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ORIGIN, TAXONOMY, AND HOMEOMORPHS OF DORYAGNOSTUS (CAMBRIAN TRILOBITA)[1]

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ABSTRACT

Iterative evolution of a preglabellar median furrow resulted in several agnostoid homeomorphs. Particularly deceptive examples are *Doryagnostus* and *Ptychagnostus*, which appear to have evolved at different times from different species of *Peronopsis*. The preglabellar median furrow reflects a parietal septum between a pair of ramified alimentary glands. The furrow tends to have stable partial or complete expressions, which in combination with other characters, are useful in generic recognition. Bergström's (1973) conclusion that the radial genal prosopon of agnostoids reflects elements of the alimentary system whereas the radial genal prosopon of polymeroids reflects elements of the circulatory system is supported by additional observations.

The taxonomic concept of *Doryagnostus* is revised. One new species, *D. wasatchensis*, is described from Utah. *Ceratagnostus magister* Whitehouse is retained in synonymy with the type species, *D. incertus* (Brögger). The genus also includes *D. deltoides* Robison.

INTRODUCTION

Doryagnostus was established in 1939 by Kobayashi, who designated *Agnostus incertus* Brögger, 1878, as the type species. Ten days later Whitehouse (1939) named *Ceratagnostus magister*, which was subsequently suppressed as a junior synonym of *D. incertus* by Westergård (1946, p. 82), but some Australian workers have continued to recognize *C. magister* as a separate species. Since 1946, few additional representatives have been described, and the taxonomic status and affinities of *Doryagnostus* have been subjects of disparate opinions (e.g., Howell, 1959, p. O178; Öpik, 1961a, p. 77).

Recent discovery of new material and a review of previously described specimens have provided significant new information about the phyletic origin and affinities of *Doryagnostus*. One new species from Utah, *D. wasatchensis*, is described in this paper. Another species, *D. deltoides* Robison, which is named in an accompanying paper (Jell & Robison, 1978), has been recognized among specimens previously assigned to *Euagnostus opimus* by Whitehouse (1936). From study of the new material, as well as most previously illustrated specimens, *Doryagnostus* appears to have some deceptive homeomorphs. Enough data have now been assembled that useful conclusions can be reached on the origin, taxonomy, and homeomorphs of *Doryagnostus*.

Repositories.—Materials used in this study are referred to by either specimen or collection numbers. These numbers include abbreviations that

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identify the repository as follows: 1) Canadian Geological Survey (CGS), 2) U.S. Geological Survey—Cambrian and Ordovician collections (CO), 3) University of Kansas Museum of Invertebrate Paleontology (KUMIP), and 4) University of Queensland (UQF).

Locality numbers.—Those numbers used by the author have a prefix "R" (for example, R-306), and a locality register is on file at the University of Kansas. University of Queensland locality numbers are indicated by the prefix "UQL."

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ORIGIN AND AFFINITIES OF DORYAGNOSTUS

Mainly on the basis of comparative axial form, I suggest that *Doryagnostus* and *Ptychagnostus* are close homeomorphs that evolved from different species of *Peronopsis* by heterochronous development of a preglabellar median furrow. Inferred phyletic relations are summarized in Figure 1. *Ptychagnostus praecurrens* (Pl. 1, figs. 5, 8), the ancestral species of *Ptychagnostus*, probably arose from *Peronopsis brighamensis* (Pl. 1, figs. 7, 11, 14) of early Middle Cambrian age. In addition to general axial form, those two species also show similar median nodes on the anterior thoracic segment (cf. Pl. 1, figs. 8, 14), moderately well-developed first and second transaxial furrows on the pygidium, and a prominent median tubercle on the pygidial axis. During the middle Middle Cambrian, *Doryagnostus wasatchensis* (Pl. 1, figs. 1-4, 6; Pl. 2, figs. 6, 9-13) appears to have arisen from *Peronopsis gaspensis* (Pl. 1, figs. 9, 10, 12, 13). On the pygidium, these two species have undeveloped or only incipient transaxial furrows and a small median tubercle. *Agnostus* is a late Middle Cambrian homeomorph of probable peronopsid ancestry; however, it differs from the aforementioned genera by having a more tumid posterior pygidial axis (cf. Westergård, 1922, pl. 1, figs. 1-3).

The initial species of *Doryagnostus* and *Ptychagnostus* are superficially similar, but species of *Doryagnostus* can be differentiated by their consistently undeveloped or weak transaxial furrows and generally smaller median tubercle on the pygidium. Also, the earliest species of *Ptychagnostus* lack border spines on the pygidium, whereas a pair of spines is present on all known species of *Doryagnostus*. During later evolutionary stages of *Doryagnostus* the axial terminus became slightly more constricted and a weak depression on the posterior part of the pygidial axis became more accentuated. By comparison, *Ptychagnostus* has numerous species that display a variety of evolutionary trends, but in all lines that did not secondarily undergo effacement of the axial furrow on the pygidium, the two transaxial furrows remain well defined. Some species, such as *P. intermedius* and *P. punctuosus*, show secondary reduction of the median tubercle on the pygidium, but they usually possess other features such as elongate basal lobes and a more evenly tapered cephalic axis that characterize late evolutionary stages of *Ptychagnostus*. A detailed taxonomic review of *Ptychagnostus* is in preparation and will be presented in a separate paper.

