MORPHOLOGY OF THE EXOSKELETON

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This section deals exclusively with the mineralized portion of the cuticle, the exoskeleton, other portions of the trilobite body being considered in the following section. In both these sections reference is to the exoskeleton and body of a trilobite in which the specific number of thoracic segments is present, a **holaspis.** To avoid ambiguity, all paired structures are described in the singular.

SIZE, FORM, AND ORIENTATION

The exoskeletons of trilobites are found in a wide variety of marine sediments, the original mineral matter apparently little changed or recrystallized, replaced, or removed to leave a mold. The exoskeletons may be preserved complete, or lacking ventral sclerites and librigena, partially or wholly disarticulated, or in a fragmentary state. When preserved in limestone, in a concretion, or in coarser clastic sediments, the exoskeleton may retain its original convexity; in finer clastic sediments the exoskeletons are flattened and distorted as a result of compaction of the sediment. Distortion may also result from subsequent stress of the enclosing rock, such as that producing cleavage. Exoskeletons preserved by silicification, which may be freed from the limestone matrix by dissolving it away with acid, have given much knowledge of morphology and growth. Improved methods of casting, in latex or plastic compounds, have greatly facilitated study of exoskeletal molds.

The exoskeleton is ovoid or subelliptical in outline and convex, the convexity of individual portions and of the entire exoskeleton differing greatly between taxa. It extends inward, for a distance that varies between taxa, beneath the ventral side of the animal. Spines, hollow projections from the exoskeleton, may be developed in any portion of the exoskeleton. These spines are typically closed structures, apart from the minute canals and openings described below in the section on exoskeletal microstructure and sculpture (p. 74). Another exception is the intergenal spine during the instar stages of development of *Olenellus* (PALMER, 1957, pl. 19, fig. 2, 3, 12), which is not closed on the ventral side. Presumably it became closed during the last instar stage when it was reduced to a small remnant.

While many holaspid exoskeletons are between 3 and 10 cm in length along the midline (excluding anterior or posterior spines in this line), one example, *Acanthopleurella stipulae,* is 1.07 to 1.50 mm in length and is believed to be the smallest known (FORTEY & RUSHTON, 1980). RAYMOND (1931) listed and discussed large known trilobites, including Middle Cambrian paradoxidids; Ordovician asaphids, lichids, and homalonotids; and Devonian lichids, homalonotids, and dalmanitids. Lengths range from 30 to 70 cm, the maximum being that of the Ordovician *Uralichas,* which RABANO (1989) gave as 66 cm. BERGSTRÖM and LEVI-SETTI (1978) described a specimen of *Paradoxides davidis* with a sagittal length of 37 cm, and DAILY and others (1979, p. 16) recorded an individual of *Redlichia* with a length of 35 cm. Dr. R. J. F. JENKINS, University of Adelaide, informs me (personal communication,1989) that this latter figure may be incorrect, the largest specimens he has traced being about 25 cm in length. In the early Middle Cambrian of Morocco occur an Olenellina, specimens of which attain a maximum length of 23 cm, and a paradoxidoid of a maximum length of 39 cm (GEYER, 1993). N. C. HUGHES (1993, p. 9) considered that the largest individuals of the Upper Cambrian *Dikelocephalus* were 40 to 45 cm in length. A complete exoskeleton of an isotelid of Ordovician (Ashgill) age, with a sagittal length of 43 cm, has been recorded from the Hudson Bay area of Canada (M. E. JOHNSON, SKINNER, &

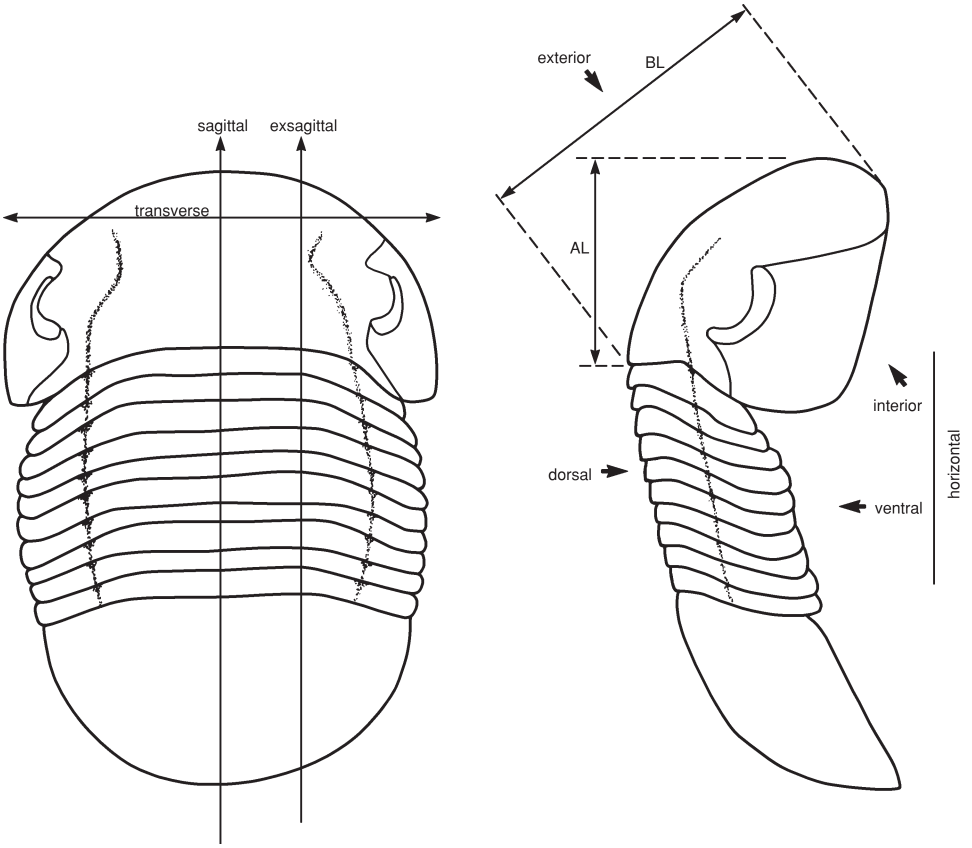


FIG. 1. Dorsal and right-lateral outlines of the Silurian illaenid *Bumastus,* ×1 (new). See text (p. 2–3) for discussion of orientation and directions.

MACLEOD, 1988, fig. 13), and REIMANN (1943) considered that the Devonian lichid *Terataspsis grandis* attained a length of at least 50 cm. It is common experience when collecting to find fragments of larger portions of the exoskeleton than any found entire (e.g., RAYMOND, 1931), and records of large Devonian dalmanitids and homalonotids appear to be based on such fragments.

In order to describe without ambiguity what is meant by length and width of an exoskeleton or any portion of it, the direction in which a measurement is being made is best referred to either a longitudinal or a transverse direction in the entire exoskeleton (Fig. 1). **Sagittal** (abbreviated to *sag.*) is the direction along the axial midline, **exsagittal** (abbreviated as *exs.*) is that direction parallel to but outside the sagittal line, and **transverse** (abbreviated as *tr.*) is the direction at right angles to sagittal. Thus an axial ring may be described as wide (tr.), i.e., wide in a transverse direction, but short (sag. and exs.), i.e., short in the midline or outside it but parallel to it. As W. ZHANG and JELL (1987, p. 35) have advocated, it would be advantageous if long and short were used uniformly with reference to longitudinal (sag. and exs.) dimensions and broad and narrow with reference to transverse (tr.) dimensions. To describe the direction away from the sagittal line, **abaxial** is used, whereas **adaxial** is toward the sagittal line. In illustrations of trilobite exoskeletons, partial or complete, conventions may be needed to explain the direction in which the specimen is being viewed. These conventions are not necessary if the specimen is flattened in the bedding plane, when a view at right angles to this plane will suffice. In specimens retaining some or all of the original convexity, views described with respect to the animal as dorsal and right lateral (Fig. 1) may be given, supplemented by anterior, posterior, ventral, or oblique views. The line AL may be considered to lie in the horizontal plane with respect to the animal, but then the dorsal view does not show fully the external surface of the cephalon. Hence WHITTINGTON and EVITT (1954) used views termed *exterior* and *interior,* taken at right angles to the vertical plane in which the line BL lies. BRUTON (1968a) preferred the term *palpebral* for the exterior view which is approximately vertical to the surface of the palpebral lobe. The problems inherent in the use of the term *horizontal* with reference to the exoskeleton were made evident by FORTEY (1975b, p. 15). How to orient the exoskeleton or its parts for the purpose of taking measurements has been debated (TEMPLE, 1975); for example, the measurement of BL rather than AL is recommended for length of cephalon (cf. BRUTON & OWEN, 1988). What is important is that each study should state precisely what has been measured and how the specimen was oriented, the latter being less obviously necessary when dealing with flattened material.

When the exoskeleton is preserved in calcareous rock, it may have been partially stripped off as the rock was split to reveal the specimen. Such specimens, where exfoliated, show a mold of the inner surface of the exoskeleton similar to the internal molds that are extracted from clastic rocks. The features shown by the external surface of the exoskeleton are different from the **visceral features**, those of the inner or **parietal surface** of the exoskeleton. It is important that the external and internal (parietal) features of an exoskeleton be described from the exoskeleton or from casts made from molds or of exfoliated specimens. Confusion arises when the parietal surface is described as it appears on the mold (of an exfoliated specimen) or an internal mold is described as if it showed the external surface of the exoskeleton.

DIVISIONS OF THE EXOSKELETON

The trilobite exoskeleton is divided by shallow infolds, evident externally as furrows, appearing on the inner surface as low ridges (Fig. 2). The longitudinal **axial furrow** isolates the convex median **axis** from the lateral portion. The axis is crossed by transverse furrows (lateral glabellar, occipital, articulating, and inter-ring furrows) at similar intervals (gradually decreasing posteriorly) from one another; these furrows are considered to correspond to the boundaries of the somites of the body. On the lateral region of the exoskeleton, each furrow (posterior border and pleural furrow) commences opposite a transverse axial furrow, and extends outward and slightly backward. The exoskeleton is also divided by transverse articulations (Fig. 2), which separate an anterior group of fused somites, the **cephalon;** each of the series of **segments** forming the **thorax;** and a posterior group of fused somites, the **pygidium.** The lateral portion of the cephalon is the **gena,** which may extend in front of the axis to the sagittal line. The **pleural region** is the lateral portion of either thorax or pygidium and in the latter may extend behind the axis to the sagittal line. The posterior border furrow of the gena and the pleural furrows of the thorax run outward and slightly backward in relation to the articulations. It has been assumed that the articulations lie at the boundaries of the somites, i.e., that each thoracic segment is the exoskeleton of a somite. Others have argued that the posterior border furrow of the cephalon and the pleural furrows of the thoracic segments and pygidium mark the boundaries of the somites and that the articulations are secondary divisions (see discussion of cephalic segmentation, p. 132). The furrows, infolds of the exoskeleton, are primary features of trilobites, some or all of

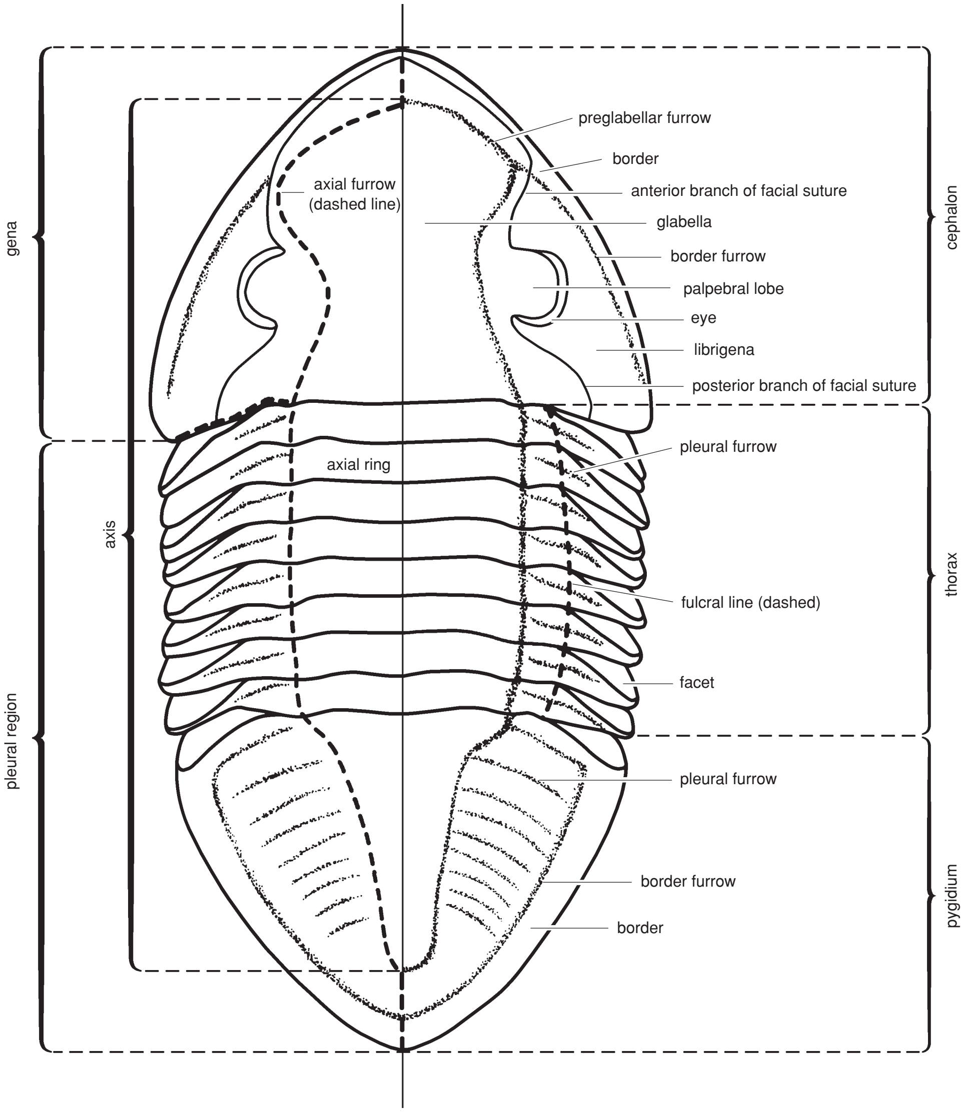


FIG. 2. Terminology of the exoskeleton illustrated by the Ordovician asaphid *Isotelus,* ×8 (new). *Dashed line* on left side outlines limits of axial region, gena, and pleural region. Articulating furrows are hidden beneath posterior margins of glabella and axial rings of thorax.

them appearing early in development (see section on ontogeny, p. 173).

The exoskeleton is continued on the ventral side beneath the outer portions of the gena and pleural region as the **doublure.** Beneath the anterior of the axis there is a ventral sclerite, the **hypostome,** which may be attached to the doublure anteriorly.

CEPHALON

The outline of the cephalon in dorsal aspect varies from subcircular to semielliptical and subtriangular and may be transversely subelliptical. The convexity varies widely between taxa. The size of the cephalon in relation to the thorax and pygidium varies considerably, and a trilobite may be described as **micropygous** (pygidium small in relation to cephalon), **isopygous** (pygidium and cephalon of similar size), or **macropygous** when the pygidium is larger than the cephalon (see section on the pygidium for further discussion of these terms, p. 59). The cephalon may be evenly convex and unfurrowed; but in most taxa the raised axial region, the **glabella**, is outlined by the **axial** and **preglabellar furrows**, and the **occipital ring** is set off from the rest of the glabella by the **occipital furrow**. The gena bears the **eye lobe** (if present), and with rare exceptions the **facial suture** traverses the eye lobe, an anterior and a posterior branch crossing the gena and extending on to the doublure. The facial suture divides the gena into an inner, adaxial portion, the **fixigena**, and an outer, abaxial portion, the **librigena**. That portion of the cephalon that lies adaxial to the facial sutures is the **cranidium**.

GLABELLA

A small circular or oval depression, the **fossula**, when developed, may be used to separate the preglabellar furrow from the axial furrow, the two furrows that are continuous and outline the glabella (Fig. 3). The fossula lies immediately in front of the junction of the eye ridge with the axial furrow. The size relative to the cephalon, shape, and convexity of the glabella vary greatly; and in some trilobites the glabella may not be outlined by furrows, but wholly or only posteriorly by a convexity differing from that of the rest of the cephalon. In the majority of trilobites the most posterior subdivision of the glabella, the **occipital ring**, is defined by the **occipital furrow**, and an occipital doublure is present, longest sagittally (Fig. 4–5). Abaxially the occipital ring may be inflated, and a **lateral occipital lobe** may be set off by its independent convexity (Fig. 3). A shallow furrow, which curves in an arc across the occipital ring, has been termed the **band furrow** in olenids (NIKOLAISEN & HENNINGSMOEN, 1985, fig. 2) and some asaphids (HENNINGSMOEN, 1960, p. 218), but it may be that in these flattened specimens this supposed furrow is an impression made by the anterior margin of the doublure of the ring. A narrow **posterior band** of the occipital ring, lower than the main body of the ring and set off from it by a change in slope is characteristic of the odontopleurid *Ceratocephala* (WHITTINGTON & EVITT, 1954, p. 55).

Further subdivision of the glabella (Fig. 3–5) in front of the occipital ring may be indicated by furrows or pits, usually in lateral pairs, the **lateral glabellar furrows**. The best defined of these furrows is generally that next to the occipital furrow, with furrows in front of this becoming successively shorter (tr.) and less well defined. In the olenid *Hypermecaspis* (FORTEY, 1974b, p. 45), however, the furrow next to the occipital is shorter (tr.) than those in front, a relatively unusual situation. A similar short furrow was termed an intervening furrow in *Asilluchus* ÖPIK (1963, p. 67) but may well be the basal lateral glabellar furrow. In the oryctocephalid *Sandoveria* (SHERGOLD, 1969, p. 13, fig. 3) a glabellar furrow regarded as the intervening furrow curves back to meet the occipital furrow, isolating an intervening glabellar lobe considered to intervene between the occipital ring and the basal lateral glabellar lobe. The occipital apodeme lies in the occipital furrow behind this intervening lobe, so that the latter might alternatively be regarded as the basal lateral lobe. In this case there would be five pairs of lateral glabellar lobes in *Sandoveria.* Up to four pairs of lateral glabellar furrows are present in many trilobites, and a fifth pair is said to be present in the immature glabella of *Daguinaspis* (HUPÉ, 1951; 1953a, p. 261). These furrows are numbered from the posterior forward as S (sulcus) O, the occipital furrow, and S1, S2, S3, etc. (Fig. 4.2–5). Between these lateral furrows are the **lateral glabellar lobes,** numbered correspondingly L (lobe) 1, L2, L3, etc.; the lateral occipital lobe is designated LO. These lateral lobes may be inflated and so have a convexity independent from that of the adjacent portions of the glabella. The

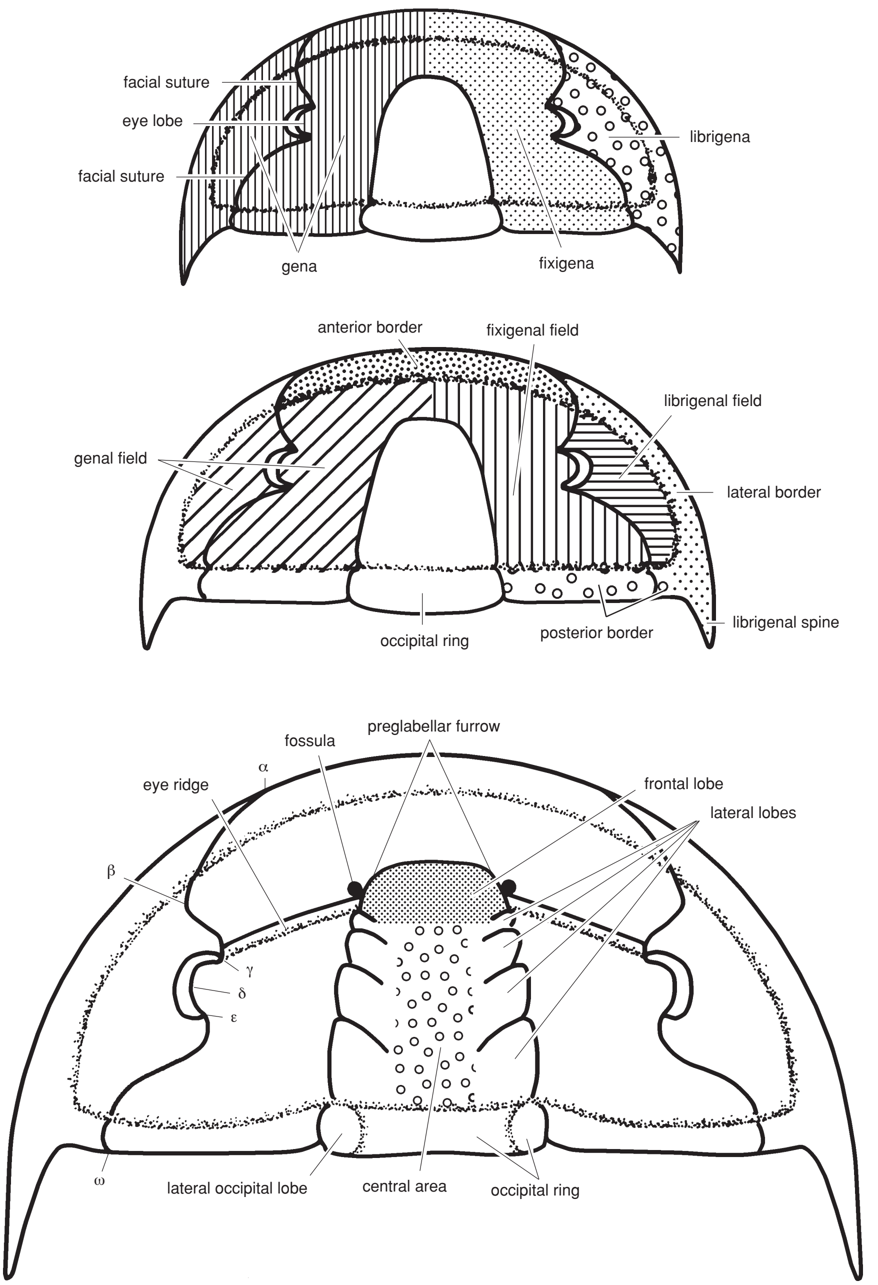


FIG. 3. Terminology of the cephalon illustrated by a ptychopariid trilobite; the labelled portions are differentiated by shading. Greek letters denote salient points on facial suture: β is farthest abaxial point of anterior branch, which reaches the cephalic margin at α; γ to ε is palpebral suture, and δ is the farthest abaxial point of this suture; posterior branch reaches cephalic margin at ω (new).

lateral glabellar furrows vary in depth, length (tr.), and direction; may extend to the axial furrow; and may be subcircular or oval depressions, adjacent to or some distance from the axial furrow. A pair may extend adaxially to form a continuous **transglabellar furrow**.

In the Agnostina a different notation and terminology, initiated by ROBISON (1964, 1982), has been applied to the glabella (Fig. 6.1). The basal lobes and narrow (sag. and exs.) occipital band are excluded from the glabella, which is divided by the transglabellar furrow into the **anteroglabella** and **posteroglabella**. The posterior portion of the posteroglabella projects back between the basal lobes as the **glabellar culmination** and may be inflated and prominent, rounded, or angulate. Lateral furrows of the glabella are numbered F1 to F3 from the posterior forward, F3 being the transglabellar furrow. Axial rings defined at the anterior margin by these furrows are numbered M1 to M3 from the posterior forward. This terminology was not applied to the Eodiscina by JELL (1975a), who regarded the basal lobe as occipital and used the notation S and L for glabellar furrows and lobes as applied to all trilobites except the Agnostina (Fig. 5). In trilobites (except Agnostina) the portion of the glabella in front of the most anterior pair of lateral furrows is the **frontal lobe** (Fig. 3), for which HENNINGSMOEN (1957a, p. 12, fig. 1) used the abbreviation LA. The portion of the glabella lying between the frontal lobe, occipital furrow, and adaxial ends of the lateral glabellar furrows is the central area of the glabella. The frontal lobe and central area may be referred to as the fronto-median glabellar lobe. Other subdivisions of the glabella are developed in particular taxa, including the **occiput** in trinucleids (C. P. HUGHES, INGHAM, & ADDISON, 1975, p. 558, fig. 1), the **intercalating ring** in phacopids (RICHTER & RICHTER, 1926, fig. 14) (both of these lying immediately anterior to the occipital furrow), and the **median preoccipital lobe** in the proetid *Ditomopyge* (WELLER, 1935). In lichids a **longitudinal furrow** may be directed exsagittally and join the inner ends of the lateral glabellar furrows, enclosing two or three lateral lobes or a single **composite lateral lobe** between the longitudinal and axial furrows (Fig. 7.2–6). There have been differing interpretations of the origins of these lobes, whether they are part of the glabella, and whether the most posterior was an occipital lobe. Studies of ontogeny have shed light on some of the problems, in particular the recognition of the **bulla** swelling in early growth stages and its development into the **bullar lobe**. The **posterolateral cranidial lobe**, a swelling adjacent to the base of the glabella, appears to belong to the fixigena and not the glabella. The history of views on glabellar lobation in lichids was reviewed by THOMAS and HOLLOWAY (1988), and the terminology they accepted is given in Figure 7. The most posterior lateral lobe is considered to be part of L1, which is consequently subdivided into L1a (the more posterior) and L1b. In two subfamilies (Selenopeltinae and Ceratocephalinae) of the Odontopleuridae, subdivisions of L1 and L2 have been recognized by RAMSKÖLD (1991b, fig. 6). L1 is subdivided into L1a (exterior), L1b (interior), and L1c (anterior) sublobes; and L2 is subdivided into L2a (interior) and L2b (exterior) sublobes.

On the inner surface of the exoskeleton, occipital and lateral glabellar furrows are reflected as ridges. In particular species, SO, S1, and S2 may be deepened a short distance adaxial to the axial furrow, and this deepening is reflected on the inner surface as a knob or bladelike extension of the ridge that projected into the body as an **apodeme** (Fig. 5). Such apodemes are characteristic of Cheirurinae and Deiphoninae but not of Acanthoparyphinae or Sphaerexochinae (CHATTERTON & PERRY, 1984), for example; are well developed in encrinurids (CHATTERTON & LUDVIGSEN, 1976, pl. 14–15; EVITT & TRIPP, 1977) and pterygometopids (LUDVIGSEN & CHATTERTON, 1982, pl. 6–7); and are less strongly developed in odontopleurids (CHATTERTON & PERRY, 1983). In Phacopoidea (CAMPBELL, 1976; STØRMER, 1980) areas of muscle attachment other than apodemes have been described as pits in the external surface or darker areas distributed widely on the exoskeleton. In asaphids (FORTEY, 1975b, p. 17; 1980c, fig. 1, 3), illaenids (JAANUSSON, 1954, p. 549–551), styginids (LANE & THOMAS, 1983, fig. 1–2), and raphiophorids (WHITTINGTON, 1965, pl. 10–12; FORTEY, 1975b, pl. 22, 24–25), smooth areas that may be slightly depressed and appear as raised areas on the internal mold are considered to be areas of muscle attachment corresponding to the glabellar furrows (see Fig. 20). As some of these examples show (Fig. 8), these areas may appear dark, particularly when the specimen is immersed in liquid. A particular such area, the **lunette**, in the illaenid *Bumastoides* (Fig. 9.1–2) is crescentic in outline and raised on the inner surface of the exoskeleton. Smooth or dark areas, representing areas of muscle attachment or glabellar furrows, have been recognized in other trilobites such as olenids (HENNINGSMOEN, 1957a, p. 92), *Telephina* (WHITTINGTON, 1965, pl. 37), and *Remopleurides* (WHITTINGTON, 1959a, pl. 5).

In Agnostina the external surface of the glabella and occipital (basal) lobes may display smooth patches, some faintly depressed (Fig. 10) (see also HUNT, 1967, pl. 22, fig. 44–47). Similar patches may be outlined by an impressed rim on the internal mold (FORTEY, 1980b, p. 30; SHERGOLD, 1975, pl. 3, fig. 3, pl. 11, fig. 5), indicating that the exoskeleton was thickened. In other specimens similar areas may appear dark (ROBISON, 1984, p. 42). These areas are considered to have been for muscle attachment, and study of these impressions in internal molds by ÖPIK (1963, 1967) and SHERGOLD (1975) has given rise to a complex terminology for them and the associated ridges, grooves, and pits (Fig. 11.1). A paired ridge, the **axial glabellar carina**, may run sagittally between the **axial glabellar node** and the **terminal glabellar node**, and a **notula** is a minute pit (in the internal mold) associated with a muscle area. A possibly analogous structure, a sagittal ridge (carina) on the internal mold of the glabella, has been recognized in such illaenids as *Panderia* (BRUTON, 1968a, pl. 1, fig. 1–3) and *Stenopareia* (OWEN & BRUTON, 1980, pl. 3, fig. 10). In asaphids rows of impressions on either side of the sagittal line of the internal mold of the glabella, in some examples separated by a low sagittal ridge, were described by HENNINGSMOEN (1960, p. 213); a low sagittal ridge is present in the glabella of *Stegnopsis* (WHITTINGTON, 1965, p. 347, pl. 22, fig. 3).

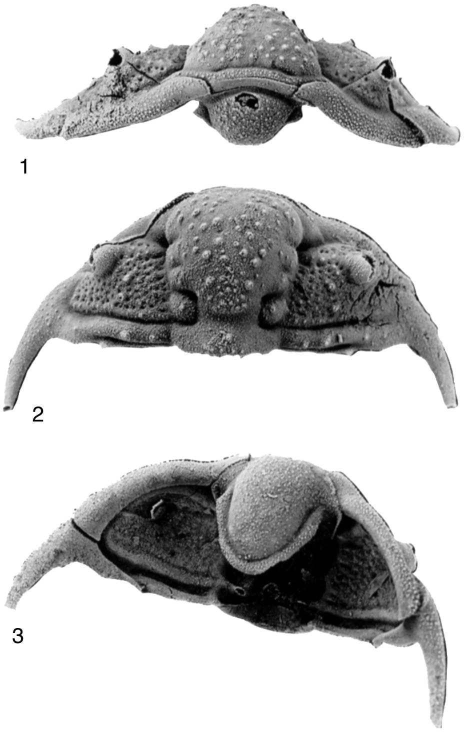


FIG. 4. Cephalon of the cheirurid *Ceraurus whittingtoni* EVITT, 1953, Middle Ordovician, Virginia, USA. The visual surface of the eye lobe is missing. *1,* Anterior view, ×3 (new); *2,3,* dorsal and oblique ventral views, ×3 (Whittington, 1960b, fig. 1a,c).

The glabella may bear median or paired spines or nodes on the frontal or frontomedian lobes, and in many taxa there is a median or paired occipital spine or node. A spectacular example is the encrinurid *Perirehaedulus* (Fig. 12), which also shows a sagittally directed **anteromedian depression** or **longitudinal median glabellar furrow** extending back from the anterior margin of the frontal glabellar lobe. Such a furrow or an associated pit or more elongate (tr.) median depression in the preglabellar furrow is characteristic of encrinurids (FORTEY, 1980b, pl. 22; EVITT & TRIPP, 1977). Similar depressions are present in some pliomerids (WHITTINGTON, 1961b), and cheirurids (muscle scars in Fig. 4.1) show a median

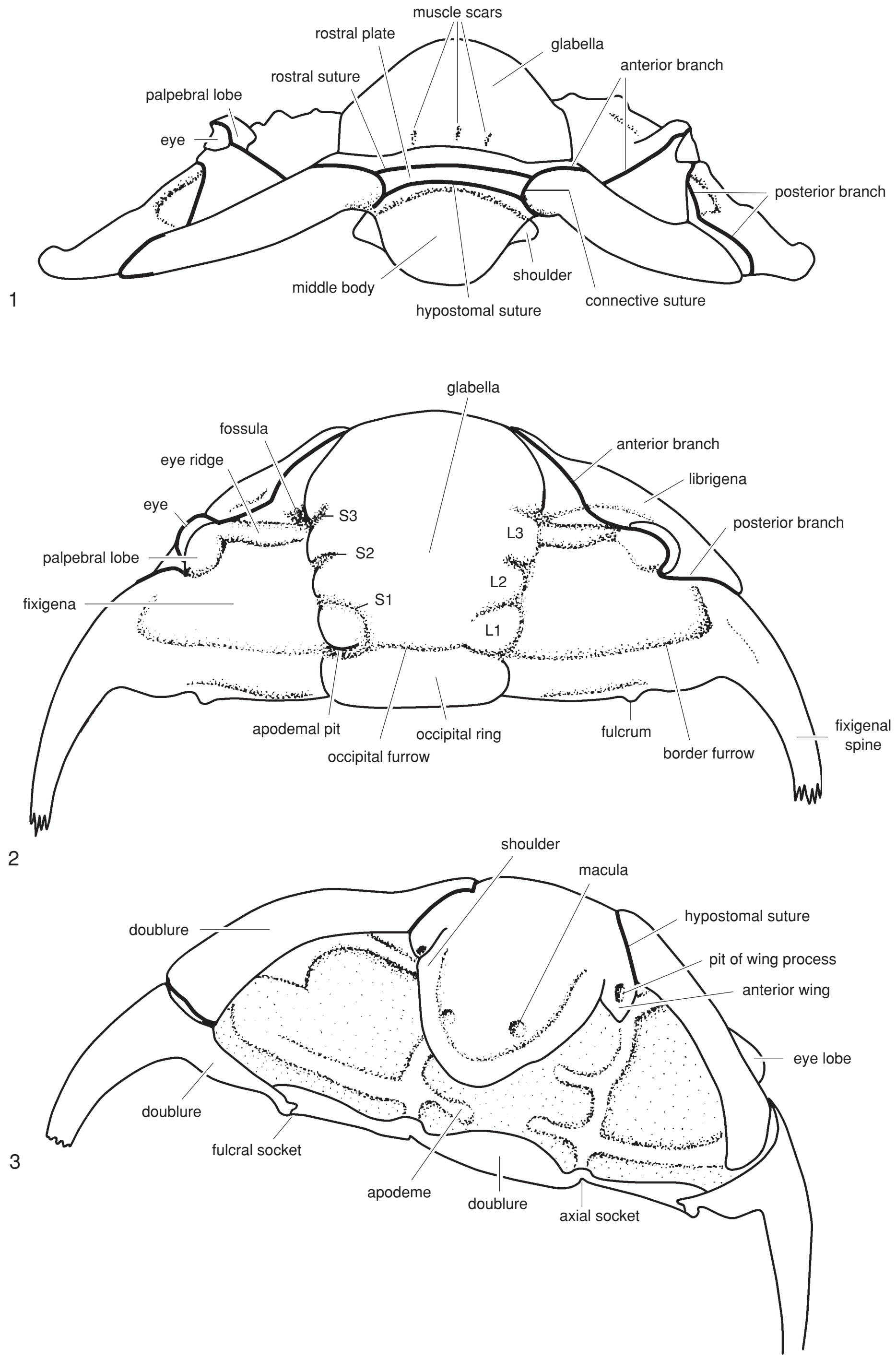
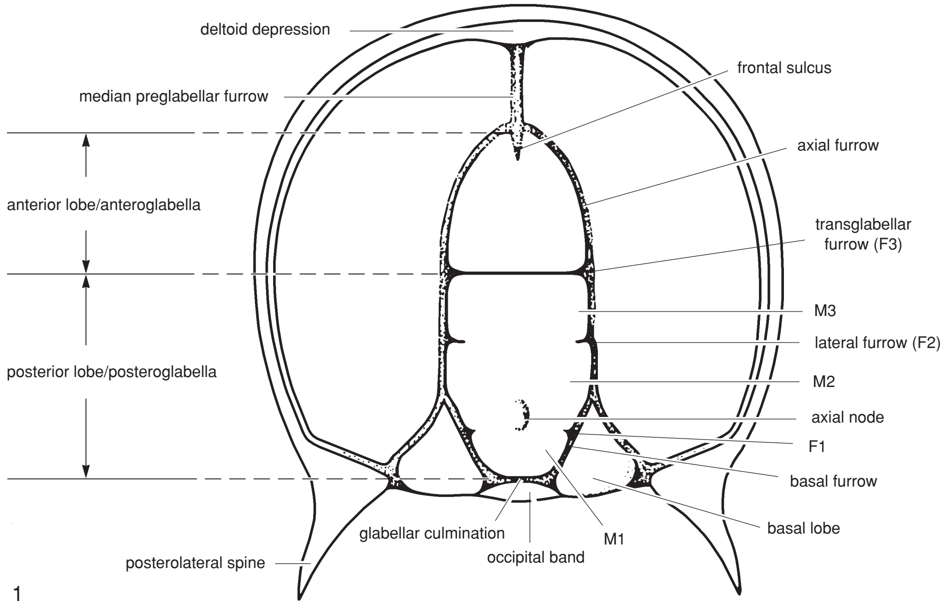


FIG. 5. Diagrammatic representation of anterior (*1*), dorsal (*2*), and oblique (*3*) views of *Ceraurus whittingtoni* EVITT, 1953 (see Fig. 4) to show terminology of the cephalic features (new).



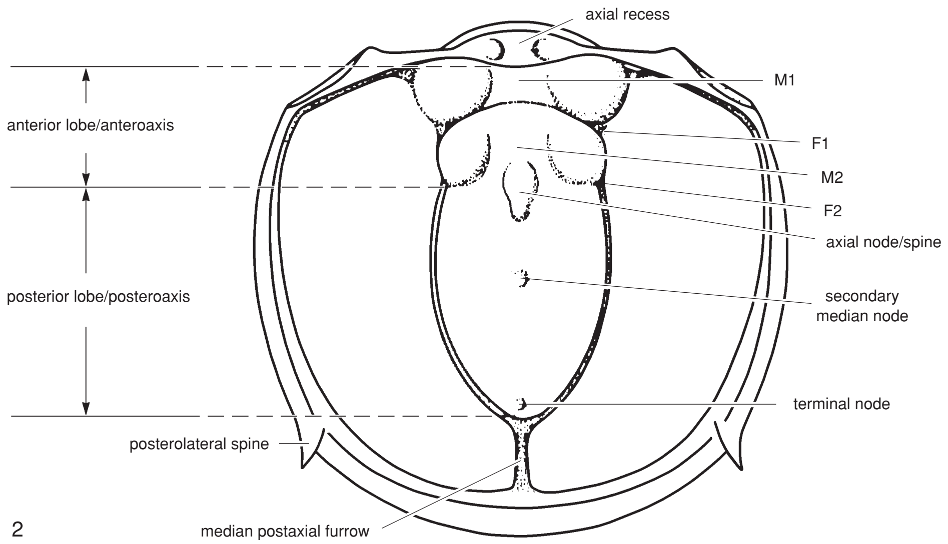


FIG. 6. Terminology applied to the external surface of the Agnostina; *1,* cephalon and *2,* pygidium (Shergold, Laurie, & Sun, 1990, fig. 1–2).

furrow flanked by a pair of depressions. A necklace arrangement of pits on the frontal lobe in phacopids (STØRMER, 1980, p. 263) has long been known and includes deep pits in the preglabellar furrow. These pits and grooves, which form projections on the inner surface, have been regarded as points of muscle attachment. In *Dalmanites* a pair of smooth areas on the frontal glabellar lobe, pierced by minute pores, were regarded as muscle-attachment areas by RAMSKÖLD (1985, p. 35).

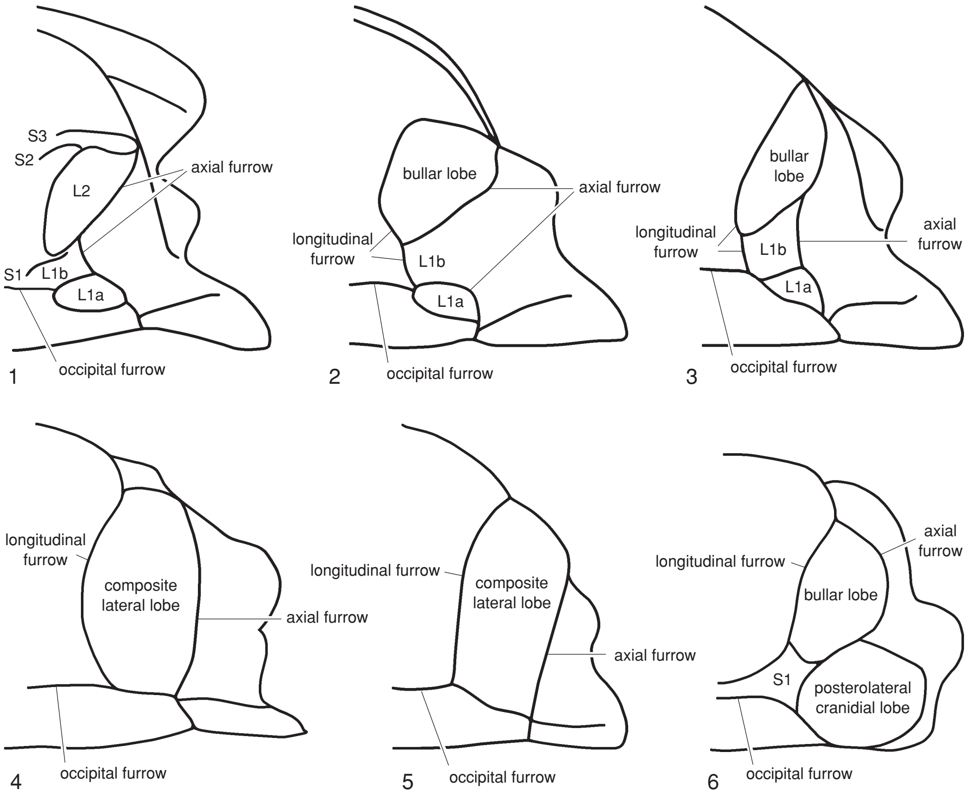


FIG. 7. Cranidial morphology of Lichida. Composite lobe formed by fusion of bullar lobe with L1b or L1a. *1, Lichakephalus; 2, Platylichas (Platylichas); 3, Dicranopeltis; 4, Echinolichas; 5, Amphilichas; 6, Acanthopyge (Jasperia)* (Thomas & Holloway, 1988, fig. 2).

GENA

The gena has a convex border in many trilobites, the area enclosed within this border being the **genal field** (Fig. 3). The term **acrolobe** (Fig. 13) was applied to the area within the border in Agnostina by ÖPIK (1967), but whether it was intended to include the axial region is not specified. The border extends to the midline in front of the glabella, and there may be a **preglabellar field** between the preglabellar furrow and the border (Fig. 14). The preglabellar field may be long (sag. and exs.) or short, flattened and gently sloping, or convex and steeply sloping. In such Cambrian trilobites as *Ctenocephalus* and *Nepea* (see Fig. 23), the preglabellar field is occupied by a prominent, subcircular **preglabellar boss**; in others there may be a **median preglabellar ridge**. This ridge may be narrow (tr.), of constant width, or may be broader, widening forward to merge with the anterior border to form the structure distinguished as the **plectrum** by

FIG. 8. *Illaenus lacertus* WHITTINGTON, Upper Ordovician, Baffin Island, Canada. Dorsal view of enrolled exoskeleton, immersed in liquid, showing darker muscle areas of glabella, ×3 (Whittington, 1954b, pl. 61, fig. 1).

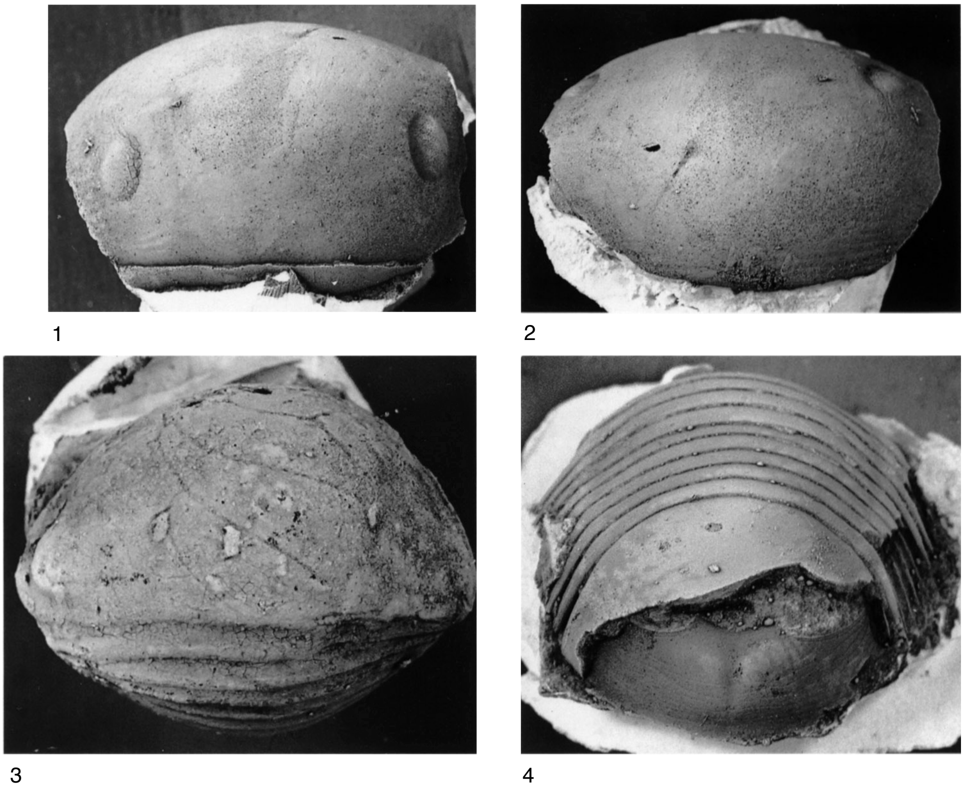


Fig. 9. *Bumastoides milleri* (Billings), Middle Ordovician, Ontario, Canada. *1,2,* Dorsal and anterior views of internal mold of cranidium, showing impression of lunette, ×3; *3,* dorsal view of cephalon of enrolled specimen, ×4.5; *4,* exterior view of thorax and pygidium, latter broken to show mold of outer surface of doublure, ×4.5 (Whittington, 1954b, pl. 62, fig. 18, 25–26, 29).

Öpik (1967, p. 58). Fortey (1990a, p. 547, fig. 9) has described the plectrum stage in the development of Ptychoparioidea. In other trilobites there may be a **median preglabellar furrow** (e.g., Fig. 6). In some proetids a **transverse preglabellar ridge** occurs immediately inside the border furrow (see Fig. 19). The gena bears the eye lobe (when present), and in many trilobites an **eye ridge** runs inwards and forward from the anterior end of the eye lobe to the axial furrow opposite the anterolateral portion of the glabella. Where present, the fossula lies immediately in front of the intersection of the eye ridge and the axial furrow. The gena is divided by the inner edge or furrow of the border, by the eye ridge, and by the facial suture; terminology for these separate areas is given in Figure 14.

The eye lobe is convex, and may be strongly so, or raised on a stalk. In trilobites having a facial suture (Fig. 5), the eye lobe is divided by the suture, in an abaxially curving arc (points γ, δ, and ε in Fig. 3), into the adaxial **palpebral lobe** and an abaxial **visual surface**. Below the visual surface there may be a ridge and furrow, the **eye socle** and **eye socle furrow** (Fig. 15), separating it from the genal field. Abaxial to the eye lobe in proetids, however, there may be a smooth **subocular area** or a depressed **subocular groove** bounded on the outside by a **subocular ridge**. The palpebral lobe, subsemicircular in dorsal outline, is separated from the fixigena by a change in slope or a **palpebral furrow**. It may be subdivided (by this change in slope or furrow) into a convex

palpebral rim bordering the facial suture and a lower adaxial portion. The **palpebral ledge** is a flattened edge or furrow abaxial to the rim. The palpebral lobe and eye ridge may form a continuous structure, the **palpebro-ocular ridge**. Olenellina lack the facial suture; consequently the gena is not subdivided by it, nor is the palpebral lobe outlined abaxially (Fig. 16). Hence a different terminology has been employed. Hupé (1953a) used ocular lobe (*lobe oculaire*) for the combined eye ridge (*crête oculaire*) and eye lobe (*lobe palpebral*), without mention of the visual surface. Öpik (1961a) termed the eye ridge and eye lobe the palpebral lobe, divided longitudinally into inner and outer portions by a furrow, the ocular striga. Bergström (1973a) used anterior and posterior (rather than outer and inner) palpebro-ocular ridge. Here **ocular lobe** is preferred for the combined eye ridge and eye lobe, including the visual surface. This lobe divides the genal field into interocular and extraocular areas and is itself divided by the **ocular furrow** into inner and outer bands (Fig. 16). The ocular furrow is the ocular striga of Öpik or epipalpebral furrow of Cowie and McNamara (1978). In many specimens of Olenellina, the ocular lobe is broken so that only the outline is preserved (e.g., Fritz, 1972; 1991). In rare specimens (e.g., Whittington, 1989, fig. 8–9) the visual surface is sharply outlined, as it is partially even when the lobe is broken (e.g., Fritz, 1972, pl. 1, fig. 7–8, pl. 15, fig. 16; 1991, pl. 11, fig. 8–9). Öpik (1967, p. 54) argued that there was a **circumocular suture** surrounding the visual surface in this and other Cambrian trilobites. In Olenellina and protolenids the inner and outer ridges of the ocular lobe may divide adjacent to the glabella, the posterior ridge reaching the axial furrow immediately in front of the outer end of glabellar S3, the anterior either merging with the anterolateral edge of the frontal glabellar lobe or the pair uniting around the anterior margin of the preglabellar furrow to form a **parafrontal band** (Hupé, 1953a, p. 105). This band is developed in ellipsocephaloids, particularly in protoleninids (Geyer, 1990b)

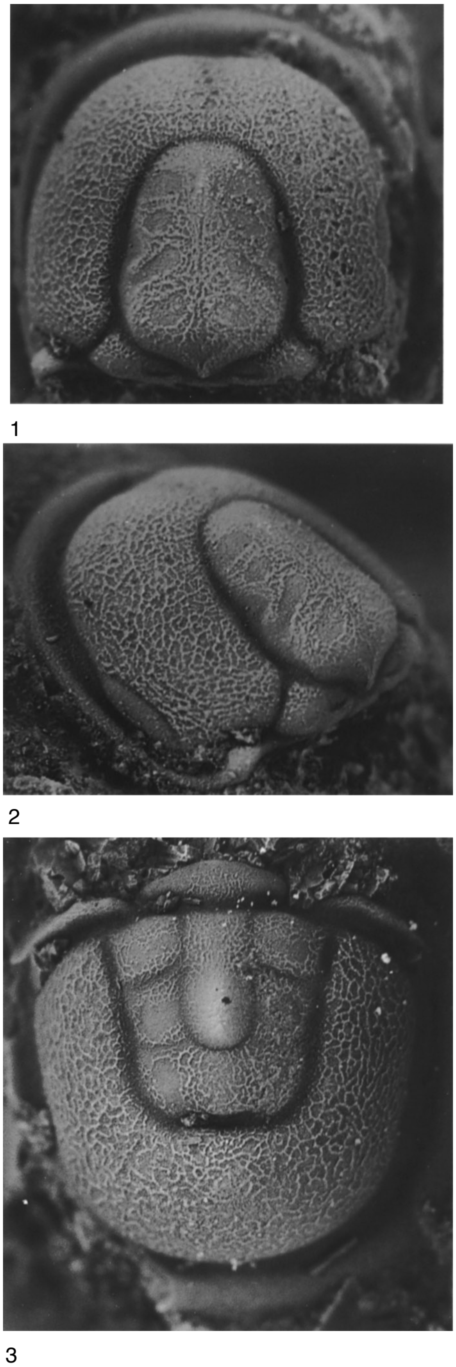


Fig. 10. *Galbagnostus galba* (Billings), Middle Ordovician, Table Head, Newfoundland. *1,2,* External surface of cephalon, dorsal and oblique views; *3,* dorsal view of pygidium, to show sculpture and smooth areas, ×20 (Whittington, 1965, pl. 3, fig. 7, 15; pl. 4, fig. 9).

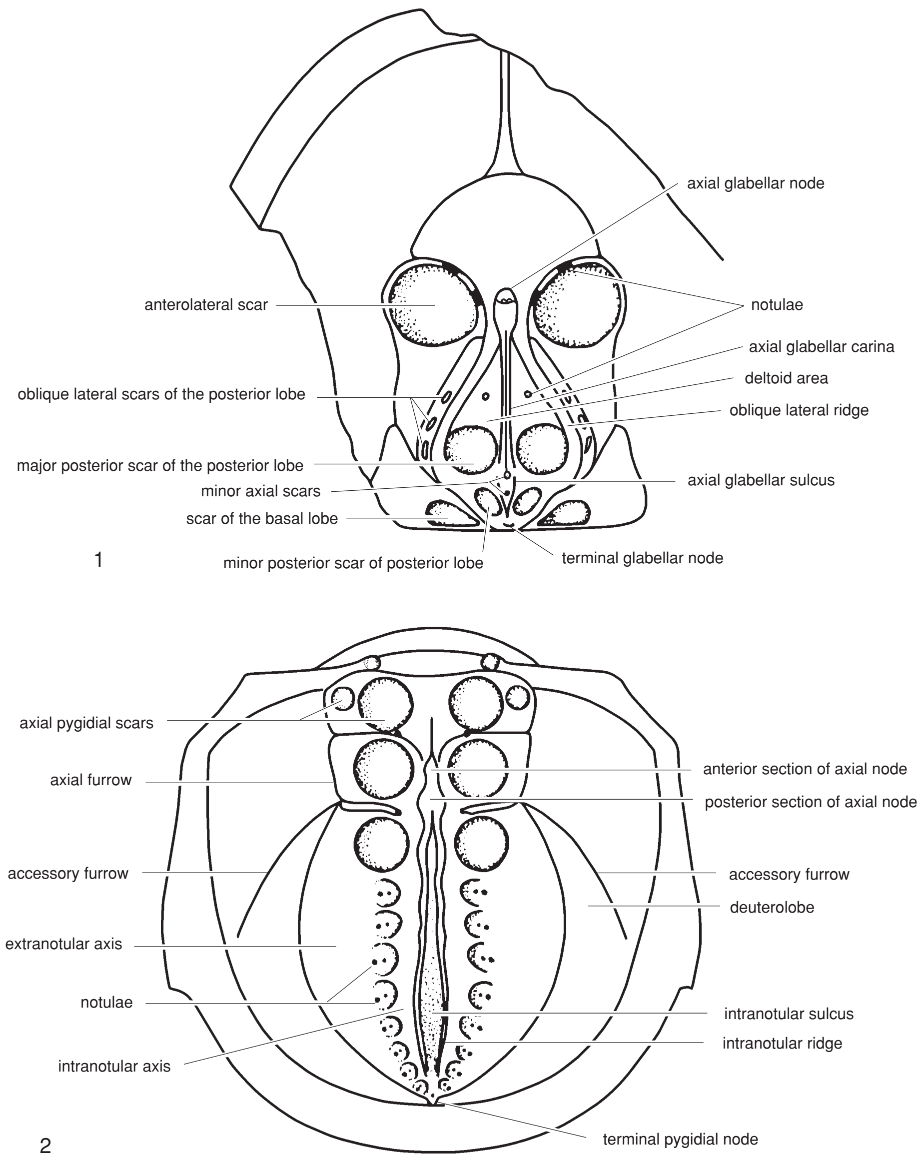


FIG. 11. Terminology applied to the visceral features of the Agnostina revealed by the parietal surface of the exoskeleton; *1,* cephalon and *2,* pygidium. This surface is preserved in many examples as an internal mold of the exoskeleton and illustrated as such (Shergold, Laurie, & Sun, 1990, fig. 6).

and in the redlichioid *Lemdadella* (SDZUY, 1978). It has been observed in the Middle Cambrian *Asthenopsis*, and in some specimens of *A. opalensis* the eye ridge is divided along most of its length into three parallel ridges (JELL, 1978b). In a small cephalon of *Daguinaspis,* HUPÉ (1951) described a third branch from the eye ridge adjacent to the glabella and illustrated similar structures in *Fallotaspis* (HUPÉ, 1953a, pl. 1, fig. 1–3); this structure was used by HUPÉ (1951) in his discussion of cephalic segmentation. The most recent consideration of the morphology of the palpebro-ocular ridge and the parafrontal band was by Pillola (1991, p. 79–84, fig. 47), who concluded that the trisegmented eye ridge is best known in Lower Cambrian trilobites. In younger forms the structure of the eye ridge is simplified.

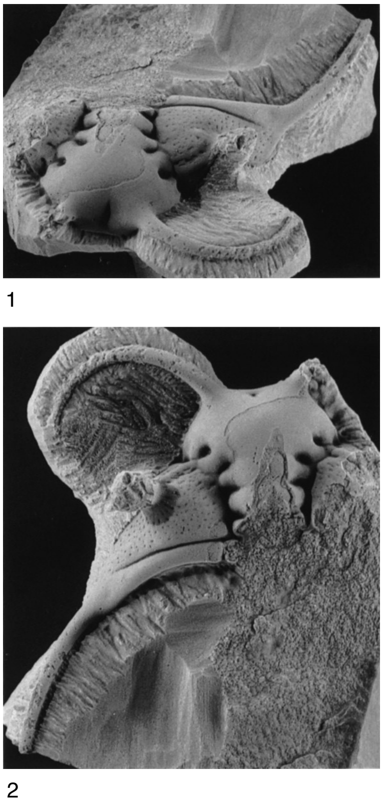


Fig. 12. *Perirehaedulus caprus* (Thomas in Thomas & Narbonne), Silurian, Arctic Canada. *1,2,* Anterior and dorsal views of the holotype, an incomplete cranidium, ×3 (Thomas & Narbonne, 1979, pl. 4, fig. c, e).

A pattern of radiating, distally anastomosing ridges, the **genal caeca**, is developed with varying intensity on the frontal area and adjacent librigenal field or over the entire genal field in many Cambrian and Ordovician trilobites (Öpik, 1961a) and in Silurian and Devonian proetids (Šnajdr, 1980, pl. 63, fig. 3–4). The ridges are numerous and narrow in comparison with the size of the cephalon. They may become stronger as they approach and cross the border furrow or may not be evident on the border. The pattern of the genal caeca is well displayed by *Harpides*, extending from the axial and preglabellar furrows across the genal field and border to the narrow marginal rim (Fig. 17.1). This cephalic border (described below as the fringe) is wide (sag. and tr.), gently concave dorsally, and bilaminar, the two lamellae lying close together. The external surface of the lamella on the underside bears a pattern of radiating ridges corresponding to those on the upper lamella (Fig. 17.2). This suggests that the ridges enclose a system of canals that lay between the lamellae [cf. Fortey's (1974b, p. 53) description of the olenid *Tropidopyge*]. Fritz (1972, p. 23) has shown that in certain Olenellina the median ridge of the preglabellar field is part of the genal caeca (Fig. 18). In *Redlichia* a ridge on the preocular area of the fixigena, directed out close to the anterior branch of the facial suture or situated more adaxially to it, was termed the **facial line** (Whitehouse, 1939, p. 189; Öpik, 1961a, fig. 8; W. Chang, 1966, fig. 1, as the preocular facial line). This ridge is similar in width to those of the genal caeca and has been considered to be part of this system of canals by some authors (Öpik, 1970b, p. 25, pl. 4, fig. 1). In harpids and harpetids, pits lie between the ridges of the genal caeca, and in some olenids (Fortey, 1974b, fig. 4), for example, pits occur in the border furrow between the ridges. The genal caeca may radiate from the eye ridge, the eye lobe, or the axial furrow behind the eye ridge (Fig. 17.1). Thus the eye ridge runs across the radiating caeca, as does the **genal ridge**, curving outward and backward toward the genal angle. The genal ridge may branch abaxially and may not reach the genal angle. It is present in Olenellina (Fig. 16), in redlichioids (the para-ocular facial line of W. Chang, 1966, fig. 1), and, for example, in *Churkinia* (Palmer, 1968, pl. 1, fig. 6). In trilobites lacking an eye lobe or eye tubercle (e.g., *Conocoryphe, Lonchodomas, Anisonotella*), a single genal ridge may extend outward from the axial furrow and curve back to the genal angle. The **intergenal ridge**

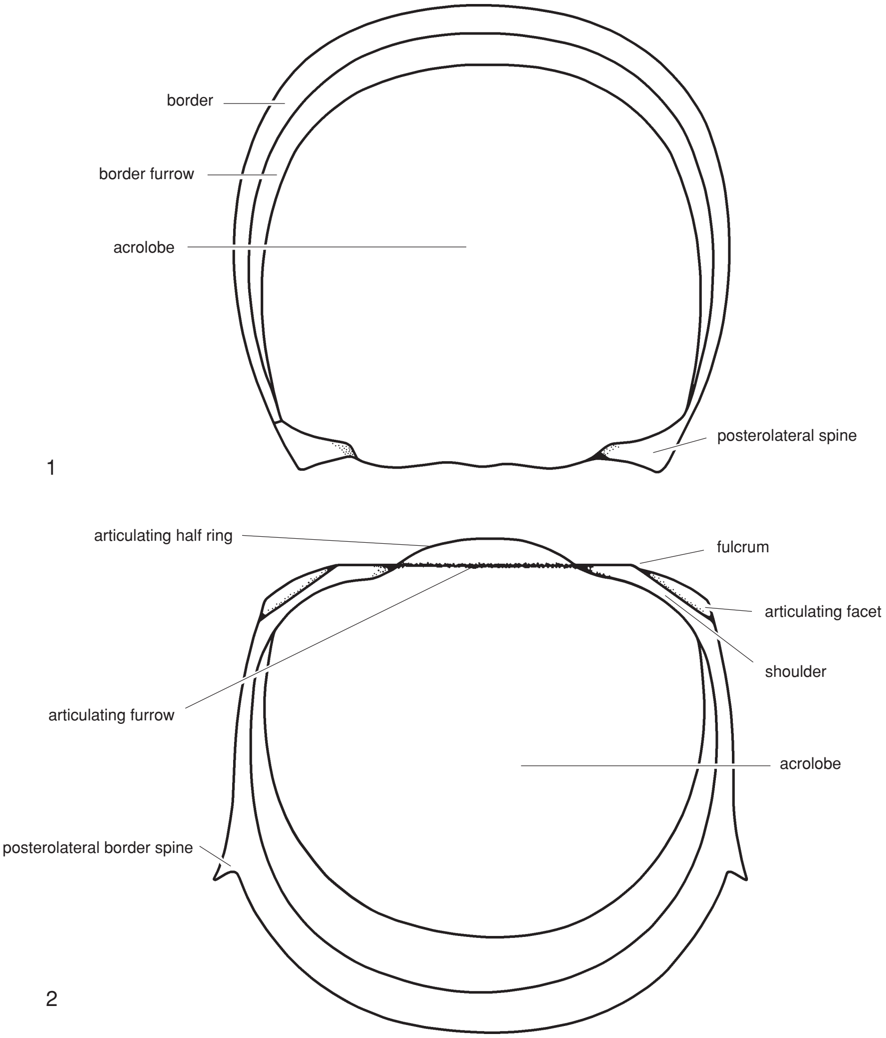


Fig. 13. Terminology applied to the external surface of the Agnostina; *1,* cephalon and *2,* pygidium (Shergold, Laurie, & Sun, 1990, fig. 1–2).

in Olenellina is a ridge that arises from the posterior end of the inflated palpebral (interocular) area and curves outward and backward to the posterior border and base of the intergenal spine (Fig. 16). The ridge is prominent in early developmental stages of *Olenellus* (Palmer, 1957) and *Elliptocephala* (Whittington, 1957a) and is retained in the holaspis. In *Elliptocephala* a less prominent ridge, the **posterior ocular line** or **ridge**, runs back from the posterior end of the eye lobe to the border, outside the intergenal ridge (Fig. 16). Both ridges are present in holaspides of *Fallotaspis* (Hupé, 1953a, pl. 1, fig. 1) and *Eofallotaspis* (Sdzuy, 1978, pl. 1, fig. 1, 4).

