

Paleontological Society

Marjuman (Cambrian) Agnostoid Trilobites of the Cow Head Group, Western Newfoundland

Author(s): Stephen R. Westrop, Rolf Ludvigsen and Cecil H. Kindle

Source: *Journal of Paleontology*, Vol. 70, No. 5 (Sep., 1996), pp. 804-829

Published by: [Paleontological Society](#)

Stable URL: <http://www.jstor.org/stable/1306483>

Accessed: 23/04/2013 14:56

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Paleontological Society is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Paleontology*.

<http://www.jstor.org>

1995. Uppermost Campanian-Maastrichtian strontium isotopic, biostratigraphic and sequence stratigraphic framework for the New Jersey Coastal Plain. *Geological Society of America Bulletin* 107:19–37.
- TUOMEY, M. 1854. Description of some new fossils from the Cretaceous rocks of the southern states. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 7:162–172.
- WARD, P. D. AND W. J. KENNEDY. 1993. Maastrichtian ammonites from the Biscay Region (France, Spain). *Paleontological Society Memoir*, 34, 58 p.
- WIEDMANN, J. 1966. Stammesgeschichte und system der posttriadischen ammoniten; ein überblick. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 125:49–79; 127, 13–81.
- ZITTEL, K.A. VON. 1884. *Handbuch der Paläontologie*. 1, Abteilung 2; Lief 3, Cephalopoda, pp. 329–522. R. Oldenbourg, Munich and Leipzig.
- . 1895. *Grundzüge der Paläontologie (Paläozoologie)*. R. Oldenbourg, Munich and Leipzig, 972 p.

ACCEPTED 20 DECEMBER 1995

J. Paleont., 70(5), 1996, pp. 804–829
Copyright © 1996, The Paleontological Society
0022-3360/96/0070-0804\$03.00

MARJUMAN (CAMBRIAN) AGNOSTOID TRILOBITES OF THE COW HEAD GROUP, WESTERN NEWFOUNDLAND

STEPHEN R. WESTROP, ROLF LUDVIGSEN, AND CECIL H. KINDLE

Department of Earth Sciences, Brock University, St. Catharines, Ontario L2S 3A1,
School of Earth and Ocean Sciences, University of Victoria, Victoria, British Columbia V8W 2Y2
(Mailing Address: 4062 Wren Road, Denman Island, British Columbia V0R 1T0) and
332 N. Midland Ave., Upper Nyack, New York 10960

ABSTRACT—Shelf-derived limestone boulders in debris flows of the Cow Head Group, western Newfoundland, have yielded rich mid- to Upper Cambrian trilobite faunas. The agnostoid component of Marjuman boulders consists of 23 species assigned to 11 genera; *Kormagnostus boltoni* and *Kormagnostus? copelandi* are new. Cladistic parsimony analysis of the Ptychagnostidae Kobayashi reduces this family to 3 genera: *Ptychagnostus* Jaekel, *Pseudophalacroma* Pokrovskaya and *Lejopyge* Hawle and Corda; *Ptychagnostus* includes three non-obligate subgenera: *P. (Ptychagnostus)* (= *Tomagnostus* Howell); *P. (Goniagnostus)* Howell and *P. (Aotagnostus)* Öpik (= *Myrmecomimus* Öpik). Correlation with zonations established in northern Canada and Utah indicates that the Cow Head Group includes a nearly complete sequence of agnostoid faunas from the mid-Cambrian *Ptychagnostus gibbus* Zone to the Upper Marjuman *Cedaria brevifrons* Zone.

INTRODUCTION

THE SLOPE debris flows of the Cow Head Group of western Newfoundland contain numerous shelf-derived limestone boulders which provide a unique record of Laurentian Cambro-Ordovician carbonate shelf-margin trilobite faunas (Kindle and Whittington, 1958; Kindle, 1982; Ludvigsen et al., 1989). During some 40 years of fieldwork, C.H. Kindle, accompanied for several years by H.B. Whittington, amassed a collection of about 20,000 mid- to Upper Cambrian trilobites from the Cow Head Group, which was acquired by the Geological Survey of Canada through a contribution from the Government of Canada under the terms of the Cultural Property Export and Import Act (Kindle, 1982). Description of these diverse faunas is a major, ongoing project and, to date, work on the trilobites of the youngest Cambrian Sunwaptan Stage (Ludvigsen et al., 1989) and on the oldest fauna from the base of the sequence (Young and Ludvigsen, 1989) has been completed. Here, we document the agnostoid trilobites of the Marjuman Stage (Ludvigsen and Westrop, 1985).

Over the past decade, agnostoid trilobites have assumed major importance in global biostratigraphic correlation of Cambrian strata (e.g. Robison, 1982, 1984, 1988, 1994; Rowell et al., 1982). They are abundant, diverse and widely distributed in deep-shelf to slope facies, although their utility is reduced greatly in inner shelf facies, where agnostids are typically very rare or absent (Robison, 1976; Melzak and Westrop, 1994). The collections described here include several biostratigraphically important taxa.

STRATIGRAPHIC SETTING

The Cow Head Group of western Newfoundland is part of the Humber Arm Allochthon (Williams, 1975), an allochthonous terrane that was transported onto the underlying autochthonous shelf sequence (e.g. James et al., 1989) during the Middle Ordovician Taconic Orogeny (Williams and Hatcher, 1982). The stratigraphy and sedimentology of the Cow Head Group have been revised recently by James and Stevens (1986), who demonstrated that it represents a deep-water debris apron that was deposited at the foot of an early Paleozoic continental margin. They divided the group into two formations (Figure 1): the Shallow Bay Formation, a proximal, coarse-grained sequence that includes carbonate conglomerates, and the Green Bay Formation, which represents the distal, shaly facies.

The Shallow Bay Formation is divided into four members (Figure 1): in ascending order, the Downes Point, Tuckers Cove, Stearing Island and Factory Cove members. All of the collections described here are from the lower part of the Downes Point Member at three localities: Cow Head Peninsula (CH prefix; Figures 2, 3), Broom Point South (BPS prefix; Figs. 2, 4) and White Rock Islets (WRI prefix; Figures 2, 5). The Downes Point Member is dominated by coarse, often amalgamated conglomerates (Figures 3–5) which contain both equant, shelf margin-derived clasts and tabular clasts from slope sources (James and Stevens, 1986). The collections described here are typically from equant clasts of light-coloured, bioclastic packstones and grainstones that were probably derived from shelf-margin sand shoals (James and Stevens, 1986). A few collections (e.g. WRI

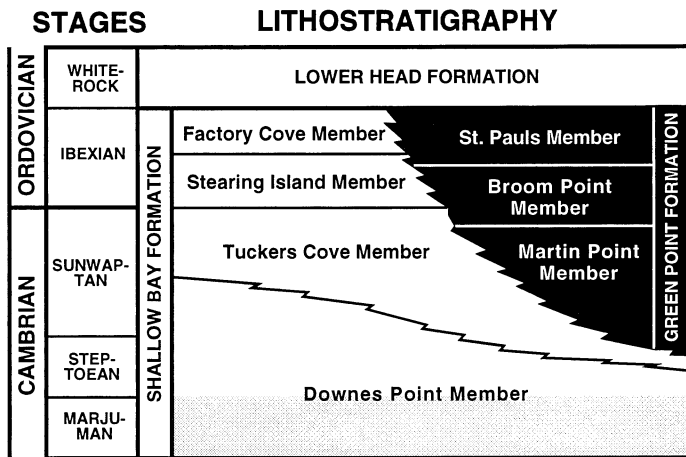


FIGURE 1—Stratigraphy of the Cow Head Group (modified from James and Stevens, 1986). The agnostoids dealt with in this paper are from the lower Downes Point Member (stippled).

619) are from dark-grey bioclastic wackestones suggestive of slope derivation and one, apparently autochthonous collection (BPS 448) is from thin, bioclastic horizons within a unit of parted lime mudstones at Broom Point South (unit 8 of James and Stevens, 1986).

AGNOSTOID ASSEMBLAGES

Complete biostratigraphic analysis of the Marjuman faunas of the Shallow Bay Formation must await description of the diverse corynexochoid and libristomate trilobites that occur with the agnostoids (Westrop and Ludvigsen, in prep.). A preliminary, agnostoid-based evaluation is presented here in the context of Kindle's (1982) informal zones. Correlations (Figure 6) can be made with both the sequence of agnostoid zones established by Robison (1976, 1982, 1984, 1994) and to the Marjuman zones of the Mackenzie Mountains (Pratt, 1992).

PRE-MARJUMAN ZONE

Kindle Zone 2.—The agnostoid fauna of Zone 2 occurs in bed 4 (Figure 4) at Broom Point South and is dominated by *Baltagnostus robustus* Öpik. *Ptychagnostus* (s.l.) *seminula* (Whitehouse) occurs with *B. robustus* and *Peronopsis segmenta* Robison in BPS 410 and 421, and with *B. robustus* and *Ptychagnostus* (*Ptychagnostus*) *fissus* (Lundgren) in BPS 409; *Peronopsis segmenta* and *P. seminula* co-occur in BPS 420. Although the boulders vary in agnostoid composition, shared corynexochoid and libristomate species (Westrop and Ludvigsen, in prep.), including *Semisphaerocephalus punctata* (Rasetti, 1963), indicate that Zone 2 is a coherent biostratigraphic assemblage. All agnostoid species of this fauna first appear in the *Ptychagnostus gibbus* Zone of Robison (1982, 1984, 1994) and one species, *P. seminula*, is confined to that zone. Thus, like the underlying Zone 1 (*Zacanthoides gilberti* Fauna of Young and Ludvigsen, 1989), Zone 2 is most likely correlative with the *P. gibbus* Zone.

Collections assigned to Zone 2 are BPS 402, 410, 413, 414, 421 and 434.

MARJUMAN ZONES

Kindle Zone 3.—The agnostoid fauna is characterized by abundant specimens of *Hypagnostus parvifrons* (Linnarsson) and is represented by collections from Broom Point South (Figure 4) and White Rock Islets (Figure 5); *Kormagnostus?* *copelandi* new species is abundant in collections from White Rock Islets. Like several other agnostoids present in at least some collections,

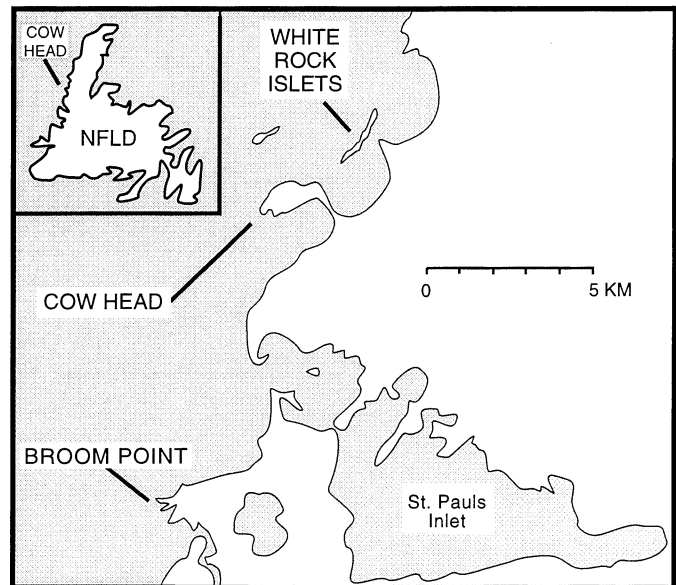


FIGURE 2—Map of the Cow Head region, western Newfoundland, showing the general location of the three sections that yielded Marjuman boulders.

including *Ptychagnostus* (s.l.) *atavus* (Tullberg), *P. hybridus* (Brögger) and *P. (Ptychagnostus) fissus* (Lundgren), *H. parvifrons* ranges through the *P. atavus* and *P. punctuosus* zones of Robison (1984); *Peronopsis interstricta* (White), which occurs with *H. parvifrons* in WRI 640, extends from the *P. gibbus* to *P. punctuosus* zones. Some collections with the eodiscid *Eodiscus scanicus* (Linnarsson; BPS 452; WRI 633; e.g. Kindle, 1982, pl. 1.2, figs. 5, 9) or the conocoryphid *Meneviella venulosa* (Salter; BPS 448, 450; e.g. Kindle, 1982, pl. 1.2.7) are most likely correlative with *P. atavus* Zone (e.g. see Hutchinson, 1962; Babcock, 1994), whereas at least one collection (BPS 451) with *Utagnostus trispinulus* Robison is probably correlative with the *P. punctuosus* Zone.

Collections assigned to Zone 3 are BPS 448, 450, 451 and 452; WRI 601, 602, 606, 607A, 608, 609, 613, 614, 615, 615B, 616, 617, 619, 621, 622, 623, 624, 625, 627, 630, 631, 632, 633, 640 and, possibly, 641.

Kindle Zone 4.—Boulders of Zone 4 occur in bed 11 at Broom Point South (Figure 4). *Kormagnostus* is the dominant agnostoid but is represented by species that are confined to the Shallow Bay Formation. Rare specimens of *Ptychagnostus aculeatus* (Angelin) and *Megagnostus glandiformis* (Angelin) indicate that Zone 4 is equivalent to the *Lejopyge laevigata* Zone of Robison (1984, 1994). This correlation is corroborated by the associated libristomate fauna (Westrop and Ludvigsen, in prep.), which includes species, such as *Bynumia metisensis* Rasetti, *Holmdalia punctata* (Rasetti) and *Exigua quebecensis* (Rasetti), that occur with *L. laevigata* in the Holm Dal Formation of northern Greenland (Robison, 1988). *Holmdalia punctata* is also shared with the lowest Marjuman zone established by Pratt (1992) in the Mackenzie Mountains, the *Cedaria minor* Zone. From the occurrence of *Kingstonia peltata* Palmer in the *L. laevigata* Zone of the Holm Dal Formation (Robison, 1988), Zone 4 is probably correlative with the Big Cove Member of the Petit Jardin Formation of the autochthonous shelf sequence of western Newfoundland (Westrop, 1992).

Collections assigned to Zone 4 are BPS 458, 460, 467 and 468.

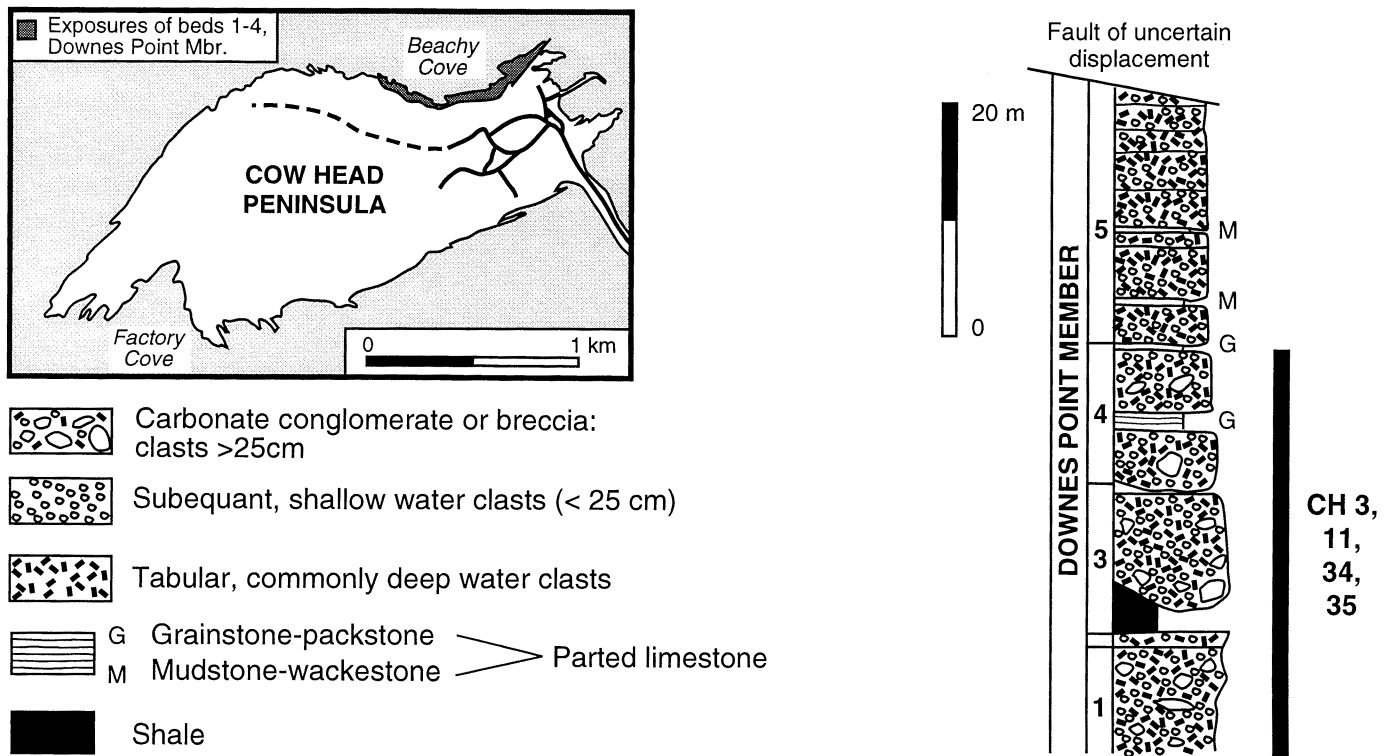


FIGURE 3—Detailed map and stratigraphic section for the Downes Point Member at Beachy Cove, Cow Head Peninsula (modified from James and Stevens, 1986). Stratigraphic intervals that yielded collections are indicated by vertical black bars.

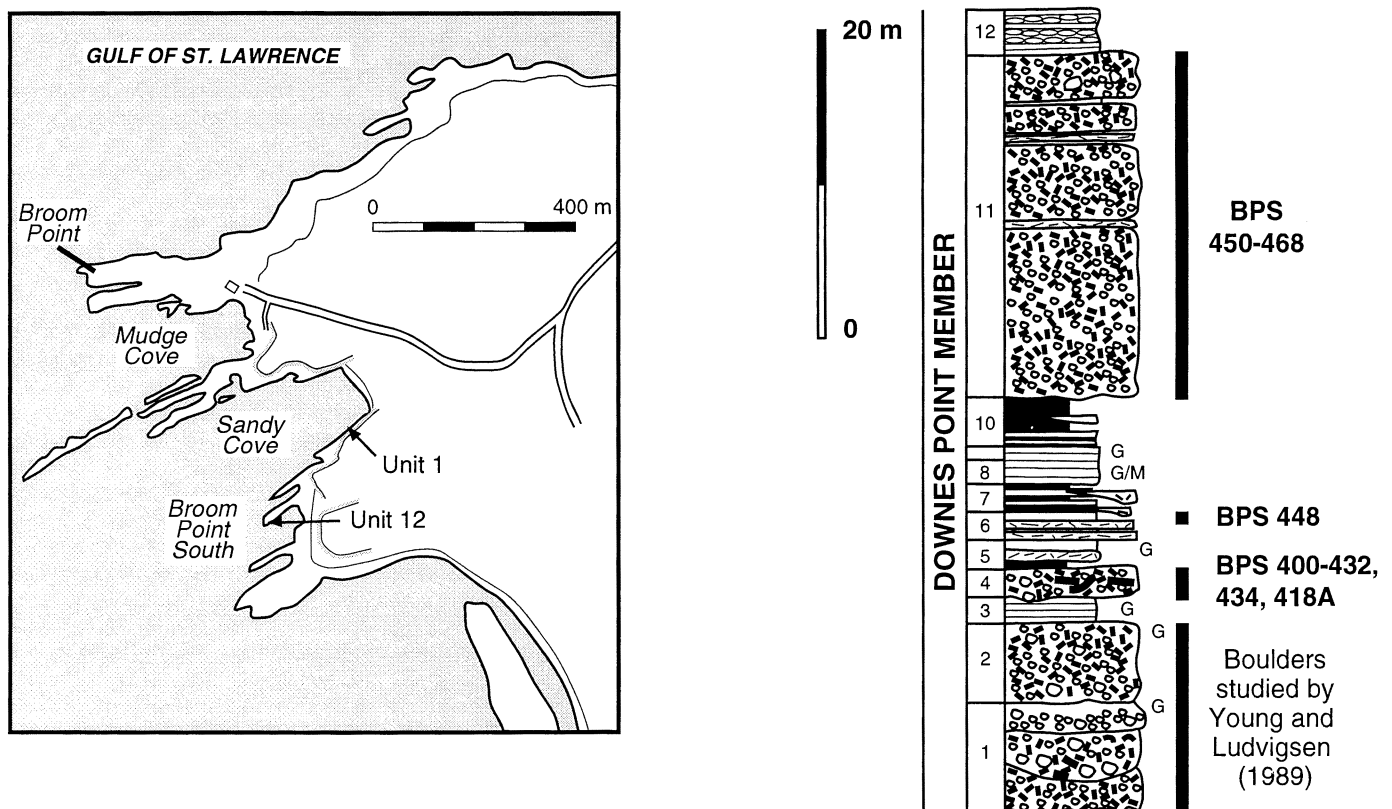


FIGURE 4—Detailed map and stratigraphic section for units 1 to 12 of the Downes Point Member, Broom Point South (modified from James and Stevens, 1986). Stratigraphic intervals that yielded collections are indicated by vertical black bars. See Figure 3 for legend.

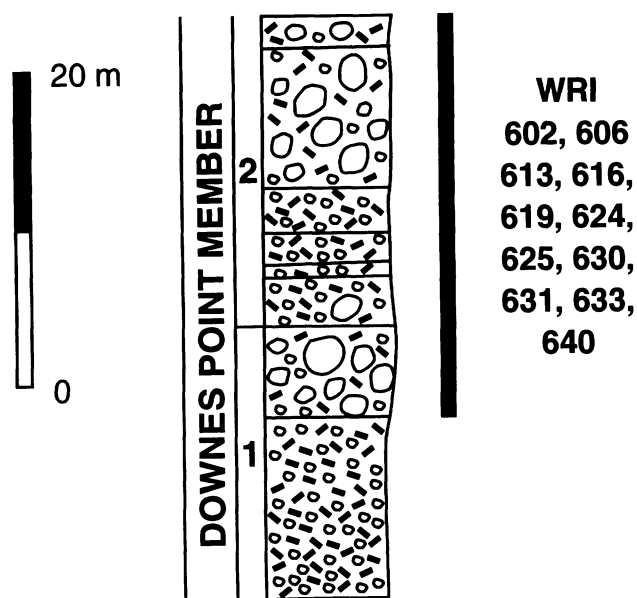


FIGURE 5—Stratigraphic section for the Downes Point Member, White Rock Islets (modified from James and Stevens, 1986). Stratigraphic intervals that yielded collections are indicated by vertical black bars. See Figure 3 for legend.

Kindle Zone 5.—Zone 5, which is confined to boulders from Cow Head Peninsula (Figure 3), is characterized by the long-ranging species, *Pseudagnostina douvillei* (Bergeron). Species present in at least some collections are *Acmarnagis typicalis* (Resser), *Connagnostus* cf. *C. fritzi* Pratt, *Kormagnostus boltoni* new species and *Nahannagnostus logani* Pratt. A diverse associated fauna of libristomates (Westrop and Ludvigsen, in prep.) includes *Crepicephalus rivus* Kindle, *Deiracephalus aster* (Walcott), *D. unicornis* Palmer, *Kingstonia walcotti* Resser, *K. vagrans* Lochman, *Meteoraspis borealis* Lochman and *Tricrepicephalus texanus* (Shumard). Taken together, the agnostoids and libristomates indicate a correlation with the *Cedaria prolifica* and *C. brevifrons* zones of the Mackenzie Mountains (Pratt, 1992) and with the *Crepicephalus* Zone of the traditional North American genus-based zonation (e.g. Lochman-Balk and Wilson, 1958).

Collections assigned to Zone 5 are CH3, 11, 12, 34 and 35.

