

Co-ossified vertebrae of mosasaurs and cetaceans: implications for the mode of locomotion of extinct marine reptiles

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Abstract.—Co-ossified pygal and caudal vertebrae in Late Cretaceous mosasaurs from the southeast Netherlands, northeast Belgium, and North America are compared with lumbar and caudal vertebrae from fossil and extant whales. Both infectious spondylitis and idiopathic vertebral hyperostosis afflicted these marine tetrapods. The causes of the infectious disease and of the idiopathic disease are similar in the compared life forms. The location of idiopathic hyperostosis along the vertebral column implicates axial locomotion in mosasaurs, as in whales.

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Introduction

Partout où il y a eu vie, il y a eu aussi maladie; la souffrance d'une créature secondaire est un trait de ressemblance de plus avec les créatures actuelles.

Gaudry 1890

Fossils may be of particular interest when they reveal extra information about lifestyle and habitat, predator patterns, and comparative physiology in addition to data on anatomy. This may occur when the consequences of diseases or injuries are documented in these ancient remains.

Paleopathological phenomena are also known from Mesozoic mosasaurs, marine squamates that inhabited the Late Cretaceous oceans and marginal seas worldwide (Fig. 1) (Williston 1904; deBraga and Carroll 1993; Bell 1997). In this paper, I discuss co-ossified (fused) mosasaurid vertebrae from the Maastrichtian type area in the southeast Netherlands and northeast Belgium and compare them with such vertebrae from North America. I also compare these vertebrae with those of fossil and extant whales, because in extant representatives of these marine tetrapods the occurrence of abnormal, co-ossified vertebrae is well recorded (Klima 1992, 1996). Vertebral fusions may develop from injuries, infection, or congenital defects (Tanke and Rothschild 1997) and are referred to as infectious spon-

dylitis whenever they are caused by infections.

Co-ossified mosasaurid vertebrae have been recorded from the Late Cretaceous Niobrara Chalk of Kansas. Martin and Rothschild (1989) described a remarkable juvenile specimen of *Platecarpus* suffering from infectious spondylitis, which resulted in a fusion of seven caudal vertebrae. The infection was evidently initiated by a shark bite, because the tip of a shark tooth is surrounded by an irregular deposition of bone in one of the vertebrae.

From the Late Cretaceous Pierre Shale Formation in South Dakota, Martin and Bell (1995) reported three examples of "club-tailed" mosasaurs, two of which were described. In one juvenile mosasaurine, probably *Clidastes*, seven caudal vertebrae are fused. The other case concerns a juvenile plioplatecarpine, in which three caudal vertebrae are fused.

Although Williston (1904: p. 49) suggested that the many cases of "hyperostosal mutilations of ante mortem origin" indicated that mosasaurs had hostile encounters throughout their lives, Martin and Bell (1995: p. 27) stated that all known "club-tailed" mosasaurs with fused caudal vertebrae were juveniles. Most of these specimens document cases of predation followed by infectious spondylitis, as illustrated in the example described by Martin and Rothschild (1989).

Nonpathologic vertebral fusions, which oc-

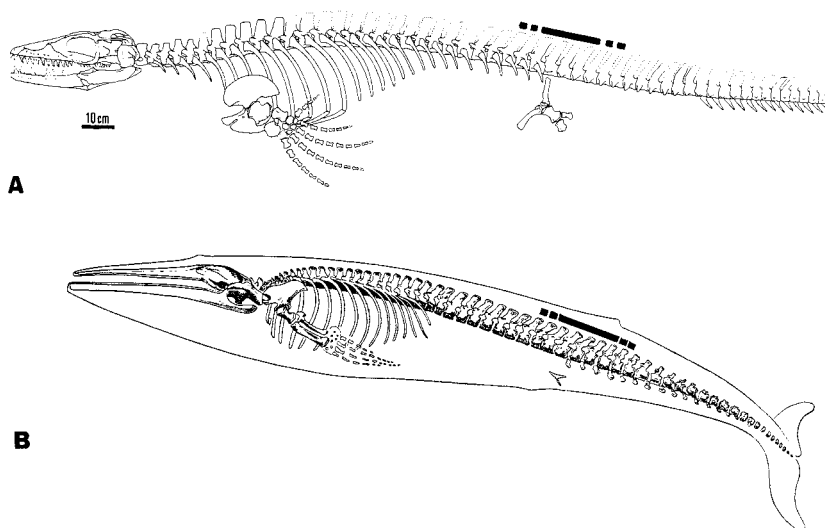


FIGURE 1. Marine tetrapods. A, A Late Cretaceous marine squamate, the mosasaur *Plioplatecarpus primaevus* (after Holmes 1996: Fig. 1; with permission). B, An extant cetacean, the blue whale *Balaenoptera musculus* (after Slijper 1958: Fig. 21, partly; not to scale). Note the area in which ligamentous ossification has been observed in mosasaurs and whales, and that both taxa are characterized by tail-propelled locomotion.

cur by ligamentous ossification, are examples of diffuse idiopathic skeletal hyperostosis (DISH). This is a commonly observed pathology and is not actually a disease but acts to strengthen the back at a structurally weak or stressed point (Tanke and Rothschild 1997: pp. 527–528). It has been observed in the literature that vertebral fusion in whales may be the result of either DISH or infectious spondylitis. Kompanje (1993, 1995, 1999) discussed these types of disease, which are both characterized by hyperostosis: an abnormal excessive bone deposition. The difference between DISH and infectious spondylitis can easily be recognized. In the latter a significant distortion of bony architecture is produced (Tanke and Rothschild 1997).

