

INFUNDIBULIPORA HUCKRIEDEI N. SP. (BRYOZ. CYCLOSTOMATA) FROM THE
UPPER CRETACEOUS OF IRAN AND WESTERN EUROPE. (WITH REMARKS
ON THE GENUS *INFUNDIBULIPORA* BROOD, 1972)

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ABSTRACT

Infundibulipora huckriedei n. sp., a mushroom-shaped Bryozoon is described and illustrated. It shows a radiate pattern of autozoecia and kenozoecia on its upper surface, and rows of smaller pits on its lower face and peduncle. It was found in the Campanian or Maastrichtian beds of the area of Kerman (Iran). It is regarded to be conspecific with some rare specimens of the Swedish Campanian and Dutch Maastrichtian. It resembles *Infundibulipora hesslandi* Brood of the Baltic Danian, but is much larger in dimensions. The generic position of *Infundibulipora hesslandi* is discussed. Brood attributed it to the Fam. Corymboporidae Smitt, but the present author has placed it in the Fam. Lichenoporidae Smitt. The morphology of the ovicell, which is a zoarial broodchamber, corresponds much more to that of the Fam. Lichenoporidae than that of the Corymboporidae. On the other hand, the ovicell of *Infundibulipora lucernaria* (Sars), the Recent type species of the genus, is quite different. Therefore, the attribution of *Inf. hesslandi* and *Inf. huckriedei* n. sp. to the Recent genus *Infundibulipora* is made with some reservation. The internal structures of *Infundibulipora lucernaria* (Sars) are studied with the help of Polyester sections.

INTRODUCTION

In 1961 the present author received from Prof. Dr. R. Huckriede (Marburg) some Bryozoa from the Upper Cretaceous of Iran (Province Kerman) with the request to determine and, if possible to date them. As a result of a preliminary survey, Huckriede (Huckriede, Kürsten & Ventzlaff 1962 p. 115) refers to the cyclostomatous Bryozoan genera "*Heteropora*", *Actinopora*, *Lichenopora*, "*Idmonea*" and some cheilostomatous ("*Membranipora*" and cribrimorph species). Other occurrences of Bryozoans in the Iranian Cretaceous are also mentioned in this publication. Since no Upper Cretaceous Bryozoan Faunas from Iran are described and our knowledge of Asiatic Cretaceous Bryozoans (e.g. Stoliczka 1872, Chiplonker 1939, Voigt 1967, Viskova and Endelman 1971) is very limited in comparison with the rich European faunas, one seems justified to publish the following note on this most interesting species, *Infundibulipora huckriedei* n. sp. It represents a "mushroom" or club-shaped cyclostomatous Bryozoan similar to the Danian *Infundibulipora hesslandi* Brood (Brood 1972 p. 322 pl. 46 Fig. 3; pl. 51 Figs. 7-8). In the meantime the present author discovered further specimens of *Infundibulipora huckriedei* in the Upper Cretaceous of Sweden and the Netherlands. They are considered to be identical with the Iranian species, and are, therefore, also described in this article.

LOCALITY AND STRATIGRAPHY

The six Iranian specimens of *Infundibulipora huckriedei* were collected by Dr. R. Huckriede within the Darmanu-Mountains (Kuh-i-Darmanu) NW Kerman on the southern side of the valley of Kischk and Kemunu northwest of the village Kemunu (Prov. Kerman). They were found within greenish marls (containing large thick-shelled *Lophospira* sp., small *Exogyra* and remains of Ophiuroids and Cidarids) intercalated within the uppermost part of the Upper Cretaceous Hippurites limestone below the Kerman conglomerate. The matrix contains very small detritic quartz grains, many spines of Echinoids but no Foraminifera. Only one fragment of a "*Hippurites*" was found and determined as *Vaccinites giganteus* (D'Hombres-Firmas) by Prof. K. Vogel (Frankfurt/M.). The range of this fossil is Coniacian-Maastrichtian. None of the Bryozoans of the locality are satisfactorily preserved. The specimens are worn by wave action, and it is very difficult to remove the adherent matrix. Therefore it is almost impossible to identify them specifically except for the cyclostomatous species (*Actinopora disticha* (v. Hagenow, 1851) *Lichenopora reticulata* (v. Hagenow, 1851) and *Crisisina carinata* (Roemer, 1840)). The stratigraphical range within the Upper Cretaceous of these three species being very wide, they give evidence of an Upper Cretaceous age only. On the other hand the newer dis-

covery of *Infundibulipora huckriedei* in the European Campanian and Maastrichtian corroborates the assumption of late Upper Cretaceous age. A more exact determination of the stratigraphical age (Campanian or Maastrichtian) is not yet possible.

Infundibulipora Brood, 1972

(Further remarks on that genus see p 232)

Infundibulipora huckriedei n. sp.

(Pl. I—1-6, Pl. II—1-7 and Pl. III—1-4)

Derivatio nominis: Named in honour of Prof. Dr. R. Huckriede (Marburg), who discovered this species.

Diagnosis: Zoarium erect, fungiform with a cup- or saucer-shaped round capitulum and a stout peduncle thickening towards the head. Upper surface of the capitulum with numerous (8-30) fascicles. Fascicles raised; in older specimens two to three cycles of fascicles are added. Centre and interspaces between the fascicles filled with the openings of numerous smaller tubes (Cancelli). Peduncle and lower surface of the head covered by straight rows of smaller pits (kenozoecia). Ovicells imperfectly known—only a zoarial brood-chamber observed in a specimen from Hemmingslycke (Sweden)—.

Description: The diagnosis is based mainly on six specimens from Iran; the preservation of the specimens is unsatisfactory. They are all worn and the peduncles are broken away below the capitulum. It is assumed that the fascicles were primarily much higher with steeper edges of the peristomes. Some other better preserved specimens are from the Swedish Campanian and the Dutch Maastrichtian (Pl. II—1-7 and Pl. III—1-4). They appear to belong to the same species although their peduncle is sometimes more conical and got so much set off against the head. Also, they have only one circle of fascicles which seem to be lowered also by detrition. Therefore it is difficult to compare them directly with the Iranian specimens and the slight differences may be caused solely by the state of preservation or by special ecological environments. The general shape of the zoaria which attain a diameter of 8 mm is saucer- or mushroom-like with short peduncle extending slowly or abruptly into the head (—capitulum). Seen from one side, the zoarium may also be club-shaped or fungiform as well with a distinct disciform or cuplike head. Neonastic zoaria may display a triangular sagittal section. This is seen especially in the Swedish and Dutch specimens (Pl. II—2-3, Pl. III—1). They possess shorter radiating fascicles with autozoecia of about the same size or a little larger than the central cancelli. In the older zoaria, the diameter of both autozoecia and kenozoecia increases a little because of the club-like form of the tubes (Pl. II—2). They may lead to a different aspect of the upper face in both younger and older zoaria

and it is evident that this difference in size means no specific difference. The slight diversity in the diameter of the autozoecia of the fascicles and the cancelli is more obvious in the adult zoaria. The center of the capitulum occupied by the cancelli is flat or a little depressed.

