astragalo-calcaneum. This fusion is present also in the procolophonid Barasaurus (Ketchum & Barrett 2004) and in mature specimens of the parareptile Macrolotherium (pers. obs. on PIN (uncatalogued) and UTM/Mezen/2001/1). The calcaneum portion is circular, flat and concave on both the ventral and dorsal surfaces (Fig. 13). It aligns distally with the astragalus. The astragalus portion is L-shaped with its proximal end articulating with the fibula and the distal part of the medial margin bearing a large, flat articular surface for the tibia (Figs 13B, 19). The lateral margin is fused to the calcaneum. Unlike Procolophon (deBraga 2003), but like Barasaurus (Ketchum & Barrett 2004), at least one centrale is present between the distal tarsals and the distal margin of the astragalus (Figs 12A, 13B), and although only a small part of it has been preserved in these specimens, the space between the elements implies that it might have been considerably larger, not unlike the centrale of Captorhinus (Fox & Bowman 1966). Five distal tarsals are also present (Fig. 12A), making the number of tarsal elements seven, one more than in Procolophon (deBraga 2003). The fourth distal tarsal is the largest. It is fairly circular and has one small foramen on the dorsal side (Fig. 12A). The other distal tarsals appear fairly smooth and rounded. The pedal phalangeal count is 2–3–4–4–2 (Fig. 12A). The first metatarsal is considerably more robust than the other metatarsals, which are long and slim in comparison to their respective phalanges (Figs 12A, 13). However, the fifth digit is an exception because its first and second phalanges seem to have merged into one long, slim phalanx. This can be seen in three specimens, BMNH R3136, R4779 and ELGNM 1978.718, and thus reflects its real condition (Figs 9A, 12A, 13). It is uncertain what would have caused this development in the fifth digit or what its use could be. All phalanges of digits 1–4 are of similar size and shape, about half the length of the metatarsals, and are followed by slightly recurved unguals that are fairly equal in length to the phalanges (Figs 12A, 13).

6. Reconstruction of the skeleton

In addition to the reconstruction of the skull (Fig. 3), a full skeletal reconstruction of Leptopleuron lacertinum is presented here in lateral view (Fig. 20). The dimensions of the reconstructed skull were based mostly on one specimen, BMNH R4779, as this is the best preserved, and largest, skull (Fig. 4). However, of the several specimens with preserved postcrania, none is as complete as the skull of BMNH R4779, and no single specimen could act as a template for the skeletal reconstruction. Thus, measurements of several skeletal dimensions were taken from 12 of the best preserved specimens (Table 1), and according to the size of correlating elements between different sized specimens, the measurements for all the elements of the largest specimen, BGS(OSM) 91093, were deducted. Accordingly, the maximum length for the skeleton of Leptopleuron, from the tip of the snout to the end of the tail, is 270 mm. However, it is possible that even this largest specimen was a subadult (see section 7.1). The details of different regions (vertebral column, girdles, limbs) were reconstructed according to the specimen that had the best preservation in that region (Figs 9–19).

The skeleton of Leptopleuron was previously reconstructed by Huene (1912, fig. 28) in lateral view. In Huene (1912), Leptopleuron is reconstructed as having an extremely long tail and a very low stature, with the head and body hanging close to the ground. This is incorrect because the scapular blade is much higher than estimated by Huene (1912), and there is no evidence for a tail longer than what can be seen in BMNH R3918 (Fig. 15). Additionally, Boulenger (1904) reconstructed Leptopleuron in dorsal view but, because of the limited material available at the time, the numbers of presacral, sacral and caudal vertebrae, among other things, are incorrect. The general appearance of Leptopleuron in Boulenger’s (1904) reconstruction is, nevertheless, more accurate than in the Huene (1912) reconstruction. However, it is the skull and mandible that are the most incorrectly depicted elements in both the Boulenger (1904) and Huene (1912) reconstructions, owing to how little was known of the skull at the time. A more accurate reconstruction of the skull in lateral view was presented by Benton & Walker (1985), but without any sutures and with some inaccuracies still remaining. Based on the new skeletal reconstruction, a fully fleshed live reconstruction illustrates how Leptopleuron might have looked like when living in its natural habitat (Fig. 21).

