# *CHELODES* AND CLOSELY RELATED POLYPLACOPHORA (MOLLUSCA) FROM THE SILURIAN OF GOTLAND, SWEDEN

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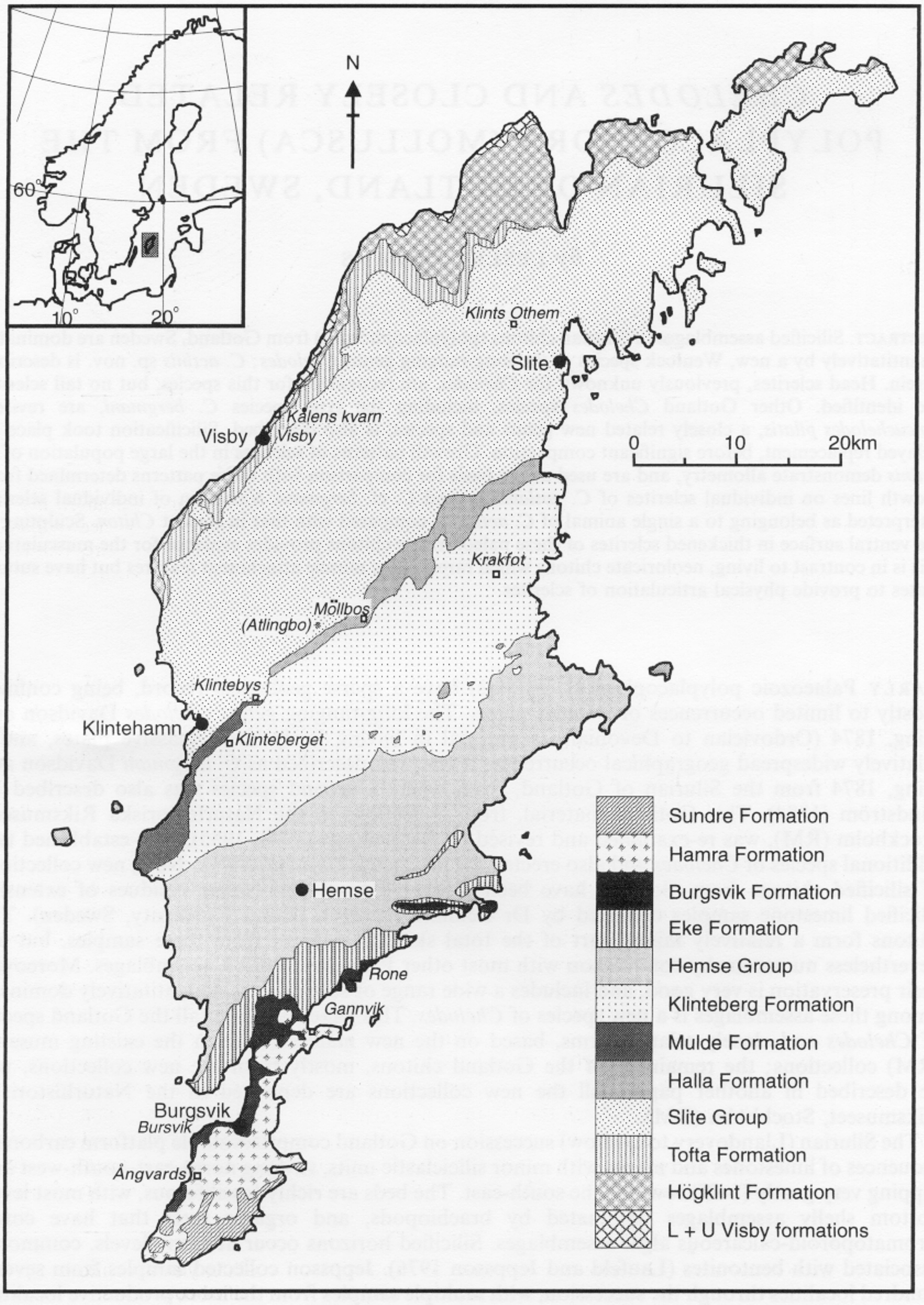
ABSTRACT. Silicified assemblages of Silurian chitons (polyplacophorans) from Gotland, Sweden are dominated quantitatively by a new, Wenlock species of the long-ranging genus *Chelodes*; *C. actinis* sp. nov. is described herein. Head sclerites, previously unknown for *Chelodes*, are recognized for this species, but no tail sclerites are identified. Other Gotland *Chelodes* species, including the type species *C. bergmani*, are revised. *Spicuchelodes pilatis*, a closely related new genus and species, is also described. Silicification took place by delayed replacement, before significant compaction. Growth patterns of sclerites in the large population of *C. actinis* demonstrate allometry, and are used as the basis for comparison with those patterns determined from growth lines on individual sclerites of *C. gotlandicus* and *C.* cf. *bergmani*. Variation of individual sclerites interpreted as belonging to a single animal of *C. actinis* is compared with that in Recent *Chiton*. Sculpting of the ventral surface in thickened sclerites of these paleoloricate chitons provides evidence for the musculature; this is in contrast to living, neoloricate chitons which rarely show muscle attachment features but have sutural plates to provide physical articulation of sclerites.

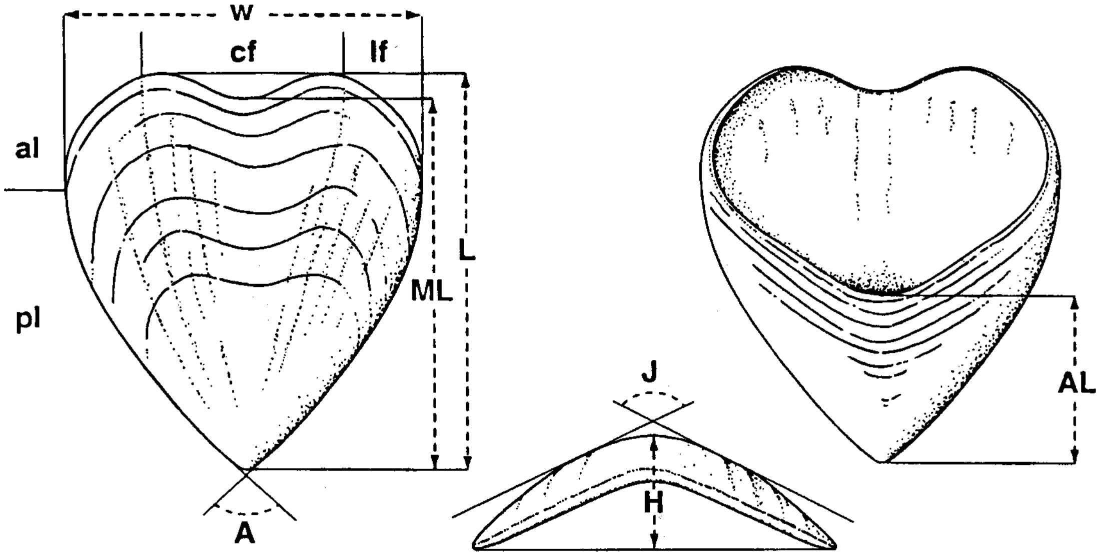
EARLY Palaeozoic polyplacophorans (chitons) have a sparse geological record, being confined mostly to limited occurrences of isolated plates. The long-ranging genus *Chelodes* Davidson and King, 1874 (Ordovician to Devonian) is unusual in having fairly large, massive plates, and a relatively widespread geographical occurrence. It was first described as *C. bergmani* Davidson and King, 1874 from the Silurian of Gotland, from where a second species was also described by Lindström (1884). This Gotland material, from collections in the Naturhistoriska Riksmuseet, Stockholm (RM), was re-examined and revised by Bergenhayn (1943, 1955), who established two additional species of *Chelodes* and also erected the new genus *Gotlandochiton*. Now, new collections of silicified chitons from Gotland have been recovered from acid-isolate residues of extensive silicified limestone samples collected by Dr Lennart Jeppsson (Lund University, Sweden). The chitons form a relatively minor part of the total skeletal material from these samples, but are nevertheless numerous by comparison with most other Palaeozoic chiton assemblages. Moreover, their preservation is very good, and includes a wide range of sclerite sizes. Quantitatively dominant among these assemblages is a new species of *Chelodes*. This paper describes all the Gotland species of *Chelodes* and closely related forms, based on the new material and on the existing museum (RM) collections; the remainder of the Gotland chitons, mostly from the new collections, will be described in another paper. All the new collections are deposited in the Naturhistoriska Riksmuseet, Stockholm (RM).

The Silurian (Llandovery to Ludlow) succession on Gotland comprises stable platform carbonate sequences of limestones and marls, with minor siliciclastic units, striking north-east–south-west and dipping very gently (1–2°) towards the south-east. The beds are richly fossiliferous, with most level-bottom shelly assemblages dominated by brachiopods, and organic reefs that have coral-stromatoporoid-calcareous algal assemblages. Silicified horizons occur at many levels, commonly associated with bentonites (Laufeld and Jeppsson 1976). Jeppsson collected samples from several hundred localities through the succession, with multiple samples from the more productive localities




TEXT-FIG. 1. For caption see opposite.




TEXT-FIG. 2. Schematic diagram of intermediate sclerite of *Chelodes* showing standard measurements and terminology in dorsal (left), ventral (right) and posterior (middle) views. L = length; ML = median length; W = width; AL = apical length; H = height; A = apical angle; J = jugal angle; al = anterolateral and pl = posterolateral portions of lateral margins; cf = central shell field; lf = lateral shell field.

('Project on Silicified Fossils from Gotland'). Chitons occur in samples from only four localities: three from the Wenlock, at Möllbos (Möllbos-1, Grid Reference Rikets nät RN 637645 165970; Liljedahl 1984), Klintebys (Klintebys 1, RN 636515 164685; Laufeld 1974) and Krakfot (Krakfot-1; RN 638020 167295; Frykman 1989); and one from the Ludlow, at Ängvards (Ängvards-4, RN 631953 164607). These, and all other localities on Gotland that have yielded chitons, are shown in Text-figure 1. *Chelodes* in museum collections come from Klinteberget, Gannvik, Bursvik and Rone (but probably not Atlingbo – see discussion of *C. gotlandicus*).

*Terminology and measurements* (Text-fig. 2). Standard measurements were taken with the dorsal median line mounted horizontally; length, median length, and width were measured in dorsal or lateral view, height in transverse profile, and apical length along the median length. The plates of the chiton shell are referred to here as sclerites rather than valves, since the latter term is more appropriate to organisms with paired shells that enclose soft parts. The total and median lengths differ by the amount of embayment of the anterior margin; the term anterior sinus is not appropriate in these chitons, which lack the sutural laminae of modern forms. Apical and jugal angles were measured in dorsal and posterior views, respectively. Where the posterior apex is rounded through abrasion, the apical angle is taken as the angle between the posterolateral margins. Changing shape of the sclerites through their progressive elongation results in convex posterolateral margins; for larger shells, estimates of apical angles in worn specimens are typically lower than measurements obtained from better preserved specimens. The jugum is the dorsal median ridge or rounded area, and the jugal angle is that formed by the side slope areas (Hoare and Smith 1984).

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TEXT-FIG. 1. Geological map of Gotland showing stratigraphical units and localities yielding chitons (□ with italicized names) from both previous museum (RM) and new silicified collections.

The term anterolateral margin is used here to describe the posteriorly directed corners and continuation of the anterior margin around to the point where the anterior growth lines cross on to the ventral surface. The posterolateral margin continues from that point to the posterior apex; along this margin, growth lines cross along the entire length. Shell fields are triangular areas of the dorsal surface delimited by a radial ridge or fold from adjacent areas; if present, there is usually a central field flanked by lateral fields, and the former may include a medial, jugal field.

In the systematic descriptions that follow, the measurements and ratios given are means, unless stated otherwise.

## SYSTEMATIC PALAEONTOLOGY

Class POLYPLACOPHORA de Blainville, 1816
Subclass PALEOLORICATA Bergenhayn, 1955
Order CHELODINA Bergenhayn, 1943
Family MATTHEVIIDAE Walcott, 1886

Genus CHELODES Davidson and King, 1874

*Type species. Chelodes bergmani* Davidson and King, 1874, p. 167, pl. 18, figs 14, 14a–d, by original designation, from the Silurian (Wenlock) of Gotland.

*Revised diagnosis* (emended from Runnegar *et al.* 1979, p. 1388). Wedge-shaped to cordate, arched intermediate sclerites with posterior apex; becoming elongate, massive. Ventral apical area flattened, up to more than half the length, anterior rim elevated slightly above smooth ventral surface. Growth lines across dorsal surface and ventral apical area, sometimes with ridged and granulate dorsal ornament. Shell fields lacking to well-defined.

