CLASSIFICATION OF THE TRILOBITE SUBORDER ASAPHINA

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ABSTRACT. We present a new phylogenetic classification of trilobites which can be included in a ptychoparioid suborder Asaphina, considerably extending the range of families included in the group as compared with existing classifications. Much of the group is known to be united by the possession of a distinctive type of inflated and effaced larva termed the asaphoid protaspis. The morphology and occurrence of this kind of protaspis is reviewed. All of the group has a ventral median suture, except where it was secondarily lost through fusion of the free cheeks, and most morphological evidence is considered to favour a monophyletic origin for this structure. Relationships between families having such a suture are based on the analysis of morphology; however, stratigraphy is relevant to the determination of the sequencing of characters within a family and to the identification of minor character reversals and parallelisms which can be discounted in the higher level analysis. Two methods of analysis are used. One produces a cladogram based on our weighted assessment of the most important characters. The other, a computer-based analysis using the PAUP program, uses a much wider range of characters to produce two trees which are equally likely. There is generally good agreement between the different methods of analysis. As thus defined, Asaphina includes Cyclopygacea (comprising Cyclopygidae, Nileidae, and Taihungshaniidae), Asaphacea (Asaphidae and Ceratopygidae), Remopleuridacea, and Dikelocephalacea, together with some more primitive families which are more difficult to classify: Dikelokephalinidae, Pterocephaliidae, and Anomocaracea. We make a case that the Trinucleacea are linked to the Asaphina by more characters than to any other group. Trilobites included within the suborder are discussed family by family. The supposed olenid *Hedinaspis* should be included in Asaphacea; on the other hand, the Olenidae, which were included in Asaphina by Bergström (1973), are unrelated to the families considered here. The Asaphina was diverse from the mid-Cambrian until the end of the Ordovician, when the group was particularly vulnerable to extinction; this may have been connected with the planktic specialization of the asaphoid larva.

HIGH level classification of the trilobites is a long-standing problem. Most authors who have reviewed the subject (Henningsmoen 1951; Bergström 1973) have stated the principle that classification should be phylogenetically based, but the agreement stops there, foundering on exactly what characters are to be taken as phylogenetically significant. The plasticity of the trilobite exoskeleton, and the recurrence of certain types of adaptive morphology from more than one phylogenetic source, has made the framing of diagnoses above the family level difficult. There are exceptions: Phacopina, for example, with the unequivocal apomorphic character of the schizochroal eye. The problems are particularly acute when it comes to relating well-characterized Ordovician and younger families to those in the Cambrian. The Cambrian–Ordovician boundary remains a taxonomic one for many groups (for a list of those that crossed it see Fortey 1983). While it is true that the Ordovician sees the inception of new trilobite morphologies that have received familial recognition, it is also probable that they have Cambrian sister groups, and the identification of these is a necessary prerequisite for a phylogenetic classification which can be incorporated in the revision of the *Treatise of Invertebrate Paleontology*. Certainly this stratigraphic boundary is of little importance to the trilobite families discussed below.

Our purpose here is to consider those families which may be classified in a suborder Asaphina, including perhaps one-fifth of the trilobites. The resulting classification differs in many ways from that used in the *Treatise* (Moore 1959), both in its arrangement of families, and in the families assigned to it. The trilobite superfamily Cyclopygacea was discussed previously (Fortey 1981) and the details are not repeated here. We do not address the wider issue of whether the Asaphina merits ordinal status, as opposed to subordinal rank within an Order Ptychopariida. This will depend on a review of the other

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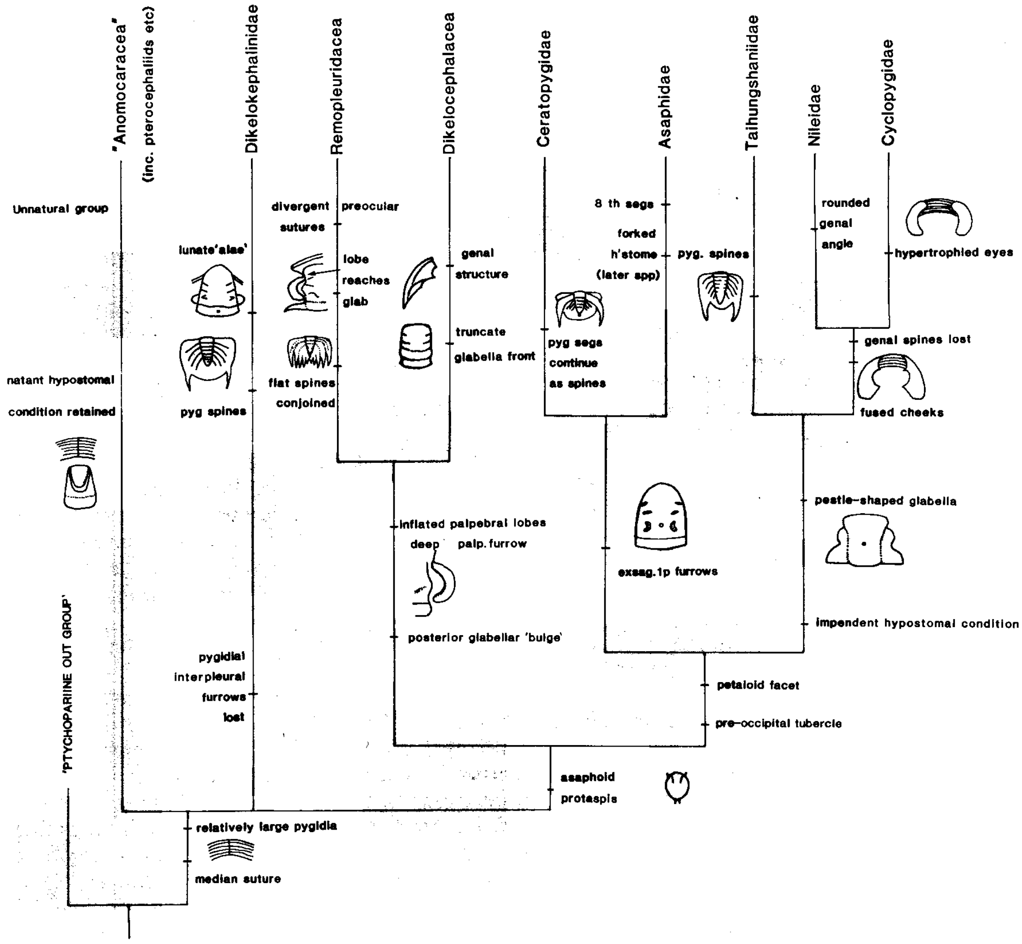
ptychoparioid trilobites and an assessment of whether that group is or is not polyphyletic. However, the recognition of an Order Asaphida including only Asaphidae and Ceratopygidae, as used by Shergold and Sdzuy (1984) for example, neither addresses this issue nor includes several related families discussed here, and seems to us a taxonomic over-elevation on insufficient grounds.

METHOD OF CONSTRUCTING CLASSIFICATION

We have used a cladistic method here for the analysis and presentation of results. We have, however, used stratigraphic criteria for the identification of primitive character states within particular families, and have accepted similar criteria for tracing out segments of trees of particular groups. Such a combination of cladistic and stratigraphic methods is not acceptable to many cladists (Eldredge and Cracraft 1980) nor is the use of cladistic analyses usual in analysing completely extinct groups. It does have the advantage of making clear exactly what characters are used in the definition of high level groups, and it frequently offers new insights into the phylogenetic arrangement of these families. Equally, it seems unwise to neglect the contribution that stratigraphy can make to an understanding of what happens to characters through time (Fortey and Jefferies 1982), although this kind of evidence tends to work better at low taxonomic levels. What we are trying to identify are synapomorphies linking accepted monophyletic units—derived characters which are considered likely to have appeared only once. We are also trying to identify autapomorphies useful for diagnosis at family level and above. Most of the families considered here are known from numerous species and have a relatively complete fossil record; hence we can use stratigraphic criteria to determine character polarity in some cases where there are ambiguities, and to observe the primitive morphology for an accepted family, which is of use in determining the most likely sister group in constructing the higher level classification.

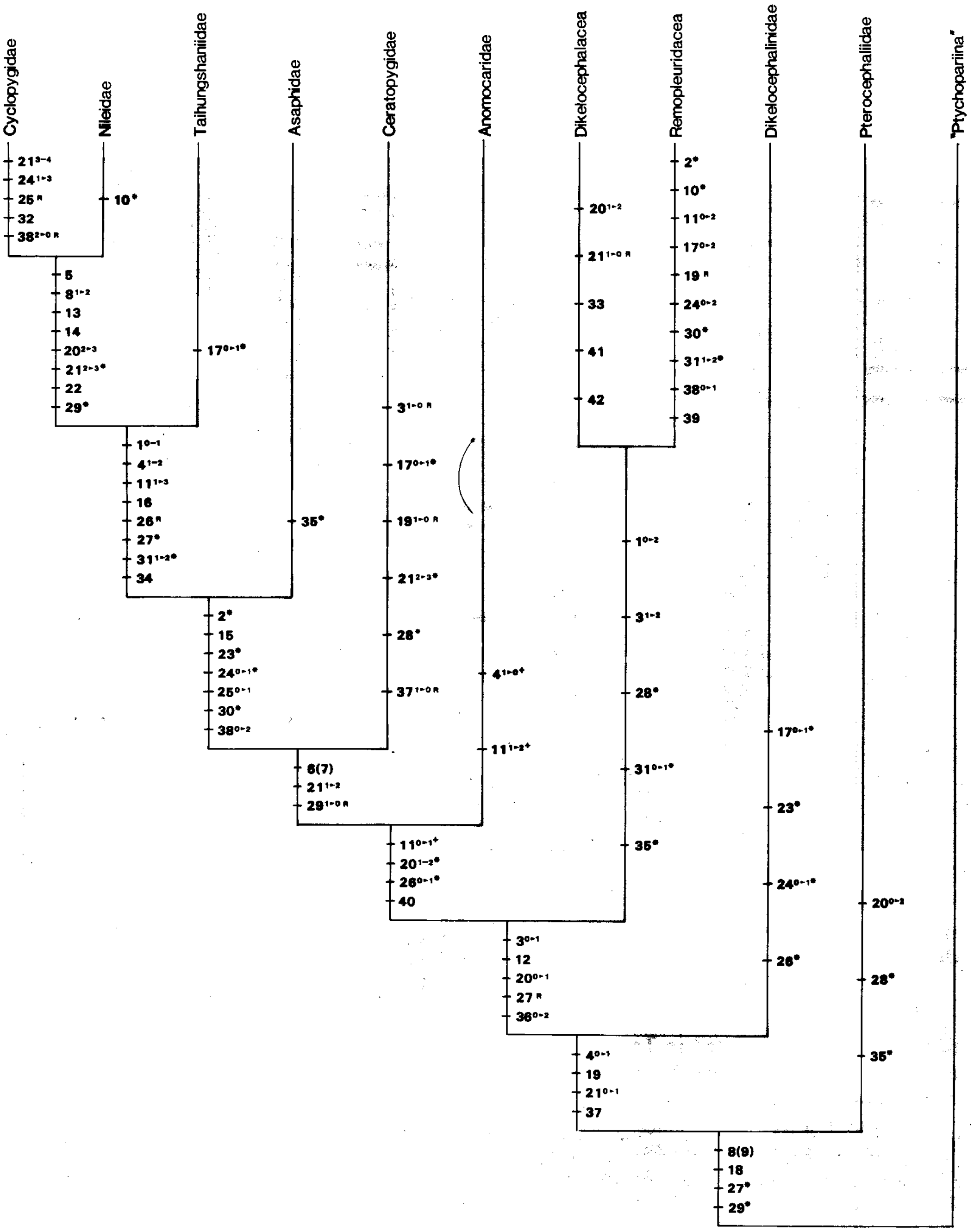
Our approach to construction of cladograms has been two-fold. We have first constructed a diagram of relationships incorporating those characters which we believe are of particular importance (i.e. weighted), especially those ontogenetic and axial characters which we discuss in detail below. This is shown as text-fig. 1. Then we constructed cladograms based on the PAUP (phylogenetic analysis using parsimony) program. This program uses a matrix of characters, which are not individually weighted, for which a polarity (primitive or derived) is assumed. Taxa are then coded for these characters, and the computer program selects from the universe of possible trees the most parsimonious tree (or trees) that can be permuted from the characters. The tree so produced is that which minimizes the number of character reversals or parallelisms. This method has previously been applied to a wholly fossil group by Forey (1987), to whom the reader is referred for technical details. Polarity of characters is determined by reference to an out-group, in our case ptychoparioid, and it was not difficult to assess polarity in this way without direct recourse to stratigraphy. We list the characters we have used in Table 2. This method allows for the inclusion and manipulation of many more characters than is possible by the more intuitive method of text-fig. 1. However, coding for characters has proved to be far from easy, and here we have found it necessary to take into account stratigraphic information *from within accepted monophyletic families* to detect such things as character reversals assumed to be at low taxonomic level, and usually concerning relatively trivial features. For example, lack of tuberculate sculpture is characteristic of a large group, Cyclopygacea + Asaphacea, but there is one genus, *Norasaphus* Fortey and Shergold, 1984, in which such sculpture is developed, and stratigraphic (as well as morphological) evidence indicates that this is a secondarily derived feature in this case. This genus is ignored; otherwise it would have to be coded entirely separately, to make a separate terminal taxon on the cladogram, which would make the process unwieldy. Advanced Remopleuridacea, *Remopleurides* and its allies, develop several peculiar autapomorphies, for example adaxial thoracic articulation; this is of use in defining a subgroup within remopleuridaceans, but does not contribute to the larger analysis of relationships. In general, such features of within-group specialization are ignored, and in contentious cases a generalized, and stratigraphically early, representative of an accepted group forms the basis for the coding. This enables us to encode more characters than would be possible if we had to allow for minor parallelisms and reversals. Most



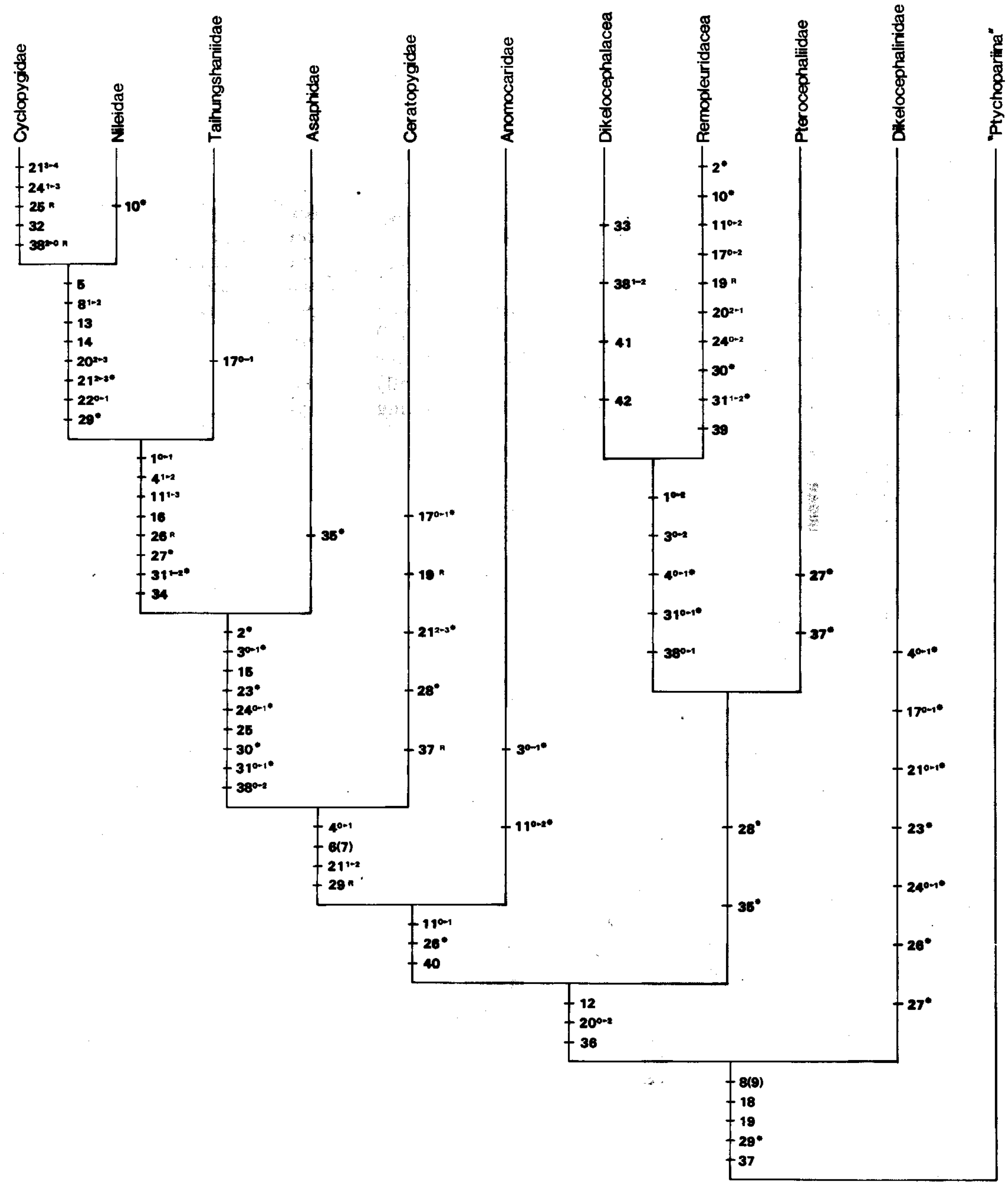
TEXT-FIG. 1. Cladogram of relationships of taxa included within Asaphina herein, based on weighting of characters which are considered particularly important in phylogeny, as discussed in text; some of these characters are sketched. A broad view of Anomocaracea is taken in this diagram.

of the characters tabulated in Table 2 should be obvious from our definitions given there. A few characters, considered of special importance by us in text-fig. 1, are discussed in some detail below. An assumption we have been obliged to make is that when a character is known from a few (maybe only one) species in a family we assume that it applied generally to that group. For example, hypostomes have been assigned to very few Dikelokephalinidae and we have made our coding from those examples. For reasons discussed below we have not included Trinucleacea in the cladistic analyses, and this group is discussed separately towards the end of this paper.

Character states which are regarded as primitive for the Asaphina are listed in Table 1. These characters have been determined from examination of a range of generalized Ptychopariina, and are those widely distributed through the various families of primitive ptychoparioids recognized in the present classification. Some of them are general for nearly all Asaphina as well and so do not reappear



TEXT-FIG. 2. Cladogram produced from the PAUP computer analysis of the characters given in Table 2. Another equally parsimonious cladogram is shown in text-fig. 3. Note that text-figs. 2 and 3 resemble each other, apart from the position of Dikelokephalinidae and Pterocephaliidae. Pterocephaliidae and Anomocaridae are coded separately (cf. text-fig. 1) rather than included in 'Anomocaracea' *sensu lato*. Numbering of characters as in Table 2. Direction of character transformation for multistate characters is indicated. For symbols see text-fig. 3.



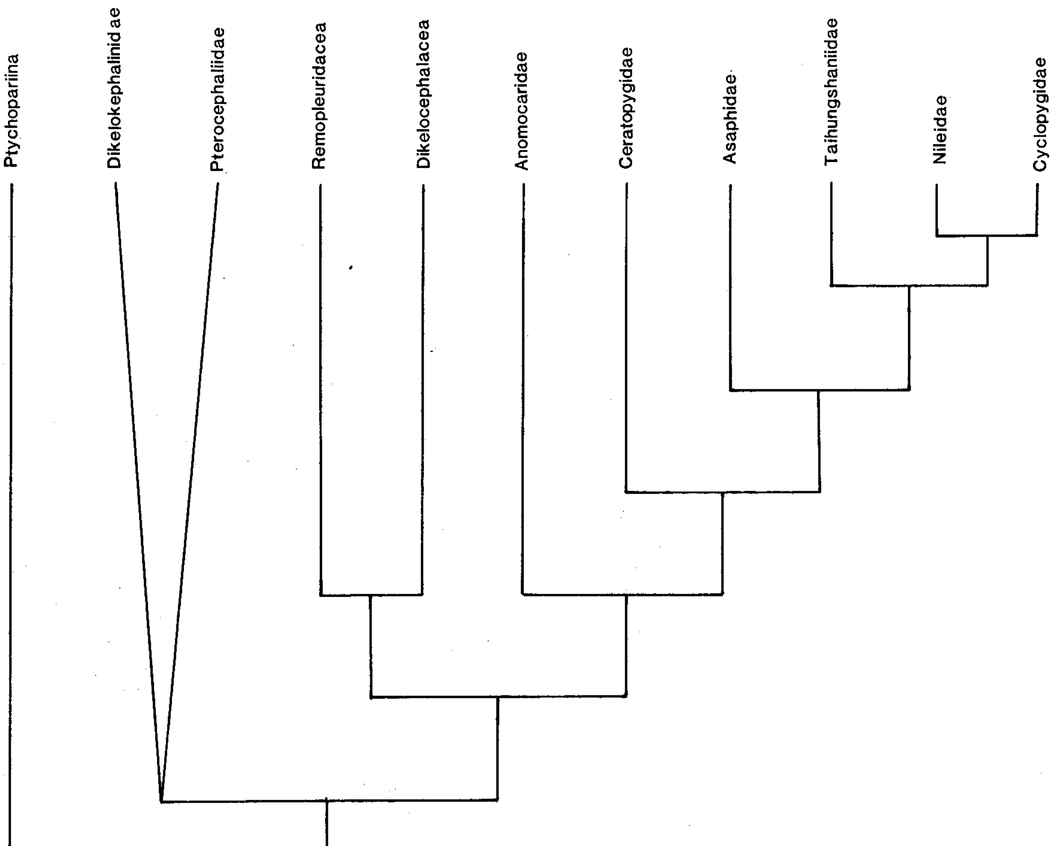
TEXT-FIG. 3. Another cladogram produced from the PAUP computer analysis of the characters given in Table 2, equally parsimonious with that shown on text-fig. 2. *, characters which are developed in parallel in more than one place on the cladogram; R, character reversals (i.e. advanced to primitive on Table 2); +, character transformations which we consider unlikely on other evidence (see text).

in Table 2 (e.g. opisthoparian sutures and terrace ridges on the doublure), but it is as well to list these to clarify those characters that *are* considered in deducing asaphine relationships. However, since Ptychopariina itself is acknowledged as an unsatisfactory taxon—a problem we cannot tackle here—the out-group to determine polarity on Table 2 has to be selected as an acceptable generalized form. We have used *Ptychoparia striata* (by definition the typical ptychoparioid) and *Elrathia kingi* as our reference.

Characters weighted in text-fig. 1

Characters on which we place particular importance, and which appear as synapomorphies linking major groups, include two categories.

1. *Character states present early in ontogeny.* In many trilobites complex developmental changes occur throughout ontogeny; we use the principle that the morphology of the early growth stages tends to be of more use in determining relationships. For example, effacement of the dorsal furrows is a general phenomenon in the asaphine trilobites. Effacement proceeds progressively both within individual ontogenies and within phylogenetic groups; it takes place repeatedly in unrelated families. The relationships of such trilobites are best judged from the immature forms in which dorsal furrows are still expressed. We argue below that a distinctive form of protaspis shared by many of the trilobites described here is also indicative of common ancestry. Characters initiated early on in ontogeny, whether or not they are subsequently lost during ontogeny or phylogeny, are regarded as likely to be of fundamental importance in demonstrating relationships, compared with characters



TEXT-FIG. 4. Consensus tree derived from text-figs. 2 and 3, according to the method of Adams (1972). Characters not included.

TABLE 1. General characters of ptychopariids, which are to be regarded as primitive when present in Asaphina.

Cephalon

Eyes with circum-ocular suture.
Eye ridges present.
Front end of palpebral lobes not reaching axial furrows.
Mid-occipital tubercle (where tubercle present).
Glabella tapering forwards or subquadrate.
Three or four pairs of glabellar furrows (unless effaced) progressively shorter anteriorly; 1s considerably the longest and directed inwards and backwards.

Venter

Hypostoma: ovoid middle body, narrow borders, pair of inward-backwardly directed middle furrows in posterior part of middle body.
Rostral plate present; rostral sutures inwardly concave.
Hypostomal condition natant.

Thorax

Thoracic segment number variable, and usually large.
Simple diagonal pleural furrows.
Unmodified articulation; fulcrum well removed from axial furrow.
Facets unspecialized.
Doublure narrow, with notches acting as vincular 'stops'.

Pygidium

Shorter (sag.) than thorax or cephalon.
Axis defined dorsally.

which may be superficially more noticeable, but which are acquired later during ontogeny, or within the course of the diversification of a family. As an example, the median suture is present in Asaphidea, Remopleurididae, and primitive Nileidae and Cyclopygidae, but in the later species of the latter two families the cheeks become yoked as a single unit. For the determination of phylogenetic relationships far more importance is attached to the presence of the suture than to its subsequent loss, partly because it appears very early on in ontogeny as a discrete structure, and partly because its loss is demonstrably polyphyletic (such sutures are lost on occasion in the asaphids too, for example).

2. *Structure of the cephalic axis.* The structure of the glabella—its shape, disposition of furrows or muscle impressions and glabellar tubercle—has proved to be an important character linking some of the high level taxa. Again we often refer to the less derived structure in a family to identify relationships, rather than subsequent modifications which can disguise significant similarities: thus Cyclopygidae became almost wholly effaced in response to their pelagic habits, but early examples (*Prospectatrix*) clearly show a glabellar form comparing with that of primitive nileids, and indicating the common ancestry of the two families (Fortey 1981). The species showing the less derived state is also the stratigraphically earliest, which is encouraging, but it is not essential to use the stratigraphic criterion in this case because the primitive nature of the glabellar structure of *Prospectatrix* would still be apparent from comparison with the out-group. Placing emphasis on glabellar form is not unreasonable, because the glabellar segmentation is likely to be related to the insertion of muscles for the cephalic limbs, and hence with the feeding mode of the trilobite, which has been shown to be significant at high taxonomic level in arthropods in general (Manton 1964).

Other characters, such as the thoracic structure and number of segments, or the incorporation of an anterior spinose segment in the pygidium, may come into play for the definition of families, as discussed below. If the relationships shown on text-figs. 1-3 are correct, spinose pygidia appeared several times in the Asaphina. Cladograms constructed on the basis that the appearance of spinose pygidia was a genuine synapomorphy are much less parsimonious than the ones shown, and result in unlikely distributions of the other characters; this

TABLE 2. Characters used in the compilation of the cladogram using the PAUP program. 0, primitive condition; 1, 2, derived conditions.