FUNCTION AND SIGNIFICANCE OF THE PREGLABELLAR MEDIAN FURROW

A preglabellar median furrow is a common feature of many agnostoid trilobites. Although discussion usually has been brief or lacking, differing taxonomic significance has been attributed to the furrow. On one hand, some authors (e.g., Howell, 1959, p. O172-186) have tacitly assigned considerable taxonomic weight to its presence or absence, particularly at the generic and family level. On the other hand, Öpik (1967, p. 67) has cited the preglabellar median furrow as an example of a feature that "illustrates the overestimation of the rank significance of some characters," and he (1967, p. 66-72) did not include the feature among seven criteria that he considered to be suitable for classifying agnostoids at suprageneric levels.

The preglabellar median furrow is part of an integrated, but not necessarily equally developed, prosopic pattern that also includes genal rugae outlined by radiating scrobiculae (Fig. 2B). On the agnostoid pygidium a postaxial median furrow is also common, but pleural rugae are rare. Based on comparative morphology, Öpik (1961b) interpreted such rugae as the surface expression of an underlying set of ramified alimentary glands. Rugae may surround the sides and front of the glabella, but are anteriorly divided by a preglabellar median furrow, and hence it is improbable that the inferred glands were anteriorly confluent. Öpik also concluded that the preglabellar furrow reflects a parietal median septum and an associated mesentery that separated and kept the gland system in place. During the phylogeny of such genera as *Doryagnostus* and *Ptychagnostus*, appearance of the preglabellar median furrow preceded development of genal scrobiculae, whereas in other forms, such as *Hypagnostus*, the two types of furrow developed simultaneously.

Peronopsis appears to be the ancestral genus of all Agnostina except for the condylopygids. Representatives of *Peronopsis* and a few other agnostoids lack a preglabellar median furrow, but as Öpik (1961b, p. 416) noted, this does not necessarily indicate the absence of a median mesenterial partition.

Based on a continuing study of agnostoid trilobites, I suggest that a partial or complete preglabellar median furrow developed independently and at different times in several evolution-

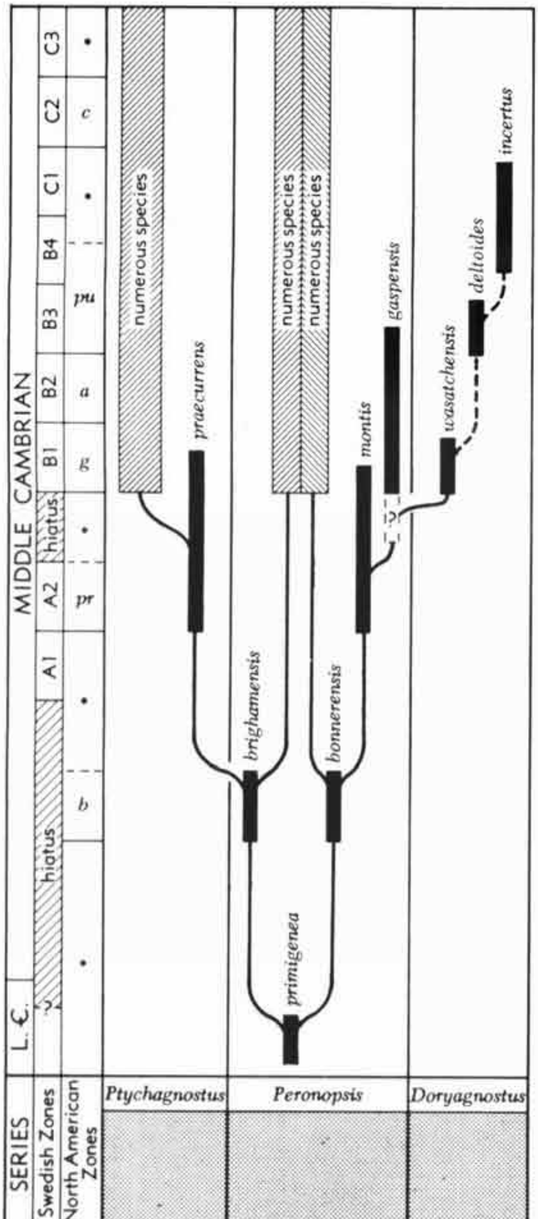


FIG. 1. Stratigraphic and inferred phyletic relations between some species of *Ptychagnostus*, *Peronopsis*, and *Doryagnostus*. Swedish zones are from Westergård (1946); symbols and zone names are: A1 *(Paradoxides insularis)*, A2 *(Paradoxides pinus)*, B1 *(Ptychagnostus gibbus)*, B2 *(Tomagnostus fissus* and *Ptychagnostus atavus)*, B3 *(Hypagnostus parvifrons)*, B4 *(Ptychagnostus punctuosus)*, C1 *(Ptychagnostus lundgreni* and *Goniagnostus nathorsti)*, C2 *(Solenopleura brachymetopa)*, and C3 *(Lejopyge laevigata)*. North American agnostoid assemblage-zones are from Robison (1976); abbreviations and assemblage-zone names are: b *(Peronopsis bonnerensis)*, pr *(Ptychagnostus praecurrens)*, g *(Ptychagnostus gibbus)*, a *(Ptychagnostus atavus)*, pu *(Ptychagnostus punctuosus)*, and c *(Lejopyge calva)*; asterisks indicate unnamed zones or undifferentiated intervals.

