EVOLUTIONARY HISTORY

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The history of the trilobites extends through some 300 million years. There is evidence that trilobites were capable of rapid evolutionary change, and refined zonal schemes of wide geographical application have been based on successions of species, especially in the Cambrian and Ordovician. Where these zones can be compared with those based on other organisms, trilobites appear to have changed relatively rapidly. For example, in the Upper Ordovician (Ashgill) Ingham (1970) recognized as many as eight shelly zones, largely based on trinucleid trilobites, spanning an interval equivalent to perhaps three graptolite zones and extending through approximately 7 to 8 million years. The Upper Cambrian zonation of Scandinavia (Henningsmoen, 1957a) is based on species of olenid trilobites (Fig. 187), and the average duration of these zones may be from one to two million years, depending on which absolute age assessment is accepted for the Cambrian. Given such rapid change over so long a time period, no short summary of trilobite evolutionary history can do justice to its complexity. Some general features of trilobite history are addressed here, together with examples of evolutionary change that can be studied directly from the stratigraphic record. The problems of trilobite phylogenetics are not considered further, and emphasis will be placed on those aspects of trilobite history that do not depend on having a completely resolved phylogenetic classification (Fortey & Owens, 1990a).

CHANGES IN MORPHOLOGY THROUGH TIME: GENERAL FEATURES

Primitive morphology is exemplified either by such Olenellina as *Olenellus* or by Redlichiina, such as *Eoredlichia* and *Redlichia.* Olenellina and Redlichiina share many features that are presumed to be primitive for the Trilobita, the main difference between the groups being the absence of facial sutures in Olenellina. This absence is regarded as primitive by most authors (Fortey & Whittington, 1989), and the presence of facial sutures, unique to trilobites, is considered to be a characteristic of Redlichiina and all higher trilobites, except where they are again secondarily lost.

Most Redlichiina and Olenellina share the following features, which may be taken as an inventory of the primitive condition in the trilobites. They have relatively low dorsoventral convexity and typically the oval exoskeleton is about two-thirds as wide as long. Genal spines are present. The thorax is composed of a large number of spinose segments, of which the third may be macropleural; the articulation was nonfulcrate (Whittington, 1990) and allowed considerable arching of the body, if not complete enrollment. The pygidium is small but appears to be composed of more than one segment. Eyes are long and extend close to the glabella anteriorly; the eye ridge and eye lobe form a continuous structure (the ocular lobe) that may be subdivided by one or more furrows (Pillola, 1991). The visual surface is surrounded by a circumocular suture, so that the eye surface is rarely found in place. Palmer and Halley (1979) have shown that the visual surface may be attached in some early olenellid growth stages, implying that the circumocular suture may not have been functional early in ontogeny. The primitive glabella tapers forward and is relatively long (sag.), with the frontal lobe bosslike or acuminate and three pairs of long (tr.) glabellar furrows that may be transglabellar; the occipital ring is defined. Fortey (1990a) maintained that the primitive hypostomal condition is conterminant (or attached by a pronglike doublural extension in some *Olenellus* species); primitive hypostomes have narrow borders, lack such features as posterior forks, and have small maculae. Olenellina, for which few ontogenies are known, apparently did not have a calcified protaspis; the development of *Redlichia* from protaspis to adult (W. Zhang, Lu, & others, 1980) was gradual without a metamorphosis at any stage.

From this bauplan the range of trilobite morphology was derived by modification of one or more features. These modifications became more extreme and more pervasive after the Cambrian, which is often described as a time when morphology was generally conservative. The changes are not easy to demonstrate quantitatively, but Foote (1991) has succeeded in showing that the range of morphology exhibited by post-Cambrian trilobites increased considerably, as revealed by the complexity of morphological maps of cranidia (Fig. 188). The same is shown by the appearance of more instances of those morphotypes associated with pelagic habits, trilobites with fringes, and other distinctive morphologies. Such changes were pervasive and tended to recur in several unrelated phylogenetic lineages.

CHANGES FROM PRIMITIVE MORPHOLOGY

Important changes from the primitive morphology as exemplified by *Eoredlichia* are summarized in Figures 189 and 190.

SHAPE OF EXOSKELETON

The general form of the exoskeleton may become transverse, i.e., wide in relation to length (*Gastropolus,* some trinucleoids), or elongate (*Opipeuter, Remopleurides*). The transverse shape may be accompanied by reduction in number of thoracic segments and widening (tr.) of the pleurae, while in elongate forms the pleurae may be reduced in width (tr.). A transverse outline is not common, but it is most typical of Trinucleoidea in the Ordovician; its most extreme manifestation is found in the Chinese genera *Taklamakania* and *Pseudampyxina* (W. Zhang, 1980) in which the thoracic segments are reduced to as few as three. Some Cambrian genera were elongate, such as *Bathynotus, Elvinia,* and some paradoxidids and Agnostina, as were many Ordovician genera, especially those associated with pelagic habits (Fortey, 1974a, 1985). The extreme in pleural reduction is attained in the bizarre trilobite *Bohemilla,* which was excluded from the class Trilobita in the last edition of the *Treatise* (Whittard in Moore, 1959), not least because it apparently lacked pleurae completely. Early bohemillids, however, retain remnants of the pleurae, and their trilobite affinity is no longer in dispute. Very elongate trilobites are uncommon after the Ordovician, which may reflect the loss of pelagic habits. The nearest proportions to those of the Ordovician forms are probably to be found in such cheirurids as *Crotalocephalus,* but in this case the long, narrow appearance is in part attributable to steep downturning of the thoracic pleurae. The vast majority of post-Ordovician trilobites have an elongate-elliptical outline not greatly different from that of a typical early trilobite.

CONVEXITY

Convexity is highly variable in trilobites. Some species, especially illaenids (Owen & Bruton, 1980) and such Upper Cambrian genera as *Plethometopus* (Stitt, 1975), are both effaced and with the cephalic shield especially convex in the sagittal direction. Such convexity may be associated with the bumastoid stance (Westrop, 1983), in which the trilobite is supposed to have burrowed backwards into the sediment, leaving only the convex cephalic shield projecting, the eyes being horizontal in this attitude. Other convex trilobites are greatly vaulted across the thorax but not especially so across the cephalon and may be generally smoother; this is particularly characteristic of Homalonotidae (Ordovician to Devonian). Hammann (1983) argued that this morphology is consistent with a burrowing habit. In many trilobite families all or part of the glabella becomes particularly convex and expanded (especially in Phacopida, Cheiruridae, Cybelinae), and this may have been associated with an expansion of the foregut be-

ZONES	SUBZONES
Acerocare	*Acerocare ecorne* *Westergaardia spp.* *Peltura costata* *Peltura transiens*
Peltura scarabaeoides	*Peltura paradoxa* *Parabolina lobata* *Ctenopyge linnarssoni* *Ctenopyge bisulcata*
Peltura minor	*Ctenopyge affinis* *Ctenopyge tumida* *Ctenopyge spectabilis* *Ctenopyge similis*
Protopeltura praecursor	*Ctenopyge flagellifera* *Ctenopyge postcurrens* *Leptoplastus neglectus*
Leptoplastus	*Leptoplastus stenotus* *Leptoplastus angostatus* *Leptoplastus crassicorne* *Leptoplastus raphidophorus* *Leptoplastus poucisegmentatus*
Parabolina spinulosa	*Parabolina spinulosa* *Parabolina brevispina*
Olenus with Homagnostus obesus	*Olenus scanicus* *Olenus dentatus* *Olenus attenuatus* *Olenus wahlenbergi* *Olenus truncatus* *Olenus gibbosus*

Fig. 187. Biozones in the Upper Cambrian of Scandinavia, based on olenid trilobites, showing fine stratigraphical subdivision (adapted from Henningsmoen, 1957a).

neath it (Eldredge, 1971). Most trilobite families display a range of convexity, and it is not a character of taxonomic importance above the generic level. Even within the Lower Cambrian a few convex genera are known (*Giordanella, Bonnia,* and some earlier eodiscoids), and dorsoventrally flattened and convex trilobites coexisted in most later trilobite faunas.

INCREASED SIZE OF PYGIDIUM

A large pygidium is believed to be an advanced character. In trilobites other than Agnostida the size of the pygidium increases on average through the Cambrian to the Ordovician but not greatly thereafter (Fig. 191). Pygidial size is easily modified via heterochronic change (see previous section on ontogeny, p. 173), and increased caudalization is not, perhaps, a character of great importance. This is shown by the fact that pygidial size may vary widely within a single family. In Olenidae the pygidium may be small to almost isopygous. Moreover, if Naraoiidae is the sister group of other trilobites, the pygidium of naraoiids has already attained its largest possible size. By the end of the Early Cambrian, isopygous trilobites had appeared in several groups (Agnostida as well as gigantopygids and yinitids in

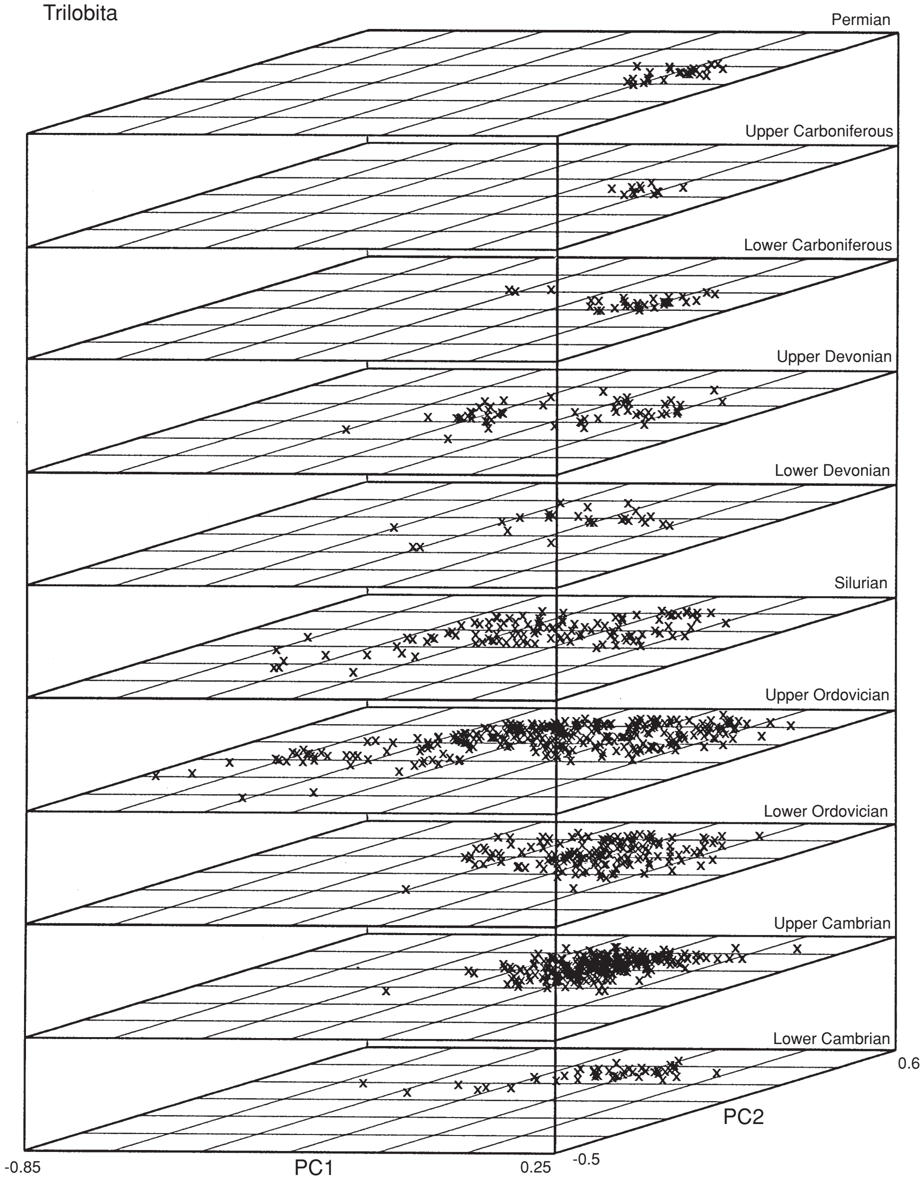

FIG. 188. Post-Cambrian trilobites occupied greater morphospace than Cambrian trilobites, as shown by morphological maps of the first two principal components (PC1 and PC2) (adapted from Foote, 1991, fig. 2).

Redlichiina), and such forms lived alongside species with smaller pygidia. This applies throughout the remainder of the history of Trilobita, although by the Devonian and later periods, elements in the fauna with small pygidia (e.g., *Aulacopleura*) were less numerous. In any case, there is no suggestion that small pygidia were heavily selected against, because the shift from generally small to generally large pygidia takes place over almost 200 million years. Species with large pygidia tend to be enrolled tightly (BERGSTRÖM, 1973a) because of the coaptation of cephalic and pygidial margins. A few

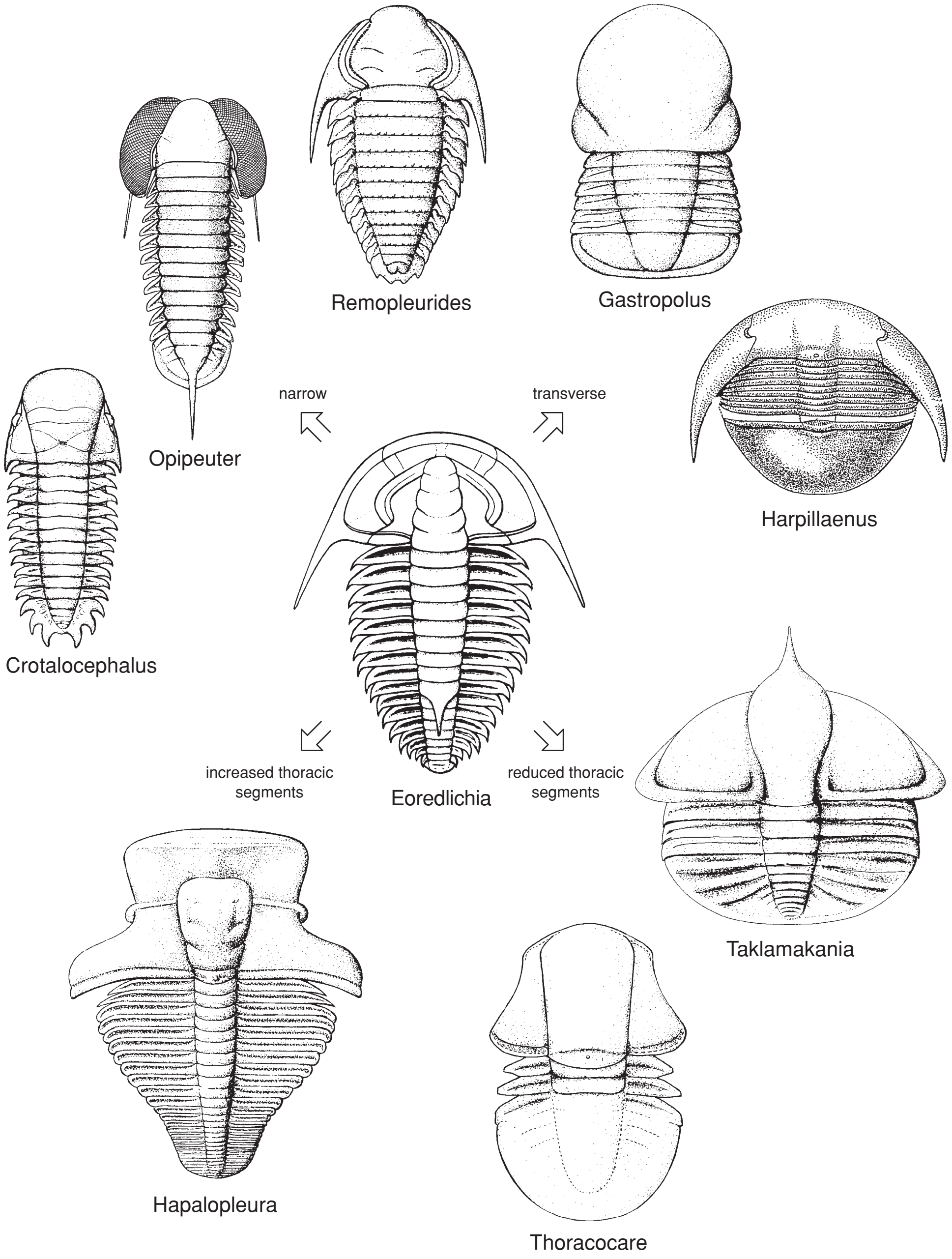

FIG. 189. Changes through time in the trilobite exoskeleton, compared with the generalized and primitive morphology exemplified by *Eoredlichia* (new).

examples are known in which a reversal to a small pygidium has taken place. Primitive remopleuridoids had large pygidia (*Apatokephalus*) with at least four segments, whereas a more derived genus (*Remopleurides*) has a minute pygidium—usually with two segments. The remopleuridid *Hypodicranotus* from the middle to the upper part of the Ordovician may have but a single segment in the pygidium (LUDVIGSEN & CHATTERTON,

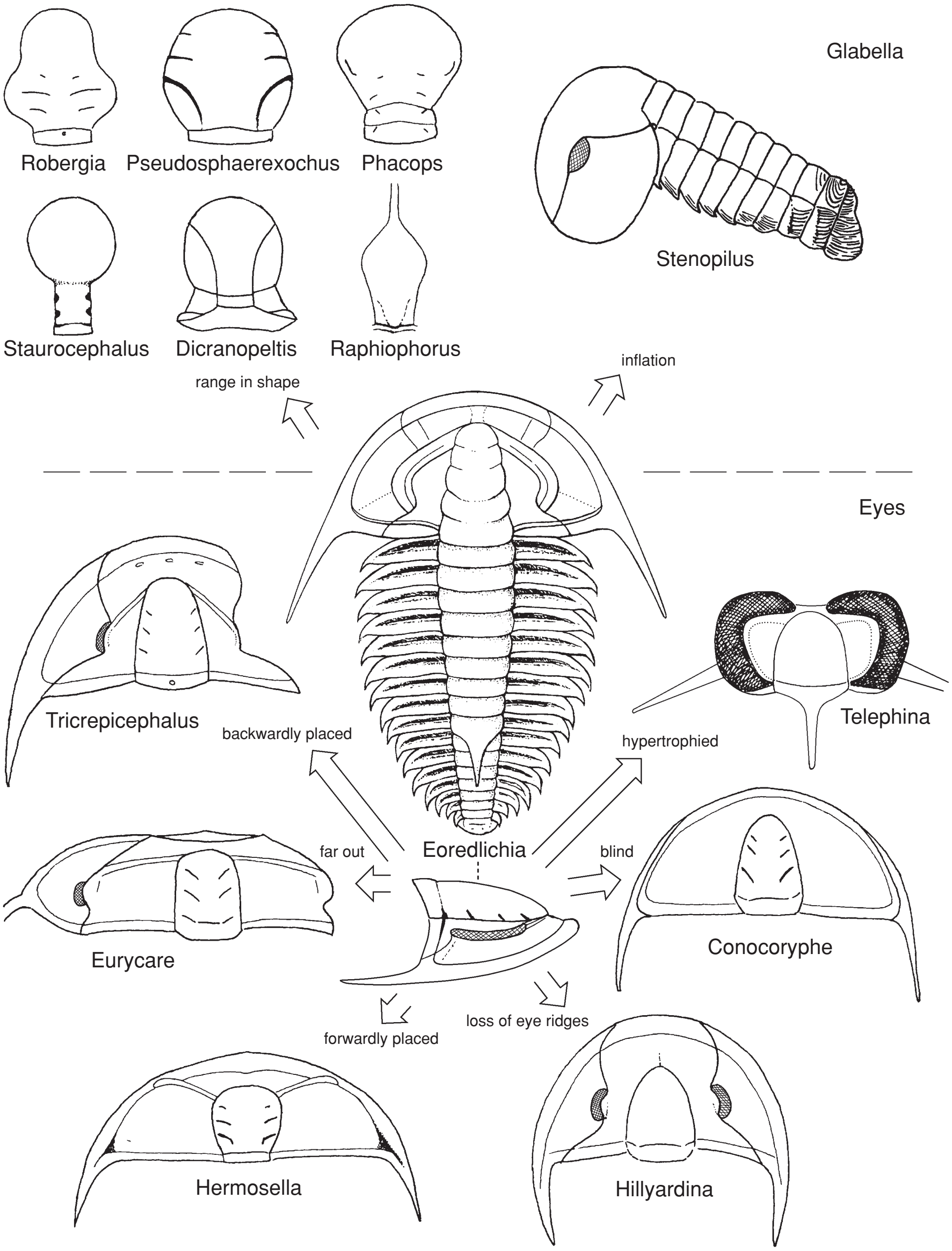

FIG. 190. Changes through time in glabella and eye morphology and position compared with the generalized and primitive morphology exemplified by *Eoredlichia* (new).

1991). It seems likely that a similar reversal has taken place in the Ordovician family Celmidae (*Celmus*), which has an extraordinarily small pygidium (BRUTON, 1983), because the families to which it may be related all have pygidia of normal proportional size. LANE (1971) has recognized a trend toward reduction in the number of pygidial segments in cheirurid lineages from the Ordovician and Silurian. However, where the pygidium and cephalic margin attained close peripheral contact in enrollment, as in asaphids and Agnostida, there was little change in pygidial size thereafter. Changes in style of enrollment were accompanied by changes in the pleural articulating facets, which are summarized in Figure 192.

LOSS OF GENAL SPINES

Genal spines were lost repeatedly. In many families the presence or absence of genal spines is of significance only at the generic level, and in some families (e.g., Olenidae) there are genera that span the range between having very long (*Olenus*), short (*Leptoplastus*), or no (*Jujuyaspis*) genal spines (Fig. 193). Short genal spines may be present in small growth stages even when absent in adults (Calymenidae, Nileidae). Nonetheless, some families typically lack genal spines—for example, Calymenidae, Cyclopygidae, Phacopidae, and Illaenidae. Presumably, exceptions (e.g., the illaenid *Thaleops*) may consititute a reversal: the reappearance of the genal spine may be paedomorphic. This has been demonstrated in the nileid *Peraspis* (Fortey, 1975b). Other families never lost their genal spines; for example, we know of no spineless member of the superfamily Trinucleoidea. In this superfamily the genal spines are presumed to play an obligatory part in the functional morphology, and all trinucleoids have a short body, which the genal spines greatly exceed in length. Normally, genal spines may have assisted in molting, added protective armory (especially in the enrolled condition when the spines increase the diameter of the animal), and prevented yawing as the trilobite sank through the water column (cf. Fisher, 1975). It is likely that several of these functions were combined. The readiness with which spines were lost in many families, however, shows that these functions could be suspended. A common tendency was for genal spines to become advanced, to originate far forwards on the cephalon. This happens early in Lower Cambrian Olenellina and Redlichiina and later in such families as Olenidae (Upper Cambrian species), Remopleurididae (Ordovician), and Telephinidae (Ordovician).

EYES

The eyes of all early trilobites are circumscribed by ocular sutures. The earliest example with the eye surface attached is a meraspid olenellid figured by Palmer and Halley (1979), but so far as we know the adults had a circumocular suture. By contrast, nearly all post-Cambrian trilobites had the visual surface attached to the free cheek. It is virtually certain that the circumocular suture was lost polyphyletically, having disappeared in parallel in several lineages (in Asaphida, in Olenina, and in Phacopida). After the Ordovician, the Calymenidae were alone in retaining the primitive condition. It is curious that loss of this suture happens in several clades within a short interval of time from the Late Cambrian to the Early Ordovician.

Clarkson has discussed evolution of the eye in an earlier section. It was primitively large, close to the glabella anteriorly, and probably had a striplike profile. Even in some Early Cambrian species the eye had moved away from the glabella (*Metadoxides;* see Pillola, 1991) to take up a position midway across the cheek; this position is highly characteristic of plesiomorphic ptychoparioids and, indeed, of most Middle to Late Cambrian trilobites. In such forms the eye ridge remains prominent and runs inwards to a homologous point near the anterolateral corner of the glabella. In many later, Ordovician to Devonian trilobites the eye ridge is effaced, but in some groups (Odontopleurida and some Aulacopleuridae) it remains distinct, even in species with stalked eyes. Species in which the eye is so far forward that the eye ridge runs inwards and backwards are very rare but occur in the Hapalopleuridae (*Jegorovaia*) and Olenidae (*Remizites*). Hypertrophied eyes and blindness are discussed below as typical evolutionary trends. Eye size

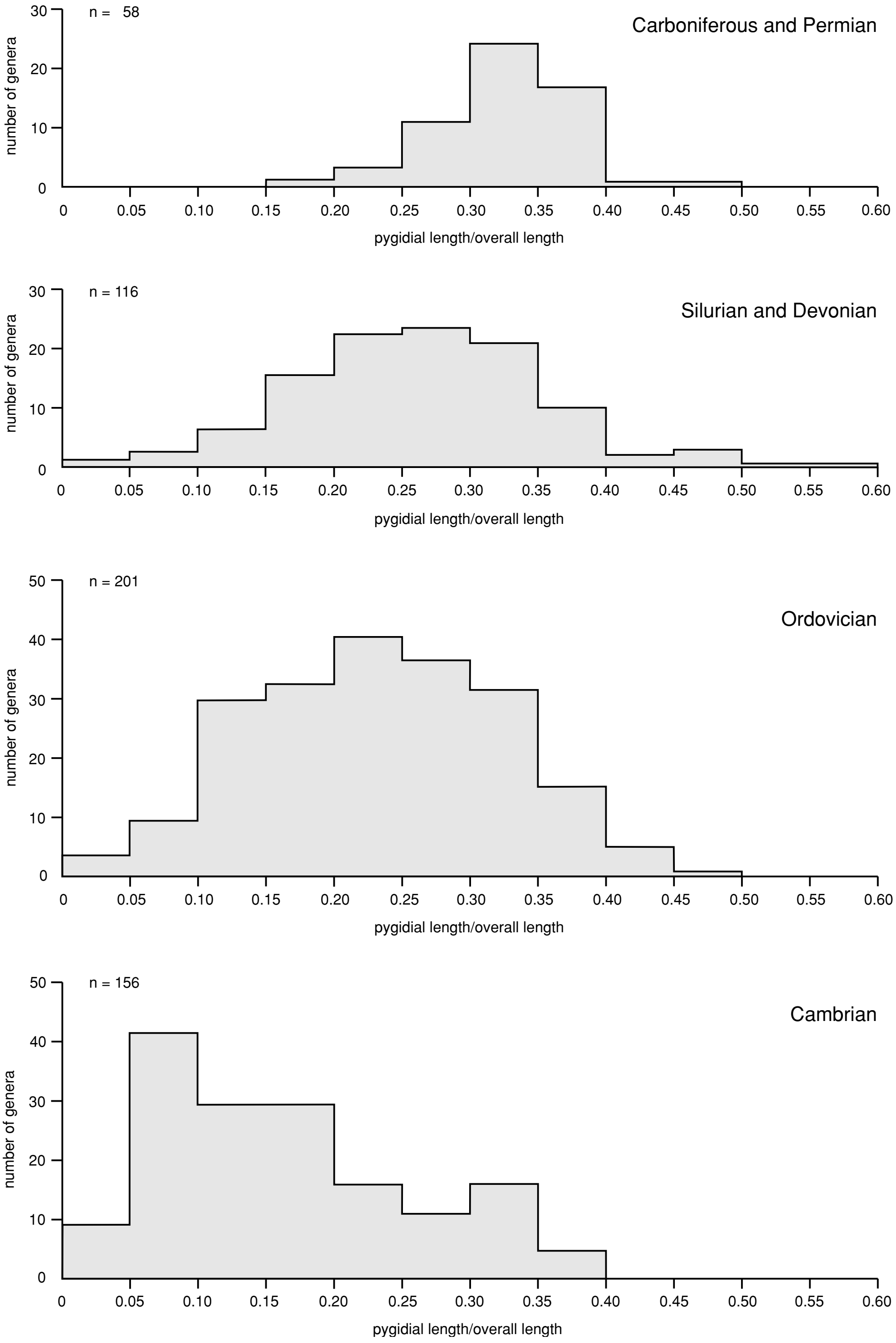

FIG. 191. General increase in the size of the pygidium through time in trilobites other than Agnostida as shown by the proportion of the total exoskeletal length occupied by the pygidium, measured from entire exoskeletons (new).

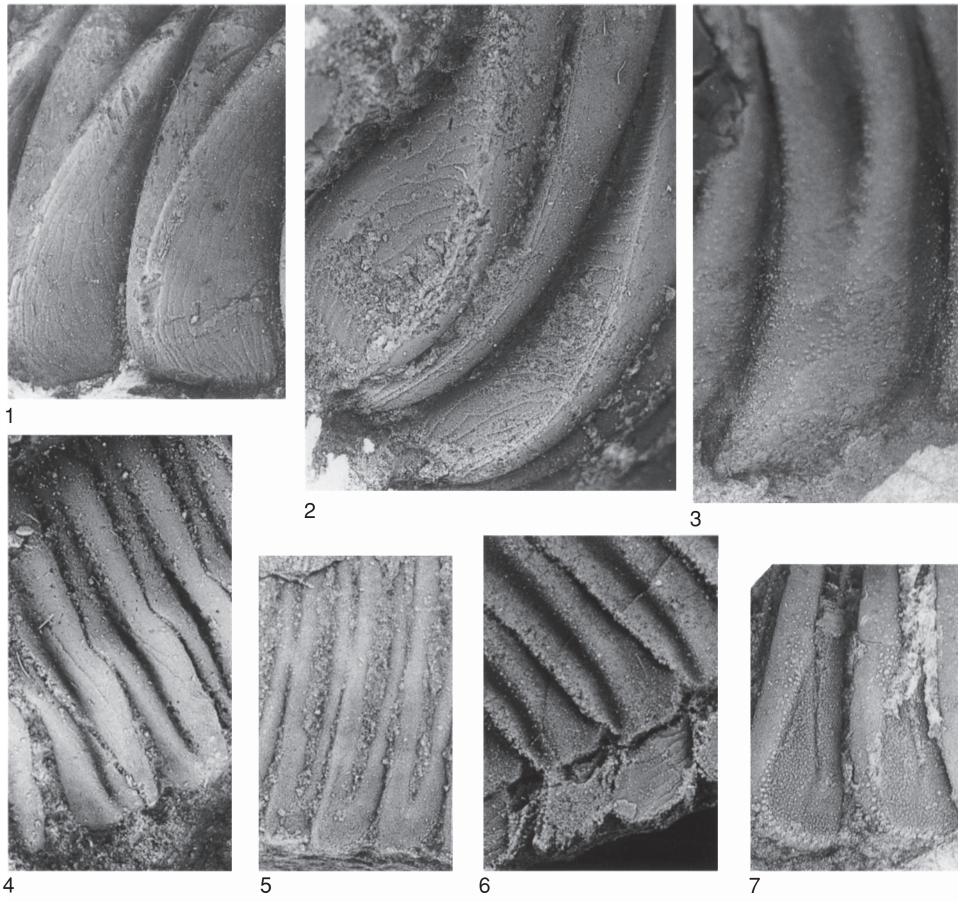

FIG. 192. Advanced and primitive types of articulating facets. *1,* Asaphid, *Asaphus* sp., BM 15430, Middle Ordovician, Russia, ×8. *2,* Nileid, *Symphysurus palpebrosus,* BM It20684, Middle Ordovician, Sweden, ×8. *3,* Granulose dalmanitoid facet, *Dalmanites caudatus,* BM 167a, Silurian, with postfacetal type of pleural furrow, ×8. *4,* Primitive type, smooth, in the Silurian aulacopleuroid *Otarion diffractum,* BM I3603, ×12. *5,6,* Primitive type in the Middle Cambrian ptychopariid *Elrathia; 5,* BM It5396, dorsal surface, ×12; *6,* BM It5397, narrow doublure with terrace ridges primitive for Asaphina, ×15. *7,* Granulose calymenoid facet, with epifacetal type of pleural furrow, *Calymene* sp., BM It20685, Upper Ordovician, Anticosti Island, ×10 (Fortey & Chatterton, 1988, fig. 13).

is a variable character of trilobites but has been rather widely used in generic diagnoses. Position of the eye in relation to the glabella is constant in many clades; interestingly, after the Late Cambrian there was a reversion to having eyes close to the glabella in several groups, including Proetidae, most Asaphidae, Remopleurididae, and Phacopidae. In several respects remopleuridids look like Olenellina (for example, in the long, curved eye lobe and small pygidium), but we know from phylogenetic analysis that this resemblance is a product of convergence. At the Permian end of their history, the trilobites had their eyes as close to the glabella as they did at the beginning but with the important difference that these stratigraphically youngest trilobites completely lacked the palpebral furrows and eye ridges of their predecessors.

GLABELLAR FORM

The glabella is one of the most variable of trilobite features and has rightly assumed great importance in taxonomy. Here we only

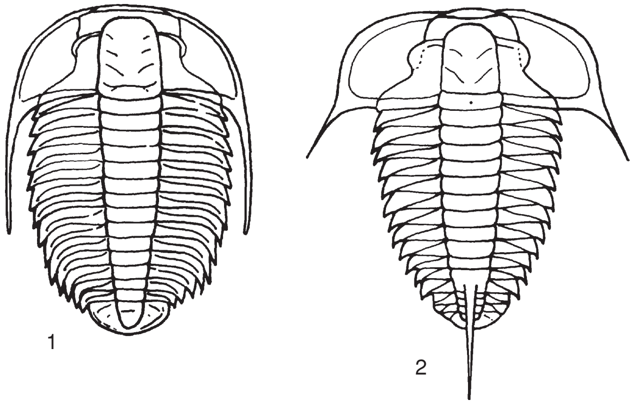

FIG. 193. Loss of genal spines within the monophyletic family Olenidae. *1, Olenus micrurus* SALTER (new); *2, Leptoplastus stenotus* ANGELIN (Henningsmoen, 1957a, pl. 2, fig. 16); *3, Jujuyaspis keideli* KOBAYASHI (Henningsmoen, 1957a, pl. 2, fig. 17).

note some broad evolutionary features. The elongate shape found in Olenellina and the more generalized Redlichiina is probably primitive and is found also in the early Eodiscina. The Agnostina soon acquired glabellar peculiarities of their own, which have led some workers to propose a separate nomenclature for furrows and other cephalic features of these trilobites (Fig. 6). Although inflation of any glabellar lobe can occur, it is perhaps commonest in the frontal lobe and is already displayed by some Early Cambrian Olenellina (*Wanneria*); in Middle Cambrian paradoxidids; in many such Ordovician families as Encrinuridae (*Oedicybele*), Bathyuridae (*Bathyurus*), Dalmanitidae as a whole, and trinucleids; and in the Silurian-Devonian Phacopida and Cheiruridae. After the demise of these groups, phillipsiids acquired similar anterior glabellar inflation in the Permo-Carboniferous. Inflation of the basal glabellar lobe occurred particularly in Ordovician-Silurian Calymenidae. One can find examples where the second glabellar lobe has become particularly inflated (*Chasmops*) or perhaps uncommonly the third lobe (certain Cybelinae). The whole glabella may be inflated in the manner of *Sphaerexochus.* No convincing functional explanation of such inflation has been advanced. A common glabellar modification is the effacement of glabellar furrows, which proceeds to completion in many families from the Lower Cambrian onwards (Agraulidae, Illaenuridae, Illaenidae, Plethopeltidae). In general, the occipital furrow and 1S are last to become effaced (see *Bollandia*), compared with the more anterior furrows. The question of effacement is considered in more detail below.

The extent to which the glabella of so-called advanced trilobites might incorporate genal material is the subject of some controversy. The ontogeny of several trilobites (Encrinuridae, see EVITT & TRIPP, 1977; Raphiophoridae, *Endymionia,* see WHITTINGTON, 1965) shows that inflated bullar lobes appear in the axial furrows of very small growth stages, and these get larger during subsequent growth stages, growing into the axial region as they do so. In adulthood such lobes would traditionally have been regarded as glabellar—strictly speaking such a glabella would not be homologous with those of other trilobites, because it would incorporate nonaxial material. It is not always clear, however, whether some specialized glabellas include extra-axial material. The curious lateral lobes of lichids (THOMAS & HOLLOWAY, 1988) can be interpreted in several ways—as wholly glabellar, wholly extraglabellar, or partly either. It is clear, however, that lateral glabellar lobes similar to the bulba have been produced several times in post-Cambrian trilobite history, in several distinctive clades (Monorakidae, Lichidae, Trinucleoidea, Encrinuridae). Bacculae adjacent to the base of the glabella may also have been incorporated into the axial lobe (*Carolinites*, see FORTEY, 1975b). It is probable that all these glabellar modifications were connected with the insertion of musculature for operation of cephalic limbs and, hence, were of fundamental importance for the life of the trilobite. However, trilobites for which limbs are known do not include species with modified glabellar structure, so one cannot say whether peculiar glabellas accompany peculiar cephalic limbs. The only exception may be *Cryptolithus,* which BERGSTRÖM (1972) claimed had appendages that differed from those of other trilobites.

