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Elasmosaur Remains from the Maastrichtian type area, and a Review of latest Cretaceous Elasmosaurs (Reptilia, Plesiosauroidea)

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Abstract

Isolated skeletal remains of elasmosaurid plesiosaurs are described from the upper Upper Maastrichtian of the type area of that stage and compared with material from the Maastrichtian of southern Belgium (Mons Basin) and Morocco. An overview of Maastrichtian elasmosaurids worldwide is presented. The rarity of elasmosaurids in the latest Cretaceous marginal seas of the type Maastrichtian as compared with their common occurrence in the oceanic waters near California and Morocco of that age may be related to food abundance in upwelling areas along the margins of continental plates.

Key-words: Elasmosaurs, Maastrichtian type area, Belgium, Morocco, North Atlantic basin.

Résumé

Des restes squelettiques isolés de plésiosaures élasmosauridés sont décrits de la partie supérieure du Maastrichtien supérieur de la région type de cet étage, replacés dans un contexte stratigraphique et comparés à du matériel provenant du Maastrichtien du Sud de la Belgique et du Maroc. Une révision globale des élasmosauridés du Maastrichtien est présentée. La rareté des élasmosauridés dans les mers marginales fini-crétacées du Maastrichtien stratotypique comparée avec leur présence dans les eaux océaniques près de la Californie et du Maroc du même age pourrait être liée à une richesse de nourriture dans des régions d'upwelling le long de bords continentaux.

Mots-clefs: Elasmosauridés, Maastrichtien stratotypique, Belgique, Maroc, bassin Nord-atlantique.

Introduction

Ever since the first unambiguous record by von MEYER (1860), it has become apparent that, amongst remains of larger vertebrates in the uppermost Maastrichtian strata of the type area of that stage (Fig. 1), those of plesiosaurs are very rare in comparison with mosasaurs and turtles. So far, only a handful of isolated elasmosaur teeth and vertebrae are on record; remains of hadrosaurid dinosaurs are even commoner, although these strata are marine (MULDER *et al.*, 1997, 1998; WEISHAMPEL *et al.*, 1999).

Records of plesiosaurs in such important contributions as the works of FAUJAS SAINT FOND (1802), BINKHORST VAN DEN BINKHORST (1859a) and UBAGHS (1879), are difficult to interpret since most of their material is now

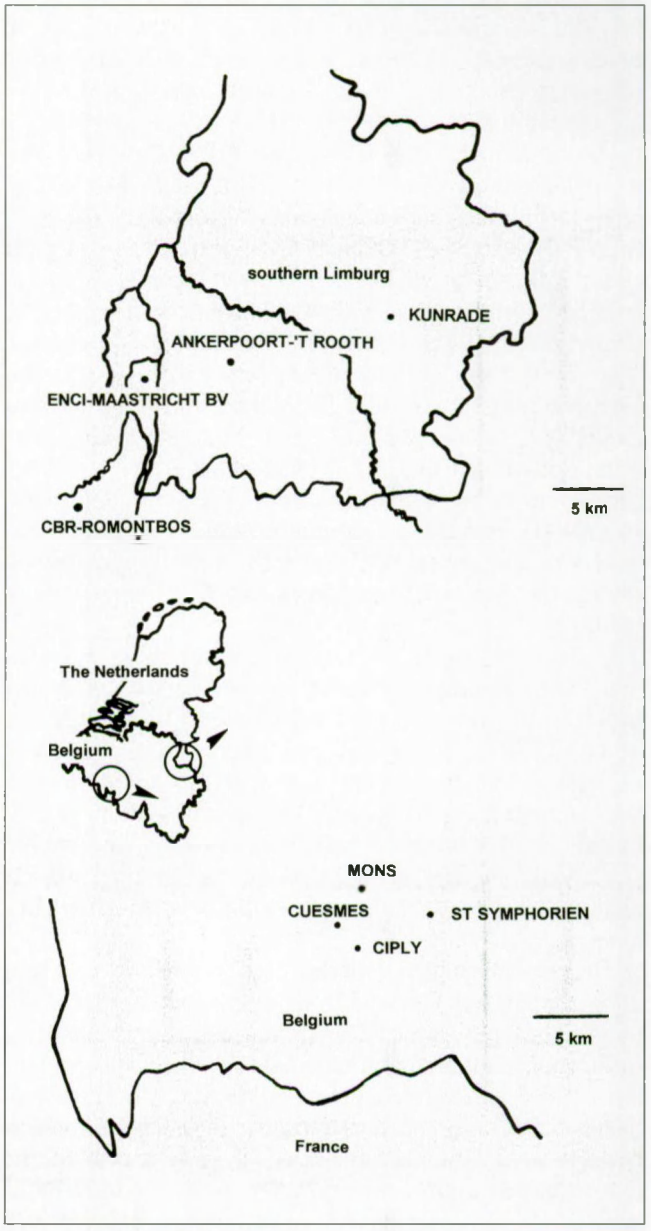


Fig. 1 — Locality map of the Maastrichtian type area (the Netherlands) and the Mons Basin (southern Belgium), showing sections that have yielded elasmosaurid remains.

lost. FAUJAS SAINT FOND (1802, pl. 18, fig. 4; pl. 19, fig. 9) illustrated, from strata at St Pietersberg south of Maastricht now assigned to the Maastricht Formation, two striated teeth which resemble the specimens described here. These specimens have not been located, if indeed they are at the Muséum national d'Histoire naturelle (Paris), but without having seen them we cannot decide whether or not they are plesiosaurian.

BINKHORST VAN DEN BINKHORST (1859a, p. 42) referred to "une dent d'un saurien lacertiforme, appartenant à un genre nouveau auquel M. Hermann von Meyer a donné le nom de *Goniosaurus Binkhorsti*" from the middle part of the Maastricht Formation (= Emael and Nekum members in current terminology). On page 112 of the same paper it reads, "Du genre *Goniosaurus* et *Plesiosaurus*(?) on n'a trouvé jusqu'aujourd'hui que des dents et vertèbres isolées" and in a listing of species which BINKHORST held to be characteristic of the "craie tuffeau" (page 117) *Goniosaurus Binkhorsti*, von MEYER and *Plesiosaurus*? sp. appear again.

BINKHORST VAN DEN BINKHORST (1859b, p. 412) also recorded remains of plesiosaurs ("Ein biconcaver Wirbel eines Reptils, das sich dem Genus *Plesiosaurus* nähert") from Folx-les-Caves (Brabant, Belgium). The Cretaceous strata exposed at that locality have recently been restudied and correlated with the Maastrichtian type area (BLESS *et al.*, 1991). Following those authors' interpretation, BINKHORST's material appears to be of (?Early) Campanian age. Items of the Binkhorst van den Binkhorst Collection, sold to the Kaiserlich Mineralogisches Museum (Universität Berlin) in 1878 (see KRUYTZER, 1963), survive in the Naturkundemuseum of the Humboldt Universität (Berlin). However, the plesiosaur material contained in that collection was most probably destroyed during the Second World War (W.-D. Heinrich, pers. comm.).

UBAGHS (1879, p. 197) reported from what he called the "Maastrichtien supérieur" (= higher part of Maastricht Formation in current terminology) the occurrence of *Goniosaurus binkhorsti* von MEYER. This record is of interest in view of the fact that the collections of the Natuurhistorisch Museum Maastricht include an elasmosaur tooth from the Upper Maastrichtian of Kunrade (The Netherlands), identified as *G. binkhorsti*. Unfortunately, the whereabouts of UBAGHS's material is unknown.

The elasmosaurid material from southern Limburg (The Netherlands) available to us is from either of the two facies types of the Maastricht Formation (Maastricht tuffaceous chalk and Kunrade Limestone facies), and all is of late Late Maastrichtian age (JAGT, 1999). Where details of stratigraphic provenance are known, it has become apparent that this material is restricted to the *Belemnitella junior* Zone of authors (= equivalent of *danica/argentea* and *baltica/danica* zones of SCHULZ & SCHMID, 1983 and SCHULZ *et al.*, 1984), and has not been found in the overlying *Belemnella (Neobelemnella) kazimiroviensis* Zone of authors (MULDER *et al.*, 1998, fig. 4C).

