CONULARIID MICROFOSSILS FROM THE SILURIAN LOWER VISBY BEDS OF GOTLAND, SWEDEN

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ABSTRACT. A conulariid fauna from the Lower Visby Beds (uppermost Llandovery–lowermost Wenlock) is described, based on microscopic exoskeletal parts found in limestones and marls prepared using standard laboratory techniques for phosphatic fossils. Although not a single complete conulariid specimen has ever been found in the unit, conulariids were evidently abundant during the deposition of the Lower Visby Beds, as inferred from the microscopic fragments. So far, five species have been identified: *Conularia sarae* sp. nov., *C. wimani* sp. nov., *C.* sp. a, *Metaconularia aspersa*, and *Pseudoconularia* aff. *scalaris*. The microscopic fragments exhibit considerable external morphological variation. They can be sorted into four discernible morphological groups, and their position in the exoskeleton can be identified. Thus, more or less complete reconstructions of the exoskeletons have been made on species unknown prior to this investigation. Characters used in species descriptions based on intact specimens are summarized and compared with characters used for microscopic fragments. The conclusion is that the general ornamentation of the exoskeleton is the most useful character in species descriptions. Moreover, microscopic fragments are not only as easily identifiable as intact specimens, but due to the fact that a larger quantity of material is obtainable, the study of microscopic fragments also gives a far better picture of the individual variation, ontogenetic development, geographical range and the stratigraphical range of conulariid species. Finally, some existing morphological terminology is modified and some new terms are introduced.

CONULARIIDS are an extinct group of marine invertebrates with a four-sided, apatitic, steeply pyramidal exoskeleton. The group has been assigned to a range of different phyla, e.g. Mollusca (e.g. Lindström 1884; Holm 1893; Slater 1907), Cnidaria (e.g. Kiderlen 1937; Moore and Harrington 1956a; Werner 1966, 1967, 1973; Bischoff 1978; Van Iten 1991a) and Chordata (Steul 1984). Babcock and Feldmann (1986a, 1986b) proposed placing conulariids in an independent phylum. This general inconsistency of conulariid systematic placement depends mainly on the morphological uniqueness of the conulariid exoskeleton which lacks distinct common characters with other groups.

Though many important papers have been published on conulariids, the group has been largely neglected compared with other Palaeozoic invertebrates. Their range is somewhat uncertain but was previously regarded as Middle Cambrian to Lower Triassic (Moore and Harrington 1956b). A better-supported stratigraphical range, Lower Ordovician to Lower Triassic, was presented by Babcock (1991). Conulariid-like fossils have also been reported from the earliest Cambrian of Yunnan Province, South China (Qian Yi and Bengtson 1989). Only a few papers, including Lindström (1884), Holm (1893), Wiman (1895), Slater (1907), Bouček (1928) and Bischoff (1978), have dealt with Silurian conulariids.

The general opinion that conulariids are rare fossils is mainly because nearly all studies are based on intact specimens. Except for a few localities e.g. in the Devonian of Bolivia (Babcock *et al.* 1987a, 1987b), and in some late Ordovician beds in the USA (Van Iten 1991b), intact specimens are often a curiosity. Accordingly, it has been very difficult to map the stratigraphical and geographical occurrences of most taxa. The rarity of intact conulariids is caused by the extremely fragile nature of their exoskeletons which broke down shortly after the death of the animal (Babcock and

Feldmann 1986c; Feldmann and Babcock 1986). The exoskeletal fragments were then scattered over the bottom by currents, wave oscillation and bioturbation. Thus, intact conulariid exoskeletons are, with a few known exceptions (see, for example, Van Iten 1991b), normally found only in units that record exceptional preservational circumstances (Babcock and Feldmann 1986a; Feldmann and Babcock 1986). Furthermore, collections of intact specimens are strongly biased towards those genera and species that had the most robust exoskeletons. However, microscopical exoskeletal fragments are preserved in many strata, often in very large numbers. For example, in the Lower Visby Beds on Gotland no complete conulariid specimens have ever been recorded, although conulariid fragments are abundant in the microfossil fauna. The present study is based on about 10000 microscopic exoskeletal fragments.

Conulariids were extracted from marls and various limestones using the same laboratory techniques as for conodonts, fish scales, polychaetes, secondarily phosphatized fossils, etc. These methods have also been applied in the study of conulariids by Bischoff (1973, 1978) and Brood (1979).

In this paper, no attempt is made to solve higher taxonomic relationships, nor are the biological affinities of conulariids discussed. Such discussions may be found in works by, among others, Slater (1907), Kiderlen (1937), Moore and Harrington (1956a), Werner (1966, 1967, 1973), Kozłowski (1968), Bischoff (1978), Steul (1984), Babcock and Feldmann (1986a), Babcock (1991) and Van Iten (1991a).

GEOLOGICAL SETTING

The Silurian of Gotland exhibits a complex variety of shallow marine, mainly carbonate, deposits formed in a tropical environment. The strata were mapped by Hede (for a brief English summary, see Hede 1960), who recognized thirteen major units. The various lithologies found on the island include biohermal limestone, stratified limestone, marlstone, oolite and siltstone (see Hede 1921, 1925, 1940; Laufeld 1974a).

The Lower Visby Beds are the oldest exposed unit found on Gotland, outcropping along the northwest coast in a 55 km long narrow strip (Text-fig. 1). The lithologies consist of alternating calcareous marlstones and
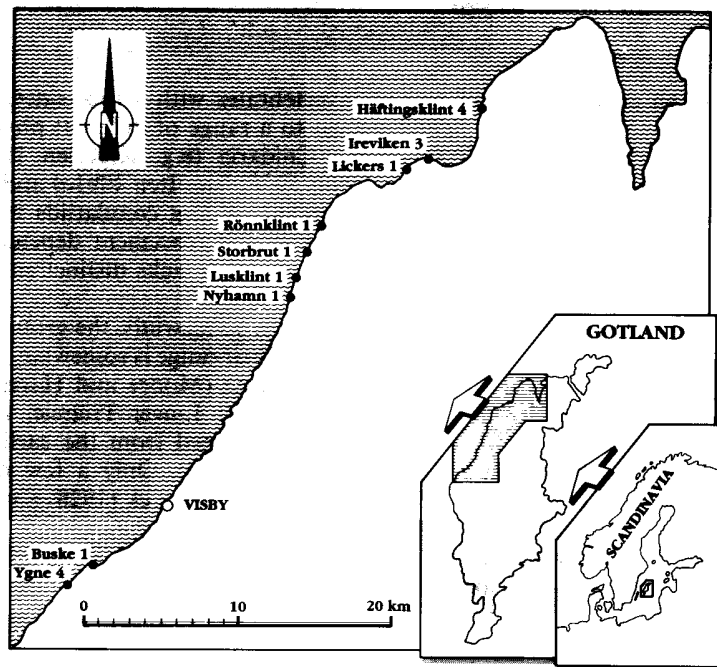
TEXT-FIG. 1. Map of the north-western part of Gotland showing the sampled localities.

argillaceous limestones (Hede 1921, 1925, 1940, 1960; Laufeld 1974a; Sandford and Moscher 1985). The thickness of the sampled sequence is about 20 m at Ireviken 3, including samples collected in submarine exposures (L. Jeppsson, pers. comm.).

A detailed conodont stratigraphy has made it possible to subdivide the Lower Visby Beds into units a to e, where unit a reaches above sea level in a small area only (L. Jeppsson, pers. comm.). Three well-defined bentonite horizons are present in the formation (Spjeldnaes 1959). The uppermost bentonite (about 10 cm thick) has been dated using K-Ar at 430,5 ± 3,0 Ma (Odin et al. 1986). The Lower Visby Beds belong to the *Pterospathodus amorphognathoides* conodont zone (Jeppsson 1983, 1987a; Odin et al. 1984). At the type locality for the base of the Wenlock, this zone spans the Llandovery–Wenlock boundary (Aldridge 1975). Thus, the boundary between Llandovery and Wenlock is to be drawn within the Lower Visby Beds, probably in the upper part (Jeppsson 1983; Odin et al. 1984).

The boundary between the Lower Visby Beds and the Upper Visby Beds was defined by differences in the macrofauna by Hede (1925). According to Laufeld (1974a) the boundary cannot be defined on lithology because the changes are gradual. However, Jeppsson (1983) has noted that the marls in the units weather differently: the Lower Visby Beds produce a sticky clay whereas the Upper Visby Beds weather to dust.

LOCALITIES AND METHODS

Localities

A total of 43 samples, weighing 291·8 kg, were collected from nine localities (Text-fig. 1). Three additional samples (25·5 kg) from the Upper Visby Beds were also briefly studied. All samples have been productive, i.e. no sample has been found to be barren of conulariids.

In addition to the Lower Visby Beds, many of the following localities expose the Upper Visby Beds and Högklint Beds. Only the studied Lower Visby Beds (abbreviated L.V.B.) are mentioned. References marked with an asterisk (*) contain a more complete description of the locality. After each sample number the total weight of dissolved rock, and the exact sample-level is listed. The sample-levels are given 'above reference level' (a.r.l.) or 'below reference level' (b.r.l.). All samples are listed in stratigraphical order. The conodont faunas in the samples will be described in a forthcoming paper by Lennart Jeppsson. The sampled localities are shown in Text-figure 1.

