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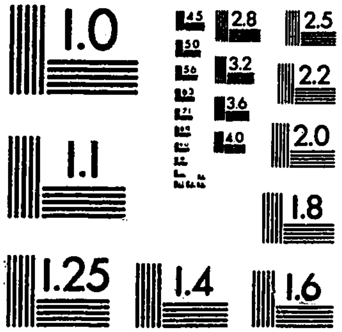

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Comparative ontogeny and phylogenetic studies of the Lower Ordovician silicified trilobites from southern Idaho, U.S.A.

by

Dong-Chan Lee ©

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of Master
of Science

Department of Earth and Atmospheric Sciences

Edmonton, Alberta

Fall 1995

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Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Comparative ontogeny and phylogenetic studies of the Lower Ordovician silicified trilobites from southern Idaho, U.S.A.** submitted by Dong-Chan Lee in partial fulfillment of the requirements for the degree of Master of Science.

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DATE: 15/August/1995

ABSTRACT

Information from cheirurine and hystricurid protaspides from the Garden City Formation (Lower Ordovician), southern Idaho, permits detailed comparative ontogenetic studies and phylogenetic analysis of these taxa.

The posteriormost axial lobe of trilobite larvae is named Lp, to emphasize its role in the proliferation of axial lobes and the homologous relationship of the Lp to the axial lobes differentiated later.

Comparison of ontogenies of *Tesselacauda depressa*, *Rossaspis pliomeris*, *Protopliomerella contracta*, and *Kawina sexapugia* with those of other cheirurine families demonstrates that there were two separate lineages of the Cheirurina: Cheiruridae, and Protopliomeropinae + Encrinuridae, the monophyly of which is defined by the presence of circumocular fixigenal tubercles and a circular L4 in protaspides, and four holaspid pygidial rib pairs.

The argument that the whole life cycle should be considered in phylogenetic analysis is supported, based on the ontogenetic transformation character concept and the 'total evidence principle'. The high reliability of the ontogenetic transformation character set is manifested by comparisons of basic tree statistics under various topological constraints, which are a possible phylogenetic hypothesis to be tested by actual character evidence. The 'character combination approach' is desirable to ontogenetic data and the character set based

on that approach is as reliable as the ontogenetic transformation character set.

Comparison of larval morphologies of Hystricuridae, other Ordovician and later Proetida, and Cambrian Ptychopariida suggests that the Hystricuridae is the earliest (mainly Tremadocian) family of the Proetida, not a Lower Ordovician member of the Ptychopariida. The existence of two separate lineages within the Hystricuridae is discovered, on the basis of two distinct protaspid morphotypes. Larvae of the Proetida including the Hystricuridae have a fusiform glabella with a distinct preglabellar furrow as the synapomorphy.

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CHAPTER I

INTRODUCTION

The trilobite orders Phacopida and Proetida have been considered to have their origin among the Cambrian Ptychopariida (Moore, 1959; Fortey, 1990). However, their detailed phylogenetic relationships to particular ptychopariids are still unknown. The origin of the Proetida to particular groups of the Ptychopariida (i.e. Solenopleuridae) can be hypothesized on the basis of their overall similarities in adult morphology. In contrast, adult features of the Phacopida are more disparate from those of Cambrian Ptychopariida, such that their relationships to subgroups in that order are less certain. One way of solving these problems is to gather and analyse data in early, Tremadocian, trilobites. Trilobites with complete growth series are particularly valuable because, apart from providing a greater amount of morphologic information, they provide data that may be used to test the role of ontogeny in the evolutionary history of these taxa. The silicified trilobites from the Garden City Formation are of primary importance to this study, since they are among the earliest members of the Phacopida or the Proetida which include well preserved early growth stages, including the larvae.

Besides the study specific to trilobite phylogeny, the information gathered gives the author an opportunity to explore how to treat ontogenetic data in cladistic analyses. Ontogeny may be viewed as a dynamic sequence (Alberch, 1985) or a catalog of characters in a static viewpoint (Mabee, 1989). Of the two, the latter is the traditional way to utilize ontogenetic information in a phylogenetic analysis. The former viewpoint has been incorporated into the context of heterochrony (Gould, 1977). However, it has rarely been used to recover the phylogenetic relationships of organisms. The growth series of trilobites from the Garden City Formation provide ontogenetic information by which the author is able to exhibit how to properly incorporate the dynamic aspect of ontogeny into the phylogenetic analysis.

Previous Works -- Ross (1951a, b, 1953) described silicified Lower Ordovician pliomerids and hystricurids from the Garden City Formation (Tremadocian and early Arenigian age) in the Great Basin. In addition, Hintze's (1952) and other colleagues' (Terrell, 1973; Demeter, 1973; Young, 1973) works on the trilobite faunas from the Fillmore Limestone in central Utah, stratigraphically equivalent to the Garden City Formation, supplemented the data of the pliomerids and hystricurids. Some of these works (e.g., Ross, 1951b; Demeter, 1973) attempted to reconstruct the evolutionary history of the trilobites, based on traditional methods in which adult morphologic transformations are used to order or organize trilobites into anagenetic lineages, or even to reveal divisions into more than one clade. The taxonomy of these trilobites, established in the Treatise (Moore, 1959), has been accepted in several other descriptive regional studies of these trilobite groups, such as those of Kobayashi (1934, 1955) and Stitt (1983). A few taxonomic revisions, e.g. the reassignment of Tesselacauda to the Cheiruridae (Whittington, 1961), were made.

One reason for such a paucity of detailed taxonomic revisions and phylogenetic studies lies in the fact that trilobite species described from the Garden City Formation have rarely been reported from the contemporaneous biostratigraphic unit sof any other continents. Indeed, only Protopliomerops, has been reported from Asia (Kobayashi, 1934), and only Hystricurus, has been described from other continents. Another reason resides in the lack of additional data, such as the description of larvae; protaspides of only two pliomerid trilobites (Rossaspis superciliosa and Pseudocybele nasuta) were described by Ross (1951b, 1953), while no hystricurid protaspides have previously been reported.

Materials -- The materials studied in this work occur in the Garden City Formation, exposed on the east and west sides of Hillyard Canyon, southern Idaho, U.S.A. (Figure I-1); these are Ross' (1951b)

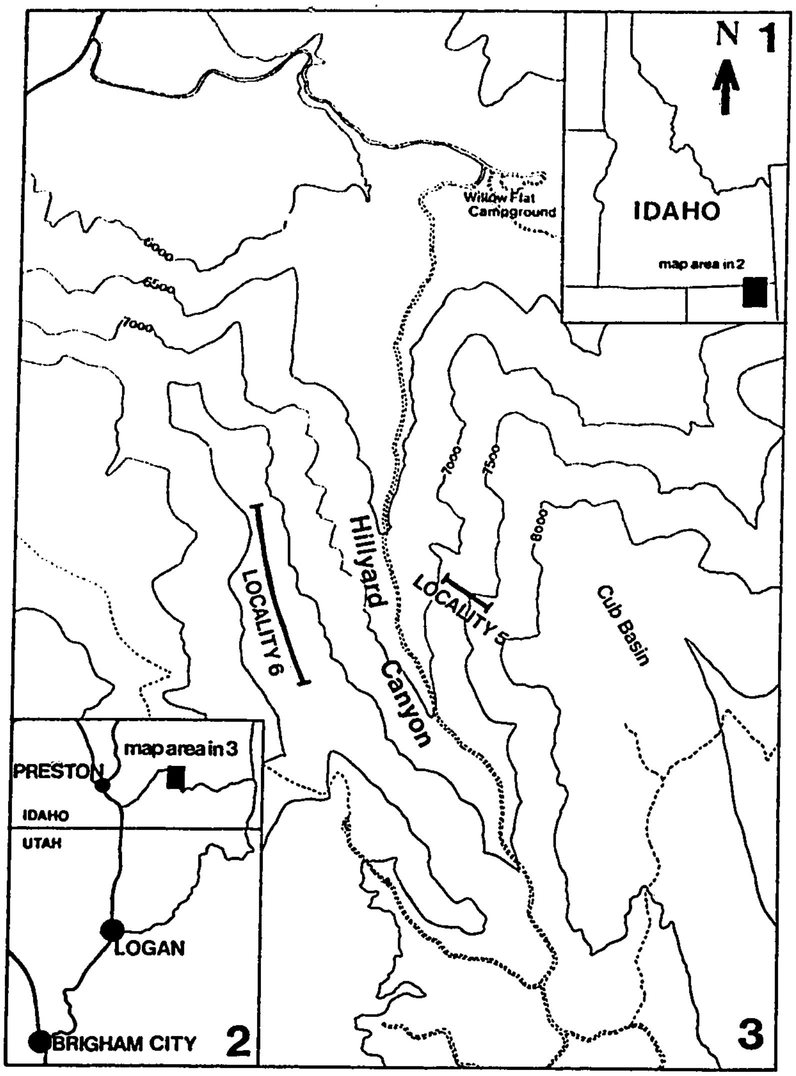

FIGURE I-1. Locality map of two sections (Ross' (1951b) Locality 5 and 6), from which the Lower Ordovician trilobites described in this work were obtained. Contours are in feet.

'Locality 5' and 'Locality 6'. The sampling horizons range from Zone C (Paraplethopeltis Zone) to Zone G (Protopliomerella contracta Zone) (Ross, 1951b; Hintze, 1973). Limestone samples were collected from 8 horizons in Locality 5 and 18 horizons in Locality 6 (Figure I-2). The collected limestone blocks (less than 5 kg) were dissolved in 10 % hydrochrolic acid and the silicified trilobite specimens were picked from the residues. Most specimens (unless, particularly noted) were photographed using back-scattered electrons on a scanning electron microscope. Specimens figured in Chapter III and V are housed in the University of Alberta Paleontological Type Collections and labeled with UA numbers.

Sedimentary Environment of the Garden City Formation -- The Garden City Formation is overlain by the Swan Peak quatzite and underlain by the St. Charles Formation (mainly composed of dolomite). The lithology of the Garden City Formation is mainly crystalline limestone, or lime mudstone. The outcrop is thinly-bedded and light-colored. The conspicuous sedimentary structures are ripple marks on some bedding planes and rare intraformational conglomerate, which are more predominant in the lower part of the formation. Towards the upper part of the formation, the chert content remarkably increases. From these lithological and structural aspects, it was suggested that the formation was deposited on a shallow carbonate shelf (Ross, 1951b) lacking reefs; the shallow depth can be inferred by ripple marks and intraformational conglomerates, which are considered to have resulted from storm activity. Besides trilobites, which mainly occur in the lower part of the formation, brachiopods, sponges, and graptolites are found in the outcrops or the silicified residues. the fauna is comparatively deep water in aspect, implying a moderate depth for the sea floor, near the storm wave base and below fair weather wave base.

Objectives -- The objective of this thesis were to use early ontogenetic data of early Ordovician trilobites to improve our understanding of the phylogenetic relationships of Ordovician and

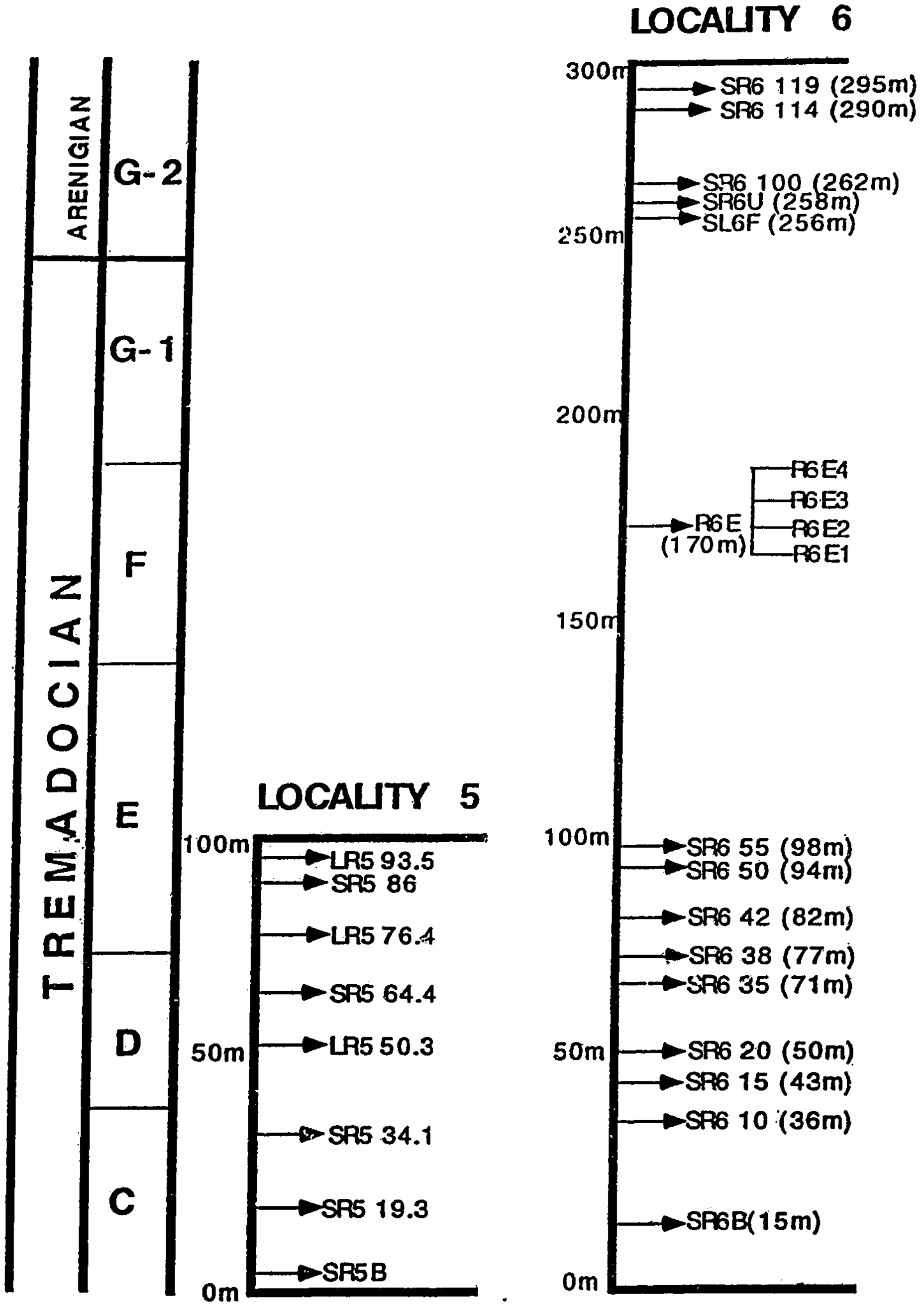

FIGURE I-2. Correlation of two sampling horizons based on faunal occurrence and North America Trilobite Zonal Scheme (Hintze, 1973, fig. 1). Numbers of each sampling horizon indicates its location in the Garden City Formation.

younger trilobites.

The studies, collected herein, re-examine the Garden City Formation trilobites, and describe their complete ontogenies, where available. Comparison of the growth stages of phacopoid trilobites permits us to establish the homology of some morphologic features (Chapter II). The significance of the pliomerid and hystricurid trilobites in these faunas is that they are among the stratigraphically earliest (and phylogenetically most primitive) members of the Phacopida and Proetida. All available ontogenetic data are used to generate plausible phylogenetic hypotheses for early members of the Cheirurina (Chapter III). In addition, a cladistic treatment of ontogenetic data from Ordovician phacopid trilobites, using the 'total evidence principle', is the basis for a new hypothesis of phylogenetic relationships within the Phacopida (Chapter IV). The phylogenetic significance of hystricurid larvae within the Proetida is evaluated in Chapter V.

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CHAPTER II

TERMINOLOGY OF GLABELLAR LOBES IN TRILOBITE LARVAE

Glabellar lobes of holaspid cranidia of trilobites have been conventionally designated L1, L2, etc. forward from the occipital ring (L0). Most trilobites have four glabellar lobes (L1 to L4) and one occipital ring (L0) (Figure II-1). The description of morphological structures with an identical term implies that are the structures are homologous throughout an organism's life cycle and across organisms; the classical homology definition (Patterson, 1982). As well, the numerical notation for glabellar lobes should be homologous throughout a trilobite's ontogeny and across different trilobite taxa. However, this conventional system only applies to and provides homology information on the ontogenetic stages which have transversely articulated somites such as the pygidium and/or thoracic segment(s), since L0 represents the occipital ring as the posteriormost axial lobe in the articulated cephalic region (Figure II-1). Such restricted application is realized when describing a phacopid protaspis with four axial lobes (stage 1 in Figure II-1); the system cannot be strictly applied to describe axial lobes of ontogenetic stages occurring before transverse demarcation at the back of the head. However, use of this system can be extended to the earlier ontogenetic stages with slight modification.

In the previous literatures, the axial lobes of those protaspides without a protopygidium are referred to as protoglabellar or glabellar lobes for the anterior ones and as occipital ring (or lobe) for the posteriormost one. The anterior three lobes seem to be homologous to the (lateral) glabellar lobes of later ontogenetic stages (Figure II-2). In contrast, the posteriormost lobe of the protaspid axis is not always strictly homologous to the occipital ring of later ontogenetic stages, because it may contain the potential to bud off future glabellar lobes and protopygidial axial ring(s), in addition to the occipital ring. These statements of homology are based on the observation that 1) the

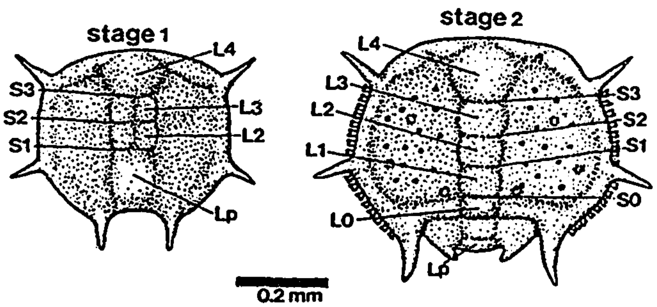

FIGURE II-1. Two protaspid stages of *Rossaspis pliomeris* Demeter, 1973. The glabellar lobes (Lp to L4) and furrows (S0 to S3) are designated following the system proposed herein.

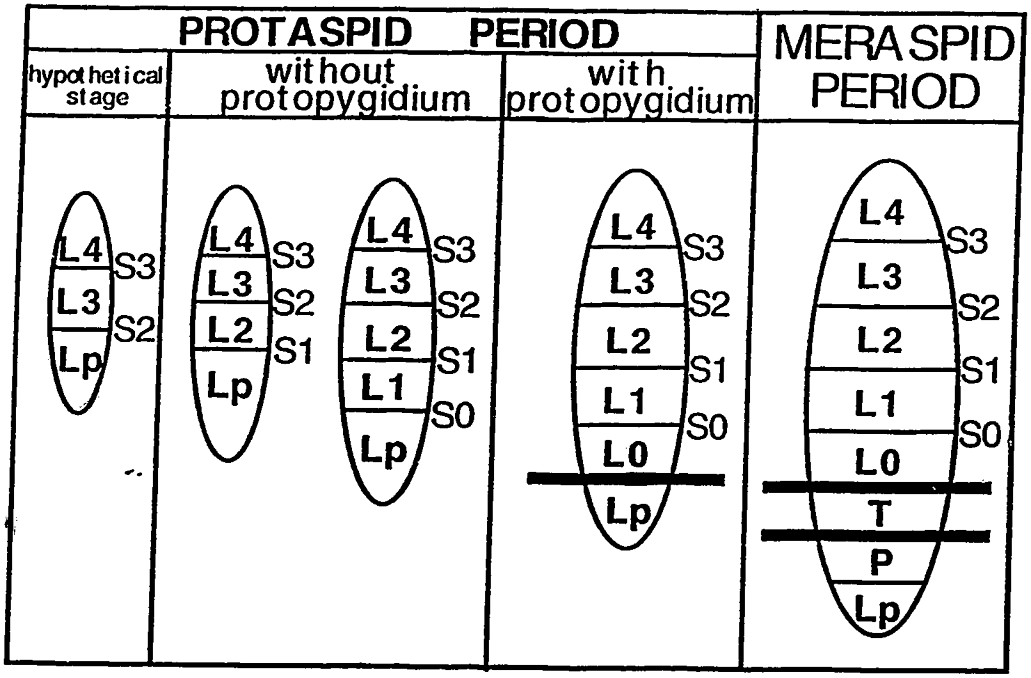

FIGURE II-2. Modified designation system of protoglabellar or glabellar and axial lobes, and glabellar furrows based on homologous relationships. Each ellipsoid represents the axial region of a trilobite. A thick, solid line indicates a boundary between two somites along which transverse articulation takes place (or will take place in the protaspis). 'T' and 'P' refer to a thoracic segment and a pygidial axial ring, respectively.

anterior three lobes are differentiated first and thus, are usually observable in the earliest phacopid protaspides, and, later in ontogeny, the lobes do not further differentiate into additional lobes, and 2) the proliferation of trilobite axial lobes takes place in the posteriormost lobe (e.g., transitory pygidia of Acanthopyge (Mephiarges) bifida (the Lichida), Chatterton, 1971; Shumardia pusilla, Stubblefield, 1926). Thus, protaspid axial lobes in front of the posteriormost lobe are designated L2, L3, and L4, from the anterior, following the conventional designation system. In contrast, the posteriormost lobe cannot be referred to as L0, since it is not strictly homologous to the occipital ring. Herein, we designate the lobe as 'Lp' (Figure II-2), implying that the lobe is topologically located most posteriorly in the axis and has the potential to proliferate additional lobes. At the beginning of the holaspid period, 'Lp' ceases to function in proliferation and is referred to as the 'pygidial terminal piece'. This modified designation system with 'Lp' carries homology information for analysis of trilobite axial lobes based on their topological (Rieppel, 1993) and functional similarity throughout ontogeny and across trilobite taxa. A comparable example of 'Lp' is the proliferation zone in front of the telson in short- and semi-long germ embryos and post-hatch juveniles of insects and some other arthropods (e.g., a proturan of Chapman, 1976, fig. 167; Patel, 1994).

For example, in Physemataspis insularis (Edgecomb, et al., 1988, fig. 2), the conventional system using L0 to L4 (or 1L to 4L) applies throughout its ontogeny, since all (proto-) glabellar lobes and the occipital ring are distinct from stage 1. On the other hand, this conventional system does not apply to those trilobites having early protaspid instars with fewer axial lobes than occur in later ontogenetic stages (e.g., stage 1 of Rossaspis pliomeris (Figure II-1) and Flexicalymene senaria (Chatterton, et al., 1990)). During ontogeny of R. pliomeris, the number of axial lobes increases from 4 to 7 during the protaspid period; the posteriormost axial lobe ('Lp') has differentiated into the posteriormost glabellar lobe (L0), an occipital ring and two protopygidial axial rings by stage 2 (Figure II-1). Following the conventional system, the posteriormost axial lobe of stage 1 protaspides would be designated as L0 (from the posterior) or L1 (from the anterior). Neither implies that further differentiation of the lobe will occur, nor does it provide evidence for homology of the lobe ('Lp') to lobes differentiated later. With the modified system, the posteriormost lobe is designated 'Lp' and the three lobes anterior to it as L2, L3 and L4, indicating homology to meraspid and holaspid glabellar lobes. For stage 2 protaspides of R. pliomeris, the four protoglabellar lobes are referred to as L1 to L4, the occipital ring as L0, and the posteriormost protopygidial axial ring as 'Lp' (Figure II-1). This system is also suitable for a trilobite having five axial lobes prior to the appearance of the protopygidium (Figure II-2), where the lobes are designated 'Lp', L1, L2, L3, and L4. This modified designation system can also be applied to hypothetical (undiscovered) protaspides with three axial lobes. In these, two anterior lobes are designated as L3 and L4 and the posteriormost lobe as 'Lp'; the furrows are designated S2 and S3 (Figure II-2). The above system also suggests that (proto-) glabellar furrows are also homologous from front to back. Each pair of glabellar furrows, designated S1, S2, and S3, seem to be homologous throughout the ontogeny of trilobite; in contrast, occipital furrow (S0) can be claimed to be homologous only after L1 is differentiated (Figure 2).

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CHAPTER III

ONTOGENIES OF THREE CHEIRURINE TRILOBITES FROM THE LOWER ORDOVICIAN GARDEN CITY FORMATION, AND THEIR PHYLOGENETIC IMPLICATIONS

INTRODUCTION

Early growth stages as well as adults of trilobites have been used for phylogenetic inferences, since no ontogenetic stages are immune to evolutionary changes (Danser, 1950; Kluge, 1988). In the past, the evolutionary (not strictly phylogenetic) relationships between different trilobite groups were largely constructed upon the basis of comparisons of adult morphologic features. These adult morphologies are still the most widely available basis for evolutionary studies (e.g., Ramsköld and Werdelin, 1991). Recently, several attempts to infer the phylogenetic relationships of trilobites using early growth stages, in particular, protaspides have been made (e.g., Edgecombe et al., 1988 - Encrinuridae; Chatterton et al., 1990 - Calymenina), as the information on early growth stages increases. Two assumptions, mainly based on Von Baer's third and fourth laws (Eldredge and Cracraft, 1980, p. 59; Rieppel, 1990, p. 181) are required to validate this phylogenetic approach: monophyletic groups of trilobites at the family or at least subordinal level share similar larvae (Chatterton and Speyer, 1995); morphologies of a trilobite individual increasingly diverge through ontogeny and thus, larval similarities are able to reflect proximity of common ancestry (Edgecombe et al., 1988). Behind these assumptions, it was postulated that there exists, to some degree, a disparity between phylogenetic relationships indicated by the different ontogenetic stages. It is not uncommon that previous classifications, based on adult materials, are frequently revised using characters based on larval morphologies (e.g., paraphyly of the Cybelinae, Edgecombe et al., 1988; supposed paraphyly of the Cheirurina, Chatterton et al., 1990). In this respect, Chatterton and

Speyer (1995) noted that there seems to be some decoupling between larval evolution and the evolution apparent in more mature stages. This may be especially true when the larvae are separated from later stages by a radical metamorphosis (e.g., Asaphida, Fortey and Chatterton, 1988) and morphologies across the metamorphosis display a great amount of variation. Thus, such a decoupling might cause incongruence between phylogenetic results solely based on morphologic features of either larvae or adults. It is important to note, however, that all growth stages share a common evolutionary history, and as a general rule, the characters of all growth stages should help us to discuss this history.

Most previous analyses used one part of the ontogenetic data to infer phylogenetic relationships and the other portion to test the relationships; for instance, holaspid synapomorphies were employed to support larval synapomorphies by Chatterton et al. (1990). In contrast, the simultaneous analysis of all available ontogenetic data based on 'total evidence principle' (Kluge, 1989; Chippindale and Wiens, 1994) is likely to allow us to resolve the disagreement between phylogenetic results based on only one portion of the whole ontogenetic data and/or thus, produce a more plausible hypothesis of relationship. This simultaneous analysis seems more applicable to the trilobites which undergo less morphologic change (e.g. trilobites with all protaspides being 'adult-like', Speyer and Chatterton, 1989) than others showing a radical metamorphosis. This radical metamorphosis may be associated with a radically different life mode change, such as from planktonic to benthic. Different parts of life cycle of the trilobites lived in different environments and came under selective pressure at different times in the evolutionary history of the trilobites. This would have led to a form of 'decoupled' evolution.

This study examines protaspides and holaspides of several subfamilies of the Cheiruridae, the Pliomeridae and the Encrinuridae from Lower and Middle Ordovician strata. The choice of taxa used here for comparison is based on the necessity for their ontogenies to be well described and to find the earliest representatives of those subfamilies. Comparisons between these trilobites are based on topological similarities (Rieppel, 1993) at comparable ontogenetic stages; the structures that occupy similar positions in the trilobite body are considered comparable or homologous ('primary homology', de Pinna, 1991). A trilobite's life cycle is traditionally divided into three comparable (homologous) periods; protaspid, meraspid and holaspid periods (Beecher, 1895; Whittington, in Harrington et al., 1959; Speyer and Chatterton, 1989). The boundary between the adjacent periods corresponds to such developmental events as calcification, segmentation of tergite and completion of adult thorax (Speyer and Chatterton, 1989, fig. 2). These three periods are considered as comparable across different trilobite taxa, since they are consistently defined by at least one character. In general, the meraspid morphologies are not considered as being suitable for comparison, since the morphologies are so variable during that period that it is not feasible to determine the meraspid states of a certain morphologic feature. In this work, the protaspid period of the phacopid trilobites is subdivided into two separate intervals, designated 'Pa' and 'Pb', prior to and after the appearance of protopygidium (see terminology). Thus, for the comparisons in this work, three comparable ontogenetic intervals, 'Pa', 'Pb' and holaspid period were chosen.

Stratigraphic distributions of the studied cheirurid and pliomerid trilobites are shown in Figure III-1. Additional information on the stratigraphic ranges of these taxa is provided by Ross (1951a, b, 1953), Hintze (1952), Demeter (1973), Terell (1973), and Young (1973); some species are described from the Fillmore Limestone, which is the same age as the Garden City Formation and exposed in the Ibex Area, Utah.

TERMINOLOGY

Palpebro-ocular ridge -- Originally this term was coined by Ross (1951b, p. 132) to describe a combined structure of ocular ridge and palpebral lobe in the holaspid cranidium of pliomerid trilobites. In most holaspid pliomerids, the ridge is clearly delimited by anterior and posterior palpebro-ocular ridge furrows. This term appears to be

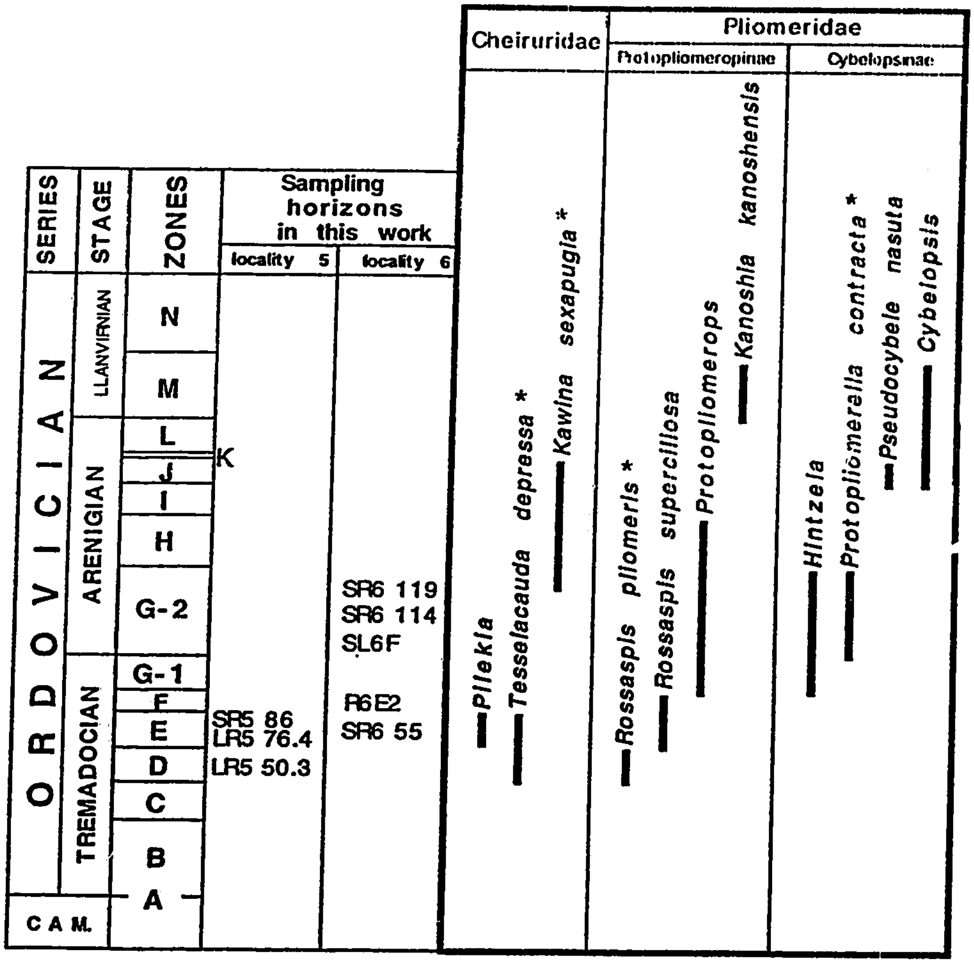

FIGURE III-1. Stratigraphic distribution of the cheirurid and pliomerid species described from the Lower Ordovician Garden City Formation in southern Idaho and equivalent Fillmore Limestone in central Utah. The relative thickness of the trilobite zones is after Hintze (1973, text-fig. 1). Species with an asterisk (*) are described and illustrated in this study.

valid for description of pliomerid protaspides, because most pliomerid trilobites have a pair of distinctly-delineated ridges extending from the abaxial side of the palpebral lobe to the axial furrow throughout their development. In the earliest protaspides of pliomerids, this ridge is not clearly differentiated from the anterior border forming a fused rim, and differentiation takes place in later protaspid stages. The development of pliomerid trilobites demonstrates homologous relationships between the holaspid palpebro-ocular ridge and the undifferentiated palpebral lobe and eye ridge, so the use of the term 'palpebro-ocular ridge' is extended into the protaspides.

'Pa' and 'Pb' -- In this work, the protaspid period of phacopide trilobites is divided into two intervals, based on whether or not protopygidium is differentiated. The earlier one, prior to the appearance of a protopygidium, is designated 'Pa'; the later one, after the appearance of a protopygidium, designated 'Pb'. 'Pa' or 'Pb' is likely to have one or more instars, separated by moulting; for example, two instars are recognized in 'Pb' of Protopliomerella contracta. In contrast, some trilobites have no instars in one of the intervals; for instance, Sphaerexochus (Kolorevium) arenosus has no instars in 'Pb' (Chatterton, 1980) and Physemataspis insularis has no instars in 'Pa' (Edgecombe et al., 1988). The absence of instars in 'Pa' or 'Pb' means that some developmental events (Speyer and Chatterton, 1989, fig. 2) might have taken place simultaneously. In development of S. (K.) arenosus, the tergite of protocranidium and protopygidium is segmented at the same time as the protopygidium appears, while no instar in 'Pb' of P. insularis indicates that the protopygidium appears as soon as the larva is calcified. The usefulness and validity of the appearance of a protopygidium as an additional developmental event in phacopoid ontogeny are justified by several morphological aspects: 1) the appearance of a protopygidium is readily recognizable in phacopid protaspides, since the protopygidium of all phacopid protaspides has distinct marginal spine pair(s); 2) the furrow to delimit the posterior margin of the protocranidium is so distinctively impressed that the event may indicate the first transverse segmentation of the whole trilobite body; 3) across the appearance of a protopygidium, several morphologic features such as the shape of protoglabella, the position of midfixigenal spine pair changes, and the number of protoglabellar lobes transform; in some trilobites, life habit may change from planktonic to benthic across the event. This event may not be as easy to recognize in other trilobite taxa, such as asaphid protaspides, where the furrow to demarcate the posterior margin of the head is not as fully developed as in phacopid protaspides, even though the region behind the head, for a future tail portion, is apparently developed (Chatterton, 1980, fig. 3).

Designation system of the axial and protoglabellar lobes -- The glabellar lobes and glabellar furrows are designated following the modified system proposed in Chapter II. In the protaspides with four axial lobes, protoglabellar lobes are denoted L4 to L2 (from the anterior), the posteriormost lobe is designated as 'Lp', and glabellar furrows are designated S3 to S1 (see Figure II-2).

SYSTEMATIC PALEONTOLOGY

Order PHACOPIDA Salter, 1864

Suborder CHEIRURINA Harrington & Leanza, 1957

Family CHEIRURIDAE Hawle & Corda, 1913

?Subfamily PILEKIINAE Sdzuy, 1955

Genus TESSELACAUDA Ross, 1951

Type Species -- _Tesselacauda depressa_ Ross, 1951 from the Garden City Formation (Early Ordovician), east side of Hillyard Canyon, southern Idaho, U.S.A.

Amended Diagnosis for Genus -- Cheirurid trilobites with pygidium possessing four paddle-shaped pleural ribs with no free ends; pygidial axis with four axial rings and triangular terminal piece; only anterior two pleural ribs have diagonal pleural furrows. Palpebro-ocular ridge continuous into anterior cranidial border. Glabella subrectangular. Hypostome subrectangular, with two pairs of lateral spines, a pair of broad swellings along posterior margin, and slightly indented posterior margin.

Taxonomic Remarks -- In the Treatise (Harrington et al., 1959), the genus *Tesselacauda* was considered to belong to the subfamily Pilekiinae Sdzuy, 1955, which was later regarded as a cheirurid subfamily (Whittington, 1961, p. 913; Lane, 1971, p. 9), based on the assumed ancestral relationship of that subfamily to younger cheirurids. The pilekiine affinity of *Tesselacauda* was noted by Ross (1951b, p. 129), based on pygidial similarities such as four pygidial rib pairs and pleural furrows. These pygidial features are shared with some, not all, pilekiines such as *Pilekia apollo* (Přibyl, 1985, pl. 1, fig. 8) and thus, the assignment of *Tesselacauda* to the Pilekiinae, based on pygidial morphology, appears not to be assured. In effect, the pilekiine morphology is highly variable and indeed, the subfamilial diagnoses of the Treatise (Henningsmoen, p. O441, *in* Harrington et al., 1959) and Lane (1971, p. 70-71) appear to encompass the morphologic features of the other cheirurid and pliomerid subfamilies. For example, the glabellar shape of the pilekiine trilobites ranges from subrectangular to forward-tapering, and the number of pygidial ribs ranges from two to four (compare *Anacheirurus frederici*, in Whittard, 1967, pl. 15, figs. 2, 7; *Pilekia trio* in Hintze, 1952, pl. 21, fig. 1c; and *Pilekia apollo* in Přibyl, 1985, pl. 1, fig. 8). In contrast, cranidial and hypostomal morphologies of *Tesselacauda* are very similar to early members of the Protopliomeropinae (Pliomeridae) such as *Rossaspis superciliosa* (Ross, 1951b, Pl. 31, figs. 18, 20). Such similarities and dissimilarities of *Tesselacauda* to the pilekiines and protopliomeropines suggest that the monotypic genus may be regarded as a separate genus which does not belong to the Pilekiinae or the Protopliomeropinae. Along with holaspid dissimilarities of pygidial morphologies, larval dissimilarities between *Tesselacauda depressa* and *Rossaspis pliomeris* (see Table III-1) further assure that *T. depressa* does not belong to the Protopliomeropinae. For the present, the genus *Tesselacauda* is questionably assigned to the Pilekiinae within the Cheiruridae, following Whittington's (1961) and Lane's

(1971) opinion. This taxonomic uncertainty of Tesselacauda could be solved by comparison of pilekiine protaspides.

Kobayashi (1955) described Tesselacauda flabella, based on two incomplete mature pygidia from the McKay Group in British Columbia. One of the illustrated pygidia (pl. 2, fig. 8a) shows at least six axial rings, pleural furrows on three pleurae and smooth exoskeleton. This does not agree with the above generic diagnosis at all. The specimens might represent the oldest cheirurid or pilekiine with more than four axial rings.

TESSELACAUDA DEPRESSA Ross, 1951

Plate III-1, 1-13; Plate III-2, 1-15, 18; Figure III-2

Tesselacauda depressa ROSS, 1951, p.129-131, pl. 31, figs. 27-31, pl. 34, figs. 1-4, 18; DEMETER, 1973, p. 48, 50, pl. 1, figs. 5, 6, 10, 14, 15.

Tesselacauda aff. T. depressa, HINTZE, 1952, p. 237, pl. 11, figs. 2, 3.

Materials and Locality -- A large number of protaspid shields and a few meraspid and holaspid specimens, mostly disarticulated, were obtained from three horizons (LR5 50.3, LR5 76.4 and SR5 86) exposed at the east side of Hillyard Canyon (equivalent to Ross', 1951b, Locality 5), and one horizon (SR6 55) exposed at the west side of the canyon (equivalent to Ross' Locality 6) in the Garden City Formation (Figure I-1). The horizons are of Tremadocian age (Figure III-1). These horizons are equivalent to Ross' Zone C to E (1951b) and Hintze's Paraplethopeltis through Tesselacauda Zone (1952).

Protaspid Description -- In the length versus width plot of protaspides (Figure III-3), there appears to be at least five distinct instars. The two largest instars (stages 1L and 2L) are assigned to Tesselacauda depressa with more confidence than the three smaller instars. The association of these smaller protaspides with the larger ones appears to be problematic (see discussion) so that these two groups of instars are designated 'Stages 1S, 2S, and 3S' for smaller protaspid instars, and 'Stages 1L and 2L' for larger instars. Instars 2S

PLATE III-1. *Tesselacauda depressa* Ross, 1951. All specimens, except 13 (from SR5 86), from horizon LR5 50.3. 1, dorsal view of stage 1s protaspis, UA 10904, x 113; 2, dorsal view of stage 2s protaspis, UA 10905, x 94; 3, dorsal view of stage 3s protaspis, UA 10906, x 77; 4, dorsal view of stage 1L protaspis, UA 10907, x 83; 5, dorsal view of stage 2L protaspis, UA 10908, x 85; 6, ventral view of stage 1s protaspis, UA 10909, x 106; 7, ventral view of stage 3s protaspis, UA 10910, x 68; 8, ventral view of stage 1L protaspis, UA 10911, x 68; 9, ventral view of stage 2L protaspis, UA 10912, x 54; 10, dorsal view of meraspid cranidium, UA 10913, x 48; 11, dorsal view of hypostome of stage 1L protaspis, UA 10914, x 102; 12, oblique lateral view of stage 1L protaspis (a secondary electron micrograph), UA 10915, x 70; 13, dorsal view of transitory pygidium, UA 10916, x 71.

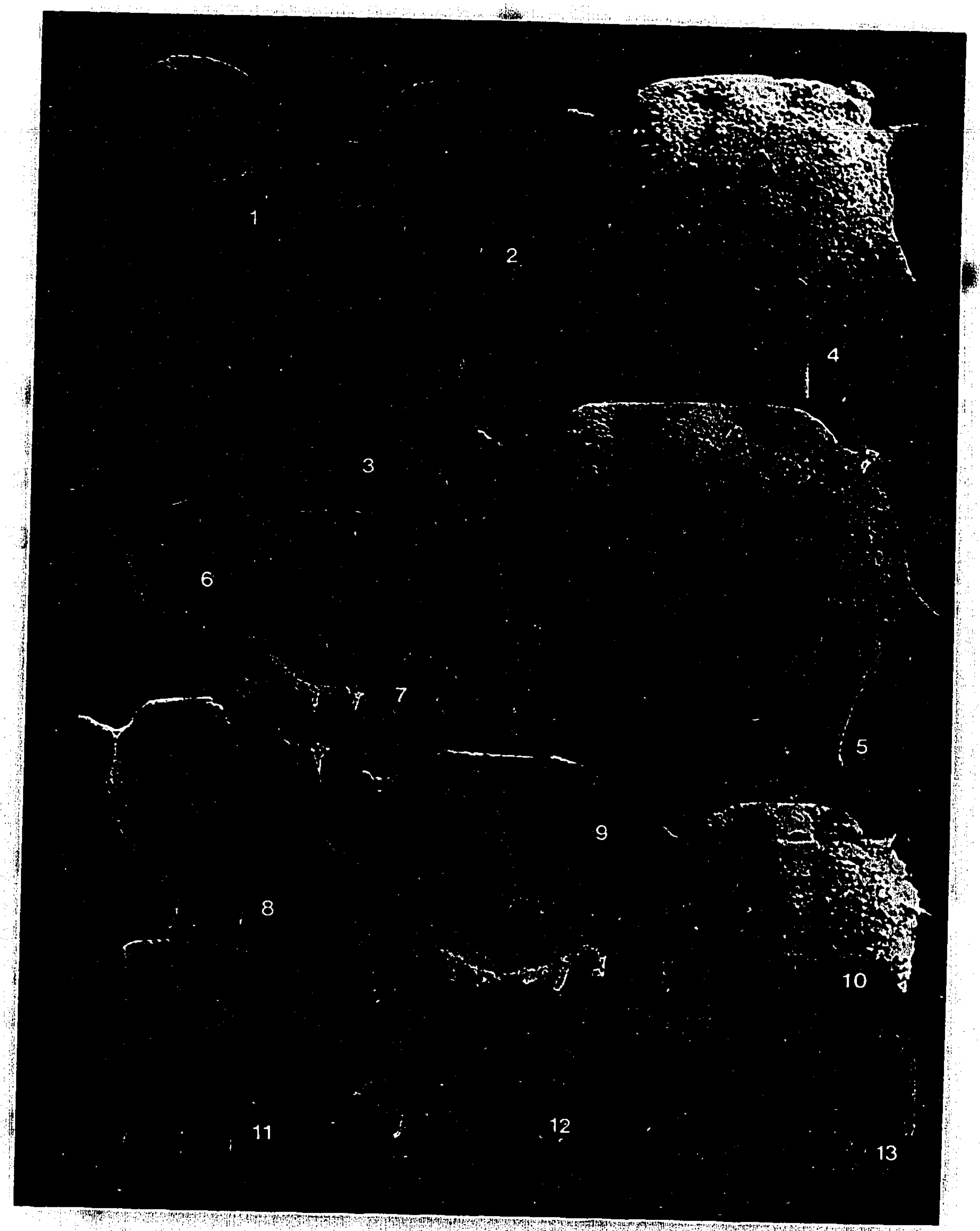
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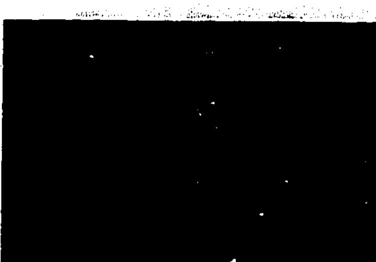
PLATE III-2. 1-15, 18, *Tesselacauda depressa* Ross, 1951. All specimens from horizon LR5 50.3 (Zone D), unless noted otherwise. 1, dorsal view of stage 1s protaspis, UA 10917, x 112; 2, dorsal view of stage 2s protaspis, UA 10918, x 90; 3, dorsal view of stage 3s protaspis, UA 10919, x 66; 4, 5, 6, dorsal views of stage 1L protaspides; 4, UA 10920, x 51; 5, UA 10921, x 48; 6, UA 10922, x 51; 7, 8, dorsal views of stage 2L protaspides; 7, UA 10923 (from SR5 86), x 43; 8, UA 10924, x 46; 9, 10, 11, dorsal views of meraspid cranidia; 9, UA 10925, x 34; 10, UA 10926, x 34; 11, UA 10927 (from LR5 76.4), x 32; 12, dorsal view of holaspid cranidium, UA 10928 (from SR6 55), x 17; 13, 14, 15, dorsal views of transitory pygidia; 13, UA 10929, x 60; 14, UA 10930 (from SR6 55), x 56; 15, UA 10931, x 73; 18, dorsal view of holaspid pygidium, UA 10932 (from LR5 76.4), x 21; 16, 17, *Kawina sexapugia* Ross, 1951 from the SR6 119 horizon (Zone G-2). 16, ventral view of early protaspid stage, UA 10933, x 65; 17, dorsal view of early protaspid stage, UA 10934, x 51.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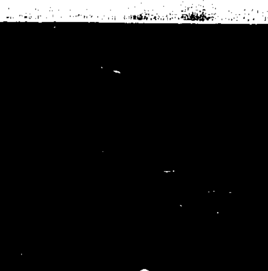
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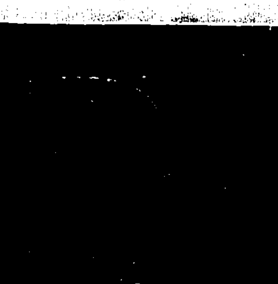
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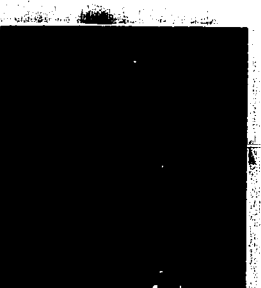
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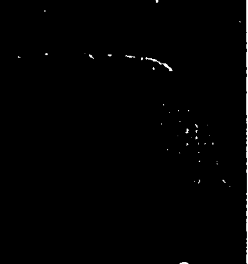
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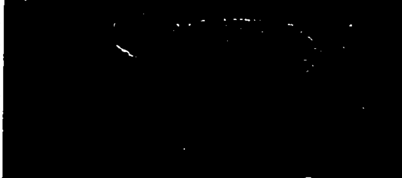
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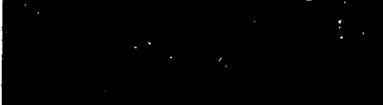
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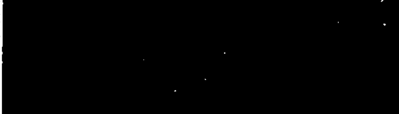
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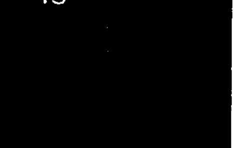
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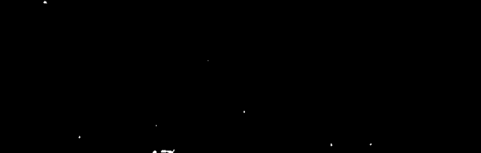
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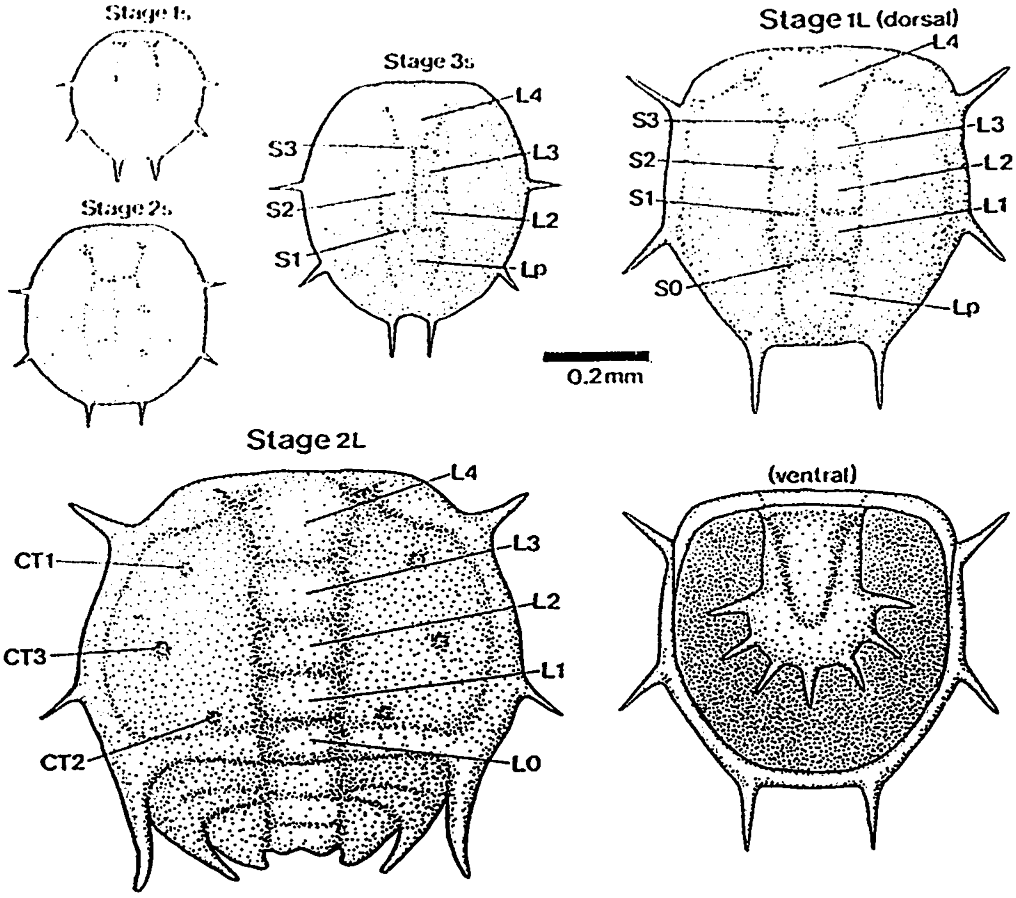

FIGURE III-2. Drawings of the protaspid stages (or instars) of Tesselacauda depressa Ross, 1951. L1 to L4, and L0 indicate glabellar lobes and occipital ring, respectively. S0 to S3 indicate glabellar furrows. 'Lp' represents the posteriormost axial lobe which has potential for proliferation. CT1, CT2, and CT3 represent "circumocular fixigenal tubercle pair".

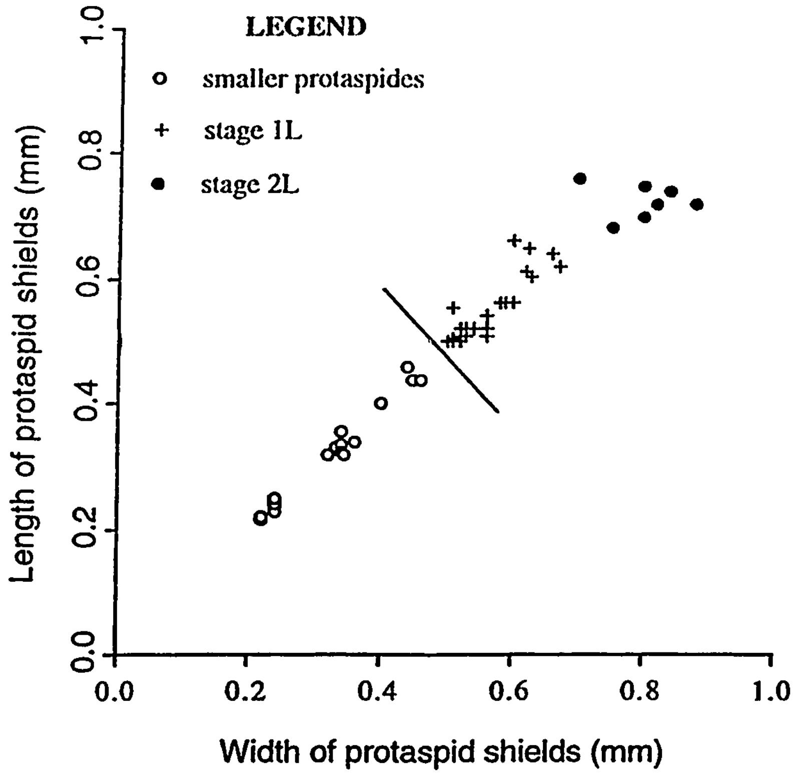

FIGURE III-3. Scatter plots of length versus width for protaspides of Tesselacauda depressa Ross, 1951 from horizon LR5 50.3. Note that the smaller protaspid stages (1s, 2s, and 3s) and the larger stages (1L and 2L) plot along a linear growth trajectory.

and 3S might be incorporated into one stage, since each instar does not show as great a morphologic difference from each other as they do with other adjacent instars, such as stages 1S and 1L.

Stage 1S protaspides are about 0.24 to 0.25 mm wide and long, with an elliptical to circular outline. Axial furrows are almost imperceptible, and pair of anterior pits is impressed at anterolateral corner of axis. Anterior border and front of axis are fused together, forming flat and depressed area. Three pairs of submarginal spines are of same length; anterior fixigenal spine is in front of but close to midlength of shield, projecting laterally; posterior ones are parallel to each other, directed backwards.

Stage 2S protaspides are 0.32 to 0.37 mm wide and long, with elliptical to circular outline. Axis is defined by shallow axial furrows. Three protoglabellar and posteriormost axial lobes are distinguishable and defined by shallow transverse furrows; Lp/L2/L3 form spindle-shaped axis; L2 and L3 are subequal in size, bilobed by shallow sagittal furrow and laterally expand to be almost twice as broad as Lp and L4; Lp is not as distinct as L2/L3/L4. Pair of anterior pits is distinctly impressed at anterolateral corner of L4. Three pairs of submarginal spines are almost the same as in stage 1 protaspides in terms of orientation and position, with anterior one being behind S3 and midfixigenal spine being behind S1.

Stage 3S protaspides are 0.4 to 0.44 wide and long, with straight and longer anterior margin. Stage 3 differs from stage 2 in that 1) anterior fixigenal spine pair is located more posteriorly with respect to whole shield length, but still remaining behind S3 and in front of S2; 2) posterior fixigenal spines are placed relatively closer to each other.

Stage 1L protaspides are 0.5 to 0.66 mm long and 0.51 to 0.67 mm wide, with inverted saucer shaped lateral profile and rounded quadrate outline, and with anterior margin relatively straight. Four glabellar and posteriormost axial lobes are well defined; L4 is subtrapezoidal and expands forward to reach anterior margin; anterior pits are depressed at anterolateral corners of L4; L1/L2/L3 are rectangular and bilobed by a sagittal furrow, and L3 is broader (tr.) than L1/L2, the three lobes still comprising spindle-shaped axis; Lp is comparatively convex upwards, well rounded, and slightly overhangs posterior margin. Palpebro-ocular ridge is laterally vaulted, lowers and tapers proximally, located in front of S3, and defined by long and backwardly-curved posterior, and shallower and shorter anterior palpebro-ocular ridge furrows. Anterior cranidial border narrows sagittally. Small triangular librigena besides distal end of palpebro-ocular ridge can be inferred from facial suture, outline of which is indented backwards. Three pairs of submarginal spines are stout, tubular and of same length; anterior fixigenal one is immediately besides lateral end of palpebro-ocular ridge, located in front of S4, and projects anterolaterally; midfixigenal one is directed posterolaterally and placed in front of S1; spines of posterior pair are parallel to each other and point posteriorly. A flat and narrow lateral border appears to connect anterior and midfixigenal spine bases. Doublure is loosely inturned, narrow and uniform in width. Shield is smooth.

Obtained protaspid hypostome is associated with this stage. Hypostome has shield-shaped outline, and almost straight anterior margin. Middle body is longer than wide; anterior lobe is long and triangular, defined by shallow middle furrow; posterior lobe is U-shaped and less convex than anterior lobe. Posterior and lateral borders are indistinct. Lateral margin is almost straight. Along margin of posterior lobe, three lateral spine pairs and posteromedian spine are developed; those spines are tubular and of same length; anterior two pairs are directed outward and ventrally and posterior pairs appear to be more horizontal.

Stage 2L protaspides are 0 72 to 0.84 mm wide and 0.68 to 0.75 mm long (sag.) with more circular outline. This stage differs from stage 1L based on the following: 1) a protopygidium (23-27% of shield length) is separated from protocranidium by shallow marginal furrow which runs straight and then strongly curves backwards at about right angle, encircling half of protopygidium; 2) protopygidium is semicircular and has two pairs of marginal spines and pair of small swellings at posterior ends; anterior two spine pairs have corresponding axial rings and pleural ribs; anteriormost pleura has shallow pleural furrow and it is separated from posterior portion of protopygidium by shallow interpleural furrow; 3) shield becomes more flattened; 4) narrow lateral border runs through all three spine pairs; 5) posterior fixigenal spine is stouter and longer than other spines; 6) three pairs of circumocular tubercles develop on fixigenal field; CT1 develops opposite L3, CT3 opposite L2, and CT2 opposite S0; 7) anterior margin becomes proportionately shorter (tr.) because facial suture moves adaxially; 8) anterior border appears as slender rim which narrows sagittally; 9) anterior palpebro-ocular ridge becomes distinct; 10) bilobation of L1/L2/L3 in stage 1L disappears; 11) small node develops on occipital ring (L0).

Meraspid and Holaspid Description -- Meraspid cranidium displays following ontogenetic changes from protocranidium of stage 2L: 1) cranidium is trapezoidal, length versus width ratio decreasing with growth; 2) glabellar furrows are no longer transverse across glabella, rather impressed as discontinuous lateral furrows alongside glabella; 3) palpebro-ocular ridge becomes more distinctively differentiated from anterior border, is placed opposite L4 and broadens distally; 4) posterior fixigenal spine becomes longer and stouter, while anterior and midfixigenal spines retain same length as in stage 5 protaspides; 5) posterior cranidial border widens abaxially and is well defined by border furrow; posterior palpebro-ocular ridge furrow, lateral cranidial border furrow and posterior border furrow appear to be continuous; 6) along anterior border and lateral border, row of short spines develops, and with growth more spines are added, resulting in irregularly distributed spines; 7) fixigenal field is granulate or decorated with tiny spines; 8) glabella is covered with irregularly distributed short spines.

Holaspid cranidium, compared to meraspid cranidium, displays following features; 1) anterior and midfixigenal spines disappear, 2) palpebro-ocular ridge bends backwards distally and moves backwards to opposite S3, 3) preglabellar furrow is clearly incised, 4) three pairs of lateral glabellar furrows are directed backwards and inwards, subequal in length and distributed with same spacing, 5) facial suture moves farther backwards, 6) genal spine pair is divergent and reduced to thorn-like projection in later stages, 7) spines on anterior border of meraspid cranidium become fine granules, while those on lateral border disappear, 8) short spines on meraspid glabella are reduced to fine granules, 9) fixigenal field is pitted and covered with short spines in smaller holaspid cranidium and later field is only pitted in larger cranidia, and 10) larger holaspid cranidia show anterior border and palpebro-ocular ridge fused together due to disappearance of anterior palpebro-ocular ridge furrow.