Table 1 — Elasmosauridae gen. et spec. indet., cervical and pectoral/sacral vertebrae, all material from the Upper Maastrichtian of the Maastrichtian type area (see text for details of provenance); measurements in mm (L - length, W - width, H - height, d-distance between nutritive foramina).

	L	W	H	d
MND K 20.01.801a	59	72	52	9
MND K 20.01.801b	59	71	49	10
MND KB 50.20.01	42	61	39	7.5
NHMM 1985141	44	76	59	18

The elasmosaurid remains from the Maastrichtian type area are amongst the most precisely dated and youngest Cretaceous occurrences known to date. Despite the fact that Maastrichtian elasmosaurid records worldwide are often poorly constrained stratigraphically, it appears that just prior to the K/T boundary, plesiosaurs were still widespread and diversified, and that their demise was sudden rather than gradual (BARDET, 1995).

Description of material

The material before us comprises three isolated teeth and five vertebrae (measurements in Table 1) from the type area of the Maastrichtian Stage, in addition to teeth and vertebrae from the Lower Maastrichtian of southern Belgium (Mons Basin) and from the Upper Maastrichtian of Morocco, including the type of *Plesiosaurus mauritanicus* ARAMBOURG, 1952.

To denote the repositories of this material, the following abbreviations are used:

ANSP	Academy of Natural Sciences, Philadelphia
IRScNB	Institut royal des Sciences naturelles de Belgique, Brussels
MND	Museum Natura Docet, Denekamp
MNHN	Muséum national d'Histoire naturelle, Paris
NHMM	Natuurhistorisch Museum Maastricht

Other abbreviations used: L - length, W - width, H - height.

Natuurhistorisch Museum Maastricht collections

An isolated tooth from Kunrade (NHMM 003842; Pl. 1, Figs. 4, 5), identified as *Goniosaurus binkhorsti* von MEYER, is well preserved. The crown is long, slender and curved, elliptical in cross section and slightly compressed bucco-lingually. The ornament consists of delicate longitudinal ridges, which are more numerous, more regular and more clearly marked on the lingual side. The root is elliptical in cross section, compressed mediolaterally, and unornamented. The general shape and pat-

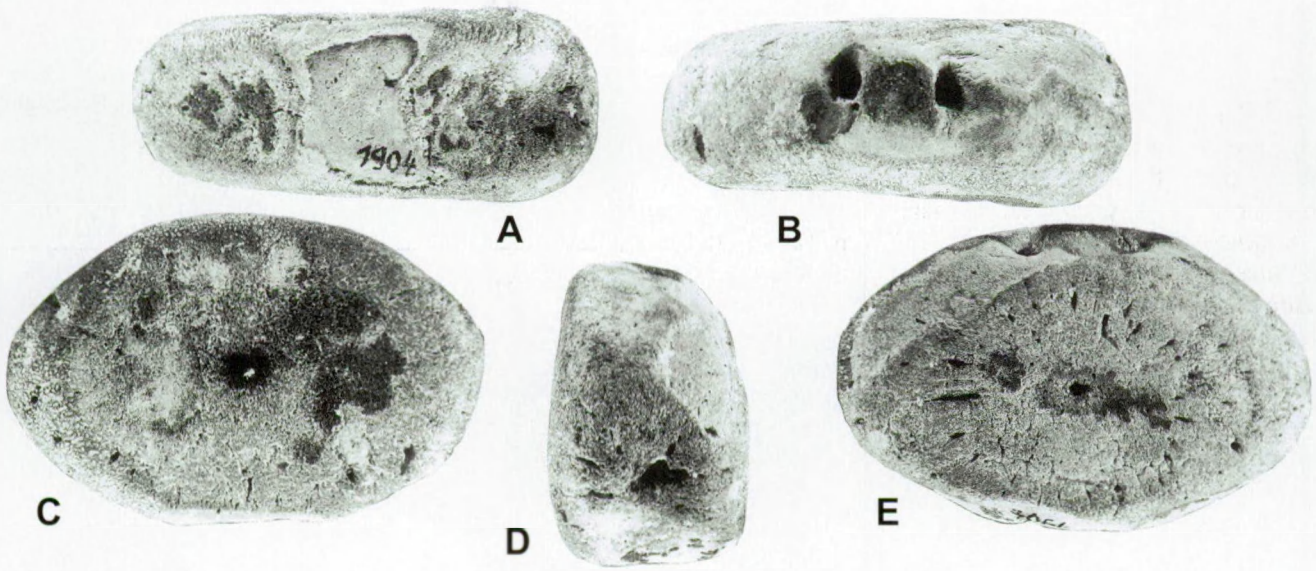


Fig. 2 — Elasmosaurid caudal centrum, NHMM K 1904, directly above Lava Horizon (Emael Member, Maastricht Formation, CBR-Romontbos quarry; Eben Emael, Bassenge, Liège); late Late Maastrichtian, in dorsal, ventral, articular and lateral aspects. Scale bar equals 10 mm.

tern of ornament of the crown are characteristic of the Elasmosauridae (see also BARDET *et al.*, 1999a).

A second tooth, from the St Pietersberg south of Maastricht (NHMM 1993062, *ex* R. Ubaghs Colln; Pl. 1, Figs. 1-3), was still embedded in matrix; matrix characters suggest provenance from the upper part of the Nekum Member or the lower portion of the overlying Meerssen Member (Maastricht Formation). This specimen is smaller and less slender, the crown being more compressed bucco-lingually and bearing more prominent longitudinal ridges; it closely resembles the tooth described by MULDER (1990), which is described and illustrated below.

A well-preserved vertebra (Pl. 2) from the Ankerpoort-'t Rooth (formerly Nekami) quarry, Bemelen (The Netherlands) (NHMM 1985141, *ex* K.C. Roos Colln, no. MK 39), was collected in the mid-1960s from excavated material on the quarry floor, from the Md (= Maastricht Formation, Meerssen Member in current terminology) according to ROOS (1966, p. 38). It is a short centrum, bearing well-developed ovoid articular facets dorsolaterally, allowing it to be identified as a pectoral or sacral centrum. The lateral faces are penetrated by a second pair of nutritive foramina, just below the insertion area. A heavily abraded caudal vertebra (NHMM K 1904; Fig. 2) is from directly above the Lava Horizon (Emael Member, Maastricht Formation), as exposed at the CBR-Romontbos quarry (Eben Emael, Bassenge, Liège).

