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Osteology of *Leptopleuron lacertinum* Owen, a procolophonoid 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 quadratojugal; 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, Leptopleuroninae, 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 rhynchosaur, a sphenodontid, a possible coelurosaur dinosaur and the procolophonid *Leptopleuron* (Benton & Walker 1985). The leptopleuronine 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 procolophonoid 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

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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), Boulenger (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).

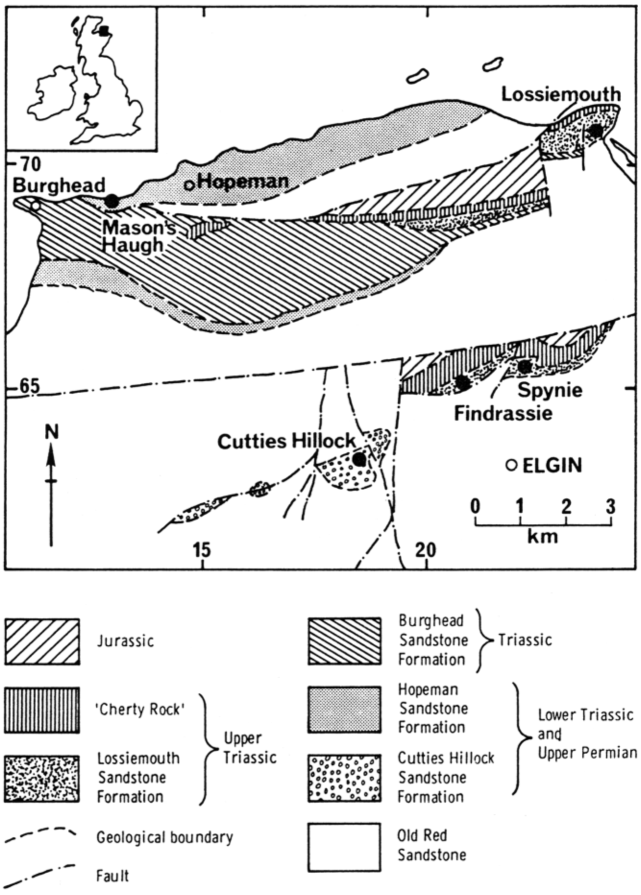

Figure 1 Geological map of the Elgin area, northeast of Scotland. *Leptopleuron* natural moulds come from the Upper Triassic Lossiemouth Sandstone near Spynie and Lossiemouth. Reproduced from Benton & Walker (1985).

3. Materials and methods

To date, nearly 40 specimens of *Leptopleuron*, ranging from articulated skeletons to partial jaws, have been collected and stored in several museums. Quality of preservation is variable, but in many cases amazingly detailed and, in addition to the holotype, 22 of the most informative specimens are illustrated in various views in this present paper. All studied specimens are natural moulds of bones, preserved as impressions in fine- to medium-grained sandstone (Fig. 2A). Most specimens have both the dorsal and ventral parts of the crania and postcrania preserved on two separated slabs. This study focuses on the casts, or positives, made with PVC plastic (by A. D. Walker; Fig. 2B) and silicone rubber of these natural moulds. Some specimens were previously cast with silicone by P. Spencer, but the majority of the silicone rubber casts were made by the present author.

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 hours 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.

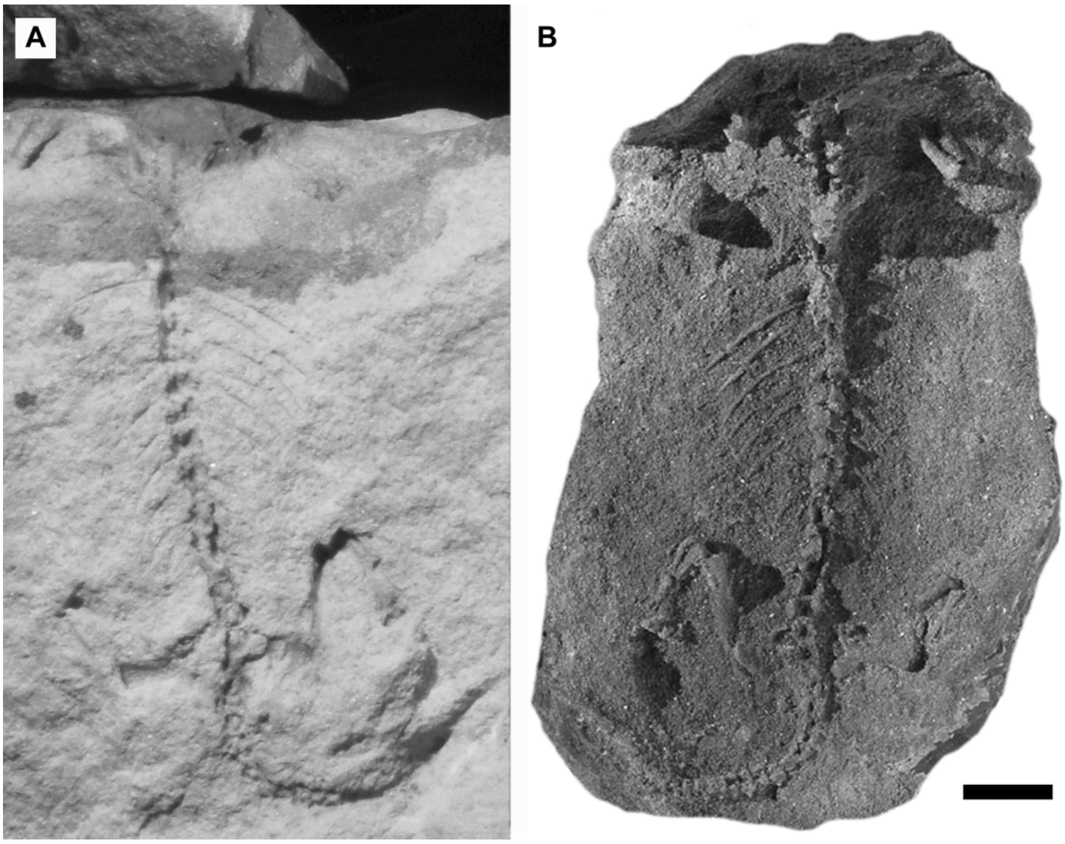

Figure 2 *Leptopleuron lacertinum* Owen, 1851, RSM 1891.92.528 (holotype): (A) natural mould of postcrania in dorsal view; (B) PVC plastic cast of the natural mould. Scale bar = 10 mm. Photograph of the natural mould courtesy of S. Stevenson (RSM).

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 Procolophonoidea, *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

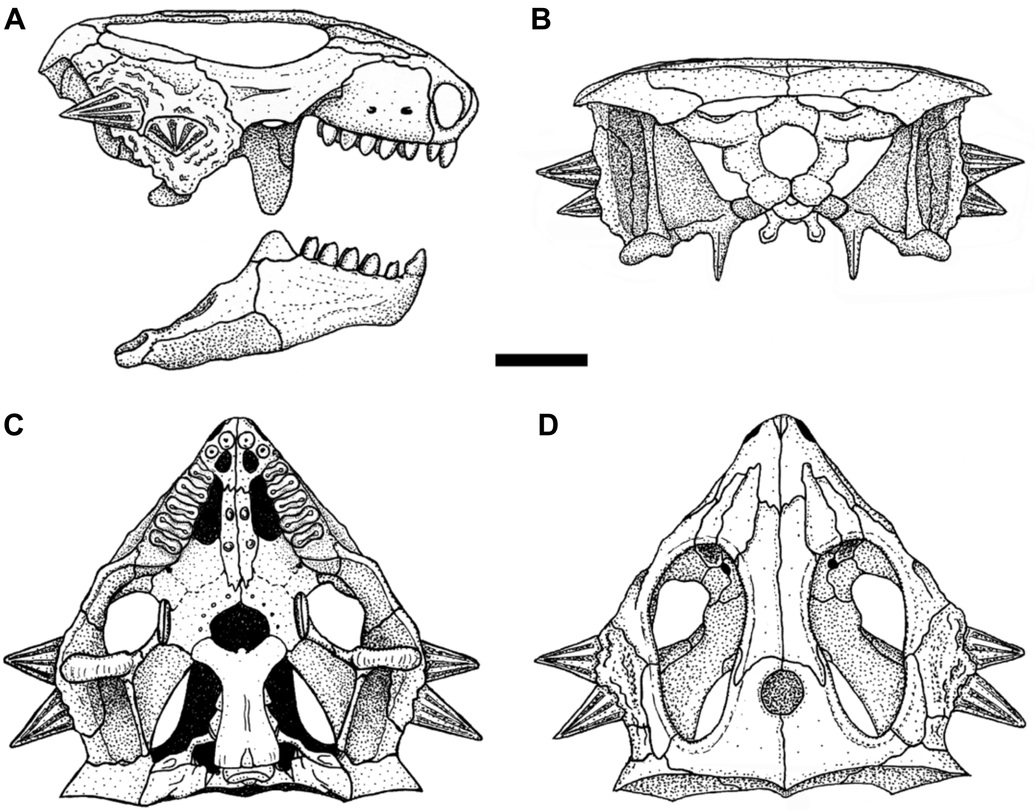

Figure 3 Reconstruction of the skull of *Leptopleuron lacertinum*: (A) lateral view; (B) occipital view; (C) palatal view; (D) dorsal view. The braincase, seen in palatal and occipital views, is reconstructed after Spencer 2000. Scale bar = 10 mm.

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 basisphenoid 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 Procolophonoidea.

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

Table 1 Skeletal dimensions (mm) of 12 *Leptopleuron lacertinum* specimens with the best-preserved skull and postcrania. Total length was estimated based on the lengths of the skull, the presacral and sacral regions and the tail, and was estimated for specimens where at least two of these dimensions could be measured.

	EM 1920.5	EM 1978.718	Holotype	EM 1978.726	BGS(GSM) 91093	BMNH R3136	BMNH R3362	BMNH R3917	BMNH R3918	BMNH R3919	BMNH R4779	GPIT/AM/682
Skull length	39	32	26	?	?	42	?	32	?	47	48	43
Presacral column	82	78	50	?	?	?	?	?	?	?	?	85
Glenoid-acet. distance	92	89	?	?	?	?	?	?	?	?	?	?
Sacrum length	12	10	8	?	?	15	?	?	?	?	18	17
Tail length	?	?	?	?	?	?	>60	?	70	?	?	?
Scapula height	?	16	?	?	?	22	?	?	?	?	?	?
Interclavicle length	?	27	?	?	?	?	?	?	?	?	?	30
Coracoid (a+p) length	21	?	?	?	?	26	?	?	?	?	?	?
Humerus length	22	22	?	?	?	24	23	?	?	24	26	25
Radius length	16	16	?	?	?	?	?	?	?	17	18	?
Ulna length	16	?	?	?	?	?	?	?	?	16	18	?
Metacarpal length	6	7	?	?	?	?	?	?	7	8	8	7
Ilium blade height	14	?	?	?	?	21	?	?	?	?	?	?
Pubis length	9	9	4	9	?	10	?	?	9	?	?	?
Ischium length	12	12	7	?	15	14	?	?	14	?	?	?
Femur length	25	22	15	25	31	29	?	23	25	?	27	27
Tibia length	20	16	12	?	24	20	18	15	16	?	21	17
Fibula length	21	?	12	?	24	?	18	15	?	?	21	17
Metatarsals i–iv	7	7	?	?	10	8	8	7	?	?	8	7
Metatarsal v	?	?	?	?	8	7	7	?	?	?	7	?
Total length (incl tail)	?	?	?	?	?	?	?	?	?	?	?	?
Estimated total length	191	175	134	–	270	210	–	–	–	–	235	217

any of the specimens. The external naris is large and oval, much as in *Procolophon* (Carroll & Lindsay 1985). The internarial bars of the premaxilla are slender and extend slightly between the nasals dorsally (Fig. 4A, D). The palatal portion of the premaxilla is very similar to that of *Hypsognathus* (pers. obs. YPM 55831) and *Soturnia* (Cisneros & Schultz 2003), with a large, round foramen (Fig. 7A–B). In *Hypsognathus* and *Soturnia*, this foramen has been called the 'foramen prepalatum' and it has been interpreted as homologous to the small foramina that punctuate the border of the premaxilla and vomer in other procolophonoids, but are lacking in *Hypsognathus*, *Soturnia* and *Leptopleuron*. These foramina served as passages for A. nasalis inferior (Heaton 1979). The extended size of the 'foramen prepalatum' is also believed to have accommodated the crown of the enlarged lower incisiform tooth in *Hypsognathus* (Sues *et al.* 2000), and this is plausible for *Leptopleuron* as well. There are two teeth on each premaxilla, the more anterior being considerably larger than the posterior. Both teeth have conical crowns (Figs 4, 7D).

