SILURIAN CALYMENID TRILOBITES FROM UNITED STATES, NORWAY, AND SWEDEN

by H. B. WHITTINGTON

ABSTRACT. The type species of *Papillicalymene* and *Liocalymene* are redescribed from type and other material; each represents a distinct morphological type. *Papillicalymene* is known from rocks of Lower Ludlow age in Gotland and Podolia, *Liocalymene* from late Llandovery strata in central and eastern United States. The type specimen of *Calymene breviceps*, Waldron Shale, Indiana, is redescribed and specimens of *Calymene* from the Brownsport Formation, Tennessee, and Ludlow age rocks in Norway briefly discussed. The species *celebra* from the Racine Dolomite, Illinois, is redescribed and referred to *Flexicalymene*. The phylogeny of early Ordovician to Devonian calymenids is considered, on the assumption that Shirley's two groups, one with, the other without, the papillate-buttress structure constitute separate evolutionary stocks. The pattern of evolution is like that in other trilobite families, showing widespread long-ranging genera from which short-ranging forms are derived at different times and in different areas. Morphological characters appear in differing combinations in each of the main stocks; the adaptive value of particular characters is difficult to assess.

IN 1916 Raymond discussed four species of Silurian calymenids from the United States, illustrating two of them but giving no new figures of the species on which he based his new genus *Liocalymene*. Among the genera erected by Shirley (1936) was *Papillicalymene*, the type species being *Calymene papillata* Lindström, 1885, a species which neither Shirley nor any subsequent author has redescribed. Thus in preparing an account of calymenids for the *Treatise on Invertebrate Paleontology*, I gave only brief diagnoses of these two genera and no new illustrations. The present redescriptions are intended to remedy this deficiency, though the available samples of each species are small, they do not reveal all details of morphology, and some specimens are not precisely localized. Nevertheless, in the characters revealed these two type species are morphologically quite distinct, and each is limited in stratigraphical and geographical range, so that their recognition as genera appears valid and useful. Exceptionally well-preserved material of two additional species of Raymond (1916) is also described here, one referred to *Calymene*, the other here placed in *Flexicalymene*, the latter genus better known from Ordovician rocks. I have attempted a partial sketch of calymenid phylogeny, and discussed taxonomic characters and their value in particular genera. It is clear that a revision of Silurian species is critical to further understanding of relationships and descent in this family.

Terminology of description follows the *Treatise of Invertebrate Paleontology* (Moore, 1959, pp. **O**117–**O**126), except that here glabella includes the occipital ring and I have preferred to use 'cheek' and 'branch' of the facial suture. The term 'anterior border' is used, and is synonymous with 'preglabellar field' of Shirley (1936). I have adopted Campbell's (1967, text-fig. 4) terms 'border sector' and 'doublure sector' for the two parts of the rostral plate which are separated by a sharp flexure. I have considered the vertical plane to be parallel to the posterior margin of the occipital or axial ring; use of 'upward' or 'downward' is with reference to this plane. I have subdivided the Ordovician System into Lower and Upper (Whittington, 1966, table 1).

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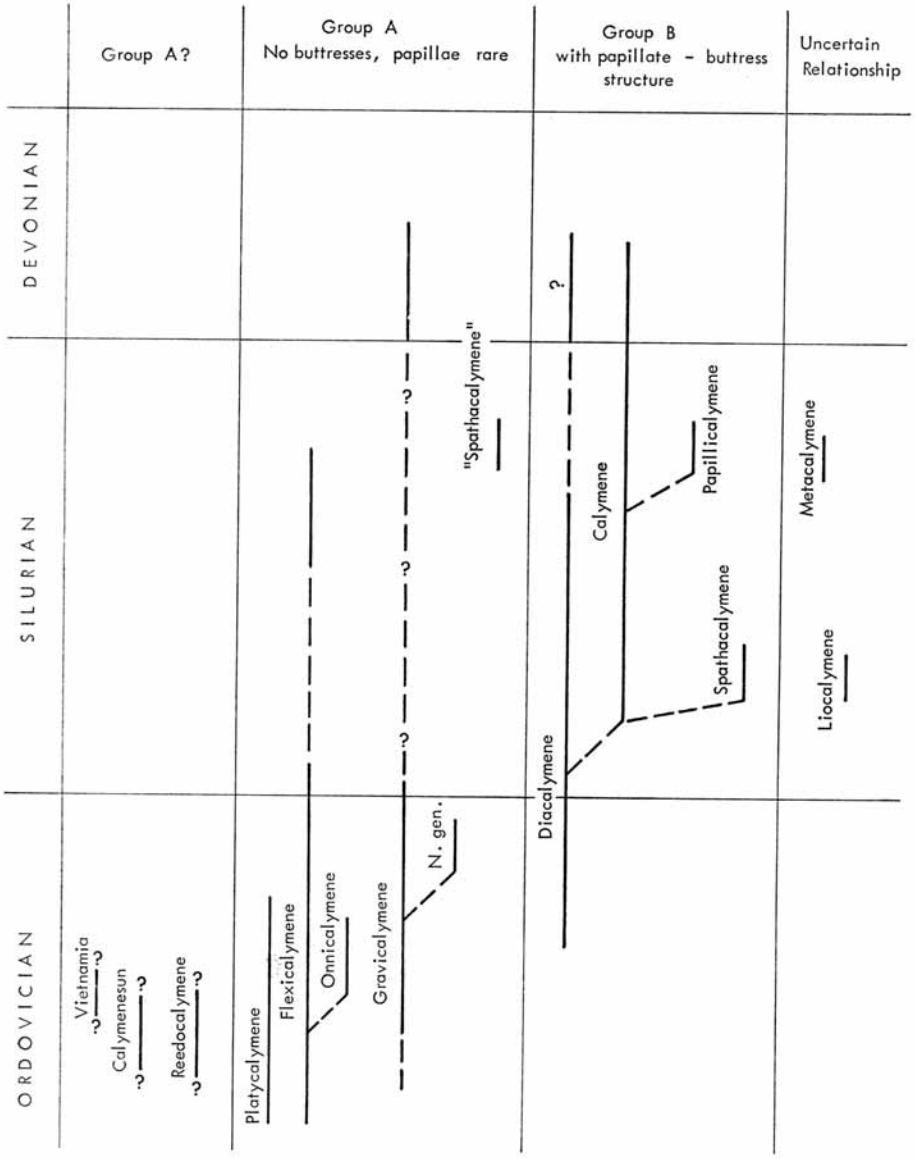
TAXONOMIC CHARACTERS AND EVOLUTION OF CALYMENIDAE

An outline sketch of phylogeny and geographical distribution of Ordovician calymenids has been given (Whittington 1966, pp. 716, 726, text-fig. 12). In that account I included *Neseuretus* and *Pharostoma* as calymenids, but Dean (1966, pp. 297–298) has advocated placing each of these genera in separate families, admitting that the use of this category rather than subfamily is somewhat arbitrary. Here I put this question aside and discuss only calymenid trilobites of post-Arenig age and their relationships (text-fig. 1). I have omitted the recently proposed Devonian taxon *Paracalymene* Pillet 1968, regarding it as of doubtful validity, and *Protocalymene* Ross 1967*a*, because of the difficulty of determining the systematic position of the small specimens on which it is based.

Flexicalymene appears in Britain in the lower Llanvirn (Hughes 1969, pp. 81–83, pl. 8, fig. 7; pl. 9, figs. 1, 2, 4, 7, 8) and in North America and Scandinavia in about mid-Caradoc time. As shown below, this genus is widespread in the Upper Ordovician and appears to be present in the middle Silurian. *Gravicalymene* (not figured in my 1966 diagram) appears in Britain at the base of the Upper Ordovician (if not earlier, Dean 1963, pp. 226–227), in North America in the mid-Caradoc (Ross 1967*b*), and is widespread geographically later in the Ordovician. Species referred to this genus are also widespread in the Lower Devonian (see discussion of *F. celebra*). These two genera, as well as several other Ordovician genera, belong within Shirley's (1936, p. 394) group A which lacks papillate glabellar lobes or buttresses on the fixed cheeks. In such genera (Pl. 87, fig. 5; Evitt and Whittington 1953, pl. 10, fig. 1; Ross 1967*b*, pls. 3–5) the axial furrow is a deep open, steep-walled trench between cheek and glabellar lobes, the furrow narrowest and the walls steepest beside lateral glabellar lobe 1p. The eye ridge may be faintly developed as a broad, low ridge directed forward and inward from the eye lobe across the cheek and down the abaxial wall of the axial furrow, dying out at the base of the furrow (Evitt and Whittington 1953, pl. 10, fig. 1). Shirley's (1936, p. 395) group B has lateral glabellar lobe 2p papillate, with a buttress projecting from the cheek (i.e. from the abaxial wall of the axial furrow) to meet it (Pl. 83, fig. 7; Pl. 84, fig. 2). The papillate-buttress structure juts out over the axial furrow, which passes beneath it as a tunnel. Additional papillae and buttresses may be developed in front of the 2p pair, the structures not in all cases being paired, and even if so, not necessarily being in contact at their extremities. Plate 84, figs. 4, 5, illustrate incipient buttressing without corresponding papillae in *Calymene*. Plate 84, figs. 8, 9; Plate 85, figs. 4–6, 10, 11, illustrate the papillate-buttress structure at its maximum known development, and show that these structures jut out over the axial furrow. The latter may be filled with matrix (Pl. 84, fig. 9), but when partially freed of matrix by weathering (Pl. 86, figs. 1, 3, 7, 8, 11, etc.)



TEXT-FIG. 1. Stratigraphical range (Ordovician to Lower Devonian) of calymenid genera and suggested relationships. See text for discussion.

shows the structures clearly. Schrank (1970, pp. 116, 121, 124, 127, 130; pl. 1, fig. 5; pl. 4, fig. 1; pl. 6, figs. 3–5) has shown that the papillate-buttress structure is not present in the meraspid stages of certain species of *Calymene*, but appears later in development. In *Liocalymene clintoni* (Pl. 89, figs. 6, 7, 10, 12) the axial furrow is exceedingly narrow, so that the truncate edge of lateral lobes 2p and 3p, and the frontal glabellar lobe, are close to the cheek; the papillate-buttress structure does not appear to be developed, so that it cannot be placed in either group A or group B.

The earliest known genus of group B, which has lateral glabellar lobe 2p papillate and a corresponding buttress, is *Diacalymene*. This genus appeared in the late Caradoc in Britain (Dean 1962, p. 116) and became widespread geographically in the late Ordovician to Middle Silurian; if the species *kockbaitalensis* Maximova, 1967 (p. 780, pl. 2, fig. 3; 1968, pp. 52–53, pl. 8, figs. 1–7) represents this genus it ranges into the Lower Devonian. It was Shirley's (1936, p. 401) contention that his two groups were separate evolutionary stocks. This would imply that *Calymene* (early Silurian to Middle Devonian), *Papillicalymene* (lower Ludlow), and *Spathacalymene* Tillman 1960 (late Llandovery in age) were derived from *Diacalymene*. If it is accepted that the presence or absence of the papillate-buttress structure at lateral glabellar lobe 2p is a taxonomic character of suprageneric rank, then relationships may be suggested as in text-fig. 1. The Asian Ordovician genera *Calymenesun* Kobayashi 1951, *Reedocalymene* Kobayashi 1951, and *Vietnamia* Kobayashi 1960, appear to lack papillae or buttresses, but this needs confirmation. Other genera are discussed below.

Shirley (1936) also used the nature of the anterior border as an important character, and it has been used as next in rank, at the genus level. The anterior border is variable in width (sag. and exs.), may be flat and upsloping, or curved convexly upward from gently to strongly, or prolonged forward as a spine or spatulate process. Schrank (1970, pp. 115–116) has used the form of the anterior border as the principal character in delineating species groups within the genus *Calymene*. Dean (1962, pp. 112–113) has used the position of the eye lobe (relatively far back in a group of Upper Ordovician species) to distinguish his genus *Onnicalymene* from *Flexicalymene*. The hypostome has been little used, but while there is a general family resemblance, for example that of *Flexicalymene* (see below) is distinct in outline from the *Calymene* type (Haas 1968, text-fig. 16*b*, *d*, *f*; Schrank 1970, pl. 2, fig. 7) which has the raised area on the anterior lobe of the middle body. *Diacalymene* and *Papillicalymene*, presumed to be related to *Calymene*, have a similar type of hypostome with the raised area on the middle body. The hypostome of *Platycalymene* (Hughes 1969, pl. 10, figs. 7, 8) has a broad (sag. and exs.) anterior border, in outline and lack of raised area on middle body like that of its presumed relative *Flexicalymene*. Thus certain taxonomic characters of the hypostome may prove to be of value both in generic and in higher subdivisions such as Shirley's groups A and B.

