AN ENIGMATIC SILURIAN METAZOAN FROM GOTLAND

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ABSTRACT. An articulated specimen of a vagile metazoan with at least twelve similar, calcitic, dorsal skeletal sclerites is described from the Hemse Beds (Silurian, Ludlow Series) of Gotland, Sweden, as *Selenoplax ogmota* gen. et sp. nov. In thin section, a sclerite shows a microstructure of posteriorly radiating, interfering spherulitic cones of calcite with fine growth lamellae; the original composition can be inferred to have been calcitic. Suprageneric taxonomic relationships are assessed but as yet it is not possible to assign the genus to any known phylum.

THE Silurian succession of Gotland, Sweden, comprises predominantly calcareous, marine sediments laid down in a shallow epicontinental sea. The sequences are richly fossiliferous and their faunas have long been the focus of much palaeontological and biostratigraphical work. The locality of Gogs I (Grid ref. on 1 : 50 000 topographical map sheet CJ 5833 5350) in the upper Hemse Beds is well known because of the occurrence there of an early vertebrate assemblage (Gross, 1968; Janvier, 1971, 1978) among a diverse invertebrate fauna (Laufeld, 1974, p. 45). During recent work on outcrop from a re-excavated section there, in connection with a detailed palaeoecological study of the Hemse Beds-Eke Beds transition (Ludlow age) on Gotland, a single articulated specimen of a metazoan with at least twelve skeletal sclerites was found. Further examination was made of material from the same horizon and of many washed marl samples from this and other Gotland localities at approximately the same level in the succession, but it failed to reveal more sclerites. However, the specimen is so unusual that it deserves description and discussion of its affinities.

SYSTEMATIC PALAEONTOLOGY

Genus SELENOPLAX gen. nov.

Type species. S. ogmota sp. nov.; the only known species.

Name. From the Greek, *selene* = moon (crescent) and *plax* = plate, to describe the crescentic shape of the sclerites and of their dorsal thickened region.

Diagnosis. Skeleton of at least twelve bilaterally symmetrical calcite sclerites; fairly small, elongate, tapering anteriorly and posteriorly. Sclerites crescentic to semicircular in outline, much wider than long, overlapping slightly; dorsal surface with prominent transverse lunate thickened region having pronounced, sometimes ornamented, crestal ridge and strongly furrowed posterior border; anterior marginal band differentiated; lateral margins slightly rolled; surface apparently without growth lines. Anterior and posterior sclerites small but all sclerites broadly similar. Nothing known of ventral side.

Selenoplax ogmota sp. nov.

Plate 33, figs. 1–8; text-figs. 1, 2

Name. From the Greek, *ogmotos* = furrowed, to describe the posterior slope of the dorsal thickened region of the sclerites.

Holotype. Naturhistoriska Riksmuseet, Stockholm X2077, from upper Hemse Beds, Gogs 1 (CJ 5833 5350), Gotland. The specimen comes from a richly fossiliferous bioclastic limestone bed. Among the associated fauna

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the beyrichiacean ostracodes *Neobeyrichia lauensis* and *N. scissa* are common, which indicates a correlation with the *Saetograptus leintwardinensis* graptolite zone of the Ludlow Series in Britain (Martinsson, 1967, p. 371). The holotype is the only known specimen of the species.

Preservation. The skeletal sclerites are mostly badly weathered. There has been some loss by breakage and partial dissolution, and much of the surface ornament and the thinner, blade-like areas of sclerites have been removed. However, the sclerite configuration is discernible from those individuals which are better preserved. The anterior margin to the anterior sclerite has been lost, so that it is possible that further sclerites have also been removed from the front of the skeleton (see p. 198). The posterior end of the skeleton is poorly preserved but the posterior sclerite appears to be complete.

Description. The specimen is interpreted as a dorsal exoskeleton with the slightly convex dorsal side exposed and with the larger and more differentiated sclerites towards the anterior end. The sclerites have been numbered from anterior to posterior, 1–12, as shown on text-fig. 1.

