

# Epibionts on upper Eifelian crinoid columnals from the Holy Cross Mountains, Poland

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Most of 378 upper Eifelian crinoid columnals collected from the lower part of Skały Beds in the Holy Cross Mountains display traces of borings produced by endobionts, but only approximately 20% of them show traces of epibionts. These infested crinoids are represented by 5 stem-based species: *Tantalocrinus scutellus*, *Schyschcatocrinus creber*, *Gilbertocrinus vetulus*, *Pentagonostipes petaloides*, and *Cycloocetocrinus* sp. They were fouled by 19 species of suspension-feeding epibionts, including saccamminid foraminiferans, rugose and tabulate corals, cyrtinitid and productid brachiopods, “ctenostome bryozoans”, “cyclostome bryozoans”, cystoporate bryozoans, and rhabdomesid? bryozoans, crinoids, and organisms of uncertain affinities. The majority of these epibionts were opportunistic commensals colonizing living crinoids, and only some utilized dead crinoids as hard substrate for attachment. At least some of these epibionts seem to have settled selectively on particular crinoid host species.

Key words: Epibionts, crinoids, host-selectivity, Skały Beds, Eifelian, Holy Cross Mountains.

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## Introduction

Many modern and ancient marine hard substratum communities have been documented by numerous authors (for review, see Taylor and Wilson 2003). These hard substrata include sedimentary hardgrounds and rock clasts, as well as the skeletons of living and dead organisms. Diverse faunas of skeletonized epibionts are also commonly preserved as encrusters of fossil crinoid columnals. These include foraminiferans, sponges, bivalves, bryozoans, brachiopods, cornulitids, serpulid worms, edrioasteroids, and crinoids (e.g., Hess 1975; Rodriguez and Gutschick 1975; Franzén 1977; Brett and Eckert 1982; Meyer and Ausich 1983; Powers and Ausich 1990; Sandy 1996; Feldman and Brett 1998; Peters and Bork 1998; Donovan and Lewis 1999; Galle and Prokop 2000). Moreover, other epi- and endobionts were adapted to drilling or becoming embedded in the skeleton of the crinoid stalk to produce stereomic swellings (e.g., Franzén 1974; Warn 1974; Welch 1976; Brett 1978, 1985; Meyer and Ausich 1983; Werle et al. 1984; Feldman and Brett 1998). Kiepura (1965, 1973) reported for the first time some bryozoans attached to crinoid columnals from the shallow-water Eifelian–Givetian sediments (Skały Beds) of the Holy Cross Mountains at Grzegorzowice-Skały section. The present study is the first attempt to comprehensively describe diverse epibionts, including foraminiferans, corals, bryozoans, brachiopods, crinoids, and some epibionts of uncertain affinities, found on the crinoid columnals from the upper Eifelian of the Grzegorzowice-Skały section.

## Geological setting

The Grzegorzowice-Skały section is situated in the eastern part of the Bodzentyn Syncline in the Łysogóry region of the Holy Cross Mountains. Investigations of Lower and Middle Devonian strata in this section have a long history (for review see Pajchłowa 1957). Lower Devonian rocks exposed in the neighborhood of Grzegorzowice village comprise terrigenous deposits of the Bostów, Barcza, and Zagórze Beds, as well as claystones, marls, and limestones of the upper Emsian–lower Eifelian Grzegorzowice Beds. The Eifelian–Givetian part of the sequence is exposed on the eastern slope of the Dobruchna river valley in the neighborhood of Skały village (Fig. 1). It includes dolostones of the Eifelian Wojciechowice Beds, marly and clayey shales interbedded with marls and limestones of the Eifelian–Givetian Skały Beds, the Givetian siliciclastic Świętomarz Beds, reef limestones of the Pokrzywianka Beds, as well as claystones, marls and limestones of the Nieczulice Beds.

The Skały Beds comprise thirteen lithologically variable units (complexes XIII–XXV *sensu* Pajchłowa 1957) and contain a rich and diverse fauna of foraminiferans, stromatopoids, corals, bivalves, gastropods, nautiloids, tentaculites, brachiopods, bryozoans, ostracods, trilobites, crinoids and conodonts. For a long time Skały Beds have been treated as Givetian in age, but data from ostracods (Adamczak 1976; Malec 1983), tentaculitids (Dzik 1981) and conodonts (Malec 1984b, 1986, 1996) suggest that the Eifelian–Givetian

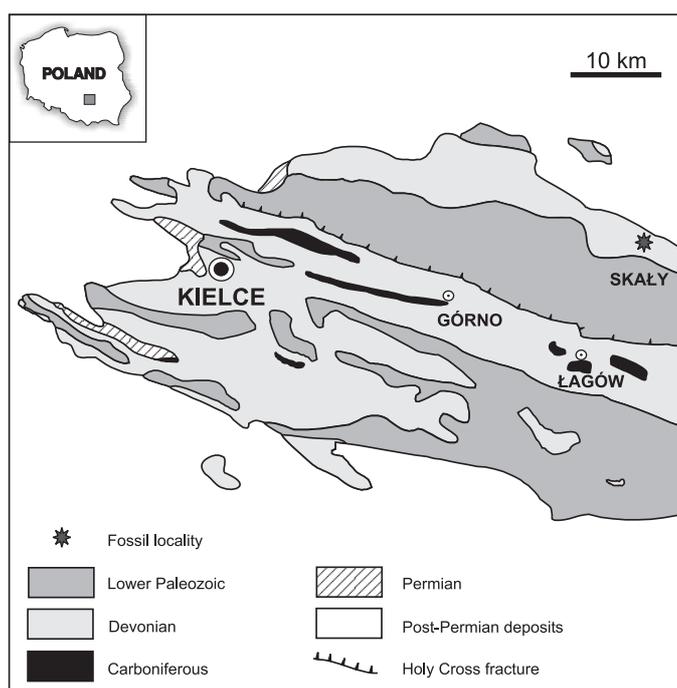


Fig. 1. Geological map of western part of the Holy Cross Mountains and location of study site. Simplified after Marynowski et. al. (2000).

boundary is contained within the Skąły Beds. According to the latest investigations of conodonts, ostracods, and miospores presented by Malec and Turnau (1997), the Skąły Beds represent the upper part of the *Tortodus kockelianus* Zone—early *Polygnathus varcus* Subzone (and perhaps also the lower part of the middle *P. varcus* Subzone, with the Eifelian–Givetian boundary within complex XIX of Pajchłowa 1957).

## Material and methods

The examined crinoid material comes from the upper Eifelian (upper part of *Tortodus kockelianus* Zone) of the lower part of the Skąły Beds exposed in Skąły village and was collected from a stratigraphic interval 0.5 m thick in the upper part of complex XVII of Pajchłowa (1957). The total collection comprises 378 crinoid stem parts, well preserved in the majority. They were obtained by disintegration through thawing in a saturated solution of Glauber's salt a bulk sample of approximately 80 kg of marly shale. The specimens discussed herein include 77 pluricolumnals with 95 epibionts occurrences counted individually for each host species. Infested crinoid pluricolumnals were cleaned with an ultrasonic disintegrator. Selected well-preserved specimens were photographed using a Philips ESEM XL 30 microscope.

*Institutional abbreviation.*—GIUS, Department of Paleontology and Biostratigraphy of the University of Silesia, Sosnowiec, Poland.

## Epibiont and crinoid host associations

The crinoid stems were colonized either during their life or after death, but in many cases, a definitive interpretation whether the attached organism colonized a live crinoid host or a stem fragment that was a sedimentary grain is not possible. Few fool-proof criteria exist to distinguish encrustation of live crinoid stems from encrustation of columnals that are no longer part of a living organism. For example, an encrusted stem composed of many columnals may indicate encrustation of a live crinoid, but it could just as easily represent postmortem encrustation because pluricolumnals may remain articulated for some time after the crinoid's death (Baumiller and Ausich 1992; Baumiller et al. 1995). On the other hand, the presence of stereomic overgrowths is unequivocal evidence that the host was alive at the time it was infested. Also life association may be inferred if the attached organisms are found around the entire circumference of the stem. However, encrustation around the entire circumference of the stem could also occur in dead material that was rolled on the sea-bed. The growth of epibionts along the axis of the stalk may also indicate that the stem was upright when fouled. However, the growth along the axis of the stalk may alternatively be a response to ambient current flow that also aligned the dead stem on the sea-bed. On the other hand, encrustation of the columnal articulum demonstrably indicates postmortem association.