The lower face including the peduncle is covered by regular radiating rows of small round or ovate pits separated by delicate ribs. Towards the periphery, they augment by dichotomous splitting where they correspond to the number of budding tubes at the edge of the capitulum. The sagittal section reveals that these pits are the apertures of short tubules budding perpendicularly from an external lamina from which also bud off the younger zoecia and cancelli (Pl. II—2). These tubules form an external supporting lattice on the surface of the zoaria. None of the specimens from Iran or Sweden nor the only small colony from Kunrade (Netherlands) show any remarkable difference in size. In contrast to these, a specimen from the Maastrichtian Chalktuff of Maastricht (Quarry Curfs) near Berg (close to Maastricht) has larger pits at the base of the peduncle and also the ribs between them are thicker and more distant (Pl. III—1). In size they surpass the size of the tubes occurring near the edge of the capitulum. It is presumed that this difference is of no specific value, since their size varies within individual specimens (Pl. II—3). The other small specimen from Kunrade (Pl. III—3-4) displays no difference in the small pits in comparison with the Iranian specimens. These pits are of the same type as those observed in the genera *Fungella* v. Hagenow, 1851, *Corymbopora* Michelin, 1846, *Trochiliopora* Gregory, 1909, *Marsoniella* Levinsen, 1925 and *Amphimarsoniella* Voigt, 1974. These small tubules form a supporting layer on the lower face and the stalk of these fungiform Cyclostomata. This kind of accessory tubes corresponds to similar kenozoecia on the dorsal face of other Cyclostomata as, e.g., in *Crisisina* d'Orbigny and *Hornera* Lamouroux.

The material is insufficient to prepare many thin sections, especially as sections of the Iranian specimens are unsatisfactory. But this defect is compensated by the Swedish specimen figured in Pl. II—2, which is split along the median line displaying clearly the internal structures. It is difficult to give exact measurements because the diameters of the apertures and of the cancelli vary with the age and state of preservation of the specimens. In the worn and recrystallized Iranian specimens there is no much difference in the diameter of autozoecia and cancelli, which is about 0.07—0.1 mm. In the long clubshaped zoarium (Pl. II—3-4) from Hemmingslycke (Sweden) the cancelli are slightly smaller than the autozoecia, which may reach a diameter of 0.13—0.16 mm. The ovicell (zoarial broodchamber) is incompletely known. Only a small specimen from the Upper Campanian of

Stafversvad (Sweden) has a broken ovicell in the center of the capitulum. Its roof is destroyed (Pl. II—5-7). There is no doubt that this hole represents a broodchamber and is not a borehole of some burrowing organism. It is widened considerably below the overhanging cover consisting of a layer of cancelli as frequently observed in damaged broodchambers of Lichenoporids. Its interior displays the well preserved bottom with the edges of the absorbed tubes and the characteristic lateral walls as well. Unfortunately the oocostome is not preserved, this is always very characteristic in Lichenoporids and was observed in *Infundibulipora hesslandi* Brood (Pl. IV—1 and 6).

Affinities : The only known species with which our species can be compared is *Infundibulipora hesslandi* Brood (Brood, 1972 p. 322 Pl. 46 Fig. 3; Pl. 51 Figs. 7-8) from the Danian of Danmark and Sweden. (Also occasionally found in Danian glacial drift boulders in Northern Germany (Pl. III—5-8, Pl. IV—1-7). Both have mushroom-like stalked zoaria which show radiating raised fascicles at the periphery and a flat or deepened center on their upper surface. This is filled with a network of polygonal tubes as observed in many Lichenoporids, where they are called cancelli. The lower surface with the peduncle displays the same pattern of smaller pits arranged in numerous radiating furrows between the thin ribs. They are often closed by a calcareous lamella. In some respects *Infundibulipora hesslandi* looks like a dwarf form of *Infundibulipora huckriedei*. Therefore young colonies of *Infundibulipora huckriedei* could be easily mistaken for *Inf. hesslandi* Brood. Also the broken zoarial broodchamber of one of our Swedish specimens (Pl. II—5-7) corresponds to that of *Inf. hesslandi* (Pl. IV—1-2 and 6. See also Voigt 1974 p. 201 Figs. 29-34). Our new species differs from *Infundibulipora hesslandi* by its much larger and stouter zoaria and the greater number of fascicles in older colonies, in which their number exceeds considerably that in *Inf. hesslandi* (20-30 instead of 8-12). A newer Tertiary species (Oligo-Miocene) of *Infundibulipora*, *Defrancia beyrichi* Reuss (Reuss, 1851 p. 176, Pl. 9 Figs. 23-24 and Reuss, 1866, p. 77 [193] Pl. 10 Figs. 7-9) is very similar to the two mentioned above. It can be distinguished by its shorter fascicles which are more closely placed and are restricted to the periphery of the zoarium.

Trochiliopora insignis (Manzoni, 1878) figured recently by Vávra (1974 p. 371 Fig. 3) belongs perhaps to the same group, but the ovicell is not yet known.

Holotype : Pl. I—1-2 (Nr. 7387 Coll. E. Voigt Hamburg).

Locus typicus : Valley of Kischk and Kemunu NW of the village Kemunu Darmanu—Mountains NW of Kerman, Prov. Kerman (Iran).

Stratum typicum : Green marl—clays between limestone of Campanian or Maastrichtian age.

Occurrence : The type specimen and paratypes are from the Campanian or Maastrichtian of the above cited locality, (6 specimens). Other specimens were collected by the present author from the Upper Campanian (zone of "*Belemnitella mucronata*") of Stafversvad (2) and Hemmingslycke (2) (Prov. Scania, Sweden) and from the Upper Maastrichtian (zone of *Belemnitella junior*) of Kunrade near Heerlen (1 specimen) and from the Upper Maastrichtian exposed around the Curfs quarry near Berg, environs of Maastricht, Southern Limburg, Netherlands (1 specimen).

SOME REMARKS ON THE GENUS *INFUNDIBULIPORA* BROOD, 1972

The genus *Infundibulipora* (type species *Tubulipora lucernaria* Sars (Sars 1851 p. 42, Pl. V—1-6) was created by Brood 1972 to replace the old invalid generic name *Defrancia* Bronn, 1825, which is a junior synonym of *Apsendesia* Lamouroux, 1821. The generic name *Defrancia* was given by Bronn, 1825 to replace the pre-occupied name *Pelagia* of Lamouroux, 1821, which was used already by Peron, 1803 for a Medusa. But the Jurassic type species *Pelagia clypeata* Lamouroux, 1821, was recognized by Pergens 1889, Gregory, 1896 and others as synonym of *Apsendesia cristata* Lamouroux, 1821. The generic name *Defrancia*—also given by Millet later for a Gastropod—is therefore superfluous. Borg (1944 p. 121) on the other hand did not accept the identity of these two species and still maintained *Defrancia*, a name used until now in the zoological literature (e.g. Kluge, 1962 p. 132) and cited the Recent *Defrancia lucernaria* (Sars) as its type species.

The fungiform Iranian Bryozoon in question is classified here provisionally within the genus *Infundibulipora* Brood, 1972 along with the allied Danian species *Infundibulipora hesslandi* Brood (Brood, 1972 p. 322). The latter species exhibits all the same general characters such as the mushroomlike pedunculated habitus of the zoaria, the lichenoporid pattern of the upper surface and the lower face provided with numerous radiating rows of smaller kenozoecia as well. It seems to be evident that these two species are closely related and that they may be congeneric although no complete ovicell of our new species could be found. Brood chose as type species for his new genus *Infundibulipora* the Recent species *Defrancia lucernaria* (Sars, 1851, Pl. V—1-6), attributed by him to the family Corymboporidae, Smitt 1866, instead of the characteristic Danian species *Inf. hesslandi* Brood, which together with our new species *Inf. huckriedei* and the Tertiary *Defrancia beyrichi* Reuss, 1851 forms a well defined and a fairly natural group. The latter three fossil species seem to be generically different from *Inf. lucernaria* since the morphology of the ovicell is quite distinct. This will be explained below.

