TWO NEW CORNUTES FROM THE LOWER ORDOVICIAN OF SHROPSHIRE AND SOUTHERN FRANCE

by P. E. J. DALEY

ABSTRACT. Two new cornutes, *Chauvelicystis vizcainoi* sp. nov., and *Prochauvelicystis semispinosa* gen. et sp. nov. are described. *C. vizcainoi*, from the lower Ordovician (Lower Arenig) of the South of France, has previously been synonymized with *Chauvelicystis spinosa* Ubaghs, 1969, and is shown to be the sister taxon of *C. ubaghsi* (Chauvel, 1966). *Prochauvelicystis semispinosa* is found in the Tremadoc stage (lowest Ordovician) of Shropshire, England, It is the smallest known cornute, and has spines along the right marginals of the head and fixed extensions of the marginal plates forming horizontal appendages on the left side of the head. The spines and appendages are for support on a soft substrate and prevention of movement in an unwanted direction during locomotion. It is the most primitive member of the new subfamily Chauvelicystinae.

THE aims of this paper are threefold: (1) to erect a new species, *Chauvelicystis vizcainoi*, for a cornute from the Lower Arenig of the South of France previously described by Ubaghs (1983), but wrongly identified by him with *Chauvelicystis spinosa* Ubaghs, 1969; (2) to describe *Prochauvelicystis semispinosa*, a new genus and species of cornute, and to consider its functional morphology; and (3) to reconstruct the phylogeny of these and related forms.

Cornutes are controversial animals, and their morphology is currently interpreted in three incompatible ways, associated respectively with the names of Ubaghs (1967, 1981), Jefferies (1967, 1986) and Philip (1979). Ubaghs and Philip regard cornutes as echinoderms, but differ in interpretation of their structures, whereas Jefferies, and Cripps (1988, 1989a, 1989b) regard them as stem chordates; this interpretation will be adopted throughout this paper.

SYSTEMATIC PALAEONTOLOGY

Superphylum DEUTEROSTOMIA Grobben, 1908
Subsuperphylum DEXIOTHETICA Jefferies, 1979
Phylum CHORDATA Bateson, 1886
(Stem group of the Chordata)
Grade CORNUTA Jaekel, 1900 (rank emended)
Family PHYLLOCYSTIDAE Derstler, 1979
Subfamily CHAUVELICYSTINAE subfam. nov.
Genus CHAUVELICYSTIS Ubaghs, 1969

Type species. *Chauvelicystis spinosa* Ubaghs, 1969

Chauvelicystis vizcainoi sp. nov.

Text-fig. 1

(non *Chauvelicystis spinosa* Ubaghs, 1969, pp. 53–56, fig. 23.)
1983   *Chauvelicystis spinosa* Ubaghs, pp. 40–45; fig. A.
1988   *Chauvelicystis spinosa* Ubaghs; Parsley, p. 348. fig. 26.1.
1988   *Chauvelicystis spinosa* Ubaghs; Ubaghs and Robison, p. 15, fig. 6.

Etymology. The species is named in honour of M. Daniel Vizcaïno of Carcassonne, France, who collected most of the relevant material.

Holotype. Specimen A, Melchior Collection, Laboratoire de Géologie Sédimentaire et Paléontologie, Université Paul-Sabatier, Toulouse, France.

Material, horizon and locality. Two nodules bearing part and counter-part of two individuals, specimens A and B, from level *f* of the Lower Arenig *schistes de St Chinian*, Pech de Cossenon, France, Melchior Collection, Université Paul-Sabatier, Toulouse, France, A quartzite nodule bearing the remains of about five individuals denoted by C1, C2, etc. from Cassagnoles, France, Lower Arenig, level *g*, Courtessole-Vizcaïno Collection, Laboratoire de Géologie Sédimentaire et Paléontologie, Université Paul-Sabatier, Toulouse, France, No. OE9.

Diagnosis. Plate b with oar-shaped horizontal flange of fibrillar stereom with three spines attached to its anterior edge, and a convex spineless left edge; spines surrounding the head are either straight or very slightly curved forwards and blunt, with splayed out ends; distance from the tip of the l appendage to the base greater than the width of base (Text-fig. 1).

TEXT-FIG. 1. Ventral view of *Chauvelicystis vizcainoi* (after Ubaghs 1983, fig. 11).
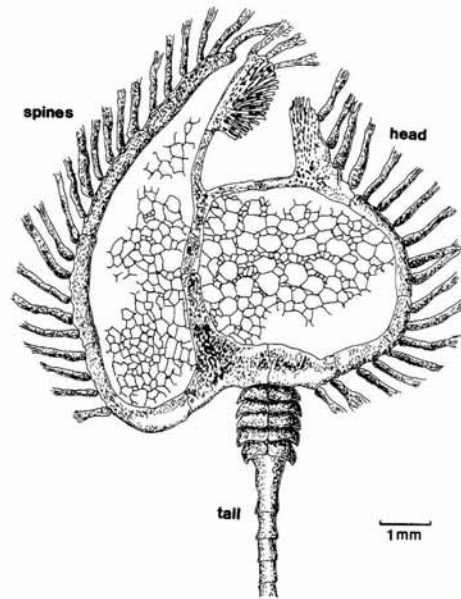
Discussion. *C. vizcainoi* differs from *C. spinosa* Ubaghs, 1969, with which it was incorrectly synonymized by Ubaghs (1983), since *C. vizcainoi* possesses an l-appendage, a flange on plate b, an open frame behind the mouth, and blunt-ended spines. In contrast, *C. spinosa* has no l-appendage, no flanges on plate b, a closed mouth frame and pointed spines. *C. vizcainoi* differs from the similar species *C. ubaghsi* Chauvel, 1966, in that the latter has a less strongly curved buccal lobe region of the head, short broadly-based l-appendage and fan-shaped distal region of plate b.

Genus PROCHAUVELICYSTIS gen. nov.

Etymology. *Pro*, before, and *chauvelicystis*, a name given by Ubaghs (1969, p. 53) in honour of the late M. Jean Chauvel, who contributed much to the study of cornutes and mitrates.

Type species. P. semispinosa sp. nov. here designated.

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Prochauvelicystis semispinosa sp. nov.

Text-figs 3–12
</div>

Etymology. semi, half and *spinosa*, spined – from the presence of spines on the right side of the head only.

Holotype. British Museum (Natural History), London; BM(MH) E63366 from the Arenaceous Beds of Shropshire, England.

Additional material, horizon and locality. Five further specimens, BM(NH) E63363–E63365, E63367 and E63477. The specimens were collected by Dr R. P. S. Jefferies and Dr R. A. Fortey of the British Museum (Natural History) and Dr R. Owens of the National Museum of Wales in March 1987.

The specimens were found in a soft yellow-green shaly horizon of the so-called Arenaceous Beds, part of the Shineton Shales formation of the Tremadoc stage in Shropshire, England (Stubblefield and Bulman 1927). The Tremadoc is now considered to be of lowest Ordovician age (Norford 1988). The collection site was the low river cliff forming the east bank of the Coundmoor Brook, near Bull Hill Cottage, Harnage Grange, Cressage, Shropshire, UK National Grid reference SJ 555 014 (Text-fig. 2), location C of Stubblefield and Bulman (1927, p. 114).

TEXT-FIG. 2. Locality map redrawn from Ordnance Survey 1/25,000 sheet SJ40/50 2nd series 1979. Collecting site marked 'X'.
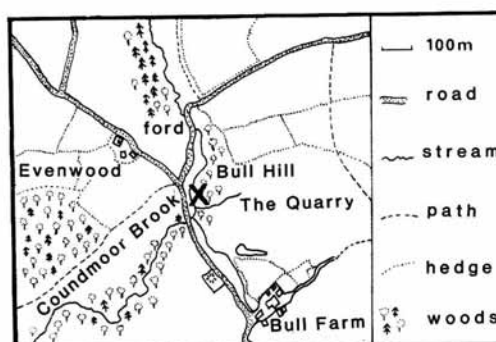
The Arenaceous Beds contain no species of the youngest British Tremadoc biozone fauna (that of *Angelina sedgwicki*), but some species of the second youngest biozone fauna (that of *Shumardia (Conophrys) salopiensis*) are present, suggesting that the lower Arenaceous Beds are slightly younger than the *S. (C.) salopiensis* Zone, but probably older than the *A. sedgwicki* Zone (Fortey and Owens 1991).

The Arenaceous Beds show evidence of having been laid down as turbidites and contain a diverse continental-shelf trilobite fauna, but the absence of graptolites implies that deposition was not in the open sea (R. A. Fortey, pers. comm., 1990). The presence of complete trilobites and remains of moulted exoskeletons in the Arenaceous Beds suggests that the fossil assemblages are *in situ*, and have not been transported.

Diagnosis. A cornute with spines on the right side of the head only; left side marginal plates extend horizontally and forward as rigid appendages; a trapezoidal x-plate and somewhat flattened ventral surface.

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METHODS AND TERMINOLOGY
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Prochauvelicystis semispinosa was reconstructed by drawing the natural moulds and latex casts to scale on a drawing board. Six projections were drawn: dorsal and ventral, anterior and posterior, right and left lateral (Text-fig. 3).