Skeleton relatively small, elongate, tapering anteriorly and posteriorly, composed of at least twelve similar, bilaterally symmetrical, calcite sclerites. Slight anterior overlap of sclerites across their entire width (see sclerites 3–5, Pl. 33, figs. 1, 4). Skeleton widest at sclerite 4, individual sclerites largest in this region; tapering backwards from sclerite 7 to 12 by approximately 40%, and forwards from 4 to 1 by approximately 50%, with individual size decreasing accordingly. Individual sclerites much wider than long (e.g. sclerite 8, see Pl. 33, fig. 5), outline crescentic to semicircular. Anterior margin gently convex; posterior margin straight to slightly concave outside broad, somewhat convex, thickened median region; lateral margins fairly straight and slightly rolled under. Dorsal surface with clearly differentiated anterior marginal band visible on sclerites 3 and 4 (Pl. 33, fig. 2 and text-fig. 1); gently convex in front of prominent ridged thickened region; ridge delimits lateral areas behind it but medially the thickened region extends to posterior margin. Sclerite outside thickened region relatively thin, broad, and plate-like (Pl. 33, fig. 1), in transverse profile very slightly arched. Ventral surface of sclerites not exposed.

Dorsal thickened region prominent, central to posterior, transverse, lunate, with a pronounced crestal ridge extending to lateral margins (text-fig. 1 t.r.). Thickened area expands rapidly posterolaterally from a median position to reach lateral margins. Thickening increases steeply posteriorly and most in the central region, less towards the lateral margins. Consequently, crestal ridge arcuate in transverse profile. Ridge with sharp to rounded crest, broadest in central part, tapering rapidly outwards to relatively narrow marginal parts, crest thus crescentic. Line of ridge having gentle curvature convex anteriorly, sometimes with further median flexure which may be slight or marked and triangular (Pl. 33, fig. 3 and text-fig. 1). Anterior border of ridge rounded, smooth, with nearby parallel row of coarse, raised, granular ornament anterior to it on rounded slope of thickened area (Pl. 33, figs. 3, 4). Posterior border of ridge rounded but interrupted by narrow triangular notches, especially

