

FUNCTIONAL MORPHOLOGY OF STYLOPHORAN ECHINODERMS

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ABSTRACT. The life orientation and mode of life of stylophorans are a subject of much ongoing debate. Examination of the ornamentation occurring both on the arm and theca in several cornutes and mitrates strongly supports the view that the life orientation was similar in all stylophorans and was 'flat-surface down'. The presence of an asymmetrical ornamentation adapted to hinder, or minimize, back slippage of the organism in all stylophorans gives strong support to their interpretation as mostly sessile organisms, feeding with the arm facing the current and the theca downstream. The examination of a wide array of thecal morphologies and sculpture patterns displayed by the various groups of cornutes and mitrates allows the identification of three main modes of life in stylophorans: (1) an epibenthic mode of life, with the theca as main anchor to the substrate (e.g. asymmetrical cornutes, *Diamphidiocystis*); (2) an epibenthic mode of life, with the arm as main anchor to the sediment (e.g. symmetrical cornutes, *Peltocystis*, primitive Mitrocystitida, some Kirkocystidae); (3) an infaunal mode of life, with the theca buried in a slightly inclined attitude (e.g. some Kirkocystidae, Mitrocystitida with cuesta-shaped ribs). The partially buried mode of life of *Lagynocystis* is intermediate between 2 and 3.

KEY WORDS: Echinoderms, Stylophorans, functional morphology.

STYLOPHORANS (Cornuta, Mitrata) are a class of bizarre-shaped, non-pentaradiate Palaeozoic echinoderms. They consist of a tripartite, highly flexible, articulated appendage (the 'aulacophore'), which is inserted into a flattened, asymmetrical theca. The unusual aspect of these fossils and the contrasted interpretations of the aulacophore as equivalent to a pelmatozoan stem (e.g. Philip 1979; Kolata *et al.* 1991), a feeding arm (e.g. Ubaghs 1961*b*; Parsley 1988), or even to a chordate tail (e.g. Jefferies 1967; Cripps and Daley 1994) have led to a wide array of speculations concerning their supposed mode of life. Almost all authors have interpreted the flattened morphology of the stylophoran theca as an adaptation to a bottom-dwelling, unattached, 'flat-fish' mode of life (but see Termier and Termier 1948). Jefferies (1968, 1969*b*, 1971) proposed that juveniles were attached to the sea floor by the tip of their appendage, whereas adult forms were vagile organisms. The presence of large protuberances on the lower surface of several forms has led some authors to interpret stylophorans as sessile epibenthic echinoderms (Bather 1913; Chauvel 1941; Ubaghs 1967*a*, 1969). The possibility that stylophorans could swim by lateral undulation of their highly flexible appendage has been advanced several times (e.g. Gislén 1930; Dehm 1934; Jefferies 1968, 1973; Jefferies and Prokop 1972; Parsley 1982, 1988, 2000; Cripps 1990). Various authors proposed that stylophorans were vagile epibenthic organisms using their aulacophore to crawl in the mud (e.g. Kirk 1911; Caster 1952; Gill and Caster 1960; Caster *et al.* 1961; Jefferies 1968, 1984, 1986; Philip 1981; Kolata and Jollie 1982; Frest 1988; Kolata *et al.* 1991; Woods and Jefferies 1992; Cripps and Daley 1994; Sutcliffe *et al.* 2000; Gee 2000). Finally, an infaunal mode of life has been suggested for several mitrates possessing a theca with ratchet sculpture (cuesta-shaped ribs, asymmetrical tubercles), by analogy with other similarly ornamented organisms (Jefferies and Prokop 1972; Jefferies and Lewis 1978; Jefferies 1982, 1984, 1986, 1999; Kolata and Jollie 1982; Savazzi *et al.* 1982; Kolata *et al.* 1991; Ruta 1997*b*; Ruta and Theron 1997; Ruta and Bartels 1998; Sutcliffe *et al.* 2000).

The goal of this paper is to discuss the mode of life of several cornute and mitrate stylophorans in the light of a detailed examination of the asymmetry, strength and extension of the ornamentation, both on the appendage and on the theca.

Material. The material referred to in this paper is preserved in the following collections: The Natural History Museum, London (BMNH); Université Claude Bernard-Lyon 1, UFR Sciences de la Terre, Villeurbanne (FSL); Institut de Géologie, Rennes (IGR); Muséum d'Histoire Naturelle, Nantes (MHNN); Courtessole-Vizcaïno collection, Muséum National d'Histoire Naturelle, Paris (MNHN); Národní Muzeum, Prague (NMP); Faculté des Sciences, Montpellier (UM); Vizcaïno collection, Carcassonne (VCBH, VOMN, VOMA).

STYLOPHORAN ANATOMY

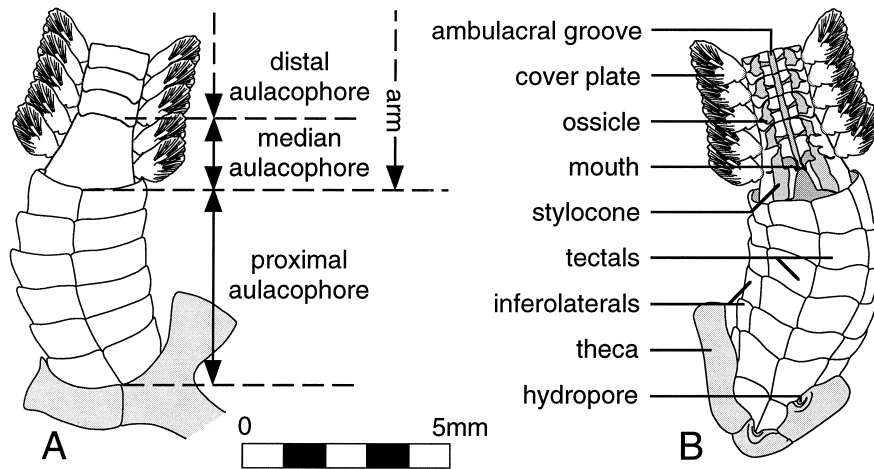
The Extraxial-Axial Theory (EAT) is a model of skeletal homologies based on ontogeny, which identifies two major components in the body wall of all echinoderms: (1) an axial region, narrowly connected to the mouth and to the water-vascular system; (2) an extraxial region, which forms the rest of the body wall and is associated with several openings such as the anus and the hydropore (Mooi *et al.* 1994; David and Mooi 1996, 1998, 1999; Mooi and David 1998). Recent application of this new model to the non-pentamerous morphology of stylophorans (David *et al.* 2000) confirms that the aulacophore is a feeding structure, as initially proposed by Ubaghs (1961*b*). The EAT also demonstrates that stylophorans do not correspond to aberrant stem-group echinoderms (Ubaghs 1975; Paul and Smith 1984) or to primitive chordates (Jefferies 1968; Cripps 1989*a*) but to highly derived echinoderms close to crinoids (Sumrall 1997). All stylophorans share the same basic organization and consist of a feeding appendage (the aulacophore) inserted into a flattened, asymmetrical theca.

The aulacophore

The stylophoran appendage shows the same tripartite regionation in all forms (Text-fig. 1). Each portion of the aulacophore is designated following its position away from the appendage insertion into the theca; the proximal region is the closest to the theca and the distal portion, the farthest. The aulacophore is a functional structure, fundamentally consisting of two distinct parts (David *et al.* 2000); its proximal region is an extraxial tegmental extension of the theca, whereas the median and distal portions form together an arm, comparable in morphology to a crinoid arm (David *et al.* 2000; see also Ubaghs 1967*a*; Nichols 1972). As in other arm-bearing echinoderms (crinoids, asterozoans), the stylophoran arm is an extension of the body wall, implying both axial and extraxial components.

The proximal aulacophore is a broad, highly flexible structure composed of several imbricated, telescoping rings, and enclosing a large internal lumen. Each proximal ring typically consists of four skeletal elements: two 'tectals' on the upper surface, and two 'inferolaterals' on the lower surface (Text-fig. 1). Most authors consider that the proximal aulacophore cavity housed powerful muscles (e.g. Jaekel 1918; Jefferies 1968; Philip 1979; Ubaghs 1981; Kolata and Jollie 1982; Parsley 1988).

The stylophoran arm (middle and distal regions of the aulacophore) consists of a series of uniseriate skeletal extraxial elements ('brachials') on the lower surface, and of two opposite rows of axial cover plates articulated to the brachials on the upper surface (Text-fig. 1). The median region of the aulacophore is characterized by a single, massive, cone-shaped brachial, the 'stylocone'. Brachials in the distal region ('ossicles') are smaller and they decrease in size distally (away from the aulacophore insertion). Interbrachial articulations are poorly developed in cornutes, which suggests that the arm was probably a rather rigid structure (Jefferies and Prokop 1972; Ubaghs 1981; Parsley 1988). Recent observations of enrolled distal portions of cornute appendages indicate that flexibility increased distally (Ubaghs and Robison 1988; Sumrall and Sprinkle 1999). Interbrachial articulations are much more complex in mitrates, as evidenced by the presence of sites for muscle insertion and of a large cavity housing ligament (Ubaghs 1967*a*, 1969, 1981; Carlson and Fisher 1981). Contrary to the situation in cornutes, interbrachial articulations allowed vertical flexion of the appendage in mitrates (Ubaghs 1967*a*; Carlson and Fisher 1981; Jefferies 1986; Parsley 1988). Mitrates are frequently preserved with their aulacophore flexed over the theca (Pl. 1, fig. 1). This preferential taphonomic position, resulting from the contraction of interbrachial muscles, has been interpreted by most authors as corresponding to a distressed or pre-mortality position (Dehm 1932; Jefferies 1984; Parsley 1988; Ruta and Bartels 1998). A longitudinal median groove runs on the upper (inner) surface of the brachials from the distal end of the arm to a

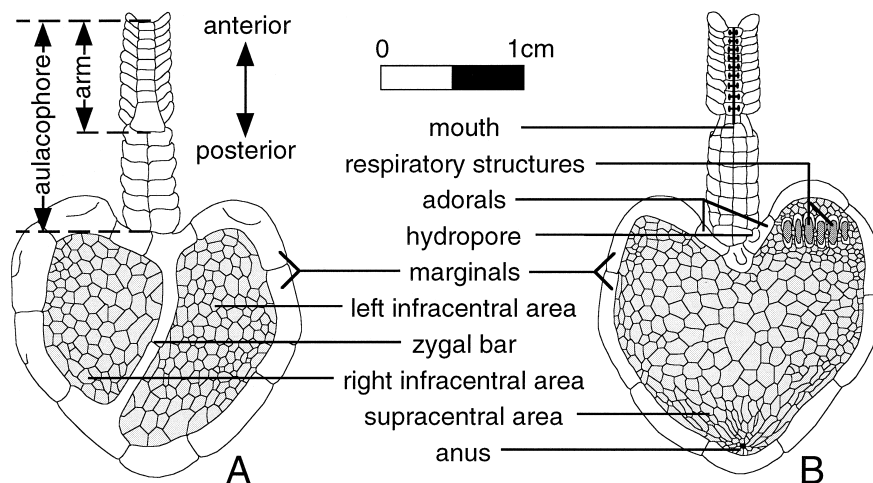


TEXT-FIG. 1. Morphology of the stylophoran aulacophore. *Phyllocystis blayaci* Thoral, 1935 (Cornuta); Saint-Chinian Formation (Lower Ordovician), Montagne Noire (France); redrawn after Ubaghs (1969). A, lower surface. B, upper surface.

proximal notch located on the stylocone (Text-fig. 1B). This groove corresponds to the imprint of a single ambulacral canal (Ubaghs 1961b, 1967a; Nichols 1972; Kolata and Guensburg 1979; Chauvel 1981; Parsley 1988; Ruta 1999c; David *et al.* 2000). The mouth was located at the proximal extremity of the ambulacral groove at, or close to, the deep notch located on the upper surface of the stylocone (Parsley 1991; David *et al.* 2000). From the location of the mouth (at the base of the arm), follows the orientation of the organism, with the arm anterior, and the theca posterior.

The ambulacral groove is roofed by two sets of movable cover plates (Text-fig. 1). Left and right series of cover plates are frequently opposite each other, but they sometimes display an alternating pattern, as in *Protocystites* (Jefferies *et al.* 1987, p. 469), or *Rhenocystis* (Ruta and Bartels 1998, p. 794). The rounded upper edge of the cover plates in cornutes and the presence of articulatory processes in the lower edge of cover plates in most stylophorans clearly demonstrate that these skeletal elements could open in life (Ubaghs 1969, 1981; Chauvel 1981; Dzik 1999). Cover plates are preserved wide open in most cornute aulacophores (Text-fig. 3B), whereas they are narrowly opened or tightly closed in mitrate appendages (Philip 1979; Chauvel 1981; Ubaghs 1981; Kolata and Jollie 1982; Jefferies 1986; Parsley 1988). As pointed out by Jefferies (1986, p. 354), 'it is risky to deduce the life habits of an animal from the precise arrangement of its parts after death'. Consequently, the difference of position of the cover plates in the two main stylophoran groups does not signify that cover plates were capable of outward opening in cornutes but not in mitrates, as proposed by Parsley (1988, 1991). The difference of preservation could rather be interpreted in terms of functional morphology, as it suggests that contrasted mechanisms were possibly involved in the articulation of cover plates in cornutes and mitrates.

Cover plates of a same series overlap each other distally and are sometimes connected by thin integumentary platelets, as in the mitrate *Chinianocarpus* (Ubaghs 1969, p. 80). This observation suggests that cover plates could not open independently, but formed two movable sheets (Ubaghs 1969, 1981; Kolata and Jollie 1982; Parsley 1988, 1991). In mitrates, the distressed, flexed, position of the aulacophore severely accentuates distal overlapping of the cover plates, which prevents them from opening (Kolata and Jollie 1982; Kolata *et al.* 1991; Parsley 1991). It is thus very improbable that mitrates fed with their aulacophore held aloft in the water column (Parsley 1988, 1991; but see Ubaghs 1967a; Sprinkle 1976; Chauvel 1981; Caster 1983; Ruta 1999c). Moreover, a stylophoran with its appendage in recurved position would have been hydrodynamically very unstable, and a current, even very weak, would have toppled the organism (Parsley 1991). In life, stylophorans probably deployed their aulacophore over the sea floor for feeding (Parsley *et al.* 2000). This position allowed the opening of the two sets of cover plates and



TEXT-FIG. 2. Morphology of the cornute *Phyllocystis blayaci* Thoral, 1935 (aulacophore and theca); Saint-Chinian Formation (Lower Ordovician), Montagne Noire (France); aulacophore and theca; modified after Ubaghs (1969). A, lower surface. B, upper surface.

minimized the intake of currents on the structure. Such a recumbent position of the appendage is observed in all cornutes (Text-fig. 3A–C). In mitrates, the relaxation of interbrachial muscles combined with the action of interossicular ligament led to the extension of the aulacophore over the sea floor.

The theca

The stylophoran theca is massive, flattened and fundamentally asymmetrical (Text-fig. 2). It shows two contrasted surfaces: a flat to slightly concave lower surface, on which the animal rested in life, and a convex upper surface (see discussion below). The theca consists of numerous extraxial skeletal elements (plates), which can be subdivided into two main categories: major plates ('marginals' and 'adorals') and integumentary platelets ('somatics'). Marginals are thick plates framing the theca. They typically extend more on the lower surface than on the upper surface. Adorals (or 'adaulacophorals') are additional marginal elements framing the aulacophore insertion at the anterior edge of the upper surface. The number, relative size, morphology and location of both marginals and adorals are extremely constant during ontogeny and are used in the distinction of the various stylophoran species. Major skeletal elements are commonly designated by the letters M (marginals) and A (adorals), following Jaekel (1918) and Ubaghs (1963). The aulacophore insertion is chosen as a landmark for the identification of these plates: elements right of the appendage insertion are designated M_n and A_n , and those left of the origin, M'_n and A'_n (with n , a number indicating the position of the plate away from the aulacophore insertion). A_0 and M_0 are major plates framing the aulacophore insertion and located in central position (M_0 is only known in the primitive stylophoran *Ceratocystis*). The appendage insertion is typically framed by five plates in stylophorans: A_1 , A_0 and A'_1 on the upper surface, M_1 and M'_1 on the lower surface (Ubaghs 1967a; Parsley 1997; Lefebvre *et al.* 1998a; Ruta 1999b).

Somatics are small, numerous, tessellated, unorganized skeletal elements. They constitute large flexible integumentary areas on the lower thecal surface ('infracentral areas') and on the upper surface ('supracentral area'), enclosed by the rigid marginal frame. On the lower surface of stylophorans, an asymmetrical structure (the 'zygial bar') resulting from the association and joining of two opposite marginals typically separates a left and a right infracentral areas (Kolata *et al.* 1991; Parsley 1997; Lefebvre *et al.* 1998a; Ruta 1999b). The number of somatic elements increases with growth in most cornutes and several mitrates (e.g. *Aspidocarpus*). In some highly derived mitrates (e.g. anomalocystitids),

the number, relative size, morphology and location of infracentral somatics ('infracentrals') and supracentral somatics ('supracentrals') become constant during ontogeny and diagnostic of a given species.

In all stylophorans, an obvious opening is present at the posterior end of the theca, opposite the aulacophore insertion (Text-fig. 2B). This orifice corresponds to the anus (Bather 1913; Chauvel 1941; Ubaghs 1967a; Kolata and Guensburg 1979; Parsley 1988; Ruta 1999c; Sumrall and Sprinkle 1999; Lefebvre and Vizcaïno 1999). The anus can open on the upper surface (e.g. *Mitrocystites*, *Scotiaecystis*) or on the lower surface (e.g. *Anatifopsis*, *Chinianocarpus*). A wide array of morphologies is displayed by the anal opening in stylophorans. It can be slit-like (e.g. *Ceratocystis*, *Placocystella*), located at the summit of an anal pyramid (e.g. *Cothurnocystis*, *Phyllocystis*), elongated and protected by numerous spike-shaped elements (e.g. *Barrandeocarpus*, *Mitrocystella*) or by a specialized anal plate (e.g. *Nanocarpus*, *Peltocystis*). Additional orifices are sometimes observed in stylophorans: the hydropore (piercing the right adoral; Ubaghs 1967a), gonopores ('lateripores' and 'paripores' opening through marginals, on the lower surface of some primitive Mitrocystitida; Parsley 1994), and various respiratory structures, comparable to those present in several other Palaeozoic echinoderms ('sutural pores', 'cothurnopores' and 'lamellipores', all located in the right anterior corner of the supracentral area of primitive stylophorans and various cornutes; Ubaghs 1967a; Parsley 1988; Lefebvre and Vizcaïno 1999). The presence of orifices on both thecal surfaces, piercing both major plates and somatics, shows that the totality of the stylophoran theca consisted of perforate extraxial elements (David *et al.* 2000).

Cornutes and mitrates

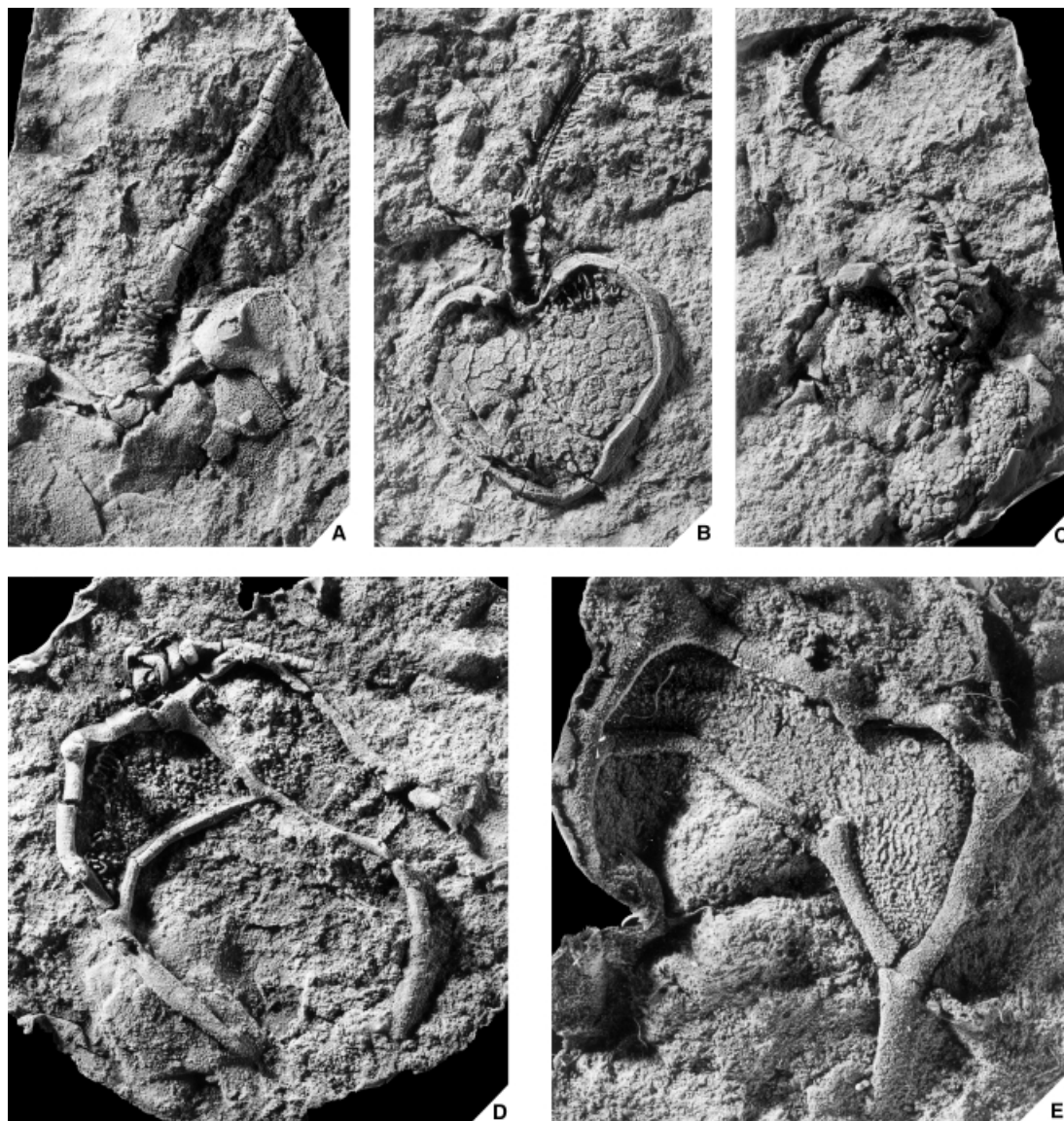
Cornutes and mitrates share the same basic 'stylophoran' organization, with an aulacophore and a flattened theca consisting of marginals and somatics (see above). Almost all authors consider that they represent two well-defined taxonomic groups (e.g. Gill and Caster 1960; Ubaghs 1967a; Jefferies 1968; Chauvel and Nion 1977; Kolata and Jollie 1982; Parsley 1988; Cripps and Daley 1994; Lefebvre and Vizcaïno 1999; Ruta 1999b; but see Parsley 1997; Ruta 1999c). Main differences between cornutes and mitrates concern (1) the morphology of marginals and adorals: these elements are typically narrow and delicate in cornutes, thick and large in mitrates; (2) the expansion of integumentary areas: infracentral areas are generally expanded and tessellate in cornutes, much smaller and comprising a reduced number of somatics in mitrates; (3) the organization of the proximal aulacophore: tectals are much smaller than inferolaterals in cornutes, subequal in size in mitrates; (4) the interbrachial articulation (see above); (5) possibly the articulation between cover plates and brachials. Additional differences have been reported elsewhere and will not be discussed further here (Ubaghs 1967a; Parsley 1988; Lefebvre and Vizcaïno 1999; Lefebvre 2000, in press).