ENROLLMENT

Articulation of the thorax and enrollment have been described in preceding sections. Trilobites having nonfulcrate articulation need further investigation, but this primitive form appears to be known only in Olenellina, some Redlichiina, and rarely in other Cambrian taxa. Nonfulcrate articulation may have allowed complete enrollment but only of the cylindrical type with a lateral gap. Complete enrollment to form a closed exoskeletal capsule characterized Agnostida, is known in the Lower Cambrian *Crassifimbra* (PALMER, 1958) and ellipsocephalids (e.g., WESTERGÅRD, 1936, pl. 11, fig. 9), and may well have become more general among Upper Cambrian trilobites; it is the dominant form of enrollment in the post-Cambrian periods. Presumably enrollment protected trilobites from predation and from sudden changes in the environment. It is now known (BRIGGS, 1994) that large predators capable of inflicting injury on trilobites were present in the Lower and Middle Cambrian. After the Cambrian more varied and swiftly moving predators (cephalopods and, later, fish) may have increased predation pressure and led to the dominance of the closed capsule and the proliferation of coaptative devices (see previous discussion of the evolution of such devices, p. 67). Pleural facets in post-Cambrian trilobites (FORTEY & CHATTERTON, 1988, fig. 13; CHATTERTON & CAMPBELL, 1993, fig. 1d, 1h, 2f, 3g–h) were in some groups large and bore sculpture.

CEPHALIC SUTURES

The opisthoparian facial suture of the Redlichiina is assumed to be primitive, and it is retained by most trilobites. The proparian pattern was derived in the Early Cambrian (Eodiscina), Middle Cambrian (*Schmalenseeia*), Late Cambrian (Norwoodiidae, Loganopeltidae), and Early Ordovician (Olenidae, Phacopida) in what are now known to be independent evolutionary lines. Because a proparian stage is present in early ontogenies of all or nearly all opisthoparian trilobites, the appearance of this feature in a range of adults has been explained as an instance of heterochrony. This appears to be a one-way process, because although opisthoparian sister groups are known or likely for proparian forms (e.g., within Pelturinae in Olenidae, see HENNINGSMOEN, 1957a), we know of no example where a proparian ancestor has been claimed for an opisthoparian trilobite. This implies that once paedomorphosis (broadly interpreted, see MCNAMARA, 1982) has happened it was not possible to revert to the ancestral condition, the later (opisthoparian) phases having been permanently lost from the development program.

On the cephalic doublure, the rostral plate might be interpreted as showing a general tendency towards reduction (Fig. 194): it decreases in width (tr.) through the major trilobite phylogenetic sequence shown by FORTEY (1990a, fig. 14). It comprises the bulk of the venter in Olenellina; in Redlichiina it is frequently still wider than the glabella, but the doublure of the free cheek occupies the rest of the cephalic doublure. In most Ptychopariina it is narrower still, being of the same width (tr.) or less than that of the glabella. The complete loss of the rostral plate followed; the earliest examples are

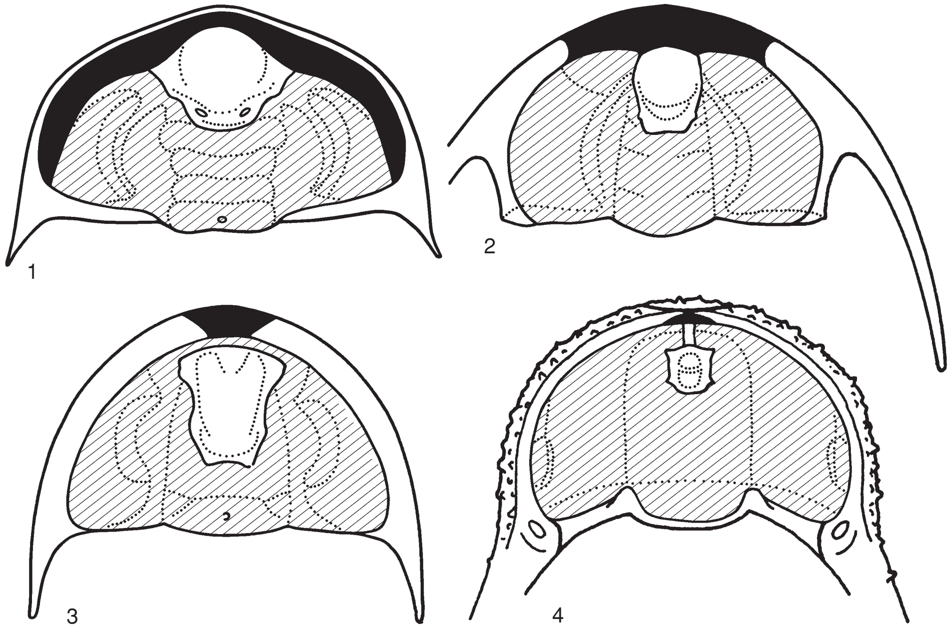

FIG. 194. Reduction in transverse width of the rostral plate (shown by blackened area), as seen in ventral views of *1, Kjerulfia, 2, Redlichia, 3, Proetus,* and *4, Dimeropyge* (*1, 4,* adapted from Moore, 1959, fig. 48b,f; *2,3,* new).

probably Middle Cambrian Anomocaroidea with a median suture (FORTEY & CHATTERTON, 1988). Yoked cheeks, in which ventral sutures have ankylosed, are known in early Late Cambrian Olenidae (*Olenus,* see HENNINGSMOEN, 1957a, fig. 12) and arose independently in numerous later and phylogenetically unrelated families such as Kainellidae, Nileidae, Trinucleidae, Phacopidae, and Shumardiidae.

Most types of ventral sutures, however, persisted side by side after the Middle Cambrian to the end of the Ordovician, when all forms with a median suture became extinct. Wide rostral plates are typical of the Illaenidae, for example, while narrower rostral plates persisted in some Bathyuridae, Odontopleuridae, and Proetidae. The evidence is that the rostral plate was a persistent structure even when it became exceedingly narrow, as it did in Encrinuridae (TRIPP, 1962) and Dimeropgyidae (WHITTINGTON, 1963). On this basis FORTEY and CHATTERTON (1988) believed that its reduction to a median suture was likely to be a character of major phylogenetic importance. However, fusion or ankylosis of the sutures appears to have happened more readily; for example, fused cheeks are known in some examples of large asaphids where median sutures are present in smaller individuals of the same species (*Isotelus*). Fused cheeks derived from loss of the median suture look identical to those derived from ankylosis of the connective sutures, and phylogenetic analysis is needed to reveal the history. We believe that the Olenidae, Shumardiidae, and Phacopidae were derived from ancestors having rostral plates, whereas Nileidae, Kainellidae, Cyclopygidae, and probably Trinucleoidea were derived from ancestors having a median suture.

HYPOSTOMAL ATTACHMENT

Different modes of attachment of the hypostome remain constant through whole trilobite clades: Odontopleurida and Lichida are always conterminant, Ptychopariina natant, and Phacopidae impendent, for example. However, it is clear that there is an evolutionary sequence in some trilobites from natant to conterminant to impendent. This is because advanced members of well-established clades have attached hypostomes, and primitive ones have natant hypostomes. Particularly good examples are known from the Remopleuridoidea and Proetida (Fig. 195). Furthermore, trilobites having impendent hypostomes were more advanced than those with conterminant hypostomes. There is no known instance of trilobites with such secondarily attached hypostomes having given rise to trilobites with natant hypostomes. Trilobites with the natant hypostomal condition correspond broadly with Ptychopariida in the sense of the 1959 *Treatise* (MOORE, 1959).

It is known that Redlichiina had conterminant hypostomes (W. ZHANG, LU, & others, 1980, pl. 20, fig. 9), and if it is assumed that this represents the primitive trilobite morphology, it is then apparent that the Ptychopariina (having a natant hypostome) were themselves a derived group. The derivation of the detached, natant hypostome can be traced to the upper Lower Cambrian, where some protolenids were undoubtedly natant but which otherwise retained many of the primitive characters of the Redlichiina. Hence, the conterminant hypostomal condition can be either primitive (primary conterminant condition) or secondarily derived from a natant condition. Primary conterminant trilobites include such important Cambrian groups as the Corynexochida and probably the Lichida, Odontopleurida, and Illaenina. Secondarily conterminant trilobites appear in the geological record after the appearance of the natant condition, as would be expected. The earliest secondary attachment of the hypostome to the doublure is probably the ceratopygid *Proceratopyge* in the upper Middle Cambrian (RUSHTON, 1983). In Proetida all known early species from the Ordovician were natant, and the conterminant and impendent forms only became prevalent in the later (Carboniferous to Permian) history of the group, after all other conterminent and impendent trilobites belonging to other trilobite orders had died out. Clearly, the hypostomal attachment condition closely reflected the feeding mode of the trilobite, and such Proetida were presumably filling niches that were previously occupied by styginid (conterminant) or phacopoid (impendent) trilobites.

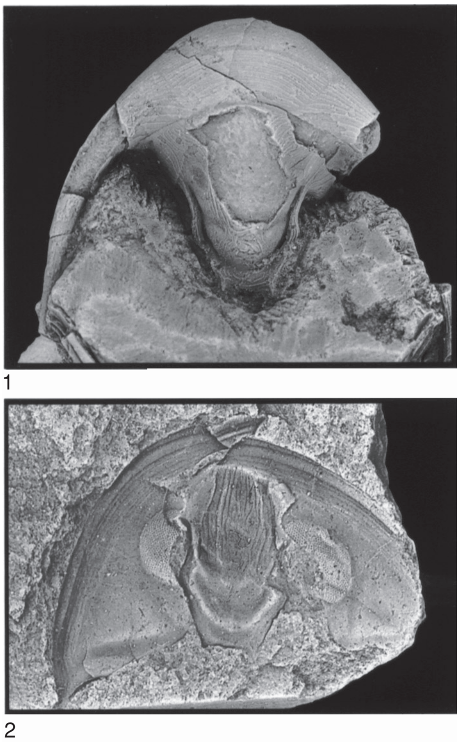

FIG. 195. Examples of secondary attachment of the hypostome in Carboniferous (Dinantian) Proetida. Primitive sister groups of these trilobites all had natant hypostomes, and the attachment of hypostome to doublure is secondary. *1,* Impendent condition in *Griffithides acanthiceps* WOODWARD, from Derbyshire, England (NMW 86.25G.2332), ×5. *2,* Secondary conterminant condition in *Archegonus (Phillibole)* sp. aff. *A. (P.) aprathensis* (RICHTER & RICHTER) from Lancashire, England (NMW 88.36G.10), ×3 (Fortey, 1990a, fig. 5b,c).

The sequence of events is illustrated in Figure 196. The paraphyletic redlichiids gave rise both to derived groups of trilobites with primary conterminant hyopstomal attachment (Corynexochida, Lichida, etc.) and to the first natant forms. The latter speciated

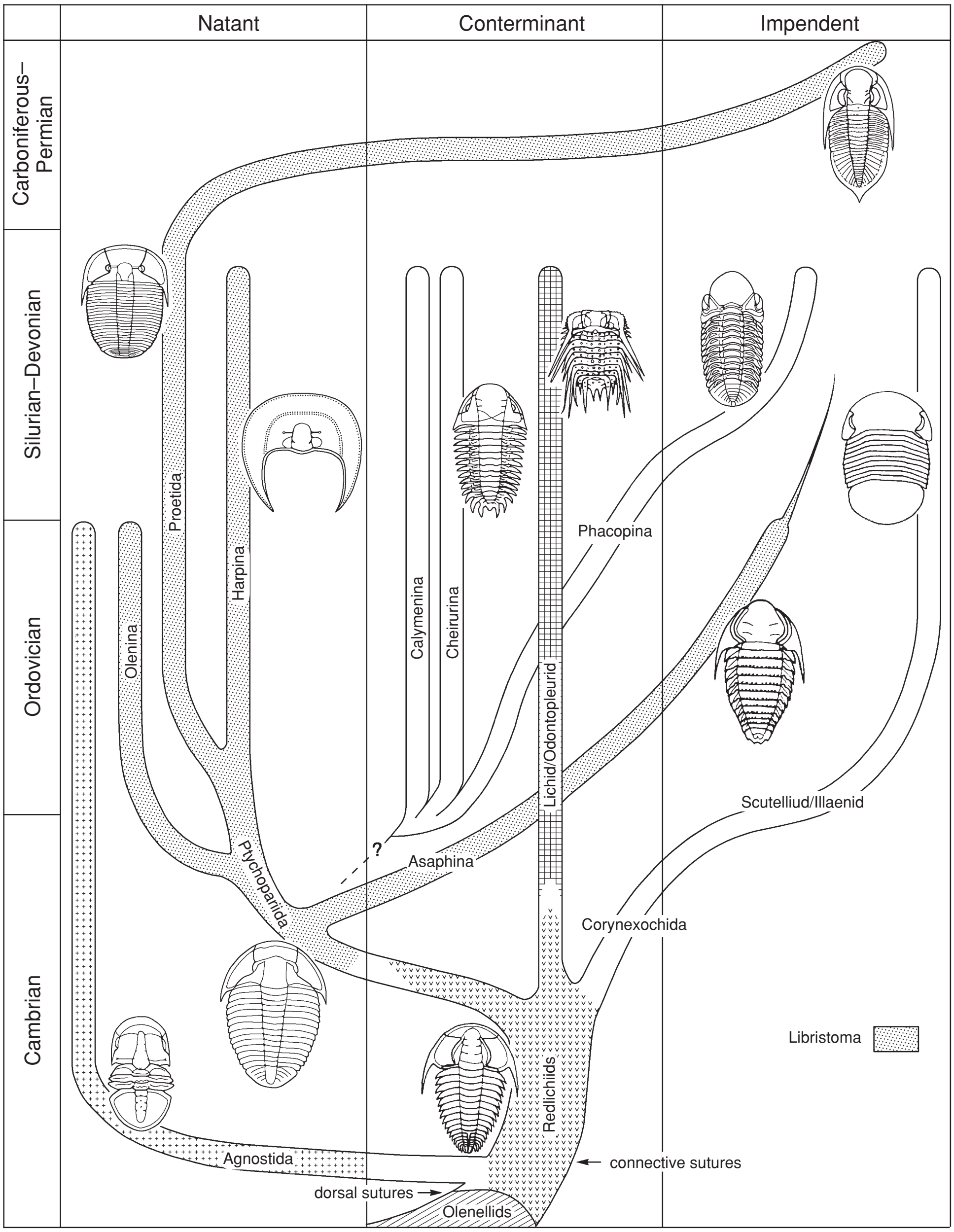

FIG. 196. Summary of the history of hypostomal attachment and the phylogeny of the Trilobita (adapted from Fortey, 1990a, fig. 19).

rapidly in the Middle to Late Cambrian, but quite soon secondary attachment of the hypostome occurred in some groups, so that by the Ordovician primary conterminant, natant, and secondary conterminant trilobites lived side by side. Impendent trilobites became common at this time. Some of the secondarily conterminant families of Asaphina became extinct at the end of the Ordovician. Later, some of the groups of

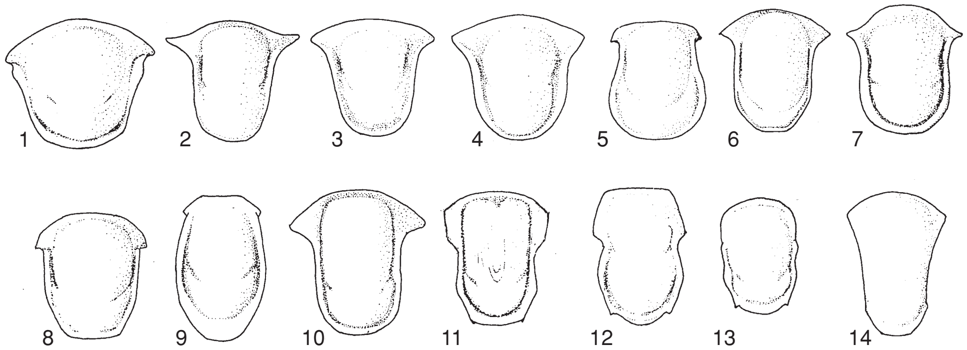

Fig. 197. Lack of morphological change through time in natant hypostomes; examples from several families ranging in age from Lower Cambrian (*2*) to Carboniferous (*14*). *1, Drepanopyge* (Yinitidae), Lower Cambrian, a primitive example of an attached hypostome, showing that this early morphology is retained in natant forms, ×2; *2, Crassifimbra* (Ptychopariidae), Lower Cambrian, ×10; *3, Conocoryphe* (Conocoryphidae), Middle Cambrian, ×4; *4, Ptychoparia striata* (Ptychopariidae), Middle Cambrian, ×2.5; *5, Dunderbergia* (Alokistocaridae), Upper Cambrian, ×10; *6, Aphelaspis* (regarded as Pterocephaliidae), Upper Cambrian, ×5; *7,* a hystricurid, Lower Ordovician, ×9; *8, Parabolinella* (Olenidae), Lower Ordovician, ×4; *9, Bathyurellus* (Bathyuridae), Lower Ordovician, ×3; *10, Paraproetus* (Proetidae), Upper Ordovician, ×7; *11, Proetus* (Proetidae), Silurian, ×4; *12, Koneprusites* (Proetidae), Devonian, ×6; *13, Voigtaspis* (Proetidae), Devonian, ×3; *14, Gitarra* (Phillipsiidae), Carboniferous, ×3 (Fortey, 1990a, fig. 11).

Proetida became secondarily conterminant, and following the Late Devonian extinctions, this group alone was the source of all modes of hypostomal attachment.

HYPOSTOMAL SPECIALIZATION

This specialization is connected with hypostomal attachment because all the known specialized hypostomal forms are associated with the conterminant or impendent condition. Natant hypostomes are remarkably similar in the many different groups in which they occur, from the Lower Cambrian to the Carboniferous (Fig. 197). They are also similar to many hypostomes of Redlichiina, characteristic features being an elongate middle body with short middle furrows, narrow borders, and the lack of prominent forks, distinctive maculae, coarse sculpture, or other specializations like the rhynchos. Hypostomes attached to the doublure were usually rigidly braced (Whittington, 1988a, 1988b). Regardless of whether they were primarily or secondarily attached, modifications of the Redlichiina bauplan follow a number of directions. Appearance of posterior forks is doubtless polyphyletic, being known from asaphids, lichids, calymenids, remopleuridids, and late Proetida. The deepest known forks are in the remopleuridid *Hypodicranotus* and the asaphid *Lycophron.* Hypostomes that are wider (tr.) than long are uncommon; the widest known is that of the cyclopygid *Degamella,* but hypostomes of some nileids (*Nileus*) and *Remopleurides* are also wide (tr.). In Nileidae much of this width is accounted for by wide lateral borders, and wide borders occur also in the hypostomes of several other families, especially Dameselloidea, Asaphidae, and Lichida. The macula is found principally upon attached hypostomes (Fig. 198). Many rigidly attached hypostomes developed a strong surface sculpture on the middle body. In some Asaphidae, Nileidae, and Illaenidae, strong terrace ridges run continuously from the cephalic doublure to the hypostome, and it is clear that together the two comprise a single functional unit. This may be the best known instance in which terrace ridge systems had a sediment-gripping function (see Schmalfuss, 1981). Other hypostomes may be granulose (invariably so in Cheiruroidea, and in most Phacopina and Odontopleurida) or even coarsely tuberculate. The inner edge of the

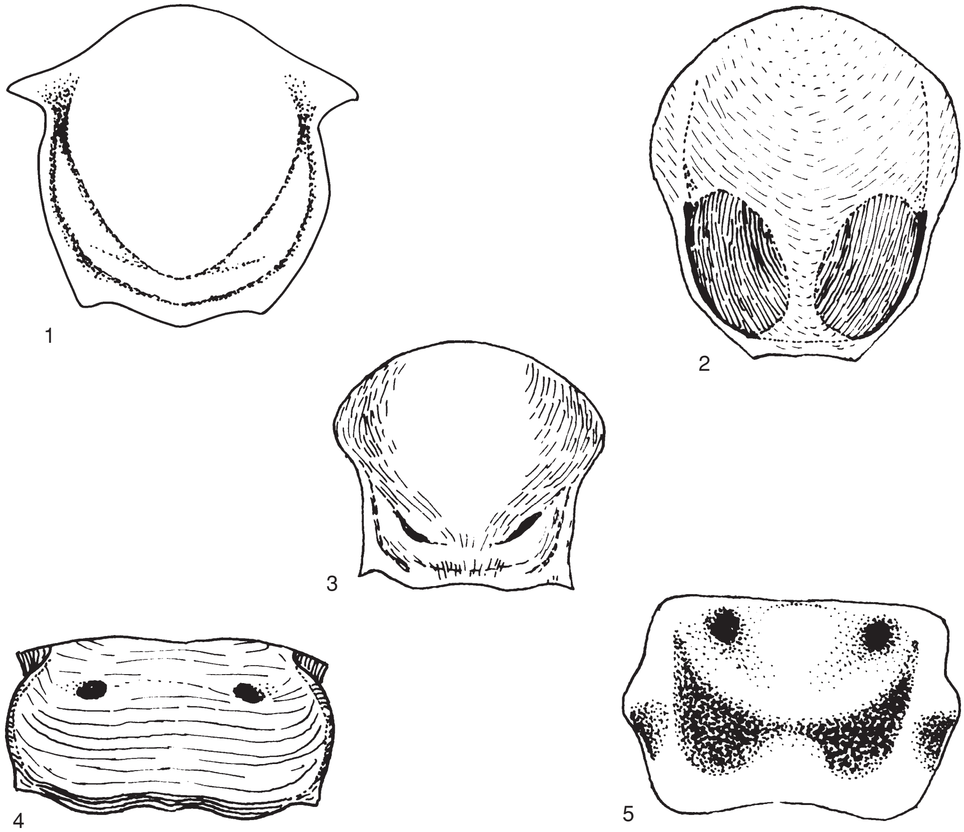

FIG. 198. Maculae in attached hypostomes. *1, Hypermecaspis latigena* FORTEY; *2, Robergia schlotheimi* (BILLINGS); *3, Paradoxides minor* (BOECK); *4, Nileus affinis* BILLINGS; *5, Ceratocephala plummeri* CHATTERTON & PERRY (new).

fork may be equipped with grinding surfaces (Silurian Odontopleurida, CHATTERTON & PERRY, 1983) or rasping surfaces (the Ordovician asaphid *Isotelus*). It is clearly not fanciful to suppose that in these trilobites the margin of the hypostome assisted in the maceration and preparation of food, and it is reasonable to add that tougher or bulkier items could be handled by trilobites equipped with these hypostomal modifications. While the hypostome (both conterminant and natant) primitively occupied quite a small part of the cephalic venter (e.g., *Elrathia,* see FORTEY, 1990a, pl. 1), in derived forms with forks and the like the hypostome can occupy a much larger area, the maximum possibly being in the Lichida. This suggests that, in addition to playing a fuller part in the preparation of food, the hypostome also protected the delicate underside of the head. Conversely, natant hypostomes remained proportionately rather small, regardless of geological age. This, coupled with their conservatism, is additional evidence that natant forms probably habitually dealt with small particles and may have included the detritivores and filter feeders among the trilobites.

SCULPTURE

Sculptural type is exceedingly variable in the trilobites. FORTEY and WILMOT (1991) showed that thicker cuticles (greater than 200µ) tend to be associated with inshore sites, at least in the Early Ordovician. Because coarse tuberculation is associated with thick cuticle, it is not surprising that this sculptural type is commonest in epeiric habitats (many Phacopidae, Brachymetopidae, etc.). However, such sculpture appears to have been relatively rare before the Late Cambrian, regardless of habitat. It may be that most early Cambrian trilobites had thin cuticles, but there are few data.

Many trilobite families have species characterized by different surface sculptures: granules, raised lines, terrace ridges, fine pits, smooth, or any combination of these. WHITTINGTON (1959a) and NIKOLAISEN (1983) have shown that various species of Ordovician Remopleurididae are typified by such sculptures. FORTEY (1974b) recognized different species of the Ordovician olenid *Balnibarbi* by their different surface sculpture. In life, sculptural patterns may have been enhanced by color patterns and functioned in species recognition or camouflage; some tubercles and pits may also have been associated with sensory organelles.

Most surface sculpture is surficial (as the name implies), and internal surfaces of the cuticle are comparatively smooth. However, in some trilobites (see illaenids in WHITTINGTON, 1965) different sculptures occur on internal and external cuticular surfaces. The smaller kinds of granules and ridges are considered to be too small to have had much function in strengthening the cuticle. They also tend to be absent over so-called muscle insertion areas. The evolution of sculptural types, if they functioned in species recognition, may have been somewhat haphazard; certainly there is no consistent progression from smooth to granulose to ridged. Some higher taxa of trilobites are broadly typified by one sculptural type. The granulose-reticulate sculpture of the cheiruroid genae is one example, the Bertillon pattern of Styginidae another. With a little experience most observers recognize the typical lichid sculpture of variously sized pustules. Nonetheless, the function of these particular kinds of surface sculpture remains obscure.

Concentric terrace ridges are present on the doublure of most trilobites, including Redlichiida, and they were probably lost in only two groups: Phacopida and Odontopleurida, where they were replaced by pustules or small, scalloped ridges. The function of terrace ridges is controversial, and hence the signficance of their loss is difficult to interpret. MILLER (1975) claimed that terrace ridges functioned as part of a system for monitoring currents. If, as claimed by SCHMALFUSS (1981), terrace ridges gripped the sediment during the creation of a filter chamber beneath the trilobite, then their loss would indicate abandonment of filter-feeding habits. MILLER (1976) and MCNAMARA (1980) have suggested that some Phacopida may have been predators, for example. On the other hand, some terrace ridges on the doublure cannot have gripped the sediment, especially in those species where the doublure is broad and reflexed against the dorsal exoskeleton to extend close to the axis, at which the appendages articulated (*Symphysurus*, FORTEY, 1986). In most Cambrian species, especially primitive libristomates, ventral terrace ridges are feeble. They become strongly developed in some younger families, especially on the cephalic doublure: Asaphidae (*Niobe*), Illaenidae, Nileidae, Brachymetopidae. In such forms the ridges may have rested on, restrained, or shoveled sediment. It does not seem possible for this function to have applied to odontopleurids with a border of downward-pointing spines, and perhaps this explains the loss of terrace ridges in this family.

EVOLUTION OF REPEATED MORPHOTYPES IN TRILOBITE HISTORY

During the course of trilobite history some designs appeared repeatedly. What is known of the phylogenetics of the group indicates that these designs appeared independently within different major taxa. FORTEY and OWENS (1990a) described these distinctive designs as morphotypes. Some morphotypes can be linked with a specific life habit; for others this habit is unknown or is the subject of debate.

Many trilobites become effaced—that is, they lose defined dorsal furrows. Often glabellar furrows are effaced first (*Eremiproetus*), followed by the occipital furrow (*Platypeltoides*), and then the axial furrows (*Illaenus*). In some trilobites effacement first occurs at the front of the glabella (*Parvigena, Geragnostella*), resulting in an entirely smooth cephalon. In others (e.g., *Leiagnostus*) the entire dorsal exoskeleton becomes effaced. As LANE and THOMAS (1983) observed, such effacement is polyphyletic, and highly effaced trilobites come to resemble one another. This causes taxonomic problems: do effaced end members really deserve the generic status they are often accorded? In some groups (Styginidae and Agnostina especially) almost any genus appears to be capable of becoming effaced. The oldest example we know of is the Early Cambrian genus *Giordanella;* the youngest is *Paraphillipsia* from the Permian. Ontogenies of effaced trilobites show that early growth stages are less effaced (e.g., *Leurostega,* ROBISON & PANTOJA-ALOR, 1968), and effacement was therefore of benefit to the adult, but what advantage it conferred is not known. Effacement may have resulted from more than one selection pressure because it is found in trilobites that lived in widely different habitats with completely different morphology. It occured in deep-water, benthic olenids with thin exoskeletons, supposedly planktonic Agnostina, and comparatively inshore illaenids and asaphids having thick cuticles. It does not contribute in any obvious way to streamlining, and although effaced trilobites are frequently convex, there are examples of effacement of trilobites of low convexity (Styginidae). Hence, effacement may not have been in response to a common external cause in all instances and is not one of the simpler examples of homeomorphy.

MORPHOTYPES AND THEIR STRATIGRAPHIC DISTRIBUTION

FORTEY and OWENS (1990a) distinguished eight trilobite morphotypes, which are common and distinctive morphologies appearing in several phylogenetic lineages. More morphotypes can be recognized, but this sample provides some measure of evolutionary activity in the trilobites because there were times at which these morphotypes were numerous and others when they are rare. The morphotypes are summarized as follows (Fig. 199–200).

PHACOMORPH

These are convex trilobites that are nearly isopygous and have tuberculate sculpture in many species. Other characteristics include a tumid glabella, which expands forward, with the posterior glabellar furrows (when present) forming the intercalating ring and a pygidium with strongly furrowed pleural fields and prominent axis. Large-eyed phacomorphs are typical shelf inhabitants. As the name implies *Phacops* is the typical representative, but phacomorphs are derived from other families such as Bathyuridae (*Bathyurus, Petigurus*), Asaphidae (*Norasaphus*), Hammatocnemidae (*Ovalocephalus*), and Phillipsiidae (*Ditomopyge*).

PELAGIC

This morphology was described by FORTEY (1985). Hypertrophied and often convex eyes and reduced (tr.) thoracic pleurae are typical features. Telephinidae, Bohemillidae, and Cyclopygidae are exemplars of this morphotype (Fig. 199.1–2).

ILLAENIMORPH

These trilobites are among the most highly effaced of all trilobites, and they are characterized by lack of a marked change in convexity between the axial and pleural areas as well as by effacement of glabellar and ring furrows. The eyes are relatively far back. Typically the sagittal convexity of the cephalon exceeds that of the thorax and pygidium, which may have been partly buried in soft sediment in the bumastoid stance described by WESTROP (1983). Illaenidae (Fig. 199.3–4) provide the type examples, but there is also a confusing range of similar forms from Plethopeltidae, Koldinioididae, Styginidae, and Proetidae.

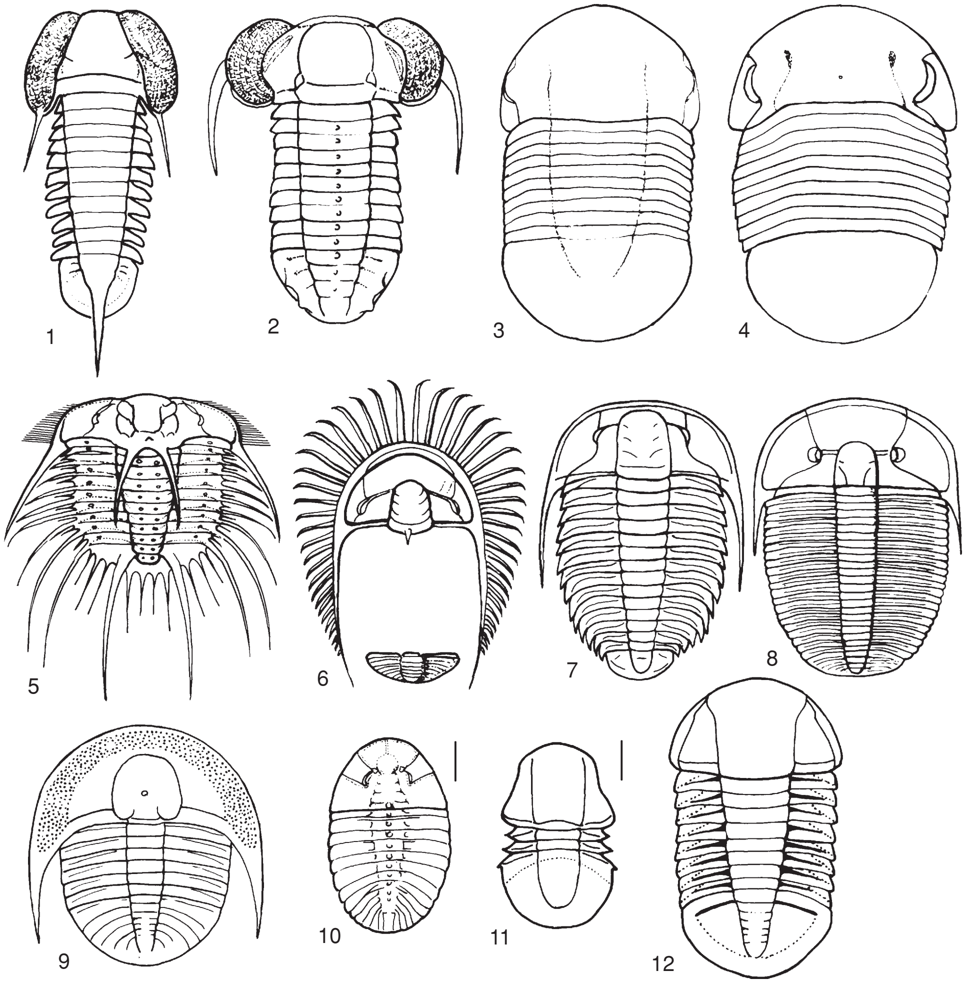

Fig. 199. Major morphotypes that have appeared several times from separate phylogenetic origins in the history of the Trilobita. *1–2,* Pelagic: *Opipeuter inconnivus* Fortey and *Carolinites genacinaca* Ross; *3–4,* Illaenimorph: *Illaenus sarsi* Jaanusson and *Bumastus barriensis* Murchison; *5–6,* Marginal cephalic spines: *Odontopleura ovata* Emmrich and *Bowmania americana* (Walcott); *7–8,* Olenimorph: *Olenus micrurus* Salter and *Aulacopleura koninckii* (Barrande); *9,* Pitted fringe: *Dionide levigena* Fortey & Owens; *10–11,* Miniaturization: *Schmalenseeia amphionura* Moberg and *Thoracocare minuta* (Resser); *12,* Atheloptic: *Illaenopsis harrisoni* (Postlethwaite & Goodchild). Magnifications range from approximately ×0.5 to ×2.5, except for views 10 and 11, where the scale bars represent 1 mm (Fortey & Owens, 1990a, fig. 5.4).

ATHELOPTIC

These trilobites have greatly reduced eyes although their close relatives are known to have had normal eyes (Fortey & Owens, 1987). (Agnostina are not atheloptic because eye reduction typifies the whole clade.) They are often but not invariably associated with deeper-water biofacies. The dalmanitinoid *Ormathops* is typical, but this is a common morphotype from the Middle Cambrian onwards.

MINIATURIZATION

Miniature trilobites, which achieve maturity at a millimeter or two in length, are possibly always the product of progenesis

(Fig. 199.10,11). *Shumardia* is a typical example.

PITTED-FRINGE TRILOBITES

The trinucleid trilobite is typical of this morphotype, in which a fringe is formed by more than one row of pits in the dorsal cephalic margin, which are opposed by a wide, lower lamella carrying corresponding pits on the external surface. Harpetids and dionidids are similarly constructed (Fig. 199.9).

OLENIMORPH

These are *Olenus*-like trilobites with thin cuticle, narrow axis, wide (tr.) but short (exsag.) thoracic pleurae, and many thoracic segments. Olenimorphs were probably adapted to cope with low oxygen concentrations, the numerous segments and the wide pleural regions increasing both the number and length of respiratory exites. Stratigraphically early examples include *Mexicella,* while the latest example is probably the aulacopleurid *Aulacopleura* (Fig. 199.8).

MARGINAL CEPHALIC SPINES

Trilobites with an array of spines around the cephalic margin are typically odontopleurid, but a similar morphology has been derived from other sources, e.g., the Upper Cambrian entomaspidid *Bowmania* (Fig. 199.5–6).

A plot of the distribution of these morphotypes through time (Fig. 200) shows that more examples were contributed by more families during the Ordovician than at any other time, after a build-up in the Late Cambrian. The end-Ordovician extinction produced a drastic decline in the number of families providing the morphotypes, and the pelagic morphotype disappeared forever. The Silurian had fewer families than the Devonian. Several more of the morphotypes, including olenimorphs and pitted fringes, disappeared at the Frasnian-Famennian extinctions. Proetida alone continued to provide several of the morphotypes until the end of the Permian.

This history of morphotypes provides, in microcosm, a pattern such as has been described for trilobite morphology as a whole and for hypostomal attachment: increase in variety through the Cambrian, a burst in the Ordovician that is curtailed by the end-Ordovician extinction, and subsequent recruitment of similar morphotypes from other families until the Late Devonian extinctions, after which the Proetida alone simulated earlier morphologies.

SPECIES-LEVEL EVOLUTION: CASE HISTORIES

In view of the number of trilobites known, there are very few well-supported examples of species-level change through stratigraphic sequences. Even fewer are supported by plausible scenarios giving a functional explanation of claimed trends. In contrast, there are many phylogenies of families, usually given at the end of a monographic treatment of the group in question in the form of a tree linking genera by dotted lines. Such phylogenetic diagrams have been proposed for the following families: Phacopidae (Chlupáč, 1977), Cheiruridae (Lane, 1971), Encrinuridae (Strusz, 1980), Olenidae (Henningsmoen, 1957a), Lichida (Thomas & Holloway, 1988), Calymenoidea (Hammann, 1983), and Proetinae (Lütke, 1980). Such analyses are useful summaries, but they are, nonetheless, theoretical constructs. Cladistic analyses of the same taxa may produce different patterns, which can also be interpreted phylogenetically. Here we refer only to case histories that are alleged to represent the evolutionary history itself, species by species.

Fig. 200. The distribution of important trilobite morphotypes through geological time, showing periods of optimal diversity of design, especially during the Ordovician, with major reduction following the late Ordovician extinction event and subsequent recovery (adapted from Fortey & Owens, 1990b, fig. 7.6).

