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PART III**

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CENTENNIAL OF THE SWEDISH SOUTH POLAR EXPEDITION (1901–1903)

The demand of science, that no part of the globe shall remain untouched by the hand of investigation, was the force that drew our little band to the land of the farthest south.

Otto Nordenskjöld, 1905

Antarctica, or, two years amongst the ice of the South Pole

Almost exactly one hundred years ago, on October 16th 1901, the Swedish South Polar Expedition, led by the explorer and geologist Dr. Otto Nordenskjöld, left Göteborg heading south on the ship *Antarctic* under the Norwegian Captain Carl Anton Larsen. After a stop in Buenos Aires and short visits to Nelson and Paulet Islands, the wintering party landed on Snow Hill Island on the February 12th 1902. Here, on the terrace above shoreline in the northernmost tip of the island that is free of ice, they found a suitable place to build the Snow Hill Station (Nordenskjöld's Hut), see Figs 1, 2.



Fig. 1. Northern and eastern sides of Snow Hill Island (upper part of the photograph) as seen from Seymour Island (Cape Lamb).
Photograph by A. Gaździcki, January 1992.

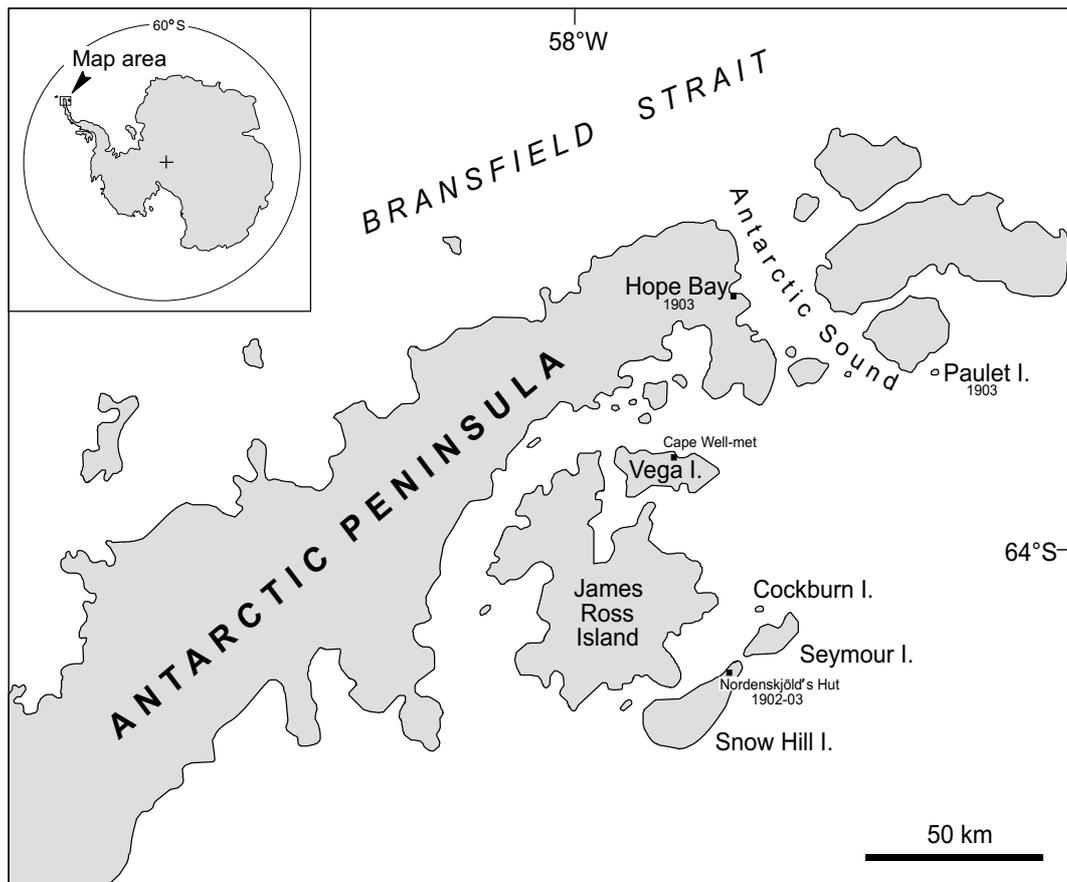


Fig. 2. Location map of Snow Hill, Seymour, Cockburn and Paulet Islands, and Hope Bay in the northern part of the Antarctic Peninsula.

On February 12th 1903 the *Antarctic* was crushed by the Weddell Sea pack ice. Having lost its ship, the Nordenskjöld's Expedition had to spend 23 months in Antarctica awaiting rescue. Their time was not wasted: they explored the northern part of the Antarctic Peninsula, including Snow Hill (Cerro Nevado), Seymour (Marambio) and Cockburn Islands, as well as the Hope Bay (Esperanza) area and Paulet Island (Fig. 2), and made many significant geological and paleontological discoveries. When rescue finally came in November 1903 with the arrival of the Argentinian corvette *Uruguay*, all but a single member of the expedition had survived. And so the Swedish South Polar Expedition remains as one of the most fascinating, incredulous, and productive in the annals of Antarctic exploration.

This volume of *Palaeontologia Polonica*, the third in the series of Palaeontological Results of the Polish Antarctic Expeditions devoted to Cretaceous and Eocene macro- and microfossils from Seymour Island, is dedicated to the brave participants of the Otto Nordenskjöld's Expedition on the occasion of its centennial to honour their scientific achievements in polar exploration accomplished under dramatic circumstances in the years 1901–1903.

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ANATOMY AND HISTOLOGY OF PLESIOSAUR BONES FROM THE LATE CRETACEOUS OF SEYMOUR ISLAND, ANTARCTIC PENINSULA

ŁUCJA FOSTOWICZ-FRELIK and ANDRZEJ GAŹDZICKI

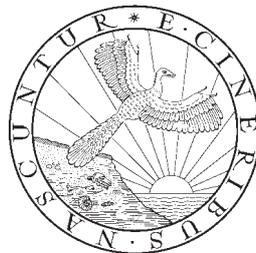
Fostowicz-Frelik, Ł. and Gaździcki, A. 2001. Anatomy and histology of plesiosaur bones from the Late Cretaceous of Seymour Island, Antarctic Peninsula. *In*: A. Gaździcki (ed.), Palaeontological Results of the Polish Antarctic Expeditions. Part III. *Palaeontologia Polonica* **60**, 7–32.

Remains of elasmosaurid plesiosaur have been collected from the lower part of the Late Cretaceous López de Bertodano Formation on Seymour Island, Antarctica. This well preserved bone material includes pectoral, dorsal, and caudal vertebral centra, femur, tibia, and fragments of the humerus, scapula, and ischia, that most probably belong to the one specimen. The microstructure of the bone tissue show rather dense structure with Haversian remodeling well underway and the areas of intensive growth, suggesting subadult stage of ontogeny. The dense pachyostotic character of the rib and girdle tissue, together with a relative small size of the bones (approximated length of the animal about two meters) may indicate that described material belongs to the not fully grown elasmosaur, which may have lived in shallow water environment. The studied remains share some similarities with those of *Mauisaurus* from the Maastrichtian of New Zealand – in the articular surface of the vertebral centra and the shape of the tibia.

Key words: Plesiosauria, bone histology, López de Bertodano Formation, Campanian–Maastrichtian, Seymour Island, Antarctica.

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INTRODUCTION

The plesiosaurs are Mesozoic group of large marine predators. They form a monophyletic order of reptiles within the Sauropterygia, probably originating from the Pistosauridae (Rieppel 1998). The first representatives of the order appeared in the Late Triassic and the latest are known from the Late Cretaceous (Brown 1981; Bardet *et al.* 1999). Plesiosaur remains from the Jurassic are found mainly in the Northern Hemisphere, until the Middle Jurassic the group is absent in the Southern Hemisphere (Persson 1963; Bartholomai 1966; Gasparini and Spalleti 1993; Gasparini 1997).

The record of marine vertebrates from the Campanian–Maastrichtian López de Bertodano Formation of Seymour Island (Marambio), West Antarctica includes remains of plesiosaurs and mosasaurs (Gasparini and del Valle 1981; Chatterjee and Zinsmeister 1982; Chatterjee, Small and Nickell 1984; Gasparini, del Valle and Goni 1984; Gasparini and Goni 1985; Chatterjee and Small 1989; Martin *et al.* 1999). Plesiosaur bone remains have been also reported from Campanian strata on Vega and James Ross Islands (del Valle, Medina