Museum Natura Docet collections

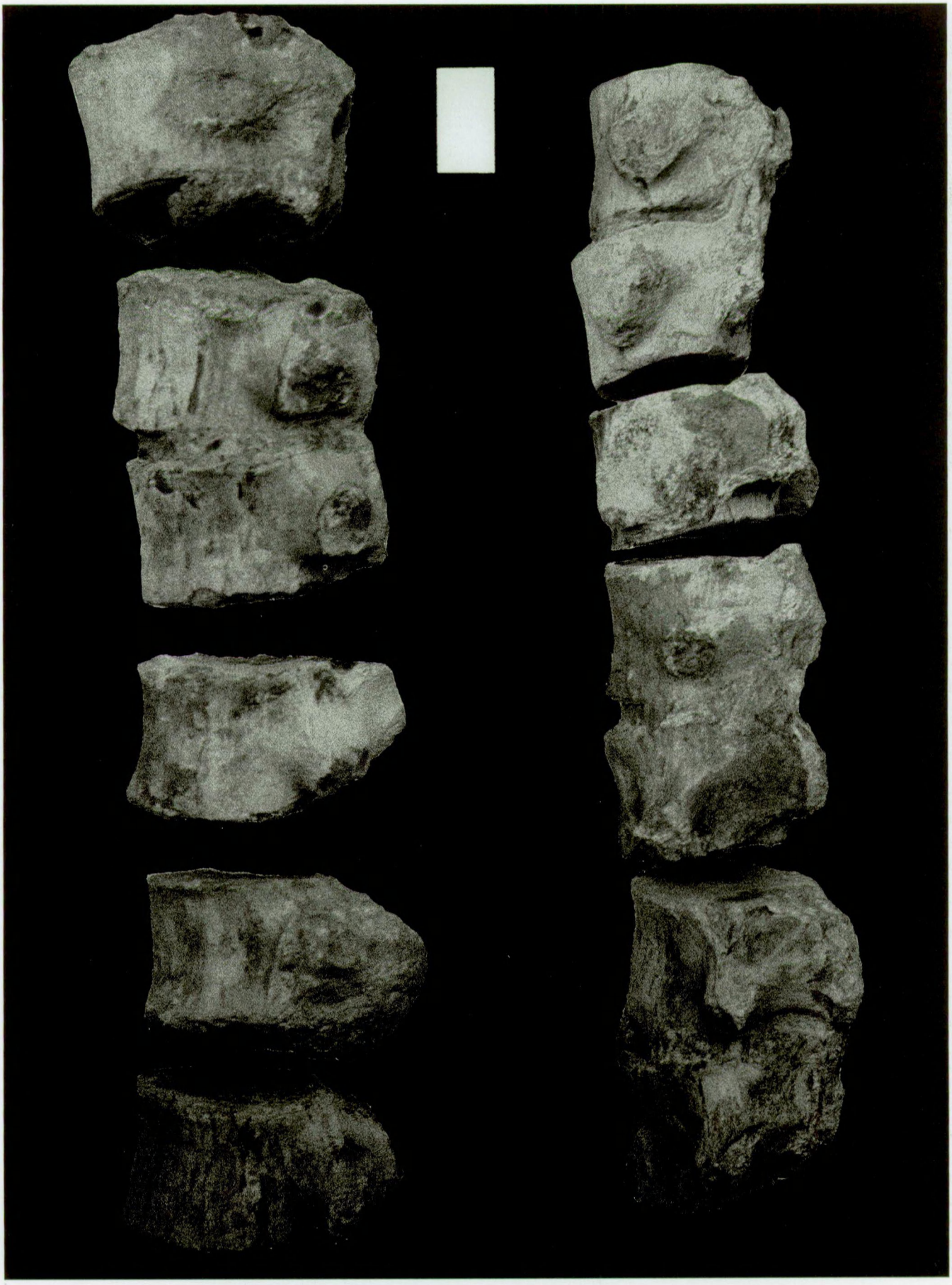
An isolated tooth (Pl. 1, Figs. 6-8; MND K 20.01.802, see also MULDER, 1990, fig. 2) is from the upper Emael Member (Maastricht Formation) at the St Pietersberg, either near or even at the ENCI-Maastricht BV quarry.

Two vertebrae (Pls. 3, 5; MND K 20.01.801a, b, *ex* L. de Heer Colln; see also MULDER, 1985, figs. 1-4) are from the Ankerpoort-'t Rooth quarry (Bemelen, collected May 27, 1961). A third specimen (Pl. 4; MND KB 50.20.01) is from the same quarry. These three vertebrae are identified as anterior cervical centra; the articular surfaces for holocephalous ribs are located very low on the lateral faces and the nutritive foramina are close together. The centra are rather elongated (L/B = 0.82-0.85; L/H > 1) and their articular surfaces typically dumbbell shaped and platycoelous. These characters are important elasmosaurid synapomorphies (BARDET *et al.*, 1999a; see discussion in BROWN, 1994). Cervical ribs and neural arches were not fused to the centra, which is a juvenile character.

Institut royal des Sciences naturelles de Belgique collections

These collections include two vertebrae (Pl. 6). The label with the first (IRScNB 204) states, "*Plesiosaurus*, Maastrichtien Saint-Symphorien. 1911". This is an eroded, small dorsal centrum (L 65 mm, W 75 mm, H 65 mm), with articular faces that are platycoelous and rounded. The ventral surface of the centrum is regularly convex, showing two widely separated nutritive foramina, while the lateral surfaces are convex without any trace of longitudinal crests or costal pits. This vertebra is from an immature individual, since the neural arch is not fused with the centrum, and is identified as elasmosaurid.

The label with the second specimen (IRScNB 205) states, "*Plesiosaurus*, Maastrichtien, Cuesmes, 1911". This is a huge, incomplete cervical centrum (L>70 mm, W 125 mm, H 95 mm), the articular surfaces of which are platycoelous with a dumbbell-shaped morphology and acute margins. The ventral surface bears closed nutritive



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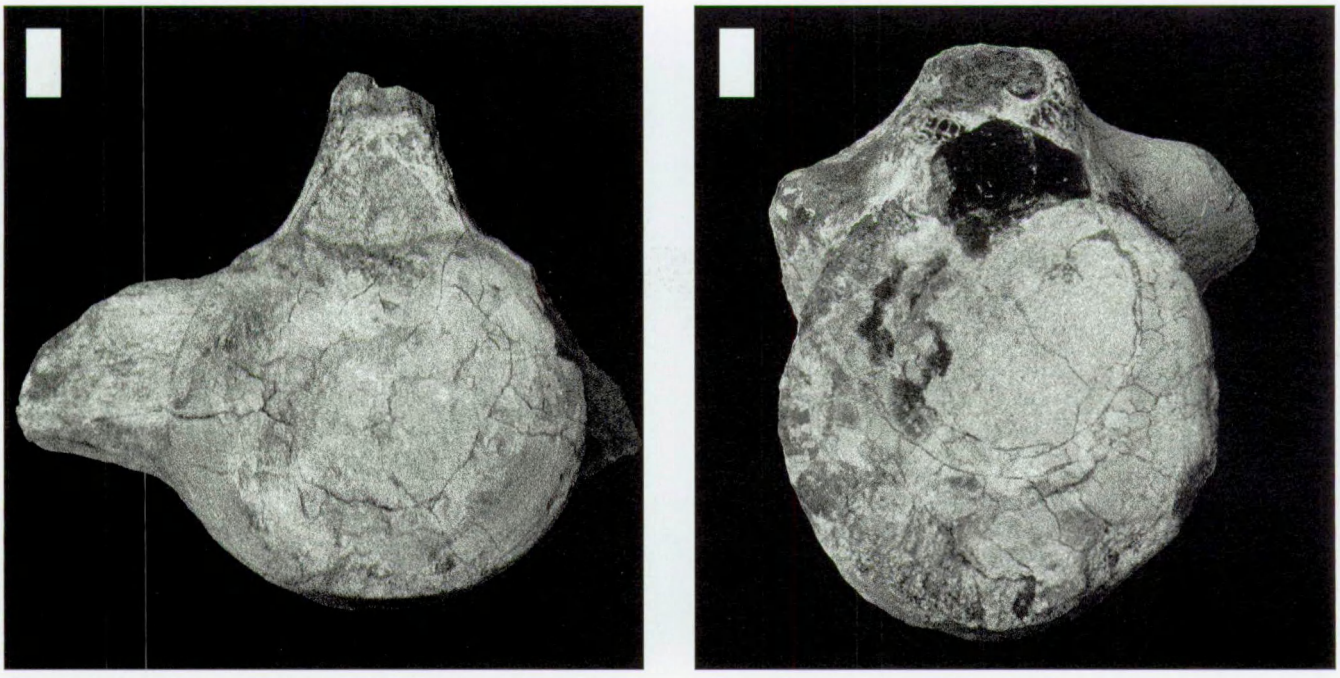

Fig. 3 — Syntypes of "*Plesiosaurus mauritanicus* ARAMBOURG, 1952", Maastrichtian of Djebel Tilda (Chichaoua, Morocco) (MNHNP Arambourg Colln, unregistered); A - original of ARAMBOURG, 1952, pl. 40, fig. 19; B, C - originals of ARAMBOURG, 1952, pl. 40, figs. 18 and 17, respectively. Scale bars equal 50 mm.

foramina, the lateral surface a strong median longitudinal crest, and a costal pit located very low. This morphology is characteristic of the Elasmosauridae.