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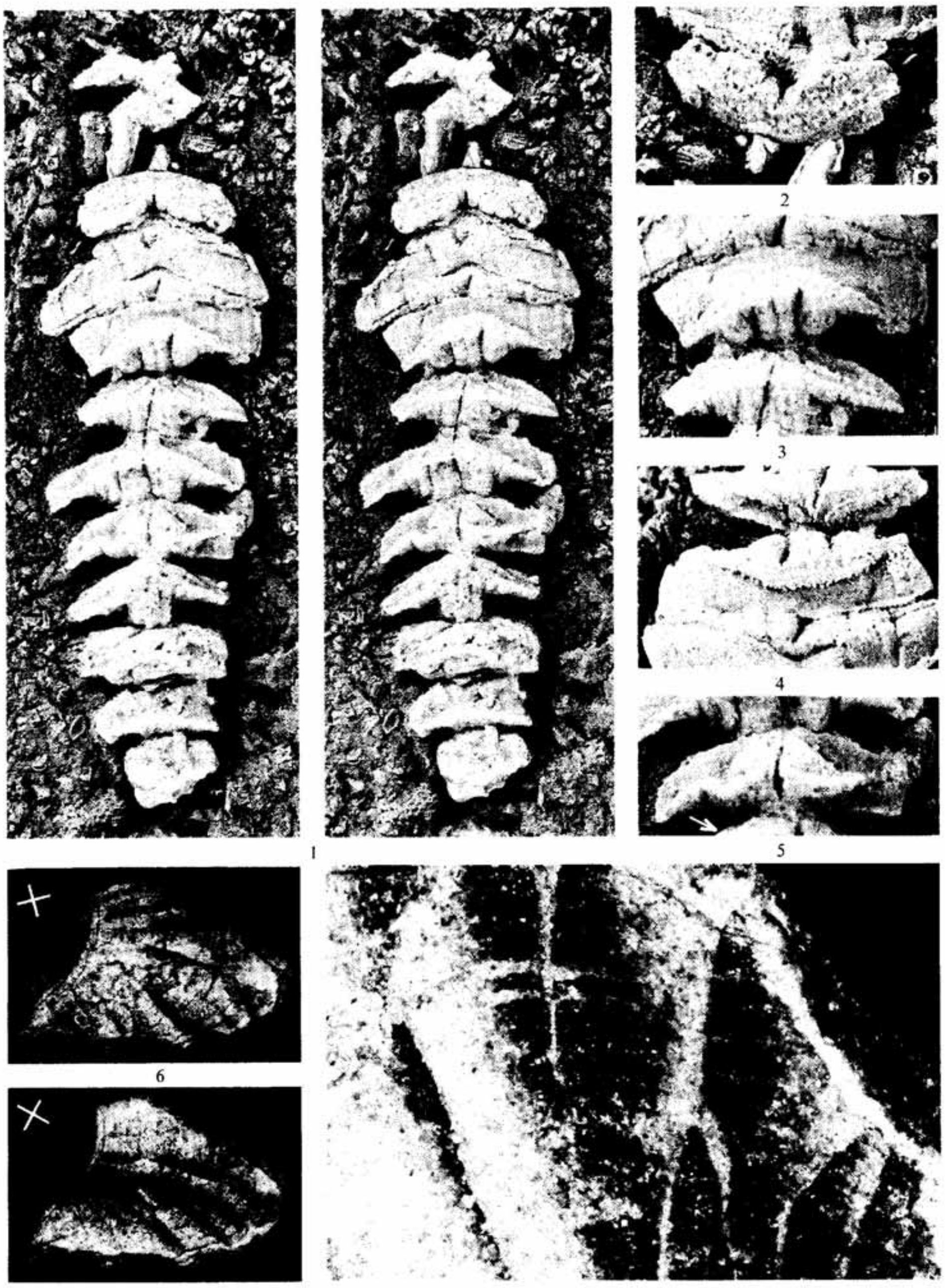
EXPLANATION OF PLATE 33

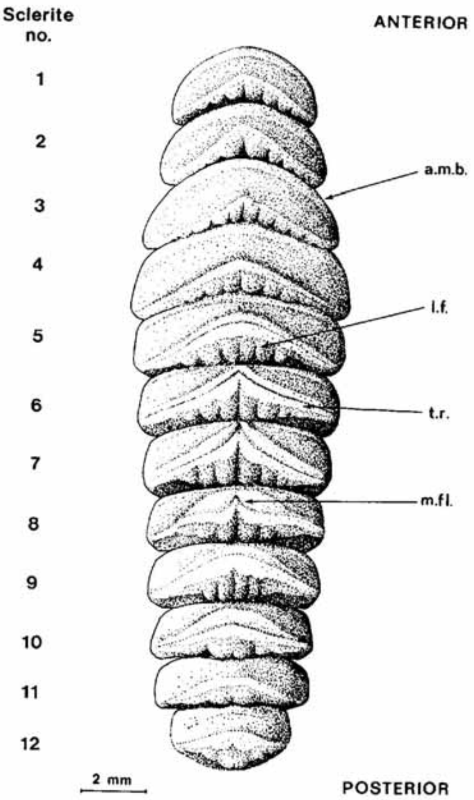
Figs. 1–8. *Selenoplax ogmota* gen. et sp. nov. Naturhistoriska Riksmuseet X2077, Holotype. 1, stereo pair, dorsal view. ×5. 2, anterior view of sclerite 3 to show the distinct anterior marginal band with fine granular ornament. Note projecting spur of calcite emerging from beneath the anterior border of the sclerite—see text pp. 198–9. ×7. 3, detail of sclerite 4 to show the strongly furrowed, posterior slope from the transverse ridge of the dorsal thickened region, and the coarse, granular ornamentation close to the crest of the ridge on its anterior slope. Note the marked forward, central deflection of the crest in sclerite 5 compared to sclerite 4. ×7. 4, Anterior view of sclerites 3–5 to show the deeply notched posterior margin to the transverse ridge, especially well seen in sclerite 4. Note the ornamented bands along the anterior crestal margins, and the slight anterior overlap of sclerites shown by sclerite 4 on to 3. ×7. 5, detail of sclerite 8 to illustrate the thin plate-like area behind the transverse ridge, seen on the right-hand side of the photograph. Note also the rapid posterior expansion of the thickened region culminating in the transverse ridge. The position of sectioning of sclerite 9 is indicated by an arrow. ×7. 6, 7, thin section of sclerite 9 taken perpendicular to the transverse ridge on its left-hand limb (see arrow on fig. 5 for position), seen under plane-polarized light. Crosses indicate the directions of nicols; the difference in orientation between figs. 6 and 7 is 45°. The anterior edge of the sclerite lies to the left, and the dorsal surface uppermost. Note the radiating and interfering cones of calcite and the distally convex lamellae which cross them, and the homogeneous but undulose extinction indicating fairly regular c-axis orientation of the calcite. ×4. 8, detail from the thin section, under plane-polarized light, to illustrate the distally convex lamellae crossing the boundaries between the calcite cones. The lamellae are picked out by lines of cryptocrystalline calcite replacement crystals. ×17.



