

THE UNIVERSITY OF KANSAS  
PALEONTOLOGICAL CONTRIBUTIONS

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June 8, 1984

Paper 109

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CAMBRIAN AGNOSTIDA OF NORTH AMERICA  
AND GREENLAND  
PART I, PTYCHAGNOSTIDAE<sup>1</sup>

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*Abstract*—Representatives of the trilobite family Ptychagnostidae are described or further documented from open-shelf lithofacies in North America and Greenland. These include 21 species distributed among the genera *Lejopyge*, *Onymagnostus*, and *Ptychagnostus*. Seventeen of the 21 species have intercontinental distributions and are important for global biostratigraphy. New species from western North America include *Lejopyge acantha*, *Lejopyge rigbyi*, *Ptychagnostus hintzei*, and *Ptychagnostus michaeli*. A new geographic subspecies, *Lejopyge laevigata rubyensis*, also is described.

Five successive interval-zones based on agnostoids are defined for the middle part of the Cambrian System. The base of each zone is defined by a biohorizon corresponding to the first appearance of a single species selected for its abundance and wide geographic distribution within the interval. In ascending order, the species and corresponding zone names are *Ptychagnostus praecurrens*, *P. gibbus*, *P. atavus*, *P. punctuosus*, and *Lejopyge laevigata*. The upper boundary of each zone is defined by the lower boundary of the one overlying it. Additional widespread agnostoid species are present in each zone. These together with the name species give each zone a distinctive character.

As defined here, the *Lejopyge laevigata* Zone is stratigraphically equivalent to the uppermost *Bolaspidella* Zone and much of the *Cedaria* Zone as traditionally used in North America. An informal lower subzone probably has close temporal correlation with the Zone of *Solenopleura brachymetopa* as commonly used in Scandinavia, and an informal upper subzone probably correlates closely with the Zone of *Lejopyge laevigata* as used in Scandinavia. These correlations further support the idea that, in reference to the standard of northwestern Europe, much of the *Cedaria* Zone of North America is Middle rather than Late Cambrian in age. Also, the lower part of the Dresbachian Stage in North America is Middle Cambrian in age.

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<sup>1</sup> Manuscript received January 15, 1984.

ABUNDANCE, wide geographic distribution, and rapid evolution make agnostoid trilobites some of the best indices for global correlation of Cambrian strata. The value of agnostoids for regional biostratigraphy was well demonstrated by A. H. Westergård (1946) in his monograph on the Middle Cambrian agnostoids of Sweden. Subsequent studies (e.g., Pokrovskaya, 1958; Öpik, 1961a, 1979; Robison, 1964, 1976, 1982; Ergaliev, 1980; Egorova and others, 1982) have

documented similar Middle Cambrian agnostoid successions elsewhere in the world. Shergold (1981) has drawn attention to the potential importance of agnostoids in Upper Cambrian biostratigraphy.

This is the first of a planned series of papers documenting the diverse Cambrian agnostoid fauna of North America and Greenland. New information about North American agnostoids is based on several hundred collections of

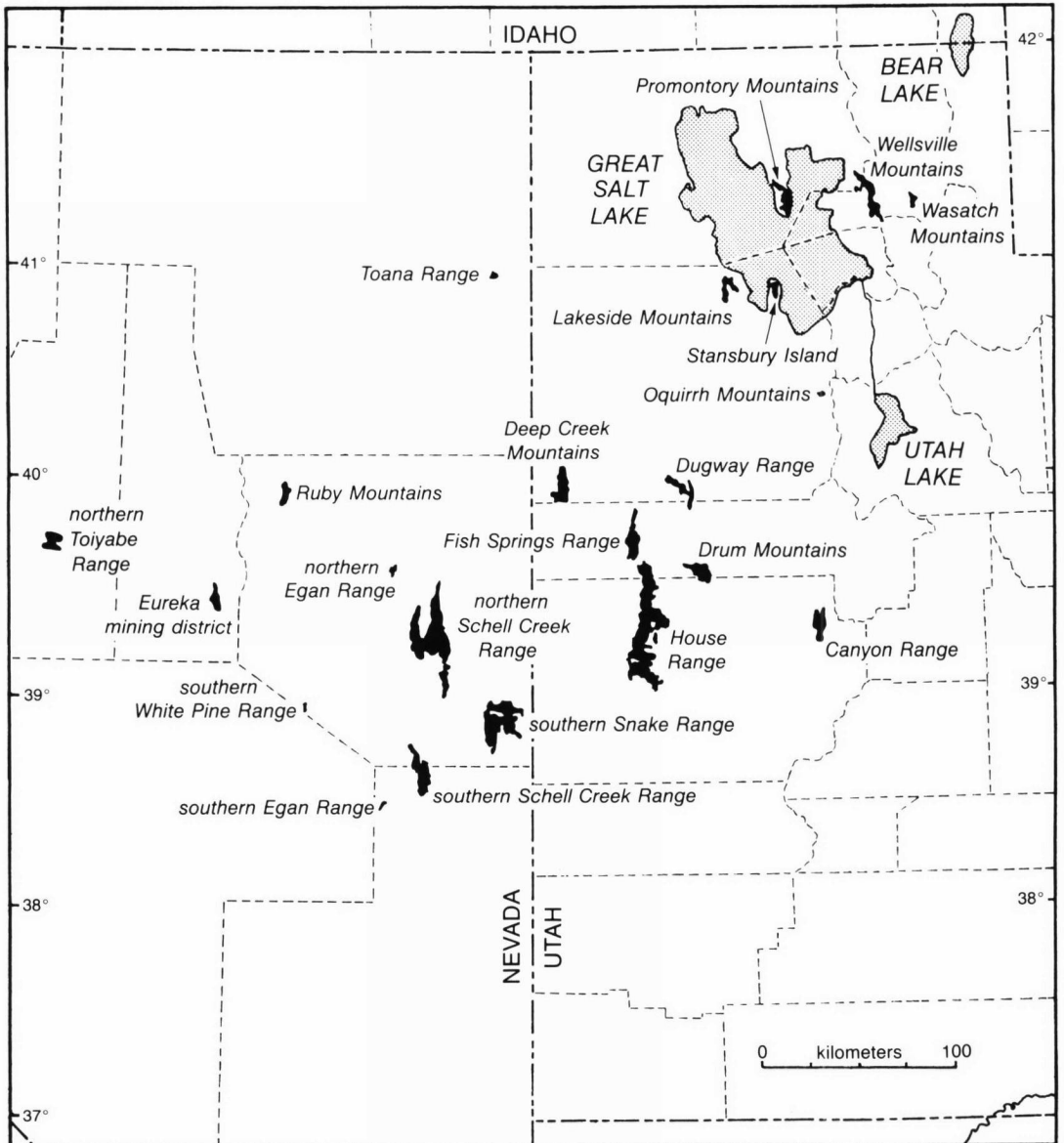


Fig. 1. Map of parts of Nevada and Utah showing outcrops of Cambrian rocks (black) in mountains or ranges mentioned in this paper (after Palmer, 1971).

Cambrian fossils that I have assembled during more than two decades. Most of these collections are from thick, generally well-exposed stratigraphic sections in the Great Basin of Nevada and Utah (Fig. 1). Other significant information has come from about 50 collections of Cambrian fossils from Peary Land in central North Greenland (Fig. 2). These were mostly collected by John S. Peel of the Geological Survey of Greenland. The Survey generously made them available for this study.

A major purpose of this paper is to provide revised or new systematic descriptions for species of one agnostoid family, the Ptychagnostidae. It is treated first because several of its species have been used by researchers around the world as zonal indices in Middle Cambrian rocks. Another purpose is to begin a global zonation based on agnostoids from the middle part of the Cambrian System.

Faunas in exotic terranes that were accreted to North America after the Cambrian Period are not included in this study. These are mainly the so-called "Atlantic province" faunas in such places as the Carolina slate belt (Secor and others, 1983) and the Avalonian terranes in parts of New England and eastern Canada. The most diverse and best documented of these faunas are in southeastern Newfoundland (Hutchinson, 1962).

*Acknowledgments.*—I am indebted to several friends who have generously contributed specimens and information used in this study. Some also have guided me to important localities and others have arranged for the loan of specimens from institutional collections. These include F. J. Collier, W. H. Fritz, Lloyd Gunther, Metta Gunther, Val Gunther, L. F. Hintze, C. H. Kindle, L. B. McCollum, M. B. McCollum, A. R. Palmer, J. S. Peel, R. L. Randolph, M. N. Rees, J. K. Rigby, A. J. Rowell, D. K. Strickland, M. E. Taylor, and W. W. White. The manuscript has been improved by the reviews of Virginia Ashlock, J. B. Jago, Rolf Ludvigsen, and A. J. Rowell. Margery Rowell translated much of the Russian literature that is cited. The illustrations were prepared by R. B. Williams, photographs were printed by Eileen Williams, and manuscript was typed by Jane Priesner. The research was supported most recently by National Science Foundation grants EAR-8024066 and EAR-8218322. For all of this help and support I am most grateful.

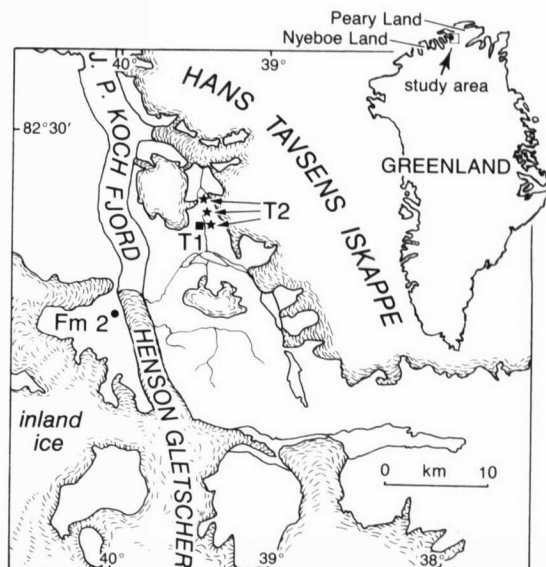


Fig. 2. Map of Henson Gletscher region, central North Greenland, indicating collecting localities (black dot, Formation 2, Brønlund Fjord Group; black square, Formation T1, Tavsens Iskappe Group; black stars, Formation T2, Tavsens Iskappe Group). Margins of permanent ice caps are indicated by broken lines.

## LITHOFACIES AND BIOFACIES

Similarities in patterns of lithofacies and biofacies indicate that Greenland and most of North America were united in a single continent during Cambrian time. Thick and widespread carbonate deposits support paleomagnetic evidence that the continent was in equatorial latitudes (e.g., Bambach and others, 1980). Lithofacies show that the craton was encircled by a broad marine shelf with shallow-water, carbonate platform deposits of variable extent (Palmer, 1973; Robison, 1976). The platform carbonates were flanked by lagoonal muds and nearshore sands on one side and by outer-shelf muds on the other side.

Two almost mutually exclusive biofacies are common in Middle Cambrian rocks of North America. Evidently the faunas were separated by salinity and temperature barriers on the shallow carbonate platforms. An inner, restricted-shelf biofacies is found in limestone, shale, and sandstone. Generally it is characterized by sparse, low-diversity, endemic, polymeroid faunules. Agnostoids are almost unknown in this inner biofacies. An outer, open-shelf biofacies found mostly in limestone and shale is characterized by common to abun-

dant, high-diversity, mixed polymeroid and agnostoid faunas. Fossils are usually most abundant near the seaward margin of the carbonate lithofacies. Polymeroid genera in the

open-shelf biofacies are widely distributed around the continent, but most lack intercontinental distribution. Agnostoid taxa also are widely distributed around the continent, but

	Agnostoid Zones	NEVADA					UTAH		
		Eureka mining district 1	northern Egan Range 2	northern Schell Creek Range 3	Snake Range 4	s. Egan & s. Schell Cr. ranges 5	central House Range 6	Deep Creek, Fish Sp., & Drum mtns. 7	
MIDDLE CAMBRIAN	<i>laevigata</i>	Hamburg Dolomite	Hamburg Formation	Lincoln Peak Formation	upper shale member	Lincoln Peak Formation	Emigrant Springs Limestone	Orr Formation	Lamb Dolomite
								Weeks Limestone	
	<i>punctuosus</i>	Secret Canyon Shale	Secret Canyon Formation	Lincoln Peak Formation	lower shale member	Lincoln Peak Formation	Patterson Pass Shale	Marjum Formation	Trippe Limestone
								Wheeler Formation	Pierson Cove Formation
	<i>atavus</i>	Geddes Limestone	Secret Canyon Formation	Lincoln Peak Formation	lower shale member	Lincoln Peak Formation	Patterson Pass Shale	Wheeler Formation	Wheeler Formation
<i>gibbus</i>							Swasey Limestone	Swasey Limestone	
<i>praecurrens</i>	Eldorado Dolomite	Eldorado Formation	Pole Canyon Limestone	Pole Canyon Limestone	Pole Canyon Limestone	Pole Canyon Limestone			

Fig. 3. Correlation chart for some Cambrian units in Nevada and Utah. Sources for stratigraphic nomenclature are: 1, Nolan, Merriam, and Williams, 1956; 2, Fritz, 1968; 3, Drewes, 1967; 4, Drewes and Palmer, 1957; 5, Kellogg, 1963; 6 and 7, Hintze and Robison, 1975. Dashed lines indicate uncertain chronocorrelation for some boundaries.

most of the genera and many species have intercontinental distributions. Regional agnostoid subfacies within the open-shelf biofacies (Jago, 1973; Robison, 1975) indicate influences from other ecological controls that are difficult to identify.

Fossils recorded here are from several formations representing open-shelf environments. A correlation of relevant stratigraphic units in Nevada and Utah is shown in Figure 3. General discussions of geologic setting and stratigraphy have been given by Palmer (1971), Hintze (1973), Hintze and Robison (1975), and Stewart (1980). Agnostoid-bearing sections in North Greenland have been divided into unnamed formations that have been discussed by Peel (1979, 1982), Palmer and Peel (1979), and Ineson and Peel (1980).

### BIOSTRATIGRAPHY

Most agnostoid trilobites were probably pelagic (Robison, 1972b), whereas most polymeroid trilobites were probably benthic. Significantly different observed geographic and stratigraphic distribution patterns are in accord with these inferred environmental adaptations. Therefore, it is desirable to establish separate sets of agnostoid and polymeroid zones (Robison, 1976).

Biozonal divisions of Cambrian strata generally have been intended only for regional, or at most continental application. Now sufficient data on widespread agnostoid faunas are available to make possible a global agnostoid zonation of open-shelf lithofacies in the middle part of the Cambrian System. A succession of five interval-zones here are defined. Preliminary descriptions of the lowest three zones were previously published (Robison, 1982:132-133). The base of each zone is defined by a biohorizon corresponding to the first appearance of a single species selected for its abundance and wide geographic distribution. In ascending order, these species and corresponding zone names are *Ptychagnostus praecurrens*, *P. gibbus*, *P. atavus*, *P. punctuosus*, and *Lejopyge laevigata*. The upper boundary of each zone is defined by the lower boundary of the one overlying it. Additional widespread agnostoid species are present in each zone. These together with the name species give each zone a distinctive character.

Individual species are not necessarily restricted to any one zone.

Brief discussions of each zone follow. Stratigraphic distributions of North American ptychagnostid species are shown in Figure 4. Distributions in North Greenland are shown in Figure 5. Detailed discussions of biostratigraphy and intercontinental stratigraphic correlations are deferred pending review or description of other important agnostoid taxa.

#### *Ptychagnostus praecurrens* Interval-zone

Lower and upper boundaries of the *P. praecurrens* Zone are defined by the first appearances of *P. praecurrens* and *P. gibbus*, respectively. Diversity of agnostoid species is low in the zone. In North America, *P. praecurrens* (= *P. burgessensis*) is known only from 21 m of the Stephen Formation in British Columbia, where it is associated with *Peronopsis columbiensis* and *Peronopsis montis* (Fritz, 1971). Representatives of the zone are not known from Greenland. In parts of Europe, Asia, and Australia, *Peronopsis fallax* is associated with *P. praecurrens* in the zone. Partly because of the few agnostoid species and partly because of significant areal restriction of favorable biofacies, this biozone is much less widely identifiable than others described here.

#### *Ptychagnostus gibbus* Interval-zone

Lower and upper boundaries of the *P. gibbus* Zone are defined by the first appearances of *P. gibbus* and *P. atavus*, respectively. Globally, the base of the zone commonly coincides with an unconformity or an abrupt lithofacies change, possibly related to a eustatic rise in sea level.

Twenty-two agnostoid species from the *P. gibbus* Zone in several countries have been listed by Rowell, Robison, and Strickland (1982, table 1). Among the more widespread and common of these are *Onymagnostus seminula*, *Peronopsis fallax*, *Peronopsis scutalis*, *Ptychagnostus gibbus*, *Ptychagnostus intermedius*, and *Tomagnostus fissus*.

In western North America, the *P. gibbus* Zone commonly includes *Doryagnostus wasatchensis*, *Onymagnostus seminula*, *Peronopsis amplaxis* (lower part), *Peronopsis fallax*, *Peronopsis gaspensis* (lower part), *Peronopsis interstricta*, *Peronopsis montis* (lower part), *Peronopsis segmenta* (middle

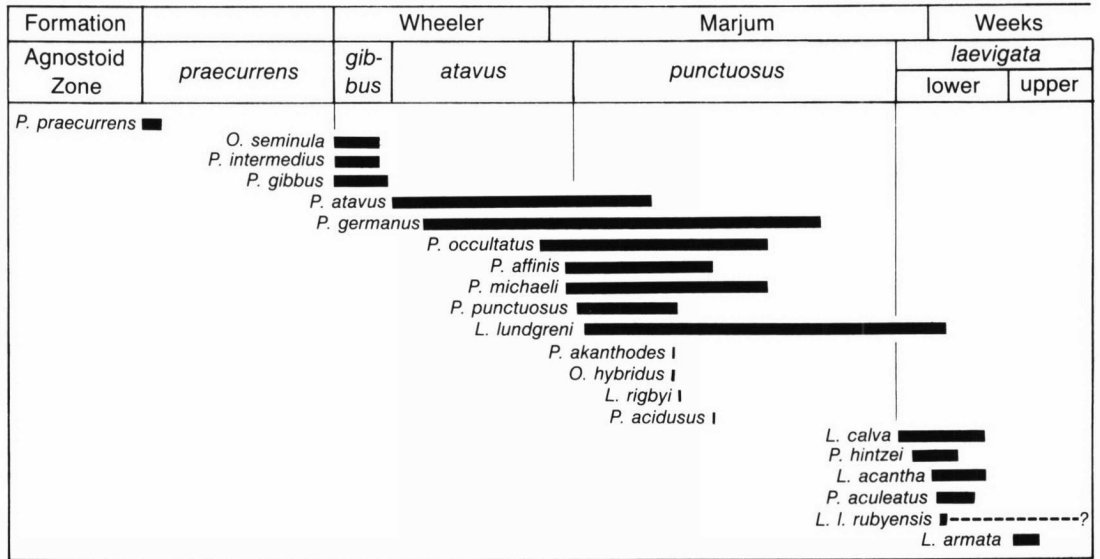


Fig. 4. Composite stratigraphic ranges of species of *Lejopyge*, *Onymagnostus*, and *Ptychagnostus* known from western North America. Thicknesses of formations in the House Range, Utah, are used as a standard.

and upper parts), *Ptychagnostus gibbus*, and *Ptychagnostus intermedius* (Robison, 1978, 1982). This assemblage is widespread in basal parts of the Geddes, Lincoln Peak, and Wheeler formations of Nevada and Utah (Fig. 3). The zone is especially well developed in the basal 70 m of the Wheeler Formation in the Drum Mountains of west-central Utah (Fig. 1; for discussion and illustrations, see Rowell, Robison, and Strickland, 1982). Characteristic species of the zone also are present in the 'black band' of the Eldon Formation in British Columbia (see Fritz, 1971, fig. 2) and the basal Meagher Formation in Montana.

Faunas of the *P. gibbus* Zone are known from only isolated localities in eastern North America. Some of the best preserved specimens are from the Taconic sequence of eastern New York (Rasetti, 1967; Bird and Rasetti, 1968). Other well-preserved specimens are in C. H. Kindle collections 362, 378, 380, 409, and 420 from boulders of Cow Head Conglomerate in western Newfoundland (see Kindle, 1981, 1982).

In North Greenland, faunas of the *P. gibbus* Zone are present in the upper half of Formation 2 of the Brønlund Fjord Group (Fig. 5). Among the agnostoid species are *Onymagnostus seminula*, *Peronopsis amplaxis*, *Peronopsis fallax*, *Peronopsis*

*gaspensis*, *Peronopsis interstricta*, *Ptychagnostus gibbus*, *Ptychagnostus intermedius*, and *Tomagnostus* sp.

The *P. gibbus* Zone as defined here probably is a close temporal correlative of the Zone of *P. gibbus* as used by Westergård (1946) in Sweden.

#### ***Ptychagnostus atavus* Interval-zone**

Lower and upper boundaries of the *P. atavus* Zone are defined by the first appearances of *P. atavus* and *P. punctuosus*, respectively. From analysis by Rowell, Robison, and Strickland (1982), chronocorrelation of the lower boundary of this zone appears to be as precise as for any known in the Cambrian System.

Thirty-five agnostoid species from the *P. atavus* Zone in several countries have been listed by Rowell, Robison, and Strickland (1982, table 2). Among the more widespread and common of these are *Hypagnostus parvifrons*, *Peronopsis fallax*, *Peronopsis ferox*, *Peronopsis scutalis*, *Ptychagnostus atavus*, *Ptychagnostus germanus*, *Ptychagnostus occultatus*, *Tomagnostus fissus*, and *Tomagnostus perrugatus*.

In western North America, the *P. atavus* Zone commonly includes *Baltagnostus euryptyx* (upper part), *Hypagnostus parvifrons*, *Peronopsis fallax* (lower part), *Peronopsis ferox* (upper part), *Peronopsis interstricta*, *Peronopsis segmenta*, *Ptychag-*

Group	Brønlund Fjord			Tavsens Iskappe		
Formation	2	3	4	T1	T2	T3
Agnostoid Zone	gibbus			punctuosus	laevigata upper	

Fig. 5. Observed stratigraphic ranges of species of *Lejopyge*, *Onymagnostus*, and *Ptychagnostus* in Peary Land, central North Greenland.

*agnostus atavus*, *Ptychagnostus germanus*, and *Ptychagnostus occultatus* (upper part). These species are especially common in the middle and upper Wheeler and lower Marjum formations of west-central Utah. Some also are present in parts of the Geddes, Lincoln Peak, and equivalent units in Nevada.

Agnostoids of the *P. atavus* Zone are rare in eastern North America. A few specimens are present in boulders of Cow Head Conglomerate in western Newfoundland (Kindle, 1981, 1982). Also, some agnostoids in conglomeratic boulders of the Levis Formation of southeastern Quebec (Rasetti, 1948) may represent the zone.

Agnostoid trilobites of the *P. atavus* Zone are not known from Greenland. Lithofacies (Ineson and Peel, 1980) of the biochron indicate restricted-shelf conditions that probably were unfavorable for agnostoids.

As defined here, the *P. atavus* Zone probably has close temporal correlation with Westergård's (1946) Zone of *Tomagnostus fissus* and *Ptychagnostus atavus* as well as his Zone of *Hypagnostus parvifrons* in Sweden. *P. atavus* and *H. parvifrons* first appear at nearly the same stratigraphic horizons in both Sweden and Utah. According to Westergård's range charts (1946: 98-103), the Zone of *H. parvifrons* in Sweden does not include a single distinctive species. Evidently, identification of that zone was based on local abundance of *H. parvifrons*.

#### ***Ptychagnostus punctuosus* Interval-zone**

Lower and upper boundaries of the *P. punctuosus* Zone are defined by the first appearances of *P. punctuosus* and *Lejopyge laevigata*, respectively. Globally, more than 60 agnostoid species have been reported from this interval.

Among the more widespread and common of these are *Cotalagnostus lens*, *Doryagnostus incertus*, *Goniagnostus nathorsti* (upper part), *Hypagnostus mammillatus*, *Hypagnostus parvifrons*, *Iniospheniscus talis*, *Lejopyge lundgreni*, *Onymagnostus hybridus*, *Peronopsis ferox*, *Pseudoperonopsis perplexus*, *Ptychagnostus acidusus*, *Ptychagnostus affinis*, *Ptychagnostus atavus* (lower part), *Ptychagnostus germanus*, *Ptychagnostus occultatus*, *Ptychagnostus punctuosus*, and *Tomagnostus ferrugatus*. As agnostoid faunas become better documented, subdivision of this interval probably will be warranted.

In western North America, the *P. punctuosus* Zone contains *Baltagnostus eurypyx*, *Cotalagnostus laevus*, *Hypagnostus parvifrons*, *Iniospheniscus talis*, *Lejopyge lundgreni*, *Lejopyge rigbyi*, *Onymagnostus hybridus*, *Peronopsis ferox*, *Peronopsis? incertus*, *Peronopsis interstricta*, *Peronopsis segmenta*, *Pseudoperonopsis perplexus*, *Ptychagnostus affinis*, *Ptychagnostus akanthodes*, *Ptychagnostus atavus*, *Ptychagnostus germanus*, *Ptychagnostus michaeli*, *Ptychagnostus occultatus*, *Ptychagnostus punctuosus*, and *Utagnostus trispinulus*. Agnostoids of this zone are common in the Marjum Formation of the House Range in western Utah. Generally, they are sparse in coeval parts of the Lincoln Peak, Patterson Pass, and Secret Canyon formations in Nevada.

Only a single locality in the eastern part of Cambrian North America has yielded a diverse, well-preserved fauna of the *P. punctuosus* Zone. This is the Stockport Station locality of Rasetti (1967) and Bird and Rasetti (1968) in the Taconic sequence of eastern New York. From three meters of exposed strata at that locality Rasetti described 21 species of trilobites, including 7 agnostoids.

In North Greenland, rich faunas of the *P.*

*punctuosus* Zone are present in the middle part of Formation T1 of the Tavsens Iskappe Group. Agnostoid species include *Baltagnostus eurypyx*, *Hypagnostus parivfrons*, *Onymagnostus hybridus*, *Peronopsis ferox*, and *Ptychagnostus occultatus*.

As defined here, the *P. punctuosus* Zone probably has close temporal correlation with Westergård's (1946) Zone of *Ptychagnostus punctuosus* as well as his Zone of *Ptychagnostus lundgreni* and *Goniagnostus nathorsti*.

### Lejopyge laevigata Interval-zone

The lower boundary of the *L. laevigata* Zone is defined by the first appearance of *L. laevigata*. Pending further study, the upper boundary is provisionally defined by the first appearance of *Aspidagnostus*. Globally, more than 50 agnostoid species have been described from this interval; however, many of these are in need of further documentation, and several synonyms appear to be included.

Such species as *Lejopyge armata*, *L. laevigata*, and *Diplagnostus planicauda* (*s. l.*) are widespread and range throughout most of the *L. laevigata* Zone. Several other widespread species seem to be mostly confined to either lower or upper parts of the zone. Therefore, I provisionally divide the zone into informal lower and upper subzones. With further documentation, these probably will warrant definition as formal zones. Among other widespread species in the lower subzone are *Agnostus neglectus*, *Clavagnostus repandus* (*s. l.*), *Goniagnostus nathorsti*, *Lejopyge calva*, *Lejopyge lundgreni*, *Peronopsis ferox*, *Phalagnostus bituberculatus*, and *Ptychagnostus aculeatus*. Other widespread species in the upper subzone include *Agnostus pisiformis*, *Clavagnostus sulcatus* (*s. l.*), *Goniagnostus spiniger*, *Hypagnostus sulcifer*, *Kormagnostus simplex*, *Oidagnostus trispinifer*, and *Triadaspis bigeneris*. Representatives of *Acmahachis* (= *Cyclagnostus*), *Agnostascus*, and *Connagnostus* are widespread in the upper subzone, but taxonomic concepts need review.

The lower *L. laevigata* subzone is stratigraphically equivalent to the *L. calva* Zone as used regionally in parts of Nevada and Utah (e.g., Robison, 1964, 1976). There *L. calva* is present in great abundance at many localities. Less common associated agnostoids include *Agnostus* aff. *A. neglectus*, *Baltagnostus eurypyx*, *Clavagnostus repandus* (*s. l.*), *Diplagnostus planicauda* (*s. l.*), *Hypagnostus* sp., *Kormagnostus se-*

*clusus*, *Lejopyge acantha*, *Lejopyge lundgreni*, *Peronopsis ferox*, *Ptychagnostus aculeatus*, *Ptychagnostus hintzei*, and *Utagnostus trispinulus*. In more seaward lithofacies of central Nevada, *L. calva* is replaced by *L. laevigata rubyensis*. Landward, in shallower water carbonates, agnostoids generally become less common and mainly include species of *Baltagnostus*, *Kormagnostus*, and *Peronopsis*. The best North American reference section for the lower subzone is the upper Marjum and lower Weeks formations in the vicinity of Marjum Pass in the House Range, Utah (Fig. 1). Elsewhere in western North America, Palmer (1968) has described *Phalagnostus bituberculatus* in association with *L. calva* and *P. aculeatus* in Alaska.

Because of areal reduction of favorable lithofacies, the upper *L. laevigata* subzone in Nevada and Utah is known from fewer localities than the lower subzone. Among the more commonly encountered agnostoids are *Acmahachis* sp., *Agnostascus* sp., *Clavagnostus sulcatus* (*s. l.*), *Connagnostus* sp., *Kormagnostus simplex*, *Lejopyge armata*, and *Triadaspis bigeneris*. Although the section is not well exposed, the best known North American development of the upper subzone is in the upper shale member of the Lincoln Peak Formation near Cleve Creek in the northern Schell Creek Range, Nevada (Fig. 1). One collection from this section also contains probable representatives of *L. laevigata rubyensis*.

