SILURIAN POLYPLACOPHORAN MOLLUSCS FROM GOTLAND, SWEDEN

by LESLEY CHERNS

ABSTRACT. A new, unusually diverse and abundant polyplacophoran (chiton) assemblage occurs in the Silurian of Gotland, Sweden, largely as silicified material. The paleoloricate fauna described here includes: *Thairoplax pelta* gen. et sp. nov., *Plectrochiton tegulus* gen. et sp. nov., *Alastega lira* gen. et sp. nov., *Heloplax papilla* gen. et sp. nov., *Enetoplax decora* gen. et sp. nov. and *Arctoplax ornata* gen. et sp. nov.; *Gotlandochiton* Bergenhayn is revised. One genus represented by an intermediate sclerite, and two unassociated end sclerites, are left under open nomenclature. Most material is from the late Wenlock Halla Formation. Three of the new genera have a holoperipheral growth style and dorsal mucronate apex, normally found only in tail sclerites; plates of these genera display prominent subapical muscle cavities. Patterns of growth banding that associate several such plates as coming from the same individual are important in suggesting that most represent intermediate, and not tail, sclerites. The morphological evidence from sclerites for musculature, and muscle function are assessed for all of the chitons. Recent chiton plates, which have sutural laminae for physical articulation, do not show comparable indications of insertion sites. Several of the Gotland chitons had elongate sclerites, and were elongate animals by comparison with Recent chitons; others had shorter, broader plates and hence a more ovoid body form.

THE only widely known early Palaeozoic polyplacophoran (chiton) genus, *Chelodes*, was first described from the Silurian of Gotland, Sweden (*C. bergmani* Davidson and King, 1874). On the basis of existing and new collections, Gotland species were revised by Cherns (1998). The new collections, from extensive sampling of silicified horizons (Laufeld and Jeppsson 1976) by Dr L. Jeppsson (Lund University, Sweden) and Dr L. Liljedahl (Liljedahl 1984), are dominated quantitatively by sclerites of the large chiton *Chelodes actinis* Cherns, 1998. However, in addition, the relatively abundant and well-preserved acid-isolate assemblages include a diverse range of other chiton taxa, which are described here. *Gotlandochiton* Bergenhayn, 1955 from museum collections is revised. All the material is deposited at the Naturhistoriska Riksmuseet, Stockholm (RM).

The general depositional setting of the stable platform carbonates that dominate the Silurian (Llandovery–Ludlow) succession of Gotland (Text-fig. 1) is discussed by Cherns (1998). Among silicified samples taken from several hundred localities throughout the succession, chitons are restricted to only four localities (Text-fig. 1); three are Wenlock (lower Silurian), of which one (Krakfot) yielded exclusively *Spicuchelodes* (Cherns 1998), and one Ludlow (upper Silurian). Productive localities for the chitons described here are Möllbos (Möllbos-1, Grid Reference Rikets nät RN 637645 165970; Liljedahl 1984), from where most material is derived, and Klintebys (Klintebys-1, RN 636515 164685; Laufeld 1974), both in the Halla Formation, and Ängvards (Ängvards-4, RN 631953 164607) in the Hamra Formation. In addition, the type locality for *Gotlandochiton interplicatus* Bergenhayn, 1955 is Klints Othem (Laufeld 1974; = Spillings 1–2, Jaanusson 1986, p. 10) in the Wenlock Slite Group, and *Thairoplax birhombivalvis* (Bergenhayn, 1955) comes from localities Visby (Lindström 1884, locality Wisby) and Kålens kvarn (Lindström 1884, Kålens qvarn) in the Upper Llandovery to Lower Wenlock, Visby to Högklint formations. All other chiton localities have yielded only *Chelodes* spp.

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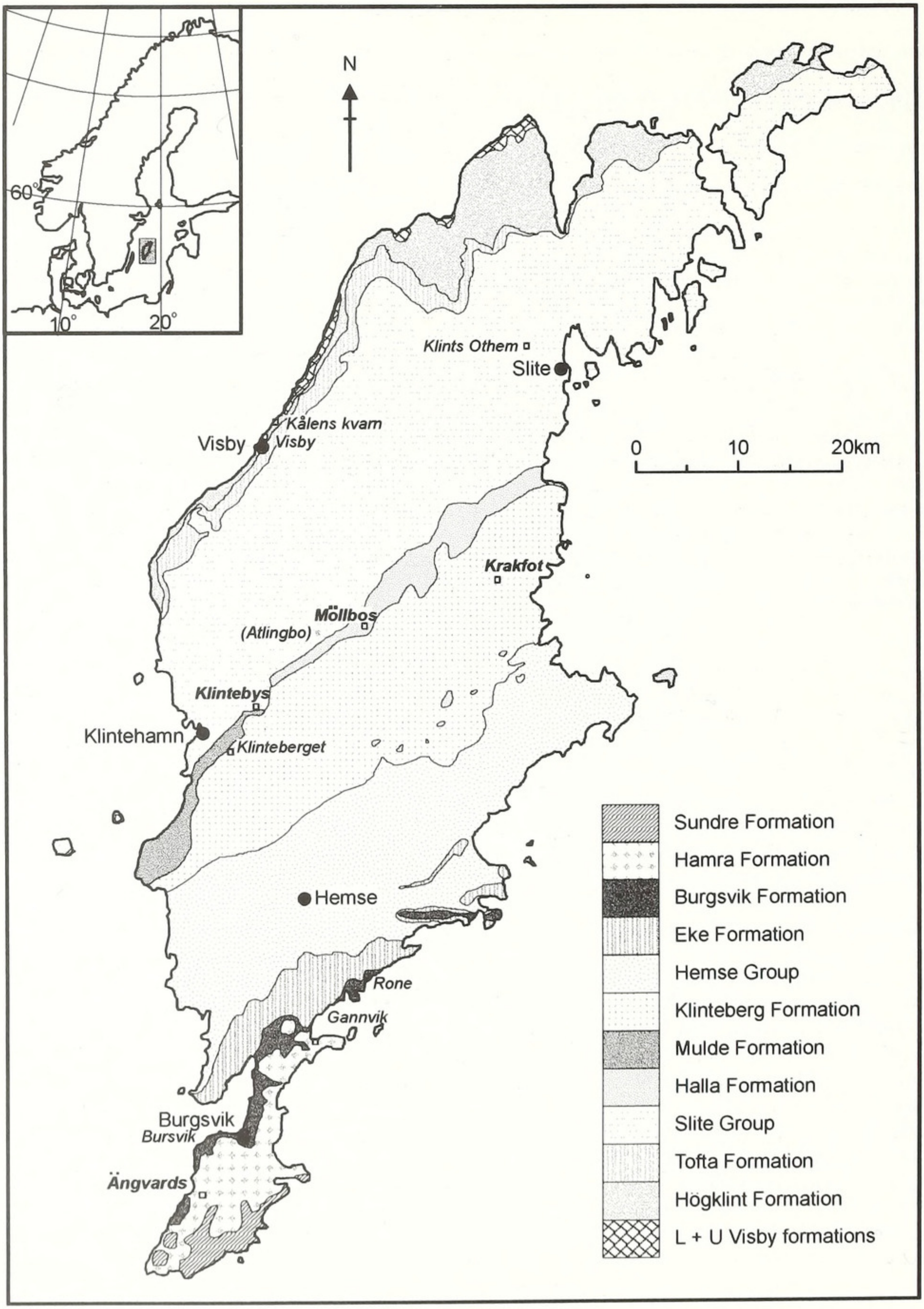


TEXT-FIG. 1. For caption see opposite.

PRESERVATION

The existing Riksmuseum collections used here are limestone specimens with sclerites partly embedded, preserved as recrystallized, coarse calcite mosaics, and with consequent loss of surface detail. These collections are from the Llandovery locality Visby (*T. birhombivalvis*), and Wenlock localities at Kålens kvarn (*T. birhombivalvis*) and Klints Othem (*G. interplicatus*). Limited taxonomic data were derived from these specimens.

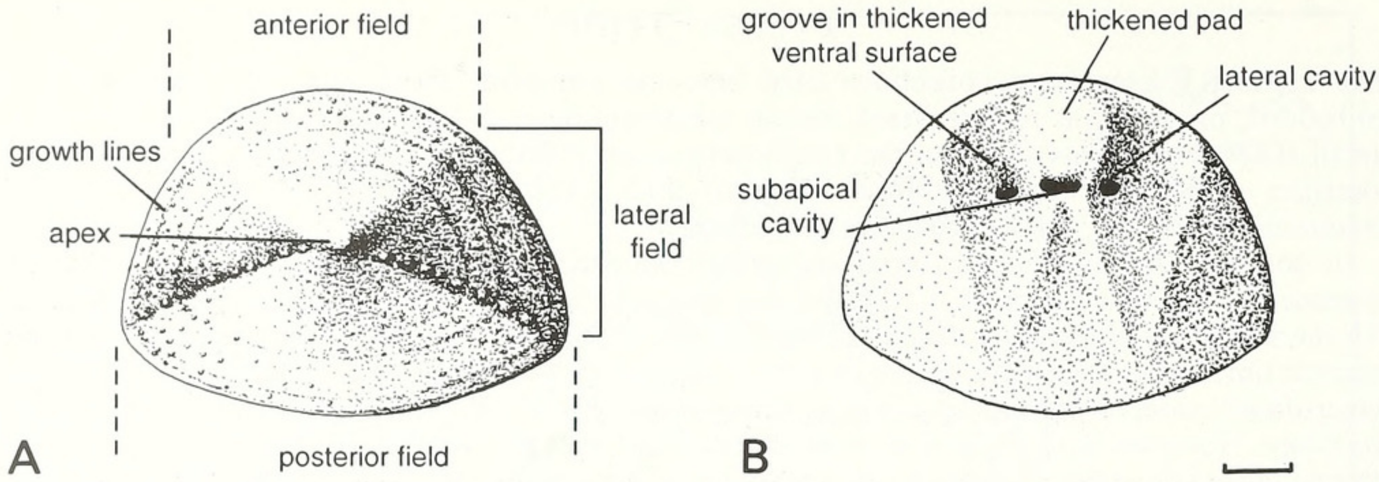
In contrast, the silicified material comprises isolated sclerites, including small and delicate specimens. The vast majority of chitons are from the Möllbos-1 locality in the Late Wenlock (Homerian) Halla Formation, from < 1 m thickness of very thin bedded (< 0·1 m), hard, pale grey micritic limestones with some thinner (< 0·05 m) marl intercalations (e.g. Liljedahl 1984, fig. 35). Macrofossil material appears sparse in hand specimen, and is difficult to extract from the compact lithology. However, acid extraction from several hundred kg of limestones has yielded a rich and diverse fauna; the total, diverse chiton material is < 300 sclerites, limited in comparison with some other groups (e.g. > 3400 determinable bivalves; Liljedahl 1984), but still unusually numerous compared with most Palaeozoic chiton occurrences. A fairly low energy depositional environment is evident from the generally small degree of wear and breakage. The chiton assemblage includes *Thairoplax pelta*, *T.*? aff. *pelta*?, *Plectrochiton tegulus*, *Alastega lira*, *Heloplax papilla*, *Enetoplax decora*, *Arctoplax ornata*, head B and head/tail C, as well as a large number of *C. actinis* (Cherns 1998). The preservation of silicified sclerites shows little distinction in crystal size between surface and inner layers, superficially a mosaic of fairly small, inward growing quartz crystals (Schmitt and Boyd 1981, cf. Pattern 1, evident in *C. actinis* from this locality; Cherns 1998). Evidence for rapid precipitation of chalcedony and fine quartz suggests relatively high silica concentrations. Details of surface features are well preserved, indicating early cementation of the micritic carbonate matrix, before delayed precipitation into dissolution cavities. Preserved shell thickness and convexity indicate replacement before significant compaction.

Some of the silicified material is from Klintebys-1, also in the Halla Formation. These specimens are more coarsely crystalline and beekitized, fairly worn, with loss of surface detail. Fragmented specimens typically have sealed edges. The preservation suggests coarser surrounding sediment, a higher energy environment producing more fragmentation, and again delayed precipitation into cavities. Coarser replacement might also indicate slower precipitation and lower silica concentrations than at Möllbos-1 (Schmitt and Boyd 1981). As with Möllbos-1, the preservation of the convexity of shells means that replacement preceded compaction. The Klintebys collections yielded only *A. lira*, including head and tail sclerites, together with *Chelodes* spp. (Cherns 1998). Gen. A from Ängvards-4 in the Hamra Formation shows similar coarse beekitization.

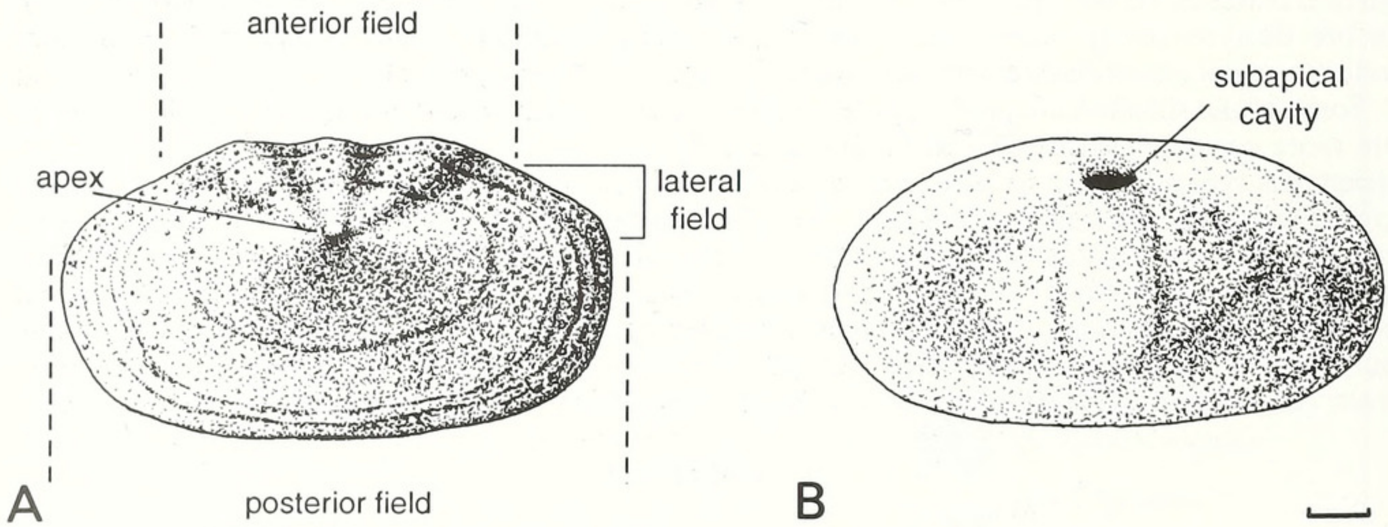
TERMINOLOGY AND MEASUREMENTS

The Silurian chitons are paleoloricates, lacking the sutural laminae for insertion beneath the adjacent plate which characterize neoloricate, and hence living chitons (e.g. Smith 1960). The measurements and terminology for paleoloricate sclerites with a posterior apex, ventral apical area and mixoperipheral growth follow those outlined by Cherns (1998, text-fig. 2). Most chitons, paleoloricates and neoloricates, have a ventral extension of the outer dorsal shell layer, the tegmentum, to form the apical area (Smith and Toomey 1964). In contrast, several of the paleoloricate chitons described here have a dorsal apex and holoperipheral growth style, typically found only in tail sclerites of Recent neoloricate chitons. These sclerites have a prominent raised dorsal apex, or mucro, which corresponds on the ventral surface to a deep subapical cavity, and

TEXT-FIG. 1. Map of Gotland showing the geological succession of Silurian (upper Llandovery to Ludlow) strata, all localities for chitons in existing Riksmuseum collections (italics) and new silicified collections (bold italics). (For discussion of the locality Atlingbo, see Cherns 1998.)



TEXT-FIG. 2. Diagram of holoperipheral sclerites of *Heloplax papilla* gen. et sp. nov., to illustrate terminology used in description of A, dorsal and B, ventral surfaces. Intermediate sclerites have a prominent mucronate subcentral apex, elevated anterior and posterior shell fields, and transverse flexure through the depressed lateral fields. A line of coarser granular ornament delimits the lateral from posterior shell fields. The sculpted ventral surface of a thickened sclerite has additional, smaller lateral cavities as well as the deep, anteriorly slanting subapical cavity, and a pattern of longitudinal and oblique furrows and pads around the cavities. Scale bar represents 1 mm.



TEXT-FIG. 3. Diagram of holoperipheral sclerites of *Enetoplax decora* gen. et sp. nov. to illustrate terminology used in description of A, dorsal and B, ventral surfaces. Intermediate sclerites have an anteriorly displaced mucronate apex, elevated short anterior shell field, long, gently curved and elevated posterior field, gentle transverse flexure through short, depressed lateral fields; lateral and posterior fields without distinct separation. The ventral surface of thickened sclerites has a deep, anteriorly slanting subapical cavity, nearer to the anterior margin and associated with shallower development of pads and longitudinal furrows than in *Heloplax papilla* (Text-fig. 2). Scale bar represents 1 mm.

dorsal shell with anterior, lateral and posterior fields. Terminology for such plates in two genera is shown in Text-figures 2–3.

In the systematic descriptions below, figured specimens are indicated by an asterisk against specimen numbers.

SYSTEMATIC PALAEONTOLOGY

Class POLYPLACOPHORA de Blainville, 1816
Subclass PALEOLORICATA Bergenhayn, 1955

Remarks. Suprageneric classification requires revision encompassing other Palaeozoic chitons, and will be considered in a wider review.