It is well documented that in whales age-related vertebral fusion as a result of ligamentous ossification (DISH) is related to life habit; the vertebrae and intervertebral disks are subject to a type of constant strain that does not occur in other large tetrapods. Whales use axial locomotion to swim (Klima 1992, 1996; Kompanje 1993), and tail-propelled locomotion involves the vertebral column in the transition zone of lumbar to anterior caudal vertebrae. It is particularly in these vertebrae that

DISH in whales mostly occurs (Klima 1992) (Fig. 1). DISH has also been documented in whale fossils, an example being an affected large but incomplete lumbar vertebra of the Miocene balaenopterid whale *Plesiocetus durinanus* (Cope 1896) found near Liessel (Province of Noord-Brabant, the Netherlands) (Fraaye and Fraaye 1995; Bol 2000; R. H. B. Fraaye personal communication 1999) (see Fig. 5:2). For a description of the vertebra, see Appendix 1 under item OMGP.

From the Maastrichtian type area, both infectious and nonpathologic fusions of mosasaurid vertebrae are recorded. The latter turn out to have implications for the mode of locomotion in mosasaurs, as they do in whales.

Records from the Maastrichtian Type Area

Abbreviations for institutions are as follows. IRScNB: Institut Royal des Sciences Naturelles de Belgique, Bruxelles; MND: Museum Natura Docet, Denekamp; MNHNP: Muséum National d'Histoire Naturelle, Laboratoire de Paléontologie, Paris; OMGP: Oertijdmuseum De Groene Poort, Boxtel.

Co-ossified vertebrae in mosasaurs were noted from the Maastrichtian type area as early as the nineteenth century. In his very first

paper on Late Cretaceous marine squamates from the Maastrichtian type area, Dollo (1882) described the then new genus and species of mosasaur, *Plioplatecarpus marshi*, based on two incomplete skeletons (IRScNB 1496, 1497 [Appendix 1]). One of the characters Dollo considered diagnostic was a "sacrum" composed of two fused pygal vertebrae (Dollo 1882; Meijer 1985) (Fig. 2). Subsequently, Dollo (1885, 1890) defined the family Plioplatecarpidae on this character. In the years that followed, however, it became clear that he had been the victim of coincidental circumstance, in that in both skeletons this supposed "sacrum" was located in the same pygal area (Dollo 1882: p. 63). In 1892, Dollo realized he had erred. At that time he had twelve specimens at his disposal, and it turned out that fused (pygal) vertebrae in *Plioplatecarpus* were an exception rather than the rule.

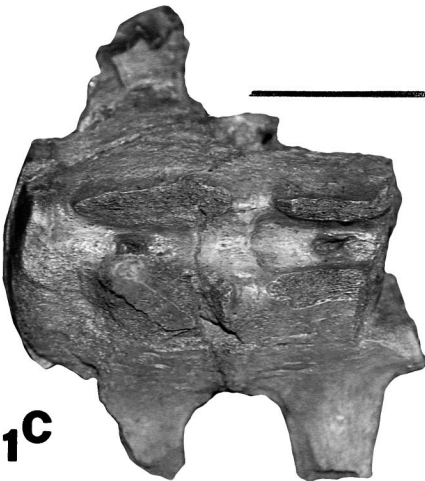
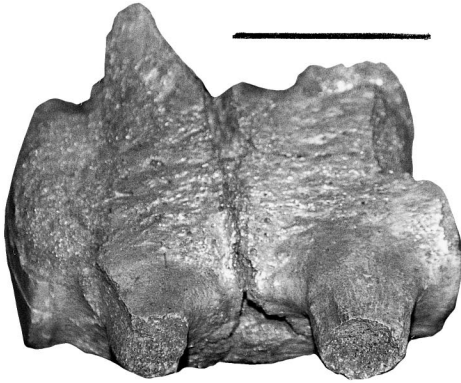
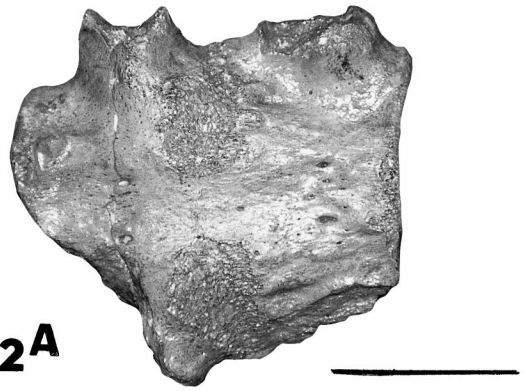
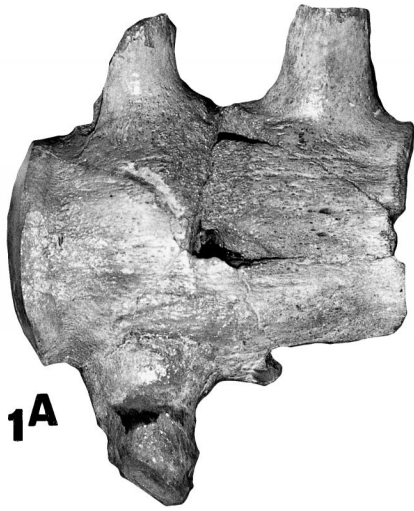
Almost a decade later than Dollo, Gaudry (1890: p. 205, Fig. 300) (see also Fig. 3) described, from the "Craie de Maëstricht (Hollande)," a substantial portion of a vertebral column of *Plioplatecarpus marshi* Dollo 1882, which, according to him, comprised 93 articulated vertebrae (26 lumbar and 67 caudals) with a total length of 3.74 m. He referred this specimen to *Mosasaurus camperi* Von Meyer 1832 (Appendix 1) and illustrated part of it, comprising 46 vertebrae. In two separate clusters, this specimen reveals fused caudal vertebrae, in Gaudry's view affected by suppurating periostitis (= infectious spondylitis in present terminology). In the anterior fusion, six vertebrae are involved, and the more posterior cluster has three. This specimen was illustrated and briefly described by Boule and Piveteau (1935: Fig. 769) and there referred to *M. giganteus* (Sömmering 1820) (Appendix 1), although rectangular foramina on the dorsal sides of the centra and articulating hemapophyses show it to be *Plioplatecarpus*. It is housed in the Laboratoire de Paléontologie des Vertébrés of the Muséum National