Smallest transitory pygidium is semicircular and 0.35 mm in sagittal length. Axis progressively tapers posteriorly. Three pairs of marginal spines are tubular; first spine pair (from anterior) is directed straight backwards, and second and third pairs point slightly inwards; corresponding axial rings are recognizable, and one pair of small swellings (represents fourth pygidial spine pair) is on posterior end of axis. Each spine has a corresponding pleural rib, which is clearly defined by interpleural furrow; first pleural furrow (from anterior) reaches corresponding pleural spine base. Following changes take place in tail portion during meraspid period: 1) up to 7 pairs of pleural spines (pygidial or protothoracic) are recognized in large transitory pygidium; 2) from sagittal length of 0.46 mm, pygidium becomes covered with small tubercles; 3) spine progressively becomes shorter and blunt; 4) in larger pygidia, anterior three pleural ribs have very distinct pleural furrows. Holaspid pygidium has strongly tapering axis with five axial rings, posteriormost one of which does not have corresponding pleural rib; four pleural ribs are discernible, anterior two of which have a diagonal pleural furrow which reaches half of pleural length (tr.); all pleural ribs have short free spinose ends and in large pygidia each rib has a blunted end; exoskeleton is tuberculate.

Discussion -- Stage 1S protaspides (Plate III-1.1, 6, Plate III-2.1) of Tesselacauda depressa with 0.24 to 0.25 mm in length and width, are the smallest phacopide protaspis described so far. The smaller protaspides of Calyptaulax callirachis (Chatterton, 1980, pl. 16, figs. 8, 9, 10, 19) and Calyptaulax annulata (Chatterton and Speyer, 1995, fig.

35K) are 0.31 to 0.34 mm in length, and P1 of Flexicalymene senaria (Chatterton et al., 1990, figs. 6-8, 9) is 0.35 mm in length. Stage 2S and 3S (Plate III-1.2, 3, 7, Plate III-2.2, 3) of T. depressa with 0.32 to 0.44 mm in length and width shows a gradual morphologic change from stage 1S. Between these smaller protaspides and stage 1L protaspides (Plate III-1.4, Plate III-2.4-6), however, there are such morphologic differences as position and orientation of submarginal spine pairs, size of librigenae, and distinctiveness of palpebral lobe and L4. These radical morphologic changes appear to render the association of these smaller protaspides with stages 1L and 2L inappropriate; those larger protaspides are more confidently assigned to T. depressa, based on gradual morphologic changes into meraspides. Several possibilities of association of these smaller instars can be hypothesized on the basis of faunal components and their morphologic features. Three possible associations below are among them, and were examined and then refuted, in order to give more confidence to the association of these smaller protaspides with stage 1L of T. depressa.

1) The stage 1S, 2S, and 3S protaspides have a great resemblance to Upper Cambrian ptychopariine protaspides, such as the 'anaprotaspis' and 'metaprotaspides' of Dunderbergia anyta (Hu, 1971, pl. 15, figs. 1 - 6 and text-figs. 44A - C) from the Dunderbergia zone and some of the 'metaprotaspides' of Genus et species indeterminata (Hu, 1986, pl. 18, figs. 1 - 4 and text-figs. 20A, B) from the Conaspis Zone. These Cambrian protaspides have a similar size range (about 0.25 - 0.36 mm in length) to these smaller protaspid instars, three distinct pairs of submarginal spines with similar positions and orientations, and a straight anterior margin. They differ from these smaller protaspides in having a more discernible axis and sagittal furrow, four protoglabellar and a posteriormost axial lobes with bilobed L1/L2/L3 (of 'metaprotaspides'), and posterior fixigenal spine expressed by a crescentic margin, not a spine proper. In spite of their great similarities, the absence of ptychopariine trilobites from any horizons of this work suggests that stages 1S to 3S do not represent the early protaspid stages of a ptychopariine trilobite. Such similarities between

stages 1S to 3S and ptychopariine protaspides, however, imply a ptychopariid origin for the Phacopida, or at least the Pliomeridae, as suggested by several workers (Henningsmoen, p. O231 in Harrington et al., 1959; Bergström, 1973).

2) The second, and least probable, is that these smaller instars might represent the earlier stages of hystricurine trilobites (e.g., Parahystricurus carinatus) which occur along with them through the horizons sampled for this work. Such an assumption was based on similarities between these smaller protaspides and ptychopariid protaspides and, in turn, similarities between holaspid hystricurine and ptychopariine trilobites, such as Onchopeltis (Fortey, 1979a). However, the hystricurine protaspides are very dissimilar to these stages 1S, 2S, and 3S, with respect to the presence of submarginal spine pairs, spindle-shaped axis, and different surface ornamentation. Thus, this association would be least reasonable, unless a considerable metamorphosis between them is supposed.

3) The remaining association, accepted herein, is with one of the pliomerid trilobites described in this work. Stratigraphic occurrence (Zones C to E, Tremadocian of age) of these protaspides precludes an association with Protopliomerella contracta, which occurs in Zone G (Arenigian) (Figure III-1). Holaspid specimens of Rossaspis pliomeris were secured from the same horizon as these smaller protaspides. Holaspid and meraspid materials of R. pliomeris were obtained from a single horizon (LR5 50.3), along with protaspid specimens of that species. In contrast, the holaspid and meraspid specimens of Tesselacauda depressa occur in three horizons (LR5 50.3, LR5 76.4 and SR5 86) along with the smaller protaspid specimens. This stratigraphic occurrence favors the association of these smaller protaspides with T. depressa rather than R. pliomeris. Furthermore, stage 2S and 3S protaspides of T. depressa differ from stage 1 (the earliest instar) of R. pliomeris, in that the former has a straight anterior margin (rounded in the latter), an elliptical or circular shield outline (subquadrate in the latter), more posteriorly located anterior fixigenal spine pair (in the latter, the pair is located besides the palpebro-ocular ridge), and an undifferentiated palpebro-ocular ridge

and anterior border, and spindle-shaped Lp/L2/L3 (parallel-sided in the latter) (Table III-1). These morphologic differences further support the association of these smaller stages with stage 1L protaspides of T. depressa. In particular, the retention of the spindle-shaped Lp/L2/L3 and bilobation of protoglabellar lobes between stages 3S and 1L support this association. Furthermore, the fact that stages 1S to 3S fall on the same ontogenetic trajectory as stage 1L and 2L of T. depressa adds support to the association (Figure III-3).

Comparison with Other Phacopoid Protaspides -- Each protaspid stage (or instar) of Tesselacauda depressa shows some similarities and dissimilarities to those of the cheirurids, the early cybelines and the calymenids; these similarities mentioned below may be used to infer their phylogenetic relationships.

Stage 2L (Plate III-1.5, Plate III-2.7, 8) of Tesselacauda depressa is similar to the larger protaspis of Kawina sexapugia (Sphaerexochinae) illustrated by Ross (1953, pl. 62, fig. 2), but differs in having a narrower (tr.) axis and a more anteriorly positioned anterior fixigenal spine. The bilobed protoglabellar lobes and subtrapezoidal L4 of the early protaspides of K. sexapugia and stage 1L of T. depressa (Table III-2) further suggest a close relationship of the latter to this early sphaerexochine.

Chatterton (1980) described the ontogenies of several cheirurids from the Middle Ordovician Esbataottine Formation. Only one instar, referred to as 'metaprotaspis', was described for each cheirurid species at that time, even if some protaspides have a protopygidium and others have unsegmented axial lobes. Herein, the comparison below was made separately for 'Pa' (instars prior to the appearance of protopygidium) and 'Pb' (instars after the appearance of protopygidium), since the protopygidium differentiation is considered a significant event for phacopid trilobite ontogeny (see terminology). Stages 1S to 3S (Plate III-1.1-3, 6, 7, Plate III-2.1-3) of Tesselacauda depressa are not comparable to these cheirurid protaspides with respect to size, position of anterior fixigenal spine pair and number of

TABLE III-1. Comparison of morphologic transformations during protaspid period (with some notes on the changes in meraspid period) of Tesselacauda depressa, Rossaspis pliomeris, and Protopliomerella contracta, described in this work.

	Tesselacauda depressa	*Rossaspis pliomeris*	*Protopliomerella contracta*
change in outline	subquadrate to circular	subquadrate to circular	subquadrate to circular
# of protoglabellar lobes	4 to 4	3 to 4	3 to 4
bilobation	present only in 'Pa'	present only in 'Pa'	present only in 'Pa'
change in shape of L4	subtrapezoidal to circular	subtrapezoidal to circular	subtrapezoidal and less convex
change in shape of Lp to L3	spindle to parallel	parallel	spindle to parallel
# of protopygidial ribs	0 to 2	0 to 1	0 to 1 to 2
midfixigenal spine	behind to opposite S2	behind to opposite S2	in front of S2
fixigenal field	smooth (spinose in meraspides and pitted in holaspides)	smooth to pitted (spinose in meraspides)	smooth (pitted in later ontogeny)
circumocular tubercles	present in 'Pb'	present in 'Pb'	absent
protoglabellar tubercle pairs	appears in meraspides	appears in meraspides	absent
width of doublure	uniform	uniform	uniform
librigenae	confined by the anterior fixigenal spine	confined by the anterior fixigenal spine	confined by the anterior fixigenal spine
palpebro-ocular ridge	combined with anterior border in later ontogeny	separated from anterior border	separated from anterior border
spines on anterior border	present in meraspides	present in meraspides	absent
marginal spines	absent	present in 'Pb' as bifurcated forms	absent

protoglabellar lobes. Stage 1L protaspides (Plate III-1.4, 8, 11, 12, Plate III-2.4-6) of T. depressa bear some resemblance to 'metaprotaspides' of the Sphaerexochinae such as Heliomeroides freschaufae (Chatterton, 1980, pl. 3, fig. 15 and pl. 12, fig. 29) and Sphaerexochus (Korolevium) arenosus (Chatterton, 1980, pl. 12, figs. 1-5) (Table III-2). The association of early growth stages of Heliomeroides was not, with confidence, ascertained by Chatterton (1980, p. 41-42), who noted that its subfamilial status as an acanthoparyphine should be reappraised if the association is correct. Herein, the genus is regarded as belonging to the Sphaerexochinae, as suggested by Whittington (1965) and Lane (1971) based on larval similarities, even if two pairs of holaspid pygidial ribs of Heliomeroides is unique among the sphaerexochines.

The acanthoparyphine and the cheirurine protaspides are comparable to stages 1L and 2L of Tesselacauda depressa with regard to several features (Tables III-3 and 4). The compared acanthoparyphine protaspides are the 'metaprotaspides' of Acanthoparypha evitti and Acanthoparypha perforata (Chatterton, 1980, pl. 10, figs. 1 - 4 and Whittington and Evitt, 1954, pl. 15, figs. 1-4, respectively), and Holia secristi (Chatterton, 1980, pl. 11, fig. 1), and early and late protaspides of Hyrokybe julli (Chatterton and Perry, 1984, pl. 12, figs. 1, 3-5; Speyer and Chatterton, 1989, figs. 8D and E; Chatterton and Speyer, 1995, fig. 38H). The 'metaprotaspides' of Ceraurinella nahanniensis, (Cheirurinae, Chatterton, 1980, pl. 9, figs. 1 - 4) share more features (subquadrate outline, stouter and longer fixigenal spines, one pair of protopygidial ribs) with the acanthoparyphine protaspides than with stage 2L of T. depressa (compare Tables III-3 and 4). However, recently, Chatterton and Speyer (1995) illustrated small and large protaspides of Ceraurinella latipyga? (figs. 38A, B, E, F), the larger one of which shows great morphologic discrepancies from the 'metaprotaspides' of C. nahanniensis as well as stage 2L of T. depressa. On the other hand, the small protaspides have some similarities to stage 1L of T. depressa, including bilobed protoglabellar lobes and seven needle-like hypostomal spines (Table III-4). Along with the two protaspid instars of C. latipyga?, one probable cheirurine protaspid specimen

TABLE III-2. Comparison of the morphologic features of protaspid instar (or stage) of 'Pa' between Tesselacauda depressa and the sphaerexochines such as Heliomeroides freschaufae, Sphaerexochus (Kolorevium) arenosus, and Kawina sexapugia.

	Stage 1L of *T. depressa*	*H. freschaufae*	*S. (K.) arenosus*	early stage of *K. sexapugia*
# of protoglabellar lobes	4	not differentiated	not differentiated	3
bilobation of protoglabellar lobe	L1/L2/L3	only sagittal furrow	no	L2/L3
protoglabellar shape	subtrapezoidal L4 and spindle-shaped Lp to L3	spindle-shaped, indistinct posterior axial furrow	spindle-shaped, indistinct posterior axial furrow	subtrapezoidal L4 and parallel-sided Lp to L3
lateral profile	flat, with lateral border	bulbous	bulbous	bulbous
width of doublure	uniform	posteriorly widening	posteriorly widening	posteriorly widening
lateral border	present	absent	absent	absent
lateral profile	rather flattened	bulbous	bulbous	bulbous
diagnostic features		backward-tapering outline; more posteriorly located midfixigenal spine	indistinct axial furrow	

TABLE III-3. Comparison of the morphologies of protaspid stages 1L ('Pa') and 2L ('Pb') of *Tesselacauda depressa* and the acanthoparyphines such as *Acanthoparypha evitti*, *Hyrokybe julli*, and *Holia secristi*.

	stage 1L (Pa)	stage 2L (Pb)	Pb of *A. evitti*	Pa of *H. julli*	Pb of *H. julli*	Pa of *H. secristi*
# of proto-glabellar lobe	4	4	4	4	4	4
bilobation of proto-glabellar lobes	L1/L2/L3	absent	absent	L1/L2/L3	absent	L1/L2/L3
proto-glabellar shape	sub-trapezoidal L4 and spindle-shaped Lp to L3	circular L4 and parallel-sided Lp to L3	sub-quadrate L4 and parallel-sided Lp to L3	sub-trapezoidal L4 and spindle-shaped Lp to L3	circular L4 and parallel-sided Lp to L3	sub-trapezoidal L4 and spindle-shaped Lp to L3
width of doublure	narrow	narrow	narrow	broad	broad	narrow
# of proto-pygidial ribs	0	2	1	0	1	0
fixigenal spines	slender and short; equal length	slender and short; longer posterior pair	stout and long; equal length	stout and long; equal length	stout and long; equal length	slender and short; equal length
fixigenal field	smooth	smooth	tuberculate	smooth	pitted	smooth
circum-ocular tubercles	absent	CT1/CT2/CT3	absent	CT1/CT2/CT3	CT1/CT2/CT3	CT1/CT2/CT3
outline	sub-quadrate	circular	sub-quadrate	sub-quadrate	sub-quadrate	sub-quadrate
proto-glabellar tubercle pairs	absent	absent	present	absent	present	absent
lateral border	present	present	present	absent	present	absent
lateral profile	flattened	flattened	flattened	bulbous	flattened	bulbous
diagnostic features			subsidiary spines		prominence of tubercle	subsidiary spines

TABLE III-4. Comparison of morphologies of 1L ('Pa') and 2L ('Pb') protaspid stages of *Tesselacauda depressa*, and such cheirurines as *Ceraurinella nahanniensis* and *Ceraurinella latipyga*?.

	Stage 1L (Pa)	Stage 2L (Pb)	Pb of *C. nahanniensis*	Pa of *C. latipyga*?	Pb of *C. latipyga*?
# of proto-glabellar lobes	4 with bilobed L1/L2/L3	4	4	3 with bilobed L2/L3	4
proto-glabellar shape	sub-trapezoidal L4 and spindle-shaped Lp to L3	circular L4 and parallel-sided Lp to L3	subcircular L4 and parallel-sided Lp to L3	sub-trapezoidal L4 and spindle-shaped Lp to L3	rectangular L4 and parallel-sided Lp to L3
width of doublure	narrow	narrow	narrow	narrow	narrow
# of proto-pygidial ribs		2	1		5
fixigenal spines	slender and short; equal length	slender and short; longer posterior pair	stout and long; shorter midfixigenal pair	slender and short; equal length	long and stout posterior pair
fixigenal field	smooth	smooth	pitted	smooth	pitted
circumocular tubercles	absent	CT1/CT2/CT3	absent	absent	absent
outline	subquadrate	circular	subquadrate	subquadrate	elliptical
proto-glabellar tubercle pairs	absent	absent	absent	absent	absent
hypostomal spines	7; needle-like		6; stouter	6; needle-like	6; stouter
lateral border	present	present	present	present	present

(Chatterton and Speyer, 1995, figs. 38C, D) was illustrated, the morphologic features of which also are different from C. nahanniensis; and the only shared feature with the latter, not T. depressa, is the pitted exoskeleton. However, stage 2L of T. depressa and this protaspid specimen share more morphologic features (two pairs of protopygidial ribs, longer posterior fixigenal spines, a lateral border, a circular outline, and a subcylindrical protoglabella) than C. nahanniensis. Such a variable larval morphology of the Cheirurinae indicates a morphologic flexibility of larvae even within a genus, which might have been caused by larval adaptation.

When reporting the possible earliest trilobite larval stage (called a 'phaselus'), Fortey and Morris (1978) illustrated an 'anaprotaspis' and a 'metaprotaspis' of Cybelurus of late Arenig - early Llanvirn of age from the Olenidsletta Member of the Valhallfonna Formation, Spitsbergen. However, these protaspides should probably be assigned to Lyrapyge which occurs in the Olenidsletta Member together with these protaspides (Fortey, 1980); Cybelurus species occur in the Profilbekken Member, stratigraphically higher than Olenidsletta Member. Their 'anaprotaspis' (1978, pl. 94, fig. 8) has a similar palpebro-ocular ridge and anterior border, orientation of fixigenal spine pair, four protoglabellar lobes (bilobed L1/L2/L3 and subtrapezoidal L4), and spindle-shaped L1/L2/L3, and a flat lateral border, to those observed in stage 1L (Plate III-1.4) of Tesselacauda depressa. However, the protaspid shield with 0.25 mm in sagittal length, is half the size of stage 1L (0.5 to 0.56 mm). On the other hand, the 'metaprotaspis' (pl. 94, fig. 9) is very different from stage 2L (Plate III-1.5) in having a pitted exoskeleton, one pair of protopygidial ribs, and much reduced anterior and midfixigenal spine pairs.

Some resemblances are detected between stage 3S and 1L of Tesselacauda depressa and P1 and P2 of Flexicalymene senaria from the Middle Ordovician Martinsburg Formation (Chatterton, et al., 1990, figs. 1-10,11, 2-1,2) (Table III-5). Stage 2L of T. depressa and B1 of F. senaria, as the first instars with a protopygidium ('Pb'), share two pairs of protopygidial marginal spines and CT1/CT3/CT2, but show more divergent morphologic discrepancies than the previous stages.

TABLE III-5. Comparison of morphologies of 3s and 1L protaspid stages of *Tesselacauda depressa* with P1 and P2 of *Flexicalymene senaria*.

	Stage 3S (Pa)	P1 (Pa)	Stage 1L (Pb)	P2 (Pb)
# of protoglabellar lobes	3	3	4	3
bilobation	L2/L3	L2/L3	L1/L2/L3	L2/L3
midfixigenal spine	behind S1	behind S1	behind S1	behind S1
anterior fixigenal spine	behind S3	in front of S3	in front of S3	in front of S3
L4	sub-trapezoidal	sub-trapezoidal	sub-trapezoidal	sub-trapezoidal
# of hypostomal spines	unavailable	unavailable	7	9
lateral profile	flattened	bulbous	flattened	bulbous
circumocular tubercles	no	no	no	CT2
lateral border	absent	absent	present	absent
characteristic features		pleural swellings		

Those differences are that the stage 2L protaspides have a more flattened lateral profile, a circular shield outline (subrectangular in B1), a distinct protocranidial marginal furrow, two discernible interpleural and pleural furrows on the protopygidium, a more anteriorly positioned (opposite S1) midfixigenal spine pair, a flat lateral border, and a facial suture which is still distally confined by an anterior fixigenal spine pair (compare to the suture of B1 or B2 of *F. senaria*, which extends into the midfixigenal spine pair dorsally as well as ventrally).

Subfamily SPHAEREXOCHINAE Öpik, 1937
Genus KAWINA Barton, 1916

Forteyops, PŘIBYL, VANĚK, AND PEK, 1985, p. 165-166.

Type Species -- *Cheirurus vulcanus* Billings, 1865.

Taxonomic Remarks -- Přibyl et al. (1985) erected a monotypic genus, *Forteyops*, with type species of *Kawina sexapugia* Ross, 1951. They distinguished the new genus from *Kawina* in that the pygidium of *K. sexapugia* has a rather pointed and long spinose end. However, the shape of pygidial ribs is highly variable in several *Kawina* species described so far, from paddle-shaped with short free ends (e.g., *Kawina* sp. B, Fortey, 1980, pl. 17, fig. 7) to rounded with longer free ends (e.g., *Kawina arnoldi*, Whittington, 1963, pl. 27, fig. 2). In addition, the size and shape of the terminal pygidial piece is even more variable than the pygidial ribs (compare long, triangular piece in *K. arnoldi* with a minute piece in *Kawina* sp. A, (Fortey, 1980, pl. 18, fig. 9). Such variable pygidial morphology is common to the Sphaerexochinae as well as the Cheiruridae. Thus, the genus *Forteyops* is regarded as a junior objective synonym of *Kawina*.

Other Species -- *Kawina arnoldi* Whittington, 1963 from Lower Table Head Formation, Newfoundland; *Kawina limbata* Whittington, 1963 from Lower Table Head Formation, Newfoundland; *Kawina*? *chazyensis* (Raymond, 1905), Shaw, 1968 from Chazy Limestone, New York; *Kawina wilsoni* Ross, 1972, from Antelope Valley Limestone, eastern Nevada; *Kawina*? *webbi* Hintze, 1952, from Zone J (late Arenigian) of the Upper Pogonip Group (Wahwah Limestone), exposed at Ibex area, midwestern Utah; *Kawina sexapugia* Ross, 1951, from Zone J of the Garden City Formation, southern Idaho.

KAWINA SEXAPUGIA Ross, 1951
Plate III-2.16, 17

Kawina sexapugia ROSS, 1951, p. 126-129, pl. 35, figs. 6, 7, 11-17, 19-21; ROSS, 1953, p. 644-645, pl. 62, figs. 1, 2, 5.

Kawina? *sexapugia* (Ross), HINTZE, 1952, p. 178, pl. 21, fig. 18.

Forteyops sexapugia (Ross), PŘIBYL, VANĚK, AND PEK, p. 165 - 166, text-fig. 14.

Materials and Locality -- A few protaspid specimens and only one transitory pygidium were obtained from SR6 119 horizon (Zone G) of the Garden City Formation, exposed at the west side of Hillyard Canyon, southern Idaho, U.S.A.

Protaspid Description -- Early protaspides are 0.47 mm long and 0.51 mm wide, with subquadrate outline. Axial furrow is distinct anteriorly, considerably shallows at midlength to be indistinct in posterior half of shield; three protoglabellar and posteriormost lobes are recognizable; L4 is subtrapezoidal and twice as broad as L2/L3; pair of distinct anterior pits is developed at half length of L4; Lp/L2/L3 form parallel-sided axis; L2 and L3 are rectangular; Lp is not as clearly defined by axial furrows as L2/L3/L4, but appears to overhang posterior margin. Palpebro-ocular ridge is inflated laterally, located anterior to S3, and defined by shallow anterior and posterior palpebro-ocular ridge furrows. Anterior border is not clearly separated from L4. Anterior fixigenal spine pair is relatively short; midfixigenal spine pair is located opposite S1; posterior fixigenal spines are parallel to each other. Posterior margin is rounded. Between anterior and midfixigenal spine pairs, indistinct lateral border is developed. Doublure (except protolibrigenae and rostral plate) is relatively broad.

Discussion -- The protaspides are very similar to protaspides of Sphaerexochus (Korolevium) arenosus (Chatterton, 1980, pl. 12, figs. 1-5) with respect to bulbous profile, rapidly-shallowing axial furrow, posteriorly widening doublure and rather short fixigenal spines. The similarities demonstrate that the protaspides belong to the Sphaerexochinae. Thus, these protaspides are, undoubtedly, associated with K. sexapugia, the only sphaerexochine trilobite described from Tremadocian strata including the Garden City Formation. Ross (1953) described a protaspid specimen, a meraspid cranidium and a transitory pygidium of K. sexapugia from Zone J of the Garden City Formation. The protaspides described in this work might represent an earlier stage than Ross' (pl. 62, fig. 2; 0.52 mm sagittal length) protaspides. If this is the case, the following ontogenetic changes during the protaspid period can be listed: 1) the anterior fixigenal spine pair moves backwards, which takes place earlier than in the ontogeny of other sphaerexochines; 2) the axis relatively widens in the larger stage, while most phacopid protaspid instars maintain similar relative width ratios of the axis; and 3) at least two protopygidial segments are differentiated. Considering that these listed changes take place in later ontogeny of the other Middle Ordovician sphaerexochine trilobites, there might have been a change in the timing of appearance of some morphologic features within this sphaerexochine lineage, based on the assumption that K. sexapugia might be ancestral to the Middle Ordovician sphaerexochines as suggested by Chatterton and Ludvigsen (1976, p. 58). This heterochronic development can be further manifested by the resemblance between meraspid cranidium and pygidium of S. (K.) arenosus (Chatterton, 1980, pl. 12, figs. 12, 19) and those of K. sexapugia (Ross, 1951b, pl. 35, figs. 11, 13). Additionally, their holaspid hypostomes uniquely share an indented posterior margin (see Ross, 1951, pl. 35, fig. 14 and Chatterton, 1980, pl. 12, fig. 25), not observed in other cheirurid species.

Family PLIOMERIDAE Raymond, 1913
Subfamily PROTOPLIOMEROPINAE Hupé, 1953
Genus ROSSASPIS Harrington, 1957

Type Species -- Protopliomerops superciliosa Ross, 1951 from Zone F (Tremadocian) of the Garden City Formation, west side of Hillyard Canyon, southern Idaho, U.S.A.

Amended Diagnosis -- Protopliomeropines with pygidium possessing 4 or 5 pleural ribs, with long free ends; glabella subrectangular; palpebro-ocular ridge elongated and clearly delineated from anterior border; hypostome subrectangular and with three pairs of lateral spines.

Other Species -- Rossaspis pliomeris Demeter, 1973 from Zone D (Tremadocian) of Fillmore Limestone, at Ibex Area; Protopliomerops rossi Harrington and Leanza, 1957 from Argentina; Rossaspis bunopasi Stait et. al., 1984 from Tarutao Formation (Tremadocian), southern Thailand.

Taxonomic Remarks -- The generic assignment of Rossaspis bunopasi was questionable when Stait et al. (1984) described the species, because of its intermediate form between Rossaspis and Kanoshia. But having a relatively wider glabella and five pygidial ribs with long free ends suggests that this species can be assigned to Rossaspis.

ROSSASPIS PLIOMERIS Demeter, 1973
Plate III-3, 1-11; Plate III-4, 1-15; Figure III-4

Rossaspis pliomeris DEMETER, 1973, p. 50, 52, pl. 2, figs. 1-4, 8, 9, 12-15.

PLATE III-3. *Rossaspis pliomeris* Demeter, 1973. All specimens from horizon LR5 50.3 (Zone E). 1, dorsal view of stage 1 protaspis, UA 10935, x 106; 2, dorsal view of stage 2 protaspis, UA 10936, x 115; 3, oblique lateral view of stage 1 protaspis (taken using secondary electrons), UA 10937, x 88; 4, oblique lateral view of stage 2 protaspis, UA 10938, x 84; 5, dorsal view of meraspid cranidium, UA 10939, x 38; 6, dorsal view of transitory pygidium, UA 10940, x 69; 7, ventral view of stage 1 protaspis, UA 10941, x 76; 8, ventral view of stage 2 protaspis, UA 10942, x 75; 9, ventral view of meraspid cranidium (bms = bifurcated marginal spine; fs = spines on fixigenal field; mfs = midfixigenal spine), UA 10943, x 315; 10, dorsal view of holaspid cranidium, UA 10944, x 19; 11, dorsal view of holaspid pygidium, UA 10945, x 31.

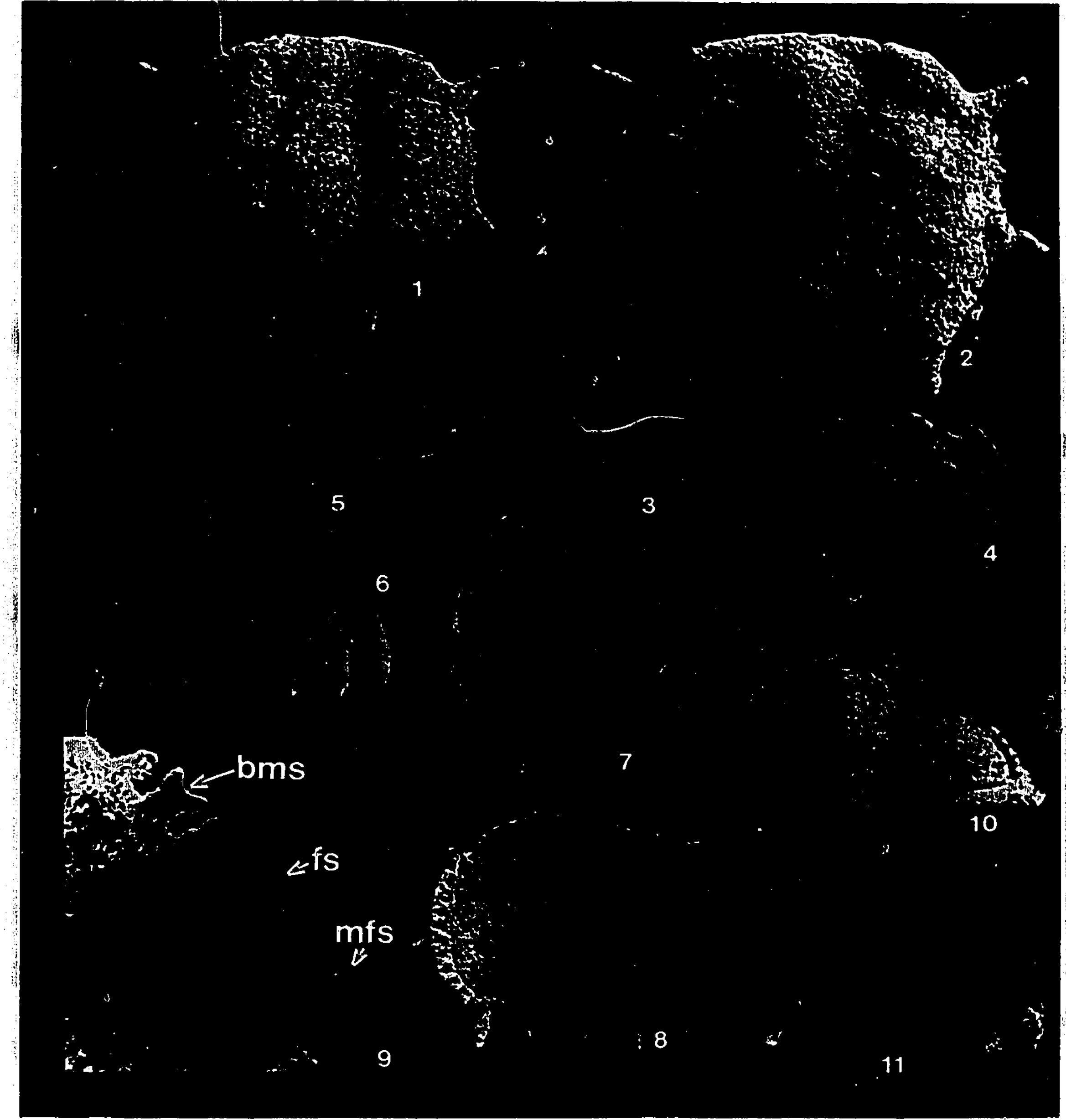
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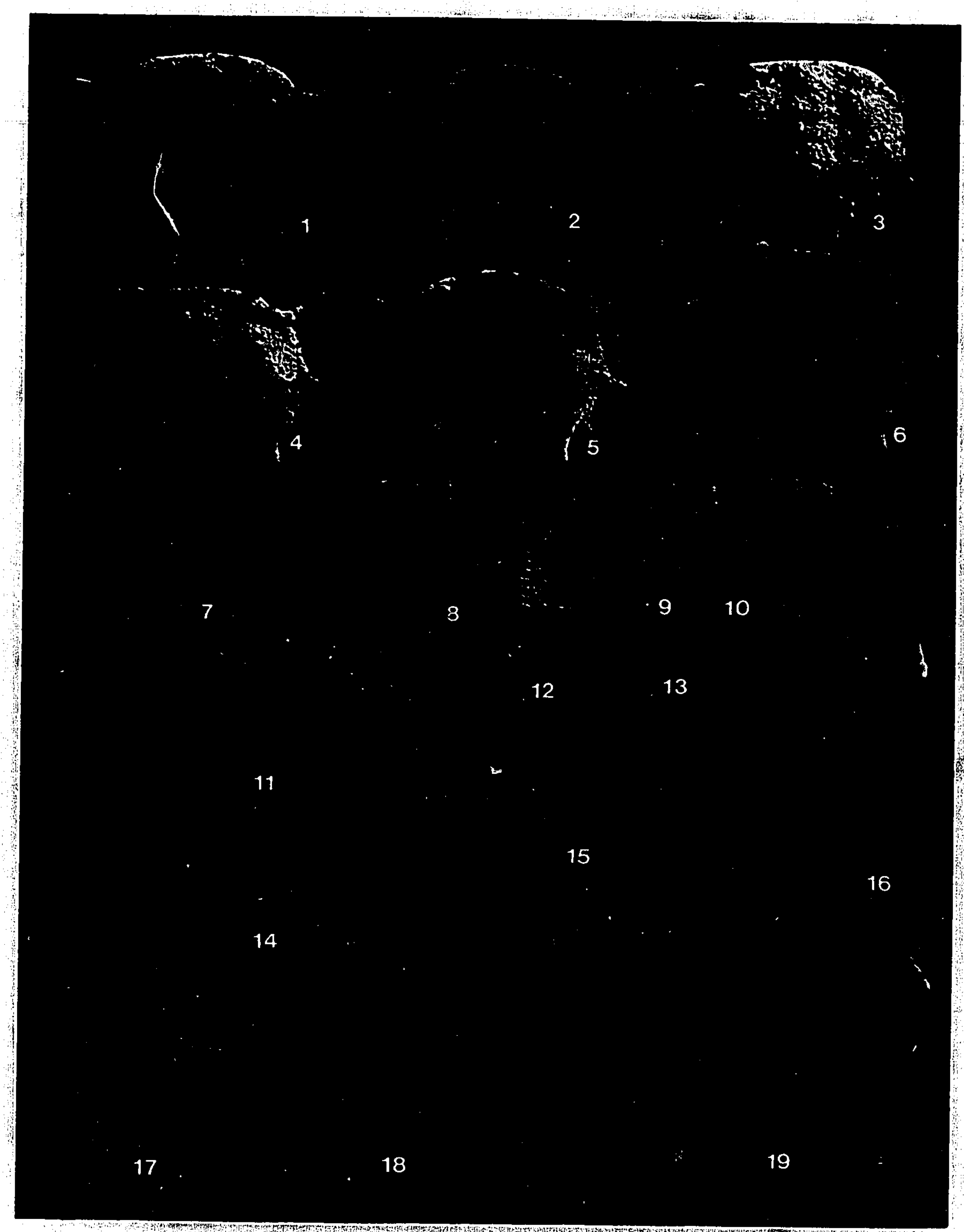
PLATE III-4. 1-15, Rossaspis pliomeris Demeter, 1973. All specimens from horizon LR5 50.3. 1, 2, 3, dorsal views of stage 1 protaspides; 1, UA 10946, x 85; 2, UA 10947, x 71; 3, UA 10948, x 71; 4, 5, 6, dorsal views of stage 2 protaspides; 4, UA 10949, x 60; 5, UA 10950, x 60; 6, UA 10951, x 66; 7, 8, dorsal views of meraspid cranidia; 7, UA 10952, x 42; 8, UA 10953, x 41; 9, ventral view (with bifurcated marginal spines) of meraspid cranidium, UA 10954, x 38; 10, 11, dorsal views of meraspid cranidia; 10, UA 10955, x 40; 11, UA 10956, x 50; 12, dorsal view of holaspid ? cranidium, UA 10957, x 23; 13, 14, 15, dorsal views of transitory pygidia; 13, UA 10958, x 64; 14, UA 10959, x 61; 15, UA 10960, x 70. 16-19, Rossaspis superciliosa Ross, 1951. All specimens from horizon R6E2. 16, dorsal view of holaspid cranidium, UA 10961, x 17; 17, dorsal view of early protaspid stage, UA 10962, x 59; 18, dorsal view of meraspid degree 0, UA 10963, x 48; 19, dorsal view of holaspid pygidium, UA 10964, x 27.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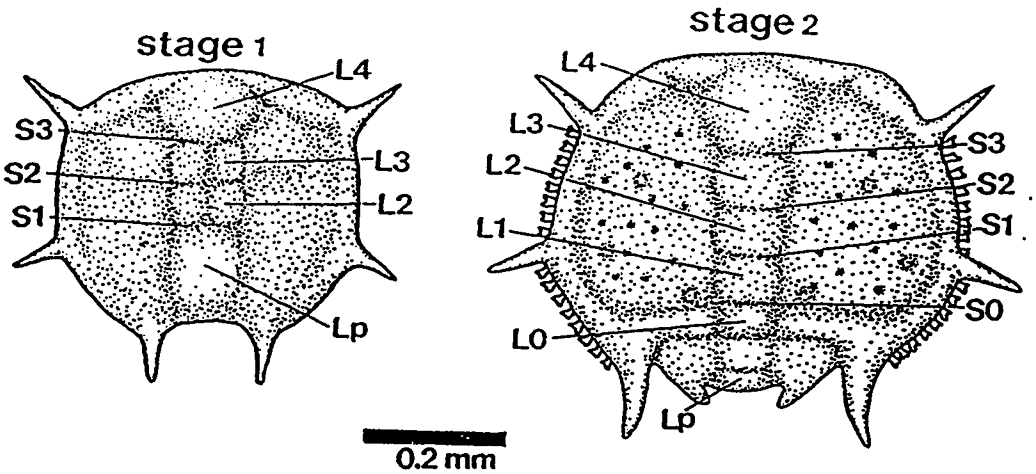

FIGURE III-4. Drawings of the dorsal view of two protaspid stages of Rossaspis pliomeris Demeter, 1973.

Taxonomic Remarks -- Demeter (1973), originally placed Rossaspis pliomeris in the cheirurid subfamily Pilekiinae Sdzuy, 1955, based on the assumption that pilekiine trilobites were derived from R. pliomeris. However, this assumption of a direct derivation appears to be questionable (see the phylogenetic consideration below). Furthermore, the only similarity shared with some, not all pilekiines and R. pliomeris is four pairs of pygidial ribs. They differ in that R. pliomeris has no pygidial pleural furrows but the lateral articulating ridge immediately in front of the anteriormost pygidial rib. Cranidial morphologies, in particular, glabellar shape, are so variable within the pilekiine trilobites that the shared possession of a subrectangular glabella of R. pliomeris with some pilekiines is not sufficient evidence that this species is a pilekiine. Thus, the genus Rossaspis is regarded as a protopliomeropine, following Harrington's (1957) original classification.

Přibyl et al. (1985, p. 116) regarded Rossaspis pliomeris as Parapilekia, without any discussion. However, between Rossaspis (Protopliomeropinae) and Parapilekia (Pilekiinae), distinguishable morphologic differences exist. First of all, protopliomeropine trilobites do not develop an anterior fixigenal area between the eye ridge and the anterior border, which is observed in Parapilekia jacquelinae (Fortey, 1980, pl. 17, fig. 1). In addition, no pleural furrows are impressed in the pygidial pleural ribs of the protopliomeropines, unlike the anterior two pygidial pleurae of P. jacquelinae which have pleural furrows. Thus, their assignment appears to be incorrect.

Materials and Locality -- Numerous protaspides and meraspides of this species were obtained from LR5 50.3 horizon of the Garden City Formation (Tremadocian), exposed in the east side of Hillyard Canyon (Figures I-1, III-1). Some noticeable changes between meraspid and holaspid periods are mentioned.

Protaspid Description -- Two instars are recognized in the protaspid period, on the basis of morphometrically distinct groupings

(Figure III-5). These instars can also be distinguished by various morphological details and are described below as two stages.

Stage 1 protaspides are 0.41 to 0.46 mm wide and 0.33 to 0.38 mm long (sag.), subquadrate in outline and gently convex in lateral profile. Anterior margin is gently convex forwards. Axis slightly tapers backwards and three protoglabellar and posteriormost axial (Lp) lobes are recognized; Lp is longer and broader than L2/L3/L4 and with a rounded posterior end, slightly overhanging posterior margin of shield; L2 and L3 are rectangular, subequal in size and bilobed by sagittal furrow, and smaller than L4; L4 is subtrapezoidal; pair of anterior pits is developed immediately opposite middle of L4. S1/S2/S3 furrows are continuous across axis, shallowing sagittally. Anterior border and L4 are not clearly separated. Palpebro-ocular ridge lowers and narrows sagittally, and is defined by shallow anterior and posterior palpebro-ocular ridge furrows. Torulus pair occurs immediately abaxial to L3, and occupies slightly more than one-half width (tr.) of fixigenal field. Anterior fixigenal spine pair is placed besides palpebro-ocular ridge, in front of S3 and directed anterolaterally. Midfixigenal spine pair is present behind S1, and directed posterolaterally. Posterior fixigenal spine pair is directed posteriorly, with spines parallel to each other. All submarginal spines are slightly directed ventrally and subequal in length. Posterior margin is deeply indented.

Stage 2 protaspides are 0.52 to 0.62 mm wide and 0.44 to 0.51 mm long (sag.). They differ from stage 1 in following features: 1) more circular outline and convex lateral profile; 2) having four lobes in subcylindrical glabella and occipital ring; occipital ring is smaller than subequal L1/L2/L3; L4 is circular and twice as long as other lobes; sagittal furrow, which subdivides L2 and L3 in stage 1, is absent; 3) anterior border narrows sagittally and palpebro-ocular ridge is more raised and inflated distally; posterior and anterior palpebro-ocular ridge furrows are deeper; 4) torulus pair is not as distinct as in stage 1; 5) three pairs of circumocular fixigenal tubercles are small; CT1 (= torular tubercle in Evitt and Tripp, 1977) develops on abaxial side of torulus; CT3 is opposite midfixigenal spine base; CT2 just in front of opposite S0; it is difficult to distinguish these tubercles because

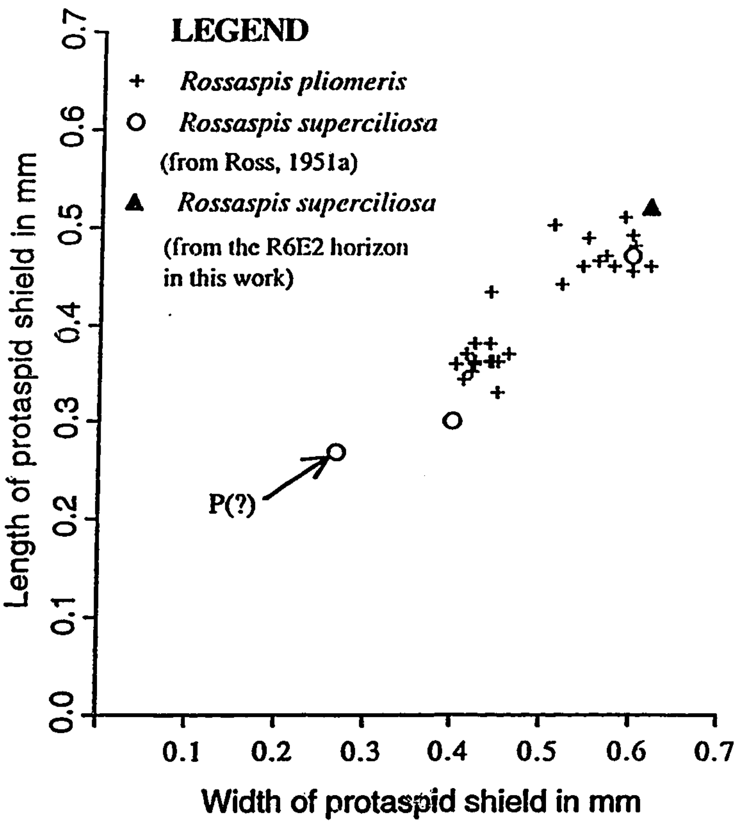

FIGURE III-5. Scatter plots of length versus width for protaspides of Rossaspis pliomeris Demeter, 1973 from horizon LR5 50.3 and Rossaspis superciliosa Ross, 1951. Note that protaspid instars of R. superciliosa (measurements from Ross, 1951b) fall within similar size ranges of those of R. pliomeris, except for the smallest, questionable instar, indicated by P(?).

fixigenal field is pitted; 6) posterior fixigenal spines are stouter and longer than other two spine pairs, and distance between posterior pair is greater (0.31 to 0.34 mm, compared to 0.12 to 0.15 mm in stage 1); 7) small protopygidium (16-23% of protaspid shield length) is differentiated behind protocranidium by moderately deep marginal furrow; pair of short, blunt and tubular protopygidial marginal spines is directed backwards and inwards; posterior margin is rounded; 8) ventral doublure between anterior and posterior fixigenal spine base is modified to splay out laterally into number of bifurcated marginal spines; 9) immediately besides palpebro-ocular ridge, facial suture is curved backwards, indicating presence of small triangular librigenae.

Meraspid and Holaspid Description -- Meraspid period appears to begin with cranidial length of 0.44 mm (smallest cranidium). Meraspid cranidium is semicircular in outline. Subcylindrical glabella occupies relatively smaller portion, compared to stage 2 protaspides; holaspid glabella becomes larger and attains a subrectangular shape. Anterior border and L4 become clearly separated by deep furrow (anterior border + preglabellar furrows) with growth. Palpebro-ocular ridge in holaspid cranidium is clearly separated from anterior border by anterior palpebro-ocular ridge furrow. Each glabellar lobe of early meraspid cranidium has pair of short glabellar tubercles adjacent to axial furrow (equivalent to I-1, II-1, III-1 and IV-1, according to Evitt and Tripp's (1977) system); with growth, one more pair of tubercles (=V-1) is added into L4, so that a larger meraspid cranidium has five distinct pairs of glabellar tubercles. In later meraspid or early holaspid cranidia, number of irregularly dispersed short spines are added to those glabellar tubercles such that those tubercles are not perceptible, and those spines and tubercles are reduced into fine granules in later holaspid cranidium. A strong node develops on occipital ring. Each glabellar furrow of early meraspid cranidium is represented by a small triangular indentation alongside glabella; in contrast, holaspid glabellar furrows are incised as relatively long furrows, and directed backwards and inwards. S3 is placed behind posterior palpebro-ocular ridge furrow on meraspid cranidium; later in holaspid cranidium, S3 is positioned opposite proximal ends of palpebro-ocular ridge, since ridge moves farther backwards. Fixigenal field of meraspid cranidium is covered by a number of small spines and pits, and that of holaspid cranidium is covered only by pits. Lateral and posterior cranidial borders are ornamented by row of spines, and in holaspides, these spines disappear. On anterior border of early holaspid cranidium, row of small spines is developed and these spines become reduced to granules with growth. Lateral and posterior cranidial border is delineated by a shallow continuous furrow. Bifurcated marginal spines on ventral side of cranidium are retained between anterior and posterior fixigenal spines only during early part of meraspid period, and then these spines disappear in later ontogeny. Posterior fixigenal spine becomes increasingly stouter and longer than other two pairs, and is directed posteriorly; in holaspid period, anterior and midfixigenal spine pairs disappear and posterior pair (genal spine) is divergent.

Smallest transitory pygidium is subsemicircular in outline and 0.30 mm long (sag.). Axis tapers backwards and bears four axial rings. Four pleural ribs develop laterally into long spines, which are tubular and gently curve inwards; anterior three pleural ribs are separated by broadly-impressed interpleural furrows. Slender (tr.) anterior pleural band (= 'lateral articulating ridge' of Ross, 1951b) develops in front of anteriormost pleural rib. Two or three short spines develop along ridge of each pleural rib and short spine pair develops on each axial ring. Holaspid pygidium has strongly tapering axis with triangular terminal piece and four pleural spines.

Discussion -- The continuous and gradual morphologic changes between stages 1 and 2, including retention of highly vaulted lateral end of the 'anterior rim', a subquadrate outline and a relatively convex lateral profile, cast no doubt in incorporating both as larval growth stages of *Rossaspis pliomeris*. Furthermore, both stages occur in the same horizon (LR5 50.3).

Ross (1951b) described the ontogeny of *Rossaspis superciliosa* from Zone F of the Garden City formation, and recognized three protaspid instars, mainly based on morphologic details, not morphometric grouping. The smallest protaspis (Ross, 1951b, pl. 32, fig. 2, fig. 4a) of R. superciliosa is 0.27 mm in length, and has four pairs of submarginal (fixigenal) spines and an unsegmented spindle-shaped axis. From his illustration, a sagittal furrow on the axis of this small protaspis appears to be evident, which was not described. The existence of the first pair (from the anterior) of fixigenal spines is dubious, because no other phacopid protaspides with four pairs of spines have been reported; the pair could be clay materials which are attached to the protaspid carapace. The association of the smallest protaspis with the larger protaspides of R. superciliosa appears not to have been well substantiated, because too many morphologic discrepancies exist between them. Similar morphologic details, except submarginal spine pairs, to this smallest protaspis are found in some Upper Cambrian ptychopariid protaspides, for instance, the 'anaprotaspis' of Arapahoia aspinosa (Hu, 1986, pl. 17, fig. 1, text-fig. 19A). For the present, it is not clear which taxon this protaspis belongs to, since no ptychopariids occur in the horizons of this work.

Stage 1 protaspides of Rossaspis pliomeris are comparable to the second large protaspid specimen of Rossaspis superciliosa (Ross, 1951b, pl. 32, fig. 3 and fig. 4b); both have a similar size range (in fact, Ross' specimen is a little smaller than stage 2 protaspides; see Figure III-5), three pairs of fixigenal spines which have the same position and orientation, highly vaulted lateral ends of 'anterior rim' and a segmented axis. The number of protoglabellar lobes and bilobation are different from each other; four lobes and absence of bilobation in R. superciliosa, and three lobes with bilobed L2/L3 in R. pliomeris. Ross' (1951b) third specimen (pl. 32, fig. 4, fig. 4c) shows a greater gross similarity to stage 2 protaspides of R. pliomeris than between the second and stage 1; Ross' specimen falls within the size range of stage 2 protaspides (Figure III-5). The only difference is the number of protopygidial spines; three spine pairs were reconstructed in Ross' drawing (1951b, fig. 4c) and description for the third specimen of R. superciliosa, whereas one pair is observed in stage 2 of R. pliomeris. However, the posteriormost pair of Ross' drawing is suspicious, since the pair is not clearly seen in the illustration. Furthermore, one protaspid specimen representing the same stage (Plate III-4.17) as Ross' third specimen was obtained from R6E2 (Zone F). The obtained specimen has two pairs of protopygidial spines and thus, Ross' third specimen is inferred to have only two pairs of marginal spines. The other difference between Ross' third specimen and stage 2 of *R. pliomeris* is the presence of bifurcated marginal spines between anterior and posterior fixigenal spine pairs of the latter, which was not described and illustrated by Ross (1951b) for *R. superciliosa*. However, the possession of those spines in *R. superciliosa* is also manifested by a specimen obtained in this work (Plate III-4.17).

Comparison of the holaspid cranidium of *Rossaspis pliomeris* with that of *Rossaspis superciliosa* (compare Plate III-3.10 and Plate III-4.16) suggests that the holaspid period begins with such morphologic details as a distinctly impressed preglabellar furrow, an anterior palpebro-ocular ridge furrow and a lateral border furrow, a rectangular glabella, the disappearance of anterior and midfixigenal spine pairs, and backwardly and inwardly directed glabellar furrows. These features are observed in a cranidium with 0.88 mm in sagittal length (Plate III-3.10) in *R. pliomeris*. Some of these features were mentioned by Ross (1951b, p. 148), who placed the boundary between the meraspid and holaspid periods of *R. superciliosa*, at between his eighth (pl. 32, fig. 9; 0.96 mm in sagittal length) and ninth cranidium specimen (pl. 32, fig. 10; 1.22 mm in sagittal length). With growth, the anterior border of *R. superciliosa* becomes narrower than in *R. pliomeris*, and the genal spine and palpebro-ocular ridge become shorter than the latter species. The other significant distinguishing feature between the adult trilobite of these two species is the number of pygidial marginal spines; five in *R. superciliosa* (Plate III-4.19; Ross, 1951b, pl. 31, fig. 19) and four in *R. pliomeris* (Plate III-3.11; Demeter, 1973, pl. 2, fig. 12). Thus, *R. superciliosa* consistently retains one more pygidial rib than *R. pliomeris* during ontogeny. It can be speculated that the number of pygidial ribs of each species increments at the equal rate, in other words, the number of pygidial ribs of the different species of the genus

Rossaspis may be controlled by an equal developmental regulation mechanism.

Comparison with Encrinurid, Pterygometopine, and Dalmanitid protaspides -- *Rossaspis pliomeris* and encrinurine and/or cybeline protaspides share several morphologic similarities, from which their phylogenetic relationships can be hypothesized. Encrinurine ontogeny has been described by several workers: 'metaprotaspides' of *Encrinuroides tholus* and *Encrinuroides neuter* (Evitt and Tripp, 1977); *Encrinuroides rarus* (Chatterton, 1980); *Physemataspis insularis* (Edgecombe, et al., 1988; Speyer and Chatterton, 1989); *Mackenziurus reimeri* (Edgecombe and Chatterton, 1990). Stage 1 protaspides (Plate III-3.1, 3, 7, Plate III-4.1-3) of *R. pliomeris* are not comparable to any encrinurine protaspides, since all of these encrinurines belong to 'Pb' (instars after protopygidium appears). However, some ontogenetic transformations between stages 1 and 2 (Plate III-3.2, 4, 8, Plate III-4.4-6) of *R. pliomeris* are shared by two instars of encrinurine protaspides (see below). The comparison in Table III-6 was mainly made with *Physemataspis insularis*, because hat species represents the earliest member (Llandeilian) of the subfamily and morphologic details were well described (Edgecombe, et al., 1988) and two similarities are explained in details below, in terms of homology and ontogenetic transformation.

Most encrinurine protaspides have a pair of distinctly raised swellings along the anterior margin, which tapers and lowers proximally and reaches the axial furrow (e.g., *Physemataspis insularis*, Speyer and Chatterton, 1989, fig. 4B). This swelling pair occurs in stages 1 and 2 protaspides of *R. pliomeris* (see Plate III-3.2) In later ontogeny, the swelling pair becomes the palpebro-ocular ridge in *R. pliomeris*, and a highly vaulted palpebral lobe + elongated (tr.) eye ridge in encrinurines. One similar protaspid structure becomes two distinguishable features in the different trilobite taxa. The protaspid similarity, however, allows establishment of homologous relationships between the palpebro-ocular ridge of *R. pliomeris* and the palpebral lobe + eye ridge of encrinurines. In fact, the separation of

TABLE III-6. Comparison of ontogenetic morphologic transformations during protaspid period (with some notes for transformations occurring in later ontogeny) of the Protopliomeropinae (*Rossaspis pliomeris*), the encrinurines (represented by *Physemataspis insularis*) and the advanced cybelines (*Cybeloides cimelia*).

	Rossaspis pliomeris	encrinurines	advanced cybelines
change in outline of protaspides	subquadrate to circular	subquadrate to circular	subtrapezoidal to circular
torulus	indistinct	very distinct	rather distinct
circumocular tubercles	only in stage 2	present in both instars (absent in some species[1])	present in both instars
change in shape of L4	subtrapezoidal to circular	circular	subtrapezoidal
bilobation of proto- or glabellar lobes	present only in stage 1	present in both instars (indistinct in some species[2])	absent
librigenae	confined by the anterior fixigenal spine	confined by the anterior fixigenal spine	confined by the anterior fixigenal spine
# of protopygidial ribs (or spines)	0 to 1	1 to 3	1 to 3
palpebral lobe and eye ridge	combined throughout the whole ontogeny as palpebro-ocular ridge	combined (separated in later ontogeny)	combined (separated in later ontogeny)
glabellar tubercles	absent (appear in meraspides)	present in both instars (addition with growth)	present in both instars (addition with growth)
spines on anterior cranidial border	absent (appear in meraspides)	present both instars (develops into tubercles)	present both instars (develops into tubercles)
position of midfixigenal spine	moves forwards from behind S1 to in front of S1	remains in front of S1	remains in front of S1
length of fixigenal spines	equally long three pairs	shorter midfixigenal spine	shorter midfixigenal spine
marginal spines	present only in stage 2 as bifurcated ones	present in both instars as unbifurcated ones	present only in stage 2 as bifurcated ones

([1] *Encrinuroides neuter*; [2] *Encrinuroides tholus* and *Encrinuroides rarus*) the palpebral lobe from the eye ridge in encrinurine holaspides is not due to the development of a furrow, but due to elevation of the palpebral lobe relative to the eye ridge. Furthermore, the eye ridge of encrinurines is clearly separated from the anterior border (e.g., Evitt and Tripp, 1977, fig. 7C) as in R. pliomeris. Such a homology statement, further, suggests that the proximal portion of the palpebral lobe of protaspides and holaspides of the pliomerid trilobites represents the eye ridge, not a proximally extended palpebral lobe.

The midfixigenal spine pair moves forward between stages 1 ('Pa') and 2 ('Pb') of Rossaspis pliomeris, relative to S1 (compare Plate III-3.1 and Plate III-3.2), while the pair remains in front of S1 during the protaspid period of encrinurines. Obviously, the character of the midfixigenal spine pair is not applicable to 'Pa' of the encrinurines, in the ontogeny of which no instars in 'Pa' exist, since calcification and appearance of protopygidium take place simultaneously. In 'Pb', each trilobite taxon shows a different condition, in front of S1 in encrinurines and opposite S1 in R. pliomeris. Each transformation of the position of the spines of both trilobite taxa, also is a valid dissimilarity for phylogenetic inference, as long as the transformation concerns the change during the interval in which the spine pair is present.

Among the morphologic differences shown in Table III-6, such features as glabellar tubercles and spines on the anterior border appear to show heterochronic patterns of development. These features appear in the meraspid period of Rossaspis pliomeris (Plate III-4.10-12) while they are present from the protaspid period of encrinurines. Based on the assumption that R. pliomeris could be ancestral to encrinurines, the earlier appearance of these features in encrinurines may be interpreted as the result of accelerated (peramorphic) development.

Evitt and Tripp (1977, pl. 19, figs. 1-4, fig. 16A) described a single protaspid stage of Cybeloides virginiensis seca from the Late Ordovician (early Caradocian) Lincolnshire Formation. Two protaspid instars of Cybeloides cimelia, designated 'small' and 'large', were described by Chatterton (1980, pl. 15, figs. 1-10, figs. 10D-10G). More morphologic features of these cybeline protaspides are shared with encrinurine protaspides than are shared with protaspides of *Rossaspis pliomeris* (Table III-6). Having bifurcated marginal spines on the protaspides is a conspicuous similarity between the advanced cybelines (see Chatterton, 1980, pl. 15, fig. 6) and *R. pliomeris* (Plate III-3.8-9) The subtrapezoidal outline of the protaspid shield and no development of bilobation of these cybeline protaspides distinguish them from *R. pliomeris* and encrinurine protaspides.