In Agnostida (Öpik, 1961a; Robison, 1978, p. 4; Jell, 1975a) a radiating, branching pattern of ridges, **rugae**, separated by furrows or **scrobiculae** that rarely anastomose, extends from the axial furrow to the border furrow. These ridges are relatively

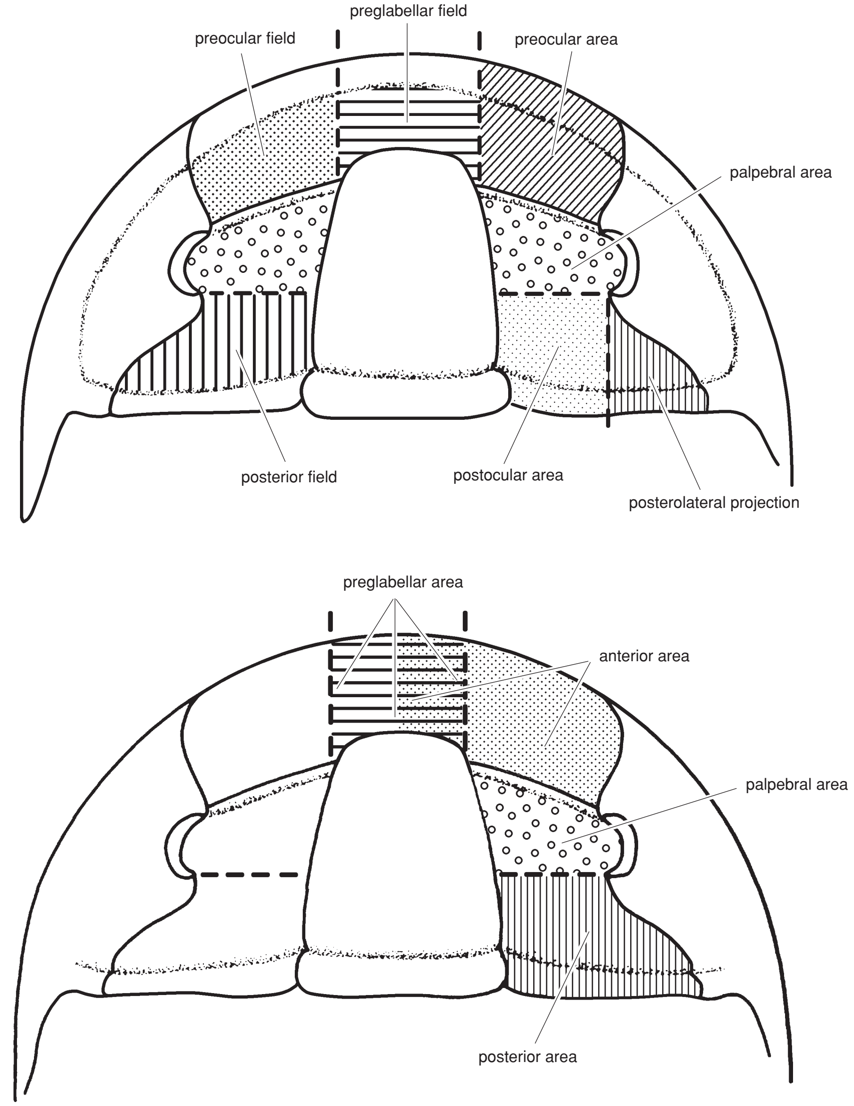


FIG. 14. Terminology of areas and fields of the cephalon illustrated by a ptychopariid trilobite, labelled portions differentiated by shading (new).

much coarser than those of other trilobites and have few main connections to the axial furrow; according to ROBISON these ridges are always anteromedially divided, unlike those in other trilobites. In the Ordovician *Galbagnostus* (WHITTINGTON, 1965, p. 307) and *Arthrorhachis* (FORTEY, 1980b, p. 31) a much finer pattern of radiating ridges has been detected crossing the border furrow.

The **tropidium** (Fig. 19) is a ridge, concentric with the cephalic margin, which traverses the preglabellar and genal fields inside the margin of the doublure (OWENS, 1973; MORZADEC, 1983, pl. 1, fig. 4–6); it may form more than one continuous ridge. OWENS termed similar discontinuous ridges **tropidial ridges**. ORMISTON (1971) described silicified material that showed that the

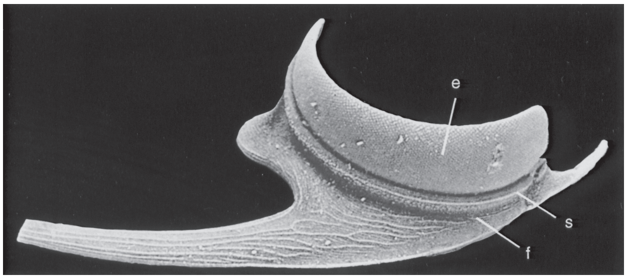


FIG. 15. *Remopleurides plaesiourus* Whittington, Middle Ordovician, Virginia. Oblique view of isolated free cheek to show visual surface of eye (*e*), eye socle (*s*), and eye socle furrow (*f*), ×6 (Whittington, 1959a, pl. 5, fig. 6–7).

tropidium was not reflected as a groove in the parietal surface. According to Šnajdr (1980, p. 18) the tropidium is present as a groove on the parietal surface in forms with a thin exoskeleton; when the exoskeleton is thick it is not so represented.

On the genal field adjacent to the base of the glabella there may be a low, elongated (exs.) swelling, the **baccula** (Fortey, 1975b) (see Fig. 73). This swelling may be connected to the anterolateral corner of the occipital ring, separated from L1 by a furrow, separated from the glabella by the axial furrow, or separated in addition from the genal field by the **baccular furrow**. The different forms of the baccula in unrelated trilobites have led some authors to consider it part of the glabella, others to regard it as part of the genal field. In *Harpides* (Fig. 17) and harpids such as *Dolichoharpes* (Chatterton & Ludvigsen, 1976, pl. 7, fig. 8–9, 16), a semicircular depressed area lacking reticulate ridges lies at the inner posterior corner of the genal field, opposite L1, and is termed the **ala.** An area in a similar position in styginids (Fig. 20), also smooth, has been called the lateral muscle impression (Fortey, 1980b, p. 59; Lane & Thomas, 1983, fig. 1–2); it has been compared with the lunette in *Bumastoides* (Fig. 9.1–2) and other illaenids. The **paraglabellar area** in homalonotids (Cooper, 1982) is in the same position. Some, if not

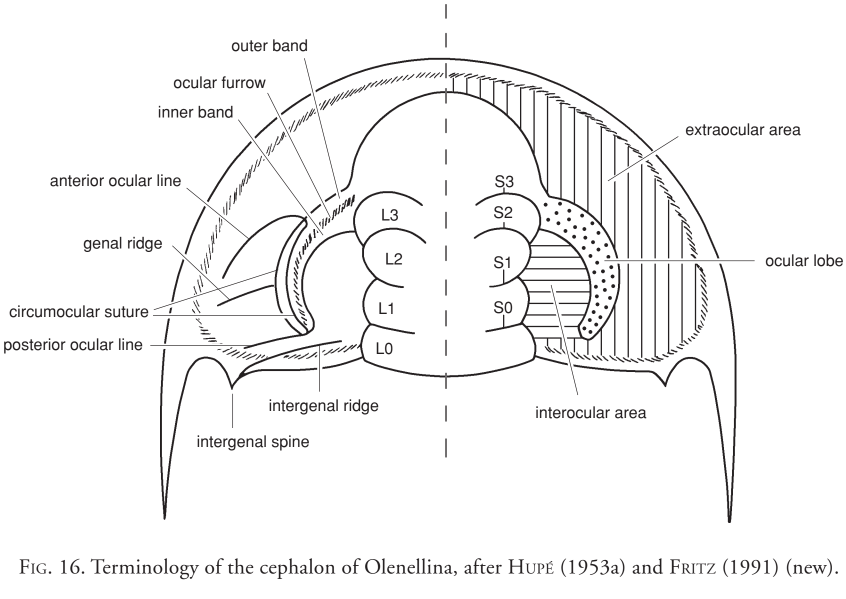


FIG. 16. Terminology of the cephalon of Olenellina, after Hupé (1953a) and Fritz (1991) (new).

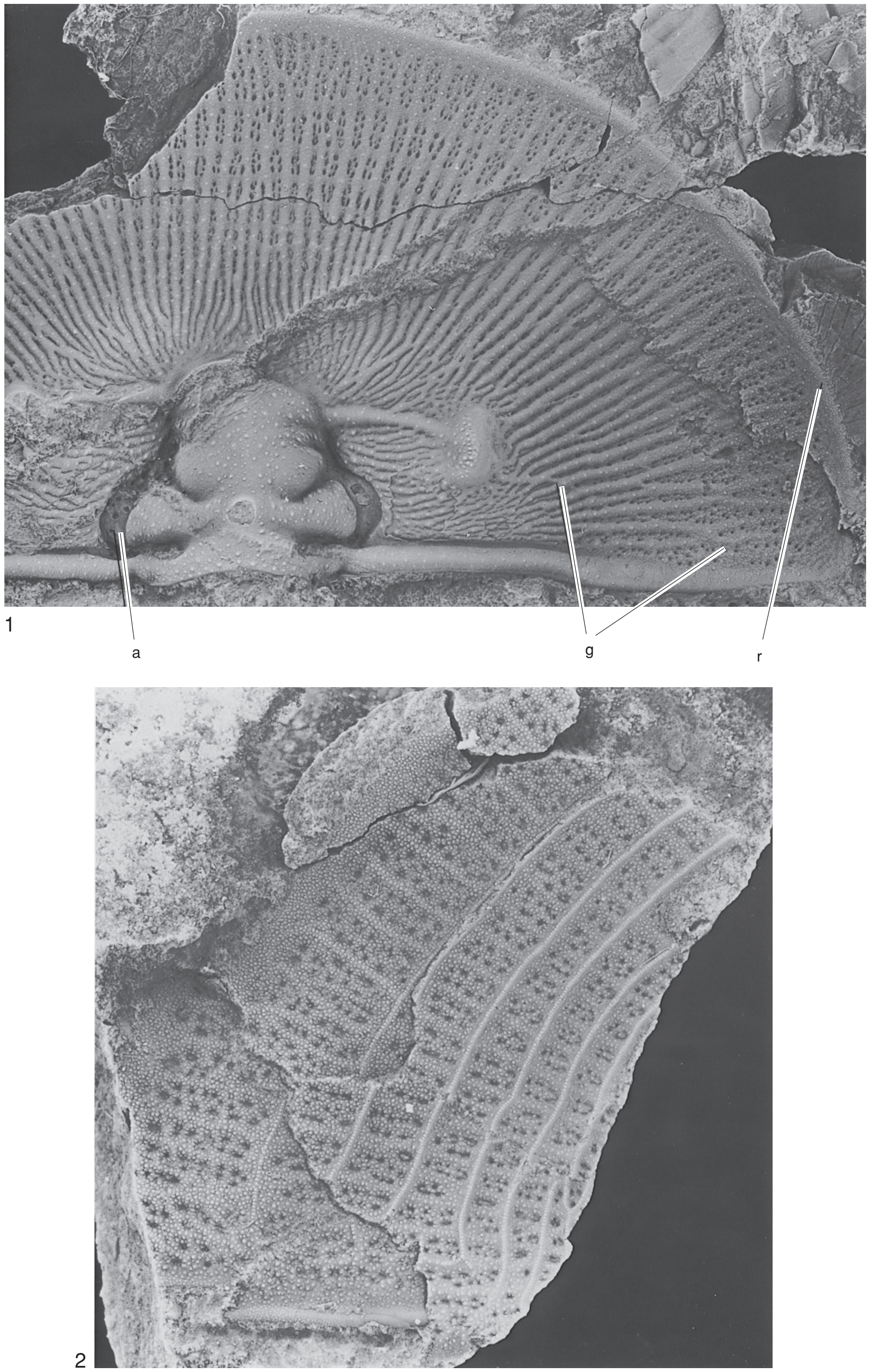


FIG. 17. *Harpides atlanticus* BILLINGS, Middle Ordovician, Table Head, Newfoundland. *1,* Dorsal view of incomplete genicranium, to show radiating pattern of genal caeca, ×5; *2,* exterior view of fragment of lower lamella of fringe, showing genal caeca as raised ridges, with intervening pits and strong concentric ridges, ×9. Abbreviations: *a,* ala; *g,* genal ridge; *r,* rim (Whittington, 1965, pl. 5, fig. 3; pl. 6, fig. 2).

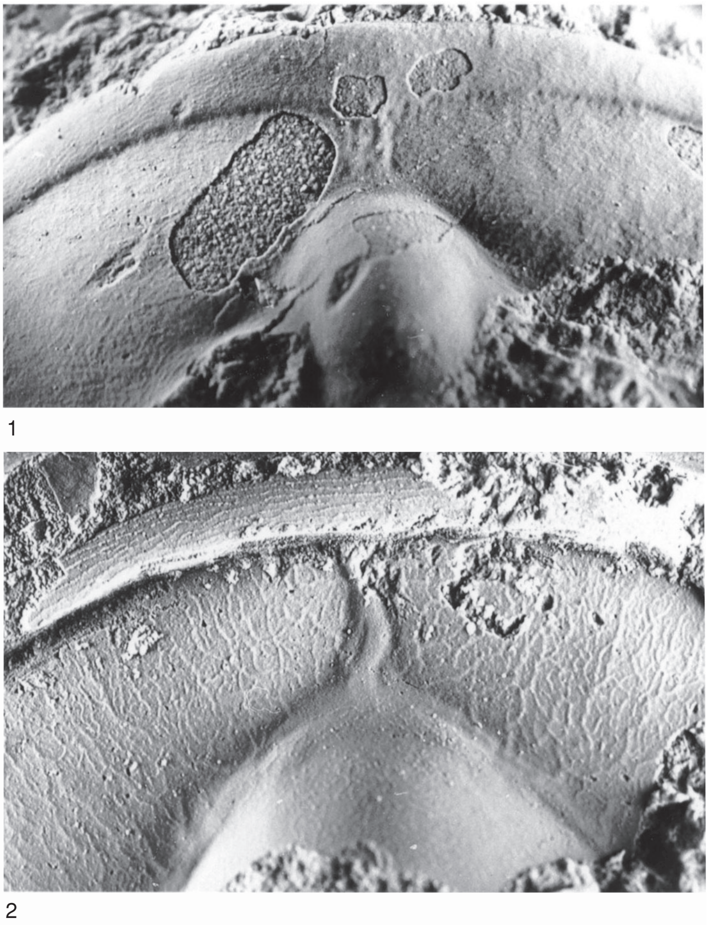


Fig. 18. The median preglabellar ridge in two Olenellina, Lower Cambrian, Canada, which suggests that the ridge is composite and part of the genal caeca. *1, Nevadella baculenta* Fritz, 1972, ×10; *2, Olenellus* sp., ×8 (Fritz,1972, pl. 5, fig. 3; pl. 13, fig. 14).

all of these areas, project from the parietal surface and appear as depressions in the internal mold. They are considered to be areas of muscle attachment, but the paraglabellar area in *Trimerus* (Whittington, 1993b) bears impressions of the genal caeca and hence cannot have been an attachment area.

The genal angle may be rounded, but in many trilobites it bears the prominent genal spine, called **librigenal** or **fixigenal** according to whether the suture is **opisthoparian** (Fig. 3) or **proparian** (Fig. 5), i.e., whether the spine is borne by the librigena or the fixigena. These terms indicate merely the position of the genal spine of the holaspid trilobite with reference to the suture and do not imply homology. The genal spine may be short or long so that it extends back beyond the rest of the body. In trilobites lacking a genal spine, the posterior branch of the suture may cross the border at the genal angle, a condition called **gonatoparian**.

The form of the anterior and lateral cephalic **border** (Fig. 3) varies. In many trilobites the border is dorsally convex, defined by border furrows (Fig. 4), and, in combination with the ventrally convex doublure, forms a tubular structure around the outer edge. This structure is continued into the base of the genal spine, where present, and into the distal extremity of the posterior border. The inner edge of the doublure of the lateral cephalic border (Fig. 4) lies a short distance ventrally of the border furrow. This tubular type of anterior and lateral cephalic border characterizes many Cambrian trilobites (see Fig. 27–28, 30, 37) and is present in many post-Cambrian forms such as proetids and Phillipsiinae (see, for example, Fig. 31.4). In the latter example, however, the doublure is flattened, giving a sharply flexed cephalic margin, as it is in Agnostina (see Fig. 27.1). This modification is associated the close fit of cephalic and pygidial doublures when fully enrolled (see section on enrollment, p. 67). In *Isotelus* (Fig. 2) lateral and anterior borders are ill-defined by the change in slope between glabella and genal field and the faintly convex border. The doublure is flat abaxially beneath the lateral border, curving up adaxially to lie close beneath the dorsal surface of the librigena (Chatterton & Ludvigsen, 1976, pl. 2). This type of border is characteristic of asaphids (Jaanusson, 1953a, 1953b; Henningsmoen, 1960) and styginids (Šnadjr, 1960); it is also developed in the bathyurid *Punka* (Fortey, 1979), but *Bathyurus* (see Fig. 31.2) has a tubular border. In trilobites in which the frontal glabellar lobe is expanded, for example in some cheirurids (see Fig. 34.1) or in phacopids (see Fig. 36.2), the anterior border faces anteriorly and may be greatly restricted, the lateral borders retaining their tubular form and facing upward and outward. In such encrinurids as *Encrinuroides* (see Fig. 34.3) the anterior border faces anteriorly, and the preglabellar field (between the preglabellar furrow and anterior border furrow) is long (sag. and exs.) and convex. The anterior branches of the suture, together with the narrow (tr.) rostral suture, divide the preglabellar field transversely. This division has resulted in the use of special terms (Evitt & Tripp, 1977)—anterior border of cranidium and precranidial lobe—the latter for the lobe of the librigena between the connective and facial sutures and anterior border furrow. Lateral and anterior borders may be lost altogether by effacement in some illaenids (see Fig. 1, 33), but the tubular form is retained laterally by the doublure.

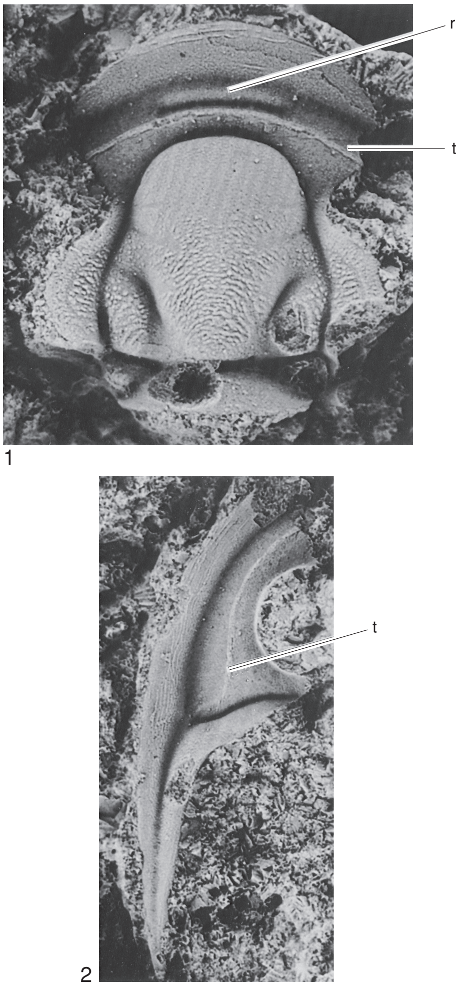


Fig. 19. *Warburgella stokesii* (Murchison), Silurian, Wenlock Limestone, U.K. *1,* Cranidium, showing transverse preglabellar ridge (*r*) and tropidium (*t*) on preglabellar field, ×13; *2,* librigena, showing tropidium continued on genal field, ×6 (Owens, 1973, pl. 13, fig. 12–13).

A different type of cephalic border is that of the trinucleid *Cryptolithus* (see Fig. 29.1, 129). The border slopes steeply downward anteriorly and laterally and has a vertical edge, the doublure underlying it closely. Pits in the outer surfaces of border and doublure join the two surfaces by opposed, funnel-shaped structures. The cephalic suture runs around the steep margin of the border and

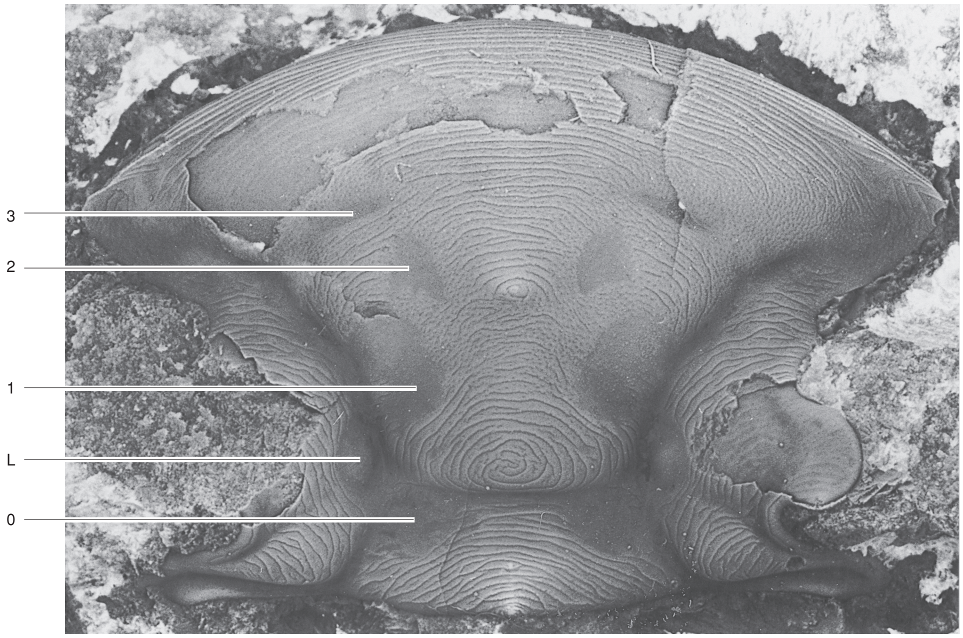


FIG. 20. *Kosovopeltis? pompilius* (BILLINGS), Lower Devonian, Maine. Dorsal view of cranidium, showing sculpture and lateral (*L*) and glabellar (*0–3*) muscle impressions, ×6 (Whittington, 1960a, pl. 54, fig. 25).

curves inward to the posterior border at the genal angle; it also divides the funnel-shaped structures. This type of border, the **fringe**, thus consists of two pitted lamellae, the **upper** and **lower lamellae**, separated by the suture, with the lower lamella extended into the genal spine. Details of the structure of the fringe in trinucleids were given by C. P. HUGHES, INGHAM, and ADDISON (1975). Similar in structure is the fringe of harpetids (WHITTINGTON, 1949; CHATTERTON & LUDVIGSEN, 1976), harpidids (Fig. 17), and dionidids (WHITTINGTON, 1952a). A single row of pits in the anterior border furrow is developed in a number of different trilobites, and in *Redlichia* (see Fig. 30.2) and certain olenids (FORTEY, 1974b) these are opposed by pits in the doublure.

The posterior cephalic border has the form of a raised ridge, defined on the inner side by a change in slope or the border furrow. This border extends transversely in the horizontal plane from the axial furrow to the **fulcrum** (Fig. 5), abaxial to which it is flexed down. The doublure extends adaxially from the genal angle, narrowing (exs.) and disappearing at the fulcrum. In trilobites, such as *Olenellus* (see Fig. 45), in which the posterior border curves outward and downward from the axial furrow, there is no fulcrum dividing the border into inner and outer portions, but the doublure extends inward to a corresponding position in an exsagittal line with the inner edge of the thoracic doublure. The posterior cephalic border thus duplicates the form of the thoracic segments in being either fulcrate or nonfulcrate (see discussion of thorax below); such duplication is necessary for articulation of cephalon and anterior thoracic segment. In trilobites in which the thoracic pleural furrow is effaced, as in illaenids (WHITTINGTON, 1963, pl. 16), the posterior border furrow is also effaced, and the posterior cephalic border consequently is not defined (see Fig. 33). Nevertheless, the posterior edge of the cephalon is fulcrate (i.e., bent down at the fulcrum) and so articulates with the fulcrate thorax.

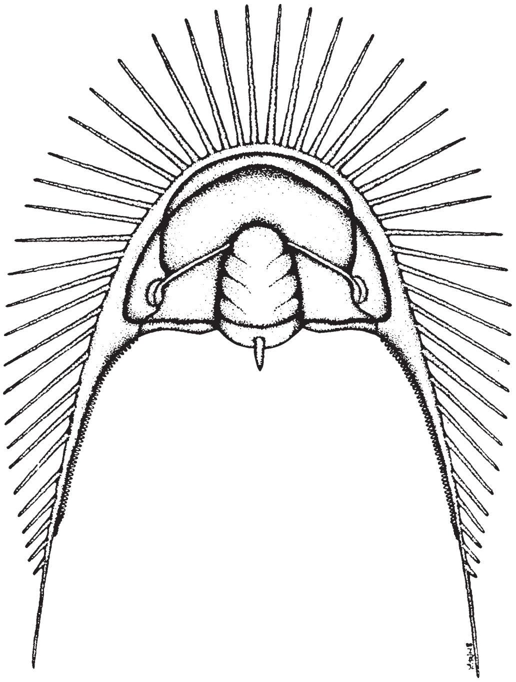


FIG. 21. Reconstruction of cephalon of *Bowmania americana* (WALCOTT), Upper Cambrian, North America; based on new material from R. LUDVIGSEN and from LUDVIGSEN, 1982, fig. 24 (new).

In many trilobites the only relatively large cephalic border spine is the **genal spine**. This spine is backwardly directed and may terminate at some point beside the thorax or extend behind the body. In most trilobites this spine tapers progressively to a sharp point. Exceptions include the Cambrian *Peachella* (PALMER & REPINA, 1993, fig. 4.2) and such Carboniferous proetids as *Spinibole* and *Cystispina* (BRAUCKMANN, 1978; OWENS & TILSLEY, 1995). In *Spinibole* the genal spine is long, tubular, and bluntly pointed; in *Cystispina* the club-shaped spine is divided into two cysts. Many additional cephalic border spines (less prominent than the genal spine) are present in such Cambrian trilobites as *Bowmania* (Fig. 21), and in some post-Cambrian odontopleurids (Fig. 22) there are many additional border spines. These spines may project almost horizontally as in *Bowmania* or be downwardly and outwardly directed as in *Acidaspsis.* The anterior border and doublure of the cephalon may be drawn out into a **frontal spine**, as in asaphids such as *Megistaspis (Megistaspidella)* (JAANUSSON, 1956b; WANDÅS, 1984). An extraordinary example of such a spine, three times the length (sag.) of the rest of the cephalon, is that of the dalmanitid *Psychopyge* (MORZADEC, 1988). In other dalmanitids the spine may be shorter, but bifid or trifid (CAMPBELL, 1977), and has been referred to as a **frontal process**. Short spines (the **median** and **anterior fixigenal** spines) project from the lateral border in holaspid cheirurids such as *Sphaerocoryphe* and are remnants of relatively longer spines in earlier growth stages. In the Devonian *Paracalmonia* a similar short spine is present on the border of the librigena. Striking is the long, upward curving **intergenal spine** in the Cambrian *Nepea* (Fig. 23). Similarly situated but smaller intergenal spines are present in the developmental stages of Olenellina, *Paradoxides* (WHITTINGTON, 1957b), and dolichometopids (ÖPIK, 1982); and remnants may be

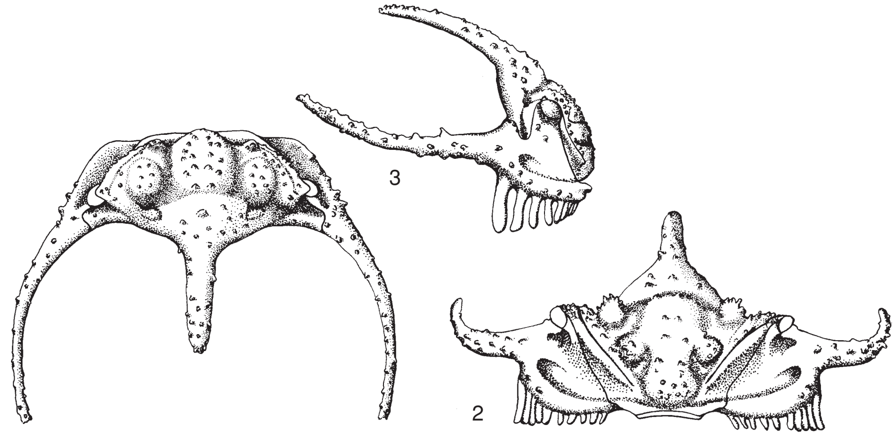


FIG. 22. Reconstruction of cephalon of *Acidaspis brighti* Murchison, Silurian, Europe, North America. *1,* Dorsal, *2,* anterior, and *3,* right lateral views, ×3 (Whittington, 1956b, fig. 1).

retained in holaspides (Fig. 16). In most trilobites the adaxial portion of the posterior cephalic border is directed transversely, the abaxial portion curved back (to different degrees) into the base of the genal spine. In some Olenellina and redlichioids, however, the genal spine is advanced, in that the base of the spine is situated on a transverse line in advance of the occipital ring at the midlength of the cephalon or even farther forward. In these forms the posterior cephalic border is flexed forward, in Olenellina at or adaxial to the intergenal spine (Fig. 16), in redlichioids at about where it is crossed by the posterior section of the facial suture. This marked flexure in the posterior border was termed the **intergenal angle** by W. Chang (1966, fig. 1). A terminology for the angle between the lateral and posterior borders and the genal spine was proposed by Henningsmoen (1957a, fig. 1). An unusual cephalic spine is the posterolateral spine of the fixigena in *Ancyropyge* (Ormiston, 1967), as prominent as the librigenal and occipital spines.

In the posterolateral corner of the genal field of the metagnostids *Geragnostus, Galbagnostus* (Fig. 10.2), and *Arthrorhachis* (Whittington, 1965, p. 297; Hunt, 1967, pl. 22, fig. 35, 47), there is a smooth, oval area that differs from the muscle areas of the glabella in being slightly raised; what this area represents is uncertain. A structure in the same position in a different metagnostid has been interpreted as an eye lobe (Ahlberg, 1988). Størmer (1980, p. 263–266) described pits and darker areas in the genal field (including the palpebral lobe and furrow) of *Chasmops* and interpreted them as areas of muscle attachment. Similar pits are present in the genal field in cheirurids, pliomerids, and encrinurids; whether these were areas of muscle insertion is an open question.

CEPHALIC SUTURES AND THE VENTRAL CEPHALIC EXOSKELETON

The **facial suture,** divided into an **anterior** and **posterior branch** (or **section**) by the eye lobe when present, may divide the dorsal cephalic exoskeleton into the cranidium and librigena (Fig. 3), and this suture may be met by other sutures in the ventral exoskeleton (Fig. 5). The dorsal and ventral sutures comprise the **cephalic sutures**. On molting the exoskeleton parted along these sutures, so that not only may the sutures be visible in entire exoskeletons, but the parts into which it separated (librigena, cranidium, rostral plate, hypostome) may be preserved. The course of the sutures is different in different trilobites, and a particular pattern has long been recognized as characteristic of some family groups (as has the form of the hypostome), hence the importance that has been placed on cephalic sutures in classification (STUBBLEFIELD, 1936). The extraction and study of silicified specimens has provided much new information, and the preservation in full relief has enabled a better appreciation of the course of the sutures. The following account of cephalic sutures, the nature of the hypostome, and its relationship to the rest of the cephalic exoskeleton is based on recent reviews (WHITTINGTON, 1988a, 1988b). FORTEY and CHATTERTON (1988, fig. 5, p. 178; see FORTEY, 1990a, for further discussion) introduced the term **natant** condition to describe that in which the hypostome was detached from the cephalic doublure, and **conterminant** condition for that in which the hypostome was attached by a suture to the doublure, the latter extending inward to a position beneath the preglabellar furrow.

PATTERNS OF CEPHALIC AND FACIAL SUTURES

In cephala having an opisthoparian facial suture (Fig. 1–3) the two branches may subtend abaxially an oblique angle, the anterior branches curving inward to become confluent along the margin. This arrangement characterizes many species and has been called **ptychopariid** (see Fig. 27.4), a term carrying the implication that the **connective suture** is present on the doublure, defining the abaxial margin of the rostral plate. In the conterminant condition this suture connects the facial suture to the hypostomal suture (Fig. 4.1–5). When in the conterminant condition only a **median suture** transects the doublure, no rostral plate is developed, and the cephalic suture is termed **asaphid** (see Fig. 35). In the remopleuridioid *Kainella* the anterior branch is strongly outwardly directed from the eye lobe, then curves inward to cross the anterior border and meet the median suture. This pattern, in which the anterior branches subtend a wide angle in front of the eye lobes, is described as **kainelliform**. In *Centropleura* (ÖPIK, 1961b, fig. 37) the anterior branch of the suture curves to run outward and backward, before curving forward to the cephalic margin and is termed **retrodivergent**. In the **cedariidiform** type of suture the posterior branch is directed outward from the eye lobe, then curves back over the posterior border to a point just inside the base of the genal spine, as in *Cedaria.* The proparian suture (Fig. 5), typical of the post-Cambrian Cheirurina and Phacopina, is also present in such unrelated Cambrian forms as *Norwoodella.* Special variants of this suture are the **burlingiiform** type (as in *Burlingia* and *Schmalenseeia*), in which both anterior and posterior branches run outward and forward from the eye lobe to the margin, and the **dalmanitidiform** (as in *Dalmanites*), where the anterior branches are confluent along the dorsal surface of the anterior border. In trilobites having either opisthoparian or proparian facial sutures, the anterior branches may be confluent; but the doublure is not crossed by a median or connective suture; this is described as the **nileiform** (see Fig. 36.1) facial suture.

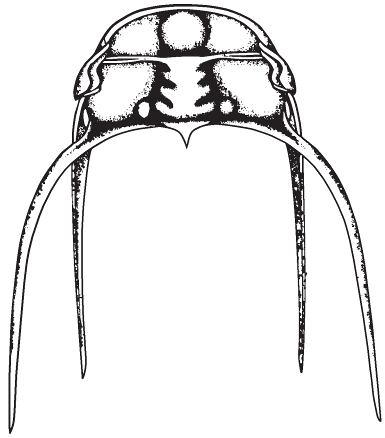


FIG. 23. Reconstruction of cephalon of *Nepea narinosa* WHITEHOUSE, Middle Cambrian, Australia, dorsal view. The upper of the two pairs of spines is the intergenal spine, ×2 (Öpik, 1970a, fig. 2).

The above kinds of facial sutures all cross the eye lobe, but facial sutures may be present when the eye lobe is absent. For

FIG. 24. Dorsal view of genicranium of *Brachymetopus ornatus* WOODWARD, Carboniferous (Dinantian), U.K., ×6 (Owens, 1986, pl. 5, fig. 10).

example, a ptychopariid facial suture is present in the Devonian proetid *Erbenicoryphe* (see Fig. 119), and a proparian suture occurs in the Devonian phacopid *Trimerocephalus* (see Fig. 118.4). On the other hand, a prominent eye lobe may be present, although the facial suture is lacking, as in *Brachymetopus* (Fig. 24).

A **marginal** or **submarginal** suture characterizes trinucleids (see Fig. 29.1), harpetids, and dionidids; and a variant is seen in *Entomaspis* (RASETTI, 1952a), where two branches run outward and backward from the eye lobe to the base of the genal spine where they join the marginal suture (**entomaspidiform** type). In trilobites with a marginal suture the cephalic exoskeleton is divided into a dorsal portion, for which HENNINGSMOEN (1959, p. 155) coined the term **genicranium**, and a ventral portion, which he called the **doublural plate**; the latter is referred to in harpetids and trinucleids as the **lower lamella** of the fringe.

In some trilobites either branch of the facial suture may be situated on or beside a narrow ridge, the **sutural ridge**. In Olenellina STØRMER (1942, fig. 14; pl. 2, fig. 1, 3–5) showed not only the intergenal and posterior ocular ridges but also described a fainter ridge curving from the anterior end of the eye lobe, outward and backward over the genal field (see Fig. 122). Some species of *Fallotaspis* HUPÉ (1953a, fig. 20, 23; pl. 1, fig. 3, 5) also have an anterior ocular line or ridge extending backward to cross the posterior border just outside the base of the genal spine. There has been much discussion of the significance of the anterior and posterior ocular lines (STØRMER, 1942, p. 137–139 and references; HUPÉ, 1953a, p. 118–119, fig. 68; HARRINGTON in MOORE, 1959, p. 62–63; BERGSTRÖM, 1973b, p. 285). HARRINGTON, following HUPÉ, concluded that they represented the fused facial suture and applied the name **metaparian** to such a suture. STØRMER was not convinced of this interpretation, and there is no evidence for it from what we know of ontogeny in Olenellina. The notion of secondary fusion of facial sutures in Olenellina is considered improbable (WHITTINGTON, 1989).

The above terms that purport to describe the course of all or part of the cephalic suture or supposed suture have only limited use because the exact course differs even between species attributed to one genus.

DOUBLURE AND ROSTRAL PLATE

At the inner edge of the doublure the exoskeleton becomes thin except along the hypostomal suture (e.g., WHITTINGTON & EVITT, 1954, pl. 12, fig. 30). As a result of compaction, the trace of the inner edge of the doublure of the lateral and anterior borders may be impressed on to the dorsal exoskeleton to give a **paradoublural line.** In uncompressed trilobites this line may be marked by a slight change in slope of the dorsal exoskeleton. The doublure may extend inward beneath the genal field for a short distance adaxially, closely beneath the dorsal exoskeleton, but never extends below the eye lobe.

The cephalic doublure may be impressed by a **vincular furrow,** subparallel to the margin (see Fig. 36.2), or by one or more notches (see Fig. 27.1) or folds below the lateral or posterolateral border. These vincular structures are coaptative (see section on enrollment and coaptation, p. 67). In certain asaphids, silicified specimens (ROSS, 1951b, pl. 12, fig. 3–8; Chatterton & Ludvigsen, 1976, pl. 2, fig. 10, 12–14) show not only a vincular fold near the lateral margin but a small opening in the doublure posterolaterally that has one margin raised, the **panderian opening** (see Fig. 35.3). In other trilobites this opening is presumed to have lain within a small embayment in the inner margin of the doublure (see Fig. 29.3, 31.4, 35.1).

In Olenellina (see Fig. 30.1) there were no facial sutures, but the cephalic doublure is divided by a **perrostral suture** that runs along the arc of the doublure from beneath one genal angle to the other, a short distance abaxially from the inner margin. This suture isolates a narrow (sag. and tr.), crescentic **rostral plate**. A similarly shaped rostral plate is isolated in the brachymetopid *Australosutura* (Fig. 25) by the **rostral suture** that curves over the doublure between the inner, posterior edges. In *Brachymetopus* (Fig. 24) the rostral plate is crescentic (Owens, 1986) as in *Australosutura* (Fig. 25), but facial sutures are absent. A crescentic ventral plate has been described in the cephalon of the metagnostid *Arthrorhachis* (see Fig. 27.1). Such ventral, rostral plates are the widest known (measured along the arc of the doublure) and are present in extremely different trilobites.

A narrower rostral plate is present in trilobites in which the connective suture crosses the anterior portion of the doublure; the shape of the plate is determined by the course of the suture, the distance separating the pair of sutures, and the form of the doublure. Jaanusson (1956a, p. 37) proposed that the ptychopariid type of cephalic suture in which a rostral plate is present should be subdivided as **euptychopariid** and **stenoptychopariid**, referring respectively to forms in which the rostral plate was broad (see Fig. 27.4) or narrow (tr.) (see Fig. 31.1). The connective suture may be straight, inward as well as backwardly directed, giving a subrectangular or rhomboidal outline to the rostral plate, or the suture may be sinuous or run in a curve concave abaxially, resulting in an hourglass-shaped outline (see Fig. 28.1b, 31.2b). In certain encrinurids (see Fig. 34.3) the connective suture is close to the midline, and the rostral plate is an extremely narrow (tr.) strip. The doublure may be flat or gently convex anteriorly but may be sharply flexed, as in calymenids (see Fig. 34.2) or illaenids (see Fig. 33). In the former group the outer, anterior portion of the rostral plate (shown in the ventral view, Fig. 34.2b) is referred to as the **border sector;** the inner portion (which is bent sharply upwards and so hidden in the ventral view but shown in section in Fig. 34.2d) is the **doublure sector.** The anterior margin of the rostral plate, the rostral suture, lies in most trilobites on the margin of the border or on the ventral side; however, in xystridurids (see Fig. 30.3) and homalonotids it is dorsal to the margin.

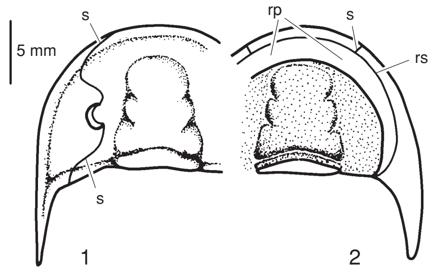


Fig. 25. Cephalon of *Australosutura* sp., Carboniferous; *1,* dorsal and *2,* ventral views. Abbreviations: *rp,* rostral plate; *rs,* rostral suture; *s,* facial suture (Whittington, 1988b, fig. 13).

NATURE OF CEPHALIC SUTURES

The course of the cephalic sutures and the nomenclature of sections of them and of the portions into which they divide the cephalon have been given above. The **hypostomal suture** is described below, a suture that separates hypostome from cephalic doublure. In entire specimens of the cephalon preserved in limestone, the suture lines may be visible as impressed lines; in such specimens in shale or silt compaction may have caused slight displacement along the suture lines so that they are readily visible. Portions of the cephalic exoskeleton, separated at the sutures, comprise the vast majority of fossils.

Such material that has been silicified has shown that the relatively thick exoskeleton is truncated at a flat edge along suture lines, and the precise fit along these lines is revealed by rare silicified specimens in which the portions are in juxtaposition (Fig. 4). This sutural edge of the exoskeleton contrasts with the thin edge at the inner margin of the doublure, to which the unmineralized ventral integument was attached. Silicified material of *Proetus* (WHITTINGTON & CAMPBELL, 1967, pl. 2, fig. 3), for example, shows the difference in appearance between these edges.

In specimens of the odontopleurid *Ceratocephala* from Bohemia (BRUTON, 1968b, p. 49) facial sutures cannot be seen, and they are described as fused and indistinct in a species described by CHATTERTON and PERRY (1983, p. 48); in other species (e.g., BRUTON, 1966, p. 25) there is clear evidence of these sutures. Other examples could be cited, and *Stelckaspis* is characterized (CHATTERTON & PERRY, 1983, p. 32) as having fused facial sutures in the holaspid stages and lacking sutural ridges. Whether facial sutures can be traced in a specimen may depend on the mode of preservation (cf. BRUTON, 1968b, p. 49), and it may also depend on whether a specimen is the exoskeleton of a molt or of a whole animal that died between molts. In the latter the suture may not have been functional, whereas in the former it would have been. In Upper Cambrian (RASETTI, 1952c, p. 892) and Ordovician trilobites (LUDVIGSEN, 1979b, p. 4) the median suture may be present in some species of a genus but absent in others. In such examples the absence of this suture does not appear to have taxonomic significance.

HYPOSTOME

The **hypostome** is a ventral cephalic exoskeletal plate, situated beneath the anterior portion of the glabella and consisting of a convex, oval or subcircular **middle body** surrounded by borders (Fig. 4, 26). The width corresponds to that of the frontal glabellar lobe, and in Cambrian trilobites the plate appears to have extended back to a point beneath L2 or L1. In younger trilobites the length (sag.) is greater, in some instances reaching to a point beneath the occipital ring. The middle body of the hypostome is subdivided into a larger **anterior lobe** and smaller **posterior lobe** by a **middle furrow** directed inward and backward from the lateral border furrow; the posterior lobe may have a convexity that is independent from that of the anterior lobe. The middle furrow dies out adaxially, and at the inner end there may be a flat or convex area, the **macula**, situated in the furrow or on either side of the slope down to the furrow, characteristically on the posterior side of this slope. The macula may be flat, lie in a deep depression, or be gently or strongly convex; it may be oval or lenticular in outline. Examples of the macula have been described in which the external surface is smooth (LINDSTRÖM, 1901; WHITTINGTON, 1988a, p. 600; 1988b, p. 336) or in which it is tuberculate (ORMISTON, 1967, pl. 2, fig. 6); examples in which the exoskeleton is thinner than in adjacent areas or shows an internal cellular structure have also been described. An anteromedian protuberance of the middle body, the **rhynchos** (see Fig. 34.2–3), is a coaptative device present, for example, in remopleuridids, calymenids, and encrinurids.

An anterior border of the hypostome may not be developed. If developed it may be flat, narrow, and downward- and forward-sloping or narrow and convex and complete or incomplete medially. The lateral and posterior borders, separated from the middle body by furrows, are of many different forms and are extended dorsally and inwardly as a doublure. In post-Cambrian species a rounded projection, the **shoulder**, is present at the anterior end of the lateral border; in older species such a projection lies farther back on the lateral border. The anterolateral edge of the hypostome is extended upward and outward as an **anterior wing**; on the inner surface of the wing a **wing process** may project,

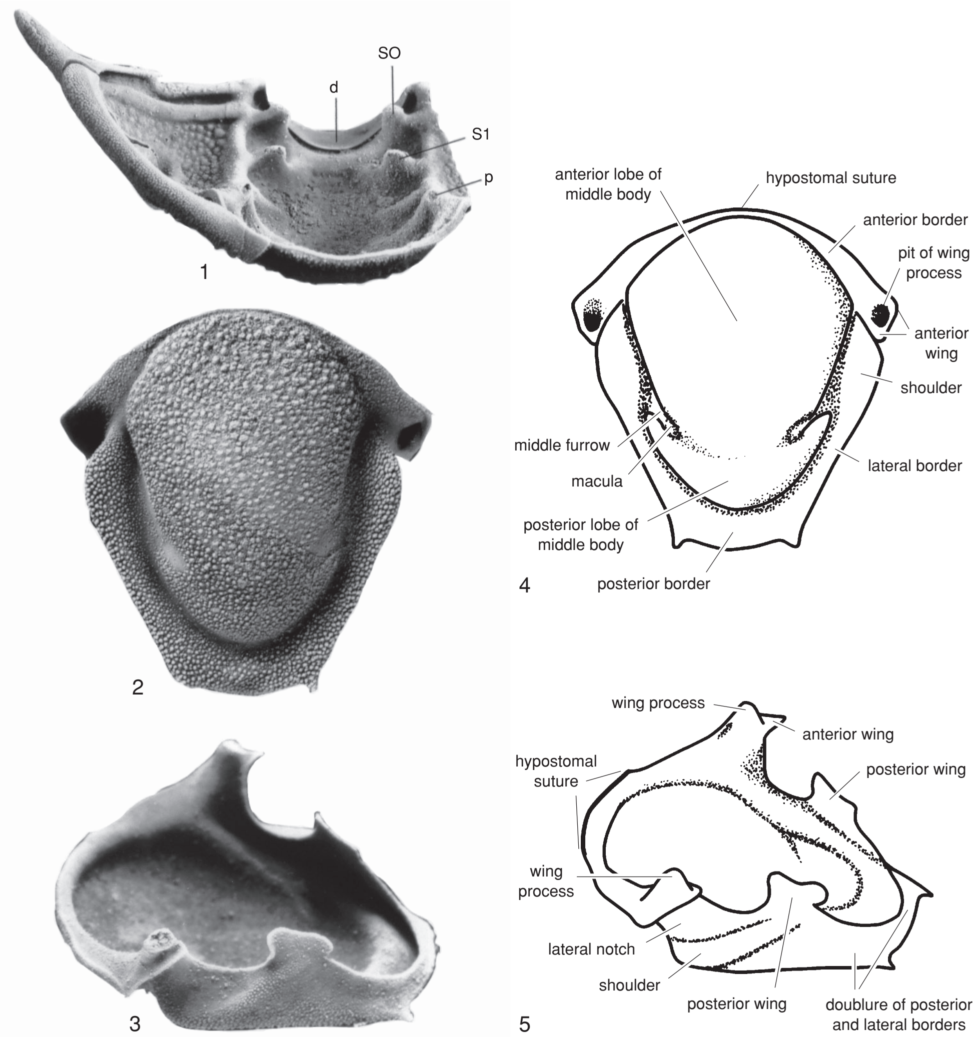


FIG. 26. Incomplete cephalon and hypostome of *Ceraurinella typa* WHITTINGTON & EVITT. *1,* Anteroventral view of cranidium with attached right free cheek, to show doublure of occipital ring (*d*), apodemes of SO and S1, and pit (*p*) in fossular apodeme, ×6 (Whittington & Evitt, 1954, pl. 10). *2,3,* Hypostome in ventral and oblique interior views, ×9 (Whittington & Evitt, 1954, pl. 11). *4,5,* Diagrammatic representation of hypostome to indicate terminology of ventral and oblique views, respectively (new).

a corresponding pit being present on the outer surface. In specimens in which the hypostome has been found in place, the tip of the wing or the wing process lies immediately beneath the fossular apodeme (Fig. 26.1) projecting from the dorsal exoskeleton. Where the internal surface of the hypostome is known, a **posterior wing** projects dorsally from the inner edge of the doublure of the lateral border, beneath the shoulder. Between the shoulder and anterior wing is the embayment of the **lateral notch**, which is broad in many Cambrian trilobites and in Proetida and is a narrow channel in such groups as Phacopida. The posterior border may bear one or more spines and may have a median notch developed or be deeply forked as in some Asaphida. The remopleuridid *Hypodicranotus* (Whittington, 1952b; Ludvigsen & Chatterton, 1991) is unique in that the prongs of the fork extend back beneath the thorax to the pygidium. The varied structures of the doublure of the posterior border, revealed by silicified specimens, include a median projection, a median groove, and sharp granulation (Whittington, 1988b, p. 335).

Hypostomal Attachment Conditions

The hypostomes of holaspid trilobites and their relationship to the rest of the cephalic exoskeleton were described by Whittington (1988a, 1988b). It was shown that in species of particular genera or families the hypostome was inserted into the ventral cephalic integument and in others that it was attached at a suture to the cephalic doublure. In the same year Fortey and Chatterton (1988, p. 178) proposed terms to describe the different attachment conditions and portrayed both holaspid and protaspid hypostomes. Fortey (1990a) discussed different hypostomal conditions in more detail, as well as their possible evolution and importance to classification. In the light of this work, the cephalic types proposed by Harrington (in Moore, 1959, p. 67), which have been little used and are known to be partly in error, are not given here. Hypostomal conditions are described in the terms of Fortey and Chatterton.

In the **natant** condition the hypostome is inserted into the ventral integument of the cephalon below the anterior portion of the glabella, not attached to the inner edge of the doublure but lying a short distance behind it. In the remarkable specimens of *Agnostus pisiformis* (Müller & Walossek, 1987), a natant hypostome is preserved in place (see Fig. 78, 80, 82); in species of other genera in which only the exoskeleton is preserved (e.g., Whittington, 1988a, pl. 55, fig. 8–9; Fortey, 1990a, pl. 1) it is slightly displaced. Many Cambrian (Fig. 27.2–4, 28) and fewer post-Cambrian trilobites (Fig. 27.1, 29) have the hypostome in this position. They are restored with the anterior wing lying beneath the anterior end of the axial furrow, in front of the intersection of this furrow with the eye ridge (if this ridge is developed), or beneath the corresponding position, the fossula, in *Cryptolithus* and *Ampyx.* In the latter two genera and in *Proetus* (Fig. 29.3), a preglabellar field is absent, this field being well developed in the Cambrian examples. In some trilobites with a natant hypostome the doublure is not crossed by sutures (Fig. 28.2; 29.1–2), while in others it is traversed by connective sutures that isolate a rostral plate of differing sizes and shapes (Fig. 27.2–3, 28.1, 29.3). In *Proetus* the anterior edge of the hypostome lay close to the inner edge of the doublure. Well-preserved silicified specimens (Whittington & Campbell, 1967, pl.

Fig. 27. Cephala with natant hypostome. *1, Arthrorhachis* sp., Middle Ordovician, with dashed outline of possible hypostome (Whittington, 1988b, fig. 1). *2, Pagetia ocellata* Jell, Middle Cambrian (Whittington, 1988a, fig. 1). *3, Dolerolenus* sp., Lower Cambrian (Whittington, 1988a, fig. 7). *4, Ptychoparia striata* (Emmrich), Middle Cambrian (Whittington, 1988a, fig. 11). All *a* views are partial dorsal, *b,* partial ventral, *c,* right lateral, and *d,* sagittal section of cephalic exoskeleton combined with a right lateral view of the hypostome. The position of the rostral suture is shown by a gap in the section; the *heavy dashed line* indicates crest of ridge formed by axial furrow on inner (parietal) surface of exoskeleton.

Abbreviations for this figure and Figures 28–37: *ab,* anterior boss; *ap,* anterior pit or fossula; *aw,* anterior wing; *bs,* border sector of rostral plate; *cs,* connective suture; *d,* doublure of cephalon; *ds,* doublure sector of rostral plate; *g,* girder; *gr,* genal ridge; *h,* hypostome; *hs,* hypostomal suture; *imd,* inner margin of cephalic doublure; *ln,* lateral notch of hypostome; *m,* median suture; *mc,* macula; *mt,* median tongue (narrow median extension inward of the posterior doublure of the hypostome); *oa,* oval area of middle body of remopleuridid hypostome; *p,* pit in anterior cephalic doublure of remopleuridid; *pa,* panderian notch; *pi,* pit in anterior border furrow or corresponding pit in doublure; *pr,* perrostral suture; *pw,* posterior wing of hypostome; *pyg,* pygidium; *rf,* rostral flange; *rh,* rhynchos; *rp,* rostral plate; *rs,* rostral suture; *s,* facial suture; *sh,* shoulder; *v,* vincular furrow or notch; *wp,* wing process.

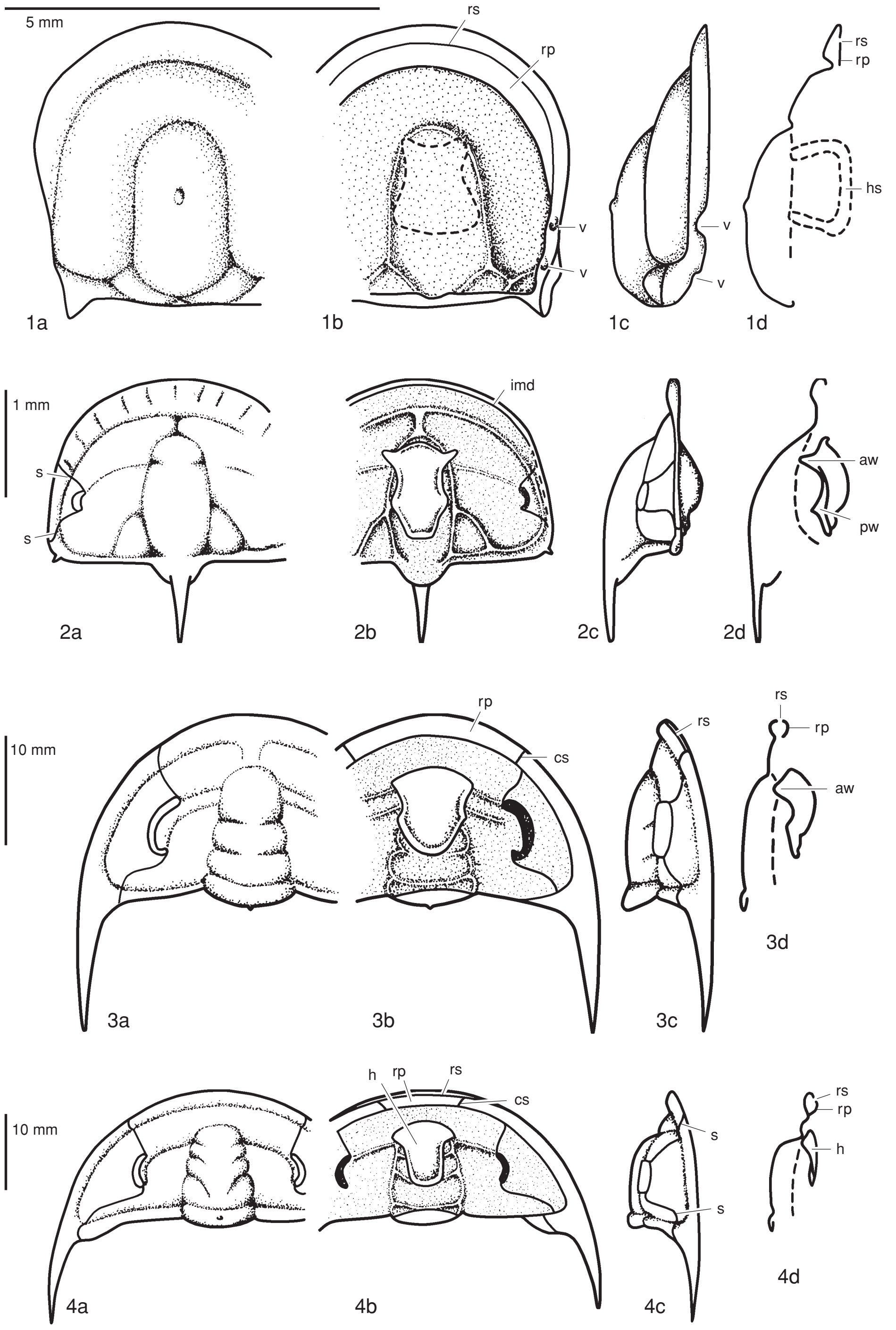


FIG. 27. *For explanation, see facing page.*

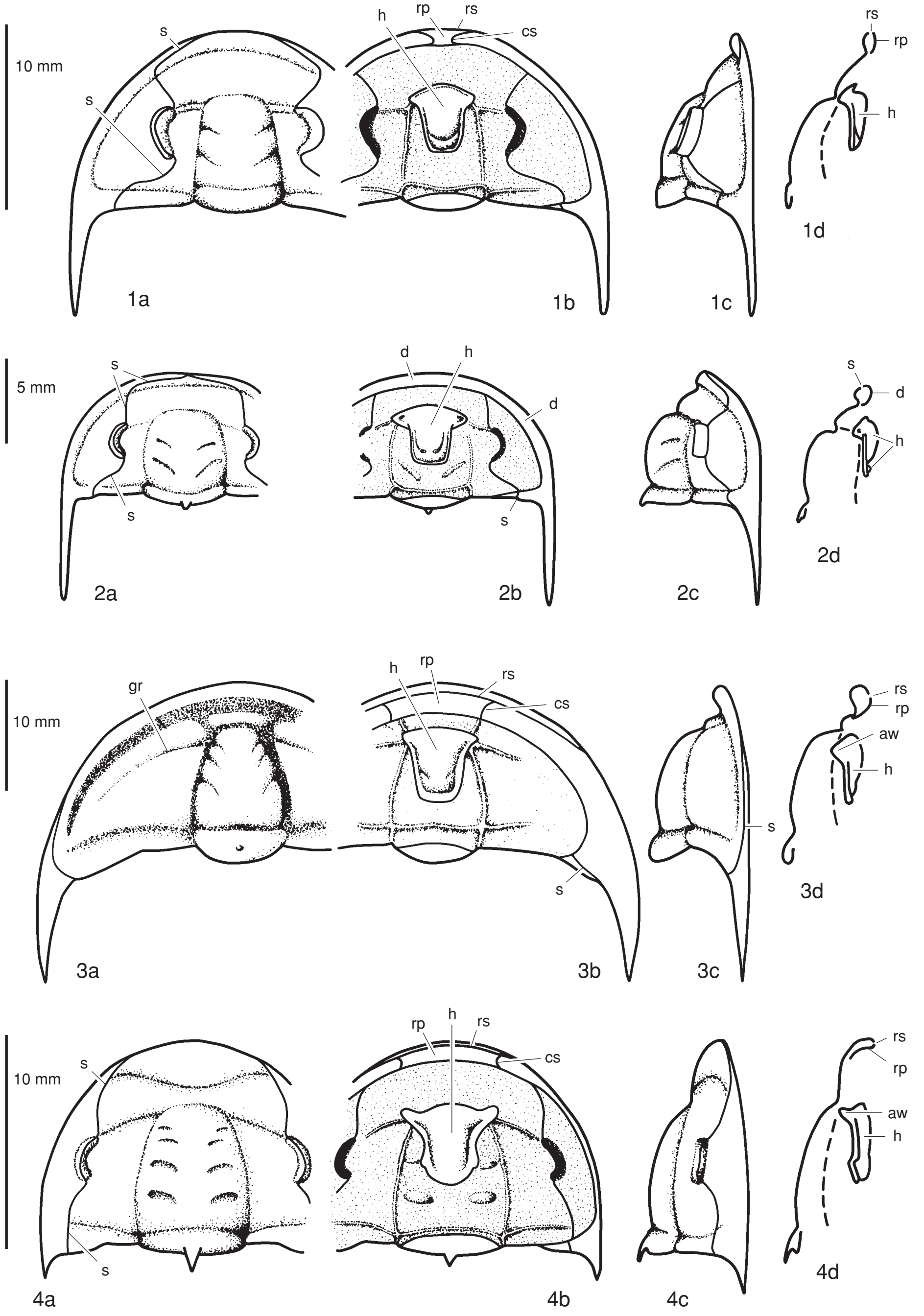


Fig. 28. Cephala with natant hypostome. *1, Aphelaspis* sp., Upper Cambrian (Whittington, 1988a, fig. 17). *2, Parabolinella* sp., Upper Cambrian (Whittington, 1988a, fig. 19). *3, Conocoryphe sulzeri* (Schlotheim), Middle Cambrian (Whittington, 1988a, fig. 12). *4, Agraulos ceticephalus* (Barrande), Middle Cambrian (Whittington, 1988a, fig. 14). All *a* views are partial dorsal, *b,* partial ventral, *c,* right lateral, and *d,* sagittal section of cephalic exoskeleton combined with a right lateral view of the hypostome. The position of the rostral suture is shown by a gap in the section; the *heavy dashed line* indicates crest of ridge formed by axial furrow on inner (parietal) surface of exoskeleton. See Figure 27 (p. 30) for list of abbreviations.

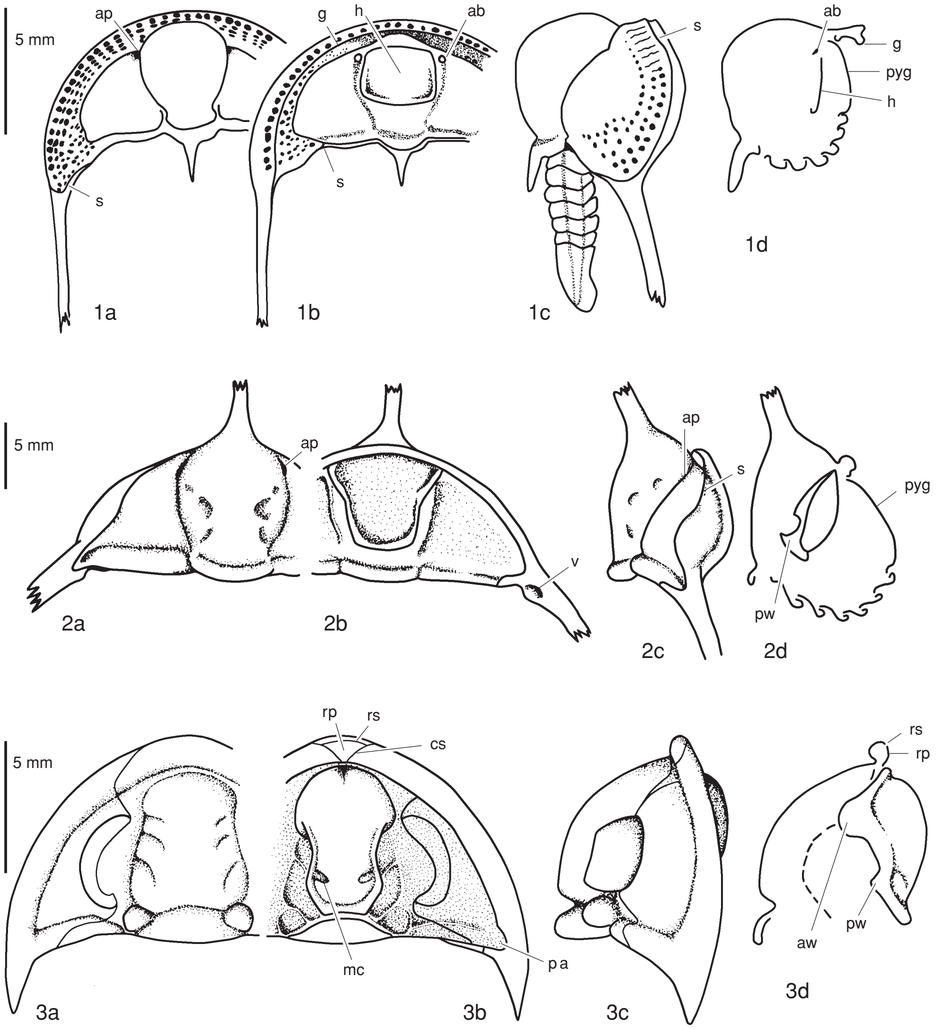


Fig. 29. Cephala of post-Cambrian trilobites with a natant hypostome. *1, Cryptolithus* sp., Ordovician (Whittington, 1988b, fig. 15). *2, Ampyx* sp., Ordovician (Whittington, 1988b, fig. 16). *3, Proetus (Proetus)* sp., Silurian (Whittington, 1988b, fig. 11). All *a* views are partial dorsal, *b,* partial ventral, *c,* right lateral (including thorax and pygidium in part 1), and *d,* sagittal section of enrolled exoskeleton (of cephalon only in part 3) combined with a right lateral view of the hypostome. The position of the rostral suture is shown by a gap in the section; the *heavy dashed line* indicates crest of ridge formed by axial furrow on inner (parietal) surface of exoskeleton. See Figure 27 (p. 30) for list of abbreviations.

2, fig. 1) show that the anterior edge of the hypostome was rounded and slotted, not a thick, flat sutural edge. This suggested that the hypostome was natant.

Fortey (1990a, fig. 11) drew attention to the similarity in morphology between examples of the natant hypostome. This generalization embraced what we know of hypostomes in Eodiscina (Fig. 27.2), but that of *Agnostus pisiformis* (Müller & Walossek, 1987, p. 11, fig. 5) and other Agnostina (Robison, 1972b) is different. The hypostome in Agnostina is highly convex and lacks borders, the more heavily sclerotized portions surround and divide the middle body, and the anterior and posterior wings are elongate and dorsally directed. The middle body is divided into a pair of oval areas, the hypostomal lobes (see Fig. 80), which were less heavily sclerotized; openings in silicified specimens described by Robison may represent similar areas. An outline of this type of hypostome is suggested for *Arthrorhachis* (Fig. 27.1), an example of a unique find among Agnostina of a species having a wide rostral plate and rostral suture. Müller and Walossek (1987, p. 44–46, fig. 26) discussed the similarities and differences between the hypostome of Agnostina and that of other trilobites and commented that the hypostome was a homologous structure in all trilobites.

In a wide range of trilobite groups the hypostome is attached to the inner margin of the cephalic doublure by the **hypostomal suture**. This is the **conterminant** condition. In *Holmia* (Fig. 30.1) the hypostome is wide (tr.) anteriorly, corresponding in width to the frontal portion of the glabella, and the anterior wing is large and triangular, its tip lying beneath the axial furrow immediately in front of the eye lobe. The hypostomal suture is narrow (tr.), the anterior wing curving up dorsal to the rostral plate. The form and relationship of the hypostome to the dorsal exoskeleton is similar in *Xystridura* (Fig. 30.3) to that in *Holmia.* In *Xystridura,* however, there is a facial and a rostral suture, the latter on the dorsal surface of the border, and the connective suture curves back to reach the inner margin of the doublure beneath the genal angle. In *Redlichia* (Fig. 30.2) the hypostome is narrower (tr.) anteriorly, corresponding to the form of the frontal lobe of the glabella, but a relatively large anterior wing is present. A furrow in the external surface of the rostral plate in *Redlichia* runs beneath the anterior border furrow, and pits in each of the furrows project inward and interlock (according to Öpik, 1958; cf. Fortey, 1990a, fig. 6).

Many post-Cambrian trilobite groups are characterized by having the hypostome attached to a doublure in which rostral and connective sutures define a rostral plate. Among Cambrian trilobites, *Welleraspis* (Fig. 31.1) is a probable example, but specimens of Cambrian trilobites showing such an arrangement, with the hypostome preserved in place, have not been figured. Among post-Cambrian trilobites, a number of such specimens are known, as well as undistorted silicified material that allows reconstruction in three dimensions. Examples are *Dysplanus* (Fig. 31.3), *Bathyurus* (Fig. 31.2), *Paladin* (Fig. 31.4), *Acanthopyge* (Fig. 32.1), and *Acidaspsis* (Fig. 32.2), in all of which the anterior wing extends up so that the tip lies closely beneath the ridge formed on the parietal surface by the axial furrow; in *Dysplanus* and *Paladin* a wing process is developed. The large size of the anterior wing in *Bathyurus* means that, if the hypostome were attached, it must have been inclined steeply downward and backward. The angle of inclination of the hypostome was less in *Paladin,* while in *Acanthopyge* it was moderate but the hypostome was large in relation to the rest of the cephalon. In *Illaenus* (Fig. 33) and *Bumastus* the rostral plate was curved posteriorly through 180° to form an inwardly facing **rostral flange**, the hypostomal suture extending along the inner edge of the flange and the adjacent edges of the doublure. The backward and upward inclination of the hypostome has been recorded in *Illaenus* (Jaanusson, 1954), and in species of this genus and of *Bumastus* the anterior wing is large; in *Bumastus* the tip may have been situated close beneath the fossular apodeme.

While in most of the above-mentioned genera the tip of the wing process lies close to, against, or in a pit in the fossular apodeme, this device is particularly well developed in such genera as *Ceraurus* (Fig. 5), *Ceraurinella* (Fig. 26), *Deiphon* (Fig. 34.1), *Encrinuroides* (Fig. 34.3), and *Calymene* (Fig. 34.2). In addition to process and apodeme being in contact, the distal portion of the wing was wrapped around the apodeme to aid in keeping the process in position. The size of the wing and its process and the convexity of the cephalon lead to a downwardly sloping attitude of the hypostome, strongly so in *Deiphon* and other cheirurids. The presence of the rhynchos in some encrinurids and calymenids appears to be related to co-

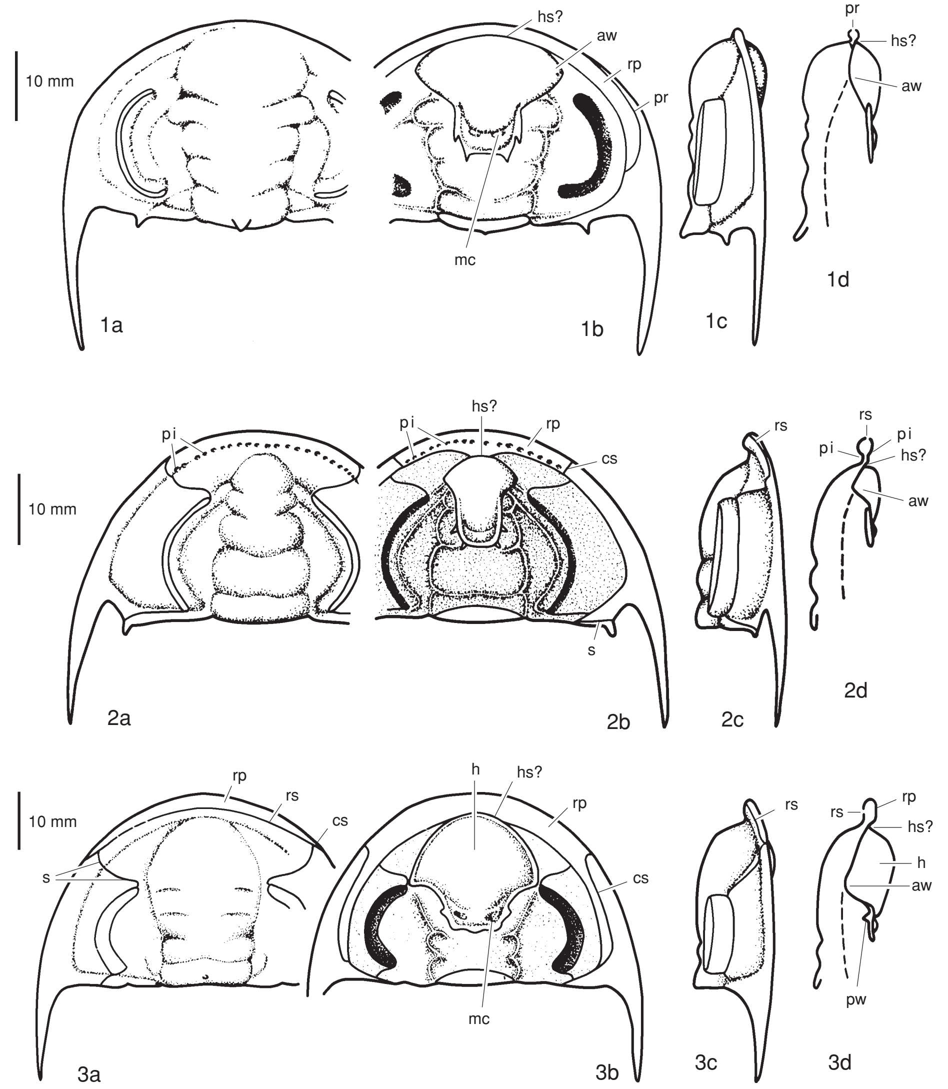


FIG. 30. Cephala in which the hypostome was probably conterminant. *1, Holmia kjerulfi* (LINNARSSON), Lower Cambrian (Whittington, 1988a, fig. 3). *2, Redlichia* sp., Lower to Middle Cambrian (Whittington, 1988a, fig. 6). *3, Xystridura* sp., Middle Cambrian (Whittington, 1988a, fig. 9). All *a* views are partial dorsal, *b,* partial ventral, *c,* right lateral, and *d,* sagittal section of cephalic exoskeleton combined with a right lateral view of the hypostome. The position of the rostral or perrostral suture is shown by a gap in the section; the *heavy dashed line* indicates crest of ridge formed by axial furrow on inner (parietal) surface of exoskeleton. See Figure 27 (p. 30) for list of abbreviations.

aptation—that is, to the fit of the pygidium below the cephalon when the hypostome is inclined downward.

The combination of an attached hypostome and a median suture crossing the doublure is known in species of the Upper Cambrian genera *Proceratopyge* and *Eurekia* (Fig. 35.1–2). In these species the hypostomal suture is narrow (tr.), and an anterior wing extends upward to the ridge formed on the ventral side of the axial furrow. The position of this ridge in *Eurekia* determines the angle of inclination of the hypostome. In Ordovician asaphids such as *Stegnopsis* (Fig.

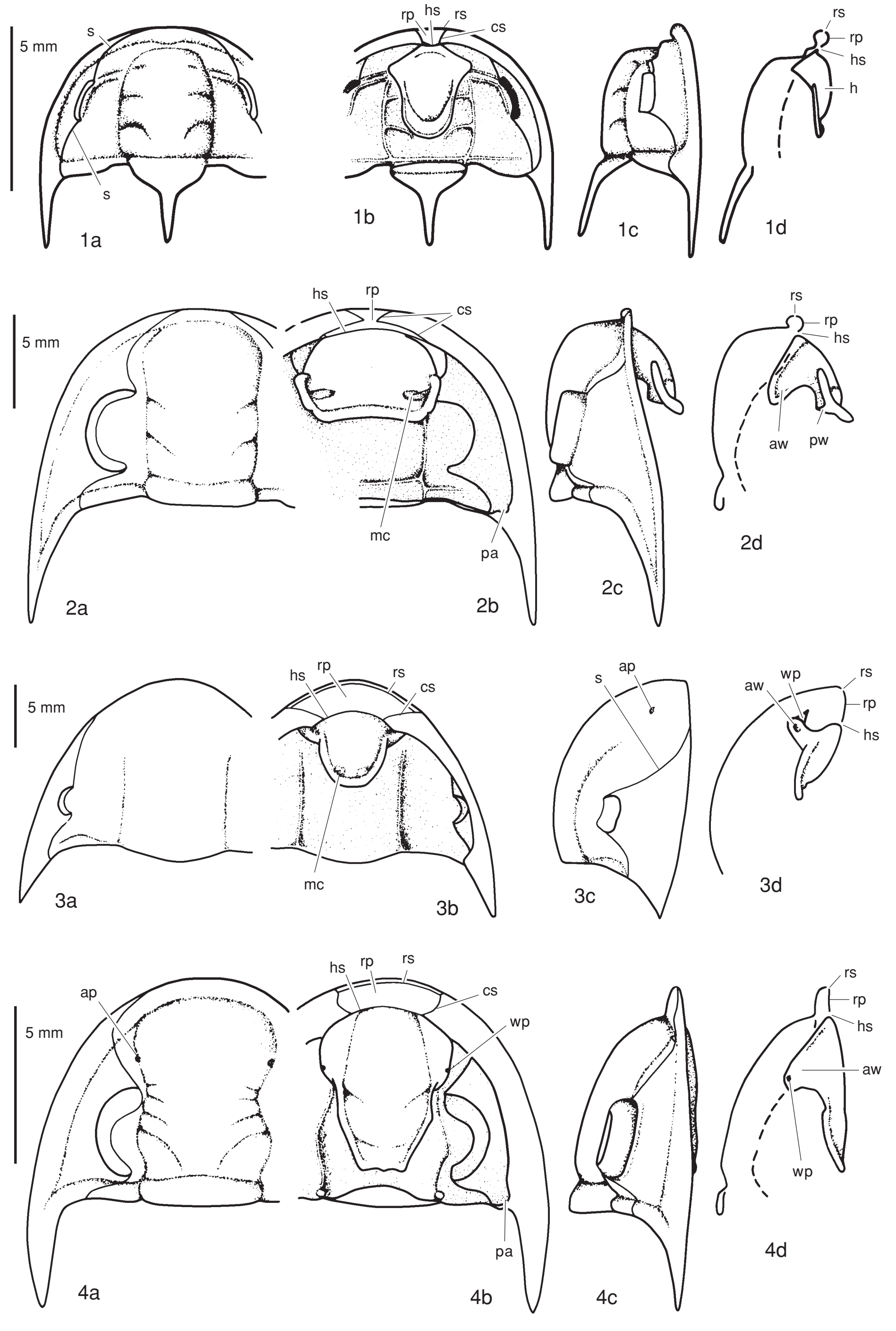


FIG. 31. *For explanation, see facing page.*

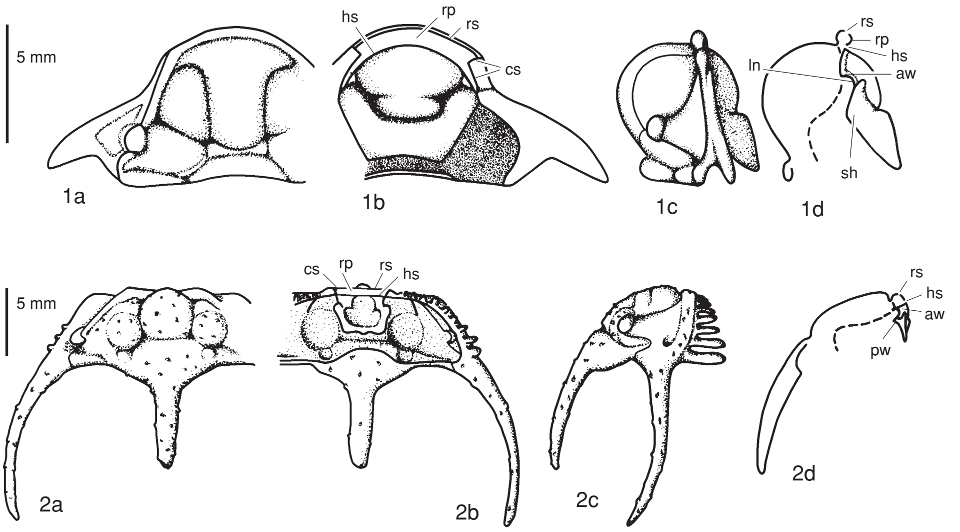


FIG. 32. Cephala with a conterminant hypostome and rostral plate. *1, Acanthopyge* sp., Silurian to Devonian (Whittington, 1988b, fig. 25). *2, Acidaspis* sp., Ordovician to Devonian (Whittington, 1988b, fig. 26). All *a* views are partial dorsal, *b,* partial ventral, *c,* right lateral, and *d,* sagittal section of cephalic exoskeleton combined with a right lateral view of the hypostome. The position of the rostral and hypostomal suture is shown by a gap in the section; the *heavy dashed line* indicates crest of ridge formed by axial furrow on inner (parietal) surface of exoskeleton. See Figure 27 for list of abbreviations.

35.3) the arrangement is similar, but the hypostomal suture is wider (tr.) and runs in a curve along the upturned doublure, so that the close fit is not in a single plane. In *Remopleurides* (Fig. 35.4) the suture also has this curved course, and a long wing process extends to the pit in the fossular apodeme and to the tip of the process formed by the pit in the anterior doublure. Peculiar to remopleuridids is the oval area that occupies much of the middle body, over which the exoskeleton is thinner and is either smooth externally or bears raised lines.

Fortey and Chatterton (1988) included in the Asaphida the Anomacaroidea, a superfamily that includes *Auritama.* In one species of this genus, Öpik (1967, fig. 75) described the marginal rostral suture, from each end of which a connective suture is directed inward, the two meeting to isolate a small triangular plate on the anterior edge of the doublure, the **rostellum**. From the posterior tip of this plate a median suture traverses the cephalic doublure. The rostellum is also known in a species of *Pterocephalia* (Chatterton & others, 1994, fig. 6.6).

In *Symphysurus* (Fortey, 1986) and *Nileus* (Fig. 36.1) the hypostome is attached and braced by a long, upwardly directed anterior wing, but the cephalic doublure is not crossed by a median or connective sutures. This latter condition is thought to be

FIG. 31. Cephala with a conterminant hypostome and rostral plate. *1, Welleraspis swartzi* (Tasch), Upper Cambrian (Whittington, 1988a, fig. 18). *2, Bathyurus* sp., Middle Ordovician (Whittington, 1988b, fig. 10). *3, Dysplanus* sp., Ordovician (Whittington, 1988b, fig. 8). *4, Paladin* sp., Carboniferous to Permian (Whittington, 1988b, fig. 12). All *a* views are partial dorsal, *b,* partial ventral, *c,* right lateral, and *d,* sagittal section of cephalic exoskeleton combined with a right lateral view of the hypostome. The position of the rostral or hypostomal suture is shown by a gap in the section; the *heavy dashed line* indicates crest of ridge formed by axial furrow on inner (parietal) surface of exoskeleton. See Figure 27 (p. 30) for list of abbreviations.

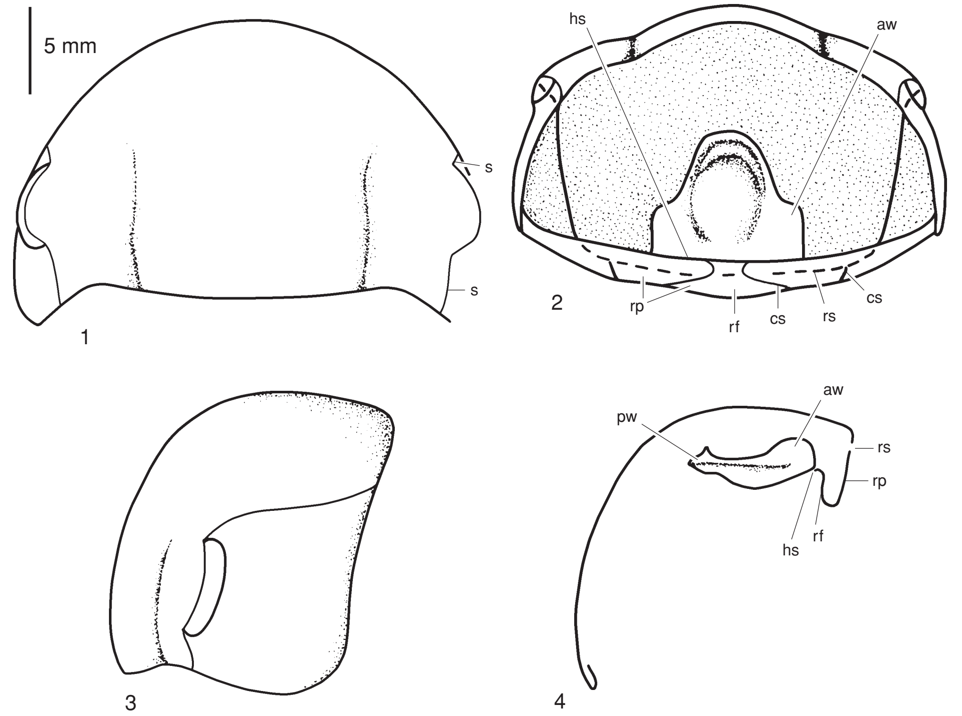


FIG. 33. Cephalon of Ordovician *Illaenus* sp.; the hypostome is conterminant and held at an unusual angle; *1,* partial dorsal view; *2,* posteroventral view, *dashed line* showing course of suture where hidden; *3,* right lateral view; *4,* sagittal section of cephalic exoskeleton combined with a right lateral view of the hypostome; position of rostral and hypostomal sutures shown by a gap in the section (Whittington, 1988b, fig. 7). See Figure 27 (p. 30) for list of abbreviations.

secondary in nileids, *Platypeltoides* (FORTEY & OWENS in OWENS & others, 1982) having a median suture. In *Phacops* (Fig. 36.2) the hypostome is attached and braced by a large anterior wing bearing a small wing process, and the cephalic doublure is entire. In early Phacopina (HENRY, 1980a) the condition of the doublure is similar, so the lack of median or connective sutures may be a cardinal character of this group. JAANUSSON (1975), however, described the Early Ordovician genus *Gyrometopus,* which is phacopid in appearance but has the cephalic doublure divided by a rostral plate. He pointed out that this species fulfills the requirements of an immediate ancestor of Phacopina but that the presence of a rostral plate might be considered to exclude it from that group.

A special case of the conterminant condition of the hypostome is fusion with the rostral plate, so far known only in Cambrian trilobites. In *Paradoxides* (Fig. 37.1) this condition is considered to be a diagnostic character of the genus, and it also obtains in *Oryctocephalus* (SHERGOLD, 1969, pl. 1, fig. 4, pl. 2, fig. 4) and many genera of corynexochoids. In *Fieldaspis* (Fig. 37.2), a corynexochoid, a long, steeply inclined anterior wing extends dorsally so that the tip lies beneath the axial furrow immediately in front of the eye ridge. In *Paradoxides* there is a similar arrangement, the wide (tr.), inflated, middle body lying beneath the expanded anterior portion of the glabella. Thus the **rostral-hypostomal plate** in these genera is rigidly braced against the rest of the cephalic exoskeleton.

The ventral cephalic sutures in the Lower Cambrian *Bathynotus* (Fig. 37.3) are unique, in that they diverge at about 100° from the

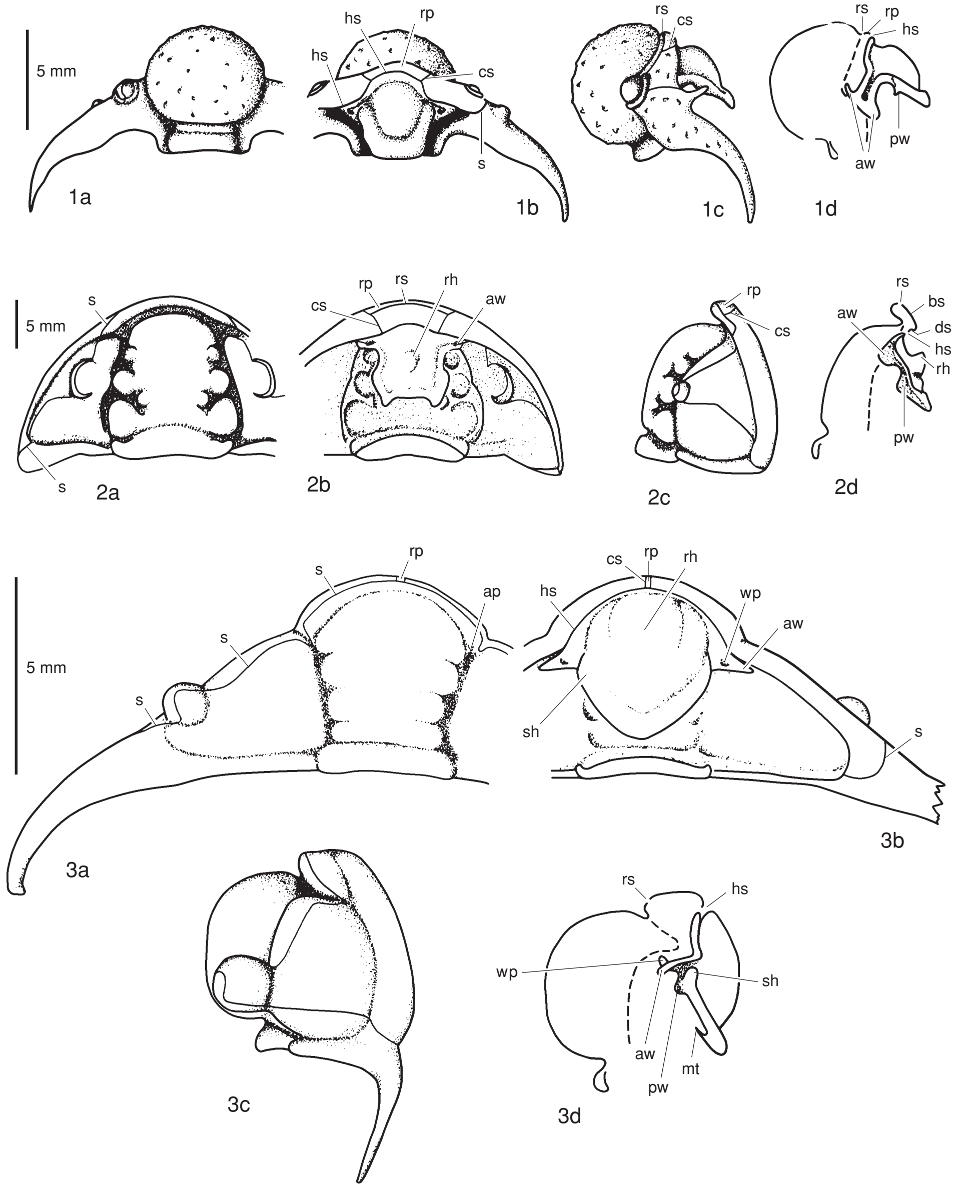


FIG. 34. Cephala with a conterminant hypostome and rostral plate. *1, Deiphon* sp., Silurian (Whittington, 1988b, fig. 19). *2, Calymene* sp., Silurian to Devonian (Whittington, 1988b, fig. 23). *3, Encrinuroides* sp., Ordovician to ?Silurian (Whittington, 1988b, fig. 20). All *a* views are partial dorsal, *b,* partial ventral, *c,* right lateral, and *d,* sagittal section of cephalic exoskeleton combined with a right lateral view of the hypostome. The position of the rostral and hypostomal suture is shown by a gap in the section; the *heavy dashed line* indicates crest of ridge formed by axial furrow on inner (parietal) surface of exoskeleton. See Figure 27 (p. 30) for list of abbreviations.

midpoint of the anterior edge of the doublure to isolate a hypostome that is pentagonal in outline. Whether these two sutures are sections of the hypostomal suture or whether they should be regarded as connective sutures is uncertain. If the latter, the supposed hypostome is composed of the true hypostome fused with a triangular rostral plate.

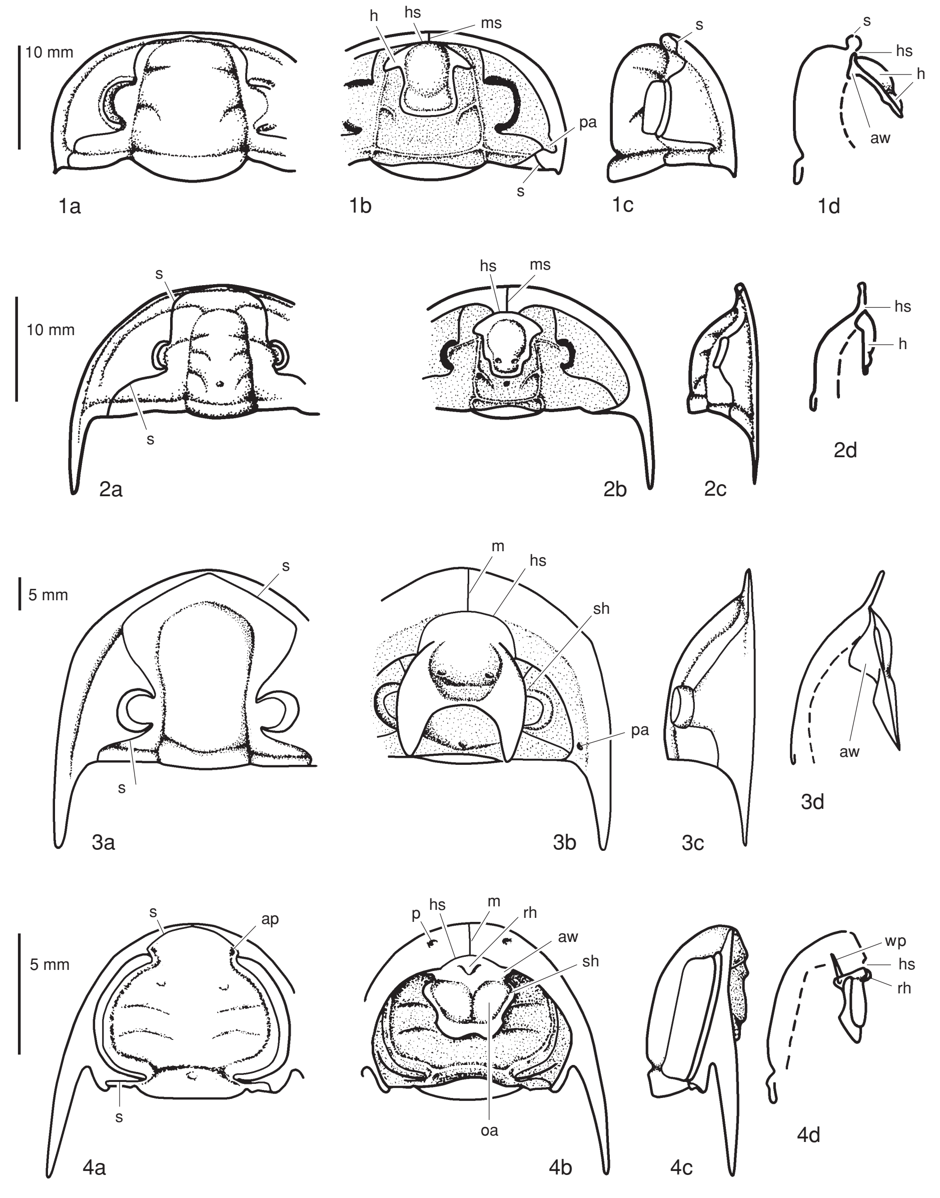


FIG. 35. Cephala with a conterminant hypostome, the doublure crossed by a median suture. *1, Eurekia ulrichi* (RASETTI), Upper Cambrian (Whittington, 1988a, fig. 20). *2, Proceratopyge* sp., Middle to Upper Cambrian, Tremadoc (Whittington, 1988a, fig. 16). *3, Stegnopsis* sp., Ordovician (Whittington, 1988b, fig. 3). *4, Remopleurides* sp., Ordovician (Whittington, 1988b, fig. 6). All *a* views are partial dorsal, *b,* partial ventral, *c,* right lateral, and *d,* sagittal section of cephalic exoskeleton combined with a right lateral view of the hypostome. The position of a suture is shown by a gap in the section; the *heavy dashed line* indicates crest of ridge formed by axial furrow on inner (parietal) surface of exoskeleton. See Figure 27 (p. 30) for list of abbreviations.

No other species is known with such a ventral structure or with a triangular rostral plate in which the apex of the triangle is directed forward.

FORTEY and CHATTERTON (1988, p. 178, fig. 5) proposed the term **impendent** for a condition seen, for example, in *Nileus* (Fig. 36.1), *Remopleurides* (Fig. 35.4), *Dysplanus*

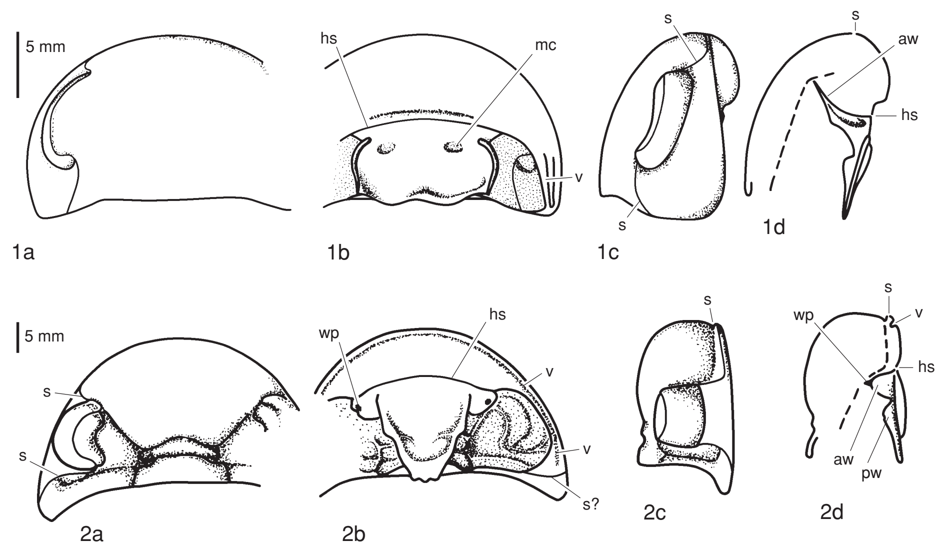


FIG. 36. Cephala with a conterminant hypostome, but lacking a connective or a median suture. *1, Nileus* sp., Ordovician (Whittington, 1988b, fig. 5). *2, Phacops* sp., Devonian (Whittington, 1988b, fig. 21). Both *a* views are partial dorsal, *b,* partial ventral, *c,* right lateral, and *d,* sagittal section of cephalic exoskeleton combined with a right lateral view of the hypostome. The position of a suture is shown by a gap in the section; the *heavy dashed line* indicates crest of ridge formed by axial furrow on inner (parietal) surface of exoskeleton. See Figure 27 (p. 30) for list of abbreviations.

(Fig. 31.3), and *Phacops* (Fig. 36.2). Here the direct relationship between the hypostomal position and the glabella is supposedly lost. As may be seen, the connection between the fossular apodeme and anterior wing process is retained in these forms, as it is in other species with the conterminant hypostome. What is different is that the glabella and presumed preglabellar area or field are merged into a continuous slope, which becomes vertical, overhangs the anterior margin, or, in the case of *Phacops,* overhangs an extremely short (sag.) anterior border. The doublure is relatively broad (sag. and exs.) so that the anterior margin of the hypostome appears to lie farther posteriorly and is not approximately beneath the preglabellar furrow in *Phacops,* for example. The impendent condition appears to reflect an expansion of the anterior glabellar lobe (possibly related to an expansion of the anterior portion of the alimentary canal) at the expense of the anterior border, with the basic relationship of hypostomal wing and fossula being retained.

The foregoing account has shown that the position of the tip of the anterior wing of the hypostome, close beneath the fossula or equivalent position in the axial furrow, was homologous in all trilobites (cf. FORTEY, 1990a, p. 531). This arrangement appears to have been maintained, whatever the hypostomal attachment condition may have been.

MOVEMENT OF THE HYPOSTOME

The possibility of such movement has long been discussed (e.g., SCHEVILL, 1936; ELDREDGE, 1971; WHITTINGTON, 1988a, 1988b). In trilobites having a conterminant hypostome (and especially in those having a fused rostral-hypostomal plate), the hypostome was held rigidly in relation to the remainder of the cephalic exoskeleton. The anterior wing resting against the fossula or inner surface of the axial furrow braced the hypostome and determined its attitude, as the lateral views and sagittal sections of Figures 30 through 37 illustrate. The

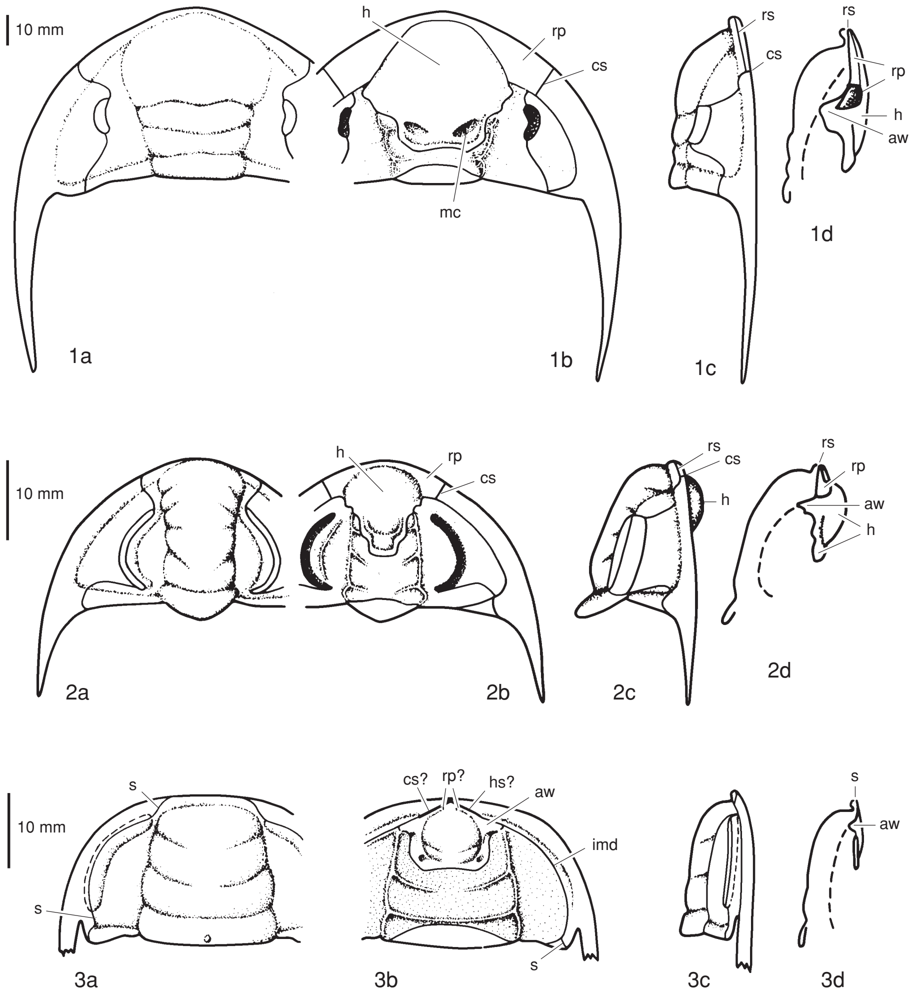


FIG. 37. Cephala in which rostral plate and hypostome are fused (possibly so in *Bathynotus*). *1, Paradoxides davidis* SALTER, Middle Cambrian (Whittington, 1988a, fig. 8). *2, Fieldaspis celer* (WALCOTT), Middle Cambrian (Whittington, 1988a, fig. 10). *3, Bathynotus holopygus* (HALL), Lower Cambrian (Whittington, 1988a, fig. 5). All *a* views are partial dorsal, *b,* partial ventral, *c,* right lateral, and *d,* sagittal section of cephalic exoskeleton combined with a right lateral view of the hypostome. The position of the rostral or facial suture is shown by a gap in the section; the *heavy dashed line* indicates crest of ridge formed by axial furrow on inner (parietal) surface of exoskeleton. See Figure 27 for list of abbreviations.

hypostome hence formed part of a capsule in the axial region of the exoskeleton, which enclosed the U-shaped anterior portion of the alimentary canal. In trilobites that had a natant hypostome (Fig. 27–29), the relationship was less rigid. Any movement of the natant hypostome would have depended upon musculature, the flexibility of the ventral integument into which it was inserted, and the nature of the link between anterior wing and fossular apodeme.

THORAX

The thoracic region of the trilobite body consists of a number of similar somites that articulate with one another and with the fused somites of the cephalic and pygidial regions. The thorax (Fig. 2) is the exoskeleton of this region, including the doublure, and the exoskeleton of each somite is referred to as a segment. Each segment consists of the **axial ring**, the exoskeleton of the axis, and the **pleura**, that of the pleural region. The number of segments in the thorax may be 2 (Agnostina) or 3 (Eodiscina), whereas in most other trilobites the number is between approximately 6 and 15. This generalization led JAEKEL (1909) to propose the terms Miomera for trilobites with 2 or 3 thoracic segments and Polymera for trilobites with 6 or more such segments. Thus Miomera could be used as an inclusive term for Agnostida and Polymera for all other trilobites. However, it is known that these other trilobites include species that had 2, 3, or 4 thoracic segments (e.g., ROBISON & CAMPBELL, 1974; W. ZHANG, 1980; FORTEY & RUSHTON, 1980); and Miomera is a junior synonym of Agnostida (MOORE, 1959, p. 172). Hence these terms cannot be used for formal taxonomic categories, but only informally as adjectives (**miomerid** and **polymerid**) to describe trilobites with few or many segments (cf. ROBISON & CAMPBELL, 1974, p. 281). In some groups of trilobites other than Agnostina and eodiscoids, a specific number of thoracic segments may be present in most if not all species, such as 6 in trinucleids, 8 in asaphids, or 13 in calymenids. In other groups the number may vary to a greater extent between species of closely related genera or species of one genus as, for example, in the 17 to 32 segments in the thorax of species attributed to *Alokistocare* (ROBISON, 1971).

The maximum number of segments known in any species appears to be 61, in an emuellid (POCOCK, 1970). The specimen on which the oft-quoted figure of 40 is based is the original of WALCOTT (1916a, pl. 26, fig. 4b,c) of *Menomonia calymenoides*. In this specimen the convex thorax of many segments narrows backward gradually, and more than 40 axial rings may be counted. Preservation is poor; it is uncertain whether the thorax is complete anteriorly, and the boundary between thorax and pygidium cannot be ascertained. This difficulty of determining, in a series of similar segments diminishing progressively backward in width (tr.) and length, where thorax ends and pygidium begins applies also to specimens of hapalopleurids (HARRINGTON & LEANZA, 1957, p. 203–205). In *Seleneceme,* a similar problem has been solved by examining new material (KENNEDY, 1989). BURLING (1916) claimed that the specimen of *Olenellus robsonensis* exhibited 44 thoracic segments, but a re-examination (WHITTINGTON, 1989) suggests that the number does not exceed 40. The pygidium is not preserved, so that the original total number of segments in the thorax is unknown. Specimens of the emuellids described by POCOCK (1970) show much of the pleural region posteriorly and the minute pygidium, so that the basis for a maximum number of 61 thoracic segments appears to be sound.

The axial ring of the thorax is separated from the pleura by the axial furrow (Fig. 2). The depth of this furrow and the transverse convexity of the axial ring vary; the transverse profile of the axial ring may be evenly curved and subtend an arc of up to 180° or may be flattened medially. The ring may be flat or convex in longitudinal (sag. and exs.) profile, the slope being steepest posteriorly; it slopes anteriorly into the transverse **articulating furrow** (Fig. 38–39) and has an anterior extension, the **articulating half ring**, the anterior edge of which curves in an arc so that the half ring is longest sagittally. This half ring projects forward beneath the similarly shaped doublure of the next ring in front (Fig. 38.2, 39) or of the occipital ring of the cephalon (Fig. 26). It acted as a guide during flexure of the thorax and covered the gap that opened between adjacent axial rings during flexure. It was absent only from the first thoracic segment of almost all species of Agnostina. In silicified examples of remopleuridids (CHATTERTON & CAMPBELL, 1993, p. 121), a small, transverse plate along the anteromedian margin of the articulating half ring is isolated by a suture. The lateral

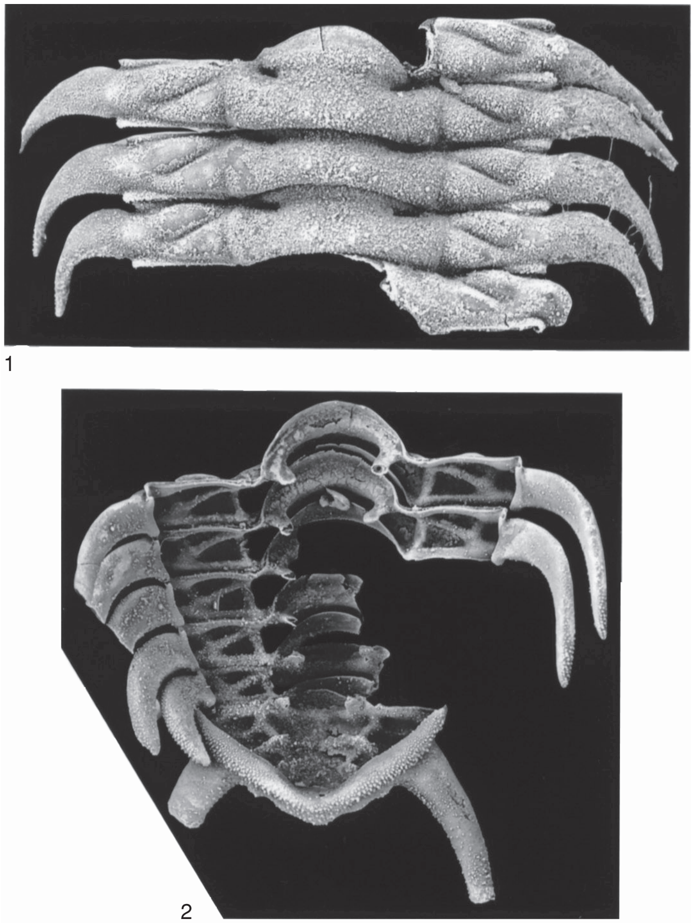


FIG. 38. *Ceraurus whittingtoni* EVITT, Middle Ordovician, Virginia, USA. *1,* Dorsal view of portions of 5 thoracic segments, ×4.5 (new). *2,* Ventral view of portions of 5 segments and the pygidium, ×4.5 (Whittington, 1960b, fig. 1g).

extremity of the articulating furrow may deepen into an **apodemal pit**, which varies in depth and projects into the body as an **apodeme**. Such apodemes form a graded morphological series with those of the cephalon (Fig. 26.1) and pygidium (Fig. 38.2, 39.2) (LUDVIGSEN & CHATTERTON, 1982, pl. 6; CHATTERTON & PERRY, 1983, pl. 1, 13). In some species the axial ring is divided (Fig. 40.2) by an intra-annular furrow into the smaller **preannulus** and a larger **postannulus.** The axial ring may bear a tubercle or **axial spine,** which may be median and borne by some or all the segments of the thorax in a size series or by only one segment. The long axial spine on the 15th segment of *Olenellus* (see Fig. 45) is well known, but equally conspicuous are the spines on the 13th segment of the Ordovician *Balnibarbi* (FORTEY, 1974b, fig. 4), on the 10th segment of the Silurian *Encrinurus* (RAMSKÖLD, 1986, pl. 39, fig. 1), and on the 6th segment of the Devonian *Otarion* (MORZADEC, 1983, pl. 3, fig. 3). Axial spines or tubercles may be paired close to the midline, and additional pairs may occur. In some trilobites the lateral extremity of the axial ring may be inflated and rounded distally, in some sufficiently so as to form a **lateral axial lobe** that may be separated from the rest of the ring by a shal-

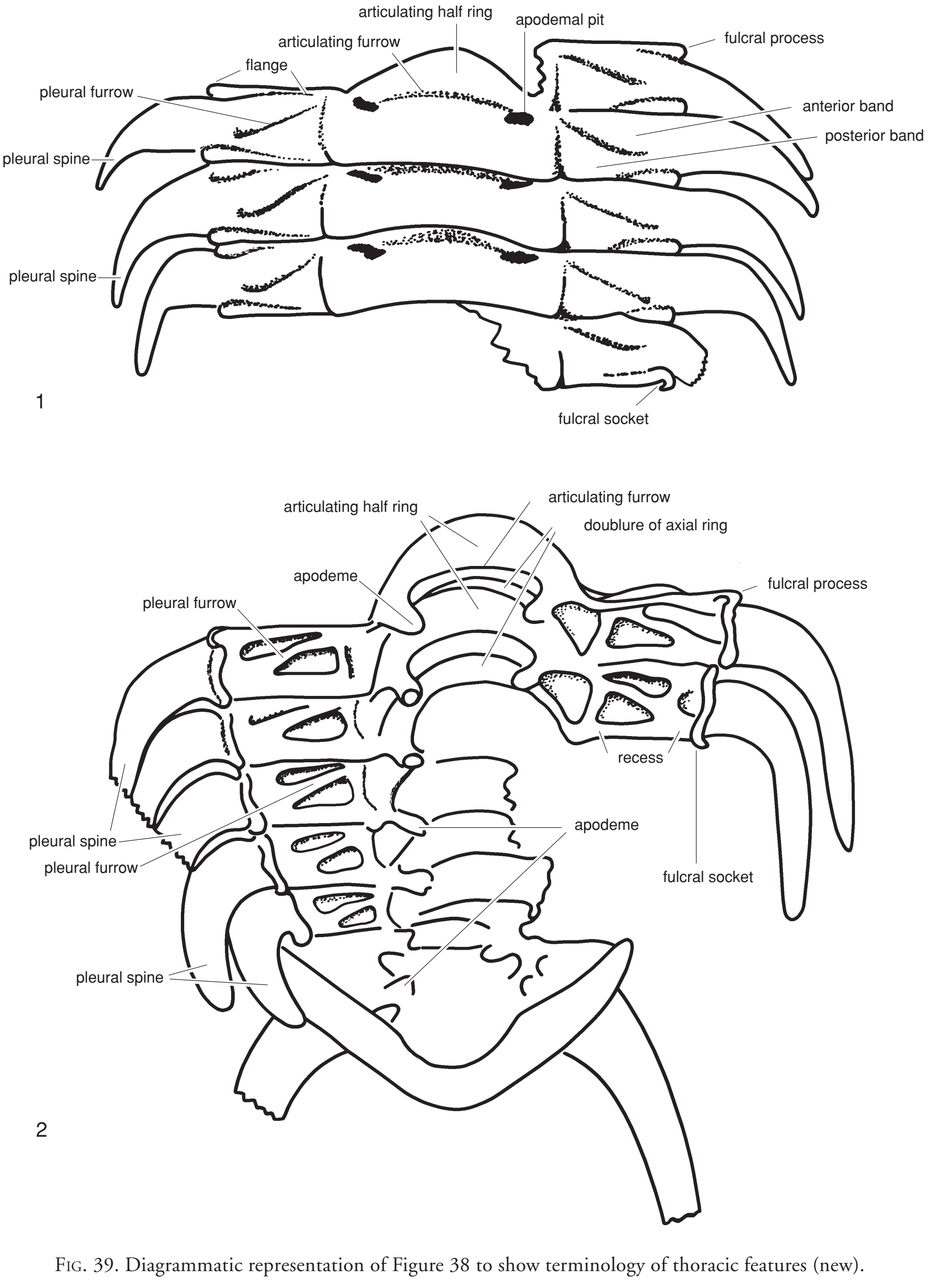


FIG. 39. Diagrammatic representation of Figure 38 to show terminology of thoracic features (new).

low furrow. A serial homology between axial rings is shown in many trilobites by their duplication of the form of the axial spine or tubercle and lateral lobes of the occipital ring. On the other hand, RAMSKÖLD (1985, p. 36) has noted that in some species of *Dalmanites* the lateral axial lobe is more prominent on particular segments.

The pleura of the segment extends outward from the axial furrow, and in most

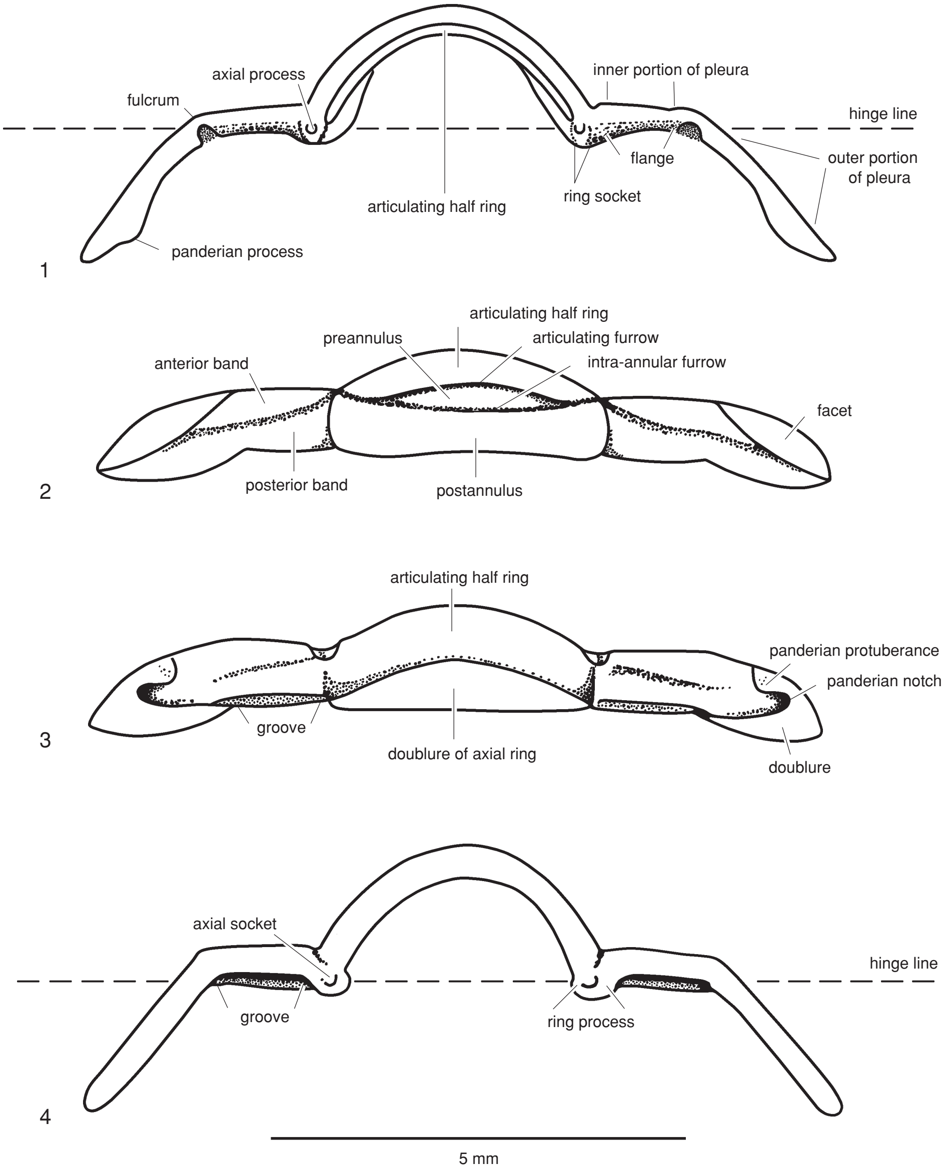


FIG. 40. Thoracic segment of *Proetus pluteus* WHITTINGTON & CAMPBELL. *1–4,* Anterior, dorsal, ventral, and posterior views, respectively, showing terminology and mode of articulation (adapted from Whittington & Campbell, 1967, pl. 2, fig. 14, 25, 31–32).

trilobites (as seen in anterior or posterior views, Fig. 40.1,4) is divided at the **fulcrum** into an **inner portion** that is horizontal and an **outer portion** that slopes downward outside the fulcrum. The same division obtains in *Ceraurus* (Fig. 38–39) at the fulcral process and socket between the inner, horizontal portion and the downwardly directed pleural spine. In contrast, in *Olenoides* the inner portion of the pleura is not horizontal (Fig. 41.5); but, after ascending from the axial furrow, it curves to slope gently downward and outward and there is no fulcrum. In *Olenellus* the pleura was similarly curved

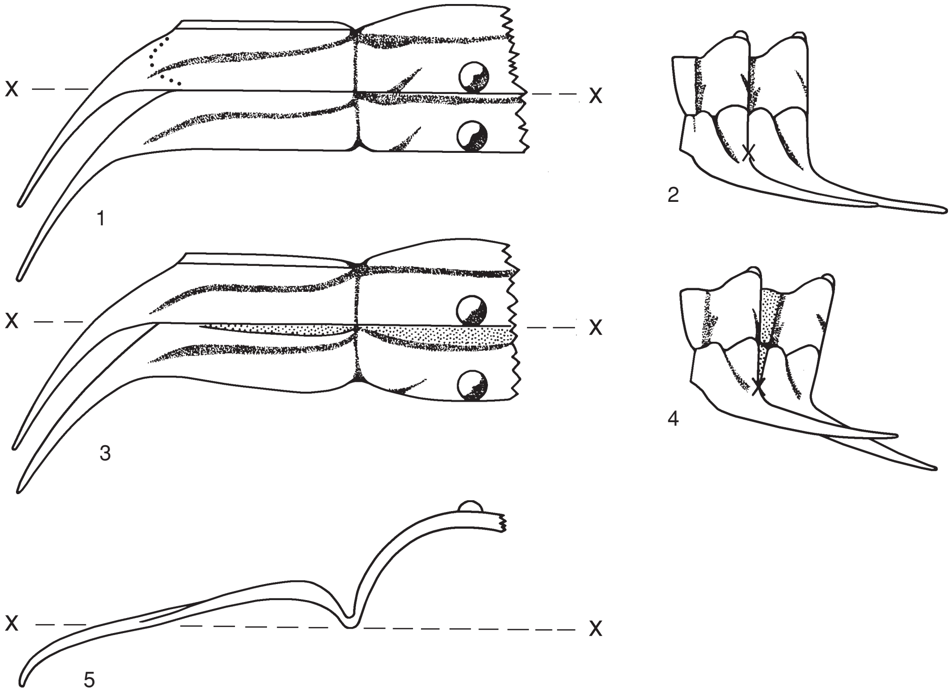


FIG. 41. Restoration of left halves of two midthoracic segments of *Olenoides serratus* (ROMINGER). *1,2,* Dorsal and left lateral views of extended position; *3,4,* dorsal and left lateral views of flexed position; *5,* posterior view. *Dashed line* and *x* indicate position of hinge line; *coarse stipple* indicates portions of flange and articulating half ring exposed by flexure; *dotted line* on left side of anterior segment in part 1 indicates position of inner margin of doublure (Whittington, 1980a, fig. 3).

and lacked the fulcrum (see Fig. 45.4). In *Remopleurides* (CHATTERTON & LUDVIGSEN, 1976, pl. 1) the fulcrum is adjacent to the axial furrow so that most of the pleura represents the outer portion; in *Cybantyx* the horizontal inner portion of the pleura is absent and the pleura continues the slope of the axial ring (see Fig. 47).

A **pleural furrow** (Fig. 39) commences at the axial furrow, opposite the outer end of the articulating furrow, and is directed outward and slightly backward across the pleura, dividing it into **anterior** and **posterior bands**. The depth and slope of the sides of this furrow vary, and the pleura may be almost flat or inflated to differing degrees. Thus the pleural furrow may be flanked by slightly inflated areas (or by ridges as in odontopleurids) or may be broad and shallow and occupy much of the dorsal area of the pleura. The pleural furrow may be absent or may be replaced by a row of pits, as in certain cheirurids (LANE, 1971, p. 44; C. P. HUGHES, 1969, pl. 8, fig. 4–5). In trilobites in which the outer portions of the pleurae overlap during enrollment (Fig. 2, 40), the anterolateral surface of this outer part is bevelled to form an articulating **facet**. The surface of this facet is gently concave (a section of a cone), to enable it to glide closely beneath the doublure in front of it. The pleural furrow may continue for a short distance on the outer portion and die out, or it may continue behind the facet (**postfacetal** condition), as in asaphids such as *Isotelus* and in the proetid *Proetus* (Fig. 40.2). In phacopids and calymenids (HAMMANN, 1983, pl. 2; CHATTERTON & CAMPBELL, 1993, fig. 1d, 1h, 2f), for example, the pleural furrow crosses the posterior margin of the facet and continues on the facet—the **epifacetal** condition. The doublure extends inward beneath the outer portion of the pleura to a varying distance; for example, in *Proetus* it extends a short distance inside the posterior and distal margins (Fig. 40), but in *Ceraurus,* in which the outer portion is a pleural spine, it extends to the fulcrum (Fig. 39). In trilobites in which the pleurae are facetted and slide closely one over another in enrollment, the doublure may carry a device to limit the amount of overlap. This device may be in the form of a notch in the narrow doublure, the **panderian notch,** the anterior side of which is raised to form a stop, the **panderian protuberance,** as in *Proetus* (Fig. 40.3) and in the Early Cambrian *Crassifimbra* (PALMER, 1958, fig. 5) or the Ordovician *Dimeropyge*. In trilobites with a wider (tr.) doublure, the stop may take the form of a sharp, raised fold directed outward and backward, as in *Symphysurus* or *Nileus.* In asaphids there may be a similar fold or a notch with a raised margin, the panderian protuberance, so called because of the small elliptical or circular opening, the **panderian opening**, immediately anterior to it. These structures have been studied by SIEGFRIED (1936) and HUPÉ (1955b) and illustrated in work on silicified (CHATTERTON & LUDVIGSEN, 1976) and other specimens (BALASHOVA, 1976; HAMMANN, 1983, p. 38, pl. 22; CHATTERTON & CAMPBELL, 1993).

The distal tip of the outer portion of the pleura may be rounded as in *Isotelus* (Fig. 2) or bluntly pointed as in *Proetus* (Fig. 41); the doublure of the outer portion of the pleura is either a narrow band around the tip and along the posterior edge or is more extensive. In forms in which the entire outer portion of the pleura forms a spine as in *Ceraurus* (Fig. 39), *Olenellus,* or *Remopleurides,* the doublure extends beneath the hollow spine to the fulcrum (or its equivalent). In encrinurids and odontopleurids (Fig. 42–43), each band of the pleura is extended into a spine, the major spine being on the longer (exs.) posterior band. The minor spine on the anterior band may be forwardly or upwardly directed or, in *Dicranurus,* vertically downward. It is apparently rare for the major spine to arise from the anterior pleural band as it does in *Dorypyge* (WESTERGÅRD, 1948, pl. 2, fig. 4; W. ZHANG & JELL, 1987, pl. 12, fig. 5).

The pleural or major pleural spines may form a graded size series, progressively more strongly backwardly directed posteriorly. Odontopleurids illustrate this well; for example, in *Miraspis mira mira* (BRUTON, 1968b, pl. 7, fig. 3), *Ceratocephala vesiculosa* (BRUTON, 1968b, pl. 8, fig. 5–6), and *Dicranurus monstrosus* (Fig. 42) the series of major pleural spines is graded in direction and length. In such trilobites as *Dicranurus hamatus elegantus* (Fig. 43), the series of major spines is not evenly graded in length, there being long major spines on segments 4, 6, and 7 but a much reduced major spine on the fifth segment. Different lengths of major spines are also shown by species of *Leonaspis*; for example, in *L. tuberculatus* (WHITTINGTON, 1956b, pl. 57, fig. 8) the series is graded but is longest anteriorly, in *L. jaanussoni* (CHATTERTON & PERRY, 1983, fig. 19) it is graded but longest posteriorly, and in *L. brittanica* (MORZADEC, 1983, pl. 32, fig. 1) the major spines on pleurae 5, 6, and 7 are much longer than others. A single, conspicuously longer spine is termed **macropleural**. In odontopleurids and *Cybeloides* (INGHAM, 1968) it is the spine, the outer portion of the pleura, that is long and stout. The inner portion of the pleura is not enlarged relative to the adjacent segments. This contrasts with the condition in *Olenellus* (see Fig. 45.1), in which the inner portion of the pleura becomes longer (exs.) abaxially. *Emuella* (POCOCK, 1970) and the olenellid *Biceratops* (Fig. 44) provide additional examples of such macropleurae, showing how the shape of the inner portions of adjacent segments are modified to accommodate the macropleura and also illustrating the great length and thickness of the outer spine compared to those of other segments. Examples of macropleurae in which the inner portion of the pleura is enlarged are rare in post-Early Cambrian trilobites, but one is the anterior thoracic segment in the raphiophorid

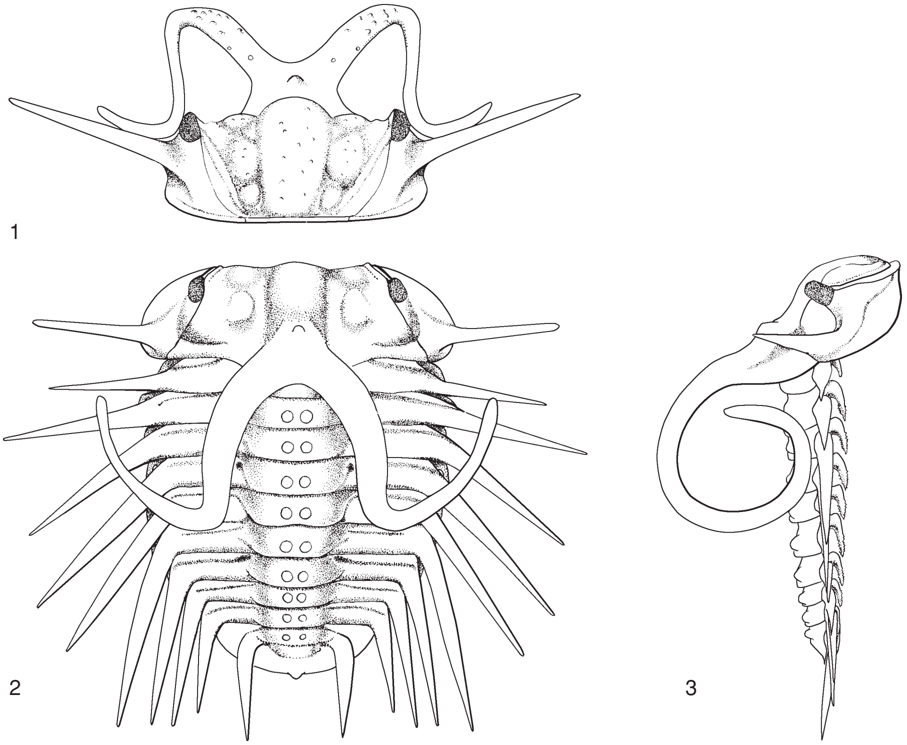


FIG. 42. *Dicranurus monstrosus* (BARRANDE), Devonian, Bohemia. *1,* Anterior view of cephalon; *2,* dorsal view of exoskeleton; *3,* right lateral view of exoskeleton, ×1 (Whittington, 1956d, fig. 18).

Cnemidopyge (C. P. HUGHES, 1969). It may be noted that the enlargement of the inner portion of the pleura in the macropleura takes place from the axial furrow outward, the axial ring being one of a graded series and not enlarged (e.g., *Olenellus* or *Biceratops*). In trilobites that lack a macropleura, thoracic segments may form a graded series, diminishing posteriorly, in length (sag.) of the axial ring and length (exs.) of the inner portion of the pleura. This is not invariably so, as was shown by RAMSKÖLD (1991b, fig. 8) in odontopleurids. His measurements of the original of Figure 43, for example, show an increase in the lengths of segments 1 to 6 (segment 5 is slightly shorter than 4 and 6) and a decrease in the lengths of 6 to 9. Such a size gradation is characteristic of one subfamily, the Selenopeltinae.