CHERNS, enigmatic Silurian metazoan

evident in central area where three deep incisions are particularly marked (Pl. 33, figs. 3, 4). Notches reflect strong longitudinal furrowing of posterior slope of thickened area (text-fig. 1). Furrows originate at base of thickening, diverge somewhat, and widen upwards towards crestal ridge. Furrowing approximately symmetrical about median furrow along transverse ridge, spacing variable; furrows become less pronounced and shallower outwards, not seen on narrow lateral limbs of ridge. Some minor longitudinal furrows also visible on posterior slope from ridge (Pl. 33, fig. 3). Posterior slope rounded, steep, thickened region extending furthest in central area where it approaches, possibly reaches, posterior edge of sclerite.

Anterior marginal band differentiated by fairly distinct and fine, granular ornament, and having slight camber against blade-like surface posterior to it. Band slightly broader in central area but tapers little towards lateral margins of sclerite, width up to about one-quarter of the length of the sclerite (Pl. 33, fig. 1—sclerites 3 and 4; fig. 2—sclerite 3; text-fig. 1). Sclerite 3 considerably narrower and smaller than sclerite 4. Sclerites 2 and 1 partly lost but the thickened areas of their transverse ridges distinguishable, although poorly preserved; 2 mainly detached from rest of specimen and rotated slightly, 1 partly detached from and rotated over 2. On sclerite 1 the clearly furrowed posterior slope from the ridge appears very similar to that of sclerites 3 and 4, with marked deep median furrow. Size of sclerites 1 and 2 decreasing from 3, thus anterior end of skeleton tapering. Although the anterior part is lost, very possibly sclerite 1 formed the front of the skeleton: or if further sclerites have been lost, the rapid tapering forwards of the skeleton suggests that they were few and yet smaller. Posterior sclerite poorly and partially preserved; however, thickening with transverse ridge discernible and morphology apparently similar to other sclerites. Posterior slope from ridge very steep. Sclerite 3 with calcite spur projecting slightly



