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THE UNIVERSITY OF ALBERTA

Systematics, ontogeny and evolution of encrinurine trilobites

by

© Gregory Donald Edgecombe

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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"...the hierarchic system best expresses the structure of the complex of relations that interconnects all organisms. Consequently we must now examine it more closely."

Hennig, 1966

THE UNIVERSITY OF ALBERTA

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 Systematics, ontogeny and evolution of encrinurine trilobites submitted by Gregory Donald Edgecombe in partial fulfilment of the requirements for the degree of Master of Science.

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Supervisor

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Date: ....Augt. 31.........1987

ABSTRACT

New data afforded by silicified Silurian encrinurine trilobites from the Avalanche Lake area of the Mackenzie Mountains permit detailed comparative ontogenetic studies and contribute to phylogenetic systematic revision of the Encrinurinae.

Comparison of growth series for late Middle Ordovician _Encrinuroides_ and descendant lineages of Silurian _Encrinurus_ suggests that divergence of the _Encrinurus punctatus_ and _variolaris_ plexi from common ancestry may be modelled by different heterochronic patterns. Dissociated cephalic and pygidial regulation in the _punctatus_ plexus, with a resultant apomorphic enrollment pattern, and peramorphic cephalic development in the _variolaris_ plexus allowed rapid morphologic and ecologic divergence in the Llandovery radiation of _Encrinurus_.

The utility of similarities in early ontogeny in phylogenetic inference, a corollary of "von Baer's Law", forms a conceptual basis for comparison of protaspides for eight Ordovician and Silurian encrinurine species. A complex of distinctive early ontogenetic synapomorphies distinguishes "advanced" cybelines, encrinurines, and staurocephalids from plesiomorphic early cybelines and pliomerids. Two closely comparable protaspid instars further unite "advanced" cybelines with Ordovician

encrinurines, while the protaspid period in Silurian Balizoma is reduced to a single ontogenetically-advanced sclerotized instar.

A new species from the Avalanche Lake area, variolaris plexus n. gen., n. sp., is designated type species for a distinctive North American Wenlock offshoot of the variolaris plexus. Including species previously assigned to Balizoma Holloway, the new genus is alternatively interpreted as a sister group to Fragiscutum Whittington and Campbell. Comparative ontogeny of the genal field in these closely-related taxa suggests that minor changes in developmental timing and rate effected substantial charater evolution, with several derived states originating as exaptive by-products shaped by ontogenetic constraints.

The traditional grouping of Ordovician encrinurines in paraphyletic Encrinuroides Reed based on symplesiomorphy obscures fundamental cladistic events. Recognition of four informal species groups emphasizes apomorphic novelties attained in lineages within "Encrinuroides". E. n. sp. from the Mackenzie Mountains is a conservative earliest Llandovery descendant of the Ordovician lineage ancestral to the Silurian Encrinurus plexi.

ACKNOWLEDGEMENT

Brian Chatterton allowed me the opportunity to study the Mackenzie Mountain encrinurines, passed on a wealth of information on trilobite ontogeny (and, seemingly, every reprint in existence), and accepted alternative ways of looking at things with an open mind. My emphasis on the significance of ontogeny in evolution was certainly influenced by his example.

These papers, and undoubtedly those to follow, benefitted from countless discussions on heterochrony, exaptation, "von Baer's Law", and other (frequently more degenerate) topics with Steve Speyer. His contribution of Chazy <u>Encrinuroides</u> material and assistance with "the protaspid paper" are particularly appreciated.

Lars Ramsköld is thanked for enthusiastic discussion on the Encrinurinae during his visit to Edmonton in 1986, as well as for providing an informative review of "the heterochrony paper". Ken McNamara's comments on that manuscript also contributed to its improvement. R. P. Tripp's insightful suggestions on manuscripts forming Chapters III and IV herein are greatly appreciated. Reillustration of specimens originally figured by Evitt and Tripp was made possible through his donation of negatives to B. D. E. Chatterton. Sections on Chinese encrinurids in Chapter V benefitted from discussion with Wu Hong-ji.

Funding for field work in the Mackenzie Mountains was

provided by a grant from the Boreal Institute for Northern Studies. I was further supported by NSERC operating grants awarded to B. D. E. Chatterton.

The unlimited supply of technical gadgets in the possession of Michael J. Ranger contributed greatly to the "arts and crafts" herein.

Lastly, hats off to Zerina, Tuffnell, Dave the conodont animal, Shawna and Robin, and occupants of the Greenhouse and South Lab for making the Edmonton experience a nifty one.

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CHAPTER I

INTRODUCTION

The subfamily Encrinurinae Angelin, 1854 typically comprises a significant element in Ordovician and, particularly, Silurian trilobite faunas. Recent years have witnessed a number of significant contributions to systematic and phylogenetic studies of this group, notably works by Evitt and Tripp (1977), Temple and Tripp (1979), Strusz (1980), and Ramsköld (1986). The studies collected herein integrate a silicified Silurian fauna from the Avalanche Lake area of the Mackenzie Mountains, Canada into a revised framework of encrinurine evolution and systematics. These new data particularly contribute to comparative ontogeny and its phylogenetic implications.

PREVIOUS DEVELOPMENTS - Early work on encrinurine systematics is summarized by Vogdes (1907) and Reed (1928). The latter includes the first major attempt to recognize species groups in Encrinurus based on complexes of cephalic and pygidial characters, and further provided hypotheses of relationships between these sexcostatus, variolaris, platynotus, multisegmentatus, punctatus, and E. (Cromus) intercostatus groups. Rosenstein (1941) emphasized patterns of cephalic tuberculation, formalized in Tripp's (1957; 1962) glabellar tubercle notation. Revision of Reed's multisegmentatus, punctatus, and variolaris groups was advanced in systematic works by Tripp (1957; 1962) and Tripp, Temple and Gass (1977), respectively. Henningsmoen (1959) and Hamada (1961) presented similar classifications of the Encrinurinae, the latter developing a model of cephalic evolution.

Whittington and Campbell's (1967) description of Silurian Fragiscutum rhytium demonstrated morphologic and early ontogenetic data afforded by silicification, further advanced in Evitt and Tripp's (1977) monographic study on Middle Ordovician encrinurids and staurocephalids from Virginia. This included description of encrinurine protaspides, refinement of morphologic terminology, and integration of new taxa in reinterpreting phylogenetic models.

Several descriptive regional studies have been revisive in scope; these include Krueger's (1971) documentation of the late Ordovician radiation of Erratencrinurus from North German glacial drift, and Silurian studies including Strusz's (1980) revision of Australian species, Chang's (1983) survey of Chinese "coronocephalines", and Ramsköld's (1986) taxonomy of Gotland encrinurines.

Strusz's (1980) work provides the most comprehensive hypotheses of evolutionary patterns to date, presenting a phylogenetic tree including all encrinurine species and revision of Encrinurus, based on recognition of three phylogenetic plexi.

Temple and Tripp's (1979) numerical taxonomic analysis of the Encrinurinae represents a bold departure from previous systematic schemes.

Discussion on encrinurine morphology and terminology applied thereto are outlined by Evitt and Tripp (1977, p. 112-118), Temple and Tripp (1979, p. 224-231), and Strusz (1980, p. 2-5).

MATERIALS - Systematic revision has required reexamination of published figures and descriptions for all taxa of Encrinurinae, essentially cosmopolitan through its late Arenig-earliest Llanvirn through early Lochkov range.

Central to these studies is continuing investigation of silicified earliest Llandovery through mid Ludlow encrinurines from seven sections located near the Silurian shelf / slope transition approximately ten kilometers east of Avalanche Lake in the Mackenzie Mountains, Northwest Territories, Canada (see Figure I-1). Locality and stratigraphic data used herein are as presented in detail by Chatterton and Perry (1983; 1984), Over (1985), and Over and Chatterton (1987) [Figure I-2]. Systematic works on the odontopleurid (Chatterton and Perry, 1983) and cheirurid (Chatterton and Perry, 1984) trilobites from these sections include stratigraphic columns for Avalanche Lake One through Four, discussions on correlation and conodont/trilobite zonation of shelf carbonates of the

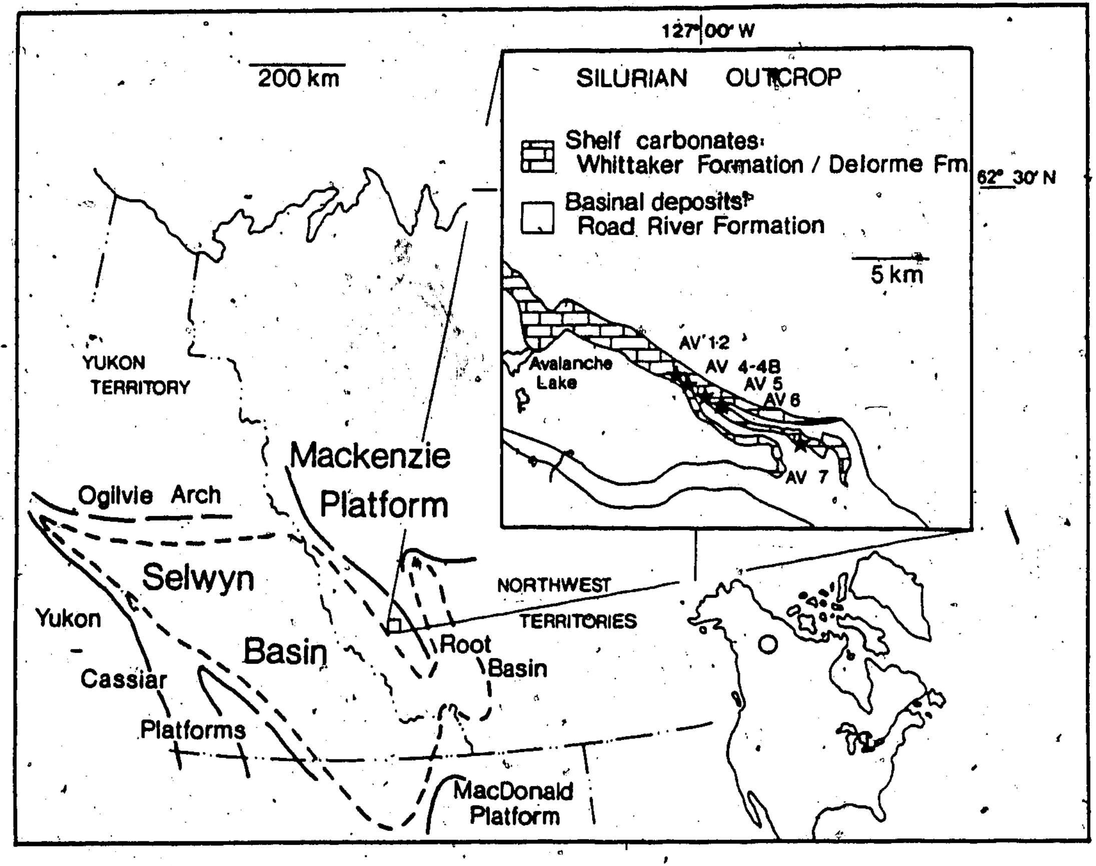
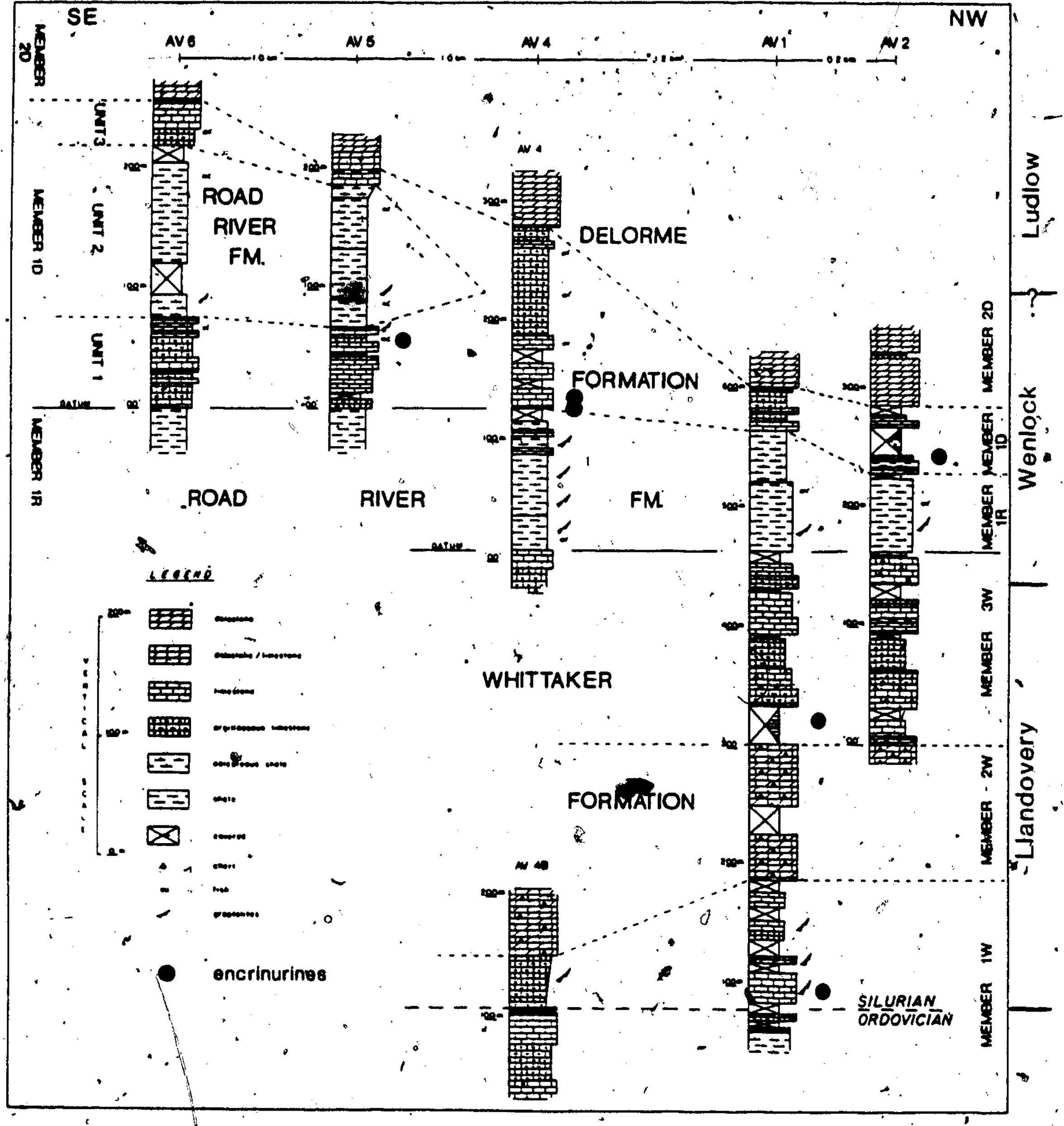


FIGURE I-1 - Location of Avalanche Lake sections on northeast flank of Avalanche Syncline (Gabrielse *et al.*, 1973). After Over and Chatterton (1987).

FIGURE I-2 - Lithostratigraphy and correlation of the Whittaker, Delorme and Road River formations in the Avalanche Lake sections. Stratigraphic horizons yielding encrinurine trilobites discussed or figured in text are indicated by bold dots to right of columns. Positions of stage boundaries based on conodont data in Over (1985); Over and Chatterton (1987). Figure after Over and Chatterton (1987).


SE
NW
AV 6
AV 5
AV 4
AV 1
AV 2
MEMBER 2D
UNIT 3
UNIT 2
UNIT 1
MEMBER 1D
MEMBER 1R
ROAD RIVER FM.
DELORME
FORMATION
ROAD
RIVER
FM.
WHITTAKER
FORMATION
DATUM
200m
100m
0m
AV 4B
LEGEND
VERTICAL SCALE
dolostone
dolostone / limestone
limestone
argillaceous limestone
calcareous shale
shale
covered
chert
fish
graptolites
encrinurines
SILURIAN
ORDOVICIAN
MEMBER 2D
MEMBER 1D
MEMBER 1R
MEMBER 3W
MEMBER 2W
MEMBER 1W
Ludlow
?
Wenlock
Llandovery

Whittaker and Delorme formations and intergrading basinal shales of the Road River Formation, and interpretation of depositional history. Studies on the conodont fauna and zonation of these sections (Over, 1985; Over and Chatterton, 1987) include stratigraphic description and environmental interpretation for sections Avalanche Lake One through Seven; unit-by-unit lithologic descriptions are further provided by Over (1985).

The studies grouped herein are part of systematic revisions involving examination of encrinurines from most of the earliest Llandovery - mid Ludlow trilobite-bearing horizons indicated by Chatterton and Perry (1983; text-figs. 4-7). These works present aspects of this broader study involving early ontogeny and systematics of *Encrinuroides* and taxa of the *Encrinurus variolaris* plexus. Encrinurines from the Avalanche Lake sections discussed or illustrated herein originate from the following stratigraphic horizons (see Figure I-2): Avalanche Lake One 86.5-97.5 and 320 meters above base of measured section; Avalanche Lake Two 248.8 meters above base; Avalanche Lake Four 126-138 meters above base; Avalanche Lake Five 58-62 meters above base; Avalanche Lake Seven 0-70 meters above base. Processed sample sizes are variable, ranging from a few kilograms of limestone up to over one-hundred kilograms. The cumulative data base for these studies includes encrinurines from samples collected in 1978 and

1979 by B. D. E. Chatterton and D. G. Perry, in 1983 by Chatterton and D. J. Over, and in 1986 by the writer, Chatterton, J. Qian, and P. A. Tuffnell. The majority of examined encrinurines were picked by the writer from previously-processed collections, and supplemented by approximately fifty samples processed in 1986. Total encrinurine yields (for species considered herein) range from approximately one-hundred sclerites for Wenlock variolaris plexus n. gen. n. sp., approximately two-hundred sclerites for early Llandovery Encrinuroides n. sp., and several hundred skeletal elements for Wenlock Balizoma spp.

Ontogenetic studies based on the Silurian Mackenzie Mountains fauna have been supplemented by encrinurines from Ordovician silicified faunas made available by B. D. E. Chatterton and S. E. Speyer. These include protaspides of Encrinuroides insularis Shaw from the Llandeilo Chazy Group, New York, and early growth stages of Encrinuroides rarus Walcott from the Llandeilo-Caradoc Esbataottine Formation, Northwest Territories. Locality and stratigraphic data for these collections are referred to in Chapter III.

All specimens illustrated in Chapters II, IV, and V are housed in the University of Alberta Paleontological Type Collections. Repositories of specimens figured in Chapter III are indicated in the introduction to that chapter. The new taxa variolaris plexus n. gen. n. sp. and Encrinuroides n. sp. are introduced in open nomenclature pending formal publication.

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CHAPTER II

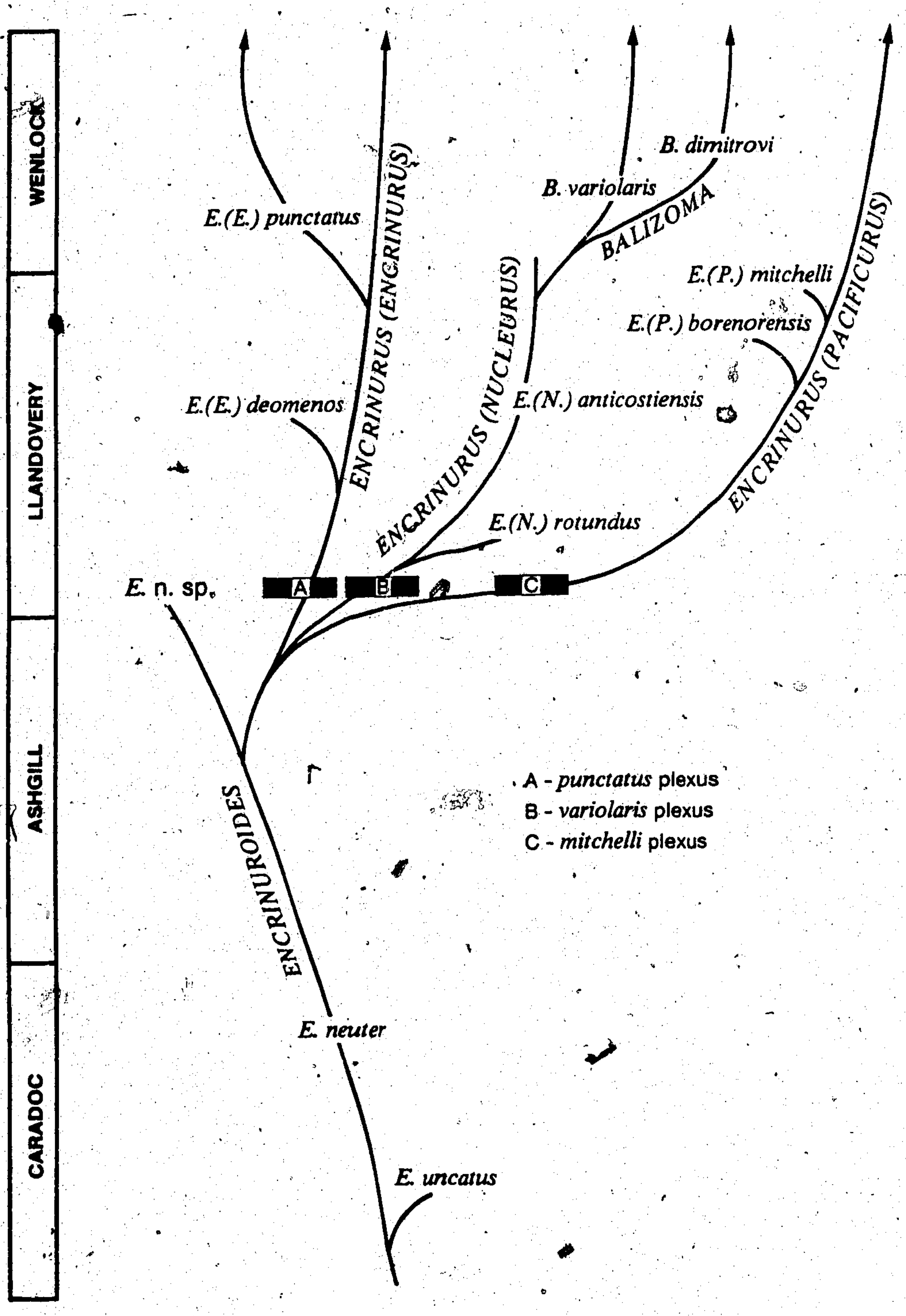
HETEROCHRONY IN THE SILURIAN RADIATION OF ENCRINURINE TRILOBITES

INTRODUCTION

The trilobite subfamily Encrinurinae underwent a major evolutionary radiation in the Lower Silurian. Strusz (1980) recognized several phylogenetic branches originating in the Llandovery, comprising the punctatus, variolaris, and mitchelli plexi of Encrinurus. Recent investigations of encrinurine phylogeny (Evitt and Tripp, 1977; Strusz, 1980; Ramskold, 1986a) have suggested that these clades shared common ancestry in a late Ordovician lineage including Encrinuroides uncatus Evitt and Tripp, 1977 and E. neuter Evitt and Tripp, 1977 from the Oranda and Martinsburg formations of Virginia (Figure II-1). This hypothesis is supported by morphologic evidence (synapomorphic development of coarse, symmetrically-distributed cephalic tuberculation), stratigraphic succession of ancestral and descendant lineages, and the occurrence of Llandovery species possessing character state complexes of both the punctatus and variolaris plexi, demonstrative of mosaic evolution.

A version of this paper has been accepted for publication. Edgecombe, G. D. and Chatterton, B. D. E. 1987. Lethaia, 20:4.

FIGURE II-1 - Phylogenetic tree depicting evolutionary relationships and stratigraphic distributions of species cited in text. Phylogenetic plexi of Encrinurus (and descendant genera in the variolaris plexus) are clades indicated by synapomorphies A-C, sharing common ancestry in late Ordovician Encrinuroides. A - mucronate pygidium with high R/P ratio, long fixigenal spines, thoracic axial spine on tenth segment; B - 1L reduced by merging of 1S with occipital furrow, broad glabella, I-1 tubercle pair forward in position; C - 1L tuberculate abaxially, four coarse tubercles on fixed cheeks along axial furrows, relatively large pygidium with 10-15 pairs of pleural ribs.


WENLOCK
LLANDOVERY
ASHGILL
CARADOC
E.(E.) punctatus
ENCRINURUS (ENCRINURUS)
B. dimitrovi
B. variolaris
BALIZOMA
ENCRINURUS (NUCLEURUS)
E.(P.) mitchelli
E.(P.) borenorensis
ENCRINURUS (PACIFICURUS)
E.(E.) deomenos
E.(N.) anticostiensis
ENCRINURUS
ENCRINURUS
E.(N.) rotundus
E. n. sp.
A
B
C
A - punctatus plexus
B - variolaris plexus
C - mitchelli plexus
ENCRINUROIDES
E. neuter
E. uncatus

A model is developed herein in which divergence from a common ancestor is interpreted as a heterochronic pattern (Figure II-2). McNamara (1986b) has recently provided a thorough summary of heterochrony in trilobite evolution. Adult character states of species of *Encrinurus* (*Encrinurus*) [the *punctatus* plexus] are suggestive of dissociation of cephalic and pygidial regulation in a hypothetical ancestor allied to the *Encrinuroides uncatus* - *neuter* lineage, as indicated by a complex of paedomorphic cranidial character states and peramorphic pygidial states. In contrast, the *variolaris* plexus, stemming from species assigned to *Encrinurus* (*Nucleurus*) Ramsköld, shows maximum phylogenetic expression of several changes in growth allometry of cephalic characters, suggestive of peramorphosis. This plexus is distinct in the early Llandovery, being represented by species such as *E.* (*N.*) *rotundus* (Männil, 1977). Growth series for Wenlock *Balizoma dimitrovi* (Perry and Chatterton, 1979) from the Mackenzie Mountains, northwestern Canada allow comparative ontogenetic studies of the *variolaris* plexus.

A test of this hypothesis involves comparison of growth series of the Caradoc *Encrinuroides uncatus* - *neuter* lineage, for which documentation by Evitt and Tripp (1977) forms the basis for discussion, with descendant Silurian lineages (Figure II-3). Additional information on the ontogeny of the hypothesized ancestral stock is provided by an early Llandovery species of *Encrinuroides* from the

FIGURE II-2 - Heterochronic patterns in the *variolaris* and *punctatus* plexi. Divergence of these clades from common ancestry in *Encrinuroides* is modelled as an effect of different changes in developmental timing. This is indicated by peramorphic cephalic character states in the *variolaris* plexus and regionally global heterochronic dissociation in the *punctatus* plexus (paedomorphic cranidial states / peramorphic pygidial states). Specific patterns in *Encrinurus* (*Encrinurus*) (neoteny / hypermorphosis) are interpreted from apparent relative size increase in the descendant, and are attributed to processes of retardation. Figured species are *Balizoma dimitrovi* (Perry and Chatterton, 1979) [*variolaris* plexus] and *Encrinurus* (*Encrinurus*) *punctatus* (Wahlenberg, 1818) cf. Form A Ramsköld, 1986 [*punctatus* plexus], which co-occur in Wenlock strata in northwestern Canada.

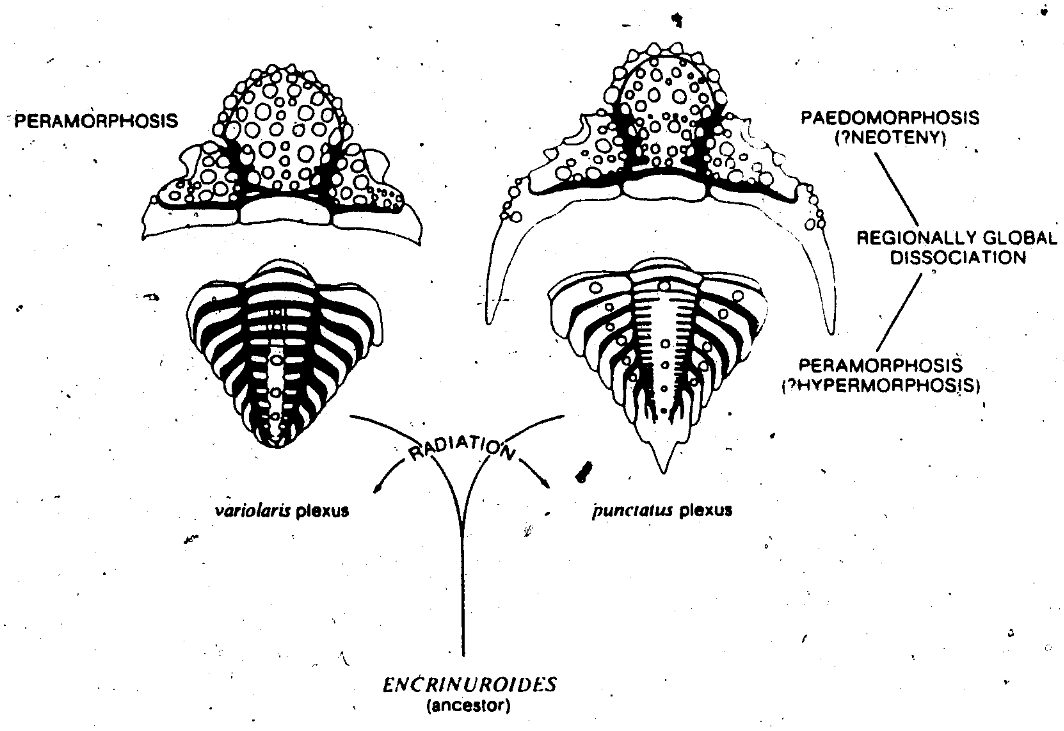
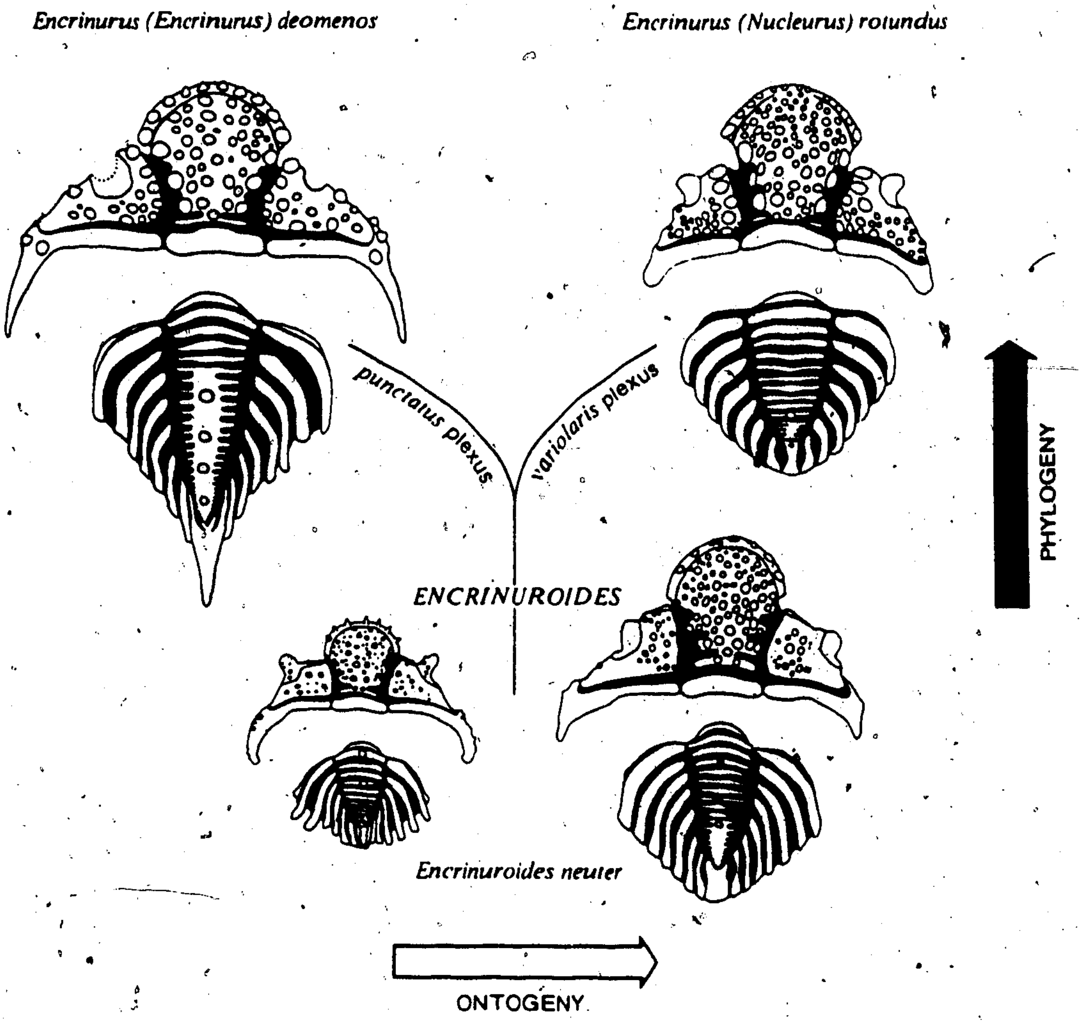

PERAMORPHOSIS
PAEDOMORPHOSIS
(?NEOTENY)
REGIONALLY GLOBAL
DISSOCIATION
PERAMORPHOSIS
(?HYPERMORPHOSIS)
RADIATION
variolaris plexus
punctatus plexus
ENCRINUROIDES
(ancestor)

FIGURE II-3 - Ontogenetic / phylogenetic relationships between ancestral *Encrinuroides* and the descendant *punctatus* and *variolaris* plexi. Illustrations of *Encrinuroides neuter* Evitt and Tripp, 1977, a species hypothesized as being allied to the common ancestor of the *Encrinurus* plexi, are based on Evitt and Tripp, 1977, Pl. 9, figs. 5a, 10 (cranidia) and Pl. 11, figs. 4, 7a (pygidia). *Encrinurus* (*Encrinurus*) *deomenos* Tripp, 1962 (reconstruction based on unpublished material from the Gun River Formation, Anticosti Island, Canada) and *Encrinurus* (*Nucleurus*) *rotundus* (Männil, 1977) (Pl. 1, figs. 1a, 2a) are the earliest-occurring species of their respective subgenera.


Encrinurus (Encrinurus) deomenos
Encrinurus (Nucleurus) rotundus
punctatus plexus
variolaris plexus
PHYLOGENY
ENCRINUROIDES
Encrinuroides neuter
ONTOGENY

Mackenzie Mountains (see Chapter V) which represents a conservative descendant of the E. uncatus - neuter lineage (see Chapter V), retaining such symplesiomorphic character states as a deep preglabellar furrow and multiple tubercles on the lateral glabellar lobes. The resultant extension of the geographic and stratigraphic range of this lineage enhances the plausibility of the proposed model, which implies cosmopolitan distribution of Llandovery descendants.

Compared character states of Encrinurus (Encrinurus) attributed to heterochronic descent are synapomorphic among the species of this mid-Llandovery - Ludlow clade, remaining relatively conservative subsequent to its origin (Strusz, 1980), and are thus represented in the stratigraphically-earliest species such as E. (E.) deomenos Tripp, 1962.

Figured specimens have been deposited in the type collections of the University of Alberta (specimen numbers 7765-7777).

CRANIDIAL CHARACTERS

(1) Glabellar width; length (sag.) of anterior border.- Encrinurine ontogeny is characterized by progressive glabellar expansion, with particular inflation of the frontal lobe to overhang the anterior border (Figure II-

4B). The relatively high glabellar length/width ratio and distinct anterior border of *Encrinurus* (*Encrinurus*) are therefore suggestive of juvenile states in the hypothesized ancestor (Figure II-4A) as well as species of the *variolaris* plexus, in which the glabella is prominently inflated in adults.

(2) Depth of preglabellar furrow.- Ontogenetic shallowing of the preglabellar furrow in late Ordovician *Encrinuroides*, a general trend in encrinurine ontogeny which attains significant phylogenetic expression in the *variolaris* plexus, is opposed by the retention of a relatively deep preglabellar furrow in adult *Encrinurus* (*Encrinurus*).