Olenellus (Fig. 45) illustrates another type of change that may take place in the series of pleurae. The long, spinose pleura of the 14th segment is directed exsagitally backward, so that the pleurae of the 15th and succeeding segments must necessarily be narrow (tr.) and the pleural spine short, to fit between the 14th pleural spines. A similar abrupt change in size of the pleurae takes place in the same position in the thorax in other species of *Olenellus,* in which the pleural spines of the 14th segment are less strongly backwardly directed. In other Olenellina a change in form of the pleurae may occur much less abruptly or not at all (WHITTINGTON, 1989). This change in the form of the thorax in Olenellina was discussed by WALCOTT (1910, p. 244–245), HUPÉ (1953a, p. 117–118, footnote; p. 122–123), and POCOCK (1970, p. 551–552), HUPÉ having introduced the terms **prothorax** and post-thorax (=**opisthothorax**) for the two portions. HUPÉ considered that the first segment of the

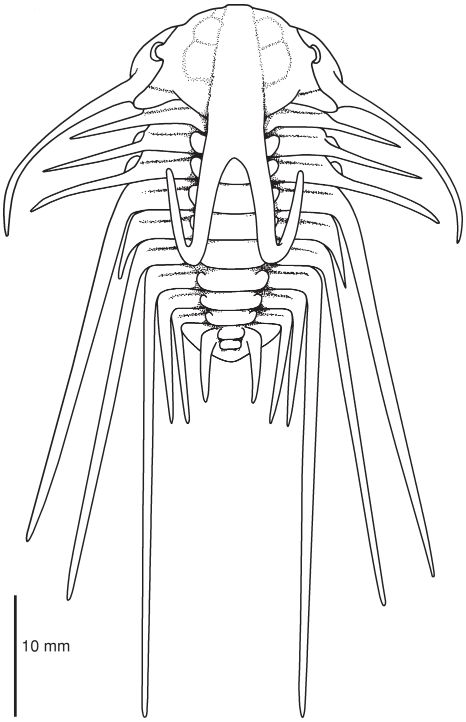


FIG. 43. Dorsal view of exoskeleton of *Dicranurus hamatus elegantus* CAMPBELL, Devonian, Oklahoma (adapted from Campbell, 1977, 1982).

opisthothorax of *Olenellus,* bearing the long median spine, was the 15th and that in this portion of the thorax the pleurae were reduced or absent. The opisthothorax in Olenellina is not well known (WHITTINGTON, 1989), but pleurae, though reduced in size, are present. A subdivision of the thorax is also well displayed by emuellids (POCOCK, 1970), the prothorax having 6 segments, the last two of which are fused, and the 6th being macropleural. The opisthothorax has from 42 to 55 segments and, as in Olenellina, has the axial rings diminishing posteriorly in a graded continuum with those of the prothorax. The pleura of the anterior opisthothoracic segment is much reduced compared to the macropleura, behind this first segment the opisthopleurae show a continuum in reduction posteriorly. Thus some Lower Cambrian trilobites show an abrupt change in the form of the entire pleura rather than the characteristic graded series of changes.

Articulation of the segments with one another and with the cephalon and pygidium is characteristic of trilobites, enabling flexure of the thorax in the vertical plane and partial or complete enrollment. Segments differ in form and convexity and in the way in which the form is modified along the thorax of a particular species to facilitate articulation, enrollment, and the close fit of coaptational devices. A thoracic segment of *Proetus* (Fig. 40) from the midportion of the thorax illustrates the mode of articulation, termed **fulcrate** (ÖPIK, 1970b, p. 4), that is most widespread in trilobites. The hinge line between segments runs through the ring and axial processes and sockets in the axial furrow and along the horizontal edge of the inner portion of the pleura to the fulcrum. The rounded, anterior edge of this inner portion forms a flange, which fits into a groove below the posterior edge of the inner portion of the pleura next in front. The articulating half ring fits below the doublure of the axial ring of this next segment; corresponding structures are present on the posterior margin of the cephalon and the anterior margin of the pygidium. On enrollment, the outer portion of each pleura slides below the one in front; the facet enables this, and the raised anterior edge (panderian protuberance) of the (panderian) notch in the doublure limits the amount of overlap. The articulation devices in hystricurids (WHITTINGTON & EVITT, 1954, fig. 10) and otarionids (WHITTINGTON & CAMPBELL, 1967) are like those of proetids, and similar structures are present in the Lower Cambrian *Crassifimbra* (PALMER, 1958) and probably in most Middle (e.g., ROBISON, 1964, pl. 87, fig. 16, pl. 89, fig. 8–9) and Upper Cambrian trilobites (e.g., STITT, 1976, 1983; LUDVIGSEN, 1982, fig. 49). Many post-Cambrian trilobites, such as calymenids (CAMPBELL, 1967; HAMMANN, 1983), phacopids (MILLER, 1976), and dalmanitids (CAMPBELL, 1977; HOLLOWAY, 1981; MORZADEC, 1983), have essentially similar segments, but a **fulcral process** and **socket** (Fig. 39) may be developed at the abaxial end of the flange as an additional aid in articulation.

A different type of articulation was first recognized by Öpik (1970b, p. 3–4) in *Redlichia* and is referred to as **nonfulcrate**. It is known also in other Cambrian trilobites such as *Olenoides* (Fig. 41), *Olenellus* (Fig. 45) and other Olenellina, and *Paradoxides* (Whittington, 1990). In these trilobites the pleura curves downward and outward and lacks the inner horizontal portion and fulcrum. The details of the structure need further investigation, but in species of *Paradoxides* (Fig. 46) there is an axial articulating process and socket, and a concave flange on the anterior margin of the pleura fits beneath a narrow strip of doublure along the posterior margin of the sclerite in front. A projection at the distal corner of the flange acted as a guide in articulation (the pleural guide of Öpik, 1970b, or the marginal connective device of Bergström, 1973a, p. 13). These devices are similar to those in *Olenellus* (Fig. 45), *Olenoides* (Fig. 41), and *Redlichia* (Öpik , 1970b) and appear to have allowed flexure of the body without the precision of the straight, horizontal hinge-line of the fulcrate form. In his study of xystridurids, Öpik (1975a, p. 23) pointed out that, while species of *Xystridura* had the nonfulcrate type of exoskeleton, that of *Galahetes* was fulcrate. Similarly in corynexochoids, *Olenoides* is nonfulcrate but *Ogygopsis* is fulcrate, and some redlichioids (for example, species of dolerolenids, Jell in Bengtson & others, 1990, p. 272, 292) were fulcrate.

In the trinucleids, raphiophorids, and harpetids (Whittington, 1959a; Campbell, 1975; Chatterton & Ludvigsen, 1976), most of the width (tr.) of the pleura is the horizontal inner portion, the outer portion being narrow (tr.) and sloping. Articulation along the wide (tr.), straight hinge line is by a flange and grooved recess that extends from the axial process or socket to the fulcrum. The outer portion of the pleura has a narrow doublure and panderian notch in *Cryptolithus* and *Dolichoharpes,* a process projecting forward from the anterolateral tip fitted into a recess in the doublure of the segment in front, serving to limit enrollment (Chatterton & Campbell, 1993, fig 8h).

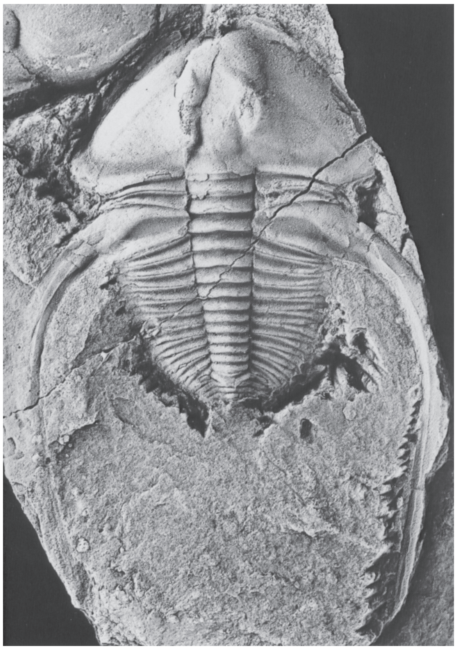


Fig. 44. *Biceratops nevadensis* Pack & Gale, Lower Cambrian, Nevada; dorsal view of paratype, ×3 (Whittington, 1989, fig. 11).

Characteristic of asaphids (Siegfried, 1936; Jaanusson, 1953a, 1953b; Balashova, 1976; Chatterton & Ludvigsen, 1976; Chatterton & Campbell, 1993, fig. 8d) is the relatively wide (tr.), steeply sloping outer portion of the pleura that is broadly facetted and has the doublure extending far inward, cut off along an exsagittal line anteriorly, posteriorly extending up to the fulcrum. This outer portion of the pleura is thus shaped like a pocket and has a panderian opening or notch and protuberance; these flattened outer portions overlap on enrollment. The horizontal inner portion of the pleura (present in most genera) articulates by an anterior flange and posterior recess, and there are axial and ring processes and sockets.

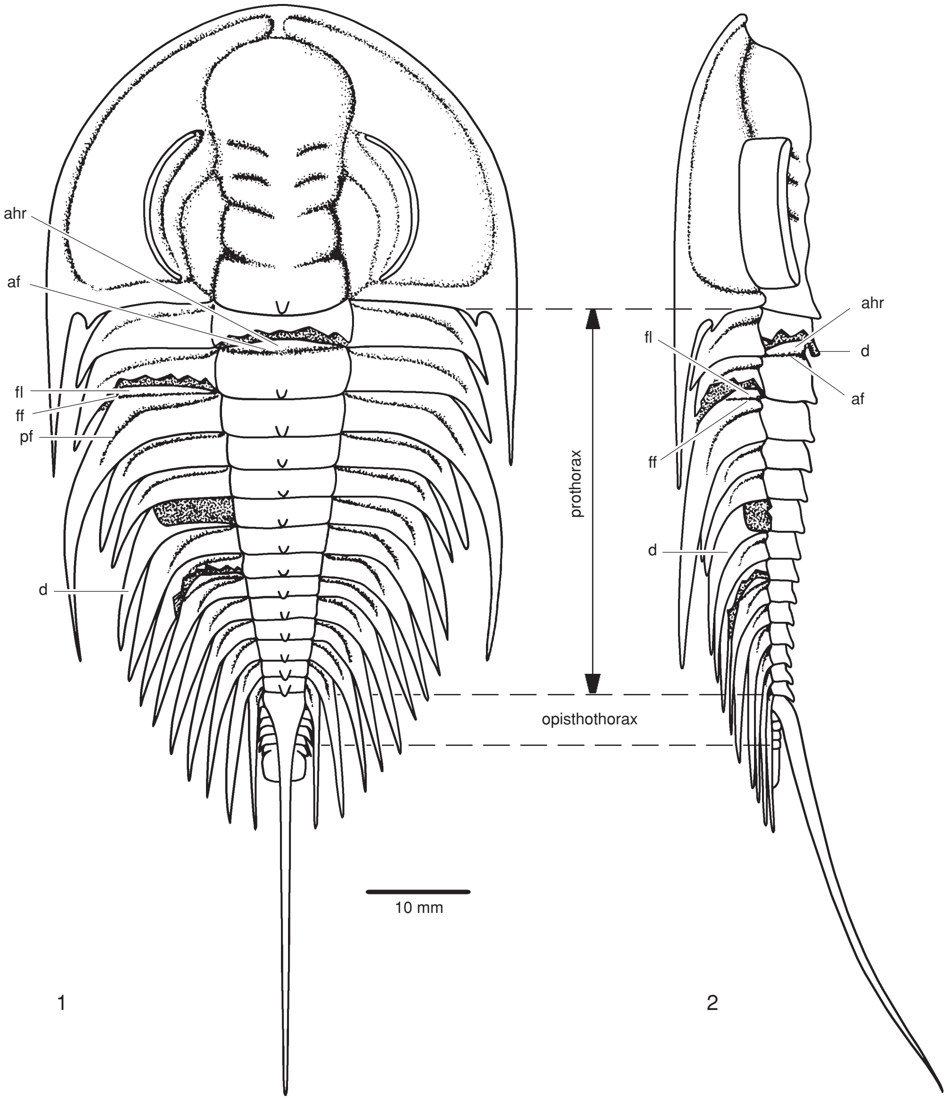


FIG. 45. Restoration of exoskeleton of *Olenellus thompsoni* (HALL), Lower Cambrian, eastern United States. *1,2,* Dorsal and left lateral views, with portions of exoskeleton cut away to show articulating half ring (*ahr*), articulating furrow (*af*), flange furrow (*ff*) and flange (*fl*), pleural furrow (*pf*), and doublure of thoracic segment (*d*); subdivisions of thorax shown; *3,* left lateral view, partly enrolled, with segments 5 and 10 numbered (*solid circles* showing position of axis of rotation between segments); *4,* posterior view, partly enrolled (Whittington, 1989, fig. 1–2).

In the related nileids (WHITTINGTON, 1965; FORTEY, 1986) the inner portion of the pleura is narrow (tr.) with large processes and sockets at the fulcrum, and the outer portion is formed like that of asaphids, a fold (directed transversely) in the doublure acting to limit enrollment. The facet in asaphids (see Fig. 74) and the nileid *Symphysurus* is relatively broad (exs.) and bears terrace ridges; it has been described as **petaloid** by FORTEY (1986) and FORTEY and CHATTERTON (1988, p. 178, fig. 13). In remopleuridids the structure of the pleura (WHITTINGTON, 1959a; CHATTERTON & LUDVIGSEN, 1976; CHAT-

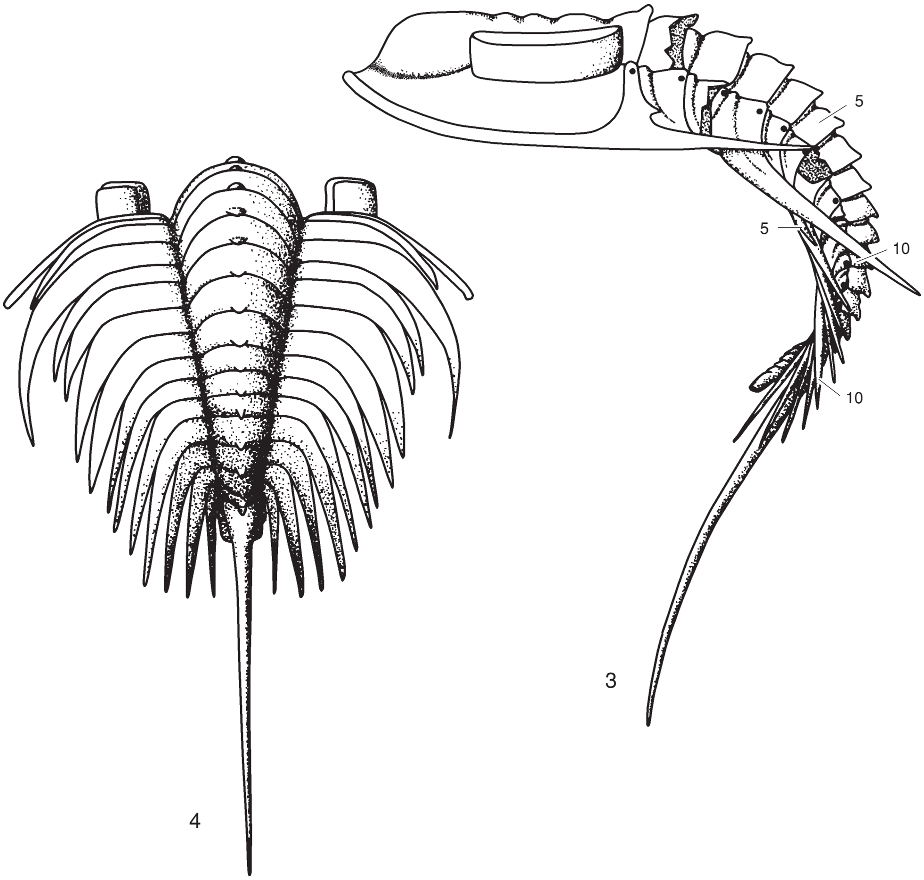


FIG. 45 (continued). *For explanation, see facing page.*

TERTON & CAMPBELL, 1993) is similar—the inner portion extremely narrow (tr.), the fulcral process and socket prominent, the doublure extending in to the fulcrum—and enrollment of the falcate outer portions is limited by a transverse fold in the doublure and the way the anterior edge of the following pleura fits into it.

In Cyclopygidae the bent-down, facetted, outer portions of the pleurae become successively wider (tr.) posteriorly, giving a thorax that is widest (tr.) across the last segment. This form of the thorax is related to the manner in which the tips of the pleurae fit into the vincular notches beneath the cephalon when enrolled (MAREK, 1961, pl. 4, fig. 3–4; HAN, 1978).

The thoracic segments of cheirurids (e.g., *Ceraurus,* Fig. 39) are known in detail from silicified specimens (WHITTINGTON & EVITT, 1954; CHATTERTON & LUDVIGSEN, 1976; HOLLOWAY, 1980; CHATTERTON & PERRY, 1984). The inner portion of the pleura is horizontal with an anterior flange and posterior recess; the outer portion is a spine, the doublure curved in beneath the fulcral process and socket to form a ventral flange in *Deiphon* (HOLLOWAY, 1980, fig. 7). The pleural spines (usually a single spine, in some species two) may be shaped and directed so that they pass one behind the other in enrollment; in *Sphaerexochus* the blunt, thick spines may have projections and corresponding recesses to give a close fit when enrolled.

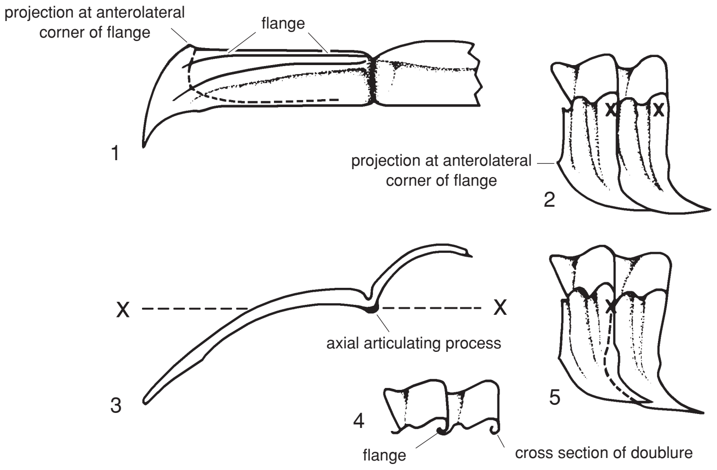


FIG. 46. *Paradoxides (Hydrocephalus) carens* BARRANDE, Middle Cambrian, Bohemia, showing articulation devices in the thorax of a nonfulcrate trilobite; *x* is the axis of rotation. *1,* Dorsal view of left half of segment (*dashed line* shows position of inner edge of doublure); *2,* left lateral view of two segments in the extended position; *3,* posterior view of left half of segment; *4,* left lateral view of two axial rings in the extended position, with inner portion of pleura shown in cross section; *5,* left lateral view of two segments in flexed position (*dashed line* shows anterior edge of pleura) (Whittington, 1990, fig. 21).

The preannulus (Fig. 40.2) has been observed in the axial ring of some species.

Thoracic segments of odontopleurids (WHITTINGTON & EVITT, 1954; BRUTON, 1966; CHATTERTON & LUDVIGSEN, 1976; CHATTERTON & PERRY, 1983) resemble in some respects those of cheirurids, particularly in the flat inner portion of the pleura, the spines (two) forming the outer portion, and the narrow doublure beneath their bases with the fulcral process and socket. A flange on the anterior edge of the inner portion of the pleura articulates with a groove on the posterior edge of the segment in front; the fulcral process and socket act as guides and limit enrollment. In such odontopleurids as *Ceratocephala* the pleural furrow is shallow and indistinct. In others, however, the pleural furrow separates an anterior and posterior ridge, the latter passing in to the base of the principal pleural spine; the ridge may be inflated into a **fulcral swelling** at the base of the spine. So far only known in *Ceratocephala* (WHITTINGTON, 1956d, p. 240; THOMAS, 1981, p. 96; CHATTERTON & PERRY, 1983, p. 48) is a peculiar posterior thoracic segment, in which anterior and posterior pleural spines are alike, and a curved suture traverses (exs.) the inner portion of the pleura. In silicified specimens this outer portion of the pleura occurs in isolation, the axial portion remains undetected. Unusual also is the **fenestra** in the exoskelton of *Laethoprusia* (RAMSKÖLD, 1991a); these openings occur in the segmental boundaries of the pleural region, from the posterior cephalic margin to within the pygidium. The exoskeleton is curved downwards (ventrally) around the margin of the ovate fenestra, and each edge projects beside an intervening trough, a form like that of the edge of the articulating flange. Less well preserved but seemingly similar structures are the unmineralized slitlike areas between the inner portions of the pleurae in the thorax of species of asteropyginids (MORZADEC, 1983; SMEENK, 1983).

The encrinurid pleura (WHITTINGTON & CAMPBELL, 1967; EVITT & TRIPP, 1977; RAMSKÖLD, 1986) has a horizontal inner portion and steeply down-curved outer portion and is characterized by the prominent posterior pleural ridge that continues into the spinose tip. WHITTINGTON and CAMPBELL

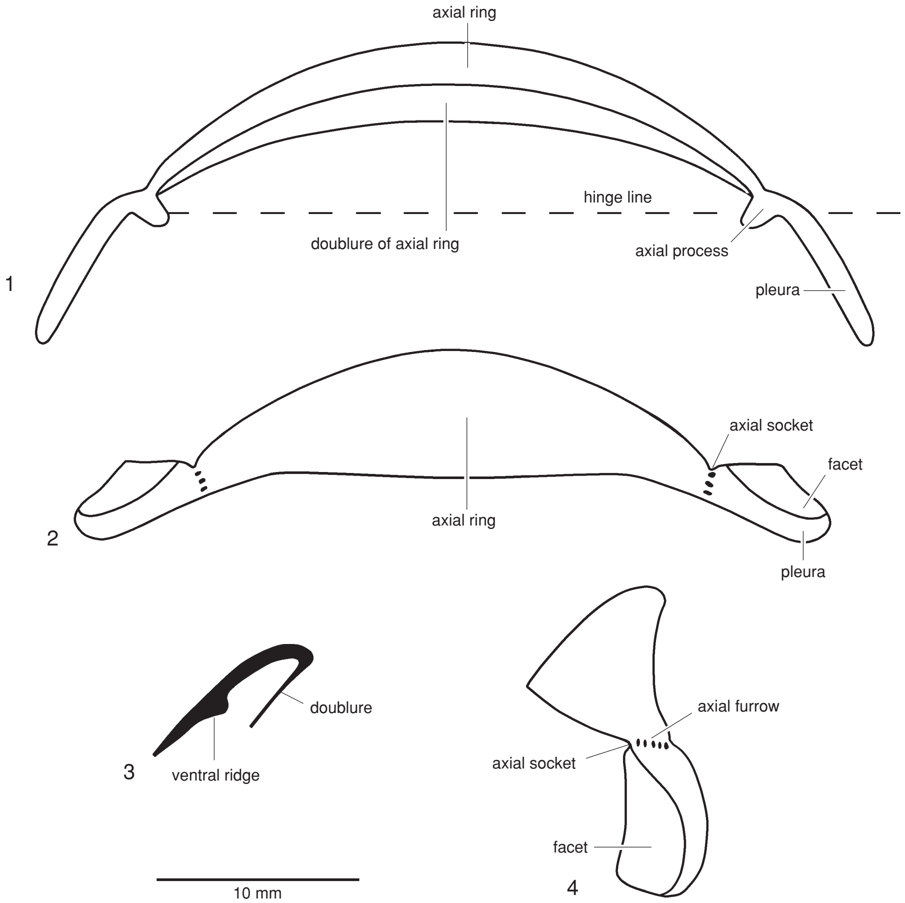


FIG. 47. Thoracic segment of *Cybantyx anaglyptos* LANE & THOMAS in THOMAS. *1,2,4,* Posterior, dorsal, and left lateral views; *3,* sagittal section of axial ring, showing thick dorsal exoskeleton and ventral ridge (new).

(1967, p. 470–471) and CAMPBELL (1967, p. 22) drew attention to the exceptional thickness of the exoskeleton along the posterior pleural ridge and the median, internal row of canals that apparently did not traverse the outermost layers of the exoskeleton. The much lower anterior pleural ridge dies out distally. The posterior pleural ridge with its fulcral swelling is so shaped on the outer portion that it acts to limit enrollment. An anterior flange and axial processes and sockets aid in articulation; the doublure extends only to the base of the spine at the tip of the outer portion of the pleura.

Articulation in the thorax of *Phacops* was described in detail by MILLER (1976), and CAMPBELL (1977) illustrated the doublure of other phacopids with its raised stop and the form of the pleural tips that fitted into vincular sockets in the cephalon (see also LESPÉRANCE, 1991; BRUTON & HAAS, 1997). CAMPBELL (1977) and SPEYER (1988) have noted that the pleural furrow is postfacetal in dalmanitids, not epifacetal as in phacopids, and that details of the articulation and the fit of the pygidium and cephalon are different in the two groups.

In the Silurian *Cybantyx* (Fig. 47), the axis is broad (tr.), the pleura narrow and curving down in a continuation of the slope of the distal portion of the axial ring; the fulcrum is absent. The axial ring, longest sagittally, curves downward and forward and is not interrupted by the downfold of an articulating furrow; the doublure has a similar downward curvature. Exfoliated specimens show that on the inner surface of the anterior portion of the ring there is a transverse ridge, steep on the posterior side, extending between the shallow axial furrows. An axial articulating process projects ventrally at the posterior edge of the ring and fits into a socket at the anterior edge of the following ring. The outer surface of the pleura is largely occupied by the facet, which has a gently concave surface. The doublure has a U-shaped inner margin, the edges of which extend in to the axial furrow. In many Ordovician species of illaenids (WHITTINGTON, 1997), the axial region of the thorax is relatively narrow (sag.), the axial ring and articulating process similar to that of *Cybantyx* and having the transverse ventral ridge. The pleura is relatively broader (sag.), fulcrate, the inner portion lacks a pleural furrow, the outer portion similar in form to that of *Cybantyx.* In contrast to the Illaenidae, the thorax of Styginidae and Scutelluidae (ŠNAJDR, 1960; CHATTERTON & CAMPBELL, 1980; ARCHINAL, 1994) has the axial ring (in many species shortest sagittally) descending to an articulating half ring that extends forward almost horizontally and underlies the almost horizontal doublure of the ring in front. The fulcrate pleura has an articulating flange on the inner portion, a fulcral articulating process and socket, and the outer portion is a spine that has the doublure extending in to the fulcrum.

The fulcrate form of articulation is seen in Agnostina and eodiscoids (WHITTINGTON, 1963, 1965; HUNT, 1967; MÜLLER & WALOSSEK, 1987; JELL, 1975a), the inner portion of the pleura horizontal, the outer portion narrow (tr.), bent down, and shaped so that the close fit enables complete enrollment (Fig. 48.3). This close fit is edge to edge; the outer portion lacks a facet, and there is no overlap between adjacent sclerites. A unique feature of Agnostina is the absence of the articulating half ring on the first thoracic segment throughout ontogeny (ROBISON, 1964, p. 515). It is present on the second segment and the pygidium. Hence, when the exoskeleton is enrolled, an elliptical opening appears in a median portion of the axial region, the **cephalothoracic aperture,** between the narrow (tr.), convex occipital band of the cephalon and a slight recess in the anterior margin of the first thoracic segment (Fig. 48; ROBISON, 1964, fig. 3). This aperture appears to be common to Agnostina, the only exception being the presence of an articulating half ring on the first segment of a species of *Leiagnostus* (PEK & SMOLA, 1989). In eodiscoids the articulating half ring is present on all segments and the pygidium.

In discussing the articulation of the pygidium of Agnostina, ÖPIK (1963, p. 31; 1967, p. 53) commented on the form of the articulating half ring and articulating furrow in different subfamilies. In the common or basic type the half ring has the shape of a segment of a circle, and the furrow is narrow (sag. and exs.). In glyptagnostoids the half ring is a narrow ridge curved forward, the furrow a wide (sag.), elliptical depression. In the clavagnostid *Aspidagnostus* the articulating half ring arched backwards, a form he termed *agnostoid* and regarded as distinct from that in glyptagnostoids. These distinctions have been used as diagnostic by SHERGOLD, LAURIE, and SUN (1990). In his later discussion of articulation in Agnostina, ÖPIK (1979, p. 25–28, 32–34) concentrated on the structures at the fulcrum, which he termed *prongs.* External prongs are short projections or spines directed backward from the posterior cephalic border and the abaxial posterior margin of each segment and are visible in dorsal view. Similar prongs may also project forward from the facet of the pygidium and the abaxial anterior margin of each segment but are concealed beneath the external prongs in dorsal view. ÖPIK considered that these fulcral prongs were the points about which the sclerites of the exoskeleton hinged. Earlier, ÖPIK (1967, p. 55) referred to the concavity of the facet of the pygidium

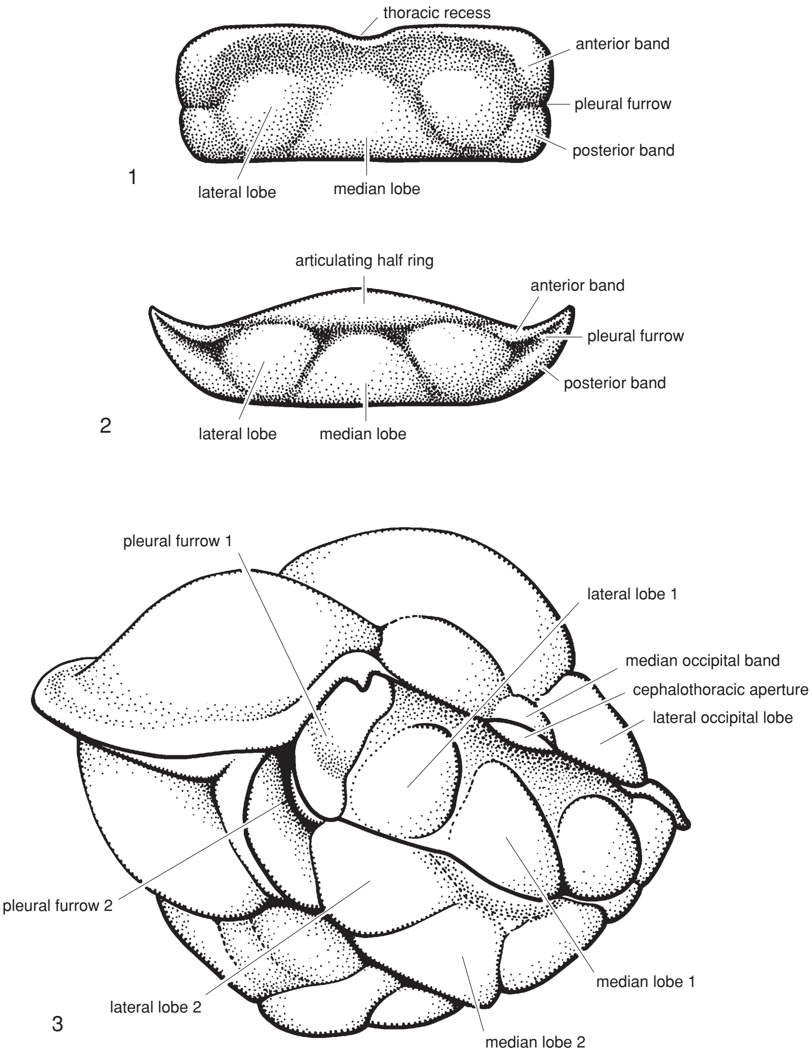


Fig. 48. *Geragnostus clusus* Whittington, Ordovician, Newfoundland. *1,2,* Dorsal views of first and second thoracic segments, showing thoracic recess, the posterior margin of the cephalothoracic aperture, and articulating half ring of second segment; axial ring of segment divided into median and lateral lobes; pleura divided by pleural furrow into anterior and posterior bands; *3,* posterolateral view of enrolled exoskeleton, to show segments, coaptation, and cephalothoracic aperture; occipital ring divided into lateral lobes and median occipital band, ×36 (Whittington, 1963, fig. 3).

in certain Agnostina in which a fulcral prong was present. Possibly this concavity fitted against the ventral side of the external prong of the second thoracic segment.

The thoracic segment of the Silurian illaenid *Cybantyx* (Fig. 47) lacks the inner, horizontal portion of the pleura and the fulcrum; the pleura continues the slope of the axial ring. This nonfulcrate form of segment differs from that of the Cambrian species described above in that the axial region is wide (tr.) and the pleural region narrow. These segments articulate with each other, and with the cephalon and pygidium, about the deep axial process. A like form of segment occurs also in the unrelated Silurian and Devonian homalonotids, in which the pleura continues the lateral slope of the broad axial ring and has no horizontal inner portion. These Silurian and Devonian homalonotids also have, as in older species, the straight, outward and backwardly directed lateral margin of the axial ring (and occipital ring), which gives a zigzag course to the axial furrow (HENRY, 1980b, p. 357; 1996), and the deep, narrow articulating furrow that is continuous across the axial furrow with the pleural furrow and dies out on the broad facet (WOLFART, 1968, pl. 1–2; THOMAS, 1977, pl. 24, fig. 12; MORZADEC, 1983, pl. 4, fig. 1; WENNDORF, 1990, pl. 15, fig. 3). The articulating half ring formed a continuous structure with the anterior band of the pleura and is relatively long (sag. and exs.). THOMAS and LANE (1984) suggested that this gave an unusual amount of dorsoventral flexibility to the thorax. The great depth of the pleural furrow and the ridge it formed on the visceral surface were shown in a Devonian example by HAAS (1981, fig. 4), and both BRASSEL and BERGSTRÖM (1978) and THOMAS and LANE (1984) regarded this ridge as a device to limit enrollment. The ridge is present in the Silurian homalonotid *Trimerus* (WHITTINGTON, 1993b) but cannot have acted to limit enrollment.

In trilobites the segments were articulated with one another and with the cephalon and pygidium so that flexure of the exoskeleton and (with rare exceptions) enrollment were possible. The straight hinge line afforded by the horizontal inner portion of the pleura (Fig. 40), the abaxial fulcrum, and the facet on the outer portion of the pleura were the most widespread articulatory devices but were not universal (Fig. 41). Back-arching of the thorax, so that it was concavely flexed dorsally, was possible to a limited extent by many trilobites, depending on the form of the axial ring. Such back-arching was facilitated if the ring had the anterior face forwardly concave in profile (as seen in dorsal view) and in longitudinal section sloped forward on the anterior side and backward on the posterior side (cf. HAMMANN, 1985). This allowed the axial rings, which were situated above the axis of articulation, to be rotated close to each other. At the same time the outer parts of the pleurae, lying below the axis, were fanned out to cover the sides of the body. CHATTERTON and PERRY (1983, p. 17) suggested that the function of the preannulus (Fig. 40) was to allow concave-dorsal flexure in odontopleurids, cheirurids, and proetids, by allowing the axial ring of the segment in front to rotate back over it. The unusual structure of the axial ring in illaenids (Fig. 47) means that dorsoventral movement between them—and between thorax, cephalon, and pygidium—is not limited, so that the maximum amount of back-arching is possible (WHITTINGTON, in press). Rarely, the flexure of the thorax appears to have been limited (e.g., in the remopleuridid *Hypodicranotus* WHITTINGTON, 1952b) by the exceptionally long fork of the hypostome. I argued (WHITTINGTON, 1981, p. 598–599) that in the Upper Cambrian *Schmalenseeia* the exoskeleton may not have hinged between the thoracic segments but may have been a rigid shield. Further studies (WHITTINGTON, 1994) have led me to rescind this argument and to consider that the burlingiid exoskeleton was articulated and had some flexibility.

The external surface of the axial ring and inner portion of the pleura of the thorax is similar in form and sculpture to the occipital ring and furrow and the posterior border and furrow of the cephalon. This is well shown, for example, by Agnostina (HUNT, 1967; ÖPIK, 1979), asaphids and nileids (HENNINGSMOEN, 1960; WHITTINGTON, 1965; SCHRANK, 1972b), and calymenids (CAMPBELL, 1967) and by the arrangement of spines in odontopleurids (CHATTERTON & PERRY, 1983). These similarities apply to the lateral lobes, smooth areas, apodemes, and course of terrace ridges. On the outer portions of the pleura and on the doublure, particular arrangements of terrace ridges are recorded, as for example in asaphids and

Symphysurus (Siegfried, 1936; Hupé, 1955b; Fortey, 1986). Granulation on the articulating facet of a calymenid was described by Chatterton and Campbell (1993, fig. 3f–h); the facet of a homalonotid (Whittington, 1993b, fig. 4g) is also granulose. Öpik (1961a) described the faint, transversely directed ridge on each band of the thoracic pleura in *Redlichia, Papyriaspsis,* and *Centropleura* and the branches from it. Such ridges have been observed in *Paradoxides* (Bergström & Levi-Setti, 1978, p. 9) but not in the thorax of other trilobites.

PYGIDIUM

This posterior region of the body consists of a number of fused somites, and the **pygidium** is the exoskeleton of this region (Fig. 2). Almost all pygidia have a convex axial region that is separated from the lateral pleural region by the axial furrow; the axial furrows merge at the terminus of the axis, and the pleural region extends behind the axis. The somites of the pygidium and thorax were similar, judging by the similarity in morphology between thoracic segments and the fused segments forming the pygidium. Like the thoracic segments, the anterior pygidial segment may have a horizontal inner portion of the pleural region, a sloping outer portion outside the fulcral line (Fig. 2), and a facet. Distally the exoskeleton extends beneath the outer portion of the pleural region as a doublure. This doublure is (in most cases) continuous behind the axis; it varies in width (tr. and sag.) and convexity and may form a tubular or flattened structure with the lateral and posterior border. The latter may be convex and defined on the inner side by a border furrow or lacking in independent convexity, not defined by a border furrow nor crossed by pleural or interpleural furrows. When the exoskeleton is sharply flexed at the margin, the border may be flattened or concave. Fenestrae, oval or slitlike areas in the interpleural furrows that are not mineralized are known in asteropyginids (Morzadec, 1983; Smeenk, 1983), and well-preserved ones have been described in an odontopleurid (Ramsköld, 1991a).

In Agnostina the axis may be subdivided by the anterior two axial rings, whereas the remainder of the axis is not divided by inter-ring furrows (Fig. 6.2). This has led to the distinction of the two rings as the **anteroaxis** and the remainder as the **posteroaxis**. A notation of M for the axial ring and F for the inter-ring furrow, numbered from the anterior ring posteriorly, is used by some authors. Agnostina having the axial lobe unmodified (Fig. 6.2) are termed **axiolobate** (Öpik, 1967, p. 53). In Pseudagnostinae, for example, the posteroaxis is expanded, defined laterally by the **accessory furrow** (Fig. 11.2) and posteriorly by the border furrow. It thus includes both axial and pleural areas, and this composite lobe is the **deuterolobe** (Öpik, 1963, p. 31). In Eodiscina the axis may be divided by many inter-ring furrows, and the terminology used in Agnostina is not applicable.

The pygidium in Olenellina (Whittington, 1989; Fritz, 1995) is formed of two to five or six fused segments with a convex axis. The pleural region in *Olenellus* is narrow (tr.) (Fig. 45), in association with the backwardly directed pleurae of the 14th thoracic segment. In *Wanneria* (Fig. 49) the posterior thoracic pleurae are more outwardly directed, so that the pleural region was relatively wider (tr.). The posterolateral margin of the pleural region was bilobed or prolonged as one or more pairs of spines, as in *Judomia* (Fig. 50). The doublure in both of these genera extended in toward the tip of the axis. The view that the pygidium in Olenellina was not like that of other trilobites but was "a true telson or caudal piece" (Harrington in Moore, 1959, p. 73) is considered to be without foundation. The small pygidium of *Redlichia* (Öpik, 1958; W. Zhang, Lu, & others, 1980, fig. 56) has three axial rings, and the pleura of the first segment extends into a short spine. Öpik described two types of pygidia as belonging to one species, which was therefore

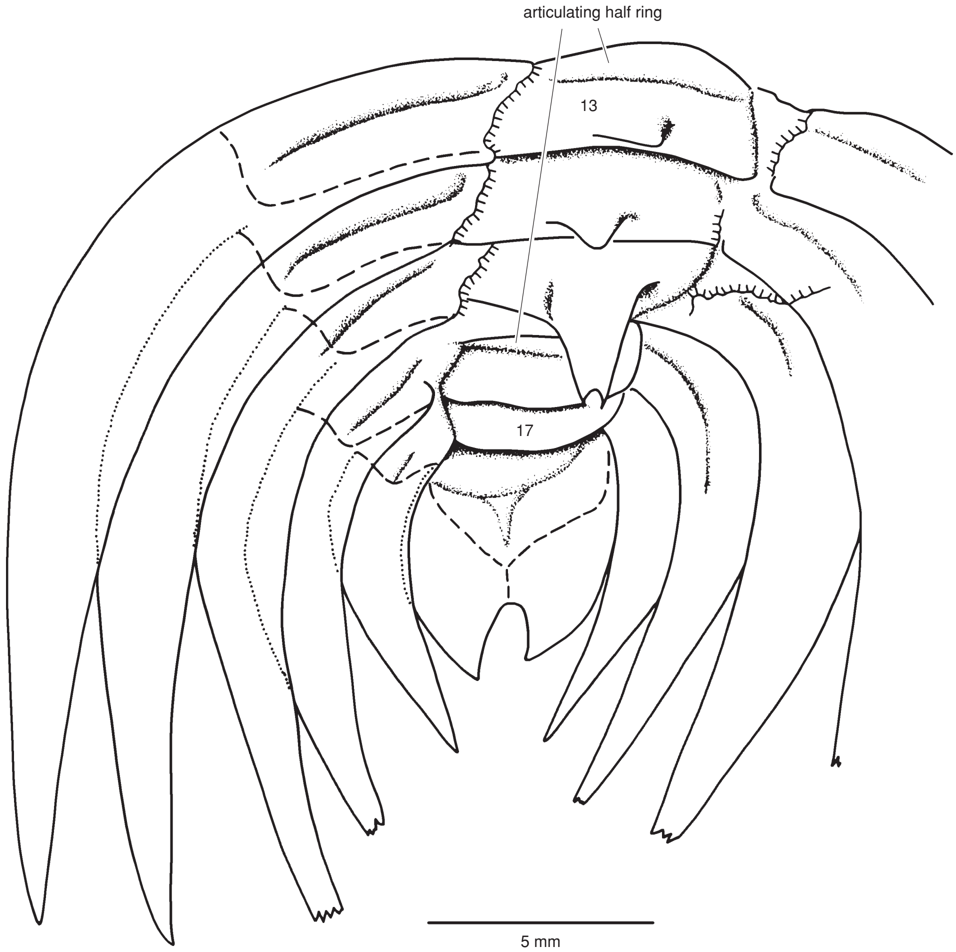


FIG. 49. Thoracic segments 13 through 17 and pygidium of *Wanneria walcottanus* (WANNER), Lower Cambrian, Pennsylvania. *Dashed line* indicates margin of doublure; *dotted line* indicates anterior margin of articulating flange; *hachures* indicate fractures in exoskeleton (Whittington, 1989, fig. 28).

dimorphic. In one type the doublure is absent along the posterior margin. The occurrence of these two types of pygidia is said by W. ZHANG and JELL (1987, p. 48) to characterize species of *Redlichia,* whereas in species of dolerolenids (JELL in BENGTSON & others, 1990, p. 287, 292) the doublure is lacking posteriorly in all examples. SDZUY (1959, p. 402–404) described a pygidium of *Saukianda* as also lacking the doublure medially but did not see this as having great taxonomic significance. *Paradoxides* (BERGSTRÖM & LEVI-SETTI, 1978; DEAN in MARTIN & DEAN, 1988) also has a small pygidium, which shows the axis and one or two rings and may be partially or completely fused to the last thoracic segment, as is the case with some species of *Redlichia*. The last thoracic segment has been termed the **semi-ankylosed segment** (W. ZHANG, LU, & others, 1980, fig. 55) because in some individual specimens it may be fused to the pygidium, in others not.

Among stratigraphically younger trilobites, many rings may occur in the pygidial axis. The Ordovician *Dionide* (WHITTINGTON, 1952a) has 20. Up to 45 have been noted in a Silurian encrinurid (TEMPLE &

Tripp, 1979, p. 233) and 27 or 28 in Permian proetids (Owens, 1983, p. 28–29). In the Ordovician *Hypodicranotus* (Ludvigsen & Chatterton, 1991), however, the axis is not defined, the pleural region is unfurrowed, there is a small pair of posterior marginal spines, and the doublure extends far forward so that the axis must have been extremely short (sag.). It is thought that this pygidium was derived from that of ancestral remopleuridids, in which the axis was defined and bore inter-ring furrows and in which pleural furrows were present. Presumably in the pygidium each axial ring (or pair of apodemes or muscle scars) indicates one somite. In *Olenoides* (Whittington, 1975, p. 128) a maximum of six pairs of appendages are known in the pygidial region, the axis having five rings and the terminal axial piece. In *Triarthrus* (Whittington & Almond, 1987) there are up to 12 pairs of limbs in the pygidial region, but the axis has only four rings and the terminal piece. Thus, the number of axial rings in the pygidium may be taken only as an indication of the minimum number of somites in the pygidial region.

In Olenellina, some Redlichiina, and paradoxidoids the pygidium is much smaller than the cephalon, and the exoskeleton may be described as **micropygous**. In most other Cambrian trilobites and in stratigraphically younger groups, the pygidum is relatively larger but not as wide (tr.) or long as the cephalon. The Agnostida are characterized by a pygidium similar in size to the cephalon, a condition described as **isopygous**. In many species of asaphids (Fig. 2) and scutelluids the exoskeleton approaches the isopygous condition. The term **macropygous** describes trilobites in which the pygidium is larger than the cephalon. Exactly what is meant by smaller or larger than the cephalon has not been defined, nor did Kobayashi (1942a, p. 145) define size in introducing the terms heteropygous and parapygous as stages intermediate between micropygous and isopygous. It is suggested here (see glossary, p. 314) that micropygous be taken to refer to a pygidium considerably shorter (sag. and exs.) and narrower (tr.) than the cephalon, while isopygous implies similarity in both maximum width (tr.) and length (sag. and exs.) of cephalon and pygidium. These terms are thus generalized, and to attempt to define intermediates between them appears unprofitable. Macropygous is taken to imply a pygidium greater in maximum width (tr.) than the cephalon. This means that in *Macropyge* (Lu & Qian, 1983), while the pygidium is longer (sag.) than the cephalon, it is considerably narrower (tr.), so that this form is not considered to be an example of a macropygous trilobite.

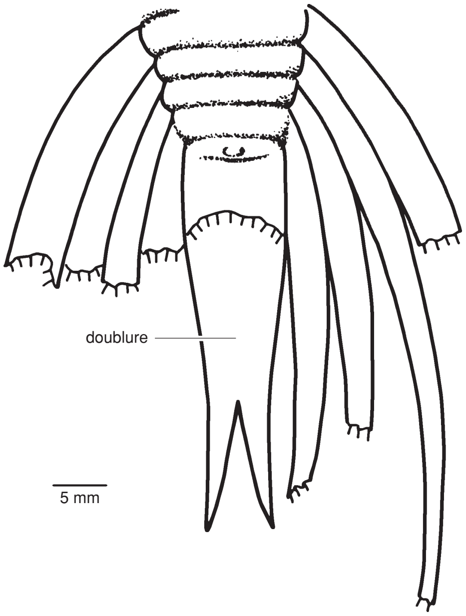


Fig. 50. Posterior four thoracic segments and pygidium of *Judomia tera* Lazarenko, Lower Cambrian, Siberia; *hachures* indicate edge of exoskeleton (Whittington, 1989, fig. 54b).

The axis of the pygidium, defined by its convexity independent of the pleural regions and by the axial furrow, may be short (sag.) or long relative to the length of the pygidium, the relative width being likewise variable, and may extend back as far as the border furrow or so that the tip lies above the inner edge of the doublure. In *Bumastus* (Fig. 1) and some homalonotids, in which the convexity of the axis is continuous with that of the pleural region and the axial furrow is effaced, the position of the axis is indicated only by the articulating furrow and articulating half ring. Characteristically the axis is divided by **inter-ring furrows** into a series of rings, the anterior ring usually defined and closely resembling those of the thorax. Thus, the special features of the thoracic axial rings—preannulus, apodemal pit, apodeme, lateral lobe, length (sag. and exs.) and form of the articulating half ring, etc.—are duplicated in the first ring of the pygidium. Succeeding rings become less convex and shorter (sag. and exs.) posteriorly, and the inter-ring furrows (and apodemal pits) become successively shallower and the apodeme lower. An undivided posterior portion of the axis is referred to as the **terminal axial piece** (see Fig. 53). In the axis of Agnostina, muscle scars may be preserved (as in the cephalic axis) as smooth areas on the external surface or as impressions, ridges, or grooves in the internal mold (SHERGOLD, 1975, pl. 4, 10) (Fig. 10.3, 11.2). In raphiophorids similar paired areas may be raised on the parietal surface of the axis or be discernible as dark patches (Fig. 51).

The pleural region (Fig. 52) may be divided by the **border furrow** into an inner **pleural field** and **border**. The border may be convex, flattened, concave upward, or sloping vertically; and the definition and depth of the border furrow differs. The border may merely be the outer, unfurrowed portion of the pleural region, lacking independent convexity or the definition of a border furrow. Dependent on the relative length (sag.) of the axis to that of the pygidium is the length (sag. and exs.) of the pleural region posteriorly. Anteriorly the pleural region conforms to the form of the thoracic segments; if the inner portion of the thoracic pleura is horizontal, so is the pleural region, and the anterior margin is straight and transverse. Outside the fulcrum the margin is directed outward and backward, and the anterolateral corner is facetted.

Behind the anterior portion the pleural region in most trilobites is reduced in width (tr.) and convexity, the outline narrowing backward. Characteristic of the pleural region (Fig. 53) is the subdivision by furrows that are successively more strongly backwardly directed. The most anterior and most prominent of these **pleural furrows** is that which extends outward and backward from the articulating furrow; successive pleural furrows originate at the axial furrow opposite the inter-ring furrow. The anterior portion of the pleural region of the pygidium is thus equivalent to the anterior band of a thoracic segment. It not only carries the facet, but there may also be a narrow (exs.) flange along the margin, similar to that on the segment.

The second series of furrows in the pleural region are **interpleural furrows**, successively arising opposite inter-ring furrows of the axis, each directed outward and less strongly backward than the pleural furrow immediately in front of it. The relation between the articulating or inter-ring furrow and the pleural and interpleural furrow of the same segment is usually clear on the first segment of the pygidium, but it may be obscured or lost posteriorly, especially when the number of axial rings greatly exceeds that of pleura. For example, in *Olenoides* (see Fig. 83) the relationship of ring and pleura is unequivocal. At the other extreme, however, is the encrinurid *Cybeloides* (Fig. 54), having some 30 axial rings but only 4 pleurae (the count of 30 axial rings being based on the assumption that the incomplete furrows on the axis behind the first axial ring are inter-ring furrows). Pleural and interpleural furrows may become less deep posteriorly and may die out on the pleural field before reaching the border furrow, or they may extend on to the border. As in the thoracic pleurae, the two pleural bands may be convex and ridgelike, the posterior band being more prominent. OWENS (1973, p. 5) observed that in proetids the anterior and posterior pleural bands differ in convexity (as seen in exsagittal profile), depending on the relative depths of pleural and interpleural furrows; three distinctive profiles were recognized. In other trilobites one convex band may occupy

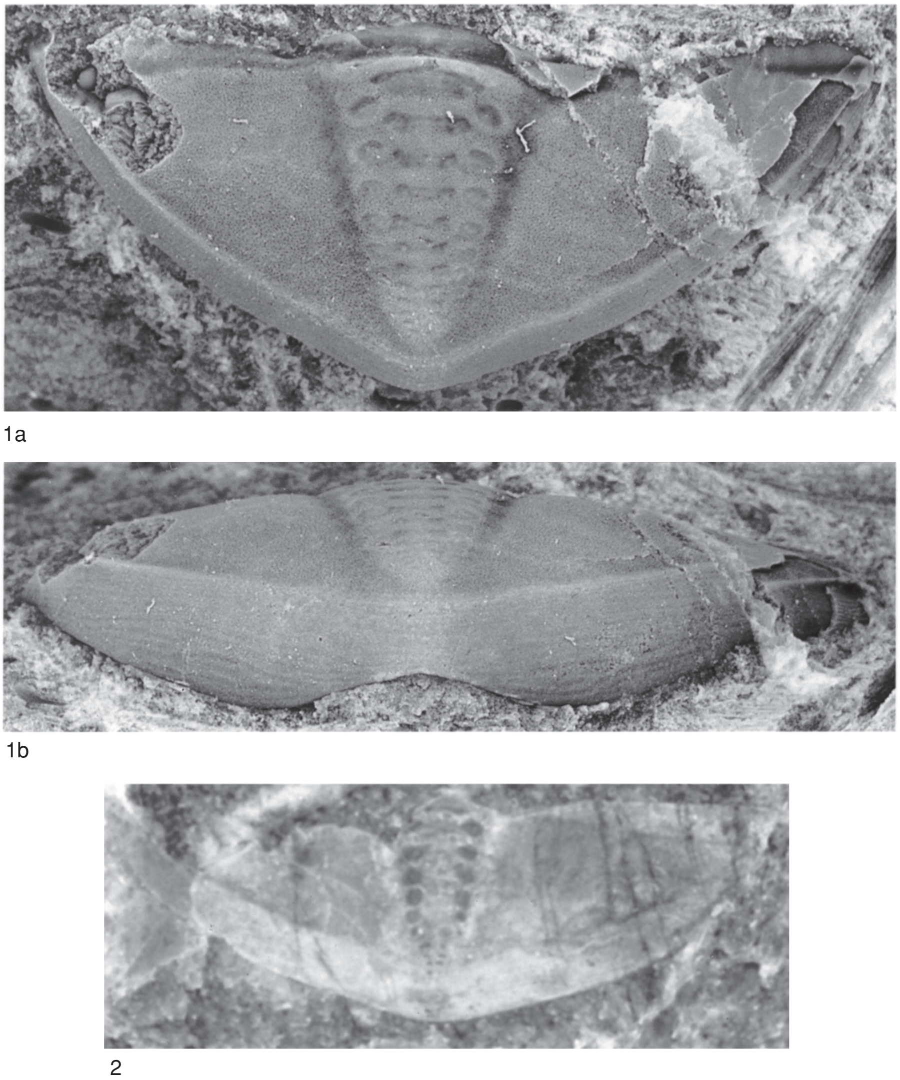


FIG. 51. *1a,b, Lonchodomas clavulus* WHITTINGTON, Ordovician, Newfoundland. Internal mold of pygidium showing impressions of raised areas on parietal surface of axis of exoskeleton and posterior embayment in outer portion of pleural region; *a,* dorsal and *b,* posterior views, ×4.5 (Whittington, 1965, pl. 11, fig. 4, 6). *2, Ampyxoides semicostatus* (BILLINGS), Ordovician, Newfoundland. Incomplete pygidium, photographed under alcohol, showing dark patches on axis, ×9 (Whittington, 1965, pl. 12, fig. 18).

the whole length (exs.) between pleural furrows as a **pleural rib** (Fig. 52), the interpleural furrow being absent. Such ribs are characteristic of scutelluids, in which the axis is short (sag.) and the ribs more and more strongly backwardly directed, the last pair of which may merge wholly or partly to form a median posterior rib on the terminal area (Fig. 55). RAMSKÖLD (1985, p. 36) has noted convex oval areas on the posterior pleural band or bands of species of *Dalmanites*; the inner surface bears numerous minute perforations. The pleural region may also lack pleural furrows except for a shallow

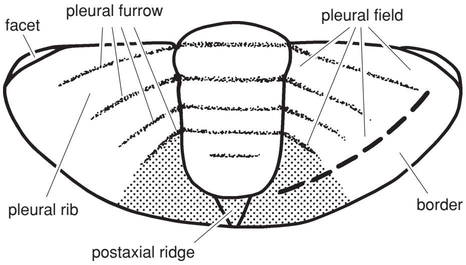


FIG. 52. Diagram to explain terminology of the pleural region of the pygidium. *Shaded portion* is the terminal area, which lies behind the posterior pair of pleural furrows; *dashed line* on right side indicates position of inner margin of doublure (new).

anterior furrow adjacent to the fulcrum; an extreme example is *Bumastus* (Fig. 1), in which pleural region and axis merge into a continuous convexity and there is no border. Most unusual is the inflated pleural field in the Upper Cambrian *Pemphigaspis* (PALMER, 1951), which bulges up above the axis and outward and backward over the narrow, vertical, lateral and posterior border. In the pygidium of Agnostina the pleural region has a well-defined border, the area within the border furrow being referred to as the **acrolobe**, an area that includes the axial region in effaced species (Fig. 13). In species in which the anteroaxis is defined, an **accessory furrow** may be directed outward and backward from the second inter-ring furrow (Fig. 11). This accessory furrow may extend to the border furrow and the pair thus enclose the **deuterolobe**, an area that may include part of the pleural field as well as the posteroaxis. The axis of the eodiscoid pygidium may have many similar rings and extend back close to the border furrow; the pleural field may have many pleural furrows or lack such furrows. Eodiscoid species with a faint or effaced axis are known. Various trilobites have a **postaxial ridge** behind the axis in the midline of the pygidium (Fig. 52, 54), and in Agnostina a **postaxial furrow** may be present (Fig. 6).

Tubercles and spines may be developed on the pygidium as they are on the thorax. On the axial rings a single median or pair of prominent tubercles, spines, or nodes like those of the thorax, may be present on the

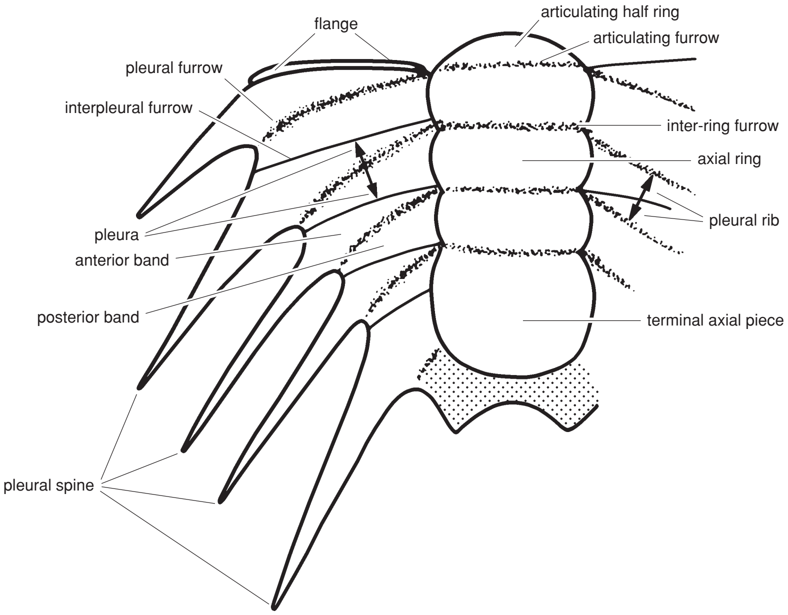


FIG. 53. *Dorypyge* sp., generalized diagram to explain terminology; terminal area shaded (adapted from Kushan, 1973).

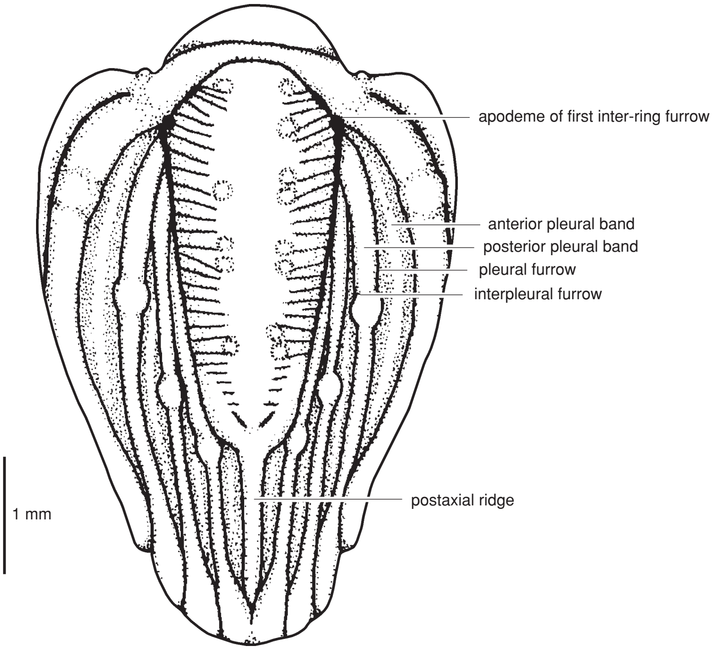


FIG. 54. Dorsal view of pygidium of *Cybeloides virginiensis virginiensis* COOPER, Ordovician, Virginia (Evitt & Tripp, 1977, fig. 15).

first few rings, diminishing posteriorly and disappearing. A single prominent spine may be present on the axis, as in some eodiscoids (RASETTI, 1966a, pl. 2), or as a **terminal axial spine** (Fig. 56). In *Encrinurus* (Fig. 57) a median tubercle occurs on particular axial rings, a smooth sagittal band surrounding and extending between these tubercles; no such structures are present on the thorax. Some species of *Encrinurus* bear a posterior spine or **mucro** that projects from the border behind the axis; similar spines are developed in asaphids and dalmanitids. The lateral margin of the pygidium may be entire or bear spines. These spines are formed in the same way as those of the thoracic pleurae, that is, as projections from both bands of the pleura, as in the dalmanitid *Greenops* (Fig. 58) or lichids; from the posterior band of the pleura as in the major spine of odontopleurids (Fig. 42–43) and many other trilobites; from the pleural rib as in scutelluids (Fig. 55); and less commonly from the anterior band of the pleura (Fig. 53). These spines are therefore termed **pleural spines;** they have also been referred to as border spines when a border is developed on the pygidium or as marginal spines when a border is not present. In the latter instance, if the margin is sharply flexed, they may be flattened in cross section and blade shaped in

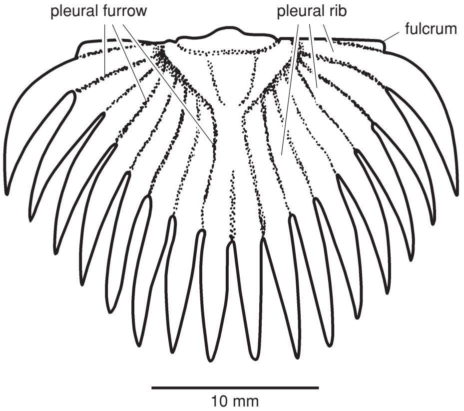


FIG. 55. Dorsal view of pygidium of *Weberopeltis* aff. *arcticum* (WEBER), Devonian, Arctic Canada (adapted from Ormiston, 1967, pl. 4, fig. 1).

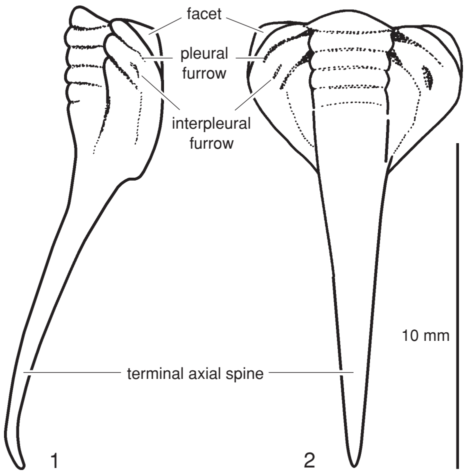


FIG. 56. *Acidiphorus spinifer* RAYMOND, Ordovician, Canada. *1,2,* Right lateral and dorsal views of pygidium (adapted from Whittington, 1965, pl. 44, fig. 4, 6, 12, 14).

outline rather than elongated-conical in form. Pleural spines of the pygidium may be graded in size, or one or more spines may be larger than those adjacent. In odontopleurids the base of the large spine may be continued by a pleural ridge across the pleural field to the axis. In the cheirurid *Holia* (WHITTINGTON & EVITT, 1954) a similar ridge forms the majority of the pleural region. In the styginid *Ancyropyge* (ORMISTON, 1967) the pleural region is largely formed of long, curved pleural spines. Some pygidia bear a single pair of large pleural spines, as in *Proceratopyge* (Fig. 59) or the redlichioid *Yinites* (W. ZHANG, LU, & others, 1980). Such spines appear to belong either to one particular segment of the pygidium (not in all examples the anterior) or, when the base is broad, to more than one segment. A postaxial ridge, extending back sagittally from the tip of the axis towards the margin, may be developed with or independently of any posterior spine (Fig. 52, 54). In addition to axial and pleural spines, large spines may arise from the pleural field, as in the odontopleurid *Apianurus* (WHITTINGTON, 1956b); these spines are upwardly directed and curve backward, rather than being outwardly directed as were pleural spines. A pattern of anastomosing ridges, similar to the genal caeca, has been described on the pleural field of Cambrian trilobites (ÖPIK, 1961a) and in one example of a styginid (Fig. 60). In this example the ridges commence at the axial furrow, and the pattern is related to segmentation, there being a major branch commencing opposite each inter-ring furrow.

