A sirenian skeleton from the Miocene of Eibergen, Province of Gelderland, The Netherlands: *Metaxytherium* cf. *medium* (Desmarest)

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A sirenian skeleton, the major part of which was excavated from Miocene deposits at Eibergen near Winterswijk, belongs to *Metaxytherium*. The temporal crests on the parietals are well separated. The foramen magnum is pointed above. The mandible has a downturned symphysial body with four shallow alveoli on each side. The wide mandibular canal opens some distance behind the alveolus of M_3. There are alveoli for one premolar (P_4) and for three molars (M_1-M_3). Only M_2 dext. is preserved; it has four main cusps and some accessory cusplets. The humerus, the shaft portion of which is missing, has a wide and marked bicipital groove. The vertebrae, with the exception of the atlas, are fragmentary. The spinous processes are solid, the centra porous. The ribs, a few of which have been reassembled rather completely from fragments, are solid except for their vertebral ends. The distal, or sternal, ends may show a porous structure internally. In the sternum, the manubrium is separate, whereas corpus and ensiform process are co-ossified. The Eibergen sirenian appears indistinguishable from *Metaxytherium medium* (Desmarest) from the Helvetian of France.

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Introduction

Some time ago Dr P. J. H. van Bree, of the Institute of Taxonomic Zoology of the University of Amsterdam, brought to my attention the existence in the collections of the Rijksmuseum van Geologie en Mineralogie at Leiden of the larger part of a skeleton of a Miocene sea cow found at Eibergen, near Winterswijk in the province of Gelderland. This consists of the proximal and distal portions of a humerus collected and donated to the museum by Mr D. J. Mol (18th February, 1970) and most of the remaining skeleton collected and donated subsequently by Dr F. J. M. Heslinga on 16th November of the same year. This find has recently been recorded as *Halitherium* in a paper by van den Bosch, Cadée & Janssen (1975; p. 97) but had not yet been described. With kind permission of the acting director of the said museum, Prof. Dr L. D. Brongersma, I obtained these sirenian remains on loan for study and report. I wish here to thank in particular Dr F. J. M. Heslinga, whose sharp eye and extraordinary skill in preparation had enabled him to put together from innumerable fragments a number of rather complete ribs, a large portion of the right mandibular ramus, and most of the sternum before the collection was first seen by me, which saved me a lot of time.

The photographs in the present paper are by Mr C. Hoorn, of the Rijksmuseum van Natuurlijke Historie, Leiden.

STRATIGRAPHY

The humerus and the other remains were found in the lower part of a clay pit, F.O.W., 34G. 3-13 (see van den Bosch, Cadée & Janssen, 1975, p. 32-35) at the type locality of the Eibergen Member; its correlation with deposits in other parts of the North Sea Basin is tentative (l.c., p. 105) but it is placed at the transition between Middle and Late Miocene (l.c., enclosure 2). Next to it, in the column headed North-western Germany, is placed the Langenfeldian Stage, considered early Late Miocene by Hinsch & Ortlam (1974, p. 12), the Badenian of the Paratethys stages. In France, *Metaxytherium medium* is found principally in the Département de Maine-et-Loire (Cottreau, 1928, p. 5) in the Helvetian — Serravallian of the Mediterranean stages — within the range of zones N 11 to N 15 of Blow, approximately 13 to 11 million years ago (Berggren & van Couvering, 1974, fig. 11 facing p. 92). In the Vienna Basin, the Late Badenian fauna of Neudorf an der March, approximately equivalent to zones N 10/N 11-N 13 (Berggren & van Couvering, 1974, p. 100), contains *Metaxytherium petersi* Abel (1904, p. 15). *Metaxytherium calvertense* Kellogg (1966, p. 71) from the Miocene Calvert Formation of Maryland, U.S.A., resembles *Metaxytherium medium,* and is interesting in that it certainly had 20 pairs of ribs (l.c., p. 86): the skeletons of *M. medium* (Cottreau, 1928, p. 15) and of *Felsinotherium serresi* (Depéret & Roman, 1920, p. 16) had 19. It is with these skeletons in particular that comparisons of the Eibergen sirenian will be made.

It soon became evident that the Eibergen sirenian does not belong to the genus *Halitherium* Kaup, typified by the best known of all fossil sirenian species, *Halitherium schinzi* Kaup of the European Oligocene, but to *Metaxytherium* de Christol of the Miocene of Europe and North America. It appears indistinguishable from the type species of that genus, *Metaxytherium medium* (Desmarest).

This species is usually being referred to as *Metaxytherium cuvieri* (de Christol, 1834), but that name (Hooijer, 1952, p. 113-114; Kellogg, 1966, p. 70) is antedated by *Hippopotamus medius* Desmarest (1822, p. 388) as given to the 'moyen hippopotame fossile' of Cuvier (1821, p. 332-333, Hippopotame fossile, pl. 7, figs. 9-10). It is also known as *Halitherium fossile* Gervais, 1852 (Flot, 1886). Cottreau (1928) described an almost complete skeleton from the Loire Basin in France; the first nearly entire mandible, from Chazé-Henri, Maine-et-Loire, was recorded by Depéret & Roman (1920, p. 27, pl. 7, figs. 2, 2a) in connexion with a monograph on *Felsinotherium serresi* (Gervais) from Montpellier.

Description of the skeleton

SKULL

The skull, like the whole skeleton of the Eibergen *Metaxytherium,* is badly fragmented and many parts are missing. However, the top and back are tolerably well preserved since three bone fragments, the anterior portion of the fused parietals, the posterior portion of the parietalia and the supraoccipital, and the left exoccipital, miraculously fit on to each other along small portions of their margins. The parieto-occipital region of the skull often is represented in sirenians because of the extraordinary thickness and density of the bone in these parts. The three fragments are shown in juxtaposition, external, left lateral, and internal views, on Pl. 1, fig. 1a-c. At the anterior end of the parietal, the — still open — fronto-parietal suture is exposed. The thickness of the bone, in the middle, is no less than 25 mm, the temporal crests, 5 mm thick and high, are 30 mm apart, and the surface between them is flat. Very little of the downward sloping sides of the parietals is preserved. The anterior fragment is only 60 mm long, and bears a sagittal crest on its internal surface, which flattens out toward the suture with the frontal bones. It is continued on he second fragment, which comprises the posterior portion of the parietalia and the supraoccipital: the area of contact between the first and the second fragment is only 2 cm wide, just to the left of the crista sagittalis interna. The suture between the parietals and the supraoccipital is closed, but is shown as a transverse groove on the internal surface: the median crest does not quite extend backward to this sutural line. The length of the parietals, in the median line, is 85 mm. The supraoccipital has an open suture with the exoccipitals, and the two bones can be fitted together along a stretch of 3 cm on the extreme left, just about one-half of the length of the suture between the supraoccipital and the left exoccipital. There is also a large portion of the right exoccipital, but unfortunately this does not fit on to the remainder of the occiput. The lower portion of the exoccipitals, with the condyles, is incomplete. The plane of the exoccipitals is at right angles to the upper surface of the parietals. The supraoccipital bears a median vertical protuberance most marked above: at its upper end, which coincides with the parieto-supraoccipital suture (not marked by any transverse occipital crest), the total thickness of the bone is 30 mm. This diminishes to 10 mm 4 cm lower down, at which point the supraoccipital is broken. As this protuberance marks the median line, and the left lower portion at the suture with the exoccipital is preserved, the total width of the supraoccipital can

