Reappraisal of an ankylosaurian dinosaur from the Upper Cretaceous of James Ross Island (Antarctica)

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ABSTRACT

The holotype of the upper Campanian ankylosaur *Antarctopelta oliveroi* n. gen., n. sp., from James Ross Island, Antarctica, is described. Diagnostic characters include short cervicals (centrum length about 70% of the centrum height), distal caudal vertebrae with transverse processes well developed (centrum width including the transverse processes exceeds 30% of the posterior articulation width) and dorsoventrally depressed, and the presence of smooth, sub-circular osteoderms, surrounded by a mosaic of smaller polygonal osteoderms with a rugose surface texture and tiny, button-like ossicles. While a number of features, such as relatively large teeth with respect to the mandible and the presence of an asymmetrical cingulum, suggest an affinity with the Nodosauridae, others such as the dorsoventrally depressed morphology of the distal caudal vertebrae and, especially, the presence of ossified tendons on their ventral side, characterize the Ankylosauridae. This uncertainty impedes evaluation of the paleobiogeographical significance of this new species of dinosaur.

KEY WORDS
Ankylosauria,
Upper Cretaceous,
James Ross Island,
Antarctica,
paleobiogeography,
new genus,
new species.

RÉSUMÉ

Réévaluation d'un dinosaure ankylosaurien du Crétacé supérieur de l'île de James Ross (Antarctique).
Nous décrivons l'holotype d'un ankylosaure du Campanien supérieur, *Antarctopelta oliveroi* n. gen., n. sp., qui provient de l'île de James Ross (Antarctique). Les caractères diagnostiques comprennent des vertèbres cervicales courtes (la longueur du centre représente environ 70 % de la hauteur), des vertèbres caudales

MOTS CLÉS
Ankylosauria,
Crétacé supérieur,
île de James Ross,
Antarctique,
paléobiogéographie,
nouveau genre,
nouvelle espèce.

distales munies de processus transverses bien développés (la largeur du centre, comprenant les processus transverses inclus, dépasse de 30 % la largeur de la surface articulaire postérieure) et dorsalement déprimés, et la présence d'ostéodermes subcirculaires plats, entourés d'une mosaïque d'ostéodermes polygonaux plus petits, à texture externe rugueuse et des petits ossicules en forme de boutons. Alors qu'un certain nombre de caractères, comme les dents relativement grandes par rapport à la longueur totale de la mandibule et la présence d'un cingulum asymétrique, suggèrent une affinité avec les Nodosauridae, d'autres comme l'existence de vertèbres caudales distales dorso-ventralement déprimées et, surtout, la présence de tendons ossifiés sur leur face ventrale, caractérisent les Ankylosauridae. Cette incertitude gêne l'évaluation de la signification paléobiogéographique de cette nouvelle espèce de dinosaure.

INTRODUCTION

The discovery of the first Antarctic dinosaur, a medium-sized ankylosaur from the Santa Marta Formation (Upper Cretaceous), was first discussed by Gasparini *et al.* (1987) and Olivero *et al.* (1991). This material was located in January 1986 by the Argentinean geologists Eduardo Olivero and Roberto Scasso. The specimen was about 2 km farther south Santa Marta Cove, in the northern part of James Ross Island (Olivero *et al.* 1991) (Fig. 1). The fossils were collected about 90 m from the base of the Gamma Member, Santa Marta Formation, in the lowermost part of the Marambio Group. Ammonite assemblages found above and below the dinosaur-bearing horizon suggest a late Campanian age (Olivero *et al.* 1991; Olivero 1992). The holotype was collected from an area of about 6 m², with many of the bones being fragmentary, having been subjected to successive freeze-thaw cycles. Additional material assumed to belong to the same specimen was recovered during subsequent fieldwork (Gasparini *et al.* 1996; Ricqlès *et al.* 2001).

We review the material belonging to the James Ross Island ankylosaur, especially those elements that have not been previously described, and other new interpretations on previously discussed material. In spite of being fragmentary, enough material of this individual is now available to present a

diagnosis of a new ankylosaur, *Antarctopelta oliveroi* n. gen., n. sp.

The specimen described herein is deposited at the Museo de La Plata (MLP), Buenos Aires Province, Argentina.

TAPHONOMIC REMARKS

The dinosaur had to be exhumed over the course of several field seasons as the fossil bearing horizons were often frozen. This notwithstanding, as observed by Olivero *et al.* (1991), these fragments appear to belong to a single specimen without signs of reworking. Moreover, several elements of the postcranium articulate (Gasparini *et al.* 1996: fig. C). Gasparini *et al.* (1996) suggested the possibility that one of the two phalanges thus far recovered may correspond to a different individual, or that the different shape and size could result from that one phalanx was from the manus and the other from the pes. In this reappraisal, the latter hypothesis is confirmed, and in agreement with Olivero *et al.* (1991), it is hereby considered that all the fragments thus far recovered belong to a single specimen.

The James Ross Island ankylosaur was collected from shallow marine deposits, associated with various marine invertebrates such as bivalves, gastropods and ammonites (Olivero *et al.* 1991).
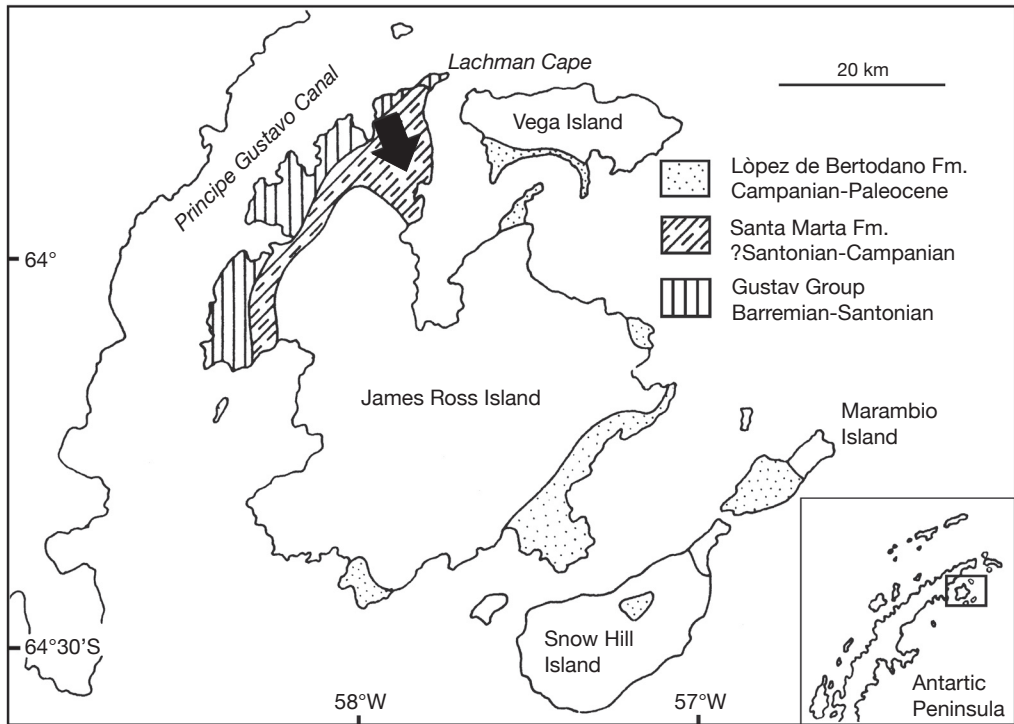
Fig. 1. — Location map of the holotype of *Antarctopelta oliveroi* n. gen., n. sp. (arrow).

