

# SYSTEMATIC DESCRIPTIONS OF THE CLASS TRILOBITA

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[Diagnoses of ordinal and higher taxa by R. A. FORTEY and H. B. WHITTINGTON; authorship of other diagnoses indicated within.]

## Class TRILOBITA Walch, 1771

[*nom. correct. ex* Trilobiten WALCH, 1771, p. 120] [This name, as "Trilobiten," was published by WALCH (1771, p. 120) in his volume III of KNORR and WALCH (1768–1774). WALCH's work was rejected for nomenclatorial purposes by the International Commission on Zoological Nomenclature (Opinion 529, 1958). However, the Commission's remit extends only to the family-group level (Article 1b(4), *International Code of Zoological Nomenclature*, 1985), hence the name, emended to "Trilobita," remains available. The designation of the genus *Dalmanites* BARRANDE as type (HENNINGSMOEN & MOORE in MOORE, 1959, p. 172) is invalid.]

Extinct marine arthropods, body divided by furrows longitudinally into median (axial) and lateral (pleural) regions, transversely into cephalon of fused segments, thorax of articulated segments, and pygidium of few to many fused segments. Length of mature individuals ranges from a little over 1 mm to about 700 mm.

Dorsal exoskeleton and periphery of venter (doublure) calcified (but see comments on Naraoiidae); calcified plate (hypostome) anterior to mouth and below anterior axial region. Anterior wing of hypostome extending dorsally to a fossula in the axial furrow. Facial suture characteristic, absent in *Olenellina*, but may be secondarily lost or modified. Rostral plate or median suture present, or cheeks conjoined. Cephalon with one pair of eyes (which may be lost), each eye lobe connected to axial region by raised ridge; eye lenses of crystalline calcite. Slightly oblique-transverse pleural furrows at posterior of cephalon, on each thoracic segment, and on pygidial segments. Growth of exoskeleton proceeded by molting from calcified protaspis about 1 mm long to adult, and by sequential release of segments into thorax. Protaspides of *Olenellina* and *Agnostina* not known. Limbs (where known) include one pair of antennae, followed posteriorly by series of generally similar biramous limbs, of which three (possibly four in one species) are

cephalic. *Lower Cambrian (Atdabanian)–Upper Permian.*

## Order AGNOSTIDA Salter, 1864

[*nom. correct.* SHERGOLD, LAURIE, & SUN, 1990, p. 32, *pro* Agnostini SALTER, 1864a, p. 2] [=Miomera JAEKEL, 1909, p. 394; Agnostida KOBAYASHI, 1935, p. 81; see discussion in ROBISON & CAMPBELL, 1974, p. 281]

Diminutive, isopygous, 2 or 3 fulcrate thoracic segments. Cephalic shield with deeply parabolic outline and maximum width (tr.) usually anterior to genal angle; border convex; glabella commonly fusiform, widest at base (except in *Condylopygidae*). Hypostome natant; rostral plate lacking or uncalcified. Outline of pygidium closely matching that of cephalon. *Lower Cambrian–Upper Ordovician.*

## Suborder AGNOSTINA Salter, 1864

[*nom. correct.* SHERGOLD, LAURIE, & SUN, 1990, p. 32, *pro* Agnostini SALTER, 1864a, p. 2]

No eye or facial suture; 2 thoracic segments; cephalothoracic aperture present; pygidium generally with wide axis, margin commonly bearing posterolateral spine. Cuticle thin. Calcified protaspis not known. *Lower Cambrian–Upper Ordovician.*

## INTRODUCTION TO THE SUBORDER AGNOSTINA

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The historical background to the classification of this suborder has recently been discussed in detail (SHERGOLD, LAURIE, & SUN, 1990, p. 1–3). The classification presented here is as developed in that paper and essentially follows ideas on relationships that have

been generated mainly in Australia, through the work of A. A. ÖPIK, and North America, particularly by R. A. ROBISON, during the past three decades.

ÖPIK (1967, p. 65) arrived at the general conclusion that due to the "combinative nature" of most taxa, "all agnostoids within their suborder are relatively close to each other, constituting a single superfamily, Agnostacea, with a restricted number of interrelated families." ÖPIK's classifications rely heavily on basic objective characteristics that allow intergrading morphologies to be independently diagnosed (e.g., ÖPIK, 1979). Although we do not follow his classifications here implicitly, we do agree that only characteristics in combination can be used for sophisticated taxonomic discrimination. Accordingly, we have made use of extended diagnoses particularly at family rank to facilitate assessment of the fullest range of permutations. In general, fewer, more succinctly diagnostic characteristics link genera at subfamilial level, as indicated in the review below. The approach has been adopted because Agnostina reiterate morphological conditions at different times in different familial groups, e.g., varyingly effacing or emphasizing external morphology, constricting acrolobes, developing zonate borders, effacing the anterior glabellar lobe or sagittally splitting it, or modifying the posterior pygidial axial lobe. We have in general made use of axial criteria to define broad groups at the familial and subfamilial level and degrees of effacement or scrobiculation at the generic and subgeneric level. As a result we emphasize morphological continuity.

Compared to treatment of Agnostina in the previous *Treatise*, we have also given more extended geographic and stratigraphic ranges. The former are given to state or province regions and the latter to local biochronological stage and zone. This is an acknowledgment of the stratigraphic and biofacies importance of these trilobites on a global scale, particularly during the Cambrian. First and last occurrences of taxa may not be the same in different zoogeographical

provinces with different biofacies relationships and biochronologic schemes.

In addition, because the Linnean system of classification relies on the concept of the type specimen, we have included what is currently known about the status of the type material, its repository, and numbers assigned. Several old collections remain unlocated; several taxa are based on syntype material requiring the designation of lectotypes; and in some instances types are known to be lost, necessitating the search for topotype material and justification of neotypes.

In almost all instances the extant type material has been illustrated, frequently supplemented by more complete material to better illustrate the generic concepts. Where type material is not identified, suitable topotypes or other subjectively selected specimens are figured.

Suborder Agnostina, as used here, is based on concepts traditionally attributed to SALTER (1864a), who recognized a Section Agnostini. This is the suborder Agnostina of MOORE (1959), RUSHTON (1966), and ÖPIK (1961b, 1967, 1975b, 1979), and the order Agnostida of RASETTI (1945a, 1948b, 1952a), SHERGOLD, LAURIE, and SUN (1990), and SHERGOLD (1991). ROBISON (1984) has also diagnosed an order Agnostida but attributed it to KOBAYASHI (1935) rather than SALTER (1864a).

A total of 190 generic and subgeneric taxa assignable to the Agnostina have been assessed. Of these, four taxa are rejected from Agnostina, and a further six are *nomina nuda*. About thirty percent of the rest are synonyms, leaving for classification 123 valid taxa. These are assigned to the superfamilies Condylopygoidea and Agnostoidea and two families of uncertain affinity, Phalacromidae and Sphaeragnostidae.

Although Condylopygoidea is based on the single family Condylopygidae RAYMOND, 1913a, itself containing only two genera, *Condylopyge* and *Pleuroctenium*, its concept is stable and goes back to the first attempted generic subdivision of *Agnostus* by HAWLE and CORDA (1847). At one taxonomic rank



or another, the constituent genera of Condylropygidae have retained independent status in all classifications. We follow KOBAYASHI (1962) in recognizing them at the superfamilial level, but the familial concept remains that advocated by RAYMOND (1913a). The characteristic expansion of the anterior glabellar lobe, the apparent presence of occipital structures instead of the basal lobes, the possible retention of a cephalothoracic aperture (if RUSHTON, 1979, p. 45 is correct), and the presence always of three anterior segments in an otherwise axiolobate pygidium differentiate Condylropygoidea from Agnostoidea. Condylropygoids are also prone to spinosity: an occipital spine may be developed, and the elongate axial cephalic node may be an aggregation of small spines (see RUSHTON, 1979, p. 47, fig. 2a). *Pleuroctenium* also displays spines developing from the axial nodes of the thoracic and anterior three pairs of pygidial segments. Fringing spines or crenulations occur on the pygidia of both genera. There is also a tendency, well illustrated by WESTERGÅRD (1946, pl. 2), for both cephalic and pygidial acrolobes to become transversely divided. Division occurs adjacent to the anterior glabellar furrow of the cephalon and the third, posteriormost (F3), transverse furrow of the pygidial axis. It is only among the Pseudagnostinae that such features are displayed among Agnostoidea. Condylropygoidea are therefore most distinctive members of the Agnostina.

The great bulk of agnostoid genera and subgenera are assigned to the superfamily Agnostoidea and distributed among seven families and ten subfamilies. A significant number of genera cannot be classified with confidence at the familial level, either because they are inadequately preserved or are not diagnosable. Many of these genera are highly effaced, and most are in need of thorough revision. Agnostoid families recognized include Agnostidae, Ptychagnostidae, Spinagnostidae, Peronopsidae, Diplagnostidae, Clavagnostidae, and Metagnostidae.

Micragnostidae (HOWELL, 1935b), Glyptagnostidae (WHITEHOUSE, 1936), Hastag-

nostidae (HOWELL, 1937), and Rudagnostidae (LERMONTOVA, 1951a) are all considered synonyms of Agnostidae. Agnostidae, the largest family of Agnostina, is presently considered to embrace three subfamilies: Agnostinae with fourteen genera and subgenera; Ammagnostinae with seven genera and subgenera; and Glyptagnostinae with two genera. A further five genera cannot be placed in subfamilies. Agnostid genera can be divided in several ways, but the axial characteristics, particularly of the pygidium, have been primarily used in the present classification. In Agnostinae the pygidium is simple and axiolobate; in Ammagnostinae the posterior lobe of the pygidial axis is invariably expanded and lengthened and contains a well-developed secondary axial node; in Glyptagnostinae, although the simple axiolobate situation is commonly obscured by scrobiculation, a secondary axial node is developed in association with a well-defined transverse depression that occurs in the rear of the posterior lobe.

Use of the subgeneric rank is made within Agnostinae to express end members of gradational morphological series. Hence, *Homagnostus* is reinstated as a subgenus of *Agnostus*, representing morphs with a laterally expanded and extended pygidial axis. *Lotagnostus* (*Lotagnostus*), *L. (Eolotagnostus)*, and *L. (Distagnostus)* represent recognizable degrees of effacement. In the revived genus *Oncagnostus* (WHITEHOUSE, 1936), the subgenus *Strictagnostus* is made available for morphs with short axes that have characteristically flared or tapered acrolobes, and the subgenus *Kymagnostus* is used for those with long axes without **deliquiate** border furrows. LUDVIGSEN, WESTROP, and KINDLE (1989) have shown that *Trilobagnostus* should not be referred to *Lotagnostus*. It is here given generic status but could also be interpreted as a subgenus of *Oncagnostus*. The species referred to the genera and subgenera *Oncagnostus*, *Strictagnostus*, *Kymagnostus*, and *Trilobagnostus* seemingly form a continuum in great need of revision. *Inmitagnostus* and *Acutatagnostus* could also be regarded as

subgenerically related. *Micragnostus*, following the suggestions of FORTEY (1980b, p. 20), is restricted in specific composition but decidedly separated from *Geragnostus* (Metagnostidae) with which it has long been associated.

Glyptagnostinae is here regarded as a subfamily of Agnostidae rather than a family in its own right (KOBAYASHI, 1938, 1939a; WESTERGÅRD, 1947; HENNINGSMOEN, 1958; ÖPIK, 1961b; SHERGOLD, 1982). It is restricted here to the genera *Glyptagnostus* and *Agnostardis*, as envisaged by ÖPIK (1963, p. 38). The previously recognized subgenus *Lispagnostus* is considered here to be synonymous with *Ammagnostus*. The highly **scrobiculate** and deuterolobate *Pseudoglyptagnostus*, which has been associated with Glyptagnostinae, is referred to Pseudagnostinae (family Diplagnostidae) and regarded as an **en grande tenue** subgenus of *Agnostotes*. We prefer to regard Glyptagnostinae here as a subfamily of Agnostidae, rather than of Diplagnostidae as proposed by ÖPIK (1967), on the basis of cephalic axial similarity with such genera as *Innitagnostus* and pygidial axial similarity with *Agnostus* itself.

Genera of the Ammagnostinae form a cohesive group with the exception perhaps of the diminutive *Kormagnostella* as recognized by ÖPIK (1967). *Tentagnostus* is considered to be an **en grande tenue** subgenus of *Ammagnostus*. *Proagnostus* is revived following ROBISON's (1988) designation of a lectotype for *P. bulbosus*. *Agnostascus* and *Agnostascus* (*Paragnostascus*) must now be regarded as synonyms of *Proagnostus*.

Of uncertain subfamilial classification, *Aistagnostus* is partially effaced, the pygidium of Agnostinae type. The cephalon, however, is not like that of members of this subfamily. The remaining unclassified genera have long or long and expanded, posterior axial pygidial lobes. *Idolagnostus* is diminutive, could be deuterolobate, and may represent a genus of Pseudagnostinae. *Acmarhachis* has been similarly classified (PALMER, 1960, 1962a), and *Connagnostus* has been regarded by ÖPIK (1967) as a Diplagnostinae. Until investi-

gated in greater detail, however, we prefer to give these genera an undefined status among Agnostidae.

The family Ptychagnostidae is here considered to represent an independent family (*vide* ROBISON, 1984, p. 10), rather than a subfamily of the Agnostidae as originally established (KOBAYASHI, 1939a, p. 151) and often considered (ÖPIK, 1967, p. 90; 1979, p. 86; ERGALIEV, 1980, p. 67; PENG, 1992, p. 82; LAURIE, 1988, p. 171). The members of this family, although sharing some features with members of the Agnostidae, do not seem to be closely related to that family. Although there has been recent debate about the validity of many of the genera belonging to Ptychagnostidae (ÖPIK, 1979; ROBISON, 1982, 1984; LAURIE, 1988), there has been general agreement with regard to the association of species in the family. Genera belonging to the Ptychagnostidae usually have a median preglabellar furrow, a relatively elongate anterior glabellar lobe, elongate basal lobes, a basic articulating device, well-developed pygidial axial F1 and F2, an acuminate posterior pygidial axial lobe, and a tendency toward spinosity. Included in this family is *Tomagnostus*, the early species of which seem to be closely related to *Onymagnostus*. Using the principle of first reviser, SHERGOLD, LAURIE, and SUN (1990) selected Ptychagnostidae (KOBAYASHI, 1939a) as the family name. It may be possible to recognize several subfamilies using some of the synonymous familial names (Triplagnostinae, Lejopyginae), but this has not been attempted herein.

The family Spinagnostidae was established by HOWELL (1935a, p. 218) to accommodate the subfamilies Spinagnostinae and Quadragnostinae, both of which were founded on only one genus, each containing one species. The types of these species are very poorly preserved. For some time now the genus *Spinagnostus* has commonly been considered synonymous with *Hypagnostus* (see WESTERGÅRD, 1946, p. 44), despite ÖPIK's (1979, p. 66) belief that it should be considered a separate genus. This synonymy is upheld herein but does not invalidate the

family name. The types of the eponymous genus of the subfamily Quadragnostinae are very poorly preserved and are largely uninterpretable. *Quadragnostus* is therefore restricted to its type material.

As understood herein, the family Spinagnostidae contains two subfamilies: Spinagnostinae and Doryagnostinae. All members of this family have nondeliquiate border furrows; a nonspinose cephalon; small, triangular basal lobes; usually broadly rounded glabellar culmination; and usually effaced pygidial axial F1 and F2. While the Spinagnostinae may be polyphyletic, all of its members have a tendency to efface the anterior glabellar lobe, usually lack the median preglabellar furrow, have the glabellar node near the F2 furrows, and lack a secondary axial node on the posterior lobe of the pygidial axis. The subfamily Doryagnostinae consists of only three genera, which form a closely related, monophyletic group. All possess a well-developed anterior glabellar lobe, have the glabellar node located from level with F1 to midway between F1 and F2 furrows, and have a small secondary axial node located on the posterior pygidial axial lobe.

One genus assigned to Spinagnostidae, *Pseudoperonopsis* (HARRINGTON, 1938), cannot be placed in a subfamily. This is because the types have never been satisfactorily illustrated and were not available to us for study. Subsequent interpretations vary considerably.

There are probably well over a hundred species that have been assigned to *Peronopsis*, and these remain there despite refinement in agnostoid taxonomy over the last few decades. This genus has for a long time been the receptacle for almost any Early to Late Cambrian agnostoid having an axiolobate, **simplimarginate** pygidium with effaced pygidial axial F1 and F2 and a cephalon with a bilobate glabella lacking a median preglabellar furrow. This has led to *Peronopsis* being, as it presently stands, probably the most morphologically diverse genus of the Agnostina. Herein, the genus is restricted to its type species and is associated with the reha-

bilitated genus *Diplorrhina* and with *Peronopsella* and *Gratagnostus* in the family Peronopsidae (WESTERGÅRD, 1936). This family is of uncertain relationships, but the included genera have a distinctive morphology.

The family Diplagnostidae is essentially reserved for agnostoids that are commonly modified axiolobate (in the sense of ÖPIK, 1967) and frequently zonate. Thus the family includes the subfamilies Diplagnostinae, Oidagnostinae, and Pseudagnostinae. The Diplagnostinae have a characteristically zonate pygidium in combination with an axiolobate or only slightly modified axiolobate condition; the cephalon has an often sulcate and occasionally bilobate anterior glabellar lobe and angulate glabellar culmination. Frequently, a transverse depression is developed behind the pygidial axial node in the anterior half of the posterior lobe. Such characteristics tend to unite the genera *Diplagnostus*, *Linguagnostus*, *Dolichagnostus*, and *Tasagnostus* into a close morphological group.

ÖPIK (1967, 1979) also included the genera *Baltagnostus* (LOCHMAN in LOCHMAN & DUNCAN, 1944) and *Oedorhachis* (RESSER, 1938) in the subfamily Diplagnostinae. In the former, it is only the type species, *B. centerensis*, that is convincingly zonate. Other species assigned to this genus by subsequent workers are simplimarginate or have thickened posterior pygidial borders that are not really zonate in the sense of *Diplagnostus* or *Linguagnostus*: they are quasizonate, having a gentle doubling of the border. Similar are the species attributed by ÖPIK (1979) to *Pseudoperonopsis* (HARRINGTON, 1938), which form a well-defined group stratigraphically but will require generic reassessment when the type species, *Aagnostus sallesi* (MUNIER-CHALMAS & BERGERON in BERGERON, 1899), is revised. As noted by ÖPIK (1967, p. 69), specimens illustrated as *Peronopsis fallax* by WESTERGÅRD (1946, pl. 2, fig. 18–24) also have an incipient zonation. All the above may, therefore, form a second group of taxa that lies intermediate between the basically nonzonate Peronopsidae and

the typically zonate Diplagnostinae. Species assigned to *Oedorhachis* are generally acceptably zonate but are also trispinose and have a variably laterally expanded posterior pygidial axial lobe, a combination of characteristics that sets them slightly apart from other Diplagnostinae.

The subfamily Oidalagnostinae also has a zonate pygidium, but there is a gap in the pygidial collar. The pygidia have a modified axiolobate condition, the posterior lobe is subquadrate and extends to the pygidial collar, and a third marginal spine is situated sagittally. The morphologies of the constituent genera, *Oidalagnostus* and *Cristagnostus* are readily related to and probably derived from Diplagnostinae. A major feature in their phylogeny is the separation of the anterior portion of the posterior axial lobe as seen in *Diplagnostus*, apparently as a third axial ring, and the manifestation of lateral bosses as appendages to this third segment (see WESTERGÅRD, 1946, pl. 9, fig. 6 for extreme condition). These features seem to foreshadow the development of the accessory furrows and deuterolobe that characterize Pseudagnostinae.

The Pseudagnostinae are usually simpli-marginate diplagnostids, which develop a deuterolobe proper and accessory furrows. They are linked to other groups of Diplagnostidae by the occasional presence of a third pygidial spine, as in *Pseudagnostus* (*Sulcatagnostus*), and triannulate anterior part of axis, as in *Xestagnostus*. The Pseudagnostinae are a large group of genera that exhibit a wide range of deuterolobe morphology and degrees of effacement. Relationships of genera and subgenera are determined by the situation of the axial glabellar node relative to the F2 and F3 furrows (SHERGOLD, 1975, 1977, 1980), falling into groups related to *Pseudagnostus*, *Neoagnostus*, and *Rhaptagnostus*, respectively. Degree of effacement varies from nearly total in *Litagnostus* to extreme scrobiculation in *Neoagnostus* (*Machairagnostus*). *Agnostotes* (*Agnostotes*) (ÖPIK, 1963) and *A.* (*Pseudoglyptagnostus*), with its synonym *Glyptagnostotes* (LAZARENKO, 1966), has been classified by authors in Glyptagnos-

tinae (for example, XIANG & ZHANG, 1985), but they are here classified among the Pseudagnostinae because their pygidia seem to be typically deuterolobate (see particularly LAZARENKO, 1966, pl. 2, fig. 1–2, 5–6, 8, 10–12). Characters of the cephalon of Glyptagnostinae, like the elaborate development of the lateral glabellar lobes and division of the anterior lobe by a median sulcus, are apparent in the scrobiculate subgenus *Pseudoglyptagnostus* but much less marked in the more effaced *Agnostotes*. Neither subgenus possesses the typical posterior axial lobe with its secondary axial node and associated transverse depression. ÖPIK (1963, 1967) has explored alternative possibilities for the classification of *Agnostotes* within the Diplagnostidae.

The definition of the deuterolobe has been debated (see PRATT, 1992, for discussion and opinion different from that below). It is a composite posterior pygidial lobe that comprises both axial and pleural elements and that extends therefore to the posterior border furrow and is anterolaterally at least circumscribed by accessory furrows. Possibly, then, such genera as *Oxyagnostus* should be excluded from Pseudagnostinae and such forms as *Idolagnostus* included. Some others, for example *Formosagnostus*, judging from its relationship with *Nahannagnostus* (i.e., the *bulgosus* species group of *Pseudagnostus*; see SHERGOLD, 1977), seem to indicate derivation from Agnostidae and suggest that the subfamily Pseudagnostinae could be polyphyletic. Further revision is required to solve such issues. FORTEY (1980b, p. 28) has regarded the Pseudagnostinae as somehow related to the Metagnostidae because some of them possess what might be taken to be an intranotular axis behind the defined extent of the pygidial axis. He also noted the glabellar furrow patterns, the deliquation of the border furrows, common pygidial articulating device, and the occurrence of a common prosopon. However, many morphological trends found among agnostoids are subsequently reiterated in apparently unrelated groups. Features of Pseudagnostinae are found in Middle Cambrian Oidalagnostinae

(Diplagnostidae) and in Glyptagnostinae (Agnostidae). The transverse division of the cephalic acrolobe of the latest Cambrian genus *Trisulcagnostus* may be observed also in Condylropygidae.

Clavagnostidae has been long recognized as an independent family, like Condylropygidae, of unknown origin and with unknown descendants. It has been discussed at length by ÖPIK (1967), whose subfamilial division into Clavagnostinae and Aspidagnostinae is followed here. Clavagnostidae are distinguished by the fused anterior and posterior glabellar lobes and generally shortened glabella. Clavagnostinae have a relatively simple pygidium, characterized by an acuminate axis posteriorly bisected by a transverse furrow somewhat similar to that of Glyptagnostinae. In Aspidagnostinae the pygidial axis has both F1 and F2 furrows, the posterior transverse one, and a secondary axial node, also rather reminiscent of Glyptagnostinae. The posterior border of taxa in Clavagnostinae is, however, zonate, and there is a gap in the collar as in *Oidalgagnostus*. A hint of a third marginal pygidial spine in Aspidagnostinae also recalls *Oidalgagnostus*. *Utagnostus* is temporarily placed with the Clavagnostidae by virtue of its trispinose pygidium and nature of its cephalic spines.

The family name Metagnostidae was revived by FORTEY (1980b, p. 24) to embrace some of the genera previously most commonly referred to Geragnostidae (HOWELL, 1935b; see also HOWELL in MOORE, 1959, p. 176). FORTEY (1980b, p. 27) also included the genera *Segmentagnostus* and *Corrugatagnostus*, those genera with a chevronate furrow separating the two main glabellar lobes. This taxonomic scheme is followed herein with modifications, notably some of those introduced by Zhiyi ZHOU (1987).

Two, long-accepted families, Phalacromidae and Sphaeragnostidae are unclassified at superfamilial rank. The former is based on the genera, *Phalacroma*, *Lisogoragnostus*, and *Dignagnostus* and the latter on *Sphaeragnostus* alone.

Phalacromidae, concept and composition, has been discussed at some length by ÖPIK

(1961b) and JAGO (1976). It has been regarded as polyphyletic (ÖPIK, 1967, p. 82). We follow ÖPIK (1961b, p. 54) in recognizing the validity of the family, but restrict it to the genera noted above. All other genera previously associated with Phalacromidae (*Phalagnostus*, *Grandagnostus*, *Valenagnostus*, *Phoidagnostus*) are classified elsewhere. The inclusion here of *Dignagnostus* (HAJRULLINA in REPINA, PETRUNINA, & HAJRULLINA, 1975) is based on pygidial characteristics, and there is no certainty that associated cephalia illustrated by this author are correctly assigned. If the association of cephalia and pygidia illustrated by HAJRULLINA is correct, then *Dignagnostus* must be rejected from Phalacromidae, which would then be restricted to *Phalacroma* as indicated by ÖPIK (1967). Pygidia of *Dignagnostus grandis* and *Phalacroma bibullatum* are unified by the long (sag.), wide (tr.), and laterally expanded axis; effacement of transverse furrows; shape and position of the axial node; and retention of a transverse depression behind the axial node, a characteristic feature of *Peronopsis* and *Diplagnostus*, which may indicate the derivation of Phalacromidae. If cephalia assigned to *Dignagnostus* are ignored, species of Phalacromidae are relatively large and mostly effaced.

Effacement also is responsible for the isolation of Sphaeragnostidae. The genus *Sphaeragnostus* is widely distributed during the Ordovician and quite characteristic. The cephalon is completely effaced, and the pygidial axis an unfurrowed, spheroidal structure of substantial width (tr.). Thoracic axial structures are also very wide (tr.), limiting the extent of the pleurae. There is no guarantee that Sphaeragnostidae or Phalacromidae are true Agnostina, as the presence of a cephalothoracic aperture is not confirmed in either group.

Twenty-one genera are left unclassified at familial level. Mostly this is because their type specimens are not readily interpreted due to effacement of diagnostic morphology (*Agnostogonus*, *Delagnostus*, *Leiagnostus*, *Monaxagnostus*, *Phoidagnostus*, *Glaberagnostus*, *Grandagnostus*, *Skryjagnostus*, and



*Valenagnostus*) or adverse preservation (*Archaeagnostus*, *Armagnostus*, *Blystagnostus*, *Hastagnostus*, and *Quadragnostus*), or both (*Ciceragnostus* and *Gallagnostus*). *Plurinodus* is a diminutive genus that may prove supra-generically classifiable when more material becomes available. *Phaldagnostus* may be classifiable when it is properly illustrated. PRATT (1992) has recently erected the family Phalagnostidae for the effaced genus *Phalagnostus*, whose relationships with other agnostoids, particularly *Grandagnostus* and *Valenagnostus*, have not been thoroughly explored.

Four genera are rejected from Agnostida. Two of them, *Discagnostus* (ÖPIK, 1963), the sole representative of the family Discagnostidae, and *Mallagnostus* (HOWELL, 1935b), on which Mallagnostidae (HOWELL, 1935b) is based, are considered better classified among Eodiscina. *Gallagnostoides*, founded by KOBAYASHI (1939b, p. 580) with *Aeglina boia* (HICKS, 1875, p. 185, pl. 10, fig. 9, 9a) as type species, is a mid-Arenig species of the cyclopygid subgenus *Microparia* (*Microparia*) HAWLE & CORDA, according to FORTEY and OWENS (1987, p. 172). *Pseudotrinodus* (KOBAYASHI & HAMADA, 1971), from the Devonian of western Malaysia, is referred to Aulacopleurinae by THOMAS and OWENS (1978, p. 74).

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## Superfamily AGNOSTOIDEA M'Coy, 1849

[*nom. transl.* SHERGOLD, LAURIE, & SUN, 1990, p. 32, ex Agnostinae M'COY, 1849, p. 402]

Agnostina with basal glabellar lobes anteriorly expanded, anterior glabellar lobe not laterally expanded. *Lower Cambrian–Upper Ordovician.*

### Family AGNOSTIDAE M'Coy, 1849

[Agnostidae M'COY, 1849, p. 402] [=Microagnostidae HOWELL, 1935b, p. 233; Glyptagnostidae WHITEHOUSE, 1936, p. 101; Rudagnostidae LERMONTOVA, 1951b, p. 7]

En grande tenue to effaced; border furrows nondeliquiate to deliquiate; cephalic border narrow and pygidial border of variable width; acrolobes usually unconstricted; median preglabellar furrow absent to well developed. Glabella with variably shaped anterior lobe; F3 straight or curved; F2 absent to well developed; glabellar culmination rounded, subquadrate, or obtusely angular; glabellar node from midway between F1 and F2 to in front of F2; basal lobes variable in size, usually simple, occasionally incorporating lateral portions of M2 lobe. Pygidium with usually long axis, commonly reaching border furrow, commonly constricted across M2; F1 variably impressed or effaced; M1 usually trilobate; F2 variably impressed or effaced; posterior lobe usually long and semioval, ogival, semicircular, or bulbous, commonly with either a secondary axial node in posterior half or with a terminal node. *Middle Cambrian–Lower Ordovician.*

### Subfamily AGNOSTINAE M'Coy, 1849

[Agnostinae M'COY, 1849, p. 402]

Pygidium bispinose or nonspinose, with agnostoid or basic articulating device; pygidial axis simple, axiolobate, usually long but not reaching border furrow; F1 and F2 variably impressed; posterior lobe with or without terminal node. *Middle Cambrian–Lower Ordovician.*

**Agnostus** BRONGNIART, 1822, p. 38 [\**Entomostracites pisiformis* WAHLENBERG, 1818, p. 42; SD JAEKEL, 1909, p. 399; lectotype cephalon (WAHLENBERG,

1818, pl. 1, fig. 5; SD SHERGOLD, LAURIE, & SUN, 1990, p. 32), Vg819a, PM, Uppsala]. Generally with relatively narrow borders. Cephalon with median preglabellar furrow; anterior glabellar lobe ogival or rounded; posterior lobe tapering forward; axial node level with or slightly behind variably developed F2; basal lobes variable in size. Pygidium with long (sag.), variably wide (tr.), and tumid axis, usually not reaching border furrow, lacking median postaxial furrow; marginal spines present. *upper Middle Cambrian–lower Upper Cambrian: Cosmopolitan.*

**A. (Agnostus)** [=*Battus* DALMAN, 1827, p. 151 (type, *Entomostracites pisiformis* WAHLENBERG, 1818, p. 42, pl. 1, fig. 5; SD JAEKEL, 1909, p. 399)]. Cephalon with ogival anterior glabellar lobe, basal lobes of moderate to large size. Pygidium with long (sag.), relatively narrow (tr.), posteriorly pointed, or narrowly rounded axis; F1 and F2 very weak or effaced. *upper Middle Cambrian–lower Upper Cambrian: northern Greenland; Sweden, Norway, Denmark, England, Wales, Canada (New Brunswick, Newfoundland), L. laevigata–A. pisiformis Zones; Australia (Queensland), E. eretes Zone. upper Middle Cambrian: Argentina.*—FIG. 217, 1a, b. \*A. (*A. pisiformis* (WAHLENBERG), Upper Cambrian (*A. pisiformis* Zone), Sweden (Hönsäter, Hallevad-Billingen, Västergötland); a, lectotype, cephalon, PM Vg819a, ×7.55 (new); b, paratype, pygidium, PM Vg819b, ×6.95 (new).

**A. (Homagnostus)** HOWELL, 1935c, p. 15 [\**Agnostus pisiformis* LINNAEUS var. *obesus* BELT, 1867, p. 294; OD; lectotype (BELT, 1867, pl. 12, fig. 4a; SD RUSHTON in ALLEN, JACKSON, & RUSHTON, 1981, pl. 16, fig. 2), I.7646, BMNH, London]. Pygidium with posteriorly broadly rounded axis extending nearly to posterior border furrow. Axis constricted across M2 with posterior lobe variably but always laterally expanded; F2 well developed; F1 always impressed laterally and only occasionally impressed medially; M1 variably tripartite. *Upper Cambrian: northern Greenland; England, Wales, O. gibbosus–O. cataractes Subzones; Sweden, Norway, Denmark, Olenus Zone; Russia (Novaya Zemlya, Yakutia, Altay Mountains), Kazakhstan, Pedinocephalina/Toxotis-Irvingella Zones; China (Zhejiang, Shandong, Liaoning), G. stolidotus Zone; South Korea, Chuangia Zone; Australia (Queensland), G. reticulatus Zone; USA (Alabama, Alaska, Oklahoma, Texas, Nevada, Wyoming), Aphelaspis-Elvinia Zones; Canada (Newfoundland, Northwest Territories), ?Cedaria minor and Irvingella major Zones.*—FIG. 217, 2a, b. \*A. (*H. obesus* (BELT), Upper Cambrian (*Olenus* Zone); a, lectotype, northern Wales (Afon Mawddach, Dolmelynlyn), ×8 (Allen, Jackson, & Rushton, 1981, pl. 16, fig. 2); b, exoskeleton, BMNH TE6, England (Nuneaton district), ×6.67 (Rushton, 1978, pl. 25, fig. 4).

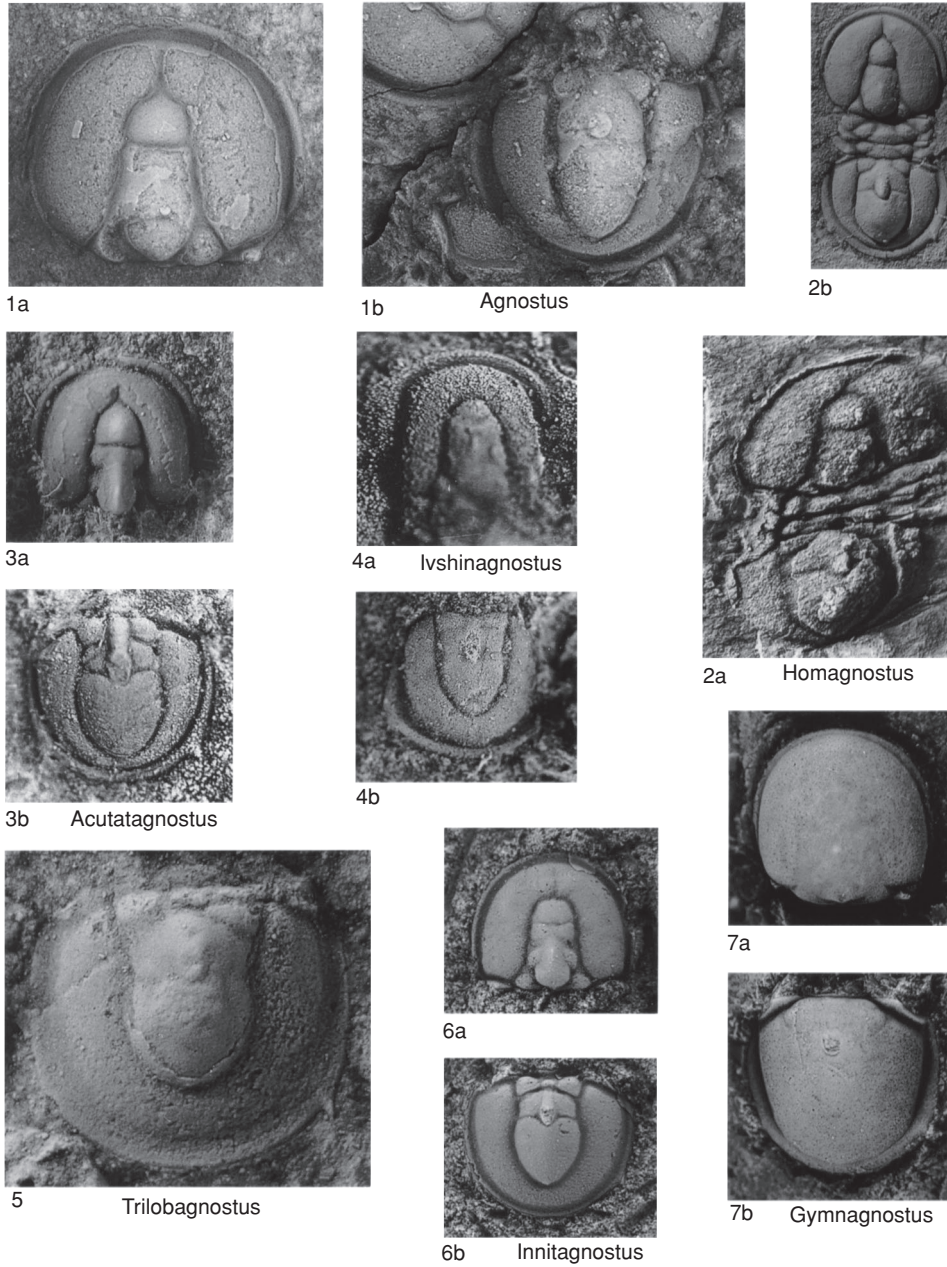


FIG. 217. Agnostidae (p. 339–344)

**Acutatagnostus** ERGALIEV, 1980, p. 91 [*A. acutatus*; OD; holotype (ERGALIEV, 1980, pl. 11, fig. 16), 1950/184, GMAN, Alma-Ata]. Like *Innitagnostus* but with median preglabellar furrow only evident proximally; anterior glabellar lobe long and ogival; F2 well developed but F1 weak. Pygidium with

retrally located spines; long axis extending almost to posterior border furrow; M1 and M2 clearly trilobate; F1 only laterally impressed. *Upper Cambrian (Sakian)*: Kazakhstan, *H. longiformis*–*P. curtare* Zones.—FIG. 217, 3a, b. \**A. acutatus* ERGALIEV, Upper Cambrian (*Oncagnostus longifrons* Zone),



- Kazakhstan (Kirshabakty River, Lesser Karatau mountains); *a*, holotype, cephalon, GMAN 1950/184,  $\times 11$ ; *b*, pygidium, GMAN 1950/185,  $\times 12$  (Ergaliev, 1980, pl. 11, fig. 16–17).
- ?**Gymnagnostus** ROBISON & PANTOJA-ALOR, 1968, p. 776 [*\*G. gongros*; OD; holotype (ROBISON & PANTOJA-ALOR, 1968, pl. 97, fig. 29), 158892, USNM, Washington, D.C.]. Almost effaced, but cephalon retaining very narrow borders, faint axial glabellar node, and partly outlined basal lobes. Pygidium with broader border, faintly constricted acrolobe, and weakly defined axial furrows and terminal node, which indicate the short axis; axial node prominent; posterolateral spines advanced. *Upper Cambrian*: Mexico, *Cordylodus proavus* Zone; Bolivia, *Neoparabolina argentina* Zone.—FIG. 217,7a,b. *\*G. gongros*, Mexico (Santiago Ixtaltepec, Nochixtlán region, Oaxaca), *Cordylodus proavus* Zone; *a*, cephalon, USNM 158887,  $\times 10$ ; *b*, holotype, pygidium, USNM 158892,  $\times 10$  (new).
- Innitagnostus** ÖPIK, 1967a, p. 98 [*\*I. innitens*; OD; holotype (ÖPIK, 1967, pl. 58, fig. 2), CPC 5853, AGSO, Canberra]. Median preglabellar furrow variably developed. Glabella with broad, trapeziform anterior lobe; F3 well impressed, nearly straight; posterior lobe with well-developed F1 and F2; lateral portions of M2 commonly separated from midmost glabella by weak longitudinal (exsag.) furrows; glabellar node located from midway between F1 and F2 to level with F2; basal lobes of moderate size, trapezoidal. Pygidial axis of moderate length, constricted across M2; M1 trilobate; F1 well impressed, bent forward; F2 straight laterally, bent rearward by strong axial node. Posterior lobe ogival to semioval, usually narrowly rounded posteriorly, not reaching border furrow. Median postaxial furrow absent. *Upper Cambrian*: China (Guizhou, Hunan); Australia (Queensland), Mindyallan–Idamean (*E. eretes* to *S. diloma* Zones); Russia (Siberia), Kazakhstan, *G. stolidotus* to *P. curtare* Zones; Canada (Northwest Territories, British Columbia, Newfoundland), *Glyptagnostus reticulatus* to *Olenaspella regularis* Zones; USA (Alabama, Nevada, Texas), *Aphelaspis* Zone.—FIG. 217,6a,b. *\*I. innitens*, Upper Cambrian (Mindyallan, *G. stolidotus* Zone), western Queensland (Boulia district); *a*, holotype, cephalon, CPC 5853,  $\times 8$ ; *b*, topotype, pygidium, CPC 5854,  $\times 8$  (new).
- ?**Ivshinagnostus** ERGALIEV, 1980, p. 65 [*\*I. ivshini*; OD; holotype (ERGALIEV, 1980, pl. 13, fig. 2), 1950/204, GMAN, Alma-Ata]. Anteriorly expanding cephalon and posteriorly expanding pygidium; median preglabellar furrow absent. Glabella strongly tapered, with small, rounded anterior lobe; posterior lobe with F2 furrows very weak, F1 furrows weak, basal furrows weak; glabellar node a short distance behind F2 furrows; basal lobes indistinct. Pygidium bispinose; axis tapered, uncontracted, short; F1 weak; M1 weakly trilobate; F2 very weak. *Upper Cambrian* (*Sakian*): Kazakhstan, *I. ivshini* Zone.—FIG. 217,4a,b. *\*I. ivshini*, Kazakhstan (Kirshabakty River, Lesser Karatau mountains); *a*, cephalon, GMAN 1950/203,  $\times 5.5$ ; *b*, holotype, pygidium, GMAN 1950/204,  $\times 6.8$  (Ergaliev, 1980, pl. 13, fig. 2–3).
- Lotagnostus** WHITEHOUSE, 1936, p. 101 [*\*Agnostus trisectus* SALTER, 1864b, p. 10; holotype by monotypy (SALTER, 1864b, pl. 1, fig. 11), BGS 8768, London]. Variably effaced, with usually nondeliquiate border furrows and uncontracted acrolobes, with or without a median preglabellar furrow. F3 furrow straight or bent backward; posterior lobe with well-developed F2 furrows; glabellar node located from midway between F1 and F2 furrows to level with F2 furrow. Basal lobes large, triangular, in some species incorporating the narrow (tr.) portions of the M2 lobe. Pygidium bispinose; axis long (sag.); M1 trilobate; F1 impressed at least laterally; M2 trilobate; F2 always impressed. Posterior lobe elongate, semioval to ogival, with well-developed terminal node. *Upper Cambrian*.
- L. (Lotagnostus)**. Commonly scrobiculate, variably deliquiate. Median preglabellar furrow present. Glabella with long (sag.), subpentagonal anterior lobe; posterior lobe with F2 furrow well developed, in some species curving forward to intersect F3 furrow, isolating anterolateral lobes. Pygidial axis weakly constricted across M2; F1 clearly impressed. *uppermost Cambrian*: Argentina; England, Wales, *P. minor* Zone; Sweden, *P. minor*–*P. scarabaeoides* Zones; Canada (Nova Scotia, Quebec), *Peltura* Zone, (Newfoundland), Sunwaptan; China (Xinjiang, Zhejiang, Hunan, Anhui, Guizhou), *L. (L.) punctatus*, *L. (L.) hedini*, *H. regalis* Zones & zones correlated with them; Kazakhstan, *E. scrobicularis* Zone; USA (Vermont, Maryland), *upper Trempealeauan*.—FIG. 218,1a,b. *\*L. (L.) trisectus* (SALTER) *sensu* WESTERGÅRD, 1922, Upper Cambrian (*Peltura minor* Zone), Sweden (Andrarum, Skåne); *a*, cephalon, SGU 127,  $\times 7.2$ ; *b*, pygidium, SGU 128,  $\times 7.2$  (new).—FIG. 218,1c. *\*L. (L.) trisectus* (SALTER), Upper Cambrian (Merioneth Series, *Peltura scarabaeoides* Zone), northern Wales (Dolgellau); plastoholotype, pygidium, wax impression, BGS 8768,  $\times 8$  (new).
- L. (Eolotagnostus)** ZHOU in Zhiqiang ZHOU, Li, & QU, 1982, p. 217 [*\*E. gansuensis*; OD; holotype (Zhiqiang ZHOU, Li, & QU, 1982, pl. 57, fig. 10), Tr 008, XIGMR, Beijing]. Cephalon weakly scrobiculate and pygidium nonscrobiculate; median preglabellar furrow absent or weakly developed. Glabella with long (sag.), semioval to ogival anterior lobe; posterior lobe with F2 furrows angled slightly forward. Pygidial axis variably constricted across M2, with F1 impressed laterally and medially effaced. *uppermost Cambrian*: China (Gansu, Xinjiang, Zhejiang), *L. punctatus*–*Hedinaspis* Zone; Kazakhstan, *E. scrobicularis* Zone; Australia (Tasmania), Iverian.—FIG. 218,2a,b. *\*L. (E.) gansuensis* (ZHOU), Upper Cambrian (Fengshanian), China (Gansu); *a*, paratype, cephalon, XIGMR Tr 007,  $\times 5$ ; *b*, holotype, pygidium, XIGMR Tr 008,  $\times 5$  (Zhiqiang Zhou, Li, & Qu, 1982, pl. 57, fig. 9–10).