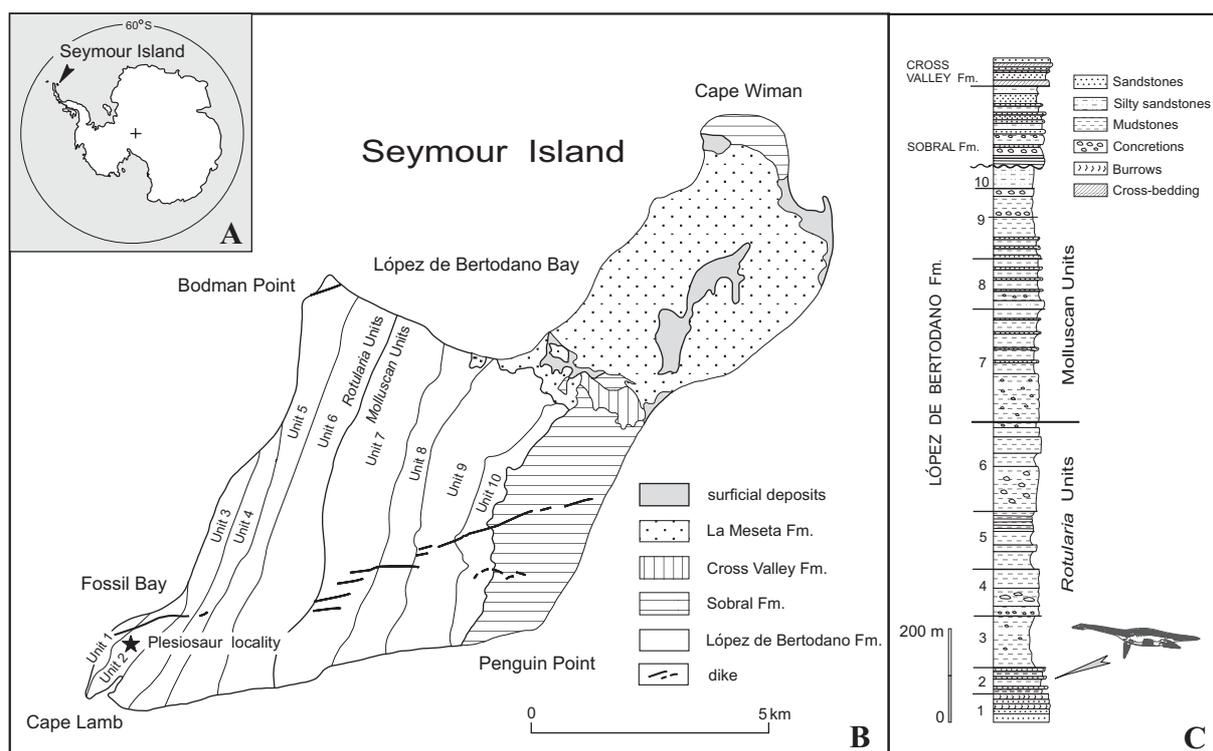


Fig. 1. Location map of Seymour Island in Antarctica (A) showing the locality where plesiosaur remains (asterisked) were collected (B) and stratigraphical column of the López de Bertodano Formation (C) along with location of plesiosaur site (arrowed). Section adopted from Macellari (1986).

and Gasparini 1977; Gasparini and Goni 1985). Most of the plesiosaur remains from Antarctica have been referred to Elasmosauridae, but Cryptoclididae are also present (Chatterjee and Small 1989). Pliosaurian genera have not yet been found in Antarctica, although they are known from Maastrichtian in Chile, New Zealand and Australia (Persson 1963; Chatterjee, Small and Nickell 1984; Gasparini, del Valle and Goni 1984; Gasparini and Goni 1985; Chatterjee and Small 1989).

The purpose of this paper is a description of plesiosaur bones and their histology based on material collected from the López de Bertodano Formation (Text-fig. 1). The plesiosaur bones were collected by one of us (AG) during the 1991–92 Argentine-Polish Field Party on Seymour Island. The specimens are housed in the Institute of Paleobiology, Polish Academy of Sciences, Warszawa, under the catalogue number ZPAL R.8.

Acknowledgements. — The field work conducted on Seymour Island during the 1991–92 austral season was made possible through an invitation from Professor Carlos A. Rinaldi, Director of the Instituto Antártico Argentino (Buenos Aires). We thank Magdalena Borsuk-Białynicka (Warszawa), Anusuya Chinsamy-Turan (Cape Town), Arthur R.I. Cruickshank (Leicester), Kristina Curry Rogers (Saint Paul, MN), and R. Evan Fordyce (Dunedin) for critical reading of the manuscript. Very special thanks go out to Andrzej Tatur (Warszawa) who assisted one of us (AG) during the course of the field program. We would like to extend our thanks to Grażyna Dziewińska for the photographs, Aleksandra Hołda for the drawings, and to Danuta Kościelska for the thin sections.

GEOLOGICAL SETTING

Seymour Island (Text-fig. 1A) is located in the northwestern part of Weddell Sea on the NE side of the Antarctic Peninsula, and contains a thick, well-exposed fossiliferous sequence of shallow marine, nonmarine, and glacial strata of Late Cretaceous to post-Pliocene age (Zinsmeister 1982; Feldmann and Woodburne 1988; Gaździcki 1998; Gaździcki *et al.* 1999). The López de Bertodano Formation (up to 1200

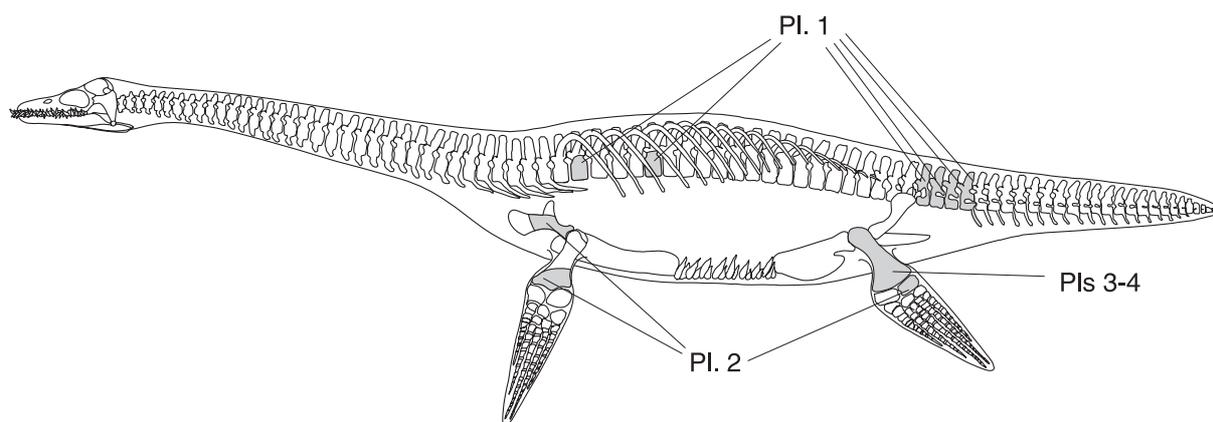


Fig. 2. Scheme of elasmosaurid skeleton with the described elements shaded.

m thick) contains these plesiosaur remains and is exposed in the southern part of the island (Text-fig. 1B, C). This clastic (poorly consolidated sandstones and siltstones) and richly fossiliferous formation represents shallow shelf marine to coastal and deltaic facies (Macellari 1986, 1988; Zinsmeister and Feldmann 1996).

The plesiosaur bones have been found in the lower part of the López de Bertodano Formation (Unit 2) within the *Rotularia* Units nearby Fossil Bay (Text-fig. 1B, C). The rocks from which the bones were collected consist of gray sandy siltstones with scarce annelid worm tubes (*Rotularia*) and poorly preserved gastropod and bivalve shells.

MATERIAL AND METHODS

The state of preservation of the bone tissue is very good, all anatomical characters of articular surfaces are easily recognizable. The bones were not articulated and appeared within a distance of about 20 m, although some of them were grouped (e.g. four caudal centra arranged closely together, more or less in articulation; Pl. 1: 6a–c). This arrangement and the similar size of the skeletal fragments suggest that all remains belong to the same specimen.

The bone histology was studied in detail using thin sections and a scanning electron microscope.

The elemental analysis (mass spectrography – EDAX) of the bone tissue supports data consistent with others found for fossil reptilian bone (Higby Schweitzer and Horner 1999). However the abundance of Sr^{2+} and Fe^{2+} is higher than expected. It could be an indicator of mild reducing environment.

SYSTEMATIC PALEONTOLOGY

Class **REPTILIA** Laurenti, 1768
 Subclass **SAUROPTERYGIA** Owen, 1860
 Order **Plesiosauria** de Blainville, 1835
 Superfamily **Plesiosauroidea** Welles, 1943
 Family **Elasmosauridae** Cope, 1869
 Gen. et sp. indet.
 (Text-figs 2–8, Pls 1–4)

Material. — The material including postcranial remains of a plesiosaur is listed in Table 1, and the anatomical situation of the remains is shown on the scheme (Text-fig. 2).

Table 1. List of the described material.

Anatomical part	Specimen number
fragment of broken cervical? vertebral centrum	ZPAL R.8/24, 27, 29
pectoral vertebral centrum	ZPAL R.8/15
anterior dorsal centrum	ZPAL R.8/5
broken dorsal centra	ZPAL R.8/19, 33, 34
anterior caudal centra	ZPAL R.8/1–4
fragments of caudal centra	ZPAL R.8/16–18, 22, 23, 25, 26, 28, 30, 35
fragments of vertebral centra – indet. region of the vertebral column	ZPAL R.8/20, 21, 31, 32
five fragments of ribs	ZPAL R.8/36–40
propodial (femur, nine pieces)	ZPAL R.8/6
head of the propodium	ZPAL R.8/7
fragment of the propodial shaft	ZPAL R.8/8
distal part of the humerus (four pieces);	ZPAL R.8/10
partly destroyed scapula (three pieces)	ZPAL R.8/11
fragment of the articular part of the scapula	ZPAL R.8/14
articular part of the girdle element (two pieces)	ZPAL R.8/12 a+b
four fragments of girdles – unrecognizable anatomical topography	ZPAL R.8/41–44
two parts of the girdle elements from the medial fusion area	ZPAL R.8/45–46
epipodial element (tibia?)	ZPAL R.8/13

ANATOMICAL DESCRIPTION

Vertebrae. — The neural arches are missing from the material, because they were not fully fused to the centra during the life of the animal. Most of the centra are represented only by fragments. They belong to three or four regions of the vertebral column: pectoral, dorsal, caudal, and, probably, cervical (Table 2). The identification of the cervical centrum is uncertain (only few fragments are present presumably belonging to a cervical centrum).

The pectoral centrum breadth-to-length ratio indicates a rather broad and short bone. The ventral surface is slightly circular in outline. The big facet for the rib is mainly formed by the centrum (parapophysis) and partly by the neural arch (diapophysis). The parapophysis is round and gently concave with pits and craters of diameters about 1–3 mm. The dorsal lip, made of the neural arch, is much smaller and triangular (Pl. 1: 2).

The dorsal region of the vertebral column is represented by one nearly complete centrum (ZPAL R.8/5; Pl. 1: 3) and a few fragments (ZPAL R.8/19, 33, 34). Specimens ZPAL R.8/5, 19 are from the anterior dorsal region. The complete anterior dorsal centrum is broad with a slightly dumbbell-shaped outline. Articular faces are slightly concave or platycoelous. There is an oval swelling with a small, shallow concavity in the center on the anterior articular face. The neural canal is broad and occupies about one third the width of the centrum. The ventral side of the centrum is circular in outline and has two pairs of nutrient foramina.