Genus GOTLANDOCHITON Bergenhayn, 1955

Type species. *G. interplicatus* Bergenhayn, 1955 (p. 15, pl. 1, fig. 6; pl. 2, fig. 4 (reconstruction)), by original designation, from the Upper Wenlock, Silurian, of Gotland, Sweden.

Diagnosis (emended from Bergenhayn 1955). Intermediate sclerites broad, arched, with straight, deep, trapezoidal side slopes; jugum rounded, jugal angle close to perpendicular; shell fields not evident. Wide anterior margin gently convex to transverse; anterolateral corners rounded, anterolateral margins short, parallel to slightly divergent; posterolateral margins longer, straight, tapering rapidly across triangulate posterior shell to posterior apex; apical angle close to perpendicular. Ornament of low rounded ridges and narrow grooves parallel to growth lines. Apical area apparently broad and short.

Remarks. *Gotlandochiton* was erected by Bergenhayn (1955) to include four new species described from Gotland. The original generic diagnosis stated that the form of the intermediate sclerites resembled that of most living chitons, with distinct shell fields and with jugal or complete coverage (across the following sclerite). The new family Gotlandochitonidae Bergenhayn, 1955 had a more discrete diagnosis of intermediate sclerites wider than long, variable in shape within the genus, and with weak but distinct shell fields. In the *Treatise on invertebrate paleontology* (Smith 1960, p. I50), relatively small size was noted as a family character.

Bergenhayn (1955) distinguished this genus from *Chelodes* on the basis of sclerites that were wider than long, and with distinct shell areas/fields. In the type species, the broad sclerite has straight side slopes flexed across the jugum, but shell fields are not evident. However, Bergenhayn (1955) also erected and included three other species within *Gotlandochiton*: *G. laterodepressus*, *G. troedssoni* and *G. birhombivalvis*. Of these, the first two, in which central and lateral shell fields are developed, have been synonymized with *C. gotlandicus* (Cherns 1998), and *Chelodes* is now recognized as including species that have distinct shell fields (Cherns 1998). For *Chelodes*, Cherns (1998) noted that sclerites only consistently become longer than wide with increasing size, so that as a criterion particularly for smaller sclerites this is of limited value. *G. birhombivalvis* is transferred here to the new genus *Thairoplax*, described below.

Smith and Toomey (1964) noted that *Gotlandochiton* should display clearly defined shell areas, and suggested an 'apical area less than 1·5 mm wide, extending across the entire posterior margin or present mainly in the vicinity of the valve apex' (p. 18). *G. hami* Smith, *in* Smith and Toomey, 1964, from the lower Ordovician of southern Oklahoma, USA, has broad, rectangular flexed sclerites which have a very narrow band-like ventral apical area and some ventral transverse thickening (Smith and Toomey 1964). The emended generic diagnosis above does not include shell fields, the approximately straight posterior margin in *G. hami* compares with a triangulate posterior shell in both *Gotlandochiton interplicatus* and *Thairoplax* gen. nov., and the very short apical area is also apparently different in form from those of both genera.

Gotlandochiton interplicatus Bergenhayn, 1955

Plate 1, figure 1a–d

v* 1955 *Gotlandochiton interplicatus* Bergenhayn, p. 15, pl. 1 fig. 6; pl. 2 fig. 4 [reconstruction].

1960 *Gotlandochiton interplicatus* Bergenhayn; Smith, p. 150, fig. 34, 4 [reconstruction, Bergenhayn 1955].
1975 *Gotlandochiton interplicatus* Bergenhayn; Van Belle, p. 125.
1977 *Gotlandochiton interplicatus* Bergenhayn; Sirenko and Starobogatov, p. 31.
1987 *Gotlandochiton interplicatus* Bergenhayn; Smith and Hoare, p. 34.

Material and locality. Holotype RM Mo6012*, intermediate sclerite, with fragment of adjacent plate; Klints Othem (= Spillings 1–2, Laufeld 1974; Jaanusson 1986), Gotland; Slite Formation, Slite g, Upper Wenlock (Homerian).

Diagnosis. As for the genus.

Description (emended from Bergenhayn 1955). Holotype an intermediate sclerite in limestone matrix obscuring ventral surface, right posterolateral edge broken; fragment of anterior left portion of second, more posterior sclerite partially covered only by apex. Broad (width 12·3 mm), arched sclerite, wider than long (length 11·3 mm), with straight and deep, trapezoidal side slopes (Pl. 1, fig. 1b–c), jugal ridge rounded, jugal angle 98°. Shell fields not evident. Anterior margin wide and gently convex, rounding into short anterolateral margins that are parallel to slightly divergent. Posterolateral margins longer, straight, tapering rapidly to posterior apex, apical angle 94°. Maximum width of sclerite near posterolateral corners, behind mid-length. Dorsal surface fairly worn, but ornament of low rounded ridges and incised narrow grooves (= ribs of Bergenhayn 1955, p. 16) parallel to growth lines, i.e. to anterior and anterolateral margins, crossing posterolateral margins (Pl. 1, fig. 1a–c). Granular sculpture identified by Bergenhayn (1955, p. 16; Pl. 1, fig. 1c) is a patchy, replacement fabric. In lateral profile, jugal ridge slightly convex (Pl. 1, fig. 1b–c). In transverse profile, shell flexed across rounded jugal ridge (Pl. 1, fig. 1d), height/length 0·38.

Remarks. On the basis of the limited overlap of the holotype onto a second sclerite, with coverage apparently confined to the jugal area, Bergenhayn (1955) deduced that the apical area was narrow and restricted to the apex. He commented that this would leave triangular areas of the body wall exposed laterally between plates (Bergenhayn 1955, p. 15). However, growth lines transect the posterolateral margins onto the ventral apical area (Cherns 1988), which would have spanned the breadth between posterolateral corners and was thus apparently wide, close to the maximum width. The broken right posterolateral margin, curved from apex to posterolateral corner (Pl. 1, fig. 1c, cf. the straight left margin in fig. 1a–b may represent breaking away of the apical area here. Its length (= median length; Cherns 1998, text-fig. 2) and shape of the anterior margin are unknown, the former at most the length from the posterolateral corners, and thus less than half the length of the sclerite. The apparently wide apical area suggests a greater degree of overlap of sclerites than is apparent in the specimen, where the plates may have separated during preservation.

EXPLANATION OF PLATE 1

Fig. 1. *Gotlandochiton interplicatus* Bergenhayn, 1955; RM Mo6012, holotype; intermediate sclerite; Klints Othem, Gotland; Slite Group, Upper Wenlock (Homerian). 1a, dorsal view, showing also fragment of following sclerite; 1b, left lateral view, showing also fragment of following sclerite; 1c, right lateral view, broken posterolateral margin; 1d, anterior view. All ×3.

Figs 2–5. *Thairoplax birhombivalvis* (Bergenhayn, 1955); intermediate sclerites. 2, holotype, RM Mo6031; Visby, Gotland; ?Lower Visby Formation, Upper Llandovery (Telychian); ventral external mould. 3, RM Mo6023; Kålens kvarn, Gotland; lower Högklint Formation, Lower Wenlock (Sheinwoodian). 3a, dorsal view; 3b, left lateral view; note coarse replacement fabric; 3c, anterior view. 4, RM Mo6024a; Kålens kvarn, Gotland; lower Högklint Formation, Lower Wenlock (Sheinwoodian); dorsal view, posterior shell broken. 5, RM Mo6024b; Kålens kvarn, Gotland; lower Högklint Formation, Lower Wenlock (Sheinwoodian); left lateral view, partly embedded sclerite. All ×3.

Fig. 6. gen. A indet.; RM Mo160.061; Ängvards-4, Gotland; Hamra Formation, Upper Ludlow (upper Ludfordian); broken intermediate sclerite. 6a, dorsal view; 6b, ventral view; 6c, left lateral view; 6d, posterior view. All ×3.

CHERNS, Silurian chitons

A silicified sample from Ängvards-4, from the younger, late Ludlow Hamra Formation, yielded one partial sclerite (gen. A, below) that has a broad form and distinctive shallow ridge-and-groove ornament somewhat similar to that of *G. interplicatus*, and an unusual, transverse anterior margin to the apical area. *Gotlandochiton birhombivalvis* Bergenhayn, 1955, in which sclerites are not notably wide, has a V-shaped ventral apical area (Bergenhayn 1955, pl. 1, fig. 7). Until more material becomes available to verify this ventral feature in *G. interplicatus*, the genus should be restricted to the type species. *G. birhombivalvis* is therefore transferred to the new genus *Thairoplax*.

gen. A indet.

Plate 1, figure 6a–d

Material, locality and horizon. One partial silicified (beekitized) intermediate sclerite, RM Mo160.061*, Gotland (RN 631953 164607), Hamra Formation, Upper Ludlow (Ludfordian).

Description. One broken and beekitized intermediate sclerite, the left side without the apex. Sclerite apparently wider than long, slightly cordate, with jugal flexure and straight side slope, without shell fields. Side slope fairly deep, trapezoidal (Pl. 1, fig. 6c). Broad, transverse, slightly rounded anterior margin having only shallow and narrow median embayment, rounding into only slightly convex to straight anterolateral margin parallel to jugal ridge, rounding sharply into straight posterolateral margin tapering steeply towards posterior apex. Anterolateral and posterolateral margins apparently roughly equal in length. Strong ornament of rounded ridges and incised grooves parallel to growth lines. Maximum width at posterolateral corners, well behind mid-length. Ventral apical area broad, triangulate, with raised transverse anterior margin across breadth of shell to posterolateral corners. Apical length/length in specimen 0·28, estimated for complete sclerite possibly *c.* 0·3. Ventral surface smooth.

Remarks. The broad shell has strong ornament of rounded ridges and narrow incised grooves parallel to growth lines that is fairly similar to that of the holotype of *G. interplicatus*, and unlike that of all other Gotland chitons. The transverse anterior margin is slightly embayed medially, by comparison with the smoothly rounded anterior in *G. interplicatus*, and the jugal angle on the broken sclerite appears to be slightly greater at *c.* 105°. The side slope is less deep, the antero- and posterolateral margins appear roughly equal in length, i.e. longer, and shorter and steeper, respectively. No shell fields are apparent. The broad apical area would imply complete coverage across the adjacent sclerite; its transverse anterior margin is unique among the Gotland chiton fauna.

The specimen is notably younger than *G. interplicatus*, from the Upper Ludlow as opposed to Upper Wenlock. Because it is only a single specimen, from a stratigraphical horizon that has previously yielded only *Chelodes gotlandicus* Lindström, 1884, it has been left under open nomenclature.

Genus THAIROPLAX gen. nov.

Derivation of name. From the Greek *thairos*, hinge, and *plax*, plate, to indicate the flexed form of sclerites.

Type species. Thairoplax pelta gen. et sp. nov.; Upper Wenlock, Silurian, Gotland, Sweden.

Diagnosis. Arched intermediate sclerites flexed longitudinally across jugum, jugal angle perpendicular to slightly obtuse, side slopes straight, trapezoidal; anterior margin transverse; posterolateral shell triangulate, posterior apex pointed, acute. Ventral apical area broad, V-shaped, less than one-third of length. Shell becoming medium to large size, typically longer than wide, thicker medially, tapering outwards; ventral surface smooth, without localized thickening. Ornament of fine growth lines. Shell fields weak. Broad central and narrower lateral fields.

Remarks. *Thairoplax* gen. nov. is similar to *Chelodes* in having fairly large, wedge-shaped sclerites with a posterior apex, but differs in its marked jugal flexure between straight trapezoidal side slopes, and in limited ventral thickening, greater medially, in contrast to the thick to massive, sculptured ventral surface in larger sclerites of *Chelodes*. *Thairoplax* differs from *Gotlandochiton*, which is similar in having flexed intermediate sclerites with straight side slopes, in having sclerites at least as long as wide, a transverse anterior margin, a more acute apex, and a distinctly V-shaped apical area.

Paleochiton Smith, 1964 (*P. kindbladensis* Smith, *in* Smith and Toomey, 1964) and *Kindbladochiton* Van Belle, 1975 (*K. arbucklensis* (Smith, *in* Smith and Toomey, 1964); Van Belle 1975) are monospecific early Ordovician genera from southern Oklahoma, USA, which have broadly rectangular intermediate sclerites, but both have transverse posterior margins, in contrast to the extended, triangulate posterior portion of the sclerite in *Thairoplax*. In *Paleochiton* the ventral apical area is short and bandlike. *Kindbladochiton* has a ventral transverse thickened ridge lacking in the smooth ventral surface of *Thairoplax*. Kluessendorf (1987) described chiton morphotype A from the middle–upper Silurian of Wisconsin, USA, for a flexed shell with flat side slopes and parallel lateral margins, which on general form and V-shaped anterior margin of the apical area could belong within *Thairoplax* (see discussion of *T. birhombivalvis* below).

Thairoplax pelta gen. et sp. nov.

Plate 2, figures 1–3

Derivation of name. From the Greek *pelte*, shield, to describe the shape of sclerites.

Material, locality and horizon. Seven intermediate sclerites, Möllbos-1, Gotland, Halla Formation, Upper Wenlock (Homerian); holotype RM Mo159.901*, isolated plate with dorsal small bryozoan encrustation; syntypes RM Mo159.937, 159.952*, 159.972, 159.973*, 160.019, 160.026.

Diagnosis. Shield-shaped intermediate sclerites flexed slightly obtusely across jugum, rounded jugal ridge, side slopes long; sclerites elongate. Ventral apical area short, apical length/length $< 0{\cdot}2$.

Description. Shield-shaped intermediate sclerites of medium size (mean length 15·3 mm, s.d. = 2·86, $n = 6$; holotype length 12·1 mm), elongate, mean length/width 1·4 (s.d. = 0·09, $n = 6$; holotype 1·38). Flexed and thickened slightly medially across rounded jugal ridge, tapering across flat, trapezoidal side slopes towards lateral margins; mean jugal angle 103° (s.d. = 3·8, $n = 7$; holotype 108°). Anterior part of shell roughly rectangular, long, with anterior margin close to transverse, very slightly embayed to convex, median length/length 0·99 (s.d. = 0·02, $n = 6$; holotype 1·0), anterolateral corners rounded. Straight anterolateral margins more than half the length of the sclerite, almost parallel, maximum width towards anterior, in front of midlength; posterolateral corners distinct; shorter, straight posterolateral margins tapering rapidly to acute posterior pointed apex, mean apical angle 69° (s.d. = 5·6, $n = 7$; holotype 70°). Dorsal sculpture of fine growth lines parallel to anterior and anterolateral margins, crossing onto ventral apical area (e.g. Pl. 2, fig. 3a, c); parallel, prominent larger growth steps (e.g. Pl. 2, figs a, c). The latest growth lines may be entirely ventral, forming a narrow ventral rim, e.g. holotype (Pl. 2, fig. 1b). Weak dorsal radial folds give poor definition of broad central and narrow posterolateral areas (Pl. 2, figs 1a, 3a).

Ventral apical area short, narrow band tapering across to posterolateral corners, to markedly V-shaped (Pl. 2, figs b), mean apical length/length 0·18 (s.d. = 0·02, $n = 5$; holotype 0·10). Apical area ornamented with growth lines, anterior margin slightly raised above smooth ventral surface.

Lateral profile (Pl. 2, figs c) shows straight jugal ridge, roughly parallel anterolateral margin, transverse anterior margin and rapidly tapering, shorter posterolateral margin. Transverse section (Pl. 2, figs d) V-shaped posteriorly, becoming more rounded anteriorly, side slopes straight and tapering. Mean height/length 0·34 (s.d. = 0·05, $n = 7$; holotype 0·37).

Remarks. *T. pelta* differs from the similar-aged (late Wenlock) *Gotlandochiton interplicatus* in having elongate sclerites, weakly defined shell areas with a broad triangular central field, a bandlike to strongly V-shaped ventral apical area, and ornament of only fine growth lines.

T. pelta is found among collections from Möllbos-1 dominated quantitatively by *C. actinis*, from which it is easily distinguished by its flexed, shield-shaped, non-massive form.

Thairoplax? aff. *pelta*?

Plate 3, figure 4

Material, locality and horizon. Möllbos-1, Gotland, Halla Formation, Upper Wenlock (Homerian); one isolated intermediate sclerite, RM Mo160.020*.

Description. Arched, medium sized intermediate sclerite, similar length to width, flexed across jugum, side slopes straight; length 12·1 mm, length/width 1·04, height/length 0·42, jugal angle 96°. Anterior margin transverse, slightly embayed, rounding through fairly long, gently convex and divergent anterolateral margins; maximum width at posterolateral corners, behind midlength. Posterolateral margins straight, similar length to anterolateral margins, tapering rapidly across triangulate posterior shell to pointed apex, apical angle 85°. Ventral apical area broad, V-shaped, tapering outwards, apical length/length 0·31. Ventral surface smooth, not greatly thickened, but with rounded, low triangular transverse ridge between posterolateral corners, tapering anteriorly, posteriorly extending as narrow median pad flanked by low furrows towards anterior rim of apical area (Pl. 3, fig. 4b). Dorsal weak low radial jugal fold across fairly narrow anterior embayment; fine growth lines.

Remarks. This specimen occurred in a sample with *T. pelta* and *C. actinis*, and is broadly similar in its flexed form with straight side slopes and V-shaped apical area to *T. pelta*. However, it differs in having rounded anterolateral margins, slightly tapering anteriorly and of similar length to the posterolateral margins, in having a relatively long apical area (apical length/length 0·31, cf. mean 0·18 for *T. pelta*), and particularly in the localized ventral thickening into a low transverse ridge. It may represent an anterior intermediate sclerite of *T. pelta*, tapering towards a typically small head sclerite, but the pattern of ventral thickening, unseen otherwise in *T. pelta*, may indicate that it does not belong within this species (or genus?).