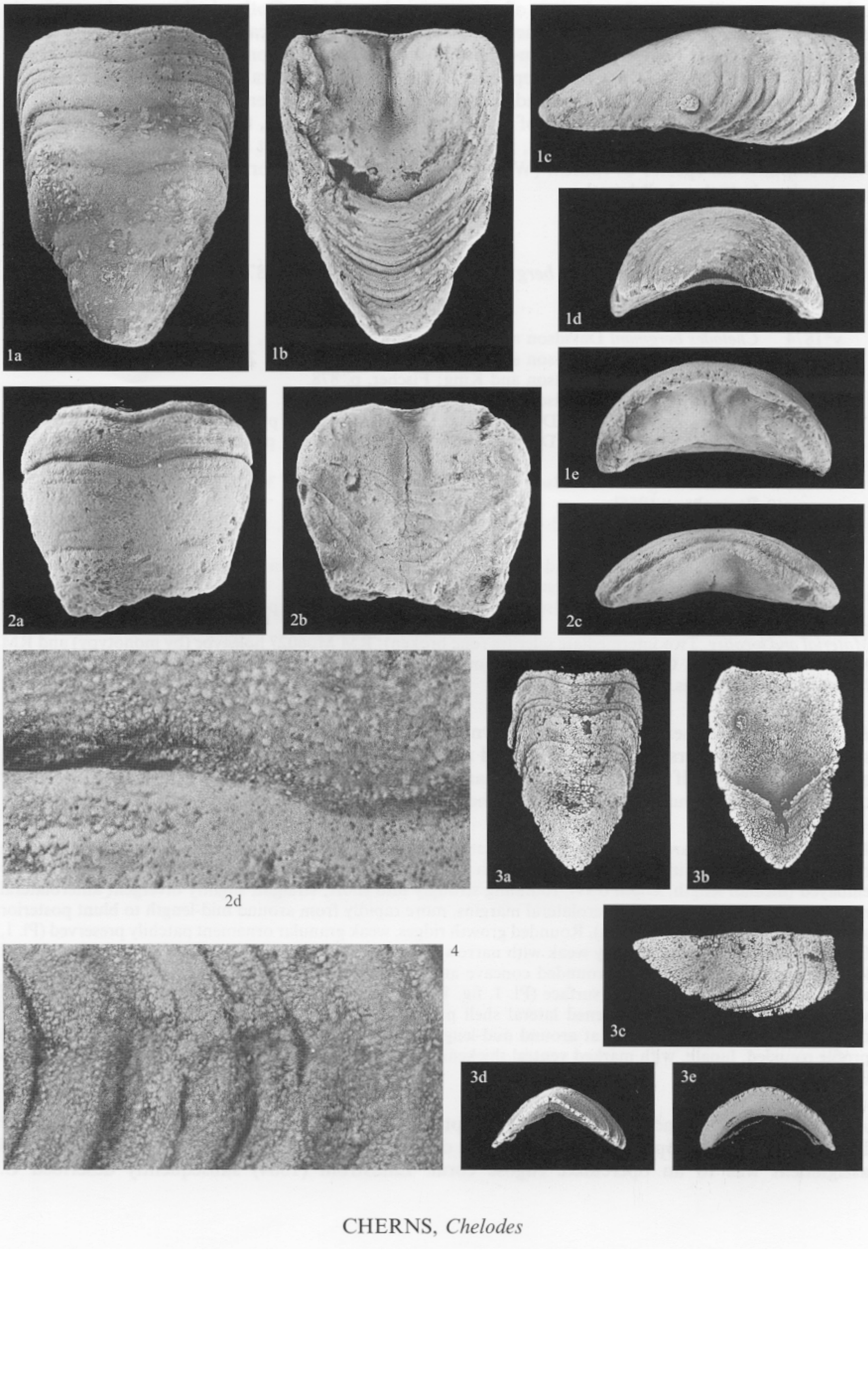
*Remarks.* Runnegar *et al.* (1979) incorporated the molluscan class Mattheva Yochelson, 1966 into the Polyplacophora, and the family Chelodidae Bergenhayn, 1943, including *Chelodes*, into the family Mattheviidae Walcott, 1886. Also included in Mattheviidae were the genera *Calceochiton* Flower, 1968, *Hemithecella* Ulrich and Bridge, 1941 and *Matthevia* Walcott, 1885. Smith and Hoare (1987, p. 7) retained the family Chelodidae to include other paleoloricate taxa not assigned to more narrowly defined families in the order Chelodina, e.g. *Eochelodes* Marek, 1962. Stinchcomb and Darrough (1995) questioned the polyplacophoran affinities of Cambrian–Ordovician hemithecellids from the Ozark area of the USA and erected a new molluscan order, Hemithecellitina; they also suggested that some elongate species of *Chelodes* might be included therein. Mattheviids differ from gotlandochitonids in having sclerites longer than wide (Bergenhayn 1943, 1955; Smith 1960; Smith and Toomey 1964; Runnegar *et al.* 1979). Further consideration of taxonomy among the

EXPLANATION OF PLATE 1

Figs 1–2. *Chelodes bergmani* Davidson and King, 1874; Klinteberg Formation, upper Wenlock (Homerian), Silurian; Klinteberget, Gotland. 1, holotype, RM Mo6027; intermediate sclerite; a–e, dorsal, ventral, right lateral, posterior and anterior views respectively; ×3. 2, RM Mo6028; intermediate sclerite; a–c, dorsal, ventral and anterior views respectively; ×3; d, detail of dorsal surface, showing granular ornament; ×15.

Fig. 3. *Chelodes* cf. *bergmani*; RM Mo160.056; Halla Formation, upper Wenlock (Homerian), Silurian; Klintebys-1, Gotland; intermediate sclerite; a–e, dorsal, ventral, right lateral, posterior and anterior views respectively; ×3.

Fig. 4. *Chelodes gotlandicus* Lindström, 1884; RM Mo6029; Hamra Formation, upper Ludlow, Silurian; Gannvik, Grötlingbo, Gotland; intermediate sclerite; detail of dorsal surface showing granular ornament; ×15.

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paleoloricates will await description of the remainder of the Gotland chitons. As currently understood, *Chelodes* is a broadly defined genus of wide morphological variability and with a long stratigraphical range (lower Ordovician–upper Silurian/Lower Devonian) and wide geographical distribution (Sweden, Britain, Czech Republic, North America, Australia). Runnegar *et al.*'s (1979) emended diagnosis for the genus included a deep anterior embayment on body sclerites, and an apical length of one-third to one-half of the sclerite length. However, the type species of *Chelodes*, *C. bergmani* Davidson and King, 1874, is characterized by a straight anterior margin. The North American Silurian species *C. raaschi* (Wenlock–Ludlow; Kluessendorf 1987) has an apical length greater than half the shell length.

### *Chelodes bergmani* Davidson and King, 1874

Plate 1, figures 1–2

v*1874 *Chelodes bergmani* Davidson and King, p. 167, pl. 18, figs 14, 14a–d.
v.1884 *Chelodes bergmani* Davidson and King; Lindström, p. 51, pl. 2, figs 1–8, 16–17.
*1885* *Chelodes bergmani* Davidson and King; Fischer, p. 878.
*1897* *Chelodes bergmani* Davidson and King; Etheridge, p. 68.
vp.1943 *Chelodes bergmanni* [*sic*] Davidson and King; Bergenhayn, p. 298.
vp.1955 *Chelodes bergmanni* [*sic*] Davidson and King; Bergenhayn, p. 12, pl. 1, figs 3a–b; pl. 2, fig. 2 [reconstruction].
1960 *Chelodes bergmani* Davidson and King; Smith, p. 149, fig. 34, 5a [reconstruction], 5b–c [cop. Bergenhayn 1955].
*1975* *Chelodes bergmani* Davidson and King; Van Belle, p. 123, pl. 1, fig. 1a–b [cop. Bergenhayn 1955].
*1977* *Chelodes bergmani* Davidson and King; Sirenko and Starobogatov, p. 31, figs 1a–b, 2a [reconstruction; cop. Bergenhayn 1955].
*1987* *Chelodes bergmani* Davidson and King; Smith and Hoare, p. 15.

*Material and locality*. Two intermediate sclerites (one broken): RM Mo6027 holotype (by monotypy) and RM Mo6028; Klinteberget, Gotland; Klinteberg Limestone Formation, upper Wenlock (Homerian), Silurian; ?*nassa*/*ludensis* biozones.

*Revised diagnosis* (emended from Bergenhayn 1955, p. 12). Wedge-shaped, low arched intermediate sclerites with transverse to weakly embayed anterior margin, elongate becoming massive. Ventral apical area nearly half of length, anterior margin rounded, concave, slightly raised. Weak granular ornament, strong, rounded growth lines. Shell fields lacking or weak.

*Description* (with measurements for holotype). Large (length 18·2 mm), wedge-shaped, elongate (length/width ratio 1·47) and massive intermediate sclerites with low arching. Anterior margin transverse, straight to weakly embayed (median length/length 0·99), rounding strongly into short, straight, slightly divergent anterolateral margins, tapering along long posterolateral margins, more rapidly from around mid-length to blunt posterior apex (apical angle 58°; Pl. 1, fig. 1a). Rounded growth ridges, weak granular ornament patchily preserved (Pl. 1, fig. 2d). Shell fields absent, or very weak with narrow, downward-sloping lateral fields (?Pl. 1, fig. 1c). Apical length/length at least 0·44, with rounded concave anterior margin and growth lines; margin raised slightly above smooth, thickened ventral surface (Pl. 1, fig. 1b). Longitudinal medial low furrow in anterior part of ventral surface, flanked by thickened lateral shell pads (Pl. 1, fig. 1b). Longitudinal profile gently convex dorsally, with slight geniculation at around mid-length (Pl. 1, fig. 1c), side slopes fairly shallow. Transverse profile rounded, lunate, with marked ventral thickening (Pl. 1, figs 1d–e, 2c); jugal angle 124°, height/length 0·28.

*Remarks*. Davidson and King (1874)'s description was based only on the holotype, supplied by Lindström, and was appended to a description of trimerellid brachiopods, although their preferred assignment was to an operculate rugose coral. Lindström (1884) subsequently described *C.*

*bergmani* as a chiton (within the Gastropoda), figured both the Klinteberg specimens (Lindström 1884, pl. 2, figs 1–8) and noted also one specimen from Grötlingbo (Gannvik; ?Hamra Formation, upper Ludlow). Bergenhayn (1955), also included in the species other, younger specimens, which in his earlier paper (Bergenhayn 1943, p. 298) he noted as coming from Gannviken (= Gannvik; RM Mo6029, Mo6030; Hamra Formation, upper Ludlow), and later (Bergenhayn 1955, p. 12) from Burgsvik ('Bursvik', RM Mo6025, Mo6030; upper Burgsvik/Hamra Formation, upper Ludlow), but he did not identify Lindström's Gannvik specimen. Lindström (1884, p. 51) noted 'traces of punctuate ornamentation' on the growth lines, indicated on the figure of the holotype (Lindström 1884, pl. 2, fig. 1). That specimen shows coarse sporadic pitting near the anterior, although this is apparently a secondary, solution feature. However, on the other Klinteberg specimen (Mo6028), there is weak, fine granular ornament patchily preserved parallel to growth lines near the anterior (Pl. 1, fig. 2d).

*C. bergmani* is characterized by an elongate, wedge-shaped form, almost straight anterior margin with no more than very slight medial embayment, only gentle transverse arching, and an apical length close to half the length. These specific characters are evident only in the holotype and the topotype. From Bergenhayn's (1943, 1955) younger material, specimen RM Mo6030 was not figured and is now missing, but Mo6029 is assigned to *C. gotlandicus* (Lindström 1884, pl. 2, figs 18–21; Pl. 2, fig. 2). RM Mo6025 is very worn, including its anterior edge, but a specific assignment to *C. bergmani* seems questionable; although growth lines are poorly preserved, they show some anterior embayment (median length/length 0·90), and the apical length/length is 0·39. On museum labels, Bergenhayn identified two further sclerites from Grötlingbo as *C. bergmani* (RM Mo6033, Mo6034); although both are worn and small, they lack features characteristic of that species. An extended stratigraphical range for the species beyond that of the type locality (i.e. upper Wenlock) through the Ludlow cannot therefore be confirmed.

### *Chelodes* cf. *bergmani* Davidson and King, 1874

Plate 1, figure 3

*Material and locality*. One silicified intermediate sclerite, RM Mo160.056; Klintebys, Gotland; Halla Formation, upper Wenlock (Homerian), Silurian.

*Description*. Small (length 11·5 mm), wedge-shaped and elongate (length/width 1·58) intermediate sclerite with blunt posterior apex (apical angle 74°), anterior margin straight, transverse (median length/length 0·98). Rounding strongly into short, straight anterolateral margins that are parallel to weakly divergent, long, gently tapering, posterolateral margins, slightly convex. Ornament of growth lines only. Shell fields lacking. Apical length/length 0·32, with rounded to V-shaped, concave anterior margin; ventral surface smooth, little thickened. Lateral profile straight dorsally, side slopes short, tapering to apex. Jugal angle 100°; transverse profile with jugal ridge flattening anteriorly, becoming rounded; height/length 0·26.

*Remarks*. This specimen is similar to *C. bergmani* in its wedge-shaped, elongate form, which lacks the anterior embayment of other Gotland *Chelodes* species, in having a blunt apex, relatively short side slopes, and a fairly long apical area. However, this apical area is shorter than in *C. bergmani*, the anterolateral margins correspondingly somewhat longer, and the specimen is small and little thickened. A length-width graph (Text-fig. 6) of growth stages in this specimen illustrates the narrow form (length/width 1·58) compared with *C. gotlandicus* (length/width 1·16). Other *Chelodes* specimens from the same locality, all of which are beekitized and poorly preserved, include two broad cordate sclerites, probably *Chelodes actinis* sp. nov. (described below). The Klintebys-1 locality is in the Halla Formation (late Wenlock), and thus is similar in age or only slightly older than the Klinteberg Limestone at Klinteberget.