Rossaspis pliomeris shares some larval morphologies with pterygometopine and dalmanitid trilobites. The ontogeny of these trilobite groups is relatively well described and illustrated for the following species: *Dalmanitina olini* (Upper Ordovician, Temple, 1952), *Dalmanitina socialis* (Lower Devonian, Whittington, 1956), *Calyptaulax annulata* (Middle Ordovician, Shaw, 1968 and Speyer and Chatterton, 1989), and *Calyptaulax callirachis* (Middle Ordovician, Chatterton, 1980). The conspicuous difference between these phacopine protaspides and protaspides of *R. pliomeris* is the lack of anterior and/or midfixigenal spine pairs in some of the phacopine protaspides (e.g. *D. olini*, Temple, 1952, pl. 4, figs. 1 - 3; *D. socialis*, Whittington, 1956, pl. 24, figs. 6 - 12). Protoglabellar furrows of these protaspides are not continuous across the protoglabella, rather represented by small and triangular depressions alongside the protoglabella (e.g., *C. annulata*, Speyer and Chatterton, 1989, fig. 10E). Of interest is that this type of glabellar furrow is observed in the early meraspid cranidium of *R. pliomeris* (Plate III-4.10). Protaspid morphologic similarities shared between pterygometopines and dalmanitids, and *R. pliomeris* are: 1) pitted fixigenal field of stage 2 of *R. pliomeris* and late protaspides of *D. olini* and *C. annulata* and *C. callirachis* (pits are retained into the holaspid period of *R. pliomeris*, while they disappear in later ontogeny of the latter three species, forming a granulate holaspid fixigenal field); 2) subtrapezoidal L4 of stage 1 of *R. pliomeris* and late pterygometopine and dalmanitid protaspides; the L4 of the latter continuously expands into the holaspid period, while the L4 of stage 1 of *R. pliomeris* becomes circular shape and later, a part of the subrectangular holaspid glabella; 3) bifurcated marginal spines of stage 2 of *R. pliomeris* and late protaspides of *C. annulata* and *C.*

calliracheis; the bifurcated spines of R. pliomeris continue to exist into the early meraspid period.

The protaspid instar of 'Pa' was reported for the pterygometopines and Dalmanitina olini. The small protaspides of the genus Calyptaulax have a peculiar morphology, and are not comparable to stage 1 of R. pliomeris. They (with 0.33 mm of length and width) have a highly bulbous form indicative of a pelagic life habit, two pairs of submarginal spines (might be equivalent to anterior and posterior fixigenal spines), and their lateral border (or in part, doublure) strongly incurves downwards and then inwards to cover a relatively larger portion of the ventral opening than in any other early protaspides of phacopid trilobites. The protaspis of D. olini (Temple, 1952, pl. 4, fig. 1) is considered to represent the poorly preserved second larger stage (pl. 4, fig. 2), since it has six axial lobes, the last of which represent a protopygidial axial ring.

Subfamily CYBELOPSINAE Fortey, 1979

Taxonomic Remarks -- Fortey (1979b) established the subfamily Cybelopsinae, mainly based on homologous relationships between the long pygidial terminal piece of Pseudocybele and the finely segmented posterior portion of the pygidial axis of Ectenonotus. Larval and adult similarities described below between Pseudocybele nasuta and Protopliomerella contracta strongly suggest that the latter belongs to the Cybelopsinae. Furthermore, the genus Hintzeia, regarded as an ancestor to the cybelopsines by Fortey (1979, p. 108), is considered as a primitive cybelopsine, since the supposed homologous relationships of the posterior portion of the pygidial axis can be extended into the small terminal piece of Hintzeia. Also, this statement is supported by the observation that all pygidial ribs of Hintzeia aemula (Hintze, 1952, pl. 22, fig. 15) are directed backwards, while the pygidial ribs of the protopliomeropines (e.g., Rossaspis superciliosa, Ross, 1951b, pl. 31, fig. 19) are radially distributed.

Genus PROTOPLIOMERELLA Harrington, 1957

Type Species -- Protopliomerops contracta Ross, 1951, from Zone F of the Garden City Formation (early Arenigian), west side of Hillyard Canyon, southern Idaho, U.S.A.

Amended Diagnosis -- Cybelopsine trilobites with forward-tapering glabella. Pygidium with 5 marginal spines with very short free ends. Palpebro-ocular ridge forward-pointed. Hypostome with elliptical middle body, three lateral spine pairs and a posteromedian spine.

PROTOPLIOMERELLA CONTRACTA (Ross, 1951)

Plate III-5; Plate III-6; Figure III-6

Protopliomerops contracta ROSS, 1951, p. 136-137, pl. 33, figs. 15-19, 22-32; HARRINGTON, 1957, p. 811; DEMETER, 1973, p. 59, pl. 4, figs. 2, 6, 11, 12.

Protopliomerops aff. P. contracta, HINTZE, 1952, p. 207-208, pl. 22, figs. 11, 18-20.

Materials and Locality -- Most of the protaspides described herein were obtained from the SL6F horizon (within Ross', 1951b, Zone G) of the Garden City Formation (early Arenigian), exposed at the west side of Hillyard Canyon (Figures I-1 and III-1); a small number are from SR6 114 horizon, slightly higher in the same section.

Protaspid Description -- Three distinct protaspid instars are recognizable on the length versus width plot (Figure III-7). Stage 1 protaspides are 0.38 to 0.44 mm long and 0.42 to 0.47 mm wide, and have subtrapezoidal outline with rather straight anterior margin. Axis is moderately well defined by axial furrow; axial furrow becomes indistinct posteriorly; three protoglabellar and posteriormost axial lobes are recognizable; Lp/L2/L3 form a spindle-shaped axis and L4 is subtrapezoidal; L2 and L3 are subequal in size, wider than Lp, and

PLATE III-5. Protopliomerella contracta (Ross, 1951). All specimens from horizon SL6F. 1, dorsal view of stage 1 protaspis, UA 10965, x 67; 2, dorsal view of stage 2 protaspis, UA 10966, x 61; 3, dorsal view of stage 3 protaspis, UA 10967, x 58; 4, ventral view of stage 1 protaspis, UA 10968, x 60; 5, ventral view (displaced hypostome and librigenae) of stage 2 protaspis, UA 10969, x 65; 6, ventral view of stage 3 protaspis, UA 10970, x 54; 7, lateral view of stage 3 protaspis, UA 10971, x 61; 8, dorsal view of meraspid cranidium, UA 10972, x 35; 9, dorsal view of transitory pygidium, UA 10973, x 50; 10, magnified ventral view of hypostome of stage 2 protaspis, UA 10969, x 153; 11, dorsal view of holaspid cranidium, UA 10974, x 20; 12, dorsal view of holaspid pygidium, UA 10975, x 31.

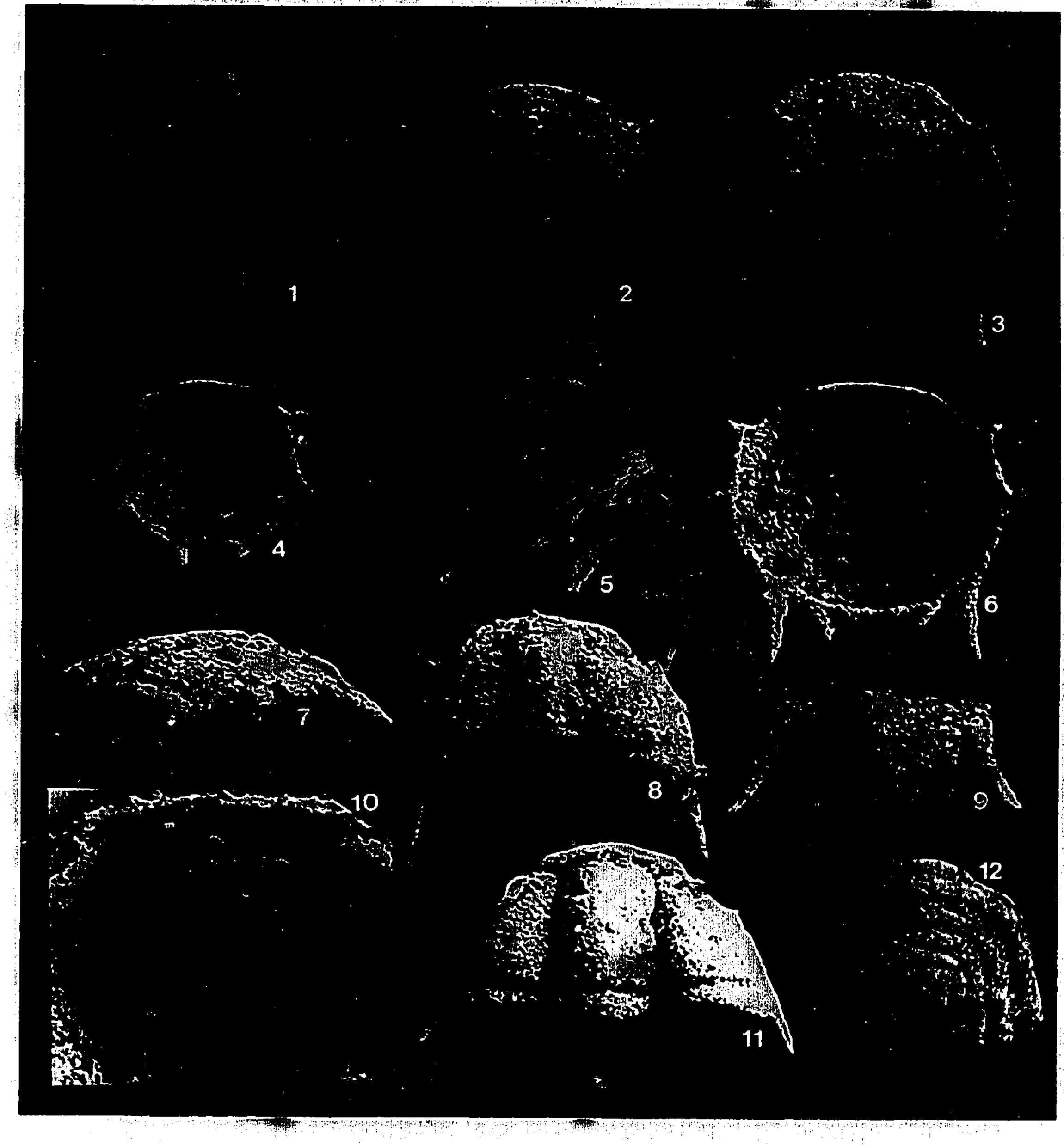
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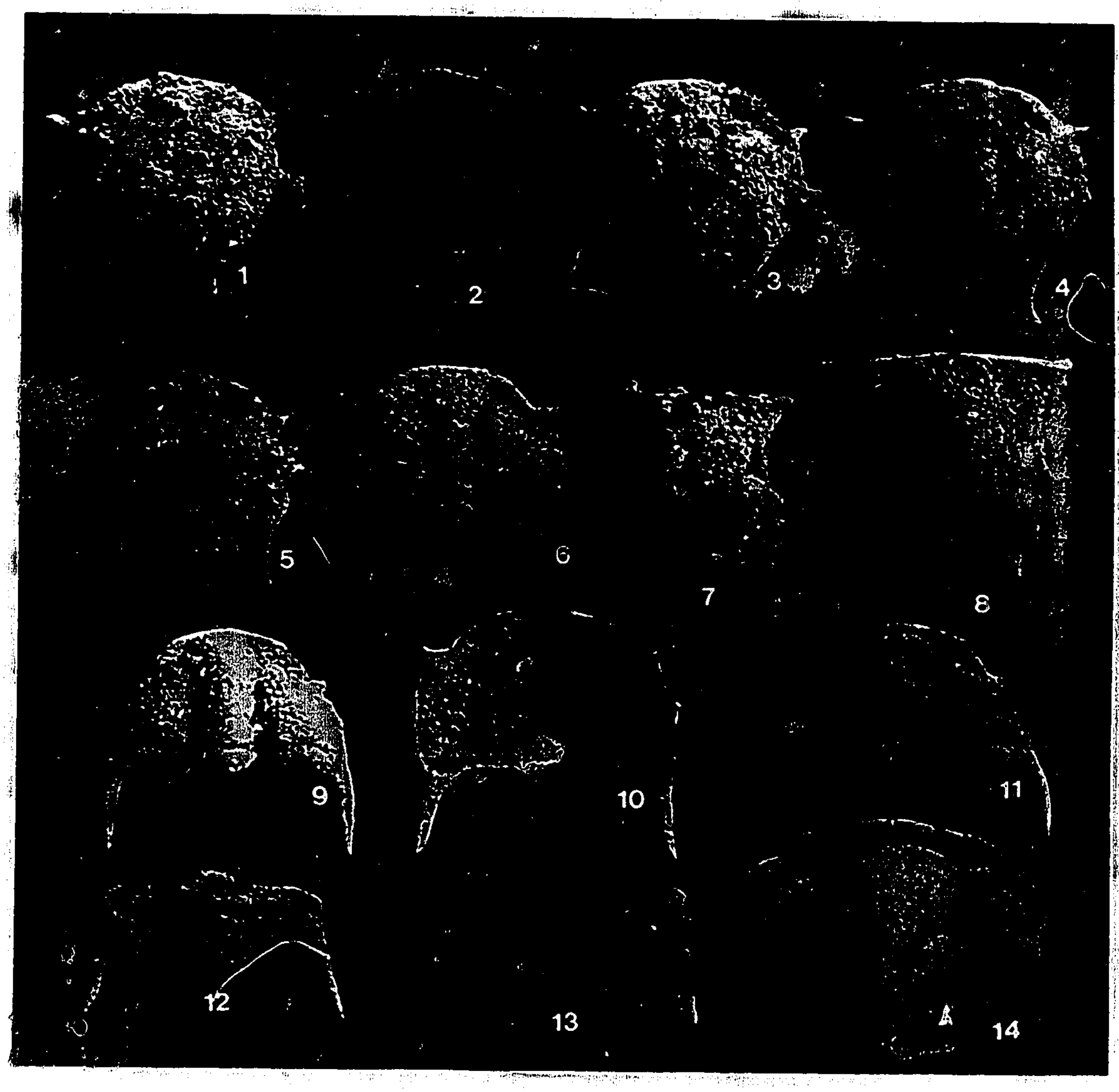
PLATE III-6. *Protopliomerella contracta* (Ross, 1951). All specimens from SL6F. 1, 2, dorsal views of stage 1 protaspides; 1, UA 10976, x 75; 2, UA 10977, x 68; 3, 4, dorsal views of stage 2 protaspides; 3, UA 10978, x 53; 4, UA 10979, x 57; 5, 6, dorsal views of stage 3 protaspides; 5, UA 10980, x 42; 6, UA 10981, x 42; 7, ventral view of late protaspid or meraspid hypostome, UA 10982, x 85; 8, ventral view of holaspid ? hypostome, UA 10983, x 40; 9, dorsal view of meraspid cranidium, UA 10984, x 26; 10, ventral view of meraspid cranidium, UA 10985, x 43; 11, dorsal view of holaspid cranidium, UA 10986, x 19; 12, 13, dorsal views of transitory pygidia; 12, UA 10987, x 52; 13, UA 10988, x 54; 14, dorsal view of holaspid cranidium, UA 10989, x 20.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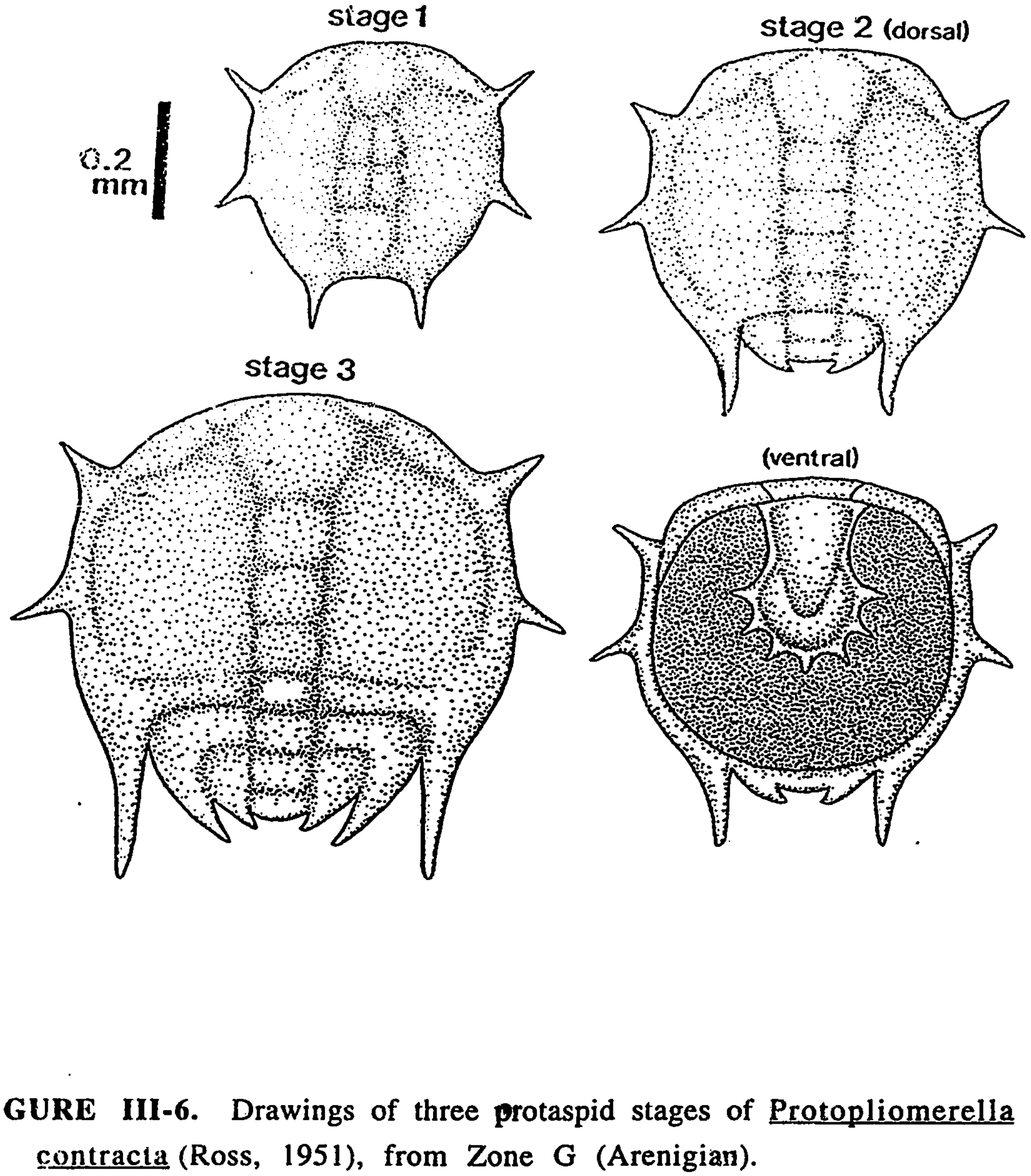


FIGURE III-6. Drawings of three protaspid stages of Protopliomerella contracta (Ross, 1951), from Zone G (Arenigian).

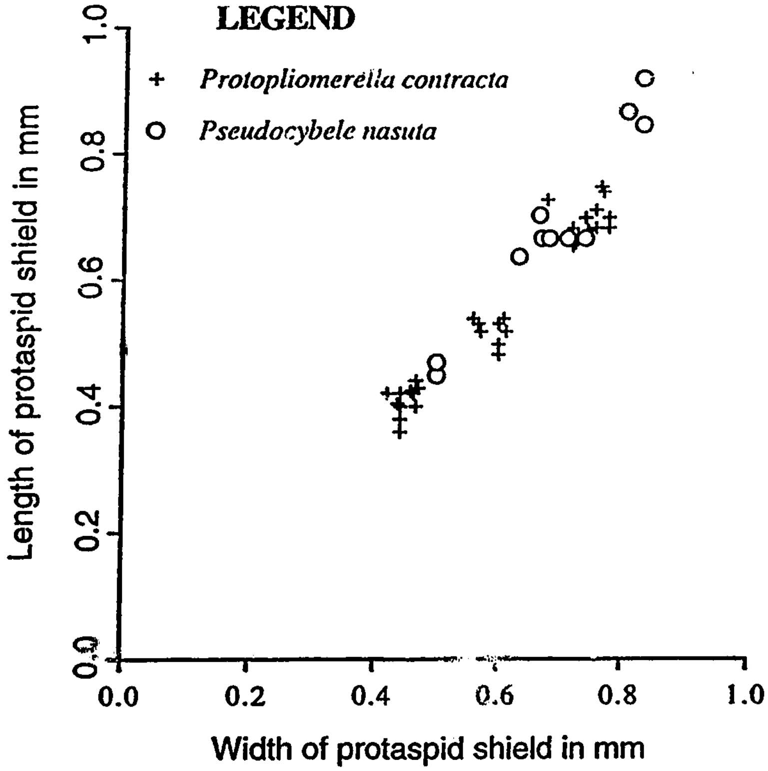


FIGURE III-7. Scatter plots of length versus width for protaspides of *Protopliomerella contracta* (Ross, 1951). Note that the three protaspid stages of *Pseudocybele nasuta* Ross, 1951 fall close to the morphometric ranges of the instars of *P. contracta*.

bilobed by sagittal furrow; transverse axial lobe furrows are shallow. Pair of anterior pits is located at anterolateral corners of L4. Anterior border and L4 are not clearly separated. Palpebro-ocular ridge is slightly defined by shallow and broad posterior palpebro-ocular ridge furrow. Three pairs of submarginal spines are of same length; anterior pair is placed in front of S3 besides palpebro-ocular ridge; midfixigenal pair is located in front of S1 or at half of sagittal length and directed posterolaterally; posterior pair runs back parallel.

Stage 2 protaspides are 0.52 to 0.54 mm long and 0.56 to 0.61 mm wide and with circular outline and more flattened profile than stage 1. Glabella is discernible, and four glabellar lobes and occipital ring are delineated; L4 is subtrapezoidal; rectangular and subequal sized L1/L2/L3 are shorter (sag.) and narrower (tr.) than L4, and form parallel-sided axis; occipital ring is narrower than L1/L2/L3; three pairs of glabellar furrows are very shallow and continuous across glabella. Palpebro-ocular ridge is distinguishable by anterior and posterior ridge furrows. Anterior and midfixigenal spines are shorter than posterior pair, and retain same orientation and relative position as in stage 1; posterior fixigenal spine pair projects posteriorly and slightly curves outwards. Lateral border is distinct and defined by border furrow which appears to be continuous into posterior palpebro-ocular ridge furrow. Protopygidium is small (12-17% of sagittal shield length), transversely elongated and separated from protocranidium by shallow marginal furrow which runs straight and then strongly turns backwards, encircling lateral margin of protopygidium. Pair of spines or small swellings develops along protopygidial posterior margin; spine pair is strongly convergent inwards. Doublure (except librigenae and rostral plate) is incurved and uniformly narrow. Hypostome is shield-shaped in outline; anterior margin gently convex; anterior wings small. Middle body is longer than broad, and inverted key-hole shaped; anterior lobe is elongated, triangular, convex and defined by narrow lateral border furrow and middle furrow and shallower anterior border furrow; posterior end of anterior lobe reaches five-sixths of hypostomal length; posterior lobe is convex, U-shaped and well defined by middle, lateral border and posterior border furrows. Lateral margin curves inwards between anterior wing and anteriormost pair of lateral border spines, positioned at one third of hypostomal length. Three lateral spine pairs and posteriormedian spine are developed along lateral and posterior border; those spines are stout and relatively short, and of same length.

Stage 3 protaspides are 0.65 to 0.75 mm in length and 0.72 to 0.78 mm in width and with more circular outline than earlier stages. This stage differs from stage 2 in following features: 1) axial furrow is deeper; 2) anterior palpebro-ocular ridge furrow becomes more impressed; posterior ridge furrow is narrower; 3) anterior fixigenal and midfixigenal spine pairs remain unchanged in relative size and position, while posterior pair is about four times longer than other spines, and distance between them is greater (0.53 mm in average) than stage 2 (0.28 mm in average); 4) lateral border furrow is more distinct; 5) protopygidium, with 20-29% of shield length, has pair of long marginal spines and pair of swellings or short spines along posterior margin; first marginal spine pair appears to be extension of posterior band of first protopygidial pleural rib, and has corresponding axial ring; first pleural rib has gently curving pleural furrow which reaches lateral pygidial margin.

Meraspid and Holaspid Description -- Meraspid period begins with cranidial length of 0.59 mm, which is continuous from protocranidium of stage 3 (protocranidial length of obtained largest stage 3 is 0.56 mm). Some morphologic changes between stage 3 protaspides and meraspid cranidium are: 1) most furrows become more deeply impressed; posterior cranidial border furrow deepens; preglabellar furrow is clearly incised; 2) glabellar furrows are discontinuous across glabella, directed backwards and inwards, and become evenly spaced; glabella becomes rectangular in shape; 3) anterior and midfixigenal spines are reduced; posterior pair is half of cranidial length in smallest meraspid cranidium and then become progressively shorter; 4) anterior palpebro-ocular ridge furrow is clearly impressed and differentiates ridge from anterior cranidial border. Holaspid cranidium is characterized by forward-tapering glabella, disappearance of anterior and midfixigenal spines, strongly divergent genal spine pair and forward-pointed palpebro-ocular ridge.

Smallest transitory pygidium is semicircular, with four pairs of marginal spines and corresponding axial rings and pleural ribs. First marginal spine (from anterior) is directed strongly outwards and reaches posterior end of pygidium; pleural ribs are defined by interpleural furrows; anterior two pleurae have shallow pleural furrows. Up to 5 pairs of pleural spines are present in the transitory pygidium. Holaspid pygidium shows strongly tapering axis with five axial rings and terminal piece; five pleural spines are coalesced along their entire length except for short free ends, and directed strongly posteriorly.

Discussion -- Stages 1 and 2 protaspides of Protopliomerella contracta are not similar to any non-pliomerid protaspides or even to pliomerid protaspides, such as Rossaspis pliomeris and Tesselacauda depressa, described herein; they are distinguished from those protaspides in having a more circular outline and relatively much flattened lateral profile. Stage 1 of P. contracta is similar to stage 1L of T. depressa, except for its relatively smaller size, three protoglabellar lobes, and more anteriorly located anterior fixigenal spine pair (Table III-1).

Ross (1951a) described and illustrated the full ontogeny of Pseudocybele nasuta from Zone J in the Garden City Formation. Additional material, which is equivalent to Ross' (1951a) 'anaprotaspid' stage, was illustrated by Fortey and Chatterton (1988, Pl. 19, fig. 15). Stage 1 protaspides of Protopliomerella contracta (Plate III-5.1, 4, Plate III-6.1, 2) are similar to Ross' (1951a) 'anaprotaspid' stage (pl. 82, figs. 1, 2; 0.45 mm in sagittal length) in both having similarly positioned and oriented submarginal spines and subtrapezoidal outline. They differ from each other in that the 'anaprotaspis' of P. nasuta has four protoglabellar lobes, which are very distinctly defined by transverse furrows, and a less discrete and shorter posterior fixigenal spine pair. Ross (1951a) recognized four 'metaprotaspid' stages in the protaspid period of P. nasuta, on the basis of relative length and number of pygidial axial segments; only three larger stages were described and illustrated. Ross' (1951a) second 'metaprotaspid' stage (pl. 82, figs. 3 to 9) was described as having two protopygidial axial rings and one pair of marginal spines; the third stage (pl. 82, figs. 10 to 12) has three axial rings and two spine pairs; and the fourth stage (pl. 82, fig. 13) has four axial rings and three spine pairs. Thus, it can be envisaged that the first stage, even if unavailable, has only one protopygidial axial ring without a corresponding spine pair. However, Ross' (1951a) second 'metaprotaspid' specimens, which were described with one pair of protopygidial marginal spines, obviously display an additional tiny pair of spines or swellings developed between the relatively long marginal spine pair (clearly shown in pl. 82, fig. 9); and this is observed in Ross' third and fourth specimens as well. The same additional small swelling or tiny spine pair also is observed in stages 2 and 3 of *P. contracta*. Thus, with respect to the number of protopygidial marginal spines, stages 2 and 3 of *P. contracta* (Plate III-5.2, 3, 5-7, 10, Plate III-6.3-6) appears to be comparable to Ross' undescribed first 'metaprotaspid' stage and the second stage, respectively. Ross' (1951a) third and fourth 'metaprotaspid' stages are likely to represent a degree 0 meraspis, as Ross (1951a, p. 585) mentioned, but he argued that only his fourth 'metaprotaspid' stage should be assigned to the meraspid period, because the smallest transitory pygidium (pl. 83, fig. 5) has three spinose segments and a terminal segment, which is structurally the same as the protopygidium of the fourth 'metaprotaspides'. However, the three pairs of pygidial marginal spines are already attained in Ross' third specimen, as mentioned earlier. Additionally, the cranidial length of the third and fourth 'metaprotaspid' stages is 0.62 and 0.66 mm (the measurement from the illustration), which is relatively longer than the length of the smallest meraspid cranidium (Figure 12.8, with 0.59 mm in sagittal length) in this work. Thus only three instar stages exist during the protaspid period of *P. nasuta*.

The described hypostomes (Plate III-5.10) of stage 2 of *Protopliomerella contracta* and of *Pseudocybele nasuta* (Fortey and

Chatterton, 1988, pl. 19, fig. 15) show three pairs of lateral spines and a posteromedian spine. The two hypostomes are dissimilar to each other in that the former has lateral and posterior border, and relatively short and stouter spines (needle-like spines in the latter). These differences might be attributed to the life habit; stage 2 of P. contracta might be benthic and stage 1 of P. nasuta be pelagic. Such a hypostomal change along with life habit change is observed in Flexicalymene senaria (Chatterton, et al., 1990, figs. 6.4 and 6.7; P2 with needle-like spines and B1 with relatively short and stout spines). As well, the holaspid morphologies (Plate III-5.11, 12, Plate III-6.14; Ross, 1951b, pl. 33, figs. 25, 23, 32) of P. contracta are similar to Pseudocybele nasuta (Ross, 1951b, pl. 33, figs. 1, 14; Hintze, 1953, pl. 24, figs. 10, 11). Those similar morphologies are the forwardly pointed palpebro-ocular ridge, all pygidial ribs that are directed posteriorly (compare the radially distributed pygidial ribs of the protopliomeropines), tightly coalesced fifth pygidial ribs, three pairs of hypostomal lateral spines and one posteriormedian spine, and a pair of additional short glabellar furrows anterior to S3.

PHYLOGENETIC RELATIONSHIPS

Morphologic comparisons between two or more trilobites are used to deduce evolutionary relationships. Determination of both similarities and dissimilarities involves a priori assumptions of homology ('classical' homology definition, Patterson, 1982; 'primary homology', de Pinna, 1991; Rieppel, 1993), since similarities and dissimilarities are variations of morphologic features considered homologous. The initial assumptions of homology can not be equated with synapomorphies (see, Patterson, 1982), and later they either are refuted as homoplastic characters of convergent origin or further substantiated as synapomorphies within a phylogenetic (or cladistic) perspective. The different states of a homologous feature are categorized into derived and primitive (determine polarity), based on whether it is an evolutionary novelty from a common ancestor (derived) or it is still observable as the same state in the common ancestor (primitive) (Schoch, 1986; Ax, 1987). However, in practice, the common ancestor is not known and thus, it is necessary to employ empirical methods to determine the polarity of the character states, such as the outgroup comparison, ontogenetic, and paleontological methods (Eldredge, 1979; Eldredge and Cracraft, 1980; Schoch, 1986; Bryant, 1991). The shared derived features (synapomorphies) are the result of either sharing a recent common ancestor or convergence. Some putative synapomorphies are later suggested to be convergent, if they do not support the clade(s) in the most parsimonious tree(s). In contrast, other synapomorphies do support the most parsimonious tree, being confirmed synapomorphies to define the clade (Patterson, 1982; de Pinna, 1991).

The phylogenetic inferences suggested below were made by treating the problem as a succession of three-taxon problems (Patterson, 1981; Schoch, 1986, fig. 1.4). Given three taxa, there are three possible fully resolved (or dichotomous) cladograms. A preferred cladogram is deductively selected by excluding the other two possibilities, based on methodological parsimony criterion (Schoch, 1986; Wiley et al., 1991) by which the number of homoplasies (ad hoc assumptions) is minimized. The morphologic features that unite two taxa may or may not be indicative of monophyly as synapomorphies. This problem was resolved by determining the polarity of the character states; polarity determination appears to be controversial with regard to whether it is a priori or a posteriori in implementation (Nixon and Carpenter, 1993). Herein, polarity determination was made employing the outgroup comparison method (Watrous and Wheeler, 1981; Maddison et al., 1984) supplemented by the paleontological method (Eldredge and Cracraft, 1980). The state that is considered as primitive is found in a taxon that is outside of the ingroup taxa but is supposed to form a monophyletic group with the ingroup taxa, and/or is stratigraphically older than the ingroup taxa. This simultaneous use of two methods in one analysis does not violate any assumptions of either method (Bryant, 1991). The choice of the three taxa of interest and the outgroup is based on assumed primary homologies and previous phylogenetic works.

Alternatively, ancestor-descendant, not sistergroup, relationships of those taxa, where possible, were assumed, mainly based on evolutionary transformation of morphologies within the stratigraphic framework. This conventional method to infer evolutionary relationships obviously necessitates more complete fossil records to fill the missing links, which is not the case in this work. Despite of lack of many intermediate taxa, this evolutionary assumption is likely to be valid for future studies.

Comparison of protaspides of Tesselacauda depressa and Kawina sexapugia (Cheiruridae), and Rossaspis pliomeris and Protopliomerella contracta (Pliomeridae), summarized in Tables III-1 to 6, suggests that these trilobites are phylogenetically related to the three cheirurid subfamilies (Sphaerexochinae, Acanthoparyphinae and Cheirurinae) and two encrinurid subfamilies (Cybelinae and Encrinurinae). Additionally, their phylogenetic relationships to the Calymenidae and the Pterygometopinae, which are more distantly related to them, were briefly mentioned.

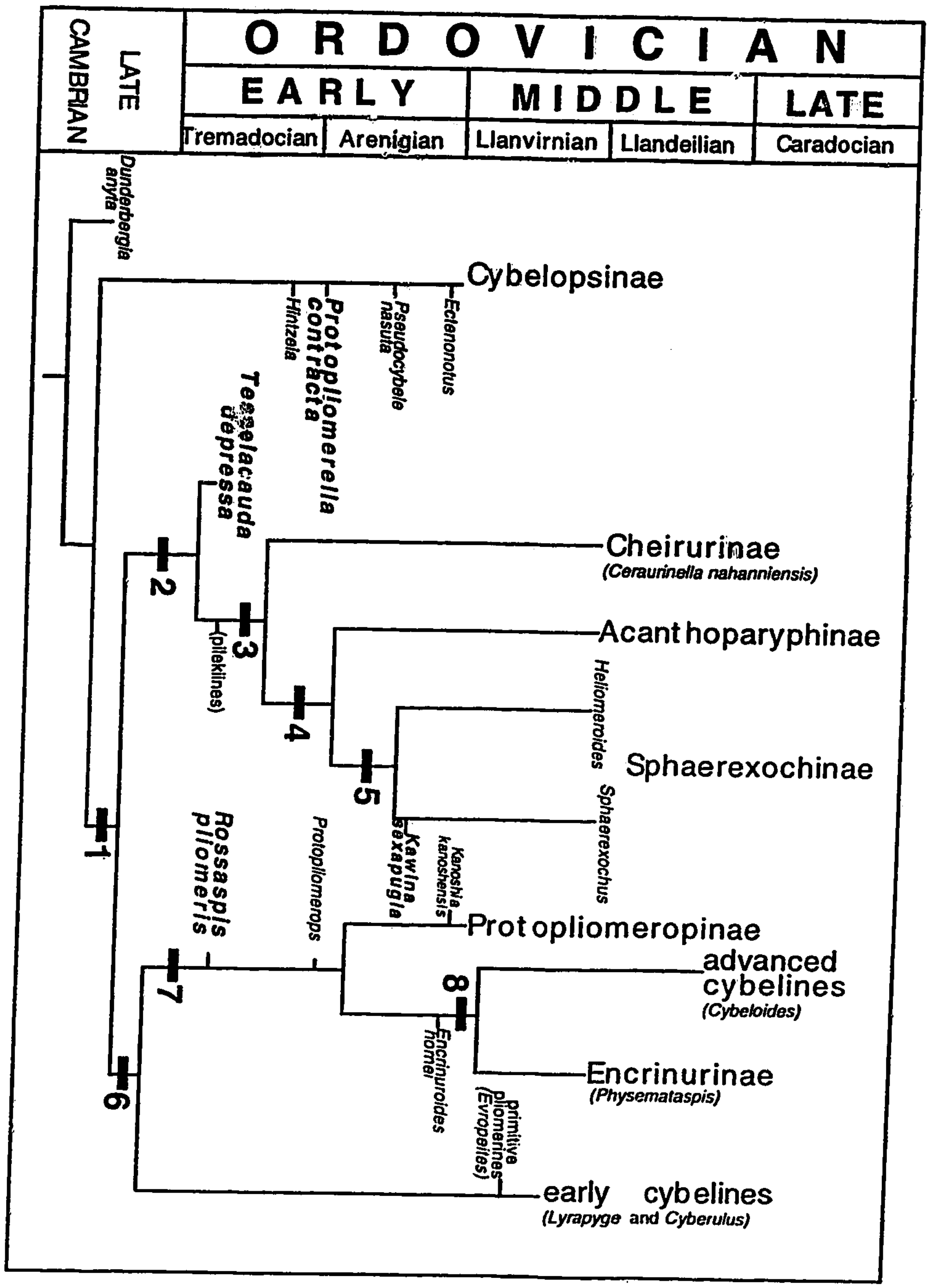
Relationships to the Cheirurid subfamilies -- Stages 1L and 2L protaspides of Tesselacauda depressa have some resemblances with protaspides of such cheirurid subfamilies as the Sphaerexochinae, the Acanthoparyphinae and the Cheirurinae (Tables III-2 to 4). The states of morphologic features found in T. depressa were considered as primitive, since the species is stratigraphically older than those subfamilies, and is less confidently considered to belong to the Cheiruridae (see remarks under Tesselacauda) so that it may be regarded as being outside of the Cheiruridae but forming a monophyletic group with those subfamilies.

Lane (1971, p. 79) noted the intermediate condition of cranidial (elongated glabella) and pygidial (larger free spines) morphologies of Kawina sexapugia between the Pilekiinae (a supposed ancestor to most younger cheirurid subfamilies) and the Sphaerexochinae, and further suggested that the later sphaerexochine members were derived from K.

sexapugia. The derivation of the sphaerexochines from K. sexapugia was also suggested by Chatterton (1980, p. 43) based on the comparison of ontogenetic transformation from meraspides to holaspides. The notion of K. sexapugia as an ancestor to the sphaerexochines may be further substantiated by similarities between early protaspides of K. sexapugia and the 'metaprotaspis' of Sphaerexochus (Korolevium) arenosus (Table III-1) and cranidial similarities between holaspides of the former and meraspides of the latter (see discussion under K. sexapugia). The indented posterior margin of the holaspid hypostomes of both species, not shared with other cheirurid species, adds support to that inference. Lane (1971, p.81) mentioned that other sphaerexochines such as Heliomeroides and Heliomera were separately derived from the above K. sexapugia - S. (K.) arenosus stock, indicative of the existence of two separate lineages within the Sphaerexochinae. Indeed, Heliomeroides freschaufae shows such unique features as backward-tapering protaspid shield, radiating holaspid glabellar furrows and two pairs of holaspid pygidial ribs, supporting Lane's suggestion. These unique features cause an unresolved taxonomic problem that Heliomeroides and Heliomera belong to the Sphaerexochinae (Whittington, 1965; Lane, 1971) or the Acanthoparyphinae (Chatterton and Perry, 1984; Chatterton, 1980). The sphaerexochines, K. sexapugia (Ross, 1951b, pl. 35, figs. 11-13), S. (K.) arenosus (Chatterton, 1980, Pl. 12, figs. 22, 26) and H. freschaufae (Chatterton, 1980, pl. 12, figs. 30, 38), share highly dorsally and/or laterally inflated glabella, narrower fixigenal area, slender (tr.) palpebral lobe and anterior border, and two or three densely granulate pygidial ribs with longer free ends. These features appear to be derived from the holaspid morphologies of T. depressa such as subrectangular glabella, five pairs of pygidial ribs, broader fixigenal area and equally long three pairs of glabellar furrows. Besides these holaspid shared features, the three sphaerexochine species share such larval features as bulbous lateral profile, indistinct posterior half of the axial furrows, more posteriorly located posterior fixigenal spine and posteriorly widening doublure, which also appear to be derived from rather flattened profile, distinct axial furrows and doublure with uniform width in protaspides of *T. depressa*. Of the above putative synapomorphies, the first three holaspid features occur in the Acanthoparyphinae (see below), so that they are likely to be synapomorphies at a more inclusive level. These synapomorphy statements demonstrate that the two lineages of the Sphaerexochinae form a monophyletic group, relative to *T. depressa* (an outgroup).

Alternatively, *Tesselacauda depressa* (Tremadocian) might be inferred as a direct ancestor of *Kawina sexapugia* (late Arenigian) which gave rise to one of the Middle Ordovician Sphaerexochinae lineage, including *Sphaerexochus* (*Korolevium*) *arenosus*. This supposed lineage may be manifested by the morphologic transformations from *T. depressa* to *S.* (*K.*) *arenosus*; *K. sexapugia* (Plate III-2.16, 17; Ross, 1951b, pl. 35, figs. 6, 7, 11-17, 19-21) displays an intermediate condition between *T. depressa* (Plate III-1; Ross, 1951b, pl. 31, figs. 27-31) and *S.* (*K.*) *arenosus* (Chatterton, 1980, pl. 12, figs. 1-5; Chatterton and Ludvigsen, 1976, pl. 13, figs. 1-48). The transformations (or evolutionary trends) of holaspid morphologies are dorsal and lateral inflation of glabella, reduction of pygidial spine number from four to three, deepening of the indentation along the posterior margin of the hypostome, narrowing of the anterior border and palpebro-ocular ridge, disappearance of anterior palpebro-ocular ridge, and from less to more densely granulate pygidial ribs. However, these supposed phylogenetic transformations (or trends) are not restricted to the supposed phyletic lineage, but observed in the possible lineage from *T. depressa* to other cheirurid subfamilies. On the other hand, the evolutionary transformations of larval features such as the posteriorly indistinct of axial furrows, the posteriorly widening doublure and shorter of fixigenal spines occur only in the supposed lineage and lend support to this ancestor-descendant hypothesis, when combined with the stratigraphic occurrences of the taxa involved. This ancestor-descendant relationship is merely a hypothesis, which will be evidenced by more complete fossil records to fill the large stratigraphic gaps between the sphaerexochines and *T. depressa*. Thus, *T. depressa* is considered as a, not immediate, sistergroup to the Sphaerexochinae, as depicted in Figure III-8.

FIGURE III-8. Inferred phylogenetic relationships of the cheirurine trilobites described herein with the cheirurid subfamilies (Cheirurinae, Acanthoparyphinae and Sphaerexochinae) and the encrinurid subfamilies (Encrinurinae and Cybelinae) with their stratigraphic distributions. The numbered synapomorphies are as follows: 1, two protaspid instars (stages), circumocular fixigenal tubercle pairs, circular L4 in 'Pb', and four pairs of holaspid pygidial ribs; 2, presence of holaspid pygidial pleural furrows; 3, narrower holaspid fixigenal field, two or three pairs of holaspid pygidial ribs, longer and posteriorly curved holaspid S1 furrow; 4, laterally inflated holaspid glabella, slender anterior border and palpebral lobe; 5, bulbous profile of protaspid shield, indistinct posterior half of protaspid axial furrow, posteriorly widening protaspid doublure, posteriorly located posterior fixigenal spine; 6, pitted protaspid fixigenal field; 7, torulus and marginal spines in protaspides; 8, shorter midfixigenal spine, protaspid fixigenal lobes abaxial to L1 to L2, all protaspid instars with protopygidium, glabellar tubercles on protaspides, size increase of tubercles on holaspid glabella and fixigenal field, more than 14 holaspid pygidial axial rings. (Species indicated by bold characters are described and illustrated in this work: trilobite taxa connected to the main lineages by a short branch, without assessing any synapomorphy, are potentially direct ancestors of descendant in those lineages).


ORDOVICIAN
EARLY
MIDDLE
LATE
Tremadocian
Arenigian
Llanvirnian
Llandeilian
Caradocian
LATE CAMBRIAN
Dunderbergia anyta
Cybelopsinae
Eclenonotus
Pseudocybele nasuta
Protopliomerella contracta
Hintzeia
Tesselacauda depressa
Cheirurinae
(Ceraurinella nahanniensis)
Acanthoparyphinae
Heliomeroides
Sphaerexochinae
Sphaerexochus
(pilekiines)
Kanoshia kanoshensis
Kawina sexapugia
Protopliomerops
Rossaspis pliomeris
Protopliomeropinae
advanced cybelines
(Cybeloides)
Encrinurinae
(Physemataspis)
Encrinuroides hornei
primitive pliomerines (Evropeites)
early cybelines
(Lyrapyge and Cyberulus)
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The derivation of acanthoparyphines from Kawina sexapugia was suggested by Chatterton and Ludvigsen (1976, p. 58), in particular, based on the similar development of pits on the thoracic pleurae and pygidial spines. If this suggestion reflects a real evolutionary history of the acanthoparyphines, K. sexapugia (the Arenig sphaerexochine) has given rise to two separate cheirurid subfamilies. The evolutionary origin of the acanthoparyphines from K. sexapugia is not as well supported as the evolutionary origin of the sphaerexochines (see above) by larval features. For the instars in 'Pa', there are numerous dissimilarities between K. sexapugia and the acanthoparyphines (e.g., Hyrokybe julli and Holia secristi) as shown in Tables III-2 and 3. Thus, the direct derivation of the acanthoparyphines from K. sexapugia is questionable. As shown in Tables III-2 and 3, the acanthoparyphine protaspides are more similar to Tesselacauda depressa than to the sphaerexochines, indicating the closer relationships of the former two taxa. However, the larval features shared by T. depressa and the acanthoparyphines are symplesiomorphies, which are also shared with cheirurine protaspides (Table III-4). Thus, the relationship of the Acanthoparyphinae and the Sphaerexochinae is best estimated by holaspid features shared by both families, such as dorsally inflated glabella, slender palpebral lobe and anterior border, and narrow fixigenal field, which are not shared with cheirurines. These features appear to have been derived from plesiomorphic states of T. depressa and unite the Acanthoparyphinae and the Sphaerexochinae as a monophyletic group. Other shared holaspid features such as less than four pygidial ribs, narrower fixigenal area, and densely granulate pygidial ribs (see Acanthoparypha evitti, Chatterton and Ludvigsen, 1976, Pl. 10, figs. 1-41) become synapomorphies at a more inclusive level, since they occur in cheirurine trilobites (see below), but not in T. depressa. The posteriorly pointed hypostomal posterior margin, not shared with the Sphaerexochinae and T. depressa, appears to uniquely characterize the Acanthoparyphinae.

The highly variable larval morphologies of the Cheirurinae make it less informative to compare only larval stages with other

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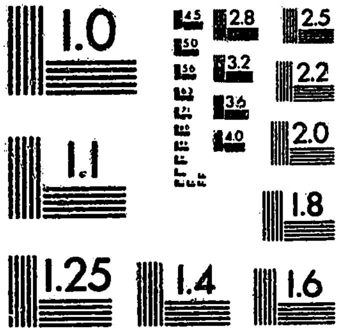
PM-1 3½"x4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT



PRECISION^{SM} RESOLUTION TARGETS

protaspides to infer phylogenetic relationships (Table III-4; see also comparison under *Tesselacauda depressa*). The larval similarities listed in Tables III-3 and 4 indicate a closer relationship of the Cheirurinae to the Acanthoparyphinae than to the Sphaerexochinae. Most of the shared features, however, occur in protaspides of *Tesselacauda depressa*, indicating that they are symplesiomorphies. As well, both subfamilies share two or three pairs of holaspid pygidial ribs with long free ends, which appears to be the synapomorphy to unite both subfamilies and the Sphaerexochinae at a more inclusive level. Thus, no larval and holaspid synapomorphies were detected to support the sistergroup relationship of the Cheirurinae and the Acanthoparyphinae. As suggested above, it is more plausible that the Cheirurinae is a sistergroup to the supposed monophyletic group of the Acanthoparyphinae + the Sphaerexochinae. These three subfamilies share one pair of protopygidial ribs, narrower holaspid fixigenal field, two or three pygidial ribs with long free ends, and longer S1 glabellar furrow. These shared features are not shared with *T. depressa* and appear to be derived from plesiomorphic conditions of protopliomeropines or cybelopsines (probable sistergroup), indicating that they are synapomorphies to unite the cheirurid subfamilies. If the smaller protaspid instars, designated stages 1S to 3S, are correctly assigned to *T. depressa*, fewer (one or two) protaspid instars (stages) might be another larval synapomorphy to define the three cheirurid subfamilies. Subrectangular glabella and broad palpebro-ocular ridge of the holaspid cheirurines (*Ceraurinella nahanniensis*; Chatterton, 1980, pl. 9, fig. 20), shared with protopliomeropines and cybelopsines as well as *T. depressa*, were independently acquired by those taxa, in other words, are of convergent origin.

Derivation of the younger cheirurid subfamilies from the Pilekiinae was suggested by Whittington (1961), Lane (1971) and Přibyl et al. (1985), all of whom included *Tesselacauda* within the Pilekiinae. However, the taxonomic position of *Tesselacauda* appears to be uncertain and it is suggested herein that *Tesselacauda* is a separate genus from the Pilekiinae and the Protopliomeropinae, based on holaspid morphologies (see above under *Tesselacauda*). Accordingly, the phylogenetic relationships between other pilekiine trilobites and *Tesselacauda depressa*, herein considered as a sistergroup to the three cheirurid subfamilies, are not clear enough to argue for and against the earlier workers' suggestion. This uncertainty is partly because the pilekiine protaspides have not been described, and partly because the holaspid morphology of the pilekiines is so variable that its subfamilial diagnosis seems to embrace the morphologic variation of the pliomerids and the cheirurids. Thus, we consider that Demeter's (1973, p. 52, text-fig. 4) suggestion that *T. depressa* was an ancestor of the pilekiines is implausible. Cheirurid trilobites, including *T. depressa*, the pilekiines and the three cheirurid subfamilies, possess holaspid pygidial pleural furrows, as a synapomorphy, derived from 'no pleural furrows' of *Rossaspis pliomeris* (Protopliomeropinae) and *Protopliomerella contracta* (Cybelopsinae). The pleural furrows have been phylogenetically lost in later members of the cheirurid lineage, which may be interpreted as a character reversal.

Relationships to the Encrinuridae -- Edgecombe et al. (1988), in their work on the Encrinuridae and the Staurocephalidae, selected *Pseudocybele nasuta* (the Cybelopsinae) as the outgroup (an immediate sistergroup). However, *Tesselacauda depressa* and *Rossaspis pliomeris*, described in this work, appear to share more larval similarities with the early cybelines (see discussion under *T. depressa*), and the advanced cybelines + the Encrinurinae (Table III-6), respectively than *P. nasuta* does. Thus, it can be inferred that both species are more closely related to the Encrinuridae than *P. nasuta*.

Monophyly of the advanced cybeline (*Cybeloides*) + the Encrinurinae (Edgecombe et al., 1988, fig. 11) is supported by two larval synapomorphies: fixigenal lobes abaxial to L1 and L2, and shorter midfixigenal spine pair. Along with Tremadoc protoplimeropines (e.g., *Rossaspis pliomeris*), the two trilobite taxa form a monophyletic group, relative to *Tesselacauda depressa* (an immediate outgroup), sharing 'two protaspid instars' and a torulus, which do not occur in the cybelopsines. Relative to *R. pliomeris* as an immediate outgroup to the encrinurine + the advanced cybelines, the last two trilobite taxa share such derived larval features as glabellar tubercle pairs, spines on the anterior border, all instars belonging to 'Pb' (with protopygidium), and highly vaulted palpebral lobe, along with the above two larval synapomorphies. Interestingly, the first two shared features occur in the meraspid period of *R. pliomeris* (Table III-6), and their presence in the protaspides of encrinurines and advanced cybelines might be interpreted as the result of heterochronic evolution. Holaspid synapomorphies, such as large tubercles on the glabella and fixigenal field, more than fourteen pygidial axial rings, eye ridge separated from a highly vaulted palpebral lobe, and inflated L4, further reinforce the sistergroup relationship of this group to *R. pliomeris* (compare *Encrinuroides rarus* and *Cybeloides cimelia*, Chatterton and Ludvigsen, pl. 15, figs. 1, 16 and pl. 14, figs. 8, 19, with Plate III-3.1-4). The last two features also occur in the early cybelines (e.g., *Cybelurus halo*, Fortey, 1980, pl. 22, figs. 4, 10) and thus, their validity as a synapomorphy at this level is lost.

The closer phylogenetic relationships of advanced cybelines + Encrinurinae to the Protopliomeropinae (*Rossaspis pliomeris*) can be better substantiated by considering two intermediate species of late Arenigian to early Llandeilian age: *Kanoshia kanoshensis* (a late protopliomeropine; Hintze, 1952, pl. 23, figs. 1-4) and *Encrinuroides hornei* (a primitive encrinurine; Dean, 1973, pl. 3, figs. 4, 7-13). The holaspid morphologies are supposed to transform between the protopliomeropines (*R. pliomeris*, Plate III-3.10, 11; *Rossaspis superciliosa*, Ross, 1951b, pl. 31, figs. 19, 20; *K. kanoshensis*) and the encrinurines (*E. hornei*; *Physemataspis insularis*, Shaw, 1968, pl. 10, figs. 10, 11), as summarized in Table III-7. The two species display intermediate conditions for all morphologic transformations. Of these transformations, the most obvious intermediate conditions are the partially coalesced fifth pair of pygidial ribs of *K. kanoshensis*, the less inflated L4 and the poorly separated posterior pygidial axial rings of *E. hornei*. A similar evolutionary trend of transformation of pygidial axial rings is also observed in the Cybelopsinae, as postulated by Fortey (1979b, p. 108). Within the cybelopsine lineage, it was postulated that a long terminal piece in *Pseudocybele nasuta* (early cybelopsine,

TABLE III-7. Phylogenetic morphologic transformations along the supposed lineage from the Protopliomeropinae (*Rossaspis pliomeris*, *Rossaspis superciliosa*, and *Kanoshia kanoshensis*) and the Encrinurinae (*Encrinuroides hornei* and *Physemataspis insularis*).

	R. pliomeris	*R. superciliosa*	*K. kanoshensis*	*E. hornei*	*P. insularis*
L4	parallel-sided	parallel-sided	parallel-sided	inflated	inflated
ornaments on glabella	granulate	granulate	granulate	tuberculate	tuberculate
posterior border of hypostome	un-extended	un-extended	posteriorly extended	posteriorly extended	posteriorly extended
# of hypostomal spine pair	3	3	2	none	none
# of pygidial ribs	4	5	5	5	6
# of pygidial axial rings	5	6	6	8	more than 15
posterior-most pygidial rib	separated from terminal piece	separated from terminal piece	partially coalesced with terminal piece	completely coalesced with terminal piece	completely coalesced with terminal piece

Hintze, 1952, pl. 24, fig. 10), a terminal piece with paired pits in *Cybelopsis* and a finely segmented posterior axis of *Ectenonotus westoni* (advanced cybelopsine, Whittington, 1961, pl. 99, fig. 2) are homologous with one another. In spite of the supposed phylogenetic transformations of holaspid morphologies of the encrinurines and the protopliomeropines, it is cautioned that these trilobites listed in Table 6 may not belong to one phyletic lineage, since the two intermediate species are of late Arenig - early Llanvirn age and there appear to be a large stratigraphic gap from the other trilobite taxa. Thus, it is considered more plausible that the "advanced" cybelines + Encrinurinae lineage split from the protopliomeropine lineage during Arenigian (Figure III-8). Evitt and Tripp (1977, p. 138) also suggested that *E. hornei* was ancestral to the advanced cybelines (*Cybeloides*), upon the basis of shared possession of five pygidial pleural ribs.

Paraphyly of the Cybelinae was suggested by Edgecombe et al. (1988), based on larval dissimilarities between advanced, represented by *Cybeloides*, and early cybelines, represented by *Lyrapyge* (= their *Cybelurus*). It was claimed in the cladogram (Edgecombe et al., 1988, fig. 11), that certain advanced cybelines share more recent common ancestry with the Encrinurinae and Staurocephalidae than with earlier cybelines; the former three taxa share two protaspid instars, the presence of a torulus pair and circumocular fixigenal spines, as synapomorphies. This paraphyly will be substantiated by larval similarities of *T. depressa* and *R. pliomeris* to these cybelines.

Protaspid stages in 'Pa' of *Tesselacauda depressa* (Plate III-1.1-3) and *Lyrapyge* (an early cybeline, Fortey and Morris, 1978) are similar to each other (see comparison under *T. depressa*). Of the shared features, four protoglabellar lobes and spindle-shaped Lp to L3 appear to be derived from such plesiomorphic conditions of stage 1 of *Rossaspis pliomeris* (an immediate outgroup) as three protoglabellar lobes and parallel-sided Lp to L3 (Plate III-3.1). However, after the protopygidium appears, *T. depressa* and *Lyrapyge* show a great morphologic divergence; for examples, smooth versus pitted fixigenal field, two versus one pair of protopygidial ribs, and long and slender versus short and stout fixigenal spines. These morphologic features of the 'metaprotaspis' of Lyrapyge, not shared by T. depressa, are found in stage 2 of R. pliomeris, suggesting an alternative sistergroup relationship of the early cybelines to R. pliomeris. Thus, larval features of 'Pa' and 'Pb' support two conflicting (or incongruent) sistergroup hypotheses between the early cybelines and T. depressa or R. pliomeris. The morphologic divergence becomes even greater in holaspides such that the comparison does not allow detection of any synapomorphies among the three trilobite taxa.

The above conflicting sistergroup relationships can be resolved by comparing morphologies of the early cybelines and the primitive pliomerines (the Pliomeridae) such as Evropeites hyperboreus (Fortey, 1980, pl. 20, figs. 1-8), since Fortey (p. 102) suggested that the Cybelinae were derived from primitive pliomerines. The holaspides of Lyrapyge ebriosus and E. hyperboreus share 'apodeme' on the preglabellar field, distinct eye ridge, and bifurcated S3. Also, of interest is that a subrectangular glabella, five pygidial ribs with no pleural furrows, and six pygidial axial rings with a terminal piece observed in E. hyperboreus occur in advanced protopliomeropines such as Kanoshia kanoshensis (late Arenig - early Llanvirn age, Hintze, 1952, pl. 23, fig. 4c). This observation suggests that the early cybelines are more closely related to the Protopliomeropinae including R. pliomeris than to T. depressa (a cheirurid) and subsequently, a sistergroup relationship between the former two trilobite taxa is preferred (Figure III-8). The monophyly of the early cybelines + the Protopliomeropinae is defined by such shared features as a pitted protaspid fixigenal field, one pair of protopygidial ribs and absence of holaspid pygidial pleural furrows. Of these putative synapomorphies, only the first appears to be informative for grouping the two taxa as a clade, since the last two features occur in the cheirurids (an immediate outgroup) and cybelopsines. 'Two protaspid instars' would be an additional synapomorphy to unite the early cybelines and the Protopliomeropinae, if the smaller protaspid stages, 1S to 3S, are correctly associated with T. depressa. The suggested paraphyly of the Cybelinae (Edgecombe et al., 1988) was further substantiated, as depicted in Figure III-8; the advanced cybelines share a more recent common ancestor with the Protopliomeropinae than the early cybelines.

Relationships between Protopliomerella contracta (Cybelopsinae), Rossaspis pliomeris (Protopliomeropinae) and Tesselacauda depressa -- The phylogenetic relationship of the early cybelines to Tesselacauda depressa and Rossaspis pliomeris, as shown in Figure III-8, portrays that the two lineages, T. depressa + the Cheiruridae, and the early cybelines + (R. pliomeris + the advanced cybelines + the Encrinuridae), may be a sistergroup to the Cybelopsinae including Protopliomerella contracta. This three-taxon problem can be resolved by comparison between T. depressa, R. pliomeris and P. contracta (Table III-1), since these three species appear to be primitive representatives of each lineage (Hennig, 1966).

The subfamily Cybelopsinae is regarded as including Protopliomerella and Hintzeia as early components of that subfamily, based on larval similarities of the former to Pseudocybele nasuta (see remarks under Protopliomerella) and holaspid similarities, such as forwardly pointed palpebro-ocular ridge, posteriorly directed pygidial ribs, three pairs of hypostomal lateral spines and posteriorly extended posterior border of the hypostome. Two previous works (Ross, 1951b, fig. 2 and Demeter, 1973, text-fig. 4) on the pliomerids suggested that the early cybelopsines (Hintzeia and Protopliomerella) were directly derived from Tesselacauda depressa or Rossaspis pliomeris. Both assumed an anagenetic lineage from these two trilobites into the early cybelopsines. In fact, the early members of cybelopsines are so similar to the early protopliomeropines including Rossaspis that some workers have assigned the cybelopsines to the Protopliomeropinae (Henningsmoen, p. O444, in Harrington et al., 1959). However, phyletically younger species of the Cybelopsinae such as Ectenonotus westoni (Whittington, 1961, pl. 99, figs. 1-4, 6-9) are very different from late protopliomeropines such as Kanoshia kanoshensis (Hintze, 1952, pl. 23, figs. 1-4). The former differs from the latter in having S3 located along the anterior glabellar margin, rhomboid L4, more posteriorly placed palpebral lobe which does not reach the axial furrow, 11 pairs of pygidial ribs with pointed and short free ends, and more than 15 pygidial axial rings. These morphologic dissimilarities ensure the phylogenetic separation of the cybelopsines from the protopliomeropines. Larval dissimilarities summarized in Table III-1 between R. pliomeris and Protopliomerella contracta further support this taxonomic statement.