Other morphological characters in calymenids appear at different times in apparently distinct stocks, for example:

(i) a new late Ordovician genus (Whittington 1971) is based on a species which shows papillation on the frontal glabellar lobe only, and no genal buttress to lateral lobes 1–3p. It thus presumably belongs in group A, in which papillation is otherwise not known;

(ii) inflation of the distal part of the axial rings is developed in *Flexicalymene* (Pl. 88, fig. 7), group A, and *Calymene* (Pl. 84, fig. 3), group B;

(iii) smooth outer part of the pleural region of the pygidium is seen in *Spathacalymene*, group B, and in *Flexicalymene celebra* (Pl. 87, figs. 9, 13), group A;

(iv) elongation of the anterior border to form a spine or spatulate projection is known in the Ordovician genera *Calymenesun*, *Reedocalymene*, and *Vietnamia*, and in the Silurian *Spathacalymene*, group B. An intriguing problem arises in connection with Tomczykowa's (1970) description of three new species from the Lower Ludlow of Poland, which she attributes to *Spathacalymene*. As she recognizes, however, these species do not show the papillate-buttress structure at lateral lobe 2p, and I consider the small ridge in the axial furrow opposite lateral furrow 3p that she describes (1970, p. 73) to represent the eye ridge, and not to be the buttress. Thus these Polish species, and others she refers to, may not belong in *Spathacalymene*, but represent a separate genus which should be placed in group A.

If the presence or absence of the papillate buttress structure is used as a suprageneric character, then application of Shirley's (1936) generic names depends primarily on the form of the anterior border. The differences in form are subtle, and must be seen on the external surface of the exoskeleton, and not only on the internal mould. Difficulties have arisen which have led to my (1954, p. 148; *in* Moore 1959, p. **O**452) rejection of *Reacalymene* as being of generic rank, to problems in the choice of *Gravicalymene* or *Flexicalymene* as the appropriate taxon for the species *celebra* (see below), and to questioning the distinction between *Platycalymene* and *Flexicalymene* (Hughes 1969, p. 84). Further study is needed to establish the value of some of the characters referred to above, and to determine new characters, so that genera may be based on a combination of several characters.

If the relationships outlined above are accepted, certain genera are long-ranging, and each includes a variety of species scattered over a wide geographical area. Such genera are, in group A, *Flexicalymene* and *Gravicalymene*, in group B, *Diacalymene* and *Calymene*. Other genera are based upon a new character or combination of characters, and include a single species which has a restricted geographical and stratigraphical range. Examples in the Silurian are *Liocalymene* and *Metacalymene* (from the Lower Ludlow Kopanina Formation of the Prague district, Czechoslovakia), and the characters they display make it difficult to suggest their derivation. *Spathacalymene* is a further example, but the presence of the papillate-buttress structure at lateral lobe 2p, and other characters, suggest a derivation from *Calymene*. The pattern of evolution displayed by calymenids is thus like that in the unrelated odontopleurids (Whittington, 1956, pp. 187–191), and shows a similar shuffling and recombination of characters in the evolving plexus.

The papillate-buttress structure is present in a wide variety of species dominantly of Silurian and early Devonian age, and is not obviously of adaptive value. It thus appears to be a suitable character to be given heavy weighting in classification. On the other hand modifications of the anterior border, and particularly the development of the snout or spine-like elongation, may well be adaptive in nature, presumably connected with balance in swimming or stability when resting on the sea bottom. Such characters should be given less weight in classification and are suitable to use at the generic or lower levels. Shirley (1936, pp. 393–394) commented on the homeomorphy between species of *Platycalymene* and *Metacalymene*, species which are widely separated in space and time. It may be assumed that this homeomorphy reflects adaptation, but Hughes (1969, p. 84)

notes that *Platycalymene* is restricted to a shaly facies, whereas the type species of *Metacalymene* is preserved in a coarse calcarenite. We are far from understanding adaptive and non-adaptive characters in trilobites, so that weighting of characters is inevitably empirical. Shirley's classification has proved useful and cannot yet be improved upon.

SYSTEMATIC PALAEONTOLOGY

Family CALYMENIDAE Burmeister, 1843
Genus CALYMENE Brongniart, 1822

Type species. C. blumenbachii Brongniart, 1822.

Discussion. Campbell (1967, pp. 24–28, pls. 9–11, text-figs. 4, 5) has made *Calymene clavicula*, from the Henryhouse Formation (late Wenlock to early Ludlow), Oklahoma, the best-known species of the genus. He distinguishes it from the similar species *C. niagarensis* and *C. breviceps*, which are of about the same age, and remarks that *C. celebra* may not belong in this genus since it lacks the buttress at lateral glabellar lobe 2p. A comprehensive re-study of Silurian calymenids is needed, here I comment on new and old material of these latter two species, and on *Calymene* sp. ind. from the Ludlow of Norway.

Calymene breviceps Raymond 1916

Plate 83, figs. 1–5

1916 *Calymene breviceps* Raymond, pp. 27–28, pl. 3, fig. 11.
1967 *Calymene breviceps* Raymond; Campbell, pp. 27–28.
1970 *Calymene breviceps* Raymond; Schrank, pp. 116, 132.

Holotype. MCZ 640, original of Raymond 1916, pp. 27–28, pl. 3, fig. 11, from the Waldron Shale (high Wenlock age), Waldron, Indiana.

Discussion. The type specimen is weathered and damaged, so that the external surface is poorly preserved. There are three lateral glabellar lobes, lobe 2p being buttressed from the fixed cheek, and the frontal lobe is relatively long, sloping vertically down to the shallow preglabellar furrow. There is an ill-defined supplementary lobe adjacent to the backward-curving, inner end of lateral furrow 1p. Distinctive of this species is the short (sag. and exs.) anterior border which, as seen in profile, is scarcely raised above the preglabellar furrow and descends steeply anteriorly. It appears, however, that the anterior border, as well as the antero-lateral borders, have been damaged by scraping, and the original shape may have been slightly more inflated. The course of each branch of the dorsal facial suture can be observed, and the rostral suture appears to run along the vertical anterior slope of the anterior border. The 13 thoracic segments show the

EXPLANATION OF PLATE 83

Figs. 1–5. *Calymene breviceps* Raymond, 1916. Holotype, extended exoskeleton, MCZ 640, original of Raymond 1916, pl. 3, fig. 11, Waldron Shale, Waldron, Indiana. Dorsal, right lateral, posterodorsal, anterodorsal views, ×1·5; part of pygidium to show external surface, ×6.

Figs. 6–8. *Calymene* cf. *breviceps* Raymond 1916. Partially enrolled exoskeleton, Brownsport Formation, south side U.S. highway 64, 4½ miles east of junction with Tennessee highway 69, east part of Savannah, Tennessee; USNM 154497. 6, 8, right lateral, anterior views, ×2; 7, dorsal view of cephalon, ×3.

convex axial rings, each of which has a small, convex lateral inflation, the pleurae with deep pleural furrows, convex posterior bands and large facets. The pygidial axis has 7 rings, the 7th defined only in the median region, between the partly effaced 6th and 7th ring furrows which do not reach the axial furrows. The tip of the axis, behind the 7th ring furrow, is inflated. There are 5 pleural furrows, the ribs between them not impressed by interpleural furrows. Scattered, irregularly placed tubercles are poorly preserved on the glabella and fixed cheeks, and on the pygidium granulation extends over the axial rings, tip of axis, pleural ribs, and border.

Schrank (1970, pp. 132–133, pl. 6, figs. 6, 7; pl. 7, figs. 1, 2) has redescribed material from the upper Wenlock of Gotland and from glacial boulders of *Calymene tuberculosa* Dalman 1827, and following Lindström's (1885, p. 66) suggestion, placed *C. breviceps* in synonomy. Comparison of the present illustrations with those of Schrank shows that in *C. breviceps* the glabella is relatively longer (sag.) and more inflated, that lobe 2p is, relative to lobe 1p, much smaller, and that the anterior border is shorter (sag. and exs.) after allowing for damage to the holotype. More material is required to define *C. breviceps* adequately, meanwhile I regard it as a species distinct from *C. tuberculosa*.

Calymenids from the Brownsport Formation, Tennessee, also of late Wenlock age, include *C. clavicula* Campbell (1967, p. 24) and a different form of which one well-preserved individual is here illustrated (Pl. 83, figs. 6–8; Pl. 84, figs. 2, 3). Similar specimens to the latter also come from 0·4 miles north of Tennessee highway 114, half mile north 26° east of Channel Cemetery, centre subquadrangle of Bath Springs quadrangle, western Tennessee. These specimens, here referred to *C.* cf. *breviceps*, come from different localities in the Brownsport Formation to those from which Campbell records *C. clavicula*. The specimen referred to *C.* cf. *breviceps* differs from the holotype of *C. breviceps* in the larger lateral glabellar lobe 1p, so that the maximum glabellar width is equal to the length (sag.), rather than considerably less in the type specimen of *C. breviceps*. Other differences include the apparently slightly longer (sag. and exs.) and higher anterior border, the wider axial furrow, smaller eye lobe, more complete 6th and 7th ring furrows on the pygidial axis, and presence of interpleural furrows on the five ribs. External surfaces are difficult to compare, but the tubercles on the glabella and cheeks may be smaller in the Tennessee specimen. It may well be that the latter represents a distinct species of *breviceps* type, but until individual variation in populations is known one cannot decide. The Tennessee specimen shows well the nature of the axial furrow on the cephalon, widening beside lateral lobe 1p, flat bottomed and steep-walled, in front of here wide and deep, bridged by the buttress to lobe 2p. *C.* cf. *breviceps* differs from *C. clavicula* most obviously in the relatively greater glabellar width across the 1p lobes, the smaller eye lobe, broader, shallower border furrows, and less coarse tuberculation of the cephalon.

Calymene sp. ind.

Plate 84, figs. 1, 4–6

Material. PMO 49987, incomplete cranidium and incomplete displaced free cheek, exoskeleton partially broken away, division 9c (Lower Ludlow), Langö, Holmestrand, Norway. Coll. J. Kjaer, 1901.

Discussion. The cranidium appears typical of *Calymene*, the glabella bell-shaped in outline, having 3 pairs of lateral lobes, lobe 2p buttressed. The lateral lobes are inflated, and set off by this inflation and shallow furrows from the median glabellar lobe. There

is a low, ill-defined inflation ('supplementary lobe') beside the inner edge of lateral furrow 1p, where it curves inward and backward to define lobe 1p; a faint inflation in the corresponding position beside furrow 2p. The axial furrow cannot be completely cleaned of matrix without damage to the adjacent walls of glabella and cheek. It is deep, steep-walled and broad beside lateral lobe 1p, bridged by the buttress at lobe 2p, and in front of here the walls are less steep. Immediately in front of buttress 2p the wall of the axial furrow on the outer side is excavated in a deep, rounded notch, at the upper, anterior edge of the notch the wall of the cheek projects slightly over the axial furrow, forming an incipient buttress. This deep notch is opposite the most anterior part of lateral lobe 2p and the adjacent part of furrow 2p; the incipient buttress is directed toward lateral lobe 3p. Two additional extremely shallow notches are visible in the cheek wall of the axial furrow, one opposite lateral furrow 3p, the other opposite the mid-length of the frontal glabellar lobe. Latter slopes vertically to the deep preglabellar furrow, anterior border convex, rolled, rising only a short distance above the preglabellar furrow and having a long (sag. and exs.) frontal slope down to the rostral suture. The exoskeleton is partially stripped from the anterior border (Pl. 84, figs. 5, 6), so that the left lateral view (Pl. 84, fig. 1) gives a false impression of the profile, making the anterior border appear lower and shorter (sag.) than the original form of the external surface. The posterior part of the left fixed cheek is bent forward, and the course of the posterior branch of the suture thus distorted; the true course of each branch of the dorsal suture is shown on the right side. The external surface, except in the furrows, bears a granulation and scattered tubercles. On the mould of the internal surface of the exoskeleton (exposed on part of the frontomedian glabellar lobe and the anterior border) are scattered, shallow depressions, in the centre of each there is a depressed ring. This ring may be the impression of the inner end of a canal through the exoskeleton; the outer end is at the summit of a tubercle. The tubercles are worn, but under alcohol some show a ring at the summit. The mould of the internal surface of the glabellar also shows, between the depressions and rings, very fine pits, that of the anterior border, granules. The mould of the internal surface of the posterior part of the fixed cheek shows a reticulate pattern of low ridges.