be given as 100 mm. The thickness of the supraoccipital as well as of the exoccipital at the extreme left of the open suture is 17 mm. Since the left exoccipital is preserved to the median line it is clear that the foramen magnum is pointed above, not rounded off, and thus exactly as in the dugong. Its height cannot be given as the basioccipital is missing, but the greatest width of the occiput, across the lower lateral margins of the exoccipitals, can be given as 165 mm. These figures agree well with those of the occipital portion of the skull of *Metaxytherium medium* described by Flot (1886, p. 485-486): basal width of occiput, 170 mm; width of supraoccipital, 90 mm. The distance between the temporal crests on the parietals varies in the various individuals (Flot, l.c., p. 488), but is 26 mm in the skull figured by Depéret & Roman (1920, pl. 7, fig. 3). The length of the parietal, from the frontal suture to the occipital protuberance, is 85 mm in *Metaxytherium medium* (Flot, l.c., p. 489): it is the same in the Eibergen skull. *Metaxytherium petersi* is of the same size as *M. medium* but has a wider and more shortened cranial portion (Abel, 1904, p. 108; Depéret & Roman, 1920, p. 28-30). In *Halitherium schinzi,* on the other hand, the temporal crests on the parietals approach each other more closely, to the point of almost touching each other, and there is a transverse supraoccipital crest (Lepsius, 1882, pl. 1). In addition, the foramen magnum is lower than that in *Metaxytherium,* the exoccipitals joining in the median line for several cm above it (Lepsius, l.c., pl. 10, fig. 97). From these and other characters to be mentioned further on, it is clear that the Eibergen sirenian cannot be accommodated in the genus *Halitherium.*

The remaining fragments of the cranium of the Eibergen sirenian are less diagnostic, and none of them fits on to any other. There are portions of the anterior and posterior zygomatic roots, a fragment of the left squamosal, a fragment of the maxillary (without teeth), and part of the perpendicular portion of the palatine, co-ossified with the basisphenoid. Two symmetrical bone fragments represent the antorbital apophyses of the jugals.

The mandible of the Eibergen sirenian is much better represented. We have the characteristic front portion, not unlike that in the Recent dugong, with four shallow but extensive alveoli above each other on either side (Pl. 3, fig. 5). These alveoli lodged rudimentary teeth: the front surface of the symphysis doubtless was covered by a thick horny plate as in the Recent form. The right and left alveolar series, however, are somewhat more widely separated than they are in the dugong. Unfortunately, the sides of the symphysis below the second alveoli from above are damaged down to the narrow antero-inferior projection where the grooves running forward and downward on either side from the huge mental foramina flatten out. The rugose triangular base of the symphysial body is much damaged, and so is the posterior face of the symphysis. The greatest symphysial width, over the outer borders between the second and third alveoli from above, is just about 60 mm, the same as in an old male dugong skull (Rijksmuseum van Natuurlijke Historie, Leiden, Dept. Mamm, reg. no. 2581). The anterior height of the symphysis of the Eibergen mandible cannot be given as it is incomplete above and below, but it must have been well over 100 mm; it is 110 mm in the Recent mandible. The diameter from the front surface with the alveoli to the postero-inferior border of the symphysis is the same in both, 70 mm. Most fortunately, the greater part of the right horizontal ramus of the mandible fits on to the symphysial portion (Pl. 2, fig. 1a), showing the downturned symphysial body so charecteristic of *Metaxytherium.* However, the inferior border of the horizontal ramus is very incomplete, exposing the wide mandibular canal, and con-

sequently the ramus height cannot be given. In the Recent specimen the mandibular canal opens above just behind and laterally of the M_3: this hole is well seen in the right half of the mandible of the Eibergen sirenian but is placed farther behind. There is a space of about 20 mm between the alveolus for M_3 and the opening for the mandibular canal. The ascending portion of the mandible is partially preserved, and appears heavier built in the fossil than in the Recent specimen: 40 mm transversely instead of only 30 mm at the level of the posterior opening of the mandibular canal, and at least 90 mm anteroposteriorly over the condyle in the fossil, against 75 mm in the Recent mandible. The angular portion is very incomplete in the fossil, and the right condyle, too. Of the left side of the mandible we have the rather excellently preserved condyle (Pl. 3, fig. 1a, b), which is 35 mm transversely and at least 25 mm anteroposteriorly. The greater part of the left ascending ramus is preserved, too, but unfortunately does not fit on to the condylar portion. The horizontal ramus of the left side, incomplete below as is the right horizontal ramus, shows the incomplete alveoli of the three molars, and that of the posterior premolar as well, but this bone fragment does not fit on to the preserved portion of the left ascending ramus, nor to the symphysis either.

In the entire mandible of *Metaxytherium medium* figured by Depéret & Roman (1920, pl. 7, fig. 2) the anterior height of the symphysis is 120 mm, and the height of the horizontal ramus below M_2 is just 90 mm. The anteroposterior diameter of the ascending ramus is approximately 110 mm. The distance from the groove running forward and downward from the mental foramen to the inferior border is the same in the Eibergen mandible and in that described by Depéret & Roman, viz., ca. 40 mm. The mandibular condyle in the specimen described by Flot (1886, p. 505) is 40 mm transversely, and 32 mm anteroposteriorly.

There is one molar preserved of the Eibergen mandible, and it is the right second molar. It is shown in situ in the internal and external views of the ramus (Pl. 2, figs. 1a, c) as well as in occlusal view (Pl. 2, fig. 1b). This element has distinct interproximal wear facets fore and aft, and is rather worn. The posterior root is the heavier of the two. The antero-internal cusp (metaconid) is the least worn (down to 11 mm from the base of the enamel), forwardly inclined and with the tip of its dentine core showing as a small island. The antero-external cusp (protoconid) is worn to a height of 7 mm, and is more extended transversely as well as anteroposteriorly than the metaconid. Antero-externally there is a cingular cuspule that would have become confluent with the protoconid occlusally upon a little more wear. The transverse valley behind the anterior pair of cusps, which runs somewhat obliquely backward toward the external side, is still wide open lingually and shows a tiny accessory cusp behind the metaconid not yet touched by wear; the buccal portion of the transverse valley is almost worn out. The dentine surfaces of the two posterior cusps, hypoconid buccally and entoconid lingually, have become confluent with each other and with that of the posterior cingulum. There is a marked enamel inflection delimiting the entoconid behind; the hypoconid is clearly the larger of the two posterior cusps. The crown of the M_2 dext. measures 30.5 mm anteroposteriorly, and 22.5 mm transversely. As the alveoli for M_1 and M_3 are only partially preserved the alveolar length M_1-M_3 may only be given approximately, as 70-75 mm.