5.1.2. Maxilla. The maxilla is extremely deep above the tooth row. The area of the maxilla behind the external naris is poorly preserved in all specimens, but there is no indication of the deep maxillary depression (Figs 4E, 5B) that is present in most procolophonids. There are five teeth on the maxilla, and the row terminates at the level of the anterior margin of the orbitotemporal opening (Fig. 4F), in contrast to *Hypsognathus* (Sues *et al.* 2000) and other leptopleuronines (Sues & Baird 1998; Cisneros & Schultz 2003) where the row terminates prior to reaching the orbitotemporal opening. However, in all other procolophonoids the row continues well past the anterior margin. Therefore, the condition in *Leptopleuron* is more similar to the other leptopleuronines than to non-leptopleuronine procolophonoids. All teeth, including the first one, are molariform with transversely broadened bases and crowns (Fig. 7B–D). The tooth bases are also mesodistally broader in lateral view (Fig. 4E–F) than in *Procolophon* (Carroll & Lindsay 1985) but not as broad as in many other procolophonids, including *Hypsognathus* (Sues *et al.* 2000). Most of the *Leptopleuron* skulls are preserved in occlusion with the mandible, exposing only the lateral view of the teeth. However, some specimens are preserved without one or both of the mandibular rami, and BMNH R3927 and R3930 both show the whole maxillary tooth row in occlusal view (Fig. 7B–C). It has also been possible to make casts of BMNH R4779 that show some of its maxillary teeth in occlusal view (Fig. 7D). This is also the only specimen where the premaxillary/maxillary tooth transition can be observed, and where both the left and right mandibular rami are connected. The first tooth is the shortest, with the following teeth fairly equal in height (Fig. 4E–F), but their labiolingual width increases considerably until the fourth tooth, which is extremely wide (Fig. 7B). The fifth tooth is less broad, more or less equal in width to the second or third tooth. Each tooth has two separate cusps that are joined together by a sharp edge. The teeth are individually oriented at a slight angle anterolabially to distolingually, relative to the middline of the skull (Fig. 7B–D), causing them to overlap somewhat in lateral view (Fig. 3A). This orientation is caused by the shape and positioning of the maxillary bone, since the transverse axis of each tooth and the long axis of the maxilla are perpendicular (Figs 3C, 7C–D). The tooth row is only slightly inset from the lateral margin of the snout but it also leans strongly towards the

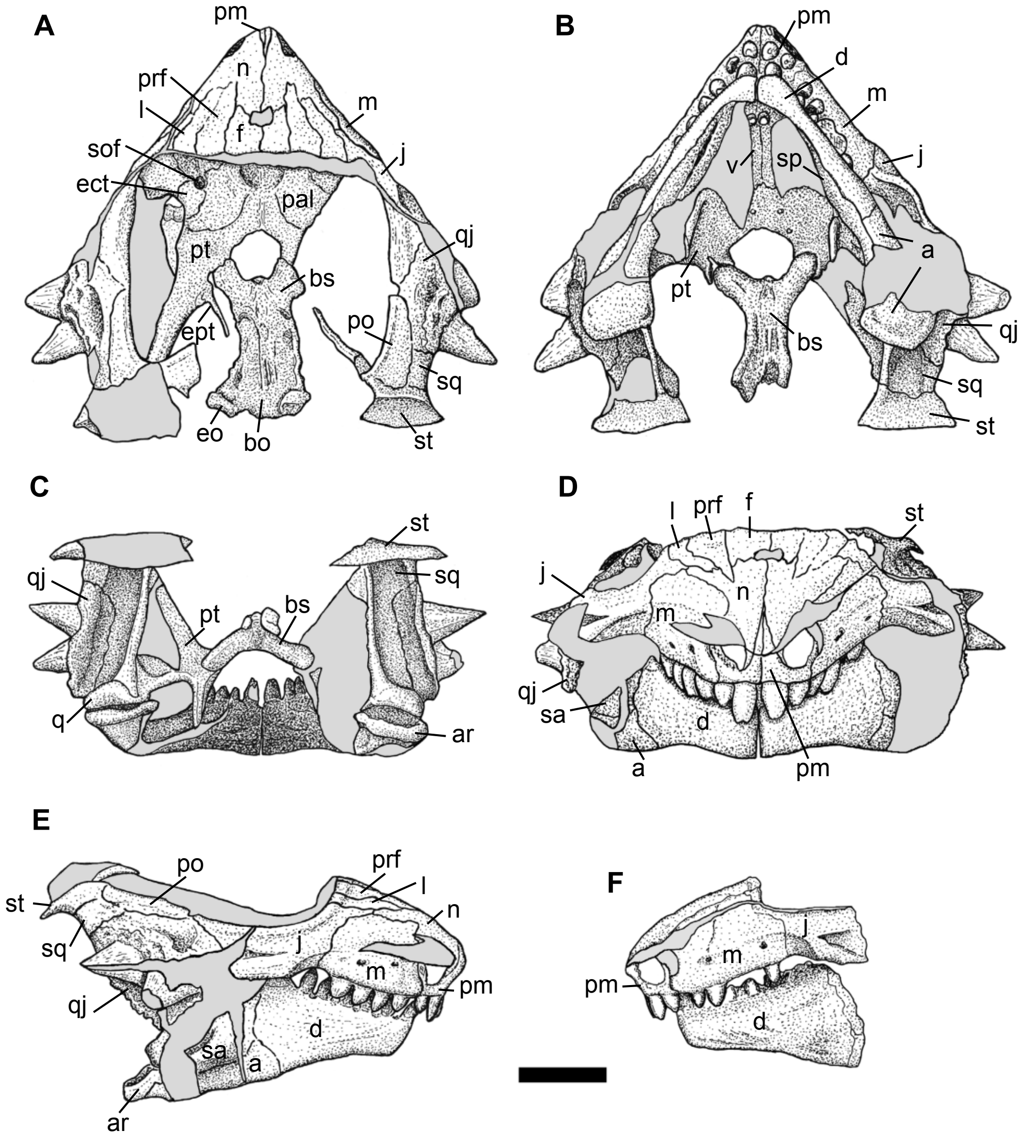

Figure 4 *Leptopleuron lacertinum* Owen, 1851, BMNH R4779. Skull and mandible in (A) dorsal view, (B) palatal view, (C) occipital view (slightly ventral angle), (D) anterior view, and (E) right lateral view; (F) snout in left lateral view. Scale bar=10 mm. Anatomical abbreviations: a=angular; ar=articular; 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=quadrate; qj=quadratojugal; sa=surangular; sof=suborbital foramen; sp=splenial; sq=squamosal; st=supratemporal; v=vomer.

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

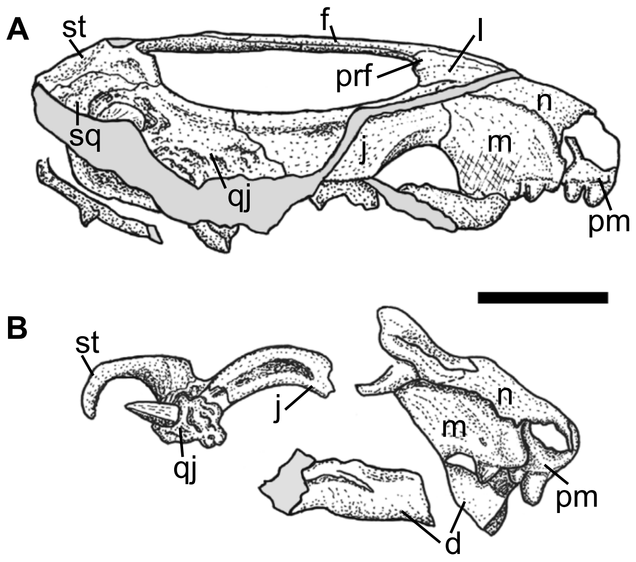

Figure 5 *Leptopleuron lacertinum* Owen, 1851. Skull of (A) BMNH R3919 and (B) BMNH R3917 in right lateral view. Scale bar = 10 mm. Anatomical abbreviations: d = dentary; f = frontal; j = jugal; l = lacrimal; m = maxilla; n = nasal; pm = premaxilla; prf = prefrontal; qj = quadratojugal; sq = squamosal; st = supratemporal.

prefrontal, present in most other procolophonoids, 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 procolophonoids. 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 posterolateral 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 pineal 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 supraoccipital (Spencer 2000). Postparietals do not appear to be present.

5.1.8. Postorbital. The postorbitals make up the posterolateral margin of the orbitotemporal openings, extending approximately half way along the opening. Only the anteriormost 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 procolophonids, but in these taxa there is also extensive contact between the postorbital and the jugal (Carroll & Lindsay 1985; Novikov & Sues 2004: Cisneros 2008a, pers. obs. SAM-PK-10192 for *Teratophon*). 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 posterolateral extension of the nasal (Fig. 4A, E).