(3) Distinctness of fixed cheek circumocular tubercles.- Ramsköld (1986a) has demonstrated the distinctness of four major tubercles on the fixed cheeks of species of *Encrinurus* (*Encrinurus*), designated as CT1 - CT4 (Figure II-5). These, along with a row of tubercles on the librigenal field and fixigenal tubercles between the eye and axial furrow, were indicated as forming a more or less distinct circumocular tubercle ring (Ramsköld, 1986a, Text-figure 2). Discussion of circumocular tubercles herein is restricted to the four major tubercles on the fixigenal field. Growth series for *Balizoma dimitrovi* show that these four spines/tubercles comprise the totality of fixigenal tuberculation in protaspid and early meraspid stages (Plate

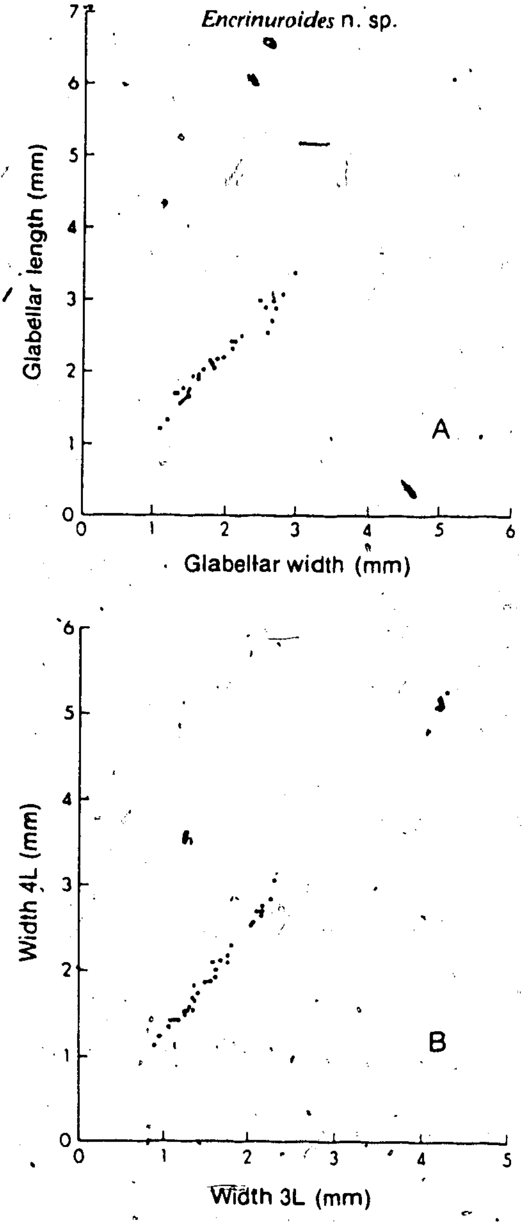
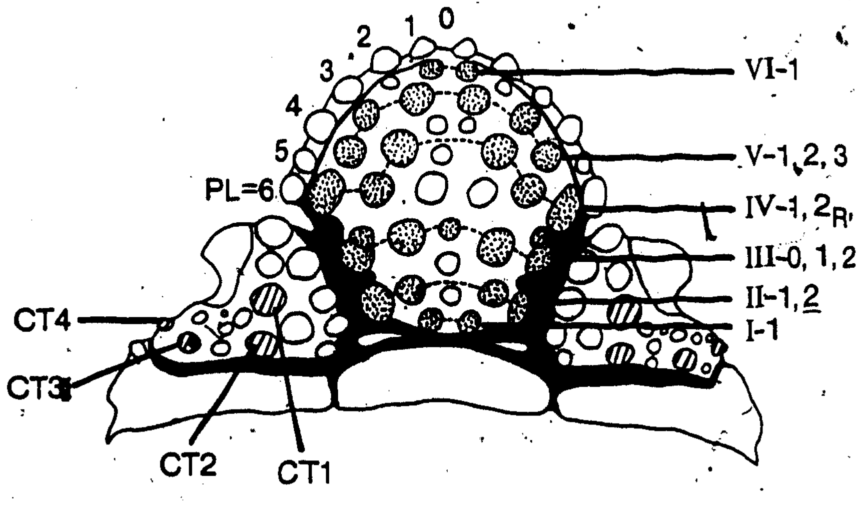


FIGURE II-4 - Scatter plots of glabellar growth in 33 holaspides of Encrinuroides n. sp. from section Avalanche Lake One, 95.5 meters above base (Chatterton and Perry, 1983). A, glabellar length versus width (across frontal lobe 4L); B, glabellar width across 4L versus 3L.

FIGURE II-5 - Cranidial tubercle notation for *Balizoma dimitrovi* (Perry and Chatterton, 1979). Glabellar tubercles are coded following Tripp (1957; 1962) with modifications by Strusz (1980) (as noted in text, p.). Major row glabellar tubercles (Rows I-VI, connected by fine dashed lines) are stippled. Fixigenal circumocular tubercles CT1-CT4 (Ramsköld, 1986a), for which homologies are indicated by ontogenetic series, are indicated by diagonal shading. Anterior border tubercles are numbered as bilaterally-symmetrical pairs 1-6, increasing abaxially. Median tubercle (0) is not developed in this species. Notation of the "preglabellar lateral lobe" (PL) on the anterior border follows Howells (1982).


2
1
0
3
4
5
PL=6
VI-1
V-1, 2, 3
IV-1, 2R, 3
III-0, 1, 2F, 3
II-1, 2
I-1
CT4
CT3
CT2
CT1

II-1). The circumocular tubercles grow with negative allometry with respect to subsequently-developing fixigenal tubercles, and are not substantially enlarged in adults (Plate II-2). Ramsköld further noted that CT1 represents the torular tubercle and CT2 the postocular tubercle of Evitt and Tripp (1977), the former positioned on the torular swelling (torulus). This is corroborated by the ontogeny of *Balizoma dimitrovi*, in which the torulus is prominent in protaspides (Plate II-1A-C) and remains distinct in small meraspides (Plate II-1E). In protaspides of this species, CT3 is positioned abaxially on the fixigenal field, intermediate (exsag.) between CT1 and CT2 (Plate II-1C). It is observed that CT4 represents a relic of the anterior fixigenal spine which is greatly elongated in the protaspid period (Evitt and Tripp, 1977, Pl. 3, figs. 8 ,9 - *Encrinuroides neuter*; Chatterton, 1980, Pl. 14, fig. 2 - *Encrinuroides rarus* (Walcott, 1877); this paper, Plate II-1A-D - *Balizoma dimitrovi*) and early meraspid stage (Plate II-1E). The distinctness of these four tubercles in adult stages of species of *Encrinurus* (*Encrinurus*) is attributed to the paedomorphic arrest of development prior to the inception of later-developing tubercles on the fixigenal field. "Circumocular tubercles" (*sensu* Ramsköld, 1986a) on the librigenal field and on the fixed cheeks overhanging the axial furrows are not apparent on *Balizoma* protaspides, although CT1 - CT4 are distinct.

PLATE II-1 - Protaspides and small (meraspid) cranidia of *Balizoma dimitrovi* (Perry and Chatterton, 1979) from section Avalanche Lake Four, 126 meters above base (Chatterton and Perry, 1983). A, dorsal view of protaspis, UA 7765, x75; B, ventral view of protaspis with free cheeks and rostral plate, UA 7766, x75; C, dorsal view of protaspis, UA 7767, x75; D, dorsal view of protaspis, UA 7768, x75; E, dorsal view of early meraspid cranidium, UA 7769, x75; F, dorsal view of small cranidium, UA 7770, x50; G, dorsal view of small cranidium, UA 7771, x 30.

[redacted]

PLATE II-2 - Growth series of cranidia of *Balizoma dimitrovi* (Perry and Chatterton, 1979) from section Avalanche Lake Four, 126 meters above base (Chatterton and Perry, 1983). All specimens in dorsal view, x10. *A*, UA 7772; *B*, UA 7773; *C*, UA 7774; *D*, UA 7775; *E*, UA 7776; *F*, UA 7777.

[redacted]

The subsequent development of these tubercles (in the meraspid period) indicates that the circumocular tubercle ring is a descriptive by-product of several tubercle series and not the result of a single ontogenetic event.

(4) Length of posterior fixigenal spines.- Encrinuroides neuter, as typifies encrinurine development, undergoes a relative ontogenetic shortening of the posterior fixigenal spines, which are of greatest relative length in protaspid / early meraspid stages. This juvenile character state is retained as a synapomorphy among species of Encrinurus (Encrinurus). In contrast, species of the variolaris plexus possess a peramorphic state of tiny thorn-like genal spines or rounded genal angles in adult stages (Plate II-2), although the posterior fixigenal spines are greatly elongated in ~~early~~ growth stages (Plate II-1C-E).

(5) Continuity of 1L.- The presence of 1L as a continuous ridge in E. (Encrinurus) serves to distinguish this clade from the variolaris plexus, in which discontinuity or loss of this glabellar lobe is induced by the progressive ontogenetic reorientation of 1S posteriorly to merge with the occipital furrow (Plate II-2). In protaspides of Balizoma dimitrovi, 1L is subequal in size to 2L and 3L and is bounded by a straight, continuous 1S furrow (Plate II-1A-D). Transglabellar furrows are common in the earliest growth stages of a wide range of trilobites. Sagittal disruption and reorientation of these furrows is common

ontogenetically.

(6) Anterior border tubercles.- Ontogenetic trends in encrinurine anterior border tuberculation, exhibited by *Encrinuroides uncatus* and *E. neuter*, typically include an increase in number of tubercles and reduction in spinosity. Paedomorphosis is suggested by the development of only eight anterior border tubercles in most species of *E.* (*Encrinurus*), in contrast to ten to twelve tubercles characterizing the *variolaris* plexus.

Balizoma dimitrovi growth series (Plates II-1, 2) provide details on patterns of anterior border tubercle development and allometries. Protaspides have two pairs of widely-spaced anterior border spines (Plate II-1D) which attain maximum [illegible]lative elongation in the meraspid period (Plate II-1E, F), in which additional spines are added abaxially. Small holaspid cranidia are characterized by enlarged anterior border tubercle pairs in the median position (which are positioned forward relative to other border tubercles), in the second abaxial pair, and in the fourth abaxial pair, while smaller tubercles characterize the third abaxial pair (slightly backward-positioned), and fifth and sixth pairs. The two pairs of spines prominent in protaspides and small meraspides are homologous with the second and fourth abaxial pairs of adults, while the median pair undergoes relative enlargement in the meraspid period (Plate II-1F). Allometric trends through the holaspid period involve enlargement of tubercle pairs in abaxial positions 3, 5, and, particularly, 6 (PL of Howells, 1982) relative to pairs 1, 2, and 4 (Figure II-5). Tubercles lining the anterior border of large cranidia (Plate II-2F) are thus subequal in size except for relatively enlarged PL.

(7) Presence / size of particular glabellar tubercles.- The ontogenies of *Encrinuroides uncatus* and *E. neuter*, substantiated by studies on Silurian encrinurines from the Mackenzie Mountains, demonstrate trends in glabellar tubercle development. Terminology used herein (Figure II-5) follows Tripp (1957; 1962) except where otherwise noted. Following Strusz (1980), the positions of tubercles on lateral glabellar lobes are underlined, and forward/rearward displacement (typically an ontogenetic phenomenon) is indicated by superscript/subscript F or R.

Development of the median IV-1 tubercle pair was initiated in protaspides (Plate II-1C), followed by position 1 tubercles in Rows III and V in small meraspides (Plate II-1E, F). Position 1 tubercle pairs in Rows VI, II, and I develop subsequently, as do abaxially-positioned (positions 2 and 3) tubercles in major rows (a term applied herein to rows designated by capital numerals in Tripp's notation; major rows I-IV align across glabellar lobes), and inter-row tubercles (small numerals in Tripp's notation) (Plate II-1G). Growth allometries in the Holaspid period involve the enlargement of these inter-row and abaxial, later-developing major row tubercles relative to the initial median pairs (Plate II-2). Positive allometry of lateral lobe tuberculation attains maximum development in the __variolaris__ plexus, in which these tubercles are enlarged relative to other glabellar tubercles.

Paedomorphosis in __Encrinurus__ (__Encrinurus__) is indicated by the following complex of "juvenile" character states of glabellar tuberculation retained into adult stages: (a) the frequent absence of inter-row tubercles in rows ii and iii, as well as frequent non-development of the I-1 tubercle pair; (b) predominance of median (position 1) major row tubercle pairs; and (c) non-enlargement of lateral lobe tubercles relative to other glabellar tubercles.

Peramorphic states of the __variolaris__ plexus, in addition to enlargement of lateral lobe tubercles, include: (a) tubercular density (an effect of the presence and relative enlargement of inter-row and abaxial major row tubercles); and (b) diagnostic presence of the I-1 tubercle pair, as well as the forward position of this pair. The ontogeny of __Balizoma__ __dimitrovi__ involves the anterior migration of I-1 from forward on 1L upon origination in the meraspid period to a position across 1S in adults (Plate II-2). This trend demonstrates that the ii-1 tubercle pair of Whittington and Campbell (1967) is actually an anteriorly-positioned I-1 pair which underwent relative ontogenetic migration. The alleged diagnostic absence of the I-1 pair in Fragiscutum rhytium Whittington and Campbell, 1967 is therefore refuted. The ontogenetic variation in position of glabellar tubercles forms the basis for the writer's usage of Tripp's (1957; 1962) original tubercle notation, which best allows for the recognition of homologies and provides for the fundamental developmental distinction between major rows and interrows, as opposed to revised notations (Strusz, 1980; Owen, 1981) based on position relative to lateral lobes / furrows in adults.

(8) Adaxial fixigenal tubercles.- Characteristic of ontogeny in the punctatus, variolaris, and mitchelli plexi is a trend towards positive allometry of a row of fixigenal tubercles overhanging the axial furrows. Optimal expression occurs in the variolaris plexus, in which enlargement of this row occurs relative to tubercles in the fixigenal field. This character state also typifies early species of the mitchelli plexus such as Encrinurus (Pacificurus) borenorensis Fletcher, 1950, and reflects recency of common ancestry between the variolaris and mitchelli plexi, also noted by Strusz (1980). Species of Encrinurus (Encrinurus) retain a "juvenile" state of a row of small adaxial tubercles on the fixed cheeks.

Encrinuroides uncatus and E. neuter do not show significant development of an adaxial tubercle row on the fixed cheeks, an evolutionary novelty presumably originating in the late Ordovician common ancestor of the Encrinurus plexi. It is noteworthy that early Llandovery Encrinuroides n. sp. from the Mackenzie Mountains shows tendencies towards several derived character states of Silurian Encrinurus, including more prominent adaxial fixigenal tubercles (8 or 9 small tubercles) and posterior reorientation of the 1S glabellar furrow (see Chapter V herein).

HYPOSTOMAL CHARACTERS

The retention of seven denticles (three lateral/posterolateral pairs and a posteromedian denticle) on the border of the hypostome throughout ontogeny in Encrinuroides uncatus and E. neuter appears to be relevant to heterochronic models. A homologous distribution of border spines or denticles is observed in the early growth stages of many encrinurines, cybelines, and staurocephalids, including Balizoma dimitrovi and Llandovery Cromus? n. sp. from the Mackenzie Mountains (see Chapter III), Fragiscutum rhytium Whittington and Campbell, 1967, Bevanopsis ulrichi Cooper, 1953 (Evitt and Tripp, 1977), Cybeloides cimelia Chatterton and Ludvigsen, 1976 (Chatterton, 1980), and Libertella corona Hu, 1971. A similar distribution of border spines is found in the adult stages of certain pliomerids such as Hintzeia aemula

(Hintze, 1952), Protopliomerella contracta (Ross, 1951), and Pseudocybele nasuta Ross, 1951, although relative proportions vary from small denticles to an elongate posteromedian spine. This provides further evidence for a close phylogenetic relationship between the Encrinuridae and the Pliomeridae, emphasized by Temple (1956), Whittington (1965, 1966) and Fortey (1980) [see also Chapter III]. The typical loss of these denticles in encrinurine ontogeny, with resultant smoothing of the margin, suggests that their retention into the adult stages in Encrinuroides uncatus and E. neuter may be paedomorphic.

Hypostomal character states of Encrinurus (Encrinurus) contrast with paedomorphic cranidial states and, in fact, more strongly approximate a peramorphic pattern. Suggestive of extension of the ancestral ontogenetic trajectory are elongation of the posterior border, loss of border denticles, and narrowing/elongation of the rhynchos to extend in front of the anterior border.

It is also noteworthy that adult hypostomes of certain cybelines [ex. Cybeloides prima (Raymond, 1905) (Shaw, 1968); C. virginiensis Cooper, 1953 (Evitt and Tripp, 1977)] resemble the early stages of encrinurines. As noted by Henningsmoen (1959), Whittington (1966), Evitt and Tripp (1977), and Strusz (1980), the ancestry of the Encrinurinae, first represented by late Arenig or earliest Llanvirn Encrinuroides hornei Dean, 1973, lies in the Cybelinae. Cybeline hypostomal character states resembling juvenile encrinurines include the forward position of the anterior wings, straightness of the anterior margin, triangular outline of the middle body, subdued rhynchos, and posterior border of uniform width with seven pronounced denticles. This suggests a peramorphic trend in the descendant Encrinurinae, also supported by the sparseness of cybeline glabellar tuberculation, typified by prominent median major row pairs distributed similar to encrinurine juvenile stages.

THORACIC CHARACTERS

Thoracic axial and pleural spines are conspicuous in early growth stages of Encrinuroides (and the descendant variolaris plexus), but are obsolete or reduced to low, rounded tubercles in adults. The retention of thoracic axial spines in Encrinurus (Encrinurus), typically elongated on the tenth thoracic segment, is suggestive of paedomorphosis. No departure from the symplesiomorphic state of eleven thoracic segments is observed, except as a derived state in lineages within/allied to the variolaris plexus (Paraencrinurus Antelo, 1973; Fragiscutum Whittington and Campbell, 1967).

PYGIDIAL CHARACTERS

In contrast to cranidial attributes suggestive of paedomorphosis, development of the mucronate pygidium of Encrinurus (Encrinurus) may be related to the peramorphic projection of an ontogenetic trajectory beyond that of ancestral Encrinuroides (Figure II-2). Although the pygidial ontogeny of Encrinurus (Encrinurus) is not well known [a late meraspid transitory pygidium of E. (E.) odvaldensis Ramsköld was figured by Ramsköld, 1986, Pl. 44, figs. 3a, b, as well as small holaspides of E. (E.) punctatus (Wahlenberg, 1818) and E. (E.) macrourus Schmidt, 1859], the highly-derived adult form of this taxon suggests the improbability of recapitulation of discrete stages in ancestral ontogeny. Peramorphic patterns are detected by ontogenetic interpretation of character states (with the possibility of dissociated allometric growth of different characters), not by postulating terminal addition onto a known ancestral growth series. Alberch (1985), emphasizing a dynamic developmental framework, demonstrated that modification of developmental timing and rates in ancestors need not produce descendants which pass through the same successive stages in their ontogenies. Comparable effects in Miocene melanopsid gastropods were modelled by Geary (1986). Peramorphosis in an ancestral-descendant sequence, generating extremely different morphologies between three successive species, was attributed to a change in timing of the underlying growth process rather than temporal shifts of developmental stages. This type of modification of parameters in ancestral ontogenetic "programs" is conceivably responsible for considerable heterochrony, although these patterns are certainly more cryptic than cases in which descendant morphologies involve simple abbreviation or extrapolation of stages in ancestral ontogeny.

Stem species of the variolaris plexus assigned to Encrinurus (Nucleurus) retain conservative pygidial character states.

(1) Number of axial rings.- Encrinurine ontogeny is characterized by addition of pygidial axial rings into the holaspid period. A large ratio of number of axial rings (generally between 20 and 30) to pleural ribs, the R/P ratio of Ramsköld, 1986a, is synapomorphic among species of Encrinurus (Encrinurus). This increase in ring number relative to the ancestral lineage (14-18 rings) may represent a peramorphic pattern.

The Australian/Asian subgenus Encrinurus (Pacificurus) Ramsköld, 1986 also shows an increased number of axial rings [usually between 20-30, but up to 35 in undescribed material (Ramsköld, personal communication, 1987)], but is distinguished from E. (Encrinurus) by a lower R/P ratio. This is achieved by development of 10-15 pleural ribs in E. (Pacificurus) in contrast to a fixed number of 7 free pleural ribs in E. (Encrinurus).

(2) Fusion of posterior pleural ribs.- The fusion of terminally-elongate posterior pleural ribs to form a mucro, involving the abaxial termination of pair 7, pair 8, and single (or paired) rib(s) 9, is a shared derived feature of species of Encrinurus (Encrinurus). The peramorphic origin of this character state is suggested by the ontogenetic increase in posterior rib fusion in Encrinuroides neuter, as well as a general ontogenetic trend towards smoothing of the pygidial margin, represented by spinose rib terminations in small growth stages (Figure II-3).

(3) Pygidial length/width ratio.- An increase in pygidial length/width ratio is demonstrated in the ontogenies of Encrinuroides uncatus, E. neuter, and E. n. sp. from the Mackenzie Mountains (Figure II-6). The extension of this ontogenetic trend is suggested by relative pygidial elongation in descendant Encrinurus (Encrinurus), largely an effect of elongation of late-developing posterior pleural ribs.

(4) Distinctness of sagittal band.- The development of a prominent, elongate sagittal axial ring discontinuity (sagittal band of Strusz, 1980) in species of Encrinurus (Encrinurus) may be related to the peramorphic extrapolation of the ontogenetic increase in axial ring discontinuity in the ancestral stock.

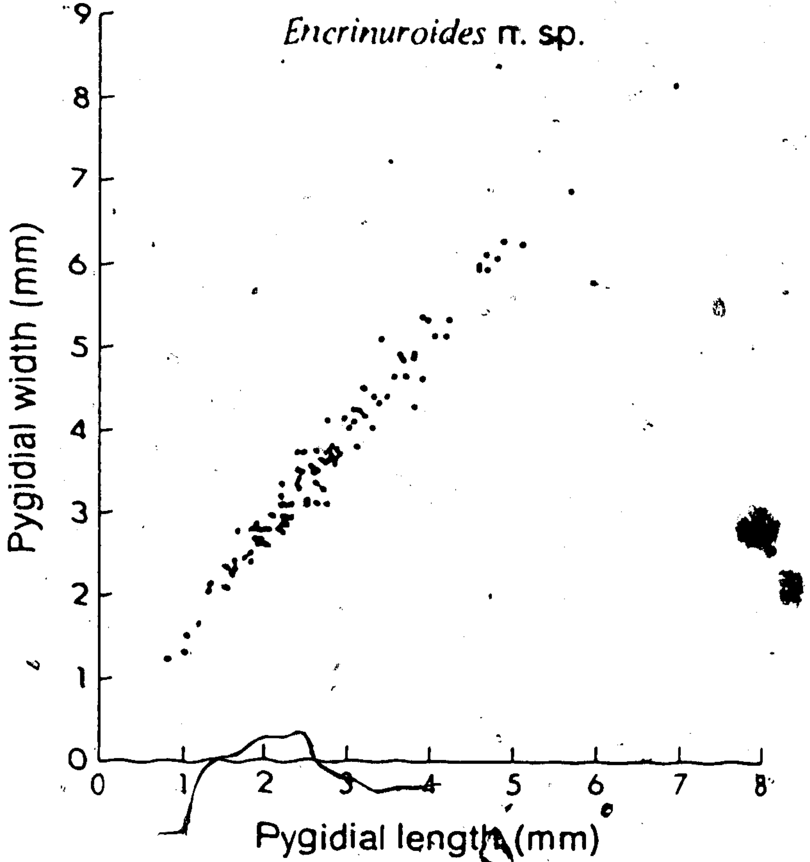


FIGURE II-6 - Scatter plot of pygidial width versus length, for 103 specimens (late meraspid through holaspid period) of Encrinuroides n. sp. from section Avalanche Lake One, 95.5 meters above base (Chatterton and Perry, 1983).

DISCUSSION

The hypothesized heterochronic descent of Encrinurus (Encrinurus) may provide a framework for investigations into regulatory dissociation. McKinney (1984) has emphasized the probable frequency of dissociation and heterochronic "mosaics". Fink (1982) specified that each trait must be analyzed separately; heterochronic patterns in one or more traits do not require that all aspects of the organism be affected by the same changes in developmental timing. This may be applicable to neotenic, accelerated, or displaced allometric changes, but contrasts with the view that progenesis and hypermorphosis are global in their effects (McNamara, 1986a). Documentation of growth allometries in species of the Eocene echinoid Oligopygus suggest that neotenic trends in isolated attributes were decoupled from otherwise global (whole organism) hypermorphosis in response to size selection (McKinney, 1984). Alberch et al. (1979) cited peramorphosis in an ammonoid lineage described by Newell (1949) as an example of the combined effects of separate processes in which acceleration, predisplacement and hypermorphosis could be recognized. Gould (1977) demonstrated the role of dissociation in human evolution by attributing certain character states to acceleration, although emphasizing the dominant effect of retardation. Furthermore, both peramorphic and paedomorphic patterns (hypermorphosis and neoteny) were attributed to the same heterochronic process of retardation. Dommergues, David and Marchand (1986) have recently outlined theoretical cases of dissociated heterochrony, and proposed examples of accelerated hypermorphosis in liparoceratid ammonites and neotenic hypermorphosis in primates.

The example documented herein is significant in suggesting regionally global effects (i.e., expression of a heterochronic pattern throughout a particular region of the body; for example, paedomorphosis in all cranidial characters), though clearly dissociated with respect to the entire organism (Figure II-2). Causal mechanisms may involve dissociated hormonal regulation of development of the cephalic and pygidial regions. The probable role of hormonal systems comparable to Recent arthropods in generating temporal shifts in trilobite ontogeny has been discussed by McNamara (1981; 1983; 1986b). A speculated trend towards increased relative size of the descendant is suggestive of retarded development involving a complex of neoteny and hypermorphosis (McNamara, 1986a).

In terms of phylogenetic significance, heterochrony provides a mechanism of explaining rapid divergence from common ancestry. It is noteworthy that, subsequent to its origin, _Encrinurus_ (_Encrinurus_) persisted through the Silurian as a relatively conservative group of species. It is hypothesized that heterochronic evolution permitted rapid establishment of morphologic, and presumably ecologic, divergence between the *punctatus* and *variolaris* plexi. This is expressed by the distinctness of these clades in the Wenlock, with enhanced potential for sympatric association.

An analogous example of heterochronic catalysis of a phylogenetic radiation has been documented by Hafner and Hafner (1986) in a macroevolutionary study of geomyoid rodents. The great diversity of this subfamily and establishment of several distinct lineages (pocket gophers, kangaroo rats, and kangaroo mice) is causally related to varying changes in developmental timing, expressed by different heterochronic patterns in various clades.

HETEROCHRONY AND ENCRINURINE ENROLLMENT

Dissociation of cephalic and pygidial development would have required modification of coaptative structures and may provide an explanation for differing enrollment strategies in encrinurines, outlined by Holloway (1980). From the convexity and slope of doublures along the contact surface in partially-enrolled specimens, Clarkson and Henry (1973) inferred that the mucronate pygidium of enrolled *Encrinurus* (*Encrinurus*) *tuberculatus* Buckland, 1836 [here regarded as a probable junior subjective synonym of *E.* (*E.*) *punctatus* (Wahlenberg, 1818)] extended beyond the cephalon, providing an open space which could have functioned for circulation of water to the enrolled trilobite [see Clarkson and Henry, 1973, Figs. 12, 16; Rosenstein, 1941, Pl. I, figs. 5, 7, Pl. II, figs. 4, 4a, 4b; Thomas, 1981, Pl. 18, figs. 1a-c; Männil, 1968, Pl. I, figs. 1-5 - partially-enrolled *E.* (*E.*) *schmidti* [=*E.* (*E.*) *schisticola* Törnquist, 1884]; Holloway, 1980, p. 45 - *E.* (*E.*) *egani* Miller, 1880]. This was contrasted with *Balizoma variolaris* (Brongniart, 1822) in which enrollment involved the rounded pygidial margin fitting exactly underneath the cephalon with no open space (Clarkson and Henry, 1973, Figs. 13-15; Levi-Setti, 1975, Pl. 31; Tripp, Temple and Gass, 1977, Pl. 113, fig. 11). Enrollment in this group apparently involved the hypostomal rhynchos fitting into a prominent U-shaped notch in the pygidial doublure. A similar condition probably obtained for species of the ancestral *Encrinuroides* lineage, with relatively rounded pygidial margins and "mirror-image" cephalic/pygidial contact surfaces. This enrollment strategy was apparently established in Llandovery species of the *variolaris* plexus such as *Encrinurus* (*Nucleurus*) *anticostiensis* (Twenhofel, 1928) (based on reexamination of partially-enrolled specimen GSC 29716 illustrated by Bolton 1981, Pl. VI, fig. 19), and appears to have been retained in late Wenlock - early Ludlow *Fragiscutum*, as demonstrated by partially-enrolled *F. glebalis* Campbell, 1967 (Pl. 8, figs. 1-4, 7-11, 14). The plesiomorphic nature of this enrollment pattern is indicated by outgroup comparison with more distantly-related encrinurine clades [ex. *Cromus*

(Encrinuraspis) storchi Šnajdr, 1983 (Šnajdr, 1985, Pl. IX, figs. 3, 4); Erratencrinurus (?Celtencrinurus) moe (Männil, 1958), Pl. VII, fig. 4]. It is noteworthy that no completely enrolled specimen of E. (Encrinurus) has ever been figured. Ramskold (personal communication, 1987) notes that "a few specimens are so nearly perfectly enrolled that they show beyond doubt that there was no space left over, but rather a perfect fit between pygidium and cephalon, with the rostral plate projecting down into the posteromedian angle formed by the inner pygidial margins in contact with these." This relationship is expressed morphologically by the development of an inflated rostral plate which projects in front of the anterior margin of the cephalon and a correspondingly narrow, V-shaped outline of the pygidial doublure (Rosenstein, 1941, Pl. III, fig. 10; Tripp, 1962, Pl. 67, fig. 7; Perry and Chatterton, 1979, Pl. 73, fig. 26; Ramsköld, 1986a, Pl. 43, fig. 10). Although refuting the "open space" hypothesis, a strategy demonstrated in several dalmanitids by Campbell (1977), it is apparent that this represents a significant modification of enrollment patterns. Peramorphic pygidial elongation in combination with paedomorphic cranidial development in Encrinurus (Encrinurus) suggests a mechanism by which this morphologic innovation may have originated. It is possible that dissociation of hypostomal and cranidial development, with particular elongation of the posterior hypostomal border, may have been structurally related to pygidial elongation. McNamara (1986b) has emphasized the role of such changes in allometric growth rate in niche partitioning and minimizing competition for resources between ancestors and descendants. It is, however, possible that this enrollment strategy resulted as a simple by-product of heterochronic dissociation in response to more immediate environmental controls. This could involve size selection (cf. McKinney, 1984; 1986b) or changes in timing of maturation as adaptive responses to ecological parameters. The relationship between heterochrony and size selection in trilobites was noted by Fortey and Rushton (1980), who stressed the correlation between adult size and particle-size utilization by deposit feeders. Paedomorphic (terminally progenetic; McNamara, 1983) shortening of the thorax in Tremadoc Acanthopleurella led to sufficient morphologic (size) difference with sympatric species, including those of its presumed ancestor, Conophrys, to minimize competition. Size displacement was also regarded by Robison (1975) as an important process in nonspatial segregation of agnostoid trilobites.

PERAMORPHOSIS IN ORDOVICIAN ENCRINUROIDES

Evitt and Tripp (1977) noted the close phylogenetic relationship between Caradoc Encrinuroides uncatus and E. neuter from Virginia, indicated by shared derived states such as denticles on the border of the adult hypostome, and thoracic and pygidial axial tubercles. The resemblence of adult E. uncatus to relatively juvenile holaspides of younger (?descendant) E. neuter suggests peramorphosis. This trend is demonstrated by the following character states of E. neuter which may have originated by extending the ontogenetic trajectory of E. uncatus: shorter, less-divergent fixigenal spines; less-prominent median major row tubercle pairs (notably III-1 and IV-1), and more-abundant inter-row tubercles; less-spinose cephalic tuberculation; less-prominent thoracic axial and pleural spines; longer rhynchos; greater number of pygidial axial rings (18 vs 16) and pleural ribs (8 vs 7); greater pygidial length/width ratio; more-prominent, elongate sagittal band.

HETEROCHRONIC PATTERNS IN LEONASPIS

Another similar example of divergent heterochronic patterns in closely-related trilobite clades during the Silurian is shown by species of the odontopleurid Leonaspis described by Chatterton and Perry (1983). In one of these clades, consisting of Leonaspis jaanussoni Chatterton and Perry, 1983, L. risbeyi Chatterton and Perry, 1983, and L. lenzi Chatterton and Perry, 1983, evolution from the first two, Lower Llandovery species to the later Wenlock species appears to be paedomorphic (possibly progenetic). Character states of juvenile holaspid stages of ancestral L.

jaanussoni (prominent subsidiary occipital and anterior margin spines on the cranidium; narrow pygidium with sharply turned backward anterodistal margins; a sparser, more-spinose prosopon) are retained into later holaspid stages of the possible descendant species *L. lenzi*. Chatterton and Perry (1983, p. 11-13, 28-30) also described a rapidly-evolving phyletic lineage from *Leonaspis beni* Chatterton and Perry, 1983 through *L. boltoni* Chatterton and Perry, 1983 and *L. besti* Chatterton and Perry, 1983 to *L. belli* Chatterton and Perry, 1983. Major changes parallel (loss of occipital spine) or run counter (movement of eye forward; loss of marginal pygidial spines) to changes found in the ontogenies of species of this lineage, and are peramorphic and paedomorphic, respectively. A trend towards decreasing size of individuals suggests that this dissociated pattern resulted from acceleration of development ["acceleration" *sensu* deBeer (1964), Gould (1977) by accelerating somatic development / progenesis by accelerating sexual maturation). Association with an environmental gradient (shallowing trend) indicates heterochronic directional evolution comparable to the peramorphoclines/ paedomorphoclines of McNamara (1982). Accelerated development may have been controlled by temperature/depth effects as outlined by McNamara (1978; 1983) in a progenetic paedomorphocline of Cambrian olenellids. Selection towards smaller size or reduced spinosity may have been significant, the latter in relation to increased substrate firmness. Analysis of heterochrony in Cenozoic echinoids by McKinney (1986a; 1986b) provides support for Gould's (1977) theory that progenesis is associated with r-selected life-history strategists inhabiting unstable environments, while neoteny is associated with K-selecting stable environments. The observed phyletic size decrease in Leonaspis (attributed to progenesis/acceleration) could be predicted by this model, in which decreasing stability is correlative with shallowing. Chatterton and Perry (1983) also suggested a more slowly-evolving branch of this clade from L. beni to L. longstaffei Chatterton and Perry, 1983 in which the first two of these three trends listed above are apparent.

All of these species occurred in the same region during the Silurian but members of the two clades are not found coexisting until the Wenlock, some time after their Llandovery first-appearance. This thus provides another example where species of closely-related clades could coexist following rapid divergence through selection of ontogenetic variation and different heterochronic patterns.

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CHAPTER III

PROTASPID LARVAE OF ENCRINURINE TRILOBITES

INTRODUCTION

Trilobite life history is traditionally divided into three periods; the protaspis, meraspis, and holaspis, approximately corresponding to larval, juvenile, and adult phases, respectively. Most faunas are represented by only holaspid, and perhaps late meraspid individuals; larvae are usually not present due to taphonomic biases. Silicified faunas, however, provide the opportunity to study trilobite larvae and allow us to evaluate the phylogenetic significance of morphologies present in early growth stages.