A tooth attributed to the chondrichthyan *Notidanodon* Cappetta, 1975 was found associated with one of the osteoderms (Cione & Medina 1987). This same type of tooth was found in the skull of the mosasaur *Lakumasaurus antarcticus* Novas, Fernández, Gasparini, Lirio, Núñez & Puerta, 2002, recently recovered 1100 m farther east from the ankylosaurian dinosaur, and 10 m above this specimen (Novas *et al.* 2002).

SYSTEMATICS

Order ORNITHISCHIA Seeley, 1888
Suborder ANKYLOSAURIA Osborn, 1923
Family indet.

Genus *Antarctopelta* n. gen.

Antarctopelta oliveroi n. sp.
(Figs 2-9)

See also Gasparini *et al.* 1987: figs 1, 2; 1996: figs 1-5; Olivero *et al.* 1991: fig. 2; Ricqlès *et al.* 2001: fig. 2.
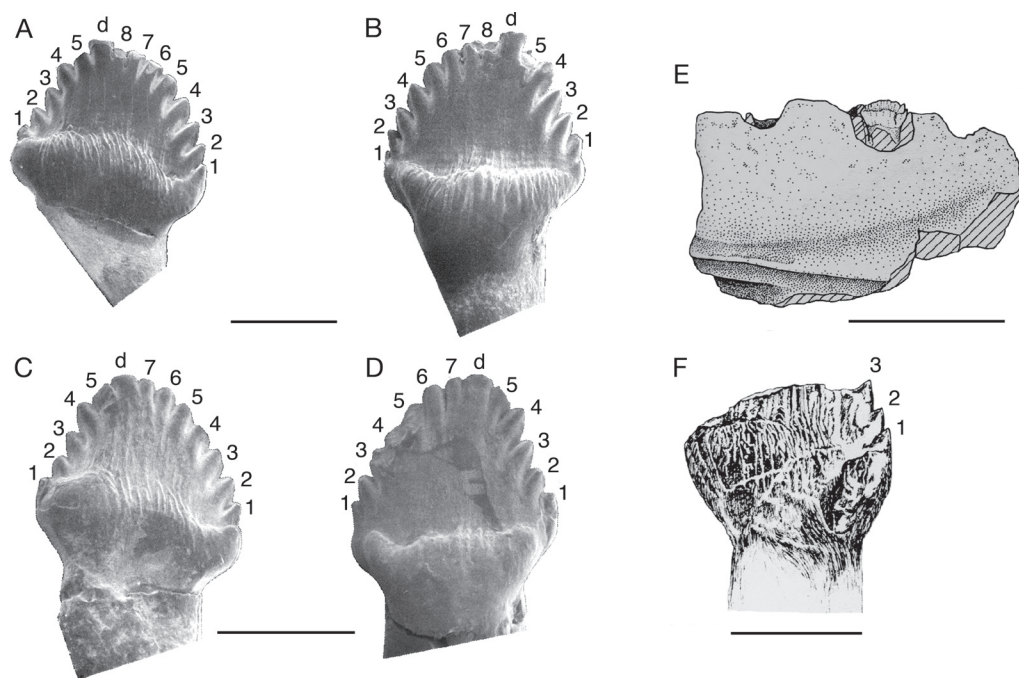
FIG. 2. — *Antarctopelta oliveroi* n. gen., n. sp., holotype (MLP 86-X-28-1): **A**, **B**, tooth I in lingual and labial views; **C**, **D**, tooth II in lingual and labial views; **E**, left dentary in medial view; **F**, tooth III in lingual view. Abbreviations: **1-8**, marginal denticles; **d**, apical denticle. Scale bars: A-D, F, 5 mm; E, 25 mm.

TYPE LOCALITY AND HORIZON. — Santa Marta Cove, North James Ross Island (Antarctica), locality D6-1 (Gasparini *et al.* 1987; Olivero *et al.* 1991) (Fig. 1).

ETYMOLOGY. — Species named for Eduardo Olivero, an outstanding Argentine geologist and paleontologist specializing in Antarctica, who discovered the holotype.

STRATIGRAPHICAL PROVENANCE. — Lower part of the Gamma Member of the Santa Marta Formation (Marambio Group) (upper Campanian) (Olivero *et al.* 1991; Olivero 1992).

DIAGNOSIS. — Medium-sized ankylosaur, estimated length of no more than 4 m; cervical centra short (centrum length about 70% of the centrum height), morphologically most similar to *Silvisaurus* Eaton, 1960, with the anterior articular faces higher than the posterior ones, as in *Edmontonia rugosidens* Gilmore, 1930; anterior caudal vertebrae with relatively slender transverse processes; centra of the posteriormost caudals notably dorsoventrally depressed, with articular faces slightly anteriorly inclined and laterally expanded, transverse processes of the posterior caudals well developed (transverse processes

length about 40% of the centrum width), dorsoventrally depressed, and positioned within the anterior half of the vertebral centrum; at least six morphotypes of postcranial osteoderms, including 1-narrow and spine-shaped, 2-ovoid plate-like with a rugose surface texture, 3-plate-like with a smooth surface texture, 4-polygonal with a rugose texture, 5-shield-shaped with a dorsal keel, and 6-small (less than 5 mm in diameter) button-like.

DESCRIPTION AND COMPARISONS
Teeth

The teeth of *Antarctopelta oliveroi* n. gen., n. sp. are leaf-like, with mesial and distal marginal denticles and a large apical denticle, slightly curved caudally (Fig. 2). The teeth have an asymmetrical cingulum (*contra* Gasparini *et al.* 1987; Olivero *et al.* 1991), similar to many nodosaurids (Coombs & Maryańska 1990). Of the four preserved teeth (designated I, II, III and IV), one remains *in situ* within the left dentary (tooth III). Tooth IV has lost most of its crown (only two denticles remain) but has a complete root.
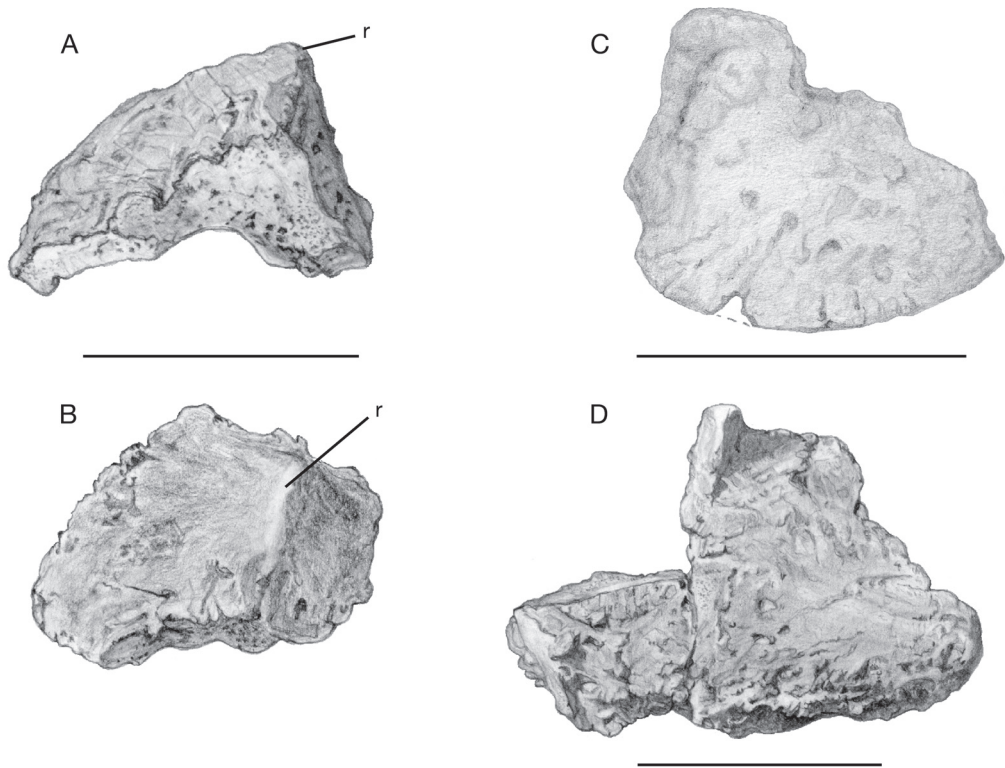
FIG. 3. — *Antarctopelta oliveroi* n. gen., n. sp., holotype (MLP 86-X-28-1), skull elements: **A**, **B**, putative supraorbital in anterior and lateral views; **C**, putative quadrato-jugal (or supraorbital) in lateral view; **D**, putative parietal in dorsal view. Abbreviation: **r**, dorsolateral ridge. Scale bars: 50 mm.

