

**Reptiles from the Senonian (U. Cret.)
of Scania (S. Sweden)**

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With 20 plates and 14 figures in the text

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Introduction

A preliminary report on Senonian reptile remains from Scania was published by the writer in 1954 on material preserved in the Palaeontological Institute of the University of Lund. The present paper deals with the material belonging to all the principal Swedish museums: the Palaeontological Department of the Swedish Museum of Nat. Hist., Stockholm, the Geological Survey of Sweden, Stockholm, the Palaeontological Institute of the University of Uppsala, the Geological-Palaeontological Institute of the University of Stockholm. In addition, the writer has had access to the private collection in possession of Architect L. Nilsson, Ignaberga.¹

The investigation of all the new material did not reveal anything of particular importance in the anatomy of the reptile groups concerned but gives as a picture of the reptile fauna existing in the northern part of the European Cretaceous sea during the Senonian time.

The writer is indebted both to the late Professor G. Troedsson, and to his successor Professor G. Regnéll, Lund, for their technical help, advice, and positive criticism. I also thank the persons who placed material at my disposal, e.g. Professor E. Stensiö, Stockholm, Professor P. Thorslund, Uppsala, Professor I. Hessland, Stockholm, Dr. F. Brotzen, Stockholm, and Architect L. Nilsson, Ignaberga. Professor S. P. Welles, University of California, examined and kindly gave me his opinion on a few casts of vertebral centra. For valuable stratigraphical information of the find localities I tender my sincere thanks to Dr. F. Brotzen, Stockholm.

Previous investigations

Reptile remains from the Upper Cretaceous of Sweden were first dealt with by Sven Nilsson in 1835 (pp. 131–136; Pl. 4). He described and figured a fragment of a large reptilian skull from Köpinge Mölla, a fragment which in his opinion was of a Plesiosaurian. Moreover, on this occasion he described three plesiosaurian vertebrae from Ivetofta (Nilsson 1835, pp. 136–138; Pl. 5, figs. 2, 3, 4) and two mosasaurian teeth (Nilsson 1835, pp. 138–140; Pl. 5, figs. 1, 5, 6); the latter he considered ichthyosaurian. All this material was mentioned and re-figured by Hisinger (1837, pp. 5–7; Pls. A, B). Schröder (1885, pp. 328–329) demonstrated that the skull fragment described by Nilsson could not be of a Plesiosaurian, but was of a Mosasaurian, which he tentatively denominated *Mosasaurus scanicus*. In addition, Schröder redescribed

¹ This valuable collection has recently been donated to the Palaeontological Institute of Lund.

(1885, pp. 325–326; Pl. 15, figs. 3a–c) and refigured one of the three vertebrae from Ivetofta under the name of *Plesiosaurus* cf. *helterseni* Kiprijanoff. Finally, the latter writer (Schröder 1885, pp. 326–327, 329–333; Pl. 17, figs. 2a–c, 3a–d) also described a few Mosasaurian teeth; one of these teeth he referred to *Mosasaurus camperi* Meyer, whilst for another one he erected a new species, *Leiodon lundgreni*. Nilsson's and Schröder's material will be discussed below (pp. 466–470).

In the years 1915–1923, G. Holm figured a considerable part of the Senonian reptile material from Scania preserved in the Swedish Museum of Natural History and had several plates printed, all of which are unpublished. The following figures from these plates have been reproduced in this paper: Pl. 3, figs. 3–4; Pl. 4, figs. a and c; Pl. 6, figs. 2–5; Pl. 8, fig. 3; Pl. 9; Pl. 14, figs. 1 and 4; Pls. 17–19; Pl. 20, figs. 1–3).

Fortuitous finds of vertebrates from the Cretaceous of Scania are listed in papers by Moberg (1884), Lundgren (1888 and 1888a), Hennig (1910), Lundegren (1934) and Troedsson (1946 and 1954).

Material and localities

The material dealt with in this paper consists chiefly of detached skeletal remains. The bones are greyish or bluish black; the enamel of some of the Plesiosaurian teeth is somewhat iridescent. Although they are well preserved with regard to their macroscopical structure, these remains are all infiltrated with a dark bituminous substance to such an extent that they show little or nothing of their minute structure.

Almost all of the material has been collected in connexion with limestone quarrying and has been given or sold to the various institutes by the quarry labourers. The principal localities are the Island of Ivö, Axeltorp in the parish of Näsrum, Balsvik in the parish of Österslöv, and Ignaberga limestone quarry in the parish of Ignaberga; all in north-east Scania. Some reptile remains comprising teeth and detached bones have, however, been found both at Båstad in the north-western corner of Scania and at Köpinge in the southern part of the same province (fig. 1).

More than $\frac{1}{4}$ of all the material dealt with, comprising hundreds of reptile teeth and bones, was collected in 1915–1925 in a small limestone deposit at Blaksudden, Ivö. Since the limestone quarrying in Blaksudden ceased in 1931 no additional material can be found at this locality. The matrix was here a very coarse shell-fragment limestone, resting upon a thick kaolin deposit. The southern part of the shell-fragment limestone was piled up against a hill of Archaean bed-rock, called Ivö Klack, which according to Voigt (1929, p. 67) and Lundegren (1934, p. 227) was an island in the Senonian sea. This shell-fragment accumulation was certainly formed by strong sea currents and breakers, and many of the reptile bones indicate by their preservation that they were rolled by the waves before being embedded in the sediment. The fact that there are remains of serpulids, bryozoans, and oysters on certain other bones proves that these bones must have lain more or less fixed on the bottom along the shore before being completely covered with sediment.

The majority of the reptile remains dealt with may be from stranded carcasses. In spite of the fact that the Plesiosaurians obviously were quite common, as is proved by the abundant occurrence of vertebral centra, no identifiable parts of the skull of this group are found in all of the material investigated. Since determinable remains of the head of other reptilian groups also are rare in the material, it may be inferred with reasonable certainty that the heads frequently were detached from the bodies

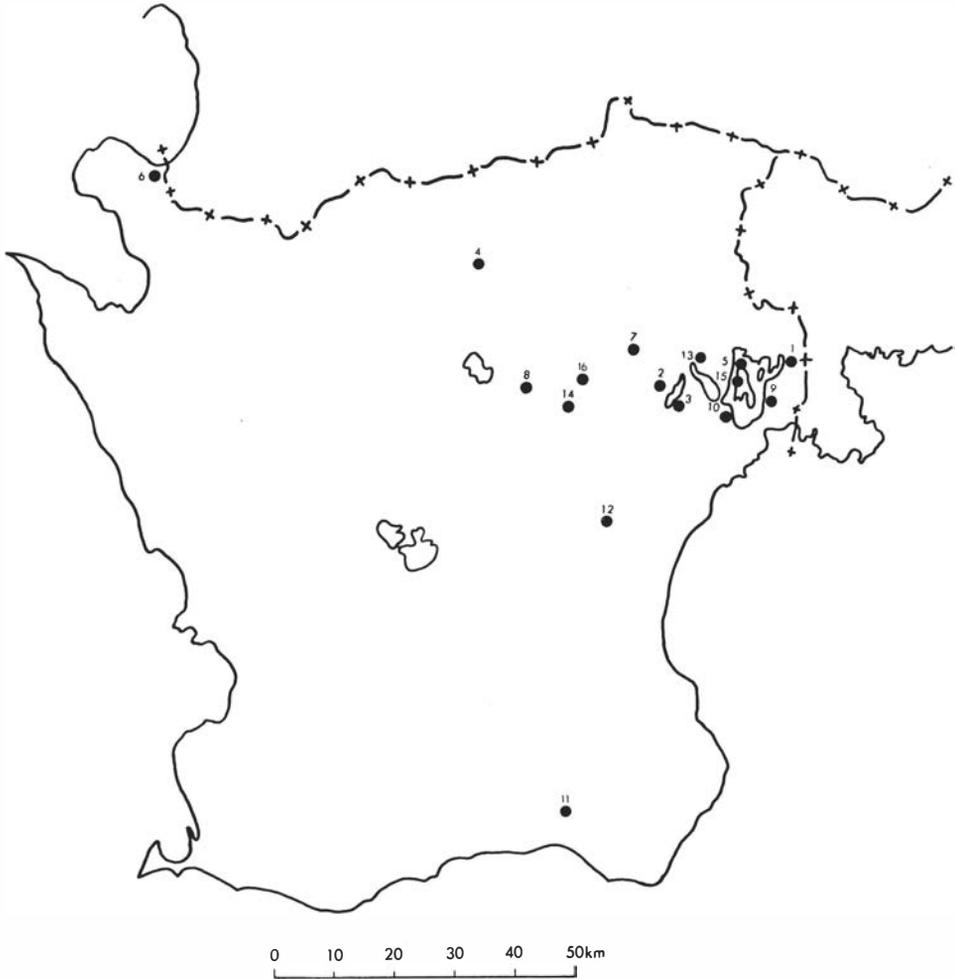


Fig. 1. Map of Scania, showing the localities from which remains of reptiles have been recorded.

- | | | | |
|--------------|---------------------------|--------------------|--------------------------------|
| 1. Axeltorp. | 5. Blaksudden, Ivö. | 9. Ivetofta. | 13. Oppmanna. |
| 2. Balsberg. | 6. Båstad. | 10. Kjuge. | 14. Ringeleslätt. ² |
| 3. Balsvik. | 7. Hanaskog. ¹ | 11. Köpinge Mölla. | 15. Ugnsmunnarna, Ivö |
| 4. Bjärnum. | 8. Ignaberga. | 12. Maltesholm. | 16. Åraslöv. |

by decaying far out at sea, or were bitten off by sharks and other beasts, whereas, distended by gas, the other parts of the carcasses drifted ashore. In harmony with this conclusion is the fact that comparatively few vertebral centra from the anterior and middle parts of the cervical region of the vertebral column have been found. Most of the cervical centra may therefore have become detached simultaneously

¹ At this locality only indeterminable fragments have been found.

² See below, p. 475.

with the heads or fairly soon afterwards. The presence of numerous isolated teeth in the littoral sediments must mean, however, that several carcasses with skulls also were carried ashore where, on account of their fragile structure as a whole, the skulls became completely smashed into pieces by the breakers.

The following stratigraphic terms are used: Emscher ("Westfalicus Senonian"); Lower Campanian ("Mammillatus Senonian"); Upper Campanian and Lower Maastrichtian ("Mucronata Senonian").

For particulars concerning the various localities mentioned in the following account the reader is referred to text-fig. 1 (see also Lundegren 1934, Brotzen 1945 and Birkelund 1957).

The names of the institutes from which material has been borrowed have been abbreviated as follows: LM, the Palaeontological Institute of the University of Lund; UM, the Palaeontological Institute of the University of Uppsala; RM, the Palaeozoological Department of the Swedish Museum of Natural History, Stockholm; S.G.U., the Geological Survey of Sweden, Stockholm; SM, the Geological Institute of the University of Stockholm.

The Cretaceous reptile material belonging to UM lacks catalogue numbers; the specimens belonging to this institute are therefore referred to with provisional designations R.p. 1-54.

Order CHELONIA Brongniart 1805 (As order Chelonii)

The material available contains several remains of turtles, most of which are very fragmentary. In one instance only (*Osteopygis?* sp), a tentative generic determination could be made.

Genus *Osteopygis* Cope 1868

Diagnosis of *Osteopygis*: see Hay (1908, p. 127).

GENOTYPE.—*Osteopygis emerginatus* Cope.

Osteopygis? sp.

Pl. I. Text-fig. 2.

MATERIAL.—The only material of this form is the holotype, specimen LM, LO 3834 t, presented to the Geol. Inst., Lund, by Mr. Nils Winquist, manager of the Cement-works, Maltesholm.

The specimen is an imperfect carapace, comprising the nuchal, 8 neurals, 8 pairs of costals, and left peripherals Nos. 1-7. Amongst these bones only the neurals, the left costals Nos. 1-4, and the left peripheral No. 1 are complete. The nuchal (*nu*, text-fig. 2) is imperfect, but its original, total width can be approximated. The right costal No. 1, the left costal No. 8 and the peripherals Nos. 6 and 7 all are fragmentarily preserved (text-fig. 2). These bones are exposed in ventral (internal) view, whereas their dorsal (external) faces are covered with rock. Since the carapace is very fragile, the latter faces could not be exposed. Taken as a whole the carapace is fractured to such an extent that one cannot everywhere distinguish clearly between cracks and true sutures. Under these circumstances it is not impossible that in

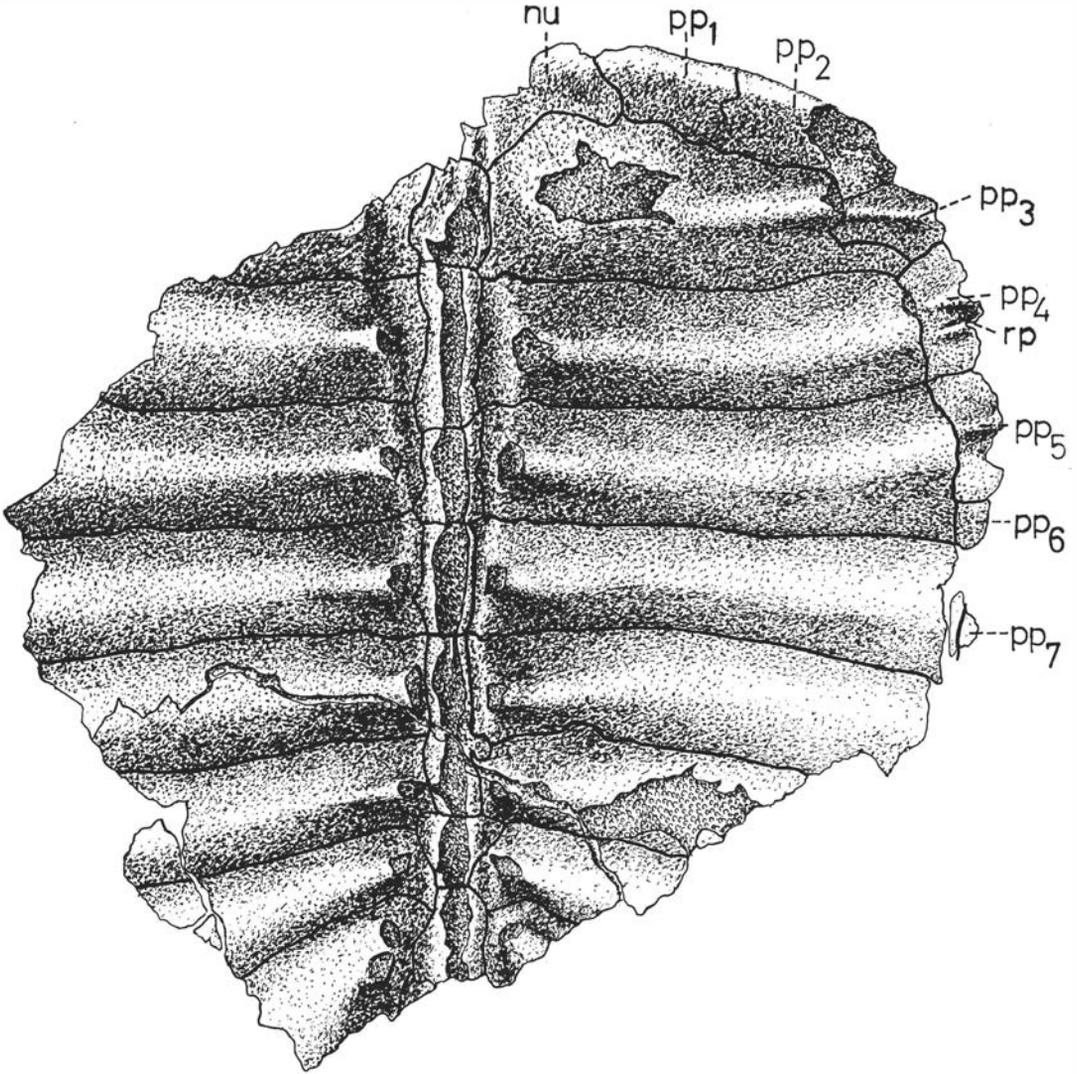


Fig. 2. *Osteopygis?* sp. Preserved parts of carapace in ventral view. LM, LO 3834 t. $\times 1/2$. nu, nuchal; pp₁-pp₇, left peripheral plates Nos. 1-7; rp, "rib pit" of 4th peripheral plate.

places the actual boundaries between the individual bones are slightly different from those shown in Text-fig. 2.

DESCRIPTION.—In its present state of preservation the carapace is 283 mm. long, and 265 mm. broad, but its original total length may be assumed to have been approximately 300-350 mm. Measurements of some details are given in table 1.

As is fully clear from its preserved parts, the carapace is well ossified and lacks

fontanels. The preserved peripheral plates are rigidly attached to the other central parts of the carapace by sutures.

Except the 1st, 7th and 8th pairs the costal plates are roughly of a rectangular shape (text-fig. 2). At the neurocostal suture the 1st left costal plate is 30 mm broad, but about 20 mm distally to this suture it widens to a breadth of 45 mm. Further towards the distal end, however, it narrows to 27 mm in breadth. The 7th and 8th pairs, on the other hand, widen considerably distally throughout their extension. The individual costal plates exhibit a low, rounded, proximo-distal ridge showing that each has incorporated a pre-existing, free rib. There are no traces of any attachment areas for the ilia of both sides.

In the 4th peripheral plate the area overlapping the free end of the rib, the "rib pit" (Hay 1908, and other writers), is a pronounced triangular depression (*rp*, text-fig. 2), 13 cm broad at its proximal border and about 18 mm long in a proximo-distal direction. The free rib end was only overgrown to some extent by the anterior and posterior margins of the "rib pit" and was hence not enclosed in this "pit". A similar condition concerning the relations between the rib ends and the peripheral plates is found in the genus *Osteopygis* (cf. Zangerl 1953, pp. 214–215).

REMARKS.—To judge from its broad, flattened shape the carapace must have belonged to a purely marine form. The absence of attachment areas for the ilia proves that one cannot be concerned in this instance with a Pleurodire. As has been mentioned, the carapace is well ossified and lacks fontanels. A carapace of a type similar to that of this specimen is found only in the non-Pleurodiran genera *Glyptops* Marsh 1890, *Baëna* Leidy 1906, and *Osteopygis* Cope 1868 (cf. Hay 1908, pp. 45–82, text-figs. 17–68, pls. 5–20; pp. 127–150, text-figs. 134–184, pls. 26–28; Russel 1934, pp. 101–110, pls. 1–6; Zangerl 1953, pp. 205–215, text-figs. 85–90, pl. 26).

Table 1. Measurements of the carapace of *Osteopygis?* sp.

Neurals and peripherals no.	A mm.	B mm.	C mm.	D mm.	E mm.	F mm.	G mm.	H mm.	I mm.
1	30	16	30	26	<i>41</i>	23	7	<i>35–40</i>	<i>65–70</i>
2	40	16	35	<i>30</i>	—	22	—		
3	27	18	30	<i>35</i>	—	—	—		
4	29	13	32	31	—	—	—		
5	32	18	30	33	—	—	—		
6	22	13	26	—	—	—	—		
7	12	10	21	—	—	—	—		
8	27	19	—	—	—	—	—		

A = Length of neurals.

B = Breadth of neurals posteriorly.

C = Breadth of left costals (proximal ends).

D = Length of the proximal suture of left peripherals.

E = Length of the external border of left peripherals.

F = Breadth of left peripherals.

G = Thickness of left peripherals.

H = Anteroposterior length of nuchal.

I = Length of anterior border of nuchal.

Estimated measurements in italics.

In *Glyptops* (represented in the Upper Cretaceous by a single species) the neurals are hexagonal, but in the present carapace they are roughly rectangular. Therefore, the specimen is most certainly not referable to *Glyptops*.

In the genus *Baëna* the limbs are decidedly more adapted for walking than for swimming (cf. Hay 1908, p. 58, and Russel 1934, pls. 2-5), and the tail is long. These features do not indicate a purely marine mode of life, and consequently the specimen here dealt with cannot possibly belong to *Baëna*.

The specimen from Scania agrees with *Osteopygis*, particularly with the holotype of *O. gibbi* Wieland 1904 (Marsh collection No. 78, Yale Univ.; cf. Hay 1908, p. 132, text-fig. 142; Pl. 26, fig. 1, Pl. 27, fig. 1) in the following respects: a) the shape and proportions of the carapace plates; b) the attachment of the peripheral plates to the costal plates; and c) the shape of the "rib pits".

As may be gathered from the above discussion, the carapace here dealt with resembles most nearly that of *Osteopygis* and it is therefore provisionally referred to this genus. Hay (1908, pp. 127-150) distinguished eight species of *Osteopygis*. In his revision of the family *Toxochelyidae*, Zangerl (1953, p. 208), however, concluded that all the material ascribed to *Osteopygis* by Hay and other previous writers is referable to one species only, viz. *O. emarginatus* Cope 1868.

The specimen from Scania is probably specifically distinct from the American species. As can be seen from a comparison between table 1 and the tables in Hay's work, it is considerably smaller than any of the American species. In spite of this it is most certainly an adult individual, the sutures between the different plates being almost obliterated.

GEOLOGICAL HORIZON.—Lower Campanian.

LOCALITY.—Maltesholm.

Chelonian remains indeterminable as to family, genus et species

Pl. 2, figs. 1-2. Text-figs. 3-4.

MATERIAL.—Amongst the numerous indeterminable Chelonian remains from different localities there are fragments of carapaces, plastrons, girdle bones and limb-bones. Of these remains only the nine following will be dealt with: 1 nuchal plate (UM, R. p. 1), 1 costal plate (LM, LO 3835 t), 1 large scapula (LM, LO 3836 t), 5 small scapulae (RM, R. 1484 d; UM, R.p. 2-5), and 1 pubis (LM, LO 3737 t).

The large scapula (LO 3836 t) and the pubis (LO 3837) are still partially concealed by the matrix, but cannot be removed from this since they are very fragile.

DESCRIPTION.—The nuchal plate (text-fig. 3) is 38 mm long in a rostro-caudal direction along the median line (*m*). The length of its anterior margin (*a-a1*) is 51 mm and the thickness at this margin is approximately 13 mm. The bone is peculiarly shaped, possessing a large postero-lateral process (*p*) possibly corresponding to a dermal bone component otherwise normally participating in the forming of the 1st costal plate. A small portion of the lateral margin of the process is thin (*t*, text-fig. 3), without rugosities, and of such a general appearance that it must be assumed to have formed part of the boundary of a small perforation or fontanel. The grooves for the nuchal horny scute and for the other horny scutes on the dorsal face of nuchal plate are all well shown.

The costal plate (Pl. 2, fig. 1) is incomplete in that its distal end is missing, but

Fig. 3. Indeterminable Chelonian. Semi-diagrammatic restoration of an incomplete nuchal plate in dorsal aspect. UM, R.p.l. $\times 1/2$. Grooves caused by the deepened margins of horny scutes denoted with broad dotted lines; uncertain outlines denoted with an interrupted line.

$a-a_1$, anterior margin; m , median line; p , postero-lateral process; t , thin part of the lateral margin participating in the boundary of a small fontanel.

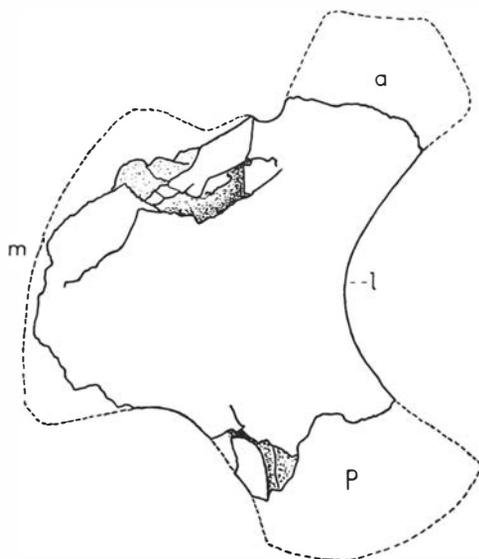
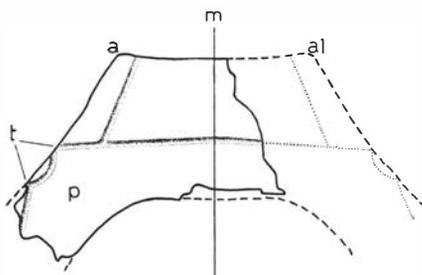


Fig. 4. Indeterminable Chelonian. Semi-diagrammatic restoration of an incomplete pubis. Out-lines of reconstructed parts denoted with interrupted lines. LM, LO 3837 t. $\times 1/4$.

a , anterior process; l , lateral margin; m , ventro-medial margin; p , posterior process.

certain parts of its neuro-costal and inter-costal sutural margins are preserved so that at least the proximal portion of the plate could be reconstructed. The dimensions of this plate are as follows: length from neuro-costal sutural margin to distal fracture, 152 mm; breadth between proximal ends of inter-costal sutural margins, 68 mm; thickness at proximal end 9 mm. In view of the fact that it is more than twice as broad as the costals in *Osteopygis?* sp. described above, it has obviously belonged to a much larger individual.