The term "protaspis" was first introduced by Beecher (1895) to identify the earliest stage in trilobite development that shows cuticle sclerotization (calcification). By definition, the protaspid tergite is not separated into body sections; the head portion (protocranidium) is fused to the tail portion (protopygidium). The protaspid period has been subdivided into ana-, meta-, and paraprotaspid stages (Beecher, 1895;

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Hu, 1971); these stages, however, are inconsistently defined (for historical review, see Hu, 1971), and do not show uniformly homologous characters. The application of these terms to different trilobite groups is, therefore, impossible (cf. Whittington, 1957). A more versatile and, perhaps, more meaningful subdivision of the protaspid period is based on the recognition of metrically and morphologically distinct subgroups. These groups presumably correspond to successive instars (cf. Palmer, 1962), and thus may be designated stages 1, 2, etc. Such stages are not to be confused with metaprotaspid "stages" as applied to encrinurid protaspides by Evitt and Tripp (1977); a modification of Ross' (1951a) division based largely on number of pygidial segments.

This study examines protaspid larvae and early development in eight species of the subfamily Encrinurinae Angelin, 1854 from Ordovician and Silurian strata. Comparisons are based largely on cladistic methodology; an analysis of primitive versus derived character states which is then related back to a temporal frame as provided by time stratigraphic distributions. This eclectic approach, advocated by Fortey and Jeffries (1982) and Henry (1984), makes optimal use of data provided by paleontology in phylogenetic reconstructions.

Studies on silicified trilobites from the Middle Ordovician Ch[illegible]oup (New York) by S. E. Speyer and from Silurian sect[illegible] in the Mackenzie Mountains (Northwest

Territories) by B. D. E. Chatterton and the author have provided much new data on the ontogeny of the Encrinurinae. At least one developmental stage is present in the protaspid period in each of the eight encrinurine species considered herein. Small, early protaspides, corresponding to the anaprotaspis stage of Hu (1971), are presently not known for encrinurines. This suggests that the stage 1 evident in Ordovician <u>Encrinuroides</u> spp. represents the earliest sclerotized stage in the development of these trlobites. Although Alberch (1985) has cautioned against homologies between discrete stages in ancestral and descendant ontogenies, it is suggested that such comparisons have validity when applied to restricted monophyletic groups and, indeed, may reveal otherwise unsuspected relationships. For example, Silurian encrinurines, best represented by <u>Balizoma</u> spp., show only one protaspid stage with attributes considered homologous with those present in <u>Encrinuroides</u> stage 2 protaspides. Arthropod ontogeny, by its very nature, is typically broken into discrete stages (or instars) as a result of ecdysis (moulting). Ecdysis is controlled by specific hormonal pathways which predispose arthropods to perturbations in ontogenetic timing (eg., acceleration or retardation). For this reason, it is important to [illegible] for homologous attributes between closely related [illegible]icularly among early growth stages where timing [illegible] sclerotization (stage 1 protaspis) represents a coarsely standardized developmental event.

In this paper are illustrated and described the early growth stages of Encrinuroides insularis Shaw, 1968 (early Middle Ordovician; Llandeilo) and Balizoma spp. (middle Silurian; Wenlock). An unpublished Wenlock species (Edgecombe and Chatterton, in prep.; Chapter IV herein), representing a new genus allied to Balizoma Holloway, 1980 and Fragiscutum Whittington and Campbell, 1967, permits a comparison of early ontogeny between taxa of the Encrinurus variolaris plexus of Strusz (1980). In addition, we illustrate the first known protaspides for Cromus Barrande, 1852; our material, very likely congeneric with Barrande's type species, is Llandovery in age from the Mackenzie Mountains. Protaspides of Encrinuroides neuter (Martinsburg Formation, Virginia; Middle Ordovician; Caradoc) and E. rarus (Walcott, 1877) (Esbataottine Formation, Northwest Territories; early Middle Ordovician; Llandeilo), originally figured by Evitt and Tripp (1977) and Chatterton (1980), respectively, are reillustrated and discussed.

Additional information is provided by a single protaspis of Encrinuroides tholus Evitt and Tripp, 1977 (lower Edinburg Formation, Virginia; early Middle Ordovician; Llandeilo) and a protaspis from the Edinburg Formation assigned by Hu (1975) to Otarion trilobus Hu, 1975 which is herein referred to Encrinuroides cf. E. tholus. The general stratigraphic and geographic distributions of materials used in this study are illustrated in Figure III-1.

Specimens figured herein are reposited in the New York State Museum (NYSM), the United States National Museum (USNM), and the University of Alberta Paleontological Collections (UA).

TERMS AND TERMINOLOGY - Terminology used throughout this paper (Figure III-2) generally follows Evitt and Tripp (1977) and Strusz (1980). Glabellar and cranidial anterior border tubercle notation used herein is as outlined by Edgecombe and Chatterton (1987, Figure 5; Figure II-5 herein). Tripp's (1957, 1962) notation is modified by underlining the positions of tubercles on lateral glabellar lobes and indicating forward/rearward displacement by superscript/subscript 'F' or 'R', as suggested by Strusz (1980). A distinction between major row tubercles (rows I-VI in Tripp's system) and inter-row tubercles (rows ii-v) was made by Edgecombe and Chatterton (1987). The glabellar frontal lobe is termed '4L' following Howells (1982). Distinction is made between anterior, mid-, and posterior fixigenal spines (Palmer, 1962). 'Circumocular tubercles' on the fixigenal field were designated as CT1-CT4 by Ramsköld (1986), and homologies with the torular tubercle (=CT1) and postocular tubercle (=CT2) of Evitt and Tripp (1977), and anterior fixigenal spine (=CT[illegible]) were discussed

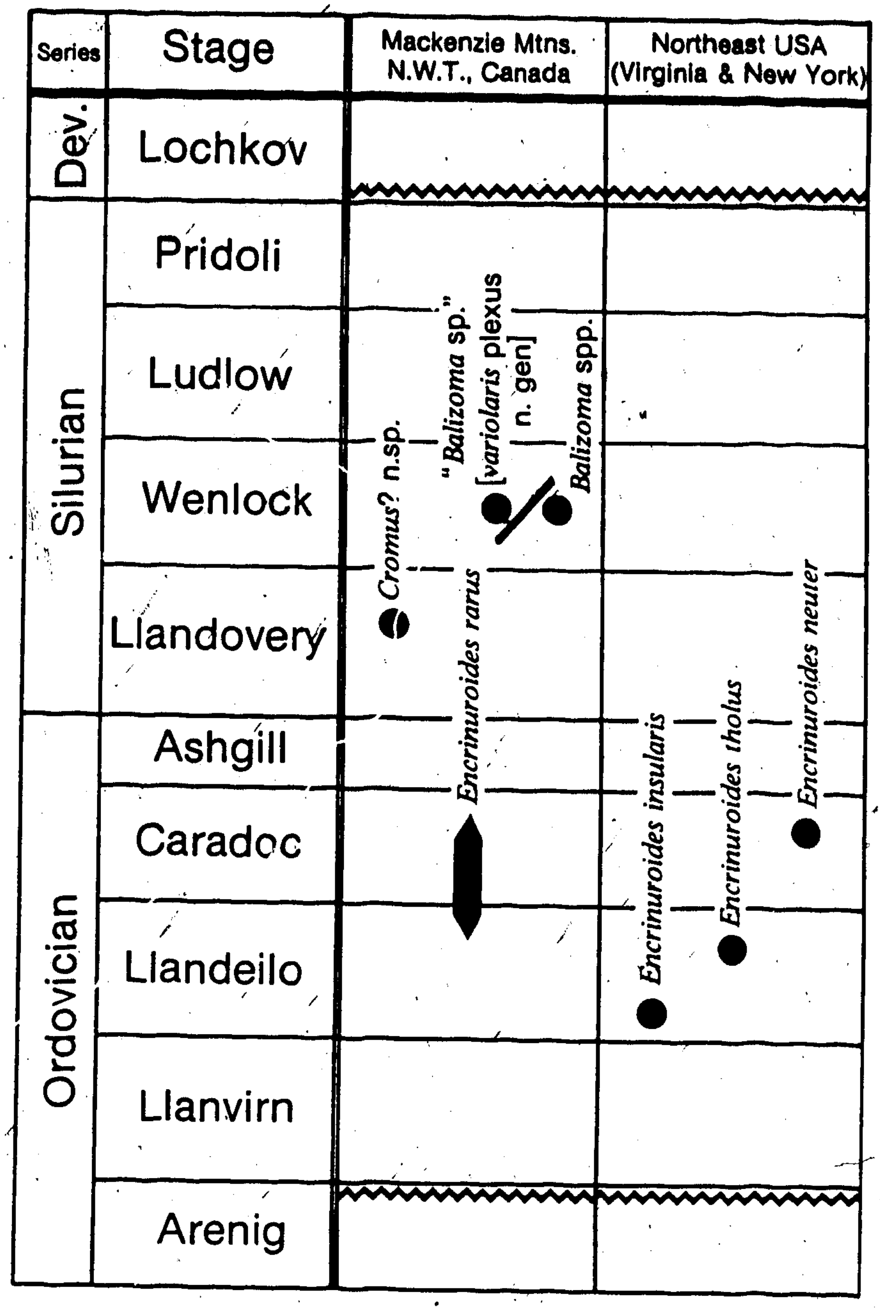
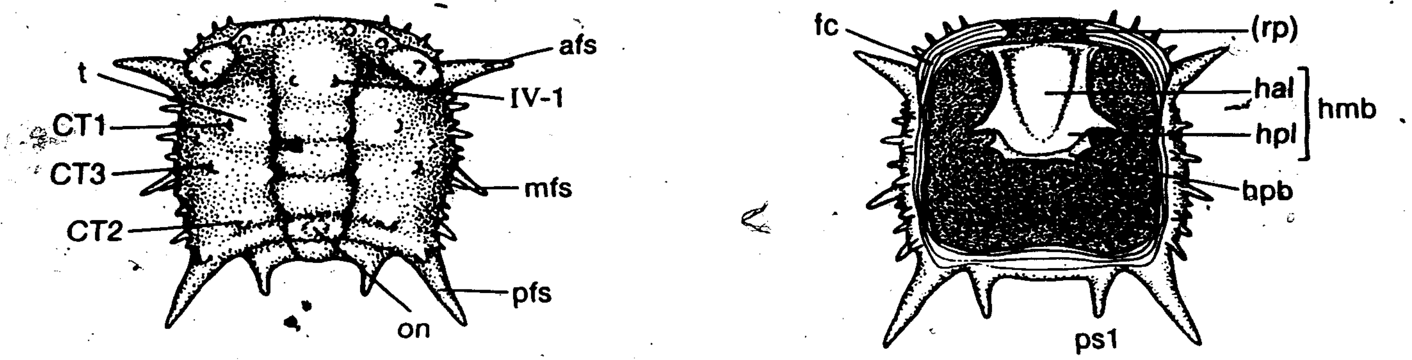


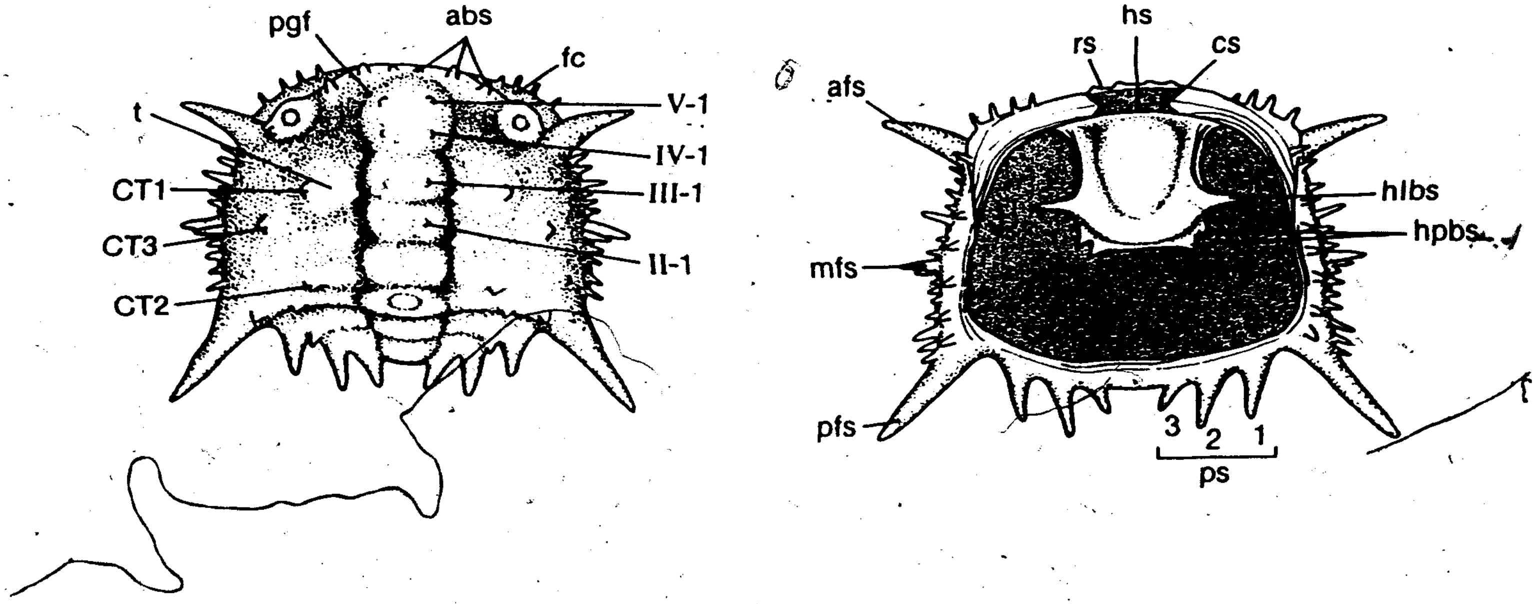
FIGURE III-1 - Stratigraphic and geographic distributions of encrinurine species for which protaspides are known. Jagged line indicates the lower and upper stratigraphic limits on the known occurrence of the Encrinurinae.

FIGURE III-2 - Dorsal (left) and ventral (right, lacking rostral plate) views of stages 1 and 2 protaspides of <u>Encrinuroides</u> <u>insularis</u> Shaw, 1968, indicating terminology applied to encrinurine protaspid morphology as follows: abs - (proto)cranidial anterior border spines; afs - anterior fixigenal spine; cs - connective suture; CT1/CT2/CT3 - fixigenal "circumocular tubercles"; fc - free cheek; hal - anterior lobe of hypostomal middle body; hlbs - hypostomal lateral border spines; hmb - hypostomal middle body; hpb - hypostomal posterior border; hpbs - hypostomal posterior border spines; hpl - posterior lobe of hypostomal middle body; hs - hypostomal suture; mfs - midfixigenal spine; on - occipital node; pfs - posterior fixigenal spine; pgf - preglabellar furrow; ps - protopygidial marginal spines; (rp) - rostral plate (inferred by course of sutures); rs - rostral suture; t - torulus; I-1, II-1, III-1, IV-1 - glabellar tubercle pairs.

Stage 1



Stage 2



by Edgecombe and Chatterton. This paper departs from Evitt and Tripp (1977), Strusz (1980) and Ramsköld (1986) in the use of the conventional term 'axis' as opposed to 'rachis'.

ENCRINURINE PROTASPID DESCRIPTIONS

Encrinuroides insularis Shaw, 1968

Pl. III-1, figs. 1-7

Numerous protaspides of this species have been obtained from the Middle Ordovician Crown Point Formation (Chazy Group; Llandeilo) exposed on Valcour Island, New York (sample locality PB81 of Shaw, 1968). Meraspid through holaspid development of this species will be described in a separate work on the Chazy trilobites (Speyer and Chatterton, in prep.).

Two distinct stages are recognized in protaspides of E. insularis on the basis of graphically distinct groupings (see Figure III-3.1); these stages are further distinguished by various morphologic details as described below.

Stage 1 protaspides are of length (sag.) 0.39 - 0.44 mm, subquadrate in outline, with sagittal length of protocranidium 73 - 81% of width across 1L. Occipital ring shorter (sag.) than subequal 1L/2L/3L, lower and narrower

PLATE III-1 --*Encrinuroides insularis* Shaw, 1968. Crown Point Formation, Chazy Group, Valcour Island, New York, locality PB81 (Shaw, 1968). *1*, ventral view of stage 1 protaspis with disarticulated hypostome and free cheeks, NYSM 15066, x115; *2*, dorsal view of stage 1 protaspis, NYSM 15067, x50; *3*, slightly posteriorly-inclined dorsal view of stage 1 protaspis, NYSM 15068, x50; *4*, *5*, dorsal views of stage 2 protaspides, *4*, NYSM 15069, *5*, NYSM 15070, x50; *6*, ventral view of stage 2 protaspis with disarticulated hypostome and and right free cheek, NYSM 16009, x50; *7*, ventral view of stage 2 protaspis with disarticulated hypostome and free cheeks, NYSM 16010, x115.

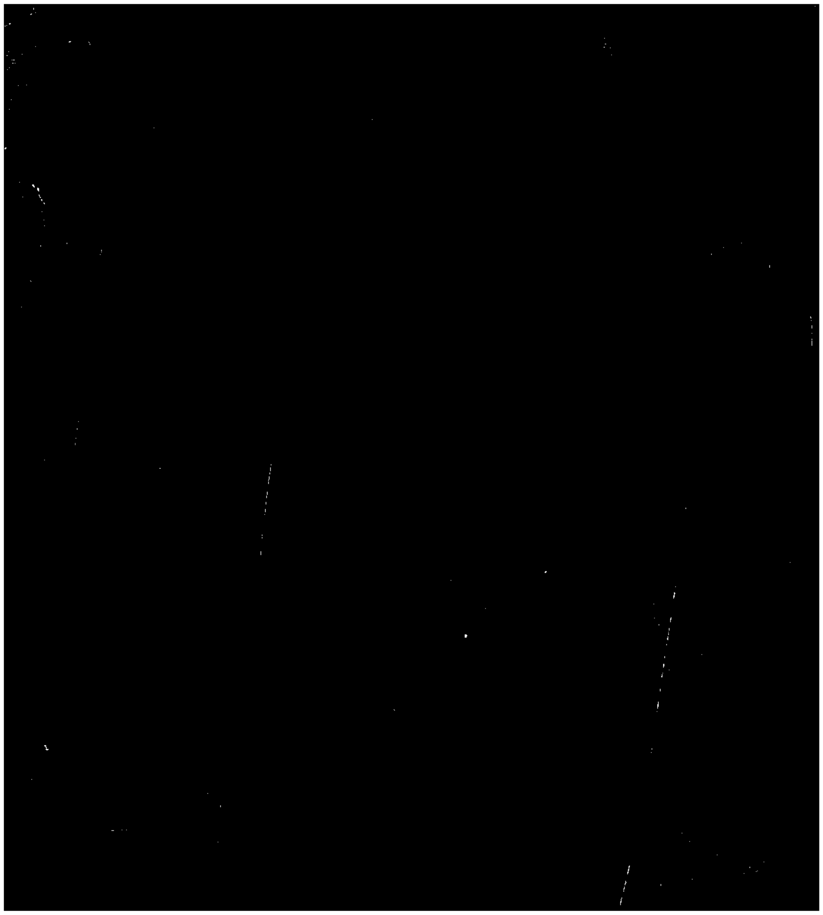
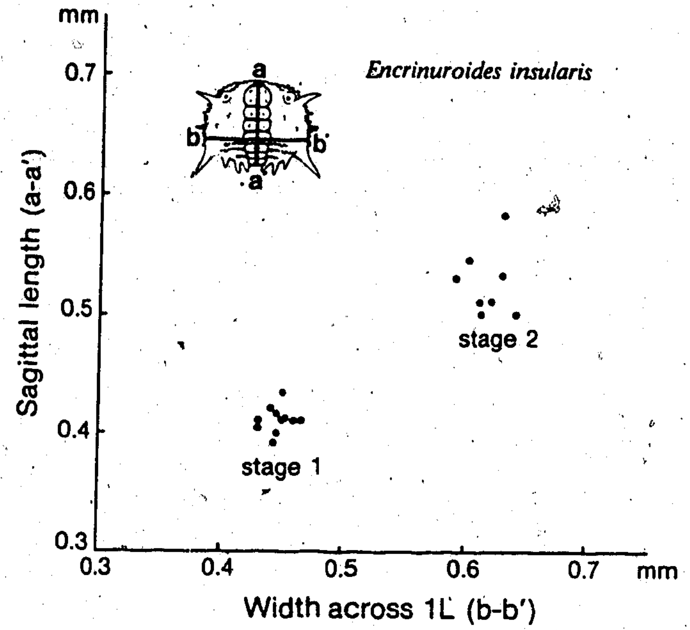
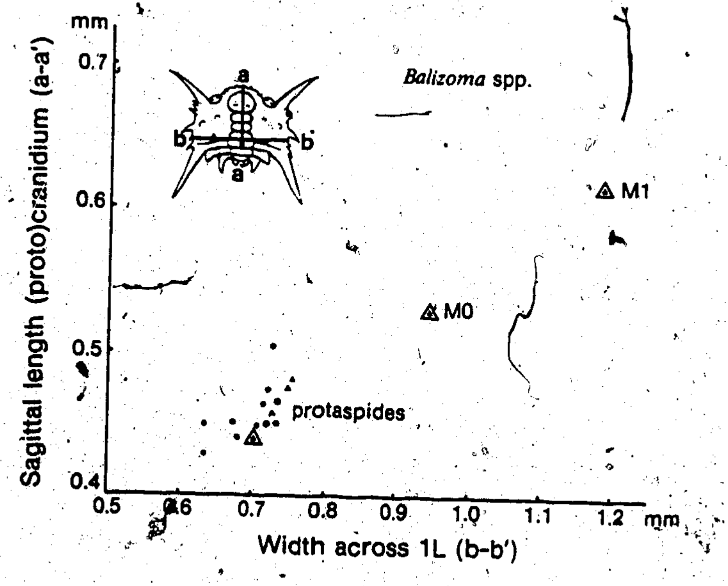


FIGURE III-3 - *1*, scatter plot of sagittal length of protaspis versus protocranidial width across midlength of 1L glabellar lobe for 19 protaspides of *Encrinuroides insularis* Shaw, 1968 [from locality PB81 (Shaw, 1968), Chazy Group, New York], indicating two discrete instars; *2*, scatter plot of (proto)cranidial sagittal length versus width across midlength of 1L for 14 protaspides and single degree 0 (M0) and degree 1 (M1) meraspides of *Balizoma* spp. Closed circles indicate specimens from locality Avalanche Lake Four, 126 meters above base; triangles from locality Avalanche Lake Two, 248.8 meters above base (locality data following Chatterton and Perry, 1983; 1984); enclosed triangles indicate specimens illustrated in Plate III-3.


Encrinuroides insularis
mm
0.7
0.6
0.5
0.4
0.3
Sagittal length (a-a')
a
b
b'
a
stage 2
stage 1
0.3
0.4
0.5
0.6
0.7
mm
Width across 1L (b-b')

1


Balizoma spp.
mm
0.7
0.6
0.5
0.4
Sagittal length (proto)cranidium (a-a')
a
b
b'
a
M1
M0
protaspides
0.5
0.6
0.7
0.8
0.9
1.0
1.1
1.2
mm
Width across 1L (b-b')

2

than 1L; 1L slightly wider than subequal 2L/3L. 4L spherical in outline and approximately as wide as 1L; very small IV-1 tubercle pair positioned on posterolateral part of 4L. 1S/2S/3S furrows continuous across glabella. Anterior border of cranidium broadest adjacent to axial furrows, narrowing sagitally. Glabella inflated proximal to gently-convex anterior margin. Preglabellar furrow shallows slightly sagittally. Two pairs of small tubercles postioned along anterior border. Palpebral furrow distinct; palpebral lobe moderately large, inflated, flexed upwards and bears small tubercles. Anterior fixigenal spine immediately beside palpebral lobe, stout, strongly divergent, may be very gently curved outwards. Palpebral furrow is convex backwards, runs around small elevated lobe. Torulus positioned abaxial to 3L, weakly bilobed, comprising large posterior lobe separated from smaller anteromedian lobe by a very shallow furrow; torulus occupies slightly less than one-half width of fixigenal field; torular tubercle (CT1) low. Postocular tubercle (CT2) distinctly raised, positioned immediately in front of posterior border furrow, slightly adaxial to middle (tr.) of fixigenal field; CT3 small, opposite 1S [between (exsag.) torulus and CT2], abaxial to middle (tr.) of field. Swollen lobe positioned adaxially on fixed cheeks opposite 1S/back of 2L; smaller lobe opposite 1L. Fixigenal field smooth, non-granulate. Lateral margin gently convex in outline. Midfixigenal spine present about half-way between anterior and posterior fixigenal spines, directed behind laterally and slightly posteriorly recurved. There are also few small equidistant anterolaterally to posterolaterally directed submarginal spines (slightly dorsal to midfixigenal spine) and some fine, spinose marginal granules. Posterior border furrow relatively broad (exsag.). Posterior fixigenal spine stout, slightly longer than anterior fixigenal spine and much less divergent, may be very gently curved outwards.

Free cheek small, curved; maximum curvature slightly behind eye which is positioned forward on low field, with relatively short anteromedian portion (developing precranidial lobe?); lateral margin with row of small spines. Facial suture originates close to second pair of small lateral submarginal spines (in front of midlength of cranidium), runs under base of anterior fixigenal spine, curving across palpebral lobe. Rostral plate (inferred by course of rostral/connective/hypostomal sutures) short (sag.), wide (tr.).

Hypostome shield-shaped in outline; anterior margin very gently convex; anterior wings small, positioned along anterior margin. Middle body small with respect to adult, slightly longer than wide, maximum convexity anteriorly; anterior lobe broadest towards front with rhynchos indistinct, defined by deep, narrow lateral border furrow, and shallower anterior border and middle furrows; middle furrow curves gently inwards near midlength of hypostome; lateral border furrow very shallow around relatively broad, flat posterior lobe of middle body, which is apparently wider than anterior lobe. Lateral margin almost straight between anterior wings and stout marginal spines positioned opposite back of middle furrow. Posterior border furrow deep, narrow (sag.), gently curved; border narrows slightly adaxially; posterolateral margin angular, apparently with two pairs of den[illegible]

[illegible]topygidium small, 12 -20% (averaging about 17%) of [illegible]l length of protaspis; separated from protocranidium b[illegible] shallow furrow. Axis slightly narrower than occipital ring, defined by shallow axial furrow; axial lobe extends almost to posterior margin; no more than one ring distinct. Pleural lobe with one pair of ribs curved gently backwards then inwards with marginal spines, extending slightly behind midlength of genal spine; adaxial interpleural furrow very shallow, indistinct. Posterior margin very weakly convex behind axis.

Doublure of protaspis quadrate in outline, uniformly narrow, with distinct terrace lines.

Stage 2 protaspides differ from stage 1 in the following cephalic characters:

(1) protaspides are larger (sagittal length 0.50 - 0.55 mm), and relatively broader (protocranidial length 63 - 68% of width across 1L) with maximum width occurring slightly

farther back, across 1L;

(2) the anterior margin is more strongly convex; anterior border spines are longer, thinner, with additional, more adaxially-positioned third pair;

(3) the torulus occupies a relatively smaller area of the enlarged fixigenal field;

(4) glabellar tubercles include small II-1, III-1, IV-1, V-1 pairs; low swellings are present on the lateral part of the 1L-3L glabellar lobes;

(5) the occipital ring is more elevated, relatively broader (subequal to 1L);

(6) maximum curvature of the free cheek is slightly farther backwards; the "[illegible]cranidial lobe" is relatively longer; the field is more elevated; lateral border spines are coarser;

(7) the anterior lobe of the middle body of the hypostome is more convex; the major lateral margin spine pair is more laterally directed;

Protopygidia of stage 2 protaspides differ from stage 1 in the following characters:

(1) the protopygidium is relatively larger (18 -27%, averaging 23%, of sagittal length of protaspis);

(2) the axis tapers slowly posteriorly, and is divided into two or three rings by shallow, continuous ring furrows;

(3) there are three pairs of pleural ribs with marginal

spines, the first pair bounded by distinct interpleural furrows which can be traced to the more deeply-incised axial furrow, the second pair of marginal spines projects almost as far back as genal spines;

(4) the inner margin of the protopygidial doublure is gently curved.

Balizoma spp.

Pl. III-2, figs. 1-8; Pl. III-3, figs. 1-6

Edgecombe and Chatterton (1987; Chapter II herein) discussed aspects of the protaspid period in Balizoma and assigned four protaspides and a growth series comprising meraspid and holaspid cranidia, to B. dimitrovi (Perry and Chatterton, 1979), a species originally described from the Delorme Range in the Mackenzie Mountains and allied to B. obtusus (Angelin, 1851) from Gotland (see Ramsköld, 1986). Further study on the ontogeny and evolutionary dynamics of Wenlock-Ludlow Balizoma from the Avalanche Lake area, however, indicates that species relationships are far more complex. Ontogenetic evidence is presented herein to suggest that B. dimitrovi as discussed by Edgecombe and Chatterton probably includes two closely related and co-occurring but ecologically-displaced species. While complete systematic treatment of these taxa will be presented elsewhere (Edgecombe and Chatterton, in prep.),

PLATE III-2 - 1-8, *Balizoma* spp. Delorme Formation, Mackenzie Mountains, Northwest Territories, Canada, locality Avalanche Lake Four, 126 meters above base (Chatterton and Perry, 1983; 1984). 1, dorsal, and 2, ventral views of protaspis with articulated free cheeks and rostral plate, UA 7824; 3, dorsal view of protaspis, UA 7825; 4, dorsal view of protaspis, UA 7826; 5, ventral view of protaspis with articulated free cheeks and rostral plate, UA 7766; 6, ventral view of small hypostome, UA 7827; 7, dorsal view of protaspis, UA 7767; 8, dorsal view of protaspis, UA 7828. 9, 10, "*Balizoma* sp." [*variolaris* plexus n. gen. n. sp. (Edgecombe and Chatterton, in prep.; Chapter IV)]. Delorme Formation, Mackenzie Mountains, Northwest Territories, Canada, locality Avalanche Lake Five, 58-60 meters above base (Over and Chatterton, 1987). 9, ventral and 10, dorsal views of protaspis, UA 7829. All specimens x50.

[redacted]

PLATE III-3 - *Balizoma* sp. Delorme Formation, Mackenzie Mountains, Northwest Territories, Canada, locality Avalanche Lake Two, 248.8 meters above base (Chatterton and Perry, 1983; 198[illegible]orsal, and *2*, ventral (with disarticulated hypostome) views of protaspis, UA 7830; *3*, dorsal, and *4*, ventral (with nearly articulated hypostome) views of degree 0 meraspis with articulated free cheeks, UA 7831; *5*, dorsal, and *6*, ventral (with disarticulated hypostome and right free cheek) views of degree 1 meraspis, UA 7832. All specimens x50.

[redacted]

preliminary results are critical [illegible] establishing relationships among protaspides.

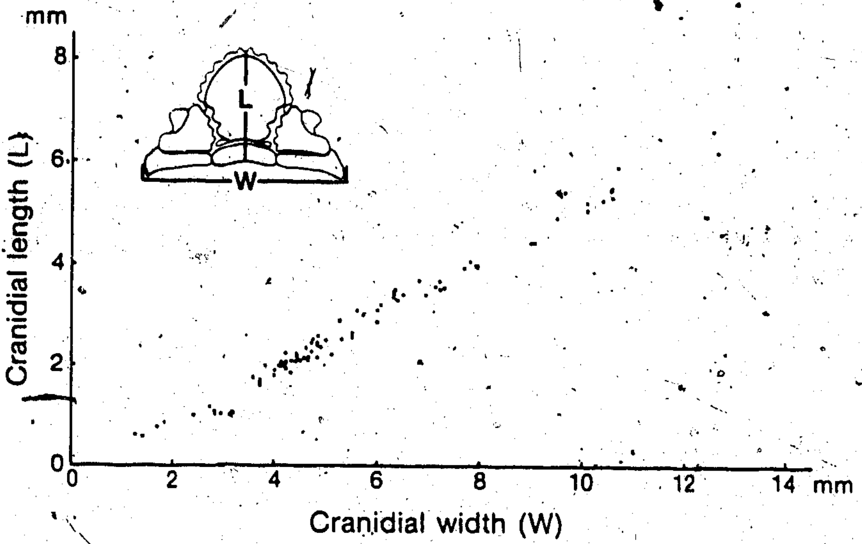
Data significant in evaluating the nature of variation in Wenlock populations of Balizoma [illegible] which protaspides have been obtained (Section Avalanche Lake Two, 248.8 meters above base; Section Avalanche Lake Four, 120.5-127 meters above base; see Chatterton and Perry, 1983, 1984) are considered below.

1) The two morphs may be distinguished on the basis of pygidial length:width ratios throughout the meraspid and holaspid periods (Figure III-4.2). Little overlap is observed even in small stages, with divergence increasing through ontogeny. However, the "wide" and "narrow" pygidial morphs both possess, on average, approximately nine pairs of pleural ribs and twelve axial rings in adult holaspides.

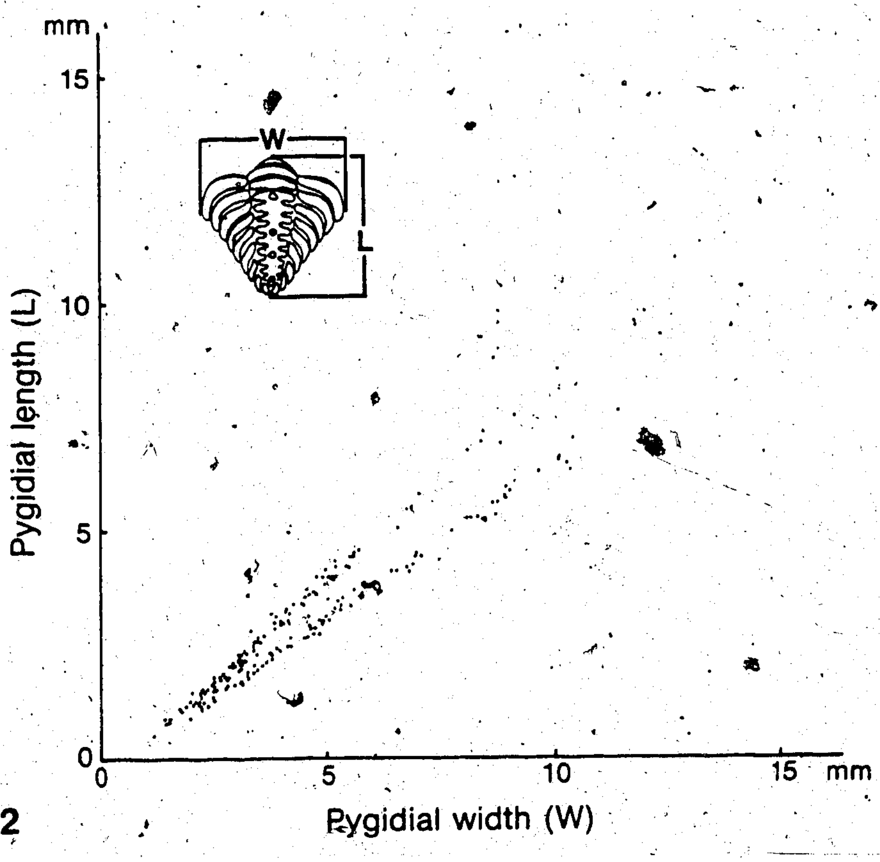
2) In contrast, cranidial length:width ratios through meraspid-holaspid ontogeny show an approximately rectilinear distribution along a single growth trajectory (Figure III-4.1).