Muséum national d'Histoire naturelle de Paris collections

Plesiosaur teeth have been collected from all Maastrichtian phosphatic deposits in Morocco, the most complete specimen amongst them being the holotype of *Plesiosaurus mauritanicus* ARAMBOURG, 1952 (pl. 40, fig. 13), from Louis Gentil (B12 level, Maastrichtian, Morocco). Two kinds of plesiosaur teeth may be recognised in this material. ARAMBOURG (1952, pl. 40, figs. 7-10) illustrated four specimens, erroneously assigned by him to a "crocodilien indéterminé", that have rounded cross-sections and enamel crowns ornamented by rough longitudinal ridges, and six with elliptical cross sections (ARAMBOURG, 1952, pl. 40, figs. 11-16). The latter, such as the type of *P. mauritanicus* (Pl. 1, Figs. 9, 10 here), are buccolingually compressed, and have their crown ornamented with fine longitudinal ridges converging towards the apex, being more marked and numerous on the lingual face. The buccal face is flatter and almost smooth. The root is devoid of ornament. In anterior view, the teeth are strongly curved. At least this latter group of teeth are characteristic of the Elasmosauridae, but they do not reveal any diagnostic character permitting them to be differentiated specifically. *Plesiosaurus mauritanicus* may thus be considered a *nomen vanum*, as already pointed out by WELLES (1962).

A series of thirteen vertebrae described and illustrated by ARAMBOURG (1952, pl. 40, figs. 17-19; see Fig. 3 here), belong together; some of the vertebrae actually remain in articulation. Collected from the C3 level at the Chichaoua outcrop (Meskala Basin, Morocco), these vertebrae are considered to be a syntype of *P. mauritanicus*. The series includes posterior cervical, pectoral and anterior dorsal vertebrae. Neural arches fused on centra prove these to have come from an adult individual (*sensu* BROWN, 1981). The cervical vertebrae (W>H>L) have flat and dumbbell-shaped articular surfaces, the costal pits strongly built and located low on the centrum. There is no trace of a lateral crest, which leads us to interpret these specimens as posterior cervicals. The pectoral vertebrae (W>H>L) have flat articular faces of a more quadrangular morphology, so that the ventral surface is almost flat. The costal pit is located both on the centrum and on the neural arch. The dorsal vertebrae (H=W>L) possess rounded articular surfaces and parapophyses located on the neural arch. The general proportions of the vertebrae, and the flat and dumbbell-shaped articular surfaces of the posterior cervical identify this material as Elasmosauridae, gen. et sp. indet.

Stratigraphy

Maastrichtian type area

Vertebrae MND K 20.01.801a and K 20.01.801b (Pls. 3 and 5, respectively) were obtained without matrix. The

amount of biocalcarenitic material that remains sticking to the specimens is hardly sufficient for an analysis of benthic foraminiferal content. The frequency and diversity of macrobiota in the type Maastrichtian are highest in the upper part of the Maastricht Formation (Nekum and Meerssen members), and quarrying activity at the Ankerpoort-'t Rooth quarry has concentrated on this part of the section during recent years. This suggests that these specimens probably originated from that part of the sequence. The same holds true for the third vertebra (MND KB 50.20.01; see Pl. 4) in the Natura Docet collections.

In view of its state of preservation it is much more likely that vertebra NHMM 1985141 came from the Nekum Member rather than from the Meerssen Member, as but the lowermost part of this latter unit is exposed at the Ankerpoort-'t Rooth quarry, which is characterised by relatively coarse-grained, bryozoa-rich calcarenites.

The single, poorly preserved vertebra from the CBR-Romontbos quarry (NHMM K 1904) was collected from directly above the Lava Horizon in the Emael Member (i.e. *Belemnitella junior* Zone of authors).

Specimen MND K 20.01.802 was still embedded in matrix at the time MULDER (1990) described it. This enabled an analysis of bioclast content; it was determined that the specimen came from the upper part of the Emael Member (Maastricht Formation).

Specimen NHMM 1993062 from the St Pietersberg also was still embedded in matrix, whose nature suggests that it was collected either from the top of the Nekum or the base of the Meerssen Member.

The label with specimen NHMM 003842 gives Kunrade as locality. Outcrops in the Kunrade area that are still accessible were referred to ecozone V by P.J. FELDER & BLESS (1989, fig. 3), and it may thus be assumed that the specimen came from the Kunderberg at Kunrade. The tooth is thus slightly older than the other remains available for study. P.J. FELDER & BLESS (1989) correlated the lower part (their ecozone IV) of the Kunrade Limestone facies as exposed in the eastern part of southern Limburg with HOFKER's (1966) benthic foraminifer zone F (= Lanaye Member, Gulpen Formation *sensu* W.M. FELDER, 1975; ALBERS & FELDER, 1979) of the Maastricht-Haccourt area, and the top with the top of foram zone H as exposed at the ENCI-Maastricht BV quarry.

The entire Maastricht Formation as currently interpreted, with the exception of the upper half of the Meerssen Member (top IVf-3 and higher), yields but one species of coleoid cephalopod, namely *Belemnitella* gr. *junior* NOWAK, 1913, index of the *junior* Zone of authors. In the upper half of the Meerssen Member appear the first representatives of the *Belemnella (Neobelemnella) kazimiroviensis* group, ranging to the K/T boundary, which equates with the Berg en Terblijt Horizon at the top of unit IVf-6 of the Meerssen Member (JAGT, 1996, 1999). This species group is index of the *kazimiroviensis* Zone (CHRISTENSEN, 1996, 1997a, b), which is also documented from the boreal latest Maastrichtian of Denmark, Poland and European Russia. More important is the recent record from the middle and upper part of the Meerssen Member of the pachydiscid ammonite *Menuites terminus* (WARD & KENNEDY, 1993), index of the *terminus* Zone of WARD & KENNEDY (1993), defined in the Bay of Biscay sections (Spain, France), exposing Tethyan uppermost Maastrichtian strata. This distinctive species is also known from Denmark (BIRKELUND, 1993), where there is additional belemnite and micromorphic brachiopod control.
Available evidence thus suggests that in the Maastrichtian type area elasmosaurid plesiosaurs are restricted to the *junior* Zone and do not range into the overlying *kazimiroviensis* Zone.

Belgium

IRScNB 204 probably came from the Saint Symphorien Chalk, since Saint Symphorien is mentioned on the accompanying label. In the Mons Basin (southern Belgium), this unit corresponds to the Upper Maastrichtian and is more or less the equivalent of the *Belemnitella junior* Zone (see ROBASZYNSKI & CHRISTENSEN, 1989; KENNEDY, 1993). It may correlate with the Lanaye Member (Gulpen Formation) of the Maastrichtian type area. IRScNB 205 is from the Cuesmes-Ciply area. Here there are several levels of Maastrichtian age. On account of its colour, this specimen must have come from another level than IRScNB 204. It probably stems from the "Craie phosphatée de Ciply", which was considered to be of late Early Maastrichtian age (*obtusa* Zone) by ROBASZYNSKI & CHRISTENSEN (1989), KENNEDY (1993), SIMON (1998) and CHRISTENSEN (1999).

Morocco

In Morocco, the fossiliferous phosphatic deposits which outcrop in the Ouled Abdoun, Ganntour and Meskala basins constitute an apparently continuous series extending from the Lower Maastrichtian to the lowermost Lutetian (Middle Eocene; see ARAMBOURG, 1952; NOUBHANI & CAPPETTA, 1997; LUCAS & PRÉVÔT-LUCAS, 1996). During the Maastrichtian, phosphatic sedimentation in these basins was supplied by an upwelling with both a Tethyan and Atlantic source of phosphorus (LUCAS & PRÉVÔT-LUCAS, 1996, pp. 379, 385).