### *Chelodes gotlandicus* Lindström, 1884

Plate 1, figure 4; Plate 2; Text-figure 3

vp*1884 *Chelodes gotlandicus* Lindström, p. 51, pl. 2, figs 9–27.
*1897* *Chelodes gotlandicus* Lindström; Etheridge, p. 69.
vp.1943 *Chelodes gotlandicus* Lindström; Bergenhayn, p. 298.
v.1955 *Chelodes gotlandicus* Lindström; Bergenhayn, p. 9, pl. 1, figs 1, 2a–b; pl. 2, fig. 1 [lectotype selected].
v.1955 *Chelodes variegatus* Bergenhayn, p. 13, pl. 1, fig. 4; pl. 2, fig. 3 [reconstruction].
v.1955 *Gotlandochiton laterodepressus* Bergenhayn, p. 17, pl. 1, fig. 8; pl. 2, fig. 5 [reconstruction].
v.1955 *Gotlandochiton troedssoni* Bergenhayn, p. 19, pl. 1, fig. 9; pl. 2, fig. 7 [reconstruction].
*1960* *Gotlandochiton laterodepressus* Bergenhayn; Smith, p. I50, fig. 34, 8 [cop. Bergenhayn 1955].
*1960* *Gotlandochiton troedssoni* Bergenhayn; Smith, p. I50, fig. 34, 7 [cop. Bergenhayn 1955].
*1975* *Gotlandochiton troedssoni* Bergenhayn; Van Belle, pl. 1, fig. 7 [cop. Bergenhayn 1955].
*1977* *Chelodes gotlandicus* Lindström; Sirenko and Starobogatov, p. 31.
*1977* *Chelodes variegatus* Bergenhayn; Sirenko and Starobogatov, p. 31.
*1977* *Gotlandochiton laterodepressus* Bergenhayn; Sirenko and Starobogatov, p. 31, fig. 2b [cop. Bergenhayn 1955].
*1977* *Gotlandochiton troedssoni* Bergenhayn; Sirenko and Starobogatov, p. 31.
?1987 Morphotype B Kluessendorf, p. 439, pl. 1, fig. 4.
*1987* *Chelodes gotlandicus* Lindström; Smith and Hoare, p. 30.
*1987* *Chelodes variegatus* Bergenhayn; Smith and Hoare, p. 58.
*1987* *Gotlandochiton laterodepressus* Bergenhayn; Smith and Hoare, p. 38.
*1987* *Gotlandochiton troedssoni* Bergenhayn; Smith and Hoare, p. 56.

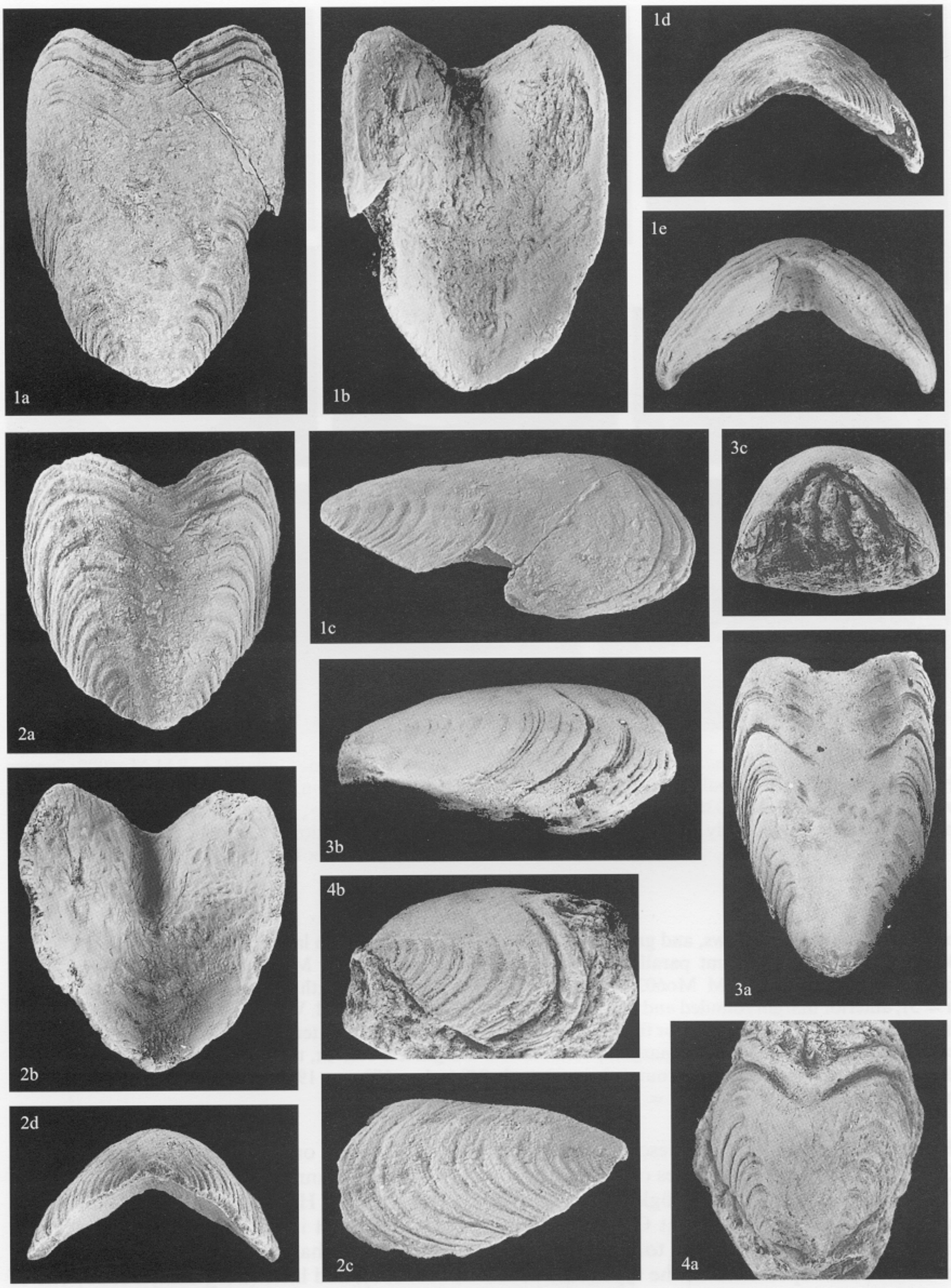
*Material and locality*. Twenty-six intermediate sclerites from Grötlingbo (Gannvik), Burgsvik (Bursvik) and Rone, Gotland; upper Hemse Group–lower Hamra Formation, upper Ludlow, Silurian; lectotype RM Mo5098 from Gannvik, lower Hamra Formation, upper Ludlow. Syntypes RM Mo5099–6001, 6003–6011, 6015–6020, 6025–6026, 6029, 6032–6034, 6036.

*Diagnosis* (emended from Bergenhayn 1955, p. 9). Cordate and arched intermediate sclerites with anterior embayment and blunt posterior apex; dorsal low radial folds defining broad elevated central shell field flanked by narrower lateral fields; ornament of rounded ridges and grooves, and growth lines, sometimes fine granular ornament; ventral apical area around one-third of sclerite length.

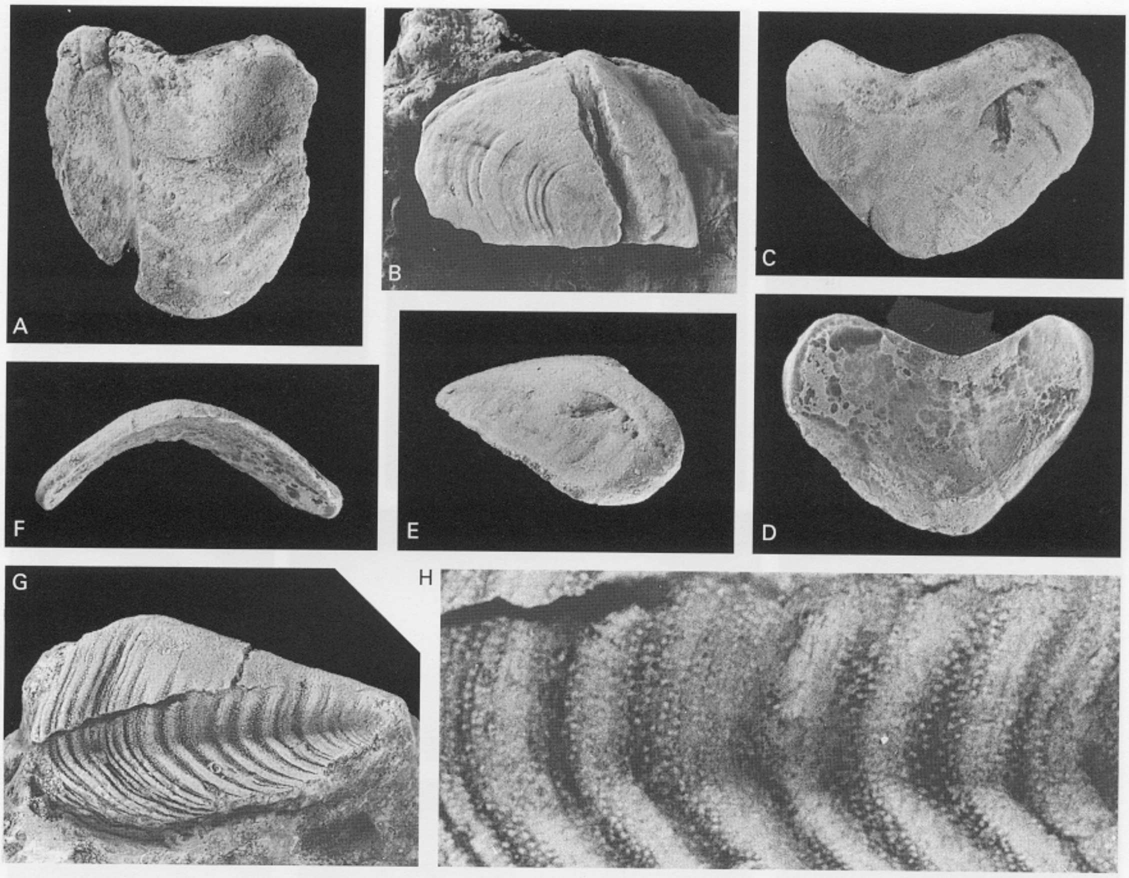
*Description*. Large, heart-shaped and arched, fairly broad intermediate sclerites (lectotype length 19·3 mm; mean length 12·65 mm, s.d. = 3·63 mm, $n = 22$; length/width 1·16, s.d. = 0·27, $n = 19$) with marked anterior embayment (median length/length 0·91, s.d. = 0·04, $n = 22$), rounding anterolaterally into fairly short, convex, divergent to parallel anterolateral margins, then into longer, gently convex posterolateral margins that taper to blunt posterior apex; apical angle 80° (s.d. = 17°, $n = 18$). Dorsal shell fields; broad, elevated and triangular central field flanked by low radial folds, 0·66 of width (s.d. = 0·11, $n = 15$), narrower and downward sloping lateral fields; central field with weak low folds elevating a jugal field in RM Mo6029 (Pl. 2, fig. 2a–c). Ornament

EXPLANATION OF PLATE 2

Figs 1–4. *Chelodes gotlandicus* Lindström, 1884; upper Ludlow, Silurian; Gotland. 1, holotype, RM Mo5098; Hamra Formation; Gannvik, Grötlingbo; intermediate sclerite; a–e, dorsal, ventral, right lateral, posterior and anterior views respectively; ×3. 2, RM Mo6029; intermediate sclerite; Hamra Formation; Gannvik, Grötlingbo; a–d, dorsal, ventral, left lateral and posterior views respectively; ×3. 3, RM Mo6006; intermediate sclerite; Hamra Formation; Burgsvik (Bursvik); a–c, dorsal, right lateral and anterior views respectively; ×3. 4, RM Mo6010; intermediate sclerite; ?upper Hemse Group; Rone; a–b, dorsal and left lateral views respectively; ×3.




CHERNS, *Chelodes*




TEXT-FIG. 3. *Chelodes gotlandicus* Lindström, 1884; upper Ludlow, Silurian; Gotland. A, RM Mo6009; ?upper Hemse Group; Rone; ventral view; ×3. B, RM Mo6020; Hamra Formation; Gannvik, Grötlingbo; left lateral view; ×3. C–F, RM Mo6036; Hamra Formation; Gannvik, Grötlingbo; dorsal, ventral, right lateral and posterior views, respectively; ×5. G–H, RM Mo6011; ?Hamra Formation; ?Gannvik, Grötlingbo. G, left lateral view; ×3. H, detail of ornament; ×15.

of growth ridges and furrows, and growth lines, mostly better preserved in lateral shell areas (Pl. 2, figs 1c, 3b, 4b). Fine granular ornament parallel to growth lines well preserved in Mo6011 (Text-fig. 3G–H), patchily preserved and weak in RM Mo6029 (Pl. 1, fig. 4). Apical length/length approximately 0·33 (s.d. = 0·05, $n = 5$); anterior margin rounded and concave to V-shaped, slightly elevated. Ventral surface smooth, thickened, developing shallow medial anterior furrow flanked by lateral shell pads. Lateral profile slightly convex dorsally, convex anterior to anterolateral margin, posterolateral margin less convex, tapering; side slopes fairly deep to deep. Transverse profile arched, rounded; jugal angle 84° (s.d. = 17°, $n = 19$), jugal field flattening anteriorly; height/length 0·44 (s.d. = 0·08, $n = 18$).

