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FIRST PLESIOSAUR REMAINS FROM THE LOWER CRETACEOUS OF THE NEUQUÉN BASIN, ARGENTINA

DARIO G. LAZO AND MARCELA CICHOWOLSKI

Departamento de Ciencias Geológicas, Universidad de Buenos Aires, Pabellón II, Ciudad Universitaria, 1428, Buenos Aires, Argentina
<dlazo@gl.fcen.uba.ar>, <mcicho@gl.fcen.uba.ar>

INTRODUCTION

PLESIOSAURS constitute a monophyletic group whose stratigraphical range is uppermost Triassic to uppermost Cretaceous (Brown, 1981). They were large predatory marine reptiles, highly adapted for submarine locomotion, with powerful paddle-like limbs and heavily reinforced limb girdles (Saint-Seine, 1955; Romer, 1966; Carroll, 1988; Benton, 1990). The Plesiosauria clade belongs to the Sauropterygia, which has recently been hypothesized as the sister-group of the Ichthyosauria. Together with that clade they form the Euryapsida (Caldwell, 1997). The Sauropterygia can be subdivided into relatively plesiomorphic stem-group taxa from the Triassic (Placodonts, Nothosauroids, and Pistosauroids), and the obligatorily marine crown-group Plesiosauria (Rieppel, 1999). Plesiosaurs are traditionally divided into two superfamilies: Plesiosauroidea, with usually small heads and long necks; and Pliosauroidae, with larger heads and shorter necks (Welles, 1943; Persson, 1963; Brown, 1981). Plesiosauroidea contains three families: Plesiosauridae, Cryptoclididae, and Elasmosauridae (Brown, 1981; Brown and Cruickshank, 1994). The validity of the Polycotylidae Cope, 1869, has long been questioned and its phylogenetic position among Plesiosauria debated, as many consider it to be related to the Pliosauridae or to be a sister-group of the Elasmosauridae (Sato and Storrs, 2000; O'Keefe, 2001).

Plesiosaurs have an almost worldwide distribution in the Jurassic and Late Cretaceous, being especially abundant in Europe (Andrews, 1910; Brown, 1981; Bardet, 1995) and North America, respectively (Welles, 1943, 1952). It is worth mentioning the scarcity of these reptiles in the cosmopolitan Lower Cretaceous (Welles, 1962; Gasparini and Goñi, 1985; Cruickshank, 1997). The only known elasmosaurid genera from this time are *Brancaesaurus* Wegner, 1914, from the Berriasian of Germany (Wegner, 1914) and *Alzadasaurus* Welles, 1943, from the Aptian of Colombia (Welles, 1962; Goñi and Gasparini, 1983). No remains of this family have been described from Valanginian or Hauterivian ages.

The oldest recorded plesiosaurs of South America are from the Sinemurian of Northern Chile (Gasparini and Fernández, 1996), and the latest ones are from the Maastrichtian of Argentina (Cabrera, 1941; Gasparini and De la Fuente, 2000; Gasparini and Salgado, 2000; Gasparini et al., 2001), Chile (Casamiquela, 1969; Gasparini, 1979), and Brazil (Carvalho and Azevedo, 1998).

In Argentina, the plesiosaurs range from Early Bajocian to Maastrichtian. The Jurassic plesiosaur records consist of bajocian, callovian, and tithonian pliosaurids, and callovian cryptoclidids and elasmosaurids from the Neuquén basin (Gasparini et al., 1982, 1997, 1999; Gasparini and Spalletti, 1993; Gasparini and Fernández, 1996; Gasparini, 1997; Spalletti et al., 1999). Cretaceous elasmosaurids and polycotylids are reported from the Campanian-Maastrichtian Atlantic transgression deposits of northern and central Patagonia (Gasparini and De la Fuente, 2000; Gasparini and Salgado, 2000; Gasparini et al., 2001), but until now, there were non Lower Cretaceous records.

The aim of this work is to report the first Lower Cretaceous plesiosaur remains from Argentina.