CLASSIFICATION OF AGNOSTOID TRILOBITES

More than any other group of trilobites in recent years, agnostoids have been subject to disparate views on classification (Öpik 1967; Robison, 1988, 1994; Shergold et al., 1990; Pratt, 1992). The content and systematic position of genera, subfamilies and families have fluctuated markedly. For example, pseudagnostines have generally been aligned with the Diplagnostidae (e.g. Shergold et al., 1990) but Pratt (1992) regarded them as a subfamily of the Agnostidae. At lower taxonomic levels, *Kormagnostus*, for example has been variously assigned to the Peronopsidae by Robison (1988), to the Ammagnostinae by Shergold et al. (1990) and to a new subfamily of the Agnostidae, the Kormagnostinae, by Pratt (1992). Numerous other examples could be cited and the various differing opinions reflect in part the fact that homoplasy is widespread among agnostids. However, part of the classification problem is a result of methodology. For example, the most recent attempt at a comprehensive revision of agnostoids (Shergold et al., 1990) used combinations of characters in extended generic and suprageneric diagnoses without determining whether those characters were plesio-

	MACKENZIE MOUNTAINS	UTAH	NFLD
MARJUMAN	<i>Cedaria brevifrons</i>	" <i>Crepicephalus</i> "	ZONE 5
	<i>C. prolifica</i>		
	<i>C. selwyni</i>		
	<i>C. minor</i>	" <i>Cedaria</i> "	?
	Zonation not established	<i>L. calva</i>	ZONE 4
		<i>Lejopyge laevigata</i>	
		<i>Bolaspidea contracta</i>	ZONE 3
		<i>P. punctuosus</i>	
		<i>Bathyriscus fimbriata</i>	
		<i>P. atavus</i>	
		" <i>Bathyriscus-Elrathina</i> "	ZONE 2
			ZONE 1

FIGURE 6—Correlation of Marjuman agnostoid faunas of the Cow Head Group with trilobite zonation for the Mackenzie Mountains (Pratt, 1992) and Utah (Robison, 1976, 1984). Zone 1 corresponds to the *Zacanthoides gilberti* Fauna of Young and Ludvigsen (1989).

morphic or apomorphic, an approach which is likely to define gradistic taxa rather than clades. Also, some workers (e.g. Robison, 1984, 1994; Laurie, 1988, 1989) have used inferred lineages to support particular arrangements of species. However, we agree with those (e.g. Forey, 1982) who have argued that apparent ancestor-descendant relationships should not be used in systematic work.

An alternative approach involves application of phylogenetic techniques, especially quantitative parsimony analysis (e.g. Swofford, 1993). Phylogenetic systematics has revolutionized systematic treatment of, for example, fossil vertebrates (e.g. Benton, 1990; Sereno, 1991) but, with a few exceptions (e.g. Fortey and Chatterton, 1988; Edgecombe and Chatterton, 1990; Hughes and Rushton, 1990; Adrain and Chatterton, 1994), application of this approach to trilobites is far from routine. A full evaluation of agnostoid classification using quantitative parsimony techniques is far beyond the scope of this paper. However, an analysis of one family, the Ptychagnostidae, is presented here as an illustration of the problems which must be overcome. The ptychagnostids were selected for a detailed study because radically different arrangements of species have been published recently by Robison (1984, 1994) and Laurie (1988, 1989).

Classification of the family Ptychagnostidae.—Originally established to accommodate *Ptychagnostus* and *Goniagnostus* by Kobayashi (1939), generic assignments of ptychagnostid species have varied greatly over the last 15 years. Öpik (1979) established four new genera for Australian material, *Aotagnostus*, *Myrmecominus*, *Onymagnostus* and *Zeteagnostus*, as well as two new subgenera of *Goniagnostus*, *Criotypus* and *Allobodochus*, and a new subgenus of *Ptychagnostus*, *Acidusus*. Robison (1982) regarded most of these new taxa as junior synonyms of *Ptychagnostus*, but modified his position two years later and concluded that the Ptychagnostidae was composed of five genera: *Ptychagnostus*, *Onymagnostus*, *Lejopyge*, *Goniagnostus* and

Myrmecomimus. Most recently, he argued that *Onymagnostus* was paraphyletic and placed it in synonymy with *Lejopyge* (Robison, 1994). He also transferred some species of *Lejopyge* to *Pseudophalacroma*, which was also regarded as a ptychagnostid genus.

Laurie (1988, 1989) advocated a classification comparable to that of Öpik (1979), but elevated *Acidusus* to full generic status. Under his scheme, the Ptychagnostidae consisted of nine genera, two of which, *Triplagnostus* and *Goniagnostus*, were divided into subgenera. However, few of the ptychagnostid genera recognized by Laurie are characterized by synapomorphies and, as discussed below, many are likely to be paraphyletic.

In resurrecting *Acidusus*, Laurie (1988, p. 179) suggested that the presence of a posteriorly located glabellar node and a large axial pygidial node made this genus "sufficiently distinct from *Ptychagnostus* to warrant generic status." However, both of these character states are present in *Triplagnostus*, as emended by Laurie (1988, p. 193–194), and cannot, therefore, contribute to the diagnosis of a demonstrably monophyletic *Acidusus*. In fact, only the presence of scrobicules on most species and a less convex, more strongly tapered glabella separate *Acidusus* from *Triplagnostus* (Laurie, 1988, p. 194). Spinosity of the exoskeleton differentiates *Triplagnostus* from *Ptychagnostus* (Laurie, 1988, p. 194) but other genera, including *Acidusus*, contain spinose species (e.g. Robison, 1984, fig. 10). In the absence of any apparent derived characters, we support Robison's (1984) synonymy of *Triplagnostus*, *Acidusus* and *Ptychagnostus*. Those species assigned to *Triplagnostus* (*Aotagnostus*) by Laurie (1988) may be more closely related to *Myrmecomimus*: both taxa share an expanded anteroglabella (e.g. Laurie, 1988, fig. 21A–E, H, J, L, M, O–P, R; Öpik, 1979, pl. 35, figs. 4–6, pl. 36, figs. 1–5) and a relatively short posteroaxis (e.g. Laurie, 1988, fig. 21F–G, I, K, N, Q; Öpik, 1979, pl. 35, figs. 4–7, pl. 36, figs. 1–6).

Onymagnostus has been diagnosed phenetically by Robison (1984) and Laurie (1988) but none of the characters used is unique to that genus. The smooth, non-scrobiculate surface is matched in *Triplagnostus* as well as in species of outgroup taxa such as *Agnostus*. The strong deflection of the pygidial F2 furrow by a large node was used by Laurie to diagnose both *Acidusus* and *Onymagnostus*, and a long pygidial axis is also shared by these, and other, genera. We are unable to find any synapomorphy that might diagnose *Onymagnostus* and, like Robison (1994), conclude that it is a paraphyletic taxon. Robison's (1994) solution to this problem was the synonymy of *Onymagnostus* and *Lejopyge*, as suggested by an apparent evolutionary sequence from *Onymagnostus hybridus* to *Lejopyge laevigata* (see also Laurie, 1989) and by parsimony analysis of species of *Lejopyge* and *Onymagnostus* (Robison, 1994, fig. 22). However, the absence of apomorphies in *Onymagnostus* is not addressed by this action because there are no derived character states which might be used to diagnose an expanded *Lejopyge*. Moreover, some character states of *Onymagnostus*, such as a large pygidial node that strongly deflects the F2 furrow, suggest a relationship with *Ptychagnostus*, rather than *Lejopyge*.

In order to explore the relationships between the ptychagnostid genera further, we used the PAUP parsimony program (version 3.1.1; Swofford, 1993). The data set for the analysis consists of 42 well-known ptychagnostid species that have been thoroughly documented by Öpik (1979), Robison (1964, 1982, 1984, 1994) and Laurie (1988, 1989). The matrix (Figure 7) includes 28 unweighted characters with a total of 70 character states (Appendix). In one set of analyses (Figures 8.1, 9), 7 characters (1, 8, 9, 14, 15, 16, 17) were ordered; in alternative runs (Figure 8.2), all states were unordered. The sister group to the Ptychagnostidae is currently uncertain and rooting of the tree was achieved using two species as outgroups: "*Peronopsis*"

brighamensis (Resser) was selected because Robison (1978, p. 2) regarded this species as the ancestor of *Ptychagnostus*, and the type species of *Agnostus*, *A. pisiformis* (Wahlenberg; Shergold et al., 1990, fig. 9.1) was somewhat arbitrarily chosen as the other outgroup (see Smith, 1994, p. 57 for the use of multiple outgroups in parsimony analysis). Because the problem was too large to use the branch-and-bound technique, the heuristic search option was used to find the most parsimonious trees. This means that trees might not be optimal with regard to length. In separate sets of analyses (Figures 7, 8), 9000 trees were saved before available memory was exhausted; the most parsimonious trees for ordered and unordered characters had lengths of 171 and 166, respectively. Analyses with ordered and unordered characters differed significantly only the positions of two species: *Agnostus fissus* Linnarsson and *Ptychagnostus cassis* Öpik.

High degrees of homoplasy are indicated and, not surprisingly, the results of our parsimony analysis do not support the finely divided, gradistic classifications of Öpik (1979) or Laurie (1988, 1989), but are consistent with Robison's (1982) more conservative approach.

Monophyletic ptychagnostid genera could be defined at several nodes. For example, *Aotagnostus* (including *Myrmecomimus*) and *Goniagnostus* both emerge as relatively small, monophyletic groupings of mainly Australian species at high levels within the trees in all analyses (Figures 7, 8). However, recognition of these taxa as separate genera leaves a paraphyletic array of species of *Acidusus* and *Triplagnostus* (as defined by Laurie, 1988) that join at successively lower nodes in the cladogram. Similarly, a large group of species with the glabellar tubercle opposite the tips of the basal lobes, encompassing *Goniagnostus*, *Aotagnostus*, *Myrmecomimus*, *Acidusus* and *Triplagnostus*, can be recognized in most trees (Figures 7.1, 8). *Tomagnostus*, together with *Ptychagnostus affinis* and *P. punctuosus*, forms the sister group but species of *Onymagnostus* are left as a paraphyletic residue. Consequently, we have opted for a broadly defined, monophyletic *Ptychagnostus* which subsumes *Onymagnostus*, *Acidusus*, *Triplagnostus*, *Aotagnostus*, *Myrmecomimus*, *Goniagnostus* and *Tomagnostus* (Figures 7, 8). *Ptychagnostus* may be diagnosed by the presence of a pygidial F2 furrow that is strongly deflected medially by a large tubercle on pygidial M2 lobe and by the possession of strongly elongate basal glabellar lobes. Character reversals are indicated by the cladograms, so that not all member species possess both of these traits: e.g. *P. punctuosus* and *P. affinis* have a weakly deflected pygidial F2, whereas species assigned formerly to *Onymagnostus* retain relatively plesiomorphic, weakly elongated or simple basal glabellar lobes. The presence of a strongly deflected pygidial F2 on at least some specimens of *Pseudophalacroma lundgreni* is interpreted from the cladogram as homoplasious. Small, monophyletic groups [*Ptychagnostus* (*Ptychagnostus*), (*P.*) *Goniagnostus* Howell and (*P.*) *Myrmecomimus* Öpik] are assigned to non-obligate subgenera (Adrain and Chatterton, 1994); the remaining species are assigned to *Ptychagnostus sensu lato* (Figures 7.1, 8). As proposed by Adrain and Chatterton (1994, p. 309), use of non-obligate subgenera allows monophyletic subsets to be recognized within genera without the necessity of naming paraphyletic arrays of sister species that occupy nodes at progressively lower levels in the cladogram.

Analyses with ordered characters (Figures 7.1, 8) revealed a monophyletic group consisting of *Tomagnostus* plus *Ptychagnostus affinis* and *P. punctuosus* that is assigned here to *Ptychagnostus* (*Ptychagnostus*). With characters unordered, one species, *Agnostus fissus* Linnarsson, changes position to become the sister taxon of "*Onymagnostus*" *barrandeii* (Figure 8.1). However, unordered analyses that were constrained to include *A. fissus* in *P. (Ptychagnostus)* increased tree length by only one

CHARACTERS SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
<i>A. punctuosus</i> Angelin	0	0	1	0	0	0	0	2	1	0	0	1	1	2	1	0	0	0	2	0	0	1	0	0	1	1	0	0
<i>A. affinis</i> Brøgger	0	0	0&1	0	0	0	0	2	1	1	0	1	1	2	1	0	0	0	2	0	0	1	0	0	1	0&1	0	0
<i>Z. incautus</i> Öpik	0	0	0	1	0	0	0	?	0	1	2	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0
<i>Z. scarifatus</i> Öpik	0	0	0	1	0	0	0	2	0	1	2	1	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0
<i>Ac. atavus</i> Tullberg	0	0	0	0&1	0	0	0	2	0&1	1&2	0	0	1	2	2	0	1	0	0	0	0	1	0&1	0	?	0	0	0
<i>Ac. acidus</i> Öpik	0	0	0	0	0	0	0	2	0&1	2	0	0	1	2	2	0	1	0	0	0	0	1	0	0	0	0	0	0
<i>Ac. germanus</i> Öpik	0	0	0	0	0	0	1	2	0&1	2	0	0	1	2	2	0	1	1	0	0	0	1	0&1	0	0	0	0	0
<i>Ac. occultatus</i> Öpik	0	0	0	0	0	0	1	2	1	2	0	0	1	2	2	0	1	1	0	0	0	1	0	0	0	0	0	0
<i>P. michaeli</i> Robison	0	0	0	1	0	0	1	2	0&1	2	0	0	1	2	2	0	0	1	0	0	0	0	1	0	0	0	0	0
<i>P. akanthodes</i> Robison	0	0	0	0	0	0	1	2	2	2	0	0	1	1	2	0	1	1	0	0	0	0	0	0	?	0&1	0	0
<i>P. cassis</i> Öpik	0	0	0	1	0	0	0	2	0	2	2	1	1	2	1&2	0	0	?	0	0	0	0	1	0	0	0	0	?
<i>A. aculeatus</i> Angelin	0	0	0	0	0	0	1	2	2	2	0	0	0	1	2	0	2	?	0	0	0&1	1	0	0	?	1	0	?
<i>A. hybridus</i> Brøgger	0	0	0	1	0	0	0	0&1	0	1	0&1	0	0&1	0&2	2	0	1	0	0	0	1	1	1	0	1	0	0	0
<i>A. seminula</i> Whitehouse	0	0	0	1	0	0	0	1	0	0	0&1	0	1	2	2	0	1	0	0	0	1	1	1	0	1	0	0	0
<i>O. semiermis</i> Öpik	0	0	0	0	0	0	0	1	0	1	0&1	0	1	2	2	0	1	0	0	0	1	1	1	0	1	0	0	0
<i>A. barrandei</i> Hicks	0&1	1	0	1	0	0	0	0	0	0	1	1	0	2	2	0	0&1	0	0	0	1	1	1	0	?	0	0	0
<i>A. praecurrens</i> Westergård	0	0&1	0	1	0	0	0	0&1	0	1	1	0	1	1	0	0	0	0	0	0	0&1	1	1	0	1	0	0	0
<i>A. gibbus</i> Linnarsson	0	0	0	0	0&1	0	1	2	0&1	2	0&1	0	1	1&2	2	0	2	1	0	0	0	0	1	0	1	0	0	0&1
<i>T. scopus</i> Öpik	0	0	0	1	0	0	1	2	0	2	0&1	0	1	1	2	0	2	1	0	0	0	0	1	0	1	0	0	1
<i>T. ultimus</i> Öpik	0	0	0	1	0	0	1	2	0	?	0	0	1	1	2	0	1	1	0	0	0	0	1	0	1	0	0	0
<i>Ao. culminosus</i> Öpik	0	0	0	1	0	0	1	1&2	0	2	3	0	1	1	2	1	2	1	0	0	0	0	1	0	?	0	0	1
<i>Ao. aotus</i> Öpik	0	0	0	1	0	0	1	0&1	0	2	3	0	1	1	2	1	1&2	1	0	1	0	1	1	0	?	0	0	1
<i>Ao. magniceps</i> Öpik	0	0	0	1	0	0	1	2	0	2	3	0	1	2	2	1	1&2	1	0	1	0	0	1	0	?	0	0	0
<i>M. tribulis</i> Öpik	0	0&1	0	1	0	0	1	2	0	2	3	0	1	0	2	2	1	0	0	1	0	1	1	0	1	0	0	0
<i>M. saltus</i> Öpik	0	1	0	1	0	0	?	2	0	2	3	0	1	0	?	2	1	0	0	1	0	1	1	0	1	0	0	0
<i>A. narhorsti</i> Brøgger	0	0	0	0	1	1	1	2	1	2	0	0	0	1	1	0	1	1	1	1	0&1	0	0	0	1	1	0	0
<i>G. scarabaeus</i> Whitehouse	0	0	0&1	0	1	1	1	2	1	2	0	0	0&1	1	1	0	2	1	1	0	0	0	0&1	0	1	1	0	1
<i>A. spiniger</i> Westergård	0	0	0&1	0	1	?	1	2	0	2	0	0	0&1	1	1	0	1	?	1	0	0	?	0	0	1	1	0	?
<i>G. (C.) oxytaurus</i> Öpik	0	0	1	0	1	1	1	2	0	2	0	0	0&1	1	1	0	2	1	?	0	0	0	0	1	1	1	0	1
<i>G. (C.) lemniscatus</i> Öpik	0	0	1	0	1	1	1	2	1	2	0	0	0&1	1	1	0	2	1	?	0	0	0	0	1	1	1	0	0
<i>A. fissus</i> Linnarsson	0	1	1	1	0	0	0	1	0	0	0	1	0	2	1	0	1	0	2	0	1	1	0&1	0	2	0&1	0	0
<i>A. perrugatus</i> Grönwall	0	1	1	0	0	0	0	2	0	1	0	1	1	1	1	0	1	0	2	0	1	0	0	1	?	?	0	0
<i>L. cantha</i> Robison	3	1	0	1	0	0	1	0	0	?	?	?	?	1	?	?	0	2	0	0	?	1	1	1	0	?	0	1
<i>A. armatus</i> Linnarsson	2	1	0	1	0	0	1	0	0	1	?	?	0	1	?	?	0	0	0	?	1	0	0&1	0	1	0	1	0
<i>L. calva</i> Robison	3	1	0	1	0	0	0	0	0	1	?	?	?	?	?	?	0	0	?	?	1	1	0&1	0	?	0	1	0
<i>Battus laevigatus</i> Dalman	2	1	0	1	0	0	0	0	0	1	?	?	0	1	?	?	0	0	0	?	1	1	1	0	?	0	1	0
<i>L. multiforma</i> Öpik	3	1	0	1	0	0	1	0	0	1	?	?	?	?	?	?	0	0	0	?	1	1	1	0	?	2	1	1
<i>Ph. dubium</i> Whitehouse	0	1	0	1	0	0	0	0	0	1	2	1	1	1	?	?	0	1	0	0	0	0	0	1	0	?	0	1
<i>A. lundgreni</i> Tullberg	0	0	0	1	0	0	0	0	0	1	2	1	1	1	1&2	0	0	0	0	0	0	1	1	0	?	0	0	0
<i>L. rigbyi</i> Robison	0	0	0	1	0	0	1	0	0	1	2	1	1	1	1	0	2	1	0	0	0	1	1	0	?	0	0	0
<i>To. bothrus</i> Robison	0	1	1	0	0	0	0	1	0	1	0	0	1	1&2	1	0	1	0	2	0	0&1	0	0	1	?	0	0	0
<i>A. elegans</i> Tullberg	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	1	0	?	0	1	1
OUTGROUP SPECIES																												
<i>A. pisiformis</i> Belt	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Pe. brighamensis</i> (Resser)	0	1	0	1	0	0	0	0	?	0	0	1	1	0	0	1	0	0	0	1	1	1	0	?	0	0	0	0

FIGURE 7—Data matrix used in PAUP analysis of the Ptychagnostidae. Characters and states are defined in the appendix. & = more than one state present for a particular character; ? = missing data. Abbreviations for genus names: *A.*, *Agnostus*; *Ac.*, *Acidus*; *C.*, *Cryotypus*; *G.*, *Goniagnostus*; *L.*, *Lejopyge*; *O.*, *Onymagnostus*; *P.*, *Ptychagnostus*; *Pe.*, “*Peronopsis*”; *Ph.*, *Phalacroma*; *T.*, *Triplagnostus*; *To.*, *Tomagnostus*; *Z.*, *Zetagnostus*.

step. Apomorphic character states of *P.* (*Ptychagnostus*) are the presence of a depression at or in front of posteroaxis midlength, a frontal sulcus on the glabella and a reversal to a weakly deflected pygidial F2 furrow (states 19[2], 3[1], 15[1] and 19[2] in Figure 9; e.g. Figure 17; Robison, 1984, fig. 9; Laurie, 1988, fig. 1; Robison, 1994, figs. 28–31). The latter two character states also occur in some species of *Ptychagnostus* (*Goniagnostus*) but, from the topology of the trees, these similarities must be interpreted as homoplasious, rather than the retention of plesiomorphies.

Apomorphic character states that can be used to diagnose *Ptychagnostus* (*Goniagnostus*) include the presence of appendiferal pits (e.g. Laurie, 1989, figs. 1–2; state 5[1] in Figure 9) and the presence of a glabellar spine (e.g. Öpik, 1979, pl. 63, fig. 1; state 6[1] in Figure 9). All members of the subgenus also have a weakly to strongly defined depression on rear half of the posteroaxis (e.g. Laurie, 1989, figs. 1–2, 4 B, E–F; state 19[1] in Figure 9).