*Remarks. C. gotlandicus* was described by Lindström (1884), based on more extensive material than *C. bergmani*, using a type series of specimens from Grötlingbo (Gannvik), Burgsvik and Rone, and from Visby (Kålens kvarn; Högklint Formation, lower Wenlock). He noted that both *C. bergmani* and *C. gotlandicus* occurred at Grötlingbo (Gannvik), although it is not known which specimens from this locality he assigned to *C. bergmani* (see above). Bergenhayn (1943, p. 298) selected two of Lindström's specimens as the type (RM Mo5098, Mo5099), and later (Bergenhayn 1955) one of them, which represents the lectotype (RM Mo5098; Lindström 1884, pl. 2, figs 11–15; Bergenhayn 1955, pl. 1, fig. 1; Pl. 2, fig. 1). Compared with *C. bergmani*, *C. gotlandicus* has more arched, broader, heart-shaped sclerites with a marked anterior embayment, and *C. bergmani* has shallow, wedge-shaped sclerites with an almost straight anterior margin, and a longer apical area. Lindström (1884, p. 51) noted the variable shape of sclerites in *C. gotlandicus*, from elongate to broad. He described marked ridges on the dorsal surface coincident with growth lines, and two longitudinal grooves that delimit the central area from narrower lateral shell areas. The latter are features evident only in the better preserved sclerites, e.g. the apical portion of the lectotype, and in RM Mo6029 which shows, in addition, a low jugal, radial fold within the central field (Lindström 1884, pl. 2, figs 18–21; Pl. 2, fig. 2a, c). The fairly evenly spaced, ridged ornament is preserved more commonly on the lateral shell fields, becoming eroded from the arched central field of several specimens. The fine, granular ornament described above, which appears similar to that in *C. bergmani* (Pl. 1, fig. 4 cf. Pl. 1, fig. 2d), is rarely preserved and, in more worn specimens, the shell between growth ridges appears smooth.

In his revision of Gotland chitons, Bergenhayn (1955) erected the species *C. variegatus* for two intermediate sclerites from Lindström's type series of *C. gotlandicus*; the holotype (RM Mo6011; Lindström 1884, pl. 2, figs 9–10; Text-fig. 3G–H) is alleged to come from Atlingbo (Slite Group, Wenlock) and a paratype from Grötlingbo (RM Mo6005; Gannvik), but there is some confusion over Atlingbo as the type locality. The locality given in Lindström's (1884, pl. 2, figs 9–10) plate description is Grötlingbo, and Lindström's (1884, pp. 52, 16–17) description and distribution table show that his *C. gotlandicus* material, including this specimen, came only from Grötlingbo, Burgsvik and Visby. The locality Atlingbo (which is one of Lindström's gastropod localities, in the older, Slite Group) is given on the boxed museum label now with this specimen, but the museum label on the specimen itself shows Grötlingbo subsequently altered to Atlingbo. The preservation of the specimen and matrix lithology are similar to other Grötlingbo (Gannvik) specimens. *C. variegatus* was distinguished from other *Chelodes* species by its distinct medial and lateral shell fields, the latter curved down ventrally, and by equally spaced growth ridges, and from *C. gotlandicus* by the lobe-and-saddle form of the anterior margin and pronounced growth ridges. The holotype is partially embedded in limestone, with only the left side of the dorsal shell exposed, and the ventral surface obscured. The emended diagnosis given here for *C. gotlandicus* emphasizes the distinction of central (medial) and lateral shell fields, and of pronounced growth ridges as ornament. These features characterize Bergenhayn's (1955) two *C. variegatus* specimens, both of which are somewhat compressed laterally but fall within the range of variation of *C. gotlandicus*. The holotype has fine granular ornament, similar to, but better preserved than that observed on RM Mo6029 (see above). The second specimen of *C. variegatus* (RM Mo6005) is worn and appears smooth between growth ridges. One or perhaps both specimens of *C. variegatus* come from the *C. gotlandicus* type locality at Gannvik, and *C. variegatus* is regarded here as a junior synonym of *C. gotlandicus*.

Bergenhayn (1955, p. 10, pl. 1, fig. 2a–b; Text fig. 3A) figured and described one specimen (RM Mo6009) as a tail sclerite. Re-examination of the specimen shows that the poorly preserved plate is compressed laterally, distorting the ventral surface, which was the side figured as dorsal. The ventral apical area is evident in Bergenhayn's (1955) figures. The new silicified collections from Gotland include no additional chiton material from Ludlow localities, and no *C. gotlandicus*. Lindström's collections are apparently all intermediate sclerites, unless possibly one notably elongate (length/width 1·58 cf. average for species 1·16), arched and narrow sclerite (RM Mo6006; Pl. 2, fig. 3), unfortunately embedded in matrix so that the ventral side is obscured, represents a tail plate (see discussion under *C. actinis* below).

Lindström's specimens from Visby (Kålens qvarn = Kolens kvarn) together with several from Grötlingbo (Gannvik), which he had included in *C. gotlandicus*, were reassigned by Bergenhayn (1955) to the new genus *Gotlandochiton*. This, with type species *G. interplicatus* Bergenhayn, 1955, was characterized by intermediate sclerites that are wider than long, with distinct shell fields, and with jugal to complete overlap along the anterior margins between sclerites. *Gotlandochiton laterodepressus* Bergenhayn, 1955 was based on a single intermediate sclerite from Grötlingbo

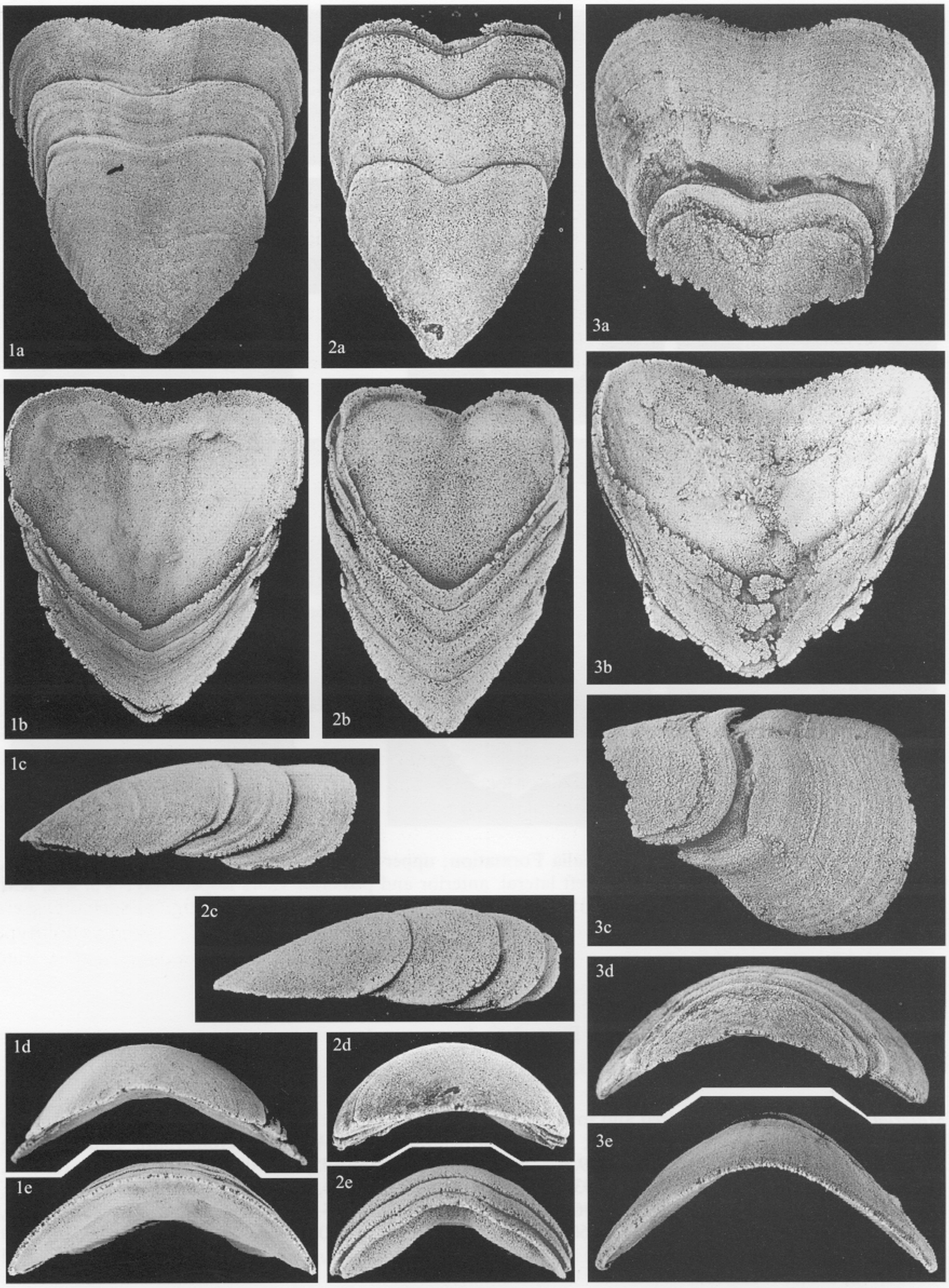
(Gannvik) embedded in limestone matrix with only the left dorsal side exposed (RM Mo6020; Bergenhayn 1955, pl. 1, fig. 8; Text-fig. 3B). The left side of the (broken) sclerite is wider than long, differentiated into a slightly elevated, triangular central field which has a broad anterior margin and tapers to the apex, and narrower lateral area with rounded anterolateral margin, long straight posterolateral margin tapering rapidly to the apex. Growth lines are more accentuated across the lateral area as shallow ridges and furrows. Across the anterior margin, curvature of the growth lines suggests a shallow embayment (cf. Bergenhayn's (1955, p. 17) description as straight). Bergenhayn (1955) distinguished this species on the basis of the much wider than long form, depressed lateral area and ornament of ridges and furrows. The redescription of *C. gotlandicus* herein emphasizes as specific features the development of shell fields, and ridged ornament, which is more commonly evident on the less abraded, lateral areas. The holotype of *G. laterodepressus*, as well as showing these features, appears to have some anterior embayment as found in *C. gotlandicus*, and it comes from the type locality of the latter (indeed, it was originally one of Lindström's (1884) syntypes for *C. gotlandicus*). There is a large variation in length/width in *C. gotlandicus*, and although the *G. laterodepressus* specimen is notably short and wide after compression, all other shell features suggest that *G. laterodepressus* should be regarded as a junior subjective synonym of *C. gotlandicus*.

*Gotlandochiton troedssoni* Bergenhayn, 1955 was based on two small, worn intermediate sclerites from Grötlingbo (Gannvik; RM Mo6032, Mo6036). Bergenhayn (1955, p. 19) noted also an unnumbered Riksmuseum specimen of a half sclerite from 'Landspitze von Grötlingbo', not now identifiable among the collections. Bergenhayn's (1955) diagnosis was of intermediate sclerites half as long as wide, with anterior and posterior margins obtuse-angled and parallel, distinct medial and lateral shell fields, and complete overlap along the anterior margin between adjacent plates. He noted strong growth ridges parallel to the lateral margins. The two sclerites are wider than long, and there is a medial embayment of the broad anterior margin. The short anterolateral (= lateral) margins are rounded and convex, curving into long, straight, rapidly tapering posterolateral (= posterior) margins transected by growth lines. The posterior apex in both examples is worn; only RM Mo6036 (Text-fig. 3C–F) shows any indication of a ventral apical area, as a poorly defined broad triangular band a minimum of 0·22 of the length of the sclerite. The worn dorsal surface shows a slightly elevated central shell field, flanked by narrower lateral areas on which growth ridges and furrows are better preserved (Text-fig. 3C; Bergenhayn 1955, pl. 1, fig. 9). These dorsal shell features and embayed anterior margin occur in *C. gotlandicus*, from which the transverse form of these small sclerites is the only notable difference. The apparently rounded, broad shape to the apex can be ascribed to abrasion. The form of *C. gotlandicus* sclerites is very variable, only reliably becoming longer than wide with age (Pl. 2; Text-fig. 6). The type localities of *C. gotlandicus* and *G. troeddsoni* are the same, and the latter is considered here to be a junior subjective synonym of the former.

