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Silurian of Gotland, Sweden

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STROMATOPOROID AND CORAL REEFS IN THE BALTIC SEA

The Swedish Island of Gotland is well known to vacationers, many of whom are also fossil collectors. They cannot miss the numerous fragments of crinoid stems spread over much of this picturesque island. The Silurian beds of Gotland, a succession of 13 stratigraphic units, range in age from Late Llandovery to Late Ludlow (around 420 million years before present) and reach a thickness of about 500 m (Fig. 96). The oldest rocks, the Lower Visby beds, are along the northwestern coast. They are composed of soft, bluish grey mudstones and contain nodules, lenses and layers of marly limestones. To the south and southeast, successively younger strata, including three elongated reef belts separated by flat mudstone areas, were laid down in a shallowing sea. The limestone reefs, predominantly composed of stromatoporoids, are surrounded by bedded, bioclastic sediments consisting largely of crinoid remains. Reefs started to grow as bioherms during the Early Wenlockian, the time of deposition of the Högklint beds. Shallowing seas and a reduced supply of terrigenous material favoured the growth of extensive reefs, which are exposed in cliffs on the northwestern coast of the island. The lower part of a typical Högklint reef was initiated by tabulate corals growing as a patch reef in deeper water on cross-bedded lenses of crinoid remains. Further reef growth was dominated by laminar stromatoporoids and topped by dome-shaped stromatoporoids, leading to a pronounced vertical profile of the structure (Kershaw 1993). These bioherms are comparable to modern reefs, their build-up being the result of the interplay between sedimentation and the growth of organisms. Reef growth continued into later Wenlock and Ludlow times. In contrast, the Hemse reefs in southeastern Gotland have low profiles and are composed entirely of stromatoporoids that grew in shallow water. Their substrate was again formed by remains of crinoids, deposited presumably by storms. The Sundre Beds, the youngest unit on Gotland, comprise mostly limestones, including stromatoporoid bioherms. Collecting is unrewarding in these beds; only two species of crinoid have been identified. Gotland contains the richest crinoid assemblage from the Silurian, with 193 species assigned to 55 genera. Most of the well-preserved fossils were found during earlier quarrying. In the few quarries still open today, manual work has been replaced by mechanical operations, making fossil collection unproductive. Ubaghs (1956a,b, 1958) devoted three papers to camerates. The study of all Gotland crinoids has been brought up to modern standards by Christina Franzén (1983).

REEF FLANKS COLONIZED BY CRINOIDS

Crinoid populations vary to some extent in the stratigraphic sequence of Gotland. The Visby Beds (Late