3) Appreciable scatter is observed in protaspid length:width and protocranidial length:width ratios (Figure III-3.1); significant instar clusters are not defined by size/shape parameters. Certain character states shared between all Balizoma protaspides suggest inclusion within a single developmental stage (three pairs of marginal spines in the protopygidium, two pairs of protocranidial anterior border spines, IV-1 glabellar tubercles only). Evidence

FIGURE III-4 - 1, scatter plot of cranidial length versus width for 78 cranidia (early meraspid through holaspid period) of *Balizoma* spp. from locality Avalanche Lake Four, 126 meters above base (Chatterton and Perry, 1983; 1984); 2, scatter plot of pygidial sagittal length versus width (late meraspid transitory pygidia exclusive of protothoracic segments through holaspid period) for 196 pygidia of *Balizoma* spp.; locality as for 1.


mm
8
6
4
2
0
L
W
Cranidial length (L)
0
2
4
6
8
10
12
14
mm
Cranidial width (W)

1


mm
15
10
5
0
W
L
Pygidial length (L)
0
5
10
15
mm
Pygidial width (W)

2

provided by Ordovician encrinurine protaspides with discrete instar clusters [notably Encrinuroides insularis, but also E. rarus (Pl. III-4, fig. 1 versus Pl. III-4, figs. 2, 3) and E. neuter (Pl. III-5, fig.1 versus Pl. III-5, figs. 2, 4)] indicates that these characters are ontogenetically transformed between instars. The relatively large size of Balizoma protaspides and possession of three pairs of protopygidial marginal spines (cf. stage 2 protaspides in E. insularis, E. rarus, E. neuter) argues strongly for homology with the second protaspid stage in Ordovician encrinurines.

Within this composite cluster, however, two subtle morphologic end-members may be distinguished on the basis of shape [i.e., subquadrate (Pl. III-2, figs. 1-3) versus subrectangular (Pl. II-2, figs. 6, 8; Pl. III-3, figs. 1, 2)]. These may correspond to the two pygidial morphs present in meraspid and holaspid collections; statistically insignificant differences in protaspides, therefore, increase through the growth series following classic "von Baerian" divergence.

Three alternate hypotheses are considered in light of these data.

1) Two protaspid stages (instars) are represented by the subquadrate and subrectangular morphs, comparable to two protaspid instars in Ordovician encrinurines. As noted above, however, this hypothesis is weakened by shared

PLATE III-4 - Encrinuroides rarus, (Walcott, 1877). Esbataottine Formation, Mackenzie Mountains, Northwest Territories, Canada. 1, 4, locality A110, 2, 3, locality A125 (Chatterton, 1980). 1, stage 1 protaspis, UA 2802; 2, 3, stage 2 protaspides, 2, UA 2804, 3, UA 2803; 4, degree 1 meraspis, UA 2806. All specimens in dorsal view, x70 (originally figured Chatterton, 1980).

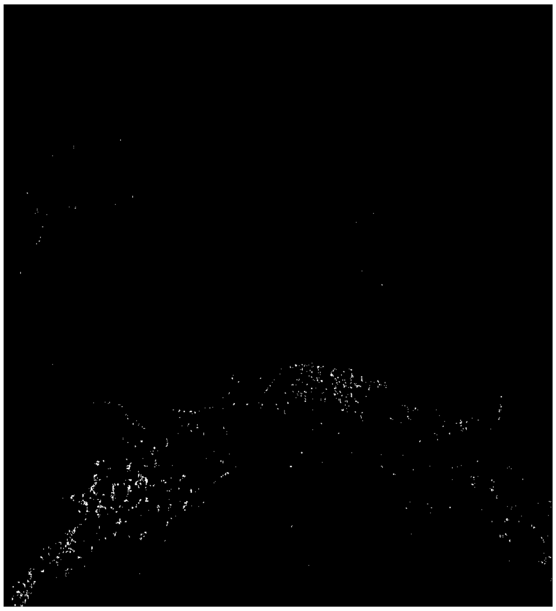


PLATE III-5 - *Encrinuroides neuter* Evitt and Tripp, 1977. Martinsburg Formation, Shenandoah Valley, Virginia, locality 10 (Evitt and Tripp, 1977). 1, dorsal view of stage 1 protaspis, USNM 217569; 2, oblique left anterolateral and 3, dorsal views of stage 2 protaspis, USNM 217570; 4, slightly oblique ventral view of stage 2 protaspis with disarticulated hypostome and right free cheek, USNM 217571. All specimens x50 (originally figured Evitt and Tripp, 1977; negatives kindly provided by R. P. Tripp).

[redacted]

states in several ontogenetically dynamic characters (number of protopygidial marginal spines and protocranidial anterior border spines; glabellar tuberculation), and insignificant size clustering/displacement. Excluding taphonomic biases, inclusion of all Balizoma protaspides in a single developmental stage (advanced states suggestive of homology with stage 2 of Encrinuroides protaspides) indicates a phylogenetic reduction in the number of sclerotized larval instars, i.e., the earlier developmental stage corresponding to stage 1 remained unsclerotized. This trend is observed elsewhere in the Trilobita; Orovician Failleana, for example, possesses an "asaphoid-like" pelagic early protaspis not known from younger illaenids or scutelluids, in which the earliest sclerotized stages are post-metamorphic benthic forms (Chatterton, 1980, p. 26-28).

2) A sexually dimorphic species is represented. This hypothesis is suggested by indistinguishable cranidia (on the basis of shape parameters and characters of tuberculation) and by progressive ontogenetic divergence between two pygidial morphs which possess similar numbers of segments and have coincidental spatial and temporal distributions (Edgecombe and Chatterton, in prep.). Sexually dimorphic pygidia have been proposed for several other phacopid trilobites (Whittard, 1934; Alberti, 1971; Holloway and Campbell, 1974; Perry and Chatterton, 1977,

1984), most relevant to the present survey being Holloway's (1980) proposed sexual dimorphism in Encrinurus (Encrinurus) egani Miller, 1880. This example similarly involves a single cephalic morph occurring with comparably-segmented narrow [illegible] pygidia.

The strongest argument against [illegible]morphism in Balizoma is the expression of presumed phenotypic differences early in ontogeny well before sexual maturation, i.e., in meraspid transitory pygidia and possibly as early as the protaspid period (subquadrate and subrectangular morphologies). It is common knowledge that secondary sexual characteristics in many extant crustacean arthropods are not manifest until a specific moult during which the adult-like juvenile spontaneously develops male or female traits (see Kaestner, 1970). Indeed, individuals within a given population are difficult to sex prior to this maturation moult (cf. "pubertal moult" of Carlisle, 1957) and are altogether undifferentiated during the first instars following hatching (i.e., external morphology and gonad appearance are identical in the two sexes; see Charnaiux-Cotton, 1960). Tessier (1960) indicated, however, that secondary sex characters in certain crustaceans appear throughout a strictly determined sequence of successive moults. Moreover, Goto and Hattori (1929) reported that sexually dimorphic traits in the xiphosuran Tachypleus tridentatus (Japanese King Crab) are not evident until individuals have attained an overall body size of 220 millimeters. This measure approximately corresponds to the twelfth moult following the so-called "trilobite stage", certainly well after development beyond typical larval attributes. These examples provide strong evidence against sexual dimorphism in early larval stages of trilobite development.

3) Two closely related, ecologically-displaced, and co-occurring species are represented. This hypothesis appears to best explain the two morph phenomenon and is most parsimonious in light of presently available evidence (i.e., least refuted by the arguments outlined above). This is particularly true if two distinct developmental trajectories are recognized throughout ontogeny. At present, it is speculated that the subquadrate and subrectangular protaspid end-members are the larvae of these two species. The variability observed in Balizoma protaspides, although probably representing the same homologous stage, is in accord with the two species hypothesis. Overlap in size and shape (Figure III-3.2) is consistent with a phylogenetic interpretation of "von Baer's Law"; i.e., early growth stages of closely related taxa are less readily distinguished than are later ontogenetic stages (Figure II-4.1). Retention of a conservative cephalic ontogenetic program and similar pygidial segmentation attest to recency of common ancestry,

closely allied to B. dimitrovi.

Protaspides of Balizoma spp. may be distinguished from stage 2 protaspides of Encrinuroides insularis by the following character states:

(1) considerably larger size (sagittal length of protaspis 0.55 - 0.63 mm);

(2) two longer pairs of protocranidial anterior border spines;

(3) the surface is covered with a granulate prosopon, notably on fixigenal field;

(4) the anterior fixigenal spines are longer and less divergent;

(5) the torulus is less conspicuously bilobate, and positioned farther abaxially to the 3L glabellar lobe;

(6) adaxial fixigenal lobes opposite 1L-2L are indistinct;

(7) 4L is relatively broader and subovate in outline;

(8) glabellar tuberculation includes only a coarse IV-1 pair;

(9) the occipital ring is relatively longer, being only slightly shorter than 1L;

(10) the lateral glabellar lobes lack the low swellings present on 1L-3L in E. insularis;

(11) the posterior fixigenal spines are longer, with half their length projecting beyond the tips of the longest protopygidial marginal spines;

(12) the midfixigenal spine is positioned slightly farther back (closer to posterior fixigenal spine), and is conspicuously larger than another more dorsal spine positioned directly above; these form a prominent spine pair in *E. insularis* not consistently present in *Balizoma* spp.;

(13) laterally-directed submarginal spines (between anterior and midfixigenal spines) are denser, with numerous tiny ventrolateral marginal spines along fixed cheek;

(14) librigenal lateral border spines are larger;

(15) the rostral plate is narrower, with 2-3 pairs of spines;

(16) small hypostomal marginal spines between the anterior wings and major lateral margin spine pair (in front of antennal notch) are prominent;

(17) the hypostomal posterior border furrow is more strongly convex;

(18) the hypostomal lateral border furrow is more distinct opposite the posterior lobe of the middle body;

(19) the middle furrow of the hypostomal middle body is shallower, and almost disappears posteromedially;

(20) the inner margin of the doublure is gently curved laterally; doublure is widest anterolaterally at maximum curvature of free cheek, narrowing sagittally (including anteromedian part of free cheek, ie. position of developing precranidial lobe, and rostral plate) with a broad anterior notch, also narrowing slightly posterolaterally where

protaspis attains maximum width; the inner margin of the protopygidial doublure is less convex medially than in E. insularis; terrace lines few and indistinct, except for submarginal ridge on free cheek.

Many of these differences (2, 4, 7, 9, 11, 12, 14, 15, 17, 18, 19) may be accounted for partly by the larger size of Balizoma protaspides, since their morphological states fall higher on or close to the ontogenetic trajectory for E. insularis. Several possibilities may explain this pattern of size increase (from which many character states are allometric correlates). Modification (retardation) of the timing of ecdysis could preserve protaspides at different developmental stages, and account for larger, more ontogenetically-advanced stages in Balizoma. Alternatively, protaspid development may have begun at a more advanced stage in B. spp. McNamara (1986) has suggested that such pre-displacement (this pattern possibly originating as a by-product of accelerated rates of pre-sclerotized development) may have been an important contributor to the "advanced" appearance of protaspides of post-Cambrian trilobites.

Changes occurring between the protaspid period and degree 0 of the meraspid period, in which articulation develops between the cephalon and transitory pygidium (Pl.

III-3, figs. 3, 4); include:

(1) increase in size (sagittal length 0.75 mm; width of cranidium across 1L 0.95 mm);

(2) broadening (tr.) of the cephalon (sagittal length 55% of width across 1L);

(3) broadening of 4L relative to more-posterior glabellar lobes;

(4) relative shortening of the anterior fixigenal spines;

(5) hypostome (sag. length) 0.33 mm, with relatively larger, more convex anterior lobe of the middle body;

(6) the rhynchos originates as a broad, low swelling on the anterior lobe;

(7) the hypostomal lateral border furrow is more deeply-incised around the anterolateral extremities of the posterior lobe of the middle body;

(8) the major hypostomal lateral margin spine pair is more strongly directed forwards; two pairs of spines originating along the margin of the slightly depressed posterior border are positioned posterolaterally;

(9) the free cheek is more gently curved;

(10) the rostral plate is narrower (tr.);

(11) the transitory pygidium is larger (sag. length 0.22 mm), with four pairs of marginal spines (first three pairs are less-strongly posteriorly-directed than in protaspides), and three pairs of pleural ribs; the axis has four (?) rings;

(12) the pygidial doublure is of uniform width, and its

r margin is evenly rounded.

An articulated degree 1 meraspis (one thoracic segment
free part extending posterolaterally as an elongate
e) [Pl. III-3, figs. 5, 6] has a sagittal length of
mm, of which the cranidium comprises 62% and the
sitory pygidium 31%. Trends occurring relative to the
ee 0 meraspis include:

progressive broadening of the cranidium (sag. length
of its width across 1L);

anterior border spines are long and stout; median pair
r 1) is distinct, small relative to two abaxial pairs;

the palpebral lobe migrates backward opposite the
le of 4L, and is separated from the axial furrow by a
ow fixigenal band;

the anterior fixigenal spines are relatively shorter,
much smaller than the posterior fixigenal spines (cf.
qual sized in protaspides);

the midfixigenal spine is much reduced in size;

the torulus is indistinct, but the torular tubercle
is large and prominent; CT2-CT3 remain the only other
enal field tuberculation; small granules are present
h are relatively smaller than in degree 0;

the occipital node forms a short spine;

the IV-1 tubercle pair is large and spinose; small
1, V-1 are also present;

(9) the rhynchos is narrower, defined by deeper furrows, and slightly overhangs the hypostomal anterior border furrow;

(10) the posterior border of the hypostome is more strongly convex;

(11) the major hypostomal lateral margin spine pair is relatively smaller, and more forward-directed;

(12) the free cheek is only gently curved, with five or six short spines along the lateral border; a very low librigenal field is rather indistinctly separated from the lateral border by a shallow border furrow; the precranidial lobe is not distinct from the anterior border of the free cheek;

(13) the transitory pygidium is of length (sag.) 0.31 mm, with four pairs of pleural ribs and five pairs of marginal spines extending almost as far back as the posterior fixigenal spines; interpleural furrows are distinctly incised.

Growth series for protaspid and meraspid hypostomes of Balizoma spp. and Encrinuroides insularis indicate that the encrinurine hypostomal border, with lateral and posterior borders intergrading in advanced stages, originates as a composite structure. In protaspides, the posterior border is completely separated from the middle body / lateral border by a deep posterior border furrow and is depressed (in ventral view) relative to the lateral border, which is continuous with the weakly-inflated posterior lobe of the middle body. The typical encrinurid distribution of seven hypostomal marginal spines, including three lateral / posterolateral pairs and an unpaired posteromedian spine (Edgecombe and Chatterton, 1987; Chapter II) is thus the product of two developmental events: 1) a prominent pair of anterolaterally-recurved spines originating from the margin of the lateral border, and 2) two smaller posterolateral spine pairs and a posteromedian spine originating from the margin of the posterior border. A small pair of marginal spines between the anterior fixigenal and major lateral border spines (in front of the antennal notch) are also conspicuous in protaspides of Balizoma spp. (Pl. III-3, fig. 2) and, particularly, in early meraspides of these species (Pl. III-2, fig. 6; Pl. III-3, figs. 4, 6) and Cromus? n. sp. (Pl. III-6, fig. 2), but are indistinctly developed in other encrinurine protaspides.

"Balizoma sp." [variolaris plexus n. gen. n. sp.]

Pl. III-2, figs. 9, 10

A single protaspis from section Avalanche Lake Five, 58-60 metres above base (Over and Chatterton, 1987) is assigned to the type species of a new genus (Edgecombe and Chatterton, in prep.; see Chapter IV herein) of the Encrinurus variolaris plexus. This species is closely related to Encrinurus sp. Tripp, Temple and Gass, 1977 and

Balizoma sp. Holloway, 1980, and is herein tentatively referred to "Balizoma sp." pending formal diagnosis of the new taxon. The overall morphology of the illustrated specimen, most notably development of three pairs of protopygidial marginal spines, suggests that it may represent a homologous late protaspid stage with that recorded in Balizoma spp. The protaspis of the new genus may be distinguished by the following character states:

(1) smaller size (sag. length 0.52 mm), with sagittal length of protocranidium 65% of its width across 1L. Small protaspid size is correlated with diminutive adult dimensions in this and other congeneric species;

(2) stouter, more strongly curved-outwards anterior fixigenal spines;

(3) more strongly-divergent posterior fixigenal spines;

(4) sparser cranidial marginal spines [an anterolaterally-directed spine immediately behind the anterior fixigenal spine, and a stout midfixigenal spine midway (exsag.) between the anterior and posterior fixigenal spine];

(5) shorter anterior border spines (two pairs);

(6) the torulus is broad [about one-half width (tr.) of fixigenal field across 3L], low, and distinctly abaxial of 3L glabellar lobe; the torular tubercle is indistinct (not obviously larger than the granular prosopon);

(8) smaller protopygidium with 3 shorter pairs of more (postero)ventrally directed marginal spines.

Cromus? n. sp.

Pl. III-6, figs. 1-3

A complete ontogenetic series, including protaspides (illustrated and discussed herein), is known for a new mid-Llandovery species from the Avalanche Lake area showing affinities to Cromus Barrande, 1852. This species shows particular similarities to C? moderatus (Poulsen, 1934) from the Llandovery of Greenland, for which Strusz (1980) presented evidence indicating a relationship (with questionable generic assignment) to Cromus. A formal diagnosis and description of this material and a revised systematics of Cromus and Encrinuraspis Webby, Moors and McLean, 1970, will be presented elsewhere (Edgecombe and Chatterton, in prep.). The protaspides are introduced in the present work for immediate comparison with other encrinurines, and to document the known range of variation among encrinurine larval stages.

Two protaspid specimens are presently known (Pl. III-6, figs. 1, 3), and although fragmentary, are comparable in size and morphology, and, therefore, probably represent the same protaspid stage. Differences with protaspides of Ordovician Encrinuroides and Silurian species of the Encrinurus variolaris plexus are striking; distinguishing character states of Cromus? n. sp. include:

(1) large size, and subcircular (versus ovate or

PLATE III-6 - <u>Cromus</u>? n. sp. Whittaker Formation, Mackenzie Mountains, Northwest Territories, Canada, locality Avalanche Lake One, 320 meters above base (Chatterton and Perry, 1983; 1984). 1, 3, dorsal views of protaspides, 1, UA 7833, 3, UA 7834; 2, ventral view of small (early meraspid?) hypostome, UA 7835. All specimens x65.

subrectangular) outline [maximum sagittal length 0.87 mm; maximum width across 1L 0.85 mm], with a relatively narrow protocranidium and large protopygidium (28% of sagittal length of most sagittally-complete protaspis);

(2) three pairs of spinose tubercles evenly spaced along anterior border of protocranidium;

(3) the frontal glabellar lobe is ovate (wider than long), and bears a faint, widely-separated IV-1 tubercle pair;

(4) the torulus and fixigenal circumocular tubercles CT1-CT3 are indistinct in protaspides (development of CT1-CT3 is retarded into the early meraspid degrees);

(5) the posterior fixigenal spines are, apparently, relatively short and non-divergent (directed backwards); the anterior fixigenal spines, while not preserved in known protaspides, are short and thin in early meraspides;

(6) the large protopygidium has, apparently, three pairs of pleural ribs and three or four axial rings.

RELATIONSHIPS INDICATED BY PROTASPIDES

Comparisons of early growth stages may be used to assess phylogenetic relationships between trilobite taxa. A phylogenetic corollary of "von Baer's Law" maintains that similarities in juvenile stages reflect proximity of common ancestry (see Gould, 1977; Lovtrup, 1978; Patterson, 1983). Early growth stages of related taxa are usually more similar than later stages, with divergence increasing through ontogeny. This concept, central to the "ontogenetic argument" in determining character state polarities in phylogenetic sequences (Nelson, 1978; Eldredge and Novacek, 1985), brings early developmental forms to the forefront of phylogenetic inference and insists, at least theoretically, on their significance. For example, the "asaphoid protaspis" (Fortey and Chatterton, 1988) is a pelagic larva characterizing the families Asaphidae, Nileidae, Remopleurididae, and Trinucleidae which shows morphologic divergence in later growth stages. To provide an example from the Encrinuridae, it is observed that the wide rostral plate of protaspides of Encrinuroides insularis resembles that of other phacopid protaspides [Pseudocybele nasuta Ross, 1951 (Fortey and Chatterton, 1988, Fig. 12B]; Ceraurinella nahanniensis Chatterton and Ludvigsen, 1976 (Chatterton, 1980, Fig. 6F; Pl. 9, fig. 3); Apocalymene quadrilobata (Chatterton, 1971) (Chatterton, 1971, Fig. 8J)], but becomes quite dissimilar in adult stages of these same species. A narrow trapezoidal rostral plate which widens slightly towards the hypostomal suture characterizes later growth stages of E. insularis and most other encrinurine holaspides. These observations contrast with Jaanusson's (1975) statement that "...in complete late protaspides of all groups of trilobites in which this ontogenetic stage is known, the ventral cephalic sutures are basically the same as in holaspides". Evolution within the protaspid period is demonstrated by the presence of a considerably narrower rostral plate (apomorphic by outgroup comparison, and supported by stratigraphic succession) in protaspides of Silurian (Wenlock) Balizoma spp.

The eight encrinurine species for which protaspides are known (Figure III-1) include several divergent lineages (see Strusz, 1980, Text-figure 9 for phylogenetic tree) ranging in age from early Llandeilo through mid Wenlock. This compilation permits comparison with protaspides of closely related groups, such as the Cybelinae, Pliomeridae, and Staurocephalidae to determine the phylogenetic significance of character states developed in protaspides of the Encrinurinae.

CYBELINAE - Encrinurine protaspides are most similar to those of cybelines, for which protaspides of Cybeloides Slocom, 1913 form a basis for comparison. The hypothesis that the Encrinurinae has ancestry in the Cybelinae (Henningsmoen, 1959; Whittington, 1966; Evitt and Tripp, 1977; Strusz, 1980) provides an outgroup for determining character state polarities in encrinurines. A single protaspis of C. virginiensis seca was illustrated by Evitt and Tripp (1977). Chatterton (1980) figured several specmens of C. cimelia Chatterton and Ludvigsen, 1976 belonging to two distinct stages designated as "small" and "large" stages. These are interpreted as homologous with stages 1 and 2, respectively, in Ordovician encrinurine protaspides. These two stages also characterize C. prima (Raymond, 1905) from the Chazy Group of New York, currently under study by Speyer and Chatterton.

Cybeline protaspides have also been figured by Fortey and Morris (1978). The illustrated "ana-" and "metaprotaspis" of Cybelurus Levitskiy, 1962 (later growth stages described in Fortey, 1980) of late Arenig-early Llanvirn age from the Valhallfonna Formation, Spitsbergen differ considerably from the stratigraphically younger cybeline Cybeloides. The specimen assigned to the anaprotaspid stage (Fortey and Morris, 1978, Pl. 94, fig. 8) represents an earlier larval stage than is known for Cybeloides or any species of the Encrinurinae, differing from a generalized "stage 1 encrinurid protaspis" as described herein by its more rounded (less trapezoidal/subquadrate) outline; absence of tubercles on the anterior border of the cranidium, fixigenal field, or glabella; indistinct torulus; longer palpebral lobes; sparser marginal spinosity (only stout anterior, mid-, and posterior fixigenal spines). A prominent sagittal furrow dividing 1L-3L into paired lobes, a plesiomorphy retained in Encrinuroides insularis, is also developed in calymenid protaspides (Chatterton, 1971; Hu, 1971; Chatterton and Siveter, in prep.) and in early protaspid stages in representatives of several cheirurid subfamilies [eg.

Kawina sexapugia Ross, 1951 (Ross, 1953); *Holia secristi* Whittington and Evitt, 1954 (Chatterton, 1980); *Hyrokybe julli* Chatterton and Perry, 1984; *Acanthoparypha perforata* Whittington and Evitt, 1954 (Hu, 1974); *Hadromeros scotti* Chatterton and Perry, 1984]. This character state, here indicated as widespread throughout the Phacopida, is retained from ptychopariine ancestry (see Whittington, 1981). Among ptychopariine families, sagittal furrowing of the glabella occurs in protaspides of alokistocarids [*Dunderbergia*? (Hu, 1971)], olenids [*Olenus* (Hu, 1971); *Acerocare* (Hu, 1971)], catillicephalids [*Pemphigaspis* (Hu, 1968)], kingstoniids [*Kingstonia* (Hu, 1968)], lonchocephalids [*Welleraspis* (Hu, 1964; 1968)], pterocephalids [*Dytremacephalus* (Hu, 1971); *Aphelaspis* (Hu and Tan, 1971; Hu, 1980b); *Housia* (Hu, 1970; 1980a)], missisqoiids [*Missisqoia* (Hu, 1971)], and ptychaspidids [*Ptychaspis* (Hu, 1971)]. The primitiveness of sagittal glabellar furrowing within the Trilobita is indicated by prominent expression of this state in protaspides of the redlichiids *Olenellus* (see Hu, 1971) and *Paradoxides* (see Westergård, 1936; Størmer, 1942; Šnajdr, 1958).

Stage 1 protaspides of *Cybeloides*, however, are extremely similar to the equivalent stage in the earliest encrinurines for which protaspides are known, particularly to *E. insularis* which, predictably, is of the stratigraphically-earliest occurrence. This stage is recognized as a small subtrapezoidal/-quadrate instar with a single pair of protopygidial marginal spines, contrasting with a larger, relatively broader, and more rounded stage 2 instar with three pairs of protopygidial marginal spines. The figured "metaprotaspis" of Cybelurus is less similar to encrinurine protaspides, differing in the lack of protocranidial tubercles (glabellar, fixigenal, or anterior border); indistinct torulus; only stout anterior, mid-, and posterior fixigenal spines; and short protopygidial margnal spines. Despite the observed stratigraphic distribution (Cybeloides first appearing in rocks of Llandeilo age, later than the late Arenig-earliest Llanvirn occurrence of the first Encrinuroides), this evidence supports more recent common ancestry between Cybeloides and Encrinuroides than between the latter and Cybelurus, and favors the choice of Cybeloides as an outgroup (i.e., plesiomorphic sister group) in cladistic analysis. These differences between protaspides of Cybelurus and Cybeloides / encrinurines are, however, shared between the former early-occurring cybeline and closely-similar protaspides of the pliomerid Pseudocybele nasuta Ross, 1951b (figured by Ross, 1951a; Fortey and Chatterton, 1988). These larval similarities substantiate Fortey's (1980) proposal that the Pliomeridae (perhaps a form allied to Evropeites Balashova, 1966) were ancestral to the Cybelinae, first represented by Middle Arenig species of Cybelurus and Lyrapyge Fortey, 1980. Comparison of pliomerid and encrinurine (Pseudocybele versus Encrinuroides) protaspides was also made by Evitt and Tripp (1977). The preservation of only two relatively advanced protaspid stages in Cybeloides and several Ordovician encrinurines (Encrinuroides insularis; E. rarus; E. neuter), with further reduction to a single sclerotized instar in Silurian Balizoma spp., contrasts with several protaspid instars of Pseudocybele nasuta, for which Ross (1951a) indicated an "anaprotaspid" and four "metaprotapid" stages. A growth series for Protopliomerops superciliosa (Ross, 1951b) also includes early protaspid stages, with at least three instars in this period. A possible phylogenetic significance (related to timing of initial sclerotization and subsequent ecdysis) is suggested (see also discussion under Balizoma spp.)

A symplesiomorphic character state (i.e., relative to other encrinurines; see discussion in "Encrinurinae" below) shared by Cybeloides and Encrinuroides insularis is the presence of median (position 1) tubercle pairs on several glabellar lobes. II-1, III-1, IV-1, and V-1 tubercles are developed in stage 2 protaspides of E. insularis. C. virginiensis seca possesses I-1, III-1, IV-1, and V-1 tubercles in stage 2 (Evitt and Tripp, 1977); this stage in C. cimelia includes I-1, III-1, and IV-1 pairs (Chatterton, 1980). In contrast, other encrinurine protaspides show development of a IV-1 tubercle pair only [E. tholus; E. neuter (not figured in Evitt and Tripp's reconstruction of stage 2, their Figure 9B, however a small, closely-spaced r is distinct on the posteromedian part of the 4L 1. III-5, figs. 2, 3 herein); *Balizoma* spp.; ia sp."; *Cromus*? n. sp.], while even this tubercle indistinct in stage 2 protaspides of *Encrinuroides* he derivation of this character state may reflect a hronic pattern; specifically, retardation of r tubercle development with delayed initiation of 1, III-1, (IV-1) and V-I tubercles into the period.

e 1 protaspides of *E. insularis* further resemble *Cybeloides cimelia* in comparable size/orientation es. The retention of stout, strongly-divergent fixigenal spines, particularily cybeline-like in aris, to a lesser degree characterizes other Middle an protaspides (*E. tholus*; *E. rarus*). This may be ed to the synapomorphic development of considerably less-divergent anterior fixigenal spines in *Balizoma* spp. and "*Balizoma* sp."

her symplesiomorphy which *E. insularis* shares with species is the presence of swellings opposite the labellar lobes on the on the fixigenal field to the axial furrows. Fixigenal lobes in stage 2 des of this species include the bilobate torulus, a swelling opposite 1S/posterior part of 2L, and a uced swelling opposite 1L. These fixigenal lobes rpreted as homologous with adaxial swellings which compromise the fixigenal portion of the cybeline pulvinus. This structure develops in the meraspid period in *Cybeloides*, incorporating lateral expansions of the glabellar lobes, the torulus (opposite 3L), and fixigenal swellings opposite the posterior glabellar lobes (Evitt and Tripp, 1977).

In addition, Middle Ordovician species (*E. insularis*; *E. tholus*; *E. rarus*) show the torulus to be positioned more proximal to 3L than in Silurian species of the *Encrinurus variolaris* plexus, in which the torular swelling "migrates" abaxially on the fixigenal field. Outgroup comparison with *Cybeloides*, in which the torulus is immediately adjacent to 3L (and ontogenetically fuses with that lobe to form the anterior part of the pulvinus), supports the observed stratigraphic succession and suggests that the former condition is plesiomorphic.

STAUROCEPHALIDAE - Discussion above demonstrates that protaspides of early cybelines retain plesiomorphic character states from pliomerid ancestry, and contrast with early growth stages in later cybelines [such as *Cybeloides*; *Bevanopsis* Cooper, 1953 (see Evitt and Tripp, 1977 for early meraspid-holaspid ontogeny of *B. ulrichi* Cooper, 1953); and possibly-related forms such as *Deacybele* Whittington, 1965], as well as with encrinurines and staurocephalids. The earliest representative of the latter family, *Libertella corona* Hu, 1971, provides a stratophenetic link between the Cybelinae and the later staurocephalids Oedicybele Whittington, 1938 and Staurocephalus Barrande, 1846, as recognized by Chatterton and Campbell (1980). Early growth stages of this species, including protaspides, have been figured and discussed by Hu (1971) and Evitt and Tripp (1977). Recency of common ancestry between these groups ("advanced" cybelines, encrinurines, and staurocephalids) is indicated by protaspid-early meraspid synapomorphies [not shared with pliomerids and early cybelines] such as the development of the torulus, distinct paired glabellar tubercles (IV-1 originating early in ontogeny), prominent paired tubercles along the protocranidial anterior border (typically two pairs), and a distinct "postocular tubercle" CT2 on the posterior part of the fixigenal field (CT3 is also typically present abaxial to this). Autapomorphies of staurocephalid protaspides (as indicated by comparing Libertella with an encrinurid outgroup) include considerable broadening of the protaspis, inflation (tr.) of 4L, reduction of the lateral glabellar furrows, development of large palpebral spines, and possibly, reduction of the torulus, and shortening of the anterior and posterior fixigenal spines. Alternatively, the weak development of the latter states may represent primitive states retained from the ancestral cybeline stock.

Tomczykowa's (1987) restriction of the Staurocephalidae to Staurocephalus and possibly Rongxiella Chang, 1974, with reassignment of Libertella and Oedicybele to the Encrinuridae, is based on interpretation of the bulbous anterior cephalic process of Staurocephalus as homologous with the encrinurid anterior border (and rostral plate/librigenal precranidial lobe) but not including the glabellar frontal lobe as described by previous workers (including Kielan, 1957; Evitt and Tripp, 1977; Chatterton and Campbell, 1980; Strusz, 1980; Thomas, 1981). However, since the narrow glabellar stalk (sensu Temple, 1956) of Staurocephalus is trilobate (1L - 3L) and indented by only two pairs of lateral furrows (1S - 2S), the conventional interpretation of the transglabellar furrow as representing 3S (with incorporation of 4L in the anterior process) is favored. Furthermore, inflation of 4L and reduction of the preglabellar furrow (with resultant merging of the glabella, cranidial anterior border, librigenal precranidial lobe, and rostral plate; see Thomas, 1981, Pl. 17, figs. 1, 3) are not uncommon trends in the evolution of the allied Encrinurinae. Such development occurs to some degree in certain lineages of the Encrinurus variolaris plexus and most notably in the Chinese "coronocephalines". These trends are particularly expressed in Rongxiella Chang, 1974, for which we follow Chang (1983) in assigning to the Encrinuridae, interpreting the swollen anterior cephalic process as homeomorphic with that of Staurocephalus. The hypostome and pygidia referred to R.

lixiensis Chang, 1983 are very distinctly "coronocephaline". As well, certain species of *Coronocephalus* show an almost comparable degree of swelling of the frontal lobe with a narrow glabellar stalk comprised of 1L-3L, the 3S furrow is transglabellar, and the preglabellar furrow is lost except for short abaxial indentations. The conventional homologies of the staurocephalid cephalon thus appear more parsimonious than Tomczykowa's proposal that implies substantial reduction of the glabella, and in particular the frontal lobe which is characteristically enlarged in related groups. *Libertella* and *Oedicybele* are herein retained in the family Staurocephalidae, as assigned by Evitt and Tripp (1977) and Strusz (1980).

As far as is known from currently-figured material, *Libertella corona* further resembles *Cybeloides* and Ordovician encrinurines in having two protaspid stages, described by Evitt and Tripp (1977) as "early" and "late metaprotaspid stage[s]" (Evitt and Tripp, Pl. 22, fig. 1; Fig. 18A, and Pl. 22, fig. 2; Fig. 18B; Hu, 1971, Pl. 22, figs. 7, 8; Text-Fig. 52 B, C, respectively). The elongate pairs of spines near the anterior margin of the (proto)cranidium, labelled by Evitt and Tripp (1977, Fig. 18) as VI-1, 2 glabellar "tubercles", are interpreted as homologous with the two pairs of anterior border spines of encrinurid early growth stages. This interpretation adds further support to similar ontogenetic relations between these families, since protaspides/early meraspides of most encrinurids described herein have IV-1 and V-1 glabellar tubercles (as labelled in Evitt and Tripp's Figure 18, originating in the later protaspid stage in Libertella), as well as two pairs of anterior border spines. In Libertella, the more abaxial pair (labelled by Evitt and Tripp as the VI-2 glabellar tubercle pair) is distinct in the first protaspid stage as tubercles positioned along the anterior margin slightly in front of the palpebral lobes. In light of new data on encrinurid ontogeny, which demonstrate that glabellar tubercles in median position 1 originate before more abaxial, position 2 tubercles, and that tubercles in major row VI originate subsequent to the IV-1 (and, typically, III-1, V-1 and, often, II-1 pairs, usually well into the meraspid period), the reinterpretation of these supposed glabellar spines as anterior border spines appears likely. As well, a shallow preglabellar furrow may be distinct into the holaspid period (see anterior view of L. corona cranidium figured by Johnson, 1985, p. 85, fig. 2), with these spine pairs clearly positioned along a short (sag.) anterior border. This Homology permits recognition of the "anterior border" portion of the inflated axial lobe of the staurocephalid cephalon, in which the preglabellar furrow is obsolete.

Chatterton and Campbell (1980) noted that Oedicybele also retains traces of cybeline ancestry. Kielan's (1957) illustrations of O. kingi Whittington, 1938 indicate paired tubercles on the frontal lobe of the glabella (including IV-1 and V-1, 2 in Figure 5), on 3L (III-1), and two pairs along the anterior margin which probably also represent anterior border tuberculation. Although the ontogeny of this species is not adequately known, the three tubercles on the fixigenal field are suggestive of CT1 - CT3 in their approximate positioning. Advanced growth stages in this staurocephalid thus display cephalic tuberculation comparable to cybelines and juvenile encrinurines.