Infundibulipora lucernaria (Sars) was described for the first time by Sars (1851) under the name *Tubulipora lucernaria* from the coast of Finmarken (Komagfjord, Norway). This species which is confined to the northern Atlantic and the Arctic Sea, was described also by d'Orbigny from Spitsbergen not knowing of Sars' paper and was named by him *Discofascigera cupula* (d'Orbigny 1852 p. 675). Sars did not publish any illustrations of his species but later gave a careful description (Sars, 1867 p. 164). The first figures were published by Busk (1856 p. 35, Pl. 1 Fig. 5 and 1875 p. 36, Pl. 33 Fig. 3). The ovicell was figured by Borg (1926 p. 378, Figs. 79-80) and by Kluge (1962 p. 133, Fig. 61). The present author is much indebted to Prof. M. Zwillow (Zoolog. Museum Univ. Hamburg) for lending a specimen and to Miss P. L. Cook (London) for the loan of specimens in the collection of the British Museum (N. H.) of that Recent species for comparison with the fossil forms.

The saucer- or cup-like form of the zoarium with its raised fascicles of autozooezia at the periphery is clearly seen on Pl. V—1-2. The lower face and the stalk is covered with irregular small kenozooezia. Their walls are granulated. I admit that the form of the zoarium is similar to that of *Infundibulipora hesslandi* Brood. But there are differences in the morphology of the ovicells and of the kenozooids within the center and of the lower face. The latter are irregularly distributed and their walls are finely granulated.

Vertical sections of the Hamburg specimen from the Kara-Sea imbedded within polyester give an excellent three dimensional impression of the internal structures of the central region flanked by the peripheral ridges (Pl. V—4-6). In its interior, the central portion of the colony is built up of an irregular tissue of large blister-like polygonal and polyedric cavities very different from ordinary kenozooezia and the regular narrow tubuliform autozooezia which are confined to the periphery of the zoarium (Pl. V—4-5). These longitudinal cavities are of different size much wider than the autozooezia and separated distally by oblique diaphragms. Distally, towards the upper face of the zoarium they become smaller and more uniform in size. They form here a meshwork of shallow oblique pocketlike cavities which are closed in most cases by a convex calcareous lamina (diaphragm) (Pl. V—3). They may also cover the bases and the sides of the fascicles and of the gonozooids. The walls of these cavities are extremely thin and fragile and show transversal growth lines. Many of the deeper cavities display incomplete walls with irregular gaps, which may be an indication of resorption of the calcareous walls. The larger cavities may be produced by resorbing the walls of the smaller ones as known from zoarial broodchambers. Unfortunately there is not enough material for making additional sections. Therefore the

question whether these cavities are connected with the ovicell cannot be answered with certainty.

Interzooidal communication pores which are very minute and hardly visible were observed only within the walls of the autozooezia. In section, the gonozooid shows a large sacklike depression (Pl. 5—6) and it is deeply sunk into the above mentioned cavities. These are supposed to occur normally within all specimens and must be regarded as kenozooezia. There is no reason to suppose that these structures are pathological or caused by parasitic or burrowing organisms. But it cannot be excluded that the size of the cavities increases by absorption of the smaller ones as mentioned above. The exterior of this zoarium is completely intact. However it is unlikely that these cavities are originally normal autozooezia.

No comparable kenozooid structures seem to be known until now in Cyclostomata, but one might refer to a section of *Infund. hesslandi* Brood (Voigt 1974 fig. 34 p. 216) which shows cavities wider than the surrounding Kenozooezia of the ovicell. The smaller ones remind somewhat of the blisterlike alveoli of the genus *Lichenopora* as described by Harmer (1896 Pl. 7, Figs. 6-7 and Pl. 8 Fig. 14). But the alveoli are all of approximately the same dimension and of different astogenetical origin. I presume these had not been observed so far because all authors concerned with that species had studied only its external morphology.

In view of the foregoing observations I am unable to agree with Borg's assumption that the smaller pocklike cavities on the surface were originally autozooezia. Borg (1926, p. 378) wrote: "One might now ask oneself whether or not these cavities are to be regarded as kenozooids . . . I wish, however, to state that, while these cavities are still a part of the common bud, they do not differ as to their outer appearance at least, from the other developing zooids; it therefore seems probable to me that at this stage they contain a polypid bud, and a little later during a brief period also an ordinary functional polypide. If this is correct, they are thus to be looked upon as ordinary, but prematurely closed autozooids."

The ovicells already described and figured by Borg (1926 p. 377, Figs. 79-80) and Kluge (1962 p. 133, Fig. 61) are common and were observed in all the four specimens studied. According to Borg, they are typical gonozooids. No ooeciostome which was figured by Borg (1926 p. 378, Fig. 80) as a tolerably long tube with triangular aperture of about the same diameter as the aperture of an autozooezium was found, perhaps because the roofs of the gonozooids are partly damaged or the ooeciostomes were closed by degeneration as presumed by Borg. All gonozooids are situated at the periphery of the center between a pair of fascicles, and may reach also in the deepened central area of the capitulum (Pl.

V—2). Most of them develop sharply limited bands or narrow lobes stretching radially between the fascicles and are often divided in two or three lobes which run together at the margin of the central area. In effect all have the same morphology and I am unable to agree with Borg who distinguishes two different types of gonozooids (Borg, 1926 p. 377) in this species.

There is a fundamental difference between normal "gonozooids" and the complex "zoarial broodchamber" with an absorption of the walls of the autozoocia and the kenozoocia as Borg was the first to state. He regarded the ovicells of *Infundibulipora* (= *Defrancia*) *lucernaria* (Sars) as normal gonozooids. These gonozooids differ from the "zoarial broodchambers" (sensu Borg) of *Infundibulipora heslandi* Brood—still unknown to Brood—and those of *Infundibulipora huckriedei* n. sp. which do not appear at the surface of the zoarium and display in *Infundibulipora heslandi* a large thickwalled oocystostome bordered by a thick rim as in *Lichenopora* (Pl. IV—1 and 6).

In the specimen of *Infundibulipora heslandi* Brood (figured on Pl. 4—1) the upper layer of the surface with the oocystostome was exposed in order to uncover the hidden hole of the supposed large typical zoarial broodchamber. It is now visible as a dark hole (Pl. IV—2) similar to the zoarial broodchamber of the specimen of *Infund. huckriedei* from the Swedish Campanian (Pl. II—5-7). In this young specimen the fascicles are much worn as also in the other Swedish and Dutch specimens. But I do not think that they represent a different species since we find the same difference in preservation in *Infundibulipora heslandi* (cf. Pl. III—5-9 and Pl. IV—1-7).

The difference of the ovicells is the reason for the present author to place *Infundibulipora heslandi* within the Fam. Lichenoporidae Smitt, 1866, rather than in the Fam. Corymboporidae as Brood suggested because he does not accept the taxonomical value of the ovicells. Therefore it seems doubtful if the Recent *Defrancia lucernaria* (Sars) and the fossil *Infundibulipora heslandi* Brood can be really considered as congeneric. It also affirms that the generic position of our *Infundibulipora huckriedei* n. sp., which is very similar to *Infund. heslandi*, is still uncertain. However, I prefer to class it provisionally with the genus *Infundibulipora* because it seems inadvisable to create a new genus before fully preserved ovicells have been found.