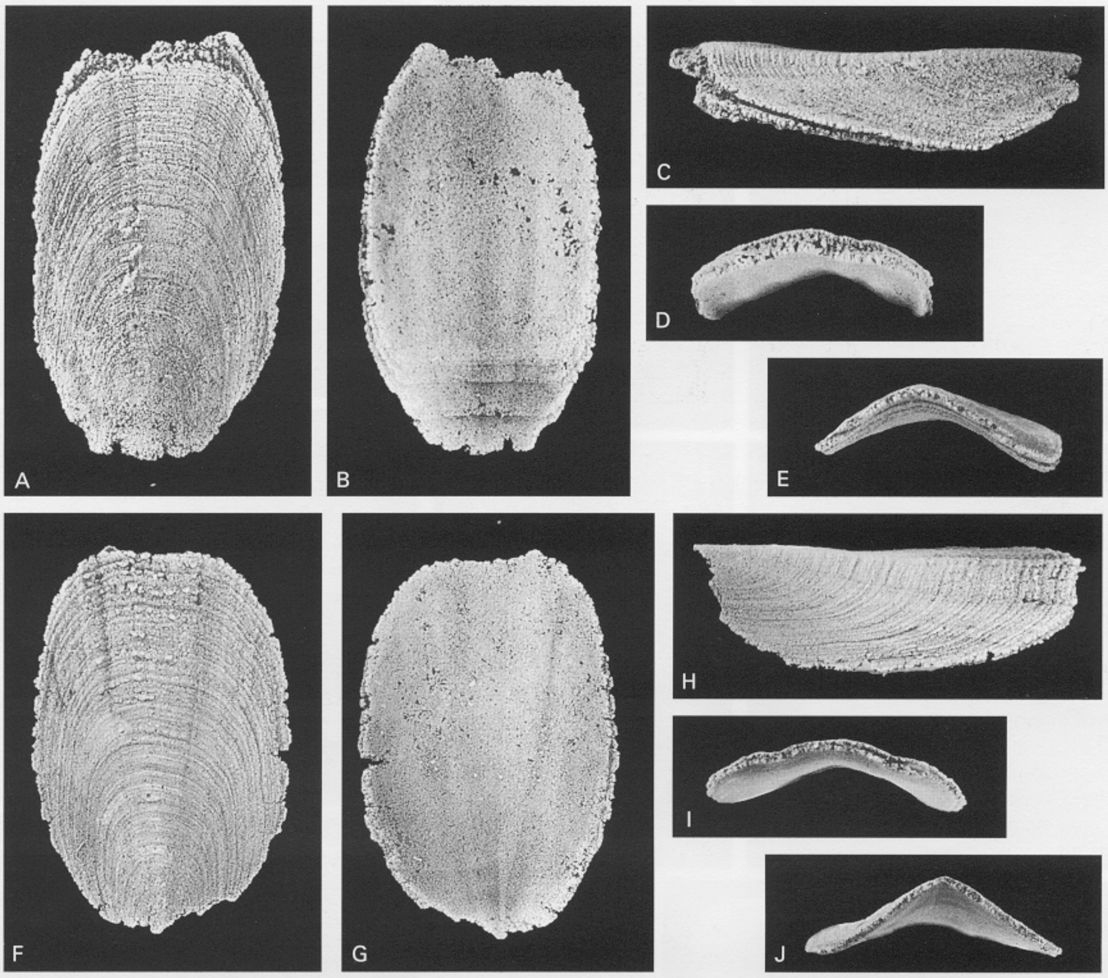
From Lindström's (1884) collections, the Visby and Kålens kvarn (Text-fig. 1) specimens are retained within *Gotlandochiton*. On the assumption that Bergenhayn's (1955) *C. variegatus* holotype is from Grötlingbo, not Atlingbo (see above), the stratigraphical range of *C. gotlandicus* is restricted to the upper Ludlow.

EXPLANATION OF PLATE 3

Figs 1–3. *Chelodes actinis* sp. nov.; Halla Formation, upper Wenlock (Homerian), Silurian; Möllbos-1, Gotland. 1, holotype, RM Mo160.004; intermediate sclerite; a–e, dorsal, ventral, right lateral, posterior and anterior views respectively; ×3. 2, RM Mo159.802; intermediate sclerite; a–e, dorsal, ventral, right lateral, posterior and anterior views respectively; ×3. 3, RM Mo159.858; intermediate sclerite; a–e, dorsal, ventral, right lateral, posterior and anterior views respectively; ×3.




CHERNS, *Chelodes*




TEXT-FIG. 4. *Chelodes actinis*, sp. nov.; Halla Formation; upper Wenlock (Homerian), Silurian; Möllbos-1, Gotland; head sclerites; dorsal, ventral, left lateral, anterior and posterior views respectively; × 5. A–E, RM Mo159.818. F–J, RM Mo160.003.

## *Chelodes actinis* sp. nov.

Plates 3–6; Text-figure 4

*Derivation of name*. From the Greek *aktis*, a ray, with reference to the weak dorsal radial folds.

*Material and locality*. One hundred and fourteen (102 used in biometric data) intermediate sclerites, and two head sclerites from Möllbos, Gotland; Halla Formation, upper Wenlock (Homerian), Silurian; Rm Mo159.802–159.824, 159.858–159.864, 159.869–159.873, 159.875, 159.895, 159.902–159.903, 159.905–159.910, 159.918–159.919, 159.922, 159.926–159.935, 159.938–159.941, 159.943, 159.945–159.947, 159.950–159.951, 159.953, 159.957–159.959, 159.961–159.967, 159.970–159.971, 159.975–159.982, 159.985, 159.988–159.995, 160.003–160.008 (160.004 is holotype), 160.012–160.015, 160.018, 160.021–160.024, 160.027, 160.031. Three intermediate sclerites from Klintebys-1, Gotland; Halla Formation, upper Wenlock (Homerian); RM Mo160.042, 160.054–160.055.

*Diagnosis.* Cordate and arched intermediate sclerites, shallow anterior embayment, pointed posterior apex; low radial folds giving weak definition of narrow lateral and broad central shell fields, and jugal field; ornament of fine growth lines; ventral apical area about one-third of length. Head sclerites fairly small, ovoid, elongate, weakly arched; transverse anterior margin, posterolateral margins tapering, becoming transverse; posterior apex slightly elevated; low dorsal radial folds, slightly elevated central shell field, lateral folds flanked by shallow furrows; ornament of fine growth lines; fairly short, transverse ventral apical area.

*Description.* Intermediate sclerites cordate and arched, highly variable in form, from broader to more elongated (holotype length 17·8 mm; mean length 11·58 mm, s.d. = 5·23 mm, $n = 83$; length/width 1·12, s.d. = 0·13, $n = 71$), anterior margin with shallow embayment (median length/length 0·96, s.d. = 0·03, $n = 79$). Rounded anterolateral corners, fairly short parallel anterolateral margins, curving into gently convex, long posterolateral margins tapering to pointed posterior apex; apical angle 76° (s.d. = 11°, $n = 84$). Maximum width anterolateral, well in front of mid-length. Ornament of fine growth lines (Pl. 5, fig. 2f); pronounced growth increments on some sclerites show anterior embayment maintained throughout growth, variable elongation relative to broadening of sclerite, although generally becoming longer than wide, whereas smaller sclerites and younger growth stages commonly wider than, or as wide as, long (Pls 3–5; Text-fig. 5). On better preserved sclerites, weak dorsal radial folds from apex indicating fairly narrow lateral and broad central fields, the latter with low medial fold representing rounded jugal field; however, fields poorly defined, sometimes with additional radial folds within fields (e.g. Pl. 3, fig. 1a, 1c; Pl. 5, figs 1a, 2a, 2f).

Ventral surface concave, flexed gently medially; apical area with slightly raised, concave anterior margin, rounded to broadly flexed medially, apical length/length variable, mean 0·34 (s.d. = 0·08, $n = 78$; e.g. Pl. 3, figs 1b, 2b). Marked growth increments record expansion and elongation of apical area (Pl. 3, figs 1b, 2b; Pl. 4, fig. 1b; Pl. 5, fig. 1b). Shallow groove more or less developed beneath apical margin and, in some larger, thickened sclerites, continuing inside the anterolateral and anterior margins (e.g. Pl. 3, fig. 2b; Pl. 4, figs 2b, 3b). Ventral surface outside apical area smooth, in larger sclerites becoming thickened and sculpted towards anterior into lateral pads outside shallow median longitudinal groove (Pl. 4, fig. 3b, d–e).

Lateral profile wedge-shaped, side slopes fairly shallow to deep (e.g. Pl. 3, figs 1c, 2c cf. 3c; Pl. 5, fig. 1c cf. 2c). Dorsally gently convex to straight, or rarely slightly concave (Pl. 5, fig. 2c); anterior to anterolateral margin convex, smoothly rounded; posterolateral margin fairly straight, tapering across apical area to apex. Posterior transverse profile arched and rounded dorsally, ventrally more flexed across jugum, side slopes tapering laterally; jugal angle 109° (s.d. = 6°, $n = 98$); height/length ratio 0·35 (s.d. = 0·04, $n = 74$). Anterior transverse profile more rounded; median longitudinal groove and secondary lateral shell pads evident on ventral surface of thickened sclerites (Pl. 4, fig. 3e; Pl. 3, fig. 2e).

Head sclerites (based on two specimens: RM Mo159.818, 160.003; Text-fig. 4) mean length 10·55 mm, ovoid, elongate (length/width 1·61, s.d. = 0·17, $n = 2$), weakly arched. Transverse anterior margin rounding into gently convex, longer anterolateral margins, which round into short, tapering posterolateral margins becoming transverse to posterior, slightly elevated apex; apical angle 180°. Low rounded radial folds from apex to anterior and lateral margins, flanked by shallow rounded furrows; low elevated central field (0·37 of width, s.d. = 0·07, $n = 2$) and less well defined pair of narrower lateral folds. Ornament of fine growth lines, parallel to anterior and anterolateral margins, crossing posterolateral margins. Ventral apical area (preserved only on RM Mo159.818) fairly short, apical length/length 0·22, flattened to slightly concave; transverse anterior margin slightly raised, curving anteriorly close to posterolateral margins. Ventral surface smooth and concave, with shallow and weak radial folds; median furrow flanked by narrower lateral pair, reflected in low folds of dorsal surface. Lateral profile shallow; dorsal low ridge straight, shell deepest at posterolateral corners, anterolateral margin tapering slightly anteriorly. Transverse profile flexed across median ridge, jugal angle 118° (s.d. = 7°, $n = 2$) flattening anteriorly; anterior edge showing weak corrugation. Tail sclerite unknown.

*Remarks.* This species differs from both *C. bergmani* and *C. gotlandicus* in having an ornament of fine growth lines only. In addition, it differs (Table 1) from *C. bergmani* in having broader and more arched, heart-shaped sclerites with an anterior embayment and a pointed broader apex, low dorsal radial folds which define weak shell fields, and a shorter ventral apical region. Compared with the cordate species *C. gotlandicus*, *C. actinis* shows weaker definition of central and lateral shell fields, oblique, shallower arching, a shallower anterior embayment and pointed apex.

*C. raaschi* Kluessendorf, 1987 from the Wenlock–Ludlow Racine Dolomite of North America has a narrower, more elongate form (Table 1), much longer apical area, and more acute apex than

*C. actinis*. *C. bohemicus* (Barrande, 1867), from the upper Wenlock (basal Homerian, *lundgreni* Biozone) of Bohemia (Barrande 1867, p. 175, pl. 16, figs 19–28) is a large, weakly cordate species that has well-defined, dorsal, low radial folds delineating narrow lateral fields and a broad elevated central field with a jugal fold, and there is an ornament of fine growth lines together with elongate granules.

The relatively large numbers of robust specimens from Möllbus might reasonably be expected to include tail sclerites. Two fairly small specimens with markedly different form from the intermediate sclerites are interpreted as head sclerites (Text-fig. 4); by comparison with other chitons, tail sclerites are commonly more similar in morphology to the intermediate sclerites, although typically with a raised apex, or mucro. For the early Ordovician *C. whitehousei*, Runnegar *et al.* (1979, pl. 2, figs 36–38, 54–59) figured triangular to rectangular, arched sclerites of similar size to the intermediate sclerites as representing the tail sclerites. In the late Cambrian *Matthevia variabilis*, the tail sclerites by comparison with the conical intermediate sclerites are shorter and laterally compressed, and they and the head sclerites each occur in the ratio of 1:5 against the intermediate sclerites (Runnegar *et al.* 1979; see discussion of *C. actinis* below). Bergenhayn (1960) described, but did not figure, laterally compressed valves with an elevated mucro as tail valves for the early Ordovician *C. intermedius*, and figured, without description, a broken specimen showing few features which he identified as a tail valve of *Chelodes*? sp. indet. (Bergenhayn 1960, p. 175, text-fig. 1, figs 17–18).

Tail sclerites are not recognized among the other Gotland (Silurian) *Chelodes* species (see above for discussion of the supposed tail sclerite for *C. gotlandicus* (RM Mo6009), identified by Bergenhayn 1955). *C. gotlandicus* sclerites are variable in length and transverse profile, and compared with the broad and fairly gently arched form of the holotype and several other specimens, RM Mo6006 is long, relatively narrow and acutely arched (Pl. 2, fig. 3; cf. figs 1–2, 4). Barrande's (1867) figured specimens of Silurian *C. bohemicus* from Bohemia are similarly variable in form, including one elongate specimen with a notably more tightly arched and narrow form than the other specimens (Barrande 1867, pl. 16, fig. 23). However, these individual specimens of the two species are within the general range of intraspecific variation, not greatly different from others, and may still represent intermediate sclerites.

For *C. actinis*, there is a similarly wide variation in form and, except where the head sclerites are included, graphical plots of the various shell parameters do not distinguish subgroups of data (e.g. length/width in Text-fig. 5). The lateral dorsal profile of sclerites is commonly slightly convex to straight, rarely slightly concave so that the apex becomes elevated (Pls 3–6, all figs c). One specimen showing the latter characteristic is RM Mo159.951, which also has notably deep side slopes and well-defined shell fields including a jugal fold (Pl. 5, fig. 2c–d; cf. Pls 3–6, all figs c–d). Within *C. gotlandicus*, RM Mo6029 (Pl. 2, fig. 2) is comparable in most respects, although the apex is not raised. However, again there is insufficient distinction from other specimens to identify any group of particular morphological characteristics as representing tail plates.

