

SILURIAN CHEIRURID TRILOBITES FROM GOTLAND

by LARS RAMSKÖLD

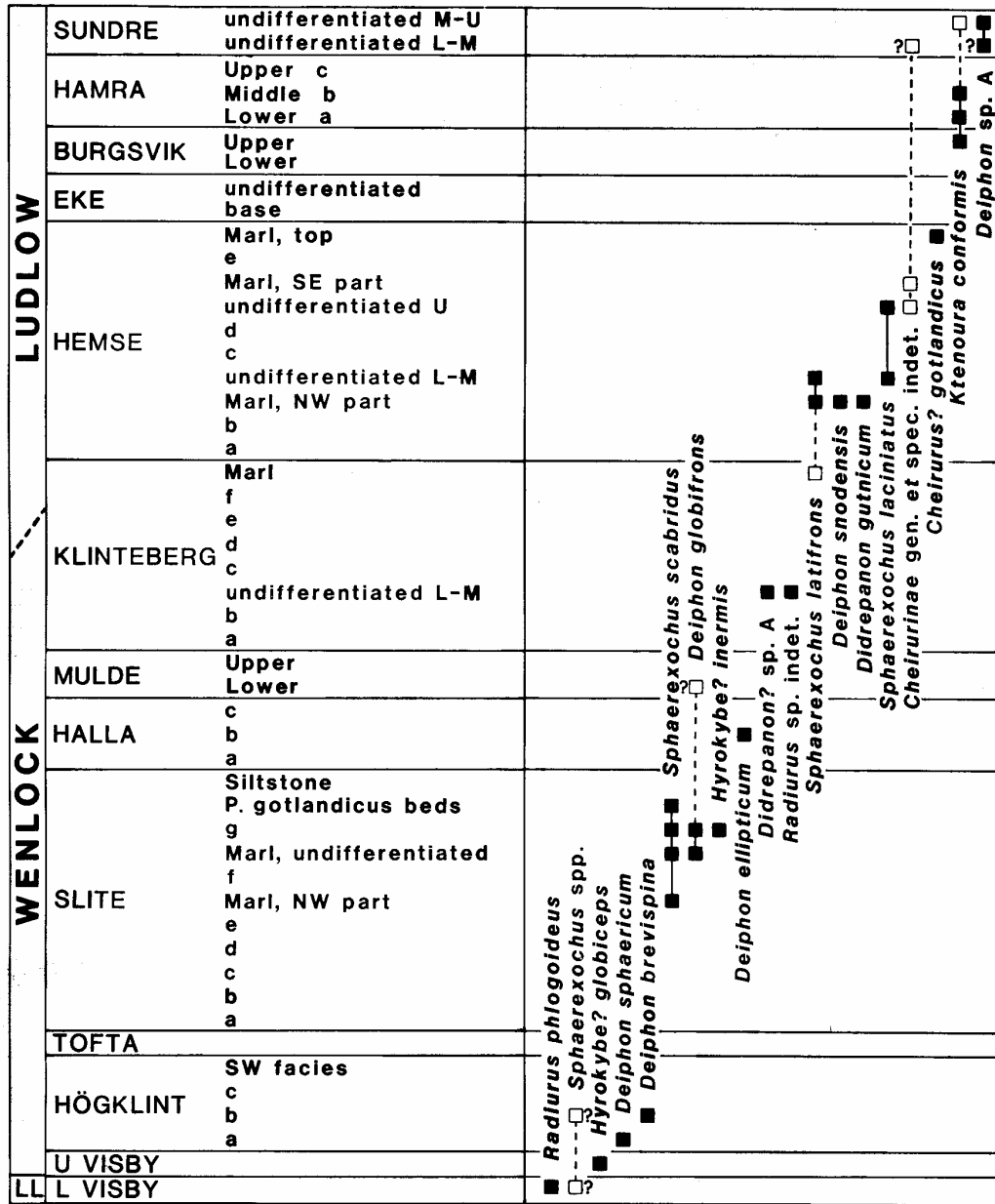
ABSTRACT. Trilobites of the family Cheiruridae are described from the Silurian of Gotland, Sweden. Nineteen species (fourteen named formally, of which six are new) are assigned to seven genera (one new). The generic composition of the fauna shows affinities with East Baltic, Bohemian, British, and Canadian faunas. None of the species is known with certainty outside Gotland. The presence of six stratigraphically successive species of *Deiphon* is noteworthy, but no phylogenetic lineage can be established. *Radiurus* gen. nov. includes the type species *R. phlogoideus* sp. nov. from the Llandovery of Gotland, together with *Cheirurus estonicus* Männil, 1958. Other new species described are *Didrepanon gutnicum*, *Deiphon sphaericum*, *Deiphon brevispina*, *Deiphon ellipticum*, and *Deiphon snodensis*.

DURING the last decade, several Silurian trilobite faunas including cheirurids have been described from various parts of the world. Lane (1971) revised the British Cheiruridae, the Wenlock species of which were reviewed by Thomas (1981), and additional Scottish Llandovery material was studied by Clarkson and Howells (1981). Holloway (1980) described several North American species, Canadian Arctic faunas have been reviewed by Perry and Chatterton (1977, 1979), and Australian cheirurids have been described by Chatterton and Campbell (1980). A number of these authors made reference to or comparisons with Gotland species, although the basis for such comparisons was rather vague since the material has not been revised since the study by Lindström (1885). This paper, which comprises a study of all known Gotland material of the family, is intended to provide a modern basis for comparative studies. The excellent preservation of the Gotland material allows detailed studies to be made of most features of cheirurid morphology.

A cheirurid was first described from Gotland by Hisinger (1837), although he identified it as the Ordovician species *Pilekia speciosus* (Dalman, 1827). Angelin (1851, 1854) then included several Gotland cheirurids in his monographic study of Scandinavian trilobites, and these were revised by Lindström (1885) who also described additional Gotland species. Following Lindström's paper, very little additional work has been done on the group, although the same author included a cheirurid (now recognized as *Ktenoura conformis*) in his study of the visual system of trilobites (1901). Some Gotland species were mentioned by Warburg (1925) in comparative discussions of Ordovician species, and Whittard (1934) redescribed *Deiphon globifrons* Angelin. More recently, Lane (1971) revised the generic allocation of some Gotland cheirurids.

STRATIGRAPHY AND LOCALITIES

Numerous workers have described aspects of the stratigraphy of Gotland for well over one hundred years. Most accounts are in Swedish, but an excellent review in English is given by Laufeld (1974a, pp. 7-13). The classification used here (text-fig. 1) is essentially that of Hede (e.g. 1921, 1925). It should be emphasized that this classification is composite in the sense that some boundaries were based on biostratigraphical criteria and others on lithostratigraphical features, Hede's main intention being to distinguish mappable units. It is now understood (e.g. Martinsson 1967, fig. 2; Laufeld and Bassett 1981, pp. 26, 27) that most of Hede's units are not synchronous, but become younger from south-west to north-east along the outcrop. Laufeld and Jeppson (1976, fig. 4) made a useful attempt to describe the lateral variations within Hede's units, which in a graphic way illustrates the complexity of the stratigraphy.



TEXT-FIG. 1. Occurrence of Cheiruridae in the different stratigraphical units of Gotland. Solid squares represent specimens assigned definitely to a taxon and open squares represent compared forms. A square with a question mark indicates that the horizon is uncertain. The stratigraphical column is a practical way of illustrating the distribution of the species within the mapped units, and is not necessarily a reflection of the chronological appearance and disappearance of various taxa. Diagram modified from Laufeld (1974a, p. 124).

The system of reference localities introduced by Laufeld (1974b) has been followed here wherever possible. However, much of the material is from old museum collections with locality data that are too vague to permit this. Locality names followed by numbers are defined in Laufeld (1974b) and Larsson (1979). Three new localities are described here in conformity with this system.

GISLE 2, 632505 164979 (CJ 3446 2396) c. 5,800 m SSW of Fide church. Topographical map-sheet 5 I Hoburgen SO & 5 J Hemse SV. Geological map-sheet Aa 152 Burgsvik. Ditch exposure along the main road, immediately south-west of the intersection of the small road from the windmill c. 210 m south-west of point 8.76 south of Burgsvik. Hamra Beds, unit a.

MOJNER 3, 639959 167789 (CJ 6824 9609) c. 1,550 m east of Boge church. Topographical map sheet 6 J Roma NV & NO. Geological map-sheet Aa 169 Slite. Ditch exposure immediately north of the main road, c. 500 m south-west of point 3.70 south of Slite. The ditch runs in line with the west side of the open field south of the road. Slite Beds, Slite Marl.

VALBYTTJE 4, 636921 164079 (CJ 2888 6865) c. 1,575 m south of Västergarn church. Topographical map-sheet 6 I Visby SO. Geological map-sheet Aa 160 Klintehamn. Shore exposure on the south-east shore of the small bight c. 100 m west of the main road, and c. 200 m west of the large barn (not marked on topographical map-sheet) east of the road. At low water levels there are exposures some metres outside the shore-line proper. Slite Beds, Slite Marl.

SYSTEMATIC PALAEOLOGY

The suprageneric classification is that of Lane (1971), except where otherwise stated. The terminology is essentially that of Harrington *et al.* (in Moore 1959, p. O117), and Lane (1971, p. 7). Lateral glabellar lobes and furrows are labelled as by Jaanusson (1956, p. 37). The term 'preoccipital depression' (in *Deiphoninae*) is explained in Holloway and Campbell (1974, pp. 418, 419). 'Eye socle' (in *Deiphon*) is the part of the fixed and free cheek between visual surface and subocular furrow. 'Width ratio fixed cheek: occipital ring' is the maximum distance between the axial furrow-posterior border furrow intersection and the lateral margin of the fixed cheek, divided by the transverse width of the occipital ring. 'Ankylosed articulating half-ring' is a purely descriptive term, with no phylogenetic or ontogenetic implications. In measurements and photographs a dorsal view indicates orientation with a vertical posterior margin of the occipital ring, or, in pygidia, a vertical anterior axial ring.

Specimen numbers with the prefix Ar belong to Naturhistoriska Riksmuseet, Stockholm. Specimens in the Type Collection of the Geological Survey of Sweden are prefixed SGU. Unless stated otherwise, the material illustrated in the plates comprises external exoskeletons. All specimens were painted with matt black opaque and coated lightly with ammonium chloride prior to photography. Dorsal views are shown unless stated otherwise in the plate explanations.

Family CHEIRURIDAE Hawle and Corda, 1847

Diagnosis. See Thomas 1981, p. 57.

Subfamily CHEIRURINAE Hawle and Corda, 1847

Genus CHEIRURUS Beyrich, 1845

Type species. *Cheirus insignis* Beyrich, 1845, from the Liteň Formation (Wenlock), Svatý Jan pod Skalou, Czechoslovakia; subsequently designated by Barton 1916.

Diagnosis. See Lane 1971, p. 11.

Cheirus? gotlandicus (Lindström, 1885)

Plate 19, figs. 1-10; text-fig. 2

v* 1885 *Chirus gotlandicus* Lindström, p. 45, pl. 12, figs. 9, 10.

1971 *Cheirus gotlandicus* Lindström; Lane, p. 11.

Lectotype. Selected here, Ar29785, internal mould of cranidium, Pl. 19, fig. 2; figured Lindström 1885, pl. 12, fig. 9; from Lau, probably uppermost Hemse Beds.

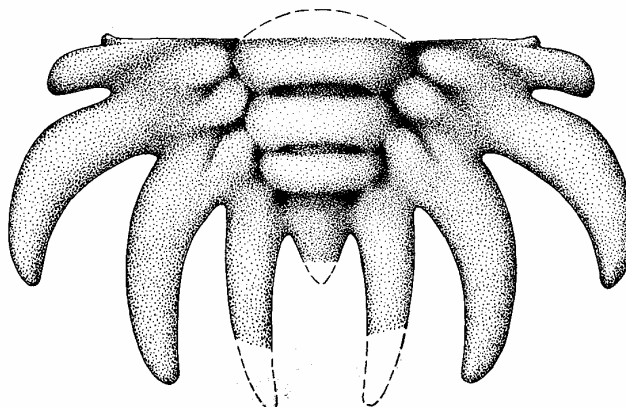
Material. All specimens appear to be from the uppermost Hemse Beds, Lau parish, mostly from Gannor 1-3 (= Lau Canal); in total five cranidia, one free cheek, one hypostome (paralectotype Ar29786), one thorax, and three pygidia.

Diagnosis. Glabella weakly convex, widening very gently anteriorly. S3 and S2 almost transverse, reaching more than two-fifths across glabella, connected medially by distinct depressions. Width ratio fixed cheek : occipital ring 0.9-1.0 : 1. Pygidium with a large anterolateral process, three pairs of spines, and a terminal mucronation.

Description. Frontal lobe slightly inflated, part of glabella behind rather flat (tr., sag.). L3 parallel-sided to widening slightly abaxially, L2 widening adaxially. Basal lobes subtriangular, circumscribed, inner angles separated by tongue-shaped posterior part of median lobe. S3 and S2 subparallel, directed very gently backwards. In some specimens S2 is shallow and constricted close to axial furrow (Pl. 19, fig. 7a-c). S1 narrow and occupied by S1 apodeme for two-thirds of its length, then running more obliquely backwards to meet occipital furrow. This is constricted abaxially with apodemal pit, medially curved in an arch, being narrow but distinct. Small median tubercle sometimes present on occipital ring. Axial furrow with deep anterior pit opposite S3. Preglabellar furrow absent on median third of frontal lobe.

Fixed cheek narrow, barely as wide as occipital ring. Free cheek small, subtriangular. Posterior cephalic margin convex backwards. Posterior border very narrow (exsag.) adaxially, a little wider lateral to fulcrum. Genal spine short. Posterior border furrow very distinct, constricted adaxially, shallowing laterally. Lateral border narrow (tr.), equal in width to posterior border. Lateral border furrow shallow, less distinct than posterior border furrow.

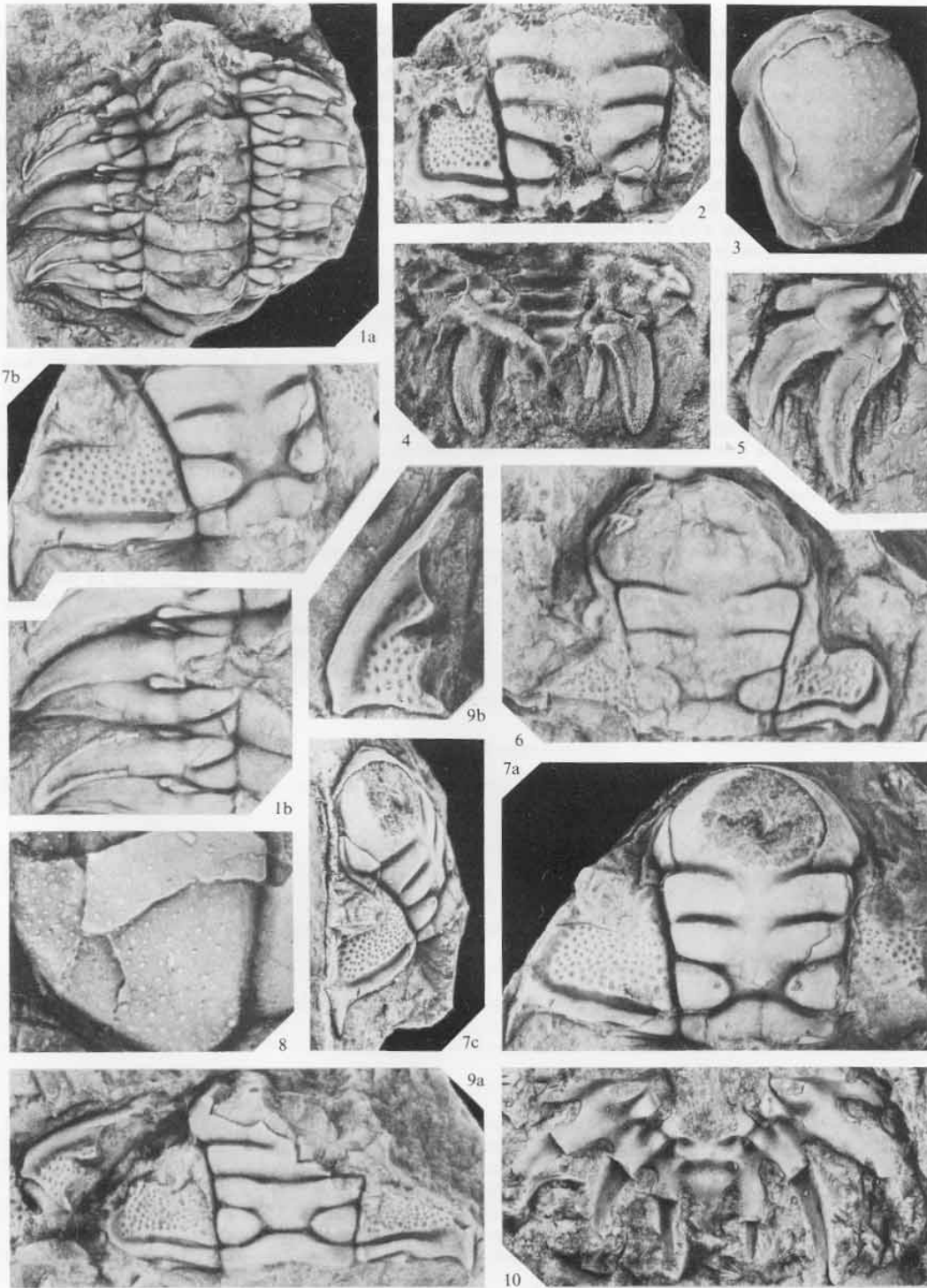
Eye fairly small, extending from opposite slightly posterior to S3 to opposite S2. Palpebral rim narrow, convex. Palpebral furrow distinct along palpebral rim and just posterior to eye. Posterior branch of facial suture



TEXT-FIG. 2. *Cheirurus? gotlandicus* (Lindström, 1885). Reconstruction of pygidium, based on Ar29792, Ar29793, and Ar30805. $\times 3$.