1, glabellar shape: 0, tapering or parallel sided; 1, expands forwards; 2, expansion at S1.
2, position of palpebral lobe: 0, does not touch axial furrow anteriorly; 1, touches axial furrow anteriorly.
3, palpebral rim: 0, defined; 1, effaced; 2, inflated, deeply described by rim furrow.
4, hypostomal condition: 0, natant; 1, conterminant; 2, impendent.
5, occipital ring: 0, defined; 1, effaced.
6, occipital tubercle: 0, present; 1, absent.
7, preoccipital tubercle: 0, absent; 1, present.
8, ventral median suture: 0, absent; 1, present; 2, lost by fusion of cheeks.
9, rostral plate: 0, present; 1, absent.
10, anterior branches of facial sutures: 0, subparallel to divergent up to 30° to sag. line; 1, more strongly divergent.
11, glabellar furrows: 0, ptychoparioid type; 1, crescentic 1s; 2, effaced abaxially; 3, entirely effaced.
12, protaspis type: 0, ptychoparioid type; 1, asaphoid type.
13, genal spines: 0, present; 1, absent.
14, posterior cephalic border furrow: 0, defined; 1, effaced.
15, thoracic facets: 0, 'ptychoparioid'; 1, petaloid (see text-fig. 13).
16, thoracic articulation: 0, first segment articulates at fulcrum at some distance from axial furrow; 1, first segment articulates at or very close to axial furrow.
17, pygidial spines: 0, marginal pygidial spines absent; 1, marginal pygidial spines anteriorly; 2, marginal pygidial spines along whole pygidial margin, conjoined at spine bases.
18, pygidial doublure: 0, narrow; 1, wide (arbitrary definition of narrow is where the width of doublure is one third, or less, the width of the pleural field inside doublure).
19, librigenal doublure: 0, narrow; 1, wide (particularly difficult to define objectively; our arbitrary definition of 'narrow' is where the doublure width is less than the width of the genal field inside doublure, to base of eye, at the anterior part of free cheek).
20, genal lateral border: 0, narrow, convex; 1, bevelled; 2, relatively wide and flattened, or gently convex; 3, obsolete (see text-fig. 6).
21, thoracic segment number: 0, group includes species with twelve or more segments; 1, group includes species with twelve to nine segments; 2, always eight segments; 3, group includes species with six to nine segments; 4, group includes species with six or fewer segments.
22, hypostomal outline: 0, elongate oval; 1, transverse.
23, hypostomal sculpture on middle body: 0, smooth, or fine pitting; 1, terrace ridges.
24, maculae and associated structures on hypostoma: 0, thin middle furrows; 1, smooth facets; 2, oval raised areas; 3, maculae lost.
25, hypostomal borders: 0, narrow; 1, wide.
26, bacculae/alae: 0, absent; 1, present, or on small growth stages, and lost in adult.
27, pygidial interpleural furrows: 0, present; 1, absent.
28, pygidial postaxial ridge: 0, absent; 1, present.
29, eye size: 0, medium (one quarter to one half glabellar length, which includes the occipital ring); 1, large (> half); 2, small (< quarter).
30, circumocular suture: 0, present; 1, absent.
31, eye ridges: 0, present; 1, absent; 2, not visible, because palpebral lobe touches axial furrow anteriorly.
32, eyes: 0, strip-like; 1, hypertrophied and inflated.
33, transglabellar glabellar furrows: 0, rarely present in group; 1, commonly present in group.
34, relationship of glabella to cephalic margin; 0, glabella does not reach furrow outlining marginal rim; 1, glabella reaches marginal rim or extends to cephalic margin.
35, course of dorsal sutures in front of glabella: 0, marginal; 1, supramarginal.
36, enrolment (after Bergström 1973): 0, not enrolled, or possibly spiral; 1, basket-and-lid; 2, sphaeroidal, or presumed to be sphaeroidal if specimen not known in enrolled condition (Bergström 1973 reported cylindrical enrolment in *Remopleurides*, but this is likely to have been secondarily derived from sphaeroidal in other remopleuridids).
37, pygidial length, excluding posterior spines; 0, shorter (sag.) than cephalon; 1, subequal to exceeding length of cephalon.

38, eye socle: 0, absent; 1, present (thin, wire-like); 2, present (band-like); see text-fig. 6.

39, postocular fixed cheek in relation to posterior border and border furrow: 0, postocular cheek includes long section of border furrow plus postocular genal field; 1, postocular fixed cheek consists almost entirely of posterior border.

40, surface sculpture: 0, often granulose/tuberculate; 1, never granulose/tuberculate (note: the only exceptions to this derived condition in Asaphacea are the genera *Norasaphus* Fortey and Shergold, 1984, and the sparsely granulose *Ceratopyge*, in both of which we regard tuberculation as secondarily derived).

41, frontal lobe of glabella: 0, broadly curved about mid-line; 1, more or less rectangular (see text-fig. 19).

42, genal spine: 0, posterior border furrow does not continue strongly into genal spine; 1, border furrows (especially continuation of posterior border furrow) curve backwards into base of genal spine (see text-fig. 7).

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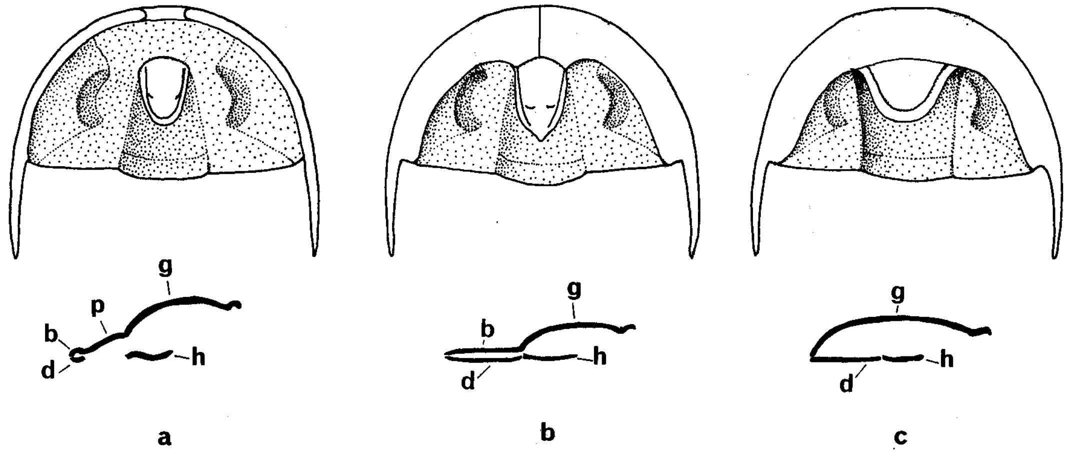
supports the high taxonomic significance accorded to cephalic structure. Characters which appear polyphyletically are often the result of heterochrony in development; such developmental changes may produce apparent 'reversals'. As an example, genal spines are lost in Nileidae, but are primitively present in the whole Asaphina (as they are in the Trilobita as a whole); they secondarily reappear in a few nileid genera (such as *Peraspis*), and here again stratigraphic criteria are of use in showing that this apparently 'primitive' condition is a derived one in this case.

Comments on characters and taxa coded in text-figs. 2 and 3

Most of the characters used should be self-explanatory from Table 2, but a few notes are necessary to show how coding decisions shown in Table 3 were reached. The taxa employed were selected to minimize the number of terminal taxa used, which required certain assumptions that need to be stated, and were for the most part the same as on the weighted cladogram (text-fig. 1). However, 'Anomocaracea' was replaced by the family Anomocaridae because, as we discuss below, the assemblage of families included in this taxon are almost certainly para- if not polyphyletic. We also coded separately the family Pterocephaliidae, another taxon which in the generality of its features is typified more by retained plesiomorphic, 'ptychoparioid' characters than by obviously derived features. Nileidae and Cyclopygidae were coded for character 8 in state 2—loss of median sutures. The earliest species currently assigned to both families (Nileidae: *Platypeltoides croftii*; Cyclopygidae: *Prospectatrix genatenta*) have median sutures, i.e. retain the primitive condition present in the sister group, Taihungshaniidae; both should really be coded separately, and on a strictly cladistic view their classification might pose problems. In other characters they appear typical of their respective families, and their 'ancestral' place in a stratigraphically determined phylogeny seems well established. To reduce the number of terminal taxa they are best omitted. Dikelocephalacea are used in the sense of Ludvigsen and Westrop (1983), to include Saukiidae, Dikelocephalidae, and Ptychaspididae. There is a good deal of information about in-group evolution

TABLE 3. Coding of characters in Table 2 used in the computer analysis of phylogeny of Asaphina.

	Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
1.	CYCLOPYGIDAE	1	1	1	2	1	1	1	2	1	0	3	1	1	1	1	1	0	1	1	3	4	1	1	3	0	0	1	0	1	1	2	1	0	1	0	2	1	0	0	1	0	0
2.	NILEIDAE	1	1	1	2	1	1	1	2	1	1	3	1	1	1	1	1	0	1	1	3	3	1	1	1	1	0	1	0	1	1	2	0	0	1	0	2	1	2	0	1	0	0
3.	TAIHUNGSHANIIDAE	1	1	1	2	0	1	1	1	1	0	3	?	0	0	1	1	1	1	1	2	2	0	1	1	1	0	1	0	0	1	2	0	0	1	0	2	1	?	0	1	0	0
4.	CERATOPYGIDAE	0	0	0	1	0	1	1	1	1	0	1	?	0	0	?	0	1	1	0	2	3	0	?	0	0	1	0	1	0	0	0	0	0	0	0	2	0	0	0	1	0	0
5.	ASAPHIDAE	0	1	1	1	0	1	1	1	1	0	1	1	0	0	1	0	0	1	1	2	2	0	1	1	1	1	0	0	0	1	2	0	0	0	1	2	1	2	0	1	0	0
6.	DIKELOCEPHALACEA	2	0	2	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	2	0	0	0	0	0	0	0	1	1	0	1	0	1	0	1	2	1	2	0	0	1	1
7.	REMOPLEURIDACEA	2	1	2	1	0	0	0	1	1	1	2	1	0	0	0	0	2	1	0	1	1	0	0	2	0	0	0	1	1	1	2	0	0	0	1	2	1	1	1	0	0	0
8.	DIKELOKEPHALINIDS	0	0	0	1	0	0	0	1	1	0	0	?	0	0	0	0	1	1	1	0	1	0	1	1	0	1	1	0	1	?	0	0	0	0	?0	?0	1	0	0	0	0	0
9.	ANOMOCARIDAE	0	0	1	0	?	?	0	1	1	0	2	?0	0	0	0	0	0	1	1	2	1	0	?	?	?	1	0	0	1	0	0	0	0	0	0	2	1	0	0	1	0	0
10.	PTEROCEPHALIIDAE	0	0	0	0	0	0	0	1	1	0	0	?0	0	0	0	0	0	1	?	2	0	?	?	?	?	0	1	1	1	0	0	0	0	0	1	?	0	0	0	0	0	0
11.	'PTYCHOPARIINA'	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0



TEXT-FIG. 5. Hypostomal attachment conditions, explaining new terminology introduced in this paper; illustrated by schematic ventral views of cephalic shield with hypostome in its life position (*above*), and by the corresponding section through the cephalic shield (*below*). *a*, *natant* hypostomal condition; hypostome is not attached at doublure, shown on a ptychoparioid with rostrum. *b*, *conterminant* hypostomal condition; doublure is docked with hypostoma, but retains position in front of glabella as in natant condition—hypostomal suture and preglabellar furrow correspond closely—shown here in Asaphina with median suture. *c*, *impendent* hypostomal condition; glabellar lobe expands forwards to cephalic margin so that its forward part is now underlain by cephalic doublure—hypostome is rigidly attached as in conterminant condition but has lost its relationship to the front of the glabella—here illustrated by species with fused cheeks. Note that the hypostomal condition is independent of the kind of ventral cephalic sutures, and the choice of illustrations is largely arbitrary. g, glabella; p, preglabellar field; b, cranidial border; d, cephalic doublure on mid-line; h, hypostome.

in the Dikelocephalacea; the ptychaspidids include a number of advanced forms in which the characters are highly modified, but whose derivation from more generalized saukiid-like forms is well documented. These latter form the basis of coding. For a very few characters (e.g. hypostomes) there is a conflict between saukiids and dikelocephalids, and in this case we have taken the least specialized condition as that coded.

Character 1. Glabellar shape. In many asaphids and one ceratopygid (*Ceratopyge* itself—see text-fig. 14*b*) the glabella expands forwards. However, all stratigraphic and out-group evidence points to these forms being secondarily derived from species with a forward-tapering to parallel-sided glabella (see below), and for the group as a whole we are obliged to score this character as 0. Secondary glabellar expansion may be of use in within-group taxonomy.

Character 3. This character is difficult to determine in some cases, especially Asaphidae. Crushed asaphid specimens can develop a false appearance of having palpebral rims. Some primitive asaphids and small growth stages show a feebly developed palpebral furrow defining a broad rim, while those species with upward-tilted palpebral lobes may also show a change in slope at the inner ends of the lobes which is not homologous with the palpebral furrow. Truly effaced palpebral furrows apply in the majority of asaphids, and this character is consequently scored 1.

Character 4. The different conditions of hypostomal attachment are defined below (see text-figs. 5 and 22).

Character 5. The occipital furrow is primitively present in all asaphid subfamilies, and its loss is secondary within-group; hence the character is scored 0 in this family.

Character 7. The pre-occipital tubercle may attain a secondarily suboccipital position in certain asaphids, as we discuss below, but its homology with tubercles in other asaphids is certain.

Character 8. A few, but not all, kainellids (Remopleuridacea) have lost the median suture (e.g. Palmer 1968, pl. 14, fig. 8) by fusion of the free cheeks; however, this is known to be a secondary condition which is not typical of the vast majority of remopleuridaceans—hence it is scored 1 for this taxon.

Character 12. The asaphoid protaspis type is discussed below. Protaspides of some groups are not known, and must be scored '?'. Hu (1971) attributed protaspides to a pterocephaliid (*Dytremacephalus*) and a ptychaspidid (*Ptychaspis*). However, several of Hu's attributions to other taxa have been questioned or discounted (e.g. Evitt and Tripp 1977, p. 158) and for this reason we are reluctant to score these families definitely for protaspis type, and both have been recorded as '?'. Both are apparently of primitive type and their inclusion would not have significantly altered the most parsimonious cladogram.

Character 13. Secondary derivation of genal spines in a nileid (*Peraspis*) from a species without has been demonstrated by Fortey (1975) from stratigraphic evidence. This reversal is discounted in coding this family for lacking genal spines. Conversely, genal spines are present in the vast majority of Asaphidae, and their secondary loss in a few genera is not reflected in the coding. We have not coded types of genal spine (broad, narrow, long, short, etc.) because of the difficulties of definition (even though most workers would probably describe asaphids as having 'broad' genal spines compared with, say, remopleuridids). This also has the effect of removing from text-figs. 2 and 3 an autapomorphy of the Nileidae ('broadly rounded genal angle') which figures on text-fig. 1.

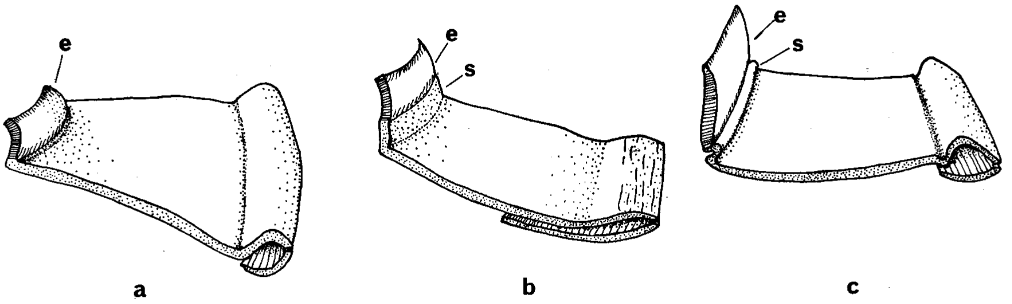
Character 15. See text-fig. 13 for explanation of petaloid thoracic facet.

Character 16. This derived character is shown clearly for *Nileus* by Schrank (1972, pl. 10, fig. 1). For most Cyclopygacea the adaxial articulation applies to the first thoracic segment, while posterior segments have the fulcral point progressively removed from the axial furrow (e.g. the cyclopygid *Degamella*: see Fortey and Owens 1987, fig. 38).

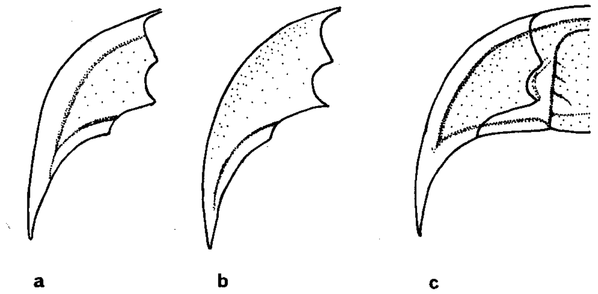
Character 17. Derived state 1 is where marginal spines are developed laterally or anterolaterally on the pygidium. Usually there is only one such pair of spines, but in some ceratopygids there are two pairs. Although this is not coded on Table 2 the marginal spines may not be strictly homologous. In ceratopygids the spinose margin is quite clearly an extension of the pygidial pleural segments, as if thoracic segments had been incorporated in the pygidium, whereas in Dikelokephalinidae and Taihungshaniidae the spines originate from the border and are wide enough to embrace more than one segment. This difference is acknowledged in text-fig. 1, where the ceratopygid pygidial spines comprise an autapomorphy of that group. In any case, these pygidial spines are different from the comb-like arrangement of remopleuridacean pygidial marginal spines which extend postaxially to conjoin at the mid-line, and comprise derived state 2.

Character 20. The different character states are shown on text-fig. 6. Wide genal borders often vary between flat and gently convex in related taxa, and these two conditions have been included in one class. Genal border furrows in nileids are absent at least laterally and posteriorly. Their atavistic appearance in *Peraspis* is, like other features of that genus, a reversal.

Character 21. There is clearly an overall reduction in thoracic segment number through time within the Asaphina, and the most advanced Cyclopygidae have the fewest, five. Within accepted monophyletic families the number is often reduced in later taxa, for example in Ceratopygidae the earliest *Proceratopyge* have nine segments while Tremadoc species of *Dichelepyge* have six. Nileids can have seven, eight, or probably nine



TEXT-FIG. 6. Genal border structure, and characteristics of eye socle (s), to illustrate characters 20 and 38 (see Table 2). Diagrammatic sections through mid part of free cheek from eye (e) through border and doublure. *a*, primitive genal structure, with convex border forming a tube with doublure and socle not well developed. *b*, gently convex border with wide, reclined doublure (this structure often intergrades with flat border) and eye elevated on wide band-like socle. *c*, remopleuridid type with narrow, wire-like eye socle below flat visual surface, flat genal field, with narrow border furrow defining bevelled border.



TEXT-FIG. 7. Dikelocephalacean genal structure to illustrate character 42 (see Table 2). Posterior border furrow continues into basal part at least of genal spine. *a*, cheek of typical saukiid with defined, gently convex lateral border. *b*, in Dikelocephalidae lateral border is generally flattened, but characteristic furrow usually remains defined. *c*, primitive ptychoparioid condition. All approximately natural size.

segments. This variability makes for difficulty of coding. However, all asaphids have eight segments, and this character appears remarkably stable in that group—and it is given as an autapomorphy of the group on our weighted cladogram (text-fig. 1). The fact that this does not appear as an autapomorphy on the PAUP treatments is a result of the way we have coded the characters. An additional coding allowing 'variability in thoracic segment number within group' as primitive, and 'stable thoracic segment number (8)' as a derived state would certainly have appeared as an autapomorphy of Asaphidae. The ancestral cyclopygid *Prospectatrix* with seven thoracic segments has not been coded for the same reason as given under character 8.

Character 24. Derived condition 2 refers to raised 'macular' areas on the hypostomes of Remopleuridacea, and is an autapomorphy of that group. While it is described from many Ordovician species there is no evidence to say whether it applied to the early species as well—the scoring is based on what evidence we have.

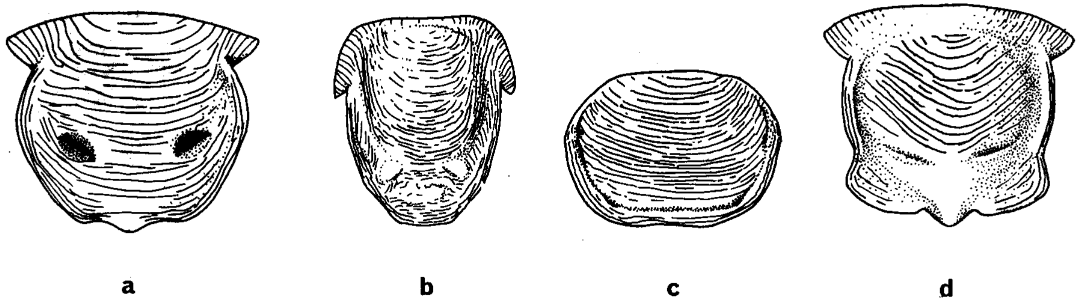
Character 26. Further discussion of bacculae is given below under the section on Trinucleacea.

Character 27. Loss of paired furrows on the pygidial pleural fields is a derived character. The remaining furrow is interpreted as pleural rather than interpleural, but this is difficult to prove. However, the resemblance of strong pygidial furrows to those pleural furrows on the thorax in Dikelokephalinidae and Taihungshaniidae is consistent with our interpretation of the homology (see Lu 1975, pl. 29, fig. 9; Courtessole *et al.* 1981, pl. 4, fig. 3).

Character 30. This character is uncertain in Dikelokephalinidae and is recorded '?'. Loss of the circumocular suture and the routine presence of the eye attached to the free cheek evidently occurred more than once independently in Asaphina. Most figured dikelokephalinid cheeks apparently show no eye attached, but one, *Hungioides* figured by Lu (1975, pl. 29, figs. 14 and 15) probably shows the eye in place, in which case the loss of the circumocular suture may have happened yet again within the dikelokephalinid clade.

Character 37. Several very derived remopleuridids, including *Remopleurides* itself, have relatively small pygidia; this is a character reversal within the group, and is not scored.

Character 42. This character is shown on text-fig. 7. That the furrow passing into the genal spine is the



TEXT-FIG. 8. Hypostomes of higher Asaphina illustrating characters 22 and 23 (see Table 2); all these types have well-developed sculpture of terrace ridges on the middle body. *a*, generalized nileid hypostome; early Ordovician *Poronileus* (after Fortey 1975, pl. 13, fig. 8). *b*, presumed primitive hypostomal morphology of Asaphidae; Upper Cambrian *Niobella* (after Westergård 1939, pl. 2, fig. 2). *c*, loss of maculae in Cyclopygidae; early Ordovician *Microparia* (after Fortey and Owens 1987, fig. 45*b*). *d*, Taihungshaniidae, showing similarity with Nileidae; early Ordovician *Taihungshania* (after Courtessole *et al.* 1981, pl. 4, fig. 7). Two to three times natural size.

continuation of the posterior border furrow, rather than the lateral border furrow, is shown by certain species in which the course of the latter is terminated before reaching the genal angle (e.g. *Hoytaspis speciosa* (Walcott) figured by Ludvigsen and Westrop 1983, pl. 14, fig. 6). The furrow is remarkable for the consistency of its presence even in such very derived Dikelocephalaceans as *Euptychaspis*.

COMPARATIVE DISCUSSION OF CLASSIFICATION

Text-figs. 1–3 show the several possibilities in producing a character-based classification of Asaphina. The two equally parsimonious trees resulting from the PAUP treatment share many points of similarity; the only significant difference between them concerns the placement of Dikelokephalinidae and Pterocephaliidae, both of them primitive groups which are problematic for several reasons, as we discuss below. Both also had a larger number of '?' characters than other taxa. Only two trees is a robust result from PAUP; some published studies have had to cope with as many as forty equally parsimonious trees. The 'consensus tree' between the two—essentially removing the problematic taxa to the lowest position as a trichotomy—has been deduced using the method of Adams (1972), and is shown in text-fig. 4.

There is a good agreement also between the PAUP trees (especially the consensus tree) and the cladogram based on our assessment of the distribution of a smaller number of key characters (text-fig. 1); the ordering of taxa left to right is virtually the same. One difference is the appearance of Anomocaridae as the sister group of Ceratopygidae to Cyclopygidae in PAUP, whereas 'Anomocaracea' appears as one of the two most primitive groups on text-fig. 1. As we discuss below, Anomocaracea is not a satisfactory taxon, and whereas text-fig. 1 attempts to treat it as a whole (including pterocephaliids within it), the PAUP treatment uses Anomocaridae alone—which could well turn out to be the sister group of the asaphacean group. The only important difference is the hierarchical treatment of Asaphidae and Ceratopygidae; on text-fig. 1 Asaphacea (Ceratopygidae + Asaphidae) is a monophyletic group, whereas the PAUP treatment produces a paraphyletic group. The latter is not strictly permissible on a phylogenetic classification. The reason for the difference is the emphasis placed on the similarity of glabellar structure of less derived asaphids and ceratopygids in our weighted classification. Since all of the characters on PAUP characterizing ceratopygids are either developed in parallel with other asaphines or are reversals, it is not unequivocally defined. However, as mentioned above, character 17 (marginal pygidial spines) may not be homologous between groups, and the way these spines are developed in ceratopygids differs from both taihungshaniids and dikelokephalinids, i.e. the marginal pygidial spines may be a better autapomorphy of Ceratopygidae than it appears in text-figs. 2 and 3. The majority of the characters separating Ceratopygidae from Asaphidae to Cyclopygidae are also parallel with those elsewhere on the cladogram, and some, particularly hypostomal characters, are poorly known for Ceratopygidae. Hence we believe that a more detailed treatment with more certain data on ceratopygid ventral structures may yet indicate a monophyletic Asaphidae + Ceratopygidae, as shown on text-fig. 1. The Asaphacea are retained in the discussion below in this sense.

Asaphidae, Nileidae, and Taihungshaniidae come out as rather poorly characterized families on text-figs. 2 and 3. All three families have a coherent stratigraphic history. Typically 'asaphid' characteristics, such as the forked hypostome and panderian openings, are not developed throughout the family and are not present on the more primitive genera—hence these characters cannot be used as autapomorphies of Asaphidae. On the other hand, the fixed number of thoracic segments—eight—does not appear as an autapomorphy of the group because of the way the thoracic segment character was coded for PAUP. The same is true of the 'broadly rounded genal angle' of Nileidae. It is, however, difficult to characterize Nileidae other than by retaining those characters shared with primitive cyclopygids, and by the lack of hypertrophied eyes. Even the autapomorphy of text-figs. 2 and 3 (divergent preocular sutures) does not apply to *all* nileids. More useful autapomorphies may emerge when more is known of the vincular structures developed on the librigenal doublure. Taihungshaniid marginal pygidial spines compare closely with those of Dikelokephalinidae, but there is no close relationship between these two families; the group retains many primitive features compared with Cyclopygidae + Nileidae.

MORPHOLOGICAL TERMS EMPLOYED IN SYSTEMATIC DISCUSSION

For most morphological terms we follow the *Treatise on Invertebrate Paleontology* (Moore 1959). The terms *ala* (plural: *alae*) and *baccula* (plural *bacculae*) are used as defined by Fortey (1975, pp. 14–15). We coin three terms to describe the relationships of the hypostome to the cephalic doublure and glabella. These are important character states which have proved of use in defining high-level taxa in the Asaphina (see text-fig. 5).