The M_2 of the Eibergen mandible agrees very well in morphology as well as in size with those of *Metaxytherium medium* figured by Cuvier (1821, Hippopotame fossile, pl. 7, fig. 10), Flot (1886, pl. 26 (the plate is numbered XXVII),

fig. 3), and Depéret & Roman (1920, pl. 7, fig. 2a). The length M_1-M_3 in these mandibles is about 70 mm. The alveolus for the P_4 is not shown on the right side but is present on the left. The lower molars of *Halitherium schinzi* are simpler in build, narrower, more lophodont, with fewer accessory cusplets (Lepsius, 1882, pl. 4), a fundamental difference from those of *Metaxytherium*.

HUMERUS

The humerus, the initial find of the Eibergen sirenian, is represented only by the proximal and distal portions, both of the right side. The total length cannot be given: the proximal fragment is barely 12 cm long, from the caput down, and the distal portion is 7.5 cm long as preserved. The caput is rather corroded, as shown in internal side view (Pl. 3, fig. 4): its diameter is ca. 60 mm. The greater and lesser tuberosities have nearly undamaged surfaces, and the bicipital groove in between is 25 mm wide and equally deep. The deltoid crest running down from the greater tuberosity is damaged already 5 cm distally from its point of origin, and the prominence of the deltoid tuberosity, therefore, cannot be determined. The greatest proximal width, over caput and lateral (greater) tuberosity, is approximately 100 mm; the diameter at right angles to this, over caput and the lesser tuberosity, is perhaps slightly less. The shaft width, 5 cm below the caput, is 60 mm, and the anteroposterior diameter, at the same level, ca. 40 mm. The distal portion, shown in anterior view on Pl. 3, fig. 8, has a greatest width of 98 mm by a trochlear width of 68 mm.

The humerus of *Metaxytherium medium* figured by Flot (1886, pl. 28, figs. 8 and 9) is incomplete proximally, but the length is given as 220 mm by a proximal width of 120 mm, a distal width of 105 mm, and a distal trochlear width of 70 mm; the diameter of the caput is given as 60 mm (Flot, l.c., p. 514-515). The humerus figured by Flot has a marked deltoid tuberosity, which tends to fold over the musculo-spiral groove: this is also shown in the specimen figured by Depéret & Roman (1920, p. 19, fig. 3C) the greatest length of which in only 195 mm if the figure is 1/3 natural size as indicated. The wide and marked bicipital groove, however, is characteristic of *Metaxytherium* in contrast to *Halitherium*, in which this groove is shallow, the articular ends weaker, less muscular, and the shaft more slender (Lepsius, 1882, pl. 6, fig. 64; Abel, 1904, p. 74). Although the length and shape of the shaft cannot be determined, the two ends of the Eibergen humerus are *Metaxytherium*-like. This is the only limb bone of the skeleton recovered.

VERTEBRAE

There is one cervical vertebra of the Eibergen skeleton, the atlas, in two parts. The facets for the occipital condyles are 55 by 31 mm, exactly the same dimensions as those given for the occipital condyles of *Metaxytherium medium* by Flot (1886, p. 487).

Of the dorsal vertebrae, there are fragmentary bodies, parts of the arches, and spinous processes, but in no case has it been possible to assemble an entire vertebra. The centrum of a dorsal vertebra shows two demifacets for articulation

with the heads of ribs. According to Cottreau (1928, p. 13) there are anterior and posterior demifacets for the rib heads only in the first nine dorsals, the more posteriorly placed dorsal vertebrae having a single capitular facet on the centrum. The anteroposterior diameter of the Eibergen vertebra is 39 mm, the transverse diameter, 88 mm. These are the dimensions of some of the anterior dorsal vertebrae of the immature skeleton of *Metaxytherium calvertense* (Kellogg, 1966, p. 87) the estimated total length of which is 3 m, the same as that of the adult skeleton of *Metaxytherium medium* described by Cottreau (1928), which is not as completely preserved as the skeleton of *M. calvertense.* A dorsal vertebra supposed to be the third is 42 mm anteroposteriorly by a height of the centrum of 40 mm (Cottreau, l.c., p. 13); the height of the body of the Eibergen vertebra is 42 mm. The smallest dorsal vertebra in the Eibergen collection is only 27 mm anteroposteriorly; the width cannot be determined as the demifacets are not complete. The first dorsal of the skeleton of *M. calvertense* is 31 mm anteroposteriorly (Kellogg, 1966, p. 87), and that of the skeleton of *M. medium* 29 mm (Cottreau, 1928, p. 13). In these skeletons the bodies of the dorsals increase in anteroposterior diameters to 55-59 mm in the twelfth to sixteenth of *M. calvertense,* and the longest dorsal of the skeleton of *M. medium,* the twelfth, even measures 63 mm. Various fragmentary centra of vertebrae in the Eibergen collection present anteroposterior diameters of 44 to 59 mm; it is impossible to determine their serial position.

The same is true for the spinous processes in the Eibergen collection, a few of which are rather complete but none of which fit on to the portions carrying the facets for the ribs, of which there are a few pertaining to the posterior dorsals as the whole capitulum articulation is placed on a single centrum. The upper portions of these parts are completely solid, with no cancellous tissue, whereas the lower parts, just like the centra of the vertebrae, are porous with only a very thin, compact, outer layer of bone. The spinous processes are compact throughout, as are the ribs except for their vertebral ends. Spongious bone is less likely to be preserved than compact bone, especially in the case of the Eibergen sirenian that was excavated rather as a salvage operation at the bottom of the clay pit under very difficult conditions. While it is, therefore, not surprising that there are few remains of vertebral bodies in the collection (eight at most), it is surprising that the solid neural spines are not present in greater numbers: only six are represented two of which are shown in profile on Pl. 3, figs. 6, 7. The longest and most complete (fig. 7) has part of the roof of the neural arch preserved, and its height to the tip is 97 mm. The thickness in the middle is 20 mm, the anteroposterior diameter 51 mm. The other (fig. 6), the height of which cannot be determined, is 25 mm in width and 54 mm anteroposteriorly. In the skeleton of *M. medium* the neural spine of the third dorsal is 112 mm high and 27 mm thick; the spines then vary in thickness, in the middle, from 23 mm in the seventh to 21 mm in the nineteenth dorsal (Cottreau, 1928, p. 13). In the skeleton of *M. calvertense* the height of the neural spine is maximal in the second to fourth dorsal (92-93 mm), diminishing to 77-82 mm in the fourteenth to sixteenth (Kellogg, 1966, p. 87); thicknesses and anteroposterior diameters are not given. These diameters in the largest neural spine in the Eibergen collection, unfortunately very incomplete, are 25 by 65 mm.