BUSKE 1. L.V.B. unit e (and unit d in the submarine part of the exposure). References: Laufeld 1974a, 1974b*; Larsson 1979; Odin et al. 1984. The reference level described by Laufeld (1974b) is imprecise, therefore an auxiliary reference level has been selected: the best visible bentonite horizon about 1·2 m below the level abundant in large, solitary rugose corals. Sample: Unit d: G88-804FJ (12·5 kg), 2·36–2·31 m below auxiliary reference level.

HÄFTINGSKLINT 4. L.V.B. unit d–e (unit c in submarine exposure). References: Hede 1933; Bergman 1989; Fredholm 1990; Jeppsson in prep.* Samples: Unit c: G84-38LJ (4·2 kg), 0·75 m below sea level. Unit d: G84-39LJ (8·5 kg), 0·05–0·00 m below sea level, G88-625LJ (6·7 kg), 0·58–0·62 m above sea level.

IREVIKEN 3. L.V.B. unit b–e (unit a in submarine exposure). References: Laufeld 1974a, 1974b*; Larsson 1979; Odin et al. 1984*, 1986; Bergman 1989. Samples: Unit a: G86-129LJ (5·3 kg), 15·38 m b.r.l. Unit b: G85-37LJ (3·7 kg), 1·95–2·05 b.r.l.; G82-1LJ (0·6 kg), 0·15–0·08 m b.r.l.; G88-802FJ (20·3 kg), 0–0·12 m b.r.l.; G82-2LJ (0·5 kg), 0·02–0·15 m a.r.l.; G88-803FJ (13·4 kg), 0·69–0·87 m a.r.l.; G82-3LJ (0·5 kg), 0·85–0·90 m a.r.l. Unit c: G81-5LJ (0·6 kg), 1·10 m a.r.l.; G82-6LJ (0·6 kg), 2·16–2·26 m a.r.l.; G82-6LJ (4·3 kg), 2·36–2·46 m a.r.l.; G85-36aLJ (10·7 kg), 2·36–2·46 m a.r.l. Unit d: G89-723LJ (16·2 kg), 2·89–2·94 m a.r.l.; G89-725LJ (13·8 kg), 3·53–3·61 m a.r.l.; G89-722LJ (11·0 kg), 4·11–4·15 m a.r.l. Unit e: G86-145LJ (5.0 kg), 4·27 m a.r.l.

LICKERS 1. L.V.B. unit b–c. Reference: Bergman 1989*. Sample: Unit b: G81-10LJ (0·5 kg), 0·1 m above sea level.

LUSKLINT 1. L.V.B. unit b–e (unit a in submarine exposure). Reference: Jeppsson in prep.* Samples: Unit a: G88-613LJ (9·4 kg), 8·98–8·83 m b.r.l.; G89-715LJ (5·4 kg), 8·56 m b.r.l.; G89-716LJ (4·4 kg), 8·28 m b.r.l. Unit b: G89-701LJ (7·7 kg), 7·68–7·58 m b.r.l.; G89-702LJ (6·2 kg), 7·18–7·13 m b.r.l.; G89-703LJ (4·8 kg), 6·48–6·33 m b.r.l.; G89-704LJ (7·4 kg), 5·91–5·76 m b.r.l.; G89-705LJ (6·3 kg), 5·26–5·09 m b.r.l.; G89-706LJ (6·2 kg), 4·67–4·63 m b.r.l.; G89-707LJ (6·1 kg), 3·97–3·82 m b.r.l.; G89-708LJ (6·8 kg), 3·45–3·33 m b.r.l.; G89-709LJ (11·7 kg), 2·75–2·70 m b.r.l.; G89-710LJ (5·6 kg), 2·10–1·97 m b.r.l.; G89-711LJ (2·8 kg), 1·50–1·35 m b.r.l.; G89-712LJ (4·3 kg), 1·08–0·97 m b.r.l.; G89-713LJ (9·6 kg), 0·53–0·43 m b.r.l.; G89-714LJ (6·5 kg), 0·26–0·15 m b.r.l.
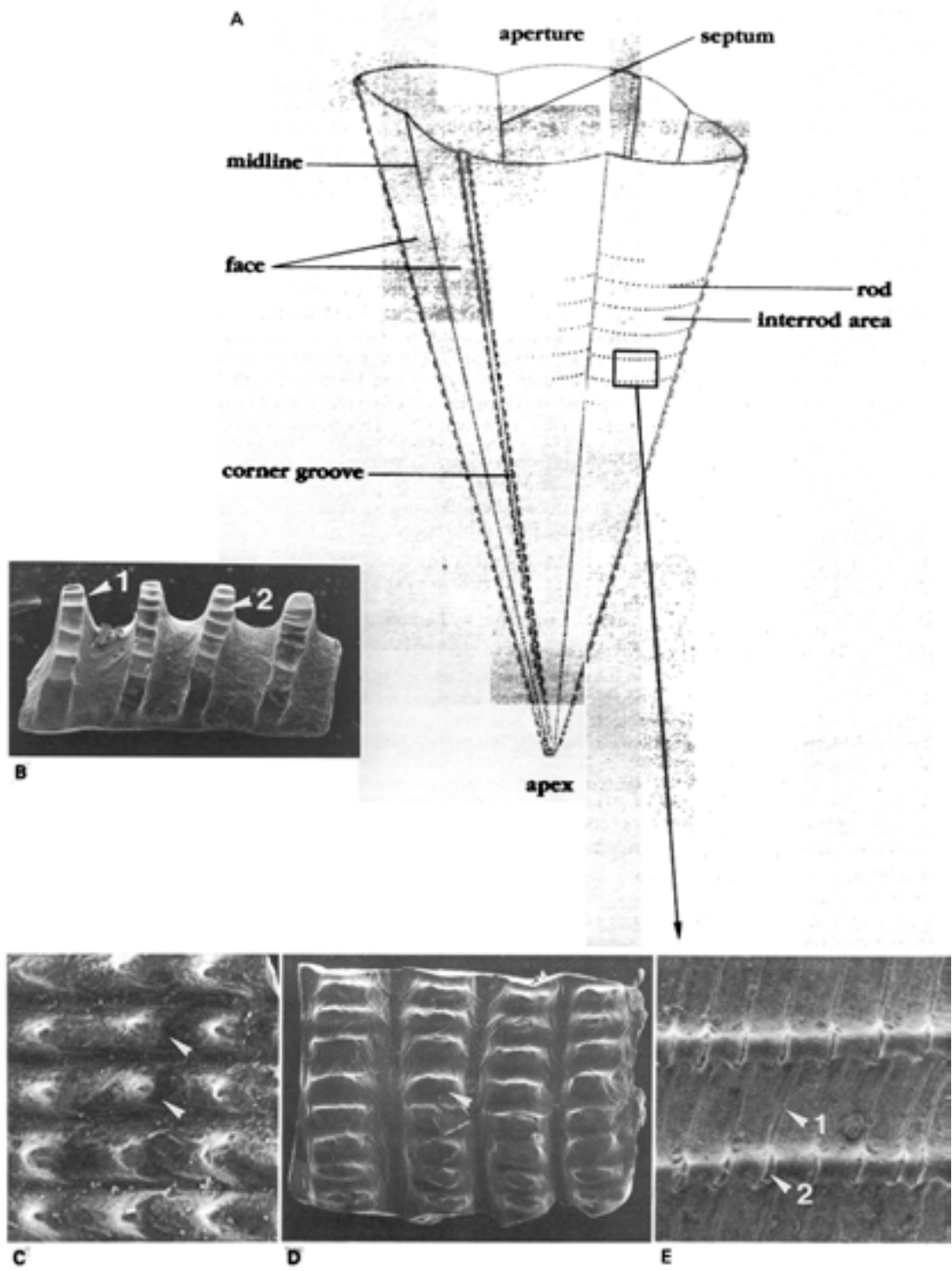
NYHAMN 1. L.V.B. unit *b*. References: Hede 1940; Martinsson 1962; Laufeld 1974*a*, 1974*b**; Larsson 1979; Bergman 1989. Sample: unit *b*: G81-28LJ (0·5 kg), 1·4 m above sea level.

RÖNNKLINT 1. L.V.B. unit *b–e*. References: Jeppsson 1983*; Ramsköld 1984; Fredholm 1990. Sample: Unit *b*: G81-11LJ (0·5 kg), at sea level.

STORBRUT 1. L.V.B. unit *b–e*. Reference: Jeppsson in prep.* Samples: Unit *b*: G88-810FJ (9·8 kg), 0·00–0·12 m b.r.l. Unit *c*: G88-633LJ (14·0 kg), 1·42–1·54 m a.r.l. Unit *d*: G88-632LJ (11·2 kg), 2·62–2·65 m a.r.l.

YGNE 4. L.V.B. unit *d–e* (unit *c* in submarine exposure). Reference: Jeppsson in prep.* Sample: Unit *e*: G85-6bLJ (5·7 kg), 1·58–1·60 m a.r.l.