Genus PAPILLICALYMENE Shirley 1936

Type species. Calymmene papillata Lindström 1885.

Diagnosis. Glabella bell-shaped in outline, axial furrow narrow beside lateral lobe 1p, wide and deep in front of this point; three pairs of lateral lobes, lobes 2p, 3p, and

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EXPLANATION OF PLATE 84

Figs. 1, 4–6. *Calymene* sp. ind. Incomplete cranidium, displaced right free cheek, exoskeleton partially exfoliated; PMO 49987, Lower Ludlow, Langö, Holmestrand, Norway. Left lateral, dorsal, antero-lateral, anterior views, ×2.

Figs. 2, 3. *Calymene* cf. *breviceps* Raymond, 1916. USNM 154497 (see explanation of Plate 83, figs. 6–8). 2, antero-lateral view of cephalon, ×4·5. 3, dorsal view of thorax, ×2.

Figs. 7–9. *Papillicalymene papillata* (Lindström 1885). Holotype, incomplete enrolled exoskeleton, partially exfoliated, Ar 6209, original of Lindström, 1885, p. 74, fig., Visby, Gotland. Left lateral, anterior of cephalon, ×2; dorsal view of glabella, ×3. *a*, indicates mould of posterior (inner) slope of anterior border; *b*, indicates mould of lower surface of buttresses 2p and 3p.

antero-lateral angle of frontal glabellar lobe papillate; genal buttresses to lateral lobes 2p and 3p. Anterior border rises vertically from preglabellar furrow, curves in the dorsal direction adjacent to frontal slope of glabella, then curves over to descend vertically, so that border is a short (sag. and exs.), high, recurved ridge; laterally it descends steeply to merge with antero-lateral border. Transverse line joining midpoints of palpebral lobes traverses anterior half of lateral lobe 2p. Inner, anterior corner of fixed cheek may be developed as a small 4p buttress. Hypostome may have low median swelling on external surface of anterior lobe of middle body.

Pleural furrows of pygidium are deepest distally and do not extend on to outer part of pleural region; shallow interpleural furrows extend on to this outer part. External surface of anterior border, cheek and outer parts of pleural regions granulate, on glabella a few low, scattered tubercles, axis (except at posterior tip) and inner parts of pleural regions apparently smooth.

Stratigraphical and geographical range. Lower Ludlow (Elton to Leintwardine stages), Gotland; Beyrichienkalk (Downton) glacial boulders, north Germany; Ludlow of Podolia.

Discussion. The diagnosis is intended to be read in conjunction with my (*in* Moore 1959, pp. **O**450–**O**451) diagnosis of the family, lines two to four of which should read 'widest across occipital ring or pre-occipital (i.e. 1p) lateral lobes; may or may not project in front of genae'. Comparison of the present, and Campbell's (1967) descriptions of species of *Calymene* with those given below will show how similar in morphology are these species to species of *Papillicalymene*. This similarity is not only general, but extends to details such as the form of the hypostome, cephalic borders and doublure, including the rostral plate, and the structures facilitating articulation (processes, facets and nature of the stop on the outer part of the doublure of the segments). However, the presence of the 3p papilla and buttress, the papilla at the antero-lateral corner of the frontal lobe, the narrow axial furrow adjacent to the lobe 1p, and its expansion in front of here, and the strongly upcurved anterior border distinguish species of *Papillicalymene*. Species of *Calymene* like *C. clavicula* and those described above are widespread in rocks of Wenlock and Ludlow age, and are characterized by the short (sag. and exs.), low ridge of the anterior border. A second group of species also of Wenlock to Ludlow age is characterized by a longer (sag. and exs.), more gently upsloping anterior border. This group includes *Calymene nodulosa* Shirley 1933, *C. pompeckji* Kummerow 1928 (= *C. neointermedia* R. and E. Richter 1954; see Schrank 1970, pp. 120–123, pl. 1, figs. 4–6; pl. 2, figs. 1–3, 7), *C. arotia* Haas 1968, etc. These two groups are Schrank's (1970, pp. 115–116) species groups 4 and 2 respectively, and that author distinguishes four other species groups mainly on the characters of the anterior border. Species of these groups of *Calymene*, exhibiting the 2p papilla and buttress, deep, trench-like axial furrow beside lateral lobe 1p and rounded frontal glabellar lobe, are known in rocks of Llandovery (Shirley 1936) to Lower Devonian age. In the Lower Devonian species *C. interjecta* (Pillet 1968, pl. D, fig. 5) there is the beginning of the development of buttress 3p, and an extremely shallow notch between buttresses 2p and 3p. In this species the inner, anterior angle of the fixed cheek is apparently sharp, suggesting the development of a buttress. In the Norwegian *Calymene* sp. ind. described above there is a faint buttress 3p separated by a deep notch from buttress 2p, and a faint buttress 4p as well as a slight projection at the inner anterior angle of the fixed cheek. Thus in certain Silurian and

Devonian species of *Calymene* the beginning of buttressing additional to that of 2p is seen, but never completely developed as in *Papillicalymene*, and not combined with papillation of the frontal glabellar lobe and the narrow axial furrow beside 1p. It seems reasonable to suggest, on account of the similarities between species of the two genera, that *Papillicalymene* is derived from *Calymene*.

Papillicalymene papillata (Lindström 1885)

Plate 84, figs. 7–9; Plate 85, figs. 1–14; Plate 86, figs. 1–4, 6

1885 *Calymmene papillata* Lindström, pp. 73–74, fig.
1933 *Calymene papillata*, Lindström; Shirley, pp. 63–64.
1936 *Papillicalymene papillata* (Lindström); Shirley, p. 396, fig. 1.
1959 *Papillicalymene papillata* (Lindström); Whittington *in* Moore, p. **O**452.
1970 *Papillicalymene moa* Schrank, pp. 141–142, pl. 12, figs. 5, 5*a*.
1971 *Papillicalymene papillata* (Lindström); Whittington, p. 131, fig. 1 *g*, *h* (*non* fig. 1 *e*, *f*).

Holotype. Ar 6209, partially enrolled incomplete individual with exoskeleton, Visby, Gotland.

Other material. Ar 6223, partially enrolled individual, exoskeleton weathered, Hablingbo, Gotland. Ar 27195, internal mould of cranidium, Östergarn, Jutenviks åker, Gotland. Ar 27196, pygidium and four segments, with exoskeleton. Ar 27197, internal mould of pygidium, Östergarn, Gotland. Ar 27198, internal mould of pygidium, 27199, incomplete enrolled individual with exoskeleton, Östergarn, Hammarn, Gotland. Ar 27201, incomplete weathered individual, Östergarnsholm, Gotland.

Geological horizon. Hemse Beds of early Ludlow age (Martinsson 1967, fig, 2). Lindström (1885, p. 94) records this species from shales of Wenlock age, while Hede (1921, p. 99; 1960) does not record it. The holotype is from 'Visby' a locality which suggests that it may have come from the Lower or Upper Visby Beds or the Högklint Beds. However, all the other specimens are from localities in the Hemse Beds, one (Ar 6223) from Hablingbo in the south-western area of outcrop of these beds, the remainder from near Östergarn or the island of Östergarnsholme in the north-eastern area of outcrop. Collecting localities in Gotland are discussed by Martinsson (1962, pp. 44–59, fig. 14).

Description. Occipital ring longest (sag.) medially, distally shorter (exs.) and curving forward, separated by a shallow axial furrow from the posterior border and inner, posterior corner of the cheek. Occipital furrow shallow medially, narrow and deep behind lateral glabellar lobe 1p. Latter elongate-oval in outline, gently convex and separated from median lobe of glabella by shallow depression. Lateral glabellar furrow 1p deep, narrow, the walls in contact, directed inward, then turning at an oblique angle to run inward and backward. Axial furrow beside lobe 1p deep and extremely narrow; at the anterolateral corner of lobe 1p the furrow widens abruptly, the adaxial wall of the

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EXPLANATION OF PLATE 85

Figs. 1–14. *Papillicalymene papillata* (Lindström 1885). 1–3. Holotype, Ar 6209, see Plate 84, figs. 7–9. Dorsal view of thorax, dorsal, postero-lateral views of pygidium, ×2. 4, 7, 10, 11. Cranidium, internal mould, Ar 27195, Hemse Beds, Gotland. Anterior, left lateral, antero-lateral, dorsal views, ×2. 5, 6, 8, 9. Partially enrolled exoskeleton, exfoliated and weathered, Ar 6223, Hemse Beds, Gotland. Dorsal and anterior views of cephalon, right lateral view, dorsal view of posterior part, ×2. 12–14. Pygidium and four incomplete segments, with exoskeleton, Ar 27196, Hemse Beds, Gotland. Dorsal, left lateral, posterior views, ×2.

furrow formed by the vertical side of the glabella. Lateral glabellar lobes 2p and 3p, and the papilla (4p) at the antero-lateral corner of the glabella, are outwardly directed, subpyramidal projections from the upper part of this wall, the upper surface gently convex, the inner edge separated by a shallow, curving depression from the gently convex median glabellar lobe. Anterior margin of glabella only slightly curved so that frontal lobe is transversely subquadrangular in outline; frontal slope curves downward and slightly posteriorly to preglabellar furrow. Anterior border a short (sag. and exs.), high, wall-like structure that is curved in dorsal and lateral aspect; the inner side curves upward and inward from the preglabellar furrow to the level of the dorsal surface of the frontal glabellar lobe; the outer side curves downward from the narrow, convex upper surface, becomes vertical and slopes downward and backward. Laterally, outside the line of the axial furrow, the anterior border loses height abruptly before it merges with the antero-lateral border. The extremity of the anterior border is slightly expanded inwardly, but does not form a discrete buttress opposed to the papilla at the antero-lateral angle of the glabella. Cheek subquadrant in outline, moderately convex, the broad, steeply sloping antero-lateral border defined by a shallow border furrow, posterior border narrow proximally, widening distally and merging with the lateral border at the rounded genal angle; posterior border furrow deep and narrow, shallowing distally. The inner edge of the cheek slopes vertically to the axial furrow; adjacent to this edge and opposite lateral lobe 2p is the palpebral lobe, gently convex and sloping steeply adaxially. Two buttresses, separated by a deep notch, project from the upper, inner edge of the cheek on either side of the palpebral lobe; the posterior (2p) is rounded distally and surrounds the sharp tip of the 2p lateral lobe; the anterior (3p) is subrectangular in shape, the flat adaxial edge lying against the tip of the 3p papilla. In the originals of Plate 85, figs. 10, 11; Plate 86, figs. 1, 3, the anterior edge of this buttress is coincident with the anterior edge of the cheek. In the original of Plate 85, figs. 5, 6, the cheek buttresses are different, in that buttress 3p is subtriangular in outline, and there is a 4p buttress at the inner, anterior corner of the cheek which projects toward the papilla at the antero-lateral angle of the glabella. It is uncertain whether or not a 4p buttress is present in the holotype. Eye lobe poorly preserved, defined on outer side by shallow furrow. Posterior branch of suture directed transversely from eye lobe for a short distance, then turning at an oblique angle to run across the lateral border furrow and curve over the border at the genal angle. Anterior branch directed exsagitally as far as the border furrow, then curving inward across the border at the base of the steeply sloping margin of the anterior border and on to the face of this border. Here it meets at an oblique angle the rostral suture, which traverses the vertical anterior face of the border (Pl. 86, fig. 3). Connective suture straight, directed inward and downward. The ventral margin of the anterior and lateral borders (Pl. 86, fig. 6) is a sharp, smooth edge at the abrupt flexure where border and doublure join; the doublure (including the doublure sector of the rostral plate) is directed upward and inward beneath the anterior border. Laterally the outer face of the doublure is concave, and it lies close beneath the dorsal exoskeleton of the border and extends in to the border furrow. This form of the cephalic doublure laterally and anteriorly makes it possible, during enrolment, for the tips of the thoracic pleurae, and the outer pleural regions of the pygidium, to be tucked inside the sharp ventral edge of the cephalon. Hypostome (Pl. 86, fig. 4) known incompletely in a poorly preserved, extended specimen. It is widest across the large, subrectangular anterior

wings, anterior margin transverse and border flexed ventrally. Middle body subdivided into wider (tr.) more convex anterior lobe and lower, gently convex posterior lobe; anterior lobe appears to bear an elongate median protuberance. Lateral border narrow and gently convex, expanding postero-laterally where it meets the posterior border; latter with semicircular median notch, postero-lateral projection sharply pointed.

