

CERATOCYSTIS PERNERI JAEKEL—A MIDDLE
CAMBRIAN CHORDATE WITH ECHINODERM
AFFINITIES

by R. P. S. JEFFERIES

ABSTRACT. *Ceratocystis perneri* Jaekel 1901 is the oldest known member of the Order Cornuta Jaekel 1901, and of the Subphylum Calcichordata Jefferies 1967; as such it is not an echinoderm, though having echinoderm affinities, but is interpreted as the oldest known member of the Phylum Chordata.

Its anatomy has been studied in detail, and new observations have also been made on *Cothurnocystis americana* Ubaghs, *Cothurnocystis primaeva* Thoral, *Cothurnocystis elizae* Bather, and *Mitrocystites mitra* Barrande. These studies throw light on the origin of the chordate heart and pericardium, reproductive system and acustico-lateralis system. They also suggest a basic similarity between the anatomy of *Ceratocystis perneri* and that of a pterobranch hemichordate resting on its right side.

It is suggested that a population of pterobranch hemichordates, that took to resting on their right sides and acquired calcite skeletons, gave rise both to the echinoderms and to the chordates.

Ceratocystis perneri Jaekel, from the Middle Cambrian of Bohemia, is interpreted as the oldest and most primitive chordate known. It is also the oldest and most primitive member of the subphylum Calcichordata Jefferies 1967, of the class Stylophora, of the order Cornuta and of the family Ceratocystidae. Unlike any known descendants, *C. perneri* had a hypopore, and this, with other features, connects it more closely than later calcichordates with the echinoderms and makes it possible to suggest how echinoderms and chordates are related to each other and to the phylum Hemichordata. Study of *C. perneri* also throws light on the origin of the chordate heart, reproductive system, acustico-lateralis system, and hypophyseal complex.

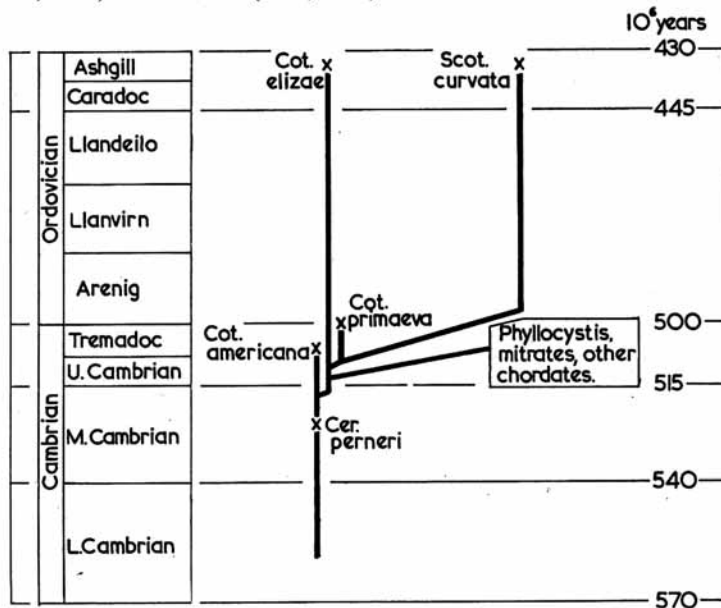
C. perneri was first described and figured by Barrande (1887, pl. 2, figs. 17–21) as 'plaquettes isolées'. Pompeckj (1896) described and figured *C. perneri* under the names *Trochocystites?* (p. 503, pl. 13, figs. 9, 11) and *Mitrocystites* (p. 504, pl. 14, figs. 1, 2). Jaekel (1901) named the species and cursorily described and figured it. Bather (1913) discovered the gill slits, whose nature was first recognized by Gislén (1930). Ubaghs (1967, summarized in 1968) has given a well-illustrated account of the species and interpreted it in a way completely different from that here adopted (see also Ubaghs 1961, 1963, 1968, and Jefferies 1967, p. 205; 1968, pp. 263, 276, 289 ff., 335). He has also selected a lectotype and given precise references to previous work (Ubaghs 1967, p. 2), except for that of Barrande and Pompeckj.

I have reconstructed *C. perneri* from natural moulds and rubber casts. As with my previous work, several projections were drawn simultaneously on a drawing-board. Reconstruction was difficult as the thecal plates have always been badly dislocated. I have made complementary observations on two species which largely bridge the gap between *C. perneri* and the previously studied *Cothurnocystis elizae*. These two species are *Cothurnocystis americana* Ubaghs and *Cothurnocystis primaeva* Thoral (text-fig. 1.)

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Systematic position. Phylum Chordata; Subphylum Calcichordata Jefferies 1967; class Stylophora Gill and Caster 1960; order Cornuta Jaekel 1901; family Ceratocystidae Jaekel 1901; genus *CERATOCYSTIS* Jaekel 1901; species *Ceratocystis perneri* Jaekel 1901.

The family Ceratocystidae, as here understood, includes the family Cothurnocystidae Bather 1913 and comprises *Ceratocystis*, *Cothurnocystis*, *Phyllocystis*, and *Nevadaecystis* (whose only known species I prefer to regard as the earliest *Cothurnocystis* known). It excludes the Scotiaecystidae Caster and Ubaghs 1968. This usage differs from Ubaghs (1963, 1967, 1968) and Jefferies (1967, 1968).



TEXT-FIG. 1. The age and phylogeny of forms mentioned in the text.

Occurrence. All the specimens studied come from near Skryje, Bohemia. Ubaghs (1967, p. 14) has given details of localities and horizon. The specimens occur in numbers scattered over bedding planes in a greenish greywacke. They are remarkably complete, and presumably died by burial. This agrees with the fact that the matrix, being a greywacke, was presumably deposited from a turbidity current. Associated trilobites prove marine, and suggest shallow-water conditions.

Material. The material of *Ceratocystis perneri* examined numbered about 100 specimens and is preserved in: Národní Muzeum, Prague (including lectotype 22123/7, 1924); Naturhistorisches Museum, Vienna (specimens W1-W27); British Museum (Natural History), London (E16071-4); Geologisch-Paläontologisches Museum der Humboldt Universität, Berlin (Ca9, 26, 30-33); Geologisch-Palaeontologisches Institut der Universität, Greifswald, German Democratic Republic; High School of Mines, Ostrava, Czechoslovakia; Ustrední Ústav Geologický, Prague; Geologisch-Paläontologisches Institut der Universität, Freiberg-i-Br., Federal German Republic; Smithsonian Institution, Washington (61503, 33324); Mineralogisk Museet, Copenhagen.

The two known specimens of *Cothurnocystis primaeva* Thoral were lent by the Institut de Géologie, Université de Lyon (1879/508), and the Institut de Géologie, Université de Montpellier (holotype). The only known specimen of *Cothurnocystis* (= *Nevadaecystis*) *americana* Ubaghs (USNM 143237) was lent by the Smithsonian Institution, Washington. Additional material of *Cothurnocystis elizae* Bather and *Scotiaecystis curvata* was lent by the Hunterian Museum, Glasgow.

GENERAL SHAPE, THECAL PLATE NOTATION, AND THECAL PLATE HOMOLOGIES

Like all calcichordates, *Ceratocystis perneri* consists of a theca and a stem (text-fig. 2). The theca is boot-shaped. On the anterior face, right oral, left oral, and left appendages can be recognized. These are equivalent to like-named appendages in *Cothurnocystis elizae* and *Coth. primaeva*. However, the right oral appendage of *Ceratocystis perneri* was fixed immoveably at the base, instead of being held by a hinge as in *Coth. primaeva* and *Coth. elizae*. The posterior right and left angles of *C. perneri* correspond to what Bather (1913, p. 399) called the 'ball of the foot' and the 'heel' of *Coth. elizae*.

The ventral surface of the theca of *C. perneri* is approximately flat but a ventral spike (S_{3R}) is always developed on plate M_{4RV} , and sometimes there are one or two ventral bosses (S_{1R} , S_{2R}) on M_{2R} (Pl. 95, fig. 1; Pl. 96, fig. 7). Also the left appendage projects somewhat downwards so that, as far as its form in *C. perneri* is concerned, it could almost equally well be called a ventral spike. It is here named the left appendage because it is homologous with the better-developed left appendages of later forms. The ventral surface curves somewhat dorsally in two regions on each side of the stem. As Ubaghs noticed (1967, p. 12), the stereom mesh of the ventral plates of *C. perneri* is denser where it would have touched the sea floor than elsewhere. It is particularly dense where it forms the ventral spikes, and the ventral surfaces of the left appendage and of the right and left oral appendages (text-fig. 17A; Pl. 95, fig. 1). These particularly dense areas represent portions of the ventral surface which would have been forced slightly into the sea floor by the weight of the animal.

The dorsal surface of the theca (text-fig. 2A) is raised into three keels which meet on the plate C_M (Pl. 95, fig. 2). The stereom forming these keels is denser than that surrounding the keels so that each forms a sort of girder. These girders are most developed where the plates that they cross are thinnest, i.e. roughly in inverse proportion to the distance from the meeting-point of the three keels.

A keel also exists dorsal to the left appendage, on plates M_{3LV} and M_{3LD} (text-fig. 2A; Pl. 95, fig. 2). In addition a rather sharp angle (peripheral keel) separates ventral from lateral surfaces in most places.

The theca of *C. perneri*, unlike that of later cornutes, was almost entirely covered by large plates. There was, however, a semicircular oral integument, (or in, in text-fig. 2C; Pl. 95, fig. 1) just ventral to and posterior to the mouth, and small, flexible flaps, containing platelets, probably covered the gill slits (text-fig. 2A, D; fpl in Pl. 98, fig. 1). The large plates of the theca can be divided into: dorsal marginals (M_D), ventral marginals (M_V), marginals that are neither dorsal nor ventral (M), centro-dorsals (C), right and left oral appendages (roap, loap) and infra-branchials (IB). The suffixes used in the plate notation are: A = anterior; P = posterior; L = left; R = right; D = dorsal; V = ventral; $1-5$ = position in sequence starting just anterior to the stem. The ascription of the same suffix number to dorsal and ventral marginals (e.g. M_{4RV} ,

M_{4RD}) is somewhat arbitrary. A plate is not necessarily homologous with a plate having the same notation in some other species of cornute.

The relation of the present notation for *C. perneri* to that of Ubaghs (1967) is as follows: $M_{PV} = M_0$; $M_{PD} = A_m$; $M_{1RV} = M'_1$; $M_{1RD} = A_g$; $M_{2R} = M'_2$; $M_{3R} = I_1$; $M_{4RV} = M_3$; $M_{4RD} = S_4$; roap = M'_4 ; $M_{5R} = I_4$; $M_{AD} = M_6, S_8$.

$M_{1LV} = M_1$; $M_{ILD} = A_d$; $M_{2L} = M_2$; $M_{3LD} = S_4$; $M_{4LV} = M_4$; $M_{4LD} = S_6$; loap = M_5 ; $M_{5L} = I_2$.

$C_A = S_5$; $C_M = S_2$; $C_{PL} = S_3$; $C_{PR} = S_1$. IB_1, IB_2, IB_3 , not shown by Ubaghs.

I_3 of Ubaghs is probably only a portion of M_{5R} . M_6 and S_8 of Ubaghs are ventral and dorsal aspects of the same plate (M_{AD}). Ubaghs did not observe the oral integument or the infra-branchial plates.

The homology of the thecal plates of *C. perneri* with those of the various species of *Cothurnocystis* and *Scotiaecystis* can be established fairly certainly in most cases (text-fig. 3). Ubaghs (1967, p. 4) seems to have been over-cautious in this matter. One important trend in the evolution of Ceratocystidae was the development of the bellows system of pumping water through the gill slits. This had much influence on the thecal plating, since it caused the thecal wall to become more and more flexible, and it must be borne in mind in examining text-fig. 3. The bellows system was rudimentary in *C. perneri*; *Coth. americana* had a flexible roof to the theca and a rigid floor crossed by a thickened strut. *Coth. primaeva*, *Coth. elizae*, and *Scotiaecystis curvata* had a flexible roof and a flexible floor, crossed by a rigid strut.

The plate homologies call for the following additional comments:

1. The strut of *Coth. americana* (str in text-fig. 4; Pl. 98, fig. 2), which has not previously been described, corresponds in position to, and must have been homologous with, the struts of later species. Comparison with *Coth. americana* allows the anterior and posterior strut plates to be recognised in *C. perneri* (M_{1RV}, M_{4LV}).

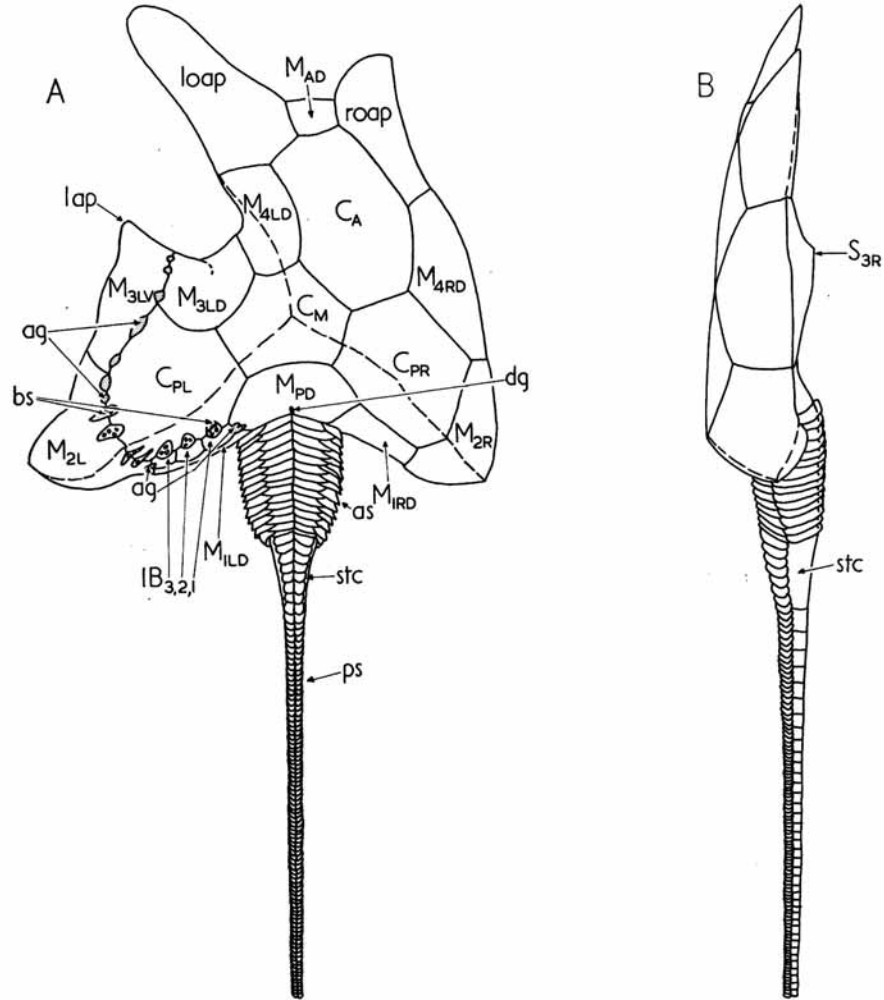
2. The left appendage, right and left oral appendages and the 'heel' and 'ball of the foot' provide good landmarks in all species, except that the right oral appendage is absent in *S. curvata*.

3. Apart from *Coth. americana*, where the relevant anatomy cannot be worked out, the plates just anterior to the stem (i.e. $M_{PV}, M_{1RV}, M_{1RD}, M_{PD}, M_{ILD}, M_{1LV}$) can be shown to have the same connections with each other in all species of cornutes and mitrates except that M_{PV} is known only in *C. perneri* while *Coth. elizae*, *S. curvata* and the mitrates have lost M_{PD} . The relative sizes of these plates, however, vary greatly from species to species.

4. M_{5LD} of *Coth. primaeva* is homologised with M_{3LD} of *C. perneri*, rather than with M_{4LD} , because (i) M_{4LD} of *C. perneri* is obviously homologous with a plate C_{1A} in the dorsal integument of *Coth. americana*, and (ii) the shape of M_{4LV} in the incomplete, only known specimen of *Coth. americana*, suggests the existence of a plate M_{4LD} (text-fig. 3c, ? pos M_{4LD} in text-fig. 4; Pl. 98, fig. 2) in the complete animal that would be intermediate in position between M_{3LD} of *C. perneri* and M_{5LD} of *Coth. primaeva*.

5. The plate M_{4RV} of *C. perneri* is homologised with M_{3R} of *Coth. primaeva*, *Coth. americana*, and *Coth. elizae*, and with M_{4R} of *S. curvata*, because a ventral spike is present, except in *Coth. elizae* and some specimens of *S. curvata*.

6. The Montpellier specimen (holotype) of *Coth. primaeva*, on which text-fig. 3 A, B

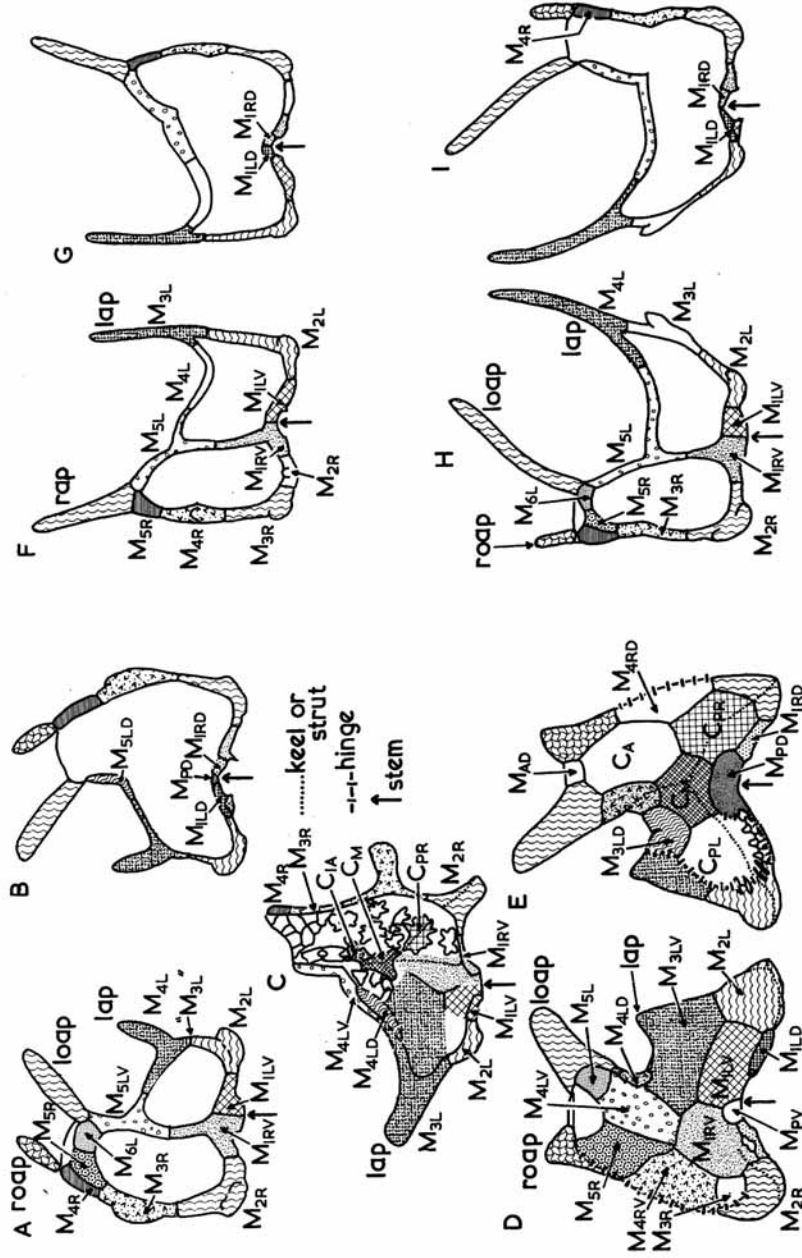


TEXT-FIG. 2

largely based, lacks M_{3L} , which exists in the only other known specimen of the species, preserved at Lyon.

7. $IB_{1, 2, 3}$ (text-fig. 2A, D; ib in Pl. 98, fig. 1) of *C. perneri* correspond to some of the posterior U-plates of *Coth. americana*, *Coth. primaeva*, and *Coth. elizae*.

The stem of *C. perneri*, like that of other calcichordates, was divided into anterior, medial and posterior parts and ended abruptly. Ubaghs himself stressed that there is no evidence for the pointed plate which he showed in his reconstruction at the posterior end of the stem (1967, text-fig. 1, p. 13.)



TEXT-FIG. 3. Plate homologies among Cornuta. A, B, *Cothurnocystis primaeva* Thoral, ventral and dorsal aspects; C, *Cothurnocystis americana* Ubachs, dorsal aspect; D, E, *Ceratocystis perneri* Jaekel, ventral and dorsal aspects; F, G, *Scoziaecystis curvata* (Bather), ventral and dorsal aspects; H, I, *Cothurnocystis elizae* Bather, ventral and dorsal aspects. Homologous plates have the same stipple. lap = left appendage; roap = right oral appendage.

Gill slits and the rudiments of the bellows system

A first complex of gaps in the thecal skeleton is disposed between the plates in the left dorsal part of the theca (ag, bs in text-fig. 2A, D). This complex consists of two types of gap. The first type is represented by seven large holes (bs). Three of these are between C_{PL} and IB_1 , IB_2 and IB_3 , while four are between C_{PL} and M_{2L} . The second type of gap, corresponding to what are here called accessory gaps (ag), is represented by holes that are variable in form, number, size, and position. They are usually much smaller than the seven holes bs. A first group of such accessory gaps is arranged anterior to the gaps bs along the sutures M_{3LD}/M_{3LV} , C_{PL}/M_{3LV} and C_{PL}/M_{2L} . A more posterior group of accessory gaps is arranged near the three most median of the gaps bs, mainly around the infra-branchial plates, along the sutures IB_3/M_{2L} , IB_3/M_{1LD} , IB_2/M_{1LD} , IB_1/M_{1LD} , IB_1/M_{PD} , and M_{PD}/M_{1LD} .

The distinction between the gaps bs and the accessory gaps is emphasized by Plate 96, fig. 2, showing the dorsal margin of M_{2L} and M_{3LV} , and by Plate 97, figs. 4, 5, showing dorsal and ventral margins of infra-branchial plates.

The gaps bs must represent branchial slits for the following reasons:

1. They closely resemble in position and number the 7 (or perhaps 8) gill slits of *Coth. americana* (bs in text-fig. 4; Pl. 98, fig. 2); each of these, in turn, is almost identical in structure to the previously studied gill slits of *Coth. elizae* (Jefferies 1967, p. 167; 1968, p. 253).

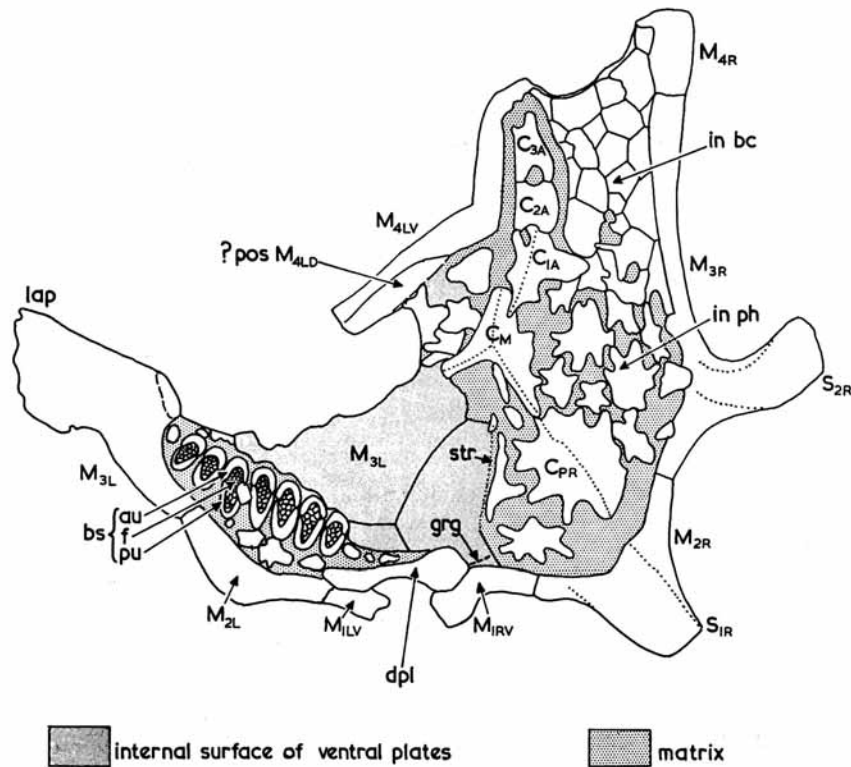
2. If the gaps bs are gill slits, the infra-branchial plates could well be homologous with some of the posterior U-plates of *Coth. americana* (pu in text-fig. 4), *Coth. elizae*, and *Coth. primaeva*.

3. Upper and lower margins of the gaps bs are not identical. Each upper margin is sharply defined and truncated by a facet (faf in Pl. 98, fig. 1) while the lower is rounded. This suggests, by analogy with *Coth. elizae*, that the upper margin bore a soft flap, attached to the facet, and this flap closed against the lower margin, so forming an outlet valve. One specimen has platelets inside one of the gaps bs (fpl in Pl. 98, fig. 1). In life these could have been imbedded in a flap, much as in *Coth. elizae*.

If the gaps bs were gill slits, the accessory gaps represent uncalcified wall spaces. Thus the posterior accessory gaps correspond closely in position to the gaps in *Coth. elizae* and *Coth. americana* between the plates in the strip of dorsal integument posterior to the gill slits. The anterior accessory gaps correspond, though less closely, to the gaps between the dorsal integument plates anterior to the gill slits in *Coth. elizae* and *Coth. americana*. Further, many of the integument plates of *Coth. americana* are star-shaped, and contact their star-shaped neighbours by the points of the stars (text-fig. 4; Pl. 98, fig. 2). They could well have evolved from polygonal plates whose sutures were affected by the enlargement of accessory gaps of the type seen in *C. perneri*.

As regards function, the accessory gaps of *C. perneri* probably contained muscles which could slightly depress the roof of the theca, so forcing a sudden jet of water out through the gill slits. This seems likely, since the gaps between the integument plates of *Coth. elizae* to which the accessory gaps correspond, seem to have contained muscle that pumped water out through the gill slits (Jefferies 1967, p. 168; 1968, p. 258) and the same is true of *Coth. americana*. There was a shallow depression in the inner face of

the theca of *C. perneri* surrounding the posterior group of accessory gaps and corresponding to a raised portion of the internal cast (iml in text-fig. 9B; see also text-fig. 10, and Pl. 95, fig. 9; Pl. 97, figs. 5, 8). This depression could have contained a patch of muscle that cooperated with the muscle of the accessory gaps in pumping.



TEXT-FIG. 4. *Cothurnocystis americana* Ubachs, dorsal aspect of only known specimen and holotype (USNM 143237 from the Lower Tremadoc of Nevada). au = anterior u-plate; bs = branchial slit; f = flap; dpl = dorsal plates of stem base region (precise morphology not discernible); grg = gonorectal groove; in bc = integument over buccal cavity; in ph = integument over pharynx; lap = left appendage; ?pos M_{4LD} = presumed position of plate M_{4LD}; pu = posterior u-plate; str = strut.

Slight contractions of the right part of the thecal cavity, which would supplement those of the left part of the theca, may also have occurred. This is suggested by the form of the edges of some of the plates near the right margin. Thus the edge of M_{4RD} where it abuts against M_{4RV} is cylindrical, rather than plane (rm in Pl. 95, fig. 1; Pl. 96, figs. 3, 6). Again the edge of M_{5R} where it touches roap and of M_{3R} where it touches M_{2R} are distinctly cylindrical. This suggests that a hinging movement was possible of the thecal plates about a hinge-line, corresponding to the sutures M_{5R}/roap, M_{4RV}/M_{4RD}, and M_{3R}/M_{2R}, near the right-hand margin of the theca (hinge in text-fig. 3D, E). This presumed

hinge-line runs along the middle of an elongate depression on the inner face of the skeleton, corresponding to a raised portion of the internal cast (imr in text-fig. 9A, C; Pl. 95, fig. 2; Pl. 96, figs. 1, 4). This depression presumably carried a sheet of muscle like the depression internal to the posterior accessory gaps. It is likely that the action of this sheet of muscle was mainly to raise the neighbouring plates of the thecal floor by rotation about the presumed hinge line.

C. perneri therefore, could probably pump water through the pharynx by flexing the thecal wall, just as later Ceratocystidae could, i.e. the bellows system of pumping water through buccal cavity and pharynx had already begun to evolve. This method of pumping, however, must have been much less efficient than in later forms, since the volume of the thecal cavity when contracted could have been only a few per cent less than the expanded volume. Indeed, in *C. perneri* flexing of the thecal walls could not have been the only method of pumping water. Some other method must have been much more important. This could have involved cilia on the inner surface of pharynx and buccal cavity, or as seems less likely, some type of muscular pumping which has left no trace in the skeleton.

The ability to flex the thecal wall in *C. perneri* was developed along sutures which, with few exceptions, correspond to the dorsal margins of the frame in later forms (text-fig. 3). This is obvious on the left side of the theca and also true on the right, for M_{4RV} of *C. perneri*, which is ventral to the right hinge-line, corresponds to the frame plate M_{3R} of *Coth. americana*, *Coth. primaeva*, and *Coth. elizae*, and M_{4R} of *S. curvata*. This situation is consistent with the fact that the thecal roof of *Coth. americana* was flexible, but the floor was not. The muscles round the presumed right hinge line must have changed their mode of action at an early stage from lifting the neighbouring floor, as in *C. perneri*, to depressing the side wall, which soon became part of the roof.

The dorsal and peripheral keels of *C. perneri* would have stiffened the roof and floor of the theca. They may owe their existence to the rudimentary bellows mechanism for, without them, contraction of the bellows muscles would have forced water towards the middle of the theca and made the floor, and especially the roof, belly out, instead of expelling water through the gill slits. As the musculature of the roof gradually spread inwards in the course of evolution, the stiffening provided by the dorsal keels became both unnecessary and disadvantageous, and they were eventually lost. The dorsal keels are still obvious in *Coth. americana*, however (text-fig. 4; Pl. 98, fig. 2), and some sign of them even occurs in *Coth. elizae*, though probably only as a functionless and variable vestige (crestal plates, Jefferies 1968, p. 259). The peripheral keels of *C. perneri*, on the other hand, became elaborated to form the thecal frame of *Coth. americana* and later species and became better adapted to a stiffening function, the need for which increased when the roof and floor of the theca became flexible.

The presence of 7 gill slits in *C. perneri* is of interest, since this is probably the primitive number for cornutes and therefore for chordates in general. That 7 is the primitive number for cornutes is supported by Table 1 which shows that all the early species of cornutes with the unspecialized *elizae* type of slit (i.e. all except *P. crassimarginata*, *S. curvata*, and *Coth. elizae* itself, which is a late form) have a similar number. The lowest value among these species is perhaps 5, probably 7; the highest value is 9.

Certain other groups of chordates with a similar number of pairs of gill slits, may have inherited this number from an unknown Upper Cambrian cornute with 7 slits on the

left side of the theca, by way of an Upper Cambrian mitrate with 7 gill slits on each side. Examples of such groups are the Cyathaspididae, which include some of the earliest known agnathous fishes and which show evidence of 6 or 7 pairs of gill slits (Denison 1964, p. 345), and gnathostomatous fishes which never have more than 8 pairs of gill slits, including the spiracles (Bertin *in* Grassé 1958, p. 1306).

TABLE 1. The number of gill slits in Cornuta

Name	Age	Type of Slit	Number
<i>Ceratocystis perneri</i> Jaekel	M. Cambrian	As here described	7
<i>Cothurnocystis americana</i> Ubaghs	L. Tremadoc	<i>elizae</i>	7 (or 8)
<i>Cothurnocystis primaeva</i> Thoral	U. Tremadoc		At least 5,
	or		probably a
	L. Arenig	„	few more.
<i>Cothurnocystis ubaghisi</i> Chauvel	„	„	7 (or 8)
<i>Phyllocystis blayaci</i> Thoral	„	„	9
<i>Phyllocystis crassimarginata</i> Thoral	„	Specialized	13
<i>Cothurnocystis elizae</i> Bather	Ashgill	<i>elizae</i>	16
<i>Scotiaecystis curvata</i> (Bather)	„	Specialized	40

Thecal openings on the right side of the theca

There are 4 thecal openings on the right side of the theca of *C. perneri* (m, h, g and an in text-fig. 2c, d; Pl. 95, fig. 1; Pl. 96, figs. 6, 7, 8, 10; Pl. 98, fig. 5). Two of these openings (g and an) are usually fused together to varying extents (cf. Pl. 96, figs. 7, 8, 10).

The identification of these four holes follows from a comparison with rhombiferan

EXPLANATION OF PLATE 95

The lengths of the scales are in mm. E = British Museum (Nat. Hist.); GPMB = Geologisch-Paläontologisches Museum der Humboldt Universität, Berlin; NM = Národní Muzeum, Prague; USNM = U.S. National Museum, Washington; W = Natur-historisches Museum, Vienna.

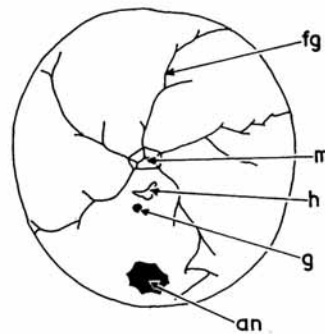
Figs. 1-7, 9. *Ceratocystis perneri*. 1, Ventral aspect of W 13; latex impression to show oral integument or in; M_{2L} is affected by a fault in the latex; an = anus; g = gonopore; h = hydropore; lap = left appendage; ng = narrow groove (lateral line); rm = rounded margin of M_{3RD} ; S_{1R} , S_{3R} = first and third right ventral spikes. 2, Reconstruction of dorsal aspect (W 8) made by glueing latex impressions of plates together. 3, Natural mould, dorsal aspect (NM 33723, same individual as Plate 97, fig. 1); br = brain; gbc = groove between buccal cavity and pharynx; pbc = pit between buccal cavity, pharynx and anterior coelom. 4, Reconstruction of ventral aspect (E 16074) made in same way as fig. 2. 5, Latex impression of part of an individual (W 10), to show inside of plate M_{4RD} ; cbc = ridge corresponding to cleft in natural mould, i.e. between buccal cavity and anterior coelom; imr = limit of groove on internal cast housing the right internal muscle. 6, Anterior aspect of natural mould representing the part of the brain in contact with M_{1RD} (specimen W 16); iskc = intraskeletal cones of right side; rf = right face of brain. 7, Anterior aspect representing part of brain in contact with M_{PD} (specimen W 16); magnification as fig. 6; adf = antero-dorsal face; dll, dlr = left and right dorsal lobes; dp = dorsal process. 9, Natural mould of inside of M_{PD} , (specimen W 26); ag = accessory gaps; iml = limit of left internal muscle.

Figs. 8, 10. *Cothurnocystis elizae*. 8, Natural mould representing posterior coelom and adjacent structures in contact with M_{1L+RV} ; cf. text-fig. 6; postero-ventral aspect, with specimen lying on its back (specimen E 28644); gd = gonoduct; grg = infilling of gonorectal groove; mlnl = left median line nerve; pco = posterior coelom; pbr = right pyriform body; r = rectum. 10, Natural mould of posterior surface of M_{ILD} of E 28658 representing terminal portion of rectum (r) and gonoduct (gd) and part of antero-dorsal surface of posterior coelom (pco); cf. text-fig. 6.



JEFFERIES, *Ceratocystis perneri*, *Cothurnocystis elizae*

and diploporitan cystoids. Jaekel (1899) established the existence in those groups of four holes in the theca, apart from pores connected with respiration (text-fig. 5). These four holes were arranged roughly in a plane that included the oral end of the theca and the base of the stem or, in stemless forms, the point of attachment. In sequence they were the mouth, at the oral end of the theca, the hydropore, the gonopore, and the anus. The holes m, h, g, and an of *C. perneri* are also distributed roughly in a plane which includes the oral (anterior) end of the theca and the stem base, but which, in this case, is parallel to the ventral surface and to the sea bottom. This comparison suggests that m of *C. perneri* is the mouth, h the hydropore, g the gonopore, and an the anus.



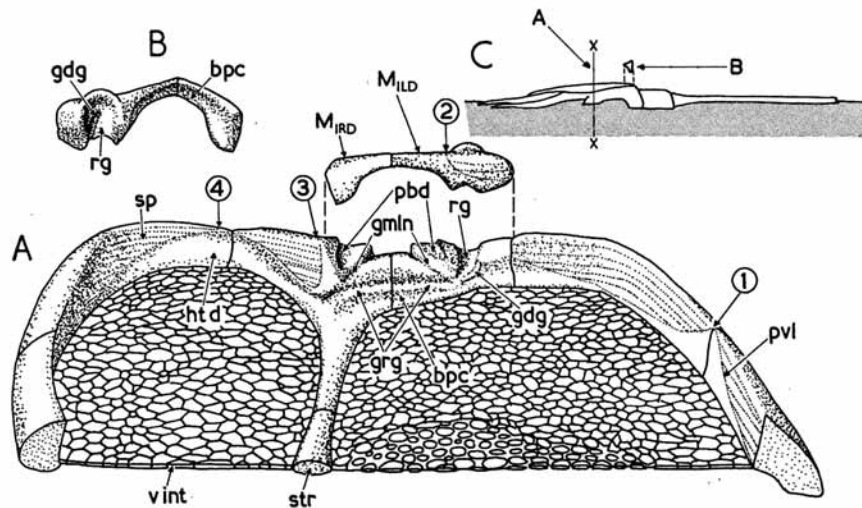
TEXT-FIG. 5. Oral surface and thecal openings of the diploporitan cystoid *Glyptosphaerites leuchtenbergi* (Volborth) redrawn after Jaekel 1899. an = anus; fg = food groove; g = gonopore; h = madreporite (corresponding to hydropore of other cystoids and of *Ceratocystis*); m = mouth.

The identification of the mouth (m) in *C. perneri* as a large opening at the anterior end of the body, agrees with the situation in other calcichordates, and with chordates in general. It agrees in particular with *Coth. elizae* (Jefferies 1967, p. 168; 1968, p. 255). The account of the mouth region of *C. perneri* given here differs greatly, even in terms of pure morphology, from that of Ubaghs (1967, p. 11, under anus), who did not observe the oral integument.

The identification of the holes g and an of *C. perneri* as gonopore and anus calls for partial restudy of the anatomy of *Coth. elizae*. In this species I have previously described an opening, which I called the 'anus', just left of the stem, where it would be in the outwash from the most median gill slits. I described the 'anus' as connected by a 'rectal groove' in the skeleton that ran under the posterior coelom to the anterior coelom in the right-hand, posterior region of the theca. Re-examination, however, reveals that the distal, vertical part of the 'rectal groove', between the 'anus' and the posterior coelom, in fact consists of two grooves—a larger and a smaller (rg and gdg in text-fig. 6, corresponding to r and gd in Pl. 95, figs. 8, 10). These two grooves must represent two contiguous tubes, one wide and one narrow, opening into the 'anus'. The narrower tube, as judged by its groove, ran ventral and posterior to the wider tube across the posterior coelom, but ran left of the wider tube where both climbed upwards after

leaving the posterior coelom, so that finally it lay dorsal and anterior to the wider tube near the opening. The situation in *Coth. primaeva* (text-fig. 7; Pl. 98, fig. 6) is essentially the same as in *Coth. elizae*.

As already mentioned, the two tubes opening into the 'anus' of *Coth. elizae* are connected by the 'rectal' groove to a point just right of the stem. This point corresponds



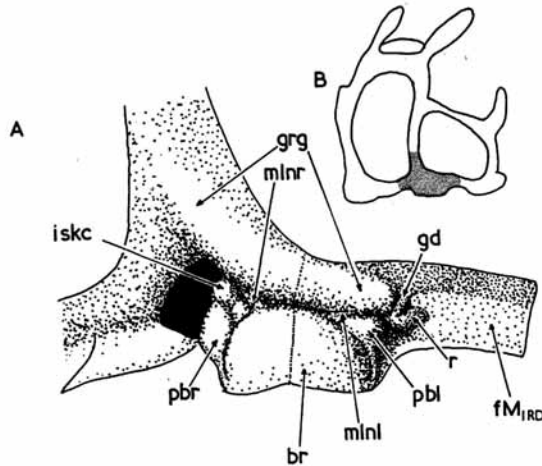
TEXT-FIG. 6. *Cothurnocystis elizae* Bather, internal anatomy of the theca (cf. Jefferies 1968, fig. 3). A, Antero-dorsal aspect of posterior part of theca, with the dorsal integument removed and M_{IL+RD} lifted upwards. B, Posterior aspect of M_{IL+RD} . C, Left lateral aspect of animal, lying on sea-floor, to show lines of sight used in A and B. Only the portion of the theca posterior to X-X is shown in A. 1, 2, 3, 4 = points where pharyngo-visceral line approaches the dorsal side of the theca; bpc = portions of skeleton in contact with posterior coelom; gdg = gonoductual groove; gmln = groove for median line nerves; grg = gonorectal groove; htd = heart depression; pbd = depressions for pyriform bodies; pvl = pharyngo-visceral line; rg = rectal groove; sp = striations of pharynx; str = strut; vint = ventral integument.

to the position of gonopore and anus in *C. perneri* (cf. text-fig. 8B-F with 8A-E). This suggests that the two tubes of *Coth. elizae* represent the rectum and the gonoduct, which had migrated in evolution to just left of the stem, so as to be in the outwash from the gill slits. Conversely, the position of these tubes in *Coth. elizae*, such that their products could be washed away, confirms that they were outlet ducts, and supports the identification of gonopore and anus in *C. perneri*. It is likely that the narrower tube in *Coth. elizae* was the gonoduct, and the wider one the rectum. Evidently the 'rectal' groove is better called the gonorectal groove, and the 'anus' should be called the gonopore-anus.

The distal part of the mitrate of a tunicate (text-fig. 8C-G) had the same basic course as in *Coth. elizae* on the one hand (text-fig. 8B-F), or a tunicate tadpole on the other (Jefferies 1967, p. 181; 1968, pp. 287 ff., p. 317). In mitrates as in tunicate tadpoles it opened into a left atrium. By comparison with *Coth. elizae*, the gonoduct of mitrates probably also

opened into the left atrium (text-fig. 8G) with the terminal portion of the gonoduct left of the rectum.

In enterogonous tunicates (text-fig. 8H) the terminal portion of the gonoduct is *right* of the rectum. Comparison of text-fig. 8G and H, however, shows that the mutual relations of rectum and gonoduct are nevertheless similar in mitrates and enterogonous tunicates. In the adult tunicate the two tubes are merely turned through 150° compared with the mitrate condition. The point x in the tadpole diagram (text-fig. 8D) indicates



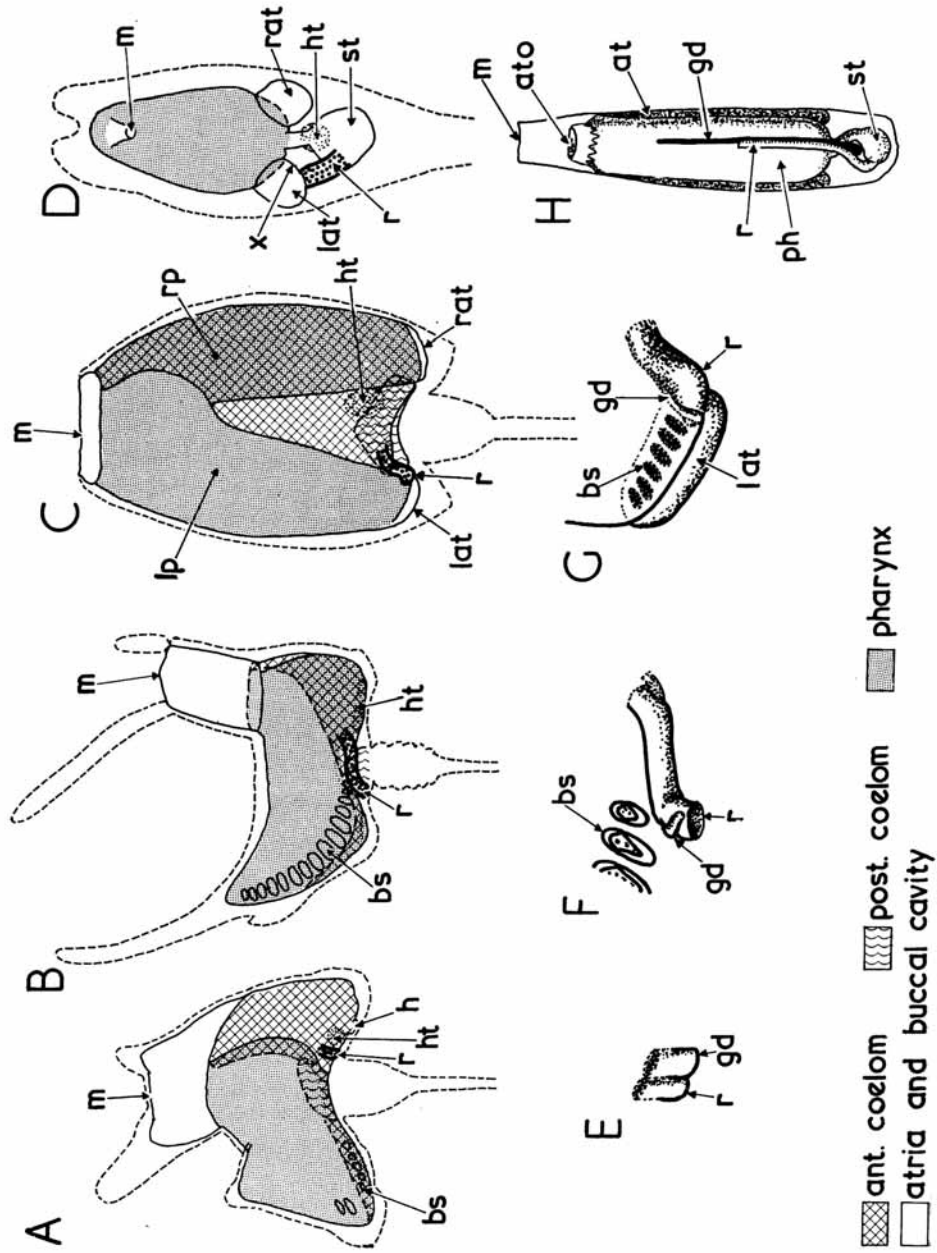
TEXT-FIG. 7. *Cothurnocystis primaeva* Thoral. A, camera lucida drawing of the ventral aspect of a portion of the natural mould of the Montpellier specimen (holotype) (cf. Pl. 98, fig. 6). B, Ventral aspect of theca; stipple indicates portion of anatomy shown in A. br = brain; fM_{IRD} natural mould of the facet on plate M_{IRV} which contacted plate M_{IRD}; gd = gonoduct; grg = infilling of gonorectal groove; iskc = intraskeletal cones, corresponding to those in *Ceratocystis perneri*; mlnl and mlnr = left and right median-line nerves; pbl and pbr = left and right pyriform bodies; r = rectum.

where the gonoduct will enter the left atrium later in ontogeny, and underlines the comparison. There is no evidence whether cornutes and mitrates were hermaphrodite like tunicates. What is here called the gonoduct may represent the male or the female duct in different individuals or, as in tunicates, one inside the other.

In *Coth. americana* the position of the gonopore-anus cannot be established. A gonorectal groove can be seen right of the stem (grg in text-fig. 4) as in other forms of *Cothurnocystis*, but cannot be followed more distally. The migration of gonopore and anus had therefore already begun, but may not yet have finished.

The leftward twist of gut and gonoducts was thus acquired by cornutes because gill slits existed only on the left side. It was retained in mitrates and tunicates, where gill slits existed on both sides, because it was no particular disadvantage.

The identification of the hydropore (h) in *C. perneri*, based on comparison with cystoids, is confirmed by its absence in all cornutes later than *C. perneri*. Thus the cornutes, in this respect as in others, evolved towards a more usual chordate condition.



The presence of a hydropore in *C. perneri*, as discussed below, has important implications for the internal anatomy and throws light on the connections between chordates, echinoderms and hemichordates.

Thecal openings related to the nervous system

Near the anterior end of the stem are two openings, the narrow groove and the dorsal groove (ng and dg in text-fig. 2A C, D), that are not represented in *Coth. elizae* (ng in Pl. 96, figs. 4, 10; dg in Pl. 96 figs. 1, 9; Pl. 98, fig. 1).

The narrow groove is excavated in the ventral surface of M_{ILD} . Ubaghs (1967, pp. 8 ff.) described it as 'hydropore'. It is here regarded as the first rudiments of the acustico-lateralis system and, since it is widely open at the surface, would have functioned as a lateral line. It is reminiscent of the lateral line of mitrates (narrow groove (ng) in Jefferies 1968, pp. 283, 307, 314, 322; lateral line (ll) in Jefferies 1967, pp. 178, etc.), and Ubaghs homologized it with this feature. It is, however, on the left of the theca, whereas the lateral line of mitrates is on the right. It will be further discussed under the nervous system.

The dorsal groove is excavated in M_{PD} , just anterior to the mid-line of the stem. Ubaghs named it 'encoche médiane' and suggested (1967, p. 11) that it might be connected with an internal mouth that he supposed to exist in this region. It is interpreted here as having carried an upward extension of the optical part of the brain, which was presumably light-sensitive. The dorsal groove certainly existed also in the cornutes *Phyllocystis blayaci* and *P. crassimarginata*. It may perhaps have existed in *Coth. primaeva*, which certainly had a plate M_{PD} that could have carried it, but this plate is not well displayed in either of the two known specimens. The dorsal groove is also further discussed under the nervous system.

THE CHAMBERS OF THE THECA

Four thecal chambers can be recognized in *C. perneri* on the basis of superficial internal anatomy, the positions of thecal openings, and the fundamental resemblance to *Coth. elizae*. These four chambers are the buccal cavity, pharynx, anterior coelom, and posterior coelom. Text-figs. 9A-C are reconstructions of the internal cast of *C. perneri*, combining details from many different specimens. Text-figs. 10A-C are an interpretation of these reconstructions. The sculpture of the internal cast is complex and includes: (1) Growth-lines, parallel to the edges of plates and not shown in the text-figures. (2) Growth traces, extending inwards perpendicular to plate edges from notches (e.g. gill slits gtbs in text-fig. 9B, C) in the plate edges (cf. Pl. 97, fig. 8). (3) Indications of muscles, associated with rudimentary flexibility of the theca, discussed above, and distributed in two areas, i.e. just ventral to the more median gill slits (iml in text-fig. 9B)

TEXT-FIG. 8. Homologies between various calcichordates and a living tunicate. A, E, *Ceratocystis perneri* (cornute); B, F, *Cothurnocystis elizae* (cornute); C, G, *Mitrocystella incipiens* (mitrate); D, tadpole of the tunicate *Ciona*; H, adult of *Ciona* (dorsal aspect) A, B, C, and D compare the anatomy of the four forms in dorsal aspect. E, F, and G show the relations of gonoduct, rectum, gill slits, and atria. at = atrium; ato = atrial opening; bs = branchial slit; g = gonoduct; h = hydropore; ht = heart; lat = left atrium; lp = left pharynx; m = mouth; ph = pharynx; r = rectum; rat = right atrium; rp = right pharynx; st = stomach; x = the point where, in the developing tunicate, the gonoduct later comes to enter the atrium.

and near the right border of the theca (imr in text-fig. 9A-C). (4) Intercameral features and indications of internal organs other than thecal chambers.

The buccal cavity was situated much as in *Coth. elizae*, occupying the 'ankle' part of the theca. Its posterior border is indicated on the internal cast: (1) By a groove (gbc in text-fig. 9C; Pl. 95, fig. 3; Pl. 96, fig. 3). (2) By a pit (pbc in text-fig. 9C; Pl. 95, fig. 3; Pl. 96, fig. 6) in the floor of the groove. (3) By a cleft (cbcr in text-fig. 9A, c; Pl. 95, fig. 5; Pl. 96, fig. 1) which appears to have divided the right-hand strip of 'bellows' muscle (imr) into two parts. (4) By a cleft on the left (cbcl in text-fig. 9A; Pl. 97, fig. 10). On general grounds the clefts and the grooves would indicate where the skeleton had filled the gap between two chambers, and the pit would indicate where it had filled the gap between three chambers (in this case, buccal cavity, anterior coelom, and pharynx).

The anterior coelom must also have been situated as in *Coth. elizae*, i.e. mainly in the posterior, right-hand part of the theca. It is from this region that gonopore, hydropore, and anus emerged, indicating that the corresponding organs, and the chamber that housed them, must have lain here. The boundary between posterior coelom and buccal cavity is indicated: (1) By the part of the groove gbc to the right of the pit pbc. (2) By the cleft cbcr. The junction of anterior coelom, pharynx, and buccal cavity is indicated by

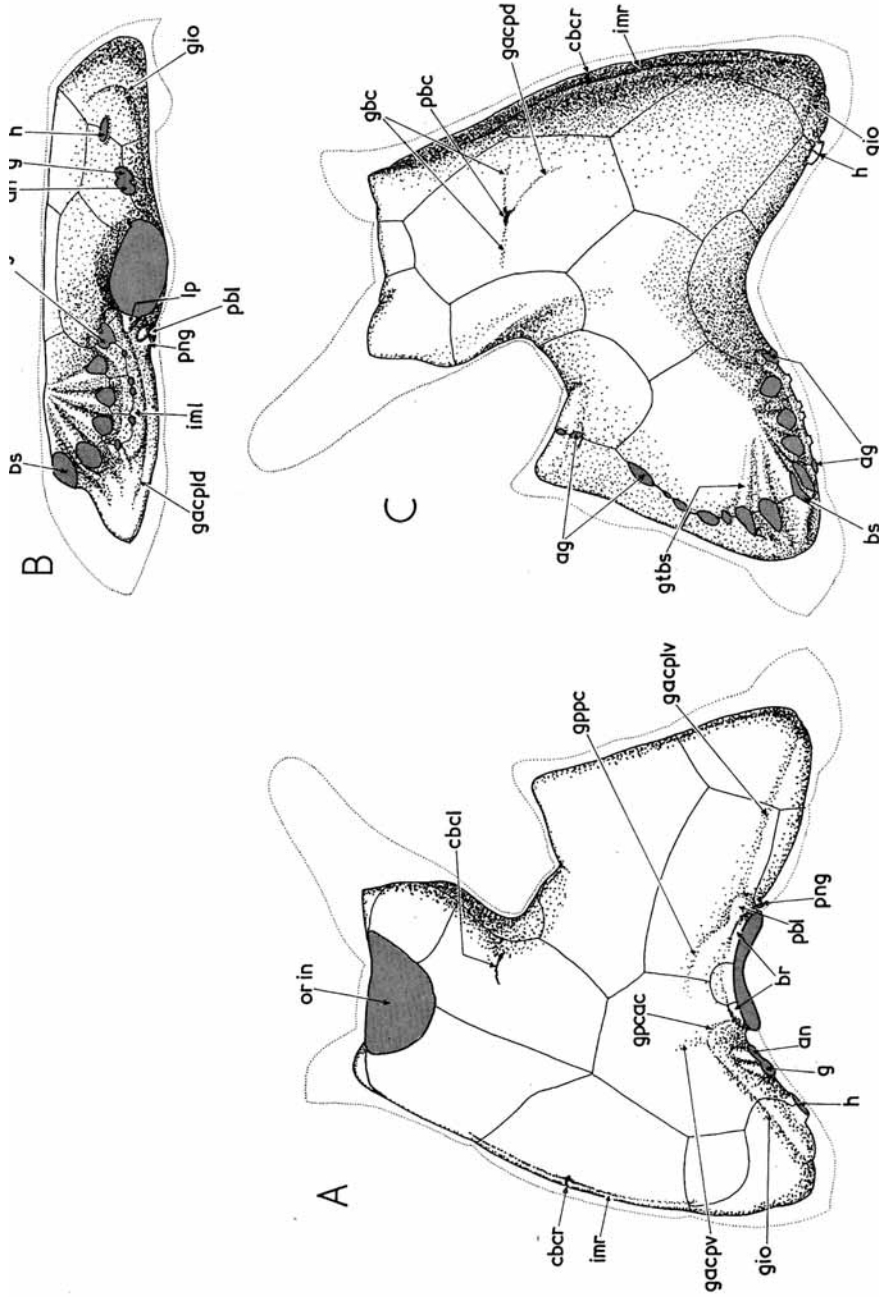
EXPLANATION OF PLATE 96

The lengths of the scales are in mm.

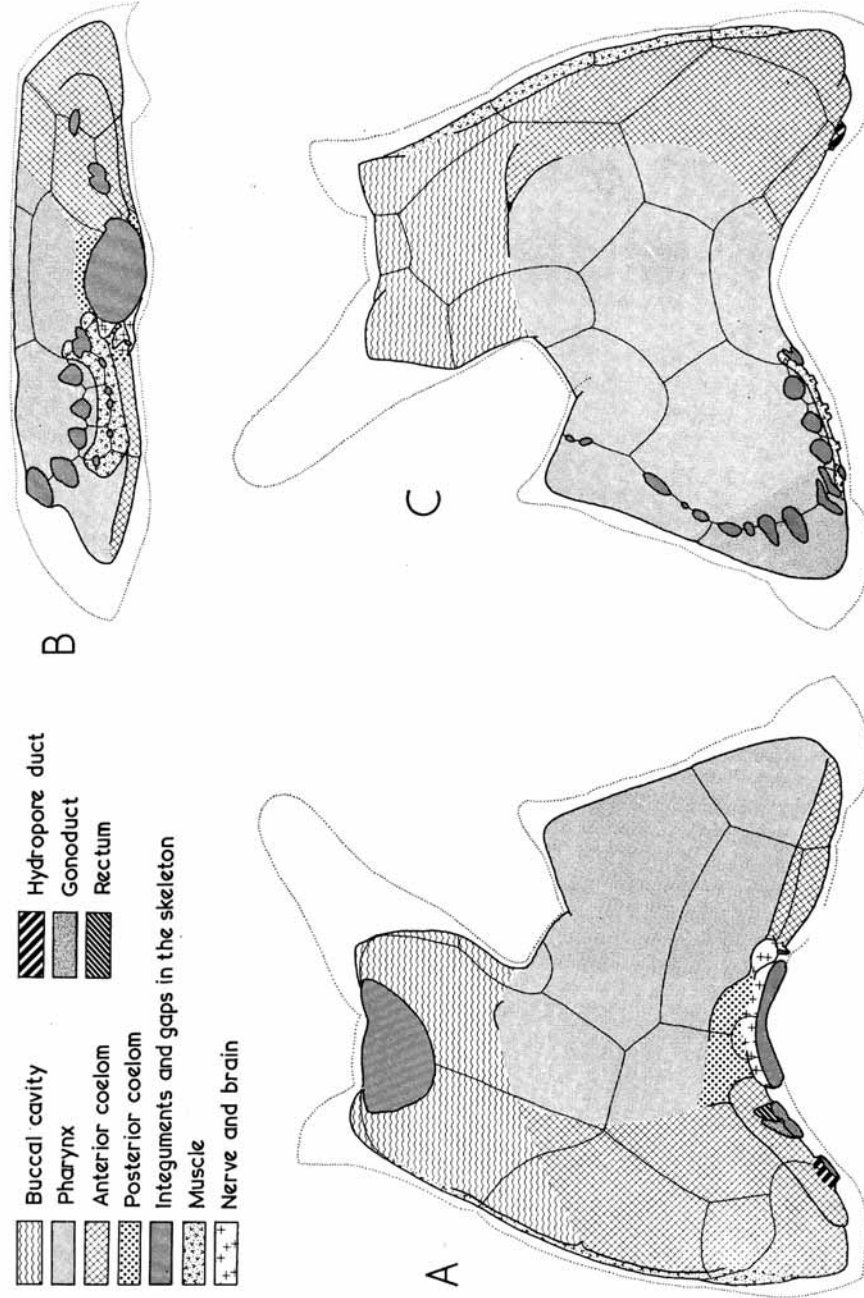
Figs. 1-10. *Ceratocystis perneri*. 1, Latex impression in dorsal aspect of W 25 to show internal features of M_{4RV} , i.e. imr = limit of groove for right internal muscle; cbcr = division between buccal cavity and posterior coelom; dg = dorsal groove in plate M_{PD} ; imr = margin of groove for right internal muscle on plate M_{4RV} . 2, Latex impression in dorsal aspect (W19) to show distinction between accessory gaps (ag) and branchial slits (bs.) 3, Latex impression in ventral aspect (Ostrava specimen) to show features on internal surface of plate C_A ; gacpd = ridge corresponding to groove on internal cast between pharynx and anterior coelom; gbc = ridge filling groove on internal cast between buccal cavity and pharynx; rm = rounded margin of M_{4RD} ; stc = stylocone. 4, Latex impression in ventral aspect of Ostrava specimen (different individual to fig. 3) to show internal surface of M_{4RD} and right oral appendage with limits of groove for right internal muscle (imr); gan = gonopore and anus; ng = narrow groove. 5, Latex impression of stem in dorsal aspect (W 9); note how dorsal plates (dpl), though dislocated after death, have nonetheless remained articulated to each other; aif = anterior imbrication facet of dorsal plate; bos = boss of ventral ossicle; bs = branchial slit; DS = dorsal plate of anterior stem; lg = lateral groove; mg = median groove; stc = stylocone; VS = ventral plate of stem. 6, Latex cast in ventral aspect of Ostrava specimen (different individual to figs. 3 and 4) to show features of inside of C_A with process (pbc) corresponding to the pit on natural mould between buccal cavity, pharynx, and anterior coelom; gan = gonopore-anus; h = hydropore; rm = rounded margin of M_{4RD} . 7, Reconstruction of right posterior region of theca in ventral aspect (W22), made by gluing latex impressions of plates together; an = anus; g = gonopore; S_{1R} , S_{2R} = first and second right, ventral spikes. 8, Natural mould in ventral aspect (GPMB Ca 33); an = anus; br = brain; g = gonopore; gacpv = groove on ventral surface between anterior coelom and pharynx; gpcac = groove between posterior coelom and anterior coelom; gppc = groove between pharynx and posterior coelom; pbl = left pyriform body. 9, Latex mould in dorsal aspect (W15), to show anterior stem, with dorsal and ventral stem plates (DS, VS); dg = dorsal groove; gan = gonopore-anus; gpcac = ridge corresponding to groove on internal cast between posterior and anterior coelom; gppc = ridge corresponding to groove on internal cast between pharynx and posterior coelom. 10, Latex mould in ventral aspect of posterior part of theca and part of stem (NM 22123/7 1924 lectotype). Note narrow groove (ng) and the gonopore (g) and anus (an) separated by a minute ridge, and lateral and ventral parts of a single ventral anterior stem plate (lpvp, vvpv); h = hydropore; stc = stylocone.



JEFFERIES, *Ceratocystis perneri*



TEXT-FIG. 9. Reconstruction of internal mould of *Ceratocystis perneri*. A, ventral; B, posterior; C, dorsal aspects. ag = accessory gap; an = anus; br = brain; bs = branchial slit; cbcl and cbr = clefts posterior to buccal cavity on left and right; gacpld and gacplv = dorsal and ventral grooves between anterior coelom and pharynx to left of stem; gacpd and gacpv = dorsal and ventral grooves between anterior coelom and pharynx to right of stem; gbc = groove posterior to buccal cavity; gio = groove round internal organ; gpcac = groove between posterior and anterior coelom; gppc = groove between pharynx and posterior coelom; gtbs = growth trace of branchial slit; h = hydropore; iml and imr = swellings of internal cast representing internal muscles, on left and right; lp = left process from brain; or in = oral integument; pbc = pit posterior to buccal cavity; pbl = left pyriform body; png = process to narrow groove (lateral-line nerve).



TEXT-FIG. 10. The chambers of the theca of *Ceratocystis perneri*—an interpretation of the reconstructed internal cast (cf. text-fig. 9).

the pit pbc. The junction of anterior coelom and pharynx is indicated: (1) By the groove gacpd (text-fig. 9C; Pl. 96, fig. 3) which meets the groove gbc at the pit pbc. (2) By the groove gacpv (text-fig. 9A; Pl. 96, fig. 8) on the ventral surface, internal to M_{IRV} . (3) By the grooves gacpld and gacplv (text-fig. 9A, B; Pl. 97, figs. 8, 9) on the left side of the internal cast, beneath the gill slits, which indicate an extension of the anterior coelom into the left part of the theca, as in *Coth. elizae*. The boundary between anterior and posterior coeloms is indicated on the right by the groove gpcac (text-fig. 9A; Pl. 96, figs. 8, 9). To the left it presumably ran left of the left pyriform body (pbl in text-fig. 9A, B; Pl. 96, fig. 8). A groove (gio in text-fig. 9A, B; Pl. 96, fig. 1; Pl. 98, fig. 5a) just beneath the gonopore and anus, and beneath and around the hydropore, may indicate the contact with the skeleton of some visceral organ inside the anterior coelom.

The pharynx would have connected with both buccal cavity and gill slits, and so would have been disposed as in *Coth. elizae*. The indications on the internal cast of its boundaries with buccal cavity and anterior coelom have been mentioned already. The boundary between pharynx and posterior coelom is shown by the groove gppc (text-fig. 9A; Pl. 96, figs. 6, 9; Pl. 97, fig. 2; Pl. 98, fig. 3).

The posterior coelom probably occupied a small volume just in front of the stem. The indications of its boundaries on the internal cast have already been mentioned.

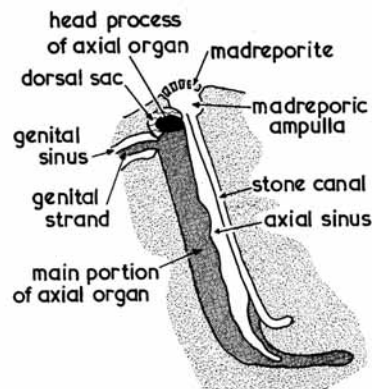
ORGANS INSIDE THE ANTERIOR COELOM

The thecal openings from the anterior coelom are the anus, the gonopore, and the hydropore. They indicate that the anterior coelom contained: (1) the rectum and the rest of the alimentary canal behind the pharynx; (2) the gonad or gonads; and (3) an axial complex, like that of echinoderms. The presence of an axial complex calls for discussion.

Living echinoderms which compare with *C. perneri* in having an axial complex that opens directly outwards by a hydropore or madreporite, comprise the echinoids, asteroids, and ophiuroids. In all such forms the axial complex has basically the same structure (Fedotov 1924, Smith 1940). This can be illustrated from an echinoid (text-fig. 11) where the following parts exist: (1) An *axial organ* divided into the *main portion* (Millott and Vevers 1968) and the *head process*. The *main portion* of the axial organ consists of a close-packed mass of canals, some of which are haemal. (2) An *axial sinus* (lumen of axial organ of Millott and Vevers 1968) which expands upwards into a *madreporic ampulla* beneath the madreporite. (3) The *stone canal* connecting the water vascular system with the madreporic ampulla. (4) The *dorsal sac* which is a coelomic chamber that has become invaginated on one side to contain the head process of the axial organ. (5) The *genital strand* which runs from the axial organ to the gonads and is surrounded by (6) the *genital sinus*.

The functions of the different parts of the axial complex are various. (1) The stone canal, opening as it does by way of the madreporic ampulla and madreporite to the outside, serves to keep the fluid of the water vascular system at the same hydrostatic pressure as the ambient sea water (Fechter 1965). (2) The main portion of the axial organ has three functions: (a) it is concerned in the degeneration of amoebocytes (Millott 1966, Millott and Vevers 1968) and presumably expels their degeneration products by way of axial sinus, madreporic ampulla, and madreporite; (b) it is certainly secretory (Millott and Vevers 1968) and possibly acts as an endocrine gland (Millott

1967, p. 63); (c) it helps to circulate fluid in the haemal system by means of contractile vessels that it contains (Booolootian and Campbell 1964). (3) The head process and dorsal sac are particularly concerned with pumping fluid through the haemal system. The head process is in fact known to be pulsatile in all the living classes where it exists. Thus, in echinoids, Booolootian and Campbell (1964) showed that it had the structure and action of a two-chambered heart and pulsation was also observed by Narasimhamurti (1931) and Prouho (1887, p. 331). In ophiuroids pulsation of the head process was recorded



TEXT-FIG. 11. The axial complex of an echinoid. Redrawn after Fedotov (1924, fig. 80).

culmination (4 in Pl. 98, fig. 4) in the pharyngo-visceral line. This bulge corresponds to a depression in the internal face of the skeleton (htd in text-fig. 6), and is similar in position to the hydropore of *C. perneri*, since both lie near the median edge of plate M_{2R} (the 'heel' plate) which is homologous in the two species. The bulge is unlikely to represent the position of an optic nerve (contrast Jefferies 1967, Pl. 168; 1968, p. 251) for it is too tumid and differs in shape from the space ventral to point 1, on the left of the theca (Pl. 98, fig. 4; text-fig. 6) which could well have carried such a nerve.

Lying in such a position the dorsal sac and the presumably pulsatile head process of *C. perneri*, *Coth. elizae*, and *Coth. primaeva* could well be homologous with the pericardium and heart of other chordates. They would be situated (ht in text-fig. 8A, B) like these features in other chordates, in the main visceral cavity, in the general region of the gonads and post-pharyngeal gut. Berrill (1955, p. 112) was therefore mistaken in asserting that, despite their morphological resemblance, the heart and pericardium of chordates could not be homologous with those of hemichordates, because located in different parts of the body. In the evolution of mitrates (text-fig. 8C) the pouching out of the right pharyngeal chamber (rp) would separate the dorsal sac and head process (henceforth called pericardium and heart) from the right wall of the theca and push them towards the right side of the gut. Their position would thus become very similar to the pericardium and heart of a tunicate larva (text-fig. 8D).

by Narasimhamurti (1933, p. 79) and Gemmill (1919), and in asteroids by Narasimhamurti (1931) and Gemmill (1919) among others.

The head process and dorsal sac of echinoderms are homologous with the heart and pericardium of hemichordates, which they resemble in structure, function and embryological origin (Fedotov 1924, p. 298, Narasimhamurti 1931, Gemmill 1914).

The head process and dorsal sac of *C. perneri*, by comparison with living echinoderms, would have lain near the aboral end of the axial complex, i.e. in the anterior coelom near the hydropore (ht in text-fig. 8A). In *C. perneri* the superficial internal anatomy does not show their exact location. In *Coth. elizae* and *Coth. primaeva*, on the other hand, the position of the dorsal sac is probably indicated by a bulge in the internal cast (ht in Pl. 98, fig. 4) ventral to a

In *C. perneri*, the stone canal, along with other parts of the water vascular system, was probably degenerate or absent. The water vascular system would have been non-functional if it did exist, for *C. perneri* shows no place that could have borne tube feet, which are the effector organs of the system.

The axial sinus and main portion of the axial organ of *C. perneri* presumably stretched forward from the hydropore, into which the axial sinus would have opened. It seems possible that the axial organ may correspond to the pituitary gland of vertebrates and the homologous neural gland of tunicates. The function of the axial organ in expelling the degeneration products of phagocytes (Millott 1966) is found also in the neural gland of tunicates (Godeaux 1964, p. 59; Pérès 1943; Millar 1953, p. 47). The possible endocrine function of the axial gland (Millott 1967, p. 63) can be paralleled in the pituitary and perhaps in the neural gland (Godeaux 1964, p. 57). The loss of the hydropore as *Ceratocystis* evolved into *Cothurnocystis* implies that a new way must have been found to eliminate the degeneration products of amoebocytes. It may be that *C. perneri*, like hemichordates, had a buccal diverticulum opening into the buccal cavity or the front of the pharynx and in contact with the axial organ, just as the buccal diverticulum is in contact with the equivalent glomerulus of hemichordates. Such a diverticulum could have provided a new pathway for the expulsion of degeneration products. Komai (1951) has already suggested that the buccal diverticulum of hemichordates (the so-called 'stomochord' or 'notochord') is homologous with the hypophysis.

THE STEM

The posterior stem (text-fig. 2A-C, 12; Pl. 96, fig. 5; Pl. 97, fig. 3) is fundamentally similar to that of *Coth. elizae* (Jefferies 1967, p. 171; 1968, p. 261) or *S. curvata* (Jefferies 1968, p. 275). Its skeleton consists dorsally of imbricating plates (dpl in text-fig. 12; Pl. 96, fig. 5), and ventrally of ossicles (vo in text-fig. 12). Unlike *Coth. elizae* or *S. curvata*, however, there is more than one pair of dorsal plates for each ventral ossicle (Pl. 97, fig. 3; Ubaghs 1967, p. 13).

The ventral ossicles are wider than deep. Their dorsal surfaces are complicated; they carry a median groove (mg in text-fig. 12; Pl. 96, fig. 5; Pl. 97, fig. 3) flanked by a longitudinal lateral groove (lg) on each side. Lateral to each longitudinal groove is a series of low bosses (bos). In the more anterior part of the posterior stem these usually number about three bosses on each ossicle on each side but in the more posterior part about two bosses on each ossicle on each side. Sometimes, however, a boss straddles an interossicular suture and, in addition, bosses on right and left sides of an ossicle do not always exactly correspond.

Right and left series of dorsal plates meet at a lax suture in the mid-line and, together with the ventral ossicles, they enclose a tunnel-like lumen. Each dorsal plate has a rough external surface (exs), a well-defined anterior imbrication facet (aif), a less well-defined posterior imbrication facet on the inner face, and an expanded base (bdp). The anterior imbrication facet fits against the posterior imbrication facet of the plate next in front. The expanded base articulates with the bosses on the ventral ossicles in such a way that each base largely covers the anterior part of one boss and the posterior part of the next boss in front. Also the base of each plate slightly overlaps the base of the next plate in front. Successive plates were probably connected to each other in life by connective tissue between adjacent imbrication facets. This is shown by

specimens in which the weak dorsal sutures have been parted after death, probably by gas released by decay of the soft parts, while the plates of a series on each side are nevertheless still articulated together as in life (Pl. 96, fig. 5).

The soft parts of the posterior stem would have been much as in *Coth. elizae* or *S. curvata*. The median groove would have carried the equivalent of the crinoid chambered organ (not in text-fig. 12), coated by the equivalent of the crinoid peduncular nerve (dnc in text-fig. 12). Comparison with mitrates suggests that the peduncular nerve (= dorsal nerve cord) was dorsal to the chambered organ (= notochord). Lateral blood vessels (lv) probably went off from the notochord, as in *Coth. elizae* and *S. curvata*, though in *C. perneri* they were not in contact with the skeleton. By comparison with *Coth. primaeva*, which has two pairs of dorsal plates, and two pairs of grooves for transverse vessels corresponding to each ossicle (personal observation), the transverse vessels of *C. perneri* would have corresponded in number to the dorsal plates and the bosses. The tunnel-like lumen between the dorsal plates and the ventral ossicles must have contained muscle (mu), since the posterior stem with its imbricating dorsal plates is adapted to flex upwards. Analogy with *S. curvata* (Jefferies 1968, p. 276) suggests that the muscle was in the form of muscle blocks, separated by the lateral vessels. Comparison with mitrates suggests that lateral ganglia (lga) connected with the dorsal nerve cord overlay the lateral vessels. There was probably a blood vessel down the middle of the notochord (pv), as deduced for *Coth. elizae* and *S. curvata*.

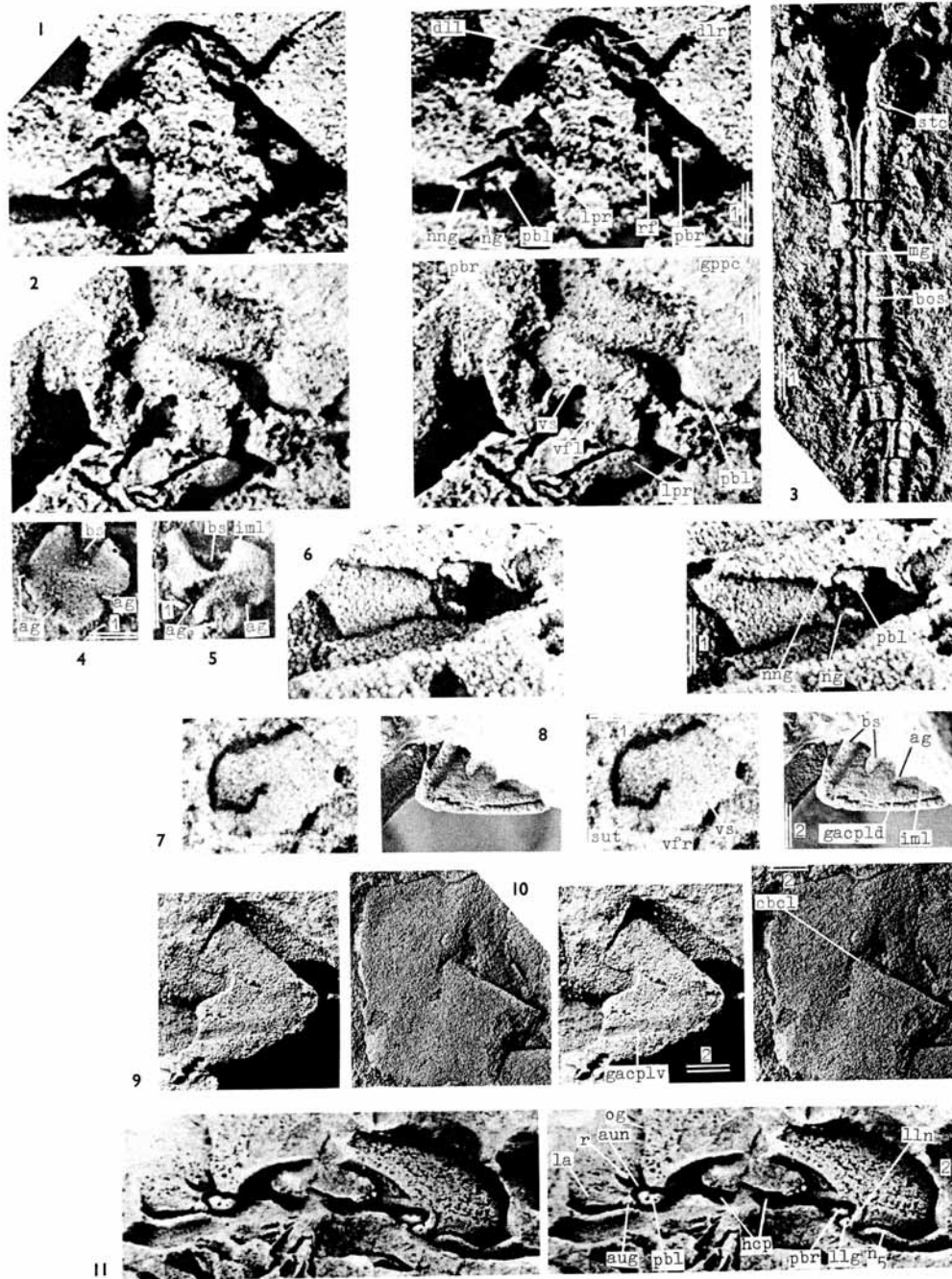
Ubahgs (1967, p. 12) has interpreted the posterior stem as carrying the water vascular system of an arm in accordance with his earlier views (1961, 1963). However, the dorsal

EXPLANATION OF PLATE 97

The lengths of the scales are in mm.

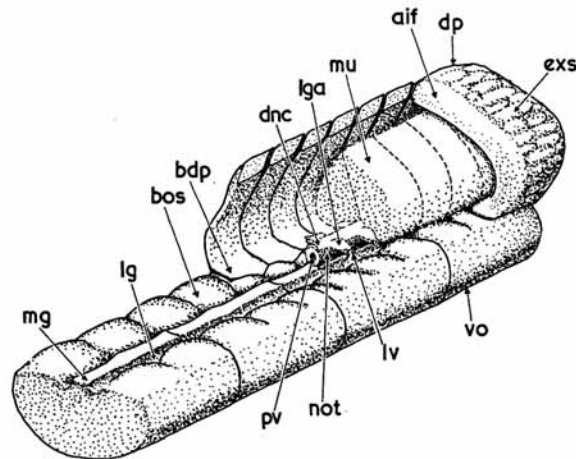
Figs. 1-10. *Ceratocystis perneri*. 1, Natural mould in dorsal aspect to show brain and associated structures (NM 33723/1951); same individual as Plate 95, fig. 3; dll and dlr = left and right dorsal lobes; lpr = left process; ng = infilling of narrow groove; nng = nerve to narrow groove; pbl and pbr = left and right pyriform bodies; rf = right face of brain. 2, Natural mould in ventral aspect to show brain and adjacent structures (W 24); gppc = groove between pharynx and posterior coelom; lpr = left process; pbl, pbr = left and right pyriform bodies; vfl = left, ventral face of brain; vs = ventral swelling. 3, Latex impression of stem in dorsal aspect (NM 221123/7 1924 lectotype); bos = boss; mg = median groove; stc = stylocone. 4, 5, Latex impression of infra-branchial plates in internal aspect (GPMB Ca 32 and W 26) to show distinction between branchial slits (bs) and accessory gaps (ag); iml = dorsal margin of depression for left internal muscle. 6, Natural mould (W13) in posterior aspect of the interior of M_{ILD} to show the nerve to the narrow groove (nng) going round the left pyriform body (pbl) to the infilling of the narrow groove (ng). 7, Natural mould of the inside of M_{pv} (specimen W 4); sut = suture with M_{IRD} ; vfr = right ventral face of brain; vs = ventral swelling. 8, Natural mould of the inside of M_{2L} , posterior aspect (W 3); ag = accessory gap; bs = branchial slit; gacpld = groove showing dorsal boundary between anterior coelom and pharynx left of the stem; iml = limit of left internal muscle. 9, As fig. 8, ventral aspect; gacplv = groove showing ventral boundary between anterior coelom and pharynx left of the stem. 10, Natural mould of inside of M_{4LV} (USNM 61503); cbcl = cleft between buccal cavity and pharynx left of stem.

Fig. 11. *Mitrocystites mitra*. Natural mould of inside of posterior part of the theca in postero-dorsal aspect (E 7517), to show (i) auditory nerve (aun) going round left pyriform body (pbl) to auditory ganglion (aug) in left atrium (la), and (ii) lateral-line nerve (lln) going round right pyriform body (pbr) to lateral line ganglion (llg); cf. Plate 98, fig. 7; hcp = cast of hypocerebral processes; n_5 = nerve n_5 of palmar complex; og = oblique groove; r = rectum.



JEFFERIES, *Ceratocystis perneri*, *Mitrocystites mitra*

plates do not resemble cover plates, for the base of each one is expanded and makes contact with the bosses by a very broad area, and successive plates on the same side seem to have been held together by connective tissue. The median dorsal suture was lax, and for this reason often split open after death. The reason for this laxity was mechanical, for when the stem flexed upwards the angle between opposite members of a pair of plates would need to change as the pair was forced downwards on to the pair next behind. The fact that left plates sometimes separated from right plates after death resulted from this laxity of the median dorsal suture and does not show that they could separate in life.

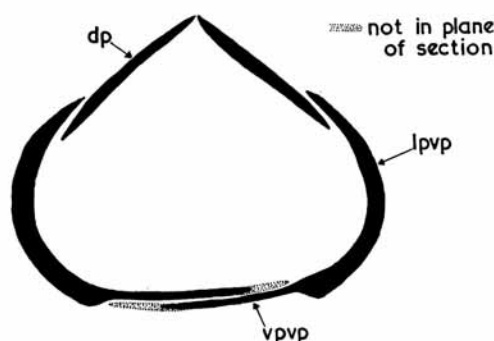


TEXT-FIG. 12. Block diagram of posterior stem of *Ceratocystis perneri*, left dorso-lateral aspect. aif = anterior imbrication facet; bdp = base of dorsal plate; bos = boss on ventral ossicle; dnc = dorsal nerve cord; dp = dorsal plate; exs = external surface of dorsal plate; lg = lateral groove; lga = lateral ganglion; lv = lateral vessel; mg = median groove; mu = muscle; not = notochord; pv = peduncular or notochordal vessel; vo = ventral ossicle.

The skeleton of the medial stem consisted of a ventral stylocone (stc in text-fig. 2A-C; Pl. 96, figs. 3, 5, 10; Pl. 97, fig. 3) surmounted by about eight pairs of dorsal plates. The stylocone has been accurately figured and described by Ubaghs (1967, p. 13, fig. 6).

The skeleton of the anterior stem was more regular than Ubaghs has suggested (1967, p. 12). It consisted of about 15 rings of plates and each ring, as in other calcichordates, contained 4 plates—left and right dorsal, and left and right ventral (Pl. 96, fig. 9). Each ventral plate consisted of a lateral and a ventral portion (lpvp and vpvp in Pl. 96, fig. 10) and the ventral portion extended across the ventral face to near the opposite side (text-fig. 13). Successive rings of plates in general imbricated so that the front part of each ring was inside the posterior part of the next ring in front. On the ventral face, however, the ventral portions of ventral plates imbricated with one another, in such a way that right and left ventral portions usually alternate (text-fig. 2c).

The soft parts of the anterior stem presumably included powerful muscles, almost filling the large lumen. In addition there must have been, on functional as well as comparative grounds, an anti-compressional structure extending through the lumen. This would be the anterior part of the notochord or chambered organ whose posterior continuation followed the median groove of the posterior stem. There would have been a nerve, the dorsal nerve cord or peduncular nerve, from the brain to the posterior stem. The functioning of the stem is dealt with below.



TEXT-FIG. 13. Transverse section through skeleton of anterior stem of *Ceratocystis perneri*. dp = dorsal plate; lpvp = lateral portion of ventral plate; vpvp = ventral portion of ventral plate.

THE BRAIN AND CRANIAL NERVES

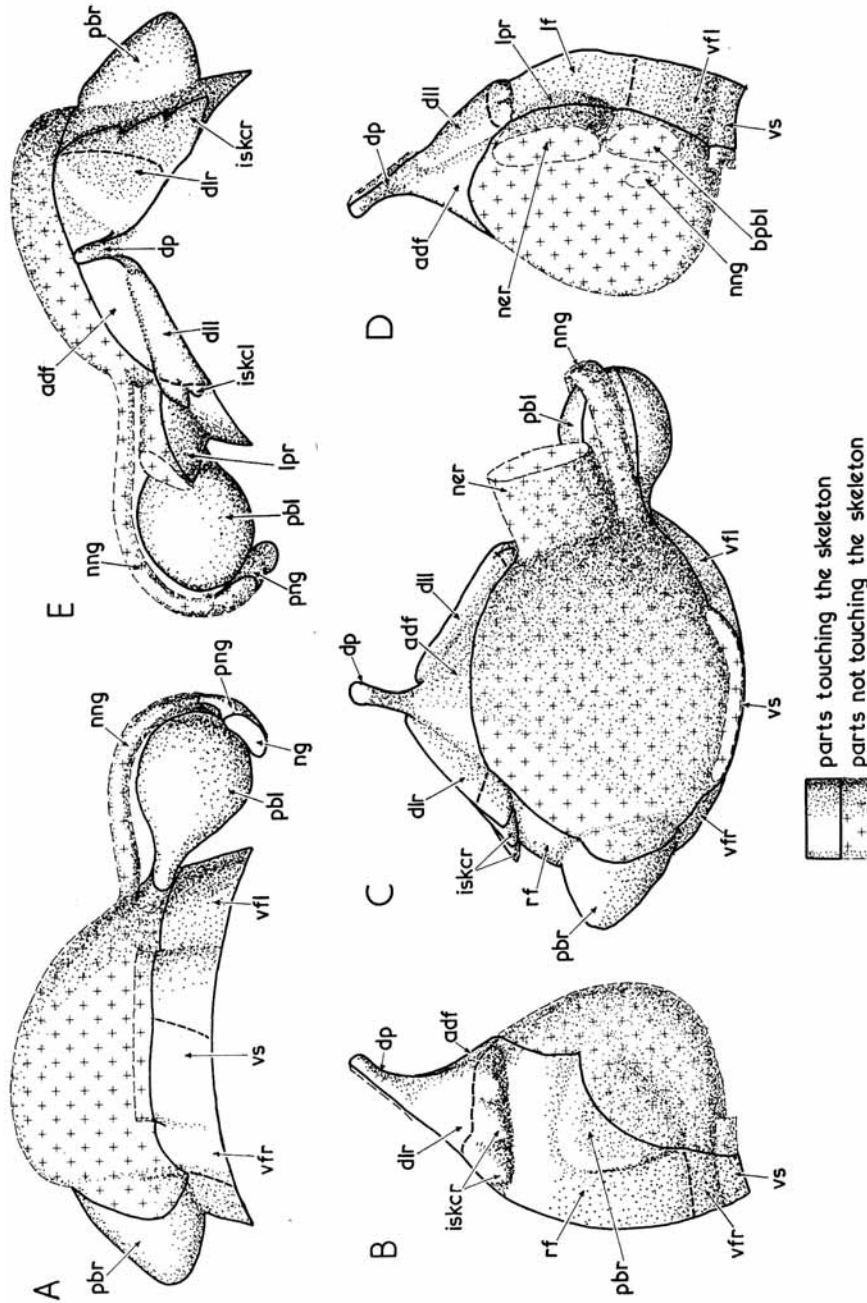
The brain of *C. perneri* (text-fig. 14A-E) can be reconstructed more fully than that of later cornutes. It lay, as in all calcichordates, and like the aboral nerve centre of crinoids, just anterior to the stem, where its position is indicated by facets on the internal cast. These facets show that it was in contact with all those plates of the theca which touched the anterior end of the stem, i.e. M_{PD} , M_{ILD} , M_{ILV} , M_{PV} , and M_{IRD} . It did not touch M_{IRV} , which did not form part of the stem insertion in *C. perneri*. The cranial nerves of *C. perneri* touched the skeleton in only a few places.

The morphology of the cerebral cast and of the associated structures may be described as follows:

1. *Right and left dorsal lobes* (dlr, dll in text-fig. 14B-E; Pl. 95, fig. 7; Pl. 97, fig. 1) are situated on right and left sides of the dorsal part of the cerebral cast. They are mainly in contact with M_{PD} but they continue downwards in contact with M_{ILD} and M_{IRD} and end in a number of points, the *intrasketal cones* (iskcr and iskcl in text-fig. 14B-E; Pl. 95, fig. 6). These presumably indicate where nerves entered the dorsal lobes from the skeleton.

2. The cerebral cast had an *antero-dorsal face* (adf) which was produced upwards into a *dorsal process* (dp in text-fig. 14B-E; Pl. 95, fig. 7). This latter was contained in the *dorsal groove* leading to the dorsal face of the theca (see above dg in text-fig. 2A, D; Pl. 96, figs. 1, 9; Pl. 98, fig. 1).

3. The *left face* of the cerebral cast (lf in text-fig. 14D) corresponds to a facet on



TEXT-FIG. 14. Reconstruction of brain of *Ceratocystis perneri*. The major part of the anterior face must have been more complicated than here shown, but cannot be reconstructed in detail. A, ventral; B, right lateral; C, anterior; D, left lateral; E, dorsal aspects. adf = antero-dorsal face; bpbl = base of left pyriform body; dll and dlr = left and right dorsal lobes; dp = dorsal process; iskcl and iskcr = left and right intraskeletal cones; lf = left face of brain; lpr = left process; ner = nerve corresponding to left process; ng = narrow groove (lateral line); nng = nerve to narrow groove (lateral line nerve); pbl and pbr = left and right pyriform bodies; png = process of internal cast to narrow groove that carried lateral-line nerve (nng); rf = right face of brain; vfl, vfr = left and right ventral faces of brain; vs = ventral swelling.

M_{ILD} (Pl. 97, fig. 1). Just anterior to it a powerful *left process* (lpr in text-fig. 14D, E; Pl. 97, fig. 1) went off leftwards.

4. Just left of the left process, and in contact with plates M_{ILD} and M_{ILV} , are indications of an approximately spherical body called the *left pyriform body* (pbl in text-fig. 14A, C-E; Pl. 96, fig. 8; Pl. 97, figs. 1, 2, 6; Pl. 98, fig. 3), since it is homologous with the like-named structure of mitrates and of other cornutes (Jefferies 1967, pp. 173, 177, 185 ff., 193; 1968, pp. 264, 276, 299 ff., 322). The right face (rf in text-fig. 14B, C; Pl. 95, fig. 6; Pl. 97, fig. 1) of the cerebral cast has anterior to it the right pyriform body (pbr in text-fig. 14A-C, E; Pl. 97, figs. 1, 2; Pl. 98, fig. 3). Both right face and right pyriform body are in contact with M_{IRD} . The right and left ventral faces (vfr and vfl in text-fig. 14A-D; Pl. 97, figs. 2, 7; Pl. 98, fig. 3) of the cerebral cast are in contact with the plates M_{PV} and M_{ILV} . The anterior boundaries of these ventral faces are better defined towards right and left sides of the cerebral cast than further ventrally where they pass into a rather vague *ventral swelling* (vs in text-fig. 14A-D; Pl. 97, figs. 2, 7; Pl. 98, fig. 3). Just left of the left pyriform body was situated the *narrow groove* (ng) in the external surface of the theca in plate M_{ILD} . This receives a projection to the narrow groove on the internal cast (png in text-fig. 14A, E; Pl. 97, fig. 6). This projection represents the infilling of a canal in the skeleton.

EXPLANATION OF PLATE 98

The lengths of the scales are in mm.

Fig. 1. *Ceratocystis perneri*. Latex impression showing dorsal surface in dorsal aspect (W 8); ag = accessory gaps; bs = branchial slits; dg = dorsal groove; faf = flap attachment facet; fpl = probable flap platelets; ib = infrabranchial plates.

Fig. 2. *Cothurnocystis americana*. Dorsal aspect of only known specimen and holotype (USNM 143237); bs = branchial slits; inbc = integument over buccal cavity; in p = integument over pharynx; ? pos M_{4LD} = probable position of plate M_{4LD} ; str = strut.

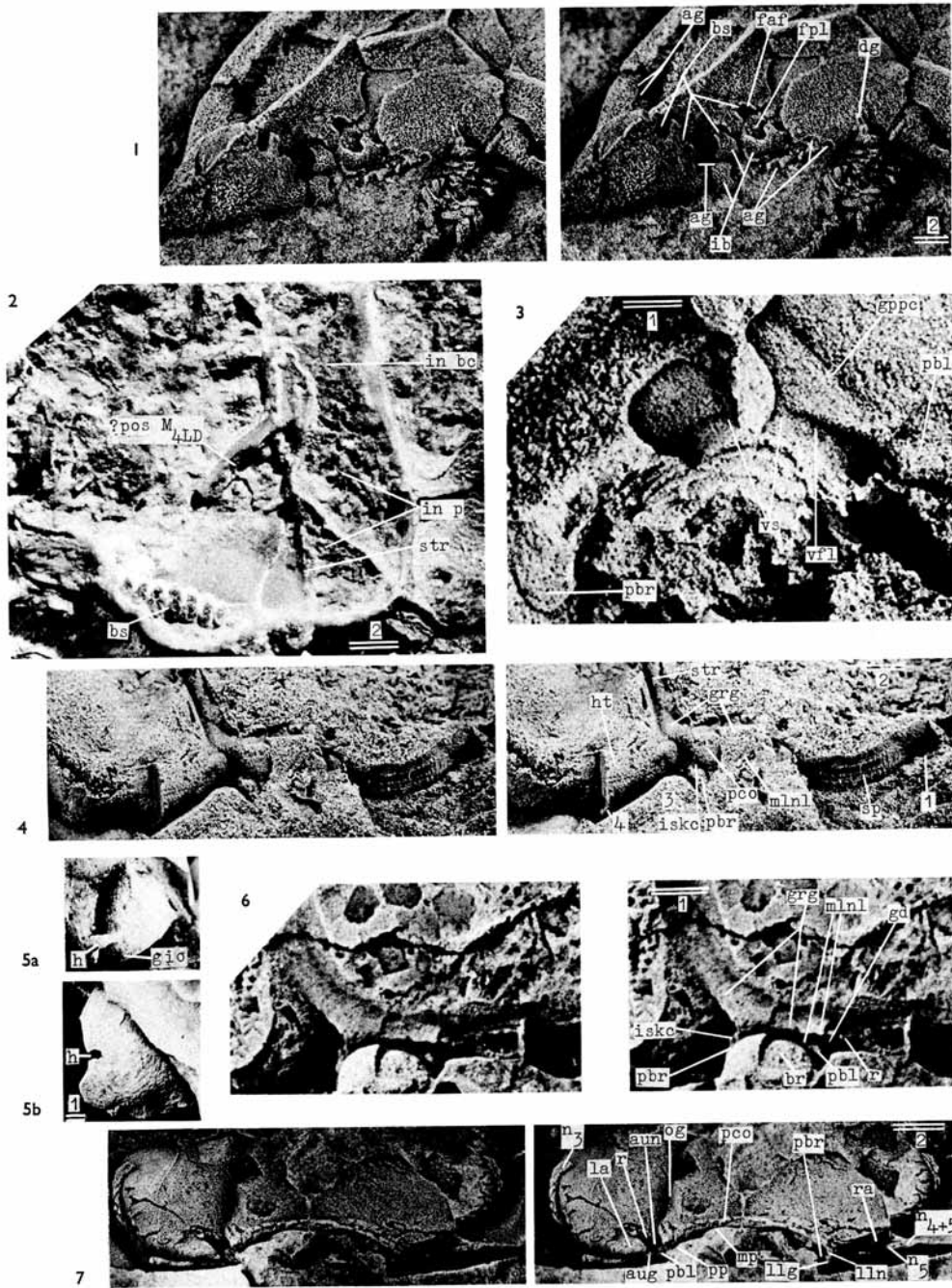
Fig. 3. *Ceratocystis perneri*. Plaster cast of silicone rubber mould of Copenhagen specimen, simulating natural mould; the ventral surface of the brain is better marked off anteriorly than in any other specimen examined; gppc = groove between pharynx and posterior coelom; pbl and pbr = left and right pyriform bodies; vfl = left ventral face of brain; vs = ventral swelling.

Fig. 4. *Cothurnocystis elizae*. Natural mould of inside of theca in postero-ventral aspect (E 28667), with the specimen lying dorsal side downwards, cf. text-fig. 6; 1, 3, 4 = points where the pharyngo-visceral line approaches the dorsal side of the theca; grg = gonorectal groove; ht = probable position of heart; pbr = right pyriform body; pco = posterior coelom; sp = striations on the inside of the pharynx; str = impression of strut.

Fig. 5. *Ceratocystis perneri*. (a) Plaster cast simulating natural internal mould of plate M_{2R} , posterior aspect; (b) Latex cast of plate M_{2R} , posterior aspect. Magnification, of (a) and (b) equal. Both are from same specimen. Národní Muzeum, no number. h = hydropore; gio = groove round internal organ.

Fig. 6. *Cothurnocystis primaeva*. Natural mould of inside of theca (Montpellier specimen) in ventral aspect, to show region just anterior to stem; cf. text-fig. 7; br = brain; gd = gonoduct; grg = infilling of gonorectal groove; iskc = intraskeletal cones; mlnl = left median-line nerve; pbl, pbr = left and right pyriform bodies; r = rectum.

Fig. 7. *Mitrocystites mitra*. Natural mould of inside of theca in postero-dorsal aspect (MCZ 566); cf. text-fig. 15 and Plate 97, fig. 11; aug = auditory ganglion; aun = auditory nerve; la = left atrium; llg = lateral line ganglion; lln = lateral line nerve; mp = median part of brain; n_3 = optic nerve; $n_4 + 5$, n_5 = other nerves of palmar complexes; og = oblique groove; pbl, pbr = left and right pyriform bodies; pco = posterior coelom; pp = posterior part of brain; r = rectum; ra = dorsal margin of right atrium.



JEFFERIES, *Ceratocystis perneri*, *Cothurnocystis* spp., *Mitrocystites mitra*

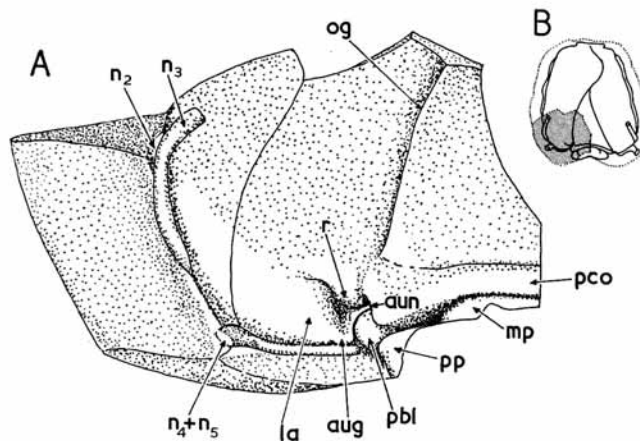
Interpretation of these features of the internal cast is possible by comparison with other cornutes and, more particularly, with mitrates (text-figs. 15, 16; Pl. 97, fig. 11; Pl. 98, fig. 7; Jefferies 1967, pp. 185 ff., 191 ff.; 1968, pp. 295 ff., 319 ff.). Taken together, the dorsal lobes (dl) and intraskeletal cones (iskc) are comparable with the anterior part of the brain of mitrates, which likewise is dorsal in position and probably also received nerves from the skeleton, sometimes by way of intraskeletal cones (e.g. *Mitrocystella incipiens miloni*, Jefferies 1967, fig. 10; 1968, figs. 19a-c). The anterior part of the brain in mitrates represented the telencephalon and was olfactory. Consequently the intraskeletal nerves of *C. perneri*, which presumably entered the dorsal lobes by way of the intraskeletal cones, would be the olfactory nerves, and the dorsal lobes would represent the telencephalon. The antero-dorsal face (adf) of the brain in *C. perneri* is ventral to the dorsal lobes, i.e. ventral to the telencephalon, and this part of the brain in mitrates and all other chordates is optic in function. The dorsal process (dp) that extended upwards on to the dorsal surface of the theca would therefore also be optic in function. It would represent a sort of primitive median eye. This, however, was probably not homologous with the pineal or parapineal eyes of vertebrates, since it runs upwards in front of the telencephalon, rather than behind it, and is absent from all known mitrates. The right and left pyriform bodies (pbr and pbl) of *C. perneri* correspond to the pyriform bodies of other calcichordates and these represent the trigemino-profundus ganglia of vertebrates (Jefferies 1967, p. 190; 1968, p. 307). The ventral swelling of the cerebral cast (vs) may possibly correspond to the places where ventrally placed nerves left the brain. These would correspond to the median-line nerves of other cornutes (1967, pp. 173, 177; 1968, pp. 264, 276). The left process (lpr) presumably represents a large nerve to the theca (ner in text-fig. 14c, D) corresponding to either posterior or medial part nerves, or both, of mitrates, i.e. to optic or medullary nerves, or both. If a corresponding right nerve existed in *C. perneri* it did not touch the skeleton.

The narrow groove (ng) on the surface of M_{ILD} recalls the narrow groove or lateral line that exists in mitrates (lateral line (ll) in Jefferies 1967, pp. 178, 190; narrow groove (ng) in Jefferies 1968, pp. 283, 299 ff., 314). If the projection to the narrow groove of *C. perneri* (png) carried a nerve, as seems likely, then the nerve supply to the groove (nng in text-fig. 14 A, C, E) was like that to the groove of mitrates in coming round the outside of a pyriform body. However, the narrow groove of *C. perneri* was left of the stem, and its nerve supply came round the left pyriform body, whereas the narrow groove of mitrates was right of the stem, and its nerve supply came round the right pyriform body.

This anomaly demands a partial restudy of the mitrates. In *Mitrocystites mitra* there is a previously unrecorded ridge on the internal cast (aun in text-fig. 15; Pl. 97, fig. 11; Pl. 98, fig. 7) which sweeps round the front and left side of the left pyriform body (pbl), behind the rectum (r), and appears to enter the left atrium (la) to end there in a little lump (aug). With respect to the pyriform body this ridge corresponds in its position on the left of the theca to the ridge in *M. mitra* representing the course of the lateral line nerve (lln) on the right. In addition, the lump (aug) is a left counterpart of the lump representing the lateral-line ganglion (llg) on the right. It therefore seems that the two sets of structures are right and left antimeres of each other, except that the left one ends in the left atrium, while the right one ends at the surface.

The acustico-lateralis system of fishes includes two parts—the lateral line which lies at or near the surface, and is directly sensitive to displacements of water (Dijkgraaf

1963, Bergeijk 1964), and the acoustic system, which is invaginated and sensitive to pressure waves, gravity and angular acceleration. It seems that the acustico-lateralis system of mitrates had two corresponding parts, i.e. external and functioning as lateral line on the right, and invaginated and presumably functioning as ear on the left. The ridge aun would therefore represent the auditory nerve and the lump aug would represent the auditory ganglion. The fact that the auditory nerve runs immediately in front of the left pyriform body, behind the rectum, suggests that the lateral line nerve (lln) probably ran immediately in front of the right pyriform body. Its proximal course was

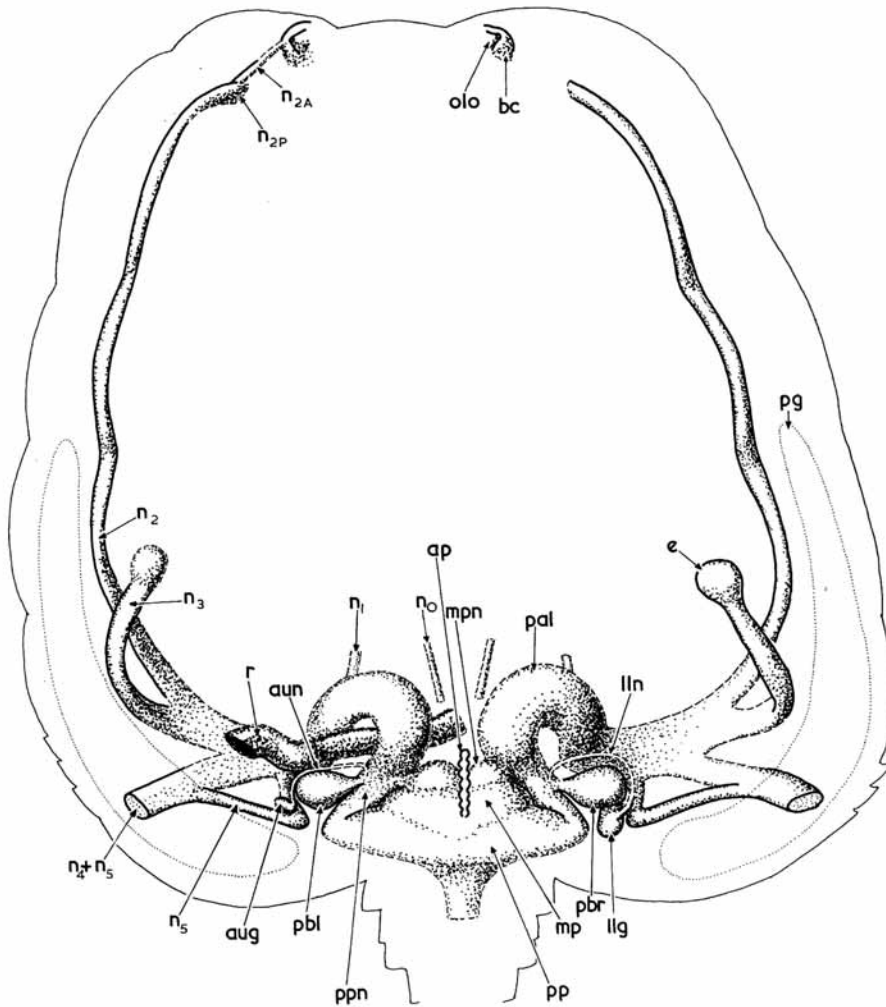


TEXT-FIG. 15. A, Portion of internal mould of *Mitrocystites mitra* to show auditory nerve and ganglion (MCZ 566, cf. Pl. 98, fig. 7). B, Diagram of dorsal aspect of theca, to show portion (stippled) included in A. aug = auditory ganglion; aun = auditory nerve; la = left atrium; mp = medial part of brain; n_2 , n_3 , n_{4+5} = nerves of left palmar complex; og = oblique groove; pco = posterior coelom; pp = posterior part of brain; r = rectum. For meaning of anatomical terms see Jefferies 1967, p. 179ff.; 1968, p. 315ff.

therefore probably different from what I previously supposed (1967, figs. 10, 14; 1968, figs. 19, 27). Text-fig. 16 is a revised reconstruction of the cranial nerves of *M. mitra* that takes these new conclusions into account.

The narrow groove (ng) of *C. perneri* and the nerve supplying it (nng) correspond closely in position to the auditory ganglion and auditory nerve of *Mitrocystites mitra*. The nerve nng must be homologous with the auditory nerve of *M. mitra* and the floor of the narrow groove presumably housed the homologue of the auditory ganglion. In *C. perneri* the narrow groove, being on the surface of the animal, would have functioned as lateral line.

The early history of the acustico-lateralis system in the chordates would therefore have been somewhat as follows. The system is first seen in *C. perneri* as a surface groove just left of the stem that functioned as lateral line, being directly sensitive to displacements of the sea water. In *Cothurnocystis* this lateral line must still have existed, but probably lay just right of the gonopore-anus, without any separate opening in the



TEXT-FIG. 16. Reconstruction of brain and cranial nerves of *Mitrocystites mitra* in dorsal aspect (modified from Jefferies 1968, fig. 27). ap = anterior part of brain; aug = auditory ganglion; aun = auditory nerve; bc = buccal cavity; e = eye; llg = lateral line ganglion; lln = lateral line nerve; mp = medial part of brain; mpn = medial part nerve; n_0 = ventral nerves of uncertain connection and homology; n_{1-5} = nerves of palmar complex including maxillary trigeminal (n_2) and optic (n_3) nerves; n_{2A+P} = branches of nerve n_2 ; olo = olfactory openings; pal = palmar nerves; pbl and pbr = left and right pyriform bodies (trigemino-profundus ganglia); pg = peripheral groove; pp = posterior part of brain; ppn = posterior part nerves; r = rectum.

skeleton. The nerve that supplied it would have swept round the front of the left pyriform body and followed the posterior surface of the rectum to the lateral line. When the left gill slits, anus, gonopore and lateral line became enclosed in the left atrium, which happened either when the mitrates evolved, or somewhat before, the lateral line changed its function. Displacement of the surrounding sea-water no longer affected it, but it would be able, in a rudimentary way, to fulfil the functions of an ear. It would thus be sensitive to pressure waves, to angular rotation that caused swirling of water in the left atrium, and to gravity, if calcareous otoconiae existed in the cupolae of the neurocasts (Pumphrey 1950, p. 13). Among mitrates, the Mitrocystitidae again became sensitive to displacements of the external sea-water by evolving a lateral line, with its nerve supply, on the right side.

The appearance of organs on the right which had previously existed only on the left was a feature of the evolution of mitrates from cornutes. It is seen in the pharynx, the gill slits, and probably the atria, as well as the acustico-lateralis system. The earliest known occurrence of a lateral line on the right side is found in *Chinianocarpus thoralis* Ubachs (Upper Tremadoc or Lower Arenig), which is the oldest mitrocystitid known. Such a feature is unknown in the Peltocystidae, which is the other family of mitrates represented at the base of the Ordovician. The way in which the primitive mitrocystitid acustico-lateralis system evolved into that of vertebrates cannot be worked out, since it would have happened in soft-bodied animals. Presumably, however, the lateral-line was replicated on the left side of the body and the acoustic system on the right. This replication on opposite sides of the body would be similar, but opposite in sense, to what had happened in the evolution of mitrates. It is interesting that the only skeletal calcium carbonate which vertebrates possess is found in the acustico-lateralis system (otoconiae and otocysts). This may represent an inheritance from calcichordates, in which the acustico-lateralis system was better developed than I previously supposed.

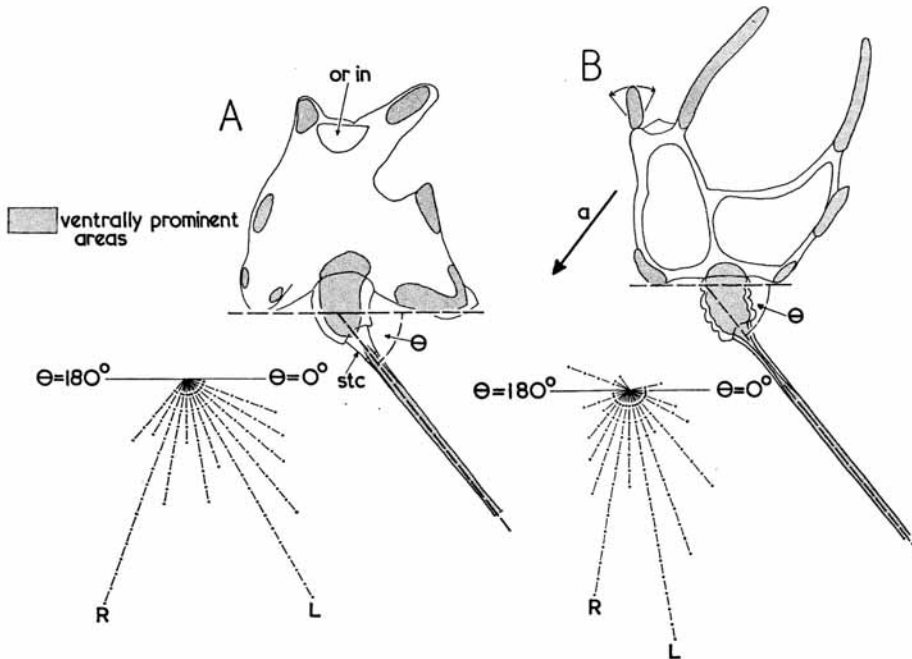
The relation between brain and blood system in *C. perneri* is of interest. The brain was in contact with the thecal skeleton all the way round the stem insertion. The blood supply to the stem must therefore have gone through the middle of the brain, just as the haemal strand goes through the aboral nerve centre of crinoids (Reichensperger 1905). Like the haemal strand, it probably continued backwards down the middle of the chambered organ (= notochord) as a notochordal vessel (Jefferies 1967, pp. 172, 184; 1968, pp. 263, 293). Anterior to the brain the notochordal vessel would presumably be connected to the axial organ, as the haemal strand is in crinoids (Reichensperger 1905).

POSTURE, HABITS, AND MODE OF FEEDING

The posture of *C. perneri* would have been very like that of *Coth. elizae*, i.e. the theca rested ventral side downwards on the bottom with the stem stretched out almost horizontal behind the theca. Certain portions of the ventral surface of the theca (stippled in text-fig. 17A) were ventrally prominent and would have touched the sea floor more frequently or sunk deeper into it than the less prominent parts. Those ventrally prominent parts would have been the places that bore most of the weight of the theca and are constructed of more massive stereom than the other parts of the ventral surface (Pl. 95, fig. 1). Indeed, the massiveness of the stereom is roughly proportional to the prominence of the part which it forms. Massive stereom would be smoother than loose-textured

stereom, and would have less soft tissue within it that could be damaged by being scraped over the sea floor.

In later members of the Ceratocystidae the ventrally projecting, weight-bearing parts of the ventral surface became better developed (e.g. *Coth. elizae*, text-fig. 17B). In such forms they had the function of raising the ventral integument clear of the sea floor,



TEXT-FIG. 17. Ventrally prominent areas (stippled) and observed positions of stem in A, *Ceratocystis perneri* and B, *Cothurnocystis elizae*. or in = oral integument; stc = stylocone. R and L = especially frequent positions of stem to right and left. The arrow *a* indicates probable easiest direction of slip in *Coth. elizae*. In the histograms each dot indicates one specimen.

so that its pumping movements would not be hindered. This raising of the ventral integument is particularly marked in *Scotiaecystis curvata* (Jefferies 1968, figs. 8c-e) but is also developed, to lesser degree, in *Coth. elizae* (figs. 1d-g) and is incipient in *Coth. primaeva*. The form of the ventral spikes and anterior appendages of these three species suggests that the theca could have slipped backwards much more easily than forwards (1968, pp. 265, 277) and this was probably also true of mitrates (1968, pp. 310, 323). The probable direction of easiest slipping in *Coth. elizae* is shown by the arrow *a* in text fig. 17B.

The form of the ventrally prominent parts of the theca of *C. perneri* suggests that the theca could already slip more easily backwards than forwards, though the tendency was less pronounced than it became in later Ceratocystidae. Thus the anterior part of

the spike S_{3R} (text-fig. 2B; Pl. 95, fig. 1) would have stuck deeper into the sea-floor than its posterior part, and the same is true of the left appendage (lap in Pl. 95, fig. 1).

The stem of *C. perneri* is in all observed specimens stretched out on a bedding plane, and could probably wave from side to side. Text-fig. 17A shows its position in 105 specimens. There are two especially frequent positions (L and R) which also existed in *Coth. elizae* (text-fig. 17B). These perhaps correspond to the most usual end positions of the stem in its side-to-side movements after burial and before death.

The massive texture of the stereom of the ossicles of the posterior stem, of the ventral surface of the anterior stem, and of part of the ventral surface of the stylocone (as stippled in text-fig. 17A, cf. Pl. 96, fig. 3; Ubaghs 1967, pl. 2, fig. 8) resembles that of the ventrally prominent parts of the theca. It is likely that the massive-textured parts of the stem, like the similar parts of the theca, were habitually in contact with the sediment of the sea bottom. Conversely, the loose-textured part of the ventral surface of the stylocone would not usually have touched the sediment, or would have touched it more lightly. The distribution of these variations in texture suggests that the stem stretched out almost horizontally in life so that the anterior and posterior parts sank somewhat into the sediment, while most of the stylocone was just clear of the sediment, or sank into it less deeply. This agrees with the observed position of the stem in fossils, parallel to the bedding. With such a posture, abrupt lateral flexion of the stem would have caused the theca to slip over the sea bottom, mainly backwards, and would have provided a clumsy but workable means of locomotion. Pulling an asymmetrical object is easier than pushing it, being directionally stable. This was the probable reason why cornutes, as here believed, took to moving backwards.

C. perneri would have been a deposit feeder like *C. elizae* (Jefferies 1968, p. 258), since its mouth was level with the bottom. It is likely that water was pumped through the pharynx mainly by ciliary action, but that the animal could also 'cough' slightly, using the rudimentary bellows mechanism of the theca.

EVOLUTION IN THE CERATOCYSTIDAE

Ceratocystis perneri, *Cothurnocystis americana*, *Cothurnocystis primaeva*, and *Cothurnocystis elizae* closely approximate to a single line of descent (text-fig. 1), and most of the changes in this line of descent can be explained functionally.

C. perneri had a boot-shaped theca formed of calcite plates. This theca rested on the sea bottom by the ventral side, which carried ventral spikes to hold the theca in the sea floor and to carry most of the thecal weight. The animal moved by dragging the theca backwards by the stem. The theca had a mouth at the anterior end, and hydropore, gonopore, and anus existed right of the stem. Left of the stem were 7 gill slits. The theca contained 4 chambers, i.e. buccal cavity, pharynx, anterior and posterior coelom. A respiratory and feeding current was created, probably mainly by ciliae on the insides of buccal cavity and pharynx. These two chambers, however, could also contract, slightly but suddenly, by the action of muscles in the thecal wall. The dorsal thecal wall was stiffened by keels which assured that this 'coughing' action caused contraction of the thecal cavity, and expulsion of water, rather than merely changing the shape of the thecal cavity without change in volume. Most of the food supply came from the organic detritus lying on the sediment, i.e. the animal was a deposit feeder. Internal organs in the

right-hand posterior corner of the theca (i.e. in the anterior coelom) included the post-pharyngeal gut, the gonads, the heart and pericardium, probably an axial gland, and perhaps parts of a degenerate water vascular system. The brain lay at the anterior end of the stem and at the anterior end of notochord and dorsal nerve cord. Olfactory and optic parts can be identified in the brain. The optic part gave rise to a sort of median eye, which lay on the dorsal surface of the theca. Just anterior and lateral to the brain were two ganglia (the pyriform bodies) homologous to the trigemino-profundus ganglia of vertebrates. Just left of the stem was a groove on the surface that represented the first beginnings of the acustico-lateralis system and was supplied by a nerve coming round the left pyriform body.

Coth. americana was functionally a major advance on *C. perneri* but is unfortunately not well known. The theca was still boot-shaped, but more like that of *Coth. elizae* than that of *C. perneri* in shape. The theca had become much more flexible than it was in *C. perneri* by the development of a dorsal integument. It seems likely that muscular pumping had become the main way of expelling water through the gill slits. The most important pumping muscles would be those in the roof of the pharynx, which would be partly housed in large spaces between the plates. The roof of the buccal cavity was flexible, but lacked comparable spaces for muscles. The gill slits of *Coth. americana*, which still numbered 7, were very similar to those of *Coth. elizae* and were well adapted as outlet valves. The hydropore had disappeared, and it is possible that the axial gland had started to discharge through a duct in the anterior part of the pharynx, i.e. had turned into the pituitary gland. Gonopore and anus had started to migrate leftwards, so as to approach the exhalent current from the gill slits, though it is not possible to say how far they had moved. The flexibility of the thecal roof meant that the floor of the theca was liable to buckle when the muscles of the dorsal integument contracted. This tendency was counteracted by thickening the floor along an antero-posterior line to form a strut.

Coth. primaeva differed principally from *Coth. americana* in having a flexible floor to the theca, crossed by a rigid strut. The pumping action of the theca therefore involved movements of the floor, as well as the roof, and would have been more efficient. Gonopore and anus were just left of the stem in *Coth. primaeva*, as they were in *Coth. elizae*. They would thus lie in the outwash from the gill slits. Heart, pericardium, gonads, most of the post-pharyngeal gut, and the pituitary gland lay in the anterior coelom, as in *C. perneri*. The rectum and the distal part of the gonoduct, however, ran across the floor of the posterior coelom, from the anterior coelom to the gonopore-anus. The brain of *Coth. primaeva* probably resembled that of *C. perneri* in most respects, including the presence of a median eye.

Coth. elizae did not much differ from *Coth. primaeva* but is better known, because more specimens are known. It lacked the median eye and had more gill slits (16 instead of about 7). Spikes on the ventral surface would have lifted the thecal floor above the sea bottom, so that movement of the ventral integument would not be hindered.