Taken as a whole the costal plate under discussion is very slightly arched in a transverse direction, and it may therefore have belonged to a species whose carapace was still more dorso-ventrally flattened than that in *Osteopygis?* sp. Moreover, it also differs from the corresponding plates of *Osteopygis?* sp. by the absence of a pleural ridge. Its dorsal face exhibits grooves marking the boundaries between one costal and two vertebral horny scutes. Somewhat further distally on this face there is a

shallow groove parallel with the longitudinal axis. This groove, which is about 44 mm long and 8 mm broad may be a scar indicating a healed injury of the shell.

The largest scapula, LO 3836 t; Pl. 2, fig. 2, lacks both its antero-ventral portions bearing the glenoid fossa, and its other end parts, i.e. the ends of the scapula proper and acromion. In its present imperfect state of preservation the bone is 240 mm long, but its total, original length may have been approximately 390 mm. Consequently we are concerned in this instance with a bone belonging to a large individual. The broader part (*a*) of the bone may be the scapula proper whilst the narrower part (*b*) probably is the acromion. If this be true, we are concerned with the remains of a scapula from the right side.

The five other scapulae available are all considerably smaller and more fragmentarily preserved than the scapula dealt with above. One of the five, minor scapulae (UM, R.p. 3) in question is flatter than the others, and the possible acromion is relatively broader. This scapula probably represents a species of its own.

The pubis (text-fig. 4) is strikingly large and may therefore have belonged to the same species as the largest scapula LO 3836 t; Pl. 2, fig. 2. The preserved piece of the bone is about 210 mm long between the fracture areas of the anterior and posterior processes (*a*, *p*, fig. 4), and about 160 mm broad between the lateral and ventro-medial margins (*l*, *m*, fig. 4).

GEOLOGICAL HORIZON.—Lower Campanian.

LOCALITIES.—The costal (LM, LO 3835 t), the large scapula (LM, LO 3836 t) and the pubis (LM, LO 3837 t) come from Ignaberga; all the other indeterminable Chelonian bones dealt with above have been found at Blaksudden, Ivö.

Sub-order PLESIOSAURIA Blainville 1835

TAXONOMY.—During the last two decades important contributions to our knowledge of the anatomy, phylogeny, and taxonomy of the Plesiosaurians have been published by White (1940, pp. 451–467), Welles (1943, pp. 196–207), Romer (1953, pp. 190–199; 595), and Saint-Seine (1955, pp. 429–456). The following classification of the group by Welles in 1943 (p. 212) is adopted in the present paper:

Sub-order PLESIOSAURIA

- A. Super-family PLIOSAUROIDEA (brachydiran forms)
 - Family 1. PLIOSAURIDAE (Jurassic–Lower Cretaceous¹)
 - Family 2. POLYCOTYLIDAE (Cretaceous)
- B. Super-family PLESIOSAUROIDEA (dolichodiran forms)
 - Family 1. PLESIOSAURIDAE (Jurassic)
 - Family 2. ELASMOSAURIDAE (Upper Jurassic and Cretaceous)

TERMINOLOGY.—Following Goodrich (1930, p. 45) and Romer (1955, p. 177) I have exchanged the frequently used inadequate term *dorsal vertebrae* for *thoracic-lumbar*

¹ One single species, *Kronosaurus queenslandicus* Longman 1924, is known from the L. Cretaceous, Queensland, Australia.

vertebrae. With regard to the terminology of the vertebral column I have else chiefly followed Welles (1943; 1952).

Since all the series of vertebral centra available to the writer are incomplete, the numerical order of the individual cervical centra from in front backwards is unknown. The centra of each series are therefore numbered in the reverse direction, i.e. from the pectoral region forwards, and are therefore referred to as *pre-pectorals* Nos. 1, 2, 3 etc. In a similar way the thoracic-lumbar centra are described as *pre-sacrals* Nos. 1, 2 etc.

The terms *brachydiran* and *dolichodiran* are used as synonyms for short-necked, respectively long-necked; these two terms are hence not used in taxonomic sense.

METHODS.—Welles (1943, pp. 135–139) listed the characters of the vertebrae from the various regions of the vertebral column in dolichodiran Plesiosaurians. On the basis of the characters thus listed and by a direct comparison with an almost complete skeleton of *Muraenosaurus durobrivensis* Lydekker 1889 in the Upsala collection, I have been able to establish to which regions of the vertebral column the series of vertebral centra in my material belong, and also to assort the numerous detached centra according to their regional position. In order further to confirm my identification of the different skeletal remains I have also studied material in the Paleontological Institute of Tübingen.

In the measuring of the vertebral centra and in the calculating of their height: length and breadth : length indices I have used the same methods as Welles (1952). Although being of little importance for specific and generic determinations, the vertebral indices, as appears in a paper by Welles (1952, pp. 50–52), are nevertheless very useful for the distinguishing of the families of the Plesiosaurians.

Super-family PLIOSAUROIDEA Welles 1943

Family POLYCOTYLIDAE Williston 1908

The remains from Scania referable to this family are so poorly preserved that I have found it necessary to describe them as indeterminable as to both genus and species.

Genus et species indet.

Pl. 3, figs. 1–2.

MATERIAL.—Under this title I group four incomplete cervical vertebrae (LM, LO 3838 t¹; RM, R. 860; UM, R.p. 6 and 7), which all seem to be of a uniform type.

DESCRIPTION.—The measurements and indices of the centra in question are given in table 2. For comparison, the corresponding figures of the 16th cervical centrum (4th or 5th pre-pectoral) of *Dolichorhynchops osborni* are added from Williston 1903, p. 36.

The neurapophysis is missing in all four vertebrae, which hence are represented by the centra and parts of the cervical ribs only. Three of the centra are damaged dorsally to such an extent that nothing is seen of the neural canal, whereas in the vertebra LO 3838 t the midmost and anterior parts of the bottom of this canal are preserved. The midmost part of the canal in question exhibits two comparatively wide foramina for nutritive vessels. In three of the vertebrae the end faces are suffi-

¹ Originally in L. Nilsson's collection; see foot-note 1, p. 432.

Table 2. Measurements and indices of four Polycotyloid cervical centra from Scania and one corresponding centrum of *Dolichorhynchops osborni*. (Estimated measurements italicized).

	Length mm.	Height mm.	Breadth mm.	H:L ind.	B:L ind.
Scanian vertebrae:					
R. 860	39	59	73	151	187
R.p. 6	43	—	76	—	177
R.p. 7	<i>40</i>	67	85	<i>168</i>	<i>213</i>
LM, LO 3838 t	38	50	60	132	158
<i>D. osborni</i> :					
16th cervical	26	38	45	142	173

ciently well preserved to enable an exact measurement of the total length of the centra (see table 2), whilst this is impossible in the vertebra R.p. 7 where the posterior end face is missing. The end faces are strongly concave with rounded off margins. The lateral and ventral faces of the centra are somewhat concave both in rostro-caudal and transverse direction. On the ventral face one finds two or (in the centrum R.p. 6) three large circular foramina for nutritive vessels (*nf*, Pl. 3, fig. 2b).

The cervical ribs are cercidopleuros and are fused with the centra without any sign of sutures. In the vertebra R.p. 6 the left rib is well preserved (*cr*, Pl. 3, fig. 2a, b).

REMARKS.—As is clear from their height : length and breadth : length indices and from the deep concavities of their end faces the vertebrae are of the Pliosauroid type. These characters and the fact already emphasised that the ribs are cercidopleurous jointly prove that the vertebrae under discussion belong to the family *Polycotylidae* amongst the *Pliosauroida* (see Cope 1870, pp. 34–38, Pl. 1, figs. 1–12; Williston 1903, pp. 13–52, text-figs. 1–12, Pls. 1–22, and pp. 57–72, Pls. 24–26 and 29).

GEOLOGICAL HORIZON.—Lower Campanian.

LOCALITIES.—The vertebrae R. 860 and R.p. 6 and 7 come from Blaksudden, Ivö; LO 3838 t was found at Ignaberga.

Fam. POLYCOTYLIDAE? Williston 1908

The material described under this title comprises several detached typical Pliosauroid teeth all of which conceivably are from forms belonging to the family *Polycotylidae*.

Genus et species indet.

Pl. 3, figs. 3–4.

MATERIAL.—Twelve detached teeth (RM, R. 1125, 1184–1186, 1254, 1298; UM, R.p. 8–13).

DESCRIPTION.—The dimensions of the best preserved tooth (UM, R.p. 8) are as follows: height of crown: 21 mm; maximum diameter of crown: 8 mm; height of root: 26 mm; maximum diameter of root: 10.1 mm. Three of the teeth—RM, R. 1125, 1185 and 1186—are considerably larger than the others; the crown in R. 1125 may have been about 40 mm high, whilst its maximum diameter amounts to 16 mm. (Pl. 3, figs. 4 a–e.) The crown in all the twelve teeth concerned is conical and recurved; it is circular in par basal sections, and its surface is ornamented with delicate apico-basal ridges, more densely set in the smaller teeth than in the larger ones. The upper part of the convex side of the crown is smooth, or almost so. The root is preserved in two teeth only; it is comparatively high, with a large pulp cavity extending a short distance upwards into the crown.

REMARKS.—To judge from what is known of the Pliosauroid teeth described by Owen (1851, pp. 56–57; Pl. 9, fig. 11; Pl. 10, figs. 7–9; Pl. 11, figs. 1–5; Pl. 45, figs. 1–5; 1861, pp. 20–22; Pl. 4, fig. 3), Lydekker (1889, p. 146, fig. 45, p. 155, fig. 51, p. 173, fig. 58), Williston (1903, pp. 15–16), Andrews (1910, vol. 2, p. 10, Pl. 2, figs. 2–4; p. 28, Pl. 3, figs. 2, 3; p. 202, Pl. 4, figs. 3–5 and Saint-Seine (1955, p. 432, fig. 12; etc.) the teeth from Scania dealt with in this instance must belong to Pliosauroid Plesiosaurians. Since they occur in the Upper Cretaceous beds they may be from Polycolylids. Under these circumstances it is possible that they belong to the same form or forms as the vertebrae dealt with above.

GEOLOGICAL HORIZON.—Lower Campanian.

LOCALITY.—Blaksudden, Ivö.

Super-family PLESIOSAUROIDEA Welles 1943

Family ELASMOSAURIDAE Cope 1869

Genus *Elasmosaurus* Cope 1868

A complete bibliography of this genus is given by Welles (1952, p. 52–53).

DIAGNOSIS.—See Welles 1952, p. 53.

In his revision of the North American Elasmosaurs, Welles (1943 and 1952) maintains that the majority of the species which earlier writers had referred to *Elasmosaurus* should not be assigned to this genus. In his opinion, *Elasmosaurus s. str.* comprises at present only two American species, viz. the genotype, *E. platyurus* Cope 1868, and *E. morgani* Welles 1949, whereas other species are referred to new genera, viz. *Thalassonomosaurus* Welles 1943, *Hydralmosaurus* Welles 1943, *Styxosaurus* Welles 1943, and *Alzadasaurus* Welles 1943.

The two European "*Elasmosaurus*" species, "*E.*" cf. *helterseni* and *E?* cf. *gigas*, both of which are dealt with below on the basis of material from Scania, are very poorly known. "*E.*" cf. *helterseni* is, however, doubtless and Elasmosaurid, probably nearest akin to *Elasmosaurus*. With regard to all of its characters so far known *E.?* cf. *gigas* also agrees with the other representatives of the family *Elasmosauridae*, but these characters are not quite sufficient to show conclusively that it actually belongs to this family.

“*Elasmosaurus*” cf. *helmerseni* (Kiprijanoff 1882)

Pl. 4.

1882 *Plesiosaurus helmersenii*. — Kiprijanoff, p. 17, Pl. 5, figs. 1, 5; Pl. 6, fig. 5; Pl. 7; Pl. 8, fig. 1-3; Pl. 9, fig. 1, 2, 4; Pl. 10-14.

1885 *Plesiosaurus helmersenii*. — Schröder, p. 310, Pl. 15, figs. 1 a-c, figs. 2 a-c; p. 325, Pl. 15, figs. 3 a-c.

1911 *Elasmosaurus helmersenii*. — Bogolubov, p. 359, Pl. 14, fig. 6; Pl. 15, fig. 6.

1914 *Plesiosaurus helmersenii*. — Wegner, p. 303.

DIAGNOSIS.—A large species with certain *Elasmosaurus*-like characters. The cervical centra lack a keel between the ventral foramina for nutritive vessels.

LECTOTYPE.—An anterior cervical centrum in the Museum of the Academy of Science, Leningrad (Kiprijanoff 1882, Pl. 11, figs. 3b-d; see below, p. 445).

MATERIAL.—The material from Scania comprises only a single centrum (RM, R. 991) from the anterior part of the cervical region.

DESCRIPTION.—The measurements and indices of the centrum from Scania just referred to are found in Table 3, where, in comparison, measurements and indices are also given of another centrum, actually that from Prussia which Schröder (1885, pp. 310-312; Pl. figs. 1 a-c) has referred to *Elasmosaurus helmersenii*. In his description of the type material Kiprijanoff did not publish any measurements which could be used for the calculation of indices. Under these circumstances and since it is also clear that the reproductions contained in his paper are incorrect with regard to the proportions, these reproductions are unsuited for the obtaining of reliable measurements for a comparison with the specimen from Scania.

Table 3. Measurements and indices of 2 cervical centra of “*Elasmosaurus*” cf. *helmerseni*.

Locality	Length mm.	Height mm.	Breadth mm.	H:L ind.	B:L ind.
Scania	60	45	69.5	75	116
Prussia	105	72	107	69	102

The centrum from Scania is fairly well preserved. The end faces are kidney-shaped in outline, with sharp-edged margins. The neurapophysis (*np*, Pl. 4, figs. a and b) is completely fused with the centrum without any sign of sutures but is broken off so that only its basal parts are shown. The neural canal is about 12 mm broad. In its midmost part there are two closely spaced foramina for nutritive vessels. The lateral face of each side, i.e. the face between the neurapophysis and the cervical rib, is somewhat concave in a rostro-caudal direction. This face is also characterised by the presence of a conspicuous, sharp-edged, longitudinal ridge (*lr*, Pl. 4, fig. b). The cervical ribs (*cr*, Pl. 4, figs. a-c), of which only the most proximal parts are preserved, are fused with the centrum. The ventral face is fairly deeply concave in both rostro-caudal and longitudinal directions. Slightly behind its middle the latter face shows

two foramina for nutritive vessels, situated approximately 6 mm apart. The bony wall separating them does not rise to form any ridge or keel.

REMARKS.—Kiprijanoff based his species upon vertebral centra and limb bones partly found “im Sewerschen Osteolith oder Kursk’schen Sandsteine (Samorod)”, partly “im grünen Sandstein im Petrov’schen Kreise des Saratow’schen Gouvernements beim Kirch-Dorfe Serdoba”. According to Lydekker (1889) these two localities would lie in the Gault. Bogolubov (1911) was of the opinion that the beds at Kursk are of a Cenomanian age; in this case those at Serdoba would belong to the Senonian. The bones from Kursk he referred to a new *Elasmosaurus* species, *E. kurskensis*, and hence it follows that only the material from Serdoba should belong to *E. helmerseni*. The latter material includes 5 cervical centra, 4 thoracic-lumbar centra, 4 caudal centra, 1 humerus and 1 fibula (Kiprijakoff 1882, Pls. 11, 12, 13).

Since Kiprijanoff’s account does not show clearly that all these bones belong to one and the same individual, it is necessary to choose a lectotype of *E. helmerseni*. As such I suggest the typical and well preserved cervical centrum figured by Kiprijanoff in Pl. 11, figs. 3b–d.

Kiprijanoff’s material is very incomplete and does not show any fully reliable characters for a proper definition of the species. A noticeable condition is, however, the absence of the keel which otherwise is normally found on the anterior cervical centra of *Elasmosaurids* between the ventral foramina for nutritive vessels. With regard to this condition the centrum from Scania agrees with the Russian ones, and I have therefore provisionally referred it to “*Elasmosaurus*” cf. *helmerseni*. Although the presence of the ventral keel concerned is said by Welles (1943, p. 135) to be one of the general characters of the dolichodiran Plesiosaurians, there can be no doubt that “*E.*” *helmerseni* is an *Elasmosaurid*. This is also proved by the relative length of its cervical centra in the material as a whole, and by the fact that the centra are equipped with a lateral longitudinal ridge. The presence of such a ridge (Cope’s “lateral angle”) is currently regarded as one of the distinctive characters of the family *Elasmosauridae* (cf. Welles 1943, p. 184). Concerning this particular character Welles (1943, p. 137) writes as follows: “Pravoslavlev (1919) considered this ridge to be an indicator of the muscular development and therefore the length of the neck. This is probably valid, as the ridge is absent in short-necked forms.”

Since the species here dealt with is still very imperfectly known, it is impossible to decide with any certainty whether it belongs to *Elasmosaurus* as defined by Welles.

On account of certain similarities to a caudal vertebra from Saratov, Schröder (1885, pp. 325–326; Pl. 15, figs. 3a–c) concluded that a sacral vertebra (LM, LO 168 t) from Ivetofta, previously described by Nilsson (1835) and Hisinger (1837), belongs to “*E.*” cf. *helmerseni*. The latter vertebra is, however, indeterminable, and Schröder’s opinion is therefore unattainable.

GEOLOGICAL HORIZON.—Lower Campanian.

LOCALITY.—Blaksudden, Ivö.

Elasmosaurus? cf. *gigas* (Schröder 1885)

Pl. 5.

1885. *Pliosaurus?* *gigas*. — Schröder, p. 322, Pl. 16, figs. 1a–b.

1911. *Elasmosaurus helmerseni*. — Bogolubov, p. 359.

1914. *Plesiosaurus gigas*. — Wegner, p. 303.

DIAGNOSIS.—A very large Plesiosaurian, possibly referable to *Elasmosaurus*. End faces of the thoracic-lumbar centra moderately concave, with an extensive, high elevation in their centres.

HOLOTYPE.—A thoracic-lumbar vertebra in the Royal Museum of Mineralogy, Königsberg (Schröder 1885, p. 322; Pl. 16, figs. 1 a–b). Locality: Altfelde near Elbing, Prussia.

MATERIAL.—One large thoracic-lumbar centrum (UM, R.p. 14).

DESCRIPTION.—This centrum is so incompletely preserved that only the breadth can be directly measured; both length and height can, however, be estimated with reasonable certainty. The measurements and indices are as follows: Length 115 mm, height 120 mm, breadth 155 mm, height : length index 104 and breadth : length index 135.

The preserved end face is moderately concave and is bounded peripherally by a sharp-edged margin. The central part of the face exhibits and extensive elevation on which a notochord pit (*nep*, Pl. 5. See Andrews 1910, I, p. 95) is clearly distinguishable. The lateral faces are rather strongly concave in a rostro-caudal direction. Their upper portions exhibit a dorso-laterally projecting thickening showing that the pleurapophysis was partly continuous with the centrum, which is a distinctive character of the posterior thoracic-lumbar centra (cf. Welles 1943, p. 135). Since the aforementioned dorso-lateral thickening decidedly lies on the anterior half of the length of the centrum, the preserved end face must have been directed forwards. The ventral face is moderately concave in a rostro-caudal direction and has three foramina for nutritive vessels. Two of these are symmetrically arranged in relation to the median line, whereas the third one, which is considerably smaller, is situated somewhat further laterally towards the right side of the centrum.

REMARKS.—The proportions of the holotype vertebra are as follows: Length 112 mm, height 129 mm, breadth 143 mm, height : length index 115, breadth : length index 128. Judging from the fact that the pleurapophysis is situated entirely above the centrum, the vertebra may be from the anterior part of the thoracic-lumbar region (cf. Welles 1943, p. 135). The most conspicuous characters of the holotype are a) the shape of the end faces, these possessing a high, extensive elevation in their centres, and b) the strikingly large size. Since the centrum from Scania agrees almost perfectly with the holotype where the two aforementioned characters are concerned, it may be provisionally ascribed to *Elasmosaurus?* cf. *gigas*.

Schröder regarded the holotype as a *Pliosaurus* species; both the holotype and the centrum from Scania differ, however, considerably from the correspondingly situated centra in the *Pliosauroides* in two essential characters, viz. their general proportions and the shape of the end faces. This being so, the two centra here concerned cannot possibly be referred to *Pliosaurus*. In addition, *Pliosaurus* is a Jurassic genus, which may not have survived into the Senonian.

On the other hand, with regard to their indices the holotype and the Scanian centrum both show an almost perfect agreement with the correspondingly situated centra in certain American *Elasmosaurids*. More precisely, these indices of an anterior thoracic-lumbar centrum in *Elasmosaurus platyurus* (Welles 1952, p. 125) are 112 and 128 (in the holotype of *Pliosaurus?* *gigas* Schröder 115 and 128, respectively); whilst the corresponding indices of a posterior thoracic-lumbar centrum in *Morenosaurus stocki* (Welles 1952, p. 125) are 103 and 135 (in the Scanian centrum 104 and

135, respectively). Taking everything into account one is led to the conclusion that both the holotype of *Pliosaurus? gigas* Schröder and the Scanian centrum here dealt with are so closely related to the *Elasmosauridae* that they may provisionally be referred to this family. At least at present there is nothing to contradict that they are nearest akin to *Elasmosaurus*, and they are therefore here described with hesitation as belonging to this genus.

The centrum from Scania is larger than any other Plesiosaurian centra known so far from the Upper Cretaceous of Europe, the next largest one being the holotype of *P.? gigas* (see above). Amongst the known North American Upper Cretaceous Plesiosaurians there is only one, the gigantic *Thalassomedon haningtoni* Welles 1943, that possesses vertebral centra larger than the one from Scania in question.

GEOLOGICAL HORIZON.—Lower Campanian.

LOCALITY.—Ignaberga.

Genus *Scanisaurus*, n.g.

Syn. *Cimoliasaurus* Leidy 1851.

DIAGNOSIS.—A dolichodiran Plesiosaurian with neck relatively shorter than in typical Elasmosaurids. The crown of the teeth high and slender, approximately elliptical in parbasal sections. The height of the cervical centra less than $\frac{2}{3}$ of the breadth; the length of, at least, the seven hindmost cervical centra increasing forwards towards the head. Cervical ribs not fused with centra. Diaphysial parts of humeri and femora short and stout.

GENOTYPE.—*Scanisaurus nazarowi* (Bogolubov 1911).

REMARKS.—In 1911 Bogolubov described and figured a posterior cervical centrum from the Senonian of Orenburg, Russia, which he referred to *Cimoliasaurus*, erecting for it a new species, *C. nazarowi*. It is now clear that several cervical centra in the Scanian material agree so well with the one described by Bogolubov that they must belong to one and the same genus. All the centra in question, both the Russian one and those from Scania, differ, however, from the genotype of *Cimoliasaurus* (*C. magnus* Leidy 1851) to such an extent that they doubtless represent a new genus, for which the name *Scanisaurus* is here introduced. More precisely *Scanisaurus* differs from *Cimoliasaurus* in the following three important characters: a) All the cervical ribs, both the anterior and the posterior ones, are attached to the centra by sutures only, whilst in *Cimoliasaurus* the ribs are fused with at least the pre-pectoral centra Nos. 12–1 (Welles 1952, p. 108). b) The length of the posterior cervical centra increases as one proceeds forwards towards the head, whereas in *Cimoliasaurus* the reverse condition is met with (Welles 1952, p. 108). c) The preserved cervical centra are much broader in proportion to their length and height than the corresponding centra in *Cimoliasaurus*.

Scanisaurus differs from the Pliosauroids in the following three characters: a) the shape of the teeth, in that the crown is high and slender and has a more or less elliptical outline in parbasal sections. b) The greater length and breadth of the cervical centra, and the condition that the end faces of the centra are plane or slightly concave, and are bounded peripherally by sharp-edged margins. c) The fact that at least in the posterior part of the cervical region (the pre-pectoral centra

Nos. 7-1) the length of the individual centra increases as one proceeds forwards towards the head.