The plate nomenclature follows the system established by Jefferies and Prokop (1972), as revised

in Jefferies, Lewis, and Donovan (1987). This system uses letters or numbers, or a combination of them, to identify homologous plates. A combination of characters implies plate fusion, e.g. plate de is believed to result from fusion of plates d and e.

DESCRIPTION

Head

The head is boot-shaped, but is less asymmetrical than in, for example, *Cothurnocystis elizae* Bather, 1913. As in all cornutes, the skeleton of the head is formed from plates of calcite stereom, histologically identical to the calcite skeleton of echinoderms. The microstructure of this stereom is mainly labyrinthic (see Smith 1980, p. 8 for stereom histology). Text-figures 3 and 5a–b show the general appearance of *Prochauvelicystis semispinosa* while Text-figure 4 shows the marginal plates of the head and their nomenclature.

On the left side of the head three similarly sized subtriangular plates, k, t, and l, are prolonged to form appendages (Text-figs 3, 4, 5a–b). The junctions between these plates are small in area and possibly allowed some relative movement. The appendages point forwards and their ventral surfaces are flat.

Plate x is a small trapezoidal plate whose left posterior edge contacts plate 1 (Text-figs 4, 5a). The anterior face of x touches the posterior part of plate b.

Plate a (Text-figs 3b, 5a–b) is produced posteriorly into a strut process which meets the strut process of plate g. The strut process of a is curved slightly to the right posteriorly and is posteriorly truncated. The mid-part of the left side sutures with the anterior right side of plate l. Anteriorly plate a contacts the posterior margin of plate b. Plate x fits on to a dorsal facet in plate a and covers almost all of the anterior half of the latter plate (Text-figs 4, 5a).

Plate b is a large blade-like plate which frames the left side of the oral region and the buccal cavity (Text-figs 3–4, 5a–b, 6). It is somewhat thickened proximally, but tapers peripherally to a flange of fasciculate stereom. The flange would increase the area of the substrate supporting the weight of the head, thus lessening any tendency to sink in the mud.

Plate c forms much of the right side of the oral lobe and of the buccal cavity (Text-figs 3–4, 6). It is similar in shape to plate b, but smaller and with a less pronounced flange. The relative positions of the sites of attachment of the buccal integument to plates b and c show that the mouth opened obliquely leftwards at about 45° to the longitudinal axis (Text-figs 3, 6).

About 15 spines articulate in a single horizontal row to the outer edge of the right marginal plates (Text-fig. 3). The spines point anteriorly, as do the appendages on the left side of the head. On all of the right marginal plates, the spines are separate from the marginals themselves, and articulate by small tubercles fitting into sockets in the marginals. They may have been capable of active movement, but scars for muscle attachment are not visible. They certainly would have been able to move passively. The row of spines begins posteriorly with the minute hindmost spine on plate g, increase in size along f, and then decrease to two-thirds of this size on the distal part of c. All spines consist of fasciculate stereom (Text-fig. 5c).

Plate de contacts the posterior part of plate c and probably results from fusion of plates d and e (Text-fig. 7). This plate has on its median surface a pronounced overhang (Text-figs 3a, 5a), the median apex of which probably marks the right posterior angle of the buccal cavity.

Plate f adjoins plate de (Text-fig. 5a). It widens and becomes higher posteriorly, from its low and narrow junction with the latter. It bears a ventral posterior flange and a roughened raised postero-dorsal ridge.

Plate g is the largest plate (Text-figs 5a–b, 8). Its right side attaches to f by a suture of complex curvature which would have prevented any movement. The posterior left part of g is expanded to form a lobe which bears on its ventral outer margin a flange directed downwards posteriorly and continuous with that of f. This flange becomes less pronounced leftwards, and is also absent at the tail-junction. At the latter region g was probably overlapped by the anterior ventral plates of the fore-tail. The right half of the cerebral basin forms a deep excavation in the left half of g lined with microperforate stereom. Just to the right of the basin, and running roughly parallel to its edge, is the reception groove for the tail insertion. As with plate f, the dorsal part of plate g is a raised area of coarse labyrinthic stereom. A right-angled excavation in the left side of the raised area is the attachment site for plate h (Text-figs 5a, 8).

Anteriorly, plate g is prolonged to form the posterior part of the strut. The strut curves leftwards anteriorly and is keeled dorsally, forming two faces sloping away from each other (Text-figs 5a, 8). Ventrally, it bears a shallow depression whose margins are parallel to the outline of the plate (Text-fig. 5b).

Plate j sutures to the left of plate g at a gently curved joint, convex leftwards in dorsal aspect (Text-figs 5a–b, 8). Like g, it has a flange on its postero-ventral edge which decreases in depth medially, disappearing at
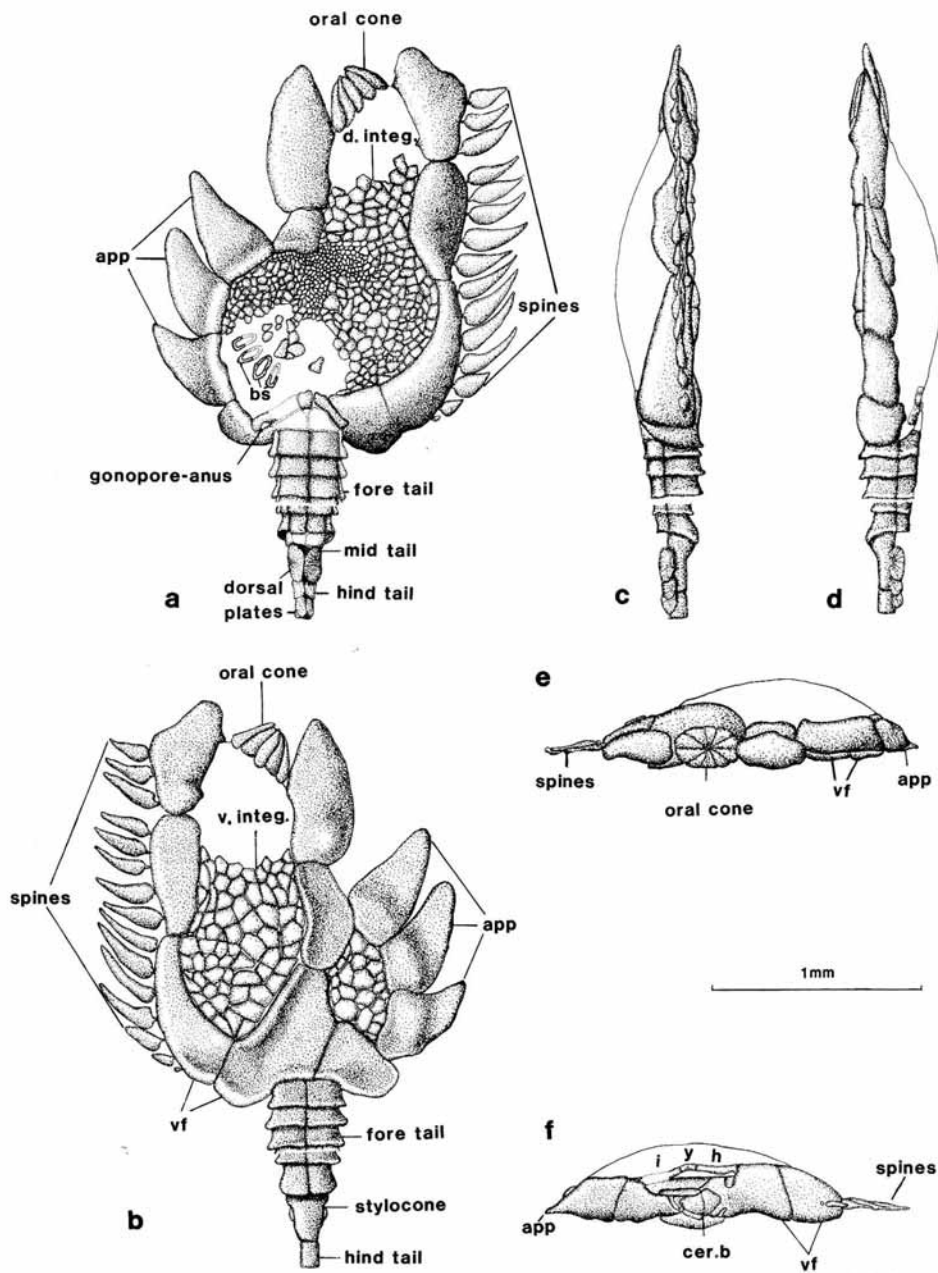
TEXT-FIG. 3. Reconstruction of *Prochauvelicystis semispinosa*: *a*, dorsal aspect; *b*, ventral aspect; *c*, right lateral aspect; *d*, left lateral aspect; *e*, anterior aspect; *f*, posterior aspect. Abbreviations: app., appendages; cer. b., cerebral basin; d. integ., dorsal integument; v.f., ventral flanges; v. integ., ventral integument.
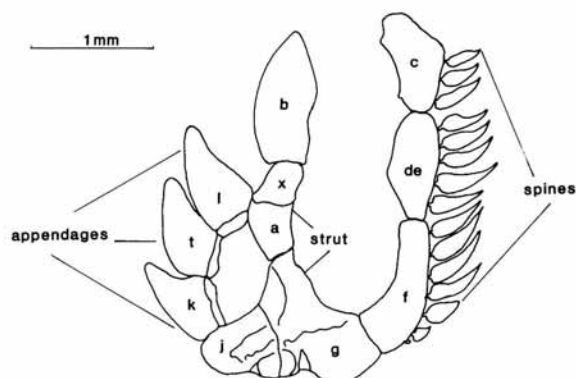
TEXT-FIG. 4. Marginal and strut plates of *Prochauvelicystis semispinosa*.

the tail junction. This flange also becomes lower towards the left margin of the plate. As in plate g, a shallow excavation occupies most of the ventral surface of the plate (Text-figs 3*b*, 5*a*). The area of raised coarse stereom forming the dorsal external surface of the plate is less pronounced than in g. On the inner face, the gonorectal groove runs leftward from the suture with g and ends in an upward-running groove (Text-figs 5*a*, 8). Parallel to the gonorectal groove, and anterior to it, is a thin wall of stereom which would have formed the rear boundary of the posterior coelom (Text-figs 5*a*, 8).

