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Transatlantic latest Cretaceous mosasaurs (Reptilia, Lacertilia) from the Maastrichtian type area and New Jersey

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Abstract

Cranial and postcranial elements of the mosasaurid reptiles *Mosasaurus hoffmanni* Mantell 1829 and *Plioplatecarpus marshi* Dollo 1882 from the Maastrichtian type area, and of *Mosasaurus maximus* Cope 1869 and *Plioplatecarpus depressus* (Cope 1869) from New Jersey are compared. Views held by previous authors are discussed. It is concluded that these European and North American taxa are conspecific.

Introduction

The type specimen of *Mosasaurus hoffmanni* Mantell 1829, an incomplete skull (Figure 1), was discovered at St Pietersberg, south of Maastricht between 1770 and 1774. The romanticised and often repeated history of this find has recently been analysed critically by Rompen (1995) and has been described in detail by Bardet & Jagt (1996).

From the start, these remains were considered to belong to a crocodile. Subsequently, P. Camper (1786) and Van Marum (1790) thought them to have come from a sperm whale. Faujas Saint Fond (1799), however, stuck to the original interpretation. When attempting to defend his father's view, A.G. Camper (1800) discovered the lacertilian nature of this fossil. Eventually, this mosasaur was to become crucial to the concept of extinction.

As early as 1800, A.G. Camper noted that a second species from the same area was represented in his father's collection (Theunissen 1980). He referred to this species as '*petite espèce*' (A.G. Camper 1812) and noted striking differences between this and the larger species. Camper's '*grande espèce*' had caudal vertebrae with fused haemapophyses, whereas the '*petite espèce*' was characterised by articulated haemapophyses. Camper's views did not become generally accepted, however, in part because Cuvier disagreed (Dollo 1890). Thus, the true nature of the second species was not recognised until 1882, when Dollo described it briefly and named it *Plioplatecarpus marshi*.

Worldwide, numerous mosasaur species inhabited the Late Cretaceous oceans and marginal seas (Russell 1967, deBraga & Carroll 1993, Bell 1997a). The following species have been identified in the Maastrichtian type area, in addition to *Mosasaurus hoffmanni* and *Plioplatecarpus marshi*: *M. lemonnieri* Dollo 1889, *Leiodon sectorius* (Cope 1871) and *Carinodens belgicus* (Woodward 1891). Mosasaurinae inc. sedis, cf. *Prognathodon solvayi* Dollo 1889 and *Platecarpus* sp. have been recorded as well (Kuypers et al. 1998, Mulder et al. 1998). Palaeoenvironmental conditions during the Late Cretaceous were discussed by Smit & Brinkhuis (1996) and Lingham-Soliar (1995) for the Maastrichtian type area, and by Gallagher (1993) for New Jersey.

For many centuries, the exploitation of the tuffaceous chalks in the Maastrichtian type area took place in an ever expanding underground system of galleries. It was in such a gallery that the abovementioned skull of *Mosasaurus hoffmanni* was discovered. In New Jersey, strata of Maastrichtian age – quarried in pits – comprise glauconitic sands. Fossil remains of numerous taxa, marine and terrestrial, vertebrate and invertebrate, have been recorded since the nineteenth century. The succession includes estuarine

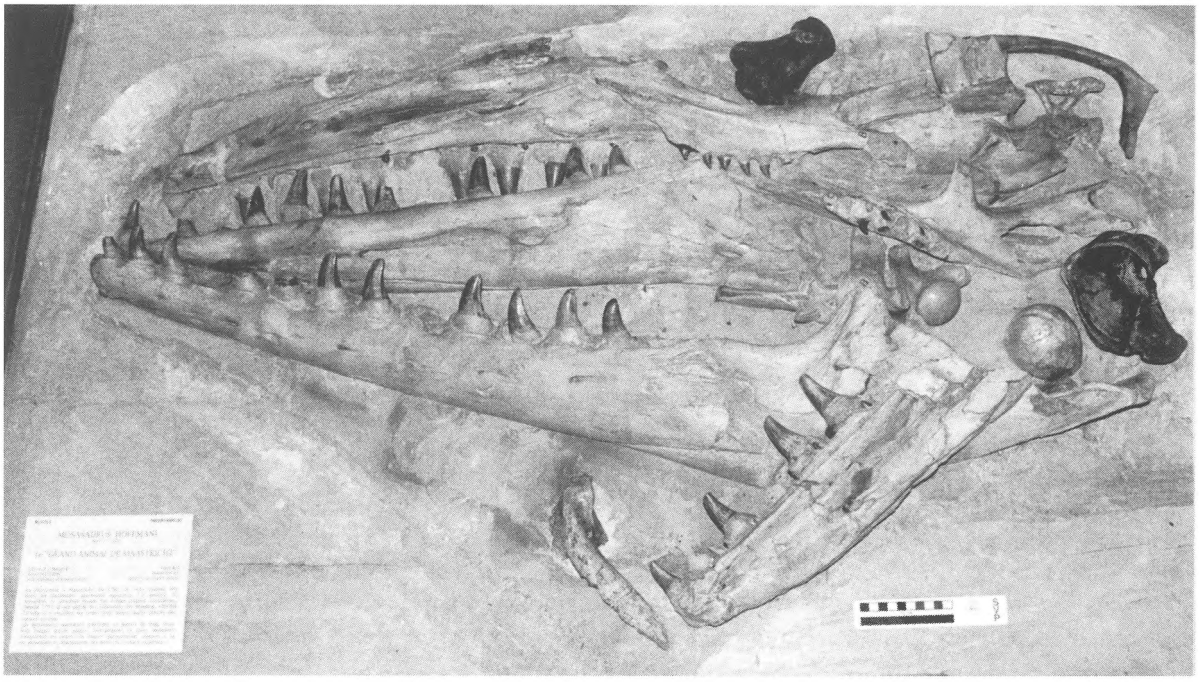

Figure 1. Mosasaurus hoffmanni, type specimen (MNHNP AC 9648). Scale bar equals 10 cm.

lagoonal-tidal channel-barrier beds (Gallagher 1993) as well as nearshore marine deposits.

The following mosasaurid taxa from the Late Maastrichtian deposits of New Jersey were listed by Gallagher (1993): *Mosasaurus maximus* Cope 1869, *M. dekayi* Bronn 1838, *M. conodon* (Cope 1881), *Plioplatecarpus depressus* (Cope 1869), *Leiodon sectorius*, *Halisaurus platyspondylus* Marsh 1869 and *Prognathodon rapax* (Hay 1902). Based on a comparison of mainly postcranial material, Baird & Case (1966) and Russell (1967) synonymised *Mosasaurus conodon* with *M. lemonnieri*. Furthermore, Russell (1967) suggested that *Mosasaurus hoffmanni* and *M. maximus* might be conspecific, a view rejected by Lingham-Soliar (1995). Recently, Kuypers et al. (1998) have noted that, with the exception of *Carinodens belgicus*, all mosasaur species from the Maastrichtian type area appeared closely related to, or even conspecific with, mosasaur taxa from the Maastrichtian of New Jersey.

In 1961, two well-preserved skulls of *Mosasaurus maximus* (Figure 2) were collected from the Inversand Company Pit, Sewell (Gloucester County, New Jersey). This is the only pit still in operation (Gallagher 1993, pers. comm.). These skulls have been re-examined for the present contribution. Based on comparative studies, the alleged conspecificity of *M. hoffmanni* and *M. maximus*, and of *P. marshi* and *P. depressus* is discussed in detail.

Material and methods

Abbreviations used to denote the repositories of specimens referred to in the text are listed in Appendix 1.

M. hoffmanni and *P. marshi* are by far the commonest species of mosasaur in the Upper Maastrichtian of the Maastrichtian type area. About one hundred teeth of each were counted in the Natuurhistorisch Museum Maastricht collections and in private collections, studied by Kuypers et al. (1998). In the New Jersey Maastrichtian, *M. maximus* is the commonest species (Russell 1967). *Plioplatecarpus* appears less common in these deposits, although Cope (1871) stated otherwise. The only cranial elements that I have recently examined in the ANSP collections are casts of three teeth (ANSP 20184, 20185). The AMNH (New York) and NJSM (Trenton) possess casts of the same teeth. Their assignment to *P. depressus* is questionable. Russell (1967: 161, fig. 88) listed and illustrated jaw elements, referred to this species, from the collections of Yale Peabody Museum (New Haven).