On the other hand, in most of its characters so far known *Scanisaurus* agrees with the Plesiosauroideans, particularly the Elasmosaurids. In one essential character, however, it differs decidedly from the Elasmosaurids, viz. that the cervical centra are shorter and broader. *Scanisaurus* is not a typical Elasmosaurid, and, as pointed out below, it may even be a representative of a third, new family of Upper Cretaceous Plesiosaurians.

In order to elucidate to which family the genera *Cimoliasaurus* and *Scanisaurus* are referable it is necessary to enter here briefly upon the former of these two genera. The genotype of *Cimoliasaurus*, *C. magnus*, was erected by Leidy in 1851 for a series of 13 vertebrae, comprising the pre-pectoral vertebrae Nos. 12-1, and the pectoral vertebra No. 1. After that time many new *Cimoliasaurus*-species have been described, most of which, however, are based on so poor and scanty materials that in fact they are indefinable. Already Williston (1903, p. 8) stated therefore that the "genus has served as a sort of waste paper basket for the reception of fragments and poorly known forms". Welles discussed *Cimoliasaurus* thoroughly in his excellent works of 1943 (p. 209) and 1952 (pp. 107-110) and demonstrated that the genotype cannot possibly be an Elasmosaurid. In his work of 1952, p. 108, he writes as follows concerning this question: "As Cope (1840) pointed out, the genus has a relatively short neck. In my present understanding of the plesiosaurs I would place it in the Polycotylidae, although it may eventually prove to be intermediate between the pliosaurs and the elasmosaurs, and therefore representative of a third group. It is based upon adequate material, and—many later finds are similar to the type." By the courtesy of Professor Welles I have been also informed privately that a revision of South American material has led him to the opinion that *Cimoliasaurus* actually represents such an intermediate group, and the material from Scania referred here to *Scanisaurus* goes decidedly to prove that this is so. However, it does not seem appropriate to establish a new family of Upper Cretaceous Plesiosaurians on the basis of the restricted material so far available. Since *Scanisaurus* certainly is more closely related to the *Elasmosauridae* than to the *Polycotylidae*, it is here provisionally referred to the former family.

Certain particular characters of interest for judgement of the taxonomic position of *Scanisaurus* are discussed on p. 456 below.

Scanisaurus cf. *nazarowi* (Bogolubov 1911)

Pl. 6, figs. 1-6; Pl. 7; Pl. 8, figs. 1-3; Pl. 9; Pl. 10, figs. 1-7; Pl. 11, figs. 1-2; Pl. 12; Pl. 13, figs. 1-2.
Text-figs. 5-7.

DIAGNOSIS.—Same as that of the genus, by monotypy.

HOLOTYPE.—A posterior cervical centrum from Orenburg, Russia (Bogolubov 1911, pp. 379-382; Pl. 13, figs. 4, 8, 12) in the Museum of the University of Moscow.

MATERIAL.—The material referable to this species, at least with a fairly great degree of probability, comprises more or less consecutive series of vertebral centra from six different individuals, a great many detached centra, teeth, and diaphysial ossifications of humeri and femora. Concerning the numbers of the different skeletal parts, find localities, etc., see Table 4.

Table 4. Number, localities and repositories of the remains of *Scanisaurus cf. nazarowi*.

Localities	Teeth	Series of vertebral centra	Detached vertebral centra						Humeri and femora
			Anterior cervical centra	Mid-most and posterior cervical centra	Pectoral centra	Thoracic-lumbar centra	Sacral centra	Caudal centra	
Blaksudden	216	4 (Nos. I, II, IV, V)	7	63	22	108	8	27	10
Axeltoorp	1	2 (Nos. III, VI)	2	2		5			3
Ignaberga				2		1		1	2
Kjuge					1	2			1
Maltesholm									
Båstad ¹				1					
Total number	217	6	9	68	23	116	8	28	16
Institutes									
LM.	13			1	2	2		2	3
RM.	64	3 (Nos. I-III)	2	23	7	33	2	16	3
S.G.U.		1 (No. IV)	1	2	1	1		1	
SM.	2					4		5	
UM.	138	2 (Nos. V, VI)	6	43	15	76	6	4	10

¹ The specimen from this locality was not found in the solid rock which here is Upper Campanian, but in a chalky moraine. As all other remains of *S. cf. nazarowi* this centrum is probably also from the Lower Campanian.

The collectors did not record the original order of the vertebral centra in the six series as found *in situ* in the rock, but after a detailed examination of the shape of the end faces and other details, and after comparison with material figured in the literature, I have been able to reconstruct these series with reasonable certainty.

The probable order of the vertebral centra forming the six different series in question (the catalogue numbers of the individual centra stated from in front backwards in the vertebral column) is as follows:

Series I. RM. Nos. R. 1069, 1068, 863, 1067, 1066, 756, 862, 757, 755, 758, 754, 759, 864, 760, 761, 1080, 762, 1079, 763.

Series II. RM. Nos. R. 951, 1003, 1002, 1001, 998, 1000, 995.

Series III. RM. Nos. R. 777, 770, 772, 768, 773, 767, 769, 765, 766, 771, 764, 775, 774, 776, 778.

Series IV. S.G.U. Nos. G, C4, C3, C1, C2, D3-1, B8-1, F, A7-5, E1-2, A4-1.

Series V. UM. Nos. R.p. 28-30.

Series VI. UM. Nos. R.p. 31, 32.

Since in the Swedish collections it is represented by a much greater number of centra than any of the other Plesiosaurians, *S. cf. nazarowi* was obviously the most

Table 5. Measurements of teeth of *Scanisaurus* cf. *nazarowi* (Bogolubov).

LM, RM and UM. (Estimated measurements in italics.)

Cat. no.	Height of crown mm.	Long diameter of parabasal section at base of crown mm.	Short diameter of parabasal section at base of crown mm.
LM			
LO 3840 t	<i>35.5</i>	<i>8.2</i>	<i>7.2</i>
RM			
R. 1121		10.1	7.3
„ 1136	<i>30.5</i>	<i>7.3</i>	<i>6.2</i>
„ 1138	<i>35.0</i>	<i>9.2</i>	<i>8.0</i>
„ 1181		<i>8.5</i>	<i>7.5</i>
„ 1140		8.8	7.3
„ 1141	<i>34.0</i>	<i>9.0</i>	<i>7.2</i>
„ 1242	<i>33.0</i>	<i>9.0</i>	<i>7.8</i>
„ 1299	<i>34.0</i>	<i>9.4</i>	<i>8.2</i>
„ 1301	<i>31.5</i>	<i>8.0</i>	<i>7.2</i>
„ 1429		<i>7.3</i>	<i>6.2</i>
„ 1439	<i>33.3</i>	<i>9.3</i>	<i>7.5</i>
UM			
R.p. 15	<i>40.0</i>	<i>11.3</i>	<i>9.2</i>
„ 16	<i>31.5</i>	<i>10.0</i>	<i>8.5</i>
„ 17	<i>34.0</i>	<i>9.0</i>	<i>7.3</i>
„ 18	<i>33.5</i>	<i>8.9</i>	<i>7.5</i>
„ 19	<i>33.0</i>	<i>7.8</i>	<i>6.8</i>
„ 20	<i>37.7</i>	<i>9.3</i>	
„ 21	<i>32.5</i>	<i>8.7</i>	<i>7.2</i>
„ 22	<i>34.5</i>	<i>9.5</i>	<i>7.7</i>
„ 23		10.1	8.3
„ 24	<i>33.5</i>	<i>9.2</i>	<i>6.5</i>
„ 25		<i>9.1</i>	<i>8.0</i>
„ 26	<i>34.0</i>	<i>8.5</i>	<i>7.3</i>
„ 27	<i>33.0</i>	<i>9.0</i>	<i>7.3</i>

common Plesiosaurian in the Senonian of Scania.¹ The teeth of the most common type met with in this division of the Scanian Cretaceous may therefore also be from *S. cf. nazarowi*.² That this must be so is also strongly supported by the condition that, according to statements by the collectors, most of these teeth were found associated with the six series of vertebral centra. For the same reason the diaphysial ossifications of the humeri and femora are also referred to *Scanisaurus* cf. *nazarowi*.

DESCRIPTION.—*Teeth*. In the majority of the teeth (Pl. 6, figs. 1a–d, 2a–b, 3a–c, 4a–d, 5a–d, 6a–d; text-fig. 5) only small parts of the roots are preserved, and in many teeth the apex of the crown is missing. Table 5 illustrates the size and proportions of some of the best preserved teeth. The crown is high, slender, and slightly lingually

¹ The centra of *S. cf. nazarowi* amount in all to 90 percent of all the determinable centra so far found in Scania.

² The total number of these teeth is 20 times as large as that of all the other Plesiosaurian teeth met with in the material investigated.

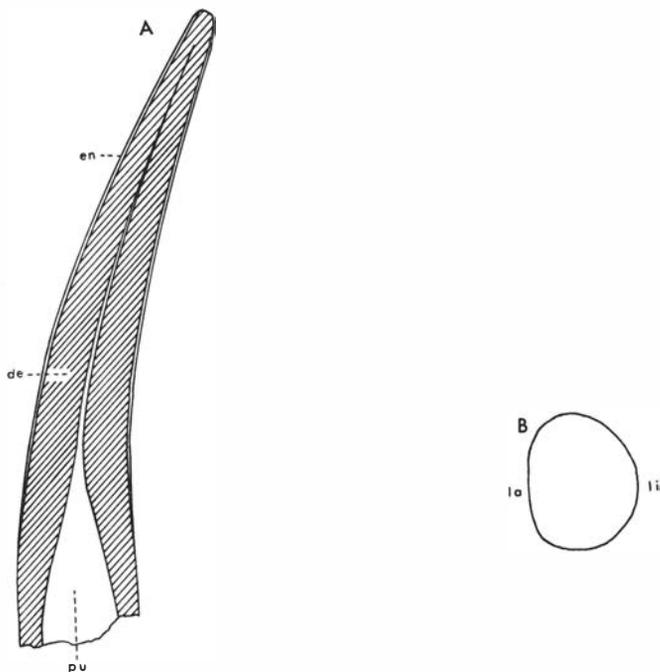


Fig. 5. *Scanisaurus* cf. *nazarowi* (Bogolubov 1911). *A*, apico-basal section of a tooth. UM, R.p. 21. $\times 2$. *B*, outline of parobasal section of the same tooth closely to the root. $\times 2$.
de, dentin; *en*, enamel; *la*, labial side; *li*, lingual side; *pu*, pulp cavity.

and posteriorly recurved. In parobasal sections it is roughly elliptical, with its labial side somewhat less convex than the lingual one (see text-fig. 5 b). The ornamentation consists of delicate apico-basal ridges, which on the lingual side are traceable almost to the tip of the crown whilst on the labial side they are confined chiefly to the basal part of the crown only, so that the whole upper part of this side is smooth. In some of the teeth the ornamentation is more conspicuous than in others. To what extent this is due to differences in the degree of abrasion, cannot be decided at present. In the root and in the basal part of the crown the pulp cavity is fairly wide, but in an apical direction it rapidly diminishes to a narrow canal which extends almost to the tip (see text-fig. 5 a). The enamel layer is thin throughout its extent.

Three of the teeth investigated show deep markings of abnormal wearing (Pl. 6, figs. 4 a-d), apparently caused by their oblique position to the teeth in the opposite jaw of the same side.

Vertebral centra (Pls. 7-12; text-fig. 6). The material of the vertebral column consists of centra only. The measurements and indices of all the centra in the six series referred to above (p. 449) are given in Table 6 (pp. 452-453). The position of the individual centra in the different regions of the vertebral column, the supposed mutual order of the centra in each region, and the gaps in the series are all shown in the aforementioned table. The gaps are denoted by dashes.

In series I and IV the pectoral region is probably complete, and in series IV this is also true of the sacral region, each of these two regions consisting of three centra.

Table 6. Measurements and indices of vertebral centra from six individuals (Series I-IV; see p. 449) of *Scanisaurus* cf. *nazarowi* (Bogolubov 1911).

Estimated measurements in italics. Gaps in the series denoted with dashes.

Series	Centrum	Length mm.	Height mm.	Breadth mm.	H:L ind.	B:L ind.
I	Pre-pectoral					
	No 2	35.5	40.5	62.5	114	175
	„ 1	36.5	41.5	65	114	178
	Pectoral					
	No 1	37	42	65	113	176
	„ 2	38	41	64.5	107	170
	„ 3	38.5	44	64.5	115	168
	Thoracic-lumbar					
	No 1	41	44	64	107	156
	„ 2	43	47	63	109	147
	„ 3	43	47	63	109	147
	„ 4	44	47	63	107	143
	„ 5	44	47	62	107	141
	„ 6	42.5	47	63	111	148
	„ 7	41.5	47	63	113	152
	„ —	—	—	—	—	—
	Pre-sacral					
	No 5	39	44	61	113	156
	„ 4	38.5	44	60	111	156
	„ 3	38	43	59	113	155
	„ 2	35	40.5	56.5	116	161
„ 1	33.5	38	55	113	165	
Sacral						
No 1	32.5	38.5	55	118	169	
„ 2	30	37	54	123	180	
II	Pre-pectoral					
	No 7	38	33	53.5	87	141
	„ 6	36	34.5	53.5	96	149
	„ 5	36	35	54.5	97	151
	„ 4	34	35.5	55	105	162
	„ 3	34.5	36	57	104	165
	„ 2	34	36	57	106	168
	„ 1	33	37	60	112	182
III	Pre-pectoral					
	No ?6	32	32.5	50	101	156
	„ —	—	—	—	—	—
	„ 4	31	34	50	110	161
	„ 3	31	34	52	110	168
	„ 2	30.5	34	52	111	170
	„ —	—	—	—	—	—
	Pectrcal					
No 1	32	34.5	55	108	172	
„ 2	32	35	57	109	178	
„ —	—	—	—	—	—	

Series	Centrum	Length mm.	Height mm.	Breadth mm.	H:L ind.	B:L ind.
IV	Thoracic-lumbar					
	No 1	36	39	54.5	108	151
	„ 2	38	40.5	52	106	137
	„ 3	36.5	40	52	109	142
	„ 4	36	40	52	111	144
	„ 5	35.5	39.5	52	111	146
	„ 6	34.5	39.5	52	114	151
	„ 7	34	39	51	115	150
	—	—	—	—	—	—
	„ ?	32	36.5	51	114	156
	—	—	—	—	—	—
	Caudal					
	No ?	20.5	28	40	136	195
	Pre-pectoral					
	No ?	39.5	44	68	111	172
	—	—	—	—	—	—
	„ ?8	40	47	74	117	185
	„ ?7	40	47	74	117	185
	„ ?6	40	48	74	120	185
	„ ?5	39.5	48.5	74	124	187
	—	—	—	—	—	—
	Pectoral					
	No 1	38.5	48	74.5	125	193
	„ 2	39	47	75	120	192
	„ 3	40	48.5	75	121	187
	Pre-sacral					
	—	—	—	—	—	—
	No ?	44	53	66	120	150
	„ ?	41.5	52	66	125	159
	—	—	—	—	—	—
	„ 6	39	—	—	—	—
	„ 5	39	47	65	121	167
„ 4	37.5	—	—	—	—	
„ 3	36	44.5	62.5	124	174	
„ 2	35	44	61	126	174	
„ 1	34	43.5	59.5	128	175	
Sacral						
No 1	32	42	60	131	188	
„ 2	30	42	62	140	207	
„ 3	29	43	62	148	214	
Caudal						
No 1	29	43	61	148	210	
„ 2	29	44	63	152	217	
„ 3	29.5	44	64.5	149	219	
„ 4	29	44	61	152	210	
„ 5	30	44	62.5	147	208	
„ 6	30	45	63	150	210	
„ 7	30	44	62	147	207	
V	Pre-pectoral					
No ?	54.5	—	85.5	—	157	
„ ?	54.5	58	85.5	106	157	
„ ?	53.5	56	86	105	161	
VI	Pre-pectoral					
No 1	49	55	87	112	178	
Pectoral						
No 1	51	56	87	110	171	

On the other hand the cervical, thoracic-lumbar and caudal regions are incomplete in all the series, and the number of their centra cannot hence be established. The thoracic-lumbar region is least incomplete in series I, where there probably is one gap only, actually between the 7th thoracic-lumbar and 5th pre-sacral centra. On account of the well-known fact that the thoracic-lumbar region varies considerably with regard to the number of its vertebrae in different genera of Plesiosaurians, the number of missing centra in this gap cannot be estimated with any certainty. It may be mentioned that in the Elasmosaurids, *Hydrotherosaurus alexandrae* and *Hydralmosaurus serpentinus* for example, the region in question consists of 17 and 19 vertebrae respectively, whereas in the Polycotylid *Dolichorhynchops osborni* it is made up of as many as 30 vertebrae. Since in the series just under discussion the 7th thoracic-lumbar and 5th pre-sacral centra differ very slightly in size and proportions (see Table 6, pp. 452–453) there is reason to believe, that they cannot have been situated particularly far apart and that hence only a few thoracic-lumbar centra are missing between them. Thus, the number of thoracic-lumbar vertebrae in *Scanisaurus* was probably comparatively small. Since the total number of centra in the vertebral column as a whole is unknown, it is still impossible to arrive even at a rough idea of the total length of the animal.

The following characters are shared by the centra in all the regions of the vertebral column of *S. cf. nazarovi*: a) the more or less low shape, so that the breadth is larger than the height; b) the fact that the end faces (*ef*, text-fig. 6) are flat or slightly concave and are bounded peripherally by sharp-edged ridges; c) the presence of a notch on the dorsal margins of the end faces, a notch which is caused by the neural canal (*nc*, text-fig. 6). d) The condition that the neural canal of the individual centra is narrowest in its midmost part and broadest in its hindmost part, and that at the bottom of the midmost part of the neural canal of each centrum there is usually a pair of foramina (*dfn*, text-fig. 6) through which nutritive vessels penetrated downwards into the centrum. e) The fact that the neurapophyses have not fused with the centra, not even in adult individuals. f) The more or less excavated shape and somewhat rough appearance of the neurapophysial facets (*nf*, text-fig. 6). g) The presence of a pair of foramina (*vfn*, text-fig. 6) for nutritive vessels on the ventral face of each centrum (one of these foramina may not infrequently be represented by two minor ones).

The *cervical* centra (*A1–C*, text-fig. 6) are characterized by the fact that their breadth is strikingly large in proportion to the length and height. Usually these centra are somewhat higher than long, but in certain cases the midmost ones of the centra in question may be as long as high, or even a little longer than high. In series II, which comprises 7 consecutive centra, actually the pre-pectoral centra Nos. 7–1, the length of the individual centra increases gradually as one proceeds forwards towards the head from 33 mm to 38 mm (see Table 6, pp. 452–453). This increase in length may possibly also have affected some of the missing centra in front of the 7th. The end faces of the anterior cervical centra are not parallel, but incline a little (maximally about 4°) downwards-forwards and downwards-backwards, respectively, and have hence such a position that they converge slightly in a ventral direction. As opposed to this the end faces of all the other centra of the vertebral column are parallel. The ventral face of each of the anterior and midmost cervical centra is occupied by a broad, shallow longitudinal groove which causes the end faces of each of the centra concerned to exhibit a broad central emargination. Similar conditions are met with in the corresponding centra of the Elasmosaurid *Hydrotherosaurus*

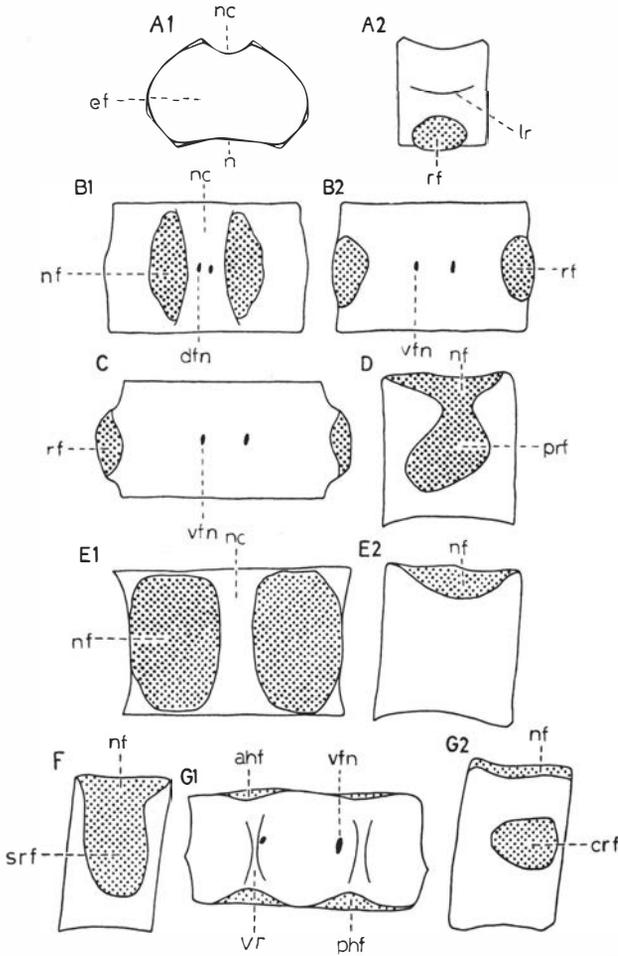


Fig. 6. *Scanisaurus* cf. *nazarowi* (Bogolubov 1911). Sketches of some vertebral centra. $\times 1/2$. A1-A2, anterior cervical centrum (RM, R. 1534) in anterior view and from the right side; B1-B2, 6th pre-pectoral centrum (RM, R. 1003) in dorsal and ventral aspects; C, 2nd pre-pectoral centrum (RM, R. 1000) in ventral aspect; D, 1st pectoral centrum (RM, R. 773) from the right side; E1-E2, 1st thoracic-lumbar centrum (RM, R. 756) in dorsal aspect and from the right side; F, 2nd sacral centrum (S.G.U., A7) from the right side; G1-G2, 5th caudal centrum (S.G.U., A₃) in ventral aspect and from the right side.

ahf, anterior haemapophysial facet; crf, caudal rib facet; dfn, foramen for nutritive vessels in neural canal; ef, end face; lr, lateral longitudinal ridge; n, emargination in the ventral margin of end face; nc, neural canal; nf, neurapophysial facet; phf, posterior haemapophysial facet; prf, pectoral rib facet; rfn, cervical rib facet; srf, sacral rib facet; vfn, ventral foramen for nutritive vessels; vr, ventral ridge.

alexandrae (Welles 1947, pp. 136–137), and in several other dolichodiran Plesiosauroians as well. The ventral groove just referred to probably housed the main vessels to and from the head. In the pre-pectoral centrum No. 4 the ventral face is flat, but in the pre-pectoral centra Nos. 3–1 this face is more or less convex in a transversal direction.

The neural canal (actually a groove) on each centrum is somewhat deeper in the cervical region than in the other regions of the vertebral column. The neuropophysial facets extend almost across the whole length of the individual centra; the facets in question are subelliptical, their median margins being less convex than the lateral ones.

With regard to the lateral faces (i.e. the faces between the facets for the neuropophysis and those for the ribs) the centra are somewhat different according to their position in the cervical region. Thus, the faces in question are more or less convex in a transverse direction on the midmost centra, whereas in the other centra (the anterior and posterior ones) they are more or less concave in both transverse and rostro-caudal directions. In addition, on the anterior cervical centra the lateral face of each side bears a more or less sharp-edged longitudinal ridge (*lr*, text-fig. 6, *A 2*).

The rib facets, which are situated somewhat posterior to the middle of the length of the centra and fairly low on the lateral faces, are almost circular; they are plane or slightly concave, and have a rough surface. In the anterior and midmost parts of the cervical region they lie directly on the centra, whereas in the posterior part of the region, i.e. on the pre-pectoral centra Nos. 4–1, they are situated on short, stout processes. In the pre-pectoral centra Nos. 2–1 the facets in question face almost laterally, whereas in the other cervical centra they face obliquely ventro-laterally, at an angle of about 45° to the vertical plane.

The following remarks concerning the cervical region should here be added. A comparison with a table published by Welles (1952, p. 125) of the measurements and indices of the vertebral centra in 18 North American Elasmosaurids shows that the cervical centra of *Scanisaurus* cf. *nazarowi* are proportionally much shorter than the corresponding centra in the American species and that, therefore, the neck of this species in all probability was shorter than in the said American forms. However, since the cervical centra of *S.* cf. *nazarowi* are proportionately very broad and their end faces are not rounded off marginally the neck in this species cannot have been flexible enough, at least not in lateral directions, unless it had been fairly long (see the analysis given by Watson in 1951, p. 179, of the flexibility in Plesiosaurian necks). There is hence reason to believe that *S.* cf. *nazarowi* was a comparatively long-necked species, but that its neck nevertheless was shorter than in the typical Elasmosaurids.