d'Histoire Naturelle in Paris (MNHN AC 9649-9775, 9776 [Appendix 1]). The two clusters of fused caudal vertebrae show signs of infectious spondylitis, similar to the conditions in the South Dakota material: abnormal excessive bone deposition and significant distortion of bony architecture. In Gaudry's specimen there are large intracentral cavities and canals, forming a system with openings at the lateral and ventral sides of the clusters involved (Fig. 3B–D,F). These were sites of severe inflammations, a conclusion already drawn by Gaudry (1890). Both clusters have a very irregular surface; the abnormal spongiform bone formation is highly developed, resulting in a clublike appearance. The process has even affected the neural arches (Fig. 3E) and the position of the hemapophyses. This is visible in the positioning of the articulation surfaces on the ventral sides of the fused centra (Fig. 3G). The excessive hyperostosis ultimately resulted in a compensation for the loss of bone tissue by suppuration in the vertebral centra.

Much more recently, Mulder (1985: Figs. 1, 2) illustrated two fused mosasaurid pygal vertebrae (MND 20.01.842), in addition to a mosasaurid dorsal vertebra (MND 20.01.826) revealing infectious reactive new bone (Figs. 4, 5.1). These specimens were collected from the late Maastrichtian as exposed at the Ankerpoort-'t Rooth (formerly Nekami) Quarry, Bemelen, The Netherlands. They are in the Museum Natura Docet Collections (*ex De Heer Colln*) and are assigned to *Plioplatecarpus marshi* because the dorsal vertebra (MND 20.01.826) shows the typical reniform articulation surfaces and one large rectangular foramen on the centrum right in the middle of the bottom of the neural canal. The same goes for the fused pygal vertebrae in MND 20.01.842 (for comparison see Kuypers et al. 1998: p. 41, Plate 8: Figs. 5–7).

MND 20.01.842 (Fig. 4) closely resembles the fused vertebrae IRSNB 1496^F and 1497^{HH}

FIGURE 2. *Plioplatecarpus marshi*, pygal vertebrae fused by ligamentous ossification. Specimens IRScNB 1496^F (1) and IRScNB 1497^{HH} (2) (compare Dollo 1882: Plate 5: Figs 5, 6). A, Ventral view. B, Right lateral view. C, Dorsal view. Scale bar, 5 cm.