Thorax of thirteen segments. Convex axial rings of thoracic segments curve forward distally and are slightly expanded, articulating furrow shallow medially, deepening as it passes into apodeme. Inner part of pleura horizontal, traversed by slightly diagonal pleural furrow, pleural bands convex, the anterior sloping down to an articulating flange that fits under the posterior band of the preceding segment. Outer part of pleura curves downward and widens (exs.) to form a facet, except for the posterior edge which is continuous with the posterior band; pleural furrow extends on to inner part of facet only. Doublure of pleura like that of *Calymene clavicula* Campbell 1967 (pl. 10, figs. 12–15), i.e. a narrow band which is thickened and raised along the anterior, distal margin to form a stop to enrolment. Articulating boss on anterior edge of segment at fulcrum fits into socket beneath posterior band. Axis of pygidium composed of seven rings and a posterior portion which merges with the smooth border area; articulating furrow and seven ring furrows, the last furrow shallow adjacent to axial furrows, and ring furrows 5–7 progressively effaced medially. Five pleural furrows, which deepen outward and terminate to leave a border area, define (with the posterior part of the axial furrow) the articulating half-rib and five ribs; each rib is traversed by an interpleural furrow which is faintly impressed on the inner pleural region, and becomes slightly impressed across the border, extending to the rounded edge.

External surface (Pl. 84, figs. 7–9; Pl. 85, fig. 1; Pl. 86, figs. 1–3, 6) of axial region (except the posterior tip) and inner part of the pleural region, and furrows, appears to lack granulation, but there are a few low tubercles scattered on the glabella. The outer parts of the pleural regions and borders, including the cheek outside the eye lobe, and border furrow of the free cheek, are densely granulate, and a finer granulation extends on to the posterior part of the thoracic facets. The sharply folded edge of the cephalon, at the junction between dorsal exoskeleton and doublure, is smooth; granulation extends on to the ventrally facing, rolled edge of the pygidium. The external surface of the exoskeleton shows an extremely fine pitting, as does the internal mould, indicating that the internal surface of the exoskeleton is finely granulate.

EXPLANATION OF PLATE 86

Figs. 1–4, 6. *Papillicalymene papillata* (Lindström 1885). 1–3, 6. Incomplete enrolled individual with exoskeleton, Ar 27199, Hemse Beds, Gotland. Dorsal, right lateral, anterior views of cephalon, dorsal view of pygidium, ×3. 4. Incomplete, weathered exoskeleton, ventral view of cephalic portion excavated to show incomplete hypostome, ×3. Ar 27201, Hemse Beds, Gotland.

Figs. 5, 7–17. *Papillicalymene excavata* (Lindström 1885). 5, 7–9. Holotype, enrolled, weathered exoskeleton, Ar 27174, original of Lindström 1885, pl. 16, figs. 1–4, Eke Beds, Gotland. Left lateral, dorsal, antero-lateral views of cephalon, dorsal view of thorax, ×3: 10, 11, 14, 15. Crushed, enrolled individual with exoskeleton, Ar 27176, Eke Beds, Gotland. 10, 14, 15, posterior, dorsal, left lateral views of pygidium; 11, dorsal view of cephalon, ×2. 12. Cephalon with exoskeleton, Ar 27172, Hemse Beds, Gotland. Ventral view showing doublure, including doublure sector of rostral plate, ×2. 13, 16, 17. Cranidium and right free cheek, Ar 27170, Hemse Beds, Gotland. Right lateral, anterior, dorsal views, ×2.

Discussion. The material of this species is limited, so that only a restricted knowledge of variation may be obtained. As described above, the buttress 3p from the fixed cheek may be relatively broad and bluntly tipped (Pl. 84, fig. 9; Pl. 86, fig. 1), or smaller and subtriangular, having adjacent to it a smaller 4p buttress (Pl. 85, fig. 6). Some variation in width (sag. and exs.) of the preglabellar furrow, and of the height and curvature of the preglabellar field, is observed. The preglabellar furrow may be narrow and the field recurved close to the frontal slope of the glabella (Pl. 84, fig. 9; Pl. 86, fig. 1), so that crest of the ridge stands above (dorsal to) the frontal glabellar lobe; in other specimens (Pl. 85, figs. 4–8, 10, 11) the preglabellar furrow appears relatively wider (sag. and exs.) and the ridge does not rise so high. In these latter specimens the exoskeleton is either broken or partially weathered away, but after allowance is made for differing modes of preservation there appears to be this variation.

Schrank (1970, pp. 141–142, pl. 12, figs. 5, 5*a*) has described a single incomplete cranidium from a boulder of 'Beyrichienkalk', of Downton age (Martinsson 1967, fig. 2), as a new species, *Papillicalymene moa.* The specimen is exfoliated, and resembles the original of Plate 85, figs. 4, 7, 10, 11, except that there is a 3p buttress and apparently a small 4p buttress, as in the original of Plate 85, figs. 5, 6. I consider this specimen falls within the range of variation here included in *P. papillata.* Schrank (1970, p. 142) also makes reference to an illustration given by O. I. Archipova of *P. papillata* from Ludlow strata, Podolia. This illustration is said to be in a guide to an excursion in Podolia (Nikiforova and Predtechenskij 1968), but this guide contains no plates. Professor C. H. Holland (pers. comm.) informs me that participants in the excursion were given an appendix to the guide in the form of a duplicated atlas with photographic copies of the plates. This appendix does not constitute a publication under Article 9 of the *International Code of Zoological Nomenclature*, whereas the guide is an available publication. The copy of the appendix I have seen shows a poorly preserved, incomplete cranidium from the Grinchuk beds, Malinovtsy horizon, Podolia. It appears to belong to *Papillicalymene*, for lateral glabellar lobes 2p and 3p are buttressed and the anterior border is a high ridge. A narrow, curved slot on the fixed cheek separates buttresses 2p and 3p, the adaxial end of the notch in line (tr.) with the posterior part of lobe 3p. This notch is narrower than that in *P. papillata*, and situated further forward. I hesitate to place this fragment in the species *papillata*, but record the genus from the Ludlow of Podolia.

Papillicalymene excavata (Lindström 1885)

Plate 86, figs. 5, 7–17

1885 *Calymmene excavata* Lindström, pp. 72–73, pl. 16, figs. 1–4.

Holotype. Ar 27174, enrolled individual with weathered exoskeleton, *Rhizophyllum* Limestone, Lau Backar (Hede 1960, pp. 81–82; Martinsson 1962, p. 57).

Other material. Ar 27169, enrolled, crushed individual with exoskeleton, Närså, a rivulet at the Lau Kanal locality (Martinsson, pers. comm.). Ar 27170–27173, one cephalon and two cranidia with exoskeleton, one incomplete exoskeleton, Lau Kanal (Gannor of Martinsson 1962, p. 57). Ar 27176–27177, crushed, enrolled individual and fragment of glabella, with exoskeleton, Lau Backar (see under holotype). Ar 27182, 27185, two specimens, one extended, incomplete, one enrolled, crushed, with exoskeleton, Lau Kanal (see above).

Geological horizon. Eke Beds of mid-Ludlow age, since Lau Backar is the type locality, and the older Hemse Beds of early Ludlow age (Martinsson 1967, fig. 2). Lindström (1885, p. 94) records the species

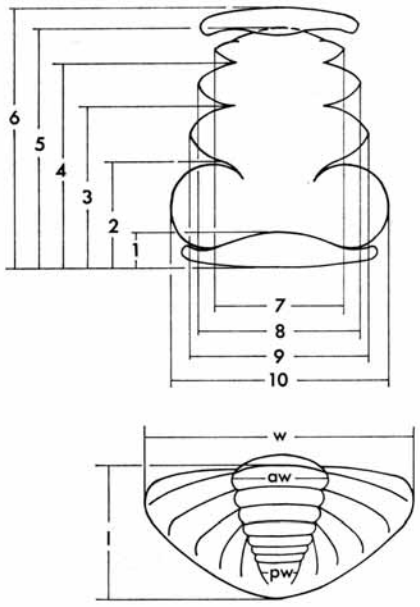
from the Wenlock Shale and Wenlock Limestone. Hede (1921, p. 99; 1960, p. 81) does not record this species from Gotland, not even from the type locality of Lau Backar. The localities of the other material indicate the Hemse Beds of the Lau Kanal section (Gannor of Martinsson 1962, p. 57), including that from Närså, a rivulet that cuts through the Hemse Beds and a little of supposed Eke Beds near the Lau Kanal locality (Martinsson, pers. comm.).

TABLE 1. Measurements in millimetres of species of *Papillicalymene* and *Calymene*, as shown in text-fig. 2. Left column is specimen number, e indicates an estimated measurement, *r* is number of axial rings in pygidium, *pl* is number of pleural furrows of pygidium.

	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*w*	*l*	*aw*	*pw*	*r*	*pl*
Papillicalymene papillata																
6209	2·5	5·6	8·3	10·3	11·4	12·5	7·1	8·8	9·7	10·9	15·6	10·3	6·1	3·0	7	5
27199	1·7	3·4	5·2	6·2	7·1	8·6	5·1	6·1	6·5	7·7	10·1	7·3	4·3	1·9	7	5
6223	2·2	4·8	7·3	9·1	10·5	12·0	7·3	9·5	9·7	11·3	16·0	8·6	6·1	3·6	7	5
27201	2·5	4·3	5·7	7·5	8·4	10·3	5·7	7·9	7·9	9·5						
27196											18·7	10·7	6·8	4·2	7	5
27197											19·5	10·9	7·1	3·0	7	5
27195	2·3e	4·5e	6·2e	7·9e	9·1e	11·0e	5·2	6·9	7·3	9·0						
Papillicalymene excavata																
27174	1·6	3·0	4·5	6·0	7·4	9·0	4·4	6·4	5·7	6·8						
27176											11·0	7·3	4·5	2·6	7	5
27173	1·9	3·9	6·1	7·8	9·2	10·7	6·2	7·7	8·1	8·7						
27170	1·8	3·1	5·1	6·8	7·9	9·4	4·8	6·4	6·4	7·0						
27172	1·7	3·8	5·6	6·9	8·6	10·3	5·8	7·4e	7·3	8·2						
Papillicalymene sp. ind. A.																
6208	2·1	4·2	6·1	7·5	8·7	10·3	6·5	7·0	7·8	9·0	12·0	8·4	5·2	3·2	7	5
Papillicalymene sp. ind. B																
27175	4·5e	8·8e	12·7e	15·9e	18·6e	23·1e	11·3e	11·2	15·1	17·2						
Calymene sp. ind.																
49987	4·0	9·1	13·0	15·6	18·3	19·8	11·8	12·2	14·6	19·0						

Description. This species is like *P. papillata* in all except minor morphological features, and the cephalon displays the broad, deep axial furrow in front of lateral furrow 1p, bridged by 2p and 3p papillae and buttresses, and the deepening at the junction of axial and preglabellar furrows. In the cephalon of *P. excavata* lateral glabellar lobe 2p is lower and relatively smaller, buttress 2p being relatively broad (exs.) and having a truncate extremity abutting against the flattened abaxial margin of the 2p lobe. There is no gap between the posterior edge of buttress 2p and the anterolateral margin of the 1p lateral lobe, for these edges are juxtaposed. Lateral glabellar lobe 3p has no convexity independent of the median glabellar lobe, but is merely a conical papilla, narrow (exs.) at the base. Buttress 3p is also narrow (exs.) but is parallel sided and truncate distally; a slight gap separates the 3p papilla and buttress. The frontal glabellar lobe is relatively longer, with a conical papilla at the antero-lateral corner directed forward and slightly outward so that it projects over the preglabellar furrow. A small 4p buttress is situated on the inner, anterior corner of the fixed cheek, directed inward and forward. This 4p buttress and the papilla on the frontal glabellar lobe are not directed towards each other, and a wide gap separates them (Pl. 86, fig. 8). The relatively greater length of the frontal glabellar lobe results in the frontal portion of the cephalon being relatively elongated (sag. and exs.) and there is a consequent difference in the cephalic outline; this elongation causes the border sector of the rostral plate and adjacent ventral-facing part of the border to slope backward and downward less steeply than in *P. papillata*, and the connective sutures converge more strongly backward.