The *pectoral* centra (*D*, text-fig. 6) resemble the cervical ones by their considerable breadth. Their end faces are approximately elliptical with the longer axis horizontal. The rib facets (*prf*, text-fig. 6, *D*) were situated partly on the diapophyses (now missing) and partly on the centra (cf. Welles 1943, p. 135), and as a result the neuropophysial facets and the rib facets are confluent and jointly occupy almost the entire dorsal and lateral faces. The ventral face of each pectoral centrum is concave in a rostro-caudal direction, but convex in a transverse direction.

The *thoracic-lumbar* centra (*E1–E2*, text-fig. 6) are decidedly higher than the cervical and pectoral ones but not so high as the corresponding centra in certain other Plesiosaurians, as *Muraenosaurus*, for example, where the end faces are even as high as to be practically sub-circular in outline (Andrews 1910. I, p. 97). Otherwise

the following should be added concerning the thoracic-lumbar centra. The large, sub-elliptical or sub-rectangular neuropophysial facets and the neural canal jointly occupy the entire dorsal face of each centrum. The foramina for nutritive vessels in the neural canal are often small, irregularly situated or absent. The lateral and ventral faces are strongly concave in a rostro-caudal direction, but convex in a transverse direction.

The *sacral* centra (*F*, text-fig. 6) are shorter and lower than the thoracic-lumbar ones. The neuropophysial facets and the foramina in the neural canal are essentially as in the thoracic-lumbar centra. In the sacral centrum No. 1 an extensive portion of the rib facet (*srj*, text-fig. 6, *F*) was obviously situated on the diapophysis (now missing), whereas in the two other sacral centra this facet also extended on to the diapophysis, but by a narrow marginal portion only. The ventral face has almost perfectly the same shape as in the pectoral centra.

At least the anterior *caudal* centra (*G1-G2*, text-fig. 6) are proportionately a little higher than the sacral ones. Their neuropophysial facets are sub-elliptical or sub-rectangular, just as those of the thoracic-lumbar centra, but narrower than those of the latter centra. In the posterior part of the caudal region the neuropophysial facets occupy the entire dorsal face on each side of the neural canal.

Rib facets (*crf*, text-fig. 6, *G2*) are absent except on the anterior caudal centra, where they extend backwards across the anterior two thirds or more of the length of the lateral faces of the centra. These facets, which are somewhat rough and have such a position as to face straight laterally, are not circular in outline as those of the cervical centra, but have rather a sub-elliptical or, at least in some instances, an almost sub-triangular shape.

In a longitudinal direction the ventral face is more or less concave in all the centra of the caudal region. On the other hand, in a transverse direction this face is convex on the foremost and hindmost centra but decidedly concave in the midmost centra. In the latter centra the ventral face is bounded on each side by a low, rounded off, rostro-caudal ridge (*vr*, text-fig. 6, *G1*). The presence of such a paired ventrallongitudinal ridge on the caudal centra is regarded by Welles (1943, p. 136) as one of the distinctive characters of dolichodiran Plesiosaurians.

Humerus and femur.—In the following account the terms humerus and femur refer to the diaphysial ossifications only of these elements.

The humerus and femur of the Plesiosaurians differ so slightly in shape and proportions that in many cases they cannot be distinguished apart with reasonable certainty when they are found detached from the limb girdles. However, in the humerus the radiar face is usually less convex than the ulnar one, whilst in the femur the tibiar face exhibit approximately the same concavity as the fibular one. This condition can be used to a certain limited extent for the identification of the bones.

In *Scanisaurus* the humerus and femur had undergone a considerable retrogressive development proximally with regard to their ossification so that they possessed at least a fairly long proximal cartilaginous epiphysis. A probable femur (LM, LO 3841 t; Pl. 13, figs. 2a–b), which is better preserved than any of the other proximal limb bones in the material available, has a total length of 165 mm, whereas the breadth at the proximal and distal ends is 61 mm and 106 mm respectively (the breadth measured across the anterior and posterior parts lined with periosteal bone). The thickness at these two ends is 53 mm and 46 mm, respectively. The extensor side is smooth, whereas on the flexor side there is an extensive rugose area for the inser-

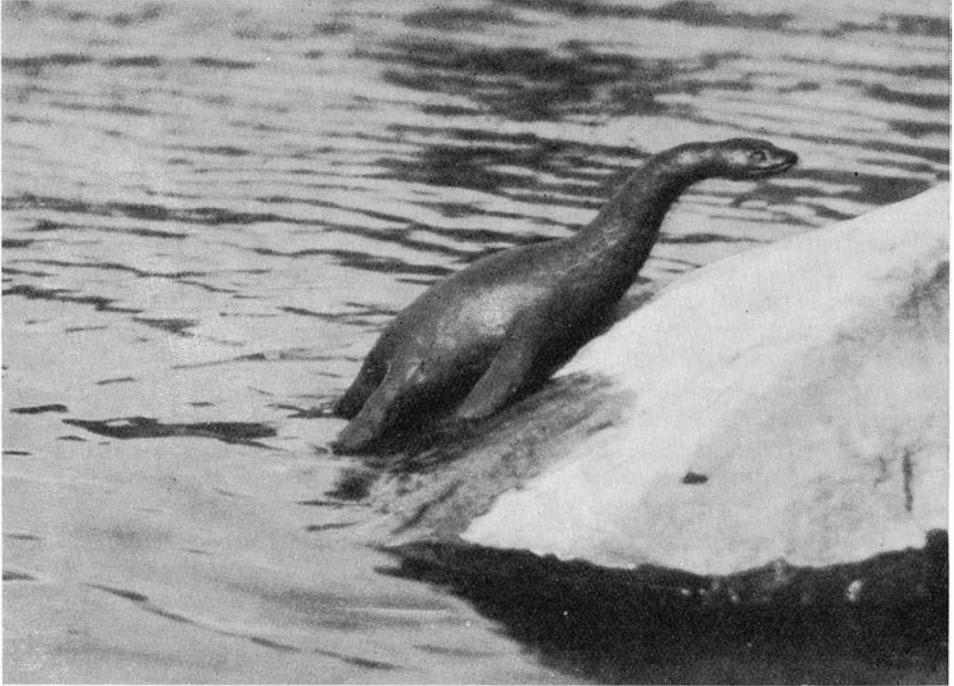


Fig. 7. *Scanisaurus* cf. *nazarowi* (Bogolubov 1911). Restoration showing the probable general shape of the animal.

tion of a muscle (*r*, Pl. 13, fig. 2b). The fibular face exhibits a similar but smaller area (*rl*, Pl. 13, fig. 2b) which also must be the place of insertion of a muscle.

The small bone figured in Pl. 11, fig. 3 (RM, R. 1578), probably a humerus, is crushed and broken in such a way as clearly to show the hour-glass shape of its cancellous enchondral bone mass. This enchondral bone mass has also been referred to by Williston (1903, p. 74), who has obviously not fully perceived its true nature and mode of embryological development.

On the extensor face of a supposed humerus (UM, R.p. 33), from Axeltorp, there are some deep scars (*s*, Pl. 13, fig. 1), and similar scars are also found on a second proximal limb bone (UM, R.p. 36) from Blaksudden, Ivö. Since they are partially filled with matrix, these scars cannot possibly have been effected by the tools of the workmen, but must be marks of sharp teeth of predacious animals such as sharks, marine reptiles, or—in view of the position of the find localities near seashores—even carrion-eating terrestrial reptiles. In the latter case the bones may have belonged to stranded carcasses in the shallow water along the beaches.

REMARKS.—On account of the condition already stressed (p. 447) that it has been erected for a single posterior cervical centrum only, *Scanisaurus nazarowi* (Bogolubov) is still actually an undefinable species. Since with regard to the similarly situated cervical centra the material of vertebral columns from Scania dealt with just above does not differ in any essential points from *S. nazarowi* the writer has preliminarily described it under the title of *S. cf. nazarowi*.

Scanisaurus cf. *nazarowi* is reminiscent of "*Plesiosaurus*" *planus* Owen (1864, pp. 2-7; Pls. 1-3) where both the proportions of the vertebral centra and the shape of their end faces are concerned. *Scanisaurus* cf. *nazarowi* differs, however, clearly from "*Plesiosaurus*" *planus* in the respect that its midmost and posterior cervical centra are decidedly broader, which proves that it cannot be identical with the latter species. Anyhow, there is reason to suspect that the two species in question are akin to each other, which is of particular interest from the point of view that *S.* cf. *nazarowi* is from the Senonian, whereas "*Plesiosaurus*" *planus* comes from Lower Cretaceous beds.

A tentative restoration of the general external appearance of *Scanisaurus* cf. *nazarowi* is given in text-fig. 7.

GEOLOGICAL HORIZON.—Lower Campanian.

LOCALITIES.—See above, table 4 (p. 449).

Remains of Elasmosaurids indeterminable as to genus and species

Pl. 14, fig. 1. Text-figs. 8-9.

Under this title I group some detached Plesiosaurian bones from different localities. The bones are decidedly of the Elasmosauridean type, but they cannot be determined as to genus and species until additional material is available. It is possible that they represent different genera and species.

MATERIAL.—Three anterior cervical centra (UM, R.p. 37; RM, R. 987 and 994), one middle or posterior cervical centra (S.G.U., Aa 103, no. 1), five thoracic-lumbar centra (S.G.U., Aa 103, nos. 2-5, 10; RM, R. 782, 783), one coracoid bone (SM, 6132), and three pubes (LM, LO 3842 t; UM, R.p. 38, 39).

DESCRIPTION AND REMARKS.—With regard to their proportions and other preserved characters the vertebral centra are decidedly Elasmosaurid-like. One of the anterior cervical centra (RM, R. 994) is figured in Pl. 14, fig. 1 a-c. The coracoid (SM, 6132; text-fig. 8) which is from the left side may have had a maximum length of approximately 195 mm; its maximum breadth and its length along the median suture amount to 145 mm and 113 mm, respectively. Unfortunately the posterior process of the bone is imperfect in such a way that the exact shape of the inter-cora-

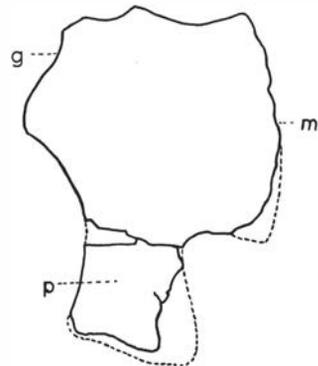


Fig. 8. *Elasmosauridae*, gen. et sp. indet. Semi-diagrammatic restoration of a left coracoid bone. Dorsal (internal) aspect. Restored parts denoted with interrupted lines. SM, 6132. $\times 1/4$.
g, glenoid face; m, median margin; p, posterior process.

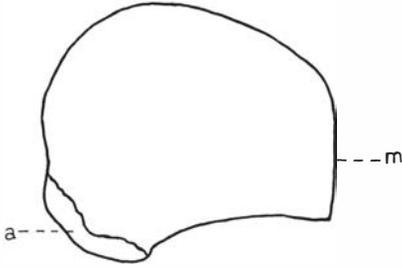


Fig. 9. *Elasmosauridae*, gen. et sp. indet. Semi-diagrammatic restoration of a left pubis. Dorsal (internal) aspect. LM, LO 3842 t. $\times 1/4$.
a, actabular-ileal margin; *m*, median margin.

coid notch (vacuity) cannot be ascertained. As well known, this notch is of great importance for generic and specific determinations. The bone is, however, of the *Elasmosauridean* type (Welles 1952, figs. 1, 2, 4, 8, 10, 13, 14, 17, 20, 22, 23, 24). This is also true of the three pubes in the material available. Of these (LM, LO 3842 t) shown in text-fig. 9 is best preserved. It is 138 mm long and 154 mm broad. The other two pubes are smaller and more poorly preserved, but of perfectly the same type as LM, LO 3842 t.

GEOLOGICAL HORIZON.—According to Brotzen the Plesiosaurian vertebrae Aa 103 Nos. 1–5 are from the Lower Maastrichtian; the other material dealt with under the above title is all from Lower Campanian beds.

LOCALITIES.—R.p. 37 is found at Axeltorp, LO 3842 at Ignaberga, and Aa 103 Nos. 1–5 and 10 at Balsvik. All the other bones described under this title come from Blaksudden, Ivö.

Plesiosaurian remains indeterminable as to family, genus and species

Pl. 14, figs. 2–4.

MATERIAL.—Numerous detached skeletal remains the following of which are briefly dealt with below: one thoracic-lumbar centrum (LM, LO 3878 t); one anterior caudal centrum (LM, LO 3891 t); a number of fragments of ribs proper; a number of pieces of gastralia (“ventral ribs”), the best preserved of which are RM, R. 1342–1344 and S.G.U., R.p. 8; diaphysial parts of two proximal limb elements (LM, LO 3839 t and LO 3877), and a number of phalanges, the best preserved of which are RM, R. 1490, 1491 and SM, 6090.

DESCRIPTION AND REMARKS.—The thoracic-lumbar centrum (LM, LO 3878 t) is 25 mm long, 42 mm high, and 41 mm broad; its height : length index is 168 and its breadth : length index 164. The end faces are almost circular and moderately concave, and are bounded peripherally by rounded off margins. The notochord pit is clearly shown. The probable anterior end of the neural canal is a little broader than the posterior one. There are 4 large foramina for nutritive vessels: an unpaired dorsal at the bottom of the neural canal, a paired lateral on the lateral face, and an unpaired on the ventral face. Since it is higher than broad and strikingly short, this centrum differs clearly from all the other Plesiosaurian centra from the Senonian of Scania so far known; it belongs probably to a Pliosauroid.

The anterior caudal centrum (LM, LO 3891 t) has the following proportions: length 63 mm, height 80 mm, breadth 93 mm, height : length index 127, breadth : length index 147. The end faces are deeply concave and are bounded by rounded off margins; at the centre of each end face there is a small elevation of a somewhat wart-like shape. The ventral face bears a paired longitudinal ridge (see above, p. 457), which, however, is low and obscure. This face shows only one foramen for a nutritive vessel. According to its proportions the anterior caudal centrum in question would be from an Elasmosaurid, whilst on the other hand the shape and appearance of its end faces rather favour the opinion that it would have belonged to a Pliosauroid.

The material does not contain any identifiable remains of cervical ribs. As is clear from the shape of the rib facets in all the Plesiosaurian cervical centra from Scania, the ribs were cercidopleurous, just as in all other Upper Cretaceous Plesiosaurians so far known. The other true ribs proper are in a poor state of preservation, being represented by fragments only. This is also true of the gastralia ("ventral ribs"), one of which is figured in Pl. 14, fig. 4.

The smallest of the two diaphysial ossifications of proximal limb elements (LM, LO 3877 t; Pl. 14, fig. 2) is about 200 mm long and 115 mm broad at its distal end. It is probable that one is concerned here with the remains of a humerus (see above, p. 457). The bone is decidedly slenderer than the corresponding ossifications in *Scanisaurus* (pp. 457-458) and seems therefore not to have belonged to any *Scanisaurus*-species.

The second, more imperfect diaphysial ossification of a proximal limb element (LM, LO 3839 t; from L. Nilsson's collection¹) is from a much larger individual than the former one in that it is 130 mm thick and may have had a total length of at least 400 mm. It must have belonged to a very large Plesiosaurian, possibly *Elasmosaurus*? cf. *gigas*.

As a rule the phalanges of the Plesiosaurians are of a stouter shape than those of the Mosasaurians. To judge from this condition the phalanges here dealt with are probably all from Plesiosaurians.

GEOLOGICAL HORIZON.—The thoracic-lumbar centrum LO 3878 t comes from the Lower Maastrichtian. All the other indeterminable bones dealt with above are from the Lower Campanian.

LOCALITIES.—Bjärnum (LO 3878 t), Ugnsnunnarna, Ivö (LO 3891 t), Maltesholm (LO 3877 t), Ignaberga (LO 3839 t) and Blaksudden, Ivö (all other bones described or mentioned under this title).

Order SQUAMATA Opperl 1811

Family MOSASAURIDAE P. Gervais 1853.

Genus *Mosasaurus* Conybeare 1822

DIAGNOSIS: see Broili and Schlosser in Zittel 1923, p. 264.

GENOTYPE.—*Mosasaurus hoffmanni* Mantell 1828.

¹ See footnote 1, p. 432.

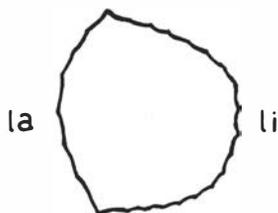


Fig. 10. *Mosasaurus* cf. *hoffmanni* Mantell 1828. Outline of a parabaasal section of a tooth crown. LM, LO 3879 t. Nat. size.
la, labial side, li, lingual side.

***Mosasaurus* cf. *hoffmanni* Mantell 1828**

Pl. 15, figs. 1-2. Text-fig. 10.

SYNONYMS.—See Kuhn 1939, pp. 66-67; Camp, pp. 44-46.

DIAGNOSIS.—As pointed out by Kuhn (1939, p. 66, footnote), *Mosasaurus hoffmanni* has not yet been properly defined. The most recent but incomplete diagnosis, given by Dollo (1925, pp. 180-181) is as follows: "Cette espèce—est caractérisée, notamment, par ses *dents robustes et facettées*, mais dont les facettes sont *larges* sur la face externe et *étroites* sur la face interne. Formule dentaire: $\frac{2 \text{ Pmx} + 13 \text{ Mx}}{14 \text{ Mn}} \times 2 + 8$
Pt $\times 2 = 58 + 16 = 74$. Le *Mosasaurus giganteus* atteignait 15 mètres de long."

HOLOTYPE.—An incomplete skull (the famous "Grand animal de Maestricht; "cf. Cuvier 1824, pp. 310-338, Pl. 18, fig. 1), in Muséum national d'histoire naturelle, Paris.

MATERIAL.—31 tooth crowns, belonging to LM (3), RM (23), SM (2) and UM (3).

DESCRIPTION.—The crown of the individual teeth is stout, conical and slightly recurved. Its labial and lingual faces are bounded off from each other both rostrally and caudally by a carinal crest ("carina" of previous writers). In a few specimens, however, the caudal carinal crest is less prominent than the rostral one. The labial and lingual faces are both ornamented with a number of apico-vasal crests which are separated from each other throughout their extent by shallowly concave fillets (the "facets" of previous writers). On the labial side there are 7-10 such crests, and 13-20 on the lingual side. A delicate striation is also visible, particularly on the basal part of the lingual face. In parabaasal sections the crown (text-fig. 10) agrees with that of the holotype (Owen 1840, Pl. 72, fig. 5; Thevenin 1896, p. 904, text-fig. 3) in the condition that its labial face is much more convex than the lingual one.

Since in the Mosasaurians the tooth replacement in all probability went on fairly rapidly (Williston 1898, p. 101), there is every reason to believe that the teeth at my disposal represent several different stages of growth. Some of the teeth are a little more recurved than the others, and may hence be pterygoid teeth (Williston 1898, p. 101, and other writers). In some tooth-crowns the apex is worn as a result of biting against tooth crowns in the opposite jaw of the same side.

REMARKS.—A proper specific determination of detached Mosasaurian teeth can hardly be made without a direct comparison with correctly determined material. By courtesy of Professor J. P. Lehman, Director of the Paleontological laboratory of Muséum national d'histoire naturelle, Paris, I have, however, received excellent casts of two mandibular teeth of the holotype of *Mosasaurus hoffmanni* from Maestricht. As is clear from these casts, the teeth from Scania are highly reminiscent of

those of the holotype where their proportions, curvature, parabasal sections and other characters are concerned. The apico-basal fillets are somewhat narrower and consequently more numerous in the Scanian teeth than they are in the casts, but in this respect there may well have been a considerable range of variation in the individual Mosasaurian specimens.

In view of their shape, ornamentation and other characters the Scanian teeth are hence such that they may be provisionally referred to *Mosasaurus hoffmanni* Mantell. To what extent a direct comparison with the Dutch, Belgian and French material may necessitate a revision of this determination remains to be seen.

M. hoffmanni has been recorded from the U. and L. Maastrichtian (Dollo 1925, p. 190). If my determination of the teeth from Scania is correct, the stratigraphic range of species now extends downwards into the Campanian as well.

GEOLOGICAL HORIZON.—Lower Campanian.

LOCALITIES.—Blaksudden, Ivö (29 teeth); Balsberg (1 tooth); Ignaberga (1 tooth).

Mosasaurus sp.

MATERIAL.—42 tooth crowns, belonging to LM (3), RM (35), S.G.U. (1) and UM (3).

DESCRIPTION.—With regard to their general shape these tooth crowns all agree with those described above under the title of *Mosasaurus* cf. *hoffmanni*. Their apico-basal fillets are, however, fairly obscure.

REMARKS.—It is not impossible that the 42 tooth crowns in question here also belong to *M.* cf. *hoffmanni*. The question whether this is so cannot, however, be decided for the reason that the range of variation of the tooth crowns in *M.* cf. *hoffmanni* still is unknown.

GEOLOGICAL HORIZON.—Lower Campanian—Lower Maastrichtian.

LOCALITIES.—Blaksudden, Ivö (37 specimens), Ignaberga (3 specimens), Balsvik (1 specimen), and Maltesholm (1 specimen).

Genus *Platecarpus* Cope 1869

Platecarpus cf. *somenensis* Thevenin 1896

Pl. 15, figs. 3a–c.

1835. *Ichthyosaurus*. — Nilsson, p. 139, Pl. 5, fig. 6.

1837. *Mosasaurus stenodon*. — Hisinger, p. 7, Pl. A, fig. 2b.

1884. *Mosasaurus* sp. II. — Schröder, p. 327, Pl. 17, figs. 2a–c.

DIAGNOSIS (compiled from Thevenin's description).—Microrhynchous form. Crowns of teeth long, slender, pointed and slightly recurved; their labial and lingual sides equally convex in parabasal sections; 7–8 fillets on the labial side, 6 on the lingual side.

HOLOTYPE.—An incomplete skull in the National Museum of Natural History, Paris. (Thevenin 1896, pp. 907–909; Pl. 30.)

MATERIAL.—29 detached tooth crowns of which 1 belongs to LM, 27 to RM, and 1 to S.G.U.

REMARKS.—With regard to their shape and their external characters the 29 tooth crowns under discussion agree perfectly with those in *Platecarpus somenensis* Thevenin except that the fillets on both the labial and the lingual sides show a somewhat wider range of variation with regard to their number. This condition could be expected, however, since Thevenin's statements refer to a single individual, whereas the tooth crowns from Scania beyond question are from several individuals.

Apart from *P. somenensis*, there are only two other known European Mosasaurians, viz. *Mosasaurus lemonnieri* Dollo and *Plioplatecarpus marchi* Dollo, which have slender tooth crowns. The two latter species both differ, however, clearly from *P. somenensis*, the former species by the conditions that the labial sides of the parabasal sections of the teeth are much less convex than the lingual sides, and that the fillets are less conspicuous, the latter species by the much more recurved shape of the tooth crowns and the probable absence of distinct fillets (see Dollo 1913, Pl. 25, fig. 2).

GEOLOGICAL HORIZON.—Lower Campanian.

LOCALITY.—Blaksudden, Ivö.

Genus ***Plioplatecarpus*** Dollo 1882

DIAGNOSIS.—See Dollo 1890, p. 159.

GENOTYPE.—*Plioplatecarpus marshi* Dollo 1882.

Plioplatecarpus? sp.

Pl. 15, fig. 4.

MATERIAL.—Two tooth crowns (LM, LO 3883 t and LO 3883 t) belonging to the Paleontological Institute of Lund, and another two in the possession of Mr. L. Larsson, Båstad.

DESCRIPTION.—The tooth crowns are slender, pointed and strongly recurved and have sub-circular parabasal sections. In all these four tooth crowns the labial side exhibits 7 distinct fillets, whereas the lingual side lacks fillets but is densely striated from the base almost to the apex.