The *Lejopyge laevigata* Zone in North Greenland is represented by only faunas of the upper subzone, which range throughout Formation T2 of the Tavsens Iskappe Group. Among diverse trilobite faunas in several collections are *Acmahachis* sp., *Agnostus* aff. *A. pisiformis*, *Connagnostus* sp., *Diplagnostus planicauda* (*s. l.*), *Hypagnostus sulcifer*, *Kormagnostus simplex*, *Lejopyge armata*, *Lejopyge laevigata*, *Oidagnostus trispinifer*, and *Triadaspis bigeneris*. The many species of associated polymeroid trilobites include representatives of *Bolaspidella*, *Cedaria*, and *Elrathia*.

As defined here, the *Lejopyge laevigata* Zone is stratigraphically equivalent to the uppermost *Bolaspidella* Zone and much of the *Cedaria* Zone as traditionally used in North America (e.g., Lochman-Balk and Wilson, 1958; Robison, 1964). Also, the lower subzone probably has close temporal correlation with Westergård's



(1946) Zone of *Solenopleura brachymetopa* in Sweden, and the upper subzone probably correlates closely with his Zone of *Lejopyge laevigata*. These correlations support the conclusion of Daily and Jago (1975) that, in reference to the stand-

ard of northwestern Europe, much of the *Cedaria* Zone of North America is Middle rather than Late Cambrian in age. Also, the lower part of the Dresbachian Stage in North America is Middle Cambrian in age.

## SYSTEMATIC PALEONTOLOGY

*Depositories.*—Materials used in this study are identified by either specimen or collection numbers that may be combined with depository abbreviations. These are: Geological Survey of Canada, GSC; Geological Survey of Greenland (Grønlands Geologiske Undersøgelse), GGU; Geologisk Museum (formerly Mineralogisk Museum), Copenhagen, MGUH; U. S. Geological Survey—Cambrian and Ordovician collections, CO; U. S. National Museum of Natural History, USNM; and University of Kansas Museum of Invertebrate Paleontology, KUMIP.

Material identified by three-digit numbers only is from my research collections. These are at the University of Kansas, where a locality description for each collection is listed in the locality file of the Museum of Invertebrate Paleontology.

Materials identified by initials and numbers were collected by M. N. Rees (MNR), A. J. Rowell and M. N. Rees (RR), and D. K. Strickland (DKS). These collections are in the University of Kansas Museum of Invertebrate Paleontology, where localities are recorded.

The C. H. Kindle collections from the Cow Head Conglomerate of western Newfoundland, cited herein, have been accessioned by the Geological Survey of Canada in Ottawa (Kindle, 1982).

*Terminology.*—Many morphological terms used in this paper are defined in the *Treatise on Invertebrate Paleontology* (Harrington, Moore, and Stubblefield, 1959). Other terms have been defined by Robison (1964, 1982) or Öpik (1967).

Phylum ARTHROPODA Siebold  
and Stannius, 1845

Class TRILOBITA Walch, 1771

Order AGNOSTIDA Kobayashi, 1935

[*nom. transl.* MOORE, 1959, p. O172, *ex suborder* Agnostida  
KOBAYASHI, 1935, p. 81]

*Diagnosis.*—Trilobites having basal lobes on cephalon, no articulating half ring on anterior thoracic segment, and no overlap between cephalon and thorax; labrum having unusually long anterior and posterior wings; thorax having two segments.

*Remarks.*—The order Agnostida includes small, eyeless, isopygous trilobites that lack facial sutures and possess only two thoracic segments in the holaspid stage. Development of a unique hinge line without overlap between the cephalon and thorax (Robison, 1964:515) was accompanied by transformation of the occipital ring into a lateral pair of triangular basal lobes and by loss of the articulating half ring on the anterior thoracic segment. The labrum, with two pairs of long, slender wings, resembles a long-legged stool (Robison, 1972a). All evidence of segmentation is effaced from pleural regions of the pygidium.

From a review of morphologic, paleoecologic, and biogeographic evidence, I previously concluded that most agnostoids were probably adapted for a pelagic lifestyle (Robison, 1972b). Recently, Fortey and Barnes (1977:306) noted that Early Ordovician agnostoids in Spitsbergen “seem to be related in occurrence to benthic communities..., and, therefore, a pelagic habitat does not seem probable for this group...” Those Spitsbergen agnostoids were

subsequently assigned by Fortey (1980) to one new species of *Micragnostus* and two new subspecies of *Arthrorhachis danica* (Poulsen). Although the three taxa of Spitsbergen agnostoids seem to be related in occurrence to benthic communities, numerous agnostoid species are not. Many agnostoid species, including several discussed here, have intercontinental distributions and each is associated with multiple polymoroid assemblages. Moreover, instances of positive correlation between agnostoid species and matrix lithology may be reflecting such factors as water chemistry, nutrients, or temperature in the general habitat rather than a relationship between an agnostoid species and a substrate condition.

### Family PTYCHAGNOSTIDAE Kobayashi, 1939

[*nom. transl.* herein, ex *Ptychagnostinae* KOBAYASHI, 1939, p. 151 (for nomenclatural history, see Öpik, 1967, p. 90)]

*Diagnosis.*—Agnostoids having preglabellar median furrow. Cephalic axis conical; unequally divided by transglabellar (F3) furrow, length of posteroglabella about twice that of anteroglabella. Pygidial axis subconical with slight lateral constriction at M2, not reaching posterior border furrow; divided by two transaxial furrows (F1, F2). Border furrows of exoskeleton narrow. Cephalic border narrow, pygidial border usually of moderate width. Furrows on cephalic and pygidial acrolobes secondarily effaced in some lineages, resulting in multiple smooth homeomorphs.

*Discussion.*—Except in secondarily effaced species, representatives of the Ptychagnostidae typically possess a preglabellar median furrow that is fairly uniform in depth and width throughout its course. The cephalic and pygidial axes are typically conical; however, lateral sides of the posteroglabella are subparallel in early species of *Ptychagnostus* Jaekel (1909) and *Onymagnostus* Öpik (1979), and the pygidial axis is considerably modified in *Myrmecomimus* Öpik (1979). A postaxial median furrow is present in the ancestral species, *Ptychagnostus praecurrens* (Westergård), and is retained in many later species. In some groups, particularly in *Onymagnostus* and in those species with pronounced effacement of other furrows, the postaxial median furrow may disappear, at least during the holaspide period. Evolution of

nodes, tubercles, spines, genal scrobicules, and surface granulation is variable.

Several genera have been defined using one or more characters derived during evolution of the ptychagnostid complex. *Lejopyge* Corda (in Hawle and Corda, 1847) was defined prior to *Ptychagnostus* and traditionally has included species characterized by extreme effacement of dorsal furrows. Other commonly used names are *Triplagnostus* Howell (1935) and *Goniagnostus* Howell (1935). Concepts of these genera, particularly that of *Goniagnostus*, have been modified by subsequent authors. In 1979, Öpik divided ptychagnostid species among 10 previously defined or new genera. At the same time, he further modified the concepts of some previously defined genera. *Goniagnostus* was revised to include species with a medial spine on the posterior glabella and *Lejopyge* was revised to include some species with well-developed dorsal furrows.

Although the complex of ptychagnostid species could be consolidated under one generic name (*Lejopyge* having priority), I prefer to assign major evolutionary lineages to separate genera. Some generic diagnoses are difficult to write, however, because homeomorphy is common.

As defined here, the Ptychagnostidae is a monophyletic family that includes *Ptychagnostus praecurrens* and all of its descendant species (Fig. 6). The family is divided into genera representing inferred monophyletic subgroups. As revised here, *Ptychagnostus* is paraphyletic and *Onymagnostus*, *Lejopyge*, *Goniagnostus*, and *Myrmecomimus* are holophyletic, each genus representing a phyletic branch arising from a different species of *Ptychagnostus*. In general, these taxonomic subdivisions parallel those of Öpik (1979); however, I prefer to recognize fewer genera.

Representatives of *Doryagnostus* are close homeomorphs of some ptychagnostids (Robison, 1978). Much of the similarity in morphology was inherited from two similar species of *Peronopsis* that independently evolved a preglabellar median furrow. *Peronopsis brighamensis* (Resser) appears to be the immediate ancestor of *Ptychagnostus praecurrens* (Westergård), and *Peronopsis gaspensis* Rasetti of *Doryagnostus wasatchensis* Robison. Axial shape in early species of *Ptychagnostus* and *Doryagnostus* is quite

similar, but other inherited characters are diagnostic. On the pygidium, *P. praecurrens* has two moderately developed transaxial furrows (F1, F2), a small median tubercle on the second axial segment (M2), and a smooth border. In contrast, the pygidium in *D. wasatchensis* has nearly effaced transaxial furrows, a median node on the second segment, and a pair of short posterolateral spines on the border.

The Ptychagnostidae have an observed stratigraphic range from the lower Middle

Cambrian (*Ptychagnostus praecurrens* Zone) to the top of the Middle Cambrian (top of *Lejopyge laevigata* Zone). Geographically, *Ptychagnostus*, *Onymagnostus*, and *Lejopyge* are cosmopolitan in open-shelf lithofacies. *Goniagnostus* (*sensu* Öpik, 1979) is common in parts of Europe, Asia, and Australia, but in North America is known from only an Avalonian terrane in New Brunswick (Howell, 1935). *Myrmecomimus* is a highly evolved genus that seems to be endemic to Australia.

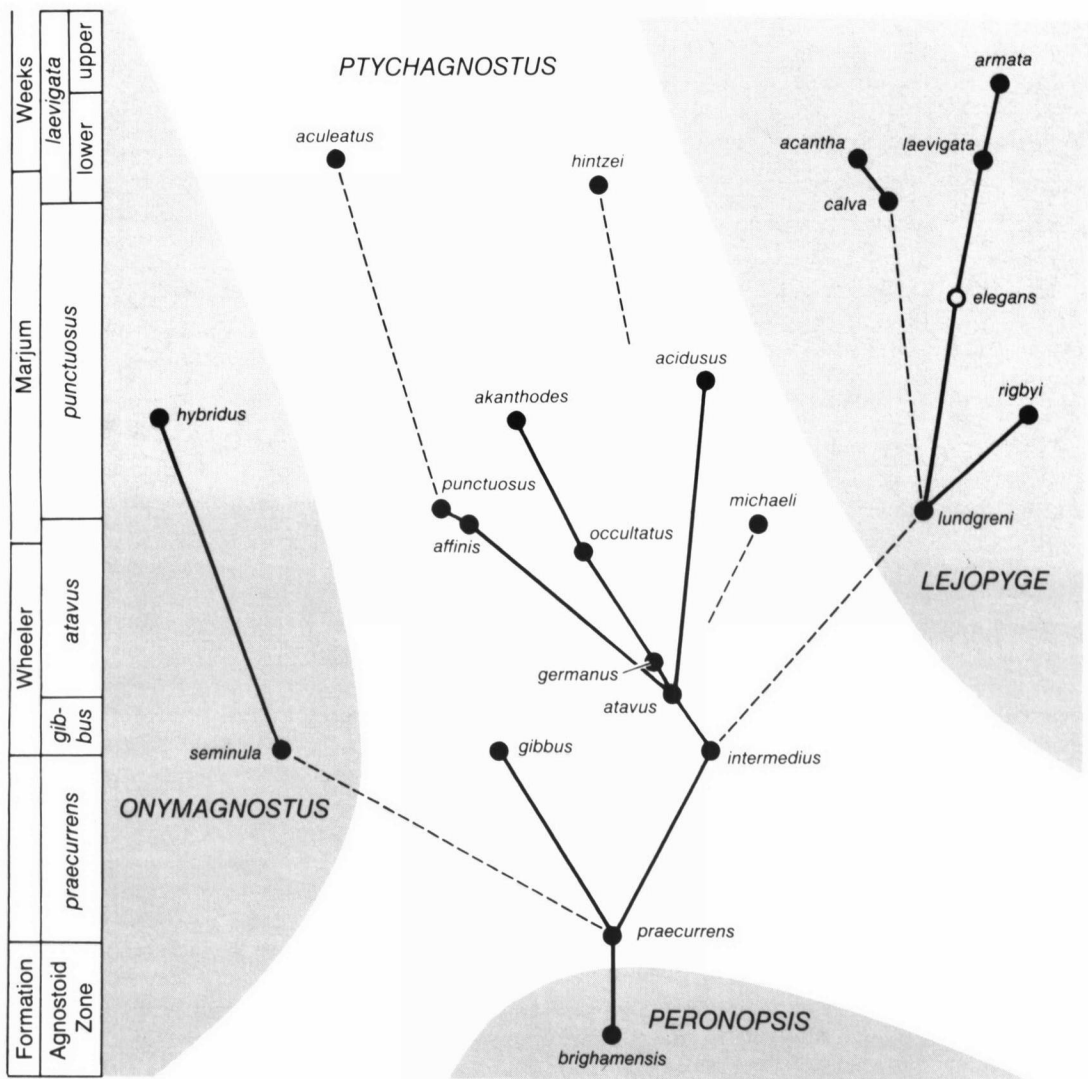


Fig. 6. Diagram of inferred phylogeny of some genera and species of Ptychagnostidae. Except for *Lejopyge elegans* (open dot), all species are known from North America or North America and Greenland. Solid dots are at observed first appearances of species within interval zones. Dashed lines indicate uncertain relationship.

### Genus PTYCHAGNOSTUS Jaekel

- Ptychagnostus* JAEKEL, 1909, p. 400 and 401; KOBAYASHI, 1939, p. 152-153; SHIMER and SHROCK, 1944, p. 600; WESTERGÅRD, 1946, p. 67-69; PALMER, 1954, p. 60; 1968, p. B28; ŠNAJDR, 1958, p. 70; HOWELL, 1959, p. O178; POKROVSKAYA in Tchernysheva, 1960, p. 58; ÖPIK, 1961a, p. 76-77; 1979, p. 88-89; ROBISON, 1964, p. 522-523; 1982, p. 135-136; LU and others, 1965, p. 37; RUSHTON, 1966, p. 35; 1978, p. 261; 1979, p. 53; JAGO, 1976a, p. 150-152; YIN, 1978, p. 387.
- Triplagnostus* HOWELL, 1935, p. 14; 1959, p. O179; KOBAYASHI, 1939, p. 145-148; LERMONTOVA, 1940, p. 127; SHIMER and SHROCK, 1944, p. 600; POKROVSKAYA in Tchernysheva, 1960, p. 58; ÖPIK, 1979, p. 115-117.
- Solenagnostus* WHITEHOUSE, 1936, p. 86.
- Pentagnostus* LERMONTOVA, 1940, p. 127; HOWELL, 1959, p. O185-O186; ÖPIK, 1967, p. 77-78; 1979, p. 139-140.
- Huaragnostus* RUSCONI, 1950, p. 92.
- Canolagnostus* RUSCONI, 1951, p. 13-14.
- Zetagnostus* ÖPIK, 1979, p. 105.
- Aotagnostus* ÖPIK, 1979, p. 128-129.

*Type species.*—*Agnostus punctuosus* Angelin, 1851:8; by original designation.

Apparently because of an error in type assembly, Jaekel's (1909) short original description of *Ptychagnostus* (top, p. 401) is separated from the brief generic discussion and the designation of "*A. punctuosus* Angelin" as "typus" (top, p. 400). The discussion and type species designation are included in a section on the family Agnostidae, but the generic description is misplaced in a section on the new family Leiagnostidae. Jaekel's inclusion of an illustration of "*Ptychagnostus reticulatus*" with those of other agnostoids indicates that he considered *Ptychagnostus* a member of that family rather than of the Leiagnostidae. Vogdes (1917:44) continued the error by listing *Ptychagnostus* as a member of the Leiagnostidae and he incorrectly listed "*A. reticulatus* Ang." as the type of *Ptychagnostus*. Although the species name was misspelled, Vogdes (1925:111) subsequently listed *A. punctuosus* as the "genotype" of *Ptychagnostus*. In 1959, Howell (p. O179) also listed *A. punctuosus* as the type species of *Ptychag-*

*nostus* but he incorrectly stated that it was established by subsequent designation of Vogdes (1925).

*Diagnosis.*—Ptychagnostids having elongate basal lobes. Axis moderately separated from anterior and posterior borders. Postaxial median furrow present.

*Description.*—Anteroglabella commonly subtriangular, entire or with rare anteromedian cleft. Posteroglabella variable in form, anterolateral sides subparallel to anteriorly convergent, back end rounded and constricted between basal lobes; median node variable in position and probably not homologous in some species. Basal lobes elongate, entire or divided. Genae smooth to strongly scrobiculate or coarsely granulose, or both. Cephalic border may possess pair of posterolateral spines. Thorax unmodified or with median spine on posterior segment. Pygidial axis moderately separated from posterior border furrow; M2 commonly hexagonal, rarely pentagonal or subrectangular. Median node, tubercle, or spine on posterior part of M2; secondary median nodes may be midway along or at tip of posteroaxis. Pleural fields commonly smooth, rarely granulose. Postaxial median furrow usually present throughout ontogeny, rarely becoming effaced in late holaspides. Pygidial border slightly wider than cephalic border, smooth or with pair of posterolateral swellings or spines.

*Remarks.*—Development of nodes, tubercles, spines, genal scrobicules, and surface granulation is highly variable within *Ptychagnostus*.

The origin, some aspects of evolution, and synonyms of *Ptychagnostus* have been recently discussed (Robison, 1982:135-136). As revised here, the concept of *Ptychagnostus* is restricted by reassignment of some species to *Onymagnostus* (as revised herein), *Goniagnostus* (*sensu* Öpik, 1979), and *Lejopyge* (as revised herein).

*Occurrence.*—*Ptychagnostus* has been reported from all continents except Africa. In North America it ranges through nearly the upper two-thirds of the Middle Cambrian (*P. praecurrens* Zone through lower *L. laevigata* subzone). The ancestral species is *P. praecurrens* and the youngest species probably is *P. aculeatus*. *Ptychagnostus?* *serus* Öpik (1967), from the lower Upper Cambrian of Australia, is based on a

single juvenile cephalon that probably represents *Glyptagnostus*.

### PTYCHAGNOSTUS ACIDUSUS ÖPIK

Figure 7

*Ptychagnostus (Acidusus) acidusus* ÖPIK, 1979:100-101, pl. 46, figs. 2-4.

*Diagnosis.*—Cephalon subquadrate. Axis moderately tapered forward. F1 undeveloped, F2 moderately developed adjacent to axial furrows. Median node behind midpoint of post-eroglabella. Basal lobes elongate and entire. Scrobicules well developed on late holaspisid genae, but depth irregular along individual furrows; weak, longitudinally directed, sub-crescentic pair usually opposite F2. Posterolateral border lacking spines, but fulcral points prominent. Thorax nonspinose; anterior segment having weak, median axial node. Pygidium semicircular. Axial F1 deepest about midway between sagittal line and axial furrows. M2 well defined, hexagonal; large, reclined, median tubercle at posterior margin. Posteroaxis ogival; bearing terminal, secondary node. Postaxial median furrow shallow. Border lacking spines.

*Discussion.*—Previously, I suggested that *P. acidusus* was probably a synonym of *P. atavus* (Robison, 1982). Upon further study, I here tentatively recognize *P. atavus* and *P. acidusus* as separate species; however, the differences are minor and of questionable taxonomic value. *P. acidusus* is known from few specimens and its range of morphologic variation is yet to be determined. The species is characterized by the combination of genal scrobicules of irregular depth, elongate and entire basal lobes, lack of spines, and a large median tubercle and a terminal node on the pygidial axis. In the

original species description, Öpik (1979) noted that, on the single cephalon known at the time, the anterior glabella is blunt and sulcate. Specimens from Nevada (Fig. 7, I) have a nonsulcate and more pointed anterior glabella; however, similar variation in shape of the anterior glabella is common in populations of *P. atavus*. Surface granules and punctae on illustrated Australian specimens of *P. acidusus* are weak and may represent only secondary effects of preservation or weathering.

Öpik (1979:99-100) designated *P. acidusus* as the type species of a new subgenus *Ptychagnostus (Acidusus)*, the distinguishing character being "its terminal pygidial axial node." In my opinion, the taxonomic importance attributed to that node is unwarranted, and I prefer not to recognize the subgenus. A terminal node is not evident from illustrations of many of the specimens that Öpik assigned to his new subgenus. Moreover, a similar node is present on specimens of various species of *Ptychagnostus* (e.g., *P. incautus*, *P. michaeli*) that otherwise are quite different from *P. acidusus*.

*P. acidusus* shares many features with *P. atavus*, from which it appears to have directly evolved. Differences are minor and mainly consist of a more constant presence of genal scrobicules and presence of a terminal axial node. Lower convexity observed in *P. acidusus* is probably due to partial flattening in shaly limestone, which also may cause reduction in width and minor changes in shape of the axis.

*Occurrence.*—Rare specimens of *P. acidusus* have been collected in Australia (Queensland) and the United States (Nevada). In addition to the specimens described by Öpik (1979), three cephalons and one pygidium are in collection 168 from 303 m above the base of the Secret Canyon Formation in the northern Egan

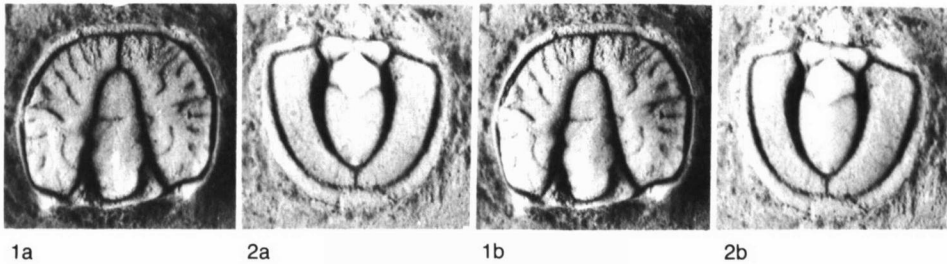


Fig. 7. *Ptychagnostus acidusus* Öpik. 1, Cephalon, KUMIP 204201,  $\times 8$ ; 2, pygidium, KUMIP 204202,  $\times 9$ ; both preserved in argillaceous limestone of collection 168, Secret Canyon Formation, northern Egan Range, Nevada.

Range, Nevada. All known specimens are associated with faunas of the *P. punctuosus* Zone.

### PTYCHAGNOSTUS ACULEATUS

(Angelin)

Figure 8

*Agnostus aculeatus* ANGELIN, 1851, p. 8, pl. 6, fig. 12; BRØGGER, 1878, p. 71, pl. 5, figs. 5a, b; TULLBERG, 1880, p. 23, pl. 1, figs. 11a, b; GRÖNWALL, 1902, p. 197; STRAND, 1929, p. 345, pl. 1, fig. 7.

*Ptychagnostus aculeatus* (Angelin) JAEKEL, 1909, p. 400; LU and others, 1965, p. 37, pl. 3, figs. 11, 12; KHAIRULLINA, 1970, p. 7, pl. 1, figs. 4, 5; 1973, p. 34, pl. 1, figs. 5-7; ROBISON, 1978, fig. 2B; XIANG and others, 1981, pl. 7, figs. 6, 7; KINDLE, 1982, pl. 1.2, figs. 16, 19, 23.

*Goniagnostus aculeatus* (Angelin) KOBAYASHI, 1939, p. 154.

*Ptychagnostus* (*Ptychagnostus*) *aculeatus* (Angelin) WESTERGÅRD, 1946, p. 79-80, pl. 12, figs. 8-11; ÖPIK, 1961a, p. 80-81, pl. 21, figs. 3, 4a, b; PALMER, 1968, p. B28, pl. 6, fig. 20; YANG, 1982, pl. 1, figs. 16, 17.

*Diagnosis.*—Mature holaspides relatively large, maximum length of complete exoskeleton probably ranging to 20 mm. Exoskeletal surface mostly covered with prominent, dense granules of uneven size.

Cephalon subquadrate to subcircular in dorsal view, convexity decreasing from moderate to low during holaspide ontogeny. F1 weak and F2 moderately developed. Median node behind midpoint of posteroglabella. Basal lobes elongate and usually divided. Genal scrobicules well developed, outlining rugae with as many as three orders of branching. Border lacking granules, posterolateral spines short to long and slender.

Thorax unknown except anterior segment (Fig. 8,4), which is weakly granulose.

Pygidium generally subquadrate with low convexity. During holaspide ontogeny, M1 becoming transversely tripartite and postaxial median furrow disappearing. Median spine on M2 unusually large, with base extending well back onto posteroaxis; length undetermined because of difficulty in preparation. Border granulose, lacking spines.

*Discussion.*—*P. aculeatus* is characterized by

prominent granules of uneven size, well-developed genal scrobicules, and spines on the cephalic border and pygidial axis. Representatives somewhat resemble those of *P. punctuosus*, but can be readily distinguished by the presence of spines on the cephalon and pygidium.

Öpik (1979:144) stated that *Agnostus aculeatus* Angelin “has a cephalon of *Goniagnostus* and is a separate genus; it is discussed in connection with *Onymagnostus*.” Neither his discussion of *Onymagnostus* nor *Goniagnostus* further mentions *aculeatus* and his notion of a “separate genus” remains unexplained. Although *P. aculeatus* is a highly evolved species, I find no compelling reason for excluding it from *Ptychagnostus*.

Specimens of *P. aculeatus* have a relatively thin exoskeleton, which seems to correlate with an unusually large holaspide size and probable retention of a pelagic mode of life. Because of the thin exoskeleton, most specimens from Nevada and Utah are flattened and deformed. Nevertheless, except for longer cephalic border spines, morphologic details closely resemble those of specimens previously assigned to the species from other continents.

The pattern of ramified genal rugae on holaspide cephalia of *P. aculeatus* is closely similar to the pattern of intestinal diverticula in larvae of the recent xyphosuran *Limulus polyphemus* (see Robison, 1978, fig. 2). This resemblance supports Öpik’s (1961b) interpretation of the ramified rugae of agnostoids as a surface expression of the internal alimentary system. The surface granules may have served an auxiliary respiratory function.

*Occurrence.*—Geographically, *P. aculeatus* is widespread; however, at most localities the number of specimens tends to be relatively low. In North America, rare specimens have been previously documented from east-central Alaska (Palmer, 1968) and western Newfoundland (Kindle, 1981, 1982). Specimens compared with *P. aculeatus* also have been reported from the District of Mackenzie (Fritz, 1981: 153). Within the conterminous United States, *P. aculeatus* here is described and illustrated for the first time from Nevada and Utah. From Nevada are more than 30 specimens in collections 155 and 156 from 1.5 and 3.0 m, respectively, above the base of member B, Emigrant Springs Limestone, in the southern Schell

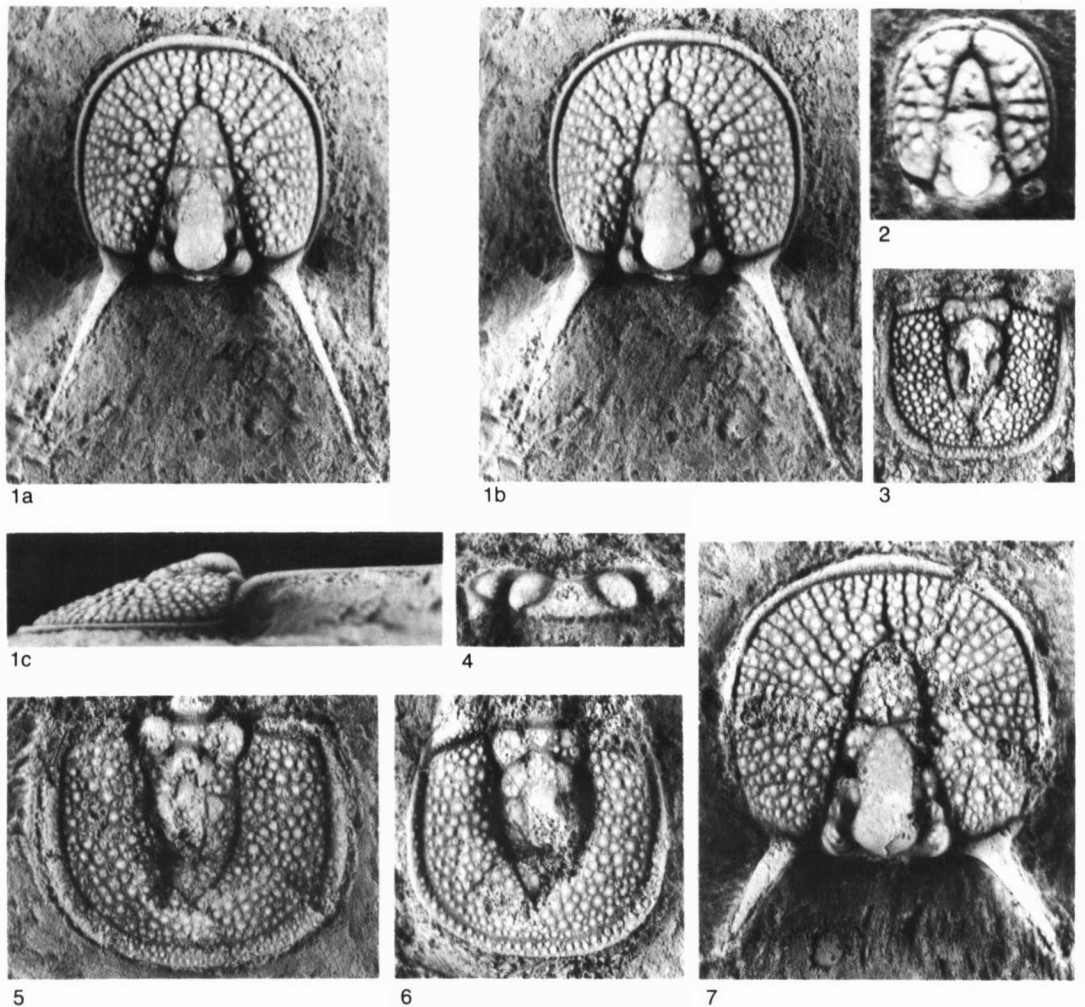


Fig. 8. *Ptychagnostus aculeatus* (Angelin); 3 is from collection 751, Weeks Limestone, House Range, Utah; all others are from collection 156, Emigrant Springs Limestone, southern Schell Creek Range, Nevada. 1, 7, Late holaspid cephala, KUMIP 204203 and 204204, both  $\times 5$ ; 2, early holaspid cephalon, KUMIP 204205,  $\times 15$ ; 3, flattened, intermediate holaspid pygidium, KUMIP 204206,  $\times 5$ ; 4, anterior thoracic segment, KUMIP 204207,  $\times 5$ ; 5, 6, flattened, late holaspid pygidia, KUMIP 204208 and 204209, both  $\times 5$ .