ENCRINURINAE - Synapomorphies of protaspides of the subfamily Encrinurinae may be assessed by determining derived character states of primitive encrinurine species (theoretically, the stem species) relative to an outgroup (theoretically, the ancestral cybeline species). This analysis may be approached by determining apomorphic character states of Encrinuroides insularis, the earliest-known species which most closely approximates the ancestral cybeline condition (i.e., relative to protaspides of Cybeloides). It is noted, of course, that these evolutionary novelties may be modified considerably (with a possible loss or character state reversal) in later, descendant species. While "a particular character condition [occurring] only in older fossils" [Hennig's (1966, p. 95) "criterion of geological character precedence"] is, by itself, not an infallible indicator of primitiveness (see, for example, Schaeffer, Hecht and Eldredge, 1972), the early occurrence of *E. insularis* provides support for the theory that character states shared between this species and *Cybeloides* (i.e., an outgroup), but contrasting with those shared by younger encrinurines, are plesiomorphic for the Encrinurinae. A similar example of application of early representatives of clades to identify characters useful in outgroup comparison is provided by Fortey and Jeffries (1982). As well, *E. insularis* diverges from a hypothetical "primitive encrinurine" (more closely approached by the earliest known species, late Arenig or earliest Llanvirn *E. hornei* Dean, 1973) in its later ontogeny and shows a number of specializations linking it to the highly-derived genus *Physemataspis* Evitt and Tripp, 1977. As listed by Evitt and Tripp (1977, p. 138), these include swelling and rounding of the glabella with reduction of the lateral lobes, swelling of the elevated, finely-tuberculate palpebral lobes and posterior band at the back of the fixigenal field (bearing the postocular tubercle CT2), and granulation of the librigenal border. Furthermore, *Cybeloides* probably has certain autapomorphic character states not shared with the immediate ancestor to the Encrinurinae (as suggested by derived adult states such as the most extreme pulvinar development of any cybeline), and its later stratigraphic occurence indicates that it is not on the main evolutionary line of encrinurine ancestry.

Indeed, certain protaspid character states of Cybeloides are presently known only from this genus (a subtriangular 4L glabellar lobe and subtrapezoidal-shaped stage 1 protaspis, for example) and are potentially autapomorphic within a restricted group of "advanced" cybelines. Stage 1 protaspides of E. insularis may be distinguished from morphologically-similar stage 1 protaspides of Cybeloides cimelia (in Chatterton, 1980, Pl. 15, figs. 3, 4) and C. prima (Raymond, 1905) [Speyer and Chatterton, in prep.] by:

1) subquadrate (versus trapezoidal) shape;

2) more laterally directed posterior fixigenal spines;

3) loss of dichotomous spines on the ventrolateral margin, with development of numerous small submarginal spines;

4) the hypostomal lateral border furrow is shallower posterolaterally (posterior lobe of middle body is more poorly-defined);

5) slightly shorter, less convergent protopygidial marginal spines.

Ontogenetic divergence of encrinurines from cybeline character states is demonstrated by more obvious differences between stage 2 protaspides of E. insularis and Cybeloides. This developmental stage is distinguished by:

1) greater relative width of the protaspis, with a more rectangular (less quadrate) outline;

2) the anterior margin of the protocranidium is more

convex;

3) 4L is more rounded, subspherical in outline, versus the somewhat triangular, anterior-widening frontal lobe of Cybeloides;

4) the posterior fixigenal spines remain more laterally directed;

5) the hypostomal posterior border furrow adopts a different course, meeting the lateral margin behind the major lateral border spine pair, distinctly separating the lateral and posterior borders;

6) protopygidial marginal spines are considerably shorter (this stage in Cybeloides indicates the substantial degree of post-axial elongation of the pleural ribs charcteristic of later growth stages); the first pair is less-strongly ventrally-directed; the third pair is distinctly shorter than the second pair (cf. subequal length in Cybeloides).

Most of these larval character states are retained in later encrinurines. In particular, the broader, more rectangular outline, convex anterior margin, more rounded (subspherical to subovate) frontal lobe, more laterally-directed posterior fixigenal spines, lack of dichotomous spines on the ventrolateral margin, and shorter protopygidial marginal spines are important character states by which encrinurine protaspides may be distinguished from those of the plesiomorphic cybeline sister group. The faint bilobation of the torulus in E.

insularis is indistinct in Cybeloides and in other encrinurines, and may thus be autapomorphic in this species.

Several other autapomorphies characterize various species and demonstrate the acquisition of evolutionary novelties in the protaspid period. Encrinuroides rarus possesses a relatively deep furrow extending across (tr.) the fixigenal field opposite IS, deliniating a "swollen posterior band" (cf. Evitt and Tripp, 1977, p. 139). Evitt and Tripp (1977) noted that this character is widespread in the Encrinuridae, with faint bands detectable in the meraspis degrees of several Ordovician taxa, and exceptional development in the encrinurine Physemataspis Evitt and Tripp, 1977 (see also Tripp, 1980). This furrow is most conspicuous in meraspid cranidia of E. rarus (Chatterton, 1980, Pl. 14, figs. 7-8), although its development in protaspides (Pl. III-4, fig. 2 herein) exceeds that in any other illustrated encrinurine species. The pronounced expression of this widespread but typically weakly-developed feature thus appears to be a derived character state. Stage 1 protaspides of E. rarus (Pl. III-4, fig. 1) may also be distinguished from other species by their greater relative width [ovate shape, in contrast to the typical (plesiomorphic) subquadrate shape].

The presence of a median (position 0) tubercle on the cranidial anterior border of Encrinuroides tholus, in addition to the two pairs developed in protaspides of other species, is autapomorphic. The five stout tubercles of the single protaspis figured by Evitt and Tripp (1977; Pl. 3, fig. 5; Fig. 7A) are extended as spines in the early meraspid stage (Pl. 3, fig. 6), and remain distinct throughout this period, possibly into the holaspid period (small cranidia figured in Pl. 4, figs. 2, 3). Large holaspides, however, have only faintly-developed anterior border tuberculation, notably two low, abaxially-positioned tubercles probably homologous with the abaxialmost pair in early growth stages.

Hu (1975) referred an Edinburg Formation encrinurine protaspis very similar of E. tholus to Otarion trilobus Hu, 1975. This specimen (Hu, 1975; Pl. 1, fig. 1; Fig. 1A) resembles E. tholus by having five coarse anterior border tubercles, a prominent pair of tubercles on the palpebral lobes, comparable size and orientation of anterior fixigenal spines, a distinctly-elevated torulus, a prominent IV-1 tubercle pair and occipital node, similar size and positions of CT2-CT3, and size of the protopygidium and orientation of the first pair of marginal spines. Hu's specimen, here referred to E. cf. E. tholus, has longer, more posteriorly-directed midfixigenal spines than Evitt and Tripp's figured protaspis of E. tholus. The apparent brevity of the posterior fixigenal spines, as represented in Hu's reconstruction (Fig. 1A), may possibly be attributed to fragmentation. Comparison with other

Middle Ordovician species of Encrinuroides suggests that both specimens represent the second protaspid stage as recognized in this study (on the basis of their large size, relatively rounded margin, and three pairs of protopygidial marginal spines), although it should be noted that Evitt and Tripp's specimen is apparently larger (sagittal length 0.55 mm versus about 0.40 mm).

Strusz's (1980, Text-figure 9) phylogenetic tree indicates close common ancestry between E. tholus and E. insularis, a relationship suggested by similar holaspid morphologies. Shared (?derived) character states include strong inflation of the densely-tuberculate glabella; elevated, finely-tuberculate palpebral lobes; a short (sag.), wide (tr.) fixigenal field with prominent pitting but sparse tuberculation; strongly-divergent posterior fixigenal spines; and sparse, low anterior border tubercles. Pygidial structure in these species resembles several other Middle Ordovician Encrinuroides, with a broadly-triangular outline, seven pairs of pleural ribs, approximately 15 - 23 axial rings with only weak development of a sagittal band, and paired granules on the anterior rings. These similarities in advanced ontogenetic stages would seem to predict closely comparable protaspides (excluding, of course, the possibility of homoplasy; synapomorphic development of the aforementioned states is, however, supported by the close temporal and geographic occurence of these species). Phylogenetic character analysis of stage 2 protaspides indicates that most of the similarities between these species are based on symplesiomorphy, as might be expected in early-occuring taxa. Prominence of palpebral tubercles may be a shared derived character state, perhaps related to tuberculation of the raised eye socle in later stages. However, important differences are recognized between protaspides of these species: E. insularis retains paired tubercles on the 2L and 3L glabellar lobes, as well as IV-1 and V-1 tubercles on 4L, and the fixigenal lobes adjacent to the axial furrow opposite the 1L-2L lobes, similar to Cybeloides; E. tholus develops only the IV-1 pair in the protaspid period (an apomorphic state present in later encrinurines) and lacks the fixigenal swellings interpreted as homologous with parts of the cybeline pulvinus. As noted above, other differences may be autapomorphic; the development of a median anterior border tubercle in E. tholus, and the bilobed state of the torulus in E. insularis.

Protaspides of late Caradoc E. neuter show similarities to both earlier Ordovician Encrinuroides as well as to Silurian Balizoma spp. and "Balizoma sp." (variolaris plexus n. gen. n. sp.). This lends support to the phylogenetic models of Evitt and Tripp (1977), Strusz (1980), Ramsköld (1986), and Edgecombe and Chatterton (1987; Chapter II herein); these proposed that a lineage including Encrinuroides uncatus Evitt and Tripp, 1977 and

ter was ancestral to Silurian Encrinurus, including
leurus) Ramsköld, 1986, the ancestral Llandovery
f the variolaris plexus from which both Balizoma and
w genus were derived (see also Chapter V herein). E.
r resembles other Ordovician Encrinuroides in
ing a small subquadrate stage 1 protaspis with a
pair of protopygidial marginal spines (Pl. III-5,
herein; Evitt and Tripp's (1977) "metaprotaspis
2", Pl. 3, figs. 7a, c]. As discussed previously,
ma spp. is apparently represented by a single
netically-advanced instar corresponding to stage 2 of
uroides, an apomorphy related to perturbation in
g of sclerotization. Insufficient data on the
pid period in variolaris plexus n. gen. does not
testing of the phylogenetic extent of this reduction
ber of protaspid stages (whether acquired by the
n ancestor of both variolaris plexus genera, or
cted to Balizoma). Synapomorphies of protaspides of
allied Silurian taxa do, however, include elongation
anterior and posterior fixigenal spines, as well as
airs of protocranidial anterior border spines, and
l positioning of the torulus on the fixigenal field
ated in E. neuter).

otaspides of Cromus? n. sp. differ greatly from all
nown encrinurine larvae, most notably in their large
subcircular shape, long protopygidium, absence of a
s, retardation of fixigenal "circumocular tubercle"

development into the meraspid period, and reduced fixigenal marginal spines. These differences are interpreted as effects of distant common ancestry of *Cromus* with other taxa for which early ontogeny is documented, with the additional possibility of apomorphic specializations acquired in the Caradoc through mid-Llandovery evolution of the lineage. Following Strusz (1980), two major clades stemming from lineages grouped in paraphyletic *Encrinuroides* are recognized; these split very early in the history of the subfamily, probably in the Arenig or early Llanvirn. The lineage giving rise to the type species, Ashgill *E. sexcostatus* (Salter, 1848), is distinguished by small irregularily-distributed glabellar tubercles, weak development of cranidial anterior border tubercles and pygidial sagittal tubercles, subquadrate multituberculate lateral glabellar lobes, and a rather large pygidium with a relatively high number of pleural ribs (often nine or more pairs) and axial rings (approximately twenty). *Cromus* (first occuring in the Caradoc of Australia), is probably also derived from or shared common ancestry with this lineage (see Chapter V). Strusz (1980) suggested that numerous Middle Ordovician species of *Encrinuroides* (including *E. rarus*, *E. insularis*, and *E. tholus*) were early offshoots of the other clade, which acquired coarse, symmetrically-distributed cephalic tuberculation in a Llandeilo - Caradoc lineage including *E. torulatus* Evitt and Tripp, 1977, *E. uncatus* Evitt and Tripp, 1977, and *E. neuter* . This evolutionary novelty was retained in descendant Silurian *Encrinurus*, and was acquired by the shared common ancestor to the endemic Chinese Silurian "coronocephalines" (*sensu* Chang, 1983, although we have reservations about the subfamilial rank proposed for this clade). The latter hypothesis is supported by *Encrinuroides zhenxiongensis* Sheng, 1964, of Caradoc - early Ashgill age from South China, which provides a stratophenetic link between the *E. uncatus* - *E. neuter* lineage and Chinese Silurian "*Encrinurodes*" near the ancestry of *Coronocephalus*. As noted by Strusz (1980, p. 45), the small subtriangular pygidium and "fairly coarse and regular" glabellar tuberculation of *E. zhenxiongensis* suggest the "main plexus leading to *E. uncatus* etc.".

The present survey of early ontogeny in the Encrinurinae indicates that this phylogenetically-important character state (coarse, symmetrically-distributed cephalic tuberculation in adult stages) is fundamental to encrinurid development. The phylogenetic expression of this character state may indicate heterochronic patterns, thus demonstrating the influence of ontogenetic disruptions on evolution in these forms. Species which develop complex tubercle distributions through advanced growth stages, such as *E. insularis*, are characterized by coarse, paired tubercles in early stages. The ontogenetic "loss" of symmetry is largely an effect of negative allometry of positon 1 tubercles relative to abaxial major row tubercles, particularily on the frontal lobe. The apparent contradiction between these ontogenetic sequences and the observed stratigraphic succession (earliest species without distinct symmetry in advanced growth stages; symmetry developed in Llandeilo - Caradoc lineage and retained in descendants) suggests the possibility of paedomorphosis.

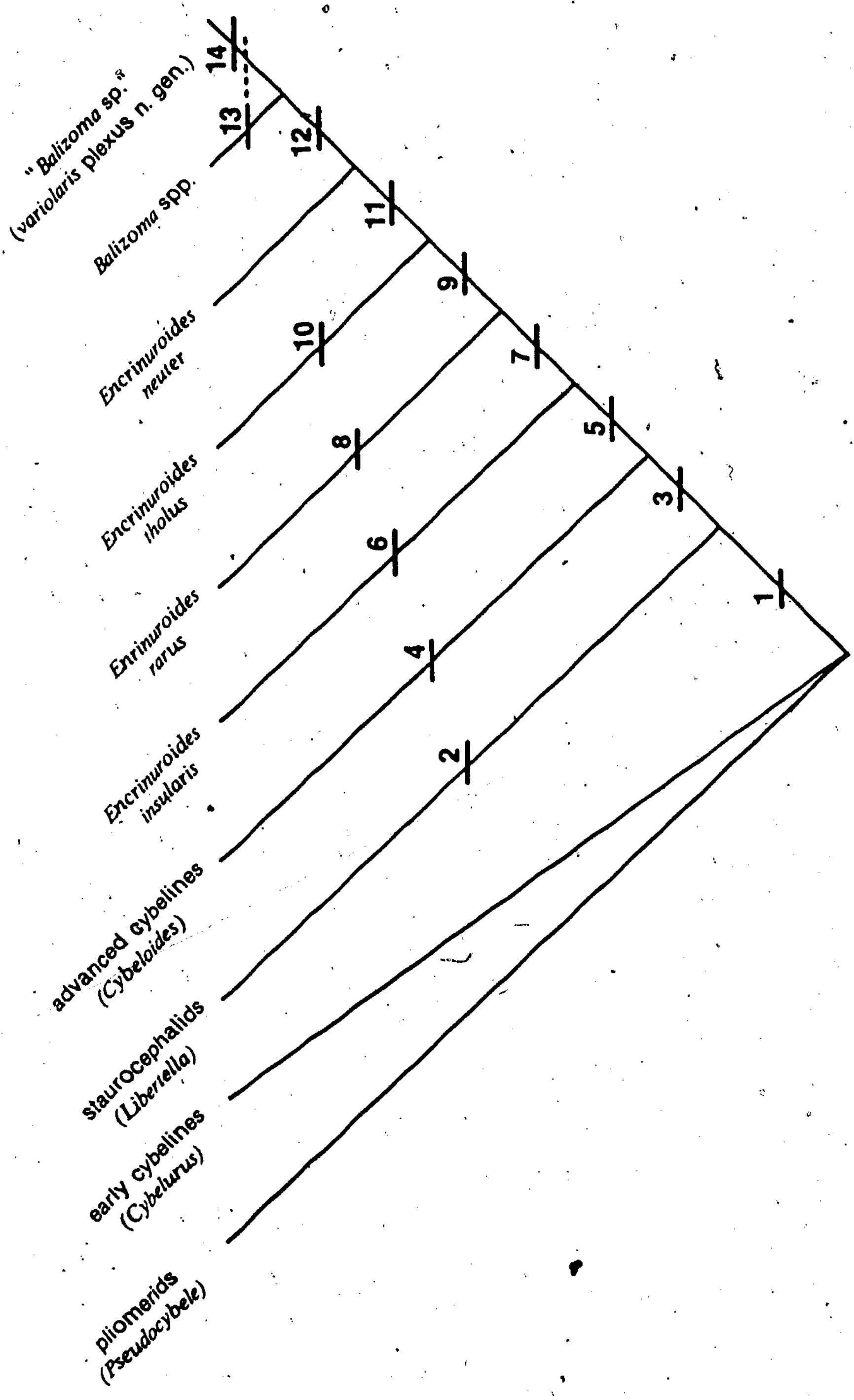
DISCUSSION AND SUMMARY

Character evolution within the framework of primitive and derived states as discussed in the text may be depicted in the form of a [illegible]ogram (Figure III-5). This provides a hypothesis of phylogenetic relationships between pliomerid, cybeline, staurocephalid, and encrinurine trilobites based on character states in early ontogeny. This statement of relationships has significant systematic implications which are explored herein.

Of particular concern is the taxonomic integrity (i.e., monophyly) of the Cybelinae. Cladistic analysis based on protaspid characters is in accordance with the conventional hypothesis that taxa included in the Cybelinae are ancestral to the Encrinurinae as well as to the Staurocephalidae (see references in text). Patterns of synapomorphy indicate that certain "advanced" cybelines share more recent common ancestry with the Encrinurinae and

FIGURE III-5 - Phylogenetic relationships between encrinurine and allied trilobite taxa indicated by protaspid character states. Bold numbers refer to apomorphies as follows: 1, only two protaspid instars, torulus and fixigenal "circumocular tubercles", paired glabellar tubercles; 2, broad protaspis, reduced lateral glabellar furrows, wide 4L, large palpebral spines; 3, fixigenal lobes abaxial to 1L-2L glabellar lobes (homologous with posterior fixigenal component of pulvinus), long divergent anterior and posterior fixigenal spines; 4, subtrapezoidal stage 1, subtriangular 4L; 5, hypostomal posterior border separated from lateral border, hypostomal lateral border furrow shallow posterolaterally (posterior lobe of middle body weakly-defined), relatively short protopygidial marginal spines; 6, torulus bilobate; 7, glabellar tubercles restricted to IV-1 only, loss of adaxial fixigenal ("pulvinar") lobes; 8, pronounced development of transverse furrow on fixigenal field opposite 1S, stage 1 protaspis subovate in outline; 9, 4L subovate; 10, median unpaired protocranidial anterior border tubercle, coarse palpebral tubercle pair; 11, weakly divergent anterior fixigenal spines, torulus abaxial to 3L on fixigenal field; 12, greatly elongate anterior and posterior fixigenal spines, long protocranidial anterior

(continued on p. 131)


" Balizoma sp. "
(variolaris plexus n. gen.)
Balizoma spp.
Encrinuroides neuter
Encrinuroides tholus
Enrinuroides rarus
Encrinuroides insularis
advanced cybelines (Cybeloides)
staurocephalids (Libertella)
early cybelines (Cybelurus)
pliomerids (Pseudocybele)
14
13
12
11
10
9
8
7
6
5
4
3
2
1

border spines; <u>13</u>, protaspid period reduced to a single sclerotized instar; <u>14</u>, reduced number of fixigenal marginal spines, strongly curved (outward) anterior and posterior fixigenal spines, ventrally-directed protopygidial marginal spines.

Staurocephalidae than with earlier cybelines. Cybeline protaspides may be readily divided into a primitive pliomerid-like group (eg. Cybelurus) and a derived encrinurine-like group (eg. Cybeloides) in which such evolutionary novelties as a two-stage protaspis, the torulus, fixigenal "circumocular tubercles", and paired glabellar and prominent cranidial anterior border tubercles are developed. These synapomorphies record a monophyletic taxon including parts of the Cybelinae, the Encrinurinae, and the Staurocephalidae. The conventional concept of the Cybelinae obscures this historical group by emphasizing certain symplesiomorphies retained into the adult stages, with the resultant recognition of a paraphyletic (sensu Farris, 1974; Wiley, 1981) group including some, but not all, descendants of a common ancestor. The goal of the present survey is not to justify or refute the validity of such groups, one of the most fundamental debates between the cladistic and evolutionary systematic schools (for review, see Schoch, 1986), but to demonstrate that current systematics do not adequately represent the observed pattern of evolutionary transformations. The lack of apomorphies shared by and restricted to cybeline protaspides corresponds with the great degree of morphologic variation in subfamilial diagnoses (based on adult stages) such as attempted by Evitt and Tripp (1977). Such diagnoses reduce to descriptions of a heterogeneous class defined without emphasis on unique derived character states. Extreme variability in many characters ("axial furrows weakly or strongly developed", "eye ridge strong or absent", "rostral plate wide or narrow") records grouping of complexes of primitive (pliomerid-like) and derived (encrinurine-like) states.

Further revision of suprageneric taxa (ideally, monophyletic) within this branch of the Cheirurina is encouraged in order to attempt to unify relationships indicated by patterns of evolution in the larva with more typically utilized (although potentially less meaningful at high taxonomic levels) holaspid character states. Do adult characters, for example, record shared ancestry between "advanced cybelines", encrinurines, and staurocephalids as indicated by several fundamental protaspid synapomorphies? The hypothesized pattern of evolutionary relationships throws a questioning light on the validity of grouping all "cybelines" and encrinurines as a taxon (Family Encrinuridae) distinct from the equivalently-ranked staurocephalids. The integration of larval characters in a cladistic framework might alternatively restrict the Encrinuridae to "advanced cybelines" and encrinurines (united by synapomorphy complex 3 in Figure III-5), or further include staurocephalids as a subfamilial sister group (united by synapomorphy complex 1).

The cladogram summarizes a very significant but previously unsuspected trend in the larval evolution of these trilobite groups; i.e., the systematic reduction in numbers of sclerotized instars present during the protaspid period. Modification of timing of initial sclerotization provides a fundamental distinction between the protaspid period in plesiomorphic pliomerids / early "cybelines" [with several sclerotized instars, including small, early "anaprotaspides"],"advanced cybelines" / staurocephalids / Ordovician encrinurines [with only two sclerotized instars, not including early "anaprotaspides"; in the cybelines/encrinurines, stages 1 and 2 may consistently be distinguished on the basis of shape parameters and possessing one versus three pairs of protopygidial marginal spines], and in apomorphic Silurian forms such as <u>Balizoma</u>, with a single large, ontogenetically-advanced instar. Associated with condensation of the protaspid period and non-sclerotized early larval stages is the increased size and advanced morphological development of such Silurian forms . These ontogenetically-advanced character states may, as noted, be simple allometric correlates of increased size, which itself may have originated as a result of selection on a timing mechanism related to the onset of sclerotization. This trend in the Cheirurina and the above-mentioned example from the Illaenina are suggestive of the adultation of larvae (Freeman, 1982) observed in lineages within numerous metazoan phyla.

In this study the phylogenetic composition and historical context of species within the Encrinurinae and closely allied groups have been evaluated on the basis of larval characters alone. The results differ radically from currently accepted systematic organizations; cybeline trilobites, for example, are divided into "early" and "advanced" groups. These differences reflect fundamental limitations constraining the utility of paraphyletic groups in phylogenetic inference (see also Wiley, 1979). It is suggested that there exist alternative ways of studying historical groups and that conventional paraphyletic classes may, out of necessity, have to be reorganized to accomodate models consistent with observed patterns of descent. For example, the distinction between "early" and "advanced" cybelines (Figure III-5) although evident in adult comparisons, is particularly significant in light of differences noted among protaspides where relatively few characters are available for such comparisons. This is a direct outgrowth of a modified "von Baer's Law" which holds characters evident during early development as paramount to recognizing realistic phylogenetic groupings and proximity of common ancestry.

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CHAPTER IV

A NEW GENUS AND COMPARATIVE ONTOGENY OF THE ENCRINURUS VARIOLARIS PLEXUS (TRILOBITA; SILURIAN)

INTRODUCTION

Strusz's (1980) recognition of three phylogenetic plexi stemming from Silurian Encrinurus has contributed greatly to establishing a systematic framework consistent with current understanding of the Silurian evolution of the Encrinurinae. Ramsköld's (1986) subgeneric revision of Encrinurus formalizes these relationships: E. (Encrinurus) and E. (Pacificurus) comprise the phylogenetically-stable spinose/mucronate punctatus and Australasian mitchelli plexi, respectively, while E. (Nucleurus) represents the plesiomorphic Llandovery core of the variolaris plexus. This latter group includes the ancestors to restricted Wenlock-Ludlow offshoots (Fragiscutum Whittington and Campbell, 1967; Frammia Holtedahl, 1914) which have been elevated to generic rank based on distinct complexes of autapomorphies, as well as to the geographically widespread and morphologically conservative Wenlock-Ludlow core of the plexus recognized as Balizoma Holloway, 1980.

While Ramsköld's revised diagnoses are closely followed herein, retention of Strusz's (1980) concept of the variolaris plexus is encouraged to emphasize that this dynamic group is a monophyletic taxon. Synapomorphies uniting species referred to *Encrinurus* (*Nucleurus*), *Balizoma*, *Fragiscutum*, *Frammia*, and a new genus proposed herein include a peramorphic complex of cephalic character states (Edgecombe and Chatterton, 1987; Chapter II herein). These may be characterized as follows: a broad glabella; shallow preglabellar furrow; nine or more (usually ten or twelve) tubercles on the adaxially-narrowing cranidial anterior border; 2L-4L lateral lobe tuberculation enlarged relative to other glabellar tubercles; 1L reduced by merging of 1S with the occipital furrow adaxially; glabellar tuberculation dense, with abundant and relatively enlarged inter-row and abaxially-positioned major row tubercles; I-1 tubercle pair present, typically positioned forward across 1S; fixigenal tubercles overhanging axial furrow enlarged relative to field tuberculation; reduced genal spines. The pygidium is broader than long, having a wide, usually tuberculate axis with a sagittal groove, posterior pleurae recurved to form a "loop", and (particularly in post-Llandovery forms) a low ratio of number of axial rings to pleural ribs.

A distinctive cluster of North American Wenlock species of the *variolaris* plexus are herein recognized as a new genus, for which *variolaris* plexus n. gen. n. sp., described from several sections located approximately ten kilometers east of Avalanche Lake in the Mackenzie Mountains, Northwest Territories, is designated as type species. Stratigraphic and locality data used herein are as presented by Chatterton and Perry (1983; 1984) and Over and Chatterton (1987). Certain Wenlock species from Illinois, Wisconsin, and Arkansas previously referred to Encrinurus and Balizoma are reassigned to variolaris plexus n. gen. Cladistic character analysis outlined below in discussion of the new genus reveals several synapomorphies with Fragiscutum which indicate a sister group relationship.

As noted in Chapter V, the conventional assignment of taxonomic rank in the Encrinurinae is not consistent with strictly cladistic ranking based on recency of common ancestry. This is particularly apparent for Silurian forms, in which numerous genera are monotypic or include only a few species (Fragiscutum; Frammia; Paraencrinurus Ankelo, 1973; Batocara Strusz, 1980; Perryus Gass and Mikulic, 1982); in contrast, Ordovician Encrinuroides includes several divergent lineages which have been retained in a single paraphyletic genus based on symplesiomorphies. The recognition of the distinctive monophyletic species group variolaris plexus n. gen. as a generic level taxon follows convention for Silurian encrinurines. By explicitly indicating hypothesized cladistic relationships within the variolaris plexus, however, a framework is presented within which potential reassessment of taxonomic rank could be accomodated.

SYSTEMATIC PALEONTOLOGY

Family ENCRINURIDAE Angelin, 1854

Subfamily ENCRINURINAE Angelin, 1854

variolaris plexus n. gen.

Type species. - variolaris plexus n. gen. n. sp. from the Delorme Formation (Wenlock), approximately ten kilometers east of Avalanche Lake, Mackenzie Mountains, Northwest Territories, Canada.

Other species. - Encrinurus sp. Tripp, Temple and Gass, 1977 from the Middle Wenlock of Illinois and Wisconsin; Balizoma sp. Holloway, 1980 from the Wenlock of Arkansas. The specific name Encrinurus laurige, referred to Tripp, Temple and Gass, 1977 by Emielty and Bradbury, 1986 for Niagaranan material from Brookfield, Wisconsin is a nomen nudum apparently based on the species left in open nomenclature by Tripp et al., 1977. R. P. Tripp (personal communication, 1987) has informed the writer that the specific name indicated by Emielty and Bradbury should read "lauriae" (Gass, in manuscript).

Diagnosis. - A genus of the Encrinurus variolaris plexus of relatively small size. Glabella widens rapidly (tr.) anterior to 3L with broad hemispherical frontal lobe; rostral plate wide (tr.), subrectangular; enlarged fixigenal tubercles positioned opposite 1S-2S overhang row; palpebral lobe small; eye opposite 3L-4L, o axial furrow, with short eye socle. Field of subequal in length (exsag.) and height (tr.) to al lobe, with a row of about six coarse ; lateral border faintly tuberculate. Hypostome nal with flat, subrounded middle body; rhynchos e inconspicuous; posterior border short. Pygidium herical, with 6-8 pairs of pleural ribs and 7-9 s (R/P ratio 1.1 - 1.3); sagittal groove narrow; ittal tubercles typically present on every second r margin of doublure lacks U-shaped posteromedian

- This new genus comprises a morphologically- emporally and geographically restricted offshoot *ncrinurus variolaris* plexus. *Fragiscutum* n and Campbell, 1967 is most comparable in its oth-margined pygidium, discontinuous 1L reduced triangular nodes, low field of the free cheek, tened hypostomal middle body (notably in early *F. rhytium*) with inconspicuous maculae, reduced tubercles in the adaxial fixigenal tubercle row d below), and non-enlargement of PL (the t anterior border tubercle; Howells, 1982) o abaxial tubercles on the anterior border. omparison with the Llandovery grade of the plexus grouped as *Encrinurus* (*Nucleurus*) suggests that [illegible] similarities are synapomorphic. This hypothesis of [illegible] common ancestry of *variolaris* plexus n. gen. and *Fragiscutum* (i.e., sister group relationship) is further corroborated by similar temporal distributions (see below), and with known geographic occurrences of both taxa restricted to North America. Ramskold (1986) suggested that *Fragiscutum* may be descended from an early Llandovery branch of the *variolaris* plexus including *Encrinurus* (*Nucleurus*) *rotundus* (Männil, 1977). This species shows cephalic features which are plesiomorphic for the plexus, and pygidial form [15 axial rings / 8 pleural ribs; R/P ratio about 1.8] comparable to *Fragiscutum* [R/P approximately 1.7-2.0]. A common ancestor of *variolaris* plexus n. gen. and *Fragiscutum* may thus have diverged from *E*. (*Nucleurus*) in the early Llandovery. There is, however, an appreciable stratigraphic gap separating the appearence of the new genus (mid Wenlock) and *Fragiscutum* (late Wenlock). We follow Tripp, Temple and Gass (1977), Strusz (1980), and Ramsköld (1986) in restricting *Fragiscutum* to the type species, *F*. *rhytium* Whittington and Campbell, 1967 from Maine, and *F*. *glebalis* Campbell, 1967 from Oklahoma. These late Wenlock - early Ludlow species are distinguished from other *variolaris* plexus taxa by the development of only ten thoracic segments and low [non-pedunculate, with a short (tr.) librigenal field], enlarged eyes. The taxonomic significance of the reduced number of thoracic segments in

F. rhytium and F. glebalis has been questioned (Perry and Chatterton, 1979; Holloway, 1980). However, since the plesiomorphic state of eleven thoracic segments is so fixed and widespread in the Encrinurinae, modification of this character in these species provides an important synapomorphy.

The new genus may be distinguished from Fragiscutum by the following autapomorphic character states (in comparison to which the latter taxon more closely resembles the primitive condition of Encrinurus (Nucleurus):

1) lower number of pygidial pleural ribs and, particularly, axial rings, with a resultant low R/P ratio (1.1 - 1.3 versus 1.7 - 2.0);

2) almost complete reduction of the hypostomal rhynchos, and associated (as coaptative structures) absence of a U-shaped posteromedian notch in the inner margin of the pygidial doublure. Holloway (1980) observed that this notch, permitting insertion of the rhynchos into the pygidial doublure during enrollment, is well-developed in species here assigned to Balizoma and Fragiscutum, while Edgecombe and Chatterton (1987; Chapter II herein) further suggested a correspondence between these coaptative structures and the plesiomorphic encrinurine enrollment pattern. Despite modification (i.e., almost complete loss) of both of these structures in variolaris plexus n. gen., the shallow vincular furrow and distinct marginal flange beneath the anterior three or four pygidial pleural ribs

are comparable to *Fragiscutum* and *Balizoma* and suggest similar cephalic/pygidial interlocking mechanisms;

3) relatively greater inflation of the frontal lobe of the glabella;

4) wider (tr.) rostral plate (possibly an allometric by-product of widening of the frontal glabellar lobe). In this character state *variolaris* plexus n. gen. most closely resembles *Frammia* (see cephalon of *F. arctica* figured by Tripp *et al.*, 1977, Pl. 115, fig. 16; text-fig. 4). The rostral plate of *Frammia* differs from that of *variolaris* plexus n. gen., however, in the inward-sloping course of the connective sutures and resultant trapezoidal (versus subrectangular) anteroventrally-narrowing shape; and,

5) further reduction of the adaxial fixigenal tubercle row to two coarse tubercles overhanging the axial furrow opposite 1S and 2S (see below).

The new genus may also be distinguished from *Fragiscutum* by its primitive character state of smaller eyes on short eye socles, presumably retained from ancestry in *Encrinurus* (*Nucleurus*). This symplesiomorphy is also apparent in certain early (Wenlock) species of *Balizoma*, such as the type species, *B. variolaris* (Brongniart, 1822). The number of thoracic segments in the new genus is unknown (to test the possibility that reduction in the number of thoracic segments to ten in *Fragiscutum* originated in a common ancestor of the *variolaris* plexus n. gen. -

Fragiscutum clade).

Species here referred to Mackenziurus n. gen. were assigned to Balizoma by Holloway (1980) and Ramsköld (1986). Shared character states are largely plesiomorphic for the variolaris plexus, and reflect descent of both genera from Llandovery lineages assigned to Encrinurus (Nucleurus). Important character states by which Mackenziurus may be distinguished from Balizoma (first appearing in the Llandovery in Northern Canada; Ludvigsen and Tripp, in review) include the following:

1) small relative size;

2) greater inflation of the frontal glabellar lobe;

3) reduction of the adaxial fixigenal tubercle row to two coarse tubercles opposite 1S-2S (versus, typically, five or six subequal-sized tubercles in Balizoma);

4) a wide (tr.), subrectangular rostral plate (versus narrower, wedge-shaped rostral plate in Balizoma);

5) subpentagonal hypostome with reduced rhynchos and maculae, and rounding/flattening of the middle body (versus rhomboid hypostomal outline, prominent rhynchos and maculae, and inflated, subovate middle body in Balizoma);

6) smaller eyes;

7) a lower, more sparsely tuberculate librigenal field (typically bearing two "rows" of tubercles in Balizoma);

8) more round-margined and convex pygidium, usually with fewer axial rings and pleural ribs (7-9 rings in variolaris plexus n. gen. versus 9-11 in Balizoma variolaris, 10-15 in

B. *obtusus* and allied species; 6-8 ribs in *variolaris* plexus n. gen. versus 7-8 in *B.* *variolaris*, 8-12 in *B.* *obtusus* and allied species). As a result, the pygidial R/P ratio is typically lower (see Ramsköld, 1986, text-figure 3); and,

9) evenly parabolic inner margin of pygidial doublure lacks U-shaped posteromedian notch.