According to ARAMBOURG (1952), plesiosaurs from the Maastrichtian phosphatic deposits occurred in all basins and were represented by isolated vertebrae and teeth. However, for most of the specimens described by ARAMBOURG the exact stratigraphical position within the Maastrichtian was not recorded. Moreover, recent field observations by one of us (NB) have shown that elasmosaurid remains occur throughout the entire Maastrichtian series. Only the above-mentioned vertebral series can be placed in a precise stratigraphical context. The label with these specimens indicates that they came from the C3 level at the Chichaoua outcrop in the Meskala Basin; they are thus of late Maastrichtian age (NOUBHANI, 1993).

An overview of Maastrichtian elasmosaurids worldwide

During the latest Cretaceous, plesiosaurs were represented by both groups of Plesiosauroidea, i.e. the long-necked elasmosaurids and the short-necked polycotylids (*sensu* CARPENTER, 1996, 1997) and by rare Pliosauroidea (BARDET, 1995; CARVALHO & AZEVEDO, 1998). They were distributed worldwide and are particularly common in the Pacific coastal zone of North America from where most of the genera were first described (see WELLES, 1962). There are also records from the uppermost Cretaceous of northwest Europe (BARDET & GODEFROIT, 1995; BARDET *et al.*, 1999b, and literature cited therein), Russia (ROZHDESTVENSKIY, 1973) and Japan (NAKAYA, 1989).

In the southern hemisphere, elasmosaurs have been recorded from South America (GASPARINI & GONI, 1985), Antarctica (GASPARINI *et al.*, 1984; CHATTERJEE & SMALL, 1989), New Zealand (WELLES & GREGG, 1971; WIFFEN & MOISLEY, 1986), Africa, the Middle East and Madagascar (WERNER & BARDET, 1996). In Africa and the Middle East, plesiosaurs have been described from the Maastrichtian of Morocco (ARAMBOURG, 1952), Angola (TELLES ANTUNES, 1964), Egypt (WERNER & BARDET, 1996), Jordan and Iraq (SIGNEUX, 1959; ARAMBOURG *et al.*, 1959). With regard to most of these areas, most material is imprecisely dated and in most cases it is difficult to differentiate between Lower and Upper Maastrichtian.

In North America, ''Middle'' to Upper Maastrichtian strata outcrop only on the east (New Jersey, Maryland) and west (California) coasts of the United States. In New Jersey, there is a continuous series from the Lower Maastrichtian into the Palaeocene. The Navesink Formation is generally dated as ''Middle'' Maastrichtian (GALLAGHER, 1993), while the overlying Hornerstown Formation is of latest Maastrichtian to Palaeocene age (BROUWERS & HAZEL, 1978; GALLAGHER *et al.*, 1986; GALLAGHER, 1993; KENNEDY & COBBAN, 1996). GRANDSTAFF (1998) noted that the presence of ''green bone'' crushing in tooth punctures on a turtle plastron supported a late Maastrichtian age for the basal Hornerstown Formation in southern New Jersey. Both the Navesink and Hornerstown formations have yielded rare plesiosaur remains, which, in part, have been assigned to *Cimoliasaurus magnus* LEIDY, 1851, the type of which consists of thirteen vertebral centra (ANSP 9235) (PARRIS, 1974). In all cases, however, these remains are indeterminate at the generic and specific levels, and should be considered as Elasmosauridae *nomina vana* (WELLES, 1962). GALLAGHER (1993) listed the names that were erected on the basis of non-diagnostic material. *Cimoliasaurus magnus* was considered by PARRIS (1974) to represent a polycotylid; it might in fact turn out to be an elasmosaurid. The articular surfaces of vertebrae assigned to *Cimoliasaurus magnus* are platycoelous, which is an elasmosaurid character, while these surfaces in polycotylid and pliosaur vertebrae are amphicoelous with rather rounded margins (LEIDY, 1865, pl. 6; BARDET *et al.*, 1999a).

In Maryland, the Severn Formation is dated as ''Middle'' Maastrichtian, being an equivalent of the Navesink Formation (BROUWERS & HAZEL, 1986; KENNEDY & COBBAN, 1996). As in New Jersey, only rare indeterminate remains of elasmosaurids have been collected, assigned with a query to *C. magnus* (see BAIRD, 1986). On the other hand, in California, the Moreno Formation of ''Middle'' to Late Maastrichtian age (POPENOE *et al.*, 1960) has yielded a rich elasmosaurid fauna: *Aphrosaurus furlongi* WELLES, 1943, *Fresnosaurus drescheri* WELLES, 1943, *Hydrotherosaurus alexandrae* WELLES, 1943, and *Morenosaurus stocki* WELLES, 1943, all of which are documented by abundant material (WELLES, 1943).

In South America, pliosaurs have recently been recorded from the Maastrichtian Gramame Formation in northeastern Brazil (CARVALHO & AZEVEDO, 1998). In Antarctica, and more precisely in Vicecomodoro Marambio Island (Seymour Island), the Lopez de Bertodano Formation represents a continuous sequence from the Upper Campanian to the Palaeocene (PIRRIE *et al.*, 1992). The fauna includes indeterminate elasmosaurs (GASPARINI *et al.*, 1984; CHATTERJEE & SMALL, 1989), some of which were collected from very close to the K/T boundary (CHATTERJEE & SMALL, 1989).

In New Zealand, the Laidmore Formation on South Island, hich is dated as Late to latest Maastrichtian (WELLES & GREGG, 1971), has yielded plesiosaur remains, including the elasmosaurid *Mauisaurus haasti* HECTOR, 1874, as well as indeterminate elasmosaurids (WELLES & GREGG, 1971; WIFFEN & MOISLEY 1986).

In Africa, only the phosphatic strata in Morocco comprise unequivocal Upper Maastrichtian deposits (i.e. upper part of C3 level). Biostratigraphical correlations are based on neoselachian faunas (ARAMBOURG, 1952; CAPPETTA, 1987; NOUBHANI, 1993; NOUBHANI & CAPPETTA, 1997).

In recent years, the similarities in fossil faunas between the Maastrichtian marine deposits of the east coast of the United States on the one hand and those of the type area on the other have received ample attention (COBBAN & KENNEDY, 1995; JAGT & COLLINS, 1999; JAGT & KENNEDY, 1994; KENNEDY & JAGT, 1998; KUYPERS *et al.*, 1998; LANDMAN & WAAGE, 1993; MULDER, 1999). These areas have also in common the extreme rarity of plesiosaur remains (BARDET & GODEFROIT, 1995; GALLAGHER, 1993; MULDER, 1990; PARRIS, 1974). PARRIS (1974, p. 32) noted that in New Jersey the suborder [*sic*] Plesiosauria declined markedly prior to the deposition of the late Maastrichtian basal Hornerstown Formation. As stated above, elasmosaurids have not been found in the latest Maastrichtian *Belemnella kazimirovensis* Zone (= upper half of Meerssen Member, Maastricht Formation) in the type area.

Discussion

When reviewing the latest Cretaceous marine fossils of the northern hemisphere, a striking contrast between New Jersey and the Maastrichtian type area on the one hand, and California and Morocco on the other, with regard to plesiosaur abundance, is noted. By comparing the marine Maastrichtian of California, the Cretaceous Western Interior Seaway, the Mississippi Embayment and the North Atlantic basin, BAKKER (1993, pp. 659, 660, fig. 18) suggested that the absence of fast-swimming plesiosaurs could be explained by the presence of an exceptionally dense algal forest. Only the California coast had an abrupt continental slope, with a narrower zone of shallow water where an algal forest could grow. The relative abundance of elasmosaurs there could be explained by the wide expanses of open water. However, we consider that the presence of an abrupt continental slope also coincided with the upwelling of nutrient-enriched water, which favoured the presence of a high biomass, being an ideal condition for open-water predators such as elasmosaurids.