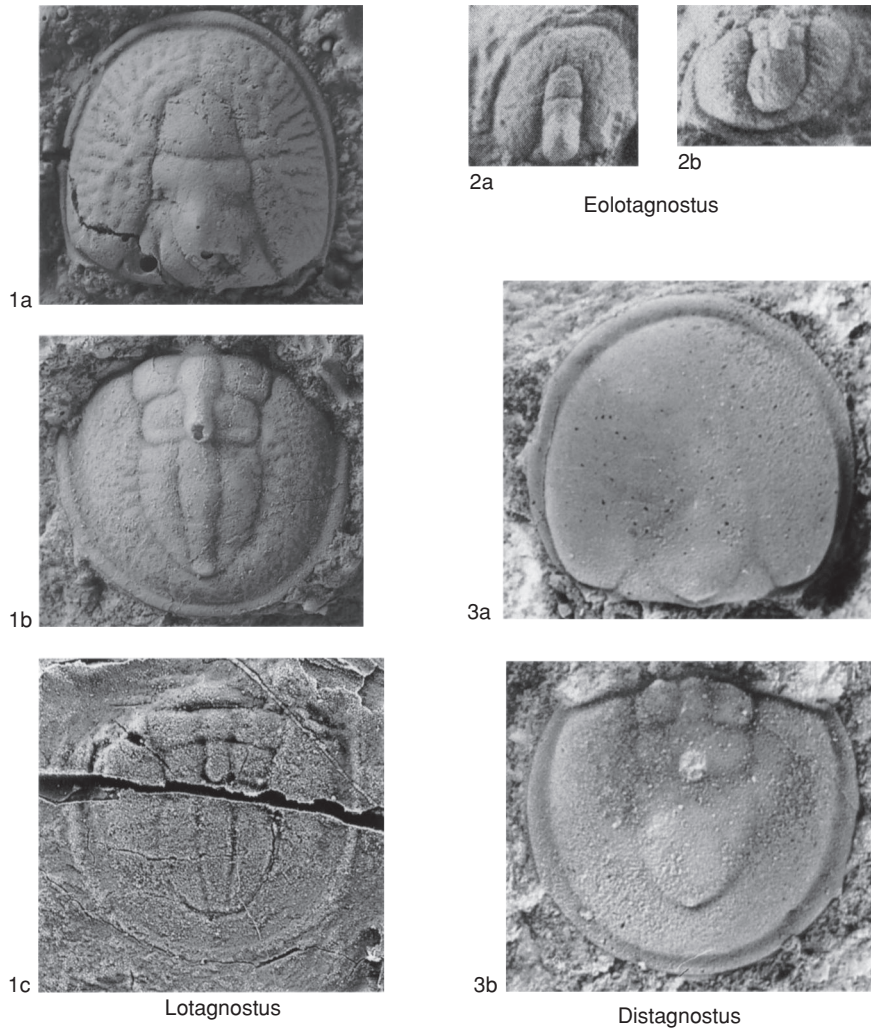


FIG. 218. Agnostidae (p. 341–342)

**L. (Distagnostus)** SHERGOLD, 1972, p. 17 [\**D. ergodes*; OD; holotype (SHERGOLD, 1972, pl. 4, fig. 3), CPC 9667, AGSO, Canberra]. Exoskeleton largely effaced with only traces of axial furrows on both cephalon and pygidium. Pygidial axis weakly constricted across M2; F1 and F2 weakly impressed. *uppermost Cambrian*: Canada (Quebec); Argentina; Australia (Queensland), *R. bifax* or *N. denticulatus* to *R. clarki maximus* or *R. papilio* Zones; USA (Nevada), *S. pyrene* Zone.—FIG. 218, 3a, b. \**L. (D.) ergodes* (SHERGOLD), Upper Cambrian (Iverian, *Rhaptagnostus clarki maximus* or *R. papilio* Assemblage-Zone), western Queensland (Momedah anticline); a,

paratype, cephalon, CPC 9671,  $\times 10$ ; b, holotype, pygidium, CPC 9667,  $\times 12$  (Shergold, 1972, pl. 4, fig. 1–3).

**Micragnostus** HOWELL, 1935b, p. 233 [\**Agnostus calvus* LAKE, 1906, p. 23; OD; lectotype (LAKE, 1906, pl. 2, fig. 18; SD FORTEY, 1980b, p. 23), A548, SM, Cambridge]. En grande tenue; non-scribulate; border furrows nondeliquate; acrolobes unconstricted; median preglabellar furrow absent. Glabella with semioval anterior lobe; F3 straight; posterior lobe parallel-sided with F2 weakly developed or absent; glabellar culmination broadly rounded; glabellar node level with or slightly behind F2. Basal lobes small. Pygidium



minutely bispinose; axis relatively short, unconstricted or weakly constricted over M2; M1 trilobate; F1 traversing axis; F2 well impressed, slightly deflected by axial node. Posterior lobe semiovate. Median postaxial furrow absent. *Upper Cambrian–Lower Ordovician (Arenig)*: Wales, Spitsbergen, *Asaphellus–D. bifidus* Zones; Argentina, *N. argentina–K. meridionalis* Zones; Sweden, *M. dalecarlicus* Zone.—FIG. 219,4. \**M. calvus* (LAKE), Lower Ordovician (Tremadoc), northern Wales (Nant Rhos Ddu); lectotype, SM A548, ×10 (new).

**Oncagnostus** WHITEHOUSE, 1936, p. 84 [\**Agnostus hoi* Y. SUN, 1924, p. 28; OD; lectotype (Y. SUN, 1924, pl. 2, fig. 2c; SD X. SUN, 1989, p. 70), 515, NIGP, Nanjing]. En grande tenue; nonscribulate; usually with deliquiate border furrows in both shields. Median preglabellar furrow absent. Glabella with semiovate, subpentagonal, or subquadrate anterior lobe; F3 straight; posterior lobe usually short with F2 variably developed; axial node level with or slightly behind F2. Pygidium bispinose; F1 impressed only laterally, curving forward to articulating furrow to isolate subtriangular to ovate anterolateral lobes; F2 well developed. *Upper Cambrian (G. reticulatus Zone)–Lower Ordovician (K. meridionalis Zone)*.

**O. (Oncagnostus)** [=*Eurudagnostus* LERMONTOVA, 1951b, p. 7 (type, *E. grandis* LERMONTOVA, 1951a, p. 8, pl. 2, fig. 1–4)]. Pygidial axis long (sag.), broad (tr.), and nearly parallel sided, with posterior lobe relatively broad. *Upper Cambrian (Glyptagnostus reticulatus to Peltura scarabaeoides Zones)*: Sweden, *P. aciculata* Zone; Russia (Siberia), Kazakhstan, *P. pseudangustilobus* to *T. trisulcus* Zones; China (Hebei, Hunan, Liaoning), *Chuangia* to *L. bella* or *A. sinensis* Zones; South Korea, *Chuangia* to *Eochuangia* Zones; Australia (Queensland), *S. diloma* to *R. maximus* or *R. papilio* Zones; Antarctica (northern Victoria Land), *Dunderbergia* Zone; USA (Alaska, Montana, Wyoming, Nevada, Texas), *Aphelaspis* to *Elvinia* Zones; Canada (Newfoundland), Sunwaptan.—FIG. 219,2a–c. \**O. (O.) hoi* (SUN), Upper Cambrian (Changshanian, *Changshania* Zone); a, b, China (Kushan, Changqingxian, Shandong); a, cephalon, NIGP 89034, b, pygidium, NIGP 89031, both ×10 (X. Sun, 1989, pl. 1, fig. 1–7); c, lectotype, pygidium, NIGP 515, China (Renzhuang, near Tangshan, Hebei), ×10 (Y. Sun, 1924, pl. 2, fig. 2c).—FIG. 219,2d, e. *O. (O.) tumidosus* (HALL & WHITFIELD), Upper Cambrian (Dresbachian, *Dunderbergia* Zone), USA (Eureka district, Nevada); d, plesiotype, cephalon, USNM 136831a, ×13; e, plesiotype, pygidium, USNM 136831b, ×13 (Palmer, 1960, pl. 4, fig. 1–2).

**O. (Kymagnostus)** HOHENSEE in HOHENSEE & STITT, 1989, p. 861 [\**K. harti*; OD; holotype (HOHENSEE & STITT, 1989, fig. 3.1), 16666a, UMC, Columbia]. Cephalic border narrow; pygidial border wide, flattened. Pygidial axis long

(sag.), broad (tr.), nearly parallel sided or expanding posteriorly, axial furrows commonly effaced around posterior lobe. *Upper Cambrian*: USA (Arkansas, Texas), *Elvinia* Zone.—FIG. 219,1a, b. \**O. (K.) harti* (HOHENSEE), USA (Ouachita Mountains, Arkansas); a, holotype, cephalon, UMC 16666a, ×16, b, paratype, thoracopygon, UMC 16667, ×16 (Hohensee & Stitt, 1989, fig. 2–3.1).

**O. (Strictagnostus)** SHERGOLD, 1975, p. 54 [\**Geragnostus (Strictagnostus) chronius*; OD; holotype (SHERGOLD, 1975, pl. 13, fig. 5), CPC 11732, AGSO, Canberra]. Cephalon anteriorly expanding with anteriorly tapering acrolobe. Pygidium posteriorly flared with posteriorly tapering, gently constricted acrolobe; short (sag.), posteriorly tapering pygidial axis, commonly slightly constricted at M2; posterior lobe short, semiovate, terminating well in advance of posterolateral spine bases. *Upper Cambrian–Lower Ordovician*: Australia (Queensland), *R. bifax* or *N. denticulatus* to *R. maximus* or *R. papilio* Zones; Argentina, Bolivia, *K. meridionalis* Zone; USA (Texas), *M. typicalis* Zone; South Korea, *Asaphellus* Zone; China (Anhui), Upper Cambrian; Afghanistan, Tremadoc; Kazakhstan, *T. trisulcus* Zone.—FIG. 219,3a, b. \**O. (S.) chronius* (SHERGOLD), Australia (Black Mountain, western Queensland); a, topotype, cephalon, CPC 11730, Upper Cambrian (Iverian, *Rhaptagnostus clarki maximus* or *R. papilio* Assemblage-Zone), ×15; b, holotype, pygidium, CPC 11732, Upper Cambrian (Iverian, *Rhaptagnostus bifax* or *Neoagnostus denticulatus* Assemblage-Zone), ×15 (Shergold, 1975, pl. 13, fig. 3, 5).

**Trilobagnostus** HARRINGTON, 1938, p. 148 [\**Agnostus innocens* CLARK, 1923b, p. 122; OD; holotype (LUDVIGSEN, WESTROP, & KINDLE, 1989, pl. 1, fig. 25), 1697, MCZ, Cambridge] [=*Rudagnostus* LERMONTOVA, 1951a, p. 7 (type, *A. princeps* var. *rudis* SALTER, 1864b, p. 4, pl. 1, fig. 3)]. Nonscribulate; unconstricted acrolobes; median preglabellar furrow generally absent. Glabella with straight or gently posteriorly curved F3; short posterior lobe with F2 usually absent; glabellar node level with F2 furrows. Pygidium widest at M1; F1 generally only impressed laterally, curving forward to isolate lateral lobes; posterior lobe relatively long (sag.); posterolateral spines retral. *Upper Cambrian–Lower Ordovician (Tremadoc)*: Wales, Sweden, Germany, Czech Republic, Poland, *P. acutidens* Zone—lower Tremadoc; Turkey, lower Tremadoc; China (Anhui, Guizhou, Hebei, Shanxi, Liaoning, Jilin, Zhejiang, Hunan), *L. punctatus* to *Yosimuruspis* Zones; South Korea, “*Dictyites*” Zone; Australia (Queensland), *R. maximus* or *R. papilio* Zone; Argentina, Bolivia, Colombia, *N. argentina* Zone; Mexico, *C. proavus* Zone; USA (Alaska, Montana, Nevada, Texas, Oklahoma, Vermont), *Saratogia* or *Drumaspis* to *C. proavus* Zones; Canada (Quebec, Newfoundland, British Columbia), Sunwaptan.—FIG. 217,5. \**T. innocens* (CLARK), uppermost Cambrian (Sunwaptan

tan), Canada (Lévis, Quebec); holotype, pygidium, MCZ 1697,  $\times 14$  (Ludvigsen, Westrop, & Kindle, 1989).

### Subfamily AMMAGNOSTINAE Öpik, 1967

[Ammagnostinae ÖPIK, 1967, p. 137]

Pygidium generally bispinose with broad, flattened border; pygidial axis long, broad, reaching border furrow, with long, expanded posterior lobe having well-developed secondary axial node in posterior half; F1 effaced or weakly impressed laterally, curving forward to intersect articulating furrow, isolating anterolateral lobes; F2 variably impressed and deflected by well-developed axial node. *upper Middle Cambrian–lower Upper Cambrian.*

**Ammagnostus** ÖPIK, 1967, p. 137 [\**A. psammius*; OD; holotype (ÖPIK, 1967, pl. 66, fig. 3), CPC 5937, AGSO, Canberra]. En grande tenue or with pygidial axial furrows effaced posteriorly. Median preglabellar furrow absent. Glabella with ogival to subpentagonal anterior lobe; F3 straight or concave forward; a broad, anteriorly tapering posterior lobe with variably developed F2 furrow and broadly rounded glabellar culmination; glabellar node immediately behind F2 furrows. *Upper Cambrian.*

**A. (Ammagnostus)** [= *Glyptagnostus (Lispagnostus)* ÖPIK, 1967, p. 169 (type, *G. (L.) lenis*; OD); *Agnostoglossa* ÖPIK, 1967, p. 145 (type, *A. bassa*; OD)]. Pygidial axis usually weakly constricted across M2 and with F2 effaced or weakly impressed. *lower Upper Cambrian:* northern Greenland; Australia (Queensland), *E. eretes* to *G. stolidotus* Zones; Kazakhstan, *K. simplex* to *G. stolidotus* Zones; China (Zhejiang), *L. sinensis* Zone, (Hunan), *A. integriceps* or *Chatiania* Zone; ?USA (Montana), *Cedaria* Zone; ?Antarctica, *Aphelaspis* Zone.—FIG. 220, 2a, b. \**A. (A.) psammius*, Upper Cambrian (Mindyallan, *Glyptagnostus stolidotus* Zone); *a*, paratype, cephalon, CPC 5936, Australia (Boulia area, western Queensland),  $\times 8$ ; *b*, holotype, pygidium, CPC 5937, Australia (Duchess area, western Queensland),  $\times 8$  (new).

**A. (Tentagnostus)** X. SUN, 1989, p. 75 [\**Pseudagnostus adchinensis* SCHRANK, 1975, p. 595; OD; holotype (SCHRANK, 1975, pl. 2, fig. 1), T934.1, HMB, Berlin]. Pygidial axis strongly constricted across M2 and with F2 strongly impressed. *lower Upper Cambrian (Changshanian):* China (Liaoning), *K. quadriceps* fauna.—FIG. 220, 1a, b. \**A. (T.) adchinensis* (SCHRANK), Upper Cambrian (Changshanian), China (Saima, Fengchenxian, Liaoning); *a*, holotype, cephalon, HMB T934.1,  $\times 13.5$ ; *b*, paratype, pygidium, HMB T904.1,  $\times 10.2$  (Schränk, 1975, pl. 2, fig. 1, 4).

**Formosagnostus** ERGALIEV, 1980, p. 92 [\**F. formosus*; OD; holotype (ERGALIEV, 1980, pl. 5, fig. 11), 1950/92, GMAN, Alma-Ata] [= *Kunshanagnostus* QIAN & ZHOU, 1984, p. 173 (type, *K. kunshanensis*; OD)]. En grande tenue, with deliquate or subdeliquate border furrow and narrow border in cephalon and poorly defined, deliquate border furrow and broad, flattened border in pygidium. Median preglabellar furrow clearly developed. Glabella with ogival to subpentagonal anterior lobe; F3 bent backward; posterior lobe with well-developed F2 furrows, F1 furrows absent or weakly developed, broadly rounded glabellar culmination; glabellar node immediately behind F2 furrows. Pygidial axis with F1 only impressed laterally, curving forward to intersect articulating furrow and isolating small, subtriangular anterolateral lobes; F2 clearly impressed, deflected strongly backward by long, low axial node. *lower Upper Cambrian:* Antarctica; Kazakhstan, *K. simplex–G. reticulatus* Zones; Australia (Queensland), *E. eretes* Zone; China (Jiangsu, Liaoning).—FIG. 221a, b. \**F. formosus*, Upper Cambrian (Ajusokkanian), Kazakhstan (Lesser Karatau mountains); *a*, holotype, cephalon, GMAN 1950/92, *Kormagnostus simplex* Zone,  $\times 8$ ; *b*, paratype, pygidium, GMAN 1950/133, *Glyptagnostus stolidotus* Zone,  $\times 7.5$  (Ergaliev, 1980, pl. 5, fig. 11; pl. 8, fig. 12).

**Hadragnostus** ÖPIK, 1967, p. 102 [\**H. las*; OD; holotype (ÖPIK, 1967, pl. 58, fig. 8), CPC 5861, AGSO, Canberra]. Cephalon and pygidium transverse; en grande tenue, with subdeliquate border furrows and narrow border on cephalon and moderately wide border on pygidium. Median preglabellar furrow broad, short. Glabella relatively long with short (sag.), subtriangular to ogival anterior lobe; F3 straight; posterior lobe with weakly developed F2 and broadly rounded glabellar culmination; glabellar node absent. Pygidial axis tapering forward from middle of posterior lobe with constriction across M2 weak or absent; F1 and F2 furrows effaced. *lower Upper Cambrian:* Australia (Queensland), *E. eretes* to *A. quasivespa* Zones; Iran, *Drepanura* Zone; Canada (Northwest Territories), *Cedaria selwyni* to *C. brevifrons* Zones; USA (Montana), *Crepicephalus* Zone.—FIG. 220, 5. \**H. las*, Upper Cambrian (Mindyallan, *Erediaspis eretes* Zone), Australia (Glenormiston district, western Queensland); holotype, pygidium, CPC 5861,  $\times 16$  (new).

?**Kormagnostella** E. ROMANENKO in ROMANENKO & ROMANENKO, 1967, p. 75 [\**K. glabrata*; OD; holotype (ROMANENKO & ROMANENKO, 1967, pl. 1, fig. 22), 152/166, ZSGU, Novokuznetsk] [= *Litagnostoides* SCHRANK, 1975, p. 593 (type, *L. minutus*; OD)]. Diminutive, partly effaced, with deliquate border furrow and narrow border in cephalon and subdeliquate border furrow and wide, flat border in pygidium. Median preglabellar furrow absent. Glabella with anterior lobe effaced; F3 curved forward; posterior lobe with F1 and F2 furrows absent; glabellar culmination broadly rounded to obtusely angular; glabellar node posteriorly located. Py-

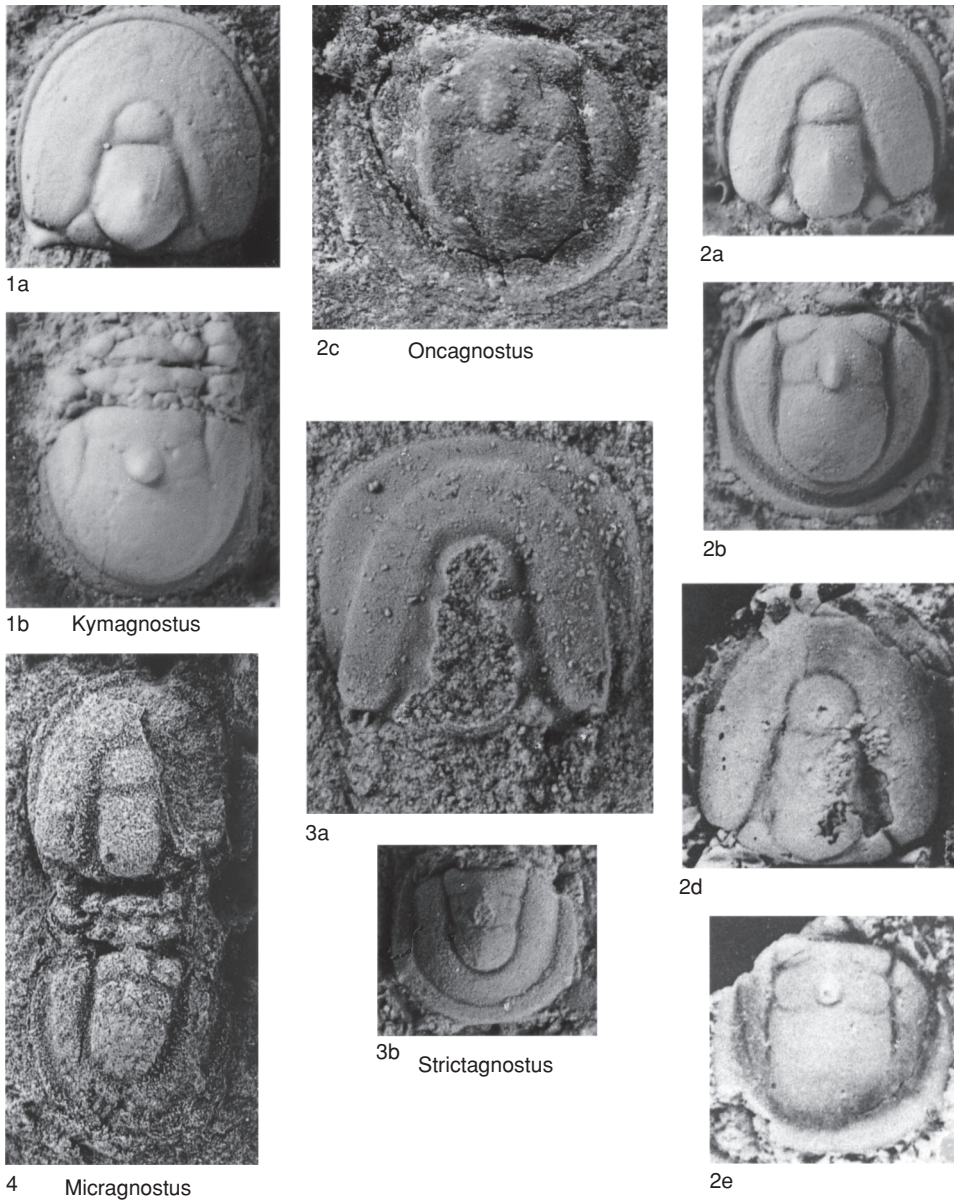


FIG. 219. Agnostidae (p. 343)

gidium nonspinose, axial furrows only impressed anteriorly, adjacent to M1 and anterior portion of M2. Axial node of moderate size. Weakly developed terminal node located adjacent to border furrow. *Upper Cambrian*: Russia (southern Siberia), Ayusokkanian–Sakian; China (Liaoning), *Kaolishania quadriceps* fauna; Australia (Queensland), *S. diloma* Zone.—FIG. 220,6. \**K. glabrata*, Upper Cambrian (Ayusokkanian, *Glyptagnostus stolidotus*

Zone), southern Siberia (Altay Mountains); holotype, cephalothorax, ZSGU 152/153, and associated pygidium, ZSGU 152/166, ×9 (Romanenko & Romanenko, 1967, pl. 1, fig. 22–23). *Kormagnostus* RESSER, 1938, p. 49 [\**K. simplex*; OD; syntypes (RESSER, 1938, pl. 9, fig. 11–13), 94842, USNM, Washington, D.C.]. Anterior glabellar lobe effaced, with deliquate border furrow in cephalon and poorly defined, deliquate border furrow and



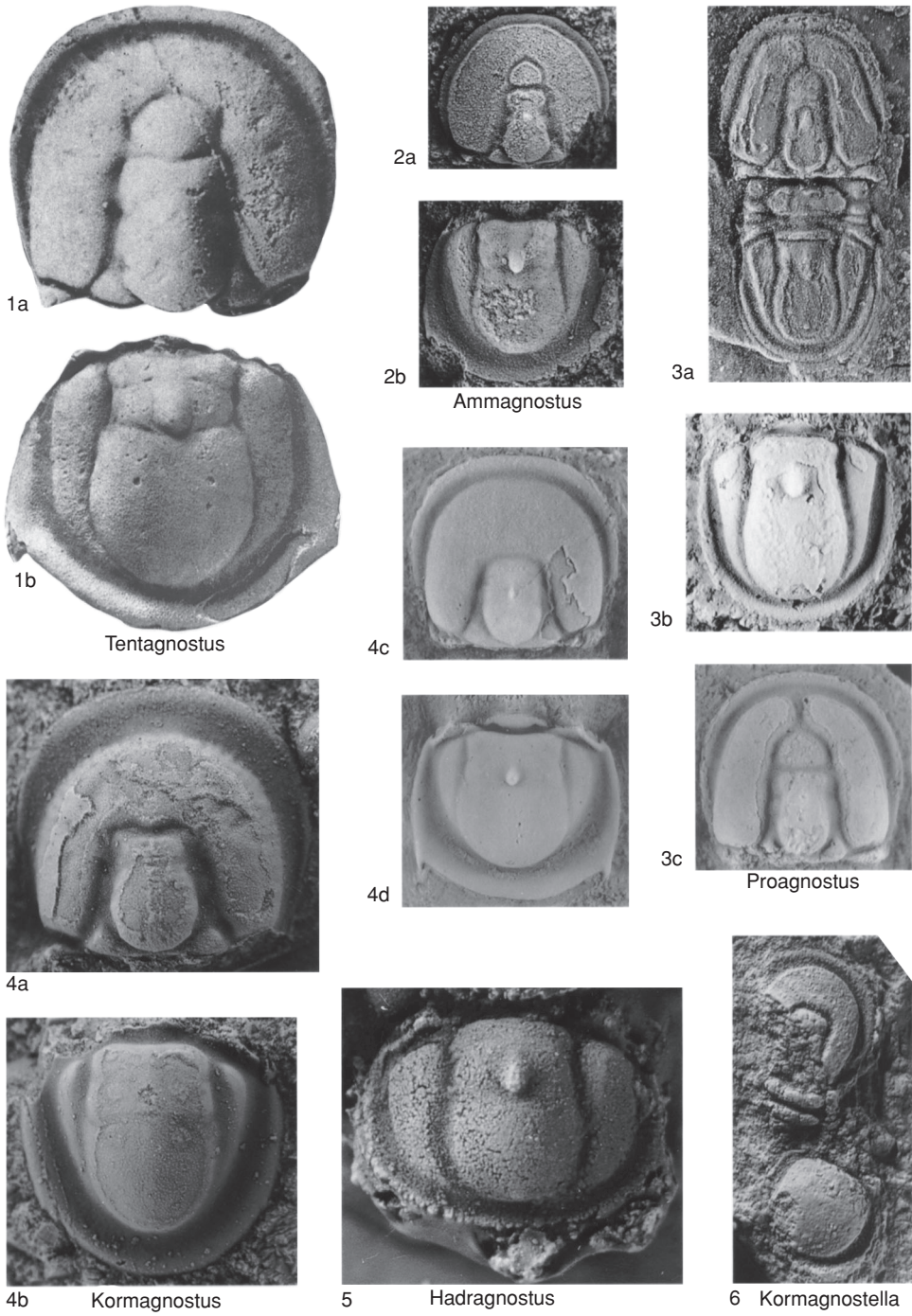


FIG. 220. Agnostidae (p. 344–347)

broad, flattened border in pygidium. Median preglabellar furrow absent. Glabella with straight F3; a broad, anteriorly tapering posterior lobe with weakly developed F2 furrows; a broadly rounded glabellar culmination; and with glabellar node immediately behind F2 furrows. Pygidial axis usually widest across posterior lobe with very slight constriction over M2; F1 and F2 effaced. *uppermost Middle Cambrian–lower Upper Cambrian*: northern Greenland; USA (Alabama, Georgia, Missouri, Montana, Nevada, Tennessee, Texas, Utah, Wyoming), *Bolaspidella* to *Crepicephalus* Zones; Canada (Quebec, Northwest Territories), *Cedaria minor–C. brevifrons* Zones; Argentina, *Bolaspidella* Zone; Australia (Queensland), *E. eretes* Zone, (Tasmania), *P. punctuosus* to *G. nathorsti* Zones; China (Hunan, Guizhou), *Paradamesops jimaensis* or *Cyclolorenzella* Zone; Kazakhstan, *K. simplex* Zone. —FIG. 220, *4a, b*. \**K. simplex*, Upper Cambrian (Dresbachian), USA (Rogersville district, Tennessee); *a*, syntype, cephalon, USNM 94842a,  $\times 10$ ; *b*, syntype, pygidium, USNM 94842b,  $\times 10$  (new). —FIG. 220, *4c, d*. *K. seclusus* (WALCOTT, 1884b), *uppermost Middle Cambrian (Lejopyge laevigata Zone)*, northern Greenland (Gustav Holm Dal, Peary Land); *c*, cephalon, MGUH 17.158,  $\times 12$ ; *d*, pygidium, MGUH 17.165,  $\times 8$  (Robison, 1988, fig. 11.7,13).

**Proagnostus** BUTTS, 1926, p. 76 [\**P. bulbus*; OD; lectotype (BUTTS, 1926, pl. 9, fig. 12; SD ROBISON, 1988, p. 41, fig. 8.12), 94867, USNM, Washington, D.C.] [= *Agnostascus* ÖPIK, 1967, p. 147 (type, *A. gravis*; OD); *Agnostascus (Paragnostascus)* PENG, 1992, p. 85 (type, *A. (P.) sinensis*; OD)]. Cephalon narrow, trapeziform or semiovate; with nondeliquate border furrows and with a narrow border in the cephalon and a wider, flattened border in the pygidium. Median preglabellar furrow well developed. Glabella with subquadrate to semiovate anterior lobe; F3 straight or bent strongly forward; posterior lobe with well-developed F2 furrows; glabellar culmination broadly rounded to obtusely angular; glabellar node in front of F2 furrows. Pygidial spines retral or advanced; axis with well-developed constriction across M2; F1 weakly impressed or effaced; F2 weakly impressed or absent, deflected posteriorly by strong axial node. *upper Middle Cambrian–lower Upper Cambrian*: northern Greenland; USA (Alabama), *Cedaria* Zone; Canada (Northwest Territories), *Cedaria minor* Zone; Australia (Queensland), *E. eretes* Zone, (Tasmania), *L. laevigata* Zone; China (Hunan, Guizhou), *Paradamesops jimaensis–Cyclolorenzella tuma* Zones, (*Xinjiang*), *Agnostascus orientalis* (= *Proagnostus orientalis*) Zone; Kazakhstan, *Kormagnostus simplex* Zone; Russia (Siberia), *L. laevigata* to *G. stolidotus* Zones. —FIG. 220, *3a–c*. \**P. bulbus*; *a*, Upper Cambrian (Dresbachian), USA (Cedar Bluff, Alabama), lectotype, exoskeleton, USNM 94867,  $\times 10$  (Resser, 1938, pl. 10, fig. 17); *b, c*, latest Middle Cambrian (*Lejopyge laevigata* Zone), northern Greenland (Gustav Holm Dal, Peary Land), *b*, pygidium, MGUH 17.128 and *c*, cephalon, MGUH 17.126,  $\times 8$  (Robison, 1988, fig. 8.14–15).

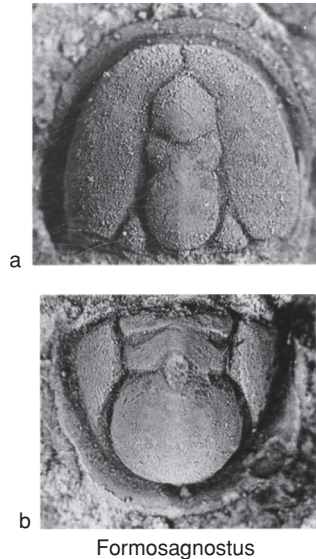


FIG. 221. Agnostidae (p. 344)

### Subfamily GLYPTAGNOSTINAE Whitehouse, 1936

[Glyptagnostinae WHITEHOUSE, 1936, p. 101]

Median preglabellar furrow well developed. Glabella with strong F2 furrow and broadly rounded culmination. Axiolobate pygidium with glyptagnostoid articulating device; secondary axial node developed in association with well-defined transverse depression occurring in rear of posterior lobe; median postaxial furrow well developed. *upper Middle Cambrian–lower Upper Cambrian*.

**Glyptagnostus** WHITEHOUSE, 1936, p. 101 [\**G. toreuma*; OD; = *Agnostus reticulatus* ANGELIN, 1851, p. 8; lectotype (SD WESTERGÅRD, 1947, pl. 1, fig. 2), Ar 9794, RM, Stockholm] [= *Barrandagnostus* IVSHIN in KHALFIN, 1960, p. 166 (type, *B. barrandei*; OD)]. Of low convexity; both cephalon and pygidium strongly scrobiculate. Glabella with anterior lobe subpentagonal to subquadrate; commonly with median sulcus; F3 straight or bent forwards. Posterior lobe with very well-developed F1 furrow and with lateral portions of M2 separated from the midmost glabella by longitudinal (exsag.) furrows. Glabellar node located from midway between F1 and F2 to level of F2. Basal lobes large, triangular. Pygidial axis constricted across M2; M1 trilobate; F1 bent forward; M2 trilobate; axial node extending well on to posterior lobe. *lower Upper Cambrian (upper Mindyallan–lower Idamean)*:



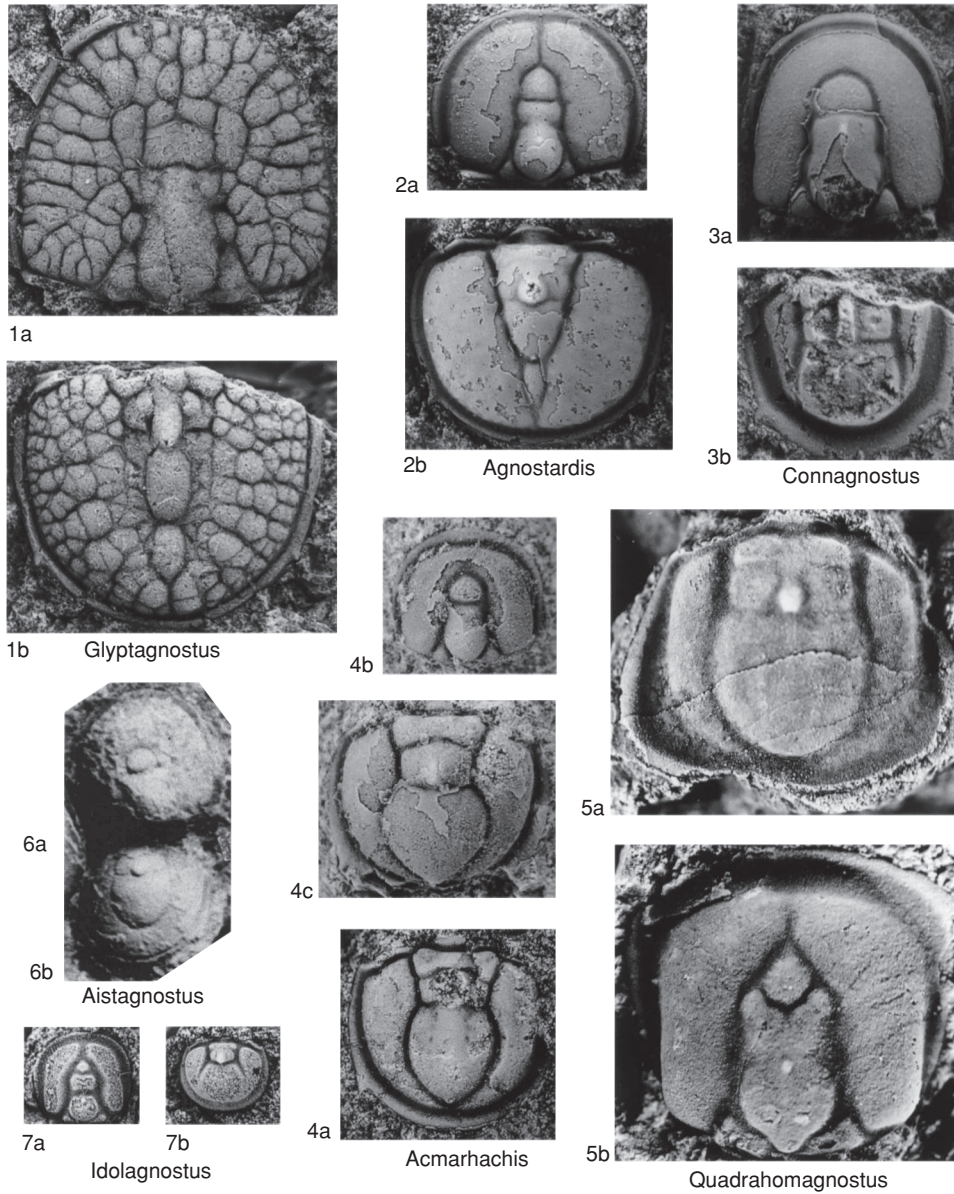


FIG. 222. Agnostidae (p. 348–350)

Cosmopolitan.—FIG. 222,1a,b. \**G. reticulatus* (ANGELIN), Upper Cambrian (*Olenus* Zone), Sweden (Andrarum, Skåne); a, lectotype, cephalon, RM Ar 9794,  $\times 8$ ; b, paralectotype, pygidium of ANGELIN (1851), RM Ar 9796,  $\times 8$  (new).

*Aagnostardis* ÖPIK, 1963, p. 39 [*A. amplinatis*; OD; holotype (ÖPIK, 1963, pl. 3, fig. 8), CPC 4270, AGSO, Canberra]. Nonscrobiculate or faintly scrobiculate. Glabella with anterior lobe ogival to

subpentagonal; F3 straight or bent backward; posterior lobe lacking F1; with glabellar node located midway between F1 and F2. Basal lobes of moderate size. Pygidial axis tapering posteriorly; F1 and F2 effaced; axial node moderately large. Posterior lobe subtriangular. *upper Middle Cambrian–lower Upper Cambrian*: Australia (Queensland), *G. stolidotus* Zone; China (Gansu, Guizhou), *L. laevigata* Zone.—FIG. 222,2a,b. \**A. amplinatis*,

Upper Cambrian (Mindyallan, *Glyptagnostus stolidotus* Zone), Australia (Wells Creek, Boullia area, western Queensland); *a*, paratype, cephalon, CPC 4265,  $\times 8$ ; *b*, holotype, pygidium, CPC 4270,  $\times 8$  (new).

### Subfamily UNCERTAIN

**Acmarhachis** RESSER, 1938, p. 47 [*\*A. typicalis*; OD; holotype (RESSER, 1938, pl. 10, fig. 5), 94858, USNM, Washington, D.C.] [= *Cyclagnostus LERMONTOVA*, 1940, p. 126 (syntypes, *Cyclagnostus elegans* LERMONTOVA, 1940, p. 127, pl. 49, fig. 10, 10a); *Wanagnostus* QIU in QIU & others, 1983, p. 30 (type, *W. anhuiensis*; OD)]. Median preglabellar furrow weak or absent. Glabella with long ogival to subquadrate anterior lobe; F3 straight; posterior lobe with forwardly directed F2 furrows, occasionally joining to form chevronate furrow; glabellar node located from well behind F2 furrows to near apex of chevronate furrow; basal lobes of moderate to large size, triangular. Pygidium with agnostoid articulating device, axiolobate, strongly constricted across M2; broad, tumid posterior lobe bearing terminal node and sometimes intranotular axis. *Upper Cambrian*: USA (Alaska, Alabama, Nevada, Maryland, Vermont), *Crepicephalus* to *Dunderbergia* Zones; Canada (British Columbia, Northwest Territories), *Cedaria minor-C. brevifrons* Zones; Australia (Queensland), *D. torosa* or *A. janitrix* to *W. iota* or *R. apsis* Zones, (Tasmania), post-Idamean; Kazakhstan, *Kormagnostus simplex* Zone; Russia (Kharaulakh), *L. laevigata* to *P. pseudangustilobus* Zones; China (Zhejiang), *L. sinensis* Zone, (Anhui), zone uncertain.—FIG. 222,4a–c. *\*A. typicalis*; *a*, Upper Cambrian (Dresbachian), USA (McCalla, Alabama), holotype, pygidium, USNM 94858,  $\times 10$  (new); *b, c*, Upper Cambrian (Dresbachian, *Crepicephalus* Zone), USA (McGill, Nevada), *b*, cephalon, USNM 143145a and *c*, pygidium, USNM 143145b,  $\times 10$  (Palmer, 1962a, pl. 2, fig. 12–13).

**Aistagnostus** XIANG & ZHANG, 1985, p. 68 [*\*A. laevigatus*; OD; holotype (XIANG & ZHANG, 1985, pl. 6, fig. 1a,b), T1415a, CAGC, Beijing]. Small, en grande tenue, with axial furrows weakly impressed and nondeliquate border furrows. Anterior glabellar lobe short, broad, subpentagonal; posterior glabellar lobe short, broad, with median node at midlength; basal lobes simple. Median preglabellar furrow absent. Pygidial axis short, broad, posteriorly rounded, tripartite, with transverse furrows weakly impressed. Median postaxial furrow absent. Pygidial marginal spines small. Possibly belongs to Agnostinae. *Upper Cambrian (Changshanian)*: China (Xinjiang), *Agnostotes tianshanicus* Zone.—FIG. 222,6a,b. *\*A. laevigatus*; *a*, paratype, cephalon, CAGC T1415a,  $\times 12$ ; *b*, holotype, pygidium, CAGC T1415b,  $\times 12$  (Xiang & Zhang, 1985, pl. 6, fig. 1a,b).