EXPLANATION OF PLATE 19

Figs. 1-10. *Cheirurus? gotlandicus* (Lindström, 1885). Hemse Beds, uppermost part. Lau Canal (1, 3-9), Lau (2), the beach at Lau fishing harbour (10). 1a, b, Ar29796, thorax, dorsal view and enlargement of pleurae, a $\times 3$, b $\times 5$. 2, lectotype Ar29785, cranidium, internal mould, figured Lindström 1885, pl. 12, fig. 9, $\times 2$. 3, Ar29786, hypostome, mainly internal mould, figured Lindström 1885, pl. 12, fig. 10, $\times 3$. 4, Ar30805, small pygidium, ventral view, $\times 6$. 5, Ar29793, partial pygidium, $\times 2$. 6, Ar29791, cranidium showing pathological? deformation of right cheek, $\times 3$. 7a-c, Ar29794, cranidium, mainly internal mould, dorsal, oblique dorsal, and oblique anterolateral views, a, b $\times 3$, c $\times 2$. 8, Ar29795, cranidium, enlargement showing granulation, $\times 7$. 9a, b, Ar29790, cranidium and displaced free cheek, continuous S2 due to distortion, a, dorsal view, $\times 3$, b, free cheek, $\times 5$. 10, Ar29792, pygidium, internal mould, $\times 2$.



RAMSKÖLD, *Cheirurus?*

turns sharply backwards just after meeting lateral border. Frontal lobe of glabella with evenly spaced, rather large granules (Pl. 19, fig. 8). Lateral lobes with no visible granulation. Lateral borders very finely and densely granulated. Field of cheek, including lateral border furrow, finely and densely pitted.

Rostral plate unknown. Hypostome with middle body fairly convex (tr., sag.), narrowing backwards. Middle furrow wide and shallow, continuous across middle body, very shallow medially. Anterior border furrow wide and shallow laterally. Anterior wing large. Lateral border narrow and convex (tr.), narrowest opposite posterior lobe of middle body. Shoulder rather pronounced, with posterior end marked by incurving of lateral margin. Lateral border furrow shallowing slightly posteriorly, but still distinct when merging with equally distinct posterior border furrow. Posterior border not preserved. Middle body with very fine and dense granulation, as on borders. Middle body with numerous pits dorsally.

Thorax of at least ten (probably eleven) segments. Axis wide, just slightly narrower (tr.) than pleural portions. On each segment abaxial to the deep pleural furrow is a rounded swelling, lateral to this is an indistinct median ridge with three to four equally spaced, faint tubercles.

Pygidium incompletely known. Axis narrowing backwards, composed of three rings and a terminal piece. A pair of pits is present laterally in each of the inter-ring furrows. Anterior pleural furrow deep, middle pleural furrow firmly impressed to indistinct. Interpleural furrows deep, widening and shallowing distally, reaching pygidial margin. Axial furrow distinct adjacent to anterior and middle rings, indistinct adjacent to posterior ring. Anterolateral process large, elongate transversely, end blunt. Anterior pair of spines long, hook-like, curving almost through 90°; middle pair equal in size to anterior one, curving backwards to an exsagittal direction; both pairs with blunt ends. Posterior pair almost exsagittally directed, possibly converging slightly backwards, more slender than the other spines, length not known. Terminal mucronation short and wide. Doublure narrow, with embayment anterior to terminal mucronation. Surface of pygidium, including doublure, covered with very dense and fine granulation.

Discussion. This species differs in several respects from other species of *Cheirurus*. The shape of S3 and S2 and the presence of a large anterolateral process on the pygidium are features in which it shows some similarity to *Didrepanon*, but it is otherwise very different from that genus. The cephalic features seem to represent a step towards the Lower Devonian Cheirurinae (e.g. *Crotalocephalus*) which have continuous S3 and S2 furrows and a rather narrow (tr.) cephalon. However, the pygidium with its large anterolateral process is different from all known Cheirurinae, and the systematic position of *C.? gotlandicus* is regarded here as uncertain.

Genus DIDREPANON Lane, 1971

Type species. *Didrepanon falcatum* Lane, 1971, from the upper Silurian (?lower Ludlow), Sedgley, West Midlands, Great Britain; by original designation.

Diagnosis. See Lane 1971, p. 21.

Didrepanon gutnicum sp. nov.

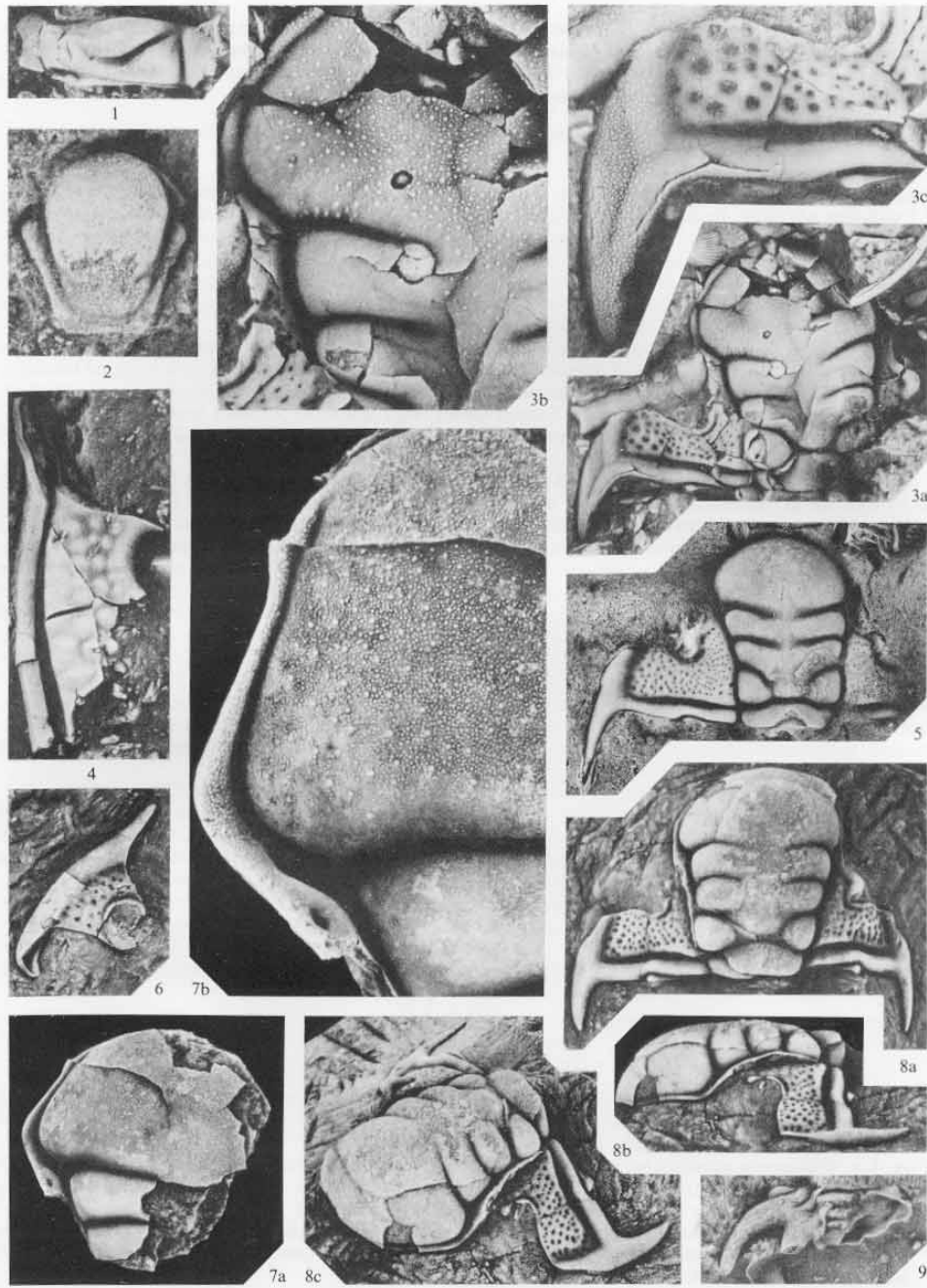
Plate 20, figs. 1–9; Plate 21, figs. 4–6; text-fig. 3

Name. Latin *gutnicus*, meaning inhabitant of Gotland.

Holotype. Ar51328, a pygidium, Pl. 21, fig. 4a, b, from Snoder 2; Hemse Marl, north-west part, Hemse Beds.

EXPLANATION OF PLATE 20

Figs. 1–9. *Didrepanon gutnicum* sp. nov. Hemse Marl, north-west part, Hemse Beds. Petesvik (5, 9), Snoder 2 (1, 2, 4, 6–8), Visne myr (3). 1, paratype Ar51293, partial left thoracic pleura, $\times 3$. 2, paratype Ar51292, small hypostome, $\times 5$. 3a–c, Ar29789, partial cranidium, dorsal view, enlargement of cheek, and enlargement of glabella, a $\times 3$, b, c $\times 7$. 4, paratype Ar51291, partial free cheek, ventral view showing doublure, $\times 3$. 5, Ar29695a, latex cast of ventrally exposed cranidium, $\times 2$. 6, paratype Ar51330, free cheek, $\times 3$. 7a, b, paratype Ar51331, partial cranidium, dorsal view and enlargement of granulation, a $\times 2$, b $\times 6$. 8a–c, paratype Ar51329, cranidium, dorsal, lateral, and oblique anterolateral views, all $\times 3$. 9, Ar29695b, partial pygidium, $\times 2$.



RAMSKÖLD, *Didrepanon*

Paratypes. From the type locality, Ar51290–51293, Ar51329–51336; from Snoder 1, Ar51287–51289. Other material referred to this species, although poorly preserved: Fardhem parish—drainage ditch in Visne myr (may include Gerete 1), Ar29789. Hablingbo parish—Petesvik, Ar29695a–b; Hablingbo kanal, Ar29784; Nissevik, Ar29726. All material is from the Hemse Marl, north-west part, Hemse Beds.

Diagnosis. Cheeks wide; width ratio fixed cheek : occipital ring 1.5 : 1, pygidium with very curved, widely separated, blunt spines.

Description. Cephalon short (sag.) and wide, length to width ratio about 1 : 1.9. L3 widening slightly abaxially, L2 widening adaxially. Basal lobes subtriangular, inner angles separated by tongue-shaped posterior part of median lobe. S3 and S2 reaching more than two-fifths across glabella, connected medially by wide, shallow depressions. S1 deep and narrow to half its length, then shallows and runs more obliquely backwards to meet occipital furrow. This is deep abaxially for the same distance as S1, then shallowing but still fairly deep and narrow, running in an arch medially. Axial furrow quite narrow and distinct, with deep anterior pit. Preglabellar furrow absent on median one-third of frontal lobe.

Fixed cheek wide (tr.) and short, broadening a little laterally. Free cheek subtriangular. Posterior border convex, narrow (exsag.), slightly wider lateral to fulcrum. Posterior border furrow slightly constricted adaxially, widening and shallowing laterally before narrowing slightly close to genal angle. Genal spine as long as length (exsag.) of fixed cheek behind eye, pointed. Lateral border twice as wide as posterior border, defined by fairly wide and shallow border furrow which narrows and deepens forwards. Doublure narrow, flat, smooth, flexed dorsally.

Eye large, extending from opposite mid L3 to almost opposite S1 (left eyes in Pl. 20, figs. 3a and 8a posteriorly dislocated due to fractures). Eye socle low, well defined by subocular furrow. Palpebral furrow distinct along palpebral rim and posterior to eye. Field of cheek of low convexity, densely pitted. Frontal lobe of glabella with granules of varying size with microgranulation in between. Granulation posterior to frontal lobe very sparse. Lateral border and genal spine very densely and finely granulated. Muscle attachments on frontal lobe visible only on internal moulds, consisting of two anteriorly diverging rows of pits with scattered pits between.

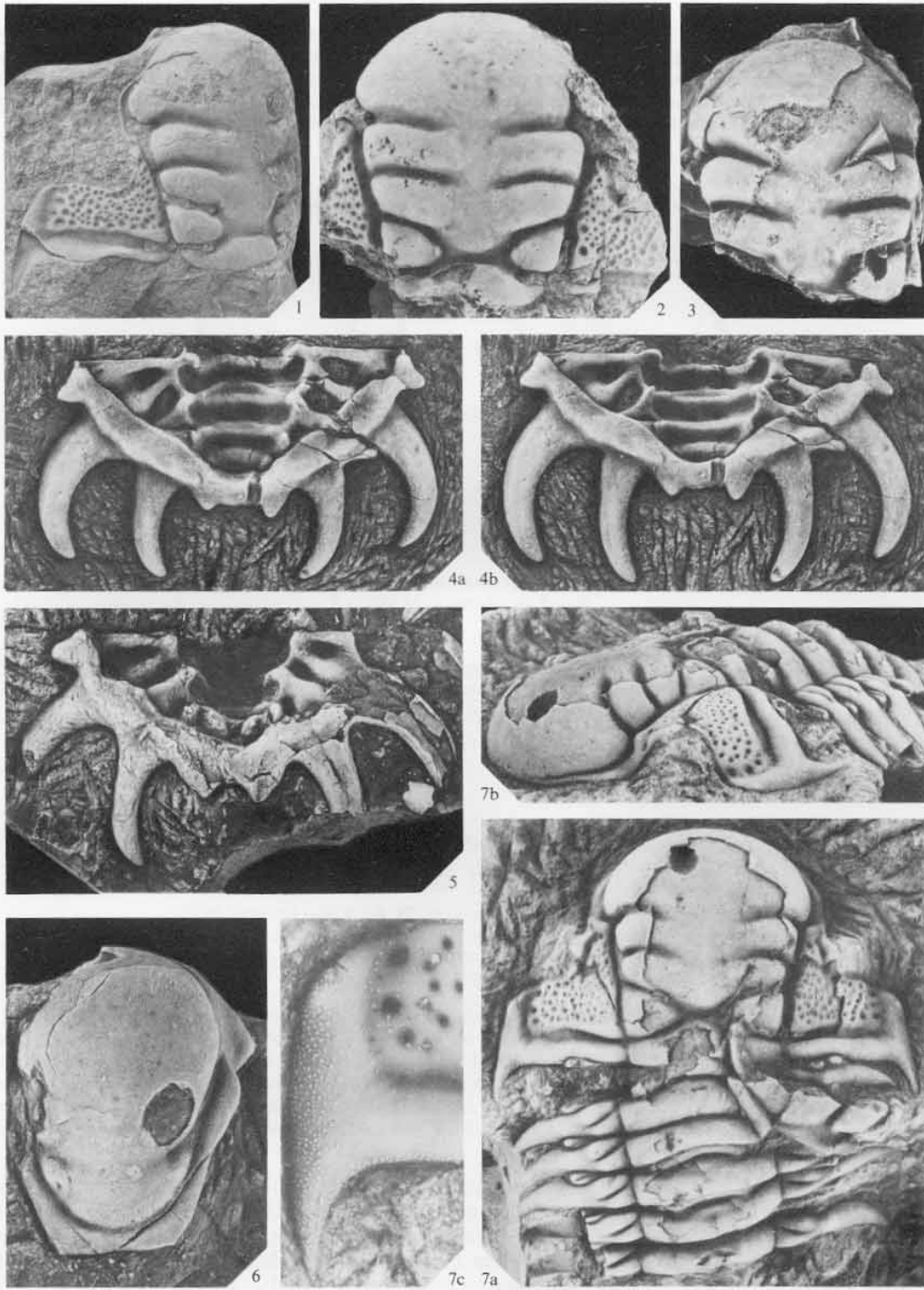
Rostral plate unknown. Hypostome lacking anterior border furrow medially. Middle furrow with deeper distal portions reaching less than one-quarter across middle body, very shallow medially. Anterior wing with indistinct median furrow. Lateral border furrow distinct, deeper than posterior border furrow. Lateral border gently convex (tr.), narrow, shoulder opposite mid length of anterior lobe of middle body. Posterior border short (sag.). Lateral and posterior margins meet at about 110°, posterior margin straight. Entire hypostome covered with microgranulation, slightly coarser on lateral borders. Middle body with numerous scattered, irregularly formed, shallow pits. Dorsal surface of middle body with equally numerous fairly large pits, seemingly not corresponding to any structures on ventral surface.

Thorax known only from proximal pleural fragments. In shape they are typical of the Cheirurinae.

