# MODE OF LIFE, HABITS, AND OCCURRENCE

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Speculation on this subject began in the middle of the last century and has broadened as appendages were discovered, the significance of facies relationships was appreciated, and the study of trace fossils intensified. The abundance and variety of trilobite remains in relatively shallow-water sediments, in contrast to the limited kinds in deeper waters farther off shore suggest that most trilobite species were part of the shelf benthos. Exoskeletal morphology and comparisons with living animals were used to interpret mode of life in earlier work by DOLLO (1910), RAYMOND (1920), and Rudolf RICHTER (see summary by SCHEVILL, 1936); and this approach continues to be valuable as, for example, in THOMAS and LANE's (1984) use of morphology in discussing the ecology of Silurian trilobites, HAMMANN's (1985) work on calymenoids, and ELDREDGE's (1970, 1971) comparisons with living animals in discussing mode of life. Comparisons with extant crustaceans are inevitable but must be used with caution because trilobites were not crustaceans. BROOKS's (1957) summary of the literature shows that from an early date authors were considering how and in what types of rock trilobites occur and the modes of life implied.

## SPECIES IN WHICH LIMBS ARE KNOWN

Widely differing views have been expressed on the mode of life of Agnostina, as deduced from exoskeletal morphology and mode of occurrence. Authors have considered these trilobites to have been not only benthic but also planktonic (ROBISON, 1972a; JAGO, 1973), parasitic (BERGSTRÖM, 1973a), or living attached to algal strands (PŘIBYL & VANĚK, 1976, p. 13; PEK, 1977; HAVLIČEK, VANĚK, & FATKA, 1993). The discovery of the ventral cuticle of *Agnostus pisiformis* (Fig. 82) has enabled the mode of life of this species to be discussed in greater detail. MÜLLER and WALOSSEK (1987) pointed out that when the animal was completely enrolled, all the appendages would have to have been packed inside (Fig. 123.1), despite the relatively large hypostome. When the trilobite was partially enrolled (Fig. 123.2), the antennae could have projected through the gape; the antennae were relatively short and were considered not to have been sensory in function, but rather to have entangled food particles and swept them back under the hypostome (as illustrated by arrows 1, 2, 3 in Fig. 124). The inward pointing spines of the inner branches of the trunk limbs may then have trapped these particles and moved them into the midline to be carried toward the mouth by the coxae (Fig. 124, arrow 4). A sucking mouth may have aided ingestion. Branches of the limbs specialized for respiration are thought to have been absent. MÜLLER and WALOSSEK suggested that the ventral integument and the club-shaped projections on the outer side of the inner branch of the trunk limb (Fig. 82) were well adapted for respiration. Perhaps the plumose setae on the outer branches of these limbs were used to create respiratory currents that bathed these structures. The second and third cephalic limbs of *A. pisiformis* had respectively either no inner branch or a much reduced one but had a long, flexible, outer branch that was spinose distally. When the exoskeleton was partly enrolled, these limbs could have been curved and swept back in a propelling stroke, curved more strongly and folded in a recovery stroke, enabling the animal to swim. This gaping, partly enrolled attitude (Fig. 123.2) appears to have been the most likely one for feeding and swimming. MÜLLER and WALOSSEK considered that when the body was outstretched (Fig. 123.3) the relative lengths of the limbs made it unlikely that the animal could have walked on the sea bottom. Furthermore, the alimentary canal appears to have been severely constricted in this

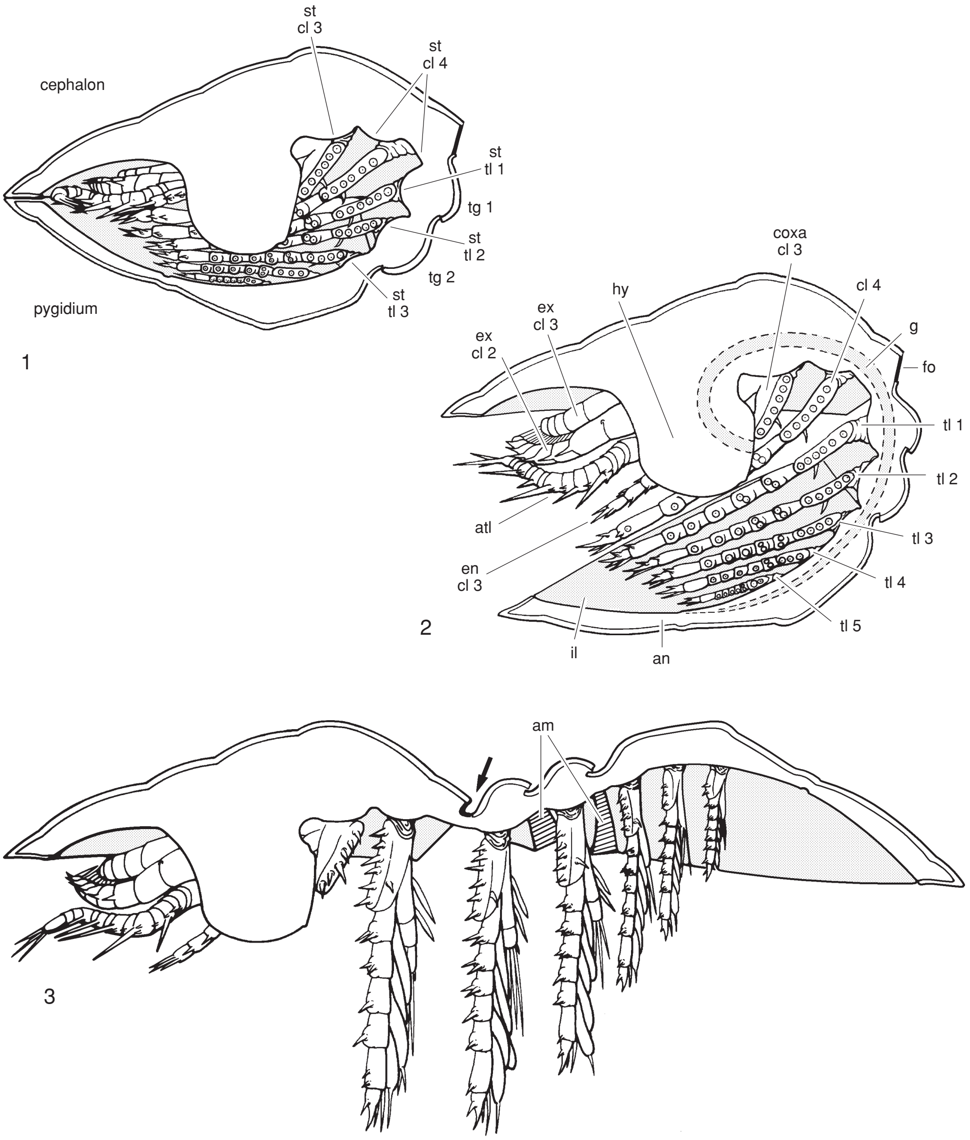

FIG. 123. *Agnostus pisiformis* (Wahlenberg), Upper Cambrian, Sweden. Possible positions in life, the right side viewed from a sagittal section; *1,* enrolled; *2,* partially open; *3,* body outstretched, with cephalic limb 4 and trunk limbs vertical (considered a most improbable position). *Arrow* in part 3 points to deformed membrane covering cephalothoracic aperture. Abbreviations: *am,* arthrodial membrane; *an,* anus; *atl,* antenna; *cl 2–4,* cephalic appendages; *en,* inner branch; *ex,* outer branch of appendage; *fo,* membrane covering cephalothoracic aperture, in which there was a foramen; *g,* gut; *hy,* hypostome; *il,* ventral integument; *st,* sternite; *tg 1–2,* thoracic segments 1 and 2; *tl 1–5,* appendages of thorax and pygidium (Müller & Walossek, 1987, fig. 25).

position and the membrane covering the cephalothoracic aperture folded. Thus, to these authors the outstretched position seemed to have been an unlikely one for either feeding or locomotion (cf. Robison, 1964, p. 515). Müller and Walossek concluded, because of its occurrence in dark, bituminous shale and the associated fauna, that *A. pisiformis* was probably a benthic animal, feeding on the abundant detritus in

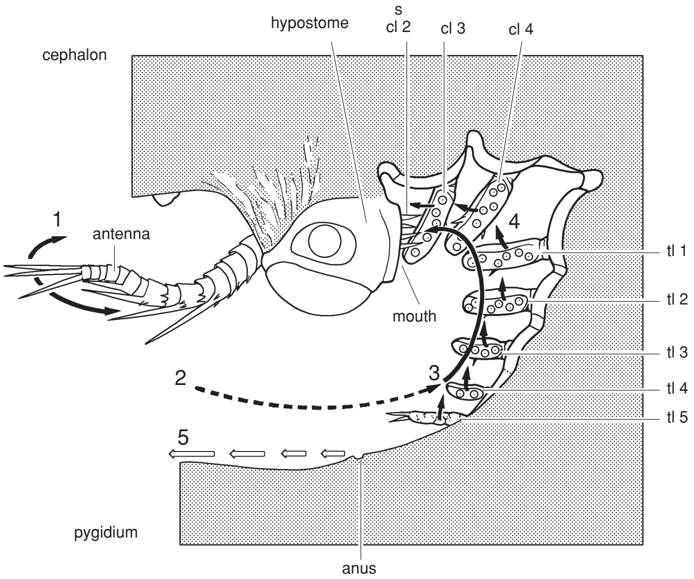

FIG. 124. *Agnostus pisiformis* (WAHLENBERG), Upper Cambrian, Sweden. Sagittal section of partially enrolled body (*stippled,* with sternites at inner edge), inside which are shown the right antenna, hypostome, position of mouth and coxae and setae (*s*) of right cephalic (*cl 2–4*) and trunk (*tl 1–5*) limbs. See text for discussion of probable mode of food intake (*arrows 1–4*); the anus and exit of feces (*arrow 5*) are shown (Müller & Walossek, 1987, fig. 24).

a flocculent zone, its limbs being not adapted for filter feeding.

The limbs of the Middle Cambrian *Olenoides* (WHITTINGTON, 1980a) are known in considerable detail (Fig. 83–85), making it possible to suggest the types of joints between the podomeres of the leg branch and the nature of the limb movements in walking (Fig. 98–99). Flexure of the leg branches, which were armed with bunches of ventral spines, may have enabled the animal to seize prey or decayed material and to have pushed it into the median groove, lined by the spinose coxae. Metachronal movements of the coxae (WHITTINGTON, 1980a, fig. 9) presumably enabled food to be squeezed and shredded as it was passed forward to the mouth, which was positioned at the back of the hypostome. The search for food on the sea bottom may have been conducted not only by walking but also by the animal launching itself off the substrate and drifting in a favorable current (Fig. 125). It is questionable, however, whether *Olenoides,* once launched off the bottom by a backward swing of a few successive pairs of limbs, had any means of swimming. The filament-bearing, outer branch of the appendage appears to have been rigidly attached to the coxa so that if the coxa swung about a transverse axis, the outer branch would have been moved up and down with it. Whether the branch itself could have been flexed is not known. Thus feeble currents may have been created as the outer branch moved toward and away from the ventral integument. Such currents would, at best, have provided only poor swimming powers.

The activities possible for *Triarthrus eatoni* (WHITTINGTON & ALMOND, 1987) appear to have been similar. In this species the inner branches are notable for the development of spinose endites on the proximal podomeres. These endites were triangular in outline and deep on the short podomeres of the posterior branches, becoming less deep on successively more anterior branches (Fig. 86.3–5). The endites may have aided in trapping food and holding it as it was conveyed into the midline. Such endites on the posterior leg branches are characteristic of trilobites otherwise very different in morphology from

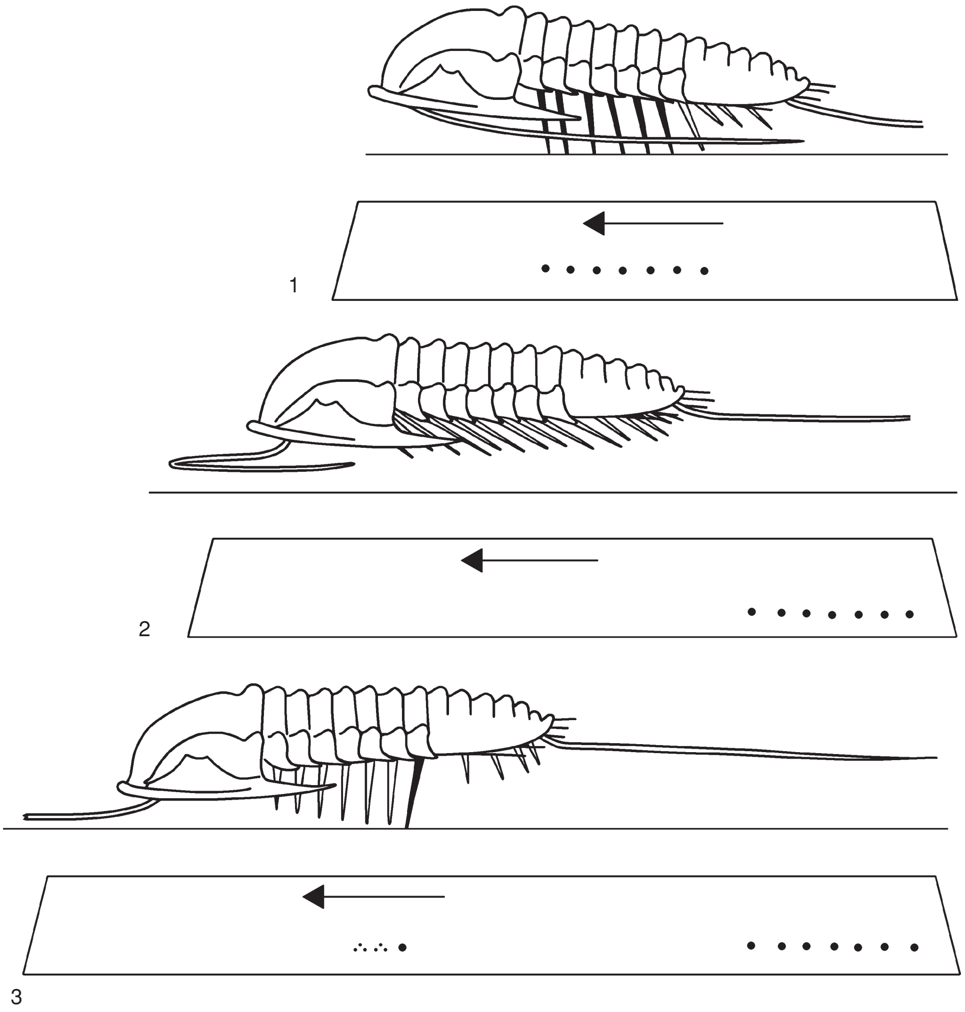

FIG. 125. Left lateral stills showing how a trilobite such as *Olenoides serratus* (ROMINGER) may have launched itself off the sea bottom (*horizontal line*) to drift or swim a short distance before descending to the bottom (compare with Figure 99). Limbs that are in contact with sea bottom are *solid black;* others are shown in *outline.* Below each drawing is a panel showing an oblique view of part of the sea floor with the imprints made by the left legs only; *arrow* shows direction of movement. *1,* Leg pairs IV to X swung back quickly to launch animal; *2,* animal drifts or swims above sea bottom with pairs of legs swung back to offer less resistance; *3,* leg pairs IV to X in promotor swing; pair X completes swing and touches bottom, to be followed in succession by pairs IX to IV, giving a second set of impressions; antenna incomplete, but cercus complete (Whittington, 1980a, fig. 13).

*Triarthrus,* for example *Cryptolithus* (RAYMOND, 1920, fig. 20), *Rhenops* (BERGSTRÖM & BRASSEL, 1984, p. 70, fig. 1–3), and *Phacops* (STÜRMER & BERGSTRÖM, 1973, p. 118–119).

*Triarthrus eatoni* could enroll completely (ROSS, 1979), the pygidium fitting closely inside the cephalic border, as could *Placoparia* (Fig. 96) and many other trilobites, the close fit achieved in different ways. In enrollment of such species, as with *Agnostus,* all the limbs would have to have been accommodated within the capsule formed by the exoskeleton, packed beside the hypostome, with the antennae folded back. Space was thus at a premium, and the body beneath the inner pleural region must have been of severely limited depth so that most of the body was concentrated within the axial region. Such considerations and the probable need for a hanging stance or upward curvature of the limbs to give stability were weighed in drawing the cross sections of *T. eatoni* (Fig. 86.3–5) and *Placoparia* (Fig. 95–96). A cross section such as that by SCHMALFUSS (1981, fig. 7), with a deep body in the pleural region, seems highly improbable for trilobites that enrolled completely.

MÜLLER and WALOSSEK (1987, p. 47–49) compared the biramous appendages of *Agnostus pisiformis* with those of other trilobites, commenting that the general construction was the same—the large coxa and gnathobase, the main branch being the inner one composed of six podomeres plus a terminal spinose one. The special form of the antenna of *A. pisiformis* and the differentiation of the anterior two biramous appendages from the remainder of the series are considered to be related to their function in food gathering and swimming. The specialization was related to the mode of life, one of swimming and drifting above the bottom but not walking on it. Other trilobites in which limbs are known have long, slim, tactile antennae followed by a series of biramous appendages of similar form, which show only gradational change in length of branches, spines, or endites. A series of inner branches of similar length and distance apart (exsag.) are essential to a gait that supported the animal along the length of the body. Thus, the similarity in form of the biramous series of limbs reflects the mode of life, walking on or digging and plowing into the sea bottom.

## FORMS IN WHICH ONLY THE EXOSKELETON IS KNOWN

However well the exoskeleton is known, inferences on mode of life and habits are restricted by uncertainty about the nature of the limbs. In the spinose odontopleurids WHITTINGTON (1956d) suggested that the form of the cephalon and relative length of border spines (Fig. 22, 42) resulted in the animal's resting on the substrate on the margins of the cephalon with the thorax and pygidium stretched out a short distance above the bottom. CLARKSON (1966a, 1966b) showed that the visual field of the eye in phacopids is striplike, restricted vertically, but covering a wide field laterally. Orientation of this field horizontally gave an attitude of the body, when resting on the sea floor, similar to that in odontopleurids. CLARKSON (1966c, 1969b) suggested that the thorax and pygidium could be stretched out above the sea bottom or inclined slightly downward to rest on the border spines (in odontopleurids) or on the margins of pleurae and pygidium (in Phacopina). CLARKSON (1966a, 1966c) drew attention to the anterior arch of the cephalic border, curving up to the sagittal line, in phacopid cephala when oriented in this fashion. Such an arch is characteristic of many trilobites, e.g., the Lower Cambrian *Crassifimbra* (PALMER, 1958), proetoids, Phacopina, cheiruroids, calymenids, and the olenid *Triarthrus eatoni* (WHITTINGTON & ALMOND, 1987, fig. 40). CLARKSON emphasized the importance of this arch as an entry for respiratory or food-bearing currents when the animal was on the sea bottom. The appendages of *T. eatoni* were well suited to such a direction of entry. The anterior arch, however, is also coaptative, a necessary form to accomodate the posterior portion of the thorax and pygidium in complete enrollment; it may not have been related to respiration or food gathering.

The evidence from exoskeletal morphology may be tested against the geological evidence of the enclosing rock and associated fossils. A recent study of this type was by N. C. HUGHES (1993) on large collections of *Dikelocephalus;* it exemplifies the problems in reaching firm conclusions on the mode of life of this probably epibenthic trilobite. The difficulties in interpreting morphology have given rise to disparate views on the habits of Illaenidae (SIEGFRIED, 1939; WHITTINGTON, 1964; BERGSTRÖM, 1973a; WHITTINGTON, 1997). In some species of illaenids, the

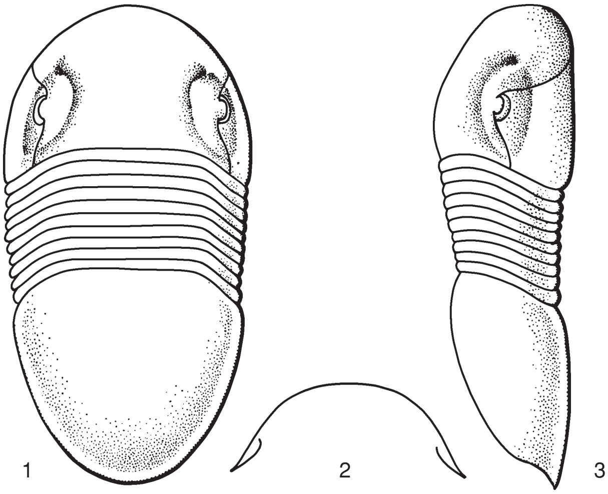

FIG. 126. *Meitanillaenus niagarensis* (WHITFIELD), Middle Silurian, Wisconsin. *1,* Dorsal view, *2,* transverse section through anterior portion of pygidium, and *3,* right lateral view, ×2 (Whittington, 1964, fig. 1c–e).

convex cephalon is deeper than the thorax and pygidium, but not in all (Fig. 126). Illaenidae lack transverse furrows—that is, they lack glabellar, articulating, inter-ring, and pleural furrows, and the axial furrow is not deeply impressed. The thorax may be fulcrate or nonfulcrate, with a wide (tr.) axis giving an even smoother, rounded form to the exoskeleton, as in *Bumastus* (Fig. 1). BERGSTRÖM (1973a) suggested that illaenids lived with the cephalic margin resting on the sea bottom, the lower margin of the eye lobe hence parallel to the bottom surface, the thorax and pygidium curved down at a steep angle in a burrow; this posture was attained by burrowing backward. Such burrows, however, have not been observed, and the specimen illustrated by BERGSTRÖM (1973a, pl. 5, fig. 5–6) is not buried in this attitude (WHITTINGTON, in press). The morphology of the illaenid thorax (Fig. 47 and discussion) gives it exceptional flexibility, and it may be that these trilobites were vagrant benthos, specially adapted to crawling over the uneven surfaces of the reef habitat in which they occur abundantly. STITT (1976) argued that the Upper Cambrian *Stenopilus* (Plethopeltidae) may have lived with the thorax and pygidium in a vertical burrow (Fig. 127) and have used the anteriorly facing terrace ridges that traversed the pygidium to assist in burrowing. STITT also thought that the morphology of the thorax was such that the animal could have walked on the bottom (Fig 127.1). For such walking to have been possible, the inner branches of the limbs would have to have been of similar length, not successively shorter as portrayed. Species of *Stenopilus* occur in association with reef mounds and may have inhabited mud patches between the mounds; no trace of burrows has been found with them. WESTROP (1983) coined the term illaenimorph for illaenids and other such trilobites as *Stenopilus,* which had a smooth convex exoskeleton, and linked this form with life in a burrow. FORTEY (1986) argued for a like habit for the Ordovician *Symphysurus,* as did BREZINSKI (1986b) for the Carboniferous proetid *Proetides.* FORTEY and OWENS (1990a; see section on evolution, p. 249) discussed the occurrence of illaenimorphs during the Paleozoic. The term illaenimorph is being used in a broad, general manner, and it is doubtful that it should imply that all such species dwelled in burrows. So-called illaenimorphs are frequently referred to as *effaced,* a term that presumably implies a species that lacks the furrows that were present in its ancestors. Unless such an ancestral relationship has been demonstrated, a particular species is best described as smooth rather than effaced.

Arguments for the long-standing view that some large-eyed Ordovician trilobites were pelagic have been marshalled by FORTEY (1974a, 1985). He considered that an elongate body with a narrow (tr.) pleural region, convex axis, and deep apodemes was to be correlated with strong musculature and good swimming powers and that the large eye gave an all-around view. A vaulted cephalon is not thought to have been consistent with a benthic life, and the eye is unusual in having increased relatively in size during ontogeny. Analogy is with extant pelagic crustaceans that have large eyes. Geological distribution, particularly of *Opipeuter* (FORTEY, 1974a) and *Carolinites* (Fig. 128.2–3)—in presumed warm waters and in all facies—is consistent with an epipelagic habit. The occurrence of cyclopygids such as *Pricyclopyge* (Fig. 128.1) is confined to what are considered to have been deeper-water, off-shelf facies and is taken to suggest that they were mesopelagic, swimming at the lower limit of the photic zone. The peculiar paired organ on the third thoracic segment of some species may have been light sensitive, a special adaptation for this habit. FORTEY also distinguished two groups of pelagic trilobites: those like *Carolinites* (Fig. 128.2–3), having a broad, globular cephalon, long genal spines, and the poorly streamlined body of a sluggish swimmer, and others like the streamlined *Novakella* (Fig. 128.4), which may have been a faster swimmer and possibly predatory.

The large eye and wide geographical distribution have also been used as arguments for a pelagic habit of the Upper Cambrian *Irvingella* (Fig. 128.5), which has a wide (tr.) pleural region and is spinose. Largely on the grounds of their worldwide distribution, I considered that burlingiids such as *Schmalenseeia* were planktonic in habit (WHITTINGTON, 1981). These grounds alone are not adequate for such an assumption; burlingiids characteristically occur in outer shelf or slope facies, and their morphology affords no compelling evidence for assuming a planktonic mode of life (WHITTINGTON, 1994).

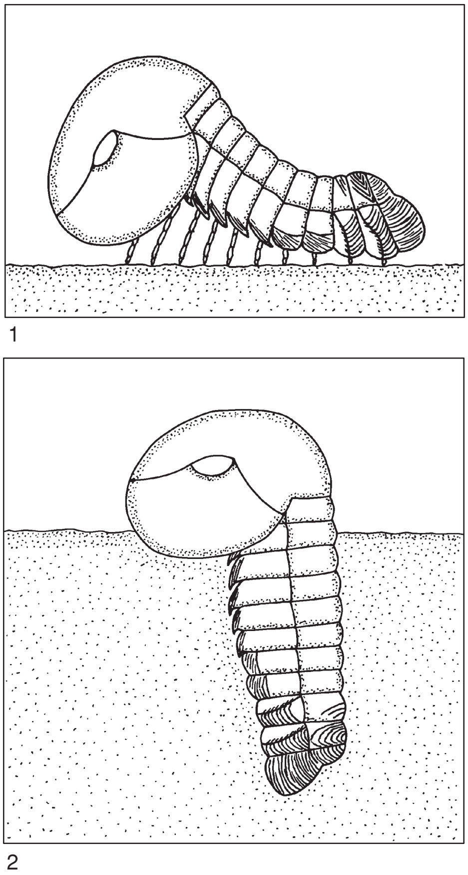

FIG. 127. *Stenopilus pronus* RAYMOND, Upper Cambrian, North America; reconstructions in lateral view; *1,* standing on the substrate and *2,* partially buried in a living position (Stitt, 1976, fig. 5–6).

Spinosity and wide distribution have long been used as arguments favoring a planktonic habit in odontopleurids. However, the convex cephalon, the border of which may bear spines including a long genal spine, appears to be well adapted, as explained above, to resting on the sea floor. CLARKSON (1969b) argued that two attitudes in life were possible for some odontopleurids, one

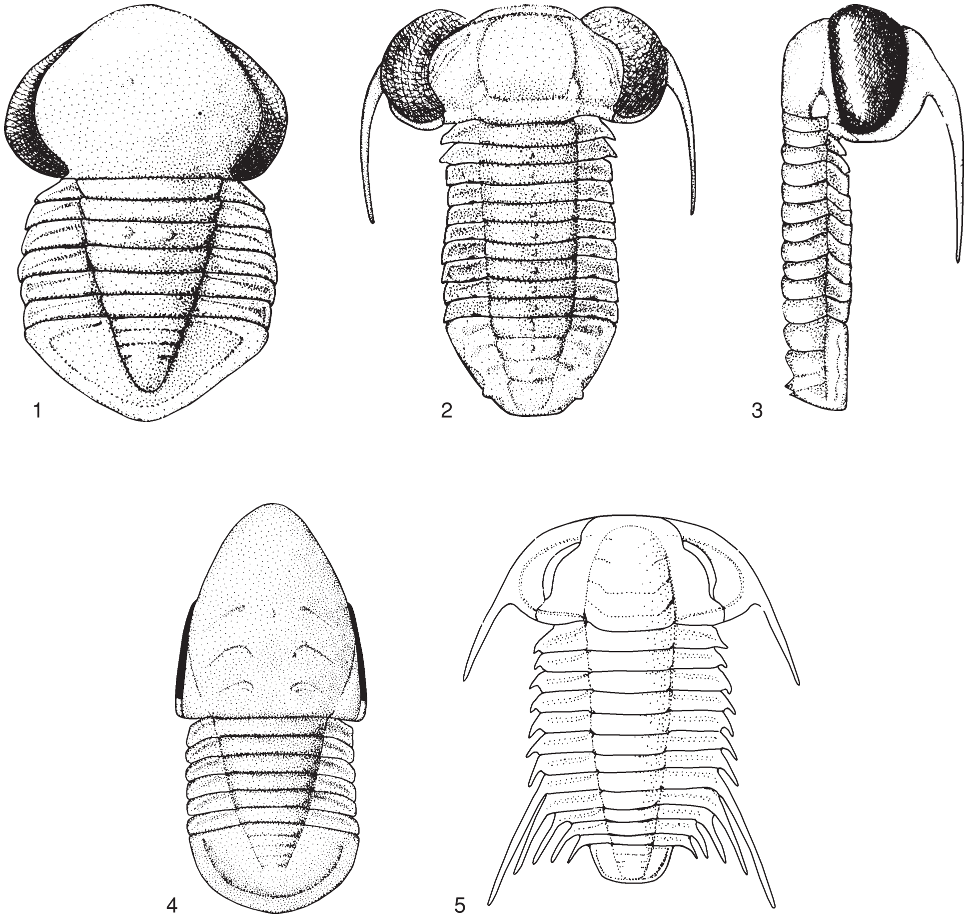

FIG. 128. Pelagic trilobites. *1,* Dorsal view of *Pricyclopyge binodosa* (SALTER), Lower Ordovician, ×1.5 to ×2. *2,3,* Dorsal and right lateral views of *Carolinites genacinaca* ROSS, Lower Ordovician, ×1.5 to ×2. *4,* Dorsal view of *Novakella bergeroni* (KLOUČEK), Ordovician, ×1. *5,* Dorsal view of *Irvingella* sp., Upper Cambrian, ×2. Reproduced by permission of the Royal Society of Edinburgh and R. A. Fortey (Fortey, 1985, fig. 1a,c,h, 5b, 9a).

with the thorax and pygidium stretched out horizontally above the bottom and a second with the cephalon tilted slightly back, the thorax and pygidium inclined downward and backward. The relative length and direction of the cephalic border and genal spines and of the pleural spines allowed these two attitudes, but in some odontopleurids the second was not possible. Arguments on habit based only on exoskeletal morphology are notoriously open to question, but a case can be made for regarding some holaspid odontopleurids as having been benthic, drifting and swimming over the sea bottom, rather than planktonic. The wide distribution may be accounted for by the early growth stages having been planktonic. On the other hand, a detailed investigation of the morphology and occurrence of the Ordovician *Selenopeltis* (HAMMANN & RABANO, 1987; cf. FORTEY & OWENS, 1987, p. 106), a characteristic odontopleurid from cooler waters, has suggested active swimming and little contact with the sea bottom, that is, an epi- or mesopelagic habit.

Exoskeletal spines may have been in part protective, projecting around and upward when the animal was resting on the sea floor and making it more difficult to attack when enrolled; they may have also inhibited sinking or aided in balance when drifting or swimming. Such spines are known in a wide range of trilobites, including *Nepea* (Fig. 23), odontopleurids such as *Apianurus* (WHITTINGTON, 1956d, fig. 19), the lichid *Ceratarges* (THOMAS & HOLLOWAY, 1988, fig. 313–317), and the styginid *Ancyropyge* (ORMISTON, 1967, pl. 2). A graduated array of genal spines (Fig. 22) and thoracic pleural and pygidial border spines may have propped the animal in position on the sea bottom, especially perhaps on a muddy bottom. The long, curving genal spines of some olenids (CLARKSON, 1973b, p. 761) and of some raphiophorids (e.g., of *Ampyx*, WHITTINGTON, 1959a, fig. 6) have been interpreted as an adaptation for this purpose (FORTEY & OWENS, 1978, p. 238), though their length and delicacy and the presence of a frontal glabellar spine in *Ampyx* and other raphiophorids suggests perhaps an additional flotational and balancing function. The long, curved macropleural spine in *Biceratops* (Fig. 44), for example, may have served a similar function. INGHAM (1968) referred to the stabilizing function of the thoracic macropleural spine of *Cybeloides* when the animal was digging into the sediment for concealment.

The frontal process was developed in very different groups—for example, in *Seleneceme* (WHITTARD, 1960), in asaphids, and in dalmanitids (where it may be bifid or trifid or an extraordinarily long spine)—and was spatulate in the calymenid *Spathacalymene* (TILLMAN, 1960) and species of the lichid *Platylichas* (THOMAS & HOLLOWAY, 1988, fig. 179). The pygidial mucro was developed in the asaphid *Megistaspis* (WANDÅS, 1984), which also has the frontal process (BOHLIN, 1960), and in some encrinurids (Fig. 57). In activity that required strong flexure of the body, the frontal process or posterior axial spine or mucro may have helped to keep the body in position on the substrate or may have aided in burrowing for concealment. Righting of the body after overturning may also have been aided by these spines, as well as by a median axial thoracic spine (cf. FORTEY, 1974b, p. 27–28). Such an activity would have required the ability to flex the body dorsally.

The mode of life of *Cryptolithus* (Fig. 129) and other trilobites with a bilaminar pitted fringe has long been a subject of discussion (RICHTER, 1921; STØRMER, 1930; PŘIBYL & VANĚK, 1986). CAMPBELL (1975) reexamined *Cryptolithus* using silicified specimens of the exoskeleton to reconstruct the musculature and combined this with what is known of the appendages and a study of trace fossils. A sound case was made for attributing these traces to the activity of *Cryptolithus,* although the role of the outer branches of the appendages in burrowing has been questioned (WHITTINGTON, 1980a, p. 189–190). CAMPBELL concluded that *Cryptolithus* was a benthic mud-feeder, able to dig down into the substrate, and with limited powers of walking and swimming. He argued that *Cryptolithus* had the ability to rapidly outroll the thorax and pygidium and that such an ability might have been used in swimming and in righting the animal if it were rolled over. The animal would have rested partially buried in the substrate on the outer portion of the fringe and genal spines, the innermost rows of pits exposed above the sediment. CAMPBELL argued that the fringe probably had a sensory function and that it contained a branching system of digestive glands. This study is exceptional in marshalling the range of evidence available in coherent support of arguments.

The general form of trinucleids such as *Cryptolithus* (Fig. 129)—the strongly vaulted cephalon, the bilaminar fringe, and long genal spine—is repeated in dionidids and is characteristic of *Harpes* and its allies, in which the fringe is prolonged posterolaterally. In harpidids (Fig. 17) and entomaspidids the form is similar, but the bilaminar fringe is less steeply inclined. LUDVIGSEN (1982) regarded *Bowmania* (Fig. 21) as an entomaspidid; the horizontal fringe of spines projecting from the cephalic border

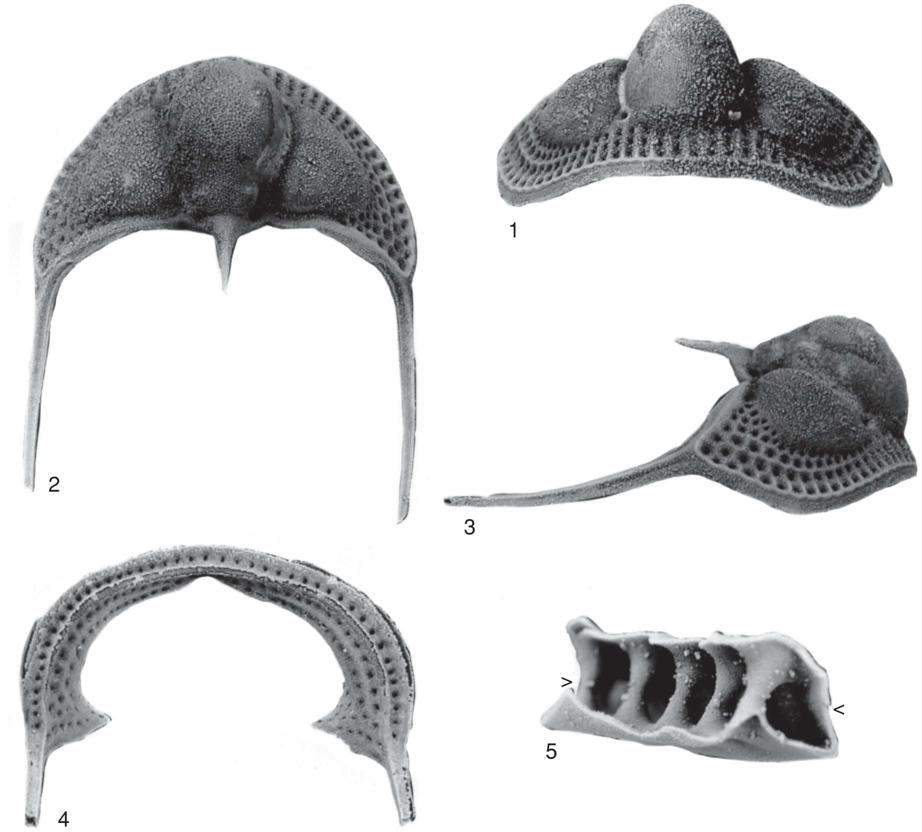

FIG. 129. *Cryptolithus tesselatus* GREEN, Middle Ordovician, Virginia, USA. *1–3,* Anterior, dorsal, and right lateral views of cephalon, ×4.5; *4,* ventral view of isolated lower lamella of fringe; genal spines incomplete, ×4.5; *5,* fragment of external portion of fringe, viewed from broken edge at girder, showing form of opposed pits; *arrows* point to position of suture, ×12.5 (Whittington, 1959a, pl. 20, fig. 1–3, 8).

and genal spine of *Bowmania* may have supported the cephalon on the sea bottom in the same manner as did the fringe of trinucleids and other groups mentioned above. These groups of trilobites were probably not all closely related; still much more distantly related were bathyurids (WHITTINGTON, 1953; LUDVIGSEN, 1978a, 1978b; FORTEY, 1979), in which the highly vaulted cephalon and concave cephalic borders, prolonged posteriorly, repeated the general form of trinucleids and harpetids. Bathyurids had large eye lobes and were typical of shallow-platform waters in North America. FORTEY (1979, p. 82) argued that bathyurids such as *Petigurus,* which had a relatively thick exoskeleton, sought partial burial in the sediment as a protection against nautiloid predators. *Punka* (FORTEY, 1979, p. 98) had a fan-shaped pygidium, and FORTEY argued that this bathyurid did not live in a burrow in the manner suggested for some illaenids but that the broad, concave border assisted the animal in gliding over the soft sediment. The convex axial region of bathyurids and other trilobites has been interpreted as providing a large area for muscle insertion, and hence as suggesting relatively powerful appendages. The vaulted cephalon and broad border seen in these very different Ordovician trilobites reappears, for example, in the Devonian *Mystrocephala* (WHITTINGTON, 1960a) and in *Cordania* (CAMPBELL, 1977), although in the latter the cephalic border is convex. The fringe, spines, or border around the vaulted cephalon of these different trilobites propped the cephalon on the sea bottom so that the thorax and pygidium were either stretched out well above it or inclined down toward it.

Articulation of the exoskeleton allowed flexure of the body in the sagittal plane, not only partial or complete enrollment but also concave-dorsal flexure (see discussion of thorax, p. 43). Many specimens of entire exoskeletons are preserved without disarticulation and show such back-arching or a sinuous combination of back-arching and partial enrollment. The *Rusophycus* type of excavation (see below) is also associated with back-arching. In odontopleurids the preannulus was most developed in anterior segments, suggesting that the strongest dorsal concavity was in this region. Geyer (1990b, p. 58–62) pointed out that the backward curvature (in dorsal view) of the anterior margin of the first four axial rings of the ellipsocephalid *Kingaspsis* made possible a dorsally concave flexure in the anterior portion of the body. The absence of such curvature in more posterior rings required dorsally convex curvature, giving an S-form in longitudinal profile. This suggested that it lived in a shallow excavation. Other ellipsocephaloids do not show this form of the anterior axial rings, and as a consequence the horizontally extended body suggests a life on the surface of the sediment.

Flexure of the body was essential to activity on the substrate, and the presence of coaptative structures in the exoskeleton of trilobites suggests that complete enrollment was a characteristic habit. It has long been urged that such enrollment was a protective reaction to attack by a predator and that a spiny exoskeleton when enrolled made an awkward target or an unwieldy mouthful. An elegant example in support of this idea is the restoration of the enrolled *Burmeisterella* by Wenndorf (1990, fig. 47). Clarkson and Henry (1973) also emphasized the function of coaptative devices in strengthening the exoskeleton against lateral shear by a predator. In studies of enrolled specimens of *Phacops* and *Greenops* from the Middle Devonian of New York State, Babcock and Speyer (1987) and Speyer (1988) discussed morphology, musculature, and enrollment behavior. They emphasized the role of rapid burial in the preservation of enrolled specimens and stressed that such enrollment was a response to such adverse conditions as a toxic environment or rapid influx of sediment. The possible musculature involved in enrollment and extension of the body has been discussed above (p. 101). A longstanding view (Raymond, 1920, p. 99) is that some trilobites used a rapid partial enrollment (i.e., a downward flick of the pygidium) to dart backward in an escape reaction. Campbell (1975), however, argued for the opposite action, rapid outrolling, as a swimming or righting action in *Cryptolithus.* Probably the ability of trilobites to flex the body into a dorsally concave curve was necessary to right the animal if accidentally overturned; a long, median, thoracic or pygidial spine may have aided in such an activity. Rapid, complete enrollment, alternating with partial outrolling (i.e., clapping the isopygous pygidium and cephalon together) has been suggested as a possible swimming mechanism. For *Agnostus pisiformis* this mode of locomotion is considered unlikely (Müller & Walossek, 1987), and it appears improbable for larger trilobites such as asaphids.

Babcock and Speyer (1987) emphasized that the complete encasement of the soft parts in tightly enrolled *Phacops* and *Greenops* protected the animal in conditions of sudden environmental change such as deoxygenation. As noted above in the discussion of enrollment in some dalmanitids, complete enrollment left a gap in the exoskeleton, and in *Symphysurus* (and possibly some other trilobites) minute passages remained. It is argued that such gaps aided in respiration while the animal was enrolled. By no means all trilobites had the soft parts sealed from the outside when enrolled, because those in which the outer portion of the pleura was spinose did not fit closely (cylindrical enrollment of Bergström, 1973a, p. 14). Complete enrollment may have been largely protective in function, but the protection was against different kinds of external factors.

The range of sculpture on the external surface of the exoskeleton and the transitions between types has been described in the section on microstructure and sculpture (p. 74–84). Prominent sculpture that thickened the exoskeleton may have strengthened it: for example, strong terrace ridges, closely spaced symmetrical ridges in an anastomosing or reticulate arrangement, or large tubercles that were not accompanied by any thinning of the cuticle. Sensory devices associated with sculpture have been described above. Miller (1975) argued that asymmetrical terrace ridges comprised a current monitoring system, while Stitt (1976) and Schmalfuss (1981) argued for the role of such ridges in burrowing and in gripping sediment. Fortey (1985, 1986) criticized aspects of these interpretations. Terrace ridges are present on the doublure of trilobites that may not have been benthic; on the other hand, such groups as cheirurids, encrinurids, calymenids, and dalmanitids lacked terrace ridges on the doublure, although probably many species were benthic. Terrace ridges and other forms of external sculpture may have had a different function in relation to behavior in different portions of the exoskeleton of species.

## TRACKWAYS, TRAILS, AND BEHAVIOR

Traces of activity are a source of information on behavior, if they may be attributed to trilobites with some confidence. The trackway produced by a trilobite walking in the manner described above (Fig. 99), however, would have had no distinctive features and been difficult to assign to its originator. More distinctive trackways were ascribed by Seilacher (1955, fig. 1; cf. Osgood, 1970, p. 351–352, fig. 17b, 20a, etc.; Seilacher, 1959, p. 390–391, fig. 2b) to trilobites walking in fashions that I have regarded as unlikely (Whittington, 1980a, p. 194–195, fig. 12). These doubts concerned the proposed relative lengths of the limbs, the suggestion that all the limbs moved in a single metachronal wave, and the idea that part of the body was dragged along. Traces that include groups of parallel scratches have been also attributed to trilobites (Osgood, 1975, p. 98–100), including the sideways raking reported by Seilacher (1955, p. 349–355, fig. 3, pl. 17, fig. 2). The manner in which such tracks were made and the supposition that they recorded a feeding activity are also open to question (Whittington, 1980a, p. 202).

The trace fossil *Rusophycus* is a bilobed hollow commensurate with a trilobite, which may show transverse or obliquely, forwardly directed grooves across the hollows. In the remarkable examples figured by Osgood (1970, pl. 57, fig. 6, pl. 58, fig. 4–5), the complete exoskeleton of *Flexicalymene meeki* closely overlies the bilobed trace and hence appears to have been its maker. Other examples of *Rusophycus* (e.g., Osgood, 1970, pl. 57, fig. 1, pl. 58, fig. 7–8; Hofmann, 1979, pl. 9) show impressions of the cephalic and pygidial doublures, genal spine, and hypostome, as well as paired impressions beside the midline. The latter are considered to have been made by the proximal portions of the appendages, the coxae. These excavations may have been made by flexure and extension of alternate limbs (Fig. 130), enabling the animal to dig vertically downward. Examples of *Rusophycus* from the Lower Cambrian of Sweden (Jensen, 1990), which intersect worm burrows, are considered to be traces of hunting burrows as trilobites dug down to capture worms. It has also been suggested that burrowing may have afforded protection from predators, for example, to trilobites that had the eye on the highest part of the gena or raised on a stalk, so that it was above the concealing sediment. Ingham (1968) and Hammann (1985) pointed out that the abilities to flex the body

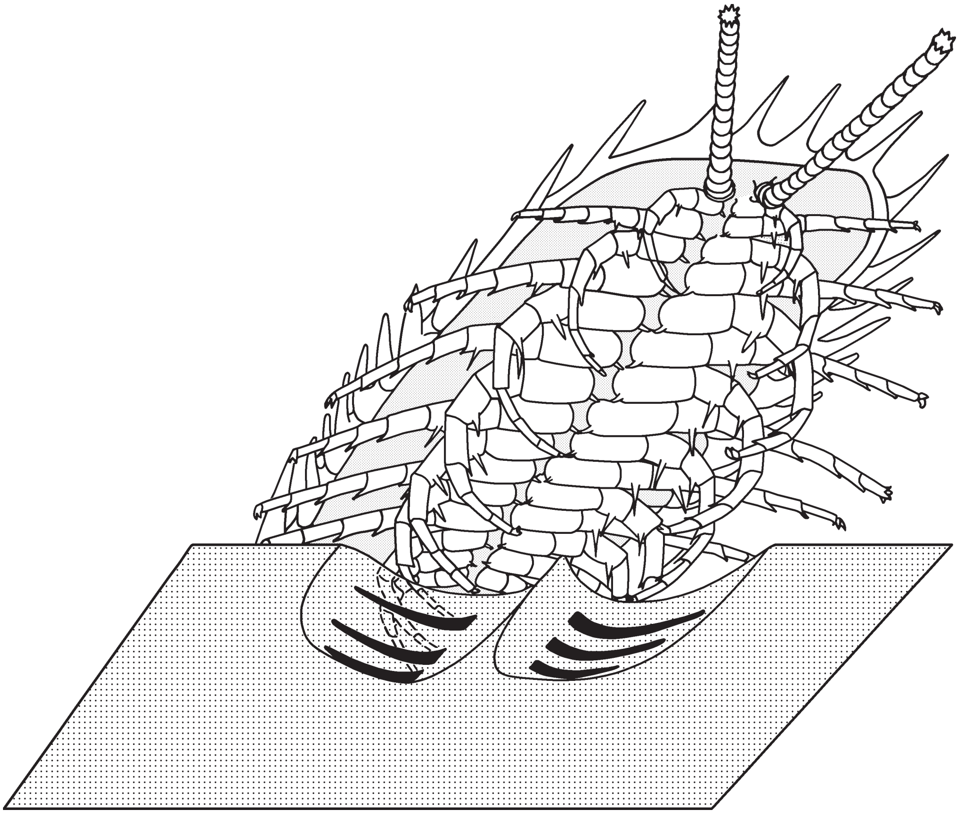

FIG. 130. Diagrammatic oblique ventral view of *Olenoides serratus* (ROMINGER) as it alternately flexed and extended pairs of limbs. Coxae and leg branches I to XV and their major ventral spines are shown; outer branches are omitted. During flexure the limbs dug into the sediment and excavated a shallow depression. Lower part of drawing shows surface of sediment (*coarse stipple*) from below, including that part of the bilobed excavation below the first seven pairs of appendages. The grooves in the excavation made by the flexure of limb pairs I, III, and V are shown in *black,* and on the left side *dashed lines* show the concealed distal portions of these limbs. Antennae assumed to be forwardly extended; cerci incomplete. Ventral integument *stippled* (Whittington, 1980a, fig. 14).

into a curve concave upward or to tilt the cephalon down may have aided in covering the dorsal surface with sand and that spines may have helped in digging and in giving stability. It may be reasonable to suggest that forward walking (Fig. 131) by a trilobite in wet sand, with the cephalon slightly lowered, may have been a form of plowing employed in search of food. Such an activity would have left a nondescript trace, since the footprints at the margins of the furrow are not likely to have been preserved. The resistance to such furrowing would have been greater the deeper the cephalon. It has been urged (SDZUY, 1957; HAMMANN, 1985) that the wedge-shaped form, high eye lobe, shovel-like anterior border of the cephalon, semicircular cross section, and smooth exterior of homalonotids are adaptations for burrowing. It seems reasonable to suggest that this form was an adaptation to making a deeper furrow. Study of trace fossils associated with Homalonotinae in the Lower Devonian led WENNDORF (1990, p. 15–21, fig. 7–12) to suggest the presence of grazing and hunting trails.

An undescribed trace fossil that shows a series of paired imprints repeated at intervals led MANTON (1977, p. 48) to suggest that a trilobite could launch itself off the bottom

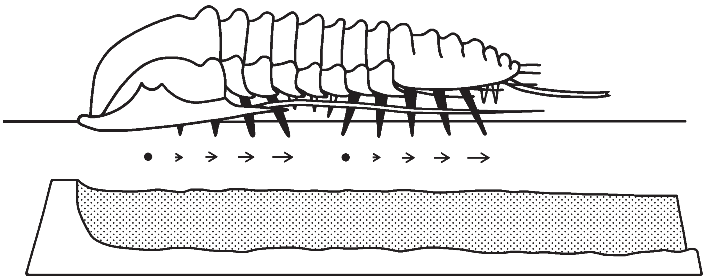

FIG. 131. Diagrammatic left-lateral view of *Olenoides serratus* (ROMINGER) in gait shown in Figure 99 but with cephalon inclined downwards and plowing shallowly into sediment; antennae curved back. *Horizontal line* shows position of sediment surface; left half of furrow (*stippled* ) shown in oblique lateral view in panel below. Other symbols as in Figure 99 (Whittington, 1980a, fig. 15).

and drift or swim before sinking again (Fig. 125). An asymmetrical Upper Cambrian trackway (BRIGGS & RUSHTON, 1980) in which scratches on one side are deep and transverse and on the other side are short or absent has been interpreted as probably having been made by a trilobite hopping in the manner suggested (Fig. 125) but under the influence of a current. This detailed description offers an alternative interpretation for dimorphic tracks of the type described by SEILACHER (1955) and OSGOOD (1970). Thus, walking on the bottom, digging and plowing shallowly in it, launching off the bottom and drifting or swimming, and oblique progress against a current are reasonable activities to suggest for benthic trilobites and appear to have been recorded by trace fossils.

The trace fossil *Cruziana* extends straight or curved for up to a meter or more, may be 5 to 6 cm wide, and is characterized by a V-shaped pattern of grooves directed forward and outward. Varied forms of the trace have been illustrated by SEILACHER (1970), CRIMES (1970), BIRKENMAJER and BRUTON (1971), and BERGSTRÖM (1976). Outside the deeper, V-shaped grooves may be a narrower zone with finer scratches, and outside these may lie a continuous, longitudinal groove. A large slab showing straight and curved trails crossing one another and associated with a bilobed *Rusophycus* excavation was figured by SEILACHER (1985, fig. 4), and the same association was earlier shown by CRIMES (1970, pl. 12a,b). *Cruziana* has been ascribed to the activities of trilobites because it is commensurate with them, is abundant in Cambrian and Ordovician shallow-water sediments, and the longitudinal groove suggests a trail left by the genal spine. A curved trace, such as might have been left by the anterior border of the cephalon, is apparently not known in *Cruziana* but is recorded from apparently similar Triassic trails, which were ascribed to xiphosurids (SEILACHER, 1985, fig. 2i). The large (maximum width 23 cm), *Cruziana*-like trail from the Triassic of South Africa may have a similar origin (SHONE, 1979); these post-Paleozoic examples lack the characteristic V-form of the grooves. The view that the early Paleozoic *Cruziana* trails were made as an open furrow in mud and subsequently cast by silt and sand (CRIMES, 1975; BALDWIN, 1977) was opposed by SEILACHER (1955, 1970, 1985) and BIRKENMAJER and BRUTON (1971). These latter authors considered that it was a furrow plowed in loose, wet sand and silt overlying a mud layer. The investigation by GOLDRING (1985) suggested that the latter view is a more likely mode of origin and emphasized the complex nature of the casting of the track.