In order to investigate an alleged conspecificity of the examined mosasaur taxa, specimens in several mu-

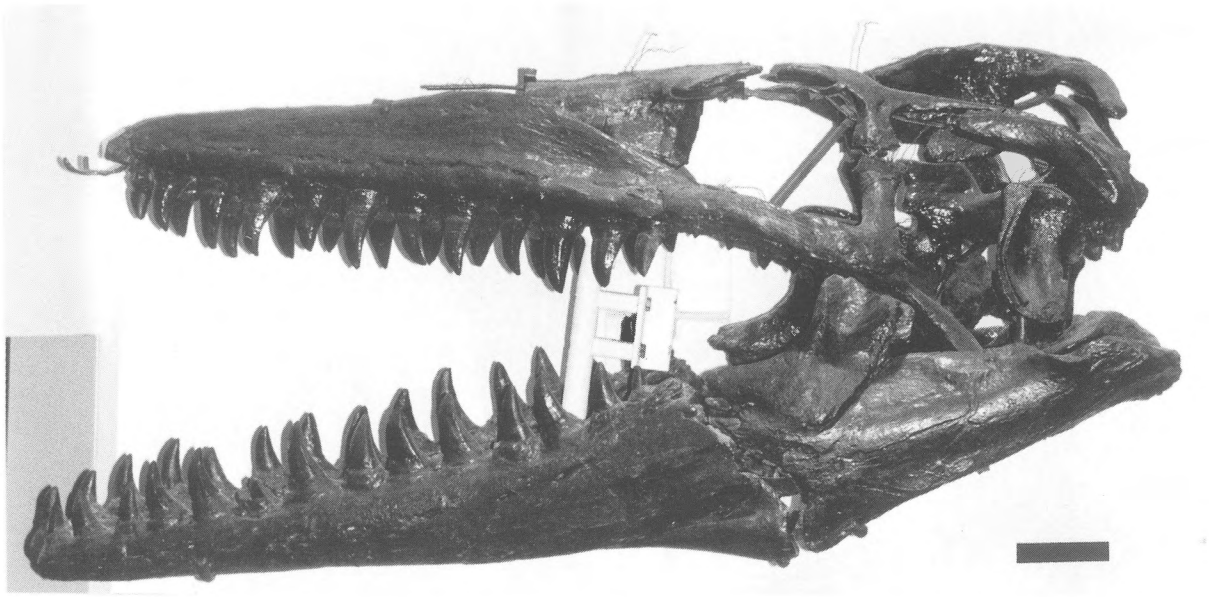

Figure 2. *Mosasaurus maximus*, mounted skull NJSM 11053, lateral view, premaxillae and frontal removed. Scale bar equals 10 cm.

seum collections, both in the USA and Europe, were compared. The majority of the studied material was collected in the nineteenth century and even earlier. It is listed in Appendix 2.

The New Jersey specimens are recorded from the Maastrichtian Navesink and basal Hornerstown Formations (Gallagher 1993). They vary in colour from brownish black to black and are prone to decay because of their high pyrite content. Many of them have been treated with a preserving fluid, and some of the elements have been partly restored. Unfortunately, details of specimens are sometimes obscured by pyrite decay and/or restoration. The material from the Maastrichtian type area varies in colour from brown to yellowish and greyish brown, and does not contain any pyrite. Specimens are often so well preserved that they do not appear fossilised. The stratigraphic distribution of the taxa was given by Mulder et al. (1998).

In the present contribution, mostly cranial elements - of which sufficiently preserved specimens have been found in both New Jersey and the Maastrichtian type area – are discussed.

Genus *Mosasaurus* Conybeare 1822

Mosasaurus hoffmanni Mantell 1829

1786 Physeteris incogniti ex Monte S. Petri – P. Camper: 444, 446, pl. 15, figs 5, 6; pl. 16

1829 *Mososaurus* [sic] *Hoffmannii* Mantell 1829: 207

1869a *Mosasaurus maximus* Cope 1869: 262

1967 *Mosasaurus maximus* Cope 1869 – Russell: 139, 140; figs 8, 24a, 80

1995 *Mosasaurus hoffmanni* Mantell 1829 – Lingham-Soliar: 158, 161; figs 1, 3, 5, 6, 9, 11, 12, 14, 16

1997b *Mosasaurus maximus* Cope 1869 – Bell: 297–308, 310–318, 320, 321, 329–332

1998 *Mosasaurus hoffmanni* Mantell 1829 – Kuypers et al.: 25, fig. 9, pl. 1, figs 1–13; pl. 3, figs 3–10; pl. 9, figs. 1–12

(See also extensive bibliographies in Russell 1967, Kuhn 1972, Lingham-Soliar 1995)

Premaxilla – The premaxillae in mosasaurs are fused with no indication of a suture and are therefore mentioned here as one unit. The same goes for frontals and parietals (Russell 1967). The premaxillae of *Mosasaurus hoffmanni* and *M. maximus* were described in detail by Lingham-Soliar (1995) and Russell (1967), respectively. In both taxa, the premaxillary teeth are somewhat pointed in a forward direction and smaller than the average size of the maxillary teeth (Figure 3). There are no significant differences between the premaxillae of these taxa.

Russell (1967) noted that the premaxilla of *M. hoffmanni* is more acutely pointed, thereby referring to the specimen illustrated by Dollo (1882: pl. 4, figs 1–2), and probably to specimen NJSM 11053 of

Figure 3. 1 – *Mosasaurus maximus*, premaxilla NJSM 11053; 2 – *M. hoffmanni*, premaxillae NHMM 006696-48; A – right lateral view, B – ventral view. Scale bar equals 5 cm.

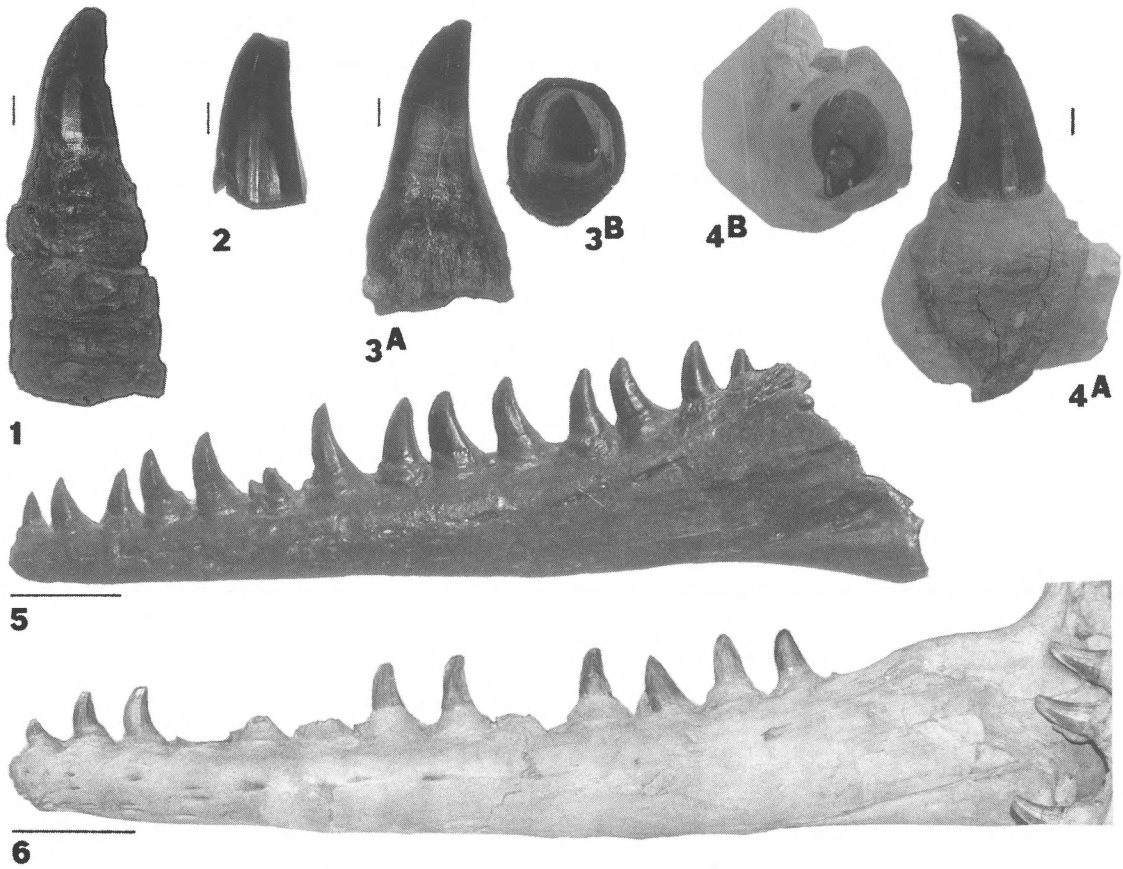

Figure 4. 1 – *Mosasaurus maximus*, tooth ANSP 8481; 2 – *M. maximus*, tooth ANSP 8507; 3 – *M. maximus*, tooth ANSP 8515; 4 – *M. hoffmanni*, tooth MND 20.01601; A – buccal view, B – occlusal view. Scale bar equals 10 mm; 5 – *M. maximus*, left dentary NJSM 11053, lateral view; 6 – *M. hoffmanni*, left dentary MNHNP AC 9648, lateral view. Scale bar equals 10 cm.

M. maximus. The shape of the premaxilla is, however, a matter of ontogeny (Kuypers et al. 1998), which means that an animal would develop a more robust structure during maturation. Actually, comparison of the premaxilla of the so-called Bemelen mosasaur (NHMM 006696-48: see Appendix 2) with that of *M. maximus* (NJSM 11053) contradicts Russell's observation (Figure 3).