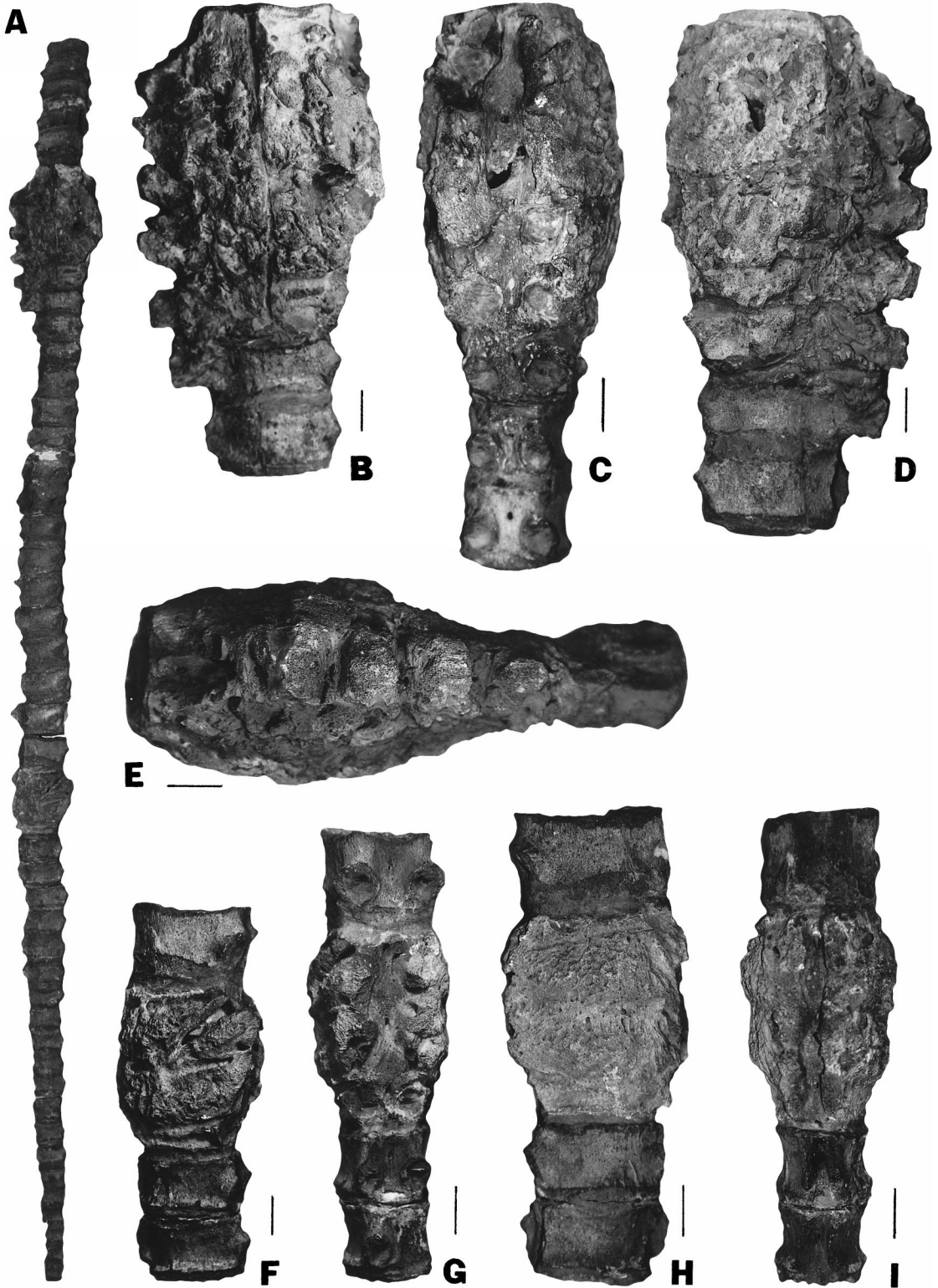


FIGURE 3. *Plioplatecarpus marshi*, tail with two clusters of vertebrae MNHNP AC 9649-9775/9776, fused by infectious spondylitis, length 113 cm (A); anterior cluster comprising six vertebrae (B–E); and posterior cluster comprising three vertebrae (F–I). A, Right lateral view (compare Gaudry 1890: Fig. 300). B, F, Right lateral view. C, G, Ventral view. D, H, Left lateral view. E, I, Dorsal view. Scale bar, 2 cm.