The doublure of the pygidium in most trilobites is narrow (tr.), convex ventrally, and curled beneath the border. Cross sections (e.g., OSMÓLSKA, 1975, pl. 2) show that the exoskeleton thins toward the inner margin. The doublure does not extend beneath the axis but may extend beneath the pleural field, as in some asaphids (Fig. 61) and scutellluids (ŠNAJDR, 1960). In illaenids the doublure may extend in toward the tip of the axis to surround it in a scalloped (Fig. 9.4, 62) or pointed projection, or the inner margin may follow the curve of the pygidial margin (JAANUSSON, 1954). In the asaphids *Ogygiocaris* (HENNINGSMOEN, 1960) and *Gog* (FORTEY, 1975b), the inner edge of the doublure has a distinctive, scalloped outline related to the pleural furrows. Silicified material has shown the structure of the

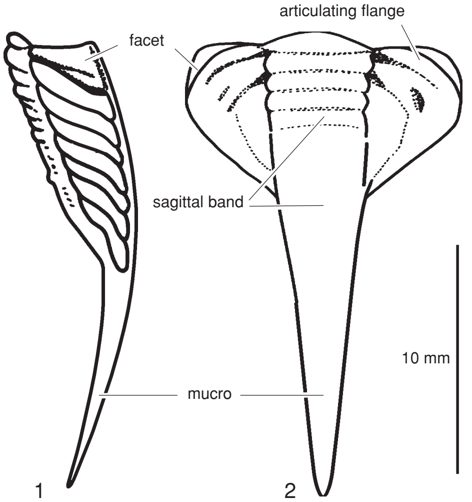


FIG. 57. *Encrinurus (Encrinurus) intersitus* RAMSKÖLD, Silurian, Sweden. *1,2,* Right lateral and dorsal views (adapted from Ramsköld, 1986, pl. 39, fig. 8a,b).

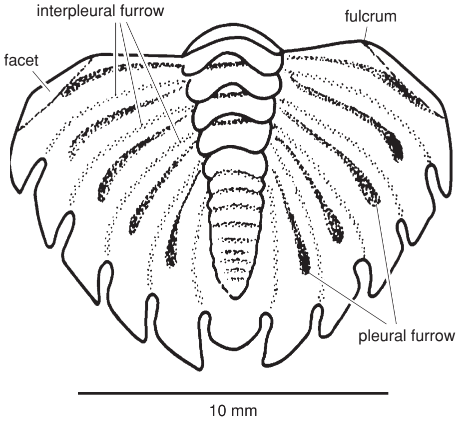


FIG. 58. Dorsal view of pygidium of *Greenops struvei* MORZADEC, Devonian, France (adapted from Morzadec, 1983, fig. 7).

doublure posteriorly: in cheirurids (WHITTINGTON & EVITT, 1954; CHATTERTON & PERRY, 1984), for example, the profile of the ventral margin of the doublure in posterior view has a median arch, and there is a small, rounded projection on the inner margin of the doublure at the tip of the axis. Many other groups of trilobites (e.g., CHATTERTON & LUDVIGSEN, 1976) show a depression in the doublure behind the axis in ventral view or an arch in posterior view. In trinucleids and raphiophorids (Fig. 51.2), in which the inner, horizontal portion of the thoracic pleurae is wide (tr.) and the outer portion narrow and steeply inclined, the outer portion of the pygidium likewise slopes steeply, and this border has a median arch in posterior view, and has an extremely narrow doublure. In Agnostina (ROBISON, 1964) a groove in the pygidial doublure, the **fibular furrow**, is a vincular structure into which the inner edge of the cephalic doublure fitted at complete enrollment. In some eodiscoids RUSHTON (1966) and RASETTI (1966b, 1967) have described vertical spines on the border of the pygidium, the tips of which on enrollment fitted beneath tubercles on the cephalic border. In *Isotelus* (CHATTERTON & LUDVIGSEN, 1976), *Annamitella* (FORTEY & SHERGOLD, 1984), and *Symphysurus* (FORTEY, 1986) a process projecting from the anterolateral margin of the doublure fitted on enrollment into a depression in the cephalic doublure.

ENROLLMENT AND COAPTATIVE STRUCTURES

E. N. K. CLARKSON and H. B. WHITTINGTON

Articulation of the thoracic segments with one another and with the cephalon and pygidium enabled enrollment in trilobites. Such enrollment is complete when a posterior portion of the thorax or the pygidium was brought into contact with the ventrally or inwardly facing inner surfaces of the cephalic doublure.

Complete enrollment is exhibited by trilobites throughout their history, from the Lower Cambrian Agnostida to Permian proetoids. Such complete enrollment is characteristic of trilobites that had a fulcrate exoskeleton, the straight, horizontal hinge-line having given a precision of movement in articulation. In such familiar examples as Agnostida (Fig. 48.3), *Calymene* (CHATTERTON & CAMPBELL, 1993, fig. 2a–c, e–g), and the phacopid *Acernaspis* (CHATTERTON & CAMPBELL, 1993, fig. 1a,b), the exoskeleton fitted together to give a closed capsule. In some forms with a fulcrate thorax and spinose pleurae, however, the exoskeleton was not closed laterally at full enrollment,

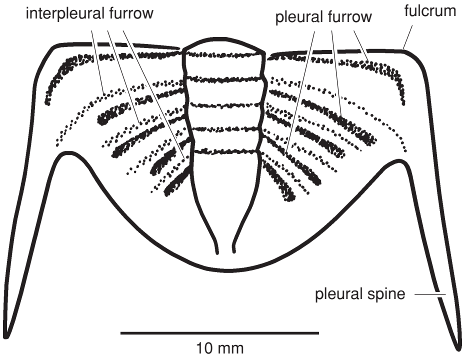


FIG. 59. *Proceratopyge* sp., Cambrian. Dorsal view of pygidium (adapted from Westergård, 1947, and Jago, 1987).

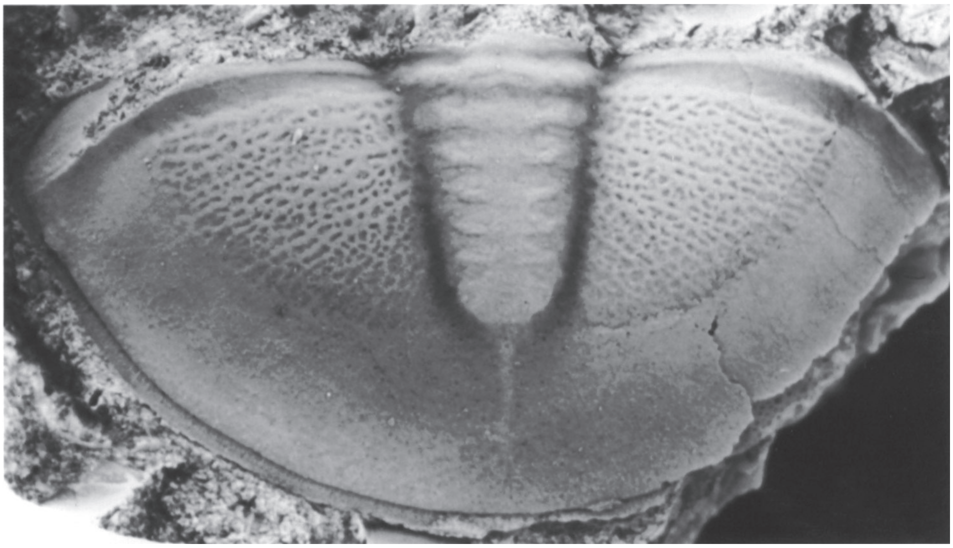


FIG. 60. *Raymondaspis reticulatus* WHITTINGTON, Ordovician, Newfoundland. Dorsal view of internal mold of pygidium, showing inter-ring furrows and lateral impressions from parietal surface of exoskeleton and caeca on pleural field, ×12 (Whittington, 1965, pl. 57, fig. 13).

the spines projecting around a lateral gap, as in *Remopleurides* (NIKOLAISEN, 1983, pl. 5; CHATTERTON & CAMPBELL, 1993, fig. 4), *Selenopeltis* (HAMMANN & RABANO, 1987), and some cheirurids (CHATTERTON & CAMPBELL, 1993, fig. 3a–c). The nonfulcrate exoskeleton is known only in Cambrian trilobites, and the amount of movement possible between sclerites suggests that complete enrollment may have been possible for some, if not all, species (WHITTINGTON, 1989, 1990). No close fit would have occurred in a completely enrolled paradoxidid, with its many thoracic segments, long pleural spines, and small pygidium, an example of which has long been known (POMPECKJ, 1896, pl. 16, fig. 1). BERGSTRÖM (1973a, p. 14, fig. 8b, pl. 1, fig. 6) used the term *cylindrical* for this type of enrollment with a lateral gap, exemplifying it by the Olenellina *Fallotaspis.* This term would apply to both fulcrate and nonfulcrate forms. Other terms purporting to characterize different types of enrollment (HARRINGTON in MOORE, 1959; BERGSTRÖM, 1973a; CHATTERTON & CAMPBELL, 1993) have been coined, but as BERGSTRÖM remarked almost any number could be added. The basic types he recognized are broadly drawn, and hence their use is limited. BERGSTRÖM (1973a) employed the manner of enrollment as a character in high-level classification. FORTEY and OWENS (1979), however, made a strong case that the exact manner of enrollment may vary between species of one genus and was not a character to be considered fundamental in classification.

Coaptative structures are complementary morphological features that ensured close interlocking of opposing surfaces (i.e., **coaptation**) when enrollment was complete. Alignment of the cephalon and pygidium in such enrollment was facilitated by the straight hinge-line of fulcrate trilobites, together with the axial and fulcral processes and sockets (Fig. 38). The facet on the outer portion of the pleura fits closely beneath the edge of the next pleura in front, and a raised stop (the panderian protuberance) limits the amount of overlap (Fig. 40). Such devices are well known in post-Cambrian trilobites (CHATTERTON & CAMPBELL, 1993) but were present in the Lower Cambrian *Crassifimbra* (PALMER, 1958), in Lower and Middle Cam-

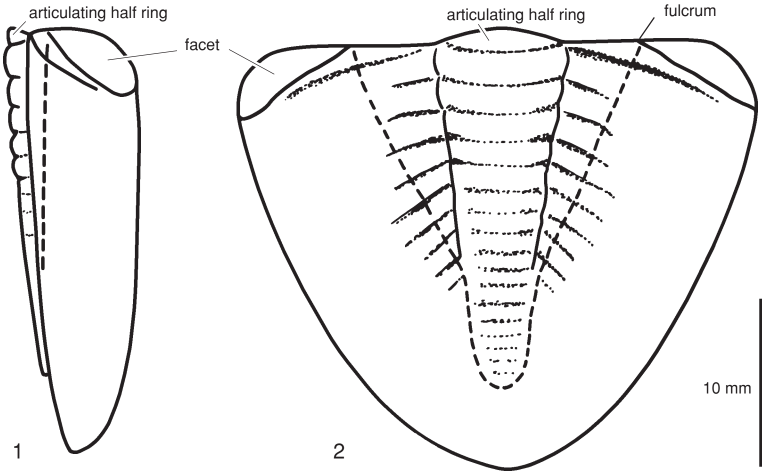


FIG. 61. *Pseudasaphus aciculatus* (ANGELIN), Ordovician, Sweden. *1,2,* Right lateral and dorsal views of pygidium, with *dashed line* showing position of inner edge of doublure (adapted from Jaanusson, 1953a, pl. 4, fig. 2, 4, 7).

brian ellipsocephalids (GEYER, 1990b, p. 55–58), in the Middle Cambrian *Bolaspidella* (ROBISON, 1964, pl. 89, fig. 8–10), and in Upper Cambrian species described by STITT (1983). In some of these Cambrian examples the width (tr.) and form of the segments and the outline of the pygidium enabled their extremities to fit closely against the inner edge of the rolled cephalic doublure; in others the posterior few thoracic segments and pygidium fitted beneath the cephalon (spiral enrollment). In the Upper Cambrian damesellinid *Stephanocare,* ÖPIK (1967) described vincular notches on the outer and ventral sides of the anterior and lateral cephalic borders. These notches received the tips of the pygidial and thoracic pleural spines on enrollment. In Agnostina the close fit of the enrolled exoskeleton is characteristic, the flat doublures of cephalon and pygidium being brought into contact and the tips of the thoracic pleurae being specially shaped to tuck in beneath the doublure of the posterior cephalic border (Fig. 48.3). HUNT (1967, pl. 22, fig. 47) illustrated a vincular notch in the posterolateral cephalic border, developed in the holaspis, into which a projection of the pygidial doublure fitted. ROBISON (in PEEL, 1988, p. 40) regarded the inflated posteroaxis of *Oidalagnostus trispinifer* as a coaptative structure to accommodate the hypostome on enrollment. In eodiscoids (JELL, 1975a) the close fit of the completely enrolled exoskeleton is well known. RUSHTON

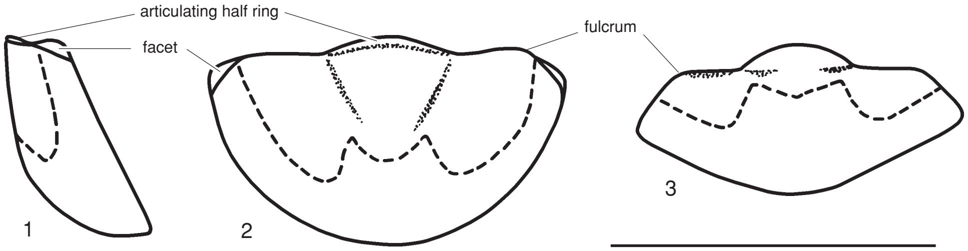


FIG. 62. Pygidium of *Illaenus tumidifrons* BILLINGS, Ordovician, Newfoundland. *1–3,* Pygidium, right lateral, dorsal, and posterior views, respectively, with *dashed line* showing position of inner edge of doublure (adapted from Whittington, 1965, pl. 15, fig. 12–13; pl. 16, fig. 14, 16).

(1966) showed that in *Serrodiscus* ventral spines on the pygidial doublure fitted beneath nodes on the cephalic border in a coaptative device and that in *Chelidiscus* the pygidial doublure fitted inside the rolled cephalic doublure in complete enrollment, the tip of the pleura of the first thoracic segment fitting beneath the posterior fixigenal cephalic spine.

In such post-Cambrian trilobites as trinucleids, coaptative structures are relatively simple, the slight projection of the pygidium behind the axis fitting into a shallow embayment in the inner edge of the lower lamella of the fringe (e.g., WHITTINGTON, 1959a, pl. 20, fig. 1, pl. 20, fig. 11). C. P. HUGHES, INGHAM, and ADDISON (1975, fig. 5) showed that there are also vincular notches on the flange of the lower lamella into which the tips of the thoracic pleurae fitted. Similar notches in the lateral or posterolateral portions of the cephalic doublure are known in such diverse trilobites as *Symphysurina* (ROSS, 1951b; HINTZE, 1953) and *Phacops* (CAMPBELL, 1967). Analogous are the ridge and groove in the cephalic doublure of some asaphids—*Kirkella* (ROSS, 1951b) and *Isotelus* (CHATTERTON & LUDVIGSEN, 1976)—although in the latter genus this structure engages with one in the doublure of the pygidium.

Coaptative devices in Ordovician and Silurian trilobites, including both lateral and median vincular structures, have been described in detail (CLARKSON & HENRY, 1973; HENRY & CLARKSON, 1975; HENRY, 1980a, 1985). Enrollment and coaptative structures in Devonian *Phacops* and *Greenops* have been compared and contrasted by SPEYER (1988). In the Ordovician dalmanitid *Crozonaspsis* (Fig. 63), CLARKSON and HENRY (1973) described the lateral vincular groove in the cephalic doublure and the median anterior projection of the cephalic border, which upon complete enrollment fitted into a notch beneath the base of the posterior pygidial spine. They emphasized how constant are the vincular structures in a single species and showed how the median projection and notch increased in size with time as the species evolved. In contrast to *Crozonaspis,* in the calymenoid *Colpocoryphe* (CLARKSON & HENRY, 1973; HAMMANN, 1985) a projection on the axis of the pygidium and a vincular furrow on the pleural region fit on enrollment into a deep anterior notch in the cephalon (Fig. 64). In *Flexicalymene* (ROSS, 1967; HAMMANN, 1985) the tip of the pygidial axis does not fit so closely into the anterior arch of the cephalon. By virtue of the sharp dorsal flexure of the inner portion of the cephalic doublure (including the doublure sector of the rostral plate), the posterior margin of the pygidium fitted against this cephalic doublure, the pygidial doublure coming to rest against the flat anterior border of the hypostome. A ridge along the posterior margin of the facet of each thoracic segment and a panderian projection and notch (HAMMANN, 1985, fig. 4e) also limited enrollment. Similar features are exhibited by the Silurian *Calymene* (CHATTERTON & CAMPBELL, 1993, fig. 2a–c, e–g).

In the Silurian *Encrinurus variolaris* (CLARKSON & HENRY, 1973; TRIPP, TEMPLE, & GASS, 1977) the pygidial and cephalic contours are identical so that the two fitted neatly when the animal was enrolled (Fig. 65.1–2). The contact surface between the two is twisted and changes in form from front to rear. Thus the pygidial doublure slopes ventrally towards its inner margin. In an enrolled specimen with the lateral part of the cephalon removed (Fig. 65.3–4), this pygidial doublure (since it is upside down) shows an outward and downward inclination, while in the thoracic doublures (which fit beneath the lateral cephalic border) the surface becomes increasingly concave and inwardly inclined. From the outer edge of the thoracic doublure arise small, flat pleural spines that fit in a groove on the cephalic doublure. The internal surfaces of these spines contacted a narrow vertical flange on the inner side of the cephalic doublural groove. The contact surface was thus twisted through some 90° from pygidial tip to genal angle, and coaptation was reinforced by the

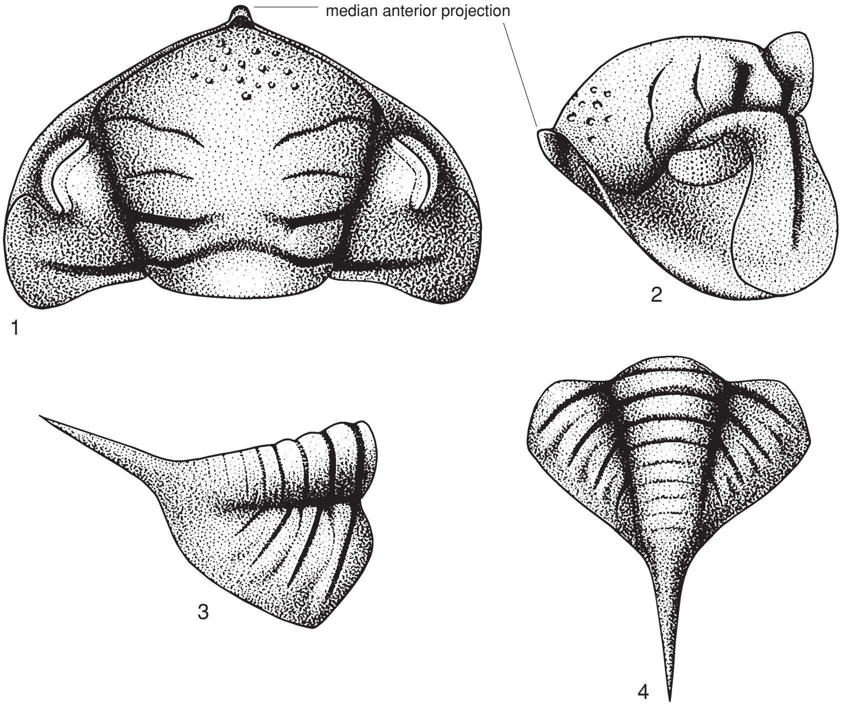


FIG. 63. *Crozonaspis dujardini* (ROUAULT), Ordovician, Brittany. *1,2,* Dorsal and left lateral views of cephalon, ×3 (approximately); *3,4,* right lateral and dorsal views of pygidium, ×3 (approximately) (Clarkson & Henry, 1973, fig. 8).

small pleural spines interlocking with the cephalic groove. In *E. tuberculatus* (CLARKSON & HENRY, 1973; TRIPP, 1962) the arrangement was similar, but the pygidium was long and mucronate, and the tip and spine projected well beyond the cephalon. CLARKSON and HENRY claimed that a gap was left where the median posterior pygidial doublure was not in contact with the cephalon. They did not, however, draw attention to the prominent rhynchos on the hypostome, which must have fitted against the inner, posterior edge of the pygidial doublure. This doublure also had a median ventral projection, and it appears at least possible that these complementary projections closed the exoskeletal capsule anteriorly. The rhynchos was also prominent in *Calymene* (CAMPBELL, 1977), and upon complete enrollment the pygidial border and doublure must have fitted closely between the doublure sector of the rostral plate and the rhynchos (Fig. 34.2). The latter appears to have been a coaptative device in these groups. In the Devonian Homalonotinae *Digonus* and *Burmeisterella,* a forwardly and downwardly directed projection on the rostral plate was coaptative, fitting against the upturned inner edge of the posterior pygidial doublure on complete enrollment (WENNDORF, 1990, fig. 13).

The Devonian *Phacops* had a single, continuous vincular furrow on the cephalic doublure, extending almost all around but becoming crenulated to form vincular notches posterolaterally; similar structures are present in many phacopids (Fig. 66) (see also CHLUPÁČ, 1977; CAMPBELL, 1977; SPEYER, 1988). On enrollment, these structures interlocked with the pygidial margin as a tongue-and-groove coupling, the vincular notches receiving the imbricated pleural tips. The different forms of vincular furrows in

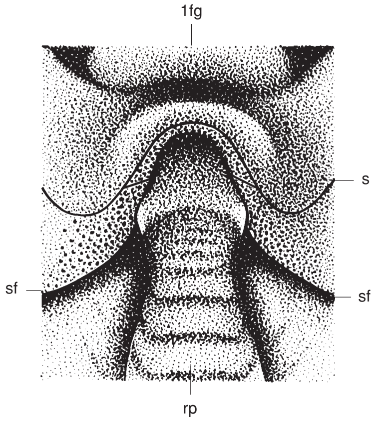


FIG. 64. *Colpocoryphe rouaulti* HENRY, Ordovician, Brittany. Anterior view showing how the axis of the pygidium fit into an anterior notch in the cephalon on complete enrollment, ×4 (approximately). Abbreviations: *1fg,* frontal lobe of glabella; *s,* facial suture; *sf,* vincular furrow of pygidium; *rp,* axis of pygidium (Clarkson & Henry, 1973, fig. 11).

phacopids and their significance in systematics were brought out by Zhiqiang ZHOU and CAMPBELL (1990) and LESPÉRANCE (1991); much new information is given by BRUTON and HAAS (1997). MILLER (1976) observed the microstructure of *Phacops rana* and noted that the vincular furrow lacked socket pits for tactile microtrichs. The pygidial margin, however, bore such pits as well as macrotrich canals, and these presumably relayed information to the central nervous system when enrollment was completed.

As mentioned above, in Ordovician dalmanitids such as *Crozonaspis,* the enrolled exoskeleton formed a closed capsule. While it may be that in some younger dalmanitoids the pygidial and cephalic doublures were everywhere in contact on enrollment, in some Silurian (Fig. 67) and Early Devonian (CAMPBELL, 1977) species this was not so. The outline of the pygidium was such that the posterior portion projected beyond the anterior border of the cephalon on enrollment and left an anterior gap in the enrolled capsule. This gap was subdivided by the median flexure in the cephalic doublure (as seen in anterior view) or partially covered by the frontal process or cephalic border spines. A similar type of anterior opening in the enrolled capsule of species of the proetid *Gerastos* was described by ŠNAJDR (1980, p. 27).

Thus complete closure of the exoskeletal capsule on enrollment was characteristic of many different groups of trilobites, but within such groups some species may have had an anterior gap. A lateral gap, between the tips of the overlapping pleurae, appears to have been present in a species of *Remopleurides* (NIKOLAISEN, 1983, pl. 5), as well as coaptative devices—a projection of the cephalic doublure fitting between the posterior pair of pygidial spines. Whether there was a similar lateral gap in trilobites with outwardly directed pleural spines when enrolled is less certain. For example, in the odontopleurid *Ceratocephala* (BRUTON, 1968b, pl. 8, fig. 1–3) there were vertical as well as outwardly directed pleural spines. The vertical spines may well have overlapped on enrollment to give lateral closure. On the other hand, in *Selenopeltis* (HAMMANN & RABANO, 1987) the flanks of the animal were open when enrolled, protected by the long, outwardly projecting spines. FORTEY (1986) showed that when the nileid *Symphysurus* is closely enrolled with the aid of coaptative devices, the arrangement of terrace ridges on the overlapping pleurae is such that minute passages to the exterior are open. Thus the exoskeletal capsule is not completely closed to the exterior. The prevalence of such devices in apparently closed capsules remains to be explored (e.g., FORTEY & CHATTERTON, 1988, fig. 13).

The fossil record suggests that new types of coaptative structures arose abruptly. Once established, however, there may have been further and more gradual evolutionary development on a smaller scale, a kind of fine-tuning process leading to an apparent improvement of the coaptative mechanism as a whole. One such example (Fig. 68) showing an evident evolutionary trend is in the Lower Silurian phacopid *Acernaspis* from northern Europe. *A. elliptifrons* (Fig. 68.1), the earliest species, has nine, narrow vincular notches deeply indenting the flat surface of the

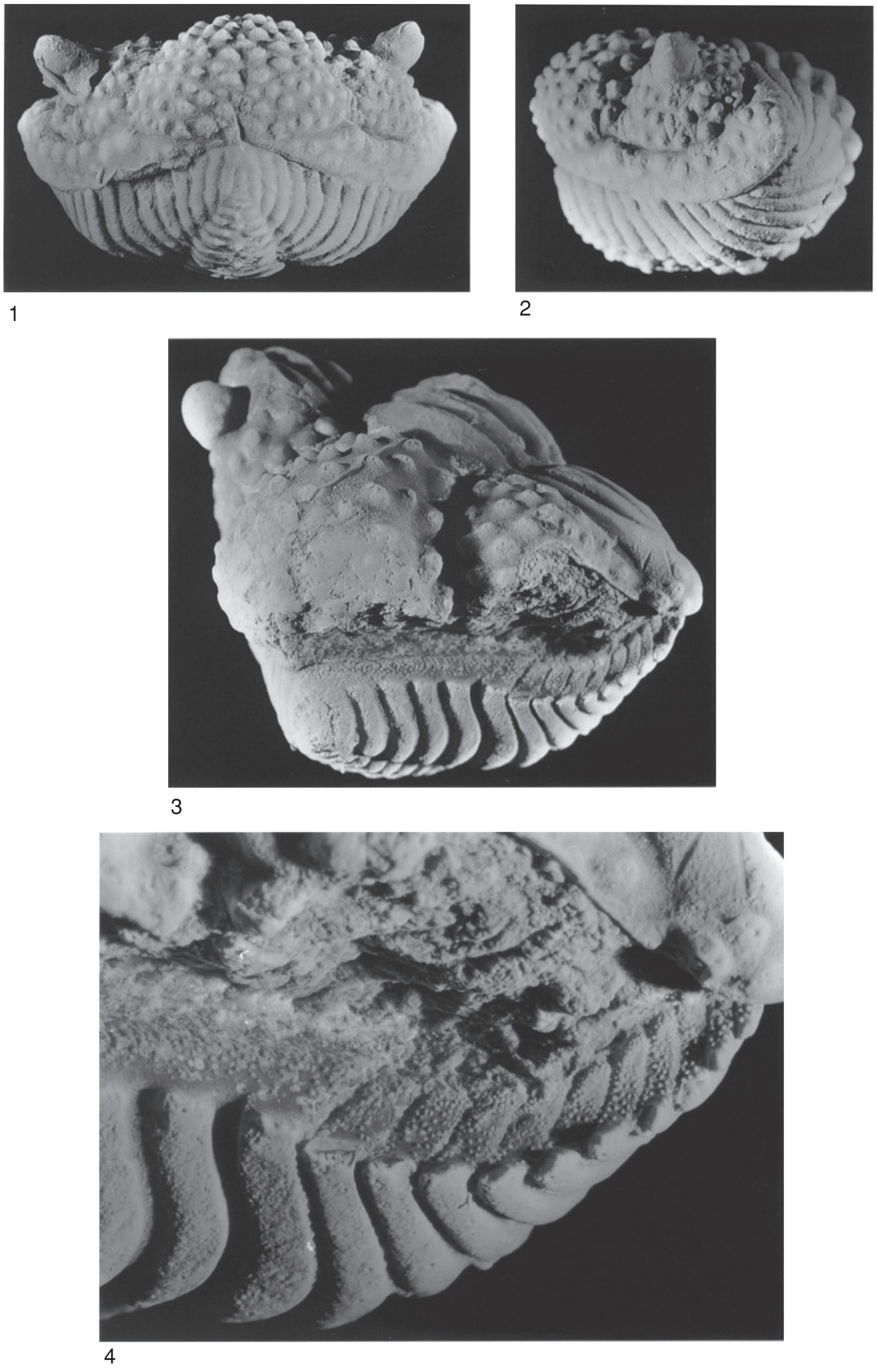


FIG. 65. *Encrinurus variolaris* (BRONGNIART), Wenlock, Silurian, England. *1,2,* Anterior and left lateral views of an enrolled specimen, ×4; *3,4,* anterolateral view of an enrolled specimen, the left librigena missing, exposing the doublure of pygidium and thorax; *3,* entire, ×3.5; *4,* detail of thoracic doublure, ×10 (Clarkson & Henry, 1973, fig. 13a,b, 14a,b).

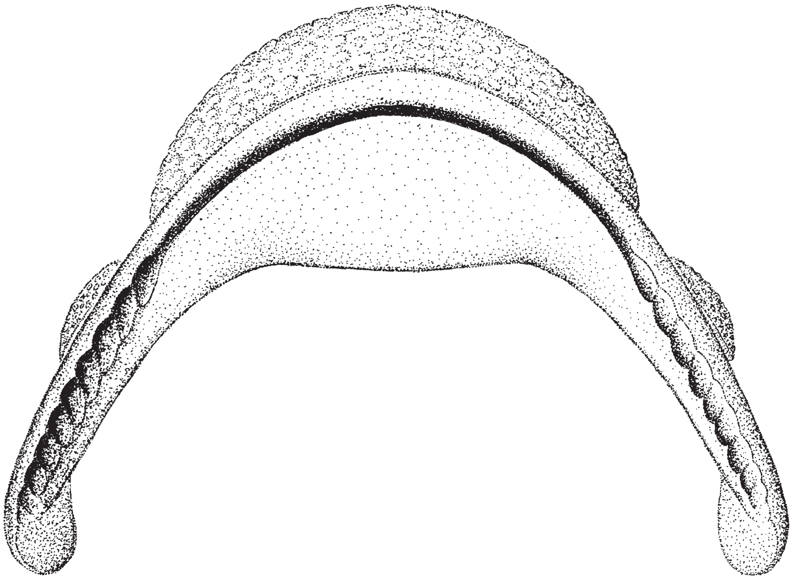


FIG. 66. *Paciphacops (Paciphacops) raymondi* (DELO), Lower Devonian, Oklahoma. Ventral view of doublure of cephalon, showing vincular furrow and lateral vincular notches (adapted from Campbell, 1977, pl. 10).

cephalic doublure, the anteriormost notch running into a deep vincular furrow. Behind this the doublure forms a flat shelf. In Scotland, the later, successive species *A. (Eskaspis) woodburnensis* and *A. (E.) sufferta* show a progressive effacement of the vincular furrow (Fig. 68.2–3), but at the same time the vincular notches broaden and deepen posteriorly and become more obliquely set. Moreover, the two doublure ridges on either side of the vincular notches become oblique to each other as seen in lateral view. The coaptative anatomy of these three stratigraphically successive Scottish species shows a clear morphological trend, and a parallel development seems to have taken place in contemporaneous Estonian species also (CLARKSON, ELDREDGE, & HENRY, 1977).

A second case is illustrated by the Ordovician genus *Placoparia*. The outer and ventral border of the librigena bears depressions into which the distal ends of the posterior thoracic pleurae and the tip of the first pygidial spine fits during enrollment. The coaptative surfaces follow a sinuous course (HENRY, 1985). In the three successive species, *P. (Coplacoparia) cambriensis, P. (C.) tournemini,* and *P. (C.) borni,* which form a stratigraphical series in the Llanvirn and Llandeilo of the Massif Armoricain, France, additional depressions appear on the anterior cephalic border (Fig. 69). These receive the tips of the posterior pygidial spines during enrollment and become increasingly pronounced through time. Contemporaneous species of *Placoparia* in Bohemia, however, show no such modification of the anterior cephalic border, and the two species groups presumably evolved in isolation (HENRY & CLARKSON, 1975; HENRY, 1985).

MICROSTRUCTURE AND SCULPTURE OF THE EXOSKELETAL CUTICLE

H. B. WHITTINGTON and
N. V. WILMOT

Studies of the cuticle since 1960 have used the scanning electron microscope, etching, and other techniques to supplement optical examinations of thin sections. Because well-preserved material in limestone is available, attention has concentrated on the Devonian *Phacops,* Ordovician species including

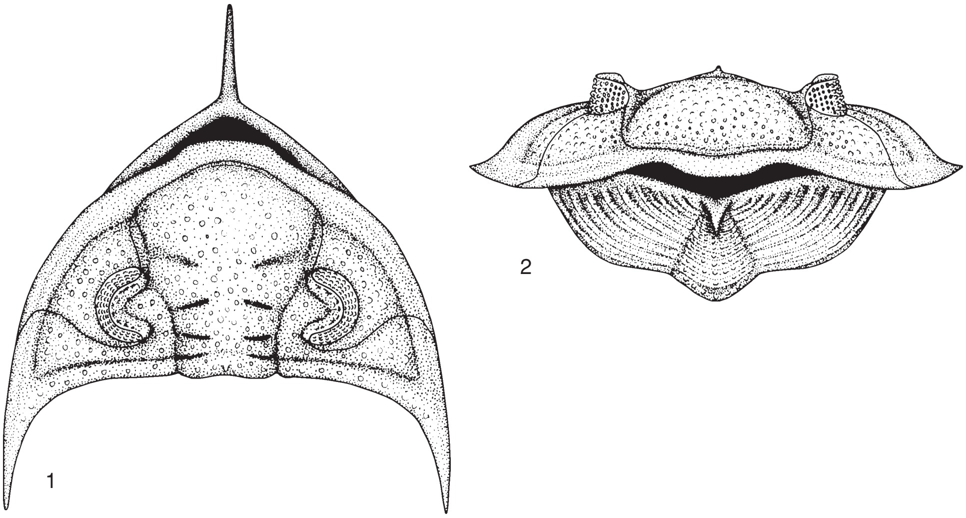


FIG. 67. *Glyptambon verrucosus* (HALL), Wenlock, Indiana, USA. *1,2,* Dorsal and anterior views of a completely enrolled individual, showing gap between cephalon and pygidium (Holloway, 1981, fig. 1).

Asaphus, and recently (DALINGWATER & others, 1993b) Silurian calymenids. The cuticular structure of the Middle Cambrian *Ellipsocephalus* has also been studied (DALINGWATER & others, 1991); otherwise few Cambrian specimens have been commented on. Uncertainties in understanding the effects of diagenesis and contradictory interpretations of what is seen in thin section show the importance of investigating primary and diagenetic microstructures (MCALLISTER & BRAND, 1989; WILMOT, 1990b). The cuticles of Lower Ordovician trilobites (FORTEY & WILMOT, 1991) show a range of thicknesses from 8 to 350 µm, 70 to 100 µm being an average range, with considerable variation in thickness shown by single species. In Devonian phacopids OSMÓLSKA (1975) has recorded a range of thicknesses from 120 to 500 µm, some proetids having a thinner cuticle, 10 to 60 µm thick; MILLER (1976) recorded cuticle as thick as 1 mm. FORTEY and WILMOT (1991) measured cuticle thickness in a sample of species across an onshore to offshore gradient, noting that greater thicknesses characterized inshore sites. Thickness does not appear to be related to size, some large species having a thin cuticle. It has been stated that the cuticle contained significant amounts of phosphate, and the outer layer in *Ellipsocephalus* appears to be composed of calcium phosphate (DALINGWATER & others, 1991). The data of WILMOT and FALLICK (1989) suggest that the exoskeleton originally had a low-magnesium calcite mineralogy. Other recent work (DALINGWATER, 1973; TEIGLER & TOWE, 1975; OSMÓLSKA, 1975) has shown that the calcite crystals have a preferred orientation of the *c* axis more or less at right angles to the surface. Decalcification of the cuticle (TEIGLER & TOWE, 1975, p. 139, pl. 5; DALINGWATER & MILLER, 1977, p. 29) leaves a delicate residue, the remains of the organic framework of the cuticle. Distinct layers (Fig. 70.1) have been recognized in the cuticle (STØRMER, 1930), and DALINGWATER (1973) considered that there is a thin, outer, prismatic layer (Fig. 70.2) one-tenth to one-thirtieth of the total thickness that overlies a principal layer. WILMOT (1990a) has shown that in some Agnostina the cuticle is only 5 to 15 µm thick and constructed like the prismatic layer.

Whether lamination is present, as seen in cross sections of modern arthropod cuticle, has been argued. A study by MUTVEI (1981) of the cuticle of a calymenid (probably

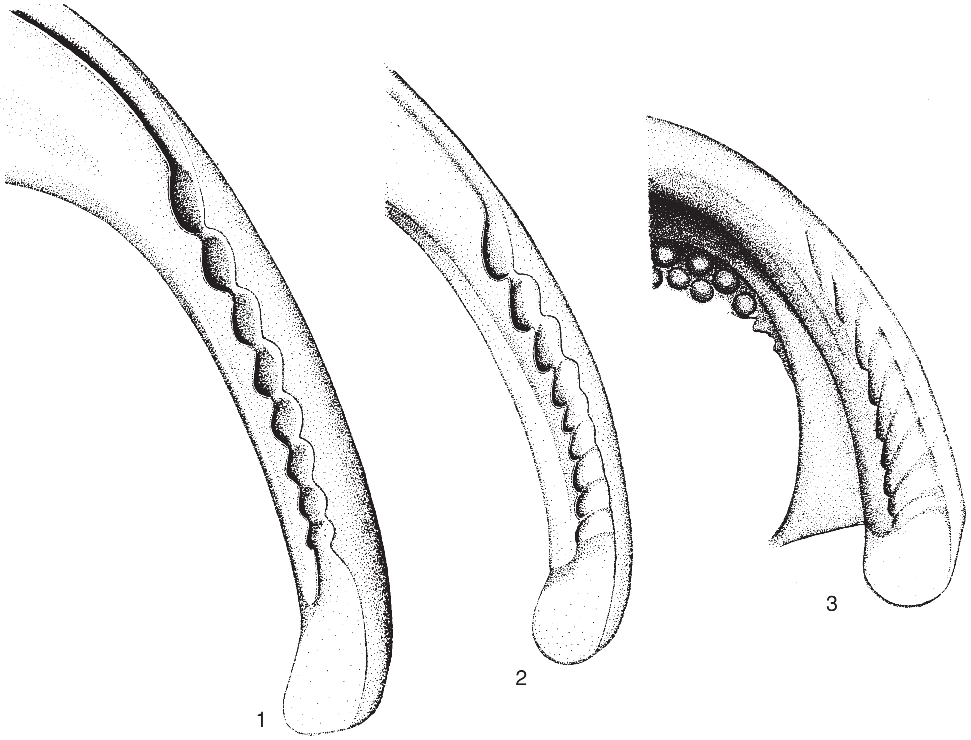


FIG. 68. Left lateral portion of the doublure of the phacopinid *Acernaspis,* showing vincular structures. *1, A. (A.) elliptifrons* (ESMARK), Llandovery, Scotland; *2, A. (Eskaspis) woodburnensis* CLARKSON, ELDREDGE, & HENRY, Llandovery, Scotland; *3, A. (E.) sufferta* (LAMONT), Llandovery, Scotland; all ×14 (Clarkson, Eldredge, & Henry, 1977, fig. 3).

Thelecalymene, see WHITTINGTON, 1971) showed an outer layer that is one-fifth in thickness of the total and horizontally laminated (compare Fig. 70.3). DALINGWATER and MILLER (1977) investigated the cuticle of *Asaphus raniceps* after breaking and etching it with EDTA (disodium salt); they distinguished three zones in the principal layer—an outer and an inner, finely laminated zone separating a much thicker, widely-laminated central zone. Using the same methods, MILLER (1976) and MILLER and CLARKSON (1980) distinguished the same zones in the principal layer of the cuticle of *Phacops rana.* The cuticle of *Ellipsocephalus* (DALINGWATER & others, 1991) appears to have a very thin outermost epicuticle, an outer laminated layer, and a principal layer. In *Tapinocalymene* (DALINGWATER & others, 1993b) the outermost layer was less than 1 µm thick; the outer layer was finely laminated, 10 to 35 µm thick; the finely foliated principal layer was 200 to 400 µm thick; and there was a very thin (about 1 µm) innermost layer. These same authors (DALINGWATER & others, 1993a) concluded that the mineralization mechanism of trilobites was similar to that of living decapod crustaceans, in contrast to TEIGLER and TOWE (1975), who compared trilobite cuticle with that of ostracodes (cf. TOWE, 1978).

The cuticle may be pierced by canals perpendicular to the surface (Fig. 70.4–5); larger diameter canals have long been recognized in thin section or in exceptionally preserved material. In silicified specimens (EVITT & WHITTINGTON, 1953, pl. 9, fig. 12–19), where the inner and outer surfaces of the exoskeleton are each represented by a thin layer, these canals may be preserved as hollow pillars connecting the two layers. Such structures and pyrite fillings of canals seen in thin section (Hammann, 1983, pl. 25) show that these canals passed through the entire thickness of the exoskeleton. These canals are considered to have been integumental glands or setal ducts (Campbell, 1977, p. 41–42; Haas, 1981), and their concentration around the margins of the exoskeleton is characteristic. Very numerous, narrow canals (about 1 µm in diameter) occur in all regions of the cuticle studied (Fig. 70.6) and were considered by Dalingwater and Miller (1977) to be similar to the pore canals in living arthropod cuticle. These authors considered that the term pore canal should be restricted to such narrow canals and not applied to canals of wider diameter, as Teigler and Towe (1975) advocated. Osmólska (1975, p. 203) drew attention to small, shallow pits (12 to 15 µm in diameter) distributed more or less evenly over the surface of the phacopid exoskeleton. Miller (1976, p. 349) observed similar pits in *Phacops,* judging them to be artifacts produced by tangential sectioning of pits that led into ducts. Størmer (1980, p. 256–259) termed these pits "Osmólska cavities" and thought that they were infilled cavities lying immediately below the outer prismatic layer of the cuticle. New studies (Wilmot, 1990b) show that these cavities lie within the prismatic layer and appear to be connected to fine, vertical canals through the exoskeleton (Fig. 71.1–2). Similar cavities in the outer layer of *Ellipsocephalus* (Dalingwater & others, 1991) are connected to canals, 3 µm in diameter, in the principal layer that extend to the inner surface of the cuticle.

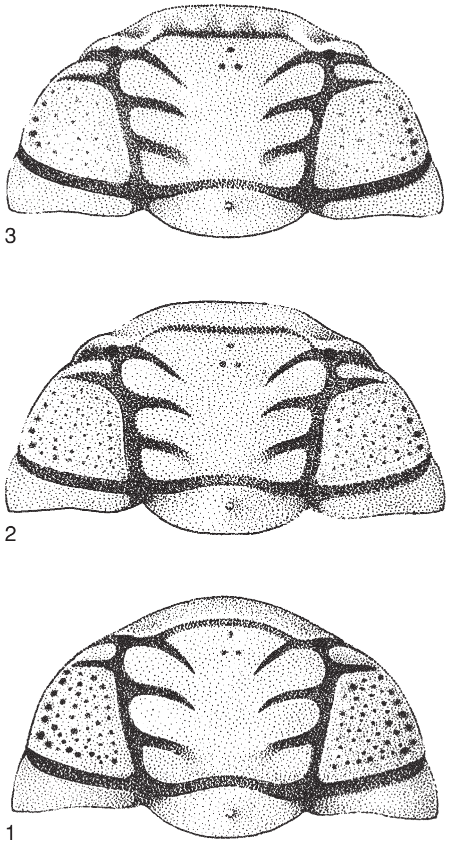


Fig. 69. Dorsal views of cranidia of *Placoparia* from the Ordovician of Brittany. *1, P. (Coplacoparia) cambriensis* Hicks, ×6; *2, P. (C.) tournemini* (Rouault), ×5; *3, P. (C.) borni* Hammann, ×4.5 (Henry & Clarkson, 1975, fig. 3).

The outer surface of the exoskeleton is smooth in the troughs of furrows, in pits, and in the areas of the axial region regarded as areas of muscle attachment. Elsewhere the surface may be sculptured in pustules of varied size and distribution, pitted, or covered by raised symmetrical or asymmetrical ridges arranged in various ways. Such surface sculpture is frequently referred to as *ornament,* but as Gill (1949) argued in proposing to call it *prosopon*, ornament is a general word that gives an erroneous impression of mere decoration, whereas surface **sculpture** has biological significance. The sculpture (or prosopon) embraces small features, not large genal, pleural, or axial spines that are hollow extensions of the entire cuticle. Miller (1976) showed that tubercles, prominences on the external surface, were of different types when seen in cross sections of the cuticle: a **dome** (Fig. 71.3) when the cuticle bulged upward and thinned at the apex of the bulge, a structure that projected from the surface and had

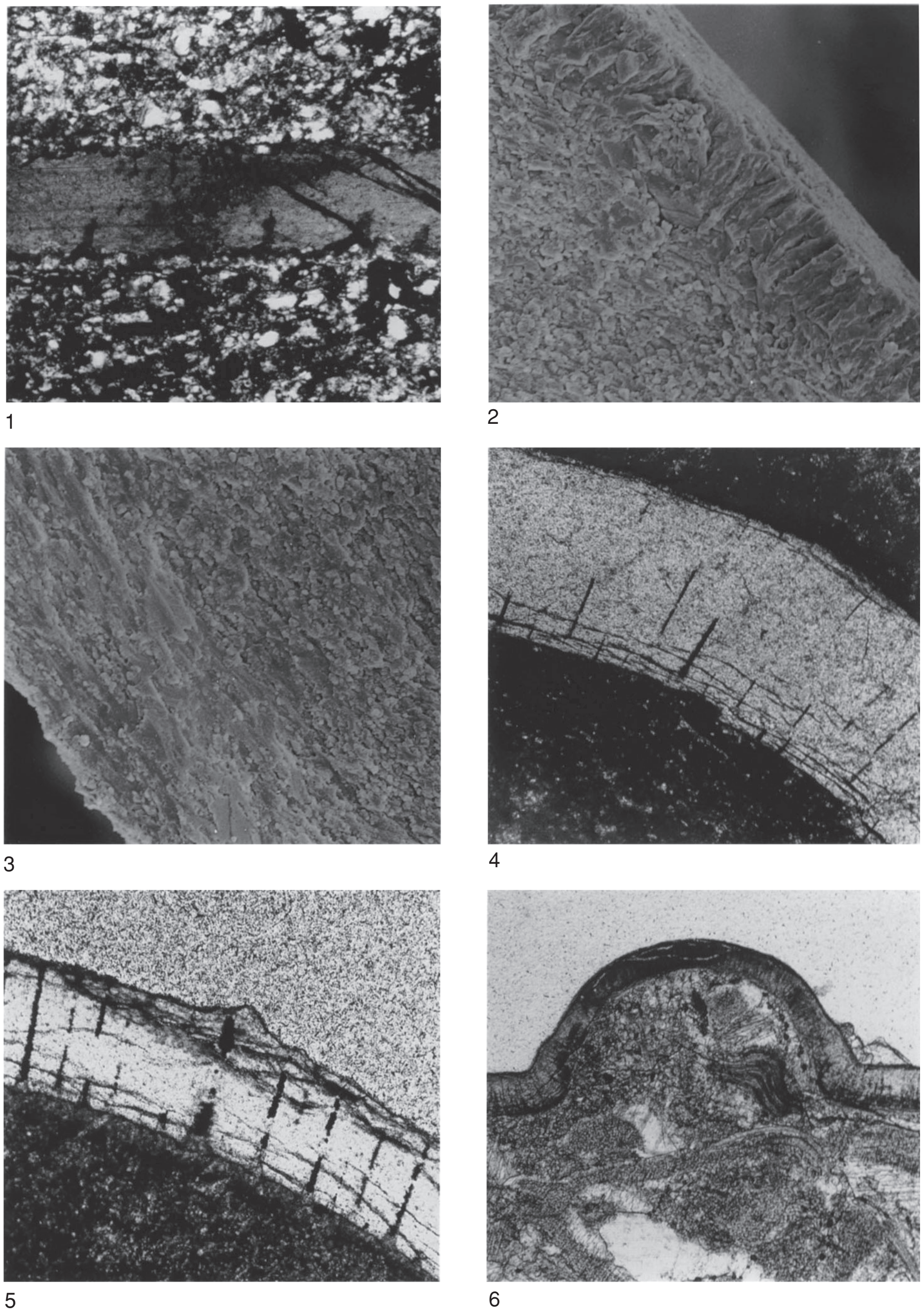


FIG. 70. Thin sections of trilobite cuticle. *1, Asaphus* sp., Asaphus Limestone, Norway, Ordovician, NMW 88.22G.16. Stained thin section revealing primary horizontal laminations within the principal layer. Large borings (30 µm diameter) are present on the visceral surface (the lower in the photograph) of the exoskeleton. The irregular external surface indicates dissolution of the cuticle, ×40 (Wilmot, 1990b, fig. 1c). *2, Phacops rana crassituberculata* STUMM, Silica Shale, Silica, Ohio, Middle Devonian, NMW 88.22G.41. SEM of prismatic layer with calcite crys-

(Continued on facing page.)

an apical pore (Fig. 71.4), or a more complex projection that he termed a *pseudotubercle* (Fig. 71.5). Størmer's (1980) investigation of phacopoid tubercles and their internal structures showed a range of types from smooth tubercles with no central opening, to domed and spiniform tubercles that had a central canal, to large composite tubercles or *pseudotubercles.* His illustrations include not only cross sections but the external surface and mold of the internal surface of the exoskeleton as well as diagrams of his interpretations of the effects of incomplete preservation and abrasion on the appearance of these features. Granulation is not invariably confined to the outer surface of the exoskeleton but has been recorded on the inner surface in illaenids (Whittington, 1965, pl. 46, fig. 19, pl. 51, fig. 11; Owen & Bruton, 1980, pl. 4, fig. 2, 6).

Studies of silicified specimens, including growth stages, have shown that thornlike pustules, spines rather than tubercles, may be prominent in meraspid growth stages but reduced later (Whittington, 1941, 1956b; Chatterton, 1980; Whittington & Evitt, 1954). Such spines may be in pairs along the axial region, reflecting segmentation, and in odontopleurids pairs of spines on the pleural regions form rows with axial pairs and may be recognizable in holaspid stages. In encrinurids paired spines or tubercles in rows on the glabella and on the fixigena are similarly recognizable during ontogeny (Evitt & Tripp, 1977). Openings at the tips of such spines or tubercles have been described, particularly in those along the border or the distal portion of an occipital, genal, or pleural spine (Whittington & Evitt, 1954). The opening may be single or multiple (Fig. 72.1), or in encrinurids (Evitt & Tripp, 1977, p. 118) may lie between the granules at the tips of axial and pleural spines.

A median occipital spine or tubercle occurs on many trilobites, and in certain odontopleurids (Fig. 72.2) and styginids (Whittington, 1965, p. 297) such a tubercle has been shown to bear at the summit four tiny pits arranged in a square. A median glabellar tubercle in front of the occipital ring is present in asaphids, nileids, and illaenids (Fortey & Clarkson, 1976). In asaphids the structure appears to be a dome, whereas in nileids and illaenids only a depression in the inner surface of the exoskeleton is visible (as a low mound in the mold of that surface) and is an area over which the exoskeleton is thinned. In the median occipital node of *Proetus,* the cuticle thins at the apex so that only the prismatic layer remains, whereas in *Harpidella* there is a central canal (Wilmot, 1991). In the cyclopygids *Pricyclopyge* and *Symphysops* (Marek, 1961; Fortey & Owens, 1987, p. 180) a pair of structures appears that on molds are either domes or pits with a raised rim and are considered to have been formed within the cuticle.

Raised ridges are another type of sculpture, the asymmetrical **terrace ridges** (Fig. 73–74) being characteristic of the outer portions of the pleural region, the border and doublure, and the hypostome. The steep slope of the ridge faces abaxially, and the ridges are strongest, long and continuous, occasionally anastomosing, on the border and doublure, running subparallel to the margin. On the dorsal side, inside the

Fig. 70. *Explanation continued from facing page.*

tals (1 × 10 µm) oriented with their c-axes perpendicular to the surface, ×1000 (Wilmot, 1990b, fig. 1a). *3, Phacops rana crassituberculata* Stumm, Silica Shale, Silica, Ohio, Middle Devonian, NE4.C, NMW 88.22G. SEM of the principal layer with calcite crystals aligned parallel to the surface, ×1000 (courtesy of N. V. Wilmot). *4, Calymene* sp., Mulde Beds, Gotland, Silurian (Wenlock), NMW 88.22G.12. Thin section through the pygidium, the canals infilled by micrite, ×30 (Wilmot, 1990b, fig. 1f). *5, Calymene* sp., Mulde Beds, Gotland, Silurian (Wenlock), NMW 88.22G.11. Thin section through the cranidium, revealing canals infilled by pyrite, ×30 (Wilmot, 1990b, fig. 1d). *6, Proetus (Proetus) concinnus* (Dalman), Silurian (Wenlock), PRO 12, NMW 88.22G, locality 64 of Thomas (1978). Transverse section through pygidium revealing numerous fine canals (1µm diameter), ×30 (courtesy of N. V. Wilmot).

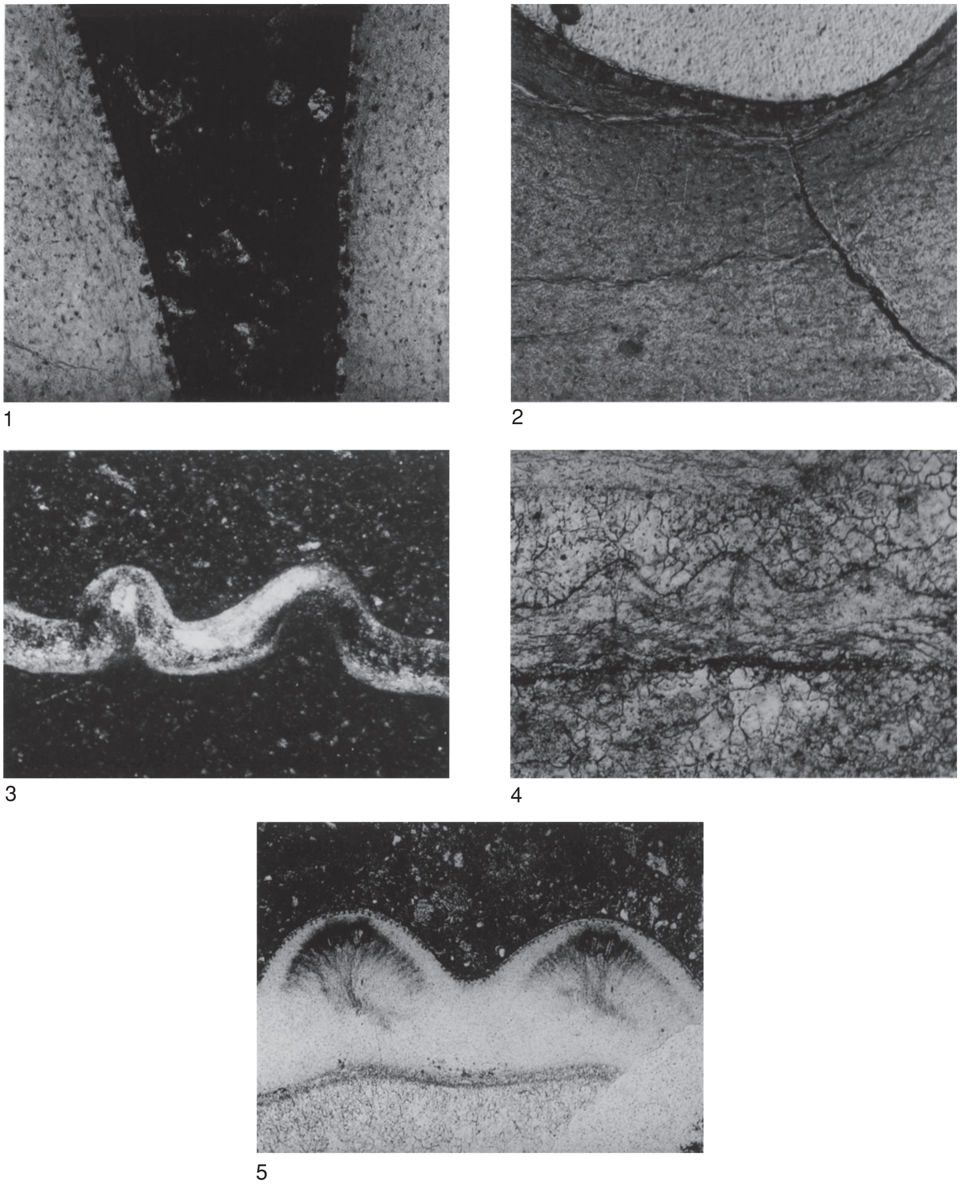


FIG. 71. Thin sections of trilobite cuticle. *1, Phacops rana crassituberculata* STUMM, Silica Shale, Silica, Ohio, Middle Devonian, NMW 88.22G.6. Longitudinal section through thoracic segments, showing Osmólska cavities within the prismatic layer, ×100 (Wilmot, 1990b, fig. 5c). *2, Phacops rana crassituberculata* STUMM, Silica Shale, Silica, Ohio, Middle Devonian, NMW 88.22G.8. Transverse section through the cephalon, showing Osmólska cavities within the prismatic layer connected to fine canals within the principal layer, ×50 (Wilmot, 1990b, fig. 5b). *3, Hemiarges bucklandii* (MILNE EDWARDS), Much Wenlock Limestone Formation, Wren's Nest, Dudley, Silurian (Wenlock), D33.3, NMW 88.22G. Longitudinal section through domes in the cranidium, ×40 (courtesy of N. V. Wilmot). *4, Cyphoproetus depressus* (BARRANDE), Dolyhir and Nash Scar Limestone Formation, near Dolyhir Bridge S0 2403 5825, Silurian (Wenlock), NW10.1, NMW 88.22G. Stained thin section through a cranidium containing tubercles with central canals, ×50 (courtesy of N. V. Wilmot). *5, Phacops granulatus* (MÜNSTER), Poland, Devonian, P.M.O A38817.1. Thin section through pseudotubercles, which contain internal tubules and show Osmólska cavities in the outer, prismatic layer, ×30 (Størmer, 1980, pl. 30, fig. 1a).

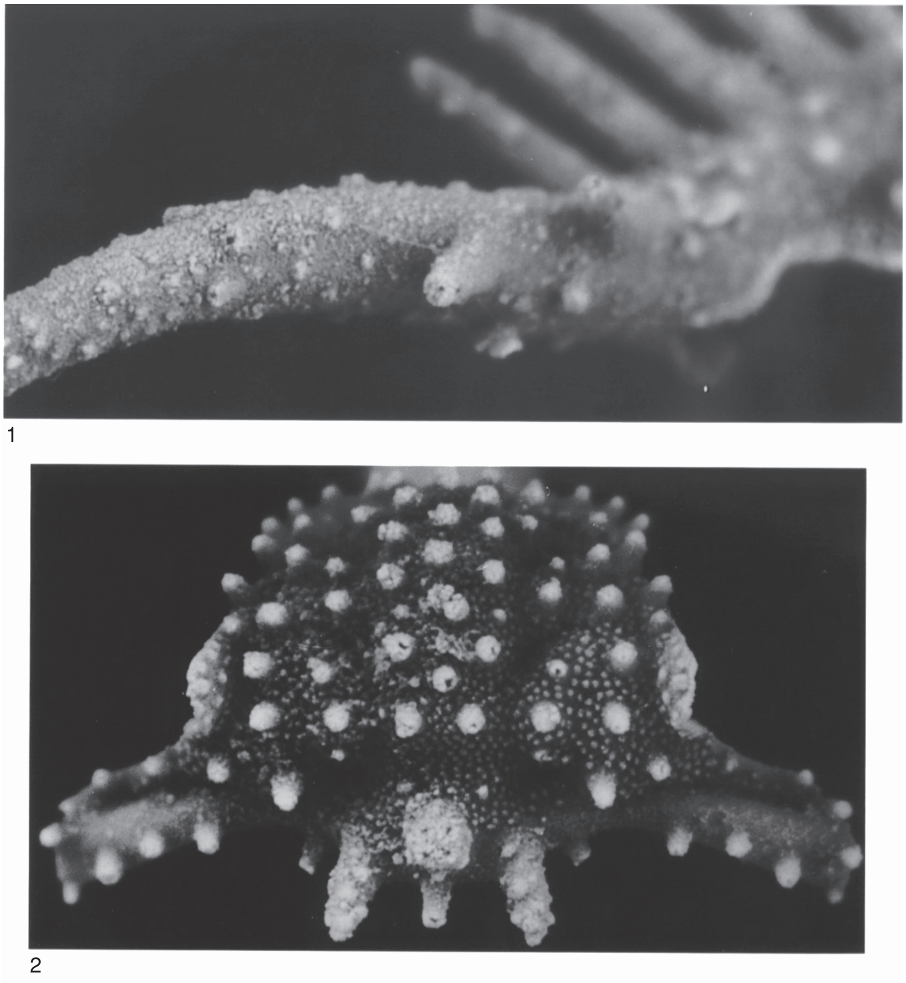


FIG. 72. *1, Diacanthaspis secretus* WHITTINGTON, Ordovician, Virginia. Basal portion of left librigenal spine bearing small spines that have single or multiple openings at the tip, ×60 (Whittington, 1956d, pl. 7, fig. 13). *2, Diacanthaspis ulrichi* WHITTINGTON, Ordovician, Virginia. Dorsal view of cranidium, showing spinose sculpture, opening at tip of spines, and four depressions at tip of median occipital spine, ×45 (Whittington, 1956d, pl. 8, fig. 30).

border, the ridges may curve to run obliquely and curve across the axial region. Such ridges are characteristic of the doublure of trilobites from a wide range of taxa and ages. Examples may be found among Cambrian trilobites (WHITTINGTON, 1988a, 1989), and younger groups including asaphids, nileids, remopleuridids (WHITTINGTON, 1965; CHATTERTON & LUDVIGSEN, 1976); illaenids (WHITTINGTON, 1965; OWEN & BRUTON, 1980); styginids (ŠNAJDR, 1960); and proetids (ŠNAJDR, 1980). As MILLER (1975) pointed out, such terrace ridges are not universally present, being seemingly unknown in Agnostida, calymenids (CAMPBELL, 1967), cheirurids (CHATTERTON & PERRY, 1984), and encrinurids (EVITT & TRIPP, 1977). Although present on the doublure of phacopids (CAMPBELL, 1967), these terrace ridges do not appear to characterize the dalmanitid doublure (HOLLOWAY, 1981; RAMSKÖLD, 1985). Using cross sections and SEM micro-

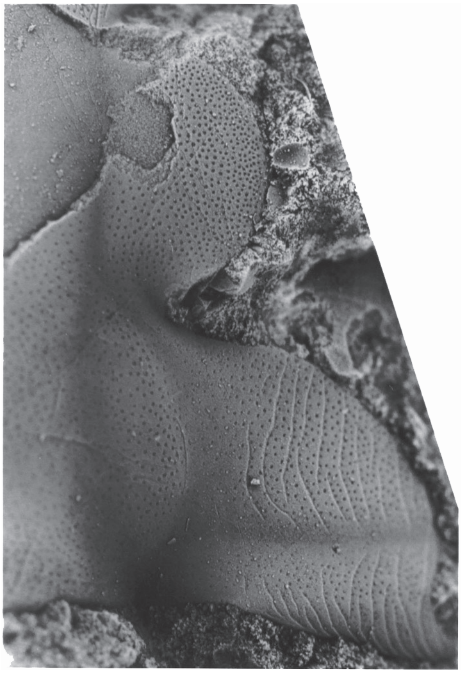


FIG. 73. *Niobe quadraticaudata* (BILLINGS), Ordovician, Newfoundland. Posterolateral portion of cranidium, showing sculpture of terrace ridges on fixigena, pits in palpebral lobe and baccula (the swelling on the adaxial portion of the fixigena, adjacent to the axial furrow), ×30 (Whittington, 1965, pl. 24, fig. 7).

graphs, MILLER (1975) described terrace ridges in several genera, showing the varied profile of the ridges and their association with scattered pits in the outer surface of the cuticle. He claimed that the outer, prismatic layer of the cuticle is absent from the steep, scarp slope of the ridge and that canals, curving through the cuticle, open in a small pit on the scarp. The former claim may not be correct, and neither OSMÓLSKA (1975, p. 204) nor STØRMER (1980, p. 256) considered that canals are present in association with terrace ridges.