In the North Atlantic basin, the Upper or uppermost Maastrichtian phosphatic deposits in Morocco are the only strata of that age which have yielded plesiosaur remains (teeth and vertebrae) in such abundance, that ARAMBOURG (1952, p. 278) hinted at "une valeur stratigraphique certaine" of the teeth. These deposits originated near the open Atlantic ocean of that time, supporting upwelling conditions in this area as well. Upwelling is closely linked to oceanic morphology and continent-ocean relations, and is generally considered to be one of the most important and efficient sources of local phosphorus supply (LUCAS & PRÉVÔT-LUCAS, 1996, p. 379).

The fossils from Belgium and the Netherlands come from epicontinental shallow seas. In the Maastrichtian type area the first appearance datum (FAD) of elasmosaurids appears to coincide with a major Tethyan incursion (MULDER *et al.*, 1998, fig. 4B), an observation which allows elasmosaurids to be regarded as a southerly Tethys/north African faunal element, in view of their abundance in the Maastrichtian of Morocco. The paucity of plesiosaur remains in the Maastrichtian type area would seem to match to BAKKER's (1993) observation to some extent; in particular, the Lanaye Member (Gulpen Formation) and the Gronsveld, Emael and Nekum members (Maastricht Formation) have yielded common to locally abundant remains of seagrass (an angiosperm), both silicified and in ferruginous imprint preservation. However, whether submarine vegetation barred plesiosaurs from epicontinental shallow seas, remains to be seen. The occurrence of plesiosaurs related to abundance of items of prey in oceanic upwelling areas is at least as plausible an explanation.

From the distribution of Maastrichtian elasmosaurids worldwide it may be concluded that, like mosasaurs, elasmosaurids were still widespread and diversified during the late(st) Maastrichtian (BARDET, 1995; LINGHAM-SOLIAR, 1998; compare LUCAS & REYNOLDS, 1993). Even if precise stratigraphical extensions are often difficult to obtain for large vertebrate remains, the extinction of elasmosaurids at the K/T boundary thus appears to be sudden rather than gradual.

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PLATE 1

Elasmosaurid teeth; scale bars equal 10 mm.

Figs. 1-3 — NHMM 1993062, in axial, buccal and lingual views, St Pietersberg, south of Maastricht; Maastricht Formation, upper Nekum Member or lower Meerssen Member.

Figs. 4-5 — NHMM 003842, in buccal and axial views, Kunrade area (?Kunderberg section); Maastricht Formation, Kunrade Limestone facies.

Figs. 6-8 — MND K 20.01.802, in axial, buccal and lingual views, respectively, St Pietersberg, south of Maastricht; Maastricht Formation, upper Emael Member.

Figs. 9-10 — Holotype of "*Plesiosaurus mauritanicus* ARAMBOURG, 1952", MNHN unregistered (Arambourg Colln), axial and lingual views; Louis Gentil (B12 level, Maastrichtian, Morocco) (original of ARAMBOURG, 1952, pl. 40, fig. 13).

PLATE 2

Figs. 1-5 — Elasmosaurid pectoral or sacral vertebra (NHMM 1985141), in dorsal, lateral, ventral views, and articular surfaces; Ankerpoort-'t Rooth quarry (formerly Nekami), Bemelen (the Netherlands); Maastricht Formation, ?Nekum Member. Scale bar equals 10 mm.

PLATE 3

Figs. 1-4 — Elasmosaurid cervical vertebra (MND K 20.01.801a), in dorsal, ventral, articular and lateral views; Ankerpoort-'t Rooth quarry (formerly Nekami), Bemelen (the Netherlands); Maastricht Formation, ?Nekum Member. Scale bar equals 10 mm.

PLATE 4

Figs. 1-4 — Elasmosaurid cervical vertebra (MND KB 50.20.01), in dorsal, ventral, articular and lateral views; Ankerpoort-'t Rooth quarry (formerly Nekami), Bemelen (the Netherlands); Maastricht Formation, ?Nekum Member. Scale bar equals 10 mm.

PLATE 5

Figs. 1-4 — Elasmosaurid cervical vertebra (MND K 20.01.801b), in dorsal, ventral, articular and lateral views; Ankerpoort-'t Rooth quarry (formerly Nekami), Bemelen (the Netherlands), Maastricht Formation, ?Nekum Member. Scale bar equals 10 mm.

PLATE 6

Figs. 1-6 — Elasmosaurid cervical and dorsal vertebrae; Mons Basin (southern Belgium), "Craie de Saint Symphorien" (Upper Maastrichtian); 1-3 - IRScNB R 205, incomplete cervical centrum, in ventral, lateral and articular views; 4-6 - IRScNB R 204, dorsal centrum, in articular, lateral and ventral views. Scale bars equal 10 mm.