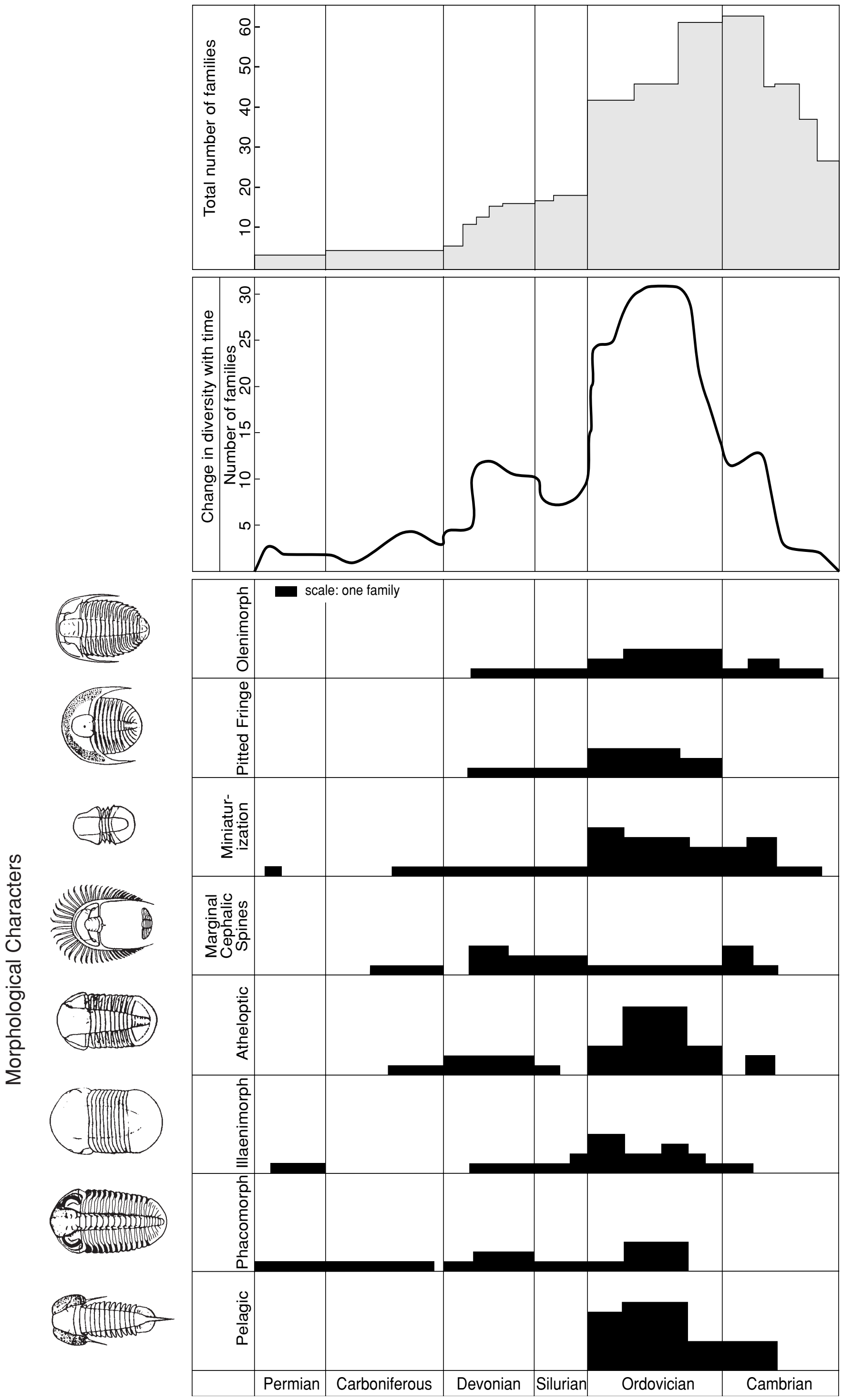

FIG. 200. *For explanation, see facing page.*

LOSS OF EYES AND BLINDNESS

Loss of eyes and blindness occur as a repeated trend in trilobite evolution. In Phacopoidea it is known to be highly polyphyletic (Fig. 201; see also Fig. 118) and can happen in two ways: the eye can migrate to a marginal position to become eventually eliminated or the number of lenses can be progressively reduced. Few examples from phacopoids, however, include all stages from ancestors with eyes to blind descendant species; most are plausible morphological series. Figure 119 gives an example of a true lineage in which much of the rest of the morphology of the trilobite remains the same, and it is clear that loss of the eyes does not involve major genetic restructuring. It is known that cave-blindness happens readily among living, aquatic arthropods.

ANTERIOR FUSION OF HYPERTROPHIED EYES

The pelagic morphotype has enlarged eyes, and there are several examples in which the eyes migrated anteriorly. In its extreme development, the eyes eventually touch on the midline to form one enormous visual organ. This morphology has its analogue in the living hyperiid crustacean *Cystosoma.* These monocular trilobites are always stratigraphically younger than closely related species with normal paired eyes, and hence this is another example of a polyphyletic trend. In the Ordovician Cyclopygidae (Marek, 1961) such anterior fusion occurs in three genera, *Cyclopyge, Pricyclopyge,* and *Microparia.* However, a species-to-species lineage recording this fusion is known only in *Pricyclopyge* through an apparently gradualistic series of subspecies of *P. binodosa* (Salter) collected from successive zones in the late Arenig to Llanvirn (Fig. 202). Although there is variation in the separation of the eyes within any one population of the earlier subspecies, the eyes are eventually conjoined in *P. binodosa synophthalma* (Klouček). Anterior enlargement and fusion of the eyes was presumably particularly useful to pelagic trilobites and occurs exclusively in this morphotype.

OLENID EVOLUTION

Olenidae often lived in oxygen-poor environments that preserve an exceptionally complete stratigraphic record. Bed-by-bed collecting through olenid-rich sequences has yielded plausible phyletic series of species (Henningsmoen, 1957a) that have been studied in great detail. Kaufmann (1933) described the succession of *Olenus* species in the earlier part of the Scandinavian Upper Cambrian, using quantitative analysis of large samples. A series of olenid species could be identified using cranidial characters that appeared suddenly in the stratigraphic record, but within these species rapid change in pygidial characters occurred. Although Kaufmann regarded the species as having been derived from a conservative stock not present in the sections studied, the succession of species could equally be regarded as an example of rapid change, i.e., punctuated equilibrium (see, however, Hoffman & Reif, 1994). Fortey (1974b) used the latter explanation to describe a lineage of olenid species from the Lower Ordovician (Arenig) of Spitsbergen, but in this lineage more aspects of morphology changed between species than in *Olenus,* including width of preglabellar field, eye position, and pygidial size. An interesting feature of the lineages from Spitsbergen was that different, closely related species were typified by different surface sculpture patterns, which may have functioned during sexual selection. Changes of surface sculpture are commonly seen in trilobites and are not otherwise readily explicable.

COAPTATIVE DEVICES IN ENROLLMENT

Changes in coaptative devices in lineages such as that of species of *Placoparia* (Fig. 69) are particularly persuasive as evolutionary examples because most of the other morphological features were little changed. The species in this series are described as part of a punctuated lineage. The inference that the evolutionary changes resulted in the capacity for tighter enrollment is a reasonable one.

TRINUCLEID FRINGES

The size, number, and arrangement of pits in the Ordovician trinucleid fringe vary greatly and provide important criteria for systematics (C. P. HUGHES, INGHAM, & ADDISON, 1975). Changes in species of *Onnia* were described by OWEN and INGHAM (1988), but no functional hypothesis explains the kind of changes that occurred.

GRADUALISTIC CHANGE IN PYGIDIAL RIBBING

SHELDON (1987) described sequential changes in pygidial ribs through a British Ordovician sequence based on very large quantitative samples. Similar increases in number of pygidial ribs at the population level take place in several co-occurring lineages from different trilobite families. Within the general trend, SHELDON observed short-lived reversals in the ribbing number. This work is important because it is one of the few quantitatively based studies where apparently gradualistic change has been demonstrated in more than one genus at one time. The fact that similar changes occur in several lineages might argue for some ecophenotypic control (rather than speciation), but SHELDON correctly noted that end members would certainly be regarded as species in conventional trilobite taxonomy.

HETEROCHRONIC CHANGES

Heterochronic lineages of species of Cambrian olenellids were described by MCNAMARA (1978). Heterochrony has been invoked as an important source of evolutionary novelty, but there are comparatively few examples where species-by-species evolution by means of heterochrony has been demonstrated, although it is plausible in many instances. See, for example, comments on origins of Agnostida in the section on classification (p. 297) and the cases of evolutionary reversal discussed above.

EVOLUTION IN RELATION TO PALEOGEOGRAPHY

Trilobites inhabited marine environments from equatorial to polar paleolatitudes. The dalmanitoid *Mucronaspis,* for example, accompanied the Late Ordovician glaciation and was adapted to cool temperatures (JAANUSSON, 1979). Conversely, the Early Ordovician family Bathyuridae was confined to paleoequatorial regions (WHITTINGTON, 1963; COCKS & FORTEY, 1982). Trilobite niches extended from inshore, even intertidal, habitats to deep-marine, continental slope habitats. Probably no other Paleozoic group of organisms had such a wide geographic spread. This leads to the possibility of evolution within different habitats and on separate continental plates. Because the Paleozoic included periods when continents drifted apart or converged, as well as major climatic fluctuations, there is a complex pattern of evolution that reflects shifting biofacies and changing paleogeography.

TRILOBITE BIOFACIES

Onshore to offshore biofacies patterns (Fig. 137) are typical of much of the history of the trilobites. These patterns may occur in relation to a former continent edge—that is, they record a transect from inner shelf to continental slope—or they may reflect paleoenvironments within intracratonic basins. There may be no genera in common between contemporaneous faunas occupying inshore and deep-water sites; these faunas from different biofacies may be as different as those from different faunal provinces (FORTEY, 1975a). Of the various terms that have been applied to describe the constant association of genera in relation to paleoenvironmental site—community, community type, constant generic association (CGA), realm, and so on—biofacies is probably most commonly used and least confusing.

Lower Cambrian faunas show some differentiation into biofacies across the carbonate shelf (W. ZHANG, LU, & others, 1980). However, deeper-water sites with trilobites are

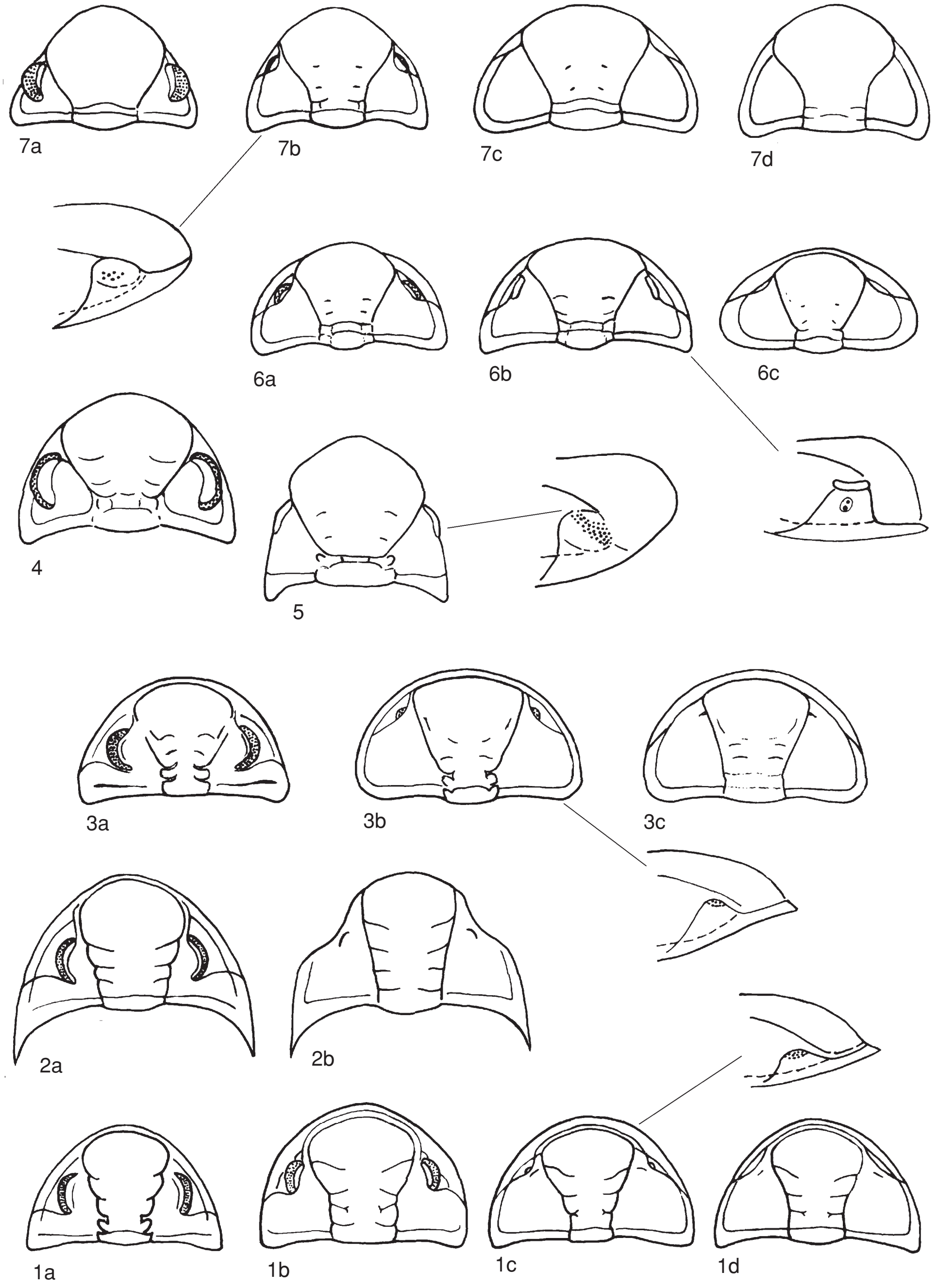

Fig. 201. Loss of eyes in Phacopoidea as an example of a polyphyletic evolutionary trend. The selected examples do not necessarily represent evolutionary lineages but illustrate the kinds of successive change that occurred.——*1a–d, Ormathops,* Ordovician, Arenig and Llanvirn series; *1a, O. borni* Dean; *1b, O. atavus* (Barrande); *1c, O. llanvirnensis* (Hicks); *1d, O. nicholsoni* (Salter).——*2a,b, Mucronaspis* and *Songxites,* Ordovician, Ashgill Series; *2a, M. mucronata* (Brongniart); *2b, Songxites* sp.——*3a–c, Phacopidella* and *Denckmannites,* Silurian, Wenlock and Ludlow series; *(Continued on facing page.)*

almost unknown at this early time in trilobite history, although some of the earlier Agnostina (late Early Cambrian) may already have occupied sites marginal to former continents (Rasetti & Theokritoff, 1967), and by the late Early Cambrian *Atops* may represent the first atheloptic trilobite (Fig. 139). By mid-Cambrian times the whole inshore to deep-water range of biofacies was occupied by trilobites, with Agnostina particularly common in more oceanward sites (Robison, 1972a), where they may have been accompanied by the diverse atheloptic assemblages attributed to the Conocoryphidae.

Similar inner-shelf to outer-shelf transects have been described by Lu (1974), who recognized what he termed bioenvironmental control of Cambrian trilobite distribution in China. Palmer (1972) has described how North American Late Cambrian trilobites relate to distribution of the inner detrital belt, carbonate belt, and outer detrital belt. In all these cases the Cambrian pattern is a comparatively simple one relating to more or less concentric facies belts running approximately parallel to an inferred shoreline (Fig. 203). Carbonate ramps in the tropical belt may have developed steep margins, thus providing a rather abrupt contact between shelf and marginal biofacies, as in the Upper Cambrian of parts of the western United States (Cook & Taylor, 1975). The deeper biofacies are often associated with olenid trilobites, as was appreciated already by Wilson (1957); at that time such biofacies were attributed to an association with geosynclines, which would now be understood to indicate proximity to a Cambrian ocean. However, the olenid sea of Scandinavia (Henningsmoen, 1957a) extended more widely over shelf areas, and this may be a reflection of the stratified nature of the Upper Cambrian oceans. Cambrian trilobites may have subdivided the habitat much more finely than is indicated by the broad shelf-to-ocean transect. Such associations of genera have been recognized by Westrop (1986b) and Ludvigsen, Westrop, and Kindle (1989) using Q- and R-mode analysis of Upper Cambrian faunas from Alberta and western Newfoundland, respectively. Such analyses may reveal something about niche width in these early faunas. It is also clear that fidelity to a biofacies was an important factor in trilobite evolution.

Similar shelf-to-ocean Ordovician biofacies were recognized by Fortey (see Fig. 137) in Spitsbergen, which was in a paleoequatorial position at that time (Fig. 204). The olenid biofacies persisted from the Cambrian and comprised the most oceanic biofacies. The open-shelf nileid biofacies was named after one of its dominant families, although shumardiids, asaphids, remopleuridids, and raphiophorids were also typical. A carbonate-mound biofacies, which may have developed at the edge of a carbonate platform in tropical areas, was typified by illaenids and cheirurids. The inner-shelf, carbonate bathyurid biofacies (Fortey, 1979) was dominated by the eponymous trilobite family but also had restricted asaphids, dimeropygids, pliomerids, and other such trilobites. Ludvigsen (1978b) recognized a similar suite of biofacies for mid-Ordovician

Fig. 201. *Explanation continued from facing page.*

3a, P. glockeri (Barrande); *3b, D. volborthi* (Barrande); *3c, D. caecus* Schrank.——*4, Phacops (Phacops) degener* Barrande, Devonian, Emsian Stage, a typical phacopid with well-developed eyes, the kind that probably lies at the beginning of the lineages shown in parts 5, 6, and 7.——*5, Phacops (Prokops) prokopi* Chlupáč, Devonian, Pragian Stage.——*6a–c, Nephranops,* Devonian, Frasnian and early Famennian stages; *6a, N. miserrimus* (Drevermann); *6b, N. incisus incisus* (Römer); *6c, N. incisus dillanus* (Richter & Richter).——*7a–d,* Devonian, Frasnian and Famennian species; *7a, Phacops granulatus* (Münster); *7b, Cryphops acuticeps* (Kayser); *7c, Trimerocephalus mastophthalmus* (Reinhard Richter); *7d, Dianops griffithides* (Richter & Richter) (adapted from Fortey & Owens, 1990b, fig. 5.2).

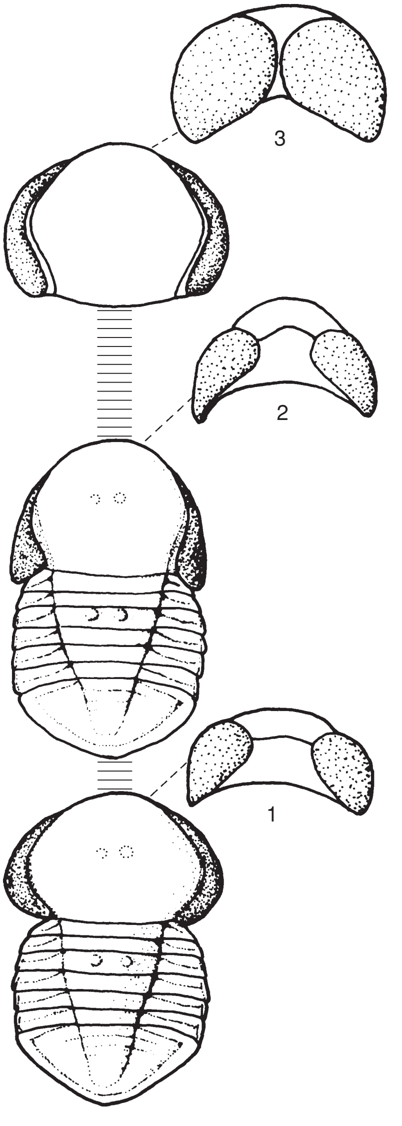

FIG. 202. Anterior convergence of the eyes of *Pricyclopyge:* an evolutionary trend repeated in several lineages of pelagic trilobites; in its extreme development the eyes are fused. *1, P. binodosa eurycephala* FORTEY & OWENS; *2, P. binodosa binodosa* (SALTER); *3, P. synophthalma* (KLOUČEK) (Fortey & Owens, 1990a, fig. 5.1b).

western Laurentia, and CISNE and others (1980) noted the influence of paleoenvironments on the evolution of some species of *Flexicalymene* and other trilobites in eastern Laurentia. A comparable suite of biofacies has been recognized off Ordovician Gondwana (FORTEY & OWENS, 1978, 1987), but because Gondwana was at a high paleolatitude, a different selection of trilobites was generally dominant in the biofacies there (see Fig. 209). The Olenid biofacies, however, could be found in deeper-water sites off both Laurentia and Gondwana—indeed, it is virtually pandemic (COCKS & FORTEY, 1990). Similar biofacies patterns persisted to the Ashgill (e.g., PRICE & MAGOR, 1984) but appear to have broken down at the Late Ordovician extinction event.

The early Silurian is regarded as a time when trilobite faunas are not well differentiated into biofacies. We know of no unequivocal deep-water trilobite biofacies from the Llandovery, for example. However, depth- and facies-related trilobite associations have been reported widely from the later Silurian (Fig. 205) and Devonian [CHLUPÁČ, 1987 (Silurian of Bohemia), CHLUPÁČ, 1983 (Devonian of Bohemia), THOMAS, 1980 (Silurian of Great Britain), MÄNNIL, 1982 (Silurian of East Baltic), CHATTERTON and PERRY, 1983 (Silurian odontopleurids of arctic Canada), and G. ALBERTI, 1969, 1970, 1981 (Devonian of Morocco)]. The most diverse of these are the Bohemian examples described by CHLUPÁČ, who matched many of the benthic associations he recognized with those defined by BOUCOT (1975). He noted persistence through time of some environmentally related assemblages but identified change in their taxonomic composition. For example, the illaenid-cheirurid assemblage was replaced in the Devonian by a styginid-proetid community.

The Old World Province in Europe and adjacent areas comprises the Rhenish and Hercynian (or Bohemian) magnafacies (ERBEN, 1964), dominated respectively by nearshore clastics and offshore carbonates (Fig. 206). The former contain a restricted trilobite fauna with homalonotids, acastomorphs, and asteropyginids dominating, while the latter contains a diverse fauna with proetids, tropidocoryphids, cheirurids, phacopids, odontopleurids, and lichids. Various subprovinces, which are probably

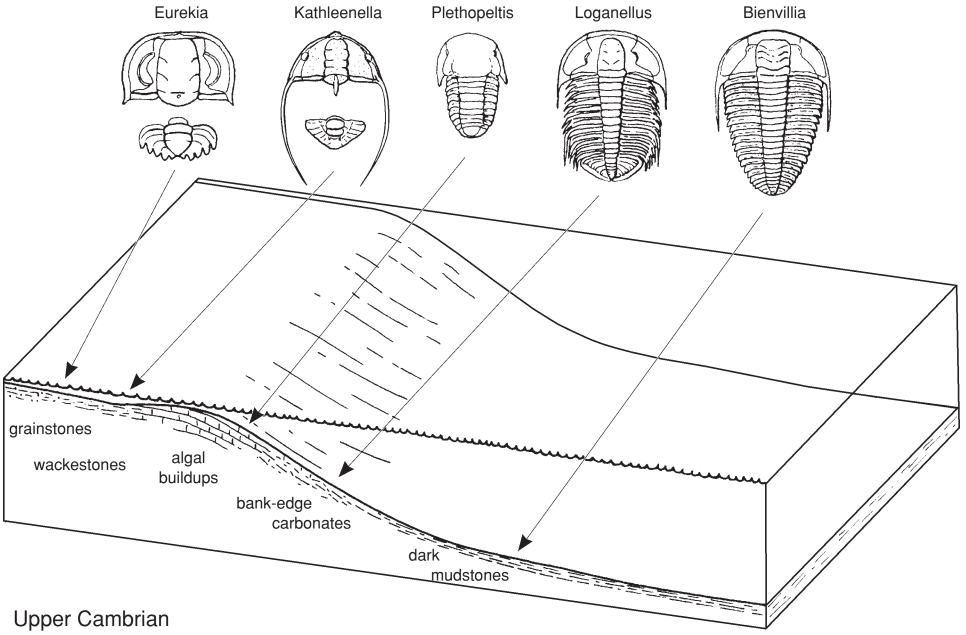

FIG. 203. Biofacies of Upper Cambrian continental shelf of Laurentia. Note in Figures 203 to 207 the persistence of paleoenvironmental associations from the Late Cambrian until the Carboniferous. Different genera and families occupied these habitats, often developing homeomorphic trends (adapted from Ludvigsen & others, 1986).

facies-controlled, have been discriminated and include Uralian (with some Appalachian elements), Tasman, and New Zealand (see HOUSE, 1979 for summary).

Figure 207 illustrates biofacies of the Lower Carboniferous of northern England. Few benthic trilobite associations have been described from the Carboniferous and Permian, but BREZINSKI (1986b) gave a detailed analysis for the Lower Carboniferous (Mississipian) of Missouri in which he recognized three such natural associations of species. He also noted variations in surface sculpture of one species that depended on the enclosing lithology. HAHN and HAHN (1988) briefly discussed associations from the Dinantian of Belgium and northeastern Germany. BREZINSKI (1992) described depth-related associations in the Permian of Texas, and CISNE (1971) observed decreasing taxonomic and numerical diversity with increase in depth in a Permian sequence in the western United States.

For the evolution of trilobites the importance of biofacies is threefold. (1) Evolution may have proceeded within biofacies, as has been described for the Olenidae above. Indeed, some families appear to have been remarkably loyal to a biofacies. LANE (1972) and FORTEY (1980a) noted the persistence of the carbonate-mound, illaenid-cheirurid biofacies from Early Ordovician until Devonian times. It is not surprising that some of the most long-lived trilobite genera (*Scotoharpes, Decoroproetus*) favored this habitat. (2) Deeper-water biofacies include more pandemic species and genera (TAYLOR & FORESTER, 1979; FORTEY, 1980b) and hence have a more limited capacity for provincial speciation. WILSON (1957) presciently noted the almost worldwide relationship of occurrences of Cambrian olenid trilobites to what were then termed geosynclinal habitats. These would now be recognized as oceanward environments fringing paleocontinents. Deep-water genera may also be long lived (FORTEY, 1980a). (3) By contrast, inshore biofacies tend to include endemics, which respond to local conditions of substrate, temperature, water chemistry,

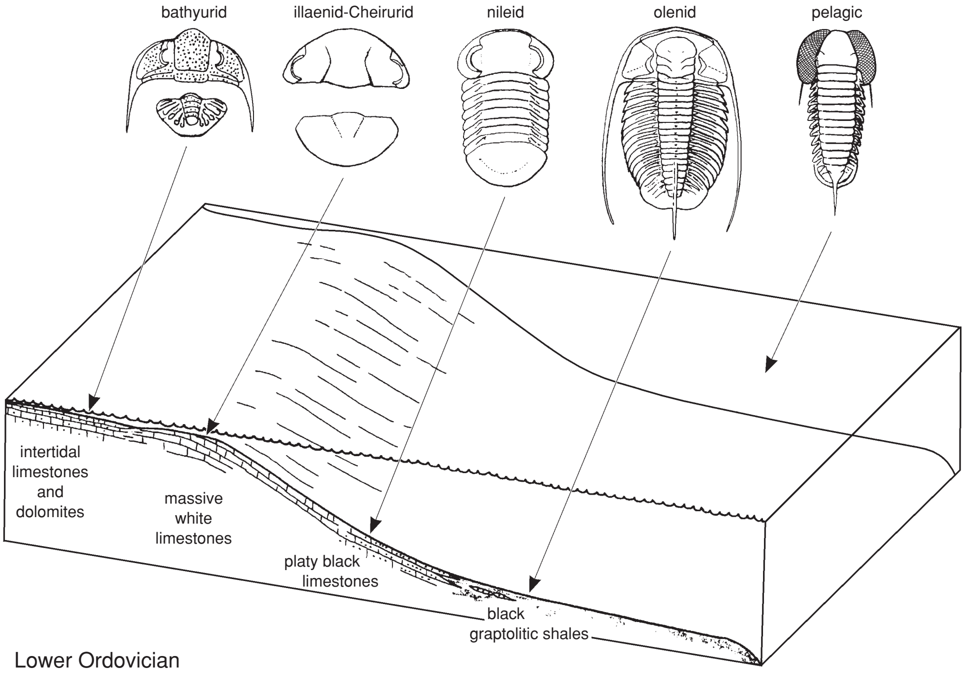

FIG. 204. Biofacies of Lower Ordovician continental shelf of Laurentia. Note in Figures 203 to 207 the persistence of paleoenvironmental associations from the Late Cambrian until the Carboniferous. Different genera and families occupied these habitats, often developing homeomorphic trends (adapted from Fortey, 1975a).

and the like. Speciation among these was more likely to relate directly to the distribution of paleocontinents by paleolatitude or to geographic separation. This has resulted in what have usually been termed trilobite provinces.

DISTRIBUTION OF ANCIENT CONTINENTS AND TRILOBITE EVOLUTION

That some kinds of trilobites were characteristic of extensive paleogeographic areas has been recognized for a long time. The application of plate tectonics to the Paleozoic to produce more reliable paleogeographic maps has made new sense of such provincial distributions, especially when they are taken in conjunction with biofacies patterns within a single paleocontinent (for example, COCKS & FORTEY, 1988, referring to Gondwana). Indeed, trilobite distributions themselves have played a part in deducing the distributions of paleocontinents, especially in the early Paleozoic (WHITTINGTON & HUGHES, 1972; COCKS & FORTEY, 1982). Because the inshore biofacies are more likely to be confined to a single paleocontinent, the distribution of such biofacies is the best guide to former distribution of continents, and evolution inshore is most likely to have proceeded as an endemic phenomenon. Some degree of endemism characterizes the greater part of trilobite history, because the climatic gradient, combined with the effects of separation of continental plates, produced endemic faunas. Hence the evolution of trilobites may have been driven as much by extrinsic, paleogeographic factors as by intrinsic, morphological change. No doubt this accounts, in part, for the repeated appearance of morphotypes, as described above.

Geographic separation of trilobite faunas is apparent from the Lower Cambrian (Atdabanian) onwards (RICHTER & RICHTER, 1941b; COWIE, 1971). The differentiation into major realms characterized by Olenel-

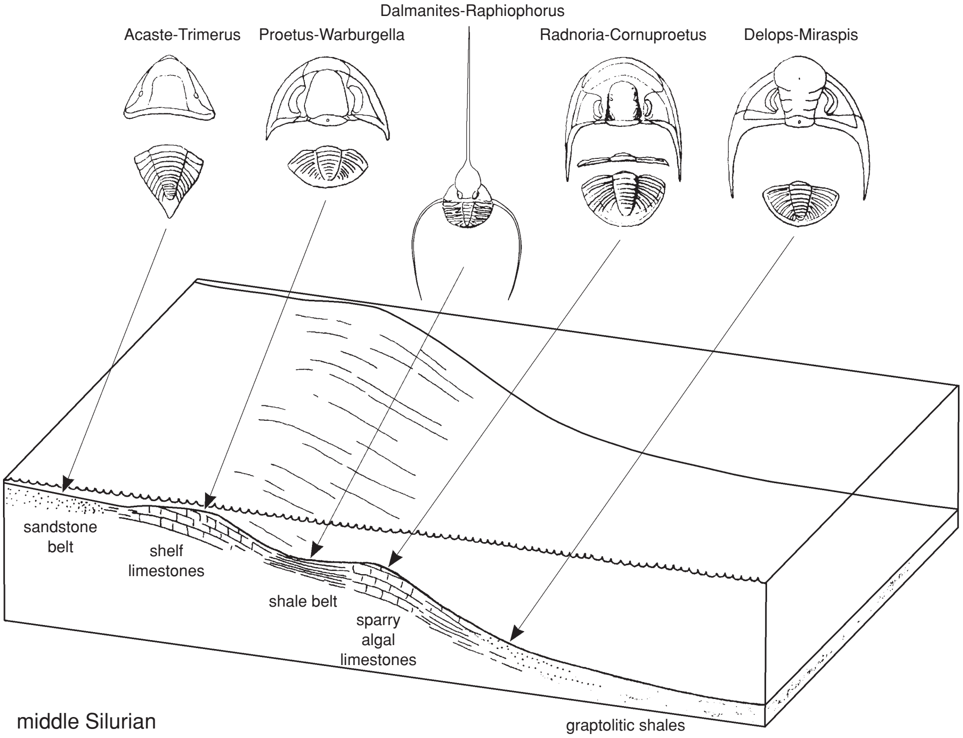

FIG. 205. Biofacies of middle Silurian continental shelf of Gondwana. Note in Figures 203 to 207 the persistence of paleoenvironmental associations from the Late Cambrian until the Carboniferous. Different genera and families occupied these habitats, often developing homeomorphic trends (adapted from Thomas, 1979).

lina (especially in Laurentia) and Redlichiina (especially in China and Australia) must, therefore, have happened in pre-Atdabanian times, but this phase of differentiation and vicariance has left no record. Hardly any genera are common to both regions, so that geographic differentiation was implicated early in the diversification of faunas (Fig. 208). There are characteristic Eodiscina and Redlichiina in China and distinctive Olenellina in Laurentia, and these are assumed to be the product of *in situ* evolution in those areas. Mixed faunas occur in Morocco and Siberia, but there are also endemics in these localities as in Scandinavia, which may indicate that there were already in the Early Cambrian still further biogeographic subdivisions. These early faunas were almost entirely inhabitants of shelves.

Later Cambrian faunas were also differentiated paleogeographically. By this time shelf faunas were differentiated from more marginal biofacies. Generally widespread faunas occur at some times, however—for example, at the *Glyptagnostus reticulatus* Zone as KOBAYASHI (1949) observed. Such widespread faunas resulted from onlap of more cosmopolitan faunas onto shelf regions at times of marine transgression. In general, Middle to Upper Cambrian trilobites differ at the generic or even familial level among biogeographic areas, and ÖPIK (1967) even described one superfamily (Rhyssometopoidea) endemic to Australia in the Mindyallan fauna. A sample horizon taken about the level of the Middle-Upper Cambrian boundary shows rich endemic eastern Gondwanan faunas characterized by Dameselloidea, Laurentian endemics especially in shelf limestones, and another suite of genera in platform Siberia, while the North Atlantic realm of authors marks the inception of the olenid

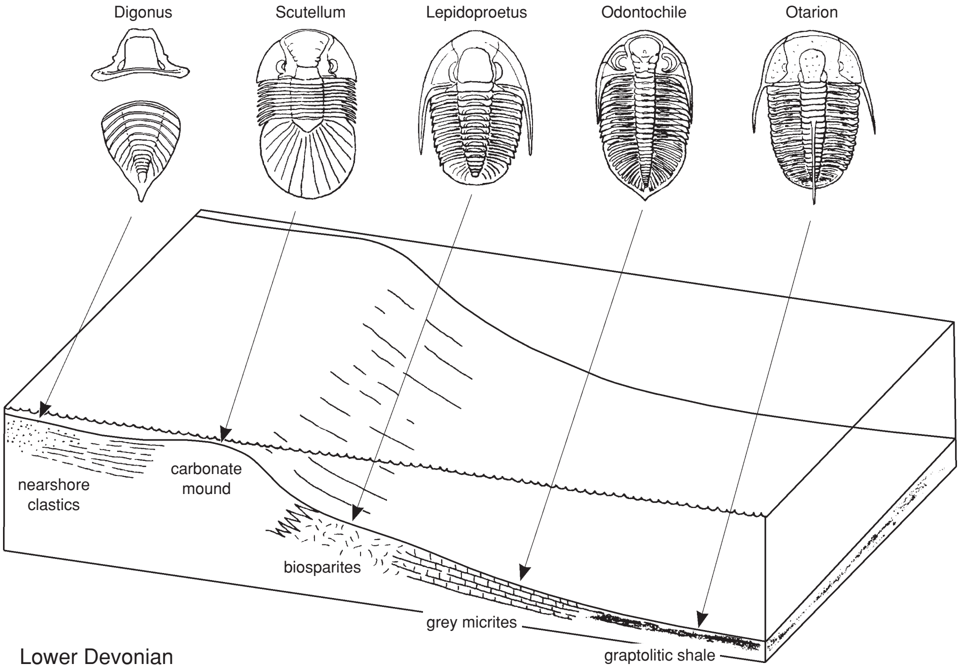

FIG. 206. Biofacies of Lower Devonian continental shelf of the Old World Province. Note in Figures 203 to 207 the persistence of paleoenvironmental associations from the Late Cambrian until the Carboniferous. Different genera and families occupied these habitats, often developing homeomorphic trends (adapted from Chlupác, 1987).

sea. There may be an element of taxonomic artifice in this pattern; for example, a critical comparison of Siberian with North American trilobites has not yet been made. Nonetheless, it seems probable that paleocontinental distribution was a prime control of trilobite speciation and distribution.