Creek Range (for lists of associated taxa, see Clark and Robison, 1969). A single cephalon of *P. aculeatus* (KUMIP 147589) is in collection DKS78-139g from the highest beds containing *Lejopyge calva* in the Lincoln Peak Formation of the southern Snake Range. From Utah are about 40 specimens in collections 749, 751, and 828 from 24 to about 45 m above the base of the Weeks Limestone in the central House Range.

Outside North America, *P. aculeatus* has been described from Australia, China, Den-

mark, Norway, the Soviet Union, and Sweden (see synonymy). Additionally, the species has been reported in faunal lists for Australia (Öpik, 1979:5), New Zealand (Cooper, 1979:54), and the Salair region of the Soviet Union (Poletaeva, 1969:27).

Stratigraphically, the reported range of *P. aculeatus* is the upper two-thirds of the *L. laevigata* Zone; however, most occurrences appear to correlate with the upper half of the lower subzone.

**PTYCHAGNOSTUS AFFINIS (Brøgger)**

Figure 9

*Agnostus punctuosus* Angelin var. *affinis* BRØGGER, 1878, p. 68, pl. 5, figs. 2a, b.

?*Agnostus punctuosus* Angelin var. *bipunctata* BRØGGER, 1878, p. 68, pl. 5, fig. 2c.

*Agnostus intermedius* THORSLUND (not Tullberg) in Asklund and Thorslund, 1935, p. 106, pl. 1, figs. 5-7.

*Ptychagnostus punctuosus affinis* (Brøgger) KOBAYASHI, 1939, p. 152-153; ОРИК, 1979, p. 91-92, pl. 39, fig. 8; pl. 40, figs. 2-7.

?*Ptychagnostus punctuosus bipunctata* (Brøgger) KOBAYASHI, 1939, p. 152-153.

*Ptychagnostus* (*Ptychagnostus*) *punctuosus affinis* (Brøgger) WESTERGÅRD, 1946, p. 79, pl. 11, figs. 26-33; PALMER, 1968, p. B28, pl. 4, figs. 26, 27.

*Diagnosis.*—Cephalon moderately to highly convex, subcircular to subquadrate in dorsal view; posterolateral borders smooth. Axis well defined, tapering anteriorly, weakly cleft ante-

romedially in some; median node usually anterior from posteroglabellar midpoint. Basal lobes elongate, entire or divided. Genae usually with well-developed scrobicules. Dorsal surface lacking granules.

Thorax relatively unmodified and non-spinose.

Pygidium low to moderately convex, commonly subquadrate, without border spines. Axis moderately well defined, constricted at hexagonal M2. Median structure on M2 varying from low, weak tubercle at posterior edge (common) to low, ill-defined, longitudinal ridge (rare). Posteroaxis centrally depressed, in some having secondary median node at midlength, and in some having as many as five pairs of characteristic, tiny, lateral pits. Postaxial median furrow usually present, but disappearing on some late holaspides. Surface of pleural fields covered with weak granules.

*Discussion.*—In his monograph on Swedish agnostoids, Westergård (1946:79) concluded that “a practically continuous evolutionary se-

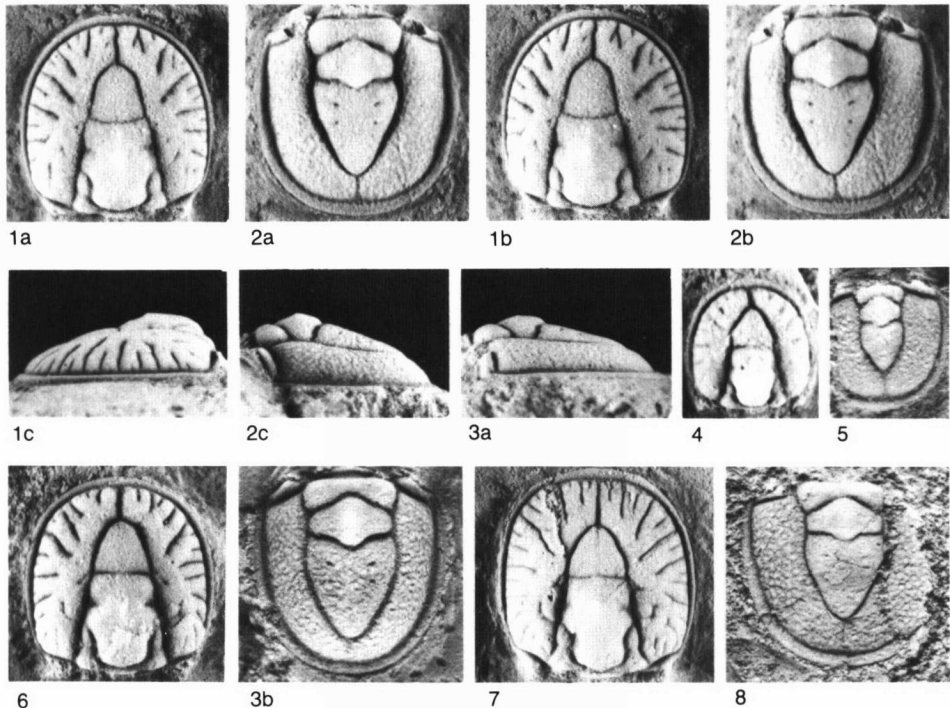


Fig. 9. *Ptychagnostus affinis* Brøgger; 1-6 are from collection 394, 7, 8 from collection 772; all Marjum Formation, House Range, Utah. 1, 4, 6, 7, Holaspide cephalons of various sizes, KUMIP 204211-204214;  $\times 8.0, 10.0, 9.0, 6.5$ , respectively. 2, 3, 5, 8, Holaspide pygidia of various sizes, KUMIP 204215-204218;  $\times 8, 8, 10, 7$ , respectively.



ries'' is formed by taxa that here are designated as *Ptychagnostus atavus*, *P. affinis*, and *P. punctuosus*. Morphologies and lowest stratigraphic appearances of these same taxa in Nevada and Utah (Fig. 4) support Westergård's conclusion concerning phylogeny. Although variation is evident, generally *P. affinis* differs from *P. atavus* by having a more constant development of genal scrobicules, lower pygidial convexity, a centrally depressed posteroaxis, and weak granules on pleural fields of the pygidium. *P. punctuosus* primarily differs from *P. affinis* by the presence of granules on the cephalon, and by addition and enlargement of granules on the pygidium. Also, within this series of three species the primary median structure on the pygidial M2 changes from a moderately large, subcircular tubercle to a low, ill-defined, longitudinal ridge.

Westergård (1946:79) noted that the median posteroglabellar node of *P. affinis* is situated slightly more forward than that of *P. atavus*. Without comment, he also illustrated (pl. 11, fig. 30) an unusual cephalon of *P. affinis* with two median nodes. The nodal position on most specimens of *P. atavus* corresponds to that of the posterior node on Westergård's binodal specimen, whereas the nodal position on most specimens of *P. affinis* corresponds to that of the anterior node on his binodal specimen. Therefore, I suggest that the glabellar nodes on most specimens of *P. atavus* and *P. affinis* are probably not homologous, and the change in position probably does not represent evolutionary migration. Rather, the posterior node was probably suppressed and an anterior, latent node was developed during the transition from *P. atavus* to *P. affinis*.

*Occurrence.*—*P. affinis* has been documented from Sweden, Norway, Denmark, Alaska, and Australia (see synonymy). Previous assignment to *P. affinis* of specimens from Wales (Kobayashi, 1939:153) is questionable (Lake, 1906, caption pl. 1; Westergård, 1946:78; see *P. punctuosus*, herein).

For the first time, specimens of *P. affinis* are illustrated herein from Nevada and Utah. In the northern Egan Range, Nevada, the species is rare in collections 167 and 169 from 301 and 317 m, respectively, above the base of the Secret Canyon Formation. In the central House Range, Utah, numerous specimens of *P.*

*affinis* are in collections (337, 393, 394, 396, 772) ranging from 15 to about 185 m above the base of the Marjum Formation.

Stratigraphically, *P. affinis* ranges through approximately the lower half of the *P. punctuosus* Zone.

## PTYCHAGNOSTUS AKANTHODES

### Robison

Figure 10

*Ptychagnostus akanthodes* ROBISON, 1964, p. 523, pl. 79, figs. 1-7.

*Aotagnostus akanthodes* (Robison) ÖPIK, 1979, p. 129.

*Diagnosis.*—Cephalon subcircular, of moderate convexity, with unusually large posterolateral border spines. Axis moderately tapered, anteroglabella usually ending in rounded point. F1 weak, F2 moderately developed. Median node behind posteroglabellar midpoint. Basal lobes elongate and varying from entire to strongly divided. Genal scrobicules well developed, outlining rugae with up to three orders of branching.

Thorax having median spine on posterior segment.

Pygidium semicircular, of moderate convexity, with pair of medium-sized spines on posterolateral borders. Axis slightly constricted at M2; median spine on M2 long, reflexed upward and backward to point over posterior border; posteroaxis ogival. Postaxial median furrow weak to moderately developed.

Dorsal surface generally smooth but may have either scattered weak granules or pits.

*Discussion.*—*P. akanthodes* is a rare species that closely resembles *P. occultatus*, from which it probably evolved. It can be differentiated from *P. occultatus*, however, by the presence of border spines on the pygidium, and it has larger spines on the cephalon and pygidial axis. The spines of *P. spinosus* Ergaliev (1980:71, pl. 1, figs. 23, 24) are similar in number and position to those in *P. akanthodes*, but appear to be considerably less robust. Further study may show these species to be synonyms. *P. akanthodes* also resembles *P. aculeatus* but differs from that species by lacking well-developed granules on the dorsal surface and by the presence of border spines on the pygidium.

Öpik (1979:129) reassigned *P. akanthodes* to

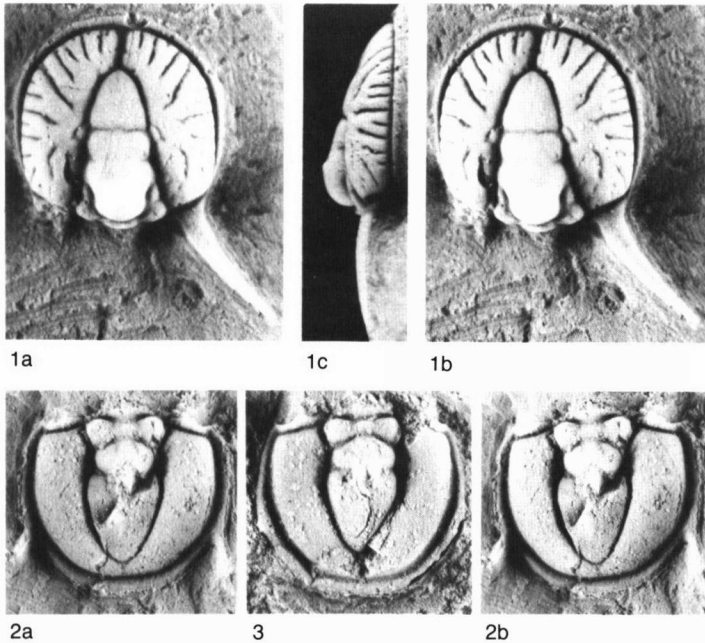


Fig. 10. *Ptychagnostus akanthodes* Robison. 1. Cephalon, USNM 374581,  $\times 8$ ; 2, pygidium, USNM 374582,  $\times 5$ ; 3, pygidium, USNM 374583,  $\times 6$ ; all paratypes from collection 3309-CO, Marjum Formation, House Range, Utah.

a new genus *Aotagnostus*, which I consider to be a junior synonym of *Ptychagnostus*. Moreover, in my opinion, *P. akanthodes* does not appear to be closely related to Australian species that Öpik assigned to *Aotagnostus*. The Australian species lack well-developed genal scrobicules and details of axial structure are different, particularly that of the posteroaxis of the pygidium.

*Occurrence.*—More than 30 specimens are in collections 3309-CO and 765, both from 134 m above the base of the Marjum Formation, central House Range, Utah. The observed occurrence is within the lower half of the *Ptychagnostus punctuosus* Zone (Fig. 4).

### PTYCHAGNOSTUS ATAVUS (Tullberg)

Figure 11

*Agnostus atavus* TULLBERG, 1880, p. 14, pl. 1, figs. 1a-d.

*Ptychagnostus atavus* (Tullberg) JAEKEL, 1909, p. 400; ÖPIK, 1979, p. 93-94, pl. 29, fig. 7; pl. 42, figs. 7, 8; pl. 43, figs. 1-4; XIANG and others, 1981, pl. 7, fig. 5; ROBISON, 1982, p. 136-139, pl. 1, figs. 1-9 (see for additional synonymy); ROWELL, ROBISON, and STRICKLAND, 1982, p. 161-182; EGOROVA, PEGEL, and TCHERNYSHEVA in Egorova and others, 1982, p. 63-64, pl. 6, fig. 7; pl. 7,

fig. 6; pl. 11, figs. 1-3; pl. 13, fig. 13; pl. 51, fig. 11; pl. 55, figs. 16, 18, 20, 21; pl. 64; KINDLE, 1982, pl. 1.2, fig. 2.

*Ptychagnostus atavus coartatus* ÖPIK, 1979, p. 94-95, pl. 42, figs. 5, 6.

*Ptychagnostus mesostatus* ÖPIK, 1979, p. 97-98, pl. 40, fig. 8; pl. 41, figs. 6, 7.

?*Ptychagnostus (Acidusus) navus* ÖPIK, 1979, p. 101-102, pl. 46, fig. 1.

not *Ptychagnostus atavus* (Tullberg) ERGALIEV, 1980, p. 67-69, pl. 1, figs. 13-17.

*Ptychagnostus intermedius* Tullberg ERGALIEV, 1980, p. 69-70, pl. 1, figs. 18-20.

*Ptychagnostus karatauensis* ERGALIEV, 1980, p. 72, pl. 1, figs. 21, 22.

*Ptychagnostus (Pt.) atavus* (Tullberg) YANG, 1982, pl. 1, fig. 18.

*Lectotype.*—In 1946, Westergård (p. 130, pl. 11, fig. 8) designated one of Tullberg's syntypes of *P. atavus* as lectotype of the species. Recently, Ergaliev (1980:69) stated that a different specimen illustrated by Westergård (1946, pl. 11, fig. 14) must be taken as the lectotype of *P. atavus*. Ergaliev's proposed change in lectotype is invalid for two reasons. According to Article 74(a)(i) of the *International Code of Zoological Nomenclature* (1961), "the first published designation of a lectotype fixes the status of the specimen." Moreover, Article 74(a) indicates

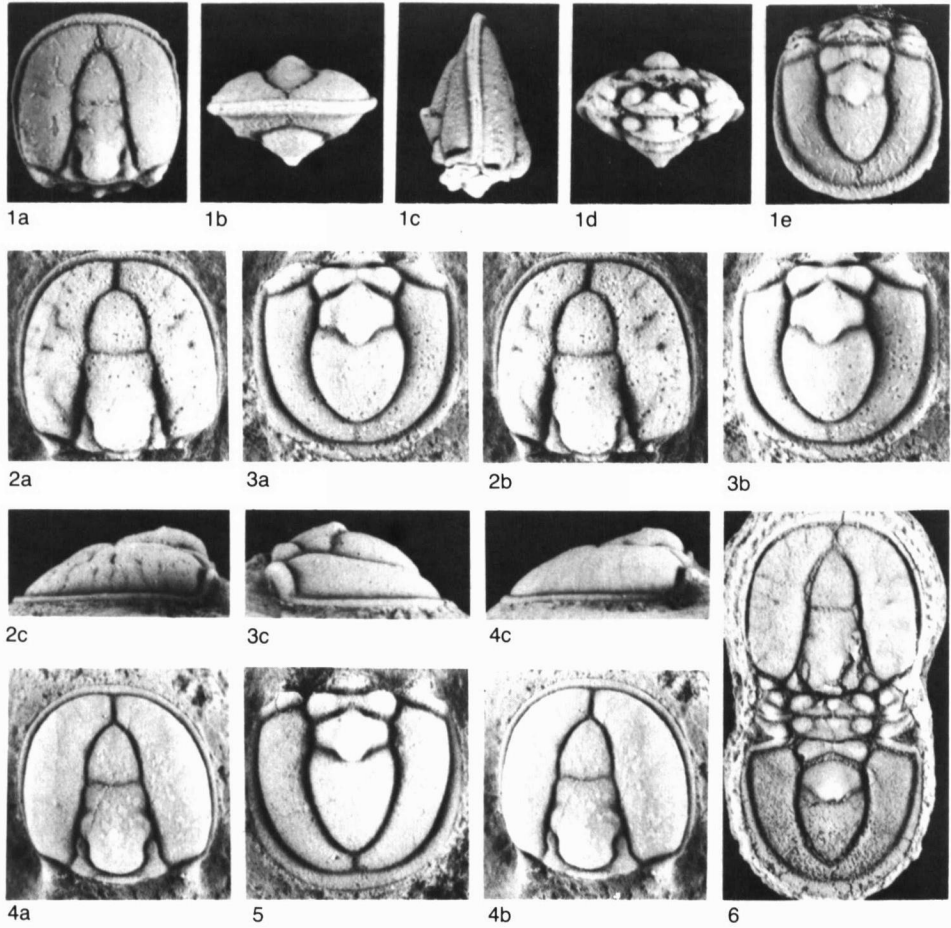


Fig. 11. *Ptychagnostus atavus* (Tullberg). 1, Enrolled specimen, KUMIP 204219,  $\times 9$ , collection 114 from middle Wheeler Formation, House Range, Utah; 1a, cephalon; 1b, anterior cephalon (above) and posterior pygidium (below); 1c, left-lateral view; 1d, thorax; 1e, pygidium. 2, 3, Cephalon and pygidium, KUMIP 204220 and 204221, both  $\times 9$ , collection 775 from lower Marjum Formation, House Range, Utah. 4, 5, Cephalon and pygidium, KUMIP 204222 and 204223,  $\times 9$  and 8, collection 789 from middle Geddes Limestone, Eureka mining district, Nevada. 6, Complete specimen from shale matrix with ventral cone-in-cone encrustation of calcite, KUMIP 204224,  $\times 9$ , collection 114 from middle Wheeler Formation, House Range, Utah.

that a lectotype must be chosen from one of the syntypes. The specimen chosen by Ergaliev is from Jämtland and is not one of Tullberg's syntypes, which are from Scania.

**Diagnosis.**—*Ptychagnostus* lacking spines, coarse surface granulation, and secondary median node on posteroaxis of pygidium; basal lobes elongate, entire or divided; median node usually behind posteroglabellar midpoint; pygidial M2 hexagonal in outline, having prominent median tubercle at rear margin; holaspide genae smooth to moderately scrobiculate.

**Discussion.**—*P. atavus*, an immediate descendant of *P. intermedius*, has been more fully diagnosed and discussed by Robison (1982: 136-139). A companion paper (Rowell, Robison, and Strickland, 1982) includes a discriminant function analysis of its morphological variation, a cladistic analysis of its phylogeny, a summary of its biogeography, and an evaluation of its use in biostratigraphy.

*P. atavus* (Tullberg) and *P. intermedius* (Tullberg) were considered by Westergård (1946:76-77) to be synonyms. Reasons for recognizing the validity of both species were inde-

pendently reached and almost simultaneously published by Öpik (1979), Ergaliev (1980), and Robison (1982). As shown by some of Tullberg's (1880) syntypes that were subsequently illustrated by Westergård (1946, pl. 11, figs. 8-10, 19-21), *P. atavus* and *P. intermedius* most obviously differ in characters of the pygidial axis. *P. atavus* has a prominent median tubercle that displaces the F2 backward in a broad V, and the M2 segment is hexagonal in outline. In comparison, *P. intermedius* usually has a small median node instead of a tubercle, the F2 is only slightly indented, and the M2 is pentagonal. On the cephalon, the median node in *P. atavus* is usually situated behind the post-eroglabellar midpoint, whereas in *P. intermedius* it is near the midpoint. Genal scrobicules are present on syntypes of both species.

As indicated by both descriptions and illustrations, Ergaliev (1980) appears to have misidentified specimens of *P. atavus* as *P. intermedius*, and vice versa. Such identification would cause *P. atavus* to precede *P. intermedius* in stratigraphic position, which is the order determined by Tullberg (1880, table on p. 10). However, Westergård (1946:77) reported that Tullberg's "type specimens of *atavus* were collected from a loose stinkstone lens" that was incorrectly believed to originate below strata containing *P. gibbus*. Further studies have produced much evidence to prove the first stratigraphic appearance of *P. atavus* to be well above the first appearance of *P. gibbus*. Without mention of Westergård's correction, Ergaliev (1980:69) cited Tullberg's table as agreeing with the vertical distribution of species recently identified in the Lesser Karatau Range of Kazakhstan. Correction of Ergaliev's taxonomic identifications also requires stratigraphic reversal of his zonal names (Ergaliev, 1980:36) that are based on *P. atavus* and *P. intermedius*.

Because most previous workers have not recognized the morphological differences between *P. atavus* and *P. intermedius*, precise stratigraphic ranges of these species are not known in most parts of the world. Moreover, from available illustrations, I suggest that some specimens from the *P. gibbus* Zone of Scandinavia and the Soviet Union that have been identified as *P. praecurrens* may actually represent *P. intermedius*. Further biostratigraphic documentation of representatives of all of these species, partic-

ularly in Scandinavia, has much potential value for refinement of global correlation.

*Ptychagnostus mesostatus* Öpik (1979:97-98, pl. 40, fig. 8; pl. 41, figs. 6, 7) is based on one complete exoskeleton and one pygidium, both poorly preserved and each from a different locality. The distinguishing characters cited by Öpik are parallel flanks of the posterior glabella, arcuate genal scrobicules, and a granular pygidial surface. In my opinion, *P. mesostatus* is a synonym of *P. atavus*, which commonly has a pair of arcuate genal scrobicules. The posterior glabella of the specimen Öpik assigned to *P. mesostatus* (pl. 41, figs. 6, 7) is practically identical in shape to that of specimens he assigned to *P. atavus* (pl. 43, figs. 1, 3). A granular pygidial surface is evident on only a latex cast of one of Öpik's specimens and is probably of secondary origin, perhaps from weathering processes.

The single known specimen of *P. (Acidusus) navus* Öpik (1979:101-102, pl. 46, fig. 1) differs from typical representatives of *P. atavus* only in the absence of a postaxial median furrow. Both in ontogenetic and phylogenetic successions, members of several species of *Ptychagnostus* exhibit a trend toward effacement of the postaxial median furrow. Therefore, I consider absence of that furrow by itself to be an inadequate character for assigning a single specimen to a new species. *P. navus* is probably a synonym of *P. atavus*.

Specimens of *P. atavus* that I illustrated in 1982 are all from the lower and middle parts of its stratigraphic range in Utah. Additional specimens illustrated herein were selected to show more fully the range of morphologic variation within the species. Also, they are from the middle and upper parts of its stratigraphic range in either Nevada or Utah.

*Occurrence.*—*P. atavus* is a common species that has been described from Sweden, Norway, Denmark, Canada, United States, Australia, China, and the Soviet Union. Many collections with *P. atavus* from Nevada and Utah were recently listed (Robison, 1982:139). Additional collections from the same states are 789 and 790 from the middle Geddes Limestone, Eureka mining district, Nevada; 822 from an unnamed formation in the Toana Range, Nevada; and 389, 393, 396, 701, 775, 796 from the upper Wheeler and lower Marjum formations in the

House Range, Utah. In Nevada and Utah, *P. atavus* has an observed range through the *P. atavus* Zone and about the lowest quarter of the *P. punctuosus* Zone.

In western Newfoundland, a few specimens of *P. atavus* are in C. H. Kindle collections 448 and 619 from boulders in the Cow Head Conglomerate.

### PTYCHAGNOSTUS GERMANUS Öpik

Figure 12

*Ptychagnostus (Acidusus) germanus* ÖPIK, 1979, p. 102-103, pl. 47, figs. 1-6.

*Ptychagnostus (Acidusus) retrotectus* ÖPIK, 1979, p. 102, pl. 46, fig. 5.

?*Ptychagnostus* sp. indet. B (aff. *atavus*) ÖPIK,

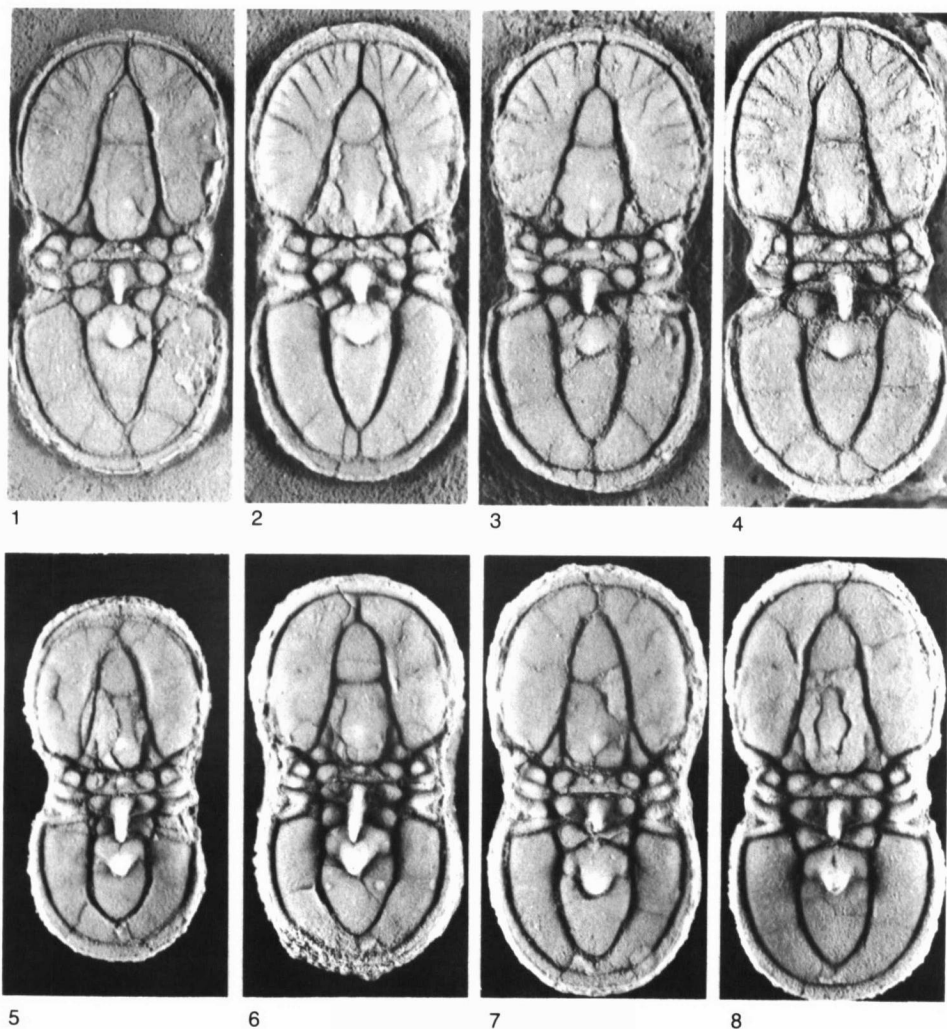


Fig. 12. *Ptychagnostus germanus* Öpik. Complete specimens, all preserved in calcareous shale, and all from the House Range, Utah. 1-4, Specimens with weak genal scrobicules from high in stratigraphic range; all from collection 716, about 300 m above base of Marjum Formation; KUMIP 204225-204228,  $\times 8$ , 8, 8, and 6.5, respectively. 5-8, Specimens with smooth genae from low in stratigraphic range, all  $\times 10$ ; 5, 6, from collection 819, about 60 m above base of Wheeler Formation, KUMIP 204229 and 204230; 7, 8, from collection 115, about 15 m below top of Wheeler Formation, KUMIP 204231 and 204232.

1979, p. 49-50, pl. 49, figs. 1-4.

*Ptychagnostus* sp. RITTERBUSH, 1983, figs. 1c,d.

*Diagnosis.*—Cephalon having pair of short posterolateral border spines. Basal lobes elongate, entire or divided. Glabella commonly pointed at anterior end, median node behind posteroglabellar midpoint. Genae smooth to weakly scrobiculate. Thorax having small median node on anterior segment and median spine, usually of moderate length, on posterior segment. Pygidium having prominent posteromedian tubercle on M2. Posteroaxis weakly oval. Pleural fields usually divided by narrow, shallow, postaxial median furrow. Pygidial border lacking spines.

*Discussion.*—*P. germanus* is morphologically intermediate between *P. atavus*, which lacks spines, and *P. occultatus*, which is characterized by a pair of cephalic spines and single median spines on the posterior thoracic segment and the pygidial M2. *P. germanus* mainly differs from *P. occultatus* by having a prominent posteromedian tubercle on the pygidial M2 rather than a spine. The recognition of separate species is supported by the overlap of stratigraphic ranges for the three species (Fig. 4) but lack of species association within most collections.

Öpik (1979:102) described a new species, *P. (Acidusus) retrotectus*, based on a single, partially flattened specimen from strata of the upper *P. punctuosus* Zone as used herein. The “blunt and sulcate glabellar front” mentioned by Öpik appears to be a secondary feature resulting from compaction. Otherwise, the specimen differs from his definition of *P. germanus*, from older strata, only by the presence of weak genal scrobicules. Because genal scrobicules comprise a variable character within several species of *Ptychagnostus*, commonly becoming better developed during the history of a species, I consider *P. germanus* and *P. retrotectus* to be synonyms representing early and late members, respectively, of a single species. In accord with the first reviser principle (ICZN, Art. 24), I select *P. germanus* as the senior subjective synonym.

Disarticulated cephalata and pygidia that Öpik (1979:98-99, pl. 49, figs. 1-4) referred to *Ptychagnostus* sp. indet. B (aff. *atavus*) likely represent *P. germanus*; however, reassignment cannot be confirmed without knowledge of thoracic morphology.