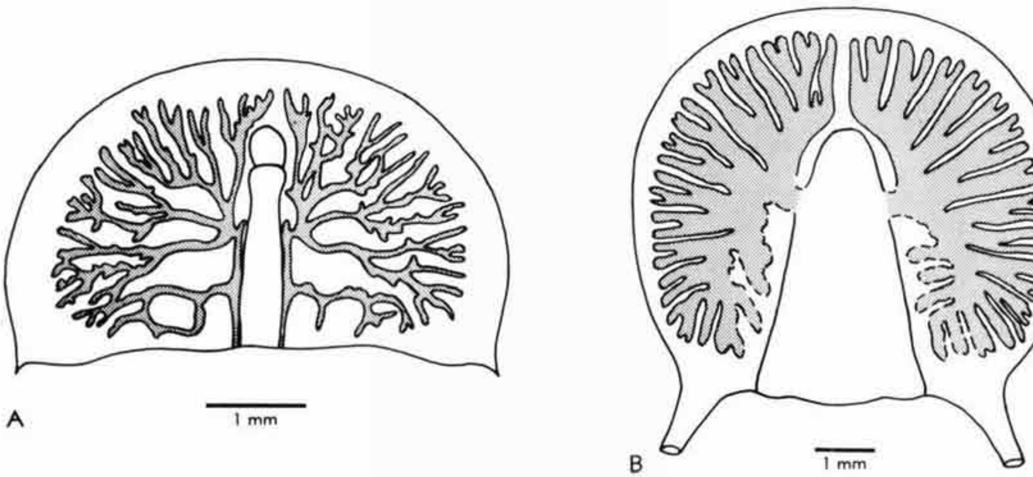


FIG. 2. Cephalothoracic intestinal diverticulae (shaded) in the second instar of the xiphosuran *Limulus polyphemus* (A) compared with the pattern of cephalic rugae (shaded) of the agnostoid trilobite *Ptychagnostus aculeatus* (B). A is after Packard (1872, pl. 5, fig. 27) and B is a camera-lucida drawing of specimen KUMIP 142608 from member B of the Emigrant Springs Limestone (upper Middle Cambrian), Schell Creek Range, Nevada.

ary lines, and particularly in several branches arising directly from *Peronopsis*. Rarely, as in *Doryagnostus wasatchensis,* initial depth of the furrow was variable. In such genera as *Baltagnostus* and *Homagnostus,* the furrow developed only in the posterior part of the preglabellar field next to the axial furrow, whereas in *Agnostus* and *Ptychagnostus,* it developed uniformly and connected with the axial and border furrows. Less commonly, a posterior extension makes a cleft in the anterior glabella, as in *Diplagnostus* and *Tomagnostus*. In most genera, however, the preglabellar median furrow, of whatever type, tends to have a stable expression.

In the most detailed analysis to date of trilobite caeca, Öpik (1961b) interpreted all of the ramified patterns of cuticular lines and ridges to be imprints of alimentary glands. Bergström (1973, p. 4-7) concurred with Öpik's conclusion that the coarse genal rugae of agnostoids are alimentary prosopon (see Figure 2 for comparison of an agnostoid with an extant xiphosuran), but he challenged Öpik's assignment of the same function to the fine, anastomosing prosopon of polymeroids. Alternatively, Bergström proposed a circulatory function for the polymeroid prosopon, which he compared with the pattern of the xiphosuran circulatory system (Fig. 3). I agree with Bergström's proposal, and as additional support for his viewpoint, note that the genal prosopon of agnostoids is always anteromedially divided whereas that of polymeroids is usually confluent. A preglabellar median furrow is extremely rare among polymeroids, and to my knowledge a medial subdivision of the anastomosing polymeroid prosopon has not been reported. In fact, a preglabellar median ridge (e.g., *Deiracephalus, Paedeumias*) or boss (e.g., *Aloķistocare,* nepeids) is much more common than a furrow among polymeroids, but is unknown among agnostoids. For these reasons, the rare preglabellar median furrow of polymeroids does not appear to be homologous with the similar furrow that is common on agnostoids.

In conclusion, because of iterative evolution, the preglabellar median furrow should not be used by itself for classifying agnostoid trilobites. Nevertheless, because of its general stability of expression within various agnostoid groups, I believe that in combination with other characters (particularly those of the axial lobe), it does warrant recognition in the definition of generic and suprageneric taxa. Within given phyletic groups, the furrow generally shows less variability than most of the seven features chosen by Öpik (1967) for classification of agnostoids. In fact, at least four of his seven features (shape of acrolobes, structure of pygidial border, shape of glabellar rear, and width of border) are variable within several genera and even some species.

SYSTEMATIC DESCRIPTIONS

Genus DORYAGNOSTUS Kobayashi

Doryagnostus Kobayashi, March 7, 1939, p. 148; Westergård, 1946, p. 82-83; Howell, 1959, p. 178; Pokrovskaja, 1960, p. 58.

Ceratagnostus Whitehouse, March 17, 1939, p. 255-256.

Type species.—Agnostus incertus Brögger, 1878, p. 70-71, by original designation.