Apomorphic characters of *Ptychagnostus* (*Aotagnostus*), regarded here as the senior synonym of *Myrmecominus* Öpik, are

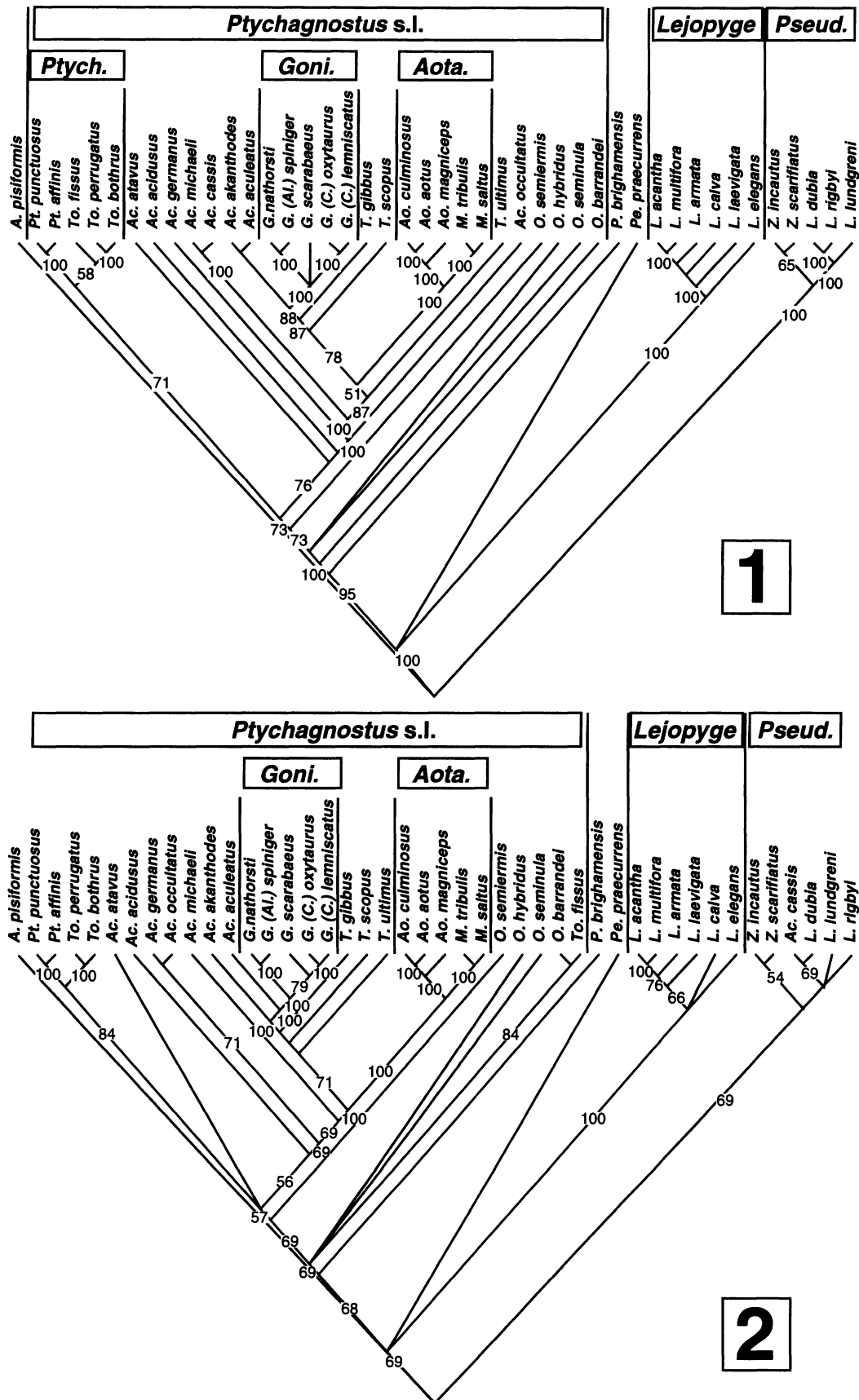


FIGURE 8—Consensus trees for 42 ptychagnostid species (from 9000 trees). Taxa indicated by abbreviations are: *Goni.*, *Goniagnostus*; *Aota.*, *Aotagnostus*; *Pseud.*, *Pseudophalacroma*; *Ptych.*, *Ptychagnostus*. In order to facilitate comparisons with the classification proposed by Laurie

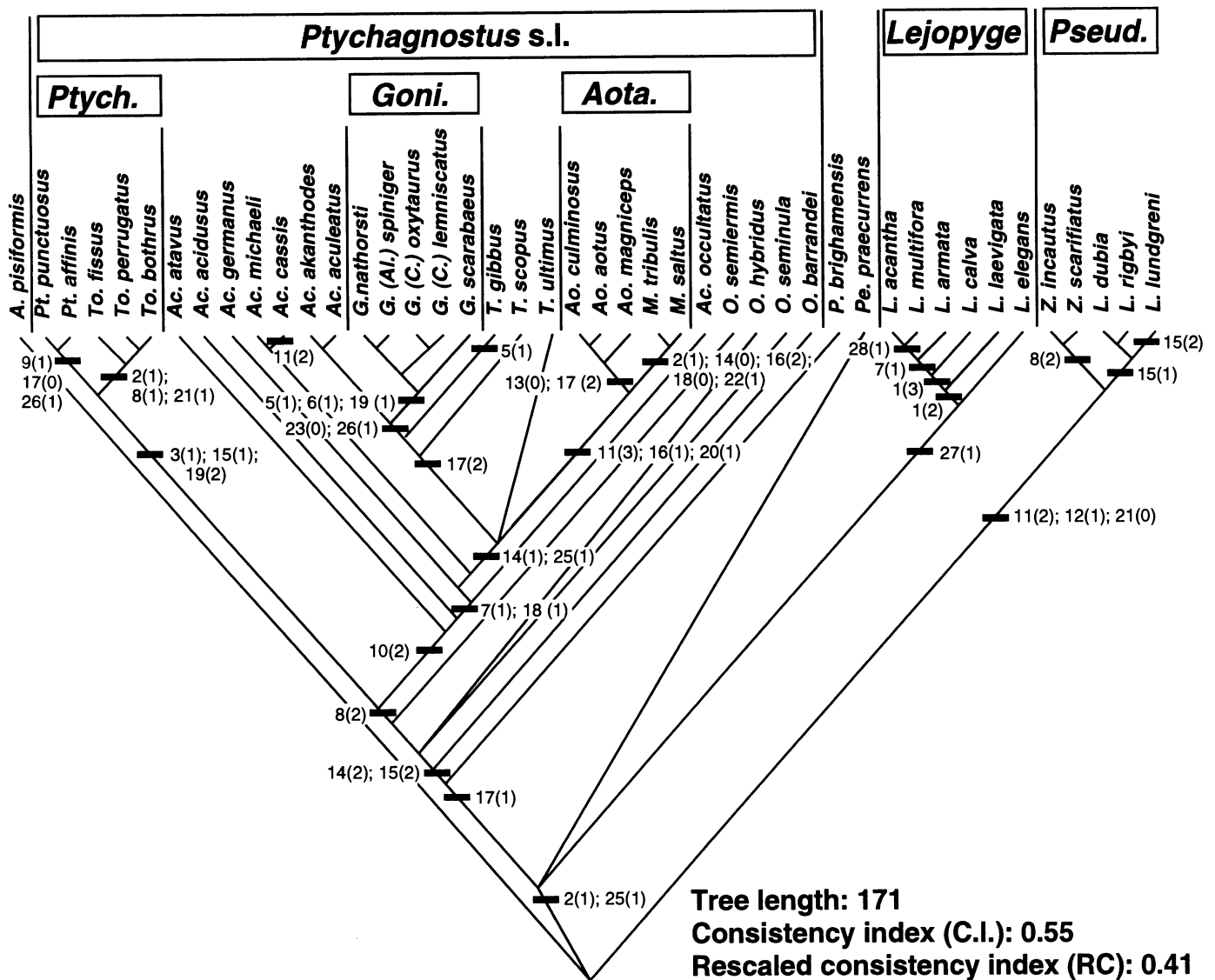


FIGURE 9—Optimized character distribution (ACCTRAN) for one of 9000 equally parsimonious trees produced with ordered characters (comparable in configuration to the 50 percent majority rule tree; Figure 8.1), generated using PAUP's "show apomorphies" option. Taxa indicated by abbreviations are: *Goni.*, *Goniagnostus*; *Aota.*, *Aotagnostus*; *Pseud.*, *Pseudophalacroma*; *Ptych.*, *Ptychagnostus*.

an expanded anteroglabella (e.g. Laurie, 1988, fig. 21 A–E, H, J, M, P; Öpik, 1979, pl. 36, figs. 1–5; state 11[3] in Figure 9) and a relatively short posteroaxis that occupies half or less of total axis length (e.g. Öpik, 1979, pl. 32, figs. 1–2, pl. 36, fig. 1–4, 6; state 20[1] in Figure 9).

In all trees, *Pseudophalacroma* Pokrovskaya emerges as a separate genus that becomes the senior synonym of *Zeteagnostus* Öpik. This genus includes *P. dubius* (Whitehouse), *P. incautus* Öpik, *P. scarifiatus* Öpik (as emended by Laurie, 1988), and, as recognized by Robison (1994), *P. lundgreni* (Tullberg) and *P. rigbyi* (Robison). All of these species possess an anteriorly tapered posteroglabella so that the glabella is constricted at the transglabellar furrow (e.g. Robison, 1984, fig. 27.1, 27.3, 27.5,

27.7, 27.8, fig. 29.1, 29.3, 29.4; Laurie, 1988, fig. 3A–G, 4A–C; Robison, 1988, fig. 11.3). The status of *Ptychagnostus cassis* Öpik is uncertain. In analyses with unordered character states this species is part of *Pseudophalacroma*. However, with ordered character states, it is nested within *Ptychagnostus* (s.l.) and the presence of an anteriorly tapered posteroglabella is, from the topology of the tree, best interpreted as homoplasous; analyses constrained to include *P. cassis* in *Pseudophalacroma* increase tree length by 2 steps. There do not appear to be any other synapomorphies that might diagnose *Pseudophalacroma* and several character states of many members are relatively plesiomorphic (e.g. simple to slightly elongate basal glabellar lobes). Thus, it may yet prove to be paraphyletic. Finally, Robison

(1988, 1989), species have been labelled according to his generic assignments: *Pt.*, *Ptychagnostus*; *To.*, *Tomagnostus*; *Ac.*, *Acidus*; *Al.*, *Allobo-*
dochus; *T.*, *Triplagnostus*; *Ao.*, *Aotagnostus*; *M.*, *Myrmecominus*; *G.*, *Goniagnostus*; *O.*, *Onymagnostus*; *Pe.*, *Pentagnostus*; *L.*, *Lejopyge*; *Z.*, *Ze-*
teagnostus. *P.* = "*Peronopsis*"; *A.* = *Agnostus*. 1, 50 percent majority rule tree generated with characters 1, 8, 9, 14, 15, 16 and 17 ordered. 2,
 50 percent majority rule tree generated with all characters unordered. Numbers indicate percentage of trees in which nodes occur.

(1994) included *Lejopyge multifora* Opik in *Pseudophalacroma* but our analyses (Figures 7, 8) include this species in *Lejopyge*.

The status of *Lejopyge* is difficult to evaluate because of information loss due to effacement; indeed, apart from the presence of a very narrow, rim-like cephalic border (character state 27[1] in Figure 9; e.g. Robison, 1984, figs. 21.7, 22.2, 23.2, 25.1, 26.2, 26.9), effacement is the primary unifying characteristic of the genus as defined here. *Lejopyge* includes *L. acantha* Robison, *L. multifora* Opik, *L. calva* Robison, *L. laevigata* (Dalman), *L. praecox* Opik, *L. elegans* (Tullberg) and *L. armata* (Linnarsson) (Figures 7, 8). The cladogram published by Robison (1994, fig. 22), which was based upon a smaller subset of ptychagnostid species, implies that the presence of small basal lobes is a synapomorphy for strongly effaced species of *Lejopyge*. However, the expanded analysis presented here indicates that this character state, present in most agnostids, is best interpreted as retention of a plesiomorphy. Finally, *Agnostus hybridus* Brøgger and *A. barrandei* Hicks were also regarded by Robison (1994) as part of the evolutionary sequence leading to *Lejopyge* but, in all of our analyses (Figures 7, 8), they share a more recent common ancestor with *Ptychagnostus* (s.l.).

The status of *Agnostus praecurrens* Westergård (1946) is also problematic and we have left it unassigned at the generic level. Laurie (1988) placed this species in *Pentagnostus* but his diagnosis of this genus is a combination of plesiomorphic (e.g. short to slightly basal glabellar lobes; subtransverse pygidial F2 furrows; absence of cephalic and pygidial spines) or ambiguous (parallel-sided posteroglabella: shared with *Triplagnostus sensu* Laurie, 1988) characters. Robison (1978, p. 2) assigned *A. praecurrens* to *Ptychagnostus* but it lacks the apomorphies used here to diagnose this genus (presence of a pygidial F2 that is strongly deflected medially by a large tubercle on pygidial M2 lobe; strongly elongate basal glabellar lobes) and joins at a low level in the cladogram. The classification of "*Peronopsis*" *brighamensis* (Resser; Robison, 1978, pl. 1, figs. 7, 11, 14) is equally uncertain. Although designated as an outgroup for rooting purposes, this species was nested within the Ptychagnostidae in all trees and shares a common ancestor with *Ptychagnostus* (s.l.). It possesses a number of plesiomorphic states (e.g. transverse pygidial F2 furrow; short basal glabellar lobes) and we have left it unassigned at the generic level.

Finally, in order to compare the classification of species produced here with those proposed by Robison (1984, 1994) and Laurie (1988, 1989), we performed separate analyses using constraint trees (Figure 10). Constraint trees depicting the alternative arrangements of species were produced using the tree manipulation window of the MacClade program (Maddison and Maddison, 1992) and, in each analysis, PAUP saved only those trees that were consistent with them. In both cases, the most parsimonious trees had greater lengths than our unconstrained analysis. Laurie's more finely divided classification increased minimum tree lengths from 171 to 182 steps. Somewhat surprisingly, Robison's classification, which includes a smaller number of genera than Laurie's, resulted in an even greater increase in minimum length to 191 steps. This probably reflects differences in group membership between Robison's classification and the one proposed here (e.g. Robison included species of "*Onymagnostus*" in *Lejopyge*, whereas these species are assigned to *Ptychagnostus* s.l. herein).

Discussion.—From a cladistic perspective, the arrangement of species produced by our analysis is an improvement on previous classifications. However, extensive homoplasy remains a significant problem. Few characters are unambiguous and, as noted above, even some of those used here to diagnose genera have isolated occurrences in sister groups. Indeed, of the 28 characters in the data matrix, only five (characters 5, 6, 15, 16

and 20 in Figure 7 and the Appendix) have consistency indices of 1.0 and only 11 of the remaining characters have consistency indices above 0.5. We suspect that similar problems will complicate analyses of many other trilobite groups, especially the plesiomorphic libristomates currently assigned to the suborder Ptychopariina. Moreover, low consistency indices in parsimony analysis of the Burgess Shale faunas (Briggs and Fortey, 1989) indicate that homoplasy is a widespread problem in early arthropod systematics and phylogeny (see also Gould, 1991; Hughes, 1994).

SYSTEMATIC PALEONTOLOGY

Illustrated material is housed in the type collections of the Geological Survey of Canada, Ottawa (GSC). Morphological terminology for agnostoid trilobites is from Shergold et al. (1990). Collection localities (Figures 3–5) are indicated by the prefixes: CH, Cow Head; BPS, Broom Point South; WRI, White Rock Islets.

Order AGNOSTIDA Salter, 1864

Superfamily AGNOSTOIDEA M'Coy, 1849

Family AGNOSTIDAE M'Coy, 1849

Genus KORMAGNOSTUS Resser, 1938

Type species.—*Agnostus seclusus* Walcott, 1884 from Cambrian strata of the Eureka District, Nevada (by synonymy with *Kormagnostus simplex* Resser, 1938; see Robison, 1988).

Remarks.—Shergold et al. (1990) followed Opik (1967) in assigning *Kormagnostus* to the Ammagnostinae, which they regarded as a subfamily of Agnostidae that is based primarily upon the presence of a long and, in some cases, expanded posteroaxis. Subsequently, Pratt (1992) argued that the presence of a posteriorly positioned pygidial node in *Kormagnostus* made a relationship with *Ammagnostus*, which is characterized by a more anteriorly positioned node, unlikely. He restricted the Ammagnostinae to the eponymous genus and established a new subfamily, the Kormagnostinae, for *Kormagnostus*. However, the posteriorly positioned pygidial node of *Kormagnostus* is shared with outgroup taxa such as *Agnostus* (Robison, 1988, fig. 7.10; Pratt, 1992, pl. 1, fig. 6) and *Lotagnostus* (Ludvigsen et al., 1989, pl. 1, fig. 11), and is likely to be plesiomorphic. There are no other apomorphic characters in Pratt's (1992, p. 30) diagnosis and we conclude that the Kormagnostinae is an artificial, most likely paraphyletic, taxon. The status of the Ammagnostinae is also uncertain. In establishing this subfamily, Opik (1967, p. 137) emphasized that it was based upon a combination of characters, none of which is unique. As such, it may also prove to be paraphyletic and, until a full phylogenetic analysis of the Agnostidae is made, *Kormagnostus* is best left unassigned at the subfamilial level.

Pratt (1992, pl. 3, figs. 4–13) tentatively assigned species with well-defined anterior glabellar lobes to *Kormagnostus* and his conclusion is followed here.

KORMAGNOSTUS BOLTONI new species

Figure 11.1–11.10

Diagnosis.—A species of *Kormagnostus* with broad, suboval pygidium in which length is about three-quarters of width. Pygidial axial furrows are ill-defined even in small holaspids and are evident only over the anterior half of the pygidium in large individuals.

Holotype.—A pygidium from CH 3 (Figure 11.4).

Etymology.—For Tom Bolton, Geological Survey of Canada.

Material and occurrence.—Ten cephalae and thirteen pygidia from CH 3 and CH 11, Zone 5.

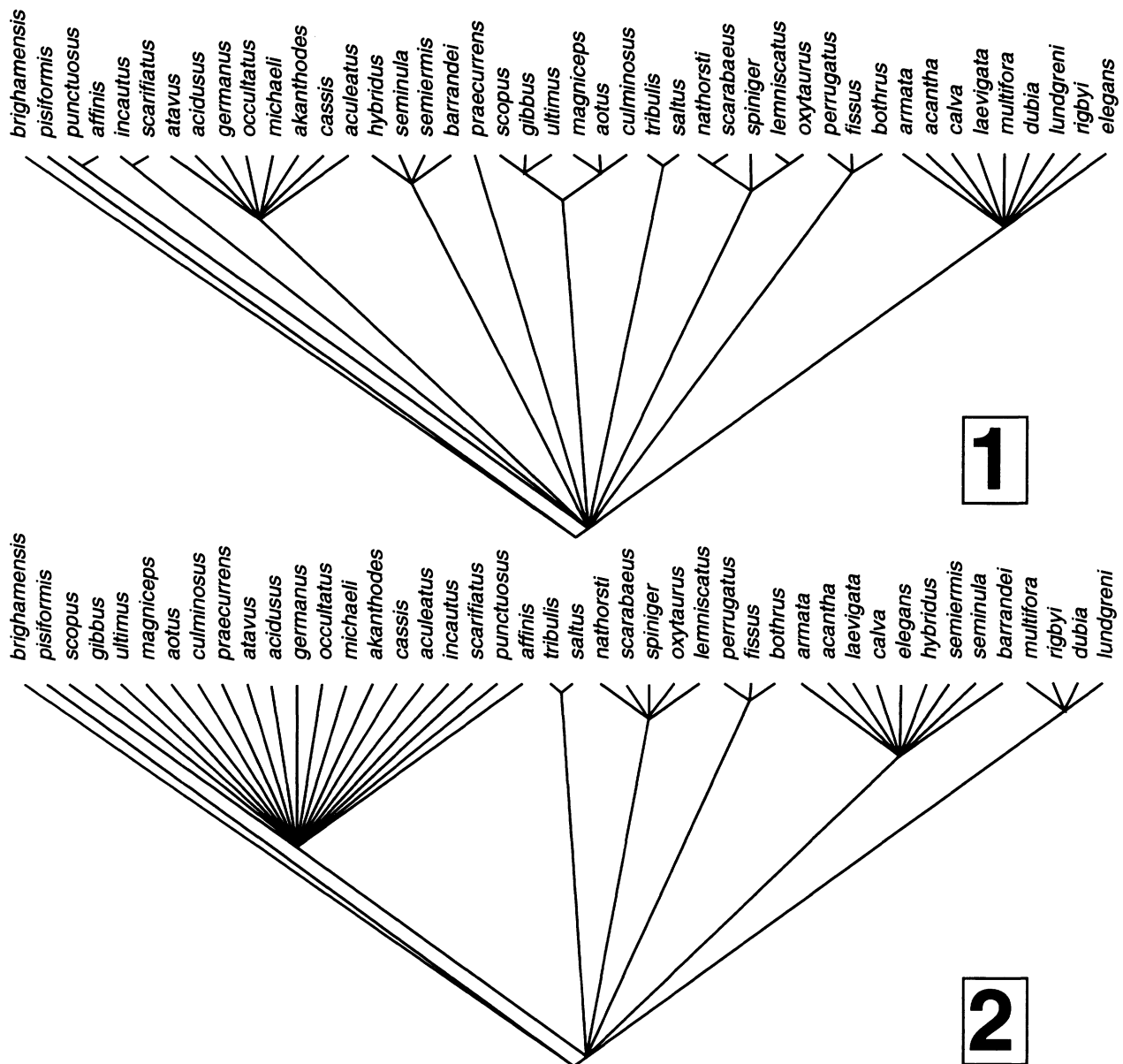


FIGURE 10—Trees used to constrain PAUP analyses in order to facilitate comparisons with classifications proposed by Robison (1984, 1994) and Laurie (1988, 1989). 1, Tree representing Laurie's classification. Under this constraint, the shortest trees found using the heuristic search method had lengths of 182. 2, Tree representing Robison's classification. Under this constraint, the shortest trees found using the heuristic search method had lengths of 191.

Description.—Convex, subelliptical posteroglabella occupies slightly less than half of cephalic length and is outlined by firmly impressed axial furrows; transglabellar furrow is shallow and roughly transverse. Basal lobes are large and triangular in outline. Axial node is located in front of posteroglabellar mid-length. Convex acrollobes are very weakly constricted and slope down to narrow, convex border and weakly deliquiate border furrow. External surface of cephalon is smooth.

Pygidium is broad and suboval in outline, with length about three-quarters of width; short pair of posterolateral spines are present. Pygidial axial furrows are ill-defined even in small holaspids and are evident only over anterior half of pygidium in large individuals. Axis is weakly convex, bulb-shaped in outline (Figure 11.3) and occupies slightly more than four-fifths of pygidial length; firmly impressed articulating furrow separates axis

from lens-shaped articulating half-ring. F1 and F2 furrows are expressed only as very faint, narrow grooves adjacent to axial furrows. Prominent axial node is present on M2 lobe. Unconstricted acrollobes slope steeply down to broad, flat border and wide, shallow border furrow.

Remarks.—*Kormagnostus* pygidia from CH 3 resemble the older type species, *K. seclusus* (Walcott; see Robison, 1988, fig. 11.5–11.15; Rasetti, 1965, pl. 1, fig. 9), in becoming progressively effaced through the holaspis ontogeny. In the largest specimens, axial furrows are well-defined only over the anterior half of the pygidium (Figure 10.3, 10.4, 10.10). The Newfoundland material differ consistently from *K. seclusus* from Greenland, the District of Mackenzie and Alberta in being significantly wider (Figure 12.; length is about 0.75, rather than 0.9, maximum pygidial width) and are thus suboval, rather than subcir-

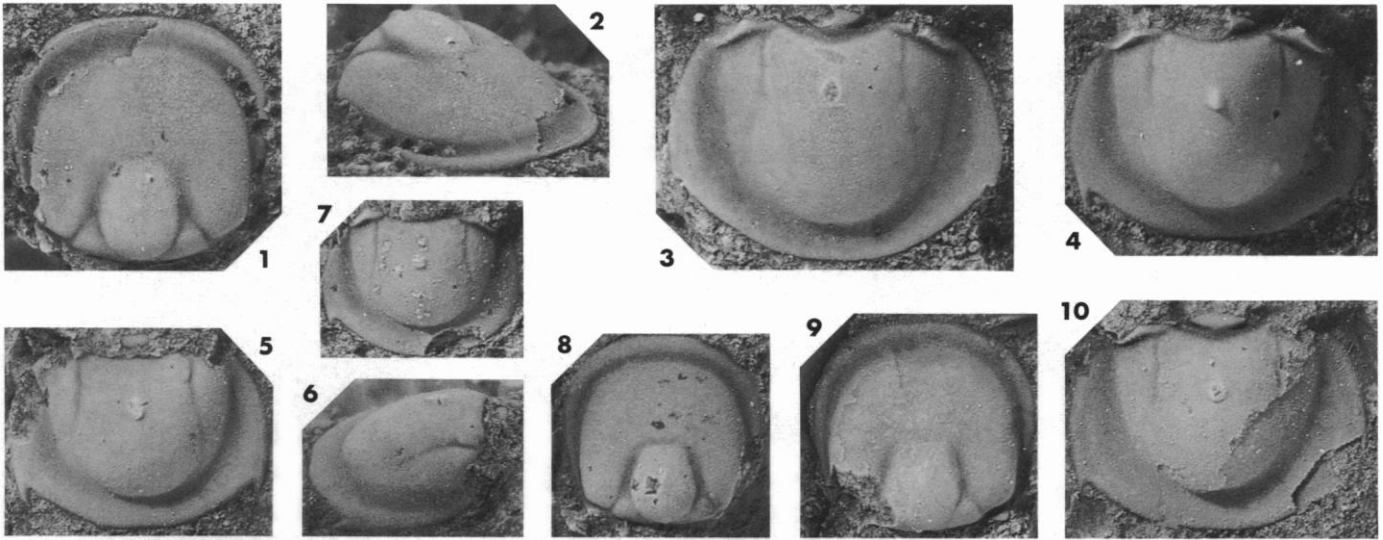


FIGURE 11—*Kormagnostus boltoni* new species, all from CH 3, all $\times 9$. 1–2, cephalon, GSC 113185; 3, pygidium, GSC 113186; 4, pygidium, GSC 113187 (holotype); 5–6, pygidium, GSC 113188; 7, pygidium, GSC 113189; 8, cephalon, GSC 113190; 9, cephalon, GSC 113191; 10, cephalon, GSC 113192.

cular, in outline. In other respects, pygidia are indistinguishable and there are no significant differences between cephalons of these two species.