ASYMMETRICAL CORNUTES

Primitive stylophorans (e.g. *Ceratocystis*) and most primitive representatives of the two main subdivisions of the Cornuta (Amygdalothecida and Cothurnocystida) are characterized by a strongly asymmetrical, 'boot-shaped' theca (Jefferies and Prokop 1972; Parsley 1988; Cripps 1989a; Ubaghs 1991; Lefebvre and Vizcaïno 1999). The plesiomorphic boot-shaped morphology is accentuated in primitive cornutes by the development of two large integumentary areas perpendicularly orientated on the lower surface: the left infracentral area is antero-posteriorly elongated, whereas the right infracentral area is transversally elongated.

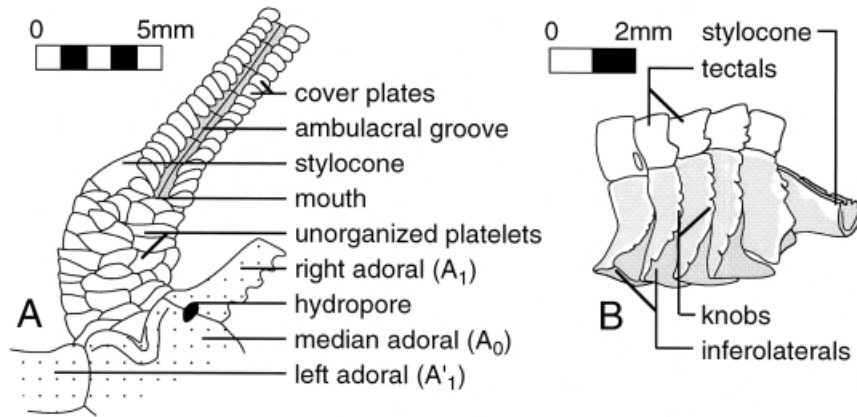
Morphology of the aulacophore

The proximal aulacophore of the primitive stylophoran *Ceratocystis* (Middle Cambrian, Bohemia) consists of numerous, unorganized, imbricated platelets (Text-figs 3A, 4A), which probably represents the plesiomorphic condition in stylophorans (Ubaghs 1967b; Jefferies 1969a; Lefebvre and Vizcaïno



TEXT-FIG. 3. A, *Ceratocystis perneri* Jaekel, 1901; VCBH 13, Skryje Shales (Middle Cambrian), Czech Republic; aulacophore and anterior portion of the lower thecal surface; $\times 2$. B, *Phyllocystis blayaci* Thoral, 1935; FSL 168704, Saint-Chinian Formation (Lower Ordovician), Montagne Noire (France); aulacophore and upper thecal surface; $\times 2$. C, *Cothurnocystis fellinensis* Ubaghs, 1969; FSL 168715 (holotype), Saint-Chinian Formation (Lower Ordovician), Montagne Noire (France); aulacophore and lower thecal surface; $\times 2$. D, *Cothurnocystis elizae* Bather, 1913; BMNH E23395, Starfish Bed (Upper Ordovician), Ayrshire (Scotland); aulacophore and lower thecal surface; $\times 2$. E, *Scotiaecystis curvata* (Bather, 1913); BMNH E28551, Starfish Bed (Upper Ordovician), Ayrshire (Scotland); lower thecal surface; $\times 5$.

1999). The proximal aulacophore of boot-shaped cornutes shows the typical cornute organization, with small tectals and large inferolaterals. The lower surface of the proximal region is frequently flat, with sometimes sharp, knob-bearing, lateral edges developed by the inferolaterals, as in *Cothurnocystis fellinensis* (Text-figs 3C, 4B) or *Phyllocystis blayaci* (Text-figs 1, 6A). The unorganized platelets of



TEXT-FIG. 4. Morphology of the aulacophore in primitive stylophorans and asymmetrical cornutes. A, *Ceratocystis perneri* Jaekel, 1901 (primitive stylophoran); Skryje Shales (Middle Cambrian), Czech Republic; aulacophore in upper view; modified after Ubaghs (1967b). B, *Cothurnocystis fellinensis* Ubaghs, 1969 (Cornuta); Saint-Chinian Formation (Lower Ordovician), Montagne Noire (France); proximal aulacophore and stylocone in right lateral aspect; modified after Ubaghs (1969).

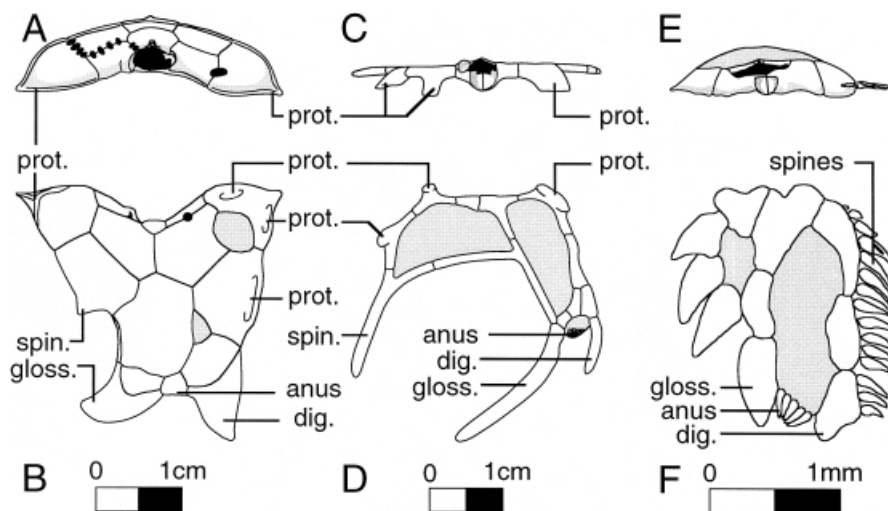
Ceratocystis and the telescoping, imbricated rings of asymmetrical cornutes allowed great flexibility of the proximal region.

The arm of *Ceratocystis* and most asymmetrical cornutes was probably a rigid structure, as suggested by the poorly developed interbrachial articulations and the flat sutures between following ossicles (Text-figs 3A–C, 6E). Lateral flexion was almost impossible, whereas ventral flexion was apparently only possible at the distal tip of the arm, as illustrated in *Archaeo-cothurnus bifida* (Ubaghs and Robison 1988) and *Ponticulocarpus rushtoni* (Sumrall and Sprinkle 1999). The lower surface of the brachials is typically smooth and rounded. Small protuberances are sometimes present on the lower surface of ossicles, as in *Cothurnocystis elizae* (Jefferies 1968, p. 261) or *Galliaecystis lignieresi* (Ubaghs 1969, p. 72). Arms are generally very long and composed of several dozen brachials: 39 ossicles have been reported in *Ceratocystis perneri* (Jefferies and Prokop 1972), around 60 in *Cothurnocystis elizae* (Jefferies 1968), and about 75 in *Proscotiaecystis melchiori* (Ubaghs 1983).

Morphology of the theca

The theca of *Ceratocystis* is massive, armoured, and comprises only large skeletal elements (Text-figs 3A, 5A–B). Height and thickness of the thecal frame decrease in a posterior direction. The lower surface is flat and formed by adjacent, expanded marginals. Infracentral areas are absent. Strong downward and laterally to posteriorly pointing protuberances are present on the lower surface of the four anterior marginals forming the lateral edges of the theca: M₂, M'₂, M₃ and M'₃ (Text-figs 3A, 5A–B; Ubaghs 1967b; Jefferies 1969a). The strong blade borne by marginal M₃ is frequently designated as the 'spinal' (Ubaghs 1967b; Lefebvre and Vizcaino 1999). At the posterior extremity of the theca, the two marginals flanking the anal opening are modified into flattened, downward pointing horn-like processes: these two plates are commonly designated as the 'glossal' (right of the anus) and the 'digital' (left of the anal opening). The convex upper thecal surface consists of three large adorals and seven massive supracentrals. It is reinforced by a strong triradiate ridge. Several sutural pores (respiratory orifices) are present in the right anterior corner of the upper surface (Text-figs 5A, 7B).

Most asymmetrical boot-shaped cornutes are characterized by a much lighter theca than that of *Ceratocystis*, and consist of large tessellated integumentary areas delimited by a delicate marginal frame (Text-figs 2, 3B–E, 5C–E, 6D–E). As in *Ceratocystis*, height and thickness of the marginal frame are maximum anteriorly, at the aulacophore insertion, and they steadily decrease rearwards. Strong downward

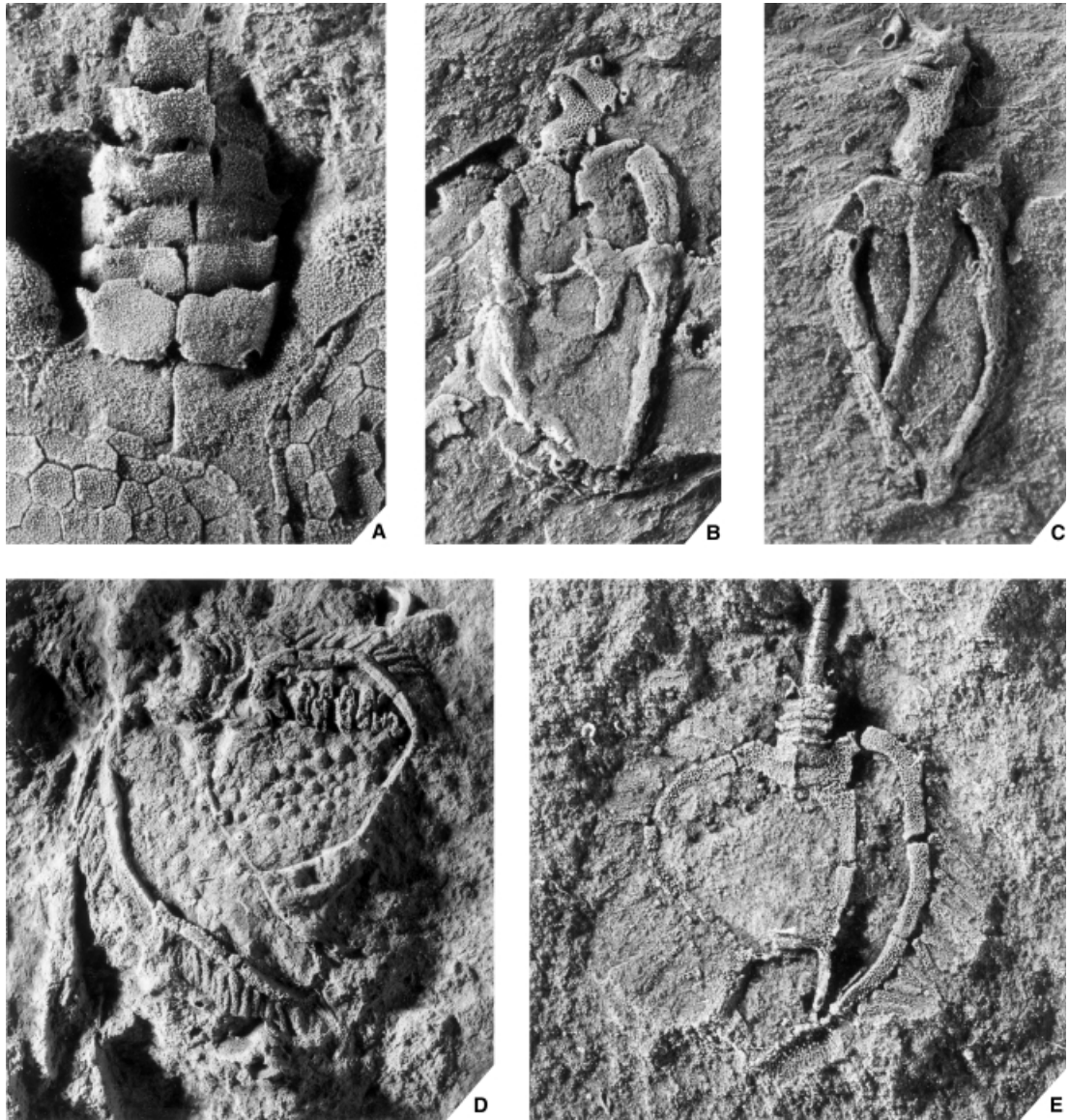


TEXT-FIG. 5. Morphology of the theca in primitive styloporans and asymmetrical cornutes. A–B, *Ceratocystis perneri* Jaekel, 1901 (primitive styloporan); Skryje Shales (Middle Cambrian), Czech Republic; modified after Ubaghs (1967b). A, anterior view of the theca. B, lower thecal surface. C–D, *Cothurnocystis elizae* Bather, 1913 (Cornuta); Starfish Bed (Upper Ordovician), Ayrshire (Scotland); redrawn after Jefferies (1968). C, anterior aspect of the theca. D, lower thecal surface. E–F, *Prochauvelicystis semispinosa* Daley, 1992 (Cornuta); Shineton Shales (Lower Ordovician), Shropshire (England); modified after Daley (1992). E, anterior aspect of the theca. F, lower thecal surface. Abbreviations: dig., digital; gloss., glossal; prot., protuberances; spin., spinal.

and posteriorly pointing protuberances are typically present on the lower surface of the anterior lateral marginals (M_2 , M'_2 , M_3 , M'_3), as for example in *Cothurnocystis fellinensis* (Text-fig. 3c), *C. elizae* (Text-figs 3D, 5C–D, 7A) or *Scotiaecystis curvata* (Text-fig. 3E). The posterior end of the theca is frequently characterized by the presence of enlarged, long and flattened thecal appendages, equivalent to the spinal, glossal and digital of *Ceratocystis*. In some asymmetrical cornutes, numerous small spines are articulated to the lateral and posterior margins of the marginal frame (e.g. *Ampelocarpus*, *Chauvelicystis*). Spines are directed downwards and rearwards (Text-figs 5E–F, 6D–E). Protuberances on the lower surface of marginals are absent in spiny cornutes. In asymmetrical cornutes, numerous respiratory structures (cothurnopores, lamellipores, sutural pores) are frequently present in the right anterior corner of the supracentral area (Text-figs 2B, 3B, 6D).

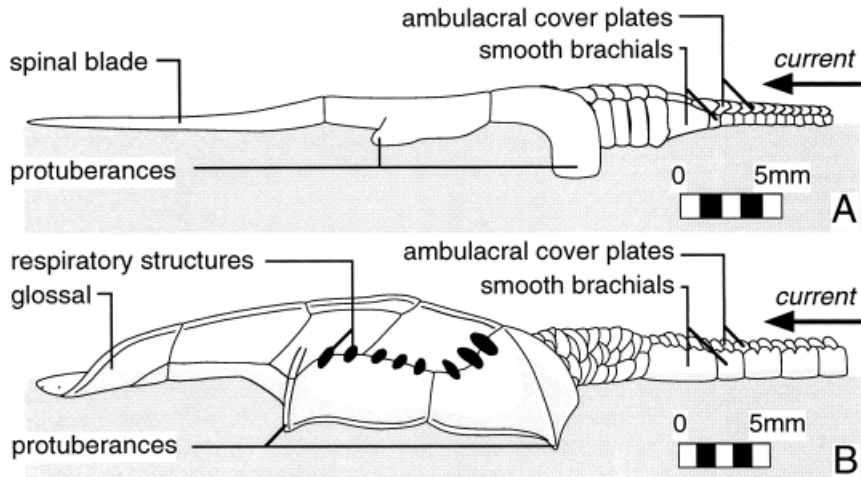
Interpretation

The presence of strong protuberances restricted to the lower surface of the theca strongly suggests that primitive styloporans and asymmetrical cornutes rested on their flat thecal surface in life (Bather 1913; Chauvel 1941; Ubaghs 1967a; Jefferies 1969a; Philip 1979; Kolata and Jollie 1982; Cripps 1988; Parsley 1988; Daley 1992; Ruta 1999c; Lefebvre and Vizcaino 1999). This 'flat-surface down' orientation of the theca is confirmed by the location of the respiratory orifices on the opposite (upper) thecal surface, and by the resulting orientation of the arm, with cover plates facing away from the substrate, which enables their opening. Ubaghs (1967b) and Jefferies (1969a) pointed out that the stereom mesh of the thecal protuberances is particularly massive, which suggests that these expansions were permanently in contact with the substrate. A comparable dense stereom can be observed on the lower surfaces of the proximal rings and brachials (Jefferies 1969a, p. 526). Consequently, the microstructure of the stereom confirms that *Ceratocystis* and asymmetrical cornutes lived 'flat-surface down', with the thecal protuberances deep into the substrate, and the aulacophore laying over the sea floor (Text-fig. 7).



TEXT-FIG. 6. A, *Phyllocystis crassimarginata* Thoral, 1935; FSL 168712, Saint-Chinian Formation (Lower Ordovician), Montagne Noire (France); lower surface of the proximal aulacophore; $\times 10$. B–C, *Nanocarpus dolambii* Ubaghs, 1991; Landeyran Formation (Lower Ordovician), Montagne Noire (France); aulacophore and lower thecal surface; $\times 10$. B, VOMN 141. C, VOMN 140 (holotype). D, *Chauvelicystis spinosa* Ubaghs, 1969; FSL 168718 (holotype), Saint-Chinian Formation (Lower Ordovician), Montagne Noire (France); upper thecal surface; $\times 5$. E, *Chauvelicystis vizcainoi* Daley, 1992; MNHN OE9, Saint-Chinian Formation (Lower Ordovician), Montagne Noire (France); aulacophore and lower thecal surface; $\times 10$.

The downward and posteriorly directed orientation of the protuberances, the thecal blades (spinal, glossal, digital) and the spiny fringe, when present, are consistent in all forms. These various structures served in anchoring the animal to the substrate and they are all well designed so as to prevent any movement in a posterior direction (Bather 1913; Ubaghs 1967a; Jefferies 1968; Philip 1979; Cripps 1988;



TEXT-FIG. 7. Life positions of primitive stylophorans and asymmetrical cornutes (in right lateral view). A, *Cothumocystis elizae* Bather, 1913 (Cornuta); Starfish Bed (Upper Ordovician), Ayrshire (Scotland). B, *Ceratocystis perneri* Jaekel, 1901 (primitive stylophoran); Skryje Shales (Middle Cambrian), Czech Republic.

Parsley 1988; Kolata *et al.* 1991; Daley 1992). The constant orientation of various thecal devices (protuberances, knobs, spines, blades) all prohibiting rearward motion of the animal has been interpreted several times as an argument suggesting that asymmetrical cornutes could move on the sea floor aulacophore first (Jefferies 1968, 1969a, 1975, 1986; Philip 1979; Jefferies *et al.* 1987; Cripps 1988; Daley 1992; Cripps and Daley 1994). First, it should be pointed out that the evidence that an animal cannot move in one way does not imply that it could do so in the opposite way. Second, locomotion of asymmetrical cornutes 'aulacophore first' hardly seems possible if one considers the rigidity of their arm and the considerable size of the protuberances on the lower thecal surface in some forms (Ubaghs 1967a, 1969, 1981, 1983; Parsley 1988, 1991; Rozhnov 1990; Kolata *et al.* 1991). Third, all locomotory cycles reconstructed for asymmetrical cornutes imply that the aulacophore is alternatively deeply thrust into the substrate on the right and on the left (Jefferies *et al.* 1987; Woods and Jefferies 1992; Daley 1992). The absence of sediment-gripping devices on the rounded lower surface of the brachials, as well as the function (feeding organ) and the delicate, extremely brittle nature of the aulacophore make it very improbable that this appendage was thrust deeply into the sediment for locomotion. On the other hand, the antero-posterior asymmetry of the thecal spikes, the presence of posterior exothecal blades, and the flexibility of the proximal aulacophore can be easily explained in the case of sessile organisms with their feeding arm upstream, facing the current (Text-fig. 7).