Nineteen epibiont taxa found on the columnals of five stem-based crinoid species were identified (Table 1). They comprise miscellaneous epibionts including encrusting foraminiferans, corals, brachiopods, bryozoans, crinoids and epibionts of uncertain affinities. Only in a few instances, more than one epibiont taxon was found on a crinoid host and only in a few cases could a succession be observed.

**Foraminiferans.**—Small, more or less rounded and collapsed vesicles with somewhat upturned edges occur on *Gilbertsocrinus vetulus* Moore and Jeffords, 1968 and *Tantalocrinus scutellus* Le Menn, 1985. They are very similar to the monothalamous arenaceous tests of the saccaminid foraminiferans *Psammospaera/Saccamina* type described by Franzén (1974) from pits in Silurian crinoid stems from Gotland. Franzén suggested that foraminiferans attached to the walls of the pits were responsible for the borings but most probably they were commensals that settled in vacated pits (Brett 1978; Meyer and Ausich 1983). The Skąły saccaminids are attached centrally on the sutures between adjoined columnals (Fig. 2A), most probably preferring the furrows for a domicile. However, the occurrence of saccaminids in furrows is a recruitment pattern, depending not only on preferential settlement by the larvae of these foraminiferans but also processes causing early mortality of recruits. It may be that settlement was random but only those individuals located in furrows actually survived to adult-

Table 1. Distribution of epibionts on crinoid hosts from the Skafy Beds (upper part of complex XVII, *Tortodus kockelianus* Zone), Skafy village, Holy Cross Mountains.

CRINOID HOSTS	<i>Cyclooctocrinus</i> sp.	<i>Gilbertocrinus vetulus</i> Moore and Jeffords, 1968	<i>Pentagonostipes petaloides</i> Moore and Jeffords, 1968	<i>Schyschcatocrinus creber</i> Dubatolova, 1975	<i>Tantalocrinus scutellus</i> Le Menn, 1985	TOTAL EPIBIONTS
<b>foraminiferans</b>		5			2	7
saccamminids		5			2	7
<b>rugose corals</b>		1		6	1	8
<i>Adradosia?</i> sp.		1		6	1	8
<b>tabulate corals</b>			1		1	2
<i>Favosites</i> sp.			1		1	2
<b>brachiopods</b>				3	1	4
cyrtinitids					1	1
<i>Poloniproductus?</i> sp.				3		3
<b>“ctenostome bryozoans”</b>	5	1	2	6	6	20
<i>Allonema moniliforme parvum</i> Kiepura, 1965	1				1	2
<i>Ascodictyon sparsiforme</i> Kiepura, 1965	2				2	4
<i>Ascodictyon vinelliforme</i> Kiepura, 1965			2	1	1	4
<i>Eliasopora stellata</i> (Nicholson and Etheridge, 1877)				2	2	4
“ <i>Ropalonaria</i> ” <i>givetiana</i> Kiepura, 1965				3		3
<i>Vinella</i> sp.	2	1				3
<b>“cyclostome bryozoans”</b>	1	1	3		3	8
<i>Hederella</i> sp.	1	1	3		3	8
<b>cystoporate bryozoans</b>		2	4	3	3	12
<i>Eridopora orbiculata</i> (Kiepura, 1973)		2	3	2	2	9
<i>Fistulipora</i> sp.			1	1	1	3
<b>rhabdomesid? bryozoans</b>				2	2	4
rhomboporids?				2	2	4
<b>crinoids</b>	1	4		1	3	9
holdfasts	1	4		1	3	9
<b>uncertain</b>	4	1	1	6	9	21
cornulitids	1				3	4
<i>Phosphannulus?</i> sp.	3			4	3	10
“spirorbids”		1	1	2	3	7
<b>TOTAL CRINOID HOSTS</b>	10	11	11	18	27	95 77

hood. These organisms occupy a small part of the stalk circumference and are situated along one side of the stem only. This may indicate that they settled on uncovered part of partially buried stem remains.

Both saccamminid genera have been previously documented in Devonian strata of the Holy Cross Mountains (see Olempska 1983; Malec 1984a, 1992). Other foraminiferans (*Tolypamma*, *Thuramminoides*) encrusting crinoid columnals have been reported from the Upper Devonian and Lower Mississippian (Rodriguez and Gutschick 1975; Powers and

Ausich 1990). Also small encrusting foraminiferans have been observed on Upper Jurassic crinoid stems (Feldman and Brett 1998).

**Rugose corals.**—Single solitary corals of *Adradosia?* sp. are attached to *Gilbertocrinus vetulus* and *Tantalocrinus scutellus*, whereas as many as three individuals can occur on each stem of *Schyschcatocrinus creber* Dubatolova, 1975 (Fig. 2E, F). The corallites are partly or completely overgrown by crinoid stereom, producing swellings on the stems, indicat-

