

## Echinoderms

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With a few exceptions, relatively little has been written on Gotland echinoderms. In 1878 Angelin's monumental work on Gotland crinoids, the *Iconographia Crinoideorum in stratis Sueciae siluricis fossilium*, was published, containing descriptions of 173 species referred to 42 genera. Prior to this only 13 species from Gotland had been described or mentioned by various authors. Angelin did not live to issue his own work, which may explain some of its shortcomings; the diagnoses of the various species are very brief, and there are no descriptions; the illustrations are often misleading, the specimens either being heavily restored (not always correctly) or composed of several individuals, in some cases even belonging to different genera. Thus, despite the great importance of the *Iconographia* it soon became evident that the Gotland crinoids were greatly in need of thorough revision. Wachsmuth & Springer (1879, 1881, 1885, 1886, 1888) revised some of the species, but did not have access to Angelin's material. Bather (1893) published a review of the Crinoidea Inadunata and Springer (1920) described the Crinoidea Flexibilia. Liljevall drew the excellent illustrations of Gotland material for both Bather and Springer.

In the past 50 years research on Gotland crinoids has been mainly on specialized groups or species (e.g. Ubags 1956a, b, 1958), and many groups are still in need of a thorough revision, particularly the Crinoidea Camerata.

Literature relating to other echinoderm classes is even more sparse. Reference should be made on the following publications. Cystoidea: Angelin 1878; Regnéll 1945. Asteroidea: Spencer 1918 (a short note on *Urasterella* without illustration); Wienberg Rasmussen 1952. Echinoidea: Regnéll 1956. Cyclocystoidea: Regnéll 1945. Edrioasteroidea: Aurivillius 1892; Regnéll 1945.

### Annotated faunal list

#### *Crinoidea*

Camerata (see Fig. 67).

*Calliocrinus* sp., *Eucalyptocrinites* n. sp. *a* (17.1 m), *E.* sp. (tegmina plate, 24.1 m), *Dimerocrinites* sp. *a* (complete crown), *Melocrinitidae* n. gen. *a*, n. sp. *a* (probably 39 specimens including complete crowns).