Methods

Samples of between 0·5 and 20 kg were dissolved in buffered acid generally following the recommendations given by Jeppsson *et al.* (1985), although the methods have been modified and improved and new methods have been developed since the publication of that article. Petroleum–ether treatment and other methods were used to disintegrate the clay (see Pokorny 1963; Swift 1987). Other methods to reduce the residues included magnetic separation to remove iron-rich minerals as pyrite, and treatment with high density solutions to concentrate the phosphatic material. In pyrite-rich samples it is often necessary to oxidize the Fe^{2+} in the pyrite to Fe^{3+} prior to magnetic separation to attain satisfactory results. This was done by soaking the sample residue in natriumhypoklorite for a maximum of one week, although it is desirable to expose the sample in the solution for as short a time as possible to avoid damage of the fossil surfaces and to avoid undesirable red staining of the fossils. The insoluble residues were washed through a 1·0 mm and a 63 μm sieve. All fractions above 63 μm were stored for future reference. The samples were originally prepared to obtain conodonts; the only technique used specifically to obtain the conulariid material was picking fragments from dried residues. The picking-technique was described by Barnes *et al.* (1987). The identifiable parts of the conulariid fragments are generally larger than 125 μm. In those cases where conulariids were not extracted at the same time as conodonts, a sieve with a 125 μm mesh was used to reduce picking time.

For a more detailed description of methodology see Jeppsson *et al.* (1985), Jeppsson and Fredholm (1987), Jeppsson (1987*b*), Fredholm (1988), Bergman (1989) and references given in these papers.

TERMINOLOGY

An understanding of conulariid morphology has often been confounded by the use of poorly-defined terms or multiple meanings for the same term. A modern morphological terminology has recently been introduced by Babcock and Feldmann (1986*a*, 1986*b*). The terminology presented by these authors is based on the assumption that the conulariid exoskeleton is made of two discrete components: rods and integument. There is insufficient evidence either presented by these authors or present in my material to verify this construction. The terms introduced by Babcock and Feldmann are, however, in most cases well chosen and function well as purely descriptive terms. Therefore the terms used here are to a large extent the same as those defined by Babcock and Feldmann.

The definitions of some of the terms listed below have been slightly modified based on more complete information from the study of microscopic exoskeletal parts. It has also been necessary to introduce some new terms for features found on microscopic parts. These, and other mentioned terms, are illustrated in Text-figure 2.

corner groove — longitudinal invagination of exoskeleton connecting points where pairs of rods from adjacent faces cross near the marginal terminations of these rods

TEXT-FIG. 2. Schematic drawing of a conulariid to illustrate terms mentioned in the text. A, previously described terms used on intact specimens (see Babcock and Feldmann 1986*a*, 1986*b*). B, rod from *Conularia sarae*; LO 4575t, sample G88-708LJ; in adapical view possessing four rod-crests with serration (arrow 1 points to a rod-crest; arrow 2 points to the serration). C, exoskeletal fragment from *Metaconularia aspersa* with nodes (same specimen as in Pl. 4, fig. 7); LO 4576t. D, exoskeletal fragment from *Pseudoconularia* aff. *scalaris*; LO 4930t; possessing four parallel ridges with tightly spaced, elongate nodes (one is arrowed). E, details from a larger exoskeletal fragment from *C. sarae*; the holotype, LO 4931T (same specimen as in Pl. 2, figs 3–5); with two rods, rod-crests and adapertural crests (arrow 1 points to an adapertural crest; arrow 2 points to a rod-crest); the aperture is upwards in the picture; note the serration on the adapical sides of the rod-crests.

face — one of four sides of the exoskeleton crossed by rods; a face is delimited by the aperture, the apex and two corner grooves

interrod area — open region located between two rods

midline — longitudinal line connecting points where either two adjacent rods on a face meet, or central to the facial terminations of each pair of adjacent rods if they do not meet; the midline can be expressed as either a thin groove, a raised line or simply a narrow, unornamented longitudinal line

node (modified term) — minute, subcircular to elongated, raised surface on a rod, ridge or directly on the mineralized, exoskeletal surface

ridge (modified term) — coarse, raised line crossing a face from corner groove to the midline; the cross section is rectangular to circular (see Pl. 4, fig. 3), sometimes also more or less triangular; differs from a rod in being a more massive structure, and in lacking rod crests.

rod — narrow, elongated structure that is semicircular in cross section; it is thickened near the marginal termination, and tapers very gradually to a blunt point at the facial termination

New or replaced terms. Terms that should be abandoned were summarized by Babcock and Feldmann (1986*b*). However, there are two terms defined by Babcock and Feldmann (1986*a*, 1986*b*) that should be changed to avoid unnecessary confusion — the terms are adapertural spine and adapical spine. The structures in question are not consistent with what is generally understood by the word spine. Instead, they are more like short ridges, or crests, pointing in an adapical or adapertural direction. Accordingly, it is proposed that these terms be replaced as follows: adapertural spine is changed to adapertural crest, and adapical spine to adapical crest.

The term septum was also abandoned by Babcock and Feldmann (1986*b*) because of its previous application for at least three different structures. It has been used for longitudinal walls interior of the midlines and the corner grooves (Wiman 1895; Kiderlen 1937), and for a convex wall found on the apical point of the exoskeleton (Slater 1907). Later, Babcock *et al.* (1987*a*) used the term carina for a longitudinal wall on the interior side of the midline. The term carina was also used by Bischoff (1978), but he restricted the term to longitudinal walls interior of the corner grooves. Septa was applied to longitudinal walls interior of the midline. Accordingly, it is recommended that carina is restricted to longitudinal walls interior of the corner grooves and septum to longitudinal walls of different shape and structure (see Bischoff 1978, p. 284) interior of the midline.

adapertural crest — crest projecting from, or near, the adapertural side of a rod, in the direction of the aperture

adapical crest — crest projecting from the side of a rod, in the direction of the apex

carinae — longitudinal wall extending inward from the corner groove, crossing the interior side of a corner from apex to aperture

node-width — the width of a node measured at its base; the diameter measured on a subcircular node

ridge-width — the width of a ridge measured at its base

rod-crest — raised line crossing a rod, usually at a right angle; continuing into the interrod areas as an adapertural or adapical crest

rod-width — the width of a rod measured at its base

septum — longitudinal wall of different shape and structure (see Bischoff 1978, p. 284), extending inward from the midline, crossing the interior side of a face from apex towards the aperture

serra — serration found on the adapical side of a rod-crest

CONULARIIDS AS MICROFOSSILS

Many fossil groups are difficult or nearly impossible to find as complete specimens. One reason is the lack of preserved soft parts in combination with poorly mineralized endo- and/or exoskeletons such as in conodonts, polychaetes and neoselachians. Another reason is the fragility of the exoskeletons of such animals as crinoids, echinoderms, fish and conulariids. All of these groups require extreme sedimentary environments, with the proper taphonomic conditions, to be preserved as intact fossils. Many species associated with high, or even moderate, energy environments will probably never be found as complete specimens. Thus, it is often necessary to include fragmentary specimens in a study in order to get a complete picture of the fauna.

As noted by previous authors (Kozłowski 1968; Bischoff 1973, 1978; Brood 1979; Babcock and Feldmann 1986*b*; Feldmann and Babcock 1986), conulariid fragments are usually found in rock units sampled for microfossils by insoluble residue techniques. I am convinced that most samples collected for conodonts, or other phosphatic or phosphatized fossils, and treated accordingly,

contain conulariid fragments. Diagnostic features can be obtained from these fragmentary specimens alone, although restudy of taxa based on intact specimens usually is needed to supplement the descriptions of these taxa. This must be done in order to avoid the introduction of a parallel nomenclature, or parataxonomy, based only on microscopic characters. A total of seventy-four intact specimens (housed in the Swedish Museum of Natural History, Stockholm) from younger strata on Gotland have been studied and compared with the microscopic fragments. The exoskeletal surfaces on these more or less intact specimens are mostly in a poor state of preservation, leaving only limited information on the original ornamentation. The poor preservation could be the result of taphonomic processes, although I suspect rough preparation techniques. Consequently, the material on which this study is based reveals details of the morphology which are possibly overlooked in studies based on intact specimens only.

The Lower Visby Beds represent a moderately bioturbated (Riding and Watts 1991) sedimentary sequence unfavourable for preserving fragile conulariids intact. Though no complete conulariid specimen has yet been found in the formation, conulariids were evidently abundant during the deposition of the Lower Visby Beds. Studied samples have revealed conulariid fragments at an average of about 30 identifiable pieces per kg of dissolved rock. The lower part of the collected section (unit a) contains even higher frequencies, up to about 200 identifiable pieces per kg. The material consists of single rods of different lengths and larger exoskeletal pieces containing several parallel rods attached to the mineralized interrod areas. The exoskeletal pieces found represent all parts of an intact specimen, except for the apex, the reasons for which are unknown. Such fragments occur, however, in my collections from younger strata on Gotland.