7. Discussion

7.1. Ontogeny

The maximum size of Leptopleuron, reaching only 270 mm, is rather small in comparison with most other procolophonids, and thus it is reasonable to raise the question of the maturity of the specimens. The variation in their size is fairly extensive. The smallest specimen, holotype RSM 1891.92.528, has an
estimated length of only 134 mm, and it has always been considered a juvenile. However, the features that are usually associated with juvenile specimens in fossil reptiles, namely unfused neurocentral sutures, lack of fully formed ends of limb bones and visible sutures on the skull (Brinkman 1988; Brochu 1996; Spencer & Lee 2000), are not determinable in the holotype. In ventral view, there is a pleurocentrum missing in the dorsal series but it is possible that the whole vertebra was damaged, as appears to be the case with many vertebrae in the holotype. The ends of long bones also appear smooth, and sutures of the skull are mostly not visible. This is also true in most of the other, larger, specimens, although cranial sutures can be observed in several specimens. However, RSM 116.43.7 has a well-preserved neural arch without the adjoining pleurocentra present (Fig. 10E–F) that indicates that they were not fused together. BMNH R3136 also has some neural arches preserved without pleurocentra, making the ventral side of the neural arch visible (Fig. 12C). These are both rather large specimens. Thus it is possible that the association of these vertebral elements in other specimens where the dorsal side is exposed might have resulted from the specimens remaining undisturbed and in life position. Also, the smoothness of the ends of the long bones could be a preservational artefact, as it is impossible to determine from these natural moulds whether the ends are cartilage polished in a quick fossilisation or actual bone. Additionally, the shoulder and pelvic girdles remain unfused in all specimens, but the astragalus and calcaneum are fused together in the large specimens with well-preserved hindlimbs (Figs 12C, 13, 19), implying that they were most likely subadults. The size of the quadratojugal spines also varies between the different-sized specimens, but even in the smallest, most immature specimen (the holotype RSM 1891.92.528) they are present, albeit rather small (Fig. 11A, C). This is different from the ontogeny of Procolophon, where juveniles lack these spines entirely (Colbert & Kitching 1975; Carroll & Lindsay 1985), and similar to the ontogeny of Hypsognathus where juveniles possess small quadratojugal spines (Sues et al. 2000). Thus, it is possible that all the specimens represent different juvenile stages, the largest being subadults.

7.2. Mode of life
It has been suggested that derived procolophonids, as exemplified by Procolophon, had a burrowing lifestyle. The main features used to support this hypothesis in Procolophon are the large, spade-like unguals (for digging more efficiently) and a pronounced overbite (to reduce ingestion of dirt), and burrow casts found together with, or attributed to, Procolophon (Groenewald 1991; deBraga 2003). Procolophon has also been likened to the horned lizards of the genus Phrynosoma, a modern day burrower, as they both have a short, triangular skull with horns, robust limbs and a very wide ribcage (deBraga 2003). However, the reconstruction of Procolophon by deBraga (2003), which depicts it with an extremely wide ribcage, is not justified. DeBraga (2003) does not present any evidence for the unusual attachment of the ribs and, together with the uncertainty of features truly attributable to Procolophon, caused by the inclusion of the indeterminate procolophonid SAM-PK-7711 (Modesto & Damiani 2007) in his descriptive study, there is no reason to assume Procolophon was especially stocky like the horned lizard. This is also true of Leptopleuron. Nevertheless, in general the ribcage of procolophonids, including Procolophon, Hypsognathus and Leptopleuron, is much wider than the ribcage of Owenetta. As for other burrowing adaptations, Leptopleuron shares a triangular head with horns and an overbite with Procolophon and the

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Figure 21  Life reconstruction of Leptopleuron lacertinum Owen, 1851. Following Benton & Walker (1985) for the reconstruction of Scleromochlus teylori Woodward, 1907, from the same location, Leptopleuron is shown in the dune-like settings of the Lossiemouth Sandstone Formation, with plants based on other comparable Late Carnian units elsewhere in the world.
horned sand lizard, but the slender phalanges and unguals on its manus and pes differ greatly from those of Procolophon, and do not appear suitably robust for digging. However, it cannot be ruled out, that Leptopleuron lived in burrows, and the coiled appearance of ELGNM 1978.718 (Fig. 9) might be indicative of it this.