Pygidium known mainly from ventral side. Axis tapering backwards, composed of three rings and a terminal piece. Anterior ring short medially, long (exsag.) laterally with swellings directed forwards. Middle and posterior rings progressively smaller, posterior ring poorly defined posterolaterally. Anterior inter-ring furrow with a distinct ankylosed articulating half-ring, middle inter-ring furrow with a similar, but smaller and less distinct, structure. Axial furrow deep adjacent to anterior ring and distinct opposite middle ring. Four pairs of apodemes present, corresponding to deep pits in the axial furrows. Anterior pleural furrow deep, middle furrow less distinct. Interpleural furrows deep adaxially, faint close to pygidial margin. Anterior and middle pairs of spines long, subequal in size, curving posterolaterally, converging distally; middle pair more gently curved. Both pairs

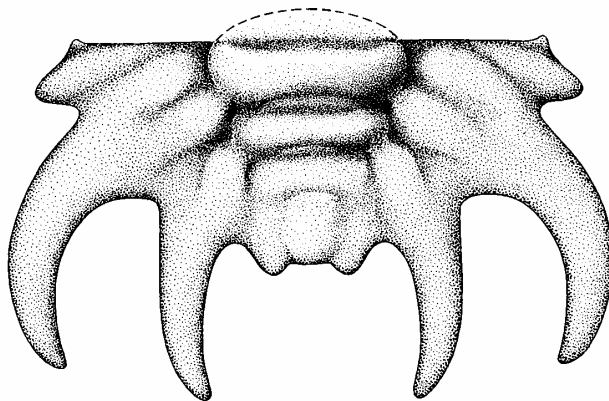
EXPLANATION OF PLATE 21

- Figs. 1–3. *Didrepanon?* sp. A. Klinteberg Beds, Klinteberget. 1, Ar46983, cranidium, internal mould, figured Hisinger 1837, pl. 39, fig. 9, refigured Angelin 1854, pl. 39, fig. 14, $\times 1$. 2, SGU 1352, cranidium internal mould, $\times 1.5$. 3, Ar29803, glabella, mainly internal mould, $\times 2$.
- Figs. 4–6. *Didrepanon gutnicum* sp. nov. Hemse Marl, north-west part, Hemse Beds. Snoder 1 (6), Snoder 2 (4, 5). 4a, b, holotype Ar51328, pygidium, ventral and posteroventral views, $\times 2$. 5, paratype Ar51288, pygidium, ventral view, $\times 2$. 6, paratype Ar51287, large hypostome, $\times 2$.
- Fig. 7a–c. *Ktenoura conformis* (Angelin, 1854). Hamra Beds, Geistermyr kanal. Ar29788, partial exoskeleton, a, dorsal view, note fragmentary hypostome and rostral plate on right pleurae, b, anterolateral view, c, enlargement of cheek, a, b $\times 2.5$, c $\times 7$.



RAMSKÖLD, *Didrepanon*, *Ktenoura*

curve gently upwards distally, and are widely separated, with furcations wide and rounded proximally. Posterior pair of spines short, blunt, subtriangular. Anterolateral process short, subtriangular, slightly posterior to transversely directed, separated from anterior pleural ridge by an oblique, shallow furrow. Doublure with a posteromedian semicircular embayment. Ventral surface of spines and outer part of doublure finely and densely granulated. Dorsal surface with dense granulation on spines and borders, less dense on pleural ridges.



TEXT-FIG. 3. *Didrepanon gutnicum* sp. nov. Reconstruction of pygidium, based mainly on Ar51288. $\times 3$.

Discussion. *D. gutnicum* differs from the type species in its larger size, smaller anterolateral processes, distinct ankylosed articulating half-ring, and much more widely spaced, more curved spines. *D. quenstedti* (Barrande, 1846) from the lower Ludlow of Bohemia has S3 and S2 more firmly impressed medially, a less curved posterior branch of facial suture, narrower lateral borders in the cephalon, and more slender, pointed, and less curved pygidial spines. (Cephalic features as figured by Přibyl and Vaněk 1964, pl. 1, fig. 7.)

Didrepanon? sp. A

Plate 21, figs. 1-3

- v. 1837 *Calymene? speciosus* Dalm.; Hisinger, p. 6, pl. 39, fig. 9, non Dalman 1827
- v. 1854 *Chirurus speciosus* His. [sic]; Angelin, p. 78, pl. 39, fig. 14, non Dalman 1827.
- v. non. 1885 *Chirurus speciosus* His.; Lindström, pl. 12, fig. 11 [= *Radiurus phlogoideus* sp. nov.].
- 1971 *Didrepanon? speciosum* (Hisinger, 1837) Lane, p. 21.

Material. Hisinger (1837) and Angelin (1854) figured the same cranium, Ar46983; refigured here Pl. 21, fig. 1. As noted by Lindström (1885, p. 44) this specimen is not related to *Calymene? speciosus* Dalman, 1827. Three more crania are known, Ar46982, Ar 29803, SGU 1352. All specimens stated to be from Klinteberget, Klinteberg Beds. Some similar specimens were collected in the 1840s by Marklin and labelled 'Burgsvik'. The lithology, however, which is not otherwise found in the Burgsvik area, is similar to that of the Klinteberget specimens, and suggests that the labelling is a mistake. These specimens are not figured, but would add no significant details.

Discussion. The course of S3 and S2 together with the general shape of the specimens suggest that this species belongs to *Didrepanon*. The only pygidium recorded from the Klinteberg Beds at Klinteberget belongs to *Radiurus* (see p. 190), but it is unlikely that the material referred here to *D.?* sp. A is related to the specimen. *D.?* sp. A is distinguished from *D. gutnicum* by its shorter and wider glabella and narrower cheek, giving a width ratio fixed cheek : occipital ring of only 1.2 : 1, as compared to 1.5 : 1. It

is also characterized by the incurved anterolateral margin of the frontal lobe and basal lobes that are better defined adaxially. *D.?* sp. A is very similar to *D. sp. A* of Lane (1971, pl. 7, fig. 22) from the British Wenlock. It seems to differ only in having broader and deeper lateral glabellar and axial furrows. The absence of pygidia, however, hampers further comparison.

Genus *KTENOURA* Lane, 1971

Type species. Ktenoura retrospinosa Lane, 1971; from the Much Wenlock Limestone Formation and Coalbrookdale Formation, Dudley, West Midlands, Great Britain; by original designation.

Diagnosis. See Lane 1971, p. 31.

Ktenoura conformis (Angelin, 1854)

Plate 21, fig. 7; Plate 22, figs. 1-16

- v. 1851 Angelin, pl. 21, fig. 3 [illustration only, without name].
- v.* 1854 *Chirurus conformis* Angelin, pp. 32, 79, pl. 39, fig. 15a.
- v. 1885 *Chirurus conformis* Ang.; Lindström, p. 45, pl. 13, figs. 13, 14.
- v. 1901 *Chirurus speciosus* His.; Lindström, p. 50, pl. 4, fig. 1.
- ?1933 *Cheirurus bicuspidatus* Bouček, pp. 5, 6, pl. 1, figs. 1-6.

Lectotype. Selected here, Ar29787, a fragmentary cranidium from Hamra Beds at Hoburgen, Pl. 22, fig. 1; figured Lindström 1885, and stated by him to be the original of Angelin 1851 and 1854. It is clear from Angelin's description that he had access to more material (which cannot be identified); the specimen he figured is therefore chosen as lectotype.

Additional material. Fragmentary material is common in the lower Hamra Beds. Localities: Gröttingbo parish—Uddvide stapelhage; east of Sallmunds allmanning; south of the south house of Sallmunds. Öja parish—Gisle 2. Sundre parish—Hoburgen 2; Kättelviken 1; Majstre 1; road ESE of the lighthouse at Hoburgen; west side of the southernmost point at Hoburgen. Vamlingbo parish—Geistemyrs kanal; Grumpevik; Snäckvik; Vallmyrs kanal. One specimen is from the Burgsvik oolite, Burgsvik Beds, from an unknown locality.

Diagnosis. Posterior border furrow wide, shallow, eye opposite L3 and S2, width ratio fixed cheek: occipital ring 0.9-1.0:1. Pygidium with ankylosed articulating half-ring in anterior inter-ring furrow, pleural furrows on both anterior and middle pleural ridges, and three pairs of spines reaching progressively further back.

Description. Frontal lobe strongly vaulted, middle and posterior part of glabella convex (tr.) and gently convex to flat (sag.). L3 widening very gently abaxially, L2 widening adaxially. Basal lobes subtriangular, circumscribed. S3 and S2 subparallel, curving slightly backwards, reaching one-third to a little more across glabella. S1 very deep and narrow from close to axial furrow to two-fifths its length, where it shallows and runs more obliquely backwards to meet the occipital furrow; this is constricted abaxially behind S1, then turns forwards in an arch, being wider and shallower between the inner angles of basal lobes. Occipital ring with a small median tubercle (Pl. 22, fig. 2). Axial furrow deepest where met by S3, shallowing backwards. Preglabellar furrow absent on median one-third of frontal lobe.

Cheeks subtriangular, gently convex (tr., exsag.). Posterior cephalic margin straight. Posterior border narrow (exsag.) adaxially, 1.5 times as wide lateral to fulcrum. Posterior border furrow constricted adaxially, curving laterally and slightly forwards while becoming broader and shallower, narrowing close to genal angle. Genal spine pointed, equal in length to sagittal length of occipital ring. Lateral border wider than posterior border, narrowing slightly forwards with increasing convexity. Lateral border furrow wide near genal angle, narrowing anteriorly.

Eye small, extending from opposite S3 to slightly behind S2. Palpebral rim strongly convex, palpebral furrow distinct. Field of cheek coarsely pitted, pits larger and more widely spaced closer to lateral border furrow, which is itself pitted. Genal spines, lateral borders, posterior edge of posterior border, and frontal lobe close to anterior margin very finely and densely granulated; larger, widely spaced granules on entire glabella, more dense on frontal lobe. On well-preserved specimens two diverging rows of pits can be seen on frontal lobe, as well as numerous pore-openings (Pl. 22, fig. 10).

Rostral plate (Pl. 21, fig. 7a) wide (tr.), very short. Hypostome with middle furrow deep abaxially, very shallow

to indistinct medially. Anterior border furrow distinct, with anterior border very short medially. Lateral border furrows wide and deep anteriorly, shallower behind middle furrows, continuing as a fairly deep posterior border furrow. Posterior margin straight. Entire surface very finely and densely granulated, granules smaller and more numerous posteriorly. Irregular, shallow pits of varying size are scattered over the middle body. Interior surface of middle body with coarse pits, larger anteriorly.

Number of thoracic segments unknown. First segment with narrower (tr.) pleurae than succeeding segments. Pleurae with a few median tubercles distally; anterior and posterior edges of pleurae lateral to fulcra densely granulated.

Pygidium with three rings and a terminal piece in axis. Inter-ring furrows long medially, constricted and deep abaxially; anterior furrow with a very distinct ankylosed articulating half-ring. Axial furrow shallow but distinct adjacent to anterior ring, very weak to absent posteriorly. Anterior and middle pleural ridges with oblique pleural furrows, the anterior one longer and deeper. Interpleural furrows very deep adaxially, shallowing distally, not reaching pygidial margin. Anterior pair of spines stoutest and longest, spine separated from well-developed anterolateral process by a marginal notch and a distinct, oblique furrow. Middle and posterior pairs of spines subequally stout and long, posterior pair reaching furthest back. Doublure with posteromedian embayment. Surface of pygidium, including doublure, finely granulated, densest on the spines.

Discussion. The range of variation in pygidial morphology is great in this species. However, even pygidia from the same locality exhibit these differences, which are therefore considered to be intraspecific. A few poorly preserved cranidia from Holmhällar 1, Hamra parish, might also belong to this species, which would extend its vertical distribution into the Sundre Beds. *K. conformis* differs from the type species in having longer (exsag.) fixed cheeks with more anteriorly situated eyes, wider posterior border furrows, a pygidium with a smaller anterior pair of spines, the middle and posterior pair reaching progressively further back than the anterior pair, longer (sag.) inter-ring furrows with an ankylosed articulating half-ring in the anterior one, and a distinct furrow on the middle pleural ridge. *K. bicuspidata* (Bouček, 1933) from the upper Wenlock-Ludlow Kopanina Beds of Bohemia is apparently closely related to *K. conformis*, but seems to differ in the pygidium by having more radially disposed spines, less distinct apodemal pits, and by lacking a middle pleural furrow. However, the figured material is rather poorly preserved, and it is possible that it is conspecific with the Gotland species.

Genus RADIURUS gen. nov.

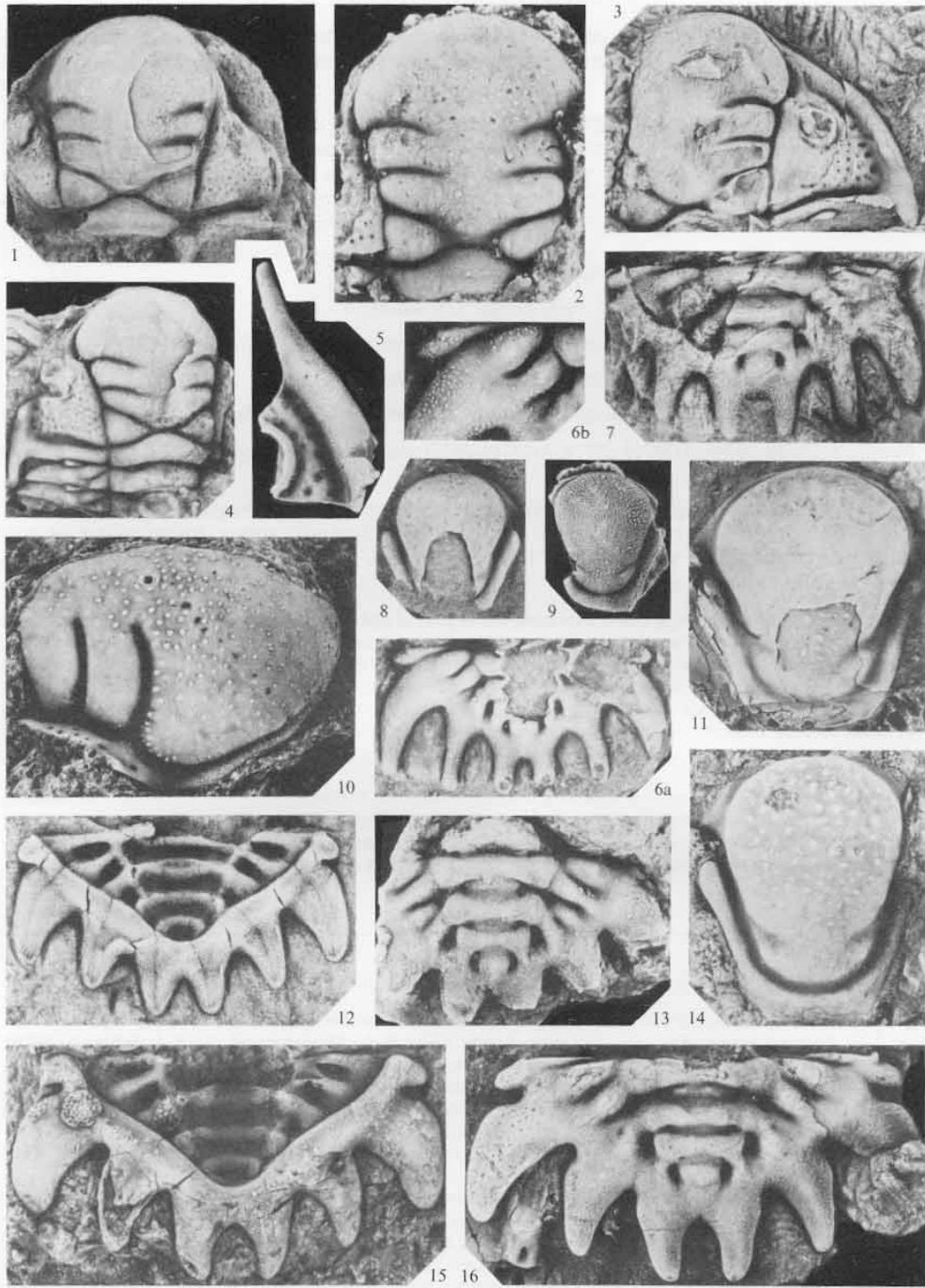
Name. Latin *radius*, ray, radial, and greek *oura*, tail; referring to the radially disposed pygidial spines.

Type species. *Radiurus phlogoideus* sp. nov; from the Lower Visby Marl (uppermost Llandoverly), Norderstrand, Visby, Gotland.

Other species. *Cheirurus estonicus* Männil, 1958; *R.* sp. (see below); *Cheirurus?* sp. of Norford 1981 (pygidium only).