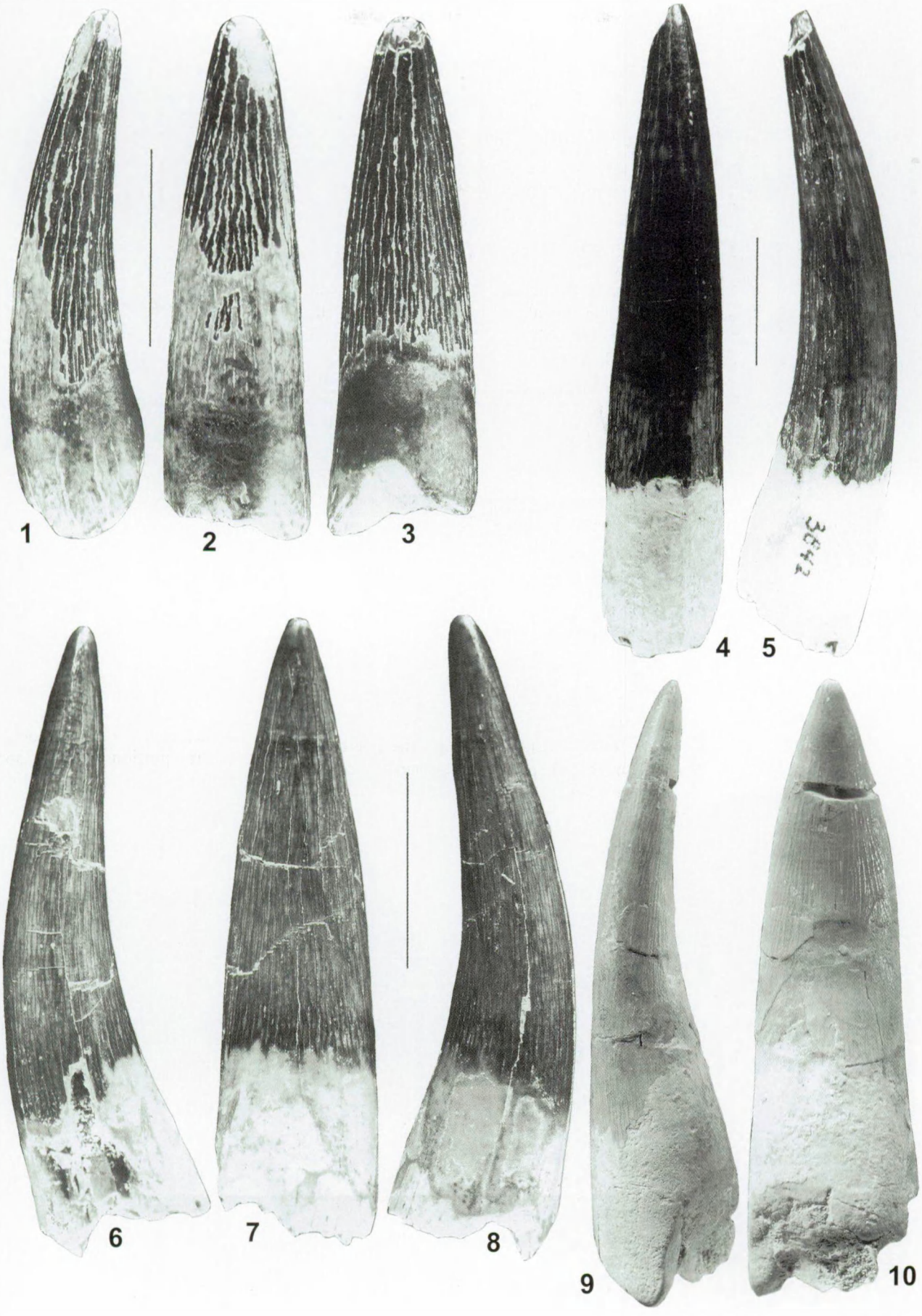

PLATE 1

PLATE 2

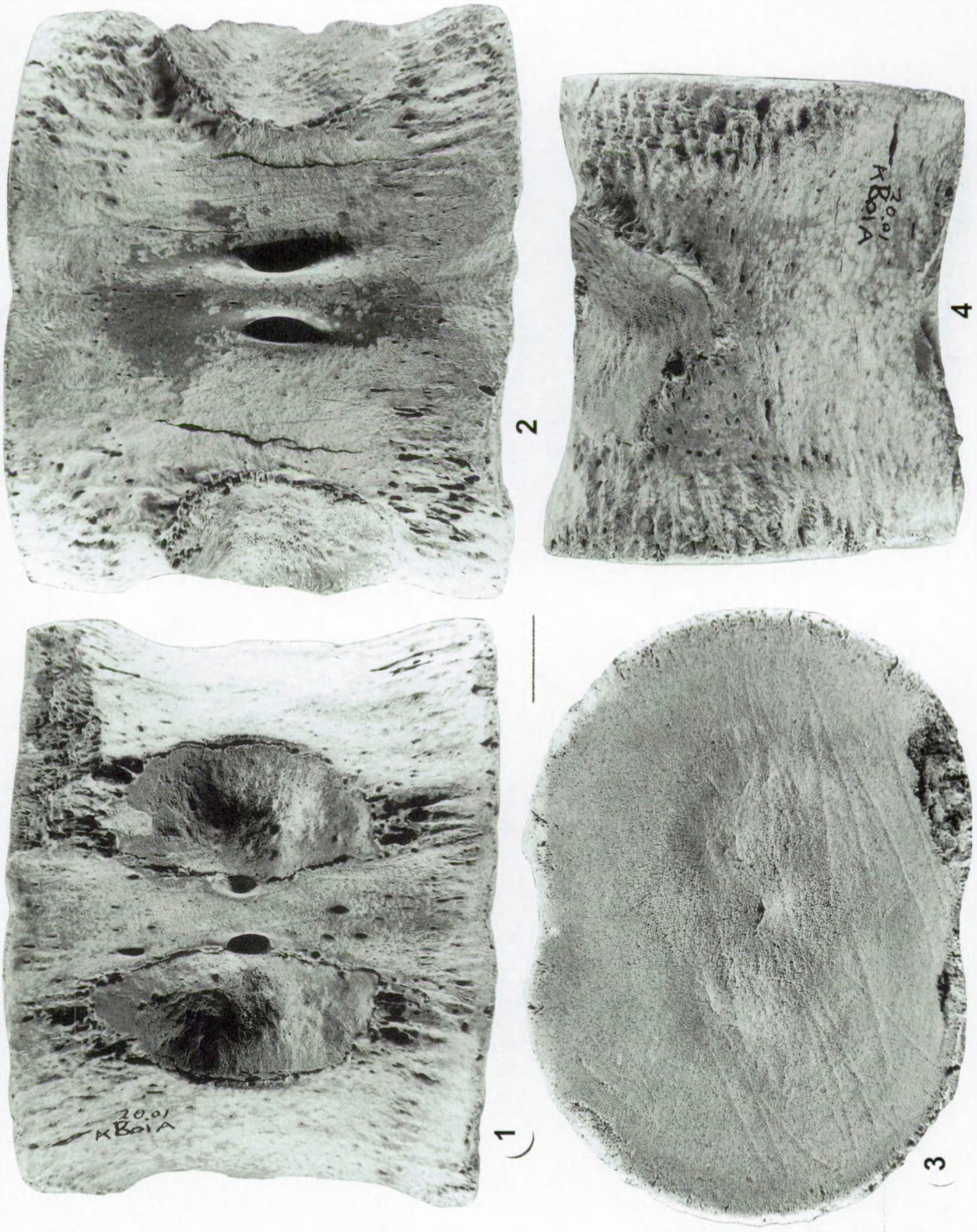

PLATE 3