The diet of Leptopleuron can only be inferred from its dentition, as no other evidence of diet has been preserved. The labiolingually broadened, two-cusped marginal teeth of Leptopleuron are like those of many other procolophonid taxa. This kind of dentition has been considered an adaptation for feeding on hard materials, perhaps vegetation (Gow 1977) or hard-shelled invertebrates (deBraga 2003; Cisneros 2008c). The larger size and relatively wider trunks of procolophonids in comparison to the slimmer owenettids, consistent with digesting vegetative material, has also been considered as additional support for herbivory in procolophonids (Cisneros 2008b). However, a wider trunk does not automatically correlate with the consumption of vegetation, as evidenced, for example, by the insectivorous horned sand lizard Phrynosoma.

7.3. Phylogenetic affinities of Leptopleuron
The phylogenetic position of Leptopleuron within the Procolophonidae is firmly established in previous studies as being one of the members of the subfamily Leptopleuroninae (Modesto et al. 2002; deBraga 2003; Piñeiro et al. 2004; Modesto & Damiani 2007; Cisneros 2008a, c; Säilä 2008). This is generally agreed, even when other relationships in the phylogenies conflict. Leptopleuroninae, defined as “taxa more closely related to Leptopleuron than to Procolophon” (sensu Modesto et al. 2002) includes Leptopleuron lacertinum and Hypsognathus ferreri in all of these analyses and, when additional taxa have been included, also Scoloparia glyphanodon, Sclerosaurus armatus and Koldskiosaurus coburgeri always fall into the Leptopleuroninae clade. Of the latter taxa, Scoloparia is known from fairly extensive cranial material (Sues & Baird 1998), justifying its inclusion in the analyses of Cisneros (2008b, c), Modesto et al. (2002), and Säilä (2008). Sclerosaurus, on the other hand, has also been considered a pareiasaur (Lee 1995) as well as a procolophonid. However, a recent study of Sclerosaurus from good quality casts (it is
preserved as natural moulds) confirmed its leptopleuronine affinities (Stues & Reisz 2008). *Kooloskiosaurus*, however, is more problematic. It is also known from natural moulds and has only ever been described from plaster casts almost a century ago (Huene 1912). Thus, information about this taxon should be treated with caution until more detailed information becomes available.

The phylogenies of Modesto & Damiani (2007) (Fig. 22A) and Sues & Reisz (2008) also found the taxon *Tichinskia* to be the most basal leptopleuronine, but this is inconsistent with all other studies, which have found that *Tichinskia* is either a procolophonid (deBraga 2003), or a procolophonid that fall outside both Leptopleuroninae and Procolophoninae in the most optimal results (Modesto et al. 2001, 2002; Piñeiro et al. 2004; Cisneros 2008a, c; Sáilá 2008). Other taxa considered as members of Leptopleuroninae by Cisneros (2008a, c) (Fig. 22C) are *Soturnia calidodon*, *Pentaedrurusaurus orsodiansus* and *Neoprocolophon asiaticus*. *Soturnia* (Cisneros & Schultz 2003) is known from only a few fragmentary remains, which is why it has been left out from analyses other than that of Cisneros (2008a, c). *Pentaedrurusaurus* and *Neoprocolophon*, however, were previously known only from brief descriptions (Young 1957; Li 1983, 1989) but Cisneros (2008a) offered more detailed information and illustrations of both taxa.

In addition to this, Sáilá (2008) found that *Kapes cf. K. majmescdae*, and *Anomoiodon illiensterni*, also fell within Leptopleuroninae, although they formed a sister-clade separate from the other leptopleuronines (Fig. 22B). However, Cisneros (2008a, c), the only other analysis that has incorporated *Kapes*, recovered it within Procolophoninae (Fig. 22C), which is defined as “the taxa more closely related to *Procolophon* than to Leptopleuron” by Modesto et al. (2002). *Anomoiodon* has not been included in any analyses other than that of Sáilá (2008). Thus, although Leptopleuron and several other taxa clearly group together and form the clade Leptopleuroninae, it is still somewhat uncertain exactly which taxa fall within or outside of this clade. A new, more inclusive and detailed analysis of the interrelationships of Procolophonoida that also addresses the composition of Leptopleuroninae is under preparation by the present author.

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9. References