As argued above and as suggested by the massive stereom on the lower surface of proximal rings and brachials, the aulacophore was probably extended over the sea floor in life in *Ceratocystis* and asymmetrical cornutes. The orientation of the various thecal gripping devices strongly supports the view that the aulacophore was facing the current, and that the theca was downstream. The distribution of the gripping structures (protuberances) shows that the animal was anchored to the substrate by the anterior portion of the theca, where the plates are the thickest and most resistant. The presence of sharp, knob-bearing surfaces on the lower edges of the inferolaterals in some cornutes could correspond to additional gripping devices. In spiny cornutes, the function of the peripheral fringe of spines is comparable to that of the anterior protuberances on the lower surface of other asymmetrical forms (Ubaghs 1983, p. 44). The role of the large, flattened, posterior thecal blades (spinal, glossal, digital) was probably to stabilize the animal on the substrate. These expanded processes could have also helped in increasing the surface/volume ratio, as is frequently the case in epibenthic forms living on soft substrates (e.g. raphiophorid trilobites; Fortey and Owens 1978). The highly flexible, muscular proximal region of the appendage probably served to keep

the arm facing the current, and could have helped the animal to reorientate favourably (Ubaghs 1967a; Ruta 1999c).

In conclusion, *Ceratocystis* and asymmetrical cornutes were adapted to an epibenthic sessile mode of life on soft substrates, with their arm resting on the sea floor and facing the current (Text-fig. 7). Active reorientation of the animal was possible thanks to the highly flexible proximal aulacophore. Anchoring to the sediment was principally realized by the strong protuberances of the anterior thickened region of the lower thecal surface, which were deeply and firmly thrust into the sediment. The flat, expanded, posterior thecal blades probably helped in stabilizing the animal on the substrate.

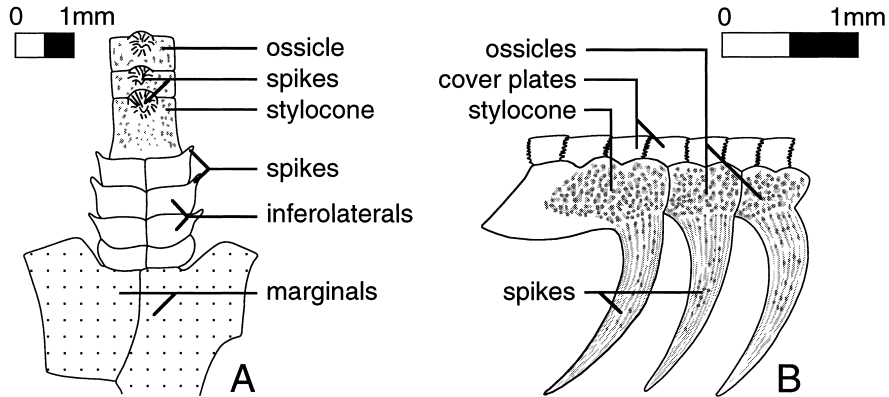
SYMMETRICAL CORNUTES

Symmetrical cornutes derive from asymmetrical boot-shaped forms (Jefferies and Prokop 1972; Cripps 1989a; Ubaghs 1991; Parsley 1997; Lefebvre and Vizcaïno 1999). Evolution towards more symmetrical thecae is a general trend in stylophorans. Identification of plate homologies shows that comparable symmetrical thecal outlines have been acquired convergently in several cornute lineages, both in the Cothurnocystida and the Amygdalothecida (Lefebvre and Vizcaïno 1999; Ruta 1999c). The transition from boot-shaped to symmetrical heart-shaped or bottle-shaped morphologies involves several drastic modifications, such as a severe reduction in size of the right infracentral area, and the frequent loss of several marginals (Lefebvre and Vizcaïno 1999). The present study focuses particularly on the functional morphology of symmetrical amygdalothecid (e.g. *Amygdalotheca*, *Domfrontia*, *Nanocarpus*) and hanusiid (*Prokopicystis*, *Reticulocarpus*) cornutes. *Juliaecarpus* is here considered as a junior synonym of *Nanocarpus*, following Lefebvre (in press).

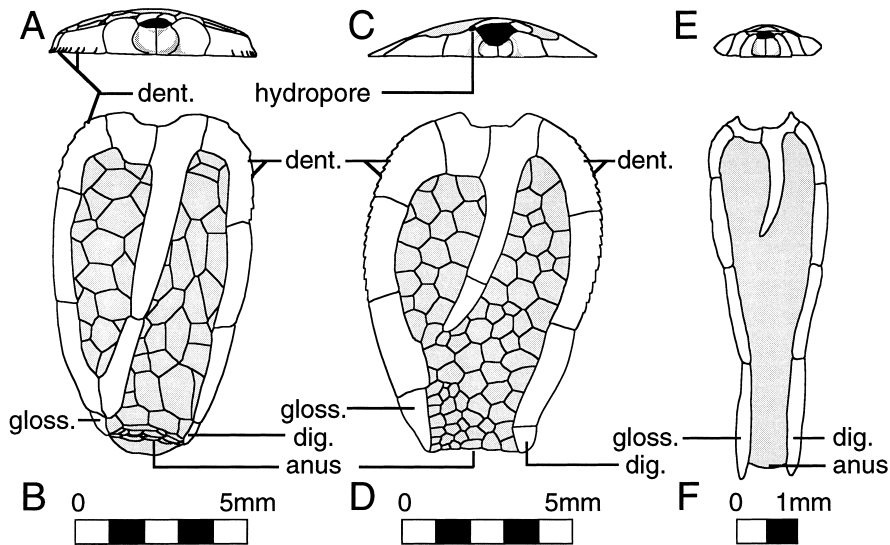
Morphology of the aulacophore

The proximal aulacophore of symmetrical cornutes is frequently disrupted and the morphology of this portion of the animal is generally poorly known (Text-fig. 6B–C; Cripps 1989a; Ubaghs 1991; Cripps and Daley 1994; Ruta 1999c). In forms where the proximal appendage is best preserved (e.g. *Beryllia*, *Domfrontia*, *Reticulocarpus*), this region shows the typical cornute organization, with tectals much smaller than inferolaterals (Text-fig. 8A). Numerous intercalary integumentary platelets are sometimes present between major proximal plates (e.g. *Reticulocarpus*). Cripps (1989a) suggested that tectals were absent in *Prokopicystis*, but this assertion has to be considered with caution given the poor preservation of this region. The lower surface of the proximal aulacophore is flat, and characterized by a coarse, granulated stereom. Sharp spikes are frequently present at the lower anterior edges of the inferolaterals (Text-fig. 8A; Jefferies and Prokop 1972; Chauvel and Nion 1977; Cripps and Daley 1994). The proximal appendage of symmetrical cornutes was a highly flexible structure which, as in boot-shaped forms, could move in nearly every direction.

The arm of symmetrical cornutes is extremely short, and does not comprise more than five brachials (stylocone and four ossicles). A possible autotomy of the distal tip (Jefferies and Prokop 1972; Cripps 1989a; Cripps and Daley 1994) and preservational artefacts (Lefebvre *et al.* 1998a; Ruta 1999c) have been advocated sometimes to explain the unusual shortness of these cornute arms. As pointed out by Ubaghs (1991), the rapid and regular decrease in size of the brachials in a distal direction rather suggests that the exceptional short size of the arm in symmetrical cornutes is likely to represent an actual phenomenon. As in boot-shaped forms, interbrachial articulations are poorly developed in symmetrical cornutes, with planar articular surfaces (Jefferies and Prokop 1972; Cripps 1989a; Ruta 1999c). This observation suggests that the arm was a rigid structure in life. Brachials are generally wider and broader than in asymmetrical forms (Text-fig. 8; Jefferies and Prokop 1972). A strong, downward to posteriorly recurved spike is present on the lower surface of the brachials in all symmetrical Amygdalothecida (Text-figs 6B–C, 8B, 10). The brachial spike is rounded to oval in cross-section, and it shows a typical fibrillar ornamentation with numerous longitudinal ridges (Jefferies and Prokop 1972; Chauvel and Nion 1977; Cripps 1989a; Ubaghs 1991; Ruta 1999c). Above the spike, the stereom of each brachial is coarse and granulated. Cover plates are rather stout and they frequently exhibit a radial striated ornamentation.



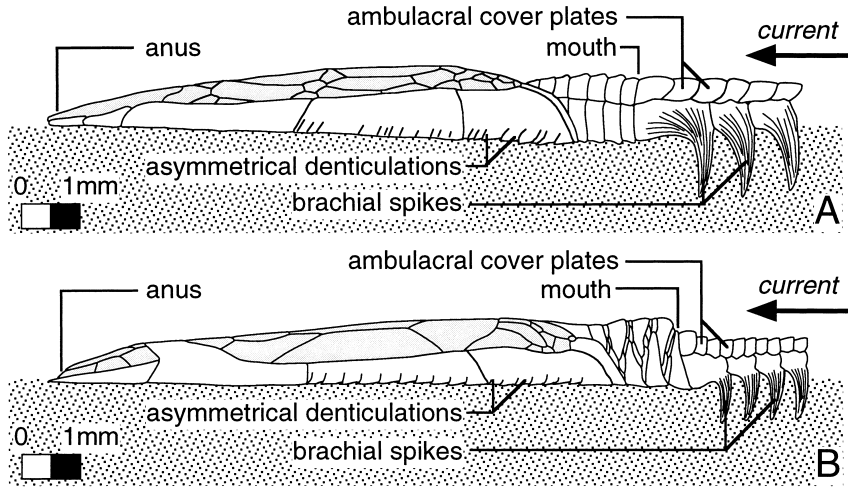
TEXT-FIG. 8. Morphology of the aulacophore in symmetrical cornutes. A–B, *Reticulocarpus hanusi* Jefferies and Prokop, 1972; Sarka Formation (Middle Ordovician), Czech Republic; modified after Jefferies and Prokop (1972). A, lower surface of the aulacophore. B, proximal portion of the arm in right lateral view.



TEXT-FIG. 9. Morphology of the theca in symmetrical cornutes. A–B, *Nanocarpus milnerorum* (Ruta, 1999c); Second Bani Formation (Upper Ordovician), Anti-Atlas (Morocco); modified after Ruta (1999c). A, anterior aspect of the theca. B, lower thecal surface. C–D, *Reticulocarpus hanusi* Jefferies and Prokop, 1972; Sarka (Middle Ordovician), Czech Republic; modified after Jefferies and Prokop (1972). C, anterior aspect of the theca. D, lower thecal surface. E–F, *Prokopicystis mergli* Cripps, 1989a; Dobrotiva Formation (Middle Ordovician), Czech Republic; modified after Cripps (1989a). E, anterior aspect of the theca. F, lower thecal surface. Abbreviations: dent., asymmetrical denticulations; dig., digital; gloss., glossal.

Morphology of the theca

The theca of symmetrical cornutes is generally extremely small and its length rarely exceeds a few millimeters: it is about 5 mm long in *Nanocarpus dolambii* (Text-fig. 6B–C), 7–10 mm in *N. milnerorum* (Text-fig. 9A–B), 6 mm in *Domfrontia* and *Beryllia*, about 9 mm in *Prokopicystis* (Text-fig. 9E–F), and 10 mm in *Reticulocarpus* (Text-fig. 9C–D). The theca of asymmetrical forms is typically two or three times larger. The thecal skeleton of Amygdalothecida is flattened, extremely light and delicate (Jefferies and



TEXT-FIG. 10. Life positions of symmetrical cornutes (in right lateral view). A, *Nanocarpus milnerorum* (Ruta, 1999c); Second Bani Formation (Upper Ordovician), Anti-Atlas (Morocco). B, *Reticulocarpus hanusi* Jefferies and Prokop, 1972; Sarka Formation (Middle Ordovician), Czech Republic.

Prokop 1972). The marginal frame is higher and slightly thicker close to the aulacophore insertion. It regularly decreases in height in a posterior direction. Marginals are thin, narrow elements, all with a flat lower surface. Protuberances and lateral blades (e.g. spinal) are absent in symmetrical cornutes. Digital and glossal are present, but they are incorporated into the marginal frame (Text-fig. 9). Their morphology is comparable to that of other marginals (Lefebvre and Vizcaïno 1999). The edges of several anterior lateral marginals (M_2 , M'_2 , M_3 , M'_3) are typically sharp and frequently serrated (e.g. *Nanocarpus*, *Reticulocarpus*). This sawtooth-shaped ornamentation is asymmetrical in all forms, with small denticulations consistently showing a steeper posterior edge (Text-figs 9A–B, D, 10). Serrations are absent on the more posterior marginals.

Integumentary areas are composed of numerous large polygonal somatics showing a typical retiform stereom (Jefferies and Prokop 1972; Chauvel and Nion 1977; Cripps 1989a; Cripps and Daley 1994; Ruta 1999c). The precise boundaries between adjacent platelets are sometimes difficult to discern, and integumentary areas give the false impression of consisting of large, uniform, reticulate surfaces (Ubaghs 1991). Respiratory orifices are absent in the right anterior corner of the upper surface (Chauvel and Nion 1977; Chauvel 1981; Ubaghs 1983, 1991; Cripps and Daley 1994; Lefebvre and Vizcaïno 1999; Ruta 1999b, c; but see Jefferies and Prokop 1972).

Interpretation

The life orientation of symmetrical cornutes was probably comparable to that of boot-shaped forms ('flat-surface down'; Text-fig. 10). This interpretation is supported by the coarse stereom of the lower surface of proximal rings and brachials, and by the concentration of all gripping devices on the lower surface of brachials (strong downward-pointing spikes), proximal rings (spikes on lower edges of inferolaterals) and marginals (asymmetrical serrations). Symmetrical cornutes differ from boot-shaped cornutes by (1) the presence of spikes on the lower surface of their brachials, (2) the shortness and stoutness of their arm, (3) their small size, (4) the absence of protuberances on the lower surface of anterior marginals, (5) the absence of large, flattened, posterior thecal blades, (6) the presence of lateral serrations on anterior marginals, (7) their more symmetrical thecal outline, (8) the reticulate stereom of their integumentary areas, and (9) the absence of respiratory structures. These numerous significant differences are probably correlated to a clearly distinct mode of life.

A first important observation concerns the contrasted distributions of anchoring devices in asymmetrical and symmetrical cornutes. In boot-shaped forms, most sediment-gripping structures are concentrated on the anterior border of the lower thecal surface (strong protuberances). The arm is not involved in the anchorage of the animal into the substrate, and rested passively over the sea floor. The situation is clearly different in symmetrical Amygdalothecida, with most of the gripping structures concentrated on the lower surface of the arm (strong brachial spikes). Contrary to the situation in boot-shaped cornutes, the theca is poorly implicated in the anchorage of the animal into the substrate in symmetrical forms (lateral serrations sometimes present on anterior marginals). Consequently, a first significant difference between asymmetrical and symmetrical cornutes concerns the location of sediment-gripping devices, concentrated on the lower surface of the theca, and of the arm, respectively.

Symmetrical and boot-shaped cornutes share very comparable proximal aulacophores, but they strongly differ as far as the morphology of the arm is concerned. Those important differences in the arm morphology are correlated with different functions in the two cornute groups. In asymmetrical forms, the long and slender arm has a single function, that of feeding the organism. In Amygdalothecida, the arm is inflated and extremely reduced in size. This massive morphology, along with the presence of strong brachial spikes, suggests that in symmetrical cornutes, the arm was not only a feeding device but also an anchoring structure. Consequently, the presence of spikes and the stout aspect of the amygdalothecidan arm probably result from its transformation into a sediment-gripping device. Anchoring the animal into the substrate certainly exerted a strong adaptative pressure on the arm, which probably prevented it from becoming longer. As pointed out by Jefferies and Prokop (1972), Amygdalothecida are adult organisms, in spite of their small size. The small size of these adult stylophorans can be interpreted as a neotenus character (Jefferies and Prokop 1972; Cripps 1989*b*), but it may also simply reflect the fact that the animals could not become much larger because the size of their feeding structure was fundamentally limited by its anchoring function. As argued by Ubaghs (1991, p.166), the extremely reduced size of the amygdalothecidan arm is correlated to the small size of the theca. Correlatively, the much larger boot-shaped cornutes are characterized by much longer feeding structures.

In boot-shaped cornutes, a large asymmetrical theca expanded on the sea bottom, strong, downward-pointing, anterior protuberances, and long, flattened, posterior blades represent adaptations to a sessile epibenthic mode of life, with the animal anchored into the substrate by the anterior border of its lower thecal surface. In Amygdalothecida, the symmetrical theca, and the absence of protuberances and expanded posterior blades are correlated with the transfer of most of the anchoring function from the theca to the arm. Anchoring devices are, nevertheless, not totally absent on the theca, as indicated by the frequent presence of lateral serrations on the edges of anterior marginals. The gripping function of these sawtooth-shaped structures is suggested by their asymmetrical morphology, with posterior steeper edges (Jefferies and Prokop 1972; Jefferies 1986). The asymmetry of the marginal serrations indicates that they were well-suited to prevent, or at least to reduce, any slippage of the theca in a posterior direction. As for protuberances on the lower thecal surface in boot-shaped cornutes, asymmetrical marginal serrations in Amygdalothecida represent efficient anchoring devices in the case of epibenthic, mostly sessile organisms facing the current aulacophore first. The asymmetry of the lateral serrations of Amygdalothecida has been interpreted by several authors as an indication that the animal could move in a forward direction (Jefferies and Prokop 1972; Jefferies 1986; Parsley 1988; Cripps 1989*a*; Cripps and Daley 1994). As already argued above, the fact that a structure prevents an organism from moving in one way does not imply that the animal was actually moving in the opposite direction. The feeding function of the aulacophore and the opening of the cover plates make it very improbable that symmetrical cornutes could crawl appendage first, by deeply thrusting the aulacophore into the mud, and one must agree with Cripps (1989*a*, p. 76) that 'locomotion in *P. mergli* . . . would have been an inefficient activity . . . In view of this, it seems probable that *P. mergli* spent most of its time stationary, moving only occasionally' (Ruta 1999*c*, p.73). Symmetrical cornutes were thus probably epibenthic sessile organisms, feeding with their appendage firmly anchored in the mud and facing the current (Text-fig. 10). The high flexibility of the proximal amygdalothecidan appendage suggests that the animal could probably move its rigid arm, so as to change its anchoring position, in order to keep it favourably orientated. Thecal gripping devices are necessary when the arm is temporarily extracted from the mud, so as to prevent the animal from slipping away in the

current. The role of the marginal serrations was probably to provide a temporary thecal anchoring of the organism, when the animal was shifting the position of its arm to keep it facing the current.

In some vagrant, bottom-dwelling, pleurocystitid cystoids, respiratory structures (rhombs) are lost (e.g. *Amecystis*), and the thick thecal plates replaced by large, tessellated, integumentary areas consisting of very thin platelets. This observation suggests the replacement of one means of respiration (using rhombs) by another (directly through the thecal walls, and possibly, anal pumping; Broadhead and Strimple 1975; Brower 1999). Analogy with these cystoids suggests that the absence of respiratory structures on the upper surface of Amygdalothecida might be correlated with the presence of large, flexible, reticulate, integumentary areas (Parsley 1988; Lefebvre and Vizcaïno 1999). Retiform stereom considerably increases the porosity of the skeleton and thus the exchange surface.

In conclusion, symmetrical cornutes were adapted to an epibenthic sessile mode of life on soft substrates (Text-fig. 10). Active reorientation of the animal was possible thanks to the highly flexible proximal aulacophore. Anchoring to the sediment was principally realized by the arm (strong spikes on the lower surface of the brachials). Gripping structures on the arm were frequently supplemented by asymmetrical serrations on the lower edges of anterior marginals. This thecal sculpture probably helped in anchoring temporarily the organism when the animal was extracting its arm from the substrate to reorientate it more favourably. The exceptional shortness of the arm and its massive aspect certainly result from its transformation into a sediment-gripping device. The small size of symmetrical cornutes could be directly correlated to the extreme reduction of their modified feeding structure.

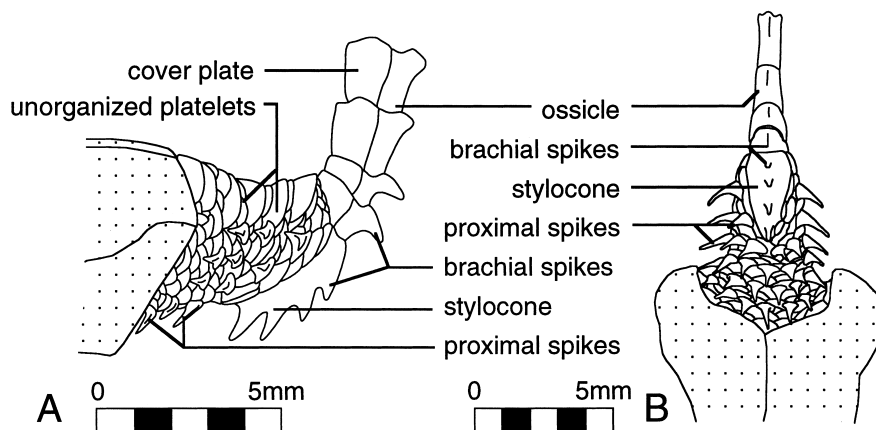
LAGYNOCYSTIS

Lagynocystis pyramidalis is the only known representative of lagynocystid mitrates. It is characterized by a remarkable stasogenesis from the Lower Arenig to the Llandeilo. The presence of *Lagynocystis* has been reported in the Lower Arenig of Montagne Noire, southern France (Ubaghs 1991), the Upper Arenig of Wales (Jefferies 1987), the Llanvirn of Spain (Gutiérrez-Marco *et al.* 1992, 1999b), the Llanvirn and Llandeilo of Bohemia (Barrande 1887; Chauvel 1941; Jefferies 1973; Parsley 2000) and Brittany (Chauvel and Nion 1977; Henry *et al.* 1997). This great stratigraphic extension at species-level is possibly correlated to the extremely stable environmental conditions prevailing in the deep, muddy sea bottoms of the northern margin of Gondwana, in which *Lagynocystis* was particularly abundant (Henry *et al.* 1997; Lefebvre *et al.* 1998b; Parsley 2000).