**Connagnostus** ÖPIK, 1967, p. 128 [*\*C. venerabilis*; OD; holotype (ÖPIK, 1967, pl. 54, fig. 11a,b), CPC 5809, AGSO, Canberra]. Nonscrobiculate, with

nondeliquate to deliquate border furrow and narrow border in cephalon; deliquate border furrow and broad, flattened border in pygidium; cephalic acrolobe unconstricted and pygidial acrolobe unconstricted to weakly constricted; median preglabellar furrow absent. Glabella with semicircular to semioval anterior lobe; F3 bent slightly forward; F2 weakly developed; glabellar culmination rounded; glabellar node elongate, keel-like, extending from level with F2 nearly to F3; basal lobes of moderate size. Pygidial axis long, broad, extending to or nearly to border furrow, with very weak constriction over M2; F1 clearly impressed, deflected forward by anterior end of axial node; F2 nearly straight, deflected by axial node. Axial node well defined, elongate, ovate. [Possibly an Ammagnostinae or a Diplagnostid.] *Lower Upper Cambrian*: Australia (Queensland), *A. quasivespa* to *G. stolidotus* Zones; Canada (Northwest Territories), *Cedaria brevifrons* Zone; USA (Alabama), *Glyptagnostus stolidotus* Zone; Russia (Siberia), Nganasan Gorizont.—FIG. 222,3a,b. *\*C. venerabilis*, Upper Cambrian (Mindyallan, *G. stolidotus* Zone), Australia (Glenormiston district, western Queensland); *a*, paratype, cephalon, CPC 5812,  $\times 8$ ; *b*, holotype, pygidium, CPC 5809,  $\times 8$  (new).

**?Idolagnostus** ÖPIK, 1967, p. 104 [*\*I. agrestis*; OD; holotype (ÖPIK, 1967, pl. 60, fig. 8), CPC 5766, AGSO, Canberra]. Small; nonscrobiculate; median preglabellar furrow well developed to absent. Glabella with small, triangular to ogival anterior lobe; F3 well developed and nearly straight; F2 usually well developed as transglabellar furrow, straight or curved forward; glabellar node a short distance behind F2 furrow; glabellar culmination elevated, broadly rounded to obtusely angular; basal lobes of moderate size. Pygidium nonspine; axis long, strongly constricted across M2; F1 clearly impressed, curved forward; F2 clearly impressed, deflected rearward by axial node; posterior lobe expanded, subcircular, extending to or nearly to border furrow; with or without small terminal node. [Possibly belongs within Diplagnostidae, Pseudagnostinae; unassigned because of configuration of glabellar furrows and greatly expanded posterior lobe of pygidial axis.] *Upper Cambrian*: Australia (Queensland), Mindyallan–Idamean (*E. eretes* to *S. diloma* Zones); China (Qinghai), lower Upper Cambrian.—FIG. 222,7a,b. *\*I. agrestis*, Upper Cambrian (Mindyallan, *G. stolidotus* Zone), Australia (Selwyn Range district, western Queensland); *a*, holotype, cephalon, CPC 5766,  $\times 8$ ; *b*, paratype, pygidium, CPC 5872,  $\times 8$  (new).

**Quadrabomagnostus** CHU, 1959, p. 91 [*\*Homagnostus (Quadrabomagnostus) subquadratus*; OD; holotype (CHU, 1959, pl. 1, fig. 21), 9429, NIGP, Nanjing]. Nonscrobiculate; median preglabellar furrow very weak to absent. Glabella with small to moderate-sized, subrhombic to subcircular anterior lobe; F3 curved strongly rearward; F2 effaced or weakly impressed, crossing glabella, and curved forward; glabellar node immediately behind F2 furrow; glabellar culmination narrowly rounded to angular; basal

lobes of moderate to large size. Pygidial axis long, parallel-sided or expanding slightly rearwards, nearly reaching border furrow. [Unassigned because of glabellar characteristics.] *lower Upper Cambrian*: China (Henan, Liaoning), *B. paronai* to *D. premesnili* Zones.—FIG. 222, 5a, b. *Q. subquad-ratus* (ZHU), Upper Cambrian (Gushanian); *a*, paratype, pygidium, NIGP 9431, China (Wutingshan, Yentai, Liaoning), *Drepanura premesnili* Zone,  $\times 10$ ; *b*, holotype, cephalon, NIGP 9429, China (Yaobao, Tienshihfu, Liaoning), *Blackwelderia paronai* Zone,  $\times 10$  (Chu, 1959, pl. 1, fig. 21, 23).

### Family PTYCHAGNOSTIDAE Kobayashi, 1939

[Ptychagnostinae KOBAYASHI, 1939a, p. 151] [=Triplagnostinae KOBAYASHI, 1939a, p. 145; Lejopyginae HARRINGTON in KOBAYASHI, 1939a, p. 128; Tomagnostinae KOBAYASHI, 1939a, p. 148; Canotagnostidae RUSCONI, 1951, p. 13]

Usually en grande tenue, with nondeliquate border furrows and unconstricted acrolobes; usually with median preglabellar furrow and elongate basal lobes; axial glabellar node variable in position. Pygidium usually simplimarginate, rarely weakly zonate, nonspinoso or bispinoso; with basic articulating device; axiolobate with F1 furrow well developed, F2 furrow rarely absent; posterior axial lobe usually long, acuminate or rounded posteriorly, occasionally with a transverse depression in anterior half; median postaxial furrow usually present. *Middle Cambrian–lower Upper Cambrian*.

*Ptychagnostus* JAEKEL, 1909, p. 401 [*Agnostus punctuosus* ANGELIN, 1851, p. 8; OD (publication date discussed by SHERGOLD & LAURIE, 1991); lectotype (SD WESTERGÅRD, 1946, p. 78, pl. 12, fig. 3a, b), Ar 9539, RM, Stockholm]. Scrobiculate; prosopon finely granulate or pustulose. Anterior glabellar lobe semiovate; posterior glabellar lobe evenly convex, with F2 furrows well developed, glabellar node slightly behind to slightly in front of F2 furrow; basal lobes divided or entire. Pygidium nonspinoso; axis with small node on M2; median postaxial furrow present. *Middle Cambrian*: Argentina; China (Liaoning); Sweden, Denmark, Norway, uppermost *H. parvifrons* to *P. punctuosus* Zones; Australia (Queensland), *P. punctuosus* to *D. notalibrae* Zones; Kazakhstan, *P. punctuosus* Zone; Russia (Siberian Platform), *A. henrici* Zone; England, Canada (Newfoundland), *P. davidis* Zone; USA (Utah, Nevada), *A. atavus* to *P. punctuosus* Zones, (New York), *Bolaspidea* Zone.—FIG. 223, 1a, b. \**P. punctuosus* (ANGELIN), Middle Cambrian (*Ptychagnostus punctuosus* Zone), Sweden (Andrarum, Skåne); *a*, lectotype, cephalon, RM Ar 9539,  $\times 8$ ; *b*, paralectotype, pygidium, RM Ar 9540,  $\times 8$  (new).

*Acidusus* ÖPIK, 1979, p. 100 [*Ptychagnostus (Acidusus) acidusus*; OD; holotype (ÖPIK, 1979, pl. 46, fig. 2–3), CPC 14248, AGSO, Canberra] [=? *Canotagnostus* RUSCONI, 1951, p. 13 (type, *C. huarpeanus*; OD)]. Commonly scrobiculate; prosopon smooth or pustulose; nonspinoso or with cephalic spines, axial spine on posterior thoracic segment, and pygidial marginal spines. Anterior glabellar lobe ogival, semiovate or trapeziform; posterior glabellar lobe tapering strongly anteriorly, evenly convex to slightly posteriorly inflated, with F2 furrows well developed; glabellar node located slightly in front of F1 furrows; basal lobes divided or entire. Pygidial axis with moderate to large, elongate node on M2 strongly deflecting F2 furrow; posterior lobe long, with or without small terminal tubercle; median postaxial furrow occasionally absent. *Middle Cambrian*: Sweden, *T. fissus* or *A. atavus* Zone; Sweden, Norway, Denmark, *S. brachymetopa* Zone; Australia (Queensland), *A. atavus* to *A. cassis* Zones, (Tasmania), *A. cassis* or *P. agra* Zone; Kazakhstan, *A. atavus* Zone, beds with *Pianaspis recta*; Russia (Siberian Platform), *T. fissus*, *A. henrici*, *L. allachjunensis* Zones, (Altay-Sayan), *A. limbataeformis* Zone; USA (Alaska), *Bolaspidea* Zone, (Utah), *B. fimbriatus* to *B. contracta* Subzones; China (Zhejiang, Hunan), *P. atavus* to *L. armata* Zones, (Guizhou), zone uncertain.—FIG. 223, 2. \**A. acidusus* (ÖPIK), Middle Cambrian (Undillan, *Doryagnostus notalibrae* Zone), Australia (northwestern Mt. Isa district, western Queensland); holotype, exoskeleton, CPC 14248,  $\times 9$  (new).

*Goniagnostus* HOWELL, 1935c, p. 13 [*Agnostus nathorsti* BRÖGGER, 1878, p. 68; OD; holotype (BRÖGGER, 1878, pl. 5, fig. 1), not traced, PMO, Oslo] [=? *Huarpeagnostus* RUSCONI, 1950b, p. 92 (type, *H. costatus*; OD)]. Usually scrobiculate; spinose, with or without cephalic spines and occipital spine, with axial spine and fulcral spines on the posterior thoracic segment and pygidial marginal spines. Anterior glabellar lobe depressed, subtriangular; posterior glabellar lobe broad, very strongly convex in posterior half, with F2 furrows very well developed; axial glabellar node located behind F1 furrows; basal lobes divided or entire, anterior extremities indistinct, associated with a well-developed apodemal pit. Pygidial axis with spine on M2 strongly deflecting F2 furrow rearward; posterior lobe with strong tubercle near midlength, centered on a variably developed rosette; median postaxial furrow well developed. *Middle Cambrian–lower Upper Cambrian*.

**G. (Goniagnostus).** Cephalon without arcuate scrobicules. Posterior lobe of pygidial axis with rosette weakly developed or absent. *upper Middle Cambrian*: Sweden, Norway, Denmark, *L. lundgreni* or *G. nathorsti* to *S. brachymetopa* Zones; Australia (Northern Territory, Queensland), *P. punctuosus* to *G. nathorsti* Zones; England, ?late *P. davidis* Zone; Canada (New Brunswick, Newfoundland), *P. hicksi* Zone; Turkestan Mountain Range, *H. brevifrons* beds; Russia (Siberian Platform), *A. henrici* to *L. laevigata* or *A. truncata* Zones. *Middle*





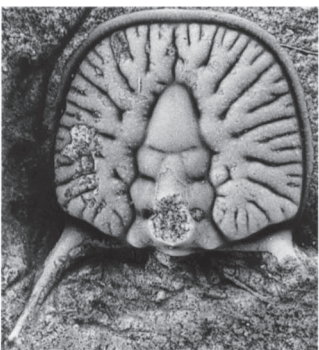
1a



1b *Ptychagnostus*



4a



4b *Allobodochus*



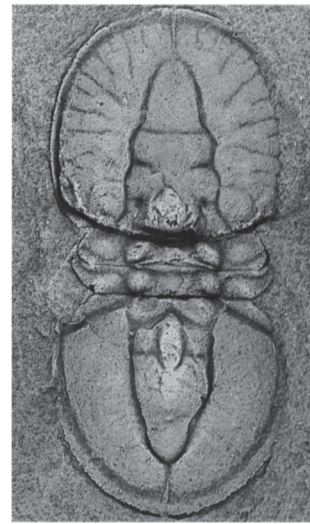
2 *Acidusus*



5b



6 *Mymecomimus*



3a



3b



3c *Goniagnostus*



5a *Criotypus*

FIG. 223. Ptychagnostidae (p. 350–352)

- Cambrian*: China (Qinghai); Argentina.—FIG. 223,3a-c. \**G. (G.) nathorsti* (BRÖGGER), Middle Cambrian (*Goniagnostus nathorsti* Zone); *a*, exoskeleton, PMO 19887, Norway (Krekling, Oslo district), ×8 (new); *b, c*, Sweden (Baskemölla, Skåne), *b*, cephalon, SGU 4957, ×8, *c*, pygidium, SGU 4958, ×8 (new).
- G. (Allobodochus)** ÖPIK, 1979, p. 144 [\**Ptychagnostus (G.) fumicola* ÖPIK, 1961b, p. 81; OD; holotype (ÖPIK, 1961b, pl. 20, fig. 14a,b), CPC 3598, AGSO, Canberra]. Cephalon lacking arcuate scrobicules; glabella with very strongly developed F1 and F2 furrows, commonly with the midmost glabella separated from the outer glabella by weak longitudinal (exsag.) furrows. Posterior pygidial axial lobe with very well developed rosette. *upper Middle Cambrian-lower Upper Cambrian*: Sweden, England, *L. laevigata* Zone; Australia (Queensland, Tasmania), *A. cassis* to *E. eretes* Zones; Kazakhstan (Lesser Karatau Mountains), ?*G. nathorsti* to *L. armata* Zones, *L. laevigata* Zone, early *K. simplex* Zone; China (Hunan, Guizhou), *P. jimaensis* or *C. tuma* Zone, (Zhejiang), *P. triangularis* to *L. sinensis* Zones.—FIG. 223,4a. \**G. (A.) fumicola* (ÖPIK), Middle Cambrian (Boomerangian, *Lejopyge laevigata* Zone), Australia (Tobermory area, Northern Territory); holotype, pygidium, CPC 3598, ×8 (new).—FIG. 223,4b. *G. (A.) spiniger* (WESTERGÅRD), Middle Cambrian (Boomerangian, *Lejopyge laevigata* Zone), Australia (Tobermory area, Northern Territory); paratype, cephalon, CPC 14342, ×8 (new).
- G. (Criotypus)** ÖPIK, 1979, p. 144 [\**G. (C.) oxytorus*; OD; holotype (ÖPIK, 1979, pl. 57, fig. 1-2), CPC 14309, AGSO, Canberra]. Cephalon with well-developed, arcuate scrobicules. Posterior lobe of pygidial axis with rosette usually absent, rarely weakly developed. *Middle Cambrian*: Australia (Queensland), *A. atavus* to *E. opimus* Zones.—FIG. 223,5a. *G. (C.) lemniscatus*, Middle Cambrian (Floran, *Euagnostus opimus* Zone), western Queensland (Camooweal area), holotype, cephalon, CPC 14311, ×8 (new).—FIG. 223,5b. \**G. (C.) oxytorus*, Middle Cambrian (Floran, *Acidusus atavus* Zone), western Queensland (Camooweal area), holotype, exoskeleton, CPC 14309, ×8 (new).
- Lejopyge** HAWLE & CORDA, 1847, p. 51 [\**Battus laevigatus* DALMAN, 1828, p. 136; OD; lectotype (SD WESTERGÅRD, 1946, p. 134, pl. 13, fig. 21a,b), Ar 287b, RM, Stockholm] [= *Miagnostus* JAEKEL, 1909, p. 401 (type, *Battus laevigatus* DALMAN, 1828, *sensu* JAEKEL, 1909, p. 401, fig. 21); *Pseudopalacroma* POKROVSKAYA, 1958, p. 79 (type, *P. creba* POKROVSKAYA, 1958, p. 79, pl. 3, fig. 4-6)]. Strongly convex, with very narrow cephalic border; en grande tenue to largely effaced; uncommonly scrobiculate; prosopon smooth; variably spinose. Anterior glabellar lobe narrow, subtriangular; posterior glabellar lobe with F2 furrows usually absent; glabellar node midway between F1 and F2; basal lobes small, simple. Pygidial axis with small node on M2 slightly deflecting F2 furrow rearward. *upper Middle Cambrian*: Sweden, Norway, Denmark, *P. punctuosus* to *L. laevigata* Zones; Australia (Queensland, Tasmania), *P. punctuosus* to *C. quasivespa* Zones; England, *P. forchhammeri* Zone; Kazakhstan, Uzbekistan, *L. armata* to *L. laevigata* Zones, *H. brevifrons* beds; Russia (Siberian Platform), *L. lundgreni* Subzone to *L. laevigata* or *A. truncata* Zone; China (Zhejiang), *P. triangularis* to *L. sinensis* Zones, (Guizhou), *L. laevigata* Zone, (Hunan), *L. laevigata*, *Paramphoton* Zone; USA (New York), *Bolaspidella* Zone, (Utah, Nevada), *P. punctuosus* to *L. laevigata* Zones; Greenland, *L. laevigata* Zone; Canada (Newfoundland, Northwest Territories), *Cedaria minor* Zone. *Middle Cambrian*: Alaska; China (Qinghai); ?Argentina.—FIG. 224,5a,b. \**L. laevigata* (DALMAN), Middle Cambrian (*Lejopyge laevigata* Zone), Sweden (Kinnekulle, Västergötland); *a*, paralectotype, pygidium, RM Ar 287a, ×12; *b*, lectotype, cephalon, RM Ar 287b, ×12 (new).
- Myrmecomimus** ÖPIK, 1979, p. 136 [\**M. tribulis*; OD; holotype (ÖPIK, 1979, pl. 36, fig. 1, 1a, 2), CPC 14179, AGSO, Canberra]. Small; strongly convex; en grande tenue or with anterior glabellar lobe, median preglabellar furrow, and median postaxial furrow effaced; nonscrobiculate; nonspinose or with short cephalic spines. Posterior glabellar lobe very strongly convex, subhexagonal or subcircular, lateral glabellar furrows absent; basal lobes elongate, entire. Thorax nonspinose. Pygidial axis usually short, with very strongly inflated M2 and posterior lobe. *Middle Cambrian*: Australia (Queensland), *P. punctuosus* to *D. notalibrae* Zones; Russia (Siberian Platform), *Pseudanomocarina* Zone.—FIG. 223,6. \**M. tribulis*, Middle Cambrian (Undillan, *Doryagnostus notalibrae* Zone), Australia (northwestern Mt. Isa, western Queensland); holotype, exoskeleton, CPC 14179, ×9 (new).
- Onymagnostus** ÖPIK, 1979, p. 107 [\**O. angulatus*; OD; = *Aagnostus gibbus* var. *hybridus* BRÖGGER, 1878, p. 62; lectotype herein designated (BRÖGGER, 1878, p. 62), 28906, PMO, Oslo] [= *Onymagnostus (Aagnostonymus)* ÖPIK, 1979, p. 114 (type, *O. (A.) semiermis*; OD)]. Usually en grande tenue; very strongly convex, particularly in the pygidium; borders in both shields moderately wide; axial furrows variably impressed; median postaxial furrow absent; uncommonly scrobiculate; nonspinose or with very small pygidial marginal spines. Anterior glabellar lobe low, semioval; posterior glabellar lobe evenly convex, with F2 furrows weak to well developed; glabellar node a short distance behind F2 furrows; basal lobes short to slightly elongate, entire, commonly indistinct anteriorly. Pygidial axis very long, with large node on M2 strongly deflecting F2 furrow; posterior lobe very long, semioval to subtriangular, narrowly rounded posteriorly. *Middle Cambrian*: Sweden, Norway, Denmark, *T. fissus* or *A. atavus* to *L. lundgreni* or *G. nathorsti* Zones; Australia (Queensland, Northern Territory), late *T. gibbus* to *G. nathorsti* Zones, (Tasmania), *P. punctuosus* or *G. nathorsti* Zone; England, Wales, *P.*



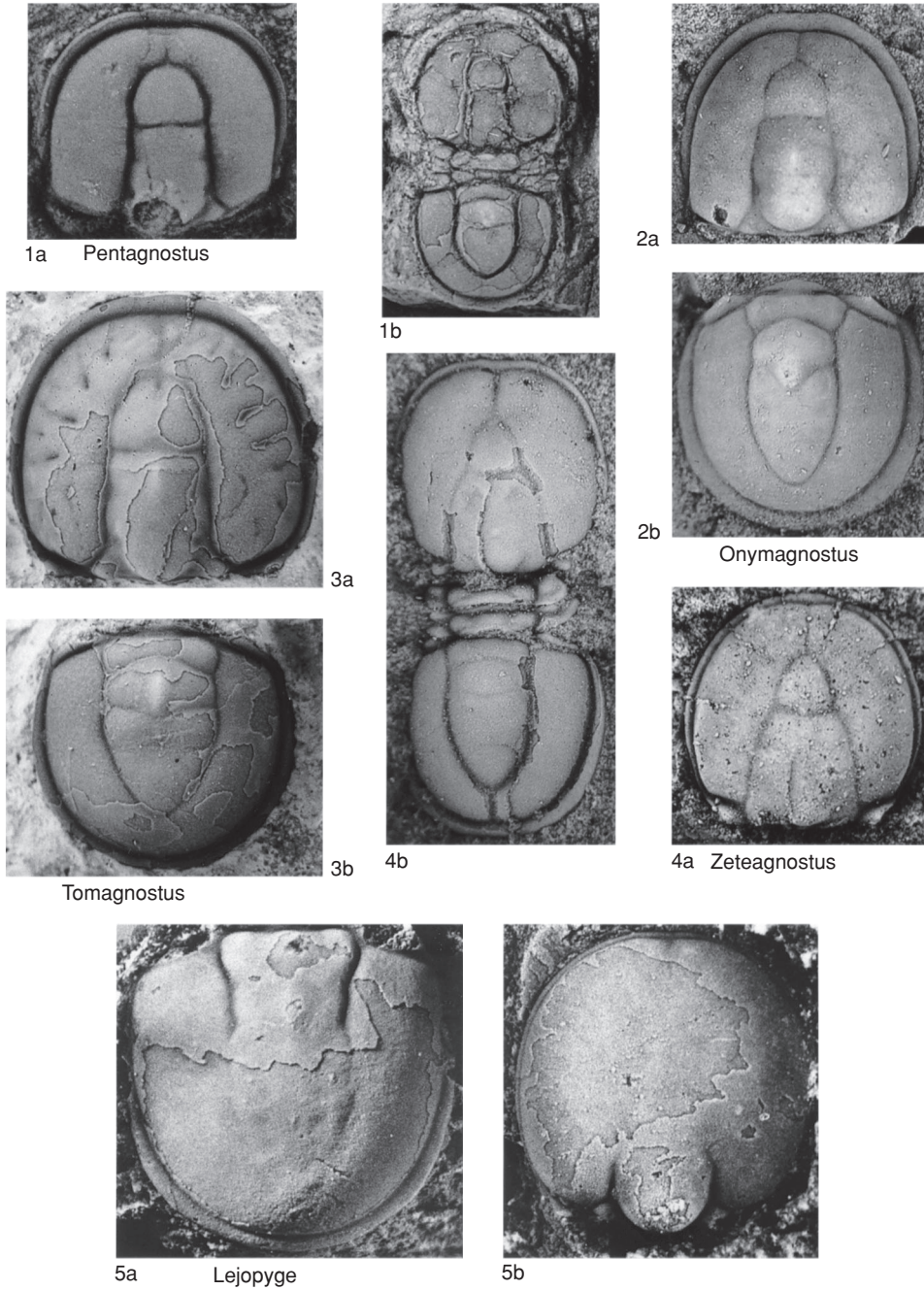


FIG. 224. Ptychagnostidae (p. 332-355)

*aurora* to early *P. davidis* Zone; Canada (Newfoundland, New Brunswick), *P. hicksi* to *P. forchhammeri* Zones; Russia (Siberian Platform), ?*Kounamkites*

Zone, *T. fissus* or *P. hicksi* to *A. limbataeformis* Zones; Kazakhstan, Uzbekistan, *Pseudanomocarina* Zone; Czechoslovakia, *E. pusillus* Zone; USA

- (Utah), *T. gibbus* Zone, *B. contracta* Subzone.—FIG. 224, 2a, b. \**O. hybridus* (BRÖGGER), Middle Cambrian (*Ptychagnostus punctuosus* Zone), Norway (Krekling, Oslo district); *a*, cephalon, PMO 28088, ×7.5 (new); *b*, lectotype (here chosen), pygidium, PMO 28096, original syntype of BRÖGGER (1878, pl. 5, fig. 4b), ×7.5 (new).
- Pentagnostus** LERMONTOVA, 1940, p. 127 [\**P. anabarensis*; OD; lectotype (LERMONTOVA, 1940, pl. 35, fig. 10c; SD SHERGOLD, LAURIE, & SUN, 1990, p. 41), 56/9182, CNIGR, St. Petersburg]. Median preglabellar furrow variably developed; median postglabellar furrow weak or absent; rarely scrobiculate; nonspine or with small pygidial marginal spines. Anterior glabellar lobe long, semiovalate; posterior glabellar lobe with subparallel sides, evenly convex or slightly inflated posteriorly with F2 furrows weakly to moderately well developed; axial glabellar node located midway between F1 and F2 furrows; basal lobes short or slightly elongate, entire. Pygidial axis with small node on M2 slightly deflecting F2 furrow. *lower Middle Cambrian*: Antarctica (Shackleton Range); Sweden, Norway, *P. insularis* to *T. gibbus* Zones; England, *P. pinus* Zone; Australia (Northern Territory, New South Wales), *T. gibbus* Zone; Russia (Siberian Platform), *Kounamkites* to *T. fissus* Zones, (Altay-Sayan), zone uncertain; Canada (British Columbia), *Bathyriscus-Elrathina* Zone.—FIG. 224, 1a, b. \**P. anabarensis*, Middle Cambrian (Amgaian, *Triplagnostus gibbus* Zone), Russia (Anabar River, Yakutia); *a*, paralectotype, exoskeleton, CNIGR 53/9182, ×10; *b*, lectotype, cephalon, CNIGR 56/9182, ×10 (Lermontova, 1940, pl. 35, fig. 10, 10c).
- Tomagnostus** HOWELL, 1935c, p. 15 [\**Agnostus fissus* LUNDGREN in LINNARSSON, 1879, p. 23; OD; neotype (SD WESTERGÅRD, 1946, pl. 7, fig. 22), 4840, SGU, Uppsala]. Usually scrobiculate; borders of moderate width; nonspine or with small pygidial marginal spines. Median preglabellar furrow commonly weakly developed. Anterior glabellar lobe subquadrate to semiovalate, usually sulcate; posterior glabellar lobe usually with well-developed F2 furrows. Axial glabellar node elongate, from a short distance behind to in front of F2 furrows; basal lobes slightly elongate, commonly indistinct anteriorly. Pygidial axis with well-developed F2 furrows; moderate to small node on M2; posterior lobe with well-developed transverse depression near midlength; median postaxial furrow rarely present. Weak, narrow (sag.) pygidial collar present in some specimens. *Middle Cambrian*: USA (South Carolina); Sweden, Denmark, England, *T. gibbus* to *H. parvifrons* Zones; Russia (Siberia), *Kounamkites*, *Pseudanomocarina*, *T. fissus*-*P. hicksi* to *A. henrici* Zones; Canada (Newfoundland), *P. hicksi* to *P. davidis* Zones; Czechoslovakia, *E. pusillus* Zone; Australia (Northern Territory), ?*A. atavus* Zone.—FIG. 224, 3a, b. \**T. fissus* (LUNDGREN), Middle Cambrian (*Triplagnostus gibbus* Zone), Sweden (south of Brantevik, Skåne); *a*, neotype, cephalon, SGU 4840, ×9; *b*, topotype, pygidium, SGU 4839, ×9 (new).
- Triplagnostus** HOWELL, 1935c, p. 14 [\**Agnostus gibbus* LINNARSSON, 1869, p. 81; OD; types not identified]. Rarely scrobiculate; spinose. Median preglabellar furrow well developed. Anterior glabellar lobe subtriangular, semiovalate or subpentagonal. Posterior glabellar lobe strongly convex in entirety or only in posterior half, with axial glabellar node located level with F1 furrows; basal lobes divided or entire. Pygidial axis with spine or large node on M2 deflecting F2 furrow rearward. Median postaxial furrow well developed or absent. *Middle Cambrian*.
- T. (Triplagnostus)** [= *Solenagnostus* WHITEHOUSE, 1936, p. 86 (type *Agnostus longifrons* NICHOLAS, 1916, p. 453, pl. 39, fig. 1); *T. (Aristarius)* ÖPIK, 1979, p. 125 (type, *T. (A.) aristarius*; OD)]. Anterior glabellar lobe low, subtriangular to semiovalate; posterior glabellar lobe very strongly convex in posterior half; F2 furrows variably developed. Pygidial axis with spine or large node on M2 strongly deflecting F2 furrow rearward; posterior axial lobe long, semiovalate to subtriangular, usually with small median tubercle near midlength. *Middle Cambrian*: England; Poland; Antarctica; Canada (Newfoundland); Sweden, Norway, Denmark, *T. gibbus* to *T. fissus* or *A. atavus* Zones; Australia (Queensland), *T. gibbus* to *G. nathorsti* Zones; Russia (Siberian Platform), upper *Kounamkites*, *T. gibbus*, *T. fissus*, *Pseudanomocarina* Zones; Kazakhstan, lower *A. atavus* Zone; USA (New York), *Bathyriscus-Elrathina* Zone, (Utah, Nevada), *T. gibbus* Zone.—FIG. 225, 1a, b. \**T. (T.) gibbus* (LINNARSSON), Middle Cambrian (*Triplagnostus gibbus* Zone), Exsulans Limestone; *a*, cephalon, SGU 4891, Sweden (Brantevik, Skåne), ×8; *b*, pygidium, SGU 4890, Sweden (Andrarum, Skåne), ×8 (new).
- T. (Aotagnostus)** ÖPIK, 1979, p. 133 [\**A. culminosus*; OD; holotype (ÖPIK, 1979, pl. 34, fig. 1), CPC 14166, AGSO, Canberra]. Anterior glabellar lobe slightly to strongly inflated, subtriangular to subpyriform; posterior glabellar lobe short, tapering forward, very strongly convex with F2 furrows very weak to absent. Pygidial axis with large spine or node on gibbous M2 strongly deflecting F2 furrow; posterior lobe of short or moderate length, semiovalate; median postaxial furrow well developed. *upper Middle Cambrian*: Australia (Queensland), *E. opimus* to *G. nathorsti* Zones.—FIG. 225, 2. \**T. (A.) culminosus* (ÖPIK), upper Middle Cambrian (Undillan, *Doryagnostus notalibrae* Zone), Australia (northwest of Mt. Isa, western Queensland); holotype, exoskeleton, CPC 14166, ×9 (new).
- Zeteagnostus** ÖPIK, 1979, p. 105 [\**Z. incautus*; OD; holotype (ÖPIK, 1979, pl. 45, fig. 1), CPC 14242, AGSO, Canberra]. Commonly scrobiculate. Anterior glabellar lobe subtriangular; posterior glabellar lobe evenly convex with F2 furrows weakly developed or absent and with axial glabellar node from a short distance in front of F1 furrow to a short distance behind F2 furrow; basal lobes divided or en-

ture, variably distinct. Pygidial axis with F2 furrow straight or slightly deflected rearward; median postaxial furrow present. *Middle Cambrian*: Australia (Queensland), *A. atavus* to *E. opimus* Zones; ?Sweden, *T. fissus* or *A. atavus* Zone; Russia (Siberia), *T. gibbus* or *T. fissus* Zone; Kazakhstan, *Z. intermedius* Zone (*sensu* ROBISON, 1984, p. 20); USA (Utah), *T. gibbus* Zone; China (Liaoning, Shandong), Canada (Newfoundland), lower Middle Cambrian.—FIG. 224, 4a, b. \**Z. incautus*, Middle Cambrian (Floran, *Acidusus atavus* Zone), Australia (northwest of Mt. Isa, western Queensland); a, holotype, cephalon, CPC 14242,  $\times 14$  (new); b, exoskeleton, CPC 14239,  $\times 14$  (new).

### Family SPINAGNOSTIDAE Howell, 1935

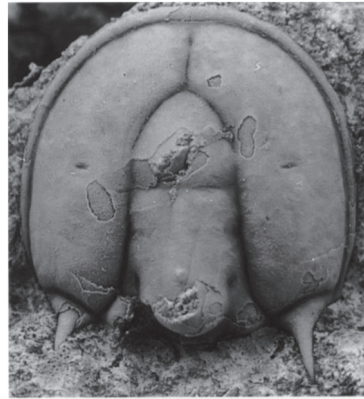
[Spinagnostidae HOWELL, 1935a, p. 218] [=Quadragnostidae HOWELL, 1935a, p. 219, *sensu* ÖPIK, 1961b, p. 55; Cyclopnagnostidae HOWELL, 1937, p. 1165]

En grande tenue or with anterior glabellar lobe variably effaced; usually nonscrobiculate; with nondeliquate border furrows and narrow to moderately wide borders; unconstricted acrolobes; cephalon nonspinose; median preglabellar furrow well developed to absent. Glabella with ogival, semiovate, subpentagonal, or effaced anterior lobe; F3 straight, variably bent forward or effaced; posterior lobe with F2 usually developed; glabellar culmination usually broadly rounded; glabellar node from level with F1 to slightly in front of F2; basal lobes small, simple. Pygidium nonspinose or bispinose, with axis usually long, not reaching border furrow, ogival, and constricted across M2; F1 and F2 usually effaced; axial node of moderate size; median postaxial furrow usually present. *upper Lower Cambrian–middle Upper Cambrian*.

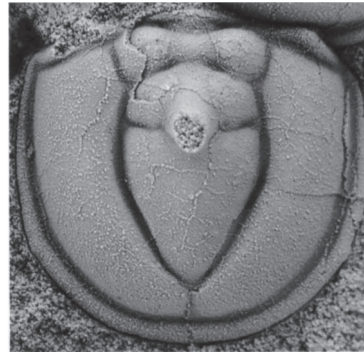
### Subfamily SPINAGNOSTINAE Howell, 1935

[Spinagnostidae HOWELL, 1937, p. 1161] [=Cyclopnagnostinae HOWELL, 1937, p. 1161; Hypagnostinae IVSHIN, 1953, p. 15; Euagnostinae ÖPIK, 1979, p. 73]

Commonly nonscrobiculate, with most species variably effacing the anterior glabellar lobe and some also effacing F3; cephalic border usually narrow; pygidial border wider; median preglabellar furrow usually absent, rarely weakly developed. Anterior glabellar lobe semiovate, subpentagonal, or



1a



1b

Triplagnostus



2

Aotagnostus

FIG. 225. Ptychagnostidae (p. 354)



more commonly effaced; posterior lobe with F2 weak or absent; glabellar node located from short distance behind F2 to short distance in front of F2. *upper Lower Cambrian–Upper Cambrian*.

**Hypagnostus** JAEKEL, 1909, p. 399 [\**Agnostus parvifrons* LINNARSSON, 1869, p. 82; OD; lectotype (LINNARSSON, 1869, pl. 2, fig. 56; SD WESTERGÅRD, 1946, p. 116), 4769, SGU, Uppsala] [= *Spinagnostus* HOWELL, 1935a, p. 219 (type, *S. franklinensis*; OD); *Cyclopagnostus* HOWELL, 1937, p. 1166 (type, *C. hesperius*; OD); *H. (Breviagnostus)* LIU, 1982, p. 296 (type, *H. (B.) brachyaxonus*; OD); *H. (Metahypagnostus)* QIU in QIU & others, 1983, p. 41 (type, *H. (M.) brachydolonus* ZHOU & YANG in QIU & others, 1983, p. 42, pl. 13, fig. 16–17, pl. 14, fig. 1)]. Commonly weakly scrobiculate. Glabella with effaced anterior lobe; F3 bent forward, rounded or chevronate; posterior lobe short, variably ovate, with F2 weak or absent; glabellar node level with or slightly in front of F2 furrows. Pygidium usually nonspinose; axis usually long, broadly ogival or less commonly short and posteriorly rounded. Median postaxial furrow usually developed. *Middle Cambrian–lower Upper Cambrian*: Argentina; Sweden, Wales, *H. parvifrons* to *L. laevigata* Zones; England, *H. parvifrons* to *A. pisiformis* Zones; Norway, *P. tessini* to *P. forchhammeri* Zones; Denmark, *P. tessini* Zone; Czechoslovakia, *P. (P.) gracilis* Zone; USA (Vermont, New York), *Bolaspidella* Zone, (Alaska), late Dresbachian, (South Carolina), zone uncertain; Canada (Newfoundland, New Brunswick, Quebec), *H. parvifrons* Zone; Australia (Queensland, Tasmania), *P. atavus* to *E. eretes* Zones; China, *H. parvifrons* to *G. stolidotus* Zones; Russia (Salaïr, Altay, southeastern Siberia), Turkestan Mountain Range, Kazakhstan, *P. atavus* Zone, *T. fissus* or *P. hicksi* to *L. laevigata* or *A. truncata* Zones; Kazakhstan, *K. simplex* to *G. reticulatus* Zones.—FIG. 226,5a,b. \**H. parvifrons* (LINNARSSON), Middle Cambrian (*Hypagnostus parvifrons* Zone), Sweden (Hällekis, Kinnekulle, Västergötland); a, lectotype, cephalon, SGU 4769, ×9; b, paralectotype, pygidium, SGU 4768, ×9 (new).

**Cotalagnostus** WHITEHOUSE, 1936, p. 92 [\**Agnostus lens* GRÖNWALL, 1902, p. 65; OD; syntypes (GRÖNWALL, 1902, pl. 1, fig. 8–9), 149, 150, MGUH, Copenhagen]. Like *Hypagnostus* but with glabellar F3 effaced and commonly with axial furrows surrounding posterior lobe of pygidial axis effaced. *Middle Cambrian*: Argentina; China (Hunan, Guizhou); Sweden, *P. atavus* to *P. forchhammeri* Zones; Denmark, *P. davidis* Zone; Norway, *P. paradoxissimus* to *P. forchhammeri* Zones; England, Wales, *H. parvifrons* to *P. punctuosus* Zones; Canada (Newfoundland, Nova Scotia), late *P. hicksi* to early *P. davidis* Zones; USA (Utah, Alaska), *B. contracta* Subzone; Australia (Queensland), *D. notalibrae* Zone; Russia (southeastern Siberia), *T. fissus* or *P. hicksi* to late *P. davidis* Zones, (Kemerov), *P.*

*forchhammeri* Zone.—FIG. 226,1a,b. \**C. lens* (GRÖNWALL), Middle Cambrian (*Hypagnostus parvifrons* Zone), Denmark (Borregård, Øle Aa, Bornholm); a, syntype, cephalon, MGUH 149, ×10; b, syntype, pygidium, MGUH 150, ×12 (new).

**Eoagnostus** RESSER & HOWELL, 1938, p. 216 [\**E. roddyi*; OD; holotype (RESSER & HOWELL, 1938, pl. 3, fig. 4), 90796, USNM, Washington, D.C.]. Small; nonscrobiculate; with moderately wide borders; median preglabellar furrow absent. Glabella with anterior lobe very faintly outlined or effaced, semiovate; F3 straight; posterior lobe strongly inflated posteriorly, overhanging occipital band; glabellar node absent; glabellar culmination rounded or obtusely angular. Pygidium nonspinose; axis of moderate length, strongly convex, semiovate, narrowly rounded posteriorly; axial node indistinct; median postaxial furrow weakly developed. *upper Lower Cambrian*: USA (Pennsylvania, Vermont, New York), *Olenellus* to *Paedumias* to *Bonnia* faunas.—FIG. 227,1a. \**E. roddyi*, Lower Cambrian (*Bonnia* to *Olenellus* Zones), USA (Lancaster, Pennsylvania); holotype, exoskeleton, USNM 90796, ×10 (new).—FIG. 227,1b,c. *E. acrorhachis*, Lower Cambrian (*Bonnia* to *Olenellus* Zones), USA (Hatch Hill, New York); b, paratype, cephalon, MCZ 8548/3, ×10; c, paratype, pygidium, MCZ 8545/4, ×10 (new).

**Euagnostus** WHITEHOUSE, 1936, p. 87 [\**E. opimus*; OD; holotype (WHITEHOUSE, 1936, pl. 8, fig. 11), 3195, UQF, Brisbane]. Glabella with anterior lobe broadly semiovate or variably effaced; F3 straight; posterior lobe broad with F2 weak to absent; glabellar node a short distance behind F2. Pygidial axis long, ogival, almost reaching border furrow, slightly constricted across M2; F1 and F2 effaced; median postaxial furrow well developed. *Middle Cambrian*: Canada (Newfoundland); Australia (Queensland), *E. opimus* to *D. notalibrae* Zones; USA (Utah, Nevada), early *T. gibbus* to *P. punctuosus* Zones.—FIG. 226,7a. \**E. opimus*, Middle Cambrian (Floran, *Euagnostus opimus* Zone), Australia (northwest of Mt. Isa, western Queensland); holotype, pygidium, UQF 3193, ×8.8 (new).—FIG. 226,7b. *E. neptis* (= *E. opimus* WHITEHOUSE), Middle Cambrian (Undillan, *Ptychagnostus punctuosus* Zone), Australia (northwest of Mt. Isa, western Queensland); holotype, exoskeleton, CPC 14068, ×8 (new).