Although the form of gonozooid of the Recent *Defrancia* (*Infundibulipora*) *lucernaria* reminds one of the gonozooid of *Coronopora truncata* (Fleming, 1828) erroneously identified in the zoological literature with the cretaceous "*Domopora stellata* (Goldfuss, 1826)" (Voigt 1975 in press, Pl. 2, Fig. 2), I cannot see that *Infundibulipora* is as closely related to the latter species as has been stressed by Borg (1926 p. 399). In *Coronopora truncata* the gonozooid is

placed transversally at the periphery between the fascicles as in *Actinopora* d'Orbigny and does not extend towards the center. It is evident that *Coronopora truncata* is more closely related to *Actinopora* d'Orbigny and allied genera of the Fam. Theonoidae Busk. The lobed shape of the gonozooid of *Infund. lucernaria* reminds somewhat of the Fam. Corymboporidae Smitt to which Brood (1974) has attributed that genus. But the Fam. Corymboporidae has no radiating fascicles of the autozoocia, and the internal structure of the central portion in *Infundibulipora lucernaria* is apparently different. Unfortunately it was not possible to investigate the wall structure of *Infund. lucernaria* with the help of the scanning microscope.

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EXPLANATION OF PLATES

PLATE I

- 1-6 *Infundibulipora huckriedei* n. sp. Campanian or Maastrichtian, Valley of Kischk and Kemunu NW of the village Kemunu, Darmanu-Mountains NW of Kerman (Prov. Kerman, Iran).
- 1-2 The type specimen, Coll. Voigt Nr. 7387.
- 1 Upper face of the capitulum, showing the marginal fascicles and the central part with the cancelli ; × 12.
- 2 Lower face with the broken peduncle, covered with smaller pits between radiating ribs ; × 6.
- 3 Similar smaller specimen, Coll. Voigt Nr. 7394 ; × 12.
- 4-5 Young specimen, Coll. Voigt Nr. 7463.
- 4 Upper face of the capitulum, showing indistinct fascicles ; × 12.
- 5 Lower face of the same specimen showing the radiating rows of pits ; × 12.
- 6 Four specimens in natural size ; × 1.

PLATE II

- 1-4 *Infundibulipora huckriedei* n. sp. Upper Campanian, Hemmingslycke, (Scania, Sweden).
- 1 Specimen in lateral view showing the capitulum with the broken peduncle, covered with the radiating pits. In the middle of the right half an incrusting young oyster is seen. Coll. Voigt Nr. 7462 ; × 12.
- 2 The same specimen, split up in the median line, showing the vertical tubes widening gradually in distal direction. The holes in the upper part of the picture are caused by burrowing acrothoracic Cirripeds. Note the short tubules at the lower periphery corresponding to the radiating pits ; abt. × 12.
- 3 Another clubformed specimen with a more conical profile and a little larger pits upon the peduncle. Coll. Voigt Nr. 7386 ; × 12.
- 4 The same specimen seen from above, showing the radiating fascicles raised a little above the apertures of the cancelli between them ; × 12.
- 5-7 *Infundibulipora huckriedei* n. sp. Young specimen displaying a broken ovicell (zoarial broodchamber) on the top. Upper Campanian Stafversvad (Scania, Sweden). Coll. Voigt Nr. 7395.
- 5 Lateral view showing the hole of the broken ovicell ; × 12.
- 6 The same showing the broken ovicell upon the top of the capitulum with the apertures of autozoocia and cancelli on its bottom ; × 12.
- 7 The same specimen in another view in order to show the widening of the broodchamber below the overhanging cover ; × 25,

PLATE III

- 1-4 *Infundibulipora huckriedei* n. sp.
- 1-2 Specimen from the Upper Maastrichtian Chalk-tuff, Quarry Curfs near Berg, east of Maastricht (South Limburg, Netherlands).
- 1 Lateral view, showing the radiating rows of pits on the lower face, which are a little larger than on the Iranian and Swedish specimens. Coll. Voigt Nr. 7478 ; × 12.
- 2 Top of the capitulum with the radiating fascicles of the autozoocia ; × 12.
- 3-4 Young specimen from the Upper Maastrichtian of Kunrade, South Limburg (Netherlands). Coll. Voigt Nr. 7479
- 3 Upper surface of the capitulum ; × 12.
- 4 Lower surface ; × 12.
- 5-8 *Infundibulipora hesslandi* Brood.
- 5-6 Specimen with shorter fascicles. Danian glacial drift boulder, Heiligenhafen (Schleswig-Holstein, Northern Germany). Coll. Voigt Nr. 2107.
- 5 Upper face of the zoarium ; × 12.
- 6 Lateral view ; × 12.

- 7-8 Specimen with raised fascicles, Danian glacial drift boulder, island of Fehmarn (Northern Germany) Coll. Voigt Nr. 7480.
 7 Lateral view ; the radiating pits on the peduncle are closed by a calcareous lamella ; $\times 12$.
 8 Top of the capitulum with the long raised fascicles ; $\times 12$.

PLATE IV

- 1-7 *Infundibulipora heslandi* Brood, 1974.
 1 Upper face of the zoarium with weakly developed or worn peripheral fascicles and thickly bordered oeciostome in the upper half of the picture (arrow). Middle Danian, Limhamn near Malmö (Sweden). Coll. Voigt Nr. 7482 ; $\times 25$.
 2 The same specimen ; the uppermost layer is artificially scratched away in order to expose the hidden zoarial broodchamber (dark cavity) below the oeciostome ; $\times 25$.
 3-4 Lower (Fig. 3) and lateral (Fig. 4) views of the same zoarium displaying the radial rows of closed kenozoocia ; $\times 25$.
 5 Another specimen with better developed fascicles at the periphery. Danian erratic drift boulder, Katharinenhof (Island of Fehmarn, Holstein, West Germany). Coll. Voigt Nr. 7481 ; $\times 25$.
 6-7 Badly preserved specimen with the upper face (fig. 6) showing the oeciostome (arrow) and the damaged lower face (Fig. 7) with the radiating Kenozoocia and some opened autozoocia. Lower Danian, Logstedt (Jutland, Denmark). Coll. Voigt Nr. 6808 ; $\times 25$. (Fig. 6 after Voigt 1974).

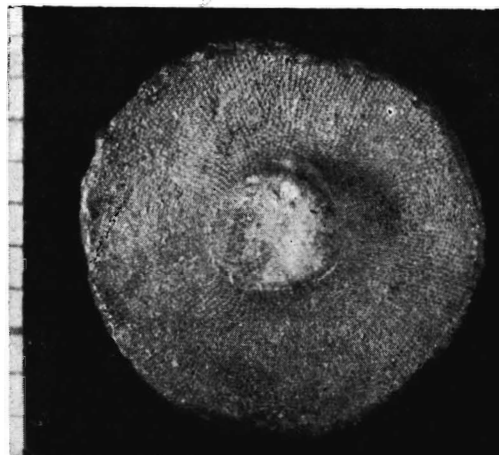
PLATE V

- 1-6 *Infundibulipora lucernaria* (Sars, 1851), Recent.
 1 Lateral view of the funnel-like zoarium showing the small irregular kenozoocia covering the stalk and the lower face of the colony Coll. British Museum (N.H.) London, Nr. 11.10.1.228 ; $\times 9$.
 2 Upper face of the same specimen showing the bifurcating fascicles and several gonozooids at the margin of the center stretched between the fascicles ; $\times 9$.
 3 Irregular polygonal meshwork of partially closed kenozoocia within the center of the same specimen ; $\times 25$.
 4 Specimen embedded with polyester and sectioned longitudinally displaying the long narrow autozoocia of the marginal portion and the large cavities (kenozoocia) within the center.
 Kara Sea, Coll. Zoological Museum Univ. Hamburg, Nr. B. 355 ; $\times 9$.
 5 Same section, enlarged part of the center within the irregular thin-walled kenozoocia (cavities) budding from the autozoocia ; $\times 25$.
 6 Another half of the sectioned zoarium showing the hole of the deeply embedded gonozooid (arrow) surrounded by irregular cavities of the kenozoocia ; $\times 20$.