The recognition of *variolaris* plexus n. gen. thus restricts the degree of morphologic variation in *Balizoma* as diagnosed by Ramsköld (1986).

The new genus demonstrates progressive ontogenetic reduction of 1L by posterior reorientation of 1S to merge with the occipital furrow, a synapomorphy of the *Encrinurus variolaris* plexus also characterizing *Encrinurus* (*Nucleurus*), *Fragiscutum*, *Balizoma*, and *Frammia*. While the type species *variolaris* plexus n. gen. n. sp. retains low, discontinuous 1L nodes, the 1L lobe is apparently "obsolete", at least dorsally, in the congeneric species of Tripp *et al.*, 1977. In this species, the wide (sag.) furrow behind 2L represents a combined 1S / occipital furrow. This character state, originating by progressive reduction / loss of 1L, is nearly attained independently in other lineages of the *variolaris* plexus [eg. *Encrinurus* (*Nucleurus*) *diabolus* (Tripp, Temple and Gass, 1977); *Fragiscutum* *gl*[illegible] Campbell, 1967; *Frammia* *arctica* (Salter, 1852)].

<u>variolaris</u> plexus n. gen. n. sp.

Pl. IV-1, figs. 1-18; Pl. IV-2, figs. 1-21;
Pl. IV-3, figs. 1-13; Fig. I-1

<u>Type locality</u>. - Avalanche Lake Five, 58-60 metres above base [Delorme Formation; (mid?) Wenlock].

<u>Type material</u>. - Holotype pygidium UA 7843 (Pl. IV-1, figs. 14, 16-18); and paratypes UA 7836-7842, 7844-7853, 7857, 7861.

<u>Other localities</u>. - Avalanche Lake Four, 138 meters above base; Avalanche Lake Seven, basal seventy meters of measured section (occurrences at AV7-0, 27, 38, and 70 meters above <u>base</u>).

<u>Diagnosis</u>. - A species of <u>variolaris</u> plexus n. gen. retaining 1L as low discontinuous lobes; maximum glabellar convexity on front of 4L, which bears small paired lateral lobe tubercles; I-1 present; genal spines bluntly pointed; axial furrow flares abruptly in front of enlarged fixigenal tubercle opposite 2S. Librigenal field bears "row" of 6-7 coarse tubercles and several smaller adventitious tubercles. Pygidial length 55-65 percent of width, with 7-8 pleural ribs, 8-9 (rarely 10) axial [illegible] alternating small and large sagittal tubercles [illegible] tubercles abaxial to sagittal groove conspicu[illegible]

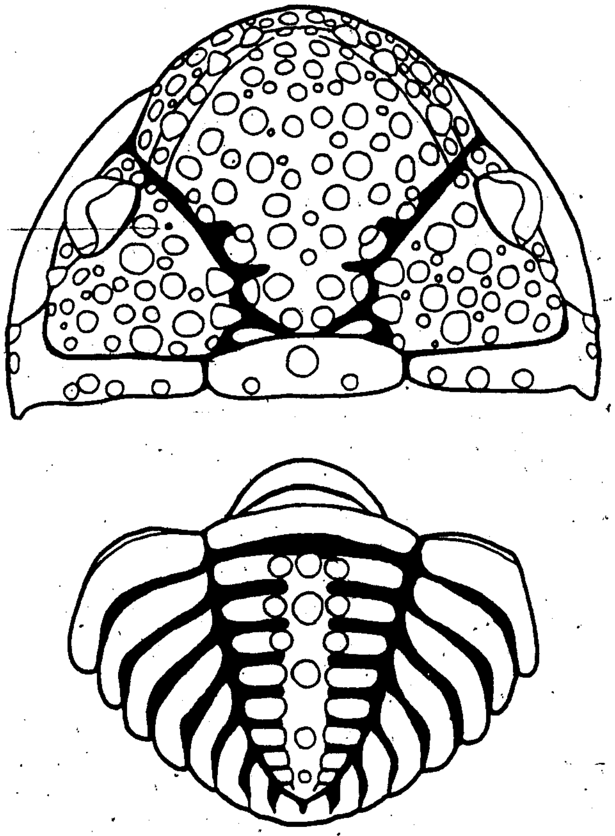


FIGURE IV-1 - Dorsal view of a reconstruction of cephalon and pygidium of *variolaris* plexus n. gen. n. sp. Reconstruction is based on specimens illustrated in Plates IV-1-3.

Plate IV-1 - *variolaris* plexus n. gen. n. sp. Delorme Formation, Mackenzie Mountains, Northwest Territories, Canada. All specimens from section Avalanche Lake Five, 58-60 meters above base (Over and Chatterton, 1987) except *13* (from section Avalanche Lake Four, 138 meters above base). Magnification x10 except where noted otherwise. *1*, dorsal view of free cheek, UA 7836; *2*-*4*, *6*, dorsal, ventral, lateral, and anterior views of cranidium, UA 7837; *5*, dorsal view of thoracic segment; *7*-*10*, anterior, dorsal, ventral, and lateral views of incomplete cranidium and free cheek, UA 7839, x5; *11*, dorsal view of cranidium, UA 7840; *12*, lateral view of cranidium, UA 7841; *13*, dorsal view of pygidium, UA 7842; *14*, *16*-*18*, ventral (x5), lateral, dorsal, and posterior views of holotype pygidium, UA 7843; *15*, external view of free cheek, UA 7844.

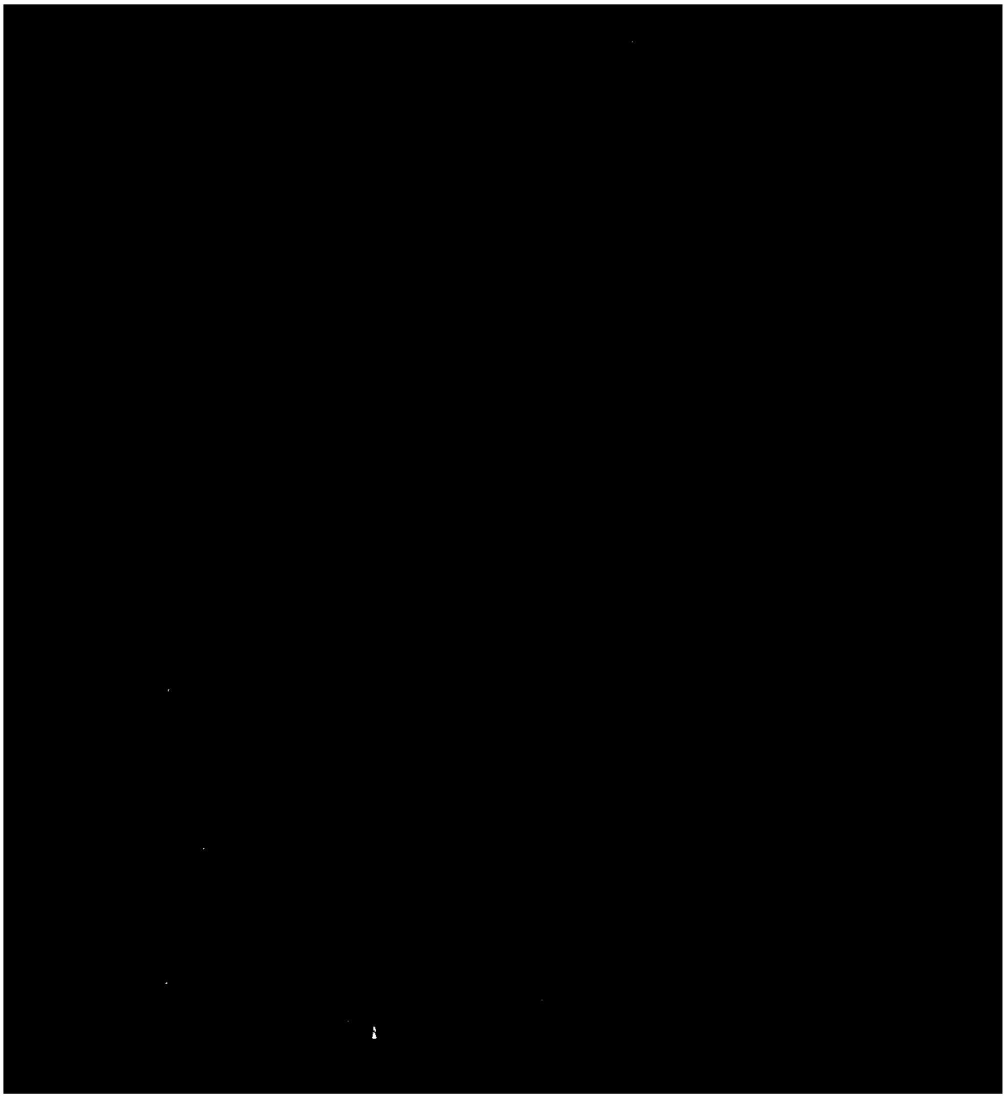


Plate IV-2 - *variolaris* plexus n. gen. n. sp. Delorme Formation, Mackenzie Mountains, Northwest Territories, Canada. All specimens from section Avalanche Lake Five, 58-60 meters above base (Over and Chatterton, 1987) except 3, 4, and 6 (from section Avalanche Lake Seven, 27 meters above base). Magnifications x10 except where otherwise noted. 1, 2, 5, dorsal, dorsolateral, and lateral views of cranidium, UA 7845; 3, 4, 6, dorsal, lateral, and anterior views of cranidium, UA 7846; 7, 8, dorsal, and anterior views of thoracic segment, UA 7847; 9-11, lateral, ventral, and anterior views of hypostome, UA 7848; 12-14, anterior, ventral, and posterior views of thoracic segment, UA 7849, x5; 15, dorsal view of cranidium, UA 7850; 16, 19-21, posterior, dorsal, ventral (x5), and lateral views of pygidium, UA 7851; 17, ventral view of hypostome, UA 7852; 18, dorsal view of pygidium, UA 7853.

[redacted]

Plate IV-3 - variolaris plexus n. gen. n. sp. Delorme Formation, Mackenzie Mountains, Northwest Territories, Canada. All specimens from section Avalanche Lake Five, 58-60 meters above base (Over and Chatterton, 1987) except 6, 10, and 11 (from section Avalanche Lake Four, 138 meters above base). All figures except 6, 10-12 are scanning electron micrographs. 1, 2, dorsal, and ventral views of protaspis, UA 7829, x75; 3, dorsal view of small (meraspid) cranidium, UA 7854, x50; 4 external view of small free cheek, UA 7855, x50; 5, dorsal view of small cranidium, UA 7856, x30; 6, 10, 11, dorsal, lateral (both x5), and ventral (x10) views of hypostome, UA 7857; 7, ventral view of small hypostome, UA 7858, x50; 8, ventral view of hypostome, UA 7859, x30; 9, dorsal view of small cranidium, UA 7860, x30; 12, external view of free cheek, UA 7861, x5; 13, dorsal view of small cranidium, UA 7862, x30.

[redacted]

- The specific diagnosis above includes Librigenal, and pygidial character states by *laris* plexus n. gen. n. sp. may be distinguished known congeneric species. Supplementary notes on ostic attributes are included below. Rostral, and thoracic character states, as well as ventral morphology, are presently known only pe species, and are thus described in greater

al length 55-65% of width; 4L 1.4 - 1.5 times n 3L, and 1.2 - 1.3 times width of occipital lla 1.1 - 1.2 times longer than width across 4L, um convexity forward on 4L. 1L present as low, us lobes bounded by posterior-directed 1S furrow es with occipital furrow behind I-1 tubercle ateral lobe bears a pair of exsagittally-aligned a small adaxially-positioned anterior tubercle, posterior tubercle), contrasting with single bercles on 2L-3L distinctly larger than more abellar tubercles. Glabellar tuberculation -1; II-1, 2; iii-0; III-1, 2(F), 3; 4L bears -1, 2, 3F/R; V-1, 2; VI-1, and smaller inter-row Occipital ring and cranidial posterior / eral border tuberculate in all but largest (see also "Ontogeny"). Preglabellar furrow axially-narrowing anterior border bears 10 -14 tubercles, abaxialmost pair ("PL") not relatively enlarged; cranidial anterior margin straight sagittally, defining wide (tr.) rostral suture. Adaxial fixigenal margin almost straight anterior to enlarged conical tubercles opposite 1S / 2S which overhang abruptly-flaring axial furrow. Palpebral lobe opposite 3S-4L and proximal to axial furrow, with one small intervening tubercle along facial suture. Fixigenal field pitted, densely tuberculate, including distinct CT1-CT4 of subequal size to coarse glabellar tubercles; CT1 adjacent to back of palpebral lobe (opposite front of 2L to back of 3L); genal angle bluntly pointed.

Pitted librigenal field with a poorly-defined "row" of 6 -7 coarse tubercles and several smaller adventitious tubercles, 80 -90% height (tr.) of faintly-tuberculate lateral border, very slightly longer (exsag.) than densely tuberculate precranidial lobe; eye socle prominent.

Cephalic apodemes expanded distally, directed inwards at outer end of occipital, 1S, 2S, and 3S furrows; 1S/2S apodemes large, longitudinally ovate and subspherical, respectively; occipital and, particularly, 3S apodemes small. In ventral view, 3S is a short anteromedially-directed furrow shallowing out just adaxial to 2L-3L lateral lobes; straight 2S weakly distinct across much of glabella. Cephalic doublure uniformly broad beneath librigenal lateral border and genal angle; cranidial doublure narrows abruptly adaxial to genal angle, librigenal doublure narrows gently beneath anterior border / precranidial lobe. Shallow vincular furrow along ventrolateral margin of cephalic doublure beneath librigenal lateral border corresponds with marginal flange beneath anterior three of four pairs of pygidial pleural ribs. Pygidial doublure broad, widening slightly posteromedially; inner margin evenly rounded, broadly parabolic.

Rostral plate (inferred by course of rostral, connective, and hypostomal sutures, including specimens with complete free cheeks articulated with cranidium) subrectangular, narrowing very slightly anteroventrally, approximately 1.5 times broader than long.

Hypostome with large flattened middle body of low convexity, subcircular, slightly broader than long; rhynchos weakly developed, defined by a faint broadly-rounded swelling on anterior margin of middle body, and very shallow furrows abaxially which are faintly-distinct in anterior 40 percent of middle body and rather strongly divergent posteriorly, incorporating about 60 percent of width of middle body where they shallow-out opposite front of anterior wings; maculae inconspicuous, forming small, low, ovate swellings on posterolateral margin of middle body; anterior border uniformly narrow and weakly flexed downwards to form a marginal rim, separated from middle body by a rather broad, shallow border furrow with distinct deeper elongate pits anterolaterally (at changes in curvature of margin); anterior margin rather straight sagittally, with abrupt posterolateral reorientation on straight anterolateral margins such that outline of hypostome is subpentagonal (particularly in small stages); anterior wings large, positioned in front of mid-length of middle body and shorter in height than middle body; short wing process near upturned edge of anterior wing; doublure narrow anteriorly and behind posterior wings (positioned almost mid-way between anterior wings and posterior margin of middle body), widening beneath posterior border, extending almost half-way to border furrow with gently concave anterior margin (lacking anterior-projecting median tongue present in Fragiscutum rhytium and many other encrinurines); middle body inflated to overhang lateral border immediately behind anterior wings; posterolateral border narrow, widening slowly posteromedially, bounded by a deep, narrow border furrow which shallows sagittally bounding posterior border; margin flexed backwards posterolaterally with distinct lengthening of broadly-rounded posterior border, angled ventrally, comprising less than 10 percent of sagittal length of hypostome.

Number of thoracic segments unknown; axial ring comprises about 35% of width of thorax, bowed gently forwards mesially and adjacent to rather deeply-impressed axial furrow; articulating half-ring about 40% of sagittal length of axial ring; ring moderately convex, rounded or weakly flattened sagittally; inner half of pleurae sloping gently inwards and fairly straight, outer half strongly recurved downwards; pleural band gently widens abaxially towards abrupt change in slope, abaxial to which it narrows and is gently flexed backwards with a weakly concave anterior margin; pleurae terminate in a bluntly rounded point. Axial processes prominent transversely ovate swellings; anterior flange uniformly narrow and about 30 percent of length of pleural band, in inner half of pleurae, widening abaxially and projecting forwards abaxial to fulcrum to form a prominent bluntly pointed facet; doublure of axial ring gently widens sagittally to almost one-half length of segment; apodemes positioned slightly inward of axial furrow, directed strongly inward and weakly downward; posterior recess well developed in inner half of pleural doublure.

Pygidium subhemispherical in outline, with length 55 - 65% of maximum width; 7 or 8 pairs of pleural ribs; downturned outer part of first rib pair inclined at 70 - 80 degrees; interpleural furrows widen towards change in slope, then narrow distally where tips of pleural ribs are expanded; posterior 2-3 pairs of interpleural furrows indistinctly continuous to ventral margin of pygidium (distal part of pleural ribs fused). 8 or 9 (rarely 10) axial rings with a narrow sagittal groove in all but the anterior 1 - 2 rings; in lateral view, axis is gently convex and weakly sloping for most of length, with abrupt steep slope in posterior rings and postaxial pleural ribs; coarse sagittal tubercles present on approximately every second ring, with smaller sagittal tubercles typically occurring on alternate rings; paired tubercles positioned abaxial to the sagittal groove on several of the anterior rings.

[illegible]<u>ion</u>. - The type species, <u>variolaris</u> plexus n. gen. [illegible] may be compared to <u>variolaris</u> plexus n. gen. sp. ([illegible]p, Temple and Gass, 1977) from the Middle Wenlock of Illinois and Wisconsin, and almost certainly congeneric pygidia from the St. Clair Limestone, Arkansas assigned to <u>Balizoma</u> sp. by Holloway (1980). Description and illustration of the former species is based on a single rather poorly preserved and fragmentary cranidium, a free cheek, and a few pygidia. The new species may be most readily distinguished from the form described by Tripp <u>et al.</u>, 1977 by its retention of 1L as low discontinuous ridges (this lobe is obsolete in the Illinois/Wisconsin species); presence of a I-1 tubercle pair, small paired tubercles on 4L, and short fixigenal spines; more anterior-positioned maximum glabellar convexity (in front of 4L versus 3L); more pronounced and abrupt flaring of the axial furrow in front of the enlarged fixigenal tubercle opposite 2S; more forward position of the palpebral lobes (opposite 3S/4L); presence of several small adventitious tubercles on the librigenal field in addition to the "aligned" 6 -7 coarse tubercles; and, a more strongly sloping pygidial profile.

Congeneric pygidia described by Holloway (1980) are more elongate and slope more steeply in lateral view (notably postaxially) than those of *variolaris* plexus n. gen. n. sp. The Arkansas species has only six pleural ribs (more strongly back- and down-turned, with the outer part of the first rib pair almost vertically inclined), seven axial rings, and a shallower sagittal groove. Holloway noted that the small number of axial rings and pleural ribs could be attributed to the small size of known specimens, apparently implying the preservation of juvenile growth stages. This possibility is weakened by comparison with similarly small adult holaspides of *variolaris* plexus n. gen. n. sp., in which a full complement of eight pairs of pleural ribs may be attained in pygidia with lengths as little as 25 percent of the largest known specimens, and by the ontogenetically advanced appearence of the smooth pygidial margin (lacking spinose rib terminations characteristic of early ontogeny in the type species and other taxa of the *variolaris* plexus).

ONTOGENY - Silicified material of *variolaris* plexus n. gen. n. sp. includes a relatively complete growth series for most sclerites, recording ontogenetic development from the protaspid through the holaspid periods.

A protaspis of this species figured by Edgecombe, Speyer and Chatterton (in review; Chapter III herein) as "*Balizoma* sp." [*variolaris* plexus n. gen. n. sp.] is reillustrated herein (Pl. IV-3, figs. 1, 2) to document ontogenetic changes across the protaspid-meraspid transition. Distinguishing character states relative to closely comparable protaspides of *Balizoma* spp. illustrated by Edgecombe and Chatterton (1987; Chapter II herein) and in Chapter III include: smaller size; stouter, more strongly curved-outwards anterior fixigenal spines; more strongly divergent posterior fixigenal spines; sparser cranidial marginal spines, including an anterolaterally-directed spine immediately behind the anterior fixigenal spine, and a stout midfixigenal spine midway (exsag.) between the anterior and posterior fixigenal spines; two pairs of shorter anterior border spines; the torulus is broad (about one-half width of fixigenal field across 3L), low, and distinstly abaxial to the 3L glabellar lobe, while the torular tubertcle (CT1) is indistinct and not obviously larger than the granular prosopon; smaller protopygidium with three pairs of shorter, more (postero-)ventrally directed marginal spines.

Trends in post-protaspid ontogeny are generally comparable to those documented by Whittington and Campbell (1967) in *Fragiscutum* and Edgecombe and Chatterton (1987) in *Balizoma*. These include the following:

(1) relative broadening of the glabella (rectilinear decrease in length/width ratio; Figure IV[illegible]) and, particularly, broadening of 4L relative to 1L-3L (Figure IV-3). Protaspides have a subovate 4L, slightly broader than subequal (in length and width) 2L-3L, with straight, transglabellar 1S - 3S furrows. The growth series demonstrates relative lengthening of 4L, becoming subhemispherical in outline, while 3S reduces to a short anteromedially-oriented furrow. 2S remains straight, but shallows out adaxially, while 1S reorients posteriorly to merge with the occipital furrow behind the I-1 tubercle pair; 1L is greatly reduced to low, discontinuous lobes in large holaspides (Pl. IV-1, fig. 8; Pl. IV-2, figs. 1, 2), although continuous 1L / straight 1S may be retained into the holaspid period (Pl. IV-1, fig. 2).

(2) Glabellar tubercle development is typical of the <u>variolaris</u> plexus, as documented in <u>Balizoma</u> by Edgecombe and Chatterton (1987; Chapter II herein). Protaspides have a IV-1 tubercle pair positioned posterolaterally on 4L, while V-1 is also present in early meraspides. A small (meraspid) cranidium (Pl. IV-3, fig. 3) shows distinct I-1; II-1; III-1; IV-1 (enlarged); V-1, 2; and VI-1 spine pairs. At this developmental stage, the lateral glabellar lobes are non-tuberculate (bearing short spines), and inter-row tubercles are indistinct. Additional major row tubercles are added abaxially through the meraspid period, on 3L (III-2F) and 4L (IV-2, V-2). Small inter-row tubercles

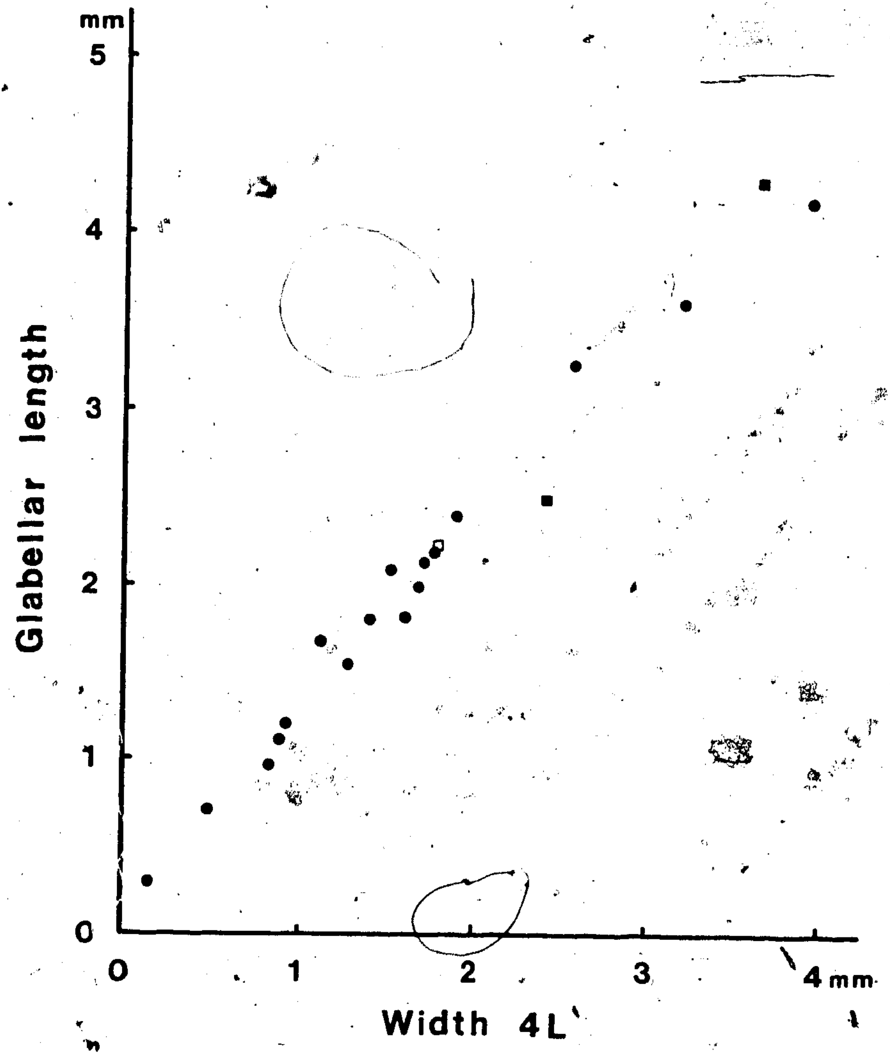


FIGURE IV-2 - Scatter plot of glabellar length (sag.) versus width across 4L for 20 specimens (protaspid through holaspid period) of variolaris plexus n. gen. n. sp. Measured specimens from section Avalanche Five, 58-60 meters above base (closed circles); and section Avalanche Lake Seven, 27 meters above base (open squares) and, 38 meters above base (closed squares).

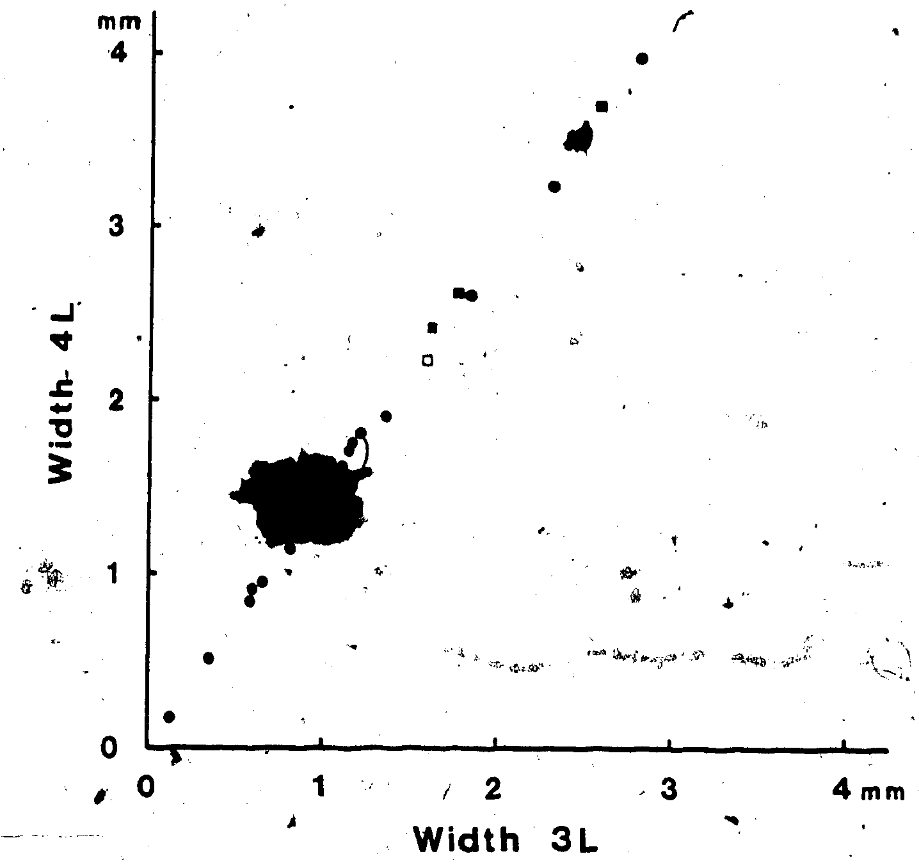


FIGURE IV-3 - Scatter plot of glabellar width across 4L versus width across 3L for 21 specimens (protaspid through holaspid period) of variolaris plexus n. gen., n. sp. Measured specimens from section Avalanche Lake Five, 58-60 meters above base (closed circles); and section Avalanche Lake Seven, 27 meters above base (open squares), and 38 meters above base (closed squares).

include iii-0 (and occasionally ii-0), and are abundant on 4L. Rounded tubercles develop on the 2L - 4L lateral lobes, finely denticulate in early stages. Large holaspides record flattening of tubercles through this period (spinose in small growth stages), enlargement of tubercles on the 2L - 3L lateral lobes relative to more medial tubercles, and an allometric trend towards subequal size of major row pairs (IV-1 notably larger in early stages) and enlargement of inter-row tubercles.

(3) The occipital ring and cranidial posterior/posterolateral border are prominently tuberculate in meraspides and small holaspides, but smooth or only faintly tuberculate in large holaspides. Occipital tuberculation includes a large median tubercle and a smaller pair posterolaterally. The occipital ring in large holaspides (Pl. IV-2, figs. 1, 2) is broad and conspicuosly furrowed (a broad, shallow furrow curved posterolaterally from abaxial edge of anterior margin and extending straight across midlength of occipital ring, separating slightly depressed anterior band from raised posterior/posterolateral band). The longitudinal swellings on the abaxial part of the occipital ring are comparably developed adjacent to the axial furrows [illegible] the thorax. Such transverse furrowing of the occipital ring and swelling of the anterolateral part of the thoracic axial rings are weakly developed in other taxa of the

variolaris plexus, being most prominen[illegible]ammia. In the type species, *F. arctica* (Salter), [illegible]ssed anterior band is very distinctly separated [illegible]m the elevated posterior band and, as noted by [illegible]p *et al.* (1977), simulates a 1L lobe.

(4) Ten to fourteen tubercles develop on the anterior cranidial border. Protaspides have two blunt spine pairs (Pl. IV-3, figs. 1, 2). These are elongate spines in small meraspides (Pl. IV-3, fig. 3), with a small third pair forming sagittally. Smaller tubercles inserted between these pairs increase in relative size through the holaspid period, resulting in a more uniformly-sized row of flattened tubercles in adults.

(5) The stout, elongate anterior fixigenal spine of protaspides (subequally long as the posterior fixigenal spine) is greatly reduced in early meraspides, and forms the rounded CT4 tubercle in holaspides. The midfixigenal spine is also reduced, and migrates posteriorly in front of the posterior fixigenal spine. The latter remain elongate in meraspides, and reorient backwards; progressive reduction occurs through the holaspid period, with the genal angle in large individuals only bluntly pointed.

(6) Small spinose fixigenal tubercles develop along the axial furrow opposite the 1S and 2S glabellar furrows (with clusters of tiny denticles in these positions in early growth stages; Pl. IV-3, figs. 3, 5). These tubercles coarsen through the growth series and assume a subconical

shape, nearly buttressing the axial furrow (Pl. IV-2, fig. 1).

(7) Small cranidia demonstrate the primary development of the CT1/CT2/CT3 fixigenal "circumocular" spines, with the torulus indistinct in early meraspides. The fixigenal field undergoes increased tuberculation, in which later-forming tubercles enlarge to a size only slightly smaller than the "circumocular" tubercles.

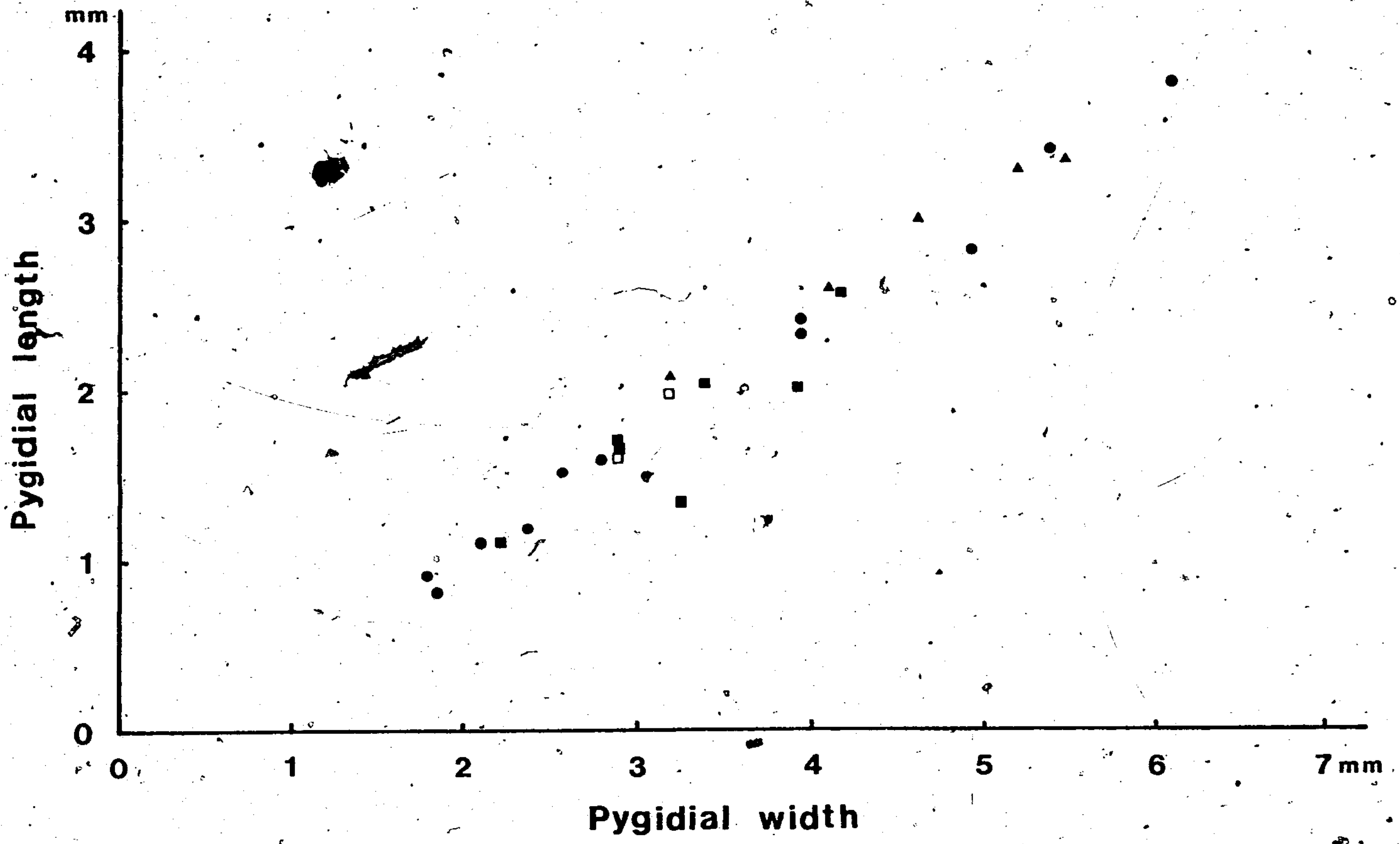
(8) The palpebral lobe, bearing short spines in early stages, migrates backwards from opposite 4L through most of the growth series to opposite 3S in large holaspides.

(9) The hypostomal middle body (widest anterolaterally in small stages and more bluntly rounded anteriorly than posteriorly) flattens, becomes rounder in outline, and inflates laterally to overhang the lateral border. A small pair of denticles on the lateral border and two pairs on the posterolateral border are present only in early growth stages (Pl. IV-3, fig. 7).

(10) The librigenal lateral border bears numerous short spines in small stages (Pl. IV-3, fig. 4) which are reduced to the faintly tuberculate adult state. Tuberculation on the lateral border precedes that on the precranidial lobe and field, which are more densely tuberculate in later ontogeny.