The production of a *Cruziana* track required considerable expenditure of energy (cf. BERGSTRÖM, 1976, p. 1618) in what was presumably a search for food. A problem I find baffling (WHITTINGTON, 1980a, p. 200–

202, fig. 16) is the nature of the limb movements required to produce the V-shaped grooves, sets of which overlap each other in succession (BIRKENMAJER & BRUTON, 1971, fig. 10). Pairs of limbs would have to have been directed forward and outward and flexed in toward the midline to produce the grooves. Such a method of dragging itself forward, through a layer of sand, would have been clumsy and inefficient because of the heavy demand on energy. It would have been far more efficient for the animal to have plowed a shallow furrow in the manner shown in Figure 131, but this activity would not have produced *Cruziana*. These considerations lead me to doubt whether the *Cruziana* trail was made by a trilobite. Diagrams such as that of BIRKENMAJER and BRUTON (1971, fig. 10) imply that a trilobite could plow or even tunnel into a mud layer. The trilobite limb, however, was inserted at the base into an apparently uncalcified ventral integument, the coxa not having been joined to a calcified sternite that was linked to the dorsal exoskeleton. Thus any push on the substrate by the limbs could not have been directly transferred to the dorsal exoskeleton, only indirectly by the extrinsic limb muscles. The implication is that the animal's power to push through sediments was severely limited. Thus I remain skeptical of the ability of the trilobite to plow deeply and consider it most unlikely that it could have made a tunnel. GOLDRING (1985) did not observe tunnels in his study.

The very limited sample we have of trilobite appendages makes speculations on modes of life and habits hazardous. This is especially so in considering the function of the outer branch. In *Agnostus pisiformis* (MÜLLER & WALOSSEK, 1987) the long, outer branches of the first two cephalic limbs are considered to have been used in swimming and those of more posterior limbs in creating respiratory currents. In *Olenoides* (WHITTINGTON, 1975) and *Triarthrus* (WHITTINGTON & ALMOND, 1987) the shaft of the outer branch was apparently rigidly attached to the coxa, the long sheets of filaments directed backward and those of the successive limbs forming an overlapping series beneath the ventral integument of the pleural region. No specimen of either *Olenoides* or *Triarthrus* shows the filaments directed in an alternating series between the inner branches in what would have been a downward direction of the filaments. Nevertheless, it has been claimed (CRIMES, 1970; BERGSTRÖM, 1973a; CAMPBELL, 1975; SEILACHER, 1985) that fine scratch marks in some trace fossils, including those in the outer portion of *Cruziana* tracks, were made by the tips of the filaments of the outer branch. I have argued (WHITTINGTON, 1980a, p. 189) that this activity was unlikely, particularly by *Olenoides,* which has fine hairs at the tips of the filaments, but also for other trilobites. It appears probable that the outer branches, their sheets of filaments forming an overlapping series beneath the ventral integument, moved up and down as the limbs swung about a transverse axis and were respiratory in function (WHITTINGTON & ALMOND, 1987, p. 40). Respiration by *A. pisiformis* (MÜLLER & WALOSSEK, 1987, p. 37) may have been via the club-shaped projections from podomeres of the inner branches and possibly also via the ventral integument. Respiration through the ventral integument has been suggested for other trilobites, but there is as yet no evidence for or against this idea. JELL (1978a) has argued that the anastomosing genal caeca and the similar structures of the thorax and pygidium aided in respiration, rather than having been branches from the alimentary canal (ÖPIK, 1961a).

It has been stated frequently that some trilobites, or even most, were filter feeders (SCHMALFUSS, 1981; SEILACHER, 1985). It is thought that the trilobite was partially buried in sediment, and a filter chamber was maintained beneath the animal, extending from the frontal cephalic arch to the tip of the pygidium. GEYER (1990b, p. 60, fig. 36) suggested that in *Kingaspis* the downward flexure of the body posteriorly, which gave the small pygidium a downward and forward inclination, closed the filter chamber

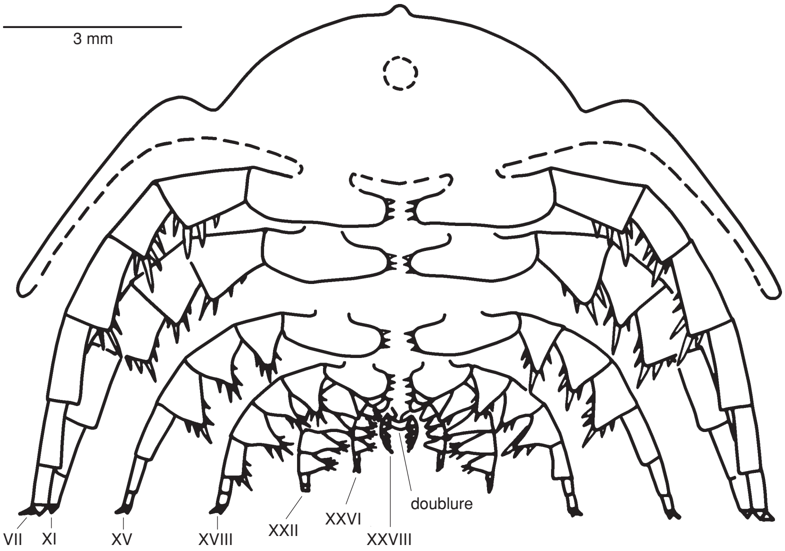

FIG. 132. *Triarthrus eatoni* (HALL), Upper Ordovician, New York, USA. Restoration of coxae and inner branches of selected appendages from the series I to XXVIII. Each pair vertical, shown looking posteriorly from cross section at fourth thoracic segment (beneath which is appendage VII). Stance as in Figure 86.2; median portion of doublure of pygidium visible in midline (Whittington & Almond, 1987, fig. 43).

posteriorly. In a cross section of a reconstructed trilobite, SCHMALFUSS (1981, fig. 7) portrayed the outer branch of the limb with the filaments vertical and held entirely above a small inner branch; the filaments are considered to have trapped particles drawn through the chamber. This reconstruction is misleading, for in no known example could the outer branch be held in this position (if we accept the evidence of taphonomy) and the downwardly directed attitude of the relatively small inner branch appears unlikely. Furthermore, the manner in which particles trapped by the sheet of filaments could be gathered and carried to the mouth is not explained. The array of spinose endites on the inner branches of the more posterior limbs of *Triarthrus* (Fig. 132) appears to constitute a food trap situated toward the rear of the animal. It is thought that this species and others displaying similar structures were predators and scavengers, as well as deposit feeders, food being carried forward in the midline to the mouth. The hypostome in some Cambrian and in most post-Cambrian trilobites was rigidly braced against the rest of the cephalon. It must have helped to guide food into the mouth and may have acted also as a plate against which the anterior coxae could scrape food (e.g., in odontopleurids). Until we have a greater knowledge of trilobite appendages, our understanding of the mode of life of these animals will remain inadequate.

## EXUVIATION AND THE FUNCTION OF SUTURES

Like other arthropods, trilobites molt. In extant arthropods, molting (HENNINGSMOEN, 1975; SKINNER, 1985) includes the processes of preparation for withdrawal from the old integument, the withdrawal and casting of the remains (exuviation or ecdysis), and the subsequent stages of growth. Presumably in trilobites the sequence of events was similar. Their relative duration is unknown, but as in living animals the stage with the fully developed exoskeleton and high activity may be assumed to have occupied a large portion of the time. Thus there presumably was a relatively short, immediately postecdysial stage when the integument was soft and rapid growth was possible. Secretion of the principal layer of the new exoskeleton followed. Support for such a sequence of events is found in two kinds of evidence.

(i) MILLER and CLARKSON (1980) and SPEYER and BRETT (1985) have described rare specimens of *Phacops* in which the exoskeleton was thin, fragile, and light colored. These specimens have the typical outer, prismatic layer of normal thickness, but the principal layer is thin, as thin as 25 µm compared to 500 µm in other specimens. The thin exoskeleton is interpreted as being postecdysial, the likelihood being that the principal layer was thickened inwardly to the final intermolt stage.

A specimen of *Olenoides serratus* from the Middle Cambrian Burgess Shale with appendages appears to be an example of an early postecdysial trilobite (Fig. 133). In contrast to other specimens from the same deposit (Fig. 85), this one shows little relief, and the surface is wrinkled (WHITTINGTON, 1975, 1980a). There is no mineralized exoskeletal layer; the pleural furrows and portions of the axial furrow are absent; and no eye lobe, eye ridge, or sutures can be seen. Thus the exoskeleton is preserved in a different manner from those of the intermolt specimens from the Burgess Shale, but the appendages are preserved in a similar manner.

(ii) Occurrence of a trilobite exoskeleton arranged in a particular pattern that involves inversion of certain portions can hardly have been chance, and the arrangement is interpreted as resulting from a manner of exuviation.

The earliest recorded example (SOWERBY in SEDGWICK & MURCHISON, 1840, p. 693, pl. 57, fig. 30; SALTER, 1864a; RICHTER, 1937, 1942) is the arrangement in the holaspid phacopid *Trimerocephalus,* the inverted cephalic exoskeleton (excluding the hypostome) lying with the posterior edge facing forward with respect to the outstretched **thoracopygon.** The dissociated hypostome may be situated anterior to and beneath the first thoracic segment. This arrangement is the so-called Salterian mode of molting. In genera of phacopids with large eyes, the facial suture (the anterior branches joined along the outer edge of the anterior border) was apparently fused; in well-preserved specimens of holaspides (CAMPBELL, 1967, pl. 15; HAAS, 1969, pl. 82) their course is only faintly visible. This fusion and the arrangements of portions of the exoskeleton suggest that exuviation may have been initiated by the opening of the hypostomal suture and facilitated by a split between cephalon and thoracopygon, enabling the newly molted animal to emerge anteriorly.

FIG. 133. *Olenoides serratus* (ROMINGER), Middle Cambrian, Canada. Photograph of specimen immersed in water; the thin, flattened, and wrinkled exoskeleton shows a trace of the alimentary canal beneath the right pleural region; portions of appendages project beyond the right side, ×2 (Whittington, 1980a, pl. 19, fig. 1).

Speyer (1985) has suggested (Fig. 134.8–12) that this split resulted from sharp flexure of the body anteriorly in an upright position.

In studies of ontogenetic series of species of *Trimerocephalus* (Maximova, 1955; Osmólska, 1963) that lacked eyes, adult molt assemblages are in the Salterian mode. In meraspides, however, molt assemblages have the dorsal exoskeleton articulated or only slightly displaced, the detached cephalic doublure lying beneath the cephalon or the anterior portion of the thorax. In these meraspides the facial suture, which crossed the lateral border and continued forward in the border furrow, was functional, so that it and the hypostomal suture opened to facilitate ecdysis. The change in mode of molting in holaspides resulted from fusion of the facial suture, and as Osmólska pointed out, this change seems to have occurred in a number of phacopid genera. Growth stages of different Phacopina (Chatterton, 1971, 1980; H. Alberti, 1972) show that the suture was functional in meraspides. Speyer's (1985) studies on molt assemblages of holaspid *Phacops rana* show that the Salterian mode was rare, arrangements in which the thoracopygon was inverted and the cephalon in various attitudes being more common. He also suggested the behavior from which such arrangements resulted (Fig. 134.1–7). Molt arrangements of other Phacopina, in which the facial suture was apparently fused, are those of *Greenops* (Speyer, 1985) and *Toxochasmops* (McNamara & Rudkin, 1984). Wenndorf (1990, p. 28–30, fig. 15) found that the remains of Homalonotinae in Lower Devonian sandstones were current-sorted, separated exoskeletal parts, the conjoined cranidium, free cheeks, and rostral plate being rarely present. In shales, however, the remains included the cranidium, free cheeks, and rostral plate joined together and the articulated thoracopygon minus the anterior two or three segments. The inverted cephalon (lacking the hypostome) lay adjacent to or under the thoracopygon, rotated 180° in relation to it. This suggested that the Salterian mode of molting occurred in Homalonotinae in addition to a mode in which the facial suture opened.

It has long been stated that in the odontopleurid *Ceratocephala* (Barrande, 1852, p. 125; Whittington & Evitt, 1954, p. 53; Bruton, 1968b, p. 49; Chatterton & Perry, 1983, p. 32, 39, 48) the facial suture was fused in larger individuals. Chatterton and Perry's studies show that such fusion took place in the holaspid period in species of several genera. In the larger specimens of these species, the cranidium and librigena are preserved fused together, but the rostral plate and hypostome are detached. Thus rostral, connective, and hypostomal sutures were functional; and, as Henningsmoen suggested (1975, p. 197), opening of these sutures may have initiated exuviation and enabled the freeing of the cephalon from the old exoskeleton. The silicified growth stages of odontopleurids (Whittington, 1956b; Chatterton & Perry, 1983) strongly suggest that the facial suture was functional. Hence, in odontopleurids, as in certain Phacopina, exuviation in meraspides was in a mode different from that in large individuals.

A presumed molt configuration of a specimen of *Paradoxides,* originally described by McNamara and Rudkin (1984), has been shown (Whittington, 1990) to consist of the **axial shield** with the librigenae and rostral-hypostomal plate inverted beneath it. I have suggested (Fig. 135) maneuvers in exuviation that would have resulted in this arrangement. I follow Henningsmoen (1975) in considering that the primary purpose of the cephalic sutures was to provide an anterior opening for exuviation. This opening freed the vital soft parts of the cephalon—the eye surface by the circumocular suture or the connective sutures, allowing the librigenae to be pushed outward by the emerging cephalon, the attached hypostome freed, and the backward facing mouth released. Egress forward was also essential to allow the newly molted animal to withdraw the genal and pleural spines and the appendages from the discarded cuticle. The dragging forward of

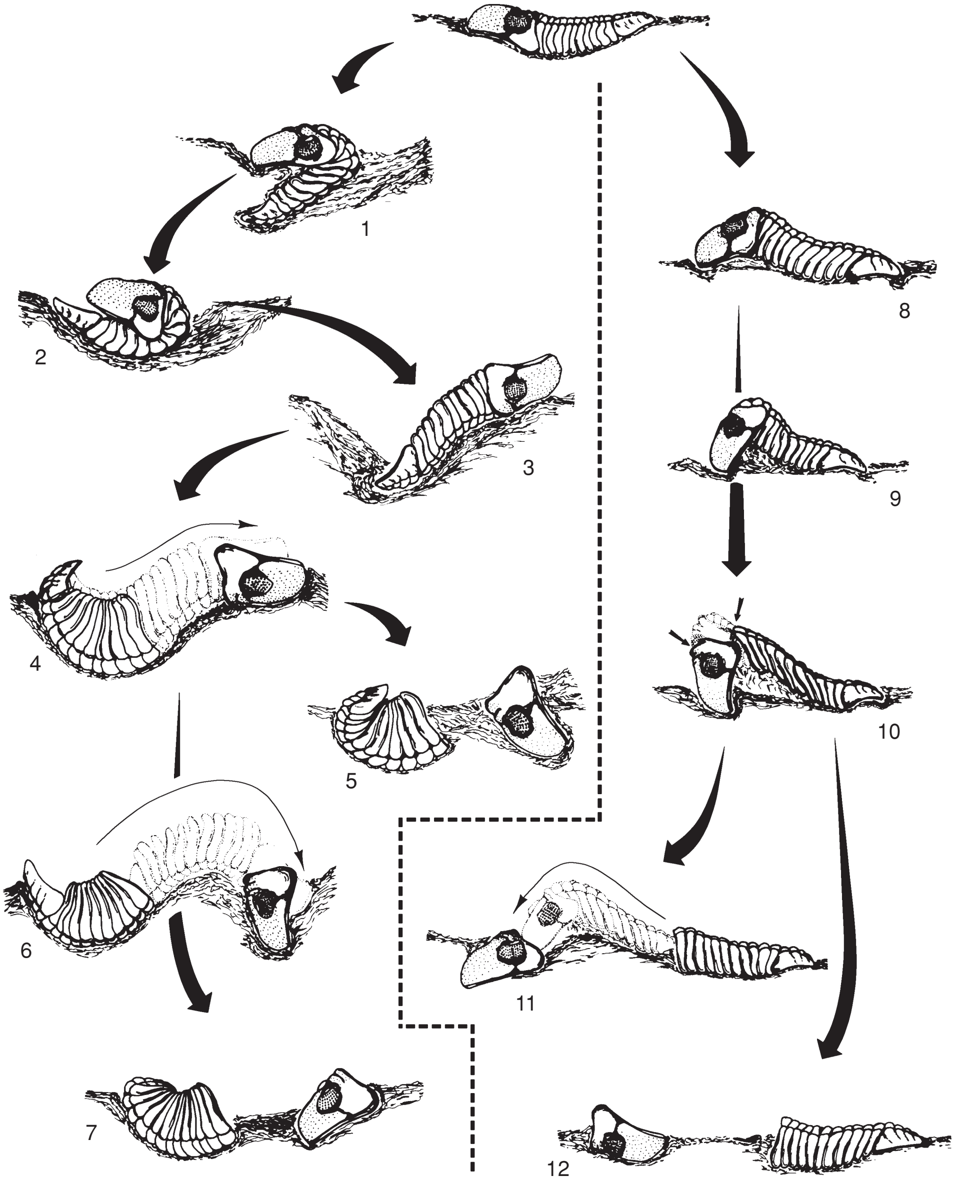

FIG. 134. Manner of exuviation in *Phacops rana* (GREEN). *1–7,* Body inversion procedure. Thoracic flexure (*1,2*) resulted in inversion of the body (*3*). Erratic contraction and expansion of longitudinal muscles (*3,2,3*) resulted in opening of sutures (*4*). As the animal withdrew from the molted exoskeleton, the cephalon may have remained inverted (*5*), or extreme arching of the body may have resulted in the cephalon lying dorsal side uppermost (*6,7*). *8–12,* Body upright procedure. The cephalon is flexed downward as the anterior portion of the thorax is arched (*8,9*) and a suture opens between cephalon and thorax (*10*). Emergence of the newly molted animal may (*12*) or may not (*11*) have inverted the cephalon (part 12 is the so-called Salterian mode). Reproduced by permission of the Royal Society of Edinburgh and S. E. Speyer (Speyer, 1985, fig. 7).

the exuviae in this withdrawal is thought to have overturned the rostral-hypostomal plate and librigenae. I consider that a split between cranidium and first thoracic segment

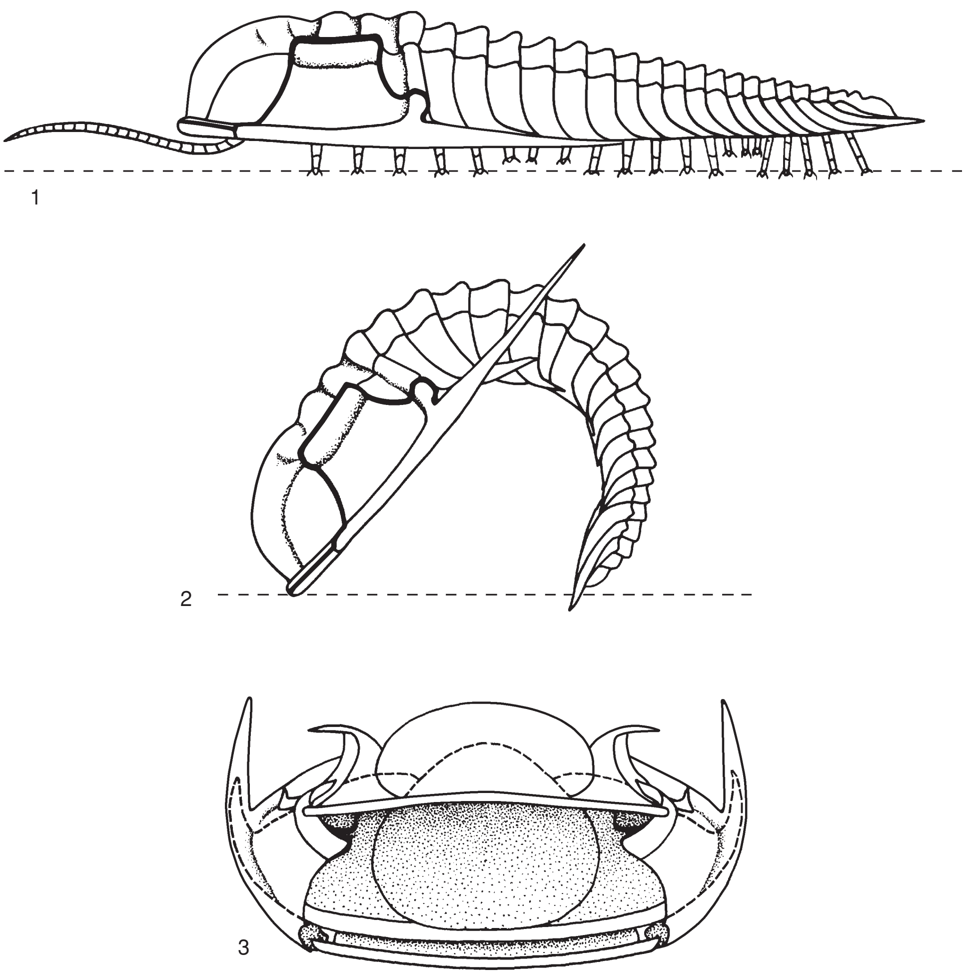

FIG. 135. Suggested maneuvers during exuviation of *Paradoxides* sp.; *1,* left lateral view, showing assumed appendages, with suture line *thick; 2,* flexure of body above substrate, with the pleural spines of thoracic segments 15 to 17 used to dig into sediment (limbs omitted); *3,* anterior view as sutures opened and cephalon of molted animal (*stippled with dashed outline*) began to withdraw from old exoskeleton and emerge; *4,* left lateral view of molted animal (*stippled, dashed outline of cephalon,* three anterior walking legs indicated) as it emerged from exuviae, which included rostral-hypostomal plate and appendages shown diagramatically; *5,* exuviae after emergence of molted animal (includes mineralized exoskeleton, cast ventral cuticle, and cuticle covering appendages), portrayed perched on substrate, the librigena and rostral-hypostomal plate having been rotated back from position shown in part 4 (Whittington, 1990, fig. 2–6).

(advocated by McNamara and Rudkin) was not necessary and hence reject the sharp downward flexure of the body anteriorly that they suggested (McNamara & Rudkin, 1984, fig. 11). Their proposals were made with reference to a species of *Ogygopsis,* but in this example, as well as those of *Oryctocephalus* they studied, I consider that maneuvers like those shown in Figure 135 may explain the specimens. A specimen of *Olenellus* (Whittington, 1989, fig. 8) has the perrostral plate inverted beneath the thorax, the posterior tips of the plate lying directly beneath their original position. I regard it as a molt configuration resulting from similar maneuvers. I agree with Hennings-

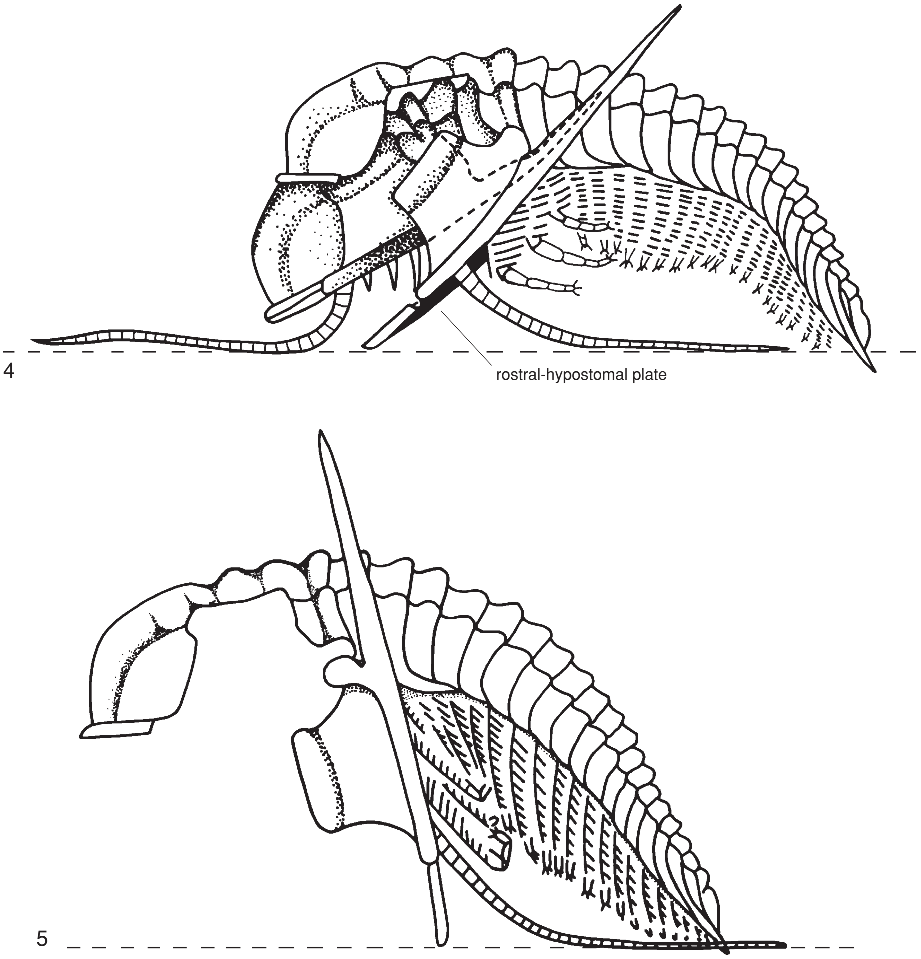

Fig. 135. *For explanation, see facing page.*

Moen (1975) that emergence forward at exuviation was normal for most trilobites in which the sutures were functional and that it was important to have no hindrance to such egress. As was pointed out in describing the course of sutures, some species with a frontal cephalic process (e.g., *Spathacalymene* or certain asaphids or dalmanitids) have sutures that would have aided in freeing these processes. While inversion of parts of the exoskeleton may have taken place in the course of exuviation, it may have occurred rarely rather than commonly.

Henningsmoen (1975) discussed aspects of molting, and descriptions and discussions of many supposed molt configurations have followed (Fortey, 1975b; Ludvigsen, 1979a, 1979b; McNamara & Rudkin, 1984; Speyer, 1985; McNamara, 1986c; Whittington, 1990). The exuviae (Fig. 135.5) were presumably abandoned on the surface of the substrate and consisted of the mineralized exoskeleton held together by articulatory membranes and ventral cuticle, including that which had sheathed the limbs. Decay of the unmineralized cuticle would lead to progressive dismemberment of the exuviae. The weakest link was that between cranidium and first thoracic segment, so that the large cranidial sclerite was likely to have been detached first and may have been inverted nearby or carried farther away. Separation of librigena, rostral plate, and hypostome and then dismemberment of the thoracopygon may have followed. Such a decay series of exuviae, at whatever point it was interrupted by burial, could be invoked to explain some specimens thought to be exuvial configurations. Rapid burial would have been essential to preserve exuviae, and I find it difficult to accept that burial could take place without some disturbance of the remains. I do not assume that portions of the old mineralized exoskeleton were carried away on the newly molted animal, but rather that exuviae were normally complete. Distinguishing between the complete (or almost complete) exoskeleton derived from a carcass and that from exuviae poses problems. Symmetrical inversions of portions of the exoskeleton beneath the axial shield may be indicative of exuviae. I have questioned (WHITTINGTON, 1990), for example, whether the specimens of *Redlichia* described by MCNAMARA (1986c) are to be regarded as derived from a decay series of exuviae or at least in part from carcasses. Because the exoskeleton of the genal spine was an elongate cone, it appears that in molting the animal must have emerged forwards in order to withdraw this spine (Fig. 135.3–4). The opening of the cephalic sutures provided the means of egress and made superfluous an opening between cephalon and first thoracic segment.

In exuviation the cephalic sutures played an essential and primary role, for even in holaspides of those species in which facial sutures were fused the connective, rostral, or hypostomal sutures were functional. Opening of a joint between cephalon and thorax was probably a secondary procedure. For most species the ability to enroll the body was necessary to the process and probably also the ability to flex the body in a concave-upward arch. CHATTERTON and PERRY (1983, p. 17) commented that the function of the preannulus in odontopleurids and other trilobites was to facilitate such arching. The remopleuridid *Hypodicranotus* (WHITTINGTON, 1952b) was unable to enroll because of the long, forked hypostome, so that opening of the cephalic sutures must have begun the process of exuviation. The role of sutures in this process has not been denied, but it has been argued that the sutures may have been lines of movement in the exoskeleton, especially the hypostomal suture. In trilobites with a conterminant hypostome, such movement about the hypostomal suture does not appear to have been possible (WHITTINGTON, 1988a, 1988b). There is thus no evidence that cephalic sutures served any purpose other than exuviation. The claim that any suture was fused needs careful consideration, for it may have been that in trilobites with a fully developed exoskeleton (between molts), the sutures were closed. A fossil from that stage would show a fused suture, but a molted exoskeleton would not.

It is widely assumed (e.g., HENNINGSMOEN, 1975) that most fossils of trilobites, which are disarticulated portions of the exoskeleton, are dissociated portions of exuviae. The less common, entire exoskeletons, extended or enrolled, are the remains of dead animals or in some cases derived from exuviae. Both types of fossils may have thick exoskeletons, up to 0.5 mm, which may include the calcified lenses of the eye (MILLER & CLARKSON, 1980). It may have been, therefore, that trilobites did not resorb the inorganic salts before ecdydsis, as many living crustaceans do. MILLER and CLARKSON pointed out the considerable effort in renewal of calcite that this would imply. Measurements by PALMER (1957) on *Olenellus,* and by HUNT (1967) on *Trinodus,* have shown the large number of instars during development, more than the number of thoracic segments. HUNT noted that growth of *Trinodus* terminated after a fixed number of instars, but it is doubtful if this was true for non-Agnostida. It is usual when collecting such trilobites to find fragments of far larger individuals than any represented by entire cranidia or pygidia, for example. Continued growth would have provided many exuviae.

## CLUSTERS AND MONOSPECIFIC OCCURRENCES

Considerable numbers of well-preserved, entire, or only partially disarticulated trilobite exoskeletons occurring close together have been remarked on by authors. One such example, a large slab from the Ordovician Bromide Formation of Oklahoma, contained some 111 complete exoskeletons of the asaphid *Vogdesia bromidensis* (LAUDON, 1939; LOEBLICH, 1940; SHAW, 1974). The individuals are similar in size, about half are inverted, and other slabs (BRANSON, 1965) show that the hypostome is present in many. The remains may be of carcasses, not of molted exoskeletons. Another occurrence of many complete, similar-sized exoskeletons of *Dalmanitina socialis* in Upper Ordovician sandstones in the former Czechoslovakia (PŘIBYL & VANĚK, 1976, pl. 8, fig. 1) is attributed to mortality following rapid burial during a storm. Different is the thin dolomitic layer from the Ordovician Maquoketa Group in Missouri (BREZINSKI, 1986a), in which 97 individual exoskeletons of the raphiophorid *Ampyxina bellatula* were found. These specimens exhibited a size range, and the absence of the librigena suggested that they were molts. BREZINSKI demonstrated size clusters in his sample and related them to instars. He interpreted this monospecific occurrence as that of an opportunistic species. These conclusions, however, have been criticized by SHELDON (1988).

Studies by SPEYER and BRETT (1985) and SPEYER (1985) draw attention to another example in Middle Devonian rocks from New York. These are considered to be *in situ* assemblages of the Phacopina *Phacops rana* and *Greenops boothi* and of the proetid *Dechenella rowi.* Each cluster is of three or more exoskeletons of a single species that are close together, of similar size, and considered to be of two types. *Body clusters* appear to be of corpses, while *molt clusters* are of thoracopyga in close proximity to corresponding cephala. The two types of clusters are of individuals of similar size and occur in close lateral proximity along a common stratigraphical horizon. It is considered that such clusters represent a related phenomenon. An analogy with living marine arthropods is drawn, suggesting that the clusters resulted from a behavioral pattern of a species gathering at a particular age (as indicated by the size), prior to synchronized ecdysis and reproduction.

The occurrence of complete enrolled holaspid Agnostina in siliceous nodules from the Ordovician of Czechoslovakia (PEK, 1977) packed closely together in a line has been interpreted as resulting from the adults having lived attached to algal strands. No trace of such strands remains, but the linear orientation is striking.

## ABNORMALITIES OF THE EXOSKELETON

Abnormalities in a single exoskeleton may include such features as a lack of symmetry between paired structures (one of the eyes or one of the major spines larger than the other), or in the pleural region of thorax or pygidium an irregularity of the segments or furrows of one side, or a marginal embayment or projection on one side. Figure 136 is a selection of examples from OWEN's review (1985); additional occurrences were described by RUDKIN (1985), ŠNADJR (1985), HESSIN (1988), and BABCOCK (1993). The latter author described healed injuries and malformation and discussed the evidence for behavioral asymmetry. Abnormalities in the anterior axial region are extremely rare, but many have been recorded in the pleural region and axis of the pygidium (e.g., RUDKIN, 1985). This may be a reflection of the greater vulnerability of the peripheral parts of the animal to injury by accident or predation and the fact that abnormalities are most readily recognizable in thorax and pygidium. The possibilities of injury from predation by other arthropods (WHITTINGTON & BRIGGS, 1985), cephalopods (ŠNADJR, 1981b; RUDKIN, 1985), sea anemones (ALPERT &

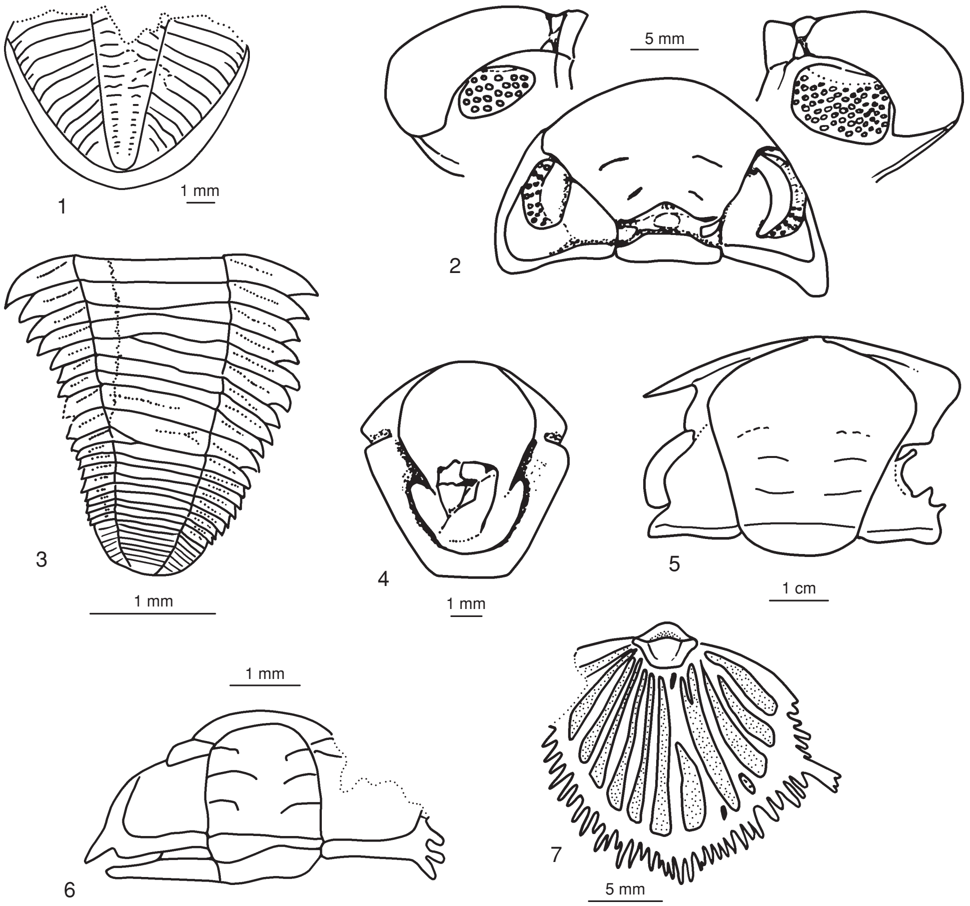

FIG. 136. Abnormalities in the exoskeleton. *1, Dechenella maclareni* ORMISTON, irregular furrows of axis and pleural field of pygidium; *2, Phacops rana* (GREEN), abnormal left gena and eye lobe; *3, Emuella polymera* POCOCK, part of thorax showing additional half segments; *4, Ceraurinella* sp., broken and partially cicatrized median body of hypostome; *5, Paradoxides gracilis* (BOECK), damaged right fixigena; *6, Rossaspis superciliosa* (ROSS), anterior two thoracic segments fused and partially incorporated into cephalon; *7, Scabriscutellum speciosum* (HAWLE & CORDA), irregular pleural spine and rib development on one side of the pygidium. Reproduced by permission of the Royal Society of Edinburgh and A. W. Owen (adapted from Owen, 1985, fig. 1b,e,g,j, 3b, 4a,h).

MOORE, 1975), starfish, and fish have been discussed; but as OWEN (1985) noted, many abnormalities may have resulted from damage sustained during or immediately after exuviation, either in the process of shedding the old exoseleton or by accidental damage or predation when the exoskeleton was thin. It is difficult to distinguish between the effects of any such injury and those that may have been caused by genetic or developmental malfunction. The unique, damaged hypostome in Figure 136.4, which shows fracture and disarrangement of fragments externally and callus internally, appears to be a clear instance of injury and repair in the same intermolt period. OWEN (1985) suggested stages over a series of molts of repairs to the trinucleid fringe. On the other hand, OWEN attributed abnormality in a cephalon of *Phacops* (Fig. 136.2) to genetic or developmental malfunction rather than to injury. Abnormalities resulting from infestation by parasites might be manifested by swellings on or borings in the exoskeleton. Exoskeletal swellings have been described (Šnadjr, 1978) and were formed during life, but it is difficult or impossible to decide whether, in a shed exoskeleton or in a carcass, borings were made when the animal was alive. As Owen (1985) pointed out, while it may be difficult to establish the causes of abnormalities, their study may shed light on paleoecology.

## DIMORPHISM

The presence of two forms, one relatively long and the other relatively broad, was noticed by Barrande (1852, p. 102–104) in many species in his collections. He suggested that these differences were not an expression of individual variation but of sexual dimorphism. Salter (1865, p. 127; 1866a, p. 132) followed this lead, regarding supposedly long (male) and broader (female) specimens as evidence of sexual dimorphism in certain asaphids, for example. Measurements by C. P. Hughes (1979, p. 126, 142), however, showed no evidence for this distinction. As Kielan (1960, p. 41–42) and Henningsmoen (1960, p. 207–210) have pointed out, these supposed differences are the result of deformation, such deformation being common in finer-grained, terrigenous, clastic sediments. When the deformation is asymmetrical it is more readily observed, but when symmetrical, either lengthening or broadening the specimen, it is less obvious; and there are many examples of its having been used as a specific distinction. Trilobites in limestones are preserved in full relief, without distortion, and supposed long and wide forms have been noted, for example of the illaenid *Stenopareia glaber* (Owen & Bruton, 1980, p. 16). In this instance, however, measurements of a larger sample (Bruton & Owen, 1988, p. 243) have shown no dimorphism. Differences between specimens in a single character, rather than in shape, have been used to discriminate dimorphs. One example is the presence or absence of the posterior doublure of the pygidium in *Redlichia* (see earlier section on the pygidial region, p. 59). While Öpik (1958) regarded this as an example of sexual dimorphism, Sdzuy (1959) attached little significance to it. More information is needed on the exact morphological differences between specimens of *Redlichia* and on their occurrence. In specimens of Ordovician *Selenoharpes* and *Bathyurellus,* the prolongation posteriorly of the genal region has been shown to differ in length and shape (Whittington, 1963, p. 23), the sample in the former case being large enough to suggest that the difference may not be merely an expression of individual variation. In *Platycalymene duplicata* C. P. Hughes (1969) noted that although wide and narrow forms could not be distinguished, the cephala could be divided into those with and without an occipital tubercle. The occurrence of specimens in the same stratum that may be separated into two distinct groups on a number of characters presents the problem of whether to regard them as dimorphs of a single species or two separate species (e.g., Hintze, 1953, p. 150; Whittington, 1965, p. 298). Hu (1964a, 1964b, 1968, 1969, 1971, 1981, 1983, 1984, 1985b, 1986) developed his views on sexual dimorphism in trilobites as a result of studying large collections and by a general analogy with such dimorphism in extant arthropods. However, the data presented on characters demonstrating the occurrence of dimorphs, in the form of drawings, photographs, and ratios of dimensions (Hu, 1968, fig. 2; 1969, fig. 2) are inadequate. A more detailed study of the eye of a Carboniferous species of *Paladin* by Clarkson (1969a) was thought to show dimorphism, but this is no longer considered to be the case (Clarkson & Zhang, 1991). The claims of dimorphism or even of polymorphism in species of phacopids (Eldredge, 1973; Campbell, 1977) were rejected by Ramsköld and Werdelin (1991), mainly on the grounds that the collections used were from more than one locality or not from a single horizon. If dimorphism in the exoskeleton of a species of trilobite does occur, it has not yet been satisfactorily demonstrated. If it is

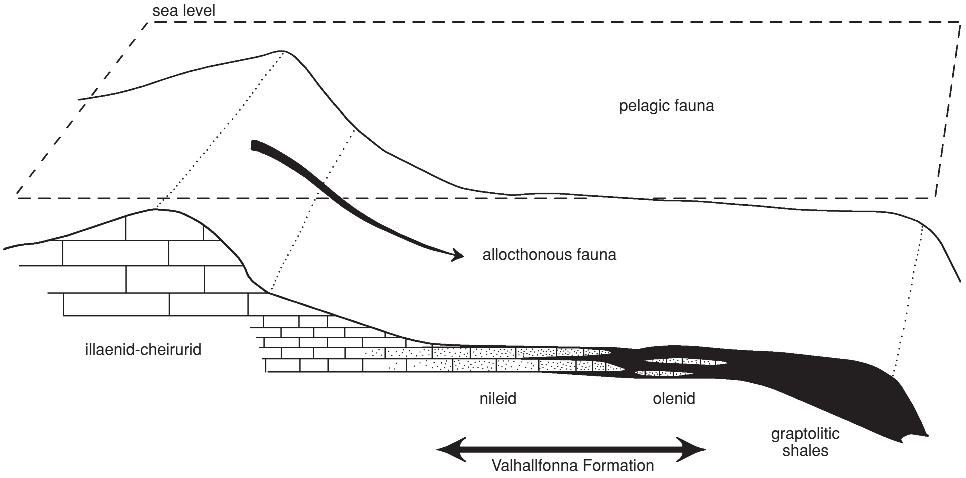

FIG. 137. Paleogeographical model showing disposition of communities of trilobites (illaenid-cheirurid, nileid, and olenid) across an Early Ordovician shelf sea. The communities are preserved in Spitsbergen in the Valhallfonna Formation, which accumulated in the area shown by the *heavy black arrow.* Remains of the shallow water illaenid-cheirurid community were brought into the area as shown by the *curved arrow.* Rock types graded from massive, light-colored limestones on the left to platy, black limestone and graptolitic shales on the right (Fortey, 1975a, fig. 3).

shown, the decision on whether to regard it as evidence of sexual dimorphism or to rank it as a subspecific or specific difference will be arbitrary.

## DISTRIBUTION IN ROCK TYPE, TIME, AND SPACE

It is clearly recognized that particular taxa occur commonly in one kind of rock; for example, olenid trilobites occur in dark shales (HENNINGSMOEN, 1957a) and trilobites with relatively smooth exoskeletons in pure, white limestones (LANE, 1972). A study of the abundance of trilobites in a section of Lower Ordovician rocks in Spitsbergen led FORTEY (1975a) to distinguish communities, each with a characteristic suite of genera. Each assemblage of species occurs in a different rock type, considered to be related to environments in shallow to deeper water (Fig. 137). The olenids occur in black, graptolitic limestones and shales, and articulated exoskeletons and growth series are preserved. These and other evidences suggest an autochthonous assemblage, and FORTEY (1989, p. 339) favored the view that olenids were adapted to the dysaerobic environment in deeper water. Dark, flaggy limestones and shales enclose nileids, raphiophorids, and other genera of the nileid community; olenids are absent; and the associated fauna more varied. The evidence suggests an environment of quiet, well-oxygenated waters. The illaenid-cheirurid assemblage occurs in thin bands of lighter limestone, the broken and disarticulated exoskeletons being part of the evidence for this being an allochthonous assemblage swept in from shallower waters. In addition to these faunas, species of *Carolinites* occur throughout the section in equal abundance in the different communities. The worldwide distribution of *Carolinites* and the unlikelihood of its having been a benthic trilobite of wide tolerance suggest that its habit was pelagic. The existence of a fourth, pelagic community is thus argued, which included other trilobites and graptolites. In other parts of the world, for example the contemporaneous rocks of southern Wales (FORTEY & OWENS, 1978, p. 237–240), the shallower-water shelf faunas were different, the deeper-water ones being more

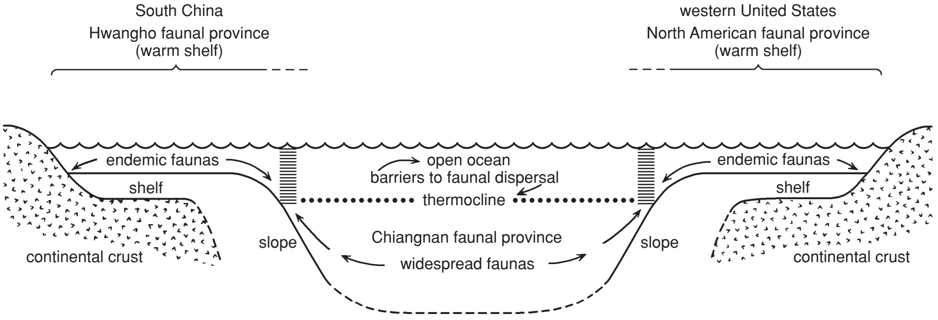

FIG. 138. Inferred habitat relationships between Upper Cambrian trilobite faunal provinces in South China and the western United States (Cook & Taylor, 1975, fig. 4).

similar to those of Spitsbergen. The contrasts are explained in terms of paleogeographical position and presumed water temperatures.

Another study (COOK & TAYLOR, 1975; TAYLOR, 1976, 1977) of autochthonous slope and allochthonous shelf trilobites of late Cambrian age from Nevada showed that some of the former were also known in China, Korea, and Alaska. From analogy with distribution of living isopod crustaceans (TAYLOR & FORESTER, 1979), it was argued that the slope faunas in lower latitudes were inhabitants of cooler water below the thermocline and hence of wide geographical distribution (Fig. 138). Similarly, it was argued by BABCOCK (1994b) that Middle Cambrian trilobites of Baltic type inhabited the cooler waters of the outer shelf facies of northern Greenland, typical Laurentian faunas occurring in contemporaneous shallow-water shelf facies. These slope faunas may also have inhabited the cold, shallow waters of high latitudes.

Associations or assemblages of trilobites in Cambrian (JAGO, 1973; REPINA, 1979; LUDVIGSEN & WESTROP, 1983a; THEOKRITOFF, 1985), Ordovician (BERGSTRÖM, 1973c; APOLLONOV, 1975; PŘIBYL & VANĚK, 1976; LUDVIGSEN, 1978b; HENRY, 1989; HAVLICEK & VANĚK, 1990; HENRY & DESTOMBES, 1991), Silurian (THOMAS, 1980; MIKULIČ & WATKINS, 1981; CHLUPAČ, 1987), Devonian (CHLUPAČ, 1983; WENNDORF, 1990), and Carboniferous (PRENTICE, 1967; BREZINSKI, 1986b, 1988a, 1988b) rocks of different facies have been discriminated as a result of detailed stratigraphical studies and the making of large, new collections. Authors emphasized the importance of the latter, to overcome the bias present in older collections that may be poorly localized. The terms *association, assemblage,* or *biofacies* are preferred to *community* because trilobites were only a portion of the original organic community. Parallels between associations of different age are commented on, particularly well-known being the similarities in composition and general morphology of trilobites found in carbonate buildups of Paleozoic age (MIKULIC, 1981). CHLUPAČ (1983, p. 64) referred to assemblages in deeper, outer, low energy to stagnant environments in which phacopids and proetids with small or no eyes were prominent. This assemblage is widespread in geosynclinal belts of the Devonian. A similar facies in Carboniferous shales and cherts (PRENTICE, 1967; cf. HAHN & HAHN, 1981; HAHN, 1990; OWENS & TILSLEY, 1995) contains small, thin-shelled proetids in which the eye was small or absent. In shallow-water, calcareous facies, species with large eyes, thick exoskeleton, and coarse tuberculation are characteristic but not universal, as BREZINSKI (1988a) showed. A benthic association in Lower Ordovician rocks that is possibly analogous to the deeper-water Devonian and Carboniferous facies, is the assemblage (FORTEY & OWENS, 1987, p. 106) of blind or nearly blind trilobites named by these authors an atheloptic (shrunken-eyed)

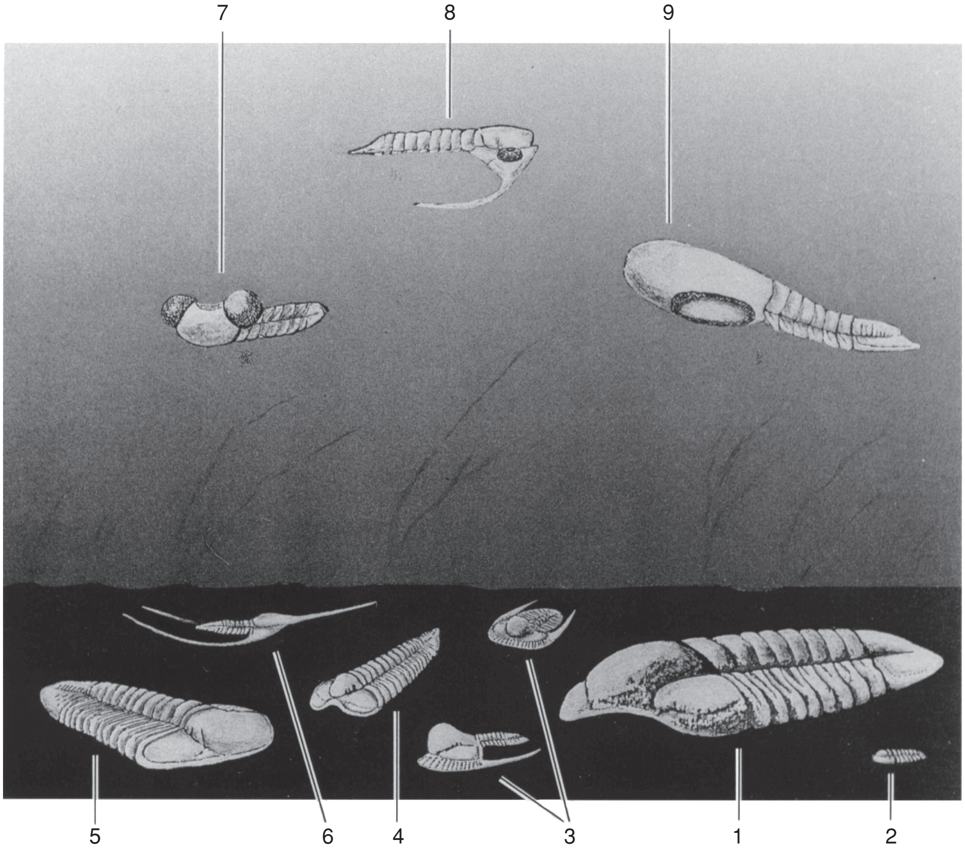

FIG. 139. *1–6,* Atheloptic assemblage of blind or nearly blind benthic trilobites; *1, Illaenopsis; 2, Shumardia; 3, Bergamia; 4, Colpocoryphe taylorum* FORTEY & OWENS; *5, Ormathops nicholsoni* (SALTER); *6, Ampyx. 7–9,* Large-eyed, mesopelagic, free-swimming forms; *7, Pricyclopyge; 8, Bohemilla (Fenniops); 9, Degamella* (Fortey & Owens, 1987, fig. 13).

assemblage (Fig. 139). Also occurring in it are large-eyed cyclopygids, considered to have been mesopelagic in habit. In describing a nautiloid assemblage from Upper Ordovician shales in Ohio, FREY (1989) remarked that species of the trilobites *Flexicalymene* and *Isotelus* are the most abundant. Attention is drawn to this and other examples of a possible predator-prey relationship between nautiloid cephalopods and trilobites.