5.1.10. Quadratojugal. The quadratojugal of *Leptopleuron* bears two spines of approximately equal size. Both are dorsoventrally flattened. The anterior one, attached slightly more ventrally, points laterally, whereas the posterior one points in a posterolateral 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 posterolateral 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 quadrate, 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 quadrate also articulates (Figs 4C, 8A). The posteroventral tip of the quadratojugal contacts the lateral side of the quadrate only slightly, as the squamosal extends between them (Figs 4C, 8A). No quadrate foramen can be seen in any

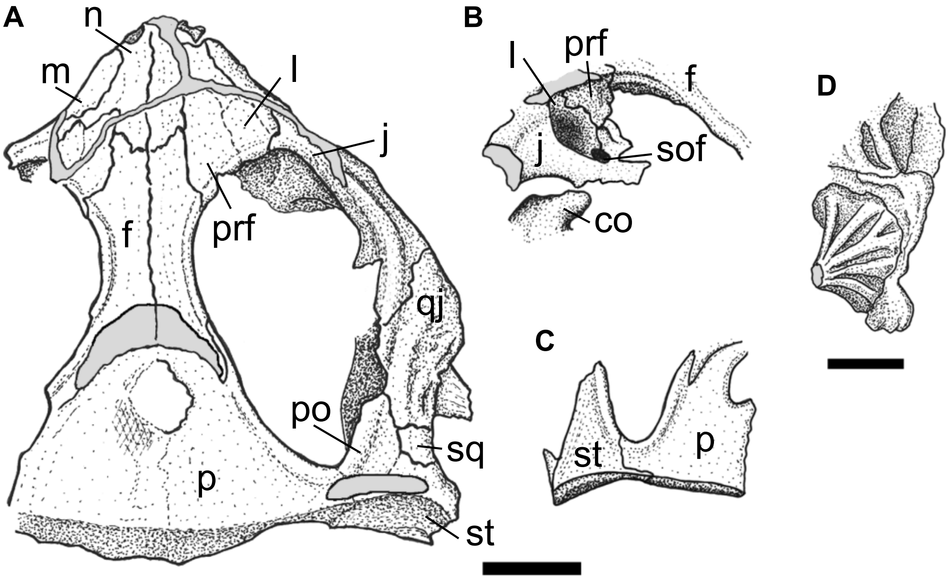

Figure 6 *Leptopleuron lacertinum* Owen, 1851: (A) BMNH R3919, dorsal view of skull; (B) GPIT/AM/00682, orbitonasal view through left orbit; (C) BMNH R3928, dorsal view of left postero-lateral corner of skull; (D), RSM 1984.20.34, quadratojugal horn in close-up. Scale bars (A–C)=10 mm; (D)=5 mm. Anatomical abbreviations: co=coronoid; f=frontal; j=jugal; l=lacrimal; m=maxilla; n=nasal; p=parietal; po=postorbital; prf=prefrontal; qj=quadratojugal; sof=suborbital foramen; sq=squamosal; st=supratemporal.

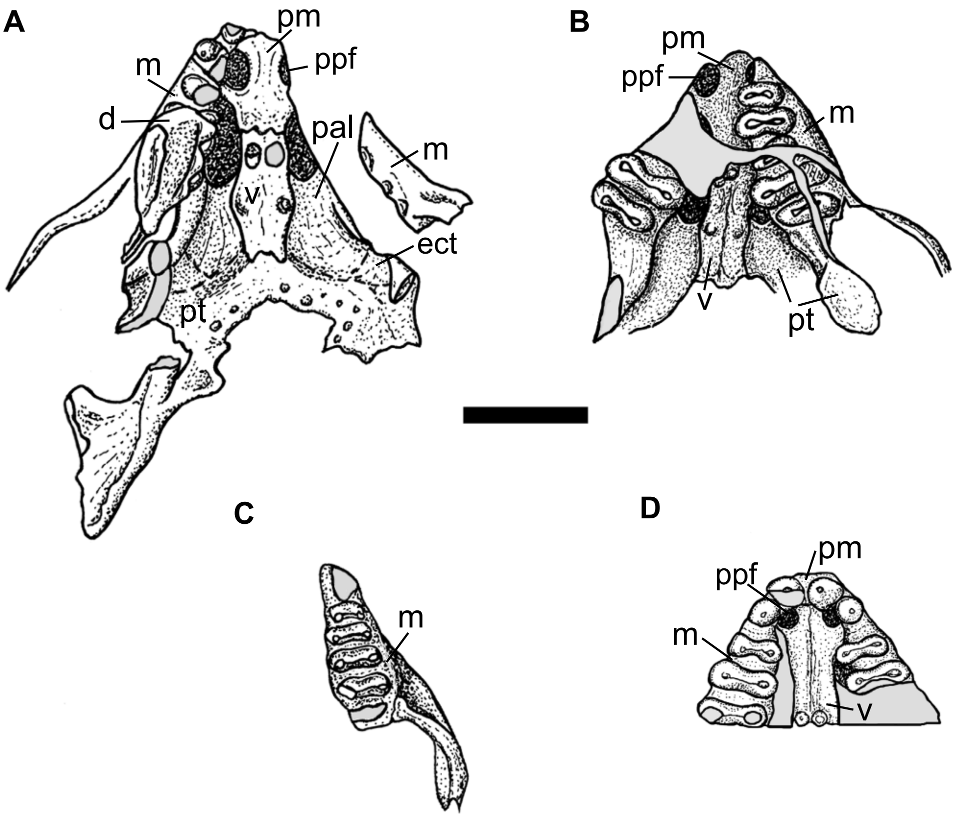

Figure 7 *Leptopleuron lacertinum* Owen, 1851, palatal region of skull and maxillary dentition: (A) BMNH R 3919; (B) BMNH R3927; (C) BMNH R3930; (D) BMNH R4779. All to same scale. Scale bar=10 mm. Anatomical abbreviations: d=dentary; ect=ectopterygoid; m=maxilla; pal=palatine; pm=premaxilla; ppf=prepalatal foramen; pt=pterygoid; v=vomer.

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

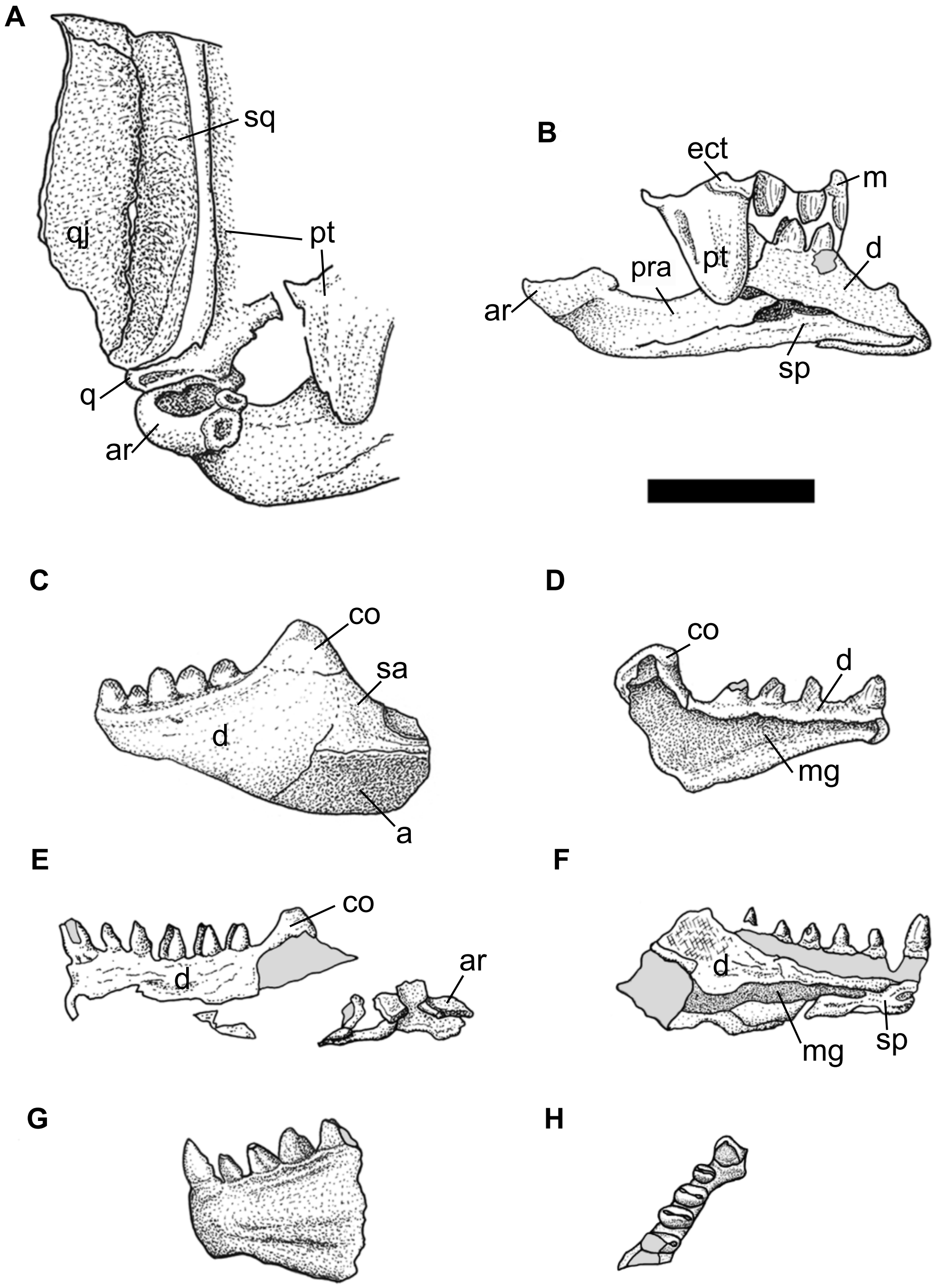

Figure 8 *Leptopleuron lacertinum* Owen, 1851. (A) RSM 1984.20.34, posteromedial view of the posterior end of skull and left mandibular ramus; (B) ELGNM 1920.5, medial view of left mandibular ramus; (C) BMNH R5487, lateral view of left mandibular ramus; (D), BMNH R3931, medial view of left mandibular ramus; (E) lateral and (F) medial views of the right mandibular ramus of BMNH R3558; (G) lateral and (H) occlusal views of the anterior end of left dentary of BMNH R4779. All to same scale; Scale bar = 10 mm. Anatomical abbreviations: a = angular; ar = articular; co = coronoid; d = dentary; ect = ectopterygoid; m = maxilla; mg = Meckelian groove; pra = prearticular; pt = pterygoid; q = quadrate; qj = quadratojugal; sa = surangular; sp = splenial; sq = squamosal.

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 internarial 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 edentulous.

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 orientated, 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 quadrate 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 R5487 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.

5.2.1. Dentary, coronoid and splenial. There are five to six teeth on the dentary. The first tooth is extremely tall, somewhat incisiform in shape and leans slightly anteriorly (Fig. 8E–G). The dentary is also deeper underneath the first tooth, elevating it above the following teeth, and making it appear even taller (Fig. 8G). The second tooth is the smallest in the row (Fig. 8C, E–G), but nevertheless has a transversely broadened crown (Fig. 8H). In teeth three to five/six the crowns are broader still, with two cusps connected by a ridge (Fig. 8B, E, H). The crowns are similar to those of the maxillary teeth (Fig. 7D), although the bases or crowns do not become as transversely broad as in the posterior maxillary teeth. The dentary of *Leptopleuron* is extremely deep, with the ventral margin diverging from the alveolar margin in a steep angle after the caniniform region (Figs 4E–F, 8C). No sculpturing of the ventral surface can be seen in any specimen. In BMNH R3931, the dentary is entirely exposed medially as the splenial is missing, and a reniform symphyseal region and the Meckelian groove are visible on the otherwise smooth surface (Fig. 8D).

The coronoid extends high above the mandible and is fairly round in lateral view (Fig. 8C). In medial view it can be seen to curve around the adductor fossa (Fig. 8D). However, the posteromedial extent of the coronoid cannot be determined, as it has not been preserved in BMNH R3931 and it is covered by the transverse flange of the pterygoid in all articulated specimens.