Teeth – The teeth of *M. hoffmanni* were described in detail and illustrated by Lingham-Soliar (1995) and Kuypers et al. (1998). Teeth of *M. maximus* were described by Leidy (1865). In both taxa, the teeth are bicarinate, the posterior carina shifting from a lateral position in the anterior teeth to a more posterior position in the teeth further posteriorly along the tooth row, notably in the dentary (compare Lingham-Soliar 1995: fig. 15, with our Figure 4: 5–6). The prominence of the prisms on the surface of the tooth crowns shows intraspecific/ontogenetic variation to a comparable extent in both *M. hoffmanni* and *M. maximus* (Kuypers et al. 1998: pl. 1, figs 1–13; our Figure 4: 1–4). A mutual comparison of the original specimens has shown that the teeth are identical in both taxa.

Two identical casts of a tooth (BMNH 11590) are present in the BMNH collections. They are labelled *Mosasaurus dekayi*, while the original specimen, ANSP 8507 (Figure 4: 2), is labelled *M. maximus*.

Palatum – The palatum of *M. hoffmanni* has recently been described and illustrated by Lingham-Soliar (1995). The palata of *M. hoffmanni* and *M. maximus* show the same constriction from the vomers to the palatines, giving the internal nare openings an identical form (Figure 5: 1–3).

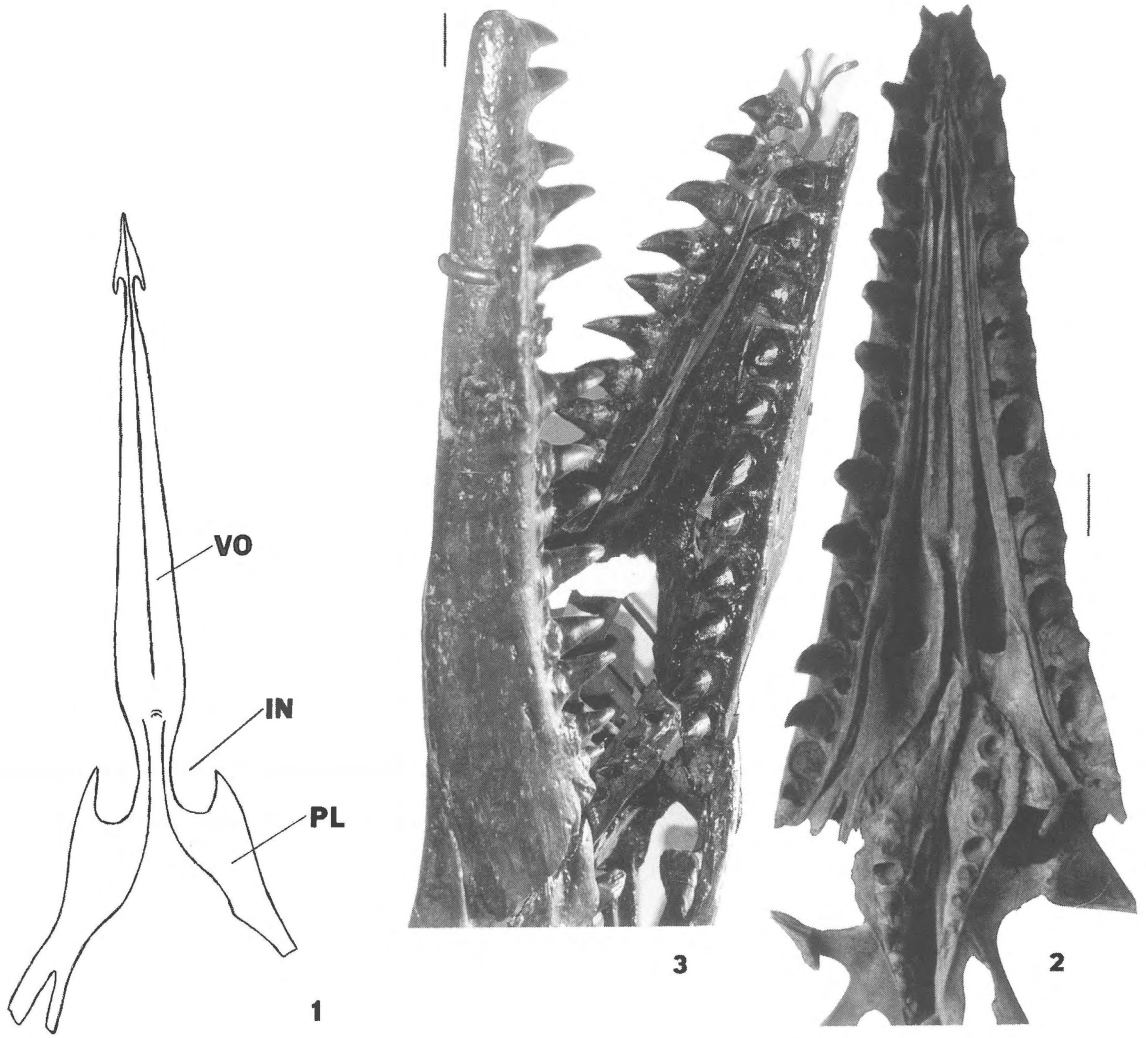

Figure 5. 1 – Palatal complex of *Mosasaurus hoffmanni*, based on IRScNB R12 (see Lingham-Soliar 1995: figs 3d, 4c; see also Appendix 3); 2 – *M. hoffmanni*, premaxillae, maxillae and palatal complex IRScNB R12, ventral view; 3 – *M. maximus*, premaxillae, maxillae and palatal complex NJSM 11053, ventrolateral view. Scale bar equals 5 cm.

Frontoparietal complex – The parietal in the genus *Mosasaurus* is covered anteriorly on either side of the midline by posterior protrusions from the frontal (Russell 1967; Bell 1997b: fig. 6). In both *M. hoffmanni* and *M. maximus*, this character is developed to exactly the same extent, as can be seen in BMNH 42929 (Figure 6) and NJSM 11052 (Figure 7): the 'frontal wings' reach equally beyond the parietal foramen in both specimens. Although the wings are partly worn in NJSM 11052, parietal dips indicate the original size of the frontal protrusions. Note in both specimens the sharp dorsolateral ridges of the parietal.

Suspensorium – The suspensorium is formed by the prootic-opisthotic-supratemporal unit (Figure 8: 2). This cranial complex was described and illustrated by Russell (1967), Welles & Gregg (1971) and Lingham-Soliar (1995). The suspensorium is identical in *M. hoffmanni* and *M. maximus*. The positions of the foramina for the seventh nerves with regard to the notches for the fifth nerves are the same (compare Lingham-Soliar 1995: fig. 13 with our Figure 8).

Posterior mandibular unit – The mosasaurid posterior mandibular unit was described by, among others, Russell (1967), Welles & Gregg (1971) and Lingham-

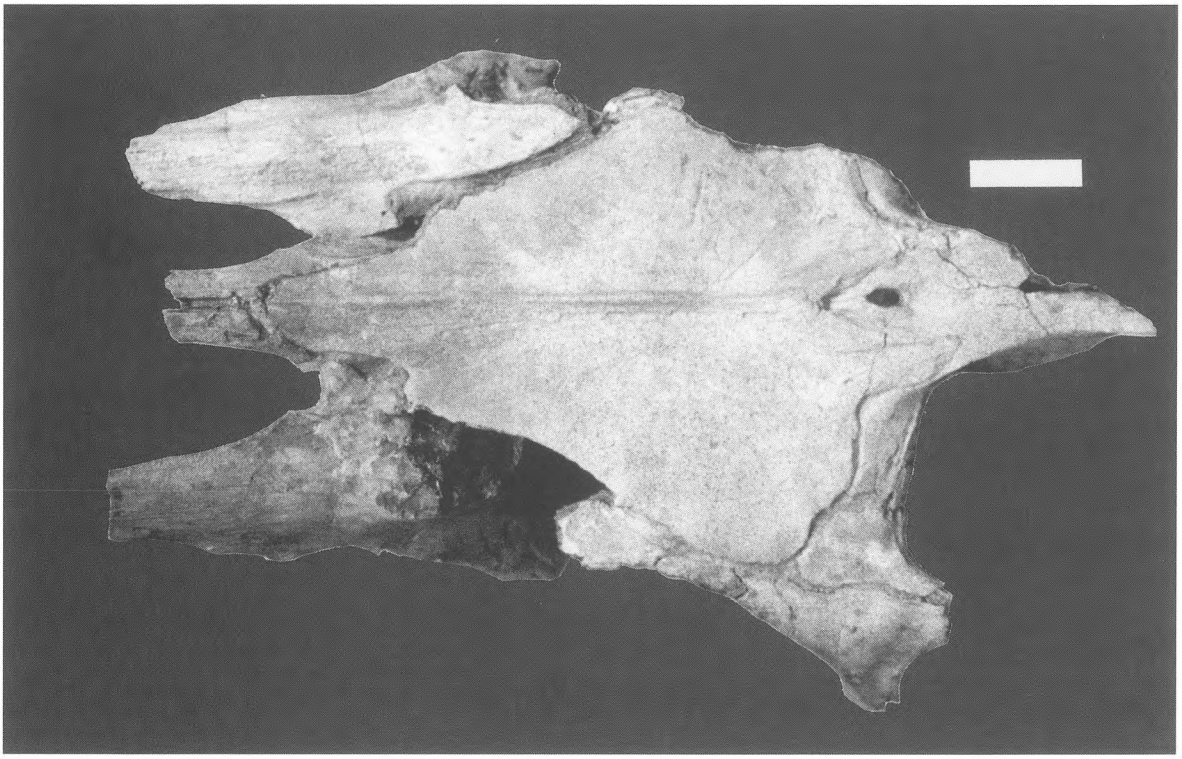

Figure 6. Mosasaurus hoffmanni, frontoparietal complex BMNH 42929, dorsal view. Scale bar equals 5 cm.