KORMAGNOSTUS cf. *K. seclusus* (Walcott, 1884)

Figure 13.1–13.5

Agnostus seclusus WALCOTT, 1884, p. 25, pl. 9, fig. 14.

Kormagnostus seclusus (Walcott). ROBISON, 1988, p. 45, fig. 11.5–11.15 (see for complete synonymy); PRATT, 1992, p. 31, pl. 3, figs. 1–3, 14–29, text-figs. 26A, 27A.

Material and occurrence.—Six pygidia from BPS 467 and 468, Zone 4.

Remarks.—*Kormagnostus* pygidia in collections from Broom Point are characterized by firmly impressed axial furrows that define completely a convex axis throughout holaspis ontogeny. By contrast, specimens of *K. seclusus* (Walcott) from Greenland (Robison, 1988, fig. 11.5–11.15), the District of Mackenzie (Pratt, 1992, pl. 3, figs. 1–3, 14–29) and Alberta (Sullivan Formation; Westrop, unpublished data) are all characterized by increasing effacement of the axial furrows during ontogeny. Two distinct types of pygidia are associated with *Kormagnostus* cephalons in the Broom Point collections: the first (Figure 13.1–13.5) is relatively narrow (sag.) and, with a length/width ratio of about 0.9, is comparable in outline to *K. seclusus*. The second (Figure 13.6–13.10) is relatively wider (length/width ratio of about 0.85) with a parallel-sided axis and very long marginal spines; it is assigned to *Kormagnostus* sp. indet. (see below). We are unable to separate associated cephalons (Figure 13.11–13.15) into two groups and are forced to identify them as *Kormagnostus* spp. (a total of 21 cephalons from BPS 460, 467 and 468).

KORMAGNOSTUS species indet.

Figure 13.6–13.10

Material and occurrence.—Sixteen pygidia from BPS 460, 467 and 468, Zone 4.

Remarks.—Pygidia with parallel-sided axes and very long marginal spines occur with *Kormagnostus* cephalons in three collections from Broom Point South. They are similar to pygidia from the Riley Formation of Texas that were assigned to *K. simplex* (= *K. seclusus*; see Robison, 1988) by Palmer (1954,

pl. 76, fig. 12) but, like *K. cf. K. seclusus*, they retain a convex, well-defined axis throughout the holaspis ontogeny. A few pygidia of *Kormagnostus* sp. indet. are present in BPS 468 with pygidia of *K. cf. seclusus*, and rare specimens of the latter occur

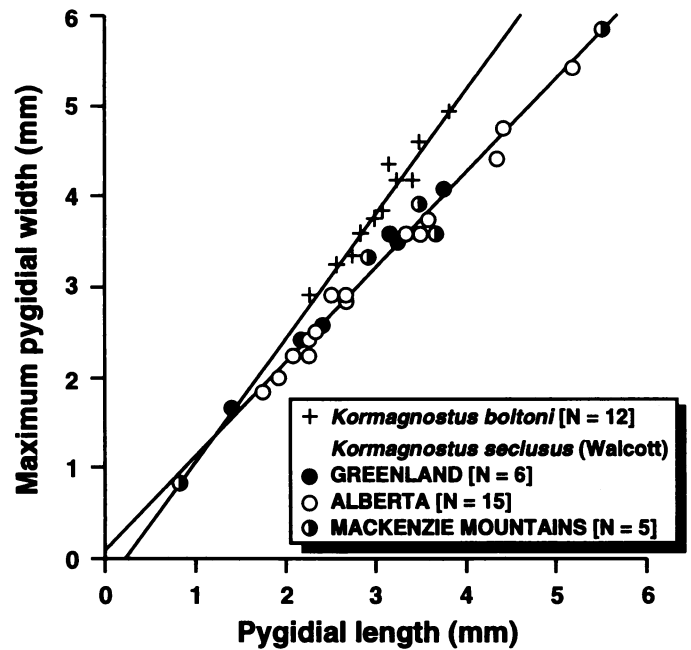


FIGURE 12—Bivariate plot with reduced major axis regressions for maximum pygidial width against pygidial length of *Kormagnostus boltoni* sp. nov. and *Kormagnostus seclusus* (Walcott). Measurements for *K. boltoni* were taken from our collections; measurements for *K. seclusus* were made from specimens from the Sullivan Formation, Alberta (Westrop, unpublished data) and from photographs in Robison (1988; Greenland) and Pratt (1992; Mackenzie Mountains). *Kormagnostus boltoni*: Pygidial width = $1.37 \text{ pygidial length} - 0.30$; $r^2 = 0.94$; standard error of slope = 0.09. *Kormagnostus seclusus*: Pygidial width = $1.05 \text{ pygidial length} + 0.09$; $r^2 = 0.99$; Standard error of slope = 0.02. Slopes of regressions are significantly different using the z-statistic (Jones, 1988) ($z = 3.5$; $p < 0.01$).

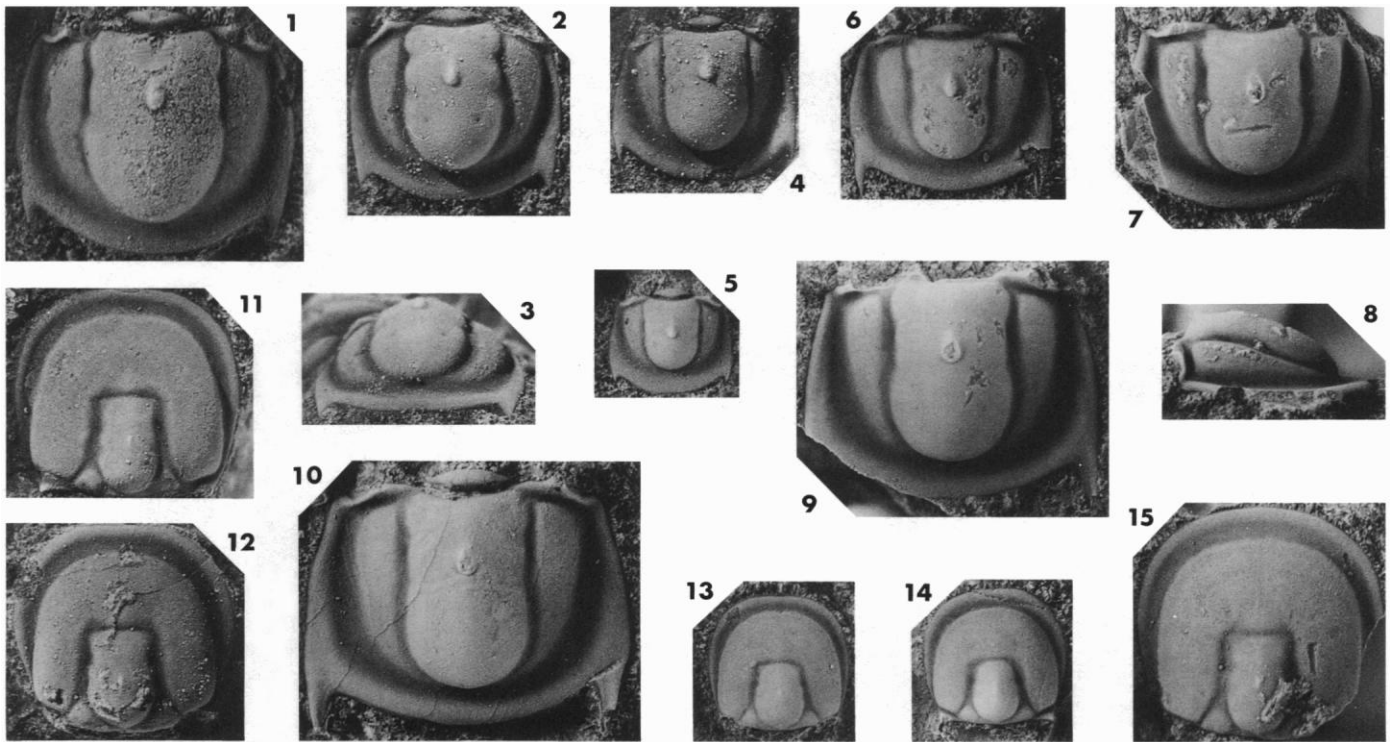


FIGURE 13—1–5, *Kormagnostus* cf. *K. seclusus* (Walcott). All x9 1, pygidium, GSC 113193, BPS 467; 2–3, pygidium, GSC 113194, BPS 468; 4, pygidium, GSC 113195, BPS 468; 5, pygidium, GSC 113196, BPS 468. 6–10, *Kormagnostus* sp. indet., all from BPS 467. 6, pygidium, GSC 113197; 7–8, pygidium, GSC 113198; 9, pygidium, GSC 113199; 10, pygidium, GSC 113200. 11–15, *Kormagnostus* spp. 11, cephalon, GSC 113201, BPS 468; 12, cephalon, GSC 113202, BPS 467; 13, cephalon, GSC 113203, BPS 468; 14, cephalon, GSC 113204, BPS 468; 15, cephalon, GSC 113205, BPS 467.

in BPS 467. Thus, there are several possible interpretations of these associations, including assignment of *K. cf. K. seclusus* and *K. sp. indet.* to a single dimorphic species. However, given the small sample size, it is equally possible that they will prove to be end-members in a continuous range of variation (cf. Bruton and Owen, 1990). The available data do not allow a confident decision to be made, and, accordingly, open nomenclature is used here.

KORMAGNOSTUS? COPELANDI new species

Figure 14.1–14.11

Diagnosis.—A species of *Kormagnostus*? with well-defined anterior glabellar lobe. Pygidium is relatively narrow with length equal to about four-fifths of width. Long, parallel-sided axis occupies about nine-tenths of pygidial length.

Holotype.—A pygidium from the Shallow Bay Formation (Figure 14.3).

Etymology.—For Murray Copeland, Geological Survey of Canada.

Material and occurrence.—Ninety cephalons and 76 pygidia from WRI 601, 603, 606, 607A, 608, 613, 614, 615, 615B, 616, 617, 619, 621, 622, 623, 627, 630, 631 and 633, Zone 3.

Description.—Convex, parallel-sided glabella occupies about seven-tenths of cephalic length and is outlined by firmly impressed axial furrows. Transglabellar furrow is transverse and faint F2 furrows may also be present. Basal lobes are small and triangular in outline. Small axial node is located slightly behind posteroglabellar midlength. Slightly constricted acrollobes slope down to narrow, convex border and deliquiate border furrow. Surfaces of most cephalons are smooth although some are weakly scrobiculate (Figure 14.1).

Pygidia are semielliptical in outline, with length equal to about 85 percent of width. Convex, parallel-sided, posteriorly rounded axis is outlined by well-defined axial furrows and occupies slightly more than four-fifths of pygidial length; very faint F1 and F2 furrows may be evident adjacent to axial furrows. Large axial node is present on M2 lobe. Unconstricted acrollobes are convex and slope down to flat border and non-deliquiate border furrow; long pair of posterolateral spines are present. External surface of pygidium is smooth.

Remarks.—The material from the Shallow Bay Formation is most similar to cephalons and pygidia of *Kormagnostus? beltensis* from the Holm Dal Formation of central North Greenland (Robison, 1988, fig. 10.1–10.5). Pygidia from Greenland are relatively narrower, with an axis that is constricted opposite the axial node, and have smaller marginal spines; there are no significant differences between the cephalons of these two species. *Kormagnostus? beltensis* is also present in the Rabbitkettle Formation of the Mackenzie Mountains, where it displays considerable intraspecific variability in pygidial morphology (Pratt, 1992, pl. 3, figs. 7–13). The Rabbitkettle collections include pygidia (Pratt, 1992, pl. 3, figs. 11–12) that differ from those illustrated here by possession of a much longer, flat border.

Genus CONNAGNOSTUS Öpik, 1967

Type species.—*Connagnostus venerabilis* Öpik, 1967 from the Georgina Limestone, Queensland (by original designation).

CONNAGNOSTUS cf. C. FRITZI Pratt, 1992

Figure 15.6

Connagnostus fritzi PRATT, 1992, p. 29, pl. 2, figs. 10–14.

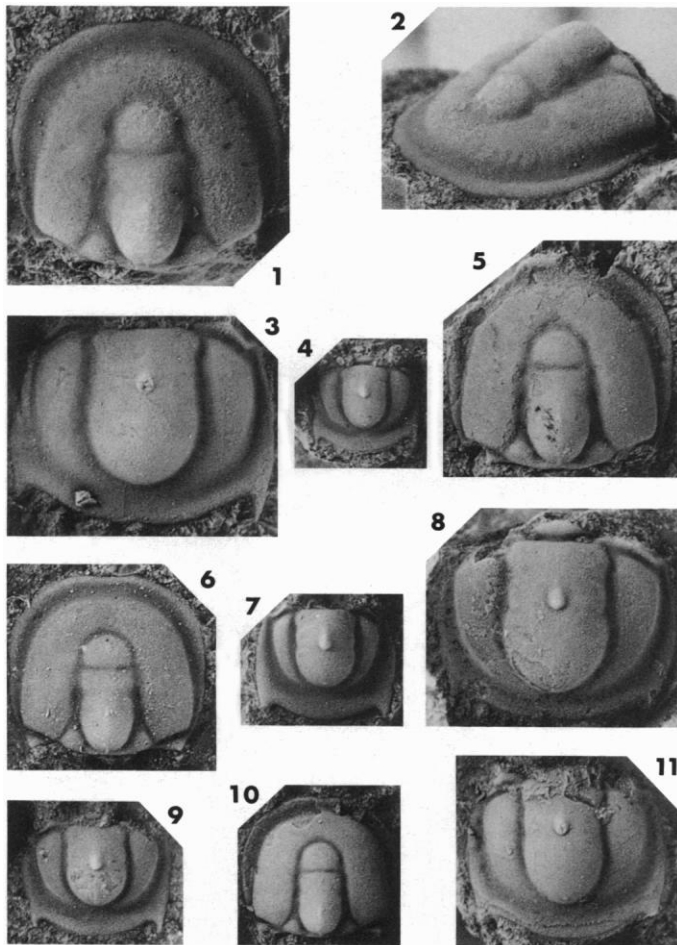


FIGURE 14—*Kormagnostus? copelandi* new species. All $\times 9$. 1–2, cephalon, GSC 113206, WRI 631; 3, pygidium, GSC 113207 (holotype), WRI 613; 4, pygidium, GSC 113208, WRI 631; 5, cephalon, GSC 113209, WRI 613; 6, cephalon, GSC 113210, WRI 630; 7, pygidium, GSC 113211, WRI 631; 8, pygidium, GSC 113212, WRI 630; 9, pygidium, GSC 113213, WRI 631; 10, cephalon, GSC 113214, WRI 615B; 11, pygidium, GSC 113215, WRI 630.

Material and occurrence.—Two cephalons from CH 34, Zone 5.

Remarks.—Two cephalons from the Shallow Bay Formation differ from cephalons of *Connagnostus fritzi* from the Mackenzie Mountains (Pratt, 1992, pl. 2, figs. 10–11) and Nevada (Palmer, 1962, pl. 1, fig. 31) only in having relatively wider borders. More material is needed for a confident identification.

Family PTYCHAGNOSTIDAE Kobayashi, 1939

Remarks.—We provisionally accept Robison's (1984) concept of the Ptychagnostidae, although a final decision on the scope and content of this family must await a broader, cladistic analysis of the ingroup relationships of the Agnostoidea.

Genus PTYCHAGNOSTUS Jaekel, 1909

Type species.—*Agnostus punctuosus* Angelin, 1851 from Cambrian strata of Sweden (by original designation).

Diagnosis.—A genus of Ptychagnostidae with pygidial F2 furrow that is strongly deflected medially by a large node or spine (weakly deflected in some plesiomorphic species). Basal lobes of glabella are strongly elongated (simple or weakly elongated in some plesiomorphic species).

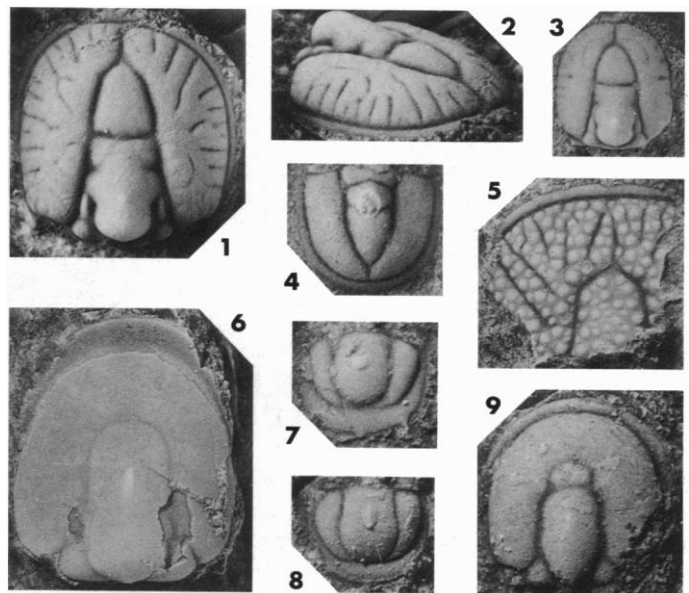


FIGURE 15—1–4, *Ptychagnostus* (s.l.) *atavus* (Tullberg). All $\times 9$. 1–2, cephalon, GSC 113216, WRI 640; 3, cephalon, GSC 113217; 4, pygidium, GSC 113218. 5, *Ptychagnostus* (s.l.) *aculeatus* (Angelin), incomplete cephalon, GSC 113219, BPS 458, $\times 9$. 6, *Connagnostus* cf. *C. fritzi* Pratt, cephalon, GSC 113220, CH 34, $\times 7.75$. 7–9, *Utagnostus trispinulus* Robison, all from BPS 451. All $\times 12$. 7, pygidium, GSC 113221; 8, pygidium, GSC 113222; 9, cephalon, GSC 113223.

Remarks.—PAUP (Swofford, 1993) parsimony analysis (Figures 8–9) suggests synonymy of *Ptychagnostus*, *Onymagnostus*, *Acidusus*, *Triplagnostus*, *Aotagnostus*, *Myrmecomimus*, *Goniagnostus* and *Tomagnostus*. *Ptychagnostus* (*Ptychagnostus*) (= *Tomagnostus*), *P.* (*Aotagnostus*) (= *Myrmecomimus*) and *P.* (*Goniagnostus*) are retained as non-obligate subgenera and the remaining species are assigned to *Ptychagnostus* (s.l.).

PTYCHAGNOSTUS (s.l.) ACULEATUS (Angelin, 1851) Figure 15.5

Agnostus aculeatus ANGELIN, 1851, p. 8, pl. 6, fig. 12.

Ptychagnostus aculeatus (Angelin). ROBISON, 1984, p. 14, fig. 8.1–8.7 (see for synonymy); LU AND LIN, 1989, p. 95, pl. 8, figs. 1–3; XIANG AND ZHANG, in WANG ET AL., 1985, p. 73, pl. 21, fig. 1.

Material and occurrence.—Two incomplete cephalons from BPS 458, Zone 4.

Remarks.—As recognized earlier by Kindle (1982), rare, incomplete cephalons from a single boulder carry the distinctive granular prosopon of *Ptychagnostus aculeatus*.

PTYCHAGNOSTUS (s.l.) ATAVUS (Tullberg, 1880) Figure 15.1–15.4

Agnostus atavus TULLBERG, 1880, p. 14, pl. 1, fig. 1a–d

Ptychagnostus atavus (Tullberg). ROBISON, 1982, p. 136, pl. 1, figs. 1–9 (see for synonymy); ROBISON, 1984, p. 18, fig. 11 (see for additional synonymy); ROBISON 1994, p. 55, figs. 10.5, 27.1, 27.2.

Acidusus atavus (Tullberg); LAURIE, 1988, p. 180, fig. 5A–F

Material and occurrence.—Five cephalons and 4 pygidia from BPS 452; WRI 619, 640 and 641 (specimens cited by Robison [1984, p. 21] from BPS 448 could not be located in the Kindle collections), Zone 3.

Remarks.—Following Robison (1982, 1984), *Ptychagnostus atavus* is regarded as a broadly defined species that displays considerable variation in cephalic scrobiculation, the position of the median glabellar node and the expression of the pygidial

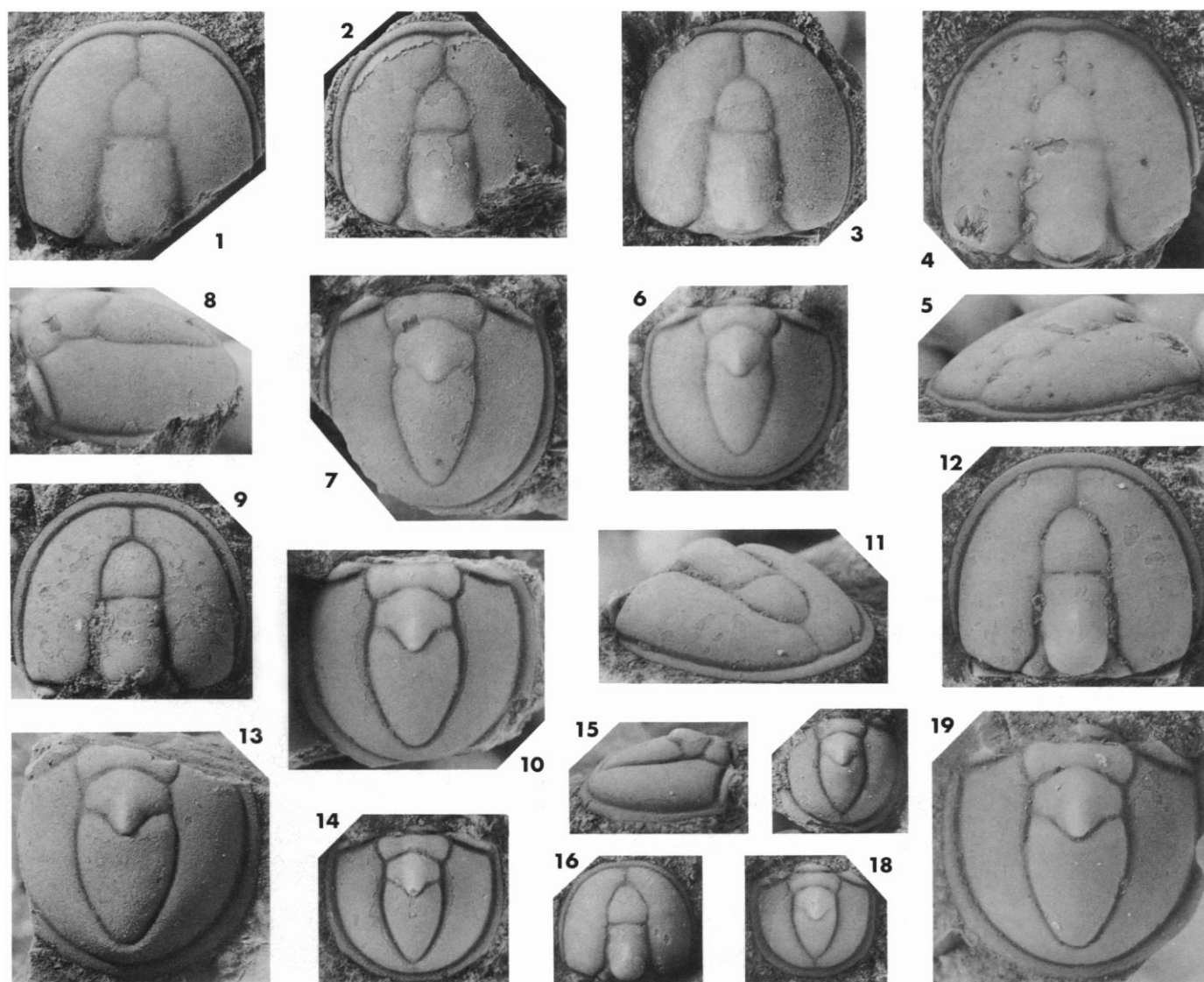


FIGURE 16—1–8, *Ptychagnostus hybridus* (Brøgger), all from WRI 602. All $\times 9$. 1, cephalon, GSC 113224; 2, cephalon, GSC 113225; 3, cephalon, GSC 113226; 4–5, cephalon, GSC 113227; 6, pygidium, GSC 113228; 7–8, pygidium, GSC 113229. 9–19, *Ptychagnostus seminula* (Whitehouse). All from BPS 409. All $\times 9$. 9, cephalon, GSC 113230; 10, pygidium, GSC 113231; 11–12, cephalon, GSC 113232; 13, pygidium, GSC 113233; 14–15, pygidium, GSC 113234; 16, cephalon, GSC 113235; 17, pygidium, GSC 113236; 18, pygidium, GSC 113237; 19, pygidium, GSC 113238.

postaxial furrow. Like the type material from Sweden (Wester-gård, 1946, pl. 11, figs. 8, 11), cephalons (Figure 15.1–15.3) from the Shallow Bay Formation have well-developed scrobiculae; pygidia (Figure 15.4) have firmly impressed postaxial furrows.