The recognition of lateral facies changes, the problems they pose in correlation, and the need for separate zonal schemes in adjacent facies are illustrated by examples from western North America (ROBISON & ROWELL, 1976) and other continents (PALMER, 1977). PALMER (1965a) also proposed the name *biomere* for a regional stratigraphic unit, the boundaries of which were defined by an abrupt, nonevolutionary change in the dominant members of a single phylum, in this case trilobites of the Upper Cambrian pterocephaliid biomere in the Great Basin (PALMER, 1965b). In his original definition, PALMER remarked that the change at the base of a biomere was not necessarily related to any break in sedimentation and might be diachronous. Further study (PALMER, 1984) has not revealed evidence of lithological change or diachroneity at the abrupt faunal change, and the advent of cooler or anoxic waters on to the shelf is regarded as a possible cause of change. That some faunal changes occurred is admitted, but it has been argued (BRIGGS, FORTEY, & CLARKSON, 1988, p. 187) that the change may have been exaggerated by the taxonomic treatment employed. The three Upper Cambrian biomeres have been proposed as stratigraphic stages by LUDVIGSEN and WESTROP (1985). These authors (1983a) have used cluster analysis to differentiate trilobite facies faunas at generic and family level in Upper Cambrian and Lower Ordovician rocks. As a result of this analysis they concluded that a catastrophic event was not required to explain the faunal change between Cambrian and Ordovician trilobites (cf. FORTEY 1983; WESTROP & LUDVIGSEN, 1987). A subsequent examination of this faunal change by FORTEY (1989) and of that at the Ordovician-Silurian boundary suggested that the data indicating such a change may have been influenced by how the trilobites had been classified. The importance of mode of life and possible oceanic events was assessed in relation to the faunal change. LUDVIGSEN and others (1986) have discussed stratigraphical problems, including zones and facies, in a wider context.

Consideration of the geographical distribution of families and genera led to the idea of faunal provinces or realms, areas to which particular taxa were limited (WALCOTT, 1890b, 1910; GRABAU, 1931; KOBAYASHI, 1944b). RICHTER and RICHTER (1941b) portrayed a *Redlichia* sea extending from the Middle East to Australia, and WILSON (1957) linked the worldwide occurrence of Upper Cambrian and Lower Ordovician olenids to a dark shale and limestone facies situated in and near the borders of troughs that were the sites of Paleozoic mountain belts. These ideas of a link between facies, tectonics, and faunas were applied to the distribution of North American Cambrian trilobites by LOCHMAN-BALK and WILSON (1958), who explained the differences between faunas of similar ages as related to three different realms—a cratonic, shallow-shelf realm; an intermediate realm at the margin of the craton; and an extracratonic realm coinciding with the mobile belt. The biogeography of Cambrian and Ordovician trilobites in relation to Tethys was discussed by SDZUY and DEAN (in ADAMS & AGER, 1967) and in relation to the Atlantic ocean by WILSON (1966). The distributions of trilobites on a present-day world map were given for the Cambrian by COWIE (1971) and PALMER (1972) and for Ordovician trilobites by WHITTINGTON (1966; in HALLAM, 1973). Meanwhile, studies on paleomagnetism and the fit of continents around the Atlantic (BULLARD, EVERETT, & SMITH, 1965) were beginning to be widely appreciated, and speculations on possible early Paleozoic paleogeography, pole positions, and climate could be compared with past distributions of animals. From such studies came the reconstructions for the Cambrian by JELL (1974) and BURRETT and RICHARDSON (1980) and for the Ordovician by WHITTINGTON and HUGHES (1972, 1973, 1974). Faunal realms are seen to have been associated with the seas around continental masses, the barriers between realms being the deeper waters between these masses, and the temperature that was determined by latitude and water depth. The influence of ocean currents on these distributions was considered by ROSS (1975), and the distribution of the cold-water, shallow-shelf *Neseuretus* fauna of the Lower Ordovician was described by FORTEY and MORRIS (1982). WILDE (1991) considered the oceanographic conditions during the Ordovician in more detail. Studies of Lower Paleozoic trilobite faunal realms are by W. ZHANG (1989) on the Cambrian, Zhiyi ZHOU and DEAN (1989) on the Ordovician, SCHRANK (1977) on the Silurian, and COCKS and FORTEY (in MCKERROW & SCOTESE, 1990) on the Ordovician and Silurian. Phanerozoic world maps, compiled using data from paleomagnetism and tectonics, were provided for a symposium on biogeography by SMITH, BRIDEN, and DREWRY (1973). Newer versions of such maps are by SCOTESE and others (1979), SMITH, HURLEY, and BRIDEN (1981), and SCOTESE and MCKERROW (1990). The data on biogeography were derived independently and so provide a test of these maps. However, an unusual fauna found in an area of structural complexity on the margin of a continental block, such as that of SAMSON and others (1990), may provide problems. Is it unusual because it belonged to a (supposedly) distant faunal realm, or does its distinctive character result from facies change at a continental margin?

## TAPHONOMY

Over the past 50 years, an increased understanding of sedimentary processes has enabled a more detailed picture to be drawn of the burial events that led to preservation. The abundance and variety of trilobites, the molting process as size increased, and the thickness of the cuticle shed caused large quantities of skeletal debris to be produced. The preservation of entire exoskeletons, of appendages, of particular arrangements of exoskeletal parts, or of exoskeletons in a characteristic orientation gives clues to the type of sedimentary process that operated as well as to behavior. Relationships between the various processes are complex (SPEYER, 1987; 1991); the processes and their interactions were discussed by BRIGGS and CROWTHER (1990, p. 213–297).

### DISARTICULATED REMAINS

In a study of the taphonomy of trilobites in Middle Devonian rocks in New York, SPEYER and BRETT (1986) used indices of fragmentation, orientation, and occurrence of articulated, enrolled, or molted exoskeletons. From these they derived divisions termed *taphofacies* that are related to type of sediment, rate of sediment supply, and water depth. This study has many parallels with the earlier studies by FORTEY (1975a) and TAYLOR (1976), which also recognized the distinctions between rocks containing assemblages of disarticulated parts of exoskeletons (some broken) and those containing complete exoskeletons and related these distinctions to depth and type of sediment.

Disarticulation and fragmentation of trilobite exoskeletons probably took place rapidly after death or exuviation if the exoskeletons were exposed at the sediment-water interface and subjected to decay, scavenging, and currents. Currents may have resulted in sorting by size, shape, and resistance to fragmentation. Assemblages recovered at different localities from a single zone in Upper Cambrian strata in western Canada (WESTROP, 1986a) show a gradation in abundance of species of two genera. Individuals of *Ellipsocephaloides* are small (having a maximum cranidial length of 12 mm) and include early ontogenetic stages, while those of *Ptychaspis* are twice this size, and early ontogenetic stages are rare or absent. The *Ellipsocephaloides* assemblage occurs in relatively fine-grained beds, the *Ptychaspis* in relatively coarse-grained strata. These beds are considered to have been generated by storms and the intergrading assemblages to be the effect of size sorting. Thus, as WESTROP pointed out, the end-members of the series might be thought to represent different facies or to be depth-related but are the outcome of taphonomic processes. Another example of sorting is from Lower Cambrian rocks in northwestern Vermont (SPEYER, 1987). Randomly oriented cephala of *Olenellus* (with or without the hypostome and perrostral plate) occur in a quartz arenite. It is thought that the relatively fragile thoracic segments and pygidium were broken down, and the cephala survived because of greater resistance to mechanical breakdown. In siltstone beds a few meters higher in the section are accumulations of either cephala or pygidia of *Billingsaspis.* These segregations appear to be examples of size sorting and breakage and are related to grain size of the sediments. The effects of fragmentation and sorting on exoskeleton parts in Middle Devonian rocks in New York (SPEYER, 1987, fig. 3) were revealed by counts of specimens in strata of different facies. Fragmentation was greatest in current-sorted deposits in which cephala of *Greenops* are rare because of their susceptibility to damage. In contrast, cephala and pygidia of *Phacops* are roughly equally represented in different types of strata. The pygidium and cephalon of *Phacops* were of similar convexity, and convex-up and convex-down specimens occur in similar numbers. In *Greenops* these two sclerites responded differently to hydrodynamic conditions. In contrast is the study of mainly disarticulated exoskeletal remains of *Dikelocephalus* from the Upper Cambrian of the northern Mississippi Valley (N. C. HUGHES, 1993). In these predominantly fine-grained rocks, transportation has been minimal, but compaction has cracked and deformed sclerites, producing shapes that are artifacts and hence not characters of taxonomic significance.

Experiments by HESSELBO (1987) using models of the *Dikelocephalus* cephalon and pygidium showed that these sclerites differed in behavior, both when falling through still water and when entrained in flowing water. Similar experiments by LASK (1993) showed that the most stable attitude for the cephalon or pygidium of *Flexicalymene* was concave-side down; enrolled exoskeletons were moved more readily than isolated sclerites. Evidently the hydrodynamic properties of sclerites need to be take into account and may be useful as paleocurrent indicators. SPEYER (1987, p. 211) considered that in the Devonian strata of New York, the occurrence of sclerites oriented randomly, obliquely, or perpendicularly to the bedding, indicated deep bioturbation. Such orientations have been recorded in coarse-grained glauconitic limestones (BOHLIN, 1949), and it was argued that burial was rapid, a settling out from a suspension of sedimentary particles and organisms or parts of skeletons.

Disarticulated parts of trilobite exoskeletons may be broken. COURTESSOLE, HENRY, and VIZCAÏNO (1991, p. 13) remarked that the exoskeletons of *Neseuretus* and *Pradoella* are never found entire in sandy, platform sediments, and the fragile free cheeks and thoracic segments rarely occur. Cranidia and pygidia found in nodules were in most instances broken before burial. It was also suggested that abrasion may have removed the external sculpture from convex portions of some exoskeletons and even the inner portion of glabellar furrows. On the other hand illustrations of silicified specimens or of those in limestones show that surface sculpture may be preserved in remarkable detail in dissociated exoskeletal parts. WILMOT's study of fragments of proetids (1991) exemplified such perfection of preservation, and she remarked that the use of sculptural detail in characterization of species is limited because of destruction of detail during diagenesis (not as a result of abrasion).

### ARTICULATED REMAINS

The occurrence of outstretched, complete exoskeletons (FORTEY, 1975a; TAYLOR, 1976) or of molt configurations (see section on exuviation and the function of sutures, p. 152) is taken to indicate burial of an autochthonous assemblage of species, and the type of rock in these examples suggests accumulation in deeper, quiet, offshore waters. Burial of entire exoskeletons does not occur only in deeper water. Those of *Dalmanitina socialis* in the Ordovician of Czechoslovakia (PŘIBYL & VANĚK, 1976, p. 20, pl. 8) are in quartzites considered to be a nearshore deposit. The occurrence of the librigenae united by a narrow strip of doublure (FORTEY, 1974b, pl. 3, fig. 1) or of the hypostome beneath the glabella (TAYLOR, 1976, pl. 2, fig. 7; FORTEY, 1990a, pl. 1) is indicative of the lack of disturbance of the remains and suggestive of rapid burial. In an analysis of articulated remains SPEYER (1987, fig. 6) drew attention to the importance of behavior in ecdysis and to burial in anaerobic or dysaerobic conditions. Thus molting behavior may account for preservation in an inverted and partly disarticulated condition (Fig. 134). Aggregations, some of them monospecific, of many complete or almost complete exoskeletons (see section on clusters and monospecific occurrences, p. 159), were discussed by SPEYER (1987), who favored the view that decay of a carcass and accumulation of gas beneath the exoskeleton caused overturning prior to burial. Complete, enrolled trilobites have been collected from pure and muddy limestone and from a wide range of terrigenous, clastic rocks; hence, the conditions under which they were preserved may have differed considerably. In the Hamilton beds of New York, enrolled trilobites are abundant in some deeper-water sediments, and the lateral persistence of horizons yielding them suggests burial during such widespread events as storms (BABCOCK & SPEYER, 1987; SPEYER, 1987). As BABCOCK and SPEYER remarked, essential conditions for preservation were rapid burial combined with reducing conditions at or just below the sediment-water interface. The manner in which specimens of *Olenoides serratus* are preserved in the Burgess Shale (WHITTINGTON, 1975; 1980b) indicates that similar factors operated—catastrophic burial and reducing conditions after entombment.

Conditions of burial and preservation of the trilobites in the Upper Ordovician Frankfort Formation with pyritized appendages (CISNE, 1973a; BRIGGS & EDGECOMBE, 1993) were similar. CISNE commented on the orientation of the specimens, noting that some were entombed in an attitude oblique to the bedding. Examples of such specimens of *Triarthrus eatoni* have been illustrated by WHITTINGTON and ALMOND (1987). The famous pyritized fossils from the Devonian Hunsrück Shale of Germany are oriented in different directions and were preserved under similar conditions (STÜRMER & BERGSTRÖM, 1973). Authors have referred to the compaction that has taken place in these fine-grained sediments in the course of lithification. Its effects on obliquely oriented specimens (WHITTINGTON, 1980b, fig. 3) were considerable, shifting the entire suite of appendages relative to the exoskeleton and greatly changing the alignment of and distance between appendages of the two sides. Such compaction also affected the exoskeleton, and in finer-grained, terrigenous clastic rocks the flattening and cracking, resulting in reduction of the original convexity, is familiar. Tectonic deformation may also have affected the exoskeleton, distorting the shape and also leading to the so-called long and broad forms (see section on dimorphism, p. 161).

The effects of diagenesis on the exoskeleton are most obvious in the dissolution that resulted in preservation as casts and molds and in replacements. Silicification of exoskeletons in limestones has enabled exceptional specimens to be extracted for morphological and ontogenetic studies; the silica may be in the form of quartz (WHITTINGTON & EVITT, 1954) or beekite in some of the trilobites from the Permian of Texas. In some specimens from the Frankfort Formation (WHITTINGTON & ALMOND, 1987), the exoskeleton is replaced by pyrite; in the Burgess Shale (WHITTINGTON, 1980a) replacement of the exoskeleton was by clay minerals of the illite group. The external sculpture of the exoskeleton has been preserved with remarkable fidelity in the course of these replacements. Decay and diagenesis of enrolled trilobites from Devonian strata was discussed by SPEYER (1987). Studies of the microstructure of the cuticle (see section on microstructure and sculpture, p. 74) reveal in detail the effects of diagenesis. Preservation of appendages was by different diagenetic processes (ALLISON & BRIGGS in DONOVAN, 1991). In the Burgess Shale the appendages are flattened and preserved as an exceedingly thin, dark film that is reflective. This film was thought to be of calcium aluminosilicate (WHITTINGTON, 1980b), but the work of BUTTERFIELD (1990) suggested that it may be composed of carbon, which may have acted as a template for diagenetic silicate minerals. The reinvestigation of the appendages of *Triarthrus eatoni* has suggested (WHITTINGTON & ALMOND, 1987) that pyrite was deposited as an infilling or lining of the cavity within the cuticle covering the limbs. How pyrite formed in such fine-grained sediments, rich in organic matter, was reviewed by ALLISON and BRIGGS (in DONOVAN, 1991);

the conditions that obtained in the beds containing pyritized *Triarthrus* have been investigated by BRIGGS, BOTTRELL, and RAISWELL (1991). The phosphatization of appendages, as either a replacement or coating of the cuticle, of *Agnostus pisiformis* from Upper Cambrian strata of Sweden, has been discussed by MÜLLER (1985), MÜLLER and WALOSSEK (1987), and ALLISON and BRIGGS (in DONOVAN, 1991). The importance of gaining some understanding of diagenesis in order to interpret what is preserved has been emphasized by authors. It makes a difference in the appearance of an appendage, if the cuticle has been infilled by mineral matter, or whether it has been replaced or coated.

# USE OF NUMERICAL AND CLADISTIC METHODS

H. B. WHITTINGTON

Linear dimensions and counts of numbers of segments, of axial rings, tubercles, and ribs of the pygidium, for example, have long been used to show the range in size of species, variation between individuals, and aspects of growth and evolution (e.g., BARRANDE, 1852; HUPÉ, 1950, 1953c; WHITTINGTON, 1957b; PALMER, 1957, 1958; BEST, 1961; HUNT, 1967; RAMSKÖLD, 1986; SHELDON, 1988; FOOTE, 1989, 1991). There have also been attempts to introduce greater precision into the description of species by measurements, for example, JAANUSSON (1953a, 1953b), SHAW (1956, 1957, 1959), C. P. HUGHES (1969, 1971, 1979) and OWEN (1981). The difficulties in discriminating between species are made evident by the detailed study of material of *Dikelocephalus* from the Upper Cambrian of the Mississippi Valley (LABANDEIRA & HUGHES, 1994). Orientation of specimens (see section on size, form, and orientation, p. 1) when they are not flattened in one plane presents problems, and standardization of procedures in orientation and measurement has been discussed (TEMPLE, 1975). Numerical methods have not been widely adopted in descriptions of species, even for well-preserved specimens in limestones or those freed from the matrix with acid. An exception is the trinucleids, because the number and arrangement of pits in the fringe may be investigated in detail. Since the pioneering work of BANCROFT (1929), numerical methods have been employed generally on trinucleids (C. P. HUGHES, 1970; C. P. HUGHES, INGHAM, & ADDISON, 1975; OWEN, 1987a, 1987b). Distinct species and subspecies have been distinguished by analysis of the arrangement and number of the pits in specimens from small samples. Larger samples, however, have shown that two or three of such forms may be present in a single, polymorphic population. This enabled OWEN (1980) to characterize some species or subspecies of the Upper Ordovician *Tretaspis* by the relative abundance of two or more forms or morphs. In their study of *Cryptolithus,* SHAW and LESPÉRANCE (1994) have found similar polymorphism in large samples from Middle and Upper Ordovician rocks in eastern North America. Morphs, originally considered to be distinct species, occur in different proportions in successive populations and appear to constitute a single polymorphic species. Species of what is thought to be a distinct genus occur in western areas and have been shown to have hybridized in the south, in Oklahoma (SHAW, 1991), with populations of *Cryptolithus.* Thus, numerical work on larger samples has radically altered earlier views on taxonomy and raised problems regarding supposed evolutionary mechanisms.

Special methods were applied to Encrinurinae (TEMPLE & TRIPP, 1979; TEMPLE & WU, 1990) and to Trinucleidae (TEMPLE, 1980), the aim having been to define each species as objectively as possible by the use of a local sample, which is of necessity assumed to be monospecific. A list of morphological attributes (e.g., presence and length of mucro, presence of particular tubercles, numbers of tubercles in encrinurinids, or characters of glabella and fringe in trinucleids) was coded for each species, based on either published descriptions or topotype collections. Each species was thus analyzed and characterized numerically, and relationships between the species were examined. Suggestions of evolutionary relationships and taxonomic groupings emerged. Important in these studies are the attempts to select attributes and to define precisely characters that may be coded. In using cladistic methods, characters must be clearly defined, be homologous for all taxa coded, and show discontinuous states, i.e., be present or absent, long or short relative to some standard, or, in the case of a furrow, be deeply impressed, weak, or absent (cf. RAMSKÖLD, 1991a). A taxon, of whatever rank, is considered to be monophyletic if it includes the stem species (the latest common ancestor of the group) and all those species derived from it (e.g., JEFFERIES, 1986, p. 2–16). In some cladistic treatments a character is determined to be either primitive for a particular taxon or derived from it and hence advanced. Such determinations have been made by comparison with closely related taxa (out-groups), by use of the premise that similarities in early ontogeny reflect a common ancestry, and from stratigraphical evidence (FORTEY & JEFFERIES, 1982). The classification arrived at is based exclusively on those characters considered to be advanced. Examples of the application of these methods include a study of encrinurid protaspides and their relevance to family and subfamily groupings (EDGECOMBE, SPEYER, & CHATTERTON, 1988), diagnosis of new encrinurid genera (EDGECOMBE & CHATTERTON, 1990a, 1990b), classification of Asaphina (FORTEY & CHATTERTON, 1988) and trilobites at a higher level (FORTEY, 1990a), and evolution in odontopleurids (RAMSKÖLD, 1991a, 1991b) and phacopids (RAMSKÖLD & WERDELIN, 1991). As many as 30 or 40 characters have been used, some of which involve measurements of length or width. Cladograms have been constructed using computer programs to examine the character data. There is considerable current debate on methodology in cladistic analyses, as a recent examination of relationships between species of *Odontopleura* shows (ADRAIN & CHATTERTON, 1990); a review of cladistics in paleontology was written by YOUNG (1995).

Relationships between assemblages of genera of trilobites occurring at particular localities and in relation to the enclosing rock type have been analyzed using different methods (ROWELL & MCBRIDE, 1972; ROWELL, MCBRIDE, & PALMER, 1973; SHAW & FORTEY, 1977; LUDVIGSEN, 1978b; LUDVIGSEN & WESTROP, 1983a). The merits and demerits of the various methods are discussed, cluster analysis appearing to be useful in discriminating biofacies in time and space (LESPÉRANCE, 1990). Studies of biogeography and faunal provinces (WHITTINGTON & HUGHES, 1972; BURRETT, 1973; JELL, 1974; BURRETT & RICHARDSON, 1980) have used other procedures, particularly those designed to assess differences between faunal assemblages.

# ONTOGENY

BRIAN D. E. CHATTERTON and STEPHEN E. SPEYER

Trilobites molted their exoskeletons at regular intervals in ontogeny. Growth and change in external form occurred when the trilobites were soft-shelled, following molting and before secretion of the next hard exoskeleton. We know little of trilobite behavior during this period. It is likely that the animals were relatively inactive because of the changes taking place in their bodies and the importance of the exoskeleton in providing leverage for proper action of many of their muscles (LOCKWOOD, 1968; REYNOLDS, 1980).

The postembryonic part of the trilobite life cycle has been divided into three main intervals, the protaspid, meraspid, and holaspid periods (Fig. 140–141). These have been subdivided into a number of stages that are usually synonymous with molts or instars (Fig. 140). The existence of an uncalcified preprotaspid stage after hatching is purely speculative; calcification probably took place very soon after emergence from the egg.

Because each calcareous exoskeleton was carried essentially unchanged for a short period during the life cycle of each trilobite animal, an excellent record is available of most of the external form. Different individuals of the same species apparently molted the same or a similar number of times during a complete life cycle, usually at similar sizes. Individuals with exoskeletons that are approximately the same size cluster as instars. As a rule, instars are more distinct early in the life cycle than later (Fig. 142), since individual variability in growth rates usually causes later instars of the same specices to overlap in size. Some species, perhaps associated with more stable environments or a stronger genetic relationship between size and onset of molting, allow the recognition of distinct instars on the basis of size late in ontogeny (Fig. 143). Instars are more easily recognized in collections taken from a single bed (or block of rock) and in samples that show little or no distortion.

Little opportunity occurred for wear, solution, or attachment of epiphytic organisms during life, since the the exoskeleton was carried by the animal only for the period between two ecdyses (a period of a few weeks to a year in modern horseshoe crabs, depending mainly upon the age of the animal; see SEKIGUCHI, SESHIMO, & SUGITA, 1988). Following molting or death, the exoskeleton was subjected to normal taphonomic processes. Some arrangements of sclerites have been regarded as the result of molting rather than death (see earlier section on exuviation and the function of sutures, p. 152).

We do not know how many molts occurred during the life cycles of most trilobites. Clearly there was considerable variation between taxa. Very large trilobites and those with many thoracic segments presumably molted a greater number of times than those that were small or had few thoracic segments. HUNT (1967) demonstrated that the Agnostina *Trinodus elspethi*, which had only two thoracic segments, had at least nine instars (three meraspid, six holaspid) during its life cycle and thus must have molted at least eight times (Fig. 143). Probably this is close to a minimum number for the class. The number of thoracic segments released into the thorax following each molt during the meraspid period was usually one, sometimes two (CHATTERTON, 1971), and rarely greater than two. This suggests that some Early and Middle Cambrian Redlichiida may have molted more than 30 times.

Small growth stages are often very different from the adults of the same species, being usually simpler in form and more conservative. Hence, considerable disparity exists between different trilobite larvae. Metamorphosis during the life cycle or radical, growth-related allometry often eliminated features present in larval stages. Larvae of closely related taxa are more similar than those of distantly related taxa (CHATTERTON & others, 1990) so that the larval stages

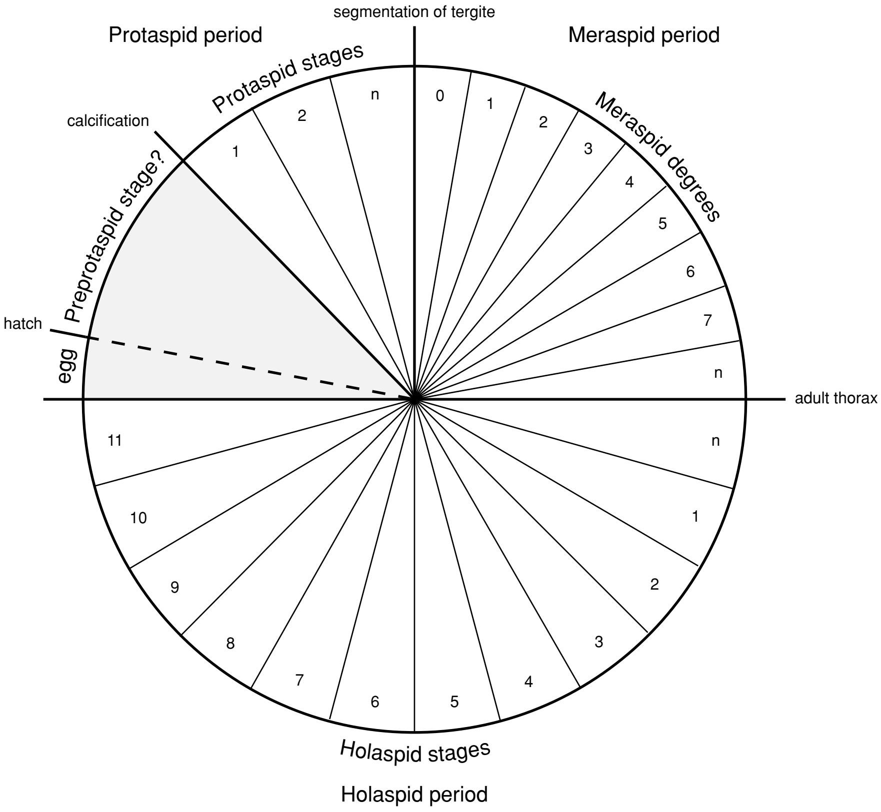

FIG. 140. Trilobite life history (adapted from Speyer & Chatterton, 1989).

contain morphological information vital for understanding trilobite taxonomy, systematics, and phylogeny.

## HISTORY OF RESEARCH

BARRANDE (1852) described the ontogeny of *Agnostus, Blainia, Paradoxides, Sao,* and *Trinucleus.* In doing so, he put into synonymy a number of taxa (10 genera and 18 species) that had been erected by HAWLE and CORDA (1847), recognizing these specimens as different growth stages of a single species, *Sao hirsuta.* BARRANDE also suggested a method for numbering growth stages during the meraspid period that is still in use today (meraspid degrees, distinguished by the number of free segments that have been released into the thorax).

BEECHER (1893a) was the first to describe the silicified larvae of trilobites, although silicified adult trilobites had been obtained from limestones earlier by RATTE (1886). Two years later, BEECHER (1895a) provided a general discussion of trilobite ontogeny and proposed the term protaspis (plural protaspides) for early growth stages where the head and tail parts of the trilobite are still fused. He subdivided the protaspid period, which often included several instars, into ana-, meta-, and paraprotaspides. These subperiods were not defined and are of limited practical value, having been used inconsistently, and lack biological meaning (see discussion of morphology and terminology, p. 183).

JAEKEL (1909) was the first to suggest heterochrony as the cause of origin of a major group of trilobites by proposing that the

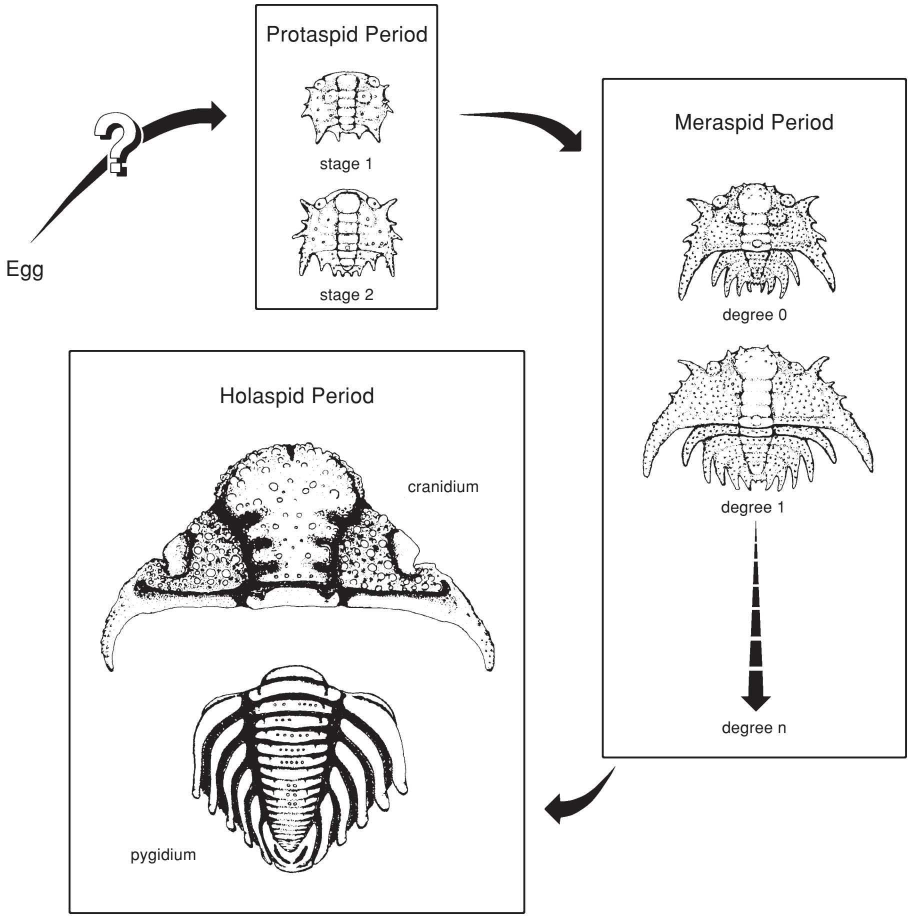

FIG. 141. Growth stages of the life history of a typical trilobite, *Encrinuroides rarus* (WALCOTT) (adapted from Speyer & Chatterton, 1989).

Agnostida, which he called miomerids, arose from polymerid trilobites through paedomorphic evolution (see section on heterochrony, p. 199). RAW (1925) added the terms meraspis and holaspis to BEECHER's term protaspis, dividing the life cycle of most trilobites into three periods. Later summaries of trilobite ontogeny include works by RAW (1927), STØRMER (1942), HUPÉ (1954), WHITTINGTON (1957a, 1959b), HU (1971), CHATTERTON (1980), MCNAMARA (1986b), CHATTERTON and SPEYER (1989, 1990), and SPEYER and CHATTERTON (1989, 1990).

STUBBLEFIELD (1926) described the addition of new segments in the trilobite thorax, originating near the back of the pygidium and migrating forward during the ontogeny of *Shumardia (Conophrys) salopiensis.* New material was described by FORTEY and OWENS (1991) but did not include protaspides. STUBBLEFIELD showed furrows crossing the axis of the protaspis, but these are not evident with SEM examination of his original material in the Natural History Museum, London.

STØRMER (1942) discussed the pattern of somitic organization of trilobites and provided additional data on growth series of *Liostracus* and *Olenus* in particular. He also discussed ontogenetic information available

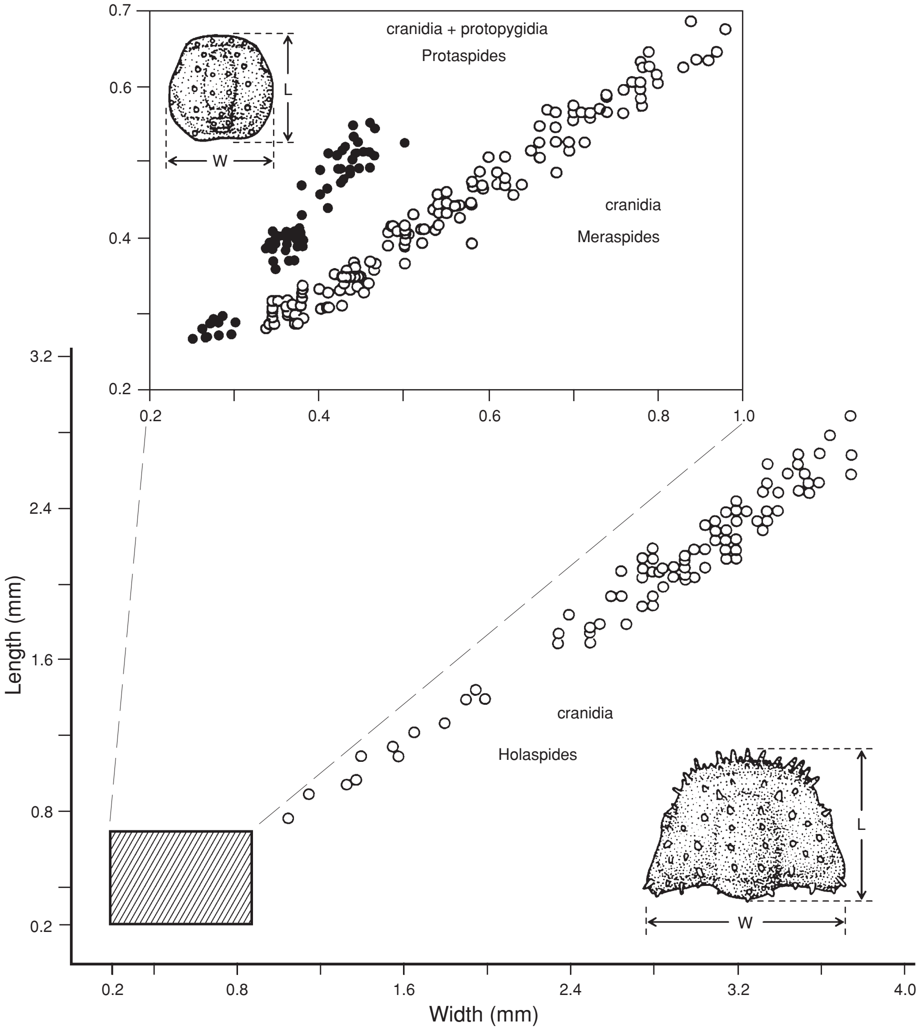

FIG. 142. Growth and recognition of instars of *Dimeropyge* (see Fig. 160) from the Middle Ordovician Esbataottine Formation in northwestern Canada. Due to individual variation in growth rates in meraspides and holaspides, recognition of instars is easier in protaspides (*solid circles*) than in later growth stages (*open circles*). This figure shows data for protaspides and cranidia; those for protaspides and transitory pygidia and pygidia are similar (new).

for higher taxa and considered the use of larval attributes in classification and understanding homologies.

Papers describing silicified trilobite larvae have substantially increased the number of known trilobite growth series and the amount of morphological information available (WHITTINGTON, 1941, 1956a, 1956c, 1956d, 1959a; EVITT, 1961; WHITTINGTON & EVITT, 1954; ROSS, 1951a, 1951b, 1953; PALMER, 1957, 1958, 1962b; HUNT, 1967; SHAW, 1968; WHITTINGTON & CAMPBELL, 1967; HU, 1971, 1974a, 1974b, 1975a, 1975b, 1976, 1985a, 1985b, 1986; CHATTERTON, 1971, 1980; CHATTERTON & PERRY, 1983, 1984; EVITT & TRIPP, 1977; TRIPP & EVITT, 1981, 1983, 1986; EDGECOMBE, SPEYER, & CHATTERTON, 1988; CHATTERTON & others, 1990; CHATTERTON & others, 1994). Larvae preserved in other manners

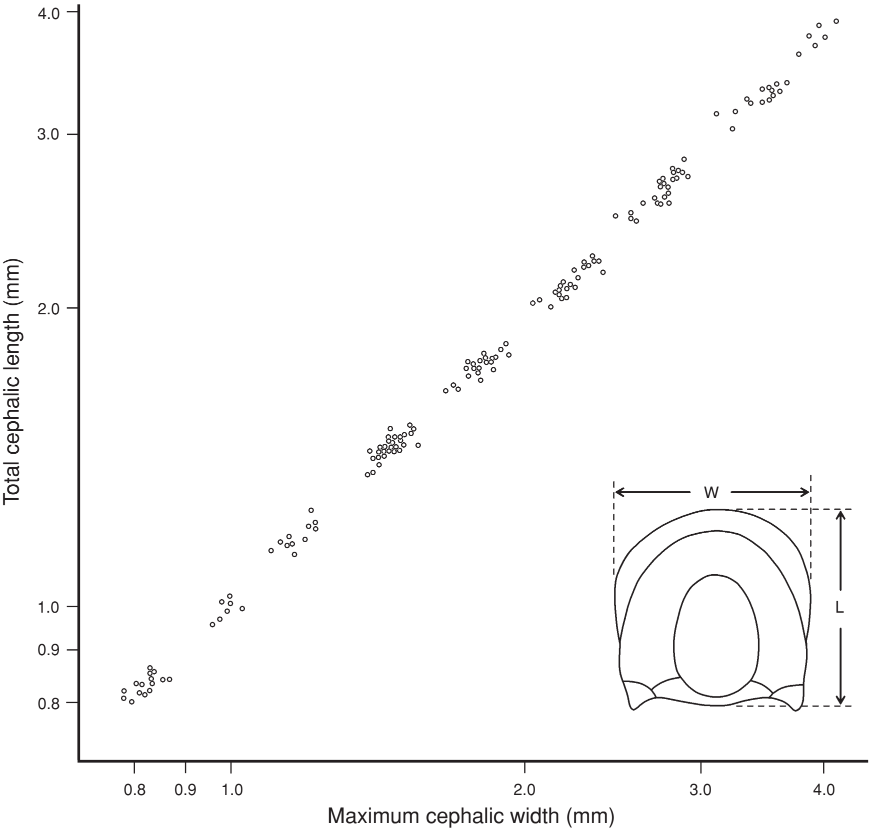

FIG. 143. Growth increments and instars in the life cycle of *Trinodus elspethi* (RAYMOND). Nine instars have been recognized, three in the meraspid period and six in the holaspid period (adapted from Hunt, 1967).

seldom provide as much morphological information, especially for the ventral surfaces of the larvae.

In recent years, phosphatized fossil collections from Australia (JELL, 1970), Spitsbergen (FORTEY & MORRIS, 1978; FORTEY & CHATTERTON, 1988), and China (X. ZHANG, 1987, 1989) have yielded well-preserved skeletons and internal molds of Cambrian and Early Ordovician trilobites.

Since 1950, studies of incremental growth and ontogenetic statistics of various taxa have provided data that are discussed below in the section on trilobite growth and population dynamics (see SHAW, 1956, 1957; BRIGHT, 1959; HUNT, 1967; PALMER, 1957; CISNE, 1973b; ROMANO, 1976; KOPASKA-MERKEL, 1981; BUSCH & SWARTZ, 1985; BREZINSKI, 1986a; SHELDON, 1988; CHATTERTON & others, 1990; CHATTERTON & SPEYER, 1990).

Since GOULD's (1977) work on ontogeny and phylogeny, paleontologists have reexamined relationships between ontogeny, phylogeny, and ecology in the context of heterochrony. Because trilobites grew by increments, they are particularly apt subjects for such studies (MCNAMARA, 1978, 1981a, 1981b, 1983, 1986a; LUDVIGSEN, 1979a; FORTEY & RUSHTON, 1980; WHITTINGTON, 1981; EDGECOMBE & CHATTERTON, 1987; RAMSKÖLD, 1988; and CHATTERTON & SPEYER, 1990).

Early growth stages have been used to solve taxonomic problems ever since BARRANDE's (1852) synonymy of HAWLE and

Corda's (1847) taxa. In the last 40 years, larval attributes have become an important source of information critical to our understanding of trilobite taxa at the ordinal level. Whittington (1954c) suggested that the Phacopida have a distinctive protaspid stage, and this criterion was used in the diagnosis of that order by Henningsmoen (in Harrington, Moore, & Stubblefield, 1959). Fortey and Owens (1975), likewise, used the similarity among early growth stages (meraspid cranidia) in erecting the Proetida. Fortey and Chatterton (1988) regarded the distinctive asaphoid protaspis as an important synapomorphy (uniting character) of the Asaphina. Fortey (1990a, 1990b) has discussed the general relationships of ontogeny to trilobite classification. In accordance with von Baer's rule (see Gould, 1977, p. 56), related taxa display a greater morphological similarity among larval stages than among adults. These larval stages are more similar to each other than to those of distantly related taxa. A number of workers have investigated the relationships and similarities of larvae of trilobite taxa that share a recent, common ancestor (Whittington, 1956a, 1959a, 1959b; Evitt & Tripp, 1977; Chatterton, 1980; Edgecombe, Speyer, & Chatterton, 1988; and Chatterton & others, 1990).

Few studies have addressed questions of larval autecology, functional morphology, and mode of life, most having concentrated on adults (e.g., Clarkson, 1969c; Whittington, 1975; Stitt, 1976; Hammann, 1985; Fortey, 1985). Whittington (1956d), however, suggested that some protaspides were pelagic but offered little evidence to support his conclusion. Cisne (1973b) argued for pelagic mode of life solely on the basis of size. More recently, Chatterton (1980), Fortey and Chatterton (1988), and Speyer and Chatterton (1989, 1990) have discussed trilobite larval ecology and functional morphology in more detail; and Chatterton and Speyer (1989) have examined the relationship between extinction, survivorship, and different trilobite life-history patterns during the Ordovician (see discussion of life-history strategies below).

## PRESERVATION AND OCCURRENCE

Early growth stages are preserved in several ways. Most commonly they are preserved in their original calcite (Fig. 144.1; Whitworth, 1970), have been silicified (Fig. 144.3–4), or occur as molds or casts in a matrix resistant to solution or weathering (Fig. 144.2; Barrande, 1852; Hu, 1971; Lu & Wu, 1982). Calcium phosphate may replace the calcareous exoskeleton (Fig. 144.6; Jell, 1970; Fortey & Morris, 1978), fill in the shell to provide an internal mold (Fig. 144.5; Fortey & Chatterton, 1988), or even, in rare instances, replace the appendages of small growth stages (Müller & Wallosek, 1987). Sclerites may be replaced by pyrite or other such minerals, but usually the crystals of the replacing mineral are too coarse to permit the preservation of morphological details. No pyritized appendages of juvenile stages have been described from the Lower Devonian Hunsrück Shales of Germany or the Ordovician Frankfort Shales of New York, for example (Whittington & Almond, 1987; Stürmer & Bergström, 1973).

The type of preservation constrains the amount and type of information available. Larvae preserved in their original calcareous material can seldom be prepared to permit analysis of their concave ventral surfaces. They may, however, display the surface sculpture in exquisite detail (Fortey & Chatterton, 1988; Clarkson & Zhang, 1991). In contrast, it is often possible to eliminate all excess matrix from diagenetically replaced larval remains during preparation (G. A. Cooper & Whittington, 1965) to permit examination of all preserved details. Unfortunately, the original shell material of early growth stages is often lost preferentially during diagenesis. Indeed it is common in many sedimentary rocks to find

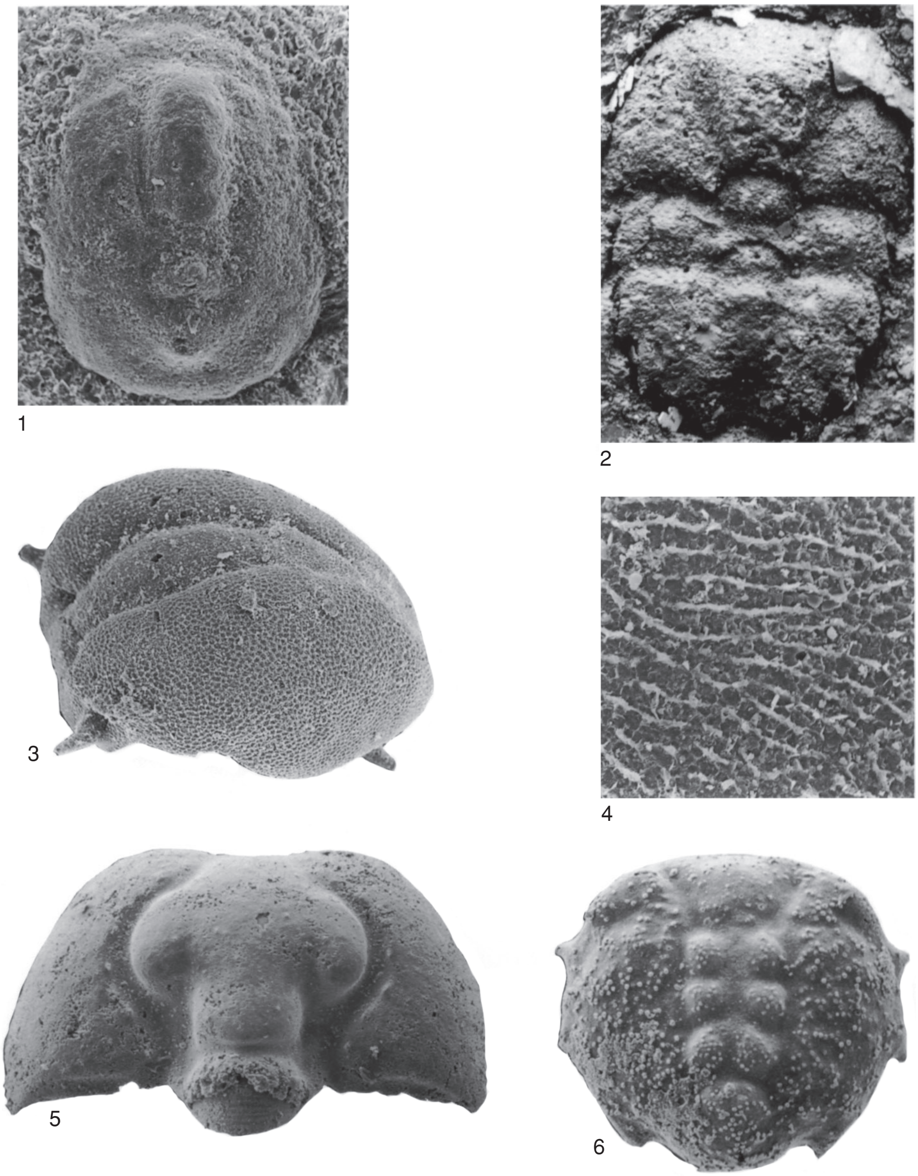

FIG. 144. Preservation of small growth stages. *1,* Preserved in original calcite, proetid protaspid from the Viola Formation, Ordovician, Oklahoma, NYSM 16296, ×115 (new, specimen courtesy of P. J. Lespérance). *2,* Preserved as a mold in shale, meraspid degree 1 of *Conophrys pusilla* (STUBBLEFIELD) from the Shineton Shale, Lower Ordovician, England, BMNH In 26812, ×94 (new, original of Stubblefield, 1926). *3,* Silicified specimen, asaphoid protaspis of *Isotelus* sp. from the Crown Point Formation, Middle Ordovician, New York, NYSM 16297, ×62.4 (new). *4,* Silicified sculpture from asaphoid protaspis of *Isotelus* sp. from the Crown Point Formation, Middle Ordovician, New York, NYSM 16029, ×2150 (new). *5,* Calcium phosphate steinkern of *Shumardia acuticaudata* FORTEY from the lower part of the Profilbekken Member, Valhallfonna Formation, Lower Ordovician, Spitsbergen, BMNH It 21250, ×190 (new). *6,* Phosphatized protaspis of *Cybelurus brutoni* FORTEY from the lower part of the Profilbekken Member, Valhallfonna Formation, Lower Ordovician, Spitsbergen, BMNH It 21251, ×93 (new).

numerous specimens of large trilobites and no larval stages at all (Sheldon, 1988). Many of these situations are clearly not the result of current sorting or other mechanical, biostratinomic processes, because articulated exoskeletons are common in the same strata.

Replacement by silica may be coarse, preserving little detail (H. Alberti, 1972), or fine enough to preserve exquisite details of the sculpture (Fig. 144.4, 145.5; Speyer & Chatterton, 1989, fig. 11). Calcium phosphate may also preserve very fine detail (Fig. 144.5; Fortey & Morris, 1978).

As a general rule, the best three-dimensional preservation occurs where the exoskeleton has been replaced by quartz or calcium phosphate in fairly pure limestone or early diagenetic calcareous concretions. Specimens preserved in shales are usually flattened as a result of postdepositional compaction, and details of marginal spines and the ventral surfaces of such specimens are rarely shown in published illustrations. Techniques for making high-quality casts of small fossils preserved in fine, indurated, siliciclastic rocks (Zapasnik & Johnston, 1984) may, however, provide an important source of information in the future.

Larval sclerites are usually disarticulated. The chances of discovering articulated stages, particularly those belonging to the meraspid period, are greater when specimens have been cracked from limestone or shale. However, some silicified specimens have been discovered with one or both free cheeks attached in life position (Fig. 145.3, 146.1–3; Speyer & Chatterton, 1989, fig. 3c), and even more rarely the rostral plate or hypostome may also be preserved in their original positions (Fig. 146.3; see Fig. 150.7–9; Speyer & Chatterton, 1989, fig. 9e). These latter specimens probably represent examples of infant mortality. Much more common are specimens with the hypostome, rostral plate, or free cheeks attached to the ventral side of the protocranidial-protopygidial fused sclerite (Fig. 145.4,6, 146.4–6). The free cheeks are likely to be located posteromedial of their life positions, and the hypostome occurs behind its life position (Fig. 145.4,6, 146.4–6; Speyer & Chatterton, 1989, fig. 4e, 8a, 8b). The samples in which all of the sclerites are present could represent either carcasses (where the sclerites were dislodged after death, perhaps by shrinking of the ventral integument) or molts, where the trilobites molted while lying on their backs, and the smaller sclerites fell into the empty shell as the animal left its molted exoskeleton. Specimens where only some of the sclerites are present could be examples of either of the above but are more likely to have resulted from the latter. We note that protaspid specimens with the hypostome, free cheek, or rostral plate still attached, either in place or out of place, are rare but are much more common in some rock units (e.g., the Middle Ordovician Crown Point Formation of the Chazy Group of New York) than in others (e.g., the Middle Ordovician Esbataottine Formation of northwestern Canada).

Association of different larval sclerites must be done on the basis of their size, morphology (including sculpture), and spatial distributions (including co-occurrence). Co-occurrence of similar sclerites or larvae at a number of different localities and horizons is often important to determine correct associations, particularly where the trilobites passed through radical metamorphoses in their ontogenies. This problem is made worse by the small number of distinctive, morphological features and broader, ecological (stratal) distributions of the globular, immature, planktonic forms that usually precede metamorphosis. A number of incorrect assignments of larvae to trilobite taxa have been published. It is important that researchers give complete faunal lists of trilobite taxa occurring with larvae that they describe, but we know of instances where the diversity of trilobite larvae exceeds that of the adults in the same samples. Articulated specimens or partly fused specimens are, of course, particularly valuable in associating different parts of a particular stage. They do not, however, provide a correct association of all of the growth stages of a taxon.