**Micagnostus** HAJRULLINA in REPINA, PETRUNINA, & HAJRULLINA, 1975, p. 115 [\**M. rectus*; OD; holotype (HAJRULLINA in REPINA, PETRUNINA, & HAJRULLINA, 1975, pl. 11, fig. 13–14), 483/179, MMG, Tashkent]. Known only from cephalon. Small, nonscrobiculate, with moderately wide border. Glabella short, broad, with anterior lobe weakly outlined, semicircular to semiovate; F3 straight; posterior lobe short, broad; F2 absent; glabellar node indistinct. *Middle Cambrian*: Uzbekistan, *Pseudanomocarina* Zone.—FIG. 226,4. \**M. rectus*, Middle Cambrian (Amgaian, *Pseudanomocarina* beds), Uzbekistan (northern Turkestan Mountain



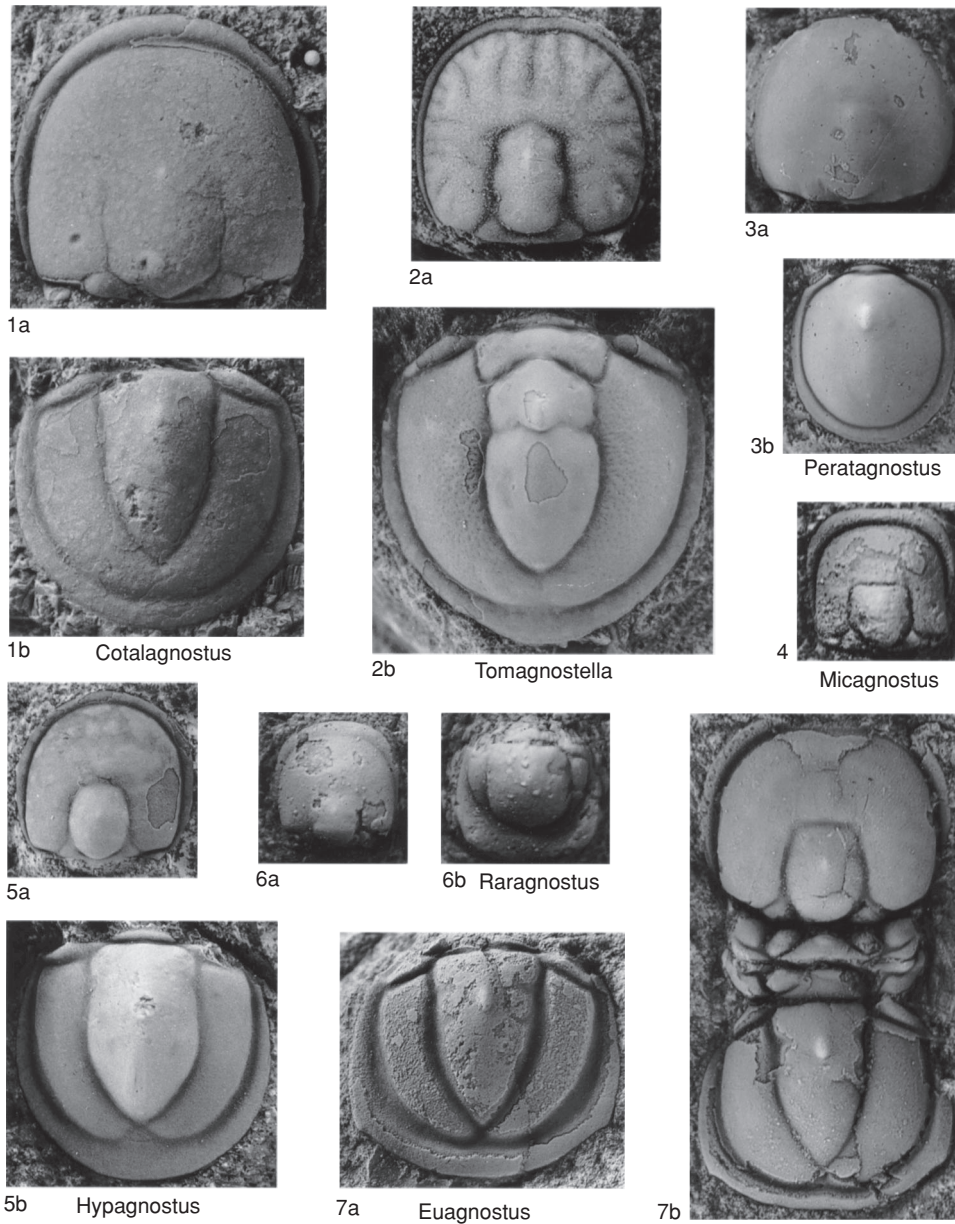


FIG. 226. Spinagnostidae (p. 356–358)

Range); holotype, cephalon, MMG 483/179,  $\times 10$  (Repina, Petrunina, & Hajrullina, 1975, pl. 11, fig. 13–14).

*Peratagnostus* ÖPIK, 1967, p. 86 [*\*P. nobilis*; OD; holotype (ÖPIK, 1967, pl. 52, fig. 11a–c), CPC 5787, AGSO, Canberra]. Almost completely effaced; nonscrobiculate or weakly scrobiculate; cephalic

border absent or very narrow; pygidial border wider, always present. Glabella with vestigial axial furrows defining rear; glabellar node advanced. Pygidium nonspinose, retaining traces of axial furrows defining a narrowly tapering axis that does not reach posterior border furrow; median postaxial furrow effaced. *Upper Cambrian*: Australia

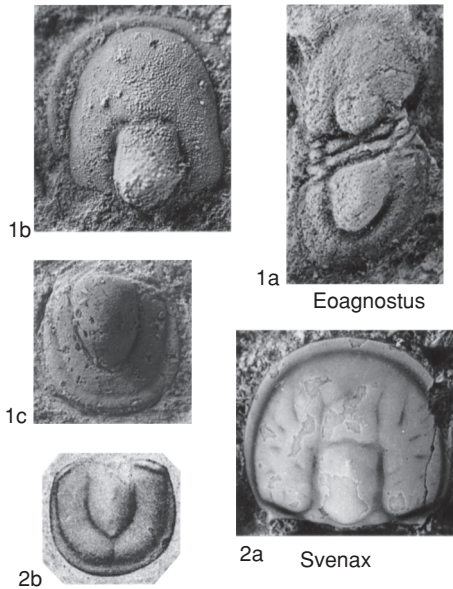


FIG. 227. Spinagnostidae (p. 356–358)

(Queensland), *E. sentum* to *R. apsis* or *W. iota* Zones; South Korea, *Eochuangia* Zone; Kazakhstan, *G. solidotus* to *H. longiformis* Zones, (Lesser Karatau Mountains), *G. reticulatus* Zone; Russia (Yakutia), *Irvingella* or *C. felix* Zone; Canada (Northwest Territories, Newfoundland), *Olenaspella evansi* to *Irvingella major* Zones; USA (Nevada), *Dunderbergia* Zone, (Alaska), Franconian; China (Zhejiang), *P. fenghuangensis* to *P. clavatus* or *S. kiangshanensis* Zones, (Hunan, Guizhou), zone uncertain.—FIG. 226,3a,b. \**P. nobilis*, Upper Cambrian (Idamean, *Erixanium sentum* Zone), Australia (Burke River Structural Belt, western Queensland); *a*, paratype, cephalon, CPC 5792,  $\times 8$ ; *b*, holotype, pygidium, CPC 5787,  $\times 8$  (new).

**Raragnostus** HAJRULLINA in REPINA, PETRUNINA, & HAJRULLINA, 1975, p. 117 [\**R. mirus*; OD; holotype (HAJRULLINA in REPINA, PETRUNINA, & HAJRULLINA, 1975, pl. 12, fig. 17–18), 483/190b, MMG, Tashkent]. Small, nonscrobiculate, with narrow cephalic border and wide, flat pygidial border. Glabella with effaced anterior lobe and with F3 effaced or weakly impressed, bent forward; posterior lobe short; F2 weak to absent; glabellar node a short distance behind F2 furrow. Pygidial axis very broad, long, posteriorly broadly rounded and in contact with border furrow across entire posterior margin; axial node indistinct. *Middle Cambrian*: Uzbekistan, Amgaian–Mayaian; Australia (Queensland), *G. nathorsti* Zone; Sweden, *P. forchhammeri* Zone.—FIG. 226,6a,b. \**R. mirus*, Middle Cambrian (northern Turkestan Mountain Range); *a*, paratype, cephalon, MMG 483/190a,  $\times 10$ ; *b*, holo-

type, pygidium, MMG 483/190b,  $\times 10$  (Repina, Petrunina, & Hajrullina, 1975, pl. 12, fig. 15, 17). **Svenax** ÖPIK, 1979, p. 64 [\**Aagnostus pusillus* TULLBERG, 1880, p. 36; OD; holotype (TULLBERG, 1880, pl. 2, fig. 30), 407T, LO, Lund]. Weakly scrobiculate. Glabella with semiovate to subpentagonal anterior lobe with adjacent axial furrows weakly impressed; F3 straight or bent slightly forward; posterior lobe with F2 weak; glabellar node level with or slightly in front of F2. Pygidial axis short, broadly ogival, with well-developed constriction across M2; median postaxial furrow clearly developed. *Middle Cambrian*: Sweden, Denmark, Norway, *P. punctuosus* Zone; Australia (Queensland), *P. punctuosus* to *D. notalibrae* Zones.—FIG. 227,2a,b. \**S. pusillus* (TULLBERG), Middle Cambrian (*Ptychagnostus punctuosus* Zone), Sweden (Andrarum, Skåne); *a*, topotype, cephalon, RM Ar 1988,  $\times 8$  (new); *b*, holotype pygidium, LO 407T,  $\times 6$  (Westergård, 1946, pl. 4, fig. 12).

**Tomagnostella** KOBAYASHI, 1939a, p. 150 [\**Aagnostus exsculptus* ANGELIN, 1851, p. 7; OD; lectotype (TULLBERG, 1880, pl. 1, fig. 10; SD WESTERGÅRD, 1946, p. 118), Ar 2007, RM, Stockholm]. Commonly weakly scrobiculate; median preglabellar furrow occasionally weakly developed, usually absent. Glabella with F3 straight, bent forward, chevronate or rarely effaced; posterior lobe with F2 commonly developed; glabellar node from slightly behind to slightly in front of F2 furrows. Pygidial axis long, commonly reaching border furrow or connected to it by median postaxial furrow; usually strongly constricted across M2; F1 clearly developed, bent forward; F2 variably developed, nearly straight, with a slight median deflection around axial node. *Middle Cambrian–lower Upper Cambrian*: northern Greenland; Sweden, *H. parvifrons* to *L. laevigata* Zones; Norway, England, *L. laevigata* Zone; Russia (Siberia), northern Turkestan Mountain Range, late *P. davidis* to *L. laevigata* Zones; Canada (Northwest Territories), *Cedaria minor* Zone; Australia (Queensland), *G. nathorsti* Zone; China (Zhejiang), *G. stolidotus* Zone, (Hunan, Guizhou), upper Middle Cambrian.—FIG. 226,2a. \**T. exsculpta* (ANGELIN), upper Middle Cambrian (*S. brachymetopa* Zone), Sweden (Andrarum Limestone, Andrarum, Skåne); lectotype, cephalon, RM Ar 2007,  $\times 10$  (new).—FIG. 226,2b. *T. sulcifer* (WALLERIUUS), upper Middle Cambrian (*Lejopyge laevigata* Zone), Sweden (Gudhem, Västergötland); topotype, pygidium, SGU 4807,  $\times 9$  (new).

### Subfamily DORYAGNOSTINAE Shergold, Laurie, & Sun, 1990

[Doryagnostinae SHERGOLD, LAURIE, & SUN, 1990, p. 28]

En grande tenue; nonscrobiculate; with borders of moderate width. Glabella with ogival to semiovate anterior lobe; F3 clear, straight or with slight median forward deflection; posterior lobe with F2 furrows

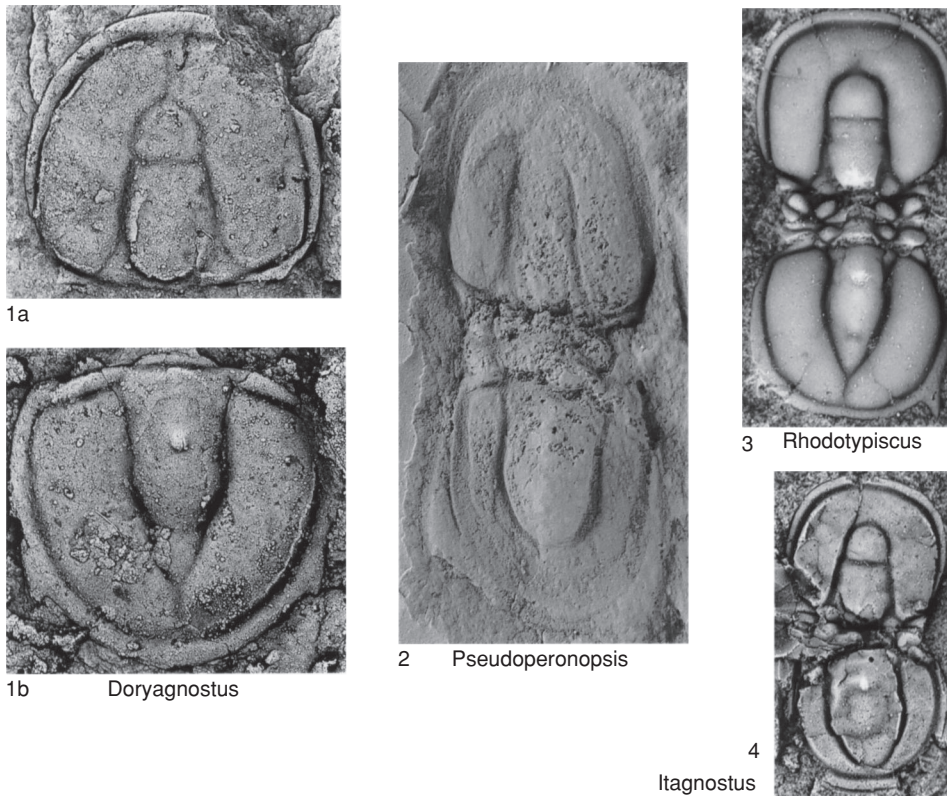


FIG. 228. Spinagnostidae (p. 359–360)

present; glabellar node located from level with F1 to midway between F1 and F2. Pygidium with long, ogival to semiovate posterior lobe; small secondary axial node, commonly associated with a transverse depression in posterior half. *Middle Cambrian*.

**Doryagnostus** KOBAYASHI, 1939a, p. 148 [\**Agnostus incertus* BRÖGGER, 1878, p. 70; OD; lectotype (NIKOLAISEN & HENNINGSMOEN, 1990, fig. 2a), 28200, PMO, Oslo] [= *Ceratagnostus* WHITEHOUSE, 1939, p. 255 (type, *C. magister*; OD)]. Median preglabellar furrow well developed, usually expanding into deltoid area anteriorly. Glabella with ogival anterior lobe; posterior lobe with weak F2 furrows; glabellar node midway between F1 and F2 furrows. Pygidium bispinose; axis ogival, acuminate posteriorly; posterior lobe ogival, commonly with transverse depression. *upper Middle Cambrian*: ?northern Greenland; England; Norway, Denmark, *P. tessini* Zone; Sweden, *P. punctuosus* Zone; Canada (Newfoundland), *P. davidis* Zone; Australia (Queens-

land), *E. opimus* to *G. nathorsti* Zones; Russia (southeastern Siberia), late *P. davidis* to *P. forchhammeri* Zones; China (Xinjiang), *G. nathorsti* or *P. punctuosus* Zone, (Hunan, Guizhou), zone uncertain.—FIG. 228, 1a, b. \**D. incertus* (BRÖGGER), Middle Cambrian (*Ptychagnostus punctuosus* Zone), southern Norway (Krekling Station, Oslo district); a, paralectotype, cephalon, PMO H2646, ×8; b, lectotype, pygidium, PMO 28200, ×8 (Nikolaisen & Henningsmoen, 1990, fig. 2a, 26).

**Itagnostus** ÖPIK, 1979, p. 60 [\**Agnostus elkedraensis* ETHERIDGE, 1902, p. 3; OD; lectotype (SD WHITEHOUSE, 1936, p. 89, pl. 9, fig. 3), 54188, AMF, Sydney]. Median preglabellar furrow absent. Glabella with semiovate anterior lobe; F3 straight; posterior lobe with F2 furrows weak or absent; glabellar node level with or a short distance in front of F1 furrows. Pygidium nonspinose or bispinose; axis broad, long, narrowly rounded posteriorly; posterior lobe semiovate, lacking transverse depression; median postaxial furrow absent. *lower Middle Cambrian*: Australia (Northern Territory), *T. gibbus* Zone; Russia (Siberian Platform), *Oryctocara* to *Kounamkites* Zones; Canada (British Columbia), *Bathyriscus-Elrathina* Zone; ?Germany, *P. insularis*



Zone; China (Guizhou), Middle Cambrian.—FIG. 228,4. \**I. elkedraensis* (ETHERIDGE), Middle Cambrian (Templetonian, *Triplagnostus gibbus* Zone), Australia (Elkedra area, Northern Territory); lectotype, exoskeleton, AMF 54188, ×8 (new).

**Rhodotypiscus** ÖPIK, 1979, p. 79 [\**R. nasonis*; OD; holotype (ÖPIK, 1979, pl. 16, fig. 1), CPC 14072, AGSO, Canberra]. Median preglabellar furrow usually weakly developed or absent. Glabella with semiovate anterior lobe; F3 straight; posterior lobe with well-developed F2 furrows; glabellar culmination strongly inflated; glabellar node level with or a short distance in front of F1 furrow. Pygidium bispinose; axis elongate ogival, acuminate posteriorly; posterior lobe ogival, commonly with well-developed transverse depression; median postaxial furrow present. *Middle Cambrian*: Canada (Quebec); Australia (Queensland), *E. opimus* Zone; USA (Utah), *T. gibbus* to lower *P. punctuosus* Zones, (Alaska), Middle Cambrian; ?Russia (Siberia), *T. fissus* Zone; China (Xinjiang), *G. nathorsti* or *P. punctuosus* Zone.—FIG. 228,3. \**R. nasonis*, Middle Cambrian (Floran, *Euagnostus opimus* Zone), Australia (Camooweal area, western Queensland); holotype, exoskeleton, CPC 14072, ×8 (new).

### Subfamily UNCERTAIN

**Pseudoperonopsis** HARRINGTON, 1938, p. 149 [\**Agnostus sallesi* MUNIER-CHALMAS & BERGERON in BERGERON, 1889, p. 337; OD; holotype (MUNIER-CHALMAS & BERGERON in BERGERON, 1889, pl. 3, fig. 5), not identified]. With tendency to efface F1 and F2 furrows of pygidial axis; deliquiate border furrows; unconstricted acrollobes. Cephalon with vestigial median preglabellar furrow; axial glabellar node at midlength of posterior lobe. Pygidium simplimarginate or narrowly (sag.) zonate; generally with short (sag.), pointed axis; with or without median postaxial furrow; with posterolateral spines. *Middle Cambrian*: France, *Paradoxides* beds; Spain, *Badulesia* to *Solenopleuropsis* Zones; USA (Utah), *B. contracta* Subzone; Australia (Queensland), *A. atavus* to *D. notalibrae* Zones; China (Liaoning, Shandong), *Crepicephalina* Zone.—FIG. 228,2. \**P. sallesi* (MUNIER-CHALMAS & BERGERON), Middle Cambrian (horizon with *Conocoryphe levyi*), France (Coulouma, Champs du Travers, Montagne Noire); plesiotype, UM Thorax H24, ×5 (new).

### Family PERONOPSIDAE Westergård, 1936

[Peronopsidae WESTERGÅRD, 1936, p. 28]

Usually en grande tenue; commonly scrobiculate; with nondeliquiate border furrows and unconstricted acrollobes; cephalon nonspinose; median preglabellar furrow occasionally weakly developed. Glabella with subrectangular, trapeziform, semicircular, or

semiovate anterior lobe; F3 straight or bent rearward; posterior lobe with F1 and F2 well developed; glabellar culmination narrowly rounded; glabellar node from a short distance behind F2 to a short distance in front of F2; basal lobes simple, inset behind a well-developed F1 furrow. Pygidium simplimarginate, nonspinose or bispinose; axis long, nearly reaching border furrow, ogival to subtriangular, variably constricted across M2; F1 well developed to effaced; F2 well developed to effaced, straight or deflected around axial node; posterior lobe semiovate to ogival with a usually well-developed transverse depression at about midlength or in anterior half. *Middle Cambrian*.

**Peronopsis** HAWLE & CORDA, 1847, p. 115 [\**Battus interger* BEYRICH, 1845, p. 44; OD; lectotype (PEK & VANĚK, 1971, p. 270, pl. 1, fig. 6), Beyrich Collection 86(530), HMB, Berlin] [= *Mesospheniscus* HAWLE & CORDA, 1847, p. 46 (type, *M. cuneifer*; OD); *Mesagnostus* JAEKEL, 1909, p. 397 (type, *Battus interger* BEYRICH, 1845, p. 44, fig. 19)]. Nonscrobiculate; narrow border in cephalon and wide, flat border in pygidium; median preglabellar furrow absent. Glabella with subquadrate to semiovate anterior lobe; posterior lobe with glabellar node a short distance behind F2. Pygidium nonspinose or bispinose; axis strongly convex, broadly ogival; F1 weak; F2 weak or absent, straight; posterior lobe broadly ogival, narrowly rounded to acuminate posteriorly, with a weakly developed transverse depression at about midlength. *Middle Cambrian*: ?Sweden; Czech Republic, *P. (P.) gracilis* Zone.—FIG. 229,1a,b. \**P. integra* (BEYRICH), Middle Cambrian (*Paradoxides gracilis* Zone), Czech Republic (Jince, Bohemia); *a*, toptype, exoskeleton, SBNM Br-190/56, ×10 (Horný & Bastl, 1970); *b*, lectotype, pygidium, HMB Beyrich Collection 86(530), ×10.7 (Pek & Vaněk, 1971, pl. 1, fig. 6–7).

**Diplorrhina** HAWLE & CORDA, 1847, p. 46 [\**D. triplicata*; SD PEK & VANĚK, 1971, p. 271; lectotype (SD ŠNAJDR, 1958, pl. 4, fig. 9), Hawle Collection 745/66, NMP, Prague]. Commonly scrobiculate, with moderately wide border in cephalon and wider border in pygidium; median preglabellar furrow absent or weakly developed. Glabella with subrectangular, trapeziform, or semicircular anterior lobe; F3 bent rearward, rounded or chevron shaped; posterior lobe with glabellar node from a short distance behind to slightly in front of F2 furrows. Pygidium bispinose; axis of low convexity, ogival to subtriangular; F1 well developed to effaced, bent forward; F2 well developed or effaced, straight; posterior lobe acuminate posteriorly. *Middle Cambrian*: Czech Republic, *P. (E.) pusillus* to *P. (P.) gracilis* Zones; Sweden, *H. parvifrons* to *S. brachy-*

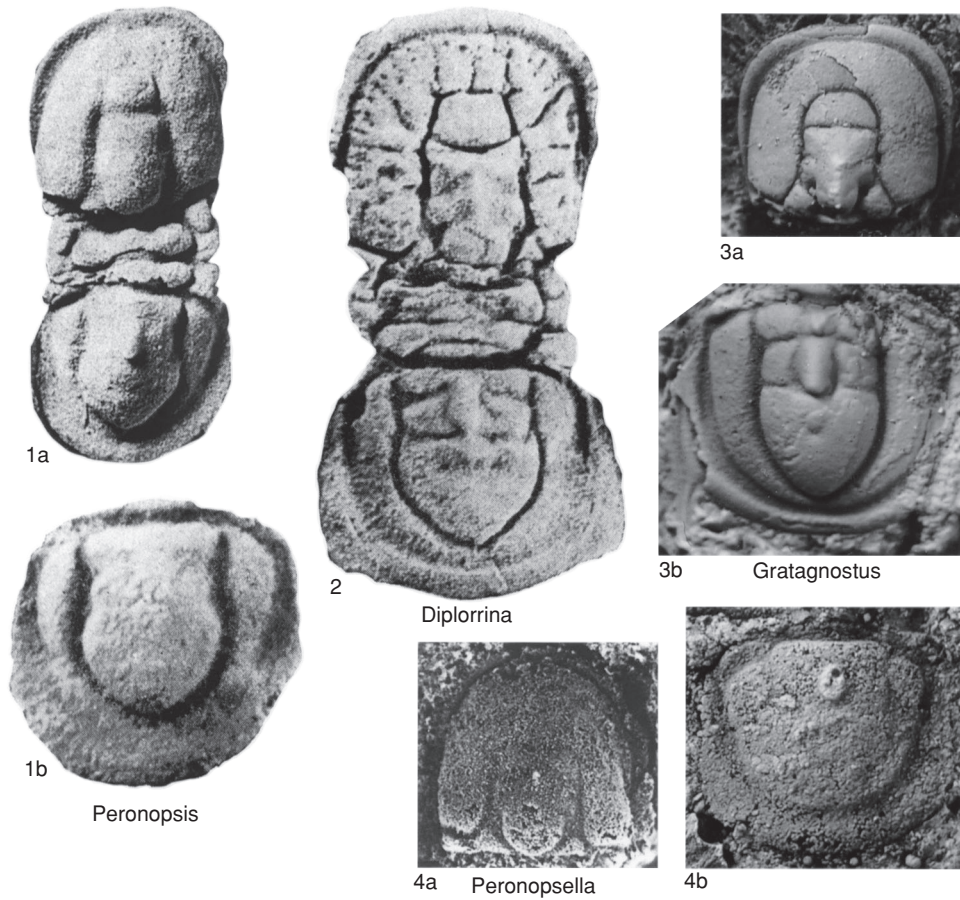


FIG. 229. Peronopsidae (p. 360–362)

*metopa* Zones; England, Canada (Newfoundland), upper *P. hicksi* to lower *P. davidis* Zone.—FIG. 229,2. \**D. triplicata*, Middle Cambrian (*Eccaparadoxides pusilla* Zone), Czech Republic (Skryje, Bohemia); lectotype, exoskeleton, NM Hawle Collection 745/66, ×10 (Pek & Vaněk, 1971, pl. 1, fig. 1).

**Gratagnostus** HAJRULLINA in REPINA, PETRUNINA, & HAJRULLINA, 1975, p. 113 [\**G. latus*; OD; holotype (HAJRULLINA in REPINA, PETRUNINA, & HAJRULLINA, 1975, pl. 11, fig. 10), 483/189, MMG, Tashkent]. Nonscrobiculate; narrow to moderately wide border in cephalon and wider border in pygidium; median preglabellar furrow absent. Glabella with trapeziform to semicircular anterior lobe; posterior lobe with glabellar node midway between F1 and F2. Pygidium bispinose; axis broad, ogival; F1 well developed; F2 well developed, deflected around axial node; posterior lobe narrowly rounded posteriorly. *Middle Cambrian*: Uzbekistan, *Pseudanomocarina* Beds; England, *P. aurora* to *T. fissus* Zones; Sweden,

*T. fissus* or *A. atavus* Zone; Canada (Newfoundland), *P. bennetti* Zone.—FIG. 229,3a,b. \**G. latus*, Middle Cambrian (Amgaian Stage beds with *Pseudanomocarina*), Uzbekistan (Shodymira region, southern Tyan-Shan Range); a, paratype, cephalon, MMG 483/176a, ×10; b, holotype, pygidium, MMG 483/189, ×10 (Repina, Petrunina, & Hajrullina, 1975, pl. 11, fig. 10, 12).

**Peronopsella** SDZUY, 1968, p. 88 [\**P. pokrovskajae*; OD; holotype (SDZUY, 1968, pl. 1, fig. 1), 24000, SMF, Frankfurt am Main]. Similar to *Peronopsis* but cephalon with F3 and F2 and axial furrows surrounding anterior half of glabella effaced. Pygidium with F1, F2, and usually axial furrows surrounding posterior axial lobe effaced. *Middle Cambrian*: Spain (Asturias), *C. ovata* beds, *Acadolenus* to *Badulesia* Zones, (Zaragoza), *Badulesia* to *Pardailhanian* Zones; Germany, *P. paradoxissimus* beds, *T. gibbus* to *A. atavus* Zones; England, lower *T. fissus* Zone; Canada (Newfoundland), *P. bennetti* Zone.—FIG. 229,4a,b. \**P. pokrovskajae*, Middle Cambrian

(beds with *Acadoparadoxides*), Spain (Riosol, Asturias); *a*, holotype, cephalon, SMF 24000,  $\times 16$ ; *b*, paratype, pygidium, SMF 24001,  $\times 12$  (Sdzuy, 1968, pl. 1, fig. 1, 6).

### Family DIPLAGNOSTIDAE Whitehouse, 1936

[Diplagnostidae WHITEHOUSE, 1936, p. 90]

Variably effaced; commonly scrobiculate; usually with deliquiate border furrows; with pygidial border simplimarginate or variably zonate; cephalon nonspinose; cephalic acrolobe usually unconstricted; pygidial acrolobe commonly constricted; median preglabellar furrow variably developed. Glabella with anterior lobe variable in shape; F3 variably impressed, straight to V-shaped; posterior lobe with glabellar culmination variably rounded to angular; glabellar node from slightly behind F2 to near F3; basal lobes of moderate to large size, simple. Pygidium with basic or glyptagnostoid articulating device; bispinose or occasionally posteriorly angulate or trispinose; axis of variable length, commonly deuterolobate; F1 variably impressed or effaced; M1 commonly trilobate; F2 usually impressed, deflected by axial node; in axiolobate forms, posterior lobe with transverse depression; deuterolobate forms with well-developed terminal node. *Middle Cambrian–Lower Ordovician*.

### Subfamily DIPLAGNOSTINAE Whitehouse, 1936

[Diplagnostinae WHITEHOUSE, 1936, p. 90]

En grande tenue; usually nonscrobiculate; with variably zonate pygidial border. Glabella with subquadrate to semicircular anterior lobe; F3 variably impressed, straight; posterior lobe with variably developed F2 and F1; glabellar node from slightly behind to slightly in front of F2. Pygidium usually bispinose, occasionally posteriorly angulate or trispinose; axis of variable length, usually slightly constricted over M2; F1 and F2 well developed to effaced; posterior lobe variable in shape, usually with transverse depression; pygidial collar usually present, incipient, arcuate or sinuous. *Middle Cambrian–lower Upper Cambrian*.

**Diplagnostus** JAEKEL, 1909, p. 396 [*\*Agnostus planicauda* ANGELIN, 1851, p. 7; OD; location of types unknown (topotypes illustrated by WESTERGÅRD, 1946, pl. 8, fig. 22–24)] [= *Enetagnostus* WHITEHOUSE, 1936, p. 91 (type, *E. humilis*; OD)]. Cephalon commonly scrobiculate; deliquiate to subdeliquiate border furrows with narrow border in cephalon and zonate border in pygidium; unconstricted acrolobes; median preglabellar furrow well developed to absent. Glabella with trapeziform to subrectangular anterior lobe, commonly with median sulcus; F3 clearly impressed; F2 well developed or absent; glabellar node level with or slightly in front of F2 furrows. Pygidium bispinose; axis long, broad, ogival, commonly extending to border furrow or connected to it by median postaxial furrow; F1 clearly impressed laterally; F2 clearly impressed; posterior lobe ogival to subtriangular, commonly with poorly defined transverse depression at about midlength; pygidial collar always well defined, extending across entire posterior margin between pygidial marginal spines, but not extending onto acrolobe. *Middle Cambrian*: Argentina; northern Greenland; Sweden, *P. punctuosus* to *L. laevigata* Zones; Denmark, Norway, *L. laevigata* Zone; England, *P. aurora* to *T. fissus* Zones; France, *Paradoxides* beds; Canada (Newfoundland), *P. davidis* Zone; Turkestan Mountain Range, Kazakhstan (Tyan-Shan Range), Amgaian; Russia (southeastern Siberia), *T. fissus* to *L. laevigata* Zones; China (Zhejiang), *P. triangularis* to *L. armata* Zones, (Hunan, Guizhou, Qinghai), upper Middle Cambrian; Australia (Queensland, Tasmania), *P. atavus* to *L. laevigata* Zones. —FIG. 230, 1a, b. *\*D. planicauda* (ANGELIN), Middle Cambrian (*Goniagnostus nathorsti* Zone), Sweden (Andrarum, Skåne); *a*, topotype, cephalon, SGU 4870,  $\times 9$ ; *b*, topotype, pygidium, SGU 4871,  $\times 9$  (new).

**Acadagnostus** KOBAYASHI, 1939a, p. 113 [*\*Agnostus acadicus* HARTT in DAWSON, 1868, p. 655; OD (*fide* ŐPIK, 1979, p. 62)] [= *Asagnostus* LAURIE, 1990, p. 318 (type, *Agnostus fallax* LINNARSSON, 1869, p. 81, pl. 2, fig. 54–55)]. Nonscrobiculate to weakly scrobiculate; surface smooth. Cephalon with deliquiate border furrow; median preglabellar furrow absent; glabella with semicircular to transversely quadrate anterior lobe; posterior glabellar lobe with well-developed F2 furrows and with glabellar node level with or immediately behind F2 furrows. Pygidium subquadrate, bispinose; occasionally with incipient or restricted zonation; border furrow deliquiate; median postaxial furrow commonly present; axis never reaching border furrow, bullet-shaped, commonly unconstricted; F1 and F2 absent to very weakly developed; axial node large; secondary axial node commonly developed on posterior lobe. *Middle Cambrian*: Norway; Turkey; Sweden, *T. (T.) gibbus* to *A. atavus* Zones; Canada (Newfoundland, New Brunswick), *P. davidis* to *P. forchhammeri* Zones; Australia (Queensland), *P. punctuosus* to *G. nathorsti* Zones; USA (Nevada, Utah), *Bolaspidella contracta* Subzone, *P. praecurrens* to early *A. atavus* Zones, (New York), *Bathyriscus–Elnathina* Zone,



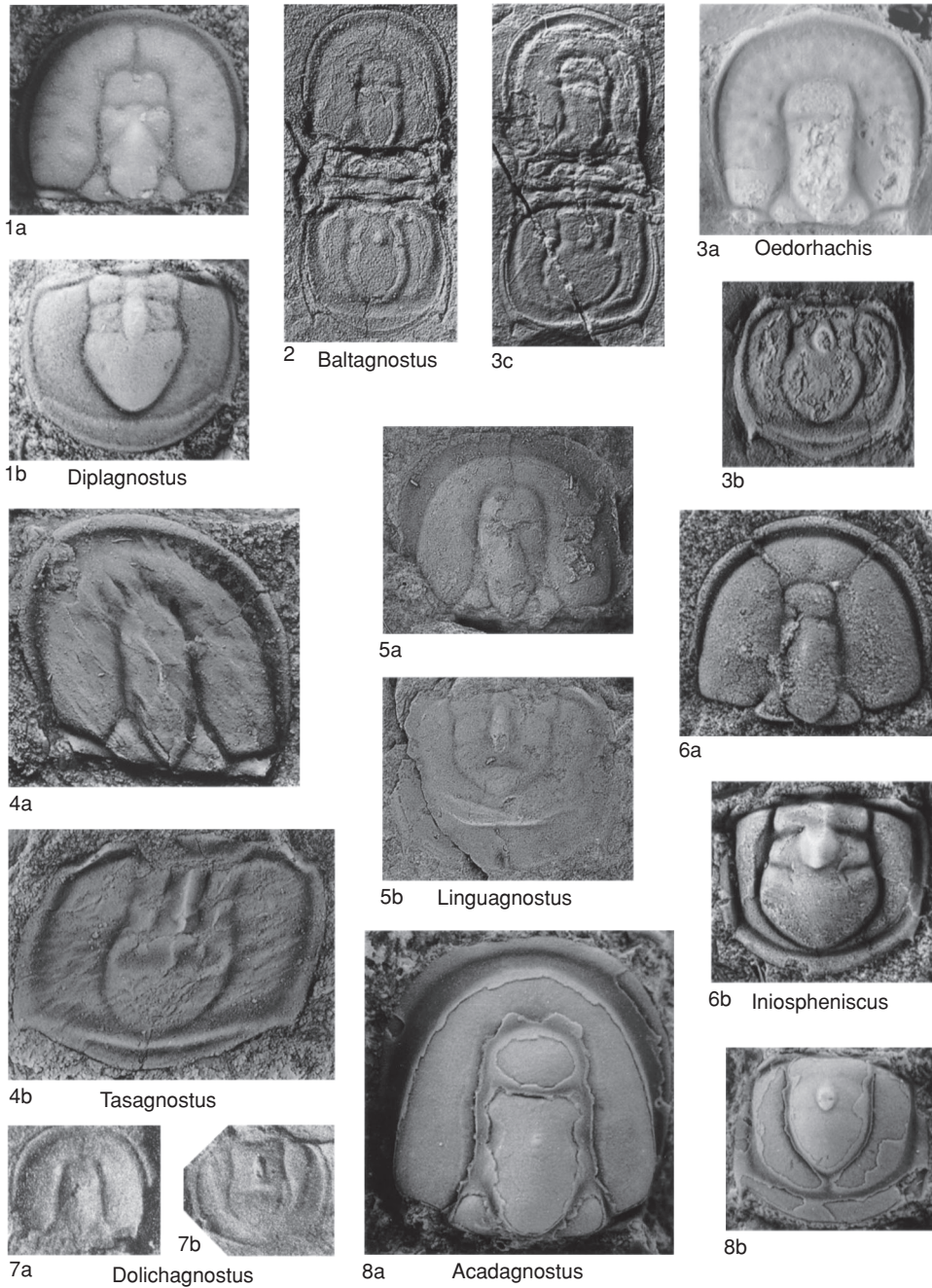


FIG. 230. Diplagnostidae (p. 362–365)

(Texas), *Bolaspidella* Zone, (South Carolina), zone uncertain; Russia (Siberia), *T. fissus*, *Pseudan-  
omocarina*, *A. henrici* Zones, (Kirgizia), Amgaian-  
Mayaian; China (Hunan, Guizhou), *D. sp. cf. D.*

*richthofeni* to lower *P. jimaensis*-*C. tuma* Zones,  
(Xinjiang), *G. nathorsti* or *P. punctuosus* Zone.—  
FIG. 230, 8a, b. \**A. fallax* (LINNARSSON), Middle  
Cambrian (*Triplagnostus gibbus* Zone), Sweden

- (Djupadalen, Västergötland); *a*, cephalon, SGU 4717, ×9; *b*, lectotype, pygidium, SGU 4716, ×9 (Laurie, 1990, fig. 1b,d).
- Baltagnostus** LOCHMAN in LOCHMAN & DUNCAN, 1944, p. 132 [\**Proagnostus? centerensis* RESSER, 1938, p. 48; OD; holotype (RESSER, 1938, pl. 10, fig. 18), 94868, USNM, Washington, D.C.]. Nonscrobiculate, with deliquiate border furrows; unconstricted acrolobes; median preglabellar furrow absent. Glabella with subquadrate to subpentagonal anterior lobe; F3 clear; posterior lobe with weak F2 furrows; glabellar culmination narrowly rounded or angular; glabellar node about level with F2 furrows. Pygidium bispinose; axis long, reaching border furrow; F1, F2 effaced; posterior lobe semiovate, broadly rounded posteriorly; pygidial collar arcuate, short (tr.), indistinct. *Middle Cambrian*: USA (Alabama, Montana, Nevada, New York, Tennessee, Texas, Utah), *Bolaspidea* Zone; Canada (Quebec), China (Liaoning), upper Middle Cambrian; southern Korea, *Tonkinella* Zone; Australia (Queensland), *E. opimus* to *D. notalibrae* Zones.—FIG. 230.2. \**B. centerensis* (RESSER), upper Middle Cambrian (Marjuman, zone uncertain), USA (Moshat, Alabama); holotype, exoskeleton, USNM 94868, ×8 (new).
- Dolichagnostus** POKROVSKAYA, 1958, p. 34 [\**D. admirabilis*; OD; holotype (POKROVSKAYA, 1958, pl. 3, fig. 1), 3534/3, GIN, Moscow]. Nonscrobiculate, with broad, deliquiate border furrows; pygidial acrolobe commonly constricted; median preglabellar furrow commonly well developed. Glabella with trapeziform anterior lobe; F3 weak; posterior lobe with F2 weak or absent; glabellar culmination narrowly rounded or angular; glabellar node about level with F2 furrows. Pygidium bispinose and angulate posteriorly; axis long, extending to pygidial collar, broadly rounded posteriorly; F1, F2 effaced; posterior lobe long, with transverse furrow in anterior half; pygidial collar sinuous, extending on to acrolobe. *upper Middle Cambrian*: Russia (Siberia), *L. laevigata* Zone; Australia (Queensland), *L. laevigata* Zone.—FIG. 230.7a,b. \**D. admirabilis*, Middle Cambrian (Mayaian, *Anomocarioides limbataeformis* Zone), Russia (Yakutia); *a*, holotype, cephalon, GIN 3534/3a, ×3; *b*, pygidium, GIN 3534/3b, ×3 (Pokrovskaya, 1958, pl. 3, fig. 1a, 3).
- ?**Iniospheniscus** ÖPIK, 1979, p. 50 [\**I. talis*; OD; holotype (ÖPIK, 1979, pl. 9, fig. 1), CPC 14021, AGSO, Canberra]. Nonscrobiculate, with subdeliquiate to deliquiate border furrows; pygidial border commonly incipiently zonate; acrolobes unconstricted; median preglabellar furrow absent. Glabella with subrectangular anterior lobe; F3 well developed; posterior lobe with weak F2 furrows; glabellar node about level with F2 furrows. Pygidium bispinose; axis long, reaching border furrow, expanding rearwards; F1, F2 impressed laterally; posterior lobe very broad, semiovate, rounded posteriorly, lacking transverse depression; pygidial collar absent or very short (tr.), indistinct. *Middle Cambrian*: Australia (Queensland), *A. atavus* to *P. punctuosus* Zones; China (Shandong, Liaoning), *Amphoton* Zone.—FIG. 230.6a,b. \**I. talis*, Middle Cambrian (Undillan, *Ptychagnostus punctuosus* Zone), Australia (Camooweal district, western Queensland); *a*, cephalon, CPC 14026, ×8; *b*, holotype, pygidium, CPC 14021, ×13 (new).
- Linguagnostus** KOBAYASHI, 1939a, p. 142 [\**Aagnostus kjerulfi* BRÖGGER, 1878, p. 65; OD; lectotype (SD WESTERGÅRD, 1946, p. 124, pl. 8, fig. 32), 28684, PMO, Oslo]. Nonscrobiculate; deliquiate border furrows; zonate pygidial border; pygidial acrolobe commonly constricted; median preglabellar furrow absent. Glabella with trapeziform to subrectangular anterior lobe, commonly with median sulcus; F3 clearly impressed; F2 weakly developed or absent; glabellar culmination narrowly rounded or angular; glabellar node about level with F2 furrows. Pygidium bispinose or trispinose, commonly with postaxial notch on margin; axis short, broadly ogival, unconstricted or slightly constricted across M2; F1 effaced to clearly impressed laterally; F2 effaced to clearly impressed; posterior lobe short, broad, subtriangular, with transverse depression at about midlength. Pygidial collar sinuous, extending onto acrolobe. *upper Middle Cambrian*: Sweden, England, *P. punctuosus* Zone; Denmark, *P. davidis* Zone; Norway, *P. forchhammeri* Zone; Wales, *P. paradoxissimus* Zone; Russia (Siberia, Tuva), Turkestan Mountain Range, Tadzhikistan; Kazakhstan, *L. laevigata*, *Anopolenus*, *L. allachjunensis* Zones; China (Hunan, Guizhou, Qinghai, Zhejiang), *L. armata* Zone; Australia (Queensland, Northern Territory), *T. gibbus* to *L. laevigata* Zones.—FIG. 230.5a,b. \**L. kjerulfi* (BRÖGGER), Middle Cambrian (*Paradoxides forchhammeri* beds), Norway (Krekling, Oslo district); *a*, paralectotype, cephalon, PMO 28682, ×5.5; *b*, lectotype, pygidium, PMO 28684, ×5.5 (new).
- Oedorhachis** RESSER, 1938, p. 50 [\**O. typicalis*; OD; holotype (RESSER, 1938, pl. 10, fig. 16, 22, 28), 94866, USNM, Washington, D.C.]. Similar to *Tasagnostus* but with incipient zonation only and lacking transverse furrow in posterior pygidial axial lobe. *upper Middle Cambrian–lower Upper Cambrian*: northern Greenland; ?Sweden; Australia (Queensland), *G. nathorsti* to *A. quasivespa* Zones; Argentina, *Bolaspidea* Zone; Canada (Northwest Territories), *Cedaria minor* Zone; USA (Alabama, Tennessee), *G. stolidotus* Zone; China (Liaoning, Qinghai), *Blackwelderia* Zone.—FIG. 230.3a–c. \**O. typicalis*; *a,b*, upper Middle Cambrian (*Lejopyge laevigata* Zone), northern Greenland (Gustav Holm Dal, Peary Land); *a*, cephalon, MGUH 17.115, ×8, *b*, pygidium, MGUH 17.118, ×8 (Robison, 1988, fig. 4, 8.1); *c*, Late Cambrian (Dresbachian, *Crepicephalus* Zone), USA (Cedar Bluff, Alabama), holotype, exoskeleton, USNM 94866, ×6 (new).
- Tasagnostus** JAGO, 1976, p. 161 [\**T. debori*; OD; holotype (JAGO, 1976, pl. 26, fig. 1), 86869e, UTGD, Hobart]. Nonscrobiculate, with broad, deliquiate border furrows; zonate pygidial border; acrolobes unconstricted; median preglabellar furrow weak. Glabella with trapeziform to subpentagonal anterior

lobe; F3 weak; posterior lobe with F2 weak or absent; glabellar culmination acutely angular; glabellar node about level with F2 furrows. Pygidium bispinose; axis long, constricted across M2; F1, F2 effaced; posterior lobe slightly bulbous, broadly rounded posteriorly, extending to pygidial collar, with well-developed transverse furrow in anterior half; pygidial collar extending across entire posterior margin between pygidial spines, but not extending onto acrolobe. *upper Middle Cambrian*: Australia (Tasmania), *L. laevigata* to ?*D. torosa* or *A. janitrix* Zones.—FIG. 230, 4a, b. \**T. debori*, Middle Cambrian (Boomerangian, *Lejopyge laevigata* Zone), Australia (Christmas Hills, northern Tasmania); a, paratype, cephalon, UTGD 86877e,  $\times 7.7$ ; b, holotype, pygidium, UTGD 86869e,  $\times 7.4$  (Jago, 1976, pl. 26, fig. 1, 9).