The four best preserved vertebral centra (ZPAL R.8/1–4; Pl. 1: 1a–b, 6a–c) come from the anterior caudal region. Centra are broader than long and high, with a general oval outline, with two grooves on dorsal and ventral side that makes them somewhat dumbbell-shaped. Anterior and posterior articular faces look very similar, and are platycoelous. In the central part of each there is an oval swelling divided into two rounded small bumps with the shallow pit between them. The margins of the articular face are smooth and turned down. The ventral surface is nearly flat with one nutrient foramen constricted by two ridges. Laterally there are two smaller nutrient foramina. The sutures for the neural arch extend from the anterior border to more than a half the centrum length. The neural canal is very shallow and hourglass-shaped with an isthmus in the middle of the length of the centrum. This isthmus possesses a single nutrient foramen.

Ribs. — Ribs are represented only by small parts without tubercles and capitula. They are slightly flattened, with oval cross-sections.

Scapula. — The preserved part of the articular surface shows a complete glenoid cavity and most of the facet for the coracoid (Pl. 2: 1b). The glenoid facet is half-elliptical, gently concave. Its surface is rather smooth, slightly wavy with few small pits for blood vessels (maximum of 1 mm in diameter). The preserved

Table 2. Measurements of the vertebral centra (in mm, approximate values italicized).

Number of the specimen	Part of the vertebral column	Length (L)	Height (H)	Breadth (B)	H/L index	B/L index	H/B index	Length of the rib facets	Height of the rib facets	Breadth of the neural canal (max.)
8/24	?cervical	23.7						15.7	12.7	
8/27	?cervical	26.2	28.4		108.4					
8/29	?cervical	26.3						18.3		
8/15	pectoral	34.4	35.8	49.1	104.1	142.7	72.9	19.2	17.8	
8/19	anterior dorsal	35.3	37.0		104.8					
8/5	anterior dorsal	34.3	34.4	53.9	100.3	157.1	63.8			18.4
8/33	?dorsal	34.1								
8/34	?dorsal		40.7	45.5			89.5			
8/1	caudal	30.8	37.8	49.5	122.7	160.7	76.4	20.6	17.2	
8/2	caudal	29.2	37.1	49.6	127.1	170.0	74.8	left 20.4 right 20.9	left 5.6 right 15.2	12.1
8/3	caudal	29.5	37.8	49.7	128.1	168.5	76.1	19.1	16.2	
8/4	caudal	28.6	38.1	48.5	133.2	169.6	78.6	19.4	15.9	
8/16	caudal	27.1	34.3		126.6			19.1	12.4	
8/17	caudal	32.3		51.0		157.9		19.0	23.0	
8/18	caudal	25.1	33.9		135.1			17.3	12.3	
8/20	?caudal	33.6								
8/21	?caudal ?cervical	21.6	26.7	40.1	123.6	185.6	66.6			
8/22	?	30.5								
8/23	?	28.3								
8/25	?	30.0								
8/26	?	31.9								
8/28	caudal	19.2		29.2		152.1				
8/30	?caudal	35.1						16.9		
8/31	?	26.5								
8/32	?	34.2								

part of the articular surface for the coracoid is slightly convex and much more wavy and porous. Pits for blood vessels are up to 3 mm in diameter. The angle between these two articular facets is 116 degrees. The collum is slender and tear-shaped in cross section. From the ventral side the bone has a gentle longitudinal ridge, from which osteons are oriented in two directions: to the dorsal process and to the ventral plate, both of which are damaged (Pl. 2: 1a).

Table 3. Measurements of the scapula remains (in mm, estimates italicized).

Specimen number	Medio-lateral diameter of the articular surface	Ventro-dorsal diameter of the articular surface	Medio-lateral length of the glenoid cavity	Medio-lateral width of the collum	Ventro-dorsal thickness of the collum
ZPAL. R.8/11	56.6 (73.8)	42.1	37.7	29.8	18.1
ZPAL. R.8/14		44.0			

Pelvic girdle element. — The pelvic girdle is represented by the articular part of ischium (Pl. 2: 2). The articular surface is divided into two triangular parts connected with the bases, one of them is longer –

55.3 mm, smoother and slightly concave and it is probably a part of the acetabulum. The second one is shorter 45.6 mm, rough and convex. Both have pits and craters for blood vessels but the shorter has much more of them and they are bigger, 2.2–2.8 mm in diameter. The breadth of the common side of two articular facets is 37.9 mm, and the angle between them is 116 degrees.

Propodials. — The propodial region of the skeleton is represented by one nearly complete left femur (Pl. 3: a–c, 4: a–c), fragments of the proximal part of the right femur, and fragment of a shaft and distal part of the humerus (Pl. 2: 3a–b). The measurements of propodial element are included in Table 4.

Femur ZPAL. R.8/6 has well preserved proximal and distal ends, it lacks only a part of a shaft. The caput is distinct and hemispherical. The articular face is nearly round with a flattened dorsal margin. The caput is connected with the trochanter only by a very thin bone bridge 7.3 mm width and 13.5 mm long, and is set at an angle, facing 33 degrees medially from the vertical. The surface of the caput is rather smooth with many small round pits about 1 mm diameter. These are the openings of canals for blood vessels passing through the cartilaginous cover of the articular face of the femoral head (Brown 1981). The trochanter is elongated, oval-shaped, and slopes obliquely ca. 36 degrees in postero-distal direction. The surface of the trochanter is slightly convex and gently slopes to the shaft surface. The section of the shaft near the caput is nearly round. Remains of a big muscle scar, partly destroyed after fossilization, are situated under the caput, on the medial side.

The distal part of the femur (ZPAL R.8/6) is flattened medio-laterally and shows two articular facets for contacting the epipodial elements. The anterior margin is little rounded and dully beveled, whereas the posterior margin is slightly elongated. The surface of the distal part of the propodial is strongly porous, showing distribution of the blood vessels (Pl. 2: 3a, Pl. 4: a).

The distal part of the propodial referred to a humerus (ZPAL R.8/10) is more flattened medio-laterally than the femur. The distal surface is spindle-shaped with slightly rounded ends. This part shows also two articular facets, but they are gently concave in contrast to the previously described in distal fragment, that are flat. This element is also strongly protruded posteriorly, whereas the anterior outline is bevelled (Pl. 2: 3b).

Table 4. Measurements of the propodial elements (in mm).

Specimen number	Total bone length (L)	Width of the caput (antero-posterior)	Thickness of the caput (medio-lateral)	Breadth of the distal end (B)	Thickness of the distal end
ZPAL. R.8/6	163.0	52.5	47.9	94.2	37.2
ZPAL. R.8/10				106.2	34.2
ZPAL. R.8/7		55.8	44.9		

Epipodial element. — Only one epipodial element was found in the material. It is flattened medio-laterally, pentagonal, 58.3 mm broad (B) and 48.5 mm long (L) with pronounced epipodial foramen (Pl. 2: 4). Its $B \times 100/L$ index is 120. The facet for the propodium is nearly straight, 44.9 mm long. It broadens medially to the 24.7 mm. The posterior side of the bone is rounded and 15.3 mm thick. From the distal side there are two articular facets for metapodial elements – posterior and anterior. The former one is shorter (26.0 mm) and 20.2 mm thick, and is oriented 23 degrees from the horizontal to the distal direction, while the latter one, 29.8 mm long and 21.2 mm thick, slopes 34 degrees. The angle between them is 123 degrees. Medial and lateral sides are slightly concave, and the thickness of the central part of the bone is 15.5 mm. All articular facets are strongly porous and show the same bone pattern as the distal parts of the propodials. Medial and lateral sides have remains of smooth, strongly compact bone. The same tissue covers the anterior part of the epipodial.

BONE HISTOLOGY

Vertebral centra. — Several transverse and longitudinal cross sections were made. The demarcation between the periosteal cortical and endosteal trabecular regions is not very distinctive. Both areas are made of dense compacted bone tissue. The outermost parts of the cortex are partly eroded, showing sometimes