EXPLANATION OF PLATE 22

Figs. 1-16. *Ktenoura conformis* (Angelin, 1854). Hamra Beds. 1, lectotype Ar29787, cranidium, Hoburgen, figured Angelin 1851, pl. 21, fig. 3; pl. 39, fig. 15, refigured Lindström 1885, pl. 13, figs. 13, 14, $\times 3$. 2, Ar29741, glabella, Sundre, $\times 3$. 3, Ar29703, partial cephalon, Uddvide stapelhage, $\times 3$. 4, Ar29707, cranidium with two thoracic segments, Uddvide stapelhage, $\times 3$. 5, Ar51299, free cheek, Kättelviken 1, $\times 5$. 6a, b, SGU 1356, pygidium, dorsal view and enlargement of granulation, west side of southernmost point at Hoburgen, $a \times 3$, $b \times 5$. 7, Ar29731, pygidium, Vallmyrs kanal, $\times 3$. 8, SGU 1357, hypostome, road ESE of the lighthouse at Hoburgen, $\times 3$. 9, Ar51337, small hypostome, Hoburgen 2, $\times 4$. 10, Ar51326, partial cranidium showing granulation, fine pore-openings and one of the two diverging rows of pits, Kättelviken 1, $\times 4$. 11, Ar29696, hypostome, Uddvide stapelhage, $\times 2.5$. 12, Ar29799, ventral view of pygidium, Vallmyrs kanal, $\times 3$. 13, Ar29747, pygidium showing well-developed middle pleural furrows, Uddvide stapelhage, $\times 3$. 14, Ar46973, hypostome, internal mould, Grumpevik, $\times 3$. 15, Ar51301, ventral view of pygidium, Kättelviken 1, $\times 3$. 16, SGU 1358, pygidium, Hoburgen, $\times 3$.



RAMSKÖLD, *Ktenoura*

Diagnosis. Cheirurinae with entire anterior border and preglabellar furrow. S3 and S2 reaching one-third to three-eighths across glabella. Pygidium with three pairs of radially disposed, equally spaced spines of subequal size.

Remarks. *Radiurus* is the only Silurian Cheirurinae having a complete anterior border and preglabellar furrow. It is also easily distinguished by its pygidial features. Lane (1971, pp. 76–79) saw *R. estonicus* as being close to an ancestor of several Silurian and Devonian Cheirurinae. The undifferentiated pygidium in *Radiurus* is certainly a likely morphological feature for such an ancestor, but to deal further with that problem is beyond the scope of this study.

Radiurus phlogoideus sp. nov.

Plate 23, figs. 2–5; text-fig. 4

v. 1885 *Chirurus speciosus* His.; Lindström, p. 44 [pars], pl. 12, fig. 11, non Hisinger 1837.

Name. Greek *phlogos*, flame; referring to the shape of the pygidial spines.

Holotype. Ar29779, a cranidium, from the Lower Visby Marl, Norderstrand, Visby; Pl. 23, figs. 2a, b.

Paratypes. Ar29742–29744, Ar29759–29778, Ar29780–29781; cranidia, seven hypostomes and one pygidium, all from the type locality.

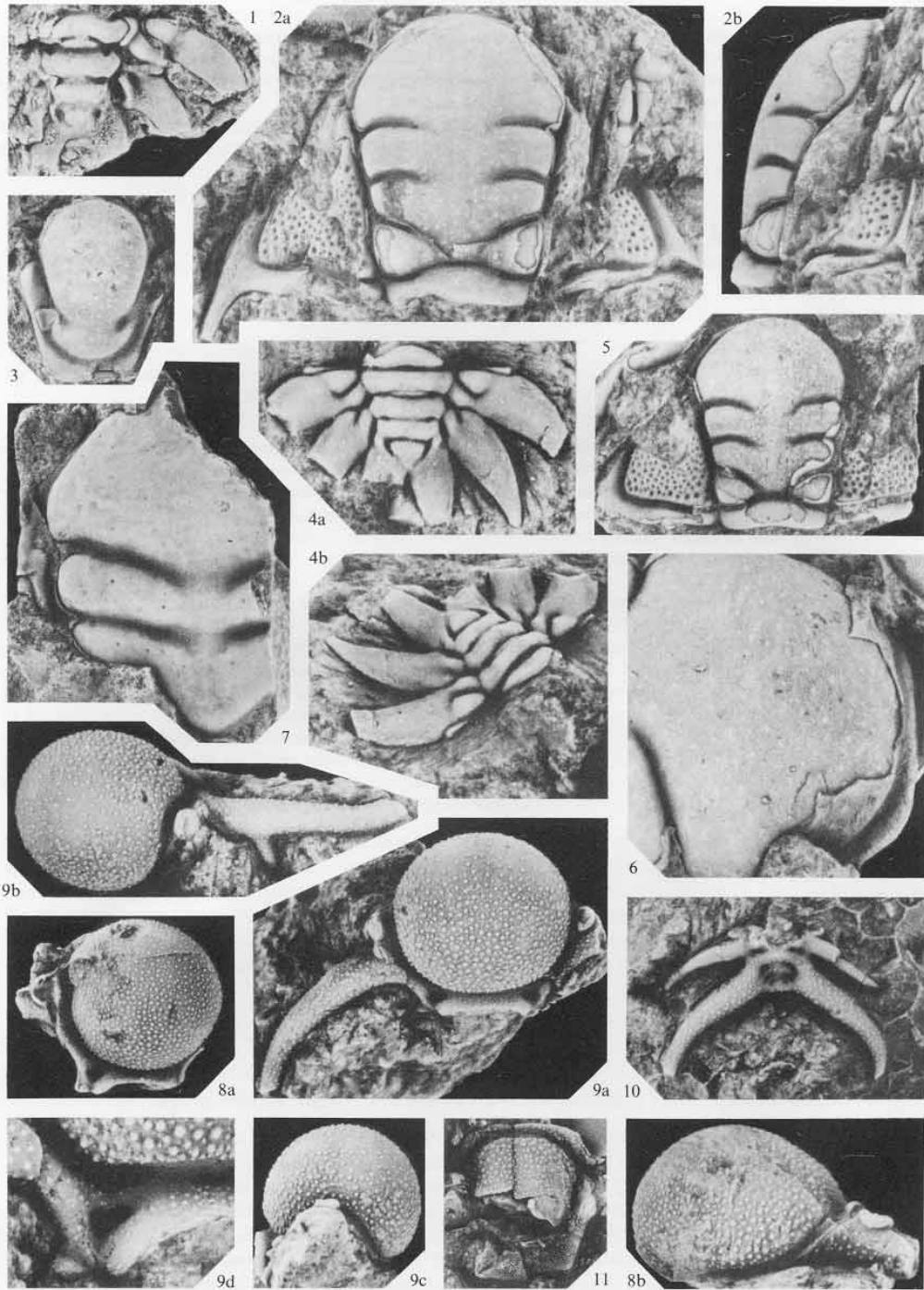
Diagnosis. Glabella strongly convex. Anterior border entire, short. Preglabellar furrow entire, distinct. Width ratio fixed cheek : occipital ring 1.3 : 1. Pygidium with spines closely spaced, at least middle pair pointed, axis with a pair of tubercles on each ring, ankylosed articulating half-ring present in anterior inter-ring furrow.

Description. Frontal lobe strongly convex, forming widest part of glabella. Portion of glabella behind frontal lobe gently convex (sag.), in large specimens less convex (sag., tr.). L3 parallel-sided to widening slightly abaxially. Basal lobes slightly inflated independently, rather poorly delimited medially on external moulds, circumscribed on internal moulds. S3 and S2 deep, narrow (exsag.). S1 deep and constricted from axial furrow to half its length. Occipital furrow deep and narrow behind S1, then shallower in an arch medially. Occipital ring with a very small median tubercle. Axial furrow rather narrow, with anterior pit opposite S3. Preglabellar furrow unbroken, but shallower medially. Anterior border short and convex (sag.), a little longer anterolaterally (Pl. 23, fig. 6).

Posterior portion of fixed cheek broadening abaxially. Posterior border short (exsag.) adaxially, broadening lateral to fulcrum. Posterior border furrow narrow, distinct, shallower close to genal angle. Genal spine fairly long, pointed, directed backwards and slightly outwards. Lateral border known from fixed cheek only, wider than posterior border, narrowing anteriorly. Lateral border furrow narrow, distinct.

EXPLANATION OF PLATE 23

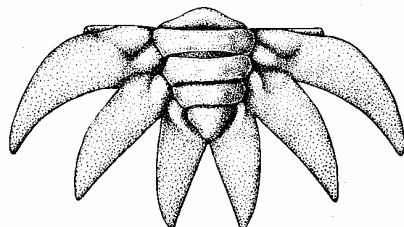
- Fig. 1. *Radiurus* sp. indet. Ar29804, pygidium, internal mould, Klinteberg Beds, Klinteberget, $\times 3$.
 Figs. 2–6. *Radiurus phlogoideus* gen. et sp. nov. Lower Visby Beds, Norderstrand. 2a, b, holotype Ar29779, cranidium, internal mould, dorsal and lateral views, $\times 3$. 3, paratype Ar29775, hypostome, internal mould, $\times 3$. 4a, b, paratype Ar29766, pygidium, dorsal and oblique anterolateral views, $\times 4$. 5, paratype Ar29780, cranidium, mainly internal mould, $\times 3$. 6, paratype Ar29764, cranidium, mainly internal mould, showing preglabellar furrow and anterior border, $\times 5$.
 Fig. 7. Cheirurinae gen. et sp. indet. Ar29724, partial cranidium, internal mould, ?Sundre Beds, Klev, Hoburgen, $\times 2$.
 Figs. 8–10. *Deiphon sphaericum* sp. nov. Possibly Högklint Beds. Visby-Lickershamn (8, 9), Lickershamn (10). 8a, b, paratype Ar6165, partial cephalon, oblique dorsal and anterolateral views, a $\times 4$, b $\times 6$. 9a–d, holotype Ar6162, cranidium, dorsal, anterolateral, lateral views, and enlargement showing L1 area, a–c $\times 4$, d $\times 10$. 10, paratype Ar6153, pygidium, figured Whittard 1934, pl. 15, fig. 12, $\times 4$.
 Fig. 11. *Deiphon brevispina?* sp. nov. Ar51269, hypostome, Högklint Beds, unit b, dump at Visby harbour, $\times 4$.



RAMSKÖLD, *Radiurus* gen. nov., *Deiphon*

Eye extending from opposite mid L3 to opposite mid L2. Palpebral furrow distinct posteriorly, less so anteriorly. Anterior branch of facial suture curves around frontal lobe close to axial and preglabellar furrows. Posterior branch runs from eye straight to gently convex forwards in a slightly anterior direction to meet lateral border opposite S2, then curves backwards across border.

Surface sculpture on entire glabella consists of rather widely spaced granules. Cheek excluding borders densely pitted, pits larger laterally and also present in lateral border furrow. Anterior and lateral borders and genal spines covered with microgranulation.



TEXT-FIG. 4. *Radiurus phlogoideus* gen. et sp. nov. Reconstruction of pygidium, based on Ar29766. $\times 4$.

Rostral plate unknown. Hypostome with middle furrow deep and wide laterally, distinct one-quarter to almost one-third distance across middle body, very shallow medially. Anterior border furrow absent medially. Lateral border furrows deep and distinct, continuing around posterior lobe as an equally distinct posterior border furrow. Lateral borders with distinct shoulders posterior to antennular notches, narrowing backwards. Posterior border convex (sag.), slightly broader than lateral borders. Posterior margin straight. Middle body with granulation similar to that of glabella. Borders with microgranulation. Dorsal surface of middle body with numerous pits.

Thorax of unknown number of segments. Axial ring with elevated middle portion, making it subtriangular in section. Segments otherwise typical for subfamily.

Pygidium with axis of three rings and a terminal piece. The rings are equally long (sag.), with a pair of tubercles on each, less distinct on anterior ring. Terminal piece posteriorly reaching median furcation. Anterior inter-ring furrow with a distinct, short, ankylosed articulating half-ring. Middle and posterior inter-ring furrows short (sag.), with lateral apodemal pits. Axial furrow distinct adjacent to anterior and middle rings, weak adjacent to posterior ring. Anterior and middle pleural ridges with deep and narrow pleural furrows. Interpleural furrows very deep proximally, shallowing distally, but still firmly impressed when reaching pygidial margin. At least middle pair of spines pointed, posterior pair probably slightly shorter than anterior and middle pair. Spines separated by equally sized, pointed furcations. Surface sculpture of microgranulation.

Discussion. This species differs from *R. estonicus* (Männil, 1958), from the upper Llandovery of Estonia, in having a more expanding-forwards glabella, eyes placed closer to axial furrows, longer (tr.) S3 and S2, and closer spaced, more curved pygidial spines. The terminal shape of the spines is not considered a difference since Männil's reconstruction of the pygidium is based on a specimen with all terminal parts apparently lost, and the Gotland specimen has only one complete spine. The hypostome figured by Lindström (1885) as '*Chirurus speciosus* His.' is typical of *R. phlogoideus* and is from the type locality.

Radiurus sp. indet.

Plate 23, fig. 1

Material. Ar29804, a fragmentary pygidium, stated to be from Klinteberget, Klinteberg Beds.

Discussion. A comparison of this single specimen with *R. phlogoideus* is difficult because the only known pygidium of the latter has the exoskeleton preserved, whereas the Klinteberget specimen is an internal mould. However, *R. sp. indet.* has more widely spaced spines, in particular the posterior pair is widely separated. Apart from this, all major features of *R. phlogoideus* seem to be present, including the pairs of tubercles on the axial rings, so that an assignment to *Radiurus* can be confirmed. Norford (1981, pl. 9, fig. 7) figured a very similar pygidium as *Cheirurus?* sp. His specimen, from the Llandovery of Canada, differs from the Klinteberget specimen by its smaller middle and

posterior axial rings and less inflated pleural ridges. The figured cephalon associated by Norford with this pygidium does not, however, fit the definition of *Radiurus*, and may in fact not be related to the pygidium.

CHEIRURINAE gen. et sp. indet.

Plate 23, fig. 7

Material. Ar29724–29725, a fragmentary cranidium, from Klev, north of Hoburgen, Sundre parish, probably Sundre Beds.

Discussion. This large specimen shows similarities both to *Didrepanon* and *Cheirurus? gotlandicus* in having the S3 and S2 connected medially by depressions. Two other, indeterminate cranidia (Ar29727 from Linde klint, south side, Linde parish, Hemse Beds, upper part; and Ar29802 from Alva parish, Hemse Marl, south-east part, Hemse Beds) also exhibit the same features. However, the relationships of these specimens cannot be evaluated until further material is available.

Subfamily DEIPHONINAE Raymond, 1913

Diagnosis. See Holloway 1980, p. 39, and Thomas 1981, p. 60.

Genus DEIPHON Barrande, 1850

Type species. *Deiphon Forbesi* Barrande, 1850, from the Liteň Formation (upper Wenlock), Lištice, near Beroun, Czechoslovakia; by original designation.

Diagnosis. Cheeks spinose, curving outwards, backwards, and downwards, with upturned tips. Ventrally on fixed cheek there is a small spine close to facial suture. Free cheek small, with doublure as large as dorsal area. Eye small, surrounded by convex rim, placed close to axial furrow on anterior part of spinose cheek. Thorax of nine segments, fulcra close to axial furrows and spinose pleurae not in contact with each other. Pygidium with axis of four rings, the small posterior two set in an oval depression. Two pairs of lateral spines, the posterior of which is the stouter, running transversely or obliquely backwards, distally recurved; and a posterior pair of short, ventrally directed spines.

Remarks. The diagnosis given by Lane (1971, p. 59) has been modified mainly to allow for the presence of the third pair of spines.

Discussion. Only *D. globifrons*, the most completely known species, is described fully here. Differences in the other species are brought out in comparative diagnosis.

Deiphon globifrons Angelin, 1854

Plate 24, figs. 6–13; Plate 25, figs. 1–4, 6–8, 11

*1854 *Deiphon globifrons* Angelin, p. 66, pl. 34, figs. 7, 7a.

v. 1934 *Deiphon forbesi* var. *globifrons* (Ang.); Whittard [*pars*], pp. 510–513, pl. 15, figs. 4–11, non fig. 12 [= *D. sphaericum* sp. nov.].

Neotype. Selected here, Ar51271, a cranidium, Pl. 24, fig. 12a, b, from Valbytte 1, Sanda parish, Slite Marl, Slite Beds.

Remarks. The specimen figured by Angelin (1854, locality given as 'Gotland') cannot be located, and there is no trace of other possible syntypes. Unfortunately, Angelin's figures are rather poor, and it is difficult to recognize diagnostic features. However, *D. globifrons* is by far the most common *Deiphon* on Gotland, and it seems likely that Angelin's concept of the species included the taxon as described here. In addition, the name has been widely used, and should be retained for stability. A neotype is therefore chosen from the specimens from Valbytte 1, the locality which has yielded the largest and best-preserved material of this species.

Additional material. Two records of *D. globifrons* are known from the Slite Beds, unit g (quarry by the windmill at Fårösund, and Lännaberget 2), otherwise the species is restricted to the Slite Marl (apparently to the upper part), where in some areas it is not uncommon. The known localities are: Bunge parish—the shore at Boviken; the shore at Fårösund village; the quarry by the old windmill c. 600 m south-west of Fårösund harbour; c. 200 m south-east of Hägur; ditch section on Ekenäs (Grundudden). Fårö parish—Braidaursvik 1; Friggars 1; Haganäs 1; Lansa; Ryssnäs; Gåsmorahammar, the shore 3 m a.s.l.; drainage ditch close to south shore of Eketräsk. Follingbo parish—locality unknown. Hejdeby parish—locality unknown. Othem parish—Lännaberget 2. Sanda parish—Valbytte 1; Valbytte 4. Stenkumla parish—Myrse 1.