1. *Natant* condition (Latin: 'floating'). Hypostome not attached to cephalic doublure, which is relatively narrow. A true preglabellar field is present, not underlain by calcified cuticle. The hypostome is sited beneath the forward part of the glabella—and the area between it and the doublure was presumably covered by soft cuticle. Work in progress by R. A. F. shows that this is the primitive condition for ptychoparioid trilobites. 2. *Conterminant* condition (Latin: 'coinciding'). Doublure extends backwards mesially as far as the preglabellar furrow *but no further*. Hypostome is docked against doublure, but still in the same relative position as in the natant condition, i.e. beneath forward part of glabella. Hence in this condition the hypostomal suture and the preglabellar furrow are spatially coincident. 3. *Impendent* condition (Latin: 'overhanging'). Direct relationship between hypostomal position and glabella is lost. Glabella extends forwards so that medially the cephalic doublure underlies its forward part; as in the conterminant condition the hypostome abuts the cephalic doublure. Note that there is no direct relationship between the state of the ventral sutures (median, rostral plate, or fused) and the condition of hypostomal attachment—so, for example, fused cheeks can and do exist with natant hypostomal condition—the choice of suture pattern in text-fig. 5 was arbitrary. In the Ptychopariida as a whole the conterminant and impendent conditions were polyphyletically derived—but are conservative enough to be of use in defining superfamilial taxa, e.g. Cyclopygacea below.

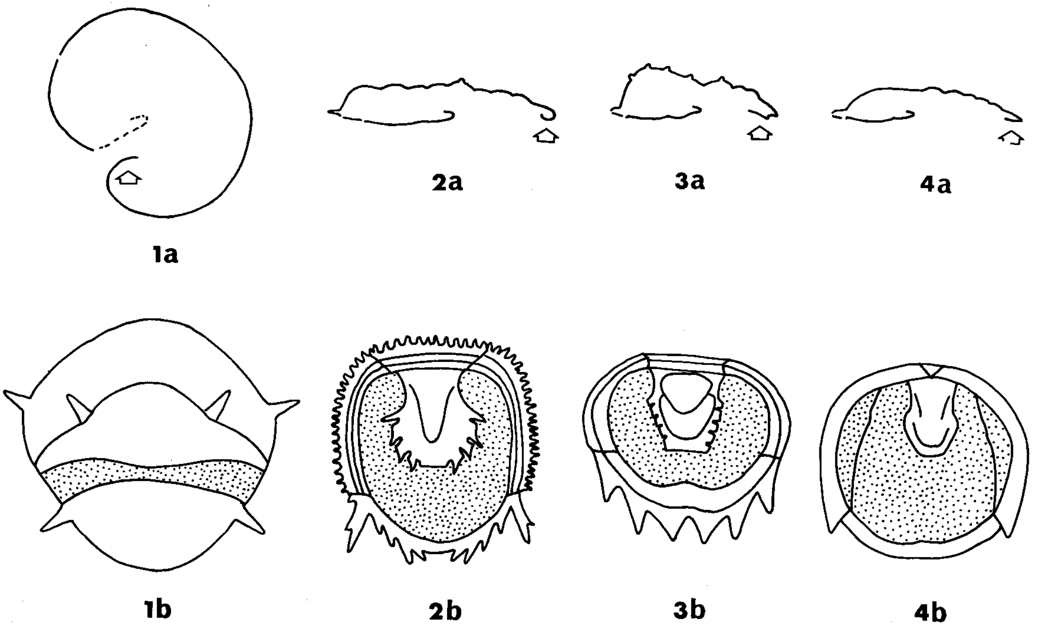
The term '*petaloid* thoracic facet' (text-fig. 13) was defined by Fortey (1987). It refers to a broad, subtriangular articulating facet on which there are terrace ridges—the upper terraces run more or less transversely while the lower ones are oblique in some cases. During enrolment the petaloid facet slides past the broad doublure of the preceding segment, which is also furnished with terrace ridges.

ASAPHOID PROTASPIS TYPE, AND THE MEDIAN SUTURE

Definition of asaphoid protaspis

Protaspides have been assigned to Asaphidae (*Isotelus*, *Anataphrus*), Nileidae (herein), Remopleurididae (*Robergiella*, *Remopleurides*), and Trinucleidae among the families that we would place in the Asaphina. These protaspides are similar enough to one another to warrant the term *asaphoid protaspis* for protaspides of this type.

Asaphoid protaspides are spherical to ovoid in shape, with an enrolled rather than inturned doublure (text-fig. 9). One or more of three prominent pairs of submarginal, sharply pointed, conical spines project from the fused cranidium/protopygidium. The free cheeks are simple, without distinct visual surfaces, and without genal spines (except for minute spines in the latest protaspis stages of *Isotelus*, see Evitt 1961), and are free, fused to each other (*R. eximius*, see Whittington 1959*a*), or fused to each other and the hypostome (smallest protaspides of *Isotelus*, see Chatterton 1980; and *Cryptolithus tesselatus*, herein). When free—later in ontogeny—they are always separated by a median connective suture, even when parts of their posterior portions may be separated by a small anterior protuberance of the hypostome (*Isotelus*, see Chatterton 1980). No rostral plate is visible at any stage, in either a fused or a free state. The genal doublure extends far back under the protaspis, and almost joins posteromedially in *Isotelus*. The hypostome has up to nine (possibly the plesiomorphic number) sharp, elongate and conical marginal spines, and it covers most of the ventral surface of the protaspis (text-fig. 10.9–11). There appear to be only two marginal spines in *Remopleurides* and four in *Cryptolithus*, described herein. In small protaspides the axial furrows are often shallow to indistinct, except for a pair of pits located at the forward limits of the axial furrows close to the anterior margin. In large, late stage protaspides a number of dorsal furrows may become distinct, including axial furrows and ring furrows, and the glabella may gain an independent convexity. The exoskeletal



TEXT-FIG. 9. Sagittal sections (*a*) and ventral views (*b*) of four protaspides to show 'enrolled' (1), 'incurved' (2), and 'inturned' doublure (3, 4). For scale, see text-figs. 10 and 11. The open arrows point towards the protopygidial doublure. 1, *Remopleurides* sp. aff. *R. eximius* Whittington (Middle Ordovician, Edinburg Formation, Virginia). 2, *Flexicalymene senaria*? (Conrad) (Middle Ordovician, Martinsburg Shale, Virginia). 3, *Acanthopyge bifida* Edgell (Lower Devonian, *Receptaculites* Limestone, nr. Yass, New South Wales). 4, *Proetus talenti* Chatterton (Lower Devonian, Warroo Limestone, nr. Yass, New South Wales).

surface, where preserved, shows a fine pattern of polygonal ridges. No protaspides assigned to the Asaphina have either a sagittal glabellar furrow dividing the glabella into paired lobes, as in some Redlichiida, Ptychopariida, and Phacopida, or a pair of lobes (?palpebral) along the anterior margin on either side of the glabella, as in some Ptychopariida (Pl. 17) and all Phacopida.

The largest asaphoid protaspides are large for the Trilobita (see Pls. 17 and 18), exceeding 1 mm in length. These late stages have more distinct ridges and furrows, including axial furrows, occipital furrows, and axial ring furrows, and may even have a furrow that shows the junction between the cranidium and the protopygidium (*Remopleurides*, see Whittington 1959*a*). Median connective and hypostomal sutures may develop during the protaspid period, as in *Isotelus*. Distinct, large (exsag.) palpebral lobes appear during the protaspid period (Asaphidae, Nileidae, and Remopleurididae). Minute librigenal spines appear near the back of the free cheeks of the largest protaspid growth stages of some species of *Isotelus* (see Evitt 1961, fig. 3), which may or may not be homologous with the genal spine of the adult.

The first two pairs of prominent submarginal spines on the cranidium/protopygidium of the Remopleuridacea are cephalic and the third pair is protopygidial. This is based on demonstrable relationships in late growth stages of species of *Remopleurides*, and in particular the work of Whittington (1959*a*). It is more difficult to determine the location of the junction between the cranidium and protopygidium in relation to these spines in Asaphidae, Trinucleidae, and Nileidae, but we suppose that they are homologous with those in *Remopleurides*. It is difficult to consider the facial suture of the protaspides in the context of the terms proparian and opisthoparian since, in most cases, the exact location of the genal angle is not clearly recognizable. However, the late protaspid stages of *Remopleurides* (Whittington 1959*a*, pl. 3, fig. 5; pl. 11, fig. 1; pl. 16, figs. 5 and 6) and *Isotelus* (Evitt 1961, pl. 117, fig. 19) are apparently opisthoparian. The sutures are definitely opisthoparian in known meraspid cranidia assigned to the Asaphina.

Median suture

The presence of a median suture (which is only secondarily lost by ankylosis in some groups, e.g. Trinucleacea and Nileidae) is considered an important apomorphic character of the Asaphina. There are two possibilities to account for its origin. It may have appeared as a result of a discrete and radical mutation; or it may have arisen as a result of the gradual disappearance of the rostral plate, associated with the 'migration' of the connective sutures medially, eventually to meet as a single median suture. The lack of a rostrum at any growth stage of the known asaphoid protaspides favours the former hypothesis. Also, in those groups of trilobites where the rostral plate has been reduced to a very small size, as in some Proetida and Encrinuridae, the rostral plate is almost never lost, even when reduced to extremely narrow transverse dimensions (see, e.g. *Ischyrotoma* in Whittington 1963, pl. 7, fig. 13). Tripp (1962, pl. 67, fig. 12) illustrated the holotype cephalon of *Encrinurus deomenos* Tripp, 1962, from the Silurian of Anticosti Island, which apparently lacks a rostrum (a second specimen in the Yale University Collections was also stated to lack this feature); he suggested that the same might have applied to *E. moe* Mannil, 1958. Specimens of Anticosti encrinurids very similar to *E. deomenos*, from slightly lower horizons (Gun River, as opposed to Jupiter River Formation) than the types, apparently do have a rostrum. If this is substantiated it is the only example we know of conversion of rostrum to median suture within a monophyletic group of post-Cambrian trilobites. Other encrinurids which approach this condition are reconstructed with small, relict rostral plates, e.g. *Physemataspis coopi* Evitt and Tripp, 1977 and *Encrinuroides torulatus* Evitt and Tripp, 1977 (Evitt and Tripp 1977, figs. 6 and 13). Since all cheiruraceans have rostral plates early in their ontogeny it is likely that its loss occurred only late in ontogeny. In some proetids the rostral plate is so reduced in size that the posterior part of the connective sutures becomes medial. However, the small triangular rostrum is always present in this order. It remains overwhelmingly true that the rostral plate is a conservative structure.

Evidence that may possibly be used to argue for the origin of the median suture from the

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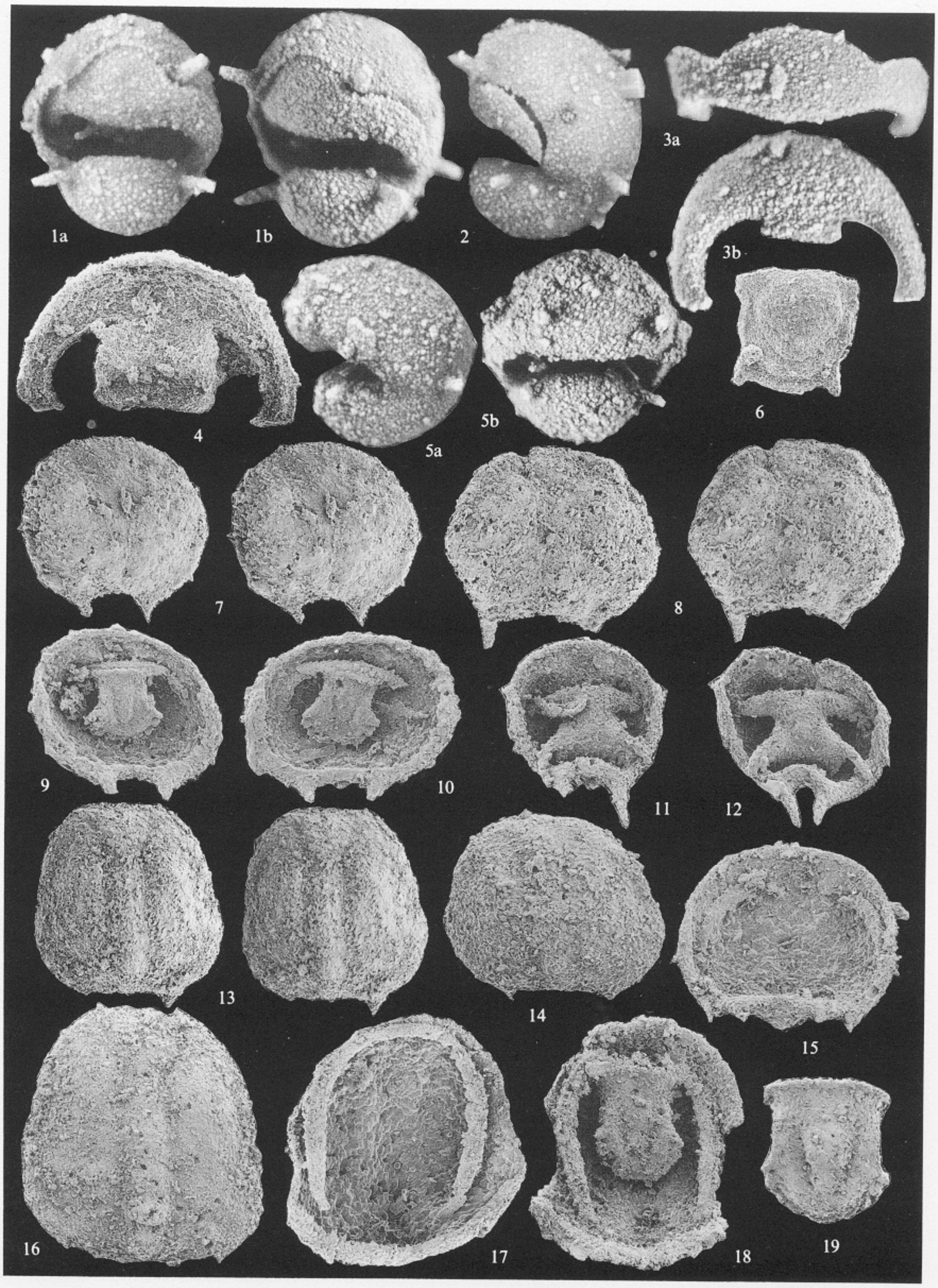
EXPLANATION OF PLATE 17

Figs. 1-6. *Remopleurides* aff. *R. eximius* Whittington, 1959, from the Edinburg Formation of Virginia. 1*a*, *b*, USNM 414581, ventral and ventrolateral views of protaspis with free cheeks and hypostome attached (slightly out of position), × 41. 2, USNM 414582, lateral view of protaspis with free cheeks attached, × 36. 3*a*, *b*, USNM 414583, free cheeks, × 55. 4, USNM 414584, internal, dorsal view of free cheeks and hypostome, × 56. 5*a*, *b*, USNM 414585, lateral and anterior views of protaspis with free cheeks attached, × 34. 6, USNM 414586, ventral view of meraspid hypostome, × 34.

Figs. 7, 9, 10, 13, 16-19. *Bathyuriscus*? sp. from a float block, probably from the Middle Cambrian Pika Formation, near Columbia Ice Fields, western Alberta. 7, UA 7750, stereo pair of small protaspis, × 62. 9, UA 7751, ventral view of small protaspis with cheeks, rostral plate, and hypostome attached, × 62. 10, UA 7752, ventral view of small protaspis with cheeks, rostral plate, and hypostome attached, × 62. 13, UA 7754, stereo pair, dorsal view of large protaspis, × 62. 16, UA 7753, dorsal view of largest protaspis stage, × 62. 17, UA 7755, ventral view of largest protaspis stage with free cheeks and rostral plate attached, × 62. 18, UA 7756, ventral view of incomplete largest protaspis stage with free cheeks, rostral plate, and hypostome attached, × 62. 19, US 7757, ventral view of small meraspid hypostome, × 62.

Figs. 8, 11, 12, 14, 15. *Spencella*? sp. from the same float block of the Middle Cambrian Pika? Formation that contained the above specimens of *Bathyuriscus*? sp. 8, US 7758, stereo pair, dorsal view of small protaspis, × 62. 11, UA 7759, ventral view of small protaspis with one free cheek and hypostome/rostral plate attached (out of original position), × 62. 12, UA 7760, ventral view of small protaspis with free cheeks and hypostome/rostral plate attached (out of original position), × 62. 14, UA 7761, dorsal view of larger protaspis, × 62. 15, UA 7762, ventral view of larger protaspis (same stage as fig. 14) with free cheeks attached, × 62.

PLATE 17



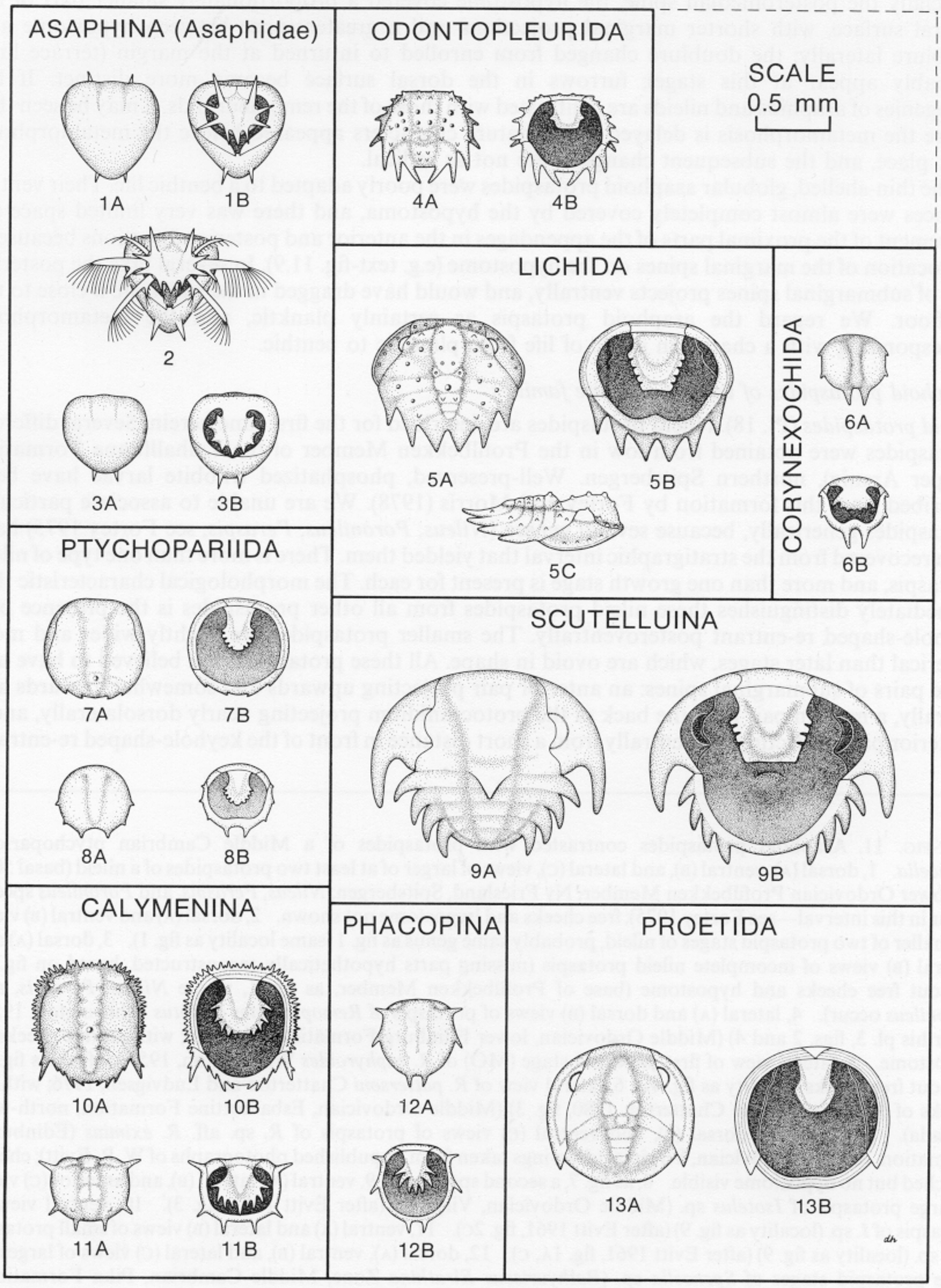
FORTEY and CHATTERTON, *Remopleurides*, *Bathyuriscus?*, *Spencella?*

progressive reduction of the rostrum is the presence of a small, tongue-like extension on the front of the hypostomes of the protaspides of some species of *Isotelus* (Evitt 1961; Chatterton 1980, figs. 1-5*b*, *c*, 2-12). It could be argued that this is a small rostral remnant fused to the hypostoma. The tongue-like extension disappears later in ontogeny. The few known ventral surfaces of Cambrian ptychopariine protaspides (text-fig. 10.6, 10.7; Palmer 1958)—which presumably represent the primitive condition—had rostral plates and separate connective sutures. In these ptychopariines the position of the connective sutures appears to vary ontogenetically in relation to the distal ends of the hypostomal suture, allowing the rostral plate to increase or decrease in width in relation to the rest of the cephalon (text-fig. 10.7B, 10.8B). Hence, if the asaphines had a ptychopariine ancestor, as is probable, the median suture either appeared as a discrete mutation early in ontogeny, or the rostral plate disappeared through medial reduction during ontogeny—and then this reduction was pushed back earlier in development during phylogeny. The latter is the more complex mechanism, of course, and it is difficult to see why the rostrum should not have been retained at small growth stages even if suppressed in the adult. Because there are also very few trilobites having median sutures which show any indication of a possible rostral homologue we favour the notion that the structure originated as a discrete mutation, although the difficulties of proving this important point are appreciated. For additional remarks see under Pterocephaliidae below.

Metamorphosis

A radical metamorphosis took place in asaphines following the protaspid period, usually between the protaspid and meraspid periods, but in some Remopleuridacea during the meraspid period. This produced a change from a globular form to a more flattened form. We consider that this change coincided with a change from a planktic to a benthic mode of life. There is some evidence to suggest that such metamorphoses in the Trilobita were associated with a greater than normal size difference between the relevant successive ecdyses (Chatterton 1980). In many cases the free cheeks have large genal spines after the metamorphosis—contrasting with small or no genal spines before the metamorphosis. At the same time the three pairs of submarginal conical spines disappeared (or became much reduced in size); the spines on the protopygidium pointed less ventrally and more to the posterior; the marginal spines on the hypostome showed a tendency to disappear or become reduced,

TEXT-FIG. 10. Dorsal and ventral views of protaspides of different orders and suborders of trilobites, showing location of facial, hypostomal, rostral, and connective sutures. The specimen of *Isotelus* with hypothetically reconstructed appendages is based on Recent nauplius stages of crustaceans (see Fryer 1983). 1, dorsal (A), and ventral (B) views of second and largest protaspides of *I. parvirugosus* Chatterton and Ludvigsen, 1976 (after Chatterton 1980, fig. 3; pl. 2, figs. 6, 9-11, 16) (Middle Ordovician, Esbataottine Formation, Mackenzie Mountains, north-west Canada). 2, as fig. 1, with hypothetical appendages added. 3, dorsal (A) and ventral (B) views of small protaspis of *I. parvirugosus* (same source as fig. 1). 4, dorsal (A) and ventral (B) views of protaspis of *Diacanthaspis cooperi* Whittington, 1956 (his fig. 9A, B, and pl. 3, figs. 1, 2, 5, 6) (Middle Ordovician, Martinsburg Shale, Virginia). 5, dorsal (A), ventral (B), and lateral (C) views of smaller of two protaspides of *Acanthopyge bifida* Edgell (after Chatterton 1971, fig. 9A, B, D; pl. 7, figs. 1-4) (Lower Devonian, *Receptaculites* Limestone, nr. Yass, New South Wales). 6, smallest protaspid stage of *Bathyuriscus*? sp. (source as figs. 7 and 8). 7, dorsal (A) and ventral (B) views of third and largest protaspid stage of *Spencella* (Middle Cambrian, ?Pika Formation, Canadian Rocky Mountains, nr. Columbia Ice Fields). 8, as fig. 7, dorsal (A) and ventral (B) views of smallest of three protaspid stages of *Spencella*. 9, dorsal (A) and ventral (B) views of protaspis of *Dentaloscutellum hudsoni* Chatterton, 1971 (after his fig. 4A, B; pl. 2, figs. 1-3; pl. 3, figs. 5 and 6) (locality as fig. 5). 10, dorsal (A) and ventral (B) views of largest of three protaspis stages of *Flexicalymene senaria*? (Conrad), nov. herein (specimens coll. W. R. Evitt; locality as fig. 4; see also Whittington 1959*b* and Hu 1971). 11, same species, smallest of three protaspid stages in dorsal (A) and ventral (B) views (locality as fig. 4). 12, dorsal (A) and ventral (B) views of small protaspis of *Pseudocybele nasuta* Ross, 1951 (see Ross 1951*a*; drawings based on photographs by B. D. E. C. from specimens loaned to us by H. B. Whittington) (Lower Ordovician, Garden City Formation, Utah). 13, dorsal (A) and ventral (B) views of late protaspid stage of *Proetus talenti* Chatterton, 1971 (after his fig. 15C, D; pl. 15, figs. 7 and 33; pl. 16, fig. 1) (Lower Devonian Warroo Limestone, nr. Yass, New South Wales).


ASAPHINA (Asaphidae)
1A
1B
2
3A
3B
ODONTOPLEURIDA
4A
4B
SCALE
0.5 mm
LICHIDA
5A
5B
5C
CORYNEXOCHIDA
6A
6B
PTYCHOPARIIDA
7A
7B
8A
8B
SCUTELLUINA
9A
9B
CALYMENINA
10A
10B
11A
11B
PHACOPINA
12A
12B
PROETIDA
13A
13B
dh

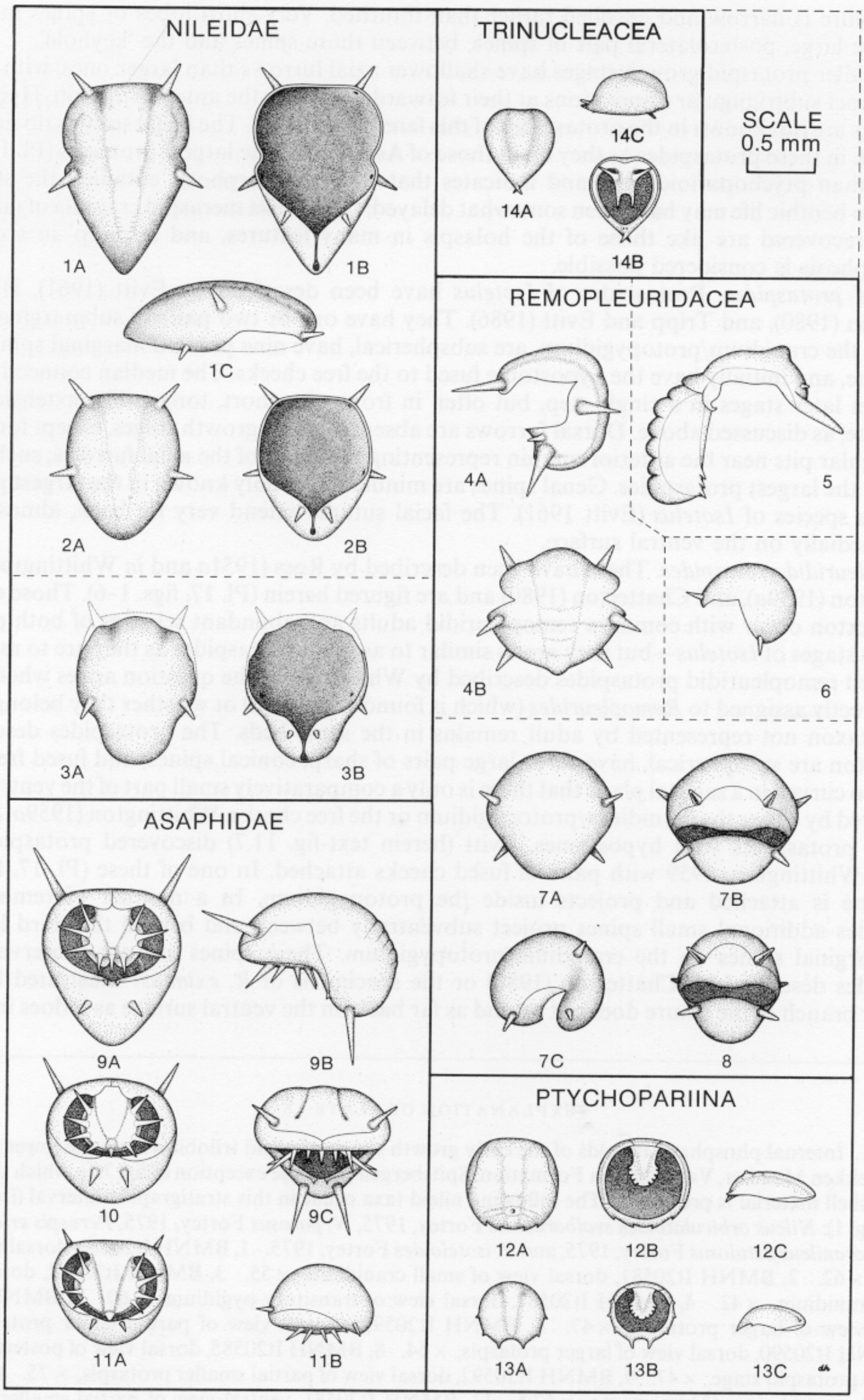
especially the posteromedian spine; the hypostome covered a proportionately smaller part of the ventral surface, with shorter marginal projections and a greater space between hypostome and doublure laterally; the doublure changed from enrolled to inturned at the margin (terrace lines probably appear at this stage); furrows in the dorsal surface became more distinct. If the ontogenies of asaphids and nileids are contrasted with those of the remopleuridids, it may be seen that where the metamorphosis is delayed more mature characters appeared before the metamorphosis took place, and the subsequent changes were not as radical.