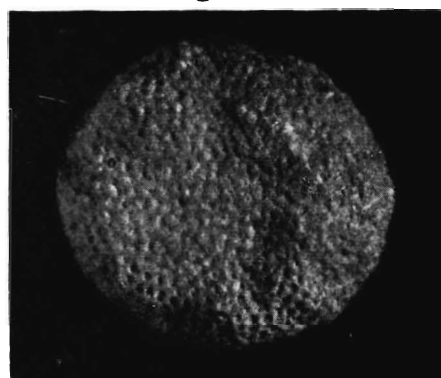
Remarks : All numbers refer to the Photo-Catalogue of the Collection E. Voigt (Hamburg).



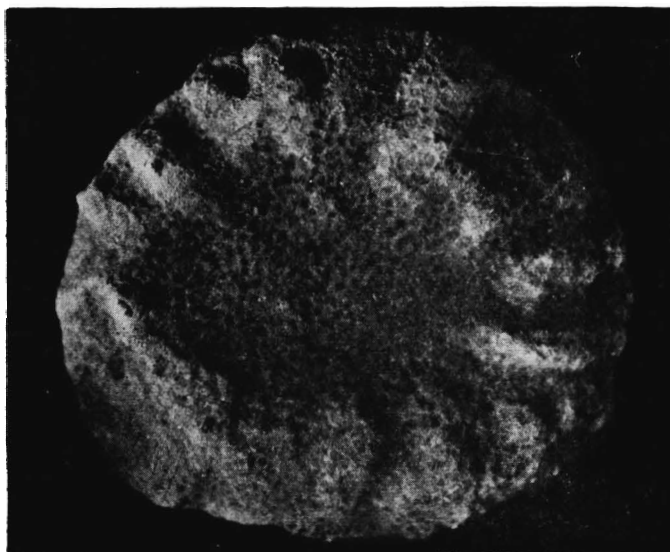
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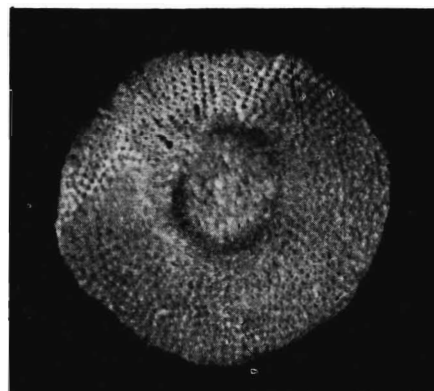
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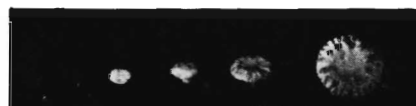
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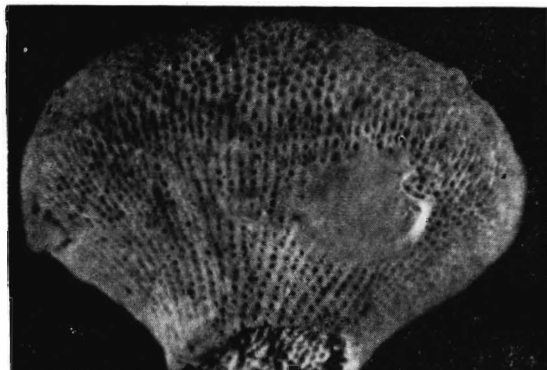
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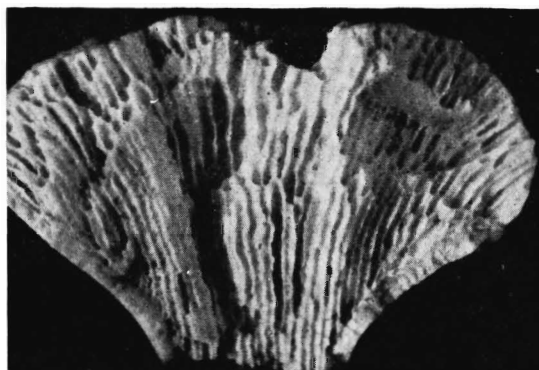
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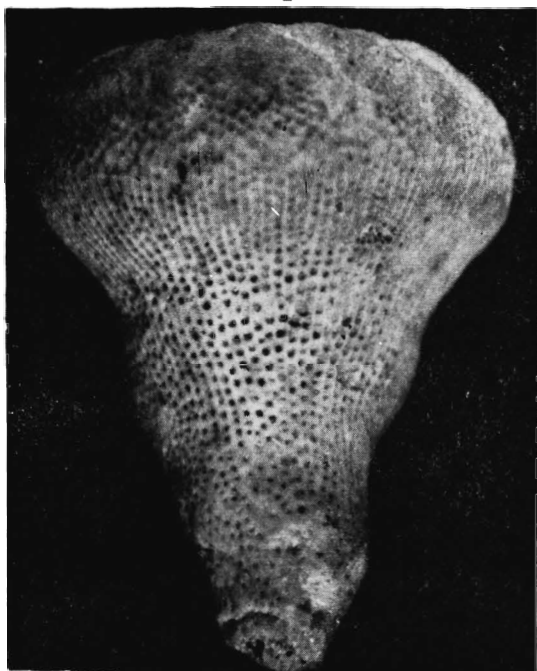
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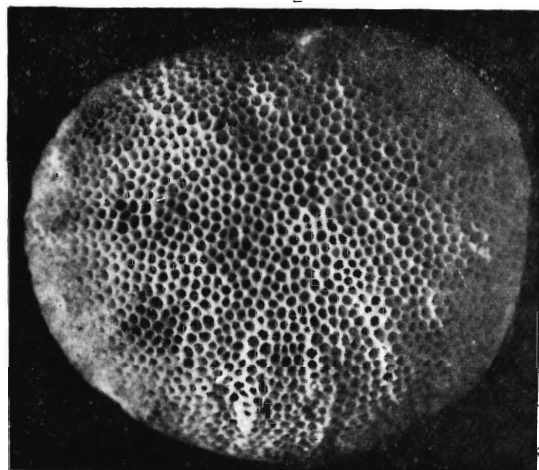
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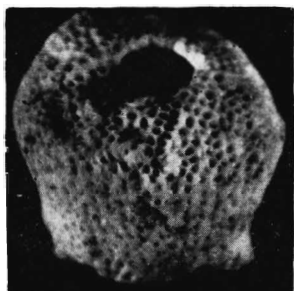