Morphology of the aulacophore

The proximal region of the appendage of *Lagynocystis* consists of very numerous, scale-like, unorganized, imbricate platelets (Text-figs 11, 24A; Jefferies 1973; Parsley 2000). Strong downward and posteriorly directed spikes are abundant on the lower surface and lateral sides of the proximal aulacophore (Text-fig. 11; Barrande 1887; Jefferies 1973; Ubaghs 1991; Parsley 2000). The unorganized plating of the proximal appendage suggests that it was certainly a highly flexible structure in life (Chauvel 1941, p. 204). The proximal aulacophore of *Lagynocystis* departs from the typical mitrate organization, characterized by well-defined telescoping rings made of inferolaterals and tectals of subequal size. The unorganized morphology of the proximal appendage of *Lagynocystis* is strongly reminiscent of the situation in *Ceratocystis* (see above; Ubaghs 1967b). This observation supports the view that *Lagynocystis* could represent a primitive mitrate (Lefebvre and Vizcaïno 1999; Lefebvre 2000; but see Parsley 1997, 1998, 2000).

The arm of *Lagynocystis* is a long and slender structure, comprising more than 30 brachials (Jefferies 1973; Parsley 2000). The lower surface of the stylocone is ornamented by four or five strong spines aligned along the mid line (Text-fig. 11A; Jaekel 1918; Chauvel 1941; Jefferies 1973; Parsley 2000). A single strong spine is also present on the lower surface of each of the two most proximal ossicles (Text-fig. 11A). More distal brachials exhibit smaller spines at the anterior edge of their lower surface. All brachial spines are laterally compressed, downward and posteriorly directed. As in other mitrates, interbrachial articulations are complex and well-developed in *Lagynocystis* (Jefferies 1973; Parsley 2000). Sites for muscle insertion and a large triangular cavity probably housing ligament (Jefferies 1973, fig. 12) suggest that the arm of *Lagynocystis* could be flexed in a vertical plane.



TEXT-FIG. 11. Morphology of the aulacophore in lagynocystid mitrates. A–B, *Lagynocystis pyramidalis* (Barrande, 1887); Sarka Formation (Middle Ordovician), Czech Republic; redrawn after Jefferies (1973). A, proximal aulacophore and proximal portion of the arm in right lateral view. B, lower surface of the proximal aulacophore and proximal portion of the arm.

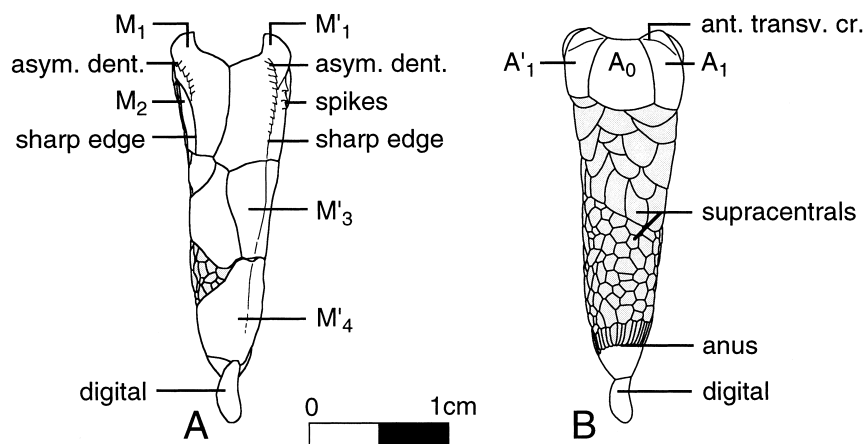
Morphology of the theca

The theca of *Lagynocystis* is narrow, elongate and subtriangular in outline (Text-figs 12, 24A). The unusual morphology of *Lagynocystis* partly results from the absence of infracentral areas on the lower surface (Lefebvre 2000). The theca comprises two distinct parts. The anterior portion of the theca is particularly high and consists of thick, tightly sutured large plates on both thecal surfaces (adorals A_1 , A_0 , A'_1 , and marginals M_1 , M'_1 , M_2). This massive anterior region slopes strongly downwards anteriorly and shows a well-developed ornamentation (Text-figs 12A, 13, 24A). Thecal sculpture in the anterior region of the theca consist of: (1) sharp lateral edges on the lower surface of M'_1 and M_1 , sometimes showing asymmetrical serrations with a consistently steeper posterior slope (Chauvel 1941, fig. 77; Ubaghs 1967a, fig. 354.1; Jefferies 1973, fig. 42; Parsley 2000, fig. 2.4); (2) frequently several strong, posteriorly and downward-pointing spikes, on the lateral side of M'_1 (Chauvel and Nion 1977; Ubaghs 1991); (3) an asymmetrical transverse crest, with a steeper posterior edge, on the anterior margins of A_1 and A'_1 (Ubaghs 1967a, 1991; Jefferies 1973; Parsley 2000). The anterior massive region houses an internal comb-like structure ('ctenoid organ'), borne by the three adorals, and located posteriorly to the aulacophore insertion (Chauvel 1941; Ubaghs 1967a; Jefferies 1973; Chauvel and Nion 1977; Parsley 2000).

The posterior region of the theca is characterized by a flat, rigid lower surface (Text-figs 12A, 13, 24A). The upper surface and lateral sides of the posterior region are flexible and consist of numerous tessellate integumentary platelets (Text-fig. 12B). The anterior portion of supracentrals is typically overlapped by the posterior margin of more anterior elements (Jefferies 1973, figs 19–20; Parsley 2000, fig. 2.1). The posterior region of the theca is subtriangular in outline. It regularly decreases in height and width in a posterior direction. The anal opening is located at the posterior end of the upper surface, anterior to a small terminal plate and a small, flattened, thecal process, homologous to the digital of cornutes (Text-fig. 12B; Lefebvre 2000). Ornamentation is absent in the posterior thecal region. The sharp lateral ridge affecting anteriorly the edge of M'_1 is present, but attenuated, in the posterior region. Contrary to the situation in the anterior portion of the theca, the sharp lateral margins of M'_3 and M'_4 are never serrated.

Interpretation

The life orientation of *Lagynocystis* was certainly comparable to that of cornutes. This 'flat-surface down' orientation is confirmed by the location and orientation of all gripping devices (Text-fig. 13). Brachial



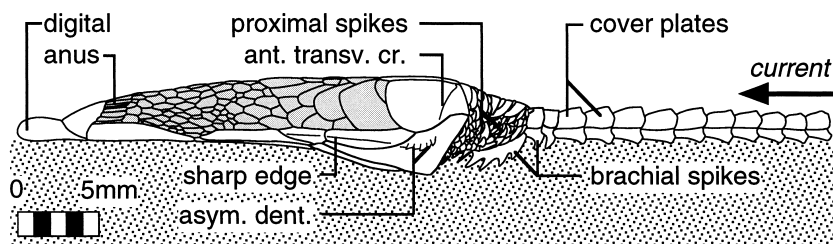
TEXT-FIG. 12. Morphology of the theca in lagynocystid mitrates. A–B, *Lagynocystis pyramidalis* (Barrande, 1887); Sarka Formation (Middle Ordovician), Czech Republic; redrawn after Jefferies (1973). A, lower thecal surface. B, upper thecal surface. Abbreviations: A, adoral; ant. transv. cr., anterior transverse crest; asym. dent., asymmetrical denticulations; M, marginal.

spines, spikes of the proximal aulacophore, asymmetrical serrations and thecal spines are consistently located on the lower surface and directed downwards and posteriorly. The life orientation is also confirmed by the respective positions of the two contrasted thecal surfaces: the flat, rigid, thicker lower surface was in contact with the substrate, and the convex, flexible, thinner upper surface faces away from the sea bottom (Ubaghs 1967a; Philip 1981; Chauvel 1981; Parsley 2000). Finally, the ‘flat-surface down’ orientation of *Lagynocystis* is in good accordance with the feeding function of the arm, as it allows the outward opening of the cover plates, away from the substrate.

The ornamentation on the lower surface of the three most proximal brachials (stylocone and two following ossicles) is clearly distinct and stronger than that on the lower surface of more distal brachials. This observation suggests that the three most proximal brachials and more distal ossicles probably fulfilled different functions in life. The presence of strong downwards and posteriorly recurved spines on the lower surface of the stylocone and of the two following brachials supports the view that these skeletal elements probably helped in anchoring the animal into the substrate. The reduced ornamentation on the lower surface of the following ossicles suggests that most of the arm was lying over the sea-floor and only fulfilled a feeding function (Text-fig. 13).

The presence of downwards and posteriorly directed spikes on the lower surface, as well as on the lateral sides of the proximal aulacophore, suggests that both the inferior and lateral surfaces of this region were in contact with the sediment and that, consequently, the proximal aulacophore was partly buried in life (Text-fig. 13). The upper surface of the proximal appendage, which lacks ornamentation and consists of larger imbricated platelets, was probably not in contact with the sediment.

Serrations on the sharp lateral edges of anterior marginals in *Lagynocystis* are comparable to those described in cornutes (see above). They are asymmetrical sculptures preventing, or reducing, slippage of the theca into a posterior direction. Their orientation is consistent with that of other gripping devices located on the theca and on the aulacophore. The presence of an anterior transverse crest on the adorals of *Lagynocystis* is a synapomorphy shared by all mitrates (Lefebvre 2000), and its presence even in indisputable epibenthic forms (see below) throws doubts on its functional, if any, significance. As suggested by Lefebvre (2000, p. 895), the anterior crest of mitrates possibly represents a plesiomorphic character reminiscent of the situation in the primitive stylophoran *Ceratocystis*. In *Ceratocystis*, adorals extend onto the lower surface and they are characterized by sharp anterior edges. Consequently, the presence of asymmetrical gripping sculpture on the lower surface (sharp serrated edges of marginals) and lateral sides (spines on M'_1) of the massive anterior portion of the theca strongly suggests that the inferior



TEXT-FIG. 13. Life position (in right lateral view) of the lagynocystid mitrate *Lagynocystis pyramidalis* (Barrande, 1887); Sarka Formation (Middle Ordovician), Czech Republic. Abbreviation: ant. transv. cr., anterior transverse crest; asym. dent., asymmetrical denticulations.

surface and lateral sides of the anterior thecal region were buried during life (Text-fig. 13). This conclusion is supported by the massive aspect and the downwards sloping of the anterior region of the theca. The long, expanded and flattened posterior region of the theca, which lacks ornamentation, possesses a planar lower surface and a posterior exothecal process (digital), probably formed a kind of large posterior buttress lying on the sea floor.

A respiratory function has been frequently proposed for the ctenoid organ of *Lagynocystis* (Ubaghs 1967a; Jefferies 1973; Kolata *et al.* 1991; Parsley 2000). Although the deep, probably deoxygenated, environments in which *Lagynocystis* lived make this function plausible, the ctenoid organ could also have represented a kind of sieving device, avoiding the ingestion of a large quantity of sediment by the organism. This alternative possible function of the ctenoid organ is suggested by its location at the anterior edge of the theca, posterior to the mouth, and by the presumed mode of life of *Lagynocystis*. If, as suggested above, the proximal appendage and the anterior region of the theca were partly buried in the mud in life, the mouth of *Lagynocystis* would have been at, or very close to, the sediment-water interface (Text-fig. 13). This location of the mouth makes ingestion of mud very probable, and the function of the ctenoid organ could have been to avoid, or minimize, sediment fouling of the gut.

Examination of the distribution of the ornamentation in *Lagynocystis* shows that sediment-gripping devices are concentrated in the region located around the aulacophore insertion. This highly ornamented region comprises the three most proximal brachials, the proximal appendage and the massive anterior region of the theca. Gripping structures regularly decrease in strength, size and number away from the aulacophore insertion, in both an anterior and a posterior direction, on the lower surface of the brachials and of the theca, respectively. This observation suggests that the region located around the aulacophore insertion, probably partly buried in life, played an important role in anchoring the animal into the mud. The asymmetry and constant orientation of all gripping devices in *Lagynocystis* (downwards and posteriorly directed) is comparable to that of anchoring structures in cornutes, and is thus very well suited for an organism facing the current aulacophore first. The polyplated proximal aulacophore of *Lagynocystis* was a highly flexible structure allowing the animal to reorientate its arm favourably, so as to keep it facing the current. Partial burial of the aulacophore insertion region into the substrate was probably realized by lateral movements of the flexible proximal appendage and of the laterally compressed, proximal brachial spikes. It possibly also involved lateral rocking of the anterior region of the theca, as suggested by the presence of sharp lateral edges on anterior marginals.

In conclusion, *Lagynocystis* was adapted to an epibenthic sessile mode of life in soft, muddy substrates. As in cornutes, active reorientation of the animal was possible thanks to the highly flexible proximal appendage, and the arm was extended upstream over the sea floor for feeding (Text-fig. 13). Anchoring to the sediment was realized by the spines of the most proximal brachials, and by the partial burial of the proximal aulacophore and of the thickened anterior region of the theca. The ctenoid organ was possibly a respiratory structure, but it could also have represented a sieving device minimizing the ingestion of mud resulting from the partial burial of the proximal aulacophore. The flat, expanded, posterior region of the theca probably helped in buttressing the animal on the sea bottom.

PELTOCYSTIDAE AND PRIMITIVE MITROCYSTITIDA

Peltocystis cornuta, from the Lower Arenig of Montagne Noire (southern France), is the single known representative of the Peltocystidae, and the most primitive peltocystidan mitrate known so far. The Peltocystida comprise two other families: the Kirkocystidae (see below), and the Jaekelocarpidae. Mitrocystitida constitute one of the most successful groups of stylophorans. Their stratigraphic range extends from the Lower Ordovician (Tremadoc) to the Middle Devonian (Eifelian). The functional morphology of several selected, primitive Mitrocystitida is discussed below: *Vizcainocarpus rutai* (Tremadoc, England), *V. dentiger*, *Chinianocarpos thorali* and *Ovocarpus moncereti* (Lower Arenig, Montagne Noire), *Mitrocystites mitra* (Llanvirn, Bohemia), *Aspidocarpus discoidalis* and *Eumitrocystella savilli* (Llandeilo, Morocco), and *Aspidocarpus bohemicus* (Caradoc, Bohemia).

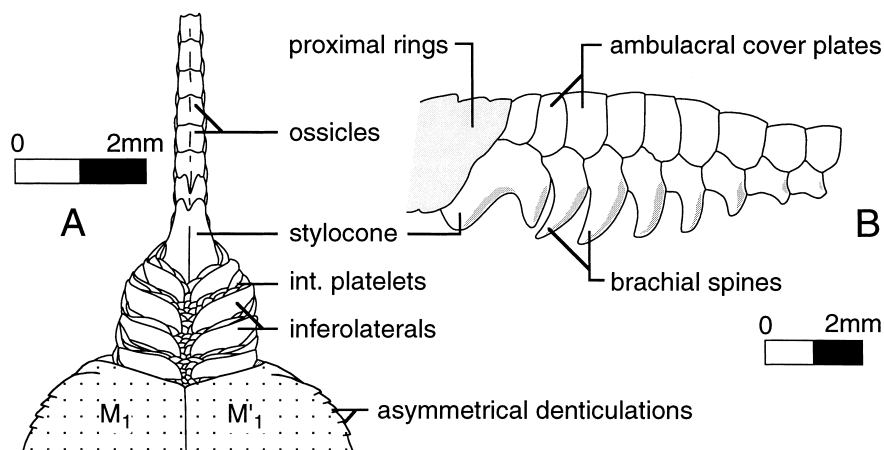
Morphology of the aulacophore

The morphology of the proximal aulacophore is very comparable in *Peltocystis* and most primitive Mitrocystitida, with a typical 'mitrate-like' organization (Text-figs 14A, 16A; Pl. 1, fig. 1). The proximal appendage is a broad and large, highly flexible structure consisting of several telescoping rings. Each ring consists of four skeletal elements. Tectals and inferolaterals are subequal in size and they typically meet in the lateral mid-line. Intercalary platelets are sometimes present between proximal rings, as in *Peltocystis* (Text-fig. 14A; Ubaghs 1969; Jefferies 1986). The lower surface of inferolaterals is flattened in *Peltocystis* (Ubaghs 1969). The proximal aulacophore of *Peltocystis* and primitive Mitrocystitida is deeply inserted into a cavity defined by anterior marginals (M_1 , M'_1) and adorals (A_1 , A'_1). The frequent greater forward extension of the two marginals flooring this aulacophore insertion cavity allows upward and lateral movements, but severely hinders potential downward flexion of the proximal appendage. In some forms (e.g. *Aspidocarpus discoidalis*, *Vizcainocarpus dentiger*), downward flexion is impossible (Cripps 1990; Ruta 1997a). The proximal aulacophore of *Chinianocarpos* differs from that of all other primitive Mitrocystitida (Text-fig. 16B). As in *Lagynocystis* and *Ceratocystis*, the proximal appendage of *Chinianocarpos* is characterized by the presence of abundant, imbricate, scale-like platelets and by the apparent absence of major skeletal elements (tectals, inferolaterals). Several downwards and posteriorly directed spikes have been described on the lower surface of the proximal aulacophore of *Chinianocarpos* (Ubaghs 1961a, 1969; Jefferies 1986).

The morphology of the arm is very similar in *Peltocystis* and primitive Mitrocystitida. Long, laterally compressed, downwards and posteriorly recurved blades are present on the lower surface of the stylocone and of the most proximal ossicles (Text-figs 14B, 16; Pl. 1, figs 1–2, 4). Those brachial spines rapidly decrease in size on the lower surface of more distal brachials. Two blades are typically present on the stylocone, the distal one being generally higher than the proximal one, as for example in *Mitrocystites* (Text-fig. 16A; Pl. 1, fig. 4; Jefferies 1968), *Chinianocarpos* (Text-fig. 16B; Ubaghs 1969; Jefferies and Prokop 1972), *Aspidocarpus* (Cripps 1990), *Eumitrocystella* (Pl. 1, figs 1–2; Beisswenger 1994), *Ovocarpus* (Ubaghs 1994), and *Vizcainocarpus* (Ruta 1997a). Complex, well-developed interbrachial articulations, comparable to those existing in *Lagynocystis*, have been described in *Peltocystis* (Ubaghs 1967a, 1969) and most primitive Mitrocystitida (Jefferies 1968; Beisswenger 1994), suggesting that the arm of these mitrates was able to flex in a vertical plane (Pl. 1, fig. 1). The length of the arm is difficult to ascertain, as the distal portion is frequently broken away (preservational artefact). Long arms, comprising several dozen brachials, have been described; at least 25 ossicles are present in *Peltocystis* (Jefferies 1986), and more than 50 in *Eumitrocystella* (Beisswenger 1994). Shorter arms probably occurred in smaller forms, such as *Ovocarpus* (Ubaghs 1994), *Chinianocarpos* (Jefferies 1986), or *Vizcainocarpus* (Ruta 1997a).

Morphology of the theca

Peltocystis and most primitive Mitrocystitida (e.g. *Aspidocarpus*, *Mitrocystites*, *Vizcainocarpus*) are characterized by a flattened theca, typically as long as wide (Text-fig. 15; Pl. 1, figs 3–6). The height of the theca progressively diminishes in a posterior direction. The lower surface is flat, rigid, thickened and

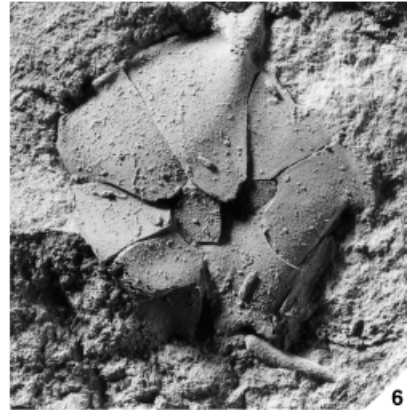
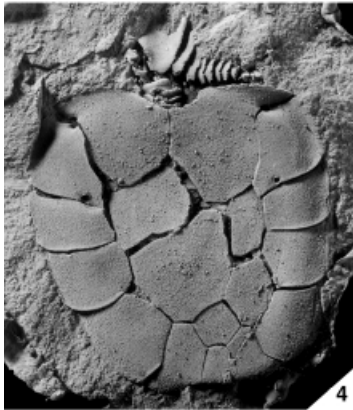
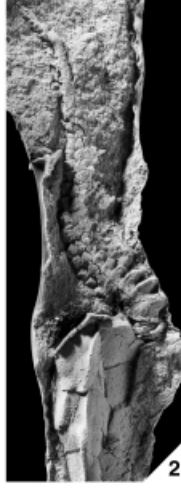


TEXT-FIG. 14. Morphology of the aulacophore of the peltocystid mitrate *Peltocystis cornuta* Thoral, 1935; Saint-Chinian Formation (Lower Arenig), Montagne Noire (France); redrawn after Jefferies (1986). A, lower surface of the proximal aulacophore and proximal portion of the arm. B, proximal portion of the arm in right lateral view. Abbreviations: int. platelets, intercalary platelets; M, marginal.