There are two transverse processes of dorsal vertebrae, probably in the region of the sixth to ninth dorsals, strong, short, and massive, both with the facet for the tuberculum of the rib on their ventral side. One shows part of the arch with

the side of the neural canal: its total length is 68 mm, and its end is 49 mm anteroposteriorly and 26 mm from above downward. Unfortunately the capitular facet is not shown on this fragment: it does not extend to the centrum. The other fragment of a transverse process is slightly more massive (52 by 28 mm in diameters) but appears shorter. The tubercular facet on its lower surface is 29 by 20 mm.

The rib facets shown on two sides of dorsal vertebrae (Pl. 3, figs. 2, 3), the upper for the tubercle, and the lower for the head, resemble those of the twelfth to sixteenth dorsals in the better known skeletons of *Metaxytherium* and *Felsinotherium:* the tubercular and capitular facets are close but not yet confluent. The postzygapophyses are preserved, too, in both specimens. One of them (fig. 3) shows the cancellous tissue in the lower half, which would join the centrum of the vertebra below the neural canal, but there is no fit in any of the specimens available. There are two similar but even less complete specimens in the Eibergen collection, representing only the upper half with the tubercular facet, but neither these nor the figured fragments fit on to the base of any of the neural spines available. The tubercular facet is about 20 by 25 mm in diameters, that for the capitulum 25 by 35 mm, with a deep, non-articular fossa in between.

There are no recognizable remains of the lumbar or caudal vertebrae in the Eibergen collection but for most of a chevron that would appear to belong to one of the caudals. The height is about 55 mm; one of its upper branches has broken off.

RIBS

The ribs, as shown in the well-preserved skeleton of *Metaxytherium* and *Felsinotherium,* form a graded series. The first ribs have a head, neck, and tubercle. Head and tubercle approach each other as we pass backward along the series of dorsals. The sternal extremity of the first few ribs is quite swollen, but it becomes flatter in the more posteriorly placed ribs. The curvature at the vertebral end is quite strong anteriorly, less so in the back portion of the thorax, in which the vertebral ends become more forwardly directed, whereas the distal ends are directed backward, giving a more nearly S-shaped curve to the posterior ribs. The skeletons of *Metaxytherium medium* (Cottreau, 1928), *Metaxytherium calvertense* (Kellogg, 1966), and *Felsinotherium serresi* (Depéret & Roman, 1920) are so complete that the respective authors have numbered all the ribs, arriving at a total of 19 pairs in *M. medium* and *F. serresi,* and 20 in *M. calvertense.* For these ribs to be arranged in a successive series, without gaps, it is imperative that they be reasonably complete, especially at their vertebral ends, so that the length of the neck and the distance between capitular and tubercular facets can be determined. The ribs of the Eibergen sirenian are far from ideally preserved: the necks of the first few ribs are missing or incomplete (there is one isolated neck portion with a head displaying two demifacets that would have fitted the figured centrum of the anterior dorsal vertebra, but it does not fit on any of the rib fragments). The vertebral ends of the ribs in general are so poorly preserved that the mutual position of the head and tubercle is far from clear. The ends of the ribs, if present, show cancellous tissue, and thus contained marrow, in contrast to the main body of the ribs, which show dense surfaces on broken parts. The distal, or sternal ends, may be solid or may show a porous structure internally, varying

in extent.

The compact structure of the ribs of *Halitherium, Metaxytherium,* and *Felsinotherium* has been considered a pathological condition, pachyostosis or osteosclerosis. Spillmann (1959) has argued against this view, still expressed by Mohr (1957, p. 10). Spillmann's manuscript dates back to 1947 (Spillmann, 1959, p. 65), and Thenius (1952, p. 34) already cites it. What Spillmann calls 'ponderosity' is seen as an adaptation to submarine life, making for passive diving and active emerging. The compact substance has increased at the expense of the spongious substance that we still find in the centra and part of the neural arches of the vertebrae. This has added considerably to the body weight of these fat animals. The Haversian canal system, however, is even better developed than that in other mammals. The same 'ponderosity' is seen in other secondarily marine vertebrates like seals and whales (Thenius & Hofer, 1960, p. 178), and thus is not confined to sirenians. Simpson (1932, p. 441) made the observation that on exposed weathered surfaces of sirenian ribs lines of growth may be seen, showing that the bone is added to in successive layers. Growth is most rapid on the outer surface, giving these ribs their 'swollen' appearance, but is seen also on the anterior and posterior sides, least so on the invariably flat internal surfaces. The same layering is observable on some specimens of ribs of the Eibergen sirenian.

The descriptions of the first rib in *M. medium, F. serresi,* and *M. calvertense* concur in this rib being very different from the others: short, slightly curved, and markedly flattened, with three processes on its vertebral end. Such a specimen is not in the Eibergen collection. There is a short rib (Pl. 4, fig. 1) that is rather flattened, just as the first costae in *Metaxytherium* and *Felsinotherium* (20 mm in thickness by an anteroposterior diameter of 55 mm), but only in the middle, over a projection at the inner curve. It has, moreover, a marked neck, and the characteristic vertebral articular end is missing. In the figured specimens of *M. calvertense* (Kellogg, 1966, p. 88) and *F. serresi* (Depéret & Roman, 1920, pl. 4, fig. 6) the anteroposterior diameter is more even throughout, and the neck is not so constricted as that in our specimen. Therefore, it may be not the first dorsal but a cervical rib, the occurrence of which in sirenians is not uncommon and which may be rather irregular in shape. The total length of the bone as preserved is 16.5 cm, and the sternal end is a flat, roughened, oval surface, 36 by 24 mm in diameters, to which doubtless a ligament was attached in life.

There is a small rib, of the left side, incomplete at either end (Pl. 4, fig. 3). It is quite slender but not flattened, with a greater diameter of 40 mm anteroposteriorly. In transverse direction it is 34 mm at the broken ends, slighly thinner (30 mm) in the middle. The broken distal end shows some spongious substance, the remainder of the rib is quite solid. The length of the rib, as preserved, is 23.5 cm in a straight line.

The rib that is most probably the second, again of the left side, is 42 cm long, along the curve: it is shown in internal view, on Pl. 4 fig. 2. There is a neck, with a small tubercular facet at its base, but the head is broken off. The diameters at mid-shaft are 52 by 28 mm, the neck diameters 32 by 14 mm, and those of the distal end maximally 62 by 40 mm.