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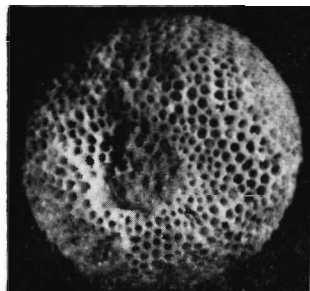
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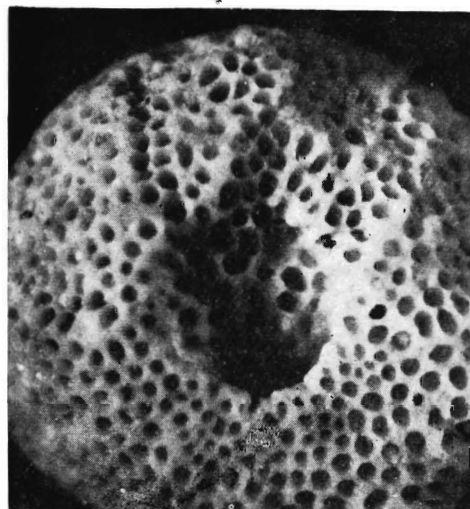
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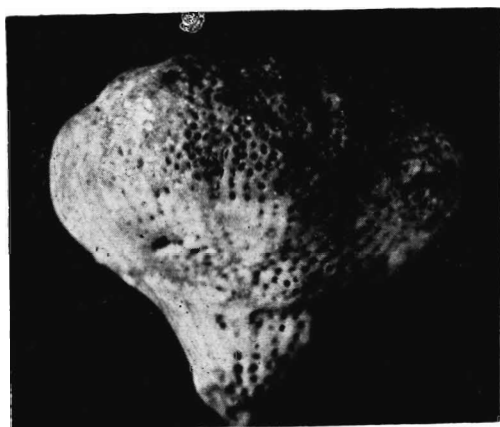
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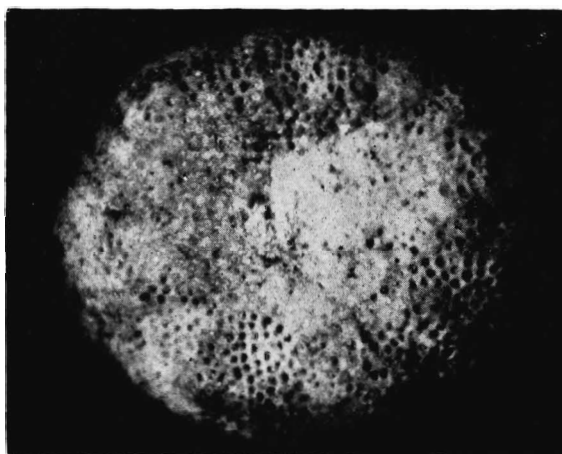
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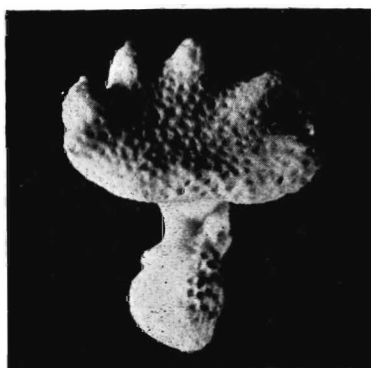
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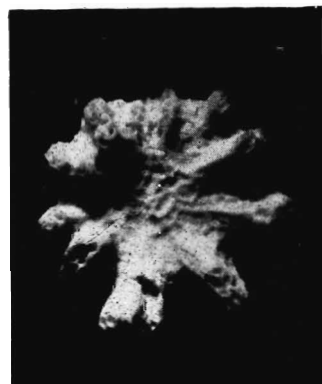
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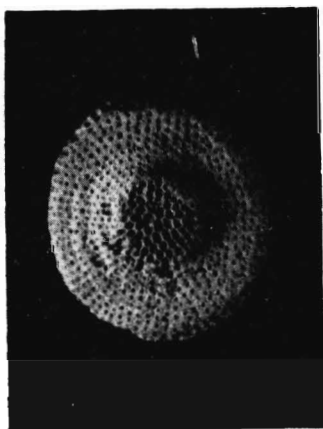
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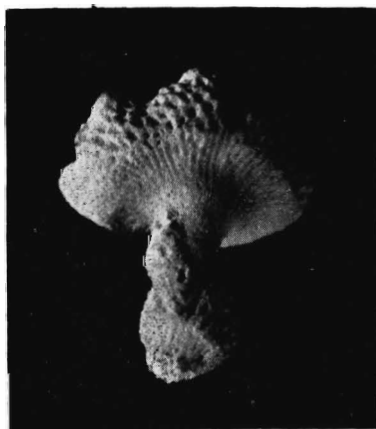
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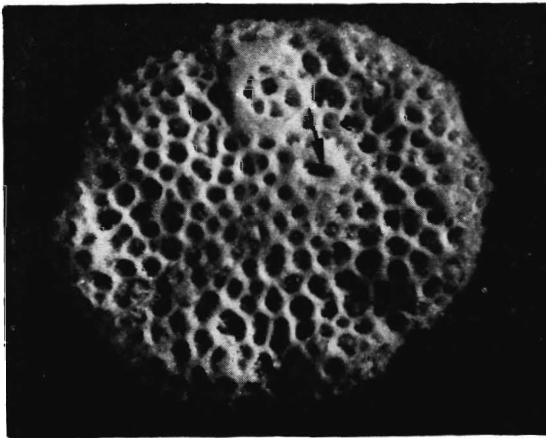
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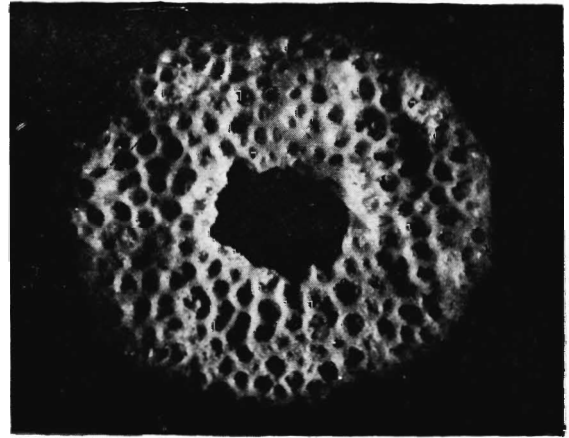