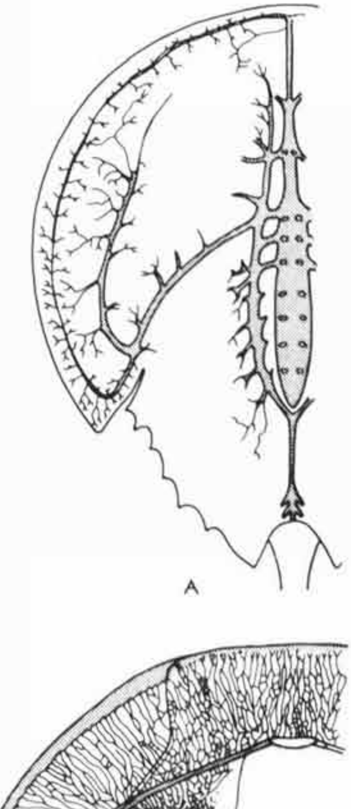
Description.—Cephalon subcircular to subquadrate; width slightly greater than length. Axial furrow well defined. Glabella slightly tapered, anterior end uncleft and commonly with blunt point, transglabellar furrow well developed and usually straight, segmentation of posterior lobe faint or undeveloped, and posterior end broadly rounded. Basal lobes short and equilaterally triangular. Genae usually smooth; divided by preglabellar median furrow. Border furrow mostly narrow to moderate in width, usually expanding into triangular depression (deltoid area) at junction with preglabellar median furrow. Border narrow posteriorly, widening moderately toward anterior, and lacking spines.

Thoracic segments with transversely tripartite axial rings that lack spines. Anterior segment with or without weak median tubercle.

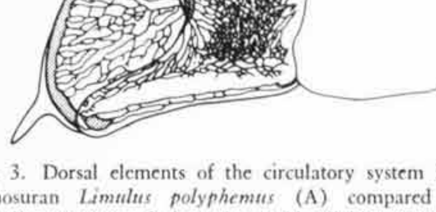
Pygidium subcircular, subquadrate, or subrectangular; width slightly greater than length. Axial furrow well defined. Axis of unmodified type (axiolobate of Öpik, 1967, p. 68); well separated from posterior border furrow; width (tr.) of first segment expands toward anterior, and is distinctly wider than remainder of axis; second segment slightly wider (tr.) than adjacent pleural fields; on larger holaspides, anterior two transverse furrows effaced or only faintly defined near junction with axial furrow; median node small, apparently situated on middle to posterior part of second segment. Posterior axis (behind second segment) acuminate, with or without weak to moderate depression centered at site of tiny secondary median node. Pleural fields smooth and separated by well-developed postaxial median furrow. Border furrow narrow. Border of uniform structure (simplimarginate of Öpik, 1967, p. 69), moderate in width, with pair of posterolateral spines.

Discussion.—Doryagnostus is characterized by an anterior border furrow that usually expands to form a triangular depression (here named **deltoid area**) at its junction with the preglabellar median furrow. The glabella is bipartite (sag.) and has simple basal lobes. The pygidial axis is widest at the anterior segment, has undeveloped or only faint transaxial furrows, a small median tubercle, and the posterior part is acuminate, usually with a weak to moderate central depression, and terminates well forward from the posterior border furrow. A postaxial median furrow and posterolateral border spines are always present.

The taxonomic status and affinities of *Doryagnostus* have been subjects of disparate opinions.



A



B

FIG. 3. Dorsal elements of the circulatory system in the xiphosuran *Limulus polyphemus* (A) compared with cephalic prosopon of the polymeroid trilobite *Papyriaspis lanceola* (B) (from Bergström, 1973, fig. 2). Shaded areas correspond to known (A) and inferred (B) vascular trunks.

Westergård (1946, p. 82-83) was the first to note that *Doryagnostus* Kobayashi, March 7, 1939, and *Ceratagnostus* Whitehouse, March 17, 1939, are obvious synonyms, and that *Doryagnostus* has priority because the name was published 10 days earlier. Westergård also expressed the opinion that "*Doryagnostus* may be closely allied to *Triplagnostus* and should possibly be regarded as another subgenus of *Ptychagnostus*," but without further comment he nevertheless recognized *Doryagnostus* as a separate genus. Based on the structure of its pygidial axis, Öpik (1961a, p. 77) considered *Doryagnostus* to be a synonym of *Ptychagnostus*, and I formerly agreed (Robison, 1964, p. 522-523). However, after further study, which includes review of most illustrated specimens as well as data from numerous undescribed collections, I now conclude that *Doryagnostus* should be recognized as a separate taxon of generic rank.

Members of *Doryagnostus* are deceptively close homeomorphs of some species of *Ptychagnostus*, and the two forms are commonly associated. Initial species of each genus probably evolved from different species of *Peronopsis* by independent heterochronus development of a preglabellar median furrow, which accounts for the close morphological similarities. Representatives of the two taxa differ, however, by the consistent effacement, or near effacement, of transaxial furrows on the pygidium of *Doryagnostus*. Two such furrows are always at least moderately well defined on all species of *Ptychagnostus* except those in later phyletic stages where most other dorsal furrows of the acrolobes are secondarily effaced. *Doryagnostus* has distinct posterolateral border spines on the pygidium of its three known species, whereas such spines appear only late in some phyletic lines of *Ptychagnostus*. Also, except in its late phylogeny (some *D. incertus* from Scandinavia), all representatives of *Doryagnostus* possess a distinctive deltoid area, a feature unknown in *Ptychagnostus*.

Öpik (1961a, p. 77) observed that some representatives of *Doryagnostus* and *Ptychagnostus* resemble each other in the possession of an accentuated central depression on the posterior part of the pygidial axis, and he considered this to be a unifying generic character. Actually, the progressive development of that feature is a common phyletic trend that can be observed in such other agnostoid genera as *Peronopsis, Tomagnostus,* and *Diplagnostus*. Its function is still unknown, but because of its considerable variability within several agnostoid lineages, I now consider its taxonomic significance to be minor, and inadequate to warrant the synonymy of *Doryagnostus* and *Ptychagnostus*.