#### Inadunata

*Myelodactylus convolutus* Hall (13.1 m), *Myelodactylus* sp. (dissociated col-

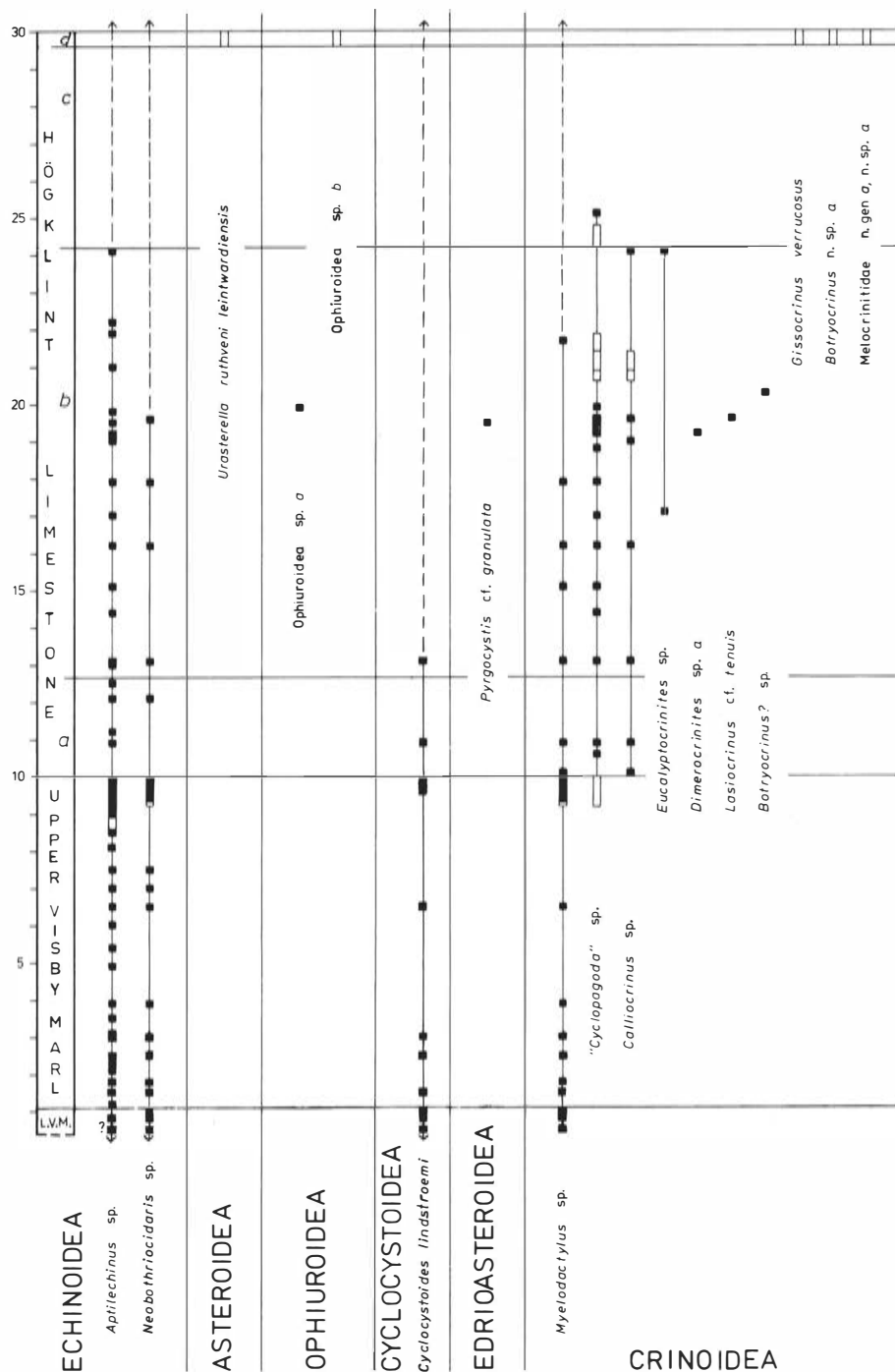


Fig. 67.

umnals), *Lasiocrinus* cf. *tenuis* (Bather) (4 calices), *Botryocrinus* n. sp. *a*, *B.*? sp., *Gissocrinus verrucosus* Bather (11 specimens), *Euspirocrinus spiralis* Angelin (Höglint *b*, exact level unknown), Crinoidea Inadunata sp. *a* (20.2–20.25 m).

Order indet.

*Cyclopagoda* sp. (columnals).

*Edrioasteroidea*

*Pyrgocystis* cf. *granulata* Aurivillius.

*Cyclocystoidea*

*Cyclocystoides lindstroemi* Regnéll.

*Ophiuroidea*

Ophiuroidea sp. *a* (one small disc), Ophiuroidea sp. *b* (Regnéll 1973, Fig. 4).

*Asteroidea*

*Urasterella ruthveni leintwardinensis* (Spencer) (Fig. 68A).

*Echinoidea*

*Aptilechinus* sp. (Fig. 68D–H), *Neobothriocidaris* sp. (Fig. 68B–C).

*Holothuroidea*

Sieve-plates (6 specimens) and hexaradiate wheels (2 specimens), all in the “*Pterygotus*” Beds.

An attempt was made to estimate the probable total number of crinoid species in various lithostratigraphical units, based on all available material from the section including dissociated columnals. According to these rough estimates the number of crinoid species is 9 in the Upper Visby Marl, 7 in Höglint *a*, 21 in Höglint *b*, 3 in Höglint *c*, and 6 in Höglint *d*. These figures are certainly not representative of the taxonomic diversity of the crinoid fauna in the section. In the Upper Visby Marl and in Höglint *a* the sampling is clearly inadequate in respect of columnals. Höglint *c* lacks marly intercalations and richly fossiliferous bedding planes which in other divisions have yielded the bulk of crinoid specimens.

## Remarks

Although echinoderm remains occur everywhere through the Silurian sequence of Gotland, the difficulties in determining what genera or species or how many individuals they represent are almost insurmountable. Completely preserved echinoderms are extremely rare. On death their skeletons generally disintegrate rapidly through tissue decay. Although crinoid columnals are the echinoderm ossicles most frequently found, virtually nothing is known of their taxonomy. Attempts have been made in the Soviet Union and U.S.A. (e.g. Moore, Jeffords & Miller 1968; Moore & Jeffords 1968) to devise a classification and nomenclature based on isolated crinoid ossicles, but they have not yet gained widespread use outside the Soviet Union.

Crinoid taxonomy is based almost exclusively on morphology of the cup, the stem being known in only a few cases. Therefore, even though individual ossicles show distinct characters in size, articulation pattern, ornamentation or relative size and shape of the axial canal, it is not possible at present to assign them to species. Since columnal size and morphology frequently vary with position in the stem, figures in the annotated faunal list given for number of crinoid species are at best uncertain.