Diagnosis. Spinose cheeks stout, sigmoidally curved in lateral profile, curving upwards distally through 90°. Secondary spines long and stout. Glabellar granulation unimodal, medium sized, coarser towards glabellar margins. Lateral borders of hypostome narrow, middle body large. Thorax with slender pleurae. Pygidium with second pair of spines curving to point straight back, or converge very slightly backwards.

Description. Glabellar bulb almost spherical, in large specimens with a tendency to become somewhat flattened anteromedially. Basal lobes present as ridges lateral to the preoccipital depression, merging with cheeks laterally. Occipital furrow rising from deep, circular occipital apodemal pit, fading into preoccipital depression. S1 longer (exsag.) than occipital furrow, rising from S1–S2 apodemal pit to merge with preoccipital depression. Occipital ring very convex (tr., exsag.), about half as wide as widest part of glabella. Axial furrow shallow adjacent to occipital ring, deepening into occipital apodemal pit before shallowing adjacent to L1, then deepening again into the very deep and fairly wide (tr.) elongate S1–S2 apodemal pit (apodemes visible on Pl. 24, fig. 9c), before shallowing half-way between L1 and eye, being very broad and shallow towards eye. Preglabellar furrow evenly distinct, gently arched upwards medially.

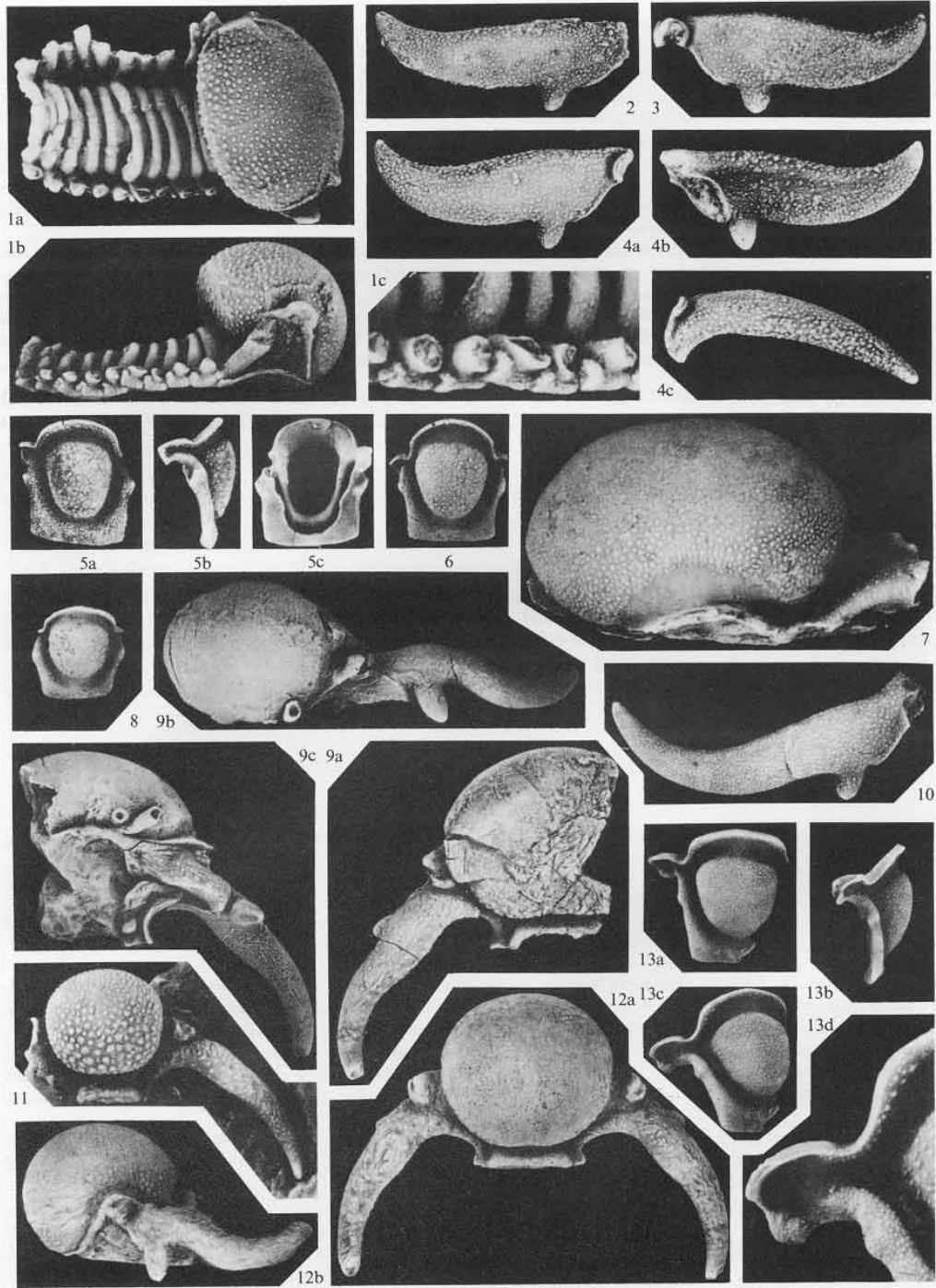
Fixed cheek posteriorly band-like, short (exsag.), curving anterolaterally to meet spinose portion behind the eye. A small, subtriangular articulating flange is separated off by an oblique, distinct furrow. The flange is wider (tr.) than cheek in front, and is laterally flexed first ventrally, then adaxially, through 180°. Spinose cheek stout, curving posterolaterally and downwards. Secondary spine situated almost immediately lateral to facial suture, cheek inflated dorsal to this. Posterior area of secondary spine and spinose cheek flattened medially to this. Spinose cheek distally circular and proximally oval in section.

Eye with reniform to oval visual surface. Subocular furrow wide and rounded in profile. Posterior branch of facial suture cuts eye socle at less than half the distance from anterior end. Glabella densely granulated, granules smallest and densest on central portion, and successively larger towards glabellar margins, largest posteromedially. Small specimens have relatively fewer, larger, and more equally sized granules (Pl. 24, fig. 11; Pl. 25, fig. 6). Granulation on cheeks intermediate in size, dense to rather widely spaced, on occipital ring very fine.

Rostral plate (Pl. 24, fig. 9c) twice as long laterally as sagittally. Hypostome with short anterior border. Anterior border furrow wide medially, narrowing and deepening laterally. Lateral border furrow deep anteriorly, shallowing and widening posteriorly, continuous with the very wide (sag.) and shallow posterior border furrow. Anterior wing (Pl. 24, fig. 13d) with median furrow deep and constricted adaxially, widening laterally into an oval, depressed area centrally on wing (corresponding to wing process). Anterior border of wing

EXPLANATION OF PLATE 24

Figs. 1–5. *Deiphon brevispina* sp. nov. Högklint Beds, unit b. Västös. 1a–c, holotype Ar6156, partial exoskeleton, dorsal and lateral views, and enlargement of thoracic segments, a, b $\times 4$, c $\times 10$. 2, holotype Ar6159, right spinose cheek, anterior view, $\times 4$. 3, holotype Ar6158, left spinose cheek, anterior view, $\times 4$. 4a–c, paratype Ar6160, right spinose cheek, anterior, posterior, and dorsal views, all $\times 4$. 5a–c, paratype Ar6157, hypostome, figured Whittard 1934, pl. 15, fig. 7a, b, ventral, lateral, and dorsal views, all $\times 4$.
Figs. 6–13. *Deiphon globifrons* Angelin, 1854. Slite Marl, Slite Beds. Valbytte 1 (6, 8, 9, 11, 12), Haganäs 1 (7, 10, 13). 6, Ar51274, hypostome, $\times 3$. 7, Ar51281, partial cranidium, posterior view, $\times 4$. 8, Ar51275, small hypostome, $\times 4$. 9a–c, Ar51272, partial cephalon, dorsal, anterolateral, and ventral views, showing free cheek and rostral plate, all $\times 2.5$. 10, Ar51298, spinose cheek, $\times 4$. 11, Ar51273, small cranidium, note coarse granulation and long preoccipital depression, $\times 5$. 12a, b, neotype Ar51271, worn cranidium, dorsal and lateral views, both $\times 2.5$. 13a–d, Ar51276, hypostome, ventral, lateral, oblique lateral views, and enlargement of anterior wing, a–c $\times 3$, d $\times 8$.



RAMSKÖLD, *Deiphon*

very narrow, lateral border narrow, overhanging part of central depression, posterior border protruding posterolaterally, narrowing adaxially, then merging with lateral hypostomal border. This is evenly raised, widening posteriorly, with a distinct shoulder which is larger in small specimens (Pl. 24, fig. 8). Posterior border fairly wide, gently convex (sag.), margin straight to slightly convex. Doublure present posterior to wing furrow, inner margin follows a course corresponding to inner margins of borders. Shoulders continue on doublure as ridges directed obliquely posteromedially. Rostral plate with granulation at least laterally. Anterior hypostomal border with an irregular row of small granules, continuing on to wing. Lateral and posterior borders finely and densely granulated. Middle body with larger, more widely spaced granules.

Thorax of unknown number of segments. Pleurae unfurrowed, very slender, adaxially oval and distally circular in section, pointed. Pleurae finely granulated.

Pygidium with anterior pair of spines slender, directed slightly backwards from the transverse direction. Second pair stout, curved backwards, much stouter and diverging at greater angle in large specimens (Pl. 25, figs. 1, 4), pointed tips directed straight back or converging slightly (Pl. 25, fig. 8). Inter-ring furrows very shallow medially, ankylosed articulating half-ring in the anterior one. Beneath posterior margin is a posterior pair of short, blunt spines, hooked backwards (Pl. 25, figs. 2, 11), reaching behind posterior margin. Surface of pygidium, at least behind anterior inter-ring furrow, finely and densely granulated.

Discussion. This is the largest *Deiphon* known, attaining a glabellar diameter of 14 mm or more. There are some differences between specimens from Valbytte 1 and those from Haganäs 1 (i.e. between the west and the east part of the Slite Marl). The latter have less sigmoidally curved spinose cheeks (Pl. 24, fig. 10) with less prominent swellings and slightly shorter secondary spines, and possibly the granulation is denser (Pl. 24, fig. 7). No other differences have been found, and they are considered to be of intraspecific nature.

In the Gotland species of *Deiphon*, mainly the cheeks and the granulation are of taxonomic value. Possibly, differences in the pygidium would also be helpful, but unfortunately it is rarely found. Each species recognized here is distinguished by a complex set of characters. There are no obvious chronological trends in these features, and the phylogenetic relationships between the species are uncertain. Some important comparative features are listed in Table 1. The two most closely related species appear to be *D. snodensis* and the type species. However, *D. forbesi* (figured Whittard 1934, pl. 15, figs. 1-3; and Horný and Bastl 1970, pl. 15, fig. 8) has even more slender spinose cheeks, denser granulation, and nodular L1.

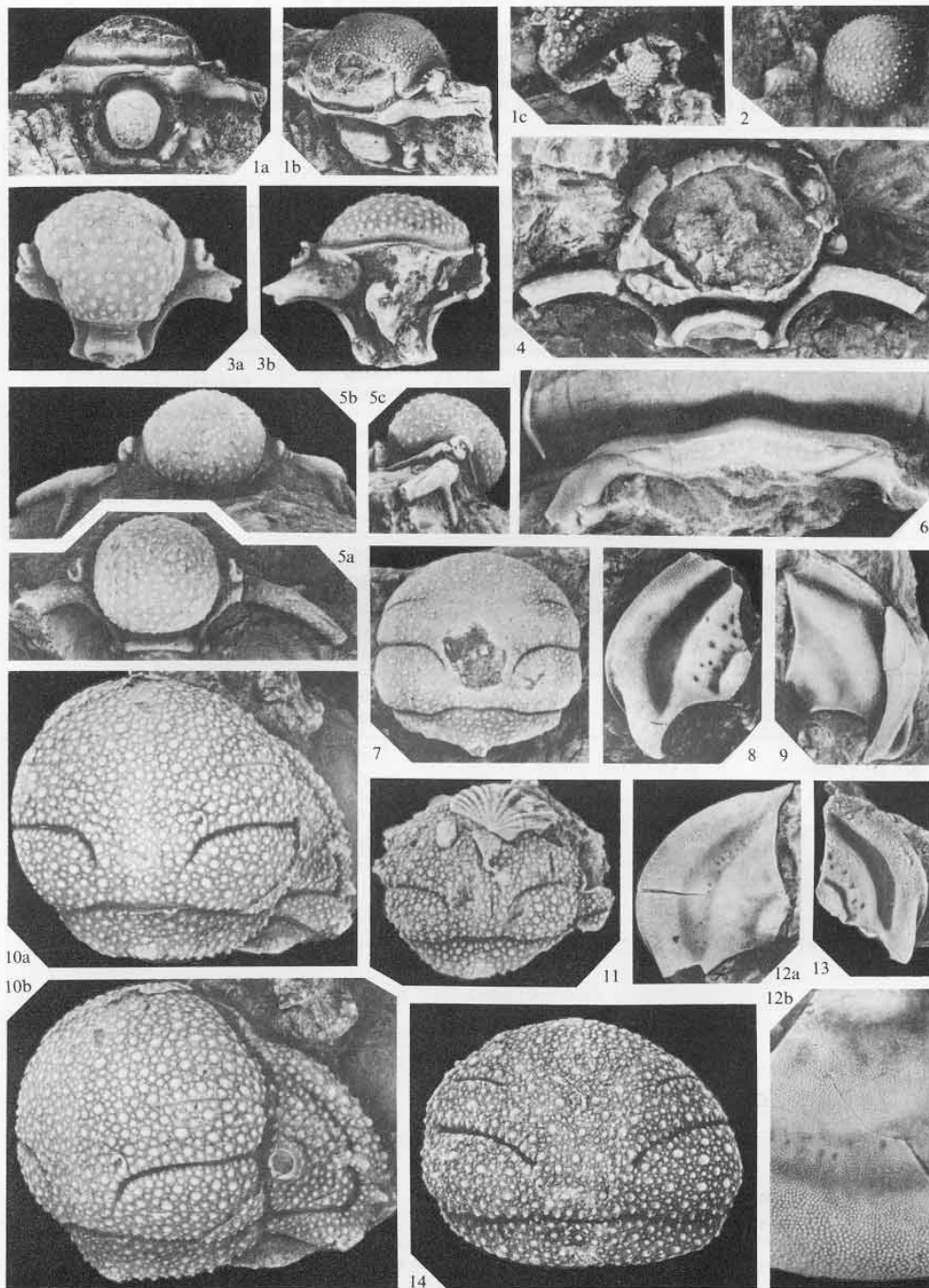
Deiphon cf. globifrons Angelin, 1854

(Not figured)

Remarks. From Djupvik, Eksta parish, two fragmentary cranidia (Ar6170-6171) are known,

EXPLANATION OF PLATE 25

- Figs. 1-4, 6-8, 11. *Deiphon globifrons* Angelin, 1854. Slite Marl (1-4, 6-8), Slite Beds, unit g (11). 1, Ar6154, worn pygidium, Fårö, figured Whittard 1934, pl. 15, fig. 11, $\times 3$. 2, Ar51294, partial pygidium, lateral view showing posterior spine, Valbytte 1, $\times 6$. 3, Ar51279, thoracic segment, Haganäs 1, $\times 3$. 4, Ar51277, pygidium, ventral view, Haganäs 1, $\times 3$. 6, Ar51314, smallest known cranium, note long preoccipital depression, Valbytte 4, $\times 6$. 7, Ar51280, thoracic segment, Haganäs 1, $\times 3$. 8, Ar51310, pygidium with unusually long spines, ventral view, Valbytte 4, $\times 4$. 11, SGU 1359, pygidium with unusually short spines, ventral view, quarry by the windmill c. 600 m south-west of Fårösund harbour, $\times 3$.
- Figs. 5, 9, 10, 12-16. *Deiphon ellipticum* sp. nov. Halla Beds, unit b. Hörsne 5 (9, 12, 15), Hörsne Canal (5, 10, 13, 14, 16). 5, paratype SGU 1361, partial cranium, $\times 6$. 9a, b, paratype Ar51296, thoracic segment, dorsal and anterior views, note faint pleural furrow, both $\times 8$. 10, paratype SGU 1362, small cranium, $\times 5$. 12a, b, paratype Ar51295, hypostome, ventral, and lateral views, both $\times 6$. 13, paratype SGU 1363, hypostome, $\times 6$. 14a-d, holotype SGU 1360, partial exoskeleton, a, b, dorsal and anterior views, c, d, enlargements of granulation and pygidium, a, b $\times 5$, c, d $\times 10$. 15, paratype Ar51297, smallest cranium known, $\times 6$. 16a-d, paratype SGU 1364, cephalon, dorsal, lateral, anterolateral, and anterior views, all $\times 4$.



RAMSKÖLD, *Deiphon*, *Sphaerexochus*, *Hyrokybe*?