Discussion. Dr. C. P. Hughes plotted various pairs of measurements of *P. papillata* and *P. excavata* (Table 1), and showed that there was little difference between the two species in relative shapes and sizes of cephalic structures. Graphs of the following pairs of measurements (text-fig. 2): 10:9; 5:2; 6:2; 10:6; indicated possible differences, but bivariate analyses, using the reduced major axis method, showed these not to be significant. However, the samples are small, such dimensions as length (sag.) of frontal glabellar lobe are difficult to measure accurately, and width of cephalon cannot be measured in this material. Further, the measurements do not include estimates of the angle of the axis of a particular papilla (or buttress) to the sagittal line. In the specimens included in *P. excavata* the 4p papilla at the antero-lateral angle of the frontal lobe is forwardly directed, not outwardly as in *P. papillata.* As a consequence, the frontal glabellar lobe appears longer (sag.) and the frontal region of the cephalon (the preglabellar furrow and anterior border) projects forward and gives a different outline to the cephalon. The downward-facing part of the anterior border has a gentler slope in profile as a result of the forward projection of the frontal region. This appears to be the major difference between the specimens assigned to *P. excavata* and those placed in *P. papillata*, but there is also the constant development of buttress 4p, its wide separation from papilla 4p, and the absence of a gap between lateral lobe 1p and the posterior edge of buttress 2p. Both species are present in the Hemse beds, though not at the same localities, and only *P. excavata* is known from the Eke beds. It is admitted by Martinsson (1962, p. 57; 1967, fig. 2, p. 381) that in certain areas it is difficult to distinguish the Eke beds from the Hemse beds, and they are shown by him as partly synchronous. I retain the name *P. excavata* for certain specimens, pending evidence from larger collections and more precise correlations.



TEXT-FIG. 2. Measurements taken on specimens of *Papillicalymene* and *Calymene*, see Table 1. Specimens were oriented with the posterior margin of the occipital ring, or the first axial ring of the pygidium, vertical. Measurements 2, 3, and 4 were made to the base of the glabellar furrow at the anterior margin of the glabellar lobe; 7, 8, 9, and 10 to the outer extremity of the glabellar lobe.

Papillicalymene sp. ind. A

Plate 87, figs. 1, 2, 4, 7, 8

1971 *Papillicalymene papillata* (Lindström); Whittington, fig. 1*e*, *f*.

Material. Ar 6208, enrolled individual with exoskeleton, from the Hemse Beds, Östergarn.

Discussion. The cephalon of this specimen differs from any of those from a similar horizon referred to *P. papillata* or *P. excavata*, in that the basal glabellar lobe is subcircular in outline, the distal part of the occipital furrow and the adjacent axial furrow is broader, the 4p buttress larger and in contact with the papillate anterolateral corner of the glabella, the anterior border does not descend abruptly laterally to the suture, but curves gently down, and the border furrow of the free cheek is deep and narrow, but shallows abruptly adjacent to each suture. This specimen may represent a variant of one of the named species, or a distinct species.

Papillicalymene sp. ind. B

Plate 87, figs. 3, 6

Material. Ar 27175, an isolated large cranidium from Fjale, a hamlet in Anga parish, from the Klinteberg Beds of early Ludlow age (Martinsson 1967, fig. 2).

Discussion. The cranidium resembles that referred to *Papillicalymene* sp. ind. A (and consequently differs from *P. papillata* or *P. excavata*) in that there is a relatively wide axial furrow beside lateral glabellar lobe 1p, a large gap separating the antero-lateral margin of this lobe from the 2p buttress, and at the inner end of lateral glabellar furrow 1p there is a small, low inflation. However, the cranidium differs from that of *Papillicalymene* sp. ind. A in that a wide gap separates the 3p papilla and buttress, the 4p papilla at the angle of the frontal lobe is directed outward and forward at about 45° to the sagittal line, the preglabellar furrow is broad, and the 4p buttress projects forward and inward over the outer part of this furrow. This cranidium is about twice the size of any others of *Papillicalymene* studied here, so is difficult to place in relation to them.

Genus FLEXICALYMENE Shirley 1936

Flexicalymene celebra (Raymond 1916)

Plate 87, figs. 5?, 9–13; Plate 88, figs. 1–10; Plate 89, figs. 8, 11?

1916 *Calymene celebra* Raymond, pp. 28–29, pl. 3, figs. 9, 10.
1936 *Calymene celebra* Raymond; Shirley, pp. 390, 392.
1967 *Calymene celebra* Raymond; Campbell, p. 27.

Lectotype (here selected). MCZ 638, internal mould of entire exoskeleton, original of Raymond 1916, pl. 3, fig. 9, Niagaran dolomites of Grafton, Illinois.

EXPLANATION OF PLATE 87

Figs. 1, 2, 4, 7, 8. *Papillicalymene* sp. ind. A. Enrolled exoskeleton, Ar 6208, Hemse Beds, Gotland. Dorsal, right lateral, anterior views of cephalon, dorsal view of thorax, dorsal view of pygidium, ×2.

Figs. 3, 6. *Papillicalymene* sp. ind. B. Incomplete, weathered cranidium, Ar 27175, Klinteberg Beds, Gotland. Dorsal, anterolateral views, ×1·5.

Fig. 5. *Flexicalymene celebra* (Raymond 1916)? Latex cast from external mould of part of cranidium, USNM 154498, coarse, granular Racine Dolomite, Milwaukee, Wisconsin; Teller coll. Dorsal view, ×3.

Figs. 9–13. *Flexicalymene celebra* (Raymond 1916). Lectotype (here selected), internal mould of exoskeleton, MCZ 638, original of Raymond, 1916, pl. 3, fig. 9, Racine Dolomite, Grafton, Illinois. Dorsal view of pygidium, anterior, dorsal views of cephalon, right lateral view, ×2; oblique view of pygidium showing incomplete pillars infilling canals through doublure, ×6.

Other material. MCZ 639, internal mould of entire exoskeleton, original of Raymond 1916, pl. 3, fig. 10, Niagaran dolomites of Grafton, Illinois. USNM 59405, counterpart moulds, Niagaran dolomites of Grafton, Illinois.

Geological horizon. The 'Niagaran' dolomites are the Racine Dolomite, probably of late Wenlock to early Ludlow age (Professor A. J. Boucot, pers. comm.).

Description. Occipital ring longest (sag. and exs.) behind median glabellar lobe, shorter and curving forward abaxially, with slight inflation at distal tip. Occipital furrow deep behind median lobe, narrower and extended into apodeme behind inner part of lateral lobe 1p, at extremity shallower. Lateral glabellar lobe 1p oval in outline, long axis longitudinal, inflated above adjacent part of median lobe. Lateral furrow 1p shallow abaxially, deepening where it curves around inner, anterior side of lobe 1p, on adaxial side of inner part a faintly inflated ovate area. Lateral lobe 2p about half length (exs.) of lobe 1p, similar in outline and inflation. Lateral lobe 3p a small inflation on the lateral slope of the glabella, furrow 3p a faint, short indentation. Axial furrow shallow beside occipital ring, beside lateral lobe 1p a deep, steep-sided trench, broader with steeply sloping sides in front of here; shallow anterior pit near anterior extremity. Preglabellar furrow narrow medially, widening abaxially; anterior border short (sag. and exs.), the slope from the preglabellar furrow flat, inclined gently upward and forward, on anterior side curving abruptly over to slope downward and backward. In anterior view border moderately arched. Eye lobe small, mid-point in transverse line with mid-point of lateral lobe 3p; anterior branch of suture directed straight inward and forward, turning more strongly inward as it crosses border, on anterior slope of border aligned with connective suture; rostral suture traverses along upper part of anterior slope. Mould of inner surface of border sector of rostral plate (Pl. 87, fig. 10) suggests that this plate is similar to that of *F. senaria* (Evitt and Whittington 1953, pl. 9, figs. 3–6). Antero-lateral cephalic border moderately convex, curled under so that doublure slopes upward and outward, the inner edge ventral to the broad, shallow border furrow. Inner part of posterior border narrow (exs.) and convex, outer part broader (exs.) and less convex; blunt genal angle. Posterior branch of suture directed straight outward and slightly backward from eye lobe, then curving through an oblique angle and continuing to the border furrow; here it curves again and is directed exsagitally to the genal angle.

Thorax of thirteen segments, axial rings with conspicuous rounded inflation adjacent to axial furrow. Articulating furrow with deep, elongate (tr.) pit distally, the external expression of the apodeme. Inner part of pleura narrow (tr.), horizontal, outer part wider (tr.) and steeply curved down from fulcrum. The deep, slightly diagonal pleural furrow shallows at the margin of the large facet, the furrow continued a short distance on the facet by a much narrower and shallower groove. Posterior band of pleura convex, continued along the margin of the facet to the tip. Articulating boss on anterior band of pleura at fulcrum. Internal moulds (Pl. 88, fig. 8) show a curved groove, deepest adaxially, extending along the anterior edge of the facet, abaxially the groove dies out and is continuous with the flat, narrow doublure which extends around the tip of the pleura and along the posterior margin of the facet. The groove on the internal mould is the mould of the ridge which forms a stop to enrollment (cf. Campbell 1967, pl. 10, fig. 15). In the internal mould slim pillars may be observed, connecting the ventrally facing outer tip of the facet to the mould of the inner surface. These are infillings of canals through the exoskeleton.

Axis of pygidium divided into six rings and the low, rounded terminal portion; first ring furrow deepest and broadest (sag. and exs.) medially, successive furrows progressively shallower medially so that sixth furrow is impressed distally only. Pleural region with first pleural furrow deepest, extending to facet; succeeding four pleural furrows progressively shorter and shallower, impressed on inner pleural region only, and successively more strongly backwardly directed. There are thus four distinct pleural ribs, only the first two impressed adjacent to the axial furrow by the beginning of an interpleural furrow. A low fifth rib runs back beside the tip of the axis, and dies out on the border. The outer part of the pleural region is smooth, the doublure curled under, the exoskeleton traversed by canals, the infillings of which appear as incomplete pillars in the internal mould (Pl. 87, fig. 13).

External surface, except in the bottom of the deep, narrow furrows and on the facets, covered by a dense, fine granulation. Scattered larger tubercles are present on the glabella, cheek inside the border furrows, axial rings, posterior pleural bands and ribs of pygidium; the largest of these tubercles are on the glabella.

Discussion. Two additional specimens from localities north of Chicago and probably the Racine Dolomite, may belong to this species. One (Pl. 87, fig. 5) shows the narrow (sag. and exs.) anterior border, the inner side of which slopes gently upward and forward, the lack of a buttress opposite lateral lobe 2p, and the sinuous course of the posterior branch of the suture. The second (Pl. 89, figs. 8, 11) shows the internal surface of part of the cephalon and thorax, and has the hypostome in place. The hypostome is like that of *Flexicalymene* (Evitt and Whittington 1953, pl. 9, figs. 8, 9), shows the pit in the anterior wing (the external expression of the wing process), and that the process rests against the anterior slope of the anterior pit of the dorsal exoskeleton.

The absence of papillation of glabellar lobes and corresponding buttresses, suggests that this species belongs in either *Gravicalymene* or *Flexicalymene*. In the present state of knowledge the form of the anterior border is decisive in distinguishing between these two genera. In Ordovician species of *Gravicalymene* (Dean 1962, 1963; Ross 1967*b*) the preglabellar furrow may be narrow or broad (sag. and exs.), the anterior border is relatively broad (sag. and exs.), stands well above the preglabellar furrow and may have a flattened upper surface. This surface may be approximately horizontal, or may slope forward and upward; at the posterior edge it joins the wall of the preglabellar furrow, at the anterior edge it curves abruptly over into the outer face of the border, which slopes downward and backward. I am not aware of any Silurian species referred to *Gravicalymene*, but a number of Lower Devonian species from Bohemia, North Africa, Turkey, Australia, and New Zealand have been referred to this genus (Shirley 1938, p. 487, pl. 44, fig. 17; Philip 1962, p. 231; Talent 1963, pp. 105–106; Strusz 1964, pp. 94–

EXPLANATION OF PLATE 88

Figs. 1–10. *Flexicalymene celebra* (Raymond, 1916). 1–7, 9, 10. Internal mould of exoskeleton and latex cast from counterpart, USNM 59405, Racine Dolomite, Grafton, Illinois. 2–4, 6, cast, dorsal, anterior, posterior, left lateral views, ×2. 1, 5, mould, dorsal, right lateral views, ×2. 7, 9, 10, enlarged views of cast to show external surface, ×6, ×6, ×4·5. 8, internal mould of exoskeleton, MCZ 639, original of Raymond 1916, pl. 3, fig. 10, Racine Dolomite, Grafton, Illinois. Outer parts of thoracic segments, showing mould of doublure (d) and pillars infilling canals through exoskeleton, ×6.