There are roughly four morphologically distinguishable types of exoskeletal fragments located in different positions on a face (Text-fig. 3). These fragments are as follows:
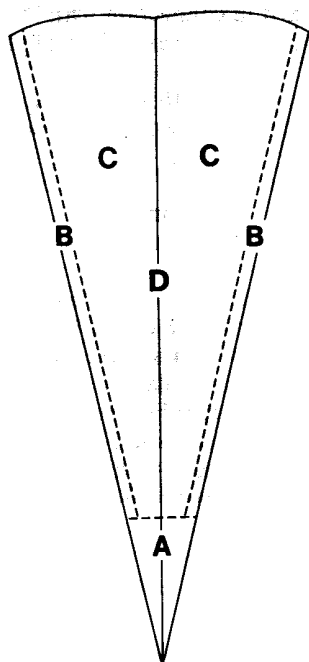
TEXT-FIG. 3. Schematic drawing of a single conulariid face. See text for explanation.

A. larger exoskeletal parts with rods connected vertically by mineralized interrod areas. These large mineralized exoskeletal fragments were probably located near the apex, reaching an unknown distance adaperaturally (Text-fig. 3). The position of the dotted line in Text-figure 3, which delimits

the area where fragments of this kind are found, probably depends both on ontogeny and species. The drawing is based on *Conularia sarae* sp. nov.

B. coarse, slightly curved rods. These rods are sometimes found connected with mineralized interrod areas, but these are generally broken and not preserved. Rods in this position form the longitudinal 'channel' of the corner groove. The morphological characters found on these rods are mostly poor species indicators, and should not be used alone for species-level identification. Species within a genus often possess strikingly similar rods in this position (compare Pl. 1, figs 2, 5 with Pl. 3, figs 5–6).

C. exoskeletal fragments in this position are mostly found as single rods with no longitudinal connection between them in the interrod areas. In a few pieces where small parts of mineralized interrod areas occur, the interrod areas are connected with the rods on the adapertural side only.

D. exoskeletal fragments formed on or in connection with the midline. The material generally consists of exoskeletal fragments with adjacent rods meeting along either a thin groove, or simply a narrow, unornamented longitudinal line. These fragments usually occur in low frequencies in the samples but are of great value when comparing microscopic fragments with complete specimens. The manner in which rods 'articulate' along the midline has been used as a diagnostic feature at the species level (Babcock and Feldmann 1986a, 1986b).

Together these four different 'types' of exoskeletal pieces represent most of the characters found on a complete conulariid specimen. Intermediate forms between these types are often found. Samples usually contain fairly large numbers of intermediate rods in the transition between positions B and C. Typically in these rods, the rod-crests are incompletely developed in shape and height close to position B, whereas in position C they are mostly well developed and long. Also obvious is the transition, when moving from corner groove horizontally towards the midline, from short rod-crests to rods that gradually possess long rod-crests. It is most likely that intermediate forms also occur between positions A and D, represented by pieces formed in connection with the midline. Thus the dotted line in Text-figure 3 should probably consist of two convex (adapically) lines connected with the midline and ending in the corner grooves.

There are also conulariids that lack rods in their exoskeletons (conulariids with nodes in the ornamentation) and these cannot be placed within the morphological types described above; they are described in detail below.

Diagnostic characters. Through the history of conulariid research, different morphological characters have been considered important in characterizing species. In early publications, authors often used the relative number of rods and ridges together with rod characteristics, as distinguishing features (e.g. Holm 1893). Holm (1893) partly based his four groups of conulariid species on rod construction. Sinclair (1952) described new species and genera using the structure of the corner grooves in addition to previously used characters. He stated that the ornamented surface of the exoskeleton was a diagnostic feature of minor use. The way in which rods articulate along the midline was used as an important character by Babcock and Feldmann (1986a, 1986b). They found four different rod articulation styles useful for species-level determinations. Babcock and Feldmann (1986a, 1986b) and Babcock *et al.* (1987a, 1987b) used the following characters to distinguish different conulariid genera and species: (1) relative spacing of rods; (2) relative proportion of rods that abut at the midline to those that alternate; (3) apical angles; (4) presence or absence of nodes and spines; and (5) spacing of nodes and spines. The relative spacing of rods should not be interpreted as a measure of the number of rods on a fixed length interval, but as the rod-width in proportion to the length of the interrod areas. This is important to remember because close to the apex the number of rods per cm is often greater than close to the aperture.

The lengths of the adapertural crests or the adapical crests are usually useful characters for specific identification. To recognize and separate these characters in fragmented material, the direction of the aperture must be identified. This is generally possible if large exoskeletal pieces (with at least four parallel rods) are available, because rods generally become wider in the apertural direction and thinner near the apex. If only single rods, or even single rod-crests, are present, their

symmetry can be used. Rods with nodes and rod-crests are together regularly asymmetrical in cross-section. The species of *Conularia* studied have rods with cross-sections shaped roughly like a breaking oscillatory wave, with the rod-crests forming the wave crest. The 'wave crest' points in the direction of the apex (Pl. 2, fig. 5). In *Metaconularia* the exoskeletal ornamentation sometimes includes almost symmetrical transverse and longitudinal rows of regularly arranged nodes. It is thus difficult to determine the apertural direction, from the four different directions that are possible, based on exoskeletal fragments only. Sometimes, however, the transverse rows can be identified because the nodes may occur with a regular spacing whereas longitudinal rows lack any regularity in spacing of the nodes. Thus, two of the four hypothetical directions of the aperture can be excluded.

When using microscopic exoskeletal fragments, all characters mentioned above were used. In addition, many other characters are present which often are neglected, or at least rarely mentioned, in the study of macroscopic specimens. I have found that the following observations preferably should be included in species-level identifications: (1) presence of rods and ridges on the exoskeleton; (2) general shape of rods and ridges; (3) presence of rod-crests and nodes; (4) general shape of rod-crests and nodes; (5) structures found on the interrod areas (mainly adapertural and adapical crests); (6) length of adapertural crests; (7) character of the midline; and (8) rod articulation along the midline. Additional characters that could be useful for identification are: the width of rod-crest, the relative spacing of rod-crests and nodes, rod- and ridge-width, and the relative spacing of rods and ridges.

Apical angle is a character of minor use when identifying species on fragmented material because most conulariids show allometric growth. The apices represent the juvenile parts of the conulariid and the apical angle of a juvenile can differ substantially from that of an adult.

It is desirable, though not always possible, for a full description to have most of these characters represented for each species. However, it is possible to identify species on as little as a single rod-crest. This is especially important when conulariids are abundant but fragmented, which is commonly the case.

COMMENTS ON QUANTIFICATION AND STRATIGRAPHICAL DISTRIBUTION

Quantification. Quantifying material of this kind presents problems. The easiest thing to count would be the number of pieces. However, the number of exoskeletal pieces per kg sample does not give accurate information on the actual number of whole conulariids represented in the sample. The number of pieces will depend on various taphonomic factors, including the degree of bioturbation, the rate of sedimentation and current strength.

The minimum number of conulariid specimens per kg of sample could be theoretically estimated by calculating the total area of hardpart-surface on a complete conulariid. This value could then be compared with the total area of hardpart-surface obtained from the exoskeletal pieces. However, this method is unreliable since the area of the hardpart-surface varies among different species, and among specimens of various ontogenetic stages and those that lived in different environments.

Because of the many difficulties inherent in the calculation described above, only rough estimates of the conulariid frequency per kg are recorded here. The intervals used to express this relative frequency are: very common, common, rare, and absent. This calculation is not a measure of the number of pieces per kg of sample but an estimate of how frequent a species is in relation to other species in the fauna.

Stratigraphical distribution. Conulariids are abundant throughout the Lower Visby Beds but their frequency generally diminishes upward.

Unit *a*, uppermost 8 m collected, 4 samples from 2 localities, together 24·5 kg produced over 2000 pieces.
Unit *b*, thickness about 9 m, 25 samples from 6 localities, together 142·3 kg produced about 5000 pieces.
Unit *c*, thickness about 1·4 m, 6 samples from 3 localities, together 34·4 kg produced about 1000 pieces.
Unit *d*, thickness about 1·8 m, 6 samples from 4 localities, together 67·5 kg produced about 1000 pieces.
Unit *e*, thickness about 1·3 m, 3 samples from 2 localities, together 23·2 kg produced about 500 pieces.

Three samples from the overlying Upper Visby Beds have also been briefly examined to confirm if some of the species cross the boundary between Lower and Upper Visby Beds. The samples are from Ireviken 3. Together the samples have a weight of 25·5 kg and contained about 100 pieces.

Conularia sarae is very common in unit *a*, common in the other units, and also continues into the Upper Visby Beds. All 44 studied samples contained this species. *Conularia wimani* is rare in units *a*, *b* and *e*; absent in units *c* and *d* and unknown from the Upper Visby Beds. *Conularia* sp. a is common in unit *a* and rare in the other units. This species has not been found in the Upper Visby Beds. *Metaconularia aspersa* is rare throughout the Lower Visby Beds and crosses the boundary with the Upper Visby Beds. *Pseudoconularia* aff. *scalaris* has only been found in one sample in unit *d*.

SYSTEMATIC PALAEONTOLOGY

Holotypes have been selected which show the maximum number of species-specific characters. In practice this generally means that the holotypes are disarticulated specimens with ornamentation representing the adult part of the exoskeleton.

Genus CONULARIA Sowerby, 1821

Type species. Conularia quadrisulcata Sowerby, 1821.