Specimens of *P. germanus* from Utah, like

those from Australia, show progressive development of weak genal scrobicules from lower to higher parts of their stratigraphic range (see Fig. 12). Utah specimens also show a slight reduction in size of the M2 tubercle and slight increase in distance between the end of the pygidial axis and the posterior border. A secondary median node near the posterior end of the pygidial axis is rare in specimens of *P. germanus* from Utah.

Two specimens identified as *Ptychagnostus* sp. were recently illustrated from the Wheeler Formation of the House Range, Utah (Ritterbush, 1983). Both appear to represent *P. germanus*. One retains a poorly preserved labrum beneath the front part of the posteroglabella.

*Occurrence.*—In addition to specimens reported from Australia, more than 200 specimens of *P. germanus* are in collections 115, 348, 716, 819, and possibly 796, which range from about 60 m above the base of the Wheeler Formation to about 300 m above the base of the Marjum Formation in the central House Range, Utah. Observed biostratigraphic range of the species is from low in the *P. atavus* Zone to the upper part of the *P. punctuosus* Zone.

### PTYCHAGNOSTUS GIBBUS (Linnarsson)

Figure 13

*Agnostus gibbus* LINNARSSON, 1869, p. 81, pl. 2, figs. 52, 53.

*Triplagnostus gibbus* (Linnarsson) HOWELL, 1935, figs. 5, 6; ERGALIEV, 1980, p. 72-73, pl. 1, figs. 11, 12; EGOROVA, PEGEL, and TCHERNYSHEVA in Egorova and others, 1982, p. 64, pl. 1, fig. 1; pl. 2, fig. 2; pl. 3, fig. 4a; pl. 52, figs. 3, 4.

*Ptychagnostus gibbus* (Linnarsson) ROBISON, 1982, p. 139-143, pl. 2, figs. 1-13 (see for additional synonymy); ROWELL, ROBISON, and STRICKLAND, 1982, p. 161-182.

*Ptychagnostus* cf. *P. gibbus* (Linnarsson) KINDLE, 1982, pl. 1.1, figs. 13, ?18.

*Diagnosis.*—*Ptychagnostus* characterized by short to moderately long spines on posterolateral borders of cephalon, posterior segment of thorax, and M2 of pygidium; middle half of glabella nearly parallel sided, posterior half of posteroglabella tumid; median node behind posteroglabellar midpoint; basal lobes elongate, entire or divided; genae usually smooth, rarely with weak scrobicules.

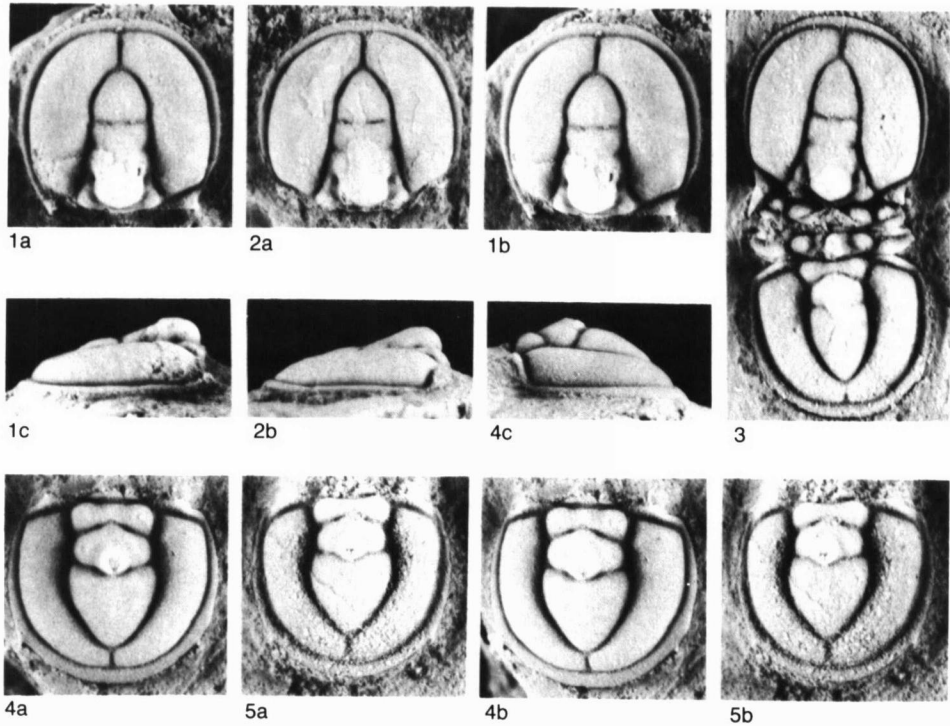


Fig. 13. *Ptychagnostus gibbus* (Linnarsson); 1, 2, 4, 5 from upper 3 m, Formation 2, Brønlund Fjord Group, North Greenland; 3 from lower Wheeler Formation, House Range, Utah. 1, Cephalon, MGUH 16.265 from GGU 271492,  $\times 10$ . 2, Partly exfoliated cephalon, MGUH 16.266 from GGU 271428,  $\times 9$ . 3, Exoskeleton, KUMIP 204233 from 157,  $\times 10$ . 4, Pygidium, MGUH 16.267 from GGU 271428,  $\times 9$ . 5, Pygidium, MGUH 16.268 from GGU 271489,  $\times 9$ .

*Discussion.*—*P. gibbus* has been more fully diagnosed and discussed by Robison (1982: 139-143). A companion paper (Rowell, Robison, and Strickland, 1982) includes a discriminant function analysis of its morphological variation, a cladistic analysis of its phylogeny, a summary of its biogeography, and an evaluation of its use in biostratigraphy.

Previously illustrated specimens (Robison, 1982, pl. 2) are representative of populations of *P. gibbus* in the Great Basin. Specimens illustrated herein are mostly from North Greenland and are representative of collections from that region. In the Great Basin, cephalic spines of *P. gibbus* usually are of moderate length; however, in rare collections from low in its stratigraphic range, the spines may be very short (see Robison, 1982, pl. 2, fig. 8). In available collections from Greenland, the opposite is observed; most specimens of *P. gibbus* possess very short spines whereas only rare specimens possess spines of moderate length.

In much of the world, *P. gibbus* is not known to have given rise to descendant species, and it rarely ranges above the zone that bears its name. In Australia, however, it ranges into the *P. punctuosus* Zone and is the apparent ancestral source of several species characterized by modification or further development of spines (Öpik, 1979).

*Occurrence.*—*P. gibbus* is a common and widespread species that has been reported from all continents except Africa and South America. Many collections with *P. gibbus* were recently listed from Nevada and Utah (Robison, 1982:142-143). In western Newfoundland, rare specimens of *P. gibbus* are in C. H. Kindle collection 362 from a boulder of Cow Head Conglomerate. In Greenland, *P. gibbus* is rare to common in collections GGU-271411, 271428, 271488, 271489, and 271492 from the upper half of Formation 2 of the Brønlund Fjord Group. *P. gibbus* disappears just below the first appearance of *P. atavus* in strata of

North America and northwestern Europe; however, in Siberia (Savitsky, 1976) and Australia (Öpik, 1979) it ranges into the *P. atavus* Zone.

**PTYCHAGNOSTUS HINTZEI, n. sp.**

Figure 14

*Etymology.*—The species name honors Prof. Lehi F. Hintze of Brigham Young University for his many contributions to our understanding of the geology and paleontology of the Great Basin.

*Holotype.*—Pygidium (Fig. 14, 8), USNM 374590.

*Diagnosis.*—Small *Ptychagnostus* lacking

spines. Basal lobes elongate and entire. Pygidium having short axis and wide anterior borders; anterior border furrows terminating against lateral border furrows, lateral furrows extending to anterior margin.

*Description.*—*Ptychagnostus* of relatively small size; length of largest cephalon or pygidium not exceeding 3 mm, maximum length of complete holaspid probably less than 7 mm.

Cephalon moderately to highly convex, length slightly greater than width. Axis markedly tapering, constricted at F3, anteroglabella pointed. F1 and F2 undeveloped. Median node slightly posterior from midpoint of post-eroglabella. Basal lobes elongate, entire. Basal

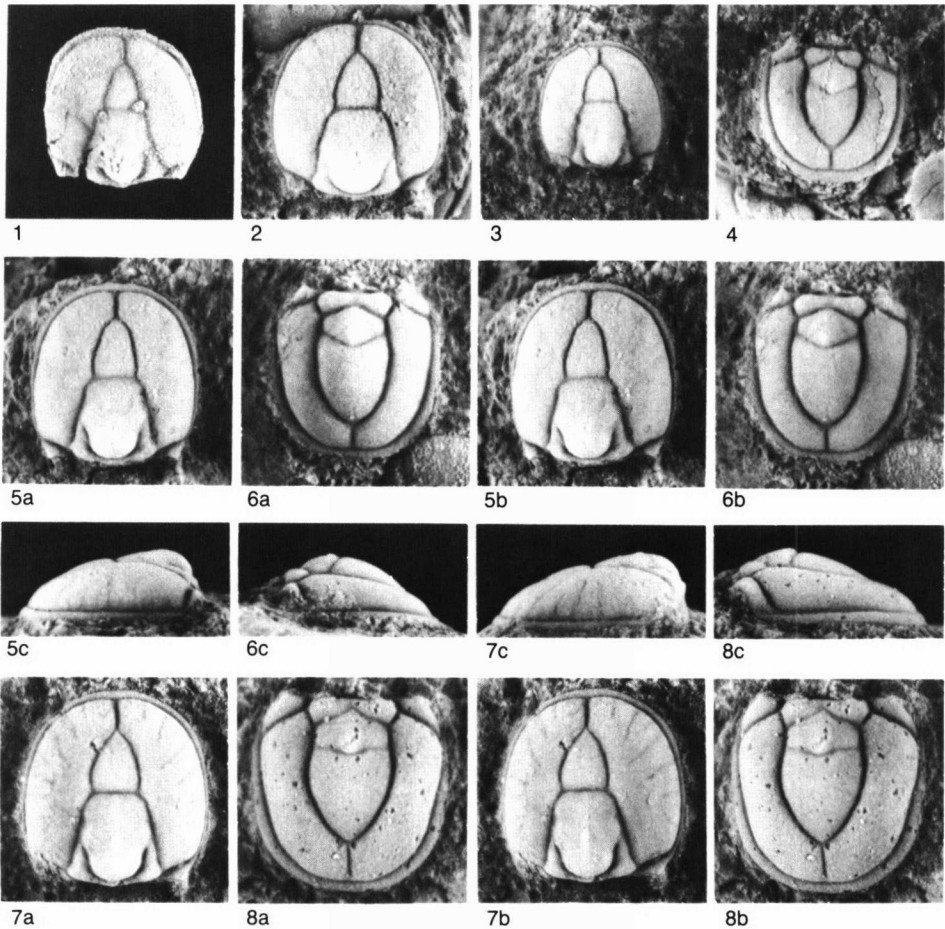


Fig. 14. *Ptychagnostus hintzei*, n. sp.; 1 is from collection 821, Marjum Formation, House Range, Utah; 2-8 are from collection 2523-CO, Emigrant Springs Limestone, southern Schell Creek Range, Nevada; all  $\times 10$ . 1, Silicified cephalon, KUMIP 204210. 2, 3, 5, 7, Cephala, USNM 374584-374587. 4, 6, Pygidia, USNM 374588, 374589. 8, Holotype pygidium, USNM 374590.



furrow geniculate, deep posteriorly, shallow near intersections with axial furrow. Genae smooth to weakly scrobiculate on late holaspides. Posterior border lacking spines.

Thorax unknown.

Pygidium moderately to highly convex, having wide (exsag.) anterior border. Lateral border furrows continuing to anterior margin and anterior border furrows terminating against lateral furrows. Axis moderately constricted at M2; M1 transversely wider than remainder of axis and sagittally constricted; M2 bearing moderate-sized, low, median tubercle near posterior edge. Posteroaxis ogival, tip well separated from posterior border furrow. Postaxial median furrow well developed. Border lacking spines.

*Discussion.*—*P. hintzei* is most similar to *P. cassis* Öpik (1961a:77-80, pl. 20, figs. 4-13); however, it lacks spines on the posterior cephalic border, whereas *P. cassis* has a pair of short spines. *P. hintzei* also resembles *Lejopyge lundgreni* (see Figs. 27, 28) and *L. rigbyi* (see Fig. 29) in axial shape, but it has elongate basal lobes, the anterior border of the pygidium is wider (exsag.), and the anterior border furrows of the pygidium terminate against the lateral border furrows.

The ancestry of *P. hintzei* is unclear, but similarity to *P. intermedius* (Robison, 1982, pl. 3; also Fig. 15, herein) in general axial shape, as well as course and depth of basal furrows, may indicate a close phyletic relationship. The two species, however, are stratigraphically well separated, and morphologically intermediate species are not known. Pygidia of *P. hintzei* differ from those of *P. intermedius* by having a more angular F2 and the lateral border furrows continue to the anterior margin.

*Occurrence.*—*P. hintzei* is a relatively rare species in the *Lejopyge calva* Zone of Nevada and Utah. All known specimens are preserved in coquinas dominated by *L. calva*. In Nevada, about 30 cephalia and pygidia are in collections 2523-CO and 155 from the uppermost part of member A and the basal 1.5 m of member B, Emigrant Springs Limestone, southern Schell Creek Range. Two cephalia are in collection 820 from about 10 m above the base of member A, Emigrant Springs Limestone, southern Egan Range. Two pygidia are in collection 111a from between 3 and 10 m above the top of the middle limestone member of the Lincoln

Peak Formation, northern Schell Creek Range. In Utah, about 40 cephalia and pygidia are in collections 733, 747, 782, 817, and 821 from an interval ranging from 18 m below the top of the Marjum Formation to about 30 m above the base of the Weeks Limestone in the central House Range.

## PTYCHAGNOSTUS INTERMEDIUS (Tullberg)

Figure 15

*Agnostus intermedius* TULLBERG, 1880, p. 17, pl. 1, figs. 4a,b; LINNARSSON, 1883, p. 32; GRÖNWALL, 1902, p. 52; STRAND, 1929, p. 344.

*Ptychagnostus intermedius* (Tullberg) JAEKEL, 1909, p. 400; KOBAYASHI, 1939, p. 152; ROBISON, 1982, p. 143-145, pl. 3, figs. 1-9; ROWELL, ROBISON, and STRICKLAND, 1982, p. 161-182.

not *Ptychagnostus intermedius* (Tullberg) ERGALIEV, 1980, p. 69-70, pl. 1, figs. 18-20.

*Ptychagnostus* (*Ptychagnostus*) *atavus* (Tullberg) WESTERGÅRD (in part), 1946, pl. 11, figs. 19-23 (not figs. 8-18, 24, 25).

*Ptychagnostus atavus* (Tullberg) ERGALIEV, 1980, p. 67-69, pl. 1, figs. 13-17.

*Ptychagnostus richmondensis* (Walcott) PALMER (in part), 1954, pl. 13, fig. 5 (not fig. 4).

*Ptychagnostus sinicus* LU, 1957, p. 259, pl. 137, figs. 17-19; LU and others, 1965, p. 37, pl. 3, figs. 16-18.

*Ptychagnostus idmon* ÖPIK, 1979, p. 95-96, pl. 43, figs. 5-8.

*Ptychagnostus scarifatus* ÖPIK, 1979, p. 96-97, pl. 44, figs. 1-5; pl. 58, fig. 2.

*Ptychagnostus* sp. aff. *scarifatus* ÖPIK, 1979, p. 97, pl. 44, fig. 6.

*Lectotype.*—Ergaliev (1980, p. 69) selected as a lectotype of *P. intermedius* a syntype cephalon illustrated by Westergård (1946, pl. 11, fig. 19). This has priority over the subsequent designation of a different lectotype (Robison, 1982:43).

*Diagnosis.*—*Ptychagnostus* without spines or surface granulation. Cephalon moderately convex; axis usually having fairly even forward taper; basal lobes elongate, entire or divided; median node near midpoint of posteroglabella; genae smooth (rare) to moderately scrobiculate (common), pair of crescentic scrobicules commonly developed near anterior end of glabella. Anterior basal furrow effaced on some late

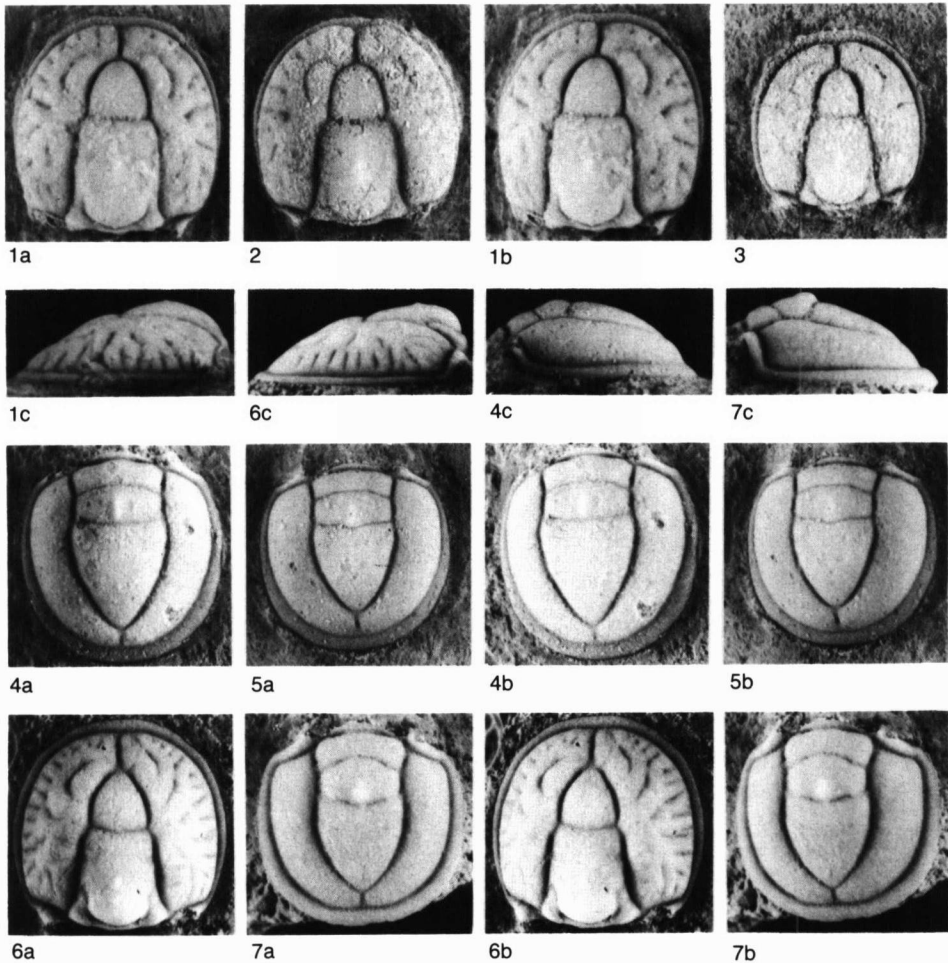


Fig. 15. Specimens of *Ptychagnostus intermedius* showing some features of either *P. atavus* or *P. idmon*; all from upper 3 m in type section of Formation 2, Brønlund Fjord Group, North Greenland. 1-3, Cephala, MGUH 16.269-16.271 from GGU 271489;  $\times 9$ , 9, 10, respectively. 4, 5, Pygidia, MGUH 16.272 and 16.273 from GGU 271489, both  $\times 9$ . 6, 7, Cephalon and pygidium, MGUH 16.274 and 16.275 from GGU 271492,  $\times 9$  and 10.

holaspides, resulting in confluence of anterior basal lobes and adjacent areas of glabella. Pygidium moderately to highly convex; axial F1 deflected forward, being broadly rounded or forming obtuse medial angle; F2 nearly straight, in some slightly indented by median node; M2 usually pentagonal in outline, rarely becoming subrectangular by straightening of F1 or rarely hexagonal by bending of F2; posteroaxis weakly ogival; postaxial median furrow usually present.

*Discussion.*—*P. intermedius* has been recently diagnosed and discussed by Robison (1982:

143-145). A discriminant function analysis of its morphologic variation and a cladistic analysis of its phylogeny have been given by Rowell, Robison, and Strickland (1982). Reasons for recognition of *P. intermedius* and *P. atavus* as separate species are given in the discussion of *P. atavus*. Further study has provided additional information about *P. intermedius* and requires some modification of previous work.

*P. intermedius* can be differentiated from most other species of *Ptychagnostus* by the pentagonal shape of its pygidial M2, a median node near the posteroglabellar midpoint, a

median node rather than a tubercle on the pygidial M2, and a lack of exoskeletal spines. *P. intermedius* differs from *P. praecurrens*, its immediate ancestor, by having a more broadly and evenly tapered cephalic axis, more elongate basal lobes, a median node that is more centrally positioned on the posteroglabella, and a node rather than small tubercle on the pygidial M2.

Generally, *P. intermedius* is one of the most common agnostoid species in collections from the *P. gibbus* Zone in North America and Greenland. In most collections, particularly in western North America, morphologic variability is relatively low (for representative specimens, see Robison, 1982, pl. 3). Collections from North Greenland are more variable, however, and include specimens (Fig. 15) with characters that are transitional to those of *P. atavus*.

From cladistic analysis, Rowell, Robison, and Strickland (1982) concluded that *P. intermedius* is the immediate ancestor of *P. atavus*. That conclusion is supported by the subsequent discovery in Greenland of specimens high in the stratigraphic range of *P. intermedius* that possess characters transitional between *P. intermedius* and *P. atavus* (Fig. 15,6,7). The median node on the posteroglabella is behind the midpoint, as in *P. atavus*. On the pygidium, the median node is slightly more enlarged than is usual in *P. intermedius*, but the course of the second transaxial furrow (F2) is displaced only slightly to the rear. Hence, the pygidial M2 remains more pentagonal than hexagonal. Because I judge the total morphological aspect of these specimens to be closer to *P. intermedius*, they are arbitrarily assigned to that species.

Öpik (1979:95-96, pl. 43, figs. 5-8) named a new species, *Ptychagnostus idmon*, which first appears in the *P. atavus* Zone of Australia. He distinguished the species "by the change of direction of the axial furrows in their passage from the slender frontal lobe to the flanks of the stout posterior glabellar lobe; and by the structure of the double basal lobes, whose anterior part is almost confluent with the glabella. The pygidial axial node is low and short, and the node on the posterior axial lobe is placed well to the rear." During the ontogeny of some specimens of *P. intermedius* in Greenland (common, GGU 271428 and 271489) and western North America (rare) the axial furrow also changes

course near junctions with the glabellar F3 (Fig. 15,1-3). By the late holaspide stage, this results in a marked difference in axial width near the F3, with the front of the posteroglabella being abruptly wider than the anteroglabella. Confluence of the basal lobes and adjacent glabella by effacement of the anterior part of the basal furrows is also observed in some late holaspides of *P. intermedius*. Rare specimens of *P. intermedius* also possess a secondary median node on the posteroaxis (Fig. 15,4). Therefore, specimens that Öpik assigned to *P. idmon* appear to represent the late stages of an evolutionary continuum from *P. intermedius*. In the absence of stable differential characters, I here consider *P. idmon* to be a junior subjective synonym of *P. intermedius*.

*Ptychagnostus scarifatus* Öpik (1979:96-97, pl. 44, figs. 1-5; pl. 58, fig. 2) and *P. sp. aff. scarifatus* Öpik (1979:97, pl. 44, fig. 6) also appear to be synonyms of *P. intermedius*. The only reported specimens of *P. scarifatus* and *P. sp. aff. scarifatus* are associated with specimens assigned to *P. idmon* in Öpik's collection M176. Specimens with an irregular axial furrow and narrow anteroglabella were assigned by Öpik (1979, pl. 43, figs. 6, 8) to *P. idmon*, whereas specimens with a more regular axial furrow and without significant difference in glabellar width near the F3 were assigned to *P. scarifatus*. From Öpik's illustrations, the morphologic differences appear to be gradational within a single, variable, species population.

With expressed reservation, Öpik (1979:95, pl. 41, fig. 8) assigned a single Australian specimen to *Ptychagnostus intermedius*. Subsequently, I (Robison, 1982:139) reassigned that specimen to *P. atavus*; however, I now consider its specific assignment to be uncertain. The specimen is flattened in siltstone and some axial features appear to have been altered. The posteroglabellar node is centrally located, as in *P. intermedius*. The pygidial M2 is hexagonal, as in *P. atavus*; however, a prominent tubercle is not evident from Öpik's illustration.

*Occurrence.*—*P. intermedius* is presently known from Norway, Sweden, Soviet Union, China, Australia, Greenland, Canada (British Columbia), and the United States (Montana, Nevada, Utah). Its distribution in western North America was recently summarized (Robison, 1982). In North Greenland, many specimens are in GGU collections 218614, 271411, 271428,

271489, and 271492 from the upper half of Formation 2 of the Brønlund Fjord Group. *P. intermedius* is a common species in the *P. gibbus* Zone. Its only documented occurrence in the *P. atavus* Zone is in Australia (= *P. idmon* Öpik, 1979; = *P. scarifatus* Öpik, 1979) where it seemingly survived longer than elsewhere in the world.

### PTYCHAGNOSTUS MICHAELI, n. sp.

Figure 16

?*Ptychagnostus* (*Acidusus*) sp. nov. ÖPIK (in part), 1979:105, pl. 48, fig. 6 (not fig. 5).

*Etymology*.—The species is named after Michael B. McCollum, who made numerous contributions to this study.

*Holotype*.—Complete holaspid exoskeleton of intermediate size, KUMIP 204283 from collection 397, 15 m above base of Marjum Formation, House Range, Utah (Fig. 16,10).

*Diagnosis*.—*Ptychagnostus* having pair of spines on posterolateral cephalon, one median spine on posterior thoracic segment, and pair of posterolateral spines on pygidium. Cephalic axis evenly tapered. Basal lobes intermediate to elongate, entire or weakly divided. Genal scrobicules weak or absent. Pygidial M2 having median tubercle.

*Description*.—Cephalon low to moderate in convexity; subcircular to subquadrate in outline, length approximately equals width. Axis rather evenly tapered to acute point. F3 straight, of moderate depth; F2 weak and F1 undeveloped. Median node behind midpoint of posteroglabella. Basal lobes intermediate to elongate, entire or weakly divided. Preglabellar median furrow deep. Genae smooth to weakly scrobiculate. Border having pair of posterolateral spines of short to moderate length.

Thorax poorly preserved on known specimens. Posterior segment having median spine.

Pygidium low to moderate in convexity, semicircular in outline. M1 sagittally constricted, forming yoked lateral swellings. M2 having slight transverse constriction; median tubercle small, posteriorly deflects F2. Posteroaxis slightly ogival on early holaspides, becoming moderately ogival on late holaspides; secondary node rare on posterior tip. Postaxial median furrow well developed throughout ontogeny. Border having pair of short to moderately long, slender, posterolateral spines pos-

terior to imaginary line drawn laterally from tip of axis.

*Discussion*.—*P. michaeli* appears to be most similar to *P. cassis* Öpik (1961:77, pl. 20, figs. 4-13) from Australia; however, *P. cassis* lacks pygidial border spines and has a more anterior secondary node on the pygidium. The thorax of *P. cassis* is unknown.

Öpik (1979:105, pl. 48, figs. 5, 6) assigned a cephalon and pygidium from different localities in Australia to *Ptychagnostus* (*Acidusus*) sp. nov. Both were reported to be from the *P. punctuosus* Zone. Öpik noted that the "shields may or may not be conspecific; the 'sp. nov.' in the title refers to the pygidium." From the illustrations, the pygidium agrees closely in all characters with *P. michaeli*, and here is questionably reassigned to this new taxon. The cephalon lacks border spines and may represent *P. atavus*; however, its taxonomic assignment remains uncertain.

Among agnostoid species in western North America, *P. michaeli* closely resembles *Lejopyge lundgreni*, with which it is commonly associated. Nevertheless, *P. michaeli* clearly differs from *L. lundgreni* by having more elongate basal lobes and by the presence of border and thoracic spines. Disarticulated cephalia also may be difficult to distinguish from those of associated *P. occultatus*; however, *P. occultatus* commonly has longer basal lobes and its genal scrobicules are usually better developed. Pygidia of *P. michaeli* can be easily distinguished from those of *P. occultatus* by their lack of a median axial spine and presence of border spines.

*Occurrence*.—*P. michaeli* is presently known from the United States (Nevada and Utah) and questionably from Australia. In Nevada, several specimens have been collected (105) from the upper Geddes Limestone in the Eureka mining district. In Utah, numerous specimens are in collections (397, 738-740, 759, 831) ranging from 15 to about 240 m above the base of the Marjum Formation in the House Range. The species has an observed range through about the lower two-thirds of the *P. punctuosus* Zone.

### PTYCHAGNOSTUS OCCULTATUS Öpik

Figures 17, 18

*Ptychagnostus* (*Acidusus*) *occultatus* ÖPIK, 1979, p. 103-104, pl. 48, figs. 1, 2.