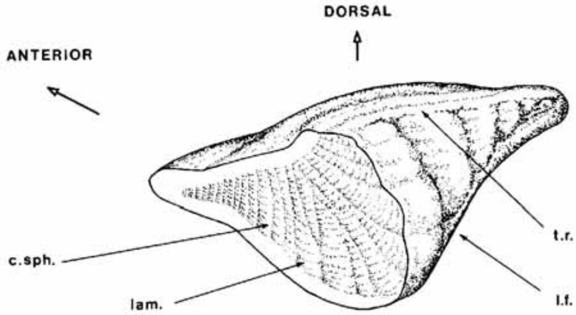
TEXT-FIG. 1. Reconstruction of *Selenoplax ogmota* (Pl. 33, fig. 1). The numbering system for sclerites is shown. Morphological features: a.m.b.—anterior marginal band: t.r.—transverse ridge of dorsal thickened region; l.f.—longitudinal furrows of posterior slope from ridge; m.fl.—median flexure of ridge.

abaxially from beneath central part of anterior margin. This could be a ventral structure of the sclerite although it may equally well be a loose fragment or even entirely unrelated to the specimen (see Pl. 33, fig. 2).

Dimensions. All measurements are minimum values because of losses from weathering. Length of skeleton—23·3 mm; width (max.) of skeleton (sclerite 4)—6·5 mm; width (min.) of skeleton (sclerite 12)— > 4·2 mm; sclerite 8, length—1·5 mm; width—5·00 mm.

Internal structure of sclerites. Sclerite 9 was sectioned perpendicular to the transverse ridge (position indicated on Pl. 33, fig. 5) to show the internal structure of the dorsal thickening. The thin section shows a structure of interfering calcite spherulites radiating from the antero-dorsal edge posteriorly and crossed by numerous, closely spaced, distally convex lamellae (Pl. 33, figs. 6, 7, 8). In plane-polarized light the extinction is homogeneous although somewhat undulose, reflecting a fairly uniform orientation of the calcite crystals with the c-axis normal to the surface (Pl. 33, figs. 6, 7). The lamellae are easily picked out because of the cryptocrystalline calcite replacement crystals lying along these interfaces (Pl. 33, fig. 8).

The relation of the shell microstructure as shown in Pl. 33, figs. 6–8 to the sclerite morphology is illustrated schematically in text-fig. 2. Because the sclerite sectioned was badly worn the blade-like thinner portions have been lost, and therefore the nature of the outer shell layers has not been speculated on in the diagram. The radiating calcite spherulites expand posteriorly and ventrally from the dorsal surface anterior to the transverse ridge. They find surface expression in the longitudinally furrowed posterior slope from the ridge, the furrows reflecting boundaries between rows and bundles of spherulites. The distal expansion of the calcite cones results in the pronounced thickening of the sclerite posteriorly.



TEXT-FIG. 2. Schematic reconstruction of a single sclerite seen in longitudinal section to show the microstructure (Pl. 33, figs. 6–8) in relation to the sclerite morphology. Morphological features: c.sph.—calcite spherulite; lam.—lamella; l.f. and t.r.—as on text-fig. 1. The outer shell layers of the section have not been drawn in because these portions were badly worn on the sclerite sectioned from the *S. ogmota* specimen.

Discussion and affinities

The classification of *Selenoplax ogmota* is a problem because the structure of the skeleton is not easily comparable with that of any other group. The articulating sclerites and bilaterally symmetrical form compare with metazoan groups that have plated exoskeletons, and with those showing metameric segmentation or serial repetition of structures, principally the Mollusca, Echinodermata, Annelida, and Arthropoda. The mineralogical composition and structure of the sclerites is of particular importance to the question. The thin section (Pl. 33, figs. 6–8) shows that the original optical characteristics and microscopical structure are preserved. This suggests that the original shell material was calcite, diagenetic changes then involving calcite-calcite alteration and not resulting in loss of fine structure. The cryptocrystalline calcite formed by recrystallization which serves to pick out the curved lamellae (Pl. 33, fig. 8) illustrates this structural preservation. SEM examination of a polished, etched surface parallel to the thin section showed that the ultrastructure was very small bladed calcite prisms with irregular boundaries, and with narrow bands of cryptocrystalline prisms along lamellae.