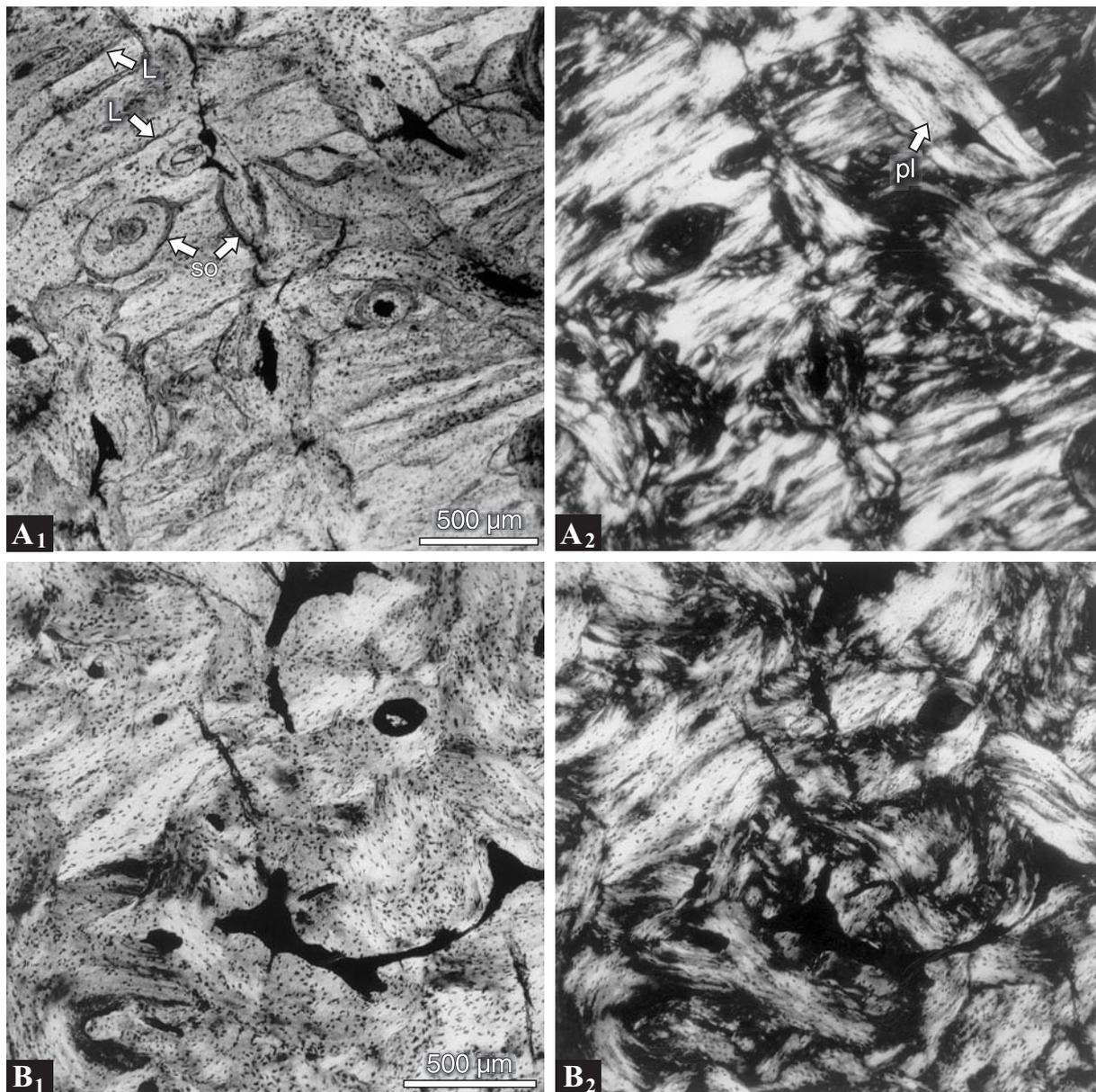


Fig. 3. Tissue of vertebral centra. **A.** Primary parallel-fibered bone overlapped by secondary osteons (so) in the deep cortex; A_1 in normal light, A_2 in polarized light. Abbreviations: L, Line of Arrested Growth (LAG); pl, pseudolamellar tissue. **B.** Endosteal compacted coarse cancellous bone from the medulla region; B_1 in normal light, B_2 in polarized light.

Sharpey's fibers. The compacta is occupied by rather small, generally circular and densely packed secondary osteons. In the periosteal region, primary parallel fibred bone occurred (with Lines of Arrested Growth – LAGs present, Text-fig. 3A₁), in which secondary osteons (Text-fig. 3A₁–A₂) consisting of pseudolamellar tissue occur (*sensu* Ricqlés 1975; Wiffen *et al.* 1995). Some small contributions of the lamellar tissue is possible. Resorption and cement lines are quite visible (Text-fig. 3A₁). In some thin sections this region is nearly completely remodeled, apart from the most external cortex, and made of compacted cancellous bone. More internally, in the medullary area, the tissue shows a typical compacted coarse cancellous character, with irregular, convoluted, and dense structure (Text-fig. 3B₁–B₂). The tissue becomes more cancellous toward the medullary region. Resorption areas are variably-shaped. Most commonly, they are narrow and convoluted. The trabeculae made of lamellar bone have sometimes the remains of primary woven-fibered bone in the cores. The areas between the trabeculae are also filled, apart from the fragments of woven-fibered bone, by lamellar tissue, which is deposited as short shreds arranged in various directions, often perpendicular to each

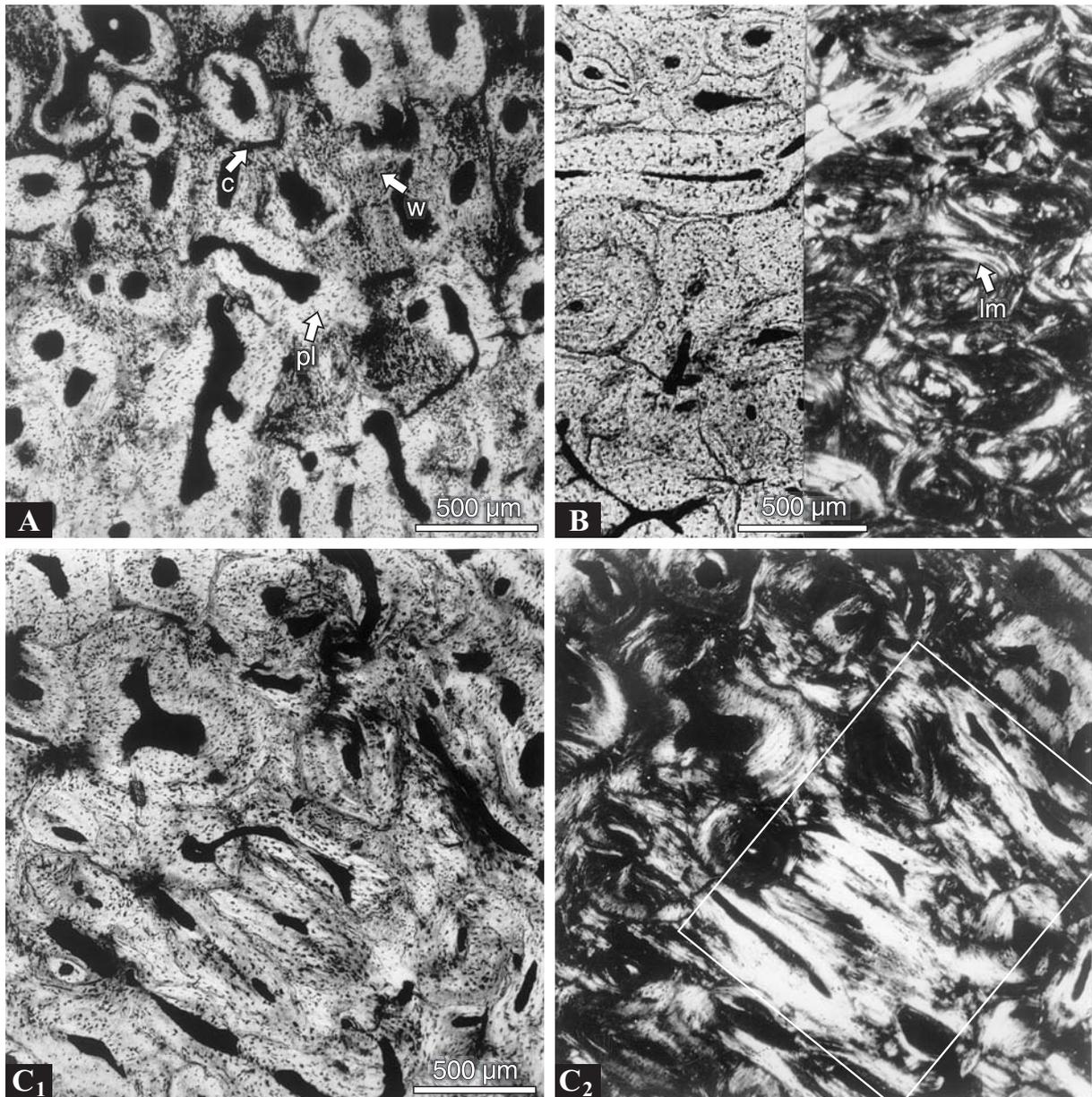


Fig. 4. Bone tissue in girdle and propodials. **A.** Propodial cortex: secondary osteons made of pseudolamellar bone (pl), and surrounded with cement (c) embedded in the woven-fibered (w) bone matrix. **B.** Dense structure of the girdle bone; left part – view in normal light, right – in polarized light; lm, lamellar bone tissue. **C.** Transition region between the deep cortex (left) and perimedulla region (right), observed change of osteon shape and orientation (frame); C₁ normal light, C₂ polarized light.

other. The most internal parts of the medulla contain also small assemblages of a globular, calcified cartilage between the trabeculae. The osteocytes of vertebral tissue are polygonal, sometimes more or less elongated, with weakly developed, or without canaliculi.

Girdle fragments and ribs. — Girdle elements and ribs show similar patterns of bone tissue type and organization. Both show very dense and compact internal structure, dominated by overlapping secondary osteons made of lamellar or, sometimes, by pseudolamellar tissue. There is no distinct division into cortex and medulla. The more external regions are occupied by densely packed secondary osteons, generally rounded or oval flattened dorso-ventrally. In the more internal regions the osteons become bigger, more elongated and sometimes slightly curved (Text-fig. 4B), but compacted in the same way as in the more external part. No calcified cartilage is incorporated into the bone, and remnants of primary woven-fibered bone are very rare. Internally the canals usually have a bigger diameter. They are surrounded by lamellar bone, but no