The distal ends of what are probably right second and fourth ribs are shown on Pl. 4, figs. 4, 5. The second, shown on its flattened internal surface, is 48 by 29 mm at the broken end; the diameter of the distal portion, which is wider, are maximally 62 by 42 mm. The swollen portion terminates in a flat, roughened oval 42 by 25 mm in diameters. Quite different is the distal end of what is prob-

ably the fourth right rib: the internal view (Pl. 4, fig. 4) shows imperfect ossification for a stretch of 7 cm, not a solid club as does the second rib, and the diameters are 66 by 35 mm maximally. Among the available right and left distal rib fragments there are no two that are perfect mirror images of each other; the distal club-like end of the rather complete left second rib, however, agrees rather closely with the right distal end of Pl. 4, fig. 5, having a roughened oval termination 34 by 21 mm in diameters, for ligamentary attachment.

Two ribs that are rather similar and both from the right side supplement each other rather nicely as the vertebral end is rather complete in one, and the sternal end in the other. The vertebral end of what is probably the seventh right rib (Pl. 5, fig. 1) is rather curved inward: it shows a small tubercular facet and the base of the neck. Then follows, at 9 cm from the broken vertebral end, a thickened portion, 60 mm anteroposteriorly and 35 mm transversely. It is at this thickened portion that the other right rib, probably the eighth (Pl. 5, fig. 2), is broken off: the diameters at the broken vertebral end are 61 by 36 mm. Then follows, sternally, a more slender portion of the rib, as is well seen in the front views. While the anteroposterior diameter remains the same, about 60 mm, the transverse diameter decreases to 28-30 mm about 10 cm distally of the thickened portion, and then increases again, to 38-39 mm, another ten cm further towards the sternal end. This flattening of the outer surface, while the internal curve of the rib remains even, is seen in a number of fragmentary ribs, but as these rather complete specimens show it is confined to the vertebral half of the rib. The distal, or sternal half of the ribs, begin to show an attenuation at about 15 cm from the sternal end: the sternal end is complete in the eighth rib, while of the seventh rib the distal 12 cm or so are missing. The eighth rib, then, decreases gradually from 60 mm anteroposteriorly and 35 mm transversely over its distal 10 cm to a blunt, flattened tip 32 by 18 mm in diameters. The total length, along the outer curve, of the eighth rib is 65 cm, to which must be added at least 10 cm for the missing vertebral end, which is preserved for the most part in the seventh rib, giving a total length of 75 cm along the curve, or 56 cm in a straight line, for the whole of the rib.

There is another pair of ribs, both from the left side however, that is rather similar, and that represent probably the twelfth and thirteenth. They are shown in posterior view, to facilitate comparison with the right ribs, on Pl. 5, figs. 3 and 4. These ribs are more massive than the seventh and eighth, and both have the tubercular as well as the capitular facets close together but not yet joined. The total length of these ribs (the twelfth lacks only a small fragment sternally) is just about 75 cm along the curve, and 57 cm in a straight line. They show the same flattened portion of their outer surface, but it is placed closer to the middle of the bone than in the seventh and eighth ribs. The thick portions bordering the external attenuation are 20-23, and 36-39 cm, respectively, from the vertebral ends, along the curve, and the maximal diameters of the ribs in these parts are 75 mm anteroposteriorly, and 45-50 mm transversely. The transverse constriction in between is 40-42 mm; there is no change in the anteroposterior diameter. The ribs gradually diminish in diameters from the middle (where they are maximal) to 60 by 30 mm at 10 cm from the sternal end: the end of the thirteenth rib presents a roughened oval 30 by 20 mm in diameters.

The vertebral half of what is probably the sixteenth rib, of the left side again, is shown in posterior view on Pl. 6, fig. 2. The capitular and tubercular facets are joined, or very nearly so, in this specimen: it is the best preserved of

the posterior ribs as far as this critical portion is concerned. This rib is more massive again than the twelfth and thirteenth, attaining diameters of 77 by 55 mm at the broken end (35 cm along the curve from the vertebral end). There is a flattened portion on the outer surface, too, as in the other ribs, but it is rather irregular and on the posterior surface there appear some transverse grooves in a broad depression, as shown in the photograph. At the point where the rib begins to curve inward, at 15 cm from the vertebral end, the diameters are 60 mm anteroposteriorly, and 42 mm transversely, and there begins a posterior longitudinal crest. At 5 cm from the vertebral end the bone is thinnest, 52 by 26 mm, to expand again transversely at the end into a rounded knob on which the facets are situated.

One of the posteriormost ribs, perhaps the seventeenth, lacks the vertebral extremity — the knob shown in the preceding rib portion — but not much is missing and the bone is preserved down to its distal end. It is shown on Pl. 6, fig. 1, in posterior view; it is of the left side. The attenuated proximal 15 cm are very much like that portion in the preceeding specimen although there is no evidence of a posterior crest. From the thinnest portion, a few cm from the broken vertebral end (49 by 24 mm) the rib expands to 70 mm anteroposteriorly at 15 cm from the end by a transverse diameter or about 45 mm. The diameters continue to increase to the middle portion of the rib, where they are 84 by 42 mm. This rib, therefore, is even wider anteroposteriorly than the preceding, and somewhat flatter transversely. The flattened portion on the outer surface cannot well be seen as this part of the bone is rather damaged externally. The distal half of the rib shows a thickening (at 16 cm from its distal end) to 48 mm transversely; at this point the anteroposterior diameter is already reduced to 73 mm. The distal end tapers to a blunt, roughened area 40 by 20 mm in diameters. The total length of this rib, along the outer curve, is 62 cm as preserved, and would not have been more than 65 cm in the complete state. In a straight line it would have been about 50 cm long.

The ribs are of the same type as those of *Metaxytherium medium* as described and figured by Cottreau (1928), who states that the largest average 55 mm in anteroposterior, and 35 mm in transverse diameters. Those of *Felsinotherium serresi* (Depéret & Roman, 1920, pl. 4) also show the external flattening and curvature observed in the Eibergen specimens: the eighteenth is already shorter than those numbered as the sixth and the eleventh. The ribs of *Metaxytherium calvertense* described in detail by Kellogg (1966, p. 86-90, pl. 42) present the same general characters although the increase in thickness as one passes backward along the series is not so marked, but the Maryland skeleton is that of an immature individual.