REGIONAL GEOLOGY AND STRATIGRAPHY

The Neuquén Basin in west-central Argentina is one of several Mesozoic basins located along the Andes of southern South America. It is a retroarc basin extending from 35–39°S lat. to 69–70°W long. along the eastern foothills of the Andes (Aguirre-Urreta et al., 1999). It is limited to the east and south by wide cratonic areas, whereas to the west it is bounded by the Andean volcanic arc (Digregorio et al., 1984).

Sedimentation in this basin began in the Late Triassic and continued during the Jurassic, Cretaceous and Cenozoic. Its fill comprised continental and marine siliciclastic, carbonate, and evaporitic deposits (Digregorio and Uliana, 1980).

The sedimentary evolution was strongly controlled by eustatic oscillations, as well as by local tectonics (Legarreta and Gulisano, 1989). This basin was open to the Pacific Ocean during most of the Mesozoic, but the Atlantic Ocean finally invaded it during the latest Cretaceous transgression.

In the latest Jurassic, there was a local marine transgressive event, followed at the beginning of the Cretaceous, by a progradation of continental facies. After this regression, in the Upper Valanginian-Lower Hauterivian, a gradual rise of sea level produced a rapid expansion of the marine facies covering the whole Neuquén Basin (Gulisano et al., 1984). The Agrio Formation was deposited during this transgression, reaching a maximum thickness of about 1,600 m. It occurs over much of the basin, forming extensive outcrops in the western half. Weaver (1931) divided the Agrio Formation into lower and upper marine members separated by a thin but laterally persistent continental sandstone, the Avilé Sandstone. The typical fauna comprises mainly invertebrates. Vertebrate records are extremely scarce. The only known publication signals a pycnodontiform vomer dentition (Bocchino, 1977; Cione and Pereira, 1986).

SEDIMENTARY FACIES AND DEPOSITIONAL ENVIRONMENT

In order to analyze the sedimentary facies association and to infer the dynamic processes and depositional environment of the strata where the remains were found, a stratigraphic section of the Lower Member of the Agrio Formation has been measured and interpreted at Agua de la Mula locality (Figs. 1 and 2). Three facies were recognized. The first one consists of black and gray mudrocks, and appears only at the base of the section. It was probably deposited in a low energy offshore subenvironment, under the stormweather wave base. Intercalated mudrocks and fossiliferous limestones compose the second facies. The limestones are tabular, 0.5 m thick in average, and comprise reworked and fragmented fauna, including plesiosaur remains PV-6894/1–2-MOZ. They were interpreted as storm deposits. The mudrocks represent pelagic background sediments and contained most of

the plesiosaur remains studied in this paper (PV-6890/1–10-MOZ, PV-6891-MOZ, PV-6892-MOZ, and PV-6893/1–23-MOZ). This facies has been interpreted as a transitional subenvironment, between the fairweather and the stormweather wave base. The last facies consists mainly of heterolithic sandstones and amalgamated coquinas, and occurs at the top of shallowing-up cycles that begin with facies two. It contains reworked mollusks and corals, and a diverse assemblage of trace fossils. It represents a lower to upper shoreface subenvironment, between low tide level and fairweather wave base. In agreement with Spalletti (1992) and Brinkmann (1994), the Lower Member of the Agrio Formation was interpreted as deposited in a relatively shallow and warm marine environment (offshore to upper shoreface) under periodical storm influence.

SYSTEMATIC PALEONTOLOGY

Repository.—The described and figured material is deposited in the following collection under the catalogue number listed in the text: Museo Juan Olsacher. Dirección General de Minería de la Provincia de Neuquén. Olascoaga 421, Zapala (8340), Neuquén, Argentina.

Superorder SAUROPTERYGIA Owen, 1860

Order PLESIOSAURIA de Blainville, 1835

Superfamily PLESIOSAUROIDEA (Gray, 1825) Welles, 1943

Family ELASMOSAURIDAE Cope, 1869

Material examined.—PV-6890/1–10-MOZ: 10 dissarticulated cervical vertebrae; PV-6891-MOZ: isolated cervical vertebra; PV-6892-MOZ: isolated cervical vertebra, and a few other undetermined bone fragments of the postcranial skeleton; PV-6893/1–23-MOZ: 23 dissarticulated vertebrae (18 cervicals, four dorsals, and one caudal) and other undetermined bone fragments of the postcranial skeleton; PV-6894/1–2-MOZ: two dissarticulated cervical vertebrae and other undetermined bone fragments of the postcranial skeleton.