TABLE 1. Comparison of some morphological features of taxonomic value in *Deiphon*. The Gotland species are listed in upwards chronological order. Four major non-Gotland species are included for comparison; the type species *D. forbesi* Barrande, 1850; the British *D. barrandei* Whittard, 1934; the Canadian *D. braybrooki* Perry and Chatterton, 1979; and the American *D. longifrons* Whittard, 1934.

SPECIES	AGE	SPINOSE CHEEK	SECONDARY SPINE	DOMINANT GLABELLAR GRANULATION	
				DENSITY	SIZE
<i>D. sp. A</i>	U Ludlow	medium?	slender?	sparse	coarse unimodal
<i>D. snodensis</i>	L Ludlow	very slender	very long slender	very sparse	very coarse unimodal
<i>D. ellipticum</i>	U Wenlock	medium	long slender	dense	fine unimodal
<i>D. globifrons</i>	Wenlock	stout	long stout	dense	medium unimodal
<i>D. brevispina</i>	L Wenlock	very stout	short stout	medium	medium bimodal
<i>D. sphaericum</i>	L Wenlock	medium	long slender	medium	medium bimodal
<i>D. forbesi</i>	Wenlock	very slender	shape uncertain	sparse	coarse bimodal
<i>D. barrandei</i>	Wenlock	stout	rel. short rel. stout	sparse	coarse unimodal
<i>D. braybrooki</i>	Wenlock	rel. stout	long slender	medium	medium bimodal
<i>D. longifrons</i>	Wenlock	medium	very long rel. stout	medium	medium bimodal

showing close affinities with *D. globifrons*. However, the lithology in these specimens is atypical of the Mulde Marl at Djupvik, and they may in fact be from the Slite Marl.

Deiphon sphaericum sp. nov.

Plate 23, figs. 8-10

v. 1934 *Deiphon globifrons* Angelin; Whittard [*pars*], pl. 15, fig. 12, *non* Angelin, 1854.

Name. Referring to the shape of the glabella.

Holotype. Ar6162, a cranidium, Pl. 23, fig. 9a-c, from unknown locality close to shore between Visby and Lickershamn.

Paratypes. From Visby-Lickershamn, Ar6161-6169, Ar6153. Vattenfallsprofilen 1, SGU 1353. Unspecified quarry south of Visby, SGU 1354. Norra Svältan Lickershamn, SGU 1355. The stratigraphic range is uncertain. Some material seems to be from the Höglint Beds, and specimens labelled Visby-Lickershamn could come from the Lower or Upper Visby Marl. Of the material from the Vattenfallet section (see Jaanusson, Laufeld and Skoglund 1979, pp. 117, 118) only the specimen from 10.7 to 10.8 m a.s.l. (lowermost Höglint Beds) can

possibly be assigned to this species. The fragmentary state of the other specimens precludes a definite assignment to any species.

Diagnosis. Glabellar bulb almost spherical, barely wider than long. Basal lobe ridge-like, merging laterally with cheek. Preoccipital depression short (sag.), rather shallow. Occipital ring slightly over half as wide (tr.) as maximum width of glabella. Band-like portion of fixed cheek short (exsag.), spinose portion emerging behind mid length of glabellar bulb, of moderate stoutness, with no swellings. Secondary spine long, slender, pointed, distance to facial suture approximately equal to its own diameter. Eye with anterior edge opposite mid length of glabellar bulb. Glabellar granulation bimodal, larger granules interspersed by a greater number of minute granules, especially antero-medially, where large granules are few. Spinose cheeks with rather sparse and coarse granulation. Pygidium behind anterior inter-ring furrow sparsely and coarsely granulated.

Deiphon brevispina sp. nov.

Plate 24, figs. 1-5

v. 1885 *Deiphon Forbesi* Barr.; Lindström, p. 51, pl. 13, figs. 9, 10; pl. 16, figs. 18-20, non Barrande, 1850.

Name. Latin *brevis*, short, and *spinus*, spine: referring to the rather short spinose cheeks.

Holotype. Ar6156, Ar6158, Ar6159; all parts belonging to the same specimen, a damaged individual lacking pygidium, partly figured Lindström 1885, pl. 13, figs. 9, 10; from ditch section at Västös, Hall parish, Högklint Beds, unit b; Pl. 24, figs. 1-3.

Paratypes. Ar6157, a hypostome, and Ar6160, a spinose cheek; from the type locality.

Specimens questionably assigned. Ar51269-51270, from dump at Visby harbour, Högklint Beds, unit b (Pl. 23, fig. 11).

Diagnosis. Basal lobe present as a low swelling, apparently not merging laterally with cheek. Occipital ring approximately half as wide (tr.) as widest part of glabella. Band-like portion of fixed cheek short (exsag.), spinose portion very stout, rather short, flat to concave posteriorly on proximal half, very high dorsoventrally, proximally reniform and distally oval in section, with short, upturned terminal part. Secondary spine short, stout, and blunt, situated very close to facial suture. Glabellar granulation bimodal, very similar to that of *D. sphaericum*, but denser and more markedly bimodal on spinose cheeks. Hypostome with rather small middle body, wide borders, and long (sag.) anterior border furrow. Thoracic pleural spines slender, circular in section close to fulcra.

Discussion. The glabella is slightly compressed anteroposteriorly, which makes it difficult to deduce its original shape. The Västös hypostome may also have belonged to the holotype, as judged from its size and preservation. (Account has not been taken of hypostome Ar51269 in the diagnosis.)

Deiphon ellipticum sp. nov.

Plate 25, figs. 5, 9, 10, 12-16

1855 *Deiphon Forbesi* Barr.; Lindström [*pars*], p. 51 [type locality mentioned], non Barrande, 1850.

Name. The specific name *ellipticum* was used on labels written by the nineteenth-century collector G. Liljevall, apparently as a working name, but it has never been published. The name refers to the shape of the glabella.

Holotype. SGU 1360, cranium, six thoracic segments and pygidium, Pl. 25, fig. 14a-d, from Hörsne kanal, Hörsne parish, Halla Beds, unit b.

Paratypes. Ar51295-51297, SGU 1361-1397; thirty-seven cranidia and cephalae, two hypostomes, one thoracic segment; all from the type locality (in Laufeld 1974b, divided into Hörsne 1-Hörsne 5).

Diagnosis. Glabellar bulb oval; length to width ratio about 5:6, low dorsoventrally. Occipital ring more than half as wide (tr.) as maximum width of glabella. Basal lobe in shape of a small swelling

connected by a ridge lateral to cheek. Axial furrow apparently curving laterally abaxial to this ridge and fading lateral to S1-S2 apodemal pit. Band-like portion of fixed cheek short (exsag.). Spinose portion of medium stoutness, without swellings, proximally oval and distally circular in section, curving upwards distally through about 45°. Secondary spine long, slender, pointed, distance to facial suture equal to its own diameter. Glabellar granulation dense, fine, regarded as unimodal although a few minute granules are scattered over the glabella, granules larger and more widely spaced close to glabellar margins. Hypostome fairly wide and short, with short (sag.) anterior border furrow. Thoracic pleurae elliptical in section, with a hint of a transverse pleural furrow on anterior one-third of proximal part. Pygidium finely and densely granulated.

Discussion. This is the Gotland species closest to the Canadian Wenlock *D. braybrooki* Perry and Chatterton, 1979. It differs mainly in having a more oval and less inflated glabella, more slender spinose cheeks, and less divergent pygidial spines. In addition, *D. braybrooki* has a coarser glabellar granulation which is equal all over, whereas in the Gotland species the granulation is much finer anteromedially, a difference that cannot be due to the different modes of preservation. The granulation of the Canadian species is also markedly bimodal, especially on the spinose cheeks. See also Table 1.

Deiphon snodensis sp. nov.

Plate 26, figs. 3-5

Name. After the type locality.

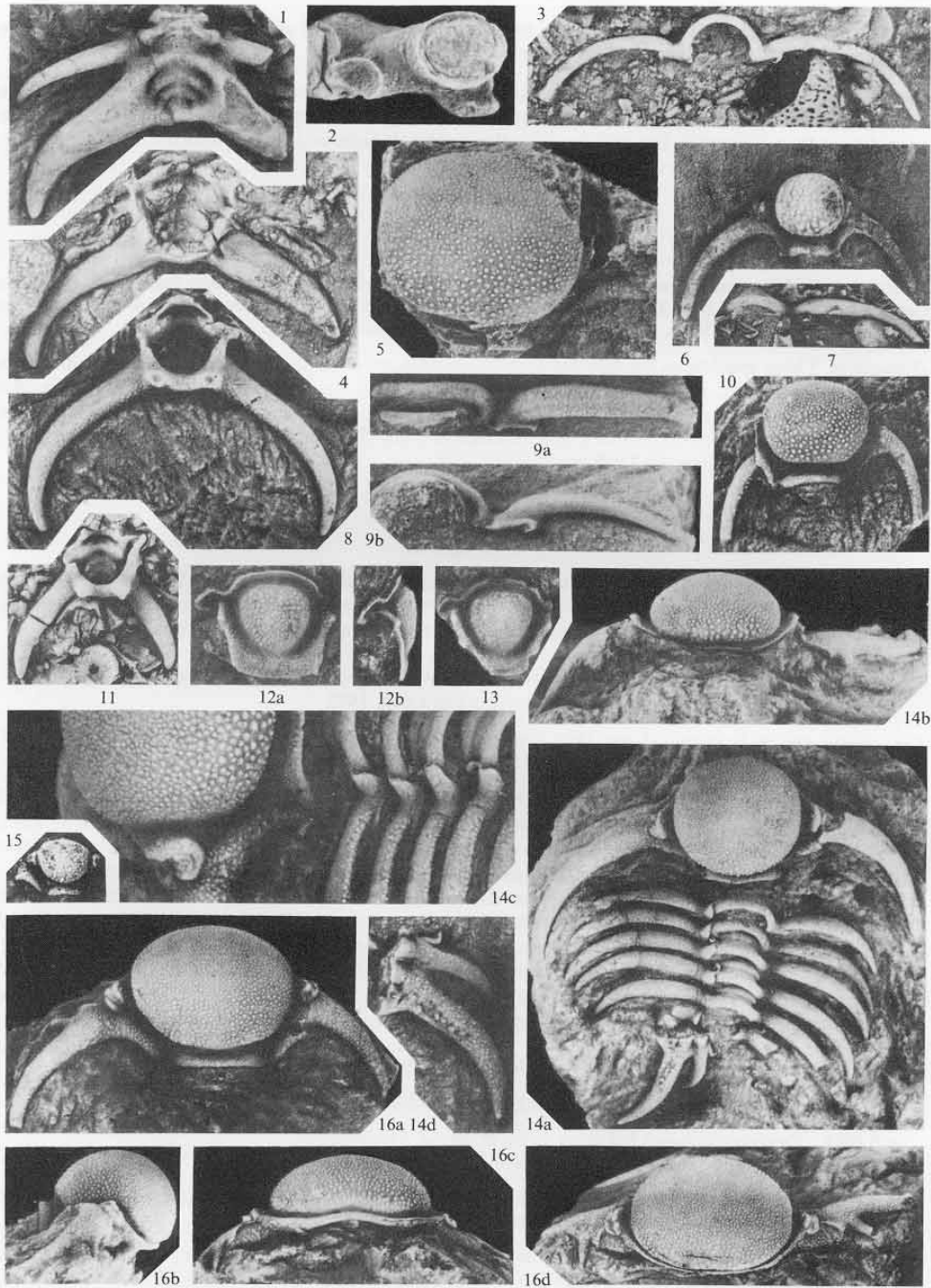
Holotype. Ar51284, a cranidium, Pl. 26, fig. 5a-c, from Snoder 2, Sproge parish, Hemse Marl, north-west part, Hemse Beds.

Paratypes. Ar51285-51286, both cranidia from the type locality.

Diagnosis. Glabellar bulb with length to width ratio 1:1. Basal lobe ridge-like, merging with cheek laterally. Occipital ring approximately half as wide (tr.) as maximum width of glabella. Band-like portion of fixed cheek long (exsag.), with only faintly concave lateral margin. Spinose cheek very slender with base opposite widest part of glabella, straight in lateral view for at least as long as diameter of glabella, without swellings, flattened posteriorly on proximal part. Secondary spine very long, slender, pointed, distance to facial suture equal to its own diameter. Glabella with very coarse,

EXPLANATION OF PLATE 26

- Figs. 1, 2. *Deiphon* sp. A. 1a-c, Ar51565, cephalon, mainly internal mould, collected by Professor H. Alberti (Göttingen), anterior, anterolateral views, and enlargement of eye, Holmhällar 1, Sundre Beds, middle to upper part, a, b × 4, c × 10. 2, Ar29815, partial cranidium, Klev, Hoburgen, probably Sundre Beds, lower to middle part, × 4.
- Figs. 3-5. *Deiphon snodensis* sp. nov. Hemse Marl, north-west part, Hemse Beds, Snoder 2. 3a, b, paratype Ar51285, cranidium with right free cheek, dorsal and ventral views, both × 4. 4, paratype Ar51286, crushed cranidium, × 4. 5a-c, holotype Ar51284, cranidium, dorsal, anterior, and lateral views, all × 4.
- Figs. 6, 8, 9, 12, 13. *Sphaerexochus scabridus* Angelin, 1854. Slite Marl (8, 9, 12, 13), Slite Beds, unit g (6). 6, Ar30042, cranidium, internal mould, anterior view showing rostral plate, Samsugn, × 5. 8, Ar51313, left free cheek, Mojner 3, × 3. 9, Ar51304, left free cheek, ventral view, lacking anterior part of doublure, Valbytte 1, × 3. 12a, b, Ar51302, left free cheek with unusually shallow lateral border furrow, dorsal view and enlargement of granulation, a × 3, b × 6. 13, Ar51323, right free cheek, Valbytte 1, × 3.
- Figs. 7, 10, 11. *Hyrokybe? globiceps* (Lindström, 1885). Upper Visby Beds. 7, SGU 1399, glabella, Själsö, × 4. 10a, b, lectotype Ar29810, partial cephalon, Visby area, figured Lindström 1885, pl. 13, fig. 11, dorsal and dorsolateral views, both × 4. 11, Ar29811, cranidium, Visby area, × 5.
- Fig. 14. *Hyrokybe? inermis* (Lindström, 1885). Holotype G238, compressed glabella, Slite Beds, unit g, Slite, × 4.



RAMSKÖLD, *Deiphon*

widely and evenly spaced unimodal granulation, equally sized and spaced anteromedially. Spinose cheek with coarse, widely spaced granulation.

Discussion. Of the Gotland species of *Deiphon* this differs most from the others (see Table 1). It has one feature in common with the only other known Ludlow species, *D. sp. A*—namely, the granulation that is equal in size and density all over the glabella within each species. However, in *D. sp. A* the granulation is less coarse and much denser.

Deiphon sp. A

Plate 26, figs. 1, 2

Material. Ar29815, a cranidium from Klev, Hoburgen, Sundre parish, probably Sundre Beds, lower to middle part; Ar30185, a glabella from Holmhällar, Vamlingbo parish; Ar51555–51565, cephalon and cranidia collected at Holmhällar 1, Sundre Beds, middle to upper part, by Professor H. Alberti (Göttingen).

Discussion. These specimens are not described here since most of the important taxonomic features are lacking. However, it is clear that the material does not belong to any described species. An interesting feature is that several of the specimens have the rostral plate, free cheeks, and hypostome *in situ*, although the thorax is obviously separated from the cephalon. The material shows that *Deiphon* survived well into the Ludlow.

Deiphon sp. indet.

(Not figured)

Remarks. From the topmost strata (of uncertain stratigraphical level in Halla or Klinteberg Beds) on the island of Lilla Karlsö several glabellae (Ar6136–6148; mainly internal moulds) are known, seemingly not belonging to *D. globifrons* or *D. ellipticum* (the species closest in age).

Subfamily ACANTHOPARYPHINAE Whittington and Evitt, 1954
Genus HYROKYBE Lane, 1972

Type species. *Hyrokybe pharax* Lane, 1972, from the ?Wenlock (?Llandovery) of Kronprins Christians Land, north-east Greenland; by original designation. (For discussion of age see Perry and Chatterton 1977, p. 287.)

Remarks. When erecting this genus, Lane (1972, p. 359) placed it in the Sphaerexochinae, but noted the similarity between *Hyrokybe* and a cranidium referred to *Youngia uralica* Tschernyschew, 1893, by Weber (1951). Dr. B. D. E. Chatterton has kindly informed me that he is working on new Canadian Llandovery material which includes several forms referable to *Youngia* and *Hyrokybe*. Both genera most probably belong to the Acanthoparyphinae. The main differences lie in the development of the cephalic spines and in the shape of the pygidium. Several species hitherto referred to *Youngia* will be reassigned to *Hyrokybe*, among them *Youngia copelandi* Perry and Chatterton, 1979. No pygidia that can be referred either to *Youngia* or *Hyrokybe* are known from Gotland, but cephalic features in the Gotland species previously assigned to *Youngia* suggest that they should be referred provisionally to *Hyrokybe*, pending the publication of the Canadian material.

Hyrokybe? globiceps (Lindström, 1885)

Plate 26, figs. 7, 10, 11

v.* 1885 *Youngia globiceps* Lindström, p. 50, pl. 13, fig. 11.

v. 1979 *Youngia sp.*; Jaanusson in Jaanusson *et al.*, pp. 117, 118.

Lectotype. Selected here, Ar29810, an incomplete cephalon, Pl. 26, fig. 10a–b, figured Lindström 1885, pl. 13, fig. 11; from the Upper Visby Marl in the Visby area.

Additional material. From 'Visby' (exact localities not known), Ar29811–29812 (these are probably Lindström's two additional specimens, i.e. paralectotypes). Vattenfallsprofilen 1, 9.6 m a.s.l., SGU 1398. Själsö, SGU 1399.

The beach at Kneippbyn, SGU 1400. This species is probably restricted to the Upper Visby Marl, although the Själsö specimen may be from the Lower Visby Marl.

Diagnosis. Glabella with S1 not reaching occipital furrow, S2 and S3 weak, reaching respectively one-third and one-fifth across glabella. Occipital ring with a small, ?short median spine. Genal spine situated close to genal angle; short, spinose tubercles present laterally on fixed cheek. Border furrows very narrow. Eye immediately adjacent to axial furrow, extending from opposite mid L1 to slightly anterior to S1. Cephalic tuberculation dense, coarse.

Description. Glabella with sagittal length (excluding occipital spine) equal to maximum width, which is reached across L1 and L2. L3 and L2 equally long (exsag.), L2 the widest (tr.). L1 1.7 times as long as L2, slightly independently inflated. S2 slightly more distinct than S3. S1 deep and narrow, directed slightly backwards, reaching two-fifths across glabella, medially flexed backwards, ending at mid length (exsag.) of L1. Occipital furrow transverse behind L1, then curves a little anteriorly, and again transverse for the medial one-fifth, where it is slightly broader and shallower than laterally. Occipital ring with a small spine-base medially on posterior margin. Axial furrow deep and narrow, preglabellar furrow (Pl. 26, fig. 10b) narrowest (sag.) medially, where it is gently arcuate.

Cheeks small. Posterior border broadening laterally, with a large spine-base close to genal angle. Lateral border of even width. Posterior border furrow evenly deep and narrow, merging with similar lateral border furrow, which is interrupted one-quarter way (of furrow length) from genal angle by a strong sutural ridge. Anterior to this ridge the furrow is shallower, close to axial furrow it ends against anterior sutural ridge.

Palpebral lobe diminutive. Anterior branch of facial suture runs from eye very close to axial furrow. Posterior branch running laterally and slightly forwards from eye until meeting lateral border, flexed backwards across the border. Surface of entire cephalon except furrows covered with more or less spinose tubercles, many of which are perforated, and granules of varying size. On posterior part of lateral margin are a few elongated tubercles; just posterior to the facial suture is a small spine (Pl. 26, fig. 10b). Rostral plate, hypostome, thorax, and pygidium unknown.

Discussion. *H.? globiceps* differs from the type species in having much denser and coarser tuberculation, better developed S2, S3 present, narrower axial and border furrows, a more laterally situated genal spine, and in having an occipital spine. A comparison with species now assigned to *Youngia* but which will be reassigned to *Hyrokybe* is hampered by the lack of pygidia. However, *Y. douglasi* Lamont, 1948 (see Clarkson and Howells 1981), from the upper Llandoverly of Scotland, appears to be very similar, but is stated to lack an occipital spine. *Y. copelandi* Perry and Chatterton, 1979, from the Canadian Wenlock, has L1 circumscribed. *Y. uralica* Tschernyschew, 1893, from the lower Ludlow of the Urals, lacks an occipital spine.

Hyrokybe? inermis (Lindström, 1885)

Plate 26, fig. 14

v.* 1885 *Youngia inermis* Lindström, pp. 50, 51, pl. 13, fig. 12.

Holotype. Specimen in the Palaeontological Institution, University of Uppsala, no. G238, a glabella, from the 'upper limestone at Slite' (= Slite Beds, unit g).

Discussion. This is the only known specimen of the species, although Lindström (1885, p. 51) considered two other fragmentary cranidia to be possible varieties. These latter specimens are too fragmentary to be recognized even at generic level. Most of the features listed by Lindström as diagnostic for *H.? inermis* can be explained by the fact that the specimen is considerably flattened, and hence should be excluded from the diagnosis. A single distinguishing feature remains—namely, the lack of an occipital spine. *H.? inermis* is too poorly known to be compared properly with other species, but seems to be close to *Y. douglasi* Lamont, 1948, and *Y. uralica* Tschernyschew, 1893.

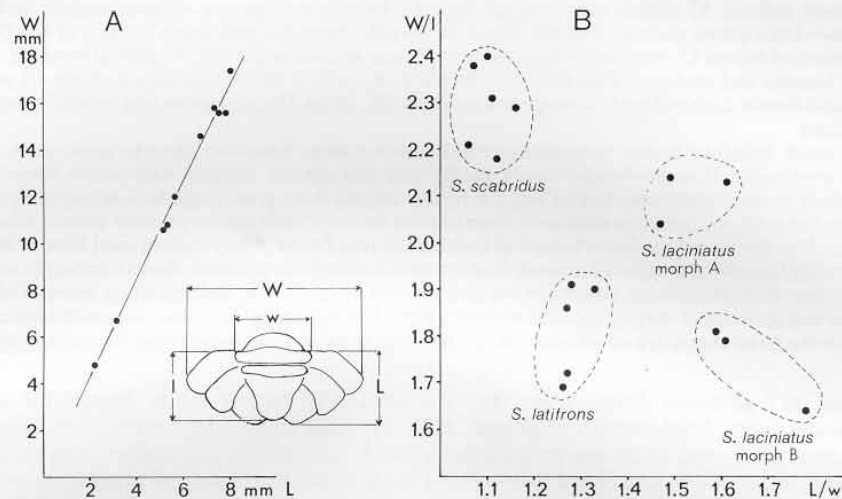
Subfamily SPHAEREXOCHINAE Öpik, 1937

Genus SPHAEREXOCHUS Beyrich, 1845

Type species. By monotypy; *Sphaerexochus [sic] mirus* Beyrich, 1845, from the Liteň Formation (upper Wenlock), Lištice, near Beroun, Czechoslovakia.

Diagnosis. See Lane 1971, p. 53.

Discussion. Some confusion has arisen concerning some Silurian *Sphaerexochus*. Dean (1971, pp. 29, 30) considered the British material to be specifically distinct from *S. mirus*, and described it as *S. britannicus*, but noted that either the species is highly variable, or the material may consist of more than one species. Thomas (1981, pp. 61–63) found no consistent differences between British and Bohemian material, and synonymized *britannicus*, and other species, with *mirus*, on the basis of overlapping variation in pygidial morphology. Variation in pygidial length–breadth proportions was stated as being due mainly to ontogeny, small individuals having a relatively wider pygidium.



TEXT-FIG. 5. *A*, *Sphaerexochus scabridus*; pygidial length plotted against pygidial width ($W = 2.20L^{0.978}$, $r = 0.998$). *B*, plot of some parameters of the pygidium in the Gotland species of *Sphaerexochus*. (Material; *A*: Ar51305–51307, Ar51338–51343, SGU 1402. *B*: Ar29857–29858, Ar29862, Ar29866, Ar29882, Ar29934, Ar30072, Ar51305–51306, Ar51338–51344, SGU 1402.)

However, plots for *S. scabridus* (text-fig. 5A) show isometric pygidial growth already from very small individuals, which probably holds for other *Sphaerexochus* as well. Both the Bohemian and British material almost certainly consist of more than one species. Figured Bohemian pygidia can be placed in two groups, one with 'long and narrow' pygidia (width:length ratio close to 1.8:1; Beyrich 1846, pl. 1, fig. 8c; Barrande 1852, pl. 42, figs. 22, 23; Barrande 1872, pl. 7, fig. 3; Shaw 1968, pl. 14, fig. 25; Thomas 1981, pl. 16, fig. 6), and one with 'wide and short' pygidia (width:length ratio 2.0–2.1:1; Thomas 1981, pl. 16, figs. 8, 10). Similarly, the British material can be divided into two such groups (Thomas 1981, pl. 16, fig. 7; and pl. 16, figs. 1, 5, 9, 11, 12, ?14, respectively). The first group (ratio 1.8:1) is very close to *S. latifrons* morph A, and the second (ratio 2.0–2.1:1) is very close to *S. scabridus*, and the respective forms may very well be conspecific. A thorough study of all Bohemian material is necessary to solve these problems. In the meantime, *S. mirus* and *S. britannicus* are regarded here as specifically distinct, and occurring both in Bohemia and Britain. *S. latifrons* may prove to be a junior synonym of *S. mirus*, if this is shown to be dimorphic, and *S. britannicus* is possibly a junior synonym of *S. scabridus*. *S. laciniatus* is well separated from the species discussed above.

Similarly to Bohemia and Britain, the Gotland material of *Sphaerexochus* is heterogenous.

However, apart from the isolated specimens referred to *S. spp.* below, the material falls into three groups, one from the Slite Beds and two from the Hemse Beds. This grouping based on morphology is supported by the stratigraphical occurrences. Unfortunately, most specimens are isolated glabellae or cranidia. As pointed out by *i.a.* Holloway (1980, p. 38), cephalic features alone are mostly insufficient for specific identification of *Sphaerexochus*. More material may therefore well make it possible to distinguish more than one species in some groups. The presence of dimorphism in at least two of the groups is also a complicating factor. For these reasons, and those outlined above, no detailed comparisons can be carried out at present between Gotland and non-Gotland species. To facilitate future studies, the diagnoses given here are detailed, although some features may prove to be generically rather than specifically diagnostic. Additional shared features are deep vincular furrows, accommodating the shortened first thoracic segment, and a small median occipital tubercle.

Sphaerexochus scabridus Angelin, 1854

Plate 26, figs. 6, 8, 9, 12, 13; Plate 27, figs. 1-11

1851 Angelin, pl. 22, fig. 9 [illustration only, without name].

*1854 *Sphaerexochus scabridus* Angelin, p. 37, pl. 33, fig. 1; pl. 38, figs. 14, 14a.

v. non 1885 *Sphaerexochus scabridus* Angelin; Lindström, pl. 15, fig. 26 [= *S. laciniatus* Lindström].

Neotype. Selected here, SGU 1402, a pygidium, from Alby 2, Rute parish, Slite Marl, Slite Beds, Pl. 27, fig. 10a-d. Angelin's original specimens cannot be located, and are considered lost (two cranidia and a pygidium were figured, locality given only as 'Gotland'). No other possible syntypes can be traced. The neotype, which agrees closely with Angelin's figure, is for diagnostic reasons a pygidium.

Material. At present all specimens from Slite Beds are referred to *S. scabridus*. Localities: Slite Beds, unit g: Follingbo parish—Stora Vede 1. Lokrume parish—drainage ditch near Lokrume (= Tomase 1?). Othem parish—Lännaberget 2; Samsugn. Slite Marl (including '*Pentamerus gothlandicus* beds'): Boge parish—Mojner 3; Tjälder. Bäl parish—Gane 2. Bunge parish—the beach at Fårösund; the beach 1 km south of Fårösund harbour. Dalhem parish—Nygårds 1. Eksta parish—Stora Karlsö. Eskelhem parish—drainage ditch south of the south farm at Valdarve. Fårö parish—Brajdaursvik 1; the beach NNW of Ryssnäs. Follingbo parish—Follingbo 6; Follingbo 7; Follingbo 8; the well near the borehole west of Rosendal. Hejdeby parish—Hajdungs 1. Hörsne parish—Bara 1. Othem parish—the beach at Slite; the beach by the shooting-range north of Länna. Roma parish—the large drainage ditch at Roma. Rute parish—Alby 2; the beach of Fardume träsk 225 m south of a in Fardume. Sanda parish—Valbytte 1; Valbytte 3; Valbytte 4; drainage ditch close to Klintehamn; drainage ditch 500 m WNW of L. Varbos. Västergarn parish—locality unknown.

Diagnosis. S3 and S2 very weak, S2 1.3 times as long (tr.) as S3. Occipital ring 0.6-0.7 times as wide (tr.) as widest part of glabella. Fixed cheek with about the same area as L1. Part of cheek between eye and posterior border furrow considerably longer (exsag.) than posterior border (in adult specimens). Posterior margin of cheek convex in large specimens, almost straight in small ones, where a small, blunt spine (Pl. 27, fig. 2c) is also present three-quarters of the way from axial furrow. Lateral border furrow deep in some specimens (Pl. 26, figs. 8, 13), shallow in others (Pl. 26, fig. 12). Palpebral furrow continuing anteriorly from eye parallel to facial suture until ending in a series of pits opposite L3.

Entire cephalon except doublure finely and densely granulated, granules almost in contact with each other, slightly coarser on anterolateral part of lateral border. Fixed cheek with a few scattered, irregular pits, area between axial furrow and anterior branch of facial suture with a few similar pits, free cheek with pits mainly beneath eye socle, sometimes also in lateral border furrow (Pl. 26, fig. 12).

Rostral plate (Pl. 26, fig. 6) with fine pitting anteromedially (on internal mould). Hypostome with anterior border at least on the lateral quarter, but possibly absent medially. Middle furrow very weak, reaching about one-quarter across middle body. Anterior wing small (Pl. 27, fig. 7 right side), cylindrical, blunt tip. Middle body and borders covered with very small granules.

Axis and pleurae of thoracic segments extremely finely and densely granulated.

Pygidium wide and short, width: length ratio 2.1-2.2: 1 (text-fig. 5A). Terminal piece short, inflated and rounded posteriorly with subhemispherical to pyramid-shaped termination. Remnants of a third inter-ring furrow present as deep notches laterally at midlength on terminal piece. Anterior pleural

ridge with a short but distinct, almost transverse pleural furrow midway between axial furrow and flexure. Pleural ridges rounded convex in profile. Interpleural furrows evenly rounded in section. Terminal piece and posterior pair of spines elevated considerably above plane of anterior and middle pleural ridges. Spines in shape of subsemicircular lobations of margin, occasionally short, broad and hook-like (Pl. 27, figs. 3, 5). Surface including doublure very densely and finely granulated.

Discussion. A few pygidia (Pl. 27, figs. 3, 5) from Slite Beds, unit g, show a rounded spinose margin, but are otherwise similar to the neotype. Also, at Valbytte 1 two types of free cheeks occur, with either a deep (Pl. 26, figs. 8, 13) or a shallow border furrow (Pl. 26, fig. 12). Whether these cases indicate dimorphism or two separate species is indeterminate at present.

Sphaerexochus latifrons Angelin, 1854

Plate 27, figs. 12-17; Plate 28, figs. 1-6

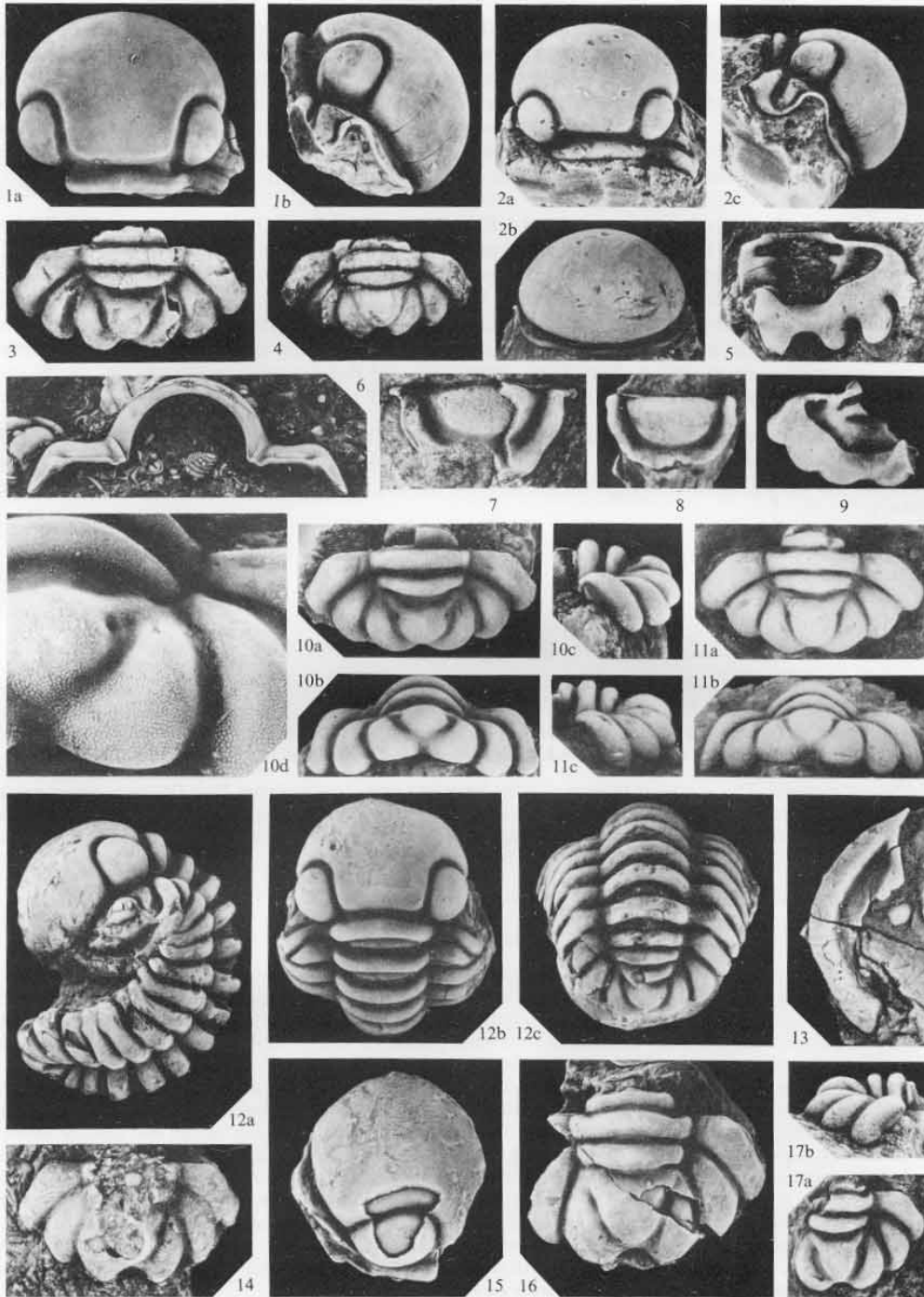
- v. 1851 Angelin, pl. 22, figs. 10 [illustration only, without name].
- *1854 *Sphaerexochus latifrons* Angelin, pp. 37, 75, pl. 38, fig. 15.
- v. 1885 *Sphaerexochus latifrons* Angelin; Lindström, pp. 46, 47, pl. 14, fig. 17.

Discussion. The cranidium (Ar30060) figured by Angelin in 1851 (and to which the 1854 description refers) is very fragmentary (Pl. 27, fig. 15), and only one of the features listed in the diagnosis below is preserved, the pointed anteroventral corner of L1. However, Angelin's (1854) illustration of the pygidium is distinctive, and the species has always been interpreted in accordance with this pygidium. Unfortunately, it cannot be located, and no locality was given. The alternative to referring material from strata presumably equivalent to those from which Angelin's cranidium came (stated by Lindström 1885, p. 47, to be from Östergarn [Hemse Beds]) to *S. latifrons* would be to consider the species a *nomen dubium*, and to erect a new species for the Hemse Beds material. Since material from this interval is rather variable, and it is possible that more than one species is present, the material is referred here as a whole to Angelin's species until further specimens are available for study. A lectotype (by necessity the 1851 cranidium) is not formally established here for the above reasons.

Material. All specimens are from the Hemse Marl of the Hemse Beds. Localities: Fardhem parish—Visne myrs kanal (may include Gerete 1). Hablingbo parish—drainage ditch west of Hablingbo railway station; Lukse 1; Petesvik. Havdhem parish—Kvinnegårde; Nissevik. Hemse parish—dump at Frigges 2 km north-east of Hemse; Likmide 1. Linde parish—Amlings 1; Rangsarve 1. Östergarn parish—unknown locality. Sproge parish—Eske 1; Snoder 1; Snoder 2.

EXPLANATION OF PLATE 27

- Figs. 1-11. *Sphaerexochus scabridus* Angelin, 1854. Slite Marl (1, 4, 6-11), Slite Beds, unit g (2, 3, ?5). Alby 2 (10), Follingbo 8 (6), Lännaberget 2 (2), Rosendal (1), Slite (3, 5), Valbytte 1 (4, 8, 9, 11), Valbytte 4 (7). 1a, b, SGU 1401, cranidium, dorsal and lateral views, $\times 1.5$. 2a-c, Ar51312, small cranidium, dorsal, anterior, and lateral views, note short genal spine, $\times 4$. 3, Ar51315, pygidium, spinose form, $\times 3$. 4, Ar51306, smallest known pygidium, $\times 6$. 5, Ar30187, pygidium, spinose form, ventral view, $\times 2$. 6, Ar51311, first thoracic segment, posterior view, $\times 2$. 7, Ar51309, hypostome, partly internal mould, $\times 3$. 8, Ar51308, hypostome, $\times 2$. 9, Ar51307, pygidium, ventral view, $\times 2$. 10a-d, neotype SGU 1402, pygidium, dorsal, posterior, lateral views and enlargement of granulation, note short transverse pleural furrow, a-c $\times 2$, d $\times 6$. 11a-c, Ar51305, small pygidium, dorsal, posterior, and lateral views, $\times 5$.
- Figs. 12-17. *Sphaerexochus latifrons* Angelin, 1854. All except fig. 15 from Hemse Marl, north-west part, Hemse Beds. 12a-c, Ar30067, complete exoskeleton, lateral view, cephalon, and pygidium, showing aberrant pygidial axis with three rings, Hablingbo, $\times 2$. 13, Ar51322, partial left free cheek, Eske 1, $\times 3$. 14, Ar51316, pygidium, morph A, Snoder 1, $\times 1.5$. 15, Ar30060, partial cranidium, ?Östergarn, figured Angelin 1851, pl. 22, fig. 10, $\times 1.5$. 16, Ar30063, pygidium, morph A, figured Lindström 1885, pl. 14, fig. 17, Visne myr, $\times 1.5$. 17a, b, Ar51324, pygidium, morph A, Likmide 1, $\times 2$.



RAMSKÖLD, *Sphaerexochus*

Diagnosis. S3 slightly shorter than S2 (tr.), both very faint. L1 with a rather pointed anteroventral corner. Occipital ring about 0.6 times as wide as maximum width of glabella. Fixed cheek with smaller area than L1. Part of cheek between eye and posterior border furrow as long (exsag.) as posterior border. Lateral border furrow deep. Palpebral furrow continues anteriorly from eye parallel to facial suture and ends opposite S3 in a series of pits. Surface sculpture with smaller and more widely spaced granules than in *S. scabridus*, so that the surface is dominated by smooth intergranule area. Fixed cheeks with a few pits, free cheek with pits beneath eye socle.

No granulation observed on thorax.

Pygidium with width:length ratio about 1.8:1, dimorphic. Morph A bulbous, morph B flatter. Morph A (Pl. 27, figs. 12, 14, 16, 17; Pl. 28, figs. 3–5) with a swollen terminal piece with blunt end, deep and wide interpleural furrows, swollen pleural ridges, and pleural spines forming subsemicircular lobes on margin. Morph B (Pl. 28, figs. 1, 6) with a subtriangular terminal piece with pointed end, narrow and shallow interpleural furrows, low, flat pleural ridges, and a very gently lobated margin. Both morphs have faint notches slightly anterior to midlength laterally on terminal piece, more pronounced on morph A. Very faint anterior pleural furrows may be present (Pl. 28, fig. 5). Surface with denser granulation than on cranidium, but still with granules clearly separate.

Discussion. This is a definite case of pygidial dimorphism. The morphs are found together, morph B less frequent. No dimorphism is observed in the cranidia. Some specimens, e.g. from Visne myr, differ in detail (Pl. 28, fig. 2) from the main bulk of the material, which is from Snoder 1 and 2 and from Eske 1.

Sphaerexochus laciniatus Lindström, 1885

Plate 28, figs. 7–17

v.* 1885 *Sphaerexochus laciniatus* Lindström, pp. 47, 48, pl. 13, figs. 2–6.

v. 1885 *Sphaerexochus scabridus* Angelin; Lindström, pl. 15, fig. 26, *non* Angelin, 1854.

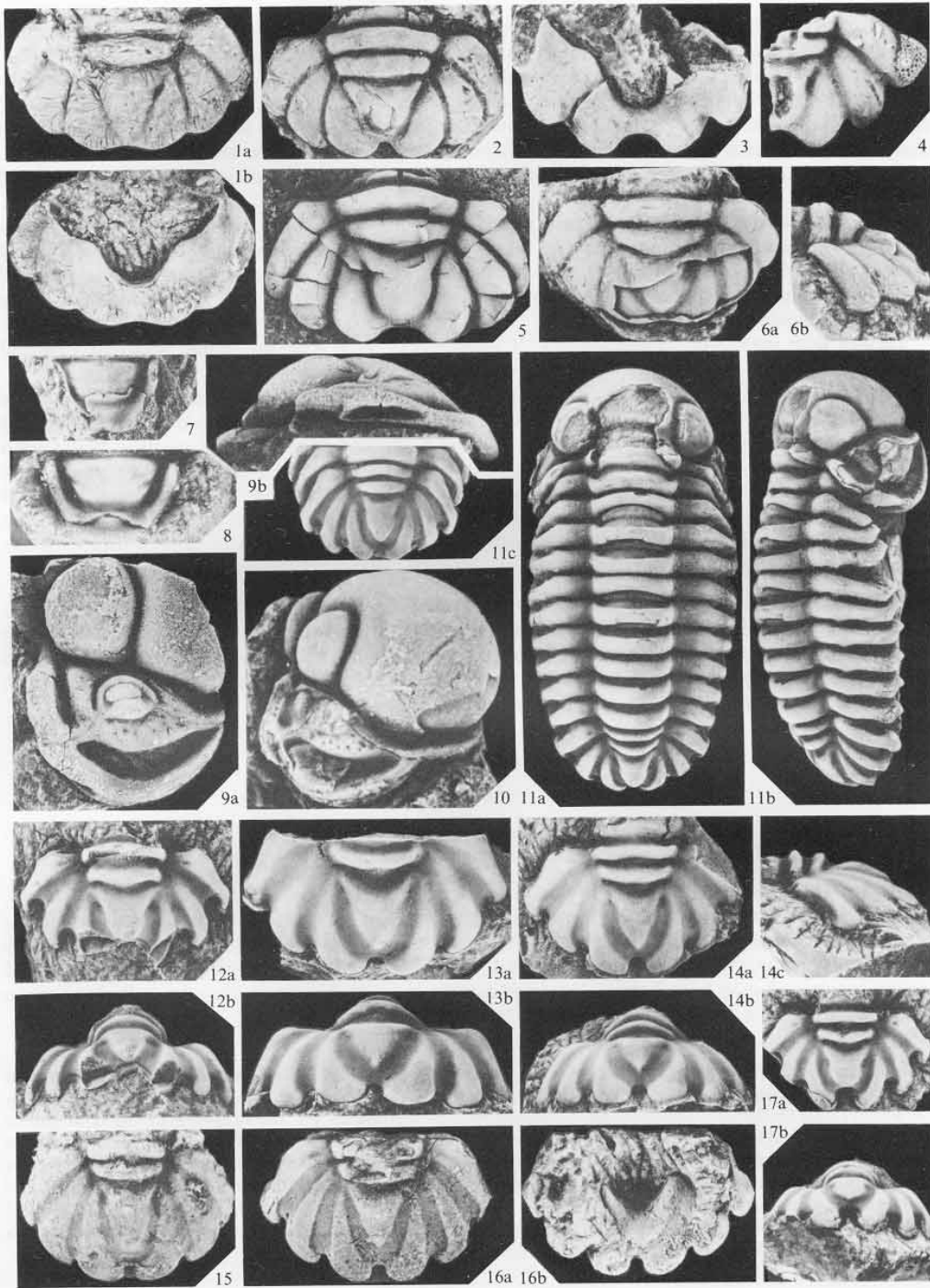
Lectotype. Selected here, Ar30072, complete exoskeleton, Pl. 28, fig. 11a–c; figured Lindström, 1885, pl. 13, figs. 2–6, stated by him to be from Kyrkviken, Fårö (Slite Marl), but this is questioned here, since material indistinguishable from this specimen occurs only in the Hemse Beds. The other material included in this species by Lindström is all from the Hemse Beds, but no specimens can be identified.

Additional material. This species is restricted to the limestone areas in the Hemse Beds (lower to upper part), where it is common in the south-western outcrops. Localities: Ardre parish—Ljugarn. Etelhem parish—Etelhem backar; Hageby träskbackar; Sigvalde 1; Tänglings hällar. Linde parish—Linde klint; Sandarve kulle. Lojsta parish—Tornklint; Asa träskbacke. Lye parish—Mannegårde.

EXPLANATION OF PLATE 28

Figs. 1–6. *Sphaerexochus latifrons* Angelin, 1854. Hemse Marl, north-west part, Hemse Beds. 1a, b, Ar51317, pygidium, morph B, dorsal and ventral views, Snoder 1, ×2. 2, Ar30065, pygidium, morph B?, Visne myr, ×2. 3, Ar51321, partial pygidium, morph A, ventral view, Eske 1, ×2. 4, Ar51320, partial pygidium, morph A, Eske 1, ×2. 5, SGU 1403, crushed and flattened pygidium, morph A, Amlings, ×2. 6a, b, Ar51318, pygidium, morph B, dorsal and lateral views, Snoder 1, ×2.

Figs. 7–17. *Sphaerexochus laciniatus* Lindström, 1885. Hemse Beds, middle to upper part. Linde Klint (8, 12–17), Sandarve kulle (7, 9, 10), unknown locality (11). 7, Ar30112, hypostome, partly internal mould, ×3. 8, Ar29831, hypostome, internal mould, ×3. 9a, b, Ar51325, partial cephalon, lateral and oblique ventral views, ×4. 10, Ar30059, cephalon, figured Lindström 1885, pl. 15, fig. 26, ×4. 11a–c lectotype Ar30072, complete exoskeleton, dorsal, lateral views, and pygidium, morph A, figured Lindström, 1885, pl. 15, figs. 2–6, ×2. 12a, b, Ar29857, pygidium, morph A, internal mould, dorsal and posterior views, ×2. 13a, b, Ar29860, pygidium, morph B, internal mould, dorsal and posterior views, ×2. 14a–c, Ar29858, pygidium, morph B, internal mould, dorsal, posterior, and lateral views, ×2. 15, Ar29866, pygidium, morph B, ×2. 16a, b, Ar29882, pygidium, morph B, dorsal and ventral views, ×2. 17a, b, Ar29862, pygidium, morph A, internal mould, dorsal and posterior views, ×2.



RAMSKÖLD, *Sphaerexochus*

Diagnosis. S3 and S2 indicated only by break in granulation, S2 1.5 times as long (tr.) as S3. Occipital ring about 0.6 times as wide as maximum width of glabella. Fixed cheek with smaller area than L1. Part of cheek between eye and posterior border furrow slightly longer or equal in length (exsag.) to posterior border. Lateral border narrow. Lateral border furrow deep and fairly wide. Palpebral furrow and rim short (exsag.), ending opposite S2, with one or two pits anterior to this. Cranidium and free cheeks with fine and dense granulation, intermediate in size and density, closer to *S. scabridus* than to *S. latifrons*. Fixed cheek with very few pits, cheek beneath eye with sparse, scattered pits.

Hypostome with very short (sag., exsag.) anterior border, and distinct, continuous anterior border furrow. Middle furrow distinct laterally, fading out one-quarter across middle body (on internal mould). Posterior border with elevated crescent-shaped central area, posterior margin notched medially. Preserved parts of middle body and lateral borders (Pl. 28, fig. 7) with fine and dense granulation, posterior border smooth.

Thorax with maximum pleural length (tr.) reached in sixth segment. Faint, short (tr.) pleural furrows on all segments midway between axial furrow and flexure.

Pygidium long and narrow, dimorphic, width:length ratio 1.6–1.8:1 depending on morph. Axis long and very narrow. Pleural ridges and interpleural furrows angular and sharply delimited. Short (tr.) pleural furrow on anterior pleural ridge. Morph A (Pl. 28, figs. 11, 12, 17) relatively wider, with inflated, elevated, blunt terminal piece, very deep interpleural furrows and pleural ridges that are gently convex in section, ending in fairly long, hooked spines, separated by wide furcations. Morph B (Pl. 28, figs. 13–16) with flat, pointed terminal piece, very shallow interpleural furrows, and flat pleural ridges that end in short, gently hooked spines, separated by narrow furcations. Both morphs with notches anterior to midlength laterally on terminal piece.

Discussion. As with *S. latifrons*, there is no doubt that this species exhibits pygidial dimorphism. More than fifty pygidia have been studied, and the two morphs occur together. A is more common than B. The peculiar shape of the very sharply delimited pleural ridges and interpleural furrows, as well as general proportions and the hooked spines, are shared by the spine-bearing specimens in *S. dimorphus* Perry and Chatterton, 1977, but not by the non-spinose ones.

Sphaerexochus spp.

(Not figured)

Material. Ar29928–29931, three pygidia and a glabella, stated to be from the Lower Visby Marl, 'Visby'; Ar30079–30080, a pygidium and a cranidium, stated to be from Högklint Beds, 'Visby'.

Remarks. These specimens are all poorly preserved. Most pygidia are indistinguishable from *S. scabridus*, and it is not improbable that the horizons given on the nineteenth-century museum labels are wrong, since reference to 'Visby' at that time could indicate a locality quite far from Visby. This supposition is supported by the fact that most of the specimens are water-worn, and were thus found on the beach, and may have been transported quite a distance. However, they are included here to indicate the possible stratigraphical range of the genus on Gotland.

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Note added in proof. Since the completion of the paper, I have collected additional cheirurid material on Gotland. *Deiphon sphaericum* sp. nov. occurs in Höglint Beds, unit a, at Ireviken 1, Stenkumla parish, which confirms the stratigraphical position suggested in text-fig. 1. From the upper Eke Beds at Lau backar 1, Lau parish, there are a few cheirurid crania and hypostomes that can be assigned almost certainly to *Ktenoura conformis*, and the vertical range of this species is thus extended downward.