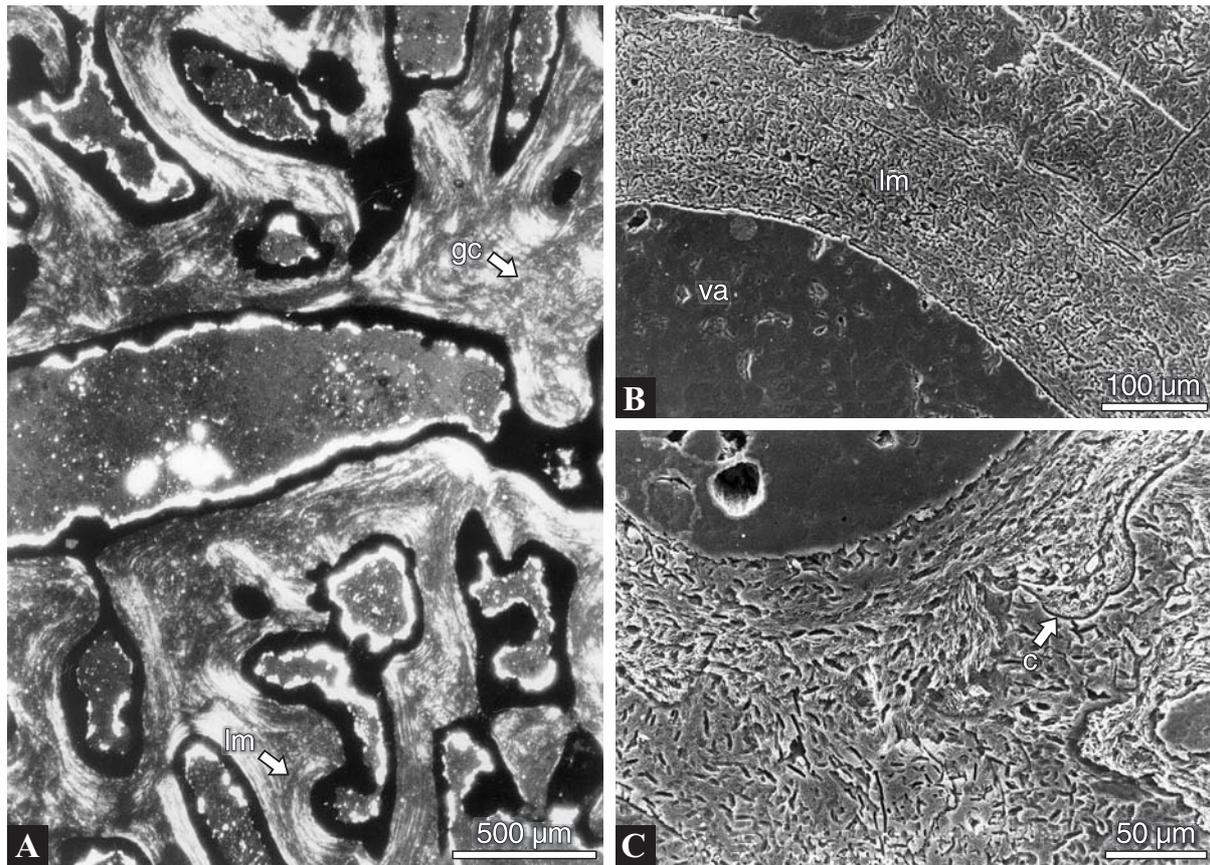


Fig. 5. **A.** Epiphyseal region of the propodium (cross section), large vacuities and well vascularized spongy structure indicate extensive growth (in polarised light); gc, globular cartilage; lm, lamellar bone tissue. **B.** Lamellar bone (lm) in the medulla of the propodium; va, vacuities in medulla. **C.** Remodelling lines (c) and the remains of woven-fibered bone in the compacted coarse cancellous bone of the propodial medulla region.

spongiosa appears. In girdle elements and rib tissue the osteocytes are variably-shaped and possess well developed canaliculi richly branching.

Propodials. — In cross section two distinct regions appear, one of them is periosteal bone tissue, which creates the cortex and the second one is the medullary region with trabeculae made of endosteal bone. The outer parts of the cortex are transparent and woven-fibered without any lamination. This region is rich in small, longitudinally oriented, vascular canals, not yet surrounded by lamellar bone. Internally the cortex displays a woven-fibered texture, very rich in osteoblasts, which is overlapped by secondary osteons densely spaced and often made of pseudolamellar bone (Text-fig. 4A). This region of the cortex frequently displays pronounced cement lines and traces of remodeling. The secondary osteons in the cortex are generally longitudinally oriented, and are more rounded and sparsely located than the osteons in the medulla, which are abundant, more elongated and variously oriented. The change in general osteon orientation occurs in the inner cortex area (Text-fig. 4C₁–C₂), where osteons become elongated radially. Inward the endosteal trabeculae made of lamellar bone show signs of remodeling and Howship's lacunae. Between them there are small areas of remaining calcified cartilage and areas of woven-fibered primary bone. Cross section of the propodial shaft described above displays intensively remodelled structure. In the most external parts of the cortex processes of intensive growth occurred. It is marked by a large number of small newly formed osteons and domination of woven-fibered bone tissue. In the medulla the tissue porosity increases, and the resorption vacuities surrounded by lamellar bone appear (Text-fig. 5B–C). A different pattern is visible in the cross section through the distal part of this bone near the articular facet (Text-fig. 5A). This part has an enormously porous structure, caused by intensive growth and vascularisation in the developing terminal part. The borders of vascular canals are covered by thin lamellar bone and between them the globular calcified cartilage is present.

DISCUSSION

INTERPRETATION OF BONE STRUCTURE IN TERMS OF INDIVIDUAL AGE AND LIFESTYLE OF THE ANIMAL DESCRIBED

The described material most probably belongs to a single individual. The similar size order of the skeletal remains and arrangement of some bones (especially vertebral centra) on the surface of the sediment seem to prove this assumption.

Anatomical investigations of the skeletal remains from Seymour Island show that they belonged to a subadult animal. The neural arches are not fused to the centra and thus indicate a juvenile or subadult ontogenetic status of the specimen (Brown 1981). Total presumed length of the described plesiosaur, approximated about two meters, indicates an animal not fully grown yet, when compared with the known range of plesiosaur body length from few meters up to 12 meters in *Hydrotherosaurus alexandrae* (Welles 1943). On the other hand, the head and the trochanter of the femur described here are well developed, and they are in fact separated, apart from a tiny connection formed by the thin bridge. This separation is not known in juvenile specimens (Brown 1981).

The microstructure of reptile bone, including that of plesiosaurs and other marine groups, is considered as indicative of ontogenetic stage, biomechanical adaptations and physiology (Enlow 1969; de Buffrenil and Mazin 1990; Chinsamy 1990, 1995; Chinsamy and Rubidge 1993; Wiffen *et al.* 1995; Cruickshank *et al.* 1996; Chinsamy 1997; Curry 1999; Horner *et al.* 1999).

Bone thin sections show features that seem to represent the ontogenetic status between dense and unorganized – typical juvenile, and highly porous and remodelled – adult tissue. The observed developed Haversian remodelling and lack of plexiform vascularization is typical for adult and subadult specimens (Wiffen *et al.* 1995; Chinsamy 1997; Curry 1999). The presence of lamellar-zonal bone with Lines of Arrested Growth (LAGs), although not very distinctive in described vertebral centrum tissue (Text-fig. 3A₁–A₂), indicates a post-juvenile age (Curry 1999), comparable features were reported by Wiffen *et al.* (1995) for an adult plesiosaur centrum from New Zealand. However, the primary woven-fibered bone (abundant in the propodial cortex and in deep vertebral centrum medulla) is characteristic, among others, for fast growing specimens (Chinsamy 1997; de Buffrenil and Mazin 1990) and indicates that intensive bone growth has not stopped. Similarly, the remnants of globular calcified cartilage show that the bone is not completely remodelled. It is known that the density of secondary osteons increases during the ontogeny in many vertebrate groups (Chinsamy 1997), and cortical region is getting thinner, also in plesiosaurs (Wiffen *et al.* 1995). Secondary osteons in the cortical regions of a described propodium are quite numerous. Observations of development and density of secondary osteons in the radius and ulna cortex of *Apatosaurus* were used by Curry (1999) to establish age classes. Although sauropods and plesiosaurs are filogenetically distant, the pattern of described plesiosaur propodial cortex corresponds to age class III (subadult) of *Apatosaurus* that could give some ideas about the ontogenetic stage of the animal. The thickness of cortical region of the described propodium (5 mm in the average, i.e. 31% of the bone radius) is less than for the juvenile (ca. 65%), and corresponds to the values found in adult, according to Wiffen *et al.* (1995).

Another problem that must be discussed is the pachyostotic character of the bone tissue, seen especially in cross sections of the ribs and the girdle elements. Three types of pachyostosis can be recognized; bones (especially ribs or mandible) can be larger and more robust, the tissue can be more dense by filling in the free spaces by new deposits, and bones can have higher mineral content (Cruickshank *et al.* 1996). The first character, which was observed in new pliosaurian species *Pachycostasaurus dawni* was also regarded as a specific character (Cruickshank *et al.* 1996). Pachyostosis has been considered characteristic for young plesiosaurs which kept close to the shore (Cruickshank *et al.* 1996). In shallow water, pachyostosis is useful to control buoyancy for an animal, as it is observed in sea cows (Cruickshank *et al.* 1996). During plesiosaur growth its bones begin to change and become more porous, and osteoporosis develops (Wiffen *et al.* 1995). This is an adaptation to an open sea habitat, found also in other marine group, ichthyosaurs and cetaceans (de Buffrenil and Mazin 1990).

The remains from the López de Bertodano Formation do not display the first mentioned kind of pachyostosis, because the rib fragments are not swollen or enlarged. In this specimen pachyostosis is manifested through the increase of bone density in girdle elements and ribs. The other parts of the skeleton do not

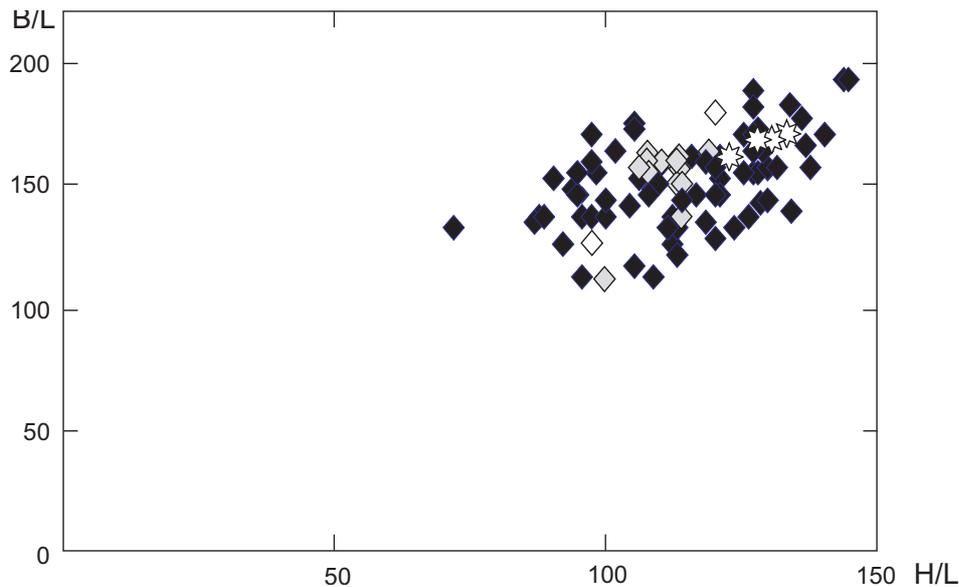


Fig. 6. Distribution of caudal centra indices in three Late Jurassic and Cretaceous plesiosaur families: elasmosaurs (black), pliosaurs (gray), cryptoclidids (white rhombs), and indices of the plesiosaur from the López de Bertodano Formations (asterisks).

display such a dense structure although vertebral centra tissue is not so porous as corresponding adult tissue described by Wiffen *et al.* (1995). This is another reason to classify the plesiosaur from the López de Bertodano Formation as subadult.