### Subfamily OIDALAGNOSTINAE

Öpik, 1967

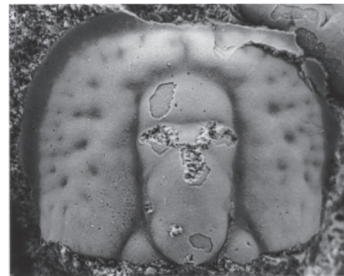
[Oidalagnostinae ÖPIK, 1967, p. 134]

En grande tenue; scrobiculate; zonate pygidial border; commonly constricted pygidial acrolobe; median preglabellar furrow usually weak. Glabella with trapeziform to subrectangular anterior lobe; F3 well developed, straight; posterior lobe with variably developed F2; glabellar culmination narrowly rounded; glabellar node about level with F2 furrows. Pygidium trispinose; axis long, extending to pygidial collar or posteriorly effaced; F1 and F2 variably impressed; posteroaxis variably quadrate with deep, transverse depression in anterior half defining a third anterior annulation and posterior portion subrectangular, tumid or effaced. *upper Middle Cambrian–lower Upper Cambrian*.

**Oidalagnostus** WESTERGÅRD, 1946, p. 65 [\**O. trispinifer*; OD; holotype (WESTERGÅRD, 1946, pl. 9, fig. 6), 4879, SGU, Uppsala] [= *Ovalagnostus* LU in LU, ZHU, & others, 1974, p. 81 (type, *Oidalagnostus changi* LU in WANG, 1964, p. 30, pl. 3, fig. 11)]. Median preglabellar furrow weakly developed. Pygidial axis long, extending to pygidial collar; posteroaxis with tumid, subrectangular posterior portion; posterior portion commonly separated from pleural field by paired bosses and weak accessory furrows; pygidial collar arcuate, with median depression. *uppermost Middle Cambrian–lower Upper Cambrian*: northern Greenland; Sweden, *L. laevigata* Zone; Australia (Queensland, Tasmania), *L. laevigata*, *C. quasivespa*, *G. stolidotus* Zones; Canada (Newfoundland), *A. pisiformis* Zone; Russia (northwestern Siberia), *Pedinocephalus* or *Toxotis* Zone, (southern Siberia), *L. laevigata* Zone; China

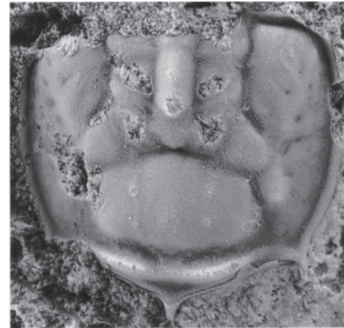


1  
Cristagnostus



2a

Oidalagnostus



2b

FIG. 231. Diplagnostidae (p. 365–366)

(Zhejiang), *L. armata* to *L. sinensis* Zones, (Hunan), *L. laevigata* Zone.—FIG. 231, 2a, b. \**O. trispinifer*, Middle Cambrian (*Lejopyge laevigata* Zone), Sweden (Gudhem, Västergötland); a, cephalon, SGU 4878,  $\times 6$ ; b, holotype, pygidium, SGU 4879,  $\times 6$  (new).

**Cristagnostus** RUSHTON, 1978, p. 262 [\**C. papilio*; OD; holotype (RUSHTON, 1978, pl. 26, fig. 5), BDA 1320–1321, BGS, London]. Very weakly scrobiculate; median preglabellar furrow variably developed. Pygidial axis with F1 well developed; F2 weak; posteroaxis with only anterior portion



defined by axial furrow and transverse depression; axial furrow effaced behind transverse depression; pygidial collar sinuous, extending on to acrolobe. *uppermost Middle Cambrian–lowest Upper Cambrian*: Russia (southwestern Siberia); England, Canada (Newfoundland), *A. pisiformis* Zone; Russia (northern Siberia), ?uppermost Middle Cambrian.—FIG. 231, *l*. \**C. papilio*, Upper Cambrian (*Agnostus pisiformis* Zone), central England (Merevale #3 borehole, Nuneaton); holotype, exoskeleton, BGS BDA 1320,  $\times 9.3$  (Rushton, 1978, pl. 25, fig. 5).

### Subfamily PSEUDAGNOSTINAE Whitehouse, 1936

[Pseudagnostinae WHITEHOUSE, 1936, p. 97]

En grande tenue to largely effaced; commonly scrobiculate; usually with wide borders; pygidial border usually simpli-marginate; pygidial acrolobe commonly constricted; median preglabellar furrow well developed to absent. Glabella with anterior lobe variable in shape; F3 variably impressed, straight to V-shaped, rarely bent forward; posterior lobe with glabellar node from a short distance behind F2 to near F3. Pygidium bispinose, rarely trispinose; axis long, deuterolobate; F1 usually effaced or weak; deuterolobe often effaced, with terminal node. *Upper Cambrian–Lower Ordovician*.

**Pseudagnostus** JAEKEL, 1909, p. 400 [\**Agnostus cyclopyge* TULLBERG, 1880, p. 26; OD; topotypes (WESTERGÅRD, 1922, pl. 1, fig. 7–8), 3066t, 3067t, LO, Lund] [= *Plethagnostus* CLARK, 1923b, p. 124 (type, *P. gyps*; OD)]. Variably convex, spectaculate pseudagnostines; en grande tenue to partly effaced; generally with wide borders; variably deliquiate border furrows; long (sag.), anteriorly rounded or pointed anterior glabellar lobe; simple, terminally angulate posterior lobe; prominent, triangular basal lobes; lateral lobes not well developed; pygidium weakly to strongly deuterolobate, occasionally trispinose. *Upper Cambrian*.

**P. (Pseudagnostus)**. Generally with deliquiate border furrows; median preglabellar furrow usually present; pygidium with single pair of marginal spines in advance of rear of deuterolobe. *Upper Cambrian*: Argentina; Antarctica; Vietnam; Afghanistan; Turkey; Spain; Sweden, England, *O. cataractes* to *L. raphidophorus* Zones; USA (Alaska, Montana, Wyoming, Nevada, Utah, Idaho, Texas, Oklahoma, Tennessee, Virginia, Maryland, Wisconsin), Canada (British Columbia, Alberta, Northwest Territories, Quebec), *Cedaria* to *Ptychaspis* or *Prosaukia* Zones, (Newfoundland), Sunwaptan; Australia (Queensland, Tasmania), *E. eretes* to *P. tertia* or *P. quarta*

Zones; South Korea, *Eochuangia* Zone; Kazakhstan, Russia (northwestern Siberia, Yakutia), *A. pisiformis* to *A. scrobicularis* Zones; China (Zhejiang), *G. stolidotus* to *L. punctatus* Zones.—FIG. 232, *1a, b*. \**P. (P.) cyclopyge* (TULLBERG), Upper Cambrian (*Parabolina spinulosa* with *Orusia lenticularis* Zone), Sweden (Andrarum, Skåne); *a*, topotype, cephalon, GMI LO 3066t,  $\times 7$ ; *b*, topotype, pygidium, GMI LO 3067t,  $\times 7$  (Shergold, 1977, pl. 15, fig. 1–2).

**P. (Pseudagnostina)** PALMER, 1962a, p. 21 [\**Pseudagnostina contracta*; OD; holotype (PALMER, 1962a, pl. 2, fig. 23), 143151, USNM, Washington, D.C.]. Effaced or partly effaced; strongly spectaculate; with subdeliquiate border furrows; lacking median preglabellar furrow; unconstricted acrolobes; clearly incised, transverse anterior glabellar furrow; pygidium weakly deuterolobate; F1, F2 furrows effaced; posterolateral spines generally close to rear of deuterolobe. *Upper Cambrian*: USA (Alabama, Nevada, Virginia), *Cedaria* to *Crepicephalus* Zones; Canada (Northwest Territories), *Cedaria minor* to *C. brevifrons* Zones; Australia (Queensland), *G. stolidotus* Zone; Kazakhstan, *G. stolidotus* Zone; South Korea, *Drepanura* to *Stephanocare* Zone; China (Hunan, Liaoning, Shandong), Gushanian.—FIG. 232, *4a, b*. \**P. (P.) contracta* (PALMER), Upper Cambrian (Dresbachian, *Cedaria* Zone), USA (Woodstock, Alabama); *a*, paratype, cephalon, USNM 143150,  $\times 16$ ; *b*, holotype, pygidium, USNM 143151,  $\times 16$  (Shergold, 1977, pl. 15, fig. 11–12).

**P. (Sulcagnostus)** KOBAYASHI, 1937b, p. 451 [\**Agnostus securiger* LAKE, 1906, p. 20; OD; holotype (LAKE, 1906, pl. 2, fig. 11), 57650, BGS, London]. En grande tenue, with deliquiate border furrows and strongly constricted acrolobes, possessing median preglabellar furrow; pygidium trispinose. *Upper Cambrian*: England, *O. cataractes* Subzone; Canada (Northwest Territories), *Olenaspella regularis* Zone; China (Zhejiang), *L. punctatus* Zone, (?Xinjiang, ?Hunan), zone uncertain; Australia (Tasmania), post-Idamean.—FIG. 232, *5*. \**P. (S.) securiger* (LAKE), Upper Cambrian (*Olenus* Zone), England (Nuneaton, Warwickshire); holotype, exoskeleton, BGS 57650,  $\times 6$  (Shergold, 1977, pl. 15, fig. 13).

**Agnostotes** ÖPIK, 1963, p. 43 [\**A. inconstans*; OD; holotype (ÖPIK, 1963, pl. 3, fig. 11), CPC 4272, AGSO, Canberra]. Large; variably en grande tenue; variably scrobiculate, with nondeliquiate border furrows, narrow borders, and unconstricted acrolobes; median preglabellar furrow well developed. Glabella with broad anterior lobe; F3 bent forward; posterior lobe with well-developed, forwardly directed F2 furrows and broadly rounded glabellar culmination; glabellar node located level with or slightly in front of F2 furrows. Pygidium bispinose; deuterolobe subcircular to subpyriform, with well-developed terminal node; notular lines usually developed. *Upper Cambrian*.

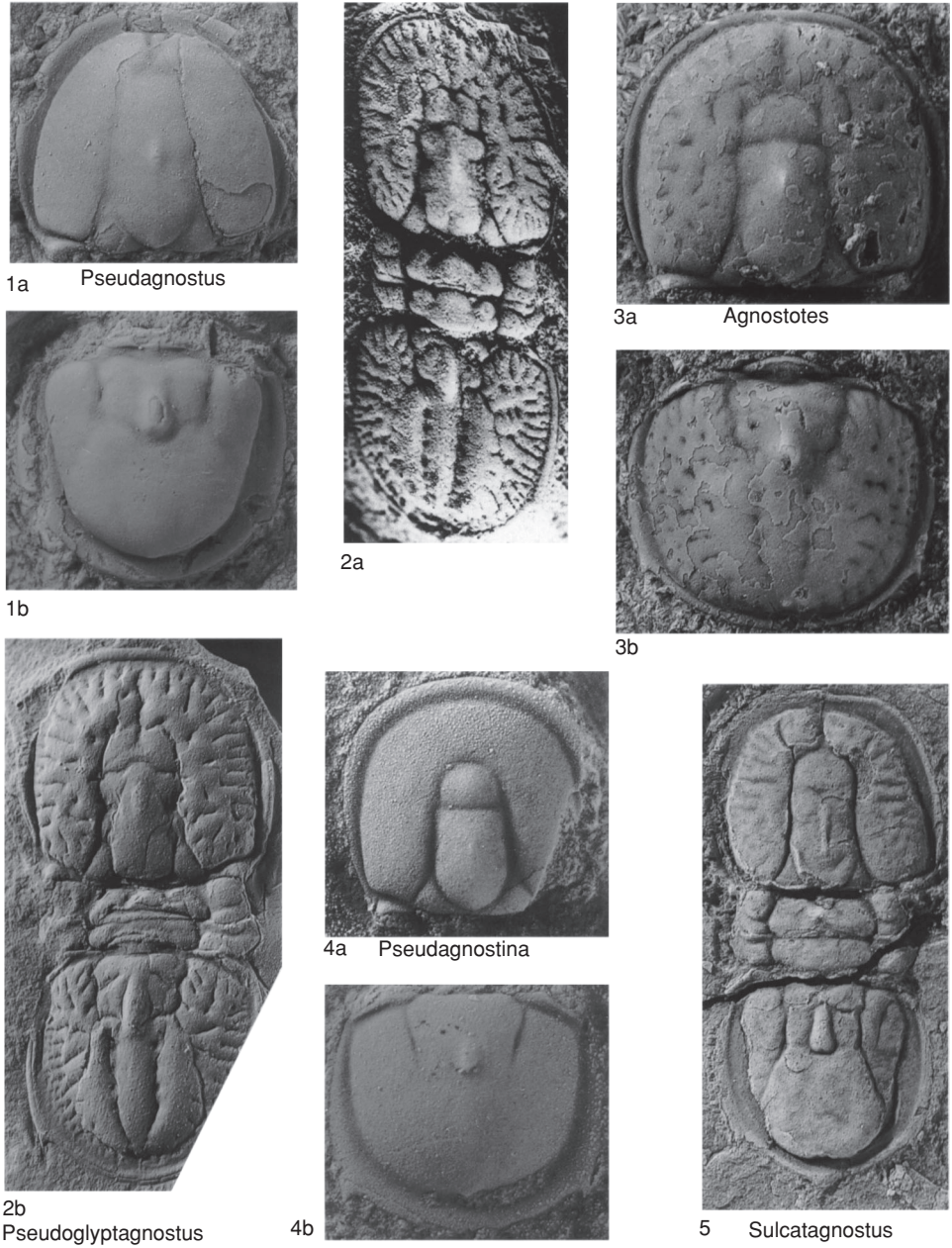


FIG. 232. Diplagnostidae (p. 366–368)

A. (*Agnostotes*). Scrobiculate; axial furrows weakly impressed. Glabella with anterior lobe broad (tr.) and subpentagonal; F3 slightly convex forward; posterior lobe with clearly developed F2; glabellar node level with or slightly in front of F2 furrows. Pygidial axis with weakly impressed

accessory furrows; axial node extending slightly onto deuterolobe; deuterolobe subcircular with notular lines erratically developed. *Upper Cambrian*: China (Qinghai); Australia (Queensland), *I. tropica* Zone.—FIG. 232,3a,b. \*A. (*A.*) *inconstans*, Upper Cambrian (post-Idamean,

- Irvingella tropica* Zone), Australia (Burke River area, western Queensland); *a*, paratype, cephalon, CPC 4274,  $\times 8.5$  (new); *b*, holotype, pygidium, CPC 4272,  $\times 7$  (new).
- A. (*Pseudoglyptagnostus*)** LU in WANG, 1964, p. 32 [*\*Pseudoglyptagnostus clavatus*; OD; holotype (LU in WANG, 1964, pl. 4, fig. 7), 23719, NIGP, Nanjing] [= *Glyptagnostotus* LAZARENKO, 1966, p. 42 (type, *G. elegans*; OD)]. Both shields strongly scrobiculate. Glabella with anterior lobe broad and trapeziform, with variably developed median sulcus; F3 bent strongly forward; posterior lobe with well-developed F2 and F1; lateral portions of M2 commonly separated from midmost glabella by longitudinal (exsag.) furrows; glabellar node located in front of F2 furrow. Pygidial axis with F1 impressed laterally and F2 clearly impressed; axial node extending well onto deuterolobe; accessory furrows clearly impressed; deuterolobe subpyriform. *Upper Cambrian*: China (Zhejiang), *P. clavatus* to *S. kiangshanensis* Zone, (Hunan), zone uncertain; Kazakhstan, *P. curtare* to *Irvingella* or *C. felix* Zones; Canada (Northwest Territories), *Proceratopyge rectispinata* Zone; USA (Nevada), *Elvinia* Zone.—FIG. 232,2a. *\*A. (P.) clavatus* (LU), Upper Cambrian (Changshanian), China (Hunan); holotype, exoskeleton, NIGP 23719,  $\times 7$  (Wang, 1964, pl. 4, fig. 7).—FIG. 232,2b. *A. (P.) elegans* (LAZARENKO), Upper Cambrian (?Sakian, *Irvingella* or *Cedarellus felix* Zone), Russia (Kyutyungda depression, Kharaulakh Mountain Range, Yakutia); holotype, exoskeleton, CNIGR 24/8907,  $\times 5$  (Lazarenko, 1966, pl. 2, fig. 1).
- Denagnostus** JAGO, 1987, p. 213 [*\*D. corbetti*; OD; holotype (JAGO, 1987, pl. 24, fig. 13), 88463, UTGD, Hobart]. Subvoid or subcircular cephalon and pygidium, almost effaced, with nondeliquiate border furrows; wide anterior cephalic border narrows posteriorly and disappears at about cephalic midlength; glabella faintly outlined, spectaculate; effaced median preglabellar furrow. Pygidium with very weakly outlined axis, acrolobe slightly constricted, marginal spines small, well in advance of rear of deuterolobe; posterior pygidial border faintly zonate. *lower Upper Cambrian*: Australia (Tasmania), Idamean.—FIG. 233,1a,b. *\*D. corbetti*, Upper Cambrian (Idamean), Australia (Denison Range, southwestern Tasmania); *a*, holotype, cephalon, UTGD 88463, *Proceratopyge cryptica* Zone,  $\times 9$ ; *b*, paratype, pygidium, UTGD 88495, *Stigmatia diloma* Zone,  $\times 9$  (Jago, 1987, pl. 24, fig. 13; pl. 25, fig. 2).
- Litagnostus** RASETTI, 1944, p. 235 [*\*L. levisensis*; OD; syntypes (RASETTI, 1944, pl. 36, fig. 5–6), 1103a,b, LU, Quebec]. Cephalon and pygidium totally effaced with exception of narrow borders and pygidial axial node; internal molds typically rhaptagnostoid. *Upper Cambrian–Lower Ordovician (Tremadoc)*: USA (Minnesota, Wisconsin, Texas); Canada (Alberta), *Taenicephalus* Zone to ?*Ellipsocephaloides silvestris* Subzone, (Newfoundland), Sunwaptan, (Quebec); England, upper Tremadoc.—FIG. 233,4a,b. *\*L. levisensis*, Upper Cambrian (Sunwaptan, *Keithia subclavata* fauna of LUDVIGSEN & others, 1989), Canada (Boulder 36, Lévis, Quebec); *a*, syntype, cephalon, LU 1103a,  $\times 5$ ; *b*, syntype, pygidium, LU 1103b,  $\times 5$  (Rasetti, 1944, pl. 36, fig. 5–6).
- Nahannagnostus** PRATT, 1992, p. 35 [*\*Pseudagnostus nganasanicus* ROZOVA, 1964, p. 27; OD; holotype (ROZOVA, 1964, pl. 16, fig. 3), 113/875, CSGM, Novosibirsk]. Cephalon and pygidium strongly convex; median preglabellar furrow well defined; anterior glabellar lobe extremely small; F3 partly effaced; axial glabellar node subcentral or slightly advanced. Pygidium with highly inflated deuterolobe; F1 and F2 mostly effaced; posterolateral spines minute. *Upper Cambrian*: Russia (Siberia), Ayusokkanian; Kazakhstan, *Kormagnostus simplex* Zone; Canada (Northwest Territories, Newfoundland), *Cedaria selwyni* to *Cedaria brevifrons* Zones; USA (Utah, Nevada, Missouri, Texas), *Cedaria* to *Crepicephalus* Zones; Australia (Queensland), *Erediaspis eretes* and *Glyptagnostus stolidotus* Zones; China (Hunan, Zhejiang), *Glyptagnostus stolidotus* Zone.—FIG. 234,1a,b. *\*N. nganasanicus* (ROZOVA), Upper Cambrian (Ayusokkanian, Nganasan Gorizont), Russia (Kulyumbe River, northwestern Siberian Platform); *a*, cephalon, CSGM 113/999,  $\times 10$ ; *b*, holotype, pygidium, CSGM 113/875,  $\times 5$  (Rozova, 1964, pl. 16, fig. 3, 11).
- Neagnostus** KOBAYASHI, 1955, p. 473 [*\*N. aspidoides*; OD; holotype (KOBAYASHI, 1955, pl. 7, fig. 5), 12745, GSC, Ottawa]. Spectaculate; partially effaced to en grande tenue, with generally wide borders and subdeliquiate to deliquiate border furrows; acrolobes weakly constricted; cephalon and pygidium frequently subquadrate. Cephalon with variably developed median preglabellar furrow; generally small, rhomboid anterior lobe; variably defined, V-shaped F3; chevronate F2 behind anterolateral lobes of posterior glabellar lobe; anterolateral lobes close together or meeting sagittally. Pygidium with third annulation in anterior part of axis; weakly to strongly deuterolobate, with retral posterolateral spines. *Upper Cambrian–Lower Ordovician*.
- N. (Neagnostus)** [= *Pseudorhaptagnostus* LERMONTOVA, 1940, p. 126 (type, *P. simplex* LERMONTOVA, 1951a, p. 12, pl. 2, fig. 11–17); *Euplethagnostus* LERMONTOVA, 1940, p. 126 (type, *E. subangulatus*; OD); *Hyperagnostus* KOBAYASHI, 1955, p. 475 (type, *H. binodosus*; OD); *Tarayagnostus* SUAREZ-SORUCO, 1975, p. 133 (type, *T. corrugatus*; OD); *Calagnostus* J. ZHANG & WANG, 1985, p. 332 (type, *C. mageshuangensis*; OD)]. En grande tenue to partly effaced; cephalon nonscrobiculate; glabella proportionately long; median preglabellar furrow variably developed; variably deuterolobate. *Upper Cambrian–Lower Ordovician*: Canada (British Columbia, Newfoundland, Quebec), *Elvinia* to *Missisquoia* Zones; USA (Alaska, Vermont, Arkansas), Franconian–Trempealeuan; Mexico,



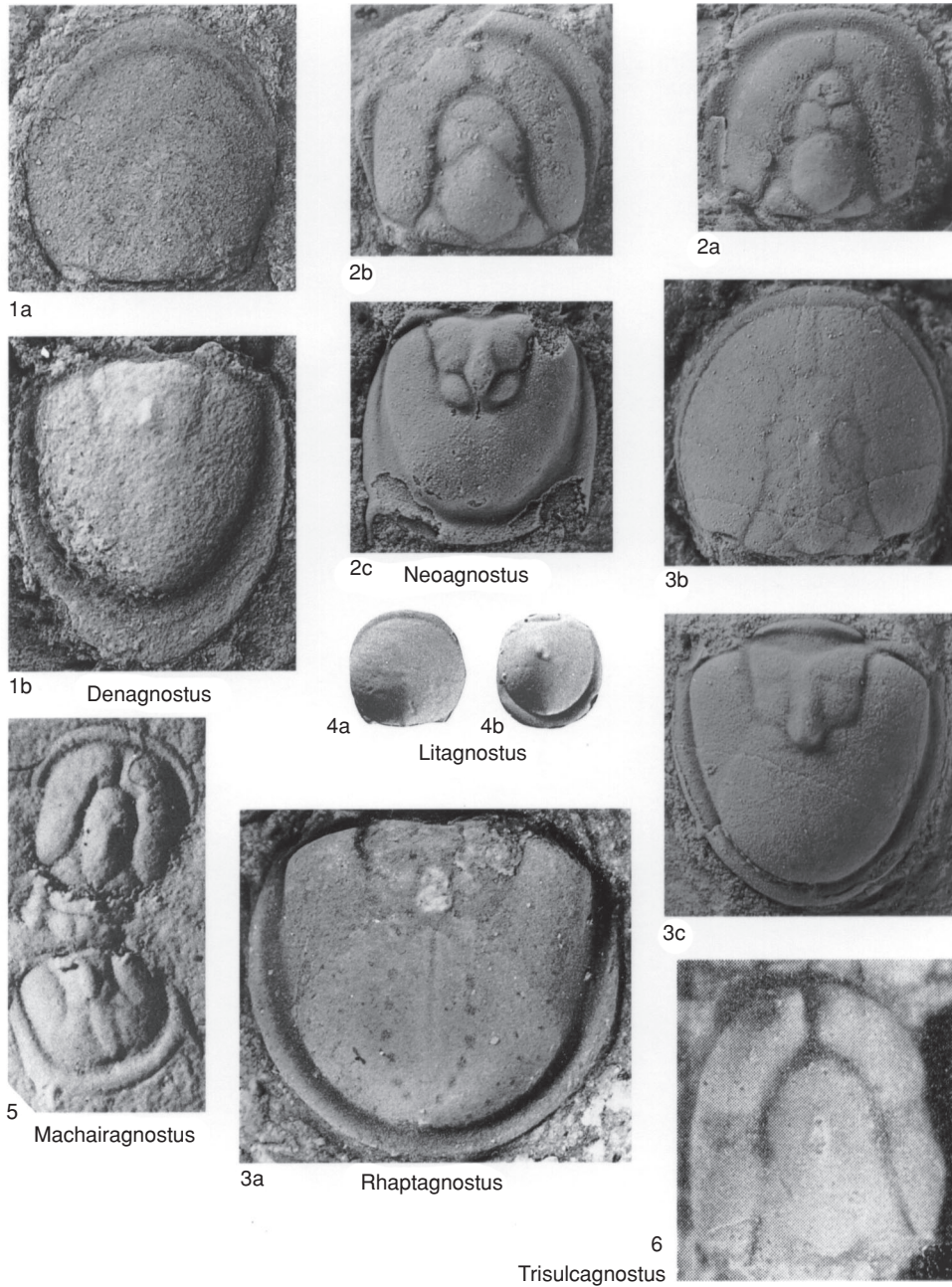


FIG. 233. Diplagnostidae (p. 368–371)

?*Cordylodus proavus* Zone; Australia (Queensland, Tasmania), *W. iota* or *R. apsis* to *N. quasibilobus* or *S. nomas* Zones; China (Anhui, Guizhou, Shanxi, Zhejiang, Xinjiang, Yunnan), *L. punctatus* to *M. perpetis* Zones, (Shandong),

*Kaolishania* Zone, (Hunan), Tremadoc; South Korea, *Kaolishania* Zone; Kazakhstan (Altay-Sayan), Russia (Kuznetsk Alatau, Yakutia), *Irvingella* to *M. mutabilis* Zones; Wales, Tremadoc; ?Argentina, lower Tremadoc; Bolivia,

*Neoparabolina argentina* Zone.—FIG. 233,2a.  
\**N. (N.) aspidoides*, ?Lower Ordovician (“*Symphysurina* fauna”), Canada (Harrogate, British Columbia); holotype, cephalon, GSC 12745,  $\times 7$  (Shergold, 1977, pl. 16, fig. 6).—FIG. 233,2b,c. *N. (N.) bilobus* (SHAW), uppermost Cambrian (*Missisquoia* Zone), USA (Highgate Falls, Vermont); *b*, paratype, cephalon, USNM 124467,  $\times 16$ ; *c*, holotype, pygidium, USNM 124468,  $\times 12.5$  (Shergold, 1977, pl. 16, fig. 7–8).

**N. (*Machairagnostus*)** HARRINGTON & LEANZA, 1957, p. 64 [\**Machairagnostus tmetus*; OD; holotype (HARRINGTON & LEANZA, 1957, fig. 7.4), 1297, BAF CB, Buenos Aires]. En grande tenue but with partially effaced glabellar furrows; cephalon scrobiculate, possessing median preglabellar furrow and proportionately short glabella; pygidium nonscrobiculate, weakly deuterolobate, preserving intranotular axis. *Uppermost Cambrian*: Argentina, *Neoparabolina argentina* Zone; Kazakhstan, *E. scrobicularis* to *P. asiatica* Zones.—FIG. 233,5. \**N. (M.) tmetus* (HARRINGTON & LEANZA), uppermost Cambrian (*N. argentina* Zone), Argentina (Iruya, Salta); holotype, exoskeleton, BAF CB 1297,  $\times 11.5$  (Harrington & Leanza, 1957, fig. 7.4).

**Oxyagnostus** ÖPIK, 1967, p. 159 [\**O. apicula*; OD; holotype (ÖPIK, 1967, pl. 63, fig. 6), CPC 5916, AGSO, Canberra]. Both cephalon and pygidium with constricted acrolobes, relatively narrow borders, and deliquiate border furrows. Cephalon lacking median preglabellar furrow; glabellar culmination angular; glabellar node advanced. Pygidium with axis constricted at M2, and long, subpentagonal, laterally expanded posterior lobe; deuterolobe not obvious externally; posterolateral spines slightly in advance of terminal axial node. *Upper Cambrian*: Australia (Queensland), *G. stolidotus* Zone; USA (Alabama), *Crepicephalus* Zone.—FIG. 234,2a,b. \**O. apicula*, Upper Cambrian (*Mindyallan, Glyptagnostus stolidotus* Zone), Australia (Boulia district, western Queensland); *a*, paratype, cephalon, CPC 5917,  $\times 8$ ; *b*, holotype, pygidium, CPC 5916,  $\times 8$  (new).

**Rhaptagnostus** WHITEHOUSE, 1936, p. 97 [\**Agnostus cyclopygeformis* Y. SUN, 1924, p. 26; OD; lectotype (Y. SUN, 1924, pl. 2, fig. 1e), 507, NIGP, Nanjing]. Characteristically with subovoid to subcircular cephalon and pygidium; effaced to partly effaced; with nondeliquiate border furrows. Cephalon papilionate, with effaced median preglabellar furrow. Pygidium variably deuterolobate, with weakly constricted acrolobe; marginal spines well in advance of rear of deuterolobe. *Upper Cambrian*: Australia (Queensland), *W. iota* or *R. apsis* to *N. quasibilobus* or *S. nomas* Zones; China (Anhui, Hebei, Liaoning, Shandong, Yunnan, Qinghai, Xinjiang), *Kaolishania* to *Tsinania* Zones, (Zhejiang), *L. punctatus* Zone, (Guizhou), zone uncertain; North and South Korea, Fengshanian, *Tsinania* to *Eoorthis* Zones; Kazakhstan, *E. scrobicularis* to *T. trisulcus* Zones, Russia (Yakutia),

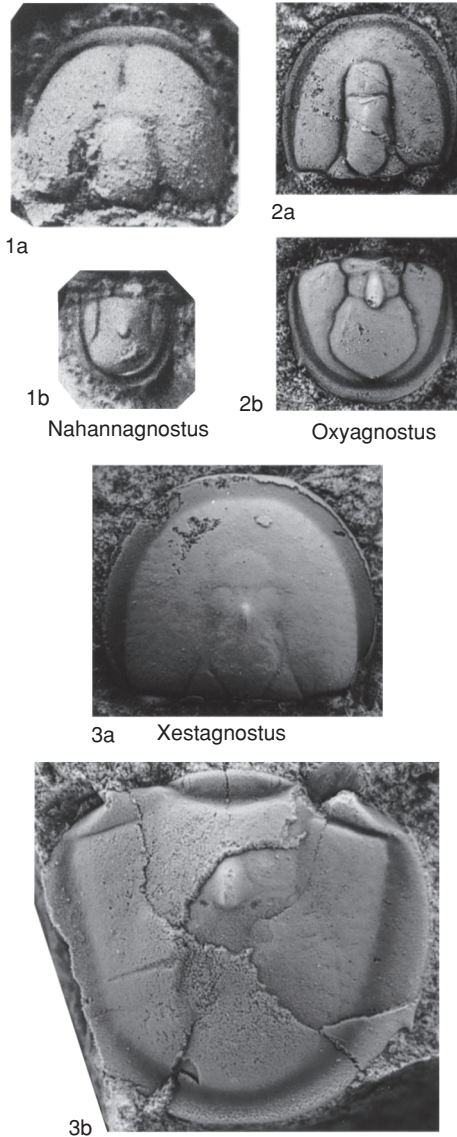


FIG. 234. Diplagnostidae (p. 368–371)

*P. perlata* Zone; Canada (Northwest Territories, Newfoundland), *Yukonaspis* Zone; USA (Alaska, Montana, Nevada, Vermont), *S. pyrene* to *S. serotina* Subzones; Mexico, pre-*Cordylodus proavus* Zone.—FIG. 233,3a. \**R. cyclopygeformis* (SUN), Upper Cambrian (Changshanian, *Kaolishania* Zone), China (Kaolishan, Taian, Shandong); lectotype, pygidium, NIGP 507,  $\times 7$  (X. Sun, 1989, pl. 5, fig. 10).—FIG. 233,3b,c. *R. convergens* (PALMER), Upper Cambrian (Trempealeuan, *Saukiella pyrene* Subzone), USA (Eureka district, Nevada); *b*,

paratype, cephalon, USNM 123563,  $\times 10$ ; *c*, holotype, pygidium, USNM 123562,  $\times 9.5$  (Shergold, 1977).

**Trisulcagnostus** ERGALIEV, 1980, p. 116 [\**T. trisulcus*; OD; holotype (ERGALIEV, 1980, pl. 18, fig. 13), 1950/289, GMAN, Alma-Ata] [= *Pseudagnostus* (*Tririmagnostus*) QIU, 1983, p. 40 (type, *P. (T.) anhuiensis*; OD)]. Like *Rhaptagnostus*, but with narrow borders and nondeliquate border furrows, well-defined median preglabellar furrow, and additionally a pair of transverse furrows crossing cephalic acrolobe from axial furrow to border furrow at level of anterolateral lobes of posterior glabellar lobe; pointed anterior lobe, papillate; pygidium unknown. *Upper Cambrian*: China (Anhui, Hunan); Kazakhstan, *E. scrobicularis* to *T. trisulcus* Zones.—FIG. 233, 6. \**T. trisulcus* ERGALIEV; *Upper Cambrian* (Batyrbaiian, *Trisulcagnostus trisulcus* Zone), Kazakhstan (Lesser Karatau Mountains); holotype, cephalon, GMAN 1950/289,  $\times 10.2$  (Ergaliev, 1980, pl. 18, fig. 13).

**Xestagnostus** ÖPIK, 1967, p. 161 [\**X. legirupa*; OD; holotype (ÖPIK, 1967, pl. 64, fig. 1), CPC 5922, AGSO, Canberra]. Moderately large; relatively flat; externally effaced. Cephalon lacking median preglabellar furrow; spectaculate; large, triangular basal lobes; glabellar culmination angulate; unstricted acrolobe; scrobiculate on internal mold. Pygidium with constricted acrolobe; internally scrobiculate pleural lobes; rectangular anteroaxis; effaced accessory furrows; weakly deuterolobate, concave articulating facets; fulcral spines; simple articulating device represented by elliptical, depressed plate; advanced posterolateral spines. *Upper Cambrian*: Australia (Queensland), *A. quasivespa* to *G. stolidotus* Zones.—FIG. 234, 3a, b. \**X. legirupa*, *Upper Cambrian* (Mindyallan, *Glyptagnostus stolidotus* Zone), Australia (Glenormiston area, western Queensland); *a*, paratype, cephalon, CPC 5924,  $\times 8$ ; *b*, holotype, pygidium, CPC 5922,  $\times 8$  (new).

### Family CLAVAGNOSTIDAE Howell, 1937

[Clavagnostidae HOWELL, 1937, p. 1164] [= Acanthagnostidae QIAN, 1982, p. 640]

En grande tenue; commonly scrobiculate, with nondeliquate to deliquate border furrow in cephalon and nondeliquate border furrow and commonly zonate border in pygidium; unstricted acrolobes and well-developed cephalic spines. Median preglabellar furrow well developed to absent. Glabella acuminate, rounded, or obtusely angular anteriorly, usually with anterior and posterior lobes fused; F2 absent or weakly developed; glabellar culmination variably rounded, or angular; glabellar node elongate,

located near midlength or in anterior half of glabella; basal lobes of small to moderate size, simple. Pygidium bispinose or trispinose, with long, usually ogival to subtriangular axis; constricted across M2; F1 effaced or clearly impressed, curving forward to articulating furrow to isolate anterolateral lobes; F2 effaced or clearly impressed, strongly deflected by long axial node; posterior axial lobe long, usually ogival, subtriangular or subpyriform, commonly extending to border furrow, with a transverse depression commonly associated with a pair of longitudinal (exsag.) pits at about midlength of lobe. *upper Middle Cambrian–lower Upper Cambrian*.

### Subfamily CLAVAGNOSTINAE Howell, 1937

[Clavagnostinae HOWELL, 1937, p. 1164]

Pygidium simplimarginate; axis with F1 and F2 effaced. *upper Middle Cambrian–lower Upper Cambrian*.

**Clavagnostus** HOWELL, 1937, p. 1164 [\**Agnostus repandus* WESTERGÅRD in HOLM & WESTERGÅRD, 1930, p. 13; OD; holotype (HOLM & WESTERGÅRD, 1930, pl. 4, fig. 11), 3131T, LO, Lund] [= *Tomorbachis* RESSER, 1938, p. 51 (type, *T. spinosa*; OD); *Culipagnostus* RUSCONI, 1952, p. 11 (type, *C. chipiquensis*; OD); *Stigmagnostus* C. POULSEN, 1960, p. 15 (type, ?*Tomagnostus canotensis* RUSCONI, 1951, p. 14, 26, fig. 29); *Acanthagnostus* QIAN, 1982, p. 640 (type, *A. longispinus*; OD); *Clavagnostus* (*Leptagnostus*) LU & LIN, 1989, p. 199 (type, *C. (L.) lanceolatus*; OD)]. Nonscrobiculate; median preglabellar furrow variably developed. Glabellar node elongate, located in anterior half of glabella. Pygidium bispinose or trispinose; posterior lobe commonly reaching border furrow or connected to it by median postaxial furrow, with a broad transverse depression and a pair of longitudinal (exsag.) pits at about lobe midlength. *upper Middle Cambrian–lower Upper Cambrian*: USA (Vermont, Alabama); Argentina; Germany; Sweden, *L. laevigata* Zone; Russia (Bennett Island), *P. forchhammeri* Zone, (southwestern Siberia, Altay Mountains, Salair), *L. laevigata* Zone, (northwestern Siberia), *L. armata* to *M. mirabilis* Zones, (southeastern Siberia), *Solenoparia* Zone; Turkestan Mountain Range, *L. laevigata* Zone; Kazakhstan, *L. armata* to *K. simplex* Zone; Canada (Northwest Territories), *Cedaria minor* Zone; Australia (Tasmania), *L. laevigata* Zone, (Queensland), *E. eretes* to *G. stolidotus* Zones; China (Zhejiang), *L. armata* to *G. stolidotus* Zones, (Shandong), *Drepanura* Zone, (Anhui, Hunan, Qinghai), zone uncertain.—FIG. 235, 2a, b. \**C.*



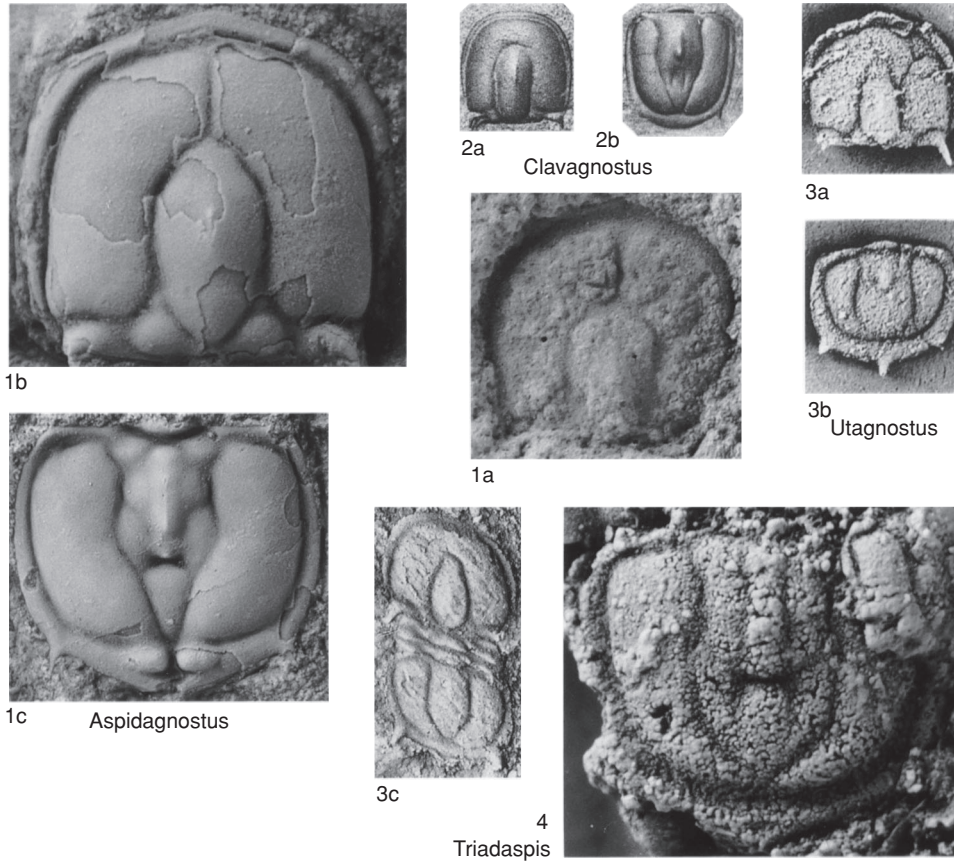


FIG. 235. Clavagnostidae (p. 371–373)

*repandus* (WESTERGÅRD), Middle Cambrian (*Paradoxides forchhammeri* Stage), Sweden (Andrarum, Skåne); *a*, holotype, cephalon, LO 3131T,  $\times 6$ ; *b*, paratype, pygidium, SGU 5461,  $\times 6$ ; (Westergård, 1946, pl. 4, fig. 19–20).

#### Subfamily ASPIDAGNOSTINAE Pokrovskaya, 1960

[Aspidagnostinae POKROVSKAYA, 1960, p. 60]

Pygidium trispinose, zonate; F1 impressed laterally, curving forward to articulating furrow to isolate subtriangular anterolateral lobes; F2 strongly deflected by long axial node extending nearly to midlength of posterior axial lobe. *Upper Cambrian*.