REMARKS.—As far as can be made out from the literature, the tooth crowns just dealt with agree most nearly with those of *Plioplatecarpus*. Dollo (1890, p. 159) characterized the *Plioplatecarpus* teeth as rather long, slender and recurved, with striated and "facetted" crowns and sub-circular in parabasal sections. In a later work he published a figure of a tooth crown (Dollo 1913, Pl. 25, fig. 2), which agrees perfectly with those from Scania just under discussion where both its shape and other general characters are concerned. (No fillets are shown in Dollo's figure, but the side directed towards the observer, apparently the lingual one, is densely striated). This being so, the four teeth from Scania in question may be provisionally referred to *Plioplatecarpus*.

GEOLOGICAL HORIZON.—Upper Campanian.

LOCALITY.—Båstad, N.W. Scania.

Genus *Leiodon* Owen 1840

GENOTYPE.—*Leiodon anceps* Owen 1851. Norfolk Chalk.

Owen originally erected this genus for a jaw fragment with two teeth (Owen 1840, pp. 261–262; Pl. 72, fig. 1). Eleven years later the same writer (Owen 1851, pp. 42–45; Pl. 9A, figs. 1–7) described and figured other jaw fragments and teeth which he considered as belonging to the same individual as the type. On the latter occasion he introduced for all these remains the species name *L. anceps*.

On the basis of an excellent material comprising large portions of skulls, Gaudry (1892, pp. 5–13, pls. 17–18) described two new species of *Leiodon* (*L. compressidens* and *L. mosasauriodes*). The latter writer also demonstrated (op. cit., p. 4) the striking agreements between *Leiodon anceps* and *Hainosaurus* Dollo with regard to the tooth crowns and concluded that these two genera are identical. On account of the condition that the two species described by Gaudry are mesorhynchous, however, Dollo (1893, p. 79) suppressed the genus *Leiodon*. Since the only known genus of the Mosasaurians of the Old World possessing a mesorhynchous premaxillary is *Mosasaurus*, Dollo (1890, p. 163), classified all the *Leiodon*-species with *Mosasaurus*.

In his discussion of *Leiodon* Thevenin (1896, p. 902) maintained that from a taxonomic point of view Dollo underrated the significance of dental characters, but overrated the shape of the premaxillary and in summarizing his opinion wrote as follows: "Il est portant difficile de placer dans une même genre des animaux aux dents longues et tranchantes et d'autres dans les dents sont plus courtes, plus fortes et presque en forme de pyramide triangulaire. Ces différences dans la dentition impliquent des différences dans la régime alimentaire et par suite dans tout l'organisme."

Depéret and Russo (1925) used the name *Leiodon* in their description of material from *Marocco*. They also pointed out that if, as seems very likely, *Leiodon* and *Hainosaurus* are synonymous, the former generic name has the priority and therefore must be retained.

Williston (1898, p. 88) stated that *Hainosaurus* and the American *Tylosaurus* are "so nearly related that decisive distinctional characters are not yet forthcoming, unless they be found in the paddles." There is hence strong reason to believe that *Tylosaurus* may also turn out to be synonymous with *Leiodon*. During a visit to Paleontological Institute of Tübingen the present writer was able to verify that the tooth crowns of *Tylosaurus dyspelor* described by Huene (1910) are essentially of the same type as the tooth crowns from Scania described below.

Leiodon cf. *anceps* Owen 1851

Pl. 15, figs. 5–7.

SYNONYMS.—See Kuhn 1939, p. 80.

DIAGNOSIS (compiled from Owen's original description). Crowns of teeth approximately half the size of those in *Mosasaurus hoffmanni*, labio-lingually compressed, and very slightly recurved; the labial and lingual sides equally convex in par basal sections; the surface of the individual tooth crowns smooth and shining.

HOLOTYPE.—Jaw fragments and teeth in the British Museum, London (cat. nos. 41639 and 41640; cf. Lydekker 1888, pp. 265–266).

MATERIAL.—8 tooth crowns, 7 of which belong to the Paleontological Institute of Lund (LM, LO 3884 t—LO 3890 t) and one to Mr. L. Larsson, Båstad.

REMARKS.—With regard to their shape and general characters the 8 tooth crowns are perfectly as in *Leiodon anceps*, but differ clearly from those of *Leiodon compressidens* Gaudry (1892, pp. 5–6; Pl. 1) and *Leiodon mosasauroides* Gaudry (1892, pp. 7–10; Pl. 2) in the condition that they are broader and more regularly biconcave in parbasal sections. Under these circumstance the present writer has found it most appropriate at present to refer the tooth crowns in question provisionally to *Leiodon anceps*.

GEOLOGICAL HORIZON.—Upper Campanian.

LOCALITY.—Båstad, N.W. Scania.

Undeterminable skull fragment of a Mosasaurian

Pl. 16. Text-figs. 11–13.

1835. *Plesiosaurus*. — Nilsson, pp. 131–136, Pl. IV; Pl. V, fig. 1.

1837. *Plesiosaurus*. — Hisinger, p. 6, Pl. B.

1885. *Mosasaurus scanicus*. — Schröder, pp. 328–329.

This specimen (LM, LO 1671 t), denominated by Schröder (1885, pp. 328–239) *Mosasaurus scanicus* was already described by Nilsson in 1835. Nilsson's description, published in Swedish, is, however, both incorrect and misleading and a new description is therefore needed.

The specimen shows the posterior half of the exoskeletal skull roof and, in addition, the anterior part of the compound premaxillary, which is exposed from the left side. The latter bone is detached and lies in the right temporal fenestra. Having been exposed to the atmospherical conditions during a long time, the individual dermal bones are much weathered in a superficio-basal direction, and in places the bones are even completely worn off so that they are represented only by more or less obscure impressions of their basal faces. Where only the superficial layers of the bones are missing the radiating structure of the middle layer is clearly visible.

Fig. 11. Undeterminable Mosasaurian skull (*Mosasaurus scanicus* Schröder 1885). LM, LO 167 T a, b. $\times 1/2$. Imperfect exoskeletal skull roof in dorsal view. The dermal bones are much weathered from above and even represented in places by impressions of their inferior faces only.

F, frontal; *P*, parietal; *Pm*, premaxillary; *Pto*, *Pf*, postorbito-postfrontal; *Sq*, squamosal; *Tab*, tabular; *X*, impressions of unidentifiable detached bones; *Y*, impression of unidentifiable dermal bone.

a–*a*₅, canals and cavities in the interior of the bones; *f*, pulp cavity of a detached tooth filled up with matrix; *g* anterior process of frontal; *i*, *i*₁, impressions of anterio-lateral parts of frontal; *j*, impression of a part of the frontal; *k*–*k*₂, impressions of the posterior part of the frontal; *l*, centre of radiation in postorbito-postfrontal; *m*, suture between frontal and postorbito-postfrontal on ventral face of exoskeletal skull roof; *n*, pineal foramen; *p*, impression of lateral parts of postorbito-postfrontal; *q*, impression of posterior process of postorbito-postfrontal; *r*, small lateral process of postorbito-postfrontal; *s*, impression of anterior part of squamosal; *t*, impression of a part of the inferior face of the left tabular; *u*, suture between tabular and postero-lateral process of parietal on ventral face of exoskeletal skull roof; *v*, impression of postero-lateral process of parietal.

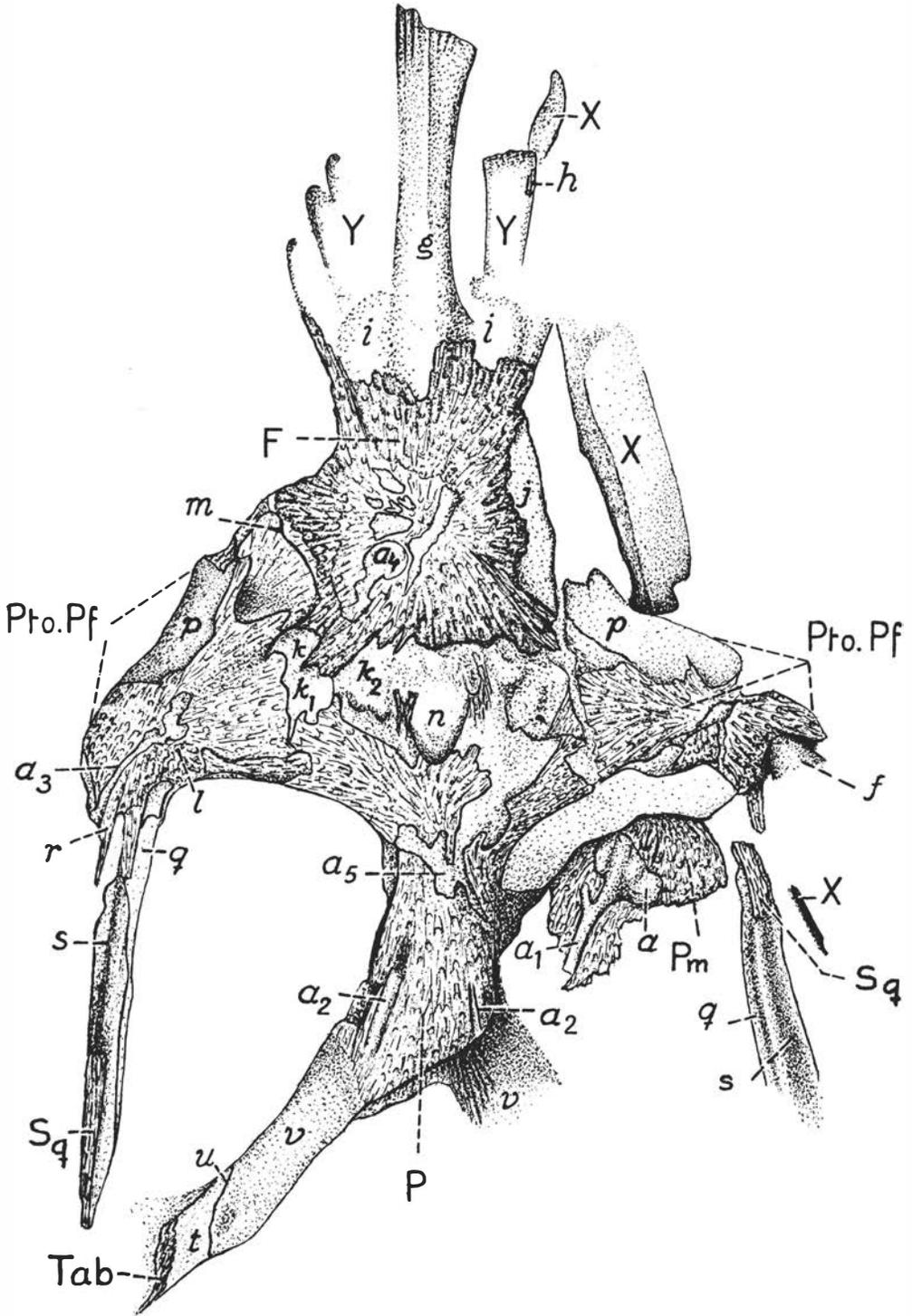


Fig. 11.

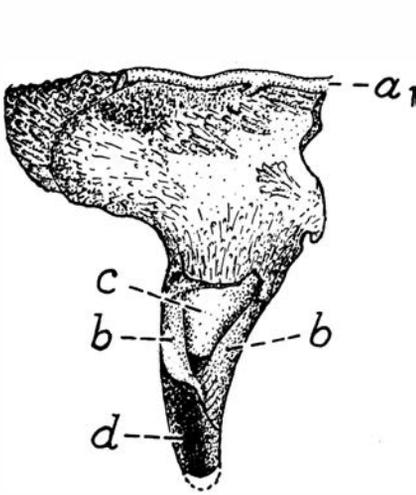


Fig. 12.

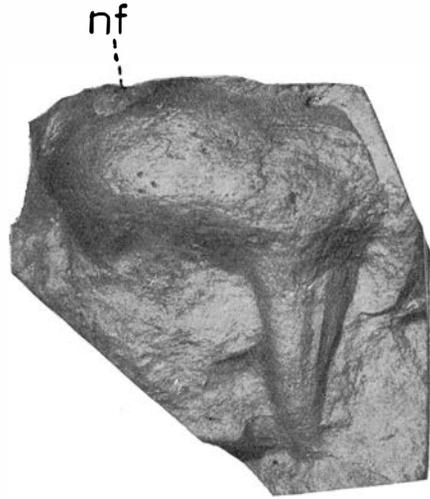


Fig. 13.

Figs. 12 and 13. Part of undeterminable Mosasaurian skull (*Mosasaurus scanicus* Schröder 1885). Foremost part of left half of compound premaxillary (text-fig. 12) with cast of counterpart showing external face (text-fig. 13). Nat. size.

a_1 , paired rostro-caudal canal in dorsal part of premaxillary; b , preserved piece of the hard tissues of the 2nd premaxillary tooth crown, counted from in front; c , cast of the pulp cavity in the 2nd premaxillary tooth; d , part of the 2nd premaxillary tooth, preserved as a cast only; nf , foramen for nerves and vessels.

In the interior of these bones one also notices special cavities and canals ($a-a_5$, text-fig. 11), some of which will be dealt with below (p. 469).

The measurements of the specimen which could be taken with reasonable certainty were as follows: total length forwards to the foremost end of the impression of the internasal process of the frontal (g , text-fig. 11) 378 mm; maximum breadth approximately 212 mm, and breadth across the foremost parts of the postfrontals 136 mm.

With the guidance of *inter alia* works by Williston (1898), Huene (1910) and Camp (1949) the writer has been able to identify most of the preserved bones in the specimen under discussion.

The *premaxillary* (Pm , text-figs. 11-13) shows that the tip of the snout is short and rounded off in front of the teeth and that one is therefore concerned in this instance with a mesorhynchous Mosasaurian (see Dollo 1889, Pl. 9, fig. 1; 1890 pp. 162-163). On the antero-dorso-lateral part of its external face the bone exhibits a fairly large foramen (nf , text-fig. 13) for nerves and vessels, which probably ran in the rostro-caudal canal a_1 shown in text-figs. 11 and 12. The foremost left premaxillary tooth is absent in the fossil. The premaxillary tooth no. 2 from in front is comparatively slender, slightly recurved and exhibits traces of crests and fillets (see p. 462 above).

A fragmentary crown of a detached tooth (f , text-fig. 11), preserved as a cast in the rock is seen lateral to the remains of the right postfrontal. This tooth was apparently larger and more robust than the premaxillary tooth no. 2.

The impressions of dermal bones (*Y*, text-fig. 11) on each side of the internasal process of the frontal are so obscure that they cannot be identified.

The compound *frontal* (*F*, text-fig. 13) has a long and narrow internasal process (*g*) which originally was overlapped by the long, median dorsal process of the premaxillary. The structures *k*, *k*₁ and *k*₂ are impressions of the posterior part of the lower side of the frontal. The latter bone overlapped the adjoining parts of the post-orbito-postfrontals of both sides, and possibly also certain adjoining parts of the compound parietal.

As normal in Mosasaurians, the postfrontal and postorbital are fused to form a *postorbito-postfrontal* (*Pto.Pf* in text-fig. 11; see Williston 1898, pp. 111–112; Huene 1910, pp. 11–12). On account of the condition already mentioned that the postorbito-postfrontal was extensively overlapped by the frontal the suture between it and the latter bone has a very different position on the dorsal and ventral sides of the exoskeletal skull roof. In the normal way, the postorbito-postfrontal was also overlapped postero-medially by the parietal. The posterior process of the bone (*g*, fig. 11) is long and seems to have extended backward along the squamosal almost as far as to the postero-lateral corner of the temporal fenestra (Owen 1877, p. 688, fig. 6). Finally, it is noticeable that the bone possesses a special minor posterior process (*r*, fig. 11), which extends somewhat backwards lateral to the foremost part of the squamosal. According to Williston (1898, Pl. 12) and Huene (1910, fig. 7) a corresponding process occurs in *Clidastes*, *Tylosaurus*, and probably in many other Mosasaurians as well.

The anterior part of the compound *parietal* (*P*, text-fig. 11) is pierced by the pineal foramen (*n*), which has a sub-elliptical shape, with the longer axis rostro-caudally. The paired, postero-lateral process of the parietal issues from the main part of the bone at an angle of about 45° to the median line of the skull. The posterior part of the bone contains a paired canal (*a*₂), which is reminiscent of the canal for the occipital artery in *Eusthenopteron* and frogs (Jarvik 1954, p. 15; cf. the temporal artery in *Sphenodon*, O'Donoghue 1920, Pl. 7, fig. 2), and hence may very well have housed an artery of a similar kind.

To judge from its remains the *squamosal* (*Sq*, text-fig. 11) stretched so far forwards that it participated in the formation of the whole of the skeletal arch constituting the lateral boundary of the temporal fenestra. In all probability it lay lateral and ventral to the posterior process of the postorbito-postfrontal.

The *tabular* (*Tab*, text-fig. 11), is preserved on the left side, where, however, it is represented only by a little piece of bone and an impression (*t*) of a part of its inferior side. As far as can be seen from this impression, the bone in question was essentially as in other Mosasaurians. Thus it was in all probability overlapped to a considerable extent by the postero-lateral process of the parietal. On the ventral face of the exoskeletal skull roof the position of the suture between the tabular and the aforementioned parietal process is as indicated by the line *u* in text-fig. 11.

Finally the skull fragment also shows remains of three detached, unidentifiable bones (*X*, text-fig. 11).

REMARKS.—Since, as may be readily gathered from the above description, it exhibits only general Mosasaurian characters the skull fragment from Scania here dealt with is actually indeterminate as to genus and species. The name *Mosasaurus scanicus* Schröder has therefore been dropped in the present paper.

GEOLOGICAL HORIZON.—Upper Campanian.

LOCALITY.—Köpinge Mölla (Stora Köpinge).

Undeterminable Mosasaurian tooth crown I

1835. *Ichthyosauri dens.* — Nilsson, pl 139, Pl. 5, fig. 5.
1837. *Mosasauri dens.* — Hisinger, p. 7, Pl. A, fig. 2b.
1884. *Mosasaurus* sp. I Schröder, p. 327.

REMARKS.—The tooth LM, LO 169 t, which in Schröder's (1884) opinion belonged a representative of the genus *Mosasaurus* is in fact indeterminable as to both genus and species.

GEOLOGICAL HORIZON.—Lower Campanian.

LOCALITY.—Oppmanna.

Undeterminable Mosasaurian tooth crown II

1885. *Leiodon lundgreni.* — Schröder, pp. 329–333; Pl. 17, figs. 3 a–d.
1939. "*Mosasaurus*" *lundgreni.* — Kuhn, p. 70.

REMARKS.—The tooth crown LM, LO 784 T, which Schröder referred to *Leiodon* and for which he erected the species *L. lundgreni*, does not either exhibit any generic or specific characters whatever and is hence also undeterminable.

GEOLOGICAL HORIZON.—Upper Campanian.

LOCALITY.—Köpinge (not Balsberg, as stated by Schröder; see Hennig 1910, p. 671).

Other undeterminable Mosasaurian remains

In addition to the material dealt with above, the collections of Scanian Cretaceous reptiles contains a great number of other Mosasaurian remains comprising tooth crowns, fragments of jaw bones, detached vertebrae etc., all of which are indeterminable.

Order CROCODILIA Wagler 1830

Family CROCODILIDAE Huxley 1860.

Sub-family CROCODILINAE Kälin 1955.

Aigialosuchus n.g.

DIAGNOSIS.—A genus of *Crocodylinae* with pre-orbital division of head (snout + corresponding parts of lower jaws of both sides) narrow and distinctly set off from the other parts of the head. Fenestrae exonarinae of both sides fused to form a fenestra exonarina communis. Nasals of both sides extending forwards to the posterior margin of this fenestra. Mandibular symphysis long; "splenia" reaching the symphysis. Teeth short.

GENOTYPE.—*Aigialosuchus villandensis* n. sp.

The new genus *Aigialosuchus* (Greek αἰγιαλος, seashore, and σοχος, Greek transcription of Egyptian name of crocodile) here introduced differs clearly from all other known long-snouted genera of Crocodylians in the forward extension of the paired

nasal bone right to the fenestra exorarina communis (see Jarvik 1942, pl. 247). The condition that the foremost part of the snout is considerably broadened and distinctly bounded off posteriorly from the rest of the cranium by a conspicuous paired notch proves that *Aigialosuchus* must belong with the sub-family *Crocililinae* as defined by Kälén (1955, p. 768). Since it is very imperfectly known, *Aigialosuchus* cannot be compared with other long-snouted genera belonging with the *Crocililinae*.

In spite of the fact that it was found in a marine sediment, *Aigialosuchus* must not necessarily have been a purely marine form, but may very well be imagined to have lived in the littoral zone or in some river on the adjacent mainland.

Most of the long-snouted Crocodiles possess long, slender teeth, which indicates that, like the recent gavials, they were piscivorous forms. Since its teeth are short and stout, *Aigialosuchus* was apparently adapted to a different mode of feeding.

Aigialosuchus villandensis n.sp.

Pls. 17–20. Text-fig. 14.

DIAGNOSIS.—The same as for the genus, which contains this species only.

HOLOTYPE AND MATERIAL.—Remains of the anterior parts of the skull and of the mandibles belonging to one and the same individual (S.G.U., A-N). Actually these remains comprise the following parts (Pls. 17–20; text-fig. 14): 1) the foremost part of the pre-orbital division of the cranium with the premaxillaries and the anterior pieces of the nasals; 2) the hindmost part of the pre-orbital division of the cranium with considerable pieces of the maxillaries and nasals; 3) a small detached fragment of the left maxillary; 4) anterior, symphyseal parts of the dentaries of both sides in connection with each other; 5) a symphyseal part of the left dentary situated further backwards than the parts referred to under point no. 4; 6) The anterior part of the right angular; 7) three detached teeth; and, finally, 8) two unidentifiable bone fragments.

The species name *villandensis* is derived from the district Volland, in which the find locality is situated.

DESCRIPTION.—From the shape of the upper jaw fragments and from the fact that the mandibular symphysis is long it can be inferred with full certainty that the pre-orbital division of the cranium was long and narrow (text-fig. 14). The premaxillaries of both sides are expanded in a lateral direction in such a way as jointly to effect a conspicuous broadening of the rostral end portion of the snout. This broadened portion is bounded off posteriorly from the rest of the snout by a conspicuous, paired notch (*n*, text-fig. 14) for the reception of the 4th mandibular tooth. The broadened portion in question has a breadth of 71 mm, whereas the breadth of the snout immediately behind, across the notches just referred to, is only 47 mm. The small fragment of the left maxillary (Pl. 19, fig. 1), which lay somewhere between the foremost, broadened portion of the snout and the posterior, broad division of the cranium has its palatal lamina completely preserved. Since the maximum breadth of the latter part (measured from the lateral margin to the medial margin of the palatal lamina) is 28 mm, the posterior, longer part of the pre-orbital division of the cranium must have been of a fairly uniform breadth which at least in most places did not exceed 56–60 mm or thereabouts. The posterior part of the pre-orbital division of the cranium is approximately 74 mm broad at the point denoted *p* in text-fig. 14, but from this

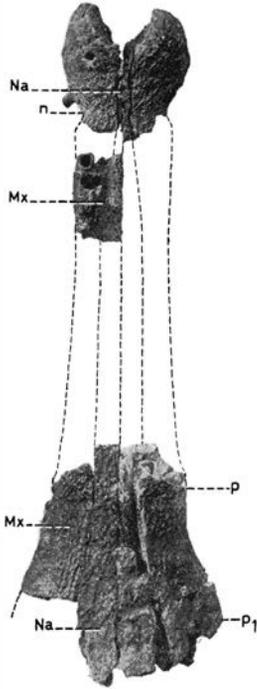


Fig. 14. *Aigialosuchus villandensis* n. sp. Reconstruction of pre-orbital part of cranium. $\times 1/4$.

Mx, maxillary; *Na*, nasal; *n*, notch for 4th mandibular tooth counted from in front; *p*, *p*₁, points used for the taking of certain measurements.

point increases rapidly in breadth backwards so that at point *p*₁ in the same text-fig., i.e. near the posterior, broad division of the cranium, it is approximately 118 mm.

As usual in crocodiles, the ornamentation of the dermal bones consist of pits and grooves, or only of pits. The latter is the case on the angular, where, however, the pits are deeper and more pronounced than on the other preserved bones.