Thairoplax birhombivalvis (Bergenhayn, 1955)

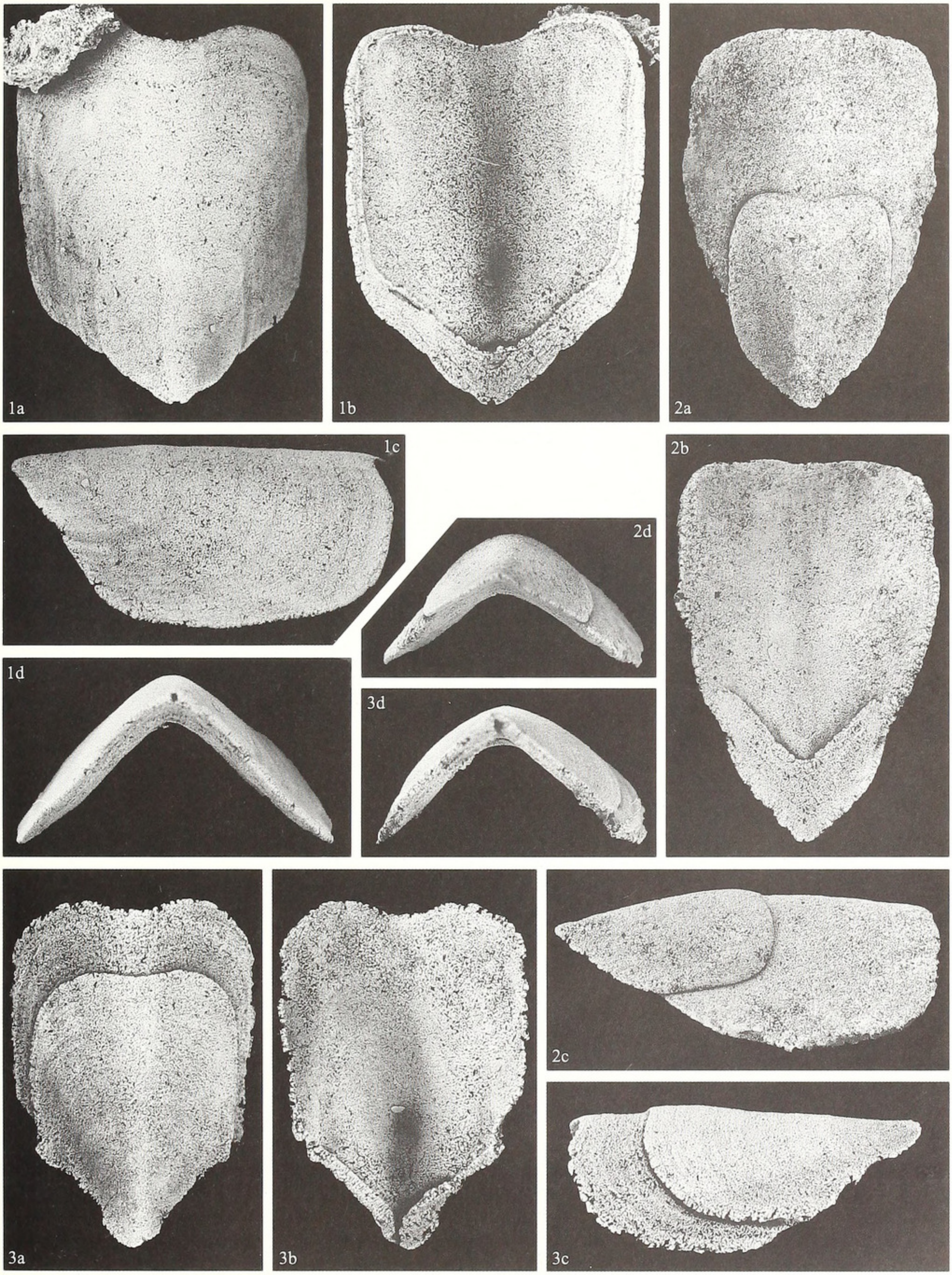
Plate 1, figures 2–5

v* 1955 *Gotlandochiton birhombivalvis* Bergenhayn, p. 18, pl. 1, fig. 7; pl. 2, fig. 6 [reconstruction].
1977 *Gotlandochiton birhombivalvis* Bergenhayn; Sirenko and Starobogatov, p. 31.
1987 *Gotlandochiton birhombivalvis* Bergenhayn; Smith and Hoare, p. 15.

Material, locality and horizon. Four intermediate sclerites; holotype RM Mo6031*, external mould of ventral surface, Visby, Gotland, Lower Visby Formation (Visby a), Upper Llandovery (Telychian); syntypes RM Mo6023* and 6024* (two specimens), Kålens kvarn (= Kolens kvarn), Visby, Gotland, Högklint Formation, Lower Wenlock (Sheinwoodian).

EXPLANATION OF PLATE 2

Figs 1–3. *Thairoplax pelta* gen. et sp. nov.; Möllbos-1, Gotland; Halla Formation, upper Wenlock (Homerian); intermediate sclerites. 1, holotype (with small bryozoan encrustation on left anterior), RM Mo159.901; 1a, dorsal view; 1b, ventral view; 1c, right lateral view; 1d, posterior view. 2, RM Mo159.973; 2a, dorsal view, showing prominent growth increment; 2b, ventral view; 2c, right lateral view; 2d, posterior view. 3, RM Mo159.952; 3a, dorsal view, showing prominent growth increment, broad central shell field; 3b, ventral view; 3c, right lateral view; note weak fold defining broad central shell field, fine growth ornament; 3d, posterior view. All ×3.



CHERNS, *Thairoplax*

Diagnosis (emended from Bergenhayn 1955, p. 18). Intermediate sclerites with deep side slopes, jugal ridge sharp to more rounded, jugal angle almost perpendicular; anterolateral margins slightly divergent, posterolateral margins longer, maximum width at posterolateral corners, apical angle acute. Ventral apical area tapering rapidly outwards, apical length/length *c.* 0·3.

Description. The holotype is a distorted, arched, ventral external mould, showing flat, deep trapezoidal side slopes diverging almost perpendicularly (87°) across a sharp jugal ridge, and with a broad, V-shaped apical area that tapers rapidly outwards from its central flexure, apical length/length 0·31. Triangulate posterior shell to pointed apex, apical angle 71°, straight posterolateral margins, longer than anterolateral margins, bordered by apical area (Pl. 1, fig. 2). RM Mo6023 (Pl. 1, fig. 3) shows only the dorsal surface, strongly arched (height/length 0·58) across a jugal flexure (86°) sharper posteriorly but becoming more rounded anteriorly, and with weakly defined, broad triangular central shell field expanding from apex to outside anterolateral corners on deep trapezoidal side slopes. Sclerite fairly large (length 13·9 mm), slightly longer than wide (length/width 1·07), not greatly thickened. Anterior margin straight across flexed central area, anterolateral corners sharply rounded into straight to only slightly convex lateral margins, and longer, straight posterolateral margins tapering rapidly to apex; apical angle 73°. Growth lines, or possibly slightly stronger ornament of very shallow ridges and grooves, follow anterior and anterolateral margins, crossing onto the ventral apical area at posterolateral corners behind mid-length; larger growth increments indicated by spaced narrow ridges/grooves (Pl. 1, fig. 3b). Two worn and coarsely replaced chiton specimens on RM 6024, both partially embedded in limestone, come from the same locality as RM Mo6023, from a slightly younger horizon than the holotype. One has the apex broken off, but shows part of the dorsal surface arched strongly across the jugal ridge, as in RM Mo6023, and appears from growth lines to have a transverse anterior margin and straight anterolateral margins (Pl. 1, fig. 4). The other specimen shows the left dorsal surface including the apex, with a long straight posterolateral margin tapering to a pointed apex (Pl. 1, fig. 5). Bergenhayn (1955) noted a granular sculpture preserved on one sclerite, presumably RM Mo6023, where coarse sparite replacement of the shell has produced an apparent surface pattern.

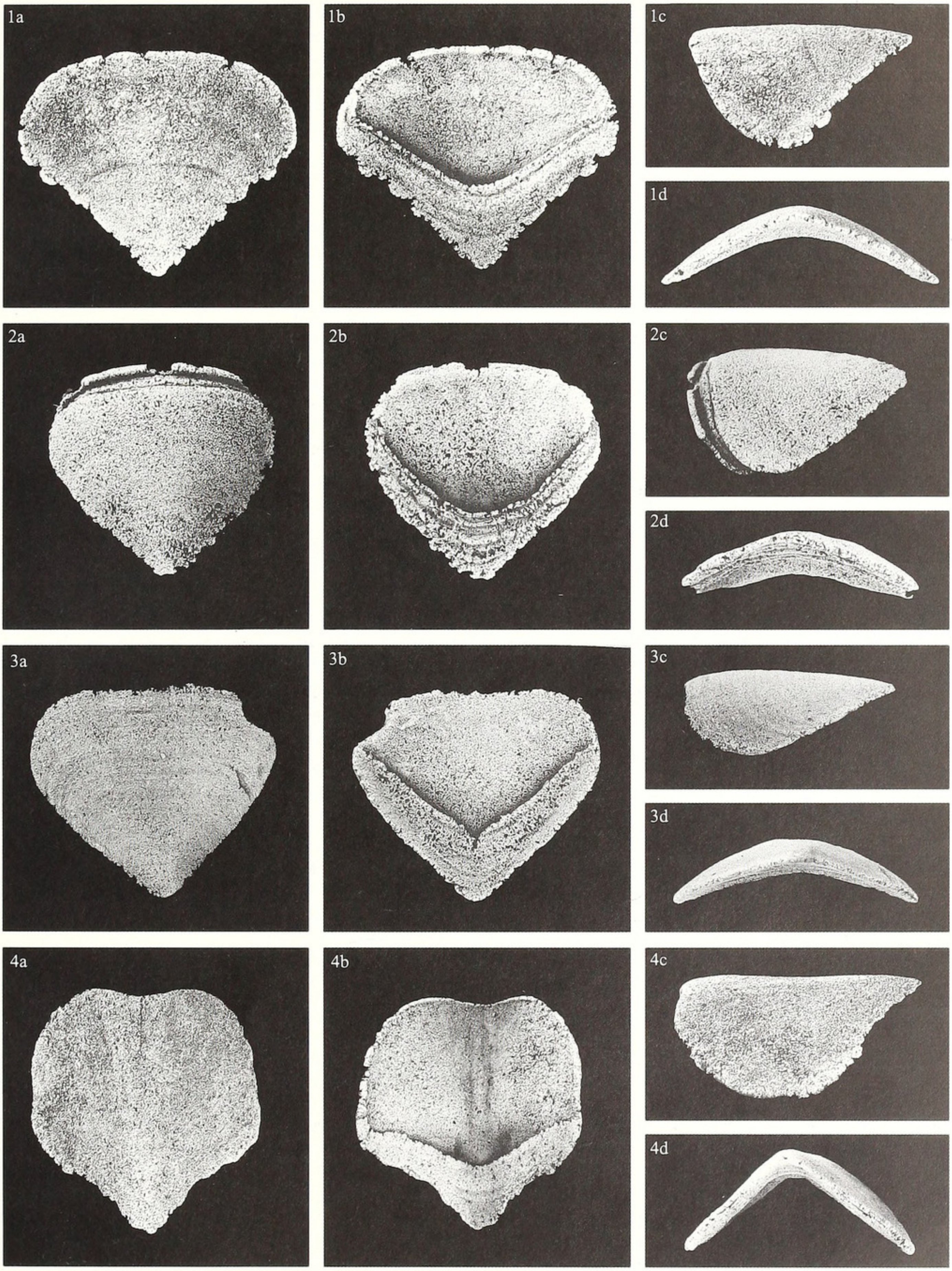
Remarks. Bergenhayn (1955, p. 18) based this species, which he considered very distinct, on the four intermediate sclerites described above from Visby and Kålens kvarn, Visby, from the Upper Llandovery to Lower Wenlock. Specific characters, of two rhomboid shaped sides hinged along the midline at a jugal angle of *c.* 90°, an ornament of very low, evenly spaced growth lines (= larger growth increments), and total coverage across the adjacent plate (indicated by a broad apical area), he noted as combined with an absence of shell fields. Despite the lack of shell fields, he still assigned the species to *Gotlandochiton* on the basis that the shell form and, more questionably, complete coverage did not belong within *Chelodes*.

In comparison with *T. pelta*, the older species *T. birhombivalvis*, based on more limited, non-isolate material, has deeper, shorter side slopes, a more perpendicular flexure, longer posterolateral margins across the triangulate posterior shell, and a longer V-shaped apical area. Intermediate sclerites are broader and less elongate.

EXPLANATION OF PLATE 3

Figs 1–3. *Plectrochiton tegulus* gen. et sp. nov.; Möllbos-1, Gotland; Halla Formation, Upper Wenlock (Homerian). 1, RM Mo160.032, holotype; intermediate sclerite. 1a, dorsal view; 1b, ventral view, note ?weak transverse ridge between anterolateral corners; 1c, left lateral view; 1d, posterior view. All × 5. 2, RM Mo159.942; intermediate sclerite. 2a, dorsal view; 2b, ventral view; 2c, left lateral view; 2d, posterior view. All × 5. 3, RM Mo159.900; intermediate sclerite. 3a, dorsal view; 3b, ventral view; 3c, left lateral view; 3d, posterior view. All × 4.

Fig. 4. *Thairoplax*? aff. *pelta*?, Möllbos-1, Gotland; Halla Formation, Upper Wenlock (Homerian); RM Mo160.020, intermediate sclerite. 4a, dorsal view showing weak narrow jugal fold; 4b, ventral view; note low transverse ridge anterior to apical area, with tapering extension beneath apical area rim; 4c, left lateral view; 4d, posterior view. All × 3.



CHERNS, *Plectrochiton*, *Thairoplax*?

Kluessendorf (1987) compared Morphotype A, an incomplete specimen showing the ventral surface, from the Racine Dolomite (Wenlock/Ludlow) of Wisconsin, USA, with *T. birhombivalvis*, on the basis of a flexed form with flat side slopes and parallel lateral margins. The elongate form and apparently short apical area are more similar to *T. pelta*, although there are insufficient diagnostic characters to allow close comparison.

PLECTROCHITON gen. nov.

Derivation of name. From the Greek *plektron*, a tool for plucking a stringed instrument, to describe the triangulate shape of sclerites.

Type species. *P. tegulus* gen. et sp. nov., from the Upper Wenlock, Silurian of Gotland, Sweden.

Diagnosis. Broad and short, small low-arched triangulate sclerites, wider than long; transverse to gently convex anterior margin, rounded anterolateral corners, tapering straight posterolateral margins to broad, pointed posterior apex, apical angle almost perpendicular. Ornament of fine growth lines; no shell fields, jugal angle obtuse, *c*. 125°. Apical area approximately one-third of length, wide, tapering outwards to anterolateral corners, V-shaped to concave anterior margin. Ventral surface smooth, concave, triangulate to lozenge-shaped.

Remarks. The small, broad and only gently arched, triangulate form of intermediate sclerites in *Plectrochiton* gen. nov., without shell fields and with only fine growth line ornament, is distinct from other genera of Palaeozoic chitons (e.g. Smith and Toomey 1964, p. 17). By comparison with other Gotland chitons, *Chelodes* Davidson and King, 1874 has commonly large, elongate, wedge- to heart-shaped intermediate sclerites, in some species with shell fields. *Gotlandochiton* Bergenhayn, 1955 and *Thairoplax* gen. nov. have medium to large, flexed sclerites with straight trapezoidal side slopes. The triangulate form distinguishes *Plectrochiton* gen. nov. from the roughly rectangular sclerites of Ordovician *Paleochiton* Smith, *in* Smith and Toomey, 1964, and *Kindbladochiton* Van Belle, 1975, and from the Ordovician–Cretaceous *Ivoechiton* Bergenhayn, 1955.

Plectrochiton tegulus gen. et sp. nov.

Plate 3, figures 1–3

Derivation of name. From the Latin *tegulus*, a tile, to describe the very low-arched form.

Material, locality and horizon. Eight intermediate sclerites from Möllbos-1, Gotland; Halla Formation, Upper Wenlock (Homerian); holotype RM Mo160.062*, isolated plate, syntypes 159.865–159.866, 159.874, 159.900*, 159.936, 159.942*, 160.009.

Diagnosis. As for the genus.

Description. Small and low-arched, short broad triangulate intermediate sclerites that are wider than long, without shell fields. Mean length 5·9 mm (s.d. = 2·2, $n = 8$; holotype 7·1 mm), mean length/width 0·87 (s.d. = 0·04, $n = 6$; holotype 0·86), mean jugal angle 125° (s.d. 3·8, $n = 8$; holotype 123°). Wide anterior margin straight to gently convex, with rounded anterolateral corners, no anterolateral margins, tapering straight posterolateral margins to broad, pointed posterior apex, mean apical angle 88° (s.d. = 9·1, $n = 8$; holotype 91°). Maximum width across anterolateral corners, well anterior of midlength. Ornament of fine growth lines parallel to anterior margin, transecting posterolateral margins onto ventral apical area. Apical area with mean apical length/length 0·29 (s.d. = 0·08, $n = 6$; holotype 0·35), wide, with a slightly raised anterior margin V-shaped to rounded and concave anteriorly (Pl. 3, figs 1b, 2b, 3b), tapering outwards along posterolateral margins to anterolateral corners. Ventral surface smooth, concave, triangulate to lozenge-shaped, may have slight transverse thickening across between anterolateral corners (Pl. 3, fig. 1b).

Lateral profile triangular, fairly shallow, with flat to slightly convex dorsal surface, gently convex anterior margin (Pl. 3, figs 1c, 2c, 3c). Transverse section shallow, shell thicker medially, tapering laterally (Pl. 3, figs 1d, 2d, 3d).