Another type of ridge, symmetrical in profile, is the **lira,** known on the dorsal surface of the cuticle of both axial and pleural regions in bathyurids, proetids, and remopleuridids (NIKOLAISEN, 1983), for example. These lirae may form a fingerprint-like pattern on the glabella and axial rings (the so-called Bertillon pattern), but as NIKOLAISEN pointed out their arrangement varies. Similar ridges in the axial region of *Peraspis* (Fig. 75) appear to be continuous with the peripheral terrace ridges, so that the two types of ridges may be transitional. BRUTON (1976) provided many illustrations of these ridges in *Phillipsinella* and of their intimate association with granules and pits. It appears that rows of granules are transitional with the ridges, and MILLER (1975) pointed out that in some styginid and homalonotid genera terrace ridges may form an anastomosing, netlike pattern. A prominent, reticulate pattern of raised, symmetrical ridges has long been recognized in some Olenellina (WHITTINGTON, 1989). In describing a species of *Wanneria,* PALMER (1964) noted that perforations on the inner surface of the exoskeleton outlined the polygons and that the exoskeleton broke along the margins of these polygons, showing that the perforations extended partway through the exoskeleton; no comparable arrangement of perforations has been described in any other trilobite. A prominent, reticulate pattern of raised ridges is known in such other trilobites as *Cryptolithus* (Fig. 76), *Galbagnostus* (Fig. 10), and *Telephina* (WHITTINGTON, 1965). MILLER (1976, fig. 2o) has claimed that there are rows of canals opening into pits along the ridge crests in *Tretaspis.* Much smaller in size (polygons 15 μm or less across) is the polygonal pattern of furrows seen on the external surface of extant arthropod cuticles (MILLER, 1976, p. 346), which appear to be a surface expression of the epidermal cells that secreted the cuticle. A reticulate pattern of raised ridges on the external surface of some Agnostina (MÜLLER & WALOSSEK, 1987, pl. 7–8; WILMOT, 1990a, 1990b) is of similar dimensions and may also result from polygonal cells. The cell polygons in proetids (WILMOT, 1991) are small, 5 μm in diameter. An extraordinary sculpture is the raised, wall-like ridges of the solenopleurid *Badelusia* (SDZUY, 1968), which in one species are extended into spines.

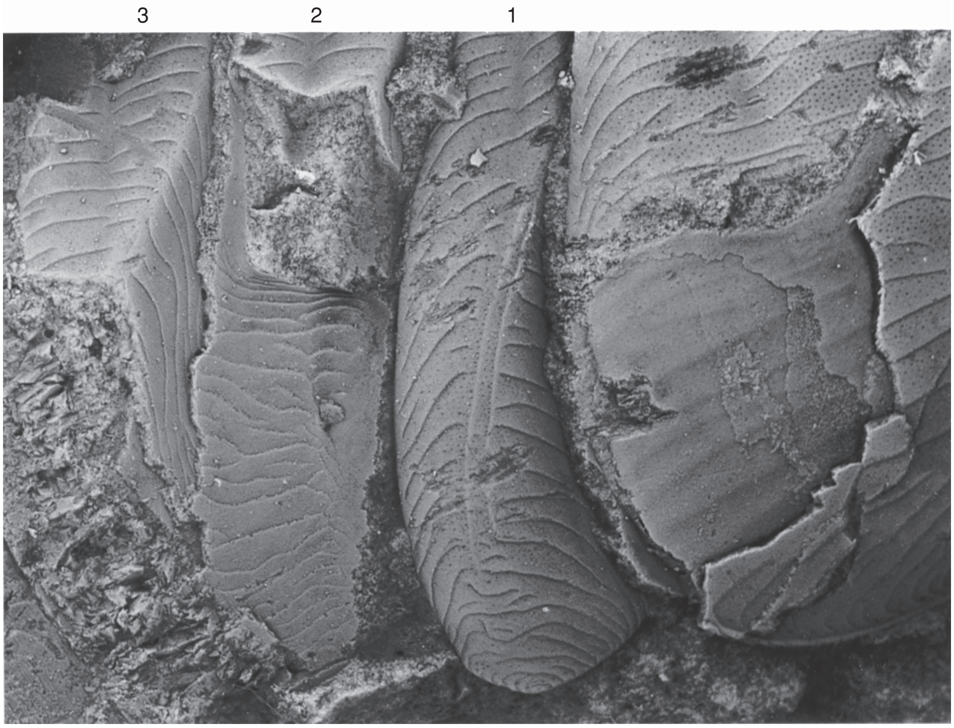


FIG. 74. *Niobe quadraticaudata* (BILLINGS), Ordovician, Newfoundland. Right posterolateral portion of librigena and outer portion of thoracic segments 1 to 3. Terrace ridges visible on external surface of segments 1 and 3 and on mold of doublure of segment 2, ×9 (Whittington, 1965, pl. 24, fig. 6).

A raised sculpture of pustules or ridges may occur in combination with pits (scattered depressions in the external surface of the cuticle), as in *Niobe* (Fig. 73), *Poronileus* (FORTEY, 1975b), *Nanillaenus* (CHATTERTON & LUDVIGSEN, 1976), and *Asteropyge* (MORZADEC, 1983, pl. 18). These pits are tiny and may be depressions rather than the openings of canals through the cuticle. Larger, deeper pits, as in the librigena of *Encrinuroides* (CHATTERTON & LUDVIGSEN, 1976, pl. 15, fig. 11–12; EVITT & TRIPP, 1977, pl. 10, fig. 1) appear to correspond to low projections on the inner surface of the cuticle. Such pits may be the opposite of domes, being depressions in which the cuticle thins at the base.

The nature and complexity of the sculpture of the exoskeleton and the variations and transitions from one type to another are shown by the references quoted. Silicified material and photographs of details of well-preserved specimens from limestone (BRUTON, 1976; ŠNAJDR, 1980, pl. 61–64; NIKOLAISEN, 1983; WILMOT, 1991) afford the best examples. While a particular type of sculpture may be widespread within a family or larger taxon, it may be neither exclusive to that taxon or universal within it. Thus while spines and tubercles are characteristic of odontopleurid sculpture, they may be absent in some species. The reticulate pattern of raised lines characteristic of some Olenellina is known in unrelated taxa, whereas both granulation and a Bertillon pattern of raised lines are known on the external surface of other Olenellina.

The microstructure and sculpture of the exoskeleton, together with the form (or architecture), enabled it to accommodate the

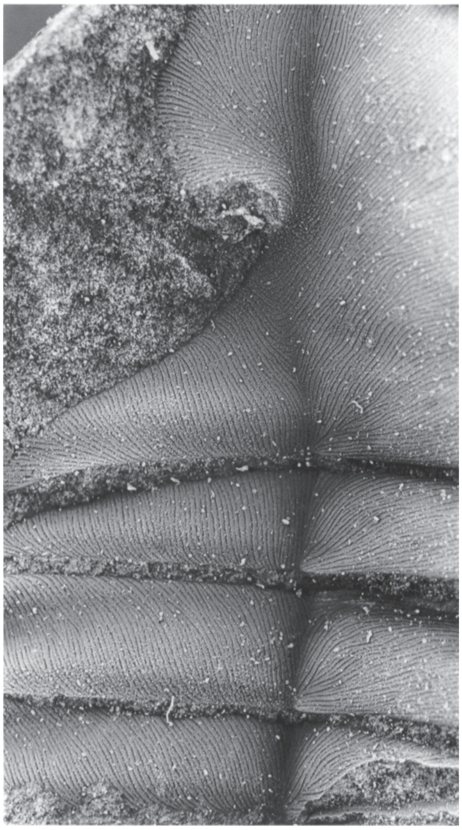


FIG. 75. *Peraspis lineolata* (RAYMOND), Ordovician, Newfoundland. Left portion of cranidium and thoracic segments 1 to 3, to show sculpture of external surface, ×22 (Whittington, 1965, pl. 36, fig. 12).

forces acting on it. These forces may have been external, the result of environmental perturbation or predators, or internal, being the site of attachment of muscles. A pioneer study of biomechanics of trilobite exoskeletons (WILMOT, 1990c) suggested that the cuticle behaved as a ceramic, in a linearly elastic manner. The exoskeleton was analogous to a monocoque shell, thin yet strong, which behaved as a stressed skin. Sculpture has been shown to be related to canals through the exoskeleton, to presumed sensory devices, and perhaps to the need to maintain aeration within the enrolled trilobite. It may have contributed to the strength of the exoskeleton, and a novel suggestion by CHATTERTON (1980, p. 6) is that granules and tubercles would have reduced the efficacy of sucker disks in obtaining a grip and so protected trilobites from predators relying on such disks.

SUPPOSED COLOR MARKINGS

H. B. WHITTINGTON

Color markings of the exoskeleton have been described as faint, light and dark gray bands crossing the pygidium of a Cambrian trilobite (RAYMOND, 1922), as dark patches outside the eye lobe, on the genal spine, and in the axial and pleural furrows of an Upper Ordovician *Isotelus* (WELLS, 1942), and as symmetrical, dark patches on the axial rings of a Carboniferous proetid (WILLIAMS, 1930). Similarly arranged dark patches on the pygidial axis of Carboniferous species were described by WHITTINGTON (1954a), HESSLER (1965, fig. 1), and PABIAN and FAGERSTROM (1972, pl. 1, fig. 12, 15) as muscle scars. They appear darker when photographed, but whether this is because of traces of original color or because the exoskeleton is of a different thickness over this area is uncertain. TEICHERT (1944, p. 458) described tiny spots scattered over the axial and pleural regions of a pygidium of a Permian proetid, and similar spots were portrayed by HESSLER (1965, fig. 1). Whether such spots are the remains of a color pattern, as TEICHERT claimed, is open to question. A remarkable example of a Silurian phacopid showing darker areas of the exoskeleton was described by CAMPBELL (1976, fig. 1, pl. A). The prominent, larger, symmetrical areas in the axial furrows and region are most probably areas of muscle attachment, as may be some of the smaller spots in the pleural region. CAMPBELL described the specimen as abraded and having associated pyrite and remarked that the tiny spots are not associated with exoskeletal sculpture, but he did not discuss the possibility that some of the small spots in the pleural region may be traces of a color pattern. Supposed color markings in the exoskeleton of the Devonian *Phacops* and *Greenops* were described by ESKER (1968) and examined in greater detail by BABCOCK (1982). The latter author considered that the original coloration in these two species, *P. rana* and *G. boothi,* consisted of irregular dark spots scattered randomly over the exoskeleton, larger spots having been concentrated adjacent to the axial furrow, outside the eye lobe, and on the adaxial portion of the pleural region. Examination of thin sections suggests that these spots are related to the Osmólska cavities and are visible externally when the exoskeleton is light in color and the cavities contain fine-grained pyrite. The lines of spots described by ESKER on the pleura of *G. boothi* are considered to be broken tubercles that were molded internally by pyrite. Diagenesis of pyrite that had formed below the exoskeleton is thought to be responsible for dark coloration in the furrows and on peripheral portions of the exoskeleton.

It appears that paired, darker-appearing areas in glabellar, articulating and inter-ring furrows of trilobites may have been areas of muscle attachment, but why such areas appear darker is not understood. Small, dark spots or bands on the exoskeleton may be traces of an original color pattern, but a reassessment of supposed examples is needed, particularly with reference to preservation and the role of diagenesis.

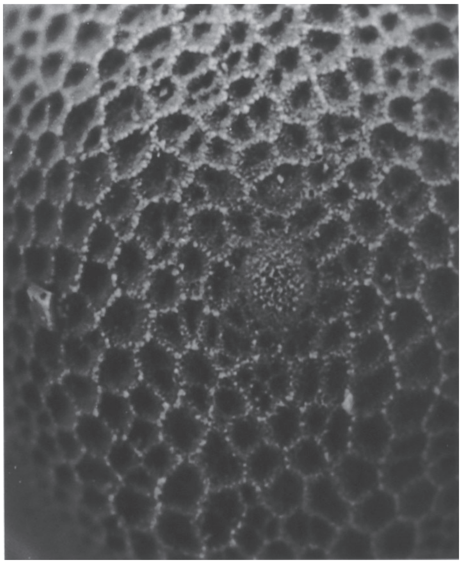


FIG. 76. *Cryptolithus tesselatus* GREEN, Ordovician, Virginia. Median area of glabella, showing tubercle and sculpture of network of raised ridges, ×50 (Whittington, 1959a, pl. 20, fig. 10).

THE TRILOBITE BODY

H. B. WHITTINGTON

INTRODUCTION

In exceptional circumstances (see the section on taphonomy below) diagenetic processes have resulted in preservation of the ventral cuticle, particularly that covering the limbs. Spectacular examples of such preservation are the enrolled specimens of *Agnostus pisiformis* less than 1.0 mm in length, described by MÜLLER and WALOSSEK (1987) and coming from localities in the Upper Cambrian of Sweden. Permineralization by phosphatic matter has not only preserved all the limbs (Fig. 77–79) but also the ventral cuticle into which they were inserted, sternites, traces of the alimentary canal, and other organs. The recognition of **sternites,** transversely rectangular plates between the insertions of the limb bases separated one from another by a transverse groove, is unique. Presumably these were sclerotized plates, not mineralized, no evidence of mineralized sternites being known in any trilobite. The ventral cuticle beneath the pleural regions is rarely preserved and when so preserved is wrinkled, suggesting that it was lightly sclerotized, thin, and flexible. Such flexibililty would be necessary in *Agnostus* and any other trilobite that enrolled completely, to allow the limbs, including the antennae, to be packed inside. The ventral cuticle must have been attached to the inner edge of the doublure. The exoskeleton thins towards this edge, but the outline of it is not ragged; rather it is sharp and distinctive in trilobites with no implication of transition. Presumably, the cuticle of the limbs of trilobites was more heavily sclerotized than that beneath the pleural regions and hence is preserved in specimens from different stratigraphical horizons in other countries (see below), by replacement with mineral matter, or by lining or infilling by pyrite. Pyritized specimens have been studied by X rays, and it is claimed that not only traces of the digestive organs and alimentary canal but also of muscles and endoskeletal bars are preserved. The anatomy of the trilobite has been conjectured from these traces and interpretations made of such exoskeletal features as muscle scars, openings, and canals.

LIMBS

Although earlier work on trilobite limbs was summarized by HARRINGTON (in MOORE, 1959, p. 76–82), detailed studies published subsequently have greatly changed our knowledge, and this account refers to the recent work. These newer studies have relied in part on X-ray photography and to a greater extent on mechanical preparation and extraction using acid. Key factors in new interpretations have been the better understanding of taphonomy, the recognition of the probable original convexity of the exoskeleton, and improved techniques.

The appendages of meraspid developmental stages of *Agnostus pisiformis* (Fig. 77–79) from the Upper Cambrian of Sweden (MÜLLER & WALOSSEK, 1987) are the best preserved of any known, despite the minuteness of the specimens. They have not been flattened by compaction or displaced in relation to the exoskeleton, hence the positions of the insertions of the limb series (Fig. 80) may be observed in relation to the morphology of the exoskeleton (Fig. 81). Thus a most detailed reconstruction could be prepared (Fig. 82). The cephalon bears four pairs of appendages, the first being the multijointed antenna having a short, basal shaft and annular podomeres bearing setae and bristles. The antenna is attached at the side of the large, bulging hypostome immediately behind the anterior hypostomal wing. The second appendage is attached on the posterolateral side of the hypostome and has a large coxa with a spinose gnathobase. From the coxa arises a long outer branch, the short

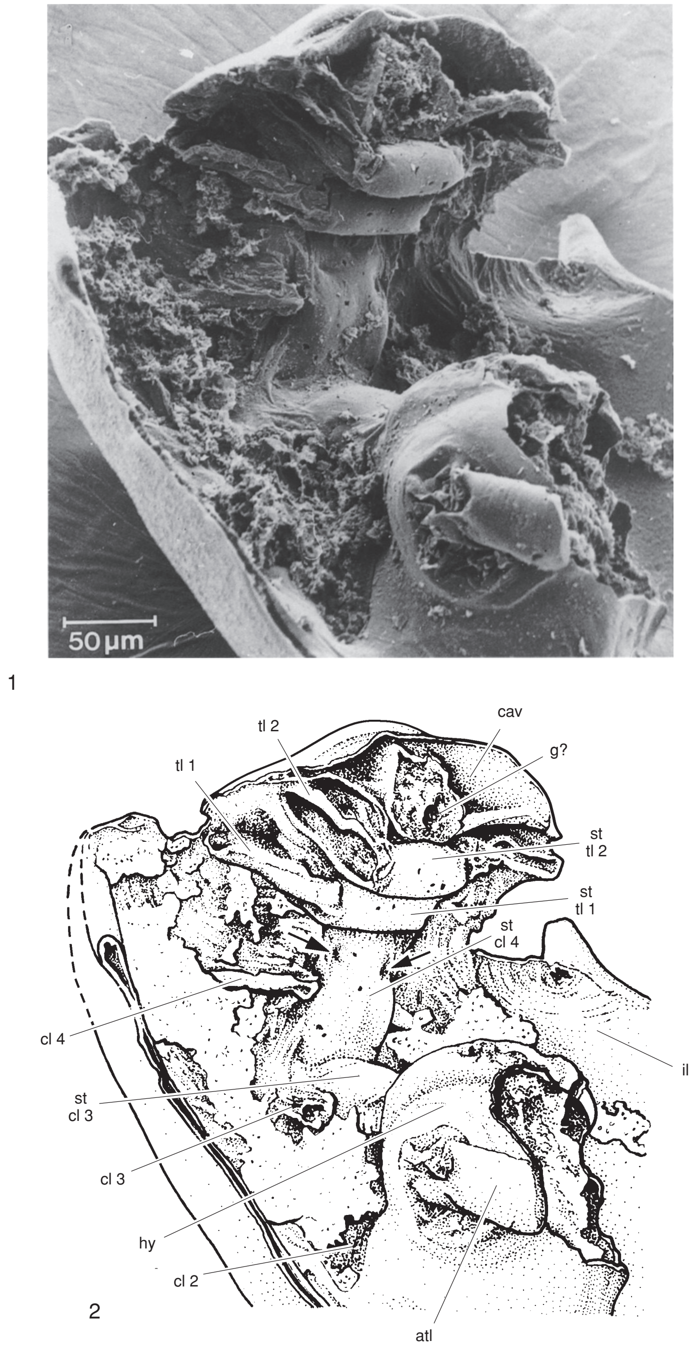


FIG. 77. *Agnostus pisiformis* (WAHLENBERG), Upper Cambrian, Sweden. Portion of enrolled specimen with cephalic border and most of trunk broken off. *1,2,* Photograph and explanatory drawing of interior, with anterior end of cephalon at bottom right. Hypostome (*hy*) and base of first antenna (*atl*) at lower right; insertions of cephalic limbs (*cl 2–4*) and thoracic limbs (*tl 1,2*) indicated. Sternites of the cephalic region (*st cl 3,4*) and trunk (*st tl 1,2*) are preserved in midregion and portions of the ventral cuticle (*il*) abaxially. Limb musculature may have caused the pair of depressions (see *arrows*) in the posterior cephalic sternite. Abbreviations: *cav,* internal cavity; *g?*, probable gut (Müller & Walossek, 1987, pl. 15, fig. 1).

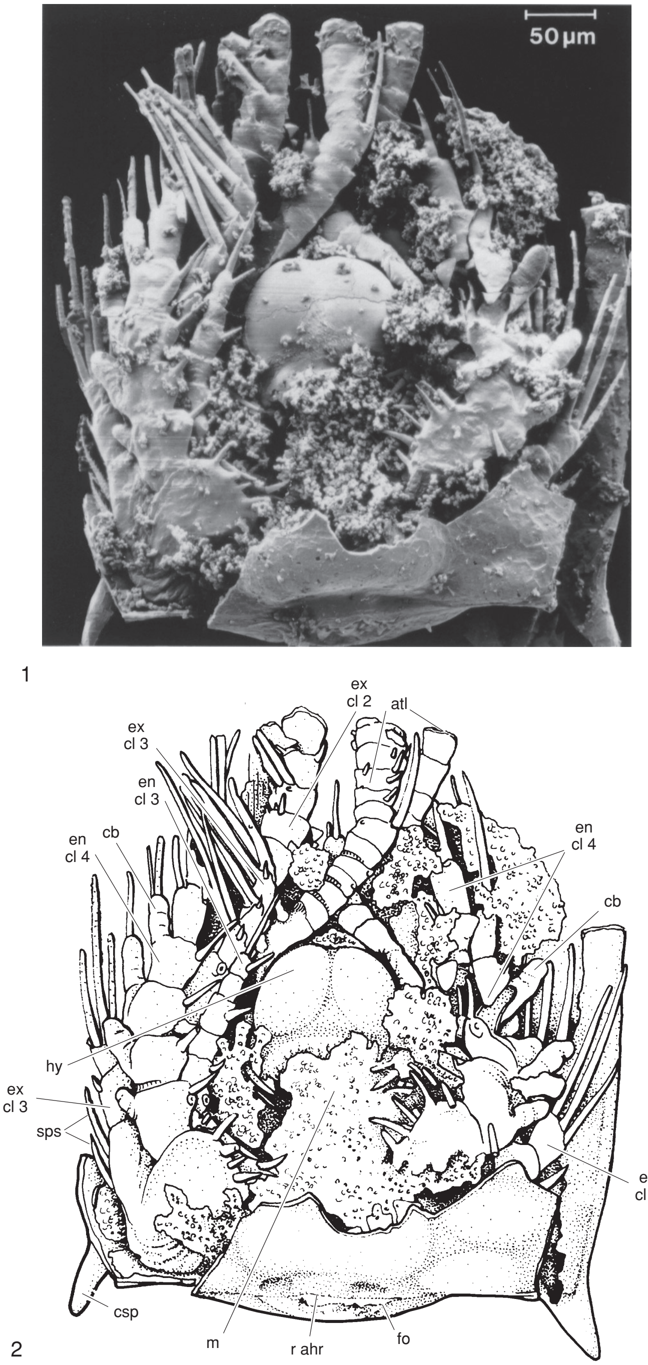


FIG. 78. *Agnostus pisiformis* (WAHLENBERG), Upper Cambrian, Sweden. *1,2,* Photograph and explanatory drawing of enrolled specimen with most of transitory pygidium removed to reveal the anteriorly directed cephalic appendages (*atl,* first antenna; *cl 2–4,* succeeding appendages; *ex,* outer branch; *en,* inner branch). Spines (*sps*) and club-shaped appendages (*cb*) of 4th cephalic appendage are preserved. The position of the mouth (*m*) is indicated. Abbreviations: *hy,* hypostome; *csp,* genal spine; *r ahr,* articulating half ring; *fo,* cephalothoracic aperture covered by membrane (Müller & Walossek, 1987, pl. 16, fig. 3).

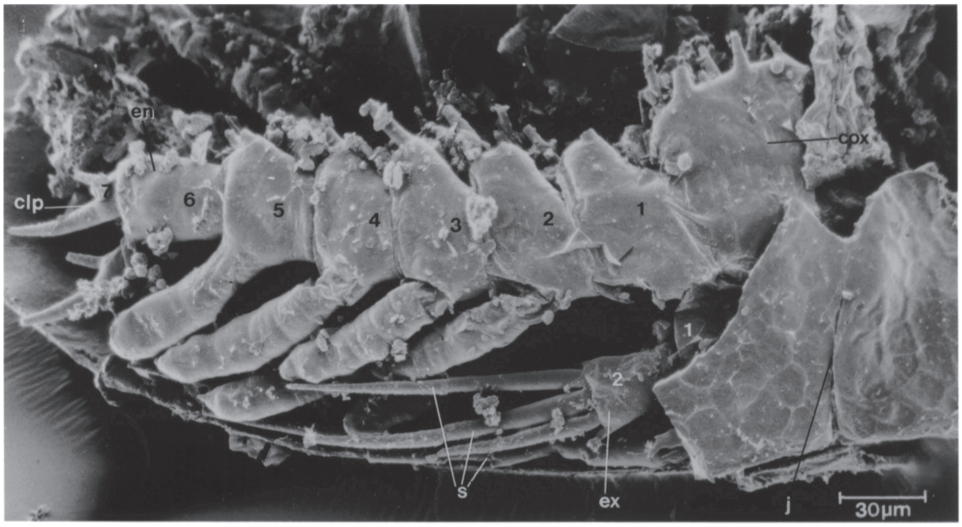


FIG. 79. *Agnostus pisiformis* (WAHLENBERG), Upper Cambrian, Sweden. First trunk limb, including coxa (*cox*), seven podomeres (*1–7*) of the inner branch (*en*), and the clawlike terminal podomere (*clp*). Two podomeres (*1, 2*) of the outer branch (*ex*) and setae (*s*) are preserved (Müller & Walossek, 1987, pl. 24, fig. 1).

podomeres of the distal portion bearing a brush of long setae; the inner branch is reduced to a small hump on the distal rim of the coxa. The third and fourth limbs have successively larger coxae with gnathobases, each pair separated by a sternite. On the third limb an inner branch bearing spines is present (shown only on the right limb in Fig. 82), and on the fourth limb the inner branch (shown only on the left limb in Fig. 82) is longer, having spines on the inner side and clublike projections on the outer side. The outer branch of the third limb is longer than the inner, but on the fourth limb the outer branch is much shorter than the inner branch. Five pairs of trunk limbs, similar to those of the fourth (posterior) cephalic limb, follow; these become progressively reduced in size posteriorly (Fig. 79, 82). In the late meraspid stage, the first of these pairs is on the single thoracic segment, and the fifth limb is rudimentary, not divided into podomeres. In the holaspid stage, the second of these five pairs belongs to the second thoracic segment, and there are three pairs on the pygidium, the last pair a short limb that has developed to become like the fourth limb of the meraspid stage of Figure 82. Sternites separate the thoracic limbs and the first pygidial pair, behind which the axial region narrows rapidly.

A reconstruction of *Olenoides serratus* from the Burgess Shale (WHITTINGTON, 1975, 1980a) shows the multijointed antenna inserted into the ventral cuticle immediately behind the anterior wing of the hypostome and probably linked by muscles to the fossula (Fig. 83). Up to 16 pairs of biramous appendages succeed the antennae, probably three on the cephalon, one on each of seven thoracic segments, and the remainder on the pygidium. Beneath the terminal axial piece of the pygidium one pair of multijointed cerci is attached—a feature unknown in any other trilobite. The biramous limb is borne by a large coxa inserted into the ventral cuticle beneath the axial region, the spinose mesial edges of each pair of coxae close together (Fig. 84). The inner (or leg) branch of the limb is attached to the abaxial edge of the coxa and consists of six podomeres and a group of terminal spines. Clusters of stout spines are present on the ventral side of podomeres 1 to 4. The outer

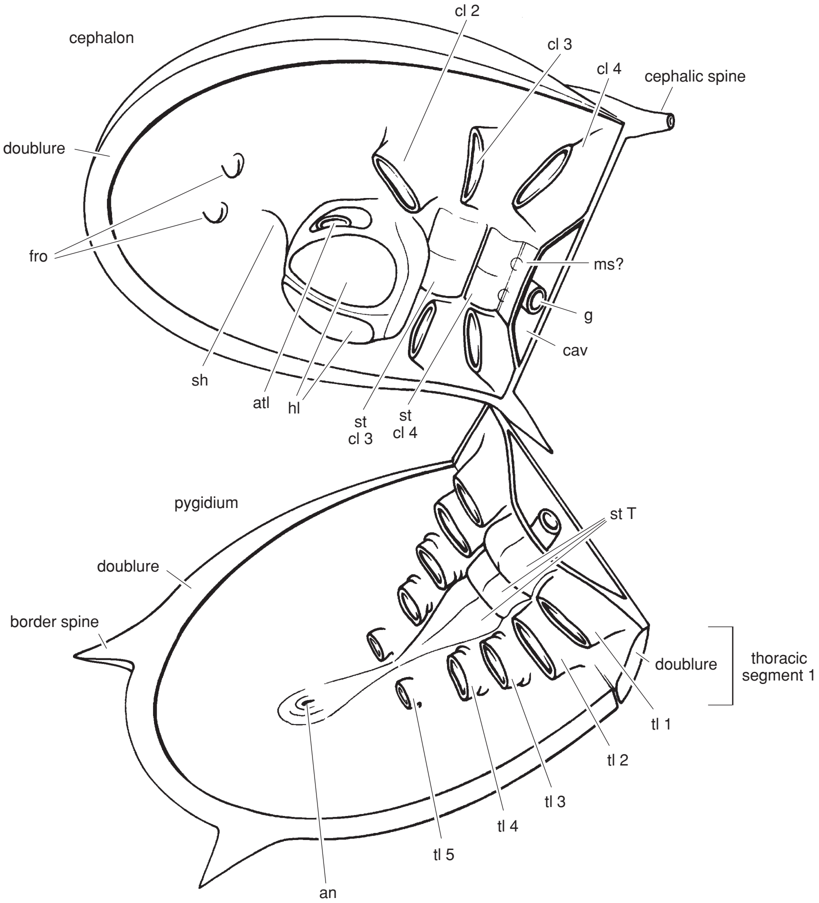


FIG. 80. *Agnostus pisiformis* (WAHLENBERG), Upper Cambrian, Sweden. Internal view of disconnected cephalon, first thoracic segment, and transitory pygidium of a meraspis. The insertions of the antenna (*atl*), cephalic limbs (*cl 2–4*), the limb of the first thoracic segment (*tl 1*), and four limbs of the transitory pygidium (*tl 2–5*) are shown, as well as the shaft (*sh*) and lobes (*hl*) of the hypostome, the frontal organ (*fro*), and the sternites of cephalic limbs (*st cl 3–4*) and trunk (*st T*); probable muscle scars (*ms?*) indicated. The body cavity (*cav*) contained the gut (*g*), which ended at the anus (*an*). Based on a specimen having a cepahlon of length (sag.) 0.64 mm (Müller & Walossek, 1987, fig. 18).

branch of the limb arises from the inner, posterolateral edge of the coxa and consists of an elongate proximal and an oval distal lobe. The proximal lobe bears long, flattened filaments, closely spaced and forming a sheet that was directed backward and slightly upward and was long enough to overlap partly the filaments of the succeeding two limbs. The way in which the series of limbs is preserved provides evidence that the outer branch was attached to the coxa in a manner that prevented it from being rotated or swung to and fro about the junction with the coxa (Fig. 85). The filaments of the outer branches are preserved in an overlapping series between the exoskeleton and the overlapping series of leg branches, never in an alternating series with the leg branches. The excellent preservation of these specimens of *O. serratus* shows details of the spinosity of coxa and leg branch, bristles on the dorsal side of the leg branch, fine hairs at the tips of the lamellae of the outer branch, and bristles on the posterior cercus. The regularity of

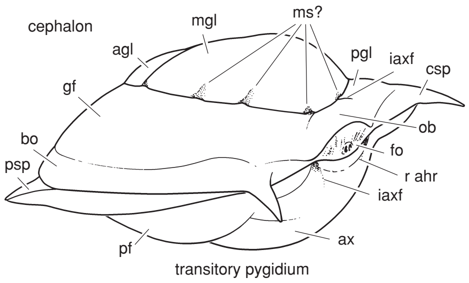


FIG. 81. *Agnostus pisiformis* (Wahlenberg), Upper Cambrian, Sweden. Posterolateral view of an enrolled meraspis, showing cephalon and transitory pygidium before the release of any segments of the thorax. Glabella divided into anteroglabella (*agl*), median portion (*mgl*), and posterior portion divided by intra-axial furrow (*iaxf*) into median occipital band (*ob*) and lateral lobes (*pgl*), probable muscle scars (*ms?*) indicated. Genal region of cephalon divided into genal field (*gf*) and border (*bo*) with genal spine (*csp*); axis (*ax*) of pygidium, pleural field (*pf*), and border spine (*psp*) shown. Abbreviations: *r ahr,* reduced articulating half ring; *fo,* membrane covering cephalothoracic aperture. Based on a specimen having a cephalon of length (sag.) 0.32 mm (Müller & Walossek, 1987, fig. 20).

arrangement of the limb series along the body shows that the limbs were held in position by the ventral cuticle during the processes of preservation. This regularity also suggests that the coxa-body junction was such as to have inhibited rotation about a vertical axis but to have allowed some degree of swing about a transverse axis. The junction itself is not preserved, and any trace of the ventral cuticle extremely rare, a possible example being the dark area surrounding the limbs in one specimen (Whittington, 1975, pl. 11, fig. 1).

The famous specimens from the Upper Ordovician of New York, displaying pyritized appendages, have attracted much attention. Most abundant is *Triarthrus eatoni,* reinvestigated using X-ray stereographs by Cisne (1981). These images were interpreted as showing three (not four as previously believed) pairs of biramous appendages on the cephalon, a coxa that revealed the coxa-body junction, with the two limb branches arising from the outer edge, and a so-called limb-bearing postpygidial abdomen projecting behind the pygidium. The triangular, spinose endites of the leg branch, known from earlier studies, were omitted from Cisne's reconstruction. A more recent investigation, based on mechanical preparation and photographs taken in reflected light (Whittington & Almond, 1987) has supported Cisne's view on the number of pairs of biramous limbs on the cephalon and has shown the prominent endites on posterior leg branches. It was considered that Cisne's portrayal of the coxa and of the postpygidial abdomen were based on misinterpretations of X-ray stereographs. The new reconstructions of *Triarthrus eatoni* (Fig. 86–87) may be compared and contrasted with that of *Olenoides serratus* as follows.

The cephalon of *Triarthrus eatoni* also has one pair of uniramous antennae and three pairs of biramous limbs and the thorax has one pair of limbs on each segment. The relatively smaller pygidium has 10 or more pairs of limbs that are crowded together, diminishing rapidly in size posteriorly. Posterior cerci are absent. The coxa is also relatively large and spinose on the adaxial edge; but the proximal three or four podomeres of the inner branch are extended ventrally as spinose **endites,** most prominent posteriorly, diminishing progressively anteriorly and disappearing on the cephalon (Fig. 86.3–5). The outer branch of the limb in *T. eatoni* (Fig. 87) consists of an annulated shaft (not a proximal lobe) and small distal lobe and is as long (tr.) as the leg branch; the shaft bears flattened, closely spaced filaments that extend back above those of the succeeding branch. As seen in lateral view, the outer branch in *T. eatoni* is exposed to a far greater extent than that of *O. serratus* (compare Fig. 86.2 with Fig. 83.2), and the long shaft is curved down distally (compare Fig. 87 with Fig. 84). Preservation of *T. eatoni* indicates that, as in *O. serratus,* the outer branch was rigidly attached to the coxa and the filaments formed an overlapping series dorsal to the inner branches. The coxa-body junction and ventral cuticle are not preserved in either species.

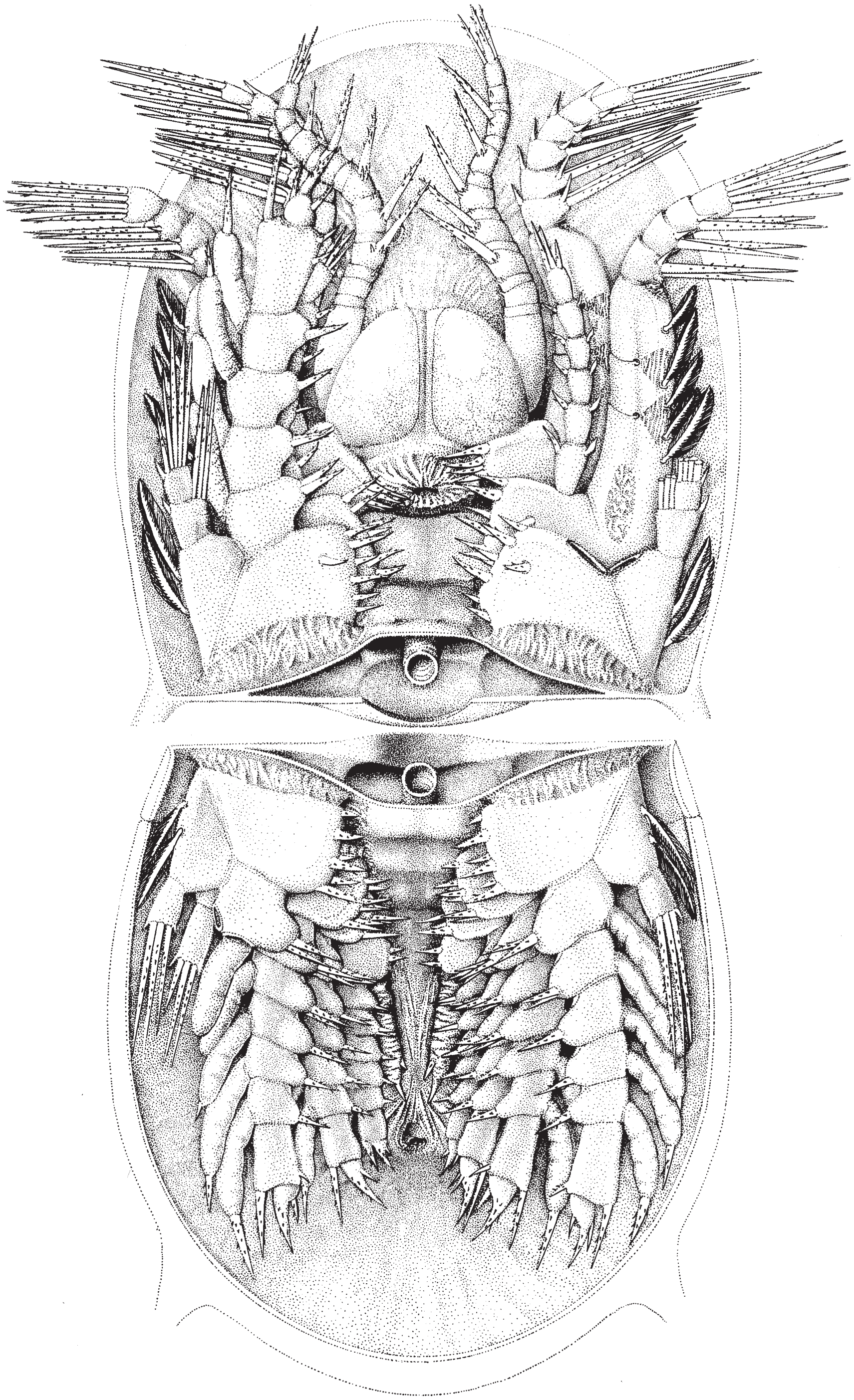


FIG. 82. *Agnostus pisiformis* (WAHLENBERG), Upper Cambrian, Sweden. Ventral view of reconstruction of meraspis with one thoracic segment, disconnected between cephalon and segment. Based on a specimen having a cephalon of length (sag.) 0.74 mm (Müller & Walossek, 1987, fig. 4).

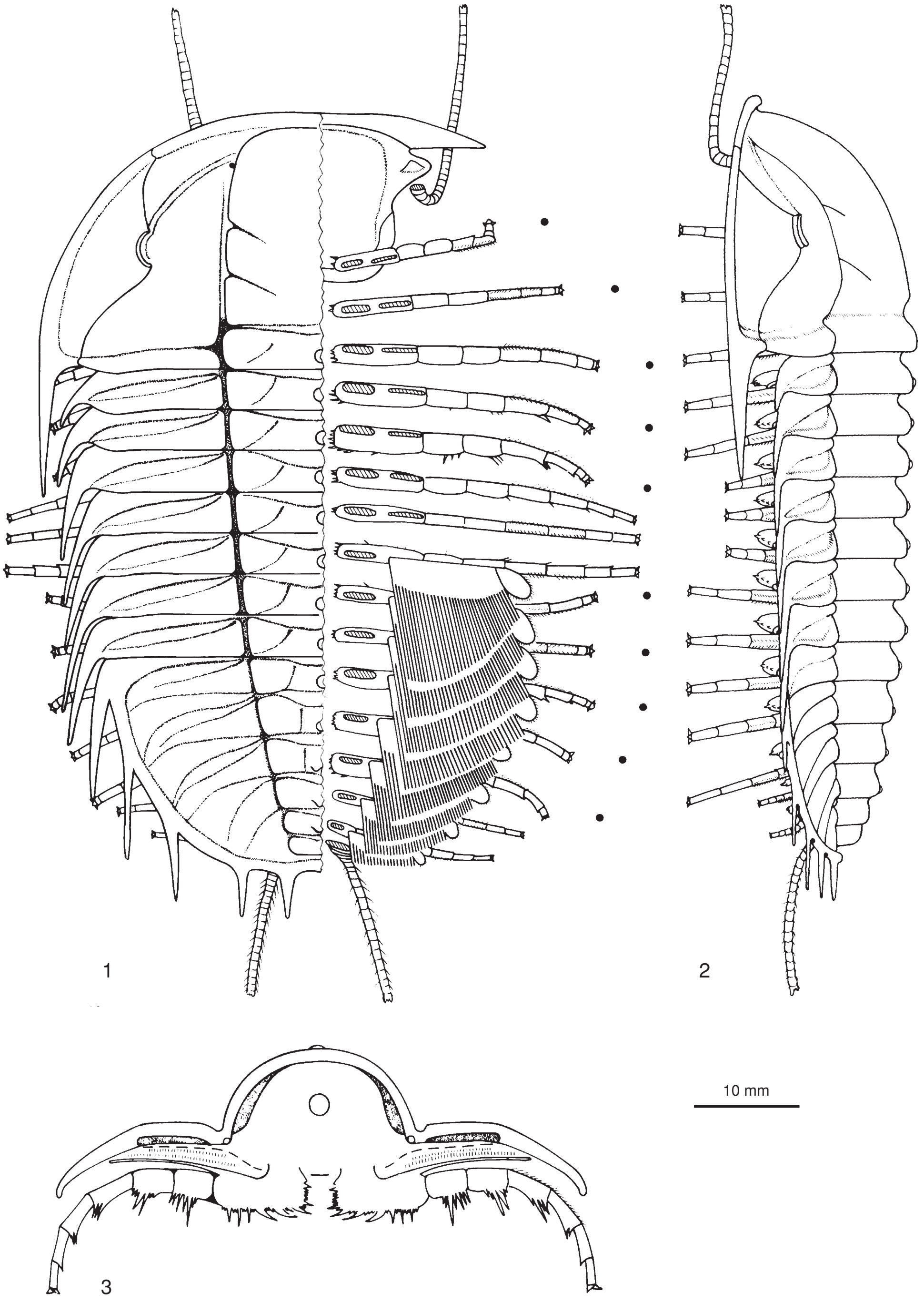


FIG. 83. *For explanation, see facing page.*

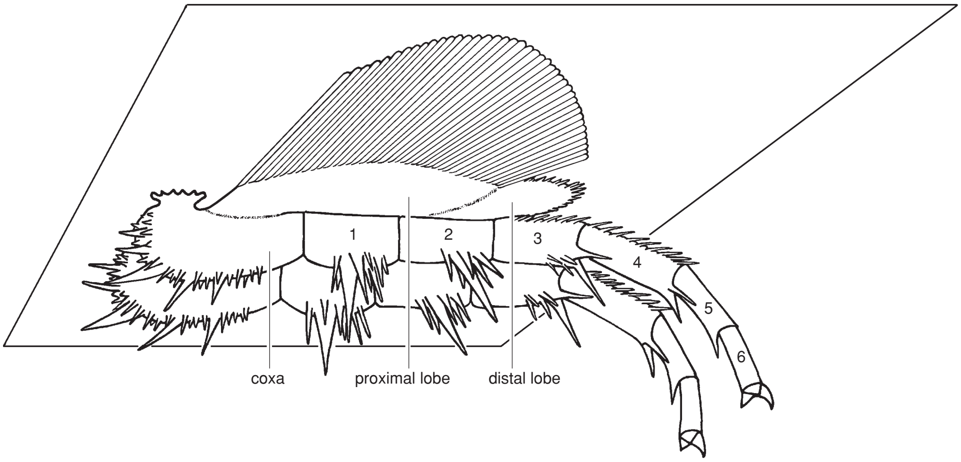


FIG. 84. *Olenoides serratus* (Rominger), Middle Cambrian, Canada. Restoration of two pairs of right appendages, as seen from below and behind; horizontal plane indicated by outline. Inner branch shows coxa and podomeres 1 through 6, podomere 6 with terminal spines. Only the outer branch of the nearer limb is visible in this view, divided into proximal and distal lobes, the long, flat filaments overlapping (Whittington, 1980a, fig. 8).

Of the trilobites with pyritized appendages from the Hunsrück Shale of West Germany, *Phacops* (Stürmer & Bergström, 1973) is most abundant and best known (Fig. 88). There is one pair of multijointed antennae and three pairs of biramous limbs on the cephalon, one pair of such limbs on each thoracic segment, and at least eight pairs on the pygidium. These posterior limbs diminish in size rapidly and are crowded together posteriorly. A spinose gnathobase has been observed at the adaxial end of the large coxa of the posterior cephalic limb. The inner branch of the limb has six podomeres and a short, distal, seventh podomere surrounded by a ring of fine bristles (Seilacher, 1962). Triangular spinose endites have been observed on distal podomeres of inner branches on posterior thoracic segments. The outer branch appears to have consisted of a relatively short (tr.) basal lobe attached to the coxa, from which long filaments are outwardly directed. The appendages of *Asteropyge* (Stürmer & Bergström, 1973) are less well known, but one specimen has a single pair of antennae and three pairs of biramous limbs on the cephalon. The single pair of antennae and the series of coxae and inner branches of the limbs of *Rhenops* were described by Bergström and Brassel (1984). It is considered that there were four pairs of biramous limbs on the cephalon. Nine or more pairs were crowded together on the pygidium and show a rapid reduction in size posteriorly; endites were developed on the more proximal podomeres.

FIG. 83. Reconstruction of *Olenoides serratus* (Rominger), Middle Cambrian, Canada. *1,* Dorsal view with right half of exoskeleton removed to show appendages and inner view of rostral-hypostomal plate. Antenna and posterior cerci incomplete; *diagonal shading* shows coxa-body junction and bases of outer branches of appendages 1 through 7 where removed. Appendages are shown in a still position of a particular gait (*solid circle* in transverse line with tip of inner branch indicates tip is stepping on sea floor; other branches are swinging forward in a recovery phase). *2,* Left lateral view of animal as shown in part 1. *3,* Posterior view of first thoracic segment, coxa and inner branch of appendage, cross section of ventral cuticle (*dashed line*), and cross section of outer branch of appendage. Between this outer branch and cuticle are cross sections of filaments of next two anterior branches of appendages (Whittington, 1975, fig. 25, 26b,e).

FIG. 85. *Olenoides serratus* (ROMINGER), Middle Cambrian, Canada. Portion of the counterpart of a specimen (GSC 34694; see WHITTINGTON, 1975, 1980a), showing the regular manner in which the series of inner branches of the appendages are arranged and posteriorly the outer branches and posterior cercus (Whittington, 1980a, pl. 20, fig. 4).

Enrolled specimens of *Ceraurus* that contained pyritized appendages were investigated (STØRMER, 1939, 1951) using serial sections; models were made from these sections. STØRMER concluded that the cephalon has one pair of antennae and four pairs of biramous appendages, with similar pairs of biramous limbs on each thoracic segment. From the large coxa arises an inner branch of six podomeres and a terminal group of spines (Fig. 89). The outer branch arises from the inner, posterior side of the coxa and consists of four podomeres and a terminal lobe bearing long, closely-spaced blade-shaped filaments. In his 1939 account STØRMER emphasized the presence of a short, precoxal podomere (Fig. 90) but was less certain about the existence of such a joint in 1951. No evidence for the presence of this joint has been put forward subsequently, but the most proximal portion of the coxa has not been clearly exposed in any specimen.

The single specimen of *Kootenia* from the Middle Combrian Burgess Shale has been redescribed (WHITTINGTON 1975), and most recently two species of redlichioids showing the antenna and biramous limbs from the Lower Cambrian of South China (SHU & others, 1995). Other species showing appendages from the Ordovician Frankfort Shale need reinvestigation. For example, three different interpretations (BERGSTRÖM, 1972, fig. 2; 1973a, fig. 15; CAMPBELL, 1975, fig. 13) of the appearance of the limbs of *Cryptolithus* have been made subsequently to RAYMOND's (1920, fig. 20) reconstruction, none based on a critical reexamination of the original material. BEECHER's (1895b) and

RAYMOND's work make it clear that endites are developed on the inner branches, most conspicuously on the pygidium.

The limbs of two additional species from the Burgess Shale are trilobite-like, though the exoskeleton is not mineralized. Best known of these is *Naraoia compacta,* which has an oval exoskeleton divided by a simple articulation into two shields (Fig. 91). Beneath the anterior shield are the multijointed antenna and three pairs of biramous limbs; below the posterior shield are up to 16 similar pairs of limbs that diminish in size posteriorly. Each biramous limb is borne on a large, triangular coxa that is spinose on the inner, adaxial side (Fig. 92). The inner branch consists of five podomeres and a short terminal spine. The proximal podomere of the inner branch is enlarged into a triangular, spinose endite. The outer branch arises from the dorsal coxal margin and consists of a slim, tapering shaft with a terminal lobe; the dorsal margin of the shaft bears many long, thin, upward and backwardly directed filaments. The outer branches form an overlapping series that lies beneath the pleural regions of the body. The limbs of the Lower Cambrian species of *Naraoia* from Yunnan, China (W. ZHANG & HOU, 1985) have not been described in detail, but these specimens show the hypostome and a filled alimentary canal.

Only two specimens of the unusually large *Tegopelte gigas* are known from the Burgess Shale (Fig. 93). The appendages include a multijointed antenna and a long series of biramous limbs, diminishing in size posteriorly, the inner branch of which is a jointed walking leg, the outer branch being a shaft bearing long, slim filaments. In this restoration the dorsal exoskeleton is shown divided into cephalon, three thoracic segments, and pygidium. There appears to have been three pairs of biramous limbs on the cephalon, three beneath each thoracic segment, probably four beneath the third segment, and up to 20 pairs on the pygidium. RAMSKÖLD and others (1996) contended that the features interpreted as subdivisions between tergites in *Tegopelte* are preservational artifacts and that the dorsal exoskeleton was undivided. This view is based on an interpretation of the features observed in the dorsal shields of other arthropods (not *Tegopelte*) preserved in the Lower Cambrian Chengjiang fauna of China.

The evidence reviewed above suggests that a single pair of uniramous antennae and many pairs of biramous limbs are characteristic of trilobites. The antenna is attached behind the anterior wing of the hypostome, the first biramous limb beside the posterior portion of the hypostome. The preservation of *Agnostus pisiformis* is such as to show unequivocally that there are three pairs of biramous limbs on the cephalon, but whether three pairs are characteristic of all trilobites is an unsolved question. During the processes of preservation (WHITTINGTON, 1975, p. 102–105; WHITTINGTON & ALMOND, 1987, p. 5–7) the entire series of limbs was held in their original relationship to one another by the ventral cuticle, but this cuticle and the attached appendages may have been moved in relation to the dorsal exoskeleton. Hence, it is difficult to be sure, in any one specimen, how appendages and exoskeleton were related. The weight of evidence available at the time of writing, however, points to three pairs of biramous appendages on the cephalon as having been characteristic of many, if not all, trilobites. The manner of preservation of the outer branch also suggests the relative stiffness of the long, slim filaments attached to it. These filaments are most frequently preserved in overlapping, backwardly directed sheets, always lying immediately below the pleural regions, between exoskeleton and inner branches. There is no evidence that the sheets of filaments were ever directed downward between the inner branches. Alignment of inner and outer branches is characteristic, arguing for a relatively rigid attachment of outer branch to coxa. The original form of the filament of the outer branch—flat sided, bladelike, and suboval or subcircular in section—is less certain. Compressed specimens suggest that

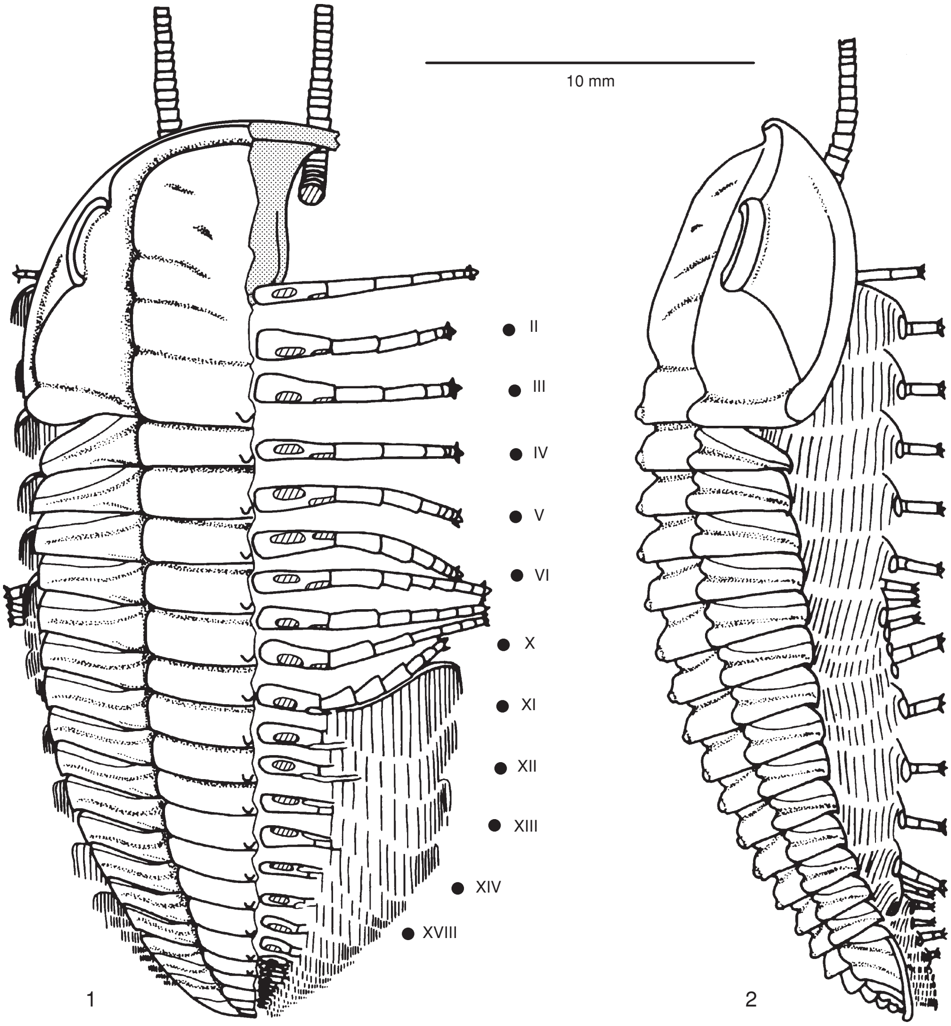


FIG. 86. Restoration of *Triarthrus eatoni* (HALL), Upper Ordovician, New York State, USA. *1,* Dorsal view, in still position of particular gait, with exoskeleton of right side removed to show hypostome and doublure (stippled) and appendages; antennae incomplete. Outer branch of right biramous limbs I through IX removed to show attitude of inner branches. *Solid circles* and *numbers* are opposite tips of inner branches that are on substrate; *diagonal shading* indicates coxa-body junction and base of outer branch where removed. *2,* Right lateral view of part 1; exoskeleton complete; outer branches diagrammatic. *3–5 (see facing page),* Cross sections through exoskeleton, showing respectively biramous limbs III, XI, and XVIII in posterior view with inner branches vertical. *Dashed lines* indicate ventral cuticle and section through alimentary canal; filaments and divisions of outer branch omitted (Whittington & Almond, 1987, fig. 38a, 39a,c,e,f).

they were slatlike (WHITTINGTON, 1980a, p. 189; WHITTINGTON & ALMOND, 1987, p. 38), and cross sections suggested the same form to STØRMER (1939, p. 184, fig. 11, 14), while CISNE (1982) argued from cross sections that the form was elongate-cylindrical.

AXIAL REGION AND ALIMENTARY CANAL

Only in *Agnostus pisiformis* is some trace of the unmineralized ventral cuticle of the axial region preserved (Fig. 77). In these remark-

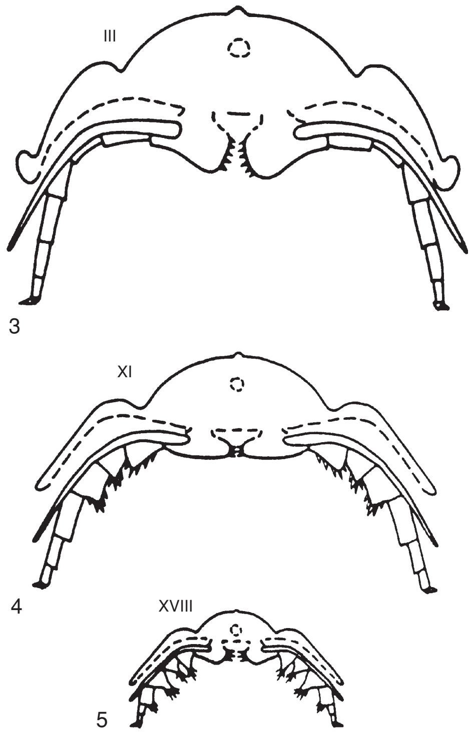


Fig. 86 (continued). *For explanation, see facing page.*

able specimens the mouth opening on the posterior side of the hypostome, the anus, and some trace of the alimentary canal may be seen. In addition, between the coxae of the third and fourth cephalic appendages and between those of the thorax and first pygidial appendage are gently convex sternites, separated from one another by a transverse furrow. Behind the posterior sternite the axial region becomes lower and tapers towards the anus.

A trace of the presumed infilling of the alimentary canal, extending from the anterior lobe of the glabella to the tip of the axis, was first described by Barrande (1852, pl. 30, fig. 38–39) in the trinucleid *Deanaspis goldfussi*. An additional specimen was figured by Přibyl and Vaňek (1969, p. 88, pl. 8, fig. 1) and many more by Šnajdr (1991). These latter show molds of the hypostome and digestive tract, one specimen showing pellets in the posterior portion of the tract, which differ in color and petrographic character from the sandy matrix. A single specimen of *Dalmanitina* also shows a mold of the canal in the thorax and pygidium. A similar trace has been described in *Naraoia compacta* (Whittington, 1977). Pyrite-filled or lined structures in *Phacops* are interpreted as showing the esophagus leading forward from the mouth above the posterior edge of the hypostome to the stomach beneath the anterior portion of the glabella, with ramified structures interpreted as the liver (Fig. 94). The intestine leads back from the stomach to the posterior tip of the pygidial axis (Fig. 88). The alimentary structures of trilobites were reviewed, and a description of these structures in a species of the Upper Cambrian *Pterocephalia* were given by Chatterton, Johansen, and Sutherland (1994). Stürmer and Bergström (1973, p. 113) considered that there was no evidence of a **metastome,** a postoral plate; and investigations of *Olenoides serratus* (Whittington, 1975) and *Triarthrus eatoni* (Whittington & Almond, 1987) have likewise shown no evidence for the existence of such a plate.

PLEURAL REGION, CAECA, AND PANDERIAN OPENINGS

In *Agnostus* (Müller & Walossek, 1987, p. 11) the unmineralized ventral cuticle is preserved, extending from the inner edge of the doublure to the axial region. Müller and Walossek emphasized that this cuticle lies close below the exoskeleton, so that the body was thin in the pleural region, a necessity if the limbs were to be accommodated during enrollment. Arguments used in reconstructing *Triarthrus* (Whittington & Almond, 1987, p. 30, 39) suggest that the bodies of most trilobites may have been shallow in the pleural region (Fig. 86). As the cross sections show (Fig. 86.3–5), this shape would have allowed a hanging stance of the inner, walking leg branches. In this stance (Manton, 1977, p. 200) the leg was at first directed upward from its origin and then curved downward so that it kept the ventral surface

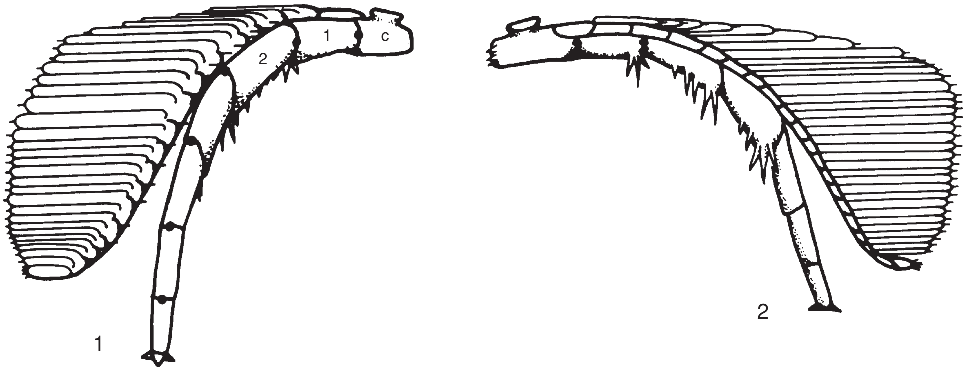


Fig. 87. Restoration of biramous limb from anterior portion of thorax of *Triarthrus eatoni* (Hall), Upper Ordovician, New York State, USA. *1,* Oblique anterolateral view; *2,* oblique view from behind in the midline. *Solid circles* show positions of pivot joint between coxa (*c*) and podomere 1, between podomeres 1 and 2, and of hinge joints between distal podomeres (Whittington & Almond, 1987, fig. 41).

of the body as close to the substrate as possible, promoting stability in cross currents. The shallow body and the flexible ventral cuticle were also necessary to allow the limbs, including the antennae, to be packed inside when the animal was completely enrolled. In trilobites in which the pygidial doublure extended inward almost to the axis (Fig. 61), the body in the pleural region was necessarily shallow. In trilobites in which the border of the cephalon or pygidium was convex, with a convex, rolled doublure below it, there was evidently a deeper, cylindrical, peripheral section of the body. This section did not extend along the tips of the thoracic pleurae.

Ridges on the external surface of the gena (including the coarse, ramifying, radiating rugae in certain Agnostina) and the genal caeca (Fig. 17) have been described above. Rugae are present on the pygidium of Agnostina, and ridges of similar dimension to the genal caeca are present on thoracic segments and pygidium (Fig. 60) of other trilobites. Öpik (1961a) considered all these impressions to be of alimentary diverticulae, by analogy with the pattern of such diverticulae in *Burgessia* (C. P. Hughes, 1975) and *Naraoia* (Fig. 91). Campbell (1975) suggested that the fringe of the trinucleid *Cryptolithus* contained ramifying digestive caeca and also outlined possible arterial and venous systems that were within the fringe and below the gena. Jell (1978a; see also Chatterton, Johansen, & Sutherland, 1994) pointed out the difference in width between the coarse rugae of Agnostina and the much finer, branching and anastomosing ridges of the genal caeca in, for example, *Harpides.* He advocated distinguishing between traces of alimentary diverticulae, the coarse ridges and grooves in Agnostina (of uncertain function), and the pattern of finer ridges to which he limited the term genal caeca. He went on to suggest, using analogies with living crustaceans, that the genal caeca were respiratory in function (auxiliary to the outer limb branch), housing a venous system that lay close beneath the exoskeleton. Such a system would have remained exposed to the surrounding water when the animal was fully enrolled.

An opening in the cephalic and pleural doublure of certain asaphids (Siegfried, 1936; Hupé, 1955b) is called the panderian opening and is the supposed opening of a segmental panderian organ. This opening may have, immediately behind it, a protuberance that acted to limit enrollment. In other asaphids there is a notch in the inner margin of the doublure, the posterior edge of the notch raised so that it limited enrollment. The notch has been regarded as surrounding a panderian opening, and the term

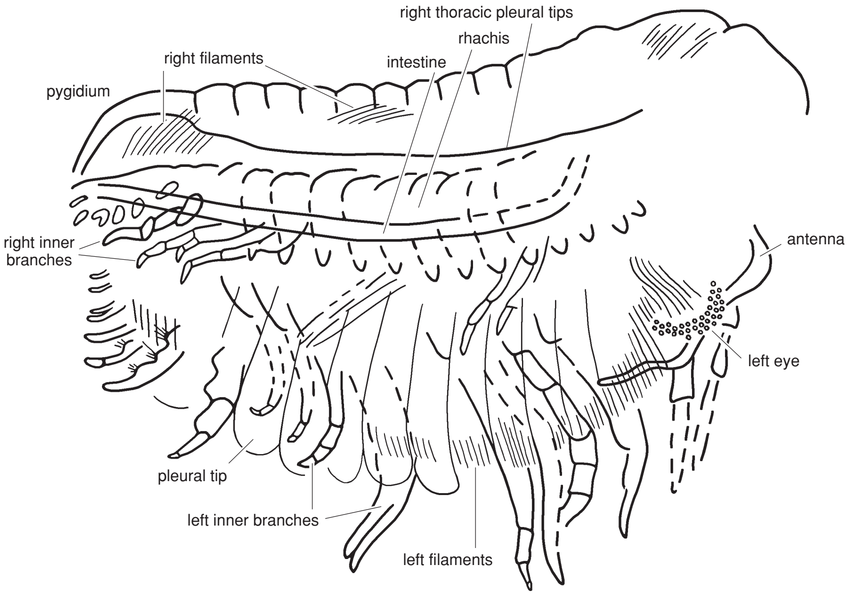


FIG. 88. *Phacops* sp., Lower Devonian, Germany. Drawing from radiograph of a pyritized specimen, buried obliquely so that it is seen from below on the right side. Only the distal portions of the inner limb branches and of the filaments of the outer limb branches are shown (Stürmer & Bergström, 1973, pl. 17b).

panderian notch has hence been applied to similar notches in the doublure of a wide variety of trilobites. Whether the notch in *Proetus,* for example (Fig. 40), surrounded a panderian opening is unknown, and hence whether the so-called panderian organ was present only in some asaphids, or generally in trilobites, may be questioned. HUPÉ (1945, 1955b) suggested that there was no opening, but merely thinner cuticle, associated with a sensory device that detected pleural overlap.