Dissociated crinoid columnals occur frequently in marl samples and on slabs from the Vattenfallet section, but it is quite obvious that the sampling has been inadequate. Intentions to erect a log and crinoid succession based on isolated columnals were abandoned as being unrealistic. There is no doubt, however, that crinoids formed a very important component of the benthic communities. One type of stem fragment (resembling the *Cyclopagoda* of Moore & Jeffords 1968, Pl. 10:1–2, 5–6) is so characteristic, that it has been included in the log. Generic affinity is not known.

Very few crinoid genera can be identified from dissociated ossicles alone. *Myelodactylus* is the only genus in the Vattenfallet section that can be identified with confidence on the basis of disarticulated columnals. *Callioocrinus* is recognized by its characteristic spines, normally attached to the calyx, while *Eucalyptocrinites* may be identified by the peculiar, elongated plates attached to the tegmen. The identification of the additional crinoid species mentioned in the faunal list is based primarily on morphology of calyx plates or brachials, and secondarily on characteristic columnals.

In Cyclocystoidea the stout submarginal plates are frequently preserved and easily identified (Regnéll 1945:216–219, Pl. 15:7–8, Textfigs. 28–29; Kesling 1966, Figs. 150:4–6, 151:3–4).

Echinoidea are represented only by dissociated plates and spines. However, the plates are so characteristic that there can be no doubt as to their generic affinity. *Aptilechinus* Kier (1973) is represented by ambulacral (Fig. 68D–F; cf. Kier 1973, Pl. 82:3, 5, Textfig. 1) and interambulacral plates (Fig. 68G–H; cf.

Kier 1973, Pls. 81, 83:1–2), the latter being found most frequently. *Neobothriocidaris* Paul (1967) is an Upper Ordovician echinoid not previously found in Silurian deposits. In the Vattenfallet material it is represented by poriferous plates (Fig. 68B–C; cf. Paul 1967, Textfigs. 2, 6). *Neobothriocidaris* plates are less common than those of *Aptilechinus*.

The Vattenfallet plates differ in surface ornament and details of morphology from the type species of *Aptilechinus* (= *A. caledonensis* Kier, 1973) and from *Neobothriocidaris* (= *N. peculiaris* and *N. minor* Paul, 1967) to such an extent, that they should probably be regarded as new species. This problem will be considered in a separate paper. In the log they are referred to as *Aptilechinus* sp. and *Neobothriocidaris* sp., respectively. Both were small species, at most 2.5 cm in diameter.

Echinoid spines are fairly common. They are small, longitudinally striated and slightly tapering towards the apex (Regnéll 1956, Pl. III:2). Both *Aptilechinus* (Kier 1973, Pl. 81–83) and *Neobothriocidaris* have spines of this type, making it impossible to refer the isolated specimens to a genus.

The “*Pterygotus*” Beds (Höglint *d*) are remarkable because of the fine preservation of the fossils; in some cases almost complete specimens are found, such as the starfish *Urasterella ruthveni leintwardinensis* (Fig. 68A; Spencer 1918:147), the ophiuroid figured by Regnéll (1973, Fig. 4; this specimen is unique among ophiuroids in having a small anal tube), and the crinoid *Gissocrinus verrucosus* (Bather 1893:172, Pl. 10:377–378; Franzén 1977, Fig. 6A). Several crowns of Melocrinitidae display arms and pinnules down to the finest detail.

The holothurian-type sclerites from the “*Pterygotus*” Beds are silicified, fairly poorly preserved and have been obtained from etched residues. Sieve-plates and wheels may also be present in ophiocistioids (Haude & Langenstrassen 1976). Although ophiocistioid teeth occur in younger strata on Gotland, they have not been found at Vattenfallet.

## Ecological notes

Crinoids are mucociliary suspension feeders, adjusting their arms with the aboral side towards the current to form a filtration fan (Magnus 1963; Breimer 1969; Macurda & Meyer 1974; Breimer & Webster 1975). The tube feet bordering the ambulacral grooves produce mucus to entangle food particles which are then sent down the food-grooves towards the mouth by ciliary movements.