Spherulitic structure is found in both aragonite (e.g. typical of Recent scleractinian corals) and calcite (e.g. the walls of some cheilostome bryozoans (Sandberg, 1971), Recent pennatulid skeletal rods (Ledger and Franc, 1978) and bird egg shells (Erben, 1970)). There has been some debate whether microstructure in aragonitic shells may be preserved after diagenetic alteration to calcite—when, typically, such changes result in a coarse, irregular mosaic of drusy calcite and loss of all original textures. Bøggild (1930, p. 11) and Sorauf (1971, pp. 28–29) have discussed this referring to Danian scleractinian corals, and Sandberg (1975) with regard to bryozoan diagenesis and composition of rugose corals. However, the regular crystal orientation and the fine microstructure seen in the *S. ogmota* section can be accounted for reasonably from an original composition of calcite. Sandberg (1975, p. 59) noted that in calcitic compared to aragonitic spherulitic arrays 'individual crystals are usually bladed or difficult to distinguish'. Among the fauna with the *S. ogmota* specimen, originally aragonitic molluscan skeletal material has been recrystallized to drusy calcite.

The lamellae are fairly closely and regularly spaced, normal to the axis of the spherulites and with distinct curvature convex distally. They can be seen to cross the boundaries between cones (Pl. 33, fig. 8). The lamellae represent growth increments of the spherulites. The structure and growth are reflected directly in the external morphology of the dorsal thickened region of sclerites (text-fig. 2). The prominent (and finer) longitudinal furrows of the posterior slope from the crest are formed by the junctions between rows of calcite spherulites. The increasing area and amount of thickening posteriorly result from the distal expansion of the cones. However, the surface of the blade-like portions of the sclerites shows no traces of marginal growth lines such as result from periodic and fluctuating growth in size of the individual as, for example, in molluscs and brachiopods. While it cannot be ruled out that the *S. ogmota* lamellae are equivalent to such growth lines it appears more probable that they relate to development of the sclerite rather than to size increase of the individual *per se*. If so, the alternative is that growth of the individual may have taken place by moulting.

The originally calcite shell and, additionally, the absence of growth lines on sclerites make affinity with the Mollusca very unlikely. This is important because in general form, if not in the number of sclerites, the skeleton bears some resemblance to that of a polyplacophoran. Also, spherulitic structure has been described for two shell layers of Recent polyplacophorans (Haas, 1972, 1976). However, the microstructure of these layers, as outlined below, is clearly different from the *S. ogmota* sclerite and they are always composed of aragonite (together with an organic component). The infrequent chiton plates from the Silurian of Gotland (*Chelodes* and *Gotlandochiton* species) are generally preserved as drusy mosaics of sparry calcite typical of diagenetic alteration of aragonite. The evidence available for early polyplacophorans goes to show that, like all Recent forms, they had aragonitic shells. Recent polyplacophorans have a complex and variable shell structure. Of the layers described by Haas, the tegmentum, or spongy outer calcareous layer, comprises longitudinal cords of radiating spherulites parallel to the dorsal surface of the plate, from which further growth takes place by extension of some of the aragonite needles lateroventrally. The outer surface of the tegmentum, generally with sculpture of low relief and pronounced marginal growth lines, has numerous fine and coarse pores from the penetration through the layer of parallel canals accommodating pallial outgrowths with apical sense organs (aesthetes). By contrast, there is no trace of pores (nor of growth lines) on *S. ogmota* sclerites and neither is there any indication in thin section of canals. The second spherulitic layer is the dense porcelanous plate-like articulamentum, which has spherulitic sectors growing outwards from a central zone and from many crystallisation centres, interspersed with frequent narrow canals. The articulamentum, which forms an insertion plate into the muscular girdle and also projects anteriorly for articulation with the adjacent shell plate, is lacking from the characteristically massive plates of early polyplacophorans (Bergenhayn, 1930). The fundamental difference in composition of the shell and the dissimilar microstructure provide sufficient reason to discount affinity of *S. ogmota* with the Polyplacophora.