The anterior and postero-dorso-medial parts of the *premaxillary* (*Pm*, Pl. 17) are missing and this is also true of the medial and postero-medial parts of the palatal lamina of the bone except at one place anteriorly where one can clearly see an emargination (*em*, Pl. 17, fig. b), which formed part of the boundary of the palatal fenestra ("palatal vacuity" in the current paleontological literature; "foramen praemaxillaire" of Kälin 1955, p. 760) and which shows that this fenestra was large and probably broader than long. The premaxillaries of both sides are separated posteriorly to the fenestra *exonarina communis* by the anterior narrow parts of the nasals. In addition, as has already been stressed (p. 471), the premaxillaries of both sides are expanded laterally so as jointly to cause the snout to be broadened most anteriorly. The paired fossa (*f*, Pl. 17, fig. b) on the palatal lamina between the two foremost preserved premaxillary teeth must have received a mandibular tooth, in all probability the second one counted from in front. The preserved part of the left premaxillary bears 4 teeth (the presence of the foremost of these teeth proved by a preserved part of an alveol), but whether most anteriorly there also existed a fifth tooth is a question which must be left unanswered. The alveoli of the teeth have somewhat raised margins.

Close to its row of teeth the palatal lamina of the large preserved part of the *maxillary* (*Mx*, Pl. 18) exhibits two circular fossae, each of which apparently received a

large mandibular tooth. In the right maxillary two replacement teeth (*st*, *st*₁, Pl. 18, figs. a, c) are exposed at the bottom of two alveols whose lateral walls are missing. It may also be mentioned here that one replacement tooth is seen in each premaxillary (*st*_a, *st*_b, Pl. 17, fig. b).

The *nasal* (*Na*, text-fig. 14; *Na*, Pls. 17, 18) is a very long bone, but does not extend forwards between the nasal openings, and, in consequence, as we have seen, the original fenestrae exonarinae of both sides have fused to form a fenestra exonarina communis. In its hindmost preserved part the nasal is comparatively broad, but tapers gradually forwards so that it is quite narrow between the postero-dorso-medial parts of the premaxillaries.

As a whole, the lower jaw is narrow, but it is clearly a little broadened anteriorly in its symphyseal part in a way similar to that of the anterior end portion of the snout. The broadening in question is, however, less pronounced than the corresponding one of the snout and is not bounded off posteriorly by any notch. The two halves of the jaw meet in a strikingly long symphysis whose total length, according to the preserved anterior pieces of the dentaries of both sides (Pl. 19, figs. 2-4; Pl. 20, fig. 2), exceeded 138 mm. In the symphysis itself there is a wide longitudinal canal, the *median symphyseal canal* (*mc*, Pl. 19, figs. 2b, 4b), which seems to be an anterior unpaired continuation of the paired groove on the median side of the dentary in *Alligator* that Nilsson (1944, fig. 19) refers to as the sulcus meckeli, a groove which is caused by the foremost part of Meckel's cartilage of each side. Provided that the opinion just set forth is true, Meckel's cartilage in *Aigialosuchus* would have fused most anteriorly with that of its opposite side to form an unpaired symphyseal bar which extended forwards between the dentaries of both sides. The median symphyseal canal widens most anteriorly to form a cavity (*cav*, Pl. 19, fig. 2b) into which there projects the crown of a small tooth (*t*, Pl. 19, fig. 2b) which points backwards and a little downwards. With regard to its size, this tooth crown is approximately as those of the replacement teeth already mentioned. As far as can be judged one is concerned here with a tooth which would have replaced the 4th or 5th dentary tooth counted from in front, and hence a tooth which has grown in a wrong direction.

The *angular* (Pl. 20, fig. 1) is imperfectly preserved, being represented only by an anterior part, bearing the area overlapped by the dentary.

The crowns of the *teeth* in both the upper and lower jaws are short, stout and slightly recurved; they are densely striated in an apico-basal direction and exhibit only slight indications of anterior and posterior carinal crests. The roots are cylindrical.

GEOLOGICAL HORIZON.—Lower Campanian.

LOCALITY.—Blaksudden, Ivö.

Undeterminable Crocodylian dermal plate

Since few Crocodylian remains occur in the Senonian of Scania, it is worth mentioning that the material investigated also contains a detached incomplete dermal plate (UM, R.p. 48) of a crocodile from the Lower Campanian at Blaksudden, Ivö.

Carnivorous Dinosaurian

Pl. 20, fig. 4.

Three tooth crowns, of which the best preserved (RM, R. 1451) is shown in Pl. 20, fig. 4, are thin in a labio-lingual direction and have therefore a shape of a somewhat thick, two-edged knife-blade. These tooth crowns are all pointed and a little recurved. Their labial and lingual faces are slightly convex and are separated anteriorly and posteriorly by sharp carinal crests. The enamel is shining and completely smooth. The figured crown, which is the largest one of the three, may have been about 45 mm high; its rostro-caudal basal breadth is 16 mm, whilst its labio-lingual basal breadth is only 6.8 mm. In view of all their characters so far known the tooth crowns just described can only have belonged to some carnivorous Dinosaurian.

GEOLOGICAL HORIZON.—Lower Campanian.

LOCALITY.—Blaksudden, Ivö.

Reptilian bone fragments undeterminable as to groups

Finally, the material from Scania also comprises three fragments of limb bones which cannot possibly belong to representatives of any of the main groups of marine reptiles. The best preserved of these fragments, SM, 6083 (Pl. 20, fig. 5), which seems to be a part of the diaphysial ossification of a long limb bone, has a length of 113 mm, whereas its maximum and minimum breadths are 113 mm and 70 mm respectively. The bone in question, which contains a large marrow cavity, may very well be from a Dinosaurian or from some other large terrestrial reptile. One of the two remaining fragmentary limb bones, UM, R. p. 51, has a length of 118 mm and a minimum breadth of 35 mm, whereas the corresponding measurements of the other bone, UM, R. p. 52, are 90 mm and 16 mm respectively. Nothing can be established with regard to the original total length of these two bones. In R. p. 52 the marrow cavity is so large that the bone fragment is of a tube-like shape with very thin walls (thickness ranging from 1.4 to 4 mm).

GEOLOGICAL HORIZON.—Lower Campanian.

LOCALITY.—Blaksudden, Ivö.

General remarks on the fauna

According to the present writer's investigation the reptile fauna from the Campanian and Lower Maastrichtian beds of Scania comprises the following forms determinable at least as to family or group.

CHELONIA	<i>Osteopygis?</i> sp.
SAUROPTERYGIA	
PLESIOSAURIA	Polycotyloid, gen. et sp. indet. Polycotyloid?, gen. et sp. indet. “ <i>Elasmosaurus</i> ” cf. <i>helterseni</i> (Kiprijanoff). <i>Elasmosaurus?</i> <i>gigas</i> (Schröder). <i>Scanisaurus</i> cf. <i>nazarowi</i> (Bogolubov).

SQUAMATA	<i>Mosasaurus</i> cf. <i>hoffmanni</i> Mantell. <i>Mosasaurus</i> sp. <i>Platecarpus</i> cf. <i>somenensis</i> Thevenin. <i>Plioplatecarpus?</i> sp. <i>Leiodon</i> cf. <i>anceps</i> Owen.
CROCODILIA	<i>Aigialosuchus villandensis</i> n. g., n. sp.
DINOSAURIA	Carnivorous Dinosaurian.

As may readily be gathered from the above list, the reptile fauna of the Upper Cretaceous of Scania is one of the richest of its kind in Europe. Concerning particularly the Plesiosaurians, this fauna is decidedly richer in forms than any contemporary one except in North America and Russia.

Two new genera, *Scanisaurus* and *Aigialosuchus*, occur in the fauna. *Scanisaurus* is of particular interest since it seems to represent a new family of Plesiosaurians. Amongst the listed forms of the fauna there are only two, *Leiodon* cf. *anceps* and *Plioplatecarpus?* sp. which occur in the Upper Campanian, whilst the remaining forms are from the Lower Campanian.

The outcrops in Scania of Cretaceous beds older than the Lower Campanian are few and small. Shell fragment limestone of the Emscherian ("Westphalicus Senonian") is quarried only at Ringeleslätt in N.E. Scania. According to statements by both Lundegren (1930, p. 119) and Troedsson (1930, pp. 91 and 117) vertebrae of reptiles have been found at the latter locality. No remains of reptile bones from this locality are, however, contained in the extensive material investigated by the present writer.

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PLATES

Plate 1

Osteopygis? sp.

Incomplete carapace in ventral aspect (see text-fig. 2). LM, LO 3834
t. Blaksudden, Ivö. $\times 1/2$; pp. 435-438.



Plate 2

Indeterminable Chelonian bones. Ignaberga

Fig. 1. LM, LO 3835 t. Incomplete costal plate. Grooves caused by the depressed margins of the horny scutes denoted with broad, white lines. Nat. size. Pp. 438-440.

Fig. 2. LM, LO 3836 t. $\times 1/2$. Incomplete scapula. P. 440.
a, scapula proper; *b*, acromion.

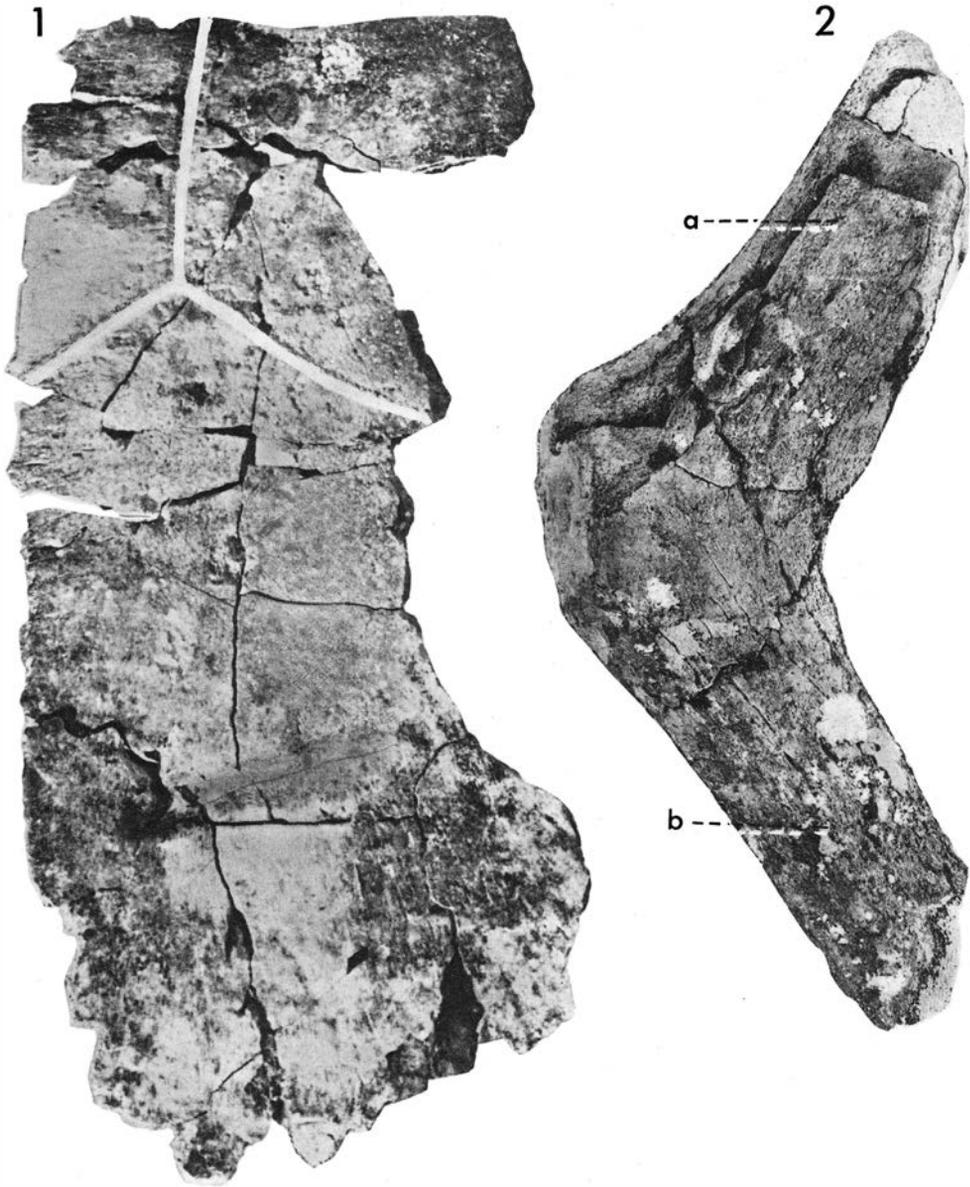


Plate 3

Figs. 1, 2. *Polycotyliidae*, gen. et sp. indet. Cervical centra. Blaksudden, Ivö. Nat. size. Pp. 441-442.

Fig. 1. RM, R. 860. Anterior aspect.

Fig. 2a, b. UM, R.p. 6. Posterior and ventral aspects, respectively.

Figs. 3-4. *Polycotyliidae?*, gen. et sp. indet. More or less incomplete teeth. Nat. size. Blaksudden, Ivö. Pp. 442-443.

Fig. 3a-f. RM, R. 1184. Labial, posterior, lingual, anterior, apical and basal aspects, respectively.

Fig. 4a-d. RM, R. 1185. Tooth crown with the apical part missing. Anterior, lingual, posterior and apical aspects, respectively.

cr, cervical rib; *nf*, foramina for nutritive vessels.

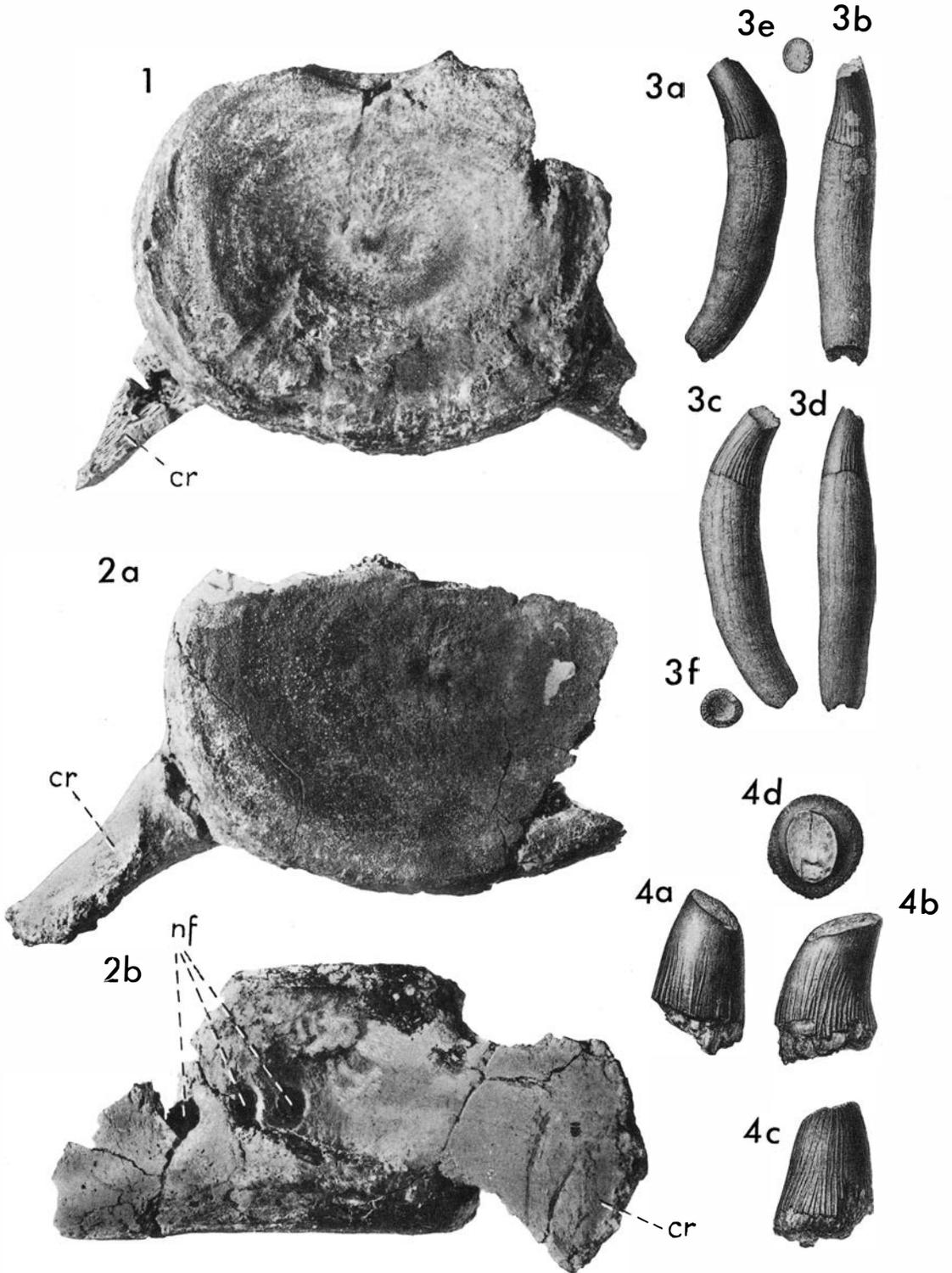


Plate 4

“*Elasmosaurus*” cf. *helmerseni* (Kiprijanoff 1882)

Cervical centrum. RM, R. 997. Nat. size. In anterior aspect (a); from the right side (b); and in ventral aspect (c). Blaksudden, Ivö. Pp. 444–445.

cr, proximal part of cervical rib; *ef*, end face; *lr*, lateral longitudinal ridge; *np*, basal part of neurapophysis.

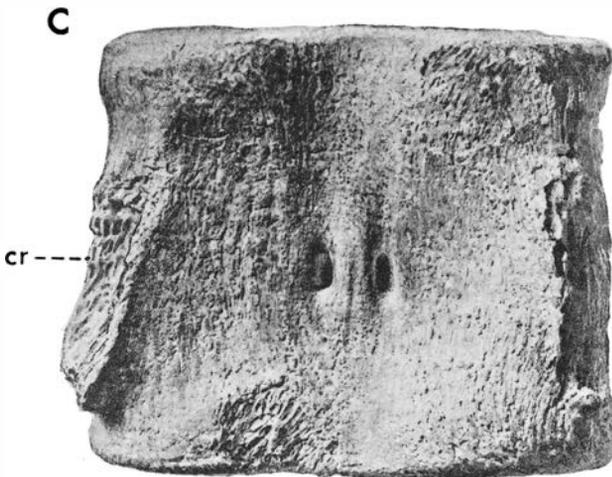
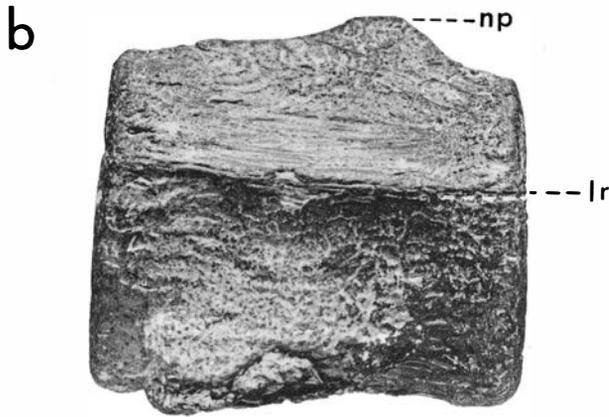
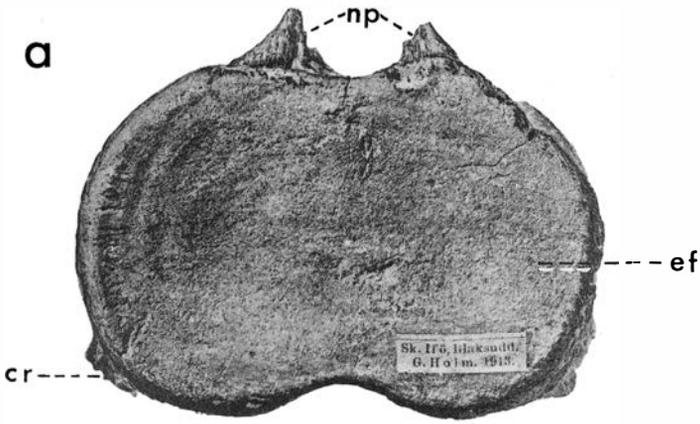


Plate 5

Elasmosaurus? gigas (Schröder 1885)

Anterior end face of a thoracic-lumbar centrum. UM, R.p. Nat. size; Ignaberga. Pp. 445-447.
nep, notochord pit.

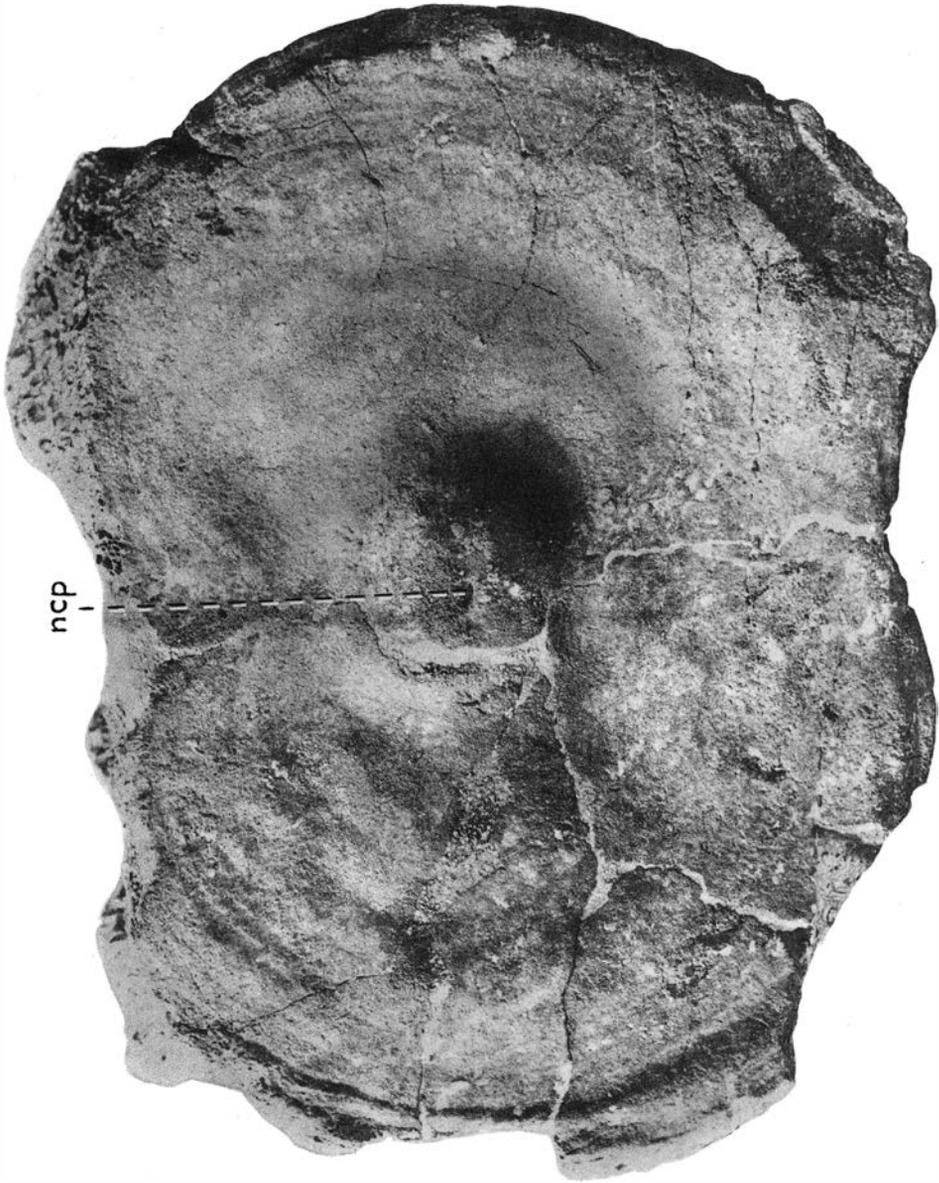


Plate 6

Scanisaurus cf. *nazarowi* (Bogolubov 1911)

More or less incomplete teeth. Blaksudden, Ivö. Pp. 450–451.

Fig. 1a–d. UM, R.p. 18. × 2. Labial, anterior, lingual and posterior aspects, respectively.

Fig. 2a, b. RM, R. 1140. × 2. Lingual and apical aspects, respectively. Apical part missing.

Fig. 3a–c. RM, R. 1122. × 2. Labial, anterior and lingual aspects, respectively.

Fig. 4a–d. RM, R. 1116. Nat. size. Labial, anterior, lingual and posterior aspects, respectively.

Fig. 5a–d. RM, R. 1121. Nat. size. a–c, labial, lingual and posterior aspects, respectively; d, basal view showing fracture area.

Fig. 6a–d. LM, LO 3840 t. Nat. size. Labial, anterior, lingual and posterior aspects, respectively.