95; Talent 1965, p. 49; Haas 1968, pp. 101–103; Alberti 1969, pp. 413–414). In these species the preglabellar furrow is deep, the anterior border of moderate width (sag. and exs.) and semicircular in cross section, not flattened on the upper surface. Certain Australian authors have expressed doubt that these species are congeneric with Ordovician species, and this question remains open—the Devonian species may be derived from a different ancestor.

The present species *celebra* has the anterior border rising in a flat slope upward and forward from the base of the preglabellar furrow, and at the anterior margin it turns abruptly over to slope downward and backward as the outer face of the border. This shape is typical of Ordovician species of *Flexicalymene* (Dean 1962, 1963; Whittington 1965; Ross 1967*b*), as is the lack of 2p papilla and buttress, though the outline of the glabella is slightly bell-shaped rather than parabolic. On balance I prefer to place it in this genus, and the hypostome attributed to it is like that of species of *Flexicalymene* rather than of *Calymene* (Campbell 1967, pl. 10, figs. 1–7; Haas 1968, pl. 29, figs. 6, 7, text-fig. 16*b*, *d*, *f*). Haas (1968, pp. 100–101) has recently described a high Llandovery to Wenlock aged species that he attributes to *Flexicalymene*, and Temple (1969, pp. 224–228) an early Llandovery form. The anterior border is not well preserved in Haas's material, and the cast figured by Temple (1969, pl. 6, fig. 1) has an anterior border apparently of *Gravicalymene* type. Thus *celebra* is the only Silurian species that I consider with some confidence may be placed in *Flexicalymene*.

Genus LIOCALYMENE Raymond 1916

Type species. Hemicrypturus clintonii Vanuxem 1842.

Diagnosis. Glabella bell-shaped in outline, three pairs of lateral glabellar lobes, lobe 1p large, subtriangular in outline, maximum length (exs.) as much as half length (sag.) of glabella, lobes 2p and 3p progressively shorter (exs.) and frontal lobe shorter (exs.) than lobe 3p; lateral glabellar furrows narrow. Axial furrow beside glabella a narrow slit throughout its length, so that cheek, lateral lobes and frontal lobe approach each other closely, but papillae and buttresses (as projections across a broad, deep furrow) are apparently not developed; anterior border low, gently convex; transverse line joining midpoints of palpebral lobes crosses junction of axial and 1p lateral furrow. Hypostome unknown.

Thorax of thirteen segments. Pygidium with median part of axis smooth behind third ring; pleural regions smooth except for narrow first pleural furrow; behind axis a short (sag.), slightly swollen band unites the pleural regions.

Stratigraphical and geographical range. Rocks of Clinton Group and equivalents, of late Llandovery age, of central and eastern United States (New York, Pennsylvania, Maryland, Virginia, and Kentucky).

Discussion. This diagnosis is intended to be read in conjunction with my (*in* Moore 1959, pp. **O**450–**O**451) diagnosis of the family, lines 2–4 of which should read 'widest across occipital ring or pre-occipital (i.e. 1p) lateral lobes; may or may not project in front of genae'. In erecting this genus Raymond (1916, p. 29) drew attention to the 'smooth pleural lobes' of the pygidium. The cephalon, with its relatively large basal glabellar lobe and narrow lateral glabellar and axial furrows, which bring lateral glabellar lobes and cheek close together without development of papillae and buttresses, appears to be

equally distinctive. No species other than the type is known, and its relationships are obscure, for no late Ordovician or early Silurian calymenid exhibiting similar characters appears to have been described.

Liocalymene clintoni (Vanuxem 1842)

Plate 89, figs. 1–7, 9, 10, 12

1842 *Hemicrypturus clintonii* Vanuxem, pp. 79, 80, fig. 11, 2.
1843 *Hemicrypturus*, Hall, p. 77, fig. 19, 2; plates, no. 9, 2.
1852 *Calymene clintoni* (Vanuxem); Hall, p. 298, pl. A66, figs. 5 *a*, *d*.
1915 *Calymene clintoni* (Vanuxem); Bassler, p. 166, giving additional early references.
1916 *Liocalymene clintoni* (Vanuxem); Raymond 1916, p. 29.
1923 *Liocalymene clintoni* (Vanuxem); Swartz and Prouty, pp. 706–707, pl. 34, figs. 1–4.
1941 *Liocalymene clintoni* (Vanuxem); Butts, pl. 104, figs. 16–19.
1959 *Liocalymene clintoni* (Vanuxem); Whittington, in Moore, p. O452.

Material. Neither the original of Vanuxem or that of Hall (1852) is preserved in the New York State Museum (pers. comm. from Dr. D. W. Fisher, 10 June 1969), and the original of Hall is not in the Field Museum of Natural History, Chicago (pers. comm. from Dr. M. H. Nitecki, 19 June 1969). MCZ 8082 (Pl. 89, fig. 1), from the Clinton Group, Clinton, Oneida County, New York State, C.D. Walcott coll., is the specimen mentioned by Raymond in erecting the genus. MCZ 8081 is from the Clinton of Pennsylvania, H. D. and W. B. Rogers coll.; MCZ 8083 from Rose Hill Shale, road cut, U.S. highway 22 and 522 at Mt. Union, Pennsylvania. USNM 154493–154496, figured herein, Crab Orchard Group, upper part, four miles south-east of Tolsboro, western part of Lewis County, Kentucky, coll. E. M. Kindle; similar specimens from *Mastigobolbina typus* zone, Clinton Group, Wills Creek, Cumberland, Maryland (U.S. Geol. Surv. locality 286i[1]). USNM 116344, internal mould, entire exoskeleton, from west portal of first tunnel on Pennsylvania turnpike, Gunther Valley, east of Roxbury, Pennsylvania.

Geological horizon. Fisher (1960) has recorded the range of this species as mid-part of the Clinton Group, late Llandovery age, in New York State. Other material I have examined is from rocks referred to the Clinton Group, and that described from Maryland (Swartz and Prouty 1923) is from the *M. typus* zone of the highest Rose Hill Formation and the overlying Keefer Sandstone member of the Rochester Formation. These beds are regarded by Professor A. J. Boucot (pers. comm.) as of late Llandovery age.

Description. Glabella of maximum width (tr.) across basal part of 1p lobes, in large cranidia this width is $\times 1{\cdot}3$ the length (sag.); gently convex. Occipital ring longest (sag.) medially, becoming progressively shorter (exs.) distally, and constricted adjacent to the shallow axial furrow where lateral glabellar lobe 1p bulges posteriorly. Occipital furrow broad and shallow medially, deep, narrow and sigmoidal behind lateral lobe 1p. Latter subtriangular in outline, in large cranidia (Pl. 89, figs. 10, 12) of maximum length (exs.)

EXPLANATION OF PLATE 89

Figs. 1–7, 9, 10, 12. *Liocalymene clintoni* (Vanuxem 1842). 1, internal mould of exoskeleton, MCZ 8082, Clinton Group, New York State. Dorsal view, $\times 2$. 2–7, 9, 10, 12, latex casts from external moulds, Crab Orchard Group, Kentucky. 2, 4, incomplete pygidium, USNM 154496, dorsal, posterior views, $\times 3$. 3, 5, incomplete pygidium, USNM 154495, dorsal, right lateral views, $\times 3$. 6, incomplete cranidium, USNM 154496, dorsal view, $\times 4{\cdot}5$. 7, 9, 10, incomplete cranidium, USNM 154493, anterior, left lateral, dorsal views, $\times 3$. 12, incomplete cranidium, USNM 154494, dorsal view, $\times 3$.

Figs. 8, 11. *Flexicalymene celebra* (Raymond 1916)? External mould of part of dorsal exoskeleton with internal mould of hypostome in place, USNM 154492, Racine Dolomite, Racine, Wisconsin. Oblique and ventral views, $\times 3$.

about half length (sag.) of glabella, defined by narrow, deep furrow 1p which has a slightly sigmoidal course, directed at about 45° to the sagittal line, adaxially curving to run inward and slightly forward; gently convex, standing above narrow (about one-quarter the maximum width of the glabella), depressed portion of median lobe which separates lobes 1p. Lateral lobe 2p defined anteriorly by straight, narrow, inward, and slightly backwardly directed furrow 2p which extends adaxially one-fifth to one-quarter width at this point; lobe 2p not inflated or separated from median lobe. Lateral lobe 3p defined anteriorly by straight, narrow, inwardly directed furrow 3p which is shorter than furrow 2p; lobe 3p slightly inflated. Anterior margin of glabella curved gently convexly forward, abaxially frontal lobe of length (exs.) less than length of lobe 3p. Course of axial furrow sigmoidal, curving abaxially anteriorly; wide and moderately deep beside occipital ring and most basal part of lobe 1p, in front of here a narrow slit so that cheek and glabella are closely juxtaposed. Preglabellar furrow broad, moderately deep, anterior border widest (exs.) abaxially, moderately convex and gently curved transversely. Cheek gently convex, posterior border longest (exs.) abaxially, antero-lateral border poorly known; eye lobe moderately convex, midpoint on a transverse line that passes approximately through junction of axial and 1p furrow. Anterior branch of suture runs straight forward and inward to cross border furrow and curve inward over border just outside the line of the axial furrow; rostral suture traverses outer surface of anterior border. Posterior branch of suture curves sigmoidally outward and backward to the genal angle. Rostral plate, doublure, and hypostome unknown.

Thorax of thirteen segments. Axial rings longest (sag.) medially, abaxially curving forward and slightly inflated. Inner part of pleura horizontal, outer part curves down to become vertical distally; pleural furrow broad, slightly diagonal, narrowing and dying out beside large facet. Axis of pygidium divided by articulating furrow and eight ring furrows, the posterior one-third smooth, gently convex; first and second ring furrows complete, but median part of second shallow, third and succeeding furrows show a progressively wider smooth median zone, and the abaxial remnants of the furrows are directed progressively more strongly backward as well as outward. Pleural region with large facet and narrow, shallow first pleural furrow ending against it; no further pleural or interpleural furrows; behind axis a short (sag. and exs.), slightly inflated band joins the pleural regions. Doublure of thorax and pygidium unknown.

External surface may be smooth, tubercles lacking; one cranidium (Pl. 89, fig. 12) suggests the presence of fine granulation on occipital ring, glabella and fixed cheek.

Discussion. Examination of calymenids in the U.S. National Museum and at the Museum of Comparative Zoology did not reveal any other North American species like *Liocalymene clintoni*. The material used herein is limited and not adequate to reveal individual variation or changes in proportion with size, so that ratios of dimensions given refer to the largest cranidia only.