Figure 7. Mosasaurus maximus, frontoparietal complex NJSM 11052, dorsal view. Scale bar equals 5 cm.

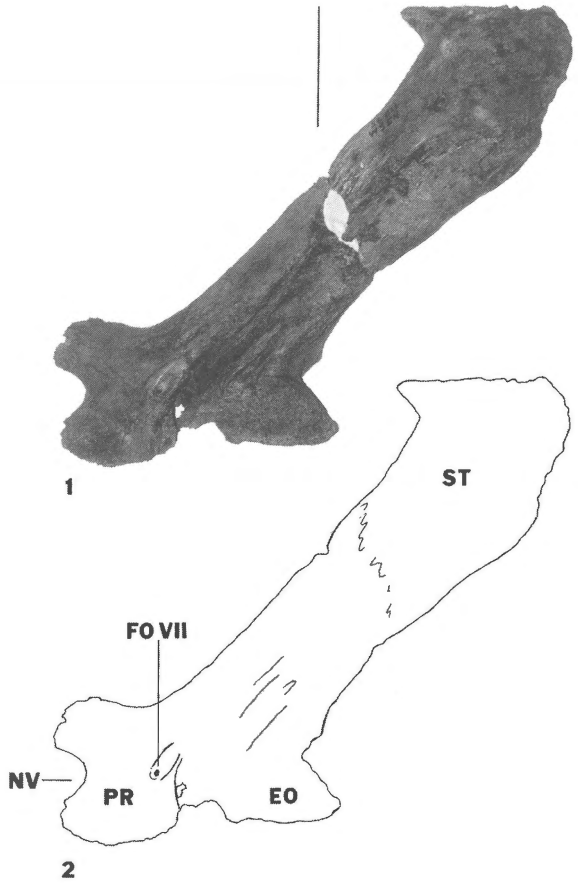

Figure 8. 1 – *Mosasaurus maximus*, left suspensorium NJSM 11895, ventrolateral view. Scale bar equals 5 cm; 2 – left suspensorium of *M. maximus/M. hoffmanni* (see Appendix 3).

Soliar (1995). These units are virtually identical in *M. hoffmanni* and *M. maximus*. In both taxa, their shape, notably the dorsal edge of surangulare, quadratal condyle and articulare (with retroarticular process) is identical (Figures 1–2). Although partly restored, the coronoideum of NJSM 11053 (*M. maximus*) allows comparison with the corresponding element in *M. hoffmanni*: these elements appear to be similar in both taxa. The angle formed by the dorsal edge varies between 65° and 68° (Figure 9).

Quadrates – Quadrates are the most diagnostic bones of the mosasaur skull (Welles & Gregg 1971). Mosasaurid quadratal features were shown by Bell (1997b). Descriptions and illustrations of the quadrates of *M. hoffmanni* and *M. maximus* were provided by Dollo (1890: pl. 8, figs 1, 3, 5, 7, 9, 11) and Cope

Figure 9. 1 – *Mosasaurus maximus*, left coronoid NJSM 11503, lateral view. Scale bar equals 10 cm; 2 – *M. hoffmanni*, left coronoid MNHNP AC 9648, lateral view.

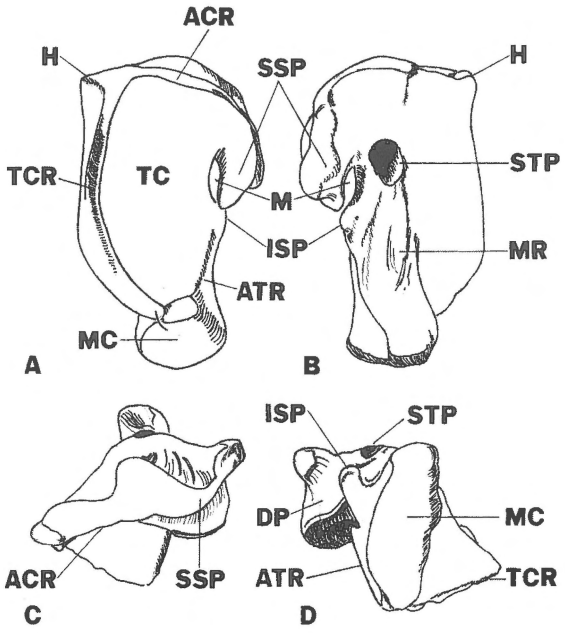

Figure 10. Quadrate of *Mosasaurus hoffmanni* (after Dollo 1890: pl. 8, figs 1, 3, 5, 7, altered; based on IRScNB EFR 27; see Appendix 3); A – lateral, B – medial, C – dorsal, D – ventral view.

(1871: fig. 48.1; 1875: pl. 37, figs 14–17), respectively (see Figure 10 for anatomy).

The following quadratal characters are found in both taxa. The main part of the quadrate is a robust vertical column (Russell 1967; Dollo 1890: fig. 11; our Figures 11: 1–2B and 12: 1–3B). Anteriorly, the shape of the quadrate is almost rectangular, with a small protrusion below midheight, close to the median ridge (Figure 11: 1–2D, 3–5). The suprastapedial process is well developed, with a prominent pit for the *m. depressor mandibulae* (Figures 11: 1A–C, 2A–B; 12; 14: 4B–C, 5B–C). The infrastapedial process is also well developed (Figure 11: 1A–C, 2A–B; Figure 12). In this context, the observation by Welles & Gregg (1971) of *M. maximus* having "extremely small suprastapedial and infrastapedial processes", is remarkable. From a dorsal view, the suprastapedial proces is constricted (Figures 13/1–4, 14/4–5a). The meatus is elliptical and vertically oriented. The stapedial pit is oval and very close to the meatus (Figure 11: 1c; Figure 12). The anterior wall of the meatus curves medially to the rim of the stapedial pit, forming the 'head' of the quadrate. The dorsal tympanic rim (alar crest) curves rather abruptly to the anterior tympanic rim (crest). A long, deep groove is present in the anterolateral edge of the ala (tympanic crest). A prominent posteroventral ascending tympanic rim is present. Its top is separated from the vertical shaft by a slit (Figure 11: 1A–B, 2A–B). Well-preserved specimens show that in both taxa, the mandibular condyles are equally convex (Figure 14: 1–3).

There are no essential differences between the quadrates of these taxa, but there may be ontogenetic differences. Even within a single skull, minor variations between both sides may exist. In an exceptionally well-preserved skull of *M. hoffmanni*, specimen IRScBN R12, described and illustrated by Lingham-Soliar (1995), the anterior tympanic rim in the left quadrate descends more abruptly to the mandibular condyle than in the right quadrate.

Russell (1967) suggested that *M. dekayi* and *M. maximus* might be conspecific. This view is supported by two fragmentary quadrates, present in AMNH, referred to as *M. dekayi*. They share all characteristics, as far as preserved, mentioned above (Figure 14: 4–5). The same goes for the quadrate AMNH 1392 of *M. oarthrus* (see Appendix 2).

Postcranial elements – No vertebrae studied by Kuypers et al. (1998) nor the specimens studied by myself show any significant differences between *M. hoffmanni* and *M. maximus* (e.g., Figure 16: 1–2; compare with Kuypers et al.'s fig. 3 and pl. 9, figs 8–10). They are virtually identical.

A metacarpal 1 (Figure 16: 5), specimen AMNH 14815, is identical with the specimen illustrated by Lingham-Soliar (1995: fig. 21).