STERNUM

What is preserved of the sternum of the Eibergen skeleton is shown on Pl. 6, figs. 3a, b. The anterior end is spatulate, dorsoventrally compressed, and slightly curved upward. This is the suture between the manubrium (which is missing) and the corpus. The thickness at the anterior suture is no more than 13 mm as preserved: in the middle there appears to have been a ridge ventrally, but the bone is eroded and rugose in this part. The greatest width, at costal facets 9 cm from the anterior edge, is 87 cm, and the thickness in the middle at this point, 24 mm. A second pair of ribs was attached 4 cm more posteriorly, at which point the

total width is 75 mm; the thickness remains 24 mm. Whereas the bone is slightly bulging transversely on the dorsal surface, and flat ventrally, the posterior end shows a median ridge ventrally and is flat dorsally. The right border of the bone is much thicker than the left, and concave anteroposteriorly; the thin left edge is broken for the most part. The sternum is rather asymmetrically developed as a whole, curving away towards the right side posteriorly. The width 6 cm from the broken posterior end is only 42 mm; the dorsoventral diameter, 18 mm. How much of the posterior process is missing, it is impossible to tell. The widths of the manubrium (anteriorly) and that of the 'xiphoid process" (more probably correctly termed the corpus) in *Metaxytherium medium* are given by Cottreau (1928, p. 16) as 96 mm and 72 mm, respectively. The total length of the sternum described by Cottreau is 38.5 cm, whereas the length of the portion preserved in the Eibergen sternum is only 25.5 cm. The Loire Basin sternum has been reconstructed with plaster and appears rather symmetrical: it is interesting that in a specimen of *Halitherium schinzi* figured by Lepsius (1882, pl. 6 fig. 62) the posterior end is as curved and asymmetrical as that in our specimen. In *Halitherium* manubrium, corpus, and ensiform process are not co-ossified, whereas in *Metaxytherium* the manubrium only is separate: the suture between corpus and ensiform process is closed. In *M. petersi* the manubrium is weak (thickness at corpus sterni only 6 mm), while the greatest thickness of the ensiform process is 18 mm and the width over the costal facets is 70 mm (Abel, 1904, p. 131-132). That width in *Felsinotherium serresi* is only 62 mm (Depéret & Roman, 1920, p. 18). Corpus and ensiform process are united with the second to fourth ribs in these sirenians, but the rib attachment areas right and left are very irregular, as they are in our specimen.

Conclusion

Whereas the characters of the skull, mandible, humerus, and sternum leave no doubt that the Eibergen sirenian should be placed in the genus *Metaxytherium*, widespread in the Miocene of Europe and North America, the specific characters of the various species proposed are not very clear-cut. It would seem from the present study that the Eibergen sirenian is indistinguishable from *Metaxytherium medium* typical of the Helvetian of France; this is also supported by the alleged geological age of the deposit which yielded the Eibergen sirenian skeleton (see Introduction). Weighing these character and stratigraphic resemblances it seems best in the present state of our knowledge to express this apparent relationship between the Dutch and the French sirenian in naming the former *Metaxytherium* cf. *medium* (Desmarest, 1822).

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Plate 1

Metaxytherium cf. *medium* (Desmarest); Eibergen.

Fig. 1. Parietals, supraoccipital and left exoccipital in juxtaposition, RGM 175 890; a: external view; b: left lateral view; c: internal view. All figs. x 0.8.

Plate 1

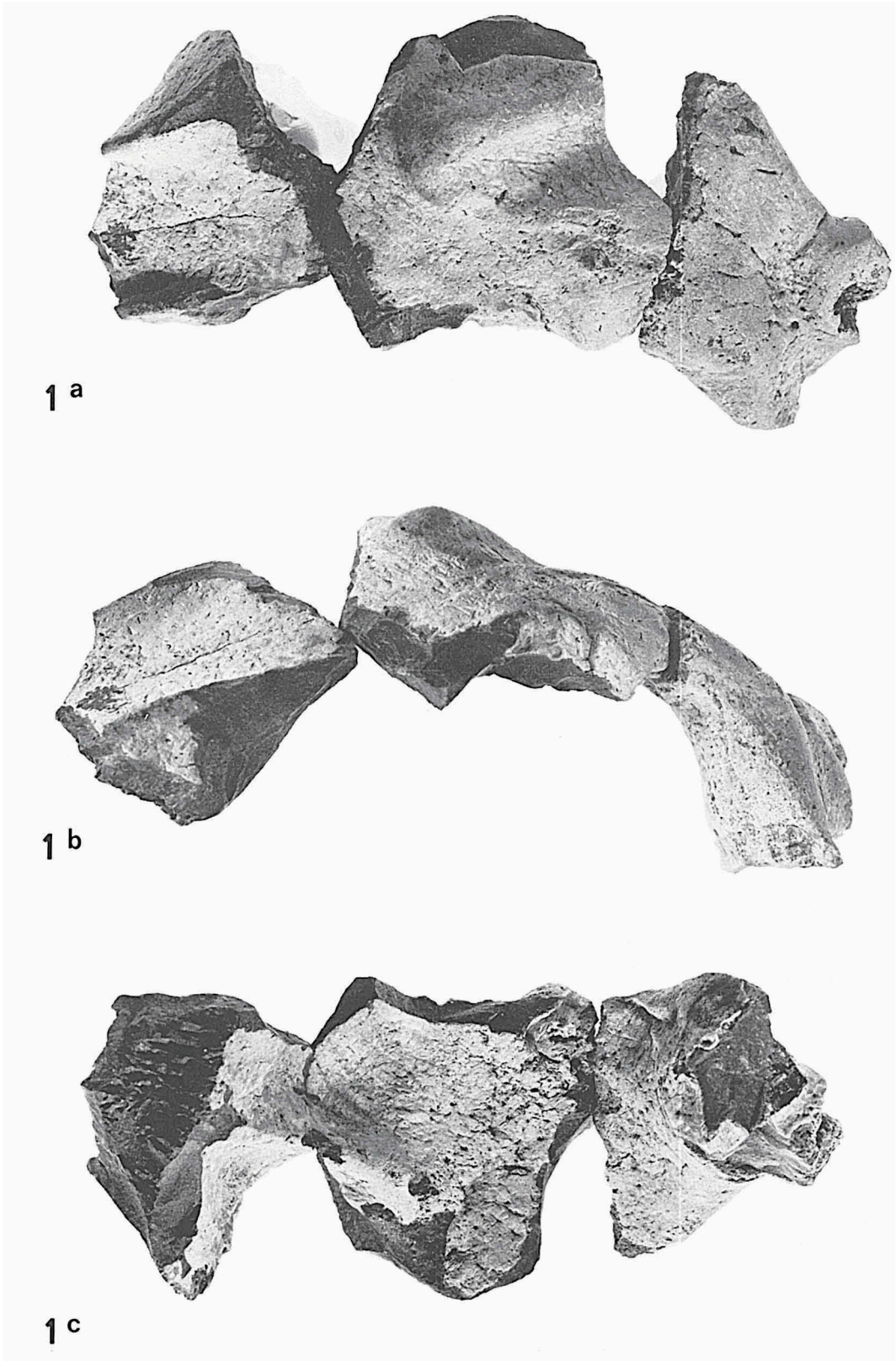

Plate 2

Metaxytherium cf. *medium* (Desmarest); Eibergen.

Fig. 1. Right half of mandible, RGM 175 900; a: external view, with symphysial portion attached to it, x 0.3; b: occlusal view, x 0.5; c: internal view, x 0.5.