All four teeth demonstrate minor morphological differences. Tooth I (Fig. 2A, B; see also Gasparini *et al.* 1996: fig. 1C, D) has eight mesial denticles, a central apical denticle and five distal denticles (8+1+5).

Along the mesial margin of teeth I and II, the most basal denticle is partially enveloped by the cingulum (Fig. 2A, B, denticle 1 and Fig. 2C, D, denticle 1).

Tooth II (Fig. 2C, D; see also Gasparini *et al.* 1996: fig. 1A, B), the smallest of the preserved crowns, has a denticle formula of (7+1+5). In lingual view (Fig. 2C), there are vertical striations continuous across the crown and cingulum. In labial view (Fig. 2D), the crown of this tooth is relatively smooth, although thin vertical striations are present along the dorsal rim of the cingulum.

Coombs (1990) has observed that larger teeth tend to have more denticles, which could explain the existence of an additional denticle in tooth I.

Tooth III has minute denticles (three have been preserved on the anterior margin, Fig. 2E, F). Lingually (Fig. 2F), the cingulum is not as pronounced as in the other teeth. However, this sector is placed clearly below the area of the cingulum that belongs to the labial side.

Although very worn and incomplete, tooth IV does have a basal denticle partially ensnared by the cingulum. The root is well preserved and virtually complete.

Fourteen or more denticles have previously been reported for nodosaurid ankylosaurs (e.g., Galton [1980] reported a tooth from the Purbeck of England with 17 [8+1+8], and a large number of denticles

is reported in replacement teeth of *Sarcolestes leedsi* Lydekker, 1893 [Galton 1983]). A high denticle count is also known for some ankylosaurids (e.g., more than 14 in *Euoplocephalus tutus* Lambe, 1902 [Coombs 1990]; probably 14 in *Ankylosaurus magniventris* Brown, 1908 [Coombs 1990] and "polacanthids" [at least 16 in *Gastonia burgei* Kirkland, 1998]). Coombs (1990), however, cautions against the taxonomic significance of denticle count.

Lower jaw
The preserved portion of the lower jaw of *Antarctopelta oliveroi* n. gen., n. sp. (Fig. 2E) was described and figured by Gasparini *et al.* (1996: see fig. 1I, J). It consists of a mid-portion of a left dentary with nine tooth positions oriented longitudinally. In dorsal view, most of these alveoli resemble figure eights, suggesting that replacement teeth were converging on the erupted series. As characteristic for ankylosaurs, the tooth row is slightly curved in dorsal view.

Within the alveolar position fifth from the anterior end is a worn *in situ* tooth (tooth III, see above). On the lingual surface of the dentary is a shallow Meckelian canal (sulcus) (Fig. 2E) opposite to which, on the labial side, are at least four foramina subparallel to the alveolar border.

Skull ossifications
Gasparini *et al.* (1987) and Olivero *et al.* (1991) had referred to the existence of cranial elements, similar to the supraorbital projections of some ankylosaurs. Gasparini *et al.* (1996) countered that at least some of these elements may represent postcranial osteoderms. This reappraisal supports the original hypothesis with various fragments of this material interpreted as skull elements.

One of these ossifications (see Olivero *et al.* 1991: fig. 2C) (Fig. 3A, B) is a two-surfaced piece with one of its external surfaces, which is interpreted as latero-ventrally oriented, slightly concave, and another one, slightly convex, which is presumed to be latero-dorsally oriented (Fig. 3A). This convex surface is rugose in the medial part. The two surfaces form a sort of ridge (Fig. 3A, B, r). In our opinion, this bone is probably a supraorbital, with the concave ventral surface representing the

dorsal surface of the orbital cavity. Unfortunately, the partial ossification impedes the recognition of articular surfaces through which their position in the skull may be accurately known.

Other two elements (Fig. 3C) also have two external surfaces, scarcely ornamented, and slightly convex, which form a dihedral angle of 45°, and an acute edge, strongly curved in lateral view. The curved flange is pointed at one of the ends, above which there is a protuberance (Fig. 3C). These elements are interpreted as quadratojugals or supraorbitals, similar to those of *Edmontonia rugosidens* (Carpenter 1990).

Another element, incompletely preserved, is rather flat with a relatively smooth surface (Fig. 3D). Toward one of its extremes (here interpreted as lateral), the bone thickens and ends in a protuberance. This bone is interpreted here as part of the skull roof, probably a right parietal.

Cervical vertebrae
Five cervical vertebrae are preserved, three of which are represented by a latex cast prepared from a natural mould by technicians of the Museo de La Plata (see Gasparini *et al.* 1996: fig. 2C) (Fig. 4A, B). Comparison with more complete material (e.g., *Silvisaurus condrayi* Eaton, 1960) suggests that these vertebrae represent the middle components of the cervical series (Eaton 1960).

All the cervical centra are proportionally short, amphicoelus, and are transversely broader than anteroposteriorly long (Fig. 4). The cervical centra become progressively proportionally shorter, being the last of the cervical centra preserved proportionally shorter than in *Ankylosaurus magniventris* (Coombs & Maryańska 1990) (*Antarctopelta* n. gen. centrum length/height ratio = 0,57, *Ankylosaurus* Brown, 1908 centrum length/height ratio = 0,78). This represents a notable difference with other ankylosaurs with relatively elongate cervical centra, such as *Stegopelta landerensis* Williston, 1905 (centrum length/height ratio = 1,14) (Carpenter & Kirkland 1998), or *Struthiosaurus austriacus* Bunzel, 1871 (centrum length/height ratio = 1,35) (Pereda-Suberbiola & Galton 2001).