Fenestrae, oval or slitlike unmineralized areas of the exoskeleton of the inner pleural region, situated along the intersegmental boundaries, have been described in asteropyginids and odontopleurids (see earlier sections on thorax and pygidium, p. 43, 59). Best preserved are those in the odontopleurid *Laethoprusia salax* (RAMSKÖLD, 1991a), in which the edges of the opening curve down ventrally, the edge in the pleura continuous with that of the articulating flange and similar in form. RAMSKÖLD speculated that the openings may have been covered by arthrodial membrane; the function of the opening is obscure.

MUSCULATURE, FLEXURE OF BODY, AND LIMB MOVEMENTS

The form of muscle scars and of invaginations of the exoskeleton (furrows, pits, and apodemes) in and adjacent to the axial region of the exoskeleton (Fig. 8, 10, 20, 26, 51) has been revealed more clearly by silicified specimens (Fig. 26.1, 38–39). These attachment areas, symmetrically arranged in the axial region, rarely median, were for muscles extrinsic to the limbs and other organs of the body and for muscles and ligaments that extended the body and maintained its form. CISNE (1974, 1975, 1981) detected the remains of such muscles in pyritized specimens of *Triarthrus*, but in almost all species in which muscle areas have been observed, traces of soft parts, including appendages, are unknown. Hence, speculations on trilobite musculature have had to

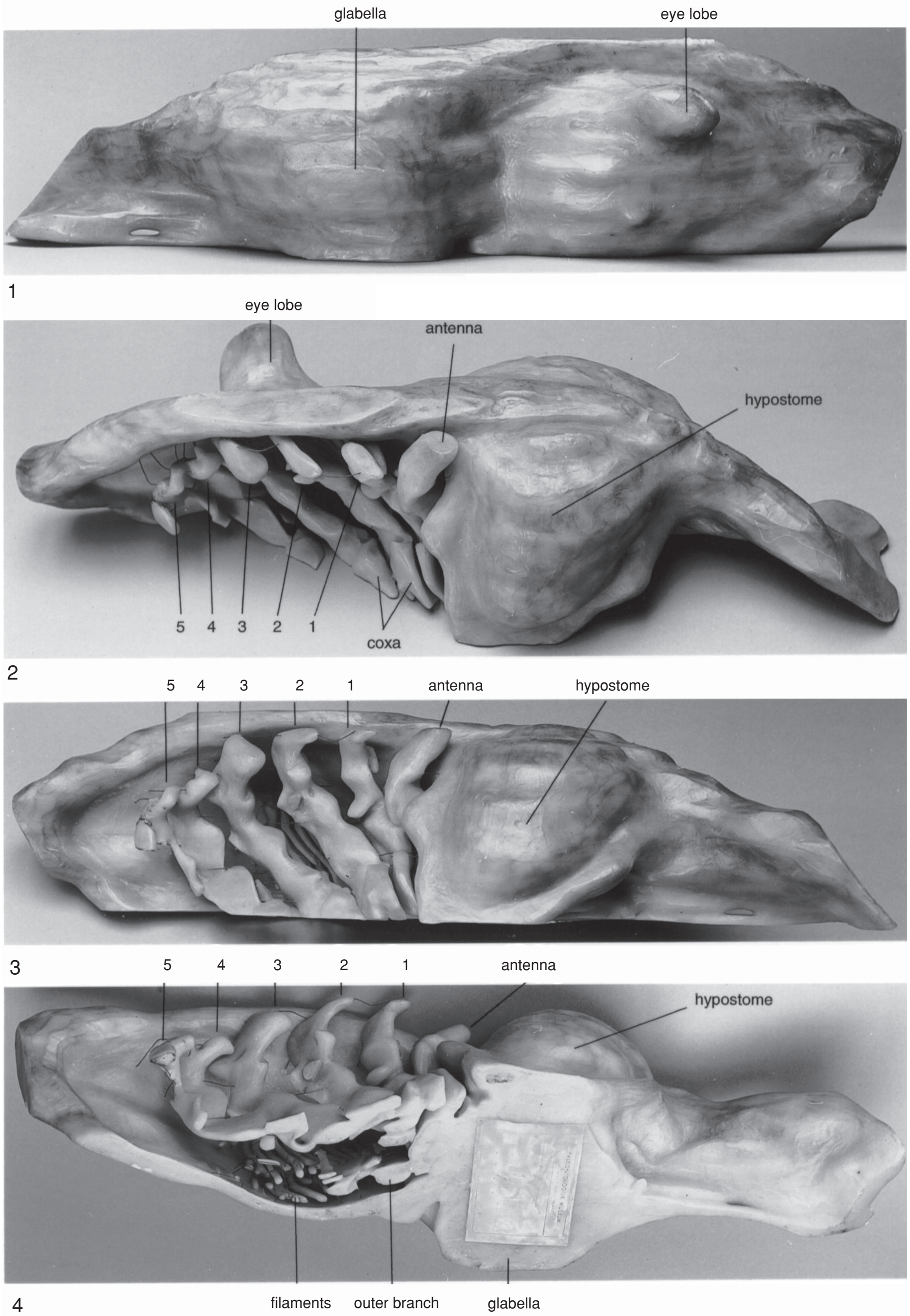


FIG. 89. Wax model (STØRMER, 1951, fig. 2, pl. 2) of part of the cephalon of *Ceraurus pleurexanthemus* GREEN, Middle Ordovician, New York, USA. *1,* Dorsal view; *2,* anterior view; *3,* ventral view; *4,* posteroventral view. *1–5,* inner branches of first 5 limbs (photographs courtesy of Per Aas, Paleontological Museum, Oslo, Norway).

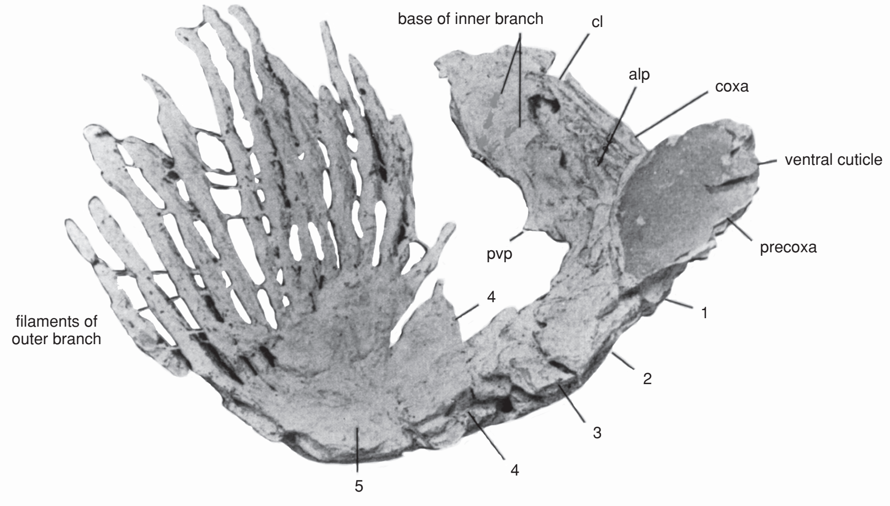


FIG. 90. *Ceraurus pleurexanthemus* GREEN, Middle Ordovician, New York State, USA. Dorsal view of wax model of third thoracic appendage, showing coxa with supposed precoxa and position of junction with ventral cuticle. Only part of the basal podomere of the inner branch is preserved, but podomeres 1 through 5 and filaments of the outer branch are shown. Abbreviations: *alp,* anterolateral process of coxa; *cl,* condyle; *pvp,* postventral process of coxa (Størmer, 1939, pl. 5, fig. 3).

rely on comparisons with extant animals and have been greatly stimulated by the work of HESSLER (1964, 1982) and MANTON (1977). In his X-ray stereographs CISNE (1981) also observed transverse endoskeletal bars, these bars situated on the ventral side of the body adjacent to the intersegmental boundaries. To these bars were attached the ventral longitudinal muscles, dorsoventral muscles (anteriorly descending, vertical, posteriorly descending), horizontal muscles, and ligaments supporting the ventral cuticle (Fig. 95). Such musculature is like that described in living crustaceans by HESSLER and was also proposed by CAMPBELL (1975, 1976, 1977). The recent discovery (WHITTINGTON, 1993a) of a specimen of *Placoparia,* apparently having the endoskeletal bars preserved as external molds, lends support to such reconstructions. Extrinsic limb muscles may also have been attached to these bars, as well as to the infold of the glabellar, occipital, and articulating furrows.

Enrolled specimens of *Placoparia* are well known (e.g., HENRY & CLARKSON, 1975), and a reconstruction shows the arc through which the body was curved and how the relaxed limbs would have been packed tightly within the enclosing capsule (Fig. 96). As HESSLER (1964, 1982) pointed out, the dorsoventral muscles and ligaments were essential to maintain the shape of the body against the pull of the contracted ventral longitudinal muscles. On enrollment the portion of the axial body below the hinge line was reduced in volume, and the larger portion above this line increased in volume. The net effect of this volume change may have reduced hydrostatic pressure within the body, facilitating enrollment and relaxation of the limbs. The fully enrolled position appears to have been essentially temporary, held by the continued contraction of the ventral longitudinal muscles. Extension of the body was effected by contraction of the dorsal longitudinal muscles, aided by contraction of the anteriorly descending dorsoventral muscles, which lay above the hinge line. The volume changes in the body, referred to above, would have been reversed, increasing the hydrostatic pressure as the dorsoventral muscles contracted to maintain the body

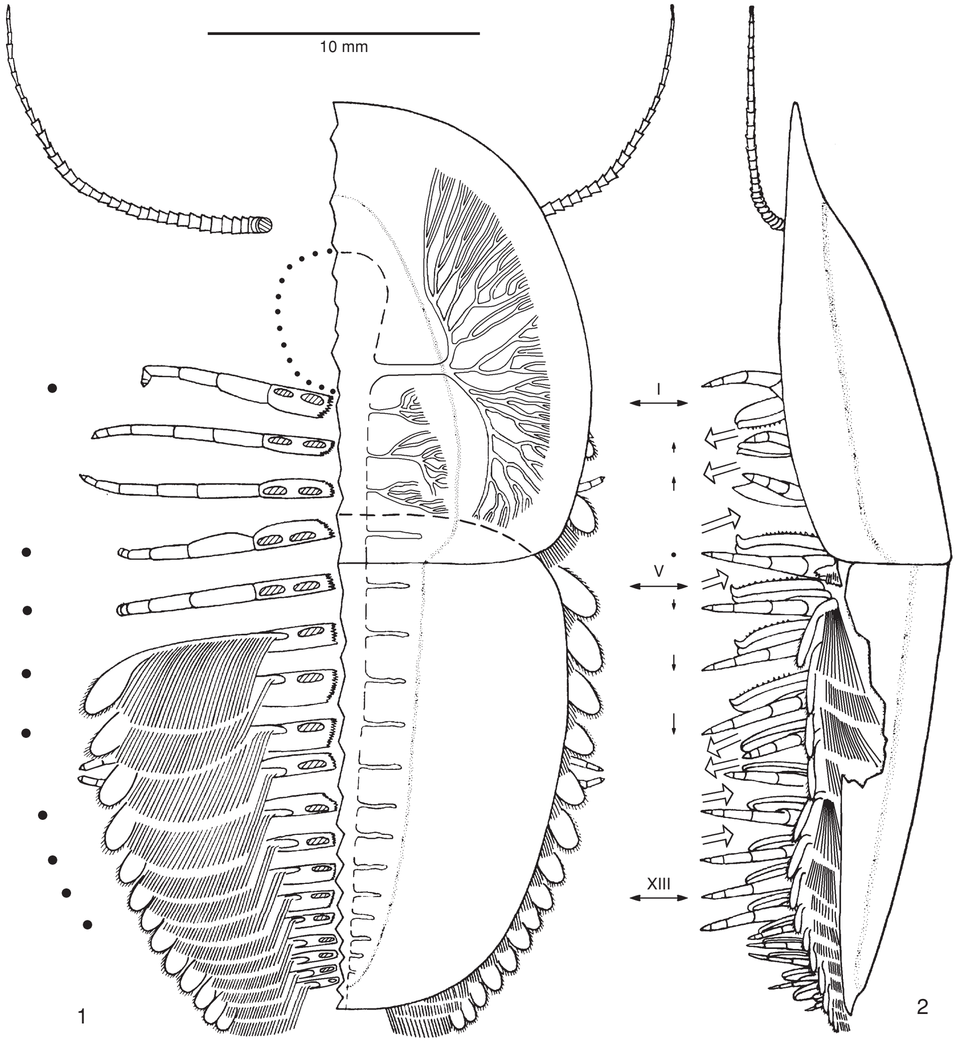


FIG. 91. *Naraoia compacta* WALCOTT, Middle Cambrian, British Columbia, Canada. *1,* Reconstruction in dorsal view, with left half of body cut away to show appendages below; insertion into ventral cuticle is *diagonally shaded.* Outer branches of biramous appendages I through V removed (insertion in coxa *diagonally shaded*). On right side *dashed line* shows outline of alimentary canal, from which diverticula arise. On left side hypostome outlined by *dotted line.* Biramous appendages shown in still position of a particular gait; *solid circle* in transverse line with tip of inner branch that is in contact with sea floor. *2,* Reconstruction in left lateral view, with outer branches of appendages I through III removed, of IV partly cut away, and part of posterior shield cut away to show appendages more completely. Biramous appendages II to VII are in different positions of one metachronal wave, the *arrows* under the tip of each inner branch showing the direction and amount of swing passed through, the *dot* under branch IV indicating the beginning of the remotor stroke. *Arrows with double shafts* indicate directions of water currents caused by movement of limbs; *numbers I, V, XIII* above *horizontal arrows* identify the cross sections shown in Figure 92 (Whittington, 1977, fig. 96).

shape; the increased hydrostatic pressure would have aided the extension. In walking, both dorsal longitudinal and dorsoventral muscles would have been active in keeping the body extended and maintaining its shape and internal pressure. It was considered by STØRMER (1939, fig. 7d) and HUPÉ (1953b, fig. 29) that extension of the body was aided

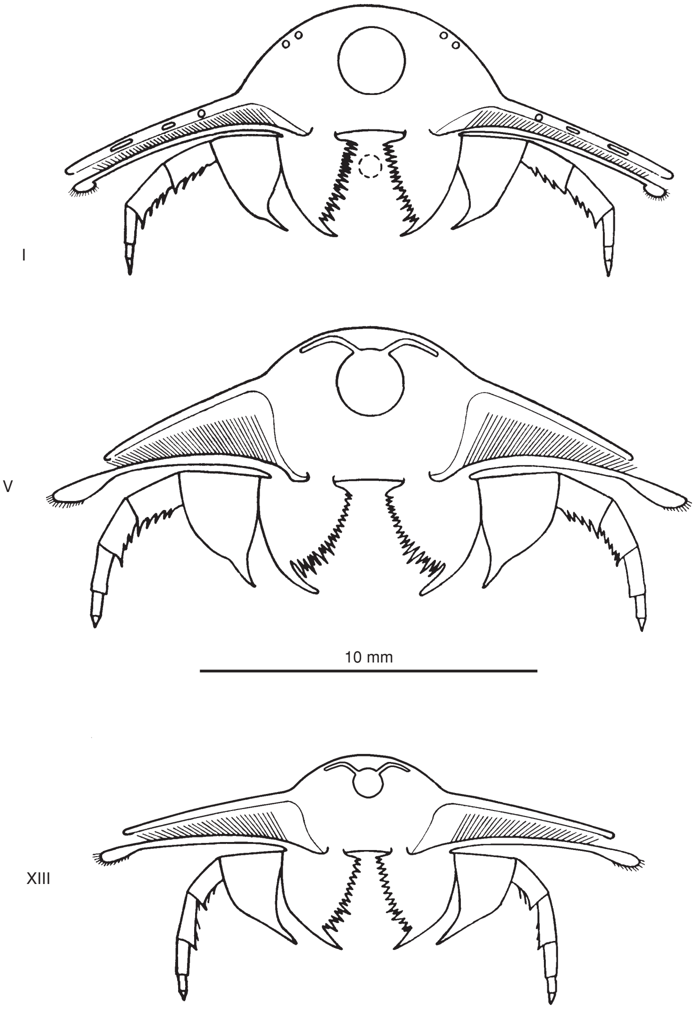


FIG. 92. *Naraoia compacta* WALCOTT, Middle Cambrian, British Columbia, Canada. Three cross sections (at biramous appendages I, V, and XIII) of the same individual shown in Figure 91. In each section the pair of appendages is seen in posterior view, the alimentary canal and diverticula *outlined;* the *dashed circle* in first cross section indicates the position of the mouth, situated a short distance in front of the section (Whittington, 1977, fig. 97).

by the contraction of auxiliary or external dorsal muscles. These were shown attached to the anterior edge of each articulating half ring and the articulating (or occipital) furrow of the segment in front. CAMPBELL (1975, p. 77; 1976, p. 173–174) argued that such muscles were necessary in *Cryptolithus* and phacopids and were effective because of being situated well above the hinge line. It does not seem necessary in the case of *Placoparia* to invoke the presence of external dorsal muscles, and the thinness of the exoskeleton of the articulating half ring makes it an unlikely site for muscle attachment.

Muscle areas in the cephalon of lower Paleozoic (mainly Ordovician) species have been investigated by RUDOLPH (1992), and a new observation is that such areas of the cuticle were traversed by narrow, vertical canals. Axial cephalic musculature is reconstructed in the raphiophorid *Ampyx* and the pterygometopid *Toxochasmops*, and paired

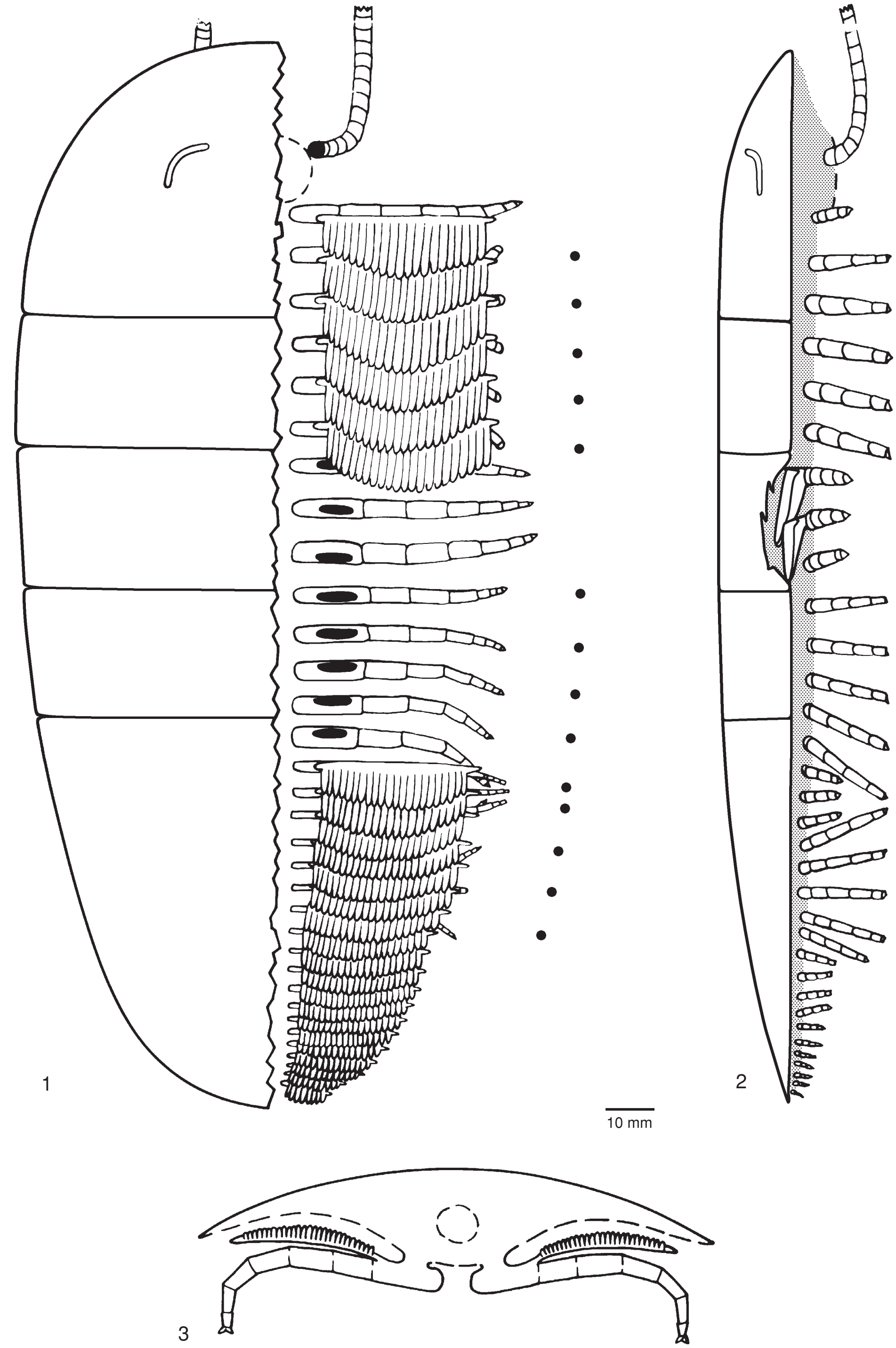


FIG. 93. *For explanation, see facing page.*

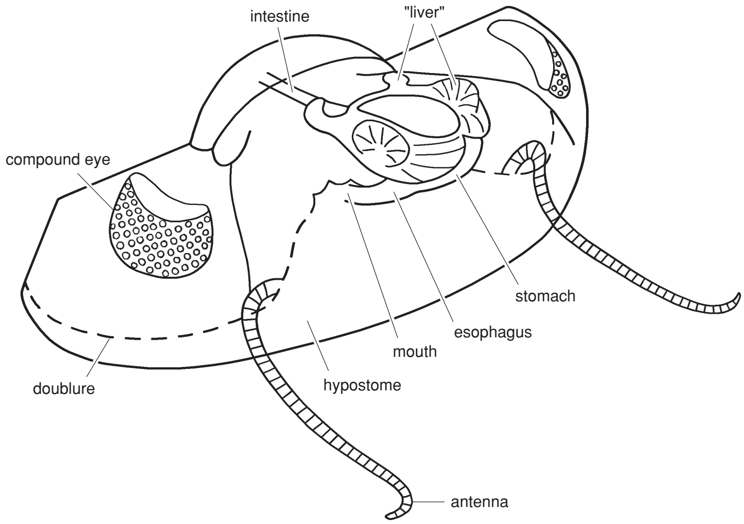


FIG. 94. Cephalon of *Phacops* sp., right anterolateral view; exoskeleton shown as if transparent; inner edge of doublure and hypostome shown by *dashed line.* Interpretation of alimentary system, internal organs, and antennae from pyritized structures (J. Bergström, new).

and median scars on the anterior glabellar lobe are regarded as having been for attachment of muscles supporting the anterior portion of the alimentary tract. Such scars in Phacopina were described by ELDREDGE (1971), CAMPBELL (1976), and STØRMER (1980), and ELDREDGE interpreted them in the same manner as RUDOLPH. CAMPBELL (1976, fig. 2), however, regarded the more anterior of these scars as providing necessary anchorage for the ventral longitudinal muscles. In *Placoparia* the most anterior transverse bar preserved is that of L2 (Fig. 95.1,4), and any more anterior extension of the ventral longitudinal muscles would have unduly restricted space for the anterior portion of the alimentary canal. The same consideration in regard to Phacopina implies that the ventral longitudinal muscles did not extend as far forward as CAMPBELL suggested. Likewise, in *Triarthrus* these ventral muscles and the bars may not have been present as far anteriorly as CISNE (1975, 1981) suggested. Muscles that controlled movement of the hypostome were shown, for example, by ELDREDGE (1971, fig. 7). However, the conterminant hypostome was apparently not movable. Muscle scars on or adjacent to the hypostome were probably for muscles attached to the most anterior portion of the alimentary tract or to the dorsal unmineralized cuticle of the hypostome. Cephalic

FIG. 93. Restoration of *Tegopelte gigas* SIMONETTA & DELLE CAVE, Middle Cambrian, Canada. *1,* Dorsal view with exoskeleton of right half removed to show appendages beneath, the outline of supposed hypostome indicated by *dashed line.* Appendages are in still position of a particular gait, with outer branches removed from limbs VII to XIV and insertion into coxa shown in *solid black.* Antenna is incomplete, its insertion into ventral cuticle shown in *solid black. Solid circles* on right are opposite tips of limbs that are on sea floor. For simplicity, filaments of outer branches are shown relatively much broader (tr.) than they were; the form of the shaft of the outer branch is generalized and does not show a lobate inner portion. *2,* Right lateral view with portion of exoskeleton removed to show outline of outer branches of limbs VII and VIII; other outer branches not shown. *3,* Posterior view of cross section through tergite 1, showing appendage VI. Ventral integument and alimentary canal shown by *dashed lines;* proximal portions of limbs conjectural (Whittington, 1985, fig. 17).

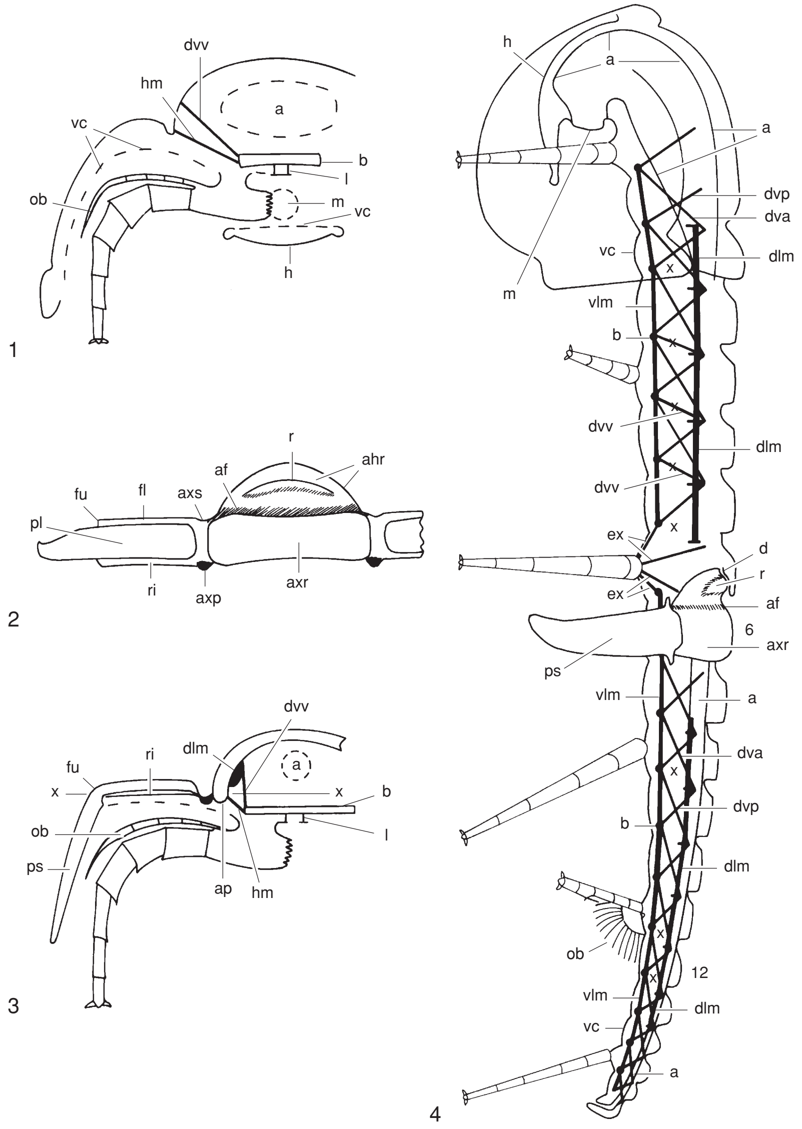


FIG. 95. *Placoparia (P.) cambriensis* HICKS, Ordovician (Llanvirn), U.K. Reconstruction of extended body with the position of the musculature (but not the bulk) shown in heavier lines.——*1,3,* Transverse sections at second glabellar lobe (L2) and sixth thoracic segment, respectively. Left biramous limb shown with inner branch vertical, outer branch (*ob*) in section. *Dashed lines* indicate outline of alimentary canal (*a*), position of mouth (*m*) in front of anterior limb, and unmineralized ventral cuticle (*vc*), which also overlies the hypostome (*h*). The transverse tendinous bar (*b*) is linked to the ventral cuticle by ligaments (*l*). A dorsoventral vertical muscle (*dvv*) and a horizontal muscle (*hm*) extend from the glabellar and axial furrows in part 1, and from the articulating furrow or apodeme (*ap*) in part 3, to the end of the bar. The dorsal longitudinal muscle (*dlm*) is shown in section in part 3; the hinge line between segments is shown by the line *x; ps* is the pleural spine.——*2,* Dorsal view of sixth thoracic segment, showing ridge (*r*) in articulating half ring (*ahr*), the axial ring (*axr*), the axial articulating socket (*axs*) and process (*axp*), the articulating furrow (*af*), the pleura (*pl*) with the anterior articulating flange (*fl*) and posterior ridge (*ri*), beneath which the flange of the following segment fits. The pleura is bent down at the fulcrum (*fu*) to form the pleural spine.——*4,* Profile of exoskeleton in left lateral view, with thoracic segments 6 and 12 (the posteriormost) numbered. Profile broken at segment 6 to show a lateral view of this segment (compare with part 2) and the doublure (*d*) of the axial ring of segment 5. The alimentary canal (*a*) is shown in the cephalon and posteriorly from segment 7. The inner branches (***continued on p. 109.***)

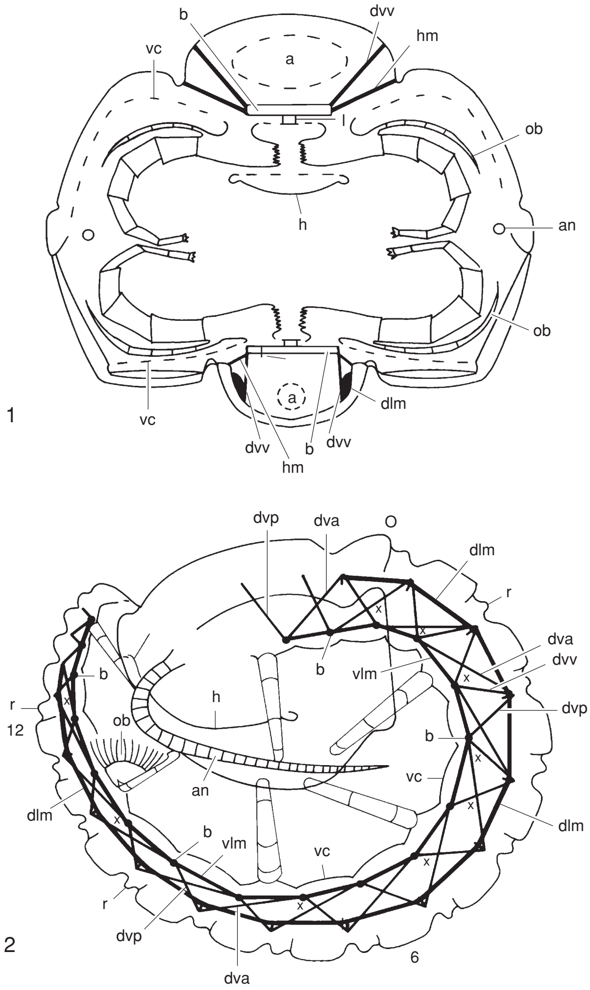


FIG. 96. *Placoparia (P). cambriensis* HICKS, Ordovician (Llanvirn), U.K. Reconstruction of body in fully enrolled attitude, to indicate the positions of muscles and the manner in which the appendages were accommodated. Position of hinge line indicated by *x. 1,* Cross section through glabellar lobe L2 and thoracic segment 7 (compare with Fig. 95.1,3). *2,* Profile of exoskeleton with antenna (*an*) in retracted position; limbs and musculature as in Figure 95.4. Abbreviations: *a,* outline of alimentary canal; *b,* tendinous bar; *dlm,* dorsal longitudinal muscle; *dva,* anteriorly descending dorsoventral muscle; *dvp,* posteriorly descending dorsoventral muscle; *dvv,* vertical dorsoventral muscle; *h,* hypostome; *hm,* horizontal muscle; *O,* occipital ring; *ob,* outer branch; *r,* ridge in articulating half ring; *vc,* ventral cuticle; *vlm,* ventral longitudinal muscle; thoracic segments 6 and 12 are numbered (Whittington, 1993a, fig. 9).

FIG. 95. *Explanation continued from facing page.*

of limbs I, V, VIII, XI, XIV (with outer branch *ob*), and XVIII are shown in the appropriate positions of the gait shown in Figure 99.2, in which pairs of limbs I to XVIII were participating. The dorsal longitudinal (*dlm*) and ventral longitudinal (*vlm*) muscles and tendinous bars (*b*) are broken between segments 5 and 7 to allow extrinsic limb muscles (*ex*) of limb VIII to be suggested. The positions of anteriorly descending (*dva*), vertical (*dvv*), and posteriorly descending (*dvp*) dorsoventral muscles are indicated, the vertical muscles only in thoracic segments 2 through 4. Position of hinge line shown by *x.* Only the antennae are known in *Placoparia*, the limbs shown being modelled on those of *Ceraurus* (STØRMER, 1939), a cheirurid, and the nearest relative to the pliomerid *Placoparia* in which limbs are known (Whittington, 1993a, fig. 8).

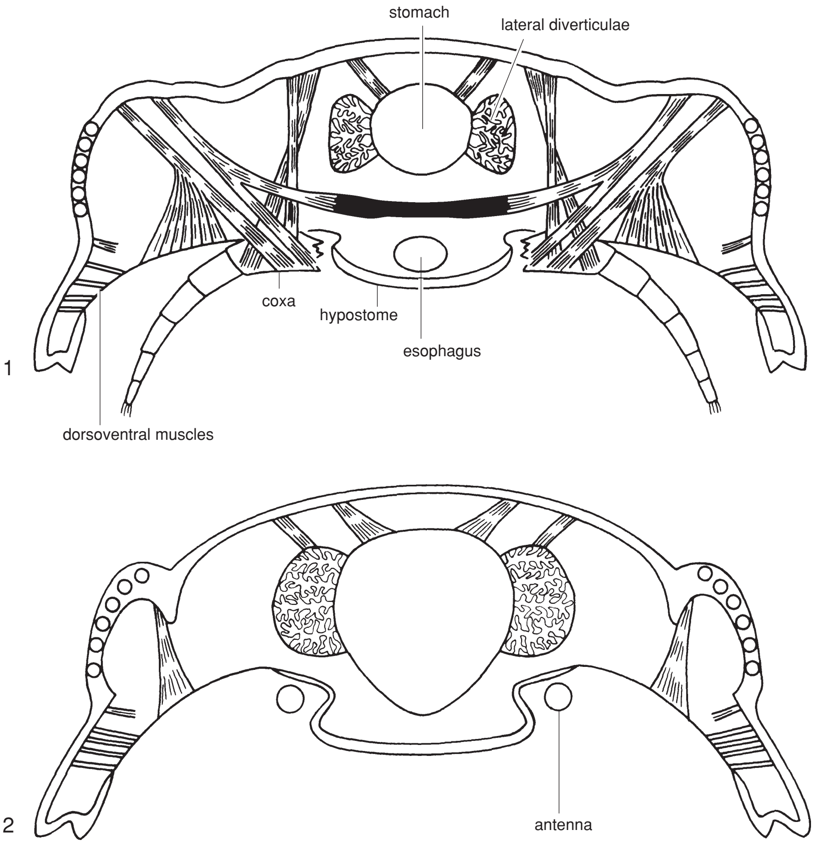


FIG. 97. Cross sections of the cephalon of a generalized phacopid at levels of *1,* posterior and *2,* anterior portions of eyes. Endoskeletal bar *solid black* (Campbell, 1976, fig. 3).

segmentation, the hypostome, and musculature in Phacopinae have been discussed by BRUTON and HAAS (1997).

CAMPBELL (1976) observed muscle attachment areas on the palpebral lobe and elsewhere on the genal area in *Eophacops*, and scars in this area were described by STØRMER (1980, p. 263–266). RUDOLPH (1992) has shown such scars to be present in other Phacopina, as well as in *Ellipsocephalus, Nileus,* and raphiophorids. CAMPBELL suggested that the palpebral scars were for muscles that supported the endoskeletal bar and possibly extrinsic limb muscles (Fig. 97). Both CAMPBELL and STØRMER suggested that muscles supporting the ventral cuticle may have been attached to the scars on the genal region. RUDOLPH (1992, p. 61) has suggested that rows of scars on the fixed cheek may be for attachment of musculature supporting intestinal diverticulae. Such diverticulae, he remarks, are distinct from the radiating, anastomosing canals of the genal caeca, which extend to the cephalic border and across the preglabellar field. CHATTERTON and CAMPBELL (1993) described not only muscle scars on the frontal glabellar lobe and hypostome of cheirurids and phacopids but also a darker-colored band on the distal area of the inner, horizontal portion of thoracic and pygidial pleurae. They suggested that this band was the attachment site for a longitudinal strip of muscles that may have assisted in maintaining the enrolled position and in resistance to twisting of the exoskeleton.

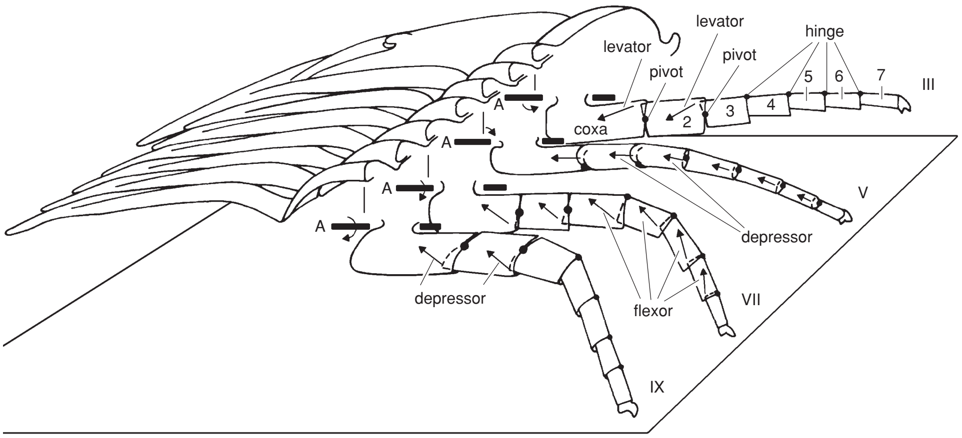


FIG. 98. Oblique diagram, based on *Olenoides serratus* (ROMINGER), Middle Cambrian, Canada, to show probable metachronal movements of right limbs III, V, VII, and IX in walking on the horizontal substrate. Limbs are in positions shown in Figure 99.3. *A* is the axis about which each coxa swung; *solid dots* indicate positions of hinge and pivot joints between podomeres 2 through 7; *arrows* show position and direction of contraction of levator, flexor, and depressor muscles (Whittington, 1980a, fig. 10).

Extrinsic limb musculature is suggested for one pair of thoracic limbs (Fig. 95.4), and such muscles in the cephalon would have been attached to glabellar furrows and endoskeletal bars. This follows the reconstruction of CISNE (1974, 1975, 1981), who suggested an additional lateral muscle attached to the pleural furrow. RUDOLPH (1992, fig. 23, 25) has suggested the possible nature of extrinsic limb musculature in the cephalon of *Ampyx* and *Toxochasmops*, the muscles being attached to the dorsal exoskeleton. Extrinsic coxal musculature was necessary to provide a promotor-remotor swing of the coxa about an approximately transverse, horizontal axis, a swing essential to walking (Fig. 98).

The basic limb movements thought to have been employed in walking are diagrammed in Figure 98 (WHITTINGTON, 1980a, p. 193–195). The leg is lifted off the substrate by levator muscles and extended by hydrostatic pressure and a promotor swing about axis A, as is shown in the figure with limb III about halfway through the swing. Limb V, extended at the beginning of the remotor swing, has its tip pressed firmly into the substrate by the action of depressor muscles on podomeres 2 and 3 (as also shown in limb IX), and the action of flexor muscles on podomeres 4 to 7 bends the limb and transmits a forward-propulsive force to the body. Limb VII is acting in the same way and has reached the midpoint of the remotor swing, the more strongly flexed leg accommodating to the reduced length between coxa and limb tip. Leg IX is extended at the conclusion of the remotor swing, the depressor muscles giving the propulsive force and keeping the tip firmly on the sediment, the flexor muscles relaxed to allow podomeres 4 to 7 to become aligned and extend the limb. The four limbs shown in Figure 98 are part (intervening limbs omitted for clarity) of a metachronal wave of eight pairs of limbs. This gait is considered to be a reasonable one, and successive stages are shown in Figure 99. These stages show how each metachronal wave of movement passed forward along the body.

SUPERFICIAL SENSORY STRUCTURES

Apart from the eye, structures that have been regarded as probably sensory in

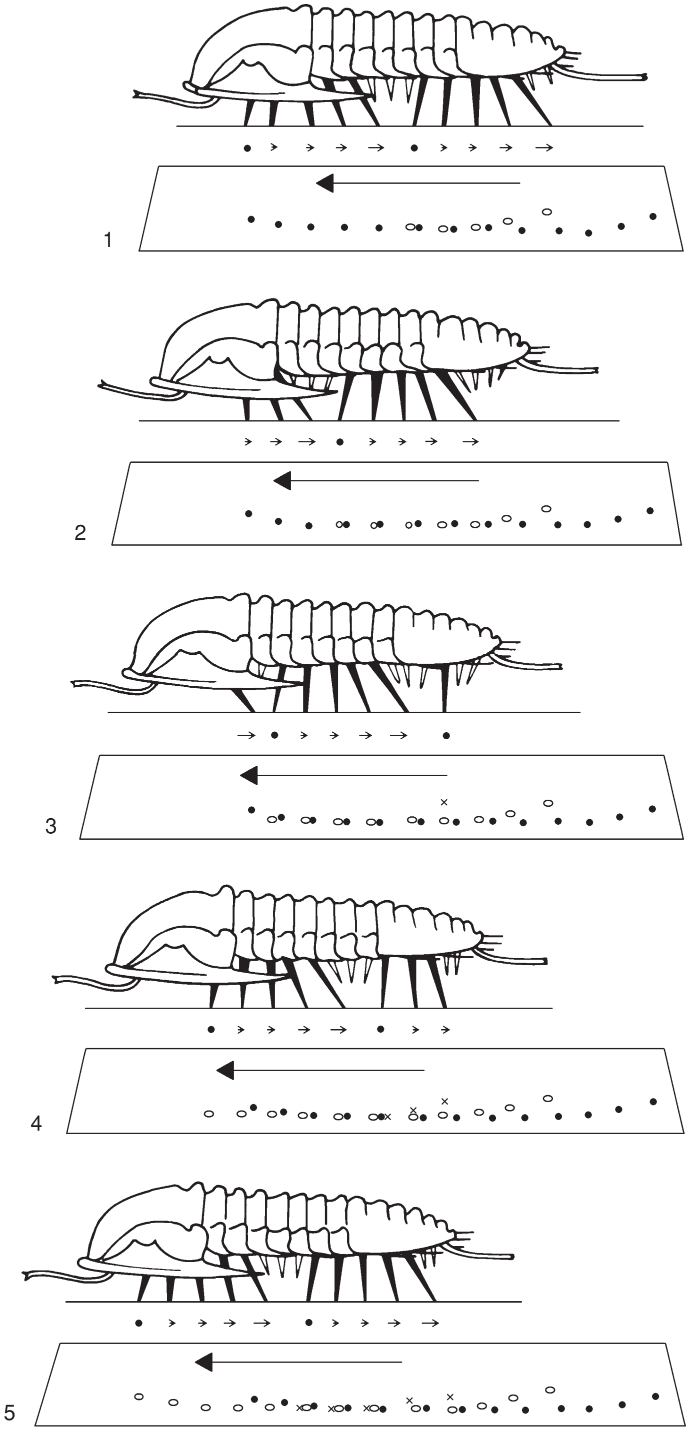


FIG. 99. *For explanation, see facing page.*

function include some on the limbs and whatever organs were associated with openings through the exoskeleton. Studies of sensory structures of living marine animals, particular those of crustaceans (LAVERACK & BARRIENTOS, 1985; BARRIENTOS & LAVERACK, 1986), have been used to interpret what is seen in trilobites.

Spines and setae on the limbs of trilobites have been regarded as assisting in swimming, in food gathering, in comminution, and in creating respiratory currents (see discussion of mode of life below). In *Olenoides,* however, rows of fine spines on the upper surface of joints 3 and 4 of the walking leg (Fig. 84) may have functioned to monitor the position of the limb relative to the outer branch or to the exoskeleton, and fine hairs at the tips of the filaments of the outer branch and around the margin of the distal lobe may also have been sensory.

Canals of larger diameter that pass through the exoskeleton (see above section on microstructure and sculpture) are considered to have been the sites of integumental glands or setal ducts. Such canals may emerge at the apex of a tubercle or the tip of a spine, or be surrounded by a rim and situated between tubercles or spines. Openings of this type are numerous around the outer surface of the cephalic and pygidial border and around the tips of pleurae and of major spines. This distribution (Fig. 100) suggests a tactile function for the setae (see also the study of the homalonotid *Trimerus* by HAAS, 1981).

A variety of other presumed sensory organs has been described. One of these is the ventral paired frontal organ anterior to the hypostome in *Agnostus* (Fig. 80). Each node of the pair has a slit at the apex, and the organ may have been a chemoreceptor. In this remarkably preserved material the axial gap in the exoskeleton between the cephalon and first thoracic segment, the **cephalothoracic aperture,** is covered by a membrane in which are a pair of openings (Fig. 81), but it is not known if these ducts to the interior had a sensory function (MÜLLER & WALOSSEK, 1987, p. 9). In *Nileus,* the exoskeleton is thinned over the glabellar tubercle, and FORTEY and CLARKSON (1976) considered it to have been the site of a light-sensitive organ; in illaenids a similar structure is the median posterior depression in the parietal surface of the glabella. Numerous pits in the visceral surface of the exoskeleton of one agnostid have been interpreted as the sites of photoreceptors (WILMOT, 1990a). In the styginid *Raymondaspsis* a low occipital tubercle is impressed by four tiny pits arranged at the corners of a square (WHITTINGTON, 1965, pl. 58, fig. 10). Similar structures in odontopleurids (Fig. 72.2), asaphids, and trinucleids have been referred to by FORTEY and CLARKSON (1976) and compared to a crustacean sense organ by WHITTINGTON (1956d, p. 177). In the latter publication examples are discussed (p. 176–177) of spines elsewhere on the cephalon (Fig. 72) that have a truncated tip pierced by several openings, which are less regularly arranged

FIG. 99. Diagrams of a probable mode of walking of *Olenoides serratus* (ROMINGER), Middle Cambrian, Canada. Parts 1 through 5 show a succession of still-stands in the gait; left limbs I through XV shown, with I through XIII being used in walking and the animal moving in the direction of the *large arrow.* Each selected still-stand shows left legs only (*in solid black* when in contact with sea-bottom, *in outline* when off the bottom and swinging forward). Below tip of each limb on sea bottom is either a *solid circle,* showing that limb tip has just been put down, or an *arrow* of length proportional to amount of backstroke completed. *1,* Legs I through V in first metachronal wave, VI through XIII in second wave. *2,* Legs I through III in first wave, IV through XI in second wave, and XII and XIII in third wave. *3,* Leg I in first wave, legs II through IX in second wave (legs II and III are off the bottom and concealed by the gena), and legs X through XIII continuing the third wave. *4,* Legs I through VII (legs I and II concealed beneath gena) in second wave, VIII through XIII in third wave. *5,* Legs I through V in second wave, VI through XIII in third wave. The panel below each still shows in oblique lateral view the left half of the symmetrical track made in this gait. *Solid circles* are footfalls of first wave, *open circles* are footfalls of second wave, and *crosses* are footfalls of third wave (Whittington, 1980a, fig. 11).

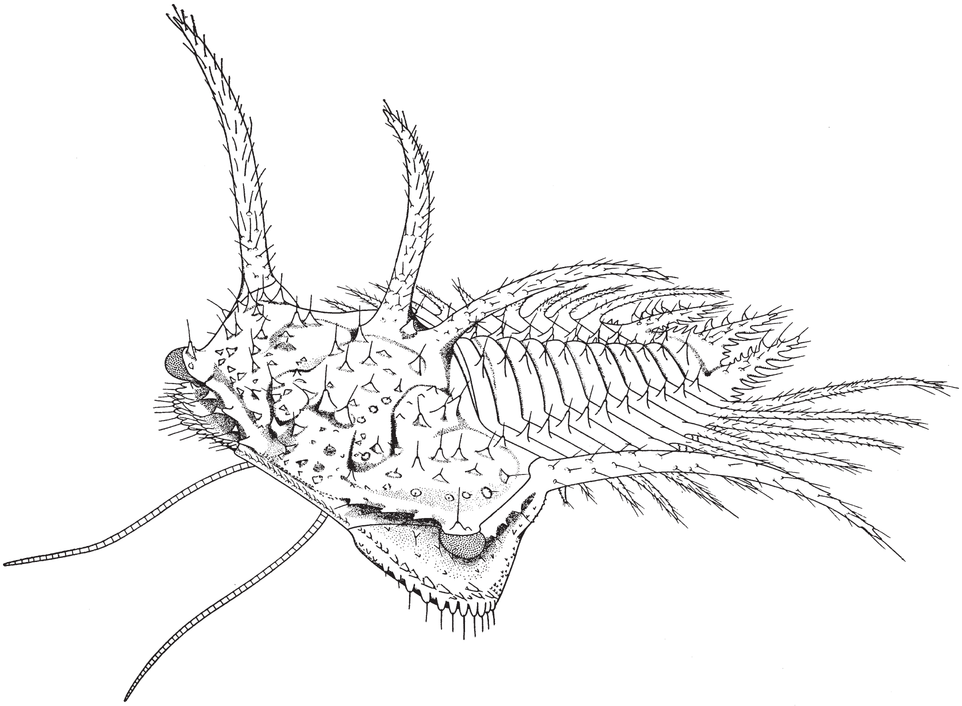


Fig. 100. *Ceratocephala laciniata* Whittington & Evitt, Middle Ordovician, Virginia, USA. Restoration assuming that there were 10 thoracic segments, that the openings in the spines and tubercles were occuped by hairs, and that antennae were present. Other appendages unknown, ×5.6 (Whittington & Evitt, 1954, fig. 1).

and hence different from the openings in the occipital tubercle or spine.

Apparently unique to *Pricyclopyge* and its close allies is a pair of structures on the axial ring of the third thoracic segment. Fortey and Owens (1987) described these as hollow, inflated structures, circular in plan, and situated within the thickness of the exoskeleton; they argued that the structures may have been luminous organs like those known in some modern crustaceans.

THE EYE: MORPHOLOGY, FUNCTION, AND EVOLUTION

E. N. K. Clarkson

Most trilobites bear one pair of compound eyes on the librigena. The eye ranges from small, consisting of only a few lenses, as in Harpetidae, to extremely large, as in Cyclopygidae. In a few species of *Cyclopyge, Ellipsotaphrus,* and *Symphysops* the eyes are confluent anteriorly (Fig. 101.2). Other than such rare instances, the eyes are separate, and most trilobite eyes are crescentic or kidney-shaped in dorsal view; in transverse section they have a convex profile. Usually the eye is sessile, though it may be set upon a narrow platform, the eye socle. This socle may be provided with sensory pits or **fossettes.** In rare instances, as in Odontopleuridae and some Asaphidae, the eye is extended into a rigid stalk. Above the lens-bearing visual surface lies the palpebral lobe, which may be flat or inflated; this is separated from the visual surface by the facial suture. That part of the facial suture lying between the visual surface and the palpebral lobe is known as the **palpebral suture.**

Since the time of the earlier workers Clarke (1889) and Lindström (1901), it has been generally recognized that two types

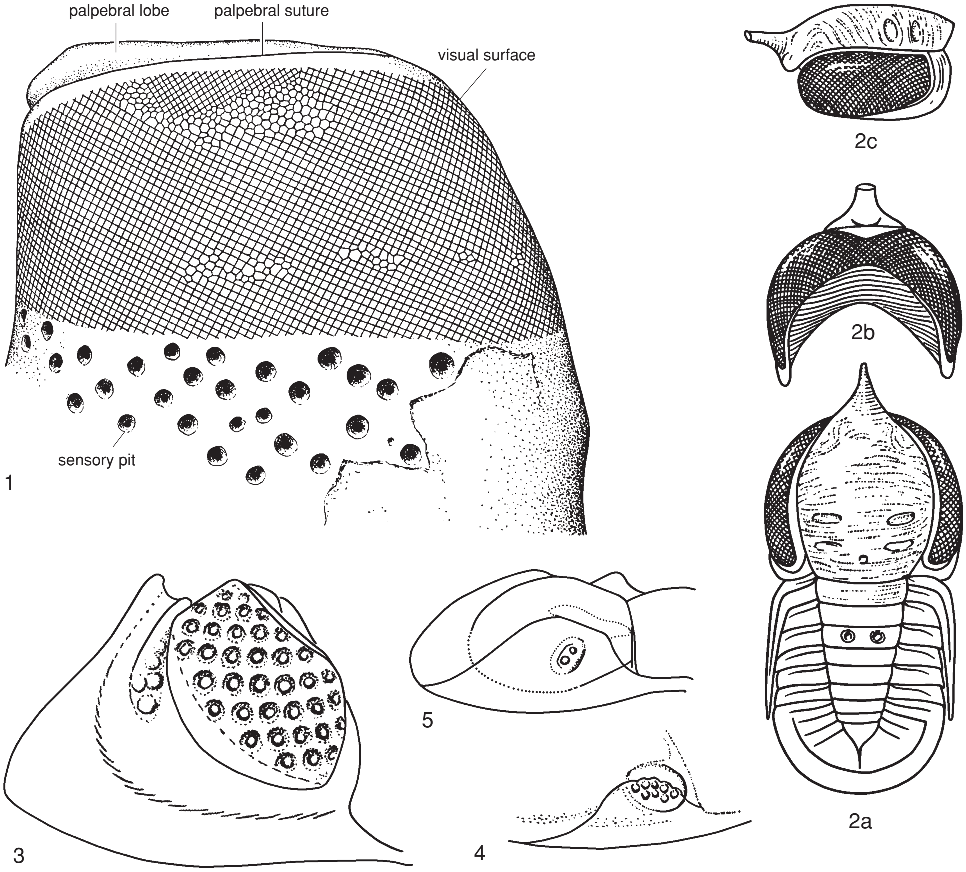


Fig. 101. *1,2,* Holochroal eyes. *1,* Eye of *Asaphus cornutus* Pander, Ordovician, Russia; the patches of large, irregular lenses might result from injury during molting, ×25 (Hupé, 1953b, fig. 31). *2a–c,* Confluent eyes of *Symphysops subarmatus* (Reed), Upper Ordovician, Great Britain, ×1.2; *2a,* dorsal view of exoskeleton; *2b,* ventral view of cephalon; *2c,* left lateral view of cephalon (Hupé, 1955a, fig. 192.2). *3–5.* Schizochroal eyes. *3,* Right eye of *Phacops latifrons* (Bronn), Middle Devonian, Germany, ×25 (Richter, 1932, fig. 2e). *4,* Right eye of *Cryphops cryptophthalmus* (Emmrich), Upper Devonian, Germany, ×7 (Richter & Richter, 1926, pl. 9, fig. 56f). *5,* Left eye of *Nephranops incisus incisus* (Roemer), Upper Devonian, Germany, ×2 (Richter & Richter, 1926, pl. 8, fig. 48d).

of eye are present in trilobites, holochroal and schizochroal (Fig. 101). A third type of eye, abathochroal, was designated by Jell (1975b).

THE HOLOCHROAL EYE

Holochroal (Clarke) or compound (Lindström) eyes have a visual surface of many closely packed, small lenses that are in direct contact with one another (Fig. 101.1–2, 102). The whole ensemble of lenses is covered by a single, thin, pellucid sheet, the cornea, which is calcitic and grades laterally into the outer layer of the cuticle. If the cornea is thin and the individual lens surfaces slightly convex, the lenses can be clearly seen and typically have hexagonal outlines.

The Lower Cambrian Olenellina seem to have had holochroal eyes, though the visual surfaces are at present only commonly found in juveniles. Indeed the record of eyes in adult Cambrian trilobites is poor, at least until the Late Cambrian. This seems to be a direct result of there having been an additional suture, the ocular suture, below the visual surface, so that on death or exuviation, the lens-bearing unit was separated from the rest of the librigena. Even if preserved, such

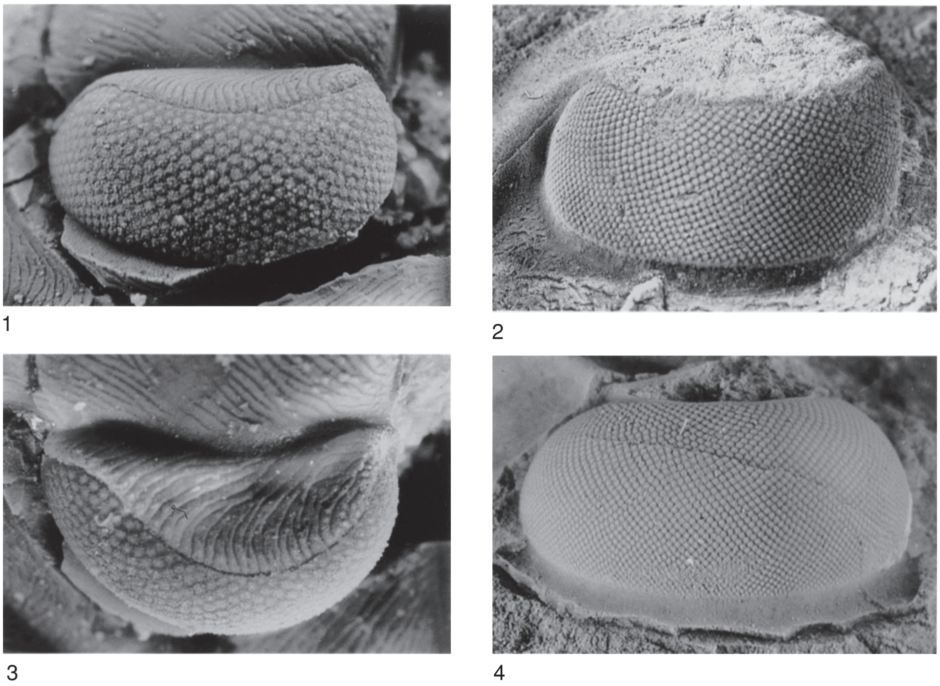


FIG. 102. Holochroal eyes. *1,3, Cornuproetus sculptus* (BARRANDE), Lower Devonian (Pragian), Hostin, Bohemia; lateral and dorsal views, ×22.5 (Clarkson, 1975, pl. 3, fig. 1–2). *2, Paralejurus brongniarti* BARRANDE, Dvorce-Prokop Limestone, Devonian, Bohemia; lateral view, ×7 (Clarkson, 1975, pl. 1, fig. 1). *4, Paralejurus campanifer* (BEYRICH), Koněprusy Limestone, Devonian, Bohemia; lateral view, ×9.5 (new).

a small object is unlikely to be retrieved. The ocular suture, first noted by ÖPIK (1967), seems not to have been functional in meraspid Olenellina and juveniles of other Cambrian trilobites, and in the latter the visual surface adheres to the librigena. It is probable that the normal pattern in Ordovician and later trilobites, where the visual surface was part of the librigena, was derived by paedomorphosis from such an ancestral state. Fully developed eyes of abathochroal type have been described in Lower Cambrian eodiscids from China (X. ZHANG & CLARKSON, 1990). Otherwise, because of the ocular suture and the comparative rarity of well-preserved juveniles, little is known about the eyes of trilobites for the first 50 or so million years of their history.

The earliest eyes that are well known (other than those of the Eodiscina) are those of the Olenidae (CLARKSON, 1973b; CLARKSON & TAYLOR, 1995). In the first representatives (*Olenus* and *Leptoplastus*), the ocular suture was functional, and the visual surface is unknown (Fig. 103). Later olenids, however, may retain the eye as part of the librigena, as in *Sphaerophthalmus* and *Ctenopyge* (Fig. 104), where the visual surface is globular and the lenses thin and biconvex, and in *Peltura* and *Parabolina,* where the eye is flatter and sessile and lenses are arranged differently.

Much more is known about the eyes of post-Cambrian trilobites, for in these, with a few exceptions (notably most Calymenidae), the ocular suture was not developed, and hence the visual surface was retained. In most Ordovician groups the diversity in the form and size of the eye is singular; although most of these trilobites have eyes of moderate size with a few hundred lenses, in some the eyes became gigantic as in some Cyclo-

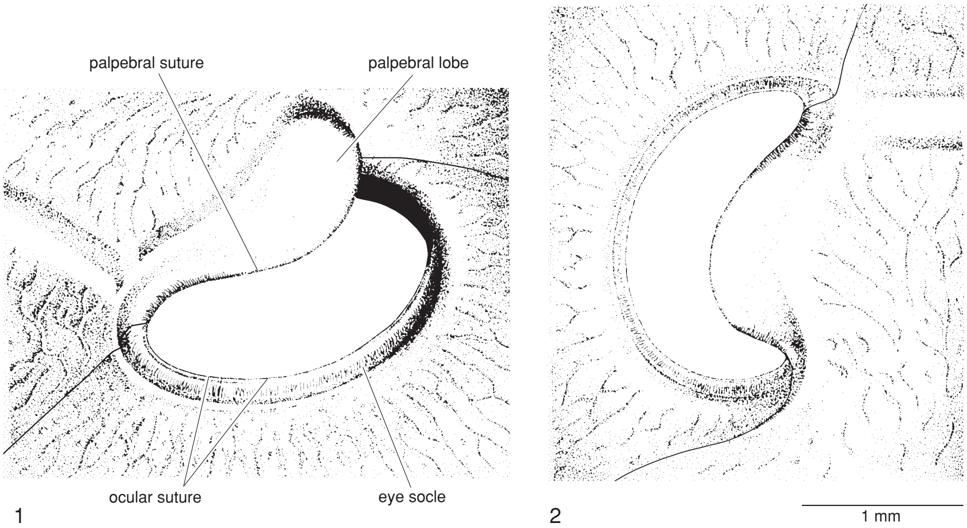


Fig. 103. Olenid eyes. *Olenus wahlenbergi* Westergaard, Upper Cambrian, Skane, Sweden. Reconstruction of eye region in adult, showing the functional ocular suture, by means of which the visual surface was separated from the librigena; *1,* oblique-lateral and *2,* dorsal views (Clarkson, 1973b).

pygidae (Fig. 105) and even fused anteriorly (Fig. 101.2). The striplike eye of *Remopleurides* has over 15,000 tiny lenses. Many Ordovician forms are blind. Holochroal eyes are normally quite large and distinct in post-Ordovician trilobites; they are usually reniform with well-developed lenses, and this kind of rather conservative organization persisted in trilobites through the Carboniferous and to the end of the Permian.

Geometry of the Visual Surface and Lens-Packing Systems

During the ontogeny of trilobites, the eye first appears in the protaspid stages at the anterolateral margin and in successive molts migrated inwards and backwards, taking the facial suture with it. The first lenses are emplaced in a generative zone lying directly below the palpebral suture, initially forming a single horizontal row. This generative zone (and the palpebral suture) has the form of a horizontal, anteriorly expanding logarithmic spiral. Subsequent lenses are always emplaced below existing ones at the bottom of the visual surface, so that as the eye grows, the generative zone moves away from the palpebral suture, all the while contributing lenses in regular sequence to the base. Characteristic patterns of lens packing emerge, which are normally constant for the species and sometimes even within a family or superfamily. On the whole these are based upon a system of hexagonal close packing, and departures from a simple pattern have little to do with the optics of the eye; they are simply solutions to the problem of accommodating (initially) disc-shaped objects on a curving surface. Two categories can be distinguished. In the first the lenses are all of the same size, and inevitable irregularities in packing develop in certain regions of the visual surface. In the second type the lenses are graduated in size and are regularly arranged. The primary control seems to be the spacing of the lens centers and whether it remains constant or changes arithmetically or logarithmically as the eye grows. Several such patterns have been analyzed by Clarkson (1975).