(11) An increase in pygidial length/width ratio occurs through the holaspid period (Figure IV-4). Other trends

FIGURE IV-4 - Scatter plot of length versus width for 25 holaspid pygidia of *variolaris* plexus n. gen. n. sp. Measured specimens from section Avalanche Lake Four, 138 meters above base (closed triangles); section Avalanche Lake Five, 58-60 meters above base (closed circles); and section Avalanche Lake Seven, 27 meters above base (open squares), and 38 meters above base (closed squares).


mm
4
3
2
1
0
Pygidial length
0
1
2
3
4
5
6
7 mm
Pygidial width

through this period (early holaspides already possessing seven or eight pairs of pleural ribs and eight or nine axial rings) include: reduced spinosity of the free rib terminations, with smoothing of the pygidial margin; deepening and broadening of the sagittal grrove; shortening of sagittal spines to rounded tubercles, and development of axial tubercle pairs lateral to the sagittal groove; loss of pleural tubercles; deepening and broadening of the axial and interpleural furrows; steepening slope of the distal part of the pleurae; and, increasing axial width relative to pygidial width (Figure IV-5).

COMPARATIVE ONTOGENY OF THE GENAL FIELD IN THE VARIOLARIS PLEXUS: CHARACTER EVOLUTION BY CHANGES IN DEVELOPMENTAL TIMING AND RATE

That minor changes in the timing and rate of developmental events affecting early ontogeny can yield substantial modification of adult morphology has long been central to the role of development in macroevolutionary theory (Goldschmidt, 1940; deBeer, 1954; see Gould, 1982; Maderson, 1982; Raff _et_ _al_., 1987 for recent perspectives). Comparative ontogenetic studies on species of several genera of the _Encrinurus_ _variolaris_ plexus (Figure IV-6) suggest that differences in "taxonomic characters" (Mayr, 1942) such as the number of tubercles in the adaxial

FIGURE IV-5 - Scatter plot of pygidial width versus axial width for 22 holaspid pygidia of *variolaris* plexus n. gen. n. sp. Measured specimens from section Avalanche Lake Four, 138 meters above base (closed triangles); section Avalanche Lake Five, 58-60 meters above base (closed circles); and section Avalanche Lake Seven, 27 meters above base (open squares), and 38 meters above base (closed squares).

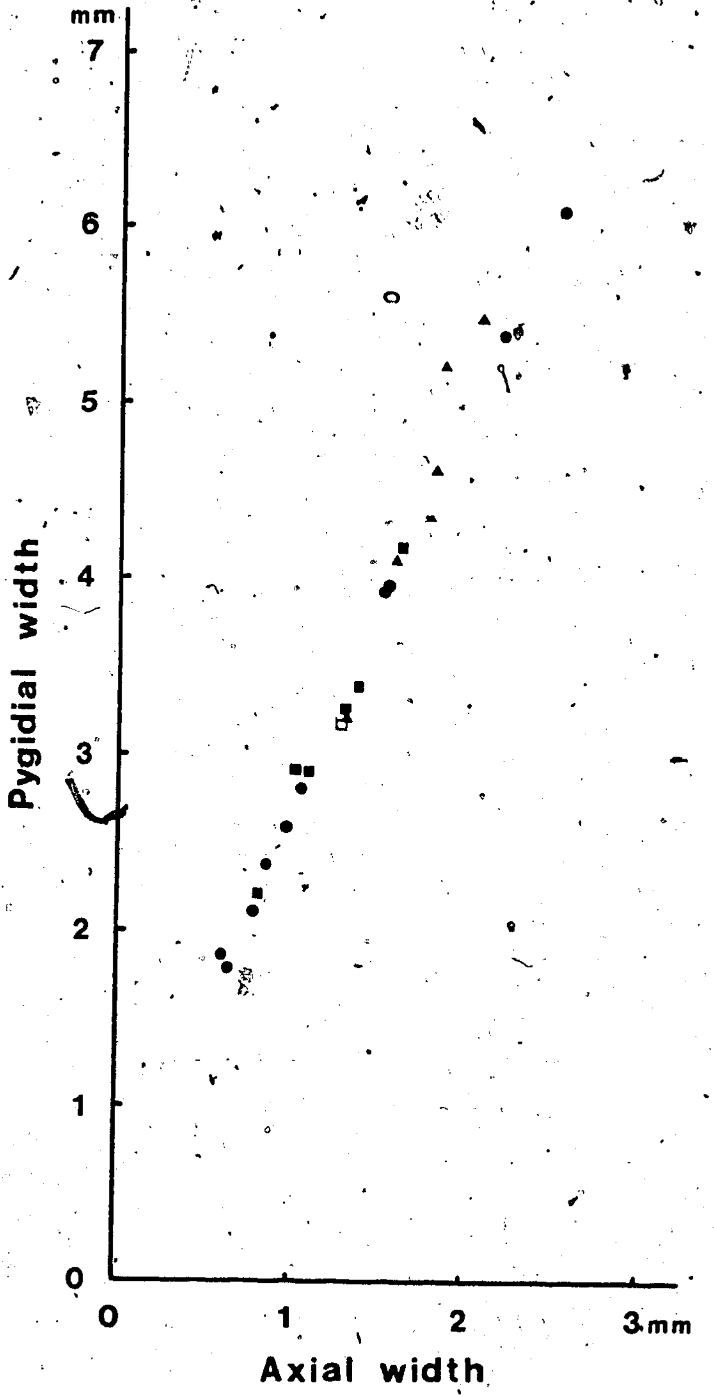
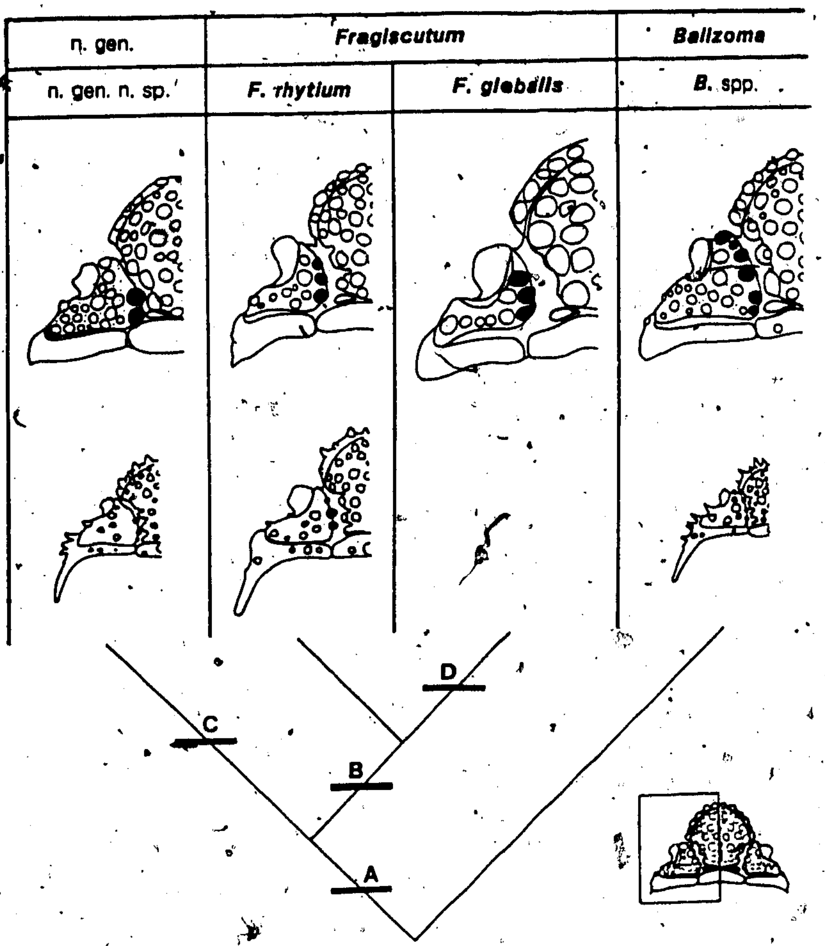

mm
7
6
5
4
3
2
1
0
Pygidial width
0
1
2
3mm
Axial width

Figure IV-6 - Comparative ontogeny of the genal field and phylogenetic relationships in the *variolaris* plexus. Adaxial fixigenal tubercles in meraspides (bottom row, approximately x11) and large holaspides (top row, approximately x5.5) shaded in black. Apomorphies include: *A*, reduction of adaxial fixigenal row to 2-4 tubercles (by postdisplaced onset timing of anterior tubercles); *B*, enlarged eyes (by accelerated rate of allometric growth); *C*, adaxial row reduced to two coarse tubercles opposite 1S-2S (paedomorphic arrest of development of tubercles opposite 3S and further anteriorly); *D*, only three tubercles opposite 1S-3S (development of anterior tubercles spatially constrained by expansion of eyes to adjacent to axial furrow).


n. gen.
Fragiscutum
Balizoma
n. gen. n. sp.
F. rhytium
F. glebalis
B. spp.
HOLASPID
MERASPID
D
C
B
A

fixigenal tubercle row, eye size, and area of the genal fields may be related to subtle temporal shifts in developmental pathways. Furthermore, certain evolutionary novelties are recognized as structurally-constrained nonadaptive by-products of timing-related selection targeted on [illegible] characters.

The adaxial fixigenal tubercle row in <u>Balizoma</u> and <u>variolaris</u> plexus n. gen. is initiated in the meraspid period as small granulose tubercles, although clusters of tiny spinose denticles along the axial furrow opposite the 1S and 2S glabellar furrows in early meraspides (Plate IV-3, fig. 3) are a precursor to tubercle development. Edgecombe and Chatterton (1987; Chapter II herein) noted that this tubercle row in <u>Balizoma</u> formed as a unified series distinct from other genal tubercles in Ramskold's (1986) "circumocular tubercle ring" [also comprised of the librigenal field tubercle row and the fixigenal field "circumocular tubercles" CT1 - CT4]. <u>Balizoma</u> meraspides show a rather uniform-sized row of small granulose tubercles opposite the glabellar furrows (and farther forward opposite the abaxial end of the preglabellar furrow), although the tubercles opposite 1S and 2S tend to be slightly larger, a result of earlier onset of development. This adaxial row enlarges through ontogeny relative to other fixigenal tubercles, and is composed of 5 or 6 (rarely 7) subequal-sized rounded tubercles in adults.

Evidence from Encrinurus (Nucleurus), probably ancestral to Balizoma as well as variolaris plexus n. gen. and Fragiscutum, indicates that 4 or 5 subequal-sized coarse tubercles are plesiomorphic for the variolaris plexus, probably primitively developing opposite the three lateral glabellar furrows, with an anterior pair abaxial to the preglabellar furrow and a posterior pair opposite the occipital furrow added later in the meraspid period. Meraspid stages in a new Llandovery species from the Avalanche Lake sections [with four nodular adaxial fixigenal tubercles in large holaspides, cf. E. (N.) anticostiensis (Twenhofel, 1928); E. (N.) inexpectatus (Šnajdr, 1975); and, E. (N.) diabolus (Tripp, Temple and Gass, 1977)] indicate three small spinose tubercles opposite 1S - 3S (Plate IV-4B).

In contrast to this plesiomorphic state of four or more tubercles in the adaxial fixigenal row, species of variolaris plexus n. gen. and Fragiscutum develop as few as 2 - 3 (variolaris plexus n. gen. n. sp.; F. glebalis) to 3 - 5 (F. rhytium) tubercles. This reduction is expressed in the meraspid period by prominence of tubercle pairs opposite 1S and 2S, with tubercles opposite 3S either absent (in variolaris plexus n. gen.) or small (in F. rhytium). This includes meraspides at degrees certainly more advanced than those at which Balizoma has developed five tubercles in the row (see Figure IV-6). Delayed timing of onset of development of ~~these~~ anterior tubercles

Plate IV-4 - Small cranidia of Encrinurus (Nucleurus) n. sp. Whittaker Formation (Llandovery), Mackenzie Mountains, Northwest Territories, Canada. Specimens from section Avalanche Lake One, 413 meters above base. (Chatterton and Perry, 1983; 1984). A, dorsal view of early meraspid cranidium, UA 7891, x75; B, dorsal view of small cranidium, UA 7892, x50.

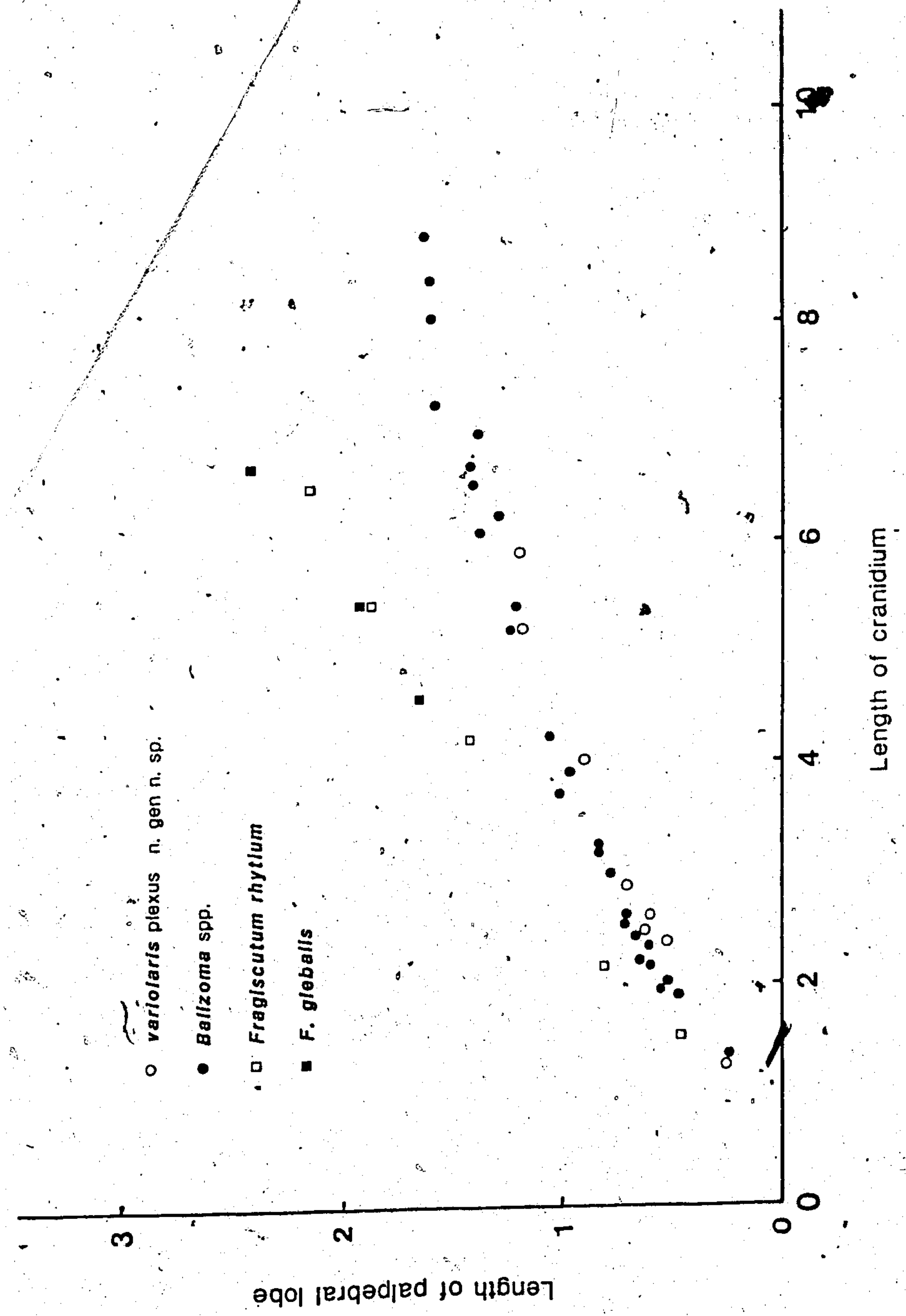
[redacted]

represents post-displacement in the terminology of Alberch et al. (1979). Further development of the adaxial row is typically completely arrested in variolaris plexus n. gen. n. sp., in which tubercles opposite 1S and 2S undergo allometric enlargement through the growth series but anterior or posterior pairs are either small or absent. This paedomorphic state differs from more plesiomorphic F. rhytium, in which a row of three to five subequal sized tubercles in adults also includes pairs positioned opposite 3S, and sometimes opposite the preglabellar and/or occipital furrows, more comparable to Encrinurus (Nucleurus) and Balizoma.

Holaspides of Fragiscutum glebalis Campbell, 1967 [complete specimens, including oustretched and partially enrolled individuals, also illustrated by Johnson, 1985; Giuseffi, 1986] record the development of three nodular tubercles opposite the 1S - 3S glabellar furrows. A correlation is apparent between expansion of the greatly enlarged eyes to immediately adjacent to the axial furrow and reduction in the area of the genal fields and reduced adaxial fixigenal tuberculation (i.e., absence of anterior tubercles sometimes developed in F. rhytium). It is hypothesized that accelerated rate of eye development resulted in positioning proximal to the axial furrow, imposing a spatial constraint on ontogenetic development of late-forming anterior tubercles in the adaxial fixigenal row.

To test this hypothesis, rate of eye development may be approximated by the allometric change in ratio of length of the palpebral lobe to length of the cranidium. The latter is selected as the independent variable representing overall body size on the basis of most species being known only from disarticulated silicified material. These data (presented in Figure IV-7 in the form of an ordinate plot to allow absolute size comparisons) suggest that differences in the "large-eyed" forms (a synapomorphy between species of _Fragiscutum_) relative to the "small-eyed" forms (_Balizoma_; _variolaris_ plexus n. gen.) are indeed results of accelerated rate of eye size increase. This refutes certain alternative scenarios which could be evoked without these ontogenetic data: i.e., variation in eye size between taxa is not a simple allometric correlate of differences in body size (see Calder, 1984 for comprehensive review of this topic) on an unmodified developmental trajectory. As well, the inferred rate perturbation in _Fragiscutum_ demonstrates that increased eye size would not be adequately modelled as a result of pre-displacement [involving earlier onset timing of a phase of eye development; size increase could therefore result from prolongation of the growth period without a change in rate or offset timing (McNamara, 1986)]. We cannot demonstrate that some aspect of pre-displaced timing was not operating in concert with rate acceleration; such difficulty in

Figure IV-7 - Scatter plot of maximum length of palpebral lobe versus sagittal length of cranidium in taxa of the *variolaris* plexus. Measurements are in millimeters. Data for *Fragiscutum rhytium* and *F. glebalis* measured from photographs in Whittington and Campbell (1967) and Campbell (1967), respectively; *variolaris* plexus n. gen. n. sp. from Avalanche Lake Five, 58-60 meters above base, and Avalanche Lake Seven, ~27 meters above base; *Balizoma* spp. from Avalanche Lake Four, 126 meters above base.


○ variolaris plexus n. gen n. sp.
● Balizoma spp.
□ Fragiscutum rhytium
■ F. glebalis
Length of palpebral lobe
0
1
2
3
Length of cranidium
0
2
4
6
8
10

distinguishing heterochrony involving selection for shape versus timing changes has been recognized by Bonner and Horn (1982).

Regardless of the specific process involved in these temporal perturbations, however, it is apparent that such derived character states as reduction in the area of the fixigenal and librigenal fields in <u>Fragiscutum</u> (and further reduction of the adaxial fixigenal tubercle row in <u>F. glebalis</u>) are exaptations (Gould and Vrba, 1982), epiphenomenal with selection on eye size. Spatial constraint on the development of the adaxial fixigenal tubercles and genal fields falls into the category of non-adaptive, non-selected character transformations of Gould and Lewontin (1979, p. 262), in which "...the form of the part is a correlated consequence of selection directed elsewhere", relationships implicit in Rensch's (1959) "material compensation" and Thompson's (1942) "mechanically forced correlations". An analogous example from the Trilobita is provided by Eldredge's (1972) proposal that a comparable reduction in area of the genal fields in certain calmoniids originated as a by-product of secondary "phacopiform" narrowing of the posterior portion of the glabella. Recognition of these structural constraints provides a substantially modified framework for assessing the "functional" significance of such character states (i.e., their "effect" in the terminology of Gould and Vrba) from that offered by strict adaptationist paradigms. The adoption of structuralist models in comparative ontogenetic studies (eg. Kauffman, 1983) is an outgrowth of perceiving development as an integrated control on the evolutionary expression of organismal form.

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CHAPTER V

SYSTEMATICS AND EVOLUTION OF <u>ENCRINUROIDES</u> REED, 1931 (TRILOBITA)

The systematics and phylogenetic relationships of encrinurine trilobites have been refined considerably in recent years, due largely to studies by Tripp (1957; 1962) and coauthors (Evitt and Tripp, 1977; Temple and Tripp, 1979; Tripp, Temple and Gass, 1977), Strusz (1980), and Ramsköld (1986). Taxonomic revisions have trended towards splitting of the once broadly-diagnosed <u>Encrinurus</u> Emmrich, 1844, with recognition of several speciose subgenera (Ramskold, 1986). From these a number of restricted Silurian genera (monotypic, or distinctive clades comprising few species) are hypothesized as derived. With the notable exception of Temple and Tripp's (1979) phenetic analysis, encrinurine systematists, although not explicitly stating so, have followed classical evolutionary systematic principles (for review, see Hull, 1970; Charig, 1982; Schoch, 1986). Ancestral plesiomorphic grades have been assigned generic ranking based on "rapid" morphologic divergence (as expressed by distinct complexes of autapomorphic character states). Such evolutionary novelties, for example, include development of only ten thoracic segments and large, low eyes in <u>Fragiscutum</u> Whittington and Campbell, 1967 (a temporally and geographically restricted clade comprising only two species), and extremely coarse, densely-arranged glabellar tuberculation and a prominent non-tuberculate ring on the fixigenal field in the monotypic genus Batocara Strusz, 1980.

Such taxonomic splitting in the Silurian Encrinurinae contrasts with currently established systematics of Ordovician encrinurines. With the exception of Physemataspis Evitt and Tripp, 1977 (including only two species), a diverse radiating assemblege of Ordovician encrinurines are assigned to either Encrinuroides Reed, 1931 or Erratencrinurus Krueger, 1972. The latter, comprising the nominate subgenus and Celtencrinurus Evitt and Tripp, 1977 (Owen, 1981; Lespérance and Tripp, 1985), is a monophyletic terminal taxon united by synapomorphies between congeneric species. As indicated in Lespérance and Tripp's (1985) diagnosis, these include six pentagonally-arranged tubercles on 1L-2S, some or all of which may merge into one to four short horns; a single row of 8-10 tubercles along the anterior cranidial border; and a subtriangular pygidium with a narrow axis consisting of 25-35 rings, and 8-11 strongly curved pleural ribs.

As diagnosed in recent revisions (Evitt and Tripp, 1977; Strusz, 1980), Encrinuroides, however, is a paraphyletic (sensu Farris, 1974; Wiley, 1981) grouping of early, mostly Ordovician, encrinurines sharing only primitive character states. Lineages grouped in this genus are ancestral to (or the plesiomorphic sister groups of) Late Ordovician and Silurian encrinurines assigned to all other genera of the subfamily. Referral of species to Encrinuroides has placed considerable weighting on the retention of a deep preglabellar furrow (in contrast to the apomorphic shallowing of this furrow independently in several different Silurian lineages), as well as such symplesiomorphies as a distinct cranidial anteromedian depression and/or longitudinal median glabellar furrow; and typically subquadrate 2L-4L lateral glabellar lobes with paired or multiple tubercles. Sharing of certain character states plesiomorphic for the subfamily (each retained in at least some descendants assigned to other genera) does not, however, imply that "Encrinuroides" is a static or conservative group, as might be used to attempt to justify paraphyly as an "adaptive grade" (sensu Simpson, 1961; see Van Valen, 1978). Indeed, evolution within distinct lineages produced considerable divergence in most characters. Thus the traditional diagnosis of Encrinuroides results in a wider range of morphologic variation than in other (monophyletic) encrinurine genera. Strusz's (1980) diagnosis, for example, includes species with five to ten pygidial pleural ribs and ten to twenty axial rings, and lists certain character states which are widespread throughout the subfamily. These include well-developed lateral glabellar furrows, a narrow cranidial anterior border, pedunculate to stalked eyes, typical presence of fixigenal spines, pitted fixigenae, eleven thoracic segments, "shallow to obscure" pygidial axial ring furrows posteriorly, and absence of a mucro.

The traditional emphasis on retention of plesiomorphies, in opposition to cladistic methodologies, obscures the evolutionary dynamics of Ordovician encrinurines. This problem is of particular significance since it is within "Encrinuroides" that the most fundamental cladistic events in the evolutionary history of the subfamily are recorded. Rather than attempting a rediagnosis of this complex paraphyletic class (in the ontological sense; Hull, 1976; reviewed in Wiley, 1981; Eldredge, 1985), emphasis is placed on apomorphic novelties attained in lineages within "Encrinuroides" by recognizing, and analyzing the relationships within and between, informal species groups. Should further examination corroborate hypotheses of monophyly (if diagnostic character states are synapomorphic), they form a natural basis for formal taxonomic splitting, as well as establishing revised taxonomic ranking based on recency of common ancestry (as indicated by nested patterns of synapomorphy). At present, these species groups are proposed in relation to the conventional concept of Encrinuroides to maintain taxonomic stability and encourage further testing. With the objective that systematics reflects phylogeny, the goal of the present study is to further discern evolutionary relationships within the Encrinurinae by analyzing a "supraspecific ancestor" (sensu Wiley, 1979)

In addition to these fundamental revisions, a new earliest Llandovery species, Encrinuroides n. sp., is described from the Mackenzie Mountains, Canada. This forms part of continuing documentation of silicified trilobite faunas from Silurian sections in the Avalanche Lake area (Chatterton and Perry, 1983; 1984). Stratigraphic and locality data cited in discussion of the new species are as outlined in these works (see also Chapter I).

SYSTEMATIC PALEONTOLOGY

Family ENCRINURIDAE Angelin, 1854

Subfamily ENCRINURINAE Angelin, 1854

Genus ENCRINUROIDES Reed, 1931

Type species.- Cybele sexcostata Salter, 1848, p. 343, Pl. viii, fig 10 (pygidium) only. Neotype complete specimen selected and described by Whittington (1950) from the Shoalshook Limestone (mid Ashgill), Shoalshook, near Haverfordwest, Pembrokeshire, South Wales. Additional material from the Rhiwlas Limestone at several localities near Rhiwlas, Bala area, Merioneth, Wales figured by Whittington (1965).

Diagnosis.- See Strusz (1980, p. 8), with remarks below.

Discussion.- The paraphyletic class conventionally grouped as Encrinuroides is perceived as comprising four major species groups. Included taxa, character analysis and relationships, and distribution of these groups are outlined herein.

a) "sexcostatus species group". - Strusz (1980) modelled a lineage stemming from late Arenig - earliest Llanvirn E. hornei Dean, 1973 including Llandeilo E. autochthon Tripp, 1954 [age following Thomas, Owens, and Rushton, 1984], E. stincharensis (Reed, 1928) and E. polypleura Tripp, 1967, Caradoc E. tuberculosis (Collie, 1903) and E. sublanceolatus (Reed, 1935), and the Ashgill type species E. sexcostatus (Salter, 1848). Caradoc E. waigatschensis Burskiy, 1966 and Llandovery E? newlandensis (Lamont, 1978) are probably derived from this lineage. The latter species, originally referred to Curriella Lamont, 1978 (here questionably placed in synonomy with Encrinuroides Reed), was reillustrated and assigned with question to Encrinurus by Howells (1982). Cephala of this group are characterized by small, irregularly-distributed glabellar tubercles, weak development of cranidial anterior border tubercles, typically rather short genal spines, and multiple tubercles on the lateral glabellar lobes. Tripp (1979) also recognized the earliest-occurring species from the Girvan district, Scotland (E. autochthon; E. stincharensis; E.

polypleura) as constituting a species group which was diagnosed as "glabella widens steadily forwards, glabellar furrows short, genal spine short, anterior border of free cheek not set at an angle to lateral border, 9 pairs of pleurae in pygidium, posterior pleurae fused abaxially, large paired granules on rachis of pygidium."

E. sexcostatus Salter has been selected as nominate species for this informal group with the intention of indicating that it is this species group which would retain the name Encrinuroides Reed should further examination favor formal subdivision of the genus. It must be noted, however, that E. sexcostatus differs considerably from the hypothetical stem species of the group (more closely approximated by E. autochthon and E. stincharensis). This is clearly an effect of the late occurrence (Ashgill) of this species. The constricted glabellar stalk and greatly inflated frontal lobe, transglabellar 1S furrow, prominent genal spines, and reduction of the number of pleural ribs to seven pairs in this species (also seen in late Caradoc E. sublanceolatus) may thus be regarded as derived character states.

E. hornei , the earliest known encrinurine trilobite, is excluded from the "sexcostatus species group" as perceived here, which shows several derived states (particularly pygidial) upon its appearence in the early Llandeilo. The early stratigraphic occurrence and cybeline-like morphology of *E. hornei* provide a useful outgroup for assessing character state polarities in younger "*Encrinuroides*". The fine, irregular glabellar tuberculation suggests, for example, that this state in the "*sexcostatus* group" is plesiomorphic, while the small, rather broad pygidium with few pleural ribs (five pairs, comparable to cybelines) and axial rings is more closely approximated by the "*tholus* group" (discussed below). Species assigned to the "*sexcostatus* group" retain a deep preglabellar furrow, a primitive state shared with the "*tholus* group". Pygidia of the former lineage do, however, indicate unique derived states (by outgroup comparison with cybelines and *E. hornei*). Most notable are the relatively elongate subtriangular shape and increased number of pleural ribs and axial rings relative to other "*Encrinuroides*" (9 rather blunt-ending rib pairs in most species; 20 or more rings). These states contrast with smaller pygidia, typically with 6-7 pairs of ribs and fewer than 20 rings, in early species of the "*uncatus*", "*tholus*", and "*zhenxiongensis*" groups (each described below). This character analysis thus provides support for Strusz's (1980) hypothesis that species here assigned to these three groups share more recent common ancestry with each other than with the "*sexcostatus* group". This is particularly indicated by synapomorphic development (possibly by paedomorphic retention of ~~a widespread~~ juvenile character state; see Chapter III) of a distinctly symmetrical distribution of glabellar tubercles in adult stages, with distinct position-1 pairs in major rows.

It is probable that *Cromus* Barrande, 1852, first represented by Caradoc *C.* (*Encrinuraspis*) *optimus* Webby, Moors and McLean, 1970, has ancestry near the "*sexcostatus* species group". This relationship is indicated by paired or trebled tubercles on the subquadrate lateral lobes, irregularly-distributed glabellar tubercles in many species [although some Llandovery and Ludlow species of *C.* (*Encrinuraspis*) possess relatively coarse, distinctly symmetrically-distributed tubercles], low eyes, reduced genal spines, and the relatively large, rather flat pygidium with a high number of pleural ribs (approximately ten pairs). Recognizing monophyletic taxa, the *Encrinuroides* "*sexcostatus* species group" - *Cromus* - *Perryus* clade [see Gass and Mikulic, 1982 for evidence linking *Perryus* to *Cromus*] is the plesiomorphic sister group of all other encrinurines (descended from a common ancestor of the "*tholus*, "*uncatus*, and "*zhenxiongensis* species groups").

The restricted geographic distribution of early species of the "*sexcostatus* group" reflects the Scoto-Appalachian origin of the Encrinurinae suggested by the occurrence of late Arenig-earliest Llanvirn *E. hornei* in northeastern Newfoundland. Llandeilo species (*E. autochthon*, *E. stincharensis*, and *E. polypleura*) are known only from the

Girvan district of Scotland. The Caradoc offshoots *E. tuberculosis* (from Pennsylvania) and *E. waigatschensis* (from the Soviet Arctic) [and possibly closely- related *Cromus* (*Encrinuraspis*) *optimus* from Australia] indicate geographic dispersal also observed in other contemporaneous encrinurine lineages, while late Caradoc *E. sublanceolatus*, Ashgill *E. sexcostatus*, and Llandovery *E*? *newlandensis* record persistent occurrence in Scotland and Wales. The increasingly cosmopolitan trend in Ordovician encrinurine biogeography is comparable to that observed in other Ordovician trilobite groups (Whittington, 1966; Whittington and Hughes, 1972), with notable Caradoc dispersal contrasting with the essentially Scoto-Appalachian Llandeilo radiation of the "*sexcostatus*" and "*tholus* groups".

b) "*uncatus* species group".- Evitt and Tripp (1977), in diagnosing *Encrinuroides torulatus*, *E. uncatus*, and *E. neuter* from the Ordovician (Llandeilo-Caradoc) of Virginia, noted that these species formed a distinct group characterized by the stratigraphically-earliest development of coarse symmetrically-distributed glabellar tubercles. This species group, extended into the Lower Llandovery by *E.* n. sp., particularly shows distinct position-1 tubercle pairs in major-rows, and single tubercles along the pygidial sagittal band. An exception is the earliest-occurring species, *E. torulatus*, in which these pygidial tubercles are paired. This plesiomorphy is shared with many other early "*Encrinuroides*" species, for example *E. insularis* Shaw, 1968 and *E. tholus* Evitt and Tripp, 1977 of the "*tholus* group", as well as early species of the "*sexcostatus* group" such as *E. autochthon*, *E. stincharensis*, and *E. polypleura*. The "*uncatus* species group" retains plesiomorphic "*Encrinuroides*" character states of a relatively deep preglabellar furrow, a distinct longitudinal median glabellar furrow, multiple small tubercles on the lateral glabellar lobes, and a poorly-defined adaxial tubercle row on the fixed cheeks (coarse and typically overhanging the axial furrows in *Encrinurus* and allied genera).

Encrinuroides sp. Westrop and Ludvigsen, 1983 from the late Caradoc of Manitoba is also assigned to this group, providing an additional morphologic link between the *Encrinuroides* "*tholus* species group" (see below) and *E. torulatus*, the earliest occurring species referred to the "*uncatus* group". *E.* sp Westrop and Ludvigsen and *E. torulatus* retain the primitive short (sag.), wide (tr.) cranidium with a rather compact glabella, and small, convex pygidium with 6-7 pairs of pleural ribs, fine sagittal granulation (not coarse tuberculation), and only weak development of a sagittal band. These forms, however, show the apomorphic ("*uncatus* group") development of coarse position-1 major row glabellar tubercles and coarse, sparsely-distributed fixigenal field tuberculation. *E.*

torulatus further resembles the cluster of species referred to the "tholus group" in its long, strongly-divergent posterior fixigenal spines and highly-elevated eyes; the fragmentary nature of material described by Westrop and Ludvigsen (1983) does not permit comparison with these plesiomorphic states which are modified in later-occurring species of the "uncatus group".

The geographic distribution of known species of the "uncatus group" (Llandeilo - Caradoc E. torulatus, E. uncatus, E. neuter from Virginia; late Caradoc E. sp. from Manitoba; early Llandovery E. n. sp. from the Mackenzie Mountains, northwestern Canada) indicates progressive dispersal of this North American lineage through the Ordovician. The occurrence of the earliest species in Virginia, thus geographically overlapping with the main Llandeilo radiation of the "tholus group", is further consistent with the hypothesis of close common ancestry for these two species groups indicated by morphological similarities.

This lineage is probably the ancestor or plesiomorphic sister group of Silurian Encrinurus (see Edgecombe and Chatterton, 1987, with references, and discussion below under E. n. sp.), as well as to Caradoc-Ashgill Erratencrinurus Krueger, 1972 (cf. Evitt and Tripp, 1977; Strusz, 1980). Several more resticted Silurian genera were descended from or shared common ancestry with Encrinurus (*sensu* Strusz, 1980; Ramsköld, 1986); these include *Fragiscutum* Whittington and Campbell, 1967; *Paraencrinurus* Antelo, 1973; *Balizoma* Holloway, 1980; and *Batocara* Strusz, 1980.