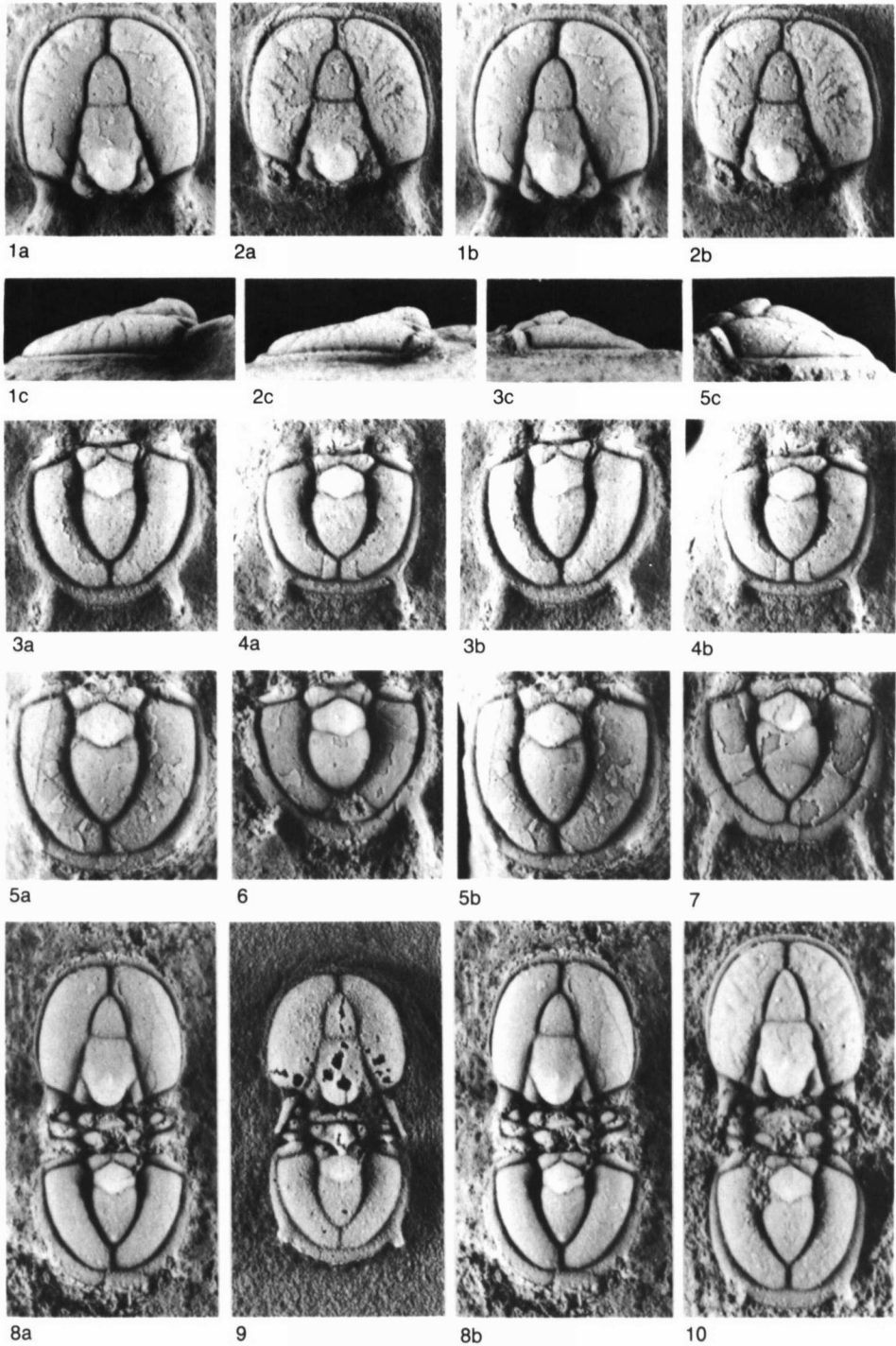


Fig. 16. *Ptychagnostus michaeli*, n. sp.; 6 and 8 from upper Geddes Limestone, Eureka mining district, Nevada, all others from Marjum Formation, House Range, Utah. 1, 2, Cephalia, KUMIP 204274 and 204275 from 397, both  $\times 9$ . 3, 4, Pygidia, KUMIP 204276 and 204277 from 397,  $\times 9$  and 10. 5, Pygidium, KUMIP 204278 from 759,  $\times 10$ . 6, 8, Pygidium and complete dorsal exoskeleton, KUMIP 204279 and 204280 from 105,  $\times 8$  and 10. 7, Pygidium, KUMIP 204281 from 740,  $\times 8$ . 9, Complete dorsal exoskeleton, KUMIP 204282 from 831,  $\times 10$ . 10, Latex cast of holotype exoskeleton, KUMIP 204283 from 397,  $\times 10$ .

*Ptychagnostus (Acidusus) sp. aff. occultatus* ÖPİK, 1979, p. 104-105, pl. 48, fig. 3.

*Ptychagnostus richmondensis* (Walcott) ROBISON (in part), 1964, p. 523-524, pl. 79, figs. 12, 16-22 (not fig. 15).

*Diagnosis.*—Cephalon subcircular to subquadrate, length approximately equaling width, convexity moderate. Axis well defined; middle half of glabella moderately tapered forward, front of glabella sharply to bluntly pointed. F1 undeveloped; F2 weakly to moderately developed adjacent to axial furrows; F3 narrow (sag.), shallowing medially. Median node slightly posterior from posteroglabellar midpoint. Basal lobes elongate and divided. Genae weakly to strongly scrobiculate, rarely smooth; depth along individual scrobicules commonly irregular, giving dimpled aspect. Posterolateral border spines well developed.

Thorax having strong median spine on posterior segment, anterior segment commonly having median node.

Pygidium semicircular to subquadrate, length about equal to or slightly less than width, convexity moderate. Axis well defined. M1 normally wide (trans.) and unequally tripartite. F1 deep abaxially, shallowing medially. M2 slightly constricted, hexagonal, and having moderate to long median spine with base deeply indenting F2. Posteroaxis variable in width, weakly ogival (common) to lanceolate (rare); secondary median node may be present at or near posterior end. Postaxial median furrow dividing pleural fields. Border lacking spines.

*Ontogeny.*—Numerous silicified specimens of *P. occultatus* in collection 337 provide information about ontogeny of the species (Fig. 18). Meraspides do not appear to possess genal scrobicules or spines; however, absence of those features may be the result of inadequate preservation. Among readily observed holaspid changes are the development and general increase in length of the characteristic spines, and increase in relative size of the posteroaxis. Late in the holaspid period, a pair of short spines develops at fulcral points on rear pleural margins of the posterior thoracic segment (compare Fig. 18, 14, 15). A secondary median node is present on the posteroaxis of only rare late holaspides (Fig. 18, 25).

*Discussion.*—Among important differential

characters of *P. occultatus* are the tapered mid glabella, elongate and divided basal lobes, and the presence of spines on the posterolateral cephalic borders, axis of the second thoracic segment, and axis of the pygidial M2. Genal scrobicules commonly are well developed but may be weak or absent, particularly during early phylogeny. Spines are absent on the pygidial border and granules are not developed on the dorsal surface. Collapse of the exoskeleton along the axial furrow during compaction in fine-grained matrix seems to have secondarily decreased the axial width in many specimens.

A morphological series from *P. atavus* to *P. germanus* to *P. occultatus* to *P. akanthodes* appears to represent a single lineage that evolved by the successive addition of new spines. This interpretation is supported by the stratigraphic first appearance of each species in the same order (Fig. 4). *P. atavus* lacks spines; *P. germanus* has a pair of posterolateral cephalic spines and a median spine on the posterior thoracic segment; *P. occultatus* has in addition a median spine on pygidial M2; *P. akanthodes* shows also a pair of posterolateral spines on the pygidial border.

The holotype of *P. occultatus* from Australia has a secondary median node at the tip of the pygidial axis (Öpik, 1979, pl. 48, fig. 1). Only a few specimens from North America and Greenland (e.g., Fig. 17, 3, 8) show a secondary node on the pygidium, and these are well forward from the tip of the axis. Whether this variation in position represents development of different latent nodes (see discussion of *P. affinis*) or node migration is unknown. However, because the nodes are rare, they are not accorded taxonomic significance at this time.

Öpik (1979:104) noted that genal scrobicules on Australian specimens of *P. occultatus* begin adaxially as "dimples." Similar dimples are present on some specimens from Utah; however, that feature is variable within single populations (compare Fig. 18, 1-12) and is lacking on many specimens (Fig. 17). Öpik also described the pygidial M1 as being bipartite, but the M1 changes from undivided to tripartite during holaspid ontogeny, and definition of lateral divisions may be variable among instars of similar size.

A reappraisal of *P. richmondensis* has led me

to the conclusion that it is an unrecognizable species (see separate discussion). Moreover,

most specimens from Utah that I formerly assigned to that species (e.g., Robison, 1964,



Fig. 17. *Ptychagnostus occultatus* Öpik from various lithologies, stratigraphic horizons, and localities. 1,3, Cephalon and pygidium in lime mudstone, KUMIP 204234 and 204235 from 159, about 300 m above base of Marjum Formation, House Range, Utah;  $\times 6$  and 10. 2,4, Cephalon and pygidium in calcareous shale, MGUH 16.276 and 16.277 from GGU 218644, 80 m above base of Formation T1, Tavstens Iskappe Group, North Greenland;  $\times 8$  and 9. 5, Pygidium in lime mudstone, KUMIP 204236 from 759, about 250 m above base of Marjum Formation, House Range, Utah;  $\times 7$ . 6, Exoskeleton from shale, ventral surface encrusted with cone-in-cone calcite; KUMIP 204237 from 115, upper 30 m of Wheeler Formation, House Range, Utah;  $\times 10$ . 7-9, Exoskeletons in lime mudstone, KUMIP 204238-204240 from 737, 397, and 758, respectively; about 40, 135, and 245 m above base of Marjum Formation, House Range, Utah;  $\times 9$ , 6, and 8, respectively.

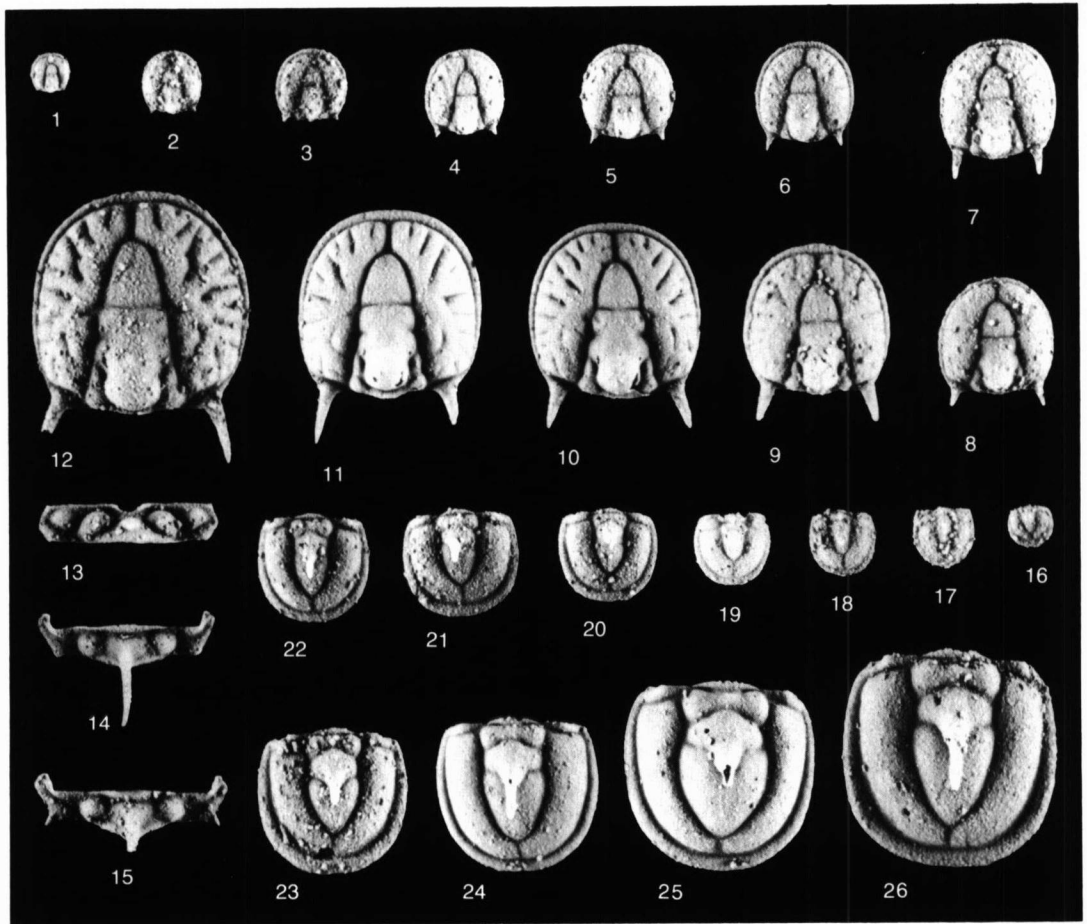


Fig. 18. Ontogeny of *Ptychagnostus occultatus* Öpik; silicified specimens from lime mudstone, collection 337, about 15 m above base of Marjum Formation, House Range, Utah; all  $\times 8$ . 1-3, Meraspid cephala, KUMIP 204241-204243. 4-12, Holaspid cephala, KUMIP 204244-204252. 13, Anterior thoracic segment of late holaspid, KUMIP 204253. 14, 15, Posterior thoracic segments of late holaspides, KUMIP 204254 and 204255. 16-19, Meraspid pygidia, KUMIP 204256-204259. 20-26, Holaspid pygidia, KUMIP 204260-204266.

1976, 1982) probably are not conspecific with the type, and few, if any, were coeval with it. Therefore, most specimens that I formerly assigned to *P. richmondensis* are here reassigned to *P. occultatus*. Other specimens, more recently collected from Nevada and Utah, together with a few specimens from North Greenland, are also assigned to this species.

*Occurrence.*—*P. occultatus* is presently known from Australia, the United States (Nevada, Utah), Greenland, and possibly Canada (District of Mackenzie). Australian occurrences have recently been documented by Öpik (1979). In Nevada, a few specimens are in collections from about 60 m above the base of

the lower shale member of the Lincoln Peak Formation in the southernmost White Pine Range (349), an undetermined level in the lower shale member of the Lincoln Peak Formation in the southern Ruby Mountains (350), and 317 m above the base of the Secret Canyon Formation in the northern Egan Range (169). In Utah, numerous specimens are in collections (113, 115, 159, 337, 347, 349, 350, 391, 393, 395, 397, 737, 739, 740, 758, 759, 772, 796, 3293-CO, 3296-CO, 3298-CO, 3302-CO, 3303-CO, 3306-CO, 3326-CO, 3430 to 3432-CO) ranging from 30 m below the top of the Wheeler Formation to about 330 m above the base of the Marjum Formation in the central



House Range. In North Greenland, a few specimens are in collections GGU 218626, 218644, and 218647 from 75 to 85 m above the base of Formation T1 of the Tavsens Iskappe Group. Fritz (1981) has reported the occurrence of *P. richmondensis*?, which may represent *P. occultatus* as used herein, from 52 m above the base of the Rockslide Formation in the Mackenzie Mountains, District of Mackenzie, Canada.

*P. occultatus* has a total observed stratigraphic range from the uppermost *P. atavus* Zone through the lower two-thirds of the *P. punctuosus* Zone. In the Great Basin, the species is most common in the *P. punctuosus* Zone, and all specimens known from Greenland are from that zone.

### PTYCHAGNOSTUS PRAECURRENS (Westergård)

Figure 19

*Agnostus gibbus praecurrens* WESTERGÅRD, 1936, p. 29, pl. 1, figs. 19-23.

*Ptychagnostus praecurrens* (Westergård) RASETTI, 1967, p. 28; ROBISON, 1982, p. 145-148, pl. 4, figs. 7-10 (see for additional synonymy).

*Diagnosis.*—Cephalon having smooth genae. Glabella elongate, sides nearly parallel; median node behind midpoint of postero-

glabella. Basal lobes slightly elongate, anteriorly ill-defined. Pygidial M2 having median tubercle of small to medium size. Spines lacking.

*Discussion.*—The species concept of Robison (1982:145-148) is followed here.

*P. praecurrens* is the oldest species of *Ptychagnostus*. It appears to have evolved directly from *Peronopsis brighamensis*, the major difference being development of a preglabellar median furrow in *P. praecurrens* (Robison, 1978:2-3).

*Occurrence.*—In North America, *P. praecurrens* is known from 21 m of the Stephen Formation at the famous Burgess quarry locality in British Columbia. There it is one of the most abundant fossils (Fritz, 1971:1166). Elsewhere the species is known from Australia, Sweden, the Soviet Union, and possibly Norway and Antarctica (see Robison, 1982:148). It ranges through the *P. praecurrens* Zone, and in Australia, Sweden, and the Soviet Union it ranges into the *P. gibbus* Zone.

### PTYCHAGNOSTUS PUNCTUOSUS (Angelin)

Figure 20

*Agnostus punctuosus* ANGELIN, 1851, p. 8, pl. 6, fig. 11; BRØGGER, 1875, p. 576, pl. 25, fig. 2; 1878, p. 67, pl. 6, figs. 12a, b; TULLBERG, 1880, p. 17, pl. 1, figs. 5a-d; LINNARSSON, 1883, p. 32; KOKEN, 1896, p. 349; MATTHEW, 1896, p. 232, pl. 16, figs. 11a, b; GRÖNWALL, 1902, p. 55; LAKE, 1906, p. 4-6, pl. 1, figs. 4-6; ILLING, 1916, p. 409, pl. 29, figs. 2, 3; NICHOLAS, 1916, p. 452-453; STRAND, 1929, p. 344.

*Agnostus laevigatus terranovicus* MATTHEW (?part), 1896, p. 233-234 [see note by Hutchinson, 1962, p. 84].

*Agnostus punctuosus* var. MATTHEW, 1897, p. 172, pl. 1, fig. 3.

*Agnostus scutalis* SALTER (part) in Hicks, 1872, p. 175, pl. 5, fig. 9 (10?).

*Agnostus scarabaeodes* SALTER in Hicks, 1872, p. 175, pl. 5, fig. 8; SALTER, 1873, p. 4.

*Ptychagnostus punctuosus* (Angelin) JAEKEL, 1909, p. 400; KOBAYASHI, 1939, p. 153; SHIMER and SHROCK, 1944, p. 600, pl. 251, fig. 20; HUTCHINSON, 1962, p. 84, pl. 9, figs. 9-19; RASETTI, 1967, p. 28, pl. 9, figs. 28-30; ALLEN, JACKSON, and RUSHTON, 1981, pl. 16, fig. 1.

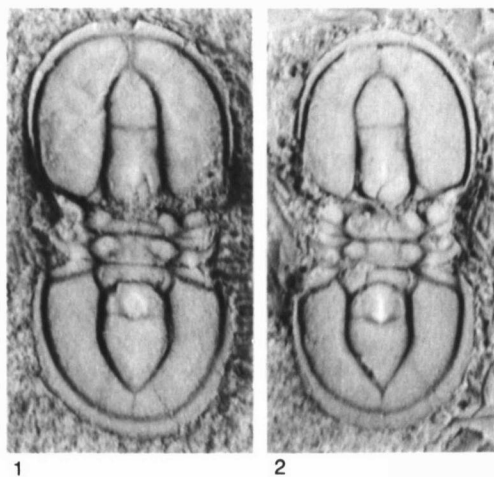


Fig. 19. *Ptychagnostus praecurrens* (Westergård); complete exoskeletons flattened in shale; Stephen Formation, British Columbia, Canada; both  $\times 10$ . 1, GSC 65861 from GSC collection 75000. 2, GSC 65863 from GSC collection 81235.

*Ptychagnostus (Ptychagnostus) punctuosus* (Angelin)  
WESTERGÅRD, 1946, p. 78-79, pl. 11, figs. 34, 35; pl. 12, figs. 1-7.

*Ptychagnostus punctuosus punctuosus* (Angelin)  
ÖPIK, 1979, p. 89-91, pl. 38, fig. 1; pl. 39, figs. 1-7, 9, 10; pl. 40, fig. 1.

*Ptychagnostus punctuosus fermexilis* ÖPIK, 1979, p. 92, pl. 41, figs. 1-5.

*Diagnosis.*—Holaspides consistently possessing genal scrobicules and lacking spines. Several other features change during ontogeny. On

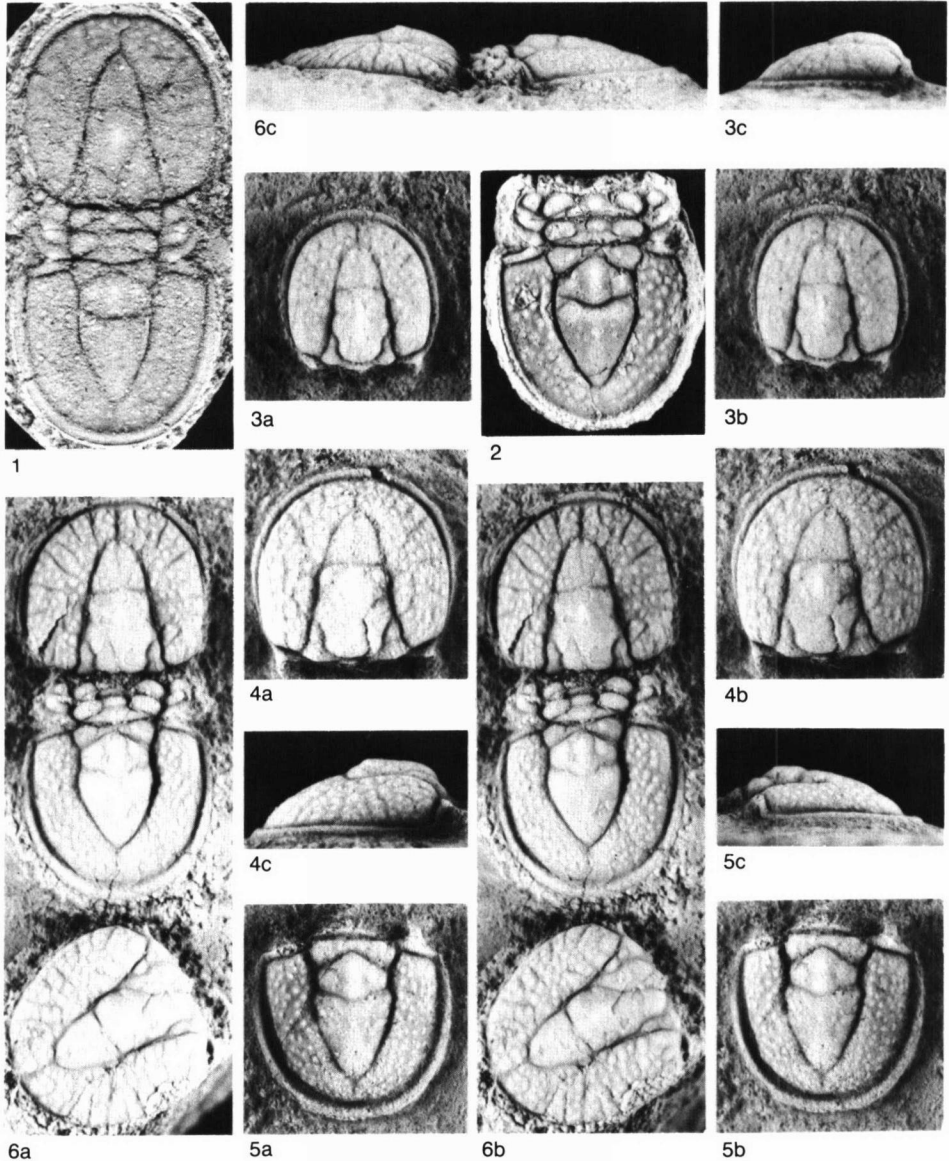


Fig. 20. *Ptychagnostus punctuosus* (Angelin); 3 is  $\times 10$ , all others are  $\times 8$ . 1, 2, Complete and partial dorsal exoskeletons, KUMIP 204267 and 204268 from 347, about 60 m above base of Marjum Formation, House Range, Utah. 3, 4, Cephala, KUMIP 204269 and 204270 from 398, about 145 m above base of Marjum Formation, House Range, Utah. 5, Pygidium, KUMIP 204271 from 398. 6, Dorsal exoskeleton and cephalon, KUMIP 204272 and 204273 from 105, upper Geddes Limestone, Eureka mining district, Nevada.

late holaspides, granules are prominent on genae and on pleural fields of pygidium, weak on cephalic and pygidial axes, and apparently absent on thoracic segments. Meraspides commonly have acutely pointed glabella and pygidial axis, well-defined postaxial median furrow, and granules may be lacking. During holaspide ontogeny, anteroglabella may become bluntly rounded in front and rarely may be weakly cleft, pygidial M2 becomes slightly constricted, and posteroaxis may become moderately to bluntly pointed. Postaxial median furrow effaced on largest holaspides. Basal lobes elongate and usually divided. Median node anterior from posteroglabellar midpoint, between F2. Primary median tubercle on pygidial M2 generally low, elongate, and poorly defined; moderately indents F2. Posteroaxis centrally depressed, may have weak secondary median node at midlength, and may have slightly concave flanks on large holaspides. Convexity of cephalon moderate to high, of pygidium low to moderate.

*Discussion.*—Holaspides of *P. punctuosus*, the type species of *Ptychagnostus*, are most easily differentiated by the combination of prominent genal scrobicules, abundant granules on surfaces of both cephalon and pygidium, and the absence of spines.

The recognition of subspecies of *P. punctuosus* has been a common practice. By far the subspecies most commonly referred to are *P. punctuosus punctuosus* and *P. punctuosus affinis*. In a few places, these taxa have been reported in association, but usually only one taxon is present. According to Westergård (1946:79), "intermediate links exist." Nevertheless, in most collections, specimens can easily be assigned to one taxon or the other, and I here prefer to assign them species rank rather than subspecies. *P. affinis* most noticeably differs from *P. punctuosus* by lacking granules on the cephalic surface, and granules on the pygidial surface are usually more weakly developed.

Öpik (1979) described a new subspecies, *P. punctuosus fermexilis*, which he differentiated primarily "by the slenderness of its glabella and by the prominence of the central node on the second lobe of the pygidial axis." These and other differences discussed by Öpik are all minor and fall within the range of variation seen in large populations of *P. punctuosus*. Thus,

I find no reason to continue recognition of this subspecies.

*Occurrence.*—Geographically, *P. punctuosus* is widely distributed. Representatives have been described and illustrated from Sweden, Norway, Denmark, England, Wales, Canada (eastern Newfoundland), United States (New York), and Australia. Additionally, the species has been reported in faunal lists for New Brunswick, Canada (Howell in Hayes and Howell, 1937:89), New Zealand (Benson, 1956:287), and the Siberian platform of the Soviet Union (Demokidov, Pisarchik, and Tchernysheva, 1966:55).

For the first time, specimens of *P. punctuosus* are illustrated herein from Nevada and Utah. About 20 specimens are in collections 105 and 804 from the upper 4 m of the Geddes Limestone, Eureka mining district, Nevada. Several other specimens are in collections 347, 396, and 398, ranging from 27 to about 140 m above the base of the Marjum Formation, central House Range, Utah.

Stratigraphically, *P. punctuosus* is restricted to the interval-zone that bears its name.

Among fossils described from Nyeboe Land, western North Greenland, are a cephalon and a pygidium that Poulsen (1969:4-5, fig. 4A,B) assigned to *P. punctuosus*. The scrobiculate cephalon is poorly preserved, but appears to lack granules on the dorsal surface. It probably does not represent *P. punctuosus*, and I consider its placement within *Ptychagnostus* to be indeterminate. The pygidium also appears to lack granules that are typical of *P. punctuosus*. On the basis of its axial shape and strong median tubercle that deeply indents the F2, I suggest an assignment to *Onymagnostus hybridus* rather than *P. punctuosus*. Hence, *P. punctuosus* is not known with certainty from Greenland.

#### PTYCHAGNOSTUS RICHMONDENSIS (Walcott)

*Discussion.*—Although I (Robison, 1964:524) previously followed Palmer's (1954:61-62) appraisal of *P. richmondensis*, further collecting and review has led me to the conclusion that the species is unrecognizable. From the Eureka mining district, Nevada, Walcott (1884:24-25, pl. 9, fig. 10) originally described a single cephalon as *Agnostus richmondensis*, which he

illustrated by a line drawing. The cephalon was reported to be from the upper portion of the "Prospect Mountain limestone," a rock unit that was later reassigned to the Geddes Limestone (see Nolan, Merriam, and Williams, 1956:9). Features mentioned in Walcott's description or shown by his figure indicate that the cephalon probably represents *Ptychagnostus*; however, it is important that he gave no indication of the presence of posterolateral border spines.

In 1954, Palmer (p. 61) reported that Walcott's original specimen could not be located among collections of the U. S. National Museum. From more recent U. S. Geological Survey collections from the Geddes Limestone of the Eureka district, Palmer described and illustrated specimens that he thought to be conspecific with *P. richmondensis*. The single illustrated cephalon from collection 965-CO has a pair of stout posterolateral border spines whereas the single illustrated pygidium from collection 901-CO lacks axial and border spines. Review of the available U. S. Geological Survey collections as well as additional collecting by me has shown that the Geddes Limestone of the Eureka district contains faunas of the *P. gibbus* to lower *P. punctuosus* zones. Among those faunas, I have been unable to find an agnostoid species with a combination of spines on the cephalon and pygidium like Palmer described as *P. richmondensis*. Moreover, I conclude that the pygidium illustrated by Palmer probably represents *P. intermedius* whereas the cephalon represents an undetermined species of *Ptychagnostus*, but not *P. intermedius*. Based on features shown in Walcott's (1884) original illustration, *P. richmondensis* may be a junior synonym of *P. atavus*, which is present in the Geddes Limestone (Robison, 1982); however, details are inadequate for confident identification.

Specimens from Utah that I (Robison, 1964:523-524, pl. 79, figs. 12, 15-22) previously assigned to *P. richmondensis* are from strata younger than the Geddes Limestone. One of the illustrated specimens (pl. 79, fig. 15) has been reassigned to *P. atavus* (Robison, 1982:137). The other illustrated specimens are here reassigned to *P. occultatus* Öpik.

### Genus LEJOPYGE Corda

*Lejopyge* CORDA in Hawle and Corda, 1847, p. 51; KOBAYASHI, 1937, p. 437-447; 1939, p. 131-132; LERMONTOVA, 1940, p. 130; WESTERGÅRD, 1946, p. 87; POKROVSKAYA, 1958, p. 72-76; in Tcherneysheva, 1960, p. 60; HOWELL, 1959, p. O178; ROBISON, 1964, p. 521; PALMER, 1968, p. 27; DAILY and JAGO, 1975, p. 527-550; JAGO, 1976b, p. 12.

*Miagnostus* JAEKEL, 1909, p. 401.