*Aspidagnostus* WHITEHOUSE, 1936, p. 104 [\**A. parmatius*; OD; holotype (WHITEHOUSE, 1936, pl. 9, fig. 5), 3213, UQF, Brisbane] [= *Biragnostus* POKROVSKAYA in KHALFIN, 1960, p. 161 (type, *B.*

*elenae*, *nom. nud.*; OD)]. Commonly scrobiculate, with nondeliquiate to deliquiate border furrow and anteriorly angulate border in cephalon; median preglabellar furrow well developed. Glabella acuminate or narrowly rounded anteriorly; glabellar culmination narrowly rounded to angular; glabellar node elongate, located at or in front of glabellar midlength; basal lobes small to moderate-sized, commonly divided. Pygidium with weak to well-developed, secondary axial node on posterior lobe; nondeliquiate border furrow and zonate border with collar crossed by deep median gap, commonly flanked by a pair of knobs. *lower Upper Cambrian*: Australia (Queensland, Tasmania), *G. stolidotus* to *G. reticulatus* Zones; Kazakhstan, *G. stolidotus* to *G. reticulatus* Zones; England, *A. pisiformis* Zone; Canada (Northwest Territories), *Cedaria brevifrons* to *G. reticulatus* Zones; USA (Nevada), upper *Crepicephalus* Zone, (Alabama, Nevada), *G. reticulatus* Zone; China (Zhejiang), *G. stolidotus* to *G. reticulatus* Zones. *Upper Cambrian*: Russia (Siberia).—FIG. 235.1a. \**A. parmatius*, Upper Cambrian (stage and zone uncertain), Australia

(Glenormiston district, western Queensland); holotype, cephalon, UQF 3213,  $\times 12.7$  (new).—FIG. 235, *1b, c*. *A. iniquilinus*, Upper Cambrian (Mindyallan, *Glyptagnostus stolidotus* Zone), Australia (Glenormiston district, western Queensland); *b*, holotype, cephalon, CPC 5828,  $\times 16$ ; *c*, paratype, pygidium, CPC 5831,  $\times 12$  (new).

*Triadaspis* ÖPIK, 1967, p. 125 [\**T. bigeneris*; OD; holotype (ÖPIK, 1967, pl. 54, fig. 6), CPC 5804, AGSO, Canberra]. Known only from poorly preserved pygidium; with nondeliquiate border furrow; zonate border lacking a gap in the collar. *lower Upper Cambrian*: Australia (Queensland), *E. eretes* Zone.—FIG. 235, *4*. \**T. bigeneris*, Upper Cambrian (Mindyallan, *Erediaspis eretes* Zone), Australia (Glenormiston district, western Queensland); holotype, pygidium, CPC 5804,  $\times 18$  (new).

### Subfamily UNCERTAIN

*Utagnostus* ROBISON, 1964, p. 533 [\**U. trispinulus*; OD; holotype (ROBISON, 1964, pl. 82, fig. 25), 141226, USNM, Washington, D.C.]. Small; en grande tenue; nonscribulate, with nondeliquiate border furrows; narrow cephalic and broad pygidial border; cephalic spines well developed; median preglabellar furrow absent. Glabella with small, low, semioval anterior lobe; F3 weakly impressed, nearly straight; glabellar node about level with F2 furrows; basal lobes very small, simple. Pygidium trispinose; F1 effaced; F2 clearly impressed, strongly deflected by elongate axial node; posterior lobe semioval, broadly rounded posteriorly, of low convexity. *upper Middle Cambrian–lower Upper Cambrian*: USA (Utah), upper *P. punctuosus* to lower *L. laevigata* Zones; Australia (New South Wales), ?*P. punctuosus* Zone.—FIG. 235, *3a, b*. \**U. trispinulus*, upper Middle Cambrian (*Bolaspidella contracta* Subzone), USA (House Range, western Utah); *a*, paratype, cephalon, USNM 141223,  $\times 9$ ; *b*, holotype, pygidium, USNM 141226,  $\times 10$  (Robison, 1964, pl. 82, fig. 21, 25).—FIG. 235, *3c*. *U. neglectus*, upper Middle Cambrian (Boomerangian, *Lejopyge laevigata* Zone), Australia (Christmas Hills, northwestern Tasmania); holotype, exoskeleton, UTGD 86844i,  $\times 11$  (Jago, 1976, pl. 23, fig. 13).

### Family METAGNOSTIDAE Jaekel, 1909

[Metagnostidae JAEKEL, 1909, p. 398] [=Trinodidae HOWELL, 1935b, p. 233; Geragnostidae HOWELL, 1935b, p. 231; Arthrorhachidae RAYMOND, 1913a, p. 139]

Usually en grande tenue; nonscribulate; border furrows nondeliquiate; acrolobes unconstricted; cephalon nonspinose; median preglabellar furrow usually absent. Glabella usually with semioval, semicircular, or subcircular anterior lobe; F3 effaced, variably chevron shaped or concave forward; posterior lobe with F2 furrows absent or chevron

shaped; glabellar culmination broadly rounded or obtusely angular; glabellar node at or near F3 furrow; basal lobes small to moderate-sized, simple. Pygidium with agnostoid articulating device, usually bispinose; axis usually short, not reaching border furrow; F1 impressed laterally, curving forward to articulating furrow, isolating anterolateral lobes; F2 impressed, straight or deflected by axial node; posterior lobe variable in length, trapeziform, subrectangular, semioval, or subtriangular, commonly with terminal node; median postaxial furrow absent. ?*Upper Cambrian–Ordovician*.

*Arthrorhachis* HAWLE & CORDA, 1847, p. 114 [\**Battus tardus* BARRANDE, 1846, p. 35; M; lectotype (BARRANDE, 1852, pl. 49, fig. 1–4) ČD 1812, NMP, Prague] [=Metagnostus JAEKEL, 1909, p. 398 (type, *M. erraticus*; OD); *Girvanagnostus* KOBAYASHI, 1939a, p. 174 (type, *Aagnostus girvanensis* REED, 1903, p. 4, pl. 1, fig. 2–4)]. Glabellar F3 effaced or with straight medial portion, lateral portions curving forward and outward; posterior lobe with F2 furrows weak; glabellar node immediately behind F3 furrow. Pygidial axis very short, tapering rearward; posterior lobe transverse, subrectangular, trapeziform or subtriangular; commonly with weak terminal node. *Ordovician*: Czechoslovakia, upper Caradoc–Ashgill; Poland, England, Ireland, Uzbekistan, Norway, Denmark, Ashgill; Scotland, Caradoc; Kazakhstan, Tremadoc–Ashgill; Argentina, upper Tremadoc; eastern USA, lower middle Ordovician; Turkey, upper Arenig; France, lower Arenig; Sweden, upper Tremadoc–lower Caradoc; Spitsbergen, upper Canadian; China (Shaanxi), upper middle Ordovician, (Jiangsu), Ashgill; Germany, middle Ordovician.—FIG. 236, *2*. \**A. tarda* (BARRANDE), Upper Ordovician (Ashgill, *Tretaspis granulata* to *T. seticornis seticornis* horizons), Czechoslovakia (Libomyšl, Bohemia); lectotype, exoskeleton, NM-ČD 1812,  $\times 10$  (Pek, 1977, pl. 8, fig. 2).

*Anglagnostus* HOWELL, 1935b, p. 233 [\**Aagnostus dux* CALLAWAY, 1877, p. 665; OD; holotype by monotypy (CALLAWAY, 1877, pl. 24, fig. 3), 693, BU, Birmingham]. Type species known from one articulated specimen having short glabella with semioval anterior lobe; F3 clearly impressed, weakly concave forward; posterior lobe with F2 furrows absent; glabellar culmination broadly rounded; glabellar node not preserved; basal lobes small, transverse. Pygidium minutely bispinose; axis very short, quadrate; posterior lobe transverse, subrectangular with terminal node; F1 and F2 impressed. *Lower Ordovician (Tremadoc)*: England; ?France; China (Hunan), *A. latilimbatus* or *T. affinis* Zone.—FIG. 236, *1*. \**A. dux* (CALLAWAY), England (Shinerton, Shropshire); holotype, exoskeleton, BU 693,  $\times 8$  (new).

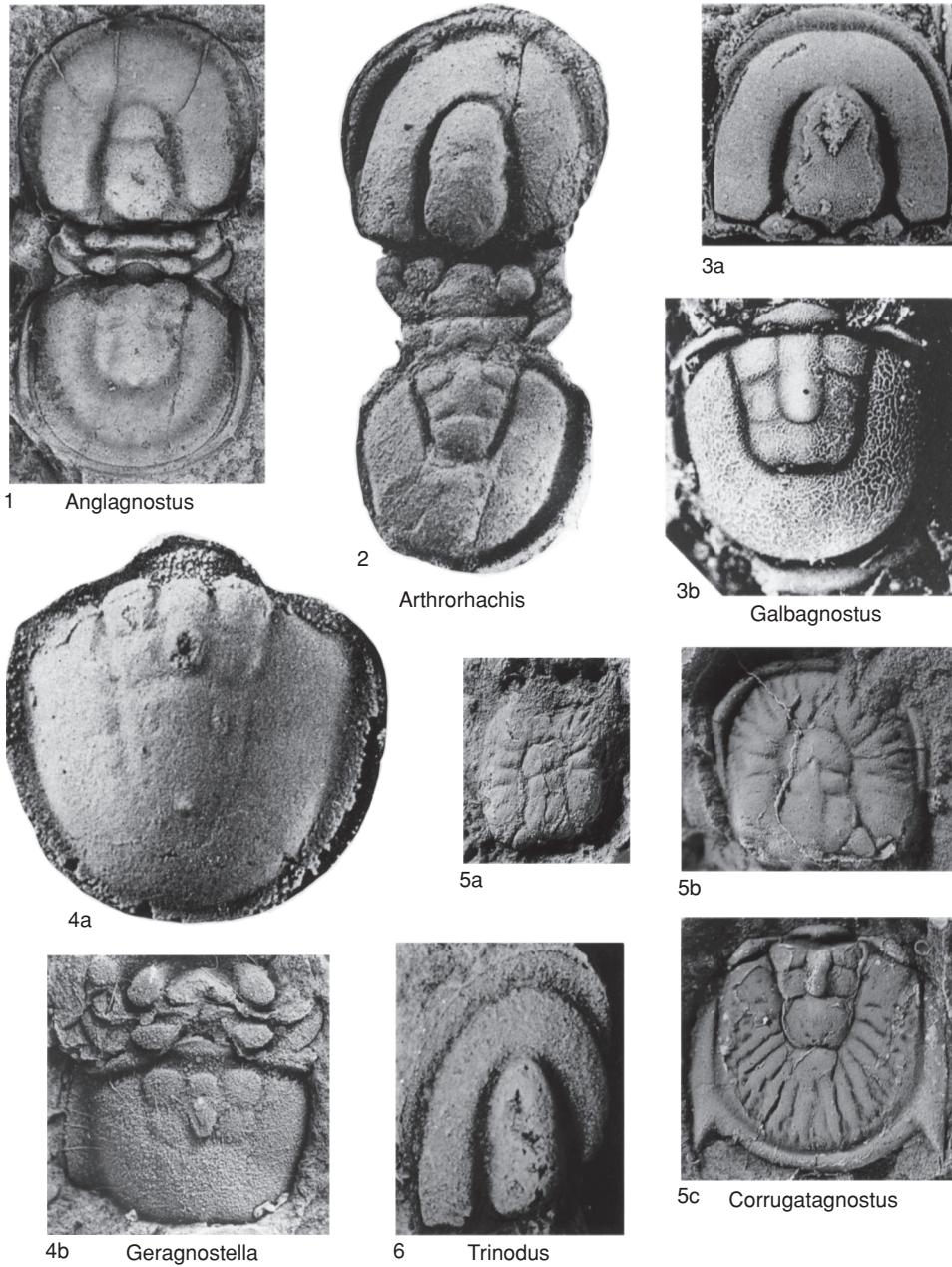


FIG. 236. Metagnostidae (p. 373–377)

**Chatkalagnostus** HAJRULLINA & ABDULLAEV in ABDULLAEV & KHALETSKAYA, 1970, p. 20 [*\*C. mirus*; OD; holotype (ABDULLAEV & KHALETSKAYA, 1970, pl. 1, fig. 1), 4/3, IGiG, Tashkent] [= *Oculagnostus* AHLBERG, 1988, p. 116 (type, *Agnostus frici* HOLUB, 1908, p. 9, pl. 1, fig. 1a,b)]. Large; en grande tenue;

usually scrobiculate; border furrows wide, deliquiate; median preglabellar furrow absent. Glabella broad, with large, subquadrate anterior lobe; F3 nearly straight, curving rearward laterally; posterior lobe with F2 furrows well developed, chevronate; glabellar node immediately behind F3 furrow. Py-



- gidium bispinose; axis short, slightly constricted across M2; posterior lobe transverse, subrectangular. *Ordovician*: Czech Republic, Llanvirn—lower Llandeilo; Uzbekistan, ?Llandeilo; Sweden, ?Arenig—Llanvirn.—FIG. 237,5a,b. \**C. mirus*, Lower Ordovician (Llandeilo), Uzbekistan (Pskem Ridge, Karakorum Range); *a*, holotype, cephalon, IGI G 4/3,  $\times 5$ ; *b*, pygidium, IGI G 4/6,  $\times 5$  (Abdullaev & Khaletskaia, 1970, pl. 1, fig. 1, 4).
- Corrugatagnostus** KOBAYASHI, 1939a, p. 173 [*\*Agnostus perrugatus* BARRANDE, 1872, p. 143; OD; =*A. morea* SALTER, 1864b, p. 7; holotype by monotypy (SALTER, 1864b, pl. 1, fig. 13), 8699, BGS, London] [= *Segmentagnostus* PEK, 1977, p. 17 (type, *Agnostus caducus* BARRANDE, 1872, p. 142, pl. 14, fig. 12–13); *Granulatagnostus* KOLOBOVA, 1981, p. 257 (type, *G. granulatus*; OD)]. En grande tenue; usually scrobiculate; median preglabellar furrow present in more strongly scrobiculate forms. Glabella with semioval to semicircular anterior lobe; F3 chevron shaped; posterior lobe with F2 very effaced, chevron shaped; glabellar node from immediately behind F3 to well onto anterior glabellar lobe. Pygidial axis very short, tapering rearward or with slight constriction across M2; posterior lobe transverse, subrectangular to trapeziform, usually with weak terminal node. ?*Upper Cambrian–Upper Ordovician*: Czechoslovakia, Llandeilo—lower Caradoc; England, Arenig—lower Llanvirn; Scotland, upper Caradoc—Ashgill; Ireland, Ashgill; Belgium, Llandeilo; France, ?lower Arenig; ?Argentina, lower Tremadoc; Russia (Altay Mountains), ?Upper Cambrian; Kazakhstan, middle—upper Caradoc; Uzbekistan, Ashgill; China (Zhejiang, Jiangsu), ?Tremadoc, upper Caradoc—Ashgill; USA (Texas), Lower Ordovician; Poland, Ashgill.—FIG. 236,5a–c. \**C. morea* (SALTER), Lower Ordovician (Llanvirn); *a*, England (Shelve Inlier, Shropshire), holotype, cephalon, BGS 8699,  $\times 5$  (new); *b,c*, England (Old Church Stoke, Shropshire), *b*, cephalon, BGS 92922,  $\times 5$ ; *c*, pygidium, BGS 92923a,  $\times 5$  (new).
- Dividuagnostus** KOROLEVA, 1982, p. 21 [*\*D. minus*; OD; holotype (KOROLEVA, 1982, pl. 1, fig. 5), 1-358, KazIMS, Alma-Ata] [= *Peziziopsis* JU in QIU & others, 1983, p. 29 (type, *P. typica*; OD)]. Glabella with bulbous, subcircular anterior lobe; F3 strong, chevronate; posterior lobe subcircular, lacking F2; glabellar node from a short distance behind to immediately behind F3 furrow. Pygidial axis short, with well-developed constriction across M2; posterior lobe nearly equidimensional, semioval to subrectangular, without terminal node. *Lower Ordovician–Upper Ordovician*: Kazakhstan, middle Ordovician; China (Zhejiang), ?Tremadoc, lower Ashgill, (Gansu), Caradoc—Ashgill, (Jiangxi), upper Caradoc; Wales, middle Arenig, Llandeilo—lower Caradoc; England, lower Llandeilo; Australia (New South Wales), upper Gisbornian—lower Eastonian; ?Canada (Newfoundland), Tremadoc.—FIG. 237,3. *D. mccoysi* (SALTER), middle Ordovician (upper Llandeilo), central Wales (Pen-Cerig Lake, Builth-Llandrindod area); exoskeleton, BMNH It 2671,  $\times 5$  (C. P. Hughes, 1969, pl. 1, fig. 3).
- Galbagnostus** WHITTINGTON, 1965, p. 304 [*\*Agnostus galba* BILLINGS, 1865, p. 297; OD; lectotype (WHITTINGTON, 1965, p. 305, pl. 3, fig. 1–2, 4), 689b, GSC, Ottawa]. Glabella short, broad; F3 effaced; F2 weak; glabellar node very advanced, near anterior margin of glabella. Pygidial axis very short, tapering rearwards; posterior lobe transverse, trapeziform, with indistinct median ridge and deepening of axial furrow behind this ridge. *Lower to Middle Ordovician—middle Ordovician*: Canada (Newfoundland), Whiterock; Ireland, ?Sweden, ?Australia, middle Arenig.—FIG. 236,3a,b. \**G. galba* (BILLINGS), middle Ordovician (Whiterock), Canada (Table Point, western Newfoundland); *a*, lectotype, cephalon, GSC 689b,  $\times 6$ ; *b*, pygidium, GSC 18395,  $\times 15$  (Whittington, 1965, pl. 3, fig. 1; pl. 4, fig. 9).
- Geragnostella** KOBAYASHI, 1939a, p. 171 [*\*Agnostus tullbergi* NOVÁK, 1883, p. 59; OD; neotype (PEK, 1977, p. 13, pl. 3, fig. 6), 1-356, OMR, Rokycany]. Mostly en grande tenue, with tendency to efface axial furrows surrounding posterior pygidial axial lobe. Glabella with F3 usually effaced or with straight median portion impressed; F2 weak; glabellar node immediately behind F3 furrow. Pygidial axis of moderate length, tapering rearward; posterior lobe semioval, variably effaced, with strong terminal node. *Ordovician*: Czech Republic, Llanvirn; Spain, lower Llanvirn; Sweden, lower Arenig—Llanvirn; Turkey, lower—upper Arenig.—FIG. 236,4a,b. \**G. tullbergi* (NOVÁK), Lower Ordovician (Llanvirn); *a*, Czech Republic (Sárka, Bohemia), pygidium, SBNM-ČD 310,  $\times 10$  (PEK, 1977, pl. 3, fig. 4); *b*, Czech Republic (Osek, near Rokycany), neotype, pygidium, MR 1-356,  $\times 6.5$  (PEK, 1977, pl. 3, fig. 6).
- Geragnostus** HOWELL, 1935b, p. 231 [*\*Agnostus sidenbladhi* LINNARSSON, 1869, p. 82; OD; lectotype (LINNARSSON, 1869, pl. 2, fig. 61; SD AHLBERG, 1989, p. 310), 25, SGU, Uppsala] [= *Geratrinodus* KOBAYASHI & HAMADA, 1978, p. 8 (type, *G. perconvexus*; OD); *Neptunagnostella* PEK, 1977, p. 14 (type, *Agnostus consors* HOLUB, 1912, p. 6, pl. 1, fig. 5)]. En grande tenue to nearly entirely effaced. Glabella with semioval anterior lobe; F3 effaced or with straight median portion, lateral portions curving forward and outward; posterior lobe with weak F2 furrows; glabellar node immediately behind F3 furrow. Pygidial axis of moderate length, commonly constricted across M2; posterior lobe nearly equidimensional, semioval to subrectangular, commonly with weak terminal node. *Ordovician*: Sweden, upper Tremadoc—Llanvirn; Norway, upper Tremadoc; France, upper Tremadoc—lower Arenig; Czech Republic, Arenig—Llanvirn; Scotland, Llandeilo; England, upper Tremadoc; Canada (Newfoundland), Whiterock; Argentina, Tremadoc; Turkey, Arenig; Tadzhikistan, Arenig; Uzbekistan, Ashgill; China (Hubei, Hunan), Tremadoc—Llanvirn; USA (Nevada), ?Lower Ordovician; Malaysia, ?middle Ordovician.—FIG. 237,4a,b. \**G. sidenbladhi* (LINNARSSON), Lower Ordovician (upper Tremadoc, *Apatokephalus serratus* Biozone);

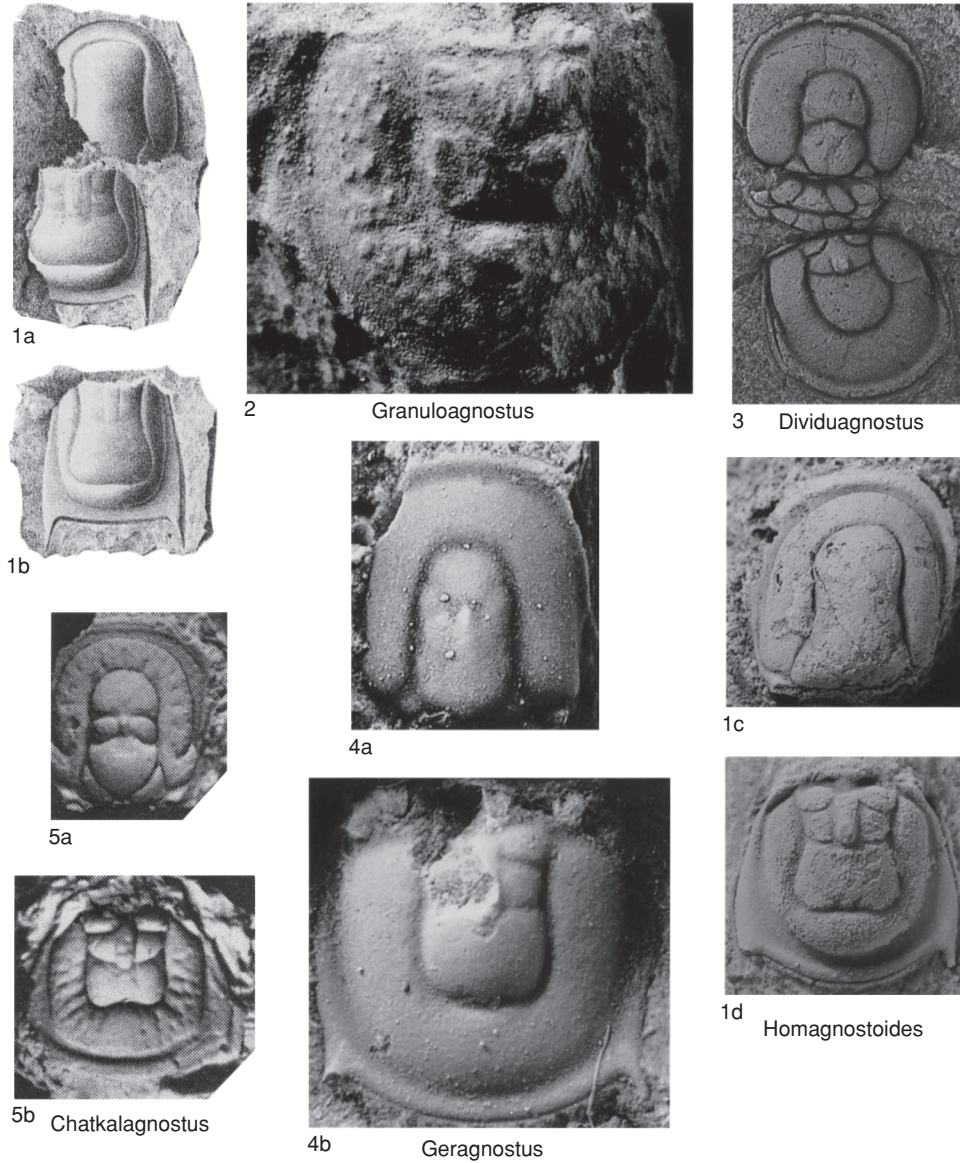


FIG. 237. Metagnostidae (p. 375–377)

*a*, Sweden (Hunneberg, Västergötland), cephalon, SGU 7886,  $\times 12$  (Ahlberg, 1989, fig. 1a,b); *b*, Sweden (Mossebo, Hunneberg, Västergötland), lectotype, pygidium, SGU 25,  $\times 11$  (Ahlberg, 1989, fig. 3a).

**Granuloagnostus** PEK, 1970, p. 129 [\**Agnostus dusli* NOVÁK, 1883, p. 58; OD; holotype by monotypy (NOVÁK, 1883, pl. 1, fig. 12a–d), ČD 314, NMP, Prague]. Known only from a pygidium; pygidium similar to that of *Galbagnostus* but with coarsely

pustulose prosopon. *Ordovician (Llanvirn)*: Czech Republic.—FIG. 237,2. \**G. dusli* (NOVÁK), Lower Ordovician (Llanvirn), Czech Republic (Ošek, Sárka, Bohemia); holotype, pygidium, NM-ČD 314,  $\times 8.5$  (Pek, 1970).

**Homagnostoides** KOBAYASHI, 1939a, p. 178 [\**Agnostus ferralsensis* MUNIER-CHALMAS & BERGERON in BERGERON, 1889, p. 342; OD; syntypes (BERGERON, 1889, pl. 4, fig. 8–9), not located]. Pygidium with short (sag.), laterally expanded, flasklike posterior

- axial lobe; posteriorly truncate; long axial node extending across entire anteroaxis; acrolobe constricted, lacking median postaxial furrow; borders wide; border furrows nondeliquiate, retral spines. *Ordovician (Tremadoc)*: France.—FIG. 237, 1a–d. \**H. ferralsensis* (MUNIER-CHALMAS & BERGERON); a, b, Lower Ordovician (Tremadoc, horizon e of COURTESOLE & PILLET in CAPÈRA, COURTESOLE, & PILLET, 1978), France (Montagne Noire, Hérault); unlocated syntypes,  $\times 4.7$  (Bergeron, 1889, pl. 4, fig. 8–9); c, d, Lower Ordovician, southern France (Montagne Noire), c, plesiotype, cephalon, IPM B 49009, upper Tremadoc,  $\times 8$  (new), d, plesiotype, pygidium, IPM B 49010, lower Arenig,  $\times 8$  (new).
- Trinodus** M'COY, 1846, p. 56 [\**T. agnostiformis*; M; holotype by monotypy (M'COY, 1846, pl. 4, fig. 3), IV-3, NMING, Dublin]. Name restricted to type specimen, an incomplete and distorted internal mold of a cephalon, by FORTEY (1980, p. 27). *Ordovician (Llandeilo)*: Ireland.—FIG. 236, 6. \**T. agnostiformis*, Ireland (Greenville, Wexford County); holotype, cephalon, NMING IV-3,  $\times 8.4$  (Whittington, 1950, pl. 68, fig. 1).
- ### Family UNCERTAIN
- Agnostogonus** ÖPIK, 1967, p. 94 [\**A. incognitus*; OD; holotype (ÖPIK, 1967, pl. 57, fig. 8), CPC 5846, AGSO, Canberra]. Cephalon and pygidium effaced but retaining narrow borders, faint indications of basal lobes and furrows, posterior margin of glabella, axial furrows of pygidial anteroaxis, and axial nodes of each shield. [May belong to either Ptychagnostinae or Spinagnostidae.] *lower Upper Cambrian*: Australia (Queensland), *G. stolidotus* Zone.—FIG. 238, 1a, b. \**A. incognitus*, Upper Cambrian (Mindyallan, *Glyptagnostus stolidotus* Zone), Australia (Burke River area, western Queensland); a, holotype, cephalon, CPC 5846,  $\times 8$ ; b, paratype, pygidium, CPC 5847,  $\times 8$  (new).
- Archaeagnostus** KOBAYASHI, 1939a, p. 112 [\**A. primigenus*; OD; lectotype (SD RASETTI & THEOKRITOFF, 1967, p. 195, pl. 20, fig. 20), 18328, USNM, Washington, D.C.]. Small; nonscrobiculate, with nondeliquiate border furrows; cephalon questionably nonspinose; median preglabellar furrow absent. Glabella parallel-sided, with elongate, subquadrate anterior glabellar lobe; F3 deep, straight; posterior lobe strongly inflated posteriorly, lacking F1 and F2; glabellar node posteriorly located; glabellar culmination narrowly rounded or angular; basal lobes small, simple. Pygidium nonspinose; axis of moderate length, broad, rounded posteriorly, not reaching border furrow; F1, F2 effaced; median postaxial furrow absent. *upper Lower Cambrian*: USA (New York).—FIG. 239, 8a, b. \**A. primigenus*, ?Lower Cambrian (?*Elliptocephala* fauna), USA (Salem, New York); a, lectotype, cephalon, USNM 18328,  $\times 17$ ; b, paratype, pygidium, USNM 18327,  $\times 14$  (new).
- Armagnostus** HOWELL, 1937, p. 1162 [\**A. megalaxis*; OD; holotype (HOWELL, 1937, pl. 2, fig. 15), 9786, YPM(PU), New Haven]. The type species of this genus is based on a poorly preserved, distorted holotype pygidium and eleven paratypes, two of which (one cephalon and one pygidium) were illustrated by HOWELL (1937, pl. 2, fig. 12, 16). These are equally poorly preserved, making this species and hence the genus very difficult to interpret. *upper Middle Cambrian*: USA (Vermont), *Centropleura vermontensis* fauna; Canada (New Brunswick).—FIG. 238, 10. \**A. megalaxis*, upper Middle Cambrian (*Centropleura vermontensis* beds), USA (St. Albans, Vermont); holotype, pygidium, YPM(PU) 9786,  $\times 2$  (Howell, 1937, pl. 2, fig. 15).
- Blystagnostus** ÖPIK, 1961b, p. 95 [\**B. laciniatus*; OD; holotype (ÖPIK, 1961b, pl. 23, fig. 5), CPC 3628, AGSO, Canberra]. Agnostoid with short, semiglobose pygidial axis, frill-like border, and granulate prosopon. *Middle Cambrian*: Australia (Queensland), *P. cassis* Zone.—FIG. 238, 9. \**B. laciniatus*, upper Middle Cambrian (Boomerangian, *Lejopyge laevigata* Zone), Australia (Burke River area, western Queensland); holotype, pygidium, CPC 3628,  $\times 8$  (new).
- Ciceragnostus** KOBAYASHI, 1937b, p. 442 [\**Agnostus barlowi* BELT, 1868, p. 11; OD; lectotype (inferred from LAKE, 1906, p. 17), 58498, BMNH, London]. Largely effaced but preserving faint indication of glabella and pygidial anteroaxis; cephalic border very narrow; pygidial border wider, possibly deuterolobate. [Type species probably referable to an effaced pseudagnostinid genus. All other species Middle Cambrian and variously assigned.] ?*Lower Ordovician (?Tremadoc)*: Wales.—FIG. 239, 2. \**C. barlowi* (BELT), Wales (Dolgellau); lectotype, exoskeleton, BMNH 58498,  $\times 9.3$  (Morris & Fortey, 1985, pl. 1, fig. 1).
- Delagnostus** ÖPIK, 1961b, p. 88 [\**D. dilemma*; OD; holotype (ÖPIK, 1961b, pl. 23, fig. 9), CPC 3633, AGSO, Canberra]. Pygidium largely effaced, without border or border furrows except anterolaterally; axial furrows only preserved anteriorly; vestigial axial node and faintly acuminate axis not reaching margin may be apparent; nonspinose; smooth. *upper Middle Cambrian*: Australia (Queensland, Northern Territory), upper *L. laevigata* Zone.—FIG. 239, 9. \**D. dilemma*, upper Middle Cambrian (Boomerangian, *Lejopyge laevigata* Zone), Australia (Burke River area, western Queensland); holotype, pygidium, CPC 3633,  $\times 9$  (new).
- Gallagnostus** HOWELL, 1935b, p. 227 [\**G. geminus*; OD; holotype (HOWELL, 1935b, pl. 22, fig. 21), Miquel Collection H 13, UM, Montpellier]. Holotype of type species is a distorted, poorly preserved, complete exoskeleton. Apparently totally effaced, apart from cephalic and pygidial border furrows; borders narrow but distinct. *Middle Cambrian*: France, *Paradoxides* beds.—FIG. 238, 5. \**G. geminus*, France (Coulouma, Hérault); holotype, exoskeleton, UM Miquel Collection H13,  $\times 7$  (new).
- Glaberagnostus** ROMANENKO, 1985, p. 57 [\**G. altaicus*; OD; holotype (ROMANENKO, 1985, pl. 5, fig. 5), 1160/4, ZSGU, Novokuznetsk]. Cephalon smooth, lacking a border, and mostly effaced, with



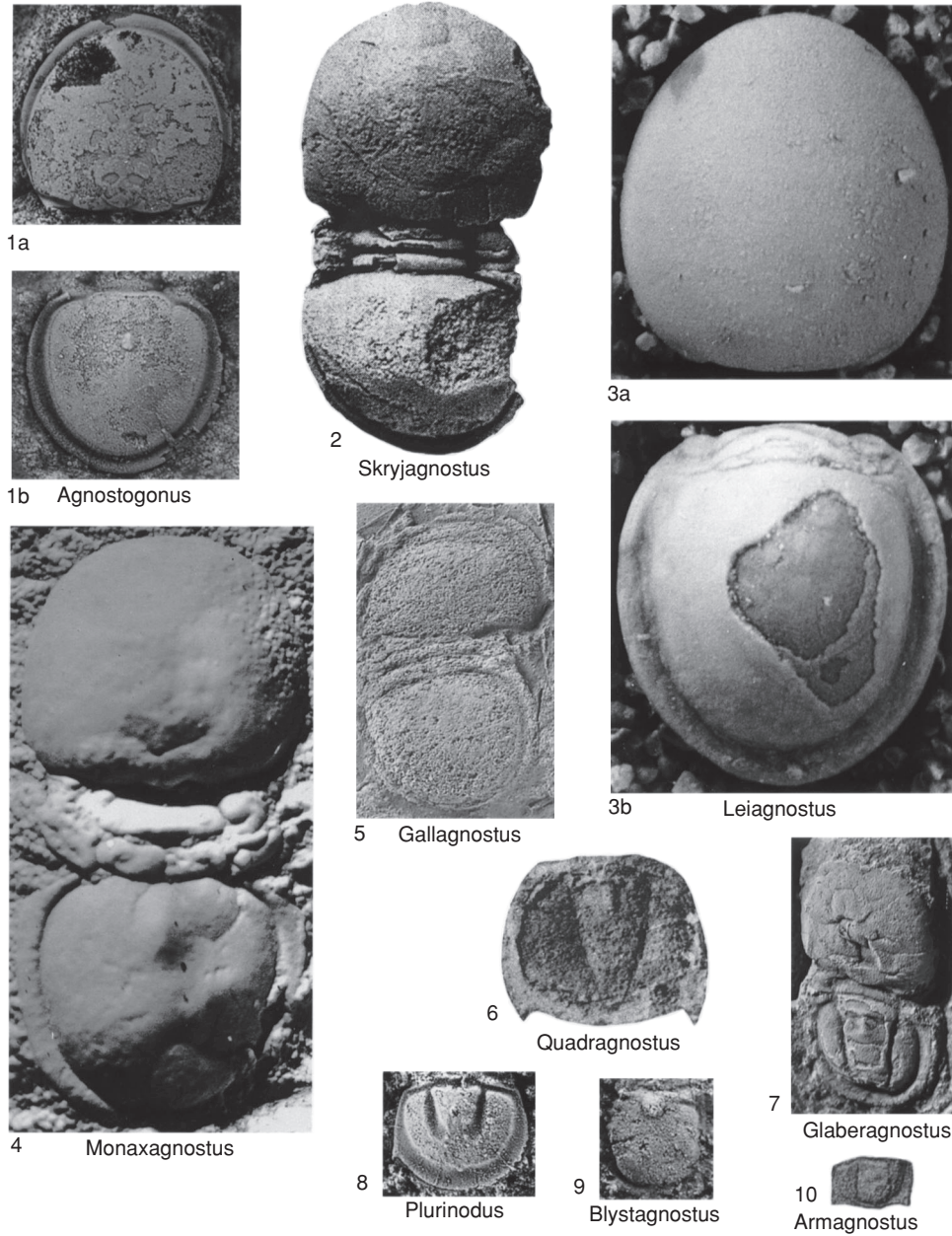


FIG. 238. Family Uncertain (p. 377–381)

glabella defined only posteriorly; basal lobes small. Pygidium smooth; smaller than cephalon, with well-developed border and wide border furrow; axis defined laterally, posteriorly indistinct; axial node indistinct; marginal spines small or absent. *lower Upper Cambrian*: Russia (Altay Mountains), *G. reticulatus* Zone.—FIG. 238.7. \**G. altaicus*, Upper Cambrian (Sakian, *Glyptagnostus reticulatus*

Zone), Russia (Altay Mountains, Siberia); holotype, exoskeleton, ZSGU 1160/4, ×4 (Romanenko, 1985, pl. 5, fig. 5).

**Grandagnostus** HOWELL, 1935a, p. 221 [\**G. vermontensis*; OD; holotype (HOWELL, 1935a, pl. 22, fig. 8), 9736, YPM(PU), New Haven]. Generic name confined to the very poorly preserved holotype cephalon of the type species by ROBISON

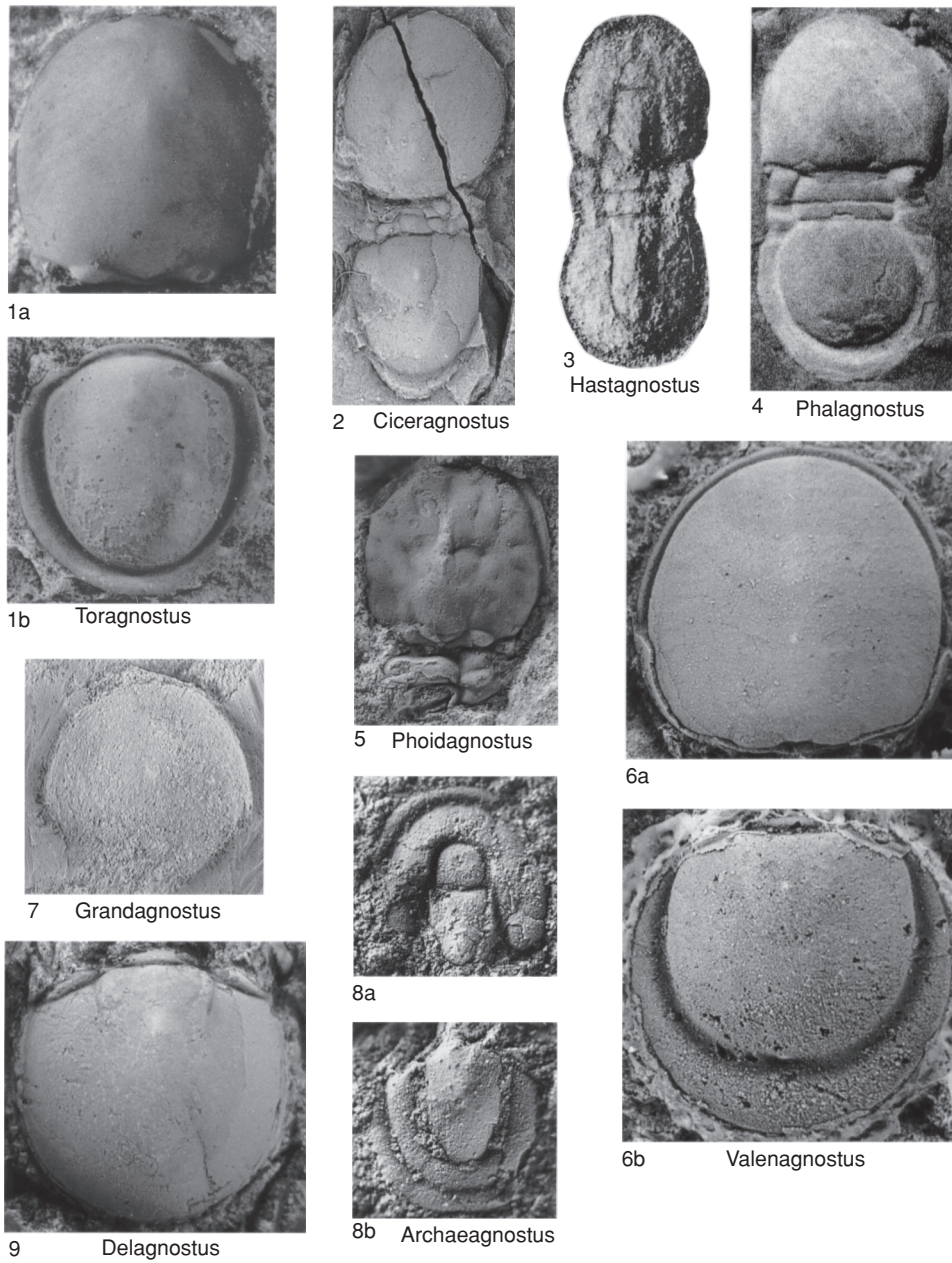


FIG. 239. Family Uncertain (p. 377–381)

(1988). Almost completely effaced; cephalic border extremely narrow (sag.) or absent; glabellar node advanced. *upper Middle Cambrian*: USA (Vermont).—FIG. 239,7. \**G. vermontensis*, *upper Middle Cambrian*, USA (St. Albans, Vermont); holotype, cephalon, YPM(PU) 9736, ×3 (Robison, 1988, fig. 12.7).