Occurrence.—PV-6890/1–10-MOZ: Arroyo Truquicó locality, south-east from the town of Chos Malal, approximately 10 km from the junction of Truquicó creek with the Neuquén River (Bodenbender, 1892; Aguirre-Urreta, 1998). *Karakaschiceras attenuatus* subzone, *Olcostephanus (O.) atherstoni* zone (Fig. 1), Upper Valanginian. PV-6891-MOZ: Cerro Negro locality, 20 km north of Zapala, near the national road 40. *Neocomites* sp. subzone, *Pseudofavrella angulatiformis* zone, Upper Valanginian. PV-6892-MOZ and PV-6893/1–23-MOZ: Agua de la Mula locality, 75 km south of Chos Malal, 3 km east of the national road 40. *Neocomites* sp. subzone, *Pseudofavrella angulatiformis* zone, Upper Valanginian, and *Hoplitocrioceras gentilii* subzone, *Hoplitocrioceras gentilii* zone, Lower Hauterivian respectively. PV-6894/1–2-MOZ: Bajada del Agrio locality (type locality of the Agrio Formation (Weaver, 1931)), on road 40, 60 km north of Zapala. *Weavericeras vacaense* zone, Lower Hauterivian. Stratigraphic range is based on ammonite zonation by Aguirre-Urreta and Rawson, (1997). All material from the Agrio Formation Lower Member (See Fig. 1).

Description.—Cervical vertebrae (Fig. 3.1–3.8). Centrum elongated, i.e., longer than central width and height (height/length less than one), and platycoelous. Articular facets subcircular in outline, slightly compressed dorsoventrally; margins form an abrupt angle with the sides of the centrum. Notochordal pit present in center of articular facets of some centra. Some vertebrae have a lateral keel. Rib articular facets, ventrolateral in position, are subcircular. Ventral part of centrum shows a longitudinal medial ridge separating two oval depressions containing a nutritive foramen each; two other nutritive foramina are located very closely together in the middle of the dorsal surface (the neural canal floor).