The posterior articular surface of the cervical vertebrae of *Antarctopelta oliveroi* n. gen., n. sp. is
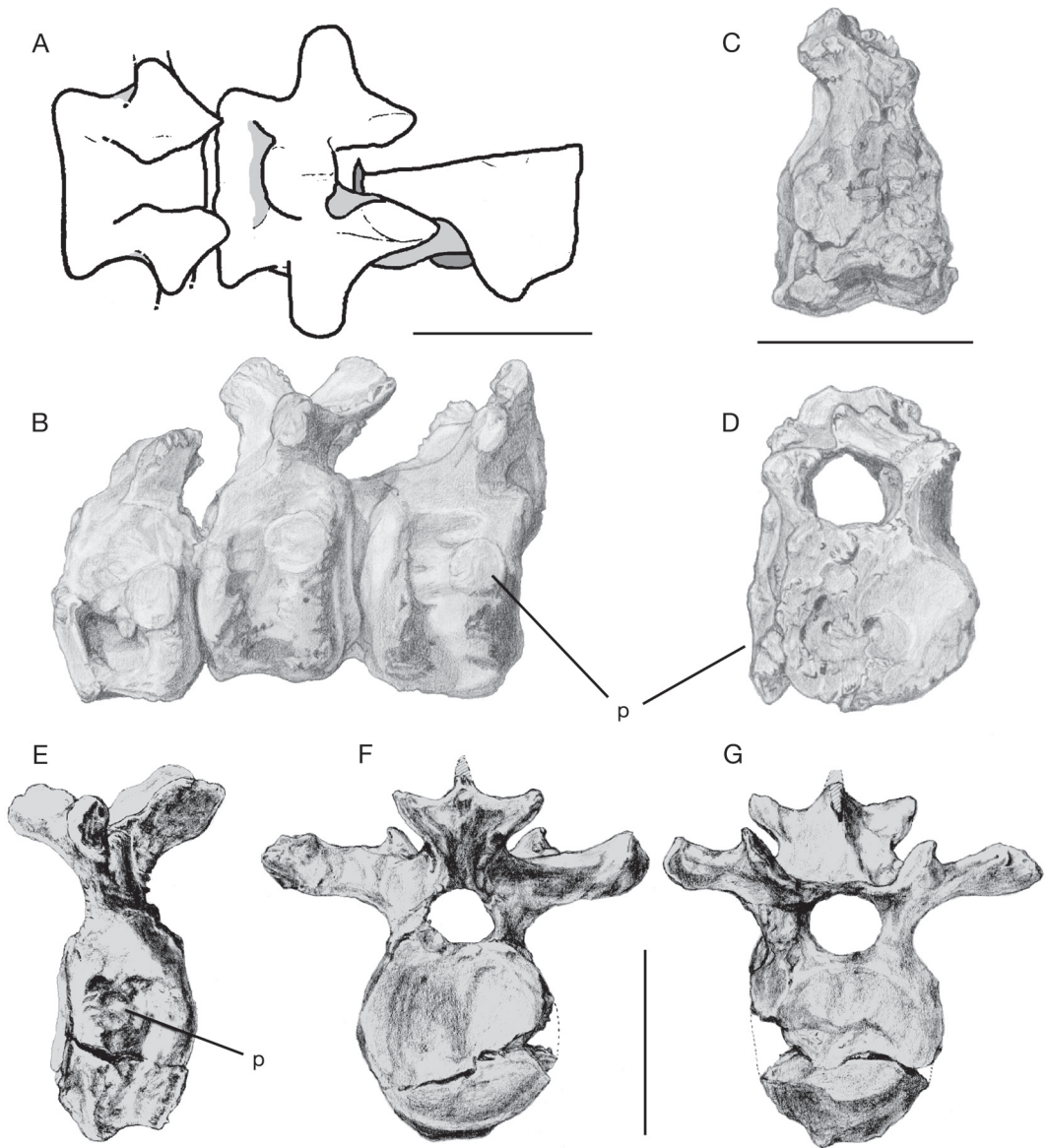
FIG. 4. — *Antarctopelta oliveroi* n. gen., n. sp., holotype (MLP 86-X-28-1): **A**, **B**, latex cast from a mould of three articulated mid-cervical vertebrae in dorsal and right lateral views; **C**, **D**, anterior cervical vertebra in right lateral and anterior views; **E-G**, posterior cervical vertebra in left lateral (**E**), posterior (**F**) and anterior (**G**) views. Abbreviation: **p**, parapophysis. Scale bars: 50 mm

lower than the anterior surface, as in *Edmontonia rugosidens* Gilmore, 1930. The neural pedicels are relatively short, and more similar to those of *Edmontonia* Sternberg, 1928, and unlike those of *Panoplosaurus mirus* Lambe, 1919, which are rela-

tively long (Carpenter 1990). The neural canal is virtually circular in cross section. The parapophyses are situated immediately below the neural arch at approximately the same level in all the preserved cervicals of *Antarctopelta oliveroi* n. gen., n. sp. The
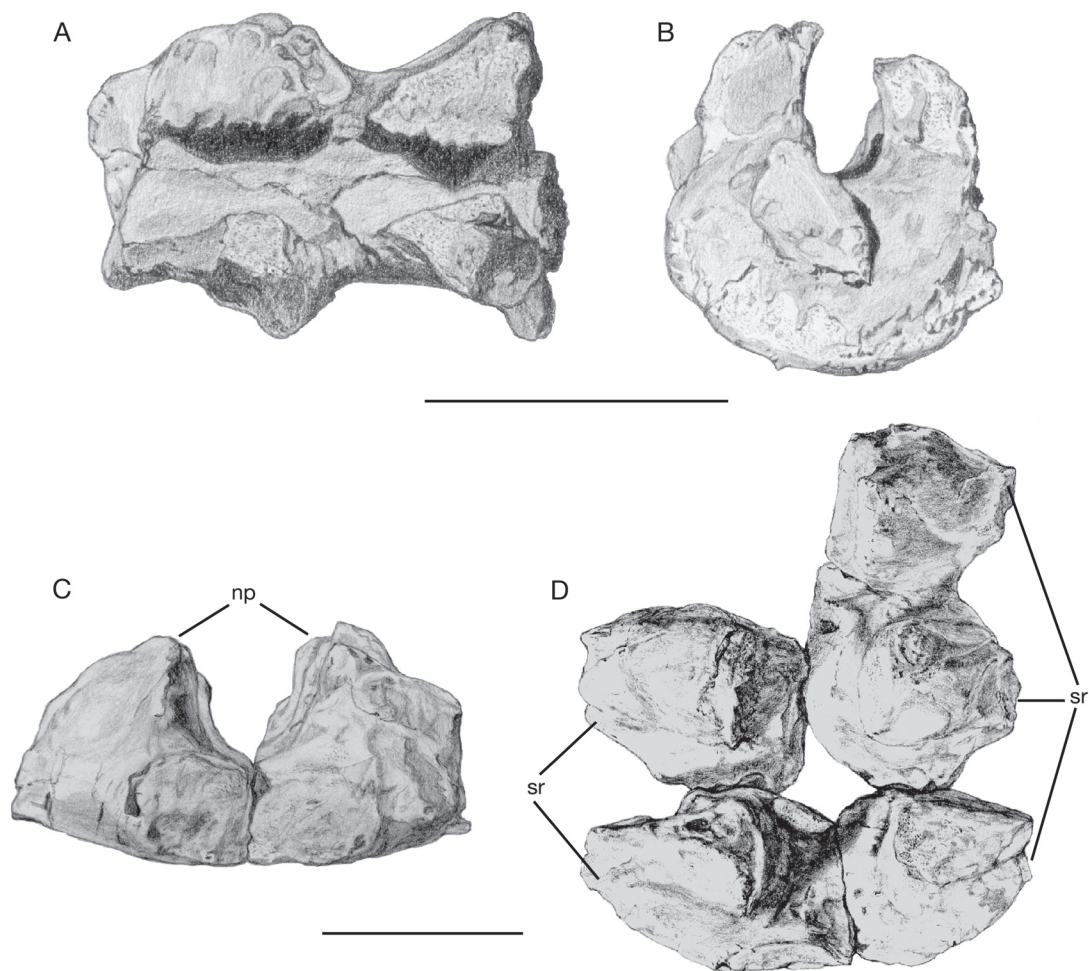
Fig. 5. — *Antarctopelta oliveroi* n. gen., n. sp., holotype (MLP 86-X-28-1): **A**, **B**, dorsal vertebrae from the presacral rod in dorsal and anterior views; **C**, **D**, sacral vertebrae in posterior and dorsal views. Abbreviations: **np**, neural pedicels; **sr**, fused proximal end of sacral ribs. Scale bars: 50 mm.

posteriormost cervical preserved is virtually complete (Fig. 4E-G). Compared to it, the prezygapophyses of the other cervical vertebrae are more widely spaced (see Gasparini *et al.* 1996: fig. 2A-C). In addition, the transverse processes of the anteriormost preserved cervical vertebrae are somewhat longer (Fig. 4A), although the degree of inclination of the transverse processes is constant throughout the series.