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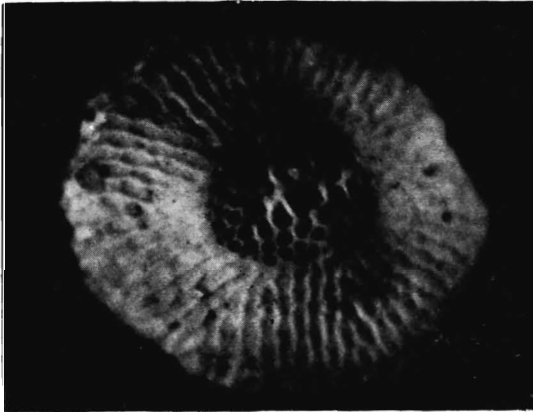
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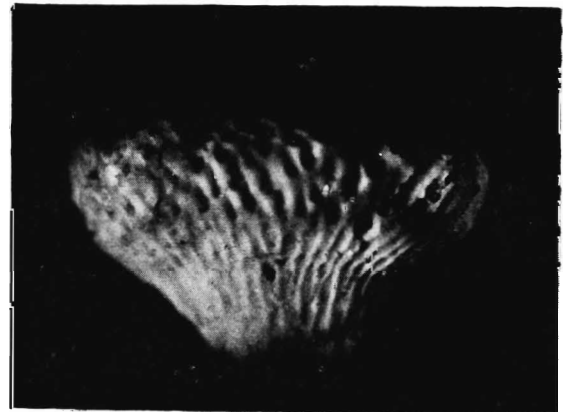
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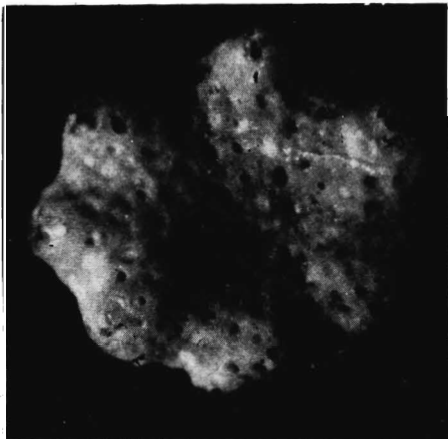
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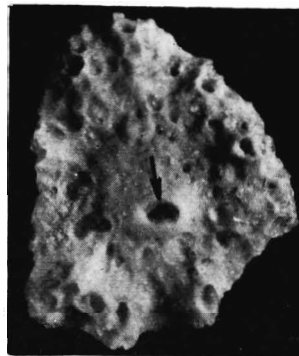
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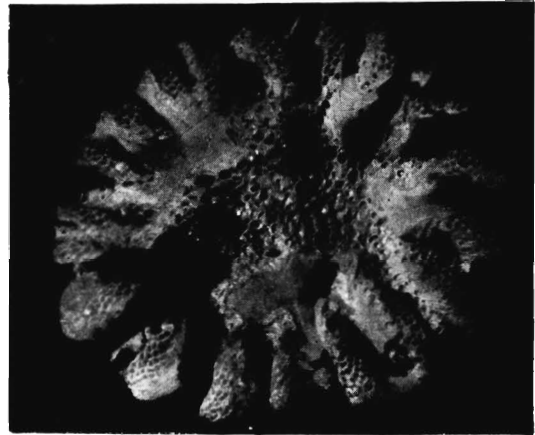
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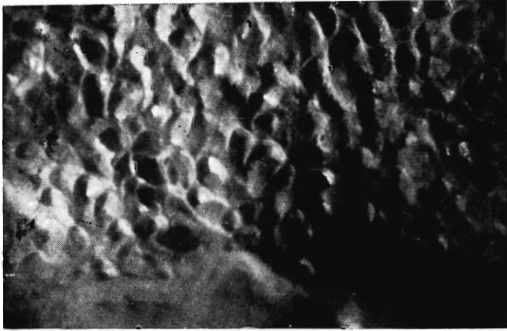
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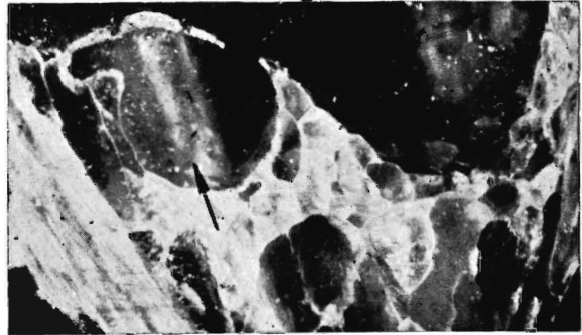
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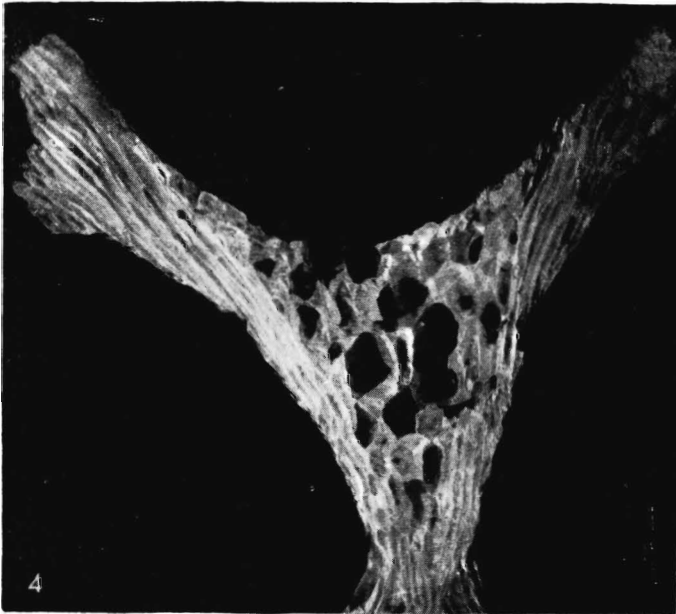
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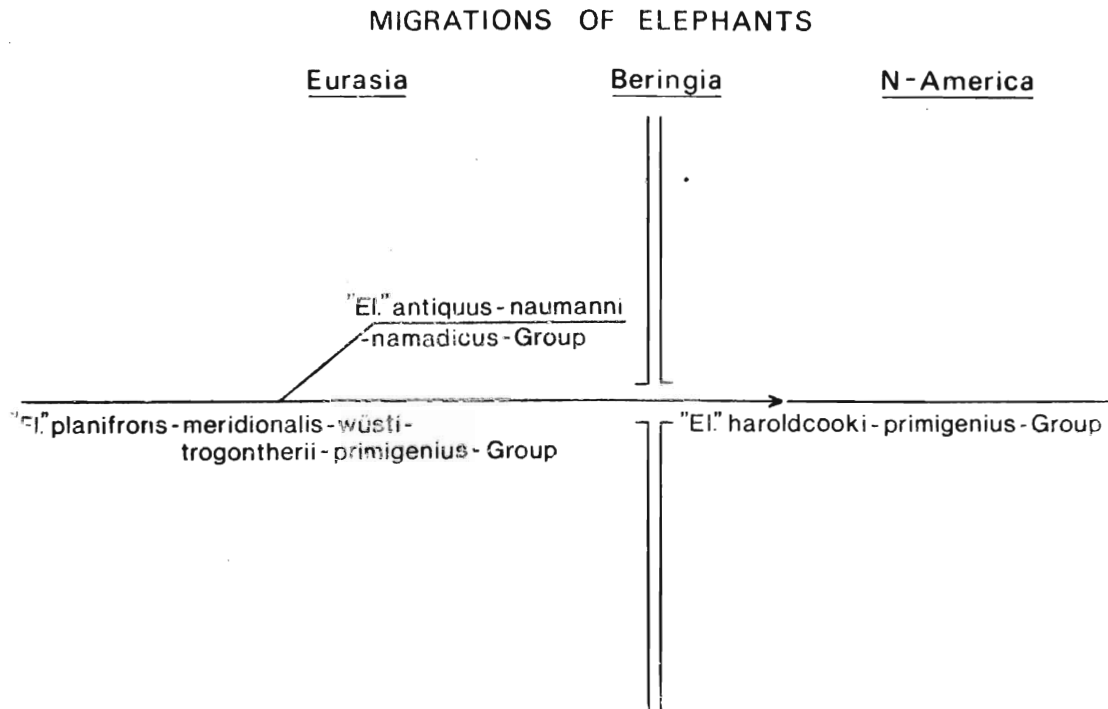