The microstructure and optical properties of the calcite in the sclerite rule out an echinoderm affinity, which is important since the Echinodermata includes a great variety of plated skeletons. It is noted here that the microstructure of the *S. ogmota* sclerite is unlike that of the calcite plates of Machaeridia (which also pose problems with their affinities) which occur quite frequently through the Silurian of Gotland. These have plates with a characteristic sculpture of distinct growth lines, and the machaeridian dorsal exoskeleton comprises paired rows of small imbricating plates (Bengtson 1978).

The segmented dorsal exoskeleton and growth by moulting would find an analogue in the Arthropoda. The inorganic composition of the trilobite cuticle is entirely calcitic and many decapods have calcified epicuticles (Stehli, 1956; Dalingwater, 1973; Dalingwater and Miller, 1977). Many trilobite cuticles have characteristic primary microstructures of horizontal laminae and perpendicular canals, and Dalingwater and Miller (1977, p. 29) considered the organization to be comparable to that of many extant arthropods. They (1977, p. 30), like Tiegler and Towe (1975, p. 144), stated that the trilobite cuticle was heavily impregnated with calcite but considered this, by comparison with other groups (ostracodes, cirripedes), to represent a functional response to environment rather than to have phylogenetic significance. A pronounced, though undulose, c-axis preferred orientation of calcite is characteristic of ostracodes and trilobites. However, no fine spherulitic microstructure similar to that of the *S. ogmota* section has been described from among arthropods, and the shell of the former shows no trace of canals normal to the surface. Even primitive arthropods have anterior segments modified into a head region; head structure forms the basis for classification at superfamily level (Manton, 1969). In the exoskeleton, cephalization may be reflected in development of a head shield, as in trilobites and chelicerates; however, all paired appendages of the fused segments remain functional, even if they become modified. The distinct anterior differentiation of the skeleton in arthropods contrasts with the externally simple head end of annelids in which the body consists of more or less uniform segments behind the head. The anterior end of the skeleton of *S. ogmota*, if complete, lacks structural differentiation or if incomplete is missing only few and small additional sclerites. Thus, any cephalization could only be minimal. However, calcareous exoskeletons in annelids are restricted to the tubes secreted by some polychaetes, e.g. serpulids. The form and microstructure of the plated skeleton of *S. ogmota* can thus be compared only with arthropods but is sufficiently different to preclude its unequivocal inclusion within this phylum.

The sclerites of *S. ogmota* show some overlap between adjacent individuals (e.g. Pl. 33, figs. 3, 4), and must have articulated together. This could have been achieved by soft tissue or flexible cuticle between sclerites, or it is possible that the calcareous spur projecting forward from beneath sclerite 3 (Pl. 33, fig. 2) might represent an articulating structure from the ventral surface of the sclerite. However, the thick, rigid structure of sclerites would restrict skeletal flexibility and preclude enrollment or rapid movement. The specimen of *S. ogmota* occurs on the undersurface of a conglomeratic hardground horizon in the upper Hemse Beds; the bed has a rich benthic invertebrate fauna and surfaces encrusted by bryozoans and spirorbids. The external resemblance to polyplacophorans may indicate some functional convergence for a similar mode of life, that is, a vagile animal adapted to adhering to surfaces.

CONCLUSIONS

The morphology and microstructure of *S. ogmota* are sufficiently different from other known metazoan phyla to preclude unequivocal suprageneric assignment at present. However, on the basis of the originally calcite composition of the sclerites, and the likelihood that growth took place by moulting and not by incremental size increase of individual sclerites, a molluscan affinity can be eliminated. External resemblance to Polyplacophora may be a response to similar life habits. The apparently segmented, plated, calcitic skeleton finds some structural analogue with the Arthropoda, but there is little or no indication of the anterior differentiation which is characteristic even of primitive arthropods. There is no comparable skeletal form in the Annelida.

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