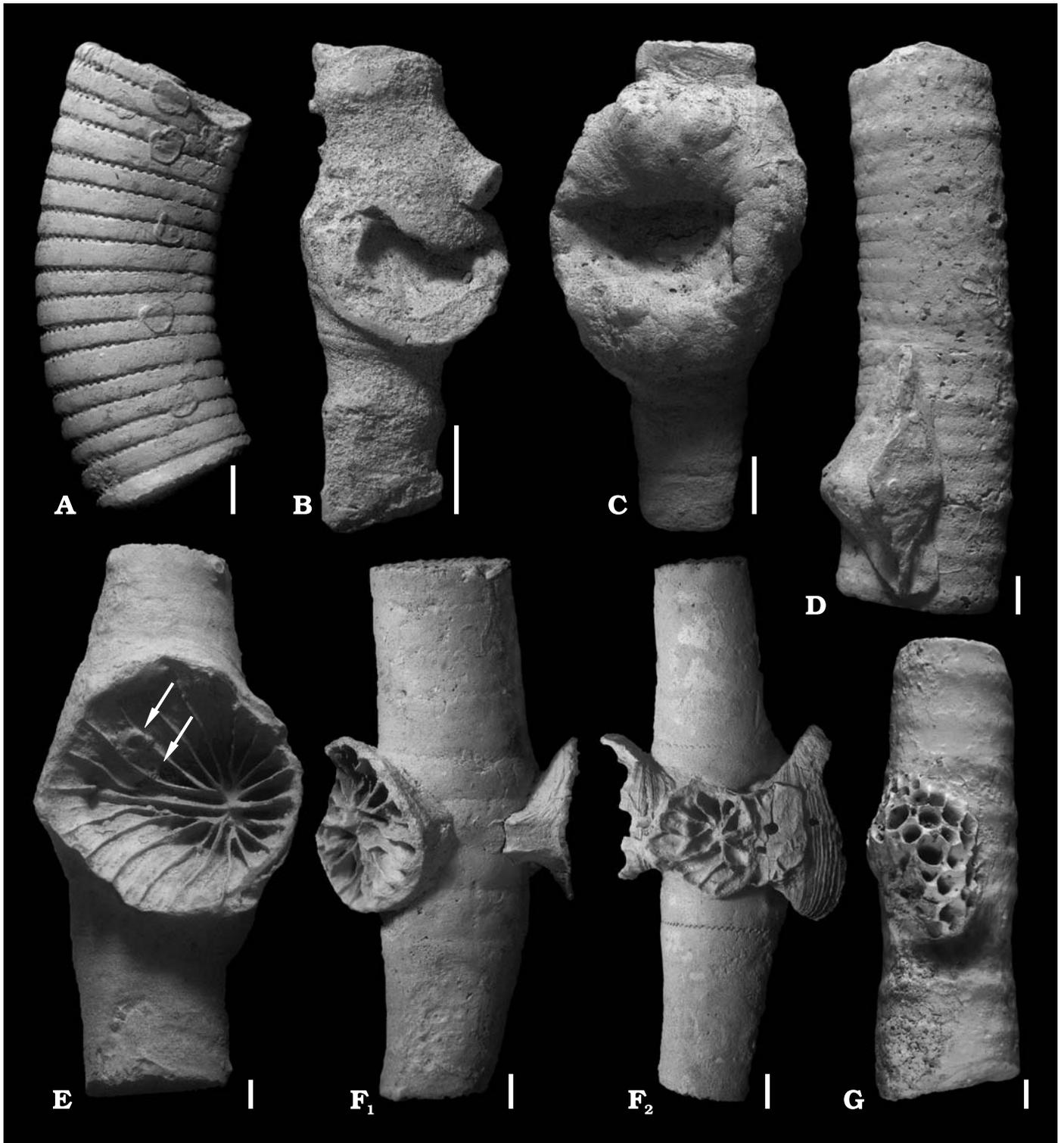


Fig. 2. Epibionts on crinoids from the Skaty Beds (upper part of complex XVII, *Tortodus kockelianus* Zone), Skaty village, Holy Cross Mountains. A. Saccamminid foraminiferans on *Gilbertsocrinus vetulus* Moore and Jeffords, 1968, GIUS-4-2445/3. B, C. *Schyschatocrinus creber* Dubatolova, 1975 malformed by attachment of the brachiopod *Poloniproductus?* sp.; stereomic overgrowth indicates that the host was alive when fouled. B. Root appendage, GIUS-4-2445/11. C. Stem fragment, GIUS-4-2445/12. D. Cyrtinitid brachiopod on *Tantalocrinus scutellus* Le Menn, 1985, GIUS-4-2445/14. E, F. Rugose coral *Adradosia?* sp. on *Schyschatocrinus creber* Dubatolova, 1975; stereomic response indicates that both epibionts and the hosts were alive contemporaneously. E. Arrows indicate later attachment of juvenile crinoids (holdfasts), GIUS-4-2445/4. F. Cluster of three individuals; note significant stereomic overgrowth (F<sub>1</sub>) and complete boreholes (*Trypanites?*) on coral on opposite side of pluricolumnal (F<sub>2</sub>), GIUS-4-2445/5. G. Tabulate coral *Favosites* sp. on *Tantalocrinus scutellus* Le Menn, 1985; oblique orientation of the coral may indicate that the crinoid stalk was upright during epibiont growth, GIUS-4-2445/9. Scale bars 1 mm.

ing that the corals lived attached to stems of living hosts. In one case, the crinoid stereom overgrows the whole epitheca, extending even somewhat inside the corallite where, additionally, minute discoidal crinoid holdfasts are visible on the septa (Fig. 2E). This may indicate that the crinoid host survived after the death of the epibiont and that juvenile crinoids settled upon the dead coral. Regular complete boreholes (*Trypanites?*) that penetrate the epitheca of another corallite (Fig. 2F<sub>2</sub>) indicate the activities of boring organisms.

The corals cannot be more precisely identified without thin sections. It must be noted, however, that *Adradosia polonica* (Sobolev, 1904) has been reported previously from the upper Eifelian of the Skąły Beds (Fedorowski 1965, 2003).

**Tabulate corals.**—Very small, irregular and poorly preserved colonies of *Favosites* sp. are attached to *Pentagonostipes petaloides* Moore and Jeffords, 1968 and *Tantalocrinus scutellus* Le Menn, 1985. They are situated only on one side of the stems, without associated swellings or deformation of the crinoid stereom. However, the oblique arrangement of corallites may indicate growth along the axis of the upright stalk of a living host (Fig. 2G).

Favositids are known from Devonian strata of the Holy Cross Mountains, and *Favosites goldfussi* d'Orbigny, 1850 was documented in the Eifelian–Givetian Skąły Beds (Stasińska 1958; Nowiński and Sarnecka 2003). Favositids that lived attached to living crinoid hosts have also been reported from the Upper Silurian (Halleck 1973; Brett and Eckert 1982; Peters and Bork 1998), Lower Devonian (Galle 1978; Galle and Prokop 2000) and Lower Carboniferous (see Meyer and Ausich 1983). Other tabulate corals (*Antholites*, *Cladochonus*, *Emmonsia*) associated with living crinoids are known from Devonian–Mississippian strata (see Meyer and Ausich 1983; Powers and Ausich 1990; Donovan and Lewis 1999).

**Brachiopods.**—A small, asymmetric shell of a cyrtinitid with a nearly flat dorsal valve and a high, concave ventral area embraces the stalk of *Tantalocrinus scutellus* (Fig. 2D). No reaction of the crinoid host to the fouler has been observed and therefore it is uncertain whether the growth of the brachiopod was on a living or dead crinoid. The shell is poorly preserved and crushed; however, it may represent *Cyrtina* or *Squamulariina*. Both these genera are known to occur in the upper Eifelian–lower Givetian of the Skąły Beds (Biernat 1966; Baliński et al. 2003).

Juvenile productid brachiopods (*Poloniproductus?* sp.) attached to a living crinoid host have been almost completely overgrown by the stereom of *Schyschcatocrinus creber* (Fig. 2B, C). While the body fossils are not preserved, deep hollows in the stem as well as root appendage swellings replicate the shape of the minute, concave-convex shells with traces of spines on their surfaces.

Productids are common in the Middle Devonian of the Holy Cross Mountains and *Poloniproductus varians* (Biernat, 1966) was described from the upper Eifelian–lower Givetian Skąły Beds (Biernat 1966; Biernat and Lazarev

1988; Baliński et al. 2003). Productid brachiopod *Linoproductus* attached with anchor spines to crinoid column have been reported from Permian strata (Grant 1963). Other productid *Heteralosia* attached to crinoid stems was mentioned from the Lower Mississippian by Powers and Ausich (1990). The Upper Ordovician atrypid *Zygospira* attached by pedicles in high density to a crinoid column was illustrated by Sandy (1996), and the Upper Silurian rhynchonellid *Stegerhynchus* oriented with the foramen against the crinoid column by Brett and Eckert (1982) and Peters and Bork (1998). In addition, attachment of the Upper Ordovician inarticulate brachiopods (*Petrocrania*, *Trematis*) to crinoid stems were mentioned by Sandy (1996), and the Upper Silurian *Crania* by Peters and Bork (1998). Other inarticulate brachiopod *Philhedra* attached to crinoid calyx was reported from the Devonian by Rodriguez and Gutschick (1975).

**“Ctenostome bryozoans”.**—These problematical, thread-like fossils described here are commonly classified as ctenostome bryozoans, however, they have calcified skeletons and cannot be ctenostomes which are entirely soft-bodied (Wilson and Taylor 2001). They represent the most numerous and taxonomically differentiated epibionts identified herein and occur on all five crinoid species infested by epibionts. They are never associated with deformations of the crinoid stereom. However, their growth around nearly the entire circumference of crinoid columnals indicates that the stems may have been upright when fouled.

Extremely delicate strings of club-like or elliptical internodes of *Allonema moniliforme parvum* Kiepura, 1965 (Fig. 3E), and poorly preserved threads of stolons connecting oval, partly embedded vesicles of *Ascodictyon sparsiforme* Kiepura, 1965 (Fig. 3G) foul *Cycloocetocrinus* sp. and *Tantalocrinus scutellus*. Delicate stolons connecting stellate groups of narrow, elongated vesicles of *Ascodictyon vinelliforme* Kiepura, 1965 (Figs. 3F, 4D) occur on *Pentagonostipes petaloides*, *Schyschcatocrinus creber*, and *Tantalocrinus scutellus*. Zoaria of *Eliasopora stellata* (Nicholson and Etheridge, 1877) (Fig. 3C) consisting of oval vesicles grouped in stellate clusters and connecting stolons encrust *Schyschcatocrinus creber* and *Tantalocrinus scutellus*. Irregularly arranged zoaria of “*Ropalonaria*” *givetiana* Kiepura, 1965 consisting of fusiform internodes and long stolons occur only on *Schyschcatocrinus creber* (Fig. 3D). This encrusting species named by Kiepura (1965) does not belong to this genus which is a true ctenostome bryozoan (Paul Taylor, personal communication 2004). Traces of embedded, radially arranged, delicate tubular stolons of *Vinella* sp. (Fig. 3G, H), are visible on the external surface of stems of *Cycloocetocrinus* sp. and *Gilbertsocrinus vetulus*.