*Phoidagnostus* WHITEHOUSE, 1936, p. 93; KOBAYASHI, 1939, p. 135-136; LERMONTOVA, 1940, p. 130; WESTERGÅRD, 1946, p. 91; IVSHIN, 1953, p. 24-25; POKROVSKAYA, 1958, p. 37-38; in Tcherneysheva, 1960, p. 60; HOWELL, 1959, p. O181.

*Lejopyge* Hawle and Corda ÖPIK, 1961a, p. 85; 1979, p. 157-159.

*Pseudophalacroma* POKROVSKAYA, 1958, p. 79; ÖPIK, 1961a, p. 90-92; 1967, p. 77; 1979, p. 163.

*Type species*.—*Battus laevigatus* Dalman, 1828:136; by monotypy.

*Diagnosis*.—Early species with little effacement of dorsal furrows on acrolobes, later species having those furrows effaced in varying degrees. Cephalic axis strongly but somewhat irregularly tapered, acutely pointed at front. Basal lobes simple. Pygidial F2 shallower than F1. Postaxial median furrow present throughout ontogeny.

*Discussion*.—Part of the preceding diagnosis necessarily pertains only to early species of *Lejopyge* that lack much effacement of furrows on the acrolobes. Effacement of furrows was common in subsequent lineages, resulting in smooth homeomorphs that may be difficult to distinguish. Development of spines was another common evolutionary trend. In one lineage, the pygidial border became unusually wide.

In most species of *Lejopyge*, the pygidial axis has a weak median node near the posterior margin of the M2; however, one new species, *L. rigbyi*, possesses a median spine on the M2. Daily and Jago (1975:530, table 1) have discussed and tabulated the variable presence or absence of weak secondary median nodes on the M1 and M3 of pygidia representing di-

fferent effaced species of *Lejopyge*. Because of apparent random variability in development of secondary nodes, I accord them no taxonomic value.

Most authors have assigned only highly effaced ptychagnostid species to *Lejopyge*. As the number of assigned species has increased, rare specimens showing vestigial features of the axis suggest that more than one phyletic lineage are represented. In 1979, Öpik significantly revised the generic concept to include species with ordinary ptychagnostid dorsal furrows. In general, I accept Öpik's revision because it adds ancestral species that unite polyphyletic lineages to form an enlarged holophyletic genus. Two new species and one new subspecies are added here, necessitating further slight modification of the generic concept. As here defined, *Lejopyge* includes *L. lundgreni* and all of its inferred descendant species (Fig. 6).

Early species of *Lejopyge* are characterized by a slightly shortened axis with a strong anterior taper to the cephalon, simple basal lobes, and a relatively shallow F2 on the pygidium. The simple condition of the basal lobes is a derived character that is homeomorphic with the condition in some species of *Onymagnostus*; however, other axial features are rather different in the two genera.

*Phoidagnostus limbatus* Whitehouse is the type species of *Phoidagnostus* Whitehouse (1936). Öpik (1961a:54, 86; 1967:76) concluded that the type specimens of *P. limbatus* are compressed representatives of either *Lejopyge laevigata* or *L. armata*. Therefore, *Phoidagnostus* is a subjective junior synonym of *Lejopyge*.

*Pseudophalacroma* was erected by Pokrovskaya (1958) to include a single new species, *P. crebra*, from Yakutia in the Soviet Union. Öpik (1961a) subsequently reassigned *Phalacroma?* *dubium* Whitehouse (1936) to *Pseudophalacroma*, and he corrected the name of the type species to *P. crebrum*. Pokrovskaya indicated that *P. crebrum* lacks a glabellar node and basal lobes; however, judging from her illustrations of type specimens, absence of those features may be due to poor preservation rather than an original condition. Otherwise, except for an unusually wide pygidial border, both *P. crebrum* and *P. dubium* agree in all essential features with some

species of *Lejopyge*. Indeed, Öpik (1979:159) later speculated that a lineage including a new species, *L. praecox*, "maintained its continuity in the species of the genus *Pseudophalacroma*." Pygidial borders in *L. praecox* and *L. multifora* Öpik (1979) are transitional in width between those in species previously assigned to either *Lejopyge* or *Pseudophalacroma*. Therefore, I find no justification for continuing to recognize *Pseudophalacroma* as a separate genus, and I consider it to be a junior synonym of *Lejopyge*.

A thorough review of the taxonomy and biostratigraphic significance of several effaced species of *Lejopyge* has been given by Daily and Jago (1975). A revision of the generic concept and a description of three new species were given by Öpik (1979). Based on further review as well as study of many additional collections, the following previously described species are here included in *Lejopyge*: *L. laevigata* (Dalman, 1828), *L. armata* (Linnarsson, 1869), *L. elegans* (Tullberg, 1880), *L. lundgreni* (Tullberg, 1880), *L. dubium* (Whitehouse, 1936), *L. crebrum* (Pokrovskaya, 1958), *L. calva* (Robison, 1964), *L. multifora* (Öpik, 1979), and *L. praecox* (Öpik, 1979). The holotype and only illustrated specimen of *L. cosfordae* (Öpik, 1979) is an early holaspid and the name may be a synonym of *L. praecox*. Three new taxa, *L. acantha*, *L. rigbyi*, and *L. laevigata rubyensis*, are described here. Four taxa, *Aagnostus laevigatus* var. *forfex* Brøgger (1878), *L. exilis* Whitehouse (1936), *L. empozadense* Rusconi (1954), and *L. eosa* Yang (1982), are considered to be indeterminate.

With regard to spelling of the generic name, Öpik (1979:157-158) used *Leiopyge* rather than *Lejopyge* because "(1) the word is classical Greek in Latin translation, and (2) 'i' (iota) cannot be expressed by 'j' which is unknown in Latin and Greek alphabets." Öpik's emendation is an invalid change in spelling (*nomen vanum*) because ICZN Article 11(b)(i) specifically states that the letter 'j,' which is common in neo-Latin, "may be used in zoological names."

*Occurrence*.—*Lejopyge* is a geographically widespread genus in open-shelf lithofacies, having been reported from all continents except Africa. It has an observed stratigraphic range from near the base of the *Ptychagnostus punctuosus* Zone to the top of the *Lejopyge laevigata* Zone.

**LEJOPYGE ACANTHA, n. sp.**

Figure 21

*Holotype*.—Cephalon (Fig. 21, 1), KUMIP 204324.

*Description*.—*Lejopyge* having paired spines of moderate size on posterolateral borders of cephalon and posterior pleural bands of posterior thoracic segment. Furrows of cephalic acrolobe usually effaced except those outlining basal lobes. Thorax having normally developed

furrows of ptychagnostid type. Pygidium lacking spines; border of moderate and uniform width posteriorly, narrowing anterolaterally. Furrows of pygidial acrolobe mostly effaced except distally shallowing axial furrows along sides of M1. On internal mold, cephalon may retain weak, anteriorly shallowing vestiges of axial furrows immediately in front of basal lobes; pygidium may retain vestiges of axial furrows to back of M2 as well as abaxial vestiges of F1. Surface of acrolobes lacking

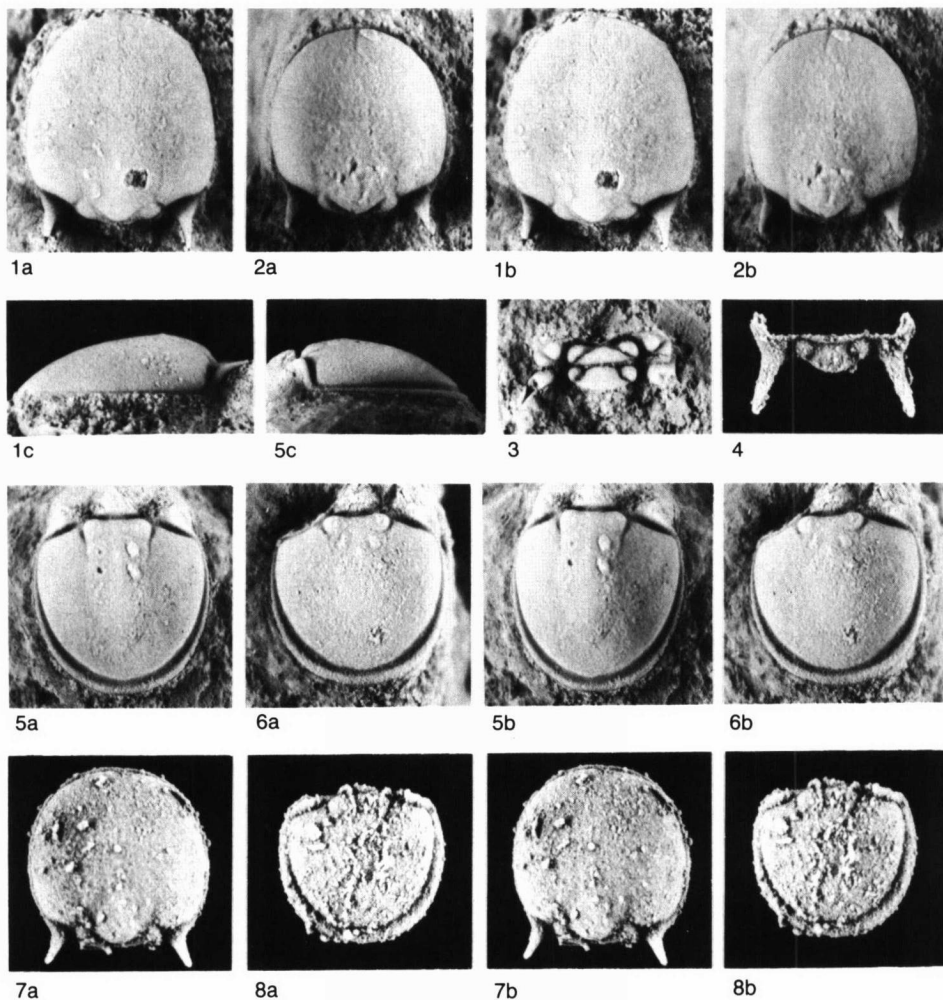


Fig. 21. *Lejopyge acantha*, n. sp.; 1-3, 5, 6 from locality 816, about 20 m above base of Weeks Limestone, House Range, Utah; 4, 7, 8 from locality 111a, about 8 m above middle limestone member of Lincoln Peak Formation, northern Schell Creek Range, Nevada. 1, Holotype cephalon in limestone, KUMIP 204324,  $\times 8$ . 2, Cephalon, KUMIP 204325,  $\times 8$ . 3, Thorax with broken pleural spines on posterior segment, KUMIP 204326,  $\times 8$ . 4, Silicified posterior thoracic segment with pleural spines, KUMIP 189183,  $\times 10$ . 5, 6, Pygidia with muscle markings on anterior axial region, KUMIP 204327 and 204328, both  $\times 8$ . 7, 8, Silicified cephalon and pygidium, KUMIP 189182 and 189184, both  $\times 10$ .

punctae.

*Discussion.*—*L. acantha* closely resembles *L. multifora* (Öpik, 1979:162-163, pl. 65, figs. 3, 4) in spine morphology. They are the only species of *Lejopyge* with one pair of spines on the cephalon, one on the thorax, and none on the pygidium. *L. acantha* differs from *L. multifora* by lacking punctate acrolobe surfaces; also, its pygidial border is only about half as wide.

*L. acantha* also closely resembles *L. calva*, which is its inferred ancestor. *L. acantha* primarily differs from *L. calva* by the presence of spines, but it also has slightly less effaced anterior axial furrows on the pygidium.

*Occurrence.*—*L. acantha* is presently known from only Nevada and Utah. In Nevada, it is abundant in collection 378 from 6 m above the base of the upper shale member of the Lincoln Peak Formation in the northern Schell Creek Range. It is also present in collection 155 from 1.5 m above the base of member B of the Emigrant Springs Formation in the southern Schell Creek Range. In Utah, it is rare to

abundant in collections 380, 732-734, and 816 from the upper meter of the Marjum Formation to about 20 m above the base of the Weeks Limestone in the central House Range. Biostratigraphically, the observed range of *L. acantha* is in the middle of the lower *L. laevigata* subzone (Fig. 4).

### LEJOPYGE ARMATA (Linnarsson)

Figure 22

*Agnostus laevigatus* var. *armata* LINNARSSON, 1869, p. 82, pl. 2, figs. 58, 59; WALLERIUS, 1895, p. 37.

*Lejopyge laevigatus armatus* (Linnarsson) KOBAYASHI, 1939, p. 131-132.

*Lejopyge armata* (Linnarsson) LERMONTOVA, 1940, p. 130, pl. 36, figs. 11a-c; DEMOKIDOV, PISARCHIK, and TCHERNYSHEVA, 1966, p. 56; ERGALIEV, 1980, p. 77-79, pl. 2, figs. 11, 13-17; YANG, 1982, p. 301, pl. 1, fig. 9.

*Lejopyge laevigata armata* (Linnarsson) WEST-

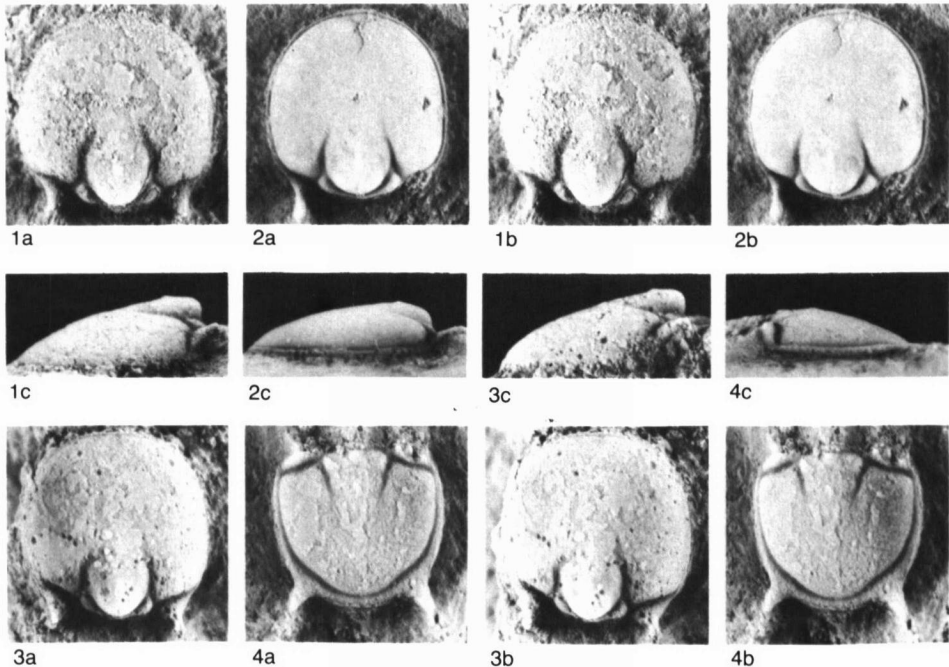


Fig. 22. *Lejopyge armata* (Linnarsson). 1, Cephalon, USNM 374591 from USNM 8m; from unknown horizon in Lincoln Peak Formation, Snake Range, Nevada;  $\times 6$ . 2, Cephalon, MGUH 16.278 from GGU 225544; 90 m above base of Formation T2, Tavsens Iskappe Group, North Greenland;  $\times 8$ . 3, 4 Cephalon and pygidium, KUMIP 204312 and 204313 from RR79-18A; about 45 m above middle limestone member, Lincoln Peak Formation, Ruby Mountains, Nevada; both  $\times 8$ .

- ERGÅRD, 1946, p. 89, pl. 13, figs. 28-36; LU and others, 1965, p. 34, pl. 3, fig. 1; DAILY, 1966, p. 95-96; KOBAYASHI, 1971, p. 176; LU and others, 1974, p. 79, pl. 1, fig. 11; DAILY and JAGO, 1975, p. 528-532, pl. 62, figs. 10-18; JAGO, 1976b, p. 13, pl. 2, figs. 3-8; YANG, 1978, p. 23, pl. 1, figs. 19, 20.
- Lejopyge laevigata* (Dalman) WESTERGÅRD (in part), 1946, pl. 13, fig. 25.
- Lejopyge laevigata ferrugata* WESTERGÅRD, 1946, p. 89-90, pl. 14, figs. 1, 2; DAILY and JAGO, 1975, pl. 63, figs. 1-3.
- Lejopyge laevigata armata* (Linnarsson) ÖPIK, 1961a, p. 87, pl. 21, fig. 10a, b; pl. 22, figs. 1-4.
- Lejopyge cos* ÖPIK, 1967, p. 93-94, pl. 57, figs. 5, 6.
- Lejopyge armata* (Linnarsson) ÖPIK, 1979, p. 161-162, pl. 64, figs. 5, 6.

*Diagnosis.*—Furrows of acrolobes usually effaced except basal furrows and distally shallowing axial furrows along most of postero-glabella and anteroaxis. Paired spines, variable in length, present on posterolateral borders of both cephalon and pygidium. Genae usually smooth, rarely with weak to moderately deep scrobicules. Pygidial acrolobe commonly having slight indentations adjacent to bases of border spines.

*Discussion.*—*L. armata* is the only species of *Lejopyge* to possess border spines on both the cephalon and pygidium. In degree of effacement of dorsal furrows, *L. armata* closely resembles *L. laevigata*, its inferred ancestor. Reasons for recognizing *L. armata* and *L. laevigata* as separate species, and for including rare specimens with genal scrobicules in *L. armata*, are given in the discussion of *L. laevigata*.

Yang (1982:30, pl. 1, figs. 10, 11) has described some pygidia from the Zhejiang Province of China under the name "*Lejopyge armata* forma *trigonospinosa*, forma nov." These pygidia are unusual in having border spines with exceptionally large bases that are much closer together than in typical representatives of *L. armata*. According to ICZN Article 45(e)(ii), the form name is to be regarded as of infrasubspecific rank and provisions of the Code do not apply to it (Article 45c). On the basis of available information, I am uncertain whether or not these specimens represent *L. armata* or a new species.

Daily and Jago (1975:529-532) presented a detailed and cogent argument for concluding that *L. cos* Öpik (1967) is a junior synonym of *L. laevigata armata* (= *L. armata* herein). I concur with that synonymy.

*Occurrence.*—*L. armata* has previously been described from Sweden, the Soviet Union, China, and Australia.

*L. armata* is here reported for the first time from three localities in Nevada. A few specimens are in collection RR79-18A from about 45 m above the base of the upper shale member of the Lincoln Peak Formation in the southern Ruby Mountains. More than 200 specimens are in collections DKS76-124v, 124z, 124-210, 124aa, and 124bb ranging from 36 to 78 m above the base of the upper shale member of the Lincoln Peak Formation in the northern Schell Creek Range. Four specimens are in USNM collection 8m, which according to the label was collected in 1900 by F. B. Weeks from "4 miles northeast of Osceola, Nevada" in the southern Snake Range. I have attempted to visit locality 8m for additional collecting, but extensive outcrops of Prospect Mountain Quartzite of Early Cambrian age in the area four miles northeast of Osceola indicates an error in the recorded locality description.

*L. armata* also is here reported for the first time from North Greenland. Two cephalae are in GGU 225544 and a few poorly preserved specimens are in GGU 271414 from 90 and 12 m, respectively, above the base of Formation T2 of the Tavsens Iskappe Group.

From worldwide reports, *L. armata* ranges throughout most of the *L. laevigata* Zone as defined herein; however, it usually is most common in the upper subzone. According to Westergård (1946:89), *L. armata* is very rare in the *Solenopleura brachymetopa* Zone (=lower *L. laevigata* subzone, herein) in Sweden. In North America and Greenland, *L. armata* has been observed in association with only faunas of the upper *L. laevigata* subzone.

### LEJOPYGE CALVA Robison

Figures 23, 24

- Lejopyge calva* ROBISON, 1964, p. 521, pl. 83, figs. 1-4; PALMER, 1968, p. B27-B28, pl. 6, figs. 15-18; DAILY and JAGO, 1975, pl. 63, figs. 7-10; ERGALIEV, 1980, p. 79-80, pl. 2, fig. 12.



*Diagnosis.*—Exoskeleton nonspinose. Furrows of acrolobes usually effaced except those outlining basal lobes on cephalon and axial furrows adjacent to M1 on pygidium. Genae

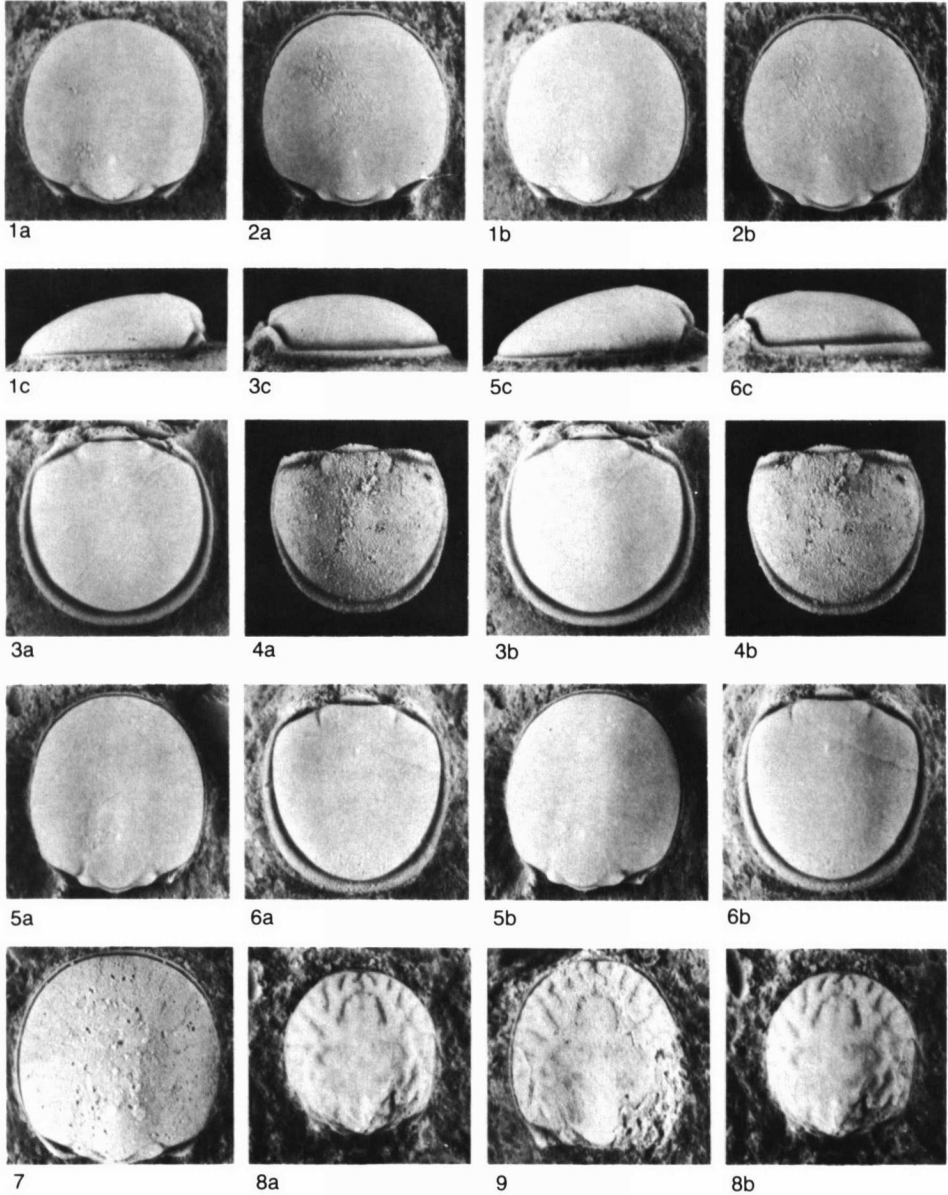


Fig. 23. *Lejopyge calva* Robison from Nevada and Utah; all preserved in limestone. 1. Cephalon, KUMIP 204314 from 156; 3 m above base, member B, Emigrant Springs Limestone, southern Schell Creek Range, Nevada;  $\times 8$ . 2. 5. Cephalon, KUMIP 204315 and 204316 from 376; 2.4 m above middle limestone member, Lincoln Peak formation, northern Schell Creek Range, Nevada; both  $\times 7$ . 3. Pygidium, KUMIP 204317 from 155; 1.5 m above base, member B, Emigrant Springs Limestone, southern Schell Creek Range;  $\times 7$ . 4. Silicified pygidium, KUMIP 204318 from 821; near top of Marjum Formation, House Range, Utah;  $\times 7$ . 6. Pygidium, KUMIP 204320 from 376.  $\times 8$ . 7. Cephalon with weak genal scrobicules, KUMIP 204321 from 751; about 43 m above base of Weeks Limestone, House Range;  $\times 7$ . 8. Small cephalon with moderately deep genal scrobicules, KUMIP 204319 from 156.  $\times 10$ . 9. Cephalon with moderately deep genal scrobicules, KUMIP 204322 from 154; top bed, member A, Emigrant Springs Limestone, southern Schell Creek Range;  $\times 8$ .

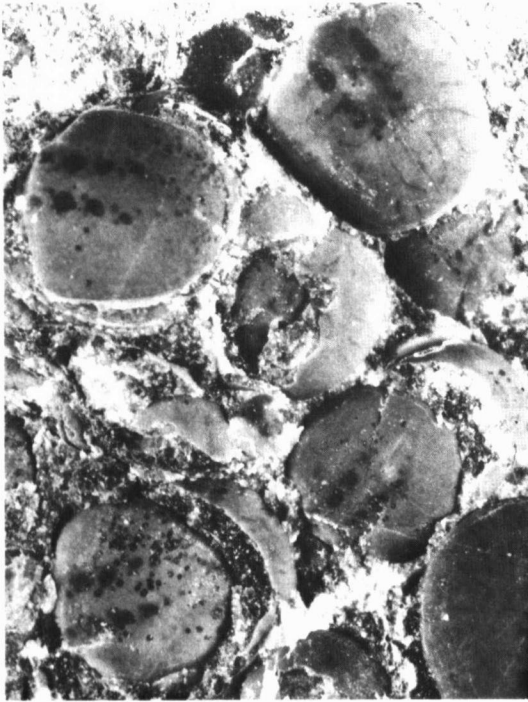


Fig. 24. *Lejopyge calva* Robison with dark markings on cephalon and pygidia; KUMIP 204323 from 155; 1.5 m above base, member B, Emigrant Springs Limestone, southern Schell Creek Range, Nevada;  $\times 10$ .

usually smooth, very rarely with weak to moderately deep scrobicules. Pygidial border of uniform and moderate width posteriorly, narrowing anterolaterally.

*Discussion.*—*L. calva* is one of the most common fossils in upper Middle Cambrian rocks of the Great Basin. At many localities, coquinas of disarticulated sclerites comprise thin to moderately thick, laterally extensive limestone beds.

Illustrated type specimens of *L. calva* (Robison, 1964, pl. 83, figs. 1-4) are mostly exfoliated internal molds. Additional specimens illustrated here are not exfoliated and were selected to demonstrate minor observed variation in morphology. In general, vestiges of axial furrows are slightly longer on internal molds than on dorsal surfaces of the cephalon and pygidium.

Genal surfaces in *L. calva* are usually smooth, but weak (Fig. 23,7) to moderately deep (Fig. 23,8,9) scrobicules are rarely developed (less than 0.1 percent of cephalon). As in *L.*

*armata* and *L. laevigata*, I consider these scrobicules to represent minor intraspecific variation rather than a character of taxonomic significance. Acrolobe shape in large populations of *L. calva* is also variable. Subcircular (e.g., Fig. 23,1-3) and slightly elongate (e.g., Fig. 23,5,6) end members of a morphologic continuum may represent sexual dimorphism, but proof is lacking.

At several localities in Nevada and Utah specimens of *L. calva* commonly show similar patterns of dark markings (Fig. 24). These markings are similar to those discussed by Harrington (1959:O94-O97). Most axial markings may represent patterns from muscle insertions on parietal surfaces. Weak, irregular lines on genae may represent parietal attachment of mesenteries that separated underlying alimentary diverticula.

Representatives of *L. calva* closely resemble those of *L. laevigata*, differing primarily in the more complete effacement of axial furrows in *L. calva*.

*Occurrence.*—*L. calva* has been described from the United States (Alaska, Nevada, Utah) and the Soviet Union (Kazakhstan).

In addition to localities recorded in previous literature, *L. calva* is here reported from several new localities in the Great Basin. Additional collections from Nevada are from the northern Schell Creek Range (111a and 376 from 2 to 8 m above base of upper shale member, Lincoln Peak Formation), southern Schell Creek Range (154-156 from top bed of member A and basal 3 m of member B, Emigrant Springs Limestone), and southern Egan Range (820 from about 10 m above base of member A, Emigrant Springs Limestone). All additional collections from Utah are from the central House Range. These include collections 728-731, 733, 734, 746-751, 766-769, 776-778, 813-815, 821, 826, and 828 ranging from 34 m below the top of the Marjum Formation to about 30 m above the base of the Weeks Limestone.

Biostratigraphically, *L. calva* is restricted to the lower subzone of the *L. laevigata* Zone.

### LEJOPYGE LAEVIGATA (Dalman)

Figure 25

*Battus laevigatus* DALMAN, 1828, p. 136-137;  
HISINGER, 1837, p. 20, pl. 4, fig. 7.  
*Lejopyge laevigata* (Dalman) CORDA in Hawle and

Corda, 1847, p. 51, pl. 3, fig. 25; WESTERGÅRD, 1946, p. 87-89, pl. 13, figs. 18-24, 26, ?27 (not 25); pl. 16, fig. 9; POKROVSKAYA, 1958, p. 76-78, pl. 5, figs. 16, 17; POLETAEVA in Khalifin, 1960, p. 163, pl. 18, figs. 3a, b; DAILY, 1966, p. 95; HUCKE and VOIGHT, 1967, p. 48, pl. 5, fig. 6; MARTINSON, 1968, p. 149, fig. 9A; PALMER, 1968, p. B28, pl. 6, fig. 19; KHAIRULLINA, 1970, p. 16, pl. 1, fig. 15; 1973, p. 50, pl. 3, figs. 11-14; HILL, PLAYFORD, and WOODS, 1971, p. cm. 20, pl. 10, figs. 5, 6; DAILY and JAGO, 1975, p. 527-550, pl. 62, figs. 1-9 (not 10); not POULSEN and ANDERSON, 1975, p. 2075-2076, pl. 2, figs. 1-9; JAGO, 1976b, p. 12, pl. 2, figs. 1, 2; YANG, 1978, p. 22-23, pl. 1, fig. 17; ERGALIEV, 1980, p. 77, pl. 3, figs. 1-9; EGOROVA, PEGEL, and TCHERNYSHEVA in Egorova and others, 1982, p. 74, pl. 25, fig. 1; pl. 28, figs. 2-5; pl. 46, fig. 6.