(c) "*tholus* species group". - A number of Llandeilo and early Caradoc species which form a major part of the initial radiation of "*Encrinuroides*" are united by a complex of character states differing from contemporaneous representatives of the "*sexcostatus*" and "*uncatus* groups". The "*tholus* species group" includes *E. periops* Tripp, 1967, *E. fallax* (Reed, 1899), *E. obesus* Tripp, 1965, *E. tholus* Evitt and Tripp, 1977, *E. capitonis* Frederickson, 1964 [see also Shaw, 1974], *E. pernodosus* (Slocum, 1913), and probably *E. contentus* (Reed, 1914) [lectotype pygidium selected and figured by Morris and Tripp, 1986]. This group is characterized by: a short (sag.), broad (tr.) cranidium with long, strongly-divergent fixigenal spines; relatively wide, typically strongly convex glabella which widens forward slowly and regularly; abundant small glabellar tubercles with faintly-distinct symmetry (position-1 pairs typically distinct); preglabellar furrow usually deeper than in species of the "*uncatus* group"; rather indistinct anterior border tuberculation; cranidial anteromedian depression variably developed, but longitudinal median furrow typically indents front of glabella; pitted fixigenal field with many small tubercles; highly raised and constricted eye stalk; a pitted librigenal field with sparse tuberculation; almost smooth (non-tuberculate) librigenal lateral border; prominently-inflated, rounded hypostomal middle body; small, rather convex, triangular pygidium with 6-8 pairs of pleural ribs and 14-23 axial rings; only slight development of a sagittal band in posterior part of axis; and, weak sagittal granulation (paired granules in many species). As noted by Evitt and Tripp (1977) and Strusz (1980), E. insularis Shaw, 1968 provides a stratophenetic link between this species group (notably E. tholus, E. periops, and E. capitonis) and Physemataspis Evitt and Tripp, 1977. Recognition of monophyletic groups including all descendants of a stem species (Hennig, 1966) [the hypothetical stem of the "tholus group"] would thus include E. insularis and Physemataspis in a higher taxon with the "tholus group". On cladistic principles, it is apparent that these fundamental splittings of "species groups" of early encrinurines which have been retained in a single paraphyletic genus (Encrinuroides) would be recognized at higher taxonomic levels and also include descendants/apomorphic sister groups to maintain monophyly. In contrast, the present systematic scheme has largely emphasized patristic relationships to establish taxonomic rank; Physemataspis, for example, was diagnosed as a monotypic genus based on apparently rapid development of a distinctive complex of autapomorphic character states.

The taxonomic integrity of the "tholus group" is supported by biogeographic relations between assigned species. The Llandeilo radiation of this group is spatially restricted to Scotland (periops, obesus, Physemataspis mirabilis Tripp, 1980), Ireland (fallax), and eastern North America (tholus, insularis, Physemataspis coopi Evitt and Tripp, 1977), further reflecting the restricted Scoto-Appalachian distribution of early Middle Ordovician encrinurines. Caradoc species such as E. capitonis (from Oklahoma) and E. pernodosus (from Iowa) indicate dispersal into the American midcontinent. As noted in discussion of the "uncatus group", the earliest species of that group (notably E. torulatus) indicate affinities (i.e., shared ancestry) with the "tholus group, consistent with overlapping geographic distributions.

Encrinuroides rarus (Walcott, 1877) [redescribed by Chatterton and Ludvigsen, 1976] is of problematic systematic position. Resemblances to the "tholus group" include the broad cranidium and general pygidial form (with seven pairs of pleural ribs and 17-19 axial rings), however the inflated glabellar frontal lobe with erratically-distributed tubercles is unique. The latter state, as well as the rather low eyes and short fixigenal spines, is more suggestive of the "sexcostatus group". This character state mosaic provides support for Strusz's (1980) proposal that E. rarus was an early offshoot of the lineage giving rise to the "*tholus* group", but retaining many primitive states from a common ancestor with the "*sexcostatus* group". This widespread and long-ranging species would thus be interpreted as representing a plesiomorphic sister group of the "*tholus*" - "*uncatus*" - "*zhenxiongensis* clade (united by symmetrically arranged glabellar tubercles in adult stages, with distinct position-1 pairs in major rows). Ontogenetic evidence reveals autapomorphies of protaspid and meraspid stages in *E. rarus* (illustrated by Chatterton, 1980; refigured and discussed in Chapter III herein) compared to other "*Encrinuroides*" for which protaspides are known (*E. tholus* and *E. insularis* of the "*tholus* group"; *E. neuter* of the "*uncatus* group"). These include the broad, ovate (rather than subquadrate) outline, and an atypically prominent transverse furrow extending across the fixigenal field opposite the 1S glabellar furrow. Evitt and Tripp (1977) noted that a swollen posterior band on the field of the fixed cheek (as delineated by this furrow) is widespread in encrinurid early ontogeny, but is particularly distinct in *Physemataspis coopi*. This further links *E. rarus* to certain taxa of the "*tholus* group". Comparison of encrinurine protaspides with a cybeline outgroup (*Cybeloides*) [see Chapter III], however, indicates that *E. insularis* of the "*tholus* group" retains the most plesiomorphic character states of known encrinurine protaspides, whereas the primitive status (i.e., distant common ancestry) of *E. rarus* may be obscured by autapomorphies.

d) "*Zhenxiongensis* species group". - This group is tentatively proposed for several rather poorly-known Chinese Ordovician and Silurian species which have been referred to *Encrinuroides* (see Chang, 1974, 1983; Wu, 1979; Strusz, 1980). These forms show the development of elongate glabellar furrows (1S commonly transglabellar) with alignment of major-row tubercles across the glabellar lobes. These character states, as well as the requisite stratigraphic distribution and endemic Chinese occurrence, suggest that this species group is near the ancestry of *Coronocephalus* Grabau, 1924, emend. Wang, 1938. Chang (1983) listed evolutionary trends leading to the development of his "subfamily" Coronocephalinae (elevated rank not recognized herein) from Chinese Late Ordovician or Early Silurian *Encrinuroides*. This was diagnosed as having a "distinct preglabellar furrow, clear anterior cranidial border, strong median furrow [=anteromedian depression], less forward expanded glabella, smooth or irregularly tuberculate lateral border of free cheeks, and small and paucisegmented pygidium".

Encrinuroides zhenxiongensis Sheng, 1964, of Caradoc-early Ashgill age from South China, is the earliest known Chinese encrinurine. As noted by Strusz (1980), the "subtriangular and rather small" pygidium and "fairly coarse and regular" glabellar tuberculation of this species suggest common ancestry with the "uncatus species group". This is further indicated by general glabellar form and "Encrinurus-like" adaxial row of fixigenal tubercles; also retained in Silurian Encrinuroides changningensis Wu, 1979 and E. songkanensis Wu, 1979. Preparation of a comprehensive list of Silurian species referrable to this group is presently hindered by inadequate knowledge of many Chinese species which have been referred to Encrinuroides. Dr. Wu Hong-ji, Nanjing Institute of Geology and Palaeontology, is currently revising many of these taxa. Preliminary results of application of Temple and Tripp's (1979) numerical taxonomic analysis to Chinese encrinurids indicates that E. zhenxiongensis, E. changningensis and two undescribed Silurian species plot closely together and are distinct from other encrinurines on principal components ordination (Wu, personal communication, 1987). Other Silurian species which have been assigned to Encrinuroides show a greater tendency towards character states intermediate with Coronocephalus, for example "E." angustigenatus Wu, 1979, particularly in the elongate pygidium with an increased number of axial rings and pleural ribs. It appears likely that several phyletic lines may be represented by Chinese "Encrinuroides". Comprehensive revision of these problematic taxa is, however, considered beyond the scope of the present study.

Silurian species assigned to Encrinuroides by Strusz (1980) but reassigned herein and by Ramskold (1986) include: "E." globosus (Maksimova, 1962) [?Perryus]; "E." hypoleprus (Stearn, 1956) [?Encrinurus (Nucleurus)]; and "E." padei (Haswell, 1865) [Encrinurus (Encrinurus)].

Caradoc Ceraurus vigilans Hall, 1847 from New York, Ontario, Illinois and Wisconsin, referred to Encrinuroides by Ludvigsen (1979), is here reassigned to Erratencrinurus (?Erratencrinurus). De Mott (1963) indicated the synonomy of Encrinurus trentonensis Walcott, 1877 and Encrinurus cybeleformis Raymond, 1921 (see also Wilson, 1947). The small, subquadrate glabella with enlarged position-1 tubercle pairs in rows I and, particularly, II-III, and few coarse fixigenal tubercles suggest affinities to Erratencrinurus spicatus (Tripp, 1974) from Wisconsin. These species record an early offshoot of Erratencrinurus in the North American Caradoc, predating the main radiation of the nominate subgenus in the late Caradoc of North Germany (Krueger, 1971).

Encrinuroides n. sp.

Pl. V-1, figs. 1-15; Pl. V-2, figs. 1-15; Pl. V-3, figs. 1-13; Fig. V-1

Type locality. - Avalanche Lake One, 95.5 meters above base

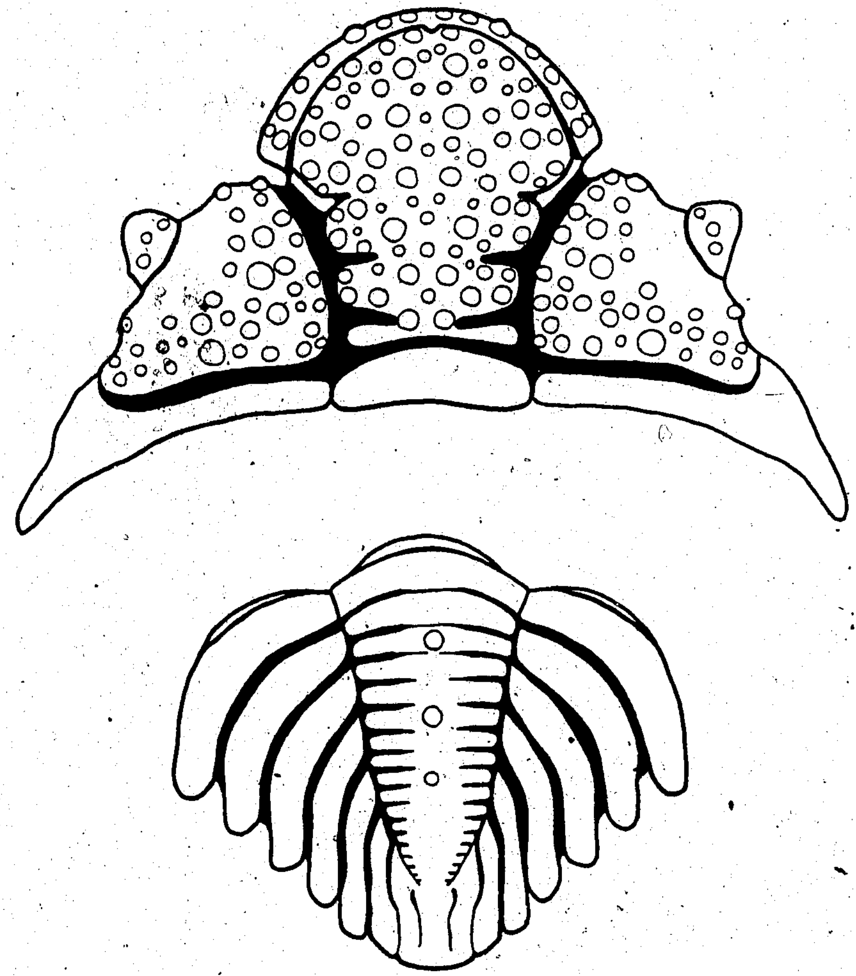

FIGURE V-1 - Dorsal view of a reconstruction of cranidium and pygidium of Encrinuroides n. sp. Reconstruction is based on specimens illustrated in Plates V-1-3.

Plate V-1 - Encr[illegible]uroides n. sp. Whittaker Formation, Mackenzie Mountains, Northwest Territories, Canada. All specimens from section Avalanche Lake One, 95.5 meters above base (Chatterton and Perry, 1983; 1984) except 5, 9 (from same locality, 97.5 meters above base). Magnifications x10 except where noted otherwise. 1-3, lateral, anterior, and dorsal views of holotype cranidium, UA 7863; 4, 6, dorsal and anterior views of thoracic segment, UA 7864, x5; 5, external view of free cheek, UA 7865; 7, dorsal view of cranidium, UA 7866; 8, dorsal view of hypostome, UA 7867; 9, external view of free cheek, UA 7868; 10, 12, posteroventral and ventral views of hypostome, UA 7869; 11, 13, 15, dorsal, lateral, and posterior views of pygidium, UA 7870; 14, ventral view of pygidium, UA 7871.

[redacted]

Plate V-2 - Encrinuroides n. sp. Whittaker Formation, Mackenzie Mountains, Northwest Territories, Canada. All specimens from section Avalanche Lake One, 95.5 meters above base (Chatterton and Perry, 1983; 1984). 1-3, dorsal, anterior, and dorsolateral views of cranidium, UA 7872, x5; 4, external view of small free cheek, UA 7873, x50; 5,6, dorsal and lateral views of pygidium, UA 7874, x5; 7-9, dorsal, lateral, and anterior views of cranidium, UA 7875, x5; 10, ventral view of small hypostome, UA 7876, x50; 11, ventral view of incomplete thoracic segment, UA 7877, x5; 12, ventral view of hypostome, UA 7878, x10, 13, dorsal view of small pygidium, UA 7879, x50; 14, dorsal view of transitory pygidium, UA 78870, x50; 15, dorsal view of pygidium, UA 7881, x30.

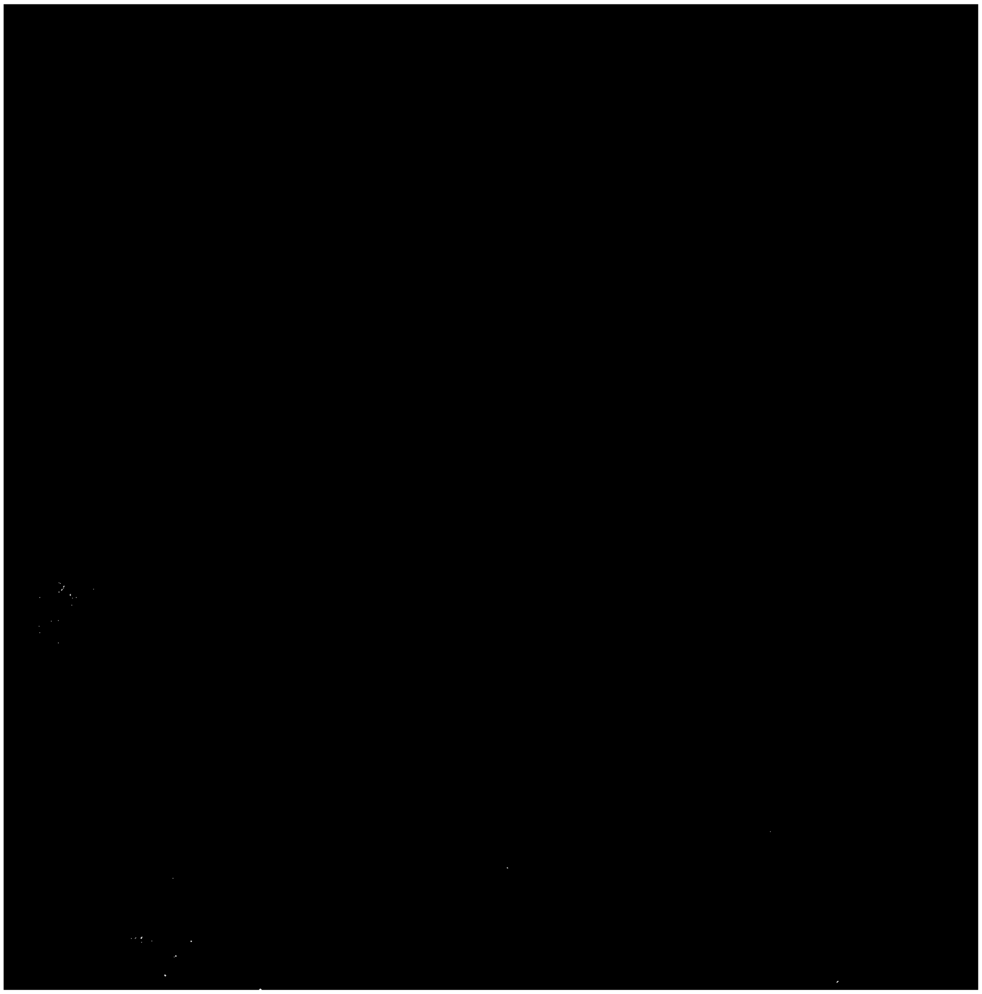

Plate V-3 - Encrinuroides n. sp. Whittaker Formation, Mackenzie Mountains, Northwest Territories, Canada. All specimens from section Avalanche Lake One, 95.5 meters above base (Chatterton and Perry, 1983; 1984). Magnifications x10 except where noted otherwise. 1, dorsal view of cranidium, UA 7882; 2, dorsal view of free cheek, UA 7883; 3, 4, dorsal and posterior views of pygidium, UA 7884; 5, ventral view of hypostome, UA 7885; 6, 7, anterior and dorsal views of incomplete thoracic segment, UA 7886, x5; 8, dorsal view of cranidium, UA 7887; 9, ventral view of cranidium, UA 7888; 10, 12, 13, dorsal, lateral, and posterior views of pygidium, UA 7889; 11, ventral view of pygidium, UA 7890.

[redacted]

(Whittaker Formation; early Llandovery).

Type material. - Holotype cranidium UA 7863 (Pl. V-1, figs. 1-3); paratypes UA 7864-7872, 7874-75, 7878, 7887-7889.

Other localities. - *E*. n. sp. is presently known through a stratigraphic interval of thirteen meters in Avalanche Lake One (84.5 to 97.5 meters above base of section), and occurs at equivalent earliest Llandovery levels in Avalanche Lake Four.

Diagnosis. - A species of the "*uncatus* group" with 1L low, reduced by 1S directed backwards, merging with occipital furrow; glabellar and fixigenal/librigenal field tuberculation fine, dense; twelve to sixteen small cranidial anterior border tubercles; fixigenal field broad, palpebral lobe forwards opposite 2S-3L; eight to ten small tubercles aligned on fixed cheek adjacent to axial furrow; moderately long, weakly divergent genal spines; hypostomal rhynchos broad, posterior border long, lacking marginal spines; pygidium with seven or eight pairs of pleural ribs, narrowow interpleural furrows; ring furrows and axial furrow weakly impressed posteriorly.

Description. - This species is sufficiently close in its morphology to late Caradoc *Encrinuroides neuter* Evitt and Tripp, 1977 from the Martinsburg Shale of Virginia such that a detailed differential description is presented. *E*. n. sp. may be distinguished by the following character states:

Glabellar length 1.1 - 1.2 times width across 4L (see Edgecombe and Chatterton, 1987, Figure 4A; Figure II-4A herein); frontal lobe slightly shorter, approximately fifty percent of glabellar length; width across 1L seventy percent of width across 4L; 1L considerably reduced, depressed relative to 2L - 4L, shortest sagittally with posterior ontogenetic reorientation of 1S, merging with occipital furrow behind I-1 tubercle pair in largest holaspides; 2S -3S slightly shorter than in *E. neuter*, extending less far adaxially across glabella in ventral view; glabellar tubercles slightly smaller, less flattened; position-1 pairs only slightly enlarged relative to more-abaxial tubercles, and only faintly distinct on frontal lobe (ie. IV-1 - VI-1); small adventitious tubercles rather irregularly distributed on frontal lobe and inter-row tubercles on posterior part of glabella (inter-rows ii and iii) typically more abundant than in *E. n[illegible]er*; cranidial anteromedian depression considerably reduced, but shallow longitudinal median glabellar furrow prominent at front of 4L; anterior border shows a more pronounced narrowing towards middle (sag.) of cranidium, with twelve to sixteen small tubercles; PL may be an exsagittally-aligned tubercle pair, comparable to small paired or trebled tubercles on 2L-4L lateral lobes; fixigenal field broader (tr.), such that eye is positioned farther abaxially from glabella;

front of palpebral lobe opposite front of 3L or 3S, back of lobe opposite middle to front of 2L, thus farther forward than in E. neuter; outer part of palpebral lobes separated by a distance about 2.2 times width of 4L; eye ridge indistinct; small fixigenal field tubercles more abundant, densely arranged except for distinct non-tuberculate ring around eye; CT1 and CT2 distinct; eight to ten small tubercles aligned on adaxial part of cheek, but not overhanging axial furrow; genal spine considerably longer, thin, and more strongly divergent, lacking incurved tip; genal spines extend back beyond occipital ring by twenty-five to thirty percent sagittal length of cranidium.

Librigenal field considerably more densely tuberculate (obscuring pitting), with two or three poorly-defined tubercle rows; field relatively shorter, subequal in height to lateral border; seven or eight slightly more prominent tubercles immediately adaxial to lateral border furrow.

Hypostome with broader rhynchos, more bluntly rounded anteriorly, projecting short of anterior margin but bounded by furrows extending backwards for at least forty percent of length of middle body and only weakly convergent anteriorly; posterior border longer, approximately twenty percent of sagittal length of hypostome, tongue-shaped; posterolateral margin smoothly rounded in large stages, lacking denticles; margin gently scalloped in small stages with three pairs of small denticles; middle pair closer to anterior pair opposite back of rhynchos than to posterior pair at corners of gently convex posterior border (cf. equidistant in E. neuter); hypostomal doublure considerably narrower (sag. and exsag.); posterior wings less incurved, extending only a short distance adaxial to lateral border furrow; short anterior-projecting median tongue beneath posterior border terminates about mid-way to border furrow.

Thoracic axial rings less convex, bowed gently forwards mesially and swollen adjacent to weakly-impressed axial furrow; axial nodes/spines absent; articulating process only weakly developed; pleural band gently curved backwards distally; anterior flange widens rapidly lateral to axial furrow, almost as long (exsag.) as pleural band along most of weakly convex inner part of pleurae, separated from band by a broad furrow.

Pygidial sagittal length seventy to eighty percent of width (see Edgecombe and Chatterton, 1987, Figure 8; Figure II-6 herein); seven or eight pairs of broad pleural ribs with interpleural furrows considerably narrower than in E. neuter; anterior ribs extend further ventrally, with a shorter marginal rim, and distal parts more gently backturned; first four or five ribs with free bluntly-pointed terminations; sixth and more-posterior interpleural furrows shallow out before reaching margin; eighth rib pair, when present, postaxial and separated by a short, pit-like furrow; axial furrow more gently impressed, shallowing and converging rapidly behind the tenth ring (approximately corresponding to fifth pair of interpleural furrows); axis comprises thirty-five to forty percent of pygidial width; ventrally, seventeen to nineteen rings may be discerned, with two congruent segments (Temple and Tripp, 1979); ring furrows shallow out mesially behind the third axial ring, forming a broad sagittal band; ring furrows short and rather indistinct in posterior part of axis (behind tenth to twelfth axial ring); three or four faint sagittal tubercles distinct dorsally; in lateral view, axis is slightly more convex, such that postaxial steepening of slope is less abrupt.

Discussion. - The close similarity of early Llandovery _Encrinuroides_ n. sp. to _E_. _uncatus_ Evitt and Tripp, 1977 and, particularly, _E_. _neuter_ Evitt and Tripp, 1977 indicates the persistence of conservative descendants of the "_uncatus_ group" into the earliest Silurian. Ramsköld (1986) previously noted that no known descendant species of this lineage have been recorded from the uppermost Ordovician. While referral of _E_. n. sp. to the "_uncatus_ group" serves to recognize this phyletic conservatism, the new species possesses certain evolutionary novelties shared with Silurian _Encrinurus_. These states, most notably coarsening of a distinct row of fixigenal tubercles adjacent to the axial furrow (eight to ten in _Encrinuroides_ n. sp.; typically five in _Encrinurus_) and posterior reorientation of the 1S glabellar furrow [already present in early Llandovery Encrinurus (Nucleurus)], provide important distinctions between Encrinuroides n. sp. and otherwise-similar Caradoc species of the lineage. These synapomorphies indicate more recent common ancestry between plesiomorphic Encrinuroides n. sp. and apomorphic Encrinurus than shared with Encrinuroides neuter, as might be expected from temporal distributions. This stratigraphic and morphologic intermediate status of the new species thus provides a further link between the Ordovician "uncatus group" and the Silurian Encrinurus plexi.

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CHAPTER VI

GENERAL DISCUSSION

The studies grouped in this volume are united by their departure from convention. Superficially, each represents an outgrowth of the writer's studies on the ontogeny and evolutionary history of the Encrinurinae, integrating a significant new silicified Silurian fauna from the Avalanche Lake area of the Mackenzie Mountains into the general framework of encrinurine systematics and phylogeny. "General discussion " could assume the predictable form of a listing of new discoveries and their implications. A new early Llandovery species of "Encrinuroides", for example, provides an important extension of the temporal range of the Ordovician lineage ancestral to the Silurian Encrinurus plexi. One could, however, look at the same trilobite from a broader angle; conservative descendant species frequently persist in time with apomorphic descendants of a common ancestor. A new Silurian species of "Encrinuroides", when placed in a temporal context, records a pattern of evolutionary stasis. Or, providing another example, the two-stage protaspis (with a torulus and paired tubercles) on the one hand tells us that "advanced cybelines", staurocephalids, and encrinurines form a previously-unrecognized monophyletic taxon, and on the other, it indicates the significance of early ontogeny in phylogenetic inference.

I suggest that the conceptual framework in which these studies were shaped forms as important a uniting link as does the homogeneity of their data base. Tracing the influence of cladistic theory and methodologies and the pervasive influence of ontogeny in evolution to the results outlined in four papers designed to speak for themselves provides more insight than reiterative conclusions.

MAKING THE CLADE. - As discussed in Chapter V, previous encrinurine workers have (although not explicitly stating so) almost invariably followed classical evolutionary systematic principles (for review and discussion, see Hull, 1970; Charig, 1982; Schoch, 1986). Explicit statements of principles applied to recognizing taxa (or, indeed, whether taxa are real units which can be recognized) are, however, scarce in the descriptive "trilobite papers" in which the systematics of the Encrinurinae have developed. Systematic revisions presented herein differ in the deliberate explication of the philosophy behind them. Anderson's (1952, fide Hennig, 1966, p. 28) observation that "...taxonomists are more like artists than like art critics; they practise their trade and don't discuss it" is, unfortunately, perceptive.

Thus, the conventional approach sees species grouped in genera (or subgenera), but taxonomic revision at the suprageneric level has not been attempted. This practice is partially an outgrowth of the common perception of "higher" taxa as rather arbitrarily-defined units of convenience, a prevalent concept in the works of influential systematists of the synthesis (see, for example Mayr, 1942; Simpson, 1961). This "generic grouping only" approach to encrinurine systematics appears to have been influenced by the traditional view that genera are somehow "more real" than other monophyletic taxa. Mayr (1942, p. 284), for example, considered that "...the delimitation of the genus is, to a considerable extent, a matter of judgement, and that this judgement in turn depends on wide experience and on some intangibles". A cladistic perspective alternatively views genera as one rank in the Linnean hierarchy, a monophyletic species group. And like all monophyletic taxa, they originate with their stem species (Hennig, 1966). The "usable and reliable" (Simpson, 1961, p. 199) nature and, frequently, ecological integrity, of such taxa are results of recency of shared ancestry between their included species, rather than the inexplicable "something" which genera share in the writings of the synthesis' systematists. Encrinurine genera have thus been perceived as clusters of related species, but suprageneric taxa (below the subfamilial level of the Encrinurinae) are not recognized because such units are not considered real or, as frequently argued, require recognition of too many taxa for practical purposes. Ramsköld, an excellent student of the Encrinurinae, for example, noted (1985) that "...the ultimate decisive factor...must be the practical utility of the taxa defined, since taxonomy for taxonomy's sake is an ivory tower of little interest". "Taxonomy" is thus not recognized as a direct statement of phylogenetic relationships between real historical entities, in this writer's opinion, the ultimate goal of systematic biology. I would further note that only monophyletic groups provide "practical" taxa since paraphyletic segments and arbitrary groupings of convenience have no reality except in the minds of their erectors (see Patterson, 1982; Schoch, 1986 for similar views). As recognized by many have chosen to consider the ontological status of taxa, only monophyletic groups (*sensu* Hennig, 1966 including *all* descendants of a stem species) are spatiotemporally-bounded historical units. They are individuals in the sense of Ghiselin (1974; see Hull, 1976; Wiley, 1981; Eldredge, 1985), with "births", histories, and "deaths".

The cladistic approach applied herein to the Encrinurinae, by recognizing the hierarchical nesting of evolutionary novelties, records relationships between taxa not recognized by other methods. Chapter IV, for example, outlines a testable hypothesis of descent within the *Encrinurus variolaris* plexus. Morphological criteria (a complex of synapomorphies), in parsimony with similar temporal and biogeographical distributions, suggest that Fragiscutum and variolaris plexus n. gen. share a common ancestor not shared with Balizoma. The perception of this hierarchy forms an objective basis for a revised taxonomic ranking by acknowledging patterns ignored by splitting into genera only. The Fragiscutum - variolaris plexus n. gen. clade (including all descendants of the unique common ancestor of these "genera") is as real and important a taxon as is either "genus", the variolaris plexus, or the subfamily Encrinurinae. It originated, probably in the early Wenlock, with a stem species acquiring diagnostic synapomorphies, had unique historical tendencies (splitting into two major lineages, each defined by a unique complex of evolutionary novelties), and terminated with the extinction of its last included species (probably a Ludlow species of Fragiscutum).

Beyond such philosophical questions as to the ontology of taxa, the applied effects of this revised conceptual framework are expressed by rigorous character analysis and renewed study of morphology. Many characters previously receiving little descriptive emphasis are herein subjected to thorough scrutiny as indices of developmental timing and keys to phylogenetic relationships; these include, for example, the adaxial fixigenal tubercle row, major row versus inter-row glabellar tubercles, and fixigenal circumocular tubercles. Darwin's (1881; fide Gould, 1983, p. 120) remark that "... 'de minimis lex non curat' [the law is not concerned with trifles] does not apply to science" remains insightful.

Indeed, one is forced to think about one's encrinurines as complexes of primitive and derived character states which record the pattern of evolution through which they originated. For example, all species conventionally grouped as Encrinuroides share a deep preglabellar furrow . The widespread occurrence of this state in early (Ordovician) encrinurines [i.e., ingroup comparison] and its presence in early ontogeny [the "ontogenetic argument"] suggest that a deep preglabellar furrow is a primitive character state. The "diagnostic" presence of this state stems from the recognition that most Silurian encrinurines have shallow (apomorphic) preglabellar furrows, although certain lineages (Erratencrinurus and Cromus, for example) retain the primitive state. Further character analysis of Encrinuroides (outlined in Chapter V) reveals that other characters are extremely variable (due to acquisition of evolutionary novelties within distinct lineages, the "species groups" of Chapter V), or are shared with at least some descendants assigned to other genera. Encrinuroides is thus recognized as a paraphyletic group united by retention of a few symplesiomorphies. In short, a deep preglabellar furrow does neither an "adaptive unit" nor a natural historical group make.

THE ROLE OF DEVELOPMENT - The most significant effect of the Mackenzie Mountains fauna has been providing previously-unknown data on the ontogeny of several taxa of Silurian encrinurines. Such information is, in itself, interesting from a descriptive viewpoint; documenting protaspides for *Balizoma*, *variolaris* plexus n. gen., and *Cromus*, or recognizing allometric trends through growth series. Of greater significance is the potential afforded by such data for comparative ontogenetic studies, an approach involving recognition of the influence of development in the evolutionary process. The writer's pervasive emphasis on the phylogenetic expression of perturbations in ontogenetic programs (i.e., changes in developmental timing and rate) has undeniably been influenced by current trends in comparative biology. Heterochrony has been resurrected, largely through Gould's (1977) landmark "Ontogeny and Phylogeny". Development is being dissected at the genomic (Dawid, 1982) and cellular levels (Gerhart, 1982), related to ecological strategies (McKinney, 1986), and to patterns of macroevolution (Maderson, 1982; Raff *et al*., 1987). Indeed, Lovtrup (1984) has defined phylogeny as the changes to which ontogeny has been subject in the course of time; Anderson (1987) reduces evolutionary change to the serial accumulation of small changes in development, constrained by the conservatism of developmental programs. Systematists (notably paleontologists) are emphasizing a comparative approach to ontogeny, and are recognizing heterochronic patterns in "their groups" (to which a glance at the titles in recent issues of <u>Paleobiology</u> will attest). Chapter II in this volume is thus, in many ways, a product of its times. The point to emphasize is that contemporary evolutionary theorists have (again) seized on the very real parallels between ontogeny and phylogeny.

The promotion of ontogeny to the forefront of phylogenetic inference (see Nelson, 1978; Fink, 1982; Patterson, 1983) is well demonstrated by current statements of the "ontogenetic argument" for determining character state polarities (in evolutionary sequences) in terms of "von Baer's Laws" of development from the general to the specific; similarities in early growth stages reflect proximity of common ancestry, with divergence increasing through ontogeny. This perception of the significance of ontogeny is a central theme through the studies presented herein. Growth series are documented in a comparative, rather than purely descriptive manner; the protaspis is no longer a curiosity in the upper left corner of photographic plates. Larval character states are used to assess phylogenetic relationships (Chapter III), with profound systematic implications rendered less immediately apparent by "von Baerian" divergence through later ontogeny.

To relate these studies in encrinurine ontogeny to more general evolutionary phenomena, two opposing roles of development in shaping the course of phylogeny should be stressed. Developmental pathways provide a potential source of variation, a means of generating substantial change in form through subtle perturbations in timing or rate [aptly summarized in Gould's, (1982) "small inputs, big outputs"]. The encrinurine examples serve to document the expression of these patterns in the fossil record. Rapid divergence of the _punctatus_ and _variolaris_ plexi from common ancestry suggests the potential role of heterochrony in macroevolutionary phenomena (cladogenesis, ecological displacement, and, indeed, adaptive radiation). As well, "taxonomic" variation within clades (the _variolaris_ plexus for example) may be recognized as results of extrapolating minor temporal shifts along growth trajectories.

The use of the term "results" in the preceding statement leads to the opposing role of development as a constraint on evolution (Gould, 1980; Alberch, 1982). "Byproducts", "allometric correlates" and the like are a pervasive theme in the interpretative sections herein, and attest to the adoption of structuralist models (see Kauffman, 1983) as a logical outgrowth of perceiving development as an integrated control on the organismal Bauplan. This marks a radical departure from the adaptationist scenarios which pervade conventional functional morphologic analysis (see Gould and Lewontin, 1979). Atomizing _Encrinurus_ (_Encrinurus_) into discrete non-correlated characters and speculating on the functional significance of derived states (long genal spines for increased soft substrate stability, to make up a typical example) is both unrealistic and misleading. "Non-adaptive" (i.e., exaptive sensu Gould and Vrba, 1982) does not imply "non-functional", nor is the role of selection denied. Indeed, E. (Encrinurus) was a long-ranging taxon including numerous species, all subtle modifications on the same general body form. Recognizing these derived states as unified ontogenetic correlates modifies instead the way we approach the target of selection. This view forms a more promising direction for unifying developmental theory with ecological theory. McKinney (1986), for example, has stressed the relationship between acceleration versus retardation and life history strategies (see Chapter II), with selection on body size (Calder, 1984) and timing of maturation of paramount importance. These issues are well demonstrated in Chapter III's discussion on protaspides of Silurian Balizoma, in which many differences with Ordovician encrinurine protaspides are simple allometric by-products of increased size of the instar. The target of selection shifts from discrete characters (anterior fixigenal spines, hypostomal posterior border furrow, etc.) to integrated organisms.

Thus, to draw on one of many examples, the recognition of a sister group relationship between Fragiscutum and variolaris plexus n. gen., as indicated by delayed onset timing of an anterior tubercle pair on the fixed cheeks along the axial furrow, is a result of documenting a new silicified fauna from the Mackenzie Mountains. Perhaps more importantly, it is an expression of a different way of looking at "the same old trilobite".

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