Genus *Plioplatecarpus* Dollo 1882

Plioplatecarpus marshi Dollo 1882

1869	*Chelonia Hoffmanni* [sic] Gray 1831 – Winkler: pl. 9, fig. 25; pl. 14, fig. 49
1869b	*Mosasaurus depressus* Cope 1869: 16
1871	*Mosasaurus depressus* Cope 1869 – Cope: 196–197; fig. 48.3; pl. 9, fig. 6
1875	*Mosasaurus depressus* Cope 1869 – Cope: pl. 37, fig. 12a-c
1882	*Plioplatecarpus marshii* [sic] Dollo 1882: 64, pl. 5, figs 5–8; pl. 6
1967	*Plioplatecarpus depressus* (Cope) 1869 – Russell: 161, fig. 88
1994	*Plioplatecarpus marshi* Dollo 1882 – Lingham-Soliar: 180–181; figs 3–8, 9a, 10–15; pls 2–4

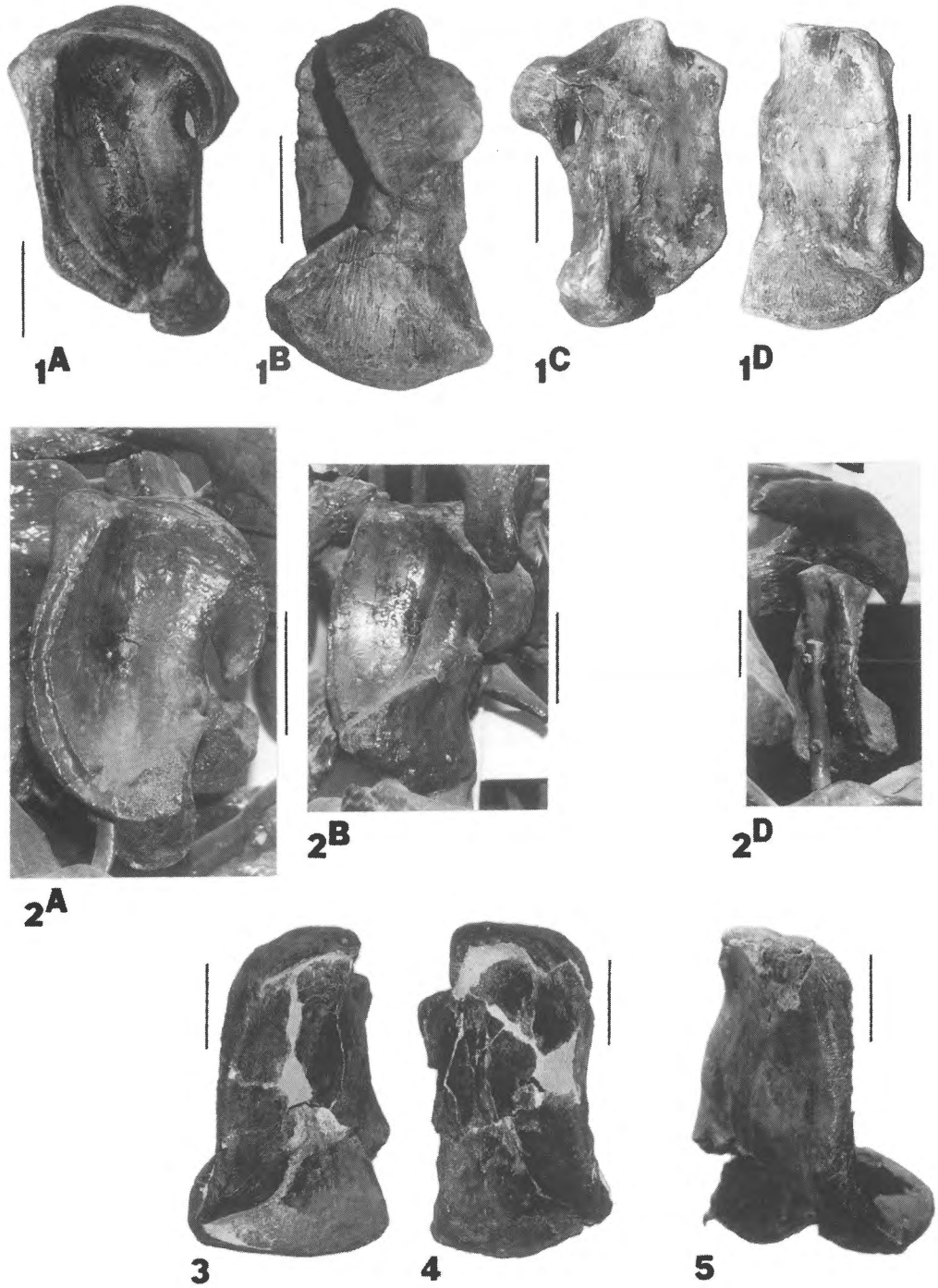

Figure 11. 1 – *Mosasaurus hoffmanni*, left quadrate MNHNP AC 9648; 2 – *M. maximus*, left quadrate NJSM 11503; A – lateral, B – posterior, C – medial, D – anterior view; 3 – *M. maximus*, right quadrate NJSM 11502, anterior view; 4 – *M. maximus*, left quadrate NJSM 11502, anterior view; 5 – *M. hoffmanni*, left quadrate NHMM 00696-02, anterior view. Scale bar equals 5 cm.

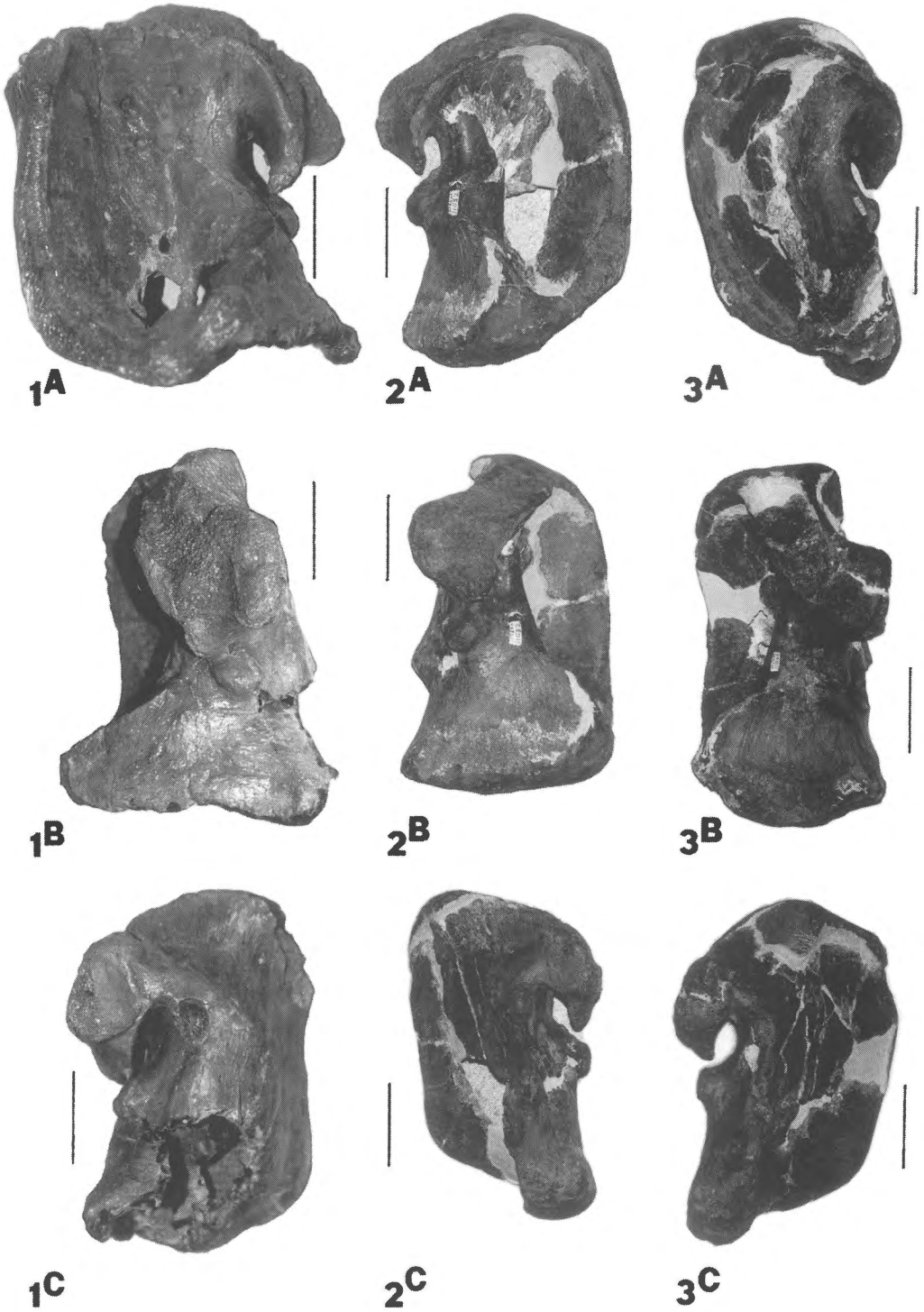

Figure 12. 1 – *Mosasaurus hoffmanni*, left quadrate NHMM 00696-02; 2 – *M. maximus*, right quadrate NJSM 11502; 3 – *M. maximus*, left quadrate NJSM 11502; A – lateral, B – posterior, C – medial view. Scale bar equals 5 cm.