The thin-shelled, globular asaphoid protaspides were poorly adapted to a benthic life. Their ventral surfaces were almost completely covered by the hypostoma, and there was very limited space for movement of the proximal parts of the appendages in the anterior and posterior directions because of the location of the marginal spines on the hypostome (e.g. text-fig. 11.9). In several taxa the posterior pair of submarginal spines projects ventrally, and would have dragged in the substrate if close to the sea-floor. We regard the asaphoid protaspis as certainly planktic, and the metamorphosis corresponding with a change in mode of life from planktic to benthic.

Asaphoid protaspides of various trilobite families

Nileid protaspides (Pl. 18). Nileid protaspides are described for the first time herein. Several different protaspides were obtained from low in the Profilbekken Member of the Valhallfonna Formation (Upper Arenig), northern Spitsbergen. Well-preserved, phosphatized trilobite larvae have been described from this formation by Fortey and Morris (1978). We are unable to associate particular protaspides generically, because several genera (*Nileus*, *Poronileus*, *Peraspis*, see Fortey 1975) have been recovered from the stratigraphic interval that yielded them. There is more than one type of nileid protaspis, and more than one growth stage is present for each. The morphological characteristic that immediately distinguishes these nileid protaspides from all other protaspides is the presence of a keyhole-shaped re-entrant posteroventrally. The smaller protaspides are slightly wider and more spherical than later stages, which are ovoid in shape. All these protaspides are believed to have had three pairs of submarginal spines: an anterior pair projecting upwards and somewhat forwards and laterally, a median pair near the back of the protocranidium projecting nearly dorsolaterally, and a posterior pair projecting subventrally from a short distance in front of the keyhole-shaped re-entrant.

TEXT-FIG. 11. Asaphoid protaspides contrasted with protaspides of a Middle Cambrian ptychoparioid, *Spencella*. 1, dorsal (A), ventral (B), and lateral (C), views of larger of at least two protaspides of a nileid (basal 50 m of Lower Ordovician Profilbekken Member, Ny Friesland, Spitsbergen; *Nileus*, *Peraspis*, and *Poronileus* species occur in this interval—see Fortey 1975); free cheeks and hypostome not shown. 2, dorsal (A) and ventral (B) views of smaller of two protaspid stages of nileid, probably same genus as fig. 1 (same locality as fig. 1). 3, dorsal (A) and ventral (B) views of incomplete nileid protaspis (missing parts hypothetically reconstructed, based on fig. 1), without free cheeks and hypostome (base of Profilbekken Member, as fig. 1, where *Nileus*, *Peraspis*, and *Poronileus* occur). 4, lateral (A) and dorsal (B) views of protaspis of *Remopleurides caelatus* Whittington, 1959*a* (after his pl. 3, figs. 2 and 4) (Middle Ordovician, lower Edinburg Formation, Virginia); without free cheeks or hypostome. 5, lateral view of first meraspid stage (MO) of *R. caphyroides* Whittington, 1959*a* (after his fig. 6); without free cheeks (locality as fig. 4). 6, lateral view of *R. pattersoni* Chatterton and Ludvigsen, 1976; without cheeks of hypostome (after Chatterton 1980, fig. 3) (Middle Ordovician, Esbataottine Formation, north-west Canada). 7, lateral (A), dorsal (B), and ventral (C) views of protaspis of *R.* sp. aff. *R. eximius* (Edinburgh Formation, Middle Ordovician, Virginia) (drawings taken from unpublished photographs of W. R. Evitt); cheeks attached but no hypostome visible. 8, as fig. 7, a second specimen. 9, ventral (A), lateral (B), and anterior (C) views of large protaspis of *Isotelus* sp. (Middle Ordovician, Virginia) (after Evitt 1961, fig. 3). 10, ventral view of protaspis of *I.* sp. (locality as fig. 9) (after Evitt 1961, fig. 2C). 11, ventral (A) and lateral (B) views of small protaspis of *I.* sp. (locality as fig. 9) (after Evitt 1961, fig. 1A, C). 12, dorsal (A), ventral (B), and lateral (C) views of largest of three protaspid stages of *Spencella* sp. (*Bathyuriscus-Elrathina* Zone, Middle Cambrian, Pika Formation?, Canadian Rocky Mountains) (based on new photographs of undescribed material). 13, dorsal (A) ventral (B) and lateral (C) views of the smallest of three protaspid stages of *Spencella* (locality as fig. 12). 14, dorsal (A), ventral (B), and lateral (C) views of protaspis of *Cryptolithus* (nov. herein) (horizon as fig. 7).


NILEIDAE
TRINUCLEACEA
SCALE
0.5 mm
1A
1B
14A
14B
14C
1C
REMOPLEURIDACEA
4A
4B
5
2A
2B
6
3A
3B
ASAPHIDAE
7A
7B
9A
9B
7C
8
10
9C
PTYCHOPARIINA
12A
12B
12C
11A
11B
13A
13B
13C

The doublure is narrow and enrolled rather than inturned. Very short lobes or spines may occur behind the large, posterolateral pair of spines, between those spines and the 'keyhole'.

The smaller protaspid growth stages have shallower axial furrows than larger ones, with a pair of more distinct subtriangular impressions at their forward ends near the anterior margin. Hypostomes and cheeks are not known in the protaspides of this family at present. The facial sutures do not extend as far back in these protaspides as they do in those of Asaphidae. The largest protaspis (Pl. 18, fig. 11) is larger than ptychoparioid ones and indicates that the metamorphosis entailing the shift from planktic to benthic life may have been somewhat delayed; the earliest meraspid cranidia of nileids that we have recovered are like those of the holaspis in many features, and a 'jump' in size during metamorphosis is considered possible.

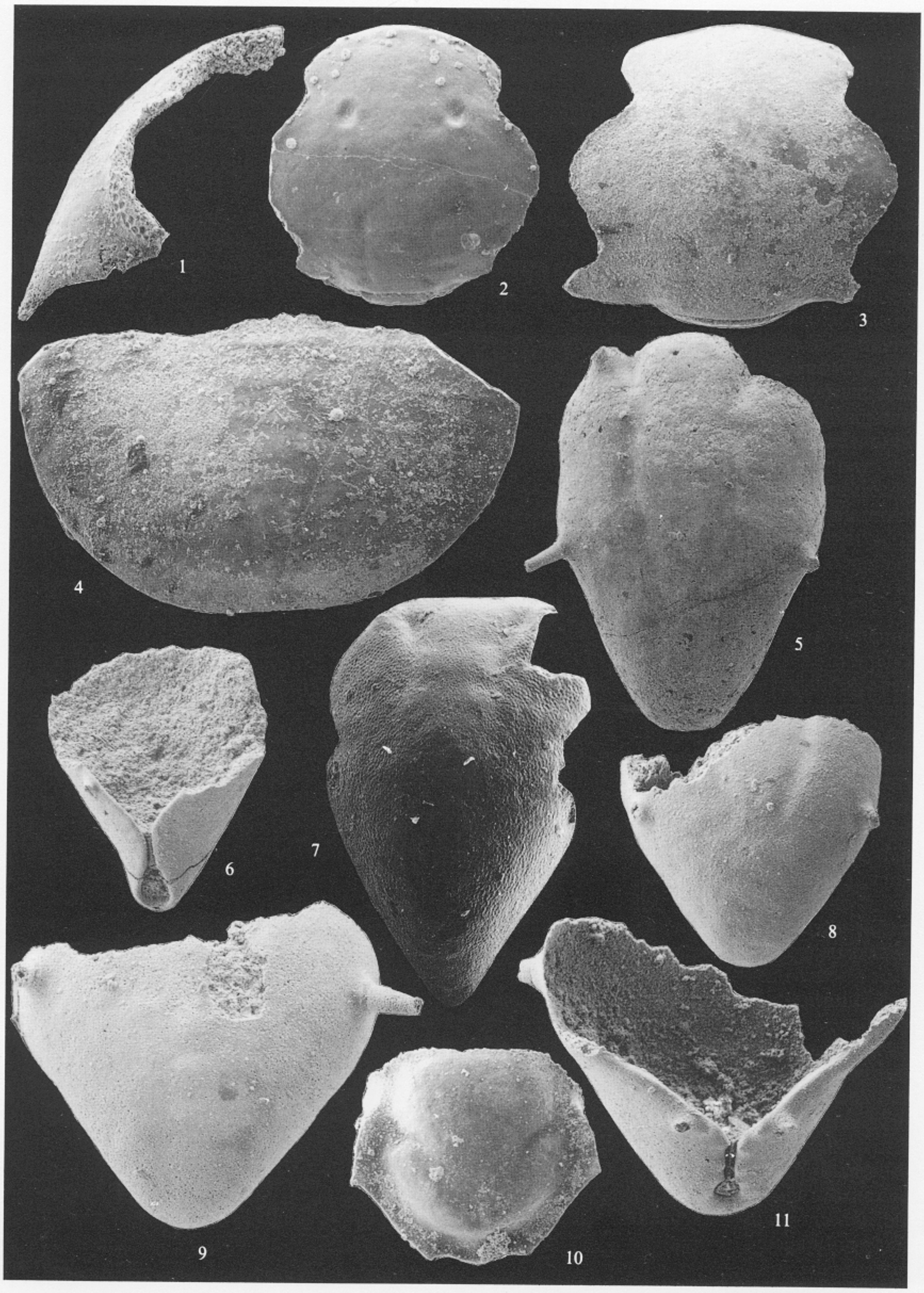
Asaphid protaspides. Protaspides of *Isotelus* have been described by Evitt (1961), Hu (1971), Chatterton (1980), and Tripp and Evitt (1986). They have one or two pairs of submarginal conical spines on the cranidium/protopygidium, are subspherical, have nine pointed marginal spines on the hypostome, and initially have the hypostome fused to the free cheeks. The median connective suture appears in later stages in a single step, but often in front of a short, tongue-like extension of the hypostome, as discussed above. Dorsal furrows are absent in small growth stages, except for a pair of subtriangular pits near the anterior margin representing the limits of the axial furrows; such furrows appear in the largest protaspides. Genal spines are minute—and only known in the largest protaspid stage of a species of *Isotelus* (Evitt 1961). The facial sutures extend very far back, almost joining posteromedially on the ventral surface.

Remopleuridid protaspides. These have been described by Ross (1951*a* and *in* Whittington 1959*b*), Whittington (1959*a*), and Chatterton (1980) and are figured herein (Pl. 17, figs. 1–6). Those described by Chatterton occur with common remopleuridid adults and abundant sclerites of both protaspid and adult stages of *Isotelus*—but they are as similar to asaphid protaspides as they are to most of the undoubted remopleuridid protaspides described by Whittington. The question arises whether these were correctly assigned to *Remopleurides* (which is found with them) or whether they belong to some asaphid taxon not represented by adult remains in the same beds. The protaspides described by Whittington are subspherical, have three large pairs of sharp, conical spines, and fused free cheeks; they are so curved in a sagittal plane that there is only a comparatively small part of the ventral surface not covered by either the cranidium/protopygidium or the free cheeks. Whittington (1959*a*, *b*) did not illustrate protaspides with hypostomes. Evitt (herein text-fig. 11.7) discovered protaspides of *R. eximius*? Whittington, 1959 with pairs of fused cheeks attached. In one of these (Pl. 17, fig. 1) the hypostome is attached and projects inside the protopygidium. In a number of remopleuridid protaspides additional small spines project subventrally between and behind the third large pair of submarginal spines on the cranidium/protopygidium. These spines are not preserved on the protaspides described by Chatterton (1980) or the specimens of *R. eximius*? illustrated here. The posterior branch of the suture does not extend as far back on the ventral surface as it does in *Isotelus*.

EXPLANATION OF PLATE 18

Figs. 1–11. Internal phosphatic moulds of the early growth stages of nileid trilobites from the lower part of the Profilbekken Member, Valhallfonna Formation, Spitsbergen (with the exception of fig. 7, in which the original calcite shell material is preserved). The following nileid taxa occur in this stratigraphic interval (from Fortey 1975, fig. 1): *Nileus orbiculatoides svalbardensis* Fortey, 1975, *N. porosus* Fortey, 1975, *Peraspis erugata* Ross, 1970, *Poronileus fistulosus* Fortey, 1975, and *P. isoteloides* Fortey, 1975. 1, BMNH It20580, dorsal view of free cheek, × 62. 2, BMNH It20581, dorsal view of small cranidium, × 55. 3, BMNH It20582, dorsal view of small cranidium, × 42. 4, BMNH It20587, dorsal view of transitory pygidium, × 60. 5, BMNH It20589, dorsal view of larger protaspis, × 47. 6, BMNH It20593, ventral view of partial larger protaspis, × 46. 7, BMNH It20590, dorsal view of larger protaspis, × 54. 8, BMNH It20585, dorsal view of posterior portion of large protaspid stage, × 47. 9, BMNH It20592, dorsal view of partial smaller protaspis, × 75. 10, BMNH It20583, ventral view of hypostome, × 57·5. 11, BMNH It20581, ventral view of partial smaller protaspis, × 74.

PLATE 18



FORTEY and CHATTERTON, nileid trilobites

Dorsal furrows and an independent convexity of the axis are present on large protaspides of this family. The metamorphosis accompanying the change from pelagic to benthic habits takes place in the meraspid period of several species of *Remopleurides* (*R. caphyroides*, *R. eximius*, *R. asperulus*, *R. plaesiourus*, see Whittington 1959*a*).

Trinucleacean protaspides. The protaspides of the Trinucleacea are similar in many ways to those of the higher Asaphina on text-figs. 1–3. Resemblances between them include the globose shape, the enrolled rather than inturned margin on the doublure, the presence of up to three pairs of submarginal conical spines on the cranidum/protopygidium, the fused free cheeks and hypostome, and the long, sharp marginal spines on the hypostome. Trinucleacean protaspides have been figured by Whittington (1959*a*: *Cryptolithus*, *Tretaspis*, *Ampyx*), Shaw (1968: *Lonchodomas*), and herein (Pl. 19: *Cryptolithus*, *Ampyxoides* or *Globampyx*). Meraspid to holaspid growth stages have also been described for this superfamily by a number of other workers, including Hu (1971). We discuss below the additional reasons that suggest that Trinucleacea might be included in an enlarged concept of Asaphina.

Trinucleacean protaspides differ from other asaphoid ones in the distinct convexity of the axis, the axial and other dorsal furrows being more distinct at the same size. The protaspides of this group are also comparatively small. The posterior pair of submarginal spines are very close to one another, and may be crossed (Whittington 1959*a*; Shaw 1968), and a second pair of spines may be present adjacent and anteroventral to this pair. This additional pair of small spines may be homologous with subsidiary marginal spines found between the large posterior pair of spines which occurs in some Remopleuridacea (see Whittington 1959*a*). The free cheeks of both protaspid and small meraspid stages (down to Meraspis degree 0) of the Trinucleacea are fused to one another to form a lower lamella,

EXPLANATION OF PLATE 19

Figs. 1–9. *Cryptolithus tesselatus* Green, 1832 from the Lower Martinsburg Shale, about 1 km along Virginia secondary highway (at the base of the roadside outcrop along the north side of the road) from its intersection with Virginia secondary highway 732 (not quite as far along this road as Loc. 12 of Whittington 1959). The trilobites from this locality have been somewhat distorted as a result of stress. 1, USNM 414587, dorsal view of protaspis, × 51. 2, USNM 414588, ventral view of protaspis, × 46·5. 3, USNM 414589, ventral view of fused partial cheeks and hypostome, × 93. 4, USNM 414590, ventral view of partial protaspis with attached fused free cheeks and hypostome, × 62. 5, USNM 414591, dorsal view of fused free cheeks and hypostome (note posterior portions of free cheeks and hypostome are missing), × 93. 6, USNM 414592, ventral view of protaspis with attached fused free cheeks and hypostome (note marginal spines and posterior part of hypostome missing), × 78. 7, USNM 414593, ventral view of protaspis with attached fused free cheeks and hypostome (note long ventrolaterally directed anterior pair of spines on hypostome), × 77. 8, USNM 414594, dorsal view of protaspis, × 62. 9, USNM 414594, ventral view of protaspis, × 62.

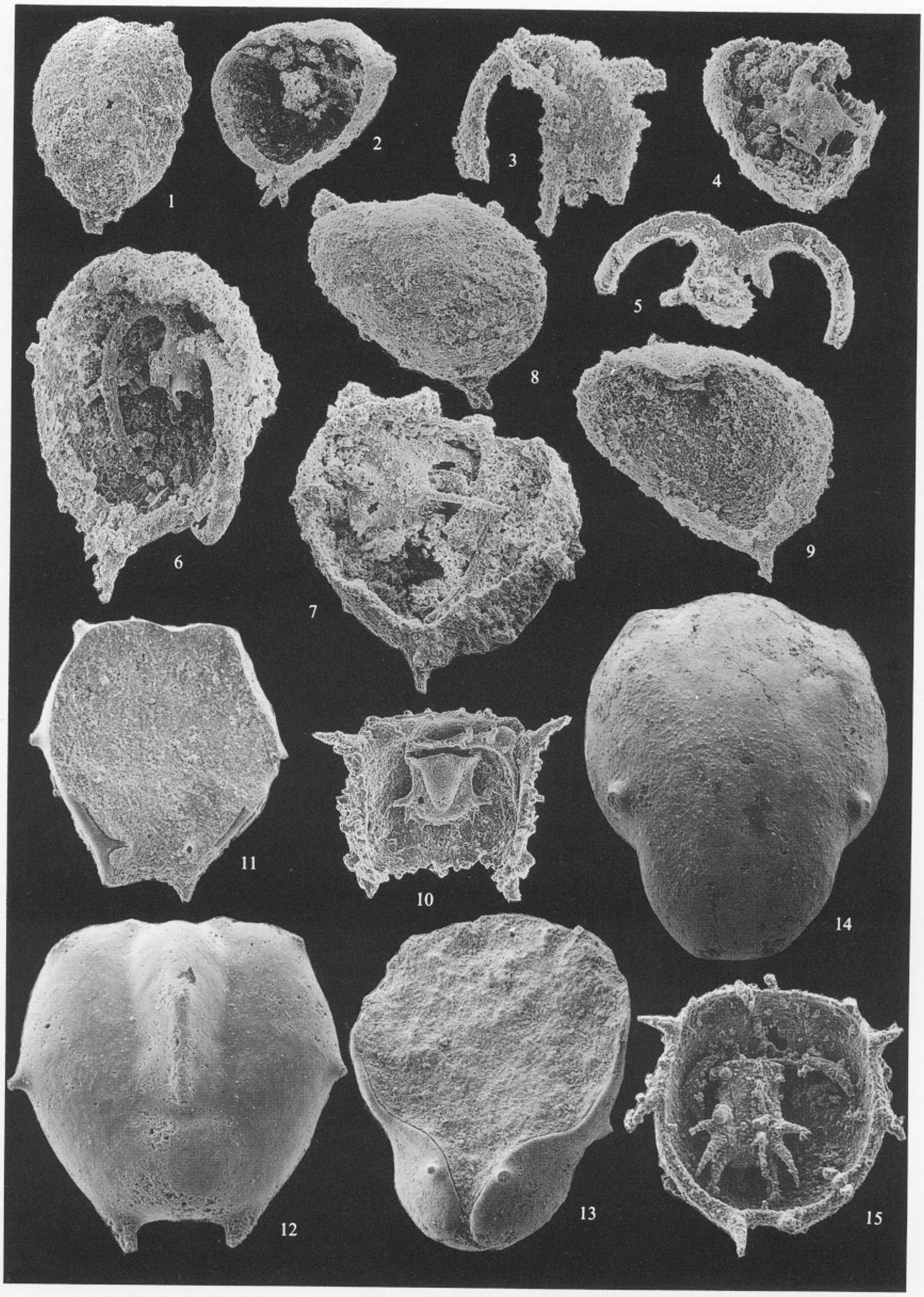
Fig. 10. *Cybeloides* sp., UA 7764, from strata of Late Ordovician Age in the Mackenzie Mountains (horizon AV1 54 of Nowlan *et al.* in press); ventral view of protaspis with attached free cheek, rostral plate, and hypostome, × 56.

Figs. 11 and 12. Raphiophorid from the Lower Ordovician, lower part of the Profilbekken Member, Valhallfonna Formation, Spitsbergen Island. *Ampyxoides inermis* Fortey, 1975 and *Globampyx trinucleoides* Fortey, 1975 occur at this horizon (Fortey 1975, fig. 1). 11, BMNH It20596, ventral view of internal phosphatic mould of protaspis, × 108. 12, BMNH It20597, dorsal view of internal phosphatic mould, × 110.

Figs. 13 and 14. Nileid from the Lower Ordovician, basal part of the Profilbekken Member, Valhallfonna Formation, Spitsbergen. The following nileids have been obtained from this interval: *Nileus orbiculatoides svalbardensis* Fortey, 1975, *N. porosus* Fortey, 1975, *Peraspis erugata* Ross, 1970, *Poronileus fistulosus* Fortey, 1975, and *P. isoteloides* Fortey, 1975 (see Fortey 1975, fig. 1). 13, BMNH It20598, ventral view of phosphatic mould of protaspis, × 50. 14, BMNH It20599, dorsal view of internal phosphatic mould of protaspis, × 55.

Fig. 15. *Pseudocybele nasuta* Ross, 1951, BMNH It20594, from the Lower Ordovician Garden City Formation (Zone J), Loc. 13 (see Ross 1951*b*), north-eastern Utah; ventral view of small protaspis stage (other later ones occur in the ontogeny of this species) with attached free cheeks, rostral plate (largely hidden under hypostome), and hypostome, × 90.

PLATE 19



FORTEY and CHATTERTON, asaphine protaspides with no connective suture visible. The protaspid cheeks are also fused to the hypostome, which has two pairs of marginal spines. The cheeks of small meraspid stages of other Asaphina are not fused to one another (although they may be fused to one another in early protaspid and late holaspid stages). No rostral plate is known for either group at any stage. The absence of connective suture(s) at any known stage in the Trinucleacea can be interpreted in more than one way. It could be the result of a complete absence of such a suture in the phylogenetic history of the group; this would set it apart from both the Asaphina as understood here, and from the Ptychopariida (even as an 'ancestral' group). Or it could be the result of retention by paedomorphosis of the larval lack of sutures; the same effect would be achieved by accelerated development with secondary fusion of the connective sutures. The earliest trilobite growth stage, the phaselus of Fortey and Morris (1978), lacks ventral sutures, and there is no reason in principle why this condition should not be fixed during subsequent development.

The resemblance of early trinucleines such as *Orometopus* to asaphines and ptychopariids, including the presence of opisthoparian sutures, is such that it does seem probable that all belong within a monophyletic group—and makes the developmental explanation the more likely origin of the fused cheeks. The resemblance of the trinucleacean protaspis to other asaphoid protaspides is one line of evidence which inclines us to include the former group within the Asaphina. The crucial test of this will be the discovery of an early representative of undoubted Trinucleacea with an ontogeny complete enough to say whether or not the primitive condition for the group was with rostrum or median suture. This is not yet known, but we present a case below for including the Cambrian family Liostracinidae in the Trinucleacea. The former family *does* include species with a median suture, and if we are correct in our use of this as a synapomorphy of Asaphina, both it and Trinucleacea can be included within the Asaphina.

Comparison of asaphoid protaspides with those of other groups

Globular protaspides with three pairs of conical submarginal spines are known also in Calymenina (*Apocalymene*, Chatterton 1971; *Flexicalymene*, Hu 1971), Phacopida (e.g. *Phacops*, Chatterton 1971), and Cheirurina (*Hyrokybe* Chatterton and Perry, 1984; ?*Sphaerexochus*, Chatterton 1980). Late stage protaspides of these groups differ in most respects from those of the Asaphina as we understand it here. However, the presence of three pairs of marginal spines could be considered plesiomorphic on the basis of out-group comparisons; but there are doubts that these spines are really homologous between different groups of trilobites, as we discuss under Phacopida below. The conical marginal spines on the hypostome *are* probably a plesiomorphic character because they are present on the majority of protaspides of various families, including those from the Lower Cambrian. The number of marginal spines is usually seven or nine in the Ptychopariida and related orders of trilobites. There appear to be nine marginal spines on the hypostomes of many Asaphina (Evitt 1961; Chatterton 1980) and some Phacopida (Calymenina and Phacopina, Chatterton 1971; Cheirurina, Chatterton 1980). However, a globular protaspid form is not a plesiomorphic character, because it is not present in protaspides of primitive ptychoparioids, nor, to employ a stratigraphic criterion, in any known protaspis from the Lower Cambrian. The sporadic occurrence of such early protaspides in groups other than the Asaphina is presumably a parallelism associated with early planktic growth stages. Later development of the protaspis avoids confusion with the asaphoid morphology.

The loss of one or two of the pairs of spines on the cranidium/protopygidium of these bulbous protaspides apparently occurred independently several times, and is not phylogenetically important (Remopleuridacea, Chatterton 1980 and herein; Trinucleacea, Whittington 1959*a*; Asaphidae, Evitt 1961). This feature is known to have varied within the single genera *Isotelus* and *Remopleurides*. The presence of additional spines on the protopygidium may prove to be an additional autapomorphy of the Remopleuridacea.