The splenial, which can be seen best in ELGNM 1920.5 and BMNH R3558 (although fragmentary in both), extends anteriorly to meet the symphyseal facet (Fig. 8F) and although most of the Meckelian groove is exposed in BMNH R3558, the splenial seems to cover at least its posterior part in ELGNM 1920.5 (Fig. 8B). Thus, the shape and extent appear very similar to the splenial of *Procolophon* (Carroll & Lindsay 1985).

5.2.2. Surangular and angular. In lateral view, the dentary meets the surangular and the angular posteriorly. The surangular forms a shelf above the suture it shares with the angular (Figs 4E, 8C), a structure similar to the horizontal crest of the surangular in *Tichvinskia* (Ivakhnenko 1973) and *Kapes* (Novikov & Sues 2004). Above the shelf, the surangular has a deep concavity and below it the smooth angular slopes ventromedially, thus making the ledge appear even more protruding (Figs 4B, 8C). The extent to which the angular wrapped itself around the ventral margin of the mandible or continued on the medial side cannot be determined in any specimen, because the suture lines in this area are not well preserved. However, the angular has a medial exposure in both *Procolophon* (Carroll & Lindsay 1985) and *Hypsognathus* (Sues *et al*. 2000), making it probable also in *Leptopleuron*.

5.2.3. Prearticular and articular. The prearticular connects with the splenial, forming the posterior medial surface of the mandible and the retroarticular process (Fig. 8B). However, its true dimensions cannot be determined, as no suture line can be seen between the prearticular and (possible) medial portion of the angular. The articular forms the transversely expanded posterior surface of the retroarticular process. The overall shape is very similar to the articular of *Hypsognathus* (Sues *et al*. 2000) and other procolophonoids, 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. 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 most other primitive reptiles. The pre- and postzygapophyses are small and unswollen and the anterior end of the neural spine is wider than the posterior end. The atlantal pleurocentrum is somewhat fragmentary but appears fairly circular and slightly concave in its anterior end (Fig. 10A) but the atlantal intercentrum, which is not well preserved, obscures this view somewhat. Only a small fragment of the axial intercentrum has been preserved and the axial pleurocentrum, which is partially hidden from view, appears to be fairly round and solid. The axial neural arch and spine are similar in general appearance to those of *Procolophon* (deBraga 2003). However, the diapophosyseal region extends farther laterally and appears to have an extremely pronounced attachment point for the axial rib (Fig. 10A). Additionally, even though the axial spine is tall, the anteroposterior length of the axial neural arch is only about half that of a dorsal vertebrae of the same specimen (Figs 10A, D). In *Procolophon* the axial neural arch is estimated to have had a similar length and robustness as the dorsal vertebrae (deBraga 2003, fig. 1). Thus, the axis of *Leptopleuron* is much more gracile.

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. Presacrals 3 to 5 are quite small. The neural spines are pillar-like, the cross-section

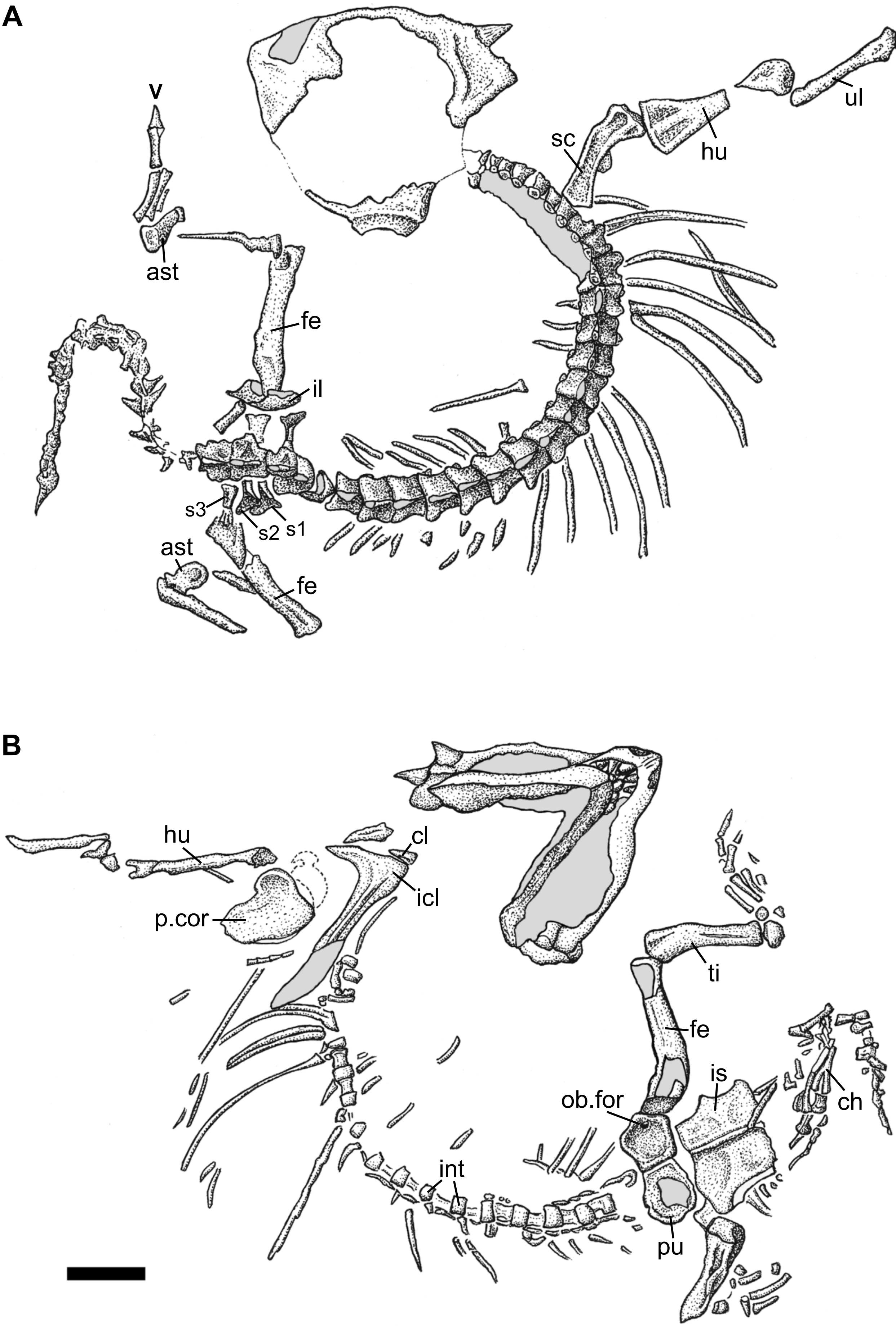

Figure 9 *Leptopleuron lacertinum* Owen, 1851. ELGNM 1978.718, skull and postcrania in (A) dorsal and (B) ventral views. Scale bar=10 mm. Anatomical abbreviations: ast=astralocalcaneum; ch=chevron; cl=clavicle; fe=femur; hu=humerus; icl=interclavicle; il=ilium; int=intercentrum; is=ischium; ob. for=obturator foramen; p. cor=posterior coracoid; pu=pubis; s1, s2, s3=sacral ribs; sc=scapula; ti=tibia; ul=ulna; V=digit number.

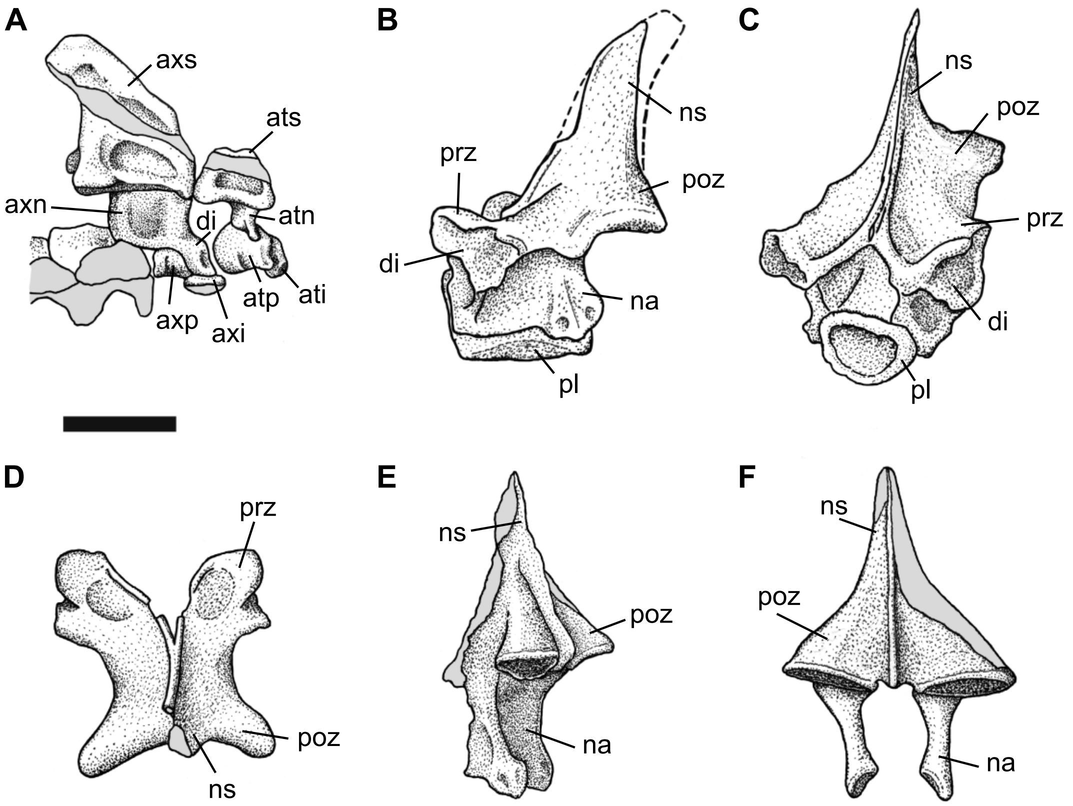

Figure 10 *Leptopleuron lacertinum* Owen, 1851. (A) BMNH R4779, right lateral view of the atlas–axis complex; (B) left lateral and (C) antero-ventral views of an isolated dorsal vertebra of BGS(GSM) 91087; (D) BMNH R4779, dorsal vertebra (13?) in ventral view; (E) lateral and (F) posterior views of the neural arch and spine of a dorsal vertebra of RSM 166.43.7. Outline of the neural spine in (B) after a complete spine in BMNH R 4779. All to the same scale; Scale bar = 5 mm. Anatomical abbreviations: ati = atlantal intercentrum; atn = atlantal neural arch; atp = atlantal pleurocentrum; ats = atlantal neural spine; axi = axial intercentrum; axn = axial neural arch; axp = axial pleurocentrum; axs = axial neural spine; di = diapophysis; na = neural arch; ns = neural spine; pl = pleurocentrum; poz = postzygapophysis; prz = prezygapophysis.