*Agnostus laevigatus* (Dalman) ANGELIN, 1851, p. 6, pl. 6, fig. 3; LINNARSSON, 1869, p. 82; 1873, p. 246; BRØGGER, 1876, p. 194, pl. 8, fig. 1; 1878, p. 74, pl. 5, fig. 6; TULLBERG,

1880, p. 27, pl. 2, fig. 17; WALLERIUS, 1895, p. 35; not MATTHEW, 1896, p. 233; KOKEN, 1896, p. 347, fig. 242; GRÖNWALL, 1902, p. 60; STRAND, 1929, p. 346.

?*Agnostus laevigatus* (Dalman) var. MATTHEW, 1897, p. 173, pl. 1, fig. 7.

?*Phoidagnostus limbatus* WHITEHOUSE, 1936, p. 93-94, pl. 9, figs. 10, 11.

*Lejopyge laevigata rugifera* WESTERGÅRD, 1946, p. 90, pl. 14, fig. 3; DAILY and JAGO, 1975, p. 529, pl. 63, fig. 6.

*Lejopyge laevigata* (Dalman) ÖPIK, 1961a, p. 85-87, pl. 21, figs. 5-9; 1979, p. 161, pl. 64, figs. 1-3.

?*Lejopyge* cf. *laevigata* (Dalman) YANG, 1982, p. 301, pl. 1, figs. 12, 13.

*Diagnosis.*—Exoskeleton nonspinose. Furrows of acrolobes usually effaced except basal furrows and distally shallowing axial furrows along most of posteroglabella and anteroaxis. Genae usually smooth, rarely with weak to moderately deep scrobicules. Pygidial border of uniform and moderate width posteriorly, narrowing anterolaterally.

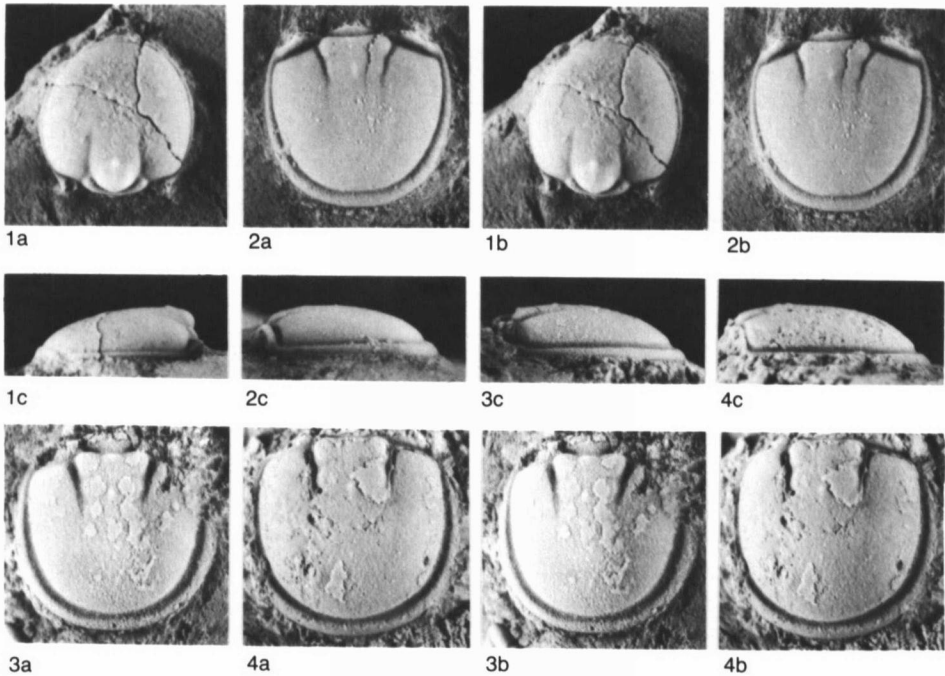


Fig. 25. *Lejopyge laevigata* (Dalman); all from Formation T2, Tavsens Iskappe Group, North Greenland. 1, 2, Cephalon and pygidium, MGUH 16.279 and 16.280 from GGU 225546, both  $\times 10$ . 3, Mostly exfoliated pygidium, MGUH 16.281 from GGU 225552,  $\times 9$ . 4, Mostly exfoliated pygidium MGUH 16.282 from GGU 225561,  $\times 7$ .

*Discussion.*—*L. laevigata* is a widely distributed species that has received much discussion (for references, see synonymy). Its origin and relationships to other species have been discussed by Westergård (1946), Pokrovskaya (1958), Öpik (1961a), and Daily and Jago (1975).

Representatives of *Lejopyge* with moderate proximal development of axial furrows on the cephalon and pygidium may possess spines of various length. Rare specimens may also possess weak to moderately deep genal scrobicules. Some authors have used these characters to differentiate varieties or subspecies of *L. laevigata* (e.g., Linnarsson, 1869; Westergård, 1946; Daily and Jago, 1975). Others have assigned the spinose forms to a separate species, *L. armata* (e.g., Lermontova, 1940; Öpik, 1979). Westergård (1946:88) justified the use of subspecies because of "considerable variability" with extreme forms being "connected by intermediate links." Although some collections contain associated nonspinose and spinose forms, many collections from widespread localities and different lithologies contain specimens that are uniformly either nonspinose or spinose. This rules out sexual dimorphism as a likely explanation for the presence or absence of spines. The observed first appearance of spinose forms is stratigraphically higher than that of nonspinose forms. Because of these distribution patterns, together with a lack of evidence for phenotypic control, I prefer to recognize separate species, *L. laevigata* (nonspinose) and *L. armata* (spinose). Spinose specimens that Westergård (e.g., 1946, pl. 13, fig. 25) assigned to *L. laevigata* I reassign to *L. armata*.

Specimens of *Lejopyge* with genal scrobicules are extremely rare. Westergård (1946) assigned two cephalons with this character to *L. laevigata rugifera*. If present, scrobicules vary from weak to moderately developed. Because of the rarity and variation of this character, together with its lack of uniform presence in any known population, I do not accord it taxonomic significance.

Specimens of *L. laevigata* are rare to common in six collections from North Greenland. Dorsal convexity of these specimens is relatively low; however, they are mostly preserved in calcareous shale and original convexity was probably reduced by compaction of the enclosing matrix.

*Occurrence.*—*L. laevigata* has been described from Sweden, Norway, Denmark, Germany (in glacial erratics), Soviet Union, China, Australia, and the United States (Alaska).

Reports of *L. laevigata* from eastern Canada are open to question. Matthew (1896:233-235) described three varieties of *Agnostus laevigatus* from eastern Newfoundland; however, all of Matthew's specimens were reassigned by Hutchinson (1962:71-72, 85-86) to genera other than *Lejopyge* and I concur with that action. Poulsen and Anderson (1975:2075-2076, pl. 2, figs. 1-9) assigned several poorly preserved specimens from southeastern Newfoundland to *L. laevigata*. Those specimens appear to lack the characteristic short, distally shallowing axial furrows on the cephalon and pygidium. In my opinion, they do not belong to *Lejopyge* and may represent *Grandagnostus*. Matthew (1897:173, pl. 1, fig. 7) also reported an unnamed variety of *A. laevigatus* from New Brunswick but his description and illustration are inadequate for verification. Absence of *L. laevigata* from later faunal lists for the same area (e.g., Hayes and Howell, 1937) leaves uncertain the presence of *L. laevigata* in New Brunswick.

*L. laevigata* here is documented for the first time from North Greenland and Nevada. Many specimens are in GGU collections 225535, 225543, 225552, 225561, and 225595 from throughout most of Formation T2 of the Tavsens Iskappe Group in North Greenland. The specimens from Nevada are assigned to a new geographic subspecies, *L. laevigata rubyensis*.

Biostratigraphically, *L. laevigata* has an observed range through the zone bearing its name.

### LEJOPYGE LAEVIGATA RUBYENSIS, n. subsp.

Figure 26

*Holotype.*—Pygidium (Fig. 26,4), KUMIP 204327.

*Description.*—*L. laevigata* having unusually deep and wide axial furrows at sides of pygidial anteroaxis. Border furrow widened in posterolateral regions of pygidium.

*Discussion.*—Some specimens of *Lejopyge* in Nevada possess characteristic features of *L.*

*laevigata* except for slight differences in width and depth of axial and border furrows on the pygidium. These differences are progressively

accentuated during holaspid ontogeny. The relative influence of genetic and phenotypic factors may never be determined. Because of

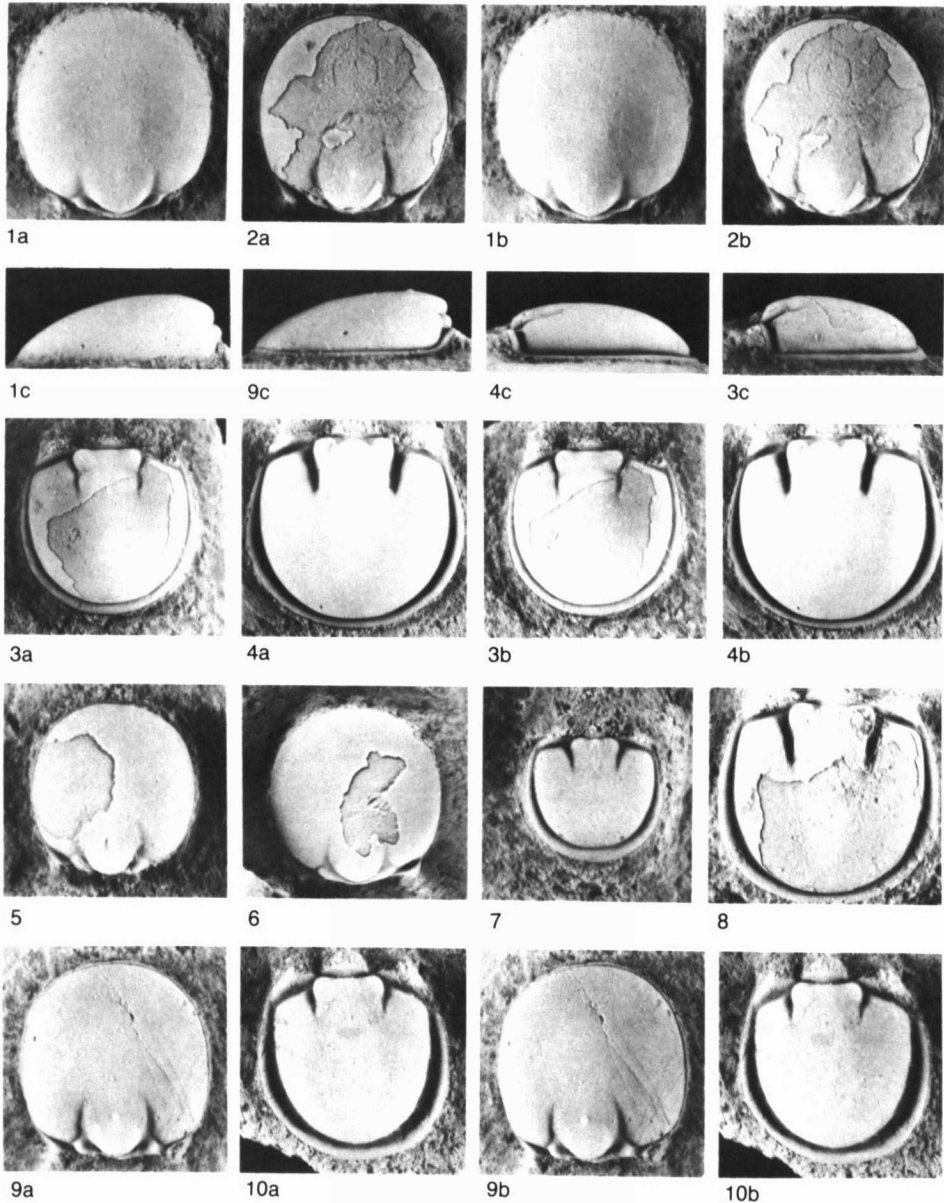


Fig. 26. *Lejopyge laevigata rubyensis*, n. subsp.; all from Lincoln Peak Formation of Nevada; 1-8 from locality RR78-35, one meter above base of upper shale member in Ruby Mountains; 9, 10 from uppermost meter of middle limestone member in southern White Pine Range. 1, Unexfoliated cephalon, KUMIP 204329,  $\times 7$ . 2, Mostly exfoliated cephalon showing weak genal scrobicules on internal mold, KUMIP 204330,  $\times 7$ . 3, Mostly exfoliated pygidium, KUMIP 204331,  $\times 7$ . 4, Unexfoliated holotype pygidium, KUMIP 204332,  $\times 7$ . 5, Partly exfoliated cephalon, KUMIP 204333,  $\times 7$ . 6, Partly exfoliated, small holaspid cephalon, KUMIP 204334,  $\times 10$ . 7, Small holaspid pygidium, KUMIP 204335,  $\times 10$ . 8, Mostly exfoliated pygidium showing faint indication of tapered posteroaxis on internal mold, KUMIP 204336,  $\times 7$ . 9, 10, Cephalon and pygidium, KUMIP 204337 and 204338, both  $\times 8$ .

morphologic gradation, particularly among early holaspides, I provisionally attribute these differences to geographic variation within *L. laevigata*.

*Occurrence.*—*L. laevigata rubyensis* is known from three localities in Nevada. More than 30 well-preserved specimens are in collections RR78-27 and RR78-35 from 2 and 1 m, respectively, above the base of the upper shale member of the Lincoln Peak Formation in the southern Ruby Mountains. Two poorly preserved pygidia of *Lejopyge*, questionably belonging to this subspecies, are in collection DKS76-124ee from 98 m above the base of the upper shale member of the Lincoln Peak Formation in the northern Schell Creek Range. About 50 specimens are in collection 795 from the upper meter of the middle limestone member of the Lincoln Peak Formation in the southern White Pine Range. If the two specimens from the Schell Creek Range represent the subspecies, it has an observed range from the middle of the lower subzone to the top of the upper subzone of the *L. laevigata* Zone. Otherwise, it is known from only the middle of the lower subzone.

*L. laevigata rubyensis* has been collected from only the most seaward *Lejopyge*-bearing lithofacies in the Great Basin. Regional biofacies relationships suggest that *L. calva* was the dominant agnostoid species in some shallower open-shelf environments whereas coeval *L. laevigata rubyensis* was dominant over some of the deeper open shelf.

### LEJOPYGE LUNDGRENII (Tullberg)

Figures 27, 28

- Agnostus lundgrenii* TULLBERG, 1880, p. 20-21, pl. 1, fig. 8; GRÖNWALL, 1902, p. 51, 197; STRAND, 1929, p. 345; COBBOLD and POCOCK, 1934, p. 342, pl. 44, figs. 20, ?21.  
*Agnostus lundgrenii* var. *nana* GRÖNWALL, 1902, p. 51-52, pl. 1, fig. 2.  
*Agnostus lundgrenii nana* (Grönwall) STRAND, 1929, p. 345, pl. 1, figs. 5, 6.  
*Agnostus atavus* (Tullberg) STRAND, 1929, p. 344, pl. 1, fig. 20.  
*Triplagnostus lundgrenii* (Tullberg) KOBAYASHI, 1939, p. 146; POULSEN, 1966, p. 121; EGOROVA, PEGEL, and TCHERNYSHEVA in Egorova and others, 1982, p. 65, pl. 54, fig. 16.  
*Triplagnostus lundgrenii nana* (Grönwall) KOBAYASHI, 1939, p. 146.

*Ptychagnostus (Triplagnostus) lundgrenii* (Tullberg) WESTERGÅRD, 1946, p. 75, pl. 10, figs. 23-25; pl. 11, figs. 1, 2.

*Ptychagnostus (Triplagnostus) lundgrenii nanus* (Grönwall) WESTERGÅRD, 1946, p. 75-76, pl. 11, figs. 3-7.

*Ptychagnostus*, species undetermined, RASETTI, 1967, p. 29, pl. 10, figs. 27-31.

*Lejopyge lundgrenii* (Tullberg) ÖPIK, 1979, p. 158.

*Lejopyge lundgrenii nanus* (Grönwall) ÖPIK, 1979, p. 158.

*Diagnosis.*—Exoskeleton nonspinose and with little effacement of dorsal furrows. Axial length compared to exoskeletal length less than in most ptychagnostid species. Cephalon moderately to highly convex, subcircular to suboval in outline. Cephalic axis broad at posterior, tapering to acute point at front; may have slight lateral constrictions at anterior ends of basal lobes and at F3. Anteroglabella low, generally flush with or little elevated above genae. F3 straight, narrow and well defined. Post-eroglabella moderately elevated above genae, F1 and F2 usually not developed. Preglabellar median furrow narrow and commonly deeper than axial furrow. Genae usually smooth, rarely having weak to moderately deep scrobicules. Pygidium semicircular and usually of moderate convexity; F2 usually shallower than F1. Posteromedian structure on M2 varying from weak node to small tubercle. Posteroaxis variable in width, slightly to moderately ogival, tapering to rather sharp point at back; may have slight central depression. Postaxial median furrow generally shallow.

*Discussion.*—*L. lundgrenii*, the ancestral species of *Lejopyge*, is characterized by normal ptychagnostid development of dorsal furrows, a slightly shortened axis, simple basal lobes, usually a weak posterior furrow (F2) on the pygidial axis, and an absence of spines. The species probably originated from a lineage containing *Ptychagnostus intermedius*. Comparative morphology indicates that the relatively short axis, simple basal lobes, and absence of genal scrobicules in late holaspides of *L. lundgrenii* (Fig. 27,7) may have been derived by paedomorphism from the early holaspid condition in *P. intermedius* (compare Robison, 1982, pl. 3, fig. 7).

In *L. lundgrenii*, as in many agnostoid species, average holaspid size in the Great Basin

(Figs. 27,1-8; 28,1-4) is approximately half that in northwestern Europe (Fig. 8,5). Paleomagnetic and lithologic evidence indicates that dur-

ing Middle Cambrian time the Great Basin terrane was positioned near the equator whereas the European terrane was in high

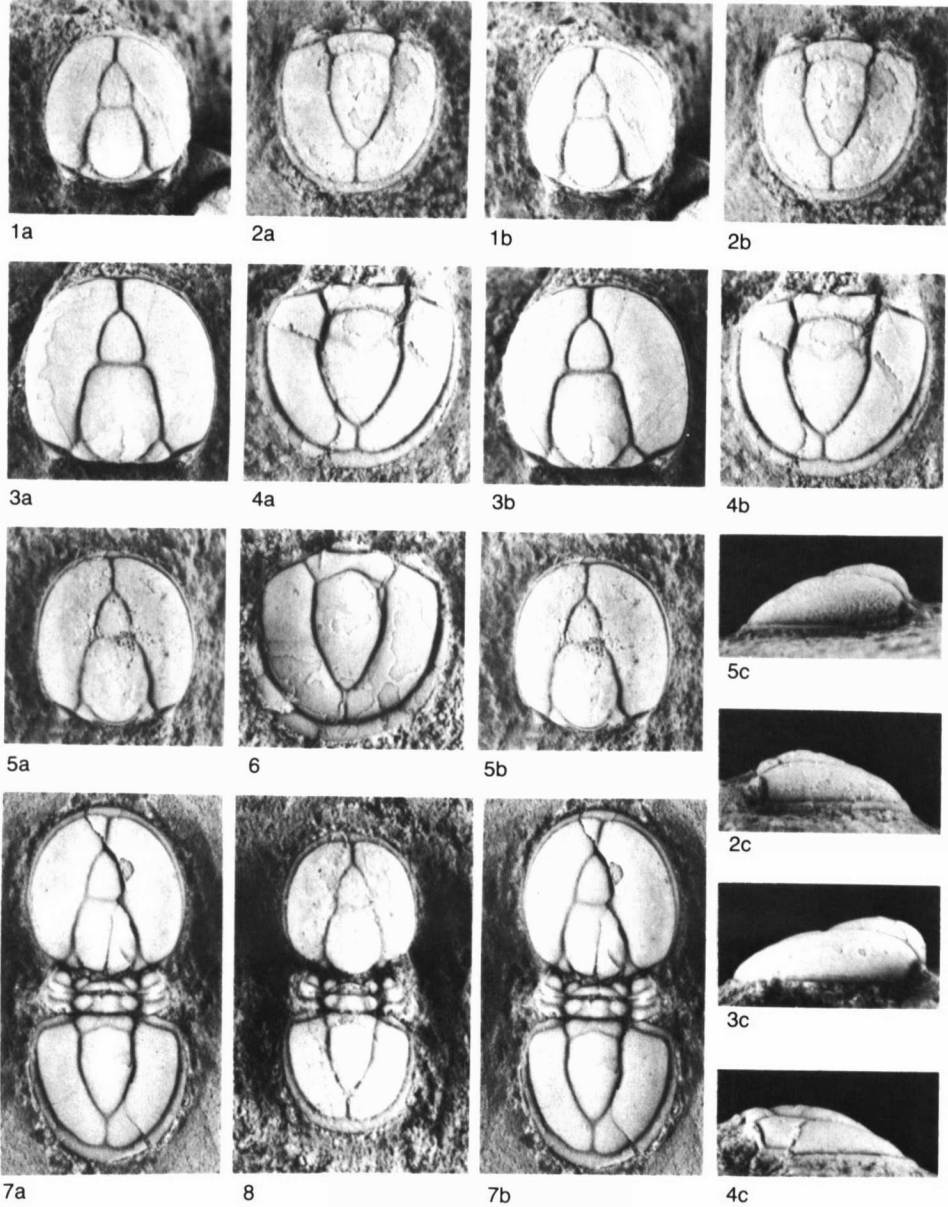


Fig. 27. *Lejopyge lundgreni* (Tullberg) from lower part of stratigraphic range in Nevada and Utah. 1, Cephalon, KUMIP 204295 from 804; 3 m below top of Geddes Limestone, Eureka mining district, Nevada;  $\times 10$ . 2, Pygidium, KUMIP 204296 from 759; about 245 m above base of Marjum Formation, House Range, Utah;  $\times 10$ . 3, Cephalon, KUMIP 204297 from 106; near base of lower shale member, Secret Canyon Shale, Eureka mining district;  $\times 8$ . 4, Pygidium, KUMIP 204298 from 398; about 140 m above base of Marjum Formation, House Range;  $\times 8$ . 5, Cephalon, KUMIP 204299 from 759;  $\times 8$ . 6, Pygidium, KUMIP 204300 from 105; probably uppermost 3 m of Geddes Limestone, Eureka mining district;  $\times 8$ . 7, Complete dorsal exoskeleton, KUMIP 204301 from 113; talus, probably between 50-70 m above base of Marjum Formation, House Range;  $\times 10$ . 8, Early holasid exoskeleton KUMIP 204302 from 398;  $\times 12$ .

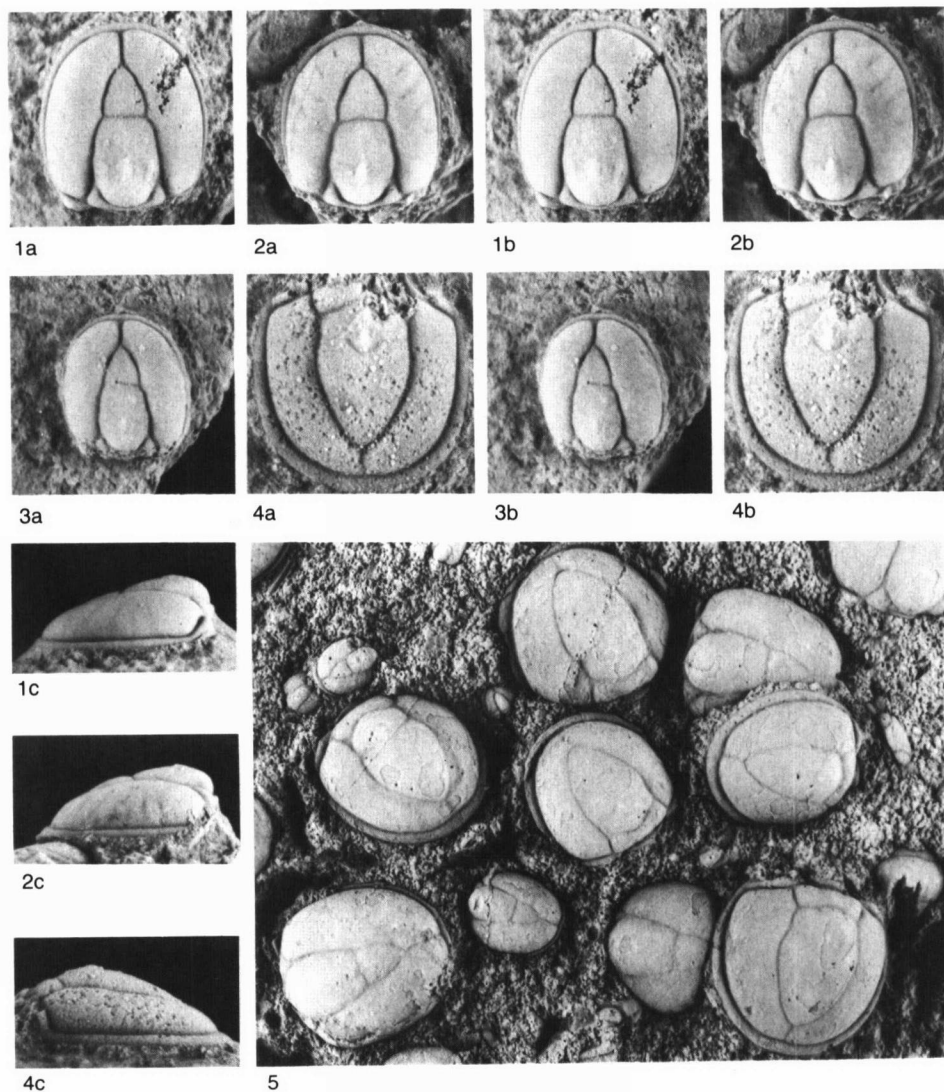


Fig. 28. *Lejopyge lundgreni* (Tullberg); 1-4, specimens from upper part of stratigraphic range in Nevada and Utah, all  $\times 10$ ; 5, specimens from Sweden,  $\times 5$ . 1, Cephalon, KUMIP 204303 from 816; about 20 m above base of Weeks Limestone, House Range, Utah. 2, Cephalon, KUMIP 204304 from 154; top bed, member A, Emigrant Springs Limestone, southern Schell Creek Range, Nevada. 3, 4, Cephalon and pygidium, KUMIP 204305 and 204306 from MNR81-187; about 285 m above base of Lincoln Peak Formation, Snake Range, Nevada. 5, Representative specimens on same piece of rock with pygidium illustrated by Westergård (1946, pl. 10, fig. 25); cast, KUMIP 204307 from Vedjéon (boulder 6), Jämtland, Sweden (original in collections of Naturhistoriska Riksmuseet, Stockholm).

latitudes (Bambach and others, 1980). Therefore, the geographic size difference in *L. lundgreni* may be related to temperature; however, such other factors as salinity and nutrients can not be ruled out. Some minor geographic variation in morphology probably relates to this difference in average size. For example, genal

scrobicules, which are accentuated with increase in cephalic size, tend to be better developed on specimens of *L. lundgreni* from Europe than on those from the Great Basin. Also, during ontogeny, the posteroaxis of the pygidium shows significant allometric size increase. As expected, larger holaspides of *L.*



*lundgreni* from Europe commonly have a wider posteroaxis than do smaller ones from the Great Basin. European specimens of *L. lundgreni* with a narrow posteroaxis have sometimes been assigned to the subspecies *nanus* (see synonymy), but because of the observed gradation in that character I find no justification for continued use of the subspecies name.

Pygidia of *L. lundgreni* illustrated by Westergård (1946, pl. 10, figs. 24, 25; pl. 11, figs. 6, 7) have a fairly well-developed F2 on the axis; however, most other specimens in the same collections have a weak F2 (e.g., Fig. 28,5). Most specimens from North America also have a weak pygidial F2. Therefore, this appears to be the more common condition throughout the species.

A few specimens from the Taconic sequence of eastern New York were assigned by Rasetti (1967) to an undetermined species of *Ptychagnostus*. Because all characters of those specimens agree with the diagnosis above, they here are reassigned to *L. lundgreni*.

Yang (1978:23, pl. 2, figs. 1, 2) illustrated agnostoids from China that were assigned to *Triplagnostus lundgreni* (Tullberg). The cephalon has elongate, divided basal lobes and does not represent *L. lundgreni*. The specimens resemble *P. atavus*; however, identification is uncertain.

**Occurrence.**—*L. lundgreni* has previously been reported from Sweden, Norway, Denmark, England, and the Soviet Union. Its occurrence in New York has been documented by Rasetti (1967, with nomenclatural emendation here).

*L. lundgreni* here is reported for the first time from many localities in the Great Basin. In Nevada, more than 50 specimens are in collections 105, 106, and 804 from the upper 3 m of the Geddes Formation and the lower few meters of the Secret Canyon Shale in the Eureka mining district. Rare specimens are in the following collections: 154 from the top bed, member A, Emigrant Springs Limestone, southern Schell Creek Range; 350 from the lower shale member, Lincoln Peak Formation, southern Ruby Mountains; and MNR81-187 from about 285 m above the base, Lincoln Peak Formation, southern Snake Range. Probable representatives include two cephalata in collection 177 from 426 m above the base of the Secret Canyon Formation in the northern Egan Range, and a few poorly preserved but com-

plete specimens in collection 183 from an unnamed formation (possibly upper part of unit B7 of Stewart and Palmer, 1967) in the Toiyabe Range. In Utah, numerous specimens are in collections 113, 391, 397, 398, 737, 740, 759, and 816 ranging from about 40 m above the base of the Marjum Formation to about 20 m above the base of the Weeks Limestone in the central House Range.