Tesselacauda depressa, Rossaspis pliomeris and Protopliomerella contracta, as earliest representatives, might have a polytomic origin (a fully unresolved cladogram) from an unknown ancestor of early Tremadocian or Late Cambrian age. Alternatively, there are three possible fully resolved cladograms to demonstrate the relationship of these three species. Among them, the sistergroup relationship of T. depressa and P. contracta is considered least possible, since both species share far fewer morphologies (see Table III-1 for larval dissimilarities) than in the other two possibilities. The sistergroup relationship of R. pliomeris and P. contracta seems to be supported by only one possible shared derived feature, densely granulate holaspid pygidial ribs. Additionally, fewer than four protaspid instars might support this relationship, if the smaller protaspid instars (1S to 3S) are correctly associated with T. depressa. The sistergroup relationship of T. depressa + R. pliomeris to P. contracta, appears to be more supported than the former two possibilities, since T. depressa and R. pliomeris share circumocular fixigenal tubercles, circular L4 in 'Pb' and four pairs of holaspid pygidial ribs. If the protaspid period of T. depressa has only two protaspid stages 1L and 2L, ' two protaspid instars (or stages)' is another shared feature. The phylogenetic trend of fewer protaspid instars towards stratigraphically younger members was also recognized in the encrinurids (from two to one; Edgecombe, et al., 1988) and the calymenids (from four to one; Chatterton et al., 1990). Thus, the sistergroup relationship of T. depressa and R. pliomeris was favored herein. In order to substantiate whether the shared features are a valid synapomorphy or not, Dunderbergia anyta was chosen as the outgroup for polarity determination, since 1) the species belong to the Ptychopariida, which was believed to have given rise to the Phacopida (Bergström, 1973), 2) protaspides of the species was well described (Hu, 1971, text-fig. 44, Pl. 15, figs. 1-40), and 3) the species occurs in the *Dunderbergia* Zone (Upper Cambrian), stratigraphically older than those cheirurine species described herein. Comparison of morphologic features of *D. anyta*, and *T. depressa* and *R. pliomeris* reveals that all of the four shared features of the last two species appear to be derived from such plesiomorphic features of *D. anyta* as absence of circumocular tubercles, subtrapezoidal L4, at least three protaspid instars, and three pairs of holaspid pygidial ribs. The monophyly of *T. depressa* + *R. pliomeris* makes it inevitable to evaluate the taxonomy of the Pliomeridae, which has been considered to include the Protopliomeropinae and Cybelopsinae. Two alternative explanations are plausible: 1) the Pliomeridae is paraphyletic, and includes some, but not all, descendants of its most recent common ancestor (Wiley et al., 1991). The synapomorphy distributions (Figure III-8) demonstrate that the Protopliomeropinae share more recent common ancestry with the Cheiruridae than the Cybelopsinae. This explanation appears to be acceptable within the evolutionary context of that the Pliomeridae is the earliest member (Tremadocian) of the Cheirurina and thus, the taxon has experienced an accelerated cladogenesis (Fortey and Owens, 1990) to give rise the younger cheirurine members. In addition, the larval similarities of *R. pliomeris* to phacopine trilobites (see below) further suggest that the Pliomeridae is the basal paraphyletic group of the Phacopida, and the apparent disappearance of the Pliomeridae at late Ordovician (Sloan, 1990) is a taxonomic pseudoextinction (Fortey, 1989); 2) the Cybelopsinae is not a subfamily of the Pliomeridae, but should be elevated into a family separated from the Pliomeridae. Indeed, the taxonomic unstableness of the earlier cheirurid and pliomerid genera, such as *Tesselacauda* and *Rossaspis*, clearly shown in Přibyl et al. (1985, p. 115-116), appears to reflect these aspects.

Comments on relationships of *Tesselacauda depressa* to the Calymenina and *Rossaspis pliomeris* to the Pterygometopinae -- Relationships of the calymenids (*Flexicalymene senaria*) to *Tesselacauda depressa* is more distant than those of the other non-pliomerid trilobites mentioned above. Based on larval similarities between stage 1L of *T. depressa* and P2 of *F. senaria*, seen in Table III-5, it can be imagined that *T. depressa* might be related to an early Tremadocian hypothetical ancestor, which was considered to have split into two calymenine lineages represented by the Calymenidae and the Homalonotidae (Henningsmoen, p. O450, *in* Harrington et al., 1959). *Rossaspis pliomeris* and the pterygometopines share such similarities as pitted protaspid fixigenal field and bifurcated marginal spines in the protaspid shield, and small indentation-like glabellar furrows in meraspides of the former and protaspides of the latter. These shared larval similarities might indicate a close relationship. However, the peculiar morphologies of an early protaspid instar (e.g., *Calpytaulax callirachis*, Chatterton, 1980, pl. 16, figs. 8-10, 19), a more posteriorly located anterior fixigenal spine pair (behind S3) in the late protaspides, a large schizochroal eye, a split S1 furrow, a rhomboid L4, and a slender pygidial marginal border (or interpleural furrows that do not cross the pygidial margin) in holaspides (e.g., *C. callirachis*, Chatterton and Ludvigsen, 1976, pl. 16, fig. 5, 10), suggest the remote relationship of the Protopliomeropinae to the Pterygometopinae.

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CHAPTER IV

ONTOGENETIC TRANSFORMATION AS A CHARACTER AND PHYLOGENY OF ORDOVICIAN PHACOPID TRILOBITES, WITH A NEW METHOD FOR COMPARING DATA SETS

INTRODUCTION

Trilobites, an extinct group of arthropods, provide a considerable amount of ontogenetic data, compared to most other fossil groups, mostly due to the extensive works on the early growth stage, called a 'protaspis' (trilobite larva) by Dr. B. D. E. Chatterton and his colleagues in the University of Alberta. As information on protaspides has increased, several studies attempted to produce phylogenetic hypotheses using the trilobites' larval features (e.g., Edgecombe et al., 1988; Chatterton et al., 1990). In their analysis, the characters were chosen only from the larval period, which implies that the entire ontogenetic data is unintentionally partitioned into larval and adult. Such partitioning appears to be less arbitrary than for other organisms, since the life cycle of arthropods, including trilobites, is divided by qualitatively discrete developmental events accompanied by moulting (Barnes, 1986; Speyer and Chatterton, 1989). However, considering that characters of separate ontogenetic data sets are causally linked together by a strongly dependent biological process, 'development' (Løvtrup, 1978; Alberch, 1985; Kluge, 1989), the unintentional division of ontogenetic data into separate character sets might not be a desirable practice for phylogenetic analysis. Furthermore, as will be exhibited in this work, separate analyses of partitioned ontogenetic data sets provide incompatible phylogenetic relationships. Such a disagreement appears to be in conflict with an ideal biological and evolutionary assumption that the phylogenetic results derived from separate ontogenetic data sets should converge onto the true phylogeny of the taxa under consideration, since those separate character sets are derived from the same organisms, but only different ontogenetic intervals. Of interest is the explanation that different evolutionary processes such as larval adaptation (Kluge, 1988; Chatterton and Speyer, 1995) may be responsible for the disagreement. In order to reveal a real evolutionary history of the organisms, the disagreement should be resolved, as Hennig (1966, p. 122) mentioned, ". . . , with proper evaluation it must always be possible to bring larval and imaginal systems into congruence." One plausible way to accomplish this is to introduce all ontogenetic characters into a phylogenetic analysis and analyze them simultaneously.

How can we fully utilize the whole ontogenetic data comprising each organism in the phylogenetic analysis? There have been proposed three methodological approaches: 'taxonomic congruence' under consensus methods (Mickevich, 1978); 'character combination approach' (Miyamoto, 1985; Kluge, 1989); 'ontogenetic transformation character concept' (de Queiroz, 1985). Several papers (e.g., Chippindale and Wiens, 1994; Miyamoto and Fitch, 1995) have been published for or against the justification of the first two approaches, mainly focusing on the independence of characters. Apart from their methodological justification, these approaches have been rarely applied to ontogenetic data sets; characters concerned are mostly morphological or biochemical (e.g., Eernisse and Kluge, 1993). The ontogenetic data sets from trilobites in the previous works have been treated by the taxonomic congruence approach, but not in a strict sense. One partition (e.g., larvae) of the ontogenetic data has been used as a main character set to provide phylogenetic relationships which were compared with the previous trilobite taxonomy mainly established by the other partition (e.g., adults). More often than not, the previous taxonomy has been revised by larval synapomorphy; for example, the paraphyly of Cybelinae (Edgecombe et al., 1988) and Cheirurina (Chatterton et al., 1990). However, taxonomic congruence appears not to be applicable to ontogenetic data sets, characters of which are strongly dependent upon one another; it has been argued that 'taxonomic congruence' is preferred for independent character sets (Bull et al., 1993; de Queiroz, 1993). The last, 'ontogenetic transformation character concept', has not drawn as much attention from phylogenetists as the first two approaches have, since de Queiroz's (1985, p. 292) argument against the traditional character concept of 'instantaneous morphologies' which comprise 'ontogenetic transformation'. Data from ontogenetic studies of trilobites adequately allow us to construct a character set which consists of ontogenetic transformations and to validate its quality as a phylogenetic character.

The aim of this paper is to justify ontogenetic transformation as a character for phylogenetic analysis using information on trilobites' ontogeny, and to demonstrate that the ontogenetic transformation character set is more reliable or informative than partitioned ontogenetic character sets. To accomplish these, available tree statistics such as tree length (L), consistency index (CI) and rescaled consistency index (RC) are compared for the shortest tree(s) derived from different data sets. Unlike the straightforward comparison, the changes of those statistical values under topological constraints are compared (see 'Choice among Data Sets' for details). The character combination approach is employed to investigate the validity of the ontogenetic transformation character set, since character combination can not be strictly applied to the original data sets consisting of unequal numbers of taxa (see below). Two assumptions are required: all specimens forming the growth series of each trilobite species are correctly associated; and the sampling of each trilobite species is adequate to approximate the whole growth series. In most ontogenetic studies of trilobites, the association of earlier growth stages with the adult is believed to be correct, if those materials occur together in the small block (usually, less than 5 kg) of limestone, which represents the same habitat where they lived together, and they show gradual changes in size and morphology from one to the other (Chatterton, 1980). This is usually supplemented by knowledge based on similar associations occurring with the same or closely related taxa from other horizons or localities.

DATA

Fifteen Ordovician trilobite species, which belong to various families of the Phacopida Salter, 1864, were chosen for analysis. Those species are *Flexicalymene senaria* (Calymenidae), *Calyptaulax annulata* (Pterygometopidae), *Protopliomerella contracta*, *Pseudocybele nasuta*, *Rossaspis pliomeris*, *Rossaspis superciliosa* (Pliomeridae), *Tesselacauda depressa*, *Kawina sexapugia*, *Ceraurinella nahanniensis*, *Acanthoparypha evitti*, *Sphaerexochus (Korolevium) arenosus*, and *Heliomeroides freschaufae* (Cheiruridae), and *Cybeloides cimelia*, *Lyrapyge ebriosus*, and *Physemataspis insularis* (Encrinuridae). The choice of taxa was based on well-described ontogenies and the earliest representative of each family or subfamily. A total of 28 morphologic characters and character states were defined (Appendix IV-I) based on available materials to the authors and the following previous publications: Ross (1951a, b, 1953), Palmer (1965), Shaw (1968), Hu (1971), Lane (1971), Demeter (1973), Chatterton and Ludvigsen (1976), Fortey and Morris (1978), Chatterton (1980), Fortey (1980), Edgecombe et al. (1988), Speyer and Chatterton (1989), Chatterton et al. (1990), Chatterton and Speyer (1995), and Chapter III.

Characters were chosen from discrete ontogenetic intervals which are considered comparable throughout phacopid trilobites. Herein, 'character' is referred to as a morphologic part (or feature) with a widely-used descriptive term of the trilobite body (see Figure IV-1, herein; Harrington et al., *in* Harrington et al., 1959: O117-O126; Chatterton and Speyer, 1995, fig. 9) or its variables (Colless, 1985; Adrain and Chatterton, 1990). Compared to other organisms, the selection of characters from separate ontogenetic intervals in trilobite analysis seems to be facilitated, since 1) trilobites, like other arthropods, shed their exoskeleton at regular intervals by moulting (Barnes, 1986; Chatterton and Speyer, 1995), so that division of life cycle is more practical and less arbitrary, and 2) as a fossil, only the shed exoskeletons of trilobites are preserved in rock records, which makes it easier to recognize instars that are the result of moultings

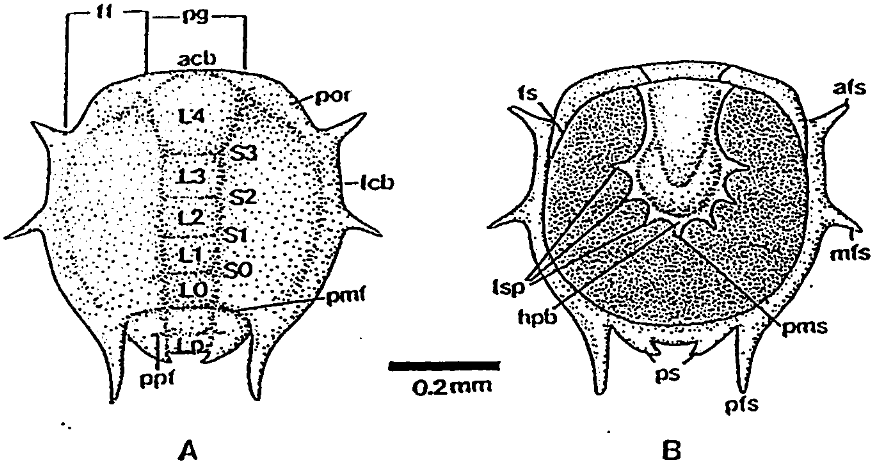

FIGURE IV-1. Drawings of dorsal (A) and ventral (B) views of protaspid stage 2 of *Protopliomerella contracta* (Ross, 1951). Abbreviations for termonologies are as follows: acb = anterior protocranidial border; afs = anterior fixigenal spine; ff = fixigenal field; fs = facial suture; hpb = hypostomal posterior border; lcb = lateral protocranidial border; lsp = lateral hypostomal spine pair; L4 to L0 = glabellar lobes; Lp = posteriormost axial lobe; mfs = midfixigenal spine; pfs = posterior fixigenal spine; pg = protoglabella; pmf = protocranidial marginal furrow; pms = posteriormedian hypostomal spine; por = palpebro-ocular ridge; ppf = protopygidial pleural furrow; ps = protopygidial marginal spine; S3 to S0 = glabellar furrows.

(Chatterton and Speyer, 1995). The life cycle of a trilobite individual is generally divided into three intervals: protaspid, meraspid and holaspid periods, each of which contains one or more instars separated by moulting. Each period is distinguished from the adjacent one by the qualitative developmental events, such as calcification, segmentation of tergite, and completion of thorax; the first event separates the protaspid period from an uncalcified and unfossilized pre-larval stage (Speyer and Chatterton, 1989, fig. 2). In addition to these periods, the protaspid period of the phacopid trilobite, herein, is subdivided into two intervals which are distinguished from each other by an additional developmental event of 'appearance of protopygidium' (Figure IV-2). The two protaspid intervals are designated 'Pa' and 'Pb' (see Chapter III). Comparability of this event throughout phacopid taxa appears to be justified on the grounds of the following observations: 1) the appearance of a protopygidium is consistently accompanied by the distinct impression of a posterior cranidial marginal furrow, and the development of distinct, long pair(s) of marginal spines, so that the event is easily recognizable and correlatable across phacopid taxa; 2) several characters, including glabellar shape and position of fixigenal spines, transform across the event. The intervals selected for comparison are equivalent to Hennig's (1966, p. 6, 65) and Wheeler's (1990, p. 230) 'semaphoront as a character bearer', since characters are invariable during each ontogenetic interval, so that each interval is characterized by at least one character. This semaphoront concept is least likely to be applied to the meraspid period, during which morphologies display a wide range of fairly continuous variation. Furthermore, seldom are these sufficient specimens to adequately represent the whole meraspid period. In fact, the comparative analysis below will demonstrate that the meraspid data had no great influence on the phylogenetic result (see discussion). Thus, three initial data matrices (designated 'PA', 'PB', and 'H') were built from three comparable ontogenetic intervals (Appendix IV-2).

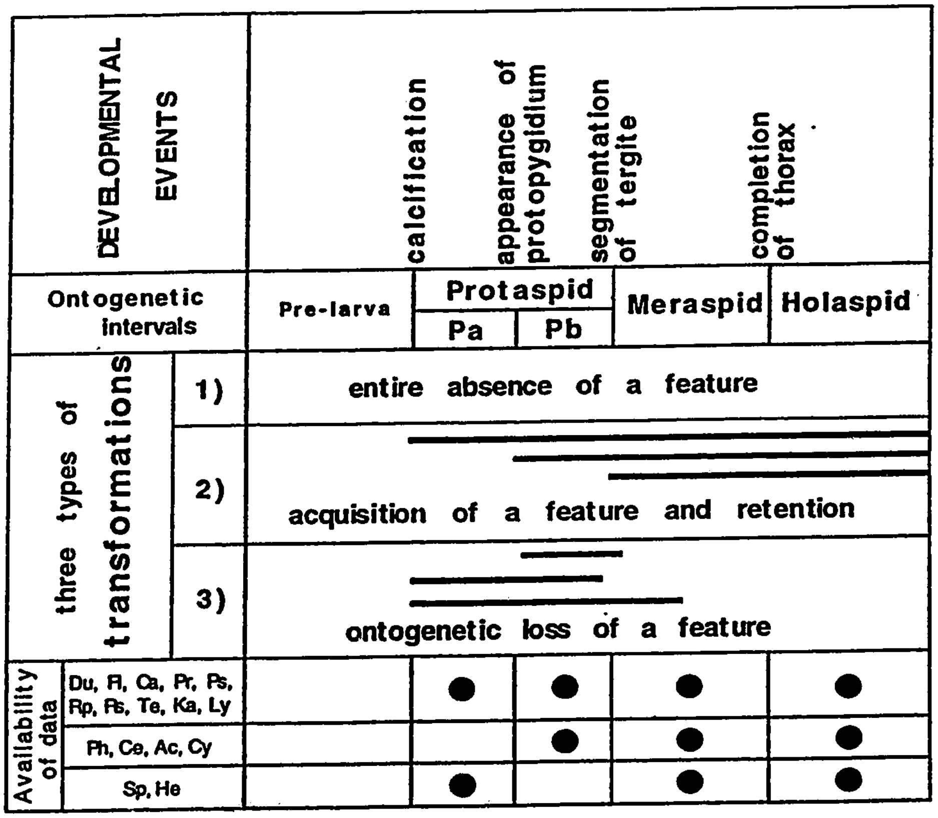

FIGURE IV-2. Three types of ontogenetic transformation characters of the phacopid trilobites in this analysis in terms of presence/absence and availability of data for each ontogenetic interval with reference to four developmental events of phacopid trilobite ontogeny. Bar indicates the duration of presence of the character. Dot depicts that the trilobites pass the ontogenetic interval with it. See Appendix IV-2 for the abbreviations of taxon name.

Ontogenetic Transformation as a Character -- In addition to the data matrices from three ontogenetic intervals, two more sets are constructed, which consist of ontogenetic transformations of 'characters'. This character concept was proposed by De Queiroz (1985, p. 292) who cautioned against the use of 'instantaneous morphologies' ("horizontal characters", Kluge, 1988) in the phylogenetic analysis. Since then, however, the concept has not drawn much attention from phylogenetists and thus, few studies have adopted this concept to generate phylogenetic hypotheses. OConnor (1984), Brooks et al. (1985), and Fuiman (1985), in their studies, used a few ontogenetic transformation characters combined with 'instantaneous morphologies'; e.g., 'copulatory stylet lost' (Brooks et al., 1985). The ontogenetic transformation characters for this analysis were defined through tracing modifications of morphologic characters during development. Character states of ontogenetic transformation characters, comprising data matrix 'T', are categorized into three types with respect to presence/absence (Figure IV-2). It is assumed that the pre-larval stage does not show the characters that appear in the interval of Pa, following a simplified restatement of Von Baer's second law, 'ontogeny proceeds from absence (more general) to presence (less general)' (Patterson, 1982, p. 54; Rieppel, 1993, p. 15). Characters such as 19, 20, and 27 (Appendix IV-1) show all three types of ontogenetic transformation in the ingroup trilobites, each of which is the character state of these characters. In contrast, characters such as 4, 9, 10, and 11 invariably display the second or third sequence in the ingroup trilobites, in which case the variable (see above) of a morphologic feature, such as shape or position, was chosen as a character. Let us consider glabellar shape (character 5) as an example. Glabella of all ingroup trilobites appears and is defined by axial furrow at the interval of Pa, and it never disappears in later ontogeny, being categorized into the second type (Figure IV-2). However, glabellar shape, as a variable, ontogenetically varies; for example of Tesselacauda depressa, from 'spindle-shaped Lp to L3 and subtrapezoidal L4' in Pa, and 'parallel-sided Lp to L3 and subtrapezoidal L4' in Pb, into 'subrectangular' in holaspides, being defined as 'forward tapering of L4 relative to L1 to L3' as ontogenetic transformation character (see Appendix IV-1). Meraspid morphologies, which are inappropriate for building their own data matrix for that period and thus, not suitable for phylogenetic analysis, allow us to trace ontogenetic modifications of morphologic features with more confidence, even if the materials are not sufficient.

In addition to the matrix, 'T', another data matrix (designated 'TH') was built upon the basis of available heterochronic information on some ontogenetic transformation characters. Applicability of heterochronic information requires that the character states occur in all ingroup and outgroup taxa, and show a variable distribution in timing of their appearance with respect to developmental events (Figure IV-2). A total of 11 characters provide suitable heterochronic information. However, as shown in Appendix IV-1, not all 'instantaneous' characters can be alternated with an equivalent ontogenetic transformation character; characters 2, 4, 12, 15, 17, and 24 are only defined at a certain ontogenetic interval, either because data for the whole life cycle are not available, or the transformation, itself, can be only defined as such general statements as 'continuous shortening' or 'increment' throughout the ingroup taxa. Among them, characters 2-Pa, 2-Pb, 15-H, 17-H, and 24-H were incorporated with ontogenetic transformation character set ('T') to construct another data set ('T+'). The reason for this incorporation is that these characters are defined for all 15 ingroup taxa and thus, are able to provide phylogenetic relationships of all trilobites under consideration, unlike the others which are not available for all 15 taxa. As a total, six different ontogenetic data sets (designated 'PA', 'PB', 'H', 'T', 'TH', 'T+') were built (Appendix IV-2).

No Instars in Certain Ontogenetic Intervals -- All three ontogenetic intervals, as a basis for character selection, are not available for some trilobites (Figure IV-2). Some trilobites do not exhibit Pa or Pb interval during their development. This indicates that two developmental events have taken place simultaneously in those trilobites' ontogeny; for example, calcification and appearance of protopygidium have taken place together during the development of Physemataspis insularis (Figure IV-2). For trilobites which have no instars in Pa or Pb, characters are not applicable for that interval. Such 'no instars' of those taxa may be scored as 'missing data (?)' for every character. In the PAUP program, one of the non-missing values would be assigned to the taxon with 'missing data' according to the parsimony criterion (Swofford and Begle, 1993, p. 21-24). However, 'missing data' for 'no instars' has wholly different initial meanings from 'missing data' for 'not available'. As an alternative, Maddison (1993) argued that taxa with inapplicable characters should be properly coded as 'absent' relative to taxa having the several applicable states of the character. However, this treatment only refers to a taxon which possesses many other applicable (thus, can be coded), but a few inapplicable characters. In contrast, no characters are applicable to Pa or Pb interval of those trilobites lacking instars in either interval, so that coding as 'no instars' for every character is not a meaningful character treatment. If a data matrix with scoring 'no instars' as a separate numerical value for every character of those trilobites is analyzed, the resultant tree(s) display a robust clade of those trilobites which is strongly but only supported by 'no instars'. Preliminary analysis using these two treatments yielded a tremendous number (over 2,000) of minimal trees for both data sets, which seems to be intractable; this may be a function of too few characters for the taxa analysed. Thus, the trilobites with 'no instars' in Pa or Pb were excluded from the analysis for the data set 'PA' or 'PB'.

Outgroup Selection -- Polarity of two or more homologous character states has been determined by three methods: ontogenetic precedence, stratigraphic precedence and outgroup comparison (Nelson, 1978; Eldredge, 1979; Eldredge and Cracraft, 1980; Bryant, 1991). Among these, the ontogenetic method, proposed by Nelson (1978, p. 327) as a restated biogenetic law, appears not to be consistently applicable to the data sets in this analysis for the following reasons: 1) the data set 'PA' consist of larval characters which occur at the earliest ontogenetic time and thus, appear to be primitive relative to character states in later ontogeny, so that ontogenetic method can not be applied to polarity determination for that data; 2) even for the data set 'PB', characters are not applicable for some trilobites lacking instars in Pb interval, so that the method is not applicable for all of the 15 taxa studied; 3) for the data set consisting of adult characters ('H'), many character states (e.g. character 5) in earlier ontogeny are not found in later ontogeny at all; the ontogenetic method is only applicable, where a character state appearing in early ontogeny is found in later ontogeny (Nelson, 1978; Patterson, 1982, 1983; Wheeler, 1991); 4) the character states of the data sets ('T' and 'TH') consisting of ontogenetic transformations, can not be polarized using the ontogenetic method, since each character includes primitive and derived states together within the context of the method (de Queiroz, 1985). For polarity determination, the outgroup method supplemented by paleontological (or stratigraphical) criteria was employed in this work. That is, the character states found in a sister taxon that occurs in stratigraphically older strata and is phylogenetically outside the presumed monophyletic ingroup are considered as primitive. This method does not violate any basic and subsidiary assumptions for both methods (Bryant, 1991). Thus, a taxon to be selected for polarity determination in this work should meet the following criteria: 1) the taxon should be older than any of the ingroup taxa; 2) the taxon should be outside the presumably monophyletic Phacopida, but have some close phylogenetic relationships; 3) specific to this analysis, its ontogeny should be fully described and illustrated. Dunderbergia anyta was selected as outgroup, because the species occurs in Upper Cambrian strata (Dunderbergia Zone of Palmer, 1965) and belongs to the Ptychopariida, some members of which were considered as a possible ancestor to the phacopid trilobites (Henningsmoen in Harrington et al., 1959; Bergström, 1973), and its ontogeny has been well described and illustrated (Hu, 1971).

METHOD

Each data matrix in Appendix IV-3 was analyzed using PAUP program, version 3.1 (Swofford, 1993). All characters are treated as unordered and equally weighted, and the ACCTRAN optimization was used. Six combinations of heuristic searching options were used to make sure that the trees found are the shortest possible. Random (with 10 replicates and steepest descent options) and simple (one tree held at each step) addition sequences, and nearest neighbor interchanges (NNI), subtree pruning-regrafting (SPR), and tree bisection-reconnection (TBR) branch swapping algorithms were utilized as combinations. These various searches produced the shortest tree(s) with little variations of tree length (L), consistency index (CI), and rescaled consistency index (RC) for each data set (Table IV-1).

CHOICE AMONG DATA SETS

Quantitative information on the shortest trees derived from each original data set are summarized in Table IV-1. Each partitioned data set provides incompatible phylogenetic hypothesis, as shown by consensus trees derived from majority rule method (Figure IV-3). In contrast, the data sets ('T', 'TH', and 'T+') which mainly consist of ontogenetic transformation characters show fewer conflicts among the consensus trees. Even the data sets with all 15 taxa ('H' and 'T', 'TH', and 'T+') do not show higher degree of congruence in their consensus trees (Figure IV-3). Such incompatibility among tree topologies seems relevant to the question of which of the original data sets provides the most reliable hypothesis, which leads to the most contentious issue in phylogenetic systematics, 'the choice of a data set or tree(s)'.

Such basic statistics as tree length (L), consistency index (CI), and rescaled consistency index (RC) are employed, but in a comparative way (see below). There appears to be considerable arguments for and against the use of these measures for choosing the best phylogenetic estimate from the same data set or choosing the more reliable ones

TABLE IV-1. Summary of quantitative information on parsimonious tree(s) derived from each original data set. Abbreviations for searching method combinations are: R = random addition sequence; S = simple addition sequence; N = nearest neighbor interchanges; B = subtree pruning-regrafting; T = tree bisection-reconnection. Abbreviations for tree statistics: M = minimum number of steps required to explain the tree topologies; L = tree length; CI = consistency index; RC = rescaled consistency index.

DATA	search	# of taxa	# of char.	# of trees	M	L	CI (M/L)	RC
PA	RN	12	10	267	15	21	0.714	0.489
	RB			272		21	0.714	0.489
	RT			272		21	0.714	0.489
	SN			238		21	0.714	0.489
	SB			272		21	0.714	0.489
	ST			272		21	0.714	0.489
PB	RN	14	19	93	25	53	0.472	0.259
	RB			112		53	0.472	0.259
	RT			113		53	0.472	0.259
	SN			51		53	0.472	0.259
	SB			112		53	0.472	0.259
	ST			112		53	0.472	0.259
H	RN	16	14	19	29	49	0.592	0.418
	RB			22		49	0.592	0.418
	RT			22		49	0.592	0.418
	SN			6		50	0.580	0.401
	SB			22		49	0.592	0.418
	ST			22		49	0.592	0.418
T	RN	16	23	1	34	72	0.472	0.283
	RB			4		72	0.472	0.283
	RT			4		72	0.472	0.283
	SN			2		72	0.472	0.283
	SB			2		72	0.472	0.283
	ST			4		72	0.472	0.283
TH	RN	16	24	2	42	89	0.472	0.274
	RB			2		89	0.472	0.274
	RT			2		89	0.472	0.274
	SN			2		89	0.472	0.274
	SB			2		89	0.472	0.274
	ST			2		89	0.472	0.274
T+	RN	16	28	7	44	95	0.463	0.274
	RB			7		95	0.463	0.274
	RT			7		95	0.463	0.274
	SN			7		95	0.463	0.274
	SB			7		96	0.458	0.268
	ST			7		96	0.458	0.268

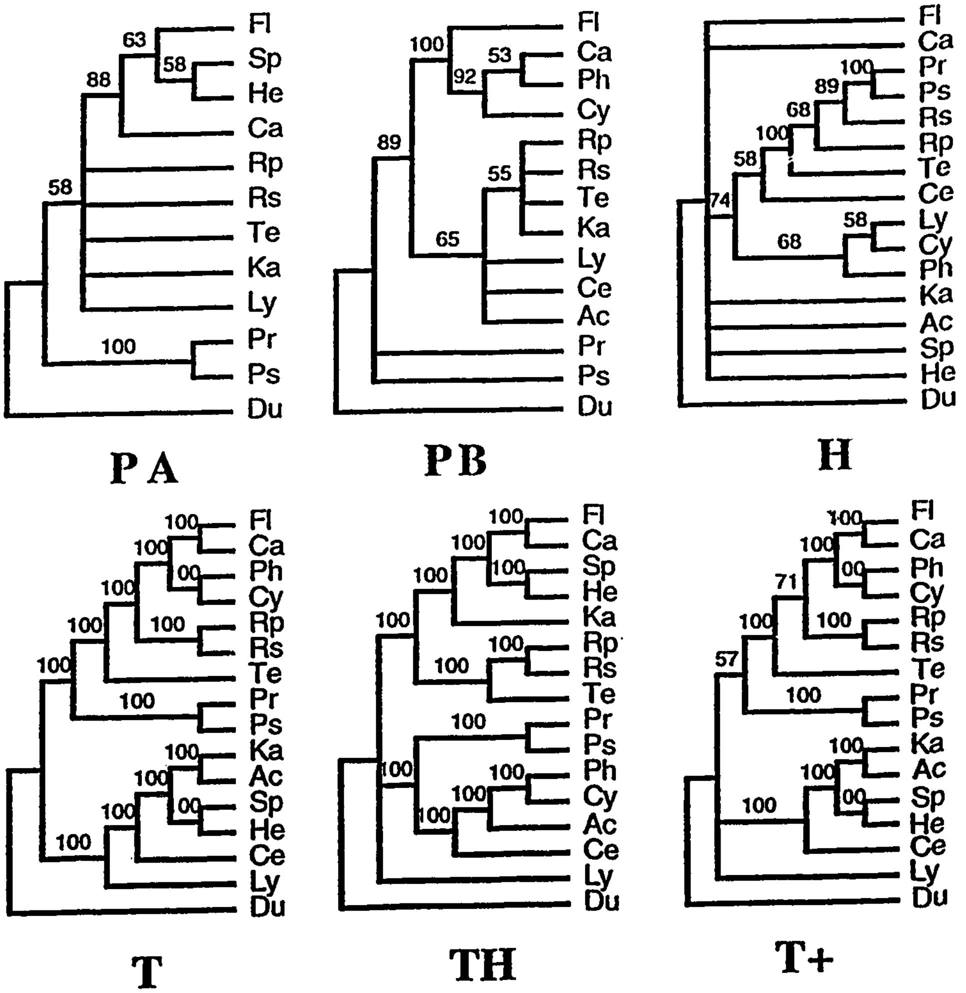

FIGURE IV-3. Majority rule consensus trees constructed from the shortest tree(s) derived from each original data set using the search combination of random addition sequence (R) and nearest neighbor interchanges (N). The number beside the internodes is the percentage in which the clade appear in the equally parsimonious trees.

among different data sets of the same taxa; for example, Archie (1989), Farris (1989), Sanderson and Donoghue (1989), Goloboff (1991), and Wiley et al. (1991), to name a few. Admittedly, higher CI and RC among the cladograms indicate less homoplasy and thus, more reliability and informativeness, which appears to be more acceptable for the same data set. In contrast, comparability of those statistics across data sets has been considered doubtful, since they, in particular CI, show a strong negative relationship to increase in the number of taxa (Archie, 1989; Sanderson and Donoghue, 1989) or characters. Most arguments have focused on the amount of homoplasy necessary to explain the phylogenetic hypothesis. Tree length of the shortest trees from different data sets is not comparable at all, since it is strongly positively related to number of taxa and character together. Thus, a straightforward comparison of these statistical values seems inappropriate for comparing data sets and choosing more reliable one. Despite these problems, it is assumed that the shortest tree(s) derived from each data set represents the best estimate of phylogeny and character evolution, and best fits into the character set.

Comparison using Topological Constraint -- A new method for comparing data sets, and deciding which of the data sets provides more reliable phylogenetic hypothesis proposed herein, is to use the minimum-length tree(s) of one data set as a topological constraint to the remaining data sets. This approach is based on the assumption that partitioned ontogenetic data sets or ontogenetic transformation character set should provide an identical phylogeny, since each set consists of characters defined at different ontogenetic interval or the whole life cycle of the same trilobite taxa. Similarly, Hennig (1966, p. 123) claimed that 'incongruence' between larval and imaginal systems (clearly exhibited in fig. 34) "must be brought into congruence in order to determine the phylogenetic relationships of the species to which they (larvae and imagoes) belong". It might be argued that evolution of each ontogenetic interval is controlled by different processes (e.g., larval adaptation or caenogenetic evolution), which have resulted in radically disparate morphologies for each interval.

Thus, the higher degree of congruence between the phylogeny estimates derived from different ontogenetic intervals can not be expected. This might be true for the trilobites showing a radical metamorphosis (e.g., asaphid, Chatterton, 1980), across which several morphologic features radically transform. Indeed, two trilobite taxa possessing only 'nonadult-like' protaspis, such as Sphaerexochus and Heliomeroides, display a highly variable distribution among the consensus trees derived from 'PA' and 'H' (Figure IV-3). However, most phacopid trilobites have 'adult-like' protaspid larvae (Speyer and Chatterton, 1989) and thus, a radical metamorphosis appears not to have been present enough to cause such a drastic morphologic change. Furthermore, characters among the ontogenetic data sets are strongly dependent to one another, since they are only sequential, not necessarily continuous, expressions of an unambiguously dependent biological mechanism, 'development' ('causal sequence', Alberch, 1985; epigenetic characters, Løvtrup, 1978). Thus, fewer conflicts can be expected among phylogenetic relationships derived from the different ontogenetic character sets.

Based on this consideration, the shortest tree(s) of each data set considered as one of the best estimate of phylogeny is used as s topological constraint(s) to the other ontogenetic data sets; each topological constraint, as a phylogenetic hypothesis, is considered an object to be tested by actual character evidences of different ontogenetic data sets. The minimal tree(s) yielded under the topological constraint(s) exhibit how well or poorly the characters of different ontogenetic data sets perform under the supposed phylogeny. The goodness of fit of one data set to the particular constraint(s) generated from the other data set is expressed in terms of negative or positive variations of the basic statistics; in all cases, tree length (L) increases, and consistency index (CI) and rescaled consistency index (RC) decrease, under each constraint. If the two data sets support an identical phylogenetic hypothesis, the variations will be nil. A relatively higher variation of a data set against a certain constraint demonstrates that more characters of the particular data set turn out to be homoplastic under the constraint, which indicates that the data set does not fit well into the topological constraint. The average value of the variations for one topological constraint indicates how much homoplasies should be introduced to explain the character evolution of the remaining data sets under the constraint environment. Thus, the higher average is interpreted as that the characters of the other data sets do not perform well under the topological constraint, and the character set which provides the constraint will be deductively rejected as an unreliable data set. The practical procedure of this approach is as follows: 1) set the most parsimonious tree(s) derived from one data set as a topological constraint(s) at search option in PAUP program (Swofford, 1993) → 2) search the parsimonious tree(s) compatible with the constraint(s) for the remaining data sets → 3) follow the first and second steps for each data set → 4) compare L, CI, and RC.

In order for all original data sets to be compared and to justify the consistency of the comparison using topological constraint, the matrices were modified as follows: 1) the original data sets are modified into matrices with equal number of taxa, since the concern is to investigate the reliability of data sets and such modification disregard the negative effect of the number of taxa to CI. The 6 trilobite taxa lacking instars in Pa or Pb were excluded in some matrices with 10 or more taxa due to inapplicability of all characters to those taxa (see above); 2) the characters with missing data (?) for any taxa were excluded, since the taxon would be analyzed to have one of the non-missing values that appears to be possible but definitely ambiguous; 3) in order to find out the applicability of character combination approach to ontogenetic data, all possible combinations of the partitioned data sets, such as 'PA'+'PB' or 'PA'+'H', etc. were made. The combination of 'PA+PB+H' is only possible for the data matrices with 10 and less taxa, since the matrices with more than 10 taxa include the 6 trilobite taxa, for Pa or Pb interval of which the characters are not applicable.

According to the above assumption, the shortest trees from each data set with the equal number of taxa are considered equally valid as a phylogeny estimate for these taxa and thus, the trees are used as a topological constraint (a hypothesis to be tested). The shortest tree(s) for these data matrices were obtained using exhaustive (for the matrices with 10 or less taxa) or heuristic (for the matrices with more than 10 taxa) searching method and the analytical results including quantitative facts are summarized in Appendix IV-3. The result of comparison for 10 taxa using the new method is depicted in Figure IV-4. The average values of the variations of L, CI, and RC with different number of taxa are graphed in Figure IV-5.

Analytical Results -- The following analytical results are obtained from the analysis of the modified data sets and the comparison using topological constraints (Figures IV-4 and IV-5).

1) The data sets, 'PA' and 'PB' show the higher average values of the variations of L, CI, and RC, indicating their low reliability and informativeness. This result is also supported by the fact that among the combined data sets, 'PA+PB', causes the greatest variation. Such a higher variation of 'PA+PB' indicates that the poor reliability of the initial data sets strongly influence the reliability of the combined data set. Furthermore, the sets are not able to provide the phylogenetic relationships of all 15 ingroup taxa (see Data). This result is exactly opposite the highest CI and RC of the original data set (Table IV-1).

2) The character set, 'H', is most reliable among the partitioned ontogenetic data sets, since it causes much lower variations (invoking much less homoplasies) and is able to produce the phylogeny of all 15 taxa. As pointed above, the higher reliability of 'H' is directly reflected in that of the combined set including 'H'.

3) The best estimates of phylogeny derived from combined character sets invoke less homoplasies for other data sets, indicating that the character combination approach is not undesirable for ontogenetic data. As shown in Appendix IV-3, this is further substantiated by the fact that the character incongruence calculated between data sets is small relative to that within a data set (Kluge, 1989). However, the combined data set ('PA+PB+H') is able to only provide the phylogenetic hypothesis of less than 10 trilobite taxa under immediate consideration (see Appendix IV-3).

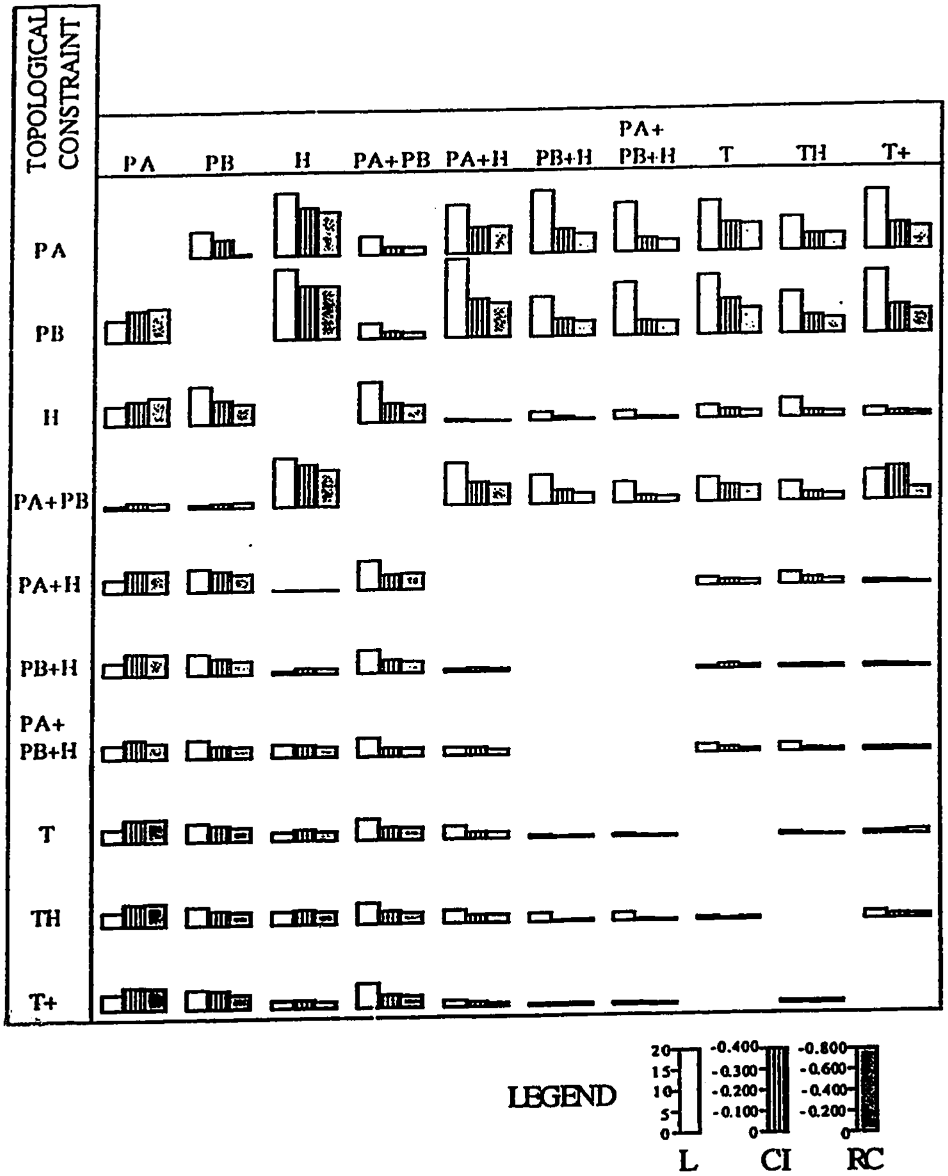

FIGURE IV-4. Variations of tree length (L), consistency index (CI), and rescaled consistency index (RC) of each modified data set with 10 trilobite taxa including the outgroup against various topological constraints. The length of each bar indicates the differences of L, CI, or RC between initial hypothesis and the constrained one.

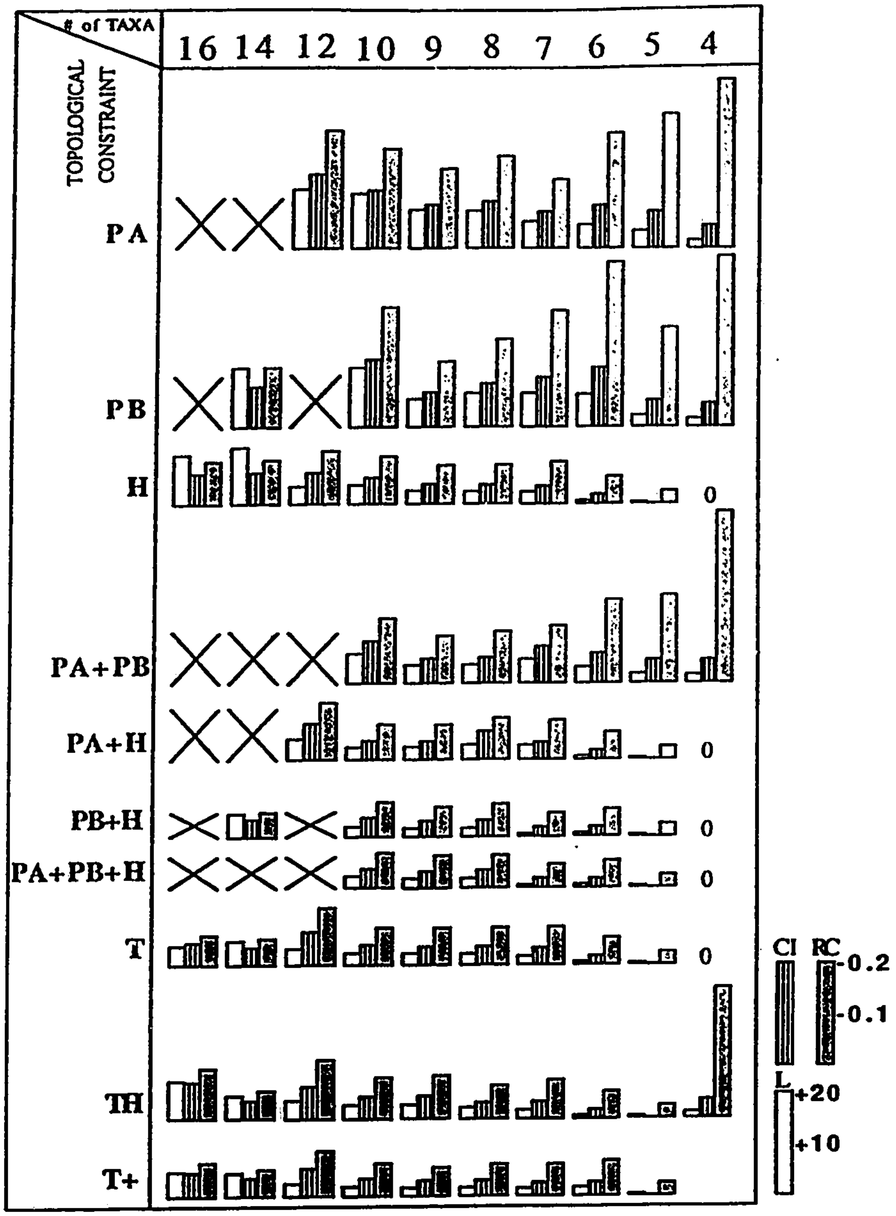

FIGURE IV-5. Summary of average values of the variation of L, CI, and RC caused by each topologic constraint with various numbers of taxa. 'X' indicates that the data sets including the combined sets are not applicable to that number of taxa due to the absence of a particular ontogenetic interval. '0' indicates that the certain topological constraint causes no homoplasy against the other ontogenetic data sets, implying that the constraint has an identical tree topology with the other sets.

4) The character sets, 'T' and 'TH', which mainly consist of ontogenetic transformations, are more reliable than partitioned ontogenetic data sets, since they result in the lower variations of L, CI, and RC than the partitioned sets. Of interest is that 'TH' with heterochronic information is consistently less reliable than 'T'. This might be interpreted as indicating that heterochronic characters are likely to be subsumed into ontogenetic transformation characters and have no great implication in phylogeny reconstruction.

5) Comparison between 'PA+PB+H' which incorporates all partitioned character sets, and 'T' (Figure IV-5 and see Table IV-2 for numerical pairwise comparison) exhibits that 'T' is more reliable, but not in a considerable difference, than 'PA+PB+H'. The possible reason for this is that the ontogenetic transformation characters are defined by tracking down the morphologies including those of meraspides, which are not included within the combined set. Alternatively, the relatively small difference between the two sets might reflect that the meraspis, as an intermediate stage, has no great bearings on phylogeny reconstruction (see Alberch, 1985, p..51).

6) For the presentation of the phylogeny of 15 Ordovician phacopid trilobites, the data set, 'T+' is chosen as the most reliable character set among all the ontogenetic data sets. This is because 'T+' causes lowest variation, invoking least homoplasies, against the other data set (Figures IV-4 and IV-5), and it includes ontogenetic transformation characters and all instantaneous characters which are able to provide phylogeny of all 15 taxa, but can not be alternated into ontogenetic transformation character; the construction of 'T+' is in accordance with the 'total evidence principle' (Kluge, 1989).

Some of the above results appear to be far from certain; in particular, the relative inferiority of heterochronic characters to plain ontogenetic transformation characters and the supposed invalidity of the intermediate ontogenetic stage (meraspis) for phylogenetic analysis. More works employing ontogenetic transformation character concept are required to substantiate these results.

TABLE IV-2. Numerical pairwise comparison of variations of L (tree length), CI (consistency index), and RC (rescaled consistency index) between ontogenetic transformation character sets ('T', 'TH', and 'T+') and the combined set ('PA+PB+H').

L	PA+PB+H	T	TH	T+
PA+PB+H		2	2	1
T	1		1	1
TH	2	1		2
T+	0.33	0	0.6	

CI	PA+PB+H	T	TH	T+
PA+PB+H		.0250	.0150	.0163
T	.0070		.0040	.0103
TH	.0100	.0090		.0206
T+	.0020	.0000	.0053	

RC	PA+PB+H	T	TH	T+
PA+PB+H		.0370	.0280	.0261
T	.0130		.0100	.0166
TH	.0190	.0270		.0330
T+	.0040	.0000	.0120	

PHYLOGENETIC RESULTS

The data set 'T+', considered as the most reliable one, provides seven equally parsimonious trees under combined heuristic searches (Table IV-1 and Figure IV-6). Seven equally parsimonious trees shown in Figure IV-6 are topologically incompatible with one another. Topologic features common in the seven trees are as follows; refer to Appendix IV-1 for the synapomorphies mentioned below.

1) The supposed monophyly of Phacopida is substantiated by at least seven synapomorphies such as 2-Pa(2), 8-T(1), 9-T(1), 14-T(2), 20-T(2), 21-T(1), and 26-T(1), some of which are shared with some terminal taxa.

2) Two inclusive clades, informally designated the 'first' and 'second', are recognized. The 'first' clade includes the following genera of various phacopid families such as Calymenidae (Flexicalymene), Pterygometopidae (Calyptaulax), Encrinuridae (Physemataspis and Cybeloides), Pliomeridae (Rossaspis) and Cheiruridae (Tesselacauda) and the 'second' clade consists of most cheirurid genera, except for Tesselacauda. The 'first' clade is defined by 6-T(1), 13-T(1), and 16-(1) and the 'second' is by 1-T(1) and 17-H(1).

3) Within the 'first' group, there are some variations of the relationships of Tesselacauda and Rossaspis among the 7 trees; in some trees, both genera forms a clade and the sistergroup to the rest genera of the 'first' group, while in others Tesselacauda is the sistergroup to the rest including Rossaspis. The first hierarchical distribution is hierarchical distribution that Rossaspis is consistently a sistergroup to the derived clades is compatible with the suggestion that Physemataspis and Cybeloides (encrinurid members of the clade) might have originated from Rossaspis (Figure III-8 in Chapter III).

4) Flexicalymene and Calyptaulax consistently form a highly derived clade defined by 3-T(1) and 19-T(1). This hierarchical distribution is in conflict with Chatterton et al.'s (1990) analysis which shows Calyptaulax is a sistergroup to Physemataspis, being defined by two larval synapomorphies.

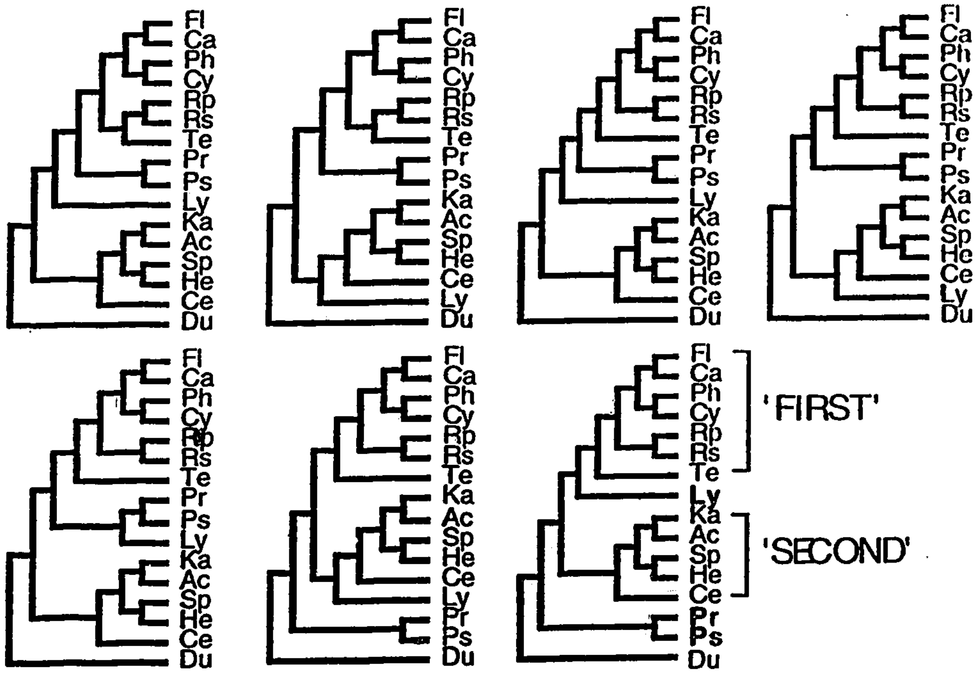

FIGURE IV-6. Seven equally parsimonious trees generated from the data set 'T+'. There are recognized two subordinate phacopid groups, 'first' and 'second', which might have been two separate lineage in the Phacopida during Lower Ordovician. The outlined are the taxa which show a highly variable distribution among the shortest trees, and the phylogenetic relationship in conflict with the previous works.

5) Within the 'second' inclusive group, the sistergroup relationship of Kawina to Acanthoparypha is in conflict with the previous suggestion (Chatterton, 1980; Chapter III, herein) that the genus is an ancestor to the Sphaerexochinae and thus, should be more closely related to the sphaerexochines, such as Sphaerexochus or Heliomeroides. Apart from the position of Kawina, the hierarchical distribution of the remaining cheirurid genera is in accordance with the hierarchical distribution of (Cheirurinae + (Acanthoparyphinae + Sphaerexochinae)) in Figure III-8 in Chapter III.

6) There are two taxa which display the most variable distribution and the greatest conflict with the previous works; they are Cybelopsinae (Protopliomerella + Pseudocybele) and "early cybeline" (Lyrapyge). The cybelopsine clade, defined by 24-H(2), 25-T(1), 27-T1(1), and 27-T2(2), consistently show the sistergroup relationships to only the 'first' group or the whole phacopids, but not to the 'second' group. This relationship disagrees with the suggestion that the cybelopsine is the sistergroup even to the cheirurids (Figure III-8 in Chapter III). However, the presumed paraphyly of Pliomeridae, as the earliest element of Phacopida, which includes Cybelopsinae and Rossaspis is further substantiated. The unstable and disputable relationship of Lyrapyge, an early member of Cybelinae, supports Edgecombe et al.'s (1988) result of the paraphyly of the Cybelinae. Most taxa which show conflicts with the previous works are stratigraphically the older and thus primitive member of a certain trilobite group, the origin of which is still problematic.

DISCUSSION

The argument that the whole life cycle of organisms should be taken into account in the phylogenetic analysis is not new. For example, Garstang (1922, p. 82) stated, "the real phylogeny of Metazoa has never been a direct succession of adult forms, but a succession of ontogenies or life cycles." and Danser (1950, p. 118) stated, "even the structure of the full-grown state, on which, in many groups, systematics is almost exclusively based, must, however great at times its importance, be only looked upon as the representation of the life-cycle." They argued against phylogenetic inference based only on adults, which is conventionally and traditionally a standardized point for depicting phylogeny (Gould, 1977, p. 212). This argument was justified with a phylogenetic perspective by de Queiroz (1985) who proposed a new character concept of ontogenetic transformation. The empirical usage of this character concept in phylogenetic analysis, i.e., the phylogenetic consideration of the whole life cycle of organisms, appears to be in accordance with 'total evidence principle' (Hempel, 1965, p. 64), since all available 'instantaneous morphologies' are introduced into the phylogenetic practice by tracing their modifications during the whole life cycle. This 'total evidence principle' has been accepted as a theoretical basis for the 'character combination approach' (Kluge, 1989; Eernessie and Kluge, 1993; Miyamoto and Fitch, 1995). Both 'PA+PB+H' (the combined set) and 'T' (ontogenetic transformation character sets) are reliable ontogenetic data sets, as shown in Figure IV-5. This result justifies their use in phylogenetic analysis using ontogenetic data. Furthermore, the data set, 'T+', which includes all ontogenetic transformation characters and all 'instantaneous' characters applicable to 15 taxa, causes fewer homoplasies than the other data sets. This indicates more information contents are closely related to higher reliability of the data set. In addition, the practical usage of ontogenetic transformation characters enables us to efficiently integrate the contradictory results derived from partitioned ontogenetic data set (Figure IV-7).

What are the differences between character combination approach and the practical use of ontogenetic transformation character concept? First of all, there is an evident difference in constructing the data set. In the 'character combination approach', characters ('instantaneous') are chosen for discrete ontogenetic stages, then a separate data matrix is constructed for each stage, and then each matrix is incorporated into one data set before analysis. On the other hand, where adopting the ontogenetic transformation character concept, characters are defined through observing variations of morphologic features (equivalent to de Queiroz's (1985) 'instantaneous morphology' and Kluge's (1988) 'vertical characters') during the whole life cycle of an organism.

Another difference is that each approach strongly supports a slightly different tree topology; as seen in Figure IV-7, the clade of Ly+(Pr+Ps) of T does not appear in PA+PB+H. This is clearly demonstrated in Hennig's (1966) fig. 35, which, he believed, is derived from the 'correct' methods of phylogenetic systematics, and appears to be similar to the current 'character combination approach'. Given that ontogenetic transformation character concept is applied to each character (cube) in fig. 35, the monophyly defined by imaginal synapomorphy ('I') is no longer supported. The reason is because each subordinate clade (defined by 'P' or 'L2') of the clade shows different ontogenetic transformations; one cube consists of the right face with square lattices ('larval') → the upper face with no pattern ('pupal') → the anterior face with dense square lattices ('imaginal'), while the other of the right face with no pattern → the upper face with dots → the anterior face with dense square lattices. Thus, the three clades in fig. 35 have their own characteristic ontogenetic transformation and then, are of a polytomic origin unless the polarity of the ontogenetic transformations is determined. Such difference of synapomorphy distribution leads us to the question of which approach is better for ontogenetic data. It appears to be precarious to choose ontogenetic transformation character set as a more reliable one, only based on its lower average value (Table IV-2) under the comparison using topological constraint. For the present, both approaches are regarded as a desirable phylogenetic practice for ontogenetic data, and further studies will be necessitated for determination of the superiority.

The practical usage of ontogenetic transformation character concept gives us a different insight of how ontogeny is integrated with phylogeny. In general, ontogeny has been treated as a process which may have been recapitulated during the course of evolution (Gould, 1977; McNamara, 1986), mainly within the context of 'heterochrony'.