Remarks. The most recent description on the generic concept is by Babcock (*in* Babcock *et al.* 1990) and is as follows: The genus is characterized by a thick exoskeleton with coarse, often closely spaced (9–84 per cm), transverse rods. Fewer than 60 per cent of the rods alternate at the midline; more than 40 per cent abut. Nodes, rod-crest, and often wide adapertural crest, with or without adapical crests, may be present and closely spaced (usually 1–10 per mm).

In addition, the midline is not marked by a raised line or groove and, according to, for example, Babcock (1991) and Van Iten (1991*a*), some species have low septa, a character that has not been observed among the *Conularia* present in my material.

Conularia sarae sp. nov.

Plate 1, figs 1–8; Plate 2, figs 1–5; Text-fig. 2B

?1978   Conodont supporting elements, Bischoff, pp. 149–151, pl. 1, fig. 8.

*Derivation of name.* Named in honour of my daughter Sara.

Types. Holotype: LO 4931T. Paratypes: LO 6410t, and LO 6415t.

Type locality. Lusklint 1. Lower Visby Beds unit *a*. The holotype is from sample G88-613LJ, 8·98–8·83 m b.r.l.

Material. More than 5000 exoskeletal fragments.

EXPLANATION OF PLATE 1

Figs 1–8, *Conularia sarae* sp. nov. 1–2, paratype, LO 6410t; Lusklint 1, sample G88-708LJ; 1, rod with rod-crests in adapertural view formed in position C, × 75; 2, detail of the middle rod-crest, × 150. 3, rod with rod-crests in adapertural view, formed in position B; LO 6411t; Ireviken 3, sample G85-36aLJ, × 75. 4, rod and rod-crest in cross-section, formed in position B; LO 6412t; Häftingsklint 4, sample G88-625LJ, × 150. 5, rod and rod-crest in cross-section, formed in position C; LO 6412t; Lusklint 1, sample G88-613LJ, × 150. 6, rod with serrated rod-crests in adapical view, formed in position B; LO 6413t; Lusklint 1, sample G88-613LJ, × 120. 7–8, LO 6414t; Lusklint 1; 7, rod with rod-crests in adapical view, formed in position C, × 75; 8, detail of the middle rod-crest; note the striation on the left side of the rod-crest, × 150.

PLATE 1
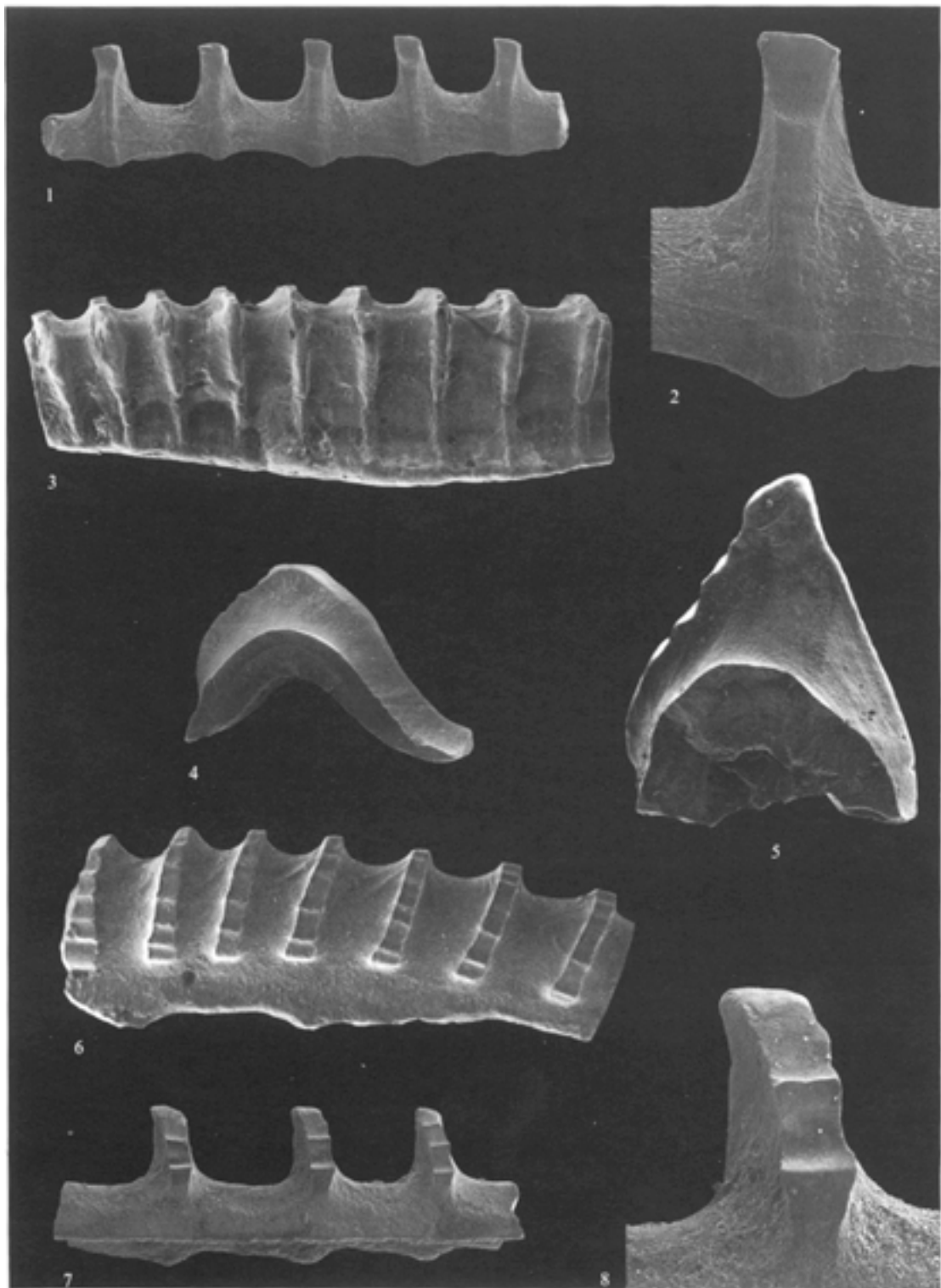
Diagnosis. Conularia with rods possessing long rod-crests in the upper part of the exoskeleton and short ones in the lower part and near the corner grooves. Rods alternate at midline (90 %). Rods and rod-crests tightly spaced. Rod-crests are serrated on the adapical sides. Adapertural crests are connected to the rod-crests, crossing the interrod areas, connecting rods longitudinally.

Description. The exoskeleton is fairly coarse with distinct rods crossing the face transversally. When the exoskeleton is seen in longitudinal cross section, the rods form a high relief, wave-like pattern (Pl. 2, fig. 5). The rods are more or less symmetrical with a roughly semicircular cross-section (Pl. 1, figs 4–5). Rod spacing is about 80 rods per cm near the apex and wider adaperturally (about 50(?) rods per cm). Both long and short rod-crests are present. The rod-crests have a more or less distinct serration on the adapical side (Pl. 1, figs 6–8; Pl. 2, fig. 4). There are an average of 2–4 crest-widths in the space between two rod-crests. The rod-crests are tightly spaced (8–18 per mm). Adapertural crests are present and they run completely across the interrod areas (Pl. 2, figs 2–5). The rod-crests are fused with the adapertural crests, forming a continuous structure. The midline is visible as an interruption of the rods and sometimes also as a shallow groove or channel (Pl. 2, figs 1–2). The rods alternate irregularly at the midline and the blunt rod-ends sometimes cross the middle. Rods that abut at the midline have also been found, but this is rare (less than 10 per cent?). Rod pattern along the midline cannot with certainty be assigned to any of those described by Babcock and Feldmann (1986*a*, 1986*b*).

 Four different types of exoskeletal fragments are present (see explanation above). Pieces that have been formed in position A (i.e. the apical part) are present in most samples. These are found as larger exoskeletal fragments with rods connected by mineralized interrod areas, and reveal a gradual development from short rod-crests near the corner groove, to longer more or less blunt ones towards the midline (see Pl. 2, figs 2–5).

 Rods from position B (i.e. fragments of the corner grooves) are represented by coarser and strongly curved rods present in fairly large amounts in the samples (these coarser rods could probably better withstand physical breakdown) (Pl. 1, figs 3–4, 6). These rods have been formed in connection with the corner grooves. Their shape indicates that the corner grooves were rather deep. On the rods are coarse, short rod-crests with distinct serrations on the adapical side (Pl. 1, fig. 6). Interrod areas are generally broken away, leaving irregular fractures along the rod margins.

 Material from position C (i.e. upper central face part, midline excluded) consists of single rods only. These rods possess long, blunt to sharp, rod-crests with well marked serrations (2–5 serrae on each rod-crest) on the adapical side (Pl. 1, figs 7–8). The adapertural side of the rod-crests are more or less smooth with a ridge-like structure running towards the interrod area adaperturally (Pl. 1, figs 1–2). The rods have not been found connected with mineralized interrod areas. There are, however, thin pieces attached to the rods on the adapertural side but this is rare. This suggests that the upper central part of the face-halves was not completely mineralized. Intermediate forms (single rods) between positions B and C occur frequently in the samples. These rods are similar to the rods found in position C but the rod-crests are shorter and closer together (see Text-fig. 2B).