The dorsal tail-junction plates h, y, and i, are poorly preserved. Plate h is long with a straight right portion and a somewhat curved left part (Text-figs 5*a*, 8).

Plate y is a small element bearing a notch posteriorly (Text-figs 3, 5*a*). In the cornute *Ceratocystis perneri*, Jefferies (1969, p. 521) suggests that this notch is associated with a nerve leading directly upward from the brain and that it could have been the site of a median eye. The same is presumably possible for *P. semispinosa*.

Plate i is very poorly preserved with only about half remaining (Text-fig. 5*a*). A poorly defined notch at one end may indicate the dorsal margin of the gonopore-anus. Plate i would overlie the gonorectal groove in life.

The skeleton of the dorsal integument of the head is formed from small rounded polygonal plates of labyrinthic stereom which vary in size in different regions of the head (Text-figs 3*a*, 5*a*, 9*c*). In the buccal cavity region, framed by plates x, b, c and de, the integument plates are larger than those covering the rest of the head, while in a small area adjoining plate x posteriorly, and to the right, they are much smaller (Text-fig. 5*a*). The dorsal integument in the branchial region is largely missing.

The skeleton of the ventral integument is formed from large polygonal plates of retiform stereom, usually about three to four times as large in area as the dorsal plates of the buccal cavity (Text-figs 2*b*, 9*b*,*d*). Much of the integument has been lost in the specimens both dorsally and ventrally. The ventral integument of the buccal cavity is particularly poorly preserved (Text-fig. 5*b*).

Openings of the head

The branchial slits open on the dorsal surface of the left part of the pharyngeal region of the head (Text-fig. 3*a*). The branchial skeleton is poorly preserved with only three or four posterior U-shaped plates, and possibly one anterior U-shaped plate, remaining in specimen E63366 (Text-fig. 5*d*). The precise number and detailed structure of the branchial elements is thus unknown.

The mouth of *P. semispinosa* would have opened leftward, as indicated by the attachment areas of the buccal integument plates band c (Text-figs 5*e*, 6). As plates b and c do not meet, the mouth was probably terminal, not dorsal as in *Phyllocystis*. In the mouth region three or four spine-shaped plates along the internal edge of plate b suggest the presence of an oral cone like that of *Cothurnocystis elizae* (Bather 1913, p. 399; Jefferies 1967, pp. 165–166, 1986, pp. 194–195; Text-figs 3*a*, 5*a* herein).

The gonopore-anus of *P. semispinosa* opens to the left of the tail-insertion (Text-figs 3*a*, 5*a*). A rounded notch in plate i and a notch in plate j in the left posterior part of the gonorectal groove indicate its position.

Chambers of the head

Jefferies (1967, 1968, 1969, 1979, 1981a, 1981b, 1986) has reconstructed several chambers in the cornute head. These are indicated by changes in the surface texture of the stereom of the internal surfaces of the marginal plates, and also by the nature of the integument plates (Text-figs 3, 5–8).

The buccal cavity of *P. semispinosa* was presumably bounded by the mouth anteriorly, and posteriorly on the right side by the apex of the overhang of plate de. On the left posterior side, it could have been bounded by the rearmost right corner of plate x. As already mentioned, the dorsal integument of the buccal cavity was plated with larger ossicles than those of the rest of the dorsal surface (Text-figs 3a, 5a).

The pharynx would have run from the posterior boundary of the buccal cavity to the region of the branchial slits. In the dorsal integument its position is indicated by smaller plates than those over the buccal cavity particularly in a small area contiguous with plate x (Text-fig. 5a).

The right anterior coelom would lie below the pharynx on the right side of the head. It would have been bounded on its right and posterior sides by plates f and g, and on its anterior side by a line which runs from the apex of the overhang of plate de to a ridge on the dorsal side of g (Text-figs 5–8). Plates f and g show evidence of the presence of this coelom by a denser stereom texture on the ventral part of their internal faces. The line separating these textures was the pharyngo-visceral line which in life would be the boundary between the pharynx and the right anterior coelom (Text-fig. 5e). The right anterior coelom is homologous to the right metacoel of the hypothetical *Cephalodiscus*-like ancestor.

The anterior limit of the gonorectal groove is marked by a weak ridge on plate g which also forms the left boundary of the right anterior coelom (Text-figs 5a, 8). The gonorectal groove is better developed on plate j, as described earlier.

The anterior boundary of the posterior coelom is marked by a thin wall of stereom on the anterior side of the gonorectal groove. The right side of this coelom is indicated by a hemispheroidal excavation on plate g (Text-figs 5a, 8, 9a, 10). The posterior coelom would have overlain the gut but it is not clear where its posterior boundary lay.

A left anterior coelom may have been present, but would have been a purely virtual chamber (Jefferies 1967, 1986; Jefferies and Lewis 1978; Jefferies *et al.* 1987). The possible presence of this coelom is inferred from the theory of descent from a *Cephalodiscus*-like ancestor, (Jefferies 1967–1986). It would correspond to the left somatocoel of echinoderms (Jefferies 1986, p. 284).

Tail

The tail of *P. semispinosa* is poorly preserved, but enough remains for a reconstruction. Apart from the dorsal plates, its skeleton is formed from labyrinthic stereom.

As in all cornutes, the tail is divided into three regions; fore-tail, mid-tail, and hind-tail (Text-figs 3, 11). The fore-tail is attached to the head at the reception grooves, as already described. The usual cornute pattern of articulating rings, each composed of four plates, is present. Ventrally the fore-tail skeleton consists of a series of paired plates. These are in the form of two adjacent hollow quarter-cylinders, whose antero-posterior length is about half the radius. They subtend an angle of a little more than 90° when viewed from behind, and consequently their ascending processes are just visible in dorsal view (Text-figs 3, 9a–b, d, 10, 12d).

The dorsal plates of the fore-tail are also paired and curved in transverse section (Text-figs 9a–b, 10, 11a–d). They are somewhat flattened dorsally, and have an almost straight suture where they meet in the mid-line. They curve sharply downward at their margins, where they join the dorsal faces of the ventral plates (Text-fig. 11d).

The plates of each fore-tail ring overlap the plates of the ring behind, and each pair of ventral plates is expanded posteriorly. The most posterior fore-tail ring overlaps the anterior part of the mid-tail and shows pronounced rearwardly expanded extensions of the two ventral plates (Text-figs 3b, 9b). The number of fore-tail rings is unknown, but comparisons with related cornutes suggest that there would have been from five to seven.