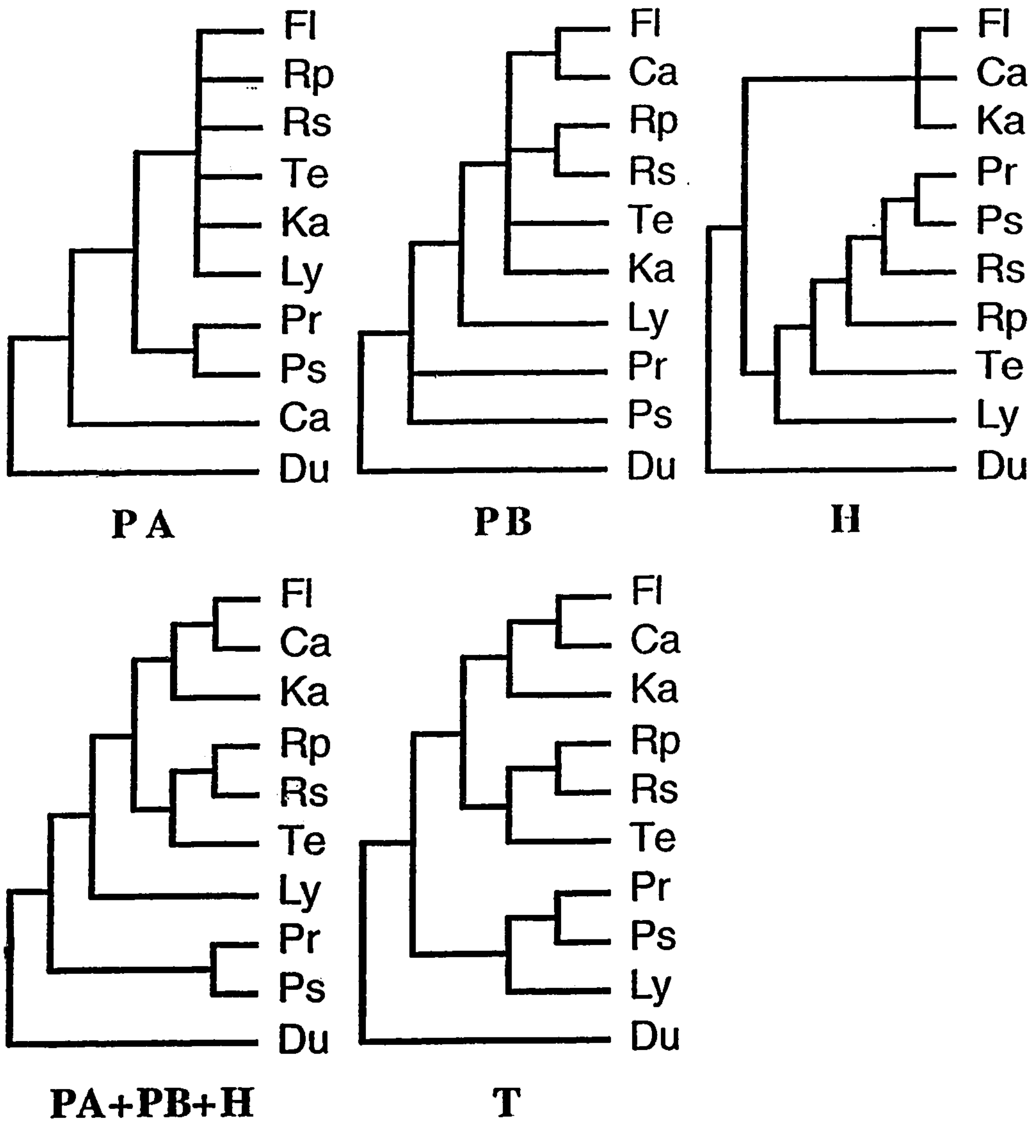

FIGURE IV-7. Majority rule consensus trees of 10 taxa derived from each partitioned data set, the combined set, and the ontogenetic transformation character set.

In contrast, the use of ontogeny as in this work places an emphasis on the descriptive aspect of ontogeny, rather than the process. This does mean that the practical use of ontogenetic transformation character concept obviously leads us to reach a more reliable hierarchical distribution pattern of the organisms, while the concept of recapitulation allows us to understand the evolutionary process using ontogenetic information. The result that heterochronic character sets are less reliable than plain ontogenetic transformation character set indicates that heterochronic information has no great implication for the phylogeny reconstruction, given that ontogenetic transformation character is employed. Other ways to use ontogenetic information are the polarity determination (Nelson, 1978; Kraus, 1988) and homology recognition (Roth, 1984; Rieppel, 1990, 1993). In contrast to the use of ontogenetic transformation character concept, these introduce the sequential property of ontogeny into phylogenetic practice, in a rather indirect way, not as an actual evidence of phylogeny reconstruction.

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CHAPTER V

HYSTRICURID PROTASPIDES FROM TREMADOCIAN OF SOUTHERN IDAHO AND THEIR TAXONOMIC AND PHYLOGENETIC IMPLICATIONS.

INTRODUCTION

Hystricurids have been considered as either the earliest member of the Proetida (Fortey and Owens, 1975; Fortey, 1990), or as Ordovician members of the Cambrian Ptychopariida (Ludvigsen et al., 1989; Shergold, 1991). The first opinion was based on similarities between early meraspid cranidia of hystricurids, in particular Hystricurus, and those of later members of the Proetida; whereas the second opinion was based on holaspid similarities. Each compared hystricurids to trilobites occurring above and below the Cambrian-Ordovician boundary which has been conceived both as extinction level (Westrop, 1989) and an interval of radiation (Fortey and Owens, 1990a). Hystricurids may be a bridging taxon between the Cambrian ptychopariids and long-lived Ordovician and later proetids. The two opinions of hystricurid taxonomy, seemingly in conflict with each other, should be integrated within the context of phylogeny of proetids and ptychopariids. New information on hystricurid protaspides provides the basis for classifying hystricurids as the earliest (Tremadocian) member of the Proetida.

Phylogenetically, several earlier workers (e.g. Chatterton, 1971, p. 71; Owens, 1973, text-fig. 11; Fortey and Owens, 1975) have suggested that hystricurids are closely related to or have given rise to younger members of the Proetida. Such phylogenetic inferences were made largely based on similarities of early growth stages, in particular, meraspid cranidia. Protaspides of several proetid families are well described, and comparison of them with hystricurid protaspides described herein gives more clear insight on the phylogeny of Proetida, especially during Lower Ordovician.

Some of newly described hystricurids do not have enough materials to acquire a formal species designation. Thus, open nomenclature based on Bengtson's (1988, p. 226) recommendations, and Jeppsson and Merrill (1982) was used for those trilobites. Synonymy list was formatted in accordance with Mattews' (1973, p. 718) example. The figured specimens in this chapter were collected from the lower part of Garden City Formation, exposed on the west side (Ross' (1951) Locality 5) of Hillyard Canyon (Figure I-1 and V-1).

SYSTEMATIC PALAEONTOLOGY

Order PROETIDA Fortey and Owens, 1975

Family HYSTRICURIDAE Hupé, 1953

Diagnosis -- For general diagnosis, see Hupé (1953, p. 198; 1955, p. 122). All pygidia which are considered to be correctly assigned to Hystricuridae have four pygidial rings and a terminal piece.

Genera Assigned -- Hystricurus Raymond, 1913, 'Paraplethopeltis' Bridge and Cloud, 1947, Amblycranium Ross, 1951, Hillyardina Ross, 1951, Pachycranium Ross, 1951, Parahystricurus Ross, 1951, Psalikilopsis Ross, 1953, Psalikilus Ross, 1951, Pseudohystircurus Ross, 1951, Hyperbolochilus Ross, 1951, Glabretina Lochman, 1965, Tanybregma Jell and Stait, 1985.

Discussion -- Taxonomic rank, familial or subfamilial, of the hystricurids have not been firmly settled down (Table V-1). Originally, Hupé (1953, p. 198) established the Family Hystricuridae to include the following genera, Hystricurus, Pachycranium, Parahystricurus, Amblycranium, Hillyardina, Psalikilus, Hyperbolochilus, Weeksina, and Jeffersonia. The last two genera were excluded from the family and assigned to Lonchocephalidae and Bathyuridae, respectively in the Treatise (Moor, 1959). Hupé's familial diagnosis includes many general features shared with other solenopleuracean families (under his classification) such as Solenopleuridae. The only feature

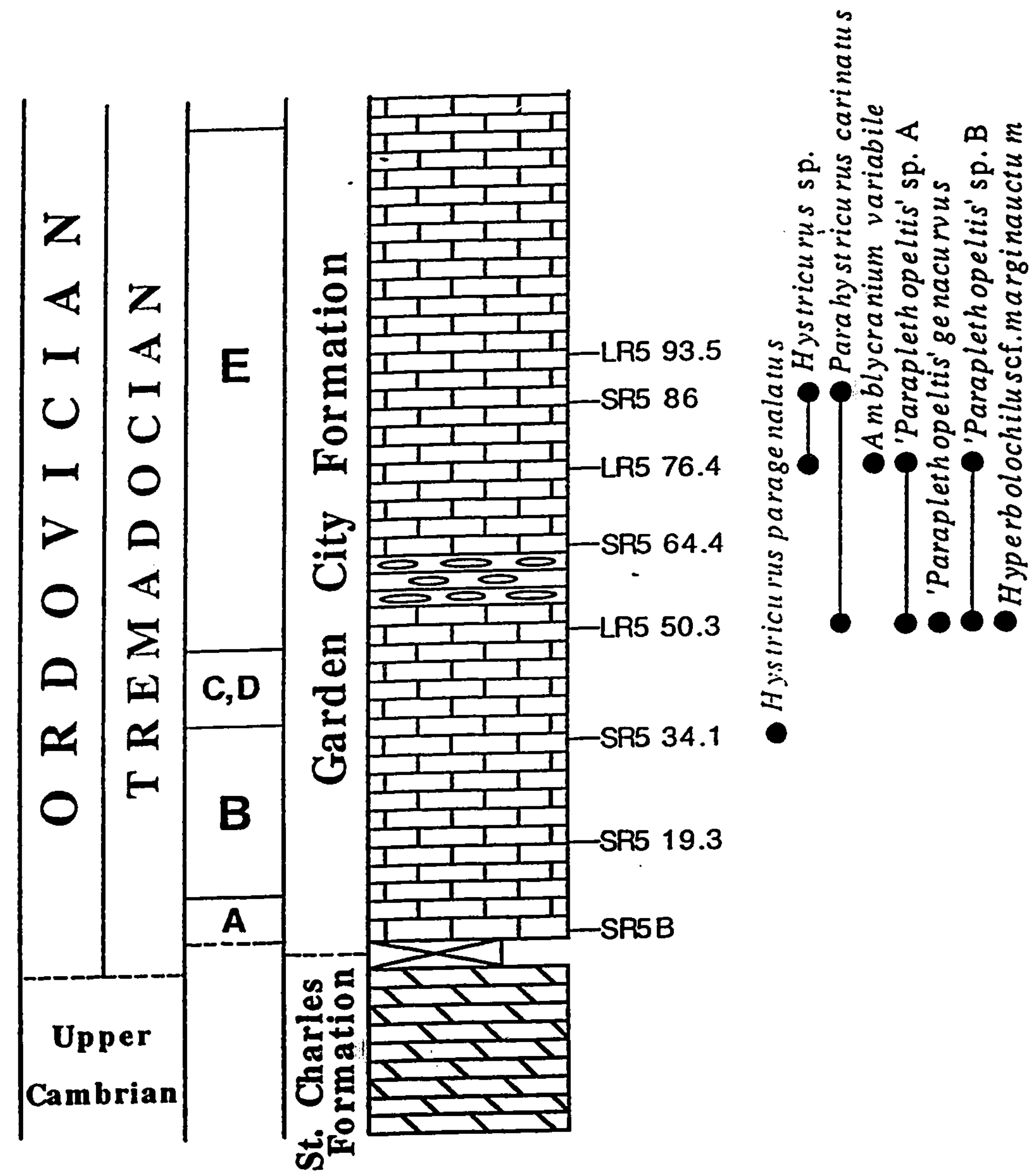


FIGURE V-1. Stratigraphic occurrence of the newly described hystricurid trilobites from the lower part of the Garden City Formation, exposed at west side of Hillyard Canyon (equivalent to Ross' (1951b) Locality 5). The boundary between underlying St. Charles Formation and Garden City Formation is covered with floats. The scale of trilobite zones is after Hintze's (1973, fig. 1) trilobite zonal scheme.

TABLE V-1. Various opinions of the taxonomic status of the hystricurid trilobites.

Authors	Subfamily	Family	Superfamily	Order
Hupé (1953)		Hystricuridae	Solenopleuroidae	
Poulsen (1954)	Hystricurinae	Solenopleuridae		
Treatise (Moore 1959)	Hystricurinae	Solenopleuridae	Solenopleuracea (includes Solenopleuroidae, Hupé, 1953)	Ptychopariida
Fortey and Owens (1975)	Hystricurinae	?	?	Order Proetida
Ludvigsen et al. (1989)		Hystricuridae	Solenopleuracea	
Shergold (1991)		Hystricuridae	Catillicephalacea	

distinguishing the Hystricuridae is the absence of an ocular ridge, and even that feature loses its validity since Hystricurus has been reported with a distinct eye ridge (e.g. Hystricurus penchiensis, see Zhou and Fortey, 1986, pl. 1, fig. 5). Poulsen (1954) lowered the taxonomic rank of the Hystricuridae to the subfamilial level, and assigned this taxon to the Solenopleuridae Angelin, 1854, a classification which was accepted in the Treatise (Moore, 1959, p. O278), even though Poulsen (p. 444) clearly stated, ". . . the following classificatory arrangement must (italicized by the author) be regarded as tentative.". Poulsen (p. 443-444) mentioned that the uncertainty about the taxonomic statement was due to inadequate knowledge of morphologic variation ranges of 'opisthoparian' (according to Størmer's (1942) classification) trilobites. Along with the Hystricurinae, Poulsen (1954) included three of Hupé's families, the Solenopleuridae, the Acrocephalitidae, and the Saoidae (a ptychoparioidean of Hupé, 1953), in the Solenopleuridae as the subfamilies. Among these subfamilies, the Acrocephalitidae, re-elevated to the familial status, was referred to as a constituent of the Superfamily Catillicephalacea (Öpik's (1967) classification) by Shergold (1991).

Since then, most researchers have agreed on the subfamilial status of hystricurid trilobites, following the Treatise, although a few researchers, such as Shergold (1991) and Westrop et al. (1993), followed Hupé's (1953) classification of hystricurid trilobites as a family. In this work, Hupé's (1953) classification is followed, because Poulsen (1954) did not clearly reveal the scientific reason for including hystricurid within the Solenopleuridae, and hystricurid protaspides, described herein, display considerable morphologic disparities from solenopleurid protaspides such as Sao hirsuta (Barrande, 1852) and Solenopleura robbi (Hupé, 1955, fig. 116). Such disparities are considered sufficient to separate hystricurids from the Solenopleuridae and to designate as a family, which is well in accordance with Ludvigsen et al.'s (1989, p. 22) comments. Thus, only two subfamilies, Saoinae Hupé, 1953 and Solenopleurinae Hupé, 1953, are regarded as belonging to the Solenopleuridae.

The superfamilial or ordinal status of the Hystricuridae (sensu herein) has not been much reviewed (Table V-1), since Hupé (1953) established a new superfamily Solenopleuroidae (incorporated into the Solenopleuracea Angelin, 1854 in the Treatise) to embrace several families, including Hystricuridae. When proposing a new order, Proetida, Fortey and Owens (1975) suggested that the included families within the Proetida might have been derived from hystricurids, mainly based on similarities of meraspid cranidia of hystricurids and those of several proetid families, and thus the hystricurids are the earliest member of the Proetida. Comparison of hystricurid protaspides with several proetid protaspides (Fortey, 1990, text-fig. 16) supports the inclusion of the Hystricuridae in the Proetida. Larval dissimilarities between hystricurids and solenopleurids (see above) indicate that most, if not all, Cambrian solenopleuraceans are not a constituent of the Ordovician and later Proetida. Fortey (1990) suggested that the Proetida might include Upper Cambrian solenopleurids, morphologies of which appear to be indistinguishable from Hystricurus. However, this extension of the Proetida into the Cambrian solenopleurids is problematic, considering that solenopleurid protaspides lack a preglabellar field, a definitive character used to define Proetida (Fortey, 1990). The same taxonomic problem caused by adult similarity and larval dissimilarity applies to Onchopeltis (an elviniid, see Westrop, 1986) which is morphologically very similar to the hystricurids (see Rasetti, 1944, pl. 39, figs 1-5) and thus, considered as a probable ancestor to the hystricurids. Ludvigsen et al. (1989) addressed a similar problem and concluded that hystricurids constitute a separate family from the solenopleurids, but were still retained within the Solenopleuracea along with dokimocephalids and elviniids, which have similar cranidial morphologies to hystricurids. However, protaspid morphologies of those Upper Cambrian solenopleuraceans (e.g., Elvinia roemeri, see Hu, 1979, pl. 8, figs 1-11, text-fig. 1) are so different from hystricurid protaspides that the Hystricuridae should be excluded from the Solenopleuracea.

Shergold (1991, p. 33) placed the Hystricuridae in the Superfamily Catillicephalacea Raymond, 1938, being in conflict with Fortey and Owens (1975). He considered that the hystricurids have similar cranidial and pygidial morphologies to the lonchocephalines (catillicephalacean, see Öpik, 1967), and, when developed, similar cranidial spines. Additionally, Shergold (1991) mentioned a modest taxonomic affinity of the hystricurids to Dokimocephalidae (an olenacean family). This is likely to be an intriguing taxonomic statement, in which some Cambrian ptychopariids are taxonomically incorporated with Ordovician hystricurids. However, the larvae of hystricurids and lonchocephalines (Welleraspis swartzi, see Rasetti, 1954, pl. 62, figs 1-4, fig. 4 and Hu, 1968, pl. 1, figs 1-9, text-fig. 1) are not similar. Thus, Hystricuridae is, herein, considered as a separate family in Proetida.

Taxonomic discussion of such hystricurid genera as Hystricurus, Parahystricurus, Amblycranium, 'Paraplethopeltis', and Hyperbolochilus will be found under the discussion of each genus. For a discussion of other hystricurid genera, see Ross (1951).

Fredrickson's (1949) genus, Apachia, (the only Cambrian hystricurid) was questionably placed in Hystricuridae in the Treatise. The type species, Apachia trigonis (Fredrickson, 1949, pl. 70, figs 14-17), exhibits similar cranidial morphologies to Hystricurus, in particular, Hystricurus globosus (Stitt, 1983, pl. 5, fig. 1), except for its triangular posterior fixigenal area and smooth surface. The features are also found in several other Upper Cambrian families, including those mentioned above. Thus, the inclusion of Apachia in Hystricuridae is problematic, and at present, the genus is not considered to definitely belong to the Hystricuridae.

Lochman (1965) established a monotypic Glabretina, as a new hystricurid genus, mainly based on its occurrence in Zone D, where few hystricurid trilobites were previously reported. The distinguishing features from Hystricurus (Lochman, 1965, p. 475-476), such as the presence of an eye ridge, a preglabellar median furrow, a more anteriorly located palpebral lobe, and a triangular posterior fixigenal area, appear to be a combination of characters which are found in different hystricurid genera; and meraspid pygidial morphologies (Lochman, 1965, pl. 62, fig. 10) are similar to '*Paraplethopeltis*'. *Glabretina* certainly belongs to the Hystricuridae, even though it is questionable whether it is a separate genus, or congeneric with another hystricurid genus. Another probable hystricurid genus worthy of discussion, *Omuliovia* Tschugaeva, 1962, was fully discussed by Zhou and Fortey (1986), who suggested that the genus is a bathyurid which was derived from a hystricurid stock, since *Omuliovia granosa*, displays similarities to some *Hystricurus* species. However, having a bilobed pygidial terminal piece (reminiscent of dimeropygids (see Ross, 1951, pl. 35, fig. 25) and strictly parallel-sided glabella makes its assignment to Hystricuridae less plausible. Jell and Stait (1985, p. 8) erected a new hystricurid genus, *Tanybregma*, which has a peculiar long preglabellar field (reminiscent of *Hyperbolochilus*). Besides that, most morphologic features, such as a forward-tapering and tuberculate glabella, a slender posterior fixigenal area, and a distinct palpebral furrow, agree with other *Hystricurus* species. *Tanybregma* is considered as a hystricurid genus with the long preglabellar field.

Genus HYSTRICURUS Raymond, 1913

Type Species -- *Bathyurus conicus* Billings, 1859 from the Canadian 'Calciferous Sandrock' of Mingan Islands, Canada (by original designation).

Other Species -- *Hystricurus crotalifrons* (Dwight), 1884; *H. cordai* (Billings), 1860; *H. ellipticus* (Cleland), 1900; *H. mammatus* Raymond, 1924; *H. ravni* Poulsen, 1927; *H. longicephalus* Poulsen, 1927; *H. quadratus* Poulsen, 1927; *H. missouriensis* Ulrich, 1930; *H. eurycephalus* Kobayashi, 1934; *H. convexus* Endo, 1935; *H. granosus* Endo, 1935; *H. armatus* Poulsen, 1937; *H. sulcatus* Poulsen, 1937; *H. nudus* Poulsen, 1937; *H. lewisi* (Kobayashi), 1940; *H. genalatus* Ross, 1951; *H. paragenalatus* Ross, 1951; *H. politus* Ross, 1951; *H. oculilunatus* Ross, 1951; *H. contractus* Ross, 1951; *H. flectimembrus* Ross, 1951; *H. acumennasus* Ross, 1951; *H. robustus* Ross, 1951; *H.*

lepidus Hintze, 1952; H. millardensis Hintze, 1952; H. platypleurus Kobayashi, 1955; H. calvus Kobayashi, 1960; H. wilsoni Gobbett and Wilson, 1960; H. sainbury Ross, 1972; H. penchiensis Lu, 1976; H. globosus Stitt, 1983; H. hillyardensis Stitt, 1983; H. paucituberculatus Fortey, 1983; H. timsheaensis Jell and Stait, 1985; H. (H.) scrofulosus Fortey and Peel, 1989.

Diagnosis -- See Raymond (1913, p. 60) and Ross (1951b, p. 39-40) for general diagnosis.

Discussion -- Raymond (1913) defined the genus Hystricurus by its forward-tapering glabella and dorsally raised palpebral area of fixigenae (= his 'the elevated ridge on the fixed cheeks outside the dorsal furrow') to distinguish it from Bathyurus Billings, 1959 (a bathyurid). Of interest is that Hystricurus species described before Ross' (1951b) extensive work on that genus, to some degree, follow Raymond's diagnosis. However, since Ross' work, the generic diagnosis was somewhat modified into a less strict one. In fact, Ross (1951b, p. 39-40) added several morphologic features to Raymond's diagnosis. For that reason, it has been common for the species described since 1951 to show a barrel-shaped glabella (e.g. Hystricurus globosus, see Stitt, 1983, pl. 5, fig. 2) and rather flat palpebral area. The morphologic deviations from the type species, Hystricurus conicus (Billings, 1859) (Whitfield, 1889, pl. 13, figs 15, 20) are summarized in Appendix V-1. The correct association of cranidia with pygidia is the most significant problem in Hystricurus taxonomy, since few Hystricurus species are completely known and the only evidence considered as plausible for a correct association is stratigraphic co-occurrence, and only one species, Hystricurus ravni (Poulsen, 1937, pl. 18, fig. 5), is known from a complete carapace. In spite of the possible incorrect association, the general pygidial morphology of Hystricurus species is more conserved than cranidial morphology listed in Appendix V-1; Ludvigsen et al. (1989, p. 22) suggested that pygidial morphologies of hystricurids are invariable enough to be used as diagnostic features for that genus.

Kobayashi (1934, p. 541) stated that the presence of a preglabellar field, a larger eye, a narrower fixed cheek, and eye-lines (probably eye ridges) are the typical features to distinguish Hystricurus from other solenopleurid trilobites. However, those features are found in only a few Hystricurus species, so that their validity as a diagnosis for the genus is questionable.

The above-listed morphologic variations render the generic concept of Hystricurus broader than Raymond's (1913) original one, since they occur in several other hystricurid genera. Indeed, due to such morphologic variations, many species have been assigned to the genus with question; for example, Ross (1951) described 9 out of a total 17 Hystricurus species without a formal species designation. This problem would extend into among hystricurid genera, since there are many species which were regarded as 'intermediate' between two other species of different genera; in some cases, 'intermediate' was interpreted as anagenetic bridging between ancestor and offsprings (see Ross, 1951, p. 61) . Nonetheless, for the present, those morphologic features are considered as being included within the generic concept.

Hystricurus paragenalatus Ross, 1951

Plate V-1.1-8; Figure V-2

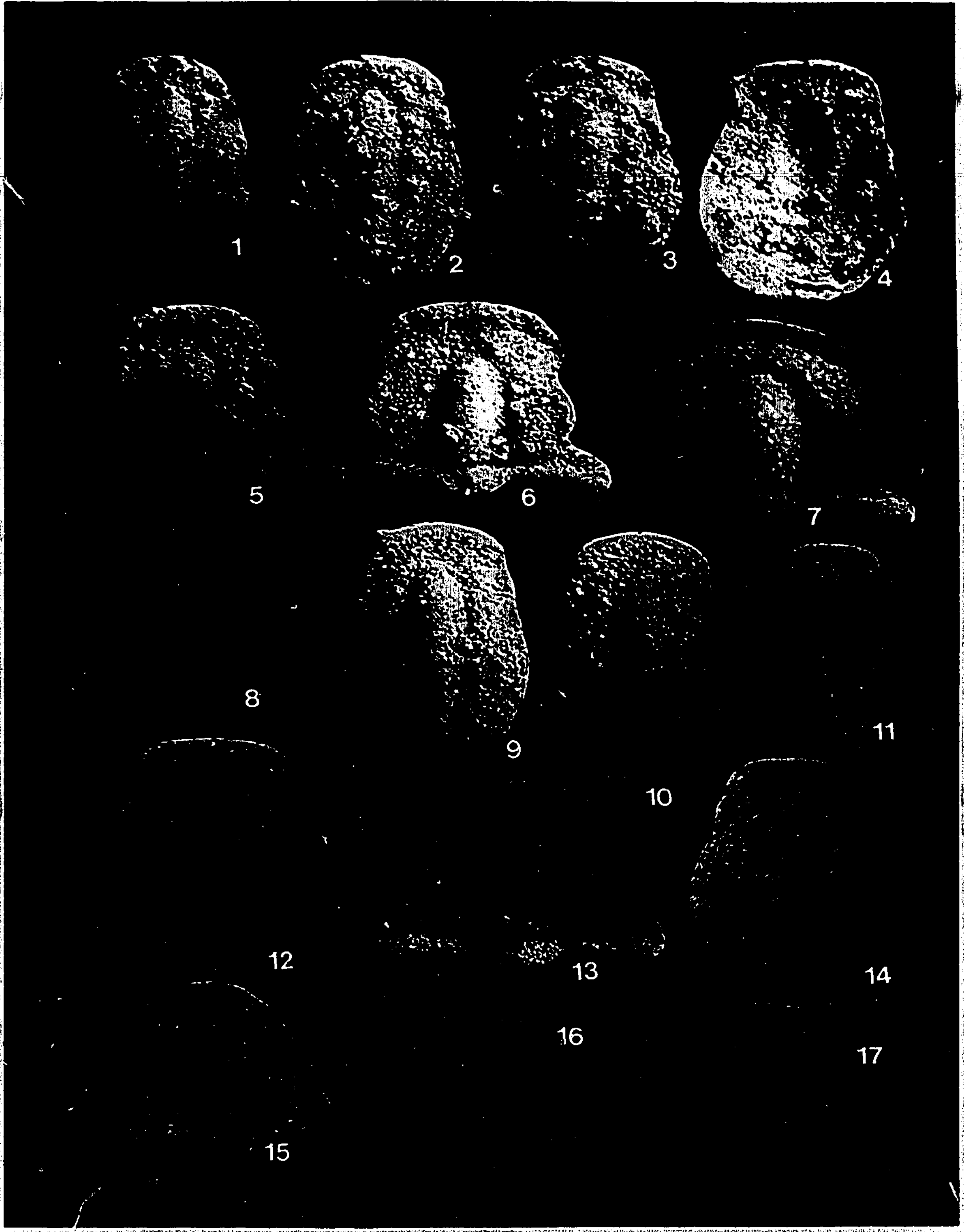
1951 Hystricurus paragenalatus n. sp. — Ross, p. 42-45, pl. 8, figs 14-26.

1952 Hystricurus paragenalatus Ross. — Hintze, p. 165, pl. 6, figs 7-11.

Holotype -- Cranidium, Y.P.M. 17934, (Ross, 1951, pl. 8, figs 14, 17, 18) from Zone B of Garden City Formation, Ross' (1951) Locality 7, southern Idaho, U.S.

Figured Material -- Protaspides; UA 10990, UA 10991, UA 10992, UA 10993: Meraspid cranidia; UA 10994, UA 10995: Holaspid cranidia; UA 10996, UA 10997.

PLATE V-1. 1-8, *Hystricurus paragenalatus* Ross, 1951, from SR5 34.1 horizon. 1, UA 10990, dorsal view of early protaspis, x 80. 2, UA 10991, dorsal view of late protaspis, x 61. 3, UA 10992, dorsal view of late protaspis, x 60. 4, UA 10993, ventral view of late protaspis, x 80. 5, UA 10994, dorsal view of meraspid cranidium, x 80. 6, UA 10995, dorsal view of meraspid cranidium, x 46. 7, UA 10996, dorsal view of holaspid (?) cranidium, x 18. 8, UA 10997, ventral view of holaspid (?) cranidium, x 15; 9-17, *Hystricurus* sp. from LR5 76.4 and SR5 86 horizons. 9, UA 10998, dorsal view of protaspis, x 63. 10, UA 10999, dorsal view of protaspis, x 66. 11, UA 11000, dorsal view of degree 0 meraspis (?), x 47. 12, UA 11001, dorsal view of meraspid cranidium, x 66. 13, UA 11002, dorsal view of meraspid cranidium, x 41. 14, UA 11003, dorsal view of protaspis, x 61. 15, UA 11004, dorsal view of degree 3 or 4 meraspis, x 24. 16, UA 11005, dorsal view of meraspid cranidium, x 30. 17, UA 11006, dorsal view of holaspid (?) cranidium, x 23.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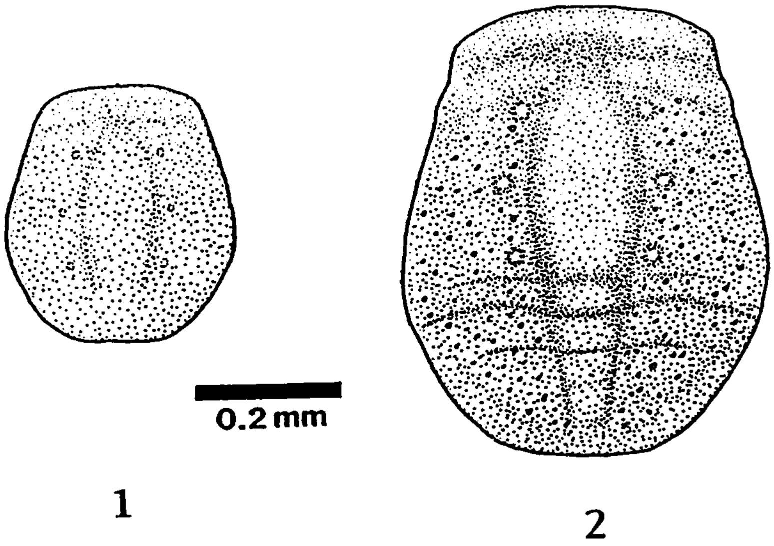


FIGURE V-2. Drawing of protaspides of *Hystricurus paragenalatus* Ross, 1951. 1, dorsal view of early stage. 2, dorsal view of late stage.

Diagnosis -- See Ross' (1951, p. 42-43) description.

Protaspid Description -- In length versus width plot of protaspid shields (Figure V-3) from SR5 34.1 horizon (Zone B, Tremadocian), three morphometric groups (instars) may be recognized. However, the morphologic features described below do not support separate existence of two distinct larger stages. Thus, only two stages, designated 'early' and 'late', are separated on the basis of the appearance of protopygidium; materials are not enough to deserve numerical denotations such as stage 1 or 2.

Shield of early protaspides is not so well-silicified that morphologic details are not clear. Early protaspides are 0.32-0.35 mm wide and 0.34-0.44 mm long, and subovate in outline. Axis is spindle-shaped, with posterior third not being clearly defined; no transverse segmentation is observed. Along with axial furrow, three pairs of inner series tubercles are developed. Frontal field comprising future preglabellar field, anterior fixigenal area and anterior border is flat and at lower-level than axis.

Late protaspides are 0.4-0.63 mm wide and 0.48-0.73 mm long and suboval in outline excluding librigenae. Protocranidium is subtrapezoidal and 62-72 % of shield length. Glabella is barrel-shaped but tapers forwards, maximum width being at midpoint; axial furrow is moderately deep. Occipital ring is narrower (tr.) than maximum glabellar width; occipital furrow is relatively deep. Anterior cranidial border slightly curves forwards and is convex upwards; border furrow is broad and shallow, being confluent with preglabellar furrow medially to form broadly depressed area immediately in front of glabella. Palpebral lobe is only recognizable by slight outward-curvature of facial suture. Eye ridge is rather convex upwards, directed anteromedially, continuous from palpebral lobe to axial furrow, and anteriorly defined by broad anterior border furrow and posteriorly by shallower furrow (posterior ridge furrow). Along and immediately outside axial furrow, three pairs of tubercles (inner series) occur and are regularly spaced; first pair (from anterior) is opposite palpebral lobe, second immediately behind mid-glabellar point, and

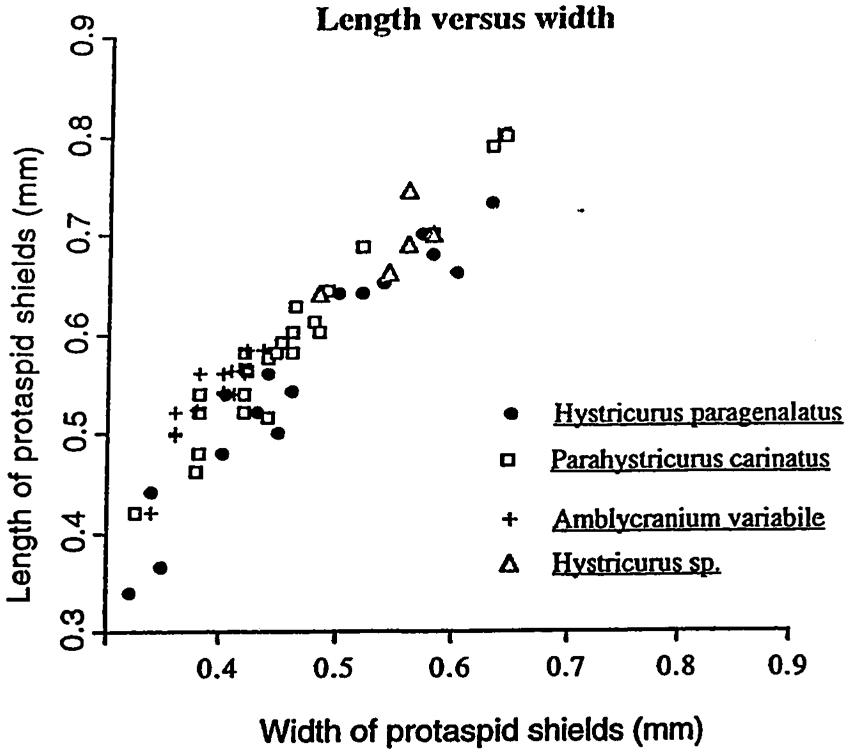


FIGURE V-3. Length versus width plots for protaspides of Hystricurus paragenalatus Ross, 1951, Hystricurus sp., Parahystricurus carinatus Ross, 1951, and Amblycranium variabile Ross, 1951. Plots for each species are so continuous that recognition of protaspid stages is based on the morphologic details (see text).

third immediately in front of posterior border furrow. Posterior cranidial marginal furrow is moderately deep, and slightly arches forwards and then strongly curves backwards distally. Facial suture is nearly straight, and gently divergent posteriorly; in larger protaspides, anterior suture becomes slightly divergent forwards and posterior one more divergent backwards. Protopygidium is semicircular; axis gently tapers backwards, with two or three axial rings; pygidial doublure is sharply inturned and uniformly narrow. Whole shield but axis and ocular ridge is covered with dispersed granules.

Meraspid and Holaspid Description -- Smallest disarticulated meraspid cranidium is 0.4 mm in sagittal length and differs from protocranidium of late protaspides only in having longer (exsag.) palpebral lobe, more divergent posterior facial suture and disappearance of eye ridge. Morphologic changes that take place during meraspid period are; 1) anterior facial suture becomes more divergent and posterior suture strongly divergent; 2) larger and more crescentic palpebral lobe in later meraspid cranidia; palpebral furrow is slightly impressed; 3) preglabellar field is longer; shallow and broad preglabellar median furrow becomes incised; 4) posterior cranidial border furrow is deeply impressed; 5) two tubercle pairs are developed on palpebral lobe. From holaspid period, cranidium has convex preglabellar field lacking median furrow, more slender posterior fixigenal area, more posteriorly situated palpebral lobe, and exoskeleton covered with interspersed tubercles, except for anterior cranidial border.

Discussion -- From this work as well as Ross' (1951), no articulated specimen is secured, so that the holaspid pygidial morphology can not be described. A detailed comparison of holaspid cranidial features of _Hystricurus paragenalatus_ and _Hystricurus genalatus_ was given by Ross (1951, p. 43-45), both being stratigraphically contemporaneous.

Hystricurus sp.

Plate V-1.9-17

Figured Material -- Protaspides; UA 10998, UA 10999, UA , UA 11003: Degree 0 meraspis; UA 11000: Degree 3 or 4 meraspis; UA 11004: Meraspid cranidia; UA 11001, UA 11002, UA 11005: Holaspid cranidium; UA 11006.

Protaspid Description -- Plots of measurements of materials including figured ones do not give any discrete groupings (Figure V-3), and all protaspid materials are considered to belong to one instar.

Protaspid shields are 0.46-0.58 mm long and 0.58-0.74 mm wide, suboval in outline. Protocranidium is 60-66 % of shield length and trapezoidal in outline. Glabella is parallel-sided or slightly inflated laterally, forward-tapering and with three pairs of lateral glabellar furrows; axial furrow is moderately deep; two pairs of glabellar furrows are short, faintly represented by non-granulated patches and are directed inwards and backwards. Anterior border moderately convex forwards; border furrow is shallow and broad. Preglabellar field is short (sag.), with indistinct preglabellar median furrow. Palpebral lobe occurs as a small outward-curvature of facial suture with palpebral tubercle. Along glabella and immediately besides axial furrow, three pairs of tubercles of inner series are developed in regular spacing; first pair (from anterior) opposite S3, second slightly behind level of S2, and third opposite L1. Occipital ring is rectangular and subequal to maximum glabellar width (tr.); occipital furrow is straight and deep. Posterior cranidial border convex upwards and gently curves backwards distally; posterior border furrow shallows distally. Posterior cranidial marginal furrow is moderately deep and gently curves backwards along with posterior border; with growth, furrow curves more strongly backwards distally. Facial suture is straight except for small stretch along convex palpebral lobe; anterior branch slightly convergent anteriorly and posterior one gently divergent posteriorly. Protopygidium semicircular in outline. Protopygidial axis gently tapers backwards and bears three to four rings, anterior two of which have pair of small tubercles on crest. Pleural field is gently convex upwards; up to two pleural ribs are recognizable; each rib has shallow pleural furrow; interpleural furrow is deep and reaches pygidial margin. Whole shield is covered with small granules.

Meraspid and Holaspid Description -- Meraspid cranidium is trapezoidal in outline and differs from protocranidium in lacking granulation on anterior border, appearance of four glabellar tubercle pairs (rachial series), more deeply incised preglabellar median furrow, more strongly divergent posterior facial suture, and addition of more tubercles on inner series and one more pair on palpebral lobe. Between meraspid and holaspid cranidia, following changes occur: 1) small granules disappear; 2) glabella becomes covered with irregularly dispersed tubercles; 3) glabella becomes wider than long and strongly tapered forwards; 4) on anterior border, fine terrace lines appear.

Discussion -- This Hystricurus species appears to be new, but the paucity of material (in particular, absence of free cheeks and pygidium) prevents its formal recognition herein. The holaspid cranidium is distinguished from other Hystricurus species in having sparsely tuberculate cranidium, strongly forward-tapering (nearly triangular in outline) glabella, preglabellar median furrow, and distally broadening posterior border. The cranidium of Hystricurus sp. C (Ross, 1951, pl. 10, fig. 22) is similar to, but dissimilar from, this species in having two pairs of glabellar furrows, smooth skeletal surface, and forwardly divergent anterior facial suture. Terrell's (1973, pl. 2, fig. 7) Hystricurus sp. L is probably conspecific with this species.

Genus PARAHYSTRICURUS ROSS, 1951

Type Species -- Parahystricurus fraudator Ross, 1951 from the Tremadoc (Lower part of Garden City Formation) of southern Idaho, U.S.

Other Species -- *Parahystricurus oculirotundus* Ross, 1951; *Parahystricurus pustulosus* Ross, 1951; *Parahystricurus carinatus* Ross, 1951.

Diagnosis -- See Ross (1951, p. 56-57) for details.

Discussion -- Taxonomic separation of *Parahystricurus* from *Hystricurus* was based on the facts that the former has triangular posterior fixigenal area, more elliptical glabella and smaller palpebral lobes (Ross, 1951, p. 57). However, just as in *Hystricurus*, the *Parahystricurus* species, all of which were collected from the Garden City Formation, show considerable morphologic variation. Indeed, Ross' diagnosis does not apply to *Parahystricurus carinatus* (Ross, 1951, pl. 13, figs 23-27, 30-32) which has similar cranidial morphologies to *Hystricurus*. However, the transitory pygidium of the complete carapace found in this work (see below) makes the assignment of the species to *Hystricurus* implausible, since the pygidium is very different from the pygidial morphology of *Hystricurus*; pygidial morphologies are considered less variable than cranidial ones within each genus of the hystricurids.

Parahystricurus carinatus Ross, 1951

Plate V-2.1-15; Plate V-3.1-4; Figures V-4, V-5

1951 *Parahystricurus carinatus* n. sp. — Ross, p. 60-61, pl. 13, figs 23-27, 30-32, 35-37.

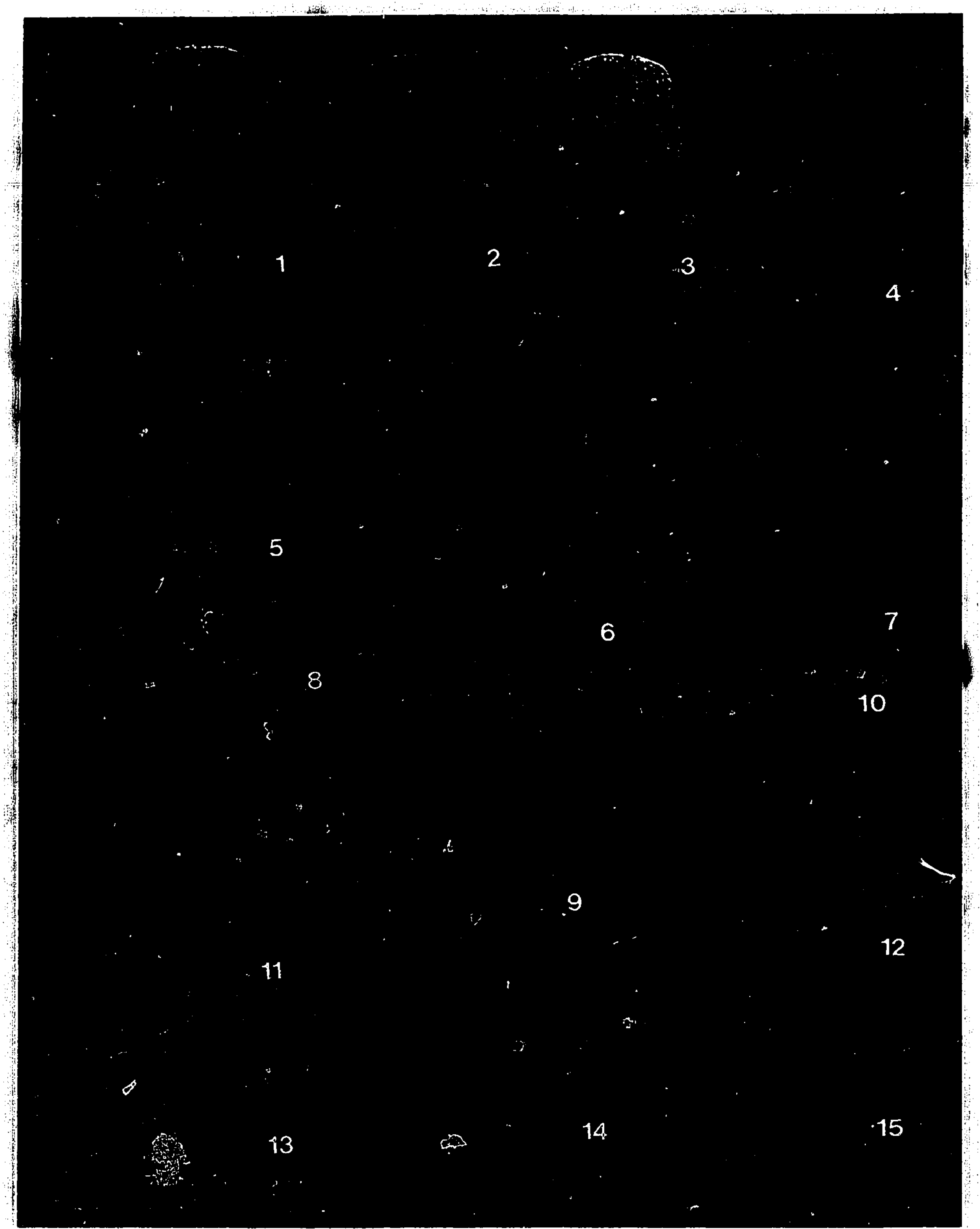
1951 Gen. and sp. ind. — Ross, pl. 19, figs 32, 35 [pygidia].

1951 Gen. and sp. ind. — Ross, pl. 19, figs 2, 21, 22, 29 [hypostomes].

?1973 *Hystricurus* sp. K. — Terrell, p. 78, pl. 4, fig. 2

Holotype -- Y.P.M. 18011 (cranidium, see Ross 1951, pl. 13, figs 26, 27, 32) from Zone E (Tremadocian), Ross' (1951) Locality 5, Garden City Formation, southern Idaho, U.S.

PLATE V-2. 1-15, *Parahystricurus carinatus* Ross, 1951 from LR5 50.3, LR5 76.4, and SR5 86 horizons. 1, UA 11007, dorsal view of early protaspis with librigenae, x 78. 2, UA 11008, dorsal view of late protaspis, x 60. 3, UA 11009, dorsal view of early protaspis, x 67. 4, UA 11010, dorsal view of early protaspis, x 85. 5, UA 11011, ventral view of early protaspis, x 72. 6, UA 11012, dorsal view of degree 0 meraspis, x 57. 7, UA 11013, dorsal view of late protaspis, x 64. 8, UA 11014, dorsal view of meraspid cranidium, x 64. 9, UA 11015, ventral view of displaced degree 7 meraspis, x 25. 10, UA 11016, dorsal view of meraspid cranidium, x 29. 11, UA 11017, dorsal view of meraspid cranidium, x 47. 12, UA 11018, dorsal view of holaspid (?) cranidium, x 18. 13, UA 11019, dorsal view of transitory pygidium with 4 thoracic segments, x 32. 14, UA 11020, dorsal view of transitory pygidium with 2 thoracic segments, x 55. 15, UA 11021, dorsal view of holaspid (?) pygidium, x 27.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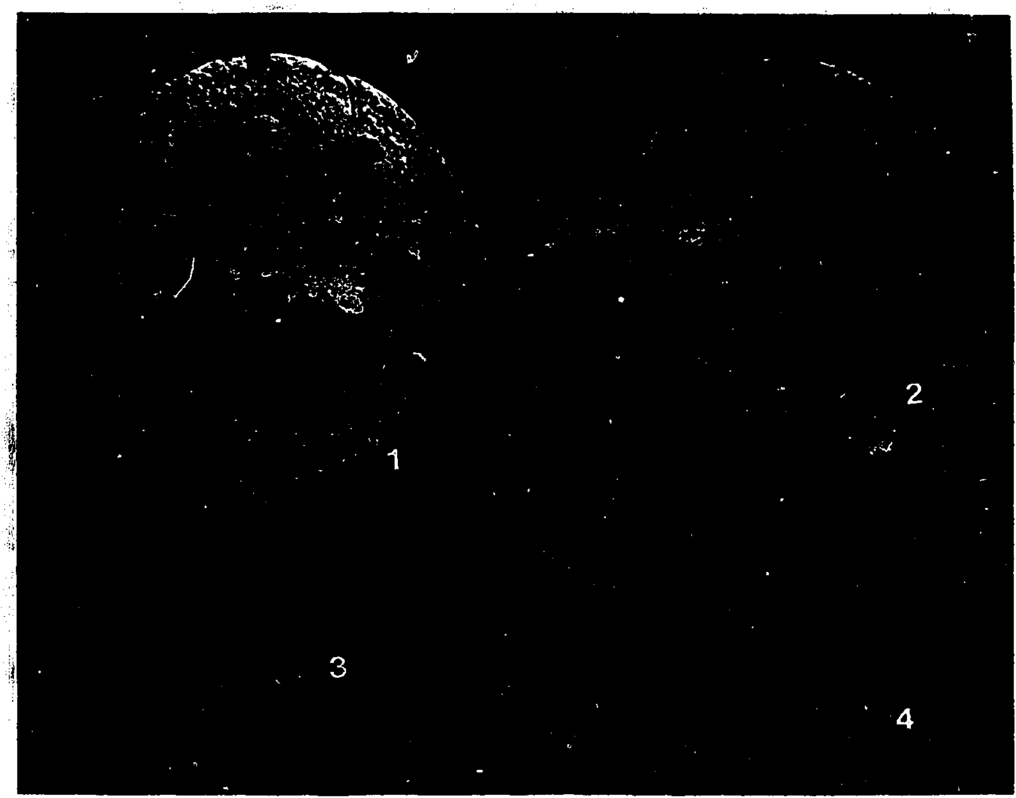


PLATE V-3. Degree 5 meraspid ([illegible]A 11022) of Parahystricurus carinatus Ross, 1951, from [illegible] 86 horizon. 1, dorsal view, x 37. 2, ventral view, x 30. 3, lateral view, x 36. 4, magnified ventral view of displaced and partially broken hypostome, x 90.

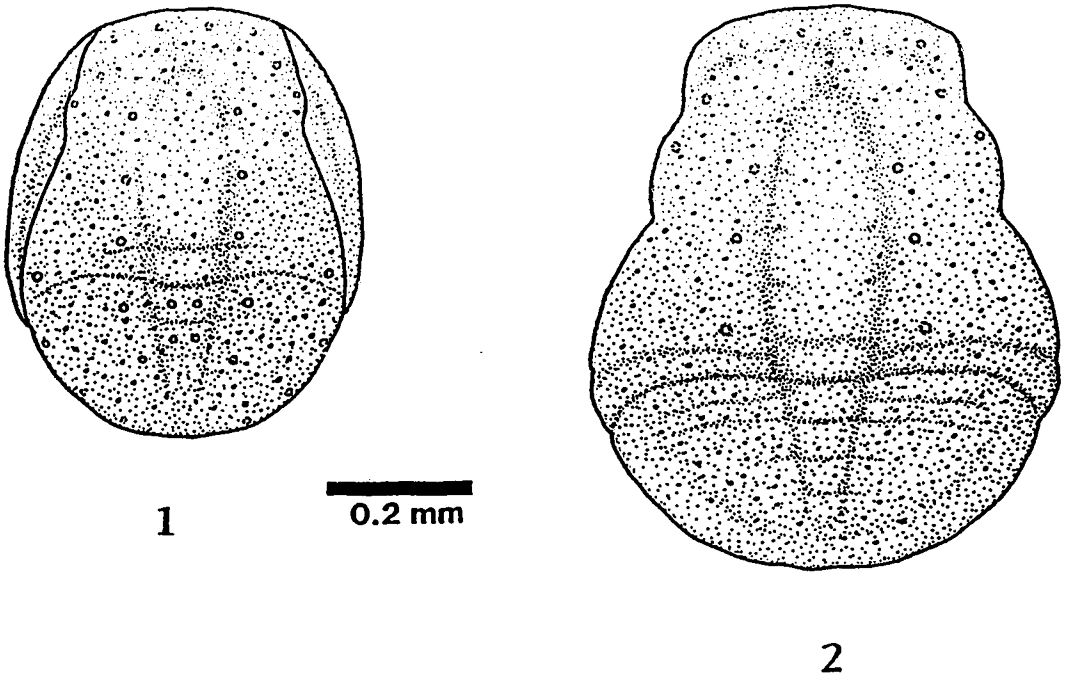


FIGURE V-4. Drawings of protaspides of Parahystricurus carinatus Ross, 1951. 1, dorsal view of early stage. 2, dorsal view of late stage

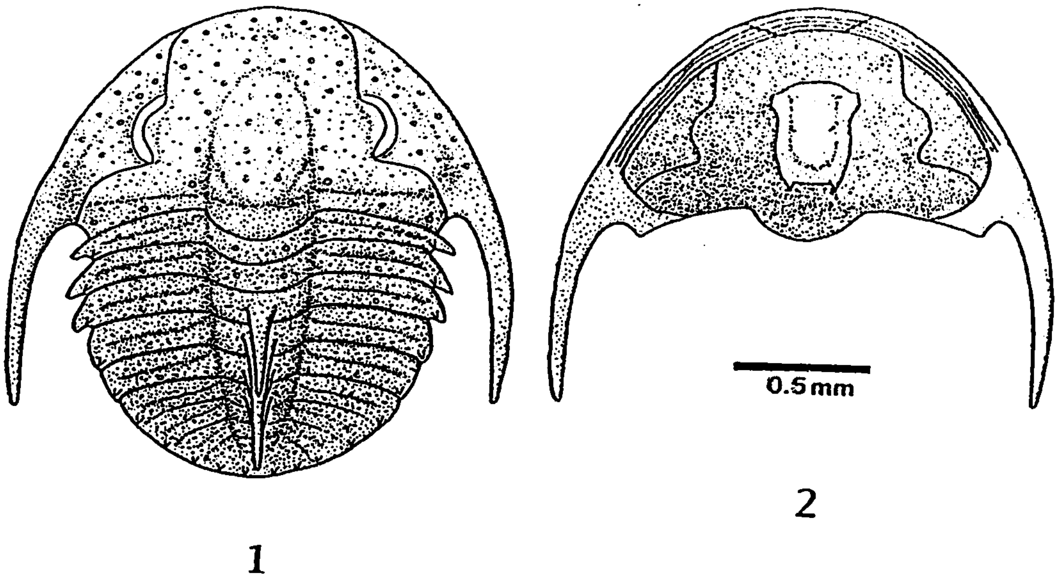


FIGURE V-5. Reconstructions of degree 5 meraspis of *Parahystricurus carinatus* Ross, 1951. 1, dorsal view. 2, ventral view with a hypostome showing a supposed natant condition.

Figured Material -- Protaspides; UA 11007, UA 11008, UA 11009, UA 11010, UA 11011, UA 11013: Degree 0 meraspis; UA 11012: Degree 5 meraspis; UA 11022: Degree 7 meraspis; UA 11015: Meraspid cranidia; UA 11014, UA 11016, UA 11017: Transitory pygidia; UA 11019, UA 11020: Holaspid cranidium; UA 11018: Holaspid pygidium; UA 11021.

Diagnosis -- See Ross' (1951, p. 60-61) description.

Protaspid Description -- Discrete instars were not recognized in length versus width plot of protaspid shields; plots are fairly continuous, without showing any distinct groups (Figure V-3); for this reason, numerical measurements are averages. Two stages, nonetheless, designated 'early' and 'late', might be separated by such morphologic features as distinctiveness of outline of palpebral lobe and number of protopygidial axial rings.

Early protaspides are 0.4 mm long and 0.43 mm wide, elliptical in outline (including librigenae), and covered with dispersed small granules. Protocranidium accounts for 67 % of whole shield length and is subtrapezoidal in outline. Glabella is parallel-sided or slightly inflated at its midpoint and tapers forwards. Occipital ring is rectangular, as wide as glabella and defined by moderately deep occipital furrow (S0); short median node develops on the ring. Preglabellar field is short, on which shallow preglabellar median furrow develops. Alongside glabella and immediately abaxial to axial furrow, three pairs of tubercles (inner series) develop in regular spacing; first pair (from anterior) is placed opposite palpebral lobe, second pair opposite midglabellar length, and third pair slightly anterior to posterior border furrow. Palpebral lobe is relatively small; each lobe bears short palpebral tubercle on its midpoint. Anterior border is gently convex forwards, and border furrow is shallow and broad; two pairs of tubercles develop on anterior border. Posterior cranidial marginal furrow shallows distally, curves slightly forward at its midpoint, and then gently turns backwards. Pair of small tubercles develops on posterolateral corner of protocranidium (consisting of outer series of cephalic region); immediately inside this tubercle pair, one more pair (posterior cranidial border tubercle) is present. Anterior facial suture is slightly convergent forwards; posterior suture is gently divergent posteriorly. Protopygidium, with 33 % of shield length, is semicircular in outline. Protopygidial axis strongly tapers backwards and has three recognizable axial rings (rachial series of pygidial region); anterior two rings possess distinct pair of tubercles, but only one tubercle appears to develop on posteriormost ring. First pleural rib is defined by distinct interpleural furrow which reaches halfway across rib. Immediately inside and along pygidial margin, three pairs of tubercles (outer series of pygidial region) develops in regular spacing; anterior pair is opposite second (from anterior) axial ring, and remaining two pairs are behind second ring. On pleural field, two pairs of small tubercles (inner series on pygidial region) develop; anterior pair is opposite first (from anterior) protopygidial axial ring and posterior one opposite posteriormost axial ring.

Late protaspides are 0.58 mm long and 0.51 mm wide, and differ from early protaspides as follows: 1) three pairs of lateral glabellar furrow are represented by non-granulated patches; each pair is placed opposite tubercle pairs developing abaxial to axial furrow; 2) preglabellar field becomes proportionately longer; 3) palpebral lobe becomes larger (exsag.), and its lateral margin arches more strongly outwards; 4) posterior cranidial marginal furrow is more distinct ,and curves strongly posteriorly at its distal end; 5) four protopygidial axial rings are recognizable; 6) anteriormost pleural furrow almost reaches protopygidial margin, and runs along posterior cranidial marginal furrow; 6) posterior margin of protopygidium is slightly indented forwards.

Meraspid and Holaspid Description -- Degree 0 meraspis (1.06 mm in sagittal length and 0.84 mm in width) displays similar morphologies to late protaspides; designation of this specimen to meraspis may be supported by its larger size and very distinct posterior cranidial marginal furrow which apparently represents segmentation. Notable differences between this stage and protaspides are that meraspis has rather straight anterior margin, more deeply indented posterior margin, more strongly divergent posterior facial suture and parallel-sided glabella.

Articulated meraspid degree 5 carapace (Plate V-3) was obtained from SR6 86 horizon. Carapace, of sagittal length 1.68 mm, is elliptical in outline excluding stout and long genal spines, and covered with a number of dispersed small granules. Cranidium, 0.8 mm long, is subtrapezoidal in outline. Glabella is 0.58 mm long (sag.), highly convex, slightly tapering forwards, with rounded anterior margin, and well defined by deep axial furrow; pair of lateral glabellar furrows (S1) strongly directed backwards and inwards, shallows sagittally to meet occipital furrow (S0), and merges with axial furrows slightly in front of posterior end of eyes; S1 appears to divide glabella into large oval anterior lobe and pair of small triangular posterior lobes (L1); posterior lobe is at far lower-level than anterior one. Occipital ring is convex, strongly curved backwards, and well defined by occipital furrow (S0); S0 shallows sagittally and becomes narrower and deeper distally. Anterior border is gently curved forwards, uniform in width, and clearly defined by border furrow; border has same width as ventral doublure; row of small tubercles is developed on border. Rostral plate is assumed to be elongated (tr.) trapezoidal in outline on basis of rostral suture and hypostomal suture. Preglabellar field is 0.13 mm long (sag.) and bears shallow and broad preglabellar median furrow; pair of small tubercles is present immediately behind anterior border and besides preglabellar median furrow. Eye is positioned at midlength of cranidium. Palpebral lobe is crescentic and defined by shallow palpebral furrow. Palpebral area of fixigena is slightly convex upwards and slopes downwards adaxially. Anterior fixigenal field is slightly inflated dorsally and bears three pairs of tubercles. Along glabella, five pairs of regularly spaced tubercles (inner series) occur immediately abaxial to axial furrow; first pair (from anterior) is immediately besides preglabellar furrow; posterior); second one is immediately in front of anterior end of eye; third is slightly behind anterior end of eye; fourth is opposite anterior end of L1; fifth is opposite midlength of L1. Posterior cranidial border broadens and inflates distally; border furrow shallows and broadens distally; two pairs of tubercles occur at half width of border and distal end of border, respectively. Anterior facial suture is parallel-sided or slightly convergent forwards, and posterior branch of suture is strongly divergent and then, strongly curves backwards.