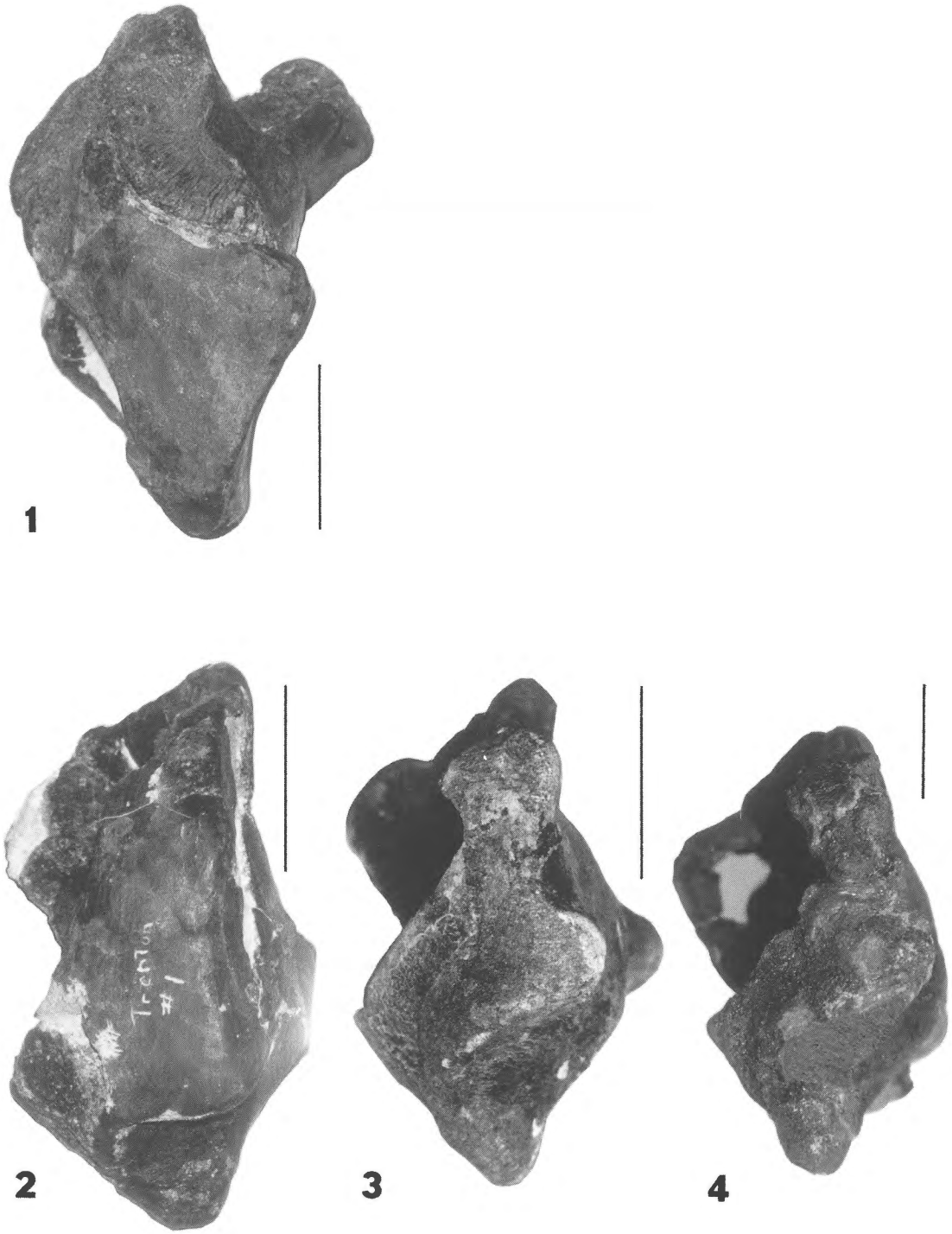

Figure 13. 1 – *Mosasaurus maximus*, right quadrate NJSM 11502; 2 – *M. maximus*, left quadrate NJSM 11502; 3 – *M. hoffmanni*, left quadrate MNHNP AC 9648; 4 – *M. hoffmanni*, left quadrate NHMM 00696-02. All figures show dorsal views. Scale bar equals 5 cm.

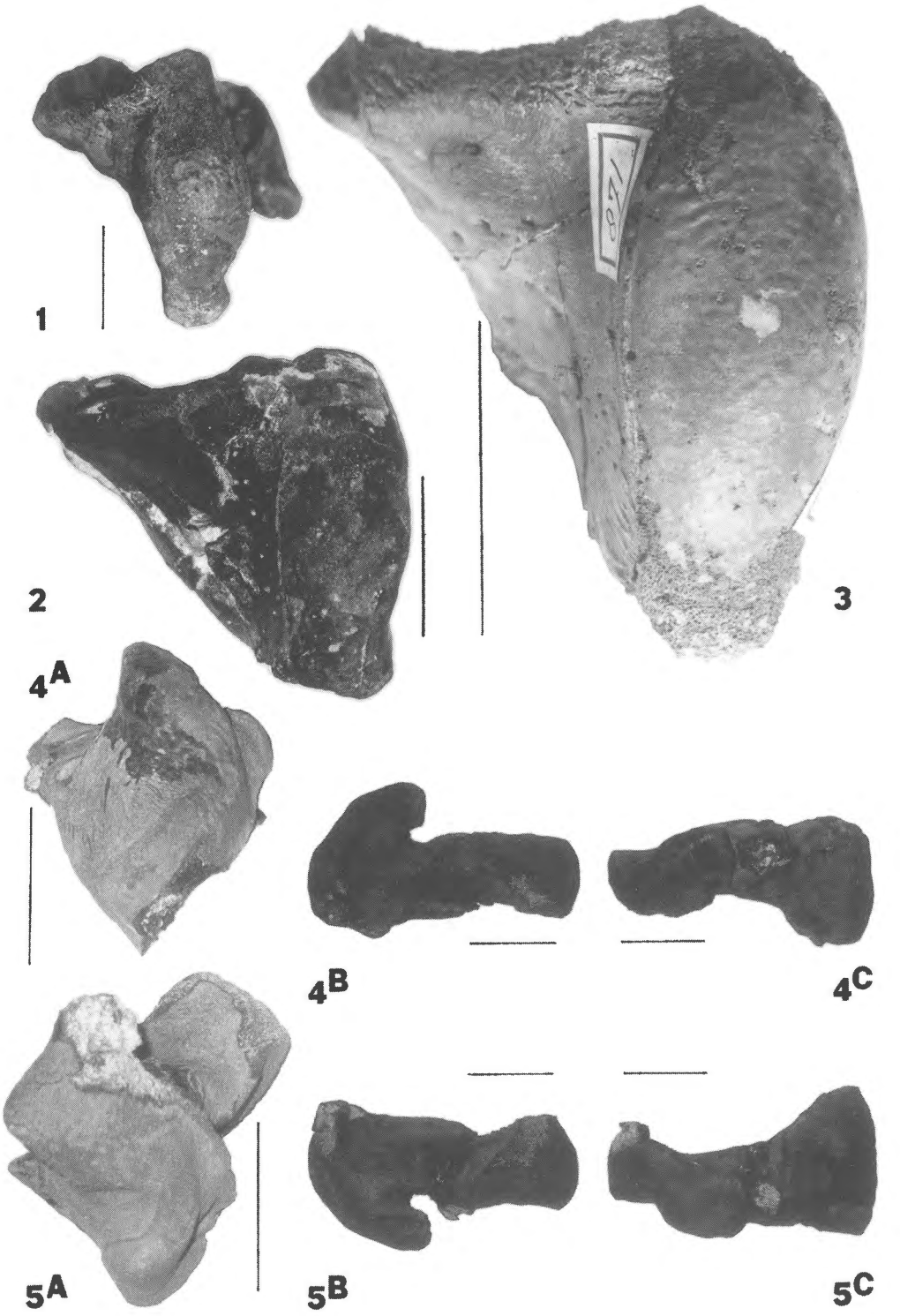

Figure 14. 1 – *Mosasaurus hoffmanni*, left quadrate MNHNP AC 9648; 2 – *M. maximus*, left quadrate NJSM 11503; 3 – *M. hoffmanni*, left quadrate TM 871, all ventral views; 4 – *M. dekayi*, left quadrate AMNH 1397; 5 – *M. dekayi*, right quadrate AMNH 1397; A – dorsal, B – lateral, C – posterior view. Scale bar equals 5 cm.