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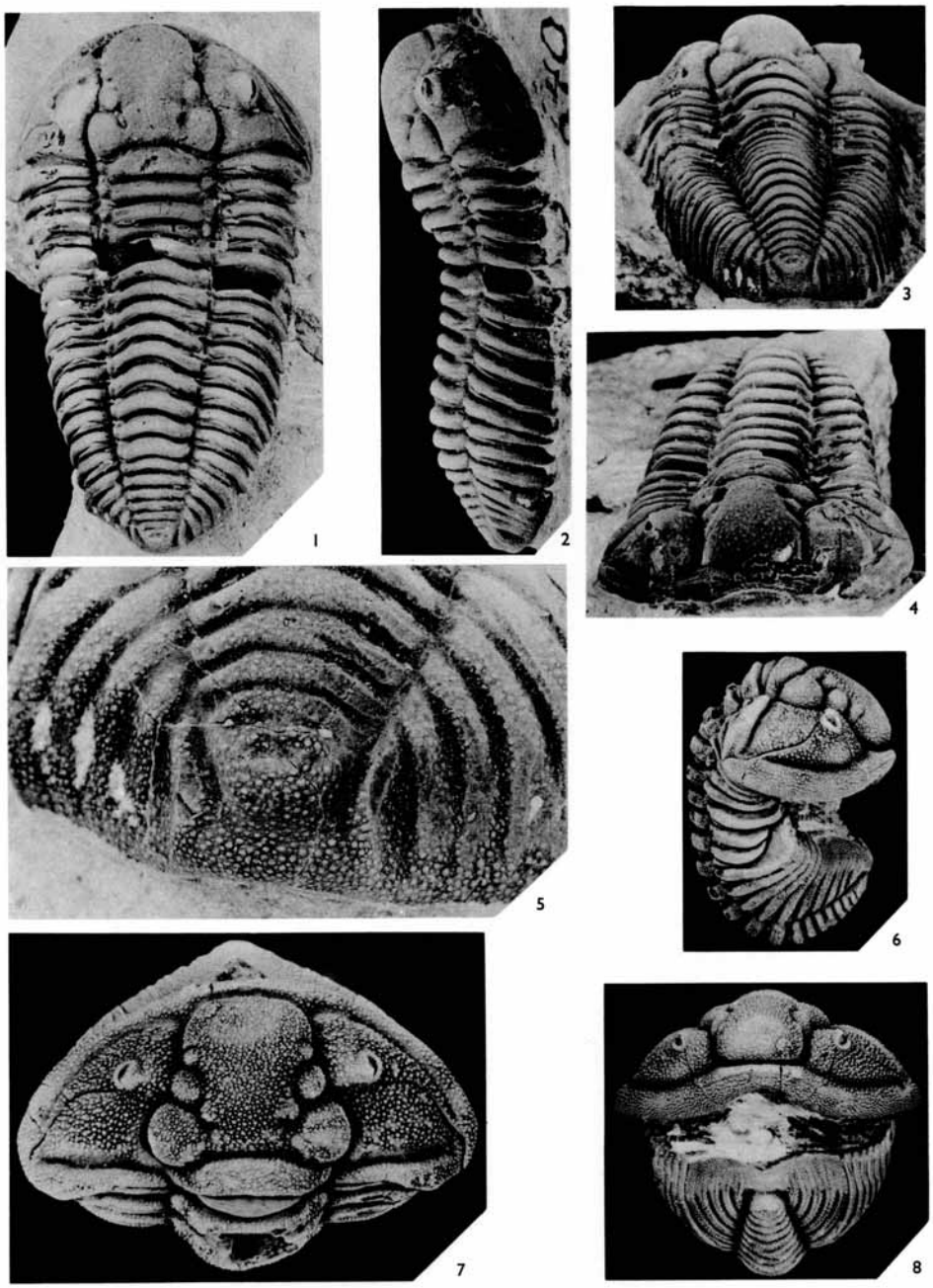
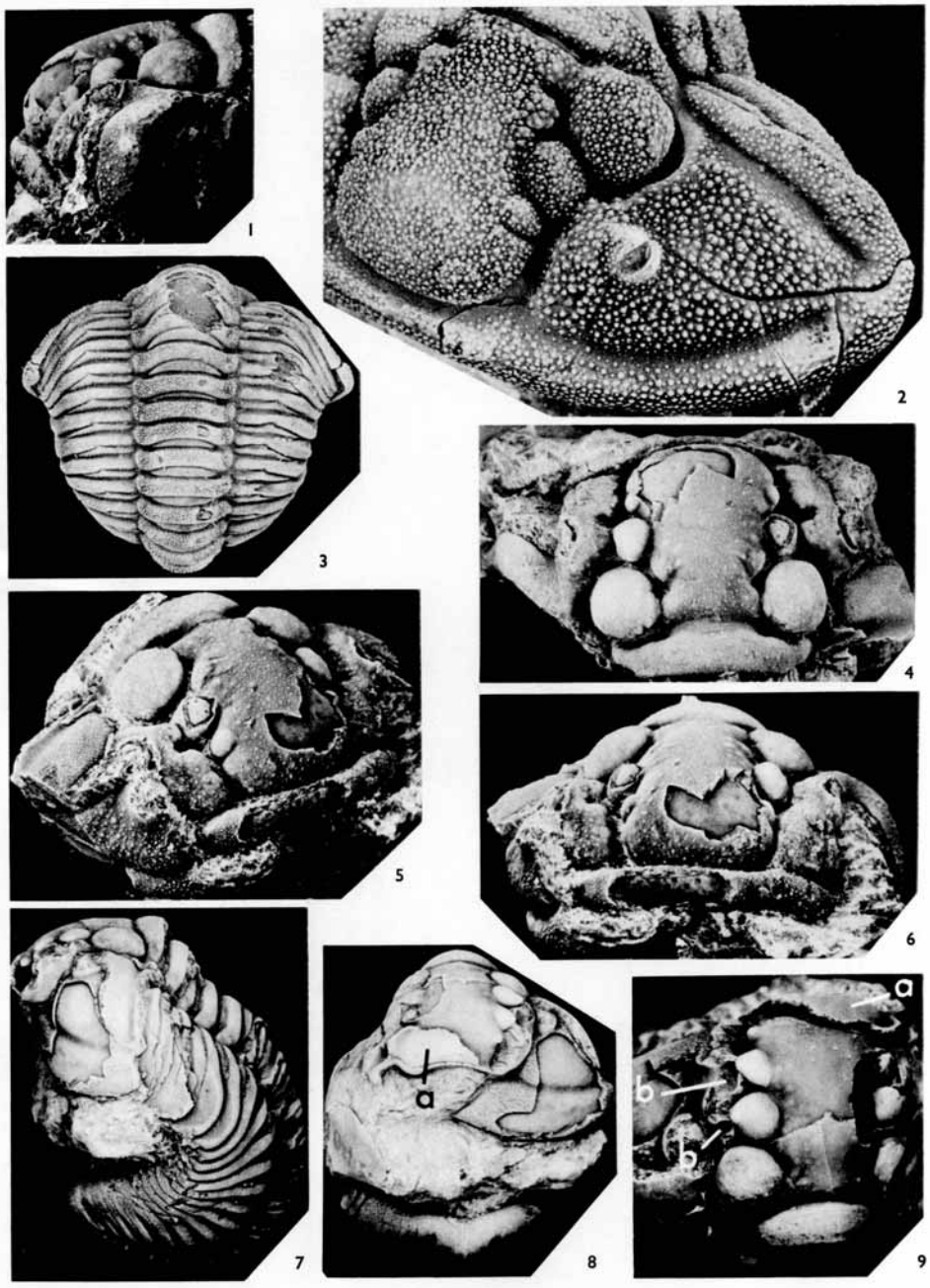


WHITTINGTON, Silurian calymenids



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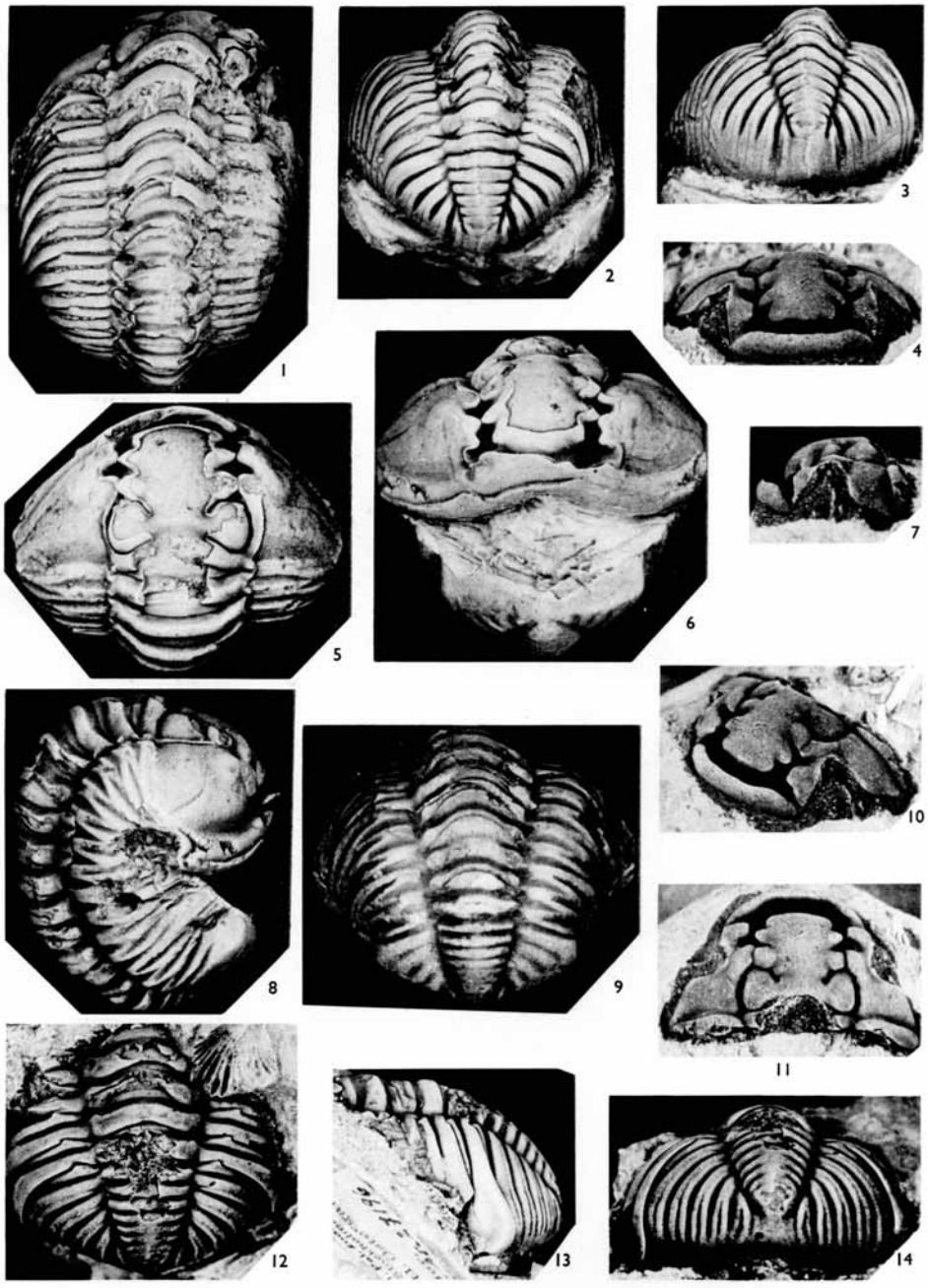

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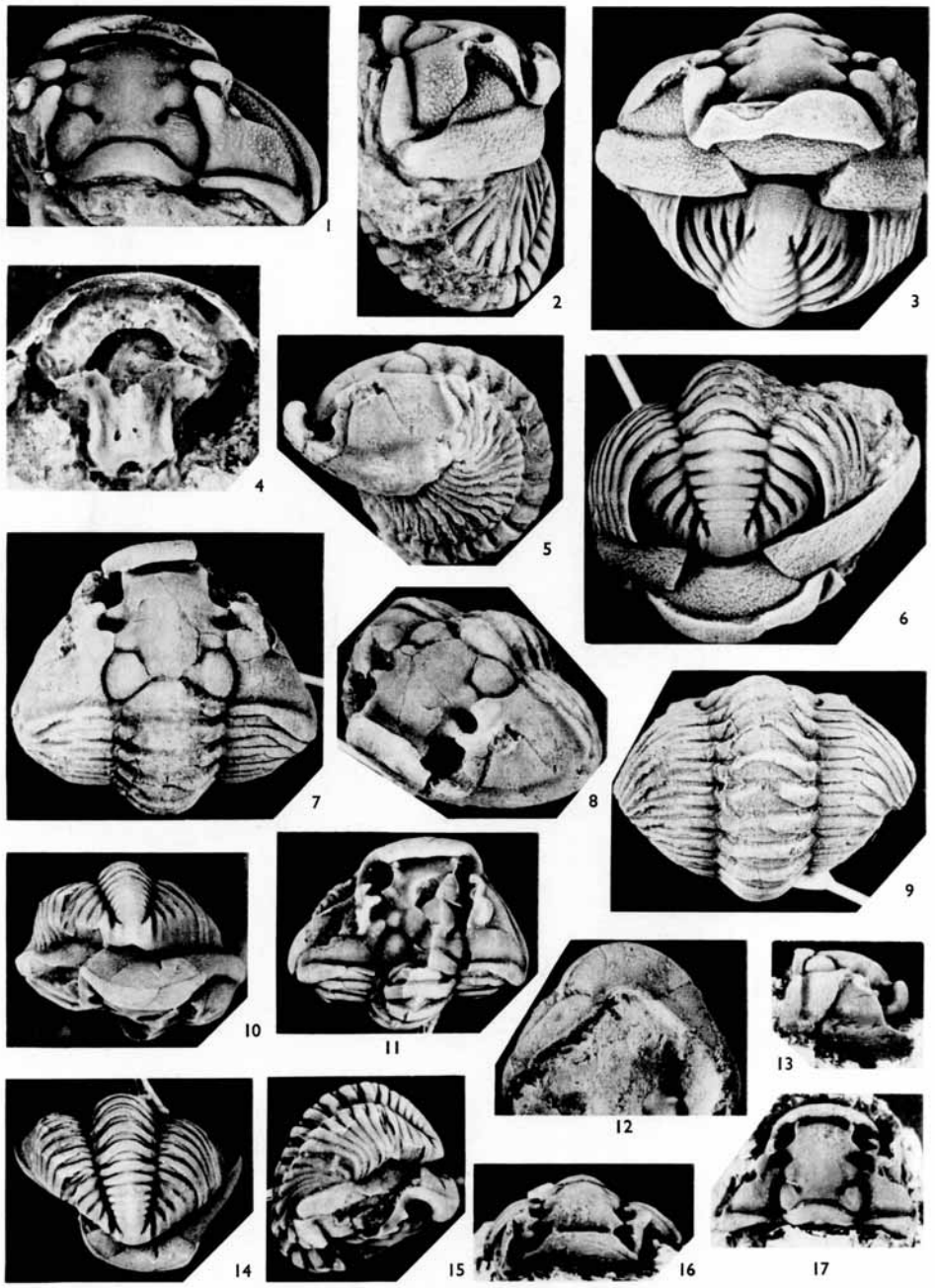