**Hastagnostus** HOWELL, 1937, p. 1165 [\**H. angustus*; OD; holotype (HOWELL, 1937, pl. 3, fig. 4), 9795, YPM(PU), New Haven]. The type species of this genus is based on a very poorly preserved, complete exoskeleton, which is difficult to interpret. *upper Middle Cambrian*: USA (Vermont), *Centropleura vermontensis* beds.—FIG. 239,3. *H. angustus*,

- USA (St. Albans, Vermont); holotype, exoskeleton, YPM(PU) 9795,  $\times 4$  (Howell, 1937, pl. 3, fig. 4).
- Leiaagnostus** JAEKEL, 1909, p. 401 [*\*L. erraticus*; OD; holotype (JAEKEL, 1909, fig. 23), K258, HMB, Berlin] [= *Phoidagnostoides* PILLET in CAPERA, COURTESOLE, & PILLET, 1978, p. 78 (type, *L. migueli* SDZUY, 1958, p. 260, pl. 1, fig. 12–15)]. Cephalon and pygidium ovoid, effaced; cephalon lacking border, totally effaced except for advanced glabellar node; pygidium nonspinose, with weak axial node and relatively broad, flat border with nondeliquate border furrow. ?uppermost Cambrian–Lower Ordovician: Germany, Tremadoc–Arenig; Czech Republic, Tremadoc–Llanvirn; France, Wales, Tremadoc; Sweden, early Arenig; Argentina, Tremadoc (*N. argentina* Zone); China (Guizhou, Hunan, Gansu, Xinjiang), ?uppermost Cambrian–lower Llanvirn; ?Kazakhstan, *Rhadinopleura pyriforme* Zone.—FIG. 238,3a,b. *\*L. erraticus*, upper Lower Ordovician (?Kundan, upper Arenig–lower Llanvirn), Germany (glacial erratic in Neukölln, Berlin); a, cephalon of enrolled holotype, HMB K258,  $\times 17$  (Neben & Kreuger, 1971, pl. 11, fig. 37–38); b, pygidium of same specimen, HMB K258,  $\times 17$  (Ahlberg, 1988, fig. 2c).
- Monaxagnostus** LIU, 1982, p. 293 [*\*M. yongshunensis*; OD; holotype (LIU, 1982, pl. 209, fig. 8), HT 8123, HBG, Changsha]. Effaced exoskeleton; cephalon totally effaced except for traces of basal lobes, lacking border and border furrow; pygidium retaining indistinct axial node and rather broad border with nondeliquate border furrow. *Middle Cambrian*: China (Hunan).—FIG. 238,4. *\*M. yongshunensis*, Middle Cambrian, China (Yongshun, Hunan); holotype, exoskeleton, HBG HT 8123,  $\times 10$  (Liu, 1982, pl. 209, fig. 8).
- Phalagnostus** HOWELL, 1955, p. 925 [*\*Battus nudus* BEYRICH, 1845, p. 46; OD; neotype (BARRANDE, 1852, pl. 49, fig. 6; SD ŠNAJDR, 1958, p. 78), ČC 229, No. 1017, NMP, Prague] [= *Phalacromina* KOBAYASHI, 1962, p. 29 (type, *Aagnostus nudus* OVALIS ILLING, 1916, p. 415, pl. 31, fig. 9–10)]. Almost totally effaced. Only glabellar culmination and small basal lobes weakly defined; otherwise cephalon totally effaced. Pygidial axis circular or ovate, defined by deep axial furrows; pygidial acrolobe undivided postaxially, forming posteriorly elongate pseudoborder, possibly with ventrally directed true border; anterolateral border furrow crossing pseudoborder and separating almost horizontal articulating facets; vestigial, elongate axial node present. *Middle Cambrian*: Sweden, *P. punctuosus* Zone; Denmark, *P. tessini* Zone; Wales, England, *H. parvifrons* Zone; France, *Paradoxides* beds; Czech Republic, *Eccaparadoxides pusillus* Zone; Russia (Bennett Island, Yakutia), Canada (Newfoundland), *P. davidis* Zone; ?Canada (Northwest Territories), *Cedaria minor* and *Olenaspella regularis* to *Proceratopyge rectispinata* Zones; ?USA (Vermont).—FIG. 239,4. *\*P. nudus* (BEYRICH); Middle Cambrian (*E. pusillus* Zone), Czech Republic (Týřovice, Bohemia); neotype, exoskeleton, NM ČC 229, No. 1017,  $\times 5$  (Šnajdr, 1958, pl. 5, fig. 3).
- Phaldagnostus** IVSHIN in KHALFIN, 1960, p. 167 [*\*P. orbiformis*; OD; holotype (KHALFIN, 1960, p. 168, fig. 48), Por-1, ZSGU, Novokuznetsk]. Ivshin's type specimen has never been satisfactorily illustrated. The description does not permit distinction between this and other effaced genera. *Upper Cambrian*: Russia (Altay Mountains), Kazakhstan (Lesser Karatau Mountain Range), *G. reticulatus* to *P. curtare* Zones.
- Phoidagnostus** WHITEHOUSE, 1936, p. 93 [*\*P. limbatus*; OD; holotype (WHITEHOUSE, 1936, pl. 9, fig. 10), 3207, UQF, Brisbane]. Only cephalon known; acrolobe moderately convex, unstricted, scrobiculate; border narrow; border furrow nondeliquate; axial furrows anteriorly effaced, weakly developed posteriorly; median preglabellar furrow clearly developed; glabellar culmination rounded; elongate axial node at about cephalic midlength, flanked by subtriangular depressions; basal lobes short, transverse, tumid; prosopon smooth. *upper Middle Cambrian*: Australia (Queensland), *P. cassis* Zone.—FIG. 239,5. *\*P. limbatus*, upper Middle Cambrian (Boomerangian, *Lejopyge laevigata* Zone), Australia (Burke River area, western Queensland); holotype, cephalon, UQF 3207,  $\times 6$  (Whitehouse, 1936, pl. 9, fig. 10).
- Plurinodus** ÖPIK, 1967, p. 170 [*\*P. discretus*; OD; holotype (ÖPIK, 1967, pl. 60, fig. 17), CPC 5889, AGSO, Canberra]. Diminutive pygidia with broad borders, deliquate border furrows, and unstricted acrolobe; anteroaxis tapers rearward, defined by deep and wide axial furrows; F1, F2 effaced; completely effaced posterior lobe; terminal node situated at border furrow; retral marginal spines; agnostoid articulating device. Cephalon with depressed or effaced anterior glabellar lobe may be associated. [May belong to Pseudagnostinae.] *lower Upper Cambrian*: Australia (Queensland), *G. stolidotus* Zone.—FIG. 238,8. *\*P. discretus*, Upper Cambrian (Mindyallan, *Glyptagnostus stolidotus* Zone), Australia (Duchess area, western Queensland); holotype, pygidium, CPC 5889,  $\times 8$  (new).
- Quadragnostus** HOWELL, 1935a, p. 219 [*\*Q. solus*; OD; holotype (HOWELL, 1935a, pl. 22, fig. 6), 9793, YPM(PU), New Haven]. The type species of this genus is based on a very poorly preserved holotype pygidium and an equally poorly preserved, fragmentary paratype cephalon, both of which are difficult to interpret. *upper Middle Cambrian*: USA (Vermont), *Centropleura vermontensis* beds.—FIG. 238,6. *\*Q. solus*, USA (St. Albans, Vermont); holotype, pygidium, YPM(PU) 9793,  $\times 8.5$  (Howell, 1935a, pl. 22, fig. 6).
- Skryjagnostus** ŠNAJDR, 1957, p. 236 [*\*S. pompeckji*; OD; holotype (ŠNAJDR, 1958, pl. 6, fig. 4), Šnajdr Collection, Br-191, NMP, Prague]. Exoskeleton almost totally effaced, except for a hint of axial furrows around rear of basal glabellar lobes and the presence of extremely narrow (sag.) border in both cephalon and pygidium. *Middle Cambrian*: Czech Republic, *E. pusillus* Zone; Russia (northwestern Siberia), *Pedinocephalus* or *Toxotis* Zone.—FIG. 238,2. *\*S. pompeckji*, Middle Cambrian (*Eccapara-*



- doxides pusillus* Zone), Czech Republic (Týřovice, Bohemia); holotype, exoskeleton, NM Br-191,  $\times 12.5$  (Horný & Bastl, 1970, pl. 1, fig. 3).
- Tornagnostus** ROBISON, 1988, p. 52–53 [*\*Agnostus bituberculatus* ANGELIN, 1851, p. 6; OD; neotype proposed herein (HOLM & WESTERGÅRD, 1930, pl. 4, fig. 4), Ar 9563a, RM, Stockholm]. Almost completely effaced, lacking cephalic border and with wide pygidial border. Cephalon strongly convex; glabella outlined posteriorly, narrow, tapering forward, with broadly rounded or obtusely angular culmination; glabellar node elongate, well in front of cephalic midlength; basal lobes simple, bulbous, strongly transverse. Pygidial axis very broad, with M1 bounded by axial furrow; axial node weak, elongate. [The lectotype selected by ROZOVA (1964, p. 19) from the material illustrated by WESTERGÅRD (1946, pl. 14, fig. 10) is invalid because WESTERGÅRD's material was not part of ANGELIN's type lot.] *upper Middle Cambrian*: USA (Alaska); Denmark; China (Hunan); Sweden, *S. brachymetopa* Zone; Russia (Siberian Platform), *C. oriens* and *A. henrici* Zones, (Bennett Island), zone unknown; Kazakhstan (Tyan-Shan Range), Mayaian; northern Greenland, *L. laevigata* Zone.—FIG. 239, 1a, b. *\*T. bituberculatus* (ANGELIN), *upper Middle Cambrian* (*Jincella brachymetopa* Zone), Sweden (Andrarum, Skåne); *a*, neotype, cephalon, RM Ar 9563a,  $\times 7.7$ ; *b*, toptype, pygidium, RM Ar 9563b,  $\times 7.7$  (new).
- Valenagnostus** JAGO, 1976, p. 144 [*\*Agnostus nudus* BEYRICH var. *marginata* BRÖGGER, 1878, p. 73; OD; holotype (BRÖGGER, 1878, pl. 6, fig. 3), not traced, PMO, Oslo]. Exoskeleton almost completely effaced; cephalic border and border furrow extremely narrow (sag.); pygidium with wide border, especially posteriorly, and deliquiate to subdeliquiate border furrow; unstricted acrollobes. Cephalic axial furrows effaced, but axial glabellar node may be present retrally. Vestigial pygidial axial furrows may define long (sag.) axis extending to border furrow and bearing terminal node; axial node almost totally effaced; nonspinose; smooth. *upper Middle Cambrian–lower Upper Cambrian*: Norway, *P. rugulosus* Zone; Sweden, *Hyolithes* Limestone; Denmark, *P. davidis* Zone; Australia (Tasmania), *?P. punctuosus* to *L. laevigata* Zones, (Queensland), *D. notalibrae* to *E. eretes* Zones.—FIG. 239, 6a, b. *V. marginatus* (BRÖGGER), *upper Middle Cambrian* (*Paradoxides forchhammeri* Zone), Norway (Aborrfallet, Ångermanland); *a*, figured specimen, cephalon, SGU 5018,  $\times 8$ ; *b*, figured specimen, pygidium, SGU 5022,  $\times 8$  (new)
- gidial axial node close to middle of axis, elongate; transverse groove or furrow present immediately behind axial node; variable border morphology and spinosity. *Middle Cambrian*.
- Phalacroma** HAWLE & CORDA, 1847, p. 43 [*\*Battus bibullatus* BARRANDE, 1846, p. 14; SD RAYMOND, 1913a, p. 139; lectotype (BARRANDE, 1852, pl. 49, fig. 6; SD ŠNAJDR, 1958, p. 74), ČC 244, NMP, Prague] [= *Platagnostus* HOWELL, 1935b, p. 228 (type, *P. immensus*; OD)]. Cephalon almost totally effaced, having barely perceptible border and axial furrows that are defined only posteriorly; basal lobes effaced. Pygidium with very wide (tr.) axis extending to narrow (sag.) posterior border; nonspinose. *Middle Cambrian*: Czech Republic, *Eccaparadoxides pusillus* Zone; France, *Paradoxides* beds; Russia (Siberia), *T. fissus* or *P. hicksi* to upper *P. davidis* Zones.—FIG. 240, 1. *\*P. bibullatum* (BARRANDE); *Middle Cambrian* (*E. pusillus* Zone), Czech Republic (Týřovice, Bohemia); lectotype, exoskeleton, NM-ČC 244, No. 1027,  $\times 8.7$  (Horný & Bastl, 1970, pl. 1, fig. 1).
- ?Dignagnostus** HAJRULLINA in REPINA, PETRUNINA, & HAJRULLINA, 1975, p. 111 [*\*D. grandis*; OD; holotype (REPINA, PETRUNINA, & HAJRULLINA, 1975, pl. 12, fig. 7–8), 483/218b, MMG, Tashkent]. With tendency to efface pygidial F1 and F2 furrows while retaining axial and border furrows. Pygidial axis pyriform, transversely expanded, long (sag.), reaching posterior border furrow; acrollobes unconstricted; pleural fields very narrow (tr.); borders of significant width; posterolaterally spinose. *Middle Cambrian*: Uzbekistan, *Sdzuyella-Aegunaspis* beds.—FIG. 240, 6. *\*D. grandis*; holotype, pygidium, MMG 483/218b,  $\times 10$  (Repina, Petrunina, & Hajrullina, 1975, pl. 12, fig. 7–8).
- Lisogoragnostus** ROZOVA in LISOGOR, ROZOV, & ROZOVA, 1988, p. 64 [*\*L. kalisae*; OD; holotype (LISOGOR, ROZOV, & ROZOVA, 1988, pl. 5, fig. 9), 848/36, CSGM, Novosibirsk]. Cephalon partly effaced, with vestigial basal lobes and glabellar culmination; well-defined border furrows. Pygidium apparently lacking border or border furrows, with wide (tr.), short (sag.) axis bearing a low axial node anteriorly and lacking F1 and F2 furrows. *Middle Cambrian*: Kazakhstan, beds with *Peronopsis fallax*; Russia (Siberian Platform), *Tomagnostus fissus* Zone.—FIG. 240, 5. *\*L. kalisae*, *Middle Cambrian* (Amgaian, beds with *Peronopsis fallax*), southern Kazakhstan (Kirshabakty River); holotype, exoskeleton, CSGM 848/36,  $\times 12$  (Lisogor, Rozov, & Rozova, 1988, pl. 5, fig. 9).

## Superfamily UNCERTAIN

### Family PHALACROMIDAE

Hawle & Corda, 1847

[Phalacromidae HAWLE & CORDA, 1847, p. 42] [=Platagnostidae HOWELL, 1935b, p. 228]

Cephalon variably effaced; pygidium with long (sag.) and laterally expanded axis; py-

### Family SPHAERAGNOSTIDAE

Kobayashi, 1939

[Sphaeragnostidae KOBAYASHI, 1939a, p. 177]

Agnostina with totally effaced cephalon, but retaining pygidial border, and short

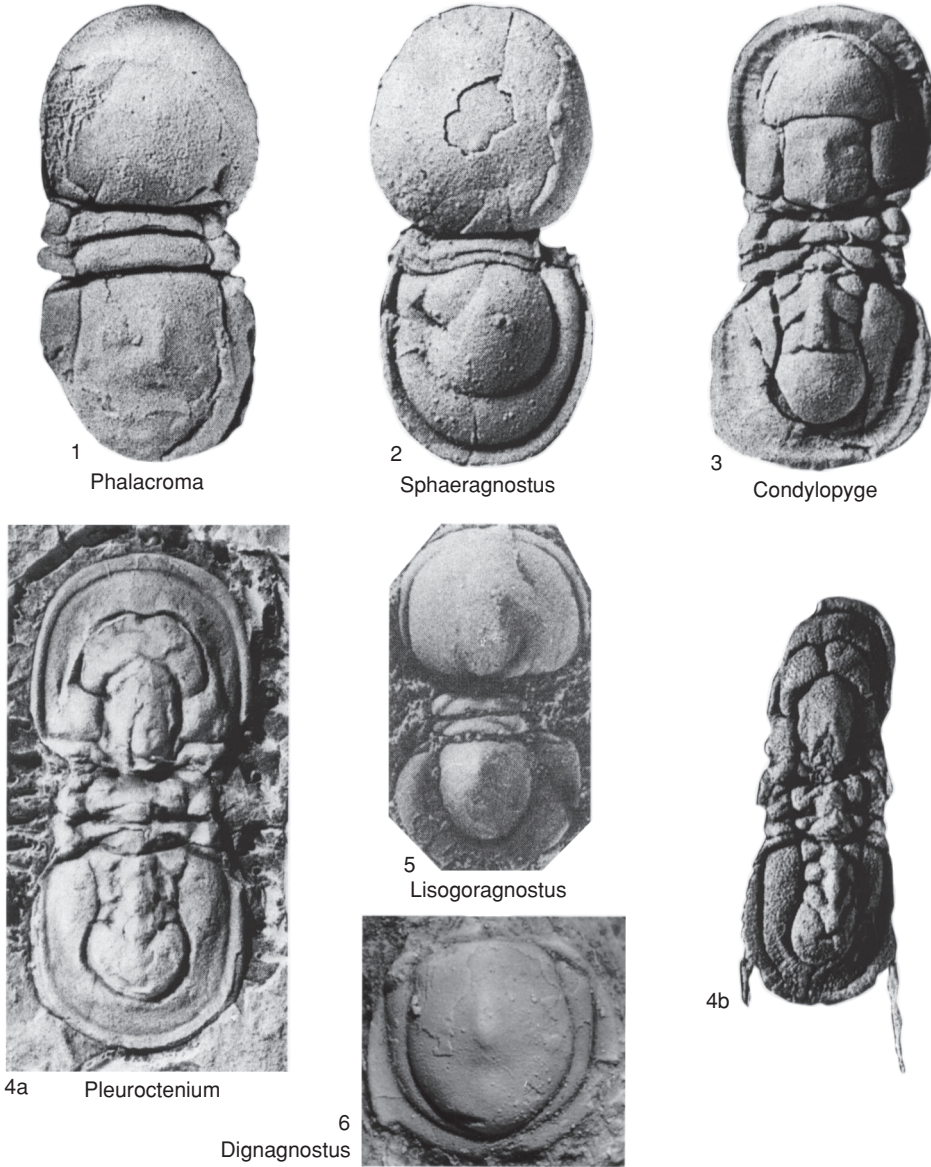


FIG. 240. Phalacromidae, Sphaeragnostidae, and Condylopygidae (p. 381–383)

(sag.), convex, subcircular pygidial axis. *Ordovician*.

**Sphaeragnostus** HOWELL & RESSER in COOPER & KINDLE, 1936, p. 361 [*Agnostus similaris* BARRANDE, 1872, p. 144; OD; holotype (BARRANDE, 1872, pl. 14, fig. 17–18), ĀD 489 (see PEK, 1977, pl. 7, fig. 6), NMP, Prague]. Cephalon totally effaced, lacking traces of border furrows, axial furrows, and glabellar node externally. Pygidium with

well-defined, nondeliquiate border furrows, narrow border, and axial furrows defining short (sag.), broad (tr.), convex (tr., sag.), subcircular, unfurrowed axis bearing both axial and terminal nodes; acrolobe unconstricted, convex, lacking median postaxial furrow; posterolateral spines minute or absent. Pleural regions of thoracic segments extremely restricted (tr.); axial portions short (sag.), very wide (tr.). *Ordovician*: Czech Republic, Llandeilo; Wales, Llandeilo–Ashgill; Denmark,

Sweden, Poland, Ashgill; Ireland, lower Ashgill; Kazakhstan, upper Tremadoc, Caradoc; Turkestan Mountain Range, Ashgill; China (Jiangxi, Zhejiang, Nei Monggol, Jiangsu), Ashgill, (Hunan), Llandeilo; Canada (Quebec), middle Ashgill.—FIG. 240,2. \**S. similaris* (BARRANDE), Middle Ordovician (Llandeilo), Czech Republic (Svatá Dobrotivá, Bohemia); holotype, exoskeleton, NM-ČD 489 (L16944), ×13.5 (Horný & Bastl, 1970, pl. 1, fig. 7).

### Superfamily CONDYLOPYGOIDEA Raymond, 1913

[Condylopygoidea RAYMOND, 1913a, p. 139] [*nom. transl.* SHERGOLD, LAURIE, & SUN, ex Condylopygidae RAYMOND, 1913a, p. 139, *partim*]

Agnostina with transverse basal glabellar lobes separated by a median plate rather than joined by connective band bearing median tubercle or spine; anterior glabellar lobe laterally expanded. Pygidial axis with triannulate anteroaxis and posteriorly rounded posteroaxis. *Lower Cambrian–Middle Cambrian.*

### Family CONDYLOPYGIDAE Raymond, 1913

[Condylopygidae RAYMOND, 1913a, p. 139]

With characteristics of superfamily. *Lower Cambrian–Middle Cambrian.*

**Condylopyge** HAWLE & CORDA, 1847, p. 50 [\**Battus rex* BARRANDE, 1846, p. 17; M; lectotype (BARRANDE, 1852, pl. 49, fig. 5; SD ŠNAJDR, 1958, p. 52), ČC 237, NMP, Prague] [= *Paragnostus* JAEKEL, 1909, p. 396 (type, *Battus rex* BARRANDE, 1846, p. 17); *Fallagnostus* HOWELL, 1935b, p. 230 (type, *F. blayaci*; OD)]. En grande tenue; cephalon and pygidium with strongly deliquiate border furrows; anterior glabellar lobe very large, approximately semicircular; posterior lobe cylindrical, with retral axial node; pygidial axis bearing elongate keel formed by fusion of axial nodes anteriorly; spines, where developed, short; prosopon smooth. *upper Lower Cambrian–Middle Cambrian:* Czech Republic, *Eccaparadoxides pusillus* Zone; England, *Protolenus* to *P. atavus* or *T. fissus* Zones; Wales, *B. oelandicus* Zone; Sweden, *A. insularis* to *P. punctuosus* Zones; France, *Paradoxides* beds; Germany, *P. insularis* to *P. paradoxissimus* Zones; Spain, *P. paradoxissimus* Zone; Canada (Newfoundland, New Brunswick), *P. hicksi* to *P. davidis* Zones; USA (Massachusetts); Russia (northern Siberia), Amgaian, *Oryctocara* to *Kounamkites* Zones, (southeastern Siberia), Mayaian Stage, *T. fissus* Zone.—FIG. 240,3. \**C. rex* (BARRANDE), Middle Cambrian (*E. pusillus* Zone), Czech Republic (Týřovice, Bohe-

mia); lectotype, exoskeleton, NM-ČC 237, No. 1034, ×5 (Horný & Bastl, 1970, pl. 1, fig. 2).

**Pleuroctenium** HAWLE & CORDA, 1847, p. 116 [\**Battus granulatus* BARRANDE, 1846, p. 15; M; lectotype (BARRANDE, 1852, pl. 49, fig. 5–7; SD ŠNAJDR, 1958, p. 56), ČC 250, No. 1008, NMP, Prague] [= *Dichagnostus* JAEKEL, 1909, p. 396 (type, *Battus granulatus* BARRANDE, 1846, p. 15)]. En grande tenue; cephalon and pygidium with narrow borders and border furrows and weakly constricted acrollobes; anterior glabellar lobe crescentic, wrapped around posterior glabellar lobe, and commonly bisected by median sulcus; long cephalic and posterolateral pygidial spines commonly developed; discrete spines developed from axial pygidial nodes; lateral and posterior margins frequently bearing fringe of small spines; prosopon granular. *Middle Cambrian:* Czech Republic, *E. pusillus* Zone; England, *P. aurora* to *P. punctuosus* Zones; Wales, Sweden, *H. parvifrons* Zone; France, *Paradoxides* beds; Canada (Newfoundland, New Brunswick), *P. hicksi* to *P. davidis* Zones.—FIG. 240,4a. *P. granulatum scanense*, Middle Cambrian (*Hypagnostus parvifrons* Zone), England (Nuneaton district, Warwickshire); exoskeleton, BGS IGS Zs 4571, ×6 (Rushton, 1979, fig. 2j).—FIG. 240,4b. \**P. granulatum* (BARRANDE), Middle Cambrian (*Eccaparadoxides pusillus* Zone), Czech Republic (Týřovice, Bohemia); lectotype, exoskeleton, NM-ČC 250, No. 1008, ×10.8 (Horný & Bastl, 1970, pl. 1, fig. 6).

### NOMINA NUDA

**Cenagnostus** WHITTARD, 1940, p. 157.  
**Clavagnostotes** LU & LIN, 1981, p. 118.  
**Kitatagnostus** ERGALIEV, 1965, p. 24.  
**Munagnostus** IVSHIN in KHALFIN, 1960, p. 17.  
**Parapseudagnostus** PETRUNINA, 1966, p. 8.  
**Pseudagnostella** KOROLEVA, 1982, p. 35.

### REJECTED GENERA

**Discagnostus** ÖPIK, 1963, p. 55 [Eodiscida; SHERGOLD, LAURIE, & SUN, 1990, p. 8].  
**Gallagnostoides** KOBAYASHI, 1939b, p. 580 [= *Microparia* (*Microparia*) HAWLE & CORDA, 1847, p. 52; FORTEY & OWENS, 1987, p. 172].  
**Mallagnostus** HOWELL, 1935b, p. 228 [Eodiscida; RUSHTON, 1966, p. 10; RASETTI & THEOKRITOFF, 1967, p. 190].  
**Pseudotrinodus** KOBAYASHI & HAMADA, 1971, p. 399 [Aulacopleurinae; THOMAS & OWENS, 1978, p. 74].

### Suborder EODISCINA Kobayashi, 1939

[*nom. correct.* MOORE, 1959, p. 187, *pro* Eodiscidi KOBAYASHI, 1939a, p. 74]

With or without eye, facial suture proparian when present; two or three thoracic segments, articulating half ring on anterior segment; pygidium with axis usually



extending close to border, pleural region segmented in some species. Protaspis calcified (known in few taxa). *Lower Cambrian–Middle Cambrian*.

## INTRODUCTION TO SUBORDER EODISCINA

P. A. JELL

### Origin and Phylogeny

Eodiscoids are generally considered to have evolved from polymerid trilobites by paedomorphosis (STUBBLEFIELD, 1936; JELL, 1975a; FORTEY, 1990a; SHERGOLD, 1991). FORTEY (1990a, p. 556) suggested that *Sinodiscus changyangensis* S. ZHANG, 1980 (in W. ZHANG, LU, & others) might be the most primitive eodiscoid. Another candidate could be the oldest genus known, *Tsunydiscus* W. CHANG, 1966. Evaluation of *Tsunydiscus* begins by comparison with *Dipharus clarki* KOROBV, 1980. That species may represent an immature redlichoid rather than an eodiscoid because of the dominant palpebro-ocular ridges, extremely long librigenae, and free pleural tips on the pygidium of variable numbers of segments. Furthermore, it occurs with several species of the redlichoid *Bulaispis* LERMONTOVA, 1956 (in TCHERNYSHEVA & others), to any one of which it may belong. Glabellae of *D. clarki* and *Tsunydiscus* are extremely similar and distinct from all other eodiscoids, prompting separation of *Tsunydiscus* at the family level in the classification below. Among the species of *Tsunydiscus* are to be found those features (well-defined dorsal furrows and eye ridges and short preglabellar field) thought by FORTEY (1990a) to characterize the primitive eodiscoid along with long librigenae as a redlichoid legacy; reduction in length of librigenae is evident on all eodiscoid lineages.

The phylogenetic scheme of JELL (1975a), which recognized three major lineages within the superfamily, is adopted here and is essentially unchanged except for reallocation and reassessment of several genera, identification of the *Tsunydiscidae* as the prob-

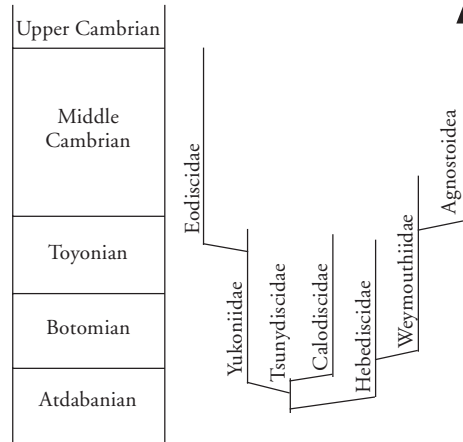


FIG. 241. Phylogenetical diagram of order with approximate relationships between superfamilies and families within Eodiscoidea.

able ancestor to all three lineages, and separation of the three lineages at family level (Fig. 241).

### Descendants

The possibility that the Agnostina descended from the Eodiscoidea has been extensively debated, with FORTEY (1990a) outlining the case for and SHERGOLD (1991) the case against this possibility. FORTEY (1990a, fig. 14) listed derived characters of Agnostida as: (1) reduction in number of thoracic segments to three or fewer, (2) loss of calcification of rostral plate, (3) an occipital width greatly exceeding width of preoccipital glabella, (4) broad, rolled cephalic border, (5) long cephalic shield (with maximum width in front of posterior margin in most species), (6) reduced or absent genal spines, and (7) fulcrate articulation. He identified the derived character of the Agnostina out of this group as the cephalothoracic aperture. Modifications to the occipital structure in miomerids (which bounds this aperture anteriorly) produce significant derived features; the trend in the Weymouthiidae to shortening and obliteration of the occipital ring is carried on in the Agnostina with the occipital ring divided into basal lobes as had evolved already in the eodiscoids *Chelediscus*

and *Tannudiscus*. *Tannudiscus* has been advanced as the eodiscoid closest to the ancestor of the Agnostina, with its bilobed glabella, basal glabellar lobes, both glabella and pygidial axis isolated from border furrow, and undivided pygidial axis. Although SHERGOLD (1991) acknowledged *Tannudiscus* as a good candidate for the ancestor of Agnostina, he argued against such ancestry on the basis of stratigraphic difficulties and poor quality of Lower Cambrian materials involved. These negative arguments are not accepted here. RASETTI (1945b, 1948a, 1952a) championed the major distinction between eodiscoids and Agnostina, and SHERGOLD regarded his discussion (1991) as supporting RASETTI's views. RASETTI (1972), however, had already rescinded his opinion on this matter, acknowledged the close relationship between the two groups, stated that the Agnostina were almost certainly derived from eodiscoids, and considered that the two groups together formed the Miomera.

Lack of a calcified protaspis in Agnostina had been employed as negative evidence for a relationship between eodiscoids and Agnostina, prior to the discovery of such a protaspis in *Neocobboldia chinlinica* by X. ZHANG (1989) and *Pagetia ocellata* by SHERGOLD (1991). SHERGOLD (1991) used this discovery to separate eodiscoids and Agnostina, although protaspides are unknown in the Weymouthiidae, the eodiscoids thought to be ancestral to Agnostina. This is despite the record of a calcified protaspis in *Pseudagnostus benxiensis* QIAN, 1982 (this record is questioned herein by CHATTERTON and SPEYER, p. 213) and the argument of FORTEY (1990a) that secondary loss of calcification in protaspides of Agnostina should be expected in light of their other specializations. Arguments based on the lack of this ontogenetic feature are surely premature in light of QIAN's (1982) possible discovery and the need to search in more detail for protaspides of Agnostina.

MÜLLER and WALOSSEK (1987) argued for isolation of the Agnostina because the appendages of *Agnostus pisiformis* are entirely

distinct from any other trilobite, but this argument must be set aside until appendages of eodiscoids are known; miomerids are specialized trilobites, with Agnostina the more specialized within the group, so appendages of Agnostina would be expected to be distinct from most other trilobites that are not so specialized.

Descent of Agnostina from Eodiscoidea has not been established beyond doubt. A large body of accepted inferential evidence makes it distinctly likely, but more research is needed.

### History of Classification

During the last century almost all eodiscoid species were assigned to *Microdiscus* (EMMONS, 1855), despite the fact that the type of that genus was known to be a juvenile of a post-Cambrian trilobite and not an eodiscoid. MATTHEW's (1896) subdivision of that genus into four sections was the first attempt at classification within the group. KOBAYASHI (1944a) thought the most significant subdivision should be based on whether there are two or three thoracic segments, with the next level of classification based on presence or absence of eyes and effacement of dorsal furrows. On this basis he arranged fifteen genera into five families, although from his table 4 showing phylogenetical relationships among the genera it is clear that he did not consider the Eodiscidae, one of his five families, a phylogenetic group.

RASETTI (1952a) repeated the observation that number of thoracic segments and presence or absence of eyes were the best characters for subdivision of the group. He recognized, however, that the number of thoracic segments could not be used at the family level. Moreover, he clearly acknowledged the likelihood that eyes and sutures had been independently lost in several lineages. Nevertheless, he proposed a classification into two families based solely on the presence or absence of eyes and facial sutures, stressing that this was a matter of expedience in view of the incomplete knowledge of the group and not necessarily relevant to phylogeny.

This classification was employed by MOORE (in HARRINGTON & others, 1959) and has been the basis of almost all classificatory schemes developed for or applied to the group since that date (including S. ZHANG in W. ZHANG, LU, & others, 1980; KOROBOV, 1980; REPINA & ROMANENKO, 1978).

A phenetic approach to classification (JELL, 1975a) showed that presence or absence of eyes and sutures was not a major discriminator, and the three lineages identified during that study each contained blind and sighted genera. By 1975 the range of morphology in the 34 genera was sufficient to start piecing together lineages with the intention of establishing a classification from the phylogeny. This was not entirely successful, and the resulting two families have not been universally accepted despite the fact that this classification is demonstrably closer to phylogeny than any previous scheme. ÖPIK (1975a) also recognized the inappropriateness of RASETTI's utilitarian classification and proposed three families that correspond roughly to the lineages identified by JELL (1975a). ÖPIK's tabulation of the features of the group indicated a mosaic pattern of morphology without clearcut family indicators.

#### Present Classification

There are now more than 50 genera. Some are intermediate between earlier established genera, but others exhibit entirely new phylogenetic branches, sometimes clarifying and sometimes complicating our understanding of the group. In the present classification the findings of JELL (1975a) and ÖPIK (1975a) are employed. These findings, along with the many new taxa described since 1976, lead to a classification into six families based on all available features, but the structure of the glabella and, in particular, modifications of the occipital area are key features. If the group evolved by neoteny from the Redlichioidea, as discussed above, the primitive structure of the eodiscoid occipital ring would be that seen in the Hebediscidae and Calodiscidae where SO is transverse and of

more or less uniform depth and where LO is of uniform length, usually the same as L1, and may have a posterior spine; this is the primitive occipital structure. The Calodiscidae have the apomorphy of a reduced number of segments in the pygidial axis, although this feature is not exclusive to that family. The Yukoniidae plus Eodiscidae have the unique feature of the expansion of the rear of the glabella (mostly L1) into a long, slender posteromedian spine that lies over and disrupts the occipital ring. The Eodiscidae have the further distinction of scrobicules developed on the anterior border. (These may be secondarily effaced on some species.) The Weymouthiidae are all blind and include forms with the rear of the glabella roundly expanded over the occipital ring or vertically spinose, forms with the occipital ring obliterated by general glabellar expansion, and forms with primitive occipital structure but greatly increased numbers of axial segments.

Eodiscoid phylogeny is still incompletely understood, and assignment of some genera to higher taxa will remain a difficult task because of the great variety of glabellar modifications, progression to effacement in numerous lineages, and demonstrated parallel evolution of certain features (e.g., border nodes in the Calodiscidae and Serrodiscidae). The suprageneric classification cannot yet be considered stable because the phylogenetic relationships between all genera are far from clear, and the evolutionary pathways of several lineages are uncertain, particularly near their origins.

### Superfamily EODISCOIDEA Raymond, 1913

[*nom. transl.* JELL, 1975a, p. 26, ex Eodiscidae RAYMOND, 1913b, p. 102] (=Eodiscidae RICHTER, 1932, p. 852, *partim*; Dawsoniidea KOBAYASHI, 1943, p. 38; Eodiscoidae HUPÉ, 1953a, p. 108]

Glabella usually well defined, and subcylindrical, tapered forward, or narrowed, or expanded near midlength; LO may be simple ring of uniform length (sag.), may be almost obliterated by enlargement posteriorly of L1 portion of glabella into



large, posterior spine overlying LO, may be shortened by rounded posteromedial expansion of the L1 portion of the glabella, or may be divided into basal lobes by such expansion. Genae elevated laterally, depressed in front of glabella. Cephalic border may be smooth or have marginal spines, tubercles, or radial grooves (scrobicules). Eye small and abathochroal, may be present in the absence of facial sutures, or may be only an eye tubercle. Thorax with second or third segment bearing posteromedian spine in some. Pygidial axis of 3 to 12 simple, unmodified rings or with ring furrows effaced; usually prominent, with axial spine or spines in some. Pleural fields furrowed or not. Border narrow, with denticulate or spinose margin. Doublure narrow. *Lower Cambrian–Middle Cambrian.*

#### Family TSUNYDISCIDAE

S. Zhang, 1980

[*nom. transl.* JELL, herein, ex Tsunydiscinae S. ZHANG in W. ZHANG, LU, & others, 1980, p. 40]

Glabella extremely narrow, lateral glabellar furrows usually obscure, with rounded and expanded frontal glabellar lobe. SO transverse, complete; LO at least as long as L1, usually expanded laterally, may bear sharp, posteriorly directed spine. Long, curved posterior fixigenal spine may be present. Librigena long. Pygidium with narrow, multisegmented axis (six or more segments). *Lower Cambrian.*

**Tsunydiscus** W. CHANG, 1966, p. 150 [\**Hebediscus niutitangensis* W. ZHANG, 1964, p. 3; OD; holotype (W. ZHANG, LU, & others, 1980, pl. 5, fig. 3), 21470, NIGP, Nanjing] [= *Mianxiandiscus* S. ZHANG & ZHU in W. ZHANG, LU, & others, 1980, p. 44 (type, *M. armatus*; OD; NIGP 37389); *Liangshandiscus* S. ZHANG in W. ZHANG, LU, & others, 1980, p. 46 (type, *L. liangshanensis*; OD; NIGP 37400); *Emeidiscus* S. LI, 1980, p. 44 (type, *E. planilimbatus*; OD; CIGMR st279); *Huheidiscus* W. CHANG in LU & others, 1974, p. 83 (type, *Hebediscus orientalis* W. ZHANG, 1953, pl. 1, fig. 1; OD; NIGP 7033); *Shizhudiscus* S. ZHANG & ZHU in W. ZHANG, LU, & others, 1980, p. 51 (type, *S. longquanensis*; OD; NIGP 37431); *Guizhoudiscus* S. ZHANG in W. ZHANG, LU, & others, 1980, p. 55 (type, *G. kaiyangensis*; OD; NIGP 37460; = *Eodiscus chintingshanensis* LU, 1942, p. 180)]. Glabella conical, slightly expanded in frontal lobe; S1 and S2 usually



Tsunyidiscus

FIG. 242. Tsunyidiscidae (p. 387)

evident but variable; SO variable but may be well impressed; border smooth or with epiborder furrow, row of nodes, or median expansion. Thorax with three segments. Pygidium with extremely narrow axis reaching close to posterior border furrow; axis multisegmented, with 6 to 10 axial rings; pleural areas with or without pleural furrows; border narrow, with or without marginal nodes. *lower Lower Cambrian–middle Lower Cambrian*: China (Hubei, Guizhou, Sichuan, Shaanxi, Yunnan).—FIG. 242. \**T. niutitangensis*, lower Lower Cambrian (Shuijingtuo Formation), Guizhou (near Zhun Yi City); holotype,  $\times 20$  (W. Zhang, Lu, & others, 1980).

#### Family HEBEDISCIDAE

Kobayashi, 1944

[*nom. transl.* JELL, herein, ex Hebediscinae KOBAYASHI, 1944a, p. 45] [= *Delgadoiinae* KOBAYASHI, 1943, p. 40; *Pagetiellinae* S. ZHANG in W. ZHANG, LU, & others, 1980, p. 23; *Dicerodiscinae* S. ZHANG in W. ZHANG, LU, & others, 1980, p. 21]

Glabella wide at base, usually without lateral furrows, tapering forward or parallel sided, separating fixigenae anteriorly. SO transverse, complete; occipital ring as long as L1, rarely spinose or bluntly expanded. Pygidium with anteriorly wide, tapering axis of four or more rings plus terminus. *Lower Cambrian–lower Middle Cambrian.*

**Hebediscus** WHITEHOUSE, 1936, p. 80 [\**Prychoparia atleborensis* SHALER & FOERSTE, 1888; OD; holotype (SHALER & FOERSTE, 1888, pl. 2, fig. 14), 18332, USNM, Washington, D.C.]. Glabella straight sided, anteriorly truncated; LO poorly

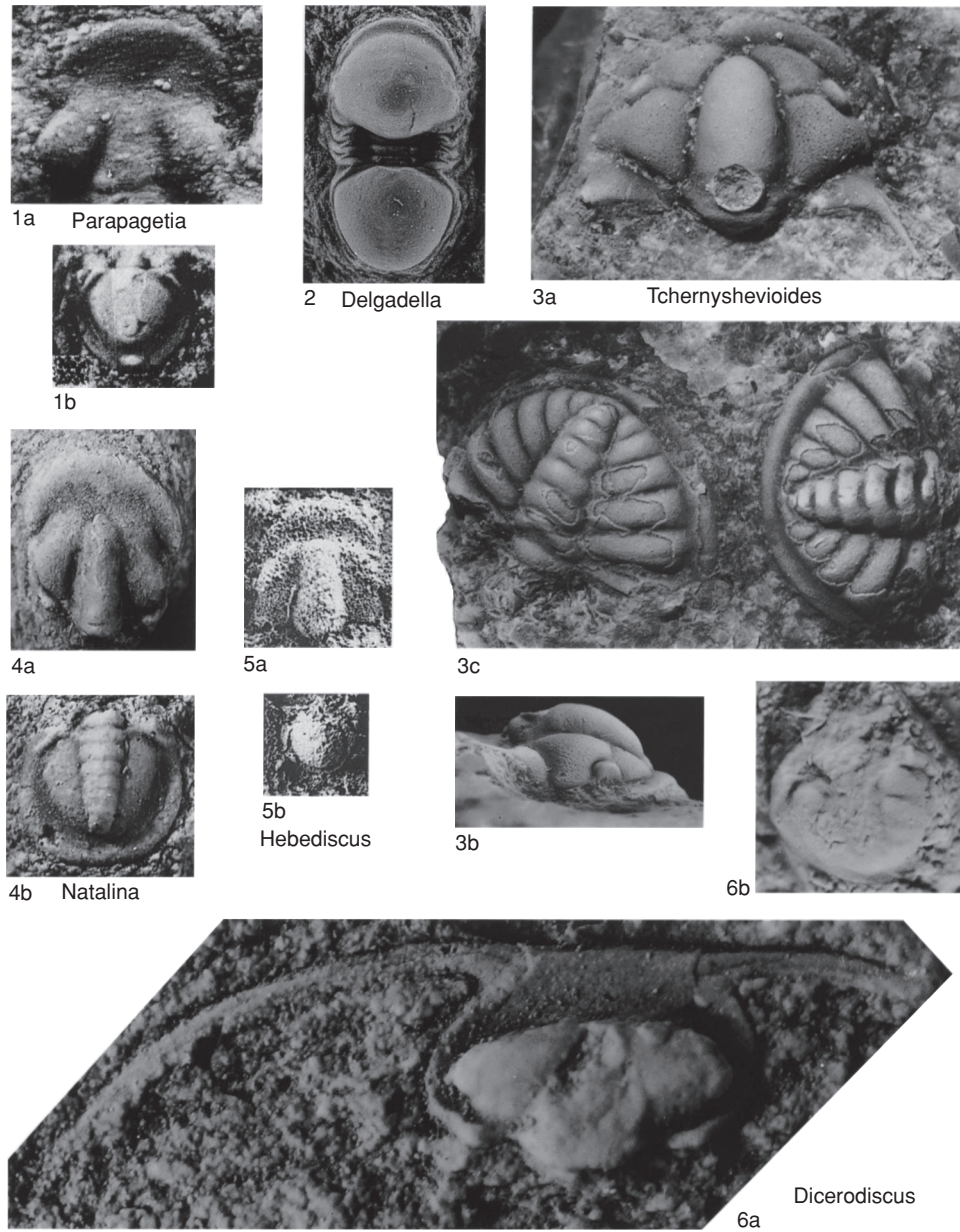


FIG. 243. Hebediscidae (p. 388–390)

defined if at all; anterior border furrow elongate; border short, flat; palpebral lobe long, usually without palpebral furrow; librigena large for family. Thorax with three segments. Pygidium semi-elliptical; axis reaching border furrow posteriorly, with seven or more rings plus small terminus; pleural area narrow, with or without furrows; border narrow, smooth or with marginal denticles. *Lower*

*Cambrian*: USA (Massachusetts), Canada (Newfoundland), England, Spain, Russia (Siberian Platform, Altay), Mongolia, Morocco.—FIG. 243, 5a, b. \**H. attleboroensis*, Lower Cambrian, Hoppin Slate, Massachusetts (North Attleboro); a, cranidium,  $\times 8$ ; b, pygidium,  $\times 8$  (Shaw, 1950).