The new silicified collections include a group of small, broad and triangulate sclerites that lack any anterior embayment, are only shallowly arched and have a short, wide apical area. These sclerites occur as single specimens among collections with *C. actinis*, which suggests that they could represent the tail sclerites of that species, yet their morphology is considerably different both from the *C. actinis* intermediate sclerites and from the tail sclerites proposed for other members of the

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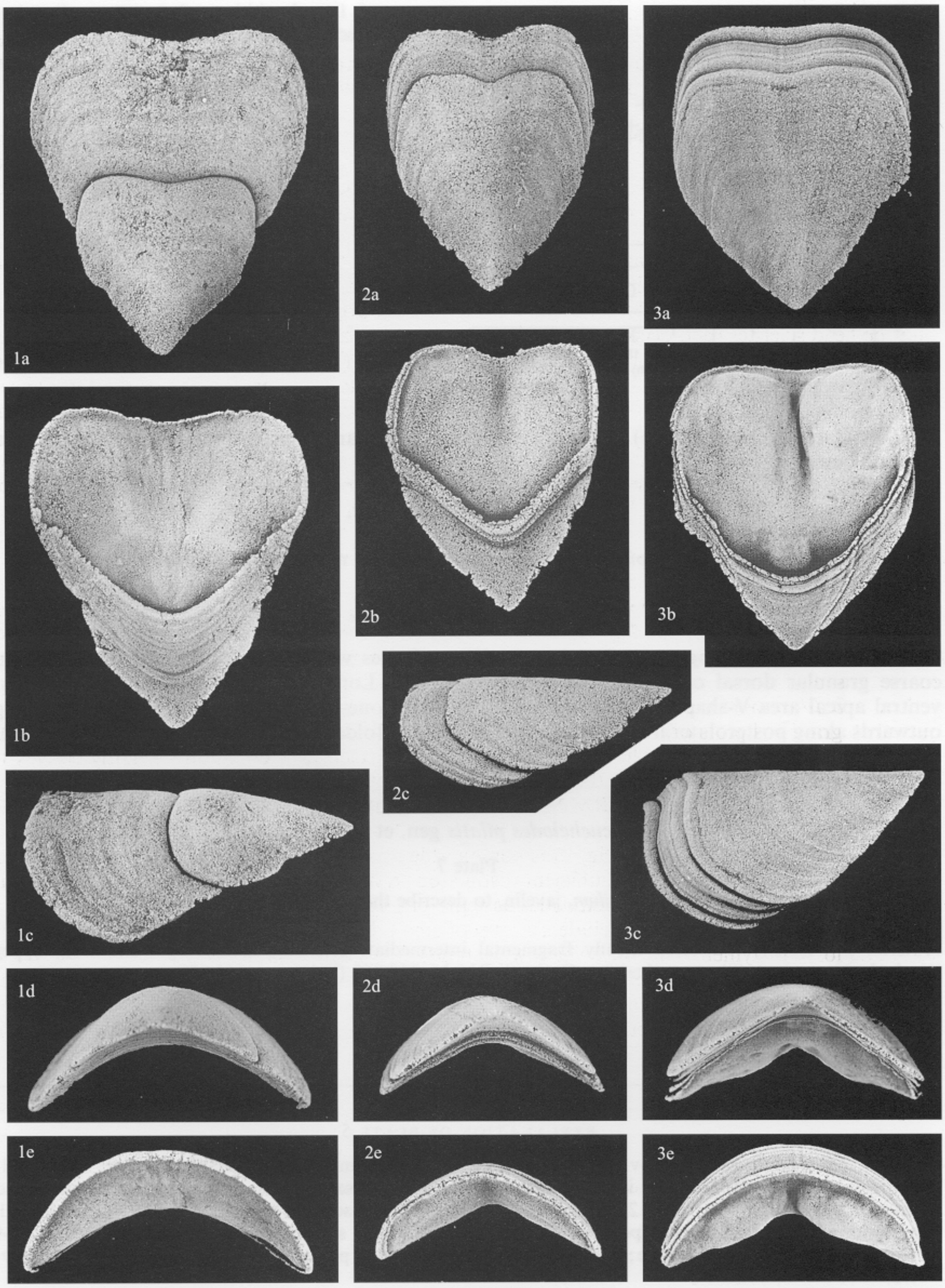
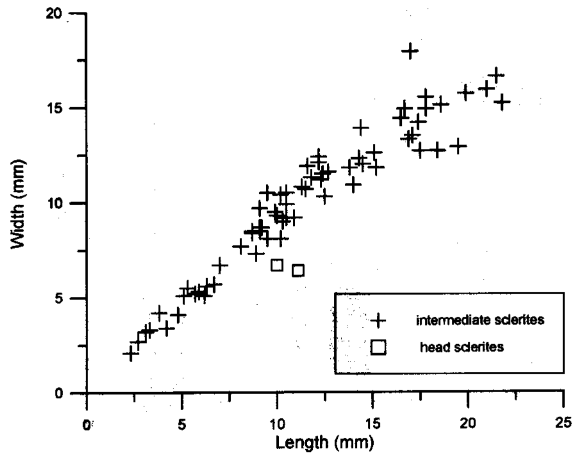
EXPLANATION OF PLATE 4

Figs 1–3. *Chelodes actinis* sp. nov.; Halla Formation, upper Wenlock (Homerian), Silurian; Möllbos-1, Gotland. 1, RM Mo159.971; intermediate sclerite; a–e, dorsal, ventral, left lateral, posterior and anterior views respectively; × 3. 2, RM Mo159.922; intermediate sclerite; a–e, dorsal, ventral, left lateral, posterior and anterior views respectively; × 3. RM Mo159.946; intermediate sclerite; a–e, dorsal, ventral, left lateral, posterior and anterior views respectively; × 3.




CHERNS, *Chelodes*




TEXT-FIG. 5. Length-width graph for intermediate and head sclerites of *Chelodes actinis* sp. nov.

Mattheviidae (described above). Alternatively, these plates are sufficiently distinct to represent a separate genus.

## SPICUCHELODES gen. nov.

*Derivation of name.* From Latin *spica*, ear of grain, to describe the raised granular ornament.

*Type species. S. pilatis* sp. nov.

*Diagnosis.* Cordate, elongate, arched intermediate sclerites with pointed posterior apex, strong, coarse granular dorsal ornament; becoming thickened. Long tapering posterolateral margins; ventral apical area V-shaped, strongly flexed and about one-third of length at midline, tapering outwards along posterolateral margins. Low dorsal radial folds, narrow central and broader lateral shell fields weakly defined.

### *Spicuchelodes pilatis* gen. et sp. nov.

Plate 7

*Derivation of name.* From the Latin *pilum*, javelin, to describe the slender pointed apex.

*Material and locality.* Nineteen mostly fragmental intermediate sclerites; Klintęberg Formation, upper Wenlock (Homerian), Silurian; Krakfot, Gotland. RM Mo160.062 (holotype)–160.079.

*Diagnosis.* As for the genus.

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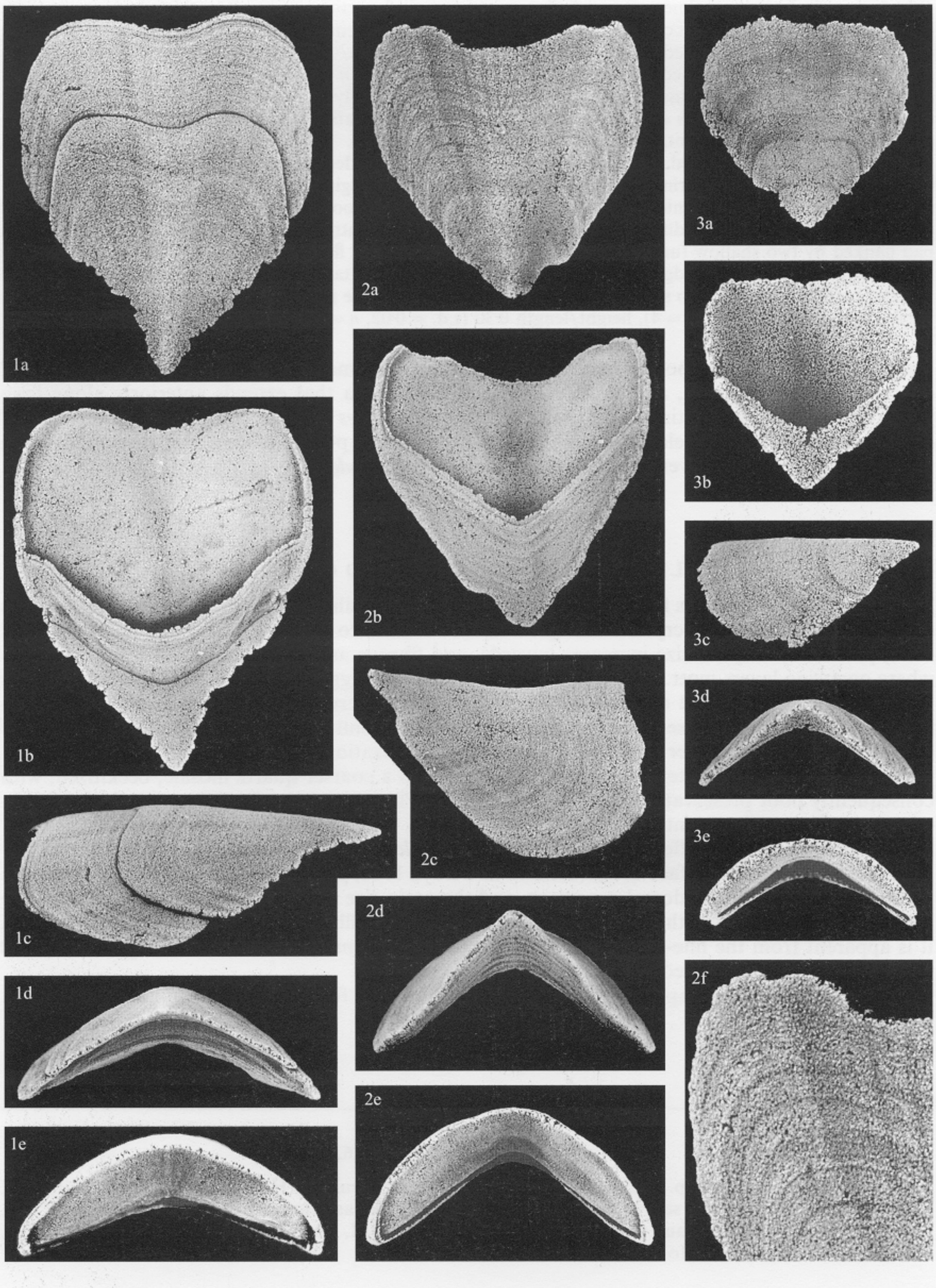
EXPLANATION OF PLATE 5

Figs 1–3. *Chelodes actinis* sp. nov.; Halla Formation, upper Wenlock (Homerian), Silurian; Möllbos-1, Gotland. 1, RM Mo160.005; intermediate sclerite; a–e, dorsal, ventral, left lateral, posterior and anterior views respectively; ×4. 2, RM Mo159.951; intermediate sclerite; a–e, dorsal, ventral, right lateral, posterior and anterior views respectively; ×4; f, detail of dorsal surface, showing ornament; ×8. 3, RM Mo159.869; intermediate sclerite; a–e, dorsal, ventral, left lateral, posterior and anterior views respectively; ×5.




CHERNS, *Chelodes*

*Description.* Beekitized specimens showing the posterior, apical portions of cordate, thickened intermediate sclerites, some with prominent coarse, spaced granular dorsal ornament arranged along growth lines (Pl. 7, figs 1a, 2a, d). Sclerites low arched, elongate and fairly slender (length/width 1·23, s.d. = 0·13, $n = 2$), with an embayed anterior margin (median length/length 0·93, s.d. = 0·04, $n = 2$) and short, rounded anterolateral corners. Posterolateral margins long, fairly straight, tapering slowly to posterior, pointed and acute apex (apical angle 54°, s.d. = 6°, $n = 8$). Low radial dorsal folds delineating weak shell fields, elevating narrow central field across embayment, lateral fields broader (Pl. 7, fig. 2a).

Ventral apical area V-shaped, with strong, angular to slightly rounded posterior flexure, apical length/length 0·36 (s.d. = 0·00, $n = 2$), tapering outwards along posterolateral margins, extending to well beyond midlength (Pl. 7, figs 1b, 2b, 3b, 4a). Anterior rim slightly elevated above smooth, concave ventral surface, which has median depression corresponding to central field (Pl. 7, fig. 3b). Ventral surface becoming thickened, median pad flanked by two shallow furrows extending into groove beneath flexure of apical rim (Pl. 7, fig. 4a).

Lateral profile shallow, wedge-shaped; straight dorsally, straight tapering posterolateral margin, embayed anterior margin rounding into short anterolateral margin. Transverse profile only gently arched and rounded, jugal angle 109° (s.d. = 9°, $n = 4$), height/length 0·30 (s.d. = 0·02, $n = 2$) (Pl. 7, figs 1c, 2c, 3d, 4b).

*Remarks.* In spite of the poor preservation and largely fragmented material, the well-developed, coarse granular ornament, and acutely V-shaped apical area that extends anteriorly along long posterolateral margins distinguish *S. pilatis* from all *Chelodes* species, and justify the erection of a new genus. The cordate, elongate and thickened shell with a posterior apex, and presence of weak shell fields indicate, however, a close relationship with *Chelodes*.