All these “ctenostome bryozoans” were described from Devonian strata in the Grzegorzowice–Skąły section by Kiepura (1965, 2003) and, except for *Eliasopora stellata*, they were observed on crinoid hosts. *Ascodictyon sparsiforme* has been reported from the Upper Emsian Grzegorzowice Beds and the Eifelian–Givetian Skąły Beds, *Eliasopora stellata*

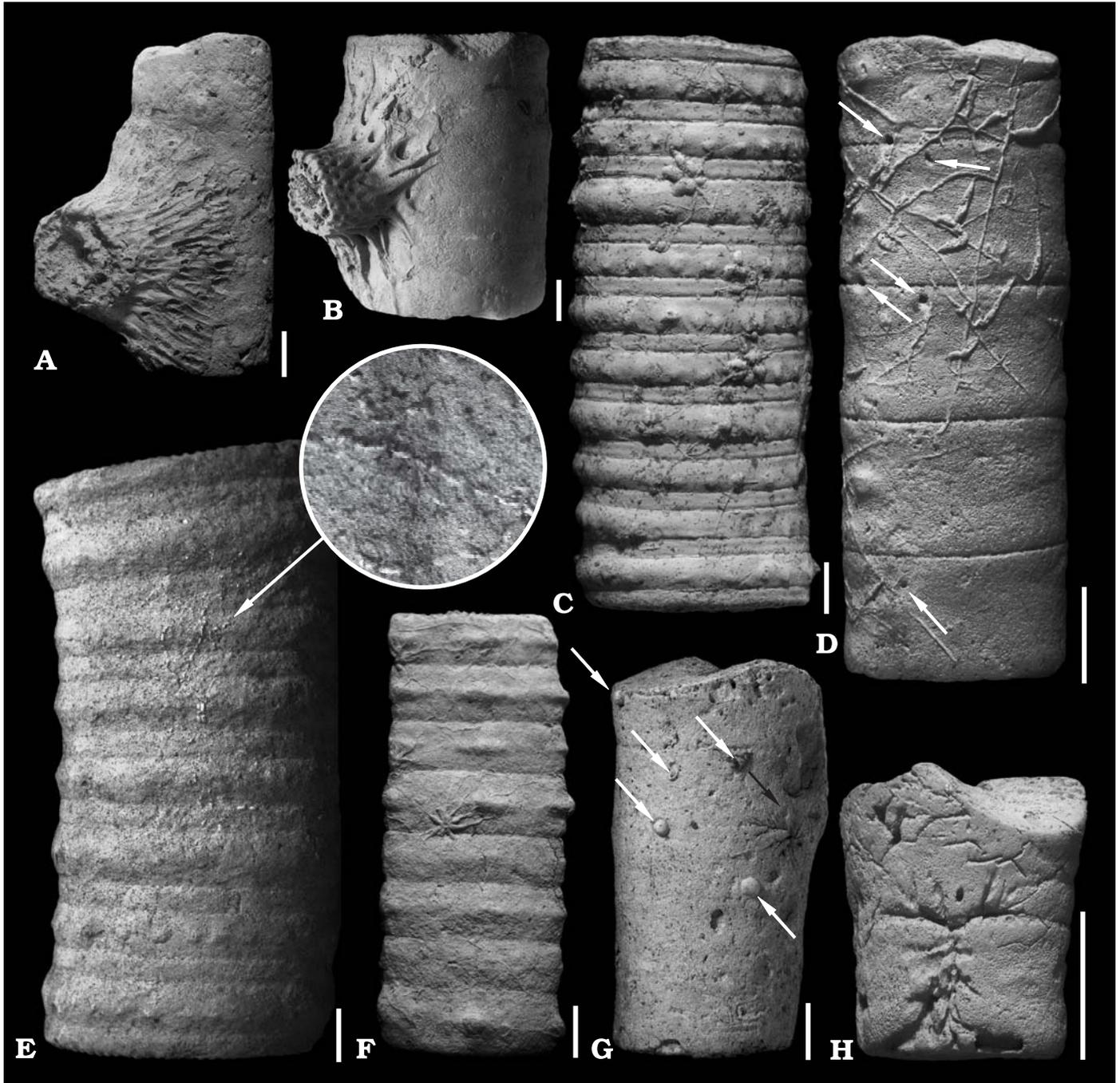


Fig. 3. Epibionts on crinoids from the Skaly Beds (upper part of complex XVII, *Tortodus kockelianus* Zone), Skaly village, Holy Cross Mountains. **A, B.** Rhomboporid? bryozoan bases on *Schyschcatocrinus creber* Dubatolova, 1975; perpendicular orientation of the zoaria to the axis of stalk may indicate that the host was dead during epibiont growth. **A.** Regularly developed base, GIUS-4-2445/58. **B.** Root-like base, GIUS-4-2445/59. **C–H.** “Ctenostome bryozoans” encrusting nearly the entire circumference of columnals that may indicate that the stalks were upright when fouled. **C.** *Eliasopora stellata* (Nicholson and Etheridge, 1877) on *Tantalocrinus scutellus* Le Menn, 1985, GIUS-4-2445/27. **D.** “*Ropalonaria*” *givetiana* Kiepura, 1965 on *Schyschcatocrinus creber* Dubatolova, 1975; arrows indicate small borings of *Trypanites*?, GIUS-4-2445/31. **E.** *Allonema moniliforme parvum* Kiepura, 1965 on *Tantalocrinus scutellus* Le Menn, 1985, GIUS-4-2445/15. **F.** *Ascodictyon vinelliforme* Kiepura, 1965 on *Pentagonostipes petaloides* Moore and Jeffords, 1968, GIUS-4-2445/21. **G.** *Ascodictyon sparsiforme* Kiepura, 1965 (white arrows) and *Vinella* sp. (black arrow) on *Cyclooctocrinus* sp., GIUS-4-2445/17. **H.** *Vinella* sp. on *Cyclooctocrinus* sp., GIUS-4-2445/34. Scale bars 1 mm.

from the upper Eifelian Skaly Beds, whereas the remaining taxa have been reported from the Eifelian–Givetian Skaly Beds. The occurrence of *Ascodictyon* sp. on a crinoid stem, also without associated deformation of the crinoid stereom

was reported from the Lower Mississippian (Powers and Ausich 1990). Unidentified ctenostome borings on crinoid pluricolumnals from the Upper Jurassic were mentioned by Feldman and Brett (1998).