 Fragments from position D (i.e. fragments from the midline) consist mostly of larger exoskeletal parts with rods connected by mineralized interrod areas (Pl. 2, fig. 1). The mineralized interrod areas indicate that these have been formed in the transition between positions A and D. The rods end bluntly along the shallow groove

EXPLANATION OF PLATE 2

Figs 1–5, *Conularia sarae* sp. nov. 1, exoskeletal piece showing alternated rods along the midline, formed in position D, possibly near position A; the aperture is upwards in the picture; LO 6415t, paratype; Häftingsklint 4, sample G88-625LJ, × 75. 2, exoskeletal piece showing the midline formed in position A in the centre part; note the rods that abut in the lower part of the specimen; aperture is upwards; LO 6416t; Lusklint 1, sample G88-613LJ, × 75. 3–5, LO 4931T, the holotype; Lusklint 1, sample G88-613LJ; 3, exoskeletal piece with rods possessing rod-crests formed in position A; note the adapertural crests, fused with the rod-crests adaperturally, and connected on the adapical side with the upper rod, × 75; 4, detail of rod in adapical view; note the incompletely developed serration and the contact between the adapertural crest and the rod, × 500; 5, sideview with the aperture upwards; the fracture forming the right side, exposing the cross-section, is probably close to the midline; note how the rod-crests gradually increase in height towards the midline and the wave-like pattern formed by the rod-crests seen in cross-section, × 75.

PLATE 2
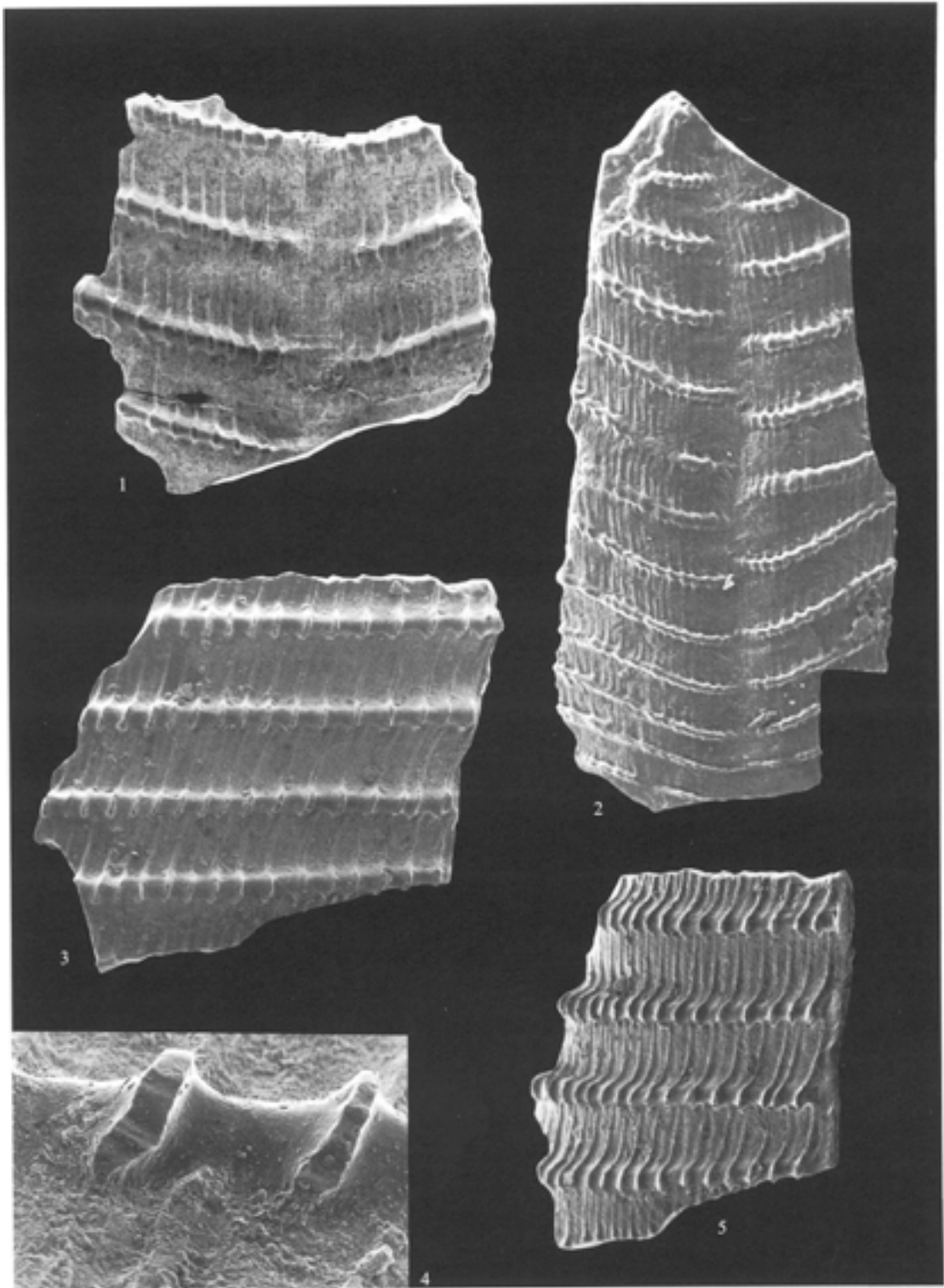
JERRE, *Conularia*

which constitutes the midline. Single rods are also found that have been formed in connection with the midline. These are identified on their blunt, rounded 'rod-ends'.

Remarks. This species, and the two described below, have most characters in common with the genus *Conularia* but also have characters that separate them from that genus. When there is more information available, *C. sarae*, *C. wimani* and possibly also *C.* sp. a could turn out to represent a hitherto undescribed genus.

A specimen illustrated by Bischoff (1978, pl. 1, fig. 8) from the *Pterospathodus amorphognathoides* conodont zone (the Llandovery–Wenlock boundary) of New South Wales, Australia, has a striking resemblance, judging from the illustration only, with rods formed in position C from *C. sarae*.

Comparisons. *Conularia sarae* could perhaps be confused with both *C. wimani* and *C.* sp. a. *C.* sp. a is separated from *C. sarae* in having rod-crests of a different shape and lacking serration.

Conularia sarae differs from *C. wimani* which has coarser rods and rod-crests, rod-crests with irregular serration on the adapical sides, and conspicuously smooth adapertural sides. *C. sarae* has 8–18 rod-crests per mm whereas *C. wimani* has' 5 rod-crests per mm. *C. sarae* differs from *Ctenoconularia monile* (Lindström, 1884), found in Upper Visby and Högklint beds, in that: (1) the rods in *C. monile* abut along the midline (nearly 100 per cent), whereas most of the rods alternate in *C. sarae*; (2) the midline has the shape of a raised line in *C. monile* whereas in *C. sarae* it has the shape of a shallow groove; and (3) the distance between rod-crests is different, with *C. monile* having 5–6 rod-crests per mm, whereas *C. sarae* has 8–18 rod-crests per mm.

Conularia wimani sp. nov.

Plate 3, figs 1–7

Derivation of name. Named in honour of the Swedish palaeontologist Carl Wiman.

Holotype. LO 6417T.

Type locality. Ireviken 3. Lower Visby Beds unit *e*. The holotype is from sample G86-145LJ, 4·27 m a.r.l.

Material. About 100 exoskeletal fragments.

Diagnosis. *Conularia* with coarse rods possessing closely spaced, broad, rectangular rod-crests. The rod-crests have distinct but irregular serration on the adapical side and are smooth on the adapertural side.

Description. Material of this species consists mainly of single rods. The rods in position C are asymmetrical but roughly subcircular in cross section (Pl. 3, fig. 5). Coarse, rectangular rod-crests occur at frequent intervals;

EXPLANATION OF PLATE 3

Figs 1–7. *Conularia wimani* sp. nov. 1–2, LO 6417T, holotype; Ireviken 3, sample G86-145LJ; 1, rod with rod-crests in adapical view formed in position C, ×75; 2, detail of the middle rod-crest; note the irregular serration, ×150. 3, rod with rod-crests in adapertural view formed in position C; LO 6418t; Ireviken 3, sample G86-145LJ, ×75. 4, exoskeletal piece showing rod adjacent to the midline, formed in position D probably in the lower part; the right rod has been worn off; aperture is upwards; LO 6419t; Ireviken 3, sample G86-145LJ, ×75. 5, rod and rod-crest in cross-section, formed in position C; LO 6420t; Ireviken 3, sample G86-145LJ, ×150. 6, rod with serrated rod-crests in adapical view, formed in position B; the corner groove is to the left of the rod; LO 6421t; Ireviken 3, sample G86-145LJ, ×75. 7, coarse rod with rod-crests in adapertural view, formed in position B; the corner groove is to the left of the rod; LO 6422t; Ireviken 3, sample G86-145LJ, ×75.