Palaeozoic crinoids were, with few exceptions, sessile, attached to the substrate by various types of holdfasts (Bather 1900: 106–107, 133–136; Ubaghs 1953: 720–722; Franzén 1977). In the Vattenfallet section, crinoid holdfasts have been obtained only from the “*Pterygotus*” Beds. In these beds wide-

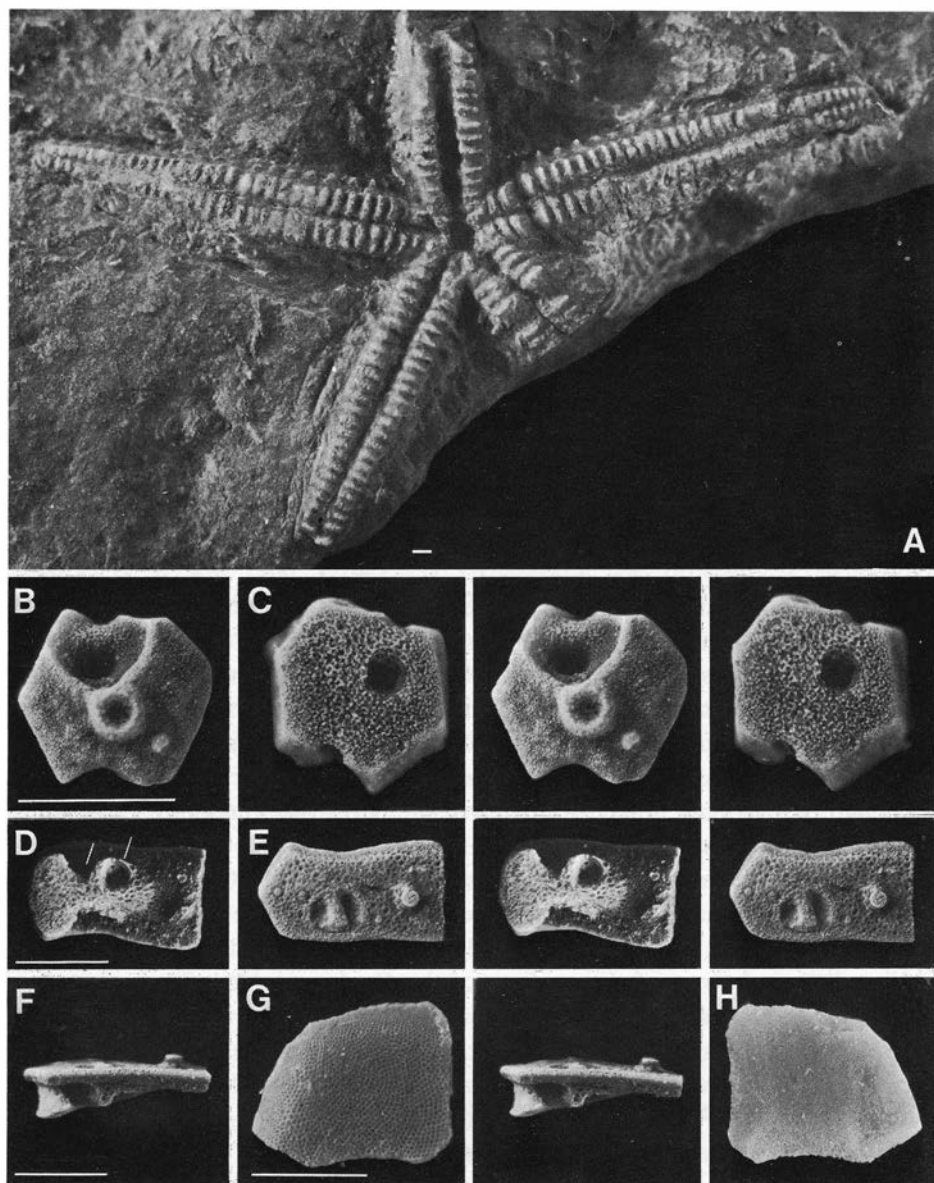


Fig. 68. A. *Urasterella ruthveni leintwardinensis*. Geological Museum, Dept. Invertebrate Palaeontology, University of Copenhagen. No. 231;  $\times 2.5$ . B. Stereo pair of external side of poriferous plate of *Neobothriocidaris* sp. (cf. Paul 1967, textfig. 2); Vattenfallet, 9.5–9.6 m. Swedish Museum of Natural History (SMNH) Ec. 27616. C. Same specimen, internal view. D. Stereo pair of ambulacral plate of *Aptilechinus* sp., internal view. Thin white lines indicate position of pore openings (cf. Kier 1973, Pl. 82:4–5, textfig. 1); Vattenfallet, 9.2–10.0 m. SMNH Ec. 27615. E. Same specimen, external view (cf. Kier 1973, Pl. 82:3). F. Same specimen from oral side. G. Interambulacral plate of *Aptilechinus* sp. viewed from the coarse-meshed side of plate (cf. Kier 1973, Pl. 80:1–2); Vattenfallet, 6.5 m. SMNH Ec. 27613. H. Same specimen, viewed from fine-meshed side. Length of scale bars: 1 mm.