These histological characters indicate that studied plesiosaur as a subadult was a shallow water form. However, it is quite possible that as a fully grown animal it led a pelagic life.

TAXONOMICAL COMPARISONS

The problem of systematics and important diagnostic features within the Plesiosauria has been discussed by many authors and is still not resolved (Welles 1943, 1952; Tarlo 1960; Persson 1963; Carpenter 1999; Storrs 1999). In the case of large water dwellers, growing throughout life, the main difficulty is a strong ontogenetic variability of the skeleton, especially in proportions and shapes of vertebral centrae and girdle bones, which are among the most common found remains in this group of animals (Godefroit 1995; Bardet and Godefroit 1995; Carpenter 1996, 1999). Brown (1981) in his monograph on Late Jurassic Plesiosauroidea of England analyzed the 38 characters used by many authors as taxonomically important (Williston 1903, 1906, 1908; Russell 1935; Welles 1943, 1949, 1952, 1962; Tarlo 1959, 1960; Welles and Gregg 1971). He classified them into four groups according to the amount of variability they were subjected to in ontogeny. The most useful for the family level taxonomy are fairly stable characters (D-group of Brown 1981); those of skull architecture and the number and special character of the cervical centra, such as ventral and lateral keels, articular surface character, and general proportions.

These characters are possibly synapomorphic for plesiosaur families. Still some characters of Brown's (1981) D-group such as the shape of ventral process of the scapula, and the proportions of the propodial bones and length of the ischia do change significantly in ontogeny and, thus, only their adult states may be valid as taxonomic features.

In his C-group Brown (1981) collected characters predisposed to parallel evolution such as body size, double- or single-headed ribs, number and proportions of epipodial elements, and extent of hyperphalangy. Groups A and B of Brown (1981) are generic and specific characters insignificant for phylogeny and others highly variable in ontogeny.

Characters concerning the proportions of the cervical centra are important and useful because of frequent finds of isolated vertebrae and incomplete skeletons with preserved parts of vertebral column. Taxonomically important are: length to width and length to height indices. These characters are connected with elongation or shortening of the neck in some groups of the plesiosaurs; the largest elongation is reported in

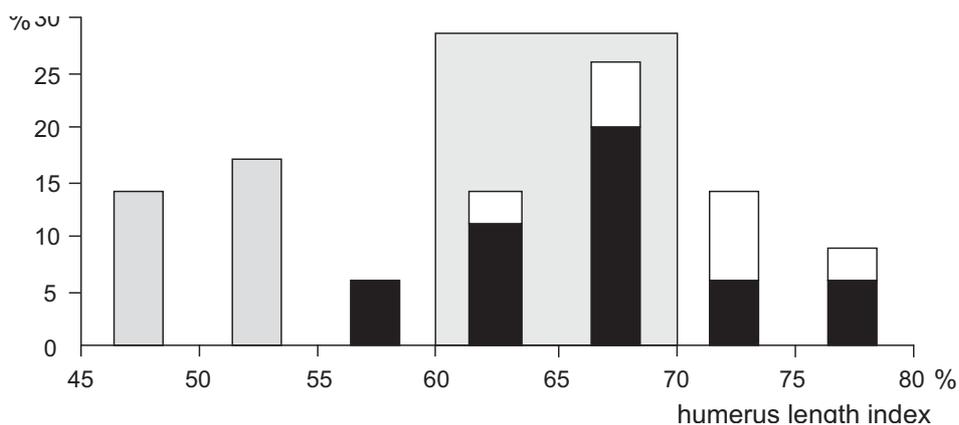


Fig. 7. Values of the humerus length index for the three Cretaceous families: pliosaurs (gray), elasmosaurs (black), and cryptoclidids (white). Striped field marks a probable range of values for the described humerus.

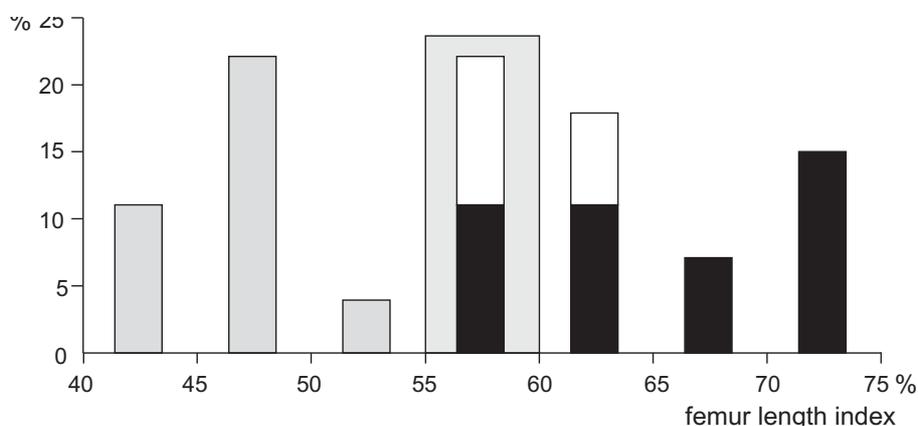


Fig. 8. Values of the femur length index for the three Cretaceous families: pliosaurs (dark gray), elasmosaurs (black), and cryptoclidids (white). Striped field marks the value for the described femur.

Elasmosauridae and the shortening in Pliosauridae (Brown 1981). Vertebral centra indices from the other parts of the vertebral column, especially presacrals, although not so characteristic, also could be useful in anatomical comparisons (Wiffen and Moisley 1986; Godefroit 1995).

The material from the López de Bertodano Formation consists of several fragments of relatively small plesiosaur skeleton. The recognition of the family and genus is uncertain due to the lack of the anterior part of the body with skull and cervical vertebrae of the animal. One can speculate about the systematic position on the basis of the shapes and proportions of the propodial elements and epipodium (Wiffen and Moisley 1986; Renesto 1993). The investigation of measurements and non-quantitative characters of the vertebral centra and their comparison with other species of plesiosaurs was also helpful.

Vertebral centra. — Caudal vertebrae indices ($B \times 100/L$ and $H \times 100/L$) of seven elasmosaurs, one pliosaur and one cryptoclidid were compared with values of indices for the López de Bertodano specimen (Text-fig. 6). The caudals show a great range of values. With the proviso that pliosaurs are poorly represented, there seem to be no taxonomic differences between the families in caudal indices or there is a great amount of overlap of variability range. Among the non-quantitative features of the vertebral centra, the surface of the articular faces may be informative. The anterior and posterior surfaces bear a central swelling with a shallow central pit (Pl. 1: 1a-b) similar to the structures found on the centra referred to paralectotype of the Maastrichtian New Zealand species *Mausaurus haasti*, and claimed to be characteristic for this species (Welles and Gregg 1971; Wiffen and Moisley 1986). The central pit is not so deep as in the dorsal vertebrae of Mangahouanga Stream specimen – NZGS, CD 430 (Wiffen and Moisley 1986: p. 222, figs 32, 33) and the vertebrae are also more flattened dorso-ventrally than in CD 430 specimen. The description of vertebrae of

Mauisaurus haasti from the Laidmore Formation (Welles and Gregg 1971) is very short and shows just a contour drawing with similar dorso-ventrally flattened central swelling (Welles and Gregg 1971: p. 26, fig. 5). The illustration, however, lacks details, and thus a full comparison of the vertebral centra of both specimens (C. M. zrf. 92 and ZPAL R.8/1–5) is impossible for the time being.

Proportions of the propodials. — Most authors emphasize the fact that pliosaurs have more slender (“pendulous”) propodial bones than elasmosaurs and cryptoclidids (Welles 1943, 1962). Indeed, among 14 elasmosaurs, one cryptoclidid and 11 pliosaur genera, there is a strict separation between the length indices ($B \times 100/L$) of pliosaurs and elasmosaurs. The pliosaur index is lower than that of the elasmosaurs. There is no distinct difference between elasmosaurs and cryptoclidids indices (Text-figs 7, 8). This relation may only hold true for Cretaceous and Late Jurassic species, because the genus *Occitanosaurus* from the Early Jurassic of France, recently reinterpreted as a new elasmosaur genus (propodial indices – 43% for humerus and 47% for femur; Bardet *et al.* 1999), is characterized by the values typical for Pliosauridae (Wiffen and Moisley 1986).

The material described from the López de Bertodano Formation contains one well preserved propodial bone (femur). Its length index (57%) is typical for Plesiosauroidea (Text-fig. 8). The value of the length index for the reconstructed length of the humerus is also between 60% and 69%, which are medium values in the range typical for Plesiosauroidea (Text-fig. 7).

Outline of the distal end of the propodials. — The majority of elasmosaurs and cryptoclidids have a horizontally expanded distal part of the propodials (Wiffen and Moisley 1986; Carpenter 1999), especially in the humerus, slightly larger than femur (Brown 1981). The specimens from the Seymour Island have a nearly flat, double articular facet with the distal end of the humerus expanded on one side (Pl. 2: 3a–b), typical for the Plesiosauroidea (Carpenter 1999; Welles 1943, 1949, 1952, 1962; Welles and Gregg 1971; Tarlo 1960). The shape of the humerus closely resembles the distal part of the humerus from Elasmosauridae from the Maastrichtian of Argentina, previously described as *Trinacromerum lafquenianum* (Gasparini and Goni 1985; Gasparini and Salgado 2000).