## SILICIFICATION OF GOTLAND CHITONS

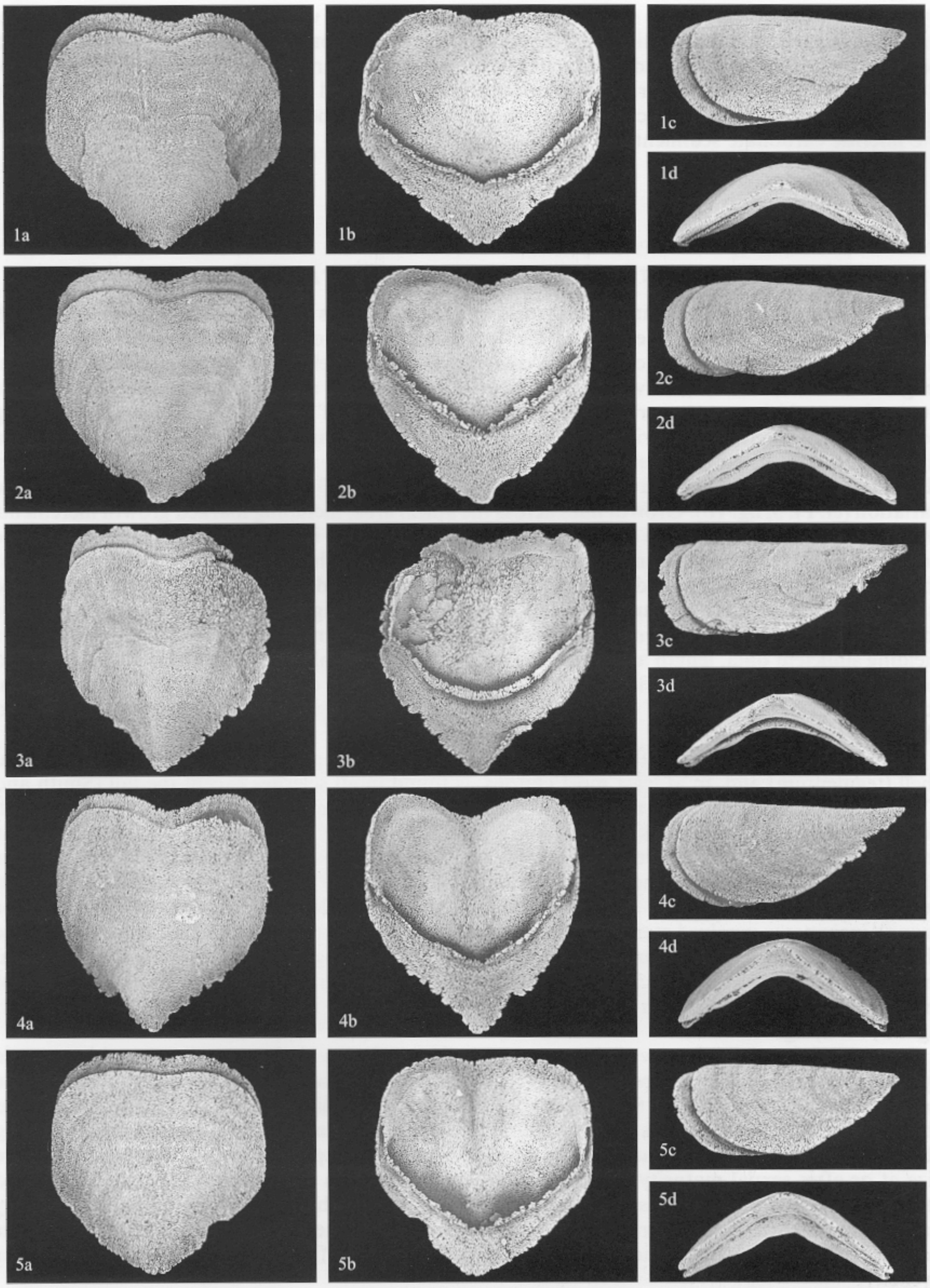
The large *Chelodes* sclerites from Möllbos show a pattern of silicification in which the skeletal rims are formed by fine quartz crystals that grow inward normal to the surface (e.g. Schmitt and Boyd 1981, pattern 1). Crystal size increases inwards, and fibrous and drusy megaquartz fill the cavity where opposing layers meet. Where incompletely filled, the jagged margin of the inner edge results from growth of individual quartz crystals. Any original internal shell structure is lost, although surface details are well preserved. The original skeletal aragonite may have been replaced earlier by a fill of sparry calcite either after dissolution or by calcitization.

In specimens from Klintebys, the shell is preserved in a coarser quartz mosaic, beekitized, with consequently poor preservation of detail. Replacement by quartz growing into a mould formed in coarser or less well cemented sediment could explain this, although reworking before or after replacement might also affect preservation. The *S. pilatis* specimens from Krakfot are patchily beekitized, with loss of surface detail (Schmitt and Boyd 1981, pattern 4). However, some specimens still preserve a distinctive dorsal ornament, and the grain size of the surface quartz except for the beekite discs is much finer than the internal shell fill, as at Möllbos. The material is fragmented, and it is apparent from the fine-grained entire surfaces forming many of the broken edges of sclerites that fragmentation preceded silicification.

All the chiton material appears to have been silicified after formation of dissolution cavities, i.e.

### EXPLANATION OF PLATE 6

Figs 1–5. *Chelodes actinis* sp. nov.; Halla Formation, upper Wenlock (Homerian), Silurian; Möllbos-1, Gotland; five intermediate sclerites from one sample, interpreted as belonging to the same individual; a–d, dorsal, ventral, left lateral and posterior views respectively; ×3. 1, RM Mo159.926. 2, RM MO159.928. 3, RM Mo159.927. 4, RM Mo159.929. 5, RM Mo159.930.




CHERNS, *Chelodes*

by delayed replacement. The specimens maintain thickness, which suggests that replacement preceded significant compaction. Higher silica concentrations would have favoured rapid precipitation of chalcedony and fine quartz, whereas the coarser internal fabric in shells indicates slower precipitation and lower silica concentrations. The good preservation of surface detail in specimens from Möllbos, particularly for originally aragonitic shells, suggests early cementation of the micritic carbonate sediment.

## GROWTH IN *C. ACTINIS* AND OTHER *CHELODES* SPP.

*C. actinis* has a heart-shaped outline that in small specimens is as wide or wider than long, but with increasing size becomes more elongate. The length-width relationship, shown in Text-figure 5, is significantly non-linear (using correlation coefficient). Similar relationships are shown for median length-width measured in individual sclerites of *C. gotlandicus* and *C.* cf. *bergmani* (Text-fig. 6). Stepped growth increments, resulting from variable rates of growth, illustrate the changing proportions of lateral to anterior extension (Pls 3–6). Length and height of sclerites also have a significantly non-linear relationship. Apical length and length are less significant: many larger, elongate specimens have relatively long apical areas (e.g. Pl. 3, fig. 2b), although there is wide variation (cf. Pl. 3, fig. 1b). Growth lines across the apical area, including marked growth increments which can be matched to those on the dorsal surface, record the increasing length. By contrast, the degree of embayment of the anterior margin (i.e. median length/length ratio) remains consistent throughout the population, and on individual sclerites (as recorded by growth lines). Growth style is demonstrated here for the large population of *C. actinis*, using a range of shell parameters. For the smaller population of *C. gotlandicus*, where length, width and height are the only parameters yielding sufficient data, length and width have a significantly nonlinear relationship, but length and height do not produce a significant correlation coefficient. The comparable graphs for individual sclerites of *C. gotlandicus* and *C.* cf. *bergmani* (Text-fig. 6) suggest that similar growth style also characterizes *C. bergmani*.

The apical area, adjacent to the apex on the ventral surface, represents an extension of the dorsal shell (tegmentum) and, in at least most chitons, is found in all sclerites except the tail (Smith and Toomey 1964). It typically has a raised rim above the smooth ventral surface (hypostracum), which becomes thickened generally as well as more locally, particularly anteriorly. Growth of the shell is thus mixoperipheral, the growth lines continuing from the dorsal shell across the lateral margins onto the ventral apical area, and involving anterior growth away from the apex on both dorsal and ventral surfaces. The isolated silicified sclerites of *C. actinis* demonstrate that successive major growth increments involved secretion of a new marginal band around the flattened cone form of the shell. Each new marginal increment protrudes beyond the existing shell, and also enlarges the apical area. In the more massive, calcite preservation of *C. gotlandicus* and *C. bergmani*, these details of growth are less clear, although both smaller and larger growth increments are evident (e.g. Pl. 1, fig. 2a; Pl. 2, fig. 4a).

The growth bands indicate variable rates of shell secretion, with fine-, medium- and large-scale cycles representing different periodicities. The Gotland Silurian chitons represent low latitude assemblages, so that marked fluctuations in growth due to climate may be less probable than through periodic spawning, as in living molluscs (e.g. Pannella and MacClintock 1968). Living chitons attain sexual maturity after one to a few years, and then spawn annually. They reach mature size at or after sexual maturity. Typically the Gotland Silurian chitons show two to five marked steps in growth, decreasing in spacing and extent after two or three, which therefore are probably annual increments. Smaller growth bands, represented by fine growth lines and subtle colour banding produced by their periodic crowding (e.g. Pl. 5, fig. 2a, f), might represent daily and lunar cyclicity.

TABLE 1. Comparative biometric data for intermediate sclerites of Silurian *Chelodes* spp.

| *Chelodes* sp. (no. of intermediate sclerites in data) | Length/width | Median length/length | Apical length/length | Height/length | Apical angle | Jugal angle |
|---|---|---|---|---|---|---|
| *C. actinis* (101) | 1·12 | 0·96 | 0·34 | 0·35 | 76° | 109° |
| *C. bergmani* (1 or 2) | 1·47 | 0·99 | 0·44 | 0·28 | 58° | 129° |
| *C.* cf. *bergmani* (1) | 1·58 | 0·98 | 0·32 | 0·26 | 74° | 100° |
| *C. gotlandicus* (26) | 1·16 | 0·91 | 0·33 | 0·44 | 80° | 84° |
| *C. raaschi* (holotype only) | 2·0 | — | 0·60 | — | 40° | — |

## SCLERITE VARIATION WITHIN ONE INDIVIDUAL OF *CHELODES ACTINIS*

Five intermediate sclerites (RM Mo159.926–159.930) in one sample from Möllbos, showing a similar, distinctive growth increment on both dorsal and ventral surfaces, may have belonged to the same individual (Pl. 6, figs 1–5; Table 2). All also show weak colour-banding on a more minor scale, and fine growth lines. These sclerites vary in size by at least 10 per cent. (means and s.d. of length, width, height and apical length), but ratios of shell parameters (length/width, apical length/length, height/length) are more consistent. The mean apical and jugal (Pl. 6, all figs d) angles also show low variation. Weak dorsal shell fields (broad central and narrow lateral fields) are more evident on three sclerites (Pl. 6, figs 1–3), and the lateral dorsal profile varies from weakly convex to straight or weakly concave (Pl. 6, figs 1c, 3c, 4c). On the heart-shaped ventral surface, where all plates have a distinct anterior and anterolateral rim around the more thickened central area, two of the sclerites show a longitudinal median furrow between thickened pads (Pl. 6, figs 4b, 5b), on the latter (Pl. 6, fig. 5b) with an additional median pad flanked by two furrows extending into the shallow groove beneath the apical area (cf. Pl. 4, fig. 3b). The total complement of sclerites in this animal is a minimum of seven, at least five intermediate plus head and tail plates.

Recent chitons have eight plates, six intermediate that vary in size along the body but are similar in form, and a head and tail plate that, morphologically, may differ considerably from the intermediate plates and from each other (e.g. Text-fig. 7). Fossil chitons belonging to the extinct order Paleoloricata (Upper Cambrian–Upper Cretaceous) differ from the Neoloricata (Carboniferous–Recent) in the lack of sutural plates formed from a middle shell layer, the articulamentum. Articulated fossil specimens are rare but, where known, those from both orders had eight plates (e.g. Hoare and Mapes 1989; Rolfe 1981). Rolfe (1981) identified a very small, eighth sclerite in the upper Ordovician *Septemchiton grayiae* (Woodward, 1885), previously thought to have only seven sclerites (= *S. vermiformis* Bergenhayn, 1955; Rolfe, 1981), and upon which the paleoloricate suborder Septemchitonina Bergenhayn, 1955 was founded. Hyman (1967, p. 121) had noted that seven sclerites appear in the late trochophore stage of chiton ontogeny, the eighth developing later, and thus pointed to *Septemchiton* as representing an early phylogenetic state. Among population of isolated sclerites, Runnegar *et al.* (1979) estimated the sclerite complement in upper Cambrian *M. variabilis* as seven (1:5:1), and accepted this as the total, based on comparison with a seven-plated *Septemchiton*. They followed Hyman (1967) in suggesting that the late ontogenetic acquisition of the eighth, tail plate observed in some living chitons (Okuda 1947) might have phylogenetic significance, although their data point to one fewer intermediate plates rather than lack of a tail plate.

The population of isolated head and intermediate sclerites of *C. actinis* does not yield further information on the sclerite complement, but in one sample (Pl. 6) at least five intermediate sclerites may have belonged to the same animal. The order of these plates along the body remains unclear; on Plate 6, they have been arranged according to development of shell fields and degree of sculpting of the ventral surface. The largest sclerites in Recent *Chiton* are typically around the third to fifth, with size diminishing to front and rear (Text-fig. 7). However, in the measured Recent specimen, the shell parameters do not vary altogether consistently (Table 3). Rolfe (1981) measured length of sclerites in articulated specimens of *S. grayiae*, and noted a marked increase through sclerites 1 to 4, then fairly similar lengths for sclerites 4 to 8 with 6 being the longest. Variation between individuals and taxa preclude any one shell dimension being taken to specify sclerite position among isolated specimens.