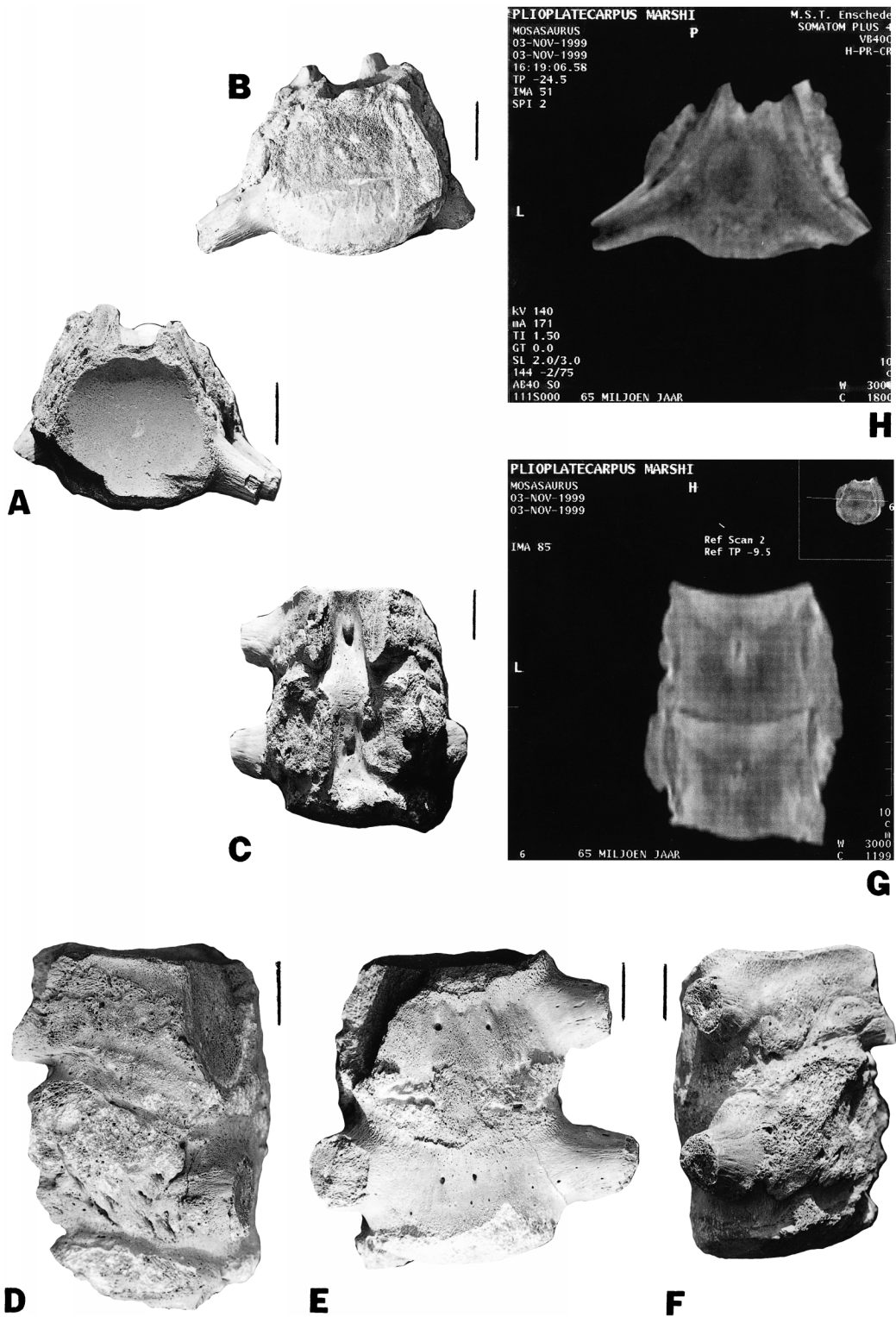


FIGURE 4. *Plioplatecarpus marshi*, pygal vertebrae MND 20.01.842 fused by ligamentous ossification. Anterior (A), posterior (B), dorsal (C), right lateral (D), ventral (E), and left lateral (F) views. Coronal (G) and transverse (H) CAT scans. Scale bar, 2 cm.

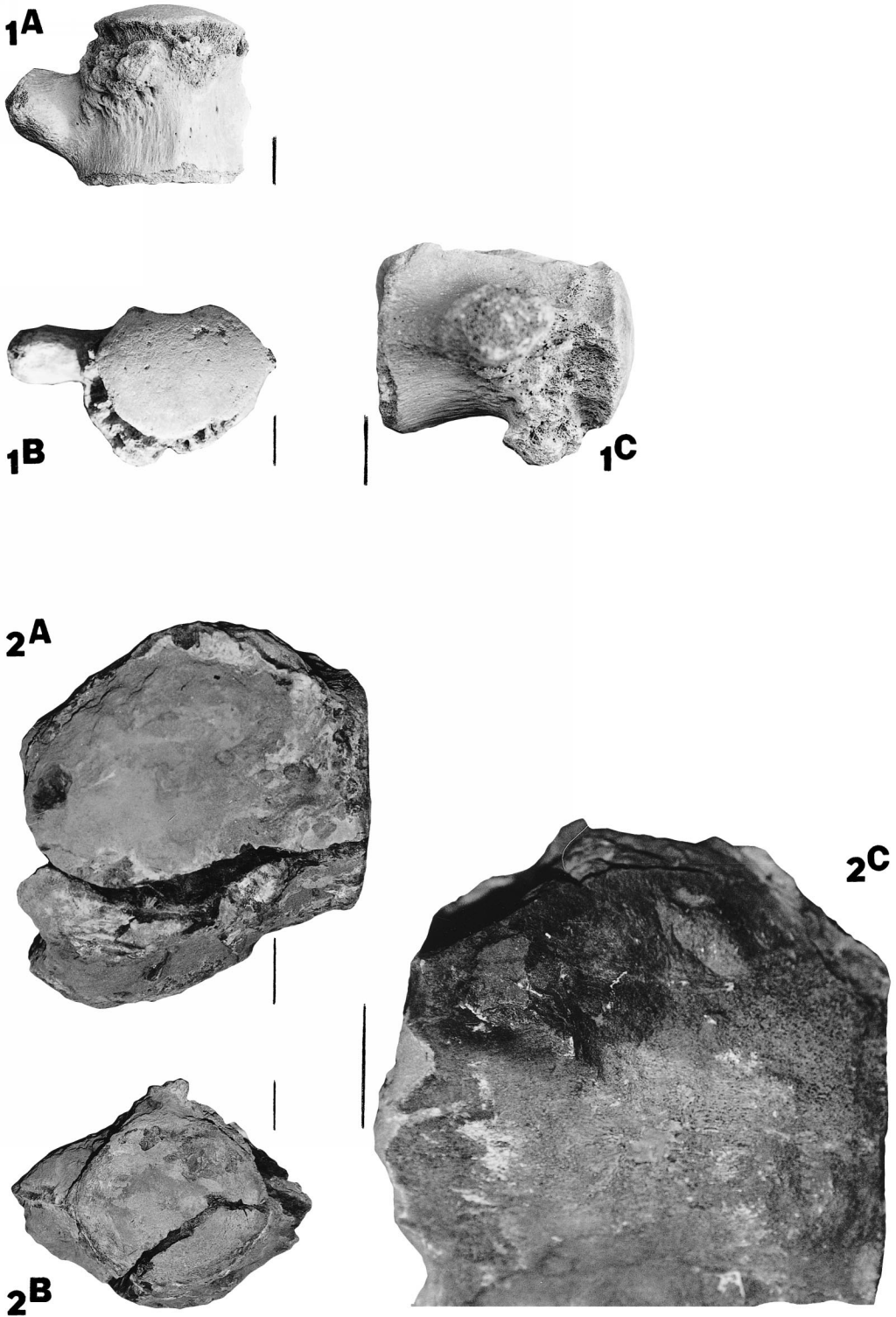


FIGURE 5. *Plioplatecarpus marshi*, dorsal vertebra MND 20.01.826 with an infectious reactive new bone formation (1). A, Ventral view. B, Posterior view. C, Left lateral view. Scale bar, 2 cm. *Plesiocetus durinasus*, balaenopterid whale, fragment of large lumbar vertebra OMGP (unnumbered) affected by ligamentous ossification (2). A, Left ventrolateral view. B, Anterior view. C, Sagittal section, showing normal bone structure. Scale bar, 5 cm.