As here redefined, *Doryagnostus* includes three species: *D. incertus* (Brögger) (= *Ceratagnostus magister* Whitehouse), *D. deltoides* Robison, and *D. wasatchensis* n. sp. The genus has an observed stratigraphic range from the *Ptychagnostus gibbus* to the *Ptychagnostus nathorsti* zones of the Middle Cambrian. Representatives are known from England, Norway, Sweden, Denmark, Canada (Newfoundland), the United States (Utah), Australia (Queensland), and the Soviet Union (Kazakhstan).

Doryagnostus wasatchensis, D. deltoides, and *D. incertus* first appear at successively higher stratigraphic horizons. If they represent parts of a phyletic continuum, the following evolutionary trends are apparent among holaspides: 1) increase in size—maximum length of the cephalon increases from about 4 to 7 mm; 2) decrease in relative width of the glabella from wider to narrower than adjacent genae at the level of the transglabellar furrow; 3) decrease in length of the anterior glabellar lobe relative to the length of the posterior lobe from about 41 to 34 percent; 4) increase in depth of the central depression on the posterior part of the pygidial axis; and 5) increase in relative size of the pygidial border spines. The most obvious feature that does not show consistent stratigraphic variation is size of the deltoid area, which is greatest in *D. deltoides* of intermediate stratigraphic position.

DORYAGNOSTUS DELTOIDES Robison

Plate 2, figures 3-5, 7

Euagnostus opimus Whitehouse (part), 1936, p. 87-88, pl. 8, fig. 10 (*not* figs. 11, 12); Hill and others, 1971, p. 18, pl. 9, fig. 4.

Doryagnostus deltoides Robison in Jell & Robison, 1978, p. 7, pl. 2, figs. 7-9, 12.

This species is described in an accompanying paper (Jell & Robison, 1978). It is characterized by its large, well-developed deltoid area. Its glabella is approximately the same width as adjacent genae at the level of the transglabellar furrow.

Occurrence.—Collection UQL256 of F. W. Whitehouse from the Currant Bush Limestone, 83 km (52 mi) north of Camooweal on Thorntonia road, northwestern Queensland; Middle Cambrian ("*Euagnostus opimus* Zone" of Öpik, 1970).

DORYAGNOSTUS INCERTUS (Brögger)

Plate 2, figures 1, 2, 8

Agnostus incertus BRÖGGER, 1878, p. 70-71, pl. 6, figs. 4a, b; TULLBERG, 1880, p. 19, pl. 1, figs. 6a, b; LINNARSSON, 1883, p. 32; GRÖNWALL, 1902, p. 52-53; LAKE, 1907, p. 29-30, pl. 3, figs. 1-3; STRAND, 1929, p. 344-345.

Doryagnostus incertus (Brögger) KOBAYASHI, 1939, p. 148; WESTERGÅRD, 1946, p. 83-84, pl. 12, figs. 20-23; pl. 13, figs. 1-3; HUTCHINSON, 1962, p. 87, pl. 10, figs. 9-11.

Ceratagnostus magister WHITEHOUSE, 1939, p. 256-257, pl. 25, fig. 27.

Doryagnostus magister (Whitehouse) HILL and others, 1971, p. 18, pl. 9, fig. 7.

Types.—Brögger (1878) did not mention types. According to D. L. Bruton (1977, written communication), part of Brögger's 1878 collection is at the Paleontologisk Museum in Oslo, but representaties of *Agnostus incertus* are missing from that collection and their whereabouts are unknown.

Diagnosis.—Size relatively large; complete specimens range up to almost 17 mm in length. One large Australian specimen (Pl. 2, fig. 8) has a cephalic length and width of 7.1 by 8.2 mm and a pygidial length and width of 7.0 by 8.2 mm.

Cephalon subcircular to subquadrate; width about equal to or slightly greater than length. Glabella distinctly narrower than genae (at level of transaxial furrow); anterior lobe ogiviform, posterior lobe with weak median node situated centrally or slightly in front of midpoint. Genae usually smooth, rarely showing faint scrobiculae; divided by consistently well-developed preglabellar median furrow. Border furrow mostly narrow, and deltoid area poorly developed or absent. Border relatively narrow, but expands slightly in width from posterior to anterior.

Thorax with tripartite (tr.) axial rings that lack spines. Weak median tubercle present on anterior segment.

Pygidium subcircular to subquadrate; width equal to or slightly greater than length. Posterior axis (behind second segment) acutely pointed, with moderate to well-developed central depression and tiny secondary median node, and axial furrow with or without slight constriction opposite depression. Border furrow narrow. Border widens slightly toward posterior, of uniform width (sag. and exsag.) between border spines; backward bow in posterior margin varies from strongly to broadly rounded. Posterolateral border spines moderate to relatively large.

Discussion.—*D. incertus* is relatively large and generally characterized by the poor development or absence of a deltoid area; however, one cephalon illustrated by Lake (1907, pl. 3, fig. 1) has a moderately well-developed deltoid area. The glabella is distinctly narrower than adjacent genae at the level of the transglabellar furrow, and the posterior part of the pygidial axis is acutely pointed and has a prominent central depression.