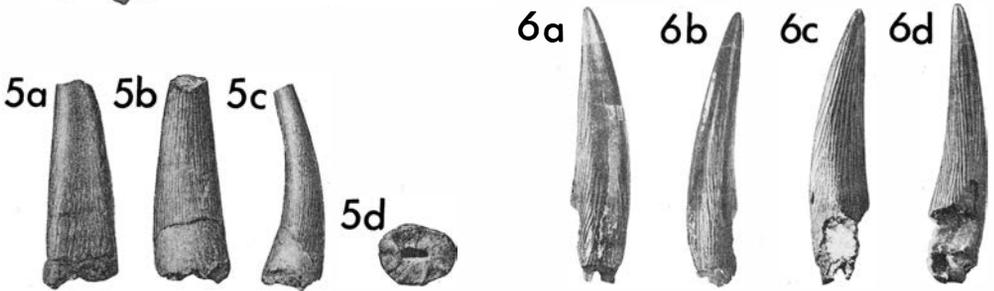
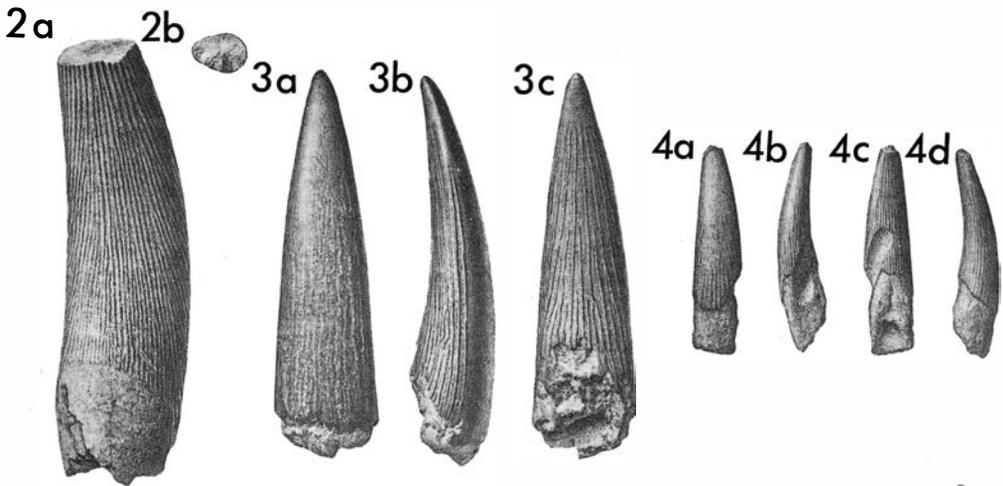
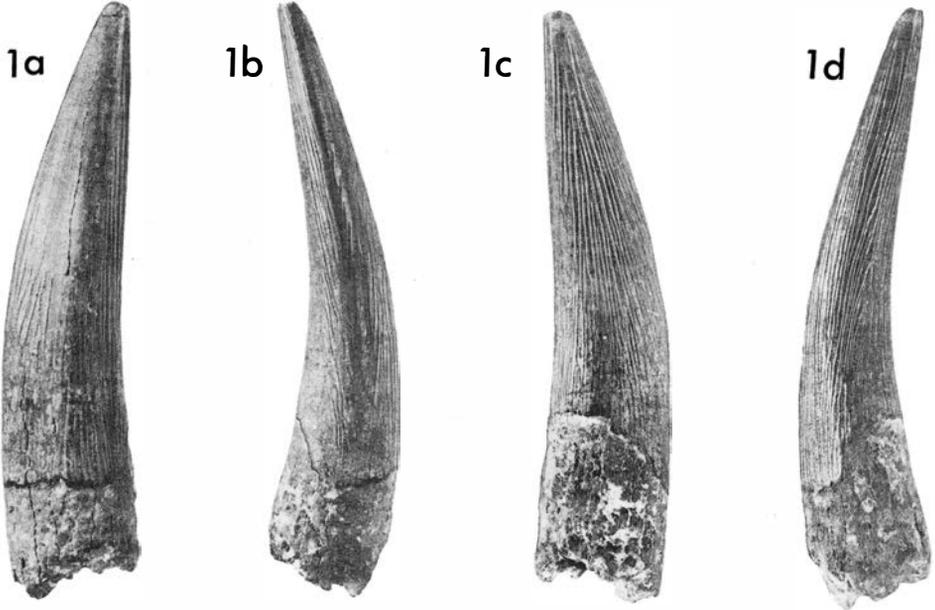


Plate 7

Scanisaurus cf. *nazarowi* (Bogolubov 1911)

Vertebral centra belonging to series I (p. 449). RM, R. 1068, R. 863, R. 1067, R. 1066, R. 756. Nat. size. Blaksudden, Ivö. Counted from above downwards in the plate: 1st pre-pectoral centrum, pectoral centra Nos. 1-3, and 1st thoracic-lumbar centrum. Pp. 451-457.

a



b

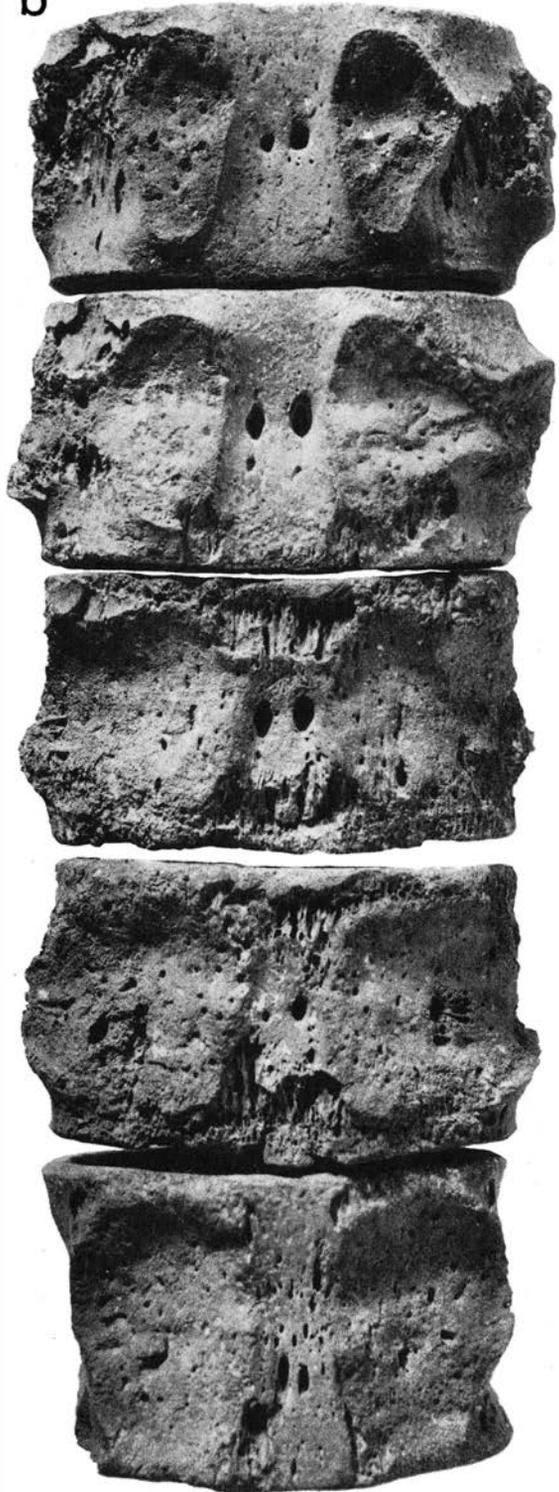


Plate 8

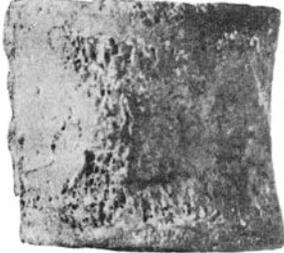
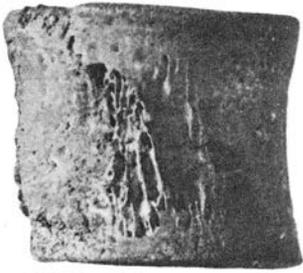
Scanisaurus cf. *nazarowi* (Bogolubov 1911)

Vertebral centra. Nat. size. Blaksudden, Ivö. Pp. 451–457.

Fig. 1. RM, R. 1080, R. 762, R. 1079, R. 763. 2nd–1st pre-sacral centra and 1st–2nd sacral centra of series I (p. 449), in left side view.

Fig. 2a, b. RM, R. 862. 2nd thoracic-lumbar centrum of series I (p. 449); a, anterior aspect; b, seen from right side.

Fig. 3a, b. RM, R. 998. 3rd pre-pectoral centrum of series II (p. 449); a, anterior aspect; b, seen from right side.



1

2a



2b



3b



3a



Plate 9

Scanisaurus cf. *nazarowi* (Bogolubov 1911)

Cervical centra belonging to series II (p. 449). RM, R. 1003, R. 1002, R. 1001, R. 998, R. 1000, R. 995. $\times 4/5$. Blaksudden, Ivö. Counted from above downwards in the plate: 6th-1st pre-pectoral centra. a, dorsal, b, ventral aspect. Pp. 451-457.

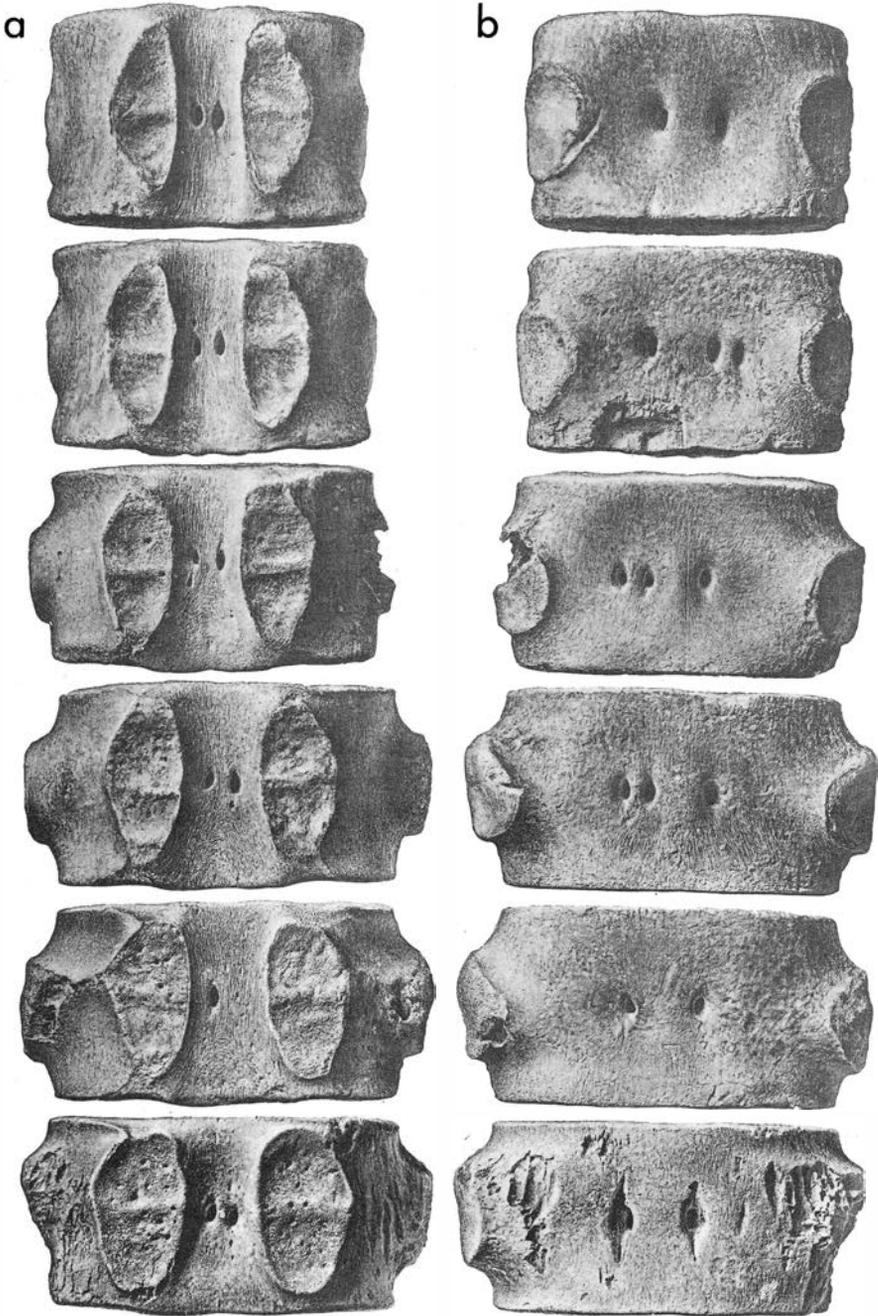


Plate 10

Scanisaurus cf. *nazarowi* (Bogolubov 1911)

Vertebral centra belonging to series III (p. 449). The mutual order of the individual centra counted from above downwards in the plate. Dorsal aspect. $\times 1/2$. Axel'torp. Pp. 451-457.

- Fig. 1. RM, R. 777. ?6th pre-pectoral centrum.
Fig. 2. RM, R. 770, R. 772, R. 768. 4th-2nd pre-pectoral centra.
Fig. 3. RM, R. 773, R. 767. 1st and 2nd pectoral centra.
Figs. 4-5. RM, R. 769, R. 765, R. 766, R. 771, R. 764, R. 775, R. 774. 1st-7th thoracic-lumbar centra.
Fig. 6. RM, R. 776. Posterior thoracic-lumbar centrum.
Fig. 7. RM, R. 778. Posterior caudal centrum.

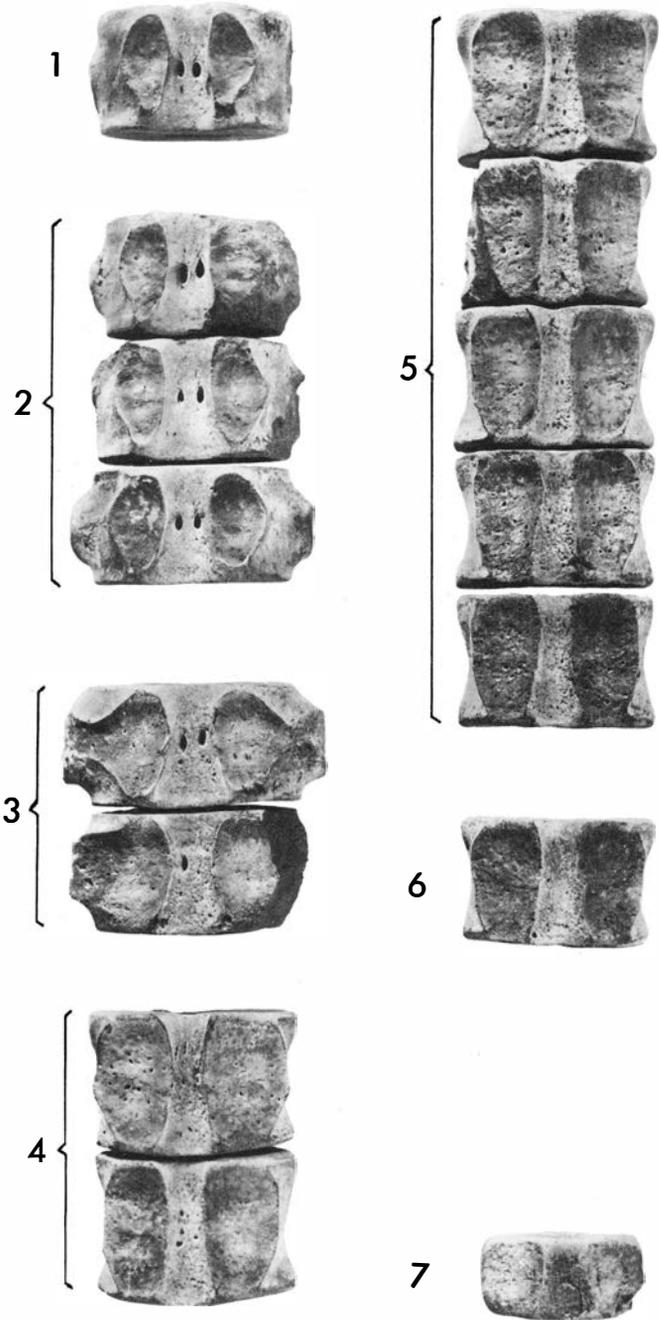


Plate 11

Scanisaurus cf. *nazarowi* (Bogolubov 1911)

Vertebral centra and a diaphysial ossification of a ?humerus.

Fig. 1. S.G.U., G. Anterior cervical centrum from series IV (p. 449) in sinistro-dorso-lateral aspect. Nat. size. Blaksudden, Ivö. Pp. 451-457.

Fig. 2 a, b. S.G.U., A₁-3. Caudal centra Nos. 5-7 in series IV (p. 449). Nat. size, Blaksudden Ivö. The mutual order of the centra counted from above downwards in the plate. a, ventral, b, dorsal aspect. Pp. 451-457.

Fig. 3. RM, R. 1578. Diaphysial ossification of a ?humerus. $\times 1/2$. Blaksudden Ivö. Pp. 457-458.

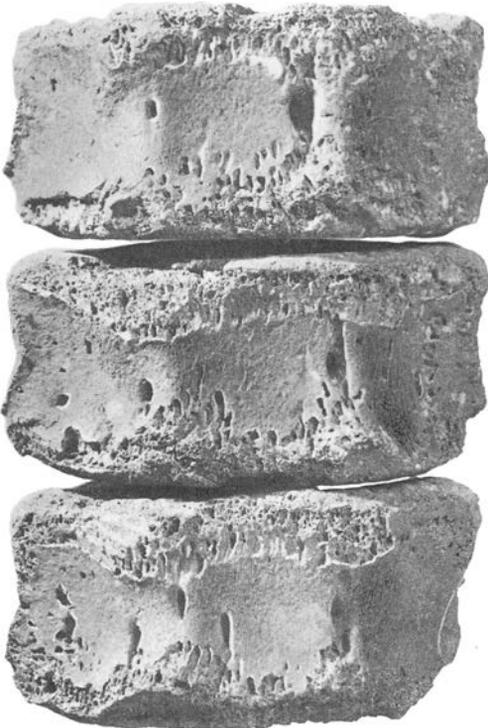
1



2b



2a



3



Plate 12

Scanisaurus cf. *nazarowi* (Bogolubov 1911)

Three of the midmost cervical centra in ventral aspect. Series V (p. 449). UM, R.p. 28, R.p. 29, R.p. 30. Nat. size. Blaksudden, Ivö. Pp. 451-457.

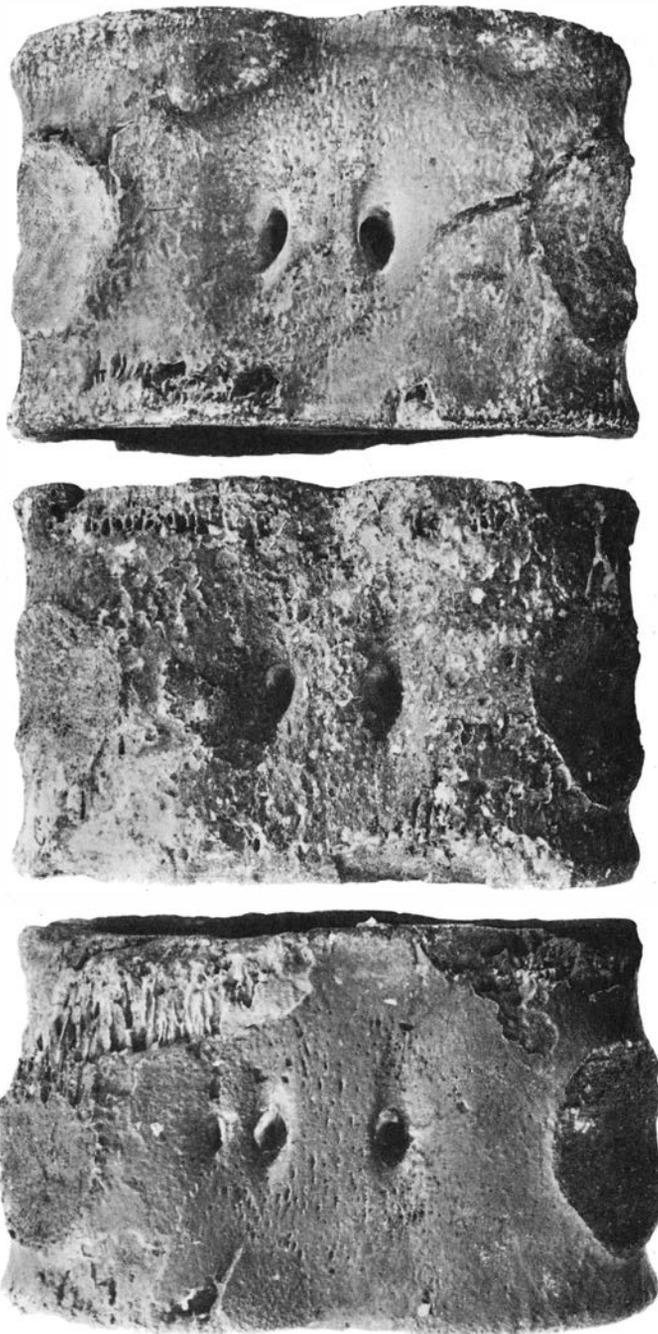


Plate 13

Scanisaurus cf. *nazarovi* (Bogolubov 1911)

Diaphysial ossifications of a ?humerus and a ?femur. Pp. 457–458.

Fig. 1. UM, R.p. 33. ?Humerus; extensor face. $\times 1/2$. Axeltoorp.

Fig. 2a, b. LM, LO 3841 t. ?Femur. $\times 1/2$. Blaksudden, Ivö. a, extensor face; b, flexor face.

r, r₁, rugose areas for the insertion of muscles; s, scars effected by a predacious vertebrate.

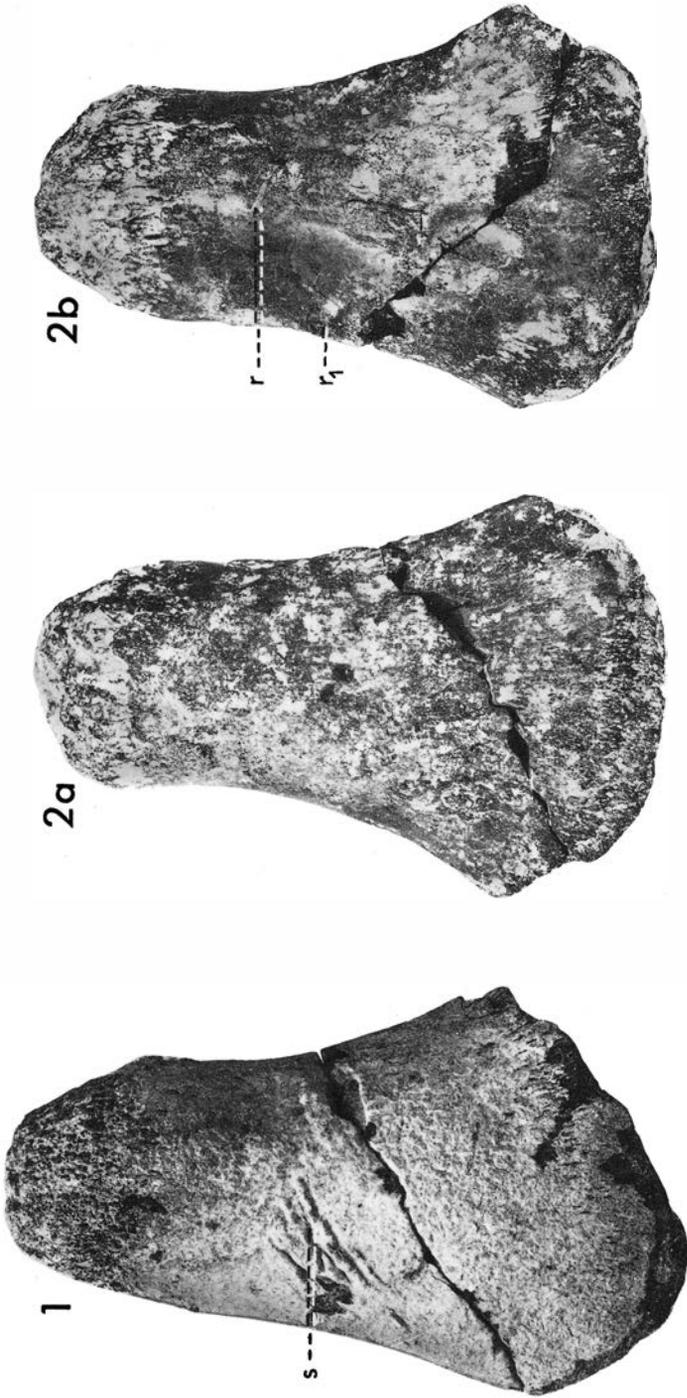


Plate 14

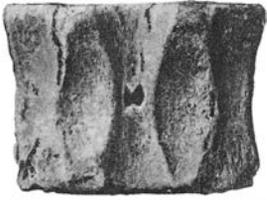
Fig. 1*a-c*. *Elasmosauridae*, gen. et sp. indet. Anterior cervical centrum. RM, R. 994. Nat. size. In dorsal aspect (a); from the left side (b); and in posterior aspect (c). Blaksudden, Ivö. Pp. 459-460.