The Early Ordovician was a time of wide continental dispersal, with the north pole in present-day North Africa. Strong faunal provinciality was the result (Fig. 209). Paleoequatorial Laurentia and Siberia were typified by trilobites of the family Bathyuridae (WHITTINGTON, 1963), which were confined to inshore carbonates and which did not survive the Ordovician. Tropical sediments at the eastern edge of Gondwana (South China, central Australia, Argentina) were not colonized by bathyurids, but a whole suite of endemic asaphids (*Lycophron*), dikelokephalinids (*Asaphopsis, Hungioides, Dactylocephalus*), dalmanitoids (*Prosopiscus*), and leiostegiids (*Annamitella*) were typical of this area. By contrast, inshore, high-latitude Gondwana (HENRY, 1980a; COCKS & FORTEY, 1988) was dominated by a calymenoid-dalmanitoid fauna including *Ormathops, Zeliszkella, Neseuretus, Calymenella,* and *Plaesiacomia.* Baltica was in temperate latitudes and was occupied by another suite of endemics, especially genera belonging to the families Asaphidae (Megistaspidinae, Ptychopygiinae) and Nileidae (*Varvia*). Enough is known about the Early Ordovician platform faunas for us to be sure that knowledge of these paleogeographic areas is not the product of biased monographic coverage. They hold their integrity through much of the Ordovician, but by the upper Caradoc the distinctions are somewhat less clear. This is because of a complex interaction between several factors: notably, the proto-Atlantic Ocean (Iapetus) had partly closed; the Caradoc transgression had brought some of the more widespread, deeper-water faunas into shelf environments; and climatic dete-

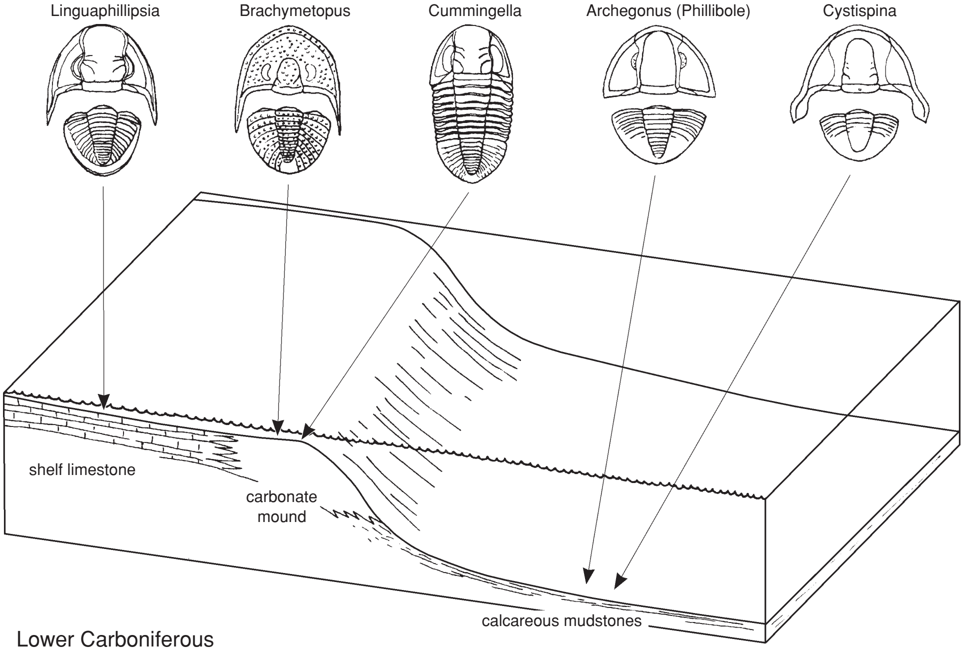

FIG. 207. Biofacies of Lower Carboniferous continental shelf of northern England. Note in Figures 203 to 207 the persistence of paleoenvironmental associations from the Late Cambrian until the Carboniferous. Different genera and families occupied these habitats, often developing homeomorphic trends (new).

rioration may have begun. Even in the late Caradoc, however, trilobite faunas are not pandemic: some genera remain restricted to eastern Gondwana (*Paraphillipsinella*), western Gondwana (*Mucronaspis*), or Laurentia (*Isotelus*).

The glaciation at the end of the Ordovician, which culminated during the Hirnantian Stage (BRENCHLEY, 1984), profoundly affected trilobite faunas. The relatively impoverished, cool-water, shelf faunas, with *Mucronaspis* (Fig. 210) and *Brongniartella,* spread at the expense of warmer-water faunas. The tropical belt was severely restricted, but reef environments survived in a few places, such as Anticosti Island.

Following the extinction of many trilobite clades at the end of the Ordovician, Llandovery trilobites are reported as showing relatively little provincial differentiation. For a while, the faunal composition was apparently dominated by those taxa that survived the Ashgill crisis. Such trilobite-based Silurian provinces as have been claimed (KOBAYASHI & HAMADA, 1974; SCHRANK, 1977) are of broad extent and embrace several paleocontinents. COCKS and FORTEY (1990) noted the generally cosmopolitan nature of Silurian faunas but discriminated several biogeographic regions in the upper part of the system. A circumpolar, low-diversity *Clarkeia* fauna, named for a characteristic brachiopod, included also a few homalonotid trilobites and is perhaps analagous to the Ordovician calymenoid-dalmanitoid fauna (Fig. 209). Temperate paleolatitudes tended to be dominated by deposits of terrigenous clastics, and there was once again a tropical carbonate belt; both of these included some endemic forms. Many Silurian trilobite genera are widespread, as are some species: the cheirurid *Sphaerexochus mirus,* for example, under several different names, occurs in North America, Europe, Japan, and eastern Australia. Those genera with a more restricted distribution were

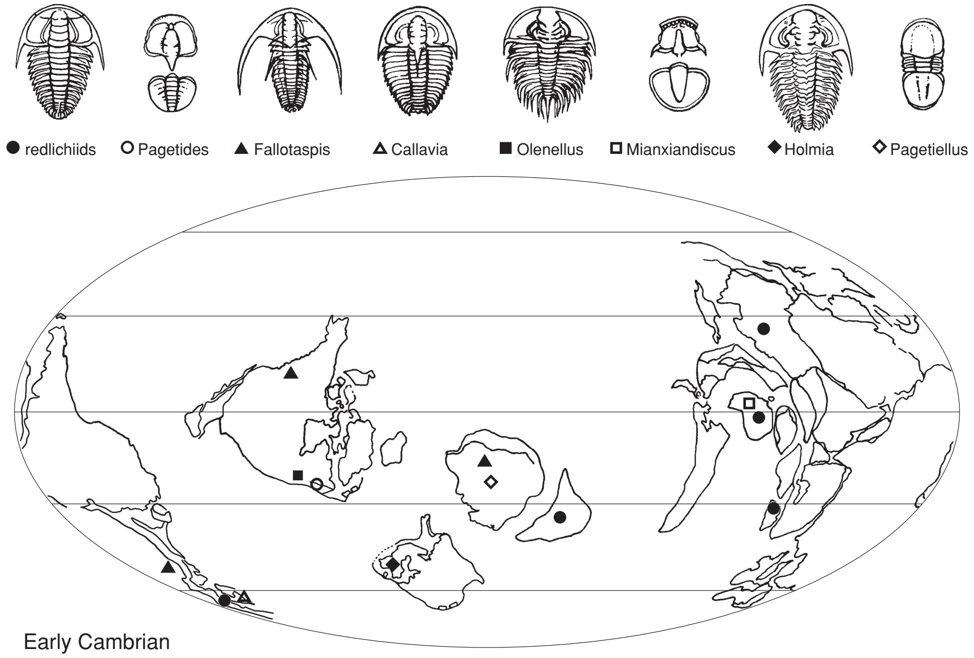

Fig. 208. Reconstruction of Early Cambrian global paleogeography (based on world maps of Scotese & McKerrow, 1990) showing the provincial distribution of shelf trilobites related to distributions and paleolatitudes of continents. Note primary division into Redlichiina and Olenellina (*Olenellus, Holmia, Callavia, Fallotaspis*) realms and local development of endemic eodiscoids (adapted from Fortey & Owens, 1990b, fig. 7.2).

presumably restricted to specific facies. *Coronocephalus* is a distinctive encrinurid that is restricted to eastern Gondwana: South China, Pamirs, Japan, and eastern Australia (Fig. 211).

Three contrasting provinces mark the earlier part of the Devonian (Fig. 212). The southern, polar Malvinokaffric Province had a taxonomically restricted fauna dominated by calmoniids (Eldredge & Ormiston, 1979; Eldredge, 1980; Eldredge & BranIša, 1980), some of which developed remarkable homeomorphy with phacopids. The remainder of the world was dominated by the Old World Province, with an Appalachian Province developed more locally in eastern North America. In the former, many taxa are widely distributed. Subspecies of *Warburgella rugulosa* occur almost worldwide at the base of the Lochkovian (G. Alberti, 1975) in the Hercynian magnafacies along with the conodont *Icriodus woschmidti* and the graptolite *Monograptus uniformis,* while species of *Acastella* occur at the same level in the Rhenish magnafacies. The common occurrence of species of *Warburgella* and *Acastella* in parts of Europe and North Africa permits correlation of widespread, lowermost Devonian strata. Old World Province faunas in some areas include locally distinctive features along with widespread taxa: arctic Canada and arctic Russia lack phacopids (Ormiston, 1967), while there are endemic phacopids in faunas from Inner Mongolia and northeastern Japan (Zhigiang Zhou & Campbell, 1990).

The Appalachian Province of eastern North America was a marine gulf opening to the south for at least some of its history. Heterogeneous local facies, which are dominated by clastics and nearshore deposits, with more limited calcareous and reef deposits, influence the kind of trilobites that are found, which include proetids, phacopids,

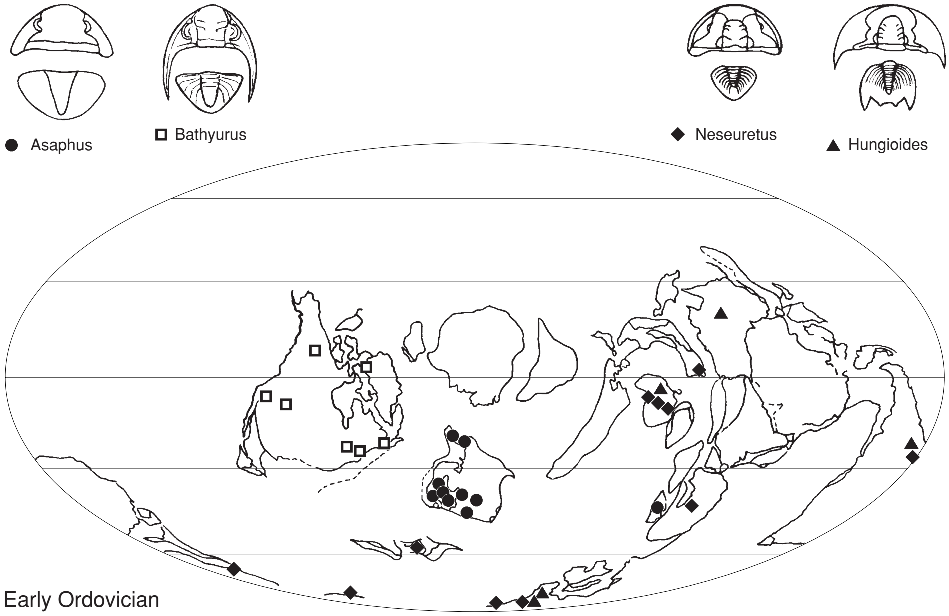

FIG. 209. Reconstruction of Early Ordovician global paleogeography (based on world maps of SCOTESE & MCKERROW, 1990) showing the provincial distribution of shelf trilobites related to distributions and paleolatitudes of continents, with differentiation of Gondwana (*Neseuretus, Hungioides*) from Baltica (*Asaphus*) and Laurentia (*Bathyurus*) (new).

and lichids belonging to genera distinct from those of the Old World Province. Some elements of the Appalachian Province fauna, however, are also known from central Kazakhstan (MAXIMOVA, 1968) and Xinjiang Province, China, which is an indication that there is an element of facies control over the occurrence of these trilobites (HOUSE, 1971).

In the Late Devonian, pelagic sediments with an atheloptic fauna were widespread over Europe, southern Urals, southeastern Asia, South China, and northwestern Australia. At the very end of the Devonian, *Phacops (Omegops) accipitrinus* was widespread in Europe, northern Africa, Afghanistan, central Asia, and China.

In Carboniferous rocks, OWENS and HAHN (1993) distinguished three broad faunal tracts in the Tournaisian and Viséan: in the former, *Breviphillipsia-Thigriffides* (North America), *Cummingella-Phillipsia* (Europe to the Urals), and *Conophillipsia* (central Asia, Japan, and eastern Australia) and in the latter, occupying the same three regions, faunas characterized by *Paladin-Griffithides, Cummingella,* and *Palaeophillipsia,* respectively (Fig. 213).

From the Namurian onwards, two major realms are recognized (Fig. 214). The North American-Andean area maintained its distinctness from Paleotethys, which embraced Eurasia, North Africa, and Australia. Typical trilobite faunas have been named after some of their characteristic constituents: for the North American-Andean area, *Paladin-Sevillia* (Namurian), *Ameura* (Westphalina-Stephanian), *Anisopyge* (Permian); and for Paleotethys, *Paladin-Cummingella* (Namurian), *Pseudophillipsia-Cummingella* (Westphalian-Stephanian), and *Pseudophillipsia* (Permian). The distinctive features of these realms can be explained in part by the separation of the landmasses of North America and Paleotethys after the Viséan (and before that time possibly by differences in local habitats, water temperature,

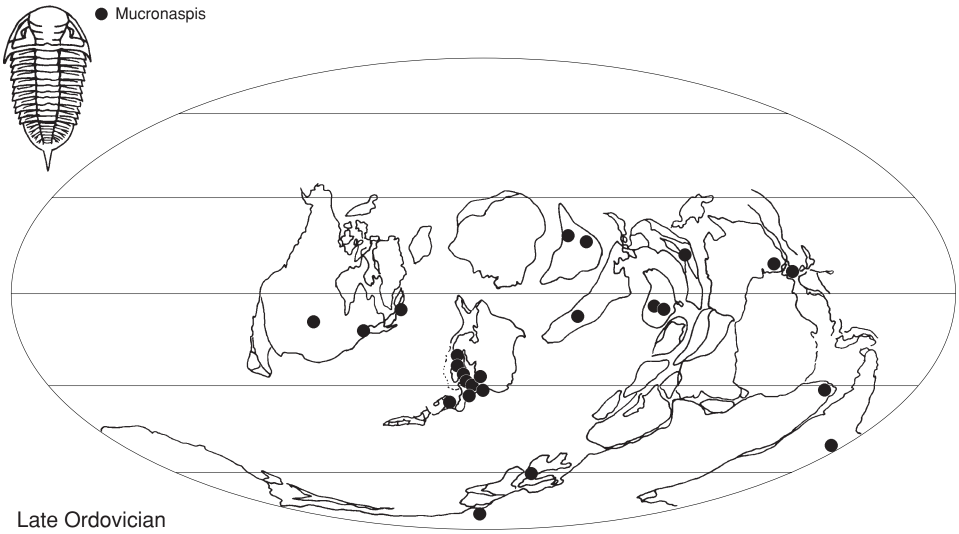

FIG. 210. Reconstruction of Late Ordovician global paleogeography (based on world maps of SCOTESE & MCKERROW, 1990) showing the wide distribution of *Mucronaspis* accompanying glaciation (new).

and depth). Some genera, however, were cosmopolitan—for example, *Pudoproetus* in the Early Carboniferous, *Brachymetopus* throughout the Carboniferous, and *Ditomopyge* in the Late Carboniferous and Permian.

TIMES OF MAJOR CHANGE IN TRILOBITE HISTORY

During some periods in the history of the Trilobita, faunal composition changed rapidly, either through extinction or through the appearance of new clades. These periods usually corresponded with similar events affecting other organisms and provide the most important extrinsic control on the history of the trilobite.

LOWER CAMBRIAN

As with many groups of marine organisms, some trilobite clades that were to last for tens of millions of years began in the Early Cambrian. In many stratigraphic sections the trilobite-bearing beds are underlain by beds containing the remains of Tommotian small shelly faunas. Most complete sections of this kind have a relatively species-poor fauna at the base, and more species appear upwards in the section (BRASIER, 1989, fig. 7.16–7.19). The appearance of new supraspecific taxa is generally quite sudden, and, with the possible exception of the Olenellina, stratigraphically based species-to-species lineages of the early trilobites are not obvious. Nor do first appearances of new clades coincide in the various sections (BRIGGS & FORTEY, 1992), so it seems likely that much of the early history of cladogenesis is not recorded in known fossils. As was discussed previously, there is also marked provincialism in these early faunas. Within the span of the Lower Cambrian, Olenellina and Redlichiina had diversified, and Corynexochida, Agnostida, and libristomate Ptychopariina had appeared. In that some of these are probably paraphyletic groups, they may well include sister groups of other higher taxa, and the so-called extinction of the Redlichiina at the top of the Lower Cambrian may have resulted primarily from their continuation within more advanced clades.

UPPER CAMBRIAN

The biomeres of the Upper Cambrian described by North American authors (PALMER, 1965a; STITT, 1975) have been de-

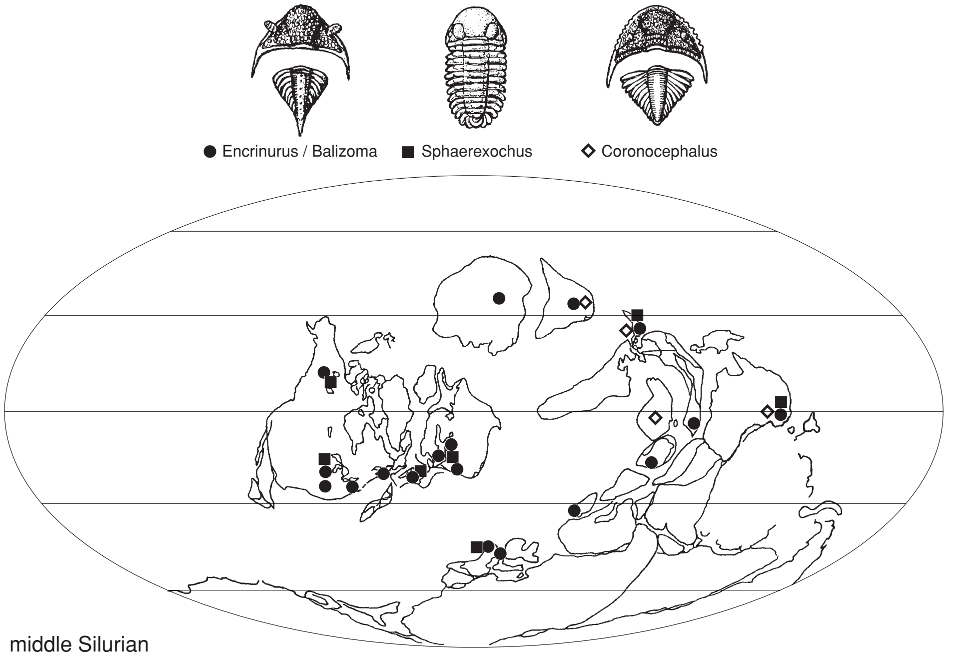

Fig. 211. Reconstruction of middle Silurian global paleogeography (based on world maps of Scotese & McKerrow, 1990) showing the provincial distribution of shelf trilobites related to distributions and paleolatitudes of continents. The wide distribution of *Sphaerexochus, Encrinurus, and Balizoma* is typical of many taxa, but *Coronocephalus* is an example of more restricted distribution (new).

scribed as packages of rapid evolution, eventually followed by widespread extinction events affecting especially shelf faunas. They have a cyclical pattern, which some authors maintain also applies to the Early Ordovician hystricurid or symphysurinid biomere. It is not clear, however, that biomeres were global phenomena; nor is there agreement about how fundamental was their influence on the taxonomic composition of faunas (Fortey, 1983). Deeper-water faunas were supposedly relatively unaffected by the biomere phenomenon. Ludvigsen (1982) and Westrop and Ludvigsen (1987) related biomeres to sedimentary cycles and the shift in biofacies disposition; the extinction events have also been related to cool water incursions onto the platform. Although platform endemics no doubt evolved and were extinguished in Cambrian epeiric seas, it is uncertain whether the biomere events were the equal of the other events listed here.

LOWER ORDOVICIAN

Many of the clades that dominated Ordovician and later trilobite faunas have their first known occurrence in the Lower Ordovician. The Cambrian-Ordovician boundary marks a period of faunal turnover, but although extinction was undoubtedly involved in this change in faunas, it is as a time of origination of clearly differentiated clades that the Early Ordovician is remarkable. Cambrian sister groups of some of these taxa are now being recognized. Insofar as they are known, the new clades do not all appear suddenly at the base of the Tremadoc, but their first occurrences lie in an interval spanning the Upper Cambrian and the lowest two Series of the Ordovician: Proetidae (Arenig); Cheiruridae (lower Tremadoc); Cyclopygoidea (uppermost Cambrian–basal Tremadoc); Dalmanitoidea (Arenig); Dimeropygidae (upper Tremadoc); Trinucleoidea (Upper

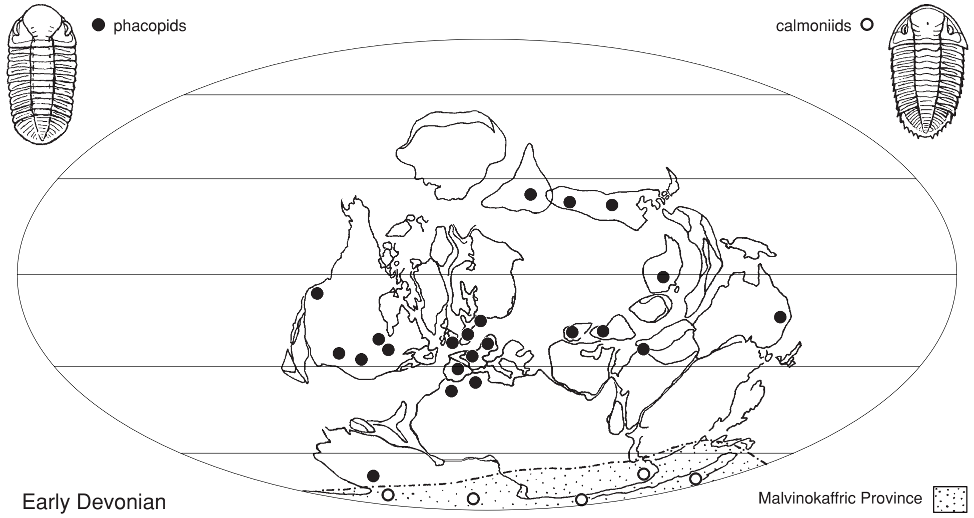

Fig. 212. Reconstruction of Early Devonian global paleogeography (based on world maps of Scotese & McKerrow, 1990) showing the provincial distribution of shelf trilobites related to distributions and paleolatitudes of continents. Note primary division of Malvinokaffric (cool-water) faunas from phacopid-bearing areas at lower paleolatitudes (new).

Cambrian); Illaenidae (basal Arenig); Harpina (uppermost Cambrian). The combination of these new families and superfamilies with those of longer pedigree (Asaphidae, Agnostina, Remopleurididae, Olenidae) lend the Ordovician faunas their distinctive characteristics.

UPPER ORDOVICIAN

The extinction event at the end of the Ordovician was one of the most important in the history of the biosphere, and the trilobites were affected drastically by it. Many families with Cambrian origins and those listed as typically Ordovician were either greatly reduced or extirpated at the end of the Hirnantian. Many families (Asaphidae, Cyclopygidae, Nileidae, and the Trinucleoidea) belong to the Asaphida, which has led some authors to conclude that the planktonic asaphoid protaspis was especially vulnerable (Speyer & Chatterton, 1990). There was a reduction in diversity before the Hirnantian (Brenchley, 1984, 1989), but many Ordovician families persisted into this short time period (Owen, 1986), and had they survived it is possible that they would readily have recovered to their former diversity. The fact that they did not argues for an exceptional crisis at the Ordovician-Silurian boundary. This has been associated with widespread anoxia in the oceans during the postglacial rebound. It seems to be true that the families of trilobites eliminated were especially those that were oceanic (all pelagics), deeper water (olenids, agnostids), or those having pelagic larvae (Asaphida). Some of the shelf-dwellers (Lichida, Dalmanitoidea, Cheiruridae, Calymenidae, Illaenidae, Harpetidae) were survivors. It is also clear that there were some Lazarus taxa (e.g., *Scharyia*) that must have existed in refugia during the crisis as they are found in strata below the uppermost Ordovician and they reappear (or a close relative does) in strata well above the base of the Silurian. There is no doubt, however, about the profound effect of the end-Ordovician extinction. The lowest Silurian (Llandovery) has faunas of relatively low diversity, but more diverse faunas are present by the late Llandovery, and cladogenesis builds continuously into the Devonian. The general composition of trilobite faunas in terms of families present remained essentially

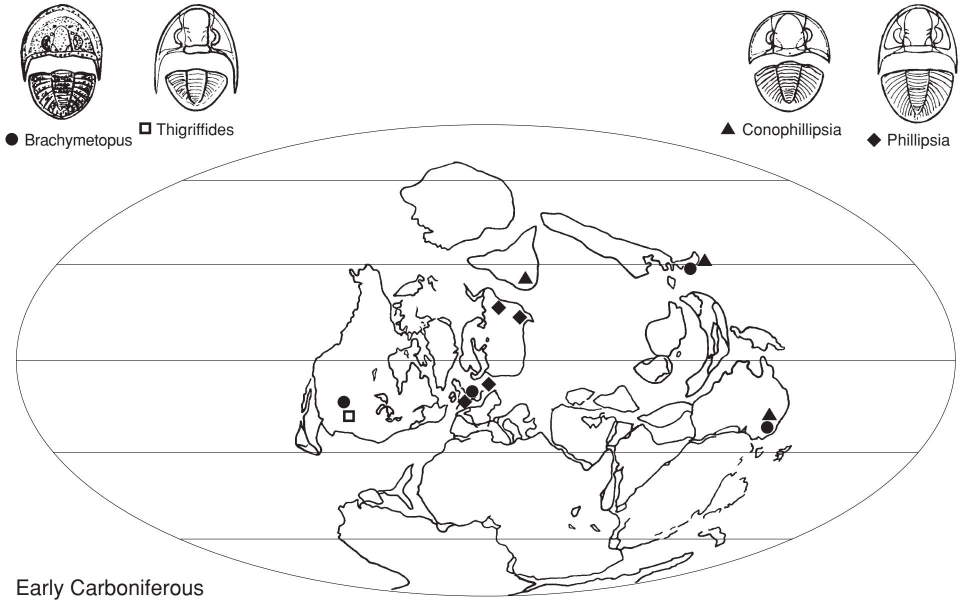

FIG. 213. Reconstruction of Early Carboniferous global paleogeography (based on world maps of SCOTESE & MCKERROW, 1990) showing the provincial distribution of shelf trilobites related to distributions and paleolatitudes of continents. *Thigriffides* (North America), *Phillipsia* (Europe), and *Conophillipsia* (Australasia) are endemics; *Brachymetopus* is more widespread (adapted from Owens & Hahn, 1993).

similar from the late Llandovery to mid-Givetian, except that the Encrinuridae became extinct in the early Lochkovian (STRUSZ, 1980), and the related Staurocephalidae, together with the Raphiophoridae (the last Asaphida), did not survive the Ludlow.

MIDDLE TO UPPER DEVONIAN

A drastic series of extinctions, brought about by global eustatic perturbations, affected the Trilobita in the Middle to Late Devonian (BRIGGS, FORTEY, & CLARKSON, 1988; FEIST, 1991; FEIST & SCHINDLER, 1994) (Fig. 215). In the late Eifelian, a change from well-oxygenated to oxygen-deficient conditions in the outer shelf (the Kačák-*otomari* event) resulted in a depletion in the number of species and the extinction of the synphoriids and rorringtoniids. A regression associated with expansion of the cool-water, Malvinokaffric, calmoniid faunas at or about this time has been interpreted as a result of a sudden lowering of global climatic gradient (BOUCOT, 1988, 1990). The mid-Givetian Taghanic or *Pharciceras* event was a marine transgression that resulted in the loss of trilobite clades adapted to life in shallow-water habitats. Lichids and cheirurids disappeared from the record at this time; in total, five families and one order became extinct. The end-Frasnian Kellwasser event (and the subsequent end-Famennian Hangenberg event) involved sudden changes of sea level leading to a break in the redox equilibrium, which has been invoked as the cause of extinction of a large number of specialized lineages (FEIST, 1991). The Kellwasser event was one of the most dramatic extinctions in the history of the Trilobita—three orders and all but five families were terminated. This event has been claimed to coincide with a major meteorite impact, but may better be accounted for by the loss of specialized groups through an influx of oxygen-depleted water (FEIST & SCHINDLER, 1994). Of the survivors, the Phacopidae disappeared with the Hangenberg event, and only Proetida

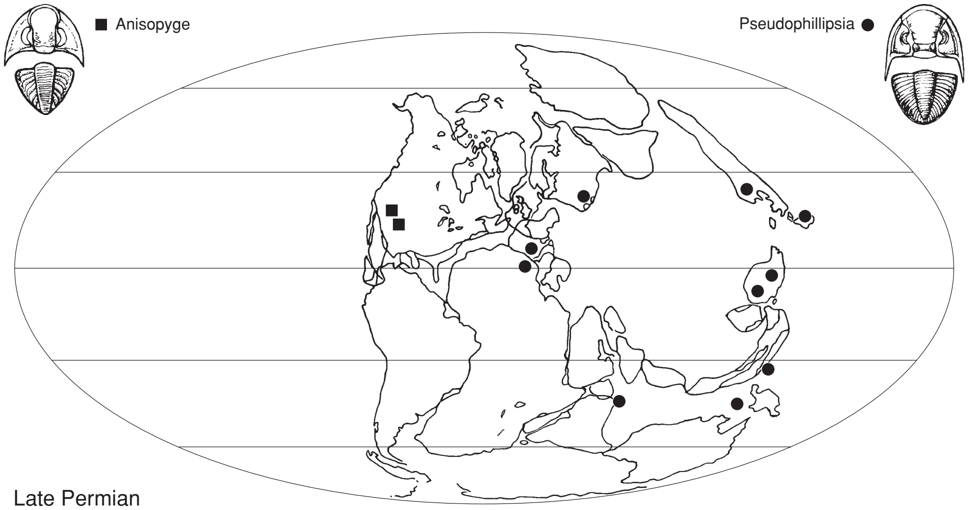

Fig. 214. Reconstruction of Late Permian global paleogeography (based on world maps of Scotese & McKerrow, 1990) showing the provincial distribution of shelf trilobites related to continent distribution and paleolatitudes. *Pseudophillipsia* and *Anisopyge* are examples of mutually exclusive distribution in Paleotethys and western North America, respectively (adapted from Owens & Hahn, 1993).

crossed into the Carboniferous. The restriction of aulacopleurids, brachymetopids, and proetids in the Late Devonian was probably an example of pseudoextinction (Owens, 1994) because several of these taxa reappeared in the Carboniferous when appropriate habitats were reestablished.

PERMIAN

No deeper-water, atheloptic trilobite faunas are known from strata younger than Namurian, although they were varied in earlier Carboniferous offshore basinal environments. The youngest trilobites are all in shallower-water, shelf habitats. Comparatively diverse faunas of Proetida remained in such habitats until the late Kazanian or Guadalupian, from which rocks seventeen genera are known belonging to five phillipsiid subfamilies, together with one proetid and one brachymetopid. However, only two genera, the ditomopyginids *Pseudophillipsia* and *Acropyge,* seem to have survived into the latest Permian. The major extinction seems to have accompanied a drastic regression that particularly affected reef and perireef habitats. The decline of the trilobites, therefore, seems to have happened shortly before the coup de grace at the end of the Paleozoic.

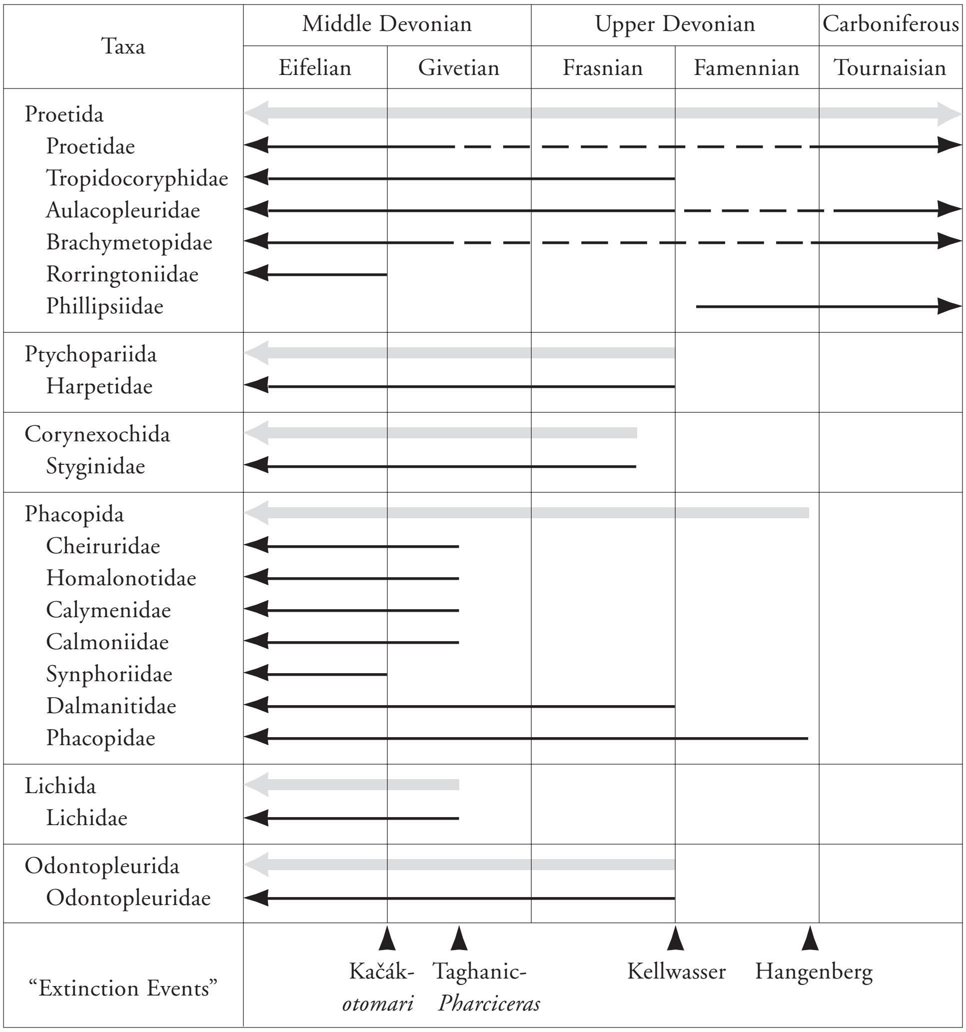

FIG. 215. Fossil record of important trilobite groups through a series of Late Devonian extinctions (recognized in Europe, but also elsewhere), showing staggered last appearances of orders (*stippled arrows*) and families. The names given to the extinction events are those currently in use (adapted from Feist, 1991).

CLASSIFICATION

RICHARD A. FORTEY

A group as large and as complex as the trilobites poses particular problems in classification. Systems of classification seek to achieve a measure of stability, but changes in taxonomic methods as well as new discoveries mean that such stability has remained elusive. HARRINGTON (in MOORE, 1959, p. 145) remarked that a "wholly satisfactory, natural classification of the trilobites is beyond possibility at the present moment." This is still true a quarter of a century later.

HARRINGTON was inclined to ascribe the difficulties in developing a higher classification to our incomplete knowledge of trilobite morphology and ontogeny. Many more ontogenies have been described in the last two decades, and these have contributed to improvements in classification. It is still true that we know the appendages of very few trilobite species, and, because appendages are among the most important criteria for classifying living arthropods, it would certainly be desirable to know more. With the exception of those of the highly specialized *Agnostus* (MÜLLER & WALOSSEK, 1987), trilobite appendages appear to be rather similar along the length of the animal. The extremes of specialization of appendages found among living crustaceans may not have generally obtained in the trilobites. On the other hand, there are many striking modifications of the dorsal and ventral exoskeletons that have no counterparts among the living arthropods, and it was the exploitation of the possibilities of a tough, calcareous cuticle that contributed to the success and adaptive range of the group. The inevitable limitations on our knowledge of trilobite limbs does not necessarily imply that a natural classification is impossible.

The history of trilobite classification shows that some groups that would still be accepted as natural—that is, monophyletic—were recognized very early by the more perceptive, early students of the group. SALTER (1864a), for example, classified trilobites into the following families: Phacopidae, Cheiruridae, Proetidae, Acidaspidae (=Odontopleuridae), Lichidae, Bronteidae (=Styginidae), Calymenidae, Cyphaspidae (=Aulacopleuridae), Asaphidae, Harpedidae (=Harpetidae), Olenidae, Trinucleidae, Agnostidae, and Conocephalidae. Of these, only the Conocephalidae is not in use today; all the others refer to good clades of trilobites, even though SALTER included more genera than are in the taxa of the same name today. More families were introduced in the latter part of the nineteenth (e.g., by BEECHER, 1897) and the first four decades of the twentieth century (GÜRICH, 1907; KOBAYASHI, 1935), and, for the most part, these are also used today. Figure 216 shows the enduring status of many of these families, which have been been passed on from one classification system to the next, with more and more families being added with the passage of time and the discovery of more fossils. The last comprehensive treatment before the 1959 edition of the *Treatise on Invertebrate Paleontology* was that of HUPÉ (1954, 1955a), who recognized some 170 families, nearly all of which are accepted today.