The mid-tail includes the stylocone which is shaped like a truncated half-cone (Text-figs 9a–b, 10, 11a–c). The ventrolateral surfaces of the stylocone, which would have been external surfaces in life, are covered with minute papillae. The dorsal surface is complex in form, with a median groove flanked by a pair of ridges, and these ridges are each interrupted by transverse grooves. Lateral to the ridges, the surface of the stylocone slopes downwards and outwards at an angle of about 15°. The stylocone bears a deep excavation anteriorly, which is triangular in plan view. This excavation is deeper at the anterior end of the stylocone and tapers into the median groove. From its broad anterior part, the stylocone tapers distally. About two-thirds of the way along its antero-posterior length, paired lateral processes exist. It is possible, but not certain, that these swellings may have articulated with dorsal plates.
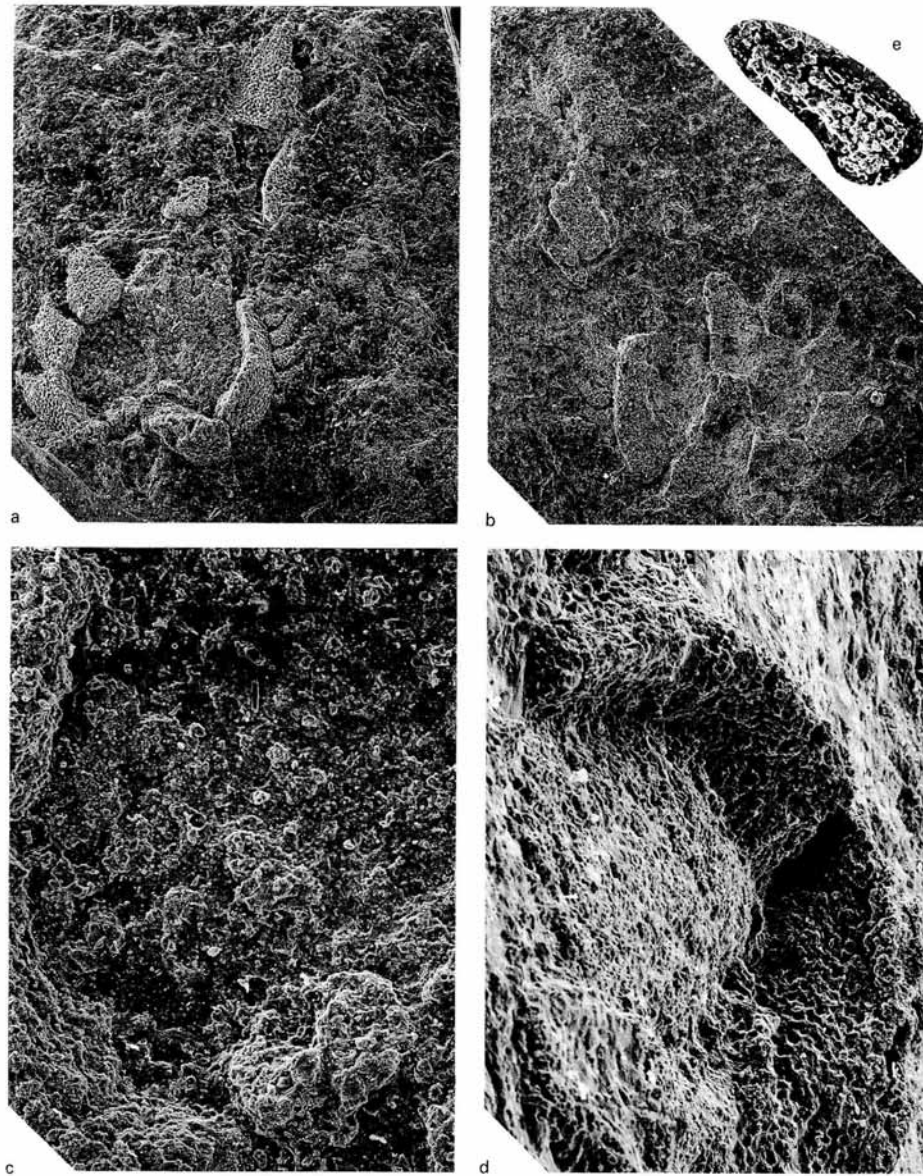
TEXT-FIG. 5. *Prochauvelicystis semispinosa* gen. et sp. nov. Scanning electron micrographs of gold/palladium coated latex casts. All specimens preserved in the British Museum (Natural History). Plate nomenclature and labelling are given in Text-figure 6. *a*, E63366*a*; holotype; showing one individual; plates of the pharyngeal area are dissociated or missing, ×20. *b*, E63366*b*; counterpart of E63366*a*; showing ventral surface, ×20. *c*, Spine of E63366*a*; dorsal view, ×90. *d*, Enlargement of E63366*a*; showing branchial skeleton, ×120. *e*, Internal view of plate f of E63366*a*; showing pharyngo-visceral line, ×67.
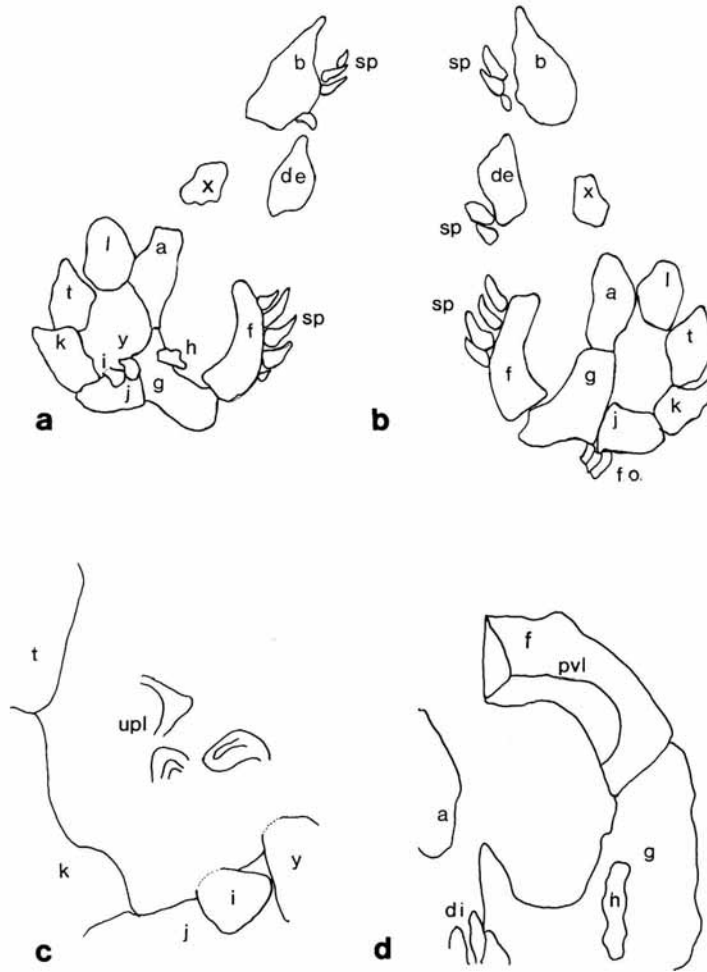
TEXT-FIG. 6. Explanatory tracing of Text-figure 5. Letters represent plate nomenclature except for: di, dorsal integument plates; fo, fore-tail plates; pvl, pharyngeo-visceral line; sp, spines; upl, U-shaped plates of branchial skeleton.

The dorsal plates of the mid-tail are elliptical structures of fasciculate stereom with a thickened, roughly semi-circular, ventral articulating surface (Text-figs 3a, 9a–b, 10, 11a–b). The edges are poorly preserved, so that the precise outline of these plates is uncertain. Two pairs of these plates probably covered the distal part of the stylocone.

The hind-tail is very poorly preserved with only one ventral ossicle remaining (Text-figs 9a–b, 11a–c). This seems very like the distal part of the stylocone, with a median groove flanked by a pair of ridges, each of which is interrupted half way along its length by a transverse groove. The dorsal surface on either side of the ridges

1mm

a   b
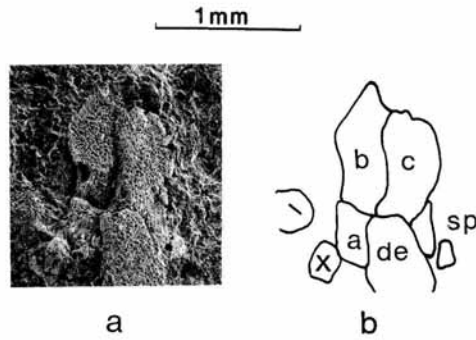
TEXT-FIG. 7. *a*, Electron micrograph of BMNH E63365*a*, showing dorsal view of plates b and c. *b*, explanatory tracing of *a*; letters represent plate nomenclature except for sp, spines.
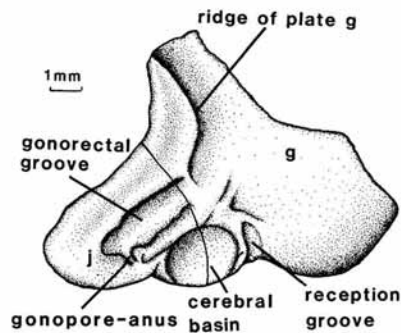
TEXT-FIG. 8. *Prochauvelicystis semispinosa*. Detail of plates g and j in dorsal aspect.

slopes downwards and outwards. The posterior part of the stylocone and the hind-tail ossicle thus have the same cross-section. The ventral and lateral surfaces of the hind-tail ossicle are papillate as in the stylocone. It is highly likely that a pair of dorsal plates articulated to this ossicle as they did to the stylocone, but these cannot be identified with certainty among the preserved material.

With only one preserved ossicle, the total number of hind-tail ossicles is indeterminate. As the cross-sectional area of the remaining ossicle is about equal to that of the distal end of the stylocone, it is likely that it was part of the proximal hind-tail. The parallel sides of this ossicle suggest that the tail did not taper steeply, and therefore there could have been more than one ossicle in the hind-tail.

FUNCTIONAL MORPHOLOGY

Spines and appendages

Spines and appendages are not synonymous in cornute morphology. Spines are defined as long narrow, pointed structures movably articulated to a marginal plate (Text-figs 3, 5*c*, 11). Appendages are horizontal prolongations of part or all of a marginal plate, fully integral with its structure and therefore not capable of relative movement.

Spines and appendages have different phylogenetic origins. The k and t appendages are developed from the k and t spikes of other cornutes, while the l appendage is found in the most primitive known forms (Jefferies *et al.* 1987, pp. 442–446). However, the spines are a new development, found only in the genera *Prochauvelicystis* and *Chauvelicystis* (Chauvel 1966; Ubaghs 1969, 1983).

Spines and appendages could support the weight of the head on the substrate, by increasing the weight-bearing surface and thus reducing the load per unit area. This would enable the animal to rest on a soft substrate. In the closely related genus *Phyllocystis*, a peripheral flange fulfilled this function (Ubaghs 1969). Compared to a flange, spines and appendages may have had the advantage that there would be less suction force to be overcome when the animal moved.

If the spines and appendages were purely supportive structures, then they would be expected to be directed radially from the centre of the head. In fact they point forwards. This orientation would hinder movement in a forward direction (Text-fig. 12). It might be suggested that *P. semispinosa* could face into a constant current, and use the spines and appendages as anchoring devices. However, judging by the fine grain of the sediment the environment was usually tranquil so this explanation is implausible. Also, the ability of the spines to fold against the side of the head only makes functional sense if *P. semispinosa* were capable of locomotion.

Locomotion

P. semispinosa was probably able to move actively across the substrate. It is possible to reconstruct the locomotory cycle of *P. semispinosa* from its morphology, although the uncertain number of fore-tail plates and hind-tail ossicles means that any reconstruction is tentative. Cornutes probably moved mainly rearwards, that is, tail first (Jefferies 1986, pp. 204, 213, 232; Jefferies *et al.* 1987, pp. 476–480; Parsley 1988, p. 352; Cripps 1989*a*, p. 234; 1989*b*, pp. 73–76; Woods and Jefferies 1992, pp. 1–25). The forwardly directed spines and appendages of *P. semispinosa* seem to confirm this view, as they would greatly hinder forward motion. Furthermore, an asymmetrical shape, such as the head of a boot-shaped cornute, is easier to pull across a surface than to push, as it is directionally stable when pulled, but directionally unstable when pushed.

P. semispinosa probably lived on the surface of the mud which formed the sea bed. The mud was likely to have been soft, as implied by its lithology, and by the weight-saving and load-spreading adaptations of *P. semispinosa* itself. Thus *P. semispinosa* could have inserted its tail into the substrate by bending it ventrally, and in doing so exerted a force which would have raised the rear part of the head, and moved the head as a whole rearwards. Horizontal force alone would not have moved the head as the flanges on the postero-ventral margins of plates f, g and j would have held the head firmly in the substrate (Text-figs 3, 5*b*).

The shape of the fore-tail rings suggests that they could have been displaced ventrally at an angle of 15° to 20° between adjacent rings. If, as seems likely, there were six or seven rings in the fore-tail, then the fully bent fore-tail would have subtended an angle of between 90° and 140° in the vertical plane, enough both to raise the head and pull it along. Similarly, the fore-tail rings could be displaced relatively by about 10° horizontally, giving an overall flexion of 60° to 70°, enough to allow the tail to move from side to side and to change the direction of movement of the head.

The papillate texture of the ventral surfaces of the stylocone and the hind-tail ossicle probably helped to make the grip on the substrate greater than it would have been had their texture been smooth, a further possible adaptation to living on soft mud.

In the following discussion, the term 'yaw' refers to movement in a horizontal plane about a vertical axis, while the term 'roll' refers to rotation about a horizontal antero-posterior axis. It is assumed that there is no effective resistance from the water, and that both the water and mud are undisturbed by currents. In Text-figure 13*a*, *P. semispinosa* is shown at rest with the spines extended roughly at right angles to the head. Locomotion started with the tail bending ventrally into the mud, raising the posterior ventral flanges of the head clear of the substrate (Text-fig. 13*d*) and pulling the head rearward (Text-fig. 13*b*), causing the spines to lie flush with the right marginal plates. The centre of mass was probably to the right of the axis of symmetry of the tail and so the ventral bending of the tail would have caused the head to yaw anticlockwise as seen from above, and to roll downwards to the right so that it is supported by the right marginal plates (Text-fig. 13*c*). The combination of roll and yaw would probably have bent the tail to the left (Text-fig. 13*c*). The appendages of the left side of the head would have been clear of the substrate.

The tail would then have been pulled out of the mud, exerting a forwardly directed force, which
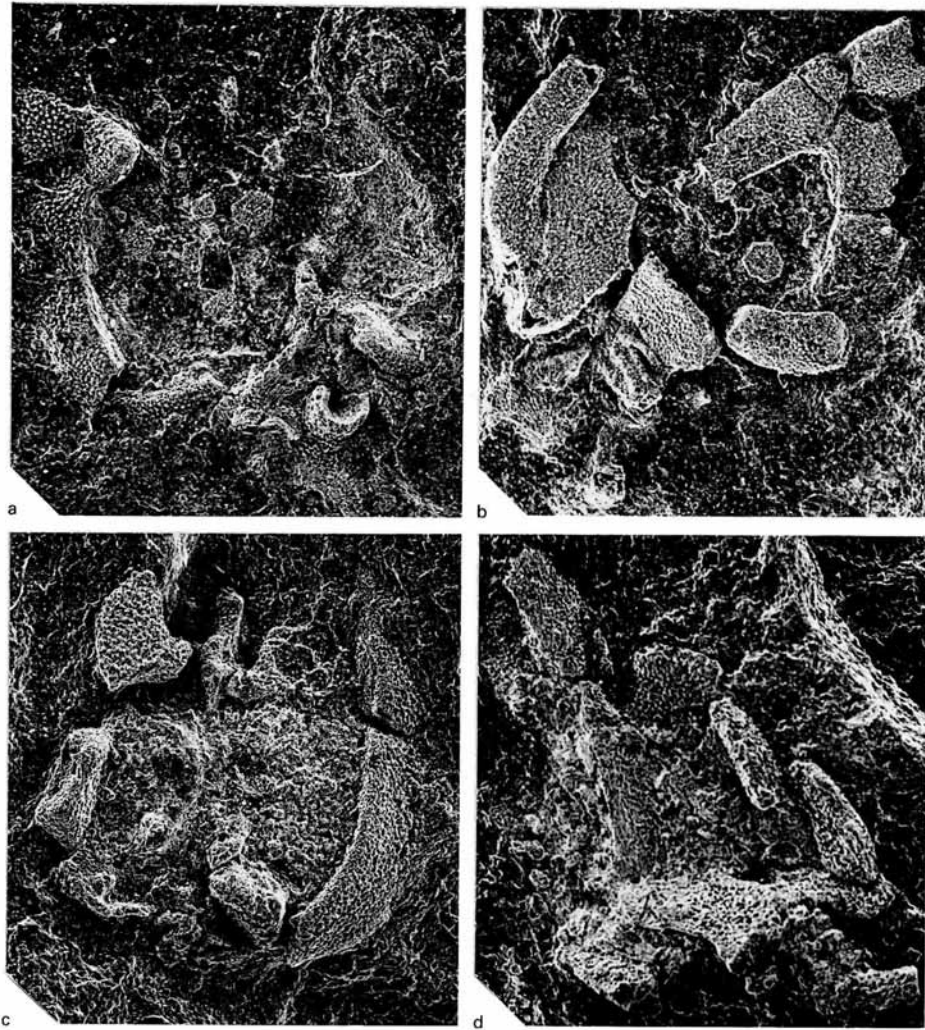
TEXT-FIG. 9. *Prochauvelicystis semispinosa* gen. et sp. nov. Light micrographs of latexes whitened with sublimated ammonium chloride. All specimens preserved in the British Museum (Natural History). Plate nomenclature and labelling are given in Text-figure 10. *a*, E63477a; dorsal view of specimen showing marginal plates, fore-tail plates, proximal part of stylocone, dorsal plates and hind-tail ossicle, ×20. *b*, E634774b; counterpart of E63477a; showing ventral views of marginal plates and hind-tail ossicle, and the distal part of the stylocone, ×20. *c*, E63367a; showing dorsal integument, plate f, and a spine, ×28. *d*, E63365c; showing left marginals, strut, isolated plates of ventral integument, fore-tail, and stylocone, ×19.
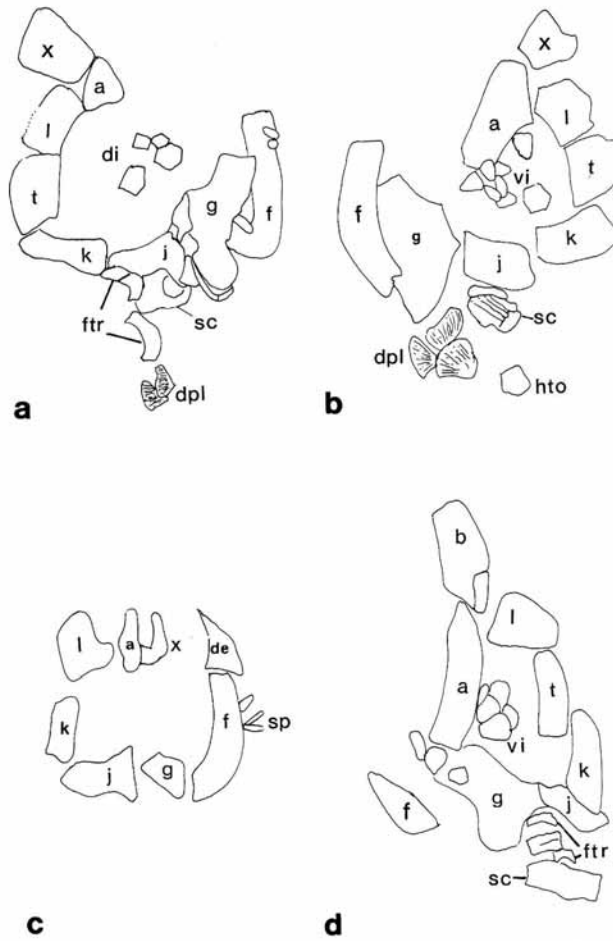
TEXT-FIG. 10. Explanatory tracing of Text-figure 9. Letters represent plate nomenclature except di, dorsal integuments; dpl, dorsal plates of mid and hind-tail; ftr, rings of fore-tail; hto, hind tail ossicle; sc, stylocone; sp, spines; vi, plates of ventral integument.