Remarks. *P. tegulus* gen. et sp. nov. is distinguished from small sclerites of *C. actinis* Cherns, 1998, which co-occur in samples from Möllbos, by the absence of anterior invagination, lower length to width ratio, and shallower transverse profile with a more obtuse jugal angle. The slightly elevated anterior rim to the apical area may indicate muscle attachment along this margin (Cherns 1998). The fairly small sized, triangulate sclerites could represent head or tail sclerites, although they lack features commonly found in such sclerites of chitons, such as distinct, commonly radiate, ornament of head sclerites, and a prominent mucro in tail sclerites (e.g. Smith 1960; Hyman 1967). For *C. actinis*, ovoid, ornamented plates that co-occur with the intermediate sclerites have been described as head sclerites (Cherns 1998).

ALASTEGA gen. nov.

Derivation of name. From the Latin *ala*, wing, and Greek *stege*, roof, to described the winged form of the sclerites.

Type species. *A. lira* gen. et sp. nov. from the Upper Wenlock, Silurian of Gotland, Sweden.

Diagnosis. Small arched sclerites, flexed across jugum, with triangulate, pointed posterior apex; slightly elevated and rounded, broad triangulate jugal shell field flattening anteriorly; apical angle nearly perpendicular, jugal angle slightly obtuse; ornament of shallow rounded ridges and furrows, growth lines, stronger on lateral fields. Intermediate sclerites small, wide and short, strongly arched and winged; jugal ridge rounded anteriorly, broad anterior embayment, side slopes deep and straight, triangulate posterior shell to apex. Ventral apical area short V-shaped band tapering across long posterolateral margins. Transverse ventral thickening forming V-shaped ridge, tapering outwards. Tail sclerites as long as wide, lower arched, more triangulate and weakly trilobed, shallower anterior embayment; jugal field elevated and rounded, side slopes shallower; apical area short, V- to U-shaped anterior margin, tapering across long posterolateral margins, ventral surface with transverse V-shaped thickening. Head sclerites small, elongate, ovoid, low arched; distinct rounded triangulate jugal field, posterior pointed apex; ventral surface smooth, concave, apical area not known.

Remarks. Small, short and wide, winged and strongly arched intermediate sclerites with distinct transverse ventral thickening at around mid-length parallel to the short V-shaped apical area are characteristic of *Alastega* gen. nov. *Ivoechiton* (*I. oklahomensis* Smith, *in* Smith and Toomey, 1964; *I. calathicolus* Smith, *in* Smith and Toomey, 1964) and *Kindbladochiton* (*K. arbucklensis* Smith, *in* Smith and Toomey, 1964) from the lower Ordovician of Oklahoma, USA, have intermediate sclerites wider than long, with a transverse thickening across the ventral surface of sclerites, and with a posterior margin swept back from the apex or transverse (Smith and Toomey 1964). *Alastega* gen. nov. differs from *Ivoechiton* in having defined shell fields, and from both in its long straight posterolateral margins tapering across the triangulate posterior shell to a pointed apex, with a corresponding V-shaped ventral apical band.

Alastega lira gen. et sp. nov.

Plate 4; Text-figure 4

Derivation of name. From the Latin *lira*, plough ridge, to describe the dorsal ornament.

Material, locality and horizon. Möllbos-1, Gotland, Halla Formation, Upper Wenlock (Homerian); 21 isolated sclerites (including four tail sclerites); holotype RM Mo159.845*, intermediate sclerite; RM Mo159.827, 159.846–159.847, 159.848*, 159.852, 159.876–159.882, 159.893–159.894, 159.917, 159.949, 159.987; tail sclerites 159.826*, 159.849*, 159.883, 160.010. Klintebys-1, Gotland, Halla Formation, Upper Wenlock (Homerian); 21 isolated sclerites (including two head, three tail sclerites); 160.036–160.037, 160.039, 160.041, 160.043–160.046, 160.048, 160.050–160.053, 160.057, 160.058*, 160.059, head sclerites 160.047, 160.060*, tail sclerites 160.038, 160.040, 160.049.

Diagnosis. As for the genus.

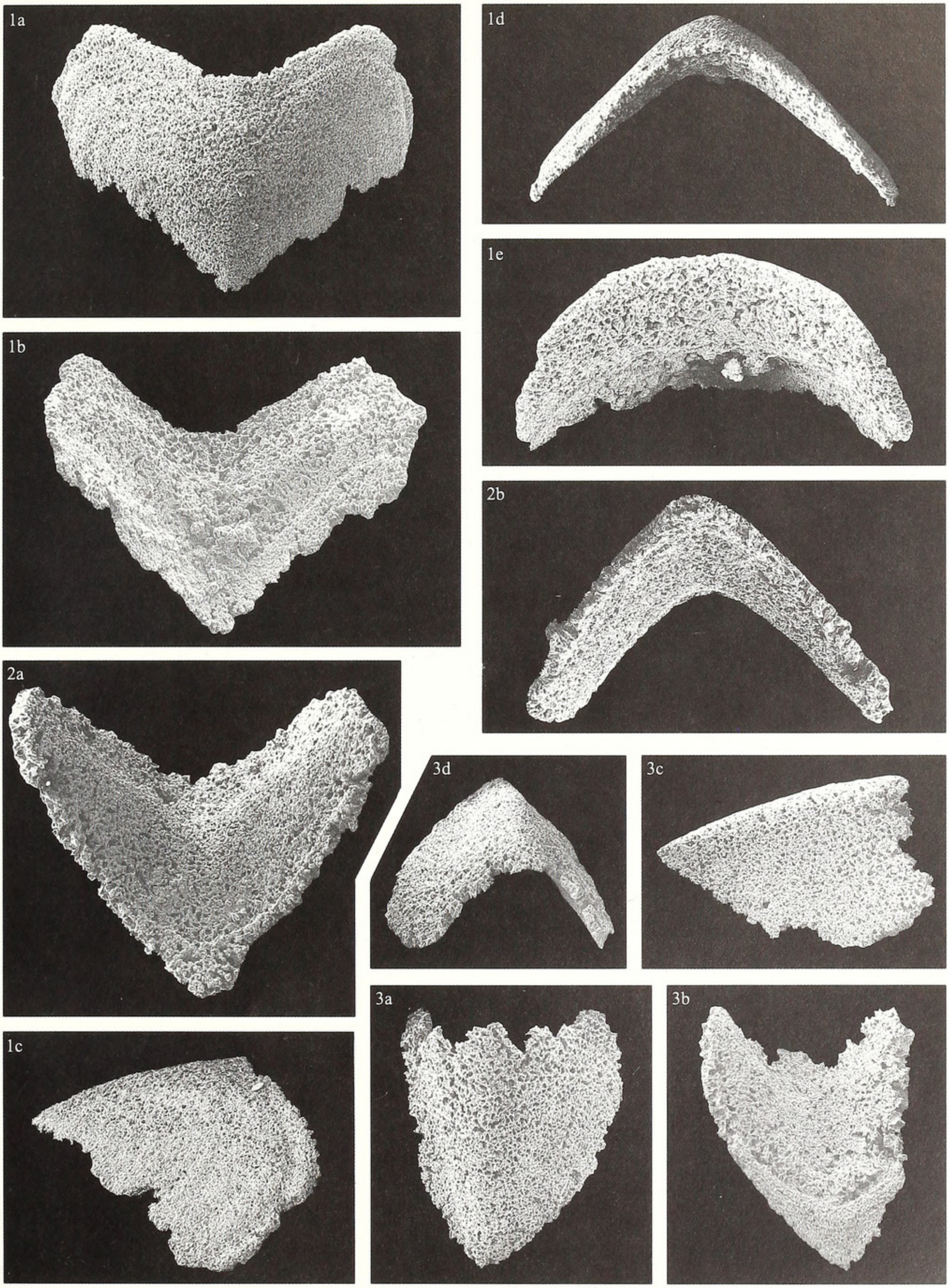
Description. Intermediate sclerites (Pl. 4, figs 1–2; Text-fig. 4D–G) small, strongly arched and winged, flexed across rounded jugum, side slopes straight and deep. Mean length 3·6 mm (s.d. = 2·0, $n = 28$; holotype 2·7 mm), smaller sclerites much wider than long, becoming less so with growth, mean length/width 0·78 (s.d. = 0·18, $n = 20$; holotype 0·66). Jugal ridge flattening anteriorly over slightly elevated and rounded, broad triangulate jugal field, mean jugal angle 96° (s.d. = 8, $n = 32$; holotype 97°). Anterior margin broad, rounding through shallow median embayment across jugal field, mean median length/length 0·88 (s.d. = 0·06, $n = 27$; holotype 0·85). Strongly rounded anterolateral corners into short, slightly convex, divergent anterolateral margins, maximum width at posterolateral corners. Posterolateral margins longer, straight, tapering rapidly across triangulate posterior to pointed broad apex; mean apical angle 88° (s.d. = 12, $n = 26$; holotype 89°). Ornament of shallow rounded ridges and furrows, and growth lines, sinuate parallel to anterior and anterolateral margins, stronger on lateral fields (Pl. 4, fig. 1a, c; Text-fig. 4D, F). Ventral surface with short, V-shaped apical area as slightly raised band across posterolateral margins, tapering outwards to posterolateral corners, mean apical length/length 0·17 (s.d. = 0·06, $n = 15$; holotype 0·19). Ventral surface smooth, with transverse thickened triangular ridge around midlength, V-shaped, thickest medially, tapering towards and flattening anteriorly and posteriorly (Pl. 4, fig. 1b, e, 2a–b; Text-fig. 4E), becoming relatively more posterior with increased size of sclerite. Lateral profile (Pl. 4, fig. 1c, Text-fig. 4F) gently convex dorsally, weak radial fold elevating low jugal area, deep side slopes to posterolateral corners, steep straight posterolateral margins, sinuate shallowing anterolateral to anterior margins. Transverse profile strongly arched across jugal flexure rounding anteriorly, side slopes straight, tapering outwards (Pl. 4, figs 1d–e, 2b; Text-fig. 4G), mean height/length 0·67 (s.d. = 0·18, $n = 28$; holotype 0·78). Thickened ventral ridge producing longitudinal flexure of ventral surface into two inclined planes, particularly evident in smaller specimens; inclined posterior profile with V-shaped ventral surface, angular ventral flexure (Pl. 4, fig. 2b), inclined anterior profile with lunate ventral surface (Pl. 4, fig. 1e).

Tail sclerites (Pl. 4, fig. 3; Text-fig. 4A–C) roughly as long as wide, mean length 3·6 mm (s.d 1·2, $n = 5$), mean length/width 1·04 (s.d. = 0·27, $n = 3$), lower arched, more triangulate and weakly trilobed. Elevated, rounded and broad triangulate jugal field, narrower, less convex lateral fields, mean jugal angle 101° (s.d. = 9, $n = 5$). Anterior margin more shallowly embayed across jugal field, mean length/length 0·93 (s.d. = 0·06, $n = 4$), strongly rounded anterolateral corners into very short anterolateral margins, long straight posterolateral margins tapering across triangulate posterior to pointed posterior apex, mean apical angle 88° (s.d. = 27, $n = 5$). Ornament of growth lines, low ridges/furrows poorly preserved. Ventral short apical area with V- to U-shaped elevated margin, tapering outwards across posterolateral margins (Pl. 4, fig. 3b; Text-fig. 4B), mean apical length/length 0·21 (s.d. = 0·04, $n = 3$). Ventral surface smooth, flexed across broad transverse triangulate thickened ridge, greatest medially, V-shaped, around midlength. Longitudinal profile showing shallower side slopes, radial fold elevating jugal field, less steep posterolateral margins (Pl. 4, fig. 3c; Text-fig. 4C). Anterior transverse profile lower arched, side slopes straight, mean height/length 0·42 (s.d. = 0·05, $n = 5$); inclined anterior ventral surface lunate, inclined posterior ventral surface with more angular flexure.

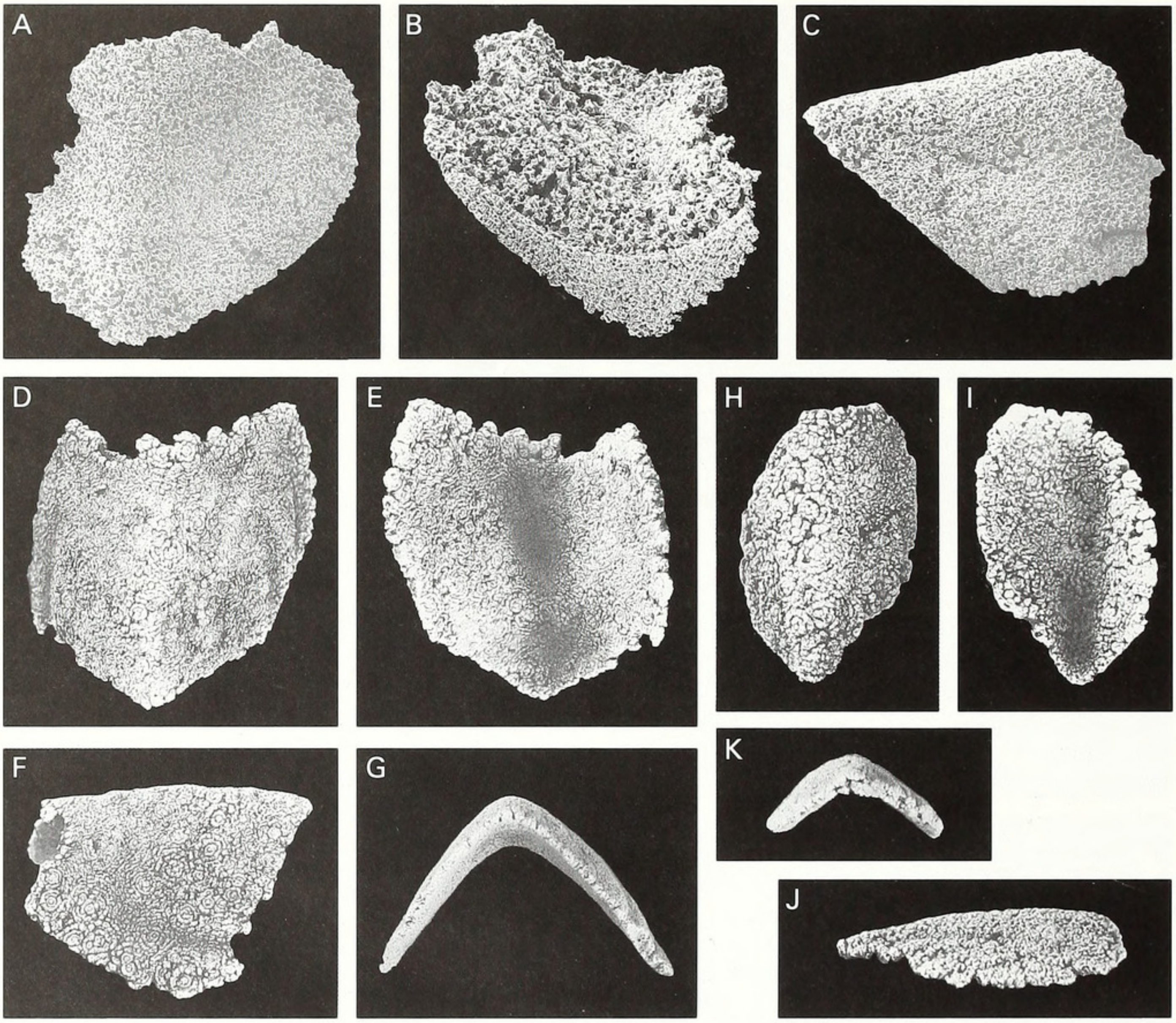
EXPLANATION OF PLATE 4

Figs 1–3. *Alastega lira* gen. et sp. nov.; Möllbos-1, Gotland; Halla Formation, Upper Wenlock (Homerian). 1, RM Mo159.845, holotype; intermediate sclerite. 1a, dorsal view; note rounded ridge-and-furrow ornament; 1b, ventral view, showing V-shaped transverse ridge; 1c, right lateral view; 1d, posterior view; 1e, anterior, slightly tilted view to show lunate anterior surface of transverse ridge. 2, RM Mo159.848; intermediate sclerite. 2a, ventral view, showing V-shaped transverse ridge further anterior than in 1b; 2b, posterior, slightly tilted view to show V-shaped posterior surface of transverse ridge. 3, RM Mo159.849; tail sclerite. 3a, dorsal view, note elevated fold of central shell field; 3b, ventral view, V-shaped transverse ridge well in front of apical area; 3c, right lateral view; 3d, anterior view. All × 15.

PLATE 4



CHERNS, *Alastega*



TEXT-FIG. 4. *Alastega lira* gen. et sp. nov. A–C, RM Mo159.826; Möllbos-1, Gotland; Halla Formation, Upper Wenlock (Homerian); tail sclerite, fragmented on left side. A, dorsal view, showing elevated fold of central shell field. B, ventral view, transverse ridge well in front of apical area. C, right lateral view, showing elevated central shell field. All ×20. D–G, RM Mo160.058; Klintebys-1, Gotland; Halla Formation, Upper Wenlock (Homerian); beekitized intermediate sclerite. D, dorsal view; note elevated shell central field, rounded ridge-and-furrow ornament. E, ventral view; note V-shaped transverse ridge. F, left lateral view, showing well developed ornament. G, posterior view. All ×5. H–K, RM Mo160.060; Klintebys-1, Gotland; Halla Formation, Upper Wenlock (Homerian); head sclerite. H, dorsal view, showing elevated central field, rounded ridged ornament on lateral fields. I, ventral view. J, lateral view, showing elevated fold of central field. K, posterior view. All ×7.