PTYCHAGNOSTUS (s.l.) HYBRIDUS (Brøgger, 1878)

Figure 16.1–16.8

Agnostus gibbus var. *hybrida* BRØGGER, 1878, p. 62, pl. 5, fig. 4a-b.
Ptychagnostus hybridus (Brøgger). ROBISON, 1964, p. 523, pl. 79, figs. 10, 13–14 [only; see Laurie, 1988, p. 188–189].
Onymagnostus hybridus (Brøgger). ROBISON, 1984, p. 51, figs. 30, 31 (see for synonymy); LAURIE, 1988, p. 187, fig. 12A–F.
Lejopyge hybridus (Brøgger). ROBISON, 1994, p. 53, fig. 25.1, 25.2, 25.3?, 25.4?
 ?*Lejopyge* cf. *seminula* (Whitehouse). ROBISON, 1994, p. 54, fig. 26.

Diagnosis.—A non-scrobiculate, strongly convex species of *Ptychagnostus* with short basal lobes. Axis occupies about four-

fifths of pygidial length in large holaspids. Many cephalons display small pit or opening at posterior end of posteroglabella.

Material and occurrence.—Six cephalons and 7 pygidia from WRI 602 and 624, Zone 3.

Remarks.—As discussed by Robison (1984, p. 53), *Ptychagnostus hybridus* is very similar to *P. seminula* (Whitehouse; see Robison, 1984, fig. 32; Young and Ludvigsen, 1989, pl. 2, figs. 3–10) and discrimination of these two, stratigraphically separate species has relied on slight differences in the length of the basal glabellar lobes (Robison, 1984; Laurie, 1988; Young and Ludvigsen, 1989), length of the glabella and pygidial axis (Robison, 1984; Young and Ludvigsen, 1989) and in the shape of the posteroglabella (Laurie, 1988). However, measurements of specimens from the Cow Head Group and of published photographs of *P. hybridus* and *P. seminula* (Figure 17) indicate that some of the pygidial dimensions, including axis width (Figure 17.3) and pygidial width, are not diagnostic. Only the regression of axis length against pygidial length (Figure 17.1) produces a sig-

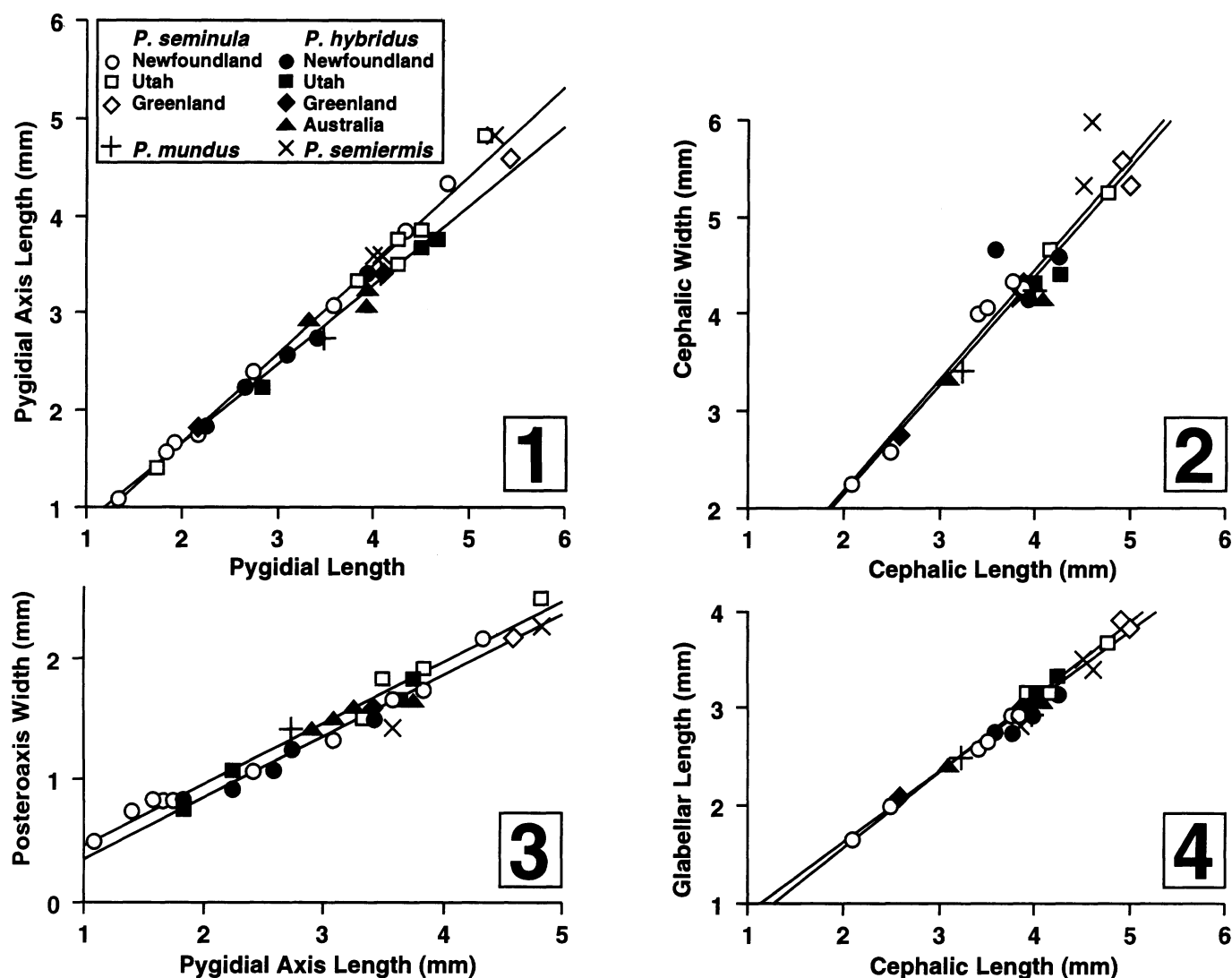


FIGURE 17—Bivariate plots with reduced major axis regressions for pygidial and cephalic dimensions of *Ptychagnostus hybridus* (Brøgger) and *P. seminula* (Whitehouse). Measurements for specimens from Newfoundland were made from our collections but measurements for specimens from other regions were made from photographs in Robison (1982, 1984) and Laurie (1988). Regressions were calculated for material from all regions. 1, Plot of pygidial axis length against pygidial length. *P. seminula*: Pygidial axis length = $0.91 \text{ Pygidial length} - 0.15$; $N = 17$, $r^2 = 0.98$; standard error of slope = 0.02. *P. hybridus*: Pygidial axis length = $0.81 \text{ pygidial length} + 0.05$; $N = 14$, $r^2 = 0.98$; standard error of slope = 0.03. Slopes are significantly different using the z statistic (Jones, 1988) ($z = 2.77$, $p < 0.01$). 2, Plot of cephalic width against cephalic length. *P. seminula*: Cephalic width = $1.13 \text{ cephalic length} - 0.09$; $N = 11$, $r^2 = 0.98$; standard error of slope = 0.05; *P. hybridus*: Cephalic width = $1.12 \text{ cephalic length} - 0.06$; $N = 10$, $r^2 = 0.77$; standard error of slope = 0.20. Slopes are not significantly different ($z = 0.05$, $p > 0.05$). 3, Plot of posteroaxis width against pygidial axis length. *P. seminula*: Posteroaxis width = $0.50 \text{ pygidial axis length} - 0.04$; $N = 17$, $r^2 = 0.98$; standard error of slope = 0.02. *P. hybridus*: Posteroaxis width = $0.51 \text{ pygidial axis length} - 0.15$; $N = 14$, $r^2 = 0.98$; standard error of slope = 0.03. Slopes are not significantly different ($z = 0.28$, $p > 0.05$). 4, Plot of glabellar length against cephalic length. *P. seminula*: Glabellar length = $0.77 \text{ cephalic length} + 0.19$; $N = 11$, $r^2 = 0.99$; standard error of slope = 0.03. *P. hybridus*: Glabellar length = $0.72 \text{ cephalic length} + 0.03$; $N = 10$, $r^2 = 0.96$; standard error of slope = 0.05. Slopes are not significantly different ($z = 0.86$, $p > 0.05$).

nificant difference between these two species: *P. hybridus* has a relatively shorter axis (see Robison, 1984; Young and Ludvigsen, 1989). However, this is expressed clearly only in larger holaspids (more than 4 mm in length), and small individuals of *P. hybridus* and *P. seminula* may be indistinguishable on the basis of axis length. Robison (1984, p. 53) noted that large holaspids of *P. seminula* often developed posterolateral swellings on the pygidial border but, according to Laurie (1988, p. 188), similar swellings may also be developed in *P. hybridus*. Laurie (1988, p. 188) diagnosed *P. hybridus* as possessing a long pygidial axis which did not extend onto the steep posterior portion of the acrolobe (e.g., Robison 1984, fig. 30.9c); by con-

trast, many specimens assigned to *P. seminula* display an axis whose posterior tip is flexed down the acrolobe (e.g., Robison, 1984, fig. 32.2c, 4c; Young and Ludvigsen, 1989, pl. 2, fig. 5). Unfortunately, there appears to be significant variation in this trait and some specimens of *P. hybridus* (e.g., Robison, 1984, fig. 30.11c) are comparable to *P. seminula*.

Many of the cephalic characters discussed by Robison, Laurie and others offer little basis for the separation of *P. hybridus* and *P. seminula*. For example, both Robison (1984) and Young and Ludvigsen (1989) suggested that these species differed in glabellar length, but plots of this dimension against cephalic length produces regression lines that are not significantly different (Fig-

ure 17.4), as does a plot of cephalic length against width (Figure 17.2). Laurie (1988, p. 187) claimed that many specimens of *P. hybridus* (e.g. Robison, 1984, fig. 30.5a, 8a, 10a) have an expanded posteroglabella but, while many specimens attributed to *P. seminula* are characterized by parallel-sided posteroglabella (e.g. Young and Ludvigsen, 1989, pl. 2, fig. 3), others are expanded (e.g. compare the cephalon assigned to *P. seminula* by Robison, 1984, fig. 30.3a, with those attributed to *P. hybridus* by Laurie, 1988, fig. 12A and Robison, 1984, pl. 79, fig. 10). The anterior glabella lobe of both species may vary from rounded to obtusely pointed (Robison, 1984).

All recent studies have agreed that *P. hybridus* typically has short, simple basal lobes (e.g. Robison, 1984, fig. 30.5a, 8a, 10a), whereas *P. seminula* has "slightly elongated" basal lobes (e.g. Robison, 1984, fig. 32.1a; Young and Ludvigsen, 1989, pl. 2, fig. 7). However, even here there is considerable variation and the two species appear to overlap in morphology (e.g. compare Laurie, 1988, fig. 12A [holotype of *Onymagnostus angulatus* Öpik, which was regarded as a junior synonym of *P. hybridus* by both Robison, 1984 and Laurie, 1988] and Robison, 1984, fig. 32.3a). Robison (1994, fig. 26) has recently illustrated cephalia with slightly elongated basal lobes that are associated with *hybridus*-type pygidia in the Henson Gletcher Formation, North Greenland.

Robison (1984, p. 52, fig. 30.5, 30.8, 30.10, fig. 31) drew attention to the presence of a small pit or opening at the posterior end of the posteroglabella in many specimens of *P. hybridus*; similar pits are evident on cephalia from WRI 602 (Figure 15.1–15.3). However, the pits are not uniformly developed in specimens of *P. hybridus* and do not offer a consistent basis for species identification.

In summary, available data indicate that it is possible to separate *P. hybridus* and *P. seminula* on length of pygidial axis length and length basal lobes, although differences in these features may not be clearly expressed in all specimens; confident identification of small pygidia may be difficult. When more information on the variability of these species is available, it may be preferable to treat them as synonyms. In particular, data are needed for large (> 5 mm) pygidia of *P. hybridus*, which were not represented in the sample analyzed here.

Collection WRI 602 includes relatively effaced cephalia (e.g., Figure 16.4–16.5) that resemble *Ptychagnostus mundus* (Öpik; Laurie, 1988, fig. 13A–B, E–G), supporting Robison's (1984, p. 52) synonymy of this species with *P. hybridus*. We are uncertain about the status of *Ptychagnostus semiermis* (Öpik), which was based on only a few specimens. Laurie (1988, p. 189–190) diagnosed this species as having a wide cephalon with deep F2 glabellar furrows. The two largest cephalia illustrated by Laurie (1988, fig. 14A, C) are distinct outliers on a plot of cephalic width against cephalic length (Figure 17.2) but both specimens show cracks suggestive of compaction; more material will be required for a confident evaluation, although Robison (1994) suggested synonymy with *P. seminula*.

PTYCHAGNOSTUS (s.l.) SEMINULA (Whitehouse, 1939)
Figure 16.9–16.19

Agnostus seminula WHITEHOUSE, 1939, p. 254, pl. 25, fig. 24.

Onymagnostus seminula (Whitehouse). ROBISON, 1984, p. 54, fig. 32 (see for synonymy); YOUNG AND LUDVIGSEN, 1989, p. 12, pl. 2, figs. 3–10.

Diagnosis.—A non-scribbulate, strongly convex species of *Ptychagnostus* with slightly elongate basal lobes. Axis occupies a little less than nine-tenths of pygidial length in large holaspids.

Material and occurrence.—Eighteen cephalia and 26 pygidia from BPS 409, 410, 420 and 421, Zone 2 (see Young and Ludvigsen, 1989 for additional occurrences in Zone 1).

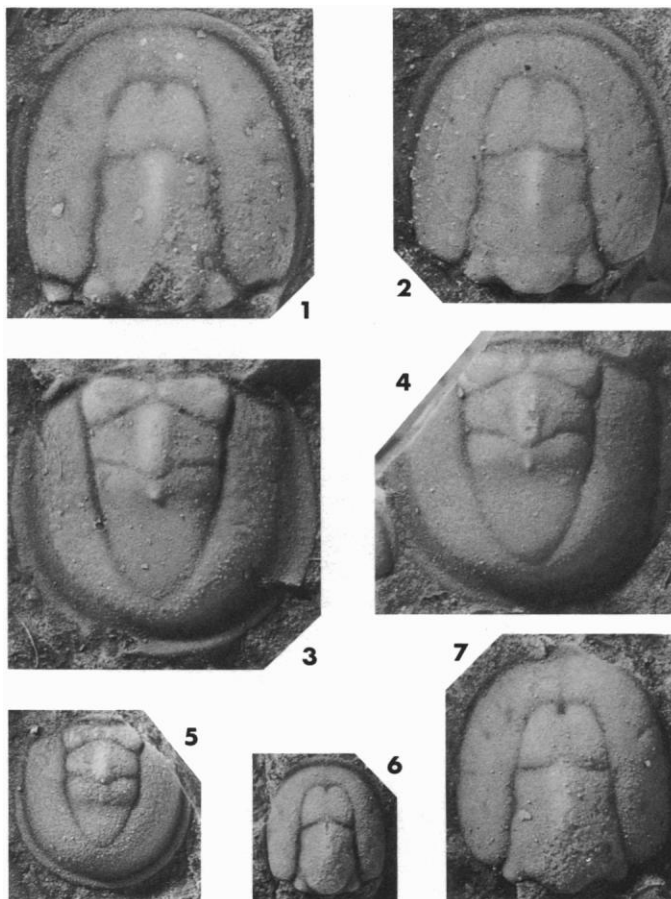


FIGURE 18—*Ptychagnostus (Ptychagnostus) fissus* (Lundgren). 1, cephalon, GSC 113239, BPS 448, $\times 7.75$; 2, cephalon, GSC 113240, BPS 448, $\times 7.75$; 3, pygidium, GSC 113241, BPS 448, $\times 7.75$; 4, pygidium, GSC 113242, BPS 448, $\times 7.75$; 5, pygidium, GSC 113243, BPS 409, $\times 9$; 6, cephalon, GSC 113244, BPS 452, $\times 9$; 7, cephalon, GSC 113245, BPS 448, $\times 7.75$.

Remarks.—Like those described by Robison (1984, fig. 32.8), small pygidia from Newfoundland (Figure 16.17, 16.18) have weak postaxial furrows which are lost in larger individuals (Figure 16.10, 16.13 16.19).

Subgenus PTYCHAGNOSTUS Jaekel, 1909

Diagnosis.—A nonspinosous subgenus of *Ptychagnostus* with weakly to strongly defined depression at or in front of mid-length of posteroaxis. Weakly to strongly developed frontal sulcus on glabella. Pygidial F2 furrow is weakly deflected medially.

PTYCHAGNOSTUS (PTYCHAGNOSTUS) FISSUS
(Lundgren, in Linnarsson, 1879)
Figure 18.1–18.7

Agnostus fissus LUNDGREN, in Linnarsson, 1879, p. 23, pl. 2, fig. 34.

Tomagnostus fissus (Lundgren). ROBISON, 1994, p. 59, fig. 30 (see for synonymy).

Diagnosis.—A species of *Ptychagnostus* with long cephalic axial node that runs along entire length of L2. Node on pygidial posteroaxis is located immediately behind F2 furrow.

Material and occurrence.—Seventy cephalia and 75 pygidia from BPS 409, 431, 448, 450 and 452; WRI 632, zones 2 and 3.

Remarks.—Pygidia from the Shallow Bay Formation vary somewhat in the length of the axis, which tends to increase in

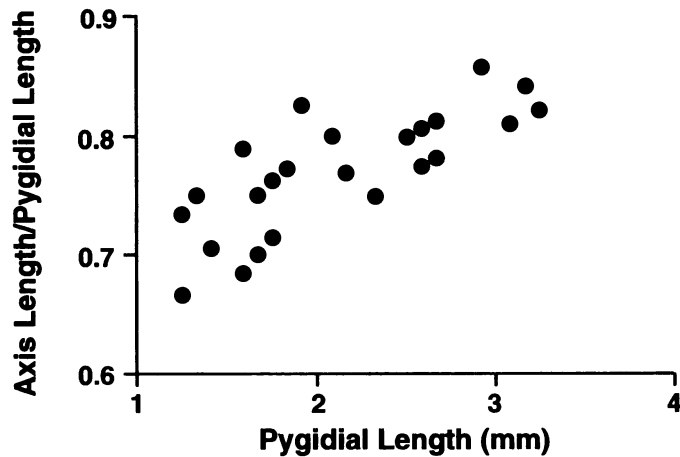


FIGURE 19—Plot of axis length/pygidial length against pygidial length for *Ptychagnostus fissus* (Lundgren) from the Shallow Bay Formation.

relative length during the holaspide ontogeny (Figure 18.3–18.5, Figure 19). *Ptychagnostus* (*Ptychagnostus*) *fissus* appears to possess two derived characters which separate it from other members of the genus: a very long, carinate cephalic axial node and a pygidial node that is located immediately behind F2 furrow. In other respects (e.g. wide glabella with frontal sulcus; weakly deflected pygidial F2 furrow), *P. (P.) fissus* resembles *P. (P.) punctuosus* (Angelin; Laurie, 1988, fig. 1) but has weakly, rather than strongly elongate, basal lobes and lacks the pustulose propodeum.

Family PSEUDAGNOSTIDAE Whitehouse, 1936

Genus PSEUDAGNOSTINA Palmer, 1962

Type species.—*Agnostus douvillei* Bergeron, 1899 from the Kushan Formation of China (by synonymy with *Pseudagnostina contracta* Palmer, 1962; see Pratt, 1992).

PSEUDAGNOSTINA DOUVILLEI (Bergeron, 1899)

Figure 20.1–20.5

Pseudagnostina douvillei (Bergeron). PRATT, 1992, p. 37, pl. 7, figs. 1–15 (see for synonymy).

Material and occurrence.—Fifteen cephalons and nine pygidia from CH 3, 11, 12 and 34, Zone 5.

Remarks.—Pratt's (1992) revision of *Pseudagnostina*, which reduced the genus to a single species, is followed here.

Genus ACMARHACIS Resser, 1938

Type species.—*Acmarhacis typicalis* Resser, 1938 from the Conasauga Formation of Alabama (by original designation).

ACMARHACIS cf. A. TYPICALIS Resser, 1938

Figure 20.6–20.10

Acmarhacis typicalis RESSER, 1938, p. 47, pl. 10, figs. 4–5; PRATT, 1992, p. 38, pl. 4, figs. 1–3 (see for synonymy).

Material and occurrence.—Nine cephalons and 1 pygidium from CH 3, Zone 5.

Remarks.—*Acmarhacis typicalis* differs from *A. acutus* Kobayashi in having two anterior axial segments of the pygidium outlined by firmly impressed transverse furrows; those of *A. acutus* are faint. Also, *A. acutus* typically possesses a pygidial axis which is well-rounded posteriorly (e.g. Palmer, 1962, pl. 2, fig. 15), whereas that of *A. typicalis* is pointed posteriorly (but see Palmer, 1968, p. 7, fig. 6 for a specimen of *A. acutus* which resembles *A. typicalis* more closely in this respect). The only pygidium recovered (Figure 20–10) is incomplete, but appears to possess well-defined, transverse furrows; more material will be needed to confirm the identification.

Cephalons from CH 3 (Figure 20.6–20.9) differ in the degree of scrobiculation and in the convexity of the glabella.

Genus NAHANNAGNOSTUS Pratt, 1992

Type species.—*Pseudagnostus nganasanicus* Rozova, 1964 from Nganasanian strata of the Siberian Platform (by original designation).