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 diapophysis 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

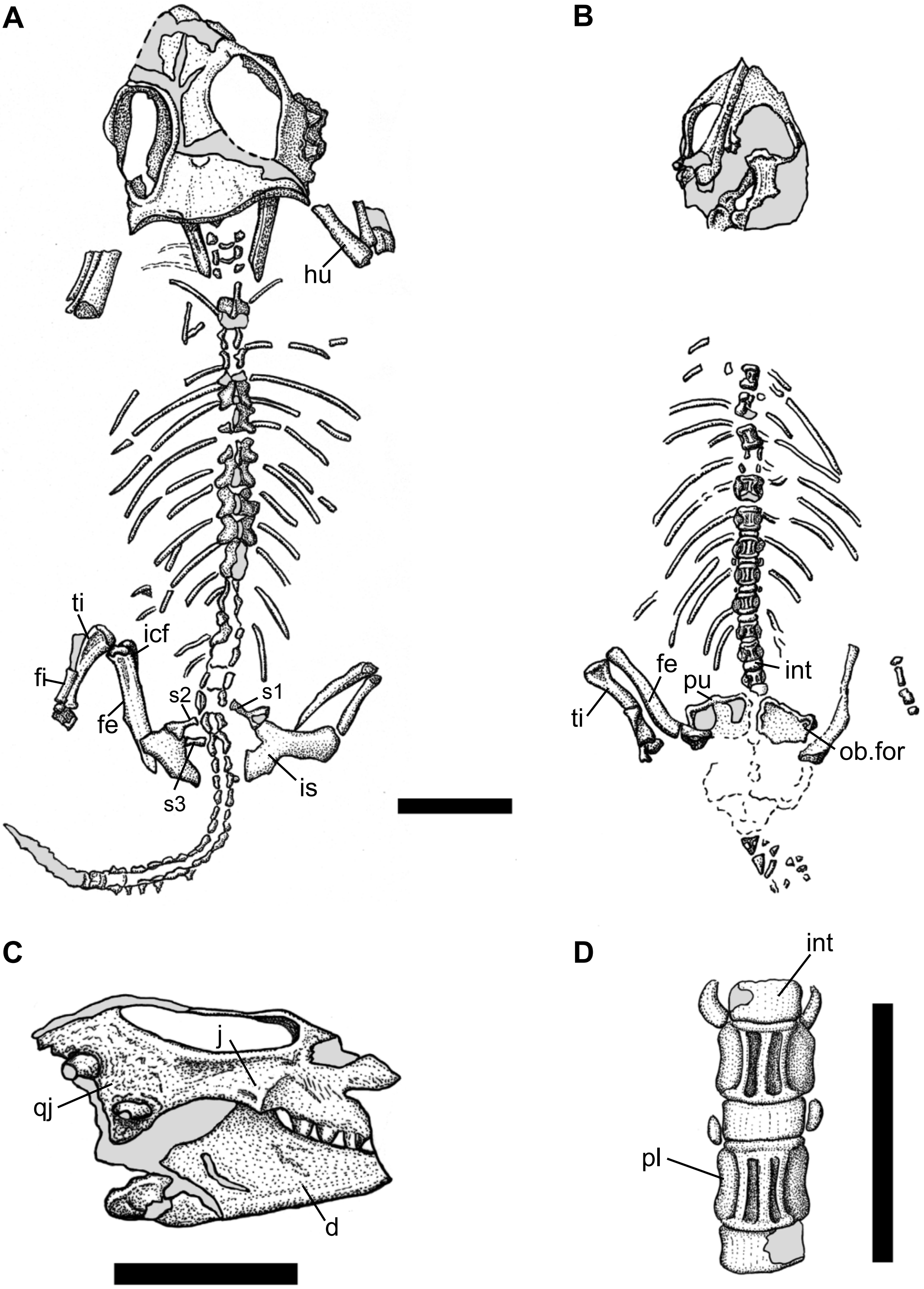

Figure 11 *Leptopleuron lacertinum* Owen, 1851, RSM 1891.92.528 (holotype): Skull and postcrania in (A) dorsal and (B) ventral views; (C) skull in right lateral view; (D) close-up of two well-preserved pleuro- and intercentra of the dorsal vertebral series. Scale bar (A–B)=10 mm; (C–D)=5 mm. Anatomical 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.

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 pleurocentra 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 presacral 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

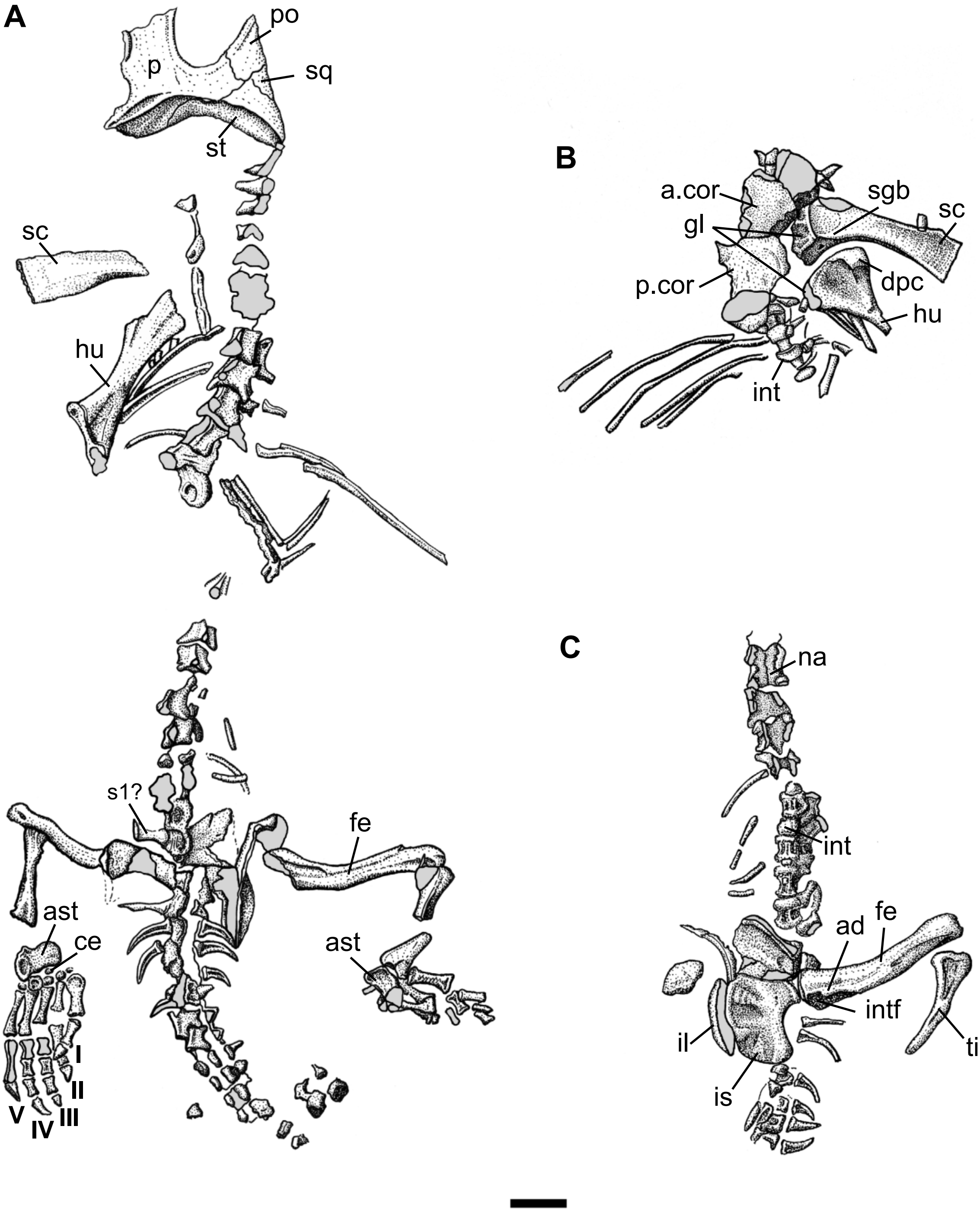

Figure 12 *Leptopleuron lacertinum* Owen, 1851. BMNH R3136: (A) partial skull and postcrania in dorsal view; (B) anterior and (C) posterior portion of postcrania in ventral view. Scale bar=10 mm. Anatomical abbreviations: a. cor=anterior coracoid; ad=adductor ridge; ast=astralocalcaneum; ce=centrale; dpc=deltopectoral crest; fe=femur; gl=glenoid facet; hu=humerus; il=ilium; int=intercentrum; intf=intratrochanteric fossa; is=ischium; na=neural arch; p=parietal; p. cor=posterior coracoid; po=postorbital; s1=sacral rib; sc=scapula; sgb=supraglenoid buttress; sq=squamosal; st=supratemporal; ti=tibia; I–V=digit numbers.

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 vertebrae (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

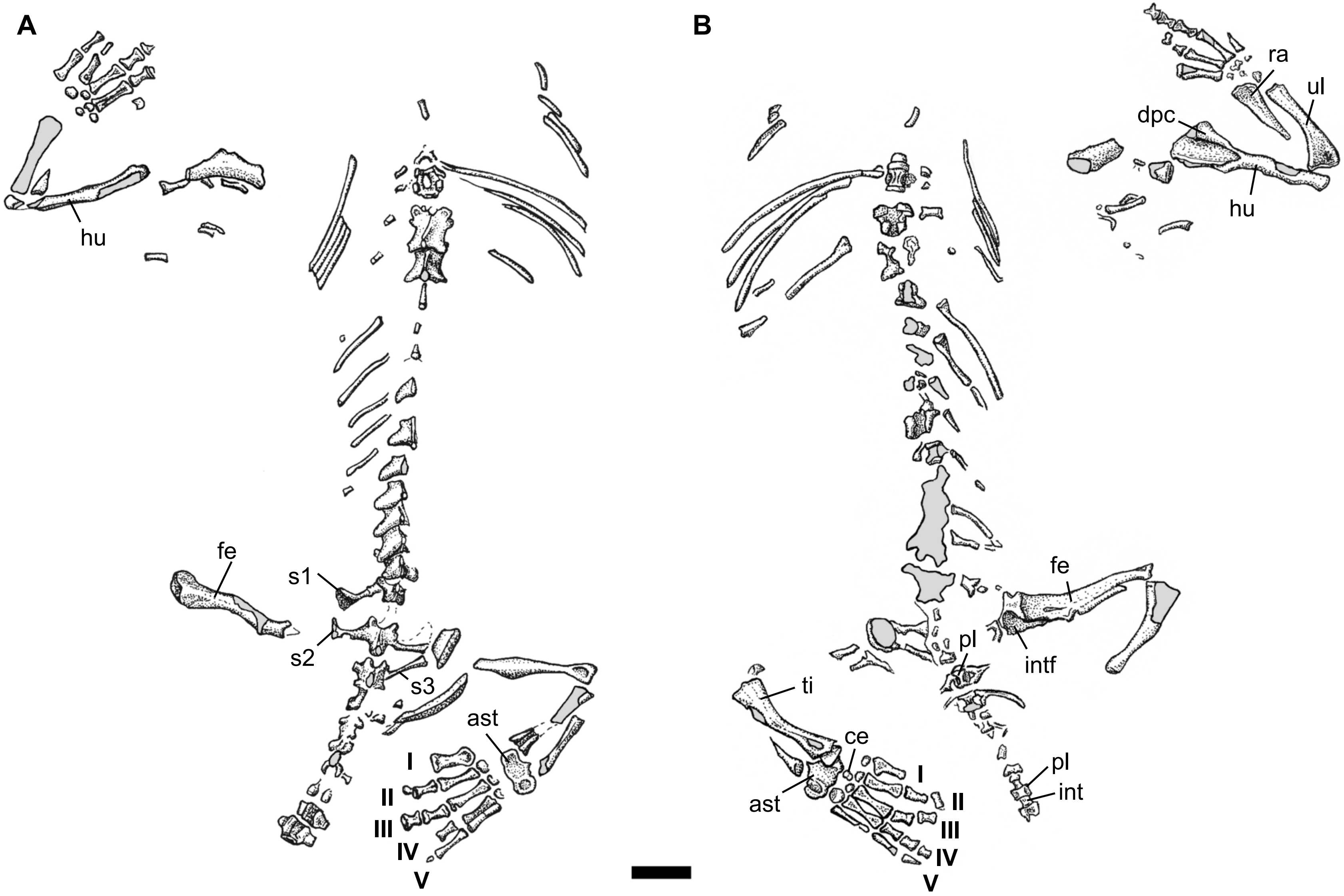

Figure 13 *Leptopleuron lacertinum* Owen, 1851. BMNH R4779, postcrania, in (A) dorsal and (B) ventral views. Scale bar = 10 mm. Anatomical abbreviations: ast = astralocalcaneum; ce = centrale; dpc = deltopectoral crest; fe = femur; hu = humerus; int = intercentrum; intf = intratrochanteric fossa; pl = 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 presacrals 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 holocephalic. 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 *Leptopleuron* 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 straight 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 sacrals 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 SAM-PK-7711 (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 *Leptopleuron*.