Visual Fields

The angular range subtended by the outermost lenses is known as the minimum

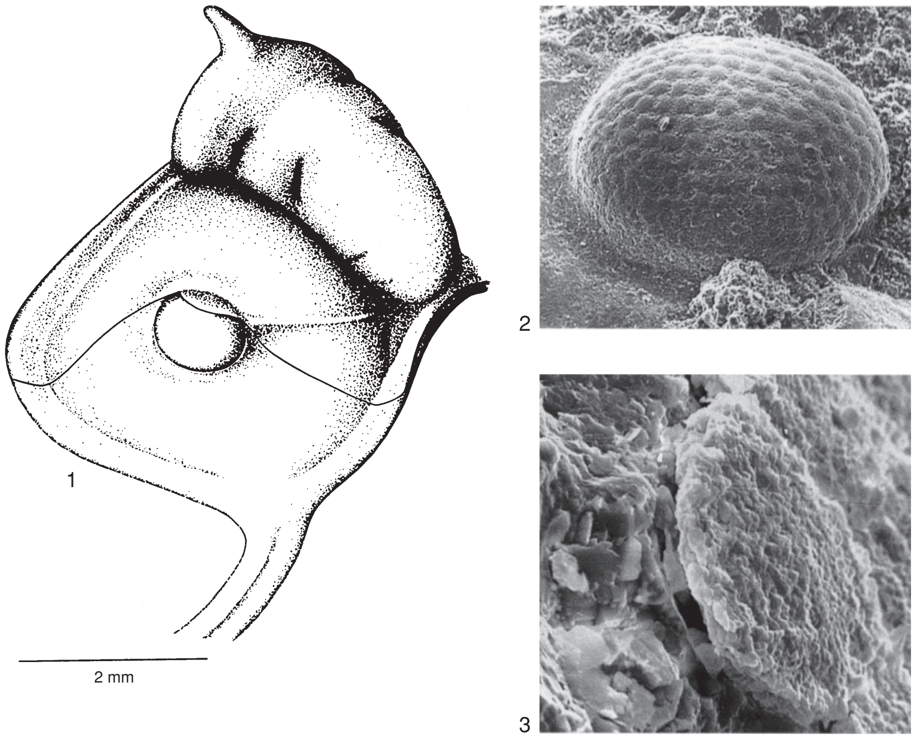


FIG. 104. Olenid eyes. *1, Ctenopyge (Mesoctenopyge) similis* HENNINGSMOEN, Upper Cambrian, Norway, ×12 (Clarkson, 1973b, fig. 6e). *2, Sphaerophthalmus alatus* (BOECK), Upper Cambrian, Sweden, ×105 (Clarkson, 1973b, pl. 95, fig. 1). *3, S. humilis* (PHILLIPS), Upper Cambrian, Sweden; single lens partly detached from matrix, ×950 (Clarkson, 1973b, pl. 95, fig. 3).

visual field. Its angular dimension depends upon the size of the eye and its surface curvature. Since in holochroal eyes the peripheral lens-axes are usually normal to the visual surface, the field of view can be worked out simply by measuring their angular bearing, at specific points along the edge of the eye. The technique was described by CLARKSON (1966a). Two basic types of angular visual field are encountered in trilobites with reniform eyes and are exemplified by the eyes of two species of the Devonian styginid *Paralejurus* (Fig. 106). *P. brongniarti* has a striplike field of view, extending from front to rear, with a latitudinal range of no more than 30° above the horizontal. In *P. campanifer,* on the other hand, the visual field extends from below the horizontal to 90° above, so that the animal could see directly upward, and the fields of the two eyes overlap at front and rear. The differences in these forms may relate directly to mode of life; they may, on the other hand, be more a

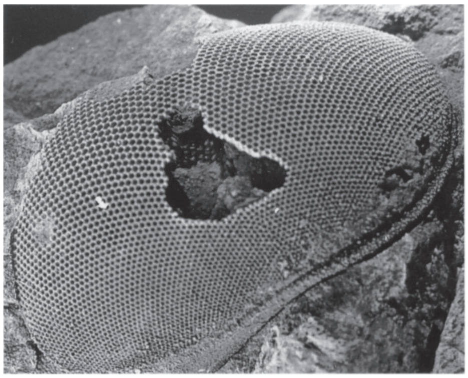


FIG. 105. *Pricyclopyge binodosa* (SALTER), Šárka beds, Ordovician, Bohemia. Internal mold of left eye in lateral view, ×6.5 (Clarkson, 1975, pl. 2, fig. 1).

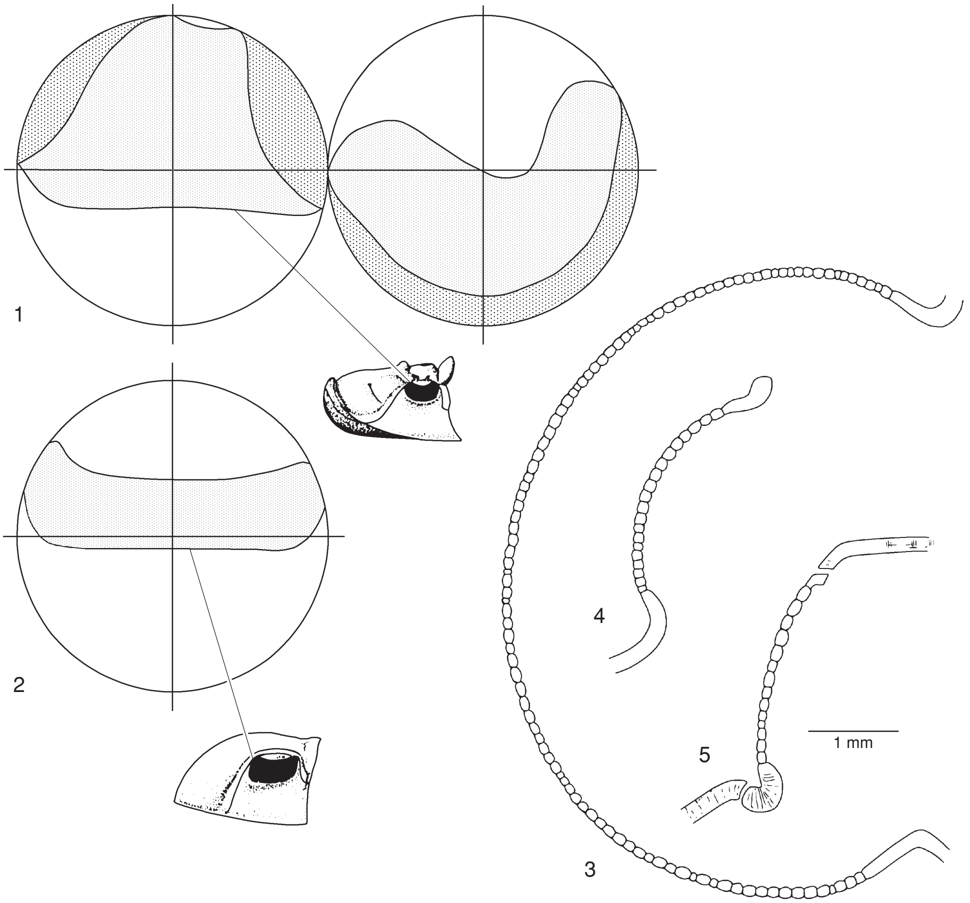


FIG. 106. *1,3,4, Paralejurus campanifer* (BEYRICH), Devonian, Bohemia; *1,* visual field of left eye plotted in equatorial (*left*) and polar (*right*) projection on a Lambert equal area stereographic net. *Coarsely stippled pattern* represents overlapping areas of the visual field; *3,4,* horizontal and vertical sections through left eye. *2,5, Paralejurus brongniarti* (BARRANDE), Devonian, Bohemia; *2,* visual field of left eye in equatorial projection; *5,* vertical section through left eye (Clarkson, 1975, fig. 4).

function of the highly vaulted form of *P. brongniarti* as opposed to the flattened *P. campanifer.* Peculiar visual fields, such as the wide, laterally directed outlook of many cyclopygids, have implications for their swimming mode of life.

Lens Composition, Structure, and Optics

The lenses of the holochroal eye (and of all other trilobite eyes) were constructed of primary calcite (TOWE, 1973), which was probably set in an organic base. Each lens (or, in some instances, small groups or domains of lenses) behaved as a single crystal with its *c* axis normal to the visual surface. In this way birefringence was minimized. Where lenses have been unaffected by diagenesis, they show a radial pattern (LINDSTRÖM, 1901; CLARKSON, 1979a) that is visible in thin sections of lenses ground parallel with their principal planes and confirmed by acid etching of whole specimens of lenses. Each lens consists of thin, originally contiguous, calcitic lamellae that are radially arranged around the *c* axis (Fig. 107). The lamellae themselves are formed of slender calcite fibers (trabeculae), which in convex lenses turn outwards in a fanlike manner so

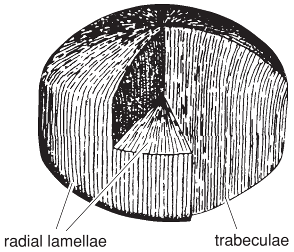


FIG. 107. Reconstruction of a single lens of a holochroal-eyed trilobite, based on *Paladin eichwaldi shunnerensis* (KING), Namurian, England (Clarkson, 1979a, fig. 1d).

that their distal terminations are nearly normal to the cambered outer surface of the lens. This apparently complex system may result from its manner of growth; possibly lenses could increase in size only by addition of trabeculae at the edges.

The lenses of thin-shelled trilobites are normally thin and biconvex, as is seen in the olenids (Fig. 104.3). Thicker lenses are more common in such post-Cambrian trilobites as styginids and proetids. They may be biconvex or planoconvex, the latter type being especially common in thick-shelled trilobites with very long columnar or prismatic lenses such as are found in *Asaphus.* In some species of this genus, the lenses form elongated calcitic pillars, like basaltic columns, as first was recognized by LINDSTRÖM (1901). These lenses have semicircular lower terminations (CLARKSON, 1973a, 1979a), and ray tracing analysis shows that they would bring light to a focus at about the same relative distance below the lens as would the thin biconvex lenses of the olenids or any of the intermediate types. The thickness of the lens is thus mainly a function of the thickness of the exoskeleton rather than being of other significance; what is important optically is the relative convexity of the surfaces.

Nothing is known of the internal structure of holochroal eyes. It is highly probable that an ommatidium-like unit lay below each lens, and both facet diameter and interommatidial angle lie within the same range as modern nocturnal compound eyes (FORDYCE & CRONIN, 1993). The function of the holochroal eye is thus considered to be similar to that of modern arthropods, adapted to moderate to dim light intensities.

THE SCHIZOCHROAL EYE

Schizochroal eyes appeared quite suddenly in the Early Ordovician and were confined to the suborder Phacopina (Lower Ordovician to Upper Devonian). Whereas the eyes of some other taxa have particular features in common with the schizochroal eyes of Phacopina, these latter have unique, distinctive characters which are unknown elsewhere in the animal kingdom. Schizochroal eyes are normally large, and the visual surface approximates to a lunate segment of a cone (Fig. 108). The lenses are thick, biconvex, and much larger and normally fewer than those of holochroal eyes. They are separated from each other by material known as **interlensar sclera,** which is identical in structure with the exoskeletal cuticle. The lenses are normally arranged in a regular system of hexagonal close packing.

When schizochroal eyes are cut in transverse section, their difference from holochroal eyes becomes most apparent (Fig. 109). Each biconvex lens is set at the outer end of a cylindrical cavity, the sublensar alveola. The outer lens surface is covered by a thin, pellucid corneal covering; this continues at the lens margin to cut through the sclera as a cylindrical ring, the **intrascleral membrane,** free of contact with the lens. In rare instances (CLARKSON, 1967a, 1969a) this membrane has been observed projecting below the visual surface as a tapering cylinder, closed off below. The sublensar alveoli, in plan, are set radially, but in vertical section, at least in *Ananaspis,* they are all parallel and horizontally disposed.

Visual Surface Geometry, Growth, and Lens Packing

In most schizochroal eyes the lenses are arranged in the economical system of hexagonal close packing, and this is usually regular. In an eye such as that of *Acaste,* the

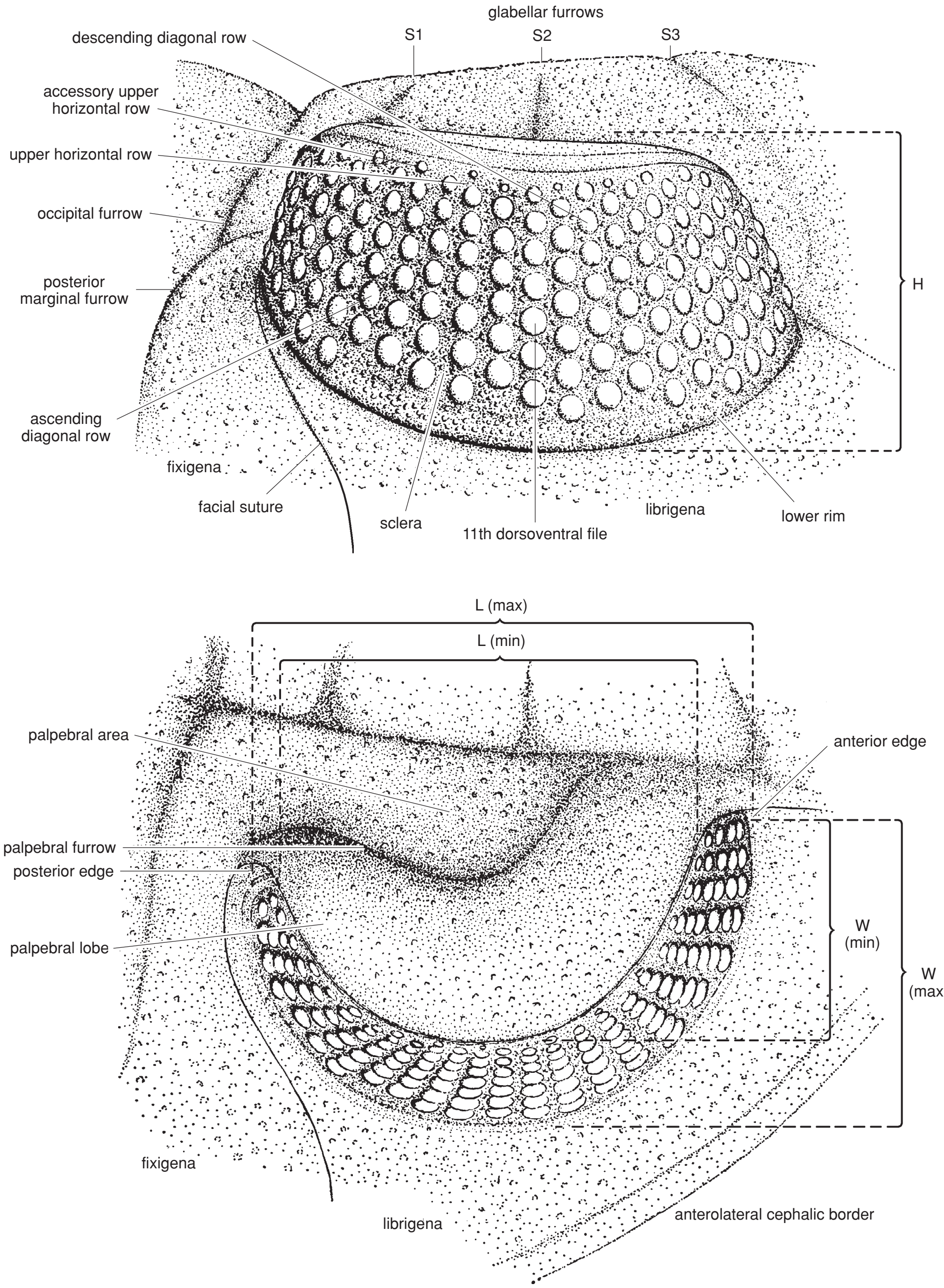


FIG. 108. *Acaste downingiae* (SALTER); external morphology of schizochroal eye and immediate environs (*H,* height; *L,* length; *W,* width), ×17.5 (Clarkson, 1966a, fig. 1a,b).

dorsoventral files and ascending and descending diagonal rows can easily be distinguished (Fig. 108). The lenses vary in size within any eye, however, and this variation is a function of the growth geometry of the visual surface.

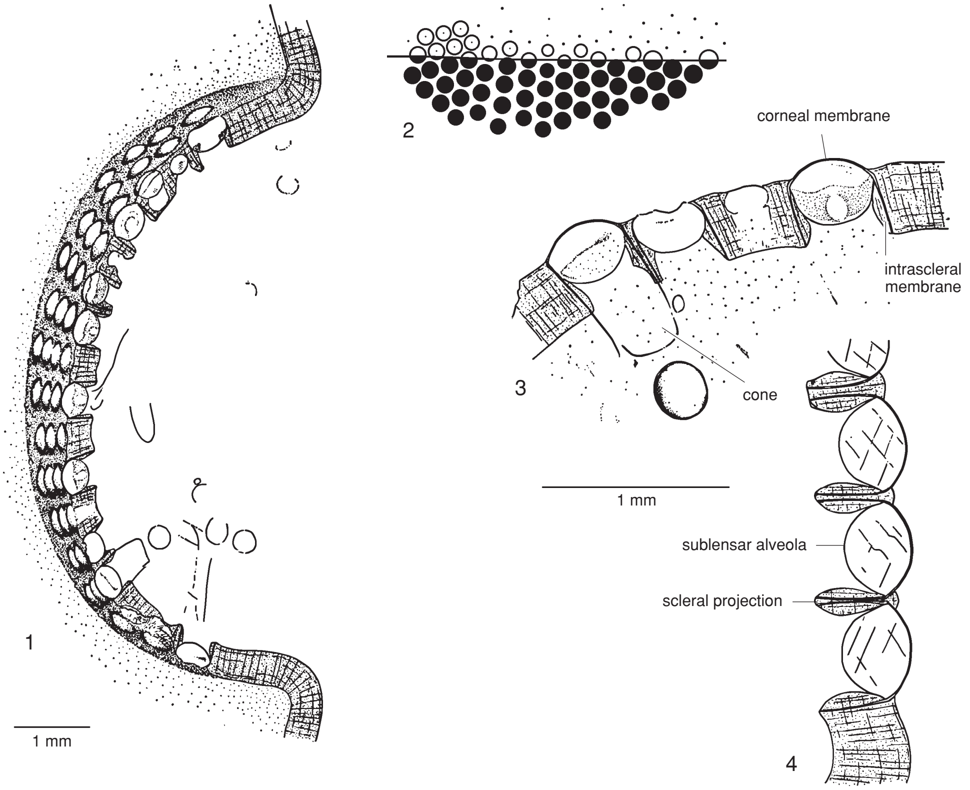


FIG. 109. *Ananaspis fecunda* BARRANDE, Silurian, Bohemia. *1,* Horizontal section through left eye along the line shown in part 2; *3,* enlargement of part of the same horizontal section to show a cone or capsule below the 14th dorsoventral file; *4,* vertical section through eye where lenses have been recrystallized (Clarkson, 1967a, fig. 1a,b,c,i).

As with holochroal eyes, the earliest formed lenses are emplaced in a generative zone that lies directly below the palpebral suture. This zone forms an anteriorly expanding logarithmic spiral that keeps the same form throughout successive molts, though it increases in size. The earliest lenses may form a single upper horizontal row, as in *Ananaspis;* but more often, especially if the eye has many lenses (*Odontochile*), there may be one or more accessory, upper, horizontal rows above the first, full, horizontal row. These were emplaced during the very first stages of growth, when the eye was very small but rapidly growing forward. New horizontal rows are always emplaced below existing ones, the lenses of each new row being offset from the ones above, so that the characteristic packing system emerges. As the eye grew the generative zone moved away from the palpebral suture, contributing lenses in regular sequence until the eye was fully grown. There is no direct relationship between the basic shape of the visual surface and the packing of the intersecting rows of lenses. The generation of the visual surface and lens emplacement were governed by different developmental programs, but since the visual surface expanded as it grew downwards, extra space became available for new lenses, a matter that had implications for the packing of lenses.

In nearly all schizochroal eyes the size of the lenses varies across the visual surface, and it is clear that the size to which the lenses grew depended upon the relative spacing of the lens-centers when newly introduced in the generative zone. If the lens-centers were closely spaced, lenses never grew large; if, on the other hand, the centers were wide apart,

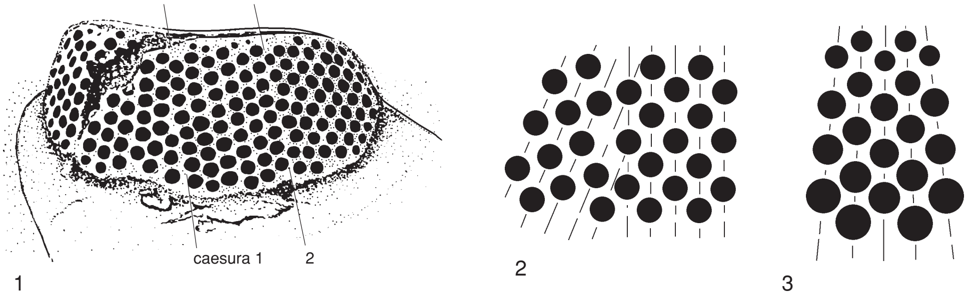


FIG. 110. *1,* Right eye of adult specimen of *Ormathops atavus* (BARRANDE), Ordovician, Bohemia, showing irregular packing and caesurae, ×10 (Clarkson, 1971, fig. 2h). *2,3,* Schematic drawing of lens packing in *2, Ormathops* and *3, Phacops* sensu lato (Clarkson, 1975, fig. 5b,c).

the lenses grew much larger. When the lens-centers were programmed to develop in sequence without any change in spacing, the lenses were all of the same size and lay in parallel dorsoventral files. In one of the earliest phacopid genera, the Ordovician *Ormathops* (Zeliszkellinae) (Fig. 110.1), this is exactly what happened (CLARKSON, 1971). Since it is geometrically impossible to pack uniformly sized lenses upon a curving, downwardly expanding surface in regular sequence, the ideal arrangement of hexagonal close packing breaks down. Sometimes areas of loose and irregular lens-packing are visible on an otherwise regular surface. In other specimens of the same species, blocks of parallel, regular dorsoventral files lie against the truncated edges of other such blocks, the line of junction being termed a **caesura**. New lenses arose when a critical spacing arose (presumably at each molt stage) between the generative zone and the lenses above it. The downward expansion of the visual surface created extra space and this was filled by one or more lenses, which were generated through the automatic operation of the program. Each new intercalated lens then acted as a focal point for the generation of further lenses, either in parallel blocks truncated by caesurae or by irregular areas, depending on the precise conformation of the eye.

In all other Phacopina the problem of achieving regularity was solved simply by the introduction of a constant arithmetical increase in spacing as the eye grew (Fig. 110.3). The result was that the lenses increased in size downwards (and usually also to the front and rear). Irregularities in such eyes are thus seldom found.

Structure and Optics of the Lenses

The internal structure of phacopid lenses is usually diagenetically altered, but in rare instances there has been no major change; and some or all of the original internal organization can be elucidated. LINDSTRÖM (1901) illustrated sections through the eye of *"Phacops macrophthalmus,"* each lens of which seems to consist of a doublet structure with two adjacent components (Fig. 111). Although LINDSTRÖM believed that these doublets were diagenetic artifacts, their presence as original structures has been amply confirmed by recent work. Schizochroal lenses, like those of holochroal eyes, were constructed of lamellae arranged radially around the *c* axis. In sections normal to the principal plane it is apparent that the lower part of each lens was occupied by an intralensar bowl; this interlocked with a mushroom-shaped upper unit. As in holochroal eyes, the *c* axis was normal to the visual surface. There are at least three patterns of lens construction within Phacopina, and these seem to have operated on slightly different optical principles. Some early Phacopina such as *Dalmanitina* have rather parabolic lenses, and the intralensar bowl in each was flattened with a central indentation (Fig. 112.2). The contemporaneous *Crozonaspis,* on the other hand, had more biconvex lenses

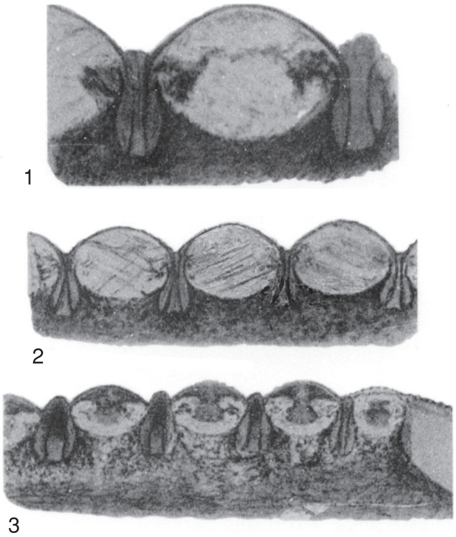


FIG. 111. Internal structure of schizochroal lenses of "*Phacops macrophthalmus* BURMEISTER," Devonian, Germany; *1,2,* longitudinal sections showing lenses separated by interlensar sclera, and *3,* with intralensar bowls present (Lindström, 1901, pl. 4, fig. 3–5).

in which the bowl was thicker and had a wavy upper surface (Fig. 112.4). It has been shown (CLARKSON & LEVI-SETTI, 1975) that the upper units of these correspond respectively to ideal, thick, but aplanatic lenses designed by Descartes and Huygens in the 17th century (Fig. 112.1,3). Experimental models have been made with intralensar bowls of differing refractive indices; these show that a slight difference in refractive index between the upper unit and the bowl, operating together with the correcting surface, focuses light very sharply a short distance below the lens.

The lenses of the Devonian *Phacops* (Fig. 113–114, 115.3–4) are ultrastructurally very complex (CLARKSON, 1979a; MILLER & CLARKSON, 1980). The bowl consists of dense calcite and thins to be absent proximally. The upper unit is built of calcite sheets, radially arranged around the *c* axis of the lens. Each of these sheets in turn consists of a palisade of calcite fibers parallel with the *c* axis proximally but fanning outwards near the outer surface of the lens. This may have minimized the effects of birefringence. As CAMPBELL (1976, 1977) noted, a central core of dense calcite may also have had a correcting function. After ecdysis the lens is reformed. In the earliest postecdysial stages, the cuticle was still flexible and the lens had the form of a small cone suspended from the center of the cornea. Subsequently, the lens spread to the periphery, thickening and becoming saucer shaped, and ultimately acquiring the characteristic wavy proximal surface of a Huygensian lens. The bowl and core differentiated last of all. HORVÁTH (in HORVÁTH & CLARKSON, 1993) calculated the successive forms of an idealized lens of *Phacops,* optimized for correction of spherical aberration at all stages of postecdysial development. The actual growth series conforms very closely to the theoretical computation; vision was bio-optimized from the earliest post-ecdysial stages. The differentiated intralensar bowl probably functioned not only as a correcting element but also reduced reflectivity and thus optimized the transmission of light to the photoreceptors below.

Origins, Functions, and Use

The earliest schizochroal eyes were probably derived paedomorphically from a holochroal ancestor (CLARKSON & ZHANG, 1991, p. 283). In the few examples in which early growth stages of holochroal eyes are known, the lenses are relatively very large and separated from each other by interstitial material. The retention of this juvenile condition by paedomorphosis into the adult phase would be the first and most important stage in the origins of the schizochroal condition. Although the earliest known eyes of Phacopina are typically schizochroal, *Ormathops* (Fig. 110.1–2) has an eye with a different lens-packing system from that of later Phacopina, contingent upon its lenses all being of the same size. It may well have retained the identical lens size from a holochroal ancestor, but this early system was abandoned and regularity was achieved at the expense of identical lens size. This must be important in some way to the functioning of the eye as a whole.

It is not yet known how the schizochroal eye operated, but certain lines of evidence are suggestive. The visual field normally formed a relatively narrow horizontal strip, with the upper limit of vision rarely rising above 40° latitude (Figure 115.1,3). The lens axes were not distributed uniformly within the visual field. They were usually clustered towards the base of the visual field (*Phacops*), and in some genera (*Acaste*) the plan curvature of the visual surface is so much greater than the profile curvature that the lens axes of the dorsoventral files tended to form visual strips traversing the narrow visual field from top to bottom (Fig. 115.2,4). Such eyes as these seem initially to be well adapted for movement perception, since a passing object would register as a flicker across the visual field. This could have been achieved, however, with much simpler lenses than the elegant lens doublets actually possessed by Phacopina, and clearly schizochroal eyes had higher levels of function than perception of movement alone. The interpretation thereof, however, depends upon the nature of the sublensar structures, and evidence is still very limited.

Stürmer interpreted the subparallel dark lines seen inside the eye facets in X-ray photographs of pyritized *Phacops* (Fig. 88) as ommatidia (Stürmer, 1970; Stürmer & Bergström, 1973, p. 112–113). Doubts as to the validity of this interpretation have been expressed by Clarkson (1973a, p. 441–442; 1979a, p. 16) and Campbell (1976, p. 175), and Professor J. Bergström (personal communication, March 1995) does not accept it. He pointed out that these supposed optical fibers form part of a series with the filaments of the outer limb branches (Fig. 88) and may continue outside the eye. Further, they are in a single, subparallel row, not in a radially arranged bunch in relation to the eye facets. Accordingly, Figure 94 has been modified from the original version (Stürmer & Bergström, 1973, fig. 5a, p. 115) to omit the ommatidia, and the label ommatidia has been removed from Figure 88.

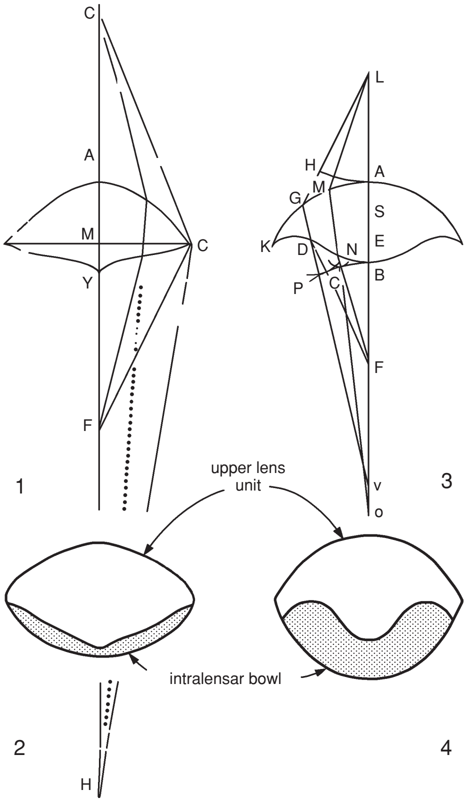


Fig. 112. *1,* An aplanatic lens in air constructed by Descartes in 1637; *2,* reconstructed lens of *Dalmanitina socialis* (Barrande), Ordovician, Bohemia; *3,* an aplanatic lens in air constructed by Huygens in 1690; *4,* reconstructed lens of *Crozonaspis struvei* Henry, Ordovician, Brittany, France (Clarkson & Levi-Setti, 1975, fig. 4).

The view is now generally held that, rather than an ommatidium, there lay below each schizochroal lens a relatively short ocellar capsule floored by a flat layer of narrow cells forming a retina. This was first proposed on the basis of poorly known, short, cylindrical tubes below the lenses (termed *cone* in Fig. 109.3) and on possible modern analogues (Clarkson, 1967a, 1979a; Campbell, 1976) (Fig. 116). More recent physicomathematical analysis of the lens optics (Haack, 1987; Fordyce & Cronin, 1989, 1993) lends considerable support to the retinal-capsule

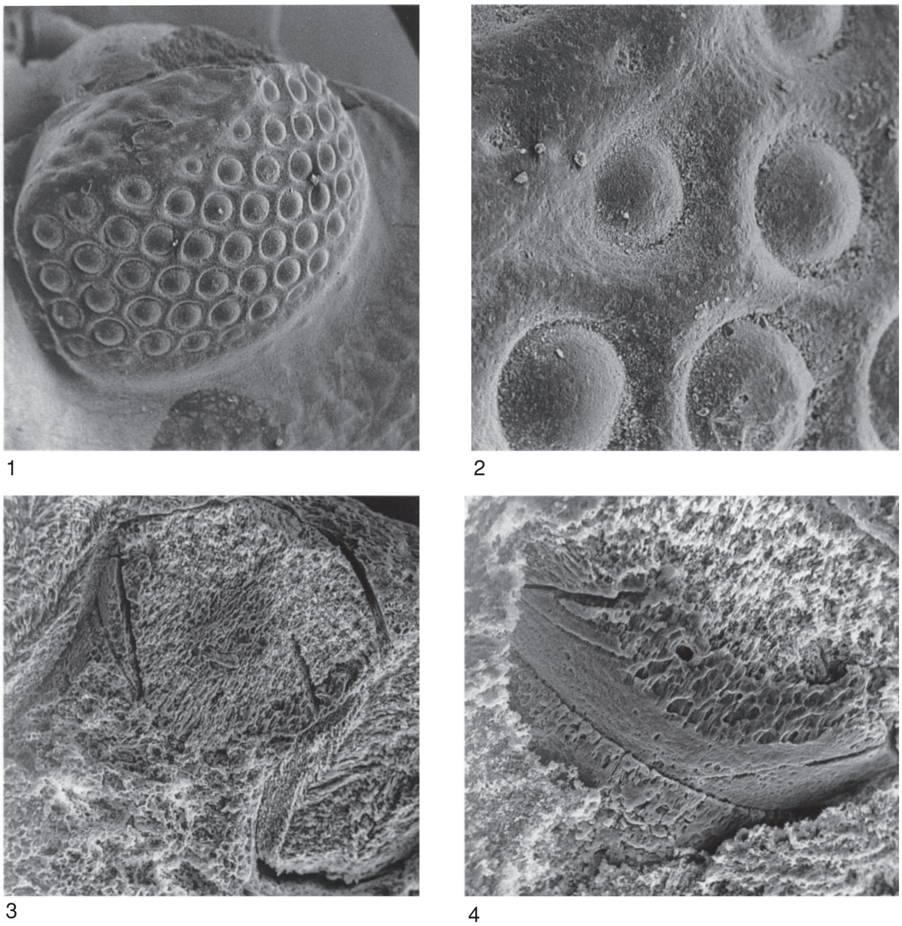


FIG. 113. Schizochroal eyes of *Phacops rana. 1,2,* Left eye of *P. rana rana* (GREEN), Middle Devonian, Ohio; *1,* anterolateral view, ×20 (new); *2,* enlarged anterolateral view, showing part of visual surface, ×105 (new). *3,4, P. rana milleri* STEWART; *3,* lens cut vertically and etched with weak acid, showing core, intralensar bowl, trabeculae, and laminae, also intralensar sclera; the etching has opened up cleavage planes in the calcite (compare with Figure 114), ×100; *4,* obliquely cut and etched lens showing junction of massive-textured intralensar bowl and more open-textured upper unit (compare with Figure 114), ×160 (Miller & Clarkson, 1980, fig. 28, 34).

model. From this work it emerges that eyes of Phacopina are best regarded as an assemblage of simple retinal eyes rather than as an ommatidial eye. In theory, starting from an array of simple visual units, visual acuity could be improved in two ways. One is by generating many identical ommatidia and packing them closely together to make a standard compound or holochroal eye. The other would be by increasing the number of light detectors beneath individual lenses—in other words, to have a retinal layer below each one. This seems to have taken place in the Phacopina, and the resolving power of each lens in a schizochroal eye of advanced type, in which the lenses are very large and relatively few, has been estimated as ten times that of modern compound eyes, comparable to that of a frog. A further consequence of retinular organization, which also takes account of the extreme convexity of each lens, is that adjacent lenses within the

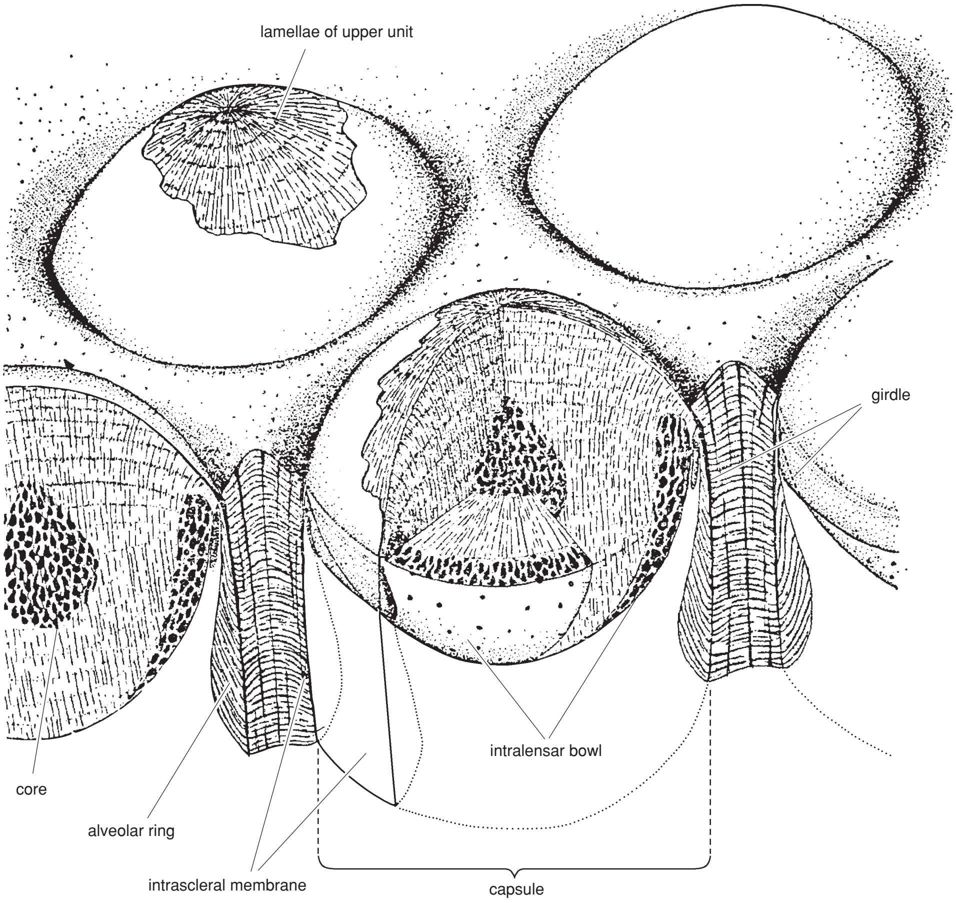


FIG. 114. *Phacops rana milleri* STEWART; reconstruction of part of lens array with lenses dissected to show internal structure (Miller & Clarkson, 1980, fig. 3).

one eye could have been used for stereoscopic vision (STOCKTON & COWEN, 1976). A pair of adjacent lenses covering a particular region of the visual field could both have picked up the same moving object on opposite sides of their respective retinas. As it moved towards or away from the trilobite, its distance could have been inferred by comparison of images in adjacent retinas at any one time, whereas its movement could be detected by comparison at successive times. The schizochroal eye might thus have functioned primarily to give a warning of the presence and movement of nearby objects and in particular a three-dimensional appreciation of actual distance. Such a system could have operated if the neural relay system had been as advanced as the lenses. Several groups of living arthropods have eyes with comparatively few and separated lenses (and those of male strepsipterid insects appear remarkably similar in many ways to the schizochroal eyes of trilobites). Other arthropods, including the larval sawfly *Perga* and the water bug *Notonecta,* have separated lenses with an internal, aplanatic doublet apparatus. Even so, none of the modern counterparts are so similar to the schizochroal eyes of trilobites that they give unequivocal evidence about how these eyes actually worked (HORVÁTH, CLARKSON, & PIX, 1997).

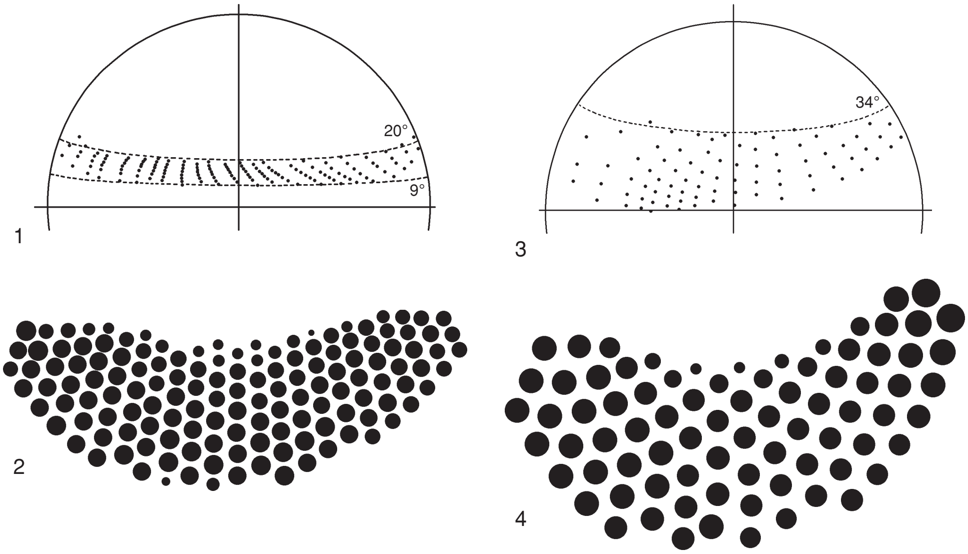


FIG. 115. Visual fields of schizochroal eyes shown by plotting the angular bearing of individual lens-axes on a Lambert equal-area net (*left* is anterior). *1,2, Acaste downingiae* SALTER, Silurian, England; *1,* visual field of adult left eye; *2,* projected visual surface of same eye (Clarkson, 1966a, fig. 1e). *3, 4, Phacops rana crassituberculata* STUMM, Devonian, Ohio; *3,* visual field of adult left eye; *4,* projected visual surface of same eye (Clarkson, 1966b, fig. 2b,c).

Clearly the eyes of Phacopina were organs of high biological quality. Although blindness is not uncommon in trilobites (in species closely related to those having either schizochroal or holochroal eyes), it may be environmentally related and does not imply that the eyes were of poor enough quality to have been easily dispensed with. There is a general correlation between the possession of large, well-developed eyes and the ability to enroll, and major changes both in eye structure and enrollment ability seem to have taken place in many early Ordovician groups at about the same time. It seems reasonable that the trilobite eyes functioned primarily as distant, early-warning sensors for the detection of approaching predators, and the combination of advanced visual and protective systems may have been a major factor in prolonging the existence of trilobites until the end of the Permian.

THE ABATHOCHROAL EYE

A third type of eye, designated abathochroal, has been described by JELL (1975b) in the Cambrian Eodiscina. First described in such Middle Cambrian genera as *Pagetia* and *Opsidiscus,* this kind of eye has recently been recorded (X. ZHANG & CLARKSON, 1990) in the Lower Cambrian *Neocobboldia* from China, making eyes of this kind among the oldest known.

The abathochroal eye superficially resembles a small schizochroal eye, having a relatively small number (50 to 70) of biconvex lenses separated from each other on the visual surface, with a semiregular arrangement of hexagonal, closely packed rows and files. It does not, however, have any indication of a deep interlensar sclera between the lenses, and evidence for an interscleral membrane is limited. It is possible instead that each lens had a separate corneal membrane, which may have been fixed to the interlensar areas round the lens margin. If these differences can be confirmed, the abathochroal eye may safely be considered a distinct type. Although the eye of *Neocobboldia* is of this kind, that of the closely related *Shizhudiscus* is of a more normal holochroal type.

Bearing in mind the ontogeny of holochroal eyes, which initially had separated lenses, it is probable that the abathochroal eye was derived by paedomorphosis from an ancester of holochroal type, as is considered likely for the origin of the much more elaborate schizochroal eye. Internal molds of *Neocobboldia* from China frequently show a small dimple in the center of each lens (Fig. 117). This indicates that the lenses were of the corrected, aplanatic kind described by Descartes, able to bring light to a sharp focus though they were of moderate thickness. Despite the elegance of these early eyes, many Eodiscina lost their visual organs altogether, and this loss may have been environmentally related.

EYE REDUCTION AND BLINDNESS

Compound eyes are primary structures in trilobites, appearing in the earliest genera and persisting in most trilobites until the final extinction of the group in the Late Permian. Secondary blindness, however, is not uncommon, especially in such long-lived major taxa as the Agnostida and Trinucleoidea, in which it is characteristic of the group. It also occurs in some representatives of taxa in which the eyes are normally developed.

There are many modern, deep-sea animals in which the eyes are either hypertrophied or reduced and lost, and blindness is also the norm in endobenthic forms. In many of the blind trilobites, the loss of the eye is likewise probably related to living in dark or infaunal habitats, and it is probably no coincidence that in some blind groups sense organs of a different kind were highly developed and seem to have been the dominant environmental monitor. The trinucleoids present a particularly interesting case. The earliest (Tremadocian) and probably ancestral genus is *Orometopus,* in which the eye and facial suture are present but the pitted fringe, so characteristic of later trinucleids, is undeveloped. In the later trinucleids, however, the fringe becomes large and prominent, with the fringe pits regularly arranged, while the suture becomes marginal, and the eye is lost. If, as has been often suggested, the fringe acted as a compound ear—a vibro- or possible chemosensory organ—it is quite possible that this became the primary sensory organ when vision was lost. A parallel situation may have existed in the Harpina, in which the pitted fringe is large but the eye is reduced to a few lenses only. The evidence for this suggestion is no more than circumstantial and is clearly not applicable to the Agnostina or other groups where there is little or no evidence of other kinds of sense organs.

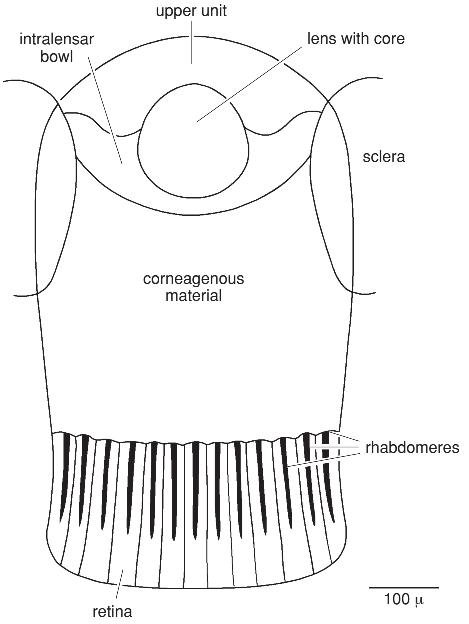


FIG. 116. Diagrammatic reconstruction of an optical unit of a phacopid trilobite, showing inferred retina with rhabdomeres, corneagenous material, sclera, and lens with core, upper unit, and intralensar bowl (Campbell, 1976, fig. 8).

A few instances are known in which secondary eyes have developed in otherwise blind groups. Thus the lateral eye spot described by STØRMER (1930) on the gena of the trinucleid *Tretaspis* was probably an organ of secondary origin. A further example was given by COURTESSOLE (1973) in the Middle Cambrian Conocoryphidae of the Montagne Noire in southern France. All conocoryphids in this region are blind except for the one species *Conocoryphe oculata,*

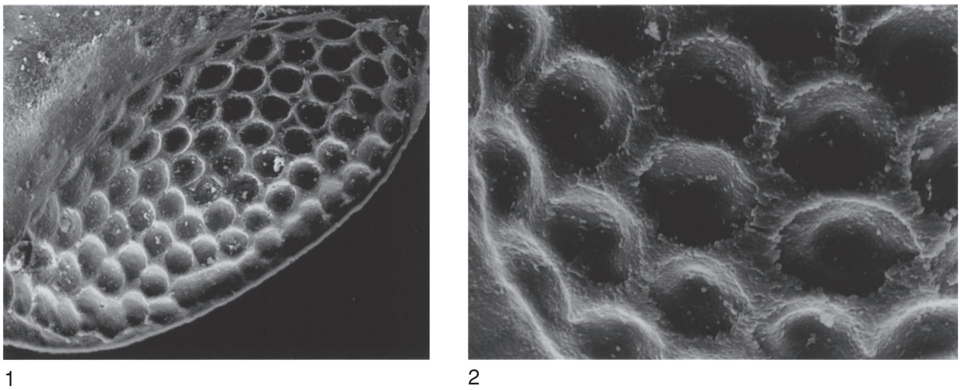


Fig. 117. Abathochroal eye of *Neocobboldia chinlinica* Lee, Lower Cambrian, southwestern China. *1,* Internal mold in phosphate, ×220; *2,* detail of internal mold, showing a dimple in the center of each lens, indicating an original lens of the aplanatic type described by Descartes, ×550 (X. Zhang & Clarkson, 1990, pl. 4, fig. 1a, 6a).

which is otherwise very similar to related species in the same area. This species has a curving lobe of normal eyelike form on the gena, though the suture remains marginal. It is poorly preserved, but there is little doubt that it is an eye. Presumably, in this case, genes for eye development were masked and not lost, and a secondary eye of a kind could develop with the removal of the masking genes.

The clearest examples of progressive reduction of eyes are to be found in Middle and Upper Devonian Proetida and Phacopina in western Europe. Richter and Richter (1926) recorded examples of both these groups from the Devonian of Germany, showing lateral migration of the facial suture accompanying eye degeneration and finally blindness. A clear morphological series in Phacopina is well known (Fig. 118), and Erben (1961) showed various paths to eye loss in Proetida. These works were based upon morphology alone, however, since at the time of writing the stratigraphy was poorly known. It has been shown, however, that in Tropidocoryphinae from southern France, eye reduction is truly progressive and can be followed through time (Feist & Clarkson, 1989). In the Middle and Upper Devonian carbonate succession in the Montagne Noire, an unbroken series of conodonts allows a precise stratigraphical zonation. Tropidocoryphinae occur throughout the sequence. Whereas these had been a stable group for some 40 million years prior to the middle Givetian, they underwent a rapid evolution in their last few million years, exhibiting some striking transformations of the cephalon and the regression and virtual disappearance of the eye within a relatively short interval of time (Fig. 119). They also diminished markedly in size and lost

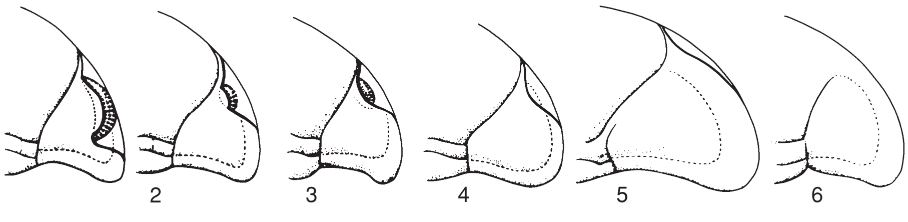


Fig. 118. Lateral migration of the facial suture accompanying migration, reduction, and disappearance of the eyes in Upper Devonian Phacopidae from Germany. *1, Phacops circumspectans* Paeckelmann; *2, Phacops wedekindi* Richter & Richter; *3, Cryphops? ensae* (Richter & Richter); *4, Trimerocephalus mastophthalmus* (Reinhard Richter); *5, Dianops limbatus* (Reinhard Richter); *6, Ductina ductifrons* (Richter & Richter) (Moore, 1959, fig. 47).

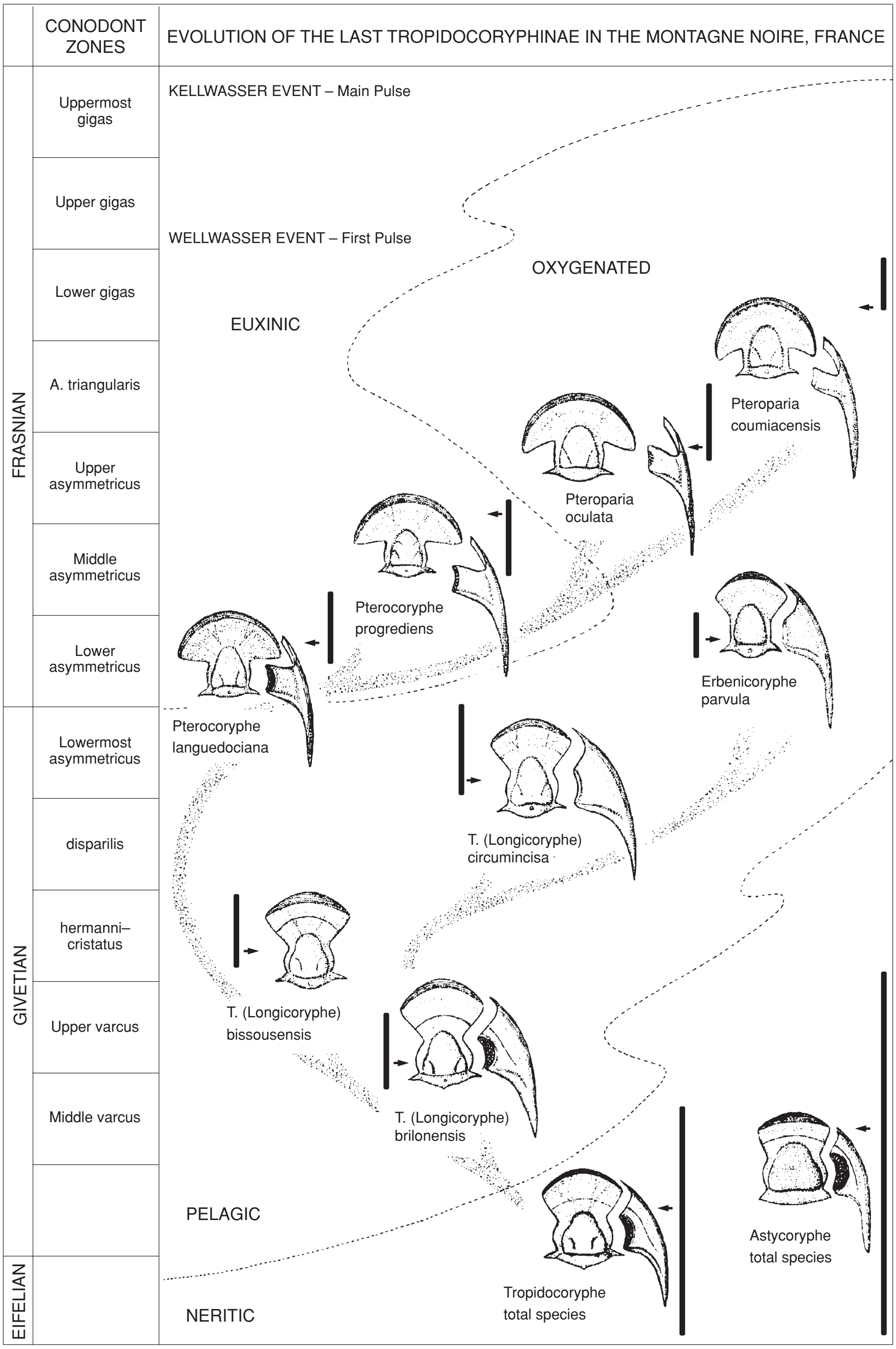


FIG. 119. Evolution of the last Tropidocoryphinae in the Devonian of France, showing two separate lineages with eye reduction. Dominant environments indicated; *vertical bars* show stratigraphical range; *stippled lines* suggest relationships (Feist & Clarkson, 1989, fig. 2).

their original relief so that the glabella became virtually flush with the surface of the cephalon, probably adaptations to an endobenthic life. Two separate lineages show eye reduction and blindness. In the first, the *Tropidocoryphe (Longicoryphe)-Erbenicoryphe* lineage, the cephalon retained the same pattern as the ancestral rootstock, but the eye was progressively reduced to a slightly convex surface, indistinctly defined and lacking lenses. The second lineage, *T. (Longicoryphe)-Pterocoryphe-Pteroparia,* shows a remarkable, backward migration of the anterior branch of the suture, which progressively swung posteriorly in successive species over about 3 million years. Here again the eye degenerated progressively so that the last forms were blind. Sutural migration and eye reduction are not genetically linked, however, and the unusual form of the cephalon and suture probably resulted from an adaptation to the euxinic environment in which *Pterocoryphe* originated. The reduction of the eye and the association with the adoption of an endobenthic habit is thus parallel in the two lineages but superimposed upon a different original cephalic configuration.

Eye reduction and blindness in these Upper Devonian Tropidocoryphinae can be related to local environmental controls. Diminution and loss of the eye, however, seem to have been widespread generally in proetids and phacopids during the Late Devonian. Among the rich proetid faunas of the late Upper Devonian of southern China (YUAN, 1988), many endemic genera and species have the eye reduced or absent (e.g., *Bapingaspsis, Skemmatocare*); and it has proved possible to trace their phylogeny. FEIST's (1995) study of eye reduction in Upper Devonian phacopids showed it to be the result of progressive paedomorphosis, so that the early larval configuration of the visual organs is retained in the adult of the descendant. FEIST suggested that Upper Devonian eye reduction on a global scale is probably linked to periods of eustatic deepening, and the trilobites became adapted to life on, or burrowing within, a muddy sea floor beyond the limit of light penetration.

CEPHALIC SEGMENTATION

H. B. WHITTINGTON

The number of segments that were originally fused to form the trilobite cephalon has been a subject for discussion because of its possible significance in high level classification of Arthropoda. It is assumed that each segment of the thorax and pygidium is the exoskeleton of a single somite. The occipital ring of the glabella, the posterior border, border furrow, and adjacent area of the gena are similar to the axial ring, posterior pleural band, and pleural furrow of a thoracic segment and hence are assumed to represent much of the posterior cephalic segment. Lateral glabellar furrows, separated by a distance (exs.) similar to the length (exs.) of the occipital ring, suggest the presence of more anterior cephalic segments. Such glabellar segmentation is most evident in early developmental stages, and clues to the number of cephalic segments have been sought from such stages, and the holaspides, of stratigraphically early trilobites. Prominent among the latter have been Olenellina, the views of WALCOTT (1910), STØRMER (1942), RAW (1953), PALMER (1957), and BERGSTRÖM (1973a, 1973d) having been derived largely from American and European species. HUPÉ (1951, 1953a) introduced new ideas into the discussion from his studies of Early Cambrian Olenellina, such as *Daguinaspis,* from Morocco. The early developmental stages of *Olenellus* (PALMER, 1957) have an occipital ring and three distinct axial segments between it and the frontal glabellar lobe, and these divisions are also shown by *Daguinaspis* and species of other genera. Differences of opinion arise over the number of segments represented by the frontal lobe. This lobe, into which the ocular lobe runs (Fig. 16), is undivided in the early developmental stages of *Olenellus,* and PALMER concluded that it represented a single segment. The ocular lobe is divided into two ridges in *Holmia,* the posterior passing into the most posterior portion of the frontal lobe, the anterior into a more anterior portion of that lobe (Fig. 120). BERGSTRÖM (1973a) there-

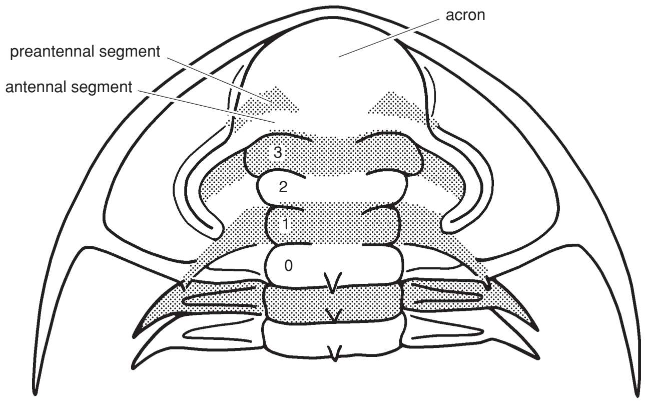


FIG. 120. *Holmia kjerulfi* (LINNARSSON), Lower Cambrian, Norway. Diagram to show the inferred segmentation; alternate segments *shaded;* the acron is a presegmental complex to which the extraocular cheeks probably belong (Bergström, 1973a, fig. 5).

fore concluded that the frontal lobe included two segments and an assumed segmental complex, which he referred to as the acron. HUPÉ concluded that the frontal lobe in cephala of *Daguinaspsis ambroggii* (about 5 mm in length) was subdivided by two pairs of lateral glabellar furrows and hence may have included three segments (Fig. 121), the antennal and preantennal segments, and segment x. STØRMER's (1942) studies of development and segmentation led him to recognize, from ridges and furrows in the adaxial genal region and the ocular lobe, that the pleural region of the preoccipital segment curved back into the intergenal spine (Fig. 122). This deduction was amply confirmed by the earliest developmental stages described by PALMER (1957). It is also clear that the ocular lobe (or the inner band of it) is the pleural region of the fourth segment in front of the occipital, and by STØRMER and BERGSTRÖM this was regarded as the antennal segment. The fossula lies in the axial furrow immediately in front of where it meets the ocular lobe, and the antenna is presumed to have been attached to the slope of the fossula. A corollary of STØRMER's recognition of this segmentation was that the pleural

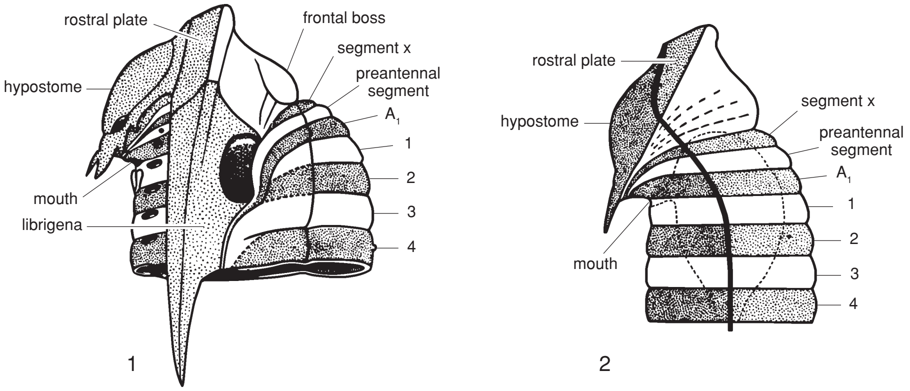


FIG. 121. Theoretical scheme of the cephalic segmentation of a trilobite; ventral surface is shown convex but was in reality concave. *1,* Cephalon in left lateral view. *2,* Schematic section of the cephalon, showing the segments, alternately *shaded; dotted line* shows the alimentary canal; *solid line* separates the tergal region on the right from the sternal region on the left. Abbreviations: *A_1,* antennal segment; *1–4,* postantennal segments (Hupé, 1951, fig. 5).

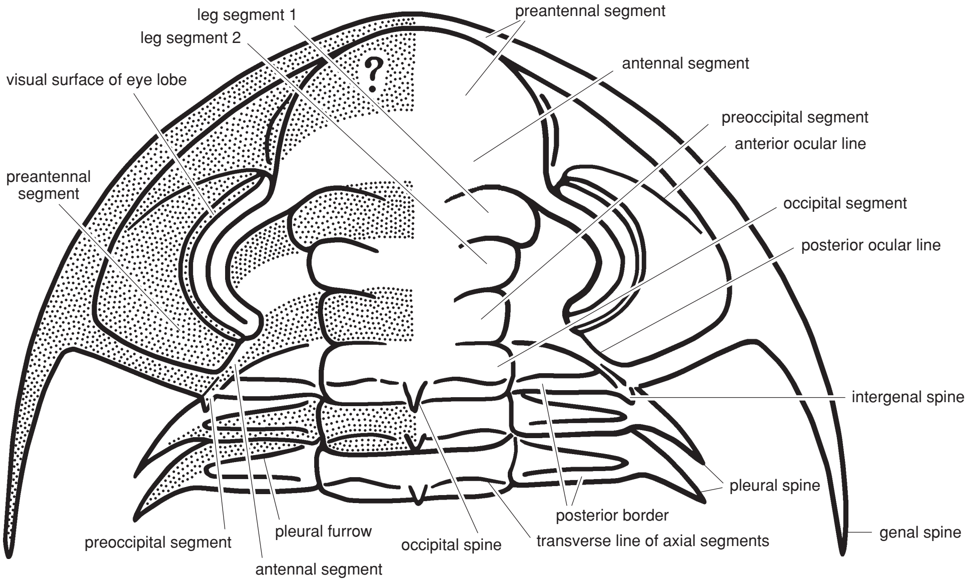


FIG. 122. *Holmia kjerulfi* (LINNARSSON), Lower Cambrian, Norway. Diagram showing the supposed relationship between primary and secondary segmentation in the cephalon and two thoracic segments; primary segments *shaded* alternately on left side (Størmer, 1942, fig. 14).

portion of the occipital segment included the anterior band and pleural spine of the first thoracic segment. Hence the joint between cephalon and first segment (and between the remainder of the thoracic joints) was secondary, cutting across original segmentation (Fig. 122). This view was embraced and extended by PALMER (1957) but rejected by BERGSTRÖM (1973a, 1973d).

It is generally accepted that the trilobite cephalon included at least five segments, the eye ridge having been part of the fourth segment in front of the occipital segment. The fossula appears to have been the apodeme of this fifth segment, to which the anterior wing of the hypostome was linked and the antenna attached. As summarized above in the section on trilobite limbs, known cephalic appendages included three (or perhaps four) pairs of biramous limbs. Presumably the three pairs were linked to the occipital (O) apodeme and those of the next two anterior segments (1, 2), segment 3 not bearing such limbs. In Olenellina only the antenna is known (DUNBAR, 1925), and appendages of protaspides are unknown. In their recent reconstruction of the protaspis of *Encrinuroides,* SPEYER and CHATTERTON (1989, fig. 15a) showed the antenna apparently attached to the apodeme of segment 3, but it was more likely to have been attached farther forward, immediately behind the anterior wing of the hypostome. How many more segments may have been fused to form the cephalon is a matter of debate. STØRMER (1942) suggested that a sixth, preantennal segment may be represented by the most anterior portion of the frontal glabellar lobe, the anterior and lateral cephalic borders, and the visual surface of the eye lobe and extraocular genal area (Fig. 122). HUPÉ (1951) added a seventh segment x in the axial region (Fig. 121) and considered that the preglabellar area, the visual surface of the eye lobe and extraocular area, and the rostral plate and hypostome were formed from the fusion of several more anterior segments. BERGSTRÖM (1973a) considered, however, that the axis terminated at the preglabellar furrow and that the area in front of it was pleural (Fig. 120). He also suggested that because a presegmental acron is present in all extant arthropods, the acron was probably present in trilobites and included the eye. He suggested that a sixth, preantennal, segment was present that extended into the outer band of the ocular lobe. PILLOLA's (1991, p. 77–84) consideration of HUPÉ's views in relation to Lower Cambrian trilobites led him to conclude that the glabella had six distinct segments at the maximum (the anterior being the preantennal segment of HUPÉ) (Fig. 121). In addition is an anterior portion, which may be part of the glabella or may form the parafrontal band. He considered that the segmental nature of segment x (of HUPÉ) is uncertain (since it includes a less prominent portion of the eye ridge), and he referred to the view of JELL (1978a) that the parafrontal band may be part of the network of genal caeca.