spread "roots" of branching radicular cirri occur, characteristic of soft substrates (Franzén 1977, Figs. 2E, 6A). At least some of them belong to *Gissocrinus verrucosus* Bather (Franzén 1977, Fig. 6A). Crinoids of the families Melocrinitidae and Botryocrinidae also occur in the "*Pterygotus*" Beds and were probably equipped with the same type of holdfasts. Fragments of cirri and dissociated cirrals have also been found at lower levels, but cannot be referred to individual genera or species because of their generalized appearance and lack of diagnostic features.

Some crinoids attach to hard objects, e.g., various shells, tabulate colonies or stromatoporoids, by cemented calcite discs (Franzén 1977, Fig. 2A). Attachment discs and other holdfasts occur in various Upper Visby and Högklint localities but, surprisingly, have not been found at Vattenfallet. There may be several reasons for this. One is simply that they have been missed due to inadequate sampling. The other is that the crinoids may have lived mainly in adjacent areas, particularly in association with reefs, where their holdfasts remained while their dissociated skeletons were deposited some distance away.

The physiological properties of the echinoderm skeleton, e.g., its porosity and lightness, permit transportation to some extent without particular abrasion of the individual ossicles. This makes it difficult to assess with certainty an allochthonous or autochthonous origin of the crinoid remains. Several genera, among them *Gissocrinus*, have been found only in fine-grained deposits while, e.g., *Calliocrinus* and *Eucalyptocrinites* on Gotland are known mainly from reefs and reef flank deposits. Remains of the latter two genera at Vattenfallet might indicate transport from the vicinity of nearby reefs.

*Myelodactylus* was probably eleutherozoic (Bather 1900: 146–147; Ehrenberg 1923). Columnals are not uncommon in the Vattenfallet material and have been obtained from fine-grained as well as coarse-grained deposits.

Very little is known of the ecology of the Cyclocystoidea. They were flat, disc-shaped animals, apparently without columns. They are generally classed as Pelmatozoa, which suggests an attached mode of life similar to that of edrioasteroids. However, some authors advocate a free-living mode of life (Nicols 1969: 109, Fig. 18C; Kesling 1966: U203).

Edrioasteroids were sessile suspension feeders using their tube feet for trapping plankton or organic particles from the surrounding sea water in a manner similar to that of the Crinoidea. Only one specimen has been found at Vattenfallet. Individuals of this genus probably lived anchored in soft mud or ooze (Regnéll 1966: U158).

Echinoids, ophiocistioids (?), holothurians (?), asteroids, and ophiuroids were all eleutherozoic epifaunal components of the Vattenfallet benthic communities. Echinoids were by far the most common (judged from the remains found). They were probably epifaunal browsers, scraping vegetable matter and

attached organisms off vegetation and substrate with their jaws, or ingesting the topmost layer of the substrate for organic matter (Moore 1966: 77–78). In the Vattenfallet section they are common in the fine-grained sediments but fairly rare in coarse-grained material.

Ophiocistioids were free-living echinoderms probably feeding on detritus (Fell & Pawson 1966:10). It is doubtful, however, if this group is truly represented in the Vattenfallet material.

Recent holothurians have three food resources: plankton, detritus and the organic contents of mud and ooze which are collected with the tentacles or ingested while the animal is burrowing through the substrate (Pawson 1966: 65). These methods of feeding were probably also typical of fossil species. Very few holothurian remains have been found in the Vattenfallet material, and it has not been possible to assess how the animals lived.

Recent asteroids can be ciliary feeders, scavengers or facultative predators, but the majority studied are active predators (Feder & Møller Christensen 1966:96). Palaeozoic asteroids had developed all these types of feeding (Spencer & Wright 1966: U24–U25). *Urasterella* was probably a carnivore, preying on benthic organisms.

Some recent ophiuroids are plankton feeders which either lie buried in the mud with the tips of their arms extended into the water or attach to corals, sponges, etc. by two or three arms while waving the others through the water to trap plankton with their sticky tube feet. Some prey on organisms in or on the substrate while others climb corals and browse on the polyps. Most ophiuroids, however, appear to be scavengers, feeding on whatever organic matter they can find (Fell 1966: 132–134). Which of these modes of life is applicable to the Vattenfallet ophiuroids is not possible to decide.

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