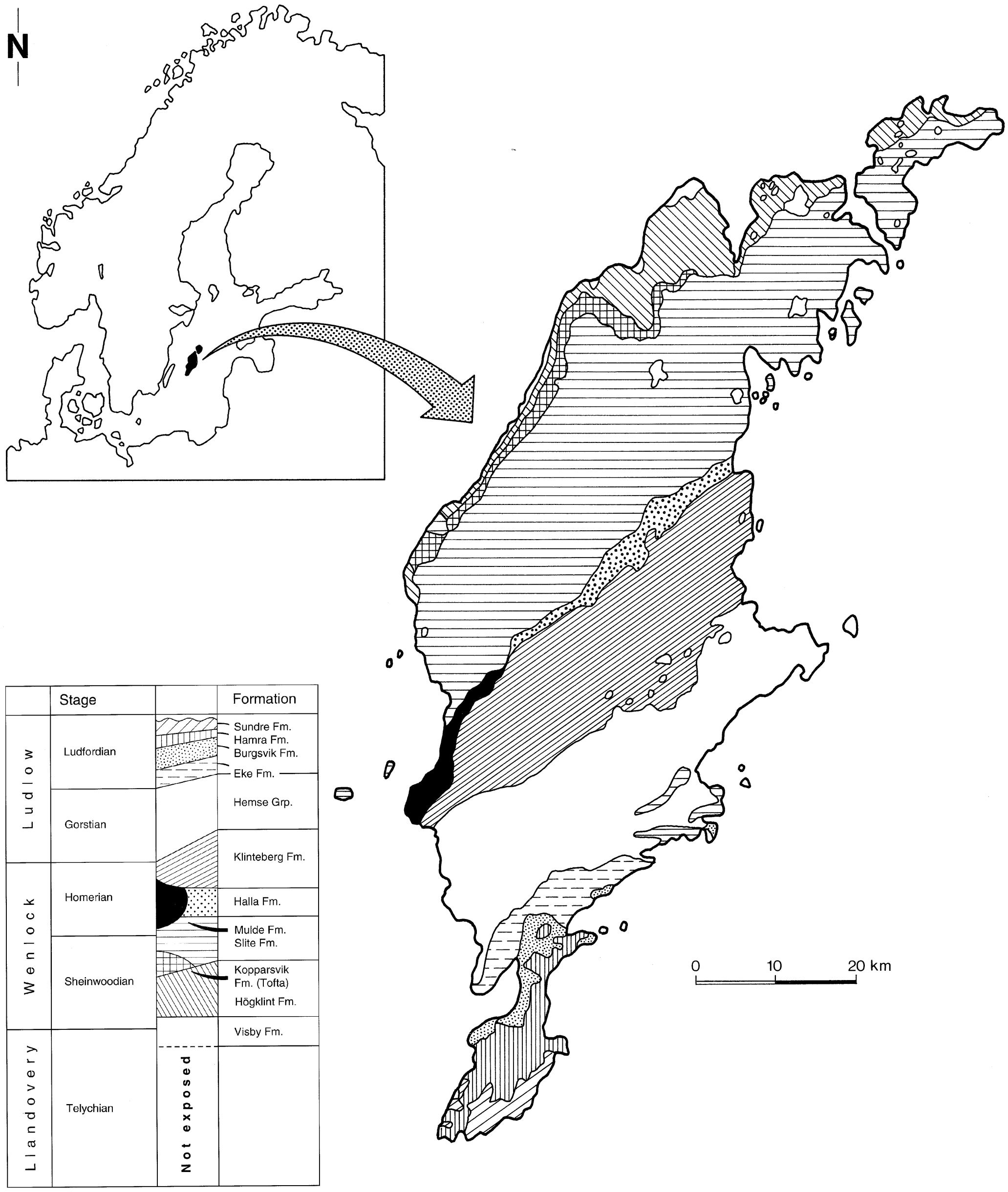


Fig. 96. Geological map and stratigraphy of Gotland. (Redrawn from Kershaw 1993.)

Llandoverian and Early Wenlockian), deposited in deeper waters at the beginning of the sequence, have yielded mostly disparids and cladids. Camerates are absent from these marlstone deposits. The Visby Bed crinoids, like those of other soft-bottom communities in deeper water, are rather small and delicate. They were anchored with branched, root-like cirri (radices) or attached with discs to hard objects on the bottom. Most of these crinoids are well preserved, but disarticulated, indicating slow sedimentation rates. The Visby marlstones were followed by the Högklint and Slite Beds. The flanks of Högklint reefs contain an abundant and diverse crinoid fauna. On the neighbouring sea floor, conditions for crinoids were less favourable. In stratified limestones and marly limestones, which were deposited at greater distances from the reefs, remains of crinoids are scattered through the sediment together with other marine invertebrates, such as brachiopods, bryozoans, corals and rare molluscs (Manten 1971). The Högklint reefs are highly fossiliferous, and well-preserved cups and even crowns occur in marly pockets within the reef structure. However, holdfasts, many of them in growth position, are considerably more common than crowns or cups. The crinoid fauna is dominated by the camerates *Calliocrinus*, *Dimerocrinites* and *Eucalyptocrinites*. In the stratigraphically higher Slite Beds, the crinoid fauna is still more diverse. Intact crowns with part of the stem occur in coarse-grained bioclastic debris composed of worn fragments of bryozoans, corals and stromatoporoids (Fig. 97). In these sediments, as in the higher strata, *Eucalyptocrinites* and the cladids *Crotalocrinites* and *Enallocrinus* are the dominant genera (for a complete listing, see Franzén 1983). Crinoid diversity diminishes in the succeeding beds. However, the best-known crinoid assemblage from Gotland is the spectacular 'När slab' (Fig. 98), a bioclastic limestone lens from the Ludlovian Eke Beds.