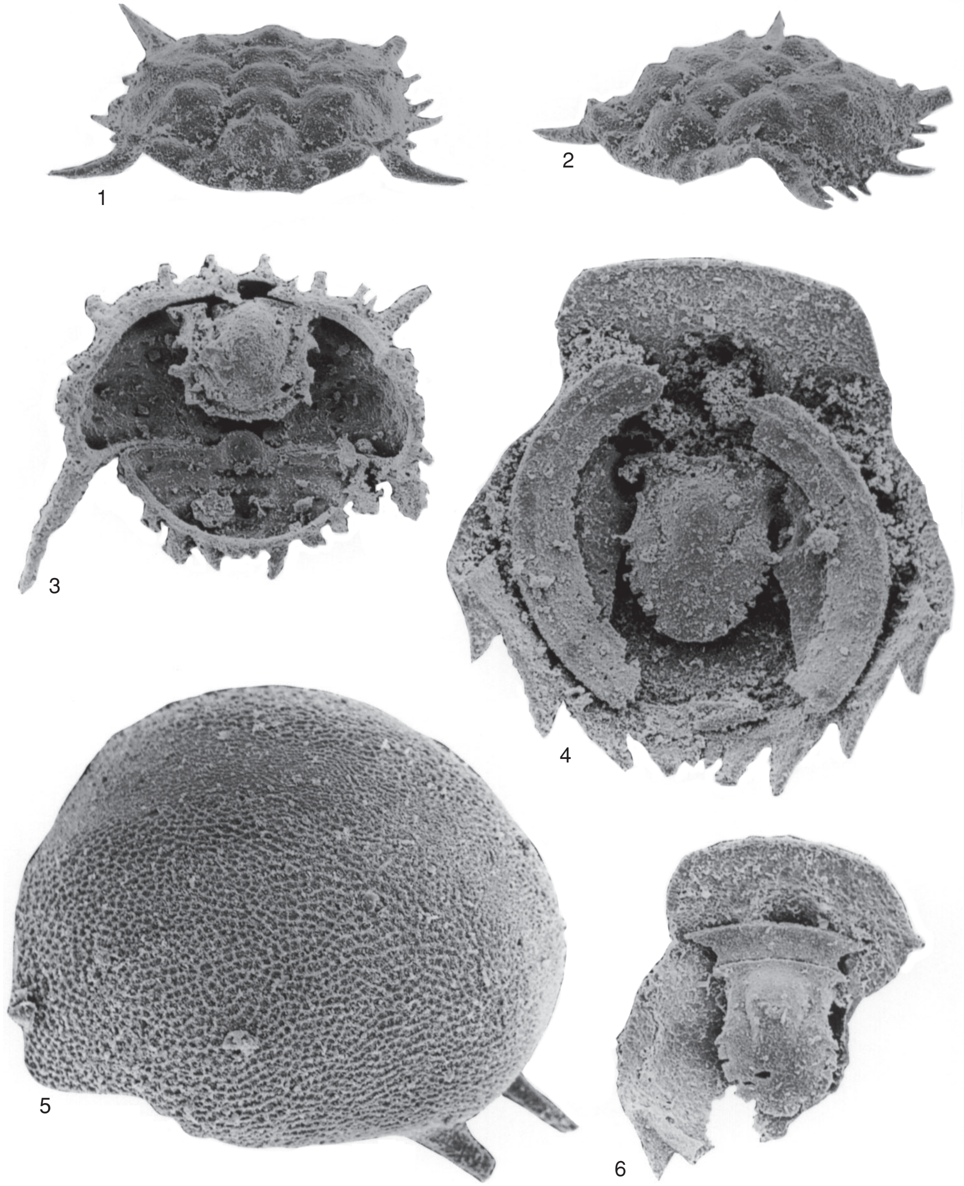

Fig. 145. Larval morphology. *1,2,* Anterodorsal and oblique anterolateral views of protaspis of the encrinurid *Physemataspis insularis* (Shaw) from the Crown Point Formation, Middle Ordovician, New York (locality PB 81), NYSM 16298, ×81 (new). *3,* Ventral view of meraspid degree 0 of encrinurid *Balizoma* sp. from the Wenlock Delorme Formation of northwestern Canada (locality AV 2 248.8); sclerites are in life position, except rostral plate, which is missing, UA 7831, ×51.25 (new). *4,* Ventral view of lichid *Hemiarges* aff. *H. turneri* Chatterton & Ludvigsen from the Crown Point Formation, Middle Ordovician, New York (locality PB81); free cheeks and hypostome are attached to ventral surface but not in life position, NYSM 16014, ×88 (new). *5,* Dorsolateral view of protaspis of asaphid *Isotelus* sp. from the Crown Point Formation, Middle Ordovician, New York (locality PB 81); sculpture of polygonal ridges is weaker in region of axis than on genae, NYSM 16299, ×97.5 (new). *6,* Ventral view of broken, small adult-like protaspis of lichid *Hemiarges* aff. *H. turneri* Chatterton & Ludvigsen from the Crown Point Formation, Middle Ordovician, New York (locality PB81); rostral plate and hypostome are attached to ventral surface, NYSM 16300, ×83 (new).

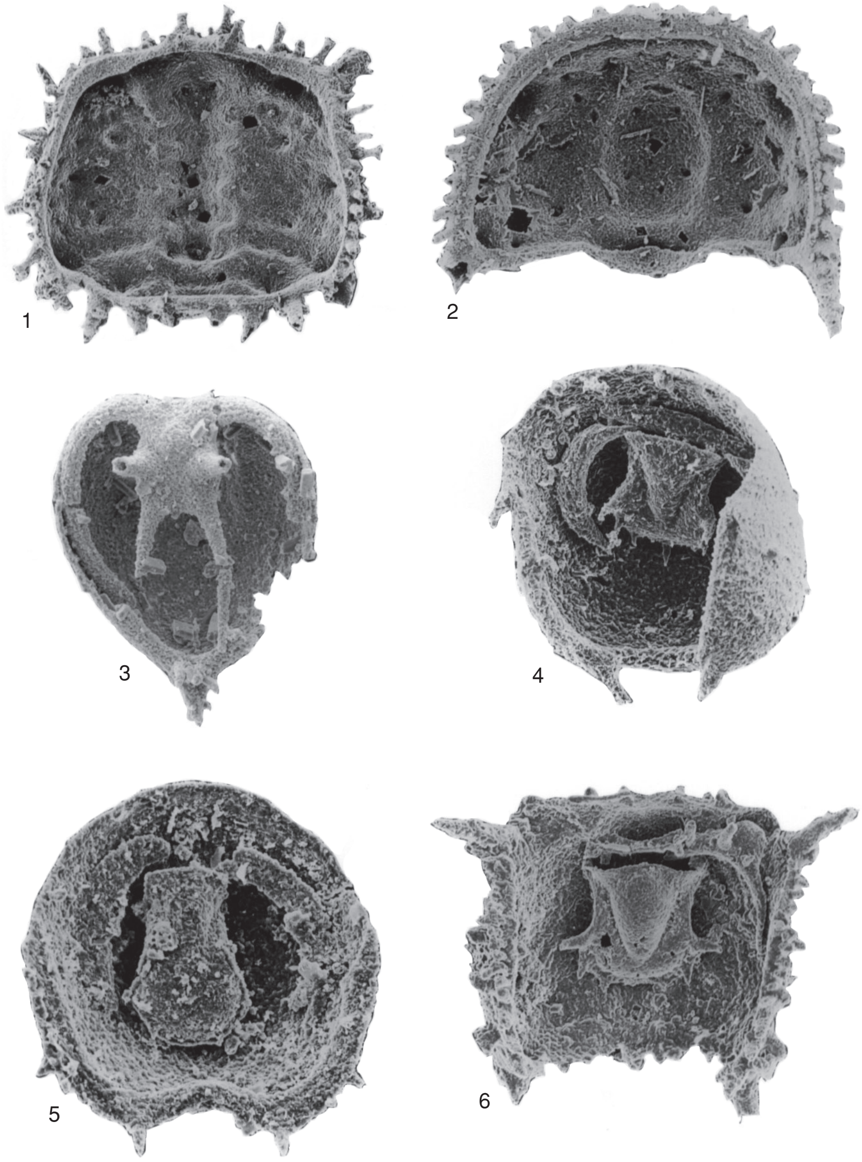

Fig. 146. Association of larval sclerites. *1,* Ventral view of protaspis of the encrinurid *Balizoma* sp. from the Delorme Formation, Mackenzie Mountains, Silurian, northwestern Canada, with attached free cheeks and rostral plate, UA 7824, ×67.25 (new). *2,* Ventral view of small meraspid cranidium of the bathyuroid *Dimeropyge* sp. from the Esbataottine Formation, Middle Ordovician, northwestern Canada, with free cheeks and rostral plate (fused to one another), UA 8420, ×94 (new). *3,* Ventral view of second protaspid stage of the trinucleid *Cryptolithus tesselatus* Green from the Martinsburg Formation, Middle Ordovician, Virginia, with free cheeks and hypostome almost in place, NYSM 16301, ×75 (new). *4,* Subventral view of smallest protaspid instar of the dalmanitoid *Calyptaulax annulata* (Raymond) from the Crown Point Formation, Middle Ordovician, New York; note free cheeks, rostral plate, and hypostome attached to ventral surface, NYSM 16302, ×123 (new). *5,* Ventral view of first protaspid stage (probably of *"Otarion" spinicaudatum* Shaw) from the Crown Point Formation, Middle Ordovician, New York; note free cheeks and hypostome attached to ventral surface, NYSM 16303, ×190 (new). *6,* Ventral view of protaspis of cheiruroid *Cybeloides* sp. from the Whittaker Formation, Mackenzie Mountains, Upper Ordovician, northwestern Canada, UA 7764, ×81 (new).

## MORPHOLOGY AND TERMINOLOGY

There is some controversy about whether the protaspid period of some trilobites was preceded by a calcified stage called the **phaselus** (see section on phaselus stage below). The phaselus lacks sutures, has an entire doublure, and is not known to have had a hypostome.

There is general agreement that the prefix *proto* should be used to denote a part of the larval stage that is homologous with a discrete sclerite in the adult. Thus the terms **protocranidium** (in protaspides) and **protothoracic segments** (in protaspides and meraspides) refer to parts of the trilobite that will ultimately become the separate cranidium and the thoracic segments, respectively. The term **protopygidium** refers to that part of the protaspis from which the thorax and pygidium subsequently develop. During the meraspid period, the corresponding tergite is called the **transitory pygidium.**

We do not advocate the usage of the terms **anaprotaspis, metaprotaspis,** and **paraprotaspis** for all trilobites. These terms were proposed by BEECHER (1895a) as subdivisions of the protaspid period (in developmental order). We feel that *paraprotaspis* should be discarded because it is undefined and little used. We also have serious reservations about *anaprotaspis* and *metaprotaspis,* which BEECHER used to describe the stages before and after a recognizable pygidial portion can be distinguished from the protocranidium, usually by the presence of a small furrow behind the head. HU's (1971, p. 49–50) definitions of these terms were based on size and morphology. They differed from those of earlier workers (HU, 1971, fig. 23), however, and are limited to only some trilobite protaspides. Many specialists judge that two separate events must occur for trilobites to develop from anaprotaspis to metaprotaspis: (1) development of enough somites, either in volume or in number behind the head for a future pygidial portion to be apparent and (2) the formation of a furrow to mark the posterior margin of the head. In some taxa the first event occurs some time before the second; in others both events occur almost simultaneously. EDGECOMBE, SPEYER, and CHATTERTON (1988) summarized many of the objections to this classification. In short, these terms bear little biological reality and confuse rather than clarify.

Although the timing of the first appearance of a distinct furrow between the protocranidium and the protopygidium may be a useful marker of ontogenetic stages of closely related trilobites, it is merely one of a number of different developmental events that may be used to monitor heterochronic changes among taxa. Large, supposedly pelagic protaspides (which usually lack such a furrow, e.g., Remopleuridioidea) are remarkably different from much smaller, supposedly benthic protaspides (which may possess such a furrow, e.g., Proetida). The possession of a differentiating furrow, then, is less of a developmental marker denoting relative maturity than a probable ecological correlate. (See discussion of ecological differences between adult-like and nonadult-like trilobite larvae below.) Some pelagic protaspides clearly possess portions that are homologous with what will later become the transitory pygidium. These parts of the protaspis are, however, quite different in form from the transitory pygidium and not delineated from the protocranidium by a distinct furrow. Should they be called anaprotaspides or metaprotaspides? While we accept that the time of origin of a distinct furrow between the protopygidium and the protocranidium can be a useful marker of a stage in the maturity of an individual (for instance in heterochronic studies), the terms *anaprotaspis* and *metaprotaspis* cannot be applied in a homologous fashion for all trilobites. They should be restricted taxonomically and used purely descriptively (perhaps as a synonym for adult-like protaspis). There is little need for retaining the term *paraprotaspis.*

Some of our criticisms of the terms *anaprotaspis, metaprotaspis,* and *paraprotaspis* could also be applied to the three periods (protaspis, meraspis, and holaspis), whose boundaries may occur in widely different ages and degrees of morphological maturity in distantly related trilobites. With very few exceptions, however (e.g., PALMER, 1958; X. ZHANG, 1989), all students of trilobite ontogeny have recognized these divisions and used them in the same fashion. These boundaries are based on individual rather than multiple developmental events, and herein lies the potential problem (see SPEYER & EDGECOMBE, 1989).

CHATTERTON and others (1990; see Fig. 179) used a system in which different protaspid instars were labelled informally with a letter prefix (P for planktonic subperiod; B for benthic subperiod) and a number suffix (1 for first instar within subperiod, 2 to *n* for later instars within the same subperiod), a convention derived from SPEYER and CHATTERTON (1989) where planktonic and benthic larvae were charted according to ecological criteria. The problem with this system is that discovery of new, earlier instars of a taxon requires renumbering of previously labelled, later instars within the same subperiod. For instance, since the earlier paper was written, new (smaller) P1 instars of the Silurian *Calymene* species described in that work have been discovered so that these growth series now consist of P1, P2, B1, and B2 (not the published P1, B1, and B2, which are equivalent to the new P2, B1, and B2). This system is stable, however, once all protaspid instars of a species are known.

Some trilobite larvae have prominent marginal, submarginal, or dorsal spines on the protocranidia. Some of these have been identified by such terms as anterior fixigenal spine, **midfixigenal spine**, and **posterior fixigenal spine** (see Fig. 148) (PALMER, 1962b). Others have been provided with a more or less formal system of terms, letters, and numbers by various authors (WHITTINGTON, 1956d; CHATTERTON, 1971) according to particular groups of trilobites (see Fig. 149; see also EDGECOMBE, SPEYER, & CHATTERTON, 1988 for terminology of encrinurid larvae). These systems can be applied to some but certainly not all trilobite early growth stages, even within the groups for which they have been invented.

Prominent spines in early growth stages are frequently lost and sometimes reemerge as a consequence of heterochronic displacement. The basic spine pattern is very conservative; and while particular spines are often lost, prominent new spines are seldom added to the basic pattern. Thus, the patterns of these spines are useful for some levels of phylogenetic analysis.

Prominent pairs of spines evident in larval stages may disappear through ontogeny or may grow at a rate consistent with the overall increases in body size. They may also be displaced or incorporated by other structures of the trilobite (i.e., cranidial lobes). Since these pairs of spines are believed to be homologous with segments of the body, they may provide important evidence for determining the homologies of structures that displace or incorporate them.

## LIFE HISTORIES

### GROWTH

Growth may occur through auxetic growth (growth of individual cells), multiplicative growth (increase in cell number but not size), and accretionary growth (some special groups of cells retaining their ability to divide mitotically after most others have ceased to do so). The balance between these different types of growth probably changed during ontogeny, perhaps entering the largely accretionary pattern at sexual maturity. Changes in balance may be apparent through changes in allometric growth curves or in the proportional increments between adjacent instars.

### REPRODUCTION

We consider that trilobites probably reproduced sexually, as do most arthropods. Certainly the extensive discussion of whether sexual dimorphism occurs in trilobites (see p.

161) would imply that this view is shared by others (e.g., Hu, 1971). Clusters and monospecific occurrences (see p. 159) have been described or illustrated for a wide range of trilobite taxa (Cambrian *Asaphiscus wheeleri* in frontispiece of Gunther & Gunther, 1981; Ordovician *Cyamops stensioei* on cover of Clarkson, 1979b; Ordovician *Cryptolithus tesselatus* on pl. 139 and *Ampyxina bellatula* on pl. 140 of Levi-Setti, 1975; Silurian *Dalmanites limulurus* in Ludvigsen, 1979a, fig. 43a; and Devonian *Greenops boothi* in T. T. Johnson, 1985, p. 147). Speyer (1985) and Speyer and Brett (1985) compiled biostratinomic details of modern taxa with clustered assemblages associated with molting or reproductive behaviors (limulid xiphosurans, varied crustaceans, and nereid polychaetes).

## EMBRYOLOGY

Barrande (1852, pl. 27, fig. 1–3) described some small structures as trilobite eggs (disputed by Raymond, 1931) and later illustrated a cephalon and six thoracic segments of *Parabarrandia crassa* with egglike structures under the cephalon (Barrande, 1872; see also Horný & Bastl, 1970). The arguments that these and similar structures under articulated *Ceraurus pleurexanthemus* (described from thin sections by Walcott, 1881, pl. 4, fig. 8) and under *Flexicalymene meeki* (described by Billings, 1870, p. 485) are trilobite eggs was refuted by Raymond (1931). Raymond reviewed all published examples of trilobite eggs and commented (p. 172) that the larger structures described are definitely not trilobite eggs (we concur), "and the smaller ones, even if correctly identified, have furnished no information of any value."

It is not known whether fertilized eggs were brooded. Egg masses are often seen attached to the undersides of extant marine crustaceans. Few of the morphological features suggested by various authors to be sexually dimorphic in trilobites (see p. 161 on dimorphism) can be correlated to brooding strategies. (An exception could be degree of vaulting or width of pygidium.) If these are really examples of sexual dimorphism, the functions may be any one of a number, and further comment would be sheer speculation. Some of the morphological features considered to be dimorphic are now known to be apparent quite early in the ontogeny of the trilobites, a considerable time before the probable time of onset of sexual maturity. The case would be stronger if these features developed rapidly immediately prior to the time of sexual maturity. If sexual dimorphism occurred and the dimorphs show extreme morphological differences, however, the differences would need to appear quite early in the ontogeny if one or both morphs were not to undergo a radical metamorphosis immediately prior to sexual maturity. In some ostracodes, however, brood pouches appear in heteromorphic individuals quite suddenly during the latter part of ontogeny.

X. Zhang (1987, fig. 8) illustrated some spheroidal, phosphatized supposed egg cases and trilobites from the Lower Cambrian of China, which he assigned, with question, to a bradoriid or trilobite. These specimens are larger than the protaspides of the eodiscid *Neocobboldia* occurring with them, but at a diameter of 0.35 mm to 0.5 mm they may have been small enough to house the embryos of polymerid trilobites (he assigned protaspides with a length of 0.36 mm to the polymerid *Ichangia ichangensis* Lee, from the same rock unit). Thus, although we assume that trilobites did produce eggs, no undoubted examples are known from the fossil record.

The size and morphology of the first calcified (protaspid) stage are highly variable between but not within different trilobite taxa. This suggests that some trilobites with large protaspides may have passed through more growth as embryos within the egg than others (Fig. 147). There is also the possibility that trilobites passed through one or more growth stages between emerging from the egg and secreting the first calcareous exoskeleton, although there is no evidence for the existence of such free, uncalcified stages.

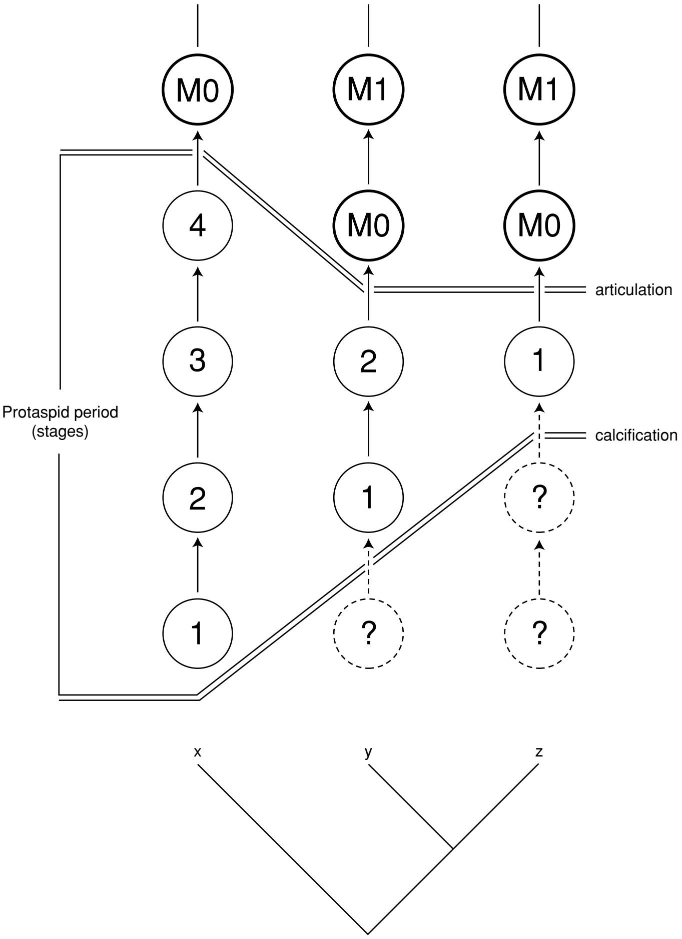

FIG. 147. Calcification and articulation may occur at different times in the life cycles of different trilobites, perhaps as a result of brooding of early instars. *Circled numbers* (or letters and numbers; M = meraspid) are discrete instars in the life cycle of three different hypothetical trilobites: x, y, and z. The *double lines* leading to calcification and articulation represent, respectively, the hypothetical timing of the first calcification and the timing of separation of the head and tail portions of the trilobites (onset of meraspid period). The small cladogram below shows hypothetical evolutionary relationship between these taxa, implying that later calcification and earlier articulation may be derived characters in some groups of trilobites (adapted from Speyer & Chatterton, 1990).

The metabolism required for calcification is not likely to be a secondary derivative within the Trilobita, such as might be argued for some heavily calcified Crustacea (e.g., brachyuran crabs, lobsters). Crustacea add carbonate into a pre-existing organic matrix that is entirely lacking in trilobite cuticle. Therefore, all free-living trilobites may have possessed a calcified exoskeleton. SPEYER and EDGECOMBE (1989) argued that calcification and hatching coincided.

## PHASELUS STAGE IN TRILOBITES

Small ovoid, phosphatized exoskeletons were described by FORTEY and MORRIS (1978) from the Lower Ordovician of Spitsbergen. These minute exoskeletons, 0.1–0.3 mm in diameter, are complete dorsally, open ventrally, and have a narrow, entire doublure. They show no sign of a facial suture, rostral plate, or hypostome. They come from two members of the Lower Ordovician Valhallfonna Formation of Spitsbergen and were assigned to *Cybelurus.* [These specimens would now be assigned to both *Cybelurus* and *Lyrapyge* (see FORTEY, 1980b).] FORTEY and MORRIS (1978) proposed that these specimens were a calcified preprotaspid stage, termed a phaselus, that they regarded as equivalent to the crustacean nauplius. They discussed the arguments for and against the phaselus being homologous with the crustacean nauplius and noted that the nauplius may be present in different crustaceans, since it is often passed in the egg stage. These arguments centered around the size of the phaselus, its form, its possible appendage number, and its position within the ontogeny of a trilobite (if it is a trilobite). They also noted on the best phaseluses the presence of a surface sculpture of cell polygons typical of early arthropod growth stages. However, they noted that with such early growth stages, similarity in size and form could be more a function of simplicity than of homology. HU (1971, p. 50) believed that early trilobite protaspides have fewer segments visible in the head than later stages, but our own observations indicate that in many taxa protaspides do not have fewer segments.

Some workers (SCHRAM, 1982; ROY & FÅHRAEUS, 1989) have considered FORTEY and MORRIS's (1978) claims to be unjustified. We have discovered (work in progress) silicified phaseluses in six formations ranging from the Middle Ordovician to the Lower Devonian. None of the hundreds of specimens recovered contains any evidence of facial sutures or hypostomes. All of the occurrences of silicified phaseluses are in beds containing numerous silicified trilobites and ostracodes as well as many other silicified fossils. In a few instances, they occur with definite protaspides that are as small as the largest phaseluses (see Fig. 150.1–2) and with bivalved ostracodes that are smaller than the phaseluses. In some instances, however, the smallest definite protaspides present are almost five times the size of the phaseluses. It is not certain that phaseluses are trilobites and not naupliuses of crustaceans or an extinct group of arthropods that has yet to be recognized. One problem confounding their correct assignment is that their minute size precludes common preservation and discovery. They are found only in exceptionally well-preserved faunas, and they may occur in one bed but not in the beds above and below, which may contain silicified protaspides and later growth stages of trilobites.

HU illustrated three specimens, which he assigned to *Norwoodia halli* RESSER from Upper Cambrian strata in Missouri, that are similar in form to Ordovician phaseluses (1963, pl. 19, fig. 18–24). These are slightly larger than most of the phaseluses that we have found to date (0.38 mm long and 0.32 mm wide, versus 0.1 to 0.2 mm in size for the phaseluses we have examined).

## PROTASPID PERIOD

Morphological terms for different protaspides are provided in Figure 148, and number and letter designations for the prominent cranidial spines of odontopleurid and lichid trilobites are given in Figure 149. These terms may be applied with varying confidence in homology to similar spines present on the cranidia of protaspides and early meraspides of the Illaenina, Phacopida, and some Ptychopariida.

The overall body plan of trilobite protaspides has been characterized as either adult-like or nonadult-like by SPEYER and CHATTERTON (1989). This distinction is based upon the dichotomy that exists among all studied stages that is neither taxon specific nor exclusive. The nonadult-like protaspides are usually more globular and three dimensional in form. The adult-like forms are more disk-shaped, with a lower profile and more planar ventral surface in lateral view, a prominent doublure, and a posteriorly tapered hypostome (Fig. 148, 150, 151). The differences would be even more apparent in Figure 150 if the free cheeks and hypostomes were present in lateral views (Fig. 150.3,9). In many nonadult-like forms, the hypo-

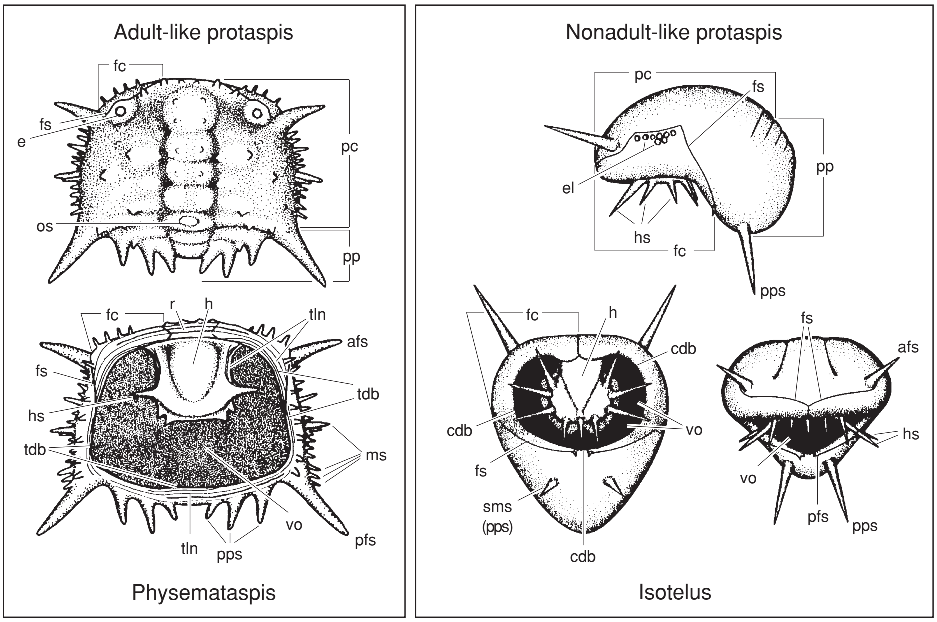

FIG. 148. Morphological terms applied to adult-like (probably benthic) and nonadult-like (or asaphoid) protaspides, based on drawings of the encrinurid *Physemataspis* and the asaphid *Isotelus.* Abbreviations: *afs,* anterior fixigenal spine; *cdb,* incurved doublure; *e,* eye; *el,* eye lens; *fc,* free cheek; *fs,* facial suture; *h,* hypostome; *hs,* hypostomal spine; *ms,* marginal spine; *os,* occipital spine (lobe); *pc,* protocephalon (protocranidium + free cheeks); *pfs,* posterior fixigenal spines; *pp,* protopygidium; *pps,* protopygidial spines; *r,* rostral plate; *sms,* submarginal spine; *tdb,* inturned doublure; *tln,* terrace ridges; *vo,* ventral opening (adapted from Speyer & Chatterton, 1989).

stomal spines extend obliquely downward well below the doublure.

EVITT and TRIPP (1977), in describing the ontogenies of encrinurid and staurocephalid trilobites, coined several terms, including **torulus** for a rounded fixigenal swelling alongside the glabella of small stages. They also applied the system of notation for glabellar tubercles introduced by TRIPP (1957) to larval stages (followed by EDGECOMBE, SPEYER, & CHATTERTON, 1988).

Ontogenetic events (as time or maturity markers) during the protaspid period may be useful for examining heterochronic relationships between rate of growth, morphological change, and timing of appearance or disappearance of specific morphologies. These include the appearance of a furrow between the protocranidium and the protopygidium, the appearance of distinct axial furrows rather than a pair of pits that were probably associated with attachment of the hypostome, the appearance of connective sutures, the appearance of a hypostomal suture, the fusion of connective sutures, a movement of the genal spine from the fixigena to the librigena (in only some taxa), the timing of a major metamorphosis (e.g., change from nonadult-like to adult-like), and a change from a concave to a convex posterior margin.

Some groups of trilobites have larval instars that are particularly diagnostic. For instance, the first benthic instar of a lichid trilobite always appears to have three pairs of marginal spines on the protopygidium, and the second instar has five pairs of marginal spines (see Fig. 183.1,5). These features of lichid larvae not only make them recognizable, but may also be useful time markers for identifying heterochronic changes occurring early in the life cycle.

Some features of protaspides are fairly general among trilobites, and others show a considerable degree of variation. For example, Figure 152 shows protaspid and early meraspid hypostomes. Most of these show

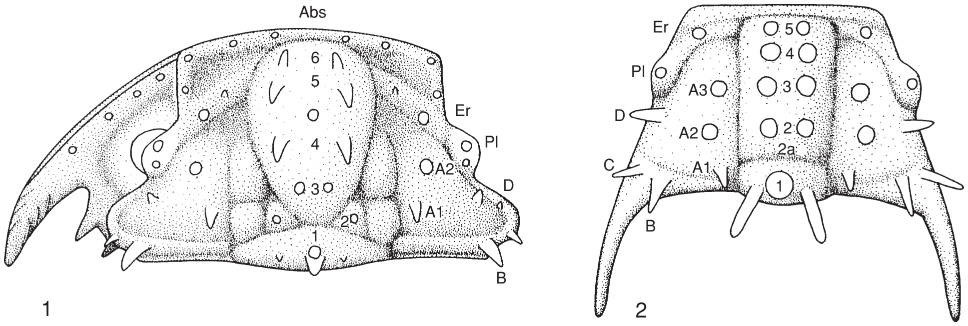

FIG. 149. Sytems for labelling prominent pairs of spines on the dorsal surfaces of meraspid cranidia; *1,* the lichid *Acanthopyge bifida* EDGELL (adapted from Chatterton, 1971); *2,* the odontopleurid *Apianurus barbatus* (adapted from Whittington, 1956d). Spines are labelled *1–6* on glabella forward from the occipital ring, *A* on the fixed cheek; *Abs* on the anterior border; *B, C* on the posterior border; *D* on fixed cheek behind palpebral lobe; *Er* on eye ridge; and *Pl* on palpebral lobe.

marginal spines. Even though the number and shape of marginal spines vary within some groups, they may be useful to characterize some taxa. As a general rule, early protaspides are more likely to have marginal spines on the hypostome than later growth stages, and those spines are more likely to be sharply conical. The presence of these marginal spines is probably a synapomorphy of trilobites (FORTEY & WHITTINGTON, 1989). Such distinctive shapes of marginal spines as the blunted, distal ends of the marginal spines of lichid and styginid, adult-like protaspides or the reduction in size or loss of marginal spines in the odontopleurids and proetids may be derived, apomorphic features. SPEYER and CHATTERTON (1989) pointed out that the marginal spines of hypostomes of nonadult-like, pelagic protaspides are generally much longer and sharper than those of adult-like benthic growth stages in the same species (contrast Fig. 152.11 with 152.7), and the hypostomes of nonadult-like protaspides cover a much greater proportion of the ventral surface than those of adult-like protaspides (Fig. 145.3, 146.3, 148).

The width of the rostral plate relative to the front of the hypostome also varies among different groups of trilobites. In some taxa the rostral plate is narrower than the hypostome (Phacopida, Fig. 152.1,3), in others it is the same width (Lichidae, Fig. 145.6; Odontopleuridae, Fig. 152.2), and in others it is much wider (Olenellina, see PALMER, 1957).

## MERASPID PERIOD

This period incorporates the growth stages in which the cephalon is separate from the thorax or the pygidial portion (transitory pygidium) but lacks a full (adult) complement of thoracic segments.

### Number of Meraspid Instars

Typically, a single thoracic segment is released into the thorax between adjacent instars, and meraspid degree numbers increase by increments of 1 during the life cycle of a trilobite. Thus the number of meraspid instars equals the number of adult thoracic segments (Fig. 153). In certain species, however, the number of meraspid instars differs from the number of adult thoracic segments. CHATTERTON (1971), for example, demonstrated that for *Dentaloscutellum campbelli* two thoracic segments are released into the thorax between instars, so the meraspid degrees mainly increased in increments of 2 (0, 1, 3, 7, and 9). Thus, there are only five meraspid instars, although there are ten thoracic segments in the adult, holaspid trilobite. Some Early and Middle Cambrian trilobites with numerous thoracic segments must either have passed through a very large

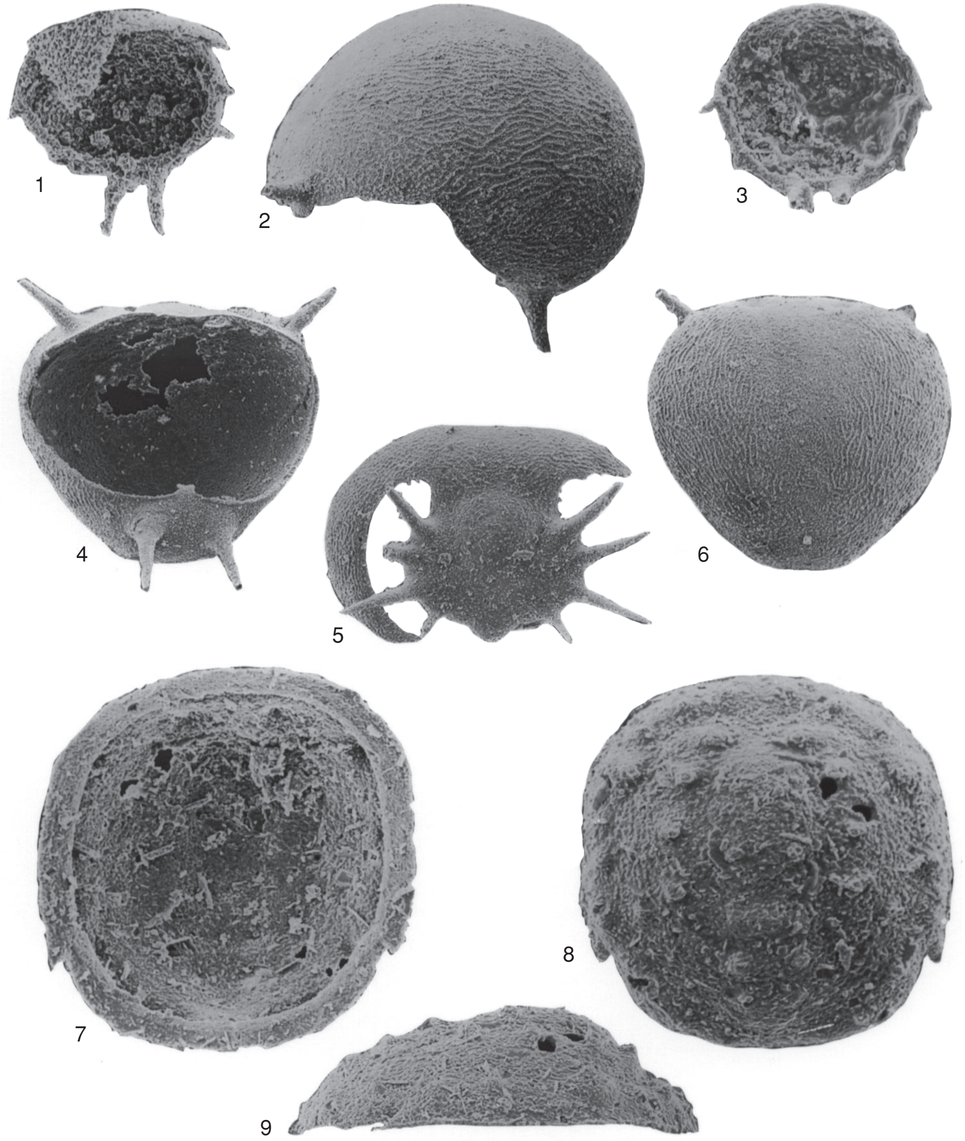

Fig. 150. Larval morphology and ecology. The smallest protaspides are shown together with adult-like and nonadult-like protaspides. *1,3,* Ventral views of two very small protaspides of uncertain assignment (possibly belonging to the Cheirurina) from the Crown Point Formation, Middle Ordovician, New York, NYSM 16304, 16305, ×136 (new). *2,4–6,* Nonadult-like protaspides assigned to the asaphid *Isotelus* sp. from the Crown Point Formation, Middle Ordovician, New York; *2,* lateral view of NYSM 16306, ×60; *4,* ventral view of NYSM 16307, ×45; *5,* ventral view of fused hypostome and free cheeks, NYSM 16308, ×60; *6,* dorsal view of NYSM 16309, ×45 (new). *7–9,* Ventral, dorsal, and right lateral views of adult-like, benthic late protaspis of bathyuroid *Dimeropyge* n. sp. from the Esbataottine Formation, Middle Ordovician, northwestern Canada, UA 7900, ×113 (new).

number of instars or released several segments into the thorax between instars (Palmer, 1957). If the number of instars of *Neocobboldia chinlinica* that X. Zhang (1989) recognized is correct (they are not very distinct on his diagrams), and if his boundary between meraspid and holaspid stages is correct (as it appears to be on

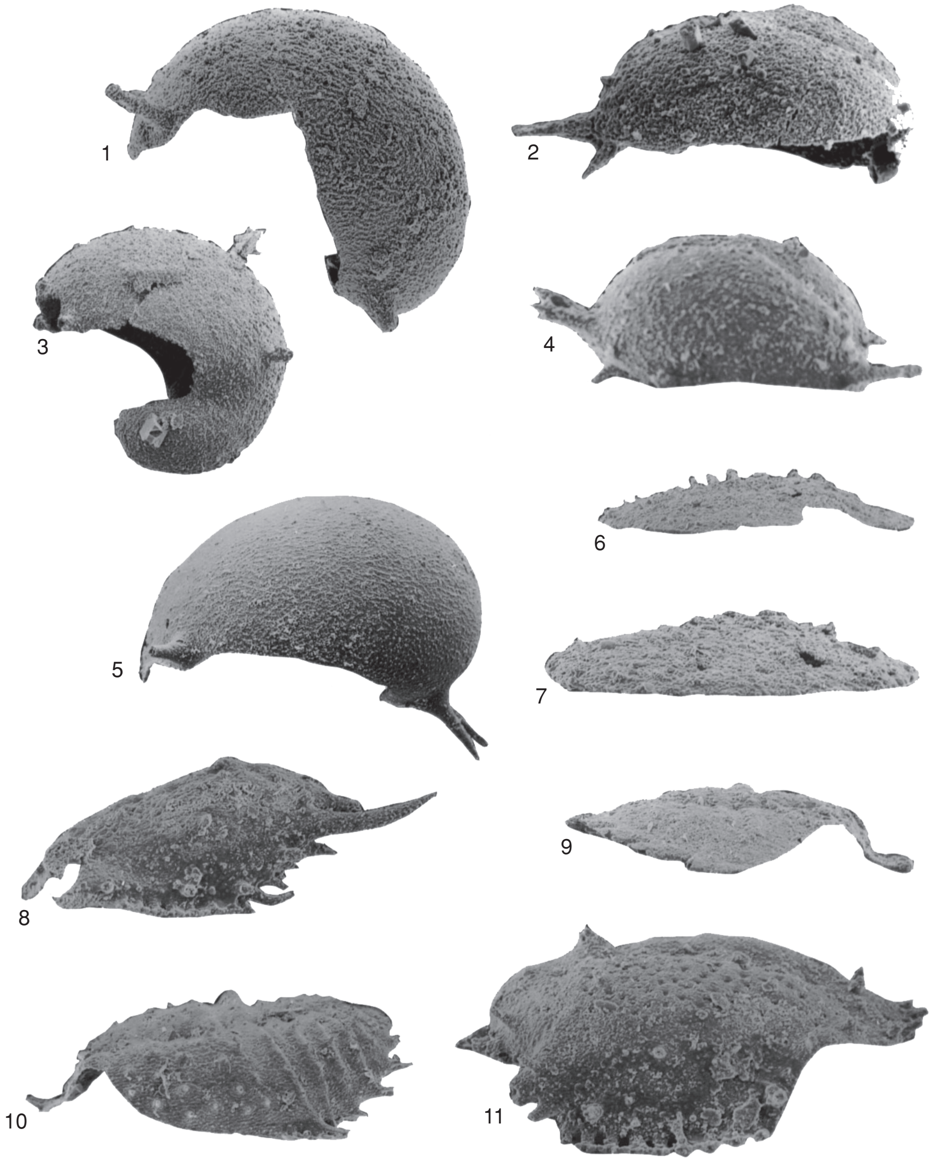

Fig. 151. Lateral views of protaspides. *1–5,* Nonadult-like, probably planktonic protaspides of Asaphida; *1, Isotelus?* sp., an asaphid, from the Crown Point Formation, Middle Ordovician, New York, NYSM 16310, ×49; *2, Cryptolithus tesselatus* (Green), a trinucleid, from the Martinsburg Formation, Middle Ordovician, Virginia, NYSM 16311, ×83; *3, Remopleurides* sp., a remopleuridid, from the Edinburg Formation, Middle Ordovician, Virginia, NYSM 16312, ×60; *4, Lonchodomas chaziensis* Shaw, a raphiophorid, from the Crown Point Formation, Middle Ordovician, New York (locality PB81), NYSM 16313, ×92; *5, Isotelus* sp., an asaphid protaspis from the Crown Point Formation, Middle Ordovician, New York, NYSM 16314, ×60 (new). *6–11,* More adult-like, probably benthic protaspides; *6,7,* aulacopleurid *Scharyia* sp. from Wenlock part of the Delorme Formation, northwestern Canada; *6,* UA 8421, ×38; *7,* UA 7902, ×56; *8,* encrinurid *Cybeloides prima* (Raymond) from the Crown Point Formation, Middle Ordovician, New York (locality PB81), NYSM 16315, ×76; *9,* lichid *Hemiarges* aff. *H. turneri* Chatterton & Ludvigsen from the Crown Point Formation, Middle Ordovician, New York, NYSM 16316, ×38; *10,* homalonotid *Brongniartella* sp. from the Martinsburg Formation, Middle Ordovician, Virginia, AMNH 43959, ×41; *11,* pterygometopid *Calyptaulax annulata* (Raymond) from the Crown Point Formation, Middle Ordovician, New York, NYSM 16317, ×108 (new).

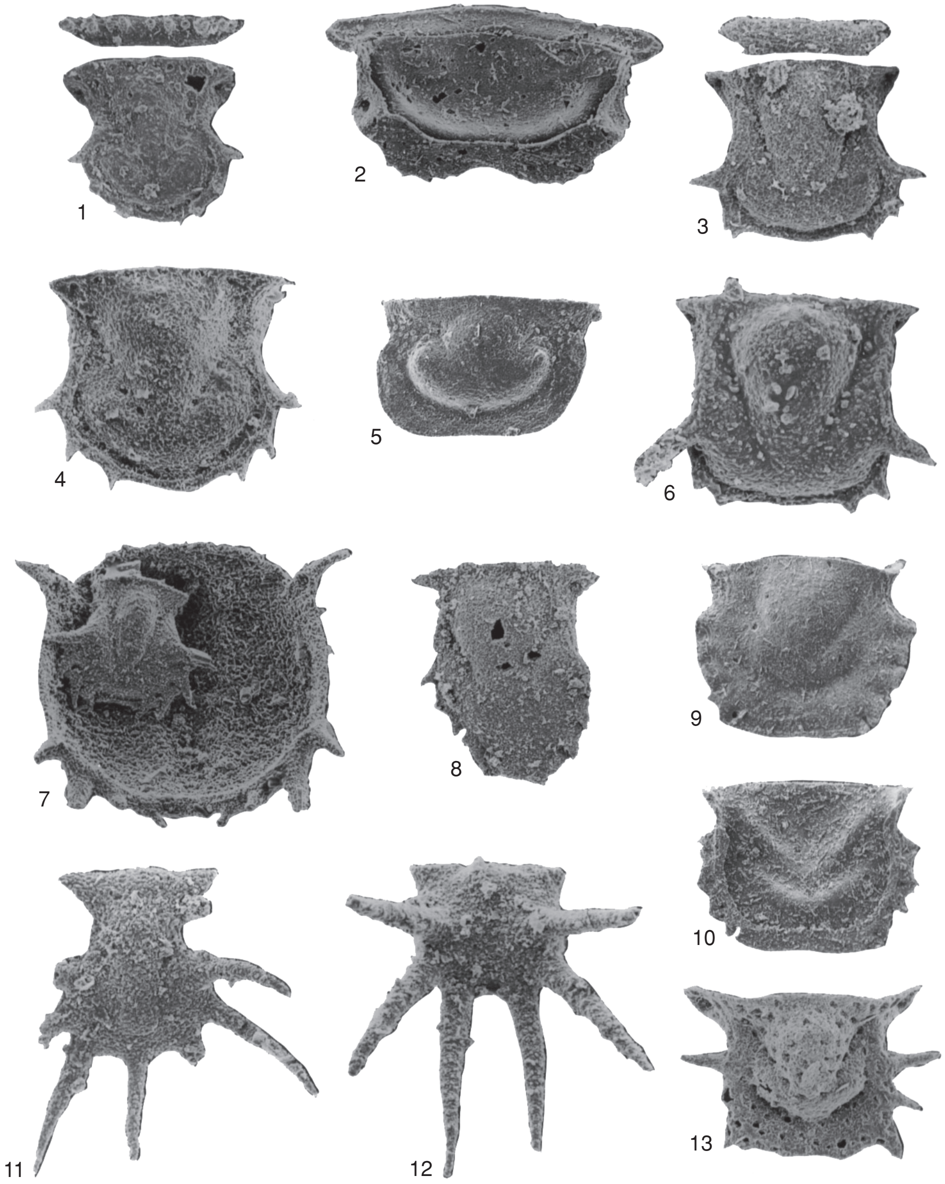

Fig. 152. Hypostomes and rostral plates. *1,* Ventral view of hypostome and rostral plate from same protaspis of pterygometopid *Calyptaulax annulata* (Raymond) from the Crown Point Formation, Middle Ordovician, New York, NYSM 16318, ×119 (new). *2,* Dorsal view of hypostome and rostral plate (meraspid?) of odontopleurid *Ceratocephala triacantheis* Whittington & Evitt from the Esbataottine Formation of the Mackenzie Mountains, Middle Ordovician, northwestern Canada, UA 8422, ×60 (new). *3,* Ventral view of hypostome and rostral plate from underside of same protaspis of encrinurid *Physemataspis insularis* (Shaw) from the Crown Point Formation, Middle Ordovician, New York, NYSM 16319, ×129 (new). *4,* Ventral view of small hypostome of pterygometopid *Calyptaulax annulata* (Raymond) from the Crown Point Formation, Middle Ordovician, New York, NYSM 16320, ×132 (new). *5,* Ventral view of small hypostome of odontopleurid *Acidaspis lesperancei* Chatterton & Perry from the Wenlock Delorme Formation, northwestern Canada, UA 4550, ×46.25 (new). *6,* Ventral view of hypostome of encrinurid *Physemataspis insularis* (Shaw) from the Crown Point Formation, Middle Ordovician, New York, NYSM

*(Continued on p. 193.)*

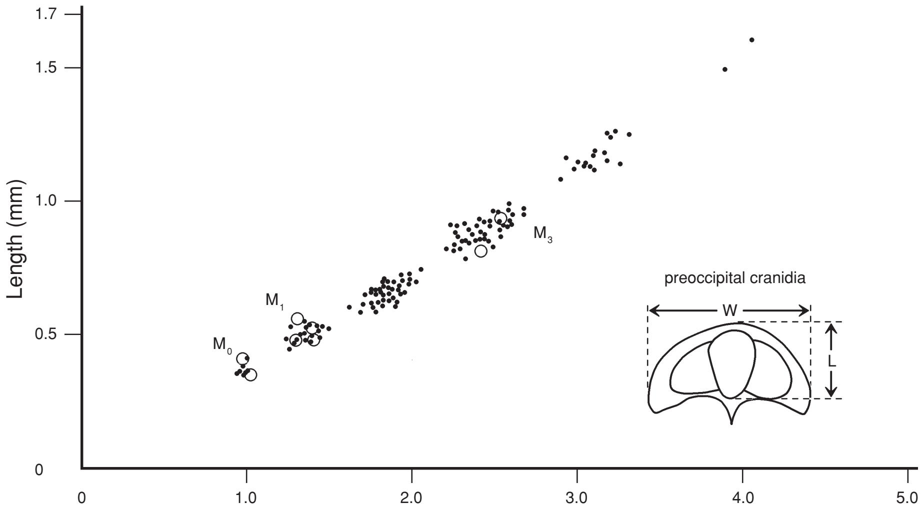

FIG. 153. Meraspid instars of trinucleid *Cryptolithus tesselatus* GREEN. *Open circles* represent articulated specimens that can be demonstrated to belong to meraspid degrees 0, 1, or 3 (M0, M1, M3). No articulated specimens were found with two free thoracic segments, representing meraspid degree 2 (M2). However, a distinct size cluster of cranidia was found between those that apparently represent meraspid degrees 1 and 3, suggesting that there was a meraspid degree 2 instar in the life cycle of *C. tesselatus,* and that each meraspid degree of this species was represented by a single instar. All articulated specimens are from a single block of the Middle Ordovician Martinsburg Limestone from north of Spring Hill, Virginia (processed by G. D. Edgecombe, collected by M. Kay); other specimens are from this locality and from locality 12 of WHITTINGTON, 1959a (processed by A. S. Hunt)(new).

morphological grounds), there are six instars during the meraspid period. Since eodiscid trilobites release only three segments into the thorax, the number of instars is twice the number of meraspid degrees; i.e., no thoracic segments were released between some instars. A similar pattern was found by HUNT (1967) for the metagnostid *Trinodus elspethi,* in which he identified three meraspid instars in a species that has only two adult thoracic segments, and by MÜLLER and WALOSSEK (1987, p. 20) for the agnostid *Agnostus pisiformis.* This similarity could be regarded as a synapomorphy for eodiscoids and Agnostina (see FORTEY, 1990a, 1990b, for more discussion); or, alternatively, it could have resulted from convergence among taxa with a reduced number of thoracic segments.

PALMER (1958, p. 165) divided the meraspid period into three subperiods, based on characters of the head. In the first, the early meraspid stage, "the glabella is continuous

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FIG. 152. *Explanation continued from facing page.*

16321, ×163 (new). *7,* Ventral view of third protaspid stage of calymenid *Flexicalymene senaria* (CONRAD) from the Martinsburg Formation, Middle Ordovician, Virginia, AMNH 43931, ×62.5 (new). *8,* Ventral view of hypostome of protaspis of lichid *Hemiarges* aff. *H. turneri* CHATTERTON & LUDVIGSEN from the Crown Point Formation, Middle Ordovician, New York, NYSM 16322, ×98 (new). *9,10,* Ventral and dorsal views of small hypostomes of illaenid *Failleana calva* CHATTERTON & LUDVIGSEN from the Crown Point Formation, Middle Ordovician, New York; *9,* UA 2717, ×36; *10,* UA 8423, ×37.5 (new). *11,* Fused hypostome and rostral plate of second protaspid stage of calymenid *Flexicalymene senaria* (CONRAD) from the Martinsburg Formation, Middle Ordovician, Virginia; most of hypostomes of this species have an extra, small pair of marginal spines between the median spine and the third pair, NYSM 16323, ×91 (new). *12,* Ventral view of hypostome of protaspid type P2 (see Fig. 174) of raphiophorid *Lonchodomas* sp. from the Crown Point Formation, Middle Ordovician, New York, NYSM 16324, ×125 (new). *13,* Ventral view of hypostome of cheirurid *Sphaerocoryphe goodnovi* RAYMOND from the Crown Point Formation, Middle Ordovician, New York, NYSM 16325, ×62.5 (new).

with the eye ridge and reaches to the anterior margin of the cranidium." In the middle meraspid stage "the glabella is separated from the border by a frontal area composed only of the brim." In the late meraspid and holaspid stage, "the frontal area is divided by a shallow marginal furrow onto [*sic*] a brim and border." He believed that these stages are "recognizable in the development of most non-olenellid trilobites with a brim and border." This may be true for a number of Cambrian ptychoparioid trilobites, but it is not applicable to most non-Olenellina. Although it may be useful in studies of heterochrony among some Cambrian trilobites, we do not advocate the use of this scheme.