Fig. 5. Schematic diagram of migrations and non-migrations of elephants via Bering landbridge during medial Pleistocene.

deinotheres to warmer climates is demonstrated by their disappearing in Europe during the Pliocene and survival in Africa into Pleistocene times.

2.2. BUNODONT MASTODONTS

More diversified is migration and non-migration in the bunodont groups. As has already mentioned above (p. 240) *Gomphotherium* populations very similar to or identical with the polymorphic *angustidens* group migrated to North America together with *Zygodont* during the late Miocene/earliest Pliocene. This holds also true for the Pliocene platybelodonts (fig. 3, 4). The descendants of Old World gomphotheres, as the tetralophodont brevirostrines (*Anancus-Pentalophodon* group) and the longirostrine *grandincisivus* form, however, did not reach N-America. It may have been partially climatic reasons, that prevented these groups from immigration; it may have been also, that the adequate ecological niches were already occupied by descendants of the North American *Gomphotherium* populations, as the brevirostrine *Rhynchotherium*, the members of the *Stegomastodon/Haplomastodon* group, and the longirostrine form with heavy lower incisors ("*Tabelodon*", "*Aybelodon*" etc.) respectively.

The Old World Mio/Pliocene genera *Choerolophodon* and *Synconolophus* likewise are not recorded from the New World (fig. 3). They paralleled the North American brevirostrines (*Stegomastodon*) in many characters and thus were perhaps unable to penetrate into those ecological

niches. Furthermore, the repartition of the Eurasiatic *Choerolophodon/Synconolophus* group seems to be restricted to warmer climatic zones.

On the other hand no members of the New World *Stegomastodon/Haplomastodon* group are known from the Old World, probably by similar ecological reasons: short-jawed bunodont mastodonts with tuskless mandibles and heavy upper incisors were widespread in Eurasia as tetralophodonts (*Anancus*, *Pentalophodon*) and trilophodonts (*Choerolophodon*, *Synconolophus*) in Pliocene and early Pleistocene times.

2.3. ZYGODONT MASTODONTS

The geographic distribution of Mio-Pliocene zygodonts (*Zygodont*, *Mammot*) is markedly different from deinotheres: Although the zygodont dentition being similar to deinotheres, and therefore having the same or similar feeding characters, zygodonts are obviously rare in sub-saharan Africa and in the Siwaliks.

From the early Miocene local fauna of Lothidok Hill (Kenya), Madden (1975) described a small, zygodont like looking cheek tooth fragment, which he ascribes to *Zygodont*. It might be possible, that the Lothidok Hill specimen is an descendant of the Oligocene zygodont *Palaeomastodon* from the Fayum, which at early Miocene times still existed in East Africa.

From the Siwaliks up to the present only a poorly preserved M³, which can be referred to a zygodont is

known from the Chinji (Tobien 1972 : 175) and in his recent review of the Siwalik Proboscidea, Sarwar (1974 : 246, fig. 76) describes a rather complete zygodont M² from the Middle Siwaliks (Dhok Pathan) of Bhandar, district Jhelum.

Zygodonts however, are known from several Mio-Pliocene places in Siberia, Mongolia and China. In contrast to deinotheres, they were adapted to a subtropical/moderate climate—so far the earlier forms are concerned—and to a moderate in the later ones. Therefore approaching Beringia and entering N-America, where adequate ecological niches were open, a climatic factor obviously was the main reason for their Nearctic distribution (fig. 4).

The moderate to cool climatic adaptation of the zygodont mastodonts is corroborated by two facts :

Zygodonts obviously never migrated to South America. In view of the climatic zonation in the New World during the Late Cenozoic and Quarternary, and in view of the fact that the last zygodonts in N-America lived under Pleistocene climate and persisted into the Postpleistocene in some places (*Mammot americanum*), the adaptational character for cooler climates of the later zygodonts is obvious.

Moreover in Europe a similar situation can be observed: *Deinotheres* disappeared during the Pliocene, whereas the zygodont *Mammot borsoni* persisted under the deteriorating climatic conditions into the Villafranchian.

2.4. STEGODONTS, STEGOLOPHODONTS

This is the *Deinotherium* case : stegodonts and stegolophodonts are descendants of zygodonts, adapted to warmer, partially oceanic climates (Osborn 1942 : fig. 691). So far stegodonts are concerned the climatic conditions in the higher latitudes at the end of the Pliocene and during the Quarternary obviously were not favourable for these animals. Furthermore the Pleistocene stegodonts were in intergroup competition with elephants, which might also have prevented northward migration (fig. 4).

2.5. ELEPHANTS

The reason, why advanced *meridionalis* or *trogontherii*-like elephants were able to penetrate into N-America, is obvious in view of what is known about the ecology of these proboscideans : They were—so far it is known from European populations—adapted to steppe habitats, with open landscapes under cooler continental conditions, which were probably realized in the early Middle Pleistocene in North-East Asia.

On the other hand, the non-migration of the *Palaeoloxodon antiquus-namadicus-naumanni* elephants is understandable : They were woodland or forest-steppe forms, adapted to warmer climatic conditions, obviously not

realised in Beringia during the middle and Late Pleistocene. (Figure 5)

GENERAL CONCLUSIONS

From the preceding pages it turns out, that an important factor for proboscidean migration and non-migration is the climatic one (see also Simpson 1947 : 685). Migrating taxa were tolerant for a rather moderate and/or relatively cooler climate in the late Neogene Beringia and its forelands, non migrating taxa were non-tolerant for these climates.

Besides the climatic factor, however, there seem to be also ecological reasons responsible for non-migration as e.g. occupation of similar ecological niches by structurally and adaptively similar, but not directly related taxa in Eurasia and North America, which might have been the case with the advanced bunodont mastodonts.

There are two possibilities analysing mammalian faunal exchanges over landbridges : (1) an overall analysis and review of most of the higher categories (e.g. Simpson 1947, Repenning 1967) (2) an investigation of single orders with a certain taxonomic diversification and a larger distribution in both landmasses. The latter—as it seems to me—may also deliver arguments which might explain the reasons for migrations and non-migrations and for the particular filtering effects of a landbridge like Beringia was in the late Cenozoic.

SUMMARY

Among Proboscideans the following trans-Beringian migrations during the late Cenozoic can be observed :

(1) Mastodonts : Both main groups, the bunodonts and the zygodonts, both of Old World origin, reached North America rather simultaneously at late Miocene/early Pliocene time : Representatives in North America are the bunodont *Gomphotherium productum* (Cope, 1875) a species nearly related to the polymorphic Eurasiatic *Gomphotherium angustidens* (Cuvier, 1806) and the zygodont *Miomastodon* Osborn, 1922 nearly related if not identical with the Old World genus *Zygodontodon* Vacek, 1877.

The platybelodonts ("shovel tuskers") likewise of Old World Origin reached North America via Beringia very probably at Pliocene time, i.e. somewhat later than *Gomphotherium* and the zygodonts.

Other Old World bunodont mastodonts, as the choerolophodonts (*Choerolophodon* Schlesinger, 1917), brevirostrine tetralophodonts, (*Anancus* Aymard, 1855) and longirostrine tetralophodonts (*Stegotetralodon*, Petrocchi, 1954) are not recorded up to now from North America.

There are no proofs of a migration or remigration of North American mastodonts to Eurasia, as for instance, brevirostrine trilophodonts (*Haplomastodon-Stegomastodon* group).

(2) Stegodonts and stegolophodonts, although wide-

spread in Asia during the Miocene, Pliocene and Pleistocene have never been encountered in North America.

(3) The same holds true with the Old World deinotheres.

(4) Only Elephants of the *meridionalis-trogontherii* group appeared in North America in the late Kansan (=early Irvingtonian), whereas members of the *Palaeoloxodon antiquus-namadicus* group obviously never reached North America.

The possible reasons for migration and non-migration via Beringia are briefly discussed. In the case of migration these are :

- (1) a trans-Beringian landbridge,
- (2) populations (mastodonts, elephants) which are adapted at the respective climates present in Beringia at the times of wandering,
- (3) free ecological niches.

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