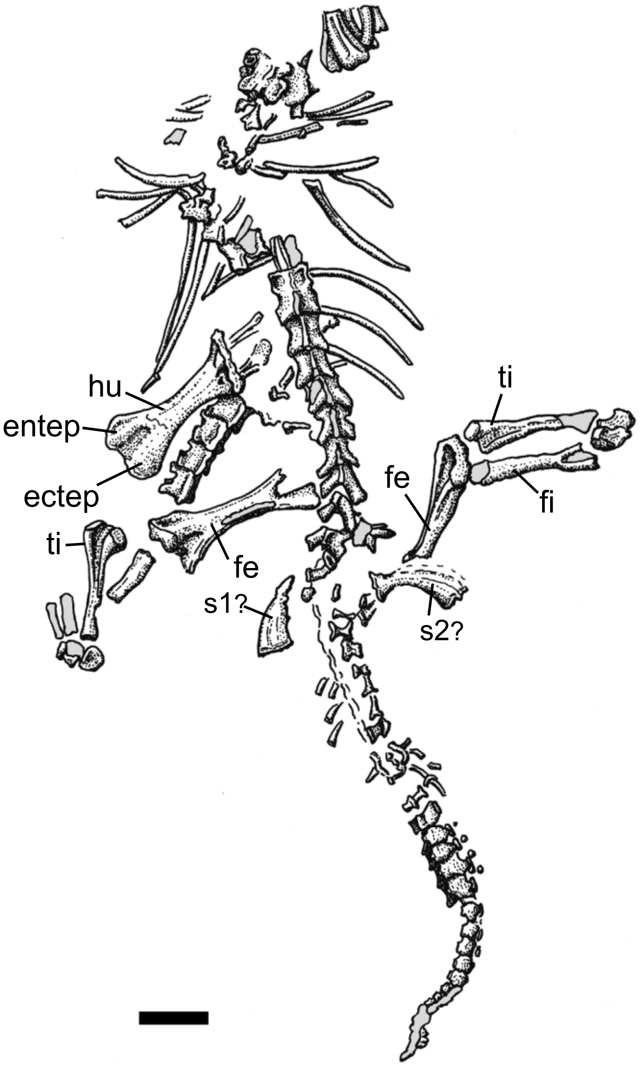

Figure 14 *Leptopleuron lacertinum* Owen, 1851. BMNH R3362, postcrania in dorsal view (together with some dorsal vertebrae from another individual). Scale bar=10 mm. Anatomical abbreviations: ectep=ectepicondyle; entep=entepicondyle; fe=femur; fi=fibula; hu=humerus; s1, s2=sacral ribs; ti=tibia.

5.4. Pectoral girdle

The pectoral girdle of *Leptopleuron* 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,

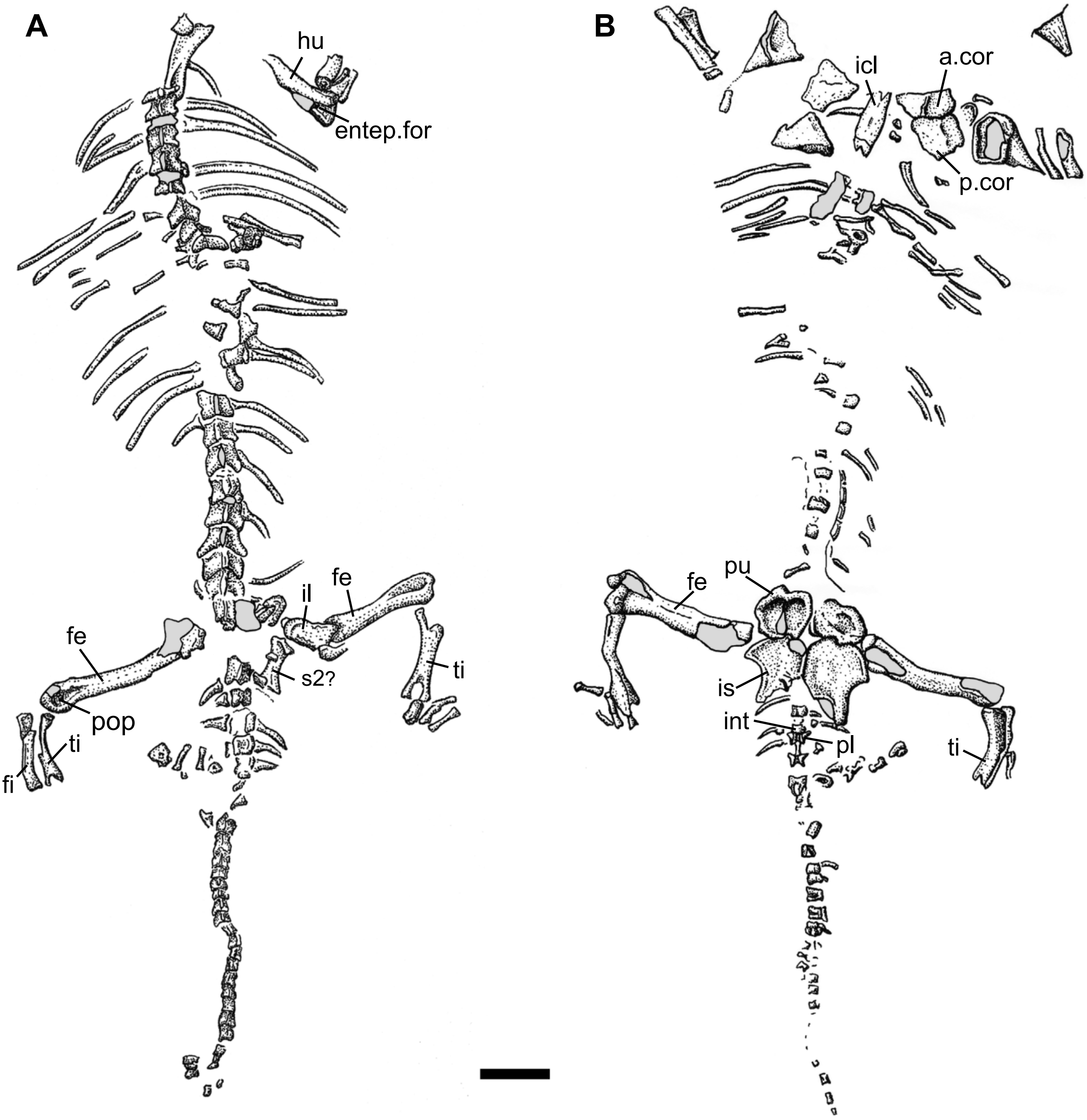

Figure 15 *Leptopleuron lacertinum* Owen, 1851. BMNH R3918, postcrania, in (A) dorsal and (B) ventral views. Scale bar = 10 mm. Anatomical abbreviations: a. cor = anterior coracoid; entep. for = enterpicondylar foramen; fe = femur; fi = fibula; hu = humerus; icl = interclavicle; il = ilium; int = intercentrum; is = ischium; p. cor = posterior coracoid; pl = pleurocentrum; pop = popliteal fossa; pu = pubis; s2 = sacral rib; ti = tibia.

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

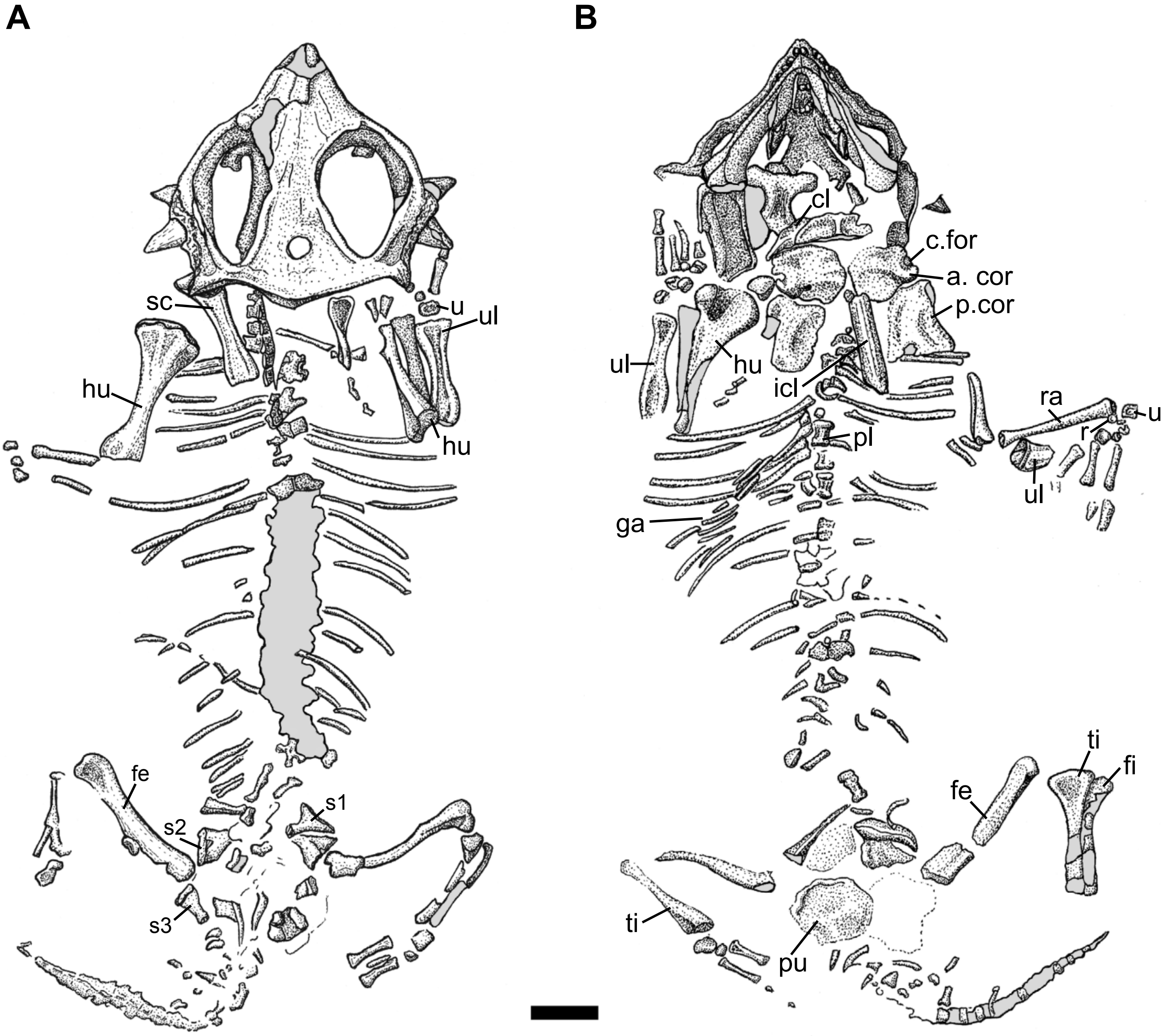

Figure 16 *Leptopleuron lacertinum* Owen, 1851. ELGNM 1920.5, skull and postcrania in (A) dorsal and (B) ventral views. Scale bar = 10 mm. Anatomical abbreviations: a. cor = anterior coracoid; c. for = coracoid foramen; cl = clavicle; fe = femur; fi = fibula; ga = gastralia; hu = humerus; icl = interclavicle; p. cor = posterior coracoid; pl = pleurocentrum; pu = pubis; ra = radius; s1, s2, s3 = sacral ribs; sc = scapula; ti = tibia; u = ulnare; ul = ulna.