Head sclerites (Text-fig. 4H–K) known only from two specimens, both beekitized, one poorly preserved. Small, ovoid, low arched, elongate, with distinct rounded, triangulate jugal field; mean length 4·6 mm (s.d. = 0·57, $n = 2$), mean length/width 1·33 (s.d. = 0·40, $n = 2$), mean jugal angle 95° (s.d. = 1, $n = 2$). Anterior margin transverse to gently convex across jugal field, rounding into long, convex anterolateral margins, short straight posterolateral margins tapering rapidly across triangulate posterior to pointed apex; apical angle *c.* 88°. Ornament of low rounded ridges and furrows, growth lines, particularly developed on lateral fields. Ventral surface smooth, concave, deepest towards posterior, apical area unknown but probably very short. Lateral profile shallow, low fold elevating jugal field. Posterior profile low arched, mean height/length 0·29 (s.d. = 0·07, $n = 2$), short straight side slopes.

Remarks. The thickened transverse ventral ridge characteristic of this genus associates the short, wide, high arched intermediate sclerites with relatively longer, more triangulate, lower arched tail sclerites. In particular, the lunate shape of the anterior ventral surface of the thickening is distinctive. In addition, in both these types of sclerite and in the elongate, ovoid and shallow arched head sclerites the dorsal surface has a triangulate, slightly elevated and rounded jugal field, and distinctive ornament of shallow rounded ridges and furrows, preserved better on the flatter lateral fields. All have almost perpendicular apical angles and slightly obtuse jugal angles. The ovoid elongate shape and shallow form of the head sclerites show similarities to those described recently for the large chiton *C. actinis* (Cherns 1998, text-fig. 4), although the *A. lira* sclerites are much smaller, with coarser ridged ornament, and a more distinct and rounded jugal field.

The material of *A. lira* comes from Möllbos-1 and Klintebys-1, both from the Late Wenlock Halla Formation. All specimens from Möllbos-1 are small but include some that are well preserved. Many of those from Klintebys-1 are poorly preserved and beekitized, but they include also larger examples, of both intermediate and tail sclerites. The size difference is notable, with several 7–9 mm long, compared with the means (including these) of 3·6 mm, and unfortunately the sclerites preserve poor detail. However, they do share the general form and characteristic ventral ridge in both intermediate and tail plates, and co-occur in samples with the more typical, small specimens; hence they are treated here as the same species.

In intermediate sclerites, the ventral thickening becomes relatively more posterior as the shell lengthens, and its anterior lunate surface develops shallow sculpting to enhance lateral pads (Text-fig. 4E, cf. Pl. 4, fig. 1b). The ventral thickening in longer (i.e. larger) intermediate sclerites produces a natural balance, and presumed life position, with gentle anterior tilt of the jugal field, leaving the ventral anterior surface horizontal and the posterior surface behind the ridge elevated slightly.

The intermediate sclerites show variation in the breadth of anterior embayment and degree of divergence of anterolateral margins. These features may relate to different positions of plates along the animal, in particular to narrowing of the broad intermediate sclerites anteriorly towards the elongate head sclerite.

HELOPLAX gen. nov.

Derivation of name. From the Greek *helos*, nail, stud, and *plax*, plate, to describe the rounded form of sclerites.

Type species. *H. papilla* gen. et sp. nov. from the Upper Wenlock (Silurian) of Gotland, Sweden.

Diagnosis. Small, transversely elongate, ovoid intermediate sclerites with subcentral elevated mucronate apex, rounded margins. Fairly broad, vaulted triangulate anterior field; broader triangulate posterior field, concave becoming flattened to convex posteriorly, elevated; depressed lateral fields across transverse flexure. Maximum shell width slightly posterior of mid-length, at posterolateral corners. Dorsal concentric growth lines; distinct granular ornament, coarser anteriorly and laterally, also coarsening outwards; quincunx pattern but with line of larger granules demarcating posterior field. Ventral surface with small deep median subapical cavity, oblique towards anterior. Ventral thickening leading to strongly sculpted surface around subapical area. ?Tail sclerites smaller, relatively broad, vaulted convex anterior and posterior fields, coarser line of ornament within lateral fields.

Remarks. *Heloplax* gen. nov. differs from all other paleoloricate chitons, except *Enetoplax* gen. nov. and *Arctoplax* gen. nov. described below, in having small ovoid intermediate plates with a dorsal mucronate apex, and concentric holoperipheral growth (Text-fig. 2). They thereby lack the ventral apical area of sclerites with a posterior apex, representing extension of the dorsal outer tegmentum onto the ventral surface, found in at least most paleoloricate chitons, and in neoloricate chitons except for tail sclerites (e.g. *Pterochiton spatulatus*, *Pedanochiton discomptus*; Smith and Toomey 1964; Debrock *et al.* 1984; Hoare 1989). In *Heloplax*, the sclerites are vaulted and convex anteriorly, and in most the concave post-apical posterior field becomes elevated. This shell morphology suggests that these are intermediate sclerites, which can become imbricated, and not tail plates. Variations in morphology suggest that both intermediate and tail plates are represented, the latter being vaulted and convex both anteriorly and posteriorly.

From the Lower Carboniferous (Mississippian) of Utah, Hoare (1989) described as a tail plate a single small sclerite of generally similar configuration to *Heloplax*, but with sutural laminae and hence a neoloricate chiton.

Heloplax papilla gen. et sp. nov.

Plates 5–6

Derivation of name. From the Greek *papilla*, bud, nipple, to describe the granular ornament.

Material, locality and horizon. Möllbos-1, Gotland, Halla Formation, Upper Wenlock (Homerian); 25 isolated sclerites; holotype RM Mo159.832*, intermediate sclerite; intermediate sclerites RM Mo159.828*, 159.829*, 159.830–159.831, 159.833, 159.867*, 159.884, 159.891–159.892, 159.896, 159.898, 159.912, 159.920, 159.954, 159.968, 159.997, 160.011, 160.017; ?tail sclerites RM Mo159.834, 159.851*, 159.886–159.887, 159.889, 159.984.

Diagnosis. As for the genus.

Description. (Text-fig. 2). Small broad intermediate sclerites, transversely ovoid, with rounded margins; mean length 3·6 mm (s.d. = 0·3, $n = 16$; holotype 3·7 mm), mean length/width 0·70 (s.d. = 0·05, $n = 16$; holotype 0·67). Prominent sub-central pointed dorsal apex is elevated and mucronate; mean 0·48 (s.d. = 0·06, $n = 17$; holotype 0·46) of length from anterior. Maximum width only slightly posterior of apex at posterolateral corners, mean 0·54 (s.d. = 0·04, $n = 16$; holotype 0·57) of length from anterior. Concentric growth lines about apex, some more distinct growth increments forming low ridges towards outer part of dorsal surface (e.g. Pl. 6, fig. 1a, d). Dorsal surface with vaulted, triangulate, transversely convex anterior and posterior fields, depressed, concave to flattened lateral fields. Anterior field fairly broad, arched, smoothly rounded and convex, elevating to apex, posterior field broader, concave behind apex, flattening and becoming convex to margins. Lateral fields rounding and becoming concave between anterior and posterior fields, most depressed close to apex, flattening outwards. Longitudinal profile strongly convex anteriorly to prominent apex, concave to flattened or becoming convex posteriorly, elevated (Pl. 5, figs 1c, 2c; Pl. 6, figs 1c, 2c). In transverse profile, gently convex, arched, deeper laterally. Granular dorsal ornament, coarser in anterior and lateral fields, and coarsening outwards, generally slightly finer granulation across posterior field. Quincunx arrangement of granules, but with band of coarser granules from apex to posterolateral corners demarcating posterior field (e.g. Pl. 5, figs 1a, b, e, 2a–b). Anterior and lateral fields not differentiated by ornament. Ornament becoming less well defined in thickened sclerites (e.g. Pl. 6, fig. 1a, c).

Ventral surface smooth, with gentle convex transverse flexure corresponding to lateral depressed fields of the dorsal surface. Small deep median cavity beneath apex, slanted obliquely towards anterior, circular to ovoid,

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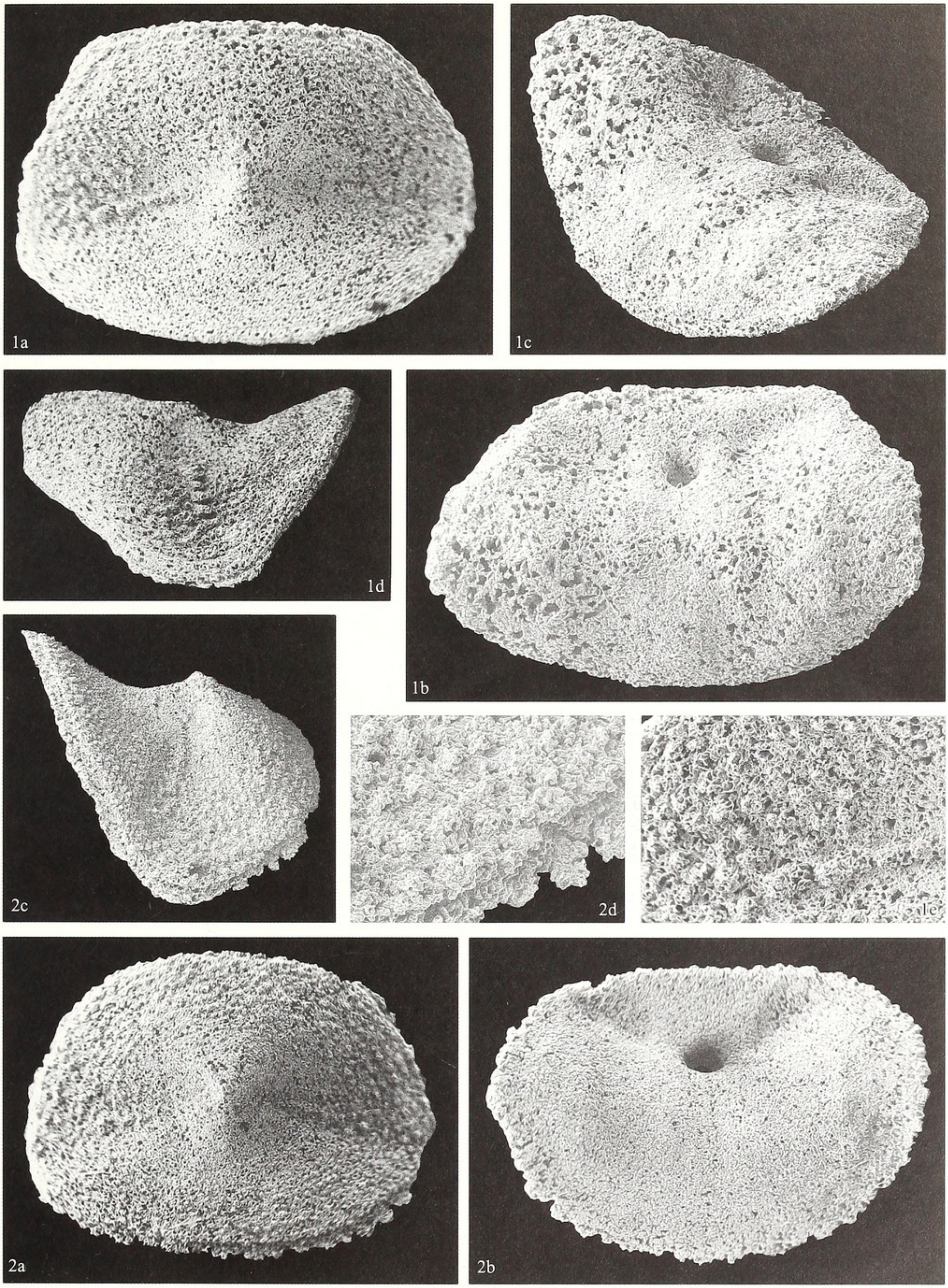
EXPLANATION OF PLATE 5

Figs 1–2. *Heloplax papilla* gen. et sp. nov.; Möllbos-1, Gotland; Halla Formation, Upper Wenlock (Homerian); intermediate sclerites. 1, RM Mo159.832, holotype. 1a, dorsal view; note sub-central mucronate apex, line of coarser granules across depressed lateral shell fields; ×15. 1b, ventral view, showing subapical cavity, flanking lateral depressions; ×15. 1c, oblique ventral view, showing transverse flexure of sclerite across lateral fields, behind subapical cavity, obliquely directed lateral depressions, deep subapical cavity slanting anteriorly; ×15. 1d, left lateral view; note line of coarser granules, elevation of posterior shell field behind mucronate apex; ×15. 1e, detail of lateral ornament, showing line of coarser granules; ×25. 2, RM Mo159.867. 2a, dorsal view; note holoperipheral quincunx granular ornament coarsening outwards; ×15. 2b, ventral view; note deep subapical cavity, flanking oblique lateral furrows, transverse flexure of sclerite; ×15. 2c, right lateral view; note line of coarser granules across lateral field, strongly elevated posterior field; ×14. 2d, detail of granular ornament from anterior edge, with new growth increment inserted from below; ×50.



CHERNS, *Heloplax*

with smooth margins; mean 0·32 (s.d. = 0·05, $n = 17$; holotype 0·30) of length from anterior. Ventral thickening leading to surface sculpting around sub-apical cavity, and development of an additional, flanking lateral pair of more anterolaterally directed, smaller shallower cavities beneath apical region; subapical cavity bordered anteriorly by thickened pad, posteriorly by shallow longitudinal furrow flattening outwards, lateral cavities in shallow anterolateral furrows (Pl. 6, fig. 1b, d; also less thickened sclerites in Pl. 5, figs 1b–c, 2b). Anterior surface and flexed region becoming strongly sculpted and thickened, posterior surface with shallow tapering median furrow, shallower outer rim to sclerite.

?Tail sclerites (Pl. 6, fig. 3) smaller and relatively broader than intermediate, mean length 2·3 mm (s.d. = 0·14, $n = 6$), mean length/width 0·55 (s.d. = 0·03, $n = 5$). Ovoid, smoothly rounded with elevated sub-central mucronate apex more anterior of maximum width; apex mean 0·40 (s.d. = 0·08, $n = 6$) of length from anterior, maximum width mean 0·54 (s.d. = 0·04, $n = 6$) of length from anterior. Vaulted convex anterior and posterior fields, without posterior elevation, lateral fields narrow, depressed (Pl. 6, fig. 3c). Transverse profile low arched, broad, deeper laterally. Granular ornament, coarsening outwards, with line of coarser granules from apex across lateral fields (Pl. 6, fig. 3a). Ventral surface with deep, slanting median cavity anterior of transverse flexure beneath apex, mean 0·33 (s.d. = 0·04, $n = 6$) of length from anterior. Ventral surface otherwise smooth, becoming thickened and sculpted particularly in subapical ad flexed region to give shallow median longitudinal furrow and anterolateral furrows flanking subapical cavity.

Remarks. By comparison with intermediate sclerites, the ovoid, rounded ?tail sclerites are smaller, relatively broad, and have a gently convex longitudinal profile, both anterior and posterior fields being vaulted. The mucronate apex is a little more anterior, ventrally the subapical pit is similarly situated. Both have outward coarsening granular ornament, but in the ?tail sclerites the characteristic line of larger granules lies within the lateral fields rather than at their posterior limit. The ?tail sclerites are distinct mainly on size, shape, and the longitudinal profile lacking post-apical concavity to posterior elevation. On the material available, and because of the line of larger granules among the lateral ornamentation of both types of sclerite, and fairly similar form overall, the smaller sclerites are proposed as possible tail plates for this species. They might otherwise represent anterior intermediate plates, but are less likely to represent head plates because those typically differ more in morphology from the other plates in chitons.

No head sclerites are identified for *H. papilla*. Two small end sclerites from Möllbos, described below (pp. 966, 968), may include the appropriate head sclerite for this species.

ENETOPLAX gen. nov.

Derivation of name. From the Greek *enete*, brooch, and Latin *plax*, plate, to describe the form.

Type species. E. decora gen. et sp. nov. from the Upper Wenlock (Silurian) of Gotland, Sweden.

Diagnosis. Small, transversely elongate, ovoid to sub-triangular intermediate sclerites with elevated mucronate apex displaced anteriorly from centre; rounded margins. Strongly vaulted short and fairly narrow triangulate anterior field to pointed apex, elevated by low folds; depressed shallow lateral fields flattening outwards across weak transverse flexure, rounding into broad long triangulate posterior field, concave becoming flattened to convex outwards. Broadening behind apex to maximum width just posterior of mid-length. Dorsal concentric growth lines; granular ornament, coarsening outwards, coarser on anterior area, finer to coarse on lateral to posterior areas. Ventral surface with small deep median subapical cavity near anterior margin, slanted anteriorly. Ventral thickening leading to only weak sculpting of surface. ?Head sclerite round, with elevated mucronate apex close to anterior, vaulted short anterior field, gently convex and long posterolateral field, granular ornament; ventral surface concave, shallow subapical cavity.

Remarks. Enetoplax gen. nov. is similar to *Heloplax* gen. nov. (above) in having small ovoid intermediate sclerites with a dorsal mucronate apex and holoperipheral growth. It differs in that sclerites are less vaulted and flexed, have the apex more anterior, and a correspondingly shorter and narrower anterior field, a longer, shallower and broader posterior field, and maximum width further displaced posteriorly behind the apex (Text-fig. 3). Ventrally the subapical cavity is more anterior, and transverse flexure is weak. Ventral thickening leads to limited surface sculpting around the subapical area, by contrast to the strong development of this surface in *Heloplax*. Granular ornament in both genera coarsens outwards, and is more developed on the anterior field which in *Enetoplax* is delimited by low radial folds. *Heloplax* has a distinct line of coarser granules radiating from the apex across the lateral fields.