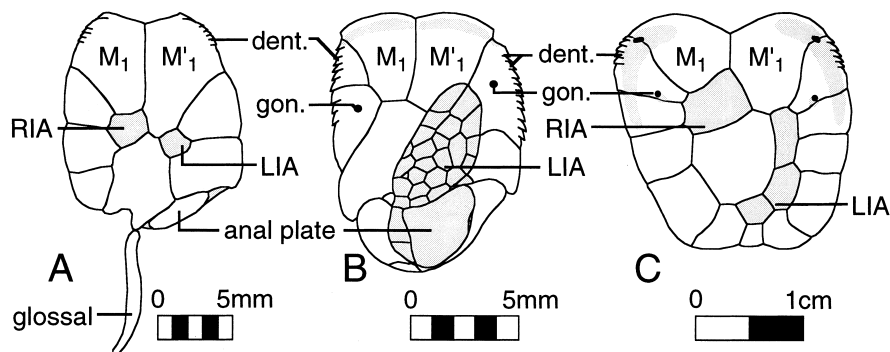
generally consists of enlarged, massive plates. The presence of tessellate infracentral areas comprising numerous platelets is a plesiomorphic feature retained in *Chinianocarpus* (Text-fig. 15B; Pl. 1, fig. 3), *Aspidocarpus*, *Ovocarpus* and *Vizcainocarpus* (Jefferies 1986; Lefebvre 2000). In more derived Mitrocystitida (e.g. *Eumitrocystella*, *Mitrocystites*) and *Peltocystis*, infracentral areas comprise a reduced and constant number of large infracentral elements (Text-figs 15A, C; Pl. 1, figs 4, 6). The sharp anterior margin of the lower thecal surface is sometimes recurved downwards, as in *Chinianocarpus* (Ubaghs 1969, p. 75), *Vizcainocarpus* (Ruta 1997a, p. 367; Lefebvre 2000, p. 901) and *Ovocarpus* (Ubaghs 1994, p. 20). The lateral edges of the lower thecal surface are frequently bent downwards anteriorly, and a sharp, serrated peripheral flange is typically present on the margin of the most anterior marginals (e.g. M_1 , M'_1 , M_2 , M'_2 , M_3). As in symmetrical cornutes and *Lagynocystis*, this saw-tooth sculpture consistently shows steeper posterior surfaces. A serrated peripheral flange is present anteriorly on the lateral edges of the lower surface of *Peltocystis* (Text-fig. 15A; Ubaghs 1969, fig. 3; Jefferies 1986, fig. 8.37), *Chinianocarpus*

EXPLANATION OF PLATE 1

- Figs 1–2. *Eumitrocystella savilli* Beisswenger, 1994. Ouine-Inirne Formation (Middle Ordovician), Anti-Atlas (Morocco). 1, VOMA 303, recurved aulacophore and anterior portion of the upper thecal surface; $\times 5$. 2, VOMA 311, extended aulacophore and anterior portion of the lower thecal surface; $\times 3$.
- Fig. 3. *Chinianocarpus thoralis* Ubaghs, 1961a; FSL 170930, Saint-Chinian Formation (Lower Ordovician), Montagne Noire (France); lower thecal surface; $\times 3$.
- Fig. 4. *Mitrocystites mitra* Barrande, 1887; BMNH E16062, Sarka Formation (Middle Ordovician), Czech Republic; aulacophore and lower thecal surface; $\times 2$.
- Figs 5–6. *Peltocystis cornuta* Thoral, 1935. Saint-Chinian Formation (Lower Ordovician), Montagne Noire (France). 5, FSL 168708, upper thecal surface; $\times 3$. 6, UM 455, lower thecal surface; $\times 3$.
- Fig. 7. *Anatifopsis papillata* (Bassler, 1943); BMNH E63140, Bromide Formation (Upper Ordovician), Oklahoma (USA); proximal aulacophore and lower thecal surface; $\times 5$.
- Fig. 8. *Balanocystites primus* (Barrande, 1872); NMP L32493, Sarka Formation (Middle Ordovician), Czech Republic; aulacophore and upper thecal surface; $\times 2$.
- Fig. 9. *Anatifopsis* cf. *barrandei minuta* (Chauvel, 1941); VOMA 122, Ouine-Inirne Formation (Middle Ordovician), Anti-Atlas (Morocco); aulacophore and lower thecal surface; $\times 2$.



LEFEBVRE, stylophoran echinoderms



TEXT-FIG. 15. Morphology of the lower thecal surface in Peltocystida and primitive Mitrocystitida. A, *Peltocystis cornuta* Thorval, 1935 (Peltocystida); Saint-Chinian Formation (Lower Arenig), Montagne Noire (France); modified after Ubags (1969). B, *Chinianocarpus thorali* Ubags, 1961a (Mitrocystitida); Saint-Chinian Formation (Lower Arenig), Montagne Noire (France); modified after Jefferies (1986). C, *Mitrocystites mitra* Barrande, 1887 (Mitrocystitida); Sarka Formation (Middle Ordovician), Czech Republic; modified after Jefferies (1968). Abbreviations: dent., asymmetrical denticulations; gon., gonopore; LIA, left infracentral area; M, marginal; RIA, right infracentral area.

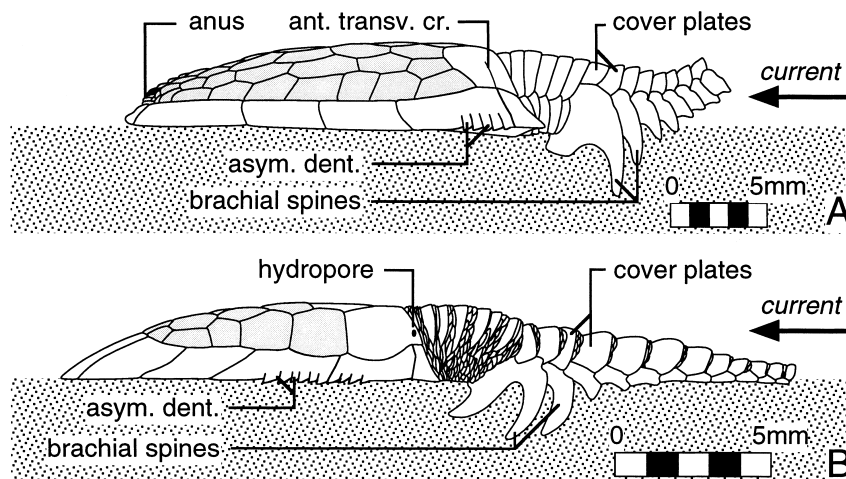
(Text-fig. 15B; Ubags 1969, fig. 29; Jefferies 1986, fig. 8.26), *Vizcainocarpus dentiger* (Ruta 1997a, fig. 2) and *Mitrocystites* (Text-fig. 15C; Ubags 1967a, fig. 342; Jefferies 1968, fig. 23). Contrary to the situation in primitive Mitrocystitida, a long and delicate, slightly curved exothecal spine is posteriorly articulated to the theca in *Peltocystis* (Text-fig. 15A; Pl. 1, figs 5–6). This posterior process is homologous to the glossal of *Ceratocystis* and cornutes (Lefebvre 2000).

In *Peltocystis* and all primitive Mitrocystitida, the upper surface is invariably convex (Pl. 1, fig. 5). As in *Lagynocystis* and all mitrates, the anterior margin of the upper thecal surface of *Peltocystis* and primitive Mitrocystitida is framed by enlarged adorals showing the typical anterior transverse crest (on A_1 and A'_1). The large flexible supracentral area comprises numerous, thin, tessellate integumentary platelets. As in *Lagynocystis*, supracentrals are sometimes imbricated (e.g. in *Eumitrocystella* and *Peltocystis*). In *Vizcainocarpus dentiger* and *V. rutai*, several supracentral elements carry strong, enlarged knobs (Ruta 1997a; Lefebvre 2000). These knobs are characterized by a very porous stereom, and they are consistently directed upwards and posteriorly. The anus opens at the distal end of the upper surface in *Peltocystis* and primitive Mitrocystitida (with the single exception of *Chinianocarpus*, in which the anus opens at the extremity of the lower surface; Text-fig. 15B).

Interpretation

The life orientation of *Peltocystis* and primitive Mitrocystitida was certainly similar to that of cornutes and *Lagynocystis* (Ubags 1981; Chauvel 1981; Kolata and Jollie 1982; Parsley 1991; Lefebvre *et al.* 1998a; Ruta 1999b). The 'flat-surface down' orientation of the organism is strongly supported by the constant orientation (rearwards and downwards) of the various sediment-gripping devices present on the lower surface of the brachials (proximal blades, distal spines and knobs), the lower surface of the proximal aulacophore (spikes in *Chinianocarpus*), and on the lower surface of the theca (asymmetrical serrations, downwards recurved, anterior thecal margin). This life orientation is also in good accordance with the presence of a massive, thickened, flat lower surface in contact with the substrate, and of a flexible, much thinner, convex upper surface, away from the sediment. Finally, the 'flat-surface down' orientation is supported by the presumed feeding posture of the organism, with the food groove exposed away from the substrate (Text-fig. 16).

Peltocystis and primitive Mitrocystitida are characterized by an extremely strong ornamentation on the lower surface of the most proximal brachials (stylocone and very first following ossicles) in the form of



TEXT-FIG. 16. Life positions of various primitive Mitrocystitida (in right lateral view). A, *Mitrocystites mitra* Barrande, 1887; Sarka Formation (Middle Ordovician), Czech Republic. B, *Chinianocarpus thoralis* Ubahgs 1961a; Saint-Chinian Formation (Lower Ordovician), Montagne Noire (France). Abbreviations: ant. transv. cr., anterior transverse crest; asym. dent., asymmetrical denticulations.

long, laterally compressed blades. Brachial spines are much stronger than those present in *Lagynocystis* (see above). This observation suggests that the proximal region of the arm was possibly more involved in the anchorage of the organism in *Peltocystis* and primitive Mitrocystitida than in *Lagynocystis*. Long, laterally compressed and posteriorly directed spines on the lower surface of the brachials are efficient sediment-gripping structures that were probably deeply thrust into the mud, thus preventing the animal from moving in a posterior direction (Text-fig. 16). Anterior and posterior edges of brachial blades can be sharp ('cutting edges') or blunt. Cutting edges can be present on both anterior and posterior margins of the brachial spines (e.g. *Chinianocarpus*, *Vizcainocarpus*; Jefferies and Prokop 1972, fig. 10; Ruta 1997a, p. 373), restricted to the anterior edges (e.g. *Peltocystis*; Jefferies 1986, fig. 8.38), or on the contrary, to the posterior edges (e.g. *Mitrocystites*; Jefferies and Prokop 1972, fig. 11). Several authors have argued that *Peltocystis* and primitive Mitrocystitida were vagile organisms crawling through the mud, aulacophore first (Jefferies and Prokop 1972; Jefferies 1975, 1984, 1986; Philip 1981; Cripps 1990; Kolata *et al.* 1991; Beisswenger 1994). In their reconstructed locomotory cycles, the arm is deeply thrust into the mud and the blunt edges of brachials provide 'bearing surfaces' that were pushed downwards against the sediment and, thus, pulled forwards the whole theca. The variable location of blunt brachial edges (on the anterior or the posterior edge of the brachials), and their absence in several forms (e.g. *Chinianocarpus*, *Vizcainocarpus*) throws serious doubts on their interpretation as 'bearing surfaces'. Another argument against this interpretation comes from the narrowness and extremely reduced total area of the so-called 'bearing surfaces', which makes it very unlikely that such small surfaces were able to drag forwards the massive posterior theca (Ruta and Bartels 1998, p. 796; Ruta 1999c, p. 72). Finally, the feeding function of the arm and the 'flat-surface down' orientation of the animal make the possibility that the organism crawled forwards by vertical flexion of the aulacophore highly improbable. On the other hand, the lateral surfaces of the long brachial blades of *Peltocystis* and Mitrocystitida constitute large potential 'bearing surfaces' (Ruta and Bartels 1998). The presence of long, laterally compressed brachial blades, along with that of a highly flexible proximal aulacophore, suggests that the animal could actively reorientate its arm. *Peltocystis* and primitive Mitrocystitida were also possibly capable of very limited forward movement, by lateral wagging of the anterior portion of the arm through the mud (Chauvel 1981; Caster 1983; Parsley 1988).

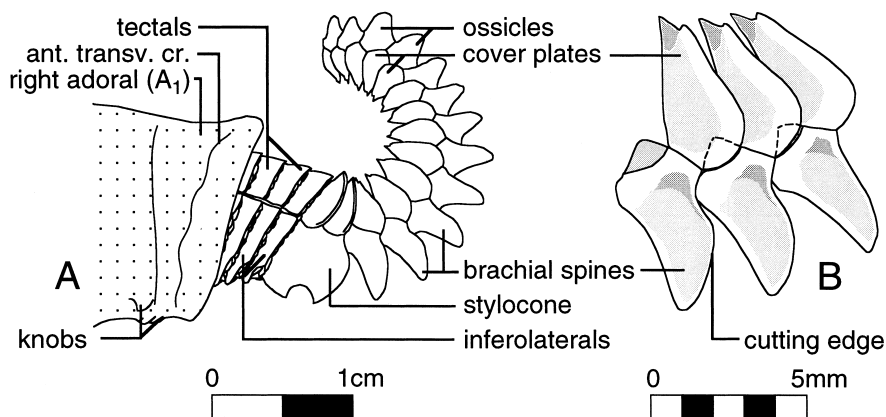
In *Peltocystis* and primitive Mitrocystitida, the insertion of the proximal aulacophore into a deep anterior thecal cavity severely reduces, and sometimes hinders (e.g. *Aspidocarpus discoidalis*, *Vizcainocarpus*

dentiger), the contact between the lower surface of the proximal appendage and the substrate. This observation suggests that, with the single possible exception of *Chinianocarpos*, the proximal appendage was probably not involved at all in the anchorage of the animal. In *Chinianocarpos*, sediment-gripping devices are present on the lower surface of the proximal aulacophore in the form of small downwards and posteriorly directed spikes. The situation in *Chinianocarpos* is nevertheless clearly different from that in *Lagynocystis* (see above). In *Chinianocarpos*, proximal spikes are restricted to the lower surface of the proximal appendage, and less numerous and smaller than in *Lagynocystis*. These differences suggest that, contrary to the situation in *Lagynocystis*, only the lower surface of the proximal appendage was in contact with the sea floor in *Chinianocarpos* (Text-fig. 16B). The morphology of the aulacophore insertion cavity suggests that movements of the highly flexible proximal region were only possible upwards and laterally. Movements in a vertical plane permitted the animal to extract the anterior brachial blades from the mud, and/or to thrust them deeply into the substrate. By lateral movements of the proximal appendage, the mitrate could reorientate its arm so as to keep it favourably orientated and facing the current.

Several strong, blunt, asymmetrical knobs are present on the upper thecal surface of *Vizcainocarpus dentiger* (Ruta 1997a) and *V. rutai* (Lefebvre 2000). The location (on the upper surface) and the orientation (rearwards and upwards) of these asymmetrical knobs in *Vizcainocarpus* questions the epibenthic mode of life of these mitrates. The extremely porous stereom texture of the knobs (Ruta 1997a) supports the view that these expansions were not in contact with the sediment in life. In stylophorans, portions of the animal frequently in contact with the substrate display a stereom texture that is either fibrillar (e.g. brachial blades of *Vizcainocarpus dentiger* and lateral edges of the lower surface of *V. rutai*), or coarse and massive (e.g. asymmetrical serrations in *V. dentiger*). Knobs in *Vizcainocarpus* thus represent a non-functional ornamentation, comparable to that displayed by the supracentrals of several cornutes: conical spines of *Cothurnocystis fellinensis* (Ubaghs 1969), and mushroom-like spikes of *Amygdalotheca griffei* and *Milonicystis kerfornei* (Ubaghs 1969, fig. 26.4; Cripps and Daley 1994, fig. 7c).

The asymmetrical serrations located on the lateral edges of the most anterior marginals of *Chinianocarpos*, *Mitrocystites* and *Peltocystis* are comparable to those described in symmetrical cornutes and *Lagynocystis* (see above). Their sediment-gripping function is supported by their downward orientation and their constant asymmetry, with steeper posterior edges. Ratchet sculpture on the lateral edges of the lower thecal surface of *Peltocystis* and several *Mitrocystitida* prevented, or at least reduced, slippage of the theca into a posterior direction. The presence of sharp and downwards recurved anterior edges of the thecal frame (e.g. *Chinianocarpos*, *Ovocarpus*, *Vizcainocarpus*), probably represents an additional anchoring device, preventing back slippage of the organism. As already argued above, the fact that the numerous anchoring structures located on the lower surface of the aulacophore and on the lower surface of the theca hindered rearward motion of the animal does not signify that the organism moved in the opposite direction. If forward locomotion cannot be totally excluded in *Peltocystis* and primitive *Mitrocystitida* (see above), it must have been extremely limited, and these mitrates probably spent most of their time feeding, immobile on the sea floor. This mostly sessile mode of life, with the arm facing the current, is strongly supported by the constant orientation and asymmetry of the numerous anchoring sculptures.

The comparable ornamentation and thecal morphologies observed in *Peltocystis*, primitive *Mitrocystitida* and symmetrical cornutes (see above) strongly suggest that the mode of life of these various stylophorans was very similar, and their comparable morphologies the result of convergent evolution. All these stylophorans are characterized by spike-bearing brachials and large, flattened thecae with asymmetrical serrations on the lateral edges of anterior marginals. Brachial spines certainly represented the main anchoring structure in life. The theca was downstream, resting on the sea floor on its planar lower surface (Text-fig. 16). As in symmetrical cornutes, asymmetrical serrations in *Peltocystis* and primitive *Mitrocystitida* possibly provided temporary anchorage of the theca when the arm was displaced or extracted from the mud. The function of the movable posterior exothecal spine (glossal) of *Peltocystis* was possibly that of a posterior buttress, stabilizing the posterior region of the theca (and the anal opening) above the sediment-water interface.



TEXT-FIG. 17. Morphology of the aulacophore in kirkocystid mitrates. *Balanocystites primus* (Barrande, 1872); Sarka Formation (Middle Ordovician), Czech Republic. A, recurved aulacophore in right lateral view. B, three proximal ossicles with their articulated cover plates, in right lateral aspect. Abbreviation: ant. transv. cr., anterior transverse crest.

KIRKOCYSTIDAE

Kirkocystidae are the most diverse and abundant group of Peltocystida. Their stratigraphic range extends from the Lower Ordovician (Tremadoc) to the Upper Ordovician (Ashgill), but Kirkocystidae may well be still present in the Lower Devonian of Germany (Dehm 1934, fig. 2; Bartels *et al.* 1998, figs 137, 139–140). Their geographic distribution is world-wide. Kirkocystidae have been reported in Bohemia (Barrande 1872, 1887; Chauvel 1941; Ubaghs 1979; Jefferies 1986; Parsley *et al.* 2000), Scotland (Jones and Woodward 1895; Reed 1907; Jefferies and Daley 1996), Montagne Noire (Thoral 1935; Vizcaïno and Lefebvre 1999), Brittany (Chauvel 1941, 1981), Korea (Kobayashi 1960), Morocco (Chauvel 1966, 1971; Cripps 1990; Beisswenger 1994), Wales (Jefferies 1987), Spain (Domínguez and Gutiérrez-Marco 1990; Gutiérrez-Marco *et al.* 1999a), Oklahoma (Bassler 1950; Parsley 1982, 1991), Tennessee (Parsley 1991), England (Vizcaïno and Lefebvre 1999; Lefebvre 2000), Nevada (Parsley *et al.* 2000), and Utah (Parsley *et al.* 2000). They were probably environmental generalists (Parsley *et al.* 2000), having been found in proximal, storm-generated deposits as well as in distal, deep environments. Kirkocystidae comprise the two genera *Anatifopsis* and *Balanocystites*. *Guichenocarpus* is here considered to be a junior synonym of *Anatifopsis*, and *Sagittacystis* a junior synonym of *Balanocystites*, following Lefebvre (in press).

Morphology of the aulacophore

The proximal aulacophore of the Kirkocystidae is closely comparable to that of *Peltocystis* and most Mitrocystitida, with a typical 'mitrate-like' organization (Text-figs 17A, 18A). It is a short and broad, highly flexible region, consisting of several telescoping rings, each made of four plates (two tectals and two inferolaterals). Tectals and inferolaterals are subequal in size. Small integumentary platelets are sometimes intercalated between proximal rings (Ubaghs 1979; Jefferies 1986). Strong, laterally compressed and rearwards-oriented spikes are sometimes present on both tectals and inferolaterals (Chauvel 1941, 1981; pers. obs.). The external surface of proximal rings is frequently smooth, but sometimes coarse and granular. As in *Peltocystis* and primitive Mitrocystitida, the proximal aulacophore of Kirkocystidae is inserted into a cavity provided by the adorals (A_1 , A'_1), and the most anterior marginals (M_1 , M'_1). The morphology of the aulacophore insertion cavity suggests that the proximal appendage of kirkocystids could be flexed in almost every direction.