Asaphoid protaspides compared with phacopid protaspides. Asaphoid protaspides differ from phacopid protaspides in lacking distinct axial and glabellar furrows, in lacking a sagittal furrow behind the frontal lobe of the glabella in all protaspid growth stages, and in lacking distinct lobes along the front of the cranidium on either side of the glabella. Evidence from late protaspid stages of phacopoids (B. D. E. C. unpublished) shows that all three pairs of prominent submarginal spines are cephalic, and therefore not homologous with those of the Asaphina, and that protopygidial spines develop behind these three pairs (see text-figs. 10–11). Many phacopoid protaspides (*Pseudocybele*, *Encrinuroides*, *Encrinurus*, *Cybeloides*, *Phacops*?) have seven marginal spines on the hypostome compared with nine on the hypostomes of Asaphidae, four in the Trinucleacea, and two in the Remopleuridacea. However, calymenids usually have nine such spines on their protaspid hypostomes (Chatterton 1971; later growth stages show loss of the ninth, posteromedian spine, as shown by Whittington 1959*a*). Protaspis hypostome marginal spine number does not seem promising as a character for high level classification. Some of the smaller protaspides of members of the Phacopida, especially Calymenina, share characters with asaphoid protaspides that are considered to be convergent, as the result of their pelagic life habits. These include a bulbous shape and an enrolled rather than inturned doublure, together with a spinose hypostoma that covers most of the ventral surface. The presence of prominent anterolateral lobes on the cranidium, paired connective sutures, and distinct sagittal furrows on the glabella clearly distinguishes them from their asaphine functional equivalents.

Asaphoid protaspides compared with bumastine protaspides. Chatterton (1980) assigned some small bulbous protaspides to the bumastine *Failleana*. These protaspides are similar, in some respects, to the asaphoid protaspis. However, they differ from the latter in having lateral connective sutures, a hypostome fused to what later becomes the rostral plate, a re-entrant posterior margin, and only one pair of submarginal spines.

Asaphoid protaspides compared with primitive ptychoparioid protaspides. Dorsal and ventral views of protaspides from several families of generalized ptychoparioids have been described by Palmer (1958, *Crassifimbra*, Lower Cambrian; 1962*a*, *Aphelaspis*, Upper Cambrian), Hu (1971, *Dunderbergia*, *Dytremacephalus*, Upper Cambrian; 1986; *Pachyaspis*, *Ehmaniella*?), and one is added herein (*Spencella*, Middle Cambrian, see Pl. 17). They are all similar to one another, and are presumed to represent the primitive condition. All have a pair of connective sutures on either side of a transverse rostral plate, three pairs of conical submarginal spines on the cranidium/protopygidium, a slightly inflated discoid shape in the smallest protaspides, with a concave posterior margin. Some of the smallest protaspid stages have a sagittal furrow subdividing the median two-thirds of the glabella into four to six lobes. The protaspid hypostomes are spinose along their margins where known.

Dorsal surfaces of ptychoparioid protaspides have been described for a much greater number of taxa, especially by Hu (1971), with a good account of olenid ontogeny (Upper Cambrian) by Whitworth (1970), but since this material is not silicified it is not possible to determine the courses of the ventral sutures, nor whether pairs of submarginal spines are present. Axial furrows are, however, distinct in ptychopariid protaspides, the glabella so defined being subparallel-sided to forward-expanding. Sagittal furrows are present in the glabellas of smallest protaspides of almost half the described ptychopariid taxa—these never continue on the frontal or occipital lobes, and usually disappear in the later protaspis. Similar sagittal furrows occur in small protaspides of redlichiids, and some phacopinids and calymenines. The occipital ring is often more inflated than the rest of the glabella. The proportion of the smallest protaspis ('anaprotaspis' of authors) occupied by the protopygidium is inconspicuous; and conspicuous, with furrows, ridges, and additional spines, in the later protaspis ('metaprotaspis').

Palmer (1962*a*) considered the three pairs of submarginal spines that occur in each of *Aphelaspis*, *Glaphyraspis*, and *Hardyoides* to be homologous, and all to be cephalic. They are probably also homologues of the three pairs of submarginal spines of the phacopoid *Pseudocybele*, which are also cephalic (see text-fig. 10; Ross 1951*b*). They are apparently not homologous with the three pairs of submarginal spines in protaspides of *Remopleurides*, only two of which have been considered cephalic (Whittington 1959*a*, pls. 3 and 10).

Differences between asaphoid and ptychoparioid protaspides include: the more bulbous shape of the former; the asaphoid always lack sagittal furrows on the glabella; they also lack distinct (?palpebro-ocular) anterior cephalic ridges; at the same size axial furrows are shallower in asaphoid protaspides; where the sutural junction between the free cheeks can be recognized in asaphoid protaspides it is single and median, and this appears as a discrete structure early in ontogeny.

The most primitive families which we include in Asaphina do not necessarily have an asaphoid protaspis: this appears as a synapomorphy uniting Remopleurididae to Cyclopygidae on text-figs. 1-3. Unfortunately, there are few described ontogenies of Cambrian forms with a median suture in the adult. As we noted above, Hu (1971) described the ontogenies of three genera of Cambrian trilobites assigned to the Pterocephaliidae (*Dytremacephalus*), Anomocaridae (*Glyphaspis*), and Dikelocephalacea (*Ptychaspis*), respectively. Of these only the anomocarid could be compared with the asaphoid protaspis in its smaller stages; the other two resemble those of ptychoparioids. As doubt has been cast on some other ontogenetic series described by Hu we did not code these examples in the computer treatment of phylogeny. *Glyphaspis* and *Ptychaspis* are known from rock specimens only. However, it is perfectly possible that the asaphoid protaspis type was acquired *after* the inception of the median suture, as implied in text-fig. 1. If the distribution of characters shown in text-figs. 1-3 is correct, and Hu's protaspis assignment to *Ptychaspis* is also correct, the primitive ptychoparioid protaspide form was retained (or achieved by reversal) in Dikelocephalacea. Clearly more information on early ontogeny of these Cambrian taxa is desirable.

If we are correct in regarding protaspis morphology as an important criterion in classification, the question arises whether Asaphina should be used in a restricted sense to embrace only the families Remopleuridacea to Cyclopygidae on text-figs. 1-3. It could even be questioned whether Asaphina in this restricted sense and Ptychopariina should be classified in the same order. There are more differences between larval stages of these two groups than between Ptychopariina and Phacopida, which are ordinally separate. The Order Proetida Fortey and Owens, 1975 is also recognizable from protaspis characteristics. Small protaspis stages of Corynexochida resemble those of Ptychopariina, nor can protaspides of Redlichiida and Agnostida be regarded as more similar to those of Asaphina. However, it is probably the case that the resemblances between ptychopariid, corynexochid, redlichiid, and even phacopoid protaspides (such as the well-defined, subparallel-sided or forward-expanding glabella with defined furrows) are shared primitive (symplesiomorphic) characters, and as such should not be employed in the definition of taxa. Certainly, if we are correct in believing that the presence of a median suture is an indication of monophyly then the Asaphina so defined is likely to have included early members which had not yet acquired the asaphoid protaspis, and the more embracing definition of Asaphina is preferred here. However, if it is subsequently shown that the median suture is polyphyletically derived, then the protaspis character will presumably again achieve prominence in the definition of Asaphina. The general conservatism of protaspis morphology, when compared with wide variations in adult morphology, increases the level of confidence one can place in using major *modifications* from the primitive morphology in the definition of high level taxa. This notion is falsifiable from our cladograms, in that we predict that the asaphoid protaspis will be discovered for numerous species, for example of Cyclopygidae, for which ontogenies are not yet known.

SYSTEMATIC DISCUSSION OF ASAPHINE SUPERFAMILIES

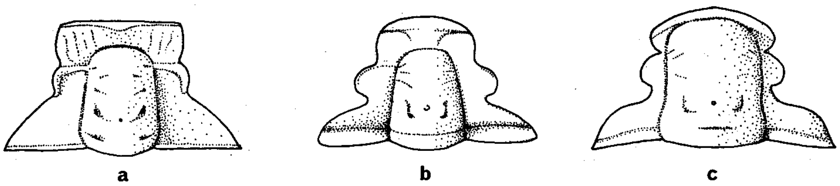
Suborder ASAPHINA Salter, 1864 emend.

Diagnosis. Trilobites having a ventral median suture initiated early in ontogeny (and only lost where cheeks are secondarily fused); protaspis commonly globular and effaced dorsally, of asaphoid type. Pre-occipital glabellar tubercle present in advanced forms.

General characters of the group may include retained primitive features: dorsal sutures opisthoparian; eyes usually moderately large to large (but some forms secondarily blind); thoracic articulation unspecialized (exception: advanced remopleuridids and later ceratopygids such as *Dichelepyge*); subisopygous to macropygous, with marginal pygidial spines in many groups; doublure with terrace ridges.

Superfamily ASAPHACEA Burmeister, 1843

The superfamily Asaphacea is regarded as including two families: Asaphidae and Ceratopygidae; the latter family has been accorded superfamilial status in previous classifications (Moore 1959;



TEXT-FIG. 12. Characteristic structure of glabella of Asaphacea, showing pre-occipital tubercle between elongate (exsag.) L_1 glabellar furrows. *a*, *Hedinaspis*, which has been classified as an olenacean (see text). *b*, *Proceratopyge* (Ceratopygidae). *c*, *Niobella* (Asaphidae). Approximately natural size.

Bergström 1973; Shergold 1975). We exclude the families Nileidae and Taihungshaniidae from the superfamily, in which they have been previously incorporated. Thus defined, the superfamily ranges from the Middle Cambrian to the end of the Ordovician.

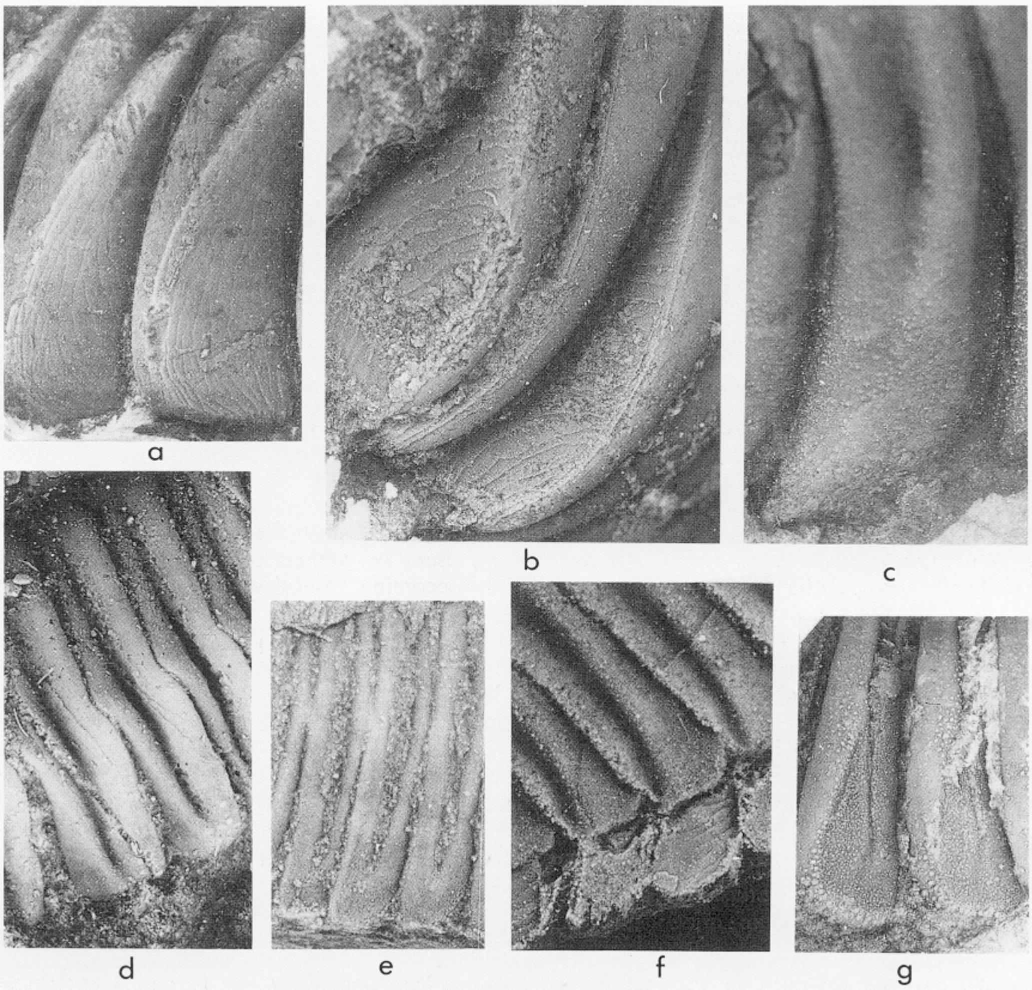
Diagnosis. Asaphina with glabellar tubercle developed on pre-occipital segment; glabellar form primitively elongate (sag.) subparallel to tapering forwards, with defined occipital ring, and with curved, apostrophe-like pair of basal glabellar furrows isolated within glabella. Hypostome attached to doublure; hypostomal condition conterminant, rarely impendent.

Discussion. The development of the glabellar tubercle, glabellar furrows, and occipital ring which are typical of the superfamily is clearly shown on the stratigraphically early ceratopygid *Proceratopyge* from the mid- to late Cambrian (Westergård 1947, pl. 2, figs. 1 and 2; Rushton 1978, pl. 26, fig. 4), and on such early asaphids as *Promegalaspides* (Westergård 1939, pl. 1, fig. 3*a*) and *Niobella* (Tjernvik 1956, pl. 4, fig. 14). The characteristic arrangement with the glabellar tubercle lying between crescentic or apostrophe-shaped basal glabellar furrows some distance forward from the occipital ring is shown on text-fig. 12; no other trilobites of which we are aware have exactly this axial structure, which is our preferred evidence for common ancestry of the Ceratopygidae and Asaphidae. As noted above, the PAUP analysis recognizes Asaphidae + Ceratopygidae as a paraphyletic group, rather than a monophyletic group, on the totality of character distribution, and whether or not Asaphacea and Ceratopygacea are recognized as distinct superfamilies depends on which interpretation is preferred. For the moment we follow previous usage (e.g. Shergold and Sdzuy 1984) in including the two families Asaphidae and Ceratopygidae within a single taxon, here given the status of superfamily Asaphacea. In any case it is clear from all our phylogenetic analyses that none of the other families included within the Asaphacea in the *Treatise* by Moore (1959: Nileidae, Taihungshaniidae, Dikelokephalinidae, and Tsinaniidae) should be included in the same group. They have different axial cephalic and pygidial structure, and are accordingly excluded from the superfamily. The characteristic arrangement of cephalic furrows and median tubercle is found in the earlier Asaphacea. Stratigraphic evidence points to modifications to this arrangement, which are considered in the following paragraphs.

Family ASAPHIDAE Burmeister, 1843

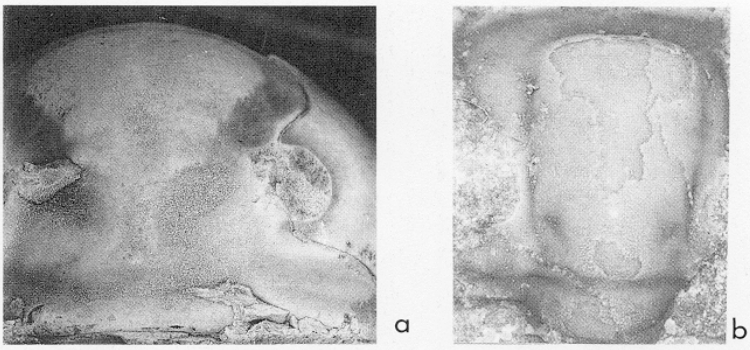
Diagnosis. Asaphaceans with eight thoracic segments; pygidial margin not incorporating anterior spinose segment; librigenal borders wide (or border furrow effaced); facial sutures supramarginal in front of glabella; later species often with forked hypostome and/or panderian openings; genal spine generally short, and wide at base.

Discussion. The generalized glabellar structure is widespread among early asaphids, but the occipital ring tends to effacement even in late Cambrian forms. On *Golasaphus* Shergold, for example, the basic structure is visible on *G. triquetrus* (Shergold 1975, pl. 56, fig. 7), but the occipital furrow has become effaced on *G. simus* (Shergold 1975, pl. 55, fig. 2). Those asaphids classified in the subfamily Niobinae



TEXT-FIG. 13. The petaloid thoracic facet (*a* and *b*), typical of higher Asaphina, compared with facets of other trilobites (*c–g*). *a*, asaphid, *Asaphus* sp. BM 15430 (Middle Ordovician, Russia), × 8. *b*, nileid, *Symphysurus palpebrosus*, BM It20684 (Middle Ordovician, Sweden), × 8. *c*, granulose dalmanitacean facet, *Dalmanites caudatus*, BM I67*a* (Silurian), with postfacetal type of pleural furrow, × 8. *d*, primitive type, smooth, in the Silurian proetide *Otarion diffractum*, BM I3603, × 12. *e*, *f*, primitive type in the Middle Cambrian ptychoparioid *Elrathia*; *e*, BM It5396, dorsal surface, × 12; *f*, BM It5397, narrow doublure with terrace ridges primitive for Asaphina, × 15. *g*, granulose calymenacean facet, with epifacetal type of pleural furrow, *Calymene* sp., BM It20685 (Upper Ordovician, Anticosti Island), × 10.

often maintain both the tubercle and the occipital ring in the same relative positions (e.g. *Niobe*, see Fortey 1975, pl. 5, fig. 2), but there is a tendency for the tubercle to migrate backwards to a nearly occipital position, a process carried furthest in *Ogygiocarella*. The pre-occipital origin of the tubercle is still betrayed by a marked backward curvature of the occipital furrow to form an embayment around the tubercle on the mid-line (*Ogygiocaris*, see Rushton and Hughes 1981, pl. 4, fig. 2). Niobines and ogygiocaridines retain an elongate glabella, but with the frontal lobe tending to enlarge;



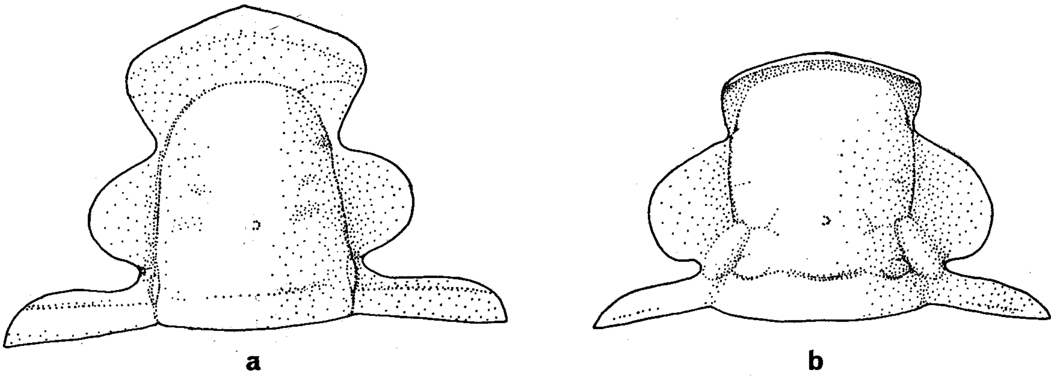
TEXT-FIG. 14. Advanced asaphid (*a*) and ceratopygid (*b*) glabellas, showing retention of pre-occipital tubercle in more derived members of these families. *a*, *Asaphus*, BM I 5701, ×2. *b*, *Ceratopyge*, BM It12895, ×4.

bacculae are present on many species, but are apparently lacking on the primitive forms figured by Westergård (1939). Baccula-like structures are present on early asaphid growth stages. In Asaphinae the glabellar shape is much modified—becoming hourglass-shaped or expanding forwards, and often incorporating genal material within the axial structure (Fortey 1980); Asaphinae attain impendent hypostomal condition. Effacement is common. The glabellar tubercle is still pre-occipital in asaphines, a fact revealed in those less effaced genera where the occipital ring is still defined dorsally (*Asaphus*, see Neben and Krueger 1971, pl. 5, fig. 7; *Norasaphus* Fortey and Shergold, 1984; text-fig. 14 herein). The constancy of the pre-occipital tubercle within this diverse family lends support to considering it a feature of taxonomic importance. All asaphids have eight thoracic segments, a character stabilized within the Cambrian and invariant thereafter; other families of Asaphina are more variable in this regard. We do not consider the subfamily division of the Asaphidae further here. The forked hypostome of many species is typical of the family but cannot be used in its definition because it is unforked in primitive species; the hypostome invariably carried smooth maculae.

Family CERATOPYGIDAE Linnarsson, 1869

Diagnosis. Asaphaceans with variable number of thoracic segments (nine to six); hypostomal condition conterminant; primitive asaphacean glabellar furrows retained throughout family; genal spines generally narrow and needle-like; cephalic rim narrow; pygidium typically incorporating one (or two) pairs of marginal spines which are extensions of pygidial segments.

Discussion. Glabellar structure in ceratopygids is conservative compared with asaphids. The characteristic asaphacean glabellar structure is shown on all genera for which well-preserved material is known, e.g. *Proceratopyge* (Westergård 1947; Shergold 1982, pl. 16, fig. 9), *Ceratopyge* (text-fig. 14*b* herein; Harrington and Leanza 1957, fig. 94.7), *Dichelepyge* (Fortey and Owens 1982, pl. 3, fig. i), *Pseudohysterolenus* (Harrington and Leanza 1957, fig. 98.2*a*), *Hysterolenus* (Lu and Lin 1984, pl. 17, fig. 3), and *Diceratopyge* (Peng 1984, pl. 5, fig. 1*b*). Later ceratopygids, especially *Ceratopyge* itself, have the glabella modified to become forward-expanding and with a corresponding reduction in the preglabellar area. The family is best defined by the inclusion in the pygidium of one or more macropleural segments, although the narrow cephalic rims of most species are also characteristic (but see *Haniwoides*, Shergold 1980, fig. 37; text-fig. 15*a* herein). The primitive glabellar structure of ceratopygids seems to us to be indistinguishable from that of primitive asaphids (text-fig. 12). Rushton (1983, text-fig. 6*b*) has shown how the doublure on *Proceratopyge* curves backwards medially to reach



TEXT-FIG. 15. Cranidia of additional taxa here included in Asaphacea, showing diagnostic glabellar structure (cf. text-fig. 11). *a*, small cranidium of *Haniwoides* (Upper Cambrian, Australia) (after Shergold 1980, pl. 4), ×8. *b*, *Macropyge*, type species *Macropyge chermi* (Tremadoc) (new restoration), ×4.

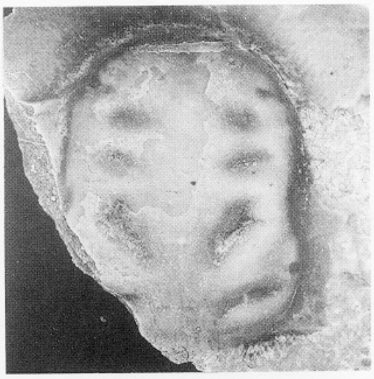
the front of the glabella, and such curvature is reflected by a paradoublural line on the dorsal surface of the preglabellar field of some species (Westergård 1947, pl. 2, fig. 1; see Dikelokephalinidae below). Hypostomal condition conterminant throughout the family.

As might be expected with the close relationship between ceratopygids and asaphids proposed here there are early members of the Asaphacea with intermediate combinations of characters which pose problems for classification. Shergold (1980, p. 86) noted the intermediate features of the subfamily Iwayaspidinae Kobayashi, 1962, between what he regarded as the superfamilies Asaphacea and Ceratopygacea. He placed this subfamily within the Ceratopygidae even though macropleural segments are lacking on the pygidium. Based on the morphology of the genus *Cermatops* Shergold, 1980, we agree with the assessment. In particular, the pygidial pleural segmentation is of a kind seen in other, macropleural ceratopygids in which the interpleural furrow encroaches closely upon the pleural furrow of the segments behind; the narrow and convex librigenal rim is also unlike the border of asaphids.

OTHER ASAPHACEA HITHERTO CLASSIFIED IN DIFFERENT SUPERFAMILIES

Subfamily MACROPYGINAE

The Tremadoc genus *Macropyge* Stubblefield, 1927, has been compared with the Remopleurididae, and was classified there in the *Treatise* (Moore 1959) and elsewhere (e.g. Peng 1984). Recent descriptions of the cephalic morphology (Fortey and Owens 1982; Shergold and Sdzuy 1984) have shown that the cephalic features are not at all like those of remopleuridids, although Shergold and Sdzuy still tentatively classified *Macropyge* with the Remopleurididae. Kobayashi (1953) had previously proposed a separate family for its reception. It is clear, however, that the features of the cephalic axis are those of the Asaphacea as described here, with a pre-occipital tubercle well in advance of a clearly defined occipital ring (Fortey and Owens 1982, pl. 2, fig. h; Shergold and Sdzuy 1984, fig. 62; text-fig. 15*b* herein). Other features of the cephalon are like those of ceratopygids such as *Haniwoides* which lack pygidial spines. In fact the free cheeks, with their narrow rims and paradoublural ridge, are characteristically ceratopygid, and the palpebral lobes lack the inflated rims typical of remopleuridids; hence it is likely that the resemblance to the latter family is one of convergence only. If *Macropyge* is a ceratopygid, it is allied to those genera lacking pygidial spines placed in the subfamily Iwayaspidinae discussed above, and Macropyginae can be a senior name for that subfamily. Two other genera were assigned to the Macropyginae by Shergold and



TEXT-FIG. 16. Glabella of type species of *Hedinaspis*, *H. regalis* Troedsson, to show asaphine construction; Hedin Collection, Riksmuseet, Stockholm, Ar 47250, × 3.

Sdzuy (1984): *Promacropyge* Lu, 1965 and *Aksapyge* Lisogor, 1977. The former is usually only regarded as a subgenus of *Macropyge* (e.g. Lu and Lin 1984), while the latter is doubtfully distinct from *Promacropyge*.

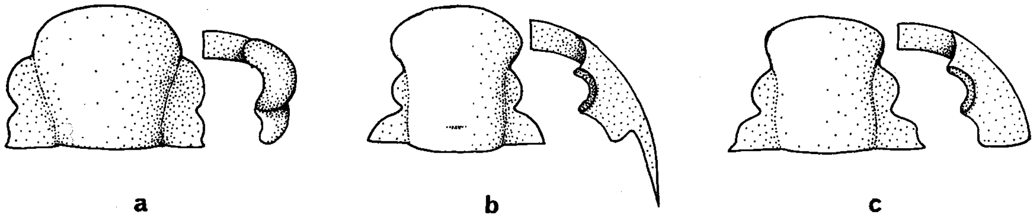
In summary, *Macropyge* and its close relatives are accommodated as subfamily Macropyginae within the Ceratopygidae, together with those genera listed by Shergold (1980) as belonging to the subfamily Iwayaspidinae. To these we add the genus *Tamdaspis* Lisogor, 1977, which is extremely like *Cermatops* Shergold, 1980. The Macropyginae spans the Cambrian–Ordovician boundary, as do the Ceratopyginae and Asaphidae.