The distal parts of the elasmosaur femur show more variable shapes, and thus sometimes are similar to pliosaur propodials, but pliosaur femora have usually more rounded and narrow distal ends (Renesto 1993; Wiffen and Moisley 1986; Tarlo 1960). The distal end of the femur from the López de Bertodano is not particularly diagnostic. However, the general outline and appearance of the caput and trochanter (presence of deep anterior and posterior grooves) and the shape of a tibia are similar to the *Mauisaurus haasti* from the Maastrichtian of New Zealand (Welles and Gregg 1971: p. 24, fig. 4). Differences are in the maximal length of the New Zealand specimen, which is twice the length than specimen referred here and has higher (67%) length index.

Shape of scapula. — The shape of the scapula, especially the ventral process, could not be identified (Pl. 2: 1a). Both processes of the scapula are damaged and their reconstruction is difficult. The body of the scapula has a long, slender neck and lacked, probably expanded, ventral process. In juvenile and subadult specimens, the development of the ventral process of the scapula varies from slender, narrow bones to expanded triangular bars (Brown 1981; Carpenter 1999). Moreover not all of Plesiosauroidea species possess ventral process of the scapula developed to the same extent (Welles 1952, 1962; Carpenter 1999).

COMPARATIVE REMARKS

Comparisons with the New Zealand and Antarctic specimens (Welles and Gregg 1971; Wiffen and Moisley 1986; Chatterjee and Small 1989; Gasparini and Salgado 2000), as well as comparisons of vertebral and propodial length indices clearly show that the material from the López de Bertodano Formation of Seymour Island represents a small (body length about two meters long), probably subadult, elasmosaur. Genus and species could not be identified, but some features of the vertebral centra articular faces, and the anatomy of tibia and femoral head and trochanter suggest that these elasmosaurid remains most likely belong to *Mauisaurus* or to a closely related genus.

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PLATES

ANATOMY AND HISTOLOGY OF PLESIOSAUR BONES FROM THE LATE CRETACEOUS
OF SEYMOUR ISLAND, ANTARCTIC PENINSULA

PLATE 1

Elasmosauridae gen. et sp. indet. 10

Fig. 1. Caudal vertebral centrum ZPAL R.8/1; *a* anterior view, *b* posterior view.

Fig. 2. Pectoral vertebral centrum ZPAL R.8/15, lateral view.

Fig. 3. Dorsal vertebral centrum ZPAL R.8/5, dorsal view.

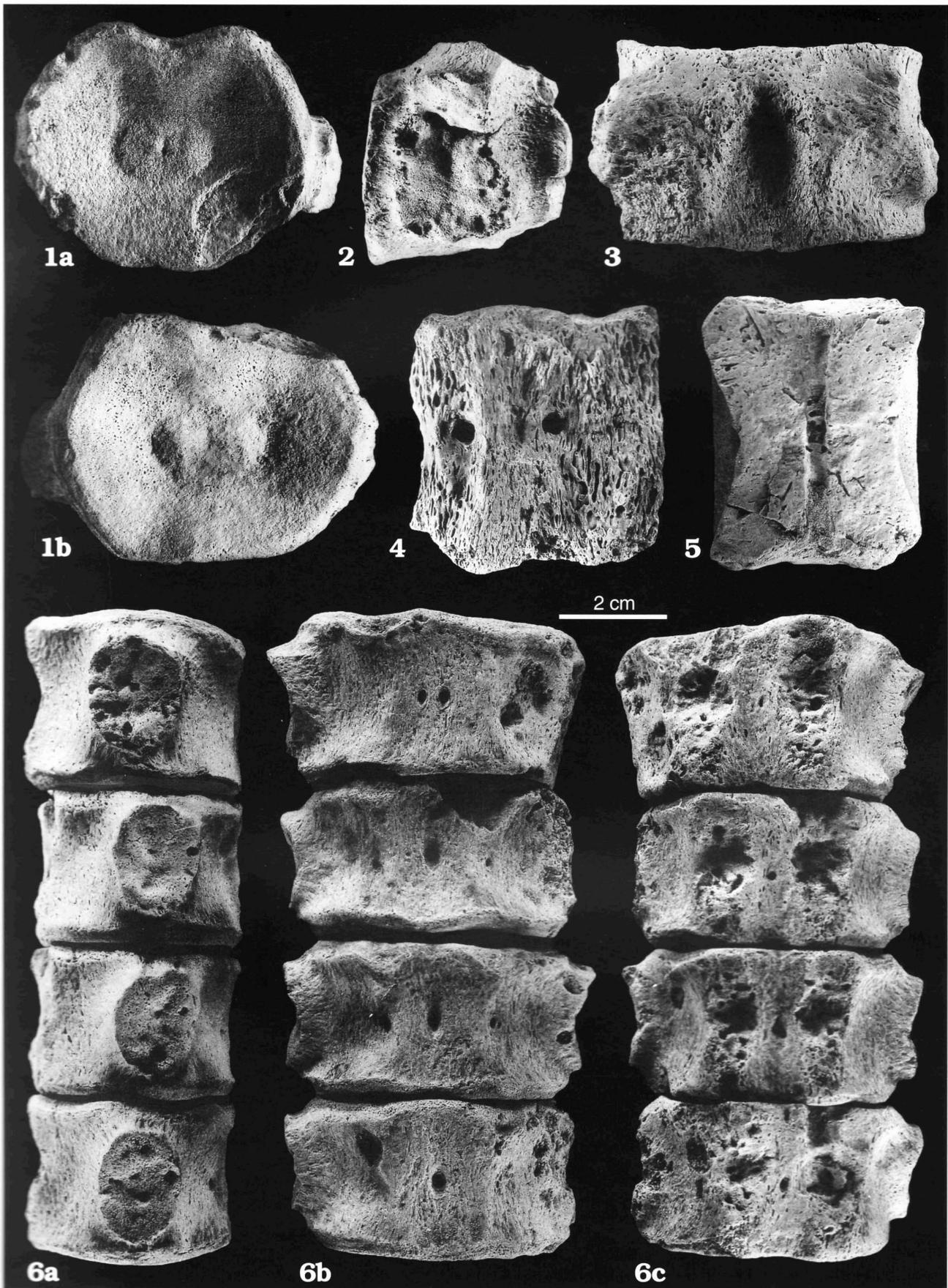
Fig. 4. Heavily weathered cervical ? centrum ZPAL R.8/27, with two well preserved ventral nutrient foramina, ventral view.

Fig. 5. Caudal vertebral centrum ZPAL R.8/17, view on the surface of the saggital section.

Fig. 6. Four caudal vertebral centra ZPAL R.8/1–4; *a* lateral view, *b* ventral view, *c* dorsal view.

All specimens natural size.

Unit 2. López de Bertodano Formation (Campanian–Maastrichtian).



L. FOSTOWICZ-FRELIK and A. GAŹDZICKI: ANATOMY AND HISTOLOGY OF PLESIOSAUR BONES FROM THE LATE CRETACEOUS OF SEYMOUR ISLAND, ANTARCTIC PENINSULA

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PLATE 2

Elasmosauridae gen. et sp. indet. 10

Fig. 1. Right scapula ZPAL R.8/11; *a* stereopair, medial view $\times 1/3$, *b* articular facet.

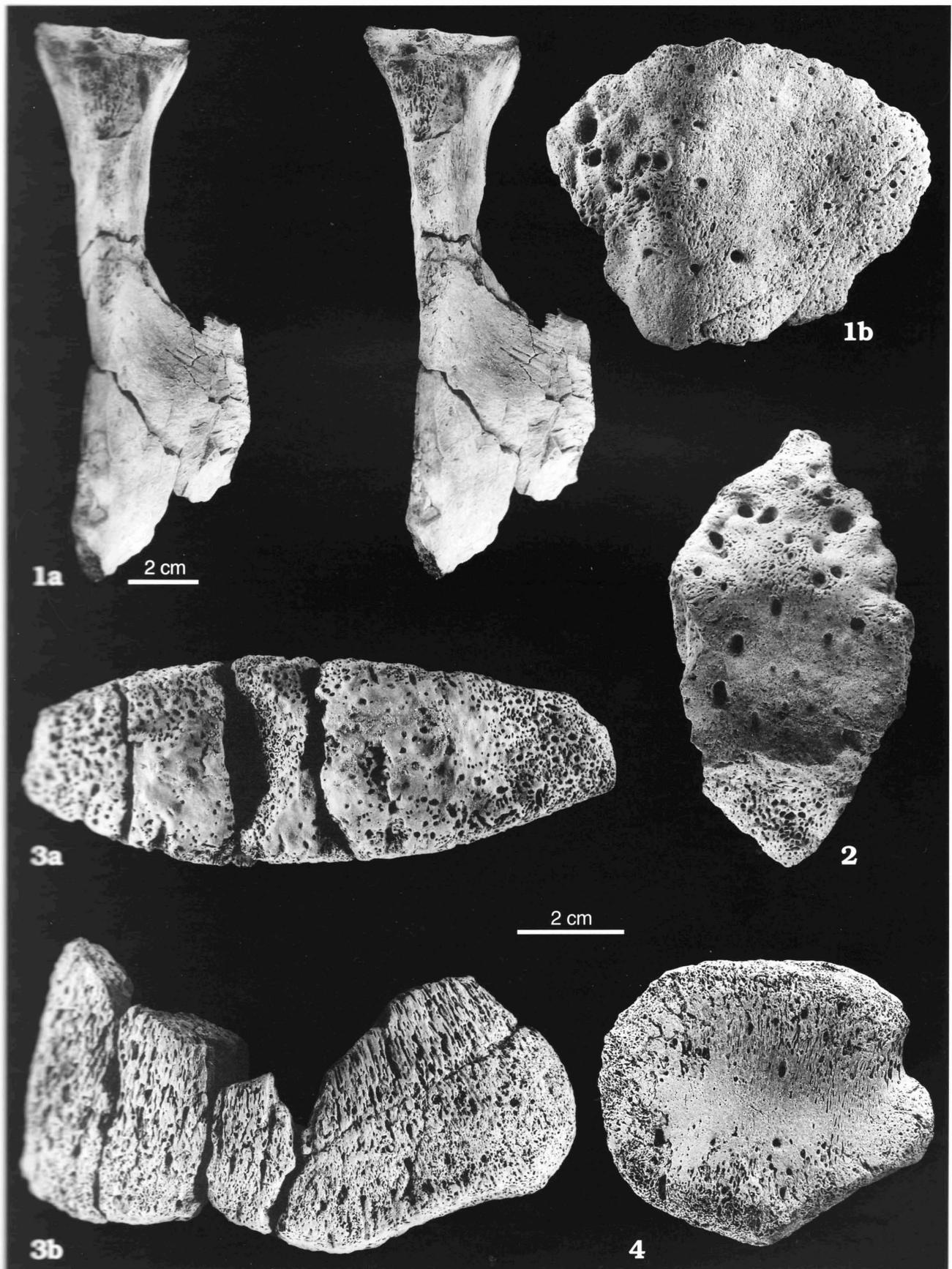
Fig. 2. Articular facet of ischium? ZPAL R.8/12.