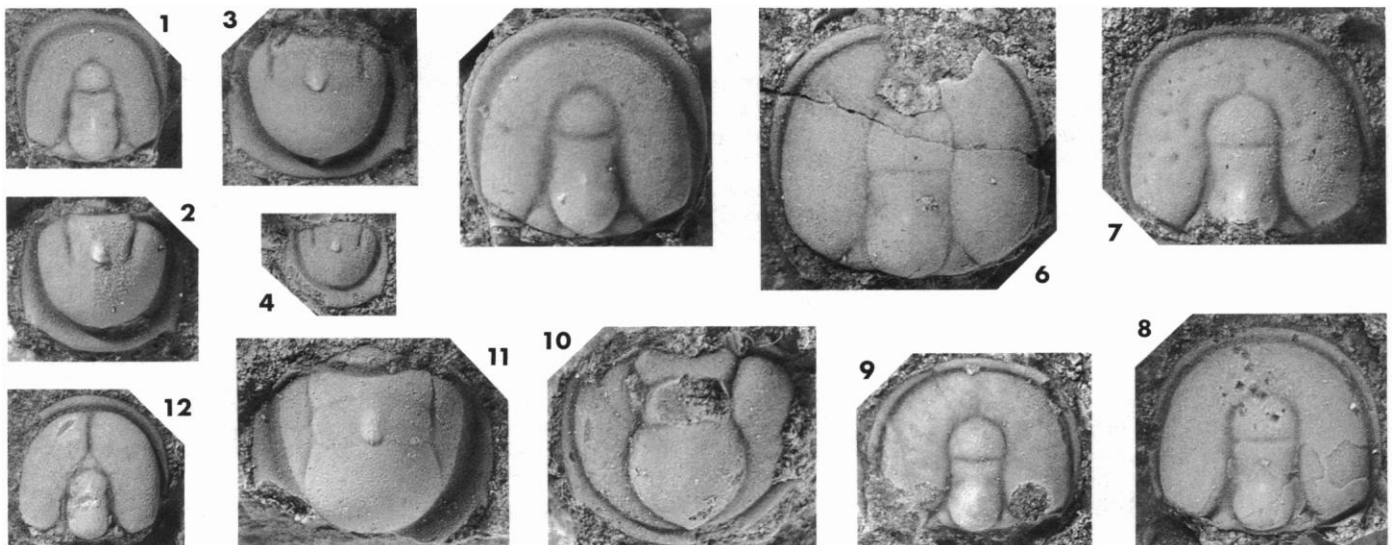


FIGURE 20—1–5, *Pseudagnostina douvillei* (Bergeron). All $\times 9$. 1, cephalon, GSC 113246, CH 34; 2, pygidium, GSC 113247, CH 3; 3, pygidium, GSC 113248, CH 3; 4, pygidium, GSC 113249, CH 34; 5, cephalon, GSC 113250, CH 3. 6–10, *Acmarhacis* cf. *A. typicalis* Resser, all from CH 3. All $\times 9$. 6, cephalon, GSC 113251; 7, cephalon, GSC 113252; 8, cephalon, GSC 113253; 9, cephalon, GSC 113254; 10, pygidium, GSC 113255. 11–12, *Nahannagnostus logani* Pratt. All $\times 9$. 11, pygidium, GSC 113256, CH 35; 12, cephalon, GSC 113257, CH 11.

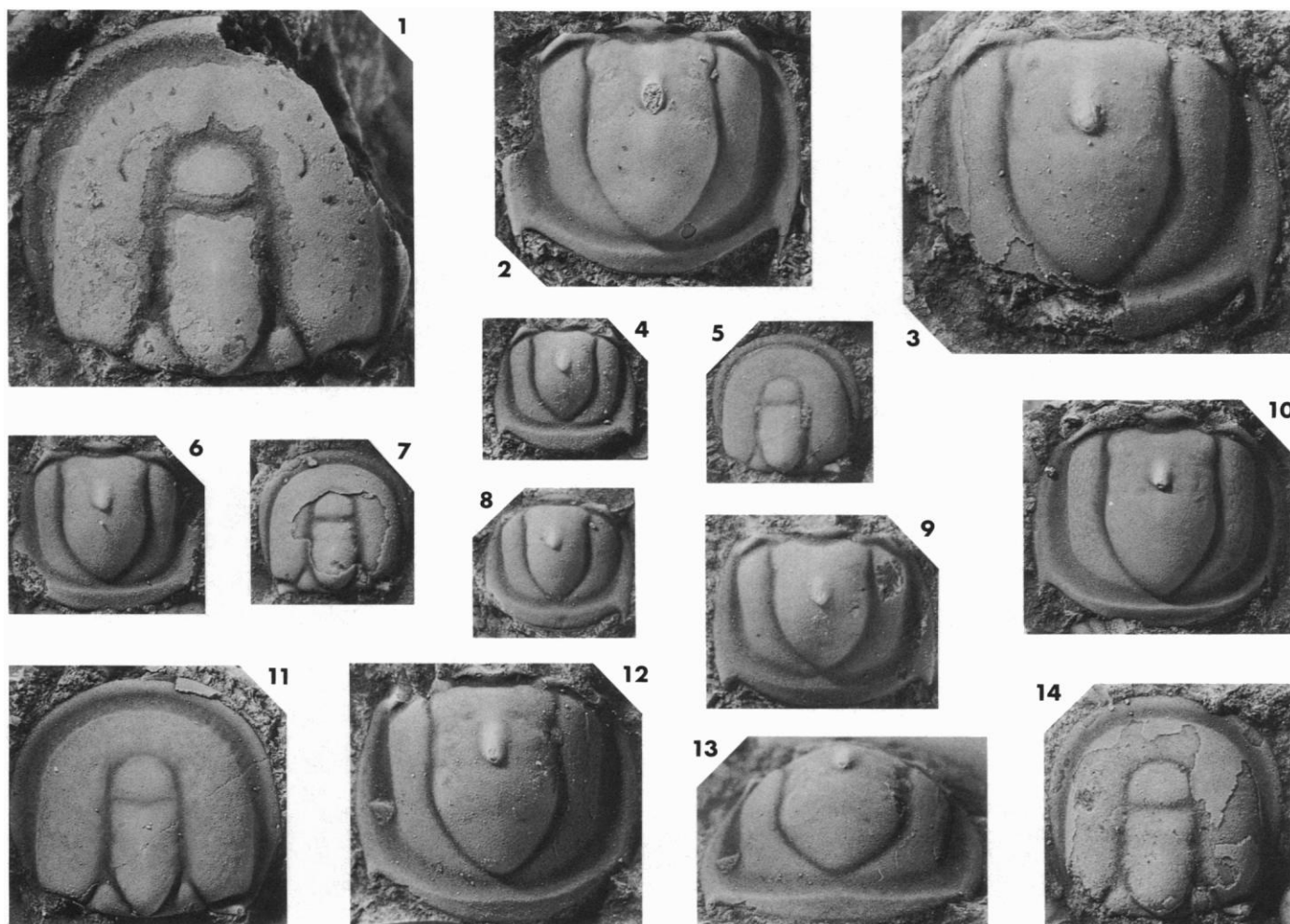


FIGURE 21—*Baltagnostus robustus* Öpik. 1, cephalon, GSC 113258, BPS 410, $\times 6$; 2, pygidium, GSC 113259, BPS 413, $\times 6$; 3, pygidium, GSC 113260, BPS 410, $\times 6$; 4, pygidium, GSC 113261, BPS 414, $\times 9$; 5, cephalon, GSC 113262, BPS 402, $\times 9$; 6, pygidium, GSC 113263, BPS 414, $\times 9$; 7, cephalon, GSC 113264, BPS 414, $\times 9$; 8, pygidium, GSC 113265, BPS 402, $\times 9$; 9, pygidium, GSC 113266, BPS 434, $\times 9$; 10, pygidium, GSC 113267, BPS 413, $\times 6$; 11, cephalon, GSC 113268, BPS 413, $\times 6$; 12–13, pygidium, GSC 113269, BPS 421, $\times 6$; 14, cephalon, GSC 113270, BPS 414, $\times 9$.

NAHANNAGNOSTUS LOGANI Pratt, 1992

Figure 20.11–20.12

Nahannagnostus logani PRATT, 1992, p. 36, pl. 6, figs. 19–23, text-fig. 28A (see for synonymy).

Material and occurrence.—One cephalon and 1 pygidium from CH 11 and 35, Zone 5.

Remarks.—The very short anterior glabellar lobe and deeply incised preglabellar median furrow of a single cephalon from CH 11 (Figure 20.12) are shared with *Nahannagnostus logani* Pratt (1992 pl. 6, figs. 19, 23). A pygidium from CH 35 (Figure 20.11) is also assigned to this species and differs from the type material only in having somewhat more firmly impressed F1 and F2 furrows and slightly larger marginal spines.

Family DIPLAGNOSTIDAE Whitehouse, 1936

Genus *BALTAGNOSTUS* Lochman,
in Lochman and Duncan, 1944

Type species.—*Proagnostus? centrensensis* Resser, 1938, from the Conasauga Group of Alabama (by original designation).

BALTAGNOSTUS ROBUSTUS Öpik, 1979

Figure 21.1–21.14

Baltagnostus robustus ÖPIK, 1979, p. 48, pl. 12, figs. 4–5, text-fig. 8.

Material and occurrence.—Sixty-seven cephalons and 85 pygidia from BPS 402, 409, 410, 413, 414, 421 and 434, Zone 2.

Description.—Cephalon is semielliptical with length about 95 percent of width. Convex, parallel-sided glabella includes large, triangular basal lobes and occupies about two-thirds of cephalic length. Axial furrows are well-defined; transglabellar furrow is firmly impressed and subtransverse. Axial node located at, or slightly in front of, posteroglabellar mid-length. Weakly constricted to unconstricted acrolabes slope down to broad border furrow and narrower, convex border. External surfaces vary from smooth to weakly scrobiculate (Figure 21.1).

Subelliptical pygidium has length equal to nearly 90 percent of width and carries pair of long, slender posterolateral spines. Prominent, lanceolate axis occupies about four-fifths of pygidial length and is outlined by firmly impressed axial furrows; F1 and F2 furrows are barely perceptible on some larger individuals

(Figure 21.2, 21.3, 21.12). Deep articulating furrow separates short, convex articulating half-ring from remainder of axis. Large axial tubercle is present on M2 lobe. Acrollobes are convex and very weakly constricted; border furrow broad and deliquate. Border is weakly zonate with collar in form of low ridge. External surface of pygidium is smooth.

Remarks.—The posteriorly pointed axis with node in front of axial midlength of the Newfoundland pygidia is matched in the two illustrated specimens of *Baltagnostus robustus* Öpik (1979, pl. 12, figs. 4–5) from Queensland. The axes of the Queensland specimens are slightly wider than those illustrated here but in other respects are closely comparable to the Newfoundland pygidia; there are no significant differences in the cephalon.

Baltagnostus sertulatus Öpik (1979, pl. 12, figs. 6–9) is similar to *B. robustus*, but comparisons are difficult because few specimens have been illustrated previously and all fall in the lower third of the size range of the material of *B. robustus* from Newfoundland. It is possible that these species will prove to be synonyms.

Apart from an axis that is rounded, rather than bluntly pointed posteriorly, *B. centrensis* (Resser) (= *B. euryptyx* Robison, 1964, pl. 80, figs. 1–16; see Schwimmer, 1988, p. 485, fig. 2.1–2.4) is also similar to *B. robustus*. Unlike *B. robustus*, *B. centrensis* possesses a median ridge at the posterior end of the glabella (Robison and Jell, 1978, p. 5), as do *B. rakuroensis* (Kobayashi) (= *Aagnostus damesi* Resser and Endo; see Zhang and Jell, 1987, p. 41, pl. 1, figs. 1–15; Jell and Robison, 1978, pl. 1, figs. 1, 2, 4, 8) and *B. australis* Robison (in Jell and Robison, 1978, pl. 1, figs. 3, 5–7). Also, both *B. rakuroensis* and *B. australis* are separable from *B. robustus* by the presence of a postaxial median furrow on the pygidium.

Baltagnostus marginalis (Rasetti, 1948, pl. 24, figs. 6, 7; Fritz et al., 1970, pl. 8, figs. 1–8) from Quebec has a narrow cephalic border and a pygidial axis that is well-rounded posteriorly, rather than bluntly pointed, as in *B. robustus*. *Baltagnostus angustilobus* Rasetti (1967, pl. 9, figs. 4–11) and *B. stockportensis* Rasetti (1967, pl. 9, figs. 12–17, 22), both from the Taconic sequence of New York, are based on very small cephalon and pygidia (1 mm sag. or smaller), so that a meaningful comparison with the material illustrated here is not possible.

Family PERONOPSIDAE Westergård, 1946
Genus PERONOPSIS Hawle and Corda, 1847

Type species.—*Battus integer* Beyrich, 1845 from Cambrian strata of Bohemia (by monotypy).

Discussion.—*Peronopsis* is used herein in the broad sense advocated by Robison (1994), even though it is based on relatively plesiomorphic characters and is most likely an artificial taxon. Evaluation of the numerous species that have been assigned to *Peronopsis* is a major problem that is beyond the scope of this paper.

PERONOPSIS cf. *P. SCUTALIS* (Hicks, 1872)
Figure 22.7, 22.9–22.12

Peronopsis scutalis (Hicks). WESTERGÅRD, 1946, p. 41, pl. 4, figs. 4–11 (see for synonymy); RUSHTON, 1979, p. 50, fig. 3G, 5C; ROBISON, 1994, p. 46–47, fig. 21.

Peronopsis (Acadagnostus) scutalis (Salter, in Hicks). HUTCHINSON, 1962, p. 72, pl. 6, figs. 1–5 (see for synonymy).

Peronopsis tenuis (Illing). ROBISON, 1988, p. 47, figs. 10.7, 10.8, 10.10–10.12.

Material and occurrence.—One cephalon and 5 pygidia from BPS 458, 467, Zone 4.

Discussion.—Incomplete pygidia and an associated cephalon appear to fall within the range of variation of *Peronopsis scutalis*

(Hicks) s.l. (see Hutchinson, 1962; Rushton, 1979; Robison, 1994 for discussion of the concept of this species). They are most similar to morphs that have previously been assigned to *P. scutalis tenuis* (Illing; Rushton, 1979, fig. 3G; see also Robison, 1988, fig. 10.7, 10.8, 10.10–10.12), but more material is needed for a confident identification.

PERONOPSIS INTERSTRICTA (White, 1874)
Figure 22.1–22.3, 22.8

Aagnostus interstrictus WHITE, 1874, p. 7.

Peronopsis interstricta (White). ROBISON, 1964, p. 530, pl. 81, fig. 29, pl. 82, figs. 1–15, 18 (see for synonymy); ROBISON, 1994, p. 45, fig. 19.8–19.10 (see for synonymy).

Material and occurrence.—Three cephalon and 2 pygidia from WRI 640, Zone 3 (see Young and Ludvigsen, 1989 for additional occurrences in Zone 1).

Remarks.—The material from WRI 640 is closely comparable to specimens of *Peronopsis interstricta* from Utah (Robison, 1964, pl. 82, figs. 1–15, 18, 1982, pl. 6, figs. 9–11) and from older boulders in the Shallow Bay Formation (Young and Ludvigsen, 1989, pl. 1, figs. 21–26, pl. 2, figs. 1–2). Cephalon from the Shallow Bay Formation are also similar both to the cephalon of *Peronopsis gaspensis* Rasetti (1948, pl. 45, fig. 1) from Quebec and to cephalon from the Geddes Formation of Nevada that were assigned to that species by Robison (1978, pl. 1, figs. 9–10). However, pygidia of *P. gaspensis* (Rasetti, 1948, figs. 2–3; Robison, 1978, pl. 1, figs. 12–13) differ from those of *P. interstricta* in possessing small marginal spines. In other respects, these two species are closely comparable and when more information is available on variability of *P. gaspensis*, it may be possible to treat them as synonyms. *Peronopsis* cf. *P. gaspensis* Rasetti (1948, pl. 45, figs. 1–2) has a cephalon that resembles cephalon of *P. interstricta* but the pygidium has a pair of marginal spines and a relatively wider axis with distinct F1 and F2 furrows.

PERONOPSIS SEGMENTA Robison, 1964
Figure 22.4–22.6

Peronopsis segmenta ROBISON, 1964, p. 530, pl. 81, figs. 24–28; ROBISON, 1982, p. 157, pl. 6, figs. 1–4.

Material and occurrence.—Three cephalon and 6 pygidia from BPS 410, 420 and 421; WRI 640, zones 2 and 3.

Discussion.—A few pygidia (Figure 22.12, 22.13) from Broom Point possess the well-developed F1 furrows that are characteristic of *Peronopsis segmenta* Robison and represent the first record of this species outside of the eastern Great Basin. Rushton (1979) placed *P. segmenta* in *Diplagnostus* but, as noted by Robison (1982, p. 157), the absence of diplagnostid apomorphies, such as a zonate pygidial margin, makes this assignment unlikely.

Genus HYPAGNOSTUS Jaekel, 1909

Type species.—*Aagnostus parvifrons* Linnarsson, 1869 from Cambrian strata of Sweden (by original designation).

Diagnosis.—A genus of Peronopsidae with effaced anteroglabella. Pygidial axis roughly parallel-sided, with weak constriction at M2 and with broadly rounded to pointed posteroaxis. Cephalic borders narrow; pygidial borders broad. Apomorphic species (“*Cotalagnostus*”) with glabella and pygidial axis largely effaced.

Discussion.—In a recent classification, Shergold et al. (1990) assigned *Hypagnostus* to the subfamily Spinagnostinae of the family Spinagnostidae. They (Shergold et al., 1990, p. 6) did concede, however, that this grouping of genera, which seems to be diagnosed primarily on effacement of the anteroglabella, might be polyphyletic. We are also doubtful about the monophyly of

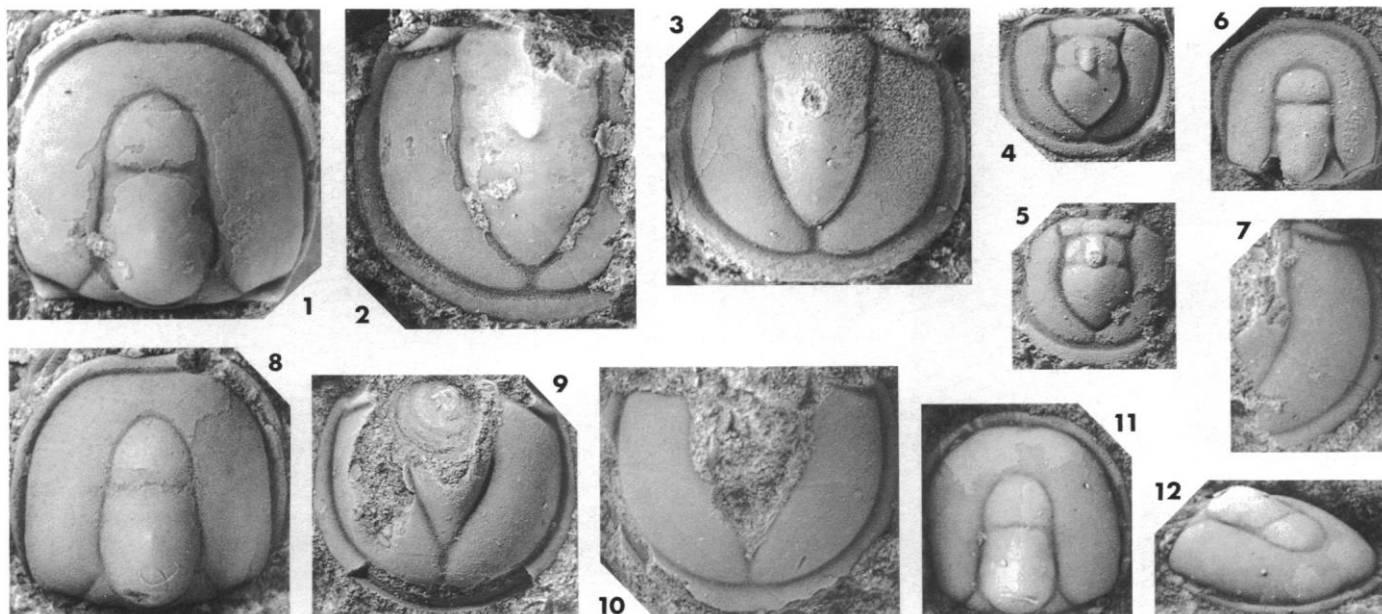


FIGURE 22—1–3, 8, *Peronopsis interstricta* (White), all from WRI 640. All $\times 9$. 1, cephalon, GSC 113271; 2, pygidium, GSC 113272; 3, pygidium, GSC 113273; 8, cephalon, GSC 113274. 4–6, *Peronopsis segmenta* Robison. All $\times 9$. 4, pygidium, GSC 113275, BPS 420; 5, pygidium, GSC 113276, BPS 421; 6, cephalon, GSC 113277, BPS 420; 7, 9–12, *Peronopsis* cf. *P. scutalis* (Hicks), all from BPS 458. All $\times 9$. 7, pygidium, GSC 113278; 9, pygidium, GSC 113279; 10, pygidium, GSC 113280; 11–12, cephalon (latex cast from external mold), GSC 113281.

the Spinagnostinae and, in the absence of any other apparent synapomorphy to define this subfamily, prefer to leave *Hypagnostus* in the family Peronopsidae (e. g. see Robison, 1994).

Cotalagnostus Whitehouse (see Westergård, 1946, pl. 7, figs. 6–20; Hutchinson, 1962, pl. 4, figs. 14–20; Robison, 1964, pl. 80, figs. 17–28) differs from *Hypagnostus* only in the greater degree of effacement of cephalic and pygidial axial furrows. As such, *Hypagnostus* is somewhat arbitrarily diagnosed by the retention of a relatively plesiomorphic character state: the presence of a distinct transglabellar furrow on the cephalon. We conclude that *Hypagnostus* is a paraphyletic grade and, in order to ensure monophyly, we regard it as a senior subjective synonym of *Cotalagnostus*.

Other “spinagnostine” genera, notably *Tomagnostella* Kobayashi (Robison, 1988, fig. 12.8–12.12), are also characterized by an effaced anteroglabella and future work may show that they should also be treated as synonyms of *Hypagnostus* (as was done, for example, by Westergård, 1946). For the present, we accept the conclusion of Robison (1988), who suggested that *Tomagnostella* and *Hypagnostus* were separable on the basis of pygidial axis morphology.

HYPAGNOSTUS PARVIFRONS (Linnarsson, 1869)

Figure 23.1–23.11

Agnostus parvifrons LINNARSSON, 1869, p. 82, pl. 2, figs. 56, 57.

Hypagnostus vortex WHITEHOUSE, 1936, p. 103, pl. 9, figs. 7, 8.

Hypagnostus clipeus WHITEHOUSE, 1936, p. 263, pl. 25, figs. 25–26; ÖPIK, 1979, p. 67, pl. 5, figs. 1, 7, text-fig. 18.

Hypagnostus parvifrons (Linnarsson). WESTERGÅRD, 1946, p. 45, pl. 4, figs. 27–31 (see for synonymy); HUTCHINSON, 1962, p. 73, pl. 4, figs. 6–7; ROBISON, 1964, p. 529, pl. 81, figs. 4–23 (see for synonymy); ÖPIK, 1979, p. 66, pl. 6, figs. 7–8; EGOROVA ET AL., 1982, p. 69, pl. 9, fig. 1, pl. 12, fig. 11, pl. 17, fig. 8, pl. 40, fig. 3; ZHANG AND JELL, 1987, p. 43, pl. 2, figs. 9–13, pl. 3, figs. 1–5; SHERGOLD ET AL., 1990, fig. 13.1a–13.1b; ROBISON, 1994, p. 41, fig. 17.

Hypagnostus cf. *vortex* Whitehouse. ÖPIK, 1979, p. 67, pl. 6, fig. 9.

Material and occurrence.—Eighty-seven cephalons and 71 pygidia from BPS 448 and 452; WRI 602, 606, 607A, 609, 614, 615B, 616, 619, 621, 622, 624, 630, 631, 633 and 640, Zone 3.

Remarks.—Numerous specimens from more than a dozen collections indicate that *Hypagnostus parvifrons* is a variable species, especially in pygidial morphology. Variation is evident in the relative length of the pygidial axis (Figure 23.4, 23.6–23.8, 23.11), with a weak trend towards increasing axis length during holaspis ontogeny (Figure 24). Different species of *Hypagnostus* have been diagnosed on the shape of the pygidial border: *H. parvifrons* has been restricted to forms which possess an expanded border behind the axis (e.g. see Westergård, 1946, ÖPIK, 1979) whereas forms that lack this expansion have been assigned to *H. clipeus* Whitehouse (ÖPIK, 1979, p. 67, pl. 5, fig. 1). However, pygidia from the Shallow Bay Formation are variable in border width and include forms in which expansion is weak or absent (e.g. Figure 23.8). Accordingly, *H. clipeus* is regarded as a junior subjective synonym of *H. parvifrons*. The poorly known *H. vortex* Whitehouse also possesses a narrow pygidial border and is also likely to be a synonym of *H. parvifrons*.