Kobayashi (1939, p. 148) designated *Agnostus incertus* Brögger, 1878, as the type species of *Doryagnostus*. Westergård (1946, p. 82-83) later considered *D. incertus* and *Ceratagnostus magister* Whitehouse, 1939, to be synonyms. Compared with Scandinavian specimens (see Westergård, 1946), those from Australia are of somewhat larger average size, tend to have a slightly shorter glabella and less constricted posterior axial furrow on the pygidium, the posterolateral border spines tend to be slightly larger, and the posterior pygidial margin is slightly less bowed. Also, Scandinavian specimens tend to lack a deltoid area, whereas that feature is poorly developed on most Australian specimens. It is arbitrary whether or not these slight differences warrant taxonomic recognition, but I tentatively concur with the synonymy proposed by Westergård.

D. incertus differs from *D. deltoides* and *D. wasatchensis* by its much less developed deltoid area, narrower glabella, and better developed depression on the posterior pygidial axis. It also differs from *D. wasatchensis* by having larger posterolateral border spines.

Occurrence.—*D. incertus* is the youngest known species of *Doryagnostus*. It has an observed range from the *Ptychagnostus punctuosus* to *P. nathorsti* zones of the late Middle Cambrian. It is known from Australia (Queensland), Canada (Newfoundland), England, Norway, Sweden, and the Soviet Union (Kazakhstan).

DORYAGNOSTUS WASATCHENSIS, n. sp.

Plate 1, figures 1-4, 6; Plate 2, figures 6, 9-13

Holotype.—Cephalon, KUMIP 142590 (Pl. 1, fig. 1a-c), from collection R-306.

Other material.—More than 100 disarticulated specimens in collections R-280c, R-305, R-306, R-333, R-369, and U.S. Geological Survey 7678-CO.

Description.—Exoskeleton moderately convex. Both cephalon and pygidium greater in width than length.

Cephalon subcircular to subquadrate; length and width of largest observed specimen 4.0 by 4.3 mm. Glabella relatively broad and slightly wider than adjacent genae (at level of transglabellar furrow); anterior lobe hemicircular, with or without slight anteromedian point; median node weak, situated slightly behind midpoint of posterior lobe. Preglabellar median furrow usually visible, but variable in depth, tending to be weakest on some large holaspides. Genae smooth. Border furrow of intermediate width, deltoid area moderately developed, even on specimens with a weak preglabellar median furrow.

Thorax unknown.

Pygidium subcircular to subrectangular; length and width of largest observed specimen 3.9 by 4.8 mm. Anterior axis usually showing faint indication of two transaxial furrows at junctions with axial furrow. Posterior axis (behind second segment) with incipient weak central depression and tiny secondary median node just behind midpoint. Posteromedian border furrow with slight forward bow, but width of adjacent border nearly constant. Posterolateral border spines relatively small.

Discussion.—*D. wasatchensis* is characterized by a moderately developed deltoid area, a preglabellar median furrow of variable depth, a broadly rounded to bluntly pointed glabella that is wider than adjacent genae at the level of the transglabellar furrow, a lanceolate pygidial axis with small median node, only an incipient weak central depression on the posterior pygidial axis, and a pair of relatively small pygidial border spines.

Compared with *D. deltoides* and *D. incertus*, *D. wasatchensis* has a wider, slightly less tapered, and a generally less anteromedially pointed glabella, and the deltoid area is intermediate in development. Few specimens of *D. deltoides* were available for comparison, but *D. wasatchensis* appears generally to have a more quadrate cephalon and pygidium, a slightly smaller average size, and smaller pygidial border spines. *D. wasatchensis* further differs from *D. incertus* by having a shallower central depression on the posterior pygidial axis and smaller pygidial border spines.

Specimens from Utah have previously been identified as *Euagnostus opimus* (Robison, 1976, p. 105), but that error is corrected here.

Occurrence.—*D. wasatchensis* is known from two localities in north-central Utah. It has an observed range through most of the *Ptychagnostus gibbus* Assemblage-zone.

Collection R-306 (= R-280c and R-305) is from the upper part of Crittenden's (1972) "Ute and Blacksmith Limestones, undivided." The locality is on a west-facing slope on the first ridge south of the South Fork Picnic Ground in the Cache National Forest, which is situated along the South Fork of the Ogden River and adjacent to Utah Highway 39 in the Wasatch Mountains, about 6.5 km (4.0 mi) northeast of Huntsville, Weber County, Utah (SE¼ SE¼ SW¼ sec. 6, T. 6 N., R. 3 E., Browns Hole Quadrangle). Abundant agnostoid trilobites are in rare concretions with a matrix of dark-gray micritic limestone, and the concretions are scattered in light-brownish-gray unfossiliferous claystone at a horizon 30.5 m above the base of the *P. gibbus* Zone. Also, the horizon is 30.5 m above the top of a carbonate unit with capping lenses of bioclastic limestone that contain a distinctive "*Glyphaspis* fauna," which elsewhere in Utah is widespread but known only from the topmost bed of the Swasey Limestone, and which has been described from the Drum Mountains in an unpublished thesis by Randolph (1973). Associated in the concretions with *D. wasatchensis* are *Elrathina* sp., *Peronopsis fallax*, *Ptychagnostus gibbus*, *Ptychagnostus intermedius*, and *Ptychagnostus seminula*.