described and illustrated by Dollo (1882). It appears that MND 20.01.842 originally comprised at least three vertebrae (Fig. 4B,D), in which the centra were fused by an abnormal irregular and crusty bone deposit. This hyperostosis is prominent on both sides of the vertebrae (Fig. 4D,F). Nutritive foramina are visible on the surface of this aberrant bone structure. In MND 20.01.842 the hyperostosis is more strongly developed than in IRSNB 1496^F and 1497^{HH}. CAT scans (Fig. 4G,H) of specimen MND 20.01.842, however, show that the fusion of the vertebrae has not proceeded internally. The articular surfaces are still distinct and there is no distortion of the internal bone structure. This means that, in contrast to the specimen described by Gaudry (1890) and the North American records, these vertebrae were not affected by infectious spondylitis. On the basis of their size the specimens described by Dollo (1882) and those in the Museum Natura Docet collections are of large animals, as was already pointed out above for Gaudry's specimen (Appendix 2).

Remarkably, all nonpathologic co-ossified pygal vertebrae described and illustrated from the Maastrichtian type area originally had a similar position in the vertebral column (Fig. 1). In view of this anatomical aspect, and the facts that (1) the articular surfaces of the centra are internally distinct, (2) there is no sign of distortion of bony architecture, and (3) evidence for infection is lacking, I conclude that these pygal vertebrae display ligamentous ossification, not infectious spondylitis. As stated above, the latter disease, which can be observed in the co-ossified caudal vertebrae described and illustrated by Gaudry (1890), is associated with all of these characteristics.

Discussion

It appears that both infectious spondylitis and ligamentous ossification along vertebrae occurred in mosasaurs, as they do in extant cetaceans (Klima 1992, 1996; Kompanje 1993, 1995, 1999; see also Introduction here). Infectious spondylitis in mosasaurs could be initiated by a predator attack, as Martin and Rothschild (1989) noted. Of course juvenile mosasaurs suffered most from predation pres-

sure, which explains the many records of juvenile "club-tailed" specimens (Martin and Bell 1995). In addition to sharks, predators of mosasaurs probably included other mosasaurs, meaning that even large animals were threatened. This could explain the infectious spondylitis in the specimen described by Gaudry (1890). If this animal was indeed attacked, it probably was bitten more than once, resulting in two clusters of affected caudal vertebrae.

The nonpathologic fusion of mosasaurid vertebrae affected by ligamentous ossification shows a striking similarity to such co-ossified vertebrae in whales and has implications for the mode of locomotion in mosasaurs. In extinct marine reptiles, various modes of locomotion have been observed. Ichthyosaur propulsion was by oscillation of the tail, with the finlike limbs used primarily for steering (Massare 1997: p. 402). Recently, Lingham-Soliar and Reif (1998) published taphonomic evidence for fast tuna-like swimming by ichthyosaurs. Plesiosaurs adopted appendicular (limb-dominated) locomotion in their adaptation to a marine life. They swam as sea lions do in present times (Storrs 1993; Rieppel 1997). Although Lingham-Soliar (1992) suggested appendicular locomotion for a plioplatecarpine mosasaur, most current ideas about propulsion of the elongate mosasaurs support axial locomotion with a major function for the tail (Massare 1997: p. 402). Recently, Lingham-Soliar (1999) reappraised subaqueous flight in plioplatecarpine mosasaurs. However, in their appearance and location in the very same lumbar region, the fused vertebrae affected by ligamentous ossification are similar in whales and mosasaurs (Fig. 1). In whales the relation between the occurrence of this vertebral ligamentous ossification and the mode of locomotion has been clearly demonstrated (Klima 1992). This is therefore an extra argument for the view that mosasaurs were tail-propelled tetrapods as well. Obviously, repeated extra strain in the vertebral column could have the same effect in these animals. Moreover, in the extinct marine crocodile *Thoracosaurus*, a lumbar vertebra affected by ligamentous ossification has been recorded (Mulder 1998: Fig. 4B–D). Such crocodiles, like mosasaurs, were

dependent on axial locomotion (Massare 1997: p. 402).

Plioplatecarpine mosasaurs, including *Plioplatecarpus marshi*, are considered to have been capable of deep dives (Dollo 1904; Quinet 1968; Rothschild and Martin 1987). In diving deeply these animals endured the upward force of the water, which makes repeated extra strain in the vertebral column even more plausible. Nevertheless, plioplatecarpines seem to have dived too deeply on occasion, resulting in decompression syndrome followed by avascular necrosis (Rothschild and Martin 1987; Martin and Rothschild 1989).