Dorsal vertebrae (Fig. 3.9, 3.10). Centrum wider than high and

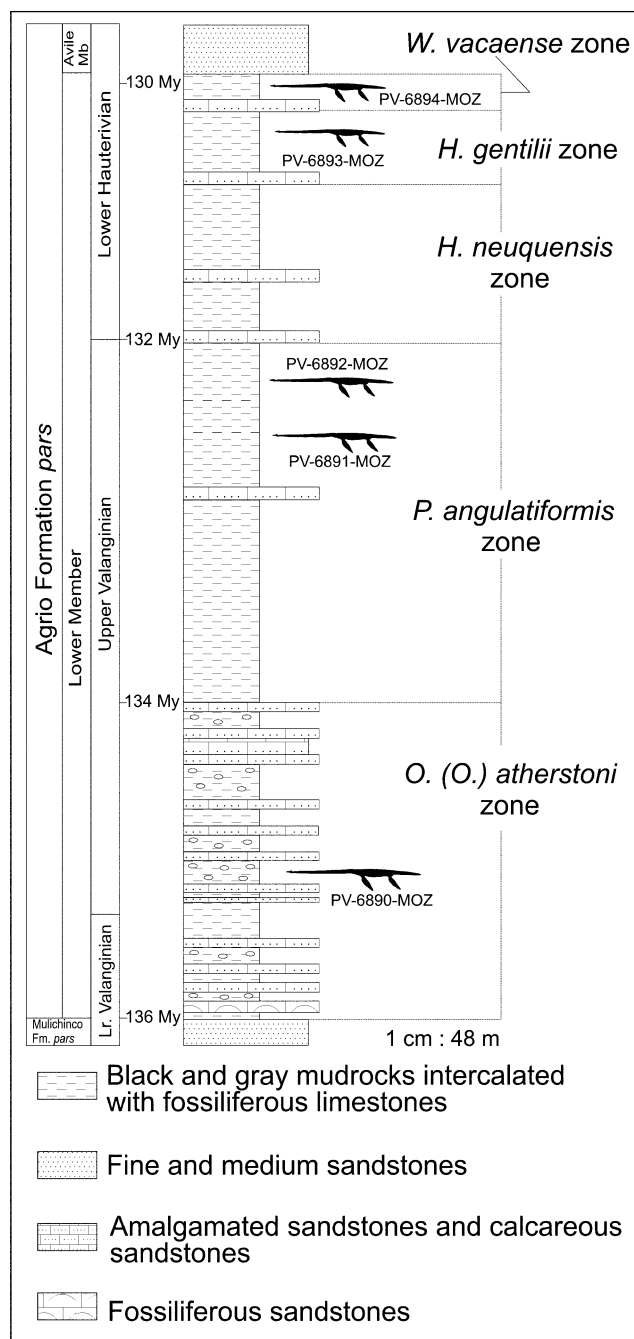


FIGURE 1—Composed stratigraphic section of the Lower Member of the Agrio Formation showing elasmosaurid remains distribution.

higher than long, and platycoelous. Articular facets subcircular in outline; their margins form an abrupt angle with the sides of the centrum. Notochordal pit present on the center of the articular facets of some of these centra as with the cervical centra. Ventral surface rounded, with two small subcentral foramina, which are not separated by a longitudinal ridge. Lateral surfaces of the centrum longitudinally concave and transversally rounded, one foramen on each side. Transverse processes project from the basis of the neural arch.

Caudal vertebrae (Fig. 3.11, 3.12). Centrum shorter than high and platycoelous. Articular facets elliptical. Two subcentral nutritive foramina are on the ventral surface. Haemal arches are not

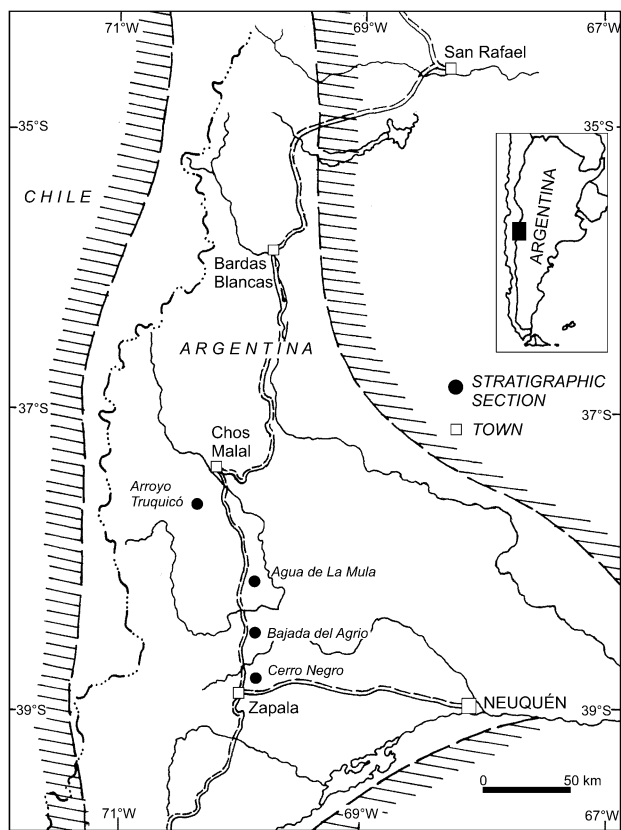


FIGURE 2—Locality map of the Neuquén Basin in west-central Argentina, showing Lower Cretaceous sections that have yielded elasmosaurid remains.

preserved. Articular facets lateral in position, with a nutritive foramen just below each rib articulation.

Discussion.—The elongated cervical centra, longer than high (height/length less than one) (Bardet et al., 1991), the margins of the articular faces forming an abrupt angle with the centrum sides (sensu Brown, 1993), the presence of a lateral keel (or lateral longitudinal ridge) in some of these centra, and single-headed ribs allows for the assignment of these remains to the family Elasmosauridae. However, being poorly preserved and fragmentary, the material found is not sufficiently complete to allow a more precise systematic identification.