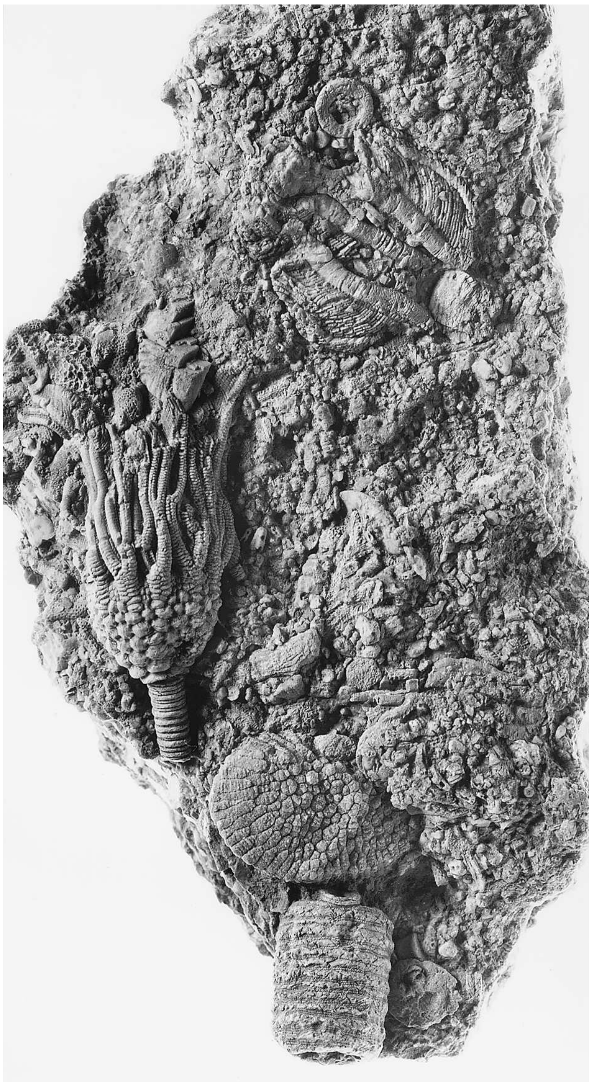


Fig. 97. Coarse bioclastic limestone of Slite Beds (Wenlock) from Follingbo with crown of the monobathrid camerate *Abacocrinus tessellatus* (left). Naturhistoriska Riksmuseet, Stockholm. (Courtesy C. Franzén.) ×1.

The Silurian rocks of Gotland were deposited in a shallow epicontinental sea with a water depth never exceeding 200 m. Crinoidal limestones formed at depths of from 5 to 50 m. Dense stands of crinoids must have covered the flanks of the larger reefs where the crinoids grew on their own debris. These faunas are dominated by camerates, but the two cladid genera mentioned earlier are also commonly found. Turbulence was high in such surroundings, leading, as a rule, to rapid disarticulation. In rare cases, more or less complete specimens were also preserved.

On a surface of approximately 1 by 1.2 m, the När slab contains 260 crinoid specimens belonging to 4 species (Franzén 1982). With the exception of three specimens of the flexible *Haereticotaxocrinus asper*, they are all monobathrid camerates. The crinoids are current-oriented and lie on a coarse-grained bed of sorted skeletal gravel made up mostly of worn *Coenites* (tabulate coral) fragments, but also with crinoid ossicles. Other fossils are absent. The crowns and stems were originally covered by *Coenites* fragments and probably also by silt. This layer, which was removed during preparation, appears to have been deposited by a storm; it rapidly buried the crinoids and protected them from scavengers. The absence of holdfasts, the orientation of the crinoids and the occurrence of crowns torn from the stem indicate that the crinoids were transported for a short distance by the current before burial. The two *Carpocrinus* species include juvenile and adult individuals, but *Desmidocrinus* specimens are adults; the reason for this difference is unknown. Stem length varies in the crinoids found on the När slab; in the camerates *Carpocrinus* and *Desmidocrinus* the stem was about 20 cm, whereas the longest stem from the flexible *Haereticotaxocrinus* measures 65 cm. The different lengths of the stems indicate that the animals were tiered, collecting food at different levels above the sea floor.