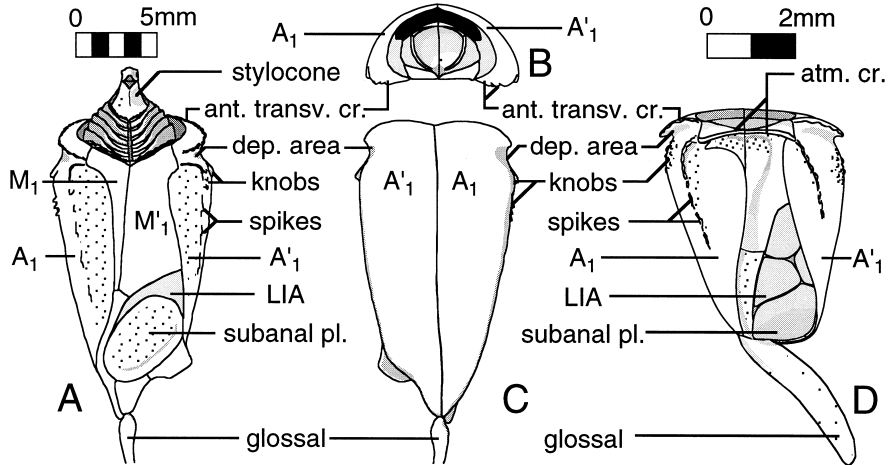
The morphology of the arm is very comparable to that described in *Peltocystis* (see above). The lower surface of the stylocone and of each proximal-most ossicle carries a long, laterally compressed,

downwards-recurved and posteriorly directed brachial spine (Text-fig. 17). Exceptionally long and enlarged proximal blades are present in several Lower Ordovician Kirkocystidae found in coarse, arenaceous lithologies (e.g. Montagne Noire, Shropshire). The anterior edge of brachial spines is generally sharper than their posterior blunt margin. The lower surface of the stylocone typically carries one (*Anatifopsis*) or two (*Balanocystites*) strong, recurved blades. When two blades are present on the lower surface of the stylocone, the distal one is typically stronger than the proximal one (Parsley *et al.* 2000; Pl. 1 fig. 9). Several small additional tubercles are sometimes aligned, posteriorly to the distal blade, in the mid-line of the lower surface of the stylocone (pers. obs.; see also Jefferies 1986, fig. 8.40). In *Anatifopsis*, a deep median furrow is excavated on each lateral side of the brachial spines. The size of the brachial spines and depth of their lateral furrows, when present, rapidly decrease in a distal direction (Text-figs 17A, 20). The lower surface of distalmost brachials is typically smooth and rounded or carries a small anterior residual knob. Examination of abundant, well-preserved material of *Anatifopsis barrandei* (Llanvirn, Bohemia) does not confirm the presence of several conical spikes on the lower surface of distalmost brachials reported by Jefferies (1986, fig. 8.40). Kirkocystidae are characterized by highly developed and complex interbrachial articulations, comparable to those described in *Peltocystis* (Ubaghs 1969) and other mitrates. The arm was thus a highly flexible structure that could be flexed in a vertical plane. The length of the arm was apparently important (see Pl. 1, fig. 9) as, for example, in *Anatifopsis papillata* (more than 45 brachials; Ubaghs 1979; Parsley 1991; Parsley *et al.* 2000).

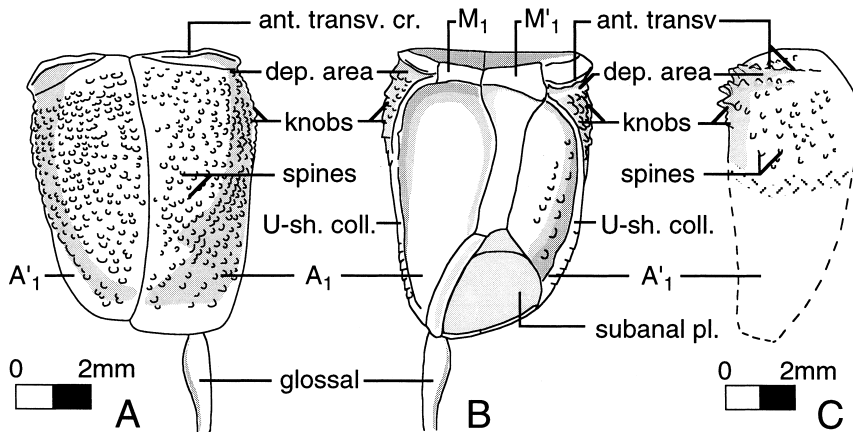
Morphology of the theca

The shape of the kirkocystid theca is that of half a walnut (Text-figs 18–20; Pl. 1, figs 7–9). This unusual morphology results from the extremely important extension of the two lateral adorals. A_1 and A'_1 form the totality of the upper surface and partly overlap the lower surface skeleton. The theca is typically longer than wide, somewhat elongate in *Balanocystites*, broader in *Anatifopsis*. The high and inflated morphology of the kirkocystid theca clearly departs from the more flattened morphologies of *Peltocystis* and primitive Mitrocystitida. The height and width of the theca regularly decrease in a posterior direction. The upper thecal surface is strongly convex, whereas the lower surface is flat to slightly concave. Both thecal surfaces are rigid. A single, movable, exothecal spine (glossal) is articulated at the distal end of the theca (Text-figs 18–20; Pl. 1, figs 8–9). The morphology of this posterior process is variable in Kirkocystidae. In *Anatifopsis trapeziiformis* (Lower Arenig, Montagne Noire), the very large, flattened morphology of the long glossal strongly recalls the situation in several asymmetrical cornutes (see above). In several other Kirkocystidae (e.g. *Anatifopsis barrandei*, *Balanocystites primus*), the narrower, slightly curved morphology of the posterior spine is very similar to that of the glossal in *Peltocystis*.

The anterior transverse crest is present on the two enlarged adorals of kirkocystids, but its morphology is clearly distinct from the faint, sinuous, asymmetrical ridge of other mitrates (see above and below). In Kirkocystidae, the transverse anterior crest is particularly high and forms a strong, crenulated, sinuous structure running from the anterior mid-line of the upper surface to the lateral edges of M_1 and M'_1 on the lower surface (Text-figs 18–20). The transverse crest is typically stronger on the lower surface (e.g. *Anatifopsis barrandei*, *Balanocystites primus*), and it carries numerous, asymmetrical, posteriorly directed tubercles. This strong, crenulated ridge is located anterior to a narrow, transversally elongated, slightly depressed, smooth area (Text-figs 18–20). Posterior to this smooth, concave anterior ring, several strong, asymmetrical knobs are typically present on the sharp lateral edges of the lower surface in the region where thecal width is maximum (Text-figs 18–20). The knobs are blunt to sharp asymmetrical sculptures, with a steeper posterior edge and a massive stereom texture. The size, number and extension of the knobs is highly variable in the Kirkocystidae. In *Anatifopsis barrandei* knobs are small and strictly restricted to the lateral edges of the lower thecal surface. In *Balanocystites primus* (Text-figs 18A, 20A) and *Anatifopsis trapeziiformis* (Text-fig. 18b) they are stronger and also extend onto the lateral sides of the adorals. Finally, even stronger knobs have been recorded in *Anatifopsis ancora* (Domínguez and Gutiérrez-Marco 1990). In *A. ancora* (Llandeilo, Spain), knobs are apparently aligned and constitute several strong, discontinuous, transverse asymmetrical ridges extending from the lower surface to the mid-line of the upper surface (Text-fig. 19C). The upper surface of *Anatifopsis ancora* is also covered by abundant, small,



TEXT-FIG. 18. Morphology of the theca in kirkocystid mitrates. A–C, *Balanocystites primus* (Barrande, 1872); Sarka Formation (Middle Ordovician), Czech Republic. A, lower thecal surface, proximal aulacophore and stylocone. B, anterior aspect of the theca. C, upper thecal surface. D, *Anatifopsis trapeziiformis* Thoral, 1935; Saint-Chinian Formation (Lower Ordovician), Montagne Noire (France); lower thecal surface. Abbreviations: A, adoral; ant. transv. cr., anterior transverse crest; dep. area, depressed area; LIA, left infracentral area; M, marginal; subanal pl., subanal plate.



TEXT-FIG. 19. Morphology of the theca in kirkocystid mitrates. A–B, *Anatifopsis papillata* (Bassler, 1943); Bromide Formation (Upper Ordovician), Oklahoma (USA); redrawn after Ubags (1967a). A, upper thecal surface. B, lower thecal surface. C, *Anatifopsis ancora* Domínguez and Gutiérrez-Marco, 1990; Guindo Shales (Middle Ordovician), Guadalajara (Spain); theca in left lateral aspect; modified after Domínguez and Gutiérrez-Marco (1990). Abbreviations: A, adoral; ant. transv. cr., anterior transverse crest; dep. area, depressed area; M, marginal; subanal pl., subanal plate; U-sh. coll., U-shaped collar.

asymmetrical, posteriorly oriented spines, which is reminiscent of the situation reported in several other Kirkocystidae (Text-figs 19A, 20B; Bassler 1950; Ubags 1979; Parsley 1982, 1991). Such a spiny ornamentation on adorals is not the rule in all kirkocystids. Several species are characterized by having a smooth upper thecal surface (e.g. *Anatifopsis barrandei*, *A. trapeziiformis*, *Balanocystites primus*; see Text-figs 18C, 20A; Pl. 1, fig. 8).

The lower surface of the theca is flat to slightly concave (Pl. 1, fig. 7). Small, asymmetrical spines,

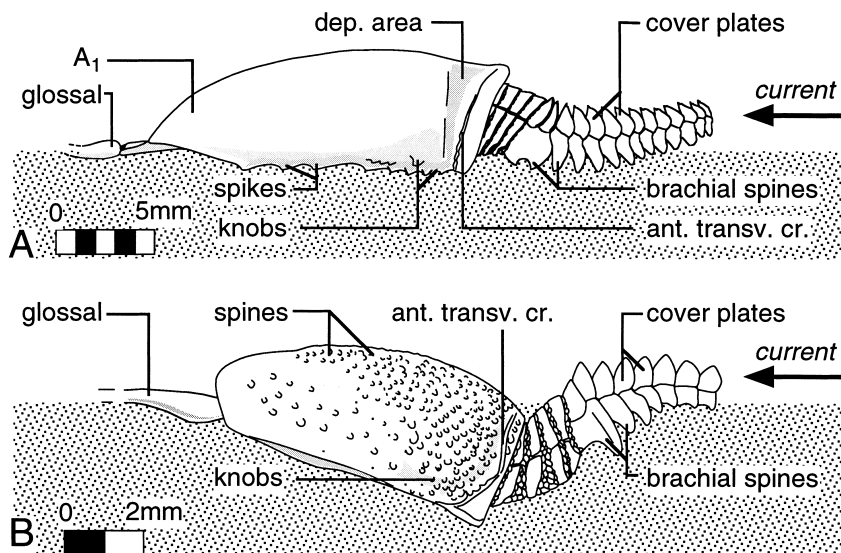
directed downwards and rearwards, are sometimes present anteriorly on the lower surface of M_1 and/or M'_1 in *Balanocystites primus* (pers. obs.). Several laterally compressed asymmetrical spikes are frequently longitudinally aligned on the lower surface of each adoral (e.g. in *Anatifopsis trapeziiformis* and *Balanocystites primus*; see Text-figs 18A, D, 20A). These sharp spikes are consistently orientated downwards and rearwards, and they regularly decrease in size in a posterior direction. The genus *Anatifopsis* is characterized by a strong, transverse, asymmetrical ridge running anteriorly on the lower surface of M_1 and M'_1 . This ridge is directed downwards, and it shows a steeper posterior edge. In *Anatifopsis*, the association of this anterior transverse marginal crest with the two lateral, longitudinal series of spikes on the lower surface of the adorals, forms a U-shaped 'collerette' (Text-fig. 18D). This U-shaped structure faces downwards and rearwards, and regularly diminishes in height and strength in a posterior direction. Lower Ordovician *Anatifopsis* found in coarse, arenaceous sediments are characterized by exceptionally high and strong U-shaped collerettes. In these forms, the anterior region of the collerette forms a high, downwards-recurved, transverse blade (Text-fig. 18D). The U-shaped collerette is much weaker and shorter in *Anatifopsis barrandei* (Pl. 1, fig. 9). In *A. papillata*, the collerette is extremely faint anteriorly, and its longitudinal portions form the sharp lateral edges of the lower surface of the theca (Text-fig. 19B; Pl. 1, fig. 7; Bassler 1950, fig. 16; Parsley 1991, pls 7–8). In all kirkocystids, the anus is protected by a large subanal plate, and opens through the left infracentral area, at the distal end of the lower surface (Text-figs 18A, D, 19B; Pl. 1, figs 7, 9).

Interpretation

All kirkocystid mitrates are characterized by the presence of long blades on the lower surface of their most proximal brachials. These brachial spines are laterally compressed and recurved rearwards. This strong ornamentation suggests that, as in *Peltocystis*, the proximal region of the arm was probably involved in firmly anchoring the organism to the substrate (Parsley *et al.* 2000). As in *Peltocystis* and primitive Mitrocystitida, the blunt posterior edges of the kirkocystid brachial spines are extremely small and narrow, and could hardly have been used as 'bearing surfaces' in the case of a presumed forward locomotion. The large lateral sides of the long, laterally compressed, brachial spines represent much larger potential 'bearing surfaces' that would have been much more efficient in the case of a lateral flexion of the proximal aulacophore. The expanded lateral surfaces of the brachial spines would then have acted as 'shovels', pushing the sediment backwards on each side. Such lateral movements of the aulacophore probably helped the organism to reorientate so as to keep its arm facing the current. Ornamentation on the lower surface of the brachials rapidly decreases in strength in a distal direction. As in other mitrates, the distal region of the arm was probably recumbent over the sea-floor, and therefore unimportant in the anchorage of the animal (Text-fig. 20).

The presence of intercalary platelets with a coarse, granular ornamentation and of asymmetrical, laterally compressed, posteriorly directed spikes on both surfaces of the proximal appendage in several kirkocystids suggest that this region was possibly buried in the sediment during life. Spikes are, nevertheless, not numerous (one or two pairs) and seldom present on the proximal appendage of Kirkocystidae (they have been recorded until now only in some specimens from Brittany; Chauvel 1941, 1981). The rare occurrence and small size of sediment-gripping devices on the proximal aulacophore of the Kirkocystidae suggest that, contrary to the situation in *Lagynocystis*, this region was probably weakly involved in anchoring the animal into the substrate.

Thecal ornamentation is very variable in strength and extension in the Kirkocystidae. Comparison of thecal ornamentation in several kirkocystids indicates that the strength of the ornamentation is correlated with the grain size of the sediment. The strongest thecal sculpture is observed in several Lower Ordovician kirkocystids from Montagne Noire (France) and Shropshire (England) occurring in coarse, arenaceous lithologies. Thousands of disarticulated skeletal elements of these highly ornamented mitrates (e.g. *Anatifopsis trapeziiformis*) are sometimes encountered in storm-generated deposits in the Lower Arenig of Montagne Noire (Saint-Chinian Formation, faunal zone 'g'). *Anatifopsis trapeziiformis* is characterized by a very strong U-shaped collerette on the lower thecal surface, and by exceptionally broad and long brachial spines (Text-fig. 18D). Ornamentation is generally much more reduced (e.g. relative size of the brachial



TEXT-FIG. 20. Life positions of various kirkocystid mitrates (Peltocystida), in right lateral view. A, *Balanocystites primus* (Barrande, 1872); Sarka Formation (Middle Ordovician), Czech Republic. B, *Anatifopsis papillata* (Bassler, 1943); Bromide Formation (Upper Ordovician), Oklahoma (USA). Abbreviation: A, adoral; ant. transv. cr., anterior transverse crest; dep. area, depressed area.

spines, height of the U-shaped collerette) in kirkocystids occurring in finer lithologies (e.g. *Anatifopsis barrandei*, *Balanocystites primus*; Text-fig. 18A–C; Pl. 1, figs 8–9).

The extension of the ornamentation on both thecal surfaces is highly variable in kirkocystids, and is probably correlated with their mode of life. A first group of Kirkocystidae is characterized by strong, abundant, sediment-gripping structures on the lower surface, and a totally smooth upper surface (e.g. *Anatifopsis barrandei*, *A. trapeziiformis*, *Balanocystites primus*). Anchoring sculptures are concentrated on the anterior margin and the lateral edges of the lower thecal surface: (1) strong, tuberculated, anterior transverse adoral crest; (2) numerous adoral knobs located posterior to this crest on the lateral edges of the theca; and (3) U-shaped collerette. All sediment-gripping devices decrease in height and size in a posterior direction. They are asymmetrical (with a steeper posterior side), rearwards- and downwards-directed. As in other stylophorans, this asymmetrical ornamentation is well suited to prevent, or at least minimize, any slippage of the theca in a posterior direction. As already argued above, this asymmetrical ornamentation is perfectly designed for mostly sessile benthic organisms living with their arm facing the current and the theca downstream. In *Anatifopsis barrandei*, the smooth upper thecal surface, and the presence of a reduced ornamentation, restricted to the anterior margin of the lower surface, suggest that this kirkocystid was probably characterized by an epibenthic mode of life, comparable to that of *Peltocystis*. In *A. trapeziiformis* and *Balanocystites primus*, ornamentation is stronger, and extends anteriorly on the lateral edges of the adorals, and more posteriorly than in *A. barrandei* on the lower surface of the theca. This observation suggests that the anterior portion of the theca of these kirkocystids was probably shallowly buried in life (Text-fig. 20A). The function of the posterior exothecal spine (glossal) of these kirkocystids was possibly to maintain the anal opening at, or slightly above, the water-sediment interface.

A second group of Kirkocystidae includes several forms from the Upper Ordovician of Europe and North America (e.g. *Anatifopsis papillata*). These mitrates are characterized by the presence of numerous small spikes covering most of the upper thecal surface, and a drastically reduced ornamentation on the lower surface (Text-figs 19, 20B; Pl. 1, fig. 7). The small spikes of the upper surface are extremely dense (about 12 per mm²; Ubaghs 1979, fig. 4E), all of the same size, and consistently asymmetrical, with a much steeper posterior side. The abundance of the small spikes regularly decreases in a posterior direction, so

that the posterior edges of the upper surface are nearly smooth (Parsley 1991, pls 7–8). Strong asymmetrical knobs are sometimes present anteriorly, on the lateral edges of the adorals, where the theca is widest (Parsley 1991). The lower thecal surface is nearly flat. The anterior transverse adoral crest is only slightly marked. Knobs and spines are absent. The U-shaped collerette comprises a faint anterior portion, and its flattened posterior branches are confluent with the sharp lateral edges of the theca. Ornamentation is thus much more important on the upper thecal surface than on the lower surface. A comparable ornamentation, much more pronounced on the upper portion of the organism, occurs in several shallow burrowers belonging to various groups of marine invertebrates (e.g. bivalves, crustaceans, gastropods). This type of ornamentation is generally referred to as the 'Fabulina-type' pattern (Seilacher 1972). It typically occurs in shallow infaunal organisms, burrowing in a horizontal to substantially inclined position (Seilacher 1972, 1973; Savazzi 1981*a, b*, 1983; Savazzi *et al.* 1982; Signor 1982). Consequently, the presence of ornamentation on both thecal surfaces and of a stronger ornamentation on the upper surface, are arguments suggesting that the mode of life of *Anatifopsis papillata* was probably infaunal.

Comparison with the paradigm for burrowing sculptures defined by Seilacher (1973) shows that the thecal ornamentation in *A. ancora* fulfills at least three of the four of its requirements. All sediment-gripping devices (small spikes on the upper surface, lateral knobs) are asymmetrical in cross section (frictional asymmetry) and perpendicular to the presumed forward-burrowing direction (cross orientation). It is difficult to know if allometric increase in density occurred in *Anatifopsis papillata*, but the extremely dense distribution of the small spikes suggests that additional elements were probably added during growth. *Anatifopsis papillata* departs from the paradigm as far as perimeter smoothing is concerned; the sculpture should be smoother where the organism is largest. The reverse situation is observed in *A. papillata*, with a much stronger sculpture occurring where the theca is the widest. This lack of compliance with the fourth requirement of the paradigm probably results from the mostly sessile mode of life of *Anatifopsis papillata*. The function of asymmetrical sculpture in infaunal kirkocystids was probably not only to provide resistance to back slippage when the animal was burrowing but also to provide efficient anchoring properties to an organism whose arm was out of the sediment and facing the current (Text-fig. 20B). An interesting parallel can be drawn with the infaunal anomuran crab *Emerita*. This is a shallow burrower, nearly totally buried in the sediment, with the exception of its large, food-collecting antennae. Ornamentation in *Emerita* is a compromise between efficient burrowing and firm anchorage of the organism in the substrate, so as to resist the pull exerted by currents on the large antennae (Seilacher 1973; Savazzi 1981*b*; Savazzi *et al.* 1982). The same was probably true for infaunal kirkocystids.

In *Anatifopsis papillata*, sediment-gripping sculptures regularly decrease in strength and density from the strongly ornamented anterior region of the upper thecal surface to the smooth posterior extremity of the theca (Text-figs 19A, 20B). A similar antero-posterior asymmetry occurs in other shallow infaunal invertebrates (e.g. the brachyuran crustacean *Corystes*; Savazzi 1983). These endobenthic organisms are all characterized by a substantially inclined living position in the sediment. In these infaunal organisms, strength and density of the ornamentation on the upper surface regularly increase with depth. Consequently, comparison with other infaunal invertebrates showing a similar asymmetrical sculpture pattern on the upper surface suggests that the living position of *Anatifopsis papillata* was probably inclined, with the more ornamented anterior region buried deeper in the sediment than the smoother posterior portion of the theca. The posterior exothecal spine (glossal) of infaunal kirkocystids possibly helped to maintain the anal opening at the water-sediment interface. The living position of *Anatifopsis papillata*, with the anterior portion of the theca deep in the substrate, requires that the proximal aulacophore was probably buried in life. As argued above, the proximal portion of the arm was firmly anchored in the sediment by the strong blades located on the lower surface of the stylocone and following ossicles. The distal region of the arm lay over the sea floor and only fulfilled a feeding function. The morphology of the feeding arm and the location of the mouth suggest that the proximal aulacophore was flexed upwards in life, so that the stylocone was proximally about level with the water-sediment interface (Text-fig. 20B). The expanded lateral surfaces provided by the long, laterally compressed, brachial spines probably helped the organism to burrow.

The ornamentation in *Anatifopsis ancora* (Text-fig. 19C) is apparently intermediate between that of epibenthic to slightly buried kirkocystids (e.g. *Balanocystites primus*) and that of infaunal forms (e.g.

Anatifopsis papillata). As in epibenthic Kirkocystidae, *Anatifopsis ancora* retains strong anterior knobs on the lower edges of the lower surface, but the presence of several small, asymmetrical spikes on the upper surface recalls the situation in endobenthic forms. *Anatifopsis ancora* probably represents a semi-infaunal, transitional form between epibenthic and endobenthic kirkocystids. This interpretation is supported by the stratigraphic occurrence of *A. ancora* (upper Middle Ordovician), which is slightly older than that of infaunal kirkocystids (all from the Upper Ordovician). Epifaunal kirkocystids are known from the Lower Ordovician (Tremadoc) to the Upper Ordovician (Ashgill).