Plate 2

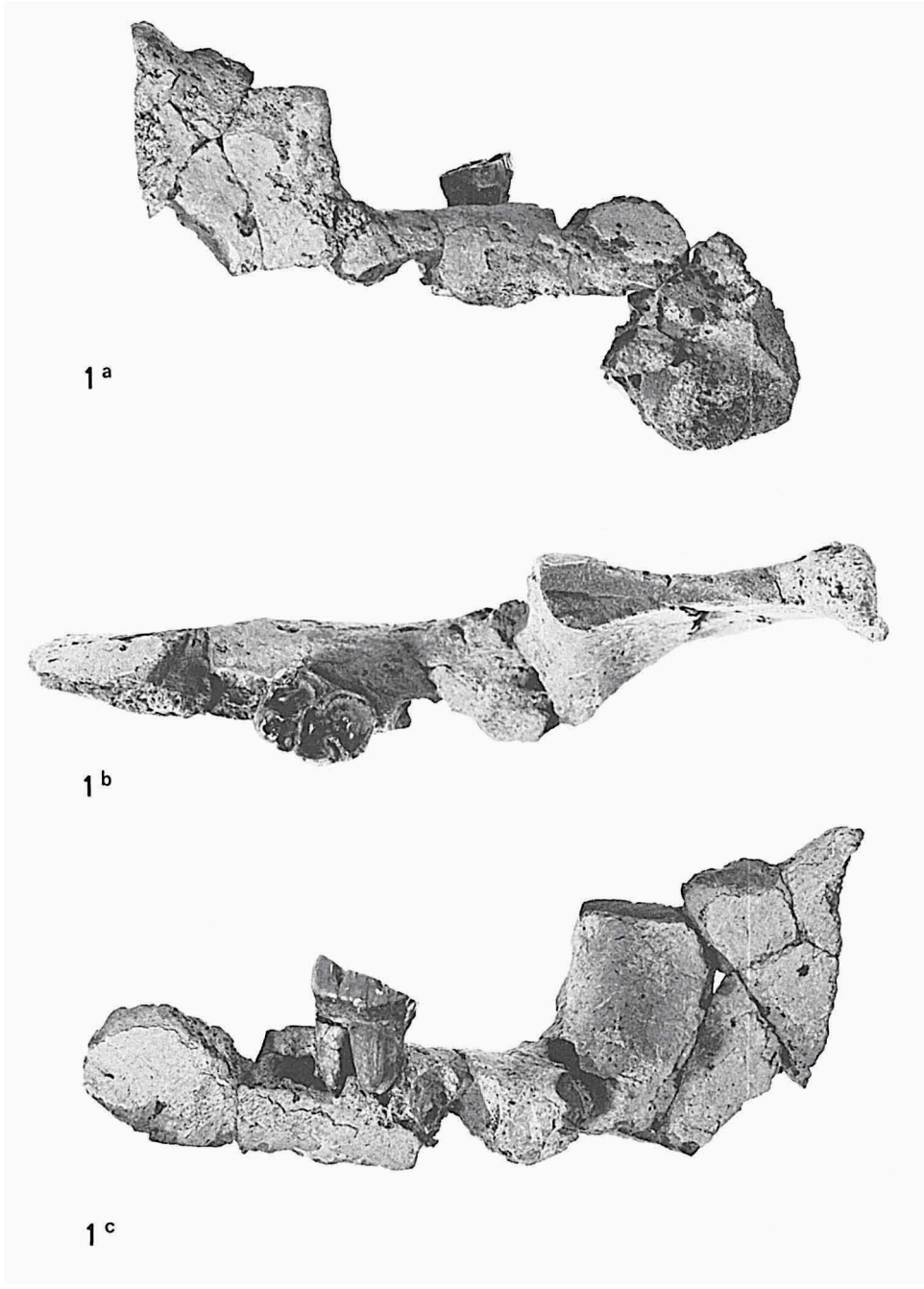

Plate 3

Metaxytherium cf. *medium* (Desmarest); Eibergen.

Fig. 1. Left mandibular condyle, RGM 175 900, x 0.5; a: anterior view; b. lateral view.

Fig. 2. Dorsal vertebra, RGM 175 902, lateral view, x 0.5.

Fig. 3. Dorsal vertebra, RGM 175 903, lateral view, x 0.5.

Fig. 4. Right humerus, proximal portion, RGM 175 952, internal view, x 0.4.

Fig. 5. Symphysial portion of mandible, RGM 175 900, anterior view, x 0.8.

Fig. 6. Neural spine, RGM 175 907, lateral view, x 0.5.

Fig. 7. Neural spine, RGM 175 908, lateral view, x 0.5.

Fig. 8. Right humerus, distal portion, RGM 175 952, anterior view, x 0.4.