Genus HEDINASPIS

Hedinaspis (type species *H. regalis* Troedsson, 1937) has been regarded as an olenacean, and has generally been assigned to the family Papyriaspididae. But the glabellar structure of the type species (Peng 1984, pl. 3, fig. 3*a*; text-fig. 16 herein) is of typical asaphacean appearance. *Papyriaspis* on the other hand has a typical generalized olenacean (or ptychoparioid) glabellar structure. There is no reason (Henningsmoen 1957, p. 20) to assume that *Hedinaspis* should be classified with the Olenacea, other than the presence of a large number of wide and narrow (exsag.) thoracic segments, a character associated with the poorly oxygenated olenid environment. The same kind of morphology has been produced in the same environment from several different phylogenetic origins, e.g. the Alsataspididae in the Trinucleacea, or the Aulacopleuridae among Proetida. Multiplication of narrow thoracic segments and their pleural extension is associated with multiplication and transverse extension of the respiratory exites and, as such, with the constraints of greater oxygen absorption in an oxygen-deficient environment. *Hedinaspis* should be classified either with the Ceratopygidae or the Asaphidae; the close resemblance of its cephalic features to those of *Proceratopyge*, together with the form of the pygidium, which is virtually identical to the immature pygidium of *Haniwoides* figured by Shergold (1980, pl. 33, fig. 4), indicate that the former is correct, i.e. *Hedinaspis* is an olenid-like ceratopygacean. *Asiocephalus* Palmer, 1968, from the Franconian of Alaska, is closely similar to *Hedinaspis* and should be classified with it.

Superfamily CYCLOPYGACEA Raymond, 1925

The superfamily Cyclopygacea included only the family Cyclopygidae in the *Treatise* (Moore 1959). Here it is considered to include three families: Cyclopygidae, Nileidae, and Taihungshaniidae, the latter two having been previously classified with the Asaphacea. This rearrangement is strongly supported by derived characters in the cladograms, text-figs. 1–3, and is consistent with stratigraphic evidence (see Fortey 1981).



TEXT-FIG. 17. Cephalic structure of the three families included in Cyclopygacea, showing similarity in glabella structure. *a*, the most primitive cyclopygid, *Prospectatrix* (Tremadoc, Shropshire). *b*, Taihungshaniidae, *Taihungshania* (Arenig, France). *c*, Nileidae, *Platypeltoides* (Tremadoc, widespread). All approximately natural size.

Diagnosis. Asaphina with glabellar lobe expanding forwards to cranidial margin (effaced in later cyclopygids); palpebral lobes, without distinct rims, touch axial furrows at anterior ends; hypostomal condition impendent; hypostome relatively transverse, often with tripartite posterior margin.

Discussion. The glabellar structure of the superfamily is distinctive (text-fig. 17). The glabella is elongate (sag.), extending to the cranidial margin and expanding in width forwards, usually immediately in front of the palpebral lobes, which touch the axial furrows at their anterior ends. The fundamental similarity of glabellar structure of Cyclopygidae to that of Nileidae and Taihungshaniidae is revealed by the earliest known cyclopygid genus *Prospectatrix* Fortey, 1981, and by growth stages of *Pricyclopyge* (Rushton and Hughes 1981, pl. 2, figs. 20 and 23); later cyclopygids develop an entirely effaced median cephalic lobe, and other adaptations for pelagic life habits, which obscure their relationships outside the group. Clearly this *glabellar structure is very different from that uniting the Asaphacea, and forms the basis for grouping these families in a different superfamily.* Glabellar furrows are not usually incised. The median suture is present in Taihungshaniidae (Lu 1975, pl. 18, fig. 9) throughout their history; it is present in only the earliest nileids, such as *Platypeltoides* (Fortey and Owens 1982, pl. 2, fig. k), and early cyclopygids (Fortey 1981, pl. 1, fig. h). Through most of their Ordovician history nileids and cyclopygids have fused free cheeks, presumably resulting from ankylosis of the two halves of the doublure. Note that the cephalic doublure of the Cyclopygacea extends *beneath* the glabella, implying the impendent hypostomal condition, whereas on most asaphaceans it is conterminant. Sharply defined palpebral rims are lost in this group. On Cyclopygidae and Nileidae the occipital ring is effaced; it is weakly indicated on some Taihungshaniidae (*Taihungshania omeishanensis*, see Lu 1975, pl. 18, fig. 13). Because the Taihungshaniidae also retain the median suture, broad (tr.) postocular cheeks, and long genal spines, they are regarded as the more primitive member of the Cyclopygacea, and hence are shown as the sister group of the Cyclopygidae + Nileidae on the cladograms. Cyclopygaceans have five to eight (?nine) thoracic segments which may have a relatively broad doublure; adaxial articulation of the first thoracic segment is characteristic. The hypostoma is rigidly attached to the doublure.

The glabellar tubercle of Cyclopygacea is clearly pre-occipital, usually being sited at a point opposite the hind end of the eyes, and far from the posterior margin of the glabella. Where cephalic muscle impressions are preserved the tubercle is near the S1 pair and well forward from the occipital pair (e.g. *Poronileus fistulosus*, see Fortey 1975, pl. 16, fig. 6). The only exception of which we are aware is the superficially asaphid-like *Peraspis lineolata* (see Whittington 1965) in which the tubercle has assumed a sub-occipital position, which we believe to be a secondary backward migration, such as happens on ogygiocaridine asaphids of comparably low convexity.

If the pre-occipital tubercles of Cyclopygacea and Asaphacea are homologous, then the two families should be regarded as sister groups because this appears to be a good synapomorphic character. The asaphoid protaspis has been proved in Nileidae (p. 184) and, from the similarity in meraspis growth series of cyclopygids and nileids, there is no reason to doubt its occurrence throughout the superfamily.

Family CYCLOPYGIDAE Raymond, 1925

Diagnosis. Subisopygous Cyclopygacea with hypertrophied eyes; free cheeks fused on all but the earliest species; fixed cheeks and librigenal borders much reduced; five or six thoracic segments. The stratigraphically earliest form has seven thoracic segments. Hypostome (where known) has lost maculae.

Discussion. Pelagic cyclopygaceans form a distinctive group. Their eyes are deep and usually inflated, unlike nileids, which may have eyes as long, but which are strip-like. The doublure of the free cheek of several cyclopygids (*Cyclopyge*, *Microparia*, *Degamella*) has been shown to carry a series of vincular notches, and this may prove to be an additional diagnostic character of the family.

The subfamily Ellipsotaphrinae Kobayashi and Hamada, 1971 has been a taxonomic problem. *Ellipsotaphrus* has very well-defined glabellar furrows, including what has been interpreted as an occipital furrow, and the presence of the latter should exclude it from the family, as did Fortey (1981). However, Fortey and Owens (1987) presented evidence that this 'occipital' furrow may be interpreted instead as pre-occipital, a conjoined pair of 1p glabellar furrows. This would allow incorporation of *Ellipsotaphrus* within the Cyclopygidae, and such an interpretation is preferred here. However, incised glabellar furrows would represent a character reversal of some importance; we did not code this group into text-figs. 2 and 3. Ontogenetic information should resolve the homologies.

Family NILEIDAE Angelin, 1854

Diagnosis. Subisopygous Cyclopygacea without anterior spinose pygidial segment; border of free cheeks not reduced and usually with broadly rounded genal angle; median suture lacking in all but earliest representatives; cephalic and pygidial doublure wide; pygidium without strong pleural furrows (secondarily developed in a few forms); seven or eight (?nine) thoracic segments. Wide hypostome with broad posterior borders and weakly tripartite margin.

Discussion. The cladistic analyses show that it is difficult to characterize Nileidae, other than by retention of characters which have been modified in Cyclopygidae. None the less it is a stratigraphically and morphologically coherent group. The relatively high divergence of the anterior branches of the facial sutures applies to virtually all species other than those in which the eyes have reached an extreme anterior position. Most nileids have large eyes, but there are several genera (e.g. *Illaenopsis*, *Psilocephalinella*) which do not, and the characters of the eye cannot be incorporated into the diagnosis, although they are never hypertrophied in cyclopygid fashion. The majority of nileids lack genal spines, but they may be present on small growth stages even if absent in the adult, and their appearance in several genera (e.g. *Homalopteon*, *Peraspis*) is regarded as a secondary result of paedomorphosis. Hence, we place loss of genal spines as an synapomorphy shared with Cyclopygidae. The same comment applies to the appearance of strong pygidial segmentation in the same genera. There is stratigraphic evidence of the secondary, probably paedomorphic derivation of these apparently primitive characters: a derivation of *Peraspis* from *Symphysurus arcticus* was proposed by Fortey (1975), while *Homalopteon* closely resembles the more usual nileid *Barrandia* which stratigraphically predates it.

A subfamily classification of Nileidae was proposed by Courtessole and Pillet (1975), involving no less than seven subfamilies. A full critique is not possible here, except to state that such fine subdivision serves no purpose and is premature. For example, two of their proposed subfamilies, Lakaspidinae and Hemibarrandiinae, are based on genera which are not nileids; another, Illaenopsinae, is listed as including three genera, *Illaenopsis*, *Borthaspidella*, and *Pseudobarrandia* (proposed therein), the last named having the same type species as *Rocykania* Přibyl and Vanek, which is not mentioned, and which is in any case a subjective synonym of *Illaenopsis* itself (Fortey and Owens 1987). Of the seventeen genera listed for the family, five (*Macelloura*, *Lakaspis*, *Benthamaspis*, *Bumastides*, and

Hemibarrandia) belong in other families according to the criteria of this paper, and were erroneously included in Nileidae by Courtessole and Pillet on the basis of general effacement, which is of no taxonomic importance. Furthermore, these authors failed to mention at least six validly proposed nileid genera (*Procephalops* Whittard, *Psilocephalinella* Kobayashi, *Homalopteon* Salter, *Eurymetopus* Postlethwaite and Goodchild, *Troedssonia* Poletaeva, and *Petrbokia* Přibyl and Vanek), the inclusion of which would have blurred their supposed subfamilial characteristics.

Subfamily SYMPHYSURININAE

One of us (Fortey 1983) has recently shown that the genus *Symphysurina* Walcott is not likely to be an asaphid. In the *Treatise* (Moore 1959) it is the eponymous genus of a supposed asaphid subfamily. However, since the Asaphidae consistently have eight thoracic segments the fact that *Symphysurina* can have nine casts doubt on its inclusion in that family; in addition, it has a series of vincular notches on the doublure of the free cheek unmatched on any asaphid genus. The glabellar tubercle does, however, appear to be pre-occipital, which places it within the Cyclopygacea or Asaphacea as understood here. The median suture is shared by primitive members of the Cyclopygacea, and, occurring as it does at the base of the Tremadoc, its presence in *Symphysurina* is only to be expected. We are uncertain how to classify it here. Cranidial and genal morphology is generally nileid-like, but the series of vincular notches can be matched in cyclopygids (Whittard 1960, pl. 24, fig. 8). On this basis it can be considered as the sister group of both Nileidae and Cyclopygidae, which is tentatively adopted. Other genera classified with *Symphysurina* in the Symphysurininae in the *Treatise* appear to be conventional asaphids, and hence at present the subfamily Symphysurininae includes only the one genus.

Family TAIHUNGSHANIIDAE Sun, 1931

Diagnosis. Taihungshaniidae are cyclopygaceans carrying a pair of pygidial spines; rarely a second pair is developed. Pygidial interpleural furrows are lacking. They retain the median suture and usually have a clearly defined glabella showing typical cyclopygacean form.

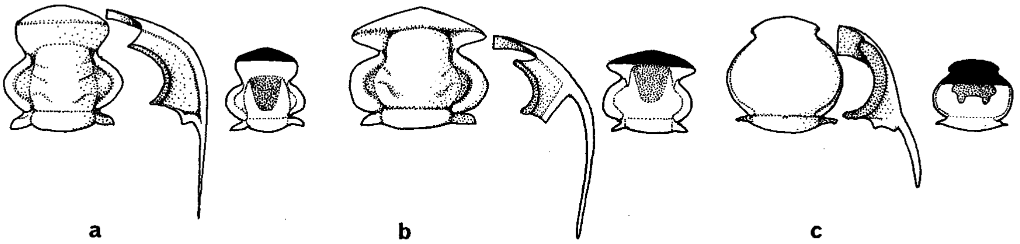
Discussion. From stratigraphic evidence, there is a trend in the group towards long pygidia with numerous segments, a trend reaching its maximum expression in *T. multisegmentata* Sheng (see Lu 1975, pl. 19, fig. 3) with at least twenty such segments. Again, stratigraphic evidence shows that this was not primitively the case: early taihungshaniids, such as *Tungtzuella*, have pygidia much like those of contemporary nileids but for the pygidial spines.

Superfamily REMOPLEURIDACEA Hawle and Corda, 1847

The asaphoid protaspis of remopleuridids has been described many times (see above), as has the presence of a median suture in later representatives of the group (e.g. Whittington 1959*a*), e.g. *Remopleurides*, *Amphytrion*, and *Robergia*. Neither the morphology not ontogeny of the earlier remopleuridaceans is as well known and comments upon these are more cautious. However, among earlier (Upper Cambrian–Tremadoc) genera ventral median sutures have been described from *Pseudokainella* (Whitworth 1969), *Menoparia* (Ross 1951*b*), and *Elkanaspis* (Ludvigsen 1982) and we assume its loss in certain kainellids is secondary. Remopleuridaceans do not have the derived glabellar structure of Cyclopygacea + Asaphacea, and also have an occipital tubercle positioned like that of other ptychoparioids.

Diagnosis. Asaphina with spinose pygidia, spines flattened, united at their bases, and extending to mid-line. Glabella bulges in transverse width in front of occipital ring; narrow, wire-like eye socle; genal borders bevelled; palpebral rims inflated, deep rim furrows, extending to axial furrows.

Discussion. The specializations of later members of the group makes the framing of a set of unequivocal uniting characters difficult. The free spinose tips on the pygidium, the bases of which are conjoined and flat and extend to the posterior mid-line, are particularly characteristic of



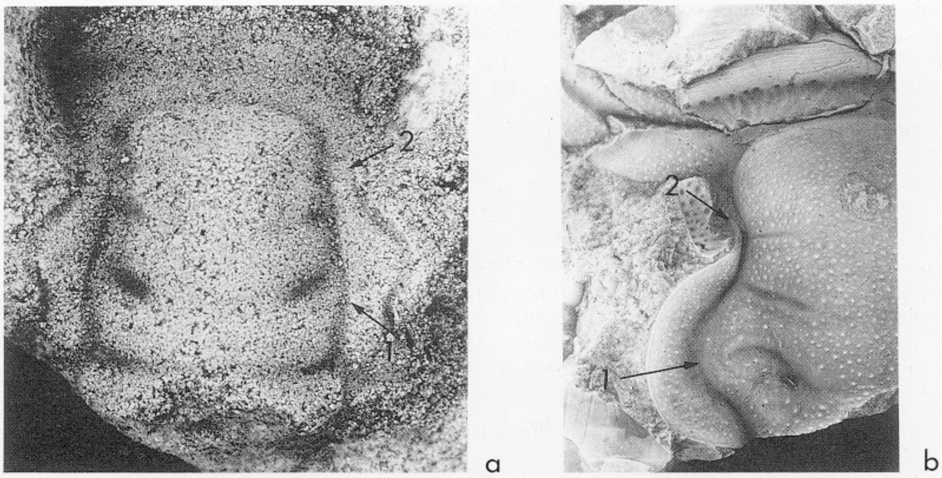
TEXT-FIG. 18. Remopleuridaceans from primitive (*a*) to advanced (*c*) types, showing change from inferred natant to impendent hypostomal condition. Smaller sketches show hypostomal position (stippled) in relation to extent of cephalic doublure (black). *a*, primitive (kainellid) natant type, *Elkanaspis* (Upper Cambrian; after Ludvigsen 1982, fig. 60). *b*, conterminant type, *Menoparia* (Tremadoc; after Ross 1951*b*, pl. 20). *c*, impendent type, *Remopleurides* (mid to late Ordovician). Approximately natural size.

remopleuridaceans. This character only fails to apply to the superfamily if loganellids are included, and see Auritamiidae (Anomocaracea) below. Slit-like glabellar furrows are developed in later species, but many taxa are effaced. The outline of the axial furrows is characteristically bowed outwards at some point in front of the occipital ring, and usually at the level of the outer end of S1 or the L2 glabellar lobe, a feature shared with generalized dikelocephalaceans. On later remopleuridids this feature dominates the glabellar outline (and the expanded glabella may incorporate the remnant genal area inside the palpebral lobes). Primitive and stratigraphically early remopleuridaceans are accommodated within the family Kainellidae (*sensu* Shergold 1975, p. 158), and here the feature is subdued but still visible—see, for example, *Kainella* (Harrington and Leanza 1957, fig. 52.2), *Richardsonella* (Ludvigsen 1982, fig. 70N), *Pseudokainella* (Whitworth 1969, pl. 75, fig. 8), and *Sigmakainella* (Shergold 1975, pl. 31, fig. 2). It is preserved in otherwise aberrant remopleuridaceans, such as *Apatokephalops* (Lu 1975, pl. 5, fig. 1), and the pelagic, specialized forms *Opipeuter* (immature cranidium Fortey 1974, pl. 14, fig. 3) and *Bohemilla* (Fortey and Owens 1987).

Remopleuridaceans have characteristically curved and inflated palpebral lobes, outlined by deep, narrow palpebral furrows, *which run into the axial furrows* (text-fig. 19). On earlier species these furrows circumscribe a small area of fixed cheek shaped like a crescent moon, which in *Remopleurides* and its allies becomes absorbed within the axial area. Genal borders are narrow and bevelled, sharply defined, and only effaced in some *Remopleurides* species. They are not broadly flattened as happens in Cyclopygacea and Asaphacea. Narrow genal spines are primitively present and almost invariably retained; on most species they are long, unlike Asaphacea.

There are three different kinds of thoracic structure in the superfamily, but the presence of one or another does not define obvious subdivisions within the group. The presumably primitive thoracic structure shown by *Pseudokainella* (Whitworth 1969, pl. 75, fig. 7), or *Kainella*, with long falcate pleurae and diagonal pleural furrows, is of a generalized ptychoparioid type. *Remopleurides* itself has powerful adaxial articulation with reduced pleurae (Whittington 1959*a*), and similar morphology is seen also on *Hypodicranotus*, *Opipeuter*, and *Bohemilla*. Another modification of this is shown by *Robergia* (Cooper 1953) and *Robergiella* with a straight-sided thorax, wide (exsag.) pleurae with straight intersegmental boundaries.

The cephalic doublure on later remopleuridids, such as *Remopleurides*, is broad and extends backwards beneath the glabellar tongue (text-fig. 18), with an impendent hypostomal condition comparable to that of Cyclopygidae and Nileidae, having the hypostome attached at the doublure. On earlier genera of the *Apatokephalus* type the doublure extends beneath the cranidial border as far as the preglabellar furrow but no farther in the conterminant condition, e.g. see Ross (1951*b*, pl. 20). The hypostome was presumably still attached at the inner edge of the doublure. However, on kainellids with a broad preglabellar field the evidence from silicified free cheeks indicates that the doublure does not extend beneath the preglabellar field (e.g. Ludvigsen 1982, fig. 64D, O, N; text-fig. 18*a*



TEXT-FIG. 19. Remopleuridacean and Dikelocephalacean cranidia compared. 1, pre-occipital glabella expansion; 2, relation of palpebral furrow to axial furrow. *a*, dikelocephalacean, the generalized saukiid *Prosaukia*, BM I3869 (Upper Cambrian), × 4. *b*, typical remopleuridacean, *Apatokephalus*, BM It7300 (early Ordovician, Tremadoc), × 6.

herein). If the hypostome on these forms lies beneath the front part of the glabella, it is hard to see how it could have been attached directly to the doublure, and the hypostomal condition was presumably natant. This is of interest because the same is true of other primitive asaphines, and is a retained character of Ptychopariina. These three ventral distinctions may afford a method of diagnosing remopleuridid subfamilies: Remopleurididae *s.s.* having impendent hypostomal condition; all Apatokephalinae conterminant; Kainellidae restricted to those forms with natant hypostomal condition. To avoid multiplication of terminal taxa on text-figs. 2 and 3 this character was arbitrarily coded as impendent there. That at least some kainellids may have lost the median suture to form yoked free cheeks is indicated by the *Richardsonella* sp. illustrated by Palmer (1968, pl. 14, fig. 8), and some *Kainella* spp.; as it is elsewhere in Asaphina, this condition is regarded as secondary.

Constituent families of Remopleuridacea. Shergold (1975) included two families, Kainellidae and Remopleurididae, in the Remopleuridacea, the latter with three subfamilies, Remopleuridinae, Apatokephalinae, and Macropyginae. Of these, the Macropyginae has been assigned to the Asaphacea herein, as discussed above. The remopleuridid subfamily Richardsonellinae was employed in the *Treatise* (Moore 1959), and was equivalent to Kainellidae in Shergold's usage. There are several additional families to be included. Two peculiar and specialized families of Ordovician pelagic trilobites are regarded as being remopleuridaceans: Bohemillidae Barrande, 1872 and Opipeuteridae Fortey, 1974. The earliest representative of the former has just been discovered (Fortey and Owens 1987), and a pygidium assigned for the first time, which is compatible with remopleuridacean affinities. *Opipeuter* is convergent with *Bohemilla*, but has a separate origin and may not be closely related. Lu (1975) proposed a family Loshanellidae for the reception of two Chinese genera *Loshanella* and *Wanliangtingia*. Glabellar furrows are effaced in these genera, and eyes are smaller than is usual in remopleuridaceans, but both (Lu 1975, pl. 5, figs. 18 and 20) show the glabellar shape typical of the superfamily. Zhou and Zhang (1978) placed *Wanliangtingia* in another new family, Apatokephalopsidae, together with *Apatokephalops* Lu, 1975 and *Jiia* Zhou and Zhang, 1978. *Apatokephalops* itself has a glabella of clear remopleuridacean shape, although unusually elongate (sag.). Ludvigsen (1982) synonymized Apatokephalopsidae with Kainellidae. Clearly, the definition of families and subfamilies within the Remopleuridacea requires a comparative assessment based on a critical evaluation of their shared characters, which is beyond the scope of our work. Provisionally, we can accept the following families within the Remopleuridacea: Remopleurididae, Kainellidae, Loshanellidae, Opipeuteridae, and Bohemillidae, possibly with the Hungaiidae, as discussed next.

Loganellidae and Hungaiidae. These two families are included in the Remopleuridacea in the *Treatise* (Moore 1959). Shergold (1975) assigned both to Dikelocephalacea. Loganellids lack the median suture of Remopleuridacea but, since this can also be lost by ankylosis in other asaphines, this does not preclude its inclusion in the group. Fortey (1983, p. 198) pointed out that loganellids resemble olenids in several features, but that this could be convergence resulting from their adaptations to similar habitats, like *Hedinaspis* described above. Several other differences from olenids were noted, perhaps making their inclusion in that family improbable. For example, *Levisella* and *Lauzonella* have broad (sag.) cephalic doublures, which is not an olenacean characteristic (below). On the other hand, the lack of pygidial spines of loganellids, their often broad genal borders, and the debatable presence of the mid-glabellar expansion makes their inclusion in the Remopleuridacea as understood here problematic. By contrast, *Hungaia* conforms to the superfamily with the exception of having short genal spines, the glabella and pygidium being typical. Unless it can be shown that Hungaiidae and Loganellidae should be classified together, we therefore favour the view that the former belong within the Remopleuridacea, and that the latter belong elsewhere, possibly with the Dikelocephalacea, following Shergold (1975).

CAMBRIAN SUPERFAMILIES INCLUDED WITHIN ASAPHINA

We have so far considered families and superfamilies sharing both median suture (unless lost by ankylosis) and asaphoid protaspis, which we claim as a monophyletic group. There are additionally several others which, we believe, belong to the same group, and are better classified, even with our present inadequate knowledge, with the Asaphina rather that in an indefinable suborder Ptychopariina. The presence of the median suture in these is a uniting character, and to disprove our classification it is necessary to show that this feature is capable of polyphyletic derivation. There is insufficient ontogenetic information on these groups to know whether they have the same protaspis type as the Asaphina described above. As shown on the cladistic analyses they share progressively more generalized ptychoparioid features.

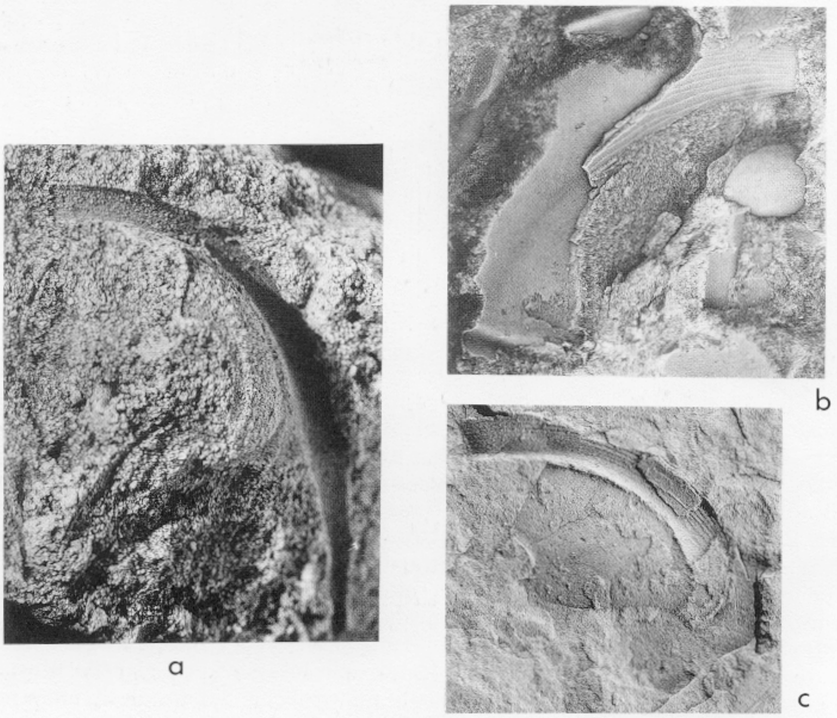
Superfamily DIKELOCEPHALACEA Miller, 1889 emend. Ludvigsen and Westrop, 1983

Discussion. The concept of the Dikelocephalacea was reviewed by Ludvigsen and Westrop (1983), who included the families Dikelocephalidae, Saukiidae, and Ptychaspididae within it, hence uniting Dikelocephalacea with Ptychaspidacea of earlier authors. The presence of the median suture (see text-fig. 20*a*) was noted by them (also Ludvigsen and Westrop 1986, fig. 4F), which may be rarely secondarily lost by fusion, as in Cyclopygacea. These authors did not say whether they would include the families Pterocephaliidae, Housiidae, or Idahoiidae within the superfamily, as in the *Treatise* (Moore 1959). Both *Pterocephalia* and *Housia* (text-fig. 20*c*) have median sutures and should on this criterion be referred to Asaphina in our usage. Taking the restricted view of Dikelocephalacea, the group comes out as the sister group of Remopleuridacea on our cladistic analyses (text-figs. 1-3). The glabella form is characteristic, as noted by Ludvigsen and Westrop, typically truncate anteriorly and squat, with deep axial and glabellar furrows of which 1p may fuse across the glabella. Most of the more primitive genera (e.g. *Prosaukia*) may show a slight mid-glabellar expansion like that noted in the Remopleuridacea, which is evidence for supposing that these two superfamilies are more closely related than to other Asaphina. Much is known about the within-group evolution of dikelocephalaceans, resulting in many departures from the generalized morphology, and mostly based on stratigraphic evidence from late Cambrian sequences in the North American platform; we shall not attempt to review this here. An important difference between the two superfamilies is in the palpebral lobes; in both superfamilies the lobes are inflated and well-defined, but in Dikelocephalacea they do not run into the axial furrows anteriorly as described for remopleuridids. Instead, the lobes are rather sharply terminated even when they closely approach the glabella (text-fig. 19*a*), i.e. they retain the ptychoparioid condition.