KOPASKA-MERKEL (1987) divided the meraspid period into two subperiods, depending on whether the number of dorsally expressed protothoracic segments is increasing (**accumulation phase**) or decreasing (**shedding phase**) between adjacent instars. Early in the meraspid period, in the accumulation phase, new segments usually form near the back of the transitory pygidium at a rate faster than they are released into the thorax at the front. Towards the middle of the meraspid period, new segments may differentiate at the back of the transitory pygidium at about the same rate as they are released into the thorax. In the later shedding phase of the meraspid period, usually all of the segments have formed, including a protopygidium; and as segments are released into the thorax, the number of segments in the transitory pygidium is reduced. These stages can be recognized for most if not all trilobite growth series. KOPASKA-MERKEL recognized an accumulation phase of five to seven instars for the pliomerid *Hintzeia* and a shedding phase of four instars. He also noted that unpublished data of LUDVIGSEN on the cheirurid *Gabriceraurus* reveal an almost identical pattern. While speculating on the value of these data in determining relationships, he noted the apparently aberrant pattern of other cheirurids, *Ceraurinella typa* and *Ceraurinella chondra,* in which the first meraspid transitory pygidium found apparently contains all of the protothoracic segments as well as those that will become the pygidium. In other words, the entire accumulation phase occurs during the protaspid period or at least before meraspid degree 1 and perhaps involves a number of instars (see reconstruction by WHITTINGTON, 1957b, fig. 27; see also *Ceraurinella* protaspis in Fig. 178.1–2, which appears to be an intermediate state). Whether the shedding phase occurs in these two species over a number of instars as small steps or as a cascade in a very few instars is not yet known. Considering the very large size of these transitory pygidia, the latter is possible. This is not so for some other species of *Ceraurinella* such as *C. nahanniensis* (see CHATTERTON & LUDVIGSEN, 1976; CHATTERTON, 1980), where the pattern is more typical.

A substantial amount of trilobite growth, from less than 25 to as much as 30 to 40 percent, probably took place during the meraspid period (WHITTINGTON, 1957a; CHATTERTON, 1971; HUNT, 1967; X. ZHANG, 1989). There is surprisingly little reliable, numerical information in the literature on the proportion of the life cycle taken up by the meraspid period. This suggests that most workers have not considered this information to be important or that it is difficult to ascertain, certainly in contrast to proportional growth increments between instars. We also know of no data that may be used to mark the end of a trilobite's life due to old age other than the size of the largest specimens discovered in any collection.

During the meraspid period the trilobite was undergoing major reorganization, the production of new segments posteriorly and their release into the thorax. Thus, the length of the meraspid period, measured by the number of instars or the amount of growth, may have been an important constraint on the life-history strategy of a trilobite. A progenetic, paedomorphic pattern could have reduced the length of the meraspid period in a trilobite switching from a K-selective towards an r-selective life-history strategy of MacArthur and Wilson (1967; see also Gould, 1977).

### HOLASPID PERIOD

In the holaspid period all of the thoracic segments have been released. Most trilobites undergo considerable growth, probably most of their growth, during the holaspid period, although the exact amount has been documented for very few trilobites (Hunt, 1967; Whittington, 1957a; Chatterton, 1971; Chatterton & Ludvigsen, 1976). Considerable allometric growth may take place during the holaspid period; however, no major metamorphoses are known. Some of these allometric changes may be useful in diagnosing heterochronic evolution (see below). The number of instars that occurred during the holaspid period is usually very difficult to determine because of variations in the rate or amount of growth or even the timing of instars between individuals. These variations, which may be minor between any two instars, are compounded through the lives of the trilobites. Thus instars may be easy to distinguish in protaspid stages, more difficult to separate upon the basis of size during the meraspid period (but often possible on the basis of morphology), and impossible to discriminate in the holaspid period. Some authors have attempted to determine the number and sizes of holaspid instars for various taxa by using such growth rules as Dyar's rule or Przibram's rule. Where the instars cannot be distinguished clearly on the grounds of size or morphology, however, the use of these rules must be teleological.

Some trilobites appear to have exercised a closer genetic control over the sizes of their instars, and these can be distinguished even in holaspid stages. One such example is the metagnostid *Trinodus elspethi* (see Hunt, 1967). This species is small, however, with only nine recorded instars in the meraspid and holaspid periods. If the number of instars is correlated with age, a greater number of instars should increase the chance that individual variation will blur the boundaries between adjacent instars in later growth stages. Thus, the factors of (1) genetic variation and control (through release of hormones), (2) the age of the trilobite (or number of instars as a measure of age), and (3) the complexity of ecology or overall morphology may determine whether holaspid instars may be discriminated. It is also easier to discriminate instars in a collection made from a single bedding plane or from a single block of limestone than from a collection obtained from a number of beds. There are exceptions even to this rule, however; and Chatterton and others (1990) found that it was possible to discriminate instars in at least very early growth stages in collections of *Flexicalymene* made from more than one locality. Another factor, well documented among modern insects, is that the type or availability of food may affect the rate of growth and the number of molts (Bernays, 1986; Bernays & Hamai, 1987). This is also documented for many long-lived crustaceans, including crabs and lobsters (Travis, 1954; Hartnoll, 1969; Lipcius & Herrnkind, 1982; Ginatzy & Romer, 1984), and for chelicerates (Jegla, 1982; Laverock, 1927; Shuster, 1982).

Indications of sexual maturity are difficult to find in trilobites. Some of the morphological features that have been suggested as sexually dimorphic appear relatively early in their life cycles, presumably before the animals reached sexual maturity. Speyer and Brett (1985) have suggested that aggregations of adult individuals of similar size were for the purpose of reproduction and that, therefore, the study of the sizes of a number of individuals composing such aggregations may provide information on the size of trilobites at the onset of sexual maturity. A change in growth allometry during ontogeny may mark the time of onset of sexual maturity (Hartnoll, 1969). This could be apparent from an inflection on a growth curve or a change in the proportional growth increment between instars. However, as noted

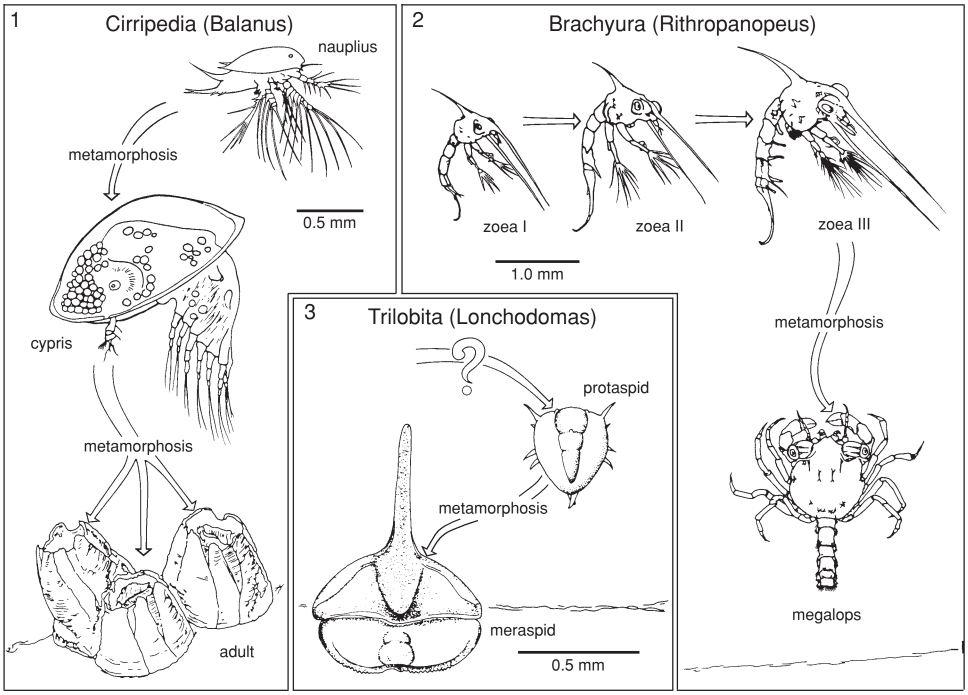


FIG. 154. Metamorphosis among marine arthropods. *1,* Barnacles (Cirripedia) undergo two ecology-related metamorphoses during development: the nauplius, a feeding and free-swimming larva transforms into a bottom-seeking nonfeeding cypris, which then transforms into a very specialized adult. *2,* Decapod crabs have an active, feeding zoea that passes through several molts before changing into a bottom-seeking megalops. *3,* The raphiophorid *Lonchodomas* passes through two protaspid instars before undergoing a metamorphosis between protaspid and meraspid periods, which, by inference, we consider to be related to a change in ecology (planktonic to benthic) (adapted from Speyer & Chatterton, 1989, fig. 12).

above, instars are usually very difficult to discriminate late in ontogeny.

## LIFE-HISTORY STRATEGIES

CHATTERTON and SPEYER (1989) have noted the more common life-history strategies, considering the larvae as either benthic or planktonic and most as heterotrophic, lecithotrophic, or planktotrophic. Some life cycles included a radical metamorphosis early in the ontogeny, usually accompanied by a change from a planktonic to a benthic mode of life, as is the case for many modern arthropods (Fig. 154). The size of the smallest known exoskeleton in the growth series of different trilobites varies greatly (from less than 0.2 mm to greater than 1.0 mm). Some trilobites passed through stages and size classes as embryos or free-swimming, uncalcified individuals that other taxa passed through calcified (Fig. 140, 147). The four life-history strategies listed below are predicated on the thesis that some larvae were planktonic and others were not. Figure 155 shows hypothetical appendages and life positions for a nonadult-like, planktonic larva and an adult-like, benthic larva. Recognition of the mode of life of larvae is based on their overall morphology (the nonadult-like being unconstrained in three dimensions, without ventral apertures and muscle attachment sites that would be expected for efficient operation of appendages that might be used for locomotion on or digging in a sedimentary substrate), their separation from more adult-like later stages by a radical metamorphosis, and their distributions (Fig. 156).

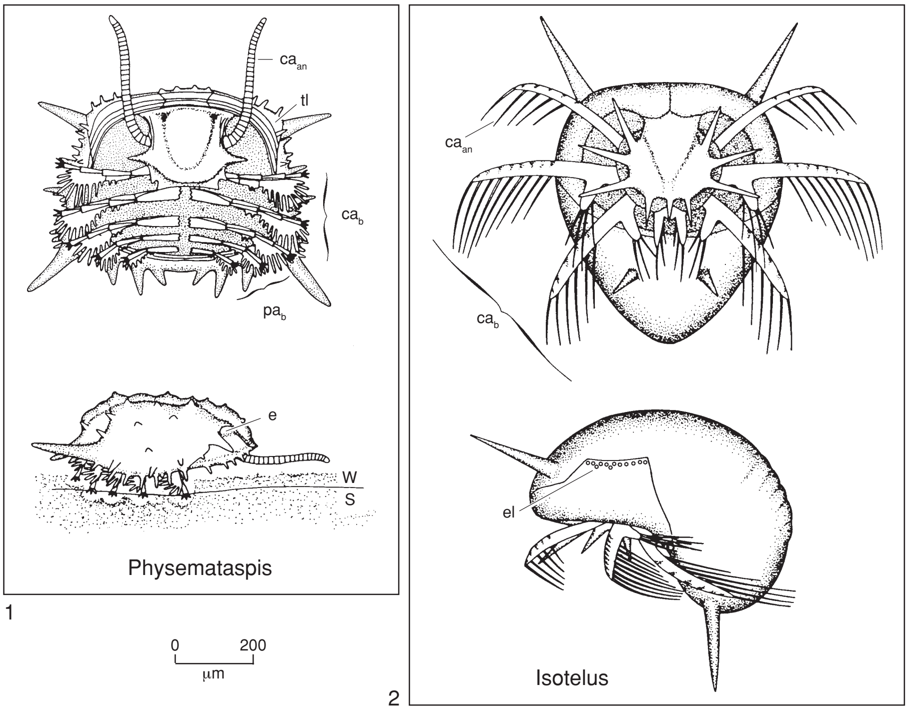


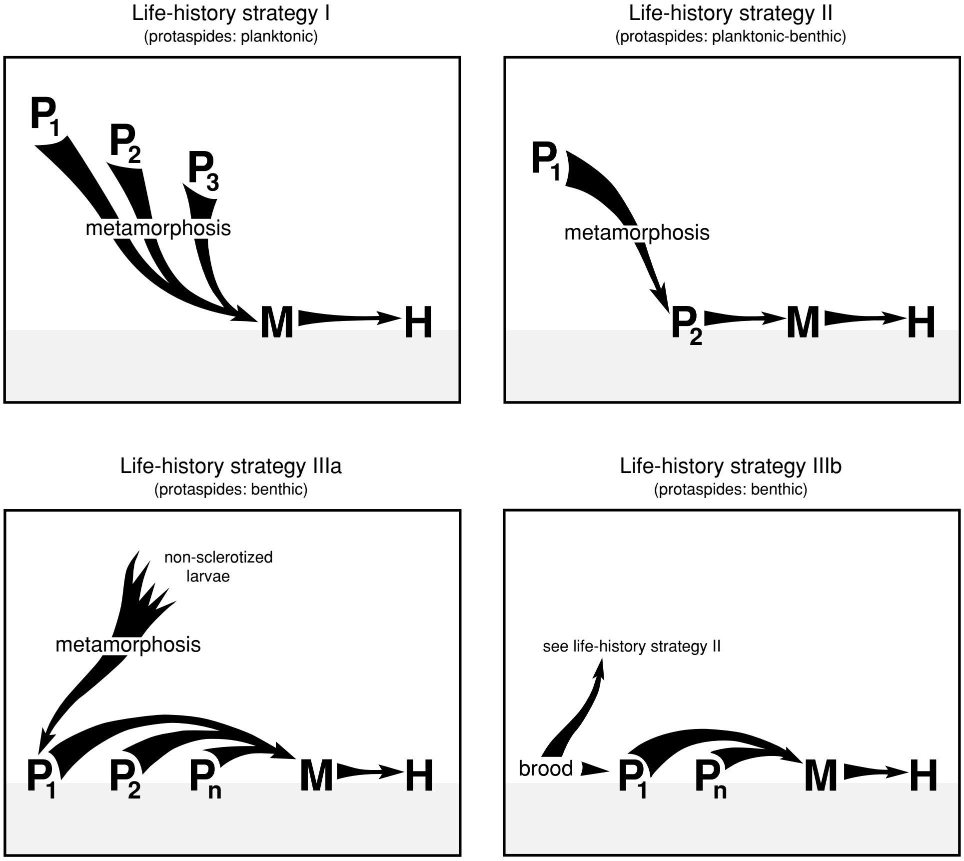
FIG. 155. Hypothetical appendages and life positions of an adult-like protaspis of encrinurid *Physemataspis* and a nonadult-like protaspis of asaphid *Isotelus.* Abbreviations: *ca,* cephalic appendage (*an,* antenna; *b,* biramous); *e,* eye; *el,* eye lenses; *pa,* pygidial appendages (*b,* biramous); *tl,* terrace ridges; *W/S,* water-sediment interface (adapted from Speyer & Chatterton, 1989).

## LIFE-HISTORY STRATEGY I

In this strategy all protaspid growth stages were planktonic (or premetamorphic) in form, with the metamorphosis into benthic, heterotrophic forms at or after the end of the protaspid period. This pattern is one of the characteristic features of the Asaphida (FORTEY and CHATTERTON, 1988). CHATTERTON and SPEYER (1989) pointed out that almost all taxa with this life-history pattern became extinct during the Ordovician (including a number of taxa in the mass extinction near the end of the Ordovician). They also demonstrated that taxa with this life-history strategy were constrained geographically to lower paleolatitudes and suffered a minor extinction at about the time of onset of the Ordovician-Silurian glaciation. Examples of trilobites with this type of life-history strategy are *Isotelus* and *Remopleurides.* In *Isotelus* (Fig. 157), the metamorphosis from nonadult-like, planktonic stages to adult-like, benthic stages apparently took place at the transition between the protaspid and meraspid periods. In *Remopleurides*, this change occurs within the meraspid period in some, if not all, species (Fig. 158).

## LIFE-HISTORY STRATEGY II

In this strategy the first calcified stage is planktonic or at least separated from later stages by a radical metamorphosis, and later stages are benthic. This pattern may have been acquired independently in several different Ordovician and younger clades. It is shared by such taxa as the Illaenina, the Lichidae, the Phacopida, and some ptychopariids. If this pattern were plesiomorphic or a synapomorphy of these groups, one might expect the smallest premetamorphosis larvae of these groups to be very similar. Since they are not and some of the taxa listed here prob-


Life-history strategy I
(protaspides: planktonic)

Life-history strategy II
(protaspides: planktonic-benthic)

Life-history strategy IIIa
(protaspides: benthic)

Life-history strategy IIIb
(protaspides: benthic)

Fig. 156. Varied developmental patterns and life-history strategies indicated by trilobite ontogenies. *P* indicates a protaspid instar; *M* indicates meraspid instars (the meraspid period); and *H* indicates an indefinite number of holaspid instars (the holaspid period). The *subscripts* in the protaspid stages refer to the first, second, third, or nth sclerotized protaspid instar. The location of letters representing growth stages corresponds to presumed ecology, that is, whether they lived in the water column or on the sea floor (adapted from Speyer & Chatterton, 1990).

ably have sister groups that are excluded from this group, this life-history strategy probably evolved several times in different groups of trilobites. Chatterton and Speyer (1989) showed that trilobites with this pattern were comparatively successful in surviving the end of the Ordovician mass extinction. Rare forms with this life-history pattern may have more than one premetamorphosis larva, as in *Flexicalymene* (see Fig. 178; Chatterton & others, 1990). It is possible that the phaselus belongs to some taxa with this strategy; Fortey and Morris (1978) assigned the phaselus to *Cybelurus,* a form with this life-history strategy. *Failleana,* an illaenid, provides an example of this life-history strategy (Fig. 159).

### LIFE-HISTORY STRATEGY III

Here all calcified growth stages are benthic. Trilobites with this life-history strategy had a comparatively high rate of survivorship during the Ordovician extinctions and gave rise to many post-Ordovician trilobites (Chatterton & Speyer, 1989). *Dimeropyge,* a bathyuroid with at least three adult-like protaspid instars, is an example of a trilobite with this life-history strategy (Fig. 160); *Scharyia* (see Fig. 180) is another (Šnajdr, 1981a). Earlier workers would have

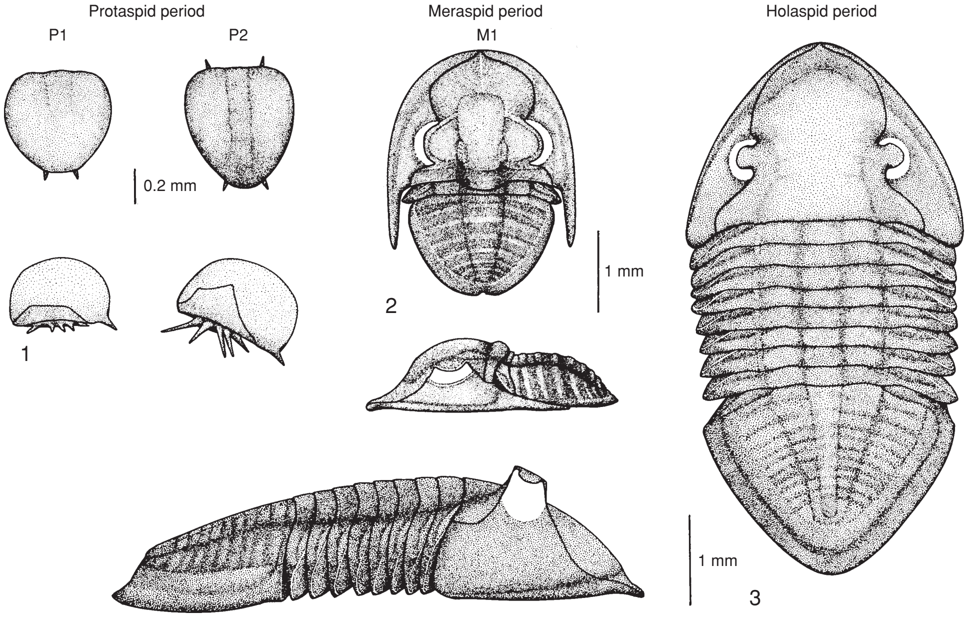


FIG. 157. Early growth stages in the life cycle of asaphid *Isotelus parvirugosus* CHATTERTON & LUDVIGSEN and a mature specimen of *Isotelus gigas* DEKAY. Drawings are of two nonadult-like protaspid instars (P1, P2), an instar representative of meraspid degree 1 (M1), and a mature holaspid. This genus appears to be a typical representative of life-history strategy I (see Fig. 156). All stages are shown in dorsal and lateral views (new).

called the smallest protaspis assigned to this growth series an anaprotaspis. Some might have argued that it was planktonic. We consider that the relatively two-dimensional form of this stage, when considered with the moderate-sized hypostome, which lacks strong marginal spines, and the moderate morphological change between this stage and the following growth stage (a large amount but less than in most planktonic to benthic metamorphoses), suggests that it was benthic rather than planktonic. Marginal spines, where they occur on the hypostomes of benthic larvae, are short and usually laterally or posteriorly directed rather than ventrodistally directed (the usual state in planktonic protaspides).

### LIFE-HISTORY STRATEGY IV

Larvae are benthic or rarely planktonic; adults are pelagic. This life-history strategy is not as relevant to early ontogeny as the preceding strategies but strongly affects the survivorship of the group. No taxa showing this life-history pattern survived the late Ordovician mass extinction. For examples of this life-history strategy, see FORTEY (1985).

Some of the stages categorized above as benthic, particularly some of the larvae, for hydrodynamic reasons could have been part planktonic or nektonic and part benthic. We have assumed that those stages that could have operated efficiently on the sea floor did so, and those that could not, did not.

The four life-history strategies discussed above are broad and encompass distantly related taxa. They do, however, affect survivorship and dispersal of trilobite taxa (CHATTERTON & SPEYER, 1989) and are relevant in evolutionary, paleoecologic, and paleobiogeographic studies.

## HETEROCHRONY

JAEKEL (1909) did not document in detail his suggestion that the Agnostida arose from

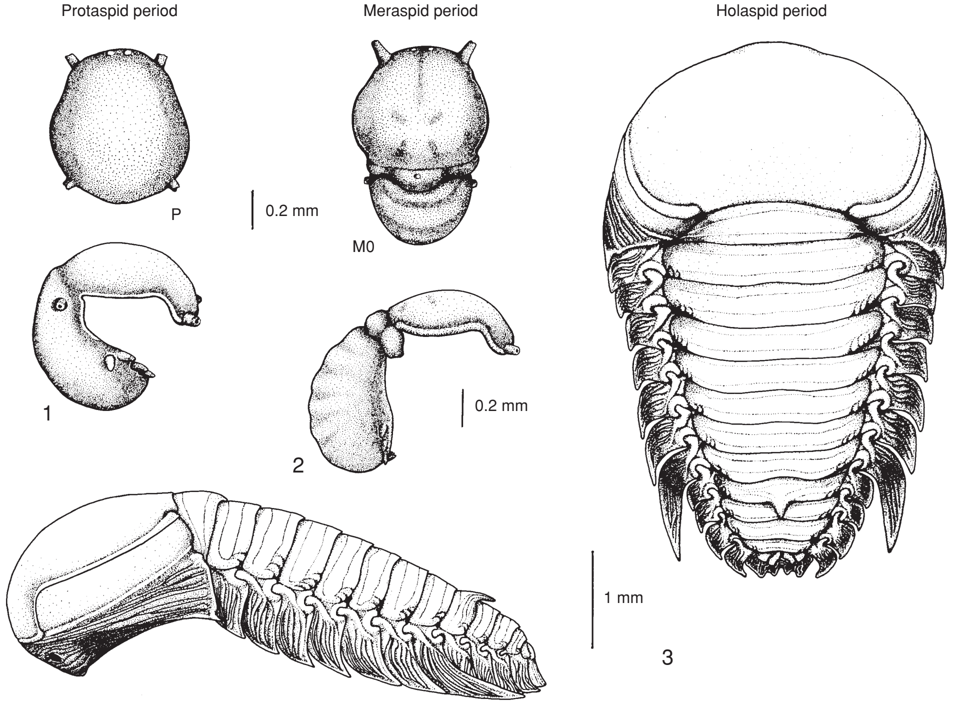


Fig. 158. The life cycle of the remopleuridid *Remopleurides eximius* Whittington. Drawings are of a late protaspis (*P*), a representative of meraspid degree 0 (M0), and a mature holaspid. This species appears to represent a variant of life-history strategy I (see Fig. 156), in which the metamorphosis from nonadult-like pelagic to adult-like benthic stages was retarded so that it took place during the meraspid period. All stages shown in both dorsal and lateral views (adapted from Whittington, 1959a).

polymerid trilobites through paedomorphosis. We presume that he was influenced by the small size of Agnostida, their small number of thoracic segments, their isopygous condition, and even, possibly, their blindness. Many of the distinctive features of Agnostida are not similar to characters known in small polymerid trilobites and cannot be interpreted as the result of paedomorphic evolution from any taxon with a well-known ontogeny. No proposed ancestor of the Agnostida has been widely accepted, and therefore any suggestions in regard to a heterochronic origin for this group must be regarded as speculative. Stubblefield (1936), Hupé (1954), Jell (1975a), and Müller and Walossek (1987) have commented on this possible mode of origin, the latter workers even suggesting that the slightly unusual form of the appendages of *Agnostus* may be explained by their derivation from larval morphologies, which are frequently quite different from adult morphologies and extensively modified during ontogeny in the related Crustacea. We do not know of any examples of preserved, larval appendages of polymerid trilobites (those of Fig. 155 are purely speculative). Comparison with the ontogenies of polymerid trilobites suggests, from the radical nature of the changes and some of the morphological details, that heterochronic changes necessary to give rise to Agnostida would have to have occurred comparatively early in the ontogeny of the ancestral forms. These changes must have affected at least meraspid and probably protaspid stages of the ancestral forms. The small size and juvenile appearance of the Agnostida would imply that most of the changes were progenetic. The

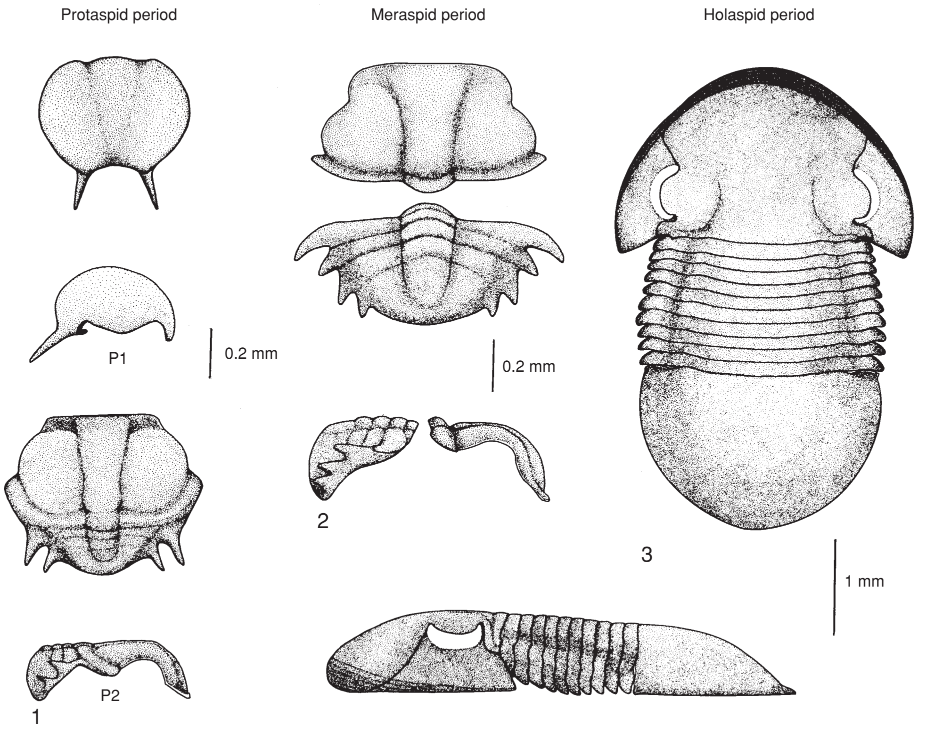


FIG. 159. The life cycle of the illaenid *Failleana calva* CHATTERTON & LUDVIGSEN. The life cycle of this species is representative of life-history strategy II (see Fig. 156). *P1* represents a nonadult-like, first protaspid instar; *P2* represents an adult-like, second protaspid instar. The meraspid period is represented by a cranidium and transitory pygidium belonging to early meraspid degree(s); and the holaspid period is represented by a reconstruction of a mature individual. All stages are shown in both dorsal and lateral views. The protaspid stages and meraspid degrees lack free cheeks, rostral plate, and hypostome (new).

Agnostida also have a number of autapomorphies that cannot be explained readily as the results of heterochronic evolution. After the separation of the Agnostida from other trilobites, considerable evolution took place within this group.

GOULD (1977) pointed out the prevalence of heterochronic evolution and suggested that there may be a relationship between heterochronic patterns of evolution and paleoecology, in particular the r and K life-history strategies of MACARTHUR and WILSON (1967).

It may be argued that the numerous evolutionary pathways available through using different heterochronic patterns (the six patterns shown by MCNAMARA, 1986b, fig. 1, plus an indefinite number of mosaic patterns based on heterochrony taking place at the organ rather than the organism level) allow organisms to radiate rapidly when the opportunity presents itself. Such an opportunity may follow a mass extinction as niches become vacant.

Some workers (STUBBLEFIELD, 1936, 1959; STØRMER, 1942; HUPÉ, 1954; CLARKSON, 1971, 1975) suggested that heterochrony, in particular paedomorphosis, was the source of important evolutionary novelties that determined higher taxa within the Trilobita. WHITTINGTON (1957a) discussed the evidence for neoteny as an evolutionary process, particularly in regard to the origins of orders of trilobites, and was not convinced by the cases that had been made by earlier workers. He favored selection at the organ

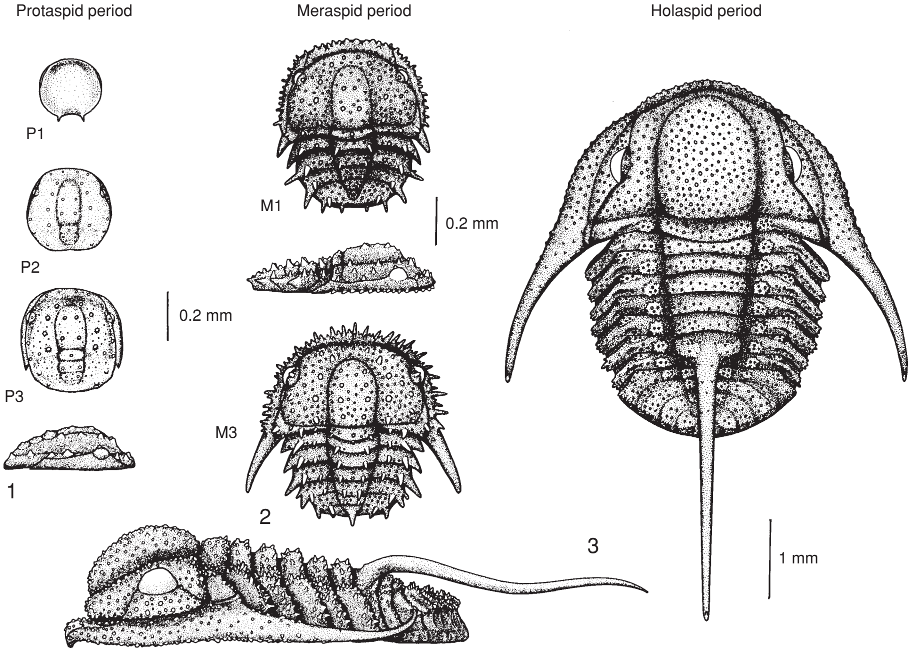


FIG. 160. The life cycle of the bathyuroid *Dimeropyge* n. sp. Drawings are of specimens from the Middle Ordovician Esbataottine Formation of northwestern Canada (see Fig. 182). The life cycle of this species is considered to represent life-history strategy III (see Fig. 156). All stages are considered to represent individuals that lived on the sea floor. *P1–P3* represent three protaspid instars; *M1* and *M3* represent meraspid degrees 1 and 3. Dorsal and lateral views are provided for the last protaspid instar (*P3*), a meraspid degree (*M1*), and a holaspid stage (new).

level in response to environmental pressures over any heterochronic process. WHITTINGTON (1981, p. 593), while accepting some documented examples of paedomorphosis, was unconvinced that this form of evolution had been demonstrated for the "derivation in this way of a species ancestral to a new family or group" and did not believe that post-Cambrian proparian trilobites evolved from a single paedomorphic species. He also commented on the cryptogenetic origin of most trilobite higher taxa.

MCNAMARA (1986a, p. 126) pointed out that most workers have concentrated on examples at the species level or on the origin of new genera (ROBISON & CAMPBELL, 1974; FORTEY, 1974b, 1975b; JELL, 1975a; MCNAMARA, 1978, 1981a, 1981b, 1983; LUDVIGSEN, 1979b; FORTEY & RUSHTON, 1980; WHITTINGTON, 1981; CHATTERTON & PERRY, 1983; RAMSKÖLD, 1988; EDGECOMBE & CHATTERTON, 1987).

MCNAMARA (1978, 1981a, 1981b, 1983, 1986a) has described heterochronic patterns of Cambrian trilobites. He found that both peramorphosis and paedomorphosis are important in trilobite evolution. He discussed the role of paedomorphosis in developing major evolutionary novelties within the Trilobita and considered that perhaps the best example is the possible paedomorphic origin of the Corynexochida from the Ptychopariida, with meraspid stages of genera such as *Crassifimbra* (see ROBISON, 1967) being very similar to adult corynexochids like *Bathyuriscus.* Most of the examples quoted by MCNAMARA are based entirely on adult allometry, which is biased in regard to the amount of morphological change that takes place and the range of ecological factors experienced by the animals. The most radical examples of heterochrony can be expected to involve morphological variation of larval as well as adult growth stages.

Clarkson (1971, 1975) has argued that the origin of the schizochroal eye of the Phacopina and the usual forward position of the eye on the cephalon may have resulted from a paedomorphic, heterochronic pattern of evolution. He based this thesis on the facts that probable ancestral taxa have fewer lenses in their juvenile eyes and the eyes of phacopid larvae are located relatively farther forward than those of the adults. Thus cases have been made for the independent evolutionary origin of three trilobite orders using paedomorphic patterns: Agnostida, Corynexochida, and Phacopida.

McNamara (1986a, p. 149) has also argued that a different pattern of heterochronic evolution may have played a part in the origin of some important post-Cambrian groups of trilobites. He noted the comparatively advanced morphological stage of the early growth stages of members of the Lichidae, Phacopida, and Illaenina. He suggested that this was an example of predisplacement, "one of the processes which result in peramorphosis" (Alberch & others, 1979). McNamara also argued that most published examples of heterochronic evolution of post-Cambrian trilobites have been of peramorphosis, although undoubtedly paedomorphosis has occurred (e.g., Ludvigsen, 1979b; Edgecombe & Chatterton, 1987). In this context, McNamara quoted Gould (1977, p. 269): "evolution by acceleration must be an important path to the development of morphological complexity in specific features." McNamara (1983) illustrated a number of small trilobites that he thought may have had a progenetic origin (Fig. 161). Fortey argued that the origin of the Proetida could have been as a result of "adult morphology displaced back to protaspis stage" or, in other words, a form of predisplacement (1990a, fig. 16, p. 558–560).

McNamara (1988, table 1) provided a list of published examples of heterochrony of trilobites. All of these are at generic or specific levels except for three: the origin of phacopids (Clarkson, 1979a), the origin of the order Corynexochida (Robison, 1967), and the origin of the subfamily Calymeninae (Siveter, 1980). Of the 36 examples that he listed, 21 are of paedomorphosis (12 Cambrian; 7 Ordovician; 2 Silurian), 13 are of peramorphosis (3 Cambrian; 8 Ordovician; 1 Silurian; and 1 Silurian-Devonian), and 2 are of mixed paedomorphosis and peramorphosis (both Silurian). Presumably, these examples provided the bulk of the data on which he based his generalization that paedomorphosis was more important among Cambrian trilobites and peramorphosis more important among post-Cambrian trilobites (McNamara, 1986a). These 36 examples represent a very small proportion of the Trilobita, and McNamara noted that some forms of heterochrony (e.g., progenesis) are more recognizable than others.

Recent work on ontogeny and heterochrony (Clarkson, 1971, 1975) has shown that some patterns of heterochrony may affect primarily organs rather than whole organisms. An organism may evolve in a variety of heterochronic patterns at the same time, some of which may be paedomorphic and some peramorphic. This form of evolution, showing mixed heterochronic patterns (mosaic heterochrony of Kopaska-Merkel, 1987), apparently occurred in the origin of the *Encrinurus punctatus plexus* from an *Encrinuroides* ancestor (Edgecombe & Chatterton, 1987). Edgecombe and Chatterton (1987) also identified a mixture of paedomorphic and peramorphic patterns in a rapidly evolving lineage of *Kettneraspis* in Silurian strata of northwestern Canada. This lineage occurs in a sequence of strata (mainly limestones) laid down during a regression, from comparatively deep and stable, presumably K-selective environments to shallower, more unstable, r-selective environments. They argued that the combination of the

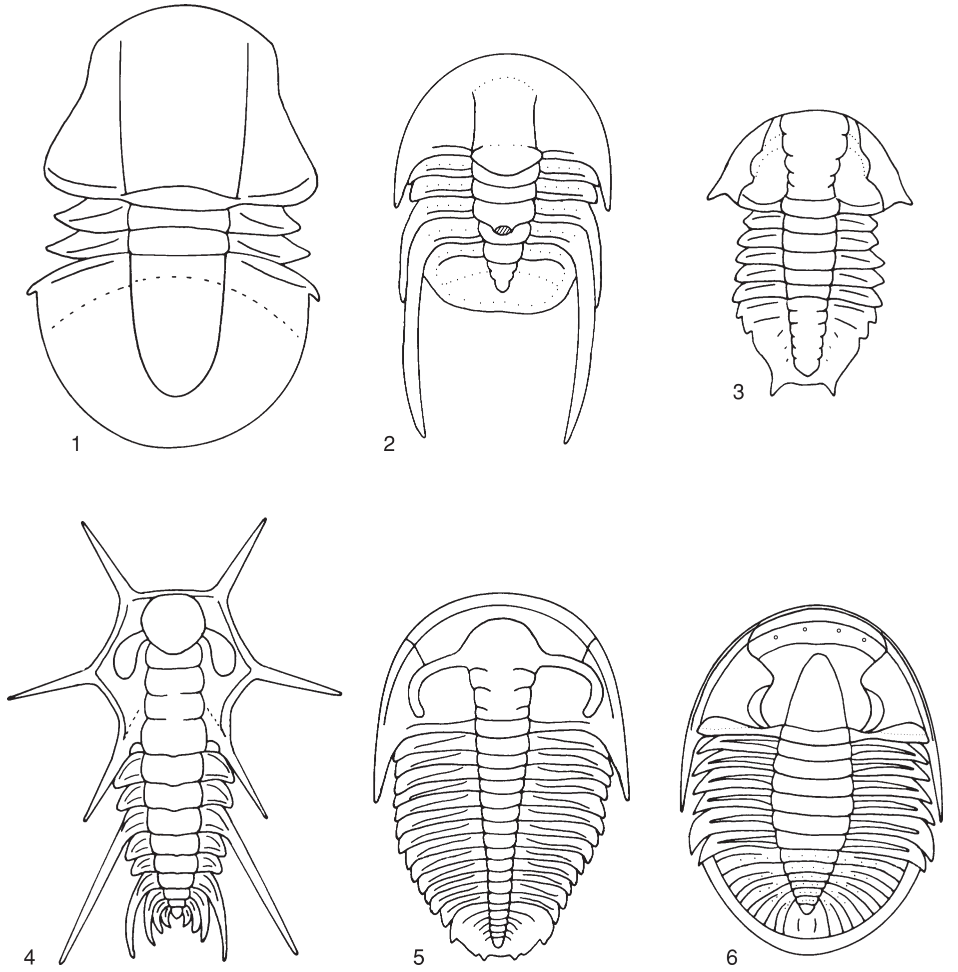


FIG. 161. Progenetic trilobites. *1, Thoracocare minuta* RESSER; *2, Acanthopleurella grindrodi* GROOM; *3, Vanuxemella nortia* WALCOTT; *4, Olenellus armatus* PEACH; *5, Galahetes fulcrosus* ÖPIK; *6, Scharyia redunzoi* PERRY & CHATTERTON (Chatterton & Speyer, 1990, fig. 4).

peramorphic acceleration and paedomorphic progenesis patterns is a consistent evolutionary response to this change in the ecology. MCKINNEY (1986) had earlier come to similar conclusions for Cenozoic echinoids. Some neontologists, however, consider the theory of r- and K-selection to be an overgeneralization: that all organisms show a mixture of such traits and that polarization of r- versus K-selection or even versus stress tolerance (VERMEIJ, 1978) is unnatural.

In order to examine heterochronic patterns in trilobites, it is necessary to select some benchmarks that may be used to determine relative rates of development and onset or timing of development of particular features. This may be accomplished by assuming that a feature increases in size at a regular rate in relation to time (such as the length of the glabella) and timing other events in relation to numerical increments in size of this feature. Alternatively, it may be done by contrasting the timing of the appearance of some morphological event in relation to that of some other morphological event considered to be a useful time marker. The number of such time markers in the ontogeny of trilobites is large and includes several features: the timing of the first distinct appearance of axial furrows on the cranidium (or protocranidium), the appearance of a furrow marginal on the protocranidium (separating the protocranidium from the prototransitory pygidium), an anterior border, a preglabellar field, a distinct visual surface, a functioning hypostomal suture, a bulla, functioning connective sutures, the first segment on the protopygidium (or a particular number of segments), and the suture that causes separation of the cephalon from the transitory pygidium (protaspid-meraspid boundary). Other important heterochronic markers may include losses (such as loss of long marginal spines on the hypostome), movements of features (transfer of genal spine from the fixed cheek to the free cheek or the release of the last segment into the thorax at the transition from meraspis to holaspis), and even expansion of features (e.g., the bullae expanding to incorporate parts of more than one cranidial somite). Not all of these markers occur in all taxa. Which markers are the most suitable for the taxa being studied and which may be most convincingly argued must be chosen for each heterochronic study.

LUDVIGSEN (1979a) argued (Fig. 162) that *Pseudogygites* arose from *Isotelus* through paedomorphic (neotenic) evolution, since mature individuals of *Pseudogygites* are very similar to meraspid individuals of *Isotelus.* He pointed out that *Pseudogygites* is abundant in a very distinct, low-diversity facies (low-temperature, low-oxygen, dark shales). However, he considered that low temperature could not be the cause of this heterochronic pattern because *Pseudogygites* apparently originated on a warm, carbonate shelf and later became abundant in deeper, colder-water, terrigenous-mud environments. (It occurs first in low numbers in the upper parts of the Cobourg Formation.) LUDVIGSEN argued that neotenic, heterochronic evolution, perhaps as a K-strategy, preadapted *Pseudogygites* for the colder, deeper, more stable environments of the Whitby Formation, which was deposited later. He suggested that this situation may have occurred more than once, producing several species of *Pseudogygites* iteratively from *Isotelus.* If so, cladists would argue that *Pseudogygites* is polyphyletic and should be subsumed within *Isotelus.*

One of the better examples of heterochronic evolution among Cambrian trilobites is that of various species of *Xystridura* and the descendant genus *Galahetes* (Fig. 163; MCNAMARA, 1981a). Morphological details found in small cranidia of such stem-form Xystriduridae as *Xystridura templetonensis* and hypothesized to occur in *Xystridura carteri* occur in adult growth stages of the later species *Xystridura altera, Xystridura dunstani, Xystridura sandoverensis,* and *Galahetes fulcrosus;* these include retention of a preglabellar field, a wide fixed cheek and cranidium, and a smaller frontal glabellar lobe. MCNAMARA also considered whether ecological factors could explain the differences between the apparently progenetic pattern that produced *G. fulcrosus* and the neotenic pattern that produced *X. altera,* two species that occur in some cases on the same bedding planes. He argued that the former, progenetic species may have been r-selective and pelagic and that the latter species may have been K-selective and benthic. However, we believe that the adult morphology of both species is typical of benthic trilobites and consider it more likely that these two forms originated in different environments, which could have favored r- over K-selective taxa, and later occurred together as a result of migrations in response to environmental changes.

Most published examples of heterochronic evolution among trilobites are based on general inferences of ancestral-descendant relationships rather than detailed arguments in support of individual phyletic lineages and demonstrations of anagenetic evolution. Also, in a number of cases, the ontogenies are not known for either the hypothesized ancestral or the descendant species but have been inferred from the known ontogeny of a

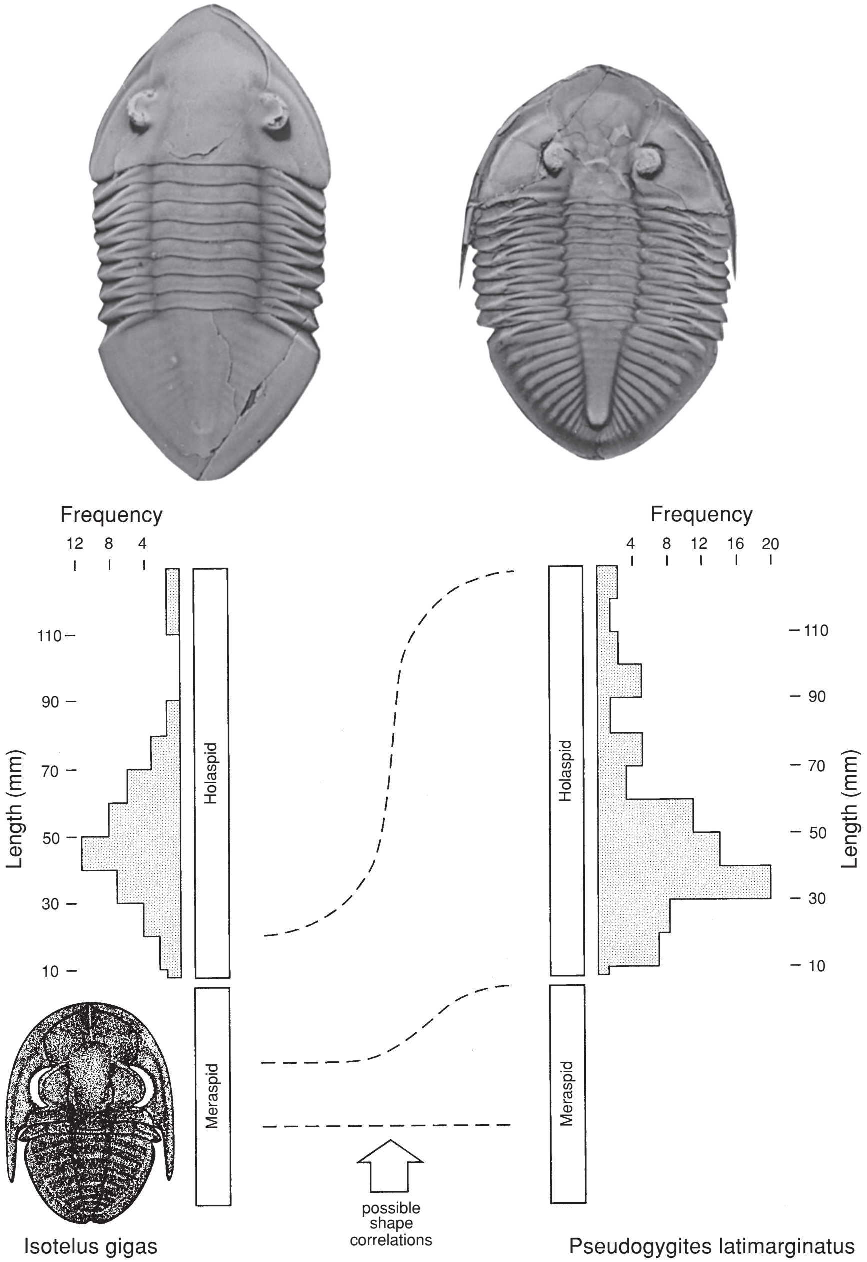


FIG. 162. Model of heterochronic (paedomorphosis, neoteny) derivation of *Pseudogygites* from *Isotelus* during the Ordovician, based on 46 specimens of *Isotelus gigas* from the Trenton Group of New York and 79 specimens of *Pseudogygites latimarginatus* from the Whitby Formation of Ontario. *Dashed lines* indicate tentative shape correlations. Drawing of *I. gigas* meraspid degree 1 based on specimen illustrated by LUDVIGSEN and silicified material of *Isotelus parvirugosus* CHATTERTON & LUDVIGSEN from the Esbataottine Formation, northwestern Canada (Chatterton & Speyer, 1990, fig. 7).

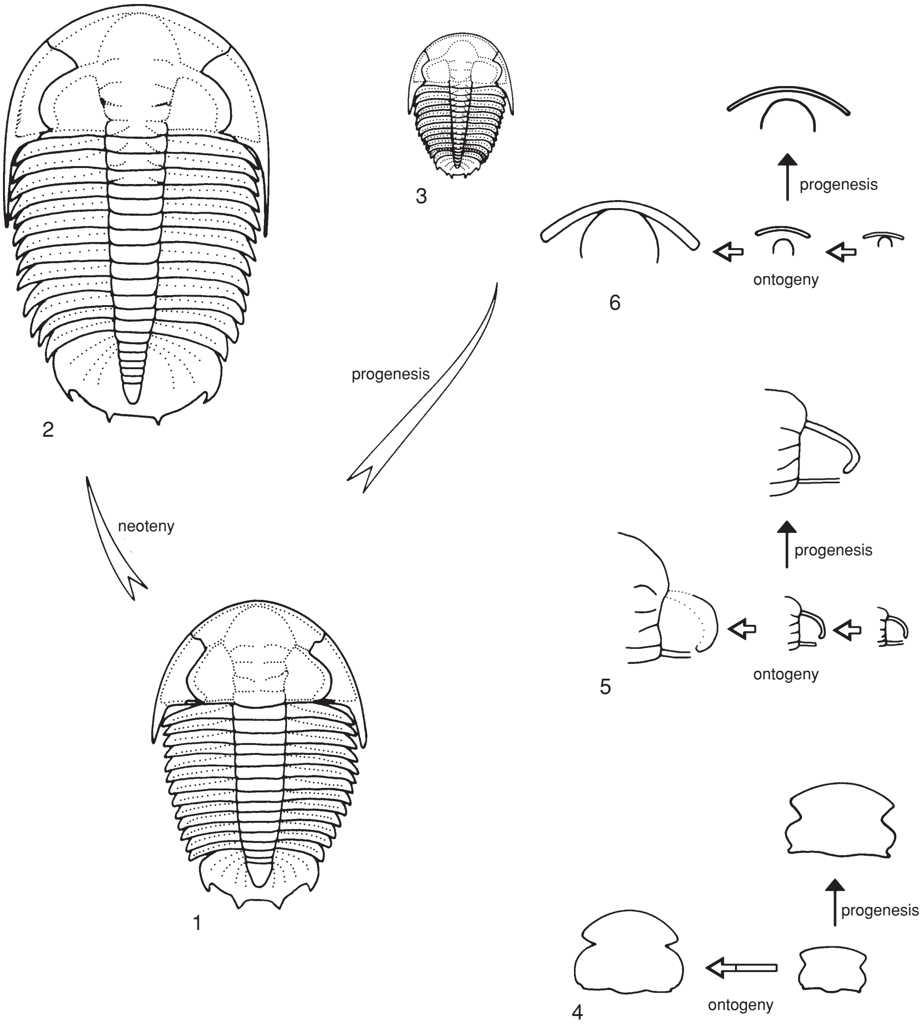


FIG. 163. Heterochronic patterns in Cambrian Redlichiina *Xystridura* and *Galahetes. 1, X. templetonensis* (CHAPMAN); *2, X. altera* ÖPIK; *3, G. fulcrosus* ÖPIK. *4–6,* Horizontal row of drawings and *open arrows* show changes during ontogeny in cranidia of *X. templetonensis; vertical arrows* show characters present in the adult *G. fulcrosus* that occur in the ontogeny of *X. templetonensis; 4,* changes in the outlines of cranidia (note curvature of anterior margin); *5,* changes in width from axial furrow to back of eye as a percentage of cranidial length; *6,* changes in the length of the preglabellar field. [In one of MCNAMARA's original diagrams used for this figure (1981a, fig. 8), *X. carteri* ÖPIK is included as the stem-form species. However, since all his examples of ontogeny within *Xystridura* were based upon *X. templetonensis* and he noted (1981a, p. 216) that *X. templetonensis* is a stem-form species of *Xystridura,* we have chosen to use the latter species in this adaptation from McNamara (1981a).]

related species. (For an exception, see FORTEY & RUSHTON, 1980.) Ideally, ontogenies of both ancestral and descendant species should be known, and a considerable amount of data should be available supporting direct descent of one species from the other in the form of morphologically overlapping intermediate collections of fossils from appropriate stratigraphic levels and geographic locations. We can think of no published examples that fulfill all of these criteria. A number of sequences of silicified trilobites have great potential as examples (Virginia, New York, the Mackenzie Mountains).