The recognition of a family implies that several genera share some well-characterized features that permit their inclusion in a higher taxon. The Asaphidae, for example, are isopygous or subisopygous trilobites with effaced glabellar furrows having eight thoracic segments with petaloid facets and a ventral median suture; many have hypostomes with a posteromedian fork. The identification of Asaphidae implies that this combination of characters did not arise more than once—and, indeed, no students of the group have claimed asaphids as polyphyletic, even though there have been many opinions on how further to subdivide them. Most trilobite families can be characterized by features that allow confidence in the monophyly of the group concerned. This is true in

	Salter 1864a	Beecher 1897	Gürich 1907	Swinnerton 1915	Poulsen 1927	Richter 1932
Agnostidae	▒	▒	▒	▨	▒	▒
Anomocaridae					▒	
Asaphidae	▒	▒	▒	▒	▒	▒
Aulacopleuridae			▨			
Bathyuridae				▒	▒	
Bathyuriscidae						▒
Burlingiidae				▒	▒	▒
Calymenidae	▒	▒	▒	▒	▒	▒
Ceratopygidae						▒
Cheiruridae	▒	▒	▒	▒	▒	▒
Conocoryphidae	▒	▒		▒	▒	▒
Corynexochidae					▒	▒
Cyclopygidae			▨	▨	▨	▒
Dikelocephalidae			▒	▒	▒	▒
Dionididae			▒			
Ellipsocephalidae			▒	▨	▒	▒
Encrinuridae		▒	▒	▒	▒	▒
Eodiscidae			▨		▒	▒
Harpetidae	▒	▒	▒	▒	▒	▒
Homalonotidae			▒	▒	▒	▒
Illaenidae				▒	▒	▒
Lichidae	▒	▒	▒	▒	▒	▒
Menomoniidae					▨	▒
Nileidae					▨	▨
Norwoodiidae					▒	▒
Odontopleuridae	▨	▨	▨	▒	▒	▒
Olenellidae			▒	▨	▒	▒
Olenidae	▒	▒	▒		▒	▒
Oryctocephalidae				▒	▒	▒
Otarionidae	▨		▨		▨	▒
Paradoxididae			▒	▒	▒	▒
Phacopidae	▒	▒	▒	▒	▒	▒
Proetidae	▒	▒	▒	▒	▒	▒
Ptychopariidae				▒	▒	▒
Raphiophoridae			▨	▒	▒	▒
Redlichiidae					▒	▒
Remopleurididae			▒	▒	▒	▒
Styginidae	▨	▨	▨	▨	▨	▒
Shumardiidae				▨	▨	▒
Solenopleuridae						▒
Trinucleidae	▒	▒	▒	▒	▒	▨
Zacanthoididae				▒	▒	▒

FIG. 216. Trilobite families in some of the principal classification systems developed through the mid-nineteenth to mid-twentienth centuries. Family-level taxa are the most enduring concepts, which, once proposed, survive into modern classification, but the list of families has been progressively augmented. Families that have always been known by the name listed in the lefthand column are *shaded gray.* Families that, while encompassing a similar concept, have undergone one or more nomenclatural changes over the period under consideration are indicated by the *diagonal shading.* For example, the family Cyclopygidae was known as Aeglinidae by some early authorities but embodies a similar suite of genera (new).

particular of families younger than Cambrian in age, because morphological gaps between clades were apparently wider then. Where problems of defining families occur (such as in Ptychopariina), they seem to come about because of problems in discriminating convincing morphological characters to define the clades. Particular Cambrian families have been discriminated on the basis of features that would not merit familial status in younger trilobites, such as details of the shape of the glabella or the size of the eyes. The traditional importance accorded to trilobites in Cambrian biostratigraphy may have contributed to these problems because the families often appear to be stratigraphically rather than morphologically bounded. Thus, there are few families found in the Ordovician that have a stratigraphic range of a span less than that of the whole system, and many that extend into the systems above or below; by contrast, there are only two families, Agnostidae and Ptychopariidae, that extend throughout the Cambrian, and the Ptychopariidae is not regarded as a satisfactory taxon. Many trilobite families regarded as typically Cambrian do not extend through more than a few biozones. Because the morphological range encompassed by Cambrian trilobites is, as a whole, less than that of Ordovician and later forms (FOOTE, 1991) and the Cambrian is also known to represent a shorter timespan than the Ordovician, it seems probable that both the short geological ranges and the difficulties with definition of some Cambrian trilobite families are to some extent a result of taxonomic practice, with the Cambrian groups being the more finely split.

More contentious problems, however, appear with classification above the family level. Whereas the families are generally diagnosable entities, the arrangement and status of superfamilies and orders have changed repeatedly, as opinions on the importance of one morphological character or another have been altered. HARRINGTON (in MOORE, 1959) ably summarized the main contributions to the higher classification made prior to the 1959 *Treatise,* and no particular purpose is served by repeating his discussion in detail here. The *Treatise* (MOORE, 1959) classification has remained the general reference for the last thirty-five years. Since 1959, LU and others (1965) published a compendium of the Chinese trilobite fauna; BERGSTRÖM (1973a) attempted a new comprehensive classification; FORTEY and OWENS (1975) proposed a new order Proetida; and a start has been made on phylogenetic analysis using cladistic methods (FORTEY & CHATTERTON, 1988; FORTEY, 1990a). In these, as in the earlier works, it is the higher taxonomic categories that have differed from one publication to another.

A few higher taxa have been stable. For example, the Phacopida has been consistently recognized as including phacopids and dalmanitids since the last century, although there have been differences of opinion as to whether the Calymenina should be classified with the Phacopida; and the status of the group has varied from superfamily to order. There are several readily recognizable morphological features that obviously unite the suborder Phacopina (Phacopoidea and Dalmanitoidea): the schizochroal eye; forwardly expanded glabella with long S3; proparian sutures combined with yoked cheeks; and typical pygidial form. These are all advanced characters, connecting what are otherwise rather disparate morphologies.

HIGH-LEVEL TAXA THAT ARE REDUNDANT

The problems with stability of other high-level taxa have stemmed from the difficulties in recognizing suites of characters appropriate for the discrimination of major natural groups. There are few groups as neatly defined as the Phacopida.

In the course of the debate about high-level classifications, some characters have come to assume particular importance. Prime among these are the patterns of cephalic sutures, which were emphasized in classical papers by BEECHER (1897) and

Stubblefield (1936). Suture patterns continue to be of importance in trilobite classification at ordinal level, although they are no longer accorded the primacy that they once had. Harrington (in Moore, 1959) sketched the voluminous history of the debate about which suture patterns were to be regarded as primitive for the group as a whole. The division of most trilobites into the two orders Proparia and Opisthoparia (or their several synonyms) on the basis of proparian and opisthoparian sutural patterns, respectively, enjoyed a widespread currency in the first half of this century (Richter, 1932; Størmer, 1942). Consideration of the total morphology, however, showed that the inclusion of such proparian families as Eodiscidae, Norwoodiidae, and Phacopidae in the same higher taxon was entirely arbitrary, and the Proparia as construed was polyphyletic. The demonstration that proparian sutures could appear within the monophyletic family Olenidae (Henningsmoen, 1957a)—most genera of which were opisthoparian—administered the coup de grace to the indiscriminate use of this suture pattern in classification. Nonetheless, it remains a useful character, among others, in the definition of clades; proparian suture pattern is a genuine derived character, and no example is known of a proparian trilobite that is ancestral to an opisthoparian one. It is abundantly clear, however, that proparian sutures in adult trilobites evolved more than once.

While it remains true that the Agnostida include the greatest number of trilobites with only two or three thoracic segments, it is no longer true that major ordinal divisions can be defined on the basis of thoracic segment number alone. This was the basis of the division of the Trilobita (Jaekel, 1909) into the orders Miomera (with two to three segments) and Polymera (six or more segments). Indubitable corynexochoids (Robison & Campbell, 1974) and trinucleoids (W. Zhang, 1980), however, have now been described with numbers of segments that are typical of Miomera but which are otherwise clearly unrelated both to each other and to any miomerid previously described. Also, a shumardiid trilobite, *Acanthopleurella,* is known that has four thoracic segments, forming a bridge between Miomera and Polymera (Fortey & Rushton, 1980). Because it is now clear that the release of segments into the thorax is under developmental control, the generation of lineages with but a few thoracic segments does not seem to be a matter of great difficulty. All that is required is a process whereby release of segments from the front of the pygidium during ontogeny is inhibited and is accompanied by precocious sexual maturation. This is a neotenous process and is more strictly described as progenesis (McNamara, 1983). As with suture patterns, the number of thoracic segments remains a useful taxonomic character, but it is not diagnostic in a simple way.

There have been various attempts to interpret the original cephalic segmentation (see discussion, p. 132), which have proved problematic with regard to the number of segments and their disposition in the preoral parts of the cephalic anatomy. Thus Hupé (1951) regarded the rostral plate, hypostome, and free cheek as comprising a single, ocular segment. Because the larval hypostome takes up much more of the venter, at which size it also shows paired, marginal spines, another interpretation might include more than one segment in the hypostome alone. None of these interpretations has contributed significantly to high-level classification, and the resolution of cephalic segmentation is still far from clear; it is probably preferable that untested and possibly untestable assumptions about homology not be built into systems of classification.

SYSTEMATIC POSITION OF OLENELLINA

Olenellus, Fallotaspis, and allied genera have occupied a special place in discussions of trilobite phylogeny and classification (Størmer, 1942; Hupé, 1954). In many stratigraphic sections spanning the Precambrian-Cambrian transition, they are the first trilobites to appear near the base of the Lower Cambrian. They have several features that have been regarded as primitive—most conspicuously, a lack of facial sutures—and this has invited speculation about how they relate to other early or primitive arthropods.

LAUTERBACH (1980, 1983) suggested that Olenellina are not trilobites at all. This interpretation of their morphology stresses alleged homologies between the tagmatization of merostome chelicerates and some of the species of Olenellina. This view has been repeated in some textbooks (AX, 1987). STØRMER (1933) had pointed out earlier the similarities between trilobites and merostomes. Cladistic analyses of the arthropods as a whole (BRIGGS, FORTEY, & WILLS, 1992) also place trilobites into a larger clade that includes *Limulus* and its allies. It seems likely that trilobites and merostomes shared a common ancestor shortly before the Cambrian radiation. However, consideration of those characters shared between undoubted trilobites and Olenellina (FORTEY & WHITTINGTON, 1989) shows that there are more features that support trilobite relationships of these Early Cambrian forms than support merostome affinities (also EDGECOMBE & RAMSKÖLD, 1991). The features shared by Olenellina and higher trilobites include the pygidium, the calcified cuticle, the structure of the hypostome, and the eye ridges; also once the cuticle was calcified, a perrostral suture facilitated molting, and the calcitic corneal surface of the eye (also unique to trilobites) was molted separately by means of a circumocular suture.

Hence it is probable that Olenellina and all other trilobites comprise a good clade, which descended from a common ancestor late in the Precambrian. The general resemblance between Olenellina and more generalized Redlichiina is striking, but the latter have functional facial sutures. This is a character unique to higher trilobites (although sutures are secondarily lost in several highly derived clades). The absence of such sutures in Olenellina is usually regarded as a primitive feature. Certainly, Olenellina retain other characters that are primitive: thin cuticle, no evidence of a calcified protaspis, nonfulcrate thoracic articulation, and minute pygidium. Moreover, some species have many additional thoracic segments grouped in a posterior opisthothorax.

The taxonomic status that should be accorded Olenellina and their close relatives is also a problem. The group as a whole is united by primitive (symplesiomorphic) characters. On the other hand, their position near the root of the trilobites has resulted in their being recognized as a higher taxon (e.g., order Olenellida in BERGSTRÖM, 1973a). Both Olenellina and Redlichiina are probably paraphyletic groups. It is considered preferable, therefore, to unite these more or less primitive trilobites into a single order Redlichiida, while recognizing that future phylogenetic studies may well further limit its scope.

The recognition that the morphology of Olenellina is primitive for the Trilobita is important in determining which characters are advanced in other trilobites and hence in determining the diagnostic features of clades within the group.

STATUS OF NARAOIIDS

Naraoia and a number of other genera placed in the family Naraoiidae cannot be included within the diagnosis of Trilobita given here because they lack a calcified cuticle, evidence of sutures, and other important features of the group. On the other hand, naraoiids have a large pygidium, a trilobite-like arrangement of cephalic limbs, and, where known in *Tarricoia* (HAMMANN, LASKE, & PILLOLA, 1990), nonfulcrate thoracic segments. *Naraoia* has been described from the Lower Cambrian of China (W. ZHANG & HOU, 1985); hence its stratigraphic occurrence is not relevant in determining its relationships other than being consistent with its being primitive.

Naraoiids have an obvious if superficial resemblance to Agnostida by virtue of their enormous pygidia. They differ, however, in that the cephalic shield is shorter than the pygidium, a condition that is otherwise known only in a few, advanced trilobites belonging to the Asaphidae and Styginidae. Furthermore, naraoiids are not progenetic (as are Agnostida) because they reach normal—even large—trilobite size. Instead, they may have arisen by a different neotenous process known as hypermorphosis. *Naraoia* resembles a giant, degree 0 meraspis in lacking a thorax and in having a relatively large pygidium.

The likely relationship of naraoiids to other calcified trilobites is that they form an uncalcified sister group of the larger, more diverse clade (WHITTINGTON, 1977; BRIGGS, FORTEY, & WILLS, 1992). They comprise a clade that, while having several peculiarities (autapomorphies) of their own, had not acquired some of the other, typical trilobite characters (e.g., calcite cuticle, sutures). In a formal classification system they might be recognized as a higher taxon commensurate with their inferred phylogenetic position, and the name Nektaspida RAYMOND (used as an order by MOORE, 1959) is available to accomodate the group. But it does not seem appropriate to use a class to encompass this handful of fossils, as would be required formally to recognize its sister group status to the class Trilobita. Instead, it is proposed to treat the family Naraoiidae as Trilobita order uncertain (essentially as a plesion in relation to the higher and diverse clade of calcified trilobites, see RAMSKÖLD & EDGECOMBE, 1991). The inclusion of Naraoiidae in the class acknowledges their systematic position, but the open, higher taxon allows the formal definition of Trilobita to be based upon the characters of calcified forms.

TAXONOMIC POSITION OF AGNOSTINA

Agnostina are remarkably abundant in Cambrian rocks and exhibit a wide range of morphology within the constraints imposed by their small size. They are clearly highly specialized: diminutive, blind, and isopygous, with two thoracic segments and various modifications of the axial segmentation. The distinctive limbs of *Agnostus pisiformis* have been described by MÜLLER and WALOSSEK (1987).

The systematic position of Agnostina has been much debated. Some maintain that the Agnostina are not trilobites, a view promulgated by C. E. RESSER in the 1930s ["This group of Crustacea . . . a subclass parallel to the Trilobita . . . " (1938, p. 47)] and espoused most recently by SHERGOLD (1991). This opinion lays emphasis upon the unique characters of Agnostina, as an indication that they must have had a phylogenetically separate arthropod origin. The same view also regards Eodiscina as not being closely related to Agnostina. No one doubts that Eodiscina are trilobites; for example, early members of the group have facial sutures, and all have typical trilobite thoracic structures. Under the view of Agnostina as nontrilobites, therefore, such similarities as there are between Agnostina and Eodiscina are a matter of convergence. Advanced Eodiscina, for example, include species that were blind and have only two thoracic segments.

The other view contends that Agnostina are trilobites, albeit of a very specialized kind. The similarities between them and Eodiscina are indicative of their shared common ancestry, with the Eodiscina representing the more primitive morphology. This is not to say that any particular species of Eodiscina is necessarily nominated as ancestor of the Agnostina. This opinion would regard the peculiar features (autapomorphies) uniquely possessed by Agnostina as not relevant to determining their systematic position, however interesting these may be in determining their life habits or evolution within the group; for example, Agnostina have a unique exoskeletal opening, the cephalothoracic aperture, between the occipital part of the cephalon and the axial part of the thorax, which is exposed during enrollment. Instead, emphasis is placed on those characters shared between Agnostina and Eodiscina (synapomorphies) as indicating common descent. Such a view on classification has been articulated recently by Jell (1975a), W. Zhang, Lu, and others (1980), and Fortey (1990a).

It is not possible completely to falsify a hypothesis invoking convergence between groups. Trilobite history has several examples of remarkable morphological convergence between groups that are not close phylogenetically. The evolution of phacopid-like Proetida late in the history of the group is one instance; and the resemblance between some early Cambrian Redlichiina and Ordovician remopleuridids is another. In these cases, the convergence is revealed by one of two methods: (1) a series of morphologically intermediate species is known connecting the homeomorph in question with its mother group, and (2) critical analysis of the homology of characters reveals fundamental similarities that betray the convergence. Thus, in the examples given, the inspection of ventral, hypostomal, or pygidial characters will reveal the origins of the phacopid-like Proetida, or the origins of the remopleuridids from Asaphina. There is, however, no final arbitration to say how far homeomorphy may proceed, and the usual procedure is to weigh up the characters to see which hypothesis of relationship is supported by the most derived (synapomorphic) characters.

For the Agnostina, a suite of species connecting the group with some other taxon is not yet known (which is perhaps not surprising, given that Agnostina go back to the Early Cambrian), and we are obliged to accept comparison of homologous characters to determine phylogenetic relationships.

In a comparison between the possible theories of the relationships of the Agnostina, Fortey (1990a) found that more shared characters supported Agnostina and Eodiscina having descended from a common ancestor than their having separate origins. In particular, the ventral surface of both groups has a narrow marginal selvage (not a wide doublure), which in one agnostid is backed by a calcified rostral plate like that of Olenellina (Hunt, 1966). In either case, the venter is certainly not like that of Redlichiina and all higher trilobites. The hypostome is not suturally attached. The long (sag.) cephalic shield, wide (tr.) occipital ring, reduction in number of thoracic segments, and features of cephalic and pygidial margin are also shared by the two groups. It seemed to Fortey (1990a) to be less parsimonious to assume that all these characters were acquired in parallel by Eodiscina and Agnostina, particularly in the absence of a plausible sister group for the latter. As discussed above, the naraoiids are not likely candidates. Shergold (1991) chose to put great emphasis on the discovery of an eodiscoid protaspis (of usual trilobite type) as an indication that this group is closer to other trilobites, especially ptychoparioids, and that the Agnostina were independently derived. No calcified protaspis of a species of Agnostina has yet been discovered. In this regard, Agnostina are like Olenellina. The simplest explanation, however, is that Agnostina have retained a primitive or plesiomorphic condition; since Olenellina are trilobites, there is nothing special in lacking a calcified protaspis. A less simple alternative would be for Agnostina to have descended from an Eodiscina-like ancestor, the loss of the calcified protaspis being secondary—a reversion to the primitive state—and another specialized character of Agnostina among many. Agnostina may well have been planktonic animals (Robison, 1972a), and both small size and accelerated development are not implausibly associated with planktonic habits. In any case there is nothing especially persuasive about the protaspis of Eodiscina as an indication of separate origins for the Agnostina and Eodiscina. In the classification below the two groups are included within a single clade, but it is noted that this opinion is not held by all specialists in Agnostida.

THE PROBLEM OF THE PTYCHOPARIINA

Beginning in the Lower Cambrian and extending into the Ordovician there occurs commonly a type of trilobite with a rather uniform bauplan. It might be termed the ptychopariid morphology and has a tapering glabella, a preglabellar field, opisthoparian sutures, rimlike cephalic borders extending into genal spines, natant hypostome, usually more than 12 thoracic segments, and a small, transverse, well-furrowed pygidium without remarkable features. Such a morphology is often referred to as generalized, but it is quite far removed from the primitive Redlichiida design, and it might be better to refer to it as exceptionally durable by virtue of a successful specialization. Where taxa of Ptychopariina occur, they often do so in great profusion. A typical example, *Elrathia kingi* (Middle Cambrian), has been extracted from its type locality in Utah in tens of thousands, and abundant specimens remain. This abundance suggests that these trilobites may have occupied a place comparatively low in the food chain, possibly by directly ingesting the sediment or living by filter feeding.

Partly because of the success and persistence of the design, Ptychopariina pose peculiar taxonomic difficulties. These difficulties stem from three sources. First, these trilobites have a range of morphological variations within a basically conservative design, which intergrade in such a way as to make the recognition of discretely bounded taxa genuinely debatable. Many of the changes that occur, concerning the size of the eye, width of border or preglabellar field, or depth of furrows, are trivial ones. Even generic diagnoses are difficult to frame using such characters, let alone those of families. Second, many of the taxa are known only from cranidia and pygidia—often only the former. It is possible that thoracic or librigenal characters may have been important. Third, in the absence of distinctive morphological characters, stratigraphic and geographical criteria have come into play in the taxonomy, and the result has probably been excessive splitting. For example, generic names applied in the Cambrian of Siberia or China are different from those in North America without critical evaluation of their morphological justification. For this group of trilobites in the Cambrian, generic stratigraphic ranges have tended to be artificially short, crossing neither stage nor biomere boundaries. The result has been a proliferation of taxa with imprecise morphological definitions.

Even the definition of Ptychopariina as a whole is problematic. So-called ptychoparioid ancestors have been invoked for several other higher trilobite taxa: Olenina, Proetida, Harpina, Asaphida, and, more doubtfully, Phacopida. These groups have distinctive characters, which unite them and ensure their discreteness, but their earliest and most primitive members have a more general resemblance to the typical Ptychopariina morphology. In the previous edition of the *Treatise* (Moore, 1959), there was no consistency about classifying these orders and suborders together in a still higher taxon, as they should be if they were ultimately descended from a common ancestor. Fortey (1990a) described the ventral sides of typical Ptychopariina and noted that in these the hypostome was natant. In many of the groups derived from Ptychopariina, the hypostome was secondarily attached to the doublure (Whittington, 1988b). Fortey applied the name Libristoma to the huge monophyletic group that includes Ptychopariina together with all those groups descended from them that had a natant hypostome.

Ptychopariina represent the primitive morphology of the libristomate groups. A paraphyletic suborder Ptychopariina can be defined as including trilobites with a natant hypostome that do not belong to one or another of the derived groups, that is, which retain the primitive exoskeletal morphology. This is not entirely satisfactory, but it does provide a phylogenetic rationale for this most difficult group. The order Ptychopariida includes also those other suborders, Harpina and Olenina, in which the bulk of the species retain the natant condition, even though they are good clades from other morphological criteria. The definition of Ptychopariida is accordingly a more restricted one than that used in the previous edition of the *Treatise* (MOORE, 1959).

It is not yet possible to resolve many of the problems within Ptychopariina at the family and generic levels. Many of the taxa will probably remain those of convenience rather than natural groups.

OUTLINE OF CLASSIFICATION

The growth in the number of trilobite genera described since the previous edition of the *Treatise on Invertebrate Paleontology* (MOORE, 1959) has made it necessary to publish the revised edition in several parts. An outline of classification is necessary to determine which families should be included in each part. This account accompanies the first part and naturally cannot anticipate what advances will be made as subsequent parts are compiled. Nor can numbers of genera within each family be given, as did HARRINGTON (in MOORE, 1959), because this will change as work proceeds. Nonetheless, it is of service briefly to describe the systematic arrangement and to note some of the changes that have occurred since 1959. Superfamily endings have been changed from -acea to -oidea following Recommendation 29A in the *International Code of Zoological Nomenclature* (1985).

Criteria relating to larval characters can now be incorporated into diagnoses of high-level taxa because many more ontogenies have been described. The descriptions of exquisitely preserved, silicified faunas over the last thirty years have probably added the most new morphological information. BERGSTRÖM (1973a) brought some features of thoracic construction to attention that are useful at a high taxonomic level, but his general system of classification has not been adopted. WHITTINGTON (1988a, 1988b) and FORTEY (1990a) have emphasized the characters of the hypostome and its attachment in high-level classification.

This first volume includes primitive trilobites that appeared early in the geological record: these are grouped together in the orders Agnostida and Redlichiida. The problems with the definition of these taxa and their status within the Trilobita have been discussed previously. The second volume will probably include the orders Corynexochida, Lichida, and Phacopida. Libristomate orders and problematica comprise a third volume.

The orders recognized at this stage are discussed below.

ORDER AGNOSTIDA

The order embraces suborders Agnostina and Eodiscina. The view that these should be classified separately was discussed previously. All Agnostina have distinctive articulating structures on their two thoracic segments and a cephalothoracic aperture between cephalic shield and thorax. Eodiscina have either two or three thoracic segments of normal trilobite form and a wide range of morphological characters (with or without eyes, different forms of pygidial segmentation, effacement) that are the basis of family divisions within the group. Classification of Agnostina is based particularly upon the work of ÖPIK (1979) and SHERGOLD, LAURIE, and SUN (1990). Advances in classification of Eodiscina were made by JELL (1975a) and W. ZHANG, LU, and others (1980).

ORDER AGNOSTIDA
 SUBORDER AGNOSTINA
  Superfamily Agnostoidea
   Family Agnostidae
   Family Ptychagnostidae
   Family Spinagnostidae
   Family Peronopsidae
   Family Diplagnostidae
   Family Clavagnostidae
   Family Metagnostidae
  Superfamily Uncertain
   Family Phalacromidae
   Family Sphaeragnostidae
  Superfamily Condylopygoidea
   Family Condylopygidae
 SUBORDER EODISCINA
  Superfamily Eodiscoidea
   Family Tsunydiscidae

- Family Hebediscidae
- Family Calodiscidae
- Family Weymouthiidae
- Family Yukoniidae
- Family Eodiscidae

ORDER REDLICHIIDA

This order includes the suborders Olenellina (PALMER & REPINA, 1993) and Redlichiina (W. ZHANG, LU, & others, 1980). Olenellina lack facial sutures and a calcified protaspis and have a wide rostral plate and nonfulcrate thoracic articulation, all characters which can be regarded as primitive. Redlichiina have facial sutures, a rostral plate bounded by connective sutures, and, where known, a calcified protaspis, characters which may be regarded as derived relative to Olenellina.

- ORDER REDLICHIIDA
  - SUBORDER OLENELLINA
    - Superfamily Olenelloidea
      - Family Olenellidae
      - Family Holmiidae
    - Superfamily Fallotaspidoidea
      - Family Fallotaspididae
      - Family Archaeaspididae
      - Family Judomiidae
      - Family Neltneriidae
      - Family Nevadiidae
  - SUBORDER REDLICHIINA
    - Superfamily Emuelloidea
      - Family Emuellidae
    - Superfamily Redlichioidea
      - Family Redlichiidae
      - Family Dolerolenidae
      - Family Yinitidae
      - Family Mayiellidae
      - Family Gigantopygidae
      - Family Saukiandidae
      - Family Metadoxididae
      - Family Abadiellidae
      - Family Kueichowiidae
      - Family Menneraspididae
      - Family Redlichinidae
      - Family Chengkouaspidae
    - Superfamily Paradoxidoidea
      - Family Paradoxididae
      - Family Centropleuridae

ORDER CORYNEXOCHIDA

This order is more inclusive here than in the previous edition of the *Treatise* (MOORE, 1959). Three suborders are placed in this group: Corynexochina, Illaenina, and Leiostegiina. All have conterminant (or impendent, derived therefrom) hypostomal attachment, often ledgelike cranidial borders, and typically elongate and pestle-shaped glabella with splayed glabellar furrows (FORTEY, 1990a). This glabellar shape resembles that of protaspides and early meraspides of other trilobites, and its presence in the adult is therefore probably neotenous. As with Agnostida, there is the question whether such a neotenous transformation could occur more than once and thus whether the Corynexochida might be polyphyletic. At the present time the evidence for this is not conclusive. Advanced members of all groups included may become effaced, which conceals their diagnostic characters. The suborder Corynexochina characteristically has the hypostome fused with the rostral plate.

- ORDER CORYNEXOCHIDA
  - SUBORDER CORYNEXOCHINA
    - Family Corynexochidae
    - Family Cheiruroididae
    - Family Chenghuiidae
    - Family Dorypygidae
    - Family Ogygopsidae
    - Family Oryctocephalidae
    - Family Dolichometopidae
    - Family Edelsteinaspididae
    - Family Jakutidae
    - Family Longduiidae
    - Family Zacanthoididae
    - Family Dinesidae

The suborder Illaenina is part of the suborder Illaenina as used by MOORE (1959). Other members formerly placed in this group have now been assigned to the order Proetida (FORTEY & OWENS, 1975). The older name Illaenina is preferred to Scutelluina. That the Illaenidae and Styginidae together comprised a monophyletic group was suggested by FORTEY (1980b, p. 59) and

LANE and THOMAS (1983). An important synapomorphy of the group is the presence of an extra-axial cephalic muscle impression, the lunette. FORTEY (1990a) added the family Tsinaniidae to the group. The relationship of the families here incorporated into the suborder Leiostegiina to those in the Corynexochina or Illaenina has not yet been determined.

SUBORDER ILLAENINA
  Superfamily Illaenoidea
    Family Styginidae (=Scutelluidae)
    Family Phillipsinellidae
    Family Illaenidae
    Family Tsinaniidae
SUBORDER LEIOSTEGIINA
  Superfamily Leiostegioidea
    Family Leiostegiidae
    Family Pagodiidae
    Family Kaolishaniidae
    Family Cheilocephalidae
    Family Lecanopygidae (=Illaenuridae)
    ?Family Shirakellidae

ORDER LICHIDA

THOMAS and HOLLOWAY (1988) regarded Lichida and Odontopleurida (*sensu* MOORE, 1959) as comprising a monophyletic group. This view depends on interpreting the complex glabellar lobes of the former as being homologous with the generally simpler lobes of the latter, as well as accepting a fundamental similarity in the protaspides of the two groups. Another view relates the lichids instead to the Styginidae. The former view is adopted here. FORTEY (1990a) regarded the superfamily Dameselloidea as likely to represent the Cambrian sister group to Odontopleuridae. Accordingly, the order Lichida is considered to include three superfamilies: Lichoidea, Odontopleuroidea, and Dameselloidea. All three superfamilies are good clades. Lichoidea have a unique glabellar structure; in addition, the pygidial structure of most lichoids is distinctive, and many have a characteristic surface sculpture comprising two sizes of granules or tubercles. Odontopleuroids have pleural tips with two kinds of spines, one of which is usually greatly extended; the short, transverse pygidium with tubular marginal spines is also characteristic. Their classification has been discussed by RAMSKÖLD (1991b). Dameselloids differ from odontopleuroids in their less specialized thoracic segments, longer pygidia with more axial segments, and thickset marginal spines.

ORDER LICHIDA
  Superfamily Lichoidea
    Family Lichidae
    Family Lichakephalidae
  Superfamily Odontopleuroidea
    Family Odontopleuridae
    Family Selenopeltidae
  Superfamily Dameselloidea
    Family Damesellidae

ORDER PHACOPIDA

The order Phacopida comprises three suborders: Calymenina, Cheirurina, and Phacopina. All three share a distinctive protaspis type; the latter two are proparian. Calymenoids and cheiruroids retain a rostral plate from their common ancestor, but in virtually all phacopoids the free cheeks are yoked as a single piece. All three groups have epifacetal pleural furrows. Phacopoids have schizochroal eyes and a typical glabellar structure. Cheiruroids have distinctive thoracic segments, and typically spinose pygidia. As WHITTINGTON (1988b) noted, the anterior wing of the hypostome of these superfamilies carries a prominent process. Granulate sculpture is very common and invariable among cheiruroids. The Calymenina include the most primitive morphology of the group, both with regard to the facial suture pattern and the presence of a circumocular suture. The coherence of this clade has been challenged by ELDREDGE (1977), who emphasized several of the ptychoparioid characters of Calymenina. More characters support its unity. It is possible that Phacopida was derived from a libristomate ancestor, but while several plausible ptychoparioids are known (eulomids and lonchocephalids among them), none is linked to the Phacopida by unequivocal characters. For this reason Phacopida are not included with other libristomate trilobites.

ORDER PHACOPIDA
 SUBORDER CALYMENINA
  Superfamily Calymenoidea
   Family Calymenidae
   Family Homalonotidae
   Family Carmonidae
   Family Bathycheilidae
 SUBORDER PHACOPINA
  Superfamily Phacopoidea
   Family Phacopidae
   Family Pterygometopidae
  Superfamily Dalmanitoidea
   Family Dalmanitidae
   Family Prosopiscidae
   Family Diaphanometopidae
  Superfamily Acastoidea
   Family Acastidae
   Family Calmoniidae
 SUBORDER CHEIRURINA
  Superfamily Cheiruroidea
   Family Cheiruridae
   Family Pliomeridae
   Family Pilekiidae
   Family Encrinuridae
   Family Staurocephalidae
   Family Hammatocnemidae

LIBRISTOMATE TRILOBITES

Trilobites that either have a natant hypostomal condition or were derived from such trilobites by secondary joining of the hypostome to the cephalic doublure were included in a subclass Libristoma by FORTEY (1990a). This formal subdivison is not adopted here, partly because the analysis necessary to determine other clades at this highest taxonomic level has not yet been done. Nonetheless, the orders below probably comprise a major clade, and hence their diagnoses are interdependent.

Order Proetida

This order was introduced by FORTEY and OWENS (1975) to include families that had been placed in the Illaenina in the previous edition of the *Treatise* (MOORE, 1959), an assignment that is not considered to reflect their true systematic affinities. After some debate (BERGSTRÖM, 1977; FORTEY & OWENS, 1979; CHATTERTON, 1980; LÜTKE, 1980), the order Proetida has achieved wider acceptance, although not invariably accorded ordinal status. The order includes those trilobites that were included by MOORE (1959) in the superfamilies Proetacea, Bathyuracea, Dimeropygacea, and Holotrachelacea, here combined into three superfamilies: Proetoidea, Aulacopleuroidea (see OWENS & HAMMANN, 1990), and Bathyuroidea. Much more is known of ontogenies of Proetida than in 1959, and these demonstrate a common likeness among protaspides (see section on ontogeny). FORTEY (1990a) suggested that the natant condition may have been initiated earlier in ontogeny in Proetida. Although the bulk of the group retains the natant condition in the adult, there are good examples of the secondarily conterminant hypostome in late Proetida and Bathyuridae.

ORDER PROETIDA
  Superfamily Proetoidea
   Family Proetidae
   Family Phillipsiidae
  Superfamily Aulacopleuroidea
   Family Aulacopleuridae
   Family Brachymetopidae
   Family Rorringtoniidae
  Superfamily Bathyuroidea
   Family Bathyuridae
   Family Dimeropygidae
   Family Celmidae
   Family Lecanopygidae
   Family Glaphuridae
   Family Holotrachelidae (downgraded from monotypic superfamily)
   Family Telephinidae

Order Asaphida

The classification of trilobites included in this group was discussed in detail by FORTEY and CHATTERTON (1988). By comparison with MOORE (1959), the Asaphidae and Ceratopygidae are united within the same superfamily, Asaphoidea, based on their glabellar structure, while the Cyclopygoidea includes other families (Nileidae, Taihungshaniidae) besides the highly specialized Cyclopygidae, again based on cephalic characters. The superfamily Remopleuridioidea includes Remopleurididae and some allied families. The superfamily Dikelocephaloidea is used as revised by LUDVIGSEN and WESTROP (1983b) to include saukiids and ptychaspidids as well as Dikelocephalidae. Primitive Asaphida are united in the Anomocaroidea, which includes a number of families retaining the natant hypostomal condition. All the above taxa have a ventral median suture, at least in primitive species, and many of the more advanced members have an inflated, globular protaspis, termed asaphoid by FORTEY and CHATTERTON (1988). The Trinucleoidea is also included within the Asaphida; it was one of the so-called ptychoparioid groups in previous classifications. The systematic position of this important and specialized group has always been difficult to decide. Numerous Ordovician species of raphiophorids and trinucleids have their free cheeks yoked together, but the protaspis invites comparison with the asaphoid protaspis. However, yoked cheeks also occur among Asaphidae and Cyclopygidae, which have a median suture in early species. Liostracinidae include Cambrian species with a probable median suture and that show other points of resemblance to advanced trinucleoids (for example, a pyriform glabella). Inclusion of Trinucleoidea in Asaphida seems to be the best hypothesis available (see CHATTERTON & others, 1994).

The median suture may have arisen by reduction and eventual loss of the rostral plate. An intermediate grade of organization is probably shown by those trilobites that have a small, triangular rostral remnant termed a rostellum by ÖPIK (1967). There is a possibility that this evolved more than once (ROBISON, 1964). While this is conceivable, there is no convincing evidence for it, and the similarity of early Asaphida (together with the Cambrian age of the rostellum-bearing forms) argues against such polyphyly.

ORDER ASAPHIDA
- Superfamily Anomocaroidea
  - Family Anomocaridae
  - Family Pterocephaliidae (includes Housiinae)
  - Family Parabolinoididae
  - Family Dikelokephalinidae
- Superfamily Asaphoidea
  - Family Asaphidae
  - Family Ceratopygidae
- Superfamily Dikelokephaloidea
  - Family Dikelokephalidae
  - Family Saukiidae
  - Family Ptychaspididae
  - Family Eurekiidae
  - Family Loganellidae
- Superfamily Remopleuridioidea
  - Family Remopleurididae
  - Family Kainellidae
  - Family Opipeuteridae
  - Family Bohemillidae
  - Family Auritamiidae
  - Family Idahoiidae
  - Family Hungaiidae
- Superfamily Cyclopygoidea
  - Family Cyclopygidae
  - Family Taihungshaniidae
  - Family Nileidae
- Superfamily Trinucleoidea
  - Family Trinucleidae
  - Family Dionididae (=?Tongxinaspididae)
  - Family Orometopidae
  - Family Raphiophoridae
  - Family Alsataspididae
  - Family Orometopidae (includes Myindidae, Hapalopleuridae, Jegorovaiidae)
  - Family Liostracinidae
- Superfamily Uncertain
  - Family Rhyssometopidae (includes Mapaniidae, Plectriferidae)
  - Family Monkaspididae (=?Chelidonocephalidae)

Order Ptychopariida

The problem of defining the Ptychopariina was discussed above. In the current classification the Ptychopariida includes only libristomates in which the secondary conterminant condition of the hypostome is not far advanced. The most primitive (plesiomorphic) families are lumped into the suborder Ptychopariina, which is dominated by families having the typical morphology as exemplified by *Ptychoparia* itself or *Elrathia.* The families are not all readily definable on unequivocal characters. When more is known of their morphology, they may be assigned as sister groups to one or another of the more derived clades, but for the moment they are retained together.