So far as is known, the cephalic doublure on dikelocephalaceans approaches the front of the glabella medially, and the hypostome is presumably attached at its inner edge beneath the frontal glabellar lobe, as is the case with most Asaphidae and *Apatokephalus*-group Remopleuridacea, i.e. the hypostomal condition is conterminant. Librigenal borders may be wide and convex, as in *Prosaukia*, or broad and flattened as in *Dikelocephalus*. Thoracic structure is of generalized ptychoparioid type. Pygidial structure is characteristic, with a convex axis having five or six axial rings and a rather sharp posterior termination, from which it is continued towards the margin as a postaxial ridge. Pygidial pleural and interpleural furrows are subequally incised (contrast dikelokephalinids) and extend on to the pygidial border, which is often flattened. On some forms the pygidial margin is spinose, but stratigraphic evidence shows that this is secondarily derived.

Superfamily ANOMOCARACEA Poulson, 1927

Discussion. Herein are included Asaphina which show a combination of characters that are mostly those of generalized ptychoparioids; they probably include some of the most primitive members of the



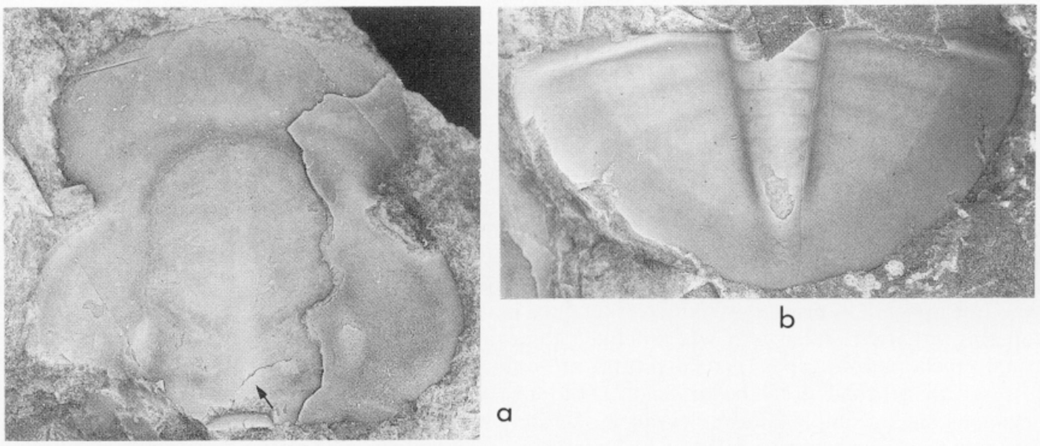
TEXT-FIG. 20. Free cheeks of Dikelocephalacea (*a*), Anomocaracea (*b*), and Housiidae (*c*) with doublure prepared to show median suture. *a*, *Saukia separata* Ulrich and Resser, USNM 84601 (Upper Cambrian), × 3. *b*, *Anomocarioides limbatus* (Angelin), Riksmuseet, Stockholm Ar 53023 (late Middle Cambrian, Andrarum Limestone, type loc., Scania, Sweden), × 4. *c*, *Housia canadensis* Walcott, USNM 5068 (Upper Cambrian, British Columbia), × 3.

suborder and may well include forms ancestral to those superfamilies discussed above (text-fig. 27). Anomocaracea *sensu lato* (including Anomocaridae and Auritamiidae at the least) plot out as a primitive group on text-fig. 1, and the group has no autapomorphies peculiar to it. The unsatisfactory nature of the taxon is shown by the fact that on text-figs. 2 and 3 the family Anomocaridae taken alone plots out as the sister group of Asaphacea (at the least). Clearly the phylogenetic position of Anomocaracea requires further scrutiny. The diagnosis given in the *Treatise* (Moore 1959) is scarcely diagnostic and would apply to most of the Asaphina. The presence of the median suture has been shown in *Anomocare* and *Anomocarioides* (see text-fig. 20*b*), and *Auritama* (see Öpik 1967); since the structure of the border in the superfamily is conservative, there seems no reason to doubt its presence throughout. Our contention is therefore that the median suture was acquired by a ptychoparioid, probably in the Middle Cambrian, and that its more generalized descendants are classified within the Anomocaracea. The primitive characters retained in the group include: 1, the glabella is mostly gently tapering or parallel-sided with, where defined, three or four pairs of glabellar furrows which may be of usual ptychoparioid type; 2, facial sutures are only slightly divergent in front of the eyes, even in forms with a broad preglabellar field; 3, thoracic structure is unspecialized, with nine or more segments having simple falcate pleurae, moderately wide facets, and diagonal pleural furrows; 4, on some anomocaraceans the hypostomal condition is assuredly natant (e.g. *A. limbatus* (Angelin), as illustrated by Egorova *et al.* 1982, pl. 44, fig. 2), i.e. they retain the character of out-group ptychoparioids. Where the cephalic doublure becomes broader (*A. novus* Tchernysheva *in* Egorova *et al.* 1982, pl. 43, fig. 1) it could be interpreted as likely to have had conterminant hypostomal condition; however, on this species the paradoublural line still stops short of the front of the glabella, and we believe that an 'advanced' natant condition still pertained. On *Auritama*, a growth series of cranidia (Öpik 1967, pl. 15, figs. 3–6) clearly shows a reduction in the width of the preglabellar field during ontogeny, and it is possible that this records the change from natant to conterminant hypostomal condition, although there is no proof that the hypostome actually docked against the cephalic doublure. The same problems apply to the Pterocephaliidae, discussed below. In any case, there is no doubt that the retention of natant hypostomal condition in anomocaraceans is primitive. Although pygidia are relatively large, there is no diagnostic characteristic which would distinguish them from those of asaphids (text-fig. 21*b*) or Dikelokephalinidae (Öpik 1967, pl. 31, fig. 3), or Remopleuridacea (Öpik 1967, pl. 15, fig. 10). A more detailed phylogenetic analysis might result in the assignment of some anomocaraceans to any of these groups. Only the inclusion of more than four segments into a relatively large and effaced pygidium is presumably to be regarded as an 'advanced' character compared with typical Ptychopariina.

In *Anomocarioides* the glabellar tubercle could be interpreted as lying in an immediately pre-occipital position (text-fig. 21*a*). It also appears to be a thinning of the exoskeleton (rather than an external tubercle) as has been described for certain nileids (Fortey and Clarkson 1976) and asaphids. If this is so, such forms record the transition into the asaphacean condition and provide further evidence for the paraphyletic, if not polyphyletic position of the superfamily, as interpreted in the tree (text-fig. 27). A strictly cladistic classification might place *Anomocarioides* in the Asaphacea. In other anomocaraceans the tubercle appears to be occipital. Palpebral lobes are long (exsag.), extending far back but not forwards to touch the glabella, often with subdued rims; their gentle curvature inwards at their posterior ends and presence of eye ridges probably afford a distinction from other asaphine superfamilies, but again these are primitive characters; they can be matched on certain species of *Proceratopyge*.

Many, but certainly not all, genera assigned to Anomocaracea have bacculae adjacent to the basal glabellar lobes (text-fig. 21*a*). These are distinct swellings (see p. 212), which we have also noted in comparable position in ceratopygids, asaphids, and macropyginids. The presence of such bacculae, in small growth stages if not in adults, is probably a uniting character of higher Asaphina (further discussion under Trinucleacea).

Further evidence of the artificial classification of the Anomocaracea is the structure of *Auritama*, and the family Auritamiidae was included in the Anomocaracea by Öpik (1967). *Auritama* retains the unmodified glabella typical of primitive forms, and the eye does not approach the axial furrow



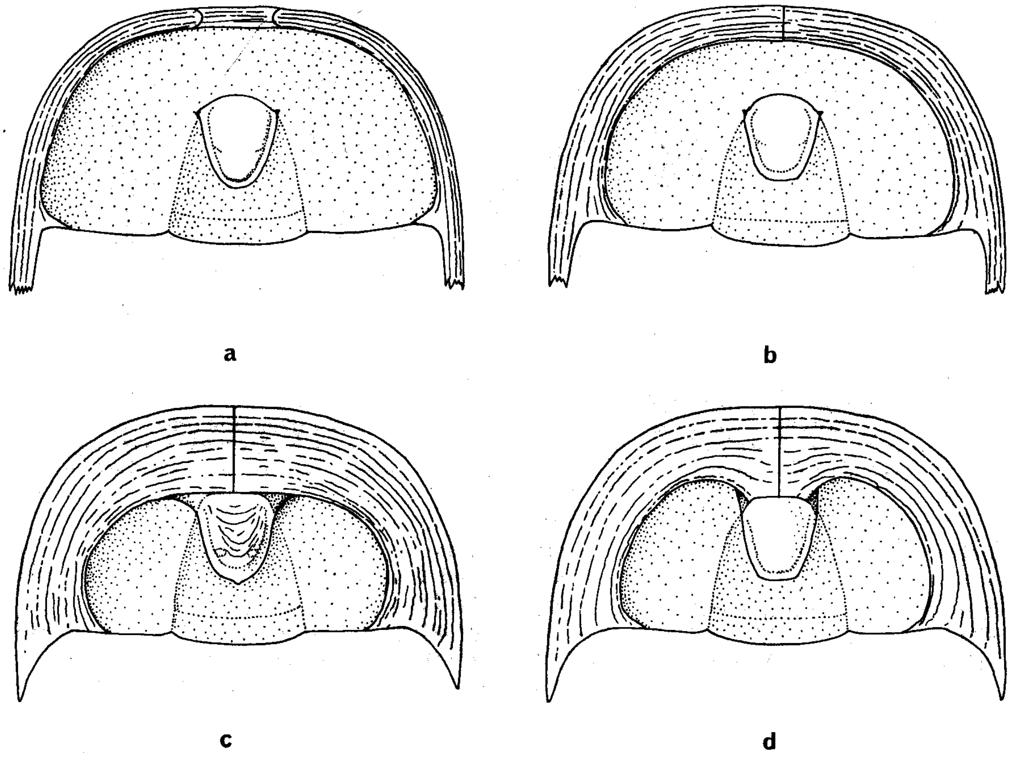
TEXT-FIG. 21. *Anomocarioides limbatus* (Angelin) (Middle Cambrian, Andrarum Limestone, Scania, Sweden). *a*, BM I668, internal mould of cranidium showing bacculae and median glabellar tubercle (arrowed); note that, in relation to occipital furrows, this could be interpreted as pre-occipital (cf. Asaphacea), × 4. *b*, BMNH It20683, pygidium, × 3.

anteriorly; however, it appears to have a narrow, wire-like eye socle, and to have lost the circumocular suture (Öpik 1967, pl. 15, fig. 1), as well as having a deeply incised palpebral rim. These are derived characters of Dikelocephalacea + Remopleuridacea, while the spinose pygidium of *Auritama* is very like that of early remopleuridids. On a cladistic classification Auritamiidae should certainly be classified with the remopleurid-dikelocephalacean clade rather than retained in Anomocaracea on primitive characters.

Family PTEROCEPHALIIDAE Kobayashi, 1935

Discussion. Pterocephaliids are an Upper Cambrian group of trilobites typifying the pterocephaliid biomere of North America (Palmer 1965). Palmer and others have included the Aphelaspidinae in the same family, and the presumption has been made that the pterocephaliids were derived from *Aphelaspis* itself (Robison 1964). *Aphelaspis* is described as having a rostral plate, and the transformation *Aphelaspis* to Pterocephaliidae is supposed to involve the loss of the rostral plate by 'shrinkage'. Since we suppose that the median suture is a synapomorphy of Asaphina there are two possibilities with regard to the median suture in Pterocephaliidae: 1, Robison (1964, p. 520) is correct, and the appearance of median sutures in Pterocephaliidae is a parallelism, and the group is not classifiable in Asaphina—presumably the stratigraphic evidence would be applied here to indicate the derivation of this group later than Anomocaracea; 2, but if we are correct, the presence of the median suture as a synapomorphy indicates that the closest relatives of pterocephaliids are other Asaphina, and not *Aphelaspis*.

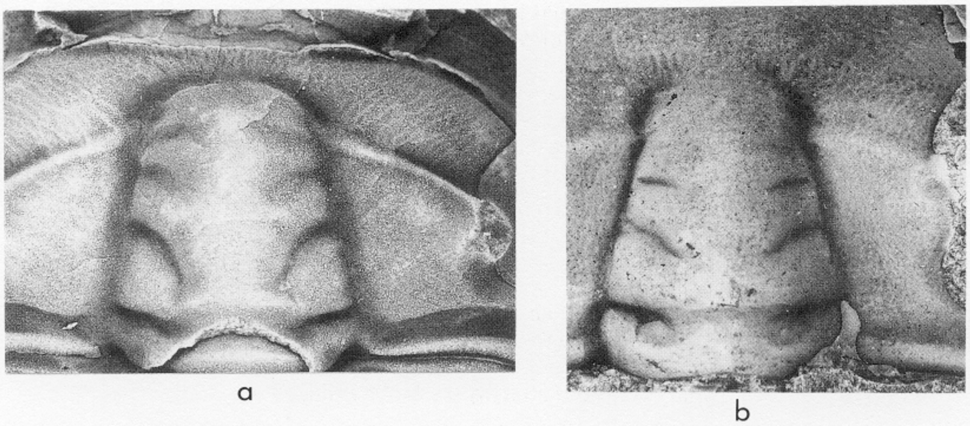
To decide in favour of the former hypothesis we would have to find characters linking *Aphelaspis* and pterocephaliids which are of convincing phylogenetic significance. We cannot find such characters. *Aphelaspis* and pterocephaliids mostly share primitive ptychoparioid characters of no use in determining relationships. For example, Robison mentions similar axial structures: text-fig. 23 shows that the glabellar structure of *Pterocephalia* is closely similar to that of *Ptychoparia striata* and hence by definition ptychoparioid; the fact that some species of *Aphelaspis* also have a comparable glabellar structure (*A. camiro* as figured by Rasetti 1965 is probably closest but other species are usually more effaced) does no more than indicate ultimate ptychoparioid ancestry. The pygidia of



TEXT-FIG. 22. Diagrammatic ventral views of cephala of Asaphina (*b–d*) compared with ptychoparioid out-group (*a*), showing development of fully conterminant condition. *a*, ptychopariine with natant hypostomal condition. *b*, median suture developed but natant hypostomal condition retained as in primitive, anomocaracean grade of Asaphina (pterocephaliids, anomocarids, auritamiids, etc.). *c*, advanced conterminant condition as in Asaphidae—hypostome strongly buttressed against doublure, and terrace ridges spread on to middle body. *d*, conterminant, by virtue of backward median curve of cephalic doublure, reflected in paradoublural line dorsally (primitive Ceratopygidae, and Dikelokephalinidae).

some species of *Aphelaspis* have backward-curved pleural furrows and facets extending far posteriorly, which can be matched on some pterocephaliids. However, other *Aphelaspis* species (e.g. *A. bridgei* Rasetti, 1965) have pygidia of primitive ptychoparioid type, while some pterocephaliids (e.g. *Pterocephalia constricta* Palmer, 1965, pl. 8, fig. 9) have pygidia of anomocaroid form, so we cannot construe a convincing synapomorphy for pterocephaliids + aphelaspids from pygidial structure alone. Backward-curved pygidial facets presumably relate to having posteriorly extended pleural tips on the thorax, which is a character developed in many trilobite families, and of little taxonomic importance.

Transformation from aphelaspid to pterocephaliid would also require an increase in the width of the doublure at the expense of the preglabellar field. There is plenty of evidence to suggest that pterocephaliids combined the natant hypostomal condition with the median suture, as is the case with anomocaraceans. For example, Palmer (1968, pl. 16, fig. 15) illustrated the genal doublure of *Strigitambus*? *blepharina* clearly showing that it must have fallen well short of the front of the glabella (as in text-fig. 22*b*) which is also shown by the paradoublural line on the cranidium. In this species the



TEXT-FIG. 23. Glabellas of *a*, the type species of *Ptychoparia*, *P. striata* (Emmrich) (Ptychopariidae), USNM 61492, × 3·5, and *b*, *Pterocephalia*, *P. sanctisabae* Roemer (Pterocephaliidae), BM It4807, × 5, to show fundamental similarity in structure—the latter is essentially primitive ptychoparioid.

doublure extends well inside the cranidial border, whereas on aphelaspids there is no example known to us in which the cephalic doublure extends beyond the marginal rim, even though the rim itself varies in width. A similar paradoublural line to that in *S*.? *blepharina* is shown also by *P. concava* Palmer (1960, pl. 9, fig. 1; 1965, pl. 17, fig. 6), *Cernuolimbus* (e.g. Palmer 1960, text-fig. 18), and *Sigmocheilus compressus* Palmer (1968, pl. 8, figs. 22–24), and these are also reasonably supposed to have combined a natant hypostomal condition with a relatively wide cephalic doublure carrying a median suture. This is a grade of organization characteristic of early Asaphina, although it cannot be used to classify a group within Asaphina because it is a combination of an advanced character with a retained primitive one: however, it is no coincidence that this grade is found in many Cambrian species. In fact, it is difficult to prove whether any pterocephaliid achieved the conterminant hypostomal condition—the only candidate is probably *P. sanctisabae* Roemer in which the cranidial paradoublural line and preglabellar furrow appear nearly (but perhaps not quite, see Palmer 1960, fig. 19) to coincide; since Palmer (1965, p. 20) shows an ancestor-descendant relationship between *P. concava*, which was natant, and *P. sanctisabae*, it is perhaps likely that the hypostome of the latter never really docked against the doublure. The cladistic analysis on text-figs. 2 and 3 shows the Pterocephaliidae in a basal relationship to the rest of the tree (see consensus tree, text-fig. 4), with Dikelokephalinidae.

Housiidae have been closely associated with pterocephaliids, indeed they were regarded as a pterocephaliid subfamily by Palmer (1965); they also have a median suture (text-fig. 20*c*). Similar arguments to those explained above would also include housiids in Asaphina. Housiidae, Pterocephaliidae, and Idahoiidae were included in the superfamily Dikelocephalacea in the *Treatise* (Moore 1959); Ludvigsen and Westrop (1983) implicitly excluded them from their revised concept of this superfamily. Most of those characters they have are retained primitive characters shared with a ptychoparioid out-group. For example Palmer's (1965, p. 57) 'diagnosis' of Pterocephaliidae would apply to most ptychoparioids. Hence it is difficult to assign them to a superfamily; we retain them in an admittedly paraphyletic Anomocaracea until more detailed phylogenetic analysis is carried out. Too little is known of ventral structures in Idahoiidae to be confident about their placement in Asaphina. Provisionally we suggest that this family is a paraphyletic group related to Dikelocephalacea + Remopleuridacea.

In summary, Anomocaracea show a combination of characters that indicates both its possible ancestral position relative to other asaphine groups, and that its closest non-asaphine relatives are ptychoparioids. Further work may show that its constituent families should be distributed between other superfamilies. Knowledge of the morphogenesis of anomocarids, and particularly of the protaspis, is highly desirable to help resolve these relationships further. Not surprisingly with such a group it is difficult to formulate a set of its own diagnostic characters, because those that it has are either primitive or shared by one or more descendant. As a grade, the combination of natant hypostomal condition with median suture is present on many of these mid- to late Cambrian trilobites. Their inclusion in Asaphina does depend on the recognition of the median suture as a monophyletic character; no compelling morphological evidence to the contrary has been found.

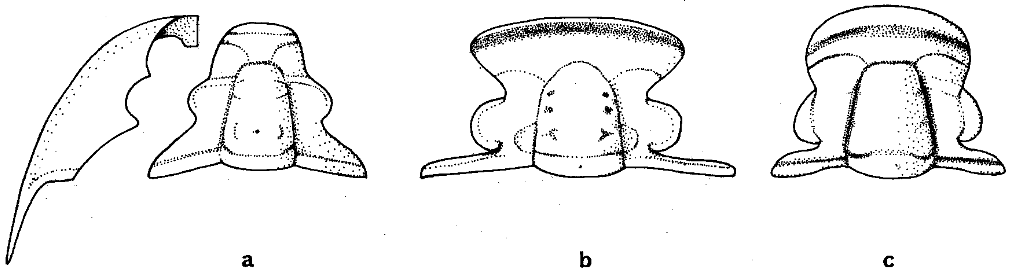
PROBLEM ASAPHINA, AND FURTHER RELEVANT TRILOBITE FAMILIES

We briefly consider here further families which are certainly Asaphina, but difficult to classify, or may prove to belong within the group, but of which knowledge is inadequate to be sure.

Family DIKELOKEPHALINIDAE Kobayashi, 1936

Discussion. This distinctive family has been classified with the Asaphacea in the *Treatise* (Moore 1959) and with the Dikelocephalacea by Öpik (1967). Although it is usually described as Ordovician, Öpik (1967) named an Upper Cambrian genus, *Nomadinis*, from the Mindyallan of Queensland which we believe he correctly referred to the family; like other families in the Asaphina stratigraphic criteria are not primarily relevant to its taxonomic position. The glabellar tubercle in Dikelokephalinidae is occipital, which is unlike Asaphacea as understood here. The distinctive autapomorphy of the group is the presence of prominent semicircular bacculae adjacent to the basal glabellar lobes. They are present wherever preservation is good (see, for example, a variety of forms figured by Lu 1975) and are often somewhat depressed rather than inflated, i.e. they have the appearance of true alae. They may not be homologous with the 'bacculae' of other Asaphina, and they appear as a parallelism on the cladogram, text-fig. 3. The cephalic doublure is broad, reaching the front of the glabella, and the paradoublural line along which this happens is preserved as a pair of concave-backward curves transversely crossing the mid-part of the preocular fixed cheeks (Lu 1975, pl. 27, fig. 1; Fortey and Shergold 1984, pl. 44, fig. 2). This is an extreme development of the outline of paradoublural line shown in some primitive asaphaceans such as *Proceratopyge* (Westergård 1947, pl. 2, fig. 1; see text-fig. 24).

The problem with classifying Dikelokephalinidae is that other characters are too general to be diagnostic. This is again reflected in the basal position of the family on the cladistic analyses. The resemblance to Dikelocephalacea is superficial, being largely that dikelokephalinids also have large



TEXT-FIG. 24. Dikelokephalinid cephalic structure and comparable forms. *a*, *Proceratopyge* (Upper Cambrian), showing form of cephalic doublure reflected in paradoublural line on preglabellar area. *b*, the dikelokephalinid *Hungioides* (early Ordovician; after Fortey and Shergold 1984, pl. 44, fig. 2), showing similarity of paradoublural line to *Proceratopyge*, presumed to reflect similar course of doublure on venter. *c*, *Chelidonocephalus* (latest Middle Cambrian; after Wittke 1984, pl. 3), again showing similar preglabellar structure to *a* and *b*.

fan-like pygidia and correspondingly extended cephalic borders. None of the critical dikelocephalacean characters described above are present. Glabellar structure of Dikelokephalinidae, especially of *Nomadinis*, is of the generalized kind (tapering glabella; lateral glabellar furrows of ptychoparioid type), although on later forms the 1S furrow tends to bifurcate, and the furrows become pit-like, isolated within the glabella. The majority of Dikelokephalinidae have anterior pygidial spines giving them a superficial pygidial similarity to taihungshaniids. This is already seen to be a polyphyletic character in Asaphina, and in any case a few dikelokephalinids do not have such spines (see, for example, *Warendia* Gilbert-Tomlinson *in* Hill *et al.*, 1969). Palpebral lobes are typically strongly curved, but do not reach the axial furrow anteriorly in remopleuridacean fashion. Pygidial interpleural furrows are absent (contrast Dikelocephalacea) or at most extremely feeble.

The best recourse seems to be to temporarily classify Dikelokephalinidae with the Anomocaracea, along with other families lacking derived characters to link them with other groups. As noted above bacculae are present in many anomocaraceans, and now that the record of Dikelokephalinidae extends to the Upper Cambrian there is no particular objection to this on stratigraphic grounds. 'Transitional' forms are to be found in the literature, e.g. *Paracoosia kingi* Wittke, 1984, from the Upper Cambrian of Iran, was assigned to the Anomocaridae by that author, but resembles a dikelokephalinid in all features but the lack of bacculae.

A cephalic border structure much like that of *Dikelokephalina* is present on the Middle–Upper Cambrian genus *Chelidonocephalus* King (see Wittke 1984, pl. 3; text-fig. 24*c* herein). The so-called 'false border furrow' on this genus is identical to the paradoublural line on dikelokephalinids. If this is an important homologue it suggests that the subfamily Chelidonocephalinae Wittke, 1984, belongs within the Asaphina, and possibly as the sister group of Dikelokephalinidae as understood here.

Superfamily LEIOSTEGIACEA

Discussion. Some leiostegiaceans show a glabellar structure generally like that of Cyclopygacea as defined here, with a pestle-shaped glabella extending forwards to the border or to the cephalic margin (*Lloydia*, *Annamitella*). The Cyclopygacea are generally effaced but it is reasonable to suppose that its relatives were less so. Some leiostegiaceans also developed spinose pygidia comparable with those of ceratopygids. Little is known about the ventral cephalic structures of leiostegiids. However, Jell (1985, pl. 22, fig. 3) has figured the genal doublure of *Leiostegium* which apparently terminates in a rostral suture. This indicates that the leiostegiaceans are not Asaphina, and that the similarities to the group are parallelisms. It would be as well to confirm the presence of the rostral plate on other leiostegiaceans, in case Jell's specimen is broken rather than suturally bounded.

Family CATILLICEPHALIDAE Raymond, 1938 (*partim*)
Family ISOCOLIDAE Angelin, 1854

Discussion. The family Catillicephalidae includes the only well-documented example of the presence of the rostral plate and the median suture within the same supposed family. *Catillicephala* itself has a rostral plate (Rasetti 1954), whereas *Acheilus* has a median suture (Rasetti 1954; Fortey 1983). If we are correct in our interpretation of the median suture as indicating a monophyletic origin of the Asaphina this means that the Catillicephalidae is likely to be a polyphyletic taxon. In fact, there is little in common between *Catillicephala* and *Acheilus* other than small size and a convex (tr.) glabella: for example *Catillicephala* has a subcircular glabella without furrows and a remnant cranidial border, whereas *Acheilus* lacks a cranidial border and has a forward-expanding glabella with three pairs of glabellar furrows. In our opinion the true relationships of these genera have yet to be proved. *Acheilus* is clearly related to several other genera: *Triarthropsis*, *Acheilops*, and *Calculites*. Fortey (1983) suggested that these in turn were related to the Ordovician family Isocolidae, for which a median suture has been demonstrated (Whittington 1963). Such isocolids are generally more similar to *Acheilus* than to *Catillicephala*. However, it is difficult to accommodate the Isocolidae within any of the superfamilies of Asaphina described above. Whether they prove to be a truly independent lineage, or whether they are related to some as yet unidentified asaphine taxon remains to be seen. For the moment we classify them as Asaphina *incertae superfamiliae* and include *Acheilus* and its allies in the same family. Because *Acheilus* has a forward-expanding glabella, palpebral lobes that touch the axial furrows, and is likely to have had an impendent hypostomal condition, it is likely that its relationships within Asaphina will prove to be with Cyclopygacea.