## GROWTH FORMULAS AND POPULATION DYNAMICS

Several rules have been formulated for the amount of growth expected between adjacent instars of various types of arthropods. HARTNOLL (1982) discussed some of these and their application to crustaceans. One of these was Dyar's rule (DYAR, 1890): $x/y$ = a constant, where $x$ is a linear measurement for an instar and $y$ is the same linear measurement for the previous instar; another was Brooks' rule, originally defined by FOWLER (1909) as $x - x/y$ = a constant but later redefined as the percentage by which the postmolt exceeds the premolt length (MAUCHLINE, 1976). HARTNOLL also discussed Przibram's rule (PRZIBRAM, 1929), where weight doubles between instars so that increase through Dyar's rule should be the cube root of 2, or 1.26.

Growth increments between molts in trilobites and their fit to these rules of growth have been discussed by PALMER (1957), HUNT (1967), CISNE (1973b), ROMANO (1976), KOPASKA-MERKEL (1981), BUSCH and SWARTZ (1985), BREZINSKI (1986a), SHELDON (1988), CHATTERTON and SPEYER (1990), and CHATTERTON and others (1990). In most examples, ontogenies have growth increments between instars that are in general agreement with these laws. However, the increments can be significantly above or below the expected values. In some, departure from these rules is associated with molts that involve radical metamorphoses. It is, however, difficult to quantify size differences between planktonic and benthic growth stages because the morphologies of the forms are so different, and volume may be more important than mere length and width. Rarely are the instars known with certainty for more than a small portion of the life cycle of the trilobite, although, as HUNT (1967) pointed out, distinct instars are usually identifiable with confidence for early growth stages.

Recent work on arthropods has demonstrated that correspondence with growth rules is far from general. Some workers have shown that the amount or type of food may affect the rate of growth, the number of instars, and thus the amount of growth between instars (e.g., BERNAYS, 1986; BERNAYS & HAMAI, 1987; LIPCIUS & HERRNKIND, 1982). The same was probably true for trilobites, and the growth increment between instars may provide evidence of genetic variation or indirect evidence of variation in environmental factors such as the availability of various types of food.

We agree with SHELDON (1988) that, while instars may often be recognized with confidence in bivariate plots (HUNT, 1967), they are usually more difficult or even impossible to identify on size-frequency histograms. An analysis of bivariate plots with distinct instars shows that the instars are usually more readily discriminated by size along one of the two axes.

Size-frequency diagrams of trilobites have sometimes been used to provide information of relevance to studies of population dynamics. These seldom involve bedding-plane assemblages and so usually represent a span of time rather than a moment frozen in time. SHELDON (1988), examining the size-frequency histograms of more than 5,000 trilobites from Ordovician shales in Wales, found that the histograms usually have normal to slightly negatively skewed distributions with very few small individuals preserved. He discussed the implications of their absence in light of the fact that the expected pattern is positive skewness. He argued that negative skewness may have resulted from high longevity and low recruitment to the fossil record of postlarval stages, with more adult than juvenile molts left behind by long-lived trilobites. A number of other factors, however, could cause negative skewness, including the poorer calcification of small sclerites (leading to preferential early taphonomic destruction), the tendency for shales to split at levels containing large but not small specimens (which does not occur with silicified faunas, where the skewness appears to us to be typically positive), the possibility that small stages lived elsewhere and arrived in the area only as adults (perhaps most likely for species with planktonic larvae), and the washing away of small growth stages (which is unlikely in SHELDON's example). SPEYER and BRETT (1986) demonstrated that size variation across numerous facies was due to biological or ecological factors and possibly represented migratory patterns such as those demonstrated by annelids and many long-lived Crustacea. Thus population dynamics of trilobites are difficult to reconstruct from size-frequency histograms taken from bulk samples, and usually such diagrams provide data that are more likely to be of value to studies of paleoecology and taphonomy than taxonomy.

## BIOGEOGRAPHY IN RELATION TO ONTOGENY

As a general rule, animals with long, pelagic growth stages will be more widely dispersed than those with purely benthic growth stages. THORSON (1936) commented that few organisms have planktotrophic larvae in high latitudes, but a high percentage of animals in equatorial latitudes have such larvae. Thus, the presence or absence of planktonic larvae in the life cycles of trilobites may be of use in determining their paleogeographic distributions. Those with planktonic larvae might be expected to be widespread in tropical or warm waters, and those with benthic growth stages may be expected to form a greater proportion of endemic faunas and faunas of high paleolatitudes. A gradient of sorts occurs between the paleogeographic extremes, with the proportion of taxa with planktonic larvae increasing towards the equator.

CHATTERTON and SPEYER (1989, 1990) and SPEYER and CHATTERTON (1990) found that some trilobites with planktonic, nonadult-like larvae had very widespread paleogeographic distributions prior to the onset of the Ordovician-Silurian glaciation. However, after the onset of that glaciation, with the introduction of a greater thermal gradient between high and low latitudes and the appearance of floating ice, the distribution of these trilobites was restricted to more equatorial latitudes. Thus the distribution of these taxa appears to have been controlled by the modes of life of their larval stages.

CHATTERTON and others (1990, p. 258) commented on the absence of known, nonadult-like protaspides among homalonotid trilobites, despite their presence in the closely related Calymenidae. They posited that the success of homalonotid trilobites in the "*Hirnantia* fauna," their survival of the Ordovician-Silurian mass extinction (CHATTERTON & SPEYER, 1989), and their later success in the cold, southern, Malvinokaffric faunas may be associated with their having had large embryos in a yolked egg and their having emerged from the egg to become large, benthic larvae.

FORTEY (1985) noted that some telephinids and cyclopygids with pelagic adults have wide geographic ranges, and these forms appear to have been more independent of facies changes than benthic trilobites found in the same collections. The cyclopygids probably also had planktonic larvae. Trilobites with mature stages that lived in deep, cold environments may also have dispersed widely (e.g., Agnostida) since the deep oceans may not have been barriers, except during periods when layering of the oceans took place, and deep water was anoxic (FORTEY, 1989).

CHATTERTON and SPEYER (1989) and SPEYER and CHATTERTON (1990) noted that trilobites with different life-history strategies were affected in different fashions at times of other extinctions in the Ordovician. Those with all pelagic larvae (strategy I) underwent a minor extinction at about the time of onset of the Ordovician-Silurian glaciation (see Fig. 164) and were virtually wiped out during the episode of mass extinction near the end of the Ordovician close to or at the level of maximum glaciation. Only one genus, *Raphiophorus,* containing very few species

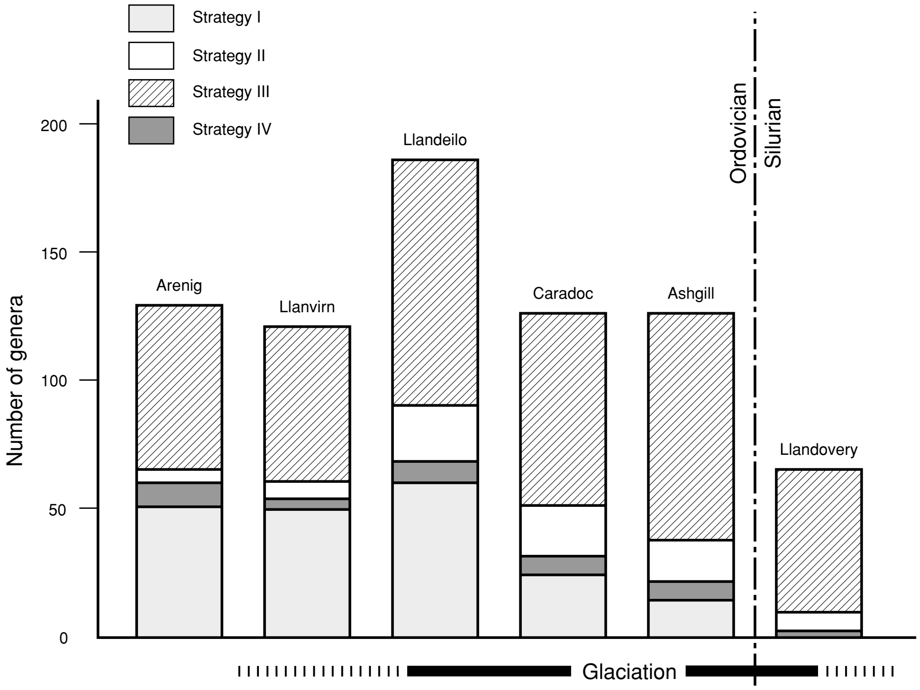


Fig. 164. Histogram of numbers of trilobite genera in Ordovician and Silurian stages. The legend refers to the life-history strategies shown in Figure 156; for strategy IV, see text. Note, in particular, the drop in diversity of trilobites with life-history strategy I between the Llandeilo and Caradoc at about the time of the start of the main part of the Ordovician-Silurian glaciation and the drops in diversity of all groups of trilobites but particularly those with life-history strategies I and IV, between the Ashgill and the Llandovery at about the time of maximum glaciation (Chatterton and Speyer, 1989, fig. 3).

survived. Trilobites with pelagic adults (strategy IV) were not obviously affected by the first of these episodes but did not survive the second. Trilobites that had a single, nonadult-like, planktonic stage with the rest of the life cycle being benthic (strategy II) were unaffected by the first episode and suffered to a lesser degree during the second. Trilobites with all known stages benthic (strategy III) were affected only slightly during the first episode and moderately during the second. Chatterton and Speyer argued that these patterns could be explained best by environmental changes associated with the onset, advances, and retreats of the Ordovician-Silurian glaciation.

An important result of this pattern of extinctions was that almost all of the trilobite taxa that survived the Late Ordovician (Fig. 165) had life-history strategies II and III, and these two groups thus gave rise to almost all of the new taxa that radiated after that extinction. The only representative with life-history strategy I to survive, *Raphiophorus,* never radiated significantly and existed only in small numbers and with low diversity to near the end of the Silurian. The life history of that genus is not known in detail but is inferred from related raphiophorid trilobites such as *Lonchodomas* (see Fig. 174). When the autecology of this genus is better understood, we may understand why it alone managed to survive the Late Ordovician mass extinction but failed to radiate to occupy niches vacated by its relatives. Examination of life-history strategies at times of other extinctions (the Late Cambrian biomere boundaries and Late Devonian, in particular) may also throw new light on the causes of those extinctions.

## ONTOGENY AND SYSTEMATICS

As a rule, monophyletic groups based on characteristics of adult growth stages have similar larvae and life-history strategies so that larval morphology appears to be a useful indicator of relationship. Despite the prevailing view that larvae may be expected to be simpler, more primitive, and more closely similar to one another than adults of the same trilobite taxa, many trilobite larvae have undergone radical evolution. Evolution apparent in larvae may not be reflected in the same manner or the same degree in more mature stages. The prevailing view, extending back to Von Baer and Haeckel (GOULD, 1977), is that changes in larval stages are necessarily added to and expanded upon in more mature stages so that they lead to even more extreme changes in mature stages. Changes in small stages, however, may not lead to equally large changes in more mature stages. Thus, there seems to be some decoupling between larval evolution and the evolution apparent in more mature stages. Some synapomorphies visible only in larval stages may be used to recognize and define large groups of trilobites (FORTEY & CHATTERTON, 1988). This may be particularly apparent when the early larvae are separated from later growth stages by a radical metamorphosis.

Work to date supports the contention that monophyletic groups of trilobites from the family at least to the subordinal level have similar larvae, which are distinct from those of other monophyletic clades (WHITTINGTON, 1956d, 1957b, 1959a, 1959b; FORTEY & OWENS, 1975; CHATTERTON, 1980; FORTEY & CHATTERTON, 1988; EDGECOMBE, SPEYER, & CHATTERTON, 1988; CHATTERTON & others, 1990). Some genera include species that have protaspides that are very similar to one another (e.g., *Scharyia,* see OWENS, 1974; ŠNAJDR, 1981a; see also Fig. 179); others show a greater degree of disparity in larval form (e.g., *Ceraurinella*); the protaspides illustrated in Figure 178 can be contrasted with those figured by CHATTERTON (1980).

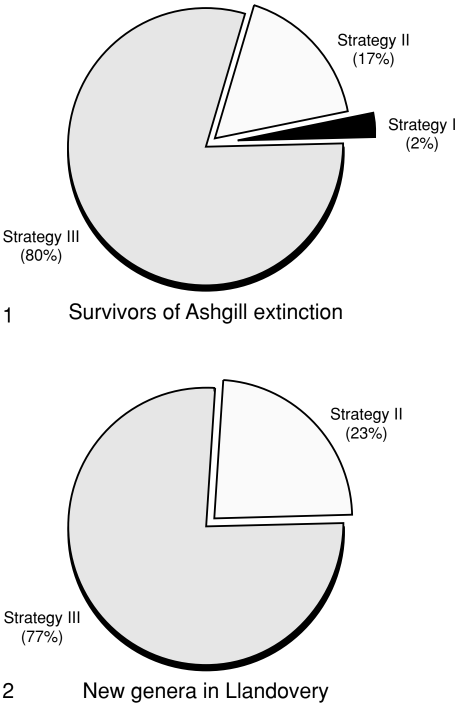


FIG. 165. Percentage of trilobite genera that survived the Ashgill extinction (*1*) and new genera that originated in the Llandovery (*2*) grouped into life-history strategy categories (for explanation of strategies, see Fig. 156 and text). Note the high proportion of forms that had benthic protaspides (strategy III).

Because radical metamorphoses occurred in the life cycles of a number of trilobites (SPEYER & CHATTERTON, 1989), a number of the nonadult-like protaspides remain unclassified with respect to growth series of individual taxa (Fig. 166). We know of a number of these early, probably planktonic, growth stages that have yet to be described because of problems with their taxonomic assignment. They can not be assigned to a species on the basis of similarity in morphology. One useful fact is that they are always earlier growth stages and therefore must, under most circumstances, be smaller than later,

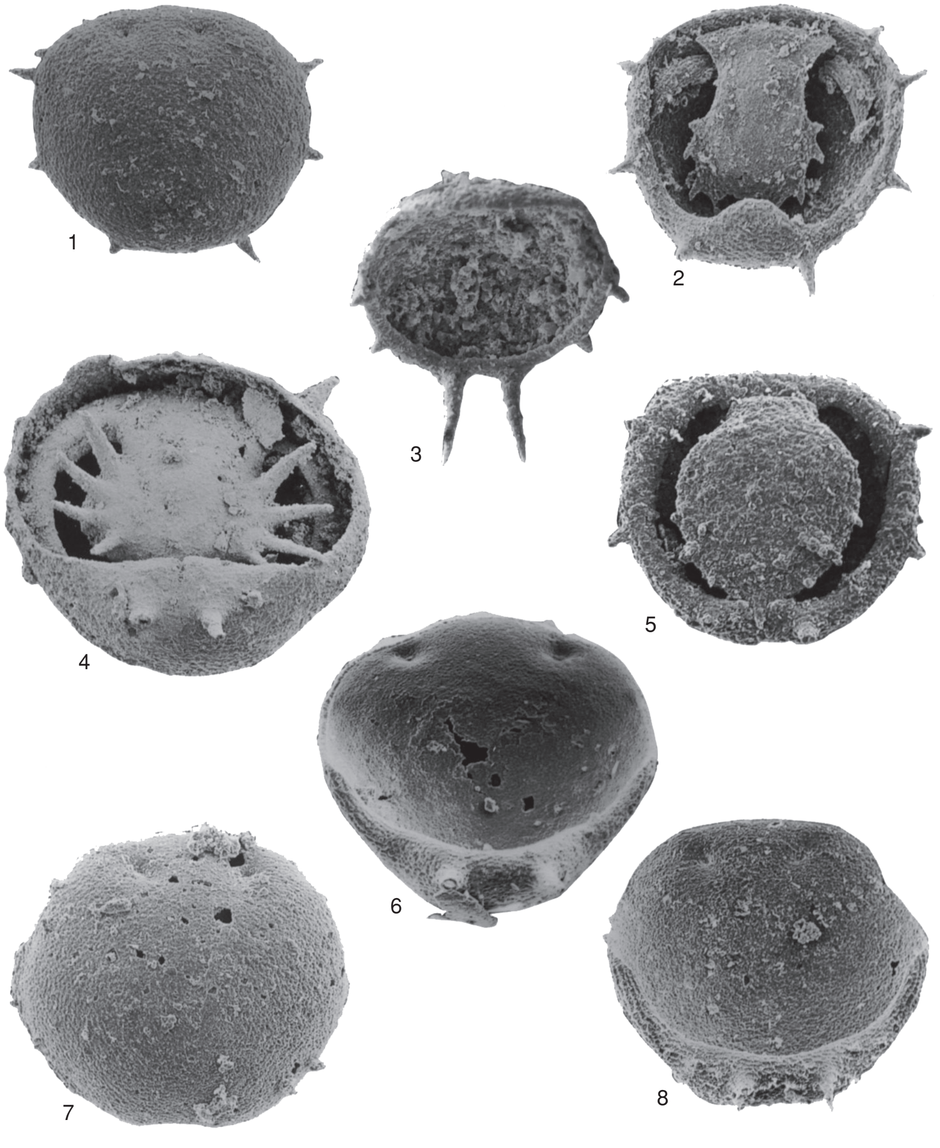


FIG. 166. Globular, nonadult-like protaspides, some of which are of uncertain attribution. *1–4,* From the Crown Point Formation, Middle Ordovician, New York (locality PB81); *1, 2,* dorsal and ventral views of a protaspid, possibly of a premetamorphic growth stage of a lichid?; *1,* NYSM 16401, ×89; *2,* NYSM 16402, ×91; *3,* anteroventral view of very small protaspis of a cheirurid?, NYSM 16403, ×153; *4,* ventral view of nonadult-like protaspis of asaphid *Isotelus* sp., NYSM 16404, ×62 (new). *5,6,* From the Wenlock Delorme Formation of northwestern Canada (locality AV4 126T); *5,* ventral view of nonadult-like early protaspis, possibly of an Illaenina, UA 8480, ×88; *6,* ventral view of protaspis of illaenid? trilobite, UA 8481, ×74 (new). *7,8,* Dorsal and ventral views of small protaspides of harpid? trilobite (*Dolichoharpes?*) from the Crown Point Formation, Middle Ordovician, New York (locality PB81); *7,* NYSM 16405, ×65; *8,* NYSM 16406, ×65 (new).

more adult-like stages in the same life cycle. The problem of correct association of these small, nonadult-like larval stages is exacerbated by the change in mode of life that apparently occurred at the same time as the radical metamorphosis. Thus, the small, nonadult-like stages did not necessarily live or die in the same place as later growth stages of the same species. This renders correct assignment through repeated stratigraphic occurrence or matching abundance more difficult.

Ontogeny aids in the correct determination of homologies by allowing the tracing of the formation of structures. Phylogenetic studies depend on the homologies of the characters used in the analyses. It is often difficult to trace these characteristics back to a common ancestor. They can usually be considered to be homologous if they have a common embryological or early ontogenetic origin from the same part of the organism. The homologies of such structures as cranidial lobes of various taxa have been suggested by studying ontogenies (Lichidae by CHATTERTON, 1971, 1980; TRIPP & EVITT, 1981; *Cybeloides* by EVITT & TRIPP, 1977).

In this section, we define the more important larval characteristics evident at the ordinal level and also for some suborders and superfamilies.

## ORDER AGNOSTIDA, SUBORDER AGNOSTINA

Meraspid to holaspid growth stages have been described by numerous authors, including BARRANDE (1852), PALMER (1955), ŠNAJDR (1958), ROBISON (1964), RUSHTON (1966, 1979), HUNT (1967), ÖPIK (1979), QIAN (1982), MÜLLER and WALOSSEK (1987), SHERGOLD (1991), and in this work (Fig. 167).

Protaspid stages assigned to *Pseudagnostus benxiensis* by QIAN (1982) come from a bed also containing *Parachangshania hsiaoshihensis.* The ontogeny of the latter was described by CHIEN (1958) from the same locality, the protaspis being different from that assigned to *P. benxiensis.* Both protaspides are very similar to those of polymerid trilobites, and X. ZHANG (1989, p. 13) expressed the opinion that they are "far more likely to be polymerid larvae." The smallest meraspides of Agnostina (including *Pseudagnostus benxiensis*) are all isopygous or almost isopygous. The largest protaspis illustrated by QIAN (1982) has a protopygidium that is considerably smaller than the cranidium, requiring a radical metamorphosis between that stage and the earliest of *P. benxiensis,* should these two stages actually belong to the same taxon. Thus, if these protaspides belong to *Pseudagnostus,* they provide strong evidence of miomerid-polymerid affinity, which is also supported by the form of eodiscoid protaspides. If they do not, then they should be assigned to some polymerid that has yet to be described from this locality.

We find it difficult to understand why no protaspides of *Agnostus* have been discovered in the Swedish Orsten fauna if they existed (MÜLLER & WALOSSEK, 1987). This phosphatized fauna is so well preserved that the appendages are known for early meraspid stages of *A. pisiformis* (Fig. 82).

The reasons why no protaspides of Agnostina have so far been found have been discussed and center in part around the mode of life of the adult. A number of workers have argued in favor of a pelagic mode of life for Agnostina (ROBISON, 1972a; STITT, 1975; X. ZHANG, 1989), citing the small size of adults and their widespread distributions. Other workers consider Agnostina to have been benthic (FORTEY, 1975b; CHATTERTON & SPEYER, 1990), living in deep, cool, marginal environments where the levels of light (accounting for blindness) and oxygen (accounting for the paucity of other benthic organisms and high organic contents of the rocks) were often low. Both modes of life could account equally well for the widespread geographic distributions and deep-shelf, marginal or basinal distributions of Agnostina. Some workers have even suggested such alternative modes of life as parasitism (BERGSTRÖM, 1973a) and epifaunal attachment to algae (PEK, 1977). We favor the benthic mode of life for several reasons (see CHATTERTON & SPEYER, 1990). (1) Almost all pelagic arthropods have large eyes, whereas Agnostina were blind. (2) It is difficult to imagine an enrolled individual staying suspended in the water column. (3) The ventral side of the exoskeleton is virtually planar, implying that it was constrained in space, as is true of most benthic trilobites. (4) The exoskeleton of Agnostina, in

FIG. 167. Agnostina. Growth stages of *Geragnostus (Micragnostus) subobesus* (KOBAYASHI) from the Rabbitkettle Formation, Section K, Mackenzie Mountains, Upper Cambrian, northwestern Canada. For adult specimens from the same horizon, see LUDVIGSEN (1982, fig. 47a–p). *1,* Dorsal view of M0, UA 8424, ×48.5; *2,* dorsal view of cranidium of M0, UA 8425, ×49; *3,* dorsal view of M0 transitory pygidium, UA 8426, ×49; *4,* dorsal view of M0, complete enrolled specimen, UA 8427, ×49; *5,* dorsal view of complete M1, UA 8428, ×52.5; *6,* dorsal view of thoracic segment, UA 8429, ×32; *7,* dorsal view of M1, UA 8430, ×22.5; *8,* dorsal view of pygidium, UA 8431, ×16.5; *9,* ventral view of small holaspid, UA 8432, ×22.5 (new).

proportion to the size of the animal, shows few signs of weight reduction. We disagree with the view that the exoskeleton of Agnostina was thin. We have found that, in the Middle Ordovician Edinburg and Upper Cambrian Rabbitkettle formations, Agnostina, although thin-shelled, are at least as thick-shelled as co-occurring, clearly benthic, usually olenid trilobites (see also data by FORTEY and WILMOT, 1991). (5) The distribution data, with beds containing enormous numbers but a low diversity of Agnostina, matches the distributions of gregarious or low-diversity, benthic organisms much better than it does the stratigraphic distributions of pelagic organisms. MÜLLER and WALOSSEK (1987, p. 1) considered that *Agnostus pisiformis* inhabited a "flocculent zone at the bottom of the Alum Sea, where the animals swam or floated around." If Agnostina were benthic, it is feasible that they passed through the protaspid stages as uncalcified embryos or larvae. Such accelerated development is common in crustaceans of small size (e.g., ostracodes and copepods). X. ZHANG (1989) presented the alternate hypothesis that the absence of a protaspis was the result of their inhabiting a different environment from the adults. If this were common in trilobites, associating larvae with more mature stages would be exceedingly difficult.

In attempting to assess whether QIAN's (1982) assignments of protaspides to the agnostid *Pseudagnostus* are correct, it is useful to consider the following points. (1) Protaspides of Agnostina have not been described from extensive collections of silicified and phosphatized trilobites, including both Agnostina extending to M0 and many small polymerid protaspides. (2) The protaspides described by QIAN (1982), at least in the shape of the simple glabella, are morphologically similar to small meraspides of Agnostina. (3) Marginal spines of the M0 transitory pygidium are not apparent, either through absence or lack of preservation on the protaspid protopygidia. (4) The disparity between the size ratio of the protopygidium to cranidium and the size ratio of the M0 transitory pygidium to cranidium is greater for *Pseudagnostus benxiensis* than for the eodiscoids *Neocobboldia chinlinica* and *Pagetia ocellata.* (5) The genal swellings, bacculae, and more anterolateral lobes apparent in the eodiscoid protaspides are not apparent on the protaspides assigned to the Agnostina. Because of the comparatively poor state of preservation of the protaspides described by QIAN (1982) and their broad morphological similarity to meraspid cranidia of Agnostina from the same locality, we are reluctant to state categorically that they are not Agnostina. However, their greater similarity in gross morphology to some polymerid protaspides, rather than to those of eodiscoids, and the comparatively radical metamorphosis required to change these protaspides into meraspides of Agnostina leads us to favor the hypothesis that these specimens are polymerid protaspides.

## ORDER AGNOSTIDA, SUBORDER EODISCINA

Protaspides have been assigned to eodiscoid trilobites by HU (1971), X. ZHANG (1989), SHERGOLD (1991), and X. ZHANG and CLARKSON (1993). JELL (1975a) and X. ZHANG (1989) suggested that the protaspis assigned to *Pagetia clytia* by HU (1971) may belong to a polymerid trilobite. However, as discussed below, we consider that this specimen is very similar to those assigned to the eodiscoids *Neocobboldia* (X. ZHANG, 1989) and *Pagetia* (SHERGOLD, 1991). There is little doubt that the latter forms are correctly assigned because of the number of specimens available, the size progression, and the clear similarity between protaspid and meraspid stages demonstrated by X. ZHANG (1989) and SHERGOLD (1991). We note here that the forms called anaprotaspides by X. ZHANG would be termed metaprotaspides by most workers (see HU, 1971, who called the similar protaspis of *Pagetia* a metaprotaspis), and the forms referred to as metaprotaspides by X. ZHANG are meraspides.

Characteristics of eodiscoid protaspides (Fig. 168.1; and X. ZHANG & CLARKSON, 1993, fig. 3, 7) include: (1) a distinct axis that extends backward almost to the posterior margin and forward to just behind a very short (sag.) anterior border and that has a distinct occipital ring and at least two poorly

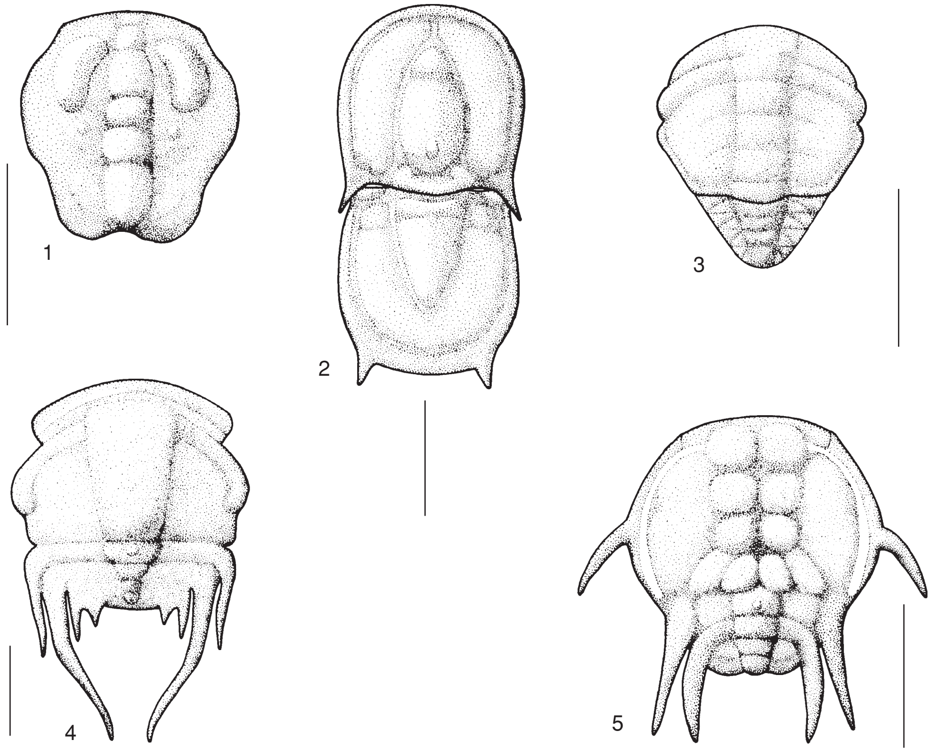


Fig. 168. Protaspides and meraspides of various Cambrian trilobite taxa. Scale bars are 0.5 mm long. *1,* Dorsal view of protaspis of *Neocobboldia* (Agnostida, Eodiscina) (adapted from X. Zhang, 1989); *2,* dorsal view of meraspid degree 0 of *Pseudagnostus benxiensis* Qian (Agnostida, Agnostina) (adapted from Qian, 1982); *3,* dorsal view of meraspid degree 0 of *Balcoracania flindersi* Pocock (Redlichiina, Emuelloidea) from the Lower Cambrian of South Australia (Pocock, 1970); *4,* dorsal view of a protaspis of *Xystridura* sp. (Redlichiina, Paradoxidoidea) (adapted from Öpik, 1975a); *5,* dorsal view of a protaspis of *Paradoxides pinus*? Holm (Redlichiina, Paradoxidoidea) (Whittington, 1957b, fig. 5a).

defined transglabellar furrows; (2) two distinct lobes on the fixigena, one subcircular a short distance anterolateral to the occipital ring (baccula?) and the other much larger (elongate-ovoid in outline and almost bicomposite), located farther anterolaterally and having an anteromedially directed axis; (3) a proparian facial suture; (4) a comparatively large protopygidium that comprises about one-third of the area of the cranidium; and (5) a protopygidium that appears to be indented posteromedially in dorsal view. The specimens of *Neocobboldia* illustrated by X. Zhang (1989) also have a sculpture of fine ridges and grooves and some tubercles, particularly posterolaterally, somewhat similar to that of asaphoid protaspides illustrated by Speyer and Chatterton (1989). The protopygidium is turned down and slightly forward posteromedially. The doublure is incurved rather than inturned. The overall form of the eodiscoid larvae is adult-like and benthic in the terms of Speyer and Chatterton (1989), and we also regard the adults as having a benthic morphology. The progressive loss of the eyes in eodiscoids appears to be an example of convergent evolution with the Agnostina. This is not surprising when the functional significance of the similarity in size and overall morphology of the two groups is considered.

X. Zhang (1989) recognized 13 instars of *Neocobboldia.* This species apparently underwent ecdysis more than once within some meraspid degrees (perhaps three times as M0, termed metaprotaspides Mp0–Mp2 by X. Zhang). The number of ecdyses suggested by X. Zhang was based on the assumption that the linear dimensions of successive instars increase at a constant geometric rate for each species. While exceptions to this rule occur, particularly in association with radical metamorphoses, it applies in general among trilobites and among other arthropods (see earlier discussion of growth). Hunt (1967) certainly demonstrated that the nine instars of *Trinodus elspethi* increased in size by a nearly constant geometric ratio (1.21 to 1.25). The ratio used by X. Zhang (1.20) was close to that determined by Hunt. X. Zhang, however, was unable to distinguish instars as distinct size clusters. Both workers demonstrated that more than one instar may occur within the same meraspid degree in the Agnostida. The comparatively small number of instars, due to the early onset of maturity, apparently was a cause of the small size and low number of thoracic segments in the Agnostida.

## ORDER REDLICHIIDA

Small growth stages of Redlichiida (Fig. 168.3–5, 169) usually have large eyes with well-developed ocular lobes that curve forward and inward to be adjacent to the glabella in the region of the frontal glabellar lobe, if distinguishable as a separate lobe. There is a short, complete anterior border and usually a very short or indistinct preglabellar field that lengthens in later meraspid stages. The rostral plate is wide (tr.), short (sag.), and curved to accommodate the curved anterior outline of the cephalon. Transverse segmentation of the glabella and even the fixed cheeks may be well developed in some taxa, which were regarded as primitive by Weller (1969).

### Superfamily Redlichioidea

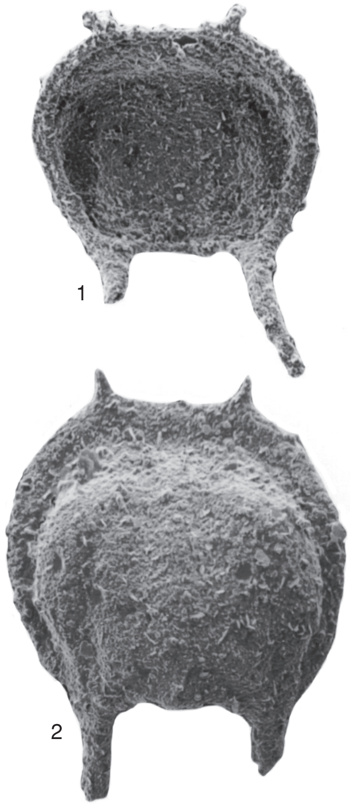


Fig. 169. Redlichiida, Olenellina. Small meraspid cranidia of *Olenellus clarki* (Resser) from the Combined Metals Bed of the Pioche Shale, Lower Cambrian, Lincoln County, Nevada (see Palmer, 1957); *1,* ventral view of BMNH It 21252, ×46; *2,* dorsal view of BMNH It 21253, ×45 (new; specimens courtesy of H. B. Whittington and A. R. Palmer).

Protaspides have been described by Lu (1940), Kautsky (1945), Kobayashi and Kato (1951), W. Zhang, Lu, and others (1980), and Pillola (1991). *Strenuella* is usually classified in the Ellipsocephalidae, but Fortey (1990a, p. 549, 563) suggested that some ellipsocephalids should be included in the Ptychopariina. These are small and ovoid and are preserved in shales; little is known of their ventral morphology. The apparent lack of intergenal spines on most specimens may be a function of this mode of preservation, or it may have been their nature in life. Drawings by W. Zhang, Lu, and others (1980) do not show any intergenal spines, but such intergenal spines are apparently present in a meraspid degree 3 of *Redlichia chinensis* (see Kobayashi & Kato, 1951, fig. 2). Some of the protaspides of that species illustrated by those authors have marginal spines, the anteriormost of which may be intergenal spines; and one specimen apparently has genal spines (Kobayashi & Kato, 1951, pl. 4, fig. 6). Some of these specimens were reassigned to *R. (Pteroredlichia) murakamii* by W. Zhang, Lu, and others (1980, pl. 26). Kobayashi and Kato (1951, pl. 4, fig. 1, 2, 11) included sagittal glabellar furrows in their drawings of some of the redlichioid protaspides. These were not, however, apparent in any of the drawings of redlichiid protaspides by W. Zhang, Lu, and others, despite the fact that one of the specimens upon which these furrows are based is reproduced in both works several times (Kobayashi & Kato, 1951, pl. 1, fig. 1, pl. 2, fig. 1, pl. 4, fig. 2; W. Zhang, Lu, & others, 1980, fig. 61.1, pl. 26, fig. 1). All workers appear to agree that transglabellar furrows are well developed in these protaspides.

### Superfamily Paradoxidoidea

Paradoxidid protaspides (Fig. 168.4,5) have been described by Barrande (1852), Raymond (1914a), Šuf (1926), Westergård (1936), Růžička (1943), Whittington (1957b), and Šnajdr (1958); and meraspides have been described by most of these workers and Šnajdr (1990). Most of the paradoxidid protaspides can be assigned to species of *Paradoxides* and others to *Hydrocephalus.*

Xystridurid protaspides (Fig. 168.4) have been described by Öpik (1975a); and meraspides were illustrated earlier by Whitehouse (1939) and later by McNamara (1981a, 1986a). Several features are shared with paradoxidid protaspides. These include a forwardly expanding glabella; long, sharply pointed intergenal spines; comparatively large and long ocular lobes that are adjacent to the anterior portion of the glabella anteriorly and separated from the glabella by a comparatively broad (tr.) fixigena posteriorly; and a complete, short anterior border. The genal spines are apparently located at the genal angle on the free cheeks of both groups. Some paradoxidid protaspides have more expanded glabellas that are often subdivided by sagittal and transverse glabellar furrows to produce as many as eight separate glabellar lobes. These furrows are often reduced in number, with only a few of the lobes distinguishable. Early meraspid cranidia of these two groups are even more similar, except that S1 and S2 are usually complete medially in paradoxidids but not in *Xystridura.* Intergenal spines disappear from both groups at a stage early in the meraspid period. Preglabellar fields are very short to insignificant in protaspides and early meraspides but lengthen during the meraspid period to become well developed in both families. Distinct occipital rings are visible in all protaspid and meraspid cephala, and occipital nodes are usually present on meraspid cranidia and in some protaspid cranidia. Protopygidia and transitory pygidia are not particularly well known, but marginal spines are present. The axis is well developed, macropleural spines can be recognized on more anterior thoracic segments early in the ontogeny, and pleural furrows are distinct on more anterior segments.

The early growth stages of paradoxidids and xystridurids are similar enough to each other to justify their inclusion in the same superfamily and similar enough to those of the redlichioids to be included in the same order.

### Superfamily Emuelloidea

Pocock (1970) described the only known ontogenetic series of this group. Its members have dorsal facial sutures and a protaspis but like Olenellina, which lack these features, have a prothorax and opisthothorax and transverse furrows on the fixed cheeks of small meraspid cranidia.

The protaspis of *Balcoracania flindersi* (Pocock, 1970, fig. 8) has a glabella and fixed cheeks with transverse furrows (SO, S1, S2, S3 on the glabella), a distinctly expanded frontal lobe that reaches the anterior margin, and a protopygidium that has an undifferentated axis and is considerably shorter than the cranidium. His photographs and drawings of early meraspid degrees are considerably more instructive (see Fig. 168.3). These have what can be interpreted as proparian facial sutures; medium-sized eyes near the midlength of the cranidium; distinct eye ridges running into the posterior half of the frontal lobe; transverse glabellar furrows (SO, S1, S2, S3 and S4); subtransverse fixigenal furrows that run outward and slightly backward; posterior border furrows on the cranidium that turn forward distally; genal spines on the free cheeks but no intergenal spines; and interpleural, axial, and ring furrows on the transitory pygidium. A short anterior border develops and increases slightly in length during the meraspid period. A sagittal furrow is not distinct but could be present in the frontal lobe of early meraspid cranidia. One of POCOCK's photographs (1970, pl. 110, fig. 2) could be interpreted as showing a very faint sagittal furrow, but no furrow was shown in his reconstruction of early meraspid cranidia. In his description of the earliest meraspid cranidia, he did mention (1970, p. 541) that the "frontal glabellar lobe is thus expanded to the anterior (although partially subdivided)." It is not clear whether this partial subdivision is longitudinal or transverse, although he noted earlier in his description that the frontal lobe is partially subdivided by an indistinct furrow aligned with the anterior edge of the eye ridge. The absence of an anterior border in the early cranidia of this superfamily, if real, is also unusual among primitive Lower Cambrian trilobites. The absence, however, could be only apparent and a function of the quality of preservation of POCOCK's material. Only one poorly preserved protaspis is illustrated in that work. A reexamination of POCOCK's material or collection of new, better-preserved specimens might resolve these problems.

### Suborder Olenellina

Small growth stages of a number of Olenellina have been described, but none is an undoubted protaspid, although some small meraspid cranidia have been referred to as protaspides (e.g., WALCOTT, 1910; C. POULSEN, 1932; STØRMER, 1942; LOCHMAN, 1956; V. POULSEN, 1974). Workers who have described small meraspid stages of Olenellina include FORD (1877, 1881), WALCOTT (1886, 1910), KIAER (1917), C. POULSEN (1932), STØRMER (1942), RICCIO (1952), LOCHMAN (1952, 1956), WHITTINGTON (1957a, 1959b), PALMER (1957), HU (1971, 1985b), FRITZ (1972), and in this publication (Fig. 169). PALMER (1957, p. 106–107, fig. 1) discussed and illustrated a silicified, ontogenetic series of *Olenellus gilberti* and *Olenellus clarki* (Fig. 169). Despite the discovery of very small meraspid cranidia, he found no protaspides. The smallest meraspid cranidia are comparable morphologically to the specimens that have been called protaspides by earlier workers. Thus, there is reason to believe that growth stages equivalent to the protaspides of other trilobites may have been passed through as embryonic stages. Olenellina share with the Agnostina the lack of known protaspid stages, and they compete for a position as the sister group of all other trilobites (FORTEY & WHITTINGTON, 1989; FORTEY, 1990a; RAMSKÖLD & EDGECOMBE, 1991). An alternative hypothesis is that the protaspis is an acquired synapomorphy of advanced trilobites. If so, the absence of a protaspis in Olenellina and Agnostina is the result of these taxa having diverged from the rest of the trilobites before this feature was acquired.

Distinctive morphological features of early meraspid cephala of Olenellina include the following: (1) well-developed intergenal spines, which usually disappear in later stages; (2) an anterior border and a preglabellar field; (3) large ocular lobes that are greater than one-third the sagittal length of cranidium; (4) a distinct, often narrow (tr.), frontal lobe opposite, adjacent to, and sometimes continuous with the anterior parts of the ocular lobes; (5) small, marginal genal and precranidial spines; (6) three glabellar lobes between distinct frontal glabellar and occipital lobes; (7) a small occipital node; (8) interocular areas that may have posterolaterally directed furrows that are often convex anterolaterally; and (9) hypostomes with numerous (usually 13) marginal spines, wide, transversely pointed anterior wings, distinct posteromedially directed middle furrows, and shallow posterior border furrows. The early thoracic segments are much narrower than the cephalon (see Palmer, 1957, pl. 19, fig. 3, 12), and macropleural spines are distinct in these early stages.

Palmer (1957, p. 126) discussed the sutures of Olenellina and commented that the "only suture whose presence is recognized by all workers with olenellid trilobites is the marginal or perrostral suture that separates the rostrum from the doublure." He also pointed out that the position of this suture does not appear to change during ontogeny (contra Størmer, 1942). The anterior and posterior ocular lines (Fig. 16) observed in holaspid Olenellina were discussed in an earlier section on the patterns of facial sutures (p. 25).

## ORDER CORYNEXOCHIDA, SUBORDER CORYNEXOCHINA

Protaspides of Corynexochina have been described by the authors listed below (see also Fig. 170.10–12).

| | |
|---|---|
| *Albertella* | Hu, 1985a |
| *Bathyuriscus* | Robison, 1967; ?Fortey & Chatterton, 1988 |
| *Corynexochides* | Rasetti, 1967 |
| *Fieldaspis* | Hu, 1985a |
| *Fuchoia* | Öpik, 1982; Lu & Qian, 1983 |
| *Glossopleura* | Hu, 1985b |
| *Ptarmigania* | Hu, 1971 |

Protaspides of *Corynexochides* and *Bathyuriscus* are similar to those of other Corynexochina. This similarity of form supports the monophyly of the group that includes these two genera. Robison (1967) argued for a heterochronic origin of this order through paedomorphosis from the Ptychopariida. One of the important synapomorphies of corynexochines, the fused hypostomal suture, could be regarded as paedomorphic since this feature is often fused in early growth stages and functional in later growth stages of other groups of trilobites. This suture remains fused throughout the life cycle of Corynexochina. We note, however, that in some taxa the hypostomal suture may be fused secondarily in later growth stages and free in early growth stages (e.g., the cheirurid *Hyrokybe,* see Chatterton & Perry, 1984). The strong similarity between Corynexochina and Ptychopariina at all growth stages certainly supports common ancestry of these two taxa.

Distinctive features of protaspides of Corynexochina appear to include: (1) a widely (tr.) anteriorly expanded frontal lobe on the glabella; (2) a glabella that is very narrow, reaches the anterior margin, and is depressed slightly below the level of the cheeks immediately behind the anterior lobe (L3); (3) a pair of pits that deepens the axial furrows adjacent to the frontal lobes of the glabella, possibly for attachment of the rostral-hypostomal plate; (4) distinct anterolateral palpebral lobes that are almost continuous with the anterolateral extremities of the frontal glabellar lobe; (5) transglabellar furrows that are very shallow to indistinct; (6) a proparian facial suture; (7) a protopygidium that is downturned to even slightly curved anteroventrally, with short marginal spines; (8) small anterior, middle, and posterior fixigenal spines; (9) a rostral plate that is fused to the hypostome in all growth stages; and (10) a hypostome that has marginal spines in small protaspides, with the anteriormost pair being longer, posterolaterally directed, and quite close to the back of the hypostome.

At least two and probably more protaspid instars occur in the life cycle of Corynexochina. Robison (1967, fig. 2) showed that there is a considerable range in the size and morphology of protaspides of *Bathyuriscus fimbriatus.* A distinct increase in width occurred with the acquisition of a protopygidium. He suggested that at least four instars occurred within the protaspid period but was unable to distinguish biometrically or morphologically separate groups for the smallest instars. The two largest protaspid instars, which have protopygidia, are morphologi-

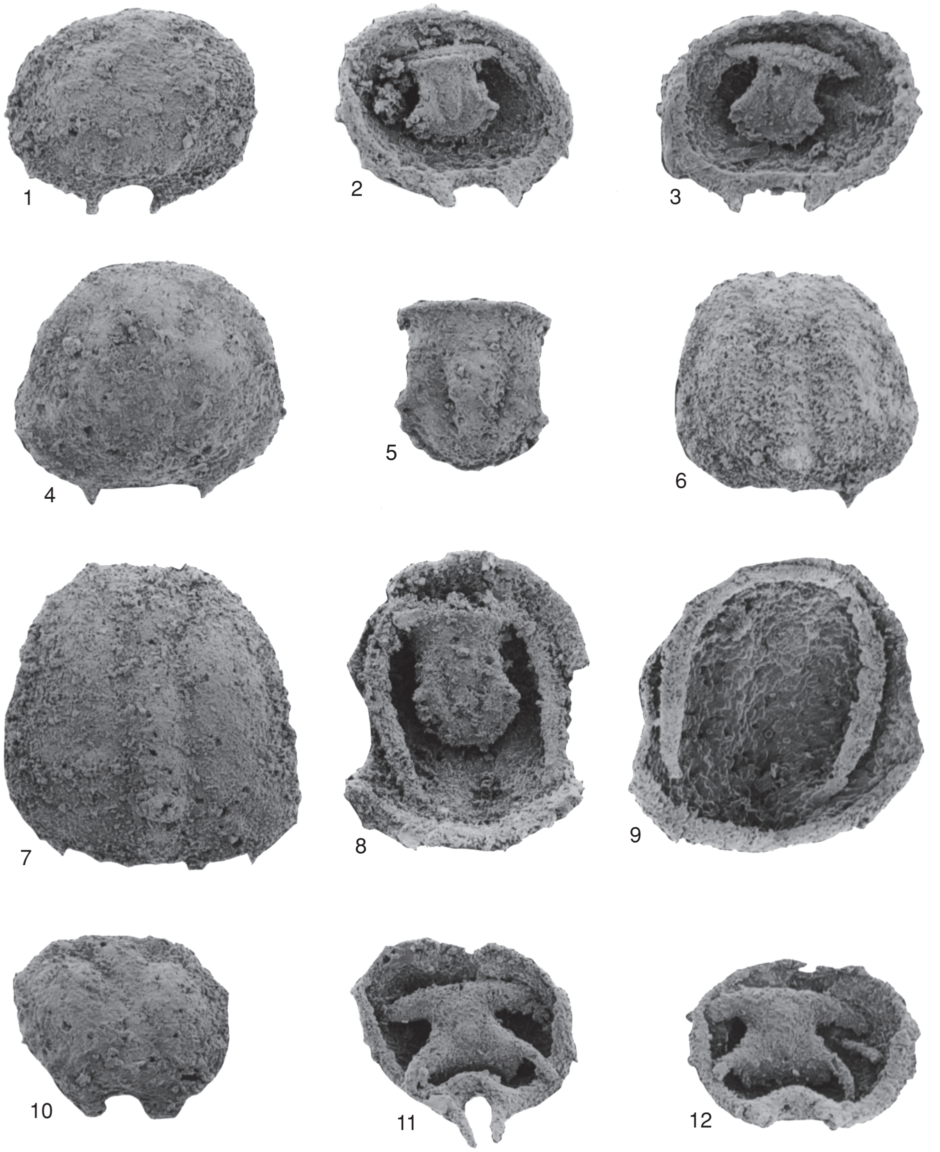


Fig. 170. Ptychopariina and Corynexochida from the Pika? Formation, Middle Cambrian, near Columbia Ice Fields, western Canada. *1–9,* Ptychoparioidea, *Spencella?* sp.; *1,* dorsal view of small protaspis, UA 8433, ×62.5 (new); *2,3,* ventral views of small protaspides (rostral plate and hypostome are attached in each case), UA 7751, 7752, ×62.5 (Fortey & Chatterton, 1988, pl. 17, fig. 9,10); *4,* dorsal view of second protaspid stage, UA 8434, ×62.5 (new); *5,* ventral view of small hypostome, UA 7757, ×62.5 (Fortey & Chatterton, 1988, pl. 17, fig. 19); *6,* dorsal view of second protaspid stage, UA 7754, ×62.5 (Fortey & Chatterton, 1988, pl. 17, fig. 13); *7,* dorsal view of largest protaspid stage, UA 7753, ×62.5 (Fortey & Chatterton, 1988, pl. 17, fig. 16); *8,* ventral view of broken largest protaspid stage (free cheeks and hypostome are attached), UA 7756, ×62.5 (Fortey & Chatterton, 1988, pl. 17, fig. 18); *9,* ventral view of largest protaspid stage (free cheeks and rostral plate are attached), UA 7755, ×62.5 (Fortey & Chatterton, 1988, pl. 17, fig. 17). *10–12,* Corynexochina, *Bathyuriscus* sp.; *10,* dorsal view of small protaspis, UA 8435, ×62.5 (new); *11,* ventral view of small protaspis (fused hypostome and rostral plate are attached to ventral surface, out of place), UA 7760, ×62.5 (Fortey & Chatterton, 1988, pl. 17, fig. 12); *12,* ventral view of small protaspis (note out-of-place attached fused hypostome and rostral plate), UA 8436, ×62.5 (new). [In Fortey & Chatterton (1988, pl. 17), the taxonomic names were inadvertently reversed in the plate explanation.]

cally and biometrically distinct and can be clearly distinguished from earlier growth stages.

## ORDER CORYNEXOCHIDA, SUBORDER ILLAENINA

Protaspides have been described by the following authors (see also Fig. 171).

| | |
|---|---|
| *Breviscutellum* | Feist, 1970 |
| *Dentaloscutellum* | Chatterton, 1971 |
| *Failleana* | Chatterton, 1980; Ludvigsen & Chatterton, 1980 |
| *Illaenus* | Hu, 1976 |
| *Kosovopeltis* | Kácha & Šaríč, 1991 |
| *Nanillaenus* | Chatterton, 1980 |
| *Raymondaspis* | Hu, 1974a |
| *Scutellum* | Chatterton, 1971 |

Hu and Chatterton included protaspides separated by a distinct metamorphosis within the ontogeny of taxa within this suborder. We now believe this to be the rule rather than the exception for species in this suborder. That is, illaenids characteristically display a Type II life-history strategy. There is, however, some doubt as to which of the small, bulbous protaspides found associated with these trilobites actually belong in the growth series as premetamorphic growth stages.

There is little doubt as to the form of later, more adult-like protaspides of this group. They are very similar to meraspides and holaspides, and distinctly different forms can be recognized for styginids and illaenids. Adult-like styginid protaspides are comparatively large (about 1 mm long) and have a distinct cranidium and protopygidium. The glabella expands forward and may reach the anterior margin; an occipital spine or node is usually present; a pattern of paired tubercles or spines may be apparent on the glabella and fixed cheeks that is similar to those of some odontopleurids, lichids, and proetids; the facial suture is opisthoparian; the connective sutures are paired and functional; a posterior border on the cranidium is usually transversely directed but may turn forward distally; the palpebral lobes are large and near the midlength of the cranidium; the protopygidium is subdivided by shallow to indistinct pleural furrows into several segments that terminate distally in tubular, pointed spines and has a distinctively shaped, slightly posterodorsally swollen and downturned posteromedian portion; the doublure is narrow and tightly incurved with a small number of terrace ridges and is usually slightly pinched posteromedially; the hypostome is subrectangular with the marginal spines short and bluntly tipped so that they appear more like a posterolateral border that is subdivided by four slits (Fig. 152.9–10). In this character, they are quite similar to the Lichida.