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 general shape of the ulna is similar to 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. 16B). 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. 13B) and it has a convex articular facet (Fig. 13A).

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

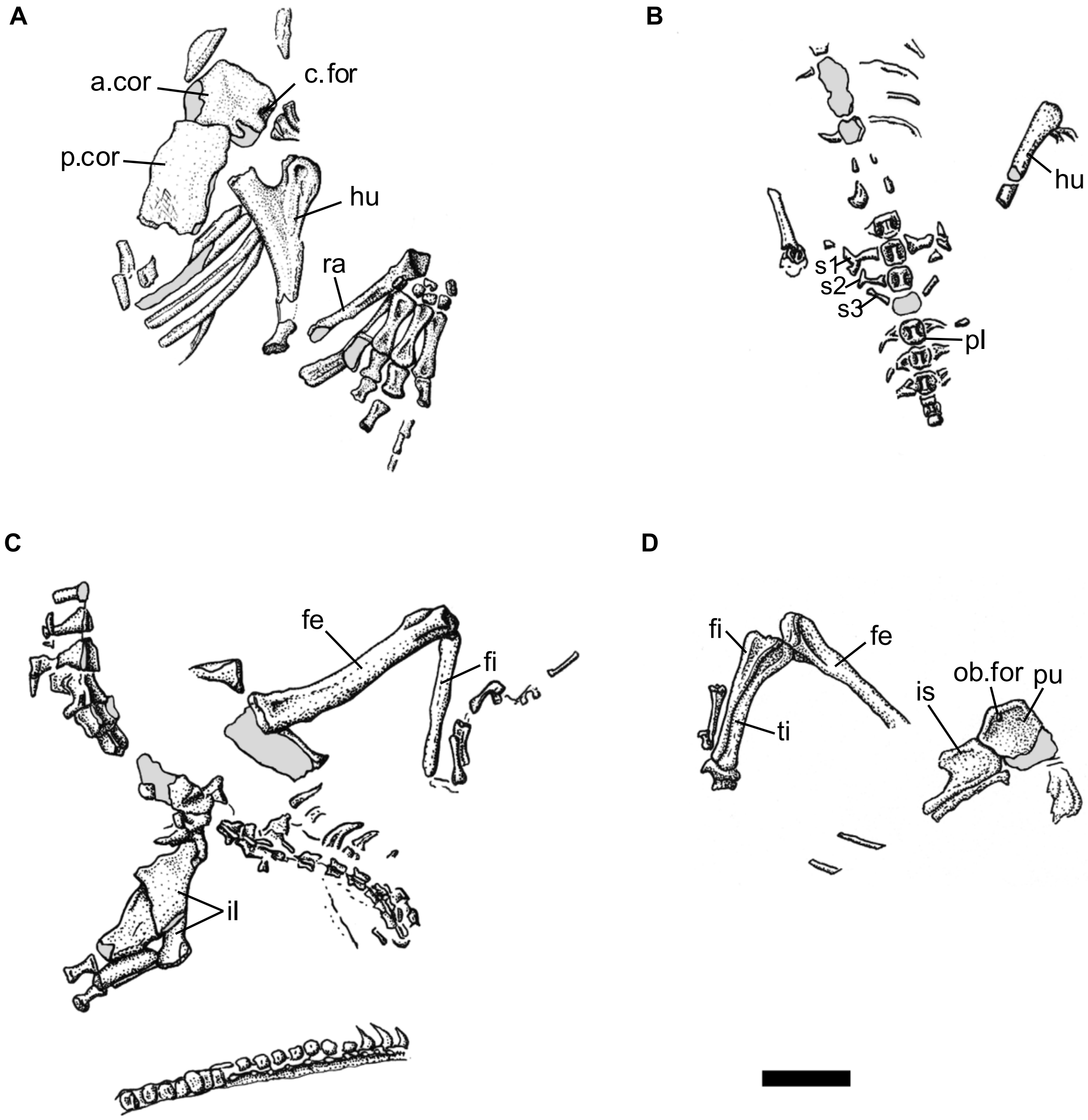

Figure 17 *Leptopleuron lacertinum* Owen, 1851. (A) BMNH R3919, ventral view of left forelimb and coracoids. (B) BMNH R3145, ventral view of the pelvic area. (C) dorsal and (D) ventral views of the pelvic girdle and hind limbs of BMNH R3917. All to same scale. Scale bar = 10 mm. Anatomical abbreviations: 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.

ELGNM 1920.5 (Fig. 16B) and the ulnare can be seen in both dorsal and ventral view in the same specimen, although it is unclear whether both left and right ulnares are exposed in the same or opposite views. The ulnare is lenticular and concave (Fig. 16A–B). Other carpal elements are poorly preserved in this specimen, but another fairly large element, surrounded by fragments of smaller elements, is tentatively identified as the lateral centrale (Fig. 16B). A medial centrale and an intermedium are also present in *Procolophon* (deBraga 2003) but, because of poor preservation, it is unclear whether they were present in the carpus of *Leptopleuron*. BMNH R3919 has four distal carpals and three well-preserved metacarpals in ventral view (Fig. 17A) and R4779 has four metacarpals that appear fairly equal in dimensions (Fig. 13). It is assumed that both specimens are missing the first metacarpal because this is shorter and stouter than the other metacarpals in *Procolophon* (deBraga 2003) and most other primitive reptiles. However, the metacarpals of *Leptopleuron* are considerably slimmer than the robust metacarpals of *Procolophon* (deBraga 2003). The associated phalanges are also slimmer than those of *Procolophon*. There are at least three phalanges on the second digit and four phalanges on the fourth digit, but other than that the phalangeal count cannot be determined. No unguals are preserved.

5.6. Pelvic girdle

5.6.1. Ilium. The shape of the right iliac blade can be seen in the holotype. The bone has fallen laterally, so that the medial side of the blade is visible in the dorsal view of the skeleton (Fig. 11A). The blade appears very tall and slim, expanding only marginally towards the dorsal end. The blade is also somewhat rounded, being thicker near the posterior edge. In posterior view, the blade is higher on its medial side and the dorsal end slopes towards the lateral side at about a 20-degree angle. The finer details, including the attachment sites for the sacral ribs, are not preserved. The iliac blade has also been preserved, although broken into two parts, in BMNH R3917 (Fig. 17C). The ventral end of the ilium, including the acetabulum, is not preserved in any specimen.

5.6.2. Pubis. The left pubis is nicely preserved on the holotype, revealing a quadrangular outline (Fig. 11B). The pubis is widest medially and narrows slightly towards the lateral end. Bony ridges run along the edges of the pubis on the cranial

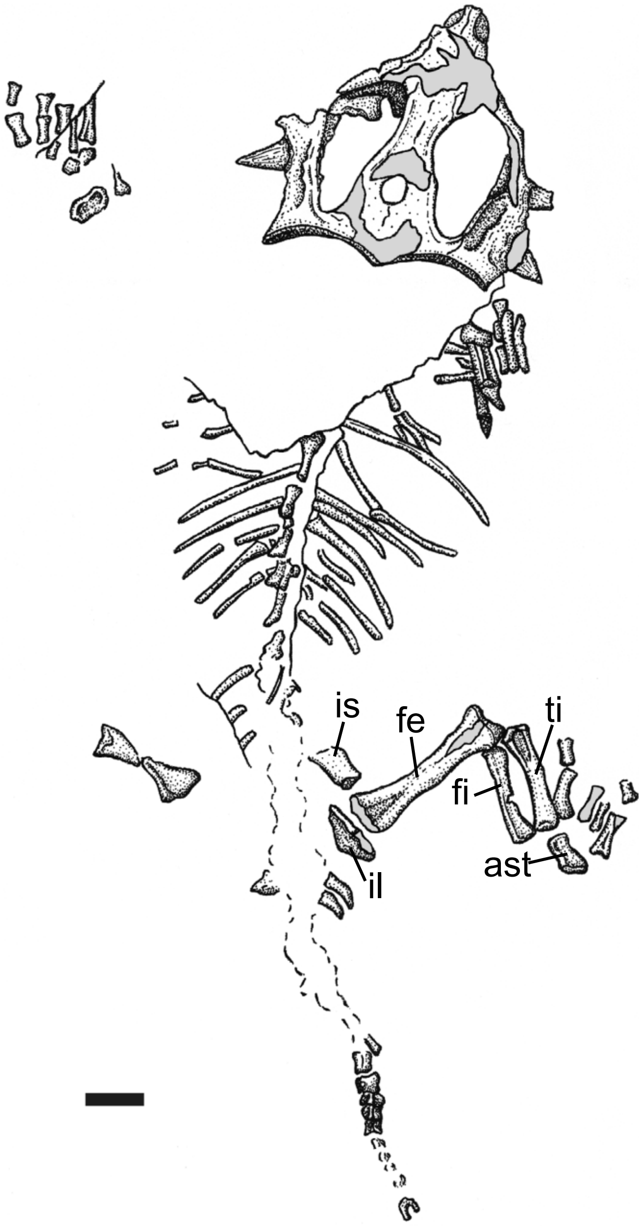

Figure 18 *Leptopleuron lacertinum* Owen, 1851. GPIT/AM/00682, skull and postcrania in dorsal view. Scale bar = 10 mm. Anatomical abbreviations: ast = astralocalcaneum; fe = femur; fi = fibula; il = ilium; is = ischium; ti = tibia.

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*.