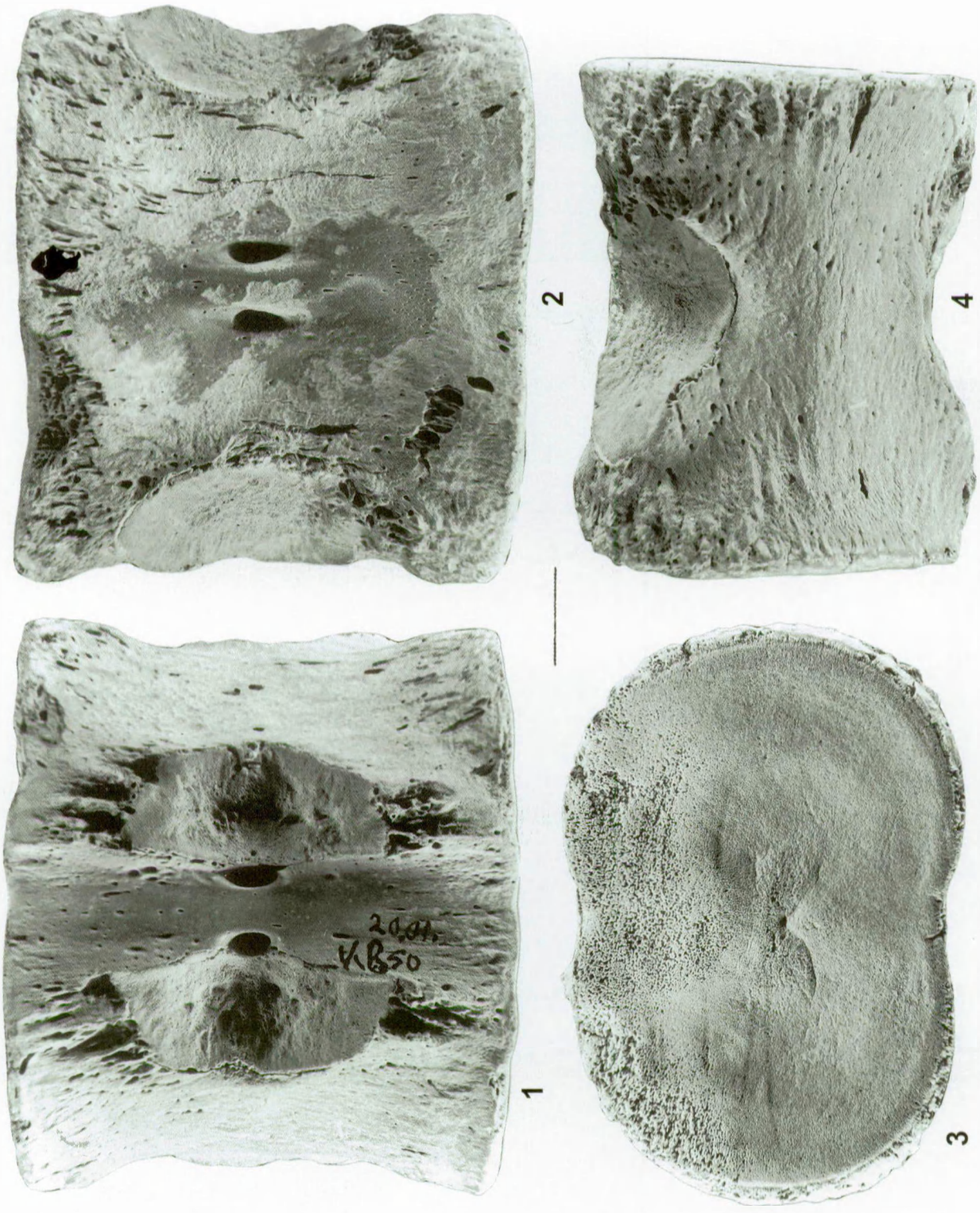

PLATE 4

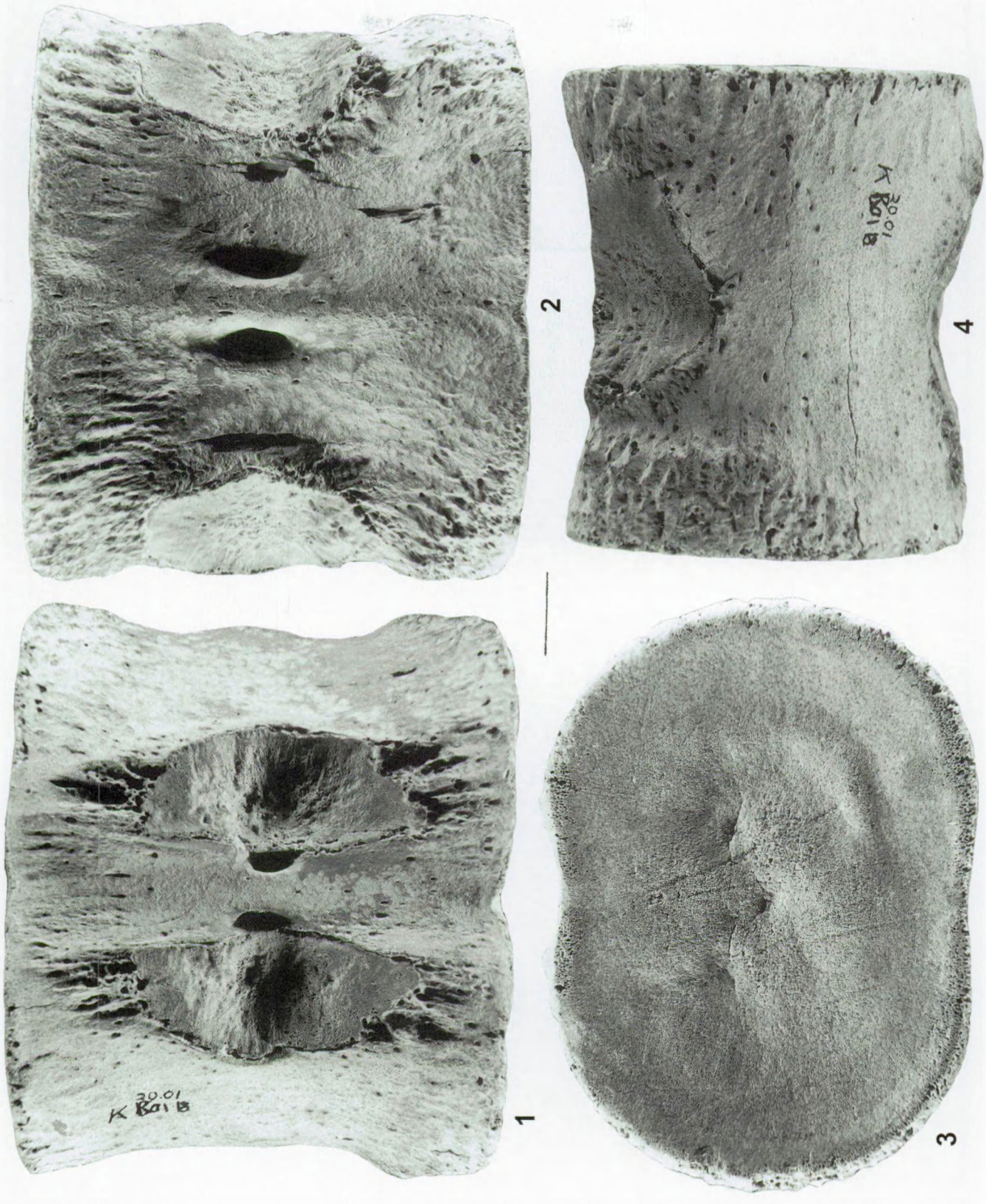

PLATE 5

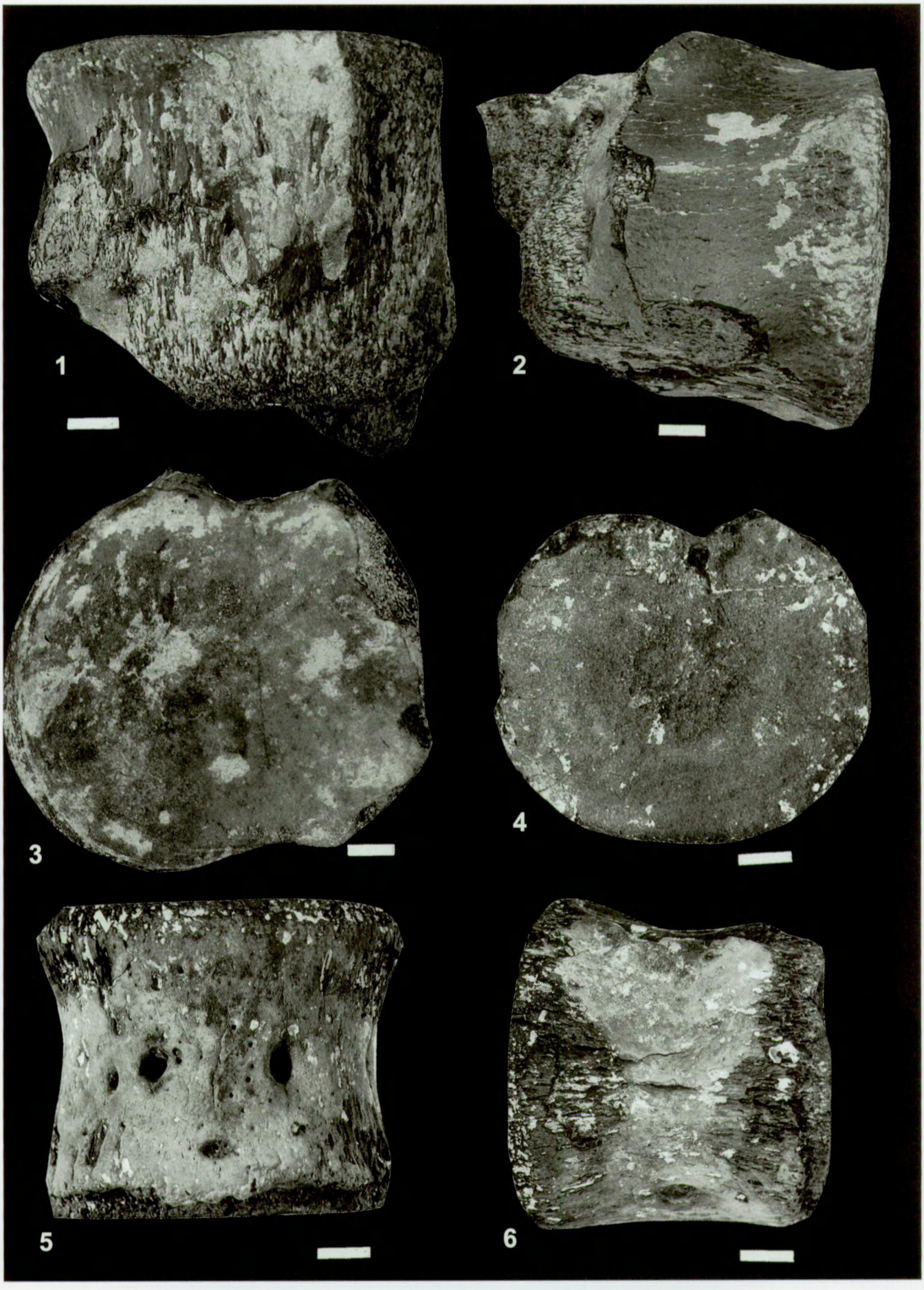

PLATE 6