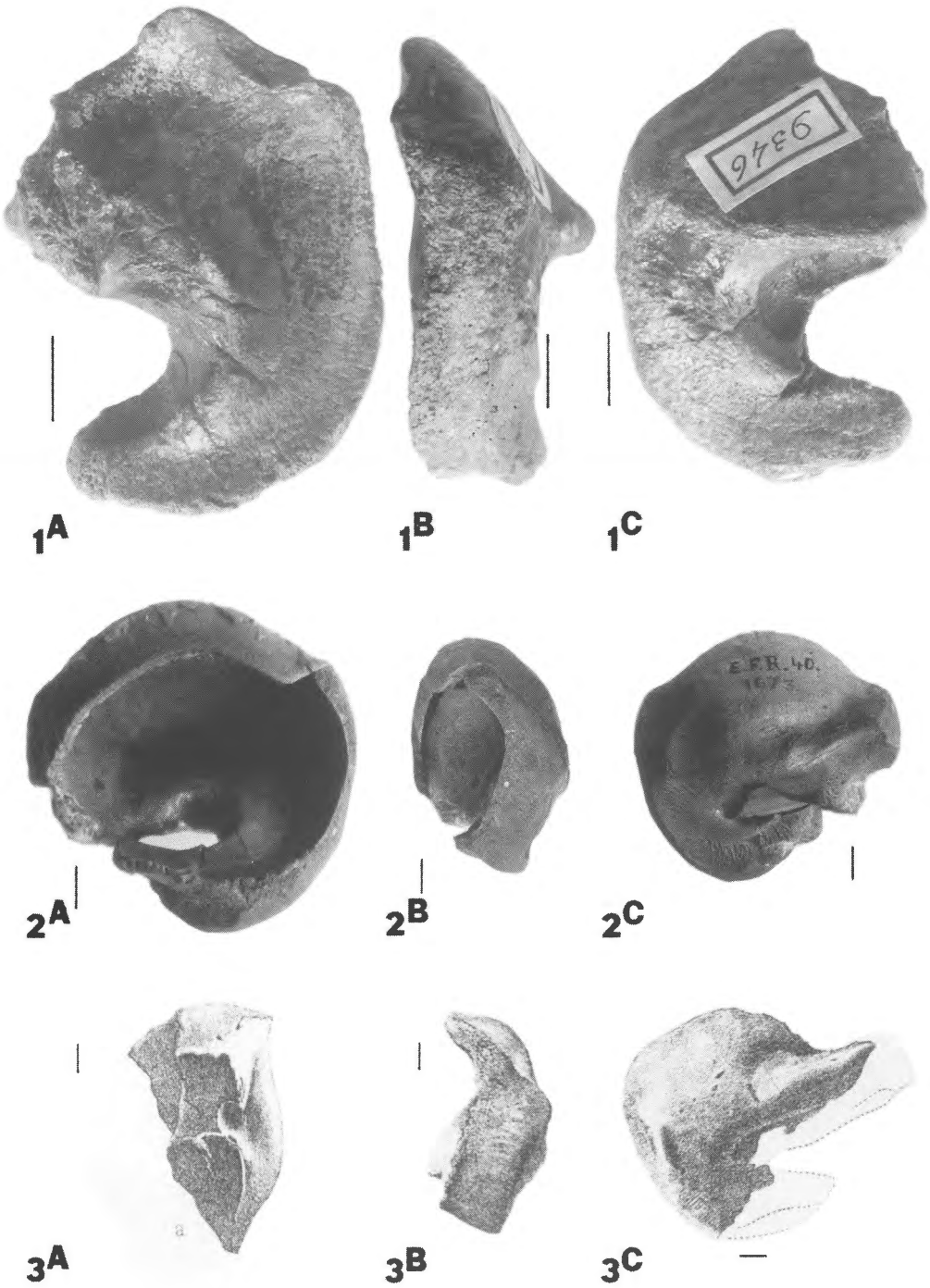

Figure 15. 1 – *Plioplatecarpus marshi*, left quadrate TM 9346; 2 – *P. marshi*, left quadrate IRSNB EFR 40; A – lateral, B – dorsal, C – medial view; 3 – *P. depressus*, copy of Cope's illustrations of left quadrate of lost type specimen (1875: pl. 37, figs 12); A – posterior, B -dorsal, C – medial view. Scale bar equals 10 mm.

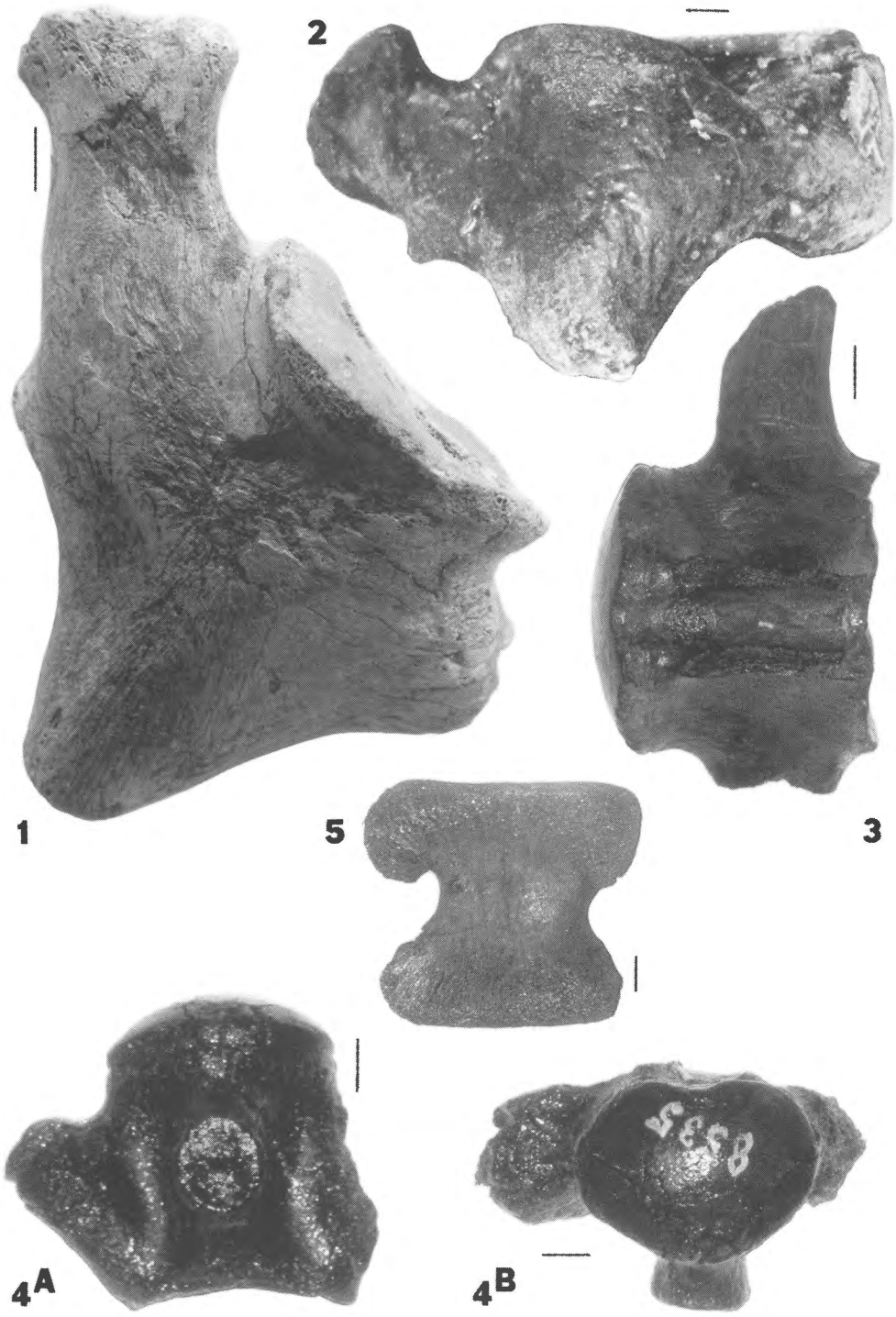

Figure 16. 1 – *Mosasaurus hoffmanni*, left atlantal arch and pleurocentrum TM 11214a, lateral view; 2 – *M. maximus*, left atlantal arch and pleurocentrum NJSM 11503, ventrolateral view; 3 – *M. maximus*, pygal vertebra ANSP 8529, dorsal view; 4 – *Plioplatecarpus depressus*, cervical vertebra ANSP 8535; A – ventral, B – posterior views; 5 – *M. maximus*(?), metacarpal 1, AMNH 14815. Scale bar equals 10 mm.

1998 *Plioplatecarpus marshi* Dollo 1882 – Kuypers et al.: 35, pl. 6, figs 1–11; pl. 8, figs 1–12

(See also extensive bibliographies in Russell 1967, Kuhn 1972, Lingham-Soliar 1994)

Quadrates – The type material of *P. depressus*, which comprised a quadrate (Cope 1871), has been lost (Gallagher 1993). Its original repository was the Academy of Natural Sciences, Philadelphia (Cope 1871). Fortunately, detailed drawings of the quadrate do exist (Cope 1871: fig. 48.3; Cope 1875: pl. 37, fig. 12a-c; our Figure 15: 3A–C). These illustrations show that the specimen was imperfect. Descriptions and illustrations of the quadrate of *P. marshi* were given by Dollo (1890: pl. 8, figs 2, 4, 6, 8, 10, 12) and Lingham-Soliar (1994). It can be deduced from Cope's drawings of *P. depressus* and the available data and material of *P. marshi* that both taxa share important quadratal characters.

The reniform stapedial pit lies almost in the meatus, which is large in relation to the quadratal size (Figure 15). A strongly developed median ridge is present from the stapedial pit downward (Figure 15: 1B–C, 2B–C, 3A–C). The dorsal articulating surface has a prominent angle medially, lying almost in line above the median ridge (Figure 15: 1B–C, 2B–C, 3B–C). The shape of the tympanic cavity (ala) is bulbous (Figure 15: 2B–C, 3B–C). The length of the quadrate is almost cut into a 3/2 ratio by the transversal plane, abutting the medial ridge (Figure 15: 2B–C).