Most cephalons from the Shallow Bay Formation have curved transglabellar furrows, but some possess more transverse furrows that approach *H. truncatus* (Brögger) in this respect. However, numerous specimens from Sweden (Westergård, 1946, pl. 5, figs. 16–18) and Siberia (Egorova, et al., 1982, pl. 6, figs. 3–5, pl. 7, figs. 1–3, pl. 8, figs. 1–2,) indicate that pygidia of *H. truncatus* usually lack a postaxial median furrow (but see, for example, Egorova, et al., 1982, pl. 14, fig. 5, pl. 15, fig. 1 for specimens attributed to *H. truncatus* that possess shallow postaxial median furrows). Pygidia of *H. parvifrons* from the Shallow Bay Formation consistently possess a postaxial median furrow and, for the present, it seems best that *H. truncatus* be retained as a separate species. *H. brevifrons* (Angelin; see Westergård, 1946, pl. 5, figs. 26–27; ÖPIK, 1961, pl. 18, fig. 8; Rozova, 1977, pl. 19, fig. 11; Ergaliev, 1980, pl. 4, fig. 11; Lu and Lin, 1989,

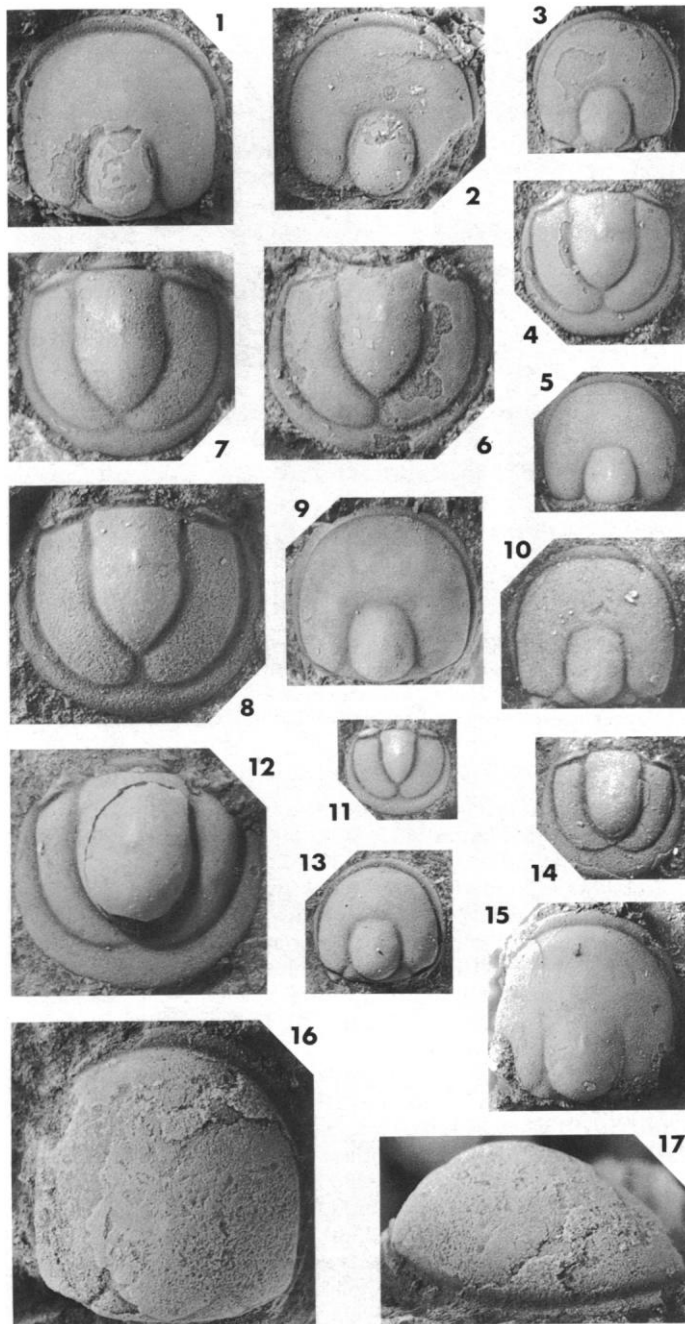


FIGURE 23—1–11, *Hypagnostus parvifrons* (Linnarsson). All $\times 9$. 1, cephalon, GSC 113282, WRI 624; 2, cephalon, GSC 113283, WRI 606; 3, cephalon, GSC 113284, WRI 633; 4, pygidium, GSC 113285, WRI 633; 5, cephalon, GSC 113286, WRI 616; 6, pygidium, GSC 113287, WRI 633; 7, pygidium, GSC 113288, WRI 616; 8, pygidium, GSC 113289, WRI 624; 9, cephalon, GSC 113290, WRI 616; 10, cephalon, GSC 113291, BPS 448; 11, pygidium, GSC 113292, BPS 448. 12–14, *Hypagnostus* cf. *H. parvifrons* (Linnarsson), all from BPS 451. All $\times 12$. 12, pygidium, GSC 113293; 13, cephalon, GSC 113294; 14, pygidium, GSC 113295. 15–17, *Hypagnostus*? cf. *H. lens* (Grönwall), all from WRI 632. All $\times 9$. 15, cephalon GSC 113296; 16–17, cephalon, GSC 113297.

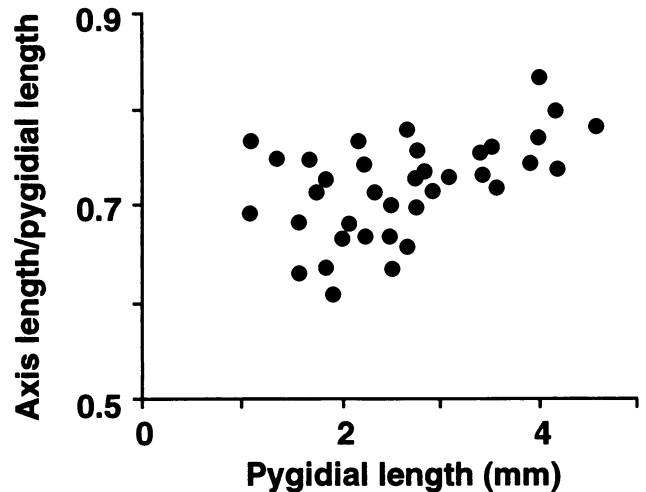


FIGURE 24—Plot of axis length/pygidial length against pygidial length for *Hypagnostus parvifrons* (Linnarsson) from the Shallow Bay Formation.

pl. 11, fig. 2; Robison, 1994, fig. 15) also differs from *H. parvifrons* in lacking the postaxial median furrow on the pygidium and, as noted by Robison (1994), has a relatively shorter pygidial axis in at least larger holaspids.

Hypagnostus mammillatus (Brögger; see Samson et al., 1990 for discussion) is separable from *H. parvifrons* on the basis of its more convex pygidial axis and longer pygidial border (e.g. Westergård, 1946, pl. 5, fig. 3b; Samson et al., 1990, fig. 5L, P). Westergård (1946) assigned scrobiculate specimens to a separate subspecies of *H. parvifrons*: *H. parvifrons cicatricosus* Westergård (1946, pl. 5, fig. 1) for scrobiculate forms. This subspecies is not present in the Cow Head collections: cephalons are uniformly smooth.

HYPAGNOSTUS cf. *H. PARVIFRONS* (Linnarsson, 1869)

Figure 23.12–23.14

Material and occurrence.—Four cephalons and 3 pygidia from BPS 451, Zone 3.

Remarks.—A few pygidia from BPS 451 differ from *Hypagnostus parvifrons* in having a relatively wider axis that is rounded posteriorly and a longer, flat border. The associated cephalons each possess a relatively wider glabella.

HYPAGNOSTUS? cf. *H. LENS* (Grönwall, 1902)

Figure 23.15–23.17

Agnostus lens GRÖNWALL, 1902, p. 65, pl. 1, figs. 9 [only; fig. 8 = *Ptychagnostus barrandei* (Hicks); see Robison, 1994, p. 50]. *Cotalagnostus lens* (Grönwall). WESTERGÅRD, 1946, p. 53, pl. 7, figs. 1–5 (see for synonymy); HUTCHINSON, 1962, pl. 4, figs. 14–17.

Material and occurrence.—Two cephalons from WRI 632, Zone 3.

Remarks.—Differentiation of isolated cephalons of weakly furrowed species of *Hypagnostus* from those of the effaced species of *Ptychagnostus*, *P. barrandei* (Hicks, as revised by Robison, 1994, p. 52, fig. 23; see also Hutchinson, 1962, pl. 9, figs. 20–23, pl. 10, figs. 1–8), is difficult (see also Westergård, 1946, p. 53; Robison, 1994, p. 52). Two cephalons are questionably assigned to *Hypagnostus* because the anterior glabellar lobe is not evident in even the smaller specimen (Figure 23.16), whereas this feature is expressed in small individuals of *P. barrandei* (e.g. Hutchinson, 1962, pl. 9, fig. 22).

In possessing distinct basal lobes in large individuals and a cephalon in which length exceeds width, the Newfoundland ce-

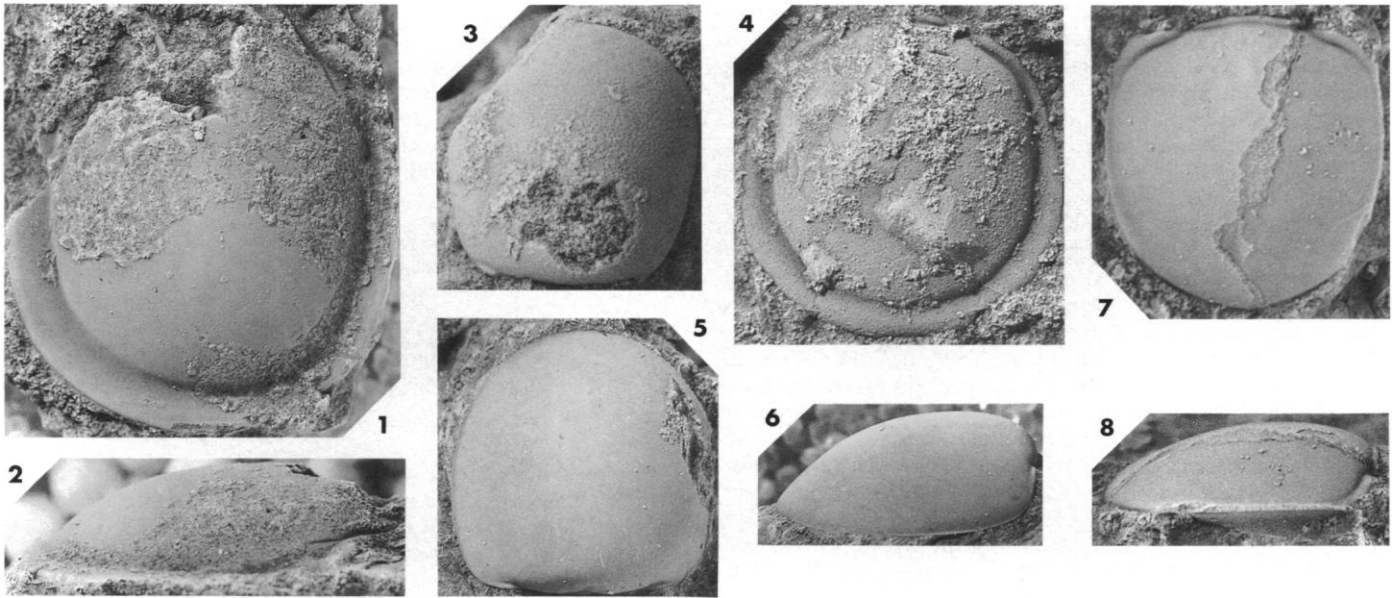


FIGURE 25—1–2, 5–6, *Megagnostus glandiformis* (Angelin), all BPS 468. Both $\times 5$. 1–2, pygidium, GSC 113298; 5–6, cephalon, GSC 113299. 3–4, *Megagnostus?* sp. indet., all BPS 458. Both $\times 9$. 3, cephalon, GSC 113300; 4, pygidium, GSC 113301, \times . 7–8, *Megagnostus* cf. *M.? resectus* (Grönwall), pygidium, GSC 113302, WRI 630, $\times 9$.

phala are comparable to *H. lens* (Grönwall; Westergård, 1946, pl. 7, figs. 1–2, 4; Hutchinson, 1962, pl. 9, figs. 14–15). *Hypagnostus confusus* (Westergård; Westergård, 1946, pl. 7, figs. 6–13, 15–20) has a relatively shorter and wider cephalon, whereas *H. laevis* (Robison, 1964, pl. 80, figs. 17–28) is much more effaced.

Family PHALACROMIDAE Hawle and Corda, 1847
Genus MEGAGNOSTUS Robison, 1994

Type species.—*Agnostus glandiformis* Angelin, 1851 from the Andrarum Limestone, Sweden (by original designation).

Remarks.—Until recently, effaced agnostids in which only the pygidial border is well-defined were assigned to *Grandagnostus* Howell (see Jago, 1976 and Rushton, 1978 for discussion). Revision of this group of species is hindered by loss of information in the most effaced members. Also, character polarities are difficult to determine because of uncertainties concerning outgroup taxa. The type species, *G. vermontensis* Howell, is very poorly preserved and Robison (1988) recommended that *Grandagnostus* be restricted to the holotype (see Robison, 1988, fig. 12.7). Consequently, *Agnostus bituberculatus* Angelin was placed in a new genus, *Toragnostus* (Robison, 1988), and an additional new genus, *Megagnostus*, was established subsequently (Robison, 1994) to house *A. glandiformis* Angelin and a new species from North Greenland; *A. cicer* Tullberg and *Ciceragnostus? falanensis* Westergård were assigned to *Peratagnostus* Öpik (Robison, 1994).

Megagnostus possesses a unique, downwardly directed flange on the pygidial doublure, which probably functioned in enrollment (Robison, 1994, p. 61, fig. 32.9a; Westergård, 1946, pl. 15, fig. 10). The pygidial doublure is not known for many species of “*Grandagnostus*” and it is possible that both the content and status of *Megagnostus* will change once this information becomes available. Species assigned previously to *Megagnostus* possess well-defined pygidial borders, but *M. cf. M.? resecta* (Grönwall) from the Shallow Bay Formation (Figure 25.7, 25.8) has a narrow border that is not expressed along the posterior pygidial margin.

Robison (1988) emphasized the presence of an anteriorly positioned median glabellar node in the diagnosis of *Toragnostus*. This character state appears to be an apomorphy, although it should be noted that in some species, including the type species of *Megagnostus*, *M. glandiformis* (Angelin; Figure 25.5, 25.6), the median node is lost through effacement, so that its position cannot be determined.

Inclusion of *Agnostus cicer* and *Ciceragnostus? falanensis* in *Peratagnostus* is based partly on interpretations of the ontogenies of *P. nobilis* by Shergold (1982) and of *A. cicer* by Robison (1994). Meraspids and early holaspids assigned to these species (Shergold, 1982, pl. 6, figs. 4–7; Robison, 1994, fig. 34.1, 34.2) have broad, convex, gently tapered, anteriorly rounded axes and wide, flat acrollobes. Both Shergold (1982, p. 23) and Robison (1994, p. 66) concluded that the development of these species included a major metamorphosis in which a true pygidial border and border furrow developed, along with convex acrollobes. Similarity in immature forms and in ontogenetic development led Robison (1994) to assign *A. cicer* to *Peratagnostus*. Shergold (1982, p. 23) and Robison (1994, p. 66) recognized the similarities between the meraspid pygidia attributed to *P. nobilis* and *A. cicer* and small pygidia of *Phalagnostus* (e.g. Snajdr, 1958, pl. 5, figs. 5, 7); Robison went so far as to conclude that *Phalagnostus* may be a paedomorphic descendant of *Peratagnostus*. In contrast, Pratt (1992) argued that Shergold (1982) had misassigned the meraspids and reinterpreted them as simply representing a diminutive species of *Phalagnostus*; a similar interpretation may be made of the meraspids attributed to *A. cicer* by Robison (1994). We concur with Pratt and remove both *A. cicer* and *C.? falanensis* from *Peratagnostus*. Removal of these species is supported by the pygidial morphology of mature holaspids. *Peratagnostus nobilis* has a relatively narrow axis (e.g. Palmer, 1968, pl. 10, fig. 24; Pratt, 1992, pl. 7, figs. 24, 26; Westrop, 1995, pl. 1, fig. 21), whereas the axis of *A. cicer* is broad (Robison, 1994, fig. 34.6a, 8b). The axis of *C.? falanensis* is completely effaced (Rushton, 1978, pl. 24, figs. 7, 12–13) but, based on the width of the articulating half-ring, it also has a broad axial lobe. This difference was recognized by Robison

(1994, p. 66), who suggested that the narrow axis of *Peratagnostus nobilis* could be pedomorphically derived from *C. falanensis* and decided to "attach trivial rather than generic significance to the late holaspis difference in axial proportions." However, differences in pygidial axes extend to outline. *Peratagnostus nobilis* has a narrow, tapered axis (Öpik, 1967, fig. 18; Westrop, 1995, pl. 1, fig. 21). The axis of *A. cicer* is defined only over the anterior half of the pygidium (Robison, 1994, fig. 34.6a, 8b) but the posteriormost portions of the axial furrows are divergent, indicating that the axis expands backwards. *Phalacroma* Hawle and Corda also has a broad, posteriorly expanding pygidial axis (Snadje, 1958, pl. 4, figs. 26–28) and we suggest that *A. cicer* is an effaced member of this genus. Ontogenetic data for *Phalacroma cicer* (Robison, 1994, figs. 34.3–34.8) indicate that posterior divergence of the pygidial axial furrows occurs relatively late in the holaspis development, suggesting that it is an apomorphic character state. Other similarities between *P. cicer* and the type species, *P. bibullatum* (Barrande; Snadje, 1958, pl. 4, figs. 25–32; Rushton, 1979, fig. 9A–B) include the presence of a long pygidial axial node. Differences between these two species are related primarily to the degree of effacement: *P. bibullatum* possesses a narrow cephalic border and the glabella is defined posteriorly by weak axial furrows (Rushton, 1979, fig. 9A); the pygidium of *P. bibullatum* has a relatively narrower border (Snadje, 1958, pl. 4, figs. 26–28; Rushton, 1979, fig. 9B). *Ciceragnostus? falanensis* differs from *P. cicer* only in the degree of effacement and it is also assigned to *Phalacroma*.

Megagnostus differs from effaced species of *Phalacroma* in the much lower degree of pygidial convexity (Robison, 1994, fig. 32.6a, 33.3b, 12b) and in the presence of a flange on the pygidial doublure. In other respects, the two genera are closely comparable and, therefore, *Megagnostus*, along with *Toragnostus*, is assigned tentatively to the Phalacromidae Hawle and Corda. We are uncertain about the relationship between the Phalacromidae, *Valenagnostus* Jago and *Phalagnostus* Howell, all of which are very similar in the degree of cephalic effacement. *Valenagnostus* (Jago, 1976, pl. 24, figs. 6–9) differs from phalacromids in possessing a pygidial border that is very long posteriorly (occupying up to half of pygidial length [sag.]) and a long, narrow, tapered pygidial axis (Jago, 1976, text-fig. 1). Pygidia of *Phalagnostus* have unique, border-like structures that apparently incorporate part of the acrolobe (e.g. see Jago, 1976 and Rushton, 1978 for discussion).

MEGAGNOSTUS GLANDIFORMIS (Angelin, 1851)

Figure 25.1, 25.2, 25.5, 25.6

Agnostus glandiformis ANGELIN, 1851, p. 5, pl. 6, fig. 1.

Megagnostus glandiformis (Angelin). ROBISON, 1994, p. 63, fig. 33 (see for synonymy).

Material and occurrence.—One cephalon and 1 pygidium from BPS 468, Zone 4.

Remarks.—The Cow Head material is closely comparable to cephalon and pygidia of *Megagnostus glandiformis* (Angelin) from the type area in Sweden (Jago, 1976, pl. 24, figs. 1–5) and from North Greenland (Robison, 1994, fig. 33). *Megagnostus diclidus* Robison (1994, fig. 32) has a narrow cephalic border and an upturned pygidial border, whereas *M. cf. M.? resectus* from the Shallow Bay Formation (Figure 25.7, 25.8) differs in having a narrow pygidial border that is developed only along the lateral margins.

Toragnostus bituberculatus (Angelin; Robison, 1988, fig. 12.4–12.6) has an anteriorly positioned median glabellar node and well-defined basal lobes on the cephalon, whereas both the median node and the basal lobes are poorly expressed or lacking

on cephalon of *M. glandiformis* (Figure 25.5, 25.6; see also Jago, 1976, pl. 24, fig. 1); *T. carinatus* (Lu and Lin, 1989, pl. 13, figs. 7–10) has a distinct cephalic border and median glabellar node close to cephalic mid-length. Pygidia of all three species are closely comparable. Finally, *Phalacroma falanensis* (Westergård), as revised by Rushton (1978, pl. 24, figs. 6–14) appears to differ from *M. glandiformis* in its much greater pygidial convexity.

MEGAGNOSTUS cf. M.? RESECTUS

(Grönwall, 1902)

Figure 25.7, 25.8

Phalacroma resectum (Grönwall). WESTERGÅRD, 1946, p. 93, pl. 14, figs. 19 a, b (see for synonymy).

Phalacroma resecta (Grönwall). JAGO, 1976, pl. 24, fig. 12.

Material and occurrence.—One pygidium from WRI 630, Zone 3.

Remarks.—A single pygidium from White Rock Islets has a ventrally directed flange on the doublure, indicating an assignment to *Megagnostus*. It is almost completely effaced and is of low convexity. The articulating half-ring is a broad, narrow band, suggesting that the axial lobe is relatively wide. A faint median node is present. The shoulder and shoulder furrow are well-developed, but a narrow border is present only along the lateral pygidial margin.

Megagnostus? resectus (Grönwall; Westergård, 1946, pl. 14, fig. 19; Jago, 1976, pl. 24, fig. 12) is very similar to the Cow Head material, but has a border that extends along the entire pygidial margin. The pygidium of the poorly documented Siberian species, *Megagnostus? laevis* Pokrovskaya (Egorova et al., 1982, pl. 11, figs. 6–7, pl. 12, fig. 4), is comparable in morphology, apparently differing in lacking a border along both the lateral and posterior margins. *Megagnostus glandiformis* Angelin (Figure 25.1, 25.2) and *M. diclidus* Robison (1994, fig. 32) are both separable from *M. cf. M.? resectus* by the presence of well-developed borders along the entire pygidial margins.

MEGAGNOSTUS? sp. indet.

Figure 25.3, 25.4

Material and occurrence.—One cephalon and 1 pygidium from BPS 458, Zone 4.

Remarks.—A single cephalon and associated weakly convex pygidium (Figure 25.3, 25.4) resemble *Megagnostus glandiformis* (Angelin; Figure 25.1, 25.2, 25.5, 25.6) but have coarsely punctate prosopon (fine punctae may be present on some specimens of *M. glandiformis*; Robison, 1995). Also, the pygidium has a subcircular, rather than subelliptical outline. We have not been able to determine whether a doublural flange is present on the pygidium and, therefore, assignment to *Megagnostus* is tentative.

Family UNCERTAIN

Genus UTAGNOSTUS Robison, 1964

Type species.—*Utagnostus trispinulus* Robison, 1964, from the Marjum Formation, western Utah (by original designation).

Diagnosis.—A genus of Agnostida with glabella composed of long, parallel-sided posteroglabella and short, narrower (tr.) anteroglabella. Pygidial border is broad and trispinose.