*Delgadella* WALCOTT, 1912c, p. 560 [*Lingulepis lusitanica* DELGADO, 1904, p. 365; OD; type not

traced] [= *Alemtejoia* KOBAYASHI, 1943, p. 40 (type, *Microdiscus souzai* DELGADO, 1904, p. 351; SD KOBAYASHI, 1944a, p. 68); *Delgadoia* VOGDES, 1917, p. 27 (type, *Microdiscus caudatus* DELGADO, 1904, p. 349); *Delgadodiscus* KOBAYASHI, 1935, p. 112 (type, *Microdiscus caudatus* DELGADO, 1904, p. 349; OD); *Pagetiellus* LERMONTOVA, 1940, p. 119 (type, *Microdiscus lenaicus* TOLL, 1899, p. 23; OD); *Pentagonalia* GEYER, 1988, p. 109 (type, *P. amouslekensis*; OD; SMF 41767)]. Cephalon convex; axial furrow almost obsolete, particularly on external surface; glabellar furrows absent; border furrow and narrow border distinct; palpebral lobe poorly defined; librigena long. Thorax with three segments. Pygidium with long axis of 10 rings; axial furrow almost obsolete; pleural area usually smooth; border and border furrow narrow. *Lower Cambrian*: Russia (Siberian Platform, Mt. Altay), Mongolia, Spain, Sardinia, Portugal, Morocco, Canada (Newfoundland).—FIG. 243,2. *D. lenaicus* (TOLL), Lower Cambrian (Botomian), Siberian Platform (Lena River, Yakutia); lectotype,  $\times 3.5$  (Lermontova, 1951a).

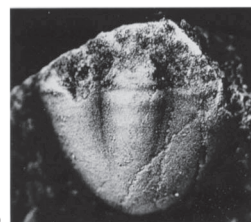
**Dicerodiscus** W. ZHANG, 1964, p. 3 [*\*D. tsunyiensis*; OD; holotype (W. ZHANG, LU, & others, 1980, pl. 1, fig. 5), 37305, NIGP, Nanjing]. Glabella conical, unfurrowed; LO usually with small spine; pair of long, anterior fixigenal spines running laterally from anterior border then curving posteriorly; border long between spines, narrow laterally; facial suture lacking; eye lobe indistinct on lateral part of cheek elevation. Thorax unknown. Pygidium convex; parallel-sided axis not reaching border furrow; three pairs of pleural furrows; border narrow. *Lower Cambrian (Qiongzhusian—Canglangpuan)*: China (Guizhou, Sichuan).—FIG. 243,6a. *\*D. tsunyiensis*, Lower Cambrian (Canglangpuan), Guizhou; holotype, cephalon,  $\times 20$ .—FIG. 243,6b. *D. pertenus*, Lower Cambrian (Qiongzhusian), Sichuan; pygidium,  $\times 15$  (W. Zhang, Lu, & others, 1980).

**Luvsanodiscus** KOROBV, 1980, p. 72 [*\*L. gammatius*; OD; holotype (KOROBV, 1980, pl. 4, fig. 16), 66, coll. 4251, PIN, Moscow]. Glabella with straight, parallel to slightly tapering sides, with truncated anterior, weak or no lateral glabellar furrows; LO poorly defined, with median tubercle; palpebral lobe overhanging border laterally; palpebral furrow shallow, exsagittal. Pygidium with axis of seven rings; ring and pleural furrows poorly impressed; border extremely narrow, with short marginal spines. *Lower Cambrian (Atdabanian)*: Mongolia.—FIG. 244,1a,b. *\*L. gammatius*, Lower Cambrian (Atdabanian, Egyngolskaya Suite), northwestern Mongolia; a, holotype, cranium,  $\times 11$ ; b, pygidium,  $\times 11$  (Korobov, 1980).

**Natalina** E. ROMANENKO in REPINA & ROMANENKO, 1978, p. 128 [*\*N. incita*; OD; holotype (REPINA & ROMANENKO, 1978, pl. 6, fig. 15), 1811/80, ZSGU, Novokuznetsk] [= *Limbadiscus* KOROBV, 1980, p. 66 (type, *L. dilatatum*; OD; PIN 58, coll. 4251)]. Glabella parallel sided, anteriorly rounded, unfurrowed, without posterior spine; border furrow long; border flat to gently convex, tapering laterally;

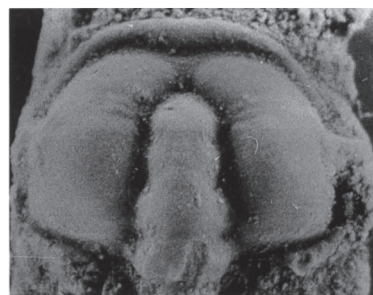


1a

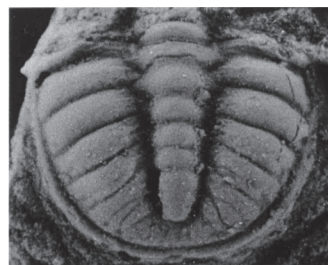


1b

Luvsanodiscus



2a



2b

Neopagetina

FIG. 244. Hebediscidae (p. 389–390)

palpebral lobe projecting from fixigenal elevation; palpebral furrow distinct; librigena small, longer than wide. Pygidium with almost parallel-sided axis of six rings plus terminus reaching into posterior border furrow; pleural area narrow, smooth; border furrow wide; border rimlike, of uniform width. *Lower Cambrian (Botomian)*: Russia (Altay, Gorno-Altayskaya).—FIG. 243,4a,b. *\*N. incita*, Lower Cambrian (Sanashtykgol), Gorno-Altayskaya (Sema River); a, holotype, cranium,  $\times 10$ ; b, pygidium,  $\times 10$  (Repina & Romanenko, 1978).

**Neopagetina** POKROVSKAYA, 1960, p. 56, *nom. nov. pro* *Pagetina* LERMONTOVA, 1940, p. 121, *non* BARNARD,



1931 [*\*Pagetina rjonsnitzkii* LERMONTOVA, 1940, p. 121; OD; holotype (LERMONTOVA, 1951a, pl. 3, fig. 7a), 34/5156, TsGM, St. Petersburg]. Glabella tapering forward to rounded anterior; preglabellar median furrow short, wide, depressed; anterior border extremely short, smooth, may be medially elongate; eye ridge anteriorly convex; librigena extremely short; LO simple, may have short occipital spine. Pygidial axis of six rings plus terminus, not reaching border furrow; pleural field with well-impressed pleural furrows; border narrow, smooth. *Lower Cambrian (Botomian, Toyonian)*: Russia (Siberian Platform, Mt. Altay), Mongolia, Greenland.—FIG. 244, 2a, b. *\*N. rjonsnitzkii*, Botomian, Kutorgina Formation, Siberia (Peleduy River); a, lectotype, cranium,  $\times 12$ ; b, pygidium,  $\times 7$  (Lermontova, 1940).

**Parapagetia** REPINA in REPINA & others, 1964, p. 258 [*\*P. limbata*; OD; holotype (REPINA in REPINA & others, 1964, pl. 38, fig. 1), 253/1, CSGM, Novosibirsk] [= *Planodiscus* KOROBV, 1980, p. 65 (type, *P. patulus*; OD; PIN 54, coll. 4251)]. Glabella parallel sided, relatively short; occipital spine absent or short; preglabellar field long; anterior border poorly defined, usually slightly elongate medially. Pygidium with short axis of four rings plus terminus; border and border furrow together wide, with poor definition between them; border sometimes elongate posteromedially. *Lower Cambrian (Botomian)*: Russia (Gorno-Altayskaya, Tuva), Mongolia.—FIG. 243, 1a. *\*P. limbata*, Lower Cambrian (Sanashtykgol), Gorno-Altayskaya (River Katun); holotype, cranium,  $\times 15$ .—FIG. 243, 1b. *P. plana* E. ROMANENKO, Lower Cambrian (Sanashtykgol), Gorno-Altayskaya (River Ul'men'); pygidium,  $\times 15$  (Repina & others, 1964).

**Tchernyshevioides** HAJRULLINA in REPINA, PETRUNINA, & HAJRULLINA, 1975, p. 100 [*\*T. ninae*; OD; holotype (REPINA, PETRUNINA, & HAJRULLINA, 1975, pl. 7, fig. 1–2), 483/160, MMG, Tashkent]. Glabella long, reaching anterior border furrow; SO well impressed; occipital ring with long posterodorsal spine; palpebral lobe short, prominent, and situated well forward; librigena tiny. Pygidium with axis of five rings plus terminus; pleural furrows impressed; border narrow, smooth. *Middle Cambrian (Amgaian)*: Asia (Tian-Shan), Morocco.—FIG. 243, 3a–c. *\*T. ninae*, Amgaian (*Pseudanomocarina* Zone), Tian-Shan (Sulyukta region); a, holotype, cranium,  $\times 8$ ; b, lateral view of cranium,  $\times 8$ ; c, pygidia,  $\times 8$  (Repina, Petrunina, & Hajrullina, 1975).

### Family CALODISCIDAE Kobayashi, 1943

[*nom. transl.* ÖPIK, 1975a, p. 25, ex Calodiscinae KOBAYASHI, 1943, p. 38] [= *Brevidiscinae* KOBAYASHI, 1943, p. 39; *Neocobboldinae* S. ZHANG in W. ZHANG, LU, & others, 1980, p. 30]

Glabella parallel sided or tapering forward, may be rounded and expanded anteriorly and may be divided by transverse glabel-

lar furrows. SO transverse, complete; LO simple, at least as long as L1 or reduced, not spinose or expanded. Palpebral lobes short and prominent when present. Pygidium with wide, tapering axis of fewer than six segments. *Lower Cambrian–lower Middle Cambrian*.

**Calodiscus** HOWELL, 1935b, p. 224, *nom. nov. pro Goniodiscus* RAYMOND, 1913b, p. 101, *non* MÜLLER & TROSCHEL, 1842 [*\*Agnostus lobatus* HALL, 1847, p. 258; OD; syntypes (RASETTI, 1952a, pl. 51, fig. 8–11), 210, AMNH, New York] [= *Brevidiscus* KOBAYASHI, 1943, p. 39 (type, *B. lunulatus*; OD; USNM 15393)]. Glabella parallel sided, with two, shallow transglabellar furrows; glabellar anterior reaching border furrow; border narrow laterally, smooth or with a few tubercles laterally; eyes and facial sutures absent. Pygidial axis of few rings (four or five), wide, reaching border furrow or close to it; border narrow, with smooth or serrated margin. *Lower Cambrian (Atdabanian, Botomian)*: Sweden, England, Germany, Morocco, Siberia (Mt. Altay), USA (Massachusetts, New York, Alaska), Canada (Newfoundland), Greenland.—FIG. 245, 4a, b. *\*C. lobatus* (HALL), Botomian (West Castleton Formation), New York (Troy); a, syntype, cephalon,  $\times 12$ ; b, syntype, pygidium,  $\times 12$  (Rasetti, 1952a).

**Chelediscus** RUSHTON, 1966, p. 18 [*\*C. acifer*; OD; holotype (RUSHTON, 1966, pl. 2, fig. 26a–e), A.57104, SM, Cambridge]. Glabella conical, bilobed (anterior lobe much smaller in type); LO depressed, forming basal lobes; median preglabellar furrow present; border furrow with line of pits; border with pair of marginal spines laterally and pair of genal spines. Thorax with two segments. Pygidium strongly convex; axis wide, tapering strongly in posterior half, of five or six rings; pleural areas with rudimentary furrows; border narrow. *Lower Cambrian (Botomian)*: England, USA (New York), Canada (Newfoundland), Russia (Siberian Platform).—FIG. 245, 1a–c. *\*C. acifer*, upper *Protolenus* Zone, Purley Shale, England (Warwickshire); a, paratype, cephalon,  $\times 8$ ; b, c, enrolled holotype in pygidial and lateral views,  $\times 8$  (Rushton, 1966).

**Korobovia** JELL in BENGTON & others, 1990, p. 263 [*\*K. ocellata*; OD; holotype (JELL in BENGTON & others, 1990, fig. 177c,f), 112656, NMVP, Melbourne]. Glabella may be subconical, reaching border furrow, with vague transverse furrow about one-third length from anterior; eye ridge convex forward, leading to small palpebral lobe situated well forward and low on fixiginal elevation; border short, rimlike, with two small nodes just behind small librigena. Pygidium transverse; axis broad, of 3 rings plus terminus, each with high, spinelike tubercle; pleural furrows impressed; border narrow, with or without marginal spines. *Lower Cambrian (Botomian)*: South Australia, Mongolia, Russia (Gorno-Altayskaya).—FIG. 245, 3a–c. *\*K. ocel-*

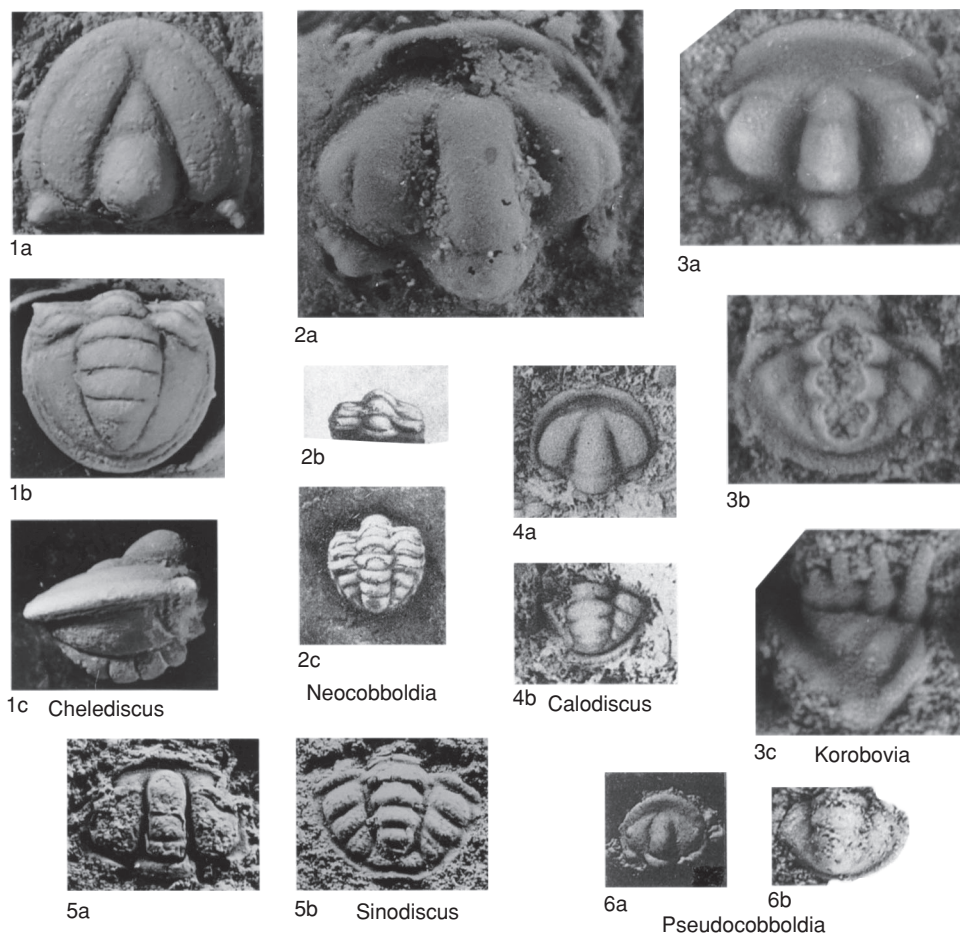


FIG. 245. Calodiscidae (p. 390–392)

*lata*, *Pararaia janeae* Zone, Oraparinna Shale, South Australia (Flinders Range); *a*, holotype, cranidium,  $\times 15$ ; *b*, pygidium,  $\times 15$ ; *c*, lateral view of pygidium,  $\times 15$  (Bengtson & others, 1990).

**Neocobboldia** RASETTI, 1952a, p. 438, *nom. nov. pro Cobboldia* LERMONTOVA, 1940, p. 120, *non* BRAUER, 1887; *nec* LEIPER, 1910 [*\*Cobboldia dentata* LERMONTOVA, 1940, p. 120; OD; holotype (LERMONTOVA, 1951a, pl. 3, fig. 2) 23/5156, TsGM, St. Petersburg] [= *Margodiscus* KOROBV, 1980, p. 54 (type, *M. rackovskii* KOROBV, 1980, p. 55; OD; PIN 18, coll. 4251)]. Glabella parallel sided, anteriorly rounded at border furrow, unfurrowed except for well-impressed, transverse SO; fixigenae narrow, separated anteriorly by short, depressed median preglabellar field; border furrow usually longer than border; anterior border short, convex, tapering only slightly laterally; palpebral furrow slitlike, exsagittal, short. Pygidium transverse; axis wide, of 3 or 4 rings plus terminus, finishing at border furrow;

pleural areas usually with well-impressed pleural furrows; border narrow, denticulate. *Lower Cambrian (Botomian)*: Russia (Siberian Platform, Gorno-Altayskaya), Mongolia. — FIG. 245, 2a–c. *\*N. dentata*, Lower Cambrian (*Protolenus* Zone), Siberia (Lena River, Yakutia); *a*, holotype, cranidium,  $\times 6.5$ ; *b, c*, thorax and pygidium,  $\times 6.5$  (Lermontova, 1951a).

**Pseudocobboldia** HUPÉ in BOUDDA, CHOUBERT, & FAURE-MURET, 1979, p. 73 [*\*Cobboldia(?) pulchra* HUPÉ, 1953a, p. 113; OD; holotype (HUPÉ, 1953a, pl. 11, fig. 21), not traced]. Glabella subconical, anteriorly rounded at border furrow, unfurrowed except for well-impressed SO; border smooth, short, and flat; prominent eye tubercle situated laterally above narrowest part of border; eye ridge running from axial furrow behind glabellar anterior to eye. Pygidium transverse; axis wide, consisting of three rings plus terminus that does not reach border furrow; pleural area narrow, with shallow pleural

furrows; border narrow, tapering posteriorly, weakly denticulate. *lower Middle Cambrian*: Morocco.—FIG. 245, 6a, b. \**P. pulchra* (HUPÉ), lower Middle Cambrian (Jbel Wawrmast Formation), Morocco (Anti-Atlas Mountains); *a*, holotype, cranidium,  $\times 4$  (Hupé, 1953a); *b*, pygidium,  $\times 14$  (Geyer, 1988).

**Sinodiscus** W. CHANG in LU & others, 1974, p. 83 [\**S. shipaiensis*; OD; holotype (W. CHANG in LU & others, 1974, pl. 31, fig. 5), 37350, NIGP, Nanjing] [= *Tologoja* KOROBOW, 1980, p. 81 (type, *T. subquadrata*; OD; PIN 99, coll. 4251)]. Glabella cylindrical except for gently expanded and rounded anterior lobe and wide LO, reaching anterior border furrow, with 2 transglabellar furrows variably impressed; LO wide, as long as L1, nonspinose; border short, upturned, uniform; palpebral lobe short, level with anterior glabellar lobe, defined by well-impressed palpebral furrow; librigena small. Thorax with three segments. Pygidial axis wide, of two to five rings plus posteriorly rounded terminus isolated from border furrow; pleural furrows well impressed; border narrow, uniform, without marginal spines. *Lower Cambrian (Botomian, upper Qiongzhusian)*: Mongolia, China (Hubei, Guizhou).—FIG. 245, 5a, b. \**S. shipaiensis*, upper Qiongzhusian (Shipai Formation), western Hubei; *a*, holotype, cranidium,  $\times 6$ ; *b*, pygidium,  $\times 6$  (Lu & others, 1974).

### Family WEYMOUTHIIDAE Kobayashi, 1943

[Weymouthiidae KOBAYASHI, 1943, p. 40, *emend.* JELL, 1975a, p. 27]  
[=Ladadiscinae SOLOVIEV, 1964, p. 34]

Most taxa in this family are large for the superfamily. Glabella wide at base, normally parallel sided but may taper gently or expand medially, usually without glabellar furrow but, if present, furrow may be incomplete or transglabellar and deeply impressed. Fixigenae normally confluent in front of glabella. SO often not impressed but dorsally complete when evident; LO simple or shortened by posterodorsal expansion of rounded L1. Without eyes. Pygidium with long, strongly tapering axis; axis with 10 or more rings (when segmentation is evident); segmentation commonly effaced. *Lower Cambrian—Middle Cambrian*.

**Weymouthia** RAYMOND, 1913b, p. 102 [\**Agnostus nobilis* FORD, 1872, p. 421; OD; types not traced, reported lost by WALCOTT, 1890b]. Cephalon effaced except for border furrow; border narrow, bearing tubercles laterally. Thorax with three segments. Pygidium effaced except for border furrow; border narrow. *Lower Cambrian*: USA (Massachusetts).—FIG. 246, 6. \**W. nobilis* (FORD), Lower Cam-

brian (Hoppin Slate), Massachusetts (North Attleboro); articulated specimen,  $\times 5$  (Shaw, 1950).

**Abakolia** BOGNIBOVA in TCHERNYSHEVA, 1971, p. 205 [\**A. pauca*; OD; holotype (TCHERNYSHEVA, 1971, pl. 24, fig. 3), P-1056a-3, CSGM, Novosibirsk] [= *Costadiscus* BABCOCK, 1994a, p. 115 (type, *C. minutus*; OD; MGUH 21.322)]. Cephalon semicircular; glabella with S1 as small pits laterally, with depressed preglabellar median furrow; border elongate anteriorly, tapering laterally; eye ridge, palpebral lobe, and eye absent. Pygidium semicircular; axis narrow, of six rings and terminal portion, not reaching border furrow; each pleural area crossed by at least six pleural furrows, and with one or two short, almost longitudinal pleural ribs at rear, partly behind axis; border extremely narrow. *Lower Cambrian (Botomian)*: Mongolia. *Middle Cambrian*: Russia (Mt. Altay), Greenland.—FIG. 247, 6a, b. \**A. pauca*, Middle Cambrian (Lower Amgaian, Abakolskaya Suite), Altay (western Sayan Mountains); *a*, holotype, cranidium,  $\times 8$ ; *b*, pygidium,  $\times 10$  (Tchernysheva, 1971).

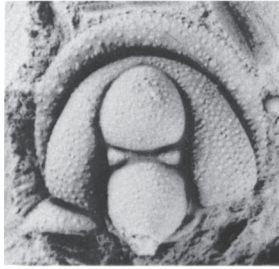
**Acidiscus** RASETTI, 1966a, p. 11 [\**A. birdi*; OD; holotype (RASETTI, 1966a, pl. 6, fig. 11–12), 145987, USNM, Washington, D.C.]. Cephalic border with one or two pairs of marginal spines; glabella isolated from border furrow, with two short, pitlike pairs of lateral furrows; occipital and genal spines present. Pygidium like *Serradiscus*; axis with ten rings; pleurae smooth; doublure may be extended into short spines. *upper Lower Cambrian*: USA (New York), Canada (Newfoundland), England.—FIG. 248, 7a, b. \**A. birdi*, upper Lower Cambrian (*Acimetopus bilobatus* faunule), New York (Griswold Farm); *a*, holotype, cranidium,  $\times 2$ ; *b*, paratype, pygidium,  $\times 2$  (Rasetti, 1966a).

**Acimetopus** RASETTI, 1966a, p. 13 [\**A. bilobatus*; OD; holotype (RASETTI, 1966a, pl. 4, fig. 1–4), 145991, USNM, Washington, D.C.]. Cephalic border strongly convex, with a pair of marginal spines laterally; glabella strongly divided by deep furrow (S1 plus S2) with large anterior lobe isolated from border furrow, with L2 as a pair of small, separated, subtriangular lobes, and with L1 large and inflated posterodorsally into a cranidial spine; LO short and low behind L1; genal spines present. Pygidial axis of type with nine rings, strongly inflated, with vertical spine on second ring; border furrow deep; border narrow, without spines. *upper Lower Cambrian*: USA (New York), England.—FIG. 246, 1a–d. \**A. bilobatus*, upper Lower Cambrian (*Acimetopus bilobatus* faunule), New York (Griswold Farm); *a*, holotype, cranidium,  $\times 5$ ; *b*, same in lateral view,  $\times 5$ ; *c*, paratype, pygidium,  $\times 5$ ; *d*, paratype, pygidium in lateral view,  $\times 5$  (Rasetti, 1966a).

**Analox** RASETTI, 1966a, p. 15 [\**A. bipunctata*; OD; holotype (RASETTI, 1966a, pl. 6, fig. 1–3), 145993, USNM, Washington, D.C.]. Glabella extending forward into merged axial and border furrows; S1 long but not deep; L1 large, drawn out posterodorsally into glabellar spine; anterior lobe wider than anterior portion of L1; LO indistinct beneath



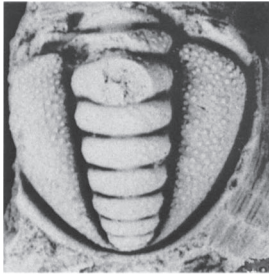
- glabellar spine. Anterior border swollen medially, defined by furrows running anterolaterally from axial furrow at front of glabella, ending in a pit; border absent laterally; posterior border furrow fading out a little in front of genal angle. Pygidium with long axis (eight rings in type); border narrow, defined by equally narrow border furrow; doublure forming vertical face without spines. *upper Lower Cambrian*: USA (New York).—FIG. 247, 1a–c. \**A. bipunctata*, upper Lower Cambrian (*Acimetopus bilobatus* faunule), New York (Griswold Farm); *a*, holotype, cranidium,  $\times 6$ ; *b*, lateral view of same,  $\times 6$ ; *c*, paratype, pygidium,  $\times 6$  (Rasetti, 1966a).
- Bathydiscus** RASETTI, 1966a, p. 16 [\**B. dolichometopus*; OD; holotype (RASETTI, 1966a, pl. 9, fig. 1–3), 145995, USNM, Washington, D.C.]. Glabella wide, convex, unfurrowed except for faint occipital furrow; median part of border gently arched in anterior view; posterior border with pair of erect spines close to axial furrow as in *Oodiscus*. Pygidial axis wide, tapering, unfurrowed; border furrow wider posteriorly; border narrow, depressed posteriorly; doublure vertical and high laterally (i.e., not reflexed parallel to dorsal exoskeleton), much lower posteriorly. *upper Lower Cambrian*: USA (New York), Canada (Newfoundland).—FIG. 247, 5a–c. \**B. dolichometopus*, upper Lower Cambrian (*Acimetopus bilobatus* faunule), New York (Griswold Farm); *a*, holotype, cranidium,  $\times 4$ ; *b*, paratype, pygidium,  $\times 3$ ; *c*, paratype, pygidium,  $\times 4$  (Rasetti, 1966a).
- Bolboparia** RASETTI, 1966a, p. 18 [\**B. superba*; OD; holotype (RASETTI, 1966a, pl. 5, fig. 1–4), 145998, USNM, Washington, D.C.]. Glabella anteriorly pointed, extended posterodorsally into a spine, with poorly defined lateral furrows; LO short, behind glabellar spine; cheeks inflated anterolaterally, hanging over border; preglabellar field depressed as broad furrow; anterior border expanded medially, with a pair of marginal spines laterally and near the genal angle one or more pairs of tubercles in front of transverse furrow running from border furrow to margin; genal spines present. Pygidial axis of ten rings, spine on second ring; narrow border extended into ventrally directed spines. Surface densely granulate in three known species. *upper Lower Cambrian*: USA (New York), Canada (Quebec).—FIG. 246, 2a, b. \**B. superba*, upper Lower Cambrian (*Acimetopus bilobatus* faunule), New York (Griswold Farm); *a*, holotype, cranidium,  $\times 4$ ; *b*, lateral oblique view of same,  $\times 4$  (Rasetti, 1966a).—FIG. 246, 2c, d. *B. elongata*, upper Lower Cambrian (*Acimetopus bilobatus* faunule), New York (Griswold Farm); *c*, paratype, pygidium,  $\times 4$ ; *d*, lateral view of same,  $\times 4$  (Rasetti, 1966a).
- Cephalopyge** GEYER, 1988, p. 123 [\**C. notabilis*; OD; holotype (GEYER, 1988, fig. 61), 41781, SMF, Frankfurt am Main]. Cephalon subcircular except for straight posterior; externally smooth, convex, and hanging over extremely narrow border; glabella evident on internal mold, conical, with SO being only furrow evident; LO short, hanging over posterior margin. Thorax with three segments. Pygidium externally smooth, convex; internal mold showing conical axis extending to posterior margin; border not present. *upper Lower Cambrian*: Morocco.—FIG. 248, 2. \**C. notabilis*, upper Lower Cambrian (Jbel Wawrmast Formation), Morocco (Anti-Atlas Mountains); holotype,  $\times 4$  (Geyer, 1988).
- Cobboldites** KOBAYASHI, 1943, p. 38 [\**Microdiscus comleyensis* COBBOLD, 1910, p. 21; OD; lectotype (COBBOLD, 1910, pl. 3, fig. 2), A18.478, SM, Cambridge]. Glabella conical, broadly rounded anteriorly at border furrow, unfurrowed; border flat, narrowing laterally. Pygidium with seven axial rings (usually not evident on exterior surface) tapering posteriorly to the border furrow; border narrow, tapering posteriorly, without spines or tubercles. *upper Lower Cambrian*: England, Morocco. ?*Middle Cambrian*: England.—FIG. 247, 4a, b. \**C. comleyensis*, upper Lower Cambrian (Comley Series, *Protolenus* Limestone), England (Shropshire); *a*, syntype, cranidium,  $\times 5$ ; *b*, syntype, pygidium,  $\times 5$  (Cobbold, 1910).
- Jinghediscus** XIANG & ZHANG, 1985, p. 92 [\**J. nummularius*; OD; holotype (XIANG & ZHANG, 1985, pl. 1, fig. 1), T1348, CAGC, Beijing]. Like *Mallagnostus*, with bilobed glabella divided by transverse furrow and posteriorly inflated. [Questionably a synonym of *Mallagnostus*.] *lower Middle Cambrian*: China (Xinjiang), ?Australia (Queensland).—FIG. 246, 4a, b. \**J. nummularius*, lower Middle Cambrian (*Xystridura* Zone), Xinjiang; *a*, holotype, cranidium,  $\times 8$ ; *b*, pygidium,  $\times 10$  (Xiang & Zhang, 1985).
- Leptochilodiscus** RASETTI, 1966a, p. 25 [\**L. punctulatus*; OD; holotype (RASETTI, 1966a, pl. 11, fig. 1–3), 146009, USNM, Washington, D.C.] [= *Kerberodiscus* BASSETT, OWENS, & RUSHTON, 1976, p. 630 (type, *K. succinctus*; OD; NMW 75.5G.7)]. Glabella long, narrow, tapering to pointed anterior, and not reaching border furrow; SO well impressed; LO short; border extremely narrow. Pygidial axis with ten axial rings, almost effaced, reaching posterior border furrow; border extremely narrow, extended ventrally with series of short spines; margin arched over median line in posterior view. *upper Lower Cambrian*: USA (New York), Canada (Quebec), Wales.—FIG. 248, 5a–c. \**L. punctulatus*, upper Lower Cambrian (*Acimetopus bilobatus* faunule), New York (Griswold Farm); *a*, holotype, cephalon,  $\times 7.5$ ; *b, c*, pygidium, posterior and dorsal views, respectively,  $\times 5$  (Rasetti, 1966a).
- Litometopus** RASETTI, 1966a, p. 26 [\**L. longispinus*; OD; holotype (RASETTI, 1966a, pl. 8, fig. 1–3), 146012, USNM, Washington, D.C.]. Cephalon almost semicircular; glabella tapering forward to border furrow, unfurrowed; border convex, with pair of small marginal spines laterally and large genal spines. Pygidium same shape as cephalon; axis tapering posteriorly to border furrow, unfurrowed to very faintly furrowed; border flat, wide, with doublure sloping adaxially, and with serrated margin. [Questionably a synonym of *Cobboldites*.]



1a



1b



1c Acimetopus



1d



6 Weymouthia



2c



2d



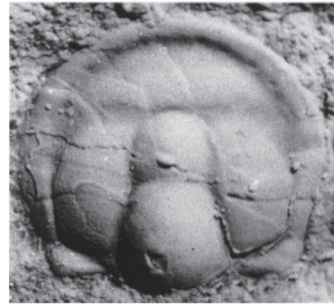
3 Semadiscus



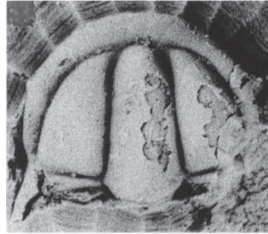
2a



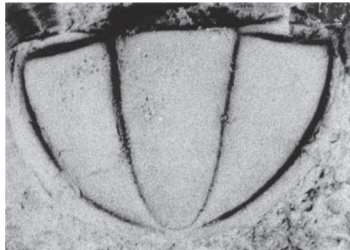
2b Bolboparia



4a



5a



5b Litometopus



4b Jinghediscus

FIG. 246. Weymouthiidae (p. 392-398)

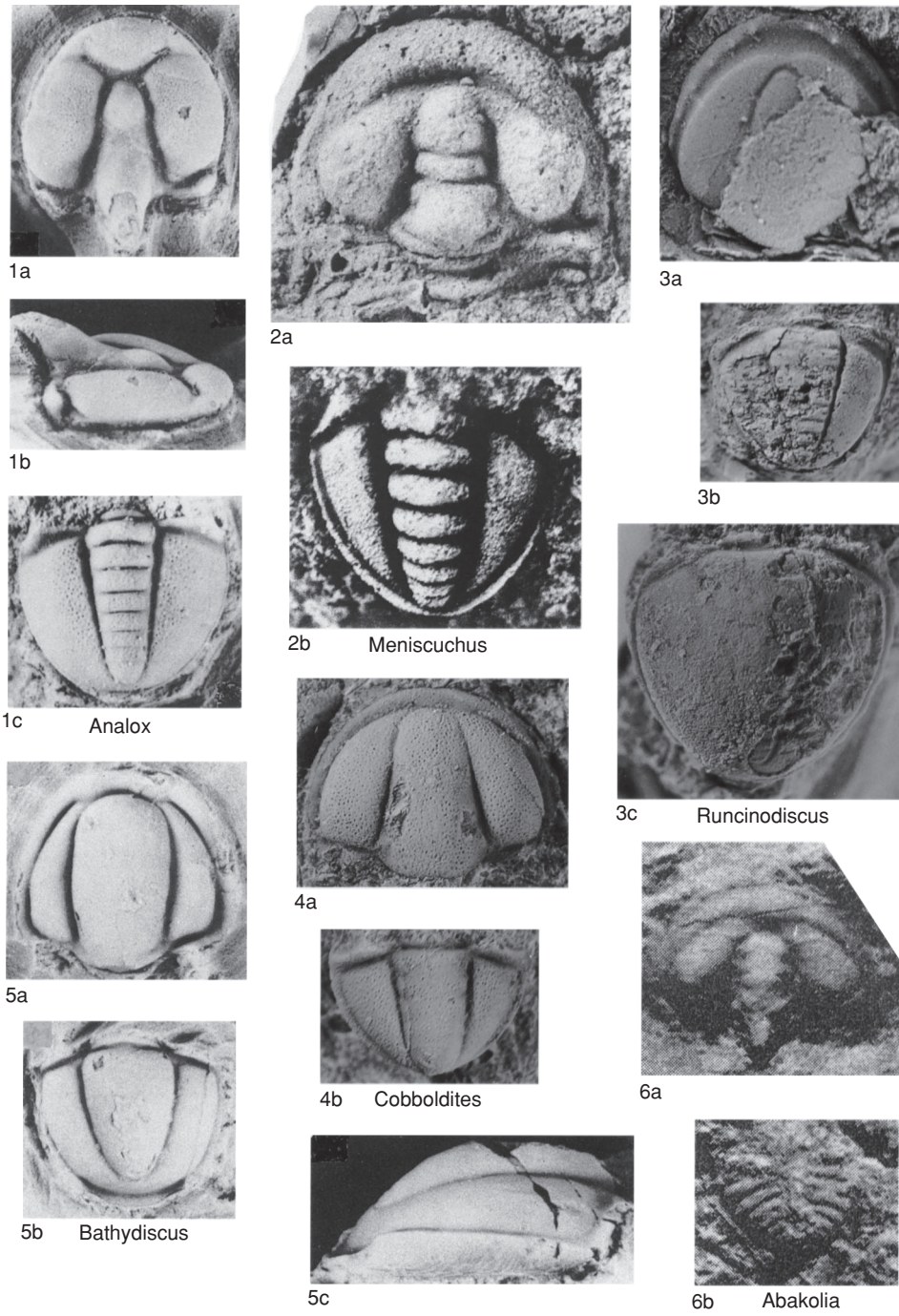


FIG. 247. Weymouthiidae (p. 392–398)



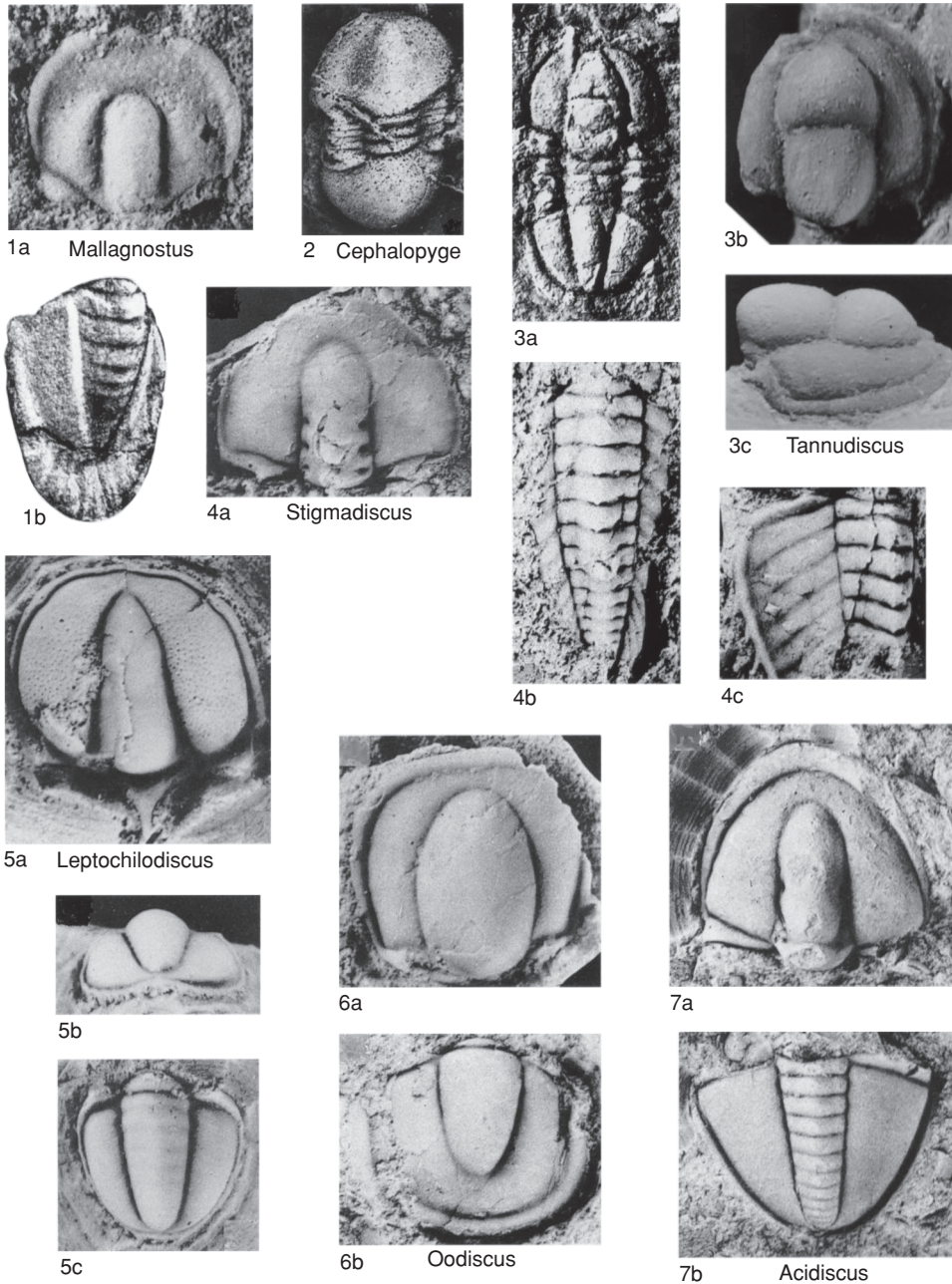


FIG. 248. Weymouthiidae (p. 392–398)

upper Lower Cambrian: USA (New York).—FIG. 246, 5a, b. \**L. longispinus*, upper Lower Cambrian (*Acimetopus bilobatus* faunule), New York (Taconic, Griswold Farm); a, holotype, cephalon,  $\times 3$ ; b, pygidium,  $\times 3$  (Rasetti, 1966a).

*Mallagnostus* HOWELL, 1935b, p. 228 [*Aagnostus desideratus* WALCOTT, 1890b, p. 629; OD; holotype (RASETTI & THEOKRITOFF, 1967, pl. 20, fig. 31), 18327, USNM, Washington, D.C.] [= *Ladadiscus* POKROVSKAYA, 1959, p. 167 (type, *L. limbatus*; OD;

VNIGNI 3536/85)]. Cephalon semielliptical; glabella unfurrowed (pits situated laterally indicate furrows in one species), finishing well behind broad border furrow; LO short, ill-defined, not spinose; anterior border long, only gently convex, tapering laterally; border furrow running to margin just anterior to genal angle. Thorax with three segments. Pygidium same shape as cephalon, with conical axis of eight or more rings, not reaching to posterior border furrow; pleural areas smooth. *upper Lower Cambrian*: USA (New York), Canada (Newfoundland), Spain, England, Russia (Tuva, Gorno-Altayskaya), Mongolia. *Middle Cambrian*: China (Tian Shan), Russia (Yakutia).—FIG. 248, 1a. \**M. desideratus* (WALCOTT), upper Lower Cambrian, New York; holotype, cranidium,  $\times 10$  (Rasetti & Theokritoff, 1967).—FIG. 248, 1b. *M. llarenai*, upper Lower Cambrian (*serratus*-Band), Herrerias-Mergel Formation, Spain (Cala); holotype, pygidium,  $\times 4$  (Richter & Richter, 1941a).

**Meniscuchus** ÖPIK, 1975a, p. 28 [\**M. menetus*; OD; holotype (ÖPIK, 1975a, pl. 4, fig. 1–2), CPC 13171, AGSO, Canberra]. Glabella rounded anteriorly at border furrow, strongly divided by complete S2 and S3; L3 of variable length (lateral lobes only in some species), posteriorly inflated and widened; LO short, low behind inflation of glabella; anterior border elongate, strongly convex, tapering laterally. Pygidium relatively narrow; axis tapering and reaching border furrow posteriorly, deeply segmented (with 4 to 10 axial rings); pleural areas unfurrowed; border uniformly narrow; doublure wide and almost vertical. *Lower Cambrian (Botomian)*: USA (Alaska, New York), Canada (Newfoundland, Quebec), Russia (Siberian Platform, Gorno-Altayskaya), Australia (New South Wales).—FIG. 247, 2a, b. \**M. menetus*, Lower Cambrian (Cymbric Vale Formation), New South Wales; a, holotype, cranidium,  $\times 8$ ; b, pygidium,  $\times 11$  (Öpik, 1975a).

**Ninadiscus** KOROBV, 1980, p. 101 [\**N. strobulatus*; OD; holotype (KOROBV, 1980, pl. 9, fig. 3), 139, coll. 4251, PIN, Moscow]. Glabella tapering gently forward to sharply rounded anterior at border furrow, with L1 expanