THE SOLUTE *DENDROCYSTOIDES SCOTICUS* FROM THE UPPER ORDOVICIAN OF SCOTLAND AND THE ANCESTRY OF CHORDATES AND ECHINODERMS

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ABSTRACT. A study of the solute *Dendrocystoides scoticus* (Bather), from the Upper Ordovician Ashgill Series, near Girvan, Scotland produces much new anatomical information. The positions of head, tail, the tube feet in the feeding arm, hydropore, gonopore, gonad, pharynx, stomach, anus, brain, left trigeminal ganglion, gill slit (at posterior left in the head), notochord, and tail muscles are deduced. In their basic structure, solutes resemble cornutes, especially the primitive cornute *Ceratocystis*, but differ in retaining a water vascular system, and in other ways. They can be compared in detail with the inferred latest common ancestor of chordates and echinoderms, visualized as resembling the hemichordate *Cephalodiscus* lying on its right side. The tail of solutes is almost certainly homologous with that of cornutes, and therefore with the tail of chordates in general. It is also probably homologous with the locomotory stalk of *Cephalodiscus*. If so, the tail (= stalk) was lost early in the evolution of the Echinodermata, while the water vascular system was lost in the early evolution of the Chordata. The Soluta, if characterized as retaining both a tail and a water vascular system, would therefore have included the latest common ancestor of chordates and echinoderms.

Dendrocystoides scoticus probably belonged to the stem group of the Chordata, on the basis of several advanced features shared with Cornuta including, especially, the posterior left position of the gill slit. The 'carpoids' placed in the group Cincta, on the other hand, probably belonged to the echinoderm stem group but were primitive for echinoderms in possessing a gill slit, located in an anterior, presumably primitive, position like the left gill slit of *Cephalodiscus*. If the tail of solutes is homologous with the tail of cornutes, then the latter organ, contrary to the 'aulacophore' interpretation of Ubaghs, cannot be a feeding arm.

THE aim of this paper is to determine the phylogenetic, and therefore systematic, position of the Soluta. These are a group of strange fossils which are characterized by a feeding arm at one end of the animal and a different appendage (in my view a locomotory tail) at the other end. They have a calcite skeleton of echinoderm type but lack any trace of radial symmetry and for this reason are traditionally placed in the 'carpoid echinoderms'. They are found in marine rocks of Lower Cambrian to Devonian age and comprise 15 described species placed in 13 genera.

I approach the problem of the systematic position of the solutes by a detailed anatomical study of one species, the late Ordovician *Dendrocystoides scoticus* (Bather), chosen because it is abundant in accessible collections. It is the only species in its genus but is very similar to *Dendrocystites* Barrande 1887 from the Ordovician of Czechoslovakia, differing mainly in having a better developed anti-brachial process. My studies convince me that the solutes are built on the same basic plan as the stem-group chordates known as Cornuta. I also believe, however, that the latest common ancestor of the echinoderms and chordates, if it were ever found, would be regarded as a solute. This means that the Soluta, characterized by the possession of a locomotory tail and a feeding arm, straddle the phylogenetic separation between chordates and echinoderms, which gives them the status of an invalid stem group of the Dexiothetica ('unechte Stammgruppe' to use the expression of Hennig 1969). Further work will be needed to decide which of them belong to the true stem group of the Dexiothetica, which of them can be assigned to the stem group of the chordates or of the echinoderms, and which of them, being close in systematic position to the latest common ancestor of chordates and echinoderms, should remain in the nodal group of the Dexiothetica.

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The conclusion, presented in this paper, that the solute tail is homologous with the cornute tail, is important to the general morphological interpretation of cornutes, since the solutes possess, in addition to this tail, an appendage clearly homologous with an echinoderm feeding arm. In such case, as Paul (1977, p. 126) pointed out, the cornute tail, contrary to the view of Ubaghs (1968) and Parsley (1988), cannot itself be a feeding arm. In a different direction, I shall argue that the tail of solutes is homologous with the locomotory and prehensile stalk of hemichordates such as *Cephalodiscus*. If so, and if the hemichordates include, or else constitute, the extant sister group of the Dexiothetica, then the latest common ancestor of echinoderms and chordates would have had such a tail. And the echinoderms, as an autapomorphy of the group Echinodermata, would have lost this organ (contrary to the view expressed in Jefferies 1988, p. 11). It follows that the mere possession of a stalk or tail does not characterize an animal as a chordate.

Which way up the solutes lay in life is a matter of dispute. Bather (1913, p. 505) and Caster (1968) oriented the animal with the arm on the left, if the tail is towards the observer, and accordingly spoke of an obverse face (presumably upper) and a reverse face (presumably lower). Kolata, Strimple and Levorson (1977), however, considered it more likely, on functional grounds, that the solutes lay the other way up and used 'aboral' for the presumed upper and 'oral' for the presumed lower surface. I agree with Kolata's orientation of the solutes, partly on functional grounds and partly because it agrees with the likely orientation, accepted by all workers, of the cornutes. I use 'dorsal' for the presumed upper and 'ventral' for the presumed lower surface. These terms, for me, are intended to imply homology with 'dorsal' and 'ventral' in chordates, but not with 'dorsal' and 'ventral' in echinoderms where the terms mean the exact opposite to what they do in chordates (Jefferies, Lewis and Donovan 1987, p. 474). For me, therefore, 'left' and 'right' in solutes mean the opposite of what they did for Caster (1968).

I studied *Dendrocystoides scoticus* by reconstructing it on a drawing board, as with previous studies done in the British Museum (Natural History) (Jefferies 1968, 1969, 1973; Jefferies and Lewis 1978; Jefferies and Prokop 1972; Jefferies *et al.* 1987; Craske and Jefferies 1989; Cripps 1988, 1989*a*, *b*, in press). Six different projections (dorsal, ventral, right, left, posterior, anterior) were drawn simultaneously, firstly of the outside and then of the superficial internal anatomy of the animal. The reconstruction was difficult since the fossils, although numerous, are all incomplete. Moreover *D. scoticus* changed shape as it grew and the plating was largely irregular.

The reconstruction of the external shape was largely based on latex casts, but silicone rubber casts were sometimes taken by pressing part and counterpart together against silicone rubber (Wacker RTV-M531 with catalyst T461). The superficial internal anatomy was reconstructed on the basis of internal moulds which, being negatives of the skeleton, can be regarded as positives of the soft parts. The *in vivo* shape of certain parts of the skeleton was reconstructed using large cardboard replicas of the plates and fixing them together with masking tape.

SYSTEMATIC PALAEONTOLOGY

Superphylum DEUTEROSTOMIA Grobben, 1908
Subsuperphylum DEXIOTHETICA Jefferies, 1979
?Phylum CHORDATA Bateson, 1886

(If a chordate, then stem group of the Chordata)

SOLUTA Jaekel, 1900 (invalid stem group of the Dexiothetica)
Genus *Dendrocystoides* Jaekel 1918
Species *Dendrocystoides scoticus* (Bather 1913)

Remarks. Dendrocystoides scoticus is probably a stem-group chordate, as argued below, though at present this conclusion is tentative. It is certain, on the other hand, that *D. scoticus* is a solute, if the Soluta are characterized as a group retaining both a feeding arm and a tail. On the other hand, the position of the Soluta, straddled across the phylogenetic separation of the Echinodermata and Chordata, makes them an invalid stem group of the Dexiothetica which further research will probably break down. These uncertainties explain the disorderliness of the above systematic 'address'. Ax (1984, 1987) has argued that Linnaean categorial ranks above the species level are arbitrary and ought to be discontinued, except for the genus which is necessary for nomenclatorial reasons. I agree with Ax on this (Craske and Jefferies 1989) and the ranks assigned above are purely traditional (superphylum, phylum) or got by interpolation (subsuperphylum). The group Soluta, set up by Jaekel (1900) as a suborder, is exactly coextensive with the Homoistelea, set up by Gill and Caster (1960) as a subclass and raised by Caster (1968) to the rank of class, Since Linnaean categorial ranks are arbitrary, not real, the difference between Homoiostelea and Soluta is purely conventional and the term 'Homoiostelea', being younger than 'Soluta', ought to be abandoned.

Dendrocystoides scoticus (Bather 1913)

Plates 1–7; text-figures 2–11, 21

1913	*Dendrocystis scotica* Bather; Bather, p. 391.
1913	*Dendrocystis scotica*; Woodward, p. 421, 423
1918	*Dendrocystoides scoticus* Bather sp.; Jaekel, p. 123.
1920	*Dendrocystis scotica*; Hawkins, p. 134.
1925	*Dendrocystis scotica*; Bather, p. 5.
1928	*Dendrocystis scotica*; Bather, p. 5.
1929	*Dendrocystis scotica*; Bather, p. 34.
1932	*Dendrocystis scotica*; Hennig, p. 170.
1934	*Dendrocystoides scotica* (Bather); Dehm, p. 39.
1937	*Dendrocystis scotica*; Woods, p. 175.
1938	*Dendrocystis scotica*; Bassler, p. 85, as type species of *Dendrocystoides* Jaekel 1918.
1941	*Dendrocystis scotica* Bather; Chauvel, p. 241.
1943	*Dendrocystoides scoticus* (Bather); Bassler and Moody, p. 150.
1947	*Dendrocystis scotica* Bather; Begg, p. 30.
1948	*Dendrocystis scotica*; Cuénot, p. 14.
1960	*Dendrocystis scotica*; Špinar, p. 668.
1960	*Dendrocystis scotica*; Termier and Termier, p. 87.
1965	*Dendrocystoides scotica*; Parsley and Caster, p. 162.
1968	*Dendrocystoides scoticus* (Bather); Caster, p. S587.
1982	*Dendrocystoides scoticus* (Bather); Meléndez, p. 688.

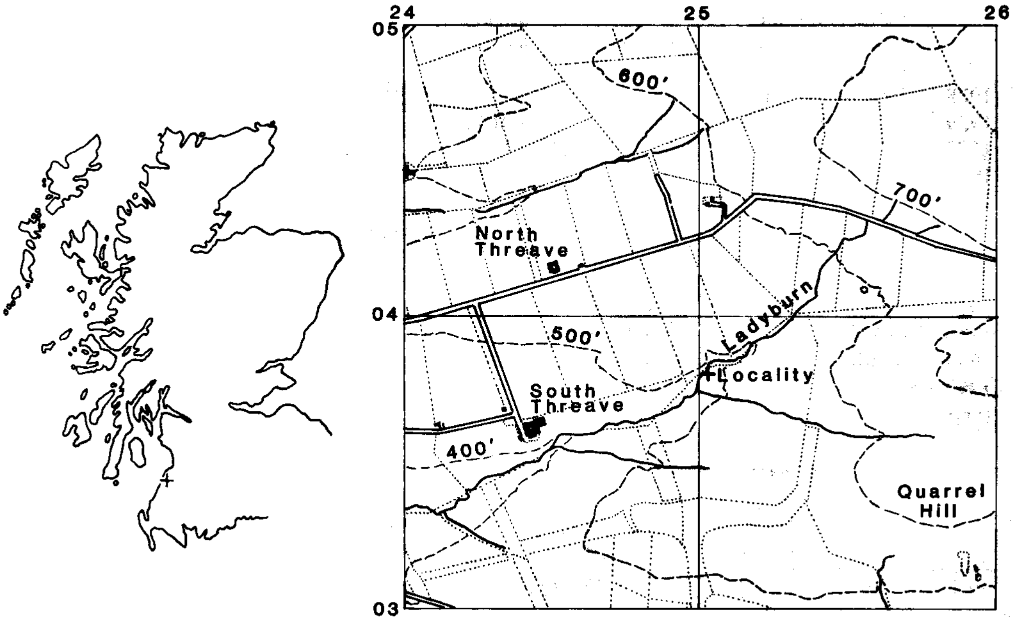
Comments on synonymy. Dendrocystoides scoticus is the only known species of its genus and is also the type species by original designation (Jaekel 1918, p. 123). *Dendrocystis* Bather 1889 is an objective junior synonym of *Dendrocystites* Barrande 1887, of which the type species is *Cystidea sedgwicki* Barrande 1867.

D. scoticus is a famous animal and Bather's reconstruction of it (1913, text-fig. 8, p. 374) has been quoted in many text books and general works without mentioning the trivial name. Such citations are not included in the above list.

History of study. The anatomy of *D. scoticus* has previously been dealt with in two important works: Bather (1913) and Caster (1968). Bather's most notable contribution was to discover the anus for the first time in solutes. Caster was responsible for a number of striking advances: he was the first to discover the pore nodes (hydropore node and gonopore node) in this species and he noted prominences which he called 'horns', though he gave no clear account of their position and relations. He also greatly clarified the systematic situation by distinguishing between *D. scoticus* Bather and the very different solute *Girvanicystis batheri* Caster which occurs in the same bed.

Material. The material examined is as follows: British Museum (Natural History): Gray Collection, E166220–E16223, E23195–E23200, E23202–E23215 (including holotype E23207), E23217–E23231, E23233–E23244, E23246–E23247, E23249–E23255, E23257–E23259, E23289, E23339, E23346–E23348, E23351, E23459, E23461, E23466, E23472, E23700, E23714, E23718, E23759, E23762, E23764, E23765, E23768, E23769, E28410–E28416, E28418, E28422, E28423, E28426, E28428, E28432–E28435, E28438–E28450, E28452–E28456, E28459, E28460, E28463–E28478, E28481, E28483–E28507, E28511, E28513–E28515, E28517, E28519, E28521–E28529, E28531–E28538, E28540–E28550, E28556, E28557, E28576–E28583, E28585–E28589, E28592–E28596, E28598–E28602, E28760–E28821, E28823, E28825–E28830, E28832–E28836, E28838–E28851, E28853, E28854, E28856–E28860, E28863–E28872, E28874–E28880, E29602–E29609, E52763, E52765, E52870, E62619, E62620, E62622–E62626, E62754, E62755; L. R. M. Cocks Collection, E29365; A. B. Smith Collection, E62521–E62533, E62537; R. P. Tripp Collection, E62778–E62779. Hunterian Museum, Glasgow: E5718, E5719, E5722–E5725, E5729–E5732, E5734–E5736, E5738, E5777, E5778, E5782, E5789, E5792, E5794, E5795, E5797, E5798, E5801–E5803, E5820–E5823, E5826, E5827, E5842, E5856, E5890, E5892, E5893, E5914, E5915, E5947. The total number of specimens examined was 399 and the number of individuals was rather greater than this.

Horizon and locality. All of the specimens examined were from the famous Starfish Bed of the Upper Ordovician Ashgill Series, near Girvan, Scotland. The locality is S6 of Harper (1982, p. 265) which is at National Grid reference NS 2503 0379 on the south bank of the stream called Ladyburn. The valley in which the Ladyburn flows is sometimes called Threave (or Thraive) Glen. For details see Harper (1981, p. 28) and text-fig. 1 herein. This locality is about 8·5 km NE of the church at Girvan (formerly in Ayrshire, now in Stratchclyde Region, Scotland).



TEXT-FIG. 1. General position and detailed map of the Starfish Bed locality (S6 of Harper 1982). Locality map traced from Ordnance Survey 1:25000, sheet NS20, Dailly. The dotted lines are field boundaries (stone walls).

According to Harper (1981), the Ladyburn Starfish Bed at this locality is 48 cm thick and divided into three beds (a, b, and c). The lowest of these (Bed a) is 22 cm thick, the famous Starfish Bed of the Gray family and it probably yielded most of the known fossils. Bed b is about 10 cm thick and relatively unfossiliferous, while Bed c is 15 cm thick and contains abundant fossils, though it is not so productive as Bed a. Stratigraphically, the Starfish Bed is near the top of the Farden Member of the South Threave Formation of the Drummuck Group and belongs to the topmost part of the Rawtheyan Stage of the Ashgill Series (Harper 1984, p. 3).

The matrix of the fossils is a greenish silty sandstone. A considerable clay-grade admixture accounts for the good histological detail of the preserved fossils. The calcite of the skeleton of *D. scoticus* has nearly always been dissolved so that the plates are now represented by rust-lined cavities in the rock.

As to conditions of deposition, the beautifully articulated condition of many of the fossils of the Starfish Bed suggests that they were killed by burial (obrution in Seilacher's terminology; see Goldring and Stephenson 1972, p. 612) or perhaps were buried immediately after death. Goldring and Stephenson considered that the Starfish Bed was laid down in shallow water, but Harper (1981) believed that the fossils did not normally live where they are now found, and that the rocks of the Ashgill Series near Girvan were deposited as a turbidite fan at the foot of the continental slope of a continent which lay NW of the Iapetus Ocean. This implies that the fossils of the Starfish Bed normally lived on the continental shelf north-west of where they are now found and died when they were carried south-eastwards, downslope and out to sea by turbidity currents.

It seems quite possible that the animals of the Ladyburn Starfish Bed were transported by turbidity currents, as Harper believes, shortly before they died. It seems unlikely that they were usually dead before burial, however. A particular reason for believing that they were killed by burial, as Goldring and Stephenson proposed, is seen in the cornute *Cothurnocystis elizae* (Jefferies 1968, p. 255), where the dorsal and ventral integuments are often separated from each other by a thin layer of rock behind the mouth and right of the strut in the head, but are in contact with each other farther away from the mouth, left of the strut. This suggests that the animal ingested a last mouthful of mud, before being killed. If after death it had then been tumbled about by turbidity currents on the sea floor, it seems almost certain that the mud inside the animal would have become evenly distributed, instead of being preferentially right of the strut as observed. I therefore believe that the articulated fossils of the Starfish Bed, such as *C. elizae* and *D. scoticus*, lived, at least for a few seconds, where they are now found, even if they had been transported downslope by a turbidity current just before death.

ANATOMICAL DESCRIPTION

General morphology

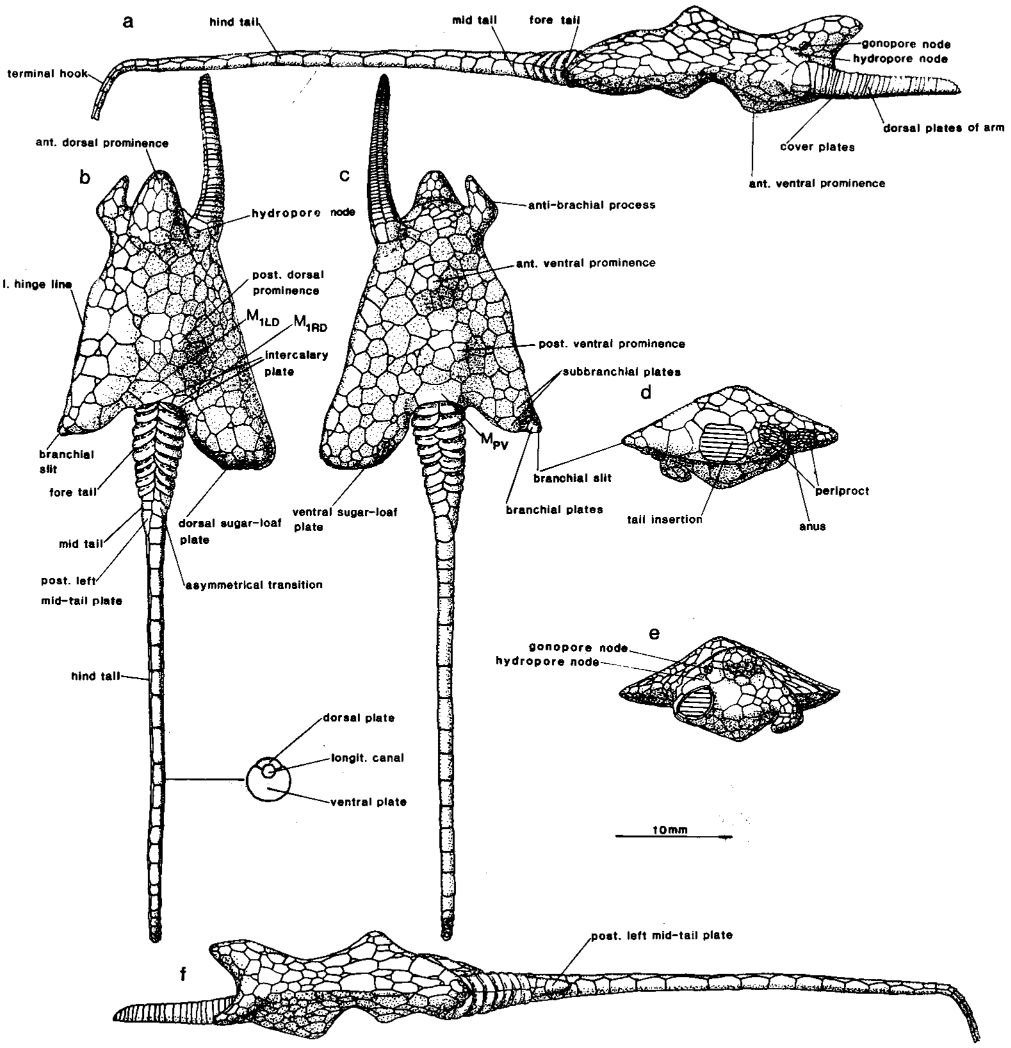
Dendrocystoides scoticus consists of a head, an arm and a tail. In the following description, I shall deal with the external anatomy first and the internal soft-part anatomy later. The main features of *D. scoticus*, in my view, can readily be compared with those of cornutes, as will gradually become clear from what follows. So far as possible, I therefore apply the cornute terminology which I have used in my previous work (see e.g. Jefferies 1986, Chap. 7). In this sense, for example, I use 'right', 'left', 'dorsal', 'ventral', 'anterior', 'posterior' and 'fore tail', 'mid tail' and 'hind tail'. When naming particular plates I use an objective notation, similar to that formerly applied to cornutes and mitrates (e.g. Jefferies 1968). In this notation: CP = cover plate of arm; D = dorsal plate of arm; M = marginal plate (of tail insertion); P = proximal plate of arm base; suffixes $_{1,2,3}$ etc. refer to position in a proximo-distal sequence; suffix $_{L}$ = left; suffix $_{R}$ = right; suffix $_{M}$ = median; suffix $_{A}$ = anterior; suffix $_{P}$ = posterior; suffix $_{D}$ = dorsal; suffix $_{V}$ = ventral.

The head is trapezium-shaped in dorsal aspect (text-fig. 2). The trapezium is widest near the posterior end of the head and becomes narrower anteriorly. The tail is inserted somewhat left of the middle of the posterior edge.

The size of *D. scoticus* can never be precisely measured in all aspects, partly because the specimens are incomplete and partly because the head was not rigid. One of the best-preserved individuals is E28768 in the BM(NH) (pl. 6, fig. 2). The total length was about 128 mm as preserved (the tail is incomplete), the head width was about 32 mm (the left side is missing), the arm was about 28 mm long, the head length was about 36 mm, and the tail length, so far as preserved, was 76 mm.

External features of the head. The head is approximately, but not accurately, bilaterally symmetrical. The most obvious departures from symmetry are that the arm is at anterior right, an antibrachial process is at anterior left, the right posterior lobe of the head (bearing the anus) is larger and more rounded than the left posterior lobe (the latter bearing, as I believe, a gill slit), and the left side of the head in dorsal aspect shows an obtuse lateral prominence, while no such prominence exists on the right.

The dorsal surface of the head is less flat than the ventral surface, though, in this respect, the difference between the two surfaces is less obvious in very large specimens (on which the reconstruction in text-fig. 2 is based; cf. pl. 1, figs. 1–3, text-fig. 4) than in smaller ones (pl. 1, figs. 4–8, text-fig. 4). On the dorsal surface there are an anterior and a posterior dorsal prominence. The anterior dorsal prominence is situated in the mid line between the base of the arm (on the right) and



TEXT-FIG. 2. *Dendrocystoides scoticus* Bather. Reconstruction of external features: (*a*) right lateral aspect; (*b*) dorsal aspect and transverse section of hind tail; (*c*) ventral; (*d*) posterior (omitting tail); (*e*) anterior (omitting arm); (*f*) left lateral.

the antibrachial process (on the left). In middle-sized individuals it is thimble-shaped and slopes equally in all directions (pl. 1, fig. 5, text-fig. 4). In large individuals, however, it projects strongly forwards, so that its anterior face is actually an overhang and visible in ventral aspect (text-fig. 2; pl. 1, fig. 3, text-fig. 4; pl. 6, figs. 2, 6, text-fig. 9), (text-fig. 2; pl. 1, fig. 3, text-fig. 4; pl. 6, figs 2, 6, text-fig. 9). The posterior dorsal prominence is situated somewhat right of the mid line. It is capped by a hemispherical plate (pl. 3, fig. 9; text-fig. 6) and usually slopes away from this plate in all directions at about 40°. Like the anterior prominence, the posterior prominence is most obvious in large individuals.

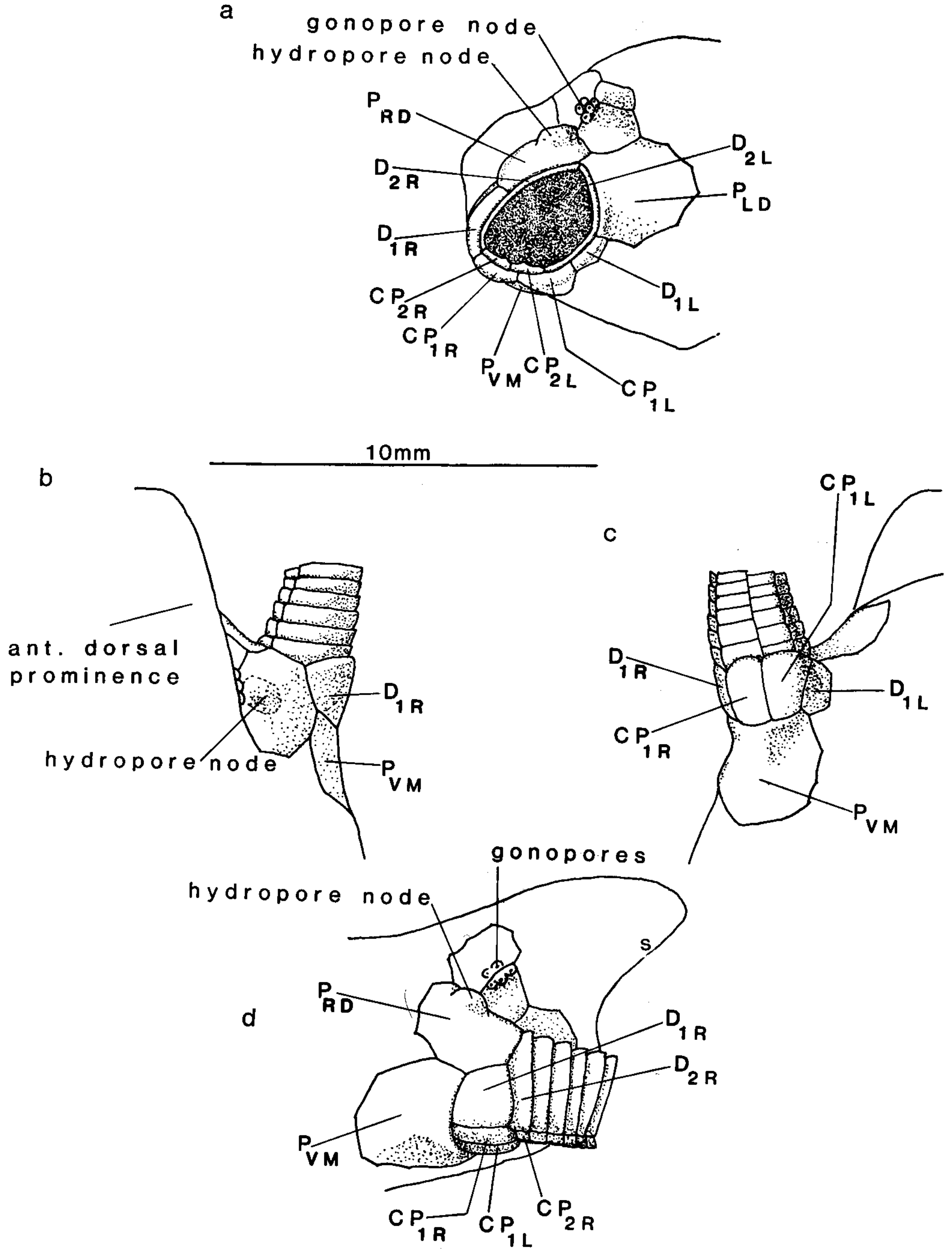
On the ventral surface, there are likewise anterior and posterior prominences. Especially in small and medium-sized individuals, however, these protrude much less than the dorsal prominences (pl. 1, fig. 5, text-fig. 4; pl. 6, fig. 4, text-fig. 9). Their summits approximately underlie the positions of the corresponding dorsal prominences, but are somewhat more posterior. Caster (1968, p. S591) referred to the anterior and posterior ventral prominences respectively as the distal and proximal obverse tumescences.

In transverse section through the head, dorsal and ventral surfaces meet at a sharp angle on the left, posterior to the obtuse lateral prominence already mentioned, and the plates of the respective surfaces meet at this edge along a rather straight line (text-fig. 2; pl. 7, figs. 1–5, text-fig. 10). This line probably functioned as a hinge, allowing the roof of the head to be raised and lowered slightly in this region. On the right side of the head, dorsal and ventral surfaces meet at a rounded contact in transverse section, with no sign of such a hinge.

The plates of the head skeleton are in general unspecialized and irregular. There are, however, some specialized and nameable plates, particularly at the arm base, at the tail insertion, in the anal region right of the tail and in the region of the gill slit left of the tail. These specialized plates will be described below when the respective parts are discussed.

The arm. The arm projects forwards and somewhat downwards from the anterior right extremity of the head (text-fig. 2; pl. 2, fig. 1, text-fig. 5; pl. 6, fig. 2, text-fig. 9). Its skeleton consists of four series of plates – two series of cover plates ventrally and two series of larger ‘flooring’ plates dorsally which, to avoid ambiguity, I shall refer to as dorsal plates. The exact length of the arm cannot be determined because it is never complete in the available specimens. The cover plates are shorter and more numerous than the dorsal plates, except in the proximal part of the arm, and there is no numerical correspondence between dorsal-plate and cover-plate series. The right and left cover plates exactly alternate with each other, whereas the right and left dorsal plates do not. The right and left cover-plate series meet at a smooth curve externally, without interdigitating, though the two series do interdigitate internally where the plates are complexly sculptured. Analogy with echinoderms suggest that the cover plates could open in life so that tube feet could emerge. The right and left dorsal series of plates, on the other hand, would have been flexibly but permanently held together at the dorsal edge of the arm. In transverse section (text-fig. 11e) the arm was not symmetrical for its dorsal edge was consistently leftward of the line of contact of right and left cover plates. The cover plates abut against each other, whereas the dorsal plates imbricate, each one being overlapped posteriorly by its more proximal neighbour. This imbrication would allow the arm to bend in life, especially upwards, rightwards and leftwards.

The plates of the arm-base region, as already mentioned, are specialized (text-fig. 3; pl. 2, fig. 2; pl. 5, figs. 3, 5, 6, text-fig. 8; pl. 6, figs. 5–7, text-fig. 9). The most proximal pair of cover plates, given the notation CP_{1L} and CP_{1R}, are much larger than more distal cover plates, some of which they strongly overlap. Right and left proximal cover plates meet each other at a flat suture and it is fairly certain that they could not open in life. This is shown by a pathological specimen (pl. 6, fig. 7, text-fig. 9) in which an extra plate is inserted distally between the two first cover plates and has formed with them a typical triple junction where the sutures meet at 120°. Such a junction shows that all three plates had always grown in mutual contact, without relative movement. The most proximal pair of dorsal plates (D_{1L}, D_{1R}) make broad contact with the most proximal cover plates, and differ from more distal dorsal plates in not meeting at the dorsal edge of the arm. Indeed, they stop dorsally far short of this edge, since the right one abuts dorsally against the right dorsal proximal plate of the arm base (P_{RD}) and the left one against the left dorsal proximal plate (P_{LD}). A third proximal plate, ventral and somewhat right of median in position with respect to the arm, is named the median ventral proximal plate (P_{VM}). It makes contact anteriorly with the two most proximal cover plates (CP_{1L}, CP_{1R}) and D_{1R}, while dorsally on the right it abuts against P_{RD}. On the left of the arm base, the gap between P_{VM} and P_{LD} is filled, behind D_{1L}, with two or three irregular plates. The right dorsal proximal plate (P_{RD}) carries a boss penetrated by small holes. The histological nature of this boss suggests that it is a node for hydropores (Caster 1968, fig. 372, p. S584) since its porosity resembles the madreporic plate of an echinoid. This suggestion is confirmed by the position of the boss near the mouth, since the latter presumably lay at the base of the arm, and the hydropore is the opening nearest the mouth in cystoids such as *Glyptosphaerites* (Jefferies 1986, fig. 7.18).



TEXT-FIG. 3. *Dendrocystoides scoticus*. External anatomy of arm-base region: (*a*) anterior aspect (arm omitted distal to D_{2R}); (*b*) dorsal; (*c*) ventral; (*d*) right lateral.

Anterior part of the head. Another set of openings is situated slightly above and left of the hydropore node, at the right base of the anterior dorsal prominence. These openings are variable. Each one is located at the summit of a small paraboloidal calcitic process. The number of these processes ranges from one to about six or seven and they are joined at their bases. The processes, with their pores, are sometimes grouped around the suture between two plates, but sometimes are situated in the middle of a plate. When best developed, the openings are obvious, circular and about 150 μm in diameter (pl. 5, fig. 3, text-fig. 8). Sometimes, however, a circular slight concavity of the same diameter is present at the distal end of a process but is not penetrated by a hole (pl. 5, figs 5, 6, text-fig. 8; pl. 6, fig. 5, text-fig. 9). Such blind processes give the impression that an opening which previously existed had been occluded with skeletal calcite during life. If the mouth was situated at the base of the arm, as seems likely on echinoderm analogies, then the pores now being discussed would be farther from the mouth than the hydropore is, since they do not penetrate one of the standardized plates of the arm base but are situated on, or between, the irregular plates just behind and above these.

The openings at the ends of the paraboloidal processes are probably gonopores. This is suggested by their position, since in cystoids such as *Glyptosphaerites* (Jefferies 1986, fig. 7–18, p. 217) the gonopore is consistently farther away from the mouth than is the hydropore. Also, if the openings were gonopores, their frequent occlusion could represent closure when not reproducing. If these openings were gonopores, then the anterior dorsal prominence of the head, at the base of which their canals emerge, probably represents the position of a gonad. As discussed later, the limits of the gonad seem to show on the surface of the natural internal mould. Despite special search, no feature was observed in these presumed gonopores which might have suggested separate sexes. I therefore cannot say whether this solute was dioecious or hermaphrodite.

The antibrachial process, situated at the left anterior extremity of the head, is, like the dorsal prominences, variable in shape and relative size. It is best developed in the largest specimens as shown in the reconstructions (text-figs. 2, 11) and in pl. 1, fig. 1 (text-fig. 4), and in these specimens it projects downwards, leftwards and forwards from the head. In some smaller specimens it is relatively small and projects leftwards (pl. 1, fig. 7, text-fig. 4). It is more prominent in *D. scoticus* than in any other known species of solute, although Bather (1889) records its presence, more weakly developed, in *Dendrocystites sedgwicki* (Barrande 1867) from the Upper Llandeilo Létna Formation of Czechoslovakia. By projecting downwards and forwards in *Dendrocystoides scoticus*, its shape and orientation are: (1) grossly the same as the arm, but on the opposite side of the head; and (2) reminiscent of the anterior appendages of cornutes, which probably functioned in locomotion to hinder forward movement and facilitate rearward movement (Jefferies 1986, p. 193). During locomotion, the arm and the antibrachial process of *D. scoticus* may well have functioned in a similar way to these cornute appendages, preventing the head from moving forwards during locomotion and helping it to slide rearwards. The position of the antibrachial process on the left side of the head suggests that it counterbalanced the arm in locomotion, resisting forces acting leftwards and forwards, whereas the arm would resist those acting rightwards and forwards.

The tail. The tail consists of three parts, the fore, the mid and the hind tail, and I believe that these regions are probably homologous with the like-named parts of the cornute tail.

The skeleton of the hind tail (text-fig. 2; pl. 6, figs. 2, 6, text-fig. 9; pl. 7, figs. 1, 2, text-fig. 10) consists of a dorsal and a ventral series of plates which between them enclose a distally tapering canal, circular in transverse section (text-fig. 2b). Except anteriorly towards the mid tail, the plates of the ventral series are thicker walled than those of the dorsal series and occupy much more of the external surface. Because of this, the canal is not central in a transverse section of the hind tail but located entirely dorsal to the centre. Dorsal and ventral plates tend to alternate in position and therefore would have interlocked. Consequently it seems almost certain that, in life, the hind tail was rigid in all directions.

At the posterior end of the hind tail there seems to have been a ventrally-directed rigid hook, ending abruptly, and the axis of the hook is at about 70° to the axis of the rest of the hind tail (text-fig. 2a, f; pl. 1, fig. 4). In the hook, the dorsal and ventral series of plates are more equally massive than anteriorly and the canal more nearly central in transverse section. A reason for doubt is that the hook as reconstructed is based on a single specimen only and this, as preserved, is not now connected to the rest of the tail. All the other specimens of the hind tail either end abruptly (pl. 6, fig. 6) or else, much more commonly, the tail runs over the edge of the block and is not seen. I believe, however, that the hook probably belongs to *D. scoticus* since it clearly is part of a solute and since Caster (1968, p. S709, fig. 382/4) has published a photograph of a similar terminal hook in *Dendrocystites barrandei* (Bather 1913), a species which in most respects is very similar to *Dendrocystoides scoticus*. Also Ubaghs (*in* Ubaghs and Robison 1985, figs. 1, 2, 8, 9; text-fig. 16a herein) has recorded a specialized terminal hook, in my view directed ventrally, in the tail of the American Middle Cambrian solute *Castericystis vali* Ubaghs and Robison 1985. Anteriorly in the hind tail of *D. scoticus* the ossicles shorten, both in the dorsal and the ventral series.

In the fore tail (text-fig. 2) the skeleton consisted of major and intercalary plates surrounding a large lumen. The major plates are in four series – right, dorsal and ventral, and left, dorsal and ventral. Each dorsal major plate is united at a suture (pl. 3, fig. 9, text-fig. 6; pl. 7, fig. 7, text-fig. 10) with a ventral major plate on the same side to form a C-shaped element built of two plates. Successive C-shaped elements have curved edges where they meet the dorsal and ventral mid-line of the tail, and these edges overlap, or are overlapped by, those of the C-shaped elements of the opposite side (pl. 3, fig. 9, text-fig. 6; pl. 6, figs. 2, 4, text-fig. 9). The number of C-shaped elements is about nine on both sides. The intercalary plates of the fore tail (pl. 1, fig. 9; pl. 6, fig. 2, text-fig. 9) are small and irregular and were evidently carried in a pliable, small-plated integument which connected the major plates together. They are most obvious near the anterior end of the fore tail, especially at the dorsal and ventral mid-lines. The exact shape of the major plates suggests that the foretail was able to flex, particularly rightwards and leftwards, but also up and down. The lumen of the fore tail was presumably largely filled with muscle and some anticompresional structure, probably a notochord, would be needed to allow flexion without telescoping. The quadriserial skeleton of the fore tail is comparable with that in most cornutes, particularly with the two least crownward of known cornutes *Ceratocystis perneri* and *Protocystites menevensis*, in which right and left ventral plates strongly overlap each other in the ventral mid line (text-fig. 14b; Jefferies 1986, p. 214; Jefferies *et al.* 1987, fig. 10b, p. 442).

The mid tail of *D. scoticus* has a complicated and rather irregular skeleton, transitional between the fore tail and hind tail (text-fig. 2). The dorsal hind-tail series of ossicles can be followed continuously forward into the right dorsal series of major plates in the fore tail (pl. 6, fig. 2, text-fig. 9). And the ventral hind-tail series of ossicles can likewise be followed forward into the right ventral series of major fore-tail plates (pl. 6, fig. 3, text-fig. 9; pl. 7, fig. 1, text-fig. 10). The left side of the mid tail is not comparable for it begins posteriorly with a single half-cone-shaped plate (the posterior left mid-tail plate; pl. 6, fig. 3, text-fig. 9; pl. 7, fig. 1, text-fig. 10) which is neither dorsal nor ventral in position, but left lateral. A dorsal and a ventral plate abut against this anteriorly, and are the posterior members of series leading respectively into the dorsal left and ventral left major plates of the fore tail.

This description of the transition between hind tail and fore tail differs from that of Caster (1968, pp. S583ff.) who considered that, in all solutes, the left ventral hind-tail series passed forward into either the left or right ventral fore-tail series, while the dorsal hind-tail series would pass forward into the diagonally opposite dorsal fore-tail series. In other words, if the ventral hind-tail series passed into the left ventral fore-tail series, then the dorsal hind-tail series would pass forward into the right dorsal fore-tail series and *vice versa*. Perhaps Caster's description is true for some solutes. It does not hold for *D. scoticus*.

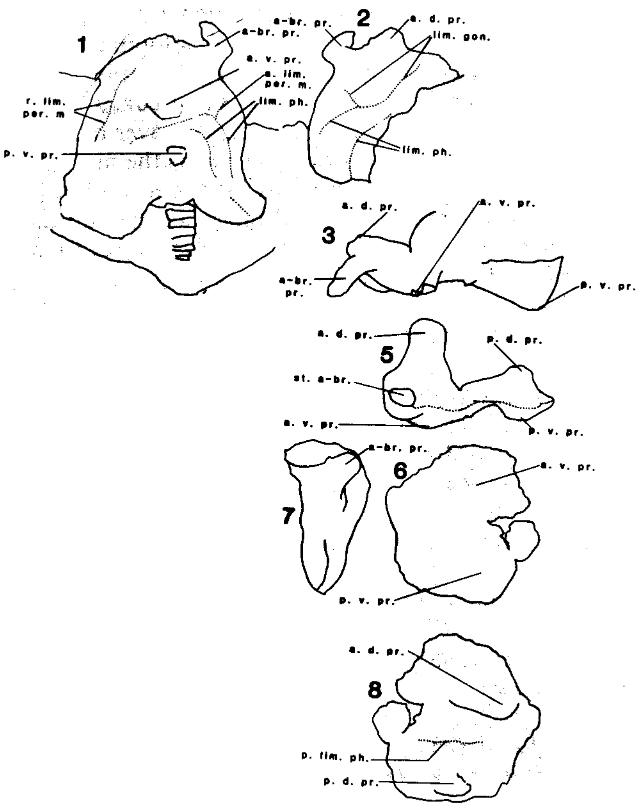
Ubaghs (1981) has argued that the tails of solutes are not homologous with those of cornutes and mitrates or, as he would say, the solute stele is not homologous with the cornute and mitrate aulacophore. This assertion reflects his view that the 'aulacophores' of cornutes and mitrates were feeding arms. In accordance with this view, he believes that what he calls the cover plates of cornutes could open to reveal a water-vascular system inside the appendage. (The Ubaghs school formerly asserted the same of the mitrate 'cover plates' but have since decided that such opening in the mid-line could not happen [Parsley 1982, 1988].) In support of his opinion that the tails of solutes are not homologous with those of cornutes, Ubaghs (1981, p.3ff.) has cited some genuine differences between them: (1) the hind-tail skeleton of solutes consists of an upper and lower series of ossicles, rather than a lower series of ossicles with paired 'cover plates'; (2) the mid-tail skeleton of solutes is made of many somewhat irregular plates whereas the mid tail of cornutes is dominated by a single element, the stylocone, with 'cover plates' above it; and, (3) the canal of the hind tail of solutes expands gradually into the funnel-shaped lumen of the mid tail which passes gradually, in turn, into the broad lumen of the fore tail, whereas in cornutes the lumen of the stylocone is sharply distinct from the canal of the more distal parts of the tail (although continuous with it). In my view these real differences do not show that the tails of solutes, cornutes and mitrates are not basically homologous. They merely show, as might be expected, that these organs are not in all ways the same.

The plates of the tail insertion (text-fig. 2; pl. 7, figs. 6, 7, text-fig. 10) do not seem to be completely standardised and the region was difficult to reconstruct since very few specimens show it in both ventral and dorsal aspect – most of the known specimens of *D. scoticus* are not preserved as part and counterpart. Normally there seem to have been seven plates: two large dorsal plates, which I classify as left and right first dorsal marginals with the notation M_{1LD} and M_{1RD}, one large posterior median ventral plate (M_{PV}), and sometimes two smaller marginal plates on the left and the right, dorsal and ventral to each other – M_{2RD} and M_{RV} on the right and M_{2LD} and M_{LV} on the left. I am doubtful whether these smaller marginal plates always number two on each side, or whether there may not sometimes be one less or one more. The internal structure of the plates of the tail insertion will be discussed below. Caster (1968, p. S592) referred to the plates of the tail insertion as the adsteleal girdle.

Posterior part of the head. As to the head openings, the gonopores and hydropores have been described already and the position of the mouth, at the base of the arm, has been implied. Two openings remain to be discussed, the anus on the posterior face of the posterior right lobe of the head, and a gill slit, as I believe, at the end of the posterior left lobe of the head.

I describe the anus first. As already mentioned, it was discovered by Bather (1913, p. 393) in *D. scoticus* for the first time in solutes. It is surrounded by an anal pyramid of long spike-shaped plates and this pyramid is set in a horizontally elongate periproct which was evidently flexible in life, and is armoured with numerous small plates (pl. 5, figs. 2, 4, text-fig. 8). The periproctal plates left of the anus are markedly elongate in a horizontal direction which suggests that the periproct here would sometimes bow outwards as part of a horizontal cylinder, which probably implies that the roof of the head could be pulled here towards the floor. Right of the anal pyramid, the periproctal plates are also horizontally elongate, but not to the same extent, which suggests that the roof here could be depressed, but not so much as left of the pyramid. The frame of the periproct is not well defined, since the integument plates tend to decrease in size towards the periproct. These framing plates tend to be imbricate, whereby the large ones outside the periproct overlap the peripheral plates of the periproct itself. Just to the right of the anus, both dorsally and ventrally, an individualised framing plate larger than its neighbours is present, which Bather called the sugar-loaf plate because of its outline. Hence there are a dorsal and a ventral sugar-loaf plate (pl. 5, figs. 2, 4, text-fig. 8; pl. 6, figs. 2, 3, 6, text-fig. 9; pl. 7, figs. 6, 7, text-fig. 10). At the sugar-loaf plates the frame of the periproct projects posteriorly. Perhaps these two plates helped the anus to protrude posteriorly during defaecation.

If a gill slit existed in *D. scoticus* we would expect, on cornute analogies, that it would be located near the left posterior angle of the head. As it happens, this region is difficult to reconstruct because few specimens show both part and counterpart and the region has usually been crushed on burial. Some specimens, however, show that there was an area of small plates in this region surrounded by a frame of larger plates (pl. 3, figs. 1, 2, text-fig. 6; pl. 7, fig. 5, text-fig. 10). The frame was made up ventrally of two or three rather thick, ventrally convex plates (subbranchial plates, pl. 3, fig. 2,



TEXT-FIG. 4. *Dendrocystoides scoticus*. Half-scale outline drawings of figs. 1–3 and 5–8 of pl. 1. Each drawing has the same number as the corresponding photograph on the plate; a.-br. pr. = antibrachial process; a. d. pr. = anterior dorsal prominence; a. lim. per. m. = anterior limit of peripheral muscle; a. v. pr. = anterior ventral prominence; lim. g. = limit of gonad; lim. ph. = limit of pharynx; p. d. pr. = posterior dorsal process; p. lim. ph. = posterior limit of pharynx; p. v. pr. = posterior ventral process; r. lim. per. m. = right limit of peripheral muscle; st. a.-br. = stump of antibrachial process.

EXPLANATION OF PLATE 1

Figs. 1–13. *Dendrocystoides scoticus*. 1–3, Hunterian Museum, E5890; ×1·2. Internal mould of head and external mould of part of fore tail; 1, ventral aspect; 2, dorsal aspect; 3, left lateral aspect; see also text-figs. 4/1, 2, 3.4, BM(NH), E29609; ×1·2. Latex of terminal hook of hind tail in left lateral aspect (determination as *D. scoticus* not certain); th = terminal hook; cr = crinoid stem on same block. 5–8, BM(NH) E23339, ×2. Natural internal mould of head (figs. 5–7) and latex of anterior left portion of head (fig. 8). See text-fig. 4 (5–8). The presence of an antibrachial process and the anterior dorsal prominence on one and the same specimen shows that these structures are different. 9, BM(NH) E28529, ×5. Natural internal and external mould of posterior part of head and adjacent fore-tail region in ventral aspect to show, especially, the left pyriform body in ventral aspect (lpb). 10, BM(NH) E28470, ×5. Natural internal mould of posterior part of head and adjacent fore-tail region in ventral aspect to show, especially the brain (br) in undissected condition. 11, BM(NH) E28494, ×5. Natural internal mould of posterior part of head (plate M_{PV}) to show cast of brain in contact with M_{PV}, so far as it can be revealed by dissection. 12,13, BM(NH) E28416; 12 ×2; 13, detail, ×5. Natural mould, mainly external, of posterior part of head, fore tail and mid tail in dorsal aspect, to show especially the left pyriform body (lpb) as an internal mould.

PLATE 1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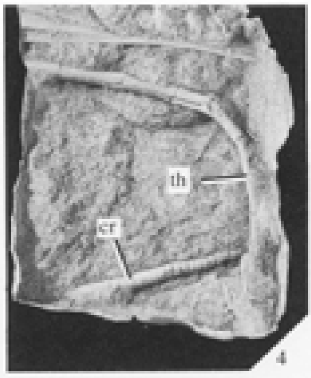

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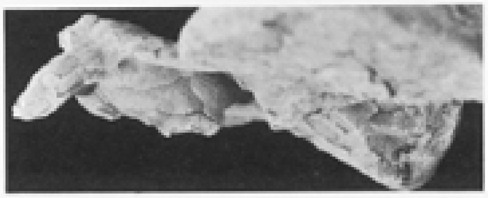
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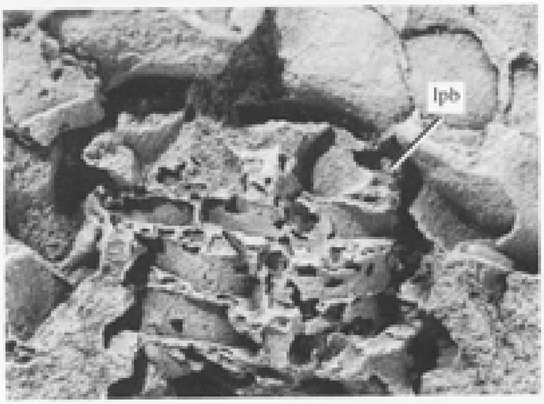

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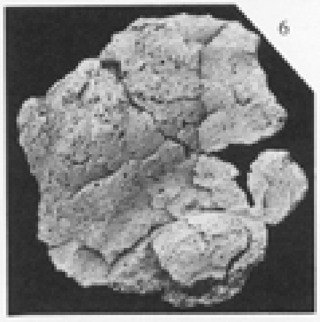
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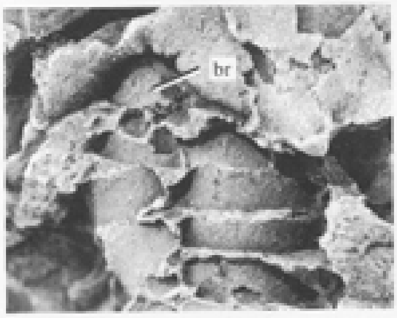

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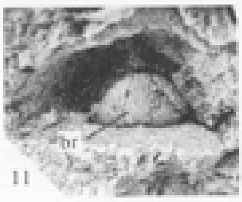

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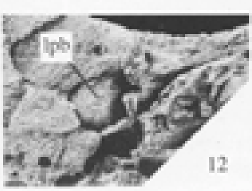

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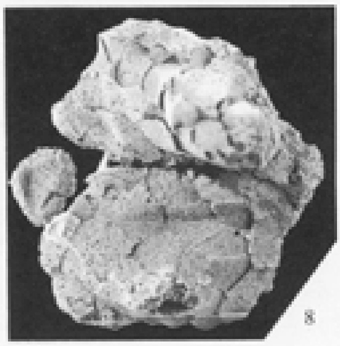
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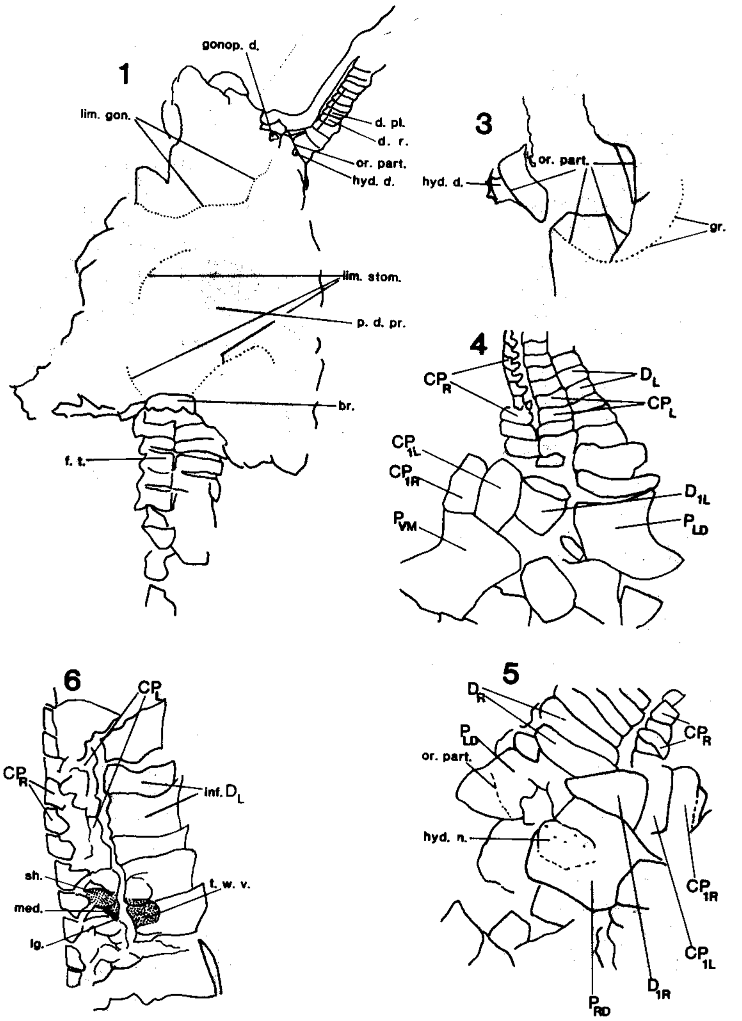
JEFFERIES, *Dendrocystoides scoticus*



TEXT-FIG. 5. Two-thirds-scale outline drawings of figs. 1 and 3–6 of pl. 2. Each drawing has the same number as the corresponding photograph on the plate; br. = brain; d. pl. = dorsal plate of arm; d. r. = dorsal ridge in infilling of arm; f. t. = fore tail; gonop. d. = gonopore duct; gr. = groove of unknown significance; hyd. d. = hydropore duct; hyd. n. = hydropore node; inf. DL = infilling of left dorsal arm plates; lim. gon. = limit of gonad; lim. stom. = limit of stomach; lg. = long tube foot of a triad; med. = medium-length tube foot of a triad; or. part. = oral partition; p. d. pr. = posterior dorsal prominence; sh. = short tube foot of a triad; t. w. v. = terminal water vessel; C_{PR}, P_{LD}, D_L etc. = plates of arm and arm-base region; cf. text-fig. 3.

EXPLANATION OF PLATE 2

Figs. 1–6. *Dendrocystoides scoticus*. All specimens in BM(NH). Compare text-fig. 5. 1, 2, E28803. 1, Dorsal aspect of natural internal mould of head, arm and fore tail, ×2. 2, arm-base region ×5. 3, E28507, ×5. Natural internal mould of arm-base region in antero-ventral aspect ×5. 4, 5, E28787. Latexes of arm-base region, ×5; 4, ventral aspect. 5, dorsal aspect. 6, 7, E28790. Natural internal mould of arm in ventral aspect to show especially the terminal water vessel and the triads of tube feet. 6, ×10; 7, ×40, to show detail.

PLATE 2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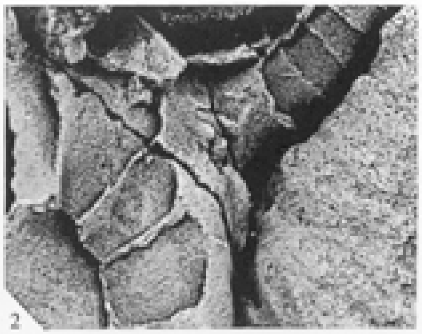
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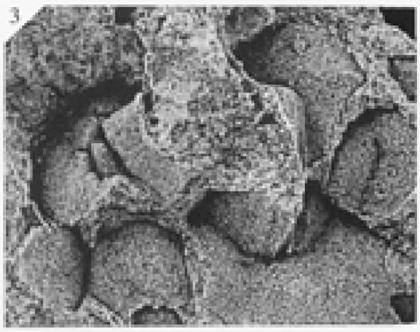
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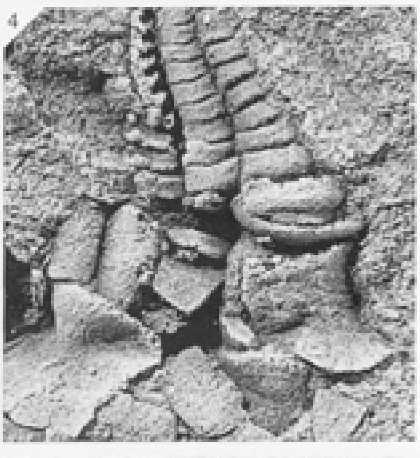
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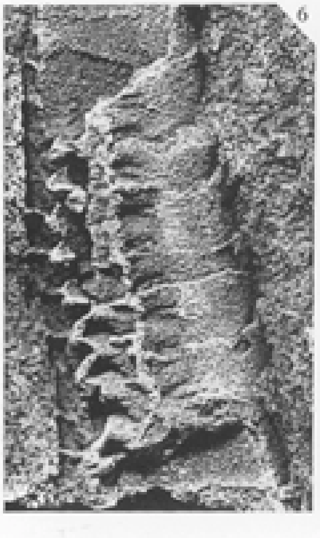
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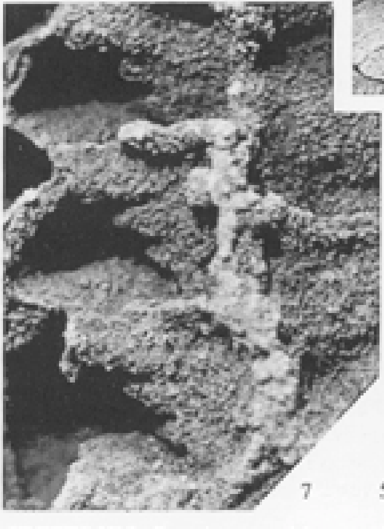
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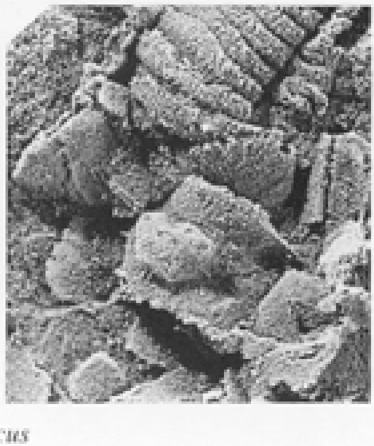
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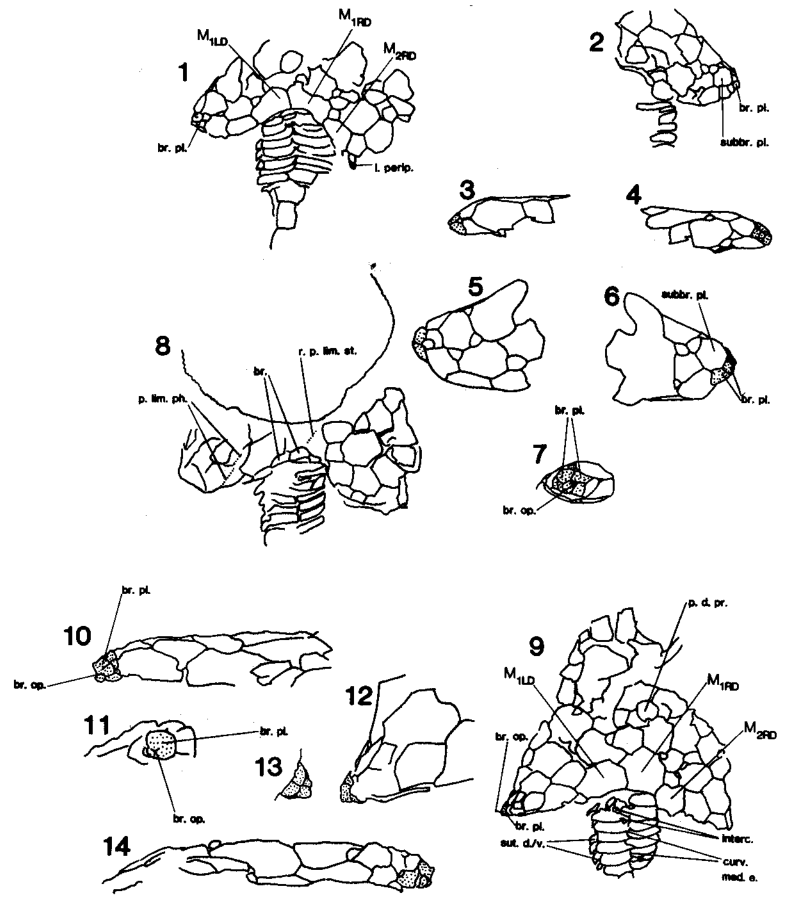
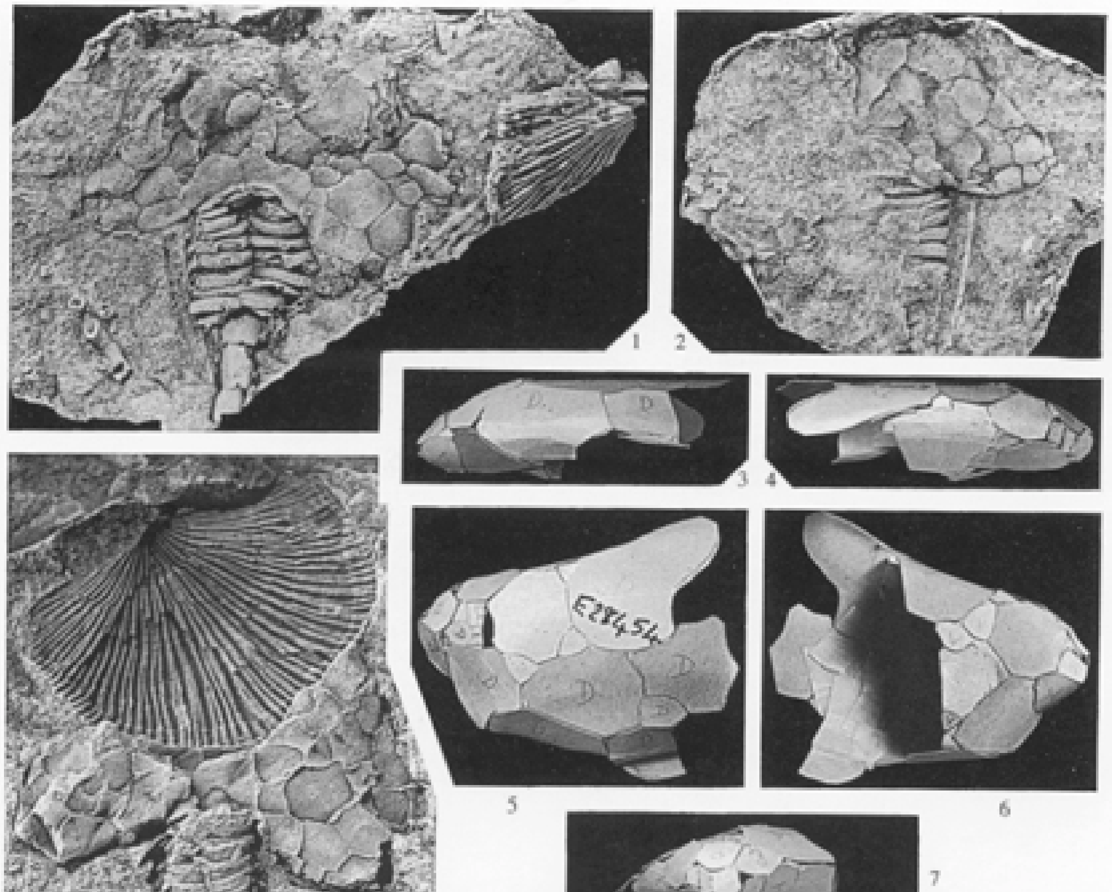
JEFFERIES, *Dendrocystoides scoticus*



TEXT-FIG. 6. Reduced-scale outline drawings (×0.6) of pl. 3, figs. 1–14. Each drawing has the same number as the corresponding photograph on the plate; br. = brain; br. op. = branchial opening; br. pl. = branchial plate; curv. med. e. = curved median edge of dorsal plate of fore tail; interc. = intercalary plate of fore tail; l. perip. = left region of periproct; p. lim. ph. = posterior limit of pharynx; r. p. lim. st. = right posterior limit of stomach; subbr. pl. = subbranchial plate; sut. d./v. = suture between dorsal and ventral plate of fore tail; M_{1LD}, M_{1RD}, M_{2RD} = plates of tail insertion; cf. text-fig. 2.

EXPLANATION OF PLATE 3

Figs. 1–14. *Dendrocystoides scoticus*, to show the gill slit (branchial opening) and associated structures. Compare text-fig. 6. Specimens in BM(NH). 1–7, E28454. 1, 2 latexes of dorsal and ventral aspects; ×2; 3–7, cardboard model based on the latexes in figs. 1, 2; ×0·36 of model, *c.* ×4·9 of specimen. 3, Posterior aspect. 4, Anterior aspect. 5, Dorsal aspect. 6, Ventral aspect. 7, Left lateral aspect. 8–14, E23239. 8, General view of natural mould in dorsal aspect (×2) and the brachiopod shell which the *Dendrocystoides scoticus* was squashed upon at death – this brachiopod probably explains the inflation with mud of the posterior parts of the head and therefore the good preservation of the branchial region. 9, General view of latex of dorsal surface of head and fore tail (×2). Figs. 10–14, details of branchial region (×5). 10, Posterior aspect. 11, Lateral aspect. 12, Dorsal aspect. 13, Ventral aspect. 14, Left antero-lateral aspect.



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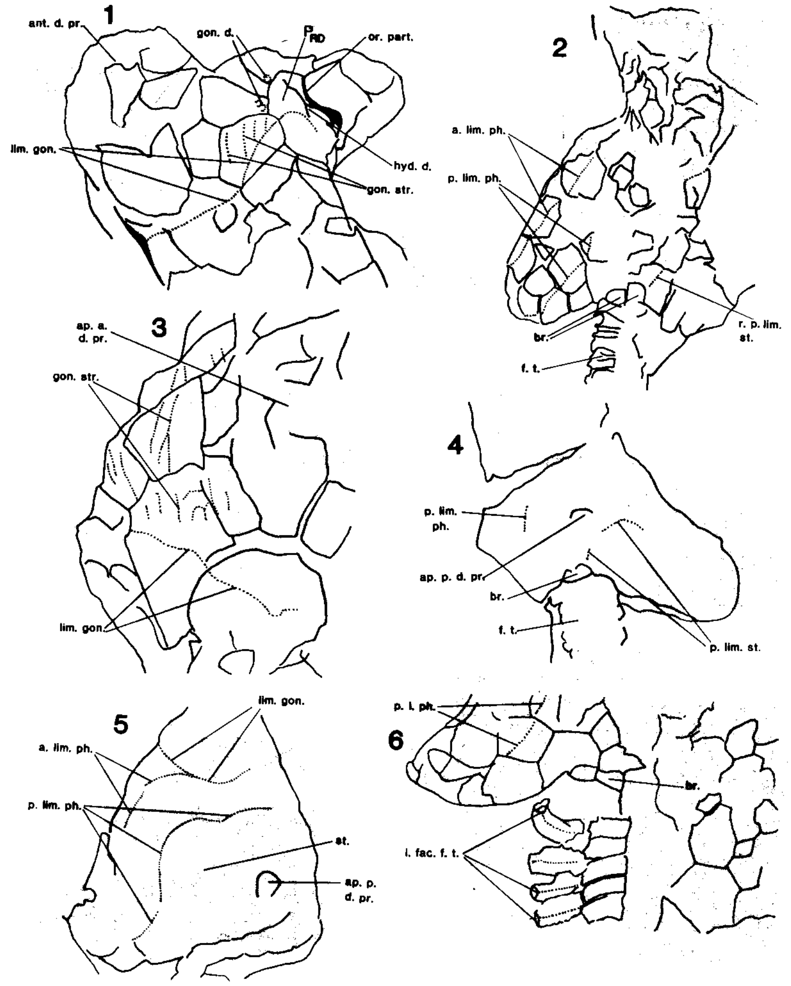
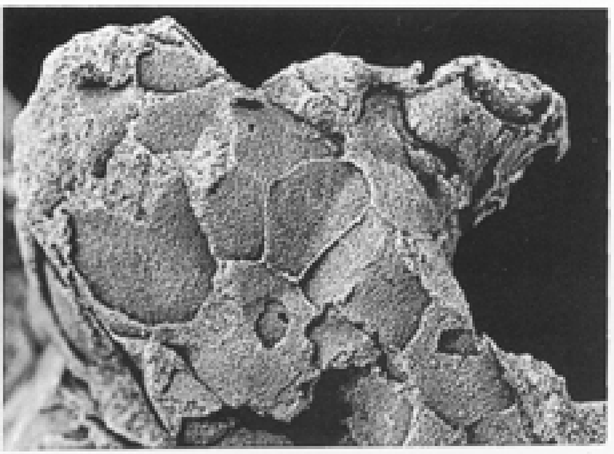


TEXT-FIG. 7. Half-scale outline drawings of pl. 4, figs. 1–6. Each drawing has the same number as the corresponding photograph on the plate; a. lim. ph. = anterior limit of pharynx; ant. d. pr. = anterior dorsal prominence; ap. a. d. pr. = apex of anterior dorsal prominence; ap. p. d. pr. = apex of posterior dorsal prominence; br. = brain; f. t. = fore tail; gon. d. = gonadial duct; gon. str. = gonadial striae on surface of gonad; hyd. d. = hydropore duct; lim. gon. = limit of gonad; l. fac. f. t. = lateral facet of dorsal plate of fore tail (making suture with corresponding ventral plate); or. part. = oral partition; p. lim. ph. = posterior limit of pharynx; p. lim. st. = posterior limit of stomach; r. p. lim. st. = right posterior limit of stomach; st. = stomach.

EXPLANATION OF PLATE 4

Figs. 1–6. *Dendrocystoides scoticus*. Natural internal moulds in dorsal aspect. Compare text-fig. 7. Specimens in BM(NH). 1, E28434, × 5. 2, E28769, Head and foretail × 2. 3, E28532, Left anterior part of head to show gonadial striae × 5. 4, E28601, Right anterior part of head × 2. 5, E23199, Posterior left part of head × 2. 6, E28439, Posterior part of head and fore tail × 3.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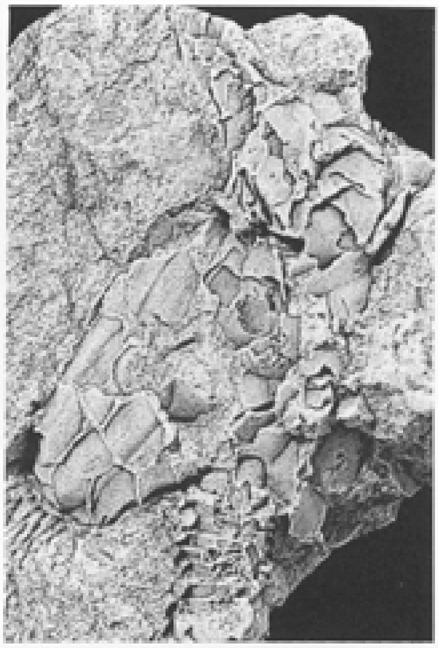
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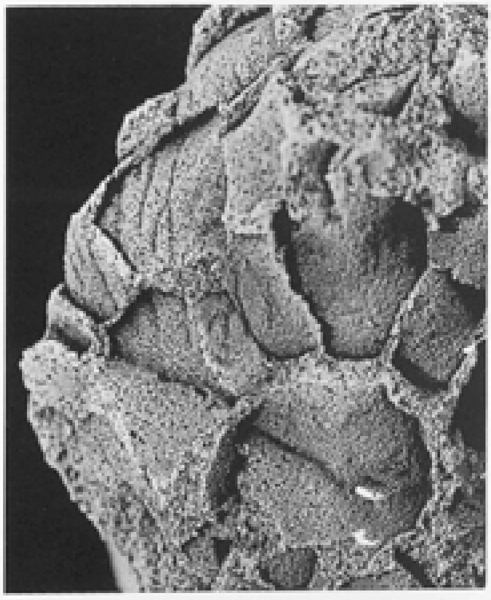
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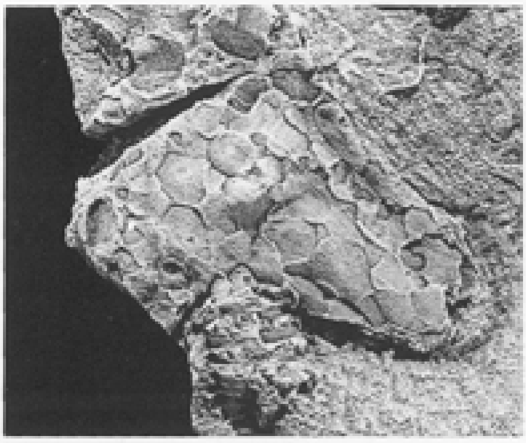
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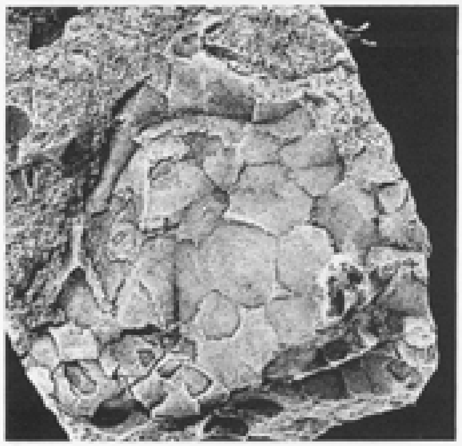
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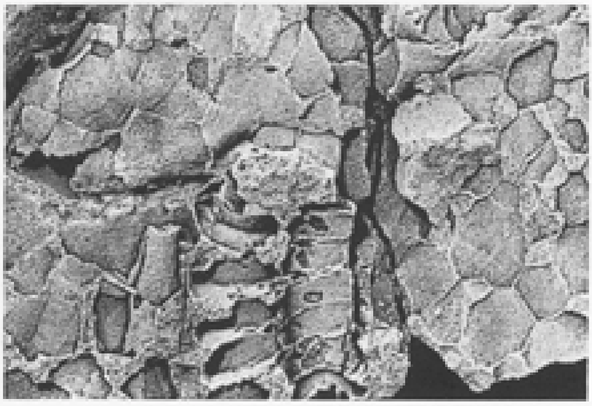
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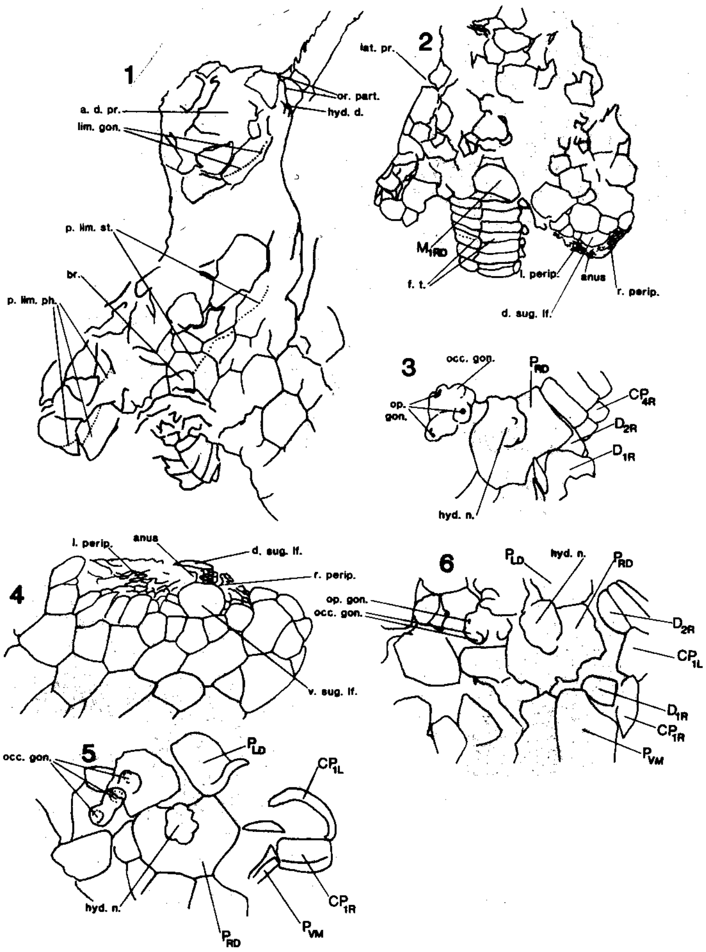
JEFFERIES, *Dendrocystoides scoticus*

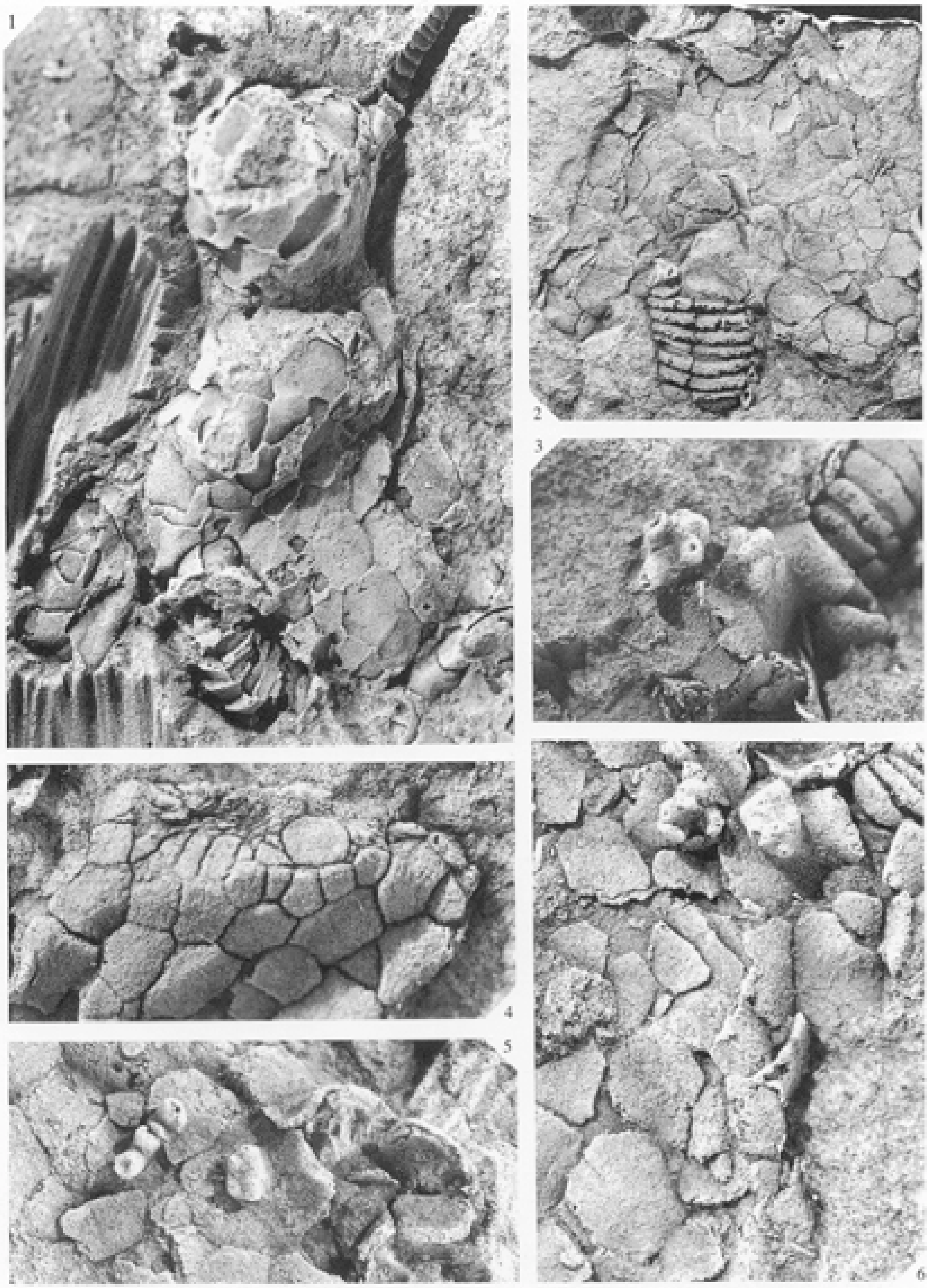


TEXT-FIG. 8. Reduced-scale outline drawings (×0.6) of pl. 5, figs. 1–6. Each drawing has the same number as the corresponding photographs on the plate; a. d. pr. = anterior dorsal prominence; anus = anus; d. sug. lf. = dorsal sugar-loaf plate; f. t. = fore tail; hyd. d. = hydropore duct; hyd. n. = hydropore node; lat. pr. = lateral prominence; lim. gon. = limit of gonad; l. perip. = left region of periproct; occ. gon. = occluded gonopore; op. gon. = open gonopore; op. part. = oral partition; r. perip. = right region of periproct; v. sug. lf. = ventral sugar loaf; CP_{1L}, M_{1RD} etc. = plates of arm, arm base and tail base as shown in text-figs. 2, 3.

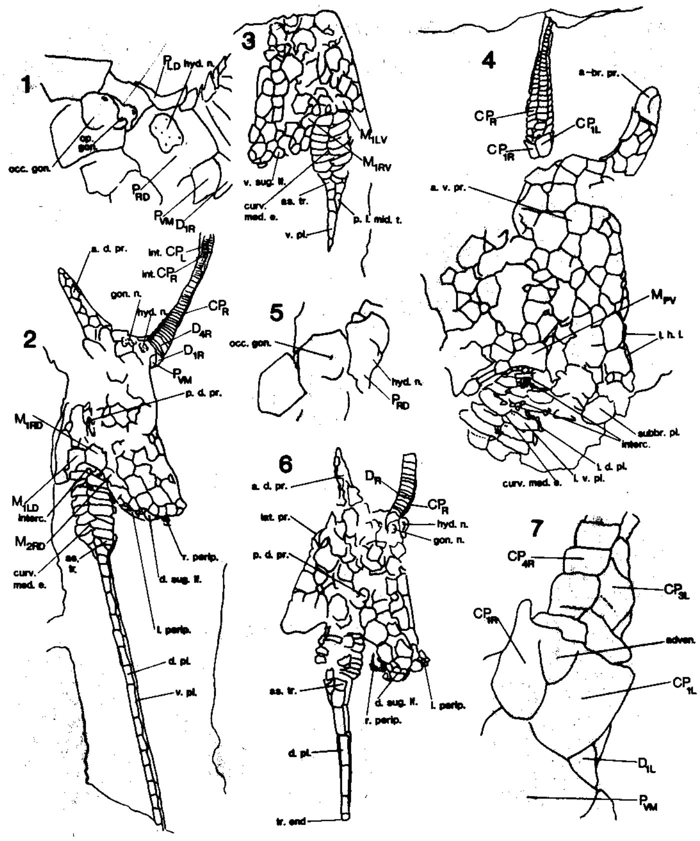
EXPLANATION OF PLATE 5

Figs. 1–6. *Dendrocystoides scoticus*. Compare text-fig. 8. Specimens in BM(NH). 1, E28439, ×3. Natural internal mould of head and fore tail in dorsal aspect. 2, E23229, ×2. Latex of dorsal surface, to show especially the anus, periproct and dorsal sugar-loaf plate. 3, E23219, ×5. Latex of arm-base region with gonopore node and hydropore mode; one of the gonopores is occluded. 4, E23237, ×5. Latex of anal region in postero-ventral aspect. 5, E28592, ×5. Latex of arm-base region with gonopore node, hydropore node and the first cover plates in dorsal aspect. The gonopores are all occluded. 6, E23718, ×5. Latex of arm-base region with gonopore node and hydropore node. Some of the gonopores are occluded.

PLATE 5



JEFFERIES, *Dendrocystoides scoticus*

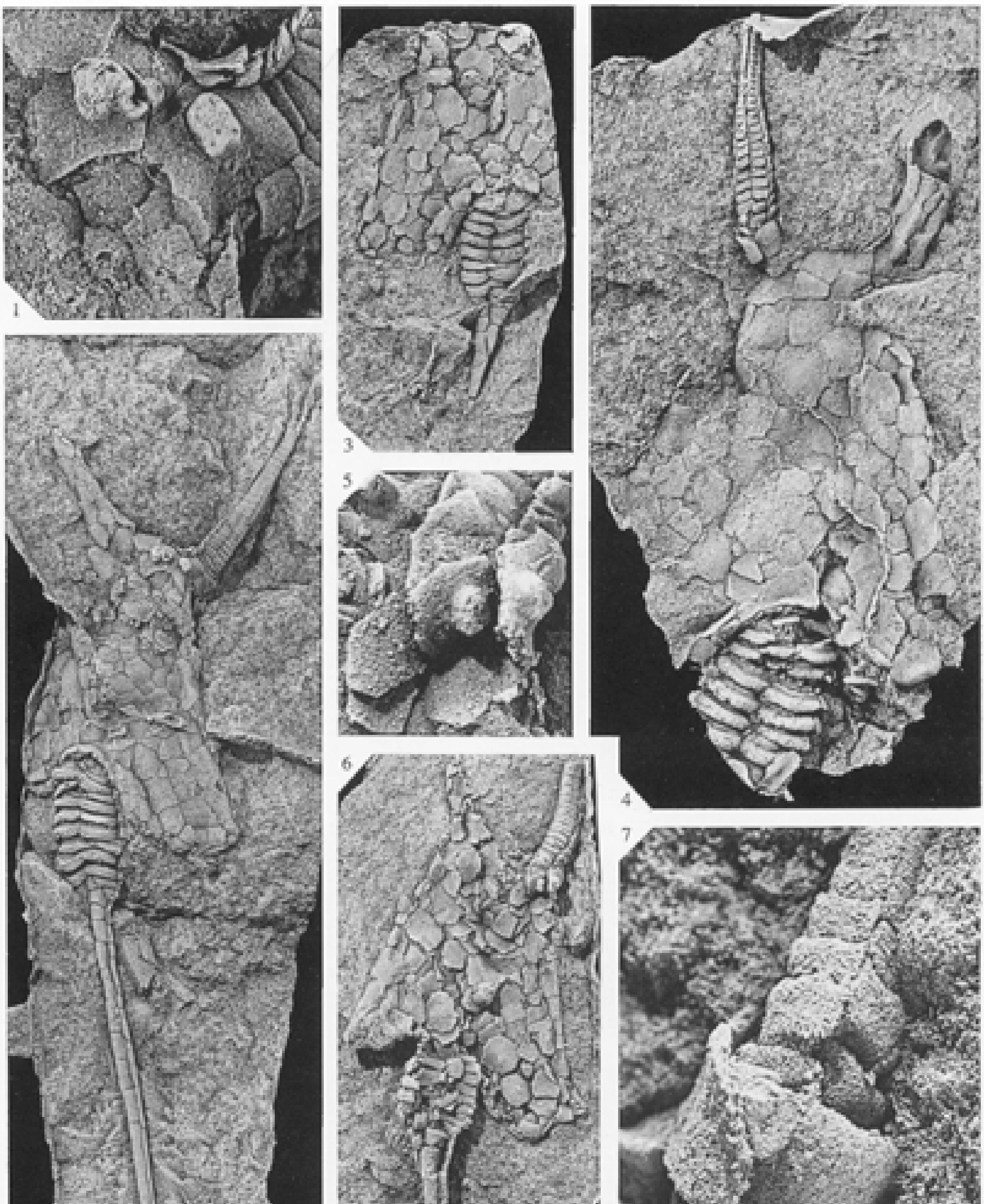


TEXT-FIG. 9. Half-scale outline drawings of pl. 6, figs. 1–7. Each drawing has the same number as the corresponding photograph on the plate; a-br. pr. = antibrachial process; a. d. pr. = anterior dorsal prominence; adven. = adventitious plate between CP_{1L} and CP_{1R}; as. tr. = asymmetrical transition between mid tail and fore tail; a. v. pr. = anterior ventral prominence; curv. med. e. = curved median edge of dorsal plates of fore tail; d. sug. lf. = dorsal sugar-loaf plate; d. pl. = dorsal plate of hind tail; gon. n. = gonopore node; hyd. n. = hydropore node; int. CPL, int. CPR = interior of left and right cover plates; interc. intercalary plate of fore tail; lat. pr. = lateral prominence; l. d. pl. = left dorsal plate of fore tail; l. v. pl. = left ventral plate of fore tail; l. perip. = left region of periproct; occ. gon. = occluded gonopore; op. gon. = open gonopore; p. l. mid. t. = posterior left plate of mid tail; p. d. pr. = posterior dorsal prominence; r. perip. = right region of periproct; subbr. pl. = subbranchial plate; tr. end. = truncated end of tail; v. pl. = ventral plate of hind tail; v. sug. lf. = ventral sugar-loaf plate; CP_{1L}, D_{1R}, P_{LD} etc. = plates of arm and arm base (see text-fig. 3); M_{1LD}, M_{PV} etc. = plates of tail insertion (see text-fig. 2).

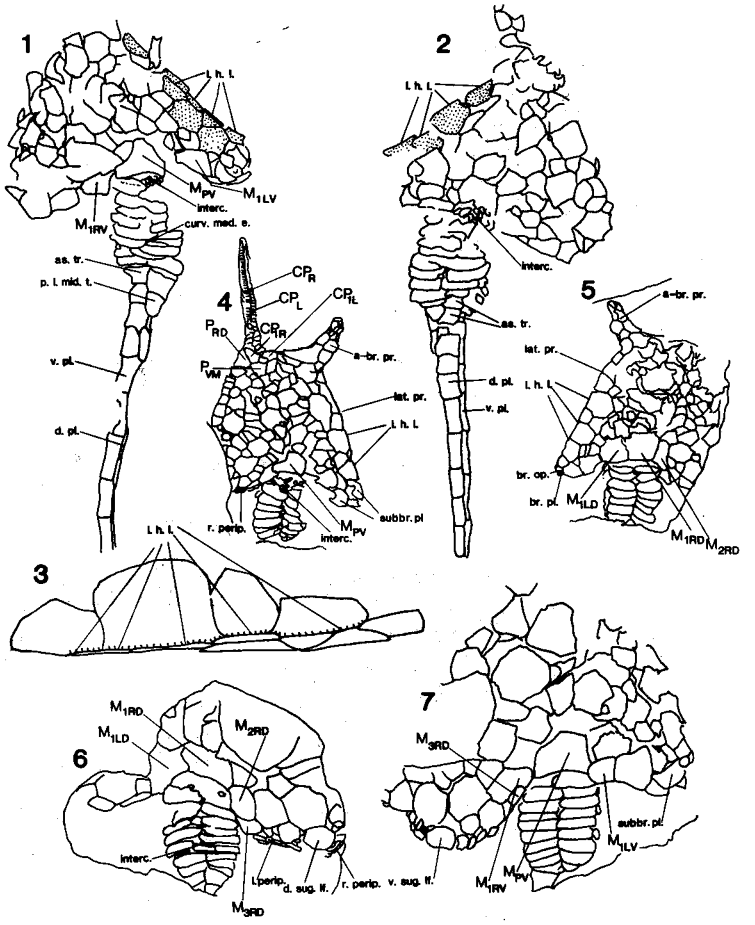
EXPLANATION OF PLATE 6

Figs. 1–7. *Dendrocystoides scoticus*. Latexes of BM(NH) specimens. Compare text-fig. 9. 1, 2, 3, E28768. 1, Arm-base region, × 5, in dorsal aspect, with the hydropore node and gonopore node; one of the gonopores is occluded. 2, General view in dorsal aspect, × 1·2. 3, ventral aspect, with the asymmetries of the mid tail. 4, E28776, × 2, ventral aspect. 5, 6, E23700, dorsal aspect. 5, Detail of arm-base region, × 5. 6, General view note truncated tail and overhanging dorsal prominence. 7, E28794, × 10. Arm-base region in ventral aspect to show pathological adventitious plate between CP_{1R} and CP_{1L}.

PLATE 6



JEFFERIES, *Dendrocystoides scoticus*



TEXT-FIG. 10. Reduced-scale outline drawings (× 0.6) of pl. 7, figs. 1–7. Each drawing has the same number as the corresponding photograph on the plate: a-br. pr. = antibrachial process; as. tr. = asymmetrical transition between mid tail and fore tail; br. op. = branchial opening (gill slit); br. pl. = branchial plate; curv. med. e. = curved median edge of ventral plate of fore tail; d. pl. = dorsal plate of hind tail; d. sug. lf. = dosal sugar-loaf plate; interc. = intercalary plate of fore tail; lat. pr. = lateral prominence; l. h. l. = left hinge line; l. perip. = left region of periproct; p. l. mid. t. = posterior left plate of mid tail; r. perip. = right region of periproct; subbr. pl. = subbranchial plate; v. pl. = ventral plate of hind tail; v. sug. lf. = ventral sugar-loaf plate; C_{PR}, P_{RD} etc. = plates of arm and arm insertion (see text-fig. 3); M_{1LD}, M_{PV} etc. = plates of tail insertion (see text-fig. 2).

EXPLANATION OF PLATE 7

Figs. 1–7. *Dendrocystoides scoticus*. BM(NH) specimens. Compare text-fig. 10. 1, 2, 3. E23198. To show structure of presumed left hinge line. 1, Latex of ventral aspect, ×2. 2, Latex of dorsal aspect, ×2. 3, Cardboard model (× 0·5 = *c*. × 8 for specimen) of the plates stippled in text-fig. 21/1, 2 to show how the dorsal and ventral plates met at a straight edge – the left hinge line. 4, 5, E23207, holotype, × 1·2. 4, Ventral aspect. 5, Dorsal aspect 42a,b. 6, 7, E28781. Latex (× 2) of posterior part of head and fore tail, to show especially the plates of the tail insertion. 6, Dorsal aspect. 7, Ventral aspect.

PLATE 7

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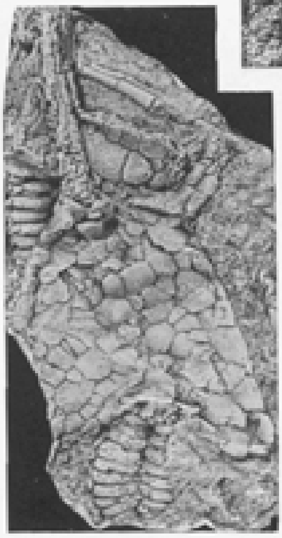

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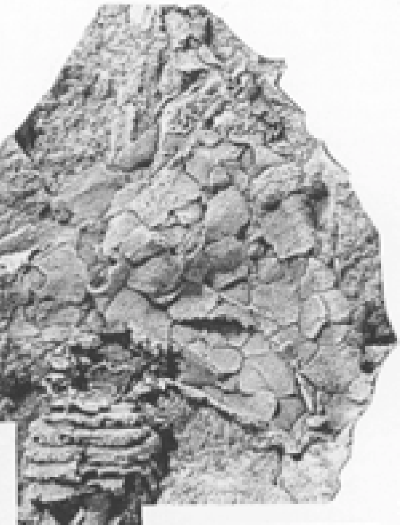

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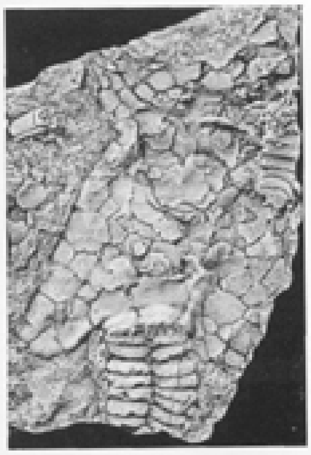

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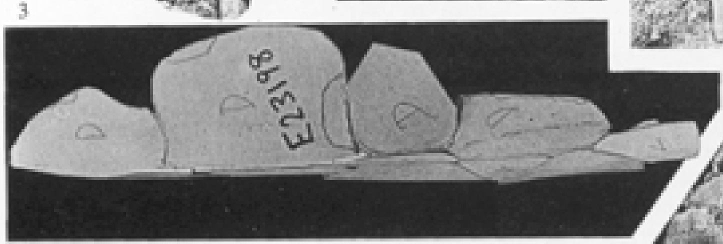

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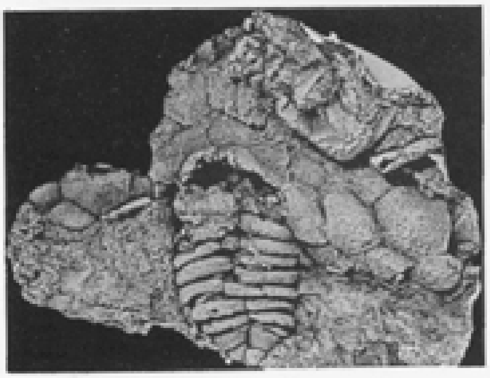

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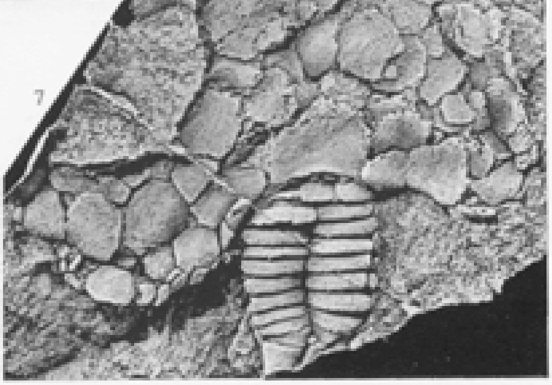


JEFFERIES, *Dendrocystoides scoticus*

text-fig. 6; pl. 6, fig. 4, text-fig. 9; pl. 7, fig. 4, text-fig. 10). These would probably have raised the posterior left angle above the sea floor. Dorsally, the frame consisted of two or three large, rather irregular plates. In one specimen (pl. 3, figs. 8–12, text-fig. 6) the small plates of the posterior left angle of the head seem to be preserved in their proper articulation and form a cone pointing leftwards and rearwards. (Under the anterior part of the head of this specimen there is a large brachiopod – perhaps the mud inside the head was squashed rearwards when the *D. scoticus* fell on top of this shell so that the posterior part of the head was preserved in an unusually inflated condition.) There is no single plate capping the cone. Indeed, the arrangement of the plates seems to be such that a small hole in the skeleton could open between the plates at the tip of the cone (pl. 3, fig. 11, text-fig. 6). I suggest that this small hole represents an outlet opening and, on cornute analogies, that it was a gill slit.

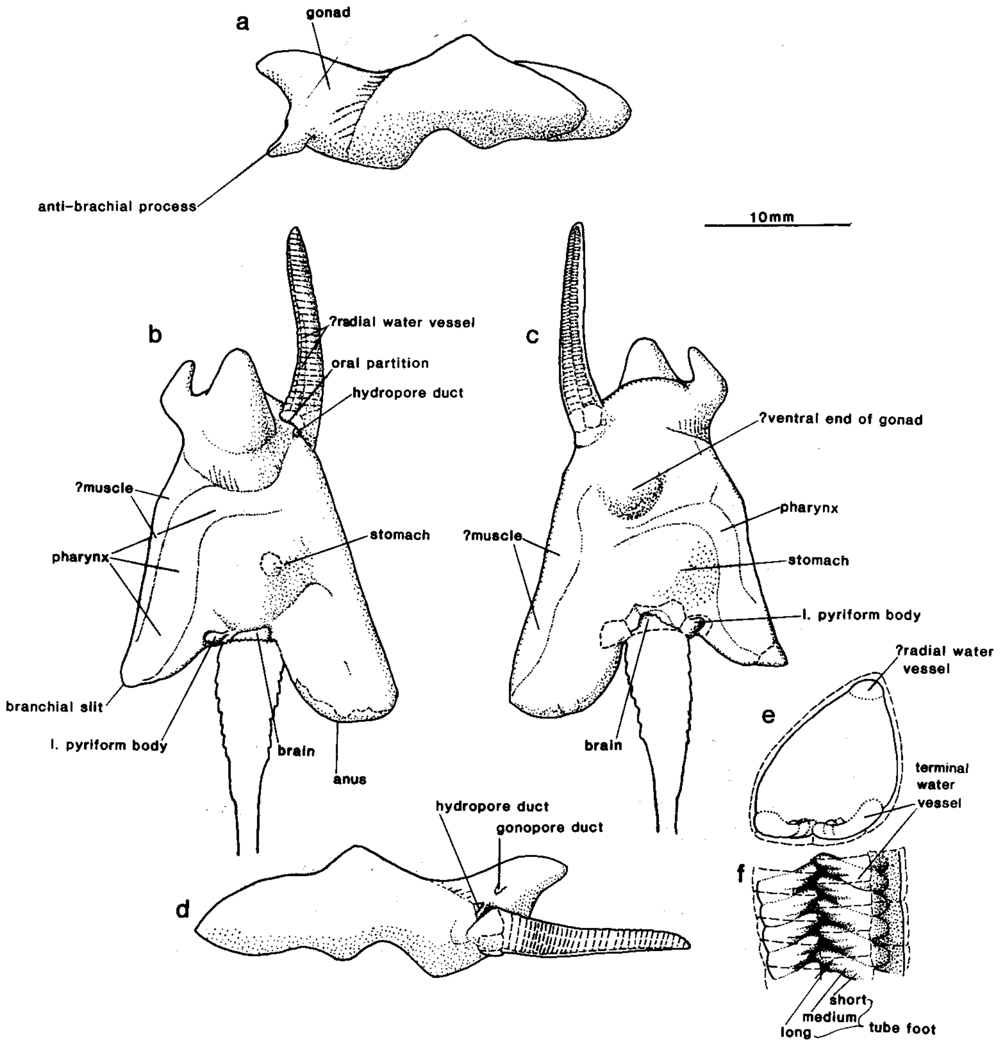
Internal anatomy

A number of grooves and other details can be seen on the internal moulds (text-fig. 11). Such grooves would correspond to ridges on the internal surface of the skeleton but it is more illuminating to consider them as indicating grooves in the surface of the soft parts and thus to use them directly in reconstructing the soft anatomy. Once again, I am influenced, at the outset, by the thought that, in basic plan, *D. scoticus* seems to be similar to the cornute *Ceratocystis*. None of the available specimens showed a complete internal mould. The diagrams of such a mould shown in text-figure 11 are highly composite.

One of the most obvious features in the internal mould is in the arm-base region. Dorsally this feature, called the oral partition (pl. 2, figs. 2, 3, text-fig. 5; pl. 4, fig. 1, text-fig. 7; pl. 5, fig. 1, text-fig. 8), is expressed as a deep groove in the natural internal mould, obliquely transverse to the arm and situated on the inner face of the dorsal arm-base plates P_{LD} and P_{RD}. Ventrally it passes into a shallow groove or break in slope, where it crosses the inner face of plate P_{VM}. In the skeleton, it would correspond to a thin, sharp-topped wall on P_{RD} and P_{LD} which would partly separate the cavity of the arm form the rest of the head. On echinoderm analogies, the arm would contain a radial water vessel and tube feet and was probably used to pick food particles from the mud. Probably the arm would graze food from the mud by sweeping left and right through or over the superficial layer of the sea bottom. If so, the food particles would be passed back towards the base of the arm and there enter the head, through the mouth. The oral partition would delimit the brachial cavity posteriorly and would arch over the mouth.

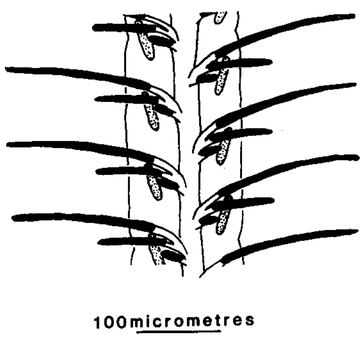
A probable indication of the tube feet is preserved on the ventral surface of the internal mould of the arm (text-fig. 11f; pl. 2, figs. 6, 7, text-fig. 8): such moulds reveal, namely, a series of approximately sausage-shaped structures equal in number to the cover plates. In the terminology which I shall adopt, the proximal end of the sausage is situated where the latter makes contact with the dorsal plate, at right or left of the arm, while the distal end is near the median line of the arm. Each sausage is obliquely disposed so that its distal end is anterior to its proximal end. The long axis of the sausage runs diagonally across the relevant cover plate. The sausage itself overlaps distally on to the next cover plate anterior, near to the median line of the arm, while proximally it overlaps on to the next cover plate posterior, away from the median line of the arm. The distal part of each sausage is divided into three lobes by two grooves which run transverse to the length of the arm. Because of these grooves, each sausage is clearly divided into three lobes towards its distal end.

A comparison of these structures with the tube feet of some crinoids is suggestive. Thus in many crinoids, such as *Antedon* (Nichols 1960), the tube feet are arranged in groups of three (text-fig. 12), each group arising from a terminal water vessel which itself branches from the radial water vessel. The three tube feet of a group differ in length, there being a long one distally, a short one proximally, and a medium-length one between the two others ('distally' and 'proximally' here refer to the position in the pinnule of the crinoid). The short and medium tube feet are in contact externally with a fold of soft tissue which is called a lappet and contains an ambulacral plate (a cover plate), whereas the long tube feet emerge between successive lappets. The lappets open when the tube feet in contact with them expand and they close when these tube feet contract. Because of their contained



TEXT-FIG. 11. *Dendrocystoides scoticus*. Reconstructed internal mould representing the superficial anatomy of the soft parts: (*a*) left lateral aspect of head; (*b*) dorsal; (*c*) ventral; (*d*) right lateral; (*e*) transverse section, seen from in front, of an arm near, but not at, its base; (*f*) soft parts of arm in ventral aspect.

TEXT-FIG. 12. The tube feet of the crinoid *Antedon bifida* in oral aspect (after Nichols 1960, text fig. 1, modified), corresponding to the ventral aspect of *Dendrocystoides*. Note the arrangement of the tube feet (black) in triads, each with a long, a medium and a short tube foot, and the relation of the triads to the cover plates (dotted) and to the radial and terminal water vessels.



musculature, the long tube feet can contract suddenly towards the ambulacral groove, the medium tube feet can contract suddenly towards or away from the groove, and the short tube feet can move in any direction. Paul and Smith (1984) have suggested that primitive echinoderms such as edrioasteroids could open the ambulacral plates or plating by pushing with their tube feet against the adradial faces of these plates, very much as crinoids do. The surfaces of the tube feet of crinoids are provided with sensitive outgrowths called papillae which, when stimulated, squirt out a stream of mucus to entangle microscopic prey. Such prey particles will normally bump first into the papillae of the long tube feet and, when once entangled, will then be passed to the medium tube feet, and from there to the short tube feet which will hand them, still wrapped in mucus, onto the ciliated tract of the ambulacral groove. By the beat of cilia in this groove, they will then be carried to the mouth.

The sausage-shaped structures observed in *D. scoticus* may each correspond to the terminal water tube of a crinoid, together with the three attached tube feet. The three terminal lobes of the sausage would, in such case, correspond to the three tube feet of a group – short, medium and long. If this suggestion is correct, then the long tube foot, as in crinoids, will be the most distal member of its group (distal with respect to the arm), the medium tube foot will be in the middle of the group, and the short tube foot will be the most proximal. Moreover, as in crinoids, the longest tube foot will coincide in position with the contact between successive cover plates (lappets) whereas the short and medium tube foot will be in contact with the inner surface of the main part of a cover plate. Presumably the cover plate would open when the contiguous terminal water tube distended. These various correspondences seem too complex to be accidental and suggest that we are dealing here with genuine homologues. If so, then the grouping of tube feet into triads, and their observed relationship to cover plates, would probably be primitive for echinoderms, and this is true whether *D. scoticus* is a stem-group chordate (as is likely) or a stem-group dexiothete or even a stem-group echinoderm. This supports Nichols' (1972, p. 536) assumption that the tube feet of eleutherozoans, which are always single rather than arranged in triads, were derived from triadic tube feet of crinoid type. There was no previous clear evidence for this assumption, however, since in hemichordates, which are the closest living relatives of the dexiothetes, the ciliated outgrowths on each arm of the mesocoel (which are perhaps homologous to tube feet and function in producing a feeding current [Lester 1985]) are never arranged in triads.

The position of the radial water vessel in *D. scoticus* is uncertain. It presumably ran the length of the arm, giving rise to branches connected with the terminal water vessels. It may be represented by a dorsal ridge on the internal mould which follows the dorsal edge of the arm (text-fig. 11e; pl. 2, fig. 1, text-fig. 5), or it may have been more ventral than this, somewhere inside the arm. The obvious flexibility of the arm suggests that there would have been large longitudinal muscles in it in life, probably filling much of its volume.

Beneath the hydropore, immediately behind the oral partition, a small upwardly pointed projection is present on the internal mould (hydropore duct; pl. 2, figs. 2, 3, text-fig. 5; pl. 4, fig. 1, text-fig. 7; pl. 5, fig. 1, text-fig. 8). This presumably represents the dorsal end of the axial sinus which opens into the hydropore in echinoderms (Fedotov 1924). By analogy with extant echinoderms, the water vascular system would have joined the axial sinus inside the animal and would thus have been connected, indirectly, with the outside world. However, any such internal connection in *D. scoticus* does not show in the internal mould. The heart of *D. scoticus*, or in echinoderm terms the dorsal sac (= madreporic vesicle), would also probably have been situated near the hydropore, but its position cannot be identified in the fossils.

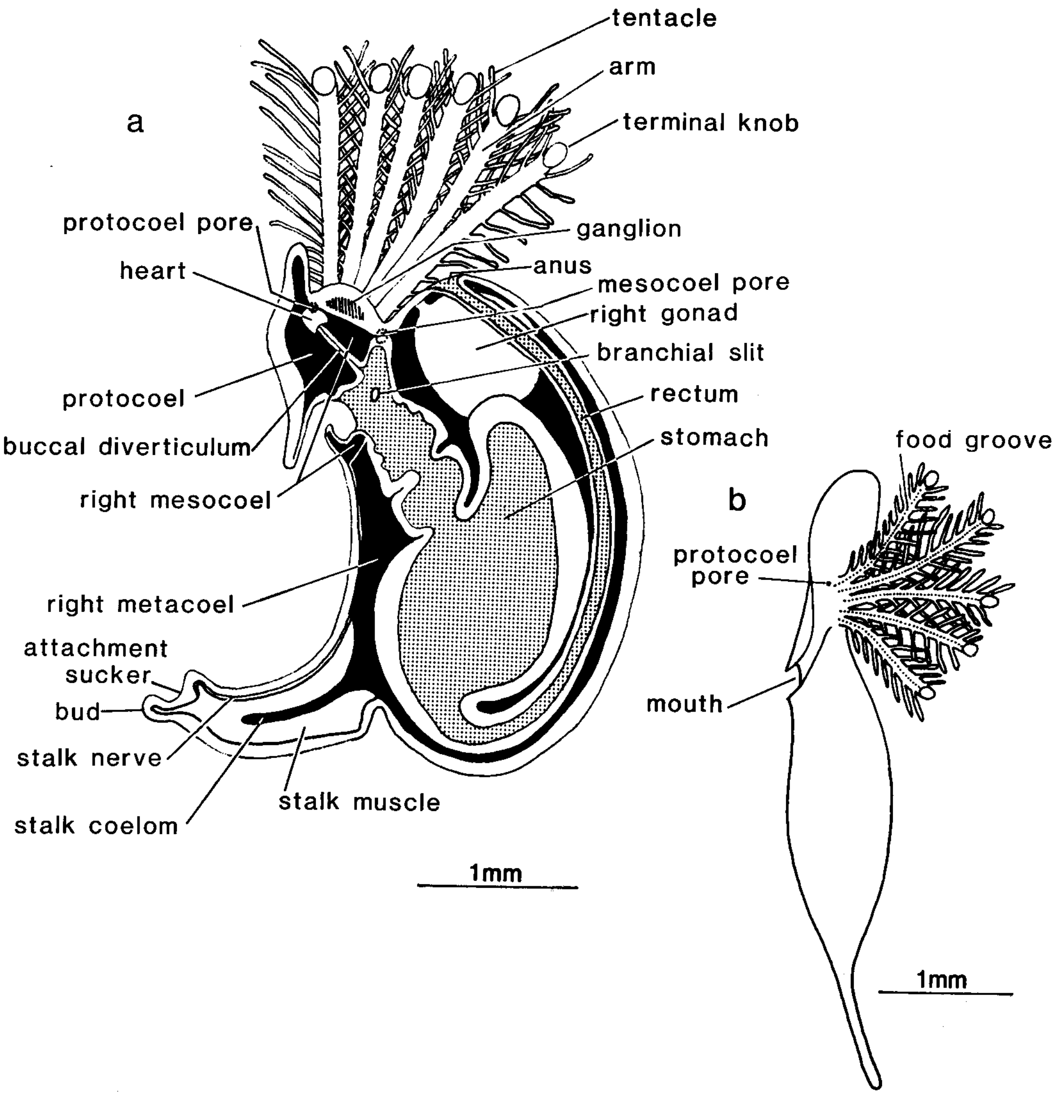
The position of the gonad, inside the anterior dorsal prominence of the head, has been suggested already. Its likely boundary on the internal mould is indicated by a slight groove which almost encircles the dorsal anterior prominence and passes at the left from the dorsal to the ventral surface (text-fig. 11; pl. 1, fig. 2, text-fig. 4; pl. 2, fig. 1, text-fig. 5; pl. 4, figs. 1, 3, 5, text-fig. 7). Corrugations on the surface of the internal mould (pl. 4, figs. 1, 3) run forwards from this groove, in some specimens, and suggest that the surface of the gonad was plicated in life. How the gonad terminated in a ventro-posterior direction is unclear: it may, in the largest individuals, have projected rearwards and downwards into the pharynx behind it (whose disposition will be explained below) so as to fill a large part of the ventral anterior prominence. Such a morphology would explain why this prominence is relatively large in the biggest of all observed individuals (pl. 1, fig. 1, text-fig. 4). On the other hand, it may be that the ventral anterior prominence corresponded to some other organ which expanded disproportionately in old age, perhaps part of the pharnyx. It is clear, from the inferred position of the gonad in the internal mould, that the most anterior part of it, at least, was dorsal to the pharynx.

The pharynx would be expected to run, as in cornutes, from the gill slit at posterior left, to the velar mouth, and the buccal cavity would run from the velar mouth to the true mouth. The likely position of the pharynx in *D. scoticus*, or of the pharynx posteriorly and the buccal cavity anteriorly, in indicated by a sinuous tract with this oblique disposition, limited at anterior left and posterior right by grooves on the dorsal and ventral surfaces of the internal mould. There is no way of saying whether *D. scoticus* had a buccal cavity or, if it did have one, where the boundary between this cavity and the pharynx may have lain.

On the dorsal surface of the internal mould, the anterior limiting groove of the presumed pharynx *plus* buccal cavity coincided in its most anterior and rightmost part with the posterior limit of the probable gonad, as proposed above (pl. 1, fig. 2, text-fig. 4; pl. 4, fig. 5, text-fig. 7). More leftward, the anterior dorsal pharyngeal groove departs from the groove bounding the gonad, and bends to pass leftward and posteriorly, parallel to the posterior left margin of the head (pl. 4, figs. 2, 5, text-fig. 7). Perhaps the groove in this region separated the pharynx from muscles which pulled the roof downwards about the left peripheral hinge line (already mentioned) and which thus squirted water through the gill slit. The groove bounding the pharynx *plus* buccal cavity to the right and behind on the dorsal surface (pl. 1, fig. 2, text-fig. 4; pl. 2, fig. 1, text-fig. 5; pl. 3, fig. 8, text-fig. 6; pl. 4, figs. 2, 5, text-fig. 7) has a sinuous course parallel to the left anterior pharyngeal groove. Its exact course gives the strong impression of being deflected by an inflated, approximately spherical organ occupying the posterior prominence, possibly the stomach. This interpretation is suggested by comparing *D. scoticus* in dorsal aspect with the recent hemichordate *Cephalodiscus* in left aspect (text-fig. 13), on the assumption, already several times presented (e.g. Jefferies 1986, pp. 50ff., 221ff., and herein below) that the Dexiothetica are descended from a *Cephalodiscus*-like ancestor which lay down on its right side. For the stomach is the largest organ in the viscera in the trunk region of *Cephalodiscus* and, like the organ filling the posterior prominence of *D. scoticus*, is situated behind the pharynx and obliquely right of it in chordate terms (behind and dorsal to it in hemichordate terms). The posterior boundary of the stomach on the dorsal surface of the internal mould may be indicated by two grooves, approximately concentric to the highest point of the posterior dorsal prominence (pl. 2, fig. 1, text-fig. 5; pl. 3, fig. 8, text-fig. 6; pl. 4, figs. 2, 4, 6, text-fig. 7; pl. 5, fig. 1, text-fig. 8). One of these grooves runs leftward and forward from the left anterior margin of the likely position of the brain, while the other one runs rightwards and forwards from the right anterior part of the brain. The rest of the non-pharyngeal gut, probably an intestine ending in a rectum, presumably ran from the stomach to the anus but there is no indication of it in the internal moulds.

On the ventral surface of the internal mould (pl. 1, fig. 1, text-fig. 4), the likely position of the pharynx *plus* buccal cavity is, once again, indicated by two weak sinuous grooves. The more posterior of these, limiting the presumed pharynx posteriorly, runs around the front of the suggested position of the stomach and then passes leftward and rearward to the region of the gill slit ('left' and 'right' here refer always to the animal, not to the reader). The groove bounding the pharynx left anteriorly is very weak in its anterior part, but becomes stronger as it approaches the left border of the head, and then turns to run leftward and posteriorly parallel to that border. Perhaps this groove represents the right edge of muscles associated with the left hinge line. A somewhat similar weak groove runs parallel to the right border of the head and possibly delimits muscle which could lower the roof of the head on the right – as already explained, the elongate shape of the periproctal plates, especially left of the anus, suggests, although there was no right hinge line, that the right part of the head roof could be depressed, presumably by the action of muscles beneath it.

The distinction between buccal cavity and pharynx, as already implied, is uncertain in *D. scoticus*. In embryological terms, this distinction ought to coincide with that between endoderm and



TEXT-FIG. 13. *Cephalodiscus* after Schepotieff (1907) and Andersson (1907); (*a*) sagittal section with the organs of the right side; (*b*) external features.

ectoderm. It is fairly certain that the epithelium lining the food groove of *D. scoticus* would be ectodermal, on echinoderm analogies, and also almost certain that the gill slit would emerge from endoderm, and therefore from pharynx. Moreover, in cornutes the distinction between buccal cavity and pharynx can usually be plausibly recognised (e.g. Jefferies 1986, in *Cothurnocystis* p. 198; *Scotiaecystis* p. 211; *Ceratocystis* p. 217; *Nevadaecystis* p. 227; *Reticulocarpos* p. 225; *Galliaecystis* p. 235) and the same is sometimes true in mitrates (Jeffferies 1986, *Placocystites* p. 269; *Lagynocystis* p. 295). In *D. scoticus*, however, there is no such visible distinction in the internal moulds. At one extreme, it seems possible that the mouth identified above was, in fact, the velar mouth, all gut inside it being endodermal. At the other extreme, it may be that the velar mouth was situated some distance internal to the identified mouth, but has left no trace on the internal moulds. The difficulty is compounded by ambiguities in the hemichordate situation, for Lester (1988, p. 116) has recorded that the region usually called pharynx in *Rhabdopleura* is ectodermal in origin. It would be interesting to know whether the same is true in *Cephalodiscus* where, unlike *Rhabdopleura*, the walls of the 'pharynx' are penetrated by gill slits.

As for the brain of *D. scoticus*, on cornute and mitrate analogies this would be expected to lie at the anterior end of the tail. (In mitrates the identification of the brain as being located here is confirmed by detailed anatomical resemblances with the brain of fishes.) The internal moulds of plates M_{1LD} and M_{1RD} dorsally and of M_{PV} ventrally in *D. scoticus* carry strong grooves which seem to delimit the anterior border of the brain (pl. 1, figs. 10, 11; pl. 2, fig. 1, text-fig. 5; pl. 4, figs. 2, 4, text-fig. 7; pl. 5, fig. 1, text-fig. 8). These moulds suggest that the brain would be an approximately hemispherical structure which made contact with the skeleton on the inside of these plates. It would be directly comparable, in these respects, with the brain of the most anticrownward cornute *Ceratocystis perneri*.

The actual anterior border of the brain on the internal moulds, if it has not been exposed by dissection, appears asymmetrical, on the right projecting farther forward than on the left. Dissection of the internal moulds reveals, however, that this asymmetry is largely illusory, at least ventrally (pl. 1, figs. 10, 11) and is due to the way in which an approximately symmetrical brain intersects the asymmetrical surface of the posterior part of the internal mould of the head. The presumed brain does not occupy the whole extent of the tail insertion, being confined to the central part of the latter. Thus the natural mould of the tail insertion is strongly bipartite in appearance. In this way it resembles the tail insertion of mitrates which, in natural moulds, shows a positive replica of the bipartite brain, the two portions there corresponding to prosencephalon and deuterencephalon (Jefferies 1986, Chap. 8). It is unlikely, however, that the bipartition of the tail insertion has this meaning in *D. scoticus* for three reasons: (1) in mitrates and cornutes the stereom in contact with the nervous tissue is characteristically smooth whereas, in *D. scoticus*, only the central anterior portion of the tail insertion has a similar smoothness; (2) the left pyriform body of *D. scoticus* (no right one, if it existed, has been observed) seems to emerge medially just anterior to the presumed brain (text-fig. 11; pl. 1, figs. 9, 12, 13) and the pyriform body, being the trigeminal ganglion, would be related to nerves coming from the deuterencephalon, not from the prosencephalon; and (3) as shown by Cripps (1989b) the highly visible bipartition of the mitrate brain seems to have been evolved in the crownward parts of the chordate stem lineage since it is incipient in crownward cornutes and is not developed in anticrownward cornutes such as *Ceratocystis*.

The features of the internal mould of the tail have been discussed already. They are simple, however, and can conveniently be repeated here. In the hind tail of the fossils, there is a strand of rock, circular in cross section, corresponding to a canal in the skeleton, and situated dorsal to the centre of the hind tail in transverse section. This strand expands forwards conically in the mid-tail region, to join the approximately cylindrical infilling of the fore tail. As previously suggested, the infilling of the fore tail probably represents the position of muscles, presumably segmentally divided like the skeleton, and of a notochord. The muscles of the fore tail would end posteriorly by insertion into the conical skeleton of the mid tail. The notochord would continue rearwards into the hind tail and would correspond in position and shape to the central canal of the hind tail i.e. to the longitudinal strand of rock preserved in this region in the fossils between upper and lower hind-tail plates. I have argued elsewhere (Jefferies 1986, p. 202) that the notochord of cornutes and mitrates probably had a blood vessel along its central axis. The same conclusion applies to the presumed notochord in the hind tail of *D. scoticus*, since some blood supply to the posterior end of the hind tail would be needed and it could only have been delivered along the central canal between dorsal and ventral series of plates.

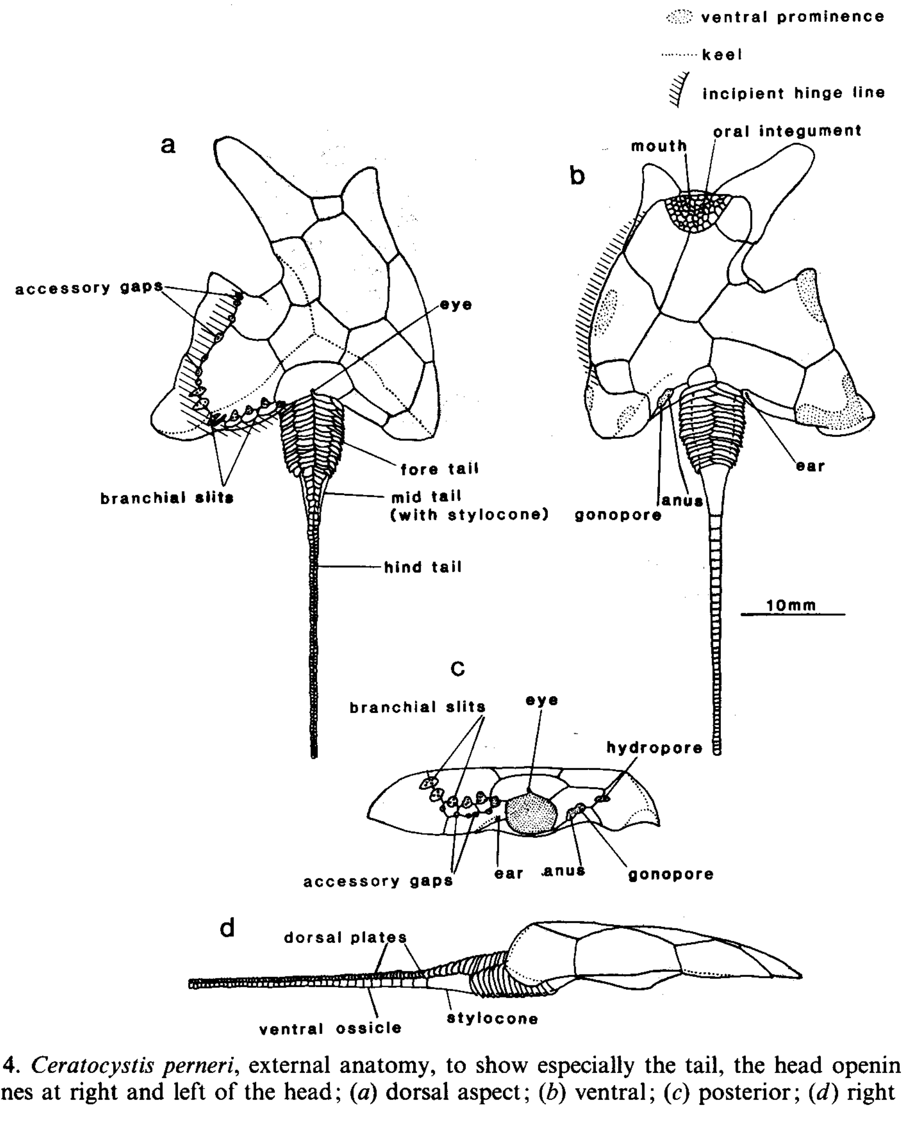
The pyriform body of *D. scoticus* has already been mentioned. It has been observed only on the left side of the brain and only in two specimens. One of these (pl. 1, figs. 12, 13) reveals it plainly in dorsal aspect inside plate M_{2LD} and the other, less clearly, in ventral aspect (pl. 1, fig. 9) inside plate M_{LV}. I have argued elsewhere that the left and right pyriform bodies of cornutes and mitrates are homologous respectively with the left and right trigeminal ganglia of vertebrates (Jefferies 1986,

p. 252, etc.) and the same would be true of this left pyriform body in a solute. It could easily be that a pyriform body existed also on the right in *D. scoticus* but has not been observed because it was never coated with calcite in life, i.e. it was never in contact with the nearest plates – in most specimens of *D. scoticus* the left pyriform body is as invisible as the possible right one.

ANATOMICAL COMPARISONS

Comparison of Dendrocystoides scoticus *with cornutes*

Ceratocystis perneri (text-fig. 14) is the only species of cornute known to have a hydropore (Jefferies 1969; 1986, p. 213ff). For this reason it is assigned to the least crownward plesion of the cornutes and is therefore the most suitable species for comparison with *D. scoticus*. (In the species *Ceratocystis vizainoi*, described by Ubaghs [1987], a hydropore may perhaps exist but has not been observed.)



TEXT-FIG. 14. *Ceratocystis perneri*, external anatomy, to show especially the tail, the head openings and the hinge lines at right and left of the head; (*a*) dorsal aspect; (*b*) ventral; (*c*) posterior; (*d*) right lateral.

D. scoticus resembles *Ceratocystis perneri* in the following respects: (1) it is divided into a head and a tail; (2) the ventral surface of the head is flatter than the dorsal surface; (3) the mouth is at anterior right of the head; (4) the anus is at right of the tail on the posterior surface of the head; (5) the gonopore and hydropore are right of the mid line and the gonopore is farther from the mouth than is the hydropore (against this, the hydropore and gonopore are anterior in position in *D. scoticus*, while the hydropore, if considered with respect to the centre of the head, is clockwise of the gonopore in *D. scoticus*, but anticlockwise of it in *C. perneri*); (6) there was an opening of the pharynx at posterior left of the head (in *D. scoticus* this seems to have been a single branchial opening or gill slit, whereas in *C. perneri* there are regularly seven gill slits); (7) the pharynx runs from anterior right towards the posterior left angle of the head – the extent of the buccal cavity, if there was one, is unknown in *D. scoticus*; (8) the non-pharyngeal gut would have lain posterior to, and right of, the pharynx, as indicated by the position of the anus in *D. scoticus*; (9) there was a brain at the tail insertion with a pyriform body (so far as observed on the left only in *D. scoticus*, but left and right of the brain in *C. perneri*); (10) there are indications that the roof of the head could be lowered in life – in *D. scoticus* these indications are the seeming hinge line on the left of the head and the horizontal elongation of the periproctal plates, while in *C. perneri* (Jefferies *et al.* 1987, p. 443) they are a probable hinge line on the right side of the head and accessory gaps, probably filled with muscle, on the left side of the head (text-fig. 14); (11) the tail is divided into fore, mid and hind regions; (12) the more massive skeletal elements of the hind tail are ventral, while the less massive are dorsal; (13) the skeleton of the fore tail is quadriserial and surrounds a large lumen, and the fore tail seems to be adapted to wave the mid and hind tail mainly from side to side. These resemblances are enough to show that *Dendrocystoides scoticus* can be regarded as built on the same basic plan as *Ceratocystis perneri* and other cornutes in general.

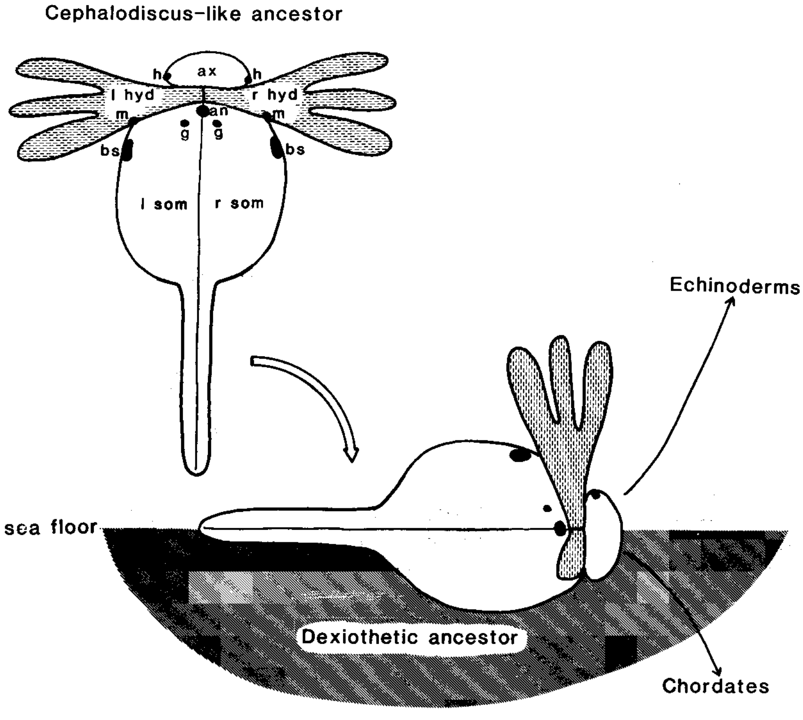
Moreover, the distal part of the hind tail was probably permanently and rigidly curved ventralwards in *D. scoticus*. Similarly, the distal part of the hind tail was able to curve ventrally in the cornute *Cothurnocystis elizae* (Jefferies 1986, p. 202). The same was probably true of the cornute *Protocystites* (Jefferies *et al.* 1987, p. 470). (Concerning *C. perneri* there is no evidence.) Both in primitive cornutes and in solutes, the downturned end of the hind tail probably served to grip the sea bottom during locomotion. It was probably used much like a punt pole in pulling the head rearwards.

However, there are obvious differences between *Dendrocystoides scoticus* and cornutes, especially *Ceratocystis perneri*. These have partly been mentioned already, but for clarity I here list them all, even when this involves repetition: (1) *D. scoticus*, like all other solutes, had a feeding arm which seems to have been constructed on a standard echinoderm pattern with cover plates and triadic groups of tube feet – there is no such arm in the cornutes; (2) *D. scoticus* had an antibrachial process which is not represented in any cornute (though it is also absent in nearly all other solutes); (3) there was an anterior prominence, probably containing a gonad, near the anterior end of the head in *D. scoticus* – there was no such prominence in any cornute and the gonad in all cornutes was probably situated near the posterior right corner of the head; (4) the hydropores, on the hydropore node, were anterior in position and just right of and behind the mouth in *D. scoticus* where they penetrated the skeleton to form a madreporic plate – in cornutes the hydropore is only known to exist in *C. perneri* where it is slit-shaped and situated near the posterior right of the head; (5) the gonopores in *D. scoticus* are anterior, just left of the mouth, multiple and sometimes occluded – in *C. perneri*, which probably represents the primitive condition for cornutes, it is a single circular hole across a suture, is never occluded and is situated posteriorly in the head, just right of the anus; (6) *D. scoticus* had presumably only one gill slit (unless the gill slits were internal and the external branchial opening was an atrial opening) whereas *C. perneri* had seven such slits and other cornutes, except the most crownward ones where the number is irregular, had more than seven; (7) the head skeleton of *D. scoticus* consisted of a large number of plates, mostly irregular, whereas that of *C. perneri* was constructed of a smaller number of regular plates (none of the plates can reliably be homologized between the two species); (8) the brain of *D. scoticus* did not occupy the whole of the tail insertion, had no auditory groove or median eye, and was linked, so far as known, to a single pyriform body (trigeminal ganglion) on the left, whereas the brain of *C. perneri* occupied the whole tail insertion, was associated with a pair of pyriform bodies and with an auditory groove and a median eye; (9) as to head chambers, there is no sign of a posterior coelom (left epicardium) in *D. scoticus*, whereas such seems to have existed in *C. perneri* and probably in all other cornutes; also it is uncertain whether or not *D. scoticus* had a buccal cavity; (10) the alternation of fore-tail plates on right and left is more irregular in *D. scoticus* than in *C. perneri* and the ventral overlap of right and left ventral plates is less extensive; (11) the mid-tail region of *D. scoticus* is altogether more irregular than that of *C. perneri* or any other cornute – in particular in *D. scoticus* there is no massive ossicle corresponding to the stylocone, while in cornutes nothing corresponds to the serial continuity of hind-tail plates with the right dorsal and right ventral plates of the fore tail in *D. scoticus*; (12) the hind tail of *D. scoticus* was rigid and its dorsal skeleton was constructed of a single unpaired series of rather long approximately hemicylindrical plates, not the right and left series of short imbricating plates seen in *C. perneri* and other cornutes.

The phylogenetic meaning of these differences from cornutes will be discussed below. Here I shall only repeat that, despite some differences, the fundamental identity of plan between solutes and cornutes seems obvious.

Comparison of Dendrocystoides scoticus *with* Cephalodiscus

The latest common ancestor of echinoderms and chordates, in my opinion, resembled the recent hemichordate *Cephalodiscus* but had become dexiothetic, i.e. had been modified to lie on its right side (Jefferies 1969, 1979, 1986, Chaps. 2 and 9; text-fig. 15 herein). In this respect, a comparison



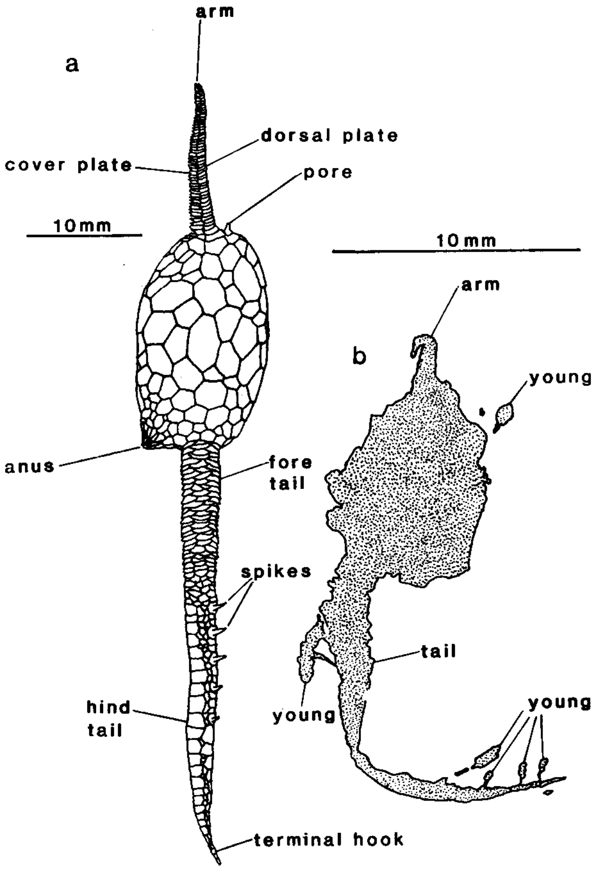
TEXT-FIG. 15. The dexiothetic rotation. In the origin of the Dexiothetica, it is likely that a *Cephalodiscus*-like ancestor fell right-side downwards onto the mud of the sea floor and lost the openings and arms of the primitive right side in consequence. The stalk was retained and became the chordate tail; an = anus; ax = axocoel (protocoel); bs = branchial slit; g = gonopore; h = hydropore (left and right mesocoel pores); l. hyd, r. hyd = left and right hydrocoels (mesocoels); l. som, r. som = left and right somatocoels (metacoels).

between *Dendrocystoides scoticus* and *Cephalodiscus* is illuminating. I discuss the tail first, and then the head, beginning at the front and working rearwards.

An evolutionary change of orientation, such as dexiothetism, brings great danger of muddle in the description. I find it necessary to use two equivalent sets of terms. Thus, with reference to *Cephalodiscus*, I write of hemichordate-ventral, hemichordate-dorsal, etc., and with reference to *D. scoticus* I write of chordate-ventral, etc. The reader will understand this most easily by remembering that: hemichordate-left = chordate-dorsal; hemichordate-right = chordate-ventral; hemichordate-dorsal = chordate-right; hemichordate-ventral = chordate-left. Posterior and anterior mean approximately the same in hemichordates and chordates. In using these terms, I do not imply that *D. scoticus* was a chordate, though this was probably true as discussed later. I merely intend to assert that, for example, the dorsal surface of *D. scoticus* was homologous with the dorsal surface of Man. The hemichordate terminology for orientation is the same as that traditionally used in describing echinoderm larvae.

The tail is the first noteworthy point of comparison. *D. scoticus*, like all other solutes and also the cornutes and mitrates, was divided into a tail and a head. In like manner, *Cephalodiscus* is divided into a stalk and the rest of the body. This stalk can be markedly lengthened or shortened and is used, in prehensile fashion, in collaboration with the head shield, for climbing up and down a horny skeletal process which projects upwards from the coenoecial cup. (In the tubeless hemichordate *Atubaria* the stalk is similarly used for clambering over hydroids [Sato 1936].) It is likely that the tail of *D. scoticus* was likewise locomotory, serving to pull the head rearwards over the sea floor like the tail of cornutes and mitrates, probably by side-to-side motion as in primitive cornutes. The stalk of *Cephalodiscus* would differ from the tail of *D. scoticus* in its mode of action, however, since the latter could bend proximally but was probably in all parts constant in length – this constancy of length certainly held for the rigid mid- and hind-tail regions but, in addition, the plates of the fore tail, because of their dorsal and ventral overlaps and sutures at right and left, suggest that the fore tail could bend right and left but not shorten or lengthen. This in turn suggests that the fore tail contained an incompressible but flexible notochord, as was probably true in cornutes and mitrates also. The notochord probably continued rearwards from the fore tail of *D. scoticus* to fill the canal between the dorsal and ventral plates of the hind tail, just as the notochord of the cornutes probably continued posteriorly into the median groove of the ventral hind-tail ossicles. There is no notochord in the stalk of *Cephalodiscus*, and its very absence allows the stalk to stretch and shorten.

An attachment sucker exists at the distal end of the stalk of *Cephalodiscus* (text-fig. 13). By means of this sucker, the animal fixes itself, at will, to the surface of the horny coenoecium – usually to the inner face of the coenoecial cup. There is no sign of such a sucker on the end of the tail of *D. scoticus*, though this may be due to ignorance, since the end of the tail has seldom been seen. It is fascinating to note, however, that Ubaghs (*in* Ubaghs and Robison 1985) observed in the Middle Cambrian solute *Castericystis vali* Ubaghs and Robison 1985 (text-fig. 16) that the adults often carry on their surface small, and therefore presumably young, individuals of the same species. These small animals are attached to the adult by distal ends of their tails. This strongly suggests that, at least in juveniles, the tail of *G. vali* had an attachment sucker at its distal end, perhaps followed in time by temporary cementation. (An alternative hypothesis, that the juveniles arose by budding from the associated adult, is unlikely because the juveniles are disposed seemingly at random on the adult body, whether on the head or the tail, with no orderly relationship between the size of the juvenile and its position on the adult.) If the tail of *C. vali* had a sucker on its end in the juvenile, a comparison with the stalk of *Cephalodiscus* is reinforced. I therefore propose that the stalk of hemichordates is homologous with the tail of solutes, and also with the tail of chordates in general. I first implied that the stalk of *Cephalodiscus* was homologous with the tail of cornutes (then called by me the stem) in Jefferies (1969). Gradually I abandoned this view for lack of evidence and in my book of 1986 I did not even mention it as a possibility. Ubaghs' interesting observations now make it likely again. I therefore now agree with the percipient remark of Eaton (1970, p. 977) when he said that: '...it is highly probable that the tail [of cornutes and mitrates] is a specialized version of the pterobranch peduncle.' Henceforth I shall stress this presumed homology by referring to the stalk of



TEXT-FIG. 16. *Castericystis vali* Ubaghs and Robison 1985 – a solute from the Middle Cambrian Marjum Formation of Utah (USA). (*a*) Reconstruction redrawn after fig. 1 of Ubaghs and Robison (1985) – the reconstruction is in an anatomically possible position for a corpse, but the hind tail is in right aspect, the head in ventral aspect and the arm in left aspect; (*b*) drawing traced from a photograph (Ubaghs and Robison 1985, fig. 11/5) to show the presence of young individuals of the species fixed to a presumed adult by the ends of their tails (×3·5).

hemichordates as the tail. In this I follow the usage of Burdon-Jones (1952) when he described the homologous organ of post-larval enteropneusts.

The planes of bilateral symmetry in the tails of *D. scoticus* and *Cephalodiscus* do not correspond to each other, if *D. scoticus* is supposed to have undergone a dexiothetic rotation: in *Cephalodiscus* the plane of symmetry in the tail is sagittal, which ought to correspond to chordate-horizontal, but the plane of symmetry in the tail of *D. scoticus*, admittedly imperfect in the mid and fore tail, is vertical. The position of the plane of symmetry has therefore rotated through 90°, either clockwise or anticlockwise when seen from behind, from hemichordate-sagittal to chordate-sagittal, thus counteracting the dexiothetic rotation.

The feeding arm of *D. scoticus*, with its ventrally-opening cover plates and its presumed ambulacral groove, water vascular canal and tube feet in probable triads, projects from the head at the opposite pole to the tail. The obviously comparable structure in *Cephalodiscus* would be part of the arm apparatus. More exactly, the best comparison would be with a single arm of the left side of *Cephalodiscus*. For the feeding arm of *D. scoticus* is presumably homologous with part of the water vascular system of echinoderms, and this system, in turn, is homologous with the left arm apparatus (left mesocoel = left hydrocoel) of *Cephalodiscus* (Jefferies 1986, p. 318).

There are difficulties in this comparison, however. For in a *Cephalodiscus* seen from the left side, the left arms present their food grooves toward the observer, whereas the food groove of *D. scoticus* in dorsal aspect faced away from the observer. If *Cephalodiscus* represents the primitive condition, therefore, the feeding arm of *D. scoticus* has rotated through 180° so that the food groove opens not towards chordate-dorsal but towards chordate-ventral. The right and left mesocoels of

Cephalodiscus open to the outside each by a mesocoel pore. In common with echinoderms, *D. scoticus* had no trace of any such pore so perhaps, as in echinoderms, the left mesocoel communicated with the axocoel (= protocoel) by a stone canal while the right mesocoel, together with its pore, had disappeared. Rehkämper and Welsch (1988) have stressed the fine-structural similarities between the stone canal of echinoderms and the mesocoel pores of *Cephalodiscus*. These resemblances suggest to me that perhaps the stone canal is homologous with the left mesocoel pore of hemichordates but has come to open into the protocoel (= axocoel) instead of direct to the outside.

The mouth of *Cephalodiscus* opens, in a hemichordate-ventral position, behind the head shield and faces posteriorly, toward the tail. The mouth of *D. scoticus*, on the other hand, is anterior and at chordate-right. In passing from the *Cephalodiscus* condition to the *D. scoticus* condition, therefore, the mouth would have rotated through some 160°, clockwise in chordate-dorsal aspect, about a vertical axis. Such a rotation would shift the left protocoel pore (equivalent to the hydropore of *D. scoticus* and the echinoderms) from a position anterior to the mouth to one where it lay, as actually observed in *D. scoticus*, chordate-right of the mouth. This suggests that, in addition to the dexiothetic rotation, *D. scoticus* differs from *Cephalodiscus* in having undergone a clockwise rotation of the anterior part of the head about a chordate-vertical axis. I shall refer to this additional rotation as anteriorisation of the mouth. The same rotation would perhaps explain another difference between *Cephalodiscus* and *D. scoticus*, namely the absence from the latter of any externally distinguishable part of the body corresponding to the head shield (protosome). Presumably, *D. scoticus* had an equivalent of the protosome, in that it would have possessed a protocoel (axocoel) buried inside the head and opening upwards at the hydropore. The burial of the protosome in the head might easily result from anteriorization of the mouth since the mouth, in moving chordate-rightwards and anteriorly, would press on the protosome. Such burial of the protosome is presumably a derived feature which *D. scoticus* shared with echinoderms and also with definite chordates, since the cornute *Ceratocystis* had a hydropore but no externally distinct protosomal body region. The heart and pericardium of *D. scoticus* would probably be near the hydropore, like the equivalent head process of the axial organ and dorsal sac of echinoderms. These structures are equivalent to the heart and pericardium in the protocoel of hemichordates, which lie anterior to the mouth in *Cephalodiscus*. The rotation involved in anteriorizing the mouth of *C. scoticus* would have shifted the heart and pericardium to their presumed new positions also.

As for the gonad, I have argued above that the anterior prominence of *D. scoticus* contained a gonad which issued by a group of gonopores at the chordate-anterior-right of the prominence. The gonad, being chordate-dorsal in position, presumably corresponds to the left gonad of *Cephalodiscus* and the gonopores to the left gonopore. In general position at the anterior end of the body farthest from the tail, the gonad of *D. scoticus* is comparable with the left gonad of *Cephalodiscus* and contrasts in both these animals with the cornute situation where the gonad was at chordate-right and posterior in the head. However, there are also differences between *Cephalodiscus* and *D. scoticus* since in the latter the gonad and gonopore lay chordate-left of the arm whereas in *Cephalodiscus* they were at chordate-right of the arms (dorsal to them in hemichordate terms). In passing from *Cephalodiscus* to *D. scoticus*, therefore, the gonopore and gonad would move chordate-leftwards. I cannot decide whether this was part of the clockwise rotation of the anterior part of the head implied by the anteriorization of the mouth, or whether it was an independent process.

The embryological origin of the gonad of echinoderms is interesting here: the primordial germ cells are said to arise from the wall of the left somatocoel in crinoids (MacBride 1914, p. 552), in asteroids (Gemmill 1914) in crinoids (Hyman 1955, p. 502) and in ophiuroids (Hyman 1955, p. 636). (No comparable statement can be made for the holothuroids, perhaps because the distinction between left and right somatocoels breaks down at an early stage.) It seems likely, therefore, that the gonad or gonads of echinoderms, like that of *D. scoticus*, correspond to the left gonad of *Cephalodiscus*.

The pharynx of *D. scoticus* seems to have been elongate, stretching from the mouth or velar mouth at anterior chordate-right to the gill slit at posterior chordate-left, with presumably an oesophageal opening posterior and right of it somewhere along its course. (A dubious point, as already mentioned, is whether *D. scoticus* had a buccal cavity.) The position of the pharynx in *D. scoticus* is broadly the same as in *Cephalodiscus* seen from the left, but the two pharynges differ in shape. The differences correspond to extension of the pharynx chordate-leftwards and rearwards and chordate-rightwards and forwards in *D. scoticus*, with the loss of a gill slit (the hemichordate right gill slit) and the migration of the remaining gill slit to a chordate-left-posterior position. In these respects, the pharynx of *D. scoticus* was more cornute-like than that of *Cephalodiscus*.

Concerning the non-pharyngeal gut, the stomach of *D. scoticus* probably coincided in position with the posterior dorsal and ventral prominences. This position, near the centre of the head, is comparable with the stomach of *Cephalodiscus* as seen from the left. The position of the anus in *Cephalodiscus* and *D. scoticus* is comparable in being, in both animals, chordate-right of the tail, but it differs in being more posterior in *D. scoticus*, nearer to the proximal end of the tail. This difference in the position of the anus implies that the intestine and rectum must also have been differently disposed, but nothing precise can be said about this since there is no evidence in *D. scoticus* of the course of the gut between stomach and anus.

Not much can be said about the positions of the coeloms in *D. scoticus*, compared with *Cephalodiscus*. If *D. scoticus* has undergone a dexiothetic rotation with respect to *Cephalodiscus*, then the right somatocoel (= right metacoel) would be downward and the left somatocoel upward, as is primitively the case in echinoderms (Jefferies 1986, p. 51) and as seems also to have been true in cornutes and mitrates (Jefferies 1986, p. 198ff. in discussing left and right anterior coeloms = left and right somatocoels). The mesentery between the two somatocoels would thus be horizontal. The left hydrocoel (= left mesocoel) would be located in the feeding arm while the right hydrocoel (= right mesocoel) would have disappeared. And the axocoel (= protocoel), buried inside the head but single and unpaired as in hemichordates, would open upwards at the hydropore, just right of the mouth and right of the arm base, the hemichordate right protocoel pore having disappeared.

Finally as for size, *D. scoticus*, like all other solutes, was about 30 mm in head length and therefore much bigger than *Cephalodiscus*, whose greatest head length is about 5 mm.

To summarize, if *D. scoticus* is compared with a *Cephalodiscus* lying on its right side, and if the latter is assumed, in all respects, to represent the primitive condition, then the following changes would have occurred in passing from *Cephalodiscus* to *D. scoticus*.

(1) The evolution of a calcite skeleton and the formation of specialized plates in some regions, especially in the tail, the tail insertion, the arm and the arm insertion.

(2) The evolution of a vertical plane of symmetry in the tail and probably the origin of the notochord so that locomotion took place by lateral bending of the tail, rather than by shortening and lengthening of it; loss of the power of budding, which had been located in *Cephalodiscus* at the distal end of the tail.

(3) Loss of all the hemichordate-right arm apparatus and all but one arm of the hemichordate-left arm apparatus; rotation of the remaining left arm through 180° so that the food groove opened chordate-downwards; development of a triadic arrangement of tube feet regularly related to the cover plates; loss of the hemichordate-left and hemichordate-right mesocoel pores. (Perhaps the hemichordate left mesocoel pore became the stone canal of dexiothetes, which in extant forms is retained in echinoderms but absent in chordates.)

(4) Anteriorization of the mouth, involving some degree of rotation of the anterior part of the body clockwise about a chordate-vertical axis, so that the hydropore came to lie chordate-right of the mouth rather than anterior to it; loss of the head shield (protosome) as an externally distinct body region, by burial of the protocoel (axocoel) in the body chordate-right of the mouth (this burial may have resulted from the anteriorization of the mouth, that is from the clockwise rotation of the anterior part of the head which such movement of the mouth implies); loss of the hemichordate-right, chordate-ventral protocoel pore; perhaps the evolution of a stone canal linking the hemichordate-left hydrocoel (= left mesocoel) with the axocoel (= protocoel).

(5) Loss of the hemichordate-right gonad and right gonopore; migration of the hemichordate-left

gonad and left gonopore chordate-leftwards, so as to lie left of the arm when *D. scoticus* is viewed in dorsal aspect.

(6) Movement of the hemichordate-left gill slit from a chordate-anterior-central to a chordate-left-posterior position, with corresponding elongation of the pharynx.

(7) Migration of the anus from chordate-anterior-right to chordate-posterior-right in the head.

(8) Evolution of a brain and a left trigeminal ganglion at the anterior end of the tail.

(9) Loss of the hemichordate-right hydrocoel (= right mesocoel); repositioning of the hemichordate-right and -left metacoels, as a result of dexiothetic rotation of the animal, to become respectively chordate-ventral and chordate-dorsal.

(10) Increase in size.

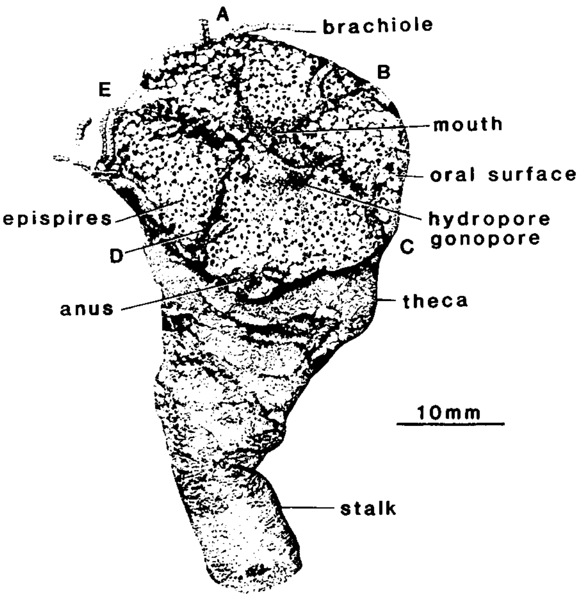
Not all these changes would actually have happened since *Cephalodiscus* is probably not in all ways more primitive than *D. scoticus.*

Comparison of Cephalodiscus *with* Kinzercystis

The 'eocrinoid' *Kinzercystis* (text-fig. 17), from the Lower Cambrian Kinzers Formation of Pennsylvania in the U.S.A., has been well described and reconstructed by Sprinkle (1973) and Paul and Smith (1984). The latter authors regard it as belonging to the crown group of the echinoderms, seeing it as a primitive member of the Pelmatozoa. I choose it for comparison here for three reasons: because it is well studied; because, unlike most primitive echinoderms, the hydropore is separate from the gonopore; and because I wish to simplify the phylogenetic argument by concentrating on one quinqueradiate echinoderm only.

Kinzercystis was a small animal about 30 mm in height and 25 mm in greatest width. It was an inverted truncated cone in shape and plated all over with calcite plates. The wide end of the cone, which would have faced upward in life, was the oral surface while the truncation of the cone, downward in life, was developed as a circular attachment area by which the animal could fix itself to objects on the sea floor.

The oral surface was approximately circular with an elongate mouth near the centre, roofed over by cover plates. Three ambulacral grooves radiate from the mouth, and two of these split into two not far from the mouth. This produces five food grooves in all, with a 2+1+2 arrangement suggesting a vestigial triradiality. The undivided food groove is conventionally labelled A and the



TEXT-FIG. 17. The eocrinoid *Kinzercystis durhami* Sprinkle 1973 from the Lower Cambrian Kinzers Formation of Pennsylvania (USA). Copied from Paul and Smith (1984, fig. 8) and relabelled.

others, in clockwise direction seen from above, are numbered B, C, D and E. Conventionally the A food groove is taken as anterior and the C–D interradius as posterior. In the C–D interradius, just behind and to the right of the mouth when seen from above, there are two openings very close to each other. The opening nearer to the mouth is spout-shaped and is identified by Paul and Smith as the hydropore while the other opening, guarded by a pyramid of small spike-shaped plates and therefore intermittently closable in life, is identified by them as the gonopore. (Sprinkle [1973, p. 74] labelled hydropore and gonopore conversely, but Paul and Smith's view is preferable because it agrees with the situation in cystoids and because it is reasonable to suppose that a gonopore could be closed intermittently.) Also in the C–D interradius, near the edge of the oral surface and left of the mouth as seen from above, was the anus guarded by an anal pyramid.

Each ambulacral groove rested on two series of flooring plates and was covered on each side by a plated lip – the plates of these lips are called cover plates. On either side of each ambulacral groove, alternating in position, was a series of flexible plated appendages called brachioles which Paul and Smith interpret, for good reasons, as plated tube feet. The interambulacra were covered with large plates which, at their sutures, carried openings called epispires. These may have had a respiratory function, each one marking the position of a thin-called external gill or papula.

The aboral suface of *Kinzercystis* was in two parts – the distal attachment area and the rest. The attachment area was approximately circular and plated with polygonal plates, whereas the remainder of the aboral surface, vaguely divided into an upper wider theca and a lower almost cylindrical holdfast, is covered with imbricating plates (Sprinkle, 1973, p.70, fig. 22). The imbrication is such that, seen from outside, lower plates overlap the lower parts of higher ones. This imbrication suggests that the aboral surface was able to elongate and shorten.

Kinzercystis can be interpreted, in its main anatomical features, by comparison with crinoids (for references see Jefferies 1986, pp. 47ff.). It is highly probable that, at least in the juvenile stages, a right and left somatocoel would have been present, with the right somatocoel located toward the attachment and the left somatocoel lying orally. Much of the gut would have been situated between the two somatocoels. The ambulacral grooves would have been occupied by radial water vessels with brachioles representing the tube feet, and this water vascular system would correspond to the left hydrocoel of the larva. The hydropore would be the opening of the axocoel and would communicate with the water vascular system by a stone canal. The attachment area would be homologous with the axocoel attachment area of the larva and thus with the ventral suface of the head shield of *Cephalodiscus*. The gonad, opening at the gonopore, would probably be homologous with the left gonad of *Cephalodiscus* as suggested above.

In comparing *Kinzercystis* with *Cephalodiscus* I shall assume, as when discussing *Dendrocystoides scoticus*, that *Cephalodiscus* in most ways represents the primitive condition. Some of the differences between *Cephalodiscus* and *Kinzercystis* are shared by the latter with *D. scoticus* and can be seen as synapomorphies of *D. scoticus* and *Kinzercystis* in a three-taxon comparison. Such include:

(1) The dexiothetic rotation, with the oral surface of *Kinzercystis* corresponding to the dorsal surface of *D. scoticus* and to the left side of *Cephalodiscus* – other results of dexiothetism include the absence of the hemichordate-right arm system and right mesocoel pore and of the hemichordate-right gill slit, gonad and gonopore.

(2) The calcitic skeleton.

(3) The disappearance of the protosome as an externally distinct body region, presumably by becoming buried in the body though still opening outwards by the hydropore.

(4) The disappearance of the right mesocoel pore, presumably because the water vascular system communicated with the protosome by a stone canal inside the body.

All four of these advanced resemblances between *Kinzercystis* and *D. scoticus* can be seen as autapomorphies of the Dexiothetica.

Some features which differentiate *Kinzercystis* from *Cephalodiscus* are not shared with *D. scoticus*. These include:

(1) The absence of a tail.

(2) Attachment by the middle of the aboral (chordate-ventral) surface to some external object.

(3) The position of the mouth at the centre of the oral surface.

(4) The recumbent position of the water vascular system on the surface of the body and its division into five branches with a distinct 2+1+2 arrangment.

(5) The absence of any gill slit.

All five of these distinguishing features of *Kinzercystis* in the three-taxon comparison can be seen as autapomorphies of the crown echinoderms, except for attachment by the aboral surface to an outside object which is perhaps an autapomorphy of the pelmatozoans.

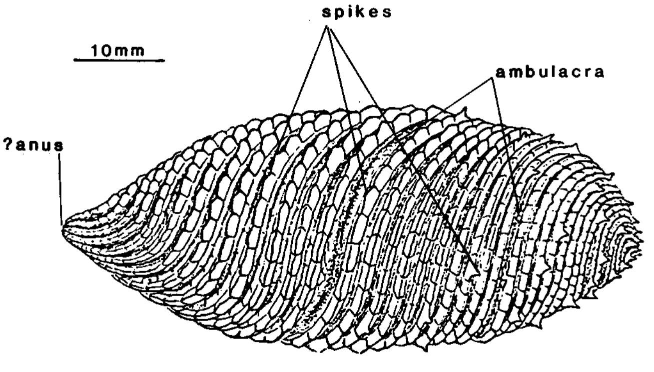
THE SYSTEMATIC POSITION OF *DENDROCYSTOIDES*

The analysis so far shows that *D. scoticus* was a member of the Dexiothetica, that it did not belong to the echinoderm crown group, nor to the chordate crown group, nor to the crownward members of the chordate stem group known as Cornuta. The methodology for placing it more exactly within the Dexiothetica is clear: if it lacked some autapomorphy of the Dexiothetica, it belongs in the stem group of that group; if it shared a synapomorphy with the chordates, particularly with the stem-group chordates of the Cornuta, it belongs in the chordate stem group; if it shared a synapomorphy with the echinoderms, it would belong in the stem group of the echinoderms; and if none of these conditions applied, it would have to remain in the nodal group of the Dexiothetica along with the latest common ancestor of chordates and echinoderms.

There are, in fact, many advanced features connecting *D. scoticus* with cornutes, which are not present in such a primitive echinoderm as *Kinzercystis* for example. In the tail these comprise: (1) the division into fore, mid and hind tail; (2) the quadriserial plating of the fore tail; and (3) the large lumen of the fore tail and its adaptation for bending from side to side, suggesting the presence of a notochord. Just anterior to the tail, *D. scoticus* shows advanced resemblances to cornutes, and to chordates in general, in having a brain and at least one pyriform body. Elsewhere in the head, advanced resemblances to cornutes include the position of the gill slit at posterior left and the corresponding leftward and posterior elongation of the pharynx.

Unfortunately, all these features relate either to the tail or to the gill slit, and both these organs are absent in echinoderms, probably having been lost. Loss of complex structures is intrinsically more likely than their origin. All these advanced resemblances are therefore dubious as synapomorphies between cornutes and *D. scoticus*, because of the possibility that the latest common ancestor of chordates and echinoderms may have had them but that they were then lost in the echinoderm stem lineage when the tail and the gill slit were lost.

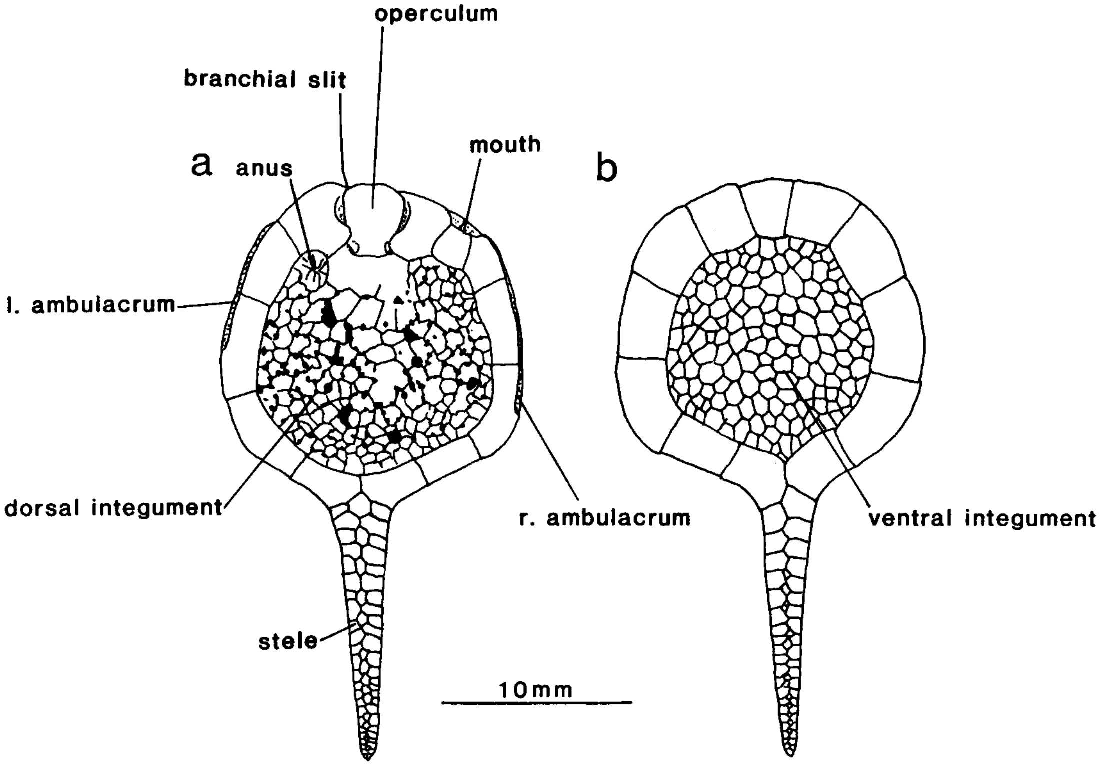
To eliminate this possibility, or perhaps to confirm it, will require study of the echinoderm stem group, to which, up till now, only one group of fossils has been assigned. These are the Helicoplacoidea (text-fig. 18) which Paul and Smith (1984) place as stem-group echinoderms on account of their triradial ambulacral system incorporated in the wall of the body, the mouth being, as Derstler (1981) suggested, at the junction of three ambulacral rays. The helicoplacoids, so far as



TEXT-FIG. 18. The helicoplacoid *Helicoplacus curtisi* Durham and Caster 1963. Reconstruction copied from Durham and Caster (1966, fig. 109a). The presence of spikes over the whole surface of the body suggests that the animal was totally buried in normal life, presumably with the long axis horizontal. About ×2.

known, probably constitute a monophyletic group because of their strongly spiral skeleton. They have no gill slit or tail and these absences confirm their position as echinoderms. Unlike Paul and Smith, I believe that helicoplacoids probably lived entirely buried in the sea bottom, burrowing earthworm-fashion with the long axis horizontal, by dilating or extending different parts of the obviously flexible body. Their spiral structure suggests that they rotated about their long axis as they moved. My reason for suggesting that they lived entirely buried is the presence of low spikes on all parts of the external surface in *Helicoplacus curtisi* (text-fig. 18), *H. gilberti* (Durham and Caster 1966, fig. 107), *Waucobella nelsoni* (Durham 1967, pl. 14, fig. 5), and *Polyplacus kilmeri* (Durham 1967, pl. 14, fig. 1). These spikes look like sediment-gripping structures which could only have functioned when the whole surface of the animal made contact with mud. The helicoplacoids suggest that a triradiate ambulacral system recumbent on the body surface, rather than borne on arms, was evolved in the echinoderm stem lineage and that later this triradiate system gave rise to the quinqueradiate system with a 2+1+2 structure. An important conclusion is that the recumbency of the ambulacral system represents an autapomorphy of echinoderms, not shared by *Cephalodiscus* with its many arms nor by solutes with their single arm.

The Cincta may also belong to the echinoderm stem group. These fossils need restudy since Ubaghs' (1968) comprehensive treatment of them is now rather old. They can be exemplified by *Trochocystites* (text-fig. 19) which is shaped much like a tennis racquet with a theca and an appendage (stele). The animal lay with one face of the theca on the sea bottom and the other upwards. The theca is surrounded by a frame of marginal plates. The appendage or stele, at least proximally, would be stiff in a right–left direction, but perhaps able to bend up and down. In its plate arrangement it resembles an extension of the frame – the major series of plates, at right and



TEXT-FIG. 19. The cinctan *Trochocystites bohemicus* Barrande 1887. Reconstruction redrawn and modified from Ubaghs (1968, fig. 363): (*a*) dorsal aspect, to show anus at anterior left; (*b*) ventral aspect. ×2·5.

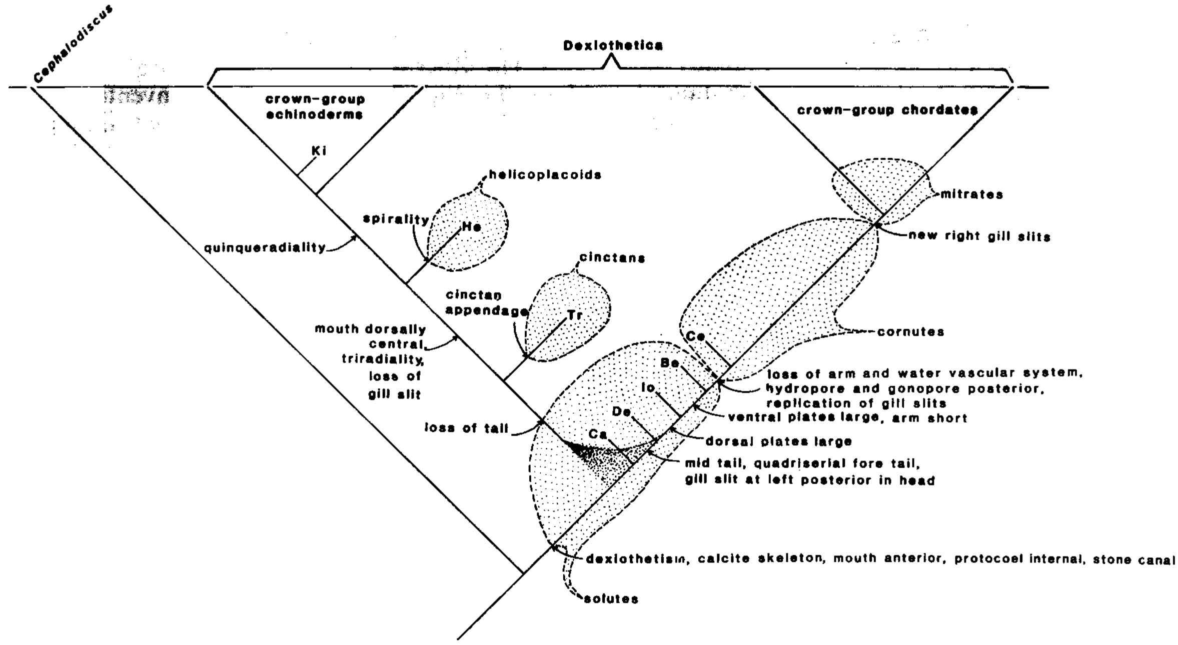
left, resemble and pass into frame plates, whereas intercalated dorsal and ventral plates in the stele resemble dorsal and ventral integument plates in the theca, and probably represent serial homologues of these integument plates. Opposite the stele, two openings have so far been recorded in the literature. The opening more to the right, when the stele is towards the observer, had a pair of ambulacral grooves converging upon it, these grooves coming to it along the marginal frame from right and left. This opening was therefore the mouth which was thus at the centre of a biradial recumbent water vascular system. The two rays presumably correspond to the rays B/C and D/E of *Kinzercystis* and other quinqueradiate echinoderms. The other opening recorded in the literature was covered by a plate, the operculum, hinged at the top. This opening is conventionally interpreted as the anus. However, there is a third opening, not yet recorded in the literature, just to the left of the operculum (Prof. K. Sdzuy, personal communication). This third opening, which is visible in Ubaghs (1968, fig. 367/1), is guarded by a pyramid of plates and is likely to be the true anus. And, in that case, the operculate opening, which in its structure suggests an outlet valve, is probably a gill slit. The recumbency of the water vascular system of cinctans, if interpreted as a synapomorphy with the recumbent water vascular system of helicoplacoids, suggests that Cincta are stem-group echinoderms. This is confirmed by the biradiality of the water vascular system in Cincta, since the 2+1+2 pattern of water vascular system, can be construed as fundamentally biradial.

However, the Cincta are probably less crownward than helicoplacoids in the echinoderm stem group. This is for several reasons: (1) they retain a gill slit; (2) they have a biradial, rather than a triradial water vascular system; and (3) the mouth is in the hemichordate–sagittal plane, as in *Cephalodiscus* – not in the centre of the chordate-dorsal surface as in crown-group echinoderms and, probably, in helicoplacoids. The position of the gill slit, anterior in the body and near to the mouth, resembles that of the left gill slit in *Cephalodiscus* and is therefore probably primitive for echinoderms. This means that the gill slit of the latest common ancestor of chordates and echinoderms would also probably have been anterior in position. And in that case, the left posterior position of the gill slit of *D. scoticus* is probably a synapomorphy with cornutes. If so, then *D. scoticus* is a stem-group chordate, less crownward than any cornute.

The stele of Cincta is difficult to interpret and there are two main possibilities: (1) its position in the animal, as far as possible away from the mouth and therefore posterior, and the fact that it is biserial in its major plating, might suggest that it is homologous with the tail of hemichordates, solutes and chordates; but, (2) the fact that the two series of plates are at right and left, not as in solutes dorsal and ventral, and the fact that in some cinctans the two series are continuous with the marginal plates of the frame (e.g. *Trochocystites*, *Gyrocystis*), might suggest that the stele arose within the Cincta, after the evolution of a marginal frame, as an extension of that frame, and that therefore it is not homologous with a tail. Further work is needed to establish which of these two alternatives is nearer the truth.

If the appendage of Cincta is genuinely a tail, then the chordate nature of *D. scoticus* is almost certain since the species would then share a large number of advanced tail features with the Cornuta which are absent in the Cincta. Such include: the brain; the left pyriform body; the fore, mid and hind regions of the tail; the large lumen of the fore tail, adapted for right–left bending and probably containing muscles and a notochord; and the ventral series of plates in the hind tail, corresponding to the ventral hind-tail ossicles of cornutes. At the moment, however, I am inclined to think that the stele of cincta is an autapomorphy of that group. If so, then the chordate nature of *D. scoticus* remains doubtful, based, as it is, on nothing but the posterior left position of the gill slit.

Whether or not *D. scoticus* is a chordate, it is almost certainly more closely related to the chordate crown group than is *Castericystis*. The conclusion is based on resemblances to *Ceratocystis* (a definite stem-group chordate) which *Castericystis* does not share: i.e., the distinctly tripartite tail of *D. scoticus*, with its stylocone-like mid tail and quadriserial fore tail. Moreover, some solutes resemble *Ceratocystis* still more closely. Thus *Iowacystis* (Caster 1968, p. S620) has the fore tail sharply distinct from the rest of the tail and the dorsal surface of the head is formed of large plates, in both respects like *Ceratocystis*. And *Belemnocystites* is still more like *Ceratocystis* in having a bigplated ventral (as well as dorsal) surface to the head and a very short arm (Caster 1968, p. S623) whereas cornutes have no arm at all. All this suggests that these four solutes are successively closer related to the chordate crown group in the sequence: *Castericystis*, *Dendrocystoides*, *Iowacystis*, *Belemnocystites*. I summarize the results of these arguments in a cladogram (text-fig. 20).



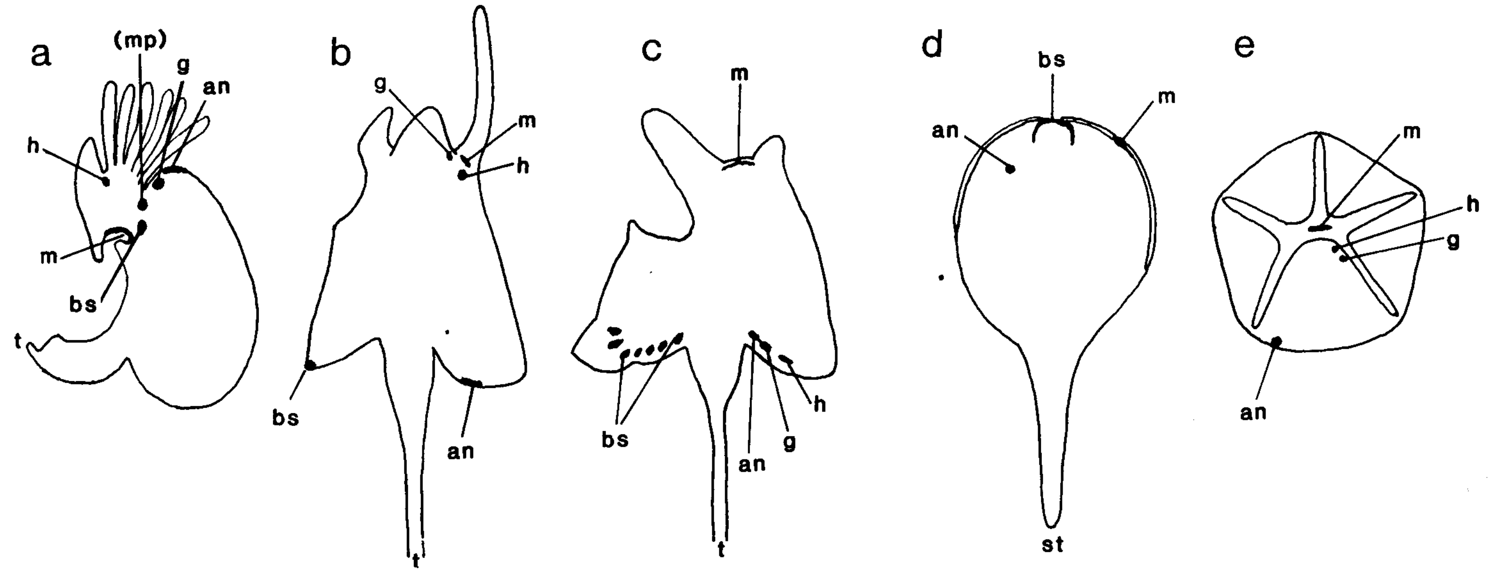
TEXT-FIG. 20. Cladogram of the deuterostomes, to show the phylogenetic position of the solutes within the Dexiothetica: Be = *Belemnocystites*; Ca = *Castericystis*; Ce = *Ceratocystis*; De = *Dendrocystoides*; He = *Helicoplacus*; Io = *Iowacystis*; Ki = *Kinzercystis*; Tr = *Trochocystites*.

As to the timing of the phylogenetic split between echinoderms and chordates, I formerly believed that this happened in the earliest Cambrian (Jefferies 1979, p. 475). This view was based on the assumption that the calcitic skeleton is homologous between echinoderms and chordates and on the further assumption that skeletons in general arose at the base of the Cambrian. The latter belief now seems to be mistaken, however, since Gehling (1987) has described an edrioasteroid-like fossil (*Arkarua adami*) from the late Precambrian Pound Quartzite of Australia. This form has a 2+1+2 symmetry and probably possessed a lightly built skeleton, since it seems to show a marginal ring of plates. If *Arkarua* is correctly regarded as a quinqueradiate echinoderm, as seems likely, then the split between echinoderms and chordates must be older than it. Perhaps the separation occurred in the late Precambrian. This raises the interesting possibility that solutes will be found in the late Precambrian.

CONCLUSIONS

The main conclusions of this paper are as follows.

(1) *Dexiothetism.* Text-figure 21 summarizes the evidence for dexiothetism on the basis of the five animals particularly discussed above. In the diagrams all five are shown in chordate-dorsal aspect, meaning that *Cephalodiscus* is seen from the left while the other animals are seen from above. The view from above is called the dorsal aspect in *Dendrocystoides* and *Ceratocystis*, the upper surface in *Trochocystites* and the oral, or sometimes 'ventral' surface in quinqueradiate echinoderms such as *Kinzercystis*.



Hemichordate	Solute	Cornute	Cinctan	Crown echinoderm
Cephalodiscus	***Dendrocystoides***	***Ceratocystis***	***Trochocystites***	***Kinzercystis***
m	m	m	m	m
h	h	h	(st)	h
(mp)	an	g	an	g
g	*t*	an	bs	an
an	bs	t		
t	g	bs		
bs				

TEXT-FIG. 21. The topological evidence for dexiothetism as shown by five deuterostomes in chordate-dorsal aspect, i.e. *Cephalodiscus* seen from the left and four dexiothetes seen from above. Tabulated below are the sequences of body openings and appendage passed in moving clockwise around each sketch, beginning at the mouth. m = mouth; h = hydropore (left protocoel pore of *Cephalodiscus*; mp = mesocoel pore (of *Cephalodiscus* only); g = gonopore; an = anus; t = tail (stalk of *Cephalodiscus*); bs = branchial slit; st = cinctan stele.

A clockwise journey around each of the five sketches, beginning at the mouth, produces the tabular statements below the sketches, in which the body openings and the tail are listed in sequence. *Cephalodiscus* and *Ceratocystis* have identical sequences, except for the absence of the mesocoel pore in *Ceratocystis*. *Dendrocystoides* is the same as *Ceratocystis* except that the gonopore is out of sequence. *Trochocystites* agrees in sequence with *Ceratocystis*, although with no hydropore, gonopore or tail the sequence has only three members and the random probability of agreement is, in any case, an unimpressive 0·5. With *Kinzercystis*, without tail or gill slit, the random probability for four items is 1/!3 = 0·17. This in itself is no more than suggestive of dexiothetism, but for quinqueradiate echinoderms in general the evidence for dexiothetism does not depend on the topology of the adults, being firmly based on embryology. The major conclusion from text-figure 21 and from embryology is that all the five animals except *Cephalodiscus* have undergone the dexiothetic rotation in their ancestry.

(2) *Failure of the aulacophore theory*. The homology of the tail of *Dendrocystoides* with that of cornutes is confirmed by evidence of the brain and left trigeminal ganglion (see especially pl. 1, figs. 12, 13) at the proximal end of the tail in *Dendrocystoides*, as well as by the division of its tail into fore, mid and hind tail and the quadriserial arrangement of the fore-tail plates. If the tail of solutes is homologous with that of cornutes, then Ubaghs' interpretation of the tail as an aulacophore or feeding-arm cannot be correct. This conclusion is confirmed by difficulties in interpreting the mitrate tail as a feeding arm since one of the leading advocates of the aulacophore theory now accepts that the hind-tail plates of mitrates could not open at the mid line in life (Parsley 1988).

(3) *Homology of the hemichordate stalk and the chordate tail*. Evidence that the early solute *Castericystis* could attach when young to hard surfaces by the distal end of its tail strongly suggests that this tail was homologous with the stalk of *Cephalodiscus* (which has a sucker at the distal end). If the pterobranch stalk is homologous with the chordate tail, and if echinoderms are the extant sister group of chordates, then the echinoderms must have lost the tail in their early phylogeny.

(4) *Similarity of body plan in cornutes and solutes*. If the solutes are orientated as here suggested with the arm at anterior right, then their basic body plan is seen to resemble that of cornutes with the mouth at anterior right, the anus posterior in the head and right of the tail, the gill slit at posterior left in the head, and the flatter surface of the head ventral.

(5) *The phylogenetic position of the solutes*. Solutes had a branchial slit (at least in *Dendrocystoides*), a water vascular system and a tail and in all these respects resembled hemichordates (in which the water vascular system is referred to as the left mesocoel). They were, however, dexiothetes, since they show signs of dexiothetism and had a calcite skeleton. They differed from the stem-group chordates called cornutes by retaining the water vascular system. And they differed from recognized stem-group echinoderms (except possibly the cinctans) in retaining the tail. The latest common ancestor of echinoderms and chordates would have had a tail, a branchial slit and an arm and therefore, if it were ever found, would be placed in the Soluta. The solutes, therefore, straddled the phylogenetic separation between echinoderms and chordates and so, to use Hennig's term, were an invalid stem group of the Dexiothetica. Further work will be needed to put the known solutes in their correct stem groups.

Acknowledgements. I am grateful to my colleague Andrew Smith for telling me, forcibly, that *Dendrocystoides scoticus* was the next animal to study. I am also grateful to a small group of devoted Scottish collectors – Mrs Eliza Gray and her daughters Alice, Agnes and Edith Gray, and Dr Archie Lamont and Mr James Begg – who, between 1880 and about 1940, accumulated the material on which this study is based (Cleevely, Tripp and Howells, 1989). Dr Keith Ingham kindly gave me access to the collections of the Hunterian Museum. Glasgow, and David Lewis was a constant help at the British Museum (Natural History) and made up the plates. I thank my students Tony Cripps, Paul Daley, Fritz Friedrich, and Ian Woods for their moral support and their patient attempts to educate me.

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