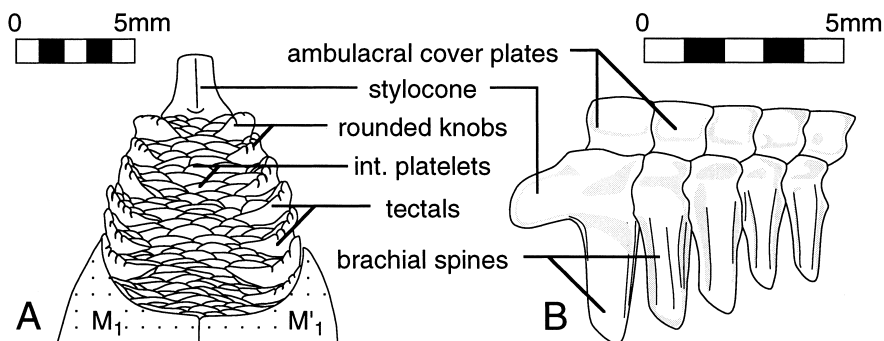
In conclusion, the strength of the ornamentation in Kirkocystidae is directly correlated with the grain size of the sediment. Two different modes of life can be deduced by analysis of the extension of the ornamentation on both thecal surfaces (Text-fig. 20). Kirkocystids are probably primitively epibenthic organisms, anchored to the substrate by their long brachial blades and the strong ornamentation present at the anterior margin of the lower thecal surface (Text-fig. 20A). Transition towards a more infaunal mode of life probably began in the late Middle Ordovician, because 'true' endobenthic forms are present in Upper Ordovician deposits. Their infaunal mode of life is strongly supported by the presence of a much stronger ornamentation on the upper thecal surface, directly comparable to the 'Fabulina-type' pattern reported in several other shallow infaunal invertebrates. Endobenthic kirkocystids probably lived slightly inclined in the sediment, with the anal opening at the water-sediment interface and the anterior region of the theca more deeply buried (Text-fig. 20B). Detailed investigation of the external morphology and ornamentation of all Kirkocystidae confirms their 'flat-surface down' orientation in life. The asymmetrical ornamentation of all kirkocystid mitrates would have been very well suited for a mostly sessile mode of life, with the theca downstream and the arm resting over the sea floor, facing the current.

MITROCYSTITIDA WITH RATCHET SCULPTURE

Ratchet or terraced sculptures are low amplitude, asymmetrical sculptures that have been described in several groups of marine hard-shelled invertebrates, such as bivalves, gastropods, brachiopods, crustaceans and trilobites (Stanley 1969; Seilacher 1972, 1973; Schmalfuss 1978*a, b*; Savazzi 1981*a, b*; Savazzi *et al.* 1982; Signor 1982, 1994). Ratchet sculptures provide frictional resistance with the substrate, and their presence is frequently associated with an infaunal mode of life (but see Schmalfuss 1978*a*; Savazzi 1983). Ratchet sculpture occurs in some primitive Mitrocystitida (e.g. *Mitrocystella*, *Promitrocystites*) and most anomalocystitid mitrates (e.g. *Barrandeocarpus*, *Enoploura*, *Placocystites*; Text-figs 24B, D-E). The presence of terraced patterns in Mitrocystitida was noticed by early authors (e.g. Barrande 1887, pl. 5), but its functional significance was long ignored until the important successive contributions of 'calcichordate' workers (Jefferies and Prokop 1972; Jefferies 1975, 1982, 1984, 1986, 1999; Jefferies and Lewis 1978; Savazzi *et al.* 1982; Craske and Jefferies 1989; Ruta 1997*b*; Ruta and Bartels 1998; Sutcliffe *et al.* 2000). The functional significance of ratchet sculpture in Mitrocystitida has been sometimes discussed (Chauvel 1981; Kolata and Jollie 1982; Kolata *et al.* 1991), but frequently ignored by echinoderm workers (Philip 1979; Parsley 1988, 1991).

Morphology of the aulacophore

The proximal aulacophore of Mitrocystitida with ratchet sculpture is a broad, large, highly flexible structure, comparable to that of more primitive forms (Text-figs 21A, 25). It shows the typical 'mitrate' organization, with tectals and inferolaterals subequal in size. Small and numerous integumentary platelets are sometimes intercalated between successive telescoping proximal rings, as in *Placocystites* (Text-figs 21A, 25A; Jefferies and Lewis 1978), *Enoploura* (Parsley 1991) or *Rhenocystis* (Ruta and Bartels 1998). Rounded knobs and tubercles (Jefferies and Lewis 1978; Ruta and Bartels 1998), and/or a coarse ornamentation (Caster and Gill 1967; Ubaghs 1979; Ruta and Jell 1999) are sometimes present on both tectals and inferolaterals. As in other mitrates, the proximal aulacophore is inserted proximally into a deep cavity provided by the adorals and anterior marginals M_1 and M'_1 . In most anomalocystitids, the two marginals flooring this cavity do not extend forwards as far as in more primitive Mitrocystitida (e.g. *Aspidocarpus*, *Mitrocystella*). This different morphology of the aulacophore insertion cavity enables



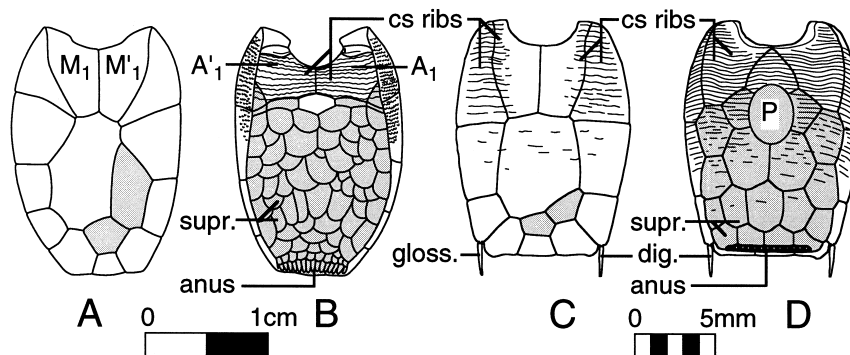
TEXT-FIG. 21. Morphology of the aulacophore in Mitrocystitida with ratchet sculpture. A, *Placocystites forbesianus* de Konick, 1869; Dudley Limestone (Upper Silurian), West Midlands (England); lower surface of the proximal aulacophore and stylocone; modified after Jefferies and Lewis (1978). B, *Rhencystis latipedunculata* Dehm, 1932; Hunsrück Slate (Lower Devonian), Rhineland (Germany); proximal portion of the arm in right lateral view; modified after Ruta and Bartels (1998). Abbreviations: int. platelets, intercalary platelets; M, marginal.

downwards flexion of the proximal appendage in anomalocystitids (Ruta and Bartels 1998). In some anomalocystitids, the proximal aulacophore is nearly as large as the anterior margin of the theca (e.g. *Rhencystis*, *Victoriacystis*), suggesting that it could be flexed in almost any direction. However, the distribution of intercalary platelets and morphology of proximal rings both suggest that the proximal region of the appendage was generally mostly flexed upwards in life (Jefferies and Lewis 1975; Jefferies 1984).

As in primitive Mitrocystitida, laterally compressed brachial spines are present on the lower surface of the stylocone and most proximal ossicles. The height and strength of the brachial spines regularly decrease in a distal direction (Text-figs 21B, 25). Brachial ornamentation is nevertheless much more variable than in more primitive forms. In *Rhencystis*, the morphology of the most proximal brachial spines is very similar to that of the long and expanded blades of primitive Mitrocystitida (Text-fig. 21B; Ruta and Bartels 1998, fig. 4). In *Enoploura* and related forms (e.g. *Placocystella*), the lower surface of the stylocone carries two large, transverse, fan-shaped ploughshare-like blades (Caster 1952, 1983; Philip 1981; Parsley 1991; Ruta and Theron 1997; Ruta and Jell 1999). Both blades are directed rearwards, and the distal one is stronger. In *Mitrocystella* and most anomalocystitids (e.g. *Ateleocystites*, *Barrandeocarpus*, *Victoriacystis*), the lower surface of the stylocone is saddle-like, with two small, laterally compressed brachial spines, and brachial ornamentation is much more reduced than in primitive Mitrocystitida (Text-fig. 25B). A coarse ornament, striations and knobs are sometimes present on the lateral surfaces of ossicles (Jefferies and Lewis 1978; Ruta and Theron 1997). Interbrachial articulations are complex and comparable to those of other mitrates, suggesting that the arm could be flexed in a vertical plane. The arm is thus a flexible and long structure, comprising several dozen brachials: about 40 segments have been reported in *Ateleocystites* (Kolata and Jollie 1982) and *Enoploura* (Parsley 1991), 55 in *Mitrocystella* (Jefferies 1984), and up to 60 in *Rhencystis* (Ruta and Bartels 1998).

Morphology of the theca

The theca of Mitrocystitida with ratchet sculpture is flattened, and sometimes as wide as long (e.g. *Placocystites*; Text-fig. 23C–D), but more frequently antero-posteriorly elongated, as in *Ateleocystites* (Text-fig. 22C–D), *Barrandeocarpus* (Text-fig. 23A–B), *Enoploura*, *Mitrocystella* (Text-figs 22A–B, 24B, E), *Rhencystis* and *Victoriacystis*. The upper thecal surface is typically gently convex and the lower surface, flat to slightly concave. As in more primitive Mitrocystitida, the anterior margin of the theca is sometimes folded downwards in anomalocystitids, as in *Placocystites* (Jefferies and Lewis 1978) or *Placocystella* (Ruta and Theron 1997). Lateral edges of the theca are frequently sharp and recurved downwards in

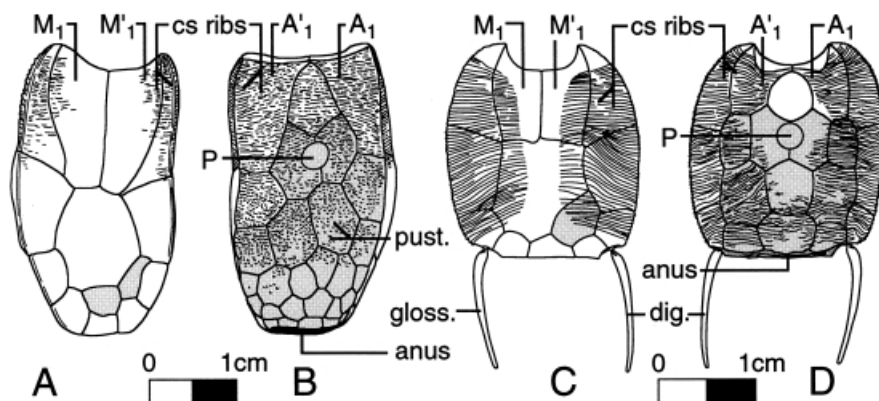


TEXT-FIG. 22. Morphology of the theca in Mitrocystitida with ratchet sculpture. A–B, *Mitrocystella incipiens* (Barrande, 1887); Traveusot Formation (Middle Ordovician), Brittany (France); modified after Jefferies (1968). A, lower thecal surface. B, upper thecal surface. C–D, *Ateleocystites guttenbergensis* Kolata and Jollie, 1982; Guttenberg Formation (Upper Ordovician), Wisconsin (USA); modified after Kolata and Jollie (1982). C, lower thecal surface. D, upper thecal surface. Abbreviations: A, adoral; cs ribs, cuesta-shaped ribs; dig., digital; gloss., glossal; M, marginal; supr., supracentrals.

anomalocystitids (Ubaghs 1979; Parsley 1991). In most Ordovician forms with ratchet sculpture, the height of the theca is greatest close to the aulacophore insertion and regularly decreases in a posterior direction (e.g. *Ateleocystites*, *Enoploura*, *Mitrocystella*). In most Siluro-Devonian anomalocystitids, the theca is more homogeneously flattened, and thecal height remains nearly constant antero-posteriorly (e.g. *Placocystella*, *Placocystites*, *Rhenocystis*).

Promitrocystites (Middle Ordovician; Bohemia) and *Mitrocystella* (Middle Ordovician; Bohemia, Brittany, Spain and Portugal; Text-figs 22A–B, 24B, E) are the most primitive and oldest Mitrocystitida with ratchet sculpture known so far. The presence of a large, tessellate, flexible supracentral area on the upper thecal surface is strongly reminiscent of the situation in more primitive forms (e.g. *Aspidocarpus*, *Mitrocystites*). The thecal outlines of *Promitrocystites* and *Mitrocystella* are, nevertheless, clearly distinct and more elongate than those of more primitive Mitrocystitida. Another important difference concerns the presence of terrace lines (or cuesta-shaped ribs) on the two lateral adorals. Cuesta-shaped ribs are parallel, transverse, asymmetrical ridges, with a gentle anterior side and a steeper posterior edge (Jefferies 1968, 1984). In *Promitrocystites*, terrace lines are faint and restricted to adorals A_1 and A'_1 (Lefebvre 2000). In *Mitrocystella*, cuesta-shaped ribs are much more obvious and extend not only on adorals but also on the lateral edges of the most anterior marginals (Text-figs 22B, 24B, E; Chauvel 1941, 1981; Jefferies 1967, 1986). A last significant difference from more primitive Mitrocystitida concerns the loss of lateripores and paripores (gonopores) on the lower surface of *Promitrocystites* and *Mitrocystella* (Parsley 1994).

Most authors consider that anomalocystitid mitrates were derived from primitive Mitrocystitida close to *Promitrocystites* and/or *Mitrocystella* (Chauvel 1941; Gill and Caster 1960; Jefferies and Lewis 1978; Derstler 1979; Jefferies 1986; Craske and Jefferies 1989; Cripps 1990; Kolata *et al.* 1991; Beisswenger 1994; Ruta and Theron 1997; Parsley 1997; Ruta 1999a; Lefebvre 2000; but see Ubaghs 1967a; Parsley 1991). The oldest recorded anomalocystitids with ratchet sculpture are Late Ordovician in age (e.g. *Ateleocystites*, *Barrandeocarpus*, *Enoploura*). Their thecal morphology strongly recalls that of *Promitrocystites* and *Mitrocystella*. An apomorphy of anomalocystitids is the presence of two posterior exothecal spines that possibly correspond to highly modified skeletal marginal plates (Kirk 1911; Ubaghs 1967a; Jefferies and Lewis 1978; Parsley 1991; Lefebvre 2000; but see Jefferies 1984; Craske and Jefferies 1989). Posterior spines are present in all anomalocystitids, with the single exception of *Barrandeocarpus* (Ubaghs 1979; Craske and Jefferies 1989; Ruta 1997c). Contrary to the situation in more primitive Mitrocystitida, both thecal surfaces are rigid in anomalocystitids with ratchet sculpture. The supracentral area comprises a reduced number of enlarged and typically tightly sutured integumentary elements (Text-figs 22D, 23B, D).

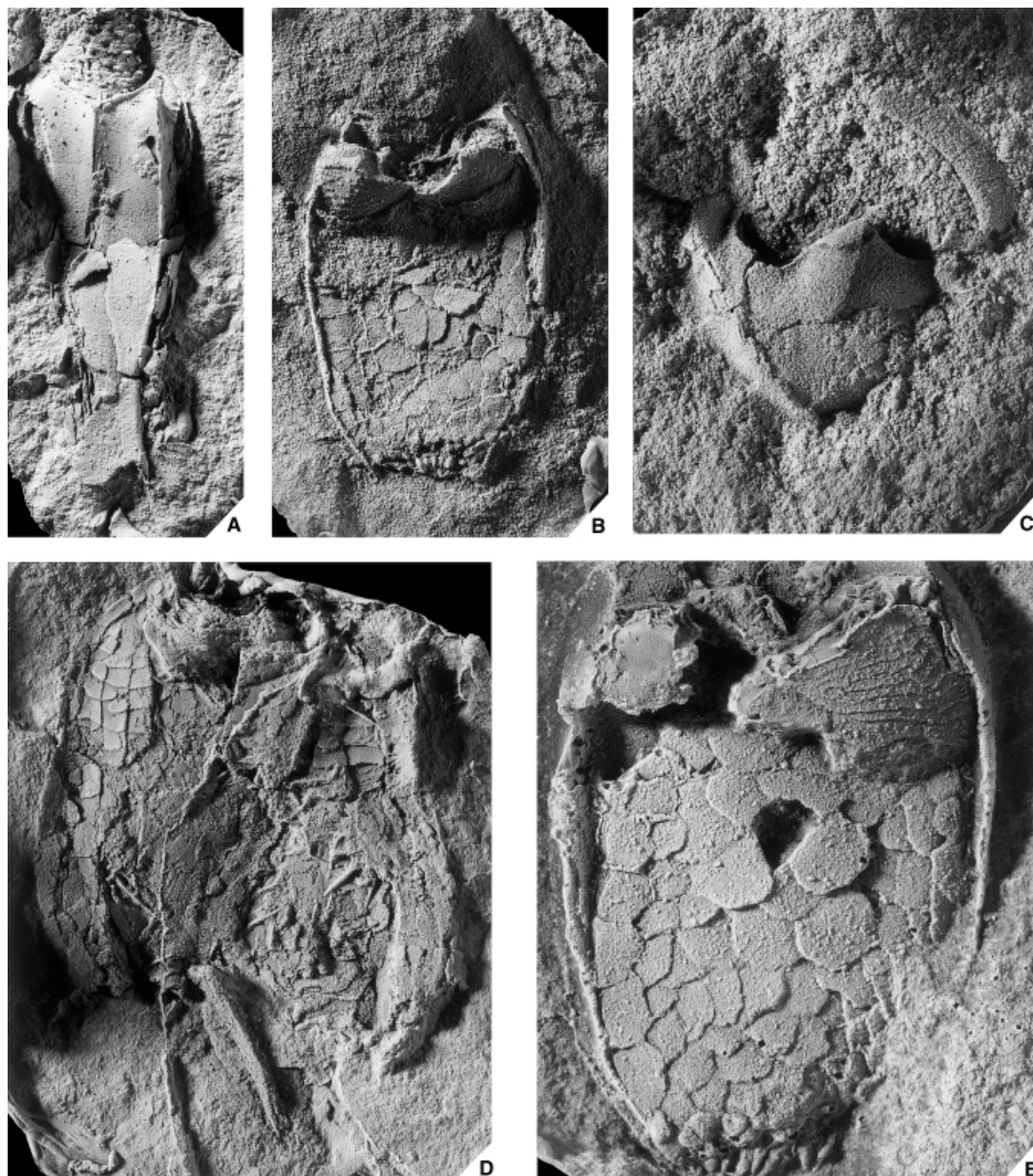


TEXT-FIG. 23. Morphology of the theca in Mitrocystitida with ratchet sculpture. A–B, *Barrandeocarpus jaekeli* Ubahgs, 1979; Letná Formation (Upper Ordovician), Czech Republic; modified after Ubahgs (1979). A, lower thecal surface. B, upper thecal surface. C–D, *Placocystites forbesianus* de Konick, 1869; Wenlock Limestone (Middle Silurian), Dudley, West Midlands (England); modified after Jefferies and Lewis (1978). C, lower thecal surface. D, upper thecal surface. Abbreviations: A, adoral; cs ribs, cuesta-shaped ribs; dig., digital; gloss., glossal; M, marginal; P, placocystid plate; pust., pustules.

Extension of ratchet sculpture on both thecal surfaces is highly variable in anomalocystitids, but in all forms ornamentation is consistently more important on the upper thecal surface than on the lower surface. As pointed out by Ruta and Bartels (1998), sculpture is generally more extensive on both surfaces when the theca is as long as it is wide (e.g. *Placocystites*) than when it is antero-posteriorly elongated (e.g. *Barrandeocarpus*). In *Placocystites*, both thecal surfaces are almost entirely covered by cuesta-shaped ribs, but terraces are clearly more abundant on the upper surface (Text-figs 23C–D, 25A). Smooth areas are restricted to the central regions of both thecal surfaces (where the theca is highest) and to the posterior edge of the lower surface (Jefferies and Lewis 1978; Jefferies 1984, 1986). Careful examination of ontogenetic series of *Placocystites* shows that the extension of cuesta-shaped ribs is very likely limited to the anterior border of the upper thecal surface in early growth stages (Jefferies 1984, p. 308). In most anomalocystitids, sculpture on the two thecal surfaces is more contrasted than in *Placocystites*. In *Barrandeocarpus jaekeli*, ornamentation covers most of the upper surface, with the exception of the posterior extremity of the theca and of a small rounded element, the ‘placocystid plate’ (P; Text-fig. 23A–B). Extension of the thecal sculpture is much more reduced on the lower surface of *Barrandeocarpus* and restricted to the lateral edges of the anterior region of the theca. On both thecal surfaces the strength of ornamentation regularly decreases rearwards, with a gradual transition from regular cuesta-shaped ribs, to broken, discontinuous ribs, and finally isolated pustules (Ubahgs 1979; Jefferies 1984). Sculptural patterns comparable to that of *Barrandeocarpus* are displayed by the thecae of various anomalocystitids, such as *Ateleocystites* (Text-fig. 22C–D; Kolata and Jollie 1982), *Placocystella* (Ruta and Theron 1997), *Victoriacystis* (Ruta 1997b), or *Rhenocystis* (Ruta and Bartels 1998).