A WEEPING WILLOW CRINOID

Among the camerates from Gotland, *Barrandeocrinus sceptrum* is the most unusual. This crinoid, which is restricted to the Slite Beds, was redescribed by Ubaghs

Fig. 98. *(On facing page)* Part of upper surface of the När slab with the conspicuous, multi-armed monobathrid camerate *Desmidocrinus pentadactylus* (bottom of photo) and the smaller 10-armed monobathrids *Carpocrinus angelini* (with bowl-shaped calyx, stout stem and arms, which are widest in the middle) and *Carpocrinus petilus* (with conical calyx, slender stem and arms). The two long stems belong to the flexible *Haereticotaxocrinus asper* (crowns outside picture). *Coenites* fragments that originally covered the slab were partly removed to expose the crinoids. Eke Beds (Ludlow). (Naturhistoriska Riksmuseet, Stockholm; courtesy C. Franzén.) ×0.9.

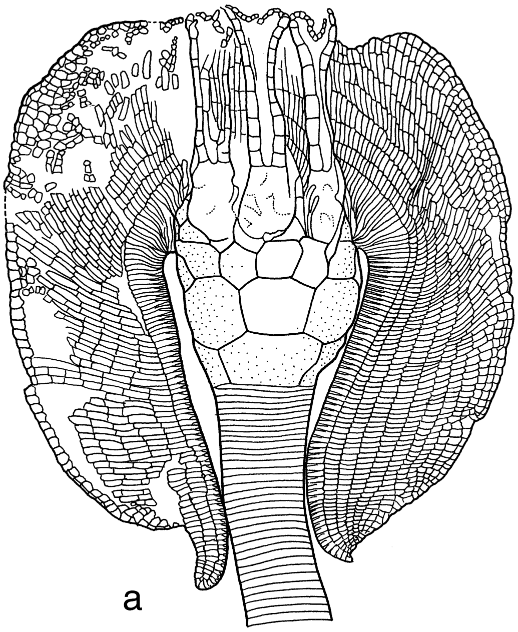
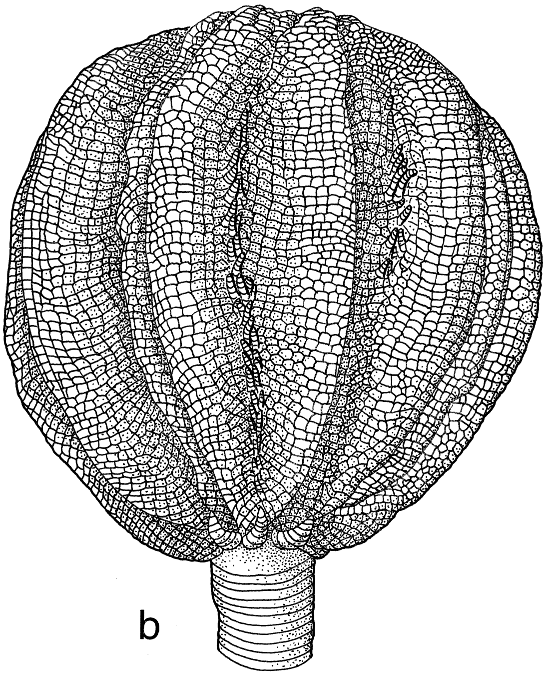
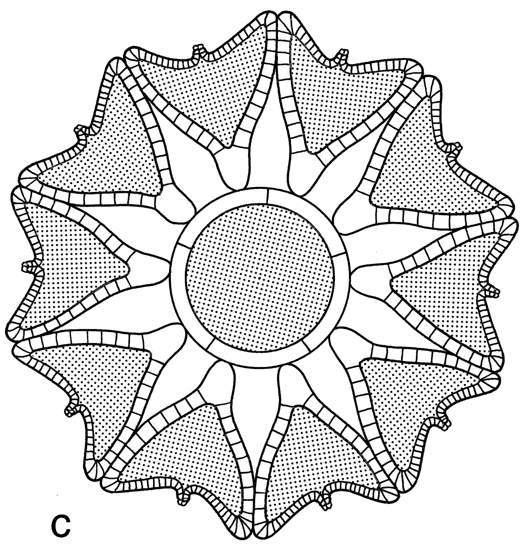