PLATE 3
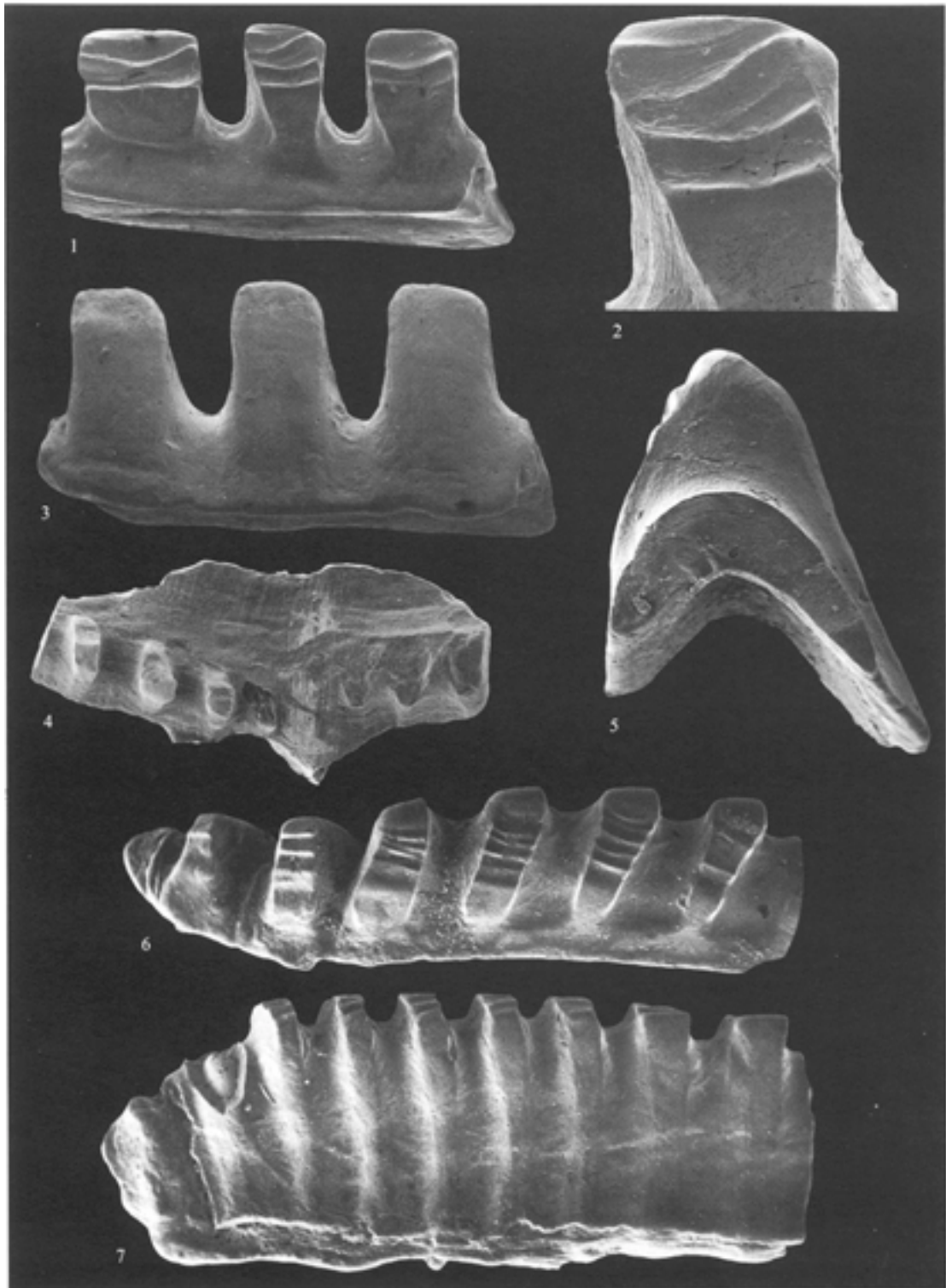
JERRE, *Conularia*
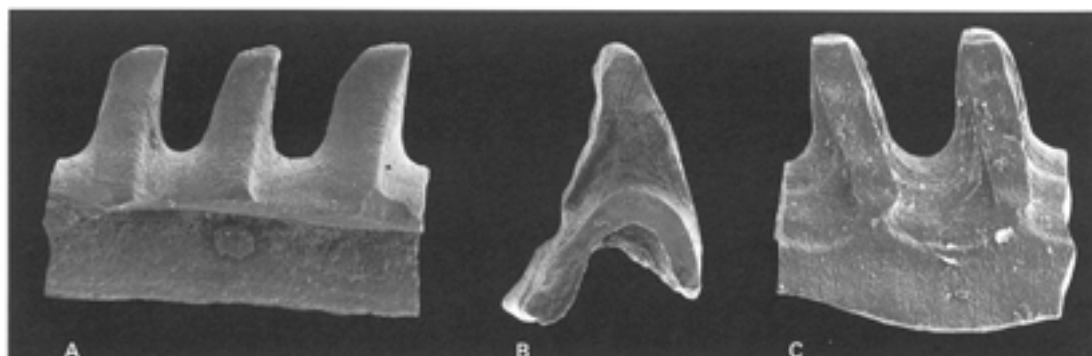
TEXT-FIG. 4. *Conularia* sp. a. SEM photographs of specimens from Lusklint 1, sample G88-613LJ. A, rod in adapertural view, formed in position C; LO 4932t, ×75. B, cross-section of a rod with a rod-crest, LO 4933t, ×100. C, rod in adapical view, formed in position C; note the lack of serration; LO 6409t, ×75.

5 rod-crests per mm (Pl. 3, figs 1, 3, 6–7). The rod-crests are remarkably broad at the top. The adapical side is characterized by a more or less rectangular, sometimes quadratic, area crossed by a distinct but irregular serration (Pl. 3, fig. 2). The margins of the rods are smooth and no pieces of the interrod areas have been found. This could indicate that there were no mineralized interrod areas present. One would expect to find fractures along the rod margins if such mineralized areas had been broken away.

Coarse rods formed near the corner grooves (i.e. in position B) are not as curved as those found on *C. sarae* (see above), which suggests that the corner grooves were more shallow. The rod-crests are more closely spaced and reduced in size towards the corner grooves (Pl. 3, figs 6–7). Mineralized interrod areas have as yet not been found. However, these rods are fractured along the rod margins, unlike rods in position C, indicating that thin mineralized interrod areas were originally present but are now broken away. One single piece has been found that exposes the midline (Pl. 3, fig. 4). The specimen is difficult to place in correct position (either position A or D) but is most likely from a position closer to the apex than to the aperture. This piece is poorly preserved with only one distinct rod present. The rod on the opposite side of the midline has been broken away. The rods seem to have abutted at the midline. There is a small piece of the interrod area connected to the rod adaperturally but the ornamentation, if there was any present originally, has been lost.

Comparison. See *C. sarae*, above.

Conularia sp. a

Text-fig. 4A–C

Material. Over 1000 exoskeletal fragments.

Description. The material consists of rods and single rod-crests only, presumably formed in position C, i.e. upper central face part (see Text-fig. 3). The rods are roughly semicircular in cross-section, possessing relatively long, broad rod-crests (Text-fig. 4B). These rod-crests are slightly tilted longitudinally. The adapertural side of the rod-crests is smooth with a distinct ridge reaching up to the top of the rod-crest (Text-fig. 4A). The adapical side is characterized by a flat, more or less rectangular, area lacking serration (Text-fig. 4c). There are no mineralized interrod areas attached to the rods. As described for *C. wimani*, the rod margins are smooth and lacking fractures from mineralized interrod areas that, if ever present, have been broken away.

Remarks. Only fragments from the upper central face part (position C) have been identified. Despite the fact that the amount of identified rods is so high (over 1000), parts from the other positions have not been recognized. These parts are probably present in the samples but could turn out to be almost indistinguishable from those found of *C. sarae*.

Conularia sp. a may represent a new species, but available material is inadequate for a complete diagnosis of the taxon.

Comparison. See *C. sarae*, above.

Genus METACONULARIA Foerste, 1928

Type species. Conularia aspersa Lindström, 1884.

Remarks. The following morphological features are of generic importance: thin, often large exoskeleton; two midlines flanked by a pair of narrow septa; ornamentation with minute nodes often arranged in transverse rows and longitudinal files; and rows arched adaperturally and crossing the corner grooves and midlines without interruption.

According to Sinclair (1940) specimens of the genus are extremely uncommon. The genus is, however, not uncommon either in the Lower Visby Beds or in other formations on Gotland. Roughly 50 per cent of the samples investigated have produced specimens of *Metaconularia*. Considering that the fragments mostly are fairly small, often less than 100 μm, and that the ornamentation within a specimen can show some variation (Sinclair 1940), a proper identification depends strongly on the size and numbers of the fragments recovered.

Metaconularia aspersa (Lindström, 1884)

Plate 4, figs 4–7; Text-fig. 2c

v* 1884   *Conularia aspersa* Lindström, p. 46, pl. 7, figs 1–3; pl. 19, fig. 1.
v. 1893   *Conularia aspersa* Lindström; Holm, p. 134, pl. 6, figs 43–46.
1907   *Conularia aspersa* Lindström; Slater, p. 19, pl. 1, figs 5–9.
1928   *Metaconularia aspersa* (Lindström); Foerste, p. 107.
1940   *Metaconularia aspersa* (Lindström); Sinclair, p. 101.