Librigenal field gently slopes down into lateral border furrow, containing row of four tubercles which are distributed parallel to border furrow. Eye socle (= Ross' (1951) infra-ocular ring) is slender and of independent convexity. Lateral border is uniform in width, moderately convex and defined by shallow border furrow; border furrow is continuous with anterior cranidial and posterior cranidial border furrows. Librigenal spine is tubular, and gently curves inwards and backwards; spine projects from in front of genal angle, so that posterior margin of free cheeks is indented. On lateral border, row of tubercles is developed, and is continuous with paired tubercles on anterior cranidial border.

Natant hypostome is slightly displaced, and partially broken laterally and anteriorly. Outline is inferred to be suboval and 0.3 mm in length. Anterior wing appears to be broad (tr.) and narrow (exsag.) distally. Middle body is oval in outline, occupying one-third of hypostomal width, and delineated by shallow lateral and posterior border furrows. Lateral and posterior borders are moderately convex ventrally and almost of uniform width. One pair of short parallel spines is present at posterolateral corner of hypostome. Macula is not distinct. Ross (1951) illustrated several unassigned hypostomes from Zone E and F, locality 5. Some of those hypostomes (pl. 19, figs 2, 21, 22) bear one pair of spines, placed at posterolateral corners, being similar in form to this degree 5 meraspis hypostome. Thus, these larger hypostomes are assigned to this species, but represent later growth stages.

Thorax consists of five segments. Axis continuously tapers backwards; each axial ring accounts for about 25 % of total width; anterior two axial rings bear pair of tubercles on crest, while each of posterior three rings possess backwardly-directed, long axial spine; each thoracic pleura has short spinose end pointing posterolaterally; pleural furrow reaches four-fifths of transverse length of each pleura;

short and small spine (equivalent to outer series of protaspides) protrude at distal end of posterior band of each pleura; in middle of each pleura, pair of small tubercles (equivalent to inner series of protaspides) is present.

Transitory pygidium is semicircular in outline; along marginal edge, five pairs of short spines (equivalent to outer series of protaspides) are present on posterior band of each pleural rib and protrude upwards, and correspond with short spines at thoracic pleural tips; three pygidial pleural ribs are distinctly delimited by interpleural furrows, each rib possessing pleural furrow; first pygidial axial ring has backwardly-directed long axial spine, as do posterior three thoracic axial rings. Doublure is sharply inturned and as wide as steeply-sloping marginal border. Degree 7 meraspis differs from degree 5 in having more distinct tubercles on cranidium, and additional tubercle pairs on palpebral lobe.

For a description for holaspid cranidium, see Ross (1951, p. 60 - 61). Distinguishing changes between meraspid and holaspid cranidia (see Ross, 1951, pl. 13, figs 25, 36) are deepening of all furrows, narrowing of preglabellar field, increase of tubercle size and number, and S1 detectable only by non-granulated patches. Holaspid pygidium is subelliptical in outline. Axis is moderately convex, strongly tapers backwards and does not reach pygidial margin; five axial rings are recognizable, on anterior three of which pair of tiny tubercles develop. Pleural field is flat; each of five pleural ribs bears a broad and shallow pleural furrow, which runs all the way across field; interpleural furrow is shallower and narrower; along edge of pleural field, short spine protrudes posteriorly at posterior band of each pleural rib; posteriormost pair of spines does not have corresponding pleural rib. Pygidial border slopes steeply downwards, and is uniform in width.

Discussion -- Holaspides, in particular cranidial morphologies of Parahystricurus carinatus are similar to those of Amblycranium? populus, as mentioned in details by Ross (1951, p. 68), but its librigenae are dissimilar from the latter. Immature cranidia of this species are similar to *Hystricurus robustus* (Ross, 1951, pl. 10, fig. 15) in having a smoothly convergent anterior facial suture and small spines on the occipital ring. However, the long (sag.) preglabellar field, relatively small palpebral lobe, and less distinct palpebral furrow of this species are indicative of a correct generic assignment. Furthermore, the transitory pygidium of the degree 5 meraspis differs from the general pygidial morphologies of *Hystricurus* by having a rather flat pleural field, a steeply inclined marginal border, a row of spines along the edge of the pleural field, and a relatively narrower (tr.) axis, strongly suggesting that this species can not be assigned to *Hystricurus*.

Genus AMBLYCRANIUM Ross, 1951

Type Species -- *Amblycranium variabile* Ross, 1951 from the Tremadoc (Lower part of Garden City Formation) of southern Idaho, U.S.

Other Species -- *Amblycranium cornutum* Ross, 1951.

Diagnosis -- See Ross (1951, p. 64) for details.

Discussion -- Ross (1951, p. 67-68) described, with less confidence, one more species, *Amblycranium* ? *populus* from Zone E, since its cranidia (1951, pl. 13, figs 20-22) are so similar to *Parahystricurus carinatus* which occurs in the same horizon, while free cheeks are very similar to other *Amblycranium* species. Such questionable taxonomic assignment of *A.*? *populus* makes it difficult to delimit the concept of *Amblycranium*. Thus, the species is, herein, excluded from the genus. Spine development on protaspid shield of *Amblycranium variabile*, described below, may serve as a feature to distinguish this genus from any other hystricurid genera.

Amblycranium variabile Ross, 1951
Plate V-4.1-9; Figure V-6

1951 Amblycranium variabile n. sp. — Ross, p. 64-66, pl. 13, figs 10-18.

Holotype -- Cranidium, Y.P.M. 18020 (Ross, 1951, pl. 13, figs 14, 17, 18) from Zone E (Tremadocian), Locality 5 in southern Idaho, U.S.

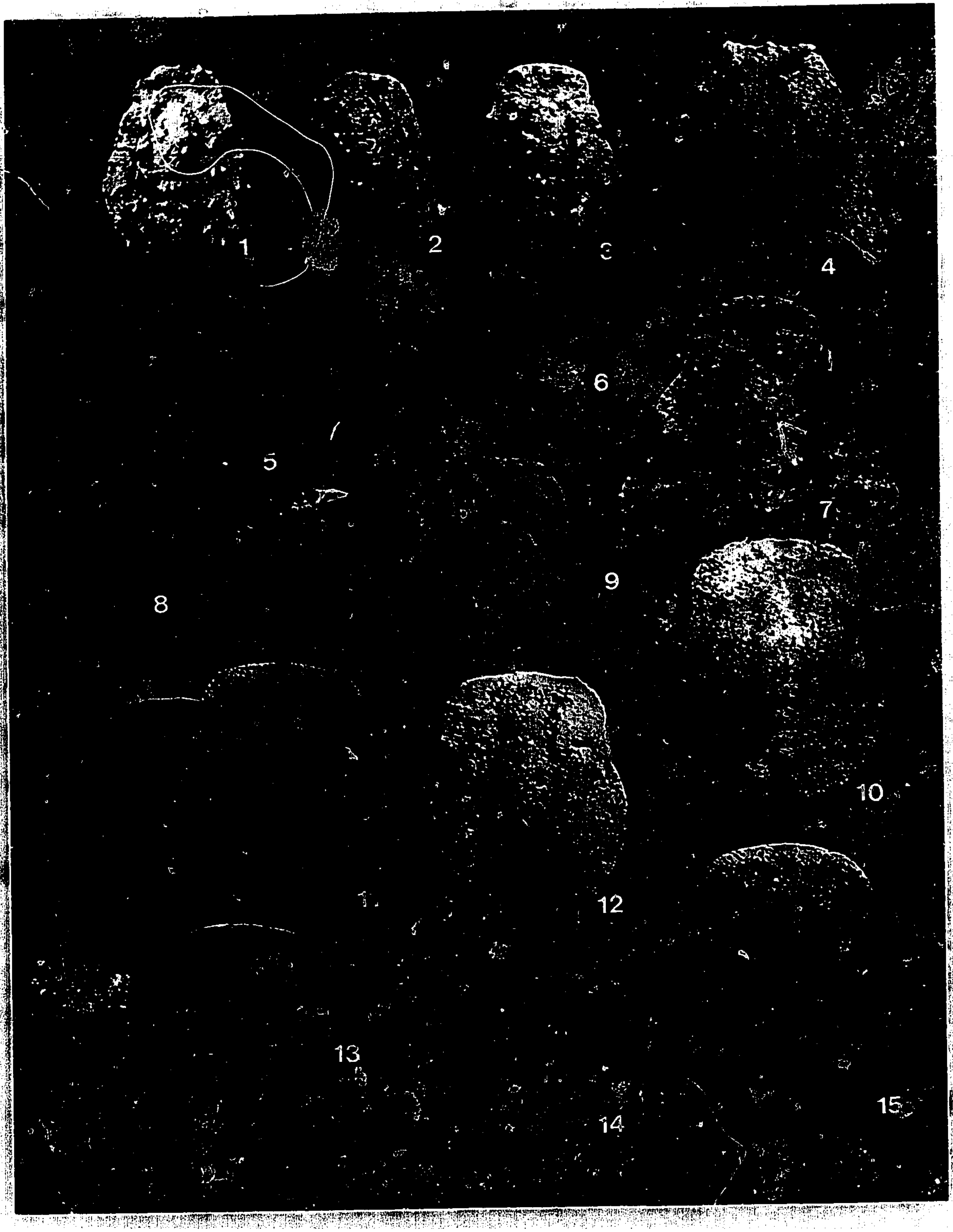
Figured Material -- Protaspides; UA 11023, UA 11024, UA 11025: Meraspid cranidia; UA 11026, UA 11027, UA 11028, UA 11029: Holaspid cranidium; UA 11031: Holaspid free cheek; UA 11030.

Diagnosis -- Refer to Ross' (1951, p. 65-66) description.

Protaspid Description -- No discrete instar stage was recognized in length versus width plot of protaspid shields and all protaspid specimens appear to belong to one stage (Figure V-3).

Protaspid shields are 0.5-0.58 mm long and 0.36-0.43 mm wide, suboval in outline excluding librigenae. Protocranidium is trapezoidal in outline and occupies 66-68% of whole shield length. Glabella is barrel-shaped, tapering anteriorly, moderately convex upwards, and 61-77 % of protocranidial length; no glabellar furrows develop; axial furrow shallows anteriorly. Preglabellar field is relatively short (less than 10 % of protocranidial length) and slightly depressed; preglabellar median furrow is broad and shallow. Anterior cranidial border is moderately convex upwards and forwards; border furrow is as broad and shallow as preglabellar furrow. Occipital ring is distinct and as wide as maximum protoglabellar width. Palpebral lobe is small (tr. and exsag.), slightly raised and located immediately behind front of glabella; palpebral furrow is indistinct. Posterior protocranidial marginal furrow is weakly impressed, shallows distally, and gently curves posteriorly. Facial suture is nearly straight except for small curvature of palpebral lobe; anterior suture convergent and posterior suture gently divergent. Protopygidium is semicircular in

PLATE V-4. 1-9, *Amblycranium variabile* Ross, 1951 from LR5 76.4 horizon. 1, UA 11023, dorsal view of protaspis, x 62. 2, UA 11024, dorsal view of protaspis, x 57. 3, UA 11025, dorsal view of protaspis, x 57. 4, UA 11026, dorsal view of meraspid cranidium, x 102. 5, UA 11027, dorsal view of meraspid cranidium, x 33. 6, UA 11028, dorsal view of meraspid cranidium, x 58. 7, UA 11029, dorsal view of meraspid cranidium, x 56. 8, UA 11030, dorsal view of holaspid free cheek, x 30. 9, UA 11031, dorsal view of holaspid (?) cranidium, x 24; 10-15, *Hyperbolochilus* cf. *marginauctum* from LR5 50.3 horizon. 10, UA 11032, dorsal view of late protaspis, x 56. 11, UA 11033, dorsal view of early protaspis, x 82. 12, UA 11034, dorsal view of early protaspis, x 83. 13, UA 11035, dorsal view of holaspid (?) cranidium (photographed by secondary electron), x 36. 14, UA 11036, dorsal view of late protaspis, x 47. 15, UA 11037, dorsal view of degree 0 meraspis, x 43.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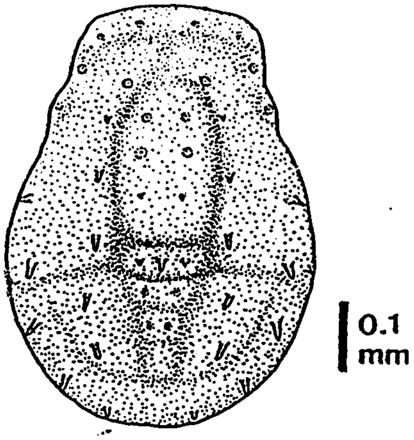


FIGURE V-6. Drawing of dorsal veiw of protaspis of *Amblycranium variabile* Ross, 1951.

outline. Axis strongly tapers backwards and is of independent convexity; axial furrow is broad, less distinct and shallows posteriorly; three axial rings are recognizable, and only anteriormost one has discernible pleural rib defined by shallow interpleural furrow. Pleural field is nearly flat; marginal border slopes downwards and is uniform in width.

Development of short spines on protaspid shield is conspicuous. Spines protrude radially from shield and exhibit unique distribution pattern. Row of three or four spines, unpaired or paired, develops on anterior protocranidial border. Glabella bears three pairs of relatively short spines (rachial series) on its crest in regular spacing; first pair (from anterior) is placed opposite palpebral lobe and third is located at posterior two thirds of glabellar length. Alongside glabella and immediately abaxial to axial furrow, four pairs of spines (inner series of cephalic region) develop; spine pairs arrange progressively farther apart towards posterior; first pair (from anterior) is placed opposite front of glabella, second opposite palpebral lobe, third slightly posterior to midpoint of protoglabella, and fourth immediately anterior to level of occipital furrow. Pair of spines develops at each distal extremities of anterior fixigenal area, posterolateral corners of protocranidium, opposite between third and fourth spine pairs of cephalic inner series, comprising cephalic portion of outer series. Immediately insides spines on posterolateral corner of protocranidium, another spine pair develops, which is equivalent to posterior cranidial border tubercle. Pair (palpebral tubercles) develops on palpebral lobe. Three spines are on occipital ring; middle one is longest. Each protopygidial axial ring has pair of spines (rachial series). Along protopygidial pleural edge, two pairs of spines (inner series) develop; anterior pair is placed halfway first pleural rib and opposite anteriormost axial ring, and posterior one opposite posteriormost axial ring. Protopygidial border is ornamented by three pairs of spines (outer series); anteriormost is opposite second axial ring (from anterior) and posterior two are behind pygidial axis.

Meraspid and Holaspid Description -- Smallest disarticulated meraspid cranidium is 0.38 mm in length, which is not as long as protocranidium. Except addition of one more pair of spines besides preglabellar median furrow, and larger and more convex palpebral lobes, there are few changes between protocranidium and smallest meraspid cranidium. Following changes take place in cranidium during meraspid period: 1) glabella becomes wider than long, retaining barrel-shape; 2) palpebral furrow is moderately impressed; 3) posterior facial suture becomes strongly divergent posteriorly; 4) anterior cranidial border furrow and preglabellar median furrow are deeper; 5) posterior cranidial border furrow is deeply impressed, and border widens distally. Changes in cranidial morphologies between meraspid and holaspid cranidia are: 1) preglabellar field and anterior fixigenal field are proportionately longer (exsag.) relative to glabellar length; 2) glabella takes more barrel-shape, and is covered with interspersed small tubercles; 3) posterior fixigenal field becomes more slender and acute, and transversely much longer; posterior border furrow shallows distally; 4) outline of palpebral lobe curves more strongly outwards; 5) spines proper are only present on occipital ring and distal extremities of posterior cranidial border, in irregular distribution pattern; 6) whole cranidium is covered with small tubercles; distribution pattern, in particular alongside protoglabella (inner series), is still recognizable, while spine arrangement on other parts of cranidium is imperceptible due to subsequent increment of number of small tubercles.

Discussion -- Distinguishing adult features of Amblycranium variabile from Amblycranium cornutum were listed by Ross (1951, p. 67).

Genus HYPERBOLOCHILUS Ross, 1951

Type Species -- Hyperbolochilus marginauctum Ross, 1951, from the Tremadoc (lower portion of Garden City Formation), southern Idaho, U.S.

Holotype -- Cranidium (Y.P.M. 18057, see Ross, 1951, pl. 17, figs 27, 34, 35), from Zone F, Locality 6.

Other Species -- Hyperbolochilus expansus Kobayashi, 1955.

Diagnosis -- See Ross' (1951, p. 77) description.

Discussion -- When establishing the genus, Ross (1951, p. 77) noted that cranidial morphologies of Hyperbolochilus marginauctum (type species) are very similar to those of Hillyardina which was included in Hystricuridae (sensu herein) in the Treatise (Moore, 1959). The close relationships of both genera were also suggested by Dean (1989, p. 25). Kobayashi (1955) placed the genus in Asaphiscidae Raymond, 1924, emphasizing that Hyperbolochilus expansus (Kobayashi, 1955, pl. 3, fig. 1) has similar cranidial architecture to the Upper Cambrian asaphiscid Homodictya, and additionally he commented on its similarity to the bathyurid Licnocephala. In the Treatise (Moore, 1959, p. O523), Hyperbolochilus was listed in Order and Family Uncertain. Since then, most workers, such as Fortey (1983) and Dean (1989), have not confidently assigned the genus to a particular family.

Protaspides of Hyperbolochilus cf. marginauctum discovered in this work are very similar to those of 'Paraplethopeltis' sp. A and 'Paraplethopeltis' genacurvus described above, indicating the close relationships of Hyperbolochilus to those hystricurid genera. Combined with the similarity of this genus to Hillyardina (Ross, 1951; Dean, 1989), Hyperbolochilus is considered to belong to Hystricuridae. One problem caused by this taxonomic assignment is that Hyperbolochilus expansus, described by Kobayashi (1955) occurs in the Upper Cambrian, which indicates that Hyperbolochilus has Upper Cambrian elements, unlike other hystricurid genera. One possible explanation is that H. expansus was not correctly assigned to Hyperbolochilus, and the species might be a Cambrian asaphiscid as a possible ancestor to Ordovician Hyperbolochilus; glabella of the species is broader than any other Hyperbolochilus species (see also Hyperbolochilus cf. H. expansus; Dean, 1989, pl. 16, figs 7, 9, 10).

However, lack of pygidium and free cheek of those described species does not support the explanation. Provisionally, H. expansus is considered as a Cambrian ptychopariid which is closely related to Ordovician Hyperbolochilus species.

Hyperbolochilus cf. marginauctum
Plate V-4.10-15.

Figured Material -- Protaspides; UA 11032, UA 11033, UA 11034, UA 11036: Degree 0 meraspis; UA 11037: Holaspid cranidium; UA 11035.

Protaspid Description -- In a length/width plot, morphologic groupings suggest the presence of two protaspid instars (Figure V-7). These two stages, 'early' and 'late', can also be discriminated by distinctiveness of posterior protocranidial marginal furrow, accompanied with appearance of protopygidium. All measurements are in average.

Early protaspides are 0.52 mm long and 0.46 mm wide, subrectangular in outline except librigenae, with straight anterior margin and indented posterior margin. Shield is covered with fine granules. Axis is subcylindrical, anterior margin being straight and posterior one being more rapidly tapered; five axial lobes are recognizable; L4 is longer than subequal and rectangular L1/L2/L3; L0 has a prominent node. Frontal area comprising future anterior border, preglabellar field and anterior fixigenal area, is flat and at lower-level than rest of shield. Palpebral lobe is identifiable through strong outward-curvature of facial suture, and is slightly raised dorsally. Posterior two thirds of shield are surrounded by rather flattened border. Anterior facial suture is convergent forwards and posterior one is gently divergent backwards. Along posterior margin, pair of short spines develops at posterior extremities.

Late protaspides are 0. 80 mm long and 0.63 mm wide, more rectangular outline and differ from early protaspides, in having protopygidium with 69 % of whole shield length and two axial rings, forwardly-divergent anterior facial suture, longer (exsag.) palpebral

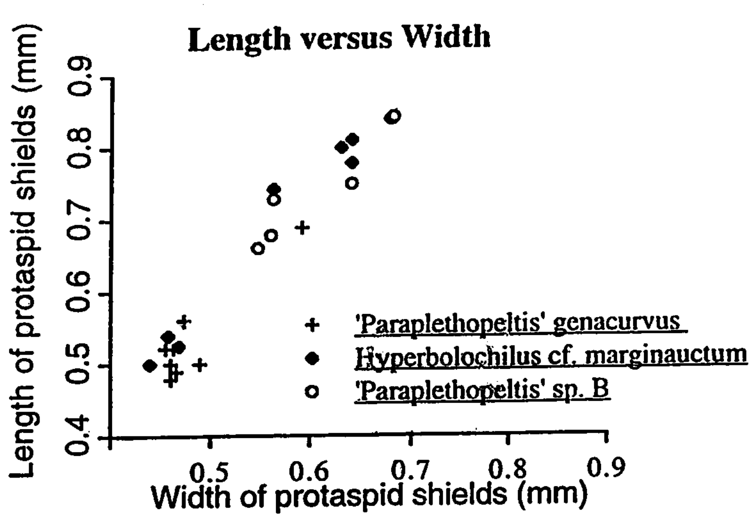


FIGURE V-7. Length versus width plots for protaspides of 'Paraplethopeltis' genacurvus Hintze, 1951, 'Paraplethopeltis' sp. B, and Hyperbolochilus cf. marginauctum. Plots appear to group into two separate stages for the last species, but the materials are not enough to ensure the numerical designations.

lobe, disappearance of pair of posterior marginal spines, discontinuous glabellar furrows, and posterior protocranidial marginal furrow strongly curved backwards distally.

Meraspid and Holaspid Description -- Meraspid degree 0 is 1.16 mm long and differs from late protaspides in having more divergent anterior facial suture, broader anterior fixigenal area, strongly backwardly curved posterior fixigenal area, four pygidial axial rings, and posterior cranidial border furrow impressed. Holaspid cranidium has long preglabellar field with median furrow and forward-tapering glabella with paired tubercles.

Discussion -- Development of tubercles on glabella and anterior fixigenal area of the holaspid cranidium precludes the possible assignment of these trilobites to *Hyperbolochilus marginauctum*. Compared with *Hyperbolochilus*? sp. (Fortey, 1983, pl. 25, figs 10,11), this species differs in having a larger glabella and a faintly tuberculated exoskeleton.

?Family HYSTRICURIDAE Hupé, 1953

Genus PARAPLETHOPELTIS Bridge and Cloud, 1947

Type Species -- *Paraplethopeltis obesa* Bridge and Cloud, 1947 from Lower Ordovician Tanyard Formation, central Texas, U.S.

Other Species -- *Paraplethopeltis depressa* Bridge and Cloud, 1947; *Paraplethopeltis carinifera* Flower, 1969.

Diagnosis -- Refer to Bridge and Cloud's (1947, p. 555-556) description of the type species.

Discussion -- Bridge and Cloud (1947) erected *Paraplethopeltis*, and distinguished the new genus from *Plethopeltis*, in having a longer preglabellar field, no spine on the occipital ring, and a more posteriorly located palpebral lobe. Hintze (1952) referred two species, *Paraplethopeltis*? *genacurvus* and *Paraplethopeltis*? *generectus*, to the genus with less confidence, since the materials show a distinct anterior cranidial border, an eye ridge, and a slender posterior fixigenal area, which are not exhibited in type species (but see Stitt, 1983, p. 22). In the *Treatise* (Moore, 1959), *Paraplethopeltis* was formally assigned to Family Plethopeltidae Raymond, 1925, which also includes *Plethopeltis*. Later, Fortey and Peel (1989, p. 9-10) placed *Paraplethopeltis* in the Hystricuridae and treated it as a subgenus of *Hystricurus*, arguing that *Hystricurus* (*Paraplethopeltis*) sp. nov. A (Fortey and Peel, 1989, fig. 7) shows the features which link *Paraplethopeltis* and *Hystricurus*. Similarly, Ludvigsen et al. (1989, p. 56-57) excluded *Paraplethopeltis* from Plethopeltidae, but did not mention an alternative systematic position.

There appear to be two taxonomic problems involved in *Paraplethopeltis*. The first is whether morphologic variations of later species, including the species described in this work, fall within the generic concept. The reason that Hintze (1952, p. 201-202) doubted the assignment of two species to *Paraplethopeltis* is their morphologic deviations, listed above, from type species. Later, Berg and Ross (1959, p. 112-113) agreed with Hintze's concerns and further regarded Hintze's species as belonging to *Hystricurus* with question rather than *Paraplethopeltis*, considering several intermediate species between *Paraplethopeltis* and *Hystricurus* such as *Hystricurus* sp. I (Ross, 1951, pl. 17, figs 1-3). However, the strict incorporation of those species with *Hystricurus* is precluded by morphologic differences of protaspides between *Hystricurus* and those species (see below). In contrast, Stitt (1983, p. 22) argued that Hintze's species really belong to *Paraplethopletis*, based on the facts that his own material of *Paraplethopeltis obesa* (type species) has a faint anterior border and an eye ridge; both morphologic features are very faint, compared to Hintze's species. Later, Fortey and Peel (1989) confidently assigned their new species to *Paraplethopeltis*, which was regarded as a subgenus of *Hystricurus*. However, morphologic features of these later described species depart so far from generic concept of *Paraplethopeltis* (Bridge and Cloud, 1947) that they are not considered to belong that subgenus. The following comparisons summarize the morphologic differences between later species that have been assigned to *Paraplethopeltis* and the type species: deeply incised versus very faint or lack of anterior border furrow; distinct versus lack of eye ridge; deeply impressed versus shallow and sagittally fading occipital furrow; wider versus longer glabella; deeper versus shallower axial furrow; and rounded versus pointed lateral end of posterior border. These features seem too different to be regarded as variations within the genus. The best solution for this taxonomic problem, for the present, is to exclude Hintze's species, along with the species described herein, from *Paraplethopeltis*, *sensu* Bridge and Cloud (1947), and to place them in a new hystricurid genus. However, paucity of materials, in particular, correctly associated holaspid free cheeks and pygidium, prevents from erecting the formal generic designation. Herein, those species were treated using quotation marks, indicating *Paraplethopeltis* is obsolete for those trilobites (Bengtson, 1988). Fortey and Peel's (1989) species is regarded as belonging to *Hystricurus*, since it displays a tuberculate cranidium; indeed, the species is very similar to *Hystricurus eurycephalus* (Shergold, 1991, pl. 6, fig. 22).

The second problem is whether *Paraplethopeltis*, *sensu* Bridge and Cloud (1947), belongs to the Hystricuridae (Fortey and Peel, 1989) or the Plethopeltidae (Moore, 1959; Stitt, 1983). The above-listed morphologic features of the type species do not agree with familial concept of the Hystricuridae (Ross, 1951, p. 39-40). Rather, those features are more in accordance with a revised diagnosis of the Plethopeltidae (Ludvigsen et al., 1989, p. 56). Thus, it is concluded that *Paraplethopeltis*, *sensu* Bridge and Cloud (1947), belongs to the Plethopeltidae, and is not a subgenus of *Hystricurus*, and does not belong to the Hystricuridae. This is further supported by morphologic differences between hystricurid and plethopeltid protaspides (e.g. *Arapahoia snowensis*, see Hu, 1986, pl. 16, figs 1-7 text-fig. 18); the latter shows a sagittal furrow in glabella and overhanging protaspid axis. The later *'Paraplethopletis'* species should be assigned to the Hystricuridae, since all of those have a distinct anterior cranidial border, a forward-tapering glabella, and a slender posterior fixigenal area. Nonetheless, a close relationship of *Paraplethopeltis* to the Hystricuridae is likely, considering the such intermediate species as *Hystricurus* ? sp. I (Ross, 1951, pl. 17, figs 1-3) and *Pachycranium* ? sp (Ross, 1951, pl. 17, figs 4, 5), as suggested by Hintze (1952, p. 202) and Berg and Ross (1959, p. 113). Tuberculation on the cranidium of these trilobite groups appears to be variable; '*Paraplethopeltis*' *genacurvus*, described below, shows sparsely distributed and smaller tubercles on the meraspid cranidium, but the holaspid cranidium has a smooth surface. '*Paraplethopeltis*' n. sp. has a smooth surface, but a probable late holaspid representative (*Hystricurus* cf. *H*. sp. B of Ross, 1951, see also Dean, 1989) has sparse, smaller tubercles.

'*Paraplethopeltis*' sp. A

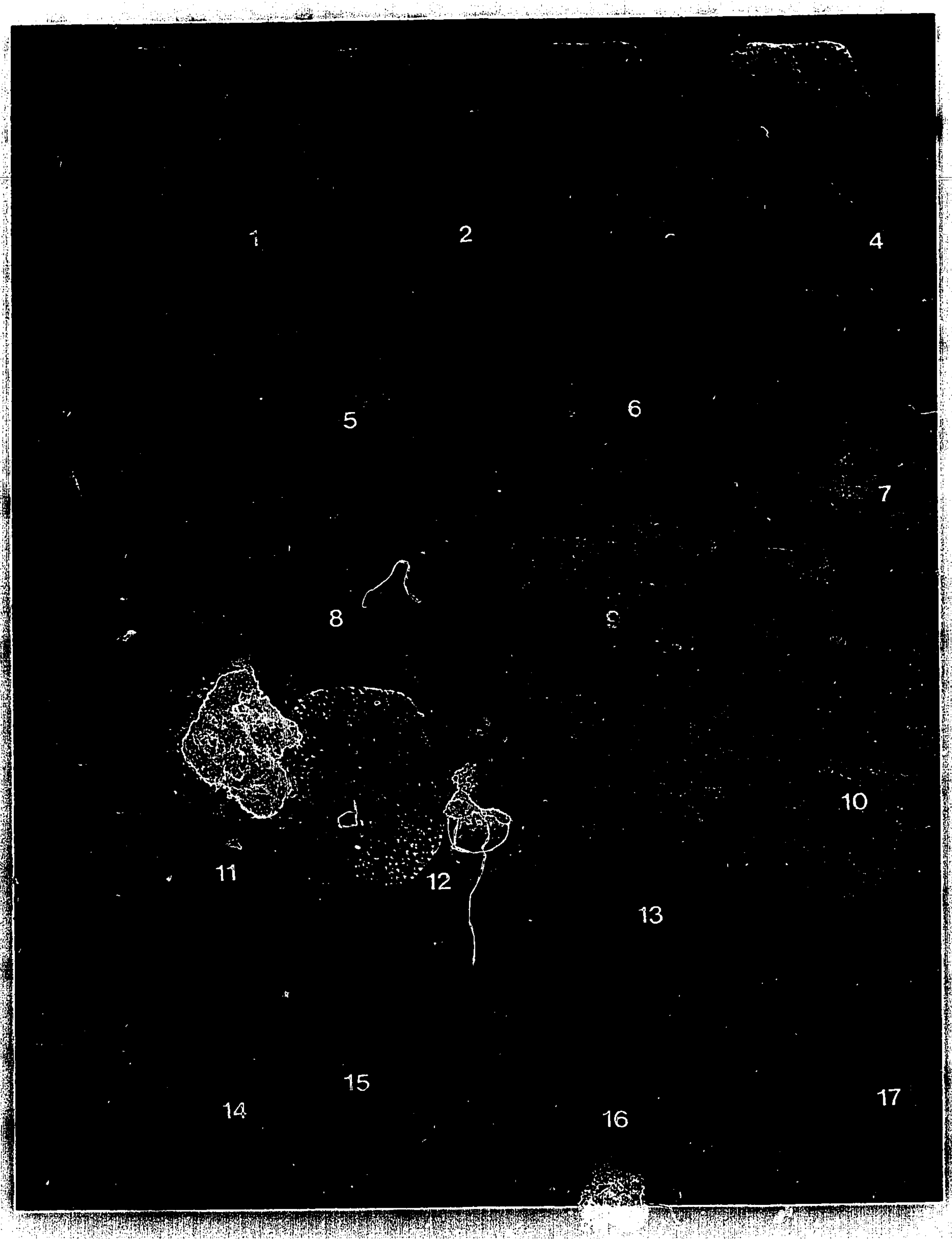
Plate V-5.1-9; Figure V-8

Figured Material -- Protaspid shields, UA 11038, UA 11039, UA 11040, UA 11041, UA 11044; Meraspid cranidia, UA 11042, UA 11043; Holaspid cranidium, UA 11045. Transitory pygidium, UA 11046.

Protaspid Description -- Two protaspid instars (stage 1 and 2) are recognized, based on groupings on the length versus width plot (Figure V-9) and morphologic criteria described below.

Stage 1 protaspides are 0.52-0.63 mm long and 0.48-0.55 mm wide, suboval in outline excluding librigenae; anterior margin is nearly straight and posterior margin is re-entrant. Protocranidium is trapezoidal and occupies 70-75 % of shield length. Anterior cranidial border is slightly convex and border furrow shallows distally. Ocular ridge is slightly convex, gently curves backwards, anteriorly defined by cranidial border furrow; palpebral lobe is slender, slightly convex upwards and arches distally in outline, located opposite S3, and continuous into ocular ridge. Axis of shield is spindle-shaped and relatively well defined by axial furrow fairly, without overhanging anterior and posterior margins. Four glabellar lobes and occipital ring are defined by shallower transglabellar and occipital furrows; L4 is

PLATE V-5. 1-9, 'Paraplethopeltis' sp. A from LR5 50.3 and LR5 76.4 horizons. 1, UA 11038, dorsal view of stage 1 protaspis, x 58. 2, UA 11039, dorsal view of stage 1 protaspis, x 58. 3, UA 11040, dorsal view of stage 2 protaspis, x 45. 4, UA 11041, dorsal view of stage 2 protaspis, x 46. 5, UA 11042, dorsal view of meraspid cranidium, x 33. 6, UA 11043, dorsal view of meraspid cranidium, x 47. 7, UA 11044, ventral view of stage 2 protaspis, x 49. 8, UA 11045, dorsal view of holaspid (?) cranidium, x 22. 9, UA 11046, dorsal view of meraspid pygidium, x 25; 10, 13, 16, 17. 'Paraplethopeltis' genacurvus Hintze, 1952, from LR5 50.3 horizon. 10, UA 11047, dorsal view of protaspis with ventral view of small pliomerid protaspis, x 61. 13, UA 11048, dorsal view of protaspis, x 59. 16, UA 11049, dorsal view of meraspid cranidium, x 31. 17, UA 11050, dorsal view of degree 0 meraspis (?), x 46; 11, 12, 14, 15. 'Paraplethopeltis' sp. B from LR5 76.4 horizon. 11, UA 11051, dorsal view of early protaspis, x 46. 12, UA 11052, dorsal view of early protaspis, x 47. 14, UA 11053, dorsal view of late protaspis, x 46. 15, UA 11054, dorsal view of meraspid cranidium, x 48.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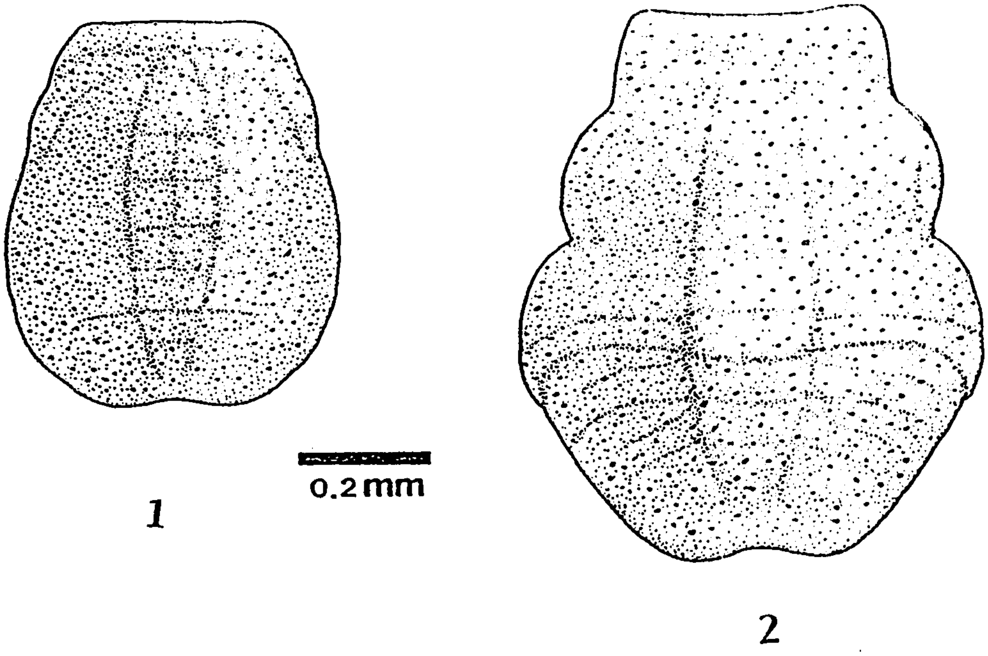

FIGURE V-8. Drawings of protaspides of '*Paraplethopeltis*' sp. A. 1, dorsal view of stage 1. 2, dorsal view of stage 2.

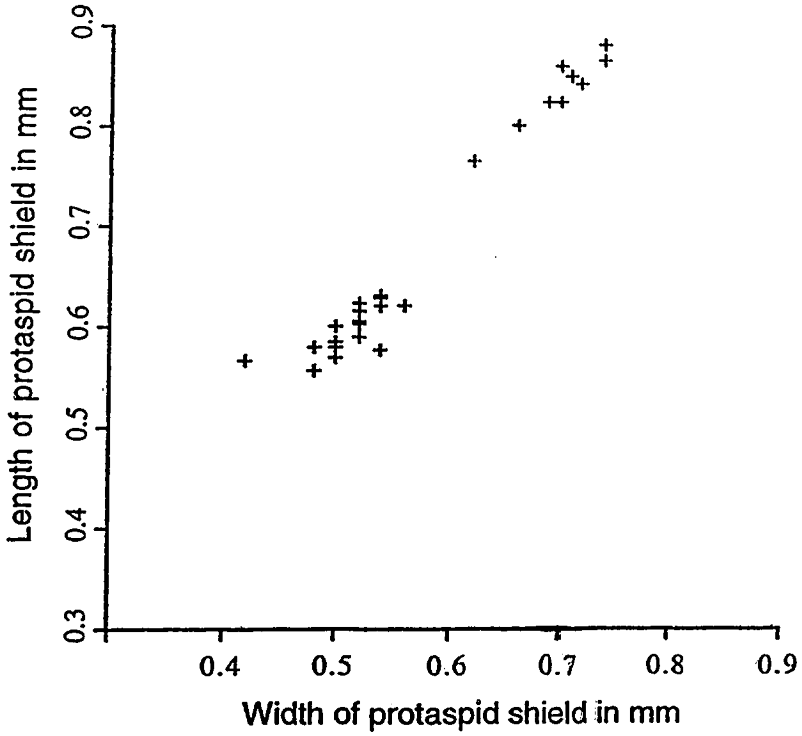

FIGURE V-9. Length versus width plots for protaspides of '<u>Paraplethopeltis</u>' sp. A. Note two distinct morphometric groupings, each of which is designated stage 1 and stage 2.

approximately two times longer (sag.) than subequal L1/L2/L3, tapers forwards and reaches the anterior cranidial border so that preglabellar field is absent; L1/L2/L3 are bilobed by very shallow sagittal furrow; and L2 is broadest (tr.). Posterior cranidial marginal furrow is not distinct and runs only halfway out across shield. Protopygidium, with 27 % (avg.) of shield length, is semicircular in outline, and has two axial rings and corresponding pleurae; interpleural furrow is not distinct. Shield is covered with large number of interspersed small granules. Protopygidial doublure is loosely incurved. Facial suture is nearly straight, except for small outward curvature of palpebral lobe.

Stage 2 protaspides are 0.76-0.88 mm long and 0.62-0.74 mm wide. Shield retains suboval outline as, but differs from stage 1 in the followings: 1) anterior margin is slightly indented medially; 2) posterior facial suture is more strongly divergent laterally and strongly curves posteriorly; 3) posterior protocranidial border furrow is more deeply impressed but still shallows distally; 4) protopygidium is about 34 % (avg.) of the shield length and two protopygidial axial rings and a terminal piece are discernible; 5) glabella becomes straight-sided rather than laterally inflated, but is still continuously forward-tapering; 6) palpebral lobe more strongly arches outwards in outline; ocular ridge is not distinct; 7) posterior protocranidial marginal furrow is very distinct, and runs straight before it strongly curves backwards distally; 8) marginal border gently slopes downwards.

Meraspid and Holaspid Description -- Meraspid cranidium shows very continuous morphogenesis from protocranidium of stage 2, and only differs in appearance of narrow preglabellar field, on which preglabellar median furrow is impressed, disappearance of transglabellar furrows, and narrow posterior fixigenal area due to continuous adaxial and backward movement of eye. Holaspid cranidium displays slender posterior fixigenal area, relatively large and strongly convex palpebral lobe, slightly divergent anterior facial suture, distinct preglabellar median furrow and convex anterior margin. Transitory pygidium is semicircular in outline; axis gradually tapers posteriorly, bears six axial segments, even if posterior ones are not as distinctively delineated as anterior ones: marginal border steeply slopes downwards.

Discussion -- The uncertainty of the assignment of this interesting species to Paraplethopeltis is because the holaspid cranidium has a forward tapering glabella, a distinct anterior border, a slender posterior fixigenal area, and a large palpebral lobe. Hystricurus sp. B, described by Ross (1951, pl. 10, figs 18, 19, 23, 24, 27, 28) must be conspecific with this species, even if the immature cranidium has a larger palpebral lobe and a more rounded anterior margin. Hystricurus cf. H. sp. B Ross, 1951 (Dean, 1989, pl. 14, figs 9, 12, 15), from Alberta, if it is correctly associated with these much smaller materials, represents a later adult stage of this species. The only objection to this interpretation is the development of tubercles on the Albertan holaspid cranidium, since the early holaspid cranidium has a smooth exoskeleton. However, the tuberclation on that Albertan cranidium is much less densely and more irregularly distributed and smaller in size than those of other hystricurid genera; in general, hystricurid species (e.g., Hystricurus sp., herein) with regularly distributed tubercles on protaspid shield show more regularly distributed and larger tubercles on the holaspid cranidium.

'Paraplethopeltis' genacurvus Hintze, 1952
Plate V-5.10, 13, 16, 17.

1952 Paraplethopletis? genacurvus n. sp. — Hintze, p. 202-204, pl. 7, figs 1-5.
1959 Hystricurus? sp. aff. H.? genacurvus. — Berg and Ross, p. 112-113, pl. 21, figs 21, 23.

Figured Material -- Protaspides; UA 11047, UA 11048: Degree 0 meraspis; UA 11050: Meraspid cranidium; UA 11049.

Diagnosis -- Refer to Hintze's (1952, p. 202-203) description.

Protaspid Description -- Two few protaspides were discovered to be able to recognize instars in length/width plot (Figure V-7). Almost all the protaspides appear to belong to one stage.

Protaspides are about 0.58 mm wide and 0.7 mm long, suboval in outline; anterior margin rounded and posterior margin slightly indented. Axis is spindle-shaped, of independent convexity, and has four glabellar lobes, occipital ring and indistinct protopygidial axial ring; L4 is longer than subequal L1/L2/L3; L1/L2/L3 are rectangular, and L2 is broadest; occipital ring is smaller (tr. and sag.) than L1; glabellar and occipital furrows are transglabellar. Anterior area, comprising future anterior cranidial border, preglabellar field and anterior fixigenal area, is flat and at lower-level than rest of shield. Palpebral lobe is only recognizable by weak outward-curvature of facial suture. Posterior protocranidial marginal furrow is shallow and narrow, runs straight halfway across pleural region and then strongly curves backwards. Facial suture is fairly straight except for palpebral lobe, and slightly convergent anteriorly and divergent posteriorly. Protopygidium accounts for 23 % of shield length; axis is very indistinct and with no discernible axial rings.

Meraspid and Holaspid Description -- Obtained meraspis degree 0 is 1.02 mm long and 0.84 mm wide, and differs from protaspides as follows: 1) anterior facial suture is slightly divergent; 2) larger and more curved outline of palpebral lobe; 3) posterior facial suture is moderately divergent, and then strongly curves inwards; 4) posterior protocranidial marginal furrow becomes impressed and shallows distally; 5) transitory pygidium, 29 % of shield length, possesses four recognizable axial rings; anterior two axial rings have corresponding pleural ribs and pleural furrows; interpleural furrow reaches pygidial margin and curves backwards at its distal end; pleural furrow is shallower and runs into only four-fifths of pleural field; 6) preglabellar field appears due to differentiation of anterior border from glabella, on which shallow median furrow is impressed.

In later ontogeny, glabella becomes parabolic in outline and loses glabellar furrows, occipital ring is better defined and curves strongly backwards; straight eye ridge is still recognizable (cf. Hintze's (1952, pl. 7, fig. 1b) larger material which shows forwardly directed eye ridge); palpebral lobe becomes deeper; fine terrace lines are developed on anterior border; posterior fixigenal area becomes progressively slender; and anterior facial suture becomes more divergent forwards.

Discussion -- This species (Hintze, 1952, pl. 7, figs 1-5) was reported from the Pogonip Group (comparable to Garden City Formation), exposed in the Ibex area, Utah. Hintze (1952, pl. 7, figs 6-9) described one more species, Paraplethopeltis? generectus. This species differs from P.? generectus in having a more slender posterior fixigenal area, a more distinct eye ridge, and a more forwardly based genal spines. It is possible that these two species are conspecific, since all specimens of the former species are smaller than those of the latter. Hystricurus? sp. aff. H.? genacurvus (Berg and Ross, 1959, pl. 21, figs 21, 23) probably represents later ontogenetic stage of this species, since it is larger than Hintze's materials.

'Paraplethopeltis' sp. B

Plate V-5.11, 12, 14, 15.

Figured Material -- Protaspides; UA 11051, UA 11052, UA 11053: Meraspid cranidium; UA 11054.

Protaspid Description -- Too few protaspides were found to be able to identify instars in the length/width plot (Figure V-7). All protaspid materials are considered to belong to one stage.

Protaspides range from 0.66 to 0.84 mm in length and 0.55 to 0.68 mm in width. Shield lacking librigenae is oval in outline, with straight anterior margin and slightly indented posterior margin. Axis is spindle-shaped, with more rounded anterior margin; axial furrow is moderately deep; four protoglabellar lobes and occipital ring are separated by shallow transglabellar furrows. Protocranidium occupies 86 % of shield length, and is subtrapezoidal in outline. Palpebral lobe is only represented by weak outward-curvature of facial suture.

Posterior protocranidial marginal furrow is shallow, runs straight and turns rather strongly backwards distally. Anterior facial suture is convergent anteriorly and posterior one is divergent posteriorly. Protopygidium is semi-circular, has more than two axial rings; and pleural and interpleural furrows are indistinct. Whole shield is covered with sparsely-dispersed granules.

Discussion -- Formal establishment of a new species is impossible due to lack of holaspid materials, but the protaspid morphologies are different from 'Paraplethopeltis' sp. A and 'Paraplethopeltis' genacurvus, so that a separate species will be erected when the holaspid materials are discovered.

COMPARISON OF HYSTRICURID PROTASPIDES AND TAXONOMIC IMPLICATIONS

Hystricurid protaspides, described herein, can be grouped into two different morphotypes. The first consists of Hystricurus, Parahystricurus, and Amblycranium and is characterized by regularly distributed tubercles; spines of the last genus are considered as a specialized condition of the tubercles of the first two. The second morphotype, consisting of 'Paraplethopeltis' and Hyperbolochilus, is characterized by a granulate (not tuberculate) exoskeleton, and the development of transglabellar furrows. Comparison between these protaspides is included in Table V-2. The most notable difference between them is the tuberculation pattern on the protaspid shield, the usefulness of which as a taxonomic character was doubted by Chatterton (1994, p. 547). In contrast, the distribution pattern of spines on meraspid otarionine trilobites was considered as a valid feature for phylogenetic inference (Adrain and Chatterton, 1994, fig. 1). Variation within the first morphotype includes the development of tubercles on both protocranidium and protopygidium or only protocranidium, and number of tubercle pairs, when comparing protaspides with a protopygidium.

The hystricurid protaspides are morphologically comparable to the following proetid protaspides described so far (Table V-2): Aulacopleuridae - *Scharyia micropyga* (Scharyiinae) (Šnajdr, 1981); *Scharyia* aff. *S. redunzoi* (Scharyiinae) (Speyer and Chatterton, 1989; Chatterton and Speyer, 1995), *Aulacopleura*? (Aulacopleurinae) (Hu, 1971; Fortey, 1990); Otarionidae - *Otarion* (*Otarion*) *dabrowni* (Chatterton, 1971), *Otarion* (*Tricornotarion*) *struszi* (Chatterton, 1971); Telephinidae - *Carrickia pinguimitra* (Chatterton, 1980); Dimeropygidae - *Dimeropyge clintonensis* (Chatterton, 1980), *Dimeropyge virginiensis* (Tripp and Evitt, 1983), *Dimeropyge speyeri* (Chatterton, 1994; Chatterton and Speyer, 1995); Bathyuridae - *Bathyurus ulu* (Chatterton, 1980); Proetidae - *Proetus* (*Proetus*) *talenti* (Proetinae) (Chatterton, 1971). In terms of the development of tuberculation, the first morphotype of hystricurid protaspides, is similar to *Aulacopleura*, *Scharyia*, *Carrickia* (= *Phorocephala*), *Otarion*, and *Dimeropyge*, even though there are generic variations, and the second hystricurid protaspid morphotype is similar to *Bathyurus* and *Proetus*. Besides this, presence of glabellar furrows is shared with the protaspides of the latter proetid group.

Cambrian ptychopariids, in particular, taxa of which were considered as the probable sistergroup to hystricurids, such as *Elvinia roemeri* (an elviniid, see Hu, 1979, text-figs 1A-C), *Welleraspis swartzi* (a lonchocephaline, see Rasetti, 1954, fig. 4 and Hu, 1968, text-figs 1A-D), *Sao hirsuta* (a solenopleurid, see Whittington *in* Moore, 1959, fig. 88), and *Solenopleura robbi* (a solenopleurid, see Hupé, 1953, fig. 116) are not similar to hystricurid protaspides. They differ from hystricurid protaspides in having a rather circular outline, an overhanging front to the glabella, and deeply impressed transglabellar furrows. In contrast, hystricurid protaspides are a typical proetide type with the fusiform glabella with distinct preglabellar furrows.

Morphologic features exhibited by hystricurid protaspides suggest the following taxonomic conclusions.

1) Hystricurids are treated as a separate family, Hystricuridae, from Solenopleuridae Angelin, 1854, in accordance with Hupe's (1953) original designation.

TABLE V-2. Comparison of larval morphologies of the Hystricuridae and several younger families of Proetida. Abbreviations of the taxon name are; Hy = Hystricurus paragenalatus; Ph = Parahystricurus carinatus; Am = Amblycranium variabile; Pp = 'Paraplethopeltis' sp. A; Hb = Hyperbolochilus cf. marginauctum; Au = Aulacopleura ?; Sc = Scharyia micropyga; Ca = Carrickia pinguimitra; Ot = Otarion (Otarion) dabrowni; Di = Dimeropyge speyeri; Ba = Bathyurus ulu; Pr = Proetus (Proetus) talenti.

TABLE V-2.

	Hy	Ph	Am	Pp	Hb
# of rachial series on glabella	none	none	three pairs	none	none
# of inner series on cranidium	three pairs	three pairs	four pairs	none	none
# of outer series on anterior border	none	two pairs	one pairs	none	none
# of outer series on fixed cheek including palpebral tubercle	none	three pairs	four pairs	none	none
# of rachial series on pygidium	none	two pairs	two pairs	none	none
# of inner series on pygidium	none	two pairs	two pairs	none	none
# of outer series on pygidium	none	three pairs	three pairs	none	none
additional pair between inner and outer series in front of posterior cranidial border	absent	present	present	absent	absent
unique tuberclation pattern			spine development	granulate	granulate

# of instars	two	two	one	two	two
protoglabellar shape	laterally inflated	laterally inflated	laterally inflated	forward-tapering	forward-tapering
protoglabellar furrows	absent	absent	absent	3 pairs, trans-glabellar	3 pairs, trans-glabellar
course of anterior facial suture	convergent forwards	convergent forwards	convergent forwards	convergent forwards	divergent forwards
preglabellar field	short	short	broad	absent	absent

TABLE V-2. (continued)

Au	Sc	Ca	Ot	Di	Ba	Pr
none	two pairs	three pairs	three pairs	two pairs		
three pairs	one pair	three pairs	four pairs	four pairs		
none	none	three pairs	three pairs	three pairs		
one pairs	two pairs	two pairs	one pair	three pairs		
none	five pairs	none	two pairs	two pairs		
one pair	seven pairs	none	none	none		
none	seven pairs	none	none	two pairs		
absent	absent	present	absent	present		
	additional pairs on pygidial pleural region		pygidial pair coalesced			
one (?)	?	two	two	three	two	two
laterally inflated	forward-tapering	laterally inflated	laterally inflated	laterally inflated	forward-tapering	forward-tapering
absent	absent	absent	absent	absent	3 pairs, discontinuous	2 pairs, discontinuous
convergent forwards	divergent forwards	divergent forwards	convergent forwards	convergent forwards	convergent forwards	convergent forwards
broad	broad	broad	absent	broad	short	absent

2) Hystricuridae should be assigned to the Order Proetida, as suggested by Fortey and Owens (1975), and should be excluded from the Ptychopariina. The Hystricuridae is the earliest (mainly of Tremadocian age) family of the Proetida and stratophenetically, separated from Upper Cambrian ptychopariid superfamilies such as Solenopleuracea or Catillicephalacea.

3) Two informal groups within the Hystricuridae are recognized, which could be separate subfamilies; one is characterized by a protaspis with tuberculation, a laterally inflated glabella, and no glabellar furrows, and the other has glabellar furrows (regardless of transglabellar or discontinuous), a forward-tapering glabella, an indented posterior margin, and no tuberclation.

4) Paraplethopeltis, sensu Bridge and Cloud (1947), does not constitute a genus (or subgenus) of the Hystricuridae and should be reassigned to the Plethopeltidae Raymond, 1925 as in the Treatise (Moore, 1959). The species assigned to 'Paraplethopeltis' belong to the Hystricuridae.

5) Hyperbolochilus is assigned to the Hystricuridae.

PHYLOGENETIC IMPLICATIONS

The above taxonomic conclusions have significant implications for our understanding of the evolution and phylogenetics of proetid trilobites. First of all, the distinct impression of a preglabellar furrow on hystricurid protaspides, regardless of presence of preglabellar field, reinforces the monophyly of the Proetida, since the glabella of most Cambrian ptychopariid protaspides overhang the anterior shield margin. Similarly, Fortey (1990) suggested that a proetid type protaspis, with a fusiform, anteriorly rounded or pointed glabella is a diagnostic character for the Proetida, derived from the forward-expanding axis, reaching far forwards, of the ptychopariid protaspis (Fortey, 1990, text-fig. 10. h-m).

The supposed two informal groups of the Hystricuridae, which are mainly discriminated by protaspid morphologies, demonstrate that there might have been two separate lineages of proetids during Lower Ordovician (Figure V-10). The first lineage is characterized by development of tuberculation pattern on protaspid shield, which might be an evolutionary novelty (putative synapomorphy) derived from Upper Cambrian ptychopariid (a probable sistergroup) with smooth protaspid shield. Among the younger proetid families, in particular, dimeropygid protaspides (e.g. *Dimeropyge speyeri*, see Chatterton, 1994, fig. 3) are much more similar to protaspides of *Hystricurus paragenalatus* (Figure V-2.2) than any other hystricurid protaspides, in having no inner series of tubercles on protopygidium, a more rounded outline, and relatively deep anterior border furrow. Compared to degree 5 meraspis of *Parahystricurus carinatus*, the M3 of *D. speyeri* shares long spine(s) on the thoracic segment(s) and three main series of tubercles on the whole carapace. These similarities further confirm that dimeropygids were derived from or are the immediate sistergroup to the first informal group of hystricurids. Chatterton (1994, fig. 1), in his cladistic analysis, presented that dimeropygid trilobites share three pygidial axial rings which appears to have been derived from more than three (in general, four) rings of hystricurids.

Whittington and Campbell (1967, p. 450) noticed that *Dimeropyge* and *Otarion* show a similar development. Later, Fortey and Owens (1975, p. 230-231) extended the similarity into such hystricurid species as *Hystricurus paragenalatus*. Protaspides of these taxa share a similar pattern of tuberculation, including the lack of an inner series of tubercles on the protopygidium. With growth, these taxa develop the inner series on thorax and pygidium (*Otarion huddyi*, see Adrain and Chatterton, 1994, fig. 7-3; *Dimeropyge speyeri*, see Chatterton,. 1994, fig. 5-19; *Parahystricurus carinatus*, herein Plate V-3.1). Comparison of hypostomes provides more similarities of these taxa, in having a pair of spines along the posterior margin (compare Adrain and Chatterton, 1994, fig. 7.6 and Plate V-3.4, herein) and a larger anterior lobe of the middle body. Based on these similarities, it can be presumed that most proetid families, except for scharyiids (see below), with tuberclate protaspides after a protopygidium appears,

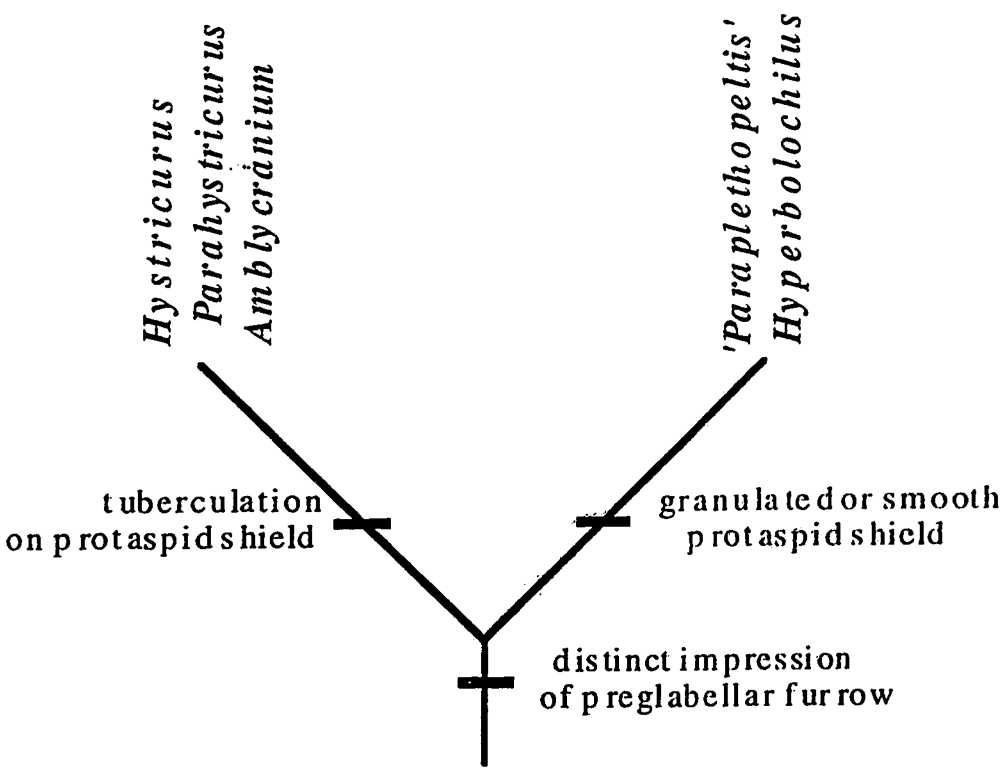

FIGURE V-10. Phylogenetic inference of the Lower Ordovician hystricurids. Two discrete protaspid morphotypes indicate that two separate lineages might have existed within the Hystricuridae during the Lower Ordovician.

were derived from the first informal hystricurid group. Of the first hystricurid group, *Amblycranium* (Plate V-4.1-3) develops all of the three main series of the tubercles in the protaspid period, probably indicating an accelerated development compared to *Hystricurus* and *Parahystricurus* occurring in stratigraphically older horizons (Figure V-1).