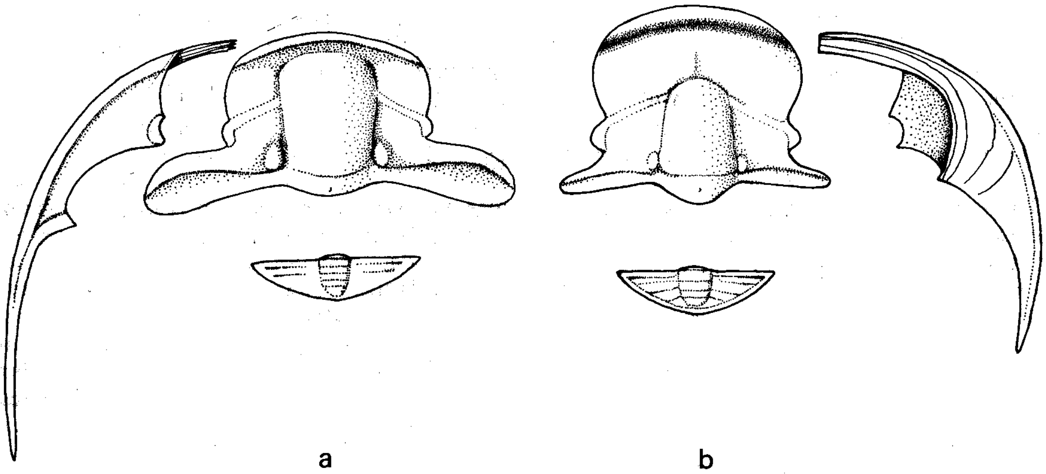
Superfamily TRINUCLEACEA Hawle and Corda, 1847 emend.

The Trinucleina are at present regarded as a suborder of Ptychopariida, but for reasons which are considered below, we consider the group as a superfamily in this work. In *Treatise* usage the taxon includes seven families: Trinucleidae, Raphiophoridae, Hapalopleuridae, Endymioniidae, Orometopidae, Dionididae, and Alsataspididae. Myindidae Hupé, 1955 should also be referred to the group, and there is now stratigraphic evidence to suggest that *Myindella* and *Myinda* are close relatives of the hapalopleurid *Araiopleura* (Rushton 1982, p. 57) which is a clear indication that separate family status for Myindidae is not necessary. Fortey and Shergold (1984) regarded Hapalopleuridae and Orometopidae as synonymous, representing the more primitive Trinucleacea retaining wide free cheeks and in most cases probably eyes. Endymioniidae have been regarded as a subfamily of Raphiophoridae. Hence, a modern view of Trinucleacea would include perhaps five families. Regardless of internal classification, so far as we are aware nobody has challenged the Trinucleacea as a monophyletic group: the convex and pyriform glabella alone may be a sufficient uniting character to support this. There are other autapomorphies: the long and narrow adaxial part of thoracic pleurae; the triangular pygidium with very narrow doublure; the basket-and-lid (Bergström 1973) style of enrolment. Dionididae and Trinucleidae have their own unique fringe structure—but although such structures adequately define the families they do not help with assessing the relationships of the trinucleaceans to other trilobites.

Although Trinucleacea is an accepted, phylogenetically based taxon, there has been little discussion of the relationships of the group to other trilobites. Their inclusion in Ptychopariida in the *Treatise* (Moore 1959) is presumably based on the presence of opisthoparian sutures in the least derived forms (Orometopidae, including Hapalopleuridae). The eventual status of the group as superfamily or suborder does depend on an assessment of its relationships to other major groups. Trinucleacea is one of those groups which apparently appear in the stratigraphic record just below the base of the Tremadoc (Rushton 1982). Clearly, it must have had Cambrian sister taxa but, as in other cases, the Cambrian–Ordovician boundary has been interpreted as a taxonomic one as well.

We present a case here that the Trinucleacea should be classified with the Asaphina. This is based on several lines of evidence: 1, the resemblance of the protaspides of the group to the asaphoid protaspis (see above); 2, the presence of a pre-occipital glabellar tubercle in many trinucleaceans; 3, the identification of stratigraphically intergrading trinucleaceans across the Cambrian–Ordovician boundary; and 4, the identification of a reasonable candidate for the Cambrian sister group which shows the cephalic median suture.

All Ordovician Trinucleacea of which we are aware have the free cheeks fused together ventrally as a single unit—which becomes extensively modified to the lower lamella of those trinucleaceans having fringes. As in other cases discussed above, this fusion is secondary, and it is obviously crucial to an assessment of relationships to discover whether the fused condition resulted from the incorporation of a rostral plate (as in olenids) or from the loss of a median suture (as in nileids). Primitive morphology of Trinucleacea may be exemplified by *Orometopus*. Text-fig. 25 compares cephalic morphology of *Orometopus* with the Upper Cambrian genus *Liostracina*. Öpik (1967, pl. 35, figs. 4 and 5) clearly figured a ventral median suture on the latter, which means, if our contention of a monophyletic origin for this character is correct, that it should be included within Asaphina in our terms. The other resemblances between *Orometopus* and *Liostracina* are compelling and include: transversely inflated glabella; eye size and position; presence of inflated bacculae; and triangular, transverse pygidium. The main differences are all primitive characters for Ptychopariida in *Liostracina*, and hence of no importance in assessing relationships. However, they merit discussion because they may be considered significant by those workers favouring classification on the basis of overall similarity.

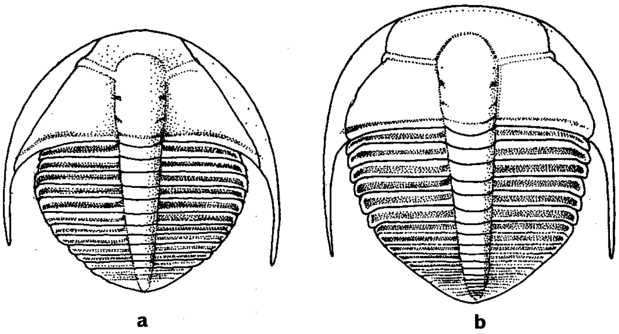


TEXT-FIG. 25. Comparative reconstructions of a primitive trinucleacean (*a*) and the late Middle Cambrian Liostracinidae (*b*), to show similarity apart from retained primitive characters of the latter. *a*, *Orometopus* (Tremadoc; new reconstruction), fused cheeks are indicated by 'broken' doublure. *b*, *Liostracina*, cranidium and cheek of *L. nolens* (after Öpik 1967, pl. 35, figs. 1 and 4), with undoubted median suture, and pygidium of same genus (after Chu 1959, pl. 1, fig. 31). Both ×8 approx.

They are: 1, tapering glabella—this is present in all primitive Asaphina, secondary derivation of forward-expanding glabella within accepted monophyletic groups of Asaphina has been demonstrated for Ceratopygidae (*Ceratopyge*) and Asaphidae (most Asaphinae) above, and there seems no special reason to regard this difference between *Liostracina* and other Trinculeacea as more significant; 2, presence of preglabellar field—again, a preglabellar field is present in Ptychopariida and primitive Asaphina, such as kainellid remopleuridaceans, and this character does not define derived groups; it is connected with 3, natant hypostomal condition—the relatively narrow width of the cephalic doublure indicates that the hypostome was not attached at the doublure in *Liostracina*; this is also a characteristic of primitive Asaphina, and is a retained primitive character from the ptychoparioid state (cf. kainellids, pterocephaliids, and most if not all anomocaraceans).

In their review of Trinucleidae, Hughes *et al.* (1975, p. 541) remarked of the hypostome that 'it appears to have had no sutural union with the inner margin of the lower lamella and it may well have been suspended entirely by the unsclerotized (*sic*) ventral cuticle' which is a description of the natant hypostomal condition. The natant condition may account for the rarity of definite assignments of hypostomes to trinucleids, as is also true of ptychopariids. During enrolment of 'basket-and-lid' (Bergström 1973) type the pygidium is tucked well beneath the inner edge of the fringe (Hughes *et al.* 1975, p. 545) and it would be difficult to imagine how the hypostome could be attached in the usual conterminant fashion at the inner edge of the doublure in a horizontal orientation. However, we have examined specimens of Raphiophoridae in which the hypostome *is* attached to the inner edge of the doublure in the conterminant position but with the hypostome tucked away up inside the frontal lobe of the glabella in a manner analogous to that in certain illaenids. It seems possible that for many Trinucleacea the natant condition was retained into the Ordovician when many of their contemporaneous Asaphina were conterminant or impendent, but that the conterminant condition was acquired by at least some raphiophorids. In any case there is nothing incompatible between the hypostomal attachment mode of *Liostracina* and that of Trinucleacea.

The noticeable bacculae adjacent to the base of the glabella in both *Orometopus* and *Liostracina* are also present in other primitive Asaphina, such as anomocarids, many ceratopygids, and all dikelokephalinids. Niobine asaphids also have bacculae, as do many small asaphid growth stages. Hughes *et al.* (1975) indicated their presence as primitive in the Trinucleidae. They are present in small growth stages of trinucleids and raphiophorids (Whittington 1959*a*; Hughes *et al.* 1975, p. 589) even when lost in the adult. Since they are not present in generalized ptychoparioids (nor apparently in meraspides of this group) it is tempting to assume that their presence is a synapomorphy of higher Asaphina. Their absence in Remopleuridacea and Cyclopygacea would then be considered a secondary loss. However, we are reluctant to be too definite about this, because there are other monophyletic groups outside the Asaphina in which the presence of bacculae is of low phylogenetic significance; for example, bacculae appear in the one genus *Carolinites* in the family Telephinidae, or are present in some species only of the genus *Shumardia.*



TEXT-FIG. 26. Trinucleaceans crossing the Cambrian-Ordovician boundary. *a*, *Jegorovaia* (Upper Cambrian; after Lu 1974, pl. 2). *b*, *Araiopleura* (Tremadoc; after Dean 1970, pl. 1, fig. 11). Both ×8 approx.

Although there is a considerable stratigraphic separation between *Liostracina* and those families usually included in Trinucleacea we do not regard this as evidence for their taxonomic separation. There *are* late Cambrian trilobites which conform to Trinucleacea which have been placed in the separate family Jegorovaiidae. They are not well known. However, Lu (1974) has already synonymized this family with Hapalopleuridae. Text-fig. 26 shows comparative reconstructions of *Jegorovaia* and the early hapalopleurid *A. beothuk* Dean; apart from the more anteriorly directed eye ridges of the former it would be difficult to place these forms in different genera, let alone families. Both have preglabellar fields, like *Liostracina*; both also have the ovoid shape of thorax + pygidium which is typical of Trinucleacea as a whole.

It is difficult to place the Trinucleacea within the classification scheme of the Asaphina as a whole. If we are correct in assigning the group here, its status should be reduced to that of superfamily, compatible with the other groups we have recognized. The preglabellar tubercle would suggest a sister group relationship with Asaphacea + Cyclopygacea. However, if stratigraphic evidence is to be believed, the early members of the group do not have a preglabellar tubercle—but they do have an occipital tubercle. *O. aridos* Bulman and Rushton, 1973 assuredly has a pre-occipital tubercle, while other forms assigned to Hapalopleuridae by Harrington and Leanza (1957) certainly have an occipital tubercle (*Hapalopleura clavata*) or are ambiguous in this regard (*A. reticulata*, their fig. 112.2*c*). *Liostracina* has an occipital tubercle. This evidence could be taken as showing the parallel derivation of the pre-occipital tubercle in what we would call trinucleaceans. The alternative would be to assume monophyletic derivation of the pre-occipital tubercle, thereby removing from the group a number of forms which resemble trinucleaceans in far more characters than the tubercle alone. We prefer the former course. This means that it becomes exceedingly difficult to rank the Trinucleacea on a cladogram, because the remaining characters are either autapomorphies of the group (e.g. pyriform glabella; adaxial extension of thoracic segment; triangular, transverse pygidium) or primitive ptychoparioid characters (natant hypostomal condition in some forms; having genal spines; narrow cephalic doublure, etc.) of no service in determining relationships. The definition of dorsal furrows in the trinucleid and raphiophorid protaspides is primitive compared with their effacement on higher Asaphina, as is the lack of terrace ridges on the known hypostomes of trinucleaceans. Hence the group has to be placed among the less derived Asaphina and probably as an unresolved trichotomy with 'Anomocaracea', itself a paraphyletic group. In any case it is clear that if we wish to include the Trinucleacea within Asaphina, its taxonomic status should be that of superfamily, like the other major groups included, rather than suborder, as at present.

Finally, a brief comment is given on what may seem the rather bold inclusion of Cambrian forms within what is regarded as an 'Ordovician' group. It has become almost axiomatic to treat resemblances between Cambrian trilobites of disparate ages—let alone Cambrian and Ordovician trilobites—as if they were likely to be the product of convergence rather than indicating phylogenetic relationships: 'every student of Cambrian trilobites knows that genera widely separated in time and space, therefore unlikely to be closely related, may appear almost identical' (Rasetti 1972, p. 44). This *assumption* of parallelism quickly becomes self-fulfilling and non-testable, because every occurrence from a different horizon or different 'space' (How are these defined? By distance in kilometres? By inferred palaeogeography? Or by the author's predelictions?) becomes subject *a priori* to different taxonomy, whether or not the morphology of the trilobites might indicate that they are 'closely related'. In our analysis of Asaphina as a whole, and the Trinucleina discussed here in particular, we prefer the opposing view that definable derived characters should form the basis of classification. If what we consider as characters indicating monophyly are regarded by another author as capable of polyphyletic development, then the burden of proof is upon the critic to demonstrate their independent origin. Hence for the Trinucleacea *Liostracina* and the rest of the Trincleacea are linked by glabellar, sutural, and pygidial characters, and differ only in retained primitive characters of the former, which are irrelevant other than for inferring ultimate 'ptychoparioid' ancestry. The median suture of the primitive form, and protaspis characters of the later ones, indicate to us that the group belongs within Asaphina. While we cannot claim that the list of uniting characters is a long one, they can be clearly stated, and our hypothesis of relationships can be disproved by demonstrating that the characters we cite are polyphyletically derived. This seems to us to be an advance on the present classification, in which Trinucleacea are unrelated to any other group, other than vaguely placed as a subgroup of Ptychopariida for unspecified reasons.

DISCUSSION OF PREVIOUS CLASSIFICATIONS IN RELATION TO THAT PROPOSED HERE

The classification given here (summary in Table 4) differs from that used in the *Treatise* (Moore 1959) and from the newer classification of Bergström (1973). The reasons for our view of Asaphina have been given in detail above, but Bergström's classification in particular deserves consideration so that our reasons for differing from it can be explicitly listed.

1. Bergström placed Ceratopygidae and Asaphidae in two different suborders of his Order Redlichiida. We consider them certainly closely related, and favour the view that they are sister groups in Asaphacea. It is difficult to see any critical characters in Bergström's diagnosis which might serve as a basis to falsify our classification. Most of the characters mentioned in his diagnosis of Ceratopygacea either apply also to his diagnosis of Asaphacea (and of Asaphina) or do not apply to the families under consideration. Certainly there are no synapomorphies mentioned linking asaphids and ceratopygids to their respective supposed superfamilies which would compare with the distinctive glabellar structure that is one of the stronger pieces of evidence for their alliance in our classification.

TABLE 4. Summary of classification of Asaphina as reviewed here, to family level.

- Suborder ASAPHINA Salter, 1864 emend.
  - Superfamily ASAPHACEA Burmeister, 1843
    - Family ASAPHIDAE Burmeister, 1843
    - Family CERATOPYGIDAE Linnarsson, 1869 [includes MACROPYGIDAE Kobayashi, 1953]
    - *Hedinaspis*, *Asiocephalus* incertae familiae
  - Superfamily CYCLOPYGACEA Raymond, 1925
    - Family CYCLOPYGIDAE Raymond, 1925
    - Family NILEIDAE Angelin, 1854
    - Family TAIHUNGSHANIIDAE Sun, 1931
  - Superfamily REMOPLEURIDACEA Hawle and Corda, 1847
    - Family REMOPLEURIDIDAE Hawle and Corda, 1847
    - Family HUNGAIIDAE Raymond, 1924
    - Family BOHEMILLIDAE Barrande, 1872
    - Family OPIPEUTERIDAE Fortey, 1974
  - Superfamily DIKELOCEPHALACEA Miller, 1889 emend. Ludvigsen and Westrop, 1983
    - Family DIKELOCEPHALIDAE Miller, 1889
    - Family SAUKIIDAE Ulrich and Resser, 1930
    - Family PTYCHASPIDIDAE Raymond, 1924 [includes EUREKIIDAE Hupé, 1953]
  - Superfamily TRINUCLEACEA Hawle and Corda, 1847, emend.
    - Family TRINUCLEIDAE Hawle and Corda, 1847
    - Family RAPHIOPHORIDAE Angelin, 1854 [includes ENDYMIONIIDAE Raymond, 1924]
    - Family OROMETOPIDAE Hupé, 1955 (includes MYINDIDAE Hupé, 1955 and HAPALOPLEURIDAE Harrington and Leanza, 1957)
    - Family DIONIDIDAE Gürich, 1907
    - Family ALSATASPIDIDAE Turner, 1940
    - Family LIOSTRACINIDAE Raymond, 1937 (?part only)
  - Superfamily ANOMOCARACEA Poulsen, 1927 (paraphyletic)
    - Family ANOMOCARIDAE Poulsen, 1927
    - Family DIKELOKEPHALINIDAE Kobayashi, 1936
    - Family PTEROCEPHALIIDAE Kobayashi, 1935 [probably includes HOUSIIDAE]
    - Family AURITAMIIDAE Öpik, 1967
    - ? Family IDAHOIIDAE Lochman, 1956
  - Incertae superfamiliae
    - ISOCOLIDAE Angelin, 1854
    - CATILLICEPHALIDAE Raymond, 1938 (part only)

2. Although Bergström placed Asaphacea and Remopleuridacea within Asaphina, and included in the former some of the families considered to belong in Asaphina here, he also included Olenacea in the same suborder. We disagree with this placement of the Olenacea for the following reasons:

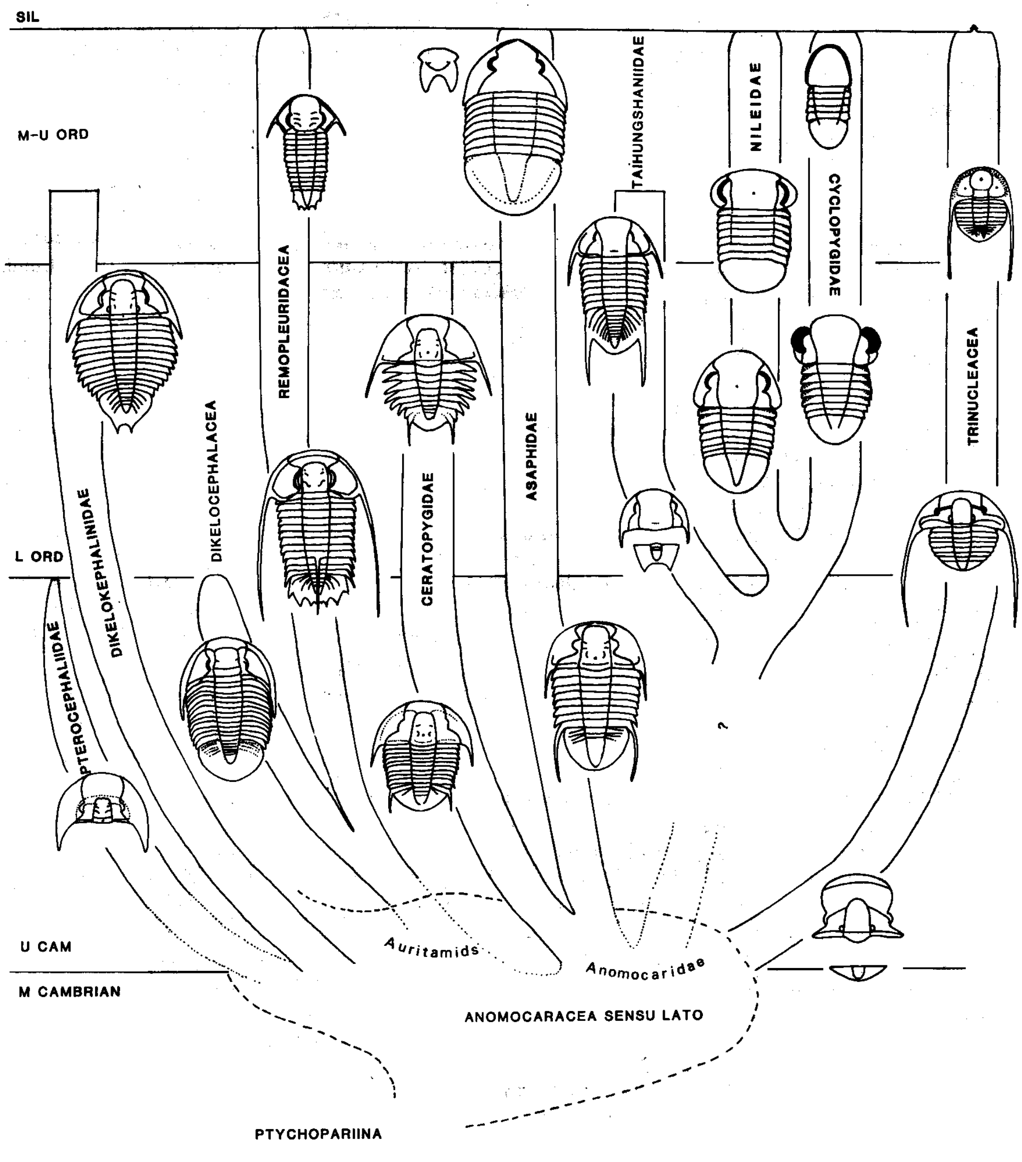
1, although most olenids have the free cheeks fused as a single piece—i.e. there is no evidence for either median suture or rostral plate—it is clear that the earliest olenids of the genus *Olenus* (*O. wahlenbergi*, see Rushton 1983) have a rostral plate and not a median suture; this allies the Olenidae with Ptychopariina and militates against an origin in Asaphina. 2, the diagnostic olenacean characters listed by Bergström are: *a*, 'hypostome probably disconnected from doublure'—this is probably a primitive ptychoparioid character, and as such is not diagnostic; *b*, 'genal spines needle-like'—this may be an autapomorphy for Olenidae, but suggests no connection with any Asaphina. 3, olenids all maintain a narrow cephalic doublure medially beneath the cranidial border, even in forms with a relatively large pygidium. This is fundamentally different from Asaphina, in which a wide cephalic doublure is present medially in all but a few of the most primitive forms, and is invariable in those species with a large pygidium.

EVOLUTIONARY HISTORY OF ASAPHINA

We can briefly summarize the account of character distribution and phylogeny in the tree shown as text-fig. 27. No attempt is made to do more than sketch the varied stratigraphically based histories of within-group evolution. We have included the Trinucleacea in this diagram. The stratigraphic record of most groups is reasonably complete, the most important 'break' being the early history of Cyclopygacea. This break may be filled when the relationships of Catillicephalidae are resolved. The origin of the group was presumably in the Middle Cambrian. The tree shows the reason for the problems with defining 'Anomocaracea' *sensu lato*, which forms a root group from which the various derived taxa originated. The Dikelokephalinidae alone of this plexus survived beyond the Cambrian. The Cambrian–Ordovician boundary closely coincides with the end of the dikelocephalacean clade, but otherwise the influence of this horizon on the group does not seem to have been profound. This is reflected by the persistence of individual genera (e.g. *Niobella*) through sections spanning the boundary. However, three of the surviving clades, Ceratopygidae, Dikelokephalinidae, and Taihungshaniidae, did not survive beyond the Middle Ordovician. Asaphidae, Nileidae, Cyclopygidae, Remopleurididae, and Trinucleacea continued as diverse elements of Ordovician faunas until the end of the System. During this long Cambrian–Ordovician interval Asaphina diversified into many habitats. Some taxa are particularly characteristic of cratonic sedimentary environments (some Asaphidae and Dikelokephalinidae, and perhaps most Dikelocephalacea). Pelagic habits probably arose on four occasions within the group (Bohemillidae with remopleuridid ancestry, Cyclopygidae, *Parabarrandia*, and *Girvanopyge*). Of these, the cyclopygids were mesopelagic and are only found in relatively exterior (off craton) facies. At least some asaphids and ceratopygids, and some aberrant small-eyed nileids, were benthic forms inhabiting deep-water sites. Trinucleids were slow moving benthos occupying various water depths, apparently on muddy substrates. Other asaphines are familiar components of limestone biofacies. Asaphina were not, in general, typical of reef-like habitats (illaenid-cheirurid trilobite biofacies), although some raphiophorids (*Lonchodomas*), asaphids (*Anataphrus*), and rare nileids (*Nileus*) have been reported from faunas of this kind. We may conclude that the group was diverse and successful within almost the whole range of marine habitats adopted by the trilobites as a whole.

Many stratigraphic case studies show that the Trinucleacea in particular evolved rapidly (Hughes *et al.* 1975), as did Asaphidae. The same is not true of Cyclopygidae, which have generic ranges extending from Arenig to Ashgill, and extraordinarily conservative morphology in a range of genera after what was presumably a rapid late Tremadoc to early Arenig radiation (Fortey and Owens 1987). Regardless of such differences, virtually the entire Asaphina was extinguished at the Ordovician–Silurian boundary. Available evidence suggests that a range of genera of the various families persisted into the last, and very short, Ordovician Stage, the Hirnantian, and so the extinction event has to be considered of some magnitude. The only survivor is the raphiophorid *Raphiophorus*, which persisted into the later Silurian. The Asaphina (particularly if we include Trinucleacea and isocolids) is the group much the most affected by the end-Ordovician event; other groups at family level which did not survive include agnostids, dimeropygids, together with the last deep-shelf olenid, and the pelagic telephinids.

Why the Asaphina proved so vulnerable to the end Ordovician extinction is an interesting question. Clearly it was not because they had become too specialized in their habitat requirements, and vulnerable to major perturbations, because they had as wide a range of adaptations as any other trilobite group. Although some of the non-asaphine genera which survived the event were reef dwellers, others were not, and the scarcity of Asaphina adapted to this habitat does not seem an adequate explanation. Because members of the group were capable of both rapid evolution in the manner of trinucleids, or exceptional stasis, as in cyclopygids, it is difficult to invoke any explanation requiring differential response to rapid environmental change. The group were also distributed world-wide, and so we cannot account for their disappearance as coinciding with the removal of some palaeobiogeographic 'province'. We are left with the fact that the very different groups of Asaphina which survived to the end of the Ordovician all had the asaphoid larva, which we have argued above



TEXT-FIG. 27. Summary in the form of an evolutionary tree of the Asaphina, as understood in this work, with sketches of some primitive and advanced examples known from stratigraphic evidence within given clades. The Anomocaracea is here shown to include the plexus of primitive forms, and is not a natural group. Only one trinucleacean genus, *Raphiophorus*, continues beyond the end of the Ordovician. Reconstructions of exoskeletons are only very approximately to scale.

was well-adapted for planktic—possibly epiplanktic—habits. Could it be that the extinction of the group was related to a change in oceanic circulation which rendered this larval type particularly vulnerable? A widespread anoxic event has been quoted at the very end of the Ordovician on other evidence, and the planktic graptolites were also seriously affected at the end of the Ordovician. Although this is speculation, it is the only explanation we can offer as to why this great group of trilobites declined suddenly after 100 million years of successful history.

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