Taking whales as a model, development of ligamentous ossification along the vertebral column during the life time of an individual mosasaur did not only depend on the evolutionarily acquired special function of the vertebral column, but also on age-related wear possibly determined by genetic constitution. Not every mosasaur suffered from vertebral ligamentous ossification. Nevertheless, the relation between tail-propelled locomotion and occurrence of this disease in both whales and mosasaurs is striking.

Acknowledgments

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Wolfgang Goethe-Universität, Frankfurt am Main), A. F. F. Oosterbaan (Ecomare, Den Burg), and G. J. J. Vennegoor (Museum Natura Docet, Denekamp).

Literature Cited

- Bell, G. L., Jr. 1997. Mosasauridae. Introduction. Pp. 281–292 in Callaway and Nicholls 1997.
- Bol, R. G. A. 2000. Upper Miocene plesiocetid crania (Cetacea; Mysticeti) from Liessel, the Netherlands: the genera *Plesiocetus* (Van Beneden, 1859) and *Metopocetus* (Cope, 1896) revisited. Master's thesis, Rijksuniversiteit Groningen, Netherlands.
- Boule, M., and J. Piveteau. 1935. Les fossiles: éléments de paléontologie. Masson and Cie, Paris.
- Callaway, J. M., and E. L. Nicholls, eds. 1997. Ancient marine reptiles. Academic Press, New York.
- deBraga, M., and R. L. Carroll. 1993. The origin of mosasaurs as a model of macro-evolutionary patterns and processes. *Evolutionary Biology* 27:245–322.
- Dollo, L. 1882. Note sur l'ostéologie des *Mosasauridae* [sic]. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique* 1:55–74 (and 3 plates).
- . 1885. Notes d'ostéologie erpétologique. *Annales de la Société Scientifique de Bruxelles* 9:309–338.
- . 1890. Première note sur les mosasauriens de Maestricht. *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie* 4:151–169.
- . 1892. Nouvelle note sur l'ostéologie des mosasauriens. *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie* 6:219–259.
- . 1904. Les Mosasauriens de la Belgique. *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie* 18: 207–216.
- Fraaye, R. H. B., and M. W. Fraaye. 1995. Miocene bracket fungi (Basidiomycetes, Aphylliphorales) from the Netherlands. *Contributions to Tertiary and Quaternary Geology* 32:27–33.
- Gaudry, A. 1890. Les enchaînements du monde animal dans les temps géologiques: fossiles secondaires. Librairie F. Savy, Paris.
- Holmes, R. 1996. *Plioplatecarpus primaevus* (Mosasauridae) from the Bearpaw Formation (Campanian, Upper Cretaceous) of the North American Western Interior Seaway. *Journal of Vertebrate Paleontology* 16:673–687.
- Klima, M. 1992. Spondylosis deformans der Wirbelsäule bei den Walen und beim Menschen—die gleiche Ursache? *Zeitschrift für Säugetierkunde*, 65. Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde, Zusammenfassungen: 23–24.
- . 1996. Anpassungen an die aquatische Lebensweise. Pp. 49–79 in D. Robineau et al., eds. *Wale und Delphine—Cetacea, Teil 1A. Einführung, Monodontidae, Phocoenidae, Delphinidae*. Band 6 (Meeressäuger) of J. Niethammer and F. Krapp, eds. *Handbuch der Säugetiere Europas*. Aula, Wiesbaden.
- Kompanje, E. J. O. 1993. Vertebral osteophytosis in Cetacea: spondylosis or spondylitis? *Zeitschrift für Säugetierkunde* 58:316–318.
- . 1995. Differences between spondylo-osteomyelitis and spondylosis deformans in small odontocetes based on museum material. *Aquatic Mammals* 21:199–203.
- . 1999. Considerations on the comparative pathology of