DISCUSSION

Fossil preservation.—Some features of the mudrocks yielding the plesiosaur remains PV-6890/1–10-MOZ, PV-6891-MOZ, PV-6892-MOZ, and PV-6893/1–23-MOZ, such as the pale color and the occurrence of benthic faunal elements and ichnofossils, suggest that these rocks have been deposited under normal oxygen level in a low energy subenvironment (Howard and Frey, 1984). These conditions allowed a relatively rapid disintegration or disarticulation of the carcasses by predators or scavengers on the sea floor. In addition, the presence of cementing oysters on some of the bones (Fig. 3.3), indicates a considerable amount of exposure time before the final burial, which probably favored the organic decomposition. Following burial, the biological and chemical processes within the sediment abraded and even destroyed many bones. Therefore, the subsurface bioturbation and scavenging, and probably slight water flows, could have scattered the remains over areas larger than the size of the articulated skeletons (Behrens-meyer, 1991). The material PV-6894/1–2-MOZ has been found

concentrated in a storm coquina within an area of approximately 0.4 m².

Ontogenetic stage.—Different ontogenetic stages are proposed for the material PV-6890/1–10-MOZ and PV-6893/1–23-MOZ, taking into account the following vertebral characters: the fusion of the neural arch with the centrum (presence or absence of neuro-central suture), the fusion of the ribs with the centrum, and the degree of ossification of the centrum.

A juvenile stage (sensu Brown, 1981) is proposed for the material PV-6890/1–10-MOZ, as the vertebrae show the neuro-central suture, smooth and free articular facets, and a low ossification degree of the centra (Fig. 3.6, 3.7). This latter character can be seen only in one of the vertebrae that is transversally broken (Fig. 3.8). An adult stage (sensu Brown, 1981) is proposed for the material PV-6893/1–23-MOZ, since the vertebrae do not show the neuro-central suture and the ribs are fused to the centra (Fig. 3.1, 3.4, 3.11). The ossification degree is higher than that observed in the material PV-6890/1–10-MOZ.

Paleoecology.—Anatomical and biomechanical studies concerning plesiosaur locomotion and feeding behavior include Tarlo (1957), Taylor (1981), Tarsitano and Riess (1982), Massare (1988), and Lingham-Soliar (2000). However, only a few attempts have been made to correlate these features with the environment in which these animals lived. In the Neuquén Basin, Gasparini et al. (1999) reviewed the Tithonian marine reptiles and concluded that almost all of these were pelagic forms. Deposits they analyzed have been interpreted as an offshore environment, where the water depth would have been 30 to 100 m, and the distance to the coast at least 60 km and probably more than 200 km (Gasparini et al., 1999). Many of these reptile remains belong to plesiosaurs. They had larger and broader limbs, more massive limb girdles, and more compact bodies than the plesiosauroids, suggesting that they were faster and more efficient sustained swimmers (Massare, 1988; Adams, 1997).

In the same basin, the elasmosaurids appeared in coastal or transitional deposits, like estuarine or lagoonal systems (Gasparini and Spalletti, 1993; Gasparini and de la Fuente, 2000; Gasparini and Salgado, 2000). In the Cretaceous from Colombia and Antarctica, other remains from the same family have been found in littoral to lagoonal and shallow marine bay deposits respectively (Goñi and Gasparini, 1983; Gasparini et al., 1984). According to these previous records, the fossils presented here came from beds interpreted as a storm dominated shallow marine shelf (Spalletti, 1992; Brinkmann, 1994). Therefore, it seems probable that these coastal marine environments were the natural habitat for the long necked elasmosaurids. This is to be expected given their poor hydrodynamic body shape and their slender limbs, which suggest they were slow and not sustained swimmers (Massare, 1988).