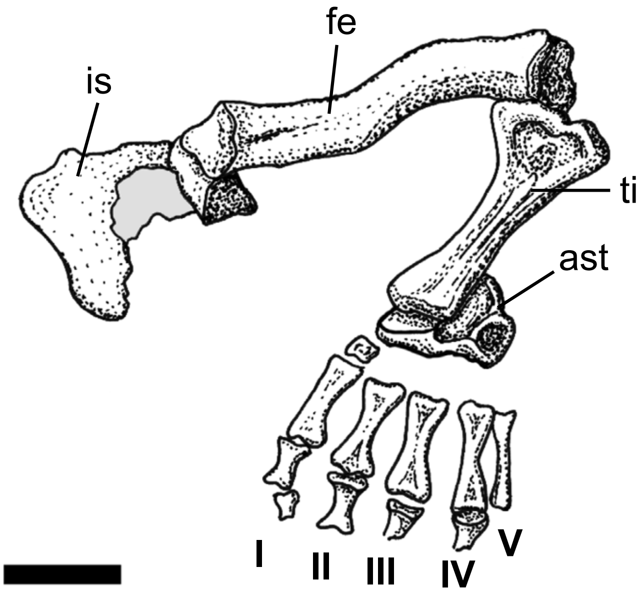

Figure 19 *Leptopleuron lacertinum* Owen, 1851. BGS(GSM) 91093, left hind limb in dorsal view. Scale bar = 10 mm. Anatomical abbreviations: ast = astralocalcaneum; fe = femur; is = ischium; ti = tibia; I–V = digit numbers.

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 BGS(GSM) 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 BGS(GSM) 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

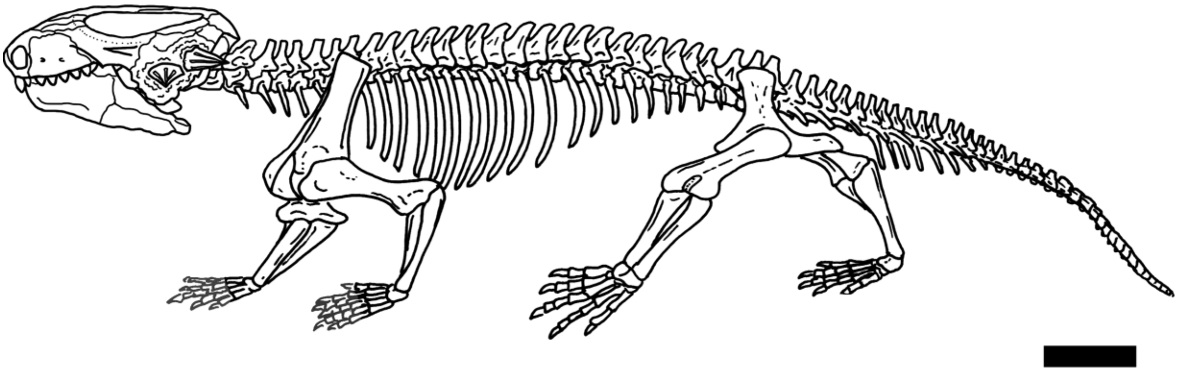

Figure 20 Skeletal reconstruction of *Leptopleuron lacertinum* Owen, 1851 in lateral view. The reconstruction is based on the several specimens illustrated in this present paper. Scale bar = 20 mm.

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 head ends 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 astragalocalcaneum. This fusion is present also in the procolophonoid *Barasaurus* (Ketchum & Barrett 2004) and in mature specimens of the parareptile *Macroleter* (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(GSM) 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

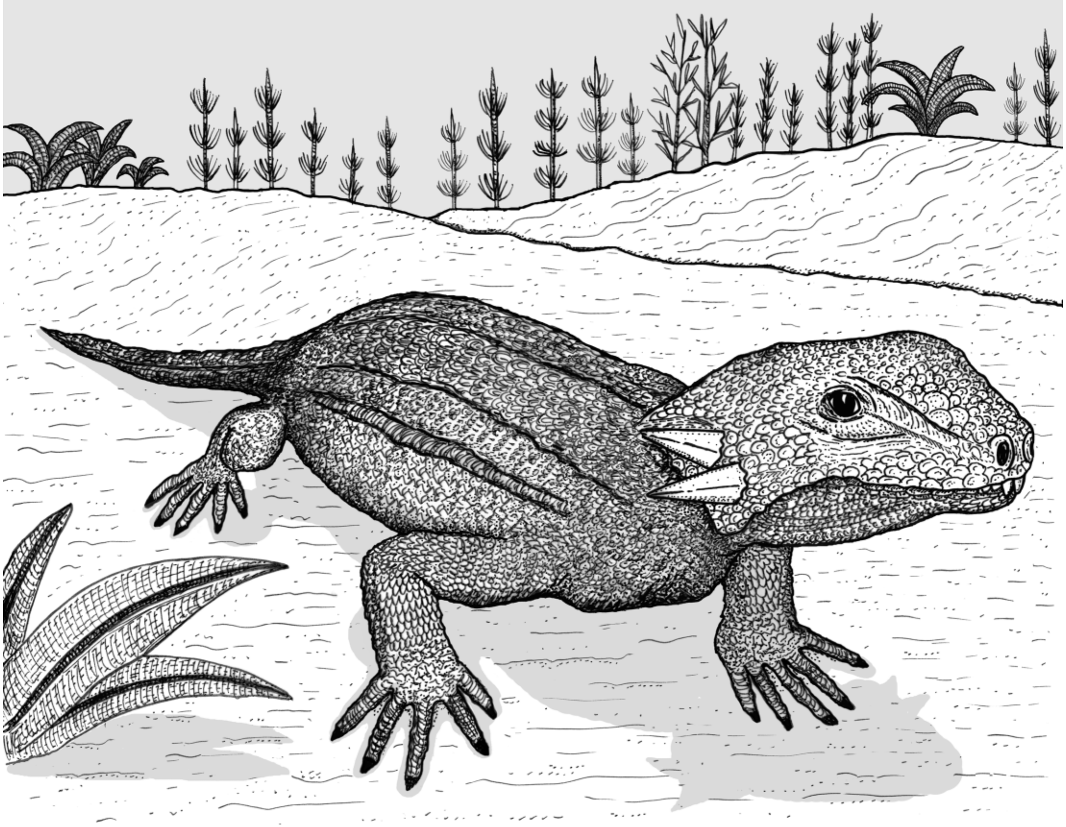

Figure 21 Life reconstruction of *Leptopleuron lacertinum* Owen, 1851. Following Benton & Walker (1985) for the reconstruction of *Scleromochlus teylori* Woodward, 1907, from the same location, *Leptopleuron* is shown in the dune-like settings of the Lossiemouth Sandstone Formation, with plants based on other comparable Late Carnian units elsewhere in the world.

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 fossilification 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

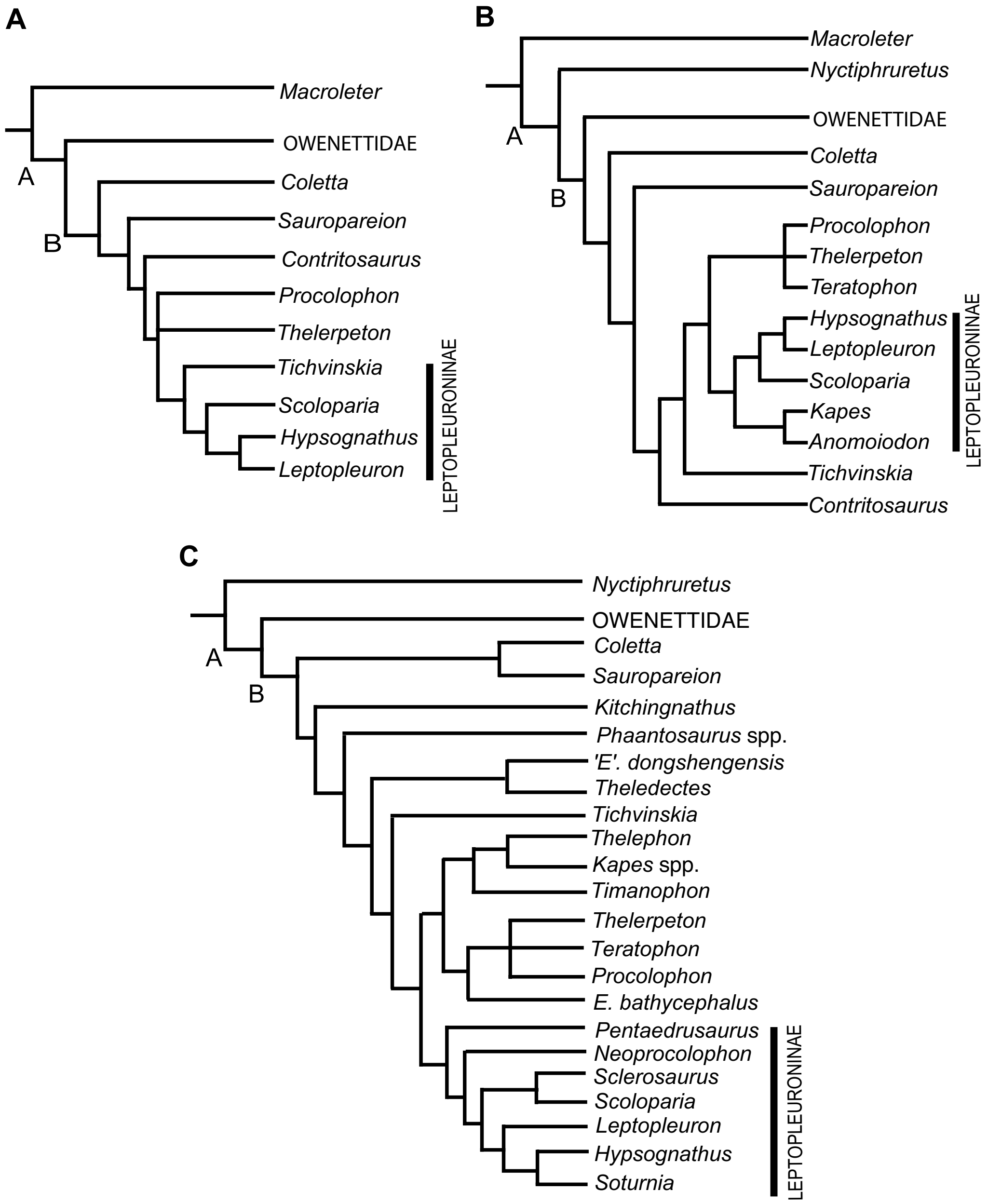

Figure 22 Results of recent phylogenetic analysis of procolophonoid interrelationships, illustrating the proposed members of Leptopleuroninae. The topology recovered in (A) the Modesto & Damiani (2007) analysis, (B) the Säilä (2008) analysis, and (C) the Cisneros (2008c) analysis. A = Procolophonoidea, B = Procolophonidae.

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 fenneri* in all of these analyses and, when additional taxa have been included, also *Scoloparia glyphanodon*, *Sclerosaurus armatus* and *Koiloskiosaurus coburgensis* 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 (Sues & Reisz 2008). *Koiloskiosaurus*, 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 *Tichvinskia* to be the most basal leptoleuronine, but this is inconsistent with all other studies, which have found that *Tichvinskia* is either a procolophonine (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; Säilä 2008). Other taxa considered as members of Leptopleuroninae by Cisneros (2008a, c) (Fig. 22C) are *Soturnia caliodon*, *Pentaedrusaurus ordosiamus* 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). *Pentaedrusaurus* 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, Säilä (2008) found that *Kapes* cf. *K. majmesculae*, and *Anomoiodon liliensterni*, 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 Säilä (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 Procolophonoidea that also addresses the composition of Leptopleuroninae is under preparation by the present author.

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