Synsacral vertebrae
The only two dorsal vertebrae preserved are those appearing to be incorporated into the presacral rod of the synsacrum (Fig. 5A, B). They were described by Gasparini *et al.* (1987, 1996: fig. 2F, G). The articular surface of the anterior vertebra is wider than high (Fig. 5B), and shows no traces of fusion with another vertebra, which suggests that it is the first vertebra of the presacral rod.

Two virtually complete sacral centra and the left portion of a third represent a portion of sacrum (Fig. 5C, D). In addition to the centra, these elements include the base of the neural pedicles and

the proximal end (head) of the sacral ribs. All three sacral vertebrae are firmly fused together.

Similar to *Silvisaurus*, the ventral surface of the sacrum is notably flat, lacking the groove or paired ridges seen in other nodosaurids (Carpenter & Kirkland 1998). In posterior view (Fig. 5C), the sacral centrum is dorsoventrally depressed. Indeed, the dorsoventral depression that characterizes the sacral vertebrae is also present in the dorsal vertebrae of the presacral rod, with a centrum width almost twice the centrum height (see Gasparini *et al.* 1996: fig. 2F, G, I, J). Among the sacral vertebrae, the width of the centra ranges from nearly twice the height anteriorly to more than three times the centrum height. The proximalmost portions of the sacral ribs are fused to each of the three sacral vertebrae with the ribs of the second and third centra being dorsoventrally deeper and more robust than the first.

Rib fragments

About eight fragments of rib exist that range in cross sectional morphology from "T" to "L". One large and several smaller osteoderms have been preserved on one of these fragments. The shield-shaped osteoderms lie on the dorsal surface of the rib at only one of its ends (Fig. 9F). The ossicles instead, are distributed on the middle part of the dorsal surface (Gasparini *et al.* 1987: lam. I3).

Caudal vertebrae

Eight fragmentary caudal vertebrae are preserved (Fig. 6). Comparison with other taxa (e.g., *Sauropelta* Ostrom, 1970, *Struthiosaurus* Bunzel, 1871) suggests that four of them are relatively proximal in the series and four are relatively distal. The anteriormost is represented only by the ventral portion of the centrum. Ventrally, this surface is concave with pronounced facet for a chevron at the posteriormost edge. Another anterior caudal vertebra was illustrated in anterior view by Gasparini *et al.* (1996: fig. 2H). As oriented, the centrum appears to be triangular. However, this vertebra is incomplete, and only represents the right half of the centrum (Fig. 6A-E). On the dorsal surface of this vertebra, the base of the right neural pedicle can be seen. The anterior caudal vertebrae of *Antarctopelta* n. gen. are rela-

tively wide (e.g., wider than in *Struthiosaurus*; see Pereda-Suberbiola & Galton 2001: fig. 3), and would have had a heart-shaped anterior articular surface, although they are morphologically similar to those typical of various nodosaurids (e.g., *Edmontonia*, *Niobrarasaurus coleii* Mehl, 1936, *Sauropelta edwardsorum* Ostrom, 1970, *Silvisaurus* and possibly *Struthiosaurus* sp. (Pereda-Suberbiola & Galton 2001; see Pereda-Suberbiola 1999: 278, fig. 3E-G). In posterior view, the outline of the articular face of the centrum was apparently sub-circular (Fig. 6D). The elliptically shaped base of the slender transverse process of this vertebra, is also preserved (Fig. 6E).

There is also a series of four more distally positioned caudal centra that have not previously been described. The neural arch is not preserved in any of these vertebrae. In relation to the anteriormost vertebrae, each centrum is elongated and dorsoventrally depressed (Fig. 6F-H) and resembles that described for some ankylosaurids (Coombs 1978). The anteriormost of the distal caudal centra (Fig. 6F-H) is wider (55 mm) than long (50 mm); two others are somewhat longer (50 mm) than wide (45 and 48 mm). Although there is a noticeable decrease in width, all the vertebrae appear to have similar lengths. Unlike *Struthiosaurus* (see Pereda-Suberbiola & Galton 2001: fig. 3) and *Sauropelta* (Carpenter, 1984), these distal caudal vertebrae are more than 40% longer than the anterior caudals, where the posterior caudals are approximately equal in length to the anterior. This latter may be a plesiomorphic condition for the Thyreophora, since it is also present in stegosaurs (Galton 1990).