Both *Enetoplax* and *Heloplax* sclerites occur in samples from Möllbos-1, both together and separately. Although the intermediate sclerites are broadly similar, and different from all other chitons described, they are easily distinguished morphologically, and are separated here at generic level.

Enetoplax decora gen. et sp. nov.

Plates 7–8

Derivation of name. From the Latin *decoris*, adorned, to describe the ornamented plates.

Material, locality and horizon. Möllbos-1, Gotland, Halla Formation, Upper Wenlock (Homerian); 40 isolated sclerites; holotype RM Mo159.999*, intermediate sclerite; intermediate sclerites RM Mo159.835* (?tail), 159.836*, 159.837–159.839, 159.840 (?tail), 159.841–159.84, 159.850, 159.868, 159.885, 159.888, 159.890, 159.897, 159.913–159.916, 159.921, 159.923, 159.924 (?tail), 159.955–159.956, 159.960, 159.969, 159.974, 159.983, 160.000*, 160.001, 160.016, 160.025, 160.028–160.029, 160.033–160.035; ?head sclerite RM Mo159.998*.

Diagnosis. As for the genus.

Description. (Text-fig. 3). Small, transversely elongate, intermediate sclerites with rounded, convex margins; mean length 3·3 mm (s.d. = 0·5, n = 38; holotype 3·3 mm), length/width 0·68 (s.d. = 0·07, n = 33; holotype 0·49). Elevated mucronate apex anterior of centre, mean 0·33 (s.d. = 0·06, n = 38; holotype 0·36) of length from anterior; ovoid to sub-triangular, broadening behind apex to maximum width slightly posterior of midlength within lateral areas, mean 0·54 (s.d. = 0·06, n = 38; holotype 0·60) of length from anterior. Strongly vaulted, short triangulate anterior field to elevated pointed apex; transversely convex, fairly narrow, elevated by low radial folds above lateral fields, low median radial fold or smoothly rounded, convex (e.g. Pl. 7, fig. 1a, c–d; Pl. 8, fig. 1a, c). Weakly defined triangulate posterior field, long and expanding from apex, shallow becoming slightly elevated; gently convex to flattened transversely, broadening outwards, broader than anterior field. Lateral fields gently concave, depressed, flattening outwards, rounding into posterior field, more clearly bounded against low folds of elevated anterior field. In longitudinal profile, convex short anterior field to apex, concave becoming flattened to slightly convex along long posterior field (Pl. 7, figs 1c, 2c; Pl. 8, figs 1c, 2d, 3c). Transverse profile shallow, broad, deeper laterally (Pl. 7, fig. 1d). Growth lines, concentric about apex, more distinct on outer part of dorsal surface, increments forming low ridges (e.g. Pl. 7, fig. 1a, c–d). Granular ornament coarsening outwards, quincunx pattern, coarser and more prominent across vaulted anterior area (e.g. Pl. 8, fig. 1), finer to coarse laterally and posteriorly (e.g. Pl. 7, figs 1a, 2c).

Ventral surface smooth, with small, deep, round to ovoid median cavity with smooth margins near anterior margin, slanting towards anterior from beneath apex (e.g. Pl. 7, fig. 2e); mean 0·22 (s.d. = 0·05, n = 38) of length from anterior. Ventral thickening leading to distinct shallow rim outside thickened surface (e.g. Pl. 7, fig. 2b, e), a pair of very shallow longitudinal furrows flanking median pad behind cavity, lateral pads (e.g. Pl. 7, fig. 1b), but relatively little sculpting of surface. Gently convex transverse flexure behind cavity, but low curvature across ventral surface.

?Tail sclerites not clearly distinct, and hence not separated from the remainder of sclerites for biometrics, but possibly represented by three relatively flatter specimens with apex and, particularly, ventral cavity somewhat more anterior (e.g. Pl. 8, fig. 2). Ovoid to sub-triangular, rounded, with elevated mucronate apex towards anterior, mean 0·27 (s.d. = 0·03, n = 3) of length from anterior; maximum width near mid-length, mean 0·51 (s.d. = 0·13, n = 3) of length from anterior. Very short, narrow, convex anterior field, elevated by low folds from lateral fields, low median radial fold; much longer, broader, concave to flattened posterior field, with slightly lobed or convex posterior margin (Pl. 8, fig. 2a, c). Lateral fields shallowly depressed, concave to flattened. Ventral surface with anteriorly slanting, round to ovoid deep subapical pit close to anterior margin, mean 0·18 (s.d. = 0·03, *n* = 3) of length from anterior (Pl. 8, fig. 2b, d). Becoming thickened, distinct shallower outer rim, otherwise smooth. Dorsal coarse granular anterior ornament, concentric growth lines.

?Head sclerite (Pl. 8, fig. 3) fairly poorly preserved, limiting biometric measurements. Small, round, with elevated mucronate apex close to anterior. Very short, convex anterior field to apex; long, gently convex posterolateral fields. Dorsal concentric growth lines, granular ornament (poorly preserved). Ventral surface smooth, concave, shallow subapical cavity.

Remarks. Tail sclerites are only tentatively proposed for *Enetoplax*, differing from intermediate sclerites in being lower arched, with the apex, and particularly the subapical cavity, closer to the anterior margin, and the longer posterior field shallower and flatter. By comparison, possible *Heloplax* tail sclerites are notably smaller than intermediate sclerites, relatively broad and have convex, vaulted anterior and posterior fields and thus a convex longitudinal profile. The round head sclerite is associated with *Enetoplax*, rather than *Heloplax*, because of the apex near to the anterior, and long posterolateral field.

ARCTOPLAX gen. nov.

Derivation of name. From the Latin *arcto*, compress, and Greek *plax*, plate, to describe the pinched form of the sclerites.

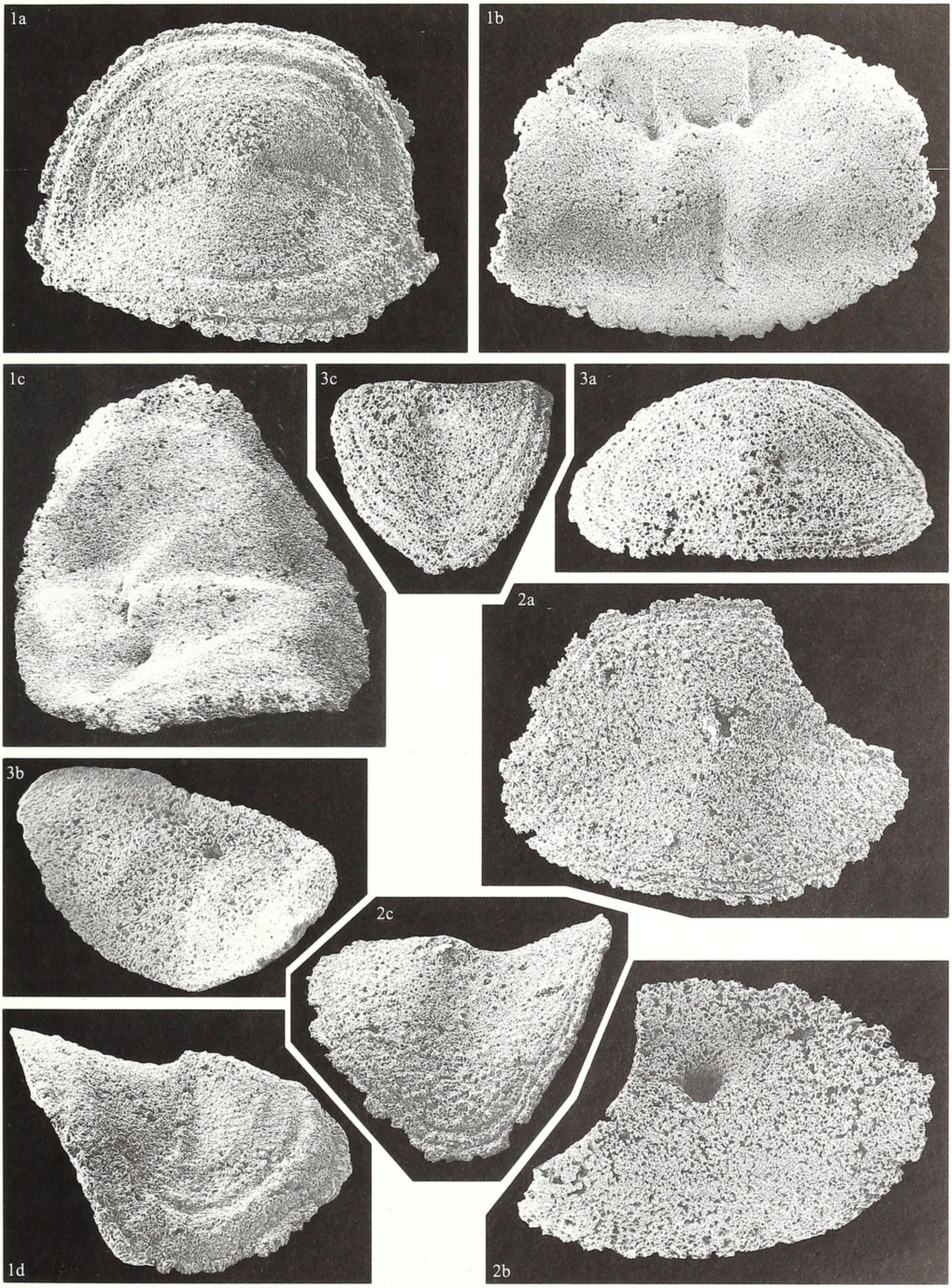
Type species. A. ornata gen. et sp. nov. from the Upper Wenlock (Silurian) of Gotland, Sweden.

Diagnosis. Small, high arched, elongate spatulate intermediate sclerites with strong constriction to sub-central mucronate apex, triangulate shell fields defined by low radial folds and furrows. Anterior and posterior shell fields vaulted, convex, lateral fields depressed; lateral and posterior fields with triangulate, angled faces; anterior field with weaker triangulate facies, rounded medially. Jugal area flat posteriorly, rounded and downward sloping anteriorly; side slopes deep, steep, tapering anteriorly, height greatest posteriorly; maximum width at anterolateral corners, but tapering little along lateral margins; anterior margin transverse to convex, rounding anterolaterally, posterior margin transverse. Ventral surface smooth; deeply concave transversely, narrowing through apical constriction, small deep narrow subapical cavity. Anterior profile rounded, low arched, posterior profile deeper, high arched, with angular corners between faces. Fine granular dorsal ornament, concentric growth lines.

Remarks. The vaulted spatulate form with sub-central mucronate apex is comparable in its holoperipheral growth, and hence lack of a ventral apical area, to *Heloplax* gen. nov. and *Enetoplax*

EXPLANATION OF PLATE 6

Figs 1–3. *Heloplax papilla* gen. et sp. nov.; Möllbos-1, Gotland; Halla Formation, Upper Wenlock (Homerian). 1, RM Mo159.828; well thickened intermediate sclerite. 1a, dorsal view, note line of coarser granules, concentric growth lines; 1b, ventral view, showing sculpted thickened ventral surface: deep, anteriorly slanting subapical cavity with anterior and posterior thickened pads, flanking smaller lateral cavities at base of anteriorly directed, expanding oblique depressions, transverse flexure of sclerite, median longitudinal furrow across posterior field. 1c, oblique ventral view showing posterior, tapering extension of furrows across lateral cavities, tapering bifurcation of pad behind anteriorly slanting subapical cavity. 1d, right lateral view, showing posterior elevation behind mucronate apex, line of coarser granules across lateral field, holoperipheral granular ornament. 2, RM Mo159.829; intermediate sclerite. 2a, dorsal view; note outward coarsening granular ornament, growth lines; 2b, ventral view, showing deep subapical cavity; 2c, left lateral view. 3, RM Mo159.851; ?tail sclerite. 3a, dorsal view; note line of coarser granules across depressed lateral fields, mucronate sub-central apex; 3b, ventral view, showing transverse flexure behind slanting subapical cavity, median longitudinal furrows across posterior field, flanked by thickened pads; 3c, left lateral view; note lack of elevation of posterior field, holoperipheral growth lines. All × 15.



CHERNS, *Heloplax*

gen. nov., and different from other chitons except for some tail sclerites. At Möllbos-1, the sclerites occur not only singly but as several within samples, including some plates of variable size with similar patterns of larger growth increments which probably belonged to the same individual. This would support an interpretation as intermediate plates, and not tail plates of another chiton. Although the ventral subapical cavity in *Arctoplax* compares with similar features in the small ovoid intermediate sclerites of *Heloplax* and *Enetoplax*, the form of *Arctoplax* sclerites is clearly distinct.

The sub-central apex and highly unusual form mean that the anterior–posterior orientation is somewhat equivocal. The normal imbrication of chiton plates produces some overlap of the posterior apical area across the anterior edge of the following plate. In *Arctoplax*, the plates lack an apical area and their form precludes overlap; the deeper, high arched end is interpreted here provisionally as posterior (e.g. Text-fig. 7).

One problematical Ordovician genus *Llandeilochiton* Bergenhayn, 1955, based on a single small specimen from the Llandeilo of southern Scotland (*L. ashbyi* Bergenhayn, 1955), has a rectangular, flexed form with a sub-central apex, and apparently folds delimiting shell areas, but with a marked jugal furrow (Bergenhayn 1955, pl. 2, fig. 12). The specimen has not been examined, and its chiton affinities have been questioned (Smith and Hoare 1987).

Arctoplax ornata gen. et sp. nov.

Plate 9

Derivation of name. From the Latin *orno*, decorate, referring to the fine granular ornament.

Material, locality and horizon. Möllbos-1, Gotland, Halla Formation, Upper Wenlock (Homerian); 15 isolated intermediate sclerites (including one anterior and three posterior fragments); holotype RM Mo159.856*, intermediate sclerite; RM Mo159.853–159.855, 159.857, 159.899*, 159.904, 159.911, 159.925, 159.944, 159.948, 159.986, 159.996*, 160.002, 160.030.

Diagnosis. As for the genus.

Description. Small and high vaulted, elongate spatulate sclerites, mean length 7·0 mm (s.d. = 0·72, $n = 11$; holotype 7·7 mm), mean length/width 1·54 (s.d. = 0·19, $n = 9$; holotype 1·35). Strong constriction to a sub-central mucronate apex, mean 0·51 (s.d. = 0·04, $n = 11$; holotype 0·58) of length from anterior, low angular to rounded radial folds and furrows from apex defining shell fields. Anterior and posterior fields broad, vaulted, convex, with anterior field shallowing from apex, posterior field deepening; steep lateral fields depressed. Lateral and posterior fields folded into triangulate, angled faces, anterior field with weaker, triangulate faces anterolaterally, becoming rounded. Low radial folds elevating anterior and posterior fields, posterior jugal field, central part of lateral fields. Maximum width at anterolateral corners but tapering little along lateral margins; maximum height at posterolateral corners; mean height/length 0·51 (s.d. = 0·08, $n = 11$; holotype 0·48). Anterior field moderately arched, sloping outward, anterior margin rounded, more transverse medially, convex anterolateral corners through steeper radial fold and flexure (Pl. 9, figs 1e, 2e). Long, slightly concave to convex, lateral margins, deepening posteriorly; lateral fields sloping steeply outwards below constricted apex, two triangulate faces flanking central low fold (Pl. 9, figs c). Squarish posterolateral

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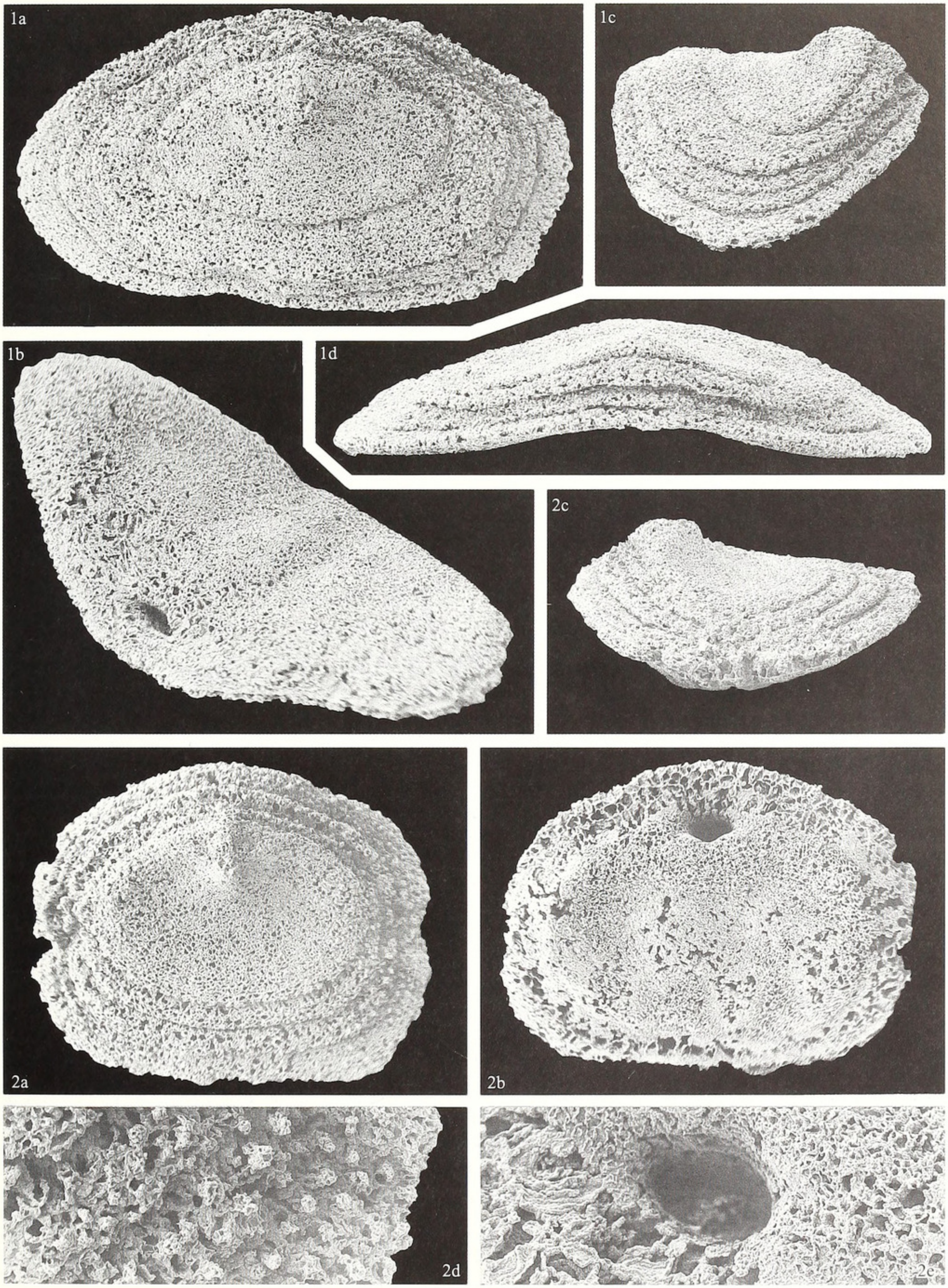
EXPLANATION OF PLATE 7

Figs 1–2. *Enetoplax decora* gen. et sp. nov.; Möllbos-1, Gotland; Halla Formation, Upper Wenlock (Homerian); intermediate sclerites. 1, RM Mo159.999, holotype. 1a, dorsal view; note anteriorly displaced mucronate apex, prominent growth increments, holoperipheral growth; 1b, oblique ventral view; note anteriorly slanting subapical cavity near anterior margin, thickened medial pad flanked by longitudinal furrows; 1c, right lateral view; lateroposterior shell field flat; 1d, anterior view showing mucronate apex, prominent growth increments. 2, RM Mo160.000. 2a, dorsal view; 2b, ventral view; note thickened surface inside marginal rim; 2c, left lateral view; 2d, detail of granular ornament from right hand side, ×50; 2e, details of subapical cavity; note smooth, anteriorly slanting walls, cavity within thickened surface, inside marginal rim, ×50. All except 2d–e ×15.