Fig. 3. Distal part of right humerus ZPAL R.8/10; *a* distal view, *b* lateral view.

Fig. 4. Epipodial element, probably the tibia ZPAL R.8/13; lateral view.

Figs 1b–4 natural size.

Unit 2. López de Bertodano Formation (Campanian–Maastrichtian).

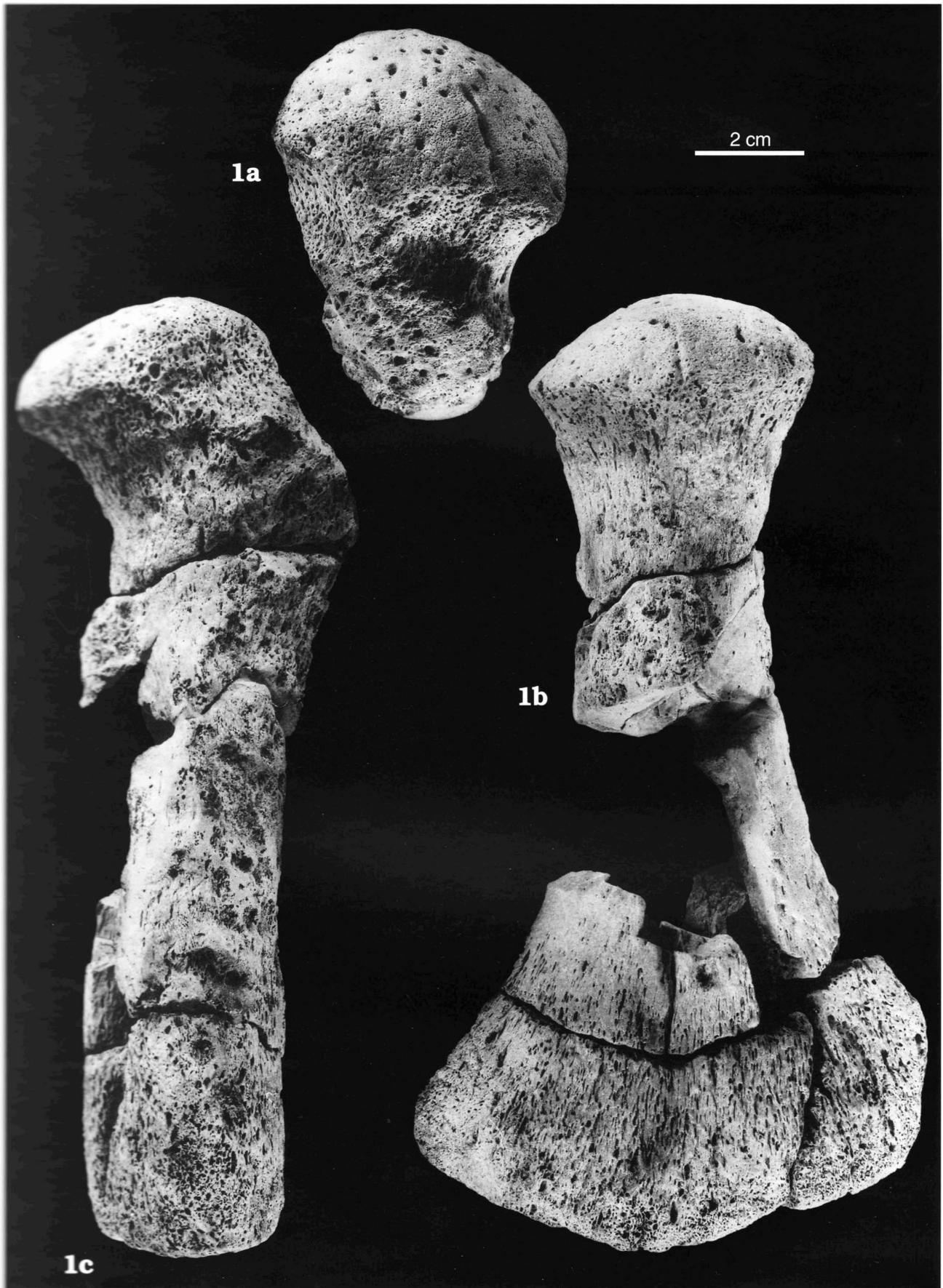


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PLATE 3

Elasmosauridae gen. et sp. indet.	10
Left femur ZPAL R.8/6; <i>a</i> proximal view, <i>b</i> medial, <i>c</i> anterior. Natural size.	
Unit 2. López de Bertodano Formation (Campanian–Maastrichtian).	

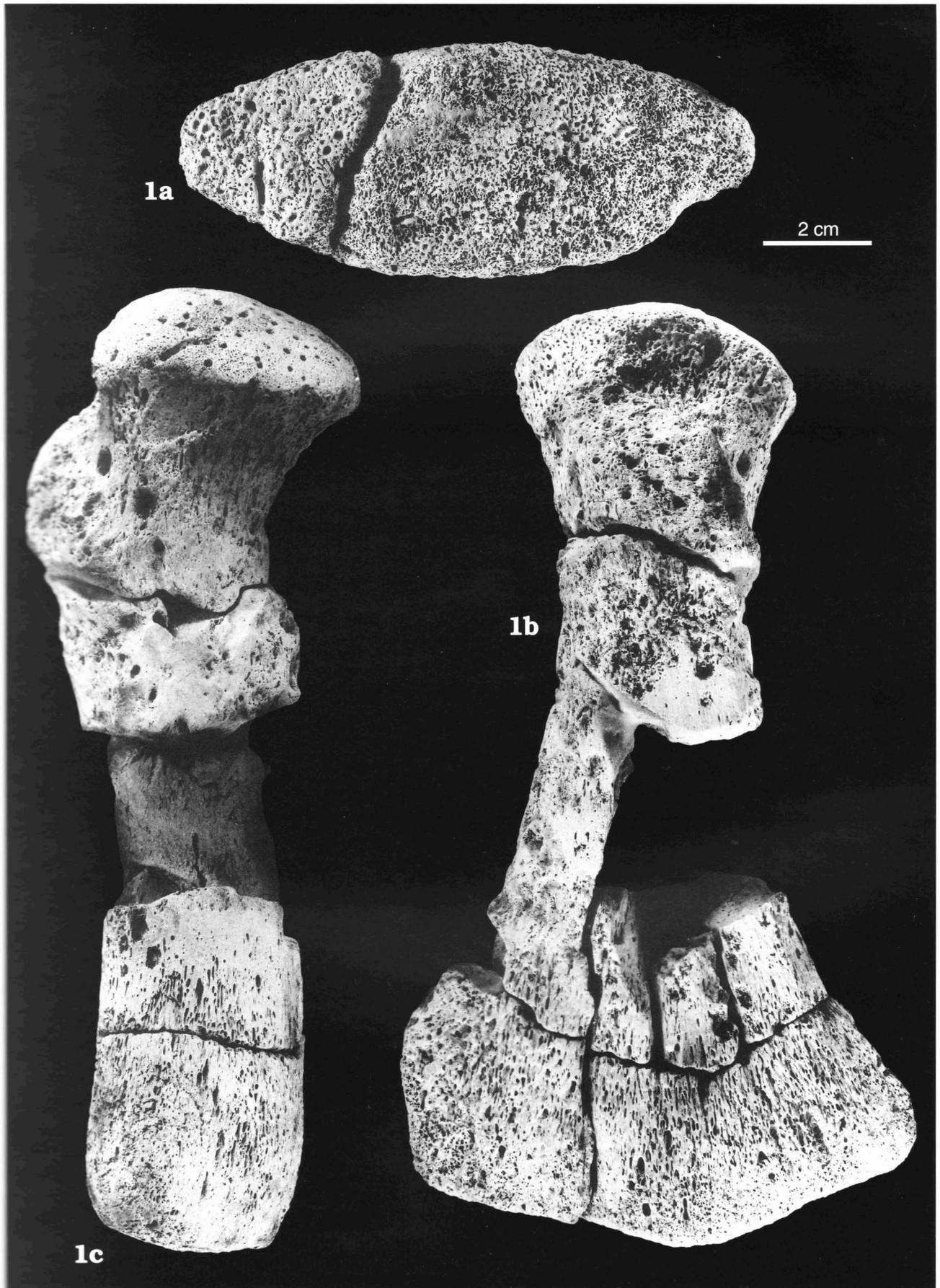


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PLATE 4

Elasmosauridae gen. et sp. indet.	10
Left femur ZPAL R.8/6; <i>a</i> distal view, <i>b</i> lateral, <i>c</i> posterior. Natural size.	
Unit 2. López de Bertodano Formation (Campanian–Maastrichtian).	



E. FOSTOWICZ-FRELIK and A. GAŹDZICKI: ANATOMY AND HISTOLOGY OF PLESIOSAUR BONES FROM THE LATE CRETACEOUS OF SEYMOUR ISLAND, ANTARCTIC PENINSULA