Remarks.—The short, narrow anteroglabella and broad, trispinose border are unusual character states that can diagnose *Utagnostus*. Shergold et al., (1990) assigned the genus to the Clavagnostidae, primarily on the basis of the cephalic and pygidial spines. However, *Utagnostus* appears to lack any of the synapomorphies that might be used to define this family. For example, both *Clavagnostus* and *Aspidagnostus* are character-

ized by a relatively narrow, posteriorly tapered pygidial axis that is depressed posteriorly (see Jago and Daily, 1974, pl. 11, figs. 2, 4, 6, 8 and Öpik, 1967, pl. 56, figs. 3–6, 8, respectively) whereas *Utagnostus* has a parallel-sided to weakly expand, posteriorly rounded pygidial axis (Figure 15.4, 15.6). *Clavagnostus* and *Aspidagnostus* also possess glabellae in which the anterior and posterior lobes are fused (see Jago and Daily, 1974, pl. 11, figs. 1, 3, 5, 7, 9 and Öpik, 1967, pl. 56, figs. 1, 2, 7, 9, 10, respectively), whereas *Utagnostus* has a transglabellar furrow and well-defined anterior glabellar lobe (Figure 15.5). We prefer to restrict the family Clavagnostidae to *Clavagnostus* Howell, *Aspidagnostus* Whitehouse and the poorly known *Triadaspis* Öpik, and leave *Utagnostus* unassigned.

UTAGNOSTUS TRISPINULUS Robison, 1964
Figure 15.7–15.9

Utagnostus trispinulus ROBISON, 1964, p. 533, pl. 82, figs. 21–28.

Material and occurrence.—One cephalon and two pygidia from BPS 451, Zone 3.

Remarks.—There are no significant differences between the cephalon and pygidia from the Cow Head Group and the type material of *Utagnostus trispinulus* from Utah (see Robison, 1964, pl. 82, figs. 21–28). *Utagnostus neglectus* Jago (1976, pl. 23, fig. 13) and *Utagnostus* (?) sp. Jago (1976, pl. 23, figs. 14–16) both differ from *U. trispinulus* in having fused anterior and posterior glabellar lobes and posteriorly tapered pygidial axes, and may be assigned incorrectly to this genus.

ACKNOWLEDGMENTS

Loan of the material from the Geological Survey of Canada was facilitated by T. Bolton and M. Copeland. D. Mucciante and the late B. 'O Donovan processed our negatives and printed many of the photographs. R.A. Robison and N.C. Hughes provided useful reviews of the manuscript and J.R. Laurie contributed helpful comments on the PAUP analysis of the Ptychagnostidae, although they do not necessarily accept all of our conclusions. Preparation of the manuscript was supported by NSERC Operating Grant 41197 to Westrop.

REFERENCES

- ADRAIN, J. M., AND B. D. E. CHATTERTON. 1994. The aulacopleurid trilobite *Otarion* with new species from the Silurian of northwestern Canada. *Journal of Paleontology*, 68:305–323.
- ANGELIN, N. P. 1851. *Palaeontologia Suecica, pars I: Iconographia crustaceorum formationis transitionis*. Lund, 24 pp.
- BABCOCK, L. E. 1994. Systematics and phylogenetics of polymeroid trilobites from the Henson Gletscher and Kap Stanton formations (Middle Cambrian), North Greenland. *Grønlands Geologiske Undersøgelse Bulletin*, 169:79–127.
- BENTON, M. J. 1990. Origin and interrelationships of dinosaurs, p. 11–30. In D.B. Weishampel, P. Dodson and H. Osmolska (eds.), *The Dinosauria*. University of California Press.
- BERGERON, M. J. 1899. Étude de quelques trilobites de Chine. *Bulletin de la Société géologique de France, series 3*, 27:499–516.
- BEYRICH, E. 1845. *Über einige böhemische Trilobiten*. Berlin, 47 p.
- BRIGGS, D. E. G., AND R. A. FORTEY. 1989. The early radiation and relationships of the major arthropod groups. *Science*, 246:241–243.
- BROGGER, W. C. 1878. Om paradoxideskifrene ved Krekling. *Nyt Magazin for Naturvidenskaberne*, 24: 18–88.
- BRUTON, D. L. AND A. W. OWEN. 1990. The Norwegian Upper Ordovician illaenid trilobites. *Norsk Geologisk Tidsskrift*, 68:241–258.
- EDGEcombe, G. D., AND B. D. E. CHATTERTON. 1990. Systematics of *Encrinuroides* and *Curriella* (Trilobita), with a new Early Silurian encrinurine from the Mackenzie Mountains. *Canadian Journal of Earth Sciences*, 27:820–833.
- EGOROVA, L. I., Y. Y. SHABANOV, T. V. PEGEL, V. E. SAVITSKY, S. S. SUCHOV, AND N. E. CHERNYSHEVA. 1982. Maya Stage of the type locality (Middle Cambrian of Siberian Platform). Academy of Sciences of the USSR, Interdepartmental Stratigraphic Committee of the USSR, Transactions, 8:1–145. (In Russian)
- ERGALIEV, G. K. 1980. Trilobites of the Middle and Upper Cambrian of the Malyi Karatau. Kazakhstan SSR Academy of Sciences, K.I. Satpaev Institute of Geological Sciences, 211 p. (In Russian)
- FOREY, P. L. 1982. Neontological analysis versus palaeontological stories, p. 119–157. In K. A. Joysey and A. E. Friday (eds.), *Problems of Phylogenetic Reconstruction*. Systematics Association Special Volume, 21.
- FORTEY, R. A., AND B. D. E. CHATTERTON. 1988. Classification of the trilobite suborder Asaphina. *Palaentology*, 31:165–222.
- FRITZ, W. H., C. H. KINDLE, AND P. J. LESPÉRANCE. 1970. Trilobites and stratigraphy of the Middle Cambrian Corner-of-the-Beach Formation, eastern Gaspé Peninsula, Quebec. *Geological Survey of Canada Bulletin*, 187:43–58.
- GRÖNWALL, K. A. 1902. Bornholms Paradoxideslag og deres fauna. *Danmark geologiske Undersøgelse (Series 2)*, 13, 220 p.
- GOULD, S. J. 1991. The disparity of the Burgess Shale arthropod fauna and the limits of cladistic analysis: why we must strive to quantify morphospace. *Paleobiology*, 17:411–423.
- HAWLE, I., AND A. J. C. CORDA. 1847. *Prodrom einer Monographie der böhemischen Trilobiten*. Prague, 176 p.
- HICKS, H. 1872. On some undescribed fossils from the Menevian Group. *Quarterly Journal of the Geological Society of London*, 28: 173–185.
- HUGHES, N. C. 1994. Ontogeny, intraspecific variation, and systematics of the Late Cambrian trilobite *Dikelocephalus*. *Smithsonian Contributions to Paleobiology*, 79, 89 p.
- , AND A. W. A. RUSHTON. 1990. Computer-aided reconstruction of a Late Cambrian ceratopygid trilobite from Wales and its phylogenetic implications. *Palaentology*, 33:429–445.
- HUTCHINSON, R. D. 1962. Cambrian stratigraphy and trilobite faunas of southeastern Newfoundland. *Geological Survey of Canada, Bulletin* 88, 156 p.
- JAELKE, O. 1909. Über die Agnostiden. *Zeitschrift deutsche geologische Gesellschaft*, 61:380–401.
- JAGO, J. B. 1976. Late Middle Cambrian agnostid trilobites from northwestern Tasmania. *Palaentology*, 19:133–172.
- , AND B. DAILY 1974. The trilobite *Clavagnostus* Howell from the Cambrian of Tasmania. *Palaentology*, 17:95–109.
- JAMES, N. P., AND R. H. STEVENS. 1986. Stratigraphy and correlation of the Cambro-Ordovician Cow Head Group, western Newfoundland. *Geological Survey of Canada, Bulletin* 366, 143 p.
- , —, C. R. BARNES AND I. KNIGHT. 1989. Evolution of a Lower Paleozoic continental-margin carbonate platform, northern Canadian Appalachians. *SEPM Special Publication* 44:123–146.
- JELL, P. A., AND R. A. ROBISON. 1978. Revision of a Late Middle Cambrian trilobite faunule from northwestern Queensland. *University of Kansas Paleontological Contributions, Paper* 90, 21 p.
- JONES, B. 1988. Biostatistics in paleontology. *Geoscience Canada*, 15: 3–22.
- KINDLE, C. H. 1982. The C.H. Kindle Collection: Middle Cambrian to Lower Ordovician trilobites from the Cow Head Group, western Newfoundland. *Geological Survey of Canada, Paper* 82–1C:1–17.
- , AND H. B. WHITTINGTON. 1958. Stratigraphy of the Cow Head region, western Newfoundland. *Geological Society of America, Bulletin*, 69:315–342.
- KOBAYASHI, T. 1939. On the agnostids (part 1). *Journal of the Faculty of Science, Imperial University of Tokyo*, 5:69–198.
- LAURIE, J. 1988. Revision of some Australian Ptychagnostinae (Agnostida, Cambrian). *Alcheringa*, 12:169–205.
- , 1989. Revision of species of *Goniagnostus* Howell and *Lejopyge* Corda from Australia (Agnostida, Cambrian). *Alcheringa*, 13:175–191.
- LINNAERSSON, J. G. O. 1869. Om Vestergötlands "Andrarumskalk". *Geologiska Föreningens i Stockholm Föreläsningar*, 1:242–248.
- , 1879. Om faunan i kalken med *Conocoryphe exsulans* ("Conrunatuskalken"). *Sveriges Geologiska Undersökning [C]*, 35:1–31.
- LOCHMAN, C., AND D. DUNCAN. 1944. Early Upper Cambrian faunas of central Montana. *Geological Society of America, Special Paper* 54, 181 p.

- LOCHMAN-BALK, C., AND J. L. WILSON. 1958. Cambrian biostratigraphy in North America. *Journal of Paleontology*, 32:312–350.
- LU, YANHAO, AND HUANLING LIN. 1989. The Cambrian trilobites of western Zhejiang. *Palaeontologia Sinica* 178, 287 p. (In Chinese with English summary)
- LUDVIGSEN, R., AND S. R. WESTROP. 1985. Three new Upper Cambrian stages for North America. *Geology*, 13:139–143.
- , —, AND C. H. KINDLE. 1989. Sunwaptan (Upper Cambrian) trilobites of the Cow Head Group, western Newfoundland, Canada. *Palaeontographica Canadiana* 6, 175 p.
- M'Coy, F. 1849. On the classification of some British fossil Crustacea with notices of some new forms in the University collection at Cambridge. *Annals and Magazine of Natural History* (2), 4:161–179, 330–335, 392–414.
- MADDISON, W. P., AND D. R. MADDISON. 1992. MacClade version 3. Sinauer Inc.
- MELZAK, A., AND S. R. WESTROP. 1994. Mid-Cambrian (Marjuman) trilobites from the Pika Formation, southern Canadian Rocky Mountains, Alberta. *Canadian Journal of Earth Sciences*, 31:969–985.
- ÖPK, A. 1961. The geology and palaeontology of the headwaters of the Burke River, Queensland. *Australian Bureau of Mineral Resources, Geology and Geophysics Bulletin*, 53, 249 p.
- . 1967. The Mindyallan Fauna of north-western Queensland. *Australian Bureau of Mineral Resources, Geology and Geophysics Bulletin*, 74, vol. 1, 404 p., vol. 2, 167 p.
- . 1979. Middle Cambrian agnostoids: systematics and biostratigraphy. *Australian Bureau of Mineral Resources, Geology and Geophysics Bulletin*, 172, vol. 1, 188 p., vol. 2, 67 plates.
- PALMER, A. R. 1954. The faunas of the Riley Formation in central Texas. *Journal of Paleontology*, 28:709–786.
- . 1962. *Glyptagnostus* and associated trilobites in the United States. United States Geological Survey Professional Paper 374F, 49 p.
- . 1968. Cambrian trilobites of east-central Alaska. United States Geological Survey Professional Paper 559B, 115 p.
- PRATT, B. R. 1992. Trilobites of the Marjuman and Steptoean stages (Upper Cambrian), Rabbitkettle Formation, southern Mackenzie Mountains, northwest Canada. *Palaeontographica Canadiana*, 9, 179 p.
- RASETTI, F. 1948. Middle Cambrian trilobites from the conglomerates of Quebec. *Journal of Paleontology*, 22:315–339.
- . 1963. Middle Cambrian ptychoparioid trilobites from the conglomerates of Quebec. *Journal of Paleontology*, 37:575–594.
- . 1965. Upper Cambrian trilobite faunas of northeastern Tennessee. *Smithsonian Miscellaneous Collections*, 148, 3, 127 p.
- . 1967. Lower and Middle Cambrian trilobite faunas from the Taconic sequence of New York. *Smithsonian Miscellaneous Collections*, 152, 4, 152 p.
- RESSER, C. E. 1938. Cambrian System (restricted) of the southern Appalachians. *Geological Society of America, Special Paper* 15, 140 p.
- ROBISON, R. A. 1964. Late Middle Cambrian faunas from western Utah. *Journal of Paleontology*, 38:510–566.
- . 1976. Middle Cambrian trilobite biostratigraphy of the Great Basin. *Geological Studies*, Brigham Young University, 23:93–109.
- . 1978. Origin, taxonomy and homeomorphs of *Doryagnostus* (Cambrian Trilobita). University of Kansas Paleontological Contributions, Paper 91, 10 p.
- . 1982. Some Middle Cambrian agnostoid trilobites from western North America. *Journal of Paleontology*, 56:132–160.
- . 1984. Cambrian Agnostida of North America and Greenland, Part 1, Ptychagnostidae. University of Kansas Paleontological Contributions, Paper 109, 59 p.
- . 1988. Trilobites of the Holm Dal Formation (late Middle Cambrian) central North Greenland. *Meddelelser om Grønland, Geoscience*, 20:20–103.
- . 1994. Agnostoid trilobites from the Henson Gletscher and Kap Stanton formations (Middle Cambrian), North Greenland. *Grønlands Geologiske Undersøgelse Bulletin*, 169:25–77.
- ROWELL, A. J., R. A. ROBISON, AND D. K. STRICKLAND. 1992. Aspects of Cambrian agnostoid phylogeny and chronocorrelation. *Journal of Paleontology*, 56:161–182.
- ROZOVA, A. V. 1964. Biostratigraphy and description of trilobites of the Middle and Upper Cambrian of the northwestern Siberian platform. Institute of Geology and Geophysics, Academy of Sciences of the USSR, Siberian Division, Novosibirsk, 148 p. (In Russian)
- . 1977. Upper Cambrian and Lower Ordovician of the Rubnoi, Khartaiki, Kureiki and Letnei river basins, p. 54–84. In N. E. Chernysheva and A. V. Rozova (eds.), *Biostratigraphy and fauna of the Upper Cambrian and its boundary layers*. Transactions of the Institute of Geology and Geophysics, Academy of Sciences of the USSR, Siberian Division, Novosibirsk. (In Russian)
- RUSHTON, A. W. A. 1978. Fossils from the Middle–Upper Cambrian transition in the Nuneaton district. *Palaeontology*, 21:245–283.
- . 1979. A review of the Middle Cambrian Agnostida from the Abbey Shales, England. *Alcheringa*, 3:43–61.
- SALTER, J. W. 1864. A monograph of the British trilobites from the Cambrian, Silurian and Devonian formations. *Paleontographical Society Monograph*, 80 p.
- SAMSON, S., A. R. PALMER, R. A. ROBISON, AND D. T. SECOR, JR. 1990. Biogeographical significance of Cambrian trilobites from the Carolina slate belt. *Geological Society of America Bulletin*, 102:1459–1470.
- SCHWIMMER, D. R. 1988. Taxonomy and biostratigraphic significance of some Middle Cambrian trilobites from the Conasauga Formation in western Georgia. *Journal of Paleontology*, 63:484–494.
- SERENO, P. C. 1991. Basal archosaurs: phylogenetic relationships and functional implications. *Society of Vertebrate Paleontology Memoir*, 2, 53 p.
- SHERGOLD, J. H. 1982. Idamean (Late Cambrian) trilobites, Burke River Structural Belt, western Queensland. *Australian Bureau of Mineral Resources, Geology and Geophysics Bulletin*, 187, 103 p.
- , J. R. LAURIE AND XIAOWEN SUN. 1990. Classification and review of the trilobite order Agnostida Salter, 1864: an Australian perspective. *Australian Bureau of Mineral Resources, Geology and Geophysics Report*, 296, 93 p.
- SMITH, A. B. 1994. Systematics and the Fossil Record. Documenting Evolutionary Patterns. Blackwell Scientific Publications, Boston, 23 p.
- SNADJR, M. 1958. Trilobiti českého středního kambria. *Rozpravy ústředního ústavu geologického* 24, 280 p.
- SWOFFORD, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1.1. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.
- TULLBERG, S. A. 1880. *Agnostus-arterna i de Kambriska aflägringarne vid Andrarum*. Sveriges Geologiska Undersökning [C], 42:1–37.
- WALCOTT, C. D. 1884. Paleontology of the Eureka district. United States Geological Survey Monograph, 8, 298 p.
- WANG, JINBIN, SHOUE CHENG, LINWEN XIANG, AND TAIRONG ZHANG. 1985. Stratigraphy and trilobite faunas of the Cambrian in the western part of northern Tianshan, Xinjiang. People's Republic of China, Ministry of Geology and Mineral Resources Geological Memoirs, Series 2, 4, 243 p. (In Chinese, with English summary)
- WESTERGÅRD, A. H. 1946. Agnostidea of the Middle Cambrian of Sweden. Sveriges Geologiska Undersökning [C], 477:1–141.
- WESTROP, S. R. 1992. Upper Cambrian (Marjuman–Steptoean) trilobites from the Port-au-Port Group, western Newfoundland. *Journal of Paleontology*, 66:228–255.
- . 1995. Sunwaptan (Upper Cambrian) from the Rabbitkettle Formation, Mackenzie Mountains, Canada. *Palaeontographica Canadiana* 12, 75 p.
- WHITEHOUSE, F. W. 1936. The Cambrian faunas of north-eastern Australia, parts 1 and 2. *Memoirs of the Queensland Museum*, 11: 59–112.
- . 1939. The Cambrian faunas of north-eastern Australia, parts 3. *Memoirs of the Queensland Museum*, new series 1:179–282.
- WILLIAMS, H. 1975. Structural succession, nomenclature and interpretation of transported rock in western Newfoundland. *Canadian Journal of Earth Sciences*, 12: 1874–1894.
- , AND R. D. HATCHER. 1982. Suspect terranes and accretionary history of the Appalachian orogen. *Geology*, 10: 530–536.
- YOUNG, G. A., AND R. LUDVIGSEN. 1989. Mid-Cambrian trilobites from the lowest part of the Cow Head Group, western Newfoundland. *Geological Survey of Canada Bulletin*, 392, 49 p.
- ZHANG, W. T., AND P. A. JELL. 1987. Cambrian Trilobites of North China—Chinese Cambrian Trilobites Housed in the Smithsonian Institution. Science Press, Beijing, 459 p.

Accepted 11 December 1995

APPENDIX
CHARACTERS USED IN THE PHYLOGENETIC ANALYSIS OF THE
FAMILY PTYCHAGNOSTIDAE

In some analyses, the following characters were ordered: 1, 8, 9, 14, 15, 16, 17.

1. Glabella: 0, outlined completely by axial furrows; 1, axial furrows effaced beyond F3 furrow; 2, axial furrows effaced beyond F2 furrow; 3, axial furrows effaced beyond basal lobes.
2. Preglabellar median furrow (Robison, 1982, p. 135, text-fig. 2): 0, complete; 1, incomplete or absent.
3. Frontal sulcus on glabella (Shergold et al., 1990, p. 12, fig. 2): 0, absent; 1, present.
4. Glabellar F2 furrow (Robison, 1982, p. 134, text-fig. 2): 0, deep to moderate; 1, weak to absent.
5. Appendiferal pit (Öpik, 1979, fig. 45): 0, absent; 1, present.
6. Glabellar spine (Öpik, 1979, fig. 45): 0, absent; 1, present.
7. Posterolateral cephalic spines (Robison, 1982, text-fig. 2): 0, absent; 1, present.
8. Basal lobe shape (Robison, 1982, p. 134, text-fig. 2): 0, simple (short, subtriangular); 1, slightly elongate; 2, strongly elongate.
9. Divided basal lobes (Robison, 1982, p. 134, text-fig. 2): 0, absent; 1, weak furrow; 2, strong furrow.
10. Cephalic axial node position: 0, in front of mid-length of posteroglabella (e.g. Laurie, 1988, fig. 1A–B); 1, between midlength of posteroglabella and anterior tip of basal lobe (e.g. Robison, 1984, Fig. 19.2); 2, opposite tip of basal lobe (e.g. Robison, 1982, pl. 2, figs. 1, 5, 10, 13). Polarity of states is uncertain.
11. Glabellar outline: 0, evenly tapered (e.g. Laurie, 1988, fig. 7A–F); 1, parallel-sided (e.g. Laurie, 1988, fig. 15A–C); 2, anteriorly tapered posteroglabella so that glabella is constricted opposite transglabellar furrow (e.g. Robison, 1984, fig. 29.1, 29.3, 29.4); 3, expanded anteroglabella (e.g. Laurie, 1988, fig. 21A–E, H, M). Polarity of states is uncertain.
12. Posteroglabella width: 0, narrow (< 50 percent cephalic width; e.g. Figure 15.1); wide (50 percent or more of cephalic width; e.g. Figure 18.1, 18.2, 18.6, 18.7). Width was measured at anterior tips of basal lobes.
13. Pygidial axis shape (Robison, 1982, p. 134, text-fig. 2): 0, lanceolate; 2, ogival. The ogival state includes a variety of posteroaxis shapes. However, variation within even a single species can be extensive [e.g. compare pygidial axes assigned to *Ptychagnostus* (s.l.) *atavus* by Robison, 1982, pl. 1, figs. 3–4; Robison, 1984, fig. 11.1e, 11.3; Laurie, 1988, fig. 5E–F] and, consequently, we have not subdivided this state further.
14. Shape of pygidial F1 furrow: 0, subtransverse (e.g. Öpik, 1979, pl. 37); 1, moderately curved forward (e.g. Robison, 1984, fig. 27.2); 2, strongly curved forward (e.g. Figure 17.3–17.5).
15. Shape of pygidial F2 furrow: 0, subtransverse (e.g. Robison, 1978, pl. 1, fig. 11a); 1, weakly deflected medially (e.g. Figure 17.3–17.5); 2, strongly deflected medially (e.g. Figure 15.6–7, 15.10, 15.13, 15.14, 15.19).
16. Inflated lobes on pygidial axis: 0, absent; 1, M2 only; M2 and posteroaxis. In species of *Aotagnostus*, the M2 lobe is inflated (e.g. 1979, pl. 34, figs. 3–4). The M2 lobe is also inflated and strongly convex in *Myrmecomimus* (e.g. Öpik, 1979, pl. 37, fig. 8) and merges posteriorly with an equally inflated posteroaxis.
17. Tubercle on pygidial M2 lobe (Robison, 1982, p. 134, text-fig. 2): 0, small; 1, large; 2, spinose.
18. Axial thoracic spines (e.g. Öpik, 1979, fig. 30, 36): 0, absent; 1, present.
19. Depression on posteroaxis: 0, absent; 1, present behind posteraxis mid-length; 2, present at or in front of posteraxis midlength. Absence of a depression is, by outgroup comparison, plesiomorphic but the polarity of the other two states is uncertain.
20. Posteroaxis length: 0, more than half of total axis length; 1, half or less of total axis length.
21. Postaxial median furrow (Robison, 1982, p. 135, text-fig. 2): 0, complete; 1, incomplete or absent.
22. Posterolateral pygidial spines (Shergold et al., 1990, fig. 2): 0, present; 1, absent.
23. Genal scrobicules (Shergold et al., 1990, p. 15): 0, strong to moderate; 1, weak to absent.
24. Arcuate genal scrobicules (e.g. Laurie, 1989, fig. 3A–B, D, F–H): 0, absent; 1, present.
25. Node on posteraxis (secondary median node of Robison, 1982, text-fig. 2): 0, at tip; 1, near mid-length; 2, at anterior.
26. Prosopon: 0, smooth; 1, granulose or pustulose; 2, coarsely punctate.
27. Cephalic border: 0, moderate to wide; 1, narrow, rim-like (e.g. Robison, 1984, figs. 21.7, 22.2, 23.2, 25.1, 26.2, 26.9).
28. Fulcral thoracic spines (e.g. Öpik, 1979, fig. 54): 0, absent; 1, present.