Two other suborders are included in Ptychopariida: Olenina and Harpina. The former has been well studied from Cambrian and Ordovician stratigraphic sections; all except the very earliest olenids (which have rostral plates) have yoked free cheeks, connected by a vary narrow strip of cephalic doublure. Extremely thin cuticles are typical. Harpina were formerly classified with Trinucleina, but the resemblance between the two groups is probably merely one of convergence. The families Entomaspididae and Loganopeltidae from the Upper Cambrian to Lower Ordovician are considered to be related to Harpina.

ORDER PTYCHOPARIIDA
 SUBORDER PTYCHOPARIINA
  Superfamily Ellipsocephaloidea
   Family Ellipsocephalidae
   Family Protolenidae
   Family Agraulidae
  Superfamily Ptychoparioidea
   Family Ptychopariidae
   Family Marjumiidae
   Family Solenopleuridae
   Family Conocoryphidae
   Family Dokimokephalidae
   Family Onchonotopsidae
   Family Nepeiidae
   Family Crepicephalidae
   Family Lonchocephalidae
   Family Kingstoniidae
   Family Shumardiidae
   Family Asaphiscidae
   Family Coosellidae
   Family Elviniidae (includes Komaspididae)
   Family Cedariidae
   Family Norwoodiidae
   Family Menomoniidae
   Family Bolaspididae
   Family Papyriaspididae
   Family Emmrichellidae
   Family Diceratocephalidae
   Family Tengfengiidae
   Family Lisaniidae
   Family Inouyiidae
   Family Wuaniidae
   Family Lorenzellidae
   Family Proasaphiscidae
   Family Ignotogregatidae
   Family Holanshaniidae
   Family Mapaniidae
   Family Acrocephalitidae
 SUBORDER OLENINA
   Family Olenidae
 SUBORDER HARPINA
   Family Harpetidae
   Family Harpididae
   Family Entomaspididae
 SUBORDER UNCERTAIN
   Family Ityophoridae
    Polyphyletic groups
   Family Catillicephalidae
   Family Raymondinidae
   Family Avoninidae
   Family Plethopeltidae

TRILOBITA ORDER UNCERTAIN

Here are included a number of distinctive taxa that are not accomodated into the broad classification given above. Burlingiidae and Bathynotidae are undoubtedly trilobites, but their place within the group is uncertain. As discussed above, Naraoiidae is regarded as the sister group of the calcified Trilobita.

Family Burlingiidae
Family Bathynotidae
Family Bestjubellidae
Family Naraoiidae

EXPLANATORY NOTES FOR THE CAMBRIAN CORRELATION CHART

By John H. Shergold

BACKGROUND

Biostratigraphic subdivision of the Cambrian probably began earlier in Scandinavia than elsewhere, particularly in Sweden and Norway where pioneering schemes for the Middle and Upper Cambrian, which foreshadowed the subdivisions shown in Table 1, were published between 1854 and 1883 (see Martinsson, 1974). Subsequently, a high-resolution biostratigraphy based on Agnostina was established for the Middle Cambrian by Westergård (1946), who also made contributions to Upper Cambrian biostratigraphy (1922, 1947). An Upper Cambrian zonation based on olenid trilobites was worked out in great detail by Henningsmoen (1957a).

Biostratigraphic division of the Lower Cambrian of Scandinavia has developed at a slower pace than that of the Middle and Upper with the use of local zones. Because the lowest Cambrian lacks trilobites, zonations using trace fossils and small shelly fossils have been established for the Precambrian-Cambrian type area in southeastern Newfoundland (see Laurentia, Table 1.4, "Tommotian" and "Nemakit-Daldynian" faunas). That part of the Lower Cambrian zoned on the basis of trilobites in Scandinavia (Table 1.3) follows the latest correlations of Mens, Bergström, and Lendzion (1990). Essentially this is the scheme of Bergström and Ahlberg (1981), Ahlberg (1985), and Shergold and Brasier (1986) with the substitution of the Zone of *Holmia inusitata* for that of *Holmia* sp. nov. (see Ahlberg, Bergström, & Johansson, 1986).

In Scandinavia, biostratigraphers use stages based on groups of zones; these stages are named after characteristic trilobites, the stage being divided into zones that are defined at specific level.

An Iberian Cambrian biostratigraphy (Table 1.3) was first established by Lotze (1961) in which thirty-two trilobite horizons were recognized and assigned to three informal series (A–C). Sdzuy (1968) described Middle Cambrian stages, subsequently demoted to substages. He also introduced three Lower Cambrian stages (Ovetian–Bilbilian) (Sdzuy, 1971a, 1971b, 1972). Liñán and Fernández-Carrasco (1984) added the Cordubian Stage. This stadial scheme has been reviewed recently by Liñán, Perejon, and Sdzuy (1993), and the trilobites that define the Lower Cambrian Ovetian–Bilbilian interval were discussed. Previously, eleven informal archaeocyathan zones (I–XI) were determined by Perejon (1986). No formal zonation by either trilobites or archaeocyathans has been published. The Cordubian Stage is defined on the basis of ichnofossils, which include *Phycodes pedum* (see Liñán, Perejon, and Sdzuy, 1993, for ranges).

The stadial divisions shown here (Table 1.3) for the Lower and lowest Middle Cambrian of Morocco are based on the recent conclusions of Geyer (1990a, 1990b, 1993). These are based essentially on the pioneering work of Hupé (1952, 1953a, 1960) and on revisions by Sdzuy (1971a, 1971b, 1972, 1978) and Geyer (1983). The two stages, Soussien and Issafénien, recognized by Hupé have been replaced by the three shown in Table 1.3. The Tissafinian Stage, the Aguilizien Substage of Hupé, is now regarded by Geyer (1990a) as lowermost Middle Cambrian following the discovery of a paradoxidoid and an Olenellina trilobite together in the *Cephalopyge notabilis* Zone. An independent archaeocyathan biostratigraphy calibrated to the Hupé (1960) trilobite zonation has been published by Debrenne (1990).

In the Cambrian of Laurentia, with the exception of the lowest Cambrian, the biostratigraphy is based on a succession of trilobite genera (Fig. 254). Assemblages of species within such generic zones are regarded variously as subzones, faunizones, and biozones, among others, but these assemblages are the most highly resolved biostratigraphic units used for correlation. Zones based on genera are grouped into stages that have developed historically and often in multiplicity. Neither the stages of the Lower nor Middle Cambrian are satisfactorily defined. WALCOTT originally called the Lower Cambrian the Georgian Epoch, but, according to RESSER and HOWELL (1938), he subsequently (1912b) substituted the name Waucoban when it was realized that the Georgian contained rocks younger than Early Cambrian. Nevertheless, LOCHMAN-BALK and WILSON (1958) and ÖPIK (1975b) have continued to use the term Georgian. PALMER (1971) preferred to use neither. Waucoban, however, is favored here because it apparently refers to definite trilobite-bearing Lower Cambrian zones in North America: *"Fallotaspis," "Nevadella,"* and *Bonnia-Olenellus* (PALMER & REPINA, 1993).

A Lower Cambrian biochronology has been developed recently for the Avalonian part of North America as a result of the deliberations on the Precambrian-Cambrian boundary. There, the biochronological interval covered by the previously proposed Etcheminian (MATTHEW, 1899a) and Hanfordian (HAYES & HOWELL, 1937) Series has been revised by LANDING (1993) and LANDING and others (1989), who recognized the Placentian and Branchian Series, in ascending order.

As with the Lower Cambrian, two series names have long been available for the Middle Cambrian of Laurentian North America: Acadian and Albertan. Because Acadian, like Georgian, has several connotations, Albertan was used for the *Bathyuriscus-Elrathina (=Ehmaniella)* and *Bolaspidella* Zones. The Upper Cambrian Croixian Series (WINCHELL, 1873), originally Potsdamian or Saratogan (WALCOTT, 1912a), traditionally contains the Dresbachian (WINCHELL, 1886), Franconian (HOWELL & others, 1944), and Trempealeauan (HOWELL & others, 1944) Stages defined from the Mississippi Valley and applied continent-wide.

An alternative stadial terminology for the upper Middle and Upper Cambrian of Laurentian North America has been applied by LUDVIGSEN and WESTROP (1985). The bases of their Marjuman, Steptoean, and Sunwaptan Stages are tied to well-defined and readily correlated trilobite assemblage-zones: *Acidusus atavus, Aphelaspis (Glyptagnostus reticulatus),* and *Irvingella major* Zones. They are shown here (Table 1.2, 1.4) as an alternative to the traditional stages. Although regarded by LUDVIGSEN and WESTROP (1985) as an initial Ordovician stage, the Ibexian is here regarded as terminal Cambrian, at least initially (see discussion below). Its base, at the first appearance of the conodont *Cordylodus proavus,* is widely correlatable.

The Lower Cambrian of the Siberian Platform, characterized by its succession of small shelly fossils and archaeocyathan biotas, has become a standard for the biostratigraphic subdivision of carbonate-platform sequences. Most of the stages shown on Table 1.3 are those recommended by SPIZHARSKI and others (1983) and SPIZHARSKI and others (1986) and are the official stage names currently recognized by the Interdepartmental Stratigraphic Committee of Russia. This committee has traditionally regarded the lowest Cambrian stage as the Tommotian. The newly defined base of the Cambrian in Newfoundland, however, now demands recognition of the Nemakit-Daldynian (KHOMENTOVSKY, 1976) as the initial Lower Cambrian stage of the Siberian Platform (ROZANOV & ZHURAVLEV, 1992).

The Middle Cambrian of the Siberian Platform, containing Agnostina, is readily correlatable, although the Lower-Middle Cambrian boundary is problematical (see below). That part of the Amgaian Stage containing *Triplagnostus gibbus* and the first appearance of *Hypagnostus parvifrons* at the base of the Mayaian Stage are significant datum points. Upper Cambrian biostratigraphic division (Table 1.1) follows IVSHIN and POKROVSKAYA (1968) in recognizing the Tuorian Stage. Their Shidertan Stage and those stages recommended by SPIZHARSKI and others (1986) are based on Kazakh units and are not used here for the Siberian Platform.

In Kazakhstan (Table 1.2, 1.4), the Upper Cambrian stadial scheme established by ERGALIEV (1980) and recommended by SPIZHARSKI and others (1983, 1986) is demonstrably incomplete, as is that of ASTASHKIN and others (1991). In Lesser Karatau sections, southern Kazakhstan, and particularly at Batyrbai, Upper Cambrian stages younger than Aksayan are recognized on the basis of both trilobites and conodonts (APOLLONOV, CHUGAEVA, & DUBININA, 1981; CHUGAEVA & APOLLONOV, 1982; APOLLONOV & CHUGAEVA, 1982; DUBININA, 1982). The Batyrbaian and Ungarian stages, defined by trilobites and conodonts, were proposed by APOLLONOV (1991) and are accepted here, even though their published correlations may not be entirely correct.

ERGALIEV (1990) introduced new stages for the Kazakh Middle Cambrian sequences. The Amgaian Stage of the Siberian Platform is replaced by Tyesaian, Mayaian by Zhanarykian, and additionally the Ayusokkanian extended downward to encompass the whole of the range of *Lejopyge laevigata.* The last goes some way to resolving the Mayaian-Ayusokkanian boundary in the earlier scheme. The Sakian remained unchanged in concept, as did the Aksayan, but a new Kazakhstanian stage was proposed to replace Batyrbaian. This seems unnecessary since nothing new is added. Accordingly, this stage is not included on the chart.

Traditionally, Chinese Cambrian biostratigraphy has been closely tied to lithostratigraphic units. All the stage names currently in use relate to formations and, by inference, the faunas they contain diagnose the stages. Facies changes are not accounted for, and the units are assumed to be correlatable across China. The Chinese column in Table 1.2, 1.4 follows the systems proposed by XIANG and others (1979, 1981) and W. CHANG (1980, 1988), which were in turn derived from the zonal biostratigraphy outlined by LU and others (1974). Following current Chinese official preference, the stage names are now given in Pinyin transliteration.

The Lower Cambrian in southwestern China has been exhaustively investigated in connection with the search for the Precambrian-Cambrian boundary, and the placement of stage boundaries and their correlation, particularly with Siberia and Kazakhstan, has fluctuated considerably since their original definition. The correlation suggested here is based on those made by SHERGOLD and BRASIER (1986), SHERGOLD, LAURIE, and SUN (1990), and BRASIER (in MCKERROW, SCOTESE, & BRASIER, 1992), in preference to those of LANDING (1992, 1993). In these correlations, the Toyonian Stage of Siberia is considered to encompass the interval from the mid-Canglangpuan to the Maozhuangian of China and most of the *Proampyx linnarssoni* Zone and *Acadoparadoxides (Baltoparadoxides) oelandicus* Stage of Scandinavia.

As elsewhere, the interval represented by the Xuzhuangian Stage is closely confined by the *Triplagnostus gibbus* and *Acidusus atavus* Zones. The Middle-Upper Cambrian transition has been addressed by DONG (1990) and XIANG (1991), who relied on the last appearance of *Lejopyge laevigata* to indicate the top of Middle Cambrian rocks (see also DAILY & JAGO, 1975), but this is recognized largely in the Chiangnan Belt (LU, ZHU, & others, 1974) and the northern marginal belt of the North China Platform. Strata of the Gushanian Stage show an endemized Australo-Sinian trilobite biofacies, which does not contain *L. laevigata.* The concepts of its constitutent zones, based on *Blackwelderia* and *Drepanura,* however, can be supported by correlation with Australia (ÖPIK, 1967; DAILY & JAGO, 1975). Zhangshanian and Fengshanian Stages are also based on the faunas of carbonate-platform environments representing Australo-Sinian Upper Cambrian biofacies (SHERGOLD, 1988), and their intercontinental utility depends also on the precision with which they can be correlated with the faunas of the Chiangnan Belt.

The history of the development of the Cambrian time scale in Australia (Table 1.2, 1.4) has been discussed at length by SHERGOLD (1989). WHITEHOUSE (1927, 1930) was the first to erect a detailed subdivision of the Cambrian in Australia, and with subsequent additions and modifications (WHITEHOUSE, 1931, 1936, 1939; WHITEHOUSE in DAVID, 1932; DAVID & BROWNE, 1950) this scheme remained current until the research of ÖPIK. With the advantage of WESTERGÅRD'S (1946) conclusions in Scandinavia, ÖPIK was able to formulate a more highly resolved Middle and lower Upper Cambrian biostratigraphy. The uppermost Cambrian series has also been intensely investigated, and a complete zonation is available for the eastern Georgina basin (SHERGOLD, 1989, 1993). A complete, local, stage nomenclature has been applied to both the Middle and Upper Cambrian in the same area. No local stage terminology has been established for the Lower Cambrian of Australia. The stage nomenclature of the Siberian Platform, however, has been applied to the archaeocyathan and small-shelly-fossil-bearing deposits of South Australia, the Amadeus basin and southwestern Georgina basin of central Australia. "Upper Atdabanian–Lower Botomian" (Qiongzhusian) trilobite zones have been proposed in South Australia (JELL in BENGTSON & others, 1990).

In northern Australian basins, the Middle Cambrian has been zoned wholly on the basis of trilobites, particularly Agnostina. Original concepts relating to the Ordian and Templetonian stages have been reviewed by SOUTHGATE and SHERGOLD (1991) with the result that the Ordian Stage (ÖPIK, 1967) has been merged with the lower Templetonian because the latter is so difficult to discriminate from it biostratigraphically. The upper Templetonian (the *Triplagnostus gibbus* Zone) logically belongs with the succeeding Floran Stage (ÖPIK, 1979), which contains the zones of *Acidusus atavus* and *Euagnostus opimus.* This is in turn was succeeded by the Undillan (ÖPIK, 1979) and Boomerangian (ÖPIK, 1979) stages, which cover the zones of *Ptychagnostus punctuosus* to *Lejopyge laevigata.* The Mindyallan Stage (ÖPIK, 1963) straddles the Middle-Upper Cambrian boundary, which was placed within the *Acmarhachis quasivespa* Zone by DAILY and JAGO (1975). Idamean (ÖPIK, 1963), Iverian (SHERGOLD, 1993), Payntonian, and Datsonian stages (JONES, SHERGOLD, & DRUCE, 1971) complete the Upper Cambrian stadial scheme, the last two subdivided by zones based on both trilobites and conodonts (NICOLL & SHERGOLD, 1991; SHERGOLD & NICOLL, 1992).

CONTENTIOUS LEVELS OF CORRELATION

Traditionally, Lower Cambrian rocks were thought to have been characterized by the occurrence of Olenellina, Redlichiina, and Protolenidae; the Middle Cambrian by Paradoxidoidea; and the Upper Cambrian by Olenidae. With increased biostratigraphic discrimination, these divisions are no longer so clear-cut.

In Spain and Morocco there is an apparent overlap of protolenid, holmiid, and ellipsocephalid with paradoxidoid trilobites (SDZUY, 1972; GEYER, 1990a, 1990b, 1993), which has led GEYER (1990a, 1990b, 1993) to correlate the Moroccan Tissafinian Stage (Table 1.3) with the *Proampyx linnarssoni* and *Acadoparadoxides insularis* Zones (i.e., lower *Acadoparadoxides (Baltoparadoxides) oelandicus* Stage) of Scandinavia and the Toyonian Stage and lower part of the Amgaian Stage in Siberia. In China and Australia (Table 1.4), late species of *Redlichia* occur in the Longwangmiaoan and Ordian Stages. Since WALCOTT'S work (1912c), Chinese authorities have regarded rocks containing *Redlichia* as Lower Cambrian, as have

Australian authorities until the mid-1950s. Öpik (1968) developed his Ordian Stage from an earlier concept of Whitehouse (1930, 1931, 1936). Characterized by the occurrence of *Redlichia,* the Ordian Stage also contains the first species of *Xystridura,* which Öpik (1975a) regarded as a possible affiliate of both Protolenidae and Paradoxididae. Hypostomal morphology suggests a relationship between *Xystridura* and *Paradoxides* (Whittington, 1988a). Thus, a relationship between Paradoxidoidea and Redlichiina is surmised. Jell (in Bengtson & others, 1990, p. 310) denied the relationship between Xystriduridae and Paradoxididae, believing that it is the result of contemporaneous homeomorphy. Accordingly, he considered the Xystriduridae to represent a family of Ellipsocephaloidea that should be classified alongside Ichangiidae, Protolenidae, and Ellipsocephalidae. The correlations suggested here favor a relationship between Xystriduridae and Paradoxididae and the conclusions of Geyer (1990a, 1990b). They are supported by the correlation of the succeeding sequences of the upper *Acadoparadoxides oelandicus* Stage (*Eccaparadoxides pinus* Zone) in Scandinavia with the Lower Templetonian of Australia and the Maozhuangian Stage of China, postdating the ranges of Olenellina, Redlichiina, and Protolenidae (see also W. Zhang & Jell, 1987; Kruse, 1990).

The placement of the Middle-Upper Cambrian boundary is debatable but less problematical than the Lower-Middle Cambrian boundary. There is a growing consensus of support for the observations of Daily and Jago (1975) that the disappearance of *Lejopyge laevigata* marks the end of Middle Cambrian time. This is indicated by current work in China (e.g., Dong, 1990; Xiang, 1991) and by the revision of the Ayusokkanian Stage by Ergaliev (1990) in Kazakhstan. The disappearance of *L. laevigata* is recorded primarily in outer-shelf environments. In carbonate-platform rocks, correlation must be made through intermediate steps via other Agnostina. Based on this criterion, the Ayusokkanian, Mindyallan, and Dresbachian stages straddle the Middle-Upper Cambrian boundary. Both the problems of this boundary and those of the Lower-Middle Cambrian boundary were avoided by Ludvigsen and Westrop (1985) and Pratt (1992), who recognized only Lower and Upper Cambrian, the boundary between them lying at the base of their Marjuman Stage, at the base of the *Bolaspidella* Zone (=*Acidusus atavus* Zone).

The exact position of the Cambrian-Ordovician boundary has yet to be agreed upon internationally. There is considerable support for defining the base of the Ordovician System at the base of the Tremadoc Series or its correlative, which in biostratigraphic terms means at the first appearance of the nematophorus graptoloids or at the conodont biostratigraphic datum closest to this event. Initial correlation of the base of the Tremadoc with the first appearance of *Cordylodus proavus* is incorrect by the magnitude of a stage. The Zone of *Cordylodus lindstromi* is regarded here as the closest correlate to that of *Dictyonema flabelliforme sociale.* Therefore, the upper *Peltura* and *Acerocare* Zones of Scandinavia, the Ungurian Stage of Kazakhstan, the Xinchangian Stage of China, the Datsonian Stage of Australia, and the basal Ibexian Stage are wholly or partly uppermost Cambrian.

TABLE 1.1. *Correlation Chart of the Cambrian (part 1).*

		Scandinavia	Iberia	Morocco	Siberia	
Ordovician	*Dictyonema*	*Dictyonema flabelliforme norvegicum*				
		Dictyonema flabelliforme flabelliforme				
		Dictyonema flabelliforme sociale				
Upper Cambrian	*Acerocare*	*Acerocare ecome*				
		Westergaardia				
		Peltura costata				
		Peltura transiens				
	Peltura	*Peltura scarabaeoides*				
		Peltura minor				
		Protopeltura praecursor				
	Leptoplastus	*Leptoplastus stenotus*				
		Leptoplastus angustatus				
		Leptoplastus ovatus				
		Leptoplastus crassicornis				
		Leptoplastus raphidophorus				
		Leptoplastus paucisegmentus				
	Parabolina	*Parabolina spinulosa*				
		Parabolina brevispina				
	Olenus Zones	*Olenus scanicus*			Tuoriam	
		Olenus dentatus				
		Olenus attenuatus				
		Olenus wahlenbergi				*Glyptagnostus reticulatus*
		Olenus truncatus				
		Olenus gibbosus				
	Agnostus pisiformis	*Agnostus pisiformis*				*Glyptagnostus stolidotus* *Agnostus pisiformis-Proagnostus fecundus*

TABLE 1.2. *Correlation Chart of the Cambrian (part 2).*

Kazakhstan		
Ungurian	*Cordylodus caseyi*	*Dikelocephalina*
	Cordylodus prion	*Euloma limitaris-Taoyuania*
	Cordylodus oklahomensis	
	Cordylodus proavus	
Batyrbaian	*Proconodontus muelleri-Eoconodontus notchpeakensis*	*Lotagn. hedini*
		Harpidoides
		Lophosaukia
Aksayan	*Westergaardodina-Furnishina*	*Trisulcagnostus trisulcus*
		Eolotagnostus scrobicularis
		Neoagnostus quadratiformis
	Oncagnostus ovaliformis	
	Oncagnostus kazachstanicus	
	Pseudagnostus pseudangustilobus	
Sakian	*Ivshinagnostus ivshini*	
	Pseudagnostus "curtare"	
	Oncagnostus longiformis	
	Glyptagnostus reticulatus	
Aryusokkanian	*Glyptagnostus stolidotus* *Agnostus pisiformis-Proagnostus fecundus*	
	Lejopyge laevigata	

China			
Xinchangian	*Cordylodus angulatus*	*Wanliangtingia*	
	Cordylodus lindstromi	*Yosimuraspis*	
	Cordylodus intermedius	*Richardsonella-Platypeltoides*	
	Cordylodus proavus	*Mictosaukia Fatocephalus*	*Missisquoia perpetis*
Fengshanian	*Cambrooistodus*		*Mict. striata* *Mict. angusti*
		Tsinania-Ptychaspis	
Changshanian	*Proconodontus muelleri*	*Kaolishania pustulosa*	
	Proconodontus posterocostatus		
	Proconodontus tenuiserratus		
	Maladioidella		
	Changshania conica		
	Chuangia batia		
Gushanian	*Drepanura*		
	Blackwelderia		

Australia	
Warendan	*Chosonodina herfurthi-Cordylodus angulatus*
	Cordylodus lindstromi
Datsonian	*Cordylodus prolindstromi Hirsutodontus simplex*
	Cordylodus proavus
Payntonian	*Mictosaukia perplexa*
	Neoagnostus quasibilobus-Shergoldia nomas
	Sinosaukia impages
Iverian	*Rhaptagnostus clarki maximus-Rhaptagnostus papilio*
	Rhaptagnostus bifax-Neoagnostus denticulatus
	Rhaptagnostus clarki prolatus-Caznaia sectatrix
	Rhaptagnostus clarki patulus-Caznaia squamosa
	Hapsidocare lilyensis
	Peichiashania tertia-Peichiashania quarta
	Peichiashania secunda-Prochuangia glabella
	Wentsuia iota-Rhaptagnostus apsis
	Irvingella tropica
Idamean	*Stigmatoa diloma*
	Erixanium sentum
	Proceratopyge cryptica
	Glyptagnostus reticulatus
Mindyallan	*Glyptagnostus stolidotus*
	Acmarhachis quasivespa
	Erediaspis eretes

Laurentia			
Canadian	Ibexian	*Symphysurina*	*Symphysurina bulbosa*
			Symphysurina brevispicata
		Missisquoia	*Missisquoia typicalis* *Missisquoia depressa*
Trempealeauan		*Saukia*	*Eurekia apopsis*
	Sunwaptan		*Saukiella serotina*
			Saukiella junia
			Saukiella pyrene-Rasettia magna
Franconian		*Ptychaspis-Prosaukia*	*Ellipsocephaloides*
			Idahoia
			Taenicephalus
			Elvinia
Dresbachian	Steptoean		*Dunderbergia*
			Aphelaspis
	Marjuman		*Crepicephalus*
			Cedaria

TABLE 1.3. *Correlation Chart of the Cambrian (part 3).*

	Scandinavia		Iberia		Morocco		Siberia	
		Agnostus pisiformis						*Glyptagnostus stolidotus* *Agnostus pisiformis-Proagnostus fecundus*
Middle Cambrian	*Paradoxides forchhammeri*	*Lejopyge laevigata*		Solenopleuropsidae free			Mayaian	*Lejopyge laevigata-Aldanaspis truncata*
		Jincella brachymetopa						*Anomocarioides limbataeformis*
		Goniagnostus nathorsti						
	Paradoxides paradoxissimus	*Ptychagnostus punctuosus*	Caesaraugustinian	*Solenopleuropsis* *Pardailhania* *Badulesia*				*Anopolenus henrici-Corynexochus perforatus*
		Hypagnostus parvifrons						
		Tomagnostus fissus-Acidusus atavus					Amgaian	*Tomagnostus fissus* *Triplagnostus gibbus* *Kounamkites*
		Triplagnostus gibbus						
	Acadoparadoxides (Baltoparadoxides) oelandicus	*Acadoparadoxides pinus*						
			Leonian	*Acadolenus* *Conocoryphe ovata* *Eoparadoxides mureroensis*	Tissafinian	*Ornamentaspis frequens* *Cephalopyge notabilis* *Hupeolenus*		
		Acadoparadoxides insularis						
								Oryctocara
? Lower Cambrian	*Protolenus*	*Proampyx linnarssoni*	Bilbilian	Archaeocyath Zone XI			Toyonian	*Anabaraspis splendens*
								Lermontovia grandis
								Bergeroniellus ketemensis
			Marianian	Archaeocyath Zones VIII–X	Banian	*Sectigena* *Antatlasia gutta-pluviae* *Antatlasia hollardi*	Botomian	*Bergeroniaspis ornata*
								Bergeroniellus asiaticus
	Holmia	*Holmia kjerulfi*						*Bergeroniellus gurarii*
			Ovetian	Archaeocyath Zones I–VII				*Bergeroniellus micmacciformis-Erbiella*
							Atdabanian	*Judomia-Uktaspis*
		Holmia inusitata						*Pagetiellus anabarus*
		Schmidtiellus mickwitzi			Issendalenian	*Daguinaspis* *Choubertella* *Fallotaspis tazemmourtensis* *Eofallotaspis*		*Fallotaspis*
								Profallotaspis jakutensis
			Cordubian				Tommotian	*Dokidocyathus lenaicus*
		sub-*Holmia*						
								Dokidocyathus regularis
								Aldanocyathus sunnaginicus
								Nemakit-Daldynian faunas

TABLE 1.4. *Correlation Chart of the Cambrian (part 4).*

Kazakhstan		China		Australia		Laurentia		
Ayusokkanian	*Glyptagnostus stolidotus* *Agnostus pisiformis-* *Proagnostus fecundus*	Gushanian	*Drepanura*	Mindyallan	*Glyptagnostus stolidotus*	Dresbachian		*Crepicephalus*
			Blackwelderia		*Acmarhachis quasivespa*			*Cedaria*
	Lejopyge laevigata							
		Zhangxian	*Damsella-Yabeia* *Leiopeishania* *Taitzuia-Poshania* *Amphoton* *Crepicephalina*		*Erediaspis eretes*			
				Boomerangian	*Lejopyge laevigata*	Albertan	Marjuman	*Bolaspidella*
Zhanarykian	*Leiopyge armata*							
				Undillan	*Goniagnostus nathorsti*			
	Goniagnostus nathorsti							
					Ptychagnostus punctuosus			
	Ptychagnostus punctuosus							
				Upper Templetonian-Floran	*Euagnostus opimus* *Acidusus atavus* *Triplagnostus gibbus*			
Tyesaian	*Acidusus atavus*	Xuzhuangian	*Bailiella-Lioparia* *Poriagraulos* *Hsuchuangia-Ruichengella*					
	Ptychagnostus intermedius							*Ehmaniella*
	Peronopsis ultimus	Maozhuangian	*Shantungaspis* *Yaojiayuella*	Ordian-Lower Templetonian	*Xystridura templetonensis-* *Redlichia chinensis*			*Glossopleura*
								Albertella
								Plagiura-Poliella
		Longwangmiaoan	*Redlichia nobilis* *Redlichia chinensis*					
						Waucoban		*Bonnia-Olenellus*
		Canglangpuan	*Megapalaeolenus* *Palaeolenus* *Drepanuroides*	Lower Cambrian	*Pararaia janeae*			
			Yunnanaspis *Yiliangella* *Malungia*					
					Pararaia bunyerooensis			
					Pararaia tatei			
		Qiongzhusian	*Eoredlichia-Wutingaspis*		*Abadiella huoi*			
			Abadiella					*"Nevadella"*
		Meishucunian	"Tommotian" faunas					*"Fallotaspis"*
						"Tommotian" faunas		
			"Nemakit-Daldynian" faunas			"Nemakit-Daldynian" faunas		

MORPHOLOGICAL TERMS APPLIED TO TRILOBITA

H. B. WHITTINGTON and S. R. A. KELLY

This glossary is based on that of HARRINGTON and others (in MOORE, 1959) and terms proposed since that date. Earlier definitions have been modified to reflect the results of research over the past 30 years. For clarity, all paired structures are referred to in the singular. Terms considered to be of lesser or greater importance are not distinguished here by typeface, but those regarded as synonyms are thought to be less desirable alternatives. Many terms are discussed and illustrated in the introductory sections.

A compilation by S. R. A. Kelly was the starting point for this glossary, the terms included and their definitions having been changed by H. B. Whittington as the introductory sections were prepared. Comments from P. D. Lane and other contributing authors are gratefully acknowledged, as are the terminology for Agnostina prepared by J. H. Shergold and J. R. Laurie (Fig. 6, 11, 13) and the collaboration of W. H. Fritz and A. R. Palmer on terms applicable to Olenellina (Fig. 16).

abathochroal eye. Similar to schizochroal eye in that lenses were separated, but lacking scleral projections and intrascleral membranes. Each lens probably with a separate cornea fixed at the lens margin to the interlensar sclera.

abaxial. Away from axial line.

accessory furrow. A diagonal furrow in the pygidium of *Pseudagnostus* arising at the posterolateral corner of the second axial ring and directed abaxially and rearward (syn., pseudofurrow).

accessory upper horizontal row. Row of lenses in eye lying above upper horizontal row but consisting of few lenses and confined to posterior part of visual surface.

acrolobe. Portion of cephalon or pygidium enclosed within border furrow in Agnostina. Described as constricted when lateral margin curves slightly adaxially and unconstricted when lateral margin maintains constant curvature.

adaxial. Toward the axial line.

aggregate eye. See schizochroal eye.

ala (pl., alae). Smooth, depressed area adjoining posterolateral portion of glabella in Harpetidae (syn., alar lobe).

alar furrow. Curved furrow bounding ala.

alar lobe. See ala.

alimentary canal. Digestive tract extending from mouth to anus.

anaprotaspis (pl., anaprotaspides). Smallest protaspides in a size series in which protopygidium is supposedly unrecognizable. Inadequately defined and not recommended as a subdivision of protaspid period.

antenna (pl., antennae). Multijointed sensory appendage attached to front part of cephalon on ventral side.

antennal notch. Notch in the anterior cephalic border immediately outside of where the connective suture crosses the border in, for example, Odontopleuridae (syn., antennular notch).

antennary pit. See fossula.

antenniform cercus (pl., cerci). Uniramous, multijointed appendage immediately behind posterior limb, probably attached to the telson; known only in *Olenoides serratus* (syn., caudal ramus, cercus).

antennular notch. See antennal notch.

antennular pit. See fossula.

anterior accessory area. See anterior pleural band.

anterior accessory ridge. Ridge on anterior pleural band separated by a flattened area (the pleural furrow) from principal pleural ridge.

anterior arch. Formed by anterior border of cephalon, as seen in anterior view, rising dorsally to midline because of convexity of cephalon.

anterior area (of fixed cheek). See anterior area (of fixigena).

anterior area (of fixigena). Portion of fixigena in front of preglabellar furrow and eye ridge. If eye ridge is absent, posterior boundary of the area is marked off by imaginary transverse line passing through anterior extremity of palpebral lobe. This area is the left or right side of the frontal area (syn., anterior area of fixed cheek, anterior fixigena, anterior region of fixigena, preocular cheek).

anterior baccular ridge. Short, low ridge running anteriorly on floor of the axial furrow from the baccula to behind the anterior lateral glabellar lobe in Eodiscidae.

anterior band of pleura. See anterior pleural band.

anterior border (of cephalon). Portion of cephalic border between anterior branches of facial sutures, when anterior branches of suture cross border; otherwise term is ill defined.

anterior border (of hypostome). Extends between anterior wings in front of middle body; bounded by anterior border furrow.

anterior border furrow (of cephalon). Portion of border furrow bounding anterior border (syn., front furrow, frontal furrow).

anterior border of cranidium (in Encrinuridae). Extends between axial furrows and is bounded by preglabellar furrow and rostral and facial sutures (previously referred to as a portion of preglabellar field) (syn., false preglabellar field, pseudoglabellar area).

anterior boss. See fossular apodeme.

anterior branch (of facial suture). Portion of facial suture lying anterior to eye [syn., anterior section (of facial suture), preocular branch (of facial suture), preocular suture].

anterior field of fixigena. Portion of fixigena in front of eye ridge and glabella and inside anterior border furrow; this area is the left or right side of frontal field (syn., anterior fixigenal field).

anterior fixigena. See anterior area (of fixigena).

anterior fixigenal field. See anterior field of fixigena.

anterior fixigenal spine. Prominent anterior spine on protocranidium of protaspis; may be adjacent to either branch of facial suture.

anterior flange. See flange.

anterior fossula. See fossula.

anterior furrow. Furrow bounding laterally the preglabellar area in *Neseuretus.* Also used for false preglabellar furrow in Encrinuridae, and for transglabellar furrow in Agnostina.

anterior glabellar furrow. See lateral glabellar furrow.

anterior half rib. See articulating half rib.

anterior limb. See frontal area.

anterior lobe (of glabella). Portion of glabella anterior to transglabellar furrow in Agnostina (syn., anteroglabella). See also frontal lobe.

anterior lobe (of hypostome). Portion of middle body of hypostome in front of middle furrows.

anterior median process. See frontal process.

anterior node. Occurring in axial furrow in the position occupied by fossula in some trilobites as in *Dechenella (Pedinodechenella).* Also used for pit in visceral surface of cephalon, situated between fossula and cephalic margin; preserved as small node on internal mold in the illaenid *Cybantyx.*

anterior ocular line. Ridge in Olenellina that curves outward and backward from anterior end of visual surface of eye toward the genal angle.

anterior pit. See fossula.

anterior pleural band. Strip of thoracic or pygidial pleura bounded posteriorly by deepest part of pleural furrow (syn., anterior accessory area, anterior band of pleura, propleura, propleuron). See also articulating half rib.

anterior pleural spine. Extension of distal end of anterior pleural band.

anterior region (of fixigena). See anterior area (of fixigena).

anterior section (of facial suture). See anterior branch (of facial suture).

anterior wing (of hypostome). Extension of anterolateral angle of hypostome.

anterior wing process (of hypostome). Rounded boss or thornlike protuberance on interior (dorsal) surface of anterior wing.

anteroaxis. Anterior portion of axis of pygidium in Agnostina, including first two axial rings (referred to as M1 and M2, numbering backward from the anterior margin).

anteroglabella. Region in front of transglabellar furrows 1S, as in *Centropleura;* alternative term for anterior lobe of glabella in Agnostina.

anterolateral furrow. Lateral portion of transglabellar furrow in Agnostina, when transglabellar furrow is interrupted by the axial glabellar node.

anterolateral lobe of posterior lobe of glabella. In Agnostina a low inflation on external surface immediately behind transglabellar or anterolateral furrow; on internal mold it forms the anterolateral muscle scar impression.

anteromedian depression. Depression in sagittal line that may be in the preglabellar furrow or extend forward from it or may join the longitudinal median glabellar furrow.

antirostral hood. Low swelling of frontal area reflecting shape of rostral plate.

apodemal pit. Excavation in external surface of exoskeleton corresponding to apodeme on internal surface (syn., appendiferal pit).

apodemal sector. Anterior portion of axis of pygidium in which inter-ring furrows have lateral apodemal pit and apodeme on inner surfaces.

apodeme. Process presumably for attachment of muscles or ligaments, formed by inbending or thickening of dorsal exoskeleton on internal side of exoskeleton (syn., appendifer).

appendage. See biramous appendage (or limb).

appendifer. See apodeme.

appendiferal pit. See apodemal pit.

arc. Curving row of pits on trinucleid fringe (syn., concentric row).

articulated pleura. See inner portion of pleura.

articulating boss (and socket). Corresponding structures on margins of thoracic segment, posterior margin of cephalon, and anterior margin of pygidium. See also axial process, axial socket, fulcral process, fulcral socket, ring process, ring socket.

articulating furrow. Transverse groove on external surface formed by transverse fold in exoskeleton separating articulating half ring from axial ring.

articulating half rib. Term applied to anterior pleural band of pygidium (syn., anterior half rib).

articulating half ring. Extension of axial ring anterior to articulating furrow that passes under posterior doublure of next anterior axial ring (syn., axial articulating half ring, half ring).

articulating socket (and boss). See articulating boss (and socket).

asaphid suture. Cephalic suture in which two anterior branches (or sections) meet in the midline, either marginally or intramarginally on the dorsal side and are continued across the doublure by a median suture (syn., isoteliform suture, niobiform suture).

asaphoid protaspis. Spherical or ovoid in form; doublure semitubular in shape, extending far back; with marginal cephalic suture and median suture in later developmental stages; librigena lacks genal spine; hypostome is relatively large and spinose. The term asaphoid as used here does not imply that all species having such a protaspis are classified in the superfamily Asaphoidea (syn., nonadult-like protaspis).

asymmetric pygidial rib. Rib that slopes steeply to the pleural furrow posterior to it and slopes less steeply anteriorly.

attached (condition). See hypostome.

axial articulating half ring. See articulating half ring.

axial bar. Convex floor of the articulating furrow of the pygidium in Agnostina.

axial furrow. Groove on external surface formed by fold in exoskeleton that outlines axial region of cephalon, thorax, and pygidium (syn., circumaxial furrow, dorsal furrow, rachial furrow).

axial glabellar carina. A narrow, exsagittal ridge between the axial and terminal nodes of the glabella, situated immediately abaxial to the sagittal, axial glabellar sulcus in internal molds of Pseudagnostinae.

axial glabellar node. In Agnostina an elongate node lying near midlength of glabella, either between (condition known as papilionate) or behind (condition known as spectaculate) the anterolateral lobes of the posterior glabellar lobe. An axial glabellar carina may run back from the node to the terminal glabellar node (syn., axial node of glabella, median node). See also glabellar node.

axial line. See sagittal line.

axial lobe. See axis.

axial node. Median (or paired) tubercle on external surface of axial ring of thorax or pygidium.

axial node of glabella. See axial glabellar node.

axial process. Projection from anterior edge of thoracic segment at axial furrow.

axial region. See axis.

axial ridge. Triangular projection of axis over posterior border of pygidium as in Proetoidea.

axial ring. Central portion of thoracic segment or of a segment of pygidium, bounded laterally by axial furrow (syn., rachial ring, ring). May be subdivided by intra-annular furrow into preannulus and postannulus.

axial shield. Articulated exoskeleton lacking librigenae, rostral plate, and hypostome (i.e., consists of articulated cranidium and thoracopygon).

axial socket. Indentation on posterior edge of axial furrow of thoracic pleura into which axial process fits.

axial spine. Median (or paired) pointed structure projecting from external surface of axial ring.

axiolobate. Referring to Agnostina with basic unmodified pygidial axial lobe.

axis (pl., axes). Median region of dorsal exoskeleton, bordered by axial furrow including preglabellar furrow (syn., axial lobe, axial region, rachis, rhachis).

axis (of pygidium). Median region of pygidium, bordered by axial furrow (syn., pygorachis). May be subdivided into apodemal and post-apodemal sectors.

axis (of thorax). Median region of thorax, outlined by axial furrow.

baccula (pl., bacculae). Swelling flanking posterior portion of glabella, which may be separated from glabella by axial furrow or may merge with anterolateral corner of occipital ring and which may be separated from fixigena by baccular furrow or may merge into fixigena.

baccular furrow. Furrow separating baccula from fixigena; may be considered the lateral part of the axial furrow if the baccula is within the axial furrow as in Eodiscidae.

band furrow. Furrow delimiting posterior band of occipital and axial thoracic rings in asaphids.

basal glabellar furrow. See lateral glabellar furrow.

basal lobe (of glabella). See lateral glabellar lobe. In Agnostina, triangular or pear-shaped in outline, situated at posterolateral corner of glabella and separated from it by curved or sinuous basal furrow; may be effaced.

beak. See frontal process.