## MUSCULATURE IN *CHELODES ACTINIS* AND *SPICUCHELODES PILATIS*

In living chitons, the musculature is complex, repeated on each intermediate sclerite, and modified on the head and tail sclerites (e.g. Hyman 1967). Multiple muscles, attached to the edges, insertion and sutural plates, hold the sclerites and can draw them closer together. Two groups of muscles run from the anterior edge down into the body-wall beneath the sclerite in front, one group cushioning the overlap of sclerites between the sutural plates and ventral posterior margin in front, and one group running marginally between sclerites from the sutural plates on to the lateral edge of the sclerite in front. From the ventral surface, which lacks evident muscle insertion sites, muscles pass into the mantle and foot. The mantle commonly embeds and partly covers the sclerites. In paleoloricate chitons, which lack an articulamentum with sutural plates, there is limited evidence of the musculature. Runnegar *et al.* (1979) interpreted deep ventral pits in late Cambrian *Matthevia* as housing dorsoventral muscles from shell to foot, but doubted whether adjacent plates were connected. They suggested an evolutionary progression in shell form from the tall conical plates of *M. variabilis* towards flattening in early Ordovician *C. whitehousei.* Associated with this, the ventral muscle attachment sites evolved from *M. variabilis* with a deep anterior and posterior cavity per plate, through *M. walcotti* which has a single, posterior cavity, to early Ordovician *Hemithecella* and only some *C. whitehousei* in which the posterior cavity is much reduced. Other *Chelodes*, including the species from the Gotland Silurian, lack any ventral muscle pit.

In *C. actinis*, although the relative length of the apical area varies between sclerites, the shape of the smooth ventral surface anterior to it remains fairly similar, cordate anteriorly, convex laterally and tapering to a rounded posterior. On the sclerites which show more sculpted thickening, the ventral surface shows a longitudinal median depression or furrow between two thickened pads anteriorly, and a narrow median pad flanked by two shallow longitudinal furrows beneath the raised rim of the apical area (Pl. 4, fig. 3b, d–e; Pl. 6, fig. 5b; also, for *S. pilatis*, Pl. 7, fig. 4a). A distinct marginal rim around the ventral surface, outside the more general thickening, continues from the slight groove beneath the apical rim (e.g. Pl. 3, fig. 2b). The depressed areas of the sculpted ventral surface, and its rim, may have housed muscles for attachment to the body-wall and to adjacent sclerites. The pattern of localized thickening of sclerites may have accommodated paired muscles extending beneath the apical rim, median longitudinal and anterior muscles (e.g. Pl. 4, fig. 3b). The pattern beneath the apical rim differs from the deep to shallow median cavity below the apical area described above from late Cambrian and early Ordovician hemithecellids, *Matthevia* spp., and *C. whitehousei* (Runnegar *et al.* 1979; Stinchcomb and Darrough 1995).

In most Recent neoloricate species, the apical area is much reduced compared with that of Palaeozoic paleoloricates such as *Chelodes*, where it occupies up to half or more of the sclerite length. Furthermore, its length and width represent the extent of overlap of successive sclerites in

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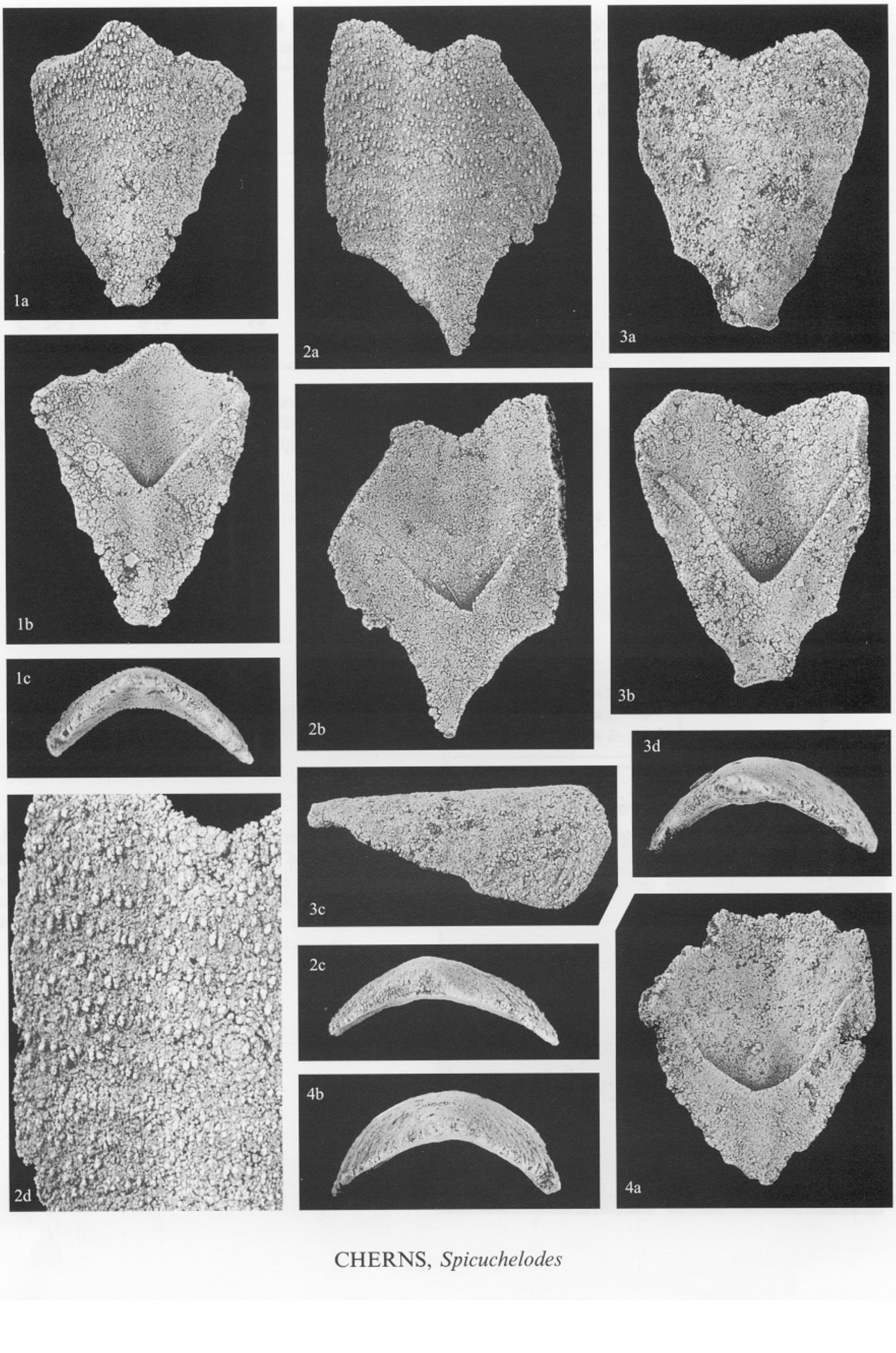
EXPLANATION OF PLATE 7

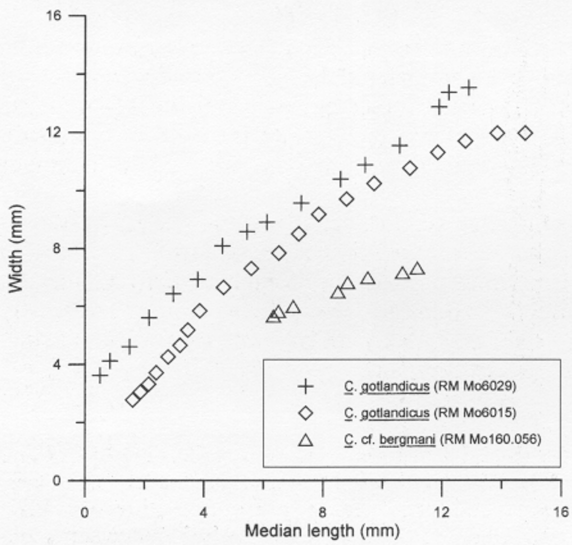
Figs 1–4. *Spicuchelodes pilatis* gen. et sp. nov.; Klinteberg Formation, upper Wenlock (Homerian), Silurian; Krakfot-1, Gotland; intermediate sclerites. 1, RM Mo160.063; a–c, dorsal, ventral and posterior views respectively; ×5. 2, RM Mo160.062, holotype; a–c, dorsal, ventral and posterior views respectively; ×5; d, detail of dorsal surface showing ornament; ×10. 3, RM Mo160.074; a–d, dorsal, ventral, right lateral and posterior views respectively; ×5. 4, RM Mo160.075; a–b, ventral and posterior views respectively; ×5.



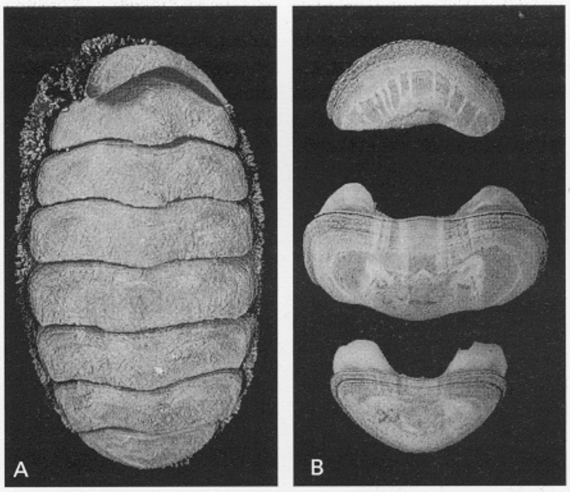

CHERNS, *Spicuchelodes*

TABLE 2. Biometric data for five intermediate sclerites of *Chelodes actinis* sp. nov. interpreted as belonging to the same individual, RM Mo159.926-159.930, Möllbos-1 (Pl. 6). *broken.

| Dimension<br>Pl. 6 | RM Mo<br>159.926<br>fig. 1 | RM Mo<br>159.928<br>fig. 2 | RM Mo<br>159.927<br>fig. 3 | RM Mo<br>159.929<br>fig. 4 | RM Mo<br>159.930<br>fig. 5 | Mean | s.d. | *n* |
|---|---|---|---|---|---|---|---|---|
| Length (mm) | 12·2 | 12·4 | 13·1 | 12·3 | 11·8 | 12·36 | 0·47 | 5 |
| Width (mm) | 12·4 | 11·5 | 11·1* | 11·2 | 11·3 | 11·6 | 0·55 | 4 |
| Length/width | 0·98 | 1·08 | | 1·10 | 1·04 | 1·05 | 0·05 | 4 |
| Apical length (mm) | 3·3 | 4·2 | 4·4 | 3·8 | 2·5 | 3·64 | 0·76 | 5 |
| Apical length/length | 0·27 | 0·34 | 0·34 | 0·31 | 0·21 | 0·29 | 0·05 | 5 |
| Height (mm) | 4·6 | 3·8 | 4·4 | 4·6 | 4·2 | 4·22 | 0·38 | 5 |
| Height/length | 0·38 | 0·31 | 0·30 | 0·37 | 0·36 | 0·34 | 0·04 | 5 |
| Apical angle (°) | 92 | 92 | 92 | 89 | 93 | 91·6 | 1·52 | 5 |
| Jugal angle (°) | 109 | 117 | 107 | 113 | 116 | 112·4 | 4·34 | 5 |




TEXT-FIG. 6. Median length-width graphs for individual intermediate sclerites of *Chelodes gotlandicus* (RM Mo6029 and Mo6015) and *C.* cf. *bergmani* (RM Mo160.056).




TEXT-FIG. 7. Recent *Chiton* sp. from the Red Sea; × 1. A, dorsal view of articulated specimen, head sclerite slightly askew in preservation, plates set into spiculate muscular body wall. B, isolated head, intermediate and tail sclerites, note sutural plates for articulation on intermediate and tail sclerites.

TABLE 3. Biometric data for individual sclerites of Recent *Chiton* sp. from the Red Sea.

| Sclerite | Length (mm) | Width (mm) | Height (mm) | Apical length (mm) | Apical angle (°) | Jugal angle (°) |
|---|---|---|---|---|---|---|
| Head | 7·3 | 14·9 | 5·4 | — | — | — |
| 2 | 11·7 | 17·6 | 6·8 | 3·5 | 115 | 110 |
| 3 | 9·6 | 21·1 | 7·0 | 3·6 | 120 | 112 |
| 4 | 10·7 | 21·2 | 7·5 | 4·0 | 121 | 114 |
| 5 | 8·5 | 20·2 | 6·9 | 2·5 | 151 | 117 |
| 6 | 7·5 | 19·8 | 6·0 | 2·2 | 125 | 118 |
| 7 | 7·4 | 18·5 | 4·9 | 2·0 | 168 | 126 |
| Tail | 6·4 | 14·7 | 4·3 | — | | |
| Mean 2–7 | 9·23 | 19·73 | 6·67 | 2·97 | 133·33 | 116·17 |
| s.d. 2–7 | 1·75 | 1·44 | 0·90 | 0·84 | 21·21 | 5·67 |

life, indicating the degree of imbrication of the commonly massive *Chelodes* sclerites. It seems unlikely that overlapping plates would not have been connected by muscles, by contrast to *Matthevia* where convex posterior faces to the conical sclerites indicate a lack of contact (Runnegar *et al.* 1979). In *Chelodes*, the close proximity of the apical rim to the anterior edge of the partly covered next sclerite, each with sculpted muscle attachment sites, makes muscular attachment between the sclerites probable.

The degree of flexibility of the body was limited by the weight and size of the plates, as well as their musculature. The large, massive plates of *Chelodes* provided effective armour, but also restricted movement. The facies relationships and distribution of Gotland Silurian chitons indicate life habits and ecology comparable to Recent assemblages (Cherns 1996). Living chitons are mostly sluggish, intertidal animals, creeping across rocky surfaces to feed, and relying on the plated shell and strength of adhesion against the substrate for protection.

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