Teeth – The teeth of *P. marshi* and *P. depressus* were described by Lingham-Soliar (1994), Kuypers et al. (1998) and Russell (1967). They show a wide range of variation. In the collections studied by myself, there are no teeth that could be assigned to *P. depressus* beyond doubt.

Postcranial elements – What is stated above for the vertebrae of *M. hoffmanni* and *M. maximus*, holds true also for *P. marshi* and *P. depressus* (compare Figure 16: 4A–B with Kuypers et al. 1998: pl. 8, figs 1–3).

Discussion

In comparing specimens of the various mosasaur taxa, it is important to study the original material, or good casts. As far as quadrates are concerned, such a comparison shows that a slight rotation of the specimen with regard to the medial plane may strongly affect the picture of the lateral view.

Regarding conspecificity, some of the previous authors may have based their observations exclusively on figures. This might explain why Russell (1967: 140) stated that the quadrates of *M. hoffmanni* and *M. maximus* were 'almost identical', whereas Lingham-Soliar (1995: 168) observed a 'striking contrast', notably with regard to the suprastapedial processes of the quadrates and the convexity of the mandibular condyles.

Conclusions

Because of the observed similarity between the compared cranial elements of *Mosasaurus hoffmanni* and *M. maximus*, it is concluded that these taxa are conspecific, the former name having priority.

Because of the similarity between the quadrate of *Plioplatecarpus marshi* and the surviving illustrations of the quadrate of the type specimen of *P. depressus*, it is concluded that these taxa are conspecific as well. Although *P. depressus* is the oldest name, it is proposed here to give priority to the former name, since *P. marshi* is very well documented by diagnostic material and *P. depressus* is not. An application for this proposal will be submitted to ICZN.

Thus, marine deposits of latest Cretaceous age in New Jersey and the Maastrichtian type area share common mosasaur taxa. To consider mosasaurs as endemic species, as implied for *M. hoffmanni* by Lingham-Soliar (1995), does not appear to be necessary. These tetrapods, being highly adapted to a marine life, could cross the then narrow northern Atlantic Ocean. These migrations may have been stimulated by an ocean-current pattern, such as suggested by Windley (1977). These patterns have affected the distributions of other marine vertebrates as well, among others those of the open-water crow shark *Squalicorax pristodontus* (Agassiz 1843), the angel shark *Squatina hassei* Leriche 1929 and thoracosaurine crocodiles (Gallagher 1993; Bardet et al. 1998; Mulder 1998). Marine invertebrates have been influenced as well, among them ostracods (Bless 1991) and ammonites (*Jeletzkytes dorfi* Landman & Waage 1993 and *Trachybaculites columna*; see Landman & Waage 1993; Jagt & Kennedy 1994; Cobban & Kennedy 1995; Kennedy & Jagt 1998).

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Appendix 1: Abbreviations used to denote repositories of specimens referred to in the text

AMNH	American Museum of Natural History (New York)
ANSP	Academy of Natural Sciences (Philadelphia)
BMNH	Natural History Museum (London)
IRScNB	Institut Royal des Sciences Naturelles de Belgique (Bruxelles)
MNHNP	Musée National d'Histoire Naturelle, Laboratoire de Paléontologie (Paris)
MND	Museum Natura Docet (Denekamp)
NHMM	Natuurhistorisch Museum Maastricht (Maastricht)
NJSM	New Jersey State Museum (Trenton)
TM	Teylers Museum (Paleontologisch Kabinet) (Haarlem)

Appendix 2: List of specimens studied

AMNH 1397	*Mosasaurus dekayi*, left and right quadrate, Greensand, Holmdel, Monmouth Co., New Jersey, Maastrichtian, *ex* Cope Colln
AMNH 1388	*Mosasaurus dekayi*, several dorsal and caudal vertebrae, New Jersey, Maastrichtian
AMNH 2393	*Mosasaurus dekayi*, several dorsal and caudal vertebrae, New Jersey, Maastrichtian
AMNH 14815	*Mosasaurus maximus*(?), 'metapodial' (metacarpal 1), ?Sewell, Gloucester Co., New Jersey, Maastrichtian, *ex* Cope Colln
AMNH 1392	*Mosasaurus oarthrus* (type material), fragmentary left quadrate, Barnsboro, Gloucester Co., New Jersey, Maastrichtian (illustrated by Cope 1875: pl. 37, fig. 17)
ANSP 8481	*Mosasaurus maximus*, tooth, Monmouth Co., New Jersey, Maastrichtian (illustrated by Leidy 1865: pl. 9, fig. 6)

ANSP 8507	*Mosasaurus maximus*, tooth, Woodbury, Gloucester Co., New Jersey, Maastrichtian (illustrated by Leidy 1865: pl. 10, fig. 3)
ANSP 8515	*Mosasaurus maximus*, tooth, Lumberton, New Jersey, Maastrichtian
ANSP 8529	*Mosasaurus maximus*, pygal vertebra, Burlington Co., New Jersey, Maastrichtian
ANSP 8535	*Plioplatecarpus depressus*, cervical vertebra, Monmouth Co., New Jersey, Maastrichtian (illustrated by Leidy 1865: pl. 7, figs 2, 3)
ANSP 20184	*Plioplatecarpus depressus*, two casts of tooth, Inversand Company Pit, Sewell, Gloucester Co., New Jersey, Maastrichtian (lower Hornerstown Formation, Main Fossiliferous Layer), collected by D.C. Parris, donated 1993
ANSP 20185	*Plioplatecarpus depressus*, cast of tooth (data: see ANSP 20184)
BMNH 42929	*Mosasaurus hoffmanni*, frontal with prefrontals, left postorbitofrontal and anterior part of parietal, Maastrichtian type area, *ex* Van Breda Colln
BMNH 11590	*Mosasaurus dekayi*, 2 casts of teeth, New Jersey (illustrated by Leidy 1865: pl. 10, fig. 3)
IRScNB R12	*Mosasaurus hoffmanni*, very well-preserved skull (Lingham-Soliar, 1995), Zichen, Late Maastrichtian (Maastricht Formation)
IRScNB EFR27	*Mosasaurus hoffmanni*, left quadrate, Kanne, Late Maastrichtian (Maastricht Formation; described and illustrated by Dollo 1890: pl. 8, figs 1, 3, 5, 7, 9, 11)
IRScNB EFR40	*Plioplatecarpus marshi*, left quadrate, Kanne, Late Maastrichtian (Maastricht Formation; described and illustrated by Dollo 1890: pl. 8, figs 2, 4, 6, 8, 10, 12)
MNHNP AC9648	*Mosasaurus hoffmanni*, type specimen (Rompen 1995; Felder & Jagt 1998): disarticulated, incomplete skull, vertebrae and a femur in matrix, St. Pietersberg, Maastricht, Late Maastrichtian (Nekum Member, Maastricht Formation)
MND 20.01601	*Mosasaurus hoffmanni*, tooth in matrix, St Pietersberg, Maastricht, Late Maastrichtian (Nekum Member, Maastricht Formation)
NHMM 006696	*Mosasaurus hoffmanni*, 'Bemelen mosasaur' (Kruytzer 1957; Kuypers et al. 1998): cranial and postcranial elements of one specimen: -02: left quadrate, lateral and medial condyle missing, -48: premaxilla, Ankerpoort-Nekami Quarry, Bemelen, Late Maastrichtian (Nekum Member, Maastricht Formation)
NJSM 11053	*Mosasaurus maximus*, mounted skull with articulated cervical vertebrae on display in NJSM, Inversand Comp. Pit, Sewell, Gloucester Co., New Jersey, Maastrichtian (upper Navesink Formation)
NJSM 11052	*Mosasaurus maximus*, disarticulated skull, same provenance as NJSM 11053
NJSM 11895	*Mosasaurus maxius*, left suspensorium: prootic-opisthotic-exoccipital-supratemporal unit, Inversand Comp. Pit, Sewell, Gloucester Co., New Jersey, Maastrichtian (lower Hornerstown Formation, Main Fossiliferous Layer)
TM 11214a	right annular part of atlas of *Mosasaurus hoffmanni*, Maastrichtian type area, *ex* Hoffmann Colln, via P. Camper Colln
TM 5214	upper part of left quadrate of *Mosasaurus hoffmanni*, Maastrichtian type area, *ex* Henckelius Colln
TM 871	lower part of left quadrate of *Mosasaurus hoffmanni*, Maastrichtian type area, *ex* Henckelius Colln (TM 5214 and TM 871 fit and are parts of the same quadrate)
TM 9346	upper part of left quadrate of *Plioplatecarpus marshi*, Maastrichtian type area, *ex* Henckelius Colln (illustrated by Winkler 1869: pl. 9, fig. 25)

Appendix 3: Osteological abbreviations

acr	alar crest
atr	posteroventral ascending tympanic rim
dp	pit for depressor mandibulae
eo	exoccipital
fo VII	foramen for nerve VII
h	head
in	internal naris
isp	infrastapedial process
mc	mandibular condyle
m	meatus
mr	median ridge
n V	notch for nerve V
pl	palatine
pro	prootic
ssp	suprastapedial process
st	supratemporale
stp	stapedial pit
tc	tympanic cavity (ala)
tcr	tympanic crest
vo	vomer

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