Bertillon pattern. Pattern of anastomosing, subconcentrically arranged, symmetrical ridges (lirae) on external surface resembling a fingerprint (syn., fingerprint pattern). See also hapsidium.

bicomposite glabellar lobe. See bullar lobe.

bigeniculate (glabellar furrow). Glabellar furrow having two marked changes in direction.

biramous appendage (or limb). Ventral appendage having an outer branch (ramus) and an inner branch (syn., appendage).

border. Outer dorsal portion of cephalon and pygidium and outer ventral portion of hypostome, usually bounded by border furrow (has been referred to as rim, marginal rim, or marginal limb, but the term rim is restricted here to narrow peripheral ridge of fringe of Trinucleidae, etc.).

border furrow. Furrow defining adaxially border of cephalon, pygidium, and hypostome (syn., marginal furrow).

border pit. One of a row of pits along anterior border furrow of cephalon as in *Angelina;* may occur also in lateral border furrow as in *Euloma* (syn., marginal pit).

border roll. Tubular border of cephalon formed by convex border and doublure that is convex ventrally.

border sector. Outer, anterior portion of rostral plate separated by sharp flexure from the inner, doublure sector.

border spine. Spine (other than genal, fixigenal, librigenal) on anterolateral border of cephalon and to pleural spine of pygidium when border is present.

brim. Peripheral portion of fringe, bounded on inward side by girder or corresponding inflexion of upper lamella as in Harpetidae, Harpididae, and Trinucleidae (formerly used for frontal field).

brim prolongation. Peripheral portion of fringe prolongation, bounded by girder; represents posterior extension of brim as in Harpetidae and Harpididae.

bulla (pl., bullae). Rudimentary swelling in early lichid growth stage (situated inside the axial furrow and opposite L2), which grew rapidly in subsequent stages to form bullar lobe or composite lobe.

bullar lobe. Lateral glabellar lobe in lichid trilobite in position of L2 and L3 and formed by growth of bulla. This term replaces bicomposite or tricomposite glabellar lobe.

burlingiiform sutures. Proparian sutures in which the anterior and posterior sections are subparallel, diverging outward and forward at an angle of about 45° to axial line of cephalon as in *Burlingia.*

buttress. Projection from abaxial wall of axial furrow of cephalon, opposing a papilla of glabellar lobe. See also papilla, papillate-buttress structure.
caecal node. Point at which diverticulum or major caecum branches.
caesura (pl., caesurae). Line of separation between two differently oriented blocks of rows of lenses in a schizochroal eye.
carapace. Term applied to Crustacea; incorrectly used for trilobite exoskeleton.
cast. A replica of an original, made from a mold.
caudal ramus (pl., rami). See antenniform cercus.
caudal shield. See pygidium.
caudal spine. See posterior spine.
cedariiform suture. Opisthoparian suture in which the posterior section runs outward (abaxially) and onto or across the lateral border before curving backward and then turning adaxially to the posterior margin (syn., pseudoproparian suture).
central area (of glabella). Middle portion of glabella between frontal lobe and occipital furrow, bounded laterally by adaxial ends of lateral glabellar furrows [syn., central region (of glabella), median cervical lobe, median lobe (of glabella)].
central body (of hypostome). See middle body (of hypostome).
central region (of glabella). See central area (of glabella).
cephalic axis. See glabella.
cephalic beak. Median anterior protuberance from doublure of cephalon that on enrollment interlocks with a depression on the median posterior doublure of the pygidium.
cephalic recess. Upwardly arched recess below occipital band, visible in posterior view of cephalon in Agnostina. See cephalothoracic aperture.
cephalic region. See cephalon.
cephalic sutures. General term for all the sutures (circumocular, connective, facial, hypostomal, perrostral, rostral) of the cephalon.
cephalon (pl., cephala). Anterior tagma composed in trilobites of a number of fused somites, applied by authors to anterior portion of exoskeleton separated from remainder of exoskeleton by an articulation (syn., cephalic region, head, head shield).
cephalothoracic aperture. An elliptical gap in the exoskeleton in Agnostina, in the median portion of the axial region, between the cephalic recess and the thoracic recess. The gap was open in the enrolled exoskeleton (Fig. 48).
cercus (pl., cerci). See antenniform cercus.
cheek. See gena.
cheek area. See gena.
cheek field. See genal field.
cheek lobe. See gena.
cheek region. See gena.
cheek roll. See genal roll.
cheek roll prolongation. See genal roll prolongation.
circumaxial furrow. See axial furrow.
circumocular suture. Suture surrounding the visual surface; in trilobites having a facial suture, it is composed of an upper section, the palpebral suture, and a lower section, the ocular suture.
coaptation (coaptative, adj.). Fitting together of two independent parts of the same animal. In trilobites coaptative structures are morphological devices that interlocked when the exoskeleton was fully enrolled.
composite internal mold. Mold of internal surface of dorsal exoskeleton and impression of external surface of ventral exoskeleton (i.e., of hypostome, rostral plate, and doublure).
composite lobe. Lobe formed by partial or complete fusion of bullar lobe with L1 in lichid trilobites.
concentric row. See arc.
connecting doublure. Bridging piece that unites the doublures of the librigenae medianly where connective sutures are lacking.
connective band: Vertical to horizontal band (depending on convexity) immediately behind the pygidial axis and anterior to the border furrow and that may connect the pleural fields of pygidium. This term has been used as a synonym for occipital band.
connective suture. One of paired longitudinal sutures transecting border or doublure in front of hypostome and defining rostral plate laterally.
constricted. See acrolobe.
conterminant (condition of hypostome). Hypostome underlies anterior portion of glabella and is attached at a suture to the anterior cephalic doublure.
cornea (corneal membrane). A thin external covering on the surface of the lens of the eye, continuous in the holochroal eye, discrete in the schizochroal and abathochroal eye.
corner angle. Angle between outer lateral and posterior margins of librigena.
corner furrow. Groove extending obliquely outward from axial furrow at anterolateral corner of glabella as in *Strenuella.*
coxa. Proximal podomere of biramous appendage, attached directly to ventral surface of body (syn., coxite, coxopodite).
coxite. See coxa.
coxopodite. See coxa.
cranidial spine. Strong occipital spine in Eodiscidae at posterior of glabella and occipital ring. Swelling of the axis obscures original site.
cranidium (pl., cranidia). Central portion of exoskeleton of cephalon, bounded laterally by facial suture.
crenal tongue. Tongue of librigena between ocular suture and retrodivergent anterior facial suture as in *Centropleura.*
cuticle. Mineralized portion of the integument, which constitutes the exoskeleton.
dalmanitidiform suture. Proparian suture in which anterior sections meet on dorsal side of cephalon near anterior margin as in *Dalmanites.*
degree of meraspid period. Stage in development characterized by number of articulated thoracic segments. Degree 0 has none, degree 1 has one freely articulating segment, etc. Meraspid degrees may be abbreviated as M0, M1, etc.
deliquiate. Condition in which border furrow in Agnostina is deep and channel-like, rather than a change in convexity.
deltoid area. Triangular depression in Agnostina, lying between oblique lateral ridge and axial glabellar carina.

deltoid depression. Triangular depression in Agnostina, formed by expansion of anterior border furrow at its junction with the median preglabellar furrow.

detached (condition). See hypostome, natant (condition) of hypostome.

deuterolobate. Agnostina in which the deuterolobe is well defined by tumidity and accessory furrow.

deuterolobe. Composite pygidial lobe of confluent pleural and axial regions, which lies between anterior lobe of axis defined by axial furrow and posterior border furrow. Laterally it is defined by the accessory furrow (syn., endlobe, pseudolobe).

distal. Portion of body away from the point of origin or sagittal line.

distal portion of pleura. See outer portion of pleura.

dome. Area of cuticle that bulges above the general level, thinning markedly at the apex of the bulge.

dorsal exoskeleton. See exoskeleton.

dorsal furrow. See axial furrow.

dorsal shield. See exoskeleton.

doublural plate. See lower lamella.

doublure. Reflexed continuation of dorsal exoskeleton onto ventral surface.

doublure sector. Inner part of rostral plate separated from border sector by sharp flexure.

E. See external.

ecdysis. Processes of preparing to cast off and casting off (exuviation) old exoskeleton.

effaced. Condition in which furrows and lobes are obliterated to give smooth or almost smooth surface. The term therefore implies that ancestral forms were not effaced, i.e., were en grande tenue.

elliptical ring. See intranotular axis.

endite. Inwardly directed lobe of podomere of inner branch.

endlobe. See deuterolobe.

endopod. See inner branch (of biramous appendage).

endopodite. See inner branch (of biramous appendage).

en grande tenue. Condition in Agnostina in which furrows and lobes are distinct (syn., non-effaced).

entomaspidiform suture. Opisthoparian facial suture in which anterior branch is retrodivergent, running outward and backward from eye to lateral margin as in *Entomaspis.*

epiborder furrow. Furrow or change in slope between the convex inner, and flattened outer portions of the cephalic border in dalmanitinids; associated with a doublure that has a flat outer portion and a steeply upturned inner portion, the latter being beneath the inner portion of the border. In eodiscoids a furrow on the cephalic border in which the distal ends of the scrobiculae lie.

epifacetal (type of pleural furrow). Outer portion of pleural furrow that crosses posterior margin of articulating facet and continues as a narrow, distinct furrow on articulating facet. See postfacetal pleural furrow.

epipalpebral furrow. See ocular furrow.

epistoma. See hypostome, rostral plate.

epistomal plate. See rostral plate.

epistome. See rostral plate.

euptychopariid rostral suture. Connective suture marginal to a broad (tr.) rostral plate (contrast with stenoptychopariid). See ptychopariid suture.

exite. See outer branch (of biramous appendage).

exopod. See outer branch (of biramous appendage).

exopodite. See outer branch (of biramous appendage).

exoskeleton. Mineralized dorsal cuticle extended onto ventral side as doublure and hypostome (syn., dorsal exoskeleton, dorsal shield, shield, test).

exsagittal. Direction parallel to, but outside sagittal (median) line (abbreviation, exs.).

external (E). Used in referring to pits in the trinucleid fringe outside girder, to arcs of pits, to individual or to irregular pits.

external mold. Mold of outer surface of exoskeleton.

external rim. Outer, raised smooth border of fringe along anterior and lateral edges extending back to posterior tip of prolongation as in Harpetidae, Harpididae, and Trinucleidae.

extranotular axis. Longitudinal portion of axis of pygidium situated between axial furrow and notular line. If axial furrow is effaced, extranotular part of axis may be mistaken for part of pleural field and the notular line regarded as the axial furrow.

extraocular area. Area of the genal field outside and behind the ocular lobe in Olenellina.

exuviae. Any or all portions of molted trilobite exoskeleton, mineralized or nonmineralized. This term for the remains of a trilobite is plural; it has no singular form.

exuviation. The active phase of ecdysis, the withdrawal of the animal from its old exoskeleton.

eye. Visual organ on external side of gena, bearing eye lenses.

eye field. See librigenal field.

eye lappet. See visual surface (of eye).

eye list. See eye ridge.

eye lobe. Ensemble of palpebral lobe and visual surface of eye.

eye platform. See librigenal field.

eye ridge. Raised band extending from anterior end of eye lobe to, or just behind, anterolateral angle of glabella; may be subdivided by ocular furrow (syn., eye list, ocular band, ocular ridge, paired eye ridge).

eye ridge fossula. See fossula.

eye socle. Rim directly below visual surface of eye and separated from the librigenal field by break in slope or furrow, the eye socle furrow.

eye socle furrow. Furrow separating eye socle from librigenal field.

eye tubercle. Raised knob bearing simple eye as in Trinucleidae.

F. In Agnostina only, used to denote lateral glabellar furrow (numbered forward from the posterior margin of the glabella) and inter-ring furrow of pygidium (numbered backward from the anterior margin).

facet. Triangular area that bevels anterolateral area of outer portion of pleura of a fulcrate thoracic segment and the corresponding area of the anterior pleural segment of the pygidium. See also epifacetal and postfacetal types of pleural furrow, petaloid facet.

facial line. Ridge in Redlichiina extending from the palpebro-ocular ridge to the border furrow of the cranidium, subparallel to, or at a slight angle to, the anterior section of the facial suture (syn., preocular facial line).

facial suture. Suture bounding adaxial margin of eye surface, which has anterior and posterior branches (sections), each of which may extend over the border and on to the doublure; suture separates librigena from fixigena. Posterior branch extends to inner margin of doublure, anterior branches may meet medially on dorsal or ventral surface of exoskeleton or may join extremity of rostral suture. Facial suture may be present when eye is absent. Particular points on the dorsal suture are denoted by Greek letters in Figure 3.

false eye ridge. See sutural ridge.

false preglabellar area. See precranidial lobe.

false preglabellar field. See anterior border of cranidium (in Encrinuridae).

false preglabellar furrow. Furrow separating precranidial lobe from border of cephalon in Encrinuridae (syn., anterior furrow).

fenestra (pl., fenestrae). An opening in the postcephalic pleural region of the dorsal exoskeleton, situated intersegmentally.

fibular furrow. Furrow separating outer flat and inner projecting portion of doublure of pygidium in Agnostina; at enrollment, inner edge of cephalic doublure lies in this furrow.

field of free cheek. See librigenal field.

fingerprint pattern. See Bertillon pattern.

fixed cheek. See fixigena.

fixigena (pl., fixigenae). Portion of cranidium abaxial to axial and preglabellar furrows and imaginary sagittal line bisecting frontal area (syn., fixed cheek).

fixigenal boss. Fixigenal protuberance at level of L1 as in *Neoredlichia.*

fixigenal eye stem. Supposed ridge separated from palpebral lobe by palpebral furrow and running posteriorly from it in Phacopida.

fixigenal field. Portion of fixigena between axial and border furrows.

fixigenal spine. A spine borne by the border of the fixigena. Anterior, mid-, and posterior fixigenal spines are recognized in certain protaspides.

flange. Inner posterior portion of lower lamella that may be expanded posteriorly in Trinucleidae [syn., inner margin (of lower lamella), integument attachment]. Also used for projecting strip along anterior edge of thoracic pleura or pleural field of pygidium, which fits below posterior flange of adjacent segment or posterior border of cephalon (syn., anterior flange).

flange furrow. Furrow defining inner edge of flange of thoracic segment.

flank. See pleural field (of pygidium).

flip. Angled edge of librigena between posterior section of facial suture and posterior margin.

fossette. One of several pits on eye socle.

fossula (pl., fossulae). Small, circular or oval depression that may occur in axial furrow at or near anterolateral edge of glabella and that lies at junction with anterior edge of eye ridge (when present) (syn., antennary pit, antennular pit, anterior fossula, anterior pit, eye ridge fossula, hypostomal pit, pore, pseudoantennary pit).

fossular apodeme. Projection from parietal surface formed by inbending of exoskeleton corresponding to fossula on external side (syn., anterior boss).

free cheek. See librigena.

free pleura. See outer portion of pleura.

fringe. External pitted portion of cephalon in Harpetidae, Harpididae, and Trinucleidae.

front furrow. See anterior border furrow (of cephalon).

frontal area. Portion of cranidium lying between anterior branches of facial suture (and rostral suture, if developed), preglabellar furrow, and eye ridge. If eye ridge is absent, posterolateral boundary of this area is marked off by imaginary line connecting anterior extremity of palpebral lobe with end of preglabellar furrow (syn., anterior limb, limb). See also frontal field.

frontal boss. See preglabellar boss.

frontal field. Portion of frontal area posterior to border furrow (syn., brim of HOWELL & others, 1947).

frontal furrow. See anterior border furrow (of cephalon).

frontal glabellar spine. Median or paired spine projecting forward from frontal part of glabella.

frontal lobe (of glabella). Lobe of glabella between preglabellar furrow and most anterior lateral glabellar furrows; may be referred to as LA. See also anterior lobe of glabella.

frontal process. Projection of anterior border and doublure of cephalon; may bifurcate or trifurcate anteriorly as in *Neoprobolium* (syn., anterior median process, beak).

frontal spine. Projection of anterior border and doublure of cephalon ending anteriorly in point (syn., median anterior border spine).

frontal sulcus. Continuation of median preglabellar furrow on to frontal glabellar lobe in Agnostina.

fronto-median lobe. Frontal lobe and central area of glabella.

fulcral joint. Pivot joint between adjoining tergites, situated at the fulcrum.

fulcral line. Imaginary exsagittal line joining the fulcra.

fulcral notch. See fulcral socket.

fulcral process. Projection from anterior edge of thoracic pleura or pygidium at fulcrum (syn., fulcral prong). See also prong.

fulcral prong. See fulcral process.

fulcral socket. Indentation on posterior edge of thoracic pleura or border of cephalon at fulcrum, into which fulcral process fits (syn., fulcral notch).

fulcral spine. Larger projection than fulcral prong in Agnostina.

fulcral swelling. Thickening of ridge at fulcrum of pleura connecting principal pleural ridge and posterior (principal) pleural spine.

fulcrate. Describes thoracic segment that has the fulcrum.

fulcrum (pl., fulcra). Geniculation of pleural region separating horizontal inner portion from inclined outer portion (syn., geniculation).

furrow process and socket. Ball and socket articulating device in the axial furrow.

gena (pl., genae). Lateral portion of dorsal exoskeleton of cephalon, abaxial to imaginary sagittal line bisecting frontal area, and to axial furrow (syn., cheek, cheek area, cheek lobe, cheek region, genal lobe, genal region).

genal angle. Posterolateral corner of cephalon.

genal artery. See genal ridge.

genal bar. Longitudinal ridge on fixigena, close to axial furrow as in *Centropleura.*

genal caecum (pl., caeca). Pattern of raised ridges on external surface (grooves on parietal surface) radiating and distally anastomosing on frontal area and genal field of cephalon; arising from the eye ridge, eye lobe, axial or preglabellar furrow. The ridges are much narrower in relation to the cephalon than the rugae of Agnostina.

genal diverticulum. See genal ridge.

genal field. Area of gena enclosed within border furrows (syn., cheek field). May be divided into librigenal field and fixigenal field.

genal flange. Area of genal roll of fringe opposite posterior margin of genal region, commonly occupied by irregularly distributed pits in Trinucleidae.

genal lobe. See gena.

genal prolongation. Portion of fringe posterior to genal region in Trinucleidae, Harpetidae, and Harpididae.

genal region. See gena.

genal ridge. Raised, narrow band running outward and backward from outer side of eye lobe, visual surface of ocular lobe in Olenellina, or eye tubercle (or axial furrow if no eye lobe or eye tubercle) toward genal angle (syn., genal artery, genal diverticulum, paraocular facial line, principal genal vein).

genal roll. Inner portion of fringe bounded on outer side by girder or corresponding inflection of upper lamella and on inner side by genal region as in Harpetidae and Trinucleidae (syn., cheek roll).

genal roll prolongation. Inner portion of genal prolongation, bounded outwardly by girder; represents extension of genal roll as in Harpetidae and Harpididae (syn., cheek roll prolongation).

genal spine. General term for hollow, posteriorly directed extension of border and doublure at genal angle, forming pointed projection. See fixigenal spine, librigenal spine.

generative zone (ocular). Narrow strip at base of visual surface of eye from which new lenses are added at exuviation.

genicranidium (pl., genicranidia). See genicranium.

genicranium (pl., genicrania). Dorsal cephalic shield of hypoparian forms and Olenellina, separated by marginal (or supramarginal in conocoryphids) suture from ventral doublural plate (syn., genicranidium).

geniculate (glabellar furrow). Glabellar furrow having single angular change in direction.

geniculation. See fulcrum.

gill branch. See outer branch (of biramous appendage).

girder. Thickening or ventrally raised flexure of lower lamella parallel to cephalic margin, found at some distance within external rim at angulation of lamella as in Harpetidae, Harpididae, and Trinucleidae.

girder list. Ridge on upper lamella of fringe in Trinucleidae corresponding in position to girder of lower lamella.

glabella (pl., glabellae). Axial portion of cephalon, bounded by axial and preglabellar furrows (syn., cephalic axis); only in Agnostina is basal lobe and occipital band excluded from the glabella.

glabellar carina. See glabellar keel.

glabellar culmination. Rounded or angulate posterior extremity of the posterior glabellar lobe (posteroglabella) in Agnostina.

glabellar furrow. See lateral glabellar furrow; transglabellar furrow.

glabellar impression. See muscle scar.

glabellar keel. Sagittal ridge on parietal surface of glabella, preserved as a groove, the axial glabellar sulcus, in internal molds of Agnostina (syn., glabellar carina).

glabellar lobe. See lateral glabellar lobe.

glabellar node. Median (or paired) tubercle developed in some part of fronto-median lobe of glabella (syn., glabellar tubercle, median glabellar tubercle). See also median sensory organ.

glabellar spine. Median (or paired) spine arising from glabella. See also cranidial spine, frontal glabellar spine, median glabellar spine, occipital spine.

glabellar tongue. Subparallel-sided axial part of cranidium anterior to eye lobes, bounded by confluent anterior sections of facial suture, and continuous with posterior portion of glabella (which occupies axial region between eye lobes as in Remopleurididae).

glabellar tubercle. See glabellar node.

glyptagnostoid articulating device. Modification in Agnostina in which articulating half ring is a narrow, raised rim and articulating furrow is a wide, elliptical depression with exsagittal pair of notulae.

gonatoparian suture. Facial suture with posterior section reaching cephalic margin at genal angle.

granule. Minute protuberance from exterior surface of exoskeleton, smaller than tubercle or pustule.

groove. Groove or recess below posterior margin of inner portion of pleura or posterior border of cephalon, into which flange fits.

half ring. See articulating half ring.

hapsidium (pl., hapsidia). Concentric cluster of closed ridges of sculpture or of loops of ridges (cf. Bertillon pattern).

head. See cephalon.

head shield. See cephalon.

hinge. Line of articulation between adjoining tergites (syn., hinge line).

hinge line. See hinge.

holaspid period. Period of growth after specific number of thoracic segments had been attained.

holaspis (pl., holaspides). Exoskeleton at any particular stage of development during holaspid period.

holcos. Concave zone parallel to and near the lateral and posterior margins of the pygidium as in some Illaenina.

holochroal eye. Compound eye consisting of numerous adjoining lenses covered by a continuous cornea.

horn. See prolongation.

hyperglabella. Term introduced for immature glabella of *Daguinaspis* because S5 is said to be present in addition to S1–S4.

hypoparian. Condition in which facial suture traverses margin of cephalon.

hypostoma. See hypostome.

hypostomal pit. See fossula.

hypostomal suture. Line of junction between posterior margin of anterior doublure, rostral or perrostral plate, and anterior margin of hypostome.

hypostome (pl., hypostomes). Ventral sclerite situated beneath anterior portion of glabella, described as conterminant (attached) when in sutural contact with rostral plate and/or doublure of librigenae and described as natant (detached) when not in such contact [syn., epistoma (partim), hypostoma].

I. Abbreviation for internal.

impendent (condition of hypostome). A modified conterminant condition of the hypostome, in which the glabella is extended forward so that the most anterior portion is underlain by the cephalic doublure.

ingluvial sac. See ingluvie.

ingluvie. Expansion of the alimentary canal; in trilobites may be bilaterally arranged sacs or an axial boss (syn., ingluvial sac).

inner branch (of biramous appendage). Inner branch (ramus) of appendage arising from coxa, composed of a number of podomeres connected to each other and the coxa by movable articulations (syn., endopod, endopodite, leg branch, telopod, telopodite, walking leg).

inner margin (of fringe). Line separating genal region and preglabellar field (if present) from pitted area and running into posterior border as in Harpetidae [syn., lateral line (of fringe)].

inner margin (of lower lamella). See flange.

inner margin (of upper lamella). Boundary between genal region and fringe on dorsal side of cephalon; coincides with inner margin of fringe as in Harpetidae and Trinucleidae.

inner portion of pleura. Portion of pleura adaxial to fulcrum (syn., articulated pleura, proximal portion of pleura).

inner spine angle. Angle between median line of genal spine and margin of posterior border of cephalon.

insloping. Situation in genal or pleural region of exoskeleton of cephalon or pygidium in which exterior surfaces face upwards or inwards toward axial surfaces.

integument. The epidermal cell layer of the body and the overlying cuticle that it has secreted.

integument attachment. See flange.

intercalary lobe. See median preoccipital lobe.

intercalating furrow. Transverse furrow at anterior margin of intercalating ring.

intercalating ring. Ring anterior to occipital ring formed by fusion of L1 lobes across glabella as in phacopids (syn., preoccipital ring).

intercheek suture. See median suture.

intergenal angle. The angle in the posterior cephalic border where it may be flexed forward, so that the base of the genal spine lies in a transverse line well in advance of the occipital ring as in certain Olenellina and Redlichiina.

intergenal ridge. Ridge in Olenellina extending from interocular area of gena opposite L1, along or across border furrow to base of intergenal spine; prominent in early growth stages (syn., metagenal ridge, posterior genal ridge).

intergenal spine. Spine projecting posteriorly from cephalic border adaxial to genal angle (syn., interocular spine, metacranidial spine, metafixigenal spine, metagenal spine).

intergenal swelling. Inflation of posterior border of cephalon at base of intergenal spine; may be present when spine is absent in holaspis.

interlamellar suture. Suture through the pillars that connect the dorsal and ventral pits in upper and lower lamellae of fringe in harpetids and trinucleids.

interlensar sclera. That part of visual surface that lies between schizochroal lenses and is not covered by cornea.

intermediate lobe. Small lobe on median glabellar lobe at anterior, adaxial end of S1 in some calymenids (syn., supplementary lobe).

internal (I). Used in referring to arcs of pits, to individual pits, or to irregularly arranged pits in trinucleid fringe adaxial to girder.

internal axial septum. Septum located on the parietal surface at the posterior end of pygidial axis in *Pseudophillipsia.*

internal mold of exoskeleton. Mold of interior (parietal) surface of dorsal exoskeleton; may be combined with mold of external surface of doublure or hypostome. See composite internal mold.

internal rim. Smooth inner border of fringe, adjacent to thorax and extending from posterior margin of genal region to posterior tip of prolongation as in Harpetidae.

interocular area. Used in Olenellina for area adaxial to ocular lobe. See also palpebral area (of fixigena).

interocular channel. Transverse channel lying immediately behind eye ridge, extending between palpebral lobe and axial furrow in *Aulacodigma.*

interocular cheek. See palpebral area (of fixigena).

interocular fixigena. See palpebral area (of fixigena).

interocular spine. See intergenal spine.

interocular swelling. Inflation by which palpebral area is swollen and repeats form of palpebral lobe.

interpleural furrow. Transverse groove extending from axial furrow across pleural region of pygidium, indicating boundary of fused pleurae (syn., interpleural groove, rib furrow).

interpleural groove. See interpleural furrow.

inter-radial plate (or ridge). Plate or ridge that separates adjacent radial rows of pits in trinucleid cephalic fringe on both upper and lower lamellae; particularly evident when radial rows of pits lie in sulci.

inter-ring furrow. Groove bounding successive axial rings of pygidium (syn., ring furrow, transaxial furrow). In Agnostina referred to as F1, F2, F3, numbering from the anterior backward.

intersulcal field. Area between outer and inner border furrows in Proetidae.

intervening furrow. Lateral glabellar furrow intervening between LO and L1, recognized in olenids and an oryctocephalid.

intervening glabellar lobe. Lateral glabellar lobe isolated by intervening furrow curving back to meet occipital furrow, considered to intervene between occipital ring and L1.

intra-annular furrow. Furrow separating anterior part of thoracic axial ring (preannulus) from posterior part (postannulus), visible on exterior but not parietal surface of exoskeleton.

intra-axial furrow. Furrow between median and lateral lobe of thoracic axial ring of Agnostina.

intralensar bowl. Differentiated lower part of compound lens in the schizochroal eye of Phacopina.

intramarginal suture. Suture running along border of cephalon, close to margin. See also marginal suture, submarginal suture.

intranotular axis. Main median part of pygidial axial lobe between notular lines or between the two lines of notulae (syn., elliptical ring, lancetoid field).

intranotular ridge. Paired ridge flanking the intranotular sulcus, anteriorly merging with axial node of pygidium.

intranotular sulcus. Sagittal groove between axial and terminal nodes of pygidial axis in Agnostina; may be impressed into axial node posteriorly.

intraoccipital furrow. Furrow on lateral portion of occipital ring defining lateral occipital lobe.

intrapalpebral ridge. Ridge on fixigena adjacent to and parallel to palpebral lobe in *Carolinites.*

intrascleral membrane. Membrane holding lenses in position in schizochroal eye.

isopygous. Having a pygidium of about the same width (tr.) and length (sag. and exs.) as the cephalon.

isoteliform suture. See asaphid suture.

kainelliform suture. Opisthoparian suture in which anterior sections first diverge strongly outward and then bend sharply inward and frontward, meeting anterior cephalic margin at its median point as in *Kainella.*

L. Abbreviation for lateral glabellar lobe or transverse division; numbered forward from posterior, LO (occipital ring), L1, L2, L3, etc.

LA. Abbreviation for frontal lobe of glabella.

lancetoid field. See intranotular axis.

larval notch. See posterior indentation.

larval ridge. Supposed combination in a single ridge of frontal glabellar lobe, ocular lobe, and intergenal ridge in such Olenellina as *Elliptocephala*.

lateral axial lobe. Lobe at lateral margin of axial ring.

lateral band. Lower half of lateral side of pygidial axis, which joins upper half at change in slope. Axial rings and inter-ring furrows are indistinct. Used for Proetoidea.

lateral border (of cephalon). Portion of cephalic border between anterior section (branch) of facial suture and genal angle.

lateral border (of hypostome). Extends from anterior wing to posterolateral corner of hypostome, bounded by lateral border furrow.

lateral border furrow (of cephalon). Portion of border furrow bounding lateral border.

lateral border furrow (of pygidium). Portion of border furrow bounding lateral border in pygidium.

lateral glabellar furrow. Bilaterally symmetrical pairs of narrow grooves on external surface formed by fold in exoskeleton, extending partway across glabella from (or near) axial furrow. Furrows vary in length, depth, and direction; they may be short (tr.), limited to pits in or close to axial furrow, or isolated from axial furrow (syn., glabellar furrow). When three pairs are present, they have been referred to as anterior, median, and basal (syn., posterior glabellar furrow, preoccipital glabellar furrow). Numbering from the back forward is preferred: occipital as SO, preoccipital as S1, and continued forward as S2, S3, etc.

lateral glabellar lobe. Portion of glabella outlined and more or less separated by successive lateral glabellar furrows, may or may not be inflated. Numbering is from posterior end forward: L1, L2, etc. (syn., glabellar lobe). In lichids it is considered that L1 is subdivided into the posterior L1a and anterior L1b, and similar subdivisions are recognized in odontopleurids. When three pairs are present they have been referred to as anterior, median, and basal lobes (syn., preoccipital glabellar lobe). See also posterior lobe (of glabella).

lateral line (of fringe). See inner margin of fringe.

lateral margin (of cephalon). Margin between anterior branch of facial suture and genal angle (if former is absent, anterior limit of lateral margin is obscure).

lateral notch (of hypostome). Deep groove crossing border and doublure between shoulder and anterior wing of hypostome.

lateral occipital lobe. Lateral or anterolateral portion of occipital ring, if differentiated; referred to as LO (syn., occipital lobe, occipital lobula).

lateral pit. See posterior fossula.

lateral preoccipital lobe. Lobe L1; lateral portion of glabellar region directly in front of occipital ring, where differentiated, as in *Otarion, Ditomopyge* (syn., pre-occipital glabellar lobe). See also posterior lobe (of glabella), lateral glabellar lobe.

lateral projection of hypostome. See shoulder (of hypostome).

lateral tongue furrow. Portion of axial furrow bounding side of glabellar tongue as in *Remopleurides.*

leg branch. See inner branch.

levisellid-type suture. See nileiform suture.

librigena (pl., librigenae). Portion of cephalon abaxial to facial suture (syn., free cheek, movable cheek, paria).

librigenal field. Portion of librigena within border furrow (syn., eye field, eye platform, field of free cheek, ocular platform).

librigenal plate. The librigenae, united by connecting doublure, not separated by connective or median suture.

librigenal spine. Spine borne by border of librigena (syn., parial spine).

libristomate. Adjective derived from Libristoma, the group of trilobites in which the hypostome was conterminant in the protaspis but became natant during the meraspid and holaspid periods.

limb. See biramous appendage, frontal area, posterior area of fixigena.

lira (pl., lirae). Symmetrical raised ridge on external surface of exoskeleton.

list. A concentric ridge on the upper lamella occurring between arcs in trinucleids.

longitudinal furrow. Posteriorly directed extension of anterior lateral glabellar furrow as in Lichidae and Odontopleuridae.

longitudinal median glabellar furrow. Furrow commencing in preglabellar furrow and extending sagittally back.

lower lamella. Ventral exoskeleton of fringe as in Harpetidae, Harpididae, and Trinucleidae (syn., doublural plate).

lower rim (external or internal). Smooth, may be raised or thickened peripheral portion of lower lamella of fringe as in Harpetidae, Harpididae, and Trinucleidae.

lunette. Raised crescentic area on inner (parietal) surface of exoskeleton at abaxial margin of axial furrow, where glabella is narrowest (tr.) and approximately in transverse line with eye lobe; characteristic of Illaenidae.

M. Used in Agnostina only to denote transverse divisions of axis of glabella (where it is equivalent to L and numbered 1 to 3 from the posterior forward) or axis of pygidium (where it is equivalent to axial ring and numbered posteriorly from anterior margin of pygidium). Also used as abbreviation for meraspid period, in numbering degrees as M0, M1, etc.

macropleura (pl., macropleurae). Pleura in which the inner portion becomes longer (exs.) abaxially and the outer portion is a long, stout spine, or in which only the pleural spine is markedly longer than those adjacent (syn., macropleural segment).

macropleural segment. See macropleura.

macropleural spine. Pleural spine of macropleura.

macropleural unit. Macropleural sixth thoracic segment that is fused to fifth as in Emuellidae.

macropygous. Having a pygidium exceeding in maximum width (tr.) that of the cephalon.

macrospine. Axial spine, much larger than those adjacent.

macula (pl., maculae). Small area lying laterally in, or on posterior side of middle furrow of hypostome; it may be sunken, flat, or elevated, smooth or with lenslike structures on the surface.

major posterior (muscle) scar of posterior glabellar lobe (posteroglabella). In Agnostina a paired, circular, depressed area situated at the maximum width of the posterior glabellar lobe.

margin. Distal edge of portion of exoskeleton.

marginal band. Narrow vertical band uniting upper and lower edges of rim as in Harpetidae and Trinucleidae.

marginal connective device. Device for articulation between adjacent pleurae at base of pleural spine.

marginal furrow. See border furrow.

marginal gutter. Broad, overdeepened border furrow of either cephalon or pygidium in Agnostina.

marginal limb. See border.

marginal pit. See border pit.

marginal rim. See border.

marginal spine. Pleural spine of pygidium when border is not defined.

marginal suture. Suture traversing marginal band of cephalon, as in Harpetidae.

median anterior border spine. See frontal spine.

median axial lobe. Median portion of axial ring between lateral axial lobes.

median body (of hypostome). See middle body (of hypostome).

median border spine. See posterior spine.

median cervical lobe. See central area (of glabella).

median gap. See pygidial collar.

median glabellar spine. Median spine arising from central area of glabella (syn., preoccipital glabellar spine).

median glabellar tubercle. See glabellar node.

median lateral glabellar furrow. Furrow S2 when three pairs are present (see lateral glabellar furrow).

median lateral glabellar lobe. Lobe L2 when three pairs are present. See lateral glabellar lobe.

median lobe (of glabella). See central area (of glabella).

median node. See axial glabellar node.

median preglabellar furrow. Furrow along sagittal line in front of glabella as in Agnostina and Dimeropygidae (syn., preglabellar median furrow).

median preglabellar ridge. Ridge along sagittal line in front of glabella.

median preoccipital lobe. Median portion of glabellar region between L1 lobes as in *Ditomopyge* (syn., intercalary lobe).

median sensory organ. Median glabellar node in which either the exoskeleton is thinner or there are symmetrically arranged pits.

median suture. Median longitudinal suture transecting doublure in front of hypostome (syn., intercheek suture).

meraspid period. Period of development from appearance of first transverse articulation in exoskeleton until specific number of thoracic segments less one had been attained (see degree of meraspid period).

meraspis (pl., meraspides). Exoskeleton at any particular degree of development during meraspid period.

mesentery. Membrane attached to inner (parietal) surface of skeleton serving as a partition between and a support for organs.

metacranidial spine. See intergenal spine.

metafixigenal spine. See intergenal spine.

metagenal ridge. See intergenal ridge.

metagenal spine. See intergenal spine.

metamere. See somite.

metaparian suture. Sutural pattern in Olenellina in which the two branches of the facial suture are supposed to have been secondarily fused.

metaprotaspis (pl., metaprotaspides). Next largest protaspides to anaprotaspides in a size series, in which protopygidium is recognizable. Not recommended as a subdivision of protaspid period.

metastoma. See metastome.

metastome. Supposed small plate lying posterior to mouth opening on ventral side of body (syn., metastoma, postoral plate).

micropygous. Having a pygidium considerably shorter (sag. and exs.) and narrower (tr.) than the cephalon.

midcheek furrow. Furrow in Agnostina extending obliquely from axial furrow adjacent to anterior portion of posteroglabella to border furrow.

middle body (of hypostome). Swollen middle portion of hypostome inside border, divided by middle furrows into anterior and posterior lobes [syn., central body (of hypostome), median body (of hypostome)].

middle furrow. Inward and backwardly directed furrow dividing middle body of hypostome into anterior and posterior lobes.

mid-fixigenal spine. Prominent spine on lateral border of protocranidium of protaspis.

midmost glabella. See posterior lobe (of glabella).

miomerid. Term originally proposed for trilobites having two or three thoracic segments (i.e., Agnostina and eodiscoids) and used as a convenient abbreviation to refer to them.

mold. See composite internal mold, external mold, internal mold of exoskeleton.

molting. The entire sequence of events, including ecdysis and postecdysis, between one shedding of the exoskeleton and the next.

movable cheek. See librigena.

mucro. Median, pointed posterior projection from posterior border of pygidium in dalmanitids and encrinurids. See posterior spine.

muscle scar (or impression). Smooth, may be slightly depressed, paired area in external surface of axial region of exoskeleton, interpreted as area of muscle attachment; may be darker in color than surrounding regions. Paired muscle impressions on glabella may be numbered from posterior forward as 1g, 2g, etc. (in Scutelluidae) or, in same manner as lateral glabellar furrows, as S1, S2, etc. In Agnostina they are preserved as shallow depressions on internal mold, reflecting raised rim of scar on parietal surface (syn., glabellar impression).

natant (condition of hypostome). Hypostome lies below anterior portion of glabella, but is not attached to the cephalic doublure.

neck furrow. See occipital furrow.

neck node. See occipital node.

neck ring. See occipital ring.

neck spine. See occipital spine.

nileiform suture. Cephalic suture in which two anterior branches (or sections) meet marginally in the midline; there is no median suture across the doublure (syn., levisellid-type suture).

niobiform suture. See asaphid suture.

node. Small subcircular or suboval swelling on exterior surface of exoskeleton.

nonadult-like protaspis. See asaphoid protaspis.

non-effaced. See en grande tenue.

nonfulcrate. Describes a thoracic segment that lacks the fulrum (i.e., has no inner horizontal portion) but curves downward and outward from the axial furrow.

notula (pl., notulae). Small pit in internal mold of exoskeleton that may be included in an area occupied by a muscle scar.

notular furrow. Longitudinal furrow developed between notulae.

notular line. A longitudinal line of notulae converging on terminal node of the pygidial axis.

nuchal furrow. See occipital furrow.

nuchal node. See occipital node.

nuchal ring. See occipital ring.

nuchal spine. See occipital spine.

O. Abbreviation for occipital ring.

oblique lateral muscle scars of posteroglabella. Grooves in Agnostina arranged in an arc running from the axial glabellar node to the basal glabellar lobe. The oblique lateral ridge flanks these grooves adaxially.

occipital band. Narrow (sag. and exsag.), depressed posterior band of occipital ring in odontopleurids; in Agnostina a narrow band that connects the basal lobes behind the posteroglabella. See also connective band.

occipital furrow. Transverse furrow (SO) that isolates occipital ring from remainder of glabella (syn., neck furrow, nuchal furrow).

occipital lobe. See lateral occipital lobe.

occipital lobula (pl., lobulae). See lateral occipital lobe.

occipital node. Median (or paired) tubercle developed on exterior of occipital ring (syn., neck node, nuchal node, occipital tubercle).

occipital ring. Axial region of most posterior segment of cephalon, bounded at sides by axial furrows, at front by occipital furrow, and at back by posterior margin. Considered part of glabella in all trilobites (syn., neck ring, nuchal ring).

occipital spine. Median (or paired) pointed structure projecting from exterior of occipital ring (syn., neck spine, nuchal spine). See also cranidial spine.

occipital tubercle. See occipital node.

occipitogenal diverticulum. Low ridge in eodiscoids that runs between occipital ring and inner, posterior corner of genal field.

occiput. Independently convex portion of glabella, bounded anteriorly by S1, lateral glabellar furrows, and posteriorly by the occipital furrow. Used in describing Trinucleidae, whereas intercalating ring is used for the similar structure in phacopids.

ocular band. See eye ridge.

ocular furrow. Furrow dividing the ocular lobe of Olenellina along its length into inner and outer bands (syn., epipalpebral furrow, ocular striga, striga).

ocular incisure. The abaxially convex curve of the margin between the eye lobe and the librigena.

ocular lobe. The ridge on the gena of Olenellina that curves outward and backward from the glabella immediately in front of S3 and bears on its outer, distal portion the curved visual surface of the eye.

ocular platform. See librigenal field.

ocular ridge. See eye ridge.

ocular striga. See ocular furrow.

ocular suture. Lower section of circumocular suture separating visual surface from librigena.

opisthoparian suture. Facial suture with posterior section cutting posterior margin of cephalon adaxial to genal angle, which is carried by librigena. See also cedariiform suture.

opisthothorax. Posterior portion of thorax when it is divisible into a wider (tr.) anterior portion (the prothorax) and narrower posterior portion (syn., postthorax).

opistopleura (pl., opistopleurae). See posterior pleural band.

orle furrow. Furrow near anterior margin of frontal glabellar lobe in *Chasmops* close to, and parallel with, preglabellar furrow.

ornament. See sculpture.

outer branch (of biramous appendage). Outer branch (ramus) of appendage arising from coxa (syn., exite, exopod, exopodite, gill branch).

outer glabellar region. See posterior lobe (of glabella).

outer portion of pleura. Portion of pleura outside fulcrum, which slopes downward and outward, may bear a facet, and has a doublure (syn., distal portion of pleura, free pleura).

outer spine angle. Angle between lateral border of cephalon and median line of genal spine.

paired eye ridge. See eye ridge.

palpebral area of fixigena. Portion of fixigena lying between eye ridge and imaginary transverse line connecting posterior corner of palpebral lobe with axial furrow (syn., interocular area, interocular cheek, interocular fixigena, palpebral region of fixigena).

palpebral furrow. Usually curved groove separating palpebral lobe from palpebral area of fixigena.

palpebral ledge. A marked ledge or groove situated on the palpebral lobe between the palpebral suture and the palpebral furrow as in *Lophosaukia.*

palpebral lobe. Protruding subsemicircular flange of fixigena bounded distally by palpebral suture. See eye lobe.

palpebral region of fixigena. See palpebral area of fixigena.

palpebral rim. Raised or thickened portion of palpebral lobe bordering palpebral suture.

palpebral suture. Portion of facial suture bounding distal edge of palpebral lobe.

palpebral view of cranidium. View normal to plane passing through palpebral lobes.

palpebro-ocular ridge. Curved ridge formed by confluence of eye ridge and palpebral lobe. The ridge may be subdivided by a longitudinal furrow into an outer (anterior) band and an inner (posterior) band.

pander organ. See panderian organ.

panderian notch. Notch in inner margin of cephalic or pleural doublure, assumed to have partially surrounded a panderian opening.

panderian opening. Small, rounded or elliptical opening in posterior genal and thoracic pleural doublure.

panderian organ. Supposed organ associated with panderian opening (syn., pander organ).

panderian protuberance. Small and rounded, elliptical, or elongate protuberance immediately adjacent to panderian opening; term also applied to raised anterior edge of panderian notch.

papilionate. See axial glabellar node.

papilla (pl., papillae). In calymenids refers to projections over axial furrow from lateral glabellar lobe or frontal lobe. See also buttress, papillate-buttress structure.

papillate-buttress structure. Projection bridging axial furrow of cephalon in calymenids, consisting of papilla and opposing buttress. See also papilla.

paradoublural line. Furrow, flexure, or ridge on dorsal exoskeleton of cephalon and pygidium, which is conformable with inner edge of doublure.

parafrontal band. Narrow, raised band following anterior border of frontal lobe of glabella and forming continuation of outer, anterior band of palpebro-ocular ridge as in protoleninids.

paraglabellar area. Arcuate, slightly depressed area at inner, posterior corner of fixigena; may be gently convex and outlined by furrow or change in slope as in homalonotids.

para-ocular facial line. See genal ridge.

para-postaxial ridge. Postaxial ridge on pygidium in which sagittal crest is prolonged into spine as in *Odontochile* and *Dalmanites.*

paraprotaspis (pl., paraprotaspides). Late protaspid stage, not precisely defined. Not recommended as a subdivision of protaspid period.

parathoracic segment. Region of transitory pygidium having the form of a thoracic segment, but still fused into pygidial exoskeleton.

paria. See librigena.

parial spine. See librigenal spine.

parietal surface. Inner surface of exoskeleton. See also visceral features.

pelturoid. Describes outline of gena when lateral and posterior margins form even curve.

pergenal spine. See procranidial spine.

peripheral pleural lobe. That part of the pygidial pleural region flanking or even enclosing deuterolobe in Agnostina.

perrostral suture. Ventral intramarginal cephalic suture crossing doublure at genal angle below spine as in Olenellina (syn., ventromarginal suture).

petaloid facet. Facet of thoracic segment crossed by subparallel terrace ridges, which are directed obliquely, the scarp slope facing downward and backward.

phaselus. Minute, oval body, deeply vaulted and widest anteriorly; narrow doublure flexed sharply, with marginal rim separating it from dorsal exoskeleton; reticulate sculpture. Thought to be a preprotaspid stage in development.

plectrum. Rearward projection of a median portion of anterior cranidial border; it may interrupt course of border furrow and may extend to front of glabella.

plethoid. Situation in *Pseudagnostus* in which accessory furrow defining deuterolobe continues to posterior border furrow.

pleura (pl., pleurae). Lateral portion of thoracic segment (syn., pleuron).

pleural band. Anterior or posterior strip resulting from transverse or oblique division of thoracic or pygidial pleura by pleural furrow.

pleural field (of pygidium). Lateral portion of pygidium bounded adaxially by axial furrow and abaxially by border furrow (syn., flank, pleural platform, pleural zone, pygopleura).

pleural furrow. Groove in external surface of thoracic pleura or pleural region of pygidium, formed by fold in exoskeleton. See epifacetal and postfacetal types.

pleural lobe. See pleural region.

pleural node. Inflated triangular area on adaxial part of thoracic pleura in Olenidae.

pleural platform. See pleural field.

pleural region. Lateral portion of thorax or pygidium abaxial to axial furrow (syn., pleural lobe, pleurothorax, side lobe).

pleural rib. See rib.

pleural ridge. Ridge along either anterior or posterior pleural band, latter commonly prominent as principal pleural ridge.

pleural spine. Hollow, pointed extension of distal end of a pleura or of either band of the pleura, of thorax or pygidium. See also border spine, marginal spine.

pleural stop. Ridge separating facet from pleural furrow in outer portion of second thoracic segment in certain Agnostina; morphologically equivalent to the anterior pleural band.

pleural zone. See pleural field.

pleuroccipital border. See posterior border (of cephalon).

pleuroccipital furrow. See posterior border furrow (of cephalon).

pleuron. See pleura.

pleurothorax. See pleural region.

podomere. Individual component of inner branch of biramous appendage, connected by movable articulation to coxa and adjoining podomeres (syn., segment).

polymerid. Term originally proposed for trilobites having six or more thoracic segments; commonly used as a convenient abbreviation to refer to all trilobites other than Agnostina and eodiscoids. This distinction cannot be made solely on numbers of thoracic segments, and the term should not be used formally as an order to include all trilobites other than Agnostina and eodiscoids.

pore. See fossula.

postannulus. Posterior part of thoracic axial ring separated by intra-annular furrow from preannulus.

post-apodemal sector. Posterior portion of axis of pygidium in which inter-ring furrows lack lateral apodeme but may show muscle scar on external surface.

postaxial furrow. Longitudinal groove bounding postaxial ridge of pygidium.

postaxial keel. See postaxial ridge.

postaxial median furrow. The pygidial median furrow behind the axis in eodiscoids and Agnostina.

postaxial region. Area on pygidium between posterior end of axis and posterior margin.

postaxial ridge. Sagittal ridge that extends back from tip of pygidial axis; latter indicated by change of slope (syn., postaxial keel, postrachial ridge).

posterior area of fixed cheek. See posterior area of fixigena.

posterior area of fixigena. Portion of fixigena lying behind imaginary transverse line connecting posterior corner of palpebral lobe with axial furrow [syn., limb, posterior area of fixed cheek, posterior fixigena, posterior limb, posterior region (of fixigena), posterolateral limb, postocular cheek, postocular fixigena].

posterior band of occipital ring. Narrow (sag. and exsag.) band, widest in midline, situated below and behind main part of occipital ring.

posterior band of pleura. See posterior pleural band.

posterior border (of cephalon). Portion of cephalic border between genal angle and occipital ring (syn., pleuroccipital border).

posterior border (of hypostome). Extends between posterolateral angles and is bounded by posterior border furrow.

posterior border furrow (of cephalon). Portion of border furrow bounding posterior border (syn., pleuroccipital furrow, posterolateral furrow).

posterior branch (of facial suture). Portion of facial suture lying behind eye [syn., posterior section (of facial suture), postocular branch, postocular suture].

posterior field (of fixigena). Portion of posterior area of fixigena lying anterior to posterior border furrow.

posterior fixigena. See posterior area of fixigena.

posterior fixigenal spine. Prominent spine at posterolateral corner of protocranidium in protaspis.

posterior flange. Narrow border extending along posterior edge of inner portion of pleura.

posterior fossula. Pit at lateral extremity of posterior border furrow opposed by a pit on flange of lower lamella in Trinucleidae (syn., lateral pit).

posterior genal ridge. See intergenal ridge.

posterior glabellar furrow. See lateral glabellar furrow.

posterior indentation. Small indentation in posterior margin of transitory pygidium in asaphids and immature proetoid pygidia (syn., larval notch).

posterior limb. See posterior area (of fixigena); see also posterolateral projection (of fixigena).

posterior lobe (of glabella). Lateral glabellar lobe L1. In Agnostina used for posterior portion of glabella (posteroglabella) lying behind transglabellar furrow. In some Agnostina a change in slope or faint exsagittal furrow divides this lobe into midmost glabella and outer glabellar regions.

posterior lobe (of hypostome). Portion of middle body of hypostome behind middle furrow.

posterior margin (of cephalon). Edge of cephalon between genal angles.

posterior median lobe of pygidium. See terminal axial piece.

posterior notch (of hypostome). Median notch in posterior border between posterolateral spines.

posterior ocular line. Ridge in Olenellina outside intergenal ridge, directed backward and outward from posterior end of ocular lobe.

posterior pleural band. Strip of thoracic or pygidial pleura bounded anteriorly by deepest part of pleural furrow (syn., opisthopleura, posterior band of pleura, postpleura).

posterior pleural spine. Pointed extension of distal end of posterior pleural band (syn., principal pleural spine).

posterior region (of fixigena). See posterior area of fixigena.

posterior section (of facial suture). See posterior branch (of facial suture).

posterior spine. Posterior extension of border and doublure of pygidium (syn., caudal spine, median border spine, mucro).

posterior wing (of hypostome). Extension of doublure of lateral border of hypostome.

posteroaxis. In Agnostina that portion of the pygidial axis lying behind the posterior inter-ring furrow (F2).

posteroglabella. Posterior portion of glabella as in *Centropleura*, formed by occipital ring plus ring formed by fusion of L1 and S1. In Agnostina synonymous with posterior lobe of glabella.

posterolateral furrow. See posterior border furrow (of cephalon).

posterolateral limb. See posterior area of fixigena.

posterolateral projection (of fixigena). Portion of fixigena lying abaxial to imaginary exsagittal line from posterior end of palpebral suture to posterior margin of cranidium (syn., posterior limb as used by some authors, but not as defined by HOWELL & others, 1947).

posterolateral spine (in Agnostina). Spine arising from posterolateral border of cephalon or pygidium.

posterolateral spine (of hypostome). Spine on posterolateral border of hypostome.

postfacetal pleural furrow. Outer portion of pleural furrow that runs behind facet in transverse direction until it becomes obsolete (in asaphids, bathyurids, etc.).

postocular area (of fixigena). Portion of posterior area of fixigena between axial furrow and imaginary exsagittal line from posterior end of palpebral suture [syn., postocular region (of fixigena)].

postocular branch. See posterior branch (of facial suture).

postocular cheek. See posterior area of fixigena.

postocular fixigena. See posterior area of fixigena.

postocular glabella. That part of the glabella behind adaxial end of eye ridge.

postocular margin. Margin of librigena defined by posterior branch of facial suture.

postocular region (of fixigena). See postocular area (of fixigena).

postocular suture. See posterior branch (of facial suture).

postocular tubercle. Tubercle at rear of field of fixigena in exsagittal line with or adaxial to palpebral lobe.

postoral plate. See metastome.

post-palpebral furrow. A furrow running from posterior end of palpebral lobe and crossing fixigena to meet posterior border furrow inside posterolateral angle of cranidium.

postpleura. See posterior pleural band.

postrachial ridge. See postaxial ridge.

post-thorax. See opisthothorax.

preannulus. Anterior portion of thoracic axial ring separated from postannulus by intra-annular furrow.

precranidial lobe. Area of librigena between facial suture, connective suture, and anterior border of cephalon in Encrinuridae (syn., false preglabellar area, pseudoglabellar area).

prefrontal furrow. Lateral portion of preglabellar furrow in *Pliomerina.*

prefrontal lobe. Lobe separated from rest of glabella by shallow furrow; it is lateral part of anterior border of cranidium in *Pliomerina.*

preglabellar area. Portion of cranidium between imaginary exsagittal lines running anteriorly from each end of preglabellar furrow, including preglabellar field if developed and median portion of anterior border.

preglabellar boss. Subcircular swelling of preglabellar field (syn., frontal boss).

preglabellar field. Portion of cranidium lying between front of glabella and anterior border furrow.

preglabellar furrow. Portion of axial furrow outlining front of glabella.

preglabellar keel. See preglabellar ridge.

preglabellar median furrow. See median preglabellar furrow.

preglabellar pit. Pit in preglabellar furrow as in Dimeropygidae.

preglabellar ridge. Sagittal ridge or fold in preglabellar field (syn., preglabellar keel). Contrast with transverse preglabellar ridge.

preoccipital glabellar furrow. See lateral glabellar furrow S1.

preoccipital glabellar lobe. See lateral glabellar lobe L1.

preoccipital glabellar spine. See median glabellar spine.

preoccipital ring. See intercalating ring.

preocular area (of fixigena). Portion of fixigena anterior to eye and eye ridge and abaxial to preglabellar area and including border.

preocular branch (of facial suture). See anterior branch (of facial suture).

preocular cheek. See anterior area (of fixigena).

preocular facial line. See facial line.

preocular field (of fixigena). Portion of preocular area inside border furrow.

preocular glabella. That part of the glabella in front of adaxial end of eye ridge; not coincident with the frontal glabellar lobe.

preocular suture. See anterior branch (of facial suture).

presulcal depression. Sagittally expanded part of outer anterior border furrow in Proetidae.

principal genal vein. See genal ridge.

principal pleural ridge. Refers to ridge of posterior pleural band when it is more prominent than ridge on anterior band; see also pleural ridge.

principal pleural spine. See posterior pleural spine.

procranidial spine. Spine on anterolateral border of cephalic shield, directed horizontally, in early developmental stages of Olenellina (syn., pergenal spine).

profixigenal spine. Spine projecting from border and doublure of fixigena in front of genal spine, as in *Sphaerocoryphe.*

prolibrigenal spine. Spine projecting from border and doublure of librigena.

prolongation. Extension of fringe beyond posterior margin of genal regions as in Harpetidae and Harpididae (syn., horn).

prong. Short projection at fulcrum at anterior margin of thoracic segment or pygidium in Agnostina. See fulcral process.

proparian suture. Facial suture with posterior branch cutting lateral margin of cephalon in front of genal angle.

propleura (pl., propleurae). See anterior pleural band.

propleuron. See anterior pleural band.

prosopon. See sculpture.

protaspid period. Period of development during which there is no transverse articulation in exoskeleton.

protaspis (pl., protaspides). Smallest known exoskeletons, subhemispherical to spherical in form; may exhibit size series, but lacking transverse articulation.

prothorax. Anterior portion of thorax when it is divisible into a wider (tr.) anterior and a narrower posterior, portion (opisthothorax).

protocephalon. Cephalic portion of protaspid exoskeleton.

protocranidium. Cranidial portion of protaspid exoskeleton.

protopygidium. Postcephalic portion of protaspis.

protothoracic segment. Segment in protopygidium or transitory pygidium destined to become thoracic segment.

proximal. End of part or organ that is nearest to point of origin or sagittal line of body.

proximal portion of pleura. See inner portion of pleura.

pseudoantennary pit. See fossula.

pseudo-articulating half ring. Lenticular or subrectangular median depression between anterior pygidial axial rings, resulting from embayment in posterior edge of ring and consequent widening of inter-ring furrow.

pseudofrontal lobe. Composite structure forming anterior part of glabella characteristically in Trinucleinae, bounded posteriorly by S2 and incorporating much reduced or absent S3.

pseudofurrow. See accessory furrow.

pseudogirder. Any concentric ridge occurring between E or I arcs on lower lamella in trinucleids.

pseudoglabellar area. See anterior border of cranidium (in Encrinuridae), precranidial lobe.

pseudolobe. See deuterolobe.

pseudopalpebral furrow. Furrow running obliquely across palpebro-ocular ridge at anterior end of palpebral rim as in *Resserops.*

pseudopostaxial ridge. A short (sag.) and narrow postaxial ridge that does not reach the posterior margin of the pygidium.

pseudoproparian suture. See cedariiform suture.

pseudotropidium. A ridge in the same position as the tropidium, but not reflected as groove on inner surface of exoskeleton.

ptychopariid suture. Opisthoparian suture in which anterior branches are directed forward and inward, librigenae are separated by connective sutures from rostral plate, and rostral plate is not suturally connected to hypostome; see euptychopariid and stenoptychopariid rostral sutures.

pulvinar furrow. Longitudinal furrow bounding pulvinus abaxially.

pulvinus. Swollen longitudinal lobe bounded adaxially by axial furrow and abaxially by pulvinar furrow in encrinurid *Cybeloides*.

pustule. Small, rounded elevation on any part of external surface of exoskeleton. See tubercle.

pygidial collar. Curved ridge on inner side of posterior border of pygidium of Agnostina; may be continuous or have a median gap.

pygidium (pl., pygidia). Posterior tagma in trilobites, composed of fused somites, applied by authors to posterior portion of exoskeleton separated from thorax by articulation (syn., caudal shield, tail, tail shield).

pygopleura (pl., pygopleurae). See pleural field (of pygidium).

pygorachis. See axis (of pygidium).

pygothorax. See thoracopygon.

rachial furrow. See axial furrow.

rachial ring. See axial ring.

rachis (pl., rachises). See axis.

rear eye ridge. Lateral continuation parallel to posterior cephalic margin of fixigenal eye stem in Phacopida. It is bounded distally by facial suture. Rear eye ridge is not a synonym of intergenal ridge.

retrodivergent suture. Anterior branch of suture that curves from eye lobe to be directed outward and backward before curving forward to margin of cephalon.

rhachis (pl., rhachises). Alternative spelling of rachis. See axis.

rhaptoid. Descriptive of Agnostina when notular line is present on pygidial axis.

rhynchos. Swollen anteromedian protuberance on anterior lobe of middle body of hypostome (as in encrinurids or calymenids).

rib. Portion of pygidial pleural region bounded by two successive pleural furrows (syn., pleural rib).

rib furrow. See interpleural furrow.

rim. Narrow peripheral ridge on either upper or lower lamella of fringe in Trinucleidae and Harpetidae; rims united at external edge by a flat, vertical marginal band. In Harpetidae rim present on external and internal edges of prolongation.

ring. See axial ring.

ring furrow. See inter-ring furrow.

ring process. Projection backward from posterolateral corner of axial ring, fitting into socket in next posterior ring.

ring socket. Hollow at extremity of articulating furrow and articulating half-ring for reception of ring process of next anterior ring.

rosette. Axial node in flared depression separating posteroaxis of pygidium in Agnostina into two parts.

rostellum. Small subtriangular plate enclosed between rostal suture and connective sutures, the latter joining as median suture posterior to rostellum.

rostral flange. Hindmost part of rostral plate when it is strongly curved in anterior or dorsal direction so as to form fold, as in *Bumastus.*

rostral-hypostomal plate. Fused rostral plate and hypostome.

rostral plate. Median cephalic ventral portion of doublure (and rarely adjacent border) of variable size and relations; may be bounded anteriorly and laterally by the perrostral suture (Olenellina) or bounded anteriorly by the rostral suture and laterally by paired connective sutures, and in Homalonotidae it is partly dorsal [syn., epistoma (partim), epistomal plate, epistome, rostrum, rostral shield)]. See also rostellum. May be subdivided into border and doublure sectors.

rostral shield. See rostral plate.

rostral suture. Suture bounding anterior edge of unpaired, median rostral plate and separating it from the cranidium.

rostrum. See rostral plate.

ruga (pl., rugae). Ramifying, relatively broad, radiating ridges on the acrolobe of Agnostina.

S. Abbreviation for occipital or lateral glabellar furrow (sulcus), numbered forward from posterior, SO (occipital), S1, S2, S3, etc.

sagittal. Direction along axial line of body (abbreviation, sag.).

sagittal band. Smooth zone along pygidial axis, level with and joining tops of axial rings, interrupting inter-ring furrows.

sagittal groove. Smooth zone along pygidial axis, depressed below axial rings, which it interrupts partly or completely.

sagittal line. Median line of body (syn., axial line).

schizochroal eye. Eye with visual surface consisting of number of biconvex lenses, rounded or polygonal in outline, each lens covered by individual cornea and separated from others by sclerotic walls (syn., aggregate eye).

sclerite. Portion of exoskeleton into which it is divided either by an articulation or (during exuviation) by a suture.

scrobicula (pl., scrobiculae). Radiating furrows between rugae in Agnostina; groove or row of pits between border and epiborder furrows in eodiscoids.

scrobiculate. Refers to presence of scrobiculae in Agnostina.

sculpture. Refers to the features of the external surface of the exoskeleton, whether it is smooth or bears lirae, terrace ridges, tubercles, granules, pits, etc. (syn., ornament, prosopon).

segment. Exoskeleton of individual thoracic somite, divided into axial ring and pleura with doublure. Also used as a synonym of podomere.

semi-ankylosed segment. Posterior thoracic segment that may or may not be fused to the pygidium as in certain Redlichiina and paradoxidids.

shield. See exoskeleton.

shoulder (of hypostome). Anterolateral part of lateral border of hypostome, separated from anterior wing by lateral notch, generally the widest and most inflated part of lateral border; ridge crosses doublure of hypostome below shoulder (syn., lateral projection of hypostome).

shoulder (of pygidium in Agnostina). Ridge on anterior edge of pleural lobe, borders facet on inner side.

shoulder furrow (of pygidium in Agnostina). Separates shoulder from acrolobe; may be continuous with border furrow or cross border to margin.

side lobe. See pleural region.

simplimarginate. Pygidium of Agnostina in which border is not modified by pygidial collar.

socle. See eye socle.

somite. Transverse division of arthropod body (syn., metamere).

spectaculate. See axial glabellar node.

spine furrow. Longitudinal furrow on genal spine, a continuation of the lateral or posterior border furrow, or of both furrows.

stenoptychopariid rostral suture. Connective suture marginal to narrow (tr.) rostral plate (contrast with euptychopariid). See ptychopariid suture.

sternite. Sclerite of ventral portion of a somite.

striga. See ocular furrow.

subcephalic furrow. See vincular structure.

subcranial furrow. See vincular structure.

subgenal notch. Notch in posterior margin of cephalon immediately inside base of genal spine.

submarginal suture. Suture following margin of cephalon, slightly inside and below distal edge.

subocular area. Small, smooth area of librigena adjoining posterior portion of eye.

subocular groove. Smooth, bandlike depression of librigena surrounding visual surface of eye.

subocular ridge. Narrow ridge confining adaxially the subocular groove.

supplementary lobe. See intermediate lobe.

sutural ridge. Narrow ridge upon (or beside) which either branch of facial suture may be present on exterior surface of dorsal exoskeleton (syn., false eye ridge).

suture. Line along which portions of cephalic exoskeleton separated at exuviation. See cephalic, circumocular, connective, facial, hypostomal, marginal, perrostral, and rostral sutures.

tail. See pygidium.

tail shield. See pygidium.

telopod. See inner branch.

telopodite. See inner branch.

telson. Postsegmental part of arthropod body, bearing anus and commonly caudal furca or pair of cerci. Postcephalic somites form successively at the anterior margin of the telson during ontogeny.

tergite. Sclerite of dorsal portion of a somite. Not precisely equivalent to thoracic segment, because latter includes doublure.

terminal area (of pygidium). That part of pleural field or pleural region (in species having a ribbed field) that lies posterior to last rib.

terminal axial piece (or ring). Portion of axis of pygidium behind last inter-ring furrow (syn., posterior median lobe of pygidium, terminal axial segment).

terminal axial segment. See terminal axial piece.

terminal axial spine. Projection of median dorsal surface of terminal portion of axis of pygidium.

terminal node (of glabella). Small node at rear of glabella in Agnostina.

terminal node (of pygidial axis). In Agnostina, node at rear extremity of posteroaxis or intranotular axis.

terminal septum. Internal septum produced by median thickening of exoskeleton at steep termination of the axis in Proetoidea.

terrace ridges. Asymmetrical ridges on external surface of exoskeleton, having a steep scarp and gentle dip slope, may be parallel, subparallel, or anastomosing.

test. See exoskeleton.

thoracic recess. Median indentation in anterior margin of first thoracic segment (which lacks the articulating half ring) in Agnostina. See cephalothoracic aperture.

thoracic segment. See segment.

thoracopygon (pl., thoracopyga). Exoskeleton of thorax and pygidium (syn., pygothorax).

thorax. Region of trilobite body between cephalon and pygidium in which successive somites are articulated; also used to refer to exoskeleton of region, the segments of thorax. The thorax may show a division into prothorax and opisthothorax.

torular tubercle. Surmounts torulus and may persist in similar position after torulus has disappeared.

torulus. Rounded swelling beside glabella (typically opposite S2) on fixigena in early growth stages of encrinurids.

transaxial furrow. See inter-ring furrow.

transglabellar furrow. Continuous furrow across glabella resulting from meeting of adaxial ends of a pair of lateral glabellar furrows. In Agnostina furrow (F3) that separates the anterior and posterior glabellar lobes, anteroglabella and posteroglabella (syn., anterior furrow).

transitory pygidium. Fused segments of posterior region of exoskeleton during meraspid period.

transmarginal genal spine. Genal spine that arises from genal field, not from border.

transverse. Term used to designate the direction at right angles to sagittal line (abbreviation, tr.).

transverse preglabellar ridge. Transverse ridge crossing preglabellar field a short distance behind anterior border furrow. Contrast with preglabellar ridge.

tricomposite glabellar lobe. See bullar lobe.

tropidial ridges. Short, discontinuous, raised ridges that occupy similar position to tropidium.

tropidium (pl., tropidia). Concentric ridge that traverses preglabellar field and librigena a short distance inside and parallel with anterior border. Not coincident with inner margin of doublure.

tubercle. Small, knoblike prominence on external surface of exoskeleton. See pustule.

unconstricted. See acrolobe.

upper lamella. Upper or dorsal plate of fringe, as in Harpetidae, Harpididae, and Trinucleidae.

upper rim (external or internal). Smooth, raised portion of upper lamella of fringe as in Harpetidae, Harpididae, and Trinucleidae.

ventromarginal suture. See perrostral suture.

vincular structure. Furrow (subcephalic, subcranial), depression (or series of depressions), protuberance, ridge, or other structure associated with enrollment. See coaptation.

visceral features. Features of inner surface of exoskeleton.

visual surface (of eye). External surface of eye that bears lenses and is bounded above by palpebral portion of facial suture (syn., eye lappet). The visual surface may be bounded below by an ocular suture, so that there is a circumocular suture.

walking leg. See inner branch.

wing (of hypostome). See anterior wing, anterior wing process, posterior wing.

zonate. Situation in pygidium of Agnostina in which border is duplicated by pygidial collar between marginal spines.