Collection R-369 (probably equivalent to R-333 and U.S. Geological Survey 7678-CO) is from an outcrop of thin-bedded, dark micritic limestone 3.0 m above the base of the *Ptychagnostus gibbus* Assemblage-zone in the Blacksmith Formation. The locality is along the north side of an unimproved U.S. Forest Service road in the Wasatch Mountains, about 6.5 km (4.0 mi) south of Mantua, Box Elder County, Utah (NE¼ NW¼ sec. 15, T. 18 N., R. 1 S.). Associated with *D. wasatchensis* at this locality are *Bathyuriscus* sp., *Elrathina* sp., *Peronopsis fallax*, *Peronopsis* cf. *P. matthewi*, *Ptychagnostus gibbus*, *Ptychagnostus intermedius*, *Ptychagnostus seminula*, *Zacanthoides* sp., and miscellaneous inarticulate brachiopods and sponge spicules.

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EXPLANATION OF PLATES

PLATE 1

FIGURE

1-4,6. *Doryagnostus wasatchensis* Robison, n. sp., Middle Cambrian, Utah (all ×6 and all from collection R-306).—*1a-c.* Dorsal stereogram and lateral view of holotype cephalon with well-developed preglabellar median furrow, KUMIP 142590.—*2a-c.* Dorsal stereogram and lateral view of pygidium with relatively slender posterior axis, KUMIP 142591.—*3.* Cephalon, KUMIP 142592.—*4a,b.* Dorsal and lateral views of pygidium with axis slightly expanded behind second segment, KUMIP 142593.—*6.* Cephalon with partially developed preglabellar median furrow, KUMIP 142594.

5,8. *Ptychagnostus praecurrens* (Westergård), Burgess Shale, Middle Cambrian, British Columbia (both ×8).—*5.* Smaller complete holaspid, CGS 81235.—*8.* Larger complete holaspid, somewhat flattened, CGS 75000.

7,11,14. *Peronopsis brighamensis* (Resser), Middle Cambrian, Idaho.—*7.* Silicified cephalon from Spence Tongue of Lead Bell Shale, ×8, KUMIP 142595.—*11a,b.* Dorsal and lateral view of undeformed pygidium from Naomi Peak Tongue of Twin Knobs Formation, ×8, KUMIP 142596.—*14.* Complete holaspid from Spence Tongue of Lead Bell Shale, ×6, KUMIP 142608.

9,10,12, 13. *Peronopsis gaspensis* Rasetti, Geddes Formation, Middle Cambrian, Northern Egan Range, Nevada (all ×6).—*9,10.* Cephala, KUMIP 142597 and 142598.—*12,13.* Pygidia, KUMIP 142599 and 142600.