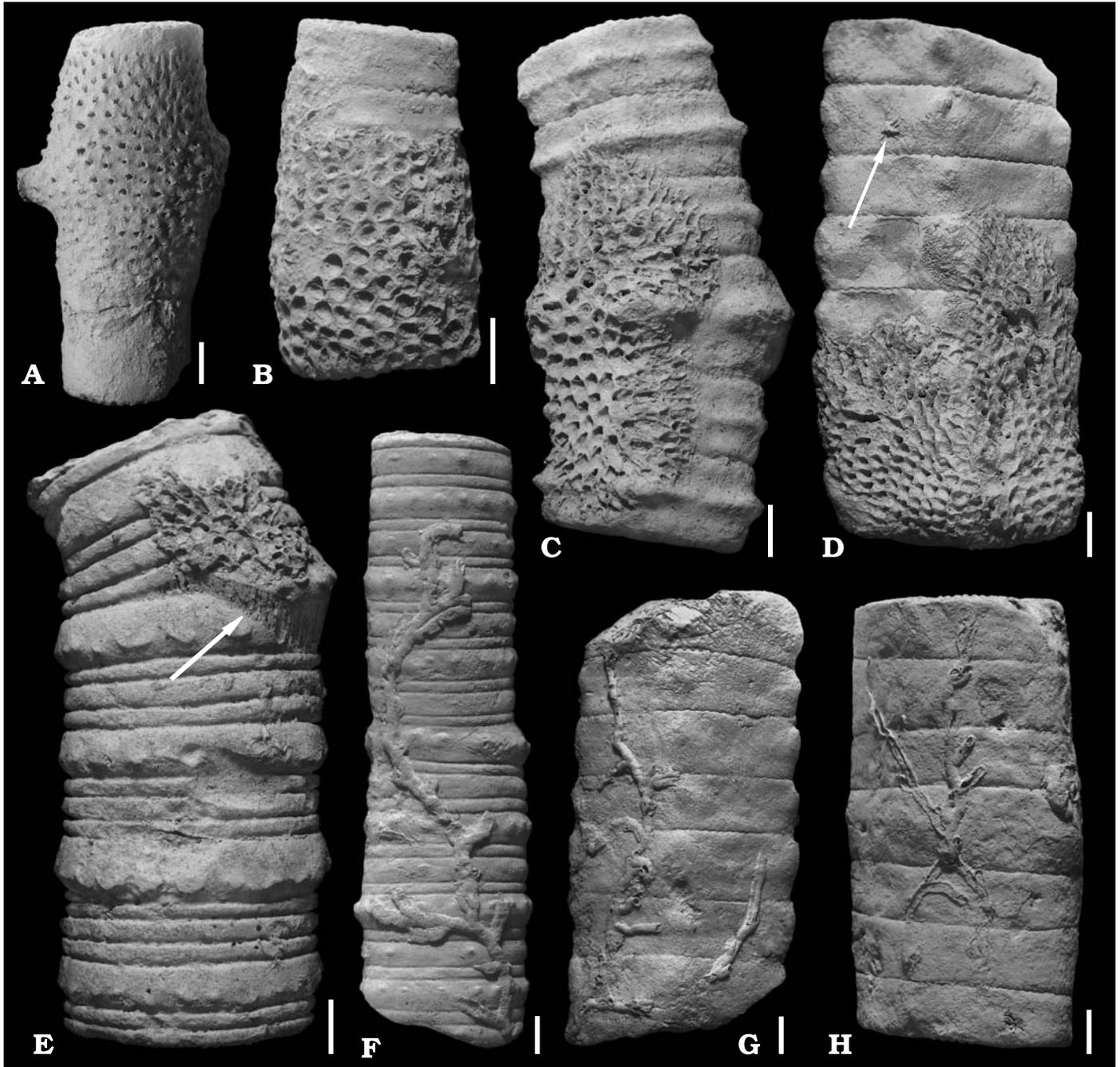


Fig. 4. Epibionts on crinoids from the Skaly Beds (upper part of complex XVII, *Tortodus kockelianus* Zone), Skaly village, Holy Cross Mountains. A. Cystoporate bryozoan *Fistulipora* sp. on *Schyschatocrinus creber* Dubatolova, 1975; growth around the entire stem circumference may indicate that the host was alive, GIUS-4-2445/53. B–E. Cystoporate bryozoan *Eridopora orbiculata* (Kiepara, 1973) on *Pentagonostipes petaloides* Moore and Jeffords, 1968 (B–D) and *Tantalocrinus scutellus* Le Menn, 1985 (E). B. Growth around the entire stem circumference may indicate that the host was alive, GIUS-4-2445/45. C. Growth on one side of the stem may indicate that the host was dead, GIUS-4-2445/46. D. Arrow indicates small “ctenostome bryozoan” *Ascodictyon vinelliforme* Kiepara, 1965, GIUS-4-2445/47. E. Arrow indicates damaged and regenerated part of the stem, GIUS-4-2445/48. F–H. “Cyclostome bryozoan” *Hederella* sp. on *Tantalocrinus scutellus* Le Menn, 1985 (F) and *Pentagonostipes petaloides* Moore and Jeffords, 1968 (G, H); zoaria occupying a significant part of the columnals circumference may indicate that they lived on the upright stalks. F. Zoarium on well ornamented, circular pluricolumnal, GIUS-4-2445/37. G. Zoarium on angularly pentagonal pluricolumnal, GIUS-4-2445/38. H. Zoarium on subpentagonal pluricolumnal, GIUS-4-2445/39. Scale bars 1 mm.

“Cyclostome bryozoans”.—Encrusting, partly damaged zoaria of *Hederella* sp. (Fig. 4F–H) are found attached to *Cycloocetocrinus* sp., *Gilbertsocrinus vetulus*, *Pentagonostipes petaloides*, and *Tantalocrinus scutellus*. Hederellids,

commonly classified among cyclostome bryozoans may not be bryozoans because they have a different budding pattern and sometimes much larger zooids than true bryozoans (Wilson and Taylor 2001). The elongate branches with zoecia

bending from a tubular axis, probably represent several species. The crinoid hosts do not display a pathologic response to the presence of these epibionts. However, zoaria occupy a significant part of the columnal circumference which may indicate that they lived attached to upright stems.

Numerous species of hederellids were described from Emsian–Givetian strata in the Grzegorzowice-Skały section (Kiepur 1973, 2003). Three of them, *Hederella* (*Hederella*) *alternata* (Hall and Whitfield, 1873), *Hederella* (*Hederella*) *canadensis* (Nicholson, 1874) and *Hederella* (*Magnederella*) *reimanni* (Bassler, 1939), were reported from the upper Eifelian of the Skały Beds, and the first two species were also found attached to crinoid stems. True cyclostome bryozoans (*Corynotrypa*) attached to crinoids were reported from the Permian (Taylor 1985) and the Lower Mississippian (Powers and Ausich 1990). Other possible Upper Silurian encrusting cyclostome bryozoans occupying approximately 270 degrees arc distance on the column were illustrated by Peters and Bork (1998). Dichotomously branching *Stomatopora* and unidentified mound-like cyclostome bryozoans partially wrapped around the columns were documented from the Upper Jurassic by Feldman and Brett (1998).

**Cystoporate bryozoans.**—Zoaria of *Eridopora orbiculata* (Kiepur, 1973) composed of tube-like, very short and oblique zoecia with pyriform apertures (Fig. 4B–E), are attached to *Gilbertsocrinus vetulus*, *Pentagonostipes petaloides*, *Schyschcatocrinus creber*, and *Tantalocrinus scutellus*. Most of the stems are encrusted circumferentially, demonstrating epibiont growth on a living host, whereas the presence of smaller disk-like zoaria may point to a postmortem association. This cystoporate species was previously reported from the upper Emsian–upper Givetian of the Holy Cross Mountains, including the upper Eifelian in the Skały locality (Kiepur 1973, 2003; Morozova et al. 2002).

Lamellar zoaria of *Fistulipora* sp. (Fig. 4A), composed of obliquely arranged zoecia with oval apertures, encrust the stems of *Pentagonostipes petaloides*, *Schyschcatocrinus creber*, and *Tantalocrinus scutellus*. They overgrow the entire circumference of the columnals, suggesting bryozoan growth on upright stems of living crinoid hosts. Two species of this cystoporate genus, the Upper Emsian *Fistulipora emphantica* Kiepur, 1973 (Kiepur 1973, 2003) and the upper Givetian *Fistulipora pavimenta* Bigey, 1988 (Morozova et al. 2002), are known to occur in the Devonian of the Holy Cross Mountains. Colonies of *Fistulipora* and *Cheilotrypa* attached to crinoid stems were also reported from the Lower Mississippian (Powers and Ausich 1990).

**Rhabdomesid? bryozoans.**—Partly preserved, thin-ramose zoaria with oval zoecial apertures arranged in regular

oblique rows are similar to bases of erect rhomboporids, however they may also represent some trepostome bryozoans (Fig. 3A, B). They are attached to the columnals of *Schyschcatocrinus creber* and *Tantalocrinus scutellus*. No associated deformations of crinoid stereom have been observed. Moreover, the bryozoan branches are oriented nearly perpendicularly to the crinoid stem axis which may indicate that they lived attached to the fragmented dead stems that lay horizontally on the sea floor.