Figs. 2-4. Undeterminable Plesiosaurian bones. Pp. 460-461.

Fig. 2. LM, LO 3877 t. $\times 1/2$. Diaphysial ossification of a ?humerus. Maltesholm.

Fig. 3*a-c*. LM, LO 3878 t. Nat. size. Thoracic-lumbar centrum. In dorsal aspect (a); from the left side (b); and in anterior aspect (c). Bjärnum.

Fig. 4. S.G.U., 8. Nat. size. Fragment of a gastral ("ventral rib"). Blaksudden, Ivö.



1a

1b



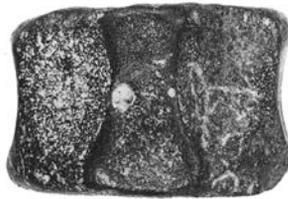
1c



2



3a



3b



3c



4



Plate 15

Figs. 1, 2. *Mosasaurus* cf. *hoffmanni*. Tooth crowns. Nat. size. Blaksudden, Ivö. Pp. 462–463.

Fig. 1 a, b. RM, R. 1292. Labial and lingual aspects, respectively.

Fig. 2 a, b. LM, LO 3879 t. Anterior and lingual aspects, respectively.

Fig. 3 a–c. *Platecarpus* cf. *somenensis* Thevenin 1896. Tooth. RM, R. 1376. Nat. size, labial, anterior and lingual aspects, respectively. Blaksudden, Ivö. Pp. 463–464.

Fig. 4. *Plioplatecarpus?* sp. Tooth crown. LM, LO 3882 t. Nat. size. Lingual aspect. Blaksudden, Ivö. P. 464.

Figs. 5–7. *Leiodon* cf. *anceps* Owen 1851. Tooth crowns. Nat. size. Båstad. Pp. 465–466.

Fig. 5 a, b. LM, LO 3884 t. Labial and anterior aspects, respectively.

Fig. 6. LM, LO 3886 t. Apical view. Apex missing.

Fig. 7 a, b. LM, LO 3886 t. Labial and anterior aspect, respectively.

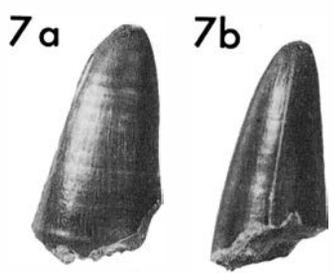
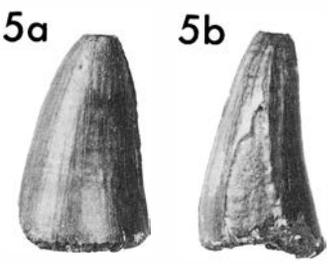
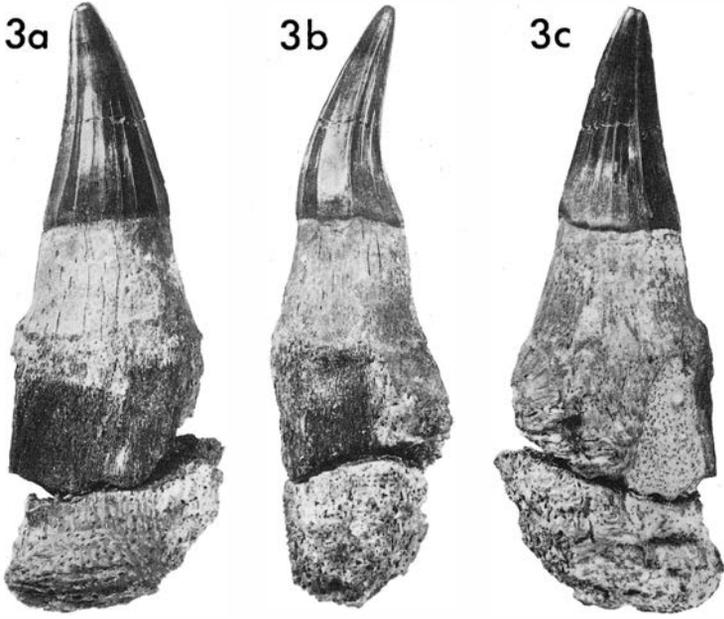
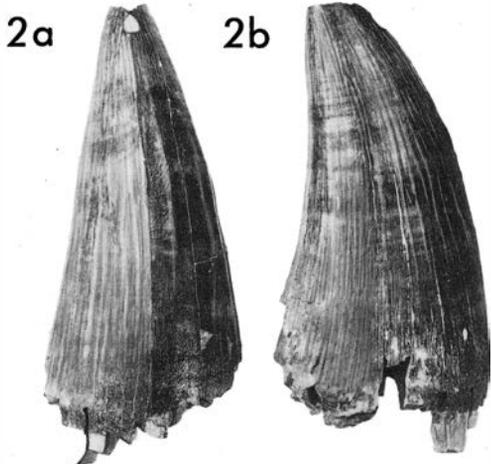
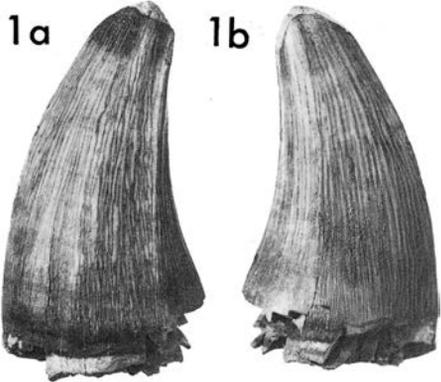


Plate 16

Indeterminable Mosasaurian skull

(*Mosasaurus scanicus* Schröder 1885) LM, LO 167 T a, b. (See text-
figs. 11-13). × 2/3. Köpinge Mölla. Pp. 466-469.

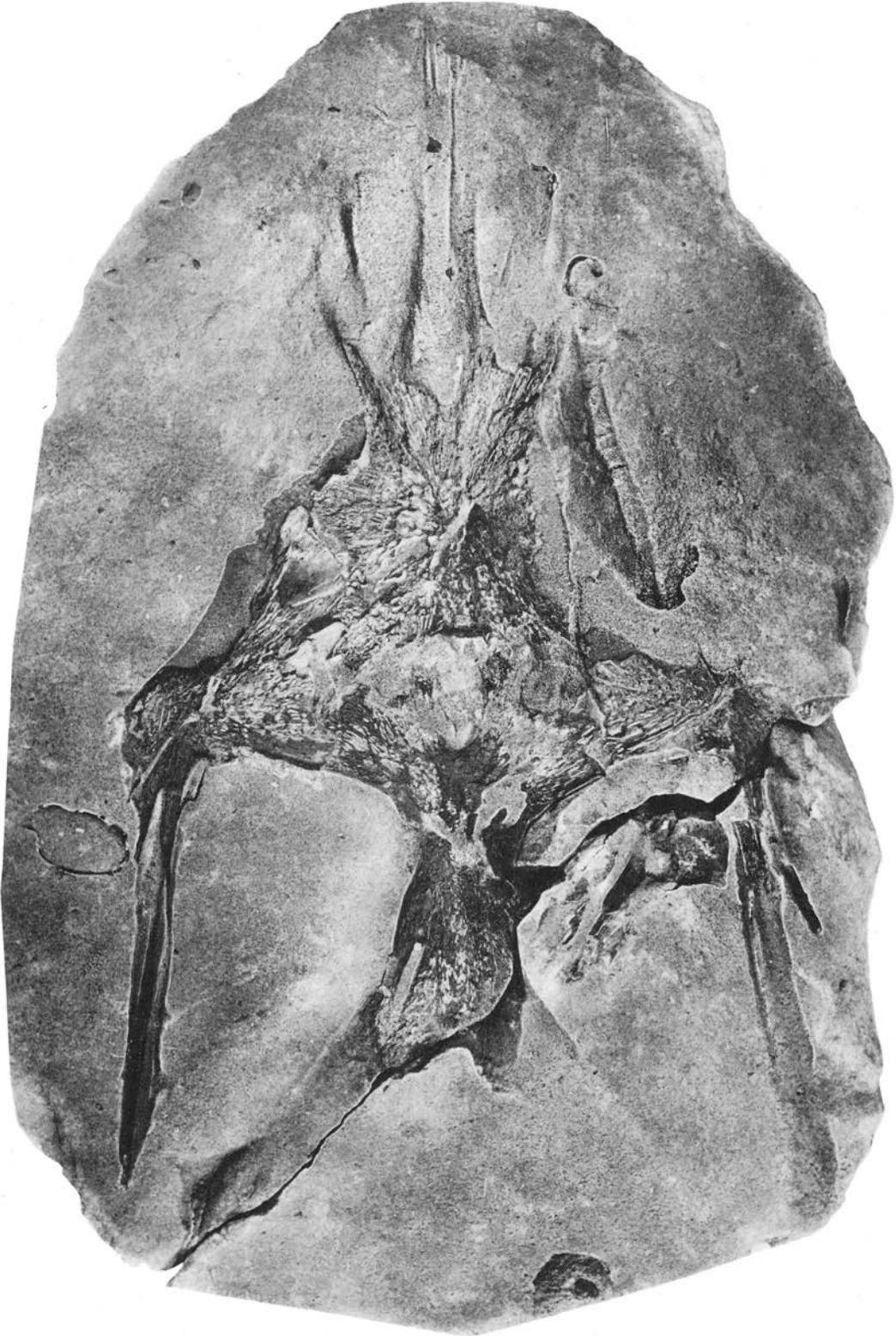


Plate 17

Aigialosuchus villandensis n.sp.

The foremost, broadened part of the pre-orbital division of the cranium showing the premaxillaries and the anterior pieces of the nasals. S.G.U., J. Nat. size. Blaksudden, Ivö. Pp. 471-473.

Figs. a, b, dorsal and ventral aspects, respectively; fig. c, from the left side.

Pm, premaxillary; *Na*, nasal; *em*, part of the margin of the palatal fenestra; *f*, fossa for the reception of a mandibular tooth; *h*, probable healed injury; *st_a*, *st_b*, replacement teeth.

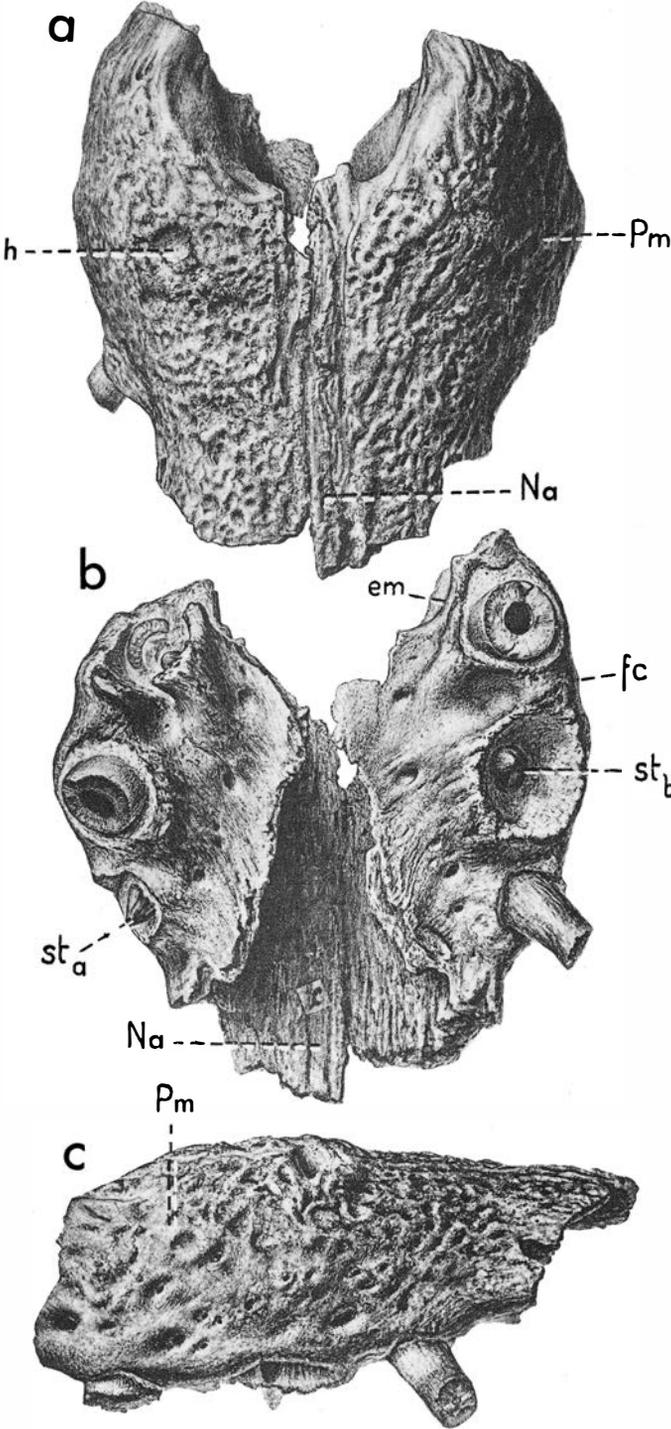


Plate 18

Aigialosuchus villandensis n.sp.

The hindmost part of the pre-orbital division of the cranium showing parts of the maxillaries and nasals. S.G.U., A, H, H₁. Nat. size. Blaks-
udden, Ivö. Pp. 471-473.

Fig. a, from the right side; fig. b, from the left side; fig. c, an-
terior aspect.

Mx, maxillary; *Na*, nasal; *st*, *st*₁, replacement teeth.

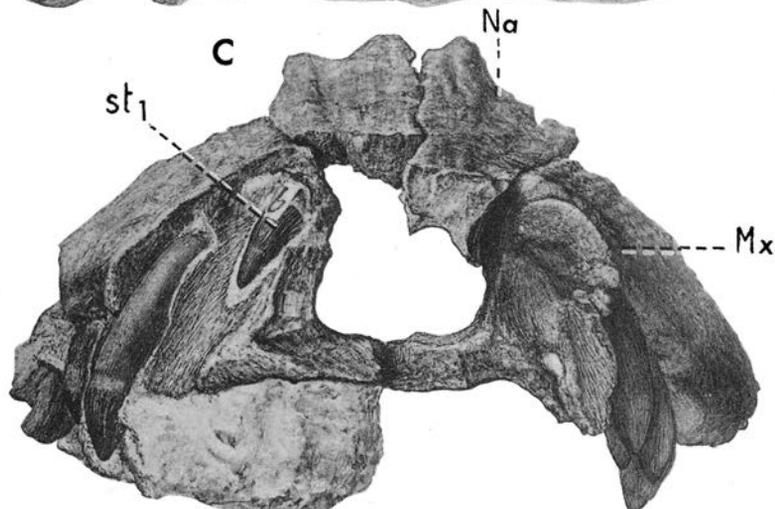
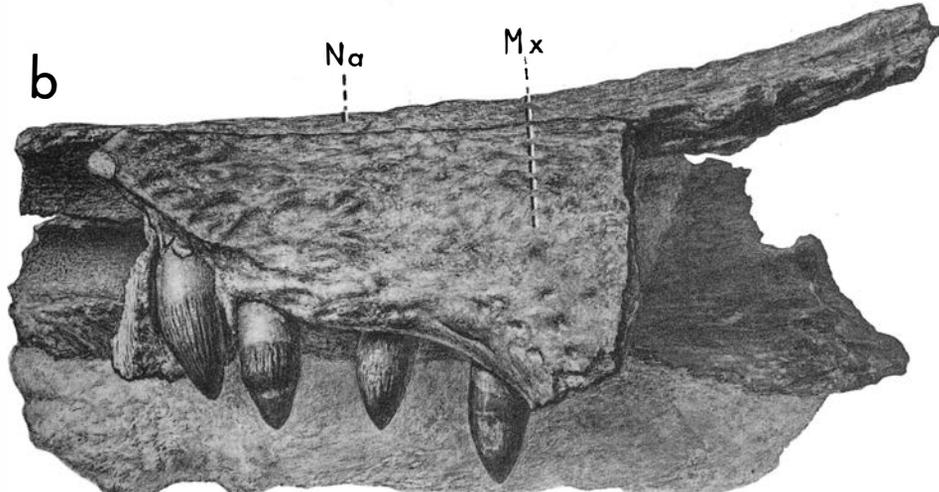
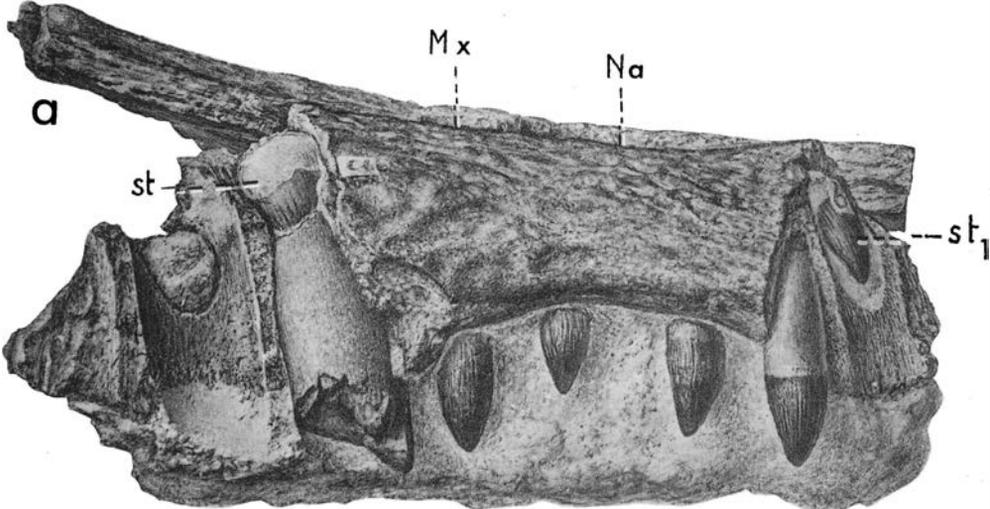


Plate 19

Aigialosuchus villandensis n.sp.

Fragments of maxillaries and dentaries of both sides. S.G.U., E.K.K₁, G. Nat. size. Blaksudden, Ivö. Pp. 471–473.

Fig. 1. Fragment of left maxillary, in medial view, showing medial (sutural) margin of palatal lamina.

Fig. 2 a, b. Foremost part of left maxillary, seen from the left side and in symphyseal (medial) view, respectively.

Fig. 3. The same bone fragment as in fig. 2, but seen in dorsal view and in its connection with a piece of the right dentary.

Fig. 4 a, b. A second fragment of the left dentary, seen from the left side and in symphyseal (medial) view, respectively.

cav, cavity formed by a widening of the median symphyseal canal; *mc*, median symphyseal canal; *sf*, area overlapped by foremost part of "splenial"; *t*, replacement tooth which has grown in a wrong direction; *t4*, 4th mandibular tooth.

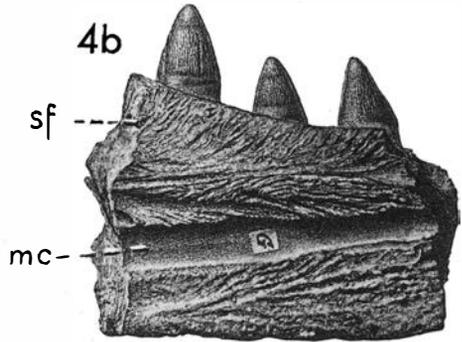
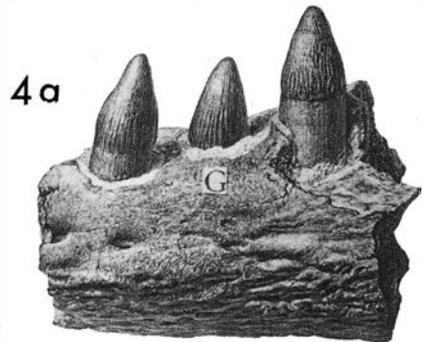
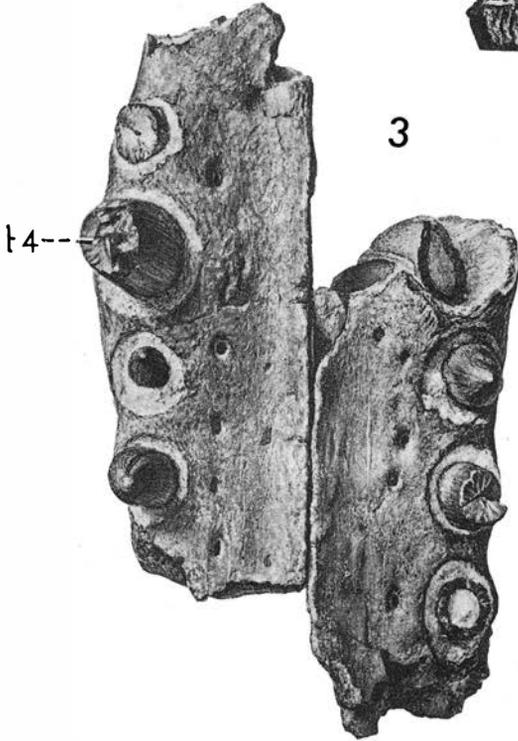
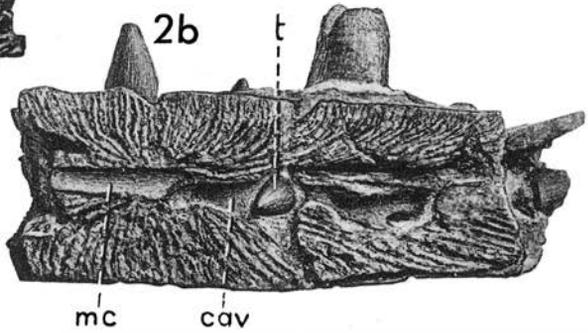
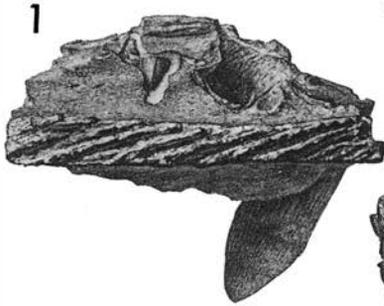
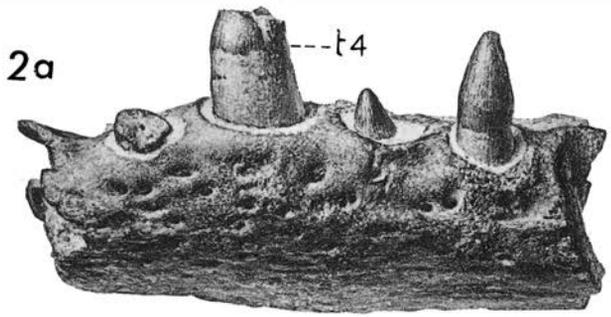


Plate 20

Figs. 1-3. *Aigialosuchus villandensis* n.sp. Fragments of the lower jaw and a detached tooth. S.G.U., N,D,G. Nat. size. Blaksudden, Ivö. Pp. 471-473.

Fig. 1. Anterior part of right angular seen from the right side.

Fig. 2a, b. Same fragment of left dentary as in Pl. 19, fig. 4; rostral and dorsal aspects, respectively.

Fig. 3a, b. Detached tooth, in labial and probable anterior aspects, respectively.

Fig. 4a, b. Tooth of a carnivorous Dinosaurian. ?Labial and anterior aspects, respectively. Apical part missing. RM, R. 1451. $\times 2$. Blaksudden, Ivö. P. 474.

Fig. 5. Reptilian bone fragment undeterminable as to group. SM, 6081. $\times 1/3$, approximately. Blaksudden, Ivö. P. 474.

df, area overlapped by the right dentary; *ms*, alveolar canal; *sf*, area overlapped by the foremost part of "splenial".