Biostratigraphically, *L. lundgreni* has an observed range from near the base of the *Ptychagnostus punctuosus* Zone to the middle of the lower subzone of the *L. laevigata* Zone (Fig. 4).

### LEJOPYGE RIGBYI, n. sp.

Figure 29

**Etymology.**—The species name honors Prof. J. Keith Rigby of Brigham Young University for his many contributions to paleontology and geology.

**Holotype.**—Nearly complete exoskeleton (Fig. 29,4), KUMIP 204311.

**Description.**—*Lejopyge* having pair of short spines on posterolateral borders of cephalon, one large median spine on posterior thoracic segment, and one large median spine on pygidial M2. Acrolobes lacking much effacement of dorsal furrows except pygidial F2. Axial length compared to exoskeletal length less than in most ptychagnostid species. Pygidial F2 usually effaced on dorsal surface, may be weakly developed on internal mold.

**Discussion.**—*L. rigbyi* is characterized by its spine morphology and its lack of much effacement of dorsal furrows on the acrolobes. Large median spines on the posterior thoracic segment and the pygidial M2 are indicated by prominent broken stumps on all available specimens. A pair of smaller, delicate spines project from the posterior cephalon, and are easily broken.

*L. rigbyi* differs from all species of *Lejopyge* by the presence of a median spine on the pygidial axis. Except for the presence of spines, it closely resembles *L. lundgreni*, its inferred ancestor. A minor difference between *L. lundgreni* and *L. rigbyi* is the greater effacement of the pygidial F2 in *L. rigbyi*.

**Occurrence.**—About a dozen specimens of *L. rigbyi* are in collection 398 from about 140 m above the base of the Marjum Formation in the

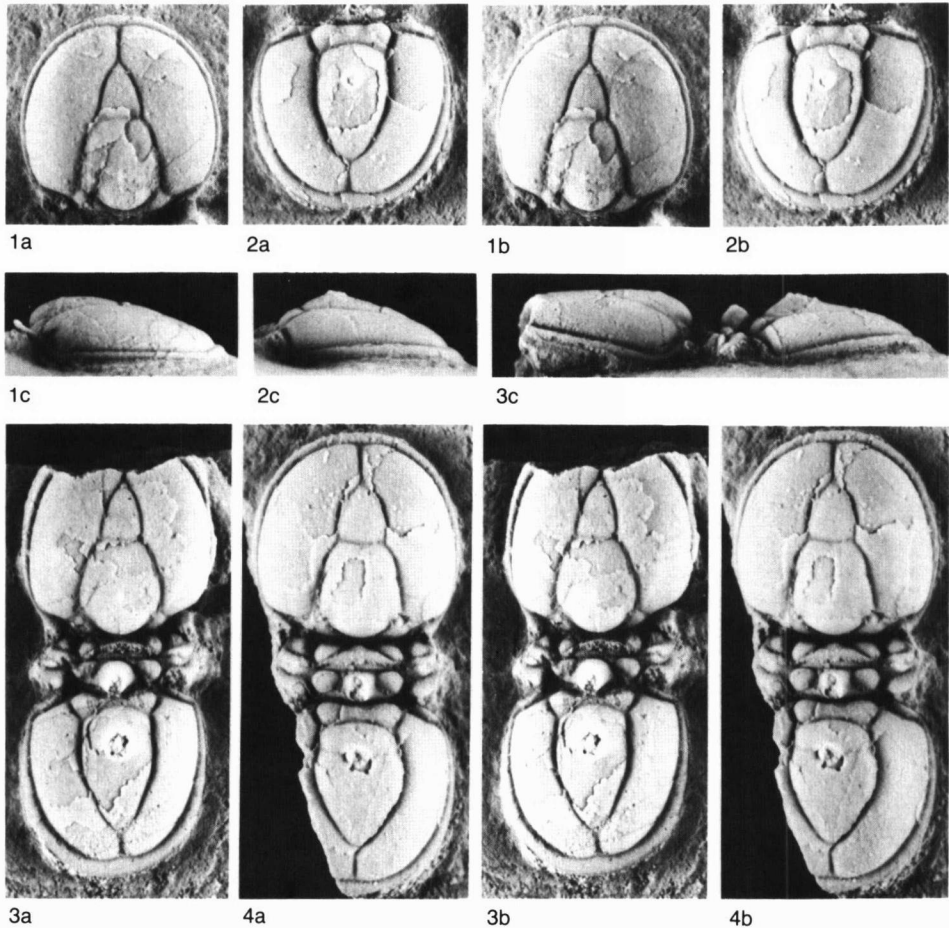


Fig. 29. *Lejopyge rigbyi*, n. sp.; all partly exfoliated and all from locality 398 in Marjum Formation, House Range, Utah. 1, Cephalon retaining short posterolateral spine on right side, spine is broken off left side, KUMIP 204308,  $\times 10$ . 2, Pygidium, showing broken base of median M2 spine, KUMIP 204309,  $\times 10$ . 3, Nearly complete exoskeleton, KUMIP 204310,  $\times 9$ . 4, Holotype, nearly complete exoskeleton, KUMIP 204311,  $\times 8$ .

central House Range, Utah. The single locality is within the *Ptychagnostus punctuosus* Zone (Fig. 4).

### Genus ONYMAGNOSTUS Öpik

*Onymagnostus* ÖPIK, 1979, p. 107-108.

*Type species.*—Öpik (1979:107) designated *Onymagnostus angulatus* as the type species of *Onymagnostus*. As revised herein, I consider *O. angulatus* to be a subjective junior synonym of *O. hybridus* (Brøgger). Therefore, the valid name of the type species of *Onymagnostus* becomes *O. hybridus*.

*Diagnosis.*—Exoskeleton of moderate to large size, in some species length probably exceeds 20 mm. Cephalic axis long, broadly rounded to obtusely pointed at front. Post-eroglabella commonly having convex lateral sides and broadly rounded rear. Basal lobes simple to slightly elongate. Pygidial axis long, M2 hexagonal with large median tubercle deeply embaying F2. Postaxial median furrow present during meraspis period, usually becoming effaced during early to middle holaspis period. Furrows on cephalic and pygidial acrols secondarily effaced in some species.

*Discussion.*—*Onymagnostus* is a ptychagnostid

genus generally having smooth genae, short basal lobes, and a long pygidial axis with a large median tubercle that deeply embays the posterior (F2) transverse furrow. During ontogeny, the postaxial median furrow usually became effaced prior to the late holaspid period. Spines are lacking except for *O. semiermis* Öpik, which has a pair of short spines on the pygidial border. As in other ptychagnostid genera, some species of *Onymagnostus* show evolutionary effacement of dorsal furrows on the acrolobes. This effacement was accompanied by secondary reduction in size of the median tubercle on the pygidial M2.

The oldest known species of *Onymagnostus* is *O. seminula* (Whitehouse), which first appears near the base of the *P. gibbus* Zone in western North America. Comparative morphology indicates that *O. seminula* was probably derived from *Ptychagnostus praecurrens* (compare Figs. 19 and 32). Both species have smooth genae, slightly elongated basal lobes that are anteriorly ill-defined, and an absence of spines. In *O. seminula* the acrolobes are more convex, the axis is slightly longer and wider, the median node on the posteroglabella is slightly more anterior, the median tubercle on the pygidial M2 is enlarged, and the postaxial median furrow is commonly effaced in late holaspides. Basal lobes are reduced to a simple condition in some later species of *Onymagnostus*.

Öpik (1979:107) assigned eight previously described species to *Onymagnostus*. Additionally, he described seven new species groups from Australia, three of which were left in open nomenclature. Based on variation observed in numerous collections of *Onymagnostus* from North America, Greenland, Europe, and Australia, as well as in illustrated material from the Siberian platform (Egorova and others, 1982), I conclude that several synonyms are represented. Herein, I recognize only five species of *Onymagnostus*; these being *O. hybridus* (Brøgger, 1878), *O. ciceroideis* (Matthew, 1896), *O. seminula* (Whitehouse, 1939), *O. grandis* (Hutchinson, 1962), and *O. semiermis* Öpik (1979). Synonyms of *O. hybridus* are listed below. Synonyms of *O. ciceroideis* are *A. laevigatus terranovicus* Matthew (part, 1896), *A. l. mammilla* Matthew (1896), *A. altus* Grönwall (1902), and *Ptychagnostus convexus* Westergård (1946).

*Occurrence.*—Of the five presently recognized species of *Onymagnostus*, *O. seminula* and *O.*

*hybridus* are geographically widespread and common. *O. semiermis* is known from only a few localities in Australia. *O. ciceroideis* and *O. grandis* are variably effaced forms known with certainty from only eastern Newfoundland and northwestern Europe. A single cephalon, possibly representing *O. grandis*, has been described from Australia (Öpik, 1979:113, pl. 53, fig. 6).

*Onymagnostus* has an observed stratigraphic range from near the base of the *P. gibbus* Zone to the upper part of the *P. punctuosus* Zone.

### ONYMAGNOSTUS HYBRIDUS (Brøgger)

Figures 30, 31

- Agnostus gibbus* var. *hybrida* BRØGGER, 1878, p. 62, pl. 5, figs. 4a, b; GRÖNWALL, 1902, p. 49, 197.
- Agnostus stenorrhachis* GRÖNWALL, 1902, p. 76-77, pl. 1, fig. 16; COBBOLD and POCKOCK, 1934, p. 342-343, pl. 44, fig. 22.
- Agnostus* cf. *intermedius* Tullberg ILLING, 1916, p. 408, pl. 28, figs. 11, 12.
- Agnostus pulchellus* ILLING, 1916, p. 410-411, pl. 30, figs. 1, 2.
- Agnostus triangulatus* ILLING, 1916, p. 412, pl. 30, figs. 7, 8.
- Agnostus gibbus hybridus* Brøgger STRAND (in part), 1929, p. 343.
- Agnostus* cf. *gibbus hybridus* Brøgger THORSLUND in Asklund and Thorslund, 1935, p. 106, fig. 1.
- Agnostus* sp. THORSLUND in Asklund and Thorslund, 1935, p. 108, pl. 1, fig. 8.
- Triplagnostus stenorrhachis* (Grönwall) KOBAYASHI, 1939, p. 146; EGOROVA, PEGEL, and TCHERNYSHEVA in Egorova and others, 1982, p. 65, pl. 11, figs. 9, 10; pl. 12, figs. 7-9; pl. 13, figs. 4, 5, 7; pl. 14, figs. 1-3; pl. 15, figs. 2, 3; pl. 18, figs. 2, 3; pl. 19, fig. 1; pl. 21, fig. 4, pl. 22, figs. 8, 9; pl. 61, figs. 1, 2.
- Triplagnostus triangulatus* (Illing) KOBAYASHI, 1939, p. 146.
- Ptychagnostus (Triplagnostus) hybridus* (Brøgger) WESTERGÅRD, 1946, p. 71-72, pl. 9, figs. 25, 26; pl. 10, figs. 1, 2; HUTCHINSON, 1962, p. 82, pl. 8, figs. 12-15.
- Ptychagnostus (Triplagnostus) stenorrhachis* (Grönwall) WESTERGÅRD, 1946, p. 72, pl. 10, figs. 3, 4; HUTCHINSON, 1962, p. 80-81, pl. 8, figs. 1-5.
- Ptychagnostus (Triplagnostus) vinicensis* ŠNAJDR (in

- part), 1958, p., 71-72, pl. 4, figs. 19, 20, 23, 24 (not figs. 21, 22).
- Ptychagnostus hybridus* (Brøgger) ROBISON, 1964, p. 523, pl. 79, figs. 10, 11, 13, 14; PALMER and others, 1984, fig. 2F.
- Ptychagnostus punctuosus* (Angelin) POULSEN (in part), 1969, p. 4-5, Fig. 4B (not 4A).
- Triplagnostus formosus* POKROVSKAYA and KHAIRULLINA in Repina, Petrunina, and Khairullina, 1975, p. 108, pl. 9, fig. 9.
- Triplagnostus urbanus* POKROVSKAYA and KHAIRULLINA in Repina, Petrunina, and Khairullina, 1975, p. 106, pl. 9, fig. 6.
- Ptychagnostus* (*Ptychagnostus*) *stenorrhachis* (Grönwall) JAGO, 1977, p. 45-46, pl. 1, figs. 7-12.
- Onymagnostus hybridus* (Brøgger) ÖPIK, 1979, p. 107.
- Onymagnostus angulatus* ÖPIK, 1979, p. 108-110, pl. 50, figs. 1-8; pl. 51, figs. 1-3.
- Onymagnostus* sp. nov. aff. *angulatus* ÖPIK, 1979, p. 110, pl. 51, figs. 4, 5.
- Onymagnostus durusacnitens* ÖPIK, 1979, p. 110-111, pl. 53, figs. 2-4.
- Onymagnostus mundus* ÖPIK, 1979, p. 111-112, pl. 51, fig. 6; pl. 52, figs. 1, 2.
- Onymagnostus seminula* (Whitehouse) ÖPIK, 1979, p. 112-113, pl. 52, figs. 3-5; pl. 53, fig. 1.
- Onymagnostus* cf. *stenorrhachis* (Grönwall) ÖPIK, 1979, p. 113-114, pl. 53, fig. 5.
- Ptychagnostus triangulatus* (Illing) RUSHTON, 1979, p. 53-54, fig. 5E-G.
- Onymagnostus prokopi* FATKA, KORDULE, and ŠNAJDR, 1981, p. 368, pl. 1, figs. 2-9.

*Diagnosis.*—Exoskeleton moderately large with well-developed dorsal furrows. Cephalon moderately convex, dorsal outline subcircular. Axis generally having irregular taper, sides rarely subparallel. Anteroglabella broadly rounded to obtusely pointed at front. Posteroglabella commonly having convex lateral sides and broadly rounded rear, F1 undeveloped and F2 weak; median node anterior from midpoint. Basal lobes simple. Genae normally smooth, rarely having very weak scrobicules. Late holaspidites may have tiny median opening or pit on back slope of glabella, above short sagittal ridge. Pygidium moderately to highly convex. Posteroaxis elongate, variable in width, weakly ovoid to lanceolate. Border lacking spines, posterolateral swellings rare.

*Discussion.*—Based on much published in-

formation as well as personal review of many collections from North America, Greenland, and Europe, I consider several described species to be synonyms of *O. hybridus* (Brøgger). These include *Agnostus stenorrhachis* Grönwall, *A. pulchellus* Illing, *A. triangulatus* Illing, *Triplagnostus formosus* Pokrovskaya and Khairullina, *T. urbanus* Pokrovskaya and Khairullina, *Onymagnostus angulatus* Öpik, *O. durusacnitens* Öpik, *O. mundus* Öpik, *O. seminula* of Öpik (not Whitehouse), and *O. prokopi* Fatka, Kordule, and Šnajdr. Most original descriptions of these species were based on few specimens. Among the diagnostic differences cited are a rounded versus obtusely pointed anterior glabella, straight versus convex sides on the posteroglabella, smooth versus slightly scrobiculate genae, differences in width of the posteroaxis on the pygidium, slight variation in depth of furrows on the acrolobes, and minor variation in width of the posterolateral border of the pygidium. Although in some collections one or more of these characters may be fairly constant, in some large collections (e.g., 765), gradations in each of the cited characters can be observed. Westergård (1946:72) mentioned unfigured Swedish specimens that are gradational between *hybridus* and *stenorrhachis*. Under the name *Triplagnostus stenorrhachis*, Egorova, Pegel, and Tchernysheva (in Egorova and others, 1982) have illustrated many specimens from the Siberian platform that show variation in some of the characters mentioned above. Width of the axis may also be secondarily decreased by collapse of the exoskeleton along the axial furrow during compaction in argillaceous matrix.

As revised here, *O. hybridus* is characterized by simple basal lobes, mostly smooth genae, a prominent median tubercle that deeply embays the pygidial F2, and an absence of spines. A postaxial median furrow is present during early ontogeny but usually becomes effaced during the early or middle holaspid period.

Many late holaspidites of *O. hybridus* from western North America and North Greenland possess an unusual, tiny, median opening or pit and a short sagittal ridge on the posterior slope of the cephalon (Figs. 30, 5, 8, 10 and 31). Similar indentations can also be seen on some specimens illustrated from eastern Newfoundland (Hutchinson, 1962, pl. 8, fig. 13a), Sweden (Westergård, 1946, pl. 9, fig. 25), the

Siberian platform (Egorova, Pegel, and Tchernysheva in Egorova and others, 1982, pl. 18, fig. 3), and possibly Australia (Öpik, 1979, pl.

51, fig. 6). Function of the opening is unknown, but it probably was glandular.

*O. hybridus* closely resembles *O. seminula*;

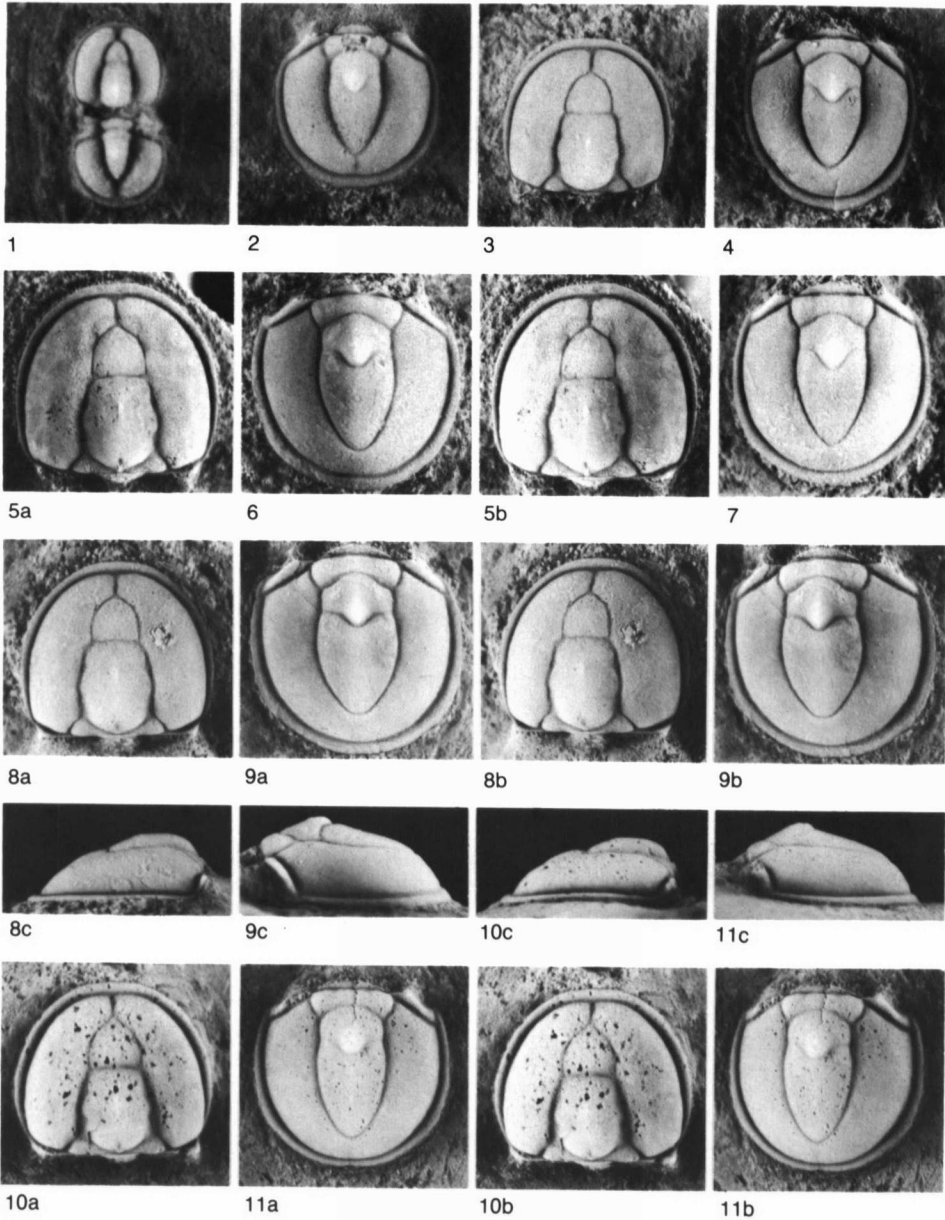


Fig. 30. *Onymagnostus hybridus* (Brøgger); 1, 2, 10, 11, from Formation T1, Tavsens Iskappe Group, North Greenland; 3-9, from Marjum Formation, House Range, Utah; all preserved in lime mudstone. 1, Early holaspid exoskeleton with wide postaxial median furrow, MGUH 16.283 from GGU 218644,  $\times 10$ . 2, Early holaspid pygidium with narrow postaxial median furrow, MGUH 16.284 from GGU 218644,  $\times 10$ . 3, 4, Middle holaspid cephalon and pygidium, latter with effaced postaxial median furrow; KUMIP 204284 and 204285 from 765, both  $\times 8$ . 5, Rare late holaspid cephalon with weak genal scrobicules; KUMIP 204286 from 765,  $\times 6$ . 6, 7, 9, Late holaspid pygidia, KUMIP 204287-204289 from 765, all  $\times 6$ . 8, Late holaspid cephalon with typically smooth genae, KUMIP 204290 from 765,  $\times 6$ . 10, 11, Cephalon and pygidium with solution-pitted surfaces; MGUH 16.285 and 16.286 from GGU 218647 and 218644, respectively; both  $\times 6$ .

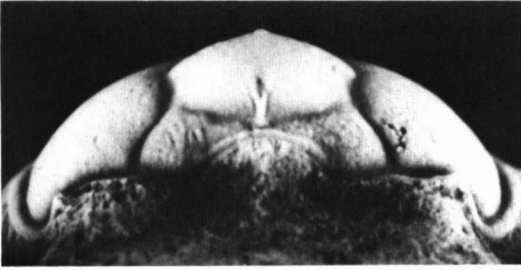


Fig. 31. Posterior cephalon of *Onymagnostus hybridus* (Brøgger); KUMIP 204286 from 765 (same specimen as Fig. 30,5),  $\times 15$ . Note the small median opening on the back slope of the glabella. Extending downward from the opening is a short sagittal ridge that crosses the edge of the glabella and a narrow occipital band, connecting to the crest of the cephalic recess. A raised, narrow rim on the cephalic recess bounded the dorsal half of a cephalothoracic aperture on the enrolled exoskeleton before disarticulation (for definitions of some terms, see Robison, 1964:515).

however, *O. hybridus* can be differentiated by its simple rather than slightly elongate basal lobes, slightly shorter axis on both cephalon and pygidium, and usual lack of posterolateral swellings on the pygidial border.

*Occurrence.*—*O. hybridus* is a widespread agnostoid. Specimens here assigned to the species have been previously described (see synonymy) from Sweden, Norway, Denmark, England, Czechoslovakia, Canada (eastern Newfoundland), United States (Texas, Utah), Australia, and the Soviet Union (Siberian platform, Turkistan).

Hayes and Howell (1937:88) reported *Triplagnostus* cf. *gibbus hybrida* from the Porter Road Formation, along Porter Road, New Brunswick, Canada; however, specimens were not described or illustrated. From the same formation and locality, I have collected (783) a few agnostoids that may represent *O. hybridus*, but poor preservation precludes confident identification.

The first report of *O. hybridus* in the United States (Robison, 1964) was based on a few specimens (collection 3309-CO) from a limestone bed 134 m above the base of the Marjum Formation, House Range, Utah. Additional collecting (765) has yielded more than 100 well-preserved specimens from the same bed. A single pygidium in collection 176 from 398 m above the base of the Secret Canyon Formation, northern Egan Range, Nevada, also probably represents this species. In the Marathon

basin of west Texas, a single early holaspid cephalon of *O. hybridus* is associated with other agnostoids in a Cambrian boulder from a conglomeratic unit of the Haymond Formation of Pennsylvanian age (Palmer and others, 1984).

In North Greenland, *O. hybridus* is common in collections (GGU 218626, 218644, 218647) from 75 to 85 m above the base of Formation T1 of the Tavsens Iskappe Group of Peary Land. A single pygidium from Nyeboe Land, which Poulsen (1969) assigned to *Ptychagnostus punctuosus*, is here reassigned to *O. hybridus* (see *P. punctuosus*, Occurrence).

*O. hybridus* has a reported range from the upper *P. atavus* Zone to the upper *P. punctuosus* Zone. Generally, it is most common in the *P. punctuosus* Zone.

### ONYMAGNOSTUS SEMINULA (Whitehouse)

Figure 32

*Agnostus seminula* WHITEHOUSE, 1939, p. 254, pl. 25, fig. 24; HILL, PLAYFORD, and WOODS, 1971, pl. 13, fig. 1.

not *Onymagnostus seminula* (Whitehouse) ÖPIK, 1979, p. 112, pl. 52, figs. 3-5; pl. 53, fig. 1.

*Ptychagnostus seminula* (Whitehouse) ROBISON, 1982, p. 148-150, pl. 4, figs. 1-6.

*Diagnosis.*—Exoskeleton moderately large with well-developed dorsal furrows. Cephalon moderately to highly convex. Axis long, averaging about 0.8 cephalic length in mature holaspides. Anteroglabella rounded to obtusely pointed at front. Posteroglabella having subparallel to slightly convex lateral sides, broadly rounded rear; F1 undeveloped and F2 weak; median node anterior from midpoint. Basal lobes entire and slightly elongate, anterior ends poorly defined. Genae smooth. Pygidium highly convex; posterior part of acrolobe rising steeply from border furrow in large holaspides. Axis long, almost reaching posterior border furrow in largest holaspides. Posteroaxis weakly ogival. Border commonly with posterolateral swellings but lacking spines.

*Discussion.*—*O. seminula* has recently been more fully diagnosed and discussed (Robison, 1982:148-150). Additional representative specimens here are illustrated from Utah and North Greenland.

*Occurrence.*—*O. seminula* is known from Aus-

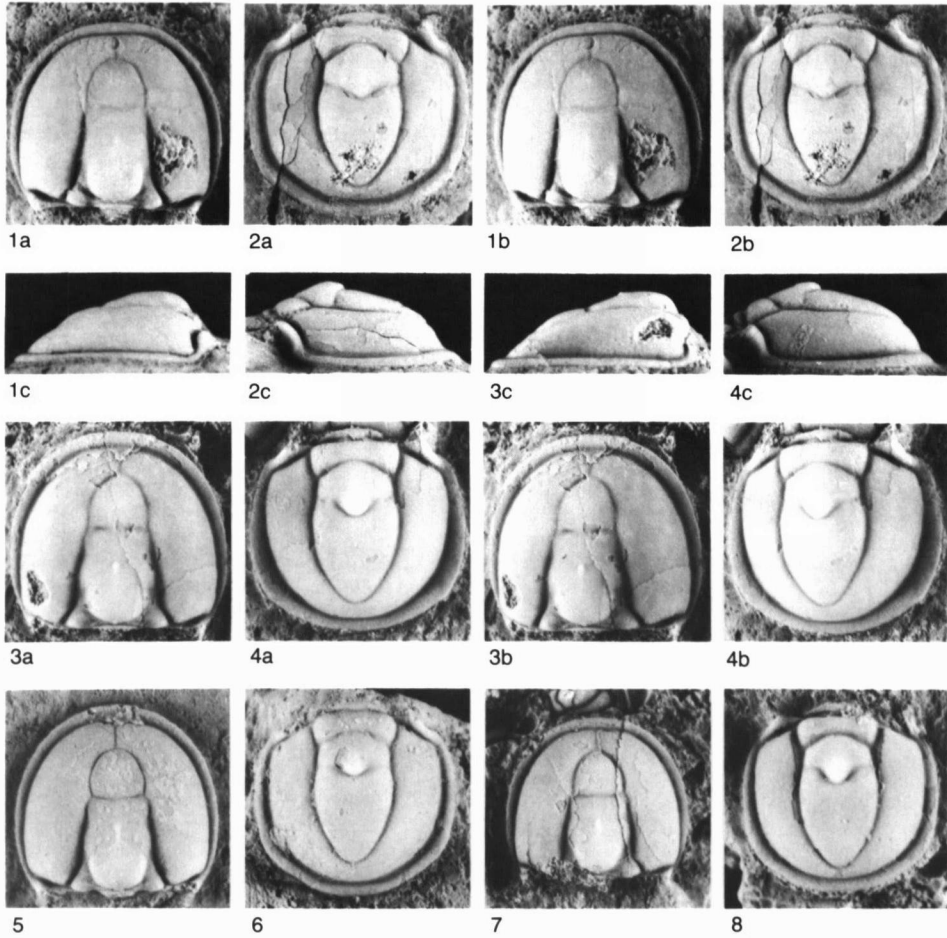


Fig. 32. *Onymagnostus seminula* (Whitehouse). Specimens preserved in limestone. 1, 2, Cephalon and pygidium, MGUH 16.287 and 16.288 from GGU 271492; Formation 2, Brønlund Fjord Group, North Greenland;  $\times 5$  and  $5.5$ . 3, 4, Cephalon and pygidium, KUMIP 204291 and 204292 from 305; Wheeler Formation, Wasatch Mountains, Utah;  $\times 5.5$  and  $6$ . 5, 6, Cephalon and pygidium, MGUH 16.289 and 16.290 from 271492, both  $\times 5$ . 7, 8, Middle holaspid cephalon and pygidium, latter with weak postaxial median furrow; KUMIP 204293 and 204294 from 305; both  $\times 6$ .

tralia, the United States (Nevada, Utah), Canada (western Newfoundland), Greenland, and probably Sweden and Norway. Many collections with *O. seminula* were recently listed from Nevada and Utah (Robison, 1982). From western Newfoundland, many specimens are in C. H. Kindle collections 362, 378, 380, 409, and

420 from boulders of the Cow Head Conglomerate. In North Greenland the species is rare to common in GGU collections 218614, 271411, 271428, 271488, 271489, and 271492 from the upper half of Formation 2 of the Brønlund Fjord Group. *O. seminula* has an observed range through most of the *Ptychagnostus gibbus* Zone.

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