The second group including '*Paraplethopeltis*' and *Hyperbolochilus* is characterized by a granulate (not tuberclate) protaspid shield and transglabellar furrow, compared to the first group. The last feature, variations of which are detected as bilobed L1/L2/L3 in 'Paraplethopeltis' sp. A (Plate V-5.1, 2), is shared with many Cambrian ptychopariids. In particular, the ptychopariid taxa considered as the possible ancestor or sistergroup to hystricurids, such as lonchocephalines (Shergold, 1991) and elviniids (Fortey, 1983; Ludvigsen et al., 1989) show the transglabellar furrow with bilobed L1/L2/L3, indicating that the feature appears to be symplesiomorphic. Of later proetid families, bathyurids and proetids ("Proetidae B" of Fortey and Owens, 1975)) may be incorporated with the second hystricurid group, since their protaspides have the glabellar furrows, regardless of whether they are transverse or lateral pairs, and a rather smooth exoskeleton of the protaspid shield. Fortey and Owens (1975, p. 229) noticed the striking similarities between '*Paraplethopeltis*' *genacurvus* (Hintze, 1952, pl. 7, figs 6-9) and *Decoroproetus*-like species ("Proetidae B" of Fortey and Owens, 1975, fig. 1D, E, F), and then further suggested their close phyletic link. However, '*Paraplethopeltis*' *genacurvus* protaspides (Plate V-5.10, 13, 17) do not show strong similarities to protaspides of *Proetus* (*Proetus*) *talenti* (Chatterton, 1971, figs 15A, B); the former differs from the latter in having narrower (tr.) protoglabella and indistinct eye ridge. More likely is that the Proetidae are phyletically linked with '*Paraplethopeltis*' through *Otarion*, as suggested by Owens (1973, text-fig. 12).

Of this second group, *Hyperbolochilus* protaspides (Plate V-4.10, 11, 12, 14, 15) are remarkably similar to scharyiid protaspides (Šnajdr, 1980, fig. 1), except for the tuberculation pattern which is similar to the first hystricurid group (Table V-2). Even the holaspid cranidium of Scharyia micropyga (Šnajdr, 1980, pl. 6, figs 1-8) are similar to that of Hyperbolochilus cf. marginauctum (herein Plate V-4.13) in having a broad preglabellar field, a moderately impressed preglabellar median furrow, a strongly divergent anterior facial suture, a smaller palpebral lobe and a forward-tapering glabella; these features are also found in Hyperbolochilus? sp. nov. described by Fortey (1983, pl. 25, figs 10, 11). In contrast, 'cedariiform' facial suture characteristic of holaspid cranidium of Scharyia (Owens, 1974, text-fig. 1) is found in Hystricurus sp. (Plate V-1.16), along with a forward-tapering glabella. The cranidium of Scharyia heothina (Ashgill sharyriine, see Owens, 1974, pl. 99, fig. 1) is similar to Hystricurus sp. L (Terrell, 1973, pl. 2, fig. 7) which probably belongs to Hystricurus sp. described herein. These disparate similarities appears to cause a confusion of phylogenetic affinities of Scharyiidae (Adrain and Chatterton, 1993), but the similarities to the Hystricuridae confirm that the Scharyiidae is phylogenetically linked with the Hystricuridae, without regard to the subordinate affinity to the first or second group.

A direct phyletic linkage of hystricurids with Upper Cambrian ptychopariids such as elviniids (Fortey, 1983, p. 182-183), dokimocephalids (Ludvigsen et al., 1989, p. 22), solenopleurids (Fortey, 1990, p. 560), and lonchocephalines (Shergold, 1991, p. 33) appears to be still problematic, since hystricurid protaspides discovered are not similar to protaspides of those taxa. Such morphologic disparity might invoke Whittington's (1981, p. 594) cryptogenetic origin of Ordovician and later taxa, which was disputed by Fortey and Owens (1990a, p. 148) who suggested that more refined phylogenetic analysis would be able to solve the problem. Based on larval and adult morphologies, the following putative synapomorphy statements are made for ptychopariids and hystricurids: 1) distinct impression of preglabellar field, i.e. distinct differentiation of anterior border from glabella, appears to be derived from overhanging glabellar front of the Upper Cambrian ptychopariid protaspides; 2) the tuberculation of the protaspid shield of the first hystricurid group and granulation of the second appears to have been derived from the smooth ptychopariid protaspides (Figure V-10), even though the development of tubercles (or spines) on the protaspid shield is considered as a readily-acquired feature; 3) the presence of a transglabellar furrow in the second hystricurid group might be a valid symplesiomorphy, which would turn out to be synapomorphy at a more inclusive level; 4) a pair of spines along hypostomal posterior margin of hystricurid holaspides seems to be an evolutionary novelty, which is likely to have been derived from an entire margin of hypostome of Cambrian ptychopariids and to be retained by even younger proetids such as Otarion.

A more corroborated analysis of the Ordovician and later proetids including the hystricurids and the Cambrian ptychopariids would be possible with the information on their earlier protaspides prior to the appearance of a protopygidium. Such earlier protaspides of the proetids and ptychopariids are shown to share a pair of short spines along the posterior margin of the shield and the absence of glabellar furrows; for example, Dimeropyge speyeri (a proetid, see Chatterton, 1994, pl. 4, figs 13-16), "Otarion" spinicaudatum (a proetid, Chatterton and Speyer, 1995, figs 41A , B), Ehmaniella waptaensis (a ptychopariid, Hu, 1986, text-fig. 11A), and Spencella ? (a ptychopariid, Chatterton and Speyer, 1995, figs 30A to F). Only Hyperbolochilus cf. marginauctum (Plate V-4.11, 12) has the equivalent protaspid stage with a pair of spines, which is, however, more than two times larger than the stage of the above taxa; the early protaspid stage (Figure V-2.1) of Hystricurus paragenalatus is not considered equivalent to those smaller protaspides, since it has an entire margin, three pairs of tubercles, and rather distinct axial furrows. It is not clear, for the present, that the appearance of the earlier protaspid stage in most hystricurids have been suppressed, or the materials representing the stage were not preserved due to a taphonomic reason. The spine pair along the posterior margin of the protaspid shield appears to be homologous to the re-entrant posterior margin of some of the Cambrian ptychopariids (e.g. Nixonella montanensis, Hu, 1972, text-fig. 2a, b). Of interest is that the scharyiid protaspides uniquely have a small spine-like projection along the anterior margin along with a pair of spines on the posterior margin (Chatterton and Speyer, 1995, figs 41C, D), which reflects the complicated similarity to the hystricurids (see above).

Various similarities of hystricurid protaspides to other proetid members are likely to be the evidence that the trilobite group is a basal paraphyletic group of the Proetida, and its later disappearance is a taxonomic pseudoextinction (Briggs et al., 1988; Fortey, 1989). Also, this morphologic disparity may be directly related to the Ordovician radiation (Sepkoski, 1981; Fortey and Owens, 1990a) that took place immediately after the Cambrian-Ordovician extinction events (Westrop, 1989), which is demonstrated by an increase in the diversity of taxa (Sloan, 1990, table 2) or in adaptive morphotypes (Fortey and Owens, 1990b). Hystricurids might have exploited many empty niches (or morphospaces, see Gould, 1989) left behind the extinction and developed a variety of morphology in the larvae as well as adults.

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CHAPTER VI

GENERAL DISCUSSION

Each subject of four papers grouped in this volume is relevant to significant issues in the field of systematic biology and/or trilobite research. It seems desirable to further discuss these relevant issues, which certainly helps the author to realize the limit of his knowledge and thus, provides a guide for the future studies. Three issues are worth being further discussed: "homology", "a role of ontogeny in phylogenetic systematics", and the "ptychopariid problem".

Homology is, without any doubt, a central theme of comparative biology (de Beer, 1971; Patterson, 1982; de Pinna, 1991), but its definition and recognition are still in dispute (e.g., de Pinna, 1991). Patterson (1982) excellently summarized several criteria and definitions of homology. It has been generally admitted that homology is a relationship between structures of different organisms (but operationally replaced by an observable feature), and it is a hypothesis to be tested. The homology of 'Lp' in Chapter II is recognized by a topographical similarity; the posteriormost axial lobe (Lp) of all phacopid trilobites is assumed homologous and thus, 'Lp' may determine the grouping of all phacopids. This is de Pinna's (1991) 'primary' homology and thus should be tested by congruence in order to logically justify the homology proposition. The homology of 'Lp' implicitly assumes that all variations of the lobe, which are detected among different trilobite taxa and different ontogenetic intervals, are homologous, just as de Pinna (1991, p. 375) said, "Recognition of the character 'hair' itself implies a grouping called mammals, i.e. a hypothesis of monophyly derived from <u>the conjecture of homology among the various expressions of the attribute hair</u>." (underlined by author). One possible way to put 'Lp' into the congruence test is to introduce another feature which is presumed to be homologous to the lobe, e.g. telson of insects. This might imply that the test of homology requires a third taxon, since homology recognition is a comparative procedure.

The second issue is the role of ontogeny in phylogeny. Ontogeny consists of a series of growth stages of an organism and thus, in ontogeny, a morphologic feature sequentially changes during an individual's life cycle. Such an ontogenetic sequence, whether continuous (Alberch et al., 1979) or discontinuous (Alberch, 1985), has been recognized as an evolutionary process which is recapitulated by phylogeny (Gould, 1977) within the heterochronic context. Another fundamental aspect is that ontogeny provides a catalog of characters (Mabee, 1989), so that we can choose a character from a certain interval which is a part of ontogeny. So far, the emphasis has been placed on that causal mechanism of evolutionary change rather than on the elucidation of particular phylogenetic relationships (Atkinson, 1992) using ontogeny. How, thus, can we elucidate phylogenetic relationship of organisms using ontogenetic information? Obviously, using characters from a certain ontogenetic interval does not necessarily require the ontogenetic sequence, only comparability of that interval across the taxa involved in the analysis is required. Two possible cladistic approaches were proposed in Chapter IV, the character combination approach and the adoption of ontogenetic transformation character concept, whereby the ontogenetic information is utilized as fully as possible and the 'incongruence' between larval and adult phylogeny is resolved. In that chapter, it was implied that heterochronic information is not necessarily introduced, where the ontogenetic transformation is used as a character; most heterochronic characters in this analysis are shifts of timing of appearance, not rates of development. It is obvious that the interpretation of heterochronic process requires a known phylogenetic framework. However, the phylogenetic relationships disclosed by ontogenetic transformation characters might be able to directly reveal the heterochronic process. For example, a clade A is defined by a-b-c-d (ontogenetic sequence) and a more inclusive clade A+B is defined by a-b-c-d-e (Figure VI-1). There can be assumed to be an evolutionary change from a-b-c-d-e to a-b-c-d between the internodes (unknown

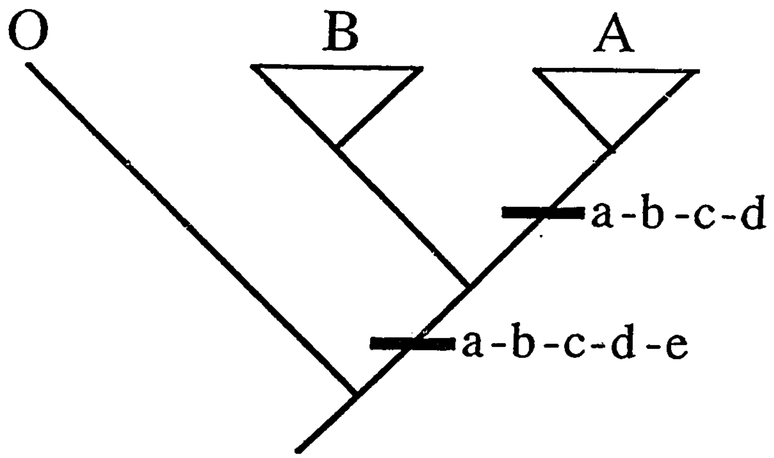

FIGURE VI-1. A hypothetical phylogenetic relationship derived from ontogenetic transformation characters. a-b-c-d and a-b-c-d-e are ontogenetic transformation characters. The cladogram is modified from Fink (1982), and Kluge and Strauss (1985).

ancestor), which, in turn, can be directly interpreted as a terminal deletion (a heterochronic process). Hence, the phylogenetic analysis using ontogenetic transformation character might be able to accomplish two disparate goals, pattern reconstruction and interpretation of evolutionary process, simultaneously.

The third issue is specific to the evolution of the Proetida and the Phacopida. Even with discovery of Tremadocian pliomerid and hystricurid larvae in this work, the 'ptychopariid problem' was not resolved. As for the Phacopida, the comparison made between ptychopariid larvae (e.g., *Dunderbergia anyta*) with three pairs of fixigenal spines and the Tremadocian phacopid larvae in Chapter III and IV provides a prospective clue towards the answer of that problem. There are several ptychopariid larvae with similar morphologies to *D. anyta*, most of which were described by Hu (1971, 1985, 1986). Such shared possession of three pairs of fixigenal spine, bilobed axial or glabellar lobes and overhanging axis to anterior and posterior margin predicts that the ptychopariids with this larval morphotype might be phylogenetically more closely related to the Ordovician and later phacopids than the other ptychopariids. In contrast, holaspid morphologies of these ptychopariids and phacopids provides much less predictive values for the phylogenetic analysis. As for the Proetida, the discovery of earlier protaspid stage ('anaprotaspis') of hystricurids will give a valuable clue to resolve the phylogenetic relationship of the hystricurids (the earliest proetid) to Cambrian ptychopariids, as mentioned in Chapter V. For the present, the larval dissimilarity between hystricurids and ptychopariids is not considered as much informative for the phylogenetic analysis as considerable adult similarity. Such a difference in the degree of morphologic similarity among different ontogenetic intervals may reflect that the evolutionary mechanism (e.g., palingenesis versus caenogenesis, Rieppel, 1990; horizontal hybridization of larvae, Williamson, 1992) which plays different roles on different ontogenetic intervals, is responsible for that ontogenetic disparity of morphologies. Remarkably intriguing is that the meta- or paraprotaspis of some ptychopariids (e.g., Gen. et species indeterminata, Hu, 1986) has similar morphologies to protaspides of 'Paraplethopeltis', while the anaprotaspis of that ptychopariid is similar to that of pliomerids. The disappearance of three pairs of fixigenal spines after a protopygidium appears is a common ontogenetic phenomenon in Cambrian ptychopariids. Such complicated similarities suggest that simultaneous phylogenetic analysis should be implemented for ptychopariids, hystricurids, and phacopids.

Another aspect of proetid and phacopid evolution is its relevance to Ordovician radiation immediately after Cambrian-Ordovician extinction events. Larval morphologic disparity of Tremadocian pliomerids and hystricurids within each family might be an evidence of the evolutionary radiation which is caused by accelerated cladogenesis or adaptive deployment (Fortey and Owens, 1990). For the phylogenetic analysis or interpretation of evolutionary pattern of the Proetida and Phacopida, the review of Cambrian ptychopariid protaspides appears to be important.

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APPENDIX IV-1. Description of characters used in this cladistic analysis and distribution of the character states and codes of 16 trilobite taxa involved in the analysis. Abbreviations: Pa = protaspid instar(s) before protopygidium appears; Pb = protaspid instar(s) after protopygidium appears; M = meraspid period; H = holaspid period; T = ontogenetic transformation character; Th = ontogenetic transformation character with heterochronic information. Refer to Appendix IV-2 for the abbreviations of the taxon names. Morphologic terminologies for protaspides are shown in Figure IV-1 and also found in Chatterton and Speyer (1995, fig. 9), and those for holaspides are found in Harrington (in Harrington et al., 1959, p. O38-O117).

1. Developmental Event: 0 = all events take place separately; 1 = calcification and appearance of protopygidium take place simultaneously; 2 = appearance of protopygidium and segmentation of tergite take place simultaneously.

NOTE-- See text for details and see also Figure IV-2.

Taxa	Pa	Pb	M	H	T(Th)
Du	present	present	present	present	0
Fl	present	present	present	present	0
Ca	present	present	present	present	0
Pr	present	present	present	present	0
Ps	present	present	present	present	0
Rp	present	present	present	present	0
Rs	present	present	present	present	0
Te	present	present	present	present	0
Ka	present	present	present	present	0
Ly	present	present	present	present	0
Ph	absent	present	present	present	1
Ce	absent	present	present	present	1
Ac	absent	present	present	present	1
Cy	absent	present	present	present	1
Sp	present	absent	present	present	2
He	present	absent	present	present	2

2. Number of Instars
2-Pa) number of instars in Pa: 0 = two; 1 = none; 2 = one.
2-Pb) number of instars in Pb: 0 = two; 1 = one; 2 = none.

NOTE -- This character is recognizable in the length versus width plot, where each morphometric grouping is assumed to represent one instar, or inter-moulting stage. Just as other morphologic characters are controlled by gene regulation, this character is considered as an expression of gene regulation for moulting frequency. The moulting frequency of meraspid and holaspid periods is not available, except only a few examples (e.g., olenellids of Palmer, 1957; eodiscid of Zhang and Clarkson, 1993). Ontogenetic transformation of this character is unlikely to be appropriate, unless the moulting frequency during the whole life cycle of each trilobite is provided. The character state of *Dunderbergia anyta* (outgroup) was assessed as two instars for Pa and Pb, respectively, even though Hu (1971) described two protaspid stages (= his ana- and metaprotaspis) in Pa and three stages (his paraprotaspis) in Pb. It is highly probable that Hu's (1971) largest paraprotaspis represents a degree 0 meraspis, because the paraprotaspis is much larger than the other two earlier paraprotaspides and the posterior protocranidial marginal furrow is so distinctly impressed that it may reflect a segmentation. For *Tesselacauda depressa* (Chapter III), such smaller stages as 1S, 2S, and 3S are not regarded as correctly being associated with that species.

Taxa	Pa		Pb		M	H
Du	two	0	two	0	not	available
Fl	two	0	two	0	not	available
Ca	one	2	one	1	not	available
Pr	one	2	two	0	not	available
Ps	one	2	two	0	not	available
Rp	one	2	one	1	not	available
Rs	one	2	one	1	not	available
Te	one	2	one	1	not	available
Ka	one	2	one	1	not	available
Ly	one	2	one	1	not	available
Ph	none	1	two	0	not	available
Ce	none	1	one	1	not	available
Ac	none	1	one	1	not	available
Cy	none	1	two	0	not	available
Sp	one	2	none	2	not	available
He	one	2	none	2	not	available

3. Life Habit

3-Pa) life habit in Pa: 0 = benthic; 1 = pelagic.

3-T) life habit change during ontogeny: 0 = remains benthic habit; 1 = changes from pelagic to benthic.

3-Th) timing of acquisition of 'benthic' life habit: 0 = at calcification; 1 = at appearance of protopygidium; 2 = at calcification accompanied with appearance of protopygidium.

NOTE -- This character is inferred from morphologic features such as lateral profile, hypostomal shape and marginal spines, and paleogeographic distribution of trilobites (Chatterton and Speyer, 1989; Speyer and Chatterton, 1989). It is conceivable that all protaspid instars in Pa of the phacopid trilobites might have a pelagic life habit, since they have needle-like hypostomal spines, rather bulbous lateral profile, and lack of marginal spines, compared to instars of Pb. It follows that in phacopid trilobite's ontogeny, the life habit change is accompanied with the appearance of protopygidium. Tentatively, only four trilobites such as *Flexicalymene senaria*, *Calyptaulax annulata*, *Sphaerexochus (Korolevium) arenosus* and *Heliomeroides freschaufae* are assessed as having pelagic life habit in their early growth stages, as suggested in the previous works (Chatterton, 1980; Chatterton et al., 1990).

Taxa	Pa		Pb	M	H	T	Th
Du	benthic	0			BENTHIC	0	0
Fl	pelagic	1			BENTHIC	1	1
Ca	pelagic	1			BENTHIC	1	1
Pr	benthic	0			BENTHIC	0	0
Ps	benthic	0			BENTHIC	0	0
Rp	benthic	0			BENTHIC	0	0
Rs	benthic	0			BENTHIC	0	0
Te	benthic	0			BENTHIC	0	0
Ka	benthic	0			BENTHIC	0	0
Ly	benthic	0			BENTHIC	0	0
Ph	NO INSTARS				BENTHIC	0	2
Cc	NO INSTARS				BENTHIC	0	2
Ac	NO INSTARS				BENTHIC	0	2
Cy	NO INSTARS				BENTHIC	0	2
Sp	pelagic	1			BENTHIC	1	1
He	pelagic	1			BENTHIC	1	1

4. Number of Glabellar Lobes

4-Pa) number of glabellar lobes in Pa: 0 = four; 1 = three; 2 = not differentiated.

4-Th) timing of attainment of 'four' glabellar lobes: 0 = at the last instar in Pa and after calcification; 1 = at the first instar in Pb and after calcification; 2 = at the first instar in Pb and simultaneous with calcification; 3 = at the degree 0 of meraspid period, and simultaneous with appearance of protopygidium and segmentation of tergite.

NOTE --All phacopid trilobites acquire four glabellar lobes at the same time that protopygidium appears, but the timing of acquisition is variable with reference to other developmental events and the first or last instar of each ontogenetic interval. Ontogenetic transformation from 3 to 4, as an increment, occurs in all trilobites.

Taxa	Pa		Pb	M	H	Th
Du	three to four	0	four	FOUR GLABELLAR LOBES		0
Fl	three to three	1	four	FOUR GLABELLAR LOBES		1
Ca	not differentiated	2	four	FOUR GLABELLAR LOBES		1
Pr	three	1	four	FOUR GLABELLAR LOBES		1
Ps	four	0	four	FOUR GLABELLAR LOBES		0
Rp	three	1	four	FOUR GLABELLAR LOBES		1
Rs	four	0	four	FOUR GLABELLAR LOBES		0
Te	four	0	four	FOUR GLABELLAR LOBES		0
Ka	three	1	four	FOUR GLABELLAR LOBES		1
Ly	four	0	four	FOUR GLABELLAR LOBES		0
Ph	NO INSTARS		four	FOUR GLABELLAR LOBES		2
Ce	NO INSTARS		four	FOUR GLABELLAR LOBES		2
Ac	NO INSTARS		four	FOUR GLABELLAR LOBES		2
Cy	NO INSTARS		four	FOUR GLABELLAR LOBES		2
Sp	not differentiated	2	NO INSTARS	FOUR GLABELLAR LOBES		3
He	not differentiated	2	NO INSTARS	FOUR GLABELLAR LOBES		3

5. Shape of Glabella

5-Pa) protoglabellar shape in Pa: 0 = spindle-shaped Lp to L3 and subtrapezoidal L4; 1 = parallel-sided Lp to L3 and subtrapezoidal L4; 2 = subcylindrical; 3 = spindle-shaped Lp to L4; 4 = invisible axial furrow.

5-Pb) protoglabellar shape in Pb: 0 = parallel-sided Lp to L3 and subtrapezoidal L4; 1 = subcylindrical.

5-H) holaspid glabellar shape: 0 = forward-tapering; 1 = subrectangular; 2 = forward-expanding; 3 = laterally inflated

5-T) ontogenetic transformation in glabellar shape: 0 = forward tapering of L4 relative to L1 to L3; 1 = forward expansion of L4 relative L1 to L3; 2 = lateral expansion of L2 and L3

NOTE -- Character states defined for each ontogenetic interval occur restricted to that interval, so that heterochronic development can not be defined as character. Transformation of the glabellar shape appears to be more radical during earlier growth stages than later stages, which might be pertinent to metamorphosis during the earlier stages. The character state for Pa of *Calyptaulax annulata* was specified as 'invisible axial furrow', because the invisible axial furrow does not mean the absence of glabella.

Taxa	Pa		Pb		H		T
Du	spindle Lp to L3; subtrapezoidal L4	0	parallel Lp to L3; subtrapezoidal L4	0	forward-tapering	0	0
Fl	parallel Lp to L3; subtrapezoidal L4	1	subcylindrical	1	forward-tapering	0	0
Ca	invisible axial furrow	4	parallel Lp to L3; subtrapezoidal L4	0	forward-expanding	2	1
Pr	spindle Lp to L3; subtrapezoidal L4	0	parallel Lp to L3; subtrapezoidal L4	0	forward-tapering	0	0
Ps	spindle Lp to L3; subtrapezoidal L4	0	parallel Lp to L3; subtrapezoidal L4	0	subrectangular	1	0
Rp	parallel Lp to L3; subtrapezoidal L4	1	subcylindrical	1	subrectangular	1	0
Rs	subcylindrical	2	subcylindrical	1	subrectangular	1	0
Te	spindle Lp to L3; subtrapezoidal L4	0	subcylindrical	1	subrectangular	1	0
Ka	spindle Lp to L3; subtrapezoidal L4	0	subcylindrical	1	forward-tapering	0	0
Ly	parallel Lp to L3; subtrapezoidal L4	1	parallel Lp to L3; subtrapezoidal L4	0	forward-expanding	2	1
Ph	NO INSTARS		subcylindrical	1	forward-expanding	2	1
Ce	NO INSTARS		subcylindrical	1	subrectangular	1	0
Ac	NO INSTARS		subcylindrical	1	laterally inflated	3	2
Cy	NO INSTARS		parallel Lp to L3; subtrapezoidal L4	0	forward-expanding	2	1
Sp	spindle-shaped	3	NO INSTARS		laterally inflated	3	2
He	spindle-shaped	3	NO INSTARS		laterally inflated	3	2

6. Ornament on Glabella

6-Pb) ornament on protoglabella in Pb: 0 = smooth; 1 = paired tubercles.

6-H) ornament on holaspid glabella: 0 = granulate; 1 = tuberclate; 2 = granulate with paired tubercles.

6-T) ontogenetic transformation of glabellar ornament: 0 = granulation without showing paired tubercles; 1 = granulation showing paired tubercles.

6-Th) timing of appearance of 'paired tubercles': 0 = entirely absent during ontogeny; 1 = at appearance of protopygidium; 2 = after segmentation of tergite.

NOTE -- Glabella in Pa interval of all trilobites is smooth. 'Timing of acquisition of granulation', as a possible heterochronic character, can not be accurately evaluated, because granulation, itself, does not appears radically during ontogeny, and is found in disarticulated meraspid or holaspid cranidia, the position of which within ontogeny can not be correctly determined. The glabellar tubercle pairs become unrecognizable in later ontogeny with exception of *Cybeloides cimelia*, since the glabella is covered with irregularly-dispersed granules or tubercles.

Taxa	Pa	Pb		M	H		T	Th
Du	smooth	smooth	0	granulate	granulate	0	0	0
Fl	smooth	smooth	0	paired tubercles	granulate	0	1	2
Ca	smooth	paired tubercles	1	paired tubercles	granulate	0	1	1
Pr	smooth	smooth	0	smooth	granulate	0	0	0
Ps	smooth	smooth	0	smooth	granulate	0	0	0
Rp	smooth	smooth	0	paired tubercles	granulate	0	1	2
Rs	smooth	smooth	0	paired tubercles	granulate	0	1	2
Te	smooth	smooth	0	paired tubercles	granulate	0	1	2
Ka	smooth	smooth	0	N/A	granulate	0	0	0
Ly	smooth	smooth	0	N/A	granulate	0	0	0
Ph	NO INSTARS	paired tubercles	1	paired tubercles	tuberclate	1	1	1
Ce	NO INSTARS	smooth	0	granulate	granulate	0	0	0
Ac	NO INSTARS	paired tubercles	1	granulate	granulate	0	1	1
Cy	NO INSTARS	paired tubercles	1	paired tubercles	granulate; with paired tubercle	2	1	1
Sp	smooth	NO INSTARS		granulate	granulate	0	0	0
He	smooth	NO INSTARS		granulate	granulate	0	0	0

7. Form of Glabellar Furrows

7-Pb) protoglabellar furrow in Pb: 0 = transglabellar; 1 = as depressions alongside glabella (phacopine-type furrows).

7-T) ontogenetic transformation of form of glabellar furrows: 0 = without showing phacopine-type furrows; 1 = with showing phacopine-type furrows.

7-Th) timing of acquisition of 'phacopine-type' glabellar furrows: 0 = entirely absent during ontogeny; 1 = at appearance of protopygidium; 2 = after segmentation of tergite.

NOTE -- Protaspides in Pa show two conditions of glabellar furrow form, 'transglabellar' and 'not impressed', which were treated in character 4. Holaspides of all trilobites show slit-like glabellar furrows. Form and direction of each pair of three glabellar furrows in holaspid trilobites are so variable and taxon-specific that those features are not informative for cladistic analysis.

Taxa	Pa	Pb		M	H	T	Th
Du	transglabellar	transglabellar	0	furrow proper	slit-like furrow	0	0
Fl	transglabellar	transglabellar	0	phacopine-type	slit-like furrow	1	2
Ca	not differentiated	phacopine-type	1	phacopine-type	slit-like furrow	1	1
Pr	transglabellar	transglabellar	0	furrow proper	slit-like furrow	0	0
Ps	transglabellar	transglabellar	0	furrow proper	slit-like furrow	0	0
Rp	transglabellar	transglabellar	0	phacopine-type	slit-like furrow	1	2
Rs	transglabellar	transglabellar	0	phacopine-type	slit-like furrow	1	2
Te	transglabellar	transglabellar	0	furrow proper	slit-like furrow	0	0
Ka	transglabellar	transglabellar	0	N/A	slit-like furrow	0	0
Ly	transglabellar	transglabellar	0	N/A	slit-like furrow	0	0
Ph	NO INSTARS	transglabellar	0	phacopine-type	slit-like furrow	1	2
Ce	NO INSTARS	transglabellar	0	furrow proper	slit-like furrow	0	0
Ac	NO INSTARS	transglabellar	0	furrow proper	slit-like furrow	0	0
Cy	NO INSTARS	transglabellar	0	phacopine-type	slit-like furrow	1	2
Sp	not differentiated	NO INSTARS		furrow proper	slit-like furrow	0	0
He	not differentiated	NO INSTARS		furrow proper	slit-like furrow	0	0

8. Length and Spacing of Glabellar Furrows

8-H) holaspid glabellar furrow pairs: 0 = posteriorly longer and more widely spaced; 1 = equally long and spaced; 2 = anteriorly longer and more widely spaced.

8-T) ontogenetic transformation of the length and spacing of glabellar furrow pairs: 0 = transform into unequal length and spacing; 1 = remain equal length and spacing.

NOTE -- Both features, length and spacing of glabellar furrows, transform consistently together during ontogeny. Protaspides in Pa and Pb intervals have equally long and spaced glabellar furrows in all trilobites. Heterochronic development appears not to be a valid character, since in all trilobites' life cycle, equally long and spaced furrows appear at the same time that larva is calcified.

Taxa	Pa	Pb	M	H		T
Du	equally long and spaced			posteriorly longer and more widely spaced	0	0
Fl	equally long and spaced			posteriorly longer and more widely spaced	0	0
Ca	equally long and spaced			anteriorly longer and more widely spaced	2	0
Pr	equally long and spaced			equally long and spaced	1	1
Ps	equally long and spaced			equally long and spaced	1	1
Rp	equally long and spaced			equally long and spaced	1	1
Rs	equally long and spaced			equally long and spaced	1	1
Te	equally long and spaced			equally long and spaced	1	1
Ka	equally long and spaced			posteriorly longer and more widely spaced	0	0
Ly	equally long and spaced			equally long and spaced	1	1
Ph	equally long and spaced			equally long and spaced	1	1
Ce	equally long and spaced			equally long and spaced	1	1
Ac	equally long and spaced			posteriorly longer and more widely spaced	0	0
Cy	equally long and spaced			equally long and spaced	1	1
Sp	equally long and spaced			equally long and spaced	1	1
He	equally long and spaced			equally long and spaced	1	1

9. Position of Anterior Fixigenal Spine Pair

9-Pa) position of anterior fixigenal spine in Pa: 0 = behind S3; 1 = in front of S3.

9-Pb) position of anterior fixigenal spine in Pb: 0 = absent; 1 = in front of S3.

9-T) ontogenetic transformation of the position of anterior fixigenal spine: 0 = remains behind S3 and disappears later; 1 = moves backwards and disappears later.

9-Th) timing of acquisition of 'behind S3' position of anterior fixigenal spine pair: 0 = at calcification; 1 = after segmentation of tergite.

NOTE -- All ingroup trilobites lose the spine pair during meraspid period, while the outgroup loses it across Pa and Pb. Anterior fixigenal spine pair of phacopid protaspides is located immediately next to palpebral lobe. Its position with reference to S3 varies with different trilobites. With growth, the spine pair continuously moves backwards due to enlargement and/or backward movement of palpebral lobe, until it disappears in the meraspid period. Character state for Pa of *Calyptaulax annulata*, *Sphaerexochus arenosus* and *Heliomeroides freschaufae* lacking protoglabellar furrows, was determined by comparisons of the relative position with other protaspides; e.g., the spine pair of the first species is more posteriorly placed and thus, the state was defined as 'behind S3'. Ontogenetic transformation of this character was defined for the interval during which the spine pair exists, without regard to the timing difference in the disappearance of the spine pair.

Taxa	Pa		Pb		M	H	T	Th
Du	behind S3	0	absent	0	absent	absent	0	0
Fl	in front of S3	1	in front of S3	1	behind S3	absent	1	1
Ca	behind S3	0	behind S3	2	behind S3	absent	0	0
Pr	in front of S3	1	in front of S3	1	behind S3	absent	1	1
Ps	in front of S3	1	in front of S3	1	behind S3	absent	1	1
Rp	in front of S3	1	in front of S3	1	behind S3	absent	1	1
Rs	in front of S3	1	in front of S3	1	behind S3	absent	1	1
Tc	in front of S3	1	in front of S3	1	behind S3	absent	1	1
Ka	in front of S3	1	behind S3	2	behind S3	absent	1	1
Ly	in front of S3	1	behind S3	2	N/A	absent	1	1
Ph	NO INSTARS		in front of S3	1	behind S3	absent	1	1
Ce	NO INSTARS		in front of S3	1	behind S3	absent	1	1
Ac	NO INSTARS		in front of S3	1	behind S3	absent	1	1
Cy	NO INSTARS		in front of S3	1	behind S3	absent	1	1
Sp	in front of S3	1	NO INSTARS		behind S3	absent	1	1
He	in front of S3	1	NO INSTARS		behind S3	absent	1	1

10. Orientation of Posterior Fixigenal Spine (Genal Spine) Pair

10-Pb) orientation of posterior fixigenal spine pair in Pb: 0 = parallel; 1 = divergent.

10-T) ontogenetic transformation of orientation of genal spine pair: 0 = from parallel to divergent; 1 = remains divergent.

10-Th) timing of acquisition of 'divergent' orientation of posterior fixigenal spine pair: 0 = after segmentation of tergite; 1 = at appearance of protopygidium; 2 = at calcification.

NOTE -- Protaspides of Pa and holaspides of all trilobites display 'parallel' and 'divergent' orientation, respectively.

Taxa	Pa	Pb		M	H	T	Th
Du	parallel	parallel	0	divergent	divergent	0	0
Fl	parallel	divergent	1	divergent	divergent	0	1
Ca	parallel	parallel	0	parallel	divergent	0	0
Pr	parallel	parallel	0	parallel	divergent	0	0
Ps	parallel	parallel	0	parallel	divergent	0	0
Rp	parallel	parallel	0	parallel	divergent	0	0
Rs	parallel	parallel	0	parallel	divergent	0	0
Te	parallel	parallel	0	parallel	divergent	0	0
Ka	parallel	parallel	0	parallel	divergent	0	0
Ly	parallel	divergent	1	N/A	divergent	1	1
Ph	NO INSTARS	divergent	1	divergent	divergent	1	2
Ce	NO INSTARS	divergent	1	divergent	divergent	1	2
Ac	NO INSTARS	divergent	1	divergent	divergent	1	2
Cy	NO INSTARS	divergent	1	divergent	divergent	1	2
Sp	parallel	NO INSTARS		divergent	divergent	1	0
He	parallel	NO INSTARS		divergent	divergent	1	0

11. Position of Midfixigenal Spine Pair

11-Pa) position of midfixigenal spine in Pa: 0 = behind S1; 1 = in front of S1; 2 = absent.

11-Pb) position of midfixigenal spine in Pb: 0 = absent; 1 = behind S1; 2 = in front of S1; 3 = opposite S1.

11-T) ontogenetic transformation of position of midfixigenal spine: 0 = remains behind S1 and disappears later; 1 = moves forwards and disappears later; 2 = remains in front of S1 and disappears later.

NOTE -- All character states described herein are not found in ontogeny of each trilobite such that heterochronic development of each character state is not applicable to all ingroup taxa. Ontogenetic transformation was defined for the interval in which the spine pair exists, regardless of shift of timing of disappearance, as in character 10.

Taxa	Pa		Pb		M	H	T
Du	behind S1	0	absent	0	absent	absent	0
Fl	behind S1	0	behind S1	1	behind S1	absent	0
Ca	absent	2	in front of S1	2	in front of S1	absent	2
Pr	in front of S1	1	in front of S1	2	in front of S1	absent	2
Ps	in front of S1	1	in front of S1	2	in front of S1	absent	2
Rp	behind S1	0	opposite S1	3	in front of S1	absent	1
Rs	behind S1	0	opposite S1	3	in front of S1	absent	1
Tc	behind S1	0	opposite S1	3	in front of S1	absent	1
Ka	behind S1	0	behind S1	1	opposite S1	absent	1
Ly	behind S1	0	behind S1	1	N/A	absent	0
Ph	NO INSTARS		in front of S1	2	in front of S1	absent	2
Ce	NO INSTARS		in front of S1	2	in front of S1	absent	2
Ac	NO INSTARS		opposite S1	3	in front of S1	absent	1
Cy	NO INSTARS		opposite S1	3	in front of S1	absent	1
Sp	behind S1	0	NO INSTARS		behind S1	absent	0
Hc	behind S1	0	NO INSTARS		behind S1	absent	0

12. Length of Midfixigenal Spine.

12-Pa) length of midfixigenal spine relative to anterior fixigenal spine in Pa: 0 = equally long; 1 = absent.

12-Pb) length of midfixigenal spine relative to anterior fixigenal spine in Pb: 0 = absent; 1 = equally long; 2 = shorter.

NOTE -- Variations of length were detected by the comparison with anterior fixigenal spine which is not much as variable as posterior fixigenal spine. The midfixigenal spine pair disappears during some stage of meraspid period. Each trilobite displays either state, 'shorter' or 'equally long', throughout the interval during which the spine pair exists, so that it is not appropriate to define heterochronic character for the spine pair.

Taxa	Pa		Pb		M	H
Du	equally long	0	absent	0	absent	absent
Fl	equally long	0	equally long	1	equally long	absent
Ca	absent	1	shorter	2	shorter	absent
Pr	equally long	0	equally long	1	equally long	absent
Ps	equally long	0	equally long	1	equally long	absent
Rp	equally long	0	equally long	1	equally long	absent
Rs	equally long	0	equally long	1	equally long	absent
Te	equally long	0	equally long	1	equally long	absent
Ka	equally long	0	equally long	1	equally long	absent
Ly	equally long	0	equally long	1	equally long	absent
Ph	NO INSTARS		shorter	2	shorter	absent
Ce	NO INSTARS		shorter	2	shorter	absent
Ac	NO INSTARS		equally long	1	equally long	absent
Cy	NO INSTARS		shorter	2	shorter	absent
Sp	equally long	0	NO INSTARS		equally long	absent
He	equally long	0	NO INSTARS		equally long	absent

13. Circumocular Fixigenal Tubercle Pairs (CTs)
13-Pa) circumocular tubercles in Pa: 0 = absent; 1 = CT2
13-Pb) circumocular tubercles in Pb: 0 = absent; 1 = CT1/CT3/CT2.
13-T) ontogenetic transformation of circumocular tubercles: 0 = entirely absent; 1 = acquired in protaspid period and retained afterwards.

NOTE -- Circumocular fixigenal tubercle pairs, designated CT1/CT2/CT3 (Ramsköld, 1986), if any, occur at the same time that protopygidium appears in all trilobite's ontogeny. The tubercle pairs become unrecognizable due to development of pits and/or tubercles on fixigenal field (see character 14); subsequent size increase of the tubercle pairs in *Cybeloides cimelia* helps to recognize them even in later ontogeny.

Taxa	Pa		Pb		M H	T
Du	absent	0	absent	0	absent	0
Fl	CT2	1	CT1/CT3/CT2	1	unrecognizable	1
Ca	absent	0	CT1/CT3/CT2	1	unrecognizable	1
Pr	absent	0	absent	0	absent	0
Ps	absent	0	absent	0	absent	0
Rp	absent	0	CT1/CT3/CT2	1	unrecognizable	1
Rs	absent	0	CT1/CT3/CT2	1	unrecognizable	1
Tc	absent	0	CT1/CT3/CT2	1	unrecognizable	1
Ka	absent	0	?	?	absent	?
Ly	absent	0	absent	0	absent	0
Ph	NO INSTARS		CT1/CT3/CT2	1	unrecognizable	1
Ce	NO INSTARS		absent	0	absent	0
Ac	NO INSTARS		absent	0	absent	0
Cy	NO INSTARS		CT1/CT3/CT2	1	recognizable	1
Sp	absent	0	NO INSTARS		absent	0
He	absent	0	NO INSTARS		absent	0

14. Ornament on Fixigenal Field except for CTs.

14-Pb) ornament on fixigenal field in Pb: 0 = smooth; 1 = pitted.

14-H) ornament on holaspid fixigenal field: 0 = granulate; 1 = pitted; 2 = granulate and pitted.

14-T) ontogenetic transformation of ornaments on fixigenal field: 0 = acquisition retention of only granules; 1 = acquisition and retention of granules, and loss of pits; 2 = acquisition and retention of pits, and loss of granules; 3 = acquisition and retention of granules and pits.

14-Th) timing of appearance of 'pits' on fixigenal field: 0 = entirely absent during ontogeny; 1 = at appearance of protopygidium; 2 = after segmentation of tergite.

NOTE -- Fixigenal field of protaspides in Pa of all trilobites is smooth. The state 'granulate' occurs from meraspid period of all trilobites, some of which retains the state and others lose it.

Taxa	Pa	Pb		M	H		T	Th
Du	smooth	smooth	0	granulate	granulate	0	0	0
Fl	smooth	smooth	0	granulate	granulate	0	0	0
Ca	smooth	pitted	1	granulate	granulate	0	1	1
Pr	smooth	smooth	0	granulate and pitted	pitted	1	2	2
Ps	smooth	smooth	0	granulate and pitted	pitted	1	2	2
Rp	smooth	pitted	1	granulate and pitted	pitted	1	2	1
Rs	smooth	pitted	1	granulate and pitted	pitted	1	2	1
Tc	smooth	smooth	0	granulate and pitted	pitted	1	2	2
Ka	smooth	pitted	1	pitted	granulate	0	1	1
Ly	smooth	pitted	1	N/A	pitted	1	2	1
Ph	NO INSTARS	smooth	0	granulate and pitted	pitted	1	2	2
Cc	NO INSTARS	pitted	1	granulate and pitted	granulate and pitted	2	3	1
Ac	NO INSTARS	pitted	1	granulate and pitted	granulate and pitted	2	3	1
Cy	NO INSTARS	smooth	0	granulate	granulate and pitted	2	3	2
Sp	smooth	NO INSTARS		granulate and pitted	granulate and pitted	2	3	2
He	smooth	NO INSTARS		granulate	granulate	0	0	0

15. Width of Fixigenal Field

15-H) ratio between maximum (tr.) width of fixigenal field relative to maximum glabellar width: 0 = about 1:1; 1 = less than 1:1; 2 = greater than 1:1.

NOTE -- Fixigenal field width (tr.) of protaspides and meraspides of all trilobites is approximately 3.5 to 4 times wider than maximum glabellar width (tr.). The field of all phacopid trilobites becomes proportionately smaller, due to inward and backward migration of facial suture at the expense of the field, or glabellar inflation.

Taxa	Pa	Pb	M	H	
Du	about 3.5	to 4 times	broader than glabella	equal	0
Fl	about 3.5	to 4 times	broader than glabella	narrower	1
Ca	about 3.5	to 4 times	broader than glabella	narrower	1
Pr	about 3.5	to 4 times	broader than glabella	equal	0
Ps	about 3.5	to 4 times	broader than glabella	equal	0
Rp	about 3.5	to 4 times	broader than glabella	equal	0
Rs	about 3.5	to 4 times	broader than glabella	equal	0
Tc	about 3.5	to 4 times	broader than glabella	equal	0
Ka	about 3.5	to 4 times	broader than glabella	narrower	1
Ly	about 3.5	to 4 times	broader than glabella	broader	2
Ph	about 3.5	to 4 times	broader than glabella	narrower	1
Cc	about 3.5	to 4 times	broader than glabella	equal	0
Ac	about 3.5	to 4 times	broader than glabella	narrower	1
Cy	about 3.5	to 4 times	broader than glabella	broader	2
Sp	about 3.5	to 4 times	broader than glabella	narrower	1
Hc	about 3.5	to 4 times	broader than glabella	narrower	1

16. Ornament on Anterior Cranidial Border

16-Pb) ornament on anterior cranidial border in Pb: 0 = smooth; 1 = row of spines.

16-T) ontogenetic transformation of ornament on anterior cranidial border: 0 = granulation without developing row of spines; 1 = granulation with developing row of spines.

16-Th) timing of acquisition of 'row of spines' on anterior cranidial border: 0 = entirely absent during ontogeny; 1 = at appearance of protopygidium; 2 = after segmentation of tergite.

NOTE -- Protaspides in Pa of all trilobites have smooth anterior border. In holaspides, the border is ornamented by fine granules which precludes from recognizing the row of spines which is developed in earlier ontogenetic intervals.

Taxa	Pa	Pb		M	H	T	Th
Du	smooth	smooth	0	granulate	granulate	0	0
Fl	smooth	row of spines	1	granulate	granulate	1	1
Ca	smooth	row of spines	1	granulate	granulate	1	1
Pr	smooth	smooth	0	smooth	granulate	0	0
Ps	smooth	smooth	0	smooth	granulate	0	0
Rp	smooth	smooth	0	row of spines	granulate	1	2
Rs	smooth	smooth	0	row of spines	granulate	1	2
Te	smooth	smooth	0	row of spines	granulate	1	2
Ka	smooth	smooth	0	row of spines	granulate	1	2
Ly	smooth	smooth	0	N/A	granulate	0	0
Ph	NO INSTARS	row of spines	1	granulate	granulate	1	1
Ce	NO INSTARS	smooth	0	granulate	granulate	0	0
Ac	NO INSTARS	smooth	1	row of spines	granulate	1	2
Cy	NO INSTARS	row of spines	1	row of spines	row of spines	1	1
Sp	smooth	NO INSTARS		?	granulate	?	?
He	smooth	NO INSTARS		row of spines	granulate	1	2

17. Sagittal Width of Anterior Cranidial Border

17-H) width of holaspid anterior cranidial border relative to sagittal glabellar length: 0 = broad (less than 1:11); 1 = narrow (more than 1:13).

NOTE -- Variations of the width were determined with respect to sagittal length of glabella. Earlier growth stages such as protaspides and meraspides show a similar width of anterior border. The border ontogenetically broadens at a certain rate of each trilobite.

Taxa	Pa	Pb	M	H	
Du	similar to sagittal glabellar length			broader	0
Fl	similar to sagittal glabellar length			broader	0
Ca	similar to sagittal glabellar length			narrower	1
Pr	similar to sagittal glabellar length			broader	0
Ps	similar to sagittal glabellar length			broader	0
Rp	similar to sagittal glabellar length			broader	0
Rs	similar to sagittal glabellar length			broader	0
Tc	similar to sagittal glabellar length			broader	0
Ka	similar to sagittal glabellar length			narrower	1
Ly	similar to sagittal glabellar length			broader	0
Ph	similar to sagittal glabellar length			broader	0
Cc	similar to sagittal glabellar length			narrower	1
Ac	similar to sagittal glabellar length			narrower	1
Cy	similar to sagittal glabellar length			narrower	1
Sp	similar to sagittal glabellar length			narrower	1
Hc	similar to sagittal glabellar length			narrower	1

18. Position of Anterior End of Palpebral Lobe

18-H) position of anterior end of palpebral lobe in holaspides: 0 = posterior to S3; 1 = anterior to S3; 2 = opposite S3.

18-T) ontogenetic transformation of the position of anterior end of palpebral lobe: 0 = moves backwards; 1 = remains anterior to S3.

NOTE -- Anterior end of palpebral lobe is located anterior to S3 in protaspides of all trilobites. With growth, palpebral lobe moves backwards and/or abaxially, and increases in size, according to the movement of anterior fixigenal spine. The backward movement take place during meraspid or holaspid period, which is difficult to accurately correlate with developmental event. The size increase of palpebral lobe in later ontogeny renders it difficult to determine its position relative to S3. Thus, the anterior ends of palpebral lobe is regarded as a reference, since it is less variable according to the ontogenetic size increase and more independent of the movement of anterior fixigenal spine than the posterior end.

Taxa	Pa	Pb	M	H		T
Du	anterior to S3	anterior to S3	opposite S3	posterior to S3	0	0
Fl	anterior to S3	anterior to S3	opposite S3	posterior to S3	0	0
Ca	not differentiated	anterior to S3	anterior to S3	opposite S3	2	0
Pr	anterior to S3	anterior to S3	anterior to S3	anterior to S3	1	1
Ps	anterior to S3	anterior to S3	anterior to S3	anterior to S3	1	1
Rp	anterior to S3	anterior to S3	anterior to S3	anterior to S3	1	1
Rs	anterior to S3	anterior to S3	anterior to S3	anterior to S3	1	1
Te	anterior to S3	anterior to S3	anterior to S3	anterior to S3	1	1
Ka	anterior to S3	anterior to S3	N/A	posterior to S3	0	0
Ly	anterior to S3	anterior to S3	N/A	posterior to S3	0	0
Ph	NO INSTARS	anterior to S3	anterior to S3	opposite S3	2	0
Ce	NO INSTARS	anterior to S3	opposite S3	posterior to S3	0	0
Ac	NO INSTARS	anterior to S3	opposite S3	posterior to S3	0	0
Cy	NO INSTARS	anterior to S3	anterior to S3	posterior to S3	0	0
Sp	anterior to S3	NO INSTARS	posterior to S3	posterior to S3	0	0
He	anterior to S3	NO INSTARS	opposite S3	posterior to S3	0	0

19. Eye Ridge

19-Pb) swelling pair along the anterior margin in Pb: 0 = reaches axial furrow; 1 = does not reach axial furrow.

19-H) holaspid eye ridge: 0 = separate eye ridge; 1 = absent; 2 = palpebro-ocular ridge

19-T) ontogenetic transformation of eye ridge: 0 = persistently present; 1 = entirely absent.

NOTE -- A swelling pair along the anterior margin in protaspides is considered as homologous with either palpebral lobe + eye ridge or only palpebral lobe in holaspides. Eye ridge, in all trilobites with it, occurs at the same time with calcification, or is entirely absent during ontogeny of other trilobites. It is considered plausible that the swelling pair in the trilobites lacking eye ridge in the holaspides only represents the palpebral lobe, without regard to whether the swelling reaches axial furrow or not. In contrast, the pair of the trilobites with 'distinguishable eye ridge' or 'palpebro-ocular ridge' in the holaspid period is considered as the combined structure of the palpebral lobe and eye ridge. Thus, the morphologic similarity of the swelling pair of the phacopide protaspides has no bearing on their homology relationships to the palpebral lobe or the palpebral lobe + eye ridge.

Taxa	Pa	Pb		M	H		T
Du	reach axial furrow	reach axial furrow	0	reach axial furrow	separate eye ridge	0	0
Fl	reach axial furrow	separated from axial furrow	1	absent	absent	1	1
Ca	not differentiated	separated from axial furrow	1	reach axial furrow	absent	1	1
Pr	reach axial furrow	reach axial furrow	0	reach axial furrow	palpebro-ocular ridge	2	0
Ps	reach axial furrow	reach axial furrow	0	reach axial furrow	palpebro-ocular ridge	2	0
Rp	reach axial furrow	reach axial furrow	0	reach axial furrow	palpebro-ocular ridge	2	0
Rs	reach axial furrow	reach axial furrow	0	reach axial furrow	palpebro-ocular ridge	2	0
Tc	reach axial furrow	reach axial furrow	0	reach axial furrow	palpebro-ocular ridge	2	0
Ka	reach axial furrow	reach axial furrow	0	N/A	absent	2	1
Ly	reach axial furrow	reach axial furrow	0	N/A	separate eye ridge	0	0
Ph	NO INSTARS	reach axial furrow	0	separable eye ridge	separate eye ridge	0	0
Cc	NO INSTARS	reach axial furrow	0	reach axial furrow	palpebro-ocular ridge	2	0
Ac	NO INSTARS	reach axial furrow	0	reach axial furrow	absent	1	1
Cy	NO INSTARS	reach axial furrow	0	separable eye ridge	distinguishable eye ridge	0	0
Sp	reach axial furrow	NO INSTARS		absent	absent	1	1
He	reach axial furrow	NO INSTARS		absent	absent	1	1

20. Lateral Cranidial Border

20-Pa) lateral border in Pa: 0 = absent; 1 = present.

20-Pb) lateral border in Pb: 0 = present; 1 = absent.

20-T) ontogenetic transformation of lateral cranidial border: 0 = ontogenetically lost; 1 = entirely absent; 2 = appears at some ontogenetic stage and remains afterwards.

20-Th) timing of appearance of 'lateral cranidial border': 0 = at appearance of protopygidium; 1 = absent; 2 = at calcification but before appearance of protopygidium; 3 = after segmentation of tergite.

NOTE -- Variations of this character are relevant to course of facial suture (character 21), particularly, in mature stage. However, protaspides of the phacopid trilobites in this analysis are assessed as presence or absence of lateral border, regardless of all having proparian suture.

Taxa	Pa		Pb		M	H	T	Th
Du	absent	0	present	0	absent		0	0
Fl	absent	0	absent	1	absent		1	1
Ca	absent	0	absent	1	present		2	3
Pr	absent	0	present	0	present		2	0
Ps	absent	0	present	0	present		2	0
Rp	present	1	present	0	present		2	2
Rs	present	1	present	0	present		2	2
Te	present	1	present	0	present		2	2
Ka	present	1	present	0	N/A		2	2
Ly	present	1	present	0	N/A		2	2
Ph	NO INSTARS		absent	1	present		2	3
Ce	NO INSTARS		present	0	present		2	0
Ac	NO INSTARS		present	0	present		2	0
Cy	NO INSTARS		present	0	present		2	0
Sp	absent	0	NO INSTARS		present		2	3
He	absent	0	NO INSTARS		present		2	3

21. Facial Suture

21-Pb) facial suture in Pb: 0 = extended backwards into midfixigenal spine; 1 = delimited in front of anterior fixigenal spine (afs).

21-H) holaspid facial suture: 0 = opisthoparian; 1 = proparian; 2 = gonatoparian.

21-T) ontogenetic transformation of facial suture: 0 = from proparian to opisthoparian; 1 = remains proparian; 2 = from proparian to gonatoparian.

NOTE -- Proparian condition of facial suture of the phacopid protaspides shows two variations of how far backwards the suture is extended, 'confined by anterior fixigenal spine' or 'extended backwards into midfixigenal spine'. These protaspid conditions seem to reflect holaspid condition of the facial suture. Trilobites with gonatoparian or opisthoparian suture in holaspides show the suture which is extended backwards into midfixigenal spine pair or behind halfway protaspid shield, while those with proparian suture in holaspides have the suture of the protaspides which is constantly delimited in front of the anterior fixigenal spine pair.

Taxa	Pa	Pb		M	H		T
Du	confined by afs	extended backwards	0	opisthoparian	opisthoparian	0	0
Fl	confined by afs	extended backwards	0	proparian	gonatoparian	2	2
Ca	confined by afs	confined by afs	1	proparian	proparian	1	1
Pr	confined by afs	confined by afs	1	proparian	proparian	1	1
Ps	confined by afs	confined by afs	1	proparian	proparian	1	1
Rp	confined by afs	confined by afs	1	proparian	proparian	1	1
Rs	confined by afs	confined by afs	1	proparian	proparian	1	1
Tc	confined by afs	confined by afs	1	proparian	proparian	1	1
Ka	confined by afs	confined by afs	1	N/A	proparian	1	1
Ly	confined by afs	confined by afs	1	N/A	proparian	1	1
Ph	NO INSTARS	confined by afs	1	proparian	proparian	1	1
Ce	NO INSTARS	confined by afs	1	proparian	proparian	1	1
Ac	NO INSTARS	confined by afs	1	proparian	proparian	1	1
Cy	NO INSTARS	confined by afs	1	proparian	proparian	1	1
Sp	confined by afs	NO INSTARS		proparian	proparian	1	1
Hc	confined by afs	NO INSTARS		proparian	proparian	1	1

22. Marginal Spines on Doublure

22-Pb) marginal spines in Pb: 0 = absent; 1 = unbifurcated; 2 = bifurcated.

22-T) ontogenetic transformation of marginal spines: 0 = entirely absent; 1 = present as unbifurcated form only in earlier ontogeny; 2 = present as bifurcated form only in earlier ontogeny.

NOTE -- No marginal spines are developed in Pa of all trilobites. The spines, if exist, appear with appearance of protopygidium and then disappear in later ontogeny.

Taxa	Pa	Pb		M	H	T
Du	absent	absent	0	absent	absent	0
Fl	absent	unbifurcated	1	disappear	disappear	1
Ca	absent	bifurcated	2	disappear	disappear	2
Pr	absent	absent	0	absent	absent	0
Ps	absent	absent	0	absent	absent	0
Rp	absent	bifurcated	2	bifurcated	disappear	2
Rs	absent	bifurcated	2	bifurcated	disappear	2
Te	absent	absent	0	absent	absent	0
Ka	absent	absent	0	N/A	absent	0
Ly	absent	absent	0	N/A	absent	0
Ph	NO INSTARS	unbifurcated	1	disappear	disappear	1
Ce	NO INSTARS	absent	0	absent	absent	0
Ac	NO INSTARS	absent	0	absent	absent	0
Cy	NO INSTARS	bifurcated	2	absent	disappear	2
Sp	absent	NO INSTARS		absent	absent	0
He	absent	NO INSTARS		absent	absent	0

23. Terrace Lines on Doublure

23-Pb) terrace lines on doublure in Pb: 0 = absent; 1 = present.

23-T) ontogenetic transformation of terrace lines on doublure: 0 = entirely absent; 1 = present only in protaspid period.

NOTE -- Only two trilobites, *Physemataspis insularis* and *Calyptaulax annulata*, acquire terrace lines on their incurved doublure at the same time that protopygidium appears, and lose them in later ontogeny. On the other hand, other trilobite larvae, even if regarded as benthic, do not have the terrace lines in the future tail portion as well as librigenae or rostral plate.

Taxa	Pa	Pb		M	H	T
Du	absent	absent	0	absent		0
Fl	absent	absent	0	absent		0
Ca	absent	terrace lines	1	absent		1
Pr	absent	absent	0	absent		0
Ps	absent	absent	0	absent		0
Rp	absent	absent	0	absent		0
Rs	absent	absent	0	absent		0
Tc	absent	absent	0	absent		0
Ka	absent	absent	0	absent		0
Ly	N/A	N/A	?	absent		?
Ph	NO INSTARS	terrace lines	1	absent		1
Cc	NO INSTARS	absent	0	absent		0
Ac	NO INSTARS	absent	0	absent		0
Cy	NO INSTARS	absent	0	absent		0
Sp	absent	NO INSTARS		absent		0
Hc	absent	NO INSTARS		absent		0

24. Number of Pygidial Rib Pair(s)

24-Pb) number of protopygidial rib pairs: 0 = one; 1 = two.

24-H) number of holaspid pygidial rib pairs: 0 = less than three; 1 = four; 2 = five; 3 = more than six.

NOTE -- Character state for Pb interval of the trilobites was determined by counting the protopygidial spine pairs which are an extension of pleural rib; the posteriormost pair of spines, represented by a tiny swelling pair, was not counted, since there is no corresponding pleural rib. In the trilobites which have more than one instars in 'Pb', the number of protopygidial ribs of the first instar in 'Pb' was chosen as a character. This is because the number of the first instar appears to be more informative than that of the last instar in 'Pb', considering the subsequent increment of the ribs throughout ontogeny. Ontogenetic transformation of this character appears to be inappropriate, since pygidial ribs subsequently are formed until accomplishing the holaspid number of each trilobite species. The pattern of increment, radical or continuous, might be considered as transformation character, only if meraspid materials are available enough to represent the whole meraspid period.

Taxa	Pa	Pb		M	H	
Du	protopygidium not differentiated	one to two	0	N/A	three	0
Fl	protopygidium not differentiated	two to four	1	N/A	seven	3
Ca	protopygidium not differentiated	two	1	N/A	eight	3
Pr	protopygidium not differentiated	one to two	0	N/A	five	2
Ps	protopygidium not differentiated	one to two	0	N/A	five	2
Rp	protopygidium not differentiated	one	0	N/A	four	1
Rs	protopygidium not differentiated	two	1	N/A	five	2
Te	protopygidium not differentiated	two	1	N/A	four	1
Ka	protopygidium not differentiated	two	1	N/A	three	0
Ly	protopygidium not differentiated	one	0	N/A	four	1
Ph	protopygidium not differentiated	one to three	0	N/A	six	3
Ce	protopygidium not differentiated	one	0	N/A	three	0
Ac	protopygidium not differentiated	one	0	N/A	two	0
Cy	protopygidium not differentiated	one to three	0	N/A	four	1
Sp	protopygidium not differentiated	NO INSTARS		N/A	three	0
He	protopygidium not differentiated	NO INSTARS		N/A	two	0

25. Pygidial Pleural Furrows

25-Pb) protopygidial pleural furrows: 0 = absent; 1 = present.