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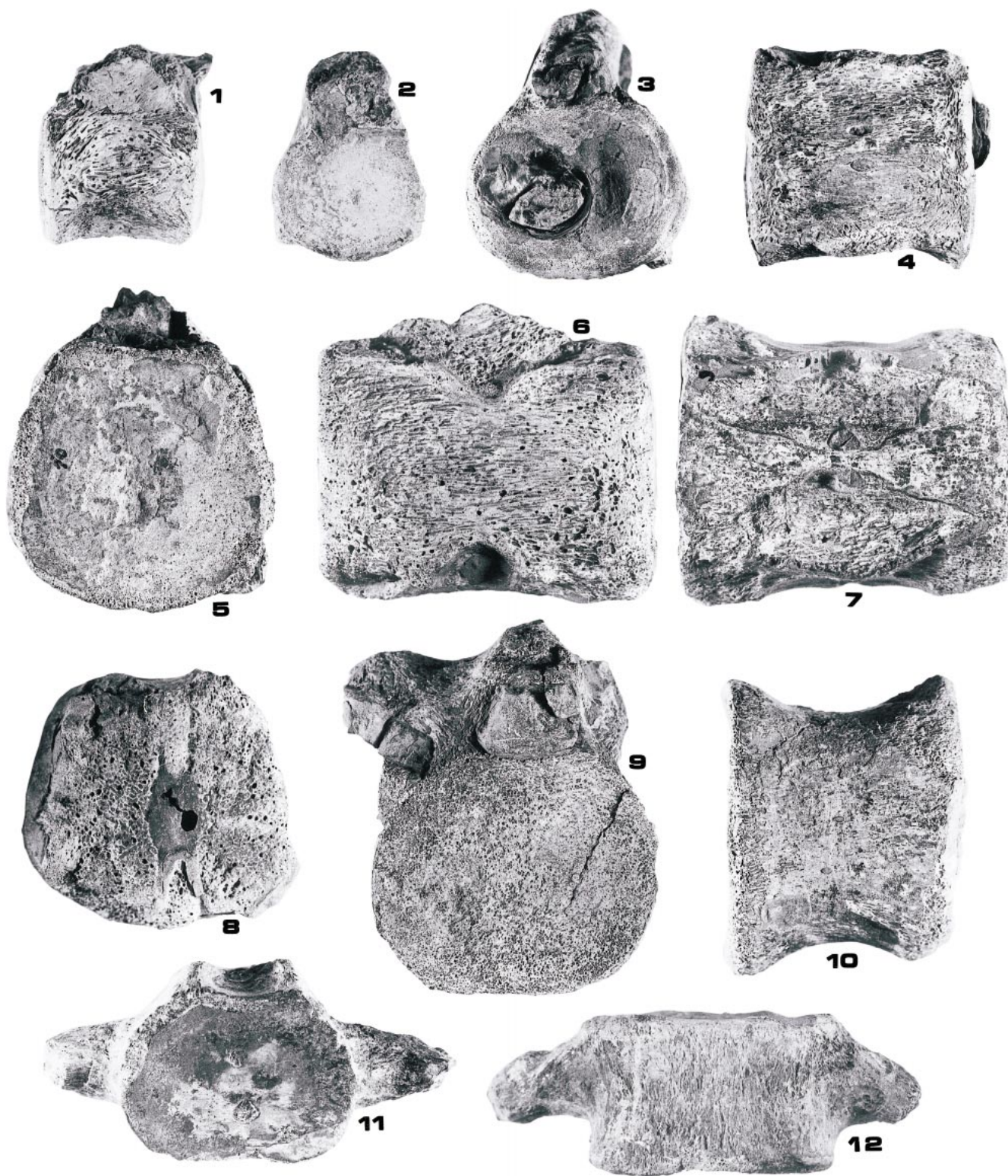


FIGURE 3—Elasmosauridae gen. and sp. indet. 1, PV-6893/2-MOZ, left lateral view; 2, PV-6893/1-MOZ, anterior view; 3–4, PV-6893/11-MOZ, anterior and ventral views; 5–7, PV-6890/10-MOZ, anterior, lateral and dorsal views; 8, PV-6890/7-MOZ, transversal section; 9–10, PV-6893/22-MOZ, anterior and ventral views; 11–12, PV-6893/23-MOZ, anterior and ventral views. All $\times 1$.

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