- the vertebrae in Mysticeti and Odontoceti: evidence for the occurrence of discarthrosis, zygarthrosis, infectious spondylitis and spondyloarthritis. *Zoologische Mededelingen, Leiden* 73:99–130.
- Kuypers, M. M. M., J. W. M. Jagt, H. H. G. Peeters, D. T. De Graaf, R. W. Dortangs, M. J. M. Deckers, D. Eysermans, M. J. Janssen, and L. Arpot. 1998. Laat-kretaceische mosasauriërs uit Luik-Limburg: nieuwe vondsten leiden tot nieuwe inzichten. *Publicaties van het Natuurhistorisch Genootschap in Limburg* 41: 4–47.
- Lingham-Soliar, T. 1992. A new mode of locomotion in mosasaurs: subaqueous flying in *Plioplatecarpus marshi*. *Journal of Vertebrate Paleontology* 12:405–421.
- . 1999. A reappraisal of subaqueous flight in mosasaurs. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 213:145–167.
- Lingham-Soliar, T., and W.-E. Reif. 1998. Taphonomic evidence for fast tuna-like swimming in Jurassic and Cretaceous ichthyosaurs. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 207:171–183.
- Martin, J. E., and G. L. Bell. 1995. Abnormal caudal vertebrae of Mosasauridae from Late Cretaceous marine deposits of South Dakota. *Proceedings of the South Dakota Academy of Sciences* 74:23–27.
- Martin, L. D., and B. M. Rothschild. 1989. Paleopathology and diving mosasaurs. *American Scientist* 77:460–467.
- Massare, J. A. 1997. Faunas, behavior, and evolution. Introduction. Pp. 401–421 in Callaway and Nicholls 1997.
- Meijer, A. W. F. 1985. Hoe wervelvergroeiingen een paleontoloog op het verkeerde spoor brachten. *Natuurhistorisch Maandblad* 74:130–131.
- Mulder, E. W. A. 1985. Beenvliesontsteking: een oude kwaal! *Natuurhistorisch Maandblad* 74:129–130.
- . 1998. Thoracosaurine vertebrae (Crocodylia; Crocodylidae) from the Maastrichtian type area. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* 100(1997):161–170.
- Quinet, G. E. 1968. Le mécanisme de l'audition chez *Plioplatecarpus Dollo*, 1882? *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 44(3):1–9.
- Rieppel, O. 1997. Sauropterygia. Introduction. Pp. 107–119 in Callaway and Nicholls 1997.
- Rothschild, B., and L. D. Martin. 1987. Avascular necrosis: occurrence in diving Cretaceous mosasaurs. *Science* 236:75–77.
- Slijper, E. J. 1958. *Walvissen*. D. B. Centen's Uitgeversmaatschappij, Amsterdam.
- Storrs, G. W. 1993. Function and phylogeny in sauropterygian (Diapsida) evolution. *American Journal of Science* 293A:63–90.
- Tanke, D. H., and B. M. Rothschild. 1997. Paleopathology. Pp. 525–530 in P. J. Currie and K. Padian, eds. *Encyclopedia of dinosaurs*. Academic Press, San Diego.
- Williston, S. W. 1904. The relationships and habits of the mosasaurs. *Journal of Geology* 12:43–51.
- is from Eben Emael, IRScNB 1497 from Zichen; both are of late Maastrichtian age (Maastricht Formation).
- MND 20.01.826
- Plioplatecarpus marshi*, dorsal vertebra with an infectious reactive new bone formation, Ankerpoort-'t Rooth Quarry, Bemelen, late Maastrichtian (Maastricht Formation, ?Nekum Member), ex De Heer Colln.
- MND 20.01.842
- Plioplatecarpus marshi*, pygal vertebrae fused by ligamentous ossification. Ankerpoort-'t Rooth Quarry, Bemelen, Late Maastrichtian (Maastricht Formation, ?Nekum Member), ex De Heer Colln.
- MNHNP AC 9649-9775
- Plioplatecarpus marshi*, substantial portion of a vertebral column with two clusters of caudal vertebrae fused by infectious spondylitis, Maastrichtian type area, late Maastrichtian (Maastricht Formation). The accompanying label reads, "*Mosasaurus giganteus* Sömm. Colonne vertébrale d'un individu de petite taille, comprenant une grande partie des v. lombaires et 67 caudales. Craie de Maëstricht (Hollande)." Gaudry (1890: p. 205) erroneously considered the articular surfaces for the hemal arches to be a juvenile character of the genus *Mosasaurus*. He reconstructed a series of 26 pygal and 67 caudal vertebrae. I counted a total of 97 vertebrae, stored in two neighboring drawers. Another accompanying label numbered MNHNP AC 9776 mentions the species name and the type region of the Maastrichtian in the same terminology. The tail fragment was formerly mounted for exhibition. Some vertebrae are still connected by iron rods; several are glued together. The anterior cluster obviously has been sectioned for investigation, the parts having been glued together again afterward. In mounting the tail, a few errors crept in: some vertebrae are fixed in a distorted position or have been inverted anteroposteriorly. Vertebral dimensions suggest that the anterior and posterior clusters of fused vertebrae may have been closer toward each other in life. The anterior central height of the first "normal" vertebra in front of the posterior cluster is 54 mm, whereas the posterior central height of the second normal vertebra in front of the posterior cluster is 49 mm. In both cases the central width is 43 mm. *Mosasaurus giganteus* (Sömmering 1820) is an invalid name for, and *Mosasaurus camperi* Von Meyer 1832 is a junior synonym of, *Mosasaurus hoffmanni* Mantell 1829.
- OMGP (unnumbered)
- Plesiocetus durinasus* (Cope 1896), balaenopterid whale, fragmentary large but incomplete pygal vertebra with irregular spongiform hyperostosis (spondylosis) in phosphorite nodule, Liessel, Miocene. (Fig. 5.2). At the surface of the phosphorite nodule, fragments of a synapophysis and the neural arch are visible. Central width at the anterior articular surface: ± 21 cm. The specimen comprises two fragments that fit together. Unfortunately, the posterior part of the vertebra is not preserved; therefore the original extension of the hyperostosis is not clear. However, the hyperostosis reaches a thickness of 5.5 cm at the area where the posterior part is lost. This makes a former presence of at least one connected (fused) vertebra plausible. The centrum shows a normal bone histology, without signs of infection, which points to a case of ligamentous ossification.

Appendix 1

List of Specimens Studied

IRScNB 1496, 1497

Plioplatecarpus marshi, specimens studied by Dollo (1882). The "sacra" are labeled 1496^f and 1497^h respectively. IRScNB 1496

Appendix 2

Measurements in mm of mosasaurid "sacra" consisting of two pygal vertebrae fused by ligamentous ossification; all material from the Maastrichtian type area (southeast Netherlands, northeast Belgium). L = length, B = breadth of anterior central articular surface.

Specimen	L	B
IRScNB 1496 ^F	110	±80
IRScNB 1497 ^{HH}	103	63
MND 20.01.842	98	61