Plate 3

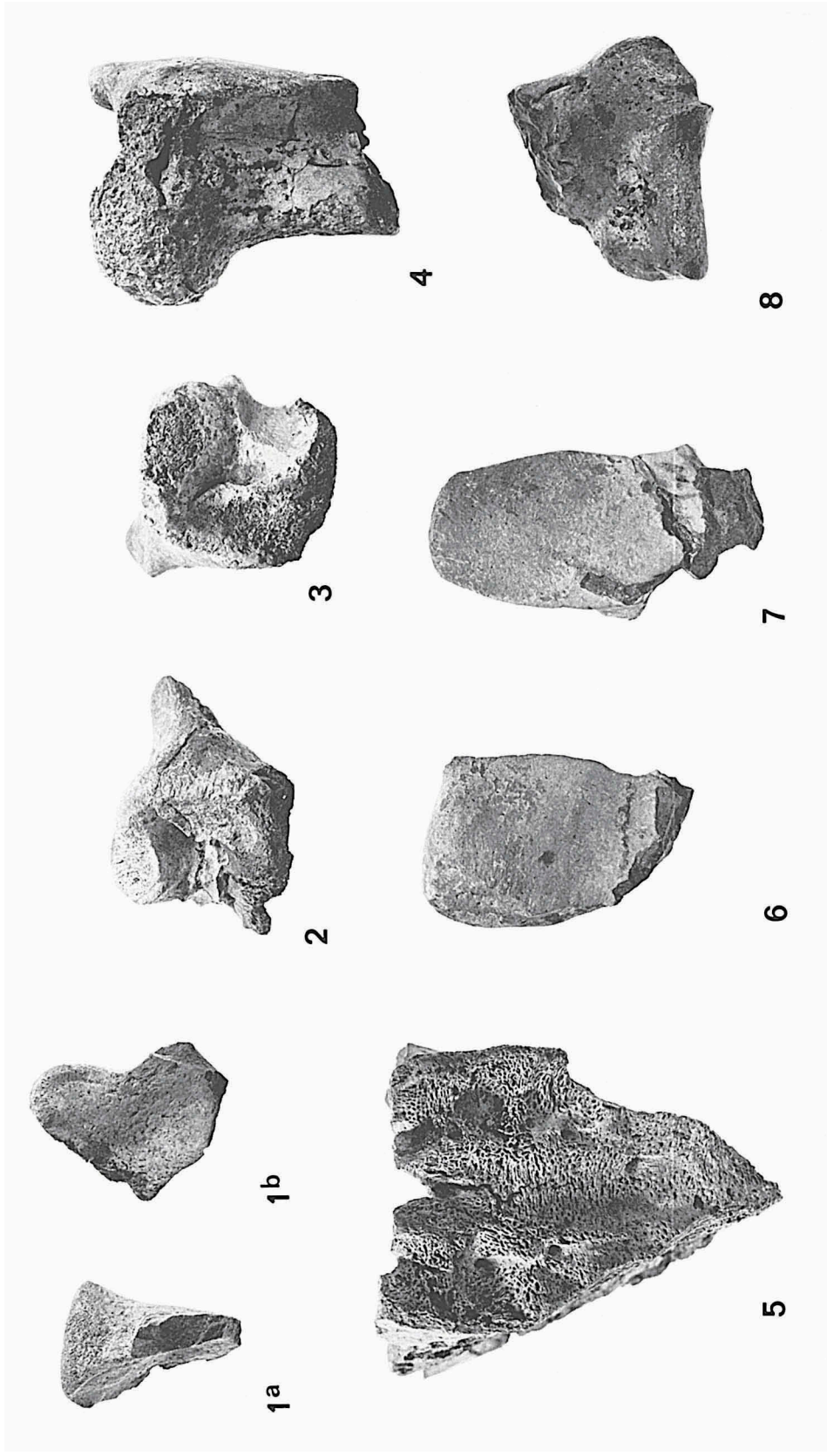

Plate 4

Metaxytherium cf. *medium* (Desmarest); Eibergen.

Fig. 1. Rib, possibly left cervical, RGM 175 915, external view, x 0.5.

Fig. 2. Left second rib, RGM 175 933, internal view, x 0.3.

Fig. 3. Rib, possibly left first, RGM 175 932, external view, x 0.5.

Fig. 4. Distal end of rib, probably right fourth, RGM 175 918, internal view, x 0.5.

Fig. 5. Distal end of rib, probably right second, RGM 175 916, internal view, x 0.5.

Plate 4

Plate 5

Metaxytherium cf. *medium* (Desmarest); Eibergen.

Fig. 1. Seventh right rib, RGM 175 921, anterior view, x 0.2.

Fig. 2. Eighth right rib, RGM 175 922, anterior view, x 0.2.

Fig. 3. Twelfth left rib, RGM 175 943, posterior view, x 0.2.

Fig. 4. Thirteenth left rib, RGM 175 944, posterior view, x 0.2.

Plate 5

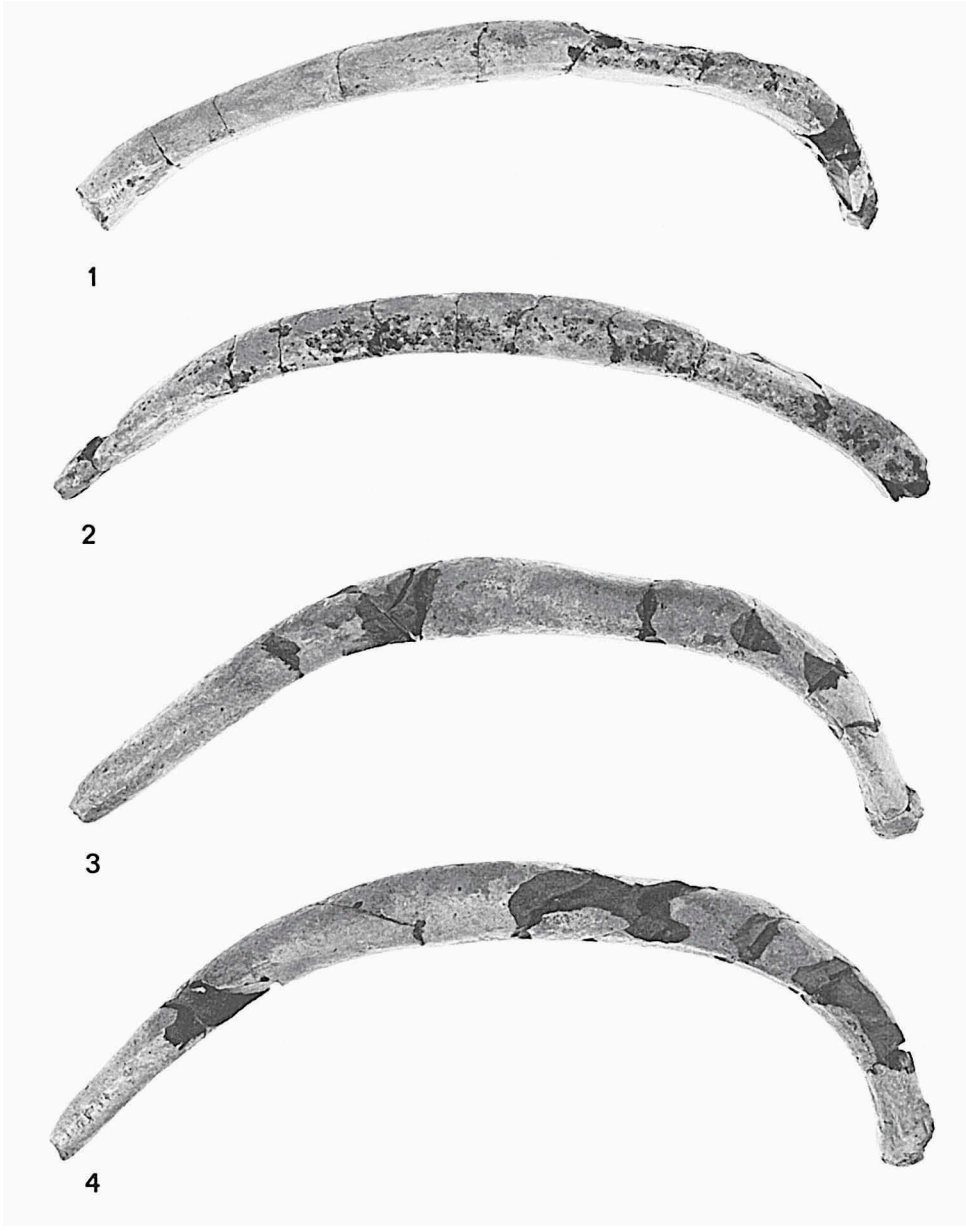

Plate 6

Metaxytherium cf. *medium* (Desmarest); Eibergen.

Fig. 1. Seventeenth left rib, RGM 175 948, posterior view, x 0.3.

Fig. 2. Sixteenth left rib, RGM 175 947, posterior view, x 0.3.

Fig. 3. Sternum, RGM 175 951, x 0.4; a: ventral view; b: dorsal view.

Plate 6