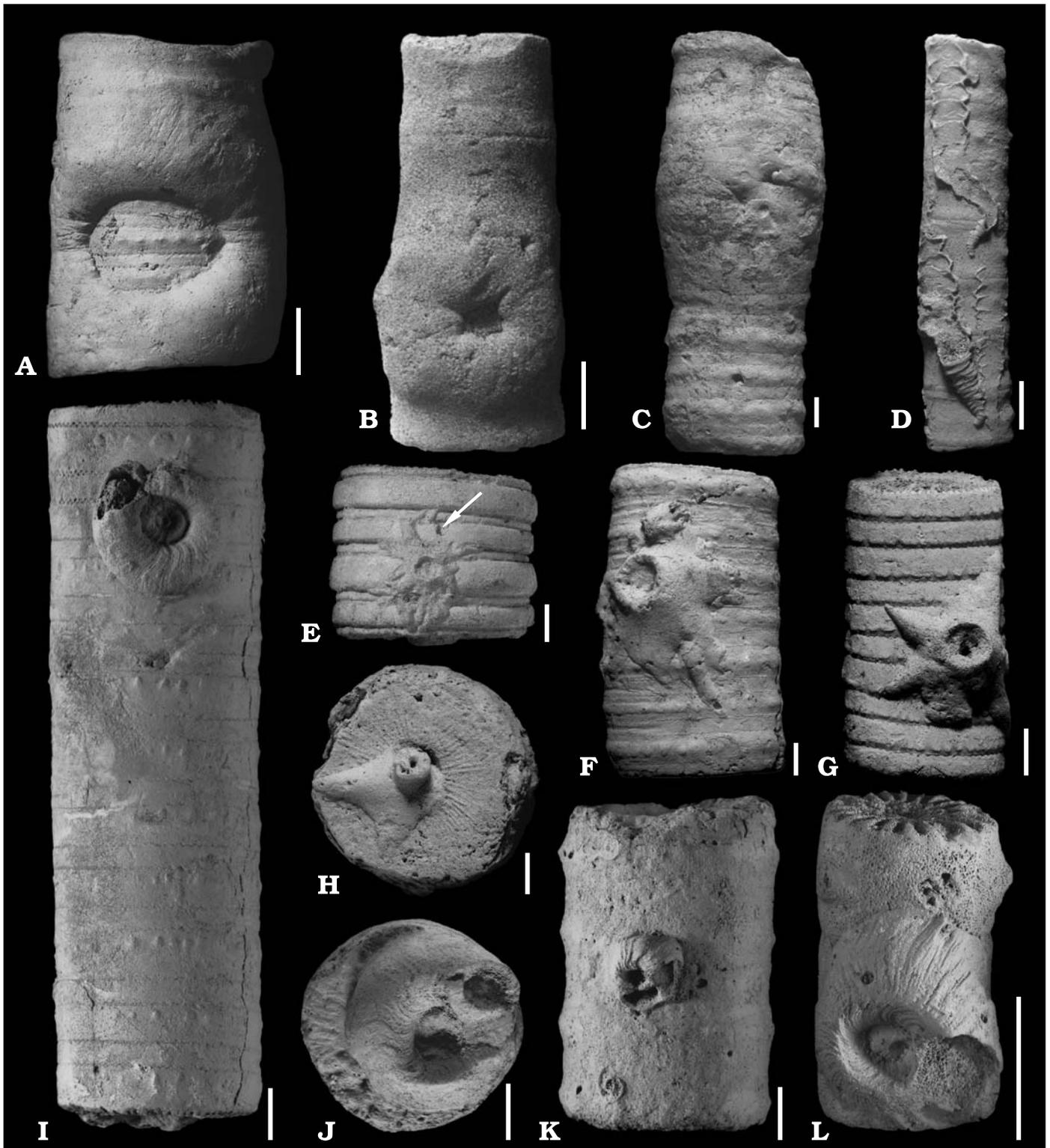
Representatives of rhomboporids (*Acanthoclema*, *Orthopora*, *Primorella*, *Rhombopora*, *Saffordotaxis*) and trepostomes (*Atactotoechus*, *Eostenopora*, *Eridotrypella*, *Leptotrypa*, *Lioclema*) were reported from some upper Givetian and middle Frasnian localities in the Holy Cross Mountains (Morozova et al. 2002). The presence of rhomboporids (*Orthopora*) in the Eifelian–Givetian of Skały village was reported by Pajchlowa (1957), whereas Kiepur (2003) mentioned also trepostomes (*Amplexopora*, *Lioclema*) from this locality.

**Crinoids.**—Small, discoidal holdfasts with strongly digitate margins of unidentified crinoid juveniles (Fig. 5E–H) are attached to *Cycloocetocrinus* sp., *Gilbertsocrinus vetulus*, *Schyschcatocrinus creber*, and *Tantalocrinus scutellus*. The stems of juveniles inserted in round depressions display traces of columnal articulation and a minute, centrally located, axial canal. No associated deformation of the crinoid hosts have been observed. A postmortem association can be inferred for the holdfasts attached to columnal articulum (Fig. 5H). In the remaining cases, the interpretation is uncertain, although the slightly oblique orientation of the discs to the stalk axis may indicate that the stem of the host was upright when fouled.

Various attachment of crinoid juveniles to living or dead adults is known from the Silurian to the Mississippian (Meyer and Ausich 1983). Coiling stems and modified discoidal holdfasts on the columns of crinoid hosts were reported from Silurian strata by Franzén (1977). Other Silurian coiling stems and dendritic holdfasts distributed on all sides of the column were documented by Peters and Bork (1998).

**Unidentified epibionts.**—These epibionts comprise organisms of unknown affinities which have not been assigned to a phylum or class, including Tentaculitidae-like cornulitids (see Fisher 1962; Richards 1974; Dzik 1991) and *Phosphannulus*, classified among the hyolithelminthids by Müller et al. (1974), as well as “spirorbids” commonly regarded as serpulid polychaetes. However, Palaeozoic spirorbids may be tentaculitoid microconchids rather than annelids (Weedon 1991, 1994). Partly damaged, small, conical and ringed tubes of cornulitids are attached along one side of the columnals of *Cycloocetocrinus* sp. and *Tantalocrinus scutellus*. They are not associated

Fig. 5. Epibionts on crinoids from the Skały Beds (upper part of complex XVII, *Tortodus kockelianus* Zone), Skały village, Holy Cross Mountains. A–C. Swellings resulted from *Phosphannulus?* sp. activity on living host *Tantalocrinus scutellus* Le Menn, 1985 (A, C) and *Schyschcatocrinus creber* Dubatolova, 1975 (B). A. Pluricolumnal with ellipsoidal, large opening, GIUS-4-2445/79. B. Pluricolumnal with narrowed, rounded opening, GIUS-4-2445/80. C. Pluricolumnal with nearly closed opening, GIUS-4-2445/81. D. Cornulitids on *Tantalocrinus scutellus* Le Menn, 1985; growth along the axis of the columnals may indicate that the stalk was upright during epibiont growth, GIUS-4-2445/77. E–H. Holdfasts of juvenile crinoids on *Gilbertsocrinus* →



*vetulus* Moore and Jeffords, 1968 (E, G), *Tantalocrinus scutellus* Le Menn, 1985 (F), and *Cycloocetocrinus* sp. (H); slightly oblique orientation to the axis of columnals may indicate that the juveniles attached to the upright host stalk (E–G). E. Holdfast on strongly heteromorphic pluricolumnal; arrow indicates boring of *Trypanites*?, GIUS-4-2445/68. F. Holdfast on heteromorphic pluricolumnal with well-marked noditaxes, GIUS-4-2445/69. G. Holdfast on slightly ornamented pluricolumnal with deep sutural furrows, GIUS-4-2445/70. H. Attachment to the articular facet indicates that the host was dead, GIUS-4-2445/71. I–L. “Spirorbids” on *Tantalocrinus scutellus* Le Menn, 1985 (I, K) and *Schyschcatocrinus creber* Dubatolova, 1975 (J, L). I. Attachment to slightly ornamented heteromorphic pluricolumnal, GIUS-4-2445/62. J. Attachment to the articular facet indicates that the host was dead, GIUS-4-2445/63. K. Attachment to heteromorphic pluricolumnal with poor-marked noditaxes, GIUS-4-2445/64. L. Attachment to nearly straight-sided pluricolumnal; note small complete boreholes (*Trypanites*?) on “spirorbid” tube, GIUS-4-2445/65. Scale bars 1 mm.

with deformation of the crinoid stereom, although orientation of the tubes parallel to the axis of the stalk may indicate growth on the erect stem of living hosts (Fig. 5D). Franzén (1974) illustrated crinoid stems malformed by the attachment of cornulitids from Silurian strata. *Cornulites* attached to crinoid columnals have also been reported from the Upper Devonian (Rodríguez and Gutschick 1975).

A different type of infestation is evident from asymmetrical spherical stereomic swellings with a central cavity involving several columnals. These have a single, variably-sized (0.5–3.5 mm), ellipsoidal to circular outwardly-flared opening to the exterior (Fig. 5A, B). The edges around the holes are bent inward as if the crinoid secreted stereom and was gradually trying to close them. Therefore, in some cases, the openings can be extremely small (Fig. 5C). They occur on *Cycloocetocrinus* sp., *Schyschcatocrinus creber*, and *Tantalocrinus scutellus*. The axial canal has never been penetrated which indicates a commensal association with the host. Moreover, in the case of a larger opening, an intact, originally ornamented lateral side of crinoid stalk is visible (Fig. 5A). These cavities in the swellings differ from the circular-parabolic pits associated with the stem deformation referred to the ichnogenus *Tremichnus* (see Brett 1978, 1985; Feldman and Brett 1998). Instead, these swellings resemble the gall morphology resulting from *Phosphannulus* activity (see Warn 1974; Welch 1976; Werle et al. 1984; Powers and Ausich 1990). However, diagnostic phosphatic material associated with the gall is lacking, but it is not clear whether this is only due to poor preservation. Since only on some specimens has the crinoid axial canal been penetrated by *Phosphannulus* holdfasts, Welch (1976) suggested that the *Phosphannulus* animal was probably a suspension-feeder using the crinoid stem as a substratum and only occasionally tapping the axial canal.