Material. Over 100 exoskeletal fragments from 23 samples from the Lower Visby Beds, the holotype and 6 other more or less complete specimens from younger strata (Högklint and Hemse Beds) on Gotland.

Description. The exoskeleton is thin with rows of fine conical nodes crossing each face transversally (Text-fig. 2c; Pl. 4, figs 6–7). The distance both between rows and between individual nodes varies considerably within the same face. Nodes may be equally spaced transversely and longitudinally, forming seemingly longitudinal rows. In some cases nodes within a single transverse row are so tightly packed that they form a knobbly ridge. In complete specimens there are two conspicuous dark lines (septa) running from apex to aperture in the middle of each face. The lines do not interrupt the ornamentation at the midline. The distance between these lines, measured on the holotype (a 50 mm long specimen), is approximately 0·5 mm near the apex, and 2 mm near the aperture where the width of the face is about 30 mm. The lines correspond with two thin septa, triangular in cross-section, on the internal surface of the exoskeleton. Pieces of these septa with attached external exoskeletal fragments are often found in the samples (see Pl. 4, fig. 5). Septa are approximately 0·3–0·5 mm in width (Pl. 4, figs 4–5).

Remarks. Ornamentation varies considerably from piece to piece: the distance between transverse rows, the distance between nodes within a single row, and the coarseness of the nodes all vary within a single sample. Such a degree of morphological variation has not been found among the studied intact specimens. It is thus possible, when more material is available and more detailed analysis is possible, that the material now included in *Metaconularia aspersa* may in the future turn out to consist of two or more species.

Comparison. Metaconularia aspersa differs from *M. biliniata* (Lindström, 1884) (found in the Slite Beds) essentially in having conical or round nodes, whereas *M. biliniata* generally has smaller and more or less elliptical nodes.

Genus PSEUDOCONULARIA Bouček, 1939

Type species. Conularia grandissima Barrande, 1867.

Remarks. This genus, called 'Grupp Longitudinales' by Holm (1893, p. 131) and 'Groupe der *Conularia grandissima*' by Bouček (1928, p. 92), is a conulariid with a unique ornamentation characterized by knobbly, longitudinal ridges, or rows of elongate, irregular nodes which also are often arranged in transverse rows (Sinclair 1941). The midline is defined by a low, often broad ridge. Apical angles are large, from 22° to 23° in *P. grandissima* and up to 40° in *P. klouceki* (Bouček, 1928). Septa are unknown.

Many of the conulariids referable to *Pseudoconularia* are of large size, as is apparent from the specific names *grandissima* (which can reach a height of 30 cm), *magnifica* and *megista* (Hessland 1949). *Pseudoconularia* is a mainly Ordovician genus but its stratigraphical range evidently extends into the Lower Silurian.

Pseudoconularia aff. *scalaris* (Holm, 1893)
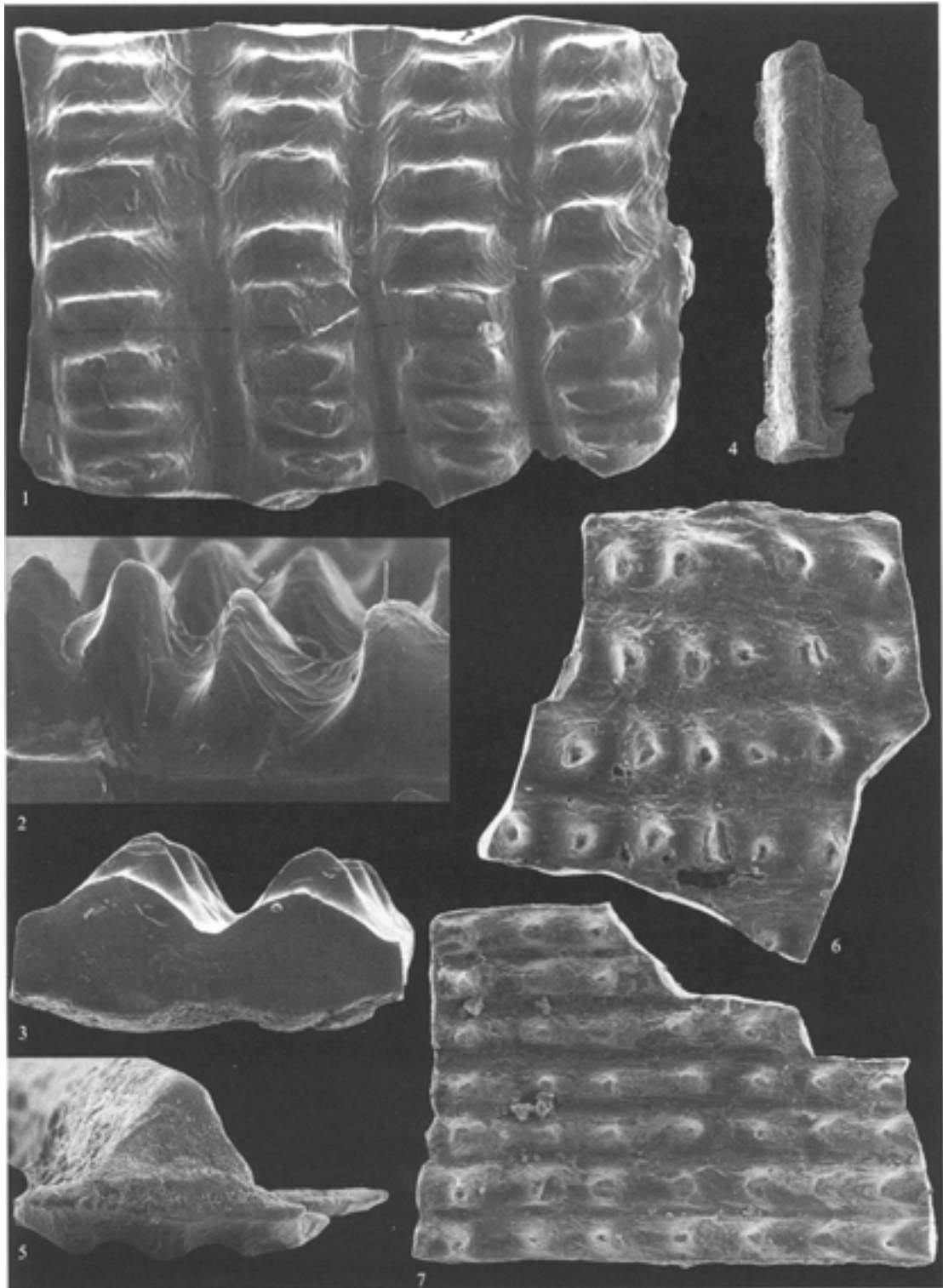
Plate 4, figs 1–3; Text-fig. 2D

Material. 12 exoskeletal fragments.

Description. The exoskeleton is covered with tightly packed, smooth rounded ridges (Pl. 4, fig. 1). The ridges are often linked together (i.e. there is hardly any interridge area visible between the ridges). However, in those places where a narrow but distinct interridge area is visible, the distance between the ridges is generally less than 0·5 ridge-widths. Numerous (15–20 per mm) depressions cut about halfway through the ridges forming elongated nodes with sharp crests on the top (Pl. 4, fig. 2). The nodes are tightly spaced with approximately one, or less than one, node-width between two nodes. In cross-section, the ridges form a sinusoidal-like pattern (Pl. 4, fig. 3). Determining the direction of the aperture and apex from this material is impossible.

Comparison. Pseudoconularia aff. *scalaris* has few morphological characters in common with the other species. Based on this fairly meagre material, the species cannot be formally named. The holotype of *P. scalaris* (Holm, 1893) has not yet been studied and a comparison with Liljevall's drawings (see Holm 1893, pl. 4, figs 49–52), is inadequate to identify *P.* aff. *scalaris* as a new species.

EXPLANATION OF PLATE 4

Figs 1–3, *Pseudoconularia* aff. *scalaris*. 1–2, LO 6423t; Storbrut 1, sample G85-16LJ; 1, large exoskeletal piece showing four parallel ridges with tightly spaced, elongated nodes; direction of the aperture is unknown, × 150; 2, sideview showing elongated nodes; note the typical striation on the sides, × 200. 3, cross-section of a specimen with two preserved ridges; LO 6424t; Storbrut 1, sample G85-16LJ, × 150. 4–7, *Metaconularia aspersa* (Lindström). 4–5, LO 6425t; Ireviken 3, sample G86-129LJ; 4, anterior side of an exoskeletal piece exposing one of the septa, × 150; 5, cross section; note the triangular shape of the septum and the ornamentation with nodes on the external surface of the exoskeleton, lowermost in the picture, × 300. 6, exoskeletal part with nodes; orientation unsure; LO 6426t; Lusklint 1, G89-715LJ, × 190. 7, nodes arranged in a symmetric pattern forming rows in both longitudinal and transverse directions; direction of the aperture is either up or down; LO 4576t; Ireviken 3, G86-129LJ, × 200.

PLATE 4

JERRE, *Pseudoconularia, Metaconularia*

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