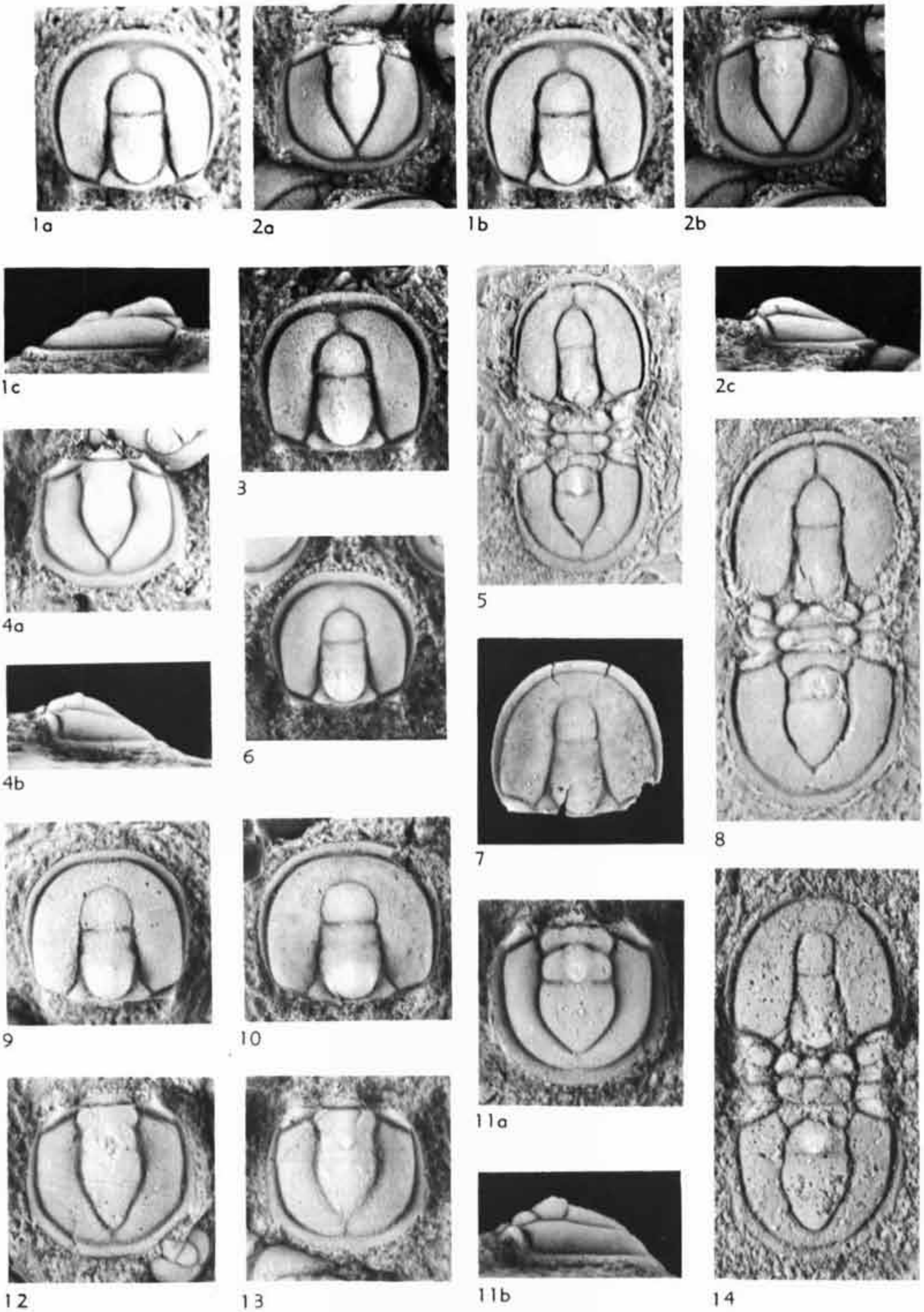
PLATE 2

FIGURE

1,2,8. *Doryagnostus incertus* (Brögger), V Creek Limestone, Middle Cambrian, Queensland.—*1a,b.* Dorsal and lateral views of complete holaspid (figured as holotype of *Ceratagnostus magister* by Whitehouse, 1939, pl. 25, fig. 27), ×5, UQF 3399.—*2.* Small complete holaspid, ×5, KUMIP 142601.—*8.* Large complete holaspid, ×4, UQF 43547.

3-5,7. *Doryagnostus deltoides* Robison, Currant Bush Limestone, Middle Cambrian, Queensland.—*3a,b.* Dorsal and lateral views of latex cast of cephalon (figured as *Euagnostus opimus* by Whitehouse, 1936, pl. 8, fig. 10), ×6, UQF 3194.—*4.* Holotype cephalon, ×6, UQF 69624.—*5a,b.* Dorsal and lateral views of pygidium, ×7, UQF 69625.—*7.* Pygidium, ×5, UQF 69626.

6,9-13. *Doryagnostus wasatchensis* Robison, n. sp., Middle Cambrian, Utah (all ×6).—*6.* Cephalon, collection R-280c, KUMIP 142602.—*9.* Three cephala with weak or partially developed preglabellar median furrows and one pygidium, collection R-306, KUMIP 142603.—*10.* Small holaspid cephalon with well-developed preglabellar median furrow and relatively large deltoid area, collection R-280c, KUMIP 142604.—*11.* Small holaspid pygidium associated with holotype, collection R-306, KUMIP 142605.—*12.* Small holaspid pygidium, collection R-280c, KUMIP 142606.—*13.* Two cephala and two pygidia associated with two partially exposed pygidia of *Ptychagnostus seminula*, collection R-306, KUMIP 142607.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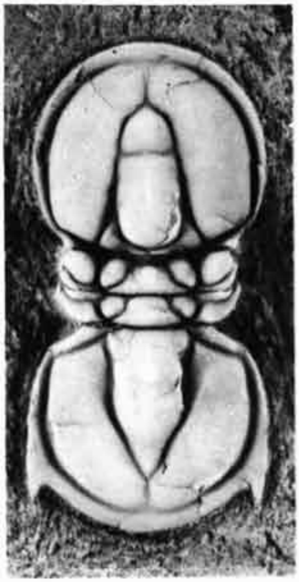
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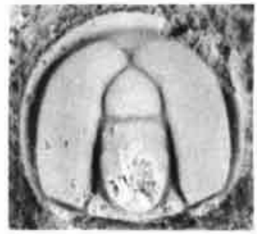
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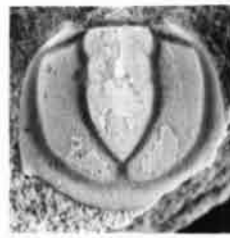
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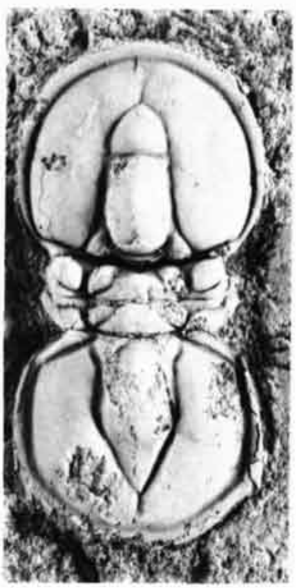
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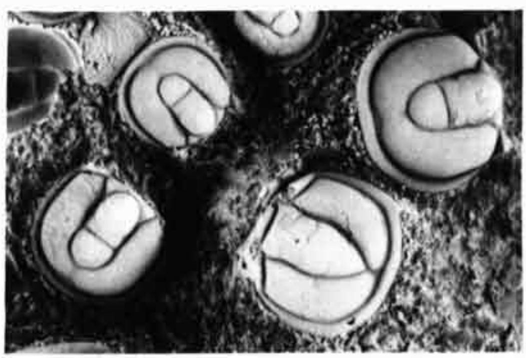
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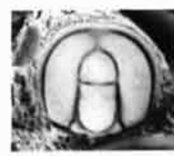
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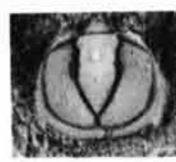
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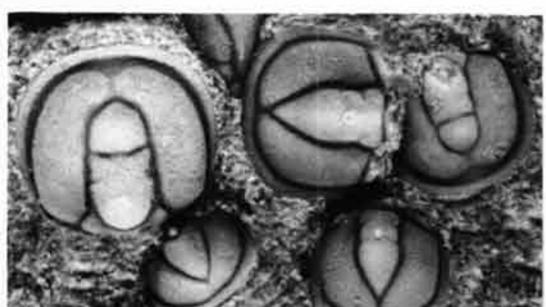
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