In dorsal view (Fig. 6F), the posterolateral surfaces of the centra are concave anterior to which are the flat, horizontally oriented transverse processes. Mid-series and distalmost caudals of *Struthiosaurus* also have well developed transverse processes (Pereda-Suberbiola & Galton 2001), a feature that is otherwise uncommon amongst nodosaurids (e.g., *Sauropelta* and *Nodosaurus textilis* Marsh, 1889) (Pereda-Suberbiola & Galton 2001). The ventral surface of the distal vertebrae of *Antarctopelta* n. gen. is slightly concave and is crossed by *in situ* ossified tendons, similar to ankylosaurids.
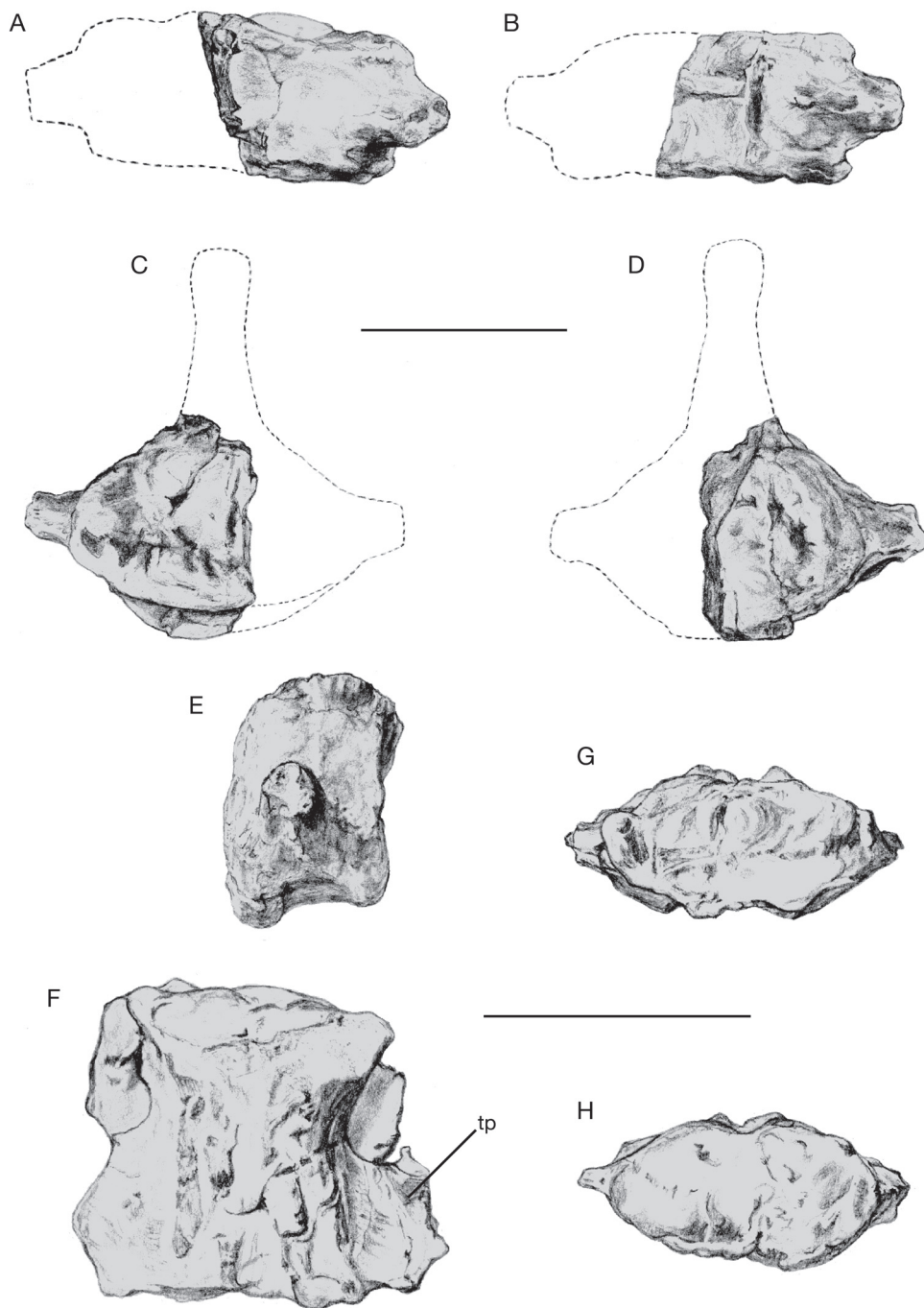
FIG. 6. — *Antarctopelta oliveroi* n. gen., n. sp., holotype (MLP 86-X-28-1): **A-E**, anterior caudal vertebra in ventral (**A**), dorsal (**B**), anterior (**C**), posterior view (**D**), and right lateral (**E**) views; **F-H**, posterior caudal vertebra in dorsal (**F**), anterior (**G**) and posterior (**H**) views. Abbreviation: **tp**, transverse process. Scale bars: 50 mm.
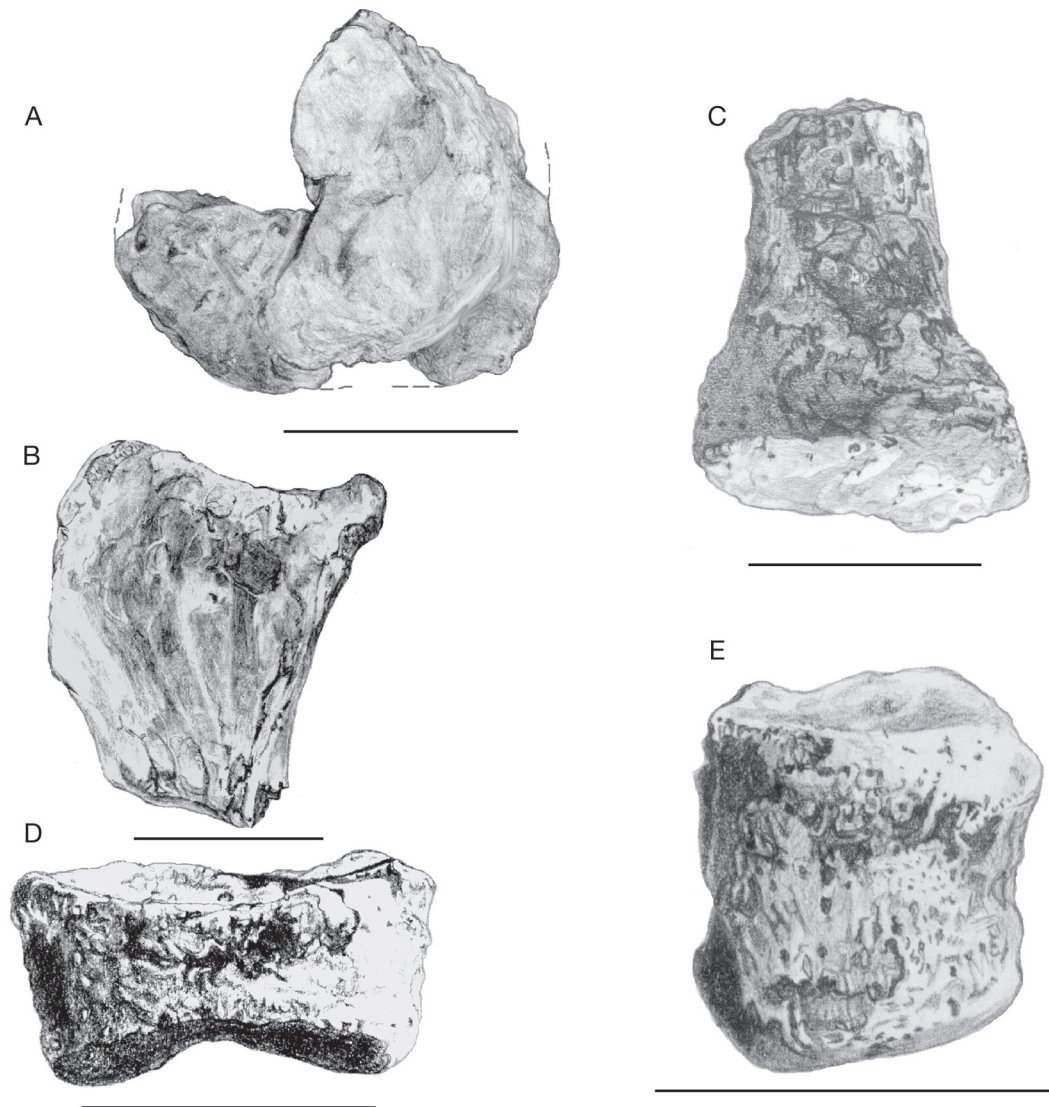
Fig. 7. — *Antarctopelta oliveroi* n. gen., n. sp., holotype (MLP 86-X-28-1): **A**, distal end of left femur in internal view; **B**, right IV? metatarsal in ventral view; **C**, distal end of metapodial; **D**, pedal? phalanges in anterior view; **E**, manual? phalanges in anterior view. Scale bars: 30 mm.

In lateral view, the distal caudals resemble a parallelogram with its articular surfaces offset from the long axis of the centrum. In contrast, nodosaurids such as *Struthiosaurus* (see Pereda-Suberbiola & Galton 2001: fig. 3) and *Sauropelta* (see Coombs & Maryaňska 1990: fig. 8C), have distal caudal vertebrae that are rectangular in profile.

Ossified tendons

These structures have been found associated with the caudal vertebral remains, arranged parallel to the long axis of the body. Numerous ossified tendons were preserved on both sides of an isolated neural spine. Other tendons arrange longitudinally on the ventral surface of the distal caudal vertebrae.
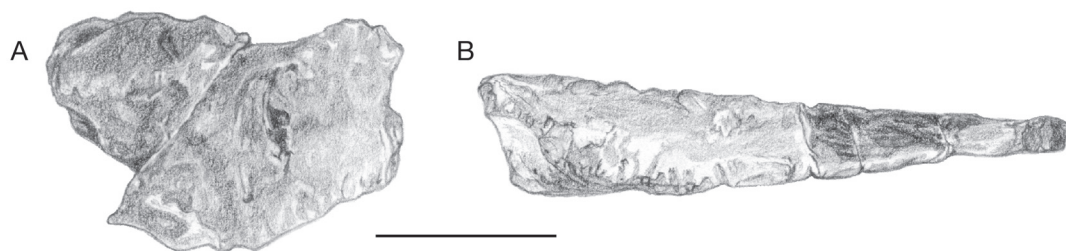
FIG. 8. — *Antarctopelta oliveroi* n. gen., n. sp., holotype (MLP 86-X-28-1): **A**, scapula in ventral view; **B**, ilium in lateral view. Scale bar: 50 mm.

Appendicular skeleton

A distal fragment of a left femur is here reported for the first time (Fig. 7A). It includes part of the medial condyle and the intercondylar furrow. The articular surface of the medial condyle is rugose, especially along its posterior surface. Reconstruction of the element based on similar material from Salitral Moreno, northwestern Patagonia (Coria & Salgado 2001) yields a total femur length of approximately 30 cm.

The holotype of *Antarctopelta* n. gen. also includes five partial metapodials (Fig. 7B, C). These elements are relatively massive, with broad, distally expanded articular surfaces (see Gasparini *et al.* 1996: fig. 4A, B) (Fig. 7C). A proximal end of a right metapodial (probably the metatarsal IV) has recently been collected (Fig. 7B). The dorsal surface of this bone is slightly convex whereas the ventral and lateral surfaces are concave. The size of the metatarsals is consistent with the estimated size of the femur.

Two phalanges are preserved. One is cuboid, albeit slightly asymmetrical (see Gasparini *et al.* 1996: fig. 4C) (Fig. 7E); the other is wider and disc-like (see Gasparini *et al.* 1996: fig. 4D) (Fig. 7D). Gasparini *et al.* (1996) suggested that the cuboid one belonged to digit I (of hand or pes). The disc-like phalanx was interpreted by these authors as the second phalanx of digit II or III (of hand or pes). In dorsal view, the outline of the proximal end of the second phalanx of digit II of the pes of the juvenile *Euoplocephalus* Lambe, 1910 is slightly convex (see Coombs 1986: fig. 4A). The morphology of the disc-like phalanx of *Antarctopelta* n. gen. matches best with the first

phalanx of digit IV in that ankylosaur; the size of this phalanx does not differ significantly from the transverse width of the distal end of the preserved metatarsal. The other phalanx is morphologically similar, although somewhat shorter, to the first phalanx of digit I of the manus of *Edmontonia rugosidens* (see Carpenter 1990: fig. 21.17 E, F).

A portion of the scapula (the glenoid region) is preserved, and shows no signs of being fused to the coracoid (see Gasparini *et al.* 1996: fig. 3A) (Fig. 8A). Other nodosaurids (e.g., *Edmontonia*) and ankylosaurids (e.g., *Euoplocephalus*) also show a similar feature (Carpenter 1990; Penkalski 2001). The lack of fusion between coracoid and scapula in *Antarctopelta* n. gen. probably results from immaturity (see Discussion). The acromion process is missing.

A fragment of the right ilium, probably the midportion of the preacetabular process, is preserved (see Gasparini *et al.* 1996: fig. 3B) (Fig. 8B).

Osteoderms

There are six different morphotypes of osteoderms thus far recognized for *Antarctopelta* n. gen. (Fig. 9), including spine-like forms, plate-like forms and small button-like ossicles.

One fragment is interpreted as a base of spine (Olivero *et al.* 1991: fig. 2d). Internally, on the fracture surface, it can be seen spongy tissue. Externally this element is very ornamented, especially on the border between ventral and lateral surfaces. This spine (described in Gasparini *et al.* 1987, and illustrated in Olivero *et al.* 1991: fig. 2d) was first interpreted as a tail club, and then by Gasparini
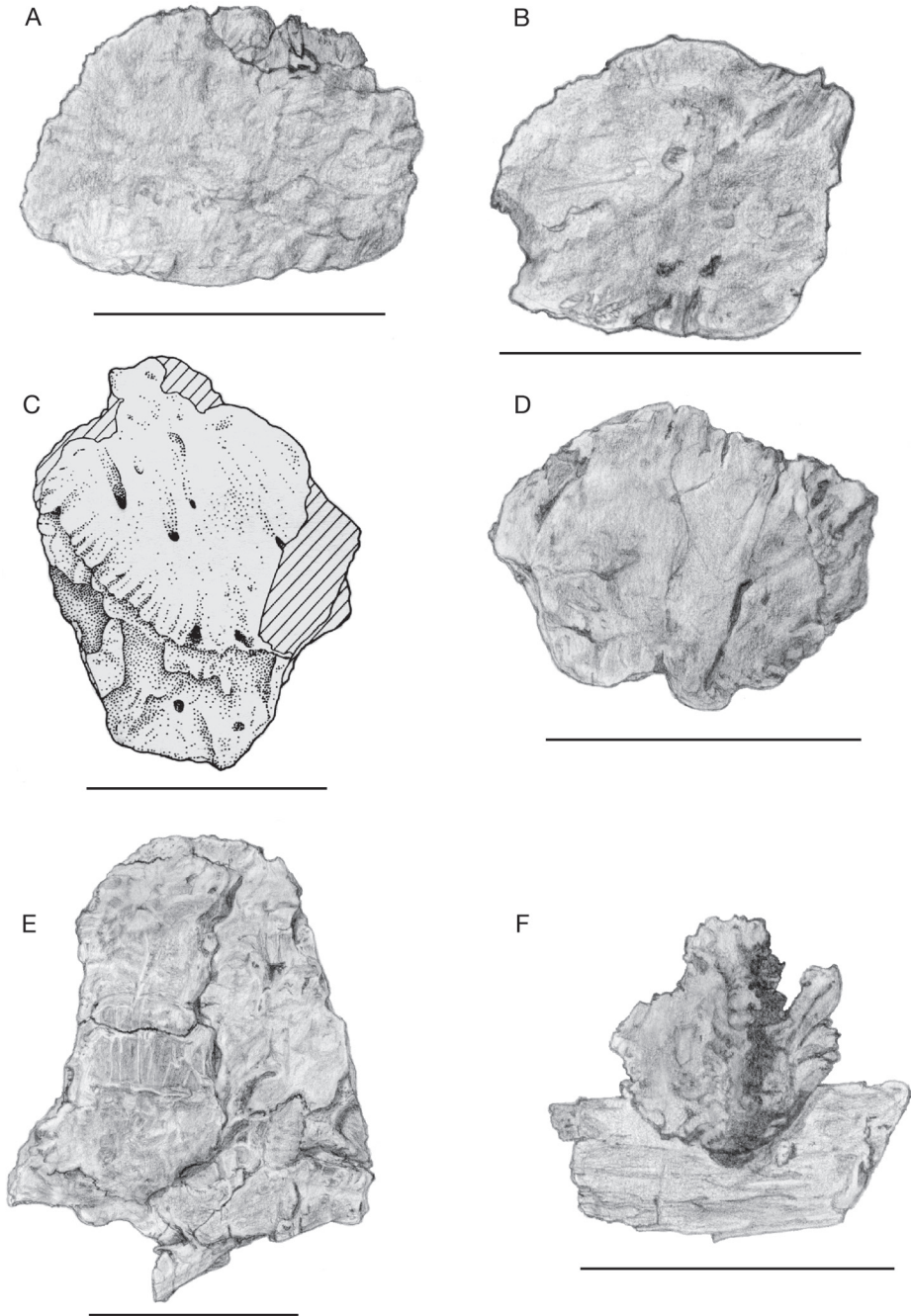
FIG. 9. — *Antarctopelta oliveroi* n. gen., n. sp., holotype (MLP 86-X-28-1), osteoderms: **A**, **B**, plate-like, ovoid forms; **C**, **D**, plate-like, sub-circular forms; **C**, **E**, plate-like, polygonal forms; **F**, elongate forms, with a dorsal keel. Scale bars: 50 mm.

et al. (1996) as a type of osteoderm (their "type b" osteoderm). According to Gasparini *et al.* (1987), the supposed tail club had a convex external surface ornamented with ossicles, and a concave internal surface. Gasparini *et al.* (1996) described the osteoderms as "large, rough-surfaced plates [with the] dorsal surface [...] sculptured with numerous small pits and rugosities. The ventral face is irregular and hollowed" (Gasparini *et al.* 1996: 588). In this review the "internal surface" of the club (Gasparini *et al.* 1987), or the "ventral surface" of the osteoderm (Gasparini *et al.* 1996) is reconsidered as the internal surface of an eroded, probably hollow, spine. The external (anterior?) surface of the base of the spine actually belongs to what Gasparini *et al.* (1996) interpreted as the dorsal surface of their "type b" osteoderm.