would have been resisted by the appendages and by the spines, the latter being extended at right-angles to the head (Text-fig. 13e). Rightward horizontal movement of the tail in the water, followed by ventral bending, caused the head both to yaw clockwise as seen from above and to roll down to the left so that it would have been supported by the appendages of the left marginal plates. The head then moved further to the rear and resumed the orientation it had when at rest (Text-fig. 13f–g).

Although the ventral flanges of *P. semispinosa* meant that the posterior part of the head must have been raised at the start of the locomotory cycle, they would have had the advantage of reducing the extent to which the head would have sunk into the substrate.

Could *P. semispinosa* have moved using its spines? Their asymmetric location, absence of obvious
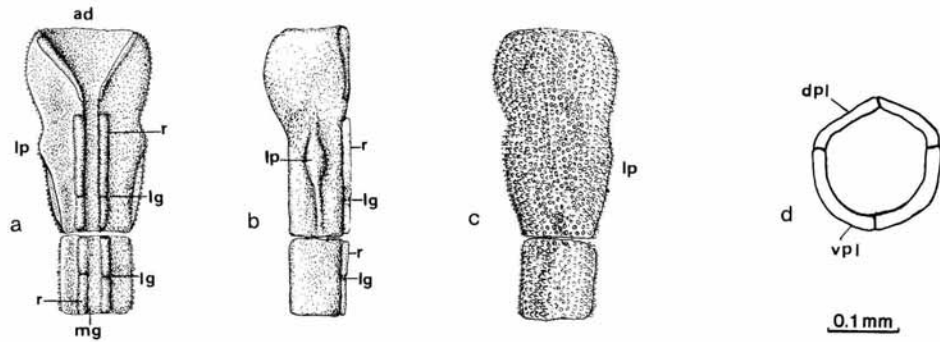
TEXT-FIG. 11. *Prochauvelicystis semispinosa*. Detail of stylocone and hind-tail: *a*, dorsal view; *b*, left lateral view; *c*, ventral view; *d*, cross-section of fore-tail. Abbreviations: ad, anterior depression; dpl, dorsal plates of hind tail; lp, lateral process; lg, lateral groove; mg, median groove; r, median ridge; vpl, ventral plates of hind tail.

muscle attachments, small size, and weak structure make this unlikely. All but the first of these reasons make it unlikely that the spines could actually raise the left side of the head to overcome the suction effect of the substrate. It seems that the tail was the only active organ of locomotion, and that the head rolled about the ventral surface of the strut to overcome suction during the locomotory cycle.

Some upholders of the aulacophore theory of the cornute tail (Ubaghs 1961, 1969, and subsequent papers; Chauvel 1966, p. 98; Fisher 1982), have suggested that the assumed feeding function of the aulacophore precluded cornutes from being motile. However, Parsley (1988, pp. 351–353) believes that the tail was both a feeding arm and a locomotory structure.

When feeding, *P. semispinosa* would rest on the substrate supported by its spines, appendages, the ventral surfaces of the marginal plates, strut, and the tail. It was very probably a deposit feeder, ingesting detritus and micro-organisms together with some organic material from the lowest layer
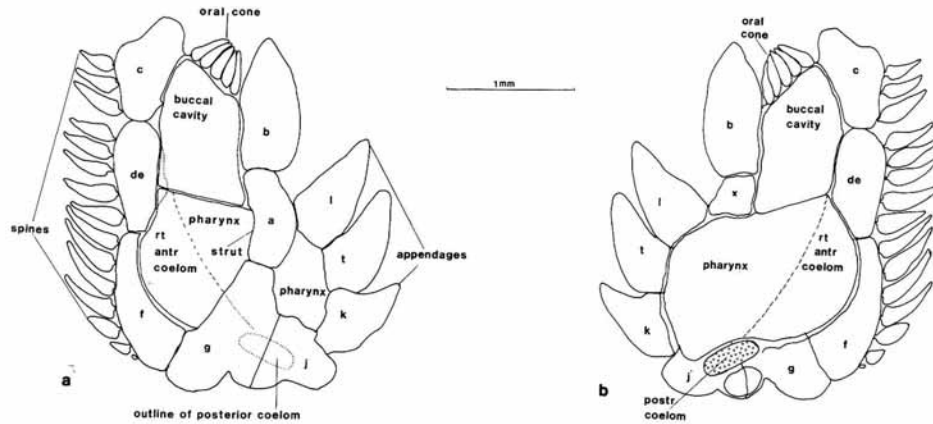
TEXT-FIG. 12. *Prochauvelicystis semispinosa*. Reconstruction of the chambers of the head; *a*, dorsal aspect; *b*, ventral aspect.
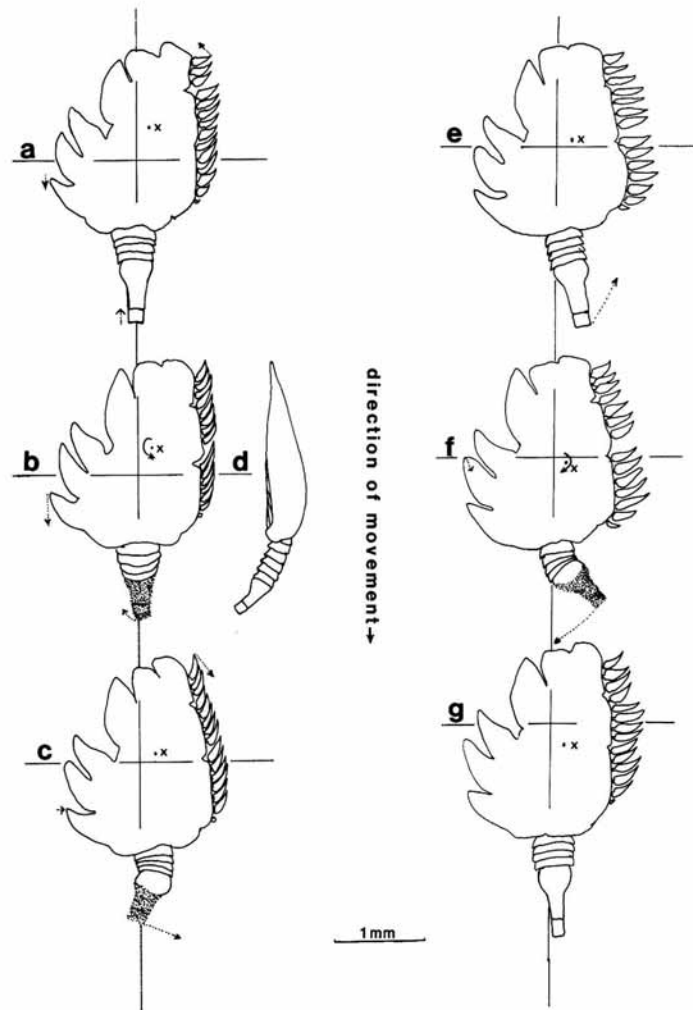
TEXT-FIG. 13. Locomotory cycle of *Prochauvelicystis semispinosa*. Arrows indicate the direction of travel of the point from which they are drawn, their lengths the displacement of the part in question in the next stage in the locomotory cycle. Stages figured are not separated by equal intervals in time but show major features of the locomotory cycle. The two lines at right angles form a space grid and thus show changes in displacement. Stippled parts of the tail are buried in the mud. The centre of mass of *P. semispinosa* is denoted by 'x'. *d*, lateral aspect of *b*, in which the tail raises the head by pushing into the substrate.

of water just above the sea-bed and the topmost layer of the substrate. The oral cone would be opened, and food particles would be ingested using inflowing water currents resulting from the ciliary and muscular action of the pharynx. Excess water and unwanted solid matter would be voided through the mouth, while food passed into the non-pharyngeal gut.

PHYLOGENY

Prochauvelicystis semispinosa is a cornute. The cornutes have been shown to be stem chordates (Jefferies 1967–1986; Jefferies *et al.* 1987; Cripps 1988, 1989a, 1989b), and are thus a paraphyletic group. The term Cornuta (cornutes) can be used to denote a grade of evolutionary organization.