The foregoing history involves some oversimplification. Thus *Coth. americana* is only known to occur at a horizon that also contains a cornute with a flexible thecal floor (*Phyllocystis* sp. Ubaghs 1963). *Coth. americana* itself, therefore, must represent a late survival of the stage with flexible roof and rigid floor, which other cornutes had already surpassed. Again the outline of the theca of *Coth. primaeva* is not intermediate between

that of *Coth. americana* and *Coth. elizae*, but suggests affinities with *Scotiaecystis curvata*. These discrepancies are probably not important.

The line connecting *C. perneri* with *Coth. elizae* was a conservative one. Other cornutes diverged more from the *C. perneri* type. The line of descent leading to *S. curvata* presumably separated from the *perneri-elizae* line after a flexible thecal floor had been acquired. It is represented by an undescribed form contemporary with *Coth. primaeva* (Ubaghs, personal communication). *S. curvata* was a suspension feeder; its mouth opened upwards and the ventral integument was lifted well above the sea floor by strong curvature of the frame so as to improve its pumping efficiency. The gill slits are also highly specialized.

The *Phyllocystis* line of descent, which includes bilaterally symmetrical forms, also separated from the *perneri-elizae* line after the acquisition of a flexible thecal floor. The increased symmetry of the theca was probably acquired by bending the 'ankle' part of the boot-shaped theca leftwards, so that the mouth also came to point leftwards. *Coth. ubaghsi* Chauvel (1966, p. 98) in which the buccal cavity is strongly bent to the left, may represent an intermediate stage in this process. The mitrates were probably derived from *Phyllocystis*. Some primitive mitrates belonging to the Mitrocystitidae have a leftward pointing mouth (e.g. *Chinianocarpos thorali* Ubaghs, Jefferies 1968, p. 314). From primitive mitrates the other chordate subphyla are probably descended.

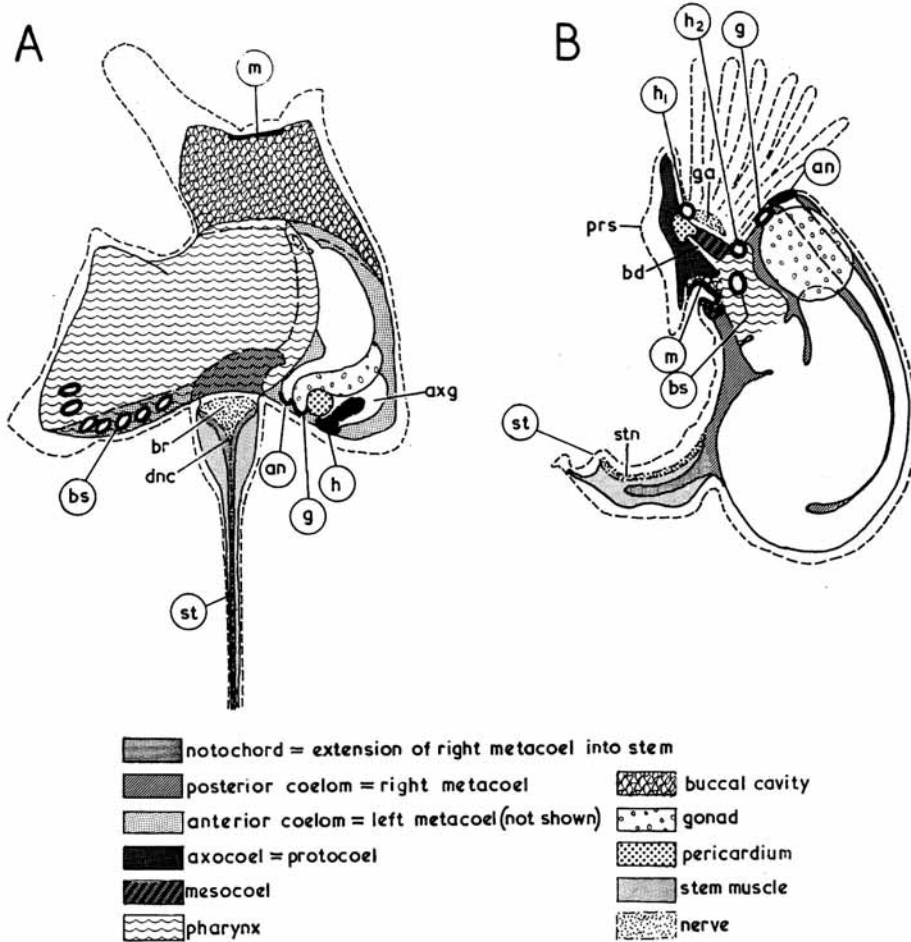
CALCICHORDATES, HEMICHORDATES, AND ECHINODERMS

The extraordinary asymmetry of *Ceratocystis perneri*, together with the position of the anus right of the stem, suggest that it evolved from a bilaterally symmetrical animal that lay down on its right-hand side. Moreover, it seems likely that the animal in question was a pterobranch hemichordate. Thus text-fig. 18 compares the reconstructed anatomy of *C. perneri*, based on echinoderm and tunicate analogies, with the anatomy of the living pterobranch *Cephalodiscus*. The disposition of organs is similar, if the ventral side of *C. perneri* is taken to correspond to the right side of *Cephalodiscus*.

A digression on the anatomy of *Cephalodiscus* is now necessary, before pursuing this comparison in detail. *Cephalodiscus* zooids (van der Horst 1935) normally live in bundles of horny tubes, but are capable of leaving the tubes to wander over the surface of the bundle. Each zooid consists of three parts, which can be called protosome (head shield) (prs in text-fig. 18B), mesosome (collar), and metasome (trunk), and the metasome is extended to form a stem (st), at whose distal end buds are produced (not shown in text-fig. 18B).

The protosome contains an unpaired coelom, the protoel. It also contains, in a dorsal position, the pericardial vesicle and heart, the buccal diverticulum (bd) ('notochord', 'stomochord') and an excretory glomerulus. A right and a left protoel pore (h_1), lateral to the heart, connect the protoel with the outside.

The mesosome contains a right and left coelom, the mesocoels, separated by a mesentery. It carries a right and a left array of tentacles and each tentacle contains an extension of the mesocoel of the same side. Down the ventral side of each tentacle runs a food groove to the region of the mouth. A ganglion (ga) is situated dorsally in the mesosome, in the mid-line, between the right and the left sets of tentacles. Right and left mesocoels open to the outside, each by a separate mesocoel pore (h_2). The mouth (m) is slit-shaped, and lies ventrally, between protosome and mesosome.



TEXT-FIG. 18. Homologies between *Ceratocystis perneri* (A) and the living hemichordate *Cephalodiscus* (B): an = anus; axg = axial gland; bd = buccal diverticulum; br = brain; bs = branchial slits; dnc = dorsal nerve cord; ga = mesosomal ganglion of *Cephalodiscus*; h = hydropore; h₁ = protocoel pore; h₂ = mesocoel pore; m = mouth; prs = protosome; st = stem; stn = peduncular nerve.

The metasome contains a right and a left coelom, the metacoels, separated by a mesentery. It also carries the whole of the gut behind the buccal cavity, and the gonads. The gut is U-shaped and consists of buccal cavity, pharynx, oesophagus, stomach, and intestine. Right and left walls of the pharynx are each penetrated by a single gill slit (bs). There are 2 gonads, one in the left and one in the right metacoel, and each opens by a single gonopore (g) to the outside.

The stem is muscular and highly innervated particularly on its ventral side (peduncular nerve stn). The coelom of the stem is an extension of the right and left metacoels, which in the stem of *Cephalodiscus* itself are not separated by mesenteries. In the related *Rhabdopleura*, however, the mesentery separating right and left metacoels continues to the end of the stem.

Animals of *Cephalodiscus* type have probably existed for a very long time. The fossil remains of *Eocephalodiscus*, described by Kozłowski (1948, p. 195), from the Tremadoc of Poland, differ very little from the skeletons of recent *Cephalodiscus* colonies. Also Kozłowski has argued (1947, 1966) that graptolites were pterobranchs, and the first graptolites are known from the Middle Cambrian (Obut 1964, p. 306).

The homologies of pterobranchs and echinoderms can be expressed in a table.

<i>Pterobranch</i>	—————	<i>Echinoderm</i>
protoceol	—————	axocoel
left protoceol pore	—————	hydropore (in part)
right protoceol pore	—————	absent
glomerulus	—————	main portion of axial gland
pericardium	—————	dorsal sac
heart	—————	head process of axial organ
buccal diverticulum	—————	absent
left mesocoel	—————	hydrocoel
left mesocoel pore	—————	hydropore (in part)
right mesocoel	—————	reduced or absent
right mesocoel pore	—————	absent
mesosome ganglion	—————	absent
left metacoel	—————	left (oral) somatocoel
right metacoel	—————	right (aboral) somatocoel
left gonopore	—————	gonopore
left gonad	—————	gonad or gonads
right gonopore	—————	absent
right gonad	—————	absent
stem	—————	stem
right metacoel extension into stem	—————	coelom of chambered organ
left metacoel extension into stem	—————	absent
innervation of stem	—————	peduncular nerve

These homologies are based largely on the discussion given by Fedotov (1924, p. 298) except that his assertion that the pericardial sac is a right antimere of the protoceol is disregarded. Also the stem homologies given here never seem to have been proposed before. It is here assumed that the hydropore of echinoids represents the fusion of the protoceol and metacoel pores of the left side of a pterobranch, instead of corresponding to one rather than the other.

It is interesting that Grobber (1924) derived echinoderms from a pterobranch that came to rest on its right side. His views on the changes involved are unnecessarily complicated, however, by his attempt to derive the echinoderm stem from the region of the hemichordate protosome. Other authors such as Bather (1900) have derived echinoderms from an essentially hemichordate and bilateral '*dipleurula*' ancestor that came to rest on its right side. The conclusion that the bilateral ancestor of echinoderms lay down on its right side is based on the absence in echinoderms of the right protoceol pore, right mesocoel pore, and right gonopore and the reduction of the right mesocoel as

compared with the left mesocoel. Also, if a pterobranch lay on its right side, the food grooves of the right tentacles would touch the sea floor, and so would become useless and disappear, while the food grooves of the left tentacles would face upwards. The absence of the originally right mesocoel and tentacles, and the upward orientation of the food grooves of the remaining, originally left, tentacles are observed features of stemmed echinoderms.

Returning now to the comparison between *Ceratocystis* and *Cephalodiscus*, the similarity can be expressed by saying that, starting from the stem of either, and proceeding clockwise round text-fig. 18A and B one passes in succession: (1) the branchial slits (bs), (2) the mouth (m), (3) the hydropore (h) or equivalent protoceol pore (h_1) and mesocoel pore (h_2), (4) the gonopore (g), and (5) the anus (an).

There are many obvious differences between *Cephalodiscus* and *Ceratocystis*. Thus *Cephalodiscus*: (1) Lacks a calcite skeleton; (2) has paired tentacles; (3) has paired protoceol and mesocoel pores, instead of a single hydropore; (4) has paired gonopores, instead of one only; (5) has a relatively smaller buccal cavity; (6) has a small pharynx with a single pair of gill slits, instead of a large pharynx with seven gill slits on the originally left (= dorsal) side; (7) has the anus, gonopores and equivalents of the hydropore much further from the stem; (8) has an important ganglion near the tentacles which, so far as known, is unrepresented in *Ceratocystis*; (9) has the stem coelom continuous with the coelom of the trunk (metacoel) instead of separated from it; (10) has no big ganglion at the proximal end of the stem; (11) has the metacoels paired and equal, by contrast with the probably equivalent, anterior and posterior coeloms of *Ceratocystis*, one of which is nearer the stem than the other. Most of these differences would represent either the loss by *Ceratocystis* of organs present in *Cephalodiscus* or else changes in the relative sizes of parts.

C. perneri shares with stemmed echinoderms many of the features which separate it from *Cephalodiscus*. The most important of such features are: (1) the calcite skeleton; (2) the position of one perivisceral coelom (right somatocoel, posterior coelom) nearer the stem than the other (left somatocoel, anterior coelom); (3) the separation of the stem coelom (coelom of the chambered organ, cavity of the notochord) from the perivisceral coelom; (4) the presence of an important ganglion at the proximal end of the stem (aboral nerve centre, brain); (5) the presence of a single hydropore (cf. cystoids), instead of paired protoceol and mesocoel pores; (6) the singleness of the gonopore (cf. cystoids).

These common features suggest that stemmed echinoderms and calcichordates have a common ancestor more recent than the common ancestor of both with *Cephalodiscus*. Also this more recent common ancestor would resemble a calcite-plated hemichordate that habitually rested on its right side.

The resemblances and differences between *Cephalodiscus*, stemmed echinoderms and *Ceratocystis* suggest the following evolutionary history. A population of Lower Cambrian animals resembling *Cephalodiscus* vacated, as *Cephalodiscus* can, the tubes in which they had normally dwelt. They took to moving over the sea floor, by the action of their muscular stems, lying on the right side of their bodies. Because of this orientation they lost the body openings of the right side, i.e. right gill slit, right protoceol pore, right mesocoel pore, and right gonopore. Further, the right tentacles found themselves with the food grooves forced downwards into the sea-floor and so became useless

and disappeared. The left tentacles found themselves with food grooves upwards and were retained. At about this time the left proto-coel pore and left mesocoel pore fused together to form a hydropore, the calcite skeleton appeared, the metacoels lost their simple paired arrangement, so that the right metacoel came nearer the stem than the left metacoel, and alone provided the stem coelom. This stem coelom then became separate from the right metacoel in the adult, so that the stem could now be bent without being shortened or lengthened, and a large ganglion evolved at its proximal end.

Evolution now proceeded in two directions. One population specialized in tentacle feeding and lost the gill slits. It gave rise to the stemmed echinoderms. Some of these lifted the mouth upwards, so that the left somatocoel came to overlie the right somatocoel and the hydropore, gonopore and anus came to be arranged in a vertical plane, as in cystoids. Another population specialized in pharyngeal feeding and lost the tentacles. This group gave rise to the calcichordates, including *Ceratocystis*. The expansion in the size of the buccal cavity and pharynx, and the increase in the number of gill slits and their migration to the downstream end of the pharynx, were adaptations for producing a more powerful pharyngeal current. The originally U-shaped gut, which may have been an adaptation to the original tubicolous habit, had been lost at some stage in the sequence described.

CALCICHORDATES AND OTHER CHORDATES

The present work does not much modify the picture previously given (Jefferies 1968, p. 331) of the evolution of the extant chordate subphyla from the Calcichordata. However, the beginnings of the acoustic part of the acustico-lateralis system seem already to have existed in mitrates; also, the left atrium of mitrates received a gonoduct as well as the rectum, and the heart and pericardium already existed in the anterior coelom. It is possible, also, that the pituitary or neural gland may have existed in mitrates, having been derived from the axial gland, and that the gill slits in mitrates may have numbered about seven on each side.

CONCLUSIONS

1. *Ceratocystis perneri* is here interpreted as the oldest chordate known, and the oldest known member of the order Cornuta. It had affinities with echinoderms, but is best regarded as a chordate; from it, or from very similar unknown forms, all later chordates are probably descended.
2. The bellows system of pumping water through the pharynx, which is well developed in later cornutes, had already begun to appear in *C. perneri*.
3. *C. perneri* had 7 gill slits, and this was probably the primitive number for cornutes, and therefore for chordates in general.
4. *C. perneri* possessed mouth, hydropore, gonopore, and anus arranged in the same order as in primitive stemmed echinoderms such as cystoids. Gonopore and anus also existed in the later cornute *Cothurnocystis*, in which rectum and gonoduct had come to be disposed fundamentally as in modern enterogonous tunicates.
5. The thecal cavity of *C. perneri*, like that of later cornutes, was divided into buccal cavity, pharynx, anterior coelom, and posterior coelom.
6. The anterior coelom of *C. perneri* would have contained, near the hydropore,

a heart and a pericardium. These resembled in position, and were presumably homologous with, the heart and pericardium of other chordates. They were also homologous with the heart and pericardium of living hemichordates and the head process of the axial organ and dorsal sac of living echinoderms.

7. The main portion of the axial organ of echinoderms may be homologous with the neural gland of tunicates and the pituitary gland of vertebrates.

8. The stem of *C. perneri* did not differ fundamentally from that of later cornutes. The anterior stem, contrary to Ubaghs (1967), was regularly tetraserial.

9. The brain of *C. perneri* had paired olfactory dorsal lobes, homologous with the telencephalon of vertebrates, and a dorsal median eye which was not homologous with the median eyes of vertebrates. Paired pyriform bodies (trigeminal ganglia) existed as in later calcichordates. A lateral line was already developed in *C. perneri*, and evidence suggests that the acustico-lateralis system of some mitrate calcichordates was already divided into acoustic and lateral-line subsystems. The blood supply to the stem of *C. perneri* must have gone through the middle of the brain.

10. *C. perneri* lay habitually on its ventral side, and could drag itself backwards by side-to-side wagging of the stem. It was a deposit feeder.

11. The reconstructed anatomy of *C. perneri* can be compared with the anatomy of a modern pterobranch hemichordate lying on its right side. On this comparison the stem of hemichordates would correspond to the stem of stemmed echinoderms and calcichordates and to the tail of other chordates. The extension of the right metacoel into the hemichordate stem would be homologous with the chambered organ of stemmed echinoderms and the notochord of chordates. It is suggested that a population of Cambrian pterobranchs took to wandering over the sea floor with right side downwards and acquired calcite skeletons. This population gave rise to the echinoderms, by elaboration of the tentacles and loss of the gill slits, and to the chordates, by loss of the tentacles and elaboration of the gill slits.

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R. P. S. JEFFERIES
Department of Palaeontology
British Museum (Natural History)
Cromwell Road
London, S.W.7

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