Fig. 99. *Barrandeocrinus sceptrum*. Slite Beds (Wenlock), Follingbo. (a) Partly dissected crown (original in the Naturhistoriska Riksmuseet, Stockholm) with three of the pendent arms removed to show the structure of arms, cup and uppermost stem; (b) reconstructed crown in lateral view, with recumbent arms, their pavement of pinnules completely covering the cup; (c) cross section of crown showing cup surrounded by the 10 brachial chambers, formed by rigid portions of the pinnules. (Redrawn from Ubaghs 1953.) ×2.





(1956a). Its 10 arms are permanently pendent and enfolded, giving the crown a hood-like appearance. The very short brachials carry close-set pinnules that are folded at midlength and attached together to form an external protective pavement enclosing 10 brachial chambers (Fig. 99). The most distal pinnules are free and would have allowed sea water to enter the chambers. It is thought that the water was expelled through a common aperture at the tip of the crown. This structure suggests that *Barrandeocrinus* may have created its own current for feeding. The longest preserved stem, measuring 14 cm, is composed of massive, circular columnals. Towards the distal end, radices were attached, as proved by the corresponding scars, and would have fixed the animal to the bottom or to some part of the reef structure. *Barrandeocrinus sceptrum* may have lived in sheltered pockets within the reef where currents were sluggish (Franzén 1983). It is not surprising that the reefs comprised a number of ecological niches, offering possibilities for crinoids with widely different morphologies and ways of feeding.

MYELODACTYLUS: A COIL ON THE BOTTOM

Of special interest are remains of the disparid *Myelodactylus* (formerly *Herpetocrinus*) from the Lower Visby Beds, discussed by Donovan and Franzén-Bengtson (1988). The stem of these crinoids is composed of bilateral columnals and has a double curvature, enabling the crown to fold back against the stem (Fig. 100). The small and slender crown is concealed by two rows of radices (radicular cirri) that are attached to the margins of the inner surface in the distal part of the coiled stem. Many theories have been put forward for the lifestyle of these peculiar crinoids. They have been thought to be free-moving, swimming, pelagic, similar to the ammonites with their coiled shells, or to have used their radicular cirri as legs for crawling or swimming. Based on the microstructure of the columnals, Donovan and Franzén-Bengtson (1988) could find no evidence in *Myelodactylus fletcheri* for the presence of contractile fibres, which would have allowed active movements of the stem. In addition, the shape of the columnals indicates coiling for life. Therefore, these authors suggested that M. *fletcheri* lived flat on its side on the sea floor.

Fig. 100. *Myelodactylus fletcheri*, lateral view of crown and column. Note long cirri in the middle (upper) part of the stem, partly covering the crown; the double row of radicular cirri is clearly visible on the distal part of the stem (right). Slite beds (Wenlock), Burgen in Endre. (Naturhistoriska Riksmuseet, Stockholm; from Bather 1893.) ×2.

The lower fringe of radicular cirri protected the crown from direct contact with the sediment, and the upper radices formed a covering roof. The curvature of the animal would have given it a fairly stable position on an unconsolidated substrate, preventing sinking into the mud. The crown could not have been raised, so that this crinoid would have had the unique properties necessary to feed with a closed crown enveloped by fringes of cirri. Feeding is thought to have been made possible by close contact with a surface layer of nutrients on the bottom, including the absorption of dissolved organic matter through the epidermis. In the absence of a modern analogue, this theory is purely conjectural.

IMPORTANT COLLECTION IN SWEDEN

Naturhistoriska Riksmuseet, Section for Paleozoology, Stockholm. The spectacular När slab is exhibited at the entrance.