The temporal range of *Phosphannulus* associations with crinoids is from Ordovician to Permian and perhaps Jurassic, although Silurian and Jurassic examples are questionable (Meyer and Ausich 1983).

Partly crushed, small, spirally coiled tubes with concentric ridges of “spirorbids” (Fig. 5I–L) are attached to *Gilbertsoocrinus vetulus*, *Pentagonostipes petaloides*, *Schyschcatocrinus creber*, and *Tantalocrinus scutellus*. It is not known whether they settled on stalks of living or dead crinoids, though at least one case of a tube attached to a columnal articulum (Fig. 5J) represents an obvious instance of postmortem association. Regular, complete boreholes that penetrate the “spirorbid” tube (Fig. 5L) point to the activities of some boring organisms (*Trypanites*?).

Numerous tubes of “spirorbids” are known from upper Emsian–upper Eifelian strata of the Grzegorzowice-Skały section in the Holy Cross Mountains (Pajchłowa 1957). “Spirorbids” attached to crinoids have been reported from the Upper Silurian (Peters and Bork 1998), from the Lower Mississippian (Meyer and Ausich 1983; Powers and Ausich 1990) and from the Upper Jurassic (Feldman and Brett 1998).

## Borings on crinoid stems

A significant portion of all the crinoid material is more or less corroded and columnal surfaces are often with minute holes. However, a number of pluricolumnals, either infested by epibionts or not, display traces of true borings of biogenic origin. These are simple, minute pocket-shaped boreholes, ranging from 0.1 to 0.3 mm in diameter, with circular to oval apertures (e.g., Figs. 3D, 5E) and they represent possible dwelling borings produced by some unknown endobionts. The boreholes occur on both lateral and articular sides of columnals and are not associated with deformation of the crinoid stereom. Therefore, at least some stalks were bored after death of the crinoid. The boreholes are also present on associated rugose corals (Fig. 2F<sub>2</sub>) and “spirorbids” (Fig. 5L). These boring structures are similar to those classified within the ichnogenus *Trypanites* and possibly result from the activities of sipunculid and/or polychaete worms (see Pamperton et al. 1980, 1988). However, they are of a much smaller size than the borings of *Trypanites* on crinoid stalks which were described from the Upper Jurassic by Feldman and Brett (1998).

## Discussion

The majority of the epibionts studied here evidently settled on living crinoid hosts. This was certainly the case for rugose corals, productid brachiopods and *Phosphannulus*?. Probably it was also true for tabulate corals, cornulitids, most crinoids, as well as “ctenostome bryozoans”, “cyclostome bryozoans” and cystoporate bryozoans. In the remaining taxa, however, a life relationship is not clear, and postmortem settlement is either possible (foraminiferans, rhabdomesid? bryozoans, cyrtinitid brachiopod and some “spirorbids”) or certain (some crinoids and “spirorbids”).

Biotic interactions between the epibionts and the crinoids cannot be demonstrated in many fossil situations (see Darrell and Taylor 1993). The settlement of an epibiont on an erect crinoid stalk most probably does not have to represent a parasitic habit, because an epibiont may simply take advantage of stronger currents above the bottom and thus avoid competition for food with other organisms attached to the substratum at the sediment-water interface (Meyer and Ausich 1983; Powers and Ausich 1990; Feldman and Brett 1998). Such organisms occupy the secondary tier of epifaunal suspension-feeding communities (Ausich and Bottjer 1982; Bottjer and Ausich 1986). According to Galle and Prokop (2000), the reaction of a host to the presence of an attached organism by secreting stereomic overgrowths to isolate it, may indicate that the epibiont inhibited the crinoid, and that their interaction represents amensalism. However, it is commonly believed that epibionts that settled on live crinoids were not detrimental to the hosts, did not

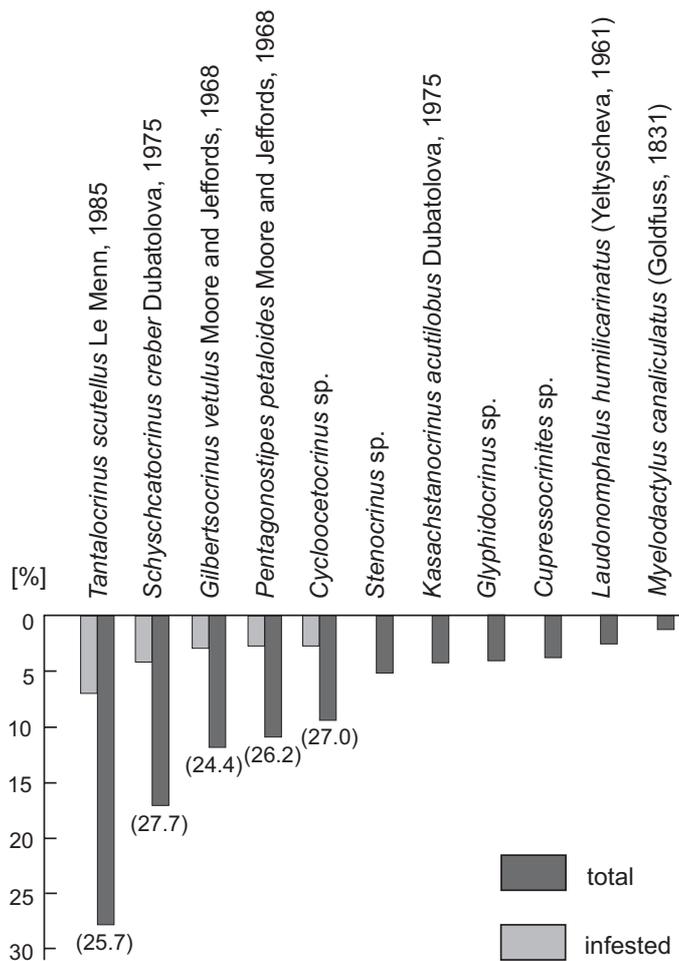


Fig. 6. Frequency distribution of crinoid stem-based taxa from the Skaly Beds (upper part of complex XVII, *Tortodus kockelianus* Zone), Skaly village, Holy Cross Mountains. Infestation rates (%) in brackets.

hinder their activities, and that the biotic interaction is best described as commensalism.

All epibionts discussed here may be regarded as commensals, even a *Phosphannulus* animal was basically an epibiotic suspension feeder, although some species of *Phosphannulus* could have been parasites on crinoids (Welch 1976; Werle et al. 1984).

Among epibionts discussed here only productid brachiopod *Poloniproductus*?, tabulate coral *Favosites*, rugose coral *Adradosia*? and *Phosphannulus*? may be regarded as obligate commensals that most probably existed solely on crinoids. Though *Phosphannulus* animals have been found on a variety of shelled organisms (Müller et al. 1974), the associated galls are known only from crinoids. The remaining epibionts examined here were facultative commensals utilizing other host substrata opportunistically, including, among others, sponges, corals, mollusks, bryozoans, brachiopods, arthropods (e.g., see Taylor and Wilson 2003).

The distribution of epibionts on hosts can be non-random, which means that distinct epibiont species settled selectively

on a given host. Host-selectivity by pit-forming epibionts among some Silurian crinoids was reported by Brett (1978). The examined material comprises ninety-five occurrences of 19 epibiont species distributed on 77 among all 378 collected crinoid stem fragments, constituting an average infestation rate of 20.4%. Among 29 crinoid stem-based taxa documented in the Eifelian–Givetian crinoid assemblage *Tantalocrinus–Gilbertsocrinus* from the Holy Cross Mountains (Gluchowski 1993), only 11 occur in complex XVII of the Skaly Beds. The presence of epibionts has been reported only on the five most common crinoid species (Fig. 6), which may indicate a random choice of hosts by epibionts. Correlation between the frequency of potential crinoid hosts and the total number of fouling epibionts seems to confirm this. Less numerous crinoid hosts were settled by fewer epibionts, while the most common, *Tantalocrinus scutellus*, was in-