CHERNS, *Enetoplax*

corners through fold and acute flexure, posterior margin straight, transverse; posterior field strongly vaulted across elevated flat triangulate jugal field, flanked either side by two steep, flat triangulate faces angled outwards and downwards respectively (Pl. 9, figs, 1d, 2d). Fine and even, granular dorsal ornament, evident only on some sclerites, coarsening and best preserved towards outer parts of shell across anterior and lateral areas (Pl. 9, figs 1a, c, f, 3a, c–d). Growth lines concentric about apex, larger growth increments more evident towards outer part of dorsal surface.

Ventral surface smooth, concave and strongly folded around a longitudinal axis, deepest posteriorly in triangulate jugal area, apical constriction flanked by depressed side slopes, shallowing anteriorly. Small, deep narrow subapical cavity. All shell areas expanding away from apical constriction, slight corrugation of surface reflecting radial folds.

Remarks. Granular ornament is well preserved on a few sclerites (holotype, Pl. 9, fig. 1, and Pl. 9, fig. 3), but not evident on several other, possibly more thickened, specimens (Pl. 9, fig. 2). Those ornamented sclerites are relatively broad and shallow, with concave lateral margins, while the more thickened sclerites are narrower and deeper, slightly convex laterally. However, differences in ornament may be preservational, and on the basis of the fairly limited material available, variation is regarded here as intraspecific. Tail sclerites have not yet been recognized for *A. ornata*, although the head sclerite may be among the two described below.

head B indet.

Text-figure 5A–E

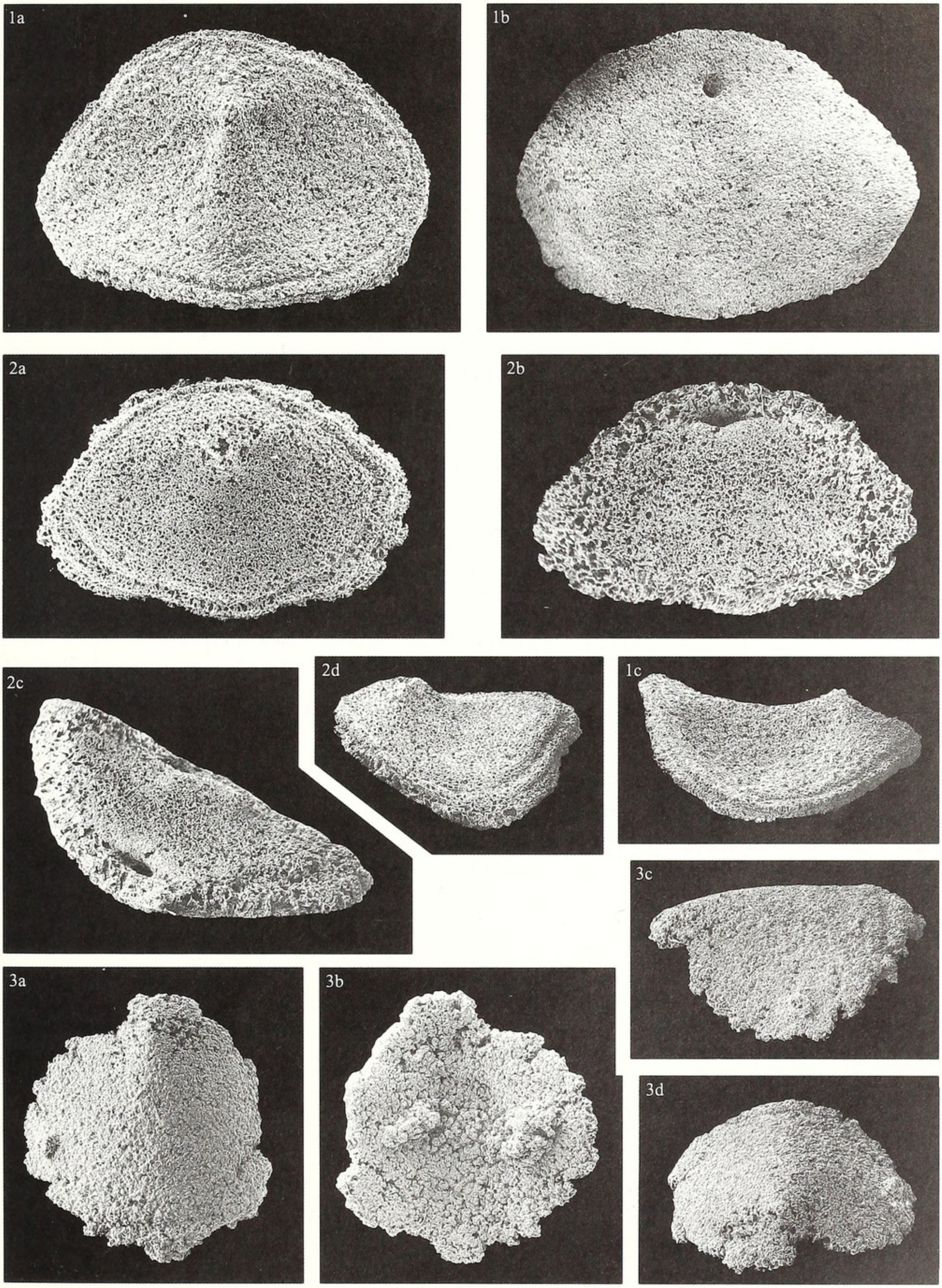
Material, locality and horizon. Möllbos-1, Gotland, Halla Formation, Upper Wenlock (Homerian); one isolated sclerite, RM Mo159.825*.

Description. Small, vaulted, convex semicircular sclerite (with some damage along the posterior edge) with elevated sub-central mucronate apex. Short, fairly broad and high; length 1·4 mm, length/width 0·58, height/length 1·0. Flat, elevated triangulate face within posterior area, steep, outward sloping, broad convex anterolateral area to rounded semicircular anterolateral margin, shallowing slightly near margin. Slight depressed radial flexure to posterolateral corners, rounding strongly into transverse, arched posterior margin (Text-fig. 5B), posterior shell arched and elevated (Text-fig. 5D), posterior margin transverse. Fine granular dorsal ornament; concentric growth lines more distinct near margins, where a new growth increment secreted from beneath is particularly evident posteriorly (Text-fig. 5E). Ventral surface deeply concave, smooth, deepest subapically and across median posterior face.

Remarks. The small, semicircular and convex form is typical of chiton end plates, and the transverse arched margin and steepness of the outward sloping face suggest that this is a head sclerite. The elevated sub-central mucronate apex, flat triangulate medial posterior face, arched and elevated posterior, and fine granular ornament across the whole shell, are features which associate it most closely with *A. ornata* (Text-fig. 7). However, the size, apical morphology and ornament are also comparable to *Heloplax*, but somewhat less so to *Enetoplax* for which a head sclerite is already tentatively recognized. All three genera are found in other samples from the same horizon.

EXPLANATION OF PLATE 8

Figs 1–3. *Enetoplax decora* gen. et sp. nov.; Möllbos-1, Gotland; Halla Formation, Upper Wenlock (Homerian). 1, RM Mo159.936; intermediate sclerite. 1a, dorsal view; note coarser granular ornament on anterior shell field; 1b, ventral view; 1c, right lateral view, posterolateral shell field gently concave, becoming elevated. 2, RM Mo159.835; ?tail sclerite. 2a, dorsal view; note trilobed, scalloped posterior margin; 2b, ventral view; subapical cavity close to anterior, thickened surface inside marginal rim; 2c, oblique ventral view, showing thickened surface inside marginal rim, medial pad inside weak longitudinal furrows. 3, RM Mo159.998; ?head sclerite. 3a, dorsal view; note mucronate apex close to anterior margin; 3b, ventral view; weak subapical cavity, surface with attached grains; 3c, left lateral view; posterolateral shell field gently convex; 3d, anterior view, showing mucronate apex, convex transverse profile. All ×15.



CHERNS, *Enetoplax*

?head or tail C indet.

Text-figure 5F–I

Material, locality and horizon. Möllbos-1, Gotland, Halla Formation, Upper Wenlock (Homerian); one isolated sclerite, RM Mo159.824.

Description. Small, transversely ovoid sclerite, convex becoming arched posteriorly, with dorsal shallow, rounded longitudinal furrows and ribs radiating posteriorly from a weakly elevated ?dorsal apex close to anterior; length 2·5 mm, length/width 0·86, height/length 0·88. Anterior area very short, arched, semicircular margin with distinct rim; strongly rounded posterolateral corners, posterior margin also semicircular, more arched (Text-figs 5F, 5H). Ventral surface smooth, concave, deepest centrally, shallowing outwards (Text-fig. 5G). Concentric growth, ?some weak granular ornament; thickened rim of anterolateral margin showing several growth increments.

Remarks. The fairly poorly preserved sclerite is broken along one edge and across the ventral surface, removing part of a later shell increment and hence the part of the dorsal margin. An apparently continuous marginal rim on an earlier shell layer suggests concentric growth around a dorsal apex, with additional shell increments added as complete layers from the ventral side, leading to significant thickening. The small size, arched convex form and semicircular margins suggest that this is an end plate, but anterior and posterior orientation are somewhat equivocal, only partly dependent upon which end plate it represents. A weak elevation near the unbroken margin apparently represents the apex, from which shallow rounded ribs and furrows, not well preserved, radiate slightly. Positioned with the apex uppermost, both margins remain moderately arched (Text-fig. 5H–I), yet if either margin is positioned flat the other margin becomes steep and raised. Radial ornament from the mucro is fairly common in both head and tail plates of neoloricate chitons (e.g. Smith 1960).

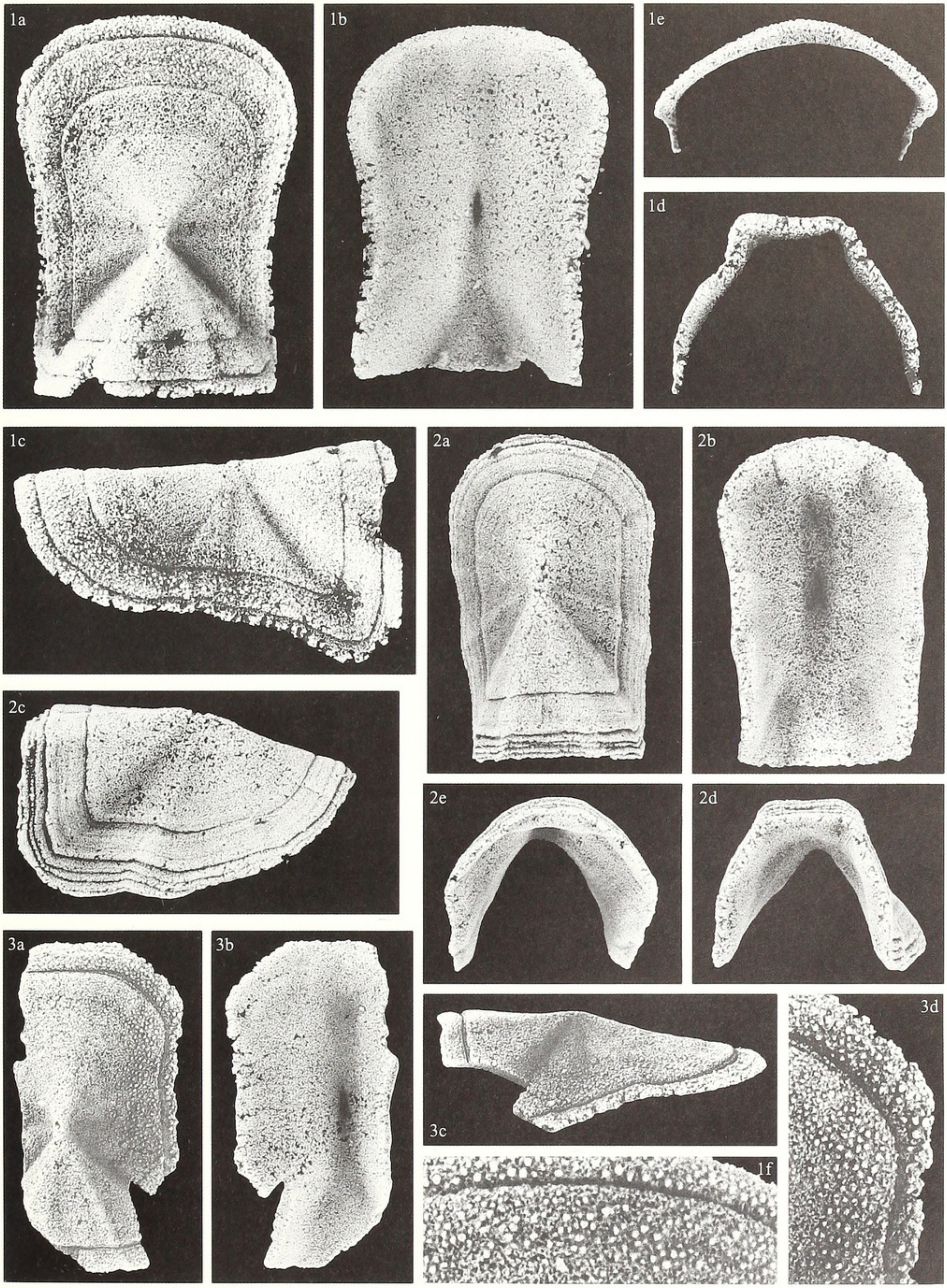
The holoperipheral growth and ovoid shape of this small sclerite are comparable to *Heloplax* and *Enetoplax*, although the ribbed ornament is different. The mode of growth is also similar to the larger, spatulate *Arctoplax*, but different from all other Gotland chitons.