Ovoid elements, but with a straight side, flat, slightly curve in lateral view (Fig. 9A, B). Their dorsal surface has no keel, flange or prominence, but is externally ornamented with a rugose surface texture. Foramina, when present, occur only on the ventral surface. The position of these osteoderms is doubtful. It most closely resembles the lateral elements of the second cervical ring of *Edmontonia rugosidens* (Carpenter 1990). However, unlike these elements, the osteoderms of *Antarctopelta* n. gen. are more convex anteroposteriorly than transversely.

Osteoderms with sub-circular dorsal profile, large and flat, and smooth external surface (Fig. 9C, D). They belong to "type c" of Gasparini *et al.* (1996: 588, fig. 5A, B). The margins are crenulated and demonstrate a few, scattered foramina. According to Gasparini *et al.* (1996), these osteoderms resemble those of the sacral region of *Sauropelta*, albeit without the central prominence.

Osteoderms relatively small and polygonal in dorsal view which were originally considered comparable with osteoderms of the previous type. However, these osteoderms differ in being smaller, with a rugose surface and relatively more foramina (Fig. 9C, E). They belong to "type c" of Gasparini *et al.* (1996: 588, fig. 5C, D) and "type D" of Coombs & Deméré (1996). These osteoderms may interdigitate along their edges with other osteoderms (Fig. 9C).

Although often intimately associated, the subcircular and polygonal osteoderms remain individually distinct (Fig. 9C). The mosaic of these elements is similar to the pattern noted for *Sauropelta* (Carpenter 1984). Probably the plates of these two types of osteoderms belong to what Blows (2001) identifies as "bosses" (elements incorporated to the pelvic-shield). These osteoderms may have contributed to a continuous armor, probably situated across the sacral area.

Shield-shaped osteoderms, with a smooth dorsal keel (Fig. 9F). These osteoderms include "type d" osteoderms of Gasparini *et al.* (1996), and resemble those of "type C" of Coombs & Deméré (1996) and the elements referred to as "scutes" by Blows (2001). These are ornamented and pierced by numerous foramina. Some have their ventral surfaces excavated whereas others have not. They are recognized by having both dorsolateral surfaces slightly concave. There is some variation with respect to the inclination of the keel. In the smallest osteoderms of this type, the keel is relatively short and the flanks less concave than in the biggest ones. Some of these osteoderms were preserved resting on ribs (Fig. 9F). Presumably, these osteoderms were arranged in one or more rows on the parasagittal surfaces of the body.

Small, ovoid to sub-rectangular osteoderms are often referred to as ossicles (e.g., Blows 2001; Ricqlès *et al.* 2001). They belong to "type e" of Gasparini *et al.* (1996), and to the "ossicles" of Blows (2001). These ossicles are smaller than those of most ankylosaurs (for example, *Minmi* Molnar, 1980: Molnar 1996, 2001). Numerous parallel and/or perpendicular fibrous-like elevations ornament their surfaces. The histological organization of these osteoderms has been studied by Ricqlès *et al.* (2001). The ossicles arrange on the external surface of the dorsal ribs. In one case they are associated with a large, flat osteoderm occupying mostly the middle part of the rib surface. In another case, the ossicles are larger occupying the entire surface of the rib.

DISCUSSION

In the original description, Gasparini *et al.* (1987) made no reference to the relative age of the specimen. Subsequently, Olivero *et al.* (1991) called the

attention to the small size of the individual element, and argued that the specimen probably represented a juvenile. Gasparini *et al.* (1996) later recognized other characters suggesting immaturity, such as the lack of fusion between splenial and dentary (assuming the portion of the dentary preserved would have contacted the splenial), and between coracoid and scapula. However, these characters alone are not enough to convincingly demonstrate an immature state of development, since they may correspond to plesiomorphic characters, as discussed for the case of *Minmi* sp. (Molnar 1996) or, it may be due to preservation artifacts. Since the vertebrae of *Antarctopelta* n. gen. show complete fusion of arch and centrum it may be interpreted that it is not a juvenile, but at least a subadult. A preliminary analysis of the histology of the bone tissue of the dorsal ribs and of the metapodials has shown the development of secondary osteons and growing rings. Newly formed bone is unlikely to have this amount of remodeling.

Olivero *et al.* (1991) originally referred the materials of James Ross Island to Ankylosauridae on the basis of a poorly developed cingulum (on tooth III), lateral projections of the cranial ornamentation and the presence of a tail club.

Gasparini *et al.* (1996) described additional teeth (I and II), which had asymmetric cingulum and well developed grooves on crown. Furthermore, they observed that the elements regarded as lateral projections of the skull were not exclusive of the ankylosaurids, since they may be found in nodosaurids. These characters persuaded these authors to reassign the Antarctic ankylosaur material to the Nodosauridae on the basis of teeth form.

Regarding the dental morphology of *Antarctopelta* n. gen., it is noteworthy that some probable ankylosaurids such as *Aletopelta coombsi* Ford & Kirkland, 2001 (a *nomen dubium*, according to Vickaryous *et al.* 2004) have relatively large teeth, with well developed asymmetric cingulum and grooves on crowns (Ford & Kirkland 2001). This peculiar dental morphology is therefore not enough to refer undoubtedly the ankylosaur to the Nodosauridae.

The cervical centra of *Antarctopelta* n. gen. are shorter than wide, a character with conflicting interpretations: Carpenter (2001) suggested it was a derived character for Nodosauridae, whereas Pereda-Suberbiola & Galton (2001) found it to be common to most ankylosaurs except *Struthiosaurus* and *Stegopelta* Williston, 1905.

On the other hand, a pelvic shield of *Antarctopelta* n. gen. seems to have been formed by strongly joined elements, probably articulated, very similar to that of the nodosaurid *Sauropelta edwardsorum* (Carpenter 1984).

The posterior distal caudal vertebra of *Antarctopelta* n. gen. closely resemble those of ankylosaurids and not nodosaurids; they are dorsoventrally depressed and elongate, and have tendons along their ventral surface, as in ankylosaurids (including the polacanthines; Blows 1987, 2001). In these ankylosaurs, such modifications have been related to the presence of a caudal club (although Carpenter & Kirkland [1998] and Pereda-Suberbiola [1994] [*contra* Blows 1987] doubted on the existence of an incipient caudal club in *Polacanthus foxii* Hulke, 1881).

In sum, *Antarctopelta* n. gen. is interpreted as demonstrating a mosaic of characters that are widely distributed among both nodosaurids and ankylosaurids. However, until the phylogenetic relationships of *Antarctopelta* n. gen. can be established, we consider it to be an Ankylosauria *incertae sedis*.

The materials from Salitral Moreno (northern Patagonia), described by Coria & Salgado (2001), similarly belong to a relatively small-sized ankylosaur. However, unlike *Antarctopelta* n. gen., the tooth described from Salitral Moreno (Coria & Salgado 2001: fig. 8.1) has a poorly developed labial cingulum that lacks superficial grooves. Furthermore, the morphology of the osteoderms does not overlap between the two taxa. At present, we conclude that the ankylosaur from Salitral Moreno corresponds to a different species than *Antarctopelta oliveroi* n. gen., n. sp.

Although the hypothesis of an Upper Cretaceous terrestrial connection between Patagonia and Antarctica has been repeatedly corroborated by geological and paleontological evidence (Lawver *et al.* 1992; Woodburne & Case 1996), it is impossible to claim yet that the fossil record of ankylosaurs supports the idea of faunal interchange between these two landmasses. This view differs from the interpretation of Gasparini *et al.* (1987) and Olivero *et al.* (1991).

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