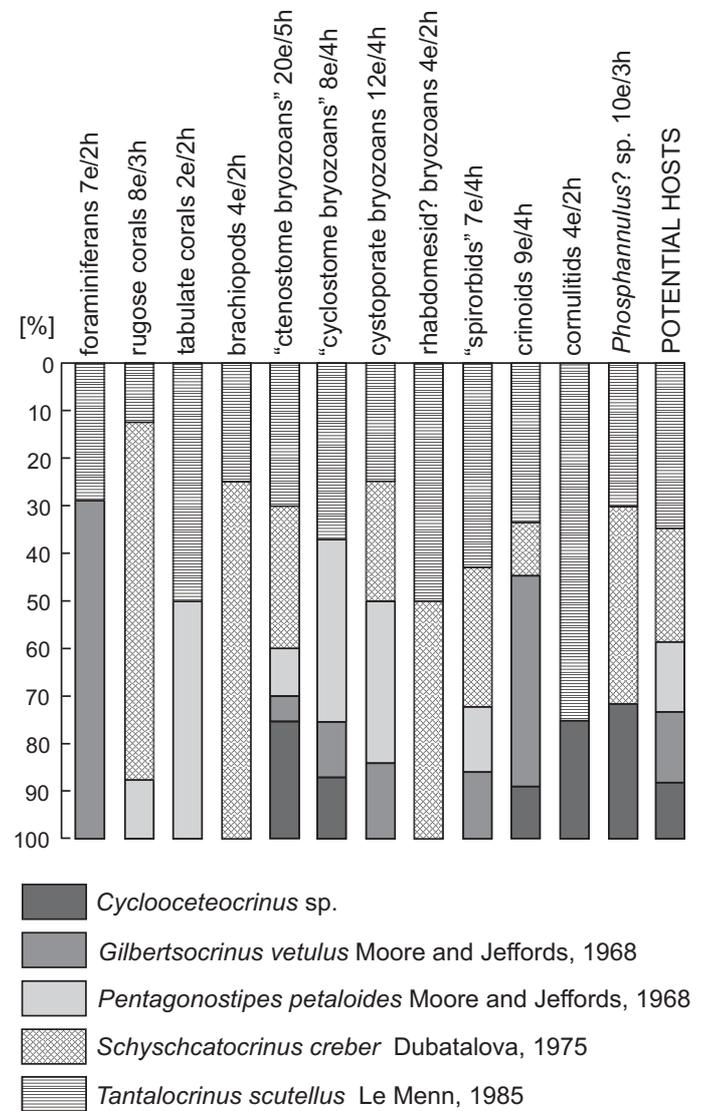


Fig. 7. Frequency distribution of epibionts on the crinoid host species from the Skaly Beds (upper part of complex XVII, *Tortodus kockelianus* Zone), Skaly village, Holy Cross Mountains; e, number of epibionts; h, number of hosts.

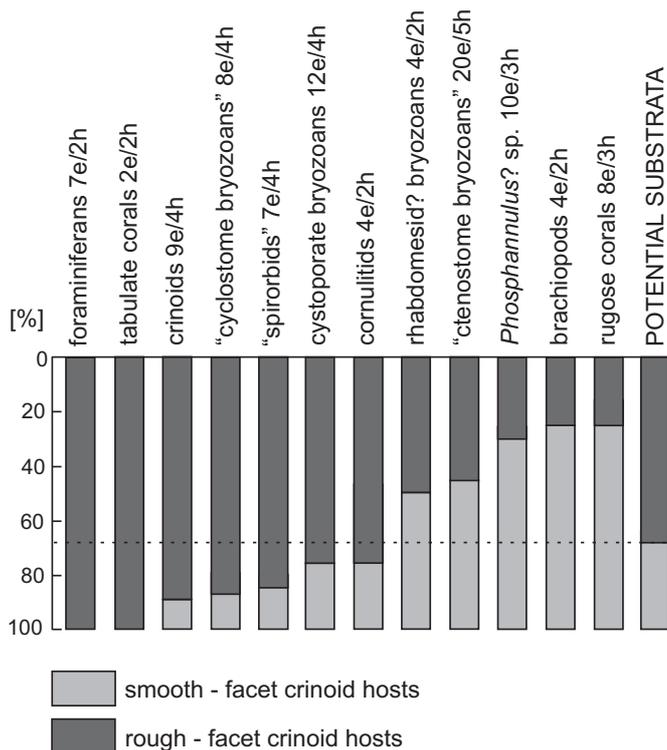


Fig. 8. Frequency distribution of epibionts on the smooth- and rough-facet crinoid hosts from the Skaly Beds (upper part of complex XVII, *Tortodus kockelianus* Zone), Skaly village, Holy Cross Mountains; frequency of potential rough-facet substrata (66.2%) marked by dashed line; e, number of epibionts; h, number of hosts.

festated most frequently and, by approximately 85% of epibiont species. Moreover, infestation rates of different crinoid species are nearly constant, falling in a narrow range from 24.4 to 27.7% (Fig. 6). Nevertheless, the distribution on crinoids of at least some of these epibionts seems to be non-random and selective (see Table 1). Also analysis of the frequency of the epibionts of higher rank, may be used to examine the host-epibiont relationships (Fig. 7). When percent-frequency of an epibiont on a hosts significantly exceeds the percent-frequency of the potential hosts, epibiont specificity may be indicated.

All epibionts reported here are generally rare, and the very low number of occurrences result in large percentages that may be misleading. However, inferences may be more reliable in epibionts with a large number of occurrences. For example, *Cyclooctocrinus* sp. could have been the preferred host of "ctenostome bryozoans" and *Phosphannulus?*, whereas cystoporate bryozoans, mainly *Eridopora orbiculata*, and "cyclostome bryozoans" (*Hederella*) display likely preferences for *Pentagonostipes petaloides*. Foraminiferans and crinoids of unknown affinities probably preferred *Gilbertsocrinus vetulus* as a host. *Schyschcatocrinus creber* could have been the favored hosts for rugose corals (*Adradosia?*). On the other hand, however, no preference by epibionts is indicated by *Tantalocrinus scutellus*. The host-selectivity by epibionts was tested statistically using procedure of binomial distribution. All these

supposed claims of selectivity are statistically robust and can be confirmed at 99% Confidence Interval (CI).

Crinoid columnals seem to be more prone sites of infestation by epibionts than crowns, probably because the stalk epidermis is thinner (Feldman and Brett 1998). Also, the settlement of epibionts on the surface of crinoids requires mutual biochemical compatibility of the epidermal tissues. Secretions of some host epidermis could have inhibited settlement of epibionts, while some crinoids could have produced substances that attracted epibionts (see Brett 1978). It is plausible that attracting epibionts to settle could have been a method of antipredatory camouflage, and thus a defensive adaptation of crinoids. An equally important factor in substratum selection for the majority of epibionts may have been surface texture (see Powers and Ausich 1990).

Among the infested upper Eifelian crinoid columnals from Skaly Beds basically two types of substratum surface can be distinguished. One of them characterizes crinoids having stems composed of columnals of uniform diameter with straight, smooth and non-ornamented lateral sides (herein called smooth-facet crinoid hosts). Generally, this type of substratum is found on columnals of *Cyclooctocrinus* sp. and *Schyschcatocrinus creber*. The second type of substratum is found among crinoids having heteromorphic stems composed of differentiated columnals with more or less convex lateral sides covered with tubercles or keels (herein called rough-facet crinoid hosts). This type of substratum was found on columnals of *Tantalocrinus scutellus*, *Pentagonostipes petaloides*, as well as *Gilbertsocrinus vetulus*. The crenulated articular facets of columnals should be also included into this type of substratum surface (see Fig. 5H, J). Generally, epibionts are distributed in proportion to the available substrata. Rough-facet hosts constitute 66.2% of potential substrata and 62.1% of all epibionts are found associated with these. However, in some cases, the percent-frequency of a particular epibiont on hosts deviates significantly from the percent-frequency of the potential host, suggesting preferential recruitment (Fig. 8). While conclusions based on so few occurrences may be tenuous, looking at more numerous occurrences of some host-epibiont associations are more robust. Delicate colonies of "ctenostome bryozoans", as well as rugose corals and *Phosphannulus?* enveloped by stereomic overgrowths seem to have recruited preferentially onto smooth-facet crinoid hosts. On the other hand, rough-facet crinoids may have been the favored hosts for foraminiferans probably providing them with inter-columnal furrows for a domicile, and for colonies of "cyclostome bryozoans" and cystoporate bryozoans, relatively larger in size, as well as for crinoids, ensuring them better attachment. The recruitment of remaining epibionts seem to be relatively random. All these epibiont preferences were tested statistically using procedure of binomial distribution. The supposed claims of preferential recruitment epibionts onto smooth-facet crinoid substrata are statistically robust (99% CI), whereas for rough-facet crinoid substrata they are less significant and can be confirmed only at 90% CI.

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