MUSCULATURE IN GOTLAND CHITONS

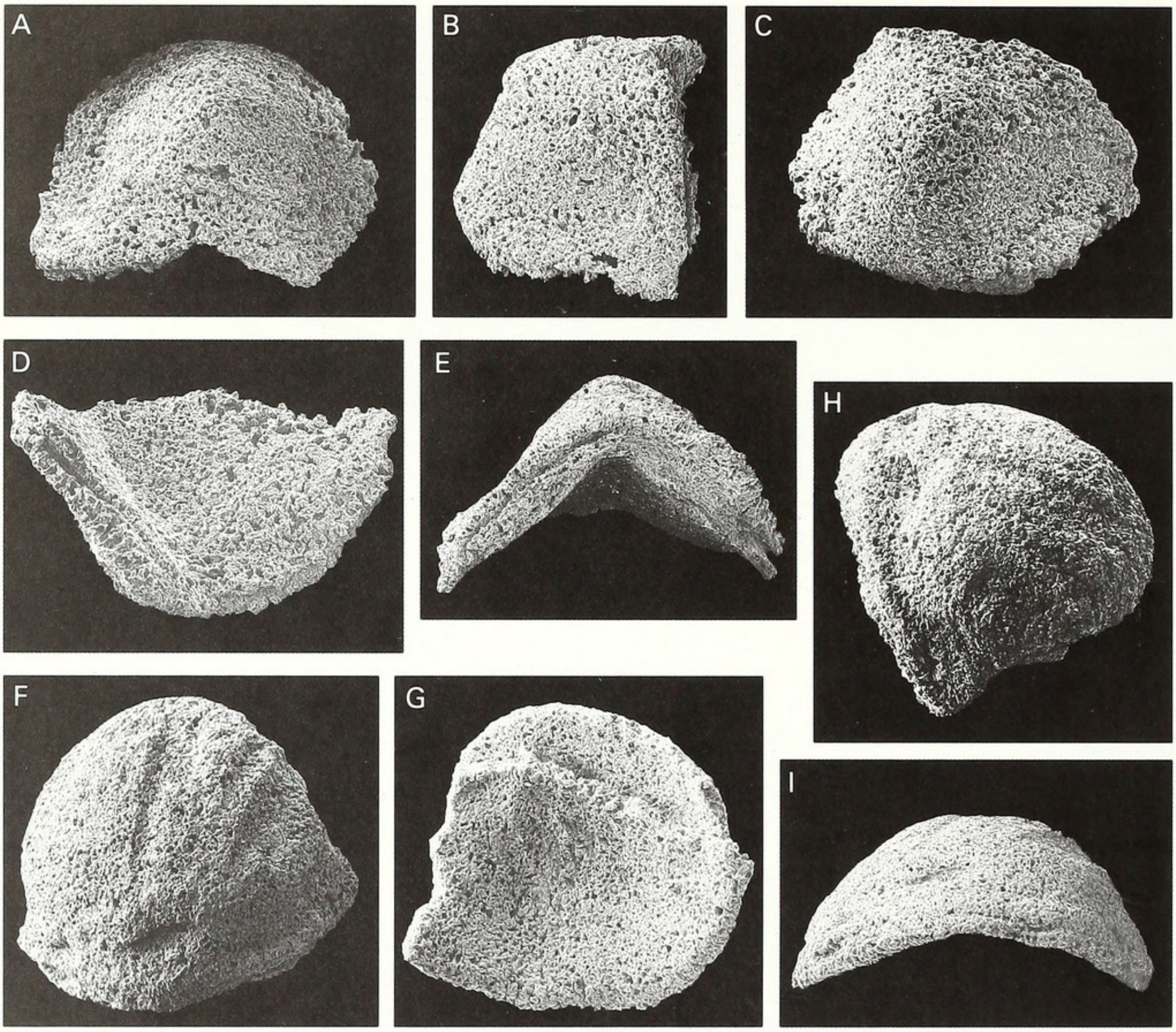
The musculature of *Chelodes actinis* was discussed from sculpting of the ventral surface in thickened sclerites (Cherns 1998). In living chitons, the complex musculature (e.g. Hyman 1967) between valves and from valves into the body wall leaves no evident insertion sites in the inner shell layer, the ventral hypostracum. The function of the various sets of muscles acting on the valves lies in drawing the plates together and holding them against the body. Sutural laminae and insertion plates, formed of the middle shell layer, the articulamentum, which is absent from paleoloricate chitons, provide physical articulation of plates and attachment to the mantle. Plates are commonly embedded in and partially covered by the mantle.

EXPLANATION OF PLATE 9

Figs 1–3. *Arctoplax ornata* gen. et sp. nov.; Möllbos-1, Gotland; Halla Formation, Upper Wenlock (Homerian); intermediate sclerites. 1, RM Mo159.856, holotype. 1a, dorsal view; note sub-central mucronate apex, radial folds within lateral and posterior shell fields, prominent growth increments; ×7. 1b, ventral view, showing narrow subapical cavity; ×7. 1c, left lateral view; ×7. 1d, posterior view; ×7. 1e, anterior view; ×7. 1f, detail of dorsal granular ornament; ×15. 2, RM Mo159.899. 2a, dorsal view; 2b, ventral view; 2c right lateral view, note prominent growth increments; 2d, posterior view; 2e, anterior view. All ×7. 3, RM Mo159.996; broken left and right posterolateral margins. 3a, dorsal view; ×7. 3b, ventral view; note narrow subapical cavity; ×7. 3c, right lateral view; ×7. 3d, detail of granular ornament; ×15.

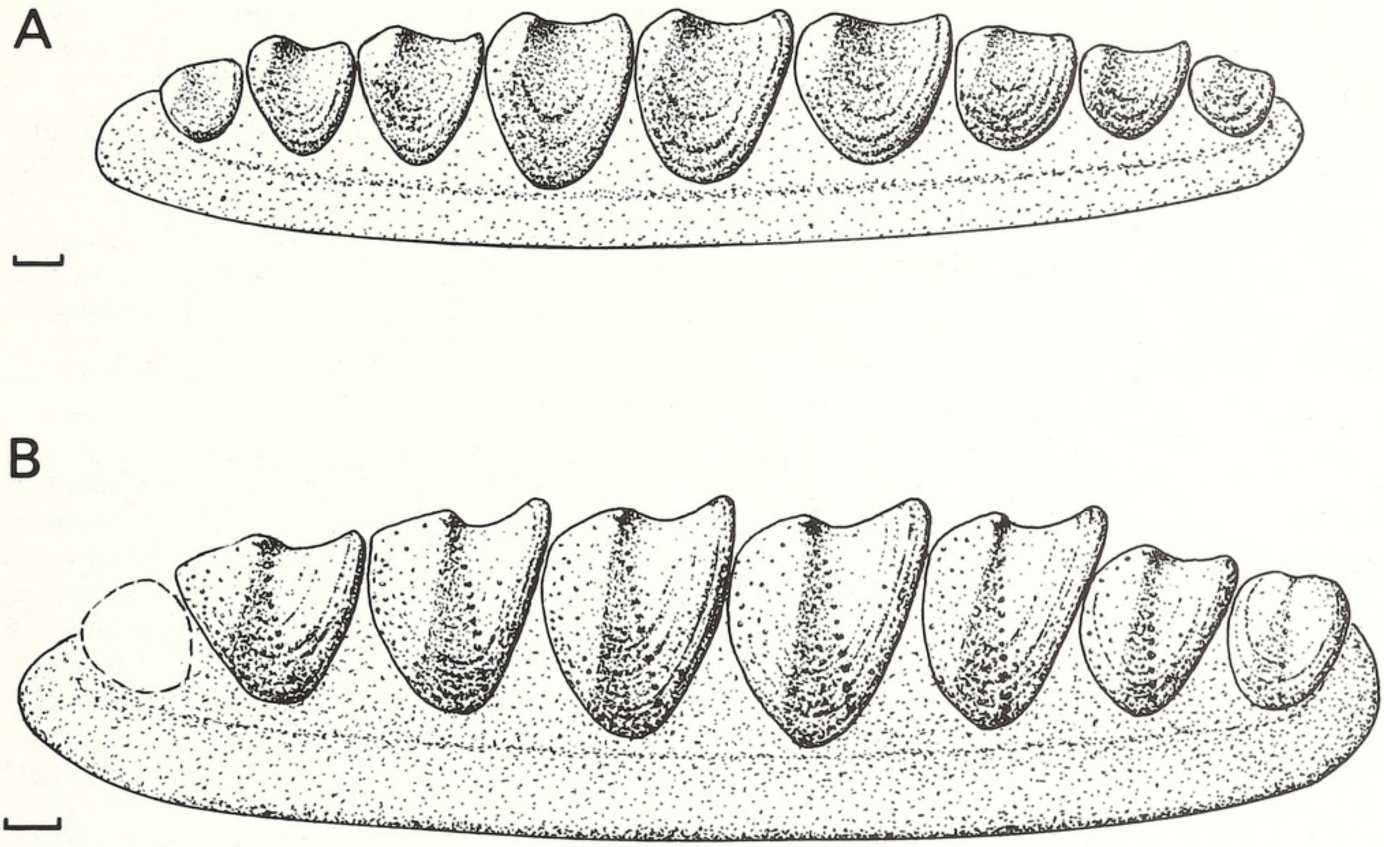


CHERNS, *Arctoplax*



TEXT-FIG. 5. A–E, head B indet.; RM Mo159.825; Möllbos-1, Gotland; Halla Formation, Upper Wenlock (Homerian). A, dorsal view; note sub-central mucronate apex, holoperipheral growth. B, left lateral view. C, oblique anterior view, showing elevated triangular posterior field. D, posterior ventral view. E, posterior view. All ×20. F–I, ?head or tail C indet.; RM Mo159.826; Möllbos-1, Gotland; Halla Formation, Upper Wenlock (Homerian). F, dorsal view, showing radial ridged ornament, thickened posterior margin with growth increment. G, ventral view; note broken growth increment beneath outer shell. H, right lateral view, showing prominent growth increment at posterior, broken anteriorly. I, posterior view. All ×15.

The elongate shield-shaped, flexed intermediate sclerites of *Thairoplax pelta* sp. nov. lack localized ventral thickening, but *T.*? aff. *pelta*? has a low triangulate transverse thickened ridge in front of, and extending medially towards, the apical area (Pl. 3, fig. 4b). Intermediate sclerites of *Plectrochiton tegulus* sp. nov. also show a slight thickening across the equivalent area, although closer to the anterior of these short triangulate sclerites (Pl. 3, fig. 1b). The small, winged intermediate and tail sclerites of *Alastega lira* sp. nov. have well-developed ventral triangulate transverse ridges. In all the genera, the apical area typically has a slightly raised rim above the smooth ventral surface. Other paleoloricate chitons which have thickened transverse ventral ridges include *Kindbladochiton* and the Ordovician *Ivoechiton* spp. (Smith and Toomey 1964). The physical effect of these ridges, which taper outwards, is to elevate slightly the posterior shell, the apical area

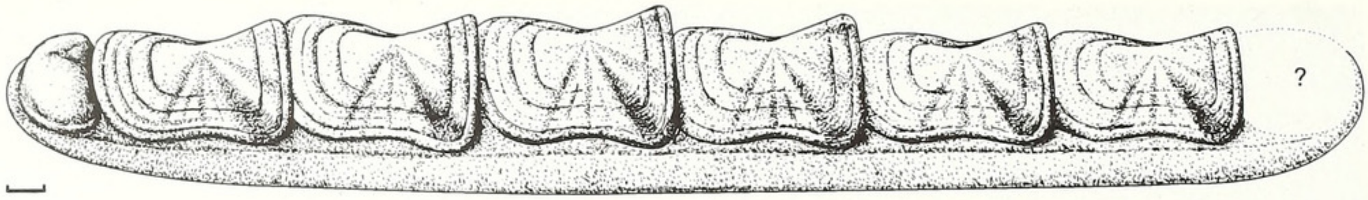


TEXT-FIG. 6. Reconstructions of A, *Enetoplax* and B, *Heloplax* as chitons, shown in left lateral view with normal plate orientations. Sclerites did not overlap but may have become imbricated through muscular rotation to elevate further the posterior shell fields. Scale bars represent 1 mm.

extending above the following sclerite. The ridge would also provide muscle attachment sites. *C. actinis* sclerites lack a similar marked thickening in front of the apical area, although developing shallow furrows flanking a medial pad towards the apical area similar to that of *T.*? aff. *pelta*? (Cherns 1998, pl. 4, fig. 3b). These furrows apparently represent muscle insertion sites, additional to the apical area rim that might serve for muscle attachment. None of the Gotland chitons has marked cavities extending beneath the apical area, as described for the Ordovician *Chelodes whitehousei* and Cambrian *Matthevia* spp. (Runnegar *et al.* 1979).

The three holoperipheral genera have mucronate sclerites with a prominent subapical cavity presumed to function for muscle insertion. In both *Heloplax* and *Enetoplax* (Text-figs 2–3), these small, deep cavities are anteriorly slanting, in front of a transverse flexure of the shell; in the former, the subapical cavity becomes flanked in some sclerites by additional, shallower, anterolaterally directed cavities (Pl. 5, fig. 1b; Pl. 6, fig. 1b). The subapical cavities are circular to transversely ovoid, with smooth margins, tapering into the valve and fairly deep, less even at the basal insertion point (Pl. 7, fig. 2d). Although the main insertion directions for the ventral cavities appear to be anterior and anterolateral, shallow furrows across the posterior field suggest that each also housed posteriorly directed muscles (Pl. 6, fig. 1b–c; Pl. 7, fig. 1b). In *Heloplax*, the posterior field of intermediate sclerites becomes elevated; in *Enetoplax*, a longer field curves more shallowly (Text-fig. 6). Thus the shell flexure serves a similar function to the thickened transverse ridges described above, for other genera; although the sclerites did not overlap, they could probably be drawn down on to the body, drawn closer, rotated and imbricated (cf. *Matthevia* reconstruction in Runnegar *et al.* 1979, text-fig. 1). The tail plates for both *Heloplax* and *Enetoplax* lack posterior elevation, the posterior fields being convex to flat (Text-fig. 6).

Arctoplax sclerites have a deep, tapering, rather slit-like sub-central subapical cavity (Pl. 9, fig. 1b), but in addition their radial angled folds and furrows across the high-arched, elongate shell might



TEXT-FIG. 7. Reconstruction of *Arctoplax* as a chiton in slightly oblique, left lateral view, with the rounded shallower end of sclerites anterior, the squarer and deeper shell field posterior. The head sclerite has been suggested as head B indet. There is no overlap of plates, but muscular rotation of plates may have produced imbrication, elevating the posterior field. Scale bar represents 1 mm.

have provided additional attachment surfaces or muscle tracks into the body wall. The subapical cavity may thus have anchored longitudinal and radial muscles, whereas those in *Heloplax* and *Enetoplax* apparently housed primarily anteriorly and anterolaterally directed muscle blocks. If the function of angled radial faces was connected primarily with the musculature, then by comparison their stronger development at the deeper end, interpreted here tentatively as posterior, might indicate the reverse orientation as more appropriate. However, the deep, long side slopes and marked apical constriction produced lateral cover for a narrow elongate body, where the incongruent, arched anterior and posterior profiles precluded overlap of sclerites. With the more rounded, shallower end as anterior (Text-fig. 7), some rotation of the shell behind the subapical muscle insertion site, to imbricate sclerites as proposed for the other genera, might elevate slightly the deeper, more arched and angular end.

Runnegar *et al.* (1979) interpreted two deep ventral pits in tall conical valves of the late Cambrian *Matthevia variabilis* Walcott, 1885 as muscle insertion sites for dorso-ventral muscles from shell to foot. A comparable single pit was present in the younger late Cambrian *M. walcotti* Runnegar, Pojeta, Taylor and Collins, 1979, and a shallow pit in the early Ordovician *Hemithecella expansa* Ulrich and Bridge, 1941. A concavity beneath the apical area in some early Ordovician *C. whitehousei* Runnegar, Pojeta, Taylor and Collins, 1979 was interpreted as equivalent, and *Matthevia* as a primitive chiton. By contrast, Stinchcomb and Darrough (1995), in discussing Cambrian–Ordovician *Hemithecella*, argued that ventral pits were not chiton features and that *Matthevia*, *Hemithecella* and some *C. whitehousei* should be considered as multi-plated problematical molluscs distinct from chitons.

THE NATURE OF THE SCLERITOME

The majority of the Gotland chitons described above represent isolated sclerites from silicified samples of late Wenlock age. Recent, neoloricate chitons typically have eight plates, of which seven are secreted in the late trochophore stage of ontogeny, the eighth, tail valve somewhat later (Okuda 1947; Hyman 1967). Limited records of articulated fossil chitons indicate a similar valve complement also in older neoloricate and in paleoloricate chitons (e.g. Rolfe 1981; Hoare and Mapes 1989). The only articulated plates among the Gotland material are the type specimen of *G. interplicatus*, which shows a fragment of a second, following sclerite (Pl. 1, fig. 1). The six similar intermediate sclerites in chitons vary in size along the body, but the head particularly, and also tail plates, can be very different (e.g. Smith 1960). The plates have posterior apices and mixoperipheral growth, with the outer tegmentum extending ventrally to form the apical area, except for some tail plates which have a dorsal mucronate apex and holoperipheral growth. In Recent chitons, the apical area is usually a narrow band, but in some early chitons may be much longer (e.g. *Chelodes raaschi*; Kluessendorf 1987).

Fine growth lines are preserved on most of the Gotland chiton sclerites, but also larger, stepped growth increments where similar patterns of growth can be used to associate plates from the same individual as well as indicating intra-individual variation (e.g. *C. actinis*; Cherns 1998, pl. 6; Pl. 7, figs 1–2). Such occurrences for all three of the new genera described here which show holoperipheral growth are important in the interpretation of these plates as intermediate and not tail sclerites. These and the more typical plates with mixoperipheral growth have highly comparable growth patterns.

Recent chitons mostly range in size up to *c.* 0·05 m, but can be much larger (*Cryptochiton stelleri*, 0·33 m; Hyman 1967), and usually have a flattened, ovoid foot. Overlap of the physically interlocking plates, relating to the length of the apical area, is generally quite small, and plates are normally broad and short. The Gotland chiton assemblage includes several with elongate rather than broad plates. Bergenhayn (1955) used formulae to estimate the length and elongation of Gotland *Chelodes* and *Gotlandochiton*, based on sclerite length, width, and length of apical area, reconstructing large sclerites with relatively long apical areas in *Chelodes* spp. as belonging to very elongate animals, *G. interplicatus* with its broad sclerite rather less so at about three times as long as wide (Bergenhayn 1955, pl. 2). Of the chitons described here, *T. pelta* has long sclerites with a short apical area, little overlap between plates, and hence must have been an elongate animal, and *Arctoplax* without overlap of plates was long but also narrow (Text-fig. 7). The remaining Gotland genera – *Plectrochiton*, *Alastega*, *Enetoplax* and *Heloplax* – had smaller, short and broad sclerites, more similar in shape to Recent chitons, the last two of these genera with no overlap of plates (Text-fig. 6). The stratigraphical evidence suggests that the late Wenlock sequences for the Gotland chiton localities represent very nearshore facies, associated with rocky shorelines (Cherns 1996). Those facies relationships indicate an ecology similar to that of most Recent chitons.

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