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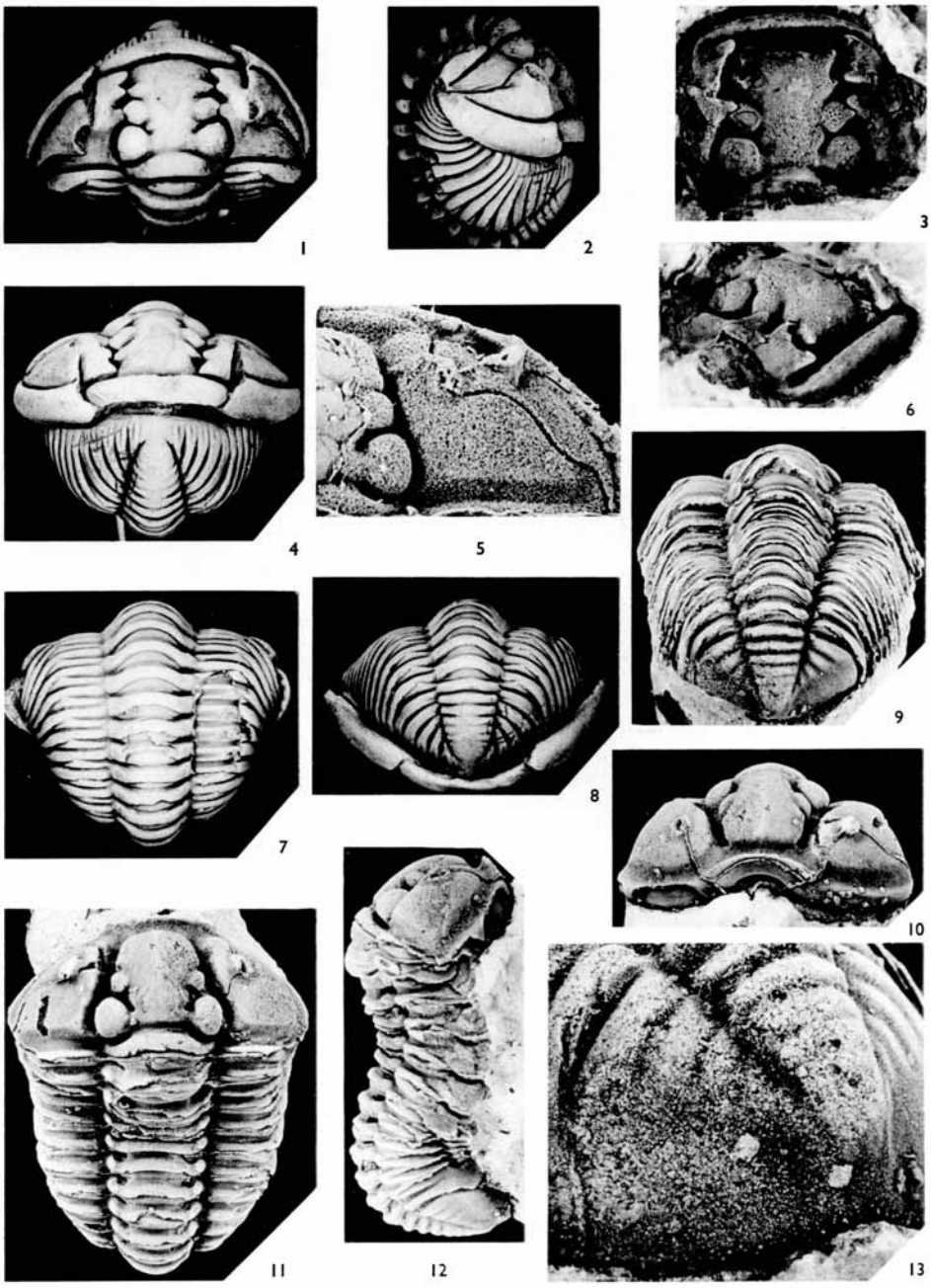

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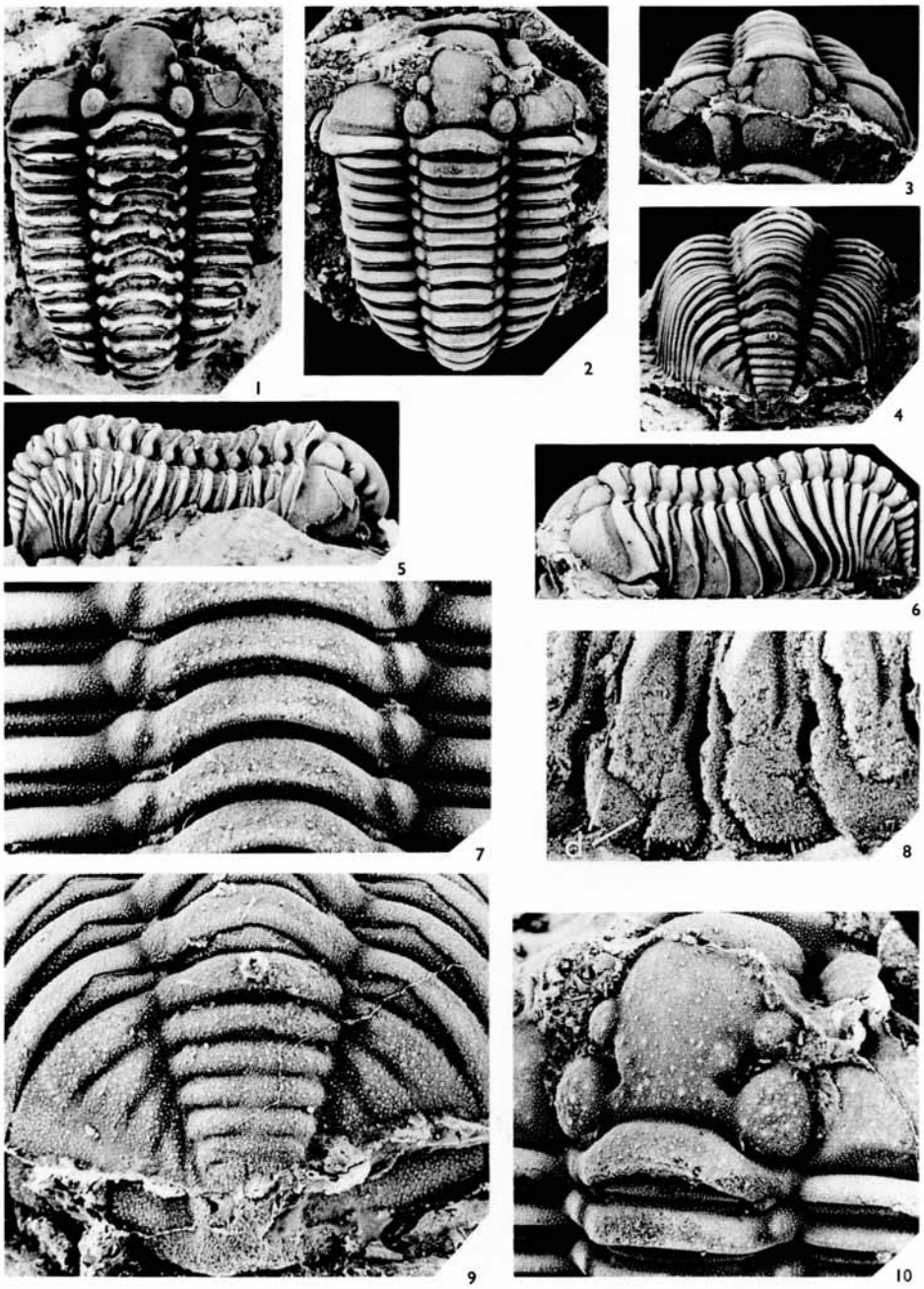

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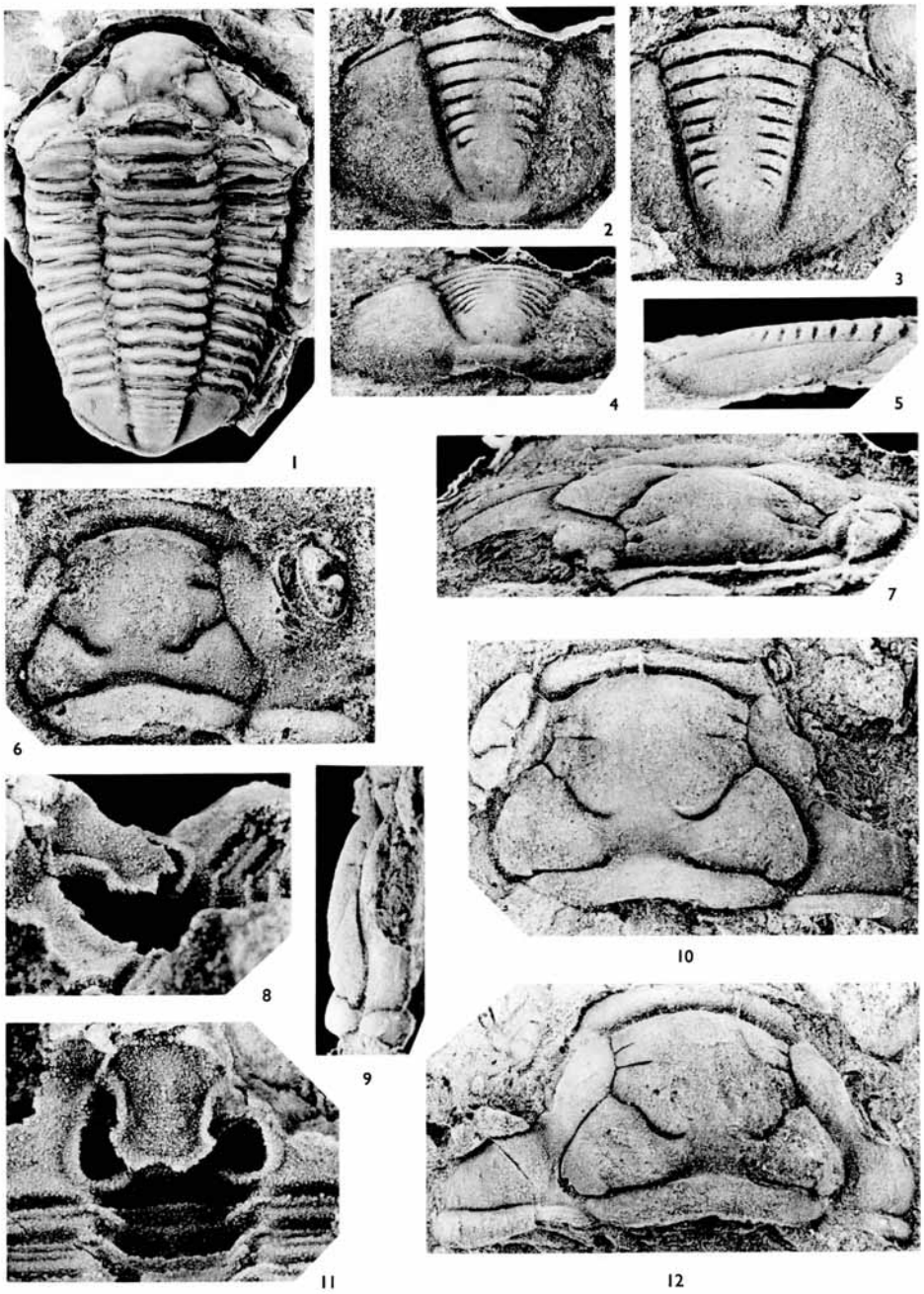

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