Illaenid adult-like protaspides differ from styginid adult-like protaspides in that the posterior border of the cranidium is usually turned backward distally; the posteromedian portion of the protopygidium is shaped differently with a strong median indentation and without posterodorsal inflation and downturning; and the marginal spines are more flattened in section and triangular (less tubular) in plan view. Chatterton (1980, pl. 3, fig. 17) illustrated a protaspid free cheek of *Nanillaenus* that has a distinct genal spine. Protaspid free cheeks are not known with certainty for any Illaenina, but we consider that they are probably similar in form (perhaps with more tubular genal spines, as shown by Chatterton, 1971, fig. 4a,b).

There is a greater problem as to the form of the earlier, premetamorphic larvae. Hu (1976, pl. 28) assigned protaspides to *Illaenus valvulus* that we would assign to three different taxa, and only the most mature of these would we assign to that species. Chatterton (1980) assigned two very different protaspides to the illaenid *Failleana calva.*

Meraspides of Illaenina have been described by several workers, in addition to those listed above, including Šnajdr (1960) and Whittington and Campbell (1967).

## ORDER CORYNEXOCHIDA, SUBORDER LEIOSTEGIINA

Hu (1970, 1971) described two protaspides of Leiostegiina: *Komaspidella* (Leiostegiidae) and *Missisquoia* (Missisquoiidae). More recently, several workers have assigned

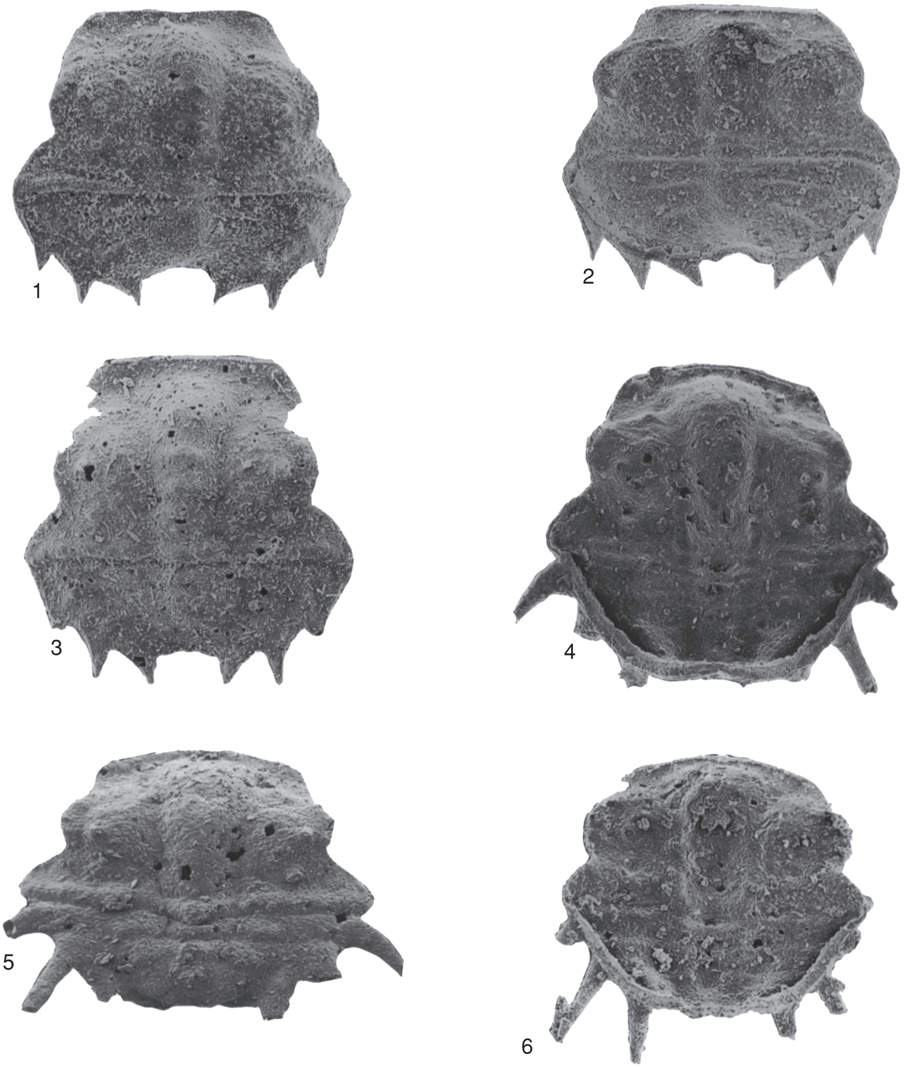


FIG. 171. Corynexochida, Illaenina. *1,2,* Dorsal and ventral views of an illaenid protaspis from the Crown Point Formation, Middle Ordovician, New York (locality PB 81), NYSM 16326, ×42.25; *3,* dorsal view of protaspis of *Bumastoides lenzi* CHATTERTON & PERRY from the lower Esbataottine Formation, northwestern Canada (locality P 17.2), UA 8437, ×50; *4–6,* Styginidae (*Kosovopeltis*? spp.) from the Wenlock Delorme Formation, northwestern Canada (locality AV4 126T); *4,5,* ventral and dorsal views of UA 8438, ×49; *6,* ventral view of UA 8439, ×49 (new).

*Missisquoia* to the Leiostegioidea, including SHERGOLD (1975), LUDVIGSEN (1982), and WESTROP (1986b). The protaspides of *Komaspidella* and *Missisquoia* are not very similar to one another. They are more similar to generalized protaspides of Ptychopariina than to those of Corynexochida, leading one to question why the Leiostegiina is included in the Corynexochida and not the Ptychopariida. Certainly, the hypostome of neither of these taxa is fused to the rostral plate, one of the distinguishing features of corynexochids.

## ORDER PTYCHOPARIIDA, SUBORDER PTYCHOPARIINA

The disparity between some of the protaspides included in this order reflects the distant relationships among some of the taxa. Thus, the protaspides are dealt with here at the superfamily level so that larval characters of very different trilobites are not confused. The ontogenies of many ptychopariids include at least three or four different protaspid instars, and few of these are very well preserved or have been illustrated with scanning electron micrographs.

### Superfamily Ptychoparioidea

Protaspides referred to genera and families mainly within the Ptychoparioidea have been described and are listed below (see also under Classification Uncertain below). [Phylacteridae Ludvigsen & Westrop (in Ludvigsen, Westrop, & Kindle, 1989) is a senior synonym of Cliffiidae Hohensee (in Hohensee & Stitt, 1989) by a few weeks.]

| | |
|---|---|
| Cedariidae | |
| *Cedaria* | Hu, 1971; Hu & Li, 1971 |
| *Cedarina* | Hu, 1971; Hu & Li, 1971 |
| *Paracedaria* | Hu, 1971; Hu & Li, 1971 |
| Coosellidae | |
| *Coosella* | Hu, 1968, 1978 |
| *Nixonella* | Hu, 1972 |
| Crepicephalidae | |
| *Crepicephalus* | Hu, 1971 |
| *Syspacheilus* | Hu, 1972 |
| Elviniidae | |
| *Elvinia* | Hu, 1979 |
| *Irvingella* | Hu, 1979 |
| Kingstoniidae (including the Shumardiidae) | |
| *Kingstonia* | Hu, 1968, 1986 |
| *Shumardia* | Stubblefield, 1926 |
| Lonchocephalidae | |
| *Glaphyraspis* | Palmer, 1962b; Hu & Tan, 1971 |
| *Welleraspis* | Rasetti, 1954; Hu, 1964b, 1968, 1969, 1978; Hu & Tan, 1971 |
| Norwoodiidae | |
| *Hardyoides* | Palmer, 1962b |
| *Holcacephalus* | Hu, 1978; Hu & Li, 1971 |
| *Norwoodella* | Hu, 1963 |
| Phylacteridae | |
| *Aphelotaxon* | Hu, 1980 |
| *Cliffia* | Hu, 1979 |
| Plethopeltidae | |
| *Arapahoia* | Hu, 1986 |
| Ptychopariidae | |
| *Amecephalus* | Hu, 1985b |
| *Chancia* | Hu, 1985b |
| *Crassifimbra* | Palmer, 1958 |
| *Dunderbergia* | Hu, 1971 |
| *Ehmaniella* | Hu, 1984, 1986; Kopaska-Merkel, 1981 |
| *Kochina* | Hu, 1985b |
| *"Liostracus"* | Brögger, 1875; Matthew, 1888, 1889 (reillustrated as *Ptychoparia*) |
| *Pachyaspis* | Hu, 1986 |
| *Piazella* | Hu, 1985b |
| Solenopleuridae | |
| *Sao* | Barrande, 1852; Whittington, 1957a; Šnajdr, 1990 |

Fortey and Rushton (1980) illustrated meraspides for *Acanthopleurella* from degree 0 up, and Fortey and Owens (1991) illustrated those of *Shumardia.*

Öpik (1970a) described some meraspides of nepiid trilobites and described the origin of typically nepeiid characters during the meraspid period. Small meraspides of this group are for the most part similar to equivalent growth stages of other ptychoparoids.

Very small ptychoparioid protaspides (Fig. 170.1–3) are shaped like an inverted saucer, with weak axial furrows. A few taxa have a sagittal furrow, particularly behind the frontal lobe and dividing L2 and L3. The frontal lobe reaches the anterior margin; the posterior margin may be convex or slightly concave; the protopygidium is usually difficult or impossible to distinguish; transverse glabellar furrows are usually indistinct, except in those taxa with a sagittal furrow, forming two pairs of glabellar lobes behind the frontal lobe; a weak, bicrescentic posterior border may be present; a palpebral lobe or ridge runs for a short distance along the anterior margin from the anterior half of the frontal glabellar lobe; the fossula may be present at the junction between the posterior edge of the palpebral ridge and the glabella; and three pairs of small marginal spines are apparent in a few taxa (e.g., *Dunderbergia, Pachyaspis, Piazella*).

Later ptychoparioid protaspides (Fig. 170.4–9) lack a sagittal furrow and usually have very short, shallow, or indistinct glabellar furrows outlining an occipital lobe (LO) and four preoccipital lobes (L1, L2, L3, and the frontal lobe). The eye ridge is slightly behind the anterior margin; a posterior border of the cranidium turns forward distally and a protopygidium becomes distinguishable;

the glabella is usually semicylindrical with a slightly wider, rounded frontal lobe; one or more segments on the protopygidium may be delineated by interpleural furrows; pleural furrows are apparent in late larval stages of very few taxa; and marginal spines are usually blunt or absent, and restricted to the genal angles and protopygidial segments. Larval hypostomes, where known, are attached to the doublure (Hu, 1971; Fortey & Chatterton, 1988) and have spinose margins, which may be blunted in later protaspides. Because in adult ptychoparioids the hypostome was natant, it must have become detached from the doublure during later ontogeny. Details of the sculpture are poorly known, but granules and small, paired tubercles are present on the glabella and genae of some taxa. The glabellas of ptychoparioid protaspides do not have the degree of narrowing and depression in height just behind the frontal lobe that is characteristic of the glabella in protaspides of Corynexochina.

Similarities between some ptychoparioid protaspides with both adult-like and nonadult-like forms and those of other, later orders, Phacopida in particular, suggest that the paraphyletic Ptychopariida includes the ancestors of several other orders.

### Superfamily Ellipsocephaloidea

Protaspides of the Ellipsocephalidae were described by Kautsky (1945, *Strenuella*). The form of the protaspis of this genus is in some ways as similar to those of Redlichiina as it is to some ptychoparioids. For instance, the sagittal subdivision of the frontal lobe of the glabella is found in the Redlichiina but absent in most ptychoparioids (with the exception of some Olenina; see below). The similarity between some of the small meraspid cranidia illustrated by Kautsky (pl. 16, fig. 4–5, 9) and those of a meraspid cranidium assigned to *Paradoxides* by Raymond (1914a) is striking. Differences, however, include an absence of glabellar furrows (except for an occipital furrow) behind the furrow that delineates the frontal lobe in *Strenuella.* Other close similarities of the protaspides of *Strenuella* are mainly with those of the Olenina.

## ORDER PTYCHOPARIIDA, SUBORDER OLENINA

Protaspides of Olenina were described by the authors listed below (see also Fig. 172).

| | |
|---|---|
| *Acerocare* | Hu, 1971 |
| *Hedinaspis* (Papyriaspididae) | Taylor, 1976 |
| *Highgatella* | Hu, 1971 |
| *Leptoplastus* | Whitworth, 1970 |
| *Olenus* | Strand, 1927; Hu, 1971; Clarkson & Taylor, 1995 |
| *Parabolinella* | Ludvigsen, 1982 |
| *Peltura* | C. Poulsen, 1923; Whittington, 1958; Hu, 1964a |
| *Triarthrus* (=*Bienvillia*) | Fortey, 1974b |

Beecher (1893b) described a protaspis of *Triarthrus,* which is not very similar to the specimen described by Fortey (1974b) of the same genus and is much more similar to those normally assigned to the Proetida (Whittington, 1957b and Chatterton, 1980, but not Cisne, 1973b). Edgecombe (personal communication, 1991) has found proetid meraspid cranidia associated with these protaspides that overlap in size with the smallest definite meraspides of *Triarthrus* so that Beecher's specimen is almost certainly a proetid and not *Triarthrus.* Walcott (1879), Whittington (1957b), and Cisne (1973b) described a series of meraspid degrees of *Triarthrus* from New York. Raw (1925) described in detail meraspid to holaspid ontogeny for *Leptoplastus.* Fortey (1974b) and Whittington (1965) also described meraspid stages of olenid trilobites.

Features shared by protaspides assigned to the Olenina include (1) well-developed, transverse glabellar furrows; (2) a transverse anterior margin without an anterior border or preglabellar field medially; (3) broad fixigenae; (4) a well-developed posterior border furrow on the cranidium that turns forward distally to delineate a lateral border extending into a sutural ridge anteriorly; (5) a weak eye ridge extending outward from

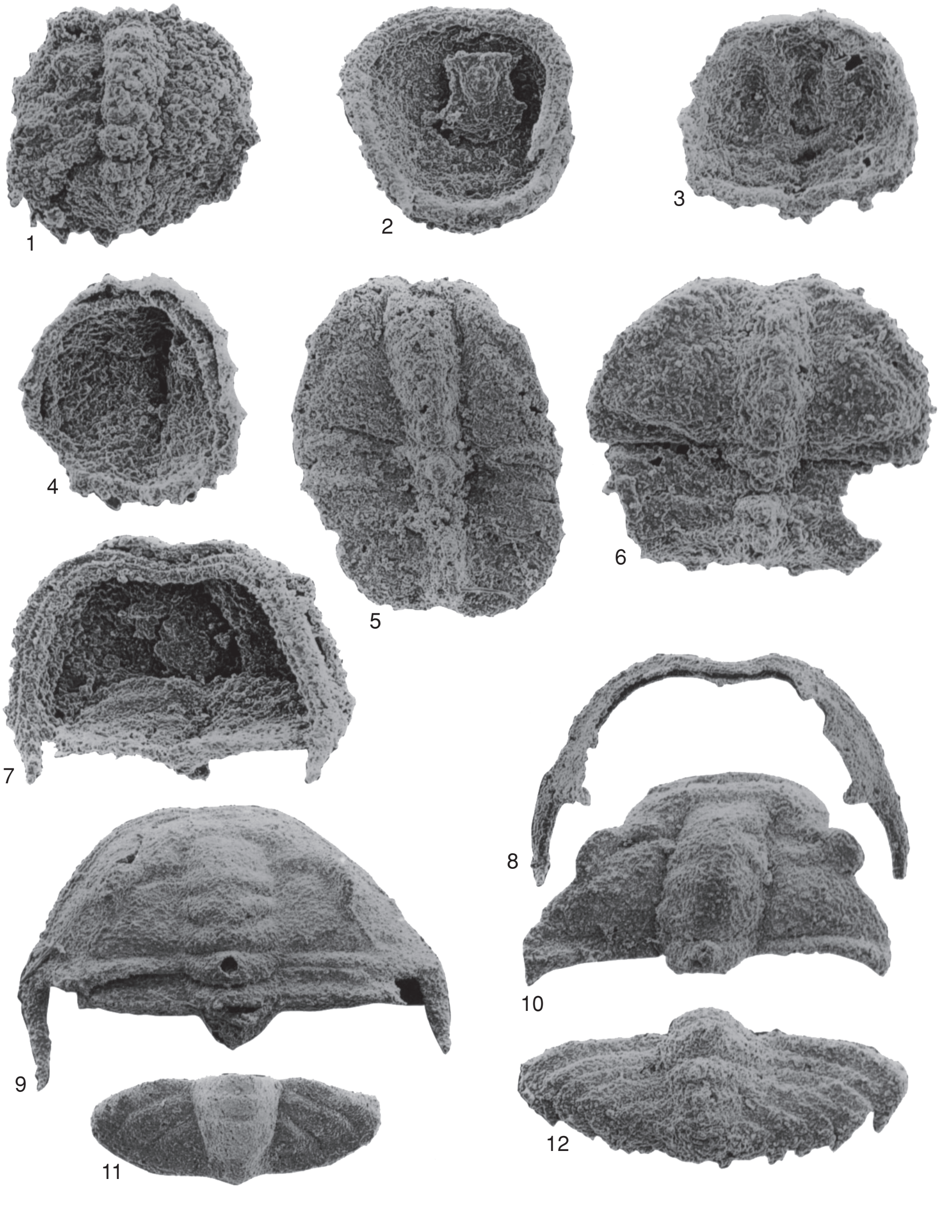


FIG. 172. Ptychopariida, Olenina. *Parabolinella panosa* LUDVIGSEN from the Rabbitkettle Formation, Lower Ordovician, northwestern Canada (locality KK113). We consider specimens assigned by LUDVIGSEN to *P.* cf. *P. prolata* ROBISON & PANTOJA-ALOR to be synonymous with *P. panosa. 1,* Dorsal view of protaspis, UA 8440, ×65; *2,* ventral view of protaspis; note attached yoked free cheeks and hypostome, UA 8441, ×61; *3,* ventral view of protaspis, UA 8442, ×60; *4,* ventral view of protaspis; note attached but out-of-place yoked free cheeks, UA 8443, ×63; *5,* dorsal view of meraspid degree 1 with free cheeks missing, UA 8444, ×44; *6,* dorsal view of outstretched meraspid degree 0 with free cheeks missing, UA 8445, ×63; *7,* ventral view of meraspid degree 0? with free cheeks present but slightly out of place, UA 8446, ×62.5; *8,* dorsal view of yoked free cheeks, transitory pygidium and free cheeks attached but out of life position, UA 8447, ×32.5; *9,* dorsal view of small cephalon and attached thoracic segments, UA 8448, ×26.25; *10,* dorsal view of small cranidium, UA 8449, ×27.5; *11,* dorsal view of small pygidium, UA 8482, ×16; *12,* dorsal view of transitory pygidium, UA 8450, ×43 (new; specimens courtesy of R. Ludvigsen).

near the front of the frontal lobe; and (6) an initial, proparian facial suture.

Features that vary among the olenid protaspides include a sagittal glabellar furrow, which is present in L2 and L3 of the smallest protaspides of *Olenus* and *Acerocare* (Hu, 1971). A sagittal glabellar furrow occurs in the anterior part of the frontal lobe of some olenid early growth stages (*Olenus* in Strand, 1927; *Balnibarbi, Cloacaspis,* and *Hypermecaspis* in Fortey, 1974b) and may persist into more mature stages of some olenids (*Cloacaspis, Hypermecaspis,* and *Plicatolina* in Fortey, 1974b). Late protaspides or early meraspides may show pitting in the genae. Examples include protaspides of *Bienvillia* (Fortey, 1974b, personal communication, 1986); *Acerocare* (Hu, 1971); meraspides of *Peltura* (C. Poulsen, 1923; Whittington, 1958); and *Olenus* (Strand, 1927; Hu, 1971). The glabella may be barrel shaped, with the frontal lobe narrower than L3 (*Peltura, Leptoplastus, Acerocare*), or may expand very slightly forward and have a frontal lobe wider than L3 (*Olenus, Bienvillia*?). The facial suture usually changes from proparian to opisthoparian well into the meraspid period. The anterior border and preglabellar field that are so distinctive of mature olenid trilobites develop comparatively late in the ontogeny and appear only in the meraspid period. Genal spines are present at the posterolateral corners of the fixigenae in protaspid and early meraspid stages, and the genal spines were presumably transferred to the librigenae some time during the meraspid period, when the suture became opisthoparian.

The smallest stages of *Parabolinella* found with librigenae attached are protaspides (see Fig. 172). These specimens, which are not very well preserved, have cheeks already fused to one another. Their preservation is such that it is not clear whether the free cheeks have genal spines until the meraspid period. There is no doubt, however, that early meraspid cranidia (degree 0) of *Parabolinella* are opisthoparian and no longer have fixigenal spines.

Fortey (1974b, p. 40) discussed the usefulness of examining morphological similarity between early meraspid cranidia within the Olenidae. He was impressed by the differences shown within the family and concluded that "ontogenies are useful only in confirming relationships between closely related genera, for example within a single subfamily."

## ORDER ASAPHIDA

Fortey and Chatterton (1988) described larval and adult stages of this group and noted that one of the more important synapomorphies is the presence of a median connective suture. Most taxa within this order also share a planktonic, nonadult-like protaspis (Fig. 148, 155); this type of protaspis was termed **asaphoid** by Fortey and Chatterton (1988, p. 178, fig. 9.1, 11.1–11, and 14). More primitive members of this order (Anomocaroidea) lack the asaphoid protaspides and have larvae that are very similar to those of the Ptychopariida.

### Superfamily Anomocaroidea

The authors listed below have described protaspides of species of genera in the superfamily Anomocaroidea.

| | |
|---|---|
| *Aphelaspis* | Palmer, 1962b; Hu, 1969, 1983; Hu & Tan, 1971 |
| *Dytremacephalus* | Hu, 1971 |
| *Glyphaspis* | Hu, 1971 |
| *Glyphopeltis* | Hu, 1986 |
| *Housia* | Hu, 1970 |
| *Parabolinoides* | Hu, 1969, 1970, 1981 |
| *Taenicephalus* | Hu, 1981 |

Anomocaroid protaspides are so similar to those of ptychoparioids that the rather general description of ptychoparioid protaspides provided above would serve equally well here. They are certainly more similar to ptychoparioid protaspides than they are to asaphoid protaspides, although shared characters are evidently primitive. The morphology suggests to us that the Anomocaroidea are more closely related to Ptychopariida than to Corynexochida, Redlichiida, or Agnostida. Classification of anomocaroids in the Asaphida is based largely upon sharing a median connective suture. One interesting possible synapomorphy between anomocaroids and other Asaphida, however, is the discovery of a rostellum in some protaspides of *Lonchodomas* (see below). This feature was first described for the anomocaroid *Auritama* and the asaphid *Griphasaphus* by Öpik (1967, p. 60).

Connective sutures have been described for the early growth stages of few anomocaroids. Palmer (1962b, fig. 2.6) showed paired connective sutures in a small protaspis assigned to the pterocephaliid *Aphelaspis*. Hu (1969, fig. 3.j) illustrated a hypostome and rostral plate that suggest a similar connective suture for an early growth stage of the same genus. This pattern is different from that found in asaphoid protaspides. However, Fortey and Chatterton (1988) noted that the width of the rostral plate in relation to the hypostome may vary ontogenetically and phylogenetically. Recent work (Chatterton & others, 1994) on the raphiophorid *Lonchodomas* suggests that the asaphoid median connective suture may have originated through narrowing of the rostral plate and its reduction into a small triangular plate separating only the anterior parts of the free cheeks in some early growth stages (the rostellum of Öpik, 1967). In the trinucleoids, this small plate apparently became fused into the yoked cheeks, but in the later Asaphida it may have been further reduced in size finally to disappear and leave only a median connective suture.

## Superfamilies with asaphoid protaspides?

Asaphoid protaspides have been described by the following authors (see also Fig. 144.3, 145.5, 146.3, 150.3–6, 151.1–5, 152.12, 173–174). Hu's (1975a) taxonomic assignment of certain sclerites seems problematical.

| | |
|---|---|
| *Ampyx* | Whittington, 1959a |
| *Ampyxoides* | Fortey & Chatterton, 1988 |
| *Cryptolithus* | Whittington, 1959a; Fortey & Chatterton, 1988; Chatterton & others, 1994 |
| *Globampyx* | Fortey & Chatterton, 1988 |
| *Isotelus* | Evitt, 1961; Hu, 1975a; Chatterton, 1980; Tripp & Evitt, 1986; Speyer & Chatterton, 1989 |
| *Lonchodomas* | Shaw, 1968; Speyer & Chatterton, 1989; Chatterton & others, 1994 |
| *Menoparia* | Ross, 1951a |
| *Remopleurides* | Whittington, 1959a; Hu, 1975a; Chatterton, 1980; Fortey & Chatterton, 1988; Speyer & Chatterton, 1989 |
| *Tretaspis* | Whittington, 1959a; Hu, 1975a |
| asaphid protaspis | Whittington, 1965 |
| possible Asaphidae | Demeter, 1973 |
| nileid | Fortey & Chatterton, 1988 |

These planktonic, asaphoid protaspides are spherical to ovoid, with up to three main pairs of submarginal spines. The doublure is curved inward in a continuous fashion with the dorsal exoskeleton or is very narrow and inturned. The hypostome is large and has up to nine marginal spines that are usually long and sharply conical. The connective suture is fused or median, and the rostral plate is either absent or a small anterior rostellum is present. There is no obvious preglabellar field or anterior border medially.

Fortey and Chatterton (1988) included the Trinucleoidea in the Asaphida on the basis of both larval and adult characters. A metamorphosis took place between these planktonic juvenile stages and more mature, usually benthic, stages (see Fig. 154, 173, 174). This metamorphosis typically took place between the protaspid and meraspid periods. In some remopleuridids, however, it took place later during the meraspid period (Fig. 158). Fortey (1985) suggested that adults of some remopleuridids may have been pelagic. The metamorphosis might have been delayed or not have been as extreme in taxa with pelagic adults. Meraspides of trinucleoids were described by Rushton and Hughes (1981).

Hu (1975a) clearly disagreed with Whittington (1959a) in the assignment of protaspides and early meraspides of *Remo-*

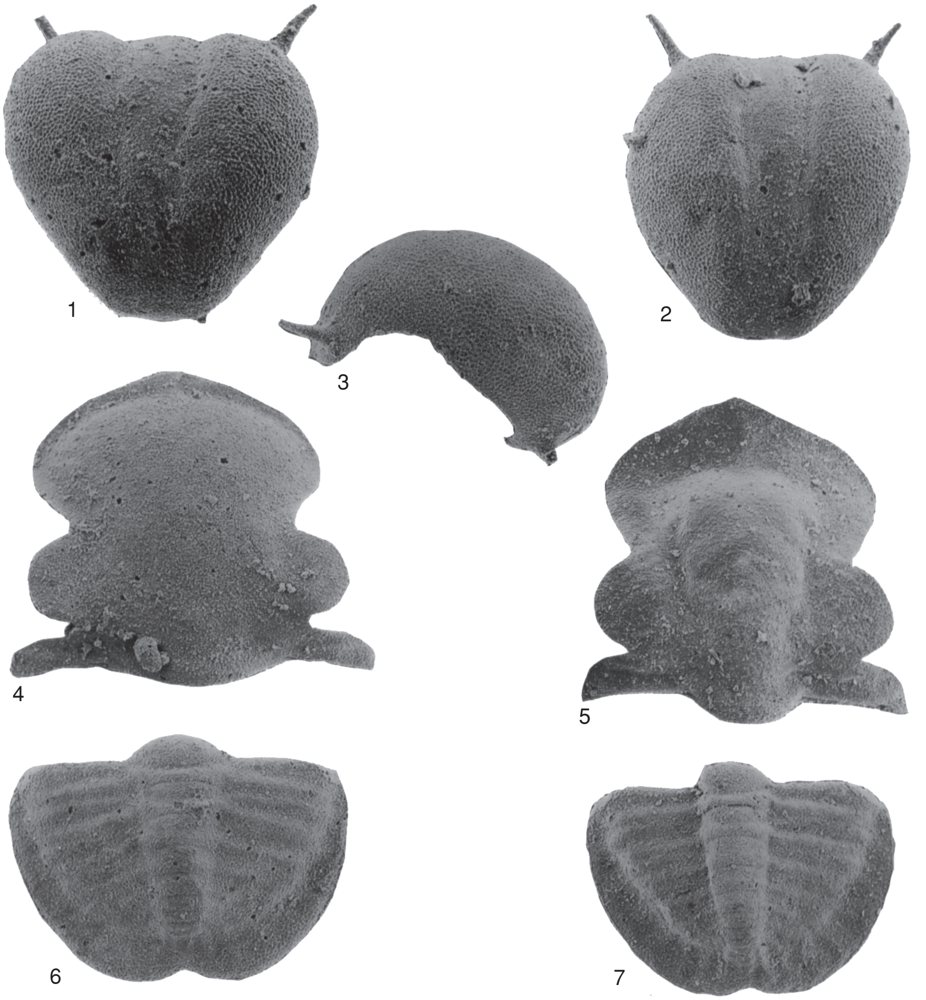


FIG. 173. Asaphida, Asaphidae. All specimens of *Isotelus* sp. from the Crown Point Formation, Middle Ordovician, New York (locality PB 81). *1–3,* Dorsal and lateral views of large protaspid stage, NYSM 16327–16329, ×45; *4,* cranidium, NYSM 16330, ×19; *5,* dorsal view of small cranidium, NYSM 16331, ×31.25; *6,7,* dorsal views of transitory pygidia; *6,* NYSM 16332, ×31.25; *7,* NYSM 16333, ×32 (new).

*pleurides* and *Isotelus*. Later workers, however, have supported WHITTINGTON's earlier work rather than HU's assignment of the protaspides to *Isotelus* (HU appears to have included protaspides of *Tretaspis* and protaspides and meraspides of *Remopleurides* in this genus). CHATTERTON (1980), however, assigned protaspides very similar to some of those assigned by HU (1975a, pl. 2, fig. 3–4, 6–7, 12–13) to *Remopleurides caelatus* to *Remopleurides pattersoni.*

Meraspides of Asaphida have been illustrated by the following workers.

| | |
|---|---|
| *Illaenopsis* | FORTEY & OWENS, 1987 |
| *Isotelus* | CHATTERTON, 1980; LUDVIGSEN, 1979a |
| *Nobiliasaphus* | KŘÍŽ & PEK, 1974 |
| *Parabarrandia* | ŠNAJDR, 1975, 1990 |
| *Pseudogygites* | LUDVIGSEN, 1979a |
| nileid meraspides | FORTEY & CHATTERTON, 1988 |

Nileid meraspides are unusually large, following large protaspid stages (FORTEY &

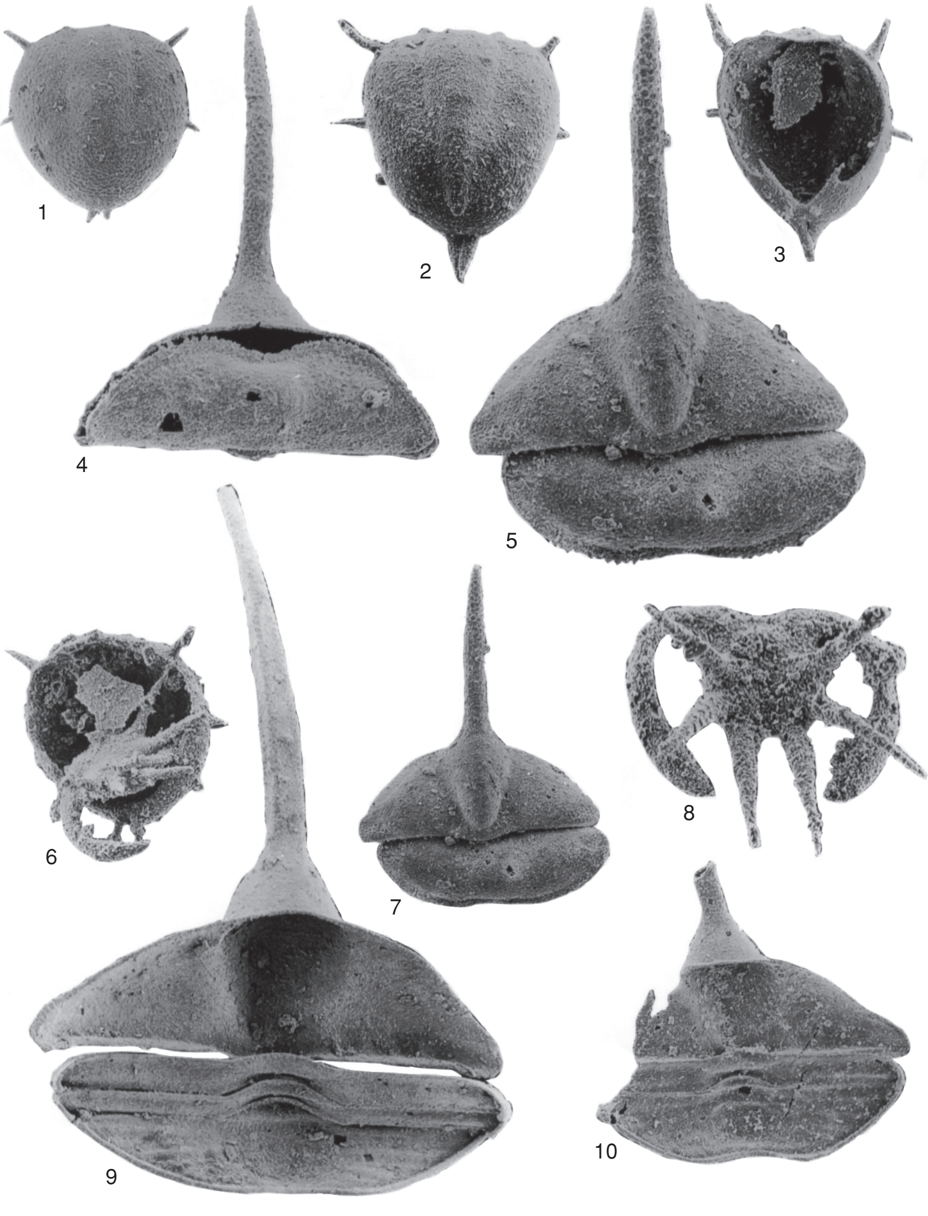


Fig. 174. Asaphida, Raphiophoridae. All specimens are of *Lonchodomas* spp. from the Crown Point Formation, Middle Ordovician, New York (locality PB 81). *1,* Dorsal view of protaspis type P1, NYSM 16334, ×62.5; *2,* dorsal view of protaspis type P2, NYSM 16335, ×62.5; *3,* ventral view of protaspis type P2, NYSM 16020, ×62.5; *4,* external view of enrolled meraspid degree 0, NYSM 16336, ×58; *5,7,* dorsal view of meraspid degree 0, NYSM 16337; *5,* ×58, *7,* ×38; *6,* ventral view of small protaspid stage; note attached, out-of-place fused cheeks and hypostome, NYSM 16338, ×62.5; *8,* ventral view of fused free cheeks and hypostome of small protaspid stage, NYSM 16339, ×90; *9,* ventral view of meraspid degree 2, NYSM 16340, ×39; *10,* ventral view of meraspid degree 1, USNM 16341, ×40 (new).

Chatterton, 1988), compared to those of most other trilobites. Meraspides of *Parabandia* illustrated by Šnajdr (1975, 1990) are very large (M1 = 7.5 mm for *P. crassa*), and the meraspid pygidium of *Illaenopsis* (Fortey & Owens, 1987, fig. 69) is the largest transitory pygidium known (approximately 18 mm wide). This may have resulted from a heterochronic pattern involved in the evolution of the Nileidae (perhaps postdisplacement). A M0 meraspid, 3.8 mm long, that was illustrated by Šnajdr (1990, p. 45) and assigned to *Zbirovia arata* is more similar to nileid meraspides than it is to illaenid meraspides.

## ORDER PHACOPIDA

Whittington (1954c) first suggested the grouping together of a number of higher taxa now included in the Phacopida on the basis of their larval characters. This suggestion was followed by Harrington, Moore, and Stubblefield (1959). Chatterton and others (1990), using cladistic methodology and morphological data from protaspides, found evidence for monophyly of the Calymenoidea and the Phacopina.

### Suborder Phacopina

Protaspides of Phacopina have been described by the authors listed below (see also Fig. 175).

| | |
|---|---|
| *Calyptaulax annulata* | Shaw, 1968; Speyer & Chatterton, 1989 |
| *Calyptaulax callirachis* | Chatterton, 1980 |
| *Calyptaulax strasburgensis* | Hu, 1971 |
| *Dalmanites puticulifrons* | Whittington & Campbell, 1967 |
| *Dalmanitina* | Šnajdr, 1990 |
| *Dalmanitina olini* | Temple, 1952 |
| *Dalmanitina socialis* | Barrande, 1852; Whittington, 1956a |

Chatterton (1971) assigned a nonadult-like protaspid to *Phacops.* We now believe that this larva should, perhaps, be assigned to the suborder Illuaenina.

Meraspid to holaspid Phacopina were described by the following authors.

| | |
|---|---|
| *Acernaspis* | Ramsköld, 1988 |
| *Dalmanitina* | Šnajdr, 1990 |
| *Dalmanitina nanchangensis* | Lu & Wu, 1983 |
| *Phacops* | Jahnke, 1969; Chatterton, 1971; H. Alberti, 1972 |
| *Trimerocephalus* | Osmólska, 1963 |

Distinctive characters of protaspides of Phacopina include (1) the highly arched (tr.) form of smaller protaspides; (2) proparian sutures; (3) eye lobes that are far forward; (4) a glabella that widens anteriorly; (5) up to four transglabellar furrows, including occipital ones; (6) fixigenae that may be pitted; (7) a short anterior border that is present medially; (8) marginal spines that are present on genae and that may splay out laterally in a radial arrangement; (9) an occipital node; (10) paired spines that are present on the anterior border and may also occur on glabella and genae; (11) a distinct, posterior marginal cephalic furrow and posterior cephalic border that are present in larger protaspides; (12) sharp, tubular marginal spines in the protopygidium; (13) paired spines that may be visible on axial rings of protopygidium; and (14) an incurled, narrow doublure that may have fine terrace ridges. Marginal spines on the cephalon may be restricted to a small pair of anterior fixigenal spines (next to the eye lobes) and a large pair of posterior fixigenal spines.

### Suborder Cheirurina

Protaspides of Cheirurina have been described by the following workers (see also Fig. 176–178).

| | |
|---|---|
| *Acanthoparypha* | Whittington & Evitt, 1954; Whittington, 1959b; Hu, 1974b (*non Ceraurinella*); Chatterton, 1980 |
| *Balizoma* | Edgecombe, Speyer, & Chatterton, 1988 |
| *Ceraurinella* | Chatterton, 1980 |
| *Cromus* | Edgecombe & Chatterton, 1992 |
| *Cybeloides* | Evitt & Tripp, 1977; Chatterton, 1980; Fortey & Chatterton, 1988 |
| *Cybelurus* | Fortey & Morris, 1978 |
| *Deiphon* | Chatterton & Perry, 1984 |
| *Encrinuroides* | Hu, 1975b (assigned to *"Otarion trilobus"*); Evitt & Tripp, 1977; Chatterton, 1980; Edgecombe, Speyer, & Chatterton, 1988 |
| *Hadromeros* | Chatterton & Perry, 1984 |
| *Heliomeroides* | Chatterton, 1980 |

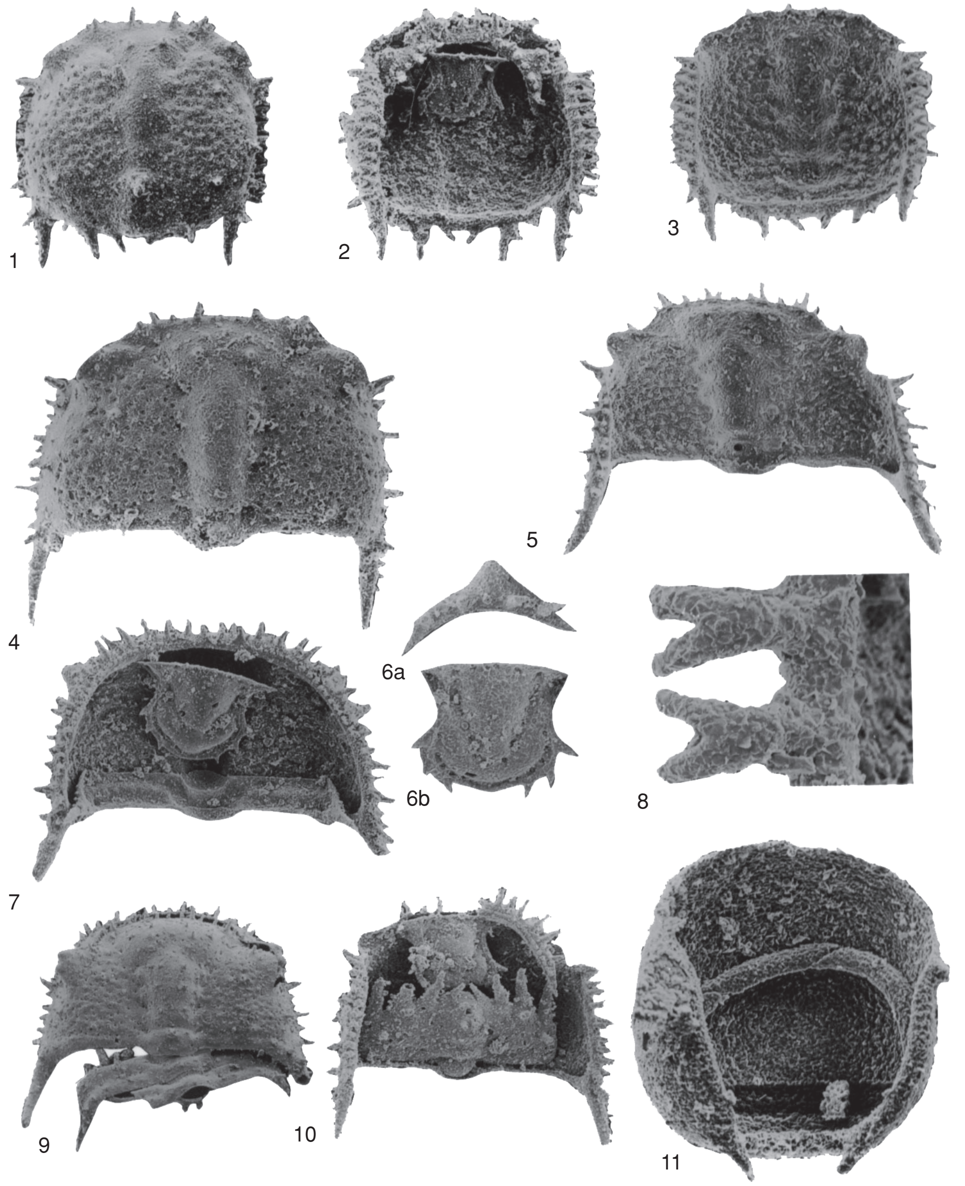


Fig. 175. Phacopida, Pterygometopidae. All specimens are of *Calyptaulax annulata* (Raymond) from the Crown Point Formation, Middle Ordovician, New York (locality PB 81); *1–3,* examples of large protaspid; *1,* dorsal view, NYSM 16342, ×62.5; *2,* ventral view; note attached free cheeks, hypostome, and rostral plate, USNM 16343, ×62.5; *3,* ventral view, example lacking free cheeks, rostral plate, and hypostome, NYSM 16344, ×65; *4,* dorsal view of small meraspid cranidium, NYSM 16345, ×67.5; *5,* ventral view of small cranidium, NYSM 16346, ×48; *6,* lateral view of free cheek (*6a*) and ventral view of hypostome (*6b*) of same larger protaspis, NYSM 16347, ×103; *7,* ventral view of cephalon with attached hypostome and thoracic segment, NYSM 16348, ×46; *8,* detail of ventral cephalic margin of larger protaspis, NYSM 16349, ×500; *9,* dorsal view of enrolled meraspid, degree uncertain, NYSM 16350, ×31; *10,* ventral view of enrolled meraspid degree 0, NYSM 16351, ×49; *11,* ventral view of smaller protaspid stage; note free cheeks and rostral plate attached to ventral surface, NYSM 16352, ×125 (new).

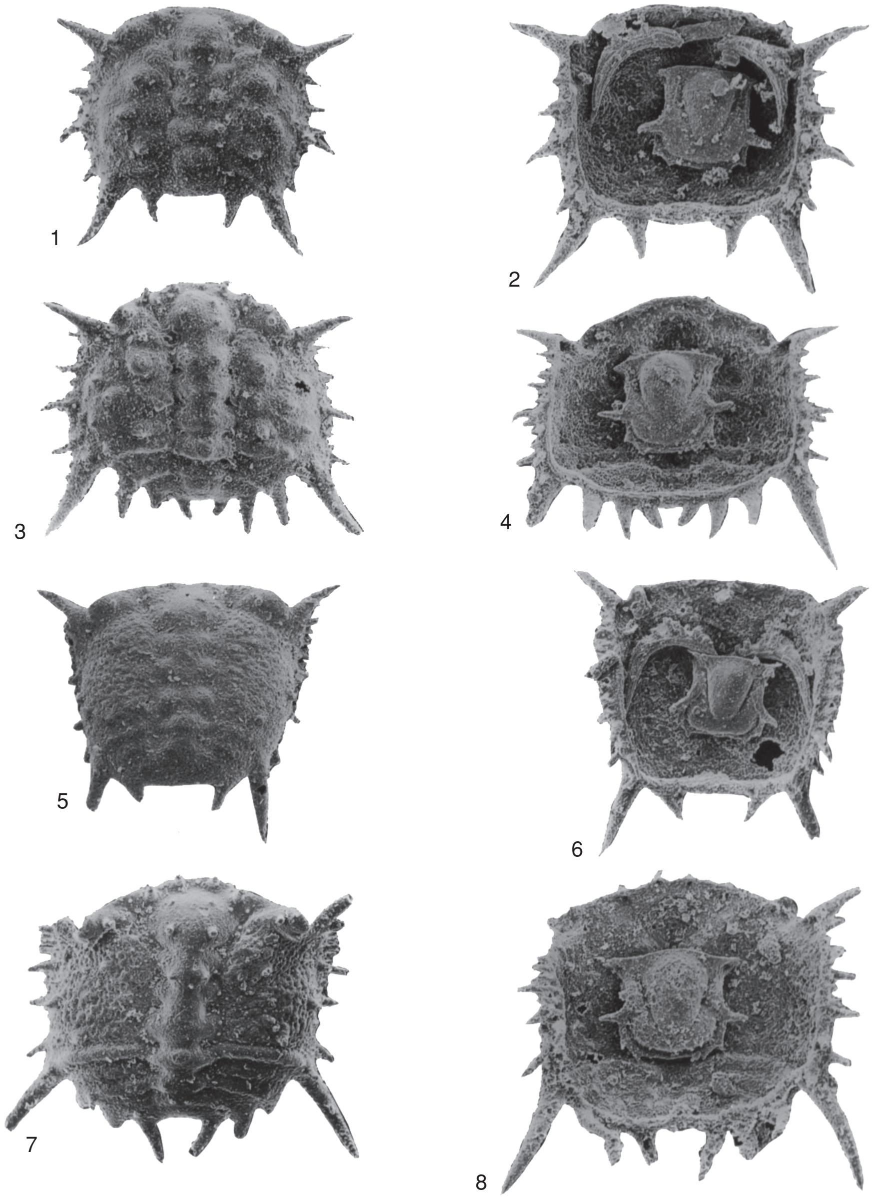


FIG. 176. Phacopida, Encrinuridae. All specimens from the Crown Point Formation, Middle Ordovician, New York (locality PB81). *1–4,* Protaspides of *Physemataspis insularis* SHAW; *1,2,* dorsal and ventral views of small protaspid stage; note attached hypostome, rostral plate, and free cheeks; *1,* NYSM 16353, ×63.5; *2,* NYSM 16354, ×74; *3,4,* dorsal and ventral views of larger protaspid stage; note attached hypostome; *3,* NYSM 16355, ×55.5; *4,* NYSM 16356, ×55.5 (new). *5–8, Cybeloides prima* (RAYMOND); *5,6,* dorsal and ventral views of small protaspid stage; note attached hypostome and free cheeks; *5,* NYSM 16357, ×62.5; *6,* NYSM 16358, ×62.5; *7, 8,* dorsal and ventral views of larger protaspid stage; *7,* NYSM 16359, ×60; *8,* NYSM 16360, ×62.5 (new).

| | |
|---|---|
| *Holia* | Chatterton, 1980 |
| *Hyrokybe* | Chatterton & Perry, 1984 |
| *Libertella* | Hu, 1971; Evitt & Tripp, 1977 |
| *Lyrapyge* | Fortey & Morris, 1978 |
| *Mackenziurus* | Edgecombe & Chatterton, 1990a |
| *Perryus* | Edgecombe, Speyer, & Chatterton, 1988 (=*Cromus*) |
| *Physemataspis* | Edgecombe, Speyer, & Chatterton, 1988 (=*Encrinuroides insularis*) |
| *Pseudocybele* | Ross, 1951a; Whittington, 1959b; Fortey & Chatterton, 1988 |
| *Rossaspis* | Ross, 1951b (=*Protopliomerops*) |
| *Sphaerexochus* | ?Chatterton, 1980; Chatterton & Perry, 1984 |

Edgecombe, Speyer, and Chatterton (1988) redescribed and discussed most known encrinurid larval stages. An important autapomorphy of this group is the presence of IV-1 and V-1 glabellar tubercles. Midfixigenal spines are apparent in early encrinurid larvae but are usually indistinguishable on later growth stages.

Larvae of Cheirurina may be divided into early and late stages. The early stages may have the glabella partly divided sagittally into two pairs of lobes behind an undivided frontal lobe, a plesiomorphic trait shared with some Ptychopariina, Redlichiina, and Calymenina. The later protaspides, without the paired glabellar lobes, are usually characterized by the following features: a proparian facial suture; eye lobes present anterolaterally; a narrow anterior border sagittally; a glabella that expands slightly forward and may be subdivided by a distinct occipital furrow and up to three glabellar furrows that are distinct laterally and usually indistinct medially; pitted genae; large anterior and posterior fixigenal spines and slightly smaller midfixigenal spines; a narrow, incurled doublure with a small number of terrace lines; prominent, sharp tubular marginal spines on the protopygidium; paired tubercles or short spines that may be present on the axis and genae; a distinct marginal furrow and posterior border usually delineating the junction between the protopygidium and the cranidium; three pairs of marginal spines occurring posterolaterally on the shield-shaped hypostome, which is usually pitted; a sculpture that usually consists of pits but may also include small tubercles; and a rostral plate that is separate and transversely widened.

### Suborder Calymenina

Protaspides of this suborder have been described by workers listed below (see also Fig. 179).

| | |
|---|---|
| *Apocalymene* | Chatterton, 1971 (only largest of three protaspides belongs to this genus) |
| *Brongniartella* | Chatterton & others, 1990 |
| *Calymene* | Chatterton & others, 1990 |
| *Flexicalymene* | Hu, 1971; Chatterton & others, 1990 |
| *Platycoryphe* | Lu & Wu, 1982 |
| *phacopoid* | Whittington, 1957b |

Siveter (1983) provided some information on allometric growth of meraspid and holaspid stages of a species of *Calymene.*

Nonadult-like protaspides (Fig. 179.1–2,11) assigned to the Calymenina are characterized by (1) a globular-quadrate form; (2) a fused rostral-hypostomal plate that lies under much of the ventral surface and has sharply pointed marginal spines (usually nine, but the number may be lower and varies intraspecifically, always with a posteromedial spine); (3) three pairs of prominent, sharp, conical submarginal cranidial spines (anterior, middle, and posterior fixigenal spines); (4) a pair of palpebral lobes adjacent to the glabella running along the anterior margin; and (5) a glabella composed of an undivided frontal lobe that extends to the anterior margin, there being no anterior border, two pairs of glabellar lobes separated by sagittal and transverse glabellar furrows, and an occipital lobe that is not obviously separated from any possible protopygidial axis that may be present. The outline of the glabella is barrel-shaped, and it is narrowest toward the back of the frontal lobe.

Adult-like protaspides succeed nonadult-like larvae in some Calymenina (Fig. 179.3–4). In the adult-like protaspides, the exoskeleton remains fairly strongly arched (tr.);

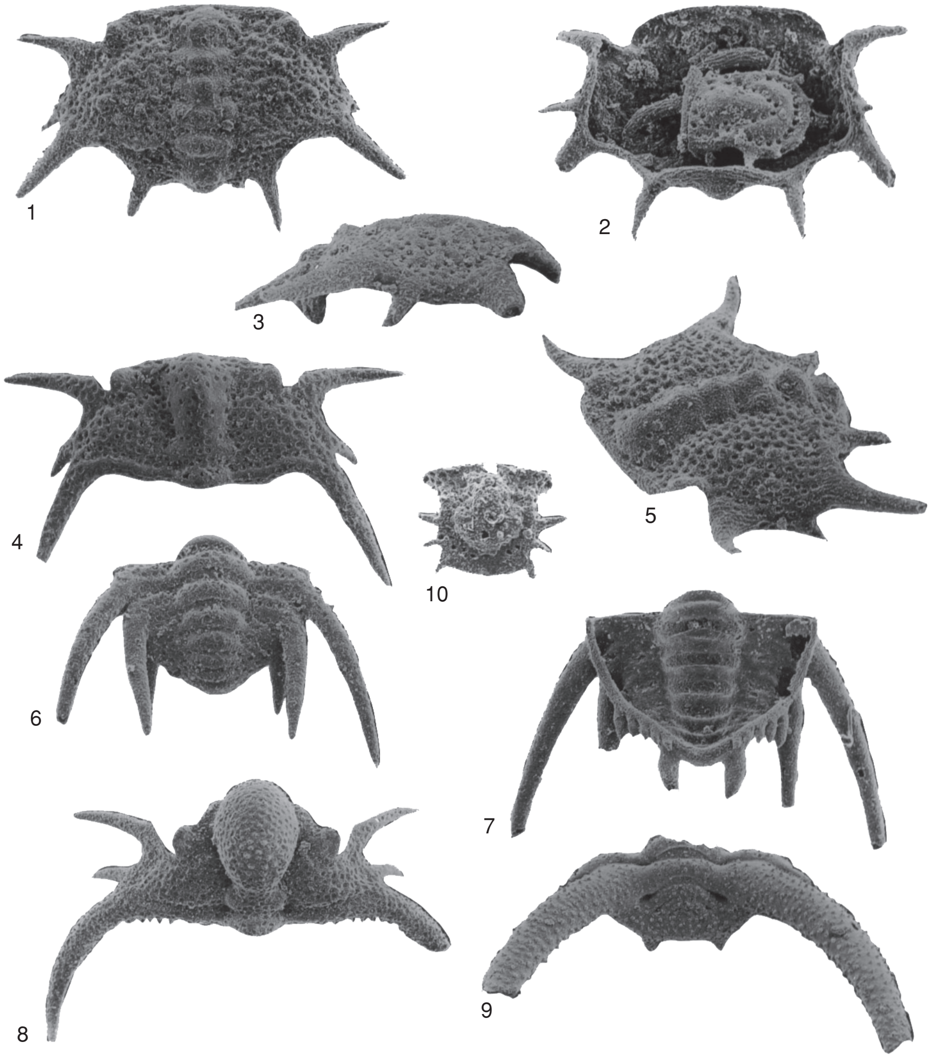


FIG. 177. Phacopida, Cheiruridae. *1–9, Sphaerocoryphe* sp. from the Crown Point Formation, Middle Ordovician, New York (locality PB 81); *1,* dorsal view of protaspis, NYSM 16361, ×47.5; *2,* ventral view of protaspis, NYSM 16362, ×50; *3,* lateral view of protaspis, NYSM 16027, ×65; *4,* dorsal view of small meraspid cranidium, NYSM 16363, ×36.5; *5,* anterodorsolateral view of protaspis, NYSM 16364, ×57.25; *6,* dorsal view of transitory pygidium, NYSM 16365, ×36.5; *7,* ventral view of transitory pygidium with six unreleased protothoracic segments, NYSM 16366, ×36.5; *8,* dorsal view of small cranidium, NYSM 16367, ×25.5; *9,* dorsal view of pygidium, NYSM 16368, ×19. *10, Deiphon* sp. from the Wenlock Delorme Formation of northwestern Canada (locality AV4 126T), ventral view of hypostome, UA 8451, ×47 (new).

the sagittal glabellar furrows have disappeared and the glabella is semicylindrical; the hypostomal suture is functional; the marginal spines of the hypostome are shorter and the median spine is lost; fine marginal spines appear on the anterior border, rostral plate, and cheeks, and the submarginal spines of earlier stages (particularly the anterior and midfixigenal spines) are relatively less prominent; an occipital ring with a tubercle is distinguishable from more anterior parts of the glabella and a protopygidial axis; the eyes are

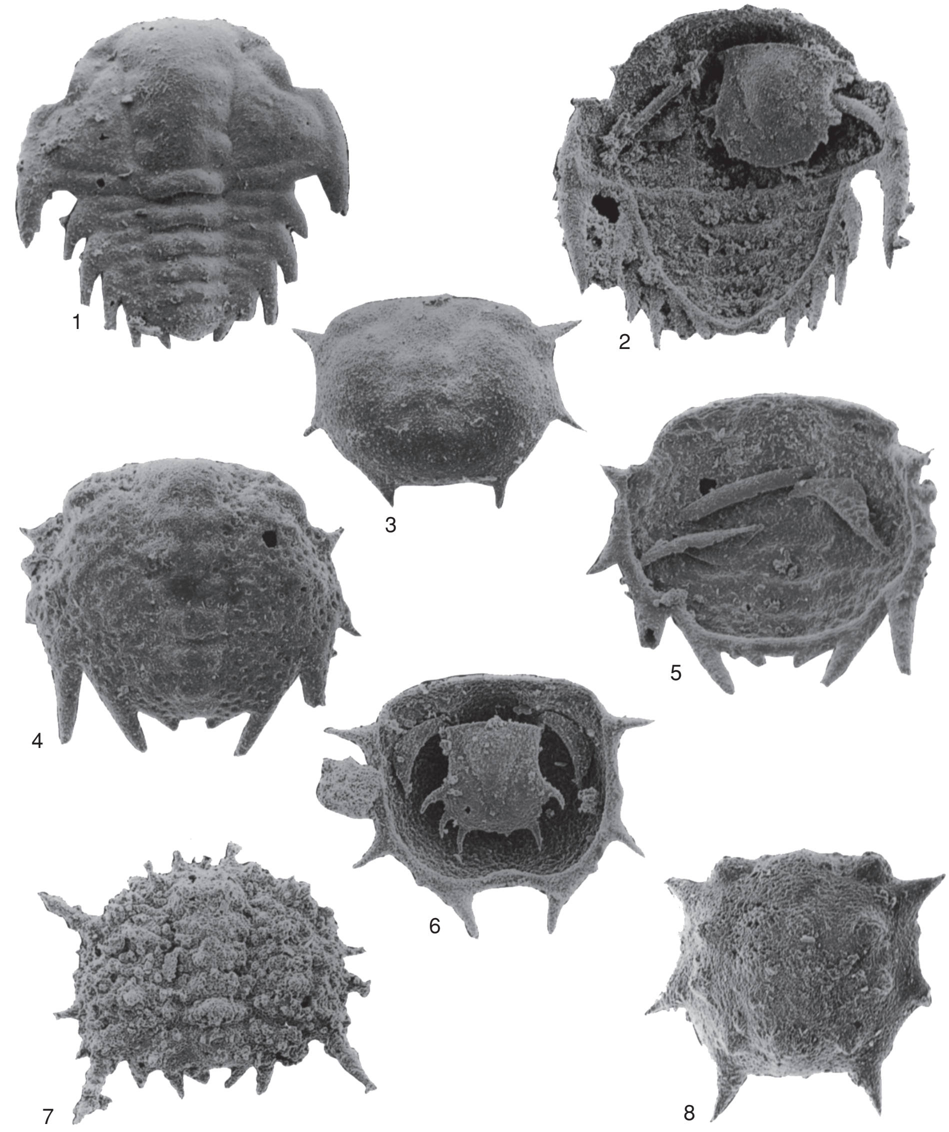


FIG. 178. Phacopida. *1–6,* From the Crown Point Formation, Middle Ordovician, New York (locality PB81); *1,2,* dorsal and ventral views of large protaspides of *Ceraurinella latipyga*? SHAW, Cheiruridae; note attached free cheeks and hypostome; *1,* NYSM 16369, ×39; *2,* NYSM 16370, ×42; *4,5,* dorsal and ventral views of small cheirurid protaspides (possibly *Acanthoparypha* or *Ceraurinella*); note presence of hypostome and free cheeks; *4,* NYSM 16371, ×61; *5,* NYSM 16372, ×75; *3, 6,* dorsal and ventral views of smaller protaspis of *Ceraurinella latipyga?,* NYSM 16373, ×62 (new). *7,8,* From the Wenlock Delorme Formation, northwestern Canada (locality AV4 126T); *7,* dorsal view of protaspis of *Balizoma* sp., Encrinuridae, UA 7826; *8,* dorsal view of small protaspis of *Hyrokybe* sp., Cheiruridae, UA 8452, ×47 (new).

comparatively far forward and opposite the frontal lobe of the glabella; an eye ridge is separated from the anterior margin by a short anterior border; a protopygidium is large and distinct, with marginal spines (two in more mature specimens) at the distal ends of the segments; paired tubercles are visible on the fixed cheeks and sometimes on the glabella; three pairs of glabellar furrows are present as shallow, marginal indentations;

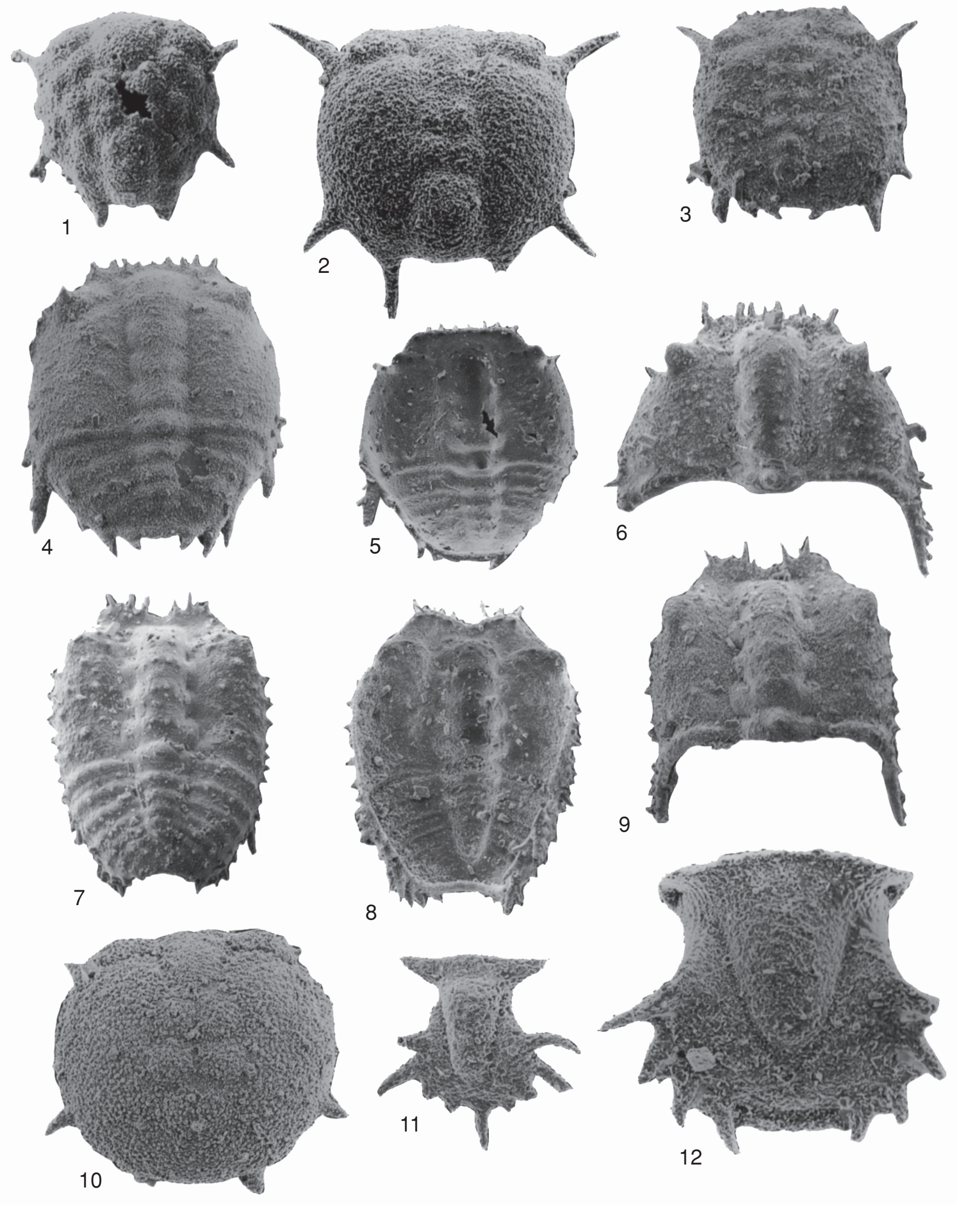


Fig. 179. Phacopida. Protaspides of species in this order may (life-history strategy II) be planktonic (P1, P2) in early stages, benthic in later stages (B1, B2); see Chatterton and others (1990, p. 257) for this terminology. *1–4, 11, 12, Flexicalymene senaria* (Conrad), Calymenidae, from the Martinsburg Formation, Middle Ordovician, Virginia; *1,* dorsal view of smallest protaspis (P1), AMNH 43943, ×75; *2,* dorsal view of second protaspid stage (P2), AMNH 43938, ×75; *3,* dorsal view of third protaspid stage (B1), NYSM 16374, ×41.7; *4,* dorsal view of fourth protaspid stage (B2), NYSM 16375, ×42.5; *11,* ventral view of fused hypostome and rostral plate from last pelagic protaspid stage (P2), AMNH 43939, ×63; *12,* ventral view of small hypostome from benthic protaspid stage, AMNH 43942, ×130 (new). *5,6, Calymene* sp., Calymenidae, from the Wenlock Delorme Formation of northwestern Canada (locality AV4 126T); *5,* ventral view of last protaspid stage (B2), UA 7928, ×33.5; *6,* dorsal view of small cranidium, UA 8453, ×34 (new). *7–9, Brongniartella* sp., Homalonotidae, from the Martinsburg Formation, Middle Ordovician, Virginia; *7,* dorsal view of protaspis (B2), AMNH 43960, ×31.4; *8,* ventral view of protaspis (B2), AMNH 43961, ×31.4; *9,* dorsal view of small cranidium, NYSM 16376, ×29 (new). *10, Apocalymene quadrilobata* (Chatterton), Calymenidae, from the Emsian *Receptaculites* Limestone of New South Wales, Australia; dorsal view of protaspis, UA 8454, ×36.8 (new).

and the doublure is narrow, curved inward, and without obvious terrace ridges.

Meraspides of Calymenina have been described by a number of workers (for details, see Chatterton & others, 1990; see also Rabano, 1990, *Colpocoryphe*). The facial suture, although it migrates backward during ontogeny, stays proparian until quite late in the ontogeny and becomes gonatoparian only in mature stages of certain taxa.

## ORDER PROETIDA

Protaspides of this order have been described by the following authors (see also Fig. 180–182).

| | |
|---|---|
| *Bathyurus* | Chatterton, 1980 |
| *Carrickia* | Chatterton & Ludvigsen, 1976; Chatterton, 1980 *(=Phorocephala)* |
| *Cyphaspis* | Chatterton, 1971 |
| *Dimeropyge* | Hu, 1976; Chatterton, 1980; Tripp & Evitt, 1983; Speyer & Chatterton, 1989 |
| *Licnocephala* | Ross, 1953 |
| *?Mesotaphraspis* | Hu, 1976 |
| *Phaseolops* | Hu, 1971 |
| *Proetus* | Chatterton, 1971; Hu, 1975b (as *"Proetus"*) |
| *Scharyia* | Owens, 1974; Šnajdr, 1980, 1981a, 1990; Speyer & Chatterton, 1989 |
| *Tricornotarion* | Chatterton, 1971 |
| proetid | Beecher, 1893b, 1895a |

There is some confusion regarding the assignment of sclerites to *Dimeropyge* and ?*Mesotaphraspis* by Hu (1976): e.g., the hypostomes belong to Cheirurina. A protaspis assigned by Hu (1975b, fig. 1a, pl. 1, fig. 1) to *Otarion trilobus* Hu is an encrinurid, *Encrinuroides* cf. *E. tholus* (see Edgecombe, Speyer, & Chatterton, 1988, p. 780).

There may be as many as four different protaspides in the ontogeny of Proetida (e.g., *Scharyia*, Fig. 180). The earliest is very small (about 0.3 to 0.4 mm long) and has a re-entrant posterior margin, usually between two sharp, spinose projections. There may be also a spinose projection anteromedially. Later protaspides lack the re-entrant posterior and have an entire protopygidial margin.

Characteristics of later protaspides include an opisthoparian facial suture; functional connective sutures; a very flat ventral profile and an elliptical to ovoid outline in dorsal view; an anterior border and usually a preglabellar field; eyes located near or just in front of the midlength of the glabella; an axis weakly defined but usually distinguishable; a glabella divided by a transverse occipital furrow but with other furrows usually shallow (e.g., S1 in largest protaspides) to indistinct; genal spines that may (*Dimeropyge*) or may not (*Scharyia*) project outward to affect the outline in dorsal view; sculpture that is smooth, finely granulose, or has a pattern of larger, paired tubercles on the axis and pleurae; a hypostome of even width; and a relatively flat doublure that is sharply turned inward and upward at the margins, with no or few terrace ridges. The hypostome is usually small and without spines or otherwise subdivided posterolateral margins in protaspid stages of this order. One feature that appears to be distinctive of protaspides of Proetida is the very early development of a preglabellar field, a feature that does not develop until the meraspid period in the otherwise rather similar Ptychopariina.

Meraspides of Proetida have been described by several workers, apart from those listed above, including Ross (1951b, 1953), Hintze (1953), Whittington and Evitt (1954), Whittington (1963), and Whittington and Campbell (1967). Fortey and Owens (1975) used similarities between meraspid cranidia to support their concept of a new order Proetida. Fortey (1990a) diagnosed this order on the basis of ontogenetic similarities. Chatterton (1980) argued that there appear to be two lineages within the Proetida, one with small growth stages having smooth protaspid and early meraspid growth stages (*Proetus, Phaseolops, Licnocephala,* and *Bathyurus*), and one with distinct, organized patterns of tubercles (hystricurinids, telephinids, dimeropygids, glaphurids, aulacopleurids, and *Scharyia*). Phylogeny and ontogeny in Proetida have been insufficiently studied, however, to

Fig. 180. Proetida. All specimens are of the brachymetopid *Scharyia* aff. *S. redunzoi* Perry & Chatterton from the Wenlock Delorme Formation of northwestern Canada (locality AV4 126T). *1,2,* Dorsal and ventral views of the largest protaspid stage (of at least three and probably four stages); *1,* UA 8455, ×32.5; *2,* UA 7901, ×30.5; *3,4,* dorsal and ventral views of the smallest protaspid stage; note free cheeks and rostral plate still attached; *3,* UA 8456, ×91; *4,* UA 8457, ×91; *5,* dorsal view of an early transitory pygidium, UA 8458, ×30.5; *6,* ventral view of an intermediate protaspid stage; note free cheeks and rostral plate attached; genal spine not apparent, UA 8459, ×91; *7,* ventral view of smallest protaspis; note that free cheeks and rostral plate are attached and the possibly natant position of hypostome is close to inferred life position, UA 8460, ×112; *8,* dorsal view of small cranidium, UA 8461, ×31; *9,* dorsal view of transitory pygidium, UA 8462, ×32.5; *10,11,* dorsal and ventral views of last protaspid stage; note attached free cheeks and absence of genal spine; *10,* ×62.5; *11,* UA 7902, ×126; *12,13,* dorsal and ventral views of transitory pygidia belonging to penultimate meraspid degree; *12,* UA 8463, ×32.5; *13,* UA 8464, ×32.5 (new).

FIG. 181. Proetida, Aulacopleuridae. *1,2,4,5,* Specimens of "*Otarion*" *spinicaudatum* SHAW from the Crown Point Formation, Middle Ordovician, New York (locality PB81); *1,2,* dorsal and ventral views of small protaspides; note out-of-place free cheeks and hypostome attached to ventral surface; *1,* NYSM 16377, ×133; *2,* NYSM 16378, ×135; *4,5,* dorsal and ventral views of later protaspid stages; note out-of-place free cheeks and hypostome still attached to ventral surface; *4,* NYSM 16379, ×107; *5,* NYSM 16380, ×107 (new). *3,6,* Dorsal and ventral views of protaspides of *Dimeropyge* sp., Dimeropygidae, from lower Edinburg Limestone of Virginia (locality 4); *3,* NYSM 16381, ×62.5; *6,* NYSM 16382, ×62.5 (new). *7,8,* Dorsal and ventral views of meraspid degree 1 of *Conopareia* n. sp. from the Wenlock Delorme Formation of northwestern Canada (locality AV4 126T), UA 8465, ×88 (new).

judge whether these are separate lineages. Certainly, prominent spines of early growth stages are often lost secondarily and perhaps sometimes regained. It is unwise to recognize large phyletic groups using a single character that may be homoplasous.

ŠNAJDR (1990, p. 40) illustrated a slab of shale from the Wenlock Liten Formation covered in late meraspid molts and carcasses of one species, *Aulacopleura konincki.* Šnajdr believed this sample to be representative of a site where a large number of individuals of this species molted. He suggested that some of the molts that are disarticulated may have been disturbed by other molting individuals.

## ORDER LICHIDA, FAMILY LICHIDAE

Ordovician to Devonian protaspides of this family have been described by workers listed below (see also Fig. 183–184).

| | |
|---|---|
| *Acanthopyge* | Whittington, 1956c; Chatterton, 1971 |
| *Amphilichas* | Chatterton, 1980; Hu, 1974a; Tripp & Evitt, 1981 |
| *Hemiarges* | Chatterton, 1980; Hu, 1974a; Tripp & Evitt, 1981; Speyer & Chatterton, 1989 |

Some problems of protaspid assignments were resolved by Tripp and Evitt (1981). Lichid protaspides are so similar to one another and so different from those of other taxa that they strongly support the monophyletic nature of this group. Protaspides have been found for members of the Lichinae (*Dicranopeltis*), Tetralichinae (*Amphilichas*), and Ceratarginae (*Hemiarges* and *Radiolichas*). The later protaspides are adult-like, very similar to meraspides of the same taxa, and clearly had a benthic life mode. It is now apparent to us that lichids (Fig. 166.1,2) may also have had an earlier nonadult-like, planktonic growth stage. As with all small stages that are separated from later growth stages by a radical metamorphosis, some uncertainty attends associating these with adult stages. Chatterton originally assigned larvae, which we now consider may belong to a lichid (*Acanthopyge*) planktonic stage, to one growth stage of *Apocalymene quadrilobata* (Chatterton, 1971, fig. 18h,i, pl. 19, fig. 8–10, pl. 21, fig. 1–3). This reassignment is still controversial, since similar stages have not been found for all other lichid ontogenies.

Features of the more adult-like protaspides of lichid trilobites were described by Chatterton (1980, p. 12) and include an opisthoparian facial suture; distinct axial and pleural regions; a comparatively wide (sag. and exsag.) anterior border; a posterior border and posterior marginal furrows to the cranidium; distinct palpebral lobes just in front of or close to the midlength of the cranidium; an occipital tubercle and a pattern of larger tubercles that is usually present on the axis and pleurae (see Chatterton, 1971 and Fig. 149 for terminology); a librigenal spine is usually absent; three or five pairs of marginal spines present on the protopygidium; interpleural furrows present on protopygidium; a doublure with terrace ridges distally and a sharp ridge around the proximal ends of marginal spines; and a hypostome with blunt-ended marginal spines that make the margins appear to be subdivided by four pairs of slits.

The distinctive anterolateral glabellar lobes or bullae of adult lichids may be absent in protaspides or present as small lobes along the axial furrows (*Acanthopyge* in Chatterton, 1971). After they appear as small lobes in or proximally adjacent to the axial furrows of later protaspid or early meraspid cranidia, they expand forward and outward but apparently remain glabellar, with the axial furrows surrounding them. The posterolateral cranidial lobes also expand outward from early meraspid stages onward and may incorporate genal as well as glabellar material as they expand (see detailed arguments in Chatterton, 1971; and Thomas & Holloway, 1988). A sequence of developmental stages of an Ordovician species of *Hemiarges* is shown in Figure 184.

## ORDER LICHIDA, FAMILY ODONTOPLEURIDAE

Protaspides of this family have been described by the workers listed below (see also Fig. 185.1,2,5,11,12).

| | |
|---|---|
| *Ceratocephala* | Chatterton, 1980 |
| *Ceratocephalina* | Chatterton, 1971 |
| *Diacanthaspis* | Whittington, 1956d; Hu, 1974b |
| *Dudleyaspis (Taemasaspis)* | Chatterton, 1971 |

Small odontopleurid meraspides have been described by the above workers as well

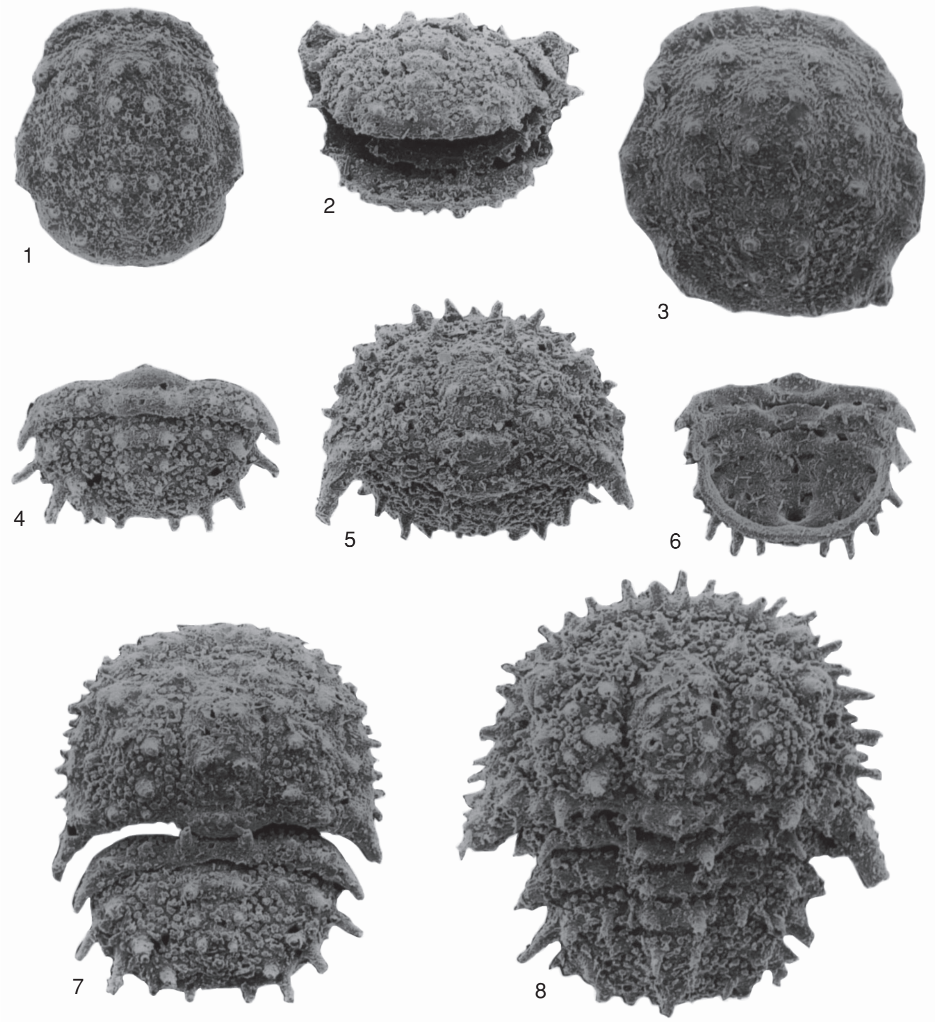


FIG. 182. Proetida. Specimens of *Dimeropyge* aff. *D. clintonensis,* Dimeropygidae, from the Esbataottine Formation, Middle Ordovician, northwestern Canada (locality P17.2); compare Figure 160. *1,* External view of protaspis P2, lacking free cheeks, UA 8466, ×80; *2,* external view of enrolled meraspid degree 0, UA 8467, ×64; *3,* dorsal view of late protaspis, UA 8468, ×97.5; *4,* dorsal view of small meraspid thoracic segment and transitory pygidium (degree 1?), UA 8469, ×63; *5,* external view of partly enrolled meraspis (degree 1), UA 8470, ×64; *6,* ventral view of meraspis (degree 2 or more), UA 8471, ×49; *7,* dorsal view of reconstructed meraspis (cephalon found separate from thoracic segment and transitory pygidium), UA 8472 and UA 8469, ×71; *8,* dorsal view of meraspid degree 2, UA 8473, ×72 (new).

as WHITTINGTON and EVITT (1954), SHAW (1968), WHITTINGTON and CAMPBELL (1967), CHATTERTON and PERRY (1979, 1983), and RAMSKÖLD and CHATTERTON (1991). Protaspides for this group are small and adult-like. No nonadult-like protaspides have been associated with this family.

The Dameselloidea are regarded as a sister group of Odontopleuroidea by FORTEY (1990a) and herein. ENDO (1939a, 1939b) provided poor illustrations considered to be of protaspides of the damesellid *Blackwelderia* from the Cambrian of China. Restudy of this material will be necessary before

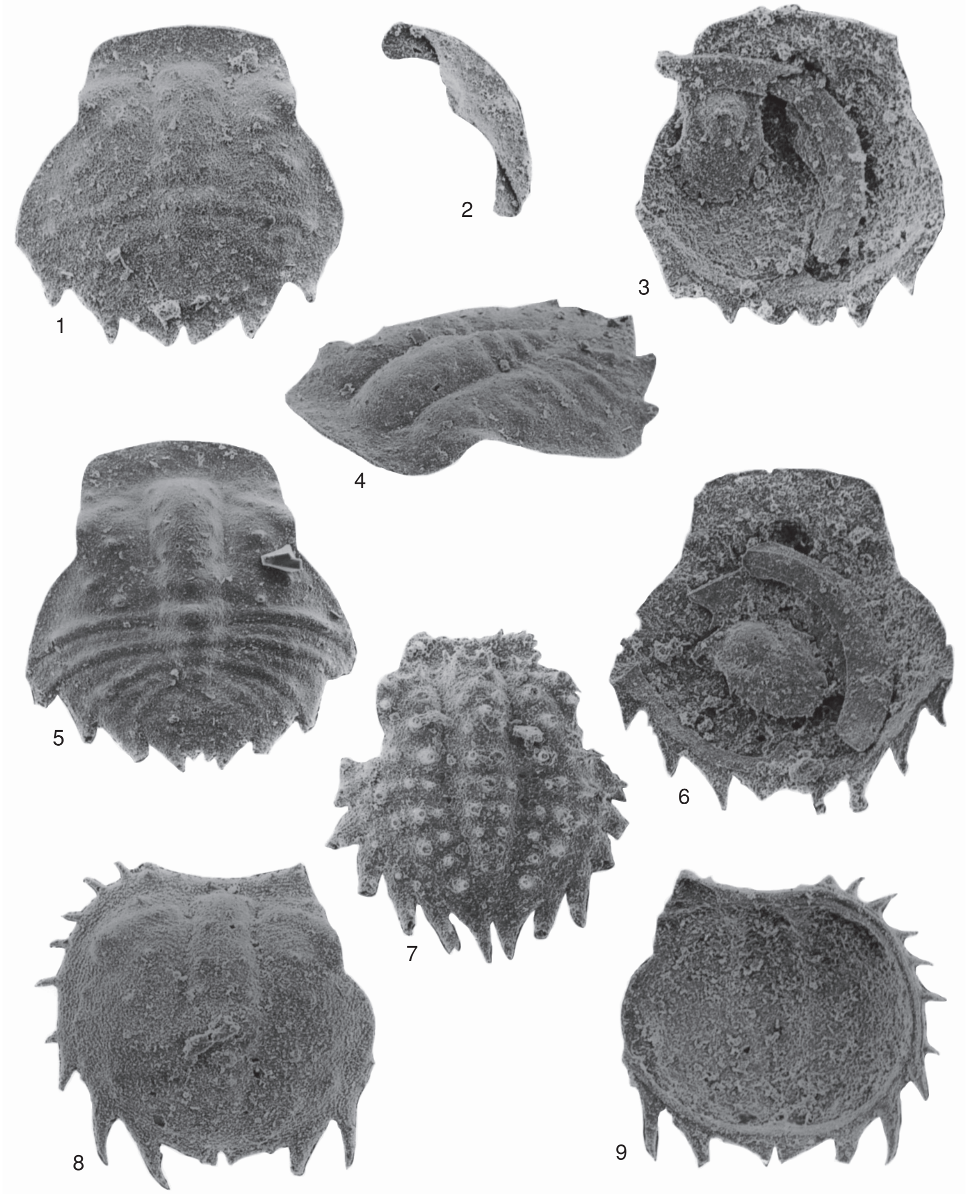


Fig. 183. Lichidae. *1–6,* Protaspides of *Hemiarges* aff. *H. turneri* Chatterton & Ludvigsen from the Crown Point Formation, Middle Ordovician, New York (locality PB81); *1,* dorsal view of small protaspis, NYSM 16383, ×62; *2,* dorsal view of protaspid free cheek, NYSM 16384, ×63.5; *3,* ventral view of small protaspid growth stage; rostral plate, hypostome, and free cheek are attached, NYSM 16385, ×62.5; *4,* anterodorsolateral view of small protaspis, NYSM 16386, ×67; *5,* dorsal view of large protaspid stage, NYSM 16387, ×53.5; *6,* ventral view of large protaspid stage, NYSM 16388, ×50. *7,* Dorsal view of large protaspid stage of *Amphilichas* sp. from the Lower Edinburg Formation, Middle Ordovician, Virginia (locality 4), NYSM 16389, ×37. *8,9,* Dorsal and ventral views of *Amphilichas minganensis?* (Billings), small protaspid growth stage with single free cheek attached, from the Crown Point Formation, Middle Ordovician, New York (locality PB81), NYSM 16390, ×61.5 (new).

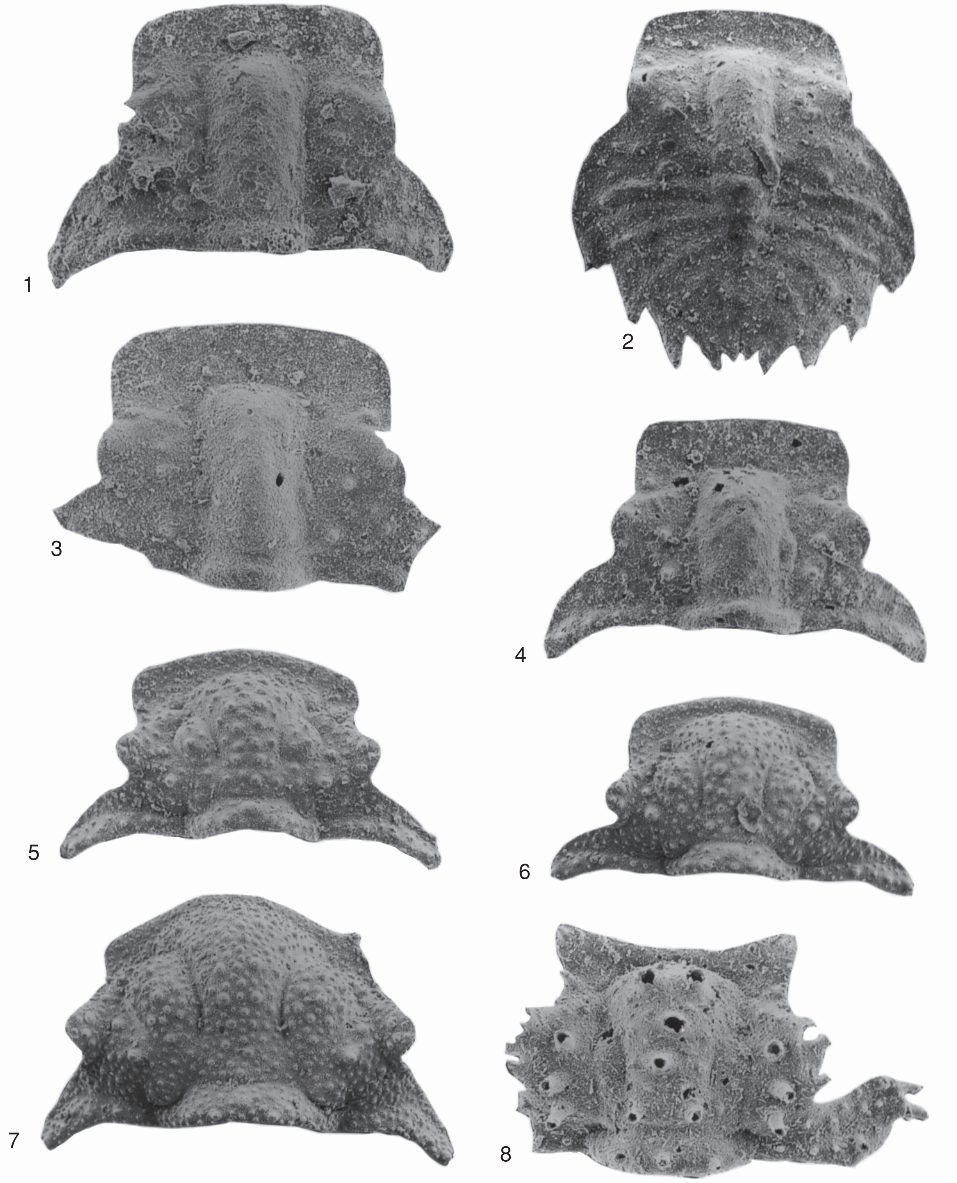


FIG. 184. Lichidae. Development of cranidial lobation in lichids. All specimens are from the Crown Point Formation, Middle Ordovician, New York (locality PB 81). *1–7,* Dorsal views of cranidia and protaspis of *Hemiarges* aff. *H. turneri* CHATTERTON & LUDVIGSEN; *1,* cranidium (bullae very small but distinguishable on glabellar side of axial furrow in L2 position), NYSM 16391, ×62; *2,* last protaspid stage (cranidial lobes indistinct; note that this is not NYSM 16014 as in SPEYER & CHATTERTON, 1989, fig. 4e), NYSM 16392, ×56.25; *3,* small cranidium (bullae expanded transversely to affect outline of glabella; posterolateral lobes barely distinguishable in L1 position as part of sides of glabella), NYSM 16393, ×62.5; *4,* small cranidium (bullae expanded outward and slightly forward; posterolateral lobes (L1) expanding slightly outward behind bullae), NYSM 16394, ×44.6; *5,* small cranidium (bullae expanded farther outward and forward to opposite at least part of L3; posterolateral lobes expanded outward but not quite as far as bullae; transverse width of glabella apparently slightly reduced towards front of posterolateral lobes, opposite fixigenal spine pair A1 of CHATTERTON, 1971), NYSM 16395, ×31.25; *6,7,* larger cranidia (bullae and *(Continued on facing page.)*

it may be used to clarify this relationship. ENDO's drawings (1939b, fig. 1b, 5b) are of larvae that show little similarity to post-Cambrian odontopleurid protaspides and a greater similarity to those of Redlichiina.

The protaspides assigned to post-Cambrian odontopleurids are similar to one another and support the thesis that these taxa form part of a monophyletic group. They share the following characteristics: the facial suture is initially proparian, then changes to opisthoparian between protaspid and meraspid periods or within the meraspid period; the librigenae have marginal spines; paired spines occur on the glabella and anterior border (see Fig. 149), an exception being *Dudleyaspis* and perhaps *Acidaspis;* the glabella is distinct and subparallel-sided to barrel-shaped, with a shallow occipital furrow and up to three indistinct transglabellar furrows farther forward; glabellar furrows often appear to constrict the glabella slightly locally; sculpture between tubercles may be absent or granulose; an occipital spine or node is present with or without subsidiary occipital spines; a distinct pattern of prominent, paired spines occurs on the genae and posterior border; sharp, tubular marginal spines are found on the protopygidium with or without spinules; the doublure is narrow, incurled to inturned, and without terrace ridges; the hypostome is slightly transverse with entire margins or very short spines; the hypostomal doublure is often embayed just behind the shoulder, sometimes later forming a hole in the doublure that is separate from its interior margin; the posterior margin of the protocranidium is delineated by a distinct furrow; and the ventral profile is subhorizontal.

The glabellar lobes of odontopleurids appear to have originated through lateral expansion of the glabella, with the glabellar furrows deepening and lengthening; and the individual glabellar lobes sometimes swell so as to be separated from the median part of the glabella by sublongitudinal furrows. Their proximity to the palpebral lobe in some taxa appears to be a combination of expansion of the glabella and migration inward of the eye. The movement of the facial suture from a proparian pattern to an opisthoparian pattern between protaspid and meraspid periods or during the early part of the meraspid period (Fig. 186) is well documented.

## CLASSIFICATION UNCERTAIN

Ontogenies of Cambrian taxa that have not been placed with confidence into any superfamily or order include those of Plethopeltidae (HU, 1986, *Arapahoia*), *Plagiura* (HU, 1985b), *Missisquoia* (HU, 1971; see also under Corynexochida, Leiostegiina above), and *Paranumia* HU (1973).

HU (1986) commented on the similarity of the protaspides of the plethopeltid *Arapahoia* to those of the norwoodiid *Norwoodella* (Ptychoparioidea) and the cedariids *Cedaria* and *Cedarina* (Ptychoparioidea). We agree with HU that the morphological similarities of early growth stages of these taxa imply relative recentness of common ancestry; the Plethopeltidae should be included with the Norwoodiidae and the Cedariidae in the Ptychoparioidea.

FIG. 184. *Explanation continued from facing page.*

posterolateral lobes slightly more expanded than in smaller cranidia; axial furrows shallow, particularly opposite A1; posterolateral part of fixigena in front of border furrow slightly swollen so that boundary between anterior part of posterolateral lobe and fixigena is not very distinct); *6,* NYSM 16396, ×21.5; *7,* NYSM 16397, ×21. *8, Amphilichas conradi* CHATTERTON & LUDVIGSEN from the lower Esbataottine Formation, Middle Ordovician, northwestern Canada (locality P17.2); bullae not delineated posteriorly by distinct furrow, but longitudinal furrow separating bullae from rest of glabella is very shallow to indistinct behind L2, and axial furrows are distinct, UA 8474, ×47 (new).

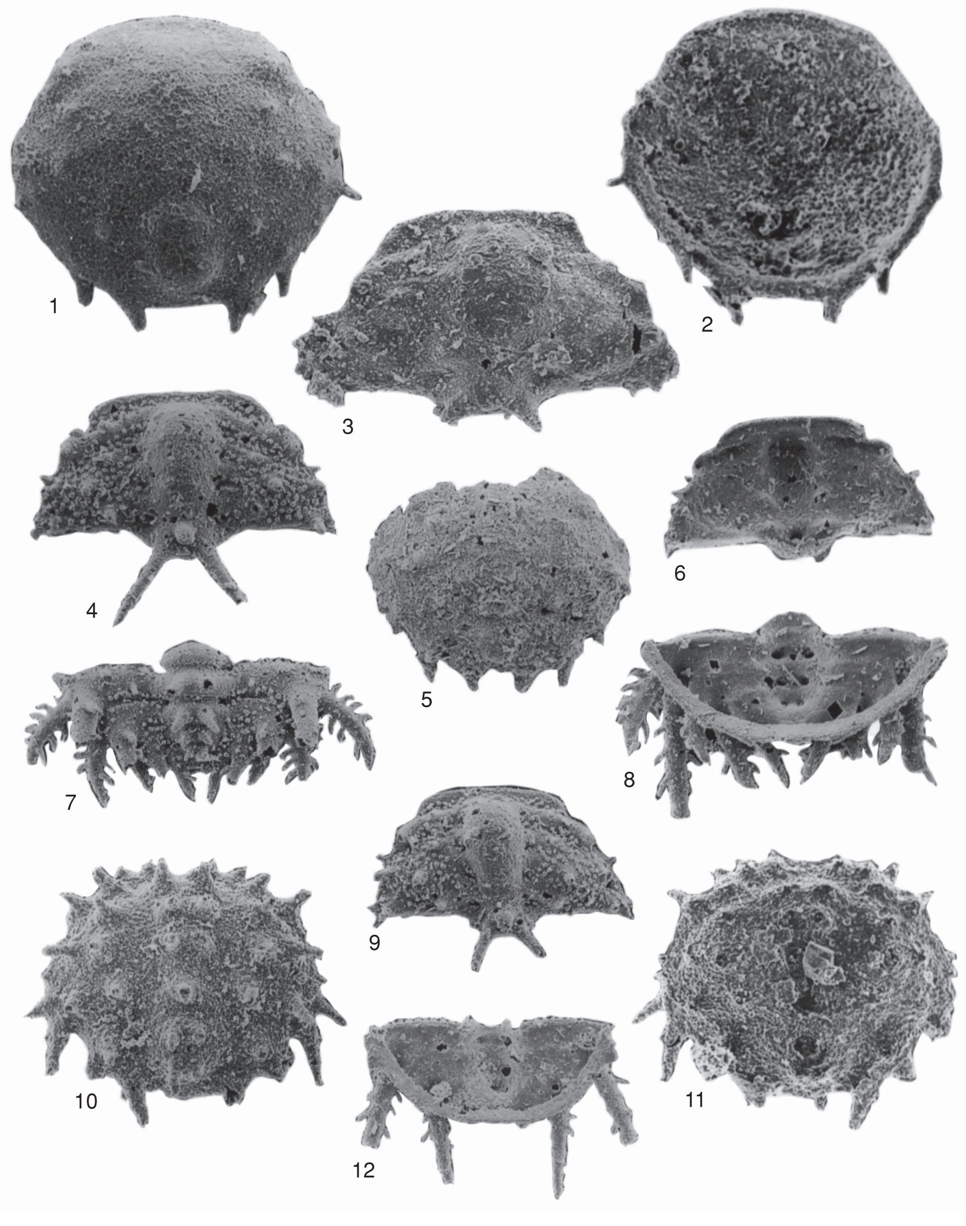


FIG. 185. Odontopleuridae. *1–9,12, Ceratocephala triacantheis* WHITTINGTON & EVITT; *1–3,* from the Crown Point Formation, Middle Ordovician, New York (locality PB81); *1,2,* dorsal and ventral views of protaspis, NYSM 16398, ×117; *3,* small cranidium, NYSM 16399, ×67 (new). *4–9,12,* from the Esbataottine Formation, Middle Ordovician, northwestern Canada (locality P17.2); *4,* dorsal view of small cranidium, UA 8175, ×64; *5,* dorsal view of incomplete protaspis, UA 8475, ×65; *6,* ventral view of cranidium, UA 8173, ×64; *7,* dorsal view of transitory pygidium (lost specimen), ×50; *8,* ventral view of transitory pygidium, UA 8179, ×64; *9,* dorsal view of small cranidium, UA 8174, ×64; *12,* ventral view of transitory pygidium, UA 8176, ×64. *10,11,* Dorsal and ventral views of protaspis of *Diacanthaspis secretus* WHITTINGTON from the lower Edinburg Limestone of Virginia (locality 4), NYSM 16400, ×80 (new).

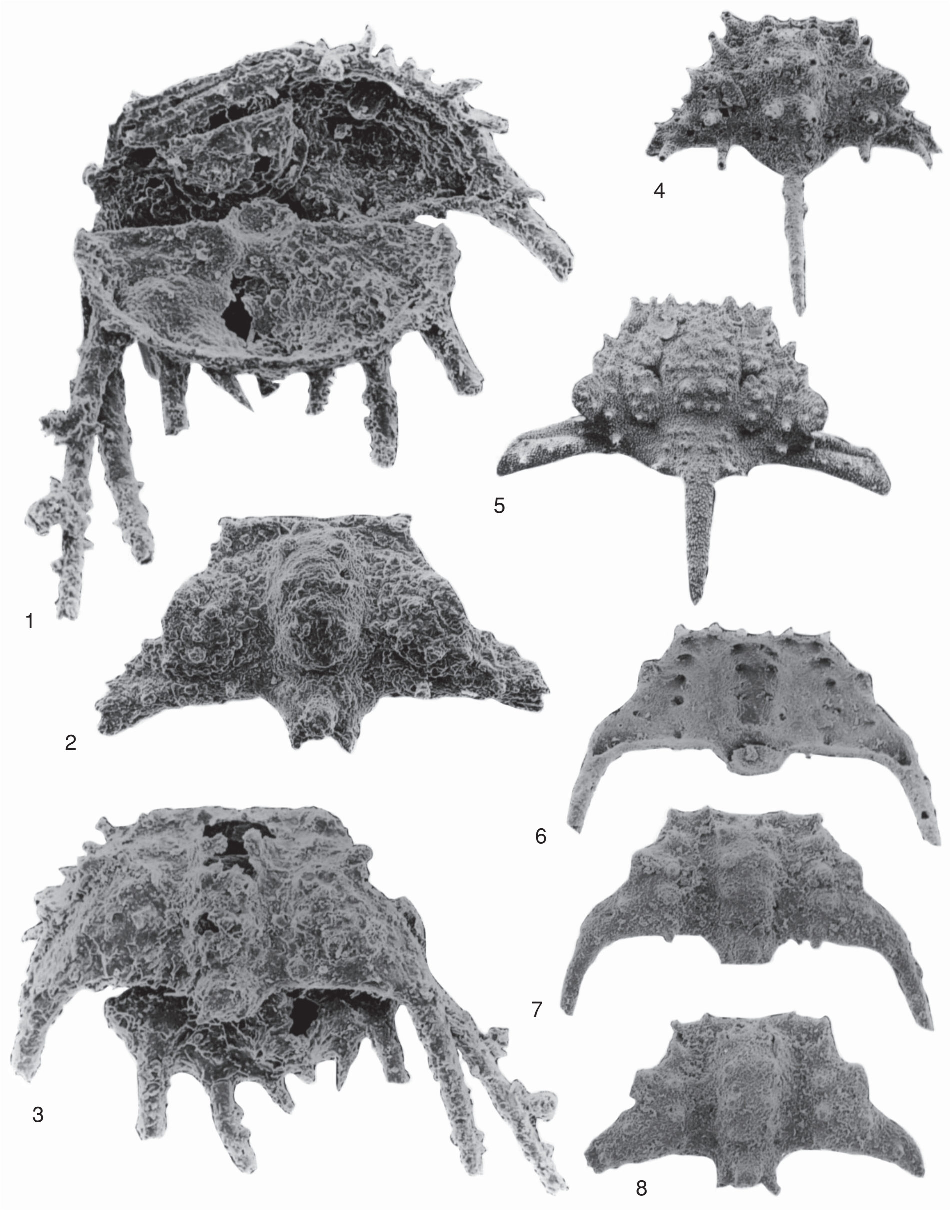


FIG. 186. Odontopleuridae. *1–3,* From the Mackenzie Mountains, early Llandovery, northwestern Canada (locality AV1-95.5); *1,3,* ventral and dorsal views of meraspid degree 0 of *Kettneraspis jaanussoni* CHATTERTON & PERRY, with genal spine on fixigena, not on free cheek, and attached rostral plate and hypostome, UA 8271, ×86; *2,* dorsal view of meraspid cranidium of *K. jaanussoni;* facial suture has migrated inward so genal spine is now on free cheek, UA 8476, ×60 (new). *4–8,* From the Wenlock Delorme Formation of northwestern Canada (locality AV4 126T); *4,5,* dorsal views of cranidia of *K. longstaffei;* in this clade of *Kettneraspis* small cranidia have a large occipital spine and reduced or absent subsidiary occipital spines; *4,* UA 8477, ×32.5; *5,* UA 8478, ×13.9; *6,7,* ventral and dorsal views of small meraspid cranidium of *K. lenzi,* UA 8273, ×45.5; *8,* dorsal view of meraspid cranidium of *K. lenzi.* Note that in *K. lenzi* the facial suture migrates inward to displace the genal spine from the fixed cheek to the free cheek. Also, it is quite clear from the similarities of the small cranidia of *K. jaanussoni* and *K. lenzi* (including prominent pairs of subsidiary occipital spines and a short, knoblike occipital tubercle) that they form part of a clade that is distinct from the clade that includes *K. longstaffei* (and *K. belli* CHATTERTON & PERRY, *K. besti* CHATTERTON & PERRY and *K. boltoni* CHATTERTON & PERRY) and has a prominent, long, sharp occipital spine in small cranidia. The patterns of the other prominent spines or tubercles on the cranidia of both of these clades are essentially the same, UA 8479, ×45.5 (new).