The concepts of crown group and stem group are useful in constructing phylogenies (Jefferies 1979, pp. 449–451; Text-fig. 14 herein). The crown group of any taxon is defined as the latest common ancestral species of all extant forms of a group, plus all descendants of that species, living or dead. The crown group corresponds to the *group of Hennig (1983, pp. 12, 29–30). A stem group is defined as all those extinct taxa more closely related to one crown group than another, but which are not themselves members of the crown group. A stem group and a crown group together form a total group. Given two monophyletic members of a stem group, or plesions (Patterson 1981), the one that is more closely related to the crown group is said to be more crownward. A plesion plus all taxa more crownward than it in the total group forms a scion, which is named after the least crownward plesion in it (Craske and Jefferies 1989, p. 74).
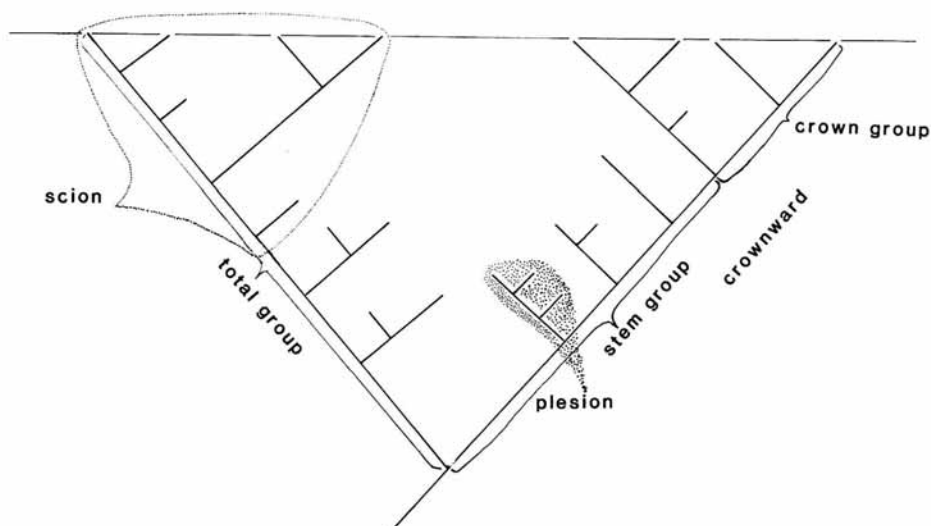
TEXT-FIG. 14. Explanation of the terms stem group, crown group, total group, plesion and scion.

The data matrix in Tables 1 and 2 was used to produce the cladogram (Text-fig. 15) using the computer program Hennig 86, devised by Dr J. S. Farris, of the State University of New York, Stony Brook, New York, USA. Relationships are based on shared derived characters only (Wiley 1981, chapter 3). To polarize the characters of the cornutes, the Soluta as described by Caster (1967) and Jefferies (1990) have been used as an outgroup.

The program initially produced 38 equally parsimonious trees from the data matrix. From these, a consensus tree was produced using the method of successive weighting in which characters found

TABLE 1. Characters used in the cladistic analysis of cornutes. The derived state is specified.

1.	Loss of feeding arm.
2.	Association of the gonopore with the anus.
3.	Loss of the water vascular system.
4.	Multiple branchial openings.
5.	Flexible dorsal integument with several separate dorsal plates.
6.	Gonopore–anus opens left of the tail junction.
7.	Loss of hydropore.
8.	Plates w, a and x form plate wax.
9.	Plate y smaller than plates h or i.
10.	Anterior u-plates of branchial skeleton.
11.	Fully flexible dorsal integument.
12.	Strut as a thickening of the floor.
13.	Flexible ventral integument and clearly demarcated strut.
14.	Plate t.
15.	Loss of plates v and w.
16.	Pointed spines on the right side of the head.
17.	Buccal lobe of head curves leftwards.
18.	Spines on left side of the head.
19.	Blunt spines.
20.	Suture between plates b and c forms a mouth frame.
21.	Gonopore–anus opens over tail junction.
22.	L-shaped plate x.
23.	Heart-shaped head with peripheral flange.
24.	Plates b and c fused to form a single plate.
25.	Anterior strut plate.
26.	Posterior u-plates of branchial skeleton.
27.	Separation of plates b and c to give a terminal mouth.
28.	Separate plate x.
29.	Paired dorsal hind-tail plates.
30.	Plate h subequal in size to plate y.
31.	Proximal fore-tail plates overlap onto ventral surfaces of plates g and j.
32.	Plate s.
33.	Interbranchial elements.
34.	Dorsal bar formed from plates a and d.
35.	Specialized plates of the branchial skeleton.
36.	l-appendage.
37.	Optic embayments.
38.	Ventral hind-tail ossicles bear downwardly directed spines.
39.	Convex ventral surface of the head.
40.	Marginal plates of the head expand onto the dorsal surface.
41.	Development of the right pharynx.
42.	Loss of cornute mid- and hind-tail.
43.	Absence of plate y.

to indicate relationships consistently among the initial trees are given higher weight than those that are less consistent (Farris 1969).

In the following discussion, the numbers in square brackets (e.g. [2]) refer to the characters as listed in Table 1, and shown on the cladogram (Text-fig. 15). Nodes on the cladogram are represented by horizontal lines and denoted by capital letters, e.g. node A (Text-fig. 15).

The cladogram shows that the cornutes (node A) are characterized by loss of the solute feeding arm [1], close association of the gonopore and the anus [2], loss of the water vascular system [3],

TABLE 2. Data matrix for the solutes, twenty-three cornute taxa and the mitrates. In the matrix the symbol '1' denotes a derived character state as specified in table 1, '0' a plesiomorphic character state, and '?' the absence of information on the state of a character.

| Character nos	1	6	11	16	21	26	31	36	41
Solutes	00000	00000	00000	00000	00000	00000	00000	00000	000
Ceratocystis perneri	11110	00100	00000	00000	00000	01110	00000	10001	000
Protocystites menevensis	11111	11010	00000	00000	11000	01110	00000	10001	000
Nevadaecystis americana	11111	110?1	1100?	00000	?1000	1??1?	??0?1	10??0	00?
Cothurnocystis primaeva	11111	11011	11100	01000	?1000	?1??0	0000?	10?00	00?
Phyllocystis blayaci	11111	11011	11111	01001	10110	10110	00001	00000	000
P. crassimarginata	11111	11011	11111	01001	10110	10110	00001	00000	000
Milonicystis kerfornei	11111	11010	11111	00001	10101	00110	0000?	00000	000
Domfront cornute	11111	110?0	?1101	00000	?0001	01110	00000	01100	00?
Amygdalotheca griffei	11111	110?0	11111	00000	?0101	01?10	00000	00?00	000
Chauvelicystis spinosa	11111	11011	11111	11101	01000	1?110	00001	00?00	000
C. ubaghsi	11111	11011	11111	11110	??000	11110	00001	10000	000
C. vizcainoi	11111	11011	11111	11110	?1000	11110	00001	10000	000
Prochauvelicystis semispinosa	11111	11011	11111	10000	00000	11110	00001	10000	000
Cothurnocystis fellinensis	11111	11011	11110	00000	01000	11110	00001	10?00	000
C. elizae	11111	110?1	11110	00000	00000	11010	00001	10000	001
C. courtessolei	11111	110??	11110	00000	?1000	?1110	0000?	10?00	00?
Scotiacystidae	11111	11010	11101	00000	00000	00111	11101	10000	000
Progalliaecystis ubaghsi	11111	110??	11101	01000	?0001	0?01?	10010	10000	001
Galliaecystis lignieresi	11111	110??	11101	00000	?0001	0?01?	00000	00000	001
Hanusia spp.	11111	110?0	01101	01000	00001	0?01?	00010	10000	001
Reticulocarpos hanusi	11111	110?0	11101	00000	00001	01010	00010	01100	001
R. pissotensis	11111	110?0	01101	00000	00001	0?011	00000	0?111	001
Prokopicystis mergli	11111	110?0	11101	00000	00000	01011	10010	0?111	001
Mitrates	11111	110?0	00001	00000	00000	01001	10010	01011	111

multiple branchial openings [4], paired dorsal plates of the hind-tail [29], separation of plates b and c to form a terminal mouth, and presence of an l-appendage [36].

The most plesiomorphic ('primitive') cornute known is *Ceratocystis perneri* Jaekel, the only cornute to retain the hydropore. The next most plesiomorphic cornute is *Protocystites menevensis* Hicks. It shares six characters with all more crownward cornutes (node B), flexible dorsal integument [5], opening of the gonopore-anus to the left of the tail junction [6], loss of the hydropore [7], plate y smaller than plates h or i [9], posterior U-shaped plates of the branchial skeleton [26] and a separate plate x [28].

All cornutes more crownward than *C. perneri* and *P. menvensis* (node C) share a fully flexible dorsal integument [11], a strut as a thickening of the ventral integument of the head [12], a flexible ventral integument with a clearly demarcated strut [13], and specialized plates of the branchial skeleton [35].