25-H) pygidial pleural furrows: 0 = present; 1 = absent.

25-T) ontogenetic transformation of pygidial pleural furrows: 0 = acquired and retained; 1 = entirely absent; 2 = ontogenetically lost.

25-Th) timing of appearance of 'pygidial pleural furrows': 0 = after segmentation of tergite; 1 = at appearance of protopygidium; 2 = entirely absent during ontogeny.

NOTE -- This character, along with character 24, is only applicable to the ontogenetic intervals after Pb.

Taxa	Pa	Pb		M	H		T	Th
Du	protopygidium not differentiated	absent	0	present	present	0	0	0
Fl	protopygidium not differentiated	present	1	present	present	0	0	1
Ca	protopygidium not differentiated	absent	0	present	present	0	0	0
Pr	protopygidium not differentiated	present	1	present	absent	1	2	1
Ps	protopygidium not differentiated	absent	0	absent	absent	1	1	2
Rp	protopygidium not differentiated	absent	0	absent	absent	1	1	2
Rs	protopygidium not differentiated	absent	0	absent	absent	1	1	2
Tc	protopygidium not differentiated	present	1	present	present	0	0	1
Ka	protopygidium not differentiated	absent	0	absent	absent	1	1	2
Ly	protopygidium not differentiated	absent	0	N/A	present	0	0	0
Ph	protopygidium not differentiated	absent	0	absent	absent	1	1	2
Cc	protopygidium not differentiated	absent	0	absent	present	0	0	0
Ac	protopygidium not differentiated	absent	0	absent	absent	1	1	2
Cy	protopygidium not differentiated	present	1	present	present	0	0	1
Sp	protopygidium not differentiated	NO INSTARS		absent	absent	1	1	2
Hc	protopygidium not differentiated	NO INSTARS		absent	absent	1	1	2

26. Pygidial Margin

26-H) holaspid pygidial margin: 0 = entire; 1 = spinose.

26-T) ontogenetic transformation of pygidial margin: 0 = acquires entire margin; 1 = remains spinose.

NOTE -- Pygidial margin of protaspides and meraspides is spinose throughout the phacopid trilobite taxa. The holaspid state of 'entire margin' is expressed by distinct marginal border as in *Dunderbergia anyta*, or the condition that the interpleural furrow does not reach the pygidial margin as in *Flexicalymene senaria* and *Calyptaulax annulata*.

Taxa	Pa	Pb	M	H		T
Du	protopygidium not differentiated	spinose	spinose	entire	0	0
Fl	protopygidium not differentiated	spinose	spinose	entire	0	0
Ca	protopygidium not differentiated	spinose	spinose	entire	0	0
Pr	protopygidium not differentiated	spinose	spinose	spinose	1	1
Ps	protopygidium not differentiated	spinose	spinose	spinose	1	1
Rp	protopygidium not differentiated	spinose	spinose	spinose	1	1
Rs	protopygidium not differentiated	spinose	spinose	spinose	1	1
Tc	protopygidium not differentiated	spinose	spinose	spinose	1	1
Ka	protopygidium not differentiated	spinose	spinose	spinose	1	1
Ly	protopygidium not differentiated	spinose	spinose	spinose	1	1
Ph	protopygidium not differentiated	spinose	spinose	spinose	1	1
Ce	protopygidium not differentiated	spinose	spinose	spinose	1	1
Ac	protopygidium not differentiated	spinose	spinose	spinose	1	1
Cy	protopygidium not differentiated	spinose	spinose	spinose	1	1
Sp	protopygidium not differentiated	spinose	spinose	spinose	1	1
He	protopygidium not differentiated	spinose	spinose	spinose	1	1

27. Hypostomal Spines

27-Pa) number of hypostomal spines in Pa: 0 = seven; 1 = nine.

27-Pb) number of hypostomal spines in Pb: 0 = seven; 1 = eight; 2 = six.

27-H) number of hypostomal spines in holaspides: 0 = none; 1 = two; 2 = seven; 3 = six; 4 = four.

27-T1) ontogenetic transformation in lateral hypostomal spine pairs (lsp): 0 = partially or completely lost; 1 = completely retained

27-T2) ontogenetic transformation in posteromedian spine (pms): 0 = lost; 1 = entirely absent; 2 = retained.

NOTE -- Protaspid hypostome of phacopid trilobites is spinose, the number of spines including lateral spine pairs and posteriormedian spine being variable with ingroup taxa. In later ontogeny, the spines are completely or partially lost, or retained. The entire number of protaspid hypostomal spines was employed as the characters for Pa and Pb. Holaspid number of hypostomal spines appears not to be accurately determined, since the remnants of the spines of some trilobites appear to be expressed by change in curvature of hypostomal outline. It is not clear that those remnants are homologous with the protaspid spines and thus, the remnants were not calculated into the spine number. As for ontogenetic transformation, the lateral spine pairs and the posteromedian spine were treated separately, since they pass through the different ontogenetic pathways.

Taxa	Pa		Pb		M	H		T1	T2
Du	3 lsp and 1 pms	0	3 lsp and 1 pms	0	3 lsp and 1 pms	none	0	0	0
Fl	4 lsp and 1 pms	1	4 lsp	1	4 lsp	1 lsp	1	0	0
Ca	3 lsp and 1 pms	0	3 lsp	2	2 lsp	none	0	0	0
Pr	N/A	?	3 lsp and 1 pms	0	3 lsp and 1 pms	3 lsp and 1 pms	2	1	2
Ps	3 lsp and 1 pms	0	3 lsp and 1 pms	0	3 lsp and 1 pms	3 lsp and 1 pms	2	1	2
Rp	N/A	?	N/A	?	N/A	3 lsp	3	1	?
Rs	N/A	?	N/A	?	N/A	3 lsp	3	1	?
Te	3 lsp and 1 pms	0	N/A	?	N/A	2 lsp	4	0	0
Ka	N/A	?	N/A	?	N/A	none	0	0	?
Ly	N/A	?	N/A	?	N/A	none	0	0	?
Ph	NO INSTARS		3 lsp	2	N/A	none	0	0	1
Ce	NO INSTARS		3 lsp	2	1 lsp	none	0	0	1
Ac	NO INSTARS		N/A	?	2 lsp	none	0	0	?
Cy	NO INSTARS		3 lsp and 1 pms	0	3 lsp and 1 pms	3 lsp and 1 pms	2	1	2
Sp	4 lsp and 1 pms	1	NO INSTARS		none	none	0	0	0
Hc	N/A	?	NO INSTARS		N/A	N/A	?	?	?

28. Posterior Border of Hypostome

28-H) posterior border of hypostome: 0 = not extended; 1 = extended; 2 = indented.

28-T) ontogenetic transformation of posterior border of hypostome: 0 = not extended; 1 = extended backwards in later ontogeny; 2 = indented in later ontogeny.

NOTE -- Posterior border is differentiated from middle body of hypostome with the appearance of protopygidium and is as broad (sagittally) as lateral border. However, the border is extended or indented in holaspides of some ingroup trilobites.

Taxa	Pa	Pb	M	H		T
Du	not differentiated	N/A	not extended	not extended	0	0
Fl	not differentiated	not extended	not extended	indented	2	2
Ca	not extended	not extended	extended	extended	1	1
Pr	N/A	not extended	extended	extended	1	1
Ps	not differentiated	N/A	extended	extended	1	1
Rp	N/A	N/A	N/A	not extended	0	0
Rs	N/A	N/A	N/A	not extended	0	0
Te	not differentiated	N/A	N/A	not extended	0	0
Ka	N/A	N/A	N/A	indented	2	2
Ly	N/A	N/A	N/A	extended	1	1
Ph	NO INSTARS	not extended	extended	extended	1	1
Ce	NO INSTARS	not extended	not extended	not extended	0	0
Ac	NO INSTARS	N/A	not extended	not extended	0	0
Cy	NO INSTARS	not extended	not extended	not extended	1	1
Sp	not differentiated	NO INSTARS	indented	indented	2	2
He	N/A	NO INSTARS	N/A	N/A	?	?

APPENDIX IV-2. Data matrices for cladistic analysis in this work. See Appendix IV-1 for abbreviations for the characters. Abbreviations for taxon name are: Du = *Dunderbergia anyta*; Fl = *Flexicalymene senaria*; Ca = *Calyptaulax annulata*; Pr = *Protopliomerella contracta*; Ps = *Pseudocybele nasuta*; Rp = *Rossaspis pliomeris*; Rs = *Rossaspis superciliosa*; Te = *Tesselacauda depressa*; Ka = *Kawina sexapugia*; Ly = *Lyrapyge ebriosus*; Ph = *Physemataspis insularis*; Ce = *Ceraurinella nahanniensis*; Ac = *Acanthoparypha evitti*; Cy = *Cybeloides cimelia*; Sp = *Sphaerexochus (Korolevium) arenosus*; He = *Heliomeroides freschaufae*. Abbreviations for data matrix: 'PA' = characters from Pa interval of protaspid period; 'PB' = characters from Pb interval of protaspid period; 'H' = characters from holaspid period; 'T' = ontogenetic transformation characters; 'TH' = including some heterochronic characters; 'T+' = including all transformation characters and some of instrantaneous characters which cannot be alternated with transformation characters.

APPENDIX II-1. Data matrix of 'PA'

	Du	Fl	Ca	Pr	Ps	Rp	Rs	Te	Ka	Ly	Ph	Ce	Ac	Cy	Sp	He
2-Pa	0	0	2	2	2	2	2	2	2	2	1	1	1	1	2	2
3-Pa	0	1	1	0	0	0	0	0	0	0					1	1
4-Pa	0	1	2	1	0	1	0	0	1	0					2	2
5-Pa	0	1	4	0	0	1	2	0	0	1					3	3
9-Pa	0	1	0	1	1	1	1	1	1	1					1	1
11-Pa	0	0	2	1	1	0	0	0	0	0					0	0
12-Pa	0	0	1	0	0	0	0	0	0	0					0	0
13-Pa	0	1	0	0	0	0	0	0	0	0					0	0
20-Pa	0	0	0	0	0	1	1	1	1	1					0	0
27-Pa	0	1	0	?	0	?	?	0	?	?					1	?

APPENDIX II-2. Data matrix of 'PB'

	Du	Fl	Ca	Pr	Ps	Rp	Rs	Te	Ka	Ly	Ph	Ce	Ac	Cy	Sp	Hc
2-Pb	0	0	1	0	0	1	1	1	1	1	0	1	1	0	2	2
5-Pb	0	1	0	0	0	1	1	1	1	0	1	1	1	0		
6-Pb	0	0	1	0	0	0	0	0	0	0	1	0	1	1		
7-Pb	0	0	1	0	0	0	0	0	0	0	0	0	0	0		
9-Pb	0	1	2	1	1	1	1	1	2	2	1	1	1	1		
10-Pb	0	1	0	0	0	0	0	0	0	1	1	1	1	1		
11-Pb	0	1	2	2	2	3	3	3	1	1	2	2	3	3		
12-pb	0	1	2	1	1	1	1	1	1	1	2	2	1	2		
13-Pb	0	1	1	0	0	1	1	1	?	0	1	0	0	1		
14-Pb	0	0	1	0	0	1	1	0	1	1	0	1	1	0		
16-Pb	0	1	1	0	0	0	0	0	0	0	1	0	1	1		
19-Pb	0	1	1	0	0	0	0	0	0	0	0	0	0	0		
20-Pb	0	1	1	0	0	0	0	0	0	0	1	0	0	0		
21-Pb	0	0	1	1	1	1	1	1	1	1	1	1	1	1		
22-Pb	0	1	2	0	0	2	2	0	0	0	1	0	0	2		
23-Pb	0	0	1	0	0	0	0	0	0	?	1	0	0	0		
24-Pb	0	1	1	0	0	0	1	1	1	0	0	0	0	0		
25-Pb	0	1	0	1	0	0	0	1	0	0	0	0	0	1		
27-Pb	0	1	2	0	0	?	?	?	?	?	2	2	?	0		

APPENDIX II-3. Data matrix of 'H'

	Du	Fl	Ca	Pr	Ps	Rp	Rs	Te	Ka	Ly	Ph	Ce	Ac	Cy	Sp	Hc
5-H	0	0	2	0	1	1	1	1	0	2	2	1	3	2	3	3
6-H	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0
8-H	0	0	2	1	1	1	1	1	0	1	1	1	0	1	1	1
14-H	0	0	0	1	1	1	1	1	0	1	1	2	2	2	2	0
15-H	0	1	1	0	0	0	0	0	1	2	1	0	1	2	1	1
17-H	0	0	1	0	0	0	0	0	1	0	0	1	1	1	1	1
18-H	0	0	2	1	1	1	1	1	0	0	2	0	0	0	0	0
19-H	0	1	1	2	2	2	2	2	2	0	0	2	1	0	1	1
21-H	0	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1
24-H	0	3	3	2	2	1	2	1	0	1	3	0	0	1	0	0
25-H	0	0	0	1	1	1	1	0	1	0	1	0	1	0	1	1
26-H	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
27-H	0	1	0	2	2	3	3	4	0	0	0	0	0	2	0	?
28-H	0	2	1	1	1	0	0	0	2	1	1	0	0	1	2	?

APPENDIX II-4. Data matrix of 'T'

	Du	Fl	Ca	Pr	Ps	Rp	Rs	Te	Ka	Ly	Ph	Ce	Ac	Cy	Sp	He
1-T	0	0	0	0	0	0	0	0	0	0	1	1	1	1	2	2
3-T	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1
5-T	0	0	1	0	0	0	0	0	0	1	1	0	2	1	2	2
6-T	0	1	1	0	0	1	1	1	0	0	1	0	1	1	0	0
7-T	0	1	1	0	0	1	1	0	0	0	1	0	0	1	0	0
8-T	0	0	0	1	1	1	1	1	0	1	1	1	0	1	1	1
9-T	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1
10-T	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
11-T	0	0	2	2	2	1	1	1	1	0	2	2	1	1	0	0
13-T	0	1	1	0	0	1	1	1	?	0	1	0	0	1	0	0
14-T	0	0	1	2	2	2	2	2	1	2	2	3	3	3	3	0
16-T	0	1	1	0	0	1	1	1	1	0	1	0	1	1	?	1
18-T	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0
19-T	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	1
20-T	0	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2
21-T	0	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1
22-T	0	1	2	0	0	2	2	0	0	0	1	0	0	2	0	0
23-T	0	0	1	0	0	0	0	0	0	?	1	0	0	0	0	0
25-T	0	0	0	2	1	1	1	0	1	0	1	0	1	0	1	1
26-T	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
27-T1	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	?
27-T2	0	0	0	2	2	?	?	0	?	?	1	1	?	2	0	?
28-T	0	2	1	1	1	0	0	0	2	1	1	0	0	1	2	?

APPENDIX II-5. Data matrix of 'TH'.

	Du	Fl	Ca	Pr	Ps	Rp	Rs	Tc	Ka	Ly	Ph	Cc	Ac	Cy	Sp	Hc
1-Th	0	0	0	0	0	0	0	0	0	0	1	1	1	1	2	2
3-Th	0	1	1	0	0	0	0	0	0	0	?	2	2	2	1	1
4-Th	0	1	1	1	0	1	0	0	1	0	2	2	2	2	3	3
5-T	0	0	1	0	0	0	0	0	0	1	1	0	2	1	2	2
6-Th	0	2	1	0	0	2	2	2	0	0	1	0	1	1	0	0
7-Th	0	2	1	0	0	2	2	0	0	0	2	0	0	2	0	0
8-T	0	0	0	1	1	1	1	1	0	1	1	1	0	1	1	1
9-Th	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1
10-Th	0	1	0	0	0	0	0	0	0	1	2	2	2	2	0	0
11-T	0	0	2	2	2	1	1	1	1	0	2	2	1	1	0	0
13-T	0	1	1	0	0	1	1	1	?	0	1	0	0	1	0	0
14-Th	0	0	1	2	2	1	1	2	1	1	2	1	1	2	2	0
16-Th	0	1	1	0	0	2	2	2	2	0	1	0	2	1	?	2
18-T	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0
19-T	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	1
20-Th	0	1	3	0	0	2	2	2	2	2	3	0	0	0	3	3
21-T	0	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1
22-T	0	1	2	0	0	2	2	0	0	0	1	0	0	2	0	0
23-T	0	0	1	0	0	0	0	0	0	?	1	0	0	0	0	0
25-Th	0	1	0	1	2	2	2	1	2	0	2	0	2	1	2	2
26-T	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
27-T1	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	?
27-T2	0	0	0	2	2	?	?	0	?	?	1	1	?	2	0	?
28-T	0	2	1	1	1	0	0	0	2	1	1	0	0	1	2	?

APPENDIX II-6--Data matrix of 'T+'

	Du	Fl	Ca	Pr	Ps	Rp	Rs	Te	Ka	Ly	Ph	Ce	Ac	Cy	Sp	He
1-T	0	0	0	0	0	0	0	0	0	0	1	1	1	1	2	2
2-Pa	0	0	2	2	2	2	2	2	2	2	1	1	1	1	2	2
2-Pb	0	0	1	0	0	1	1	1	1	1	0	1	1	0	2	2
3-T	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1
5-T	0	0	1	0	0	0	0	0	0	1	1	0	2	1	2	2
6-T	0	1	1	0	0	1	1	1	0	0	1	0	1	1	0	0
7-T	0	1	1	0	0	1	1	0	0	0	1	0	0	1	0	0
8-T	0	0	0	1	1	1	1	1	0	1	1	1	0	1	1	1
9-T	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1
10-T	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
11-T	0	0	2	2	2	1	1	1	1	0	2	2	1	1	0	0
13-T	0	1	1	0	0	1	1	1	?	0	1	0	0	1	0	0
14-T	0	0	1	2	2	2	2	2	1	2	2	3	3	3	3	0
15-H	0	1	1	0	0	0	0	0	1	2	1	0	1	2	1	1
16-T	0	1	1	0	0	1	1	1	1	0	1	0	1	1	?	1
17-H	0	0	1	0	0	0	0	0	1	0	0	1	1	1	1	1
18-T	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0
19-T	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	1
20-T	0	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2
21-T	0	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1
22-T	0	1	2	0	0	2	2	0	0	0	1	0	0	2	0	0
23-T	0	0	1	0	0	0	0	0	0	?	1	0	0	0	0	0
25-T	0	0	0	2	1	1	1	0	1	0	1	0	1	0	1	1
26-T	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
27-T1	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	?
27-T2	0	0	0	2	2	?	?	0	?	?	1	1	?	2	0	?
28-T	0	2	1	1	1	0	0	0	2	1	1	0	0	1	2	?

APPENDIX IV-3. Quantitative information on shortest trees derived from modified data sets with various numbers of trilobite taxa. (R = minimum number of evolutionary steps; L = tree length; e = extra steps; CI = consistency index; RC = rescaled consistency index)

16 Taxa

DATA	# of char.	# of tree	R	L	e (L-R)	CI (R/L)	RC
H	12	38	23	39	16	0.590	0.427
T	17	2	26	52	26	0.500	0.314
TH	18	111	33	70	37	0.471	0.264
T+	22	97	36	77	41	0.468	0.276

14 taxa (exclude *Sphaerexochus* and *Heliomeroides*)

DATA	# of char.	# of tree	R	L	e (L-R)	CI (R/L)	RC	character congruence	
								within data sets	between data sets
PB	16	67	21	50	29	0.420	0.194		
H	14	3	29	47	18	0.617	0.422		
PB+H	30	7	50	103	53	0.485	0.254	0.456	0.058
T	19	11	28	56	28	0.500	0.281		
TH	21	1	36	74	38	0.486	0.276		
T+	25	3	38	81	43	0.469	0.252		

12 Taxa (exclude *Physemataspis*, *Cybeloides*, *Acanthoparypha*, and *Ceraurinella*)

DATA	# of char.	# of tree	R	L	e (L-R)	CI (R/L)	RC	character congruence	
								within data sets	between data sets
PA	9	32	14	19	5	0.737	.0532		
H	12	2	21	28	7	0.750	0.608		
PA+H	21	10	35	52	17	0.673	0.465	0.231	0.096
T	17	2	25	38	13	0.658	0.459		
TH	18	2	29	49	20	0.592	0.355		
T+	22	4	34	53	19	0.642	0.438		

10 Taxa (exclude *Physemataspis*, *Cybeloides*, *Acanthoparypha*, *Ceraurinella*, *Sphaerexochus*, *Heliomeroides*)

DATA	# of char.	# of tree	R	L	e (L-R)	CI (R/L)	RC	character congruence	
								within data sets	between data sets
PA	9	32	13	18	5	0.722	0.444		
PB	16	1	21	33	12	0.636	0.382		
H	13	2	25	33	8	0.758	0.574		
PA+PB	25	6	34	53	19	0.642	0.358	0.321	0.038
PA+H	22	1	38	54	16	0.704	0.459	0.241	0.056
PB+H	29	5	46	72	26	0.639	0.375	0.278	0.083
PA+PB+H	38	7	59	93	34	0.634	0.351	0.269	0.097
T	19	9	26	41	15	0.634	0.408		
TH	20	5	31	52	21	0.594	0.346		
T+	24	3	34	54	20	0.630	0.392		

9 Taxa (exclude *Rossaspis superciliosa* from the above data sets with 10 taxa)

DATA	# of char.	# of tree	R	L	e (L-R)	CI (R/L)	RC	character congruence	
								within data sets	between data sets
PA	9	12	12	17	5	0.706	0.412		
PB	16	4	21	33	12	0.636	0.331		
H	13	2	25	33	8	0.758	0.541		
PA+PB	25	2	33	51	18	0.647	0.332	0.333	0.020
PA+H	22	2	37	53	16	0.698	0.419	0.245	0.057
PB+H	29	3	46	70	24	0.657	0.360	0.286	0.057
PA+PB+H	38	4	58	90	32	0.644	0.327	0.278	0.078
T	19	9	26	41	15	0.634	0.362		
TH	20	8	31	52	21	0.596	0.298		
T+	24	3	34	53	19	0.642	0.371		

8 Taxa (exclude *Pseudocybele* from the above data set with 9 taxa)

DATA	# of char.	# of tree	R	L	e (L-R)	CI (R/L)	RC	character congruence	
								within data sets	between data sets
PA	9	164	12	17	5	0.706	0.353		
PB	16	3	21	33	12	0.636	0.304		
H	13	7	25	33	8	0.758	0.494		
PA+PB	25	2	33	51	18	0.647	0.294	0.333	0.020
PA+H	22	5	37	52	15	0.712	0.388	0.250	0.038
PB+H	29	2	46	69	23	0.667	0.333	0.290	0.043
PA+PB+H	38	6	58	89	31	0.652	0.291	0.281	0.067
T	19	3	26	40	14	0.650	0.347		
TH	20	1	31	50	19	0.620	0.283		
T+	24	2	34	52	18	0.654	0.344		

7 Taxa (exclude *Rossaspis pliomeris* from the above data sets with 8 taxa)

DATA	# of char.	# of tree	R	L	e (L-R)	CI (R/L)	RC	character congruence	
								within data sets	between data sets
PA	9	7	12	16	4	0.750	0.375		
PB	16	2	21	30	9	0.700	0.350		
H	13	5	24	31	7	0.774	0.473		
PA+PB	25	11	33	49	16	0.673	0.259	0.265	0.061
PA+H	22	5	36	49	13	0.735	0.367	0.224	0.041
PB+H	29	1	45	64	19	0.703	0.332	0.250	0.047
PA+PB+H	38	1	57	82	25	0.695	0.300	0.244	0.061
T	19	3	26	36	10	0.722	0.378		
TH	20	2	31	45	14	0.689	0.303		
T+	24	2	34	48	14	0.708	0.366		

6 Taxa (exclude *Kawina* from the above data sets with 7 taxa)

DATA	# of char.	# of tree	R	L	e (L-R)	CI (R/L)	RC	character congruence	
								within data sets	between data sets
PA	9	2	12	15	3	0.800	0.400		
PB	16	1	21	29	8	0.724	0.338		
H	13	1	24	26	2	0.923	0.769		
PA+PB	25	1	33	46	13	0.717	0.273	0.239	0.043
PA+H	22	1	36	43	7	0.837	0.512	0.116	0.047
PB+H	29	1	45	57	10	0.789	0.439	0.175	0.000
PA+PB+H	38	1	57	74	17	0.770	0.373	0.176	0.054
T	19	1	25	31	6	0.806	0.522		
TH	20	1	30	40	10	0.750	0.393		
T+	24	2	33	42	9	0.786	0.464		

5 Taxa (exclude *Tesselacauda* from the above data sets with 6 taxa)

DATA	# of char.	# of tree	R	L	e (L-R)	CI (R/L)	RC	character congruence	
								within data sets	between data sets
PA	9	4	12	15	3	0.800	0.320		
PB	16	5	20	27	7	0.741	0.269		
H	13	1	22	23	1	0.957	0.797		
PA+PB	25	2	32	42	10	0.762	0.286	0.238	0.000
PA+H	22	1	34	39	5	0.872	0.476	0.103	0.026
PB+H	29	1	42	50	8	0.840	0.445	0.160	0.000
PA+PB+H	38	1	54	66	12	0.818	0.372	0.167	0.015
T	19	1	24	27	3	0.889	0.646		
TH	20	1	28	35	7	0.800	0.333		
T+	24	1	32	37	5	0.865	0.556		

4 Taxa (exclude *Calyptaulax* from the above data sets with 5 taxa)

DATA	# of char.	# of tree	R	L	e (L-R)	CI (R/L)	RC	character congruence	
								within data sets	between data sets
PA	8	3	8	10	2	0.800	0.267		
PB	14	3	16	18	2	0.889	0.296		
H	12	1	19	19	0	1.000	1.000		
PA+PB	22	3	24	28	4	0.857	0.286	0.143	0.000
PA+H	20	1	27	29	2	0.931	0.621	0.069	0.000
PB+H	26	1	35	37	2	0.946	0.631	0.054	0.000
PA+PB+H	34	1	43	47	4	0.915	0.508	0.085	0.000
T	19	1	22	22	0	1.000	1.000		
TH	20	2	24	27	3	0.889	0.356		
T+	23	1	29	29	0	1.000	1.000		

APPENDIX V-1. Morphologic deviations of Hystricurus species from the type species (Hystricurus conicus).

morphologic features	type species	deviations in other *Hystricurus* species
width of anterior cranidial border	uniform	'sagittally broader' in Hystricurus paucituberculatus (Fortey, 1983, pl. 23, fig. 7)
anterior facial suture	slightly divergent	'forwardly convergent' in Hystricurus penchiensis (Zhou and Fortey, 1986, pl. 1, fig. 5)
glabellar furrows	less distinct and confined within the glabella	'connected with axial furrow' in Hystricurus genalatus (Ross, 1951, pl. 8, fig. 11)
posterior fixigenal area	slender	'broad and triangular' in Hystricurus paucituberculatus (Fortey, 1983, pl. 23, fig. 1)
exoskeleton	tuberculate	'smooth' in Hystricurus politus, see Ross, 1951b, pl. 9, fig. 28)
eye ridge	absent	'present' in Hystricurus penchiensis (Kuo et al., 1982, pl. 1, fig. 8)
occipital spine	absent	'present' in Hystricurus armatus (Poulsen, 1937, pl. 2, fig. 3)
spines on posterior border	absent	'present' in Hystricurus flectimembrus (Ross, 1951, pl. 10, fig. 33)
pygidial marginal border	less convex	'distinct and convex' in pygidia tentatively assigned to Hystricurus (Ross, 1951, pl. 9, figs 1-13, 17-19)

TABLE V-2. (continued)

Au	Sc	Ca	Ot	Di	Ba	Pr
none	two pairs	three pairs	three pairs	two pairs		
three pairs	one pair	three pairs	four pairs	four pairs		
none	none	three pairs	three pairs	three pairs		
one pairs	two pairs	two pairs	one pair	three pairs		
none	five pairs	none	two pairs	two pairs		
one pair	seven pairs	none	none	none		
none	seven pairs	none	none	two pairs		
absent	absent	present	absent	present		
	additional pairs on pygidial pleural region		pygidial pair coalesced			
one (?)	?	two	two	three	two	two
laterally inflated	forward-tapering	laterally inflated	laterally inflated	laterally inflated	forward-tapering	forward-tapering
absent	absent	absent	absent	absent	3 pairs, dis-continuous	2 pairs, dis-continuous
convergent forwards	divergent forwards	divergent forwards	convergent forwards	convergent forwards	convergent forwards	convergent forwards
broad	broad	broad	absent	broad	short	absent

CHAPTER VI

GENERAL DISCUSSION

Each subject of four papers grouped in this volume is relevant to significant issues in the field of systematic biology and/or trilobite research. It seems desirable to further discuss these relevant issues, which certainly helps the author to realize the limit of his knowledge and thus, provides a guide for the future studies. Three issues are worth being further discussed: "homology", "a role of ontogeny in phylogenetic systematics", and the "ptychopariid problem".

Homology is, without any doubt, a central theme of comparative biology (de Beer, 1971; Patterson, 1982; de Pinna, 1991), but its definition and recognition are still in dispute (e.g., de Pinna, 1991). Patterson (1982) excellently summarized several criteria and definitions of homology. It has been generally admitted that homology is a relationship between structures of different organisms (but operationally replaced by an observable feature), and it is a hypothesis to be tested. The homology of 'Lp' in Chapter II is recognized by a topographical similarity; the posteriormost axial lobe (Lp) of all phacopid trilobites is assumed homologous and thus, 'Lp' may determine the grouping of all phacopids. This is de Pinna's (1991) 'primary' homology and thus should be tested by congruence in order to logically justify the homology proposition. The homology of 'Lp' implicitly assumes that all variations of the lobe, which are detected among different trilobite taxa and different ontogenetic intervals, are homologous, just as de Pinna (1991, p. 375) said, "Recognition of the character 'hair' itself implies a grouping called mammals, i.e. a hypothesis of monophyly derived from the conjecture of homology among the various expressions of the attribute hair." (underlined by author). One possible way to put 'Lp' into the congruence test is to introduce another feature which is presumed to be homologous to the lobe, e.g. telson of insects. This might imply

9. Position of Anterior Fixigenal Spine Pair

9-Pa) position of anterior fixigenal spine in Pa: 0 = behind S3; 1 = in front of S3.

9-Pb) position of anterior fixigenal spine in Pb: 0 = absent; 1 = in front of S3.

9-T) ontogenetic transformation of the position of anterior fixigenal spine: 0 = remains behind S3 and disappears later; 1 = moves backwards and disappears later.

9-Th) timing of acquisition of 'behind S3' position of anterior fixigenal spine pair: 0 = at calcification; 1 = after segmentation of tergite.

NOTE -- All ingroup trilobites lose the spine pair during meraspid period, while the outgroup loses it across Pa and Pb. Anterior fixigenal spine pair of phacopid protaspides is located immediately next to palpebral lobe. Its position with reference to S3 varies with different trilobites. With growth, the spine pair continuously moves backwards due to enlargement and/or backward movement of palpebral lobe, until it disappears in the meraspid period. Character state for Pa of *Calyptaulax annulata*, *Sphaerexochus arenosus* and *Heliomeroides freschaufae* lacking protoglabellar furrows, was determined by comparisons of the relative position with other protaspides; e.g., the spine pair of the first species is more posteriorly placed and thus, the state was defined as 'behind S3'. Ontogenetic transformation of this character was defined for the interval during which the spine pair exists, without regard to the timing difference in the disappearance of the spine pair.

Taxa	Pa		Pb		M	H	T	Th
Du	behind S3	0	absent	0	absent	absent	0	0
Fl	in front of S3	1	in front of S3	1	behind S3	absent	1	1
Ca	behind S3	0	behind S3	2	behind S3	absent	0	0
Pr	in front of S3	1	in front of S3	1	behind S3	absent	1	1
Ps	in front of S3	1	in front of S3	1	behind S3	absent	1	1
Rp	in front of S3	1	in front of S3	1	behind S3	absent	1	1
Rs	in front of S3	1	in front of S3	1	behind S3	absent	1	1
Tc	in front of S3	1	in front of S3	1	behind S3	absent	1	1
Ka	in front of S3	1	behind S3	2	behind S3	absent	1	1
Ly	in front of S3	1	behind S3	2	N/A	absent	1	1
Ph	NO INSTARS		in front of S3	1	behind S3	absent	1	1
Ce	NO INSTARS		in front of S3	1	behind S3	absent	1	1
Ac	NO INSTARS		in front of S3	1	behind S3	absent	1	1
Cy	NO INSTARS		in front of S3	1	behind S3	absent	1	1
Sp	in front of S3	1	NO INSTARS		behind S3	absent	1	1
He	in front of S3	1	NO INSTARS		behind S3	absent	1	1

23. Terrace Lines on Doublure

23-Pb) terrace lines on doublure in Pb: 0 = absent; 1 = present.

23-T) ontogenetic transformation of terrace lines on doublure: 0 = entirely absent; 1 = present only in protaspid period.

NOTE -- Only two trilobites, *Physemataspis insularis* and *Calyptaulax annulata*, acquire terrace lines on their incurved doublure at the same time that protopygidium appears, and lose them in later ontogeny. On the other hand, other trilobite larvae, even if regarded as benthic, do not have the terrace lines in the future tail portion as well as librigenae or rostral plate.

Taxa	Pa	Pb		M H	T
Du	absent	absent	0	absent	0
Fl	absent	absent	0	absent	0
Ca	absent	terrace lines	1	absent	1
Pr	absent	absent	0	absent	0
Ps	absent	absent	0	absent	0
Rp	absent	absent	0	absent	0
Rs	absent	absent	0	absent	0
Tc	absent	absent	0	absent	0
Ka	absent	absent	0	absent	0
Ly	N/A	N/A	?	absent	?
Ph	NO INSTARS	terrace lines	1	absent	1
Ce	NO INSTARS	absent	0	absent	0
Ac	NO INSTARS	absent	0	absent	0
Cy	NO INSTARS	absent	0	absent	0
Sp	absent	NO INSTARS		absent	0
Hc	absent	NO INSTARS		absent	0

6 Taxa (exclude Kawina from the above data sets with 7 taxa)

DATA	# of char.	# of tree	R	L	c (L-R)	CI (R/L)	RC	character congruence	
								within data sets	between data sets
PA	9	2	12	15	3	0.800	0.400		
PB	16	1	21	29	8	0.724	0.338		
H	13	1	24	26	2	0.923	0.769		
PA+PB	25	1	33	46	13	0.717	0.273	0.239	0.043
PA+H	22	1	36	43	7	0.837	0.512	0.116	0.047
PB+H	29	1	45	57	10	0.789	0.439	0.175	0.000
PA+PB+H	38	1	57	74	17	0.770	0.373	0.176	0.054
T	19	1	25	31	6	0.806	0.522		
TH	20	1	30	40	10	0.750	0.393		
T+	24	2	33	42	9	0.786	0.464		

5 Taxa (exclude Tesselacauda from the above data sets with 6 taxa)

DATA	# of char.	# of tree	R	L	c (L-R)	CI (R/L)	RC	character congruence	
								within data sets	between data sets
PA	9	4	12	15	3	0.800	0.320		
PB	16	5	20	27	7	0.741	0.269		
H	13	1	22	23	1	0.957	0.797		
PA+PB	25	2	32	42	10	0.762	0.286	0.238	0.000
PA+H	22	1	34	39	5	0.872	0.476	0.103	0.026
PB+H	29	1	42	50	8	0.840	0.445	0.160	0.000
PA+PB+H	38	1	54	66	12	0.818	0.372	0.167	0.015
T	19	1	24	27	3	0.889	0.646		
TH	20	1	28	35	7	0.800	0.333		
T+	24	1	32	37	5	0.865	0.556		

4 Taxa (exclude Calyptaulax from the above data sets with 5 taxa)

DATA	# of char.	# of tree	R	L	c (L-R)	CI (R/L)	RC	character congruence	
								within data sets	between data sets
PA	8	3	8	10	2	0.800	0.267		
PB	14	3	16	18	2	0.889	0.296		
H	12	1	19	19	0	1.000	1.000		
PA+PB	22	3	24	28	4	0.857	0.286	0.143	0.000
PA+H	20	1	27	29	2	0.931	0.621	0.069	0.000
PB+H	26	1	35	37	2	0.946	0.631	0.054	0.000
PA+PB+H	34	1	43	47	4	0.915	0.508	0.085	0.000
T	19	1	22	22	0	1.000	1.000		
TH	20	2	24	27	3	0.889	0.356		
T+	23	1	29	29	0	1.000	1.000		

2) Hystricuridae should be assigned to the Order Proetida, as suggested by Fortey and Owens (1975), and should be excluded from the Ptychopariina. The Hystricuridae is the earliest (mainly of Tremadocian age) family of the Proetida and stratophenetically, separated from Upper Cambrian ptychopariid superfamilies such as Solenopleuracea or Catillicephalacea.

3) Two informal groups within the Hystricuridae are recognized, which could be separate subfamilies; one is characterized by a protaspis with tuberculation, a laterally inflated glabella, and no glabellar furrows, and the other has glabellar furrows (regardless of transglabellar or discontinuous), a forward-tapering glabella, an indented posterior margin, and no tuberclation.

4) Paraplethopeltis, sensu Bridge and Cloud (1947), does not constitute a genus (or subgenus) of the Hystricuridae and should be reassigned to the Plethopeltidae Raymond, 1925 as in the Treatise (Moore, 1959). The species assigned to 'Paraplethopeltis' belong to the Hystricuridae.

5) Hyperbolochilus is assigned to the Hystricuridae.

PHYLOGENETIC IMPLICATIONS

The above taxonomic conclusions have significant implications for our understanding of the evolution and phylogenetics of proetid trilobites. First of all, the distinct impression of a preglabellar furrow on hystricurid protaspides, regardless of presence of preglabellar field, reinforces the monophyly of the Proetida, since the glabella of most Cambrian ptychopariid protaspides overhang the anterior shield margin. Similarly, Fortey (1990) suggested that a proetid type protaspis, with a fusiform, anteriorly rounded or pointed glabella is a diagnostic character for the Proetida, derived from the forward-expanding axis, reaching far forwards, of the ptychopariid protaspis (Fortey, 1990, text-fig. 10. h-m).

The supposed two informal groups of the Hystricuridae, which are mainly discriminated by protaspid morphologies, demonstrate that

that the test of homology requires a third taxon, since homology recognition is a comparative procedure.

The second issue is the role of ontogeny in phylogeny. Ontogeny consists of a series of growth stages of an organism and thus, in ontogeny, a morphologic feature sequentially changes during an individual's life cycle. Such an ontogenetic sequence, whether continuous (Alberch et al., 1979) or discontinuous (Alberch, 1985), has been recognized as an evolutionary process which is recapitulated by phylogeny (Gould, 1977) within the heterochronic context. Another fundamental aspect is that ontogeny provides a catalog of characters (Mabee, 1989), so that we can choose a character from a certain interval which is a part of ontogeny. So far, the emphasis has been placed on that causal mechanism of evolutionary change rather than on the elucidation of particular phylogenetic relationships (Atkinson, 1992) using ontogeny. How, thus, can we elucidate phylogenetic relationship of organisms using ontogenetic information? Obviously, using characters from a certain ontogenetic interval does not necessarily require the ontogenetic sequence, only comparability of that interval across the taxa involved in the analysis is required. Two possible cladistic approaches were proposed in Chapter IV, the character combination approach and the adoption of ontogenetic transformation character concept, whereby the ontogenetic information is utilized as fully as possible and the 'incongruence' between larval and adult phylogeny is resolved. In that chapter, it was implied that heterochronic information is not necessarily introduced, where the ontogenetic transformation is used as a character; most heterochronic characters in this analysis are shifts of timing of appearance, not rates of development. It is obvious that the interpretation of heterochronic process requires a known phylogenetic framework. However, the phylogenetic relationships disclosed by ontogenetic transformation characters might be able to directly reveal the heterochronic process. For example, a clade A is defined by a-b-c-d (ontogenetic sequence) and a more inclusive clade A+B is defined by a-b-c-d-e (Figure VI-1). There can be assumed to be an evolutionary change from a-b-c-d-e to a-b-c-d between the internodes (unknown

10. Orientation of Posterior Fixigenal Spine (Genal Spine) Pair

10-Pb) orientation of posterior fixigenal spine pair in Pb: 0 = parallel; 1 = divergent.

10-T) ontogenetic transformation of orientation of genal spine pair: 0 = from parallel to divergent; 1 = remains divergent.

10-Th) timing of acquisition of 'divergent' orientation of posterior fixigenal spine pair: 0 = after segmentation of tergite; 1 = at appearance of protopygidium; 2 = at calcification.

NOTE -- Protaspides of Pa and holaspides of all trilobites display 'parallel' and 'divergent' orientation, respectively.

Taxa	Pa	Pb		M	H	T	Th
Du	parallel	parallel	0	divergent	divergent	0	0
Fl	parallel	divergent	1	divergent	divergent	0	1
Ca	parallel	parallel	0	parallel	divergent	0	0
Pr	parallel	parallel	0	parallel	divergent	0	0
Ps	parallel	parallel	0	parallel	divergent	0	0
Rp	parallel	parallel	0	parallel	divergent	0	0
Rs	parallel	parallel	0	parallel	divergent	0	0
Te	parallel	parallel	0	parallel	divergent	0	0
Ka	parallel	parallel	0	parallel	divergent	0	0
Ly	parallel	divergent	1	N/A	divergent	1	1
Ph	NO INSTARS	divergent	1	divergent	divergent	1	2
Ce	NO INSTARS	divergent	1	divergent	divergent	1	2
Ac	NO INSTARS	divergent	1	divergent	divergent	1	2
Cy	NO INSTARS	divergent	1	divergent	divergent	1	2
Sp	parallel	NO INSTARS		divergent	divergent	1	0
He	parallel	NO INSTARS		divergent	divergent	1	0

24. Number of Pygidial Rib Pair(s)
24-Pb) number of protopygidial rib pairs: 0 = one; 1 = two.
24-H) number of holaspid pygidial rib pairs: 0 = less than three; 1 = four; 2 = five; 3 = more than six.

NOTE -- Character state for Pb interval of the trilobites was determined by counting the protopygidial spine pairs which are an extension of pleural rib; the posteriormost pair of spines, represented by a tiny swelling pair, was not counted, since there is no corresponding pleural rib. In the trilobites which have more than one instars in 'Pb', the number of protopygidial ribs of the first instar in 'Pb' was chosen as a character. This is because the number of the first instar appears to be more informative than that of the last instar in 'Pb', considering the subsequent increment of the ribs throughout ontogeny. Ontogenetic transformation of this character appears to be inappropriate, since pygidial ribs subsequently are formed until accomplishing the holaspid number of each trilobite species. The pattern of increment, radical or continuous, might be considered as transformation character, only if meraspid materials are available enough to represent the whole meraspid period.

Taxa	Pa	Pb		M	H	
Du	protopygidium not differentiated	one to two	0	N/A	three	0
Fl	protopygidium not differentiated	two to four	1	N/A	seven	3
Ca	protopygidium not differentiated	two	1	N/A	eight	3
Pr	protopygidium not differentiated	one to two	0	N/A	five	2
Ps	protopygidium not differentiated	one to two	0	N/A	five	2
Rp	protopygidium not differentiated	one	0	N/A	four	1
Rs	protopygidium not differentiated	two	1	N/A	five	2
Te	protopygidium not differentiated	two	1	N/A	four	1
Ka	protopygidium not differentiated	two	1	N/A	three	0
Ly	protopygidium not differentiated	one	0	N/A	four	1
Ph	protopygidium not differentiated	one to three	0	N/A	six	3
Ce	protopygidium not differentiated	one	0	N/A	three	0
Ac	protopygidium not differentiated	one	0	N/A	two	0
Cy	protopygidium not differentiated	one to three	0	N/A	four	1
Sp	protopygidium not differentiated	NO INSTARS		N/A	three	0
He	protopygidium not differentiated	NO INSTARS		N/A	two	0

APPENDIX V-1. Morphologic deviations of Hystricurus species from the type species (Hystricurus conicus).

morphologic features	type species	deviations in other *Hystricurus* species
width of anterior cranidial border	uniform	'sagittally broader' in Hystricurus paucituberculatus (Fortey, 1983, pl. 23, fig. 7)
anterior facial suture	slightly divergent	'forwardly convergent' in Hystricurus penchiensis (Zhou and Fortey, 1986, pl. 1, fig. 5)
glabellar furrows	less distinct and confined within the glabella	'connected with axial furrow' in Hystricurus genalatus (Ross, 1951, pl. 8, fig. 11)
posterior fixigenal area	slender	'broad and triangular' in Hystricurus paucituberculatus (Fortey, 1983, pl. 23, fig. 1)
exoskeleton	tuberculate	'smooth' in Hystricurus politus, see Ross, 1951b, pl. 9, fig. 28)
eye ridge	absent	'present' in Hystricurus penchiensis (Kuo et al., 1982, pl. 1, fig. 8)
occipital spine	absent	'present' in Hystricurus armatus (Poulsen, 1937, pl. 2, fig. 3)
spines on posterior border	absent	'present' in Hystricurus flectimembrus (Ross, 1951, pl. 10, fig. 33)
pygidial marginal border	less convex	'distinct and convex' in pygidia tentatively assigned to Hystricurus (Ross, 1951, pl. 9, figs 1-13, 17-19)

there might have been two separate lineages of proetids during Lower Ordovician (Figure V-10). The first lineage is characterized by development of tuberculation pattern on protaspid shield, which might be an evolutionary novelty (putative synapomorphy) derived from Upper Cambrian ptychopariid (a probable sistergroup) with smooth protaspid shield. Among the younger proetid families, in particular, dimeropygid protaspides (e.g. Dimeropyge speyeri, see Chatterton, 1994, fig. 3) are much more similar to protaspides of Hystricurus paragenalatus (Figure V-2.2) than any other hystricurid protaspides, in having no inner series of tubercles on protopygidium, a more rounded outline, and relatively deep anterior border furrow. Compared to degree 5 meraspis of Parahystricurus carinatus, the M3 of D. speyeri shares long spine(s) on the thoracic segment(s) and three main series of tubercles on the whole carapace. These similarities further confirm that dimeropygids were derived from or are the immediate sistergroup to the first informal group of hystricurids. Chatterton (1994, fig. 1), in his cladistic analysis, presented that dimeropygid trilobites share three pygidial axial rings which appears to have been derived from more than three (in general, four) rings of hystricurids.

Whittington and Campbell (1967, p. 450) noticed that Dimeropyge and Otarion show a similar development. Later, Fortey and Owens (1975, p. 230-231) extended the similarity into such hystricurid species as Hystricurus paragenalatus. Protaspides of these taxa share a similar pattern of tuberculation, including the lack of an inner series of tubercles on the protopygidium. With growth, these taxa develop the inner series on thorax and pygidium (Otarion huddyi, see Adrain and Chatterton, 1994, fig. 7-3; Dimeropyge speyeri, see Chatterton,. 1994, fig. 5-19; Parahystricurus carinatus, herein Plate V-3.1). Comparison of hypostomes provides more similarities of these taxa, in having a pair of spines along the posterior margin (compare Adrain and Chatterton, 1994, fig. 7.6 and Plate V-3.4, herein) and a larger anterior lobe of the middle body. Based on these similarities, it can be presumed that most proetid families, except for scharyiids (see below), with tuberclate protaspides after a protopygidium appears,

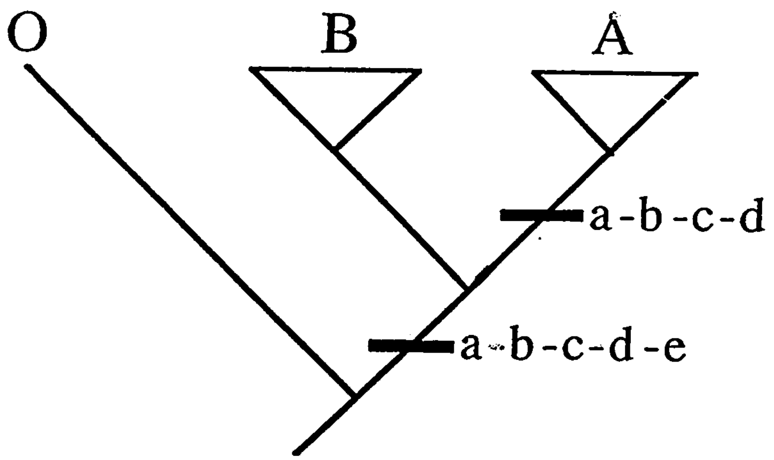

FIGURE VI-1. A hypothetical phylogenetic relationship derived from ontogenetic transformation characters. a-b-c-d and a-b-c-d-e are ontogenetic transformation characters. The cladogram is modified from Fink (1982), and Kluge and Strauss (1985).

11. Position of Midfixigenal Spine Pair

11-Pa) position of midfixigenal spine in Pa: 0 = behind S1; 1 = in front of S1; 2 = absent.

11-Pb) position of midfixigenal spine in Pb: 0 = absent; 1 = behind S1; 2 = in front of S1; 3 = opposite S1.

11-T) ontogenetic transformation of position of midfixigenal spine: 0 = remains behind S1 and disappears later; 1 = moves forwards and disappears later; 2 = remains in front of S1 and disappears later.

NOTE -- All character states described herein are not found in ontogeny of each trilobite such that heterochronic development of each character state is not applicable to all ingroup taxa. Ontogenetic transformation was defined for the interval in which the spine pair exists, regardless of shift of timing of disappearance, as in character 10.

Taxa	Pa		Pb		M	H	T
Du	behind S1	0	absent	0	absent	absent	0
Fl	behind S1	0	behind S1	1	behind S1	absent	0
Ca	absent	2	in front of S1	2	in front of S1	absent	2
Pr	in front of S1	1	in front of S1	2	in front of S1	absent	2
Ps	in front of S1	1	in front of S1	2	in front of S1	absent	2
Rp	behind S1	0	opposite S1	3	in front of S1	absent	1
Rs	behind S1	0	opposite S1	3	in front of S1	absent	1
Tc	behind S1	0	opposite S1	3	in front of S1	absent	1
Ka	behind S1	0	behind S1	1	opposite S1	absent	1
Ly	behind S1	0	behind S1	1	N/A	absent	0
Ph	NO INSTARS		in front of S1	2	in front of S1	absent	2
Ce	NO INSTARS		in front of S1	2	in front of S1	absent	2
Ac	NO INSTARS		opposite S1	3	in front of S1	absent	1
Cy	NO INSTARS		opposite S1	3	in front of S1	absent	1
Sp	behind S1	0	NO INSTARS		behind S1	absent	0
He	behind S1	0	NO INSTARS		behind S1	absent	0

25. Pygidial Pleural Furrows
25-Pb) protopygidial pleural furrows: 0 = absent; 1 = present.
25-H) pygidial pleural furrows: 0 = present; 1 = absent.
25-T) ontogenetic transformation of pygidial pleural furrows: 0 = acquired and retained; 1 = entirely absent; 2 = ontogenetically lost.
25-Th) timing of appearance of 'pygidial pleural furrows': 0 = after segmentation of tergite; 1 = at appearance of protopygidium; 2 = entirely absent during ontogeny.

NOTE -- This character, along with character 24, is only applicable to the ontogenetic intervals after Pb.

Taxa	Pa	Pb		M	H		T	Th
Du	protopygidium not differentiated	absent	0	present	present	0	0	0
Fl	protopygidium not differentiated	present	1	present	present	0	0	1
Ca	protopygidium not differentiated	absent	0	present	present	0	0	0
Pr	protopygidium not differentiated	present	1	present	absent	1	2	1
Ps	protopygidium not differentiated	absent	0	absent	absent	1	1	2
Rp	protopygidium not differentiated	absent	0	absent	absent	1	1	2
Rs	protopygidium not differentiated	absent	0	absent	absent	1	1	2
Tc	protopygidium not differentiated	present	1	present	present	0	0	1
Ka	protopygidium not differentiated	absent	0	absent	absent	1	1	2
Ly	protopygidium not differentiated	absent	0	N/A	present	0	0	0
Ph	protopygidium not differentiated	absent	0	absent	absent	1	1	2
Cc	protopygidium not differentiated	absent	0	absent	present	0	0	0
Ac	protopygidium not differentiated	absent	0	absent	absent	1	1	2
Cy	protopygidium not differentiated	present	1	present	present	0	0	1
Sp	protopygidium not differentiated	NO INSTARS		absent	absent	1	1	2
Hc	protopygidium not differentiated	NO INSTARS		absent	absent	1	1	2

END

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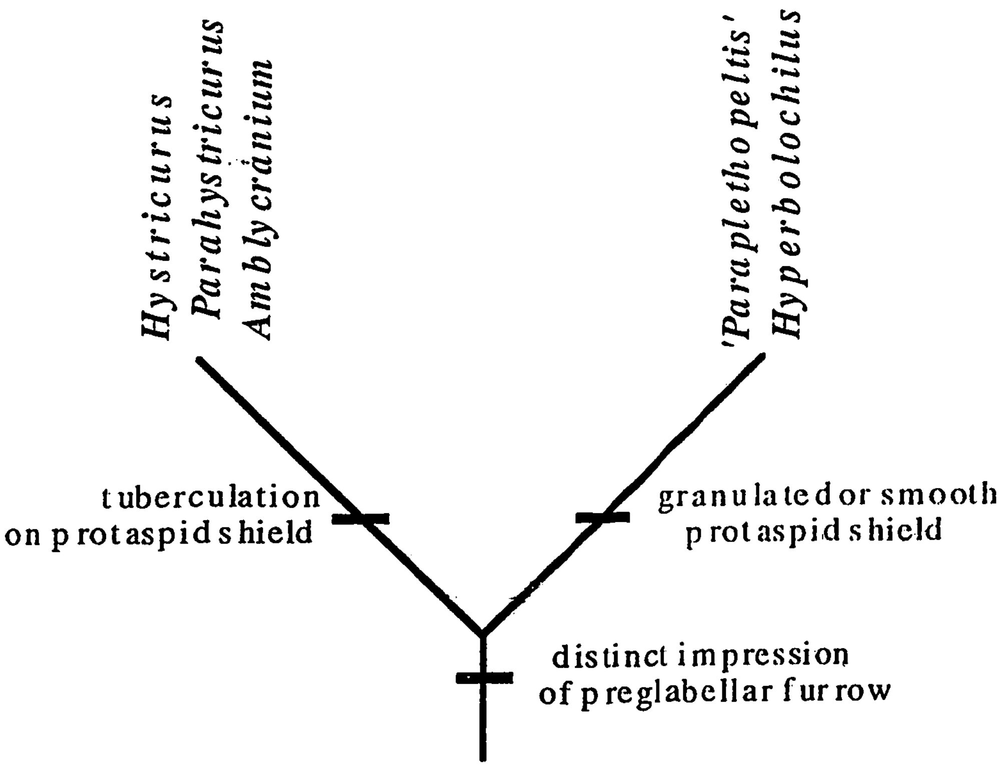

FIGURE V-10. Phylogenetic inference of the Lower Ordovician hystricurids. Two discrete protaspid morphotypes indicate that two separate lineages might have existed within the Hystricuridae during the Lower Ordovician.

ancestor), which, in turn, can be directly interpreted as a terminal deletion (a heterochronic process). Hence, the phylogenetic analysis using ontogenetic transformation character might be able to accomplish two disparate goals, pattern reconstruction and interpretation of evolutionary process, simultaneously.

The third issue is specific to the evolution of the Proetida and the Phacopida. Even with discovery of Tremadocian pliomerid and hystricurid larvae in this work, the 'ptychopariid problem' was not resolved. As for the Phacopida, the comparison made between ptychopariid larvae (e.g., *Dunderbergia anyta*) with three pairs of fixigenal spines and the Tremadocian phacopid larvae in Chapter III and IV provides a prospective clue towards the answer of that problem. There are several ptychopariid larvae with similar morphologies to *D. anyta*, most of which were described by Hu (1971, 1985, 1986). Such shared possession of three pairs of fixigenal spine, bilobed axial or glabellar lobes and overhanging axis to anterior and posterior margin predicts that the ptychopariids with this larval morphotype might be phylogenetically more closely related to the Ordovician and later phacopids than the other ptychopariids. In contrast, holaspid morphologies of these ptychopariids and phacopids provides much less predictive values for the phylogenetic analysis. As for the Proetida, the discovery of earlier protaspid stage ('anaprotaspis') of hystricurids will give a valuable clue to resolve the phylogenetic relationship of the hystricurids (the earliest proetid) to Cambrian ptychopariids, as mentioned in Chapter V. For the present, the larval dissimilarity between hystricurids and ptychopariids is not considered as much informative for the phylogenetic analysis as considerable adult similarity. Such a difference in the degree of morphologic similarity among different ontogenetic intervals may reflect that the evolutionary mechanism (e.g., palingenesis versus caenogenesis, Rieppel, 1990; horizontal hybridization of larvae, Williamson, 1992) which plays different roles on different ontogenetic intervals, is responsible for that ontogenetic disparity of morphologies. Remarkably intriguing is that the meta- or paraprotaspis of some ptychopariids (e.g., Gen. et species indeterminata, Hu, 1986) has

12. Length of Midfixigenal Spine.

12-Pa) length of midfixigenal spine relative to anterior fixigenal spine in Pa: 0 = equally long; 1 = absent.

12-Pb) length of midfixigenal spine relative to anterior fixigenal spine in Pb: 0 = absent; 1 = equally long; 2 = shorter.

NOTE -- Variations of length were detected by the comparison with anterior fixigenal spine which is not much as variable as posterior fixigenal spine. The midfixigenal spine pair disappears during some stage of meraspid period. Each trilobite displays either state, 'shorter' or 'equally long', throughout the interval during which the spine pair exists, so that it is not appropriate to define heterochronic character for the spine pair.

Taxa	Pa		Pb		M	H
Du	equally long	0	absent	0	absent	absent
Fl	equally long	0	equally long	1	equally long	absent
Ca	absent	1	shorter	2	shorter	absent
Pr	equally long	0	equally long	1	equally long	absent
Ps	equally long	0	equally long	1	equally long	absent
Rp	equally long	0	equally long	1	equally long	absent
Rs	equally long	0	equally long	1	equally long	absent
Te	equally long	0	equally long	1	equally long	absent
Ka	equally long	0	equally long	1	equally long	absent
Ly	equally long	0	equally long	1	equally long	absent
Ph	NO INSTARS		shorter	2	shorter	absent
Ce	NO INSTARS		shorter	2	shorter	absent
Ac	NO INSTARS		equally long	1	equally long	absent
Cy	NO INSTARS		shorter	2	shorter	absent
Sp	equally long	0	NO INSTARS		equally long	absent
He	equally long	0	NO INSTARS		equally long	absent

26. Pygidial Margin

26-H) holaspid pygidial margin: 0 = entire; 1 = spinose.

26-T) ontogenetic transformation of pygidial margin: 0 = acquires entire margin; 1 = remains spinose.

NOTE -- Pygidial margin of protaspides and meraspides is spinose throughout the phacopid trilobite taxa. The holaspid state of 'entire margin' is expressed by distinct marginal border as in *Dunderbergia anyta*, or the condition that the interpleural furrow does not reach the pygidial margin as in *Flexicalymene senaria* and *Calyptaulax annulata*.

Taxa	Pa	Pb	M	H		T
Du	protopygidium not differentiated	spinose	spinose	entire	0	0
Fl	protopygidium not differentiated	spinose	spinose	entire	0	0
Ca	protopygidium not differentiated	spinose	spinose	entire	0	0
Pr	protopygidium not differentiated	spinose	spinose	spinose	1	1
Ps	protopygidium not differentiated	spinose	spinose	spinose	1	1
Rp	protopygidium not differentiated	spinose	spinose	spinose	1	1
Rs	protopygidium not differentiated	spinose	spinose	spinose	1	1
Tc	protopygidium not differentiated	spinose	spinose	spinose	1	1
Ka	protopygidium not differentiated	spinose	spinose	spinose	1	1
Ly	protopygidium not differentiated	spinose	spinose	spinose	1	1
Ph	protopygidium not differentiated	spinose	spinose	spinose	1	1
Ce	protopygidium not differentiated	spinose	spinose	spinose	1	1
Ac	protopygidium not differentiated	spinose	spinose	spinose	1	1
Cy	protopygidium not differentiated	spinose	spinose	spinose	1	1
Sp	protopygidium not differentiated	spinose	spinose	spinose	1	1
He	protopygidium not differentiated	spinose	spinose	spinose	1	1