Interpretation

The presence of long blades on the lower surface of the most proximal brachials in some anomalocystitids (e.g. *Enoploura*, *Rhenocystis*) strongly recalls the situation in more primitive Mitrocystitida (e.g. *Mitrocystites*). This strong ornamentation suggests that, in these forms, the proximal region of the arm probably played an important role in the anchorage of the animal into the substrate. This anchoring function is supported by the frequent presence of striations restricted to the lateral sides of the most proximal brachials (Ruta and Theron 1997, p. 218). These striations are comparable to those observed on the brachial spikes of symmetrical cornutes (see above). The anchoring function of the proximal region of



TEXT-FIG. 24. A, *Lagyncystis pyramidalis* (Barrande, 1887); BMNH E16017, Sarka Formation (Middle Ordovician), Czech Republic; proximal aulacophore and lower thecal surface; $\times 3$. B, E, *Mitrocystella incipiens* (Barrande, 1887); Traveusot Formation (Middle Ordovician), Brittany (France); upper thecal surface. B, IGR 15047; $\times 3$. E, IGR 15090; $\times 4$. C, *Diamphidiocystis* sp.; MHNN P25931, Traveusot Formation (Middle Ordovician), Brittany (France); lower thecal surface; $\times 5$. D, anomalous mitrate indet.; FSL 170929, Icla Formation (Lower–Middle Devonian), Bolivia; lower thecal surface; $\times 5$.

the arm is optimized in *Enoploura* and related forms (e.g. *Placocystella*) by the realization of transversally elongated, fan-shaped blades on the lower surface of the stylocone. Transverse blades are more efficient anchoring devices than laterally compressed spines in the case of organisms feeding with the arm facing

the current. The reduced size of brachial spines in most anomalocystitids (e.g. *Placocystites*, *Victoriacystis*) suggests that the proximal region of the arm was less involved in the anchorage of the organism into the substrate. However, the ossicles are much higher in anomalocystitids than in more primitive Mitrocystitida. Lateral surfaces of the arm are thus comparatively larger, and could possibly have represented more efficient 'bearing surfaces' if the arm was moved from side to side (Parsley 1991; Ruta and Bartels 1998). Such lateral movements probably enabled the animal to reorientate itself, so as to keep the arm favourably oriented, but they possibly also helped in burrowing (see below). The frequent presence of knobs and/or of a coarse ornamentation on the lateral sides of the ossicles supports the view that the lower surface of the arm was probably not resting passively on the sea floor.

The frequent presence of coarse ornamentation (knobs, tubercles) both on tectals and inferolaterals, and that of integumentary platelets intercalated between proximal rings, suggest that the proximal aulacophore was possibly buried in life in most anomalocystitids (see below). Contrary to the situation in *Lagynocystis*, proximal rings in anomalocystitids lack strong asymmetrical sediment-gripping devices (e.g. spikes). This observation indicates that, in anomalocystitids, the proximal aulacophore was probably weakly involved in the anchorage of the animal into the substrate.

Extension of the ornamentation on both thecal surfaces is highly variable in Mitrocystitida with ratchet sculpture, but in all forms, ornamentation is consistently stronger on the upper thecal surface (see above). This fundamental asymmetry between the two thecal surfaces strongly recalls the situation in some Kirkocystidae (see above) and several marine infaunal invertebrates. This asymmetry is frequently referred to as the '*Fabulina*-type' pattern (Seilacher 1972) and is encountered in several shallow infaunal organisms buried in a horizontal to slightly inclined position (Seilacher 1972, 1973; Savazzi 1981*b*, 1983; Savazzi *et al.* 1982; Signor 1982). Comparison with other invertebrates belonging to various unrelated taxa (e.g. bivalves, arthropods, brachiopods), all showing a similar contrasting ornamentation on their upper and lower body surfaces, strongly supports the view that Mitrocystitida with ratchet sculpture were shallowly buried in life, with their convex, more ornamented thecal surface facing upwards (Text-fig. 25; Kolata *et al.* 1991, fig. 5). This life orientation is comparable to that of other stylophorans (see above). The elongate thecal morphology of most anomalocystitids is possibly related to their infaunal mode of life (Savazzi 1986).

In all Mitrocystitida with ratchet sculpture, ornamentation is stronger anteriorly and decreases in a posterior direction (see above). The posterior border of the upper thecal surface is always smooth, even in the most ornamented forms (e.g. *Placocystites*). A comparable asymmetrical pattern, with a regular decrease in strength of the ornamentation in an antero-posterior direction, has been described in several infaunal organisms living buried at a slightly inclined attitude in the substrate (Savazzi 1982, 1983). In these forms, the stronger ornamentation is observed on the more deeply buried parts of the animal, and smooth surfaces typically occur on the shallowest parts. Comparison with other invertebrates showing a similar antero-posterior asymmetrical pattern strongly supports the view that Mitrocystitida with ratchet sculpture were buried at a slightly inclined attitude, with the anterior region of the theca deeper in the sediment (Kolata *et al.* 1991, fig. 5). In such an inclined living position, the anus would be at, or slightly above, the water-sediment interface (Text-fig. 25). The posterior exothecal spines of most anomalocystitids are possibly devices that helped in maintaining the posterior region of the organism and the anus above the water-sediment interface. In infaunal Mitrocystitida, the respective positions of the anterior portion of the theca (deep in the sediment) and of the arm (above the substrate) require that the proximal aulacophore was strongly flexed-upwards in life. A mostly flexed-upwards position in life of the proximal aulacophore has been confirmed by a careful examination of its morphology in several anomalocystitids (Jefferies and Lewis 1975; Jefferies 1984). Burrowing into the substrate probably involved both lateral movements of the high and laterally compressed proximal region of the arm, and possibly yawing of the anterior portion of the theca (Ruta and Bartels 1998). The oblique orientation of anterior cuesta-shaped ribs in mitrates with a theca as long as wide (e.g. *Placocystites*) suggests that thecal yaw was important in these forms. In more elongate anomalocystitids (e.g. *Ateleocystites*, *Barrandeocarpus*), the course of anterior cuesta-shaped ribs is more parallel to the anterior edge of the theca, which suggests that thecal yaw was reduced.

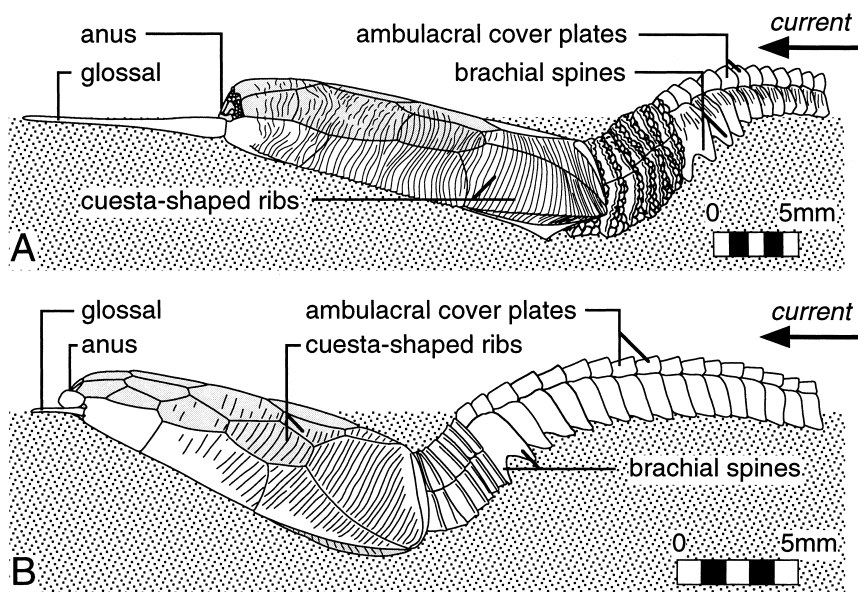
As already pointed out by Savazzi *et al.* (1982), ratchet sculpture in Mitrocystitida fulfills the four

requirements of the paradigm for burrowing sculptures devised by Seilacher (1973), which strongly supports the view that these mitrates were infaunal organisms (Jefferies and Lewis 1978; Jefferies 1984; Ruta 1997b). Cuesta-shaped ribs and broken ribs occurring on both thecal surfaces are perpendicular to the forward-burrowing direction (cross orientation; Text-fig. 24B, D–E). Thecal sculpture is asymmetrical in cross section, with consistently steeper posterior edges (frictional asymmetry). Ornamentation is reduced or absent where thecal width is maximum (perimeter smoothing); this situation is exemplified by the longitudinal smooth surfaces occurring in central position on both thecal surfaces in *Placocystites* (Text-fig. 23C–D; Jefferies and Lewis 1978; Savazzi *et al.* 1982; Jefferies 1984). Finally, careful examinations of ontogenetic series have demonstrated that the absolute size and spacing of terraces remained constant during growth (allometric increase in density), as, for example, in *Placocystites* (Jefferies and Lewis 1978) and *Placocystella* (Ruta 1997b). It should be pointed out that the close compliance of the thecal ornamentation of several *Mitrocystitida* with the paradigm for burrowing sculpture only strongly suggests that these mitrates were infaunal; it does not signify that these organisms were vagile and actively moved through the substrate. Several infaunal organisms with burrowing sculpture remain immobile once buried (e.g. crustaceans; Savazzi 1981b, 1982). The presence of several anchoring devices on the lower surface of the arm (brachial spines) and of the theca (e.g. anterior margin of the lower surface recurved downwards), as well as the presumably inclined living attitude of the organism in the substrate, strongly suggest that *Mitrocystitida* with ratchet sculpture were mostly sessile organisms. The ornamentation on the lower surface of the arm is frequently more reduced in infaunal *Mitrocystitida* than in epibenthic forms. This observation suggests a transfer of the anchoring function from the arm to the strongly ornamented theca. As a consequence, the function of thecal sculpture was probably not only to provide an efficient aid during burrowing but also, as in the mole-crab *Emerita* (see above), to anchor firmly the organism into the substrate so as to resist the pull exerted anteriorly by the currents on the feeding arm.

Evolution towards an infaunal mode of life was apparently pioneered by some Middle Ordovician primitive *Mitrocystitida*, as suggested by the presence of cuesta-shaped ribs and the realization of more elongate thecal morphologies in *Promitrocystites* and *Mitrocystella*. The loss of gonopores opening on the lower thecal surface in these two primitive *Mitrocystitida* is possibly correlated with the adoption of an infaunal mode of life. The replacement of the flexible supracentral area of early burrowers by the rigid upper surface of anomalocystitids can plausibly represent an adaptation to an infaunal mode of life. The transformation of two posterior marginals into exothecal spines in most anomalocystids is also possibly correlated with the adoption of a burrowing mode of life.

A slab from the Devonian Hunsrück Slate of Germany showing the association of two infaunal trails with four specimens of the anomalocystiid mitrate *Rhenocystis* has been described recently by Sutcliffe *et al.* (2000). The close vicinity of the trails with at least one mitrate has been interpreted by these authors as ichnological evidence that mitrates were vagile infaunal organisms, crawling forwards in the mud (Bartels *et al.* 1998; Sutcliffe *et al.* 1999; Jefferies 1999; Gee 2000). Sedimentological evidence indicates that the four mitrates were buried with their flat thecal surface upwards. This preservational orientation of the fossils is interpreted by Sutcliffe *et al.* (2000) as corresponding to the living position of the mitrates. It should be pointed out that the mitrates and their presumed trails are located in two different stratigraphical levels, but also on two distinct slabs of slate that have been glued (Sutcliffe *et al.* 2000, p. 2). The course of the two trails converges towards one of the specimens and stops abruptly at the glued contact between the two slabs. Consequently, the possibility that the trails extend further below the slab containing the mitrates cannot be entirely ruled out, and the relationship between mitrates and trails should be considered with extreme caution. Similar-looking trails occurring in the Hunsrück Slate have been attributed to arthropods and/or polychaete worms (Bartels *et al.* 1998, figs 229–230). The vicinity of such trails with one mitrate is thus possibly purely accidental. As pointed out by Ruta and Bartels (1998, p. 774), about half of the fossils are preserved upside-down in the Hunsrück Slate (Bartels and Brassel 1990; Bartels *et al.* 1998; Sutcliffe *et al.* 1999). The taxonomic preservation of four mitrates with their flat surface facing upwards is thus inconclusive as regards the life orientation of these fossils. Several examples of mitrates preserved *in situ* (e.g. sheltered under a large clast) with their flat thecal surface facing downwards have been reported (Parsley 1981; Fisher 1993; Peterson 1995).

In conclusion, the ratchet thecal sculpture of *Mitrocystitida* probably fulfilled both a burrowing and an



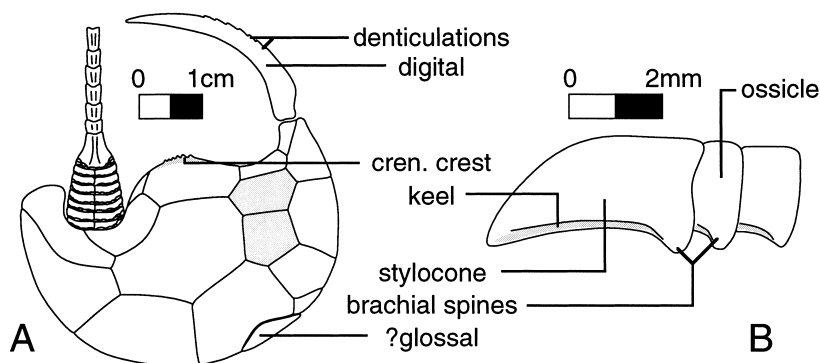
TEXT-FIG. 25. Life positions of various Mitrocystitida with ratchet sculpture (in right lateral view). A, *Placocystites forbesianus* de Koninck, 1869; Dudley Limestone (Upper Silurian), West Midlands (England). B, *Ateleocystites guttenbergensis* Kolata and Jollie, 1982; Guttenberg Formation (Upper Ordovician), Wisconsin (USA).

anchoring function. The presence of a stronger ornamentation consistently on the upper surface is directly referable to the 'Fabulina-type' pattern. Comparison with other marine invertebrates displaying a similar asymmetrical pattern suggests an infaunal mode of life and strongly supports a 'flat-surface down' orientation, comparable to that of other stylophorans. Infaunal Mitrocystitida probably lived slightly inclined in the substrate, with the anus at the water-sediment interface, and the anterior region of the theca more deeply buried (Text-fig. 25). Infaunal Mitrocystitida derive from epibenthic forms. The loss of paired gonopore openings on the lower surface, and the acquisition of posterior exothecal spines, a rigid upper surface and more elongate thecal outlines are possible adaptations to an endobenthic mode of life. Infaunal Mitrocystitida were probably mostly sessile with the theca downstream, shallowly buried in the sediment, the arm resting over the sea floor, facing the current.

Evolution towards an infaunal mode of life occurred independently in two stylophoran lineages (Peltocystida and Mitrocystitida). In both cases, the transition into a burrowing mode of life was initiated during the Middle Ordovician and fully realized early in the Late Ordovician. Interestingly, all Siluro-Devonian stylophorans known so far are either Peltocystida or Mitrocystitida. Exclusively epibenthic groups (e.g. cornutes, Lagynocystida) apparently do not survive beyond the Late Ordovician.

DIAMPHIDIOCYSTIS

Diamphidiocystis is a strongly asymmetrical, bizarre-shaped mitrate from the Middle Ordovician of Brittany (*Diamphidiocystis* sp. in Chauvel 1981; Text-fig. 24c) and the Upper Ordovician of Illinois (*D. drepanon* in Kolata and Guensburg 1979; Text-fig. 26). The unusual morphology of *Diamphidiocystis* led Kolata and Guensburg (1979) to assign this form to a distinct suborder, Diamphidiocystida (see also Chauvel 1981). As suggested by Ruta (1999a), *Diamphidiocystis* more likely represents a highly derived anomalocystitid mitrate. The discovery of several new, well-preserved specimens of the Breton *Diamphidiocystis* since the original contribution of Chauvel (1981) has led to a better knowledge of its morphology (Lefebvre in Ruta 1999a).



TEXT-FIG. 26. Morphology of *Diamphidiocystis drepanon* Kolata and Guensburg, 1979; Orchard Creek Shale (Upper Ordovician), Illinois (USA); redrawn after Kolata and Guensburg (1979). A, aulacophore and lower thecal surface. B, proximal portion of the arm, in right lateral view. Abbreviation: cren. crest, crenulated crest.

Morphology of the aulacophore

The proximal aulacophore of *Diamphidiocystis* is mostly similar to that of other anomalocystitids and consists of several telescoping rings, each made of four plates (Text-fig. 26A). Tectals and inferolaterals are subequal in size. Integumentary platelets intercalated between successive inferolaterals and a coarse ornamentation on the lower surface of proximal rings have been described in the American form (Kolata and Guensburg 1979). The deep excavation of the aulacophore insertion in the anterior border of the theca probably severely hindered lateral flexion of the proximal appendage in life (Text-figs 24C, 26A).

Ornamentation on the lower surface of the brachials is extremely reduced. It consists of a low median longitudinal keel and a small blunt distal spine (Text-fig. 26B). Brachial spines are laterally compressed, and facing downwards and slightly rearwards (Kolata and Guensburg 1979). Spines rapidly decrease in size in a distal direction. Interbrachial articulations are poorly known, but they were possibly more reduced than in other mitrates (Kolata and Guensburg 1979). Contrary to the situation in other Mitrocystitida, the arm is typically preserved in a straight, recumbent position. The original length of the arm is difficult to assess: at least 10–15 brachials are present in *D. drepanon* (Kolata and Guensburg 1979), and 7–8 elements in *Diamphidiocystis* sp. (pers. obs.).

Morphology of the theca

The theca of *Diamphidiocystis* is reniform, 'bagpipe-like' and fundamentally asymmetrical (Text-figs 24C, 26A). The unusual thecal morphology of *Diamphidiocystis* results from the 90 degree sinistral torsion of the posterior region of a 'standard' theca of Mitrocystitida (Kolata and Guensburg 1979; Ruta 1999a). As a result of this torsion, the 'old' left thecal side is anterior, the 'old' posterior extremity of the animal is on the left, and right marginals constitute both the right and posterior edges of the theca. Another consequence of this torsion is that the theca is no longer antero-posteriorly elongated, but transversally elongated. The lower thecal surface is flat and the upper surface strongly convex. The height of the theca is greatest anteriorly and decreases regularly in a posterior direction. Thecal ornamentation is reduced and consists of a strong crenulated crest at the anterior edge of the lower surface (Text-fig. 26A). This crest faces downwards and is borne by anterior marginals M'_1 and M'_2 in *Diamphidiocystis* sp., and M'_2 and M'_3 in *D. drepanon*. Two large and strongly recurved exothecal spines are present in *Diamphidiocystis* sp. (Text-fig. 24C; Lefebvre in Ruta 1999a, p. 360), and possibly in *D. drepanon* as well (Text-fig. 26A; Kolata and Guensburg 1979, p. 1133). These processes are equivalent to the posterior exothecal spines of other anomalocystitids. In *Diamphidiocystis*, the left exothecal spine (digital) is a long, scimitar-shaped, flattened blade recurved towards the aulacophore and articulated to the left anterior corner of the theca (Text-figs 24C, 26A). The right exothecal spine (glossal) is shorter and articulated to the posterior extremity of the theca. Exothecal processes are characterized by a sharp, sometimes denticulated, external margin,

and a thicker internal edge. The digital process was possibly movable in life (Kolata and Guensburg 1979, p. 1123). The supracentral area of *Diamphidiocystis* sp. is flexible and comprises numerous small, imbricated integumentary elements (Lefebvre in Ruta 1999a, p. 399). The upper surface is apparently more rigid in *D. drepanon*, and consists of a smaller number of large, tightly sutured plates (Kolata and Guensburg 1979). A faint anterior transverse crest is present on the adorals.

Interpretation

The orientation (facing downwards) and location of anchoring structures, restricted to the lower surfaces of the arm (brachial spines) and theca (crenulated crest), as well as the presence of a massive, rigid, flat lower surface and sometimes a flexible, thinner, convex upper surface strongly support the view that the life orientation of *Diamphidiocystis* was comparable to that of other stylophorans, and thus 'flat-surface down'. This orientation is also in good accordance with the presumed feeding function of the arm.

The extremely reduced ornamentation on the lower surface of the brachials suggests that in *Diamphidiocystis* the arm was probably hardly involved in the anchorage of the organism and only fulfilled a feeding function. Lateral movements of the appendage were severely limited proximally by the deeply emarginated aulacophore insertion, and distally by the extremity of the digital blade. These important limitations to the lateral flexion of the appendage, along with the presence of poorly developed interbrachial articulations, suggest that the aulacophore probably rested passively, mostly immobile, on the sea floor in life. Consequently, contrary to the situation in other stylophorans, the animal could not reorientate its arm to keep it facing the current. However, the presence of a well-developed articulation surface between the digital and the theca suggests that lateral movements of the large, scimitar-shaped anterior blade were possible and probably helped the organism to reorientate into more favourable positions.

The strongly asymmetrical outline of the large, flattened theca of *Diamphidiocystis*, as well as the presence of long exothecal blades, and protuberances restricted to the anterior edge of the theca, strongly recall the situation in asymmetrical cornutes (see above; Parsley 1988; Frest 1988). The strong, anterior crenulated crest of *Diamphidiocystis* probably fulfilled an anchoring function comparable to that of the protuberances on the lower surface of boot-shaped cornutes. Similarly, the long, expanded, exothecal processes probably served as buttressing devices, maintaining the edges of the theca at the sediment surface. The asymmetrical morphology of *Diamphidiocystis* is, thus, remarkably convergent with that of boot-shaped cornutes. This convergence can probably be correlated with the adoption of a comparable epibenthic mode of life, with most of the anchorage realized by the theca (strong anterior protuberances and long flattened blades).

In conclusion, the atypical morphology of *Diamphidiocystis* is remarkably convergent with that of boot-shaped cornutes and perfectly adapted to an epibenthic sessile mode of life, with the arm resting on the sea-floor and facing the current. Active reorientation of the animal was probably possible by lateral movements of the long anterior digital blade. Anchorage into the sediment was mainly provided by the strong, crenulated crest and the thickened anterior region of the lower thecal surface. The flat, expanded, thecal blades probably helped in stabilizing the animal on the substrate.

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