Prochauvelicystis semispinosa and the three species of the genus *Chauvelicystis* Ubaghs form a clade, the subfamily Chauvelicystinae (node G), on the basis of pointed spines on the right side of the head [16]. *P. semispinosa* is the most plesiomorphic chauvelicystine. The genus *Chauvelicystis* (node H) is characterized by the presence of spines on the left side of the head [18]. *C. vizcainoi* sp. nov. and *C. ubaghsi* (Chauvel) are sister taxa (node I) because of their possession of blunt spines [19], leaving *C. spinosa* Ubaghs as the most primitive member of its genus.

The genus *Phyllocystis* Thoral, 1935 (Ubaghs 1969; node J) has two species, *P. crassimarginata* Thoral and *P. blayaci* Thoral, and is characterized by the presence of a mouth frame [20], a heart-shaped head with a peripheral flange [23], and fusion of plate b and c [24]. The genus *Phyllocystis* and the subfamily Chauvelicystinae form the family Phyllocystidae (Derstler 1979, p. 104; node F)
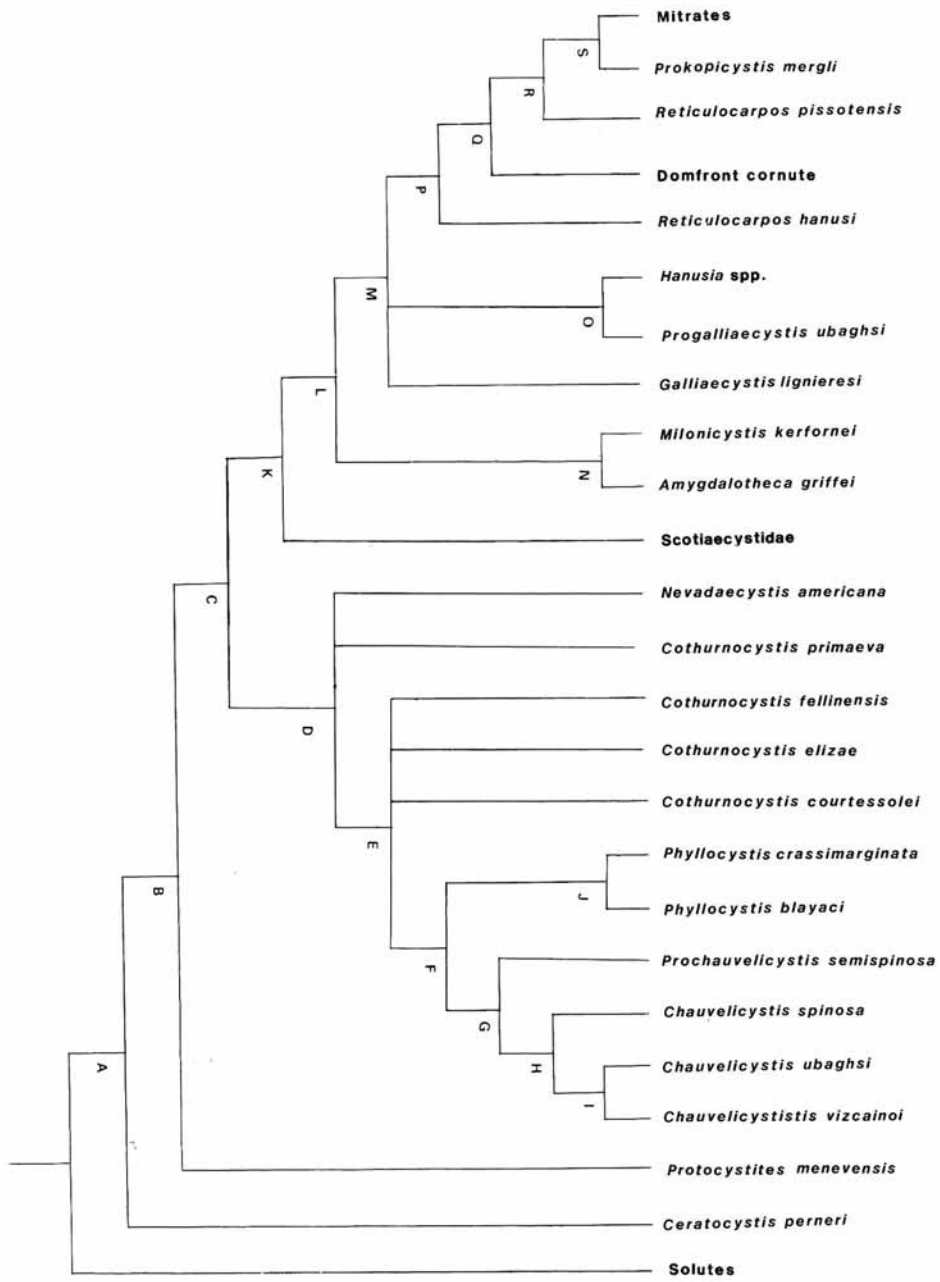
TEXT-FIG. 15. Cladogram of *Prochauvelicystis semispinosa* and other cornutes. Characters are listed in Table 1.

characterized by loss of plates v and w [15], the buccal lobe of the head curving to the left [17] and the opening of the gonopore-anus lying over the tail-junction [21].

The Phyllocystidae form an unresolved four-fold polytomy (node E) with *Cothurnocystis courtessolei* Ubaghs, *Cothurnocystis fellinensis* Ubaghs and *Cothurnocystis elizae* Bather denoted by the presence of plate t [14]. This group forms an unresolved trichotomy (node D) with *Cothurnocystis primaeva*, Thoral and *Nevadaecystis americana* Ubaghs, with the presence of an L-shaped plate x [22].

The family Scotiaecystidae (Caster and Ubaghs, in Caster 1967; Cripps 1988) share plate s [32] and interbranchial elements [33]. The scion of the Scotiaecystidae (node K) is defined by the loss of plates v and w [15], a parallelism with the phyllocystids. *Amygdalotheca griffei* Ubaghs and its sister taxon *Milonicystis kerfornei* Chauvel form the family Amygdalothecidae (Ubaghs 1969, p. 63; node N), characterized by a heart-shaped head with peripheral flange [23], a parallelism with the genus *Phyllocystis*. The amygdalothecids are related to all more crownward cornutes (node L) by possession of an anterior strut plate [25].

Progalliaecystis ubaghsi Cripps and the three species of the genus *Hanusia* Cripps form a clade (node O) with leftward curvature of the buccal lobe of the head [17], separation of plates b and c to give a terminal mouth [27], and a dorsal bar formed by plates a and d [34] (node O). Character 27 has evolved twice, as it is also found at node A. Character 17 is a parallelism with the phyllocystids. The *Hanusia–P. ubaghsi* group forms an unresolved trichotomy (node M) with *Galliaecystis lignieresi*, Ubaghs and the scion of *Reticulocarpos hanusi*, Jefferies and Prokop with absence of plate y [43].

The scion of *R. hanusi* (node P) possesses optic embayments [37] and spines on the ventral hind-tail ossicles [38], and that of an undescribed cornute from the Llandeilo of Domfront, Normandy, France (node Q) shares the overlap of the proximal ventral fore tail plates onto the ventral surfaces of plates g and j [31]. The scion of *Reticulocarpos pissotensis* Chauvel and Nion (node R) shares a convex ventral surface of the head [39] and the expansion of marginal plates of the head onto the dorsal surface [40]. *Prokopicystis mergli* Cripps is found to be the sister taxon of the mitrates (Jefferies 1986, ch. 8), from their shared dorsal bar [34], a parallelism with the *Hanusia–Progalliaecystis* group.

The mitrates all share development of a right pharynx [41] and loss of the cornute mid- and hind-tail [42]. Jefferies (1986, chapter 8) has shown that mitrates can be referred to the stem groups of the extant chordate subphyla.

CONCLUSIONS

C. vizcainoi is a previously unrecognized species of *Chauvelicystis*, differing slightly from *C. ubaghsi* but more from *C. spinosa*. Together with *P. semispinosa*, it shows that spined cornutes were more diverse and widespread than previously believed.

Prochauvelicystis semispinosa is an unusual cornute because of its small size and the presence of spines on the right side of the head only. Both these features are probably adaptations to living on a soft substrate. The orientation of the spines suggests that *P. semispinosa*, like other cornutes, was actively motile and move rearwards.

P. semispinosa has derived characters in common with the three known species of the genus *Chauvelicystis* and is the most primitive member of the Chauvelicystinae. In its gross morphology, *P. semispinosa* is intermediate between the boot-shaped cornutes of the genus *Cothurnocystis* and the more symmetrical *Chauvelicystis* and *Phyllocystis*. The boot-shaped head is probably a primitive condition inherited from the less crownward cornutes such as *Ceratocystis perneri*. *P. semispinosa* is also primitive in having spines on the right side of the head only, unlike *Chauvelicystis* which has the derived condition of spines on right and left sides of the head. Thus *P. semispinosa* is the primitive sister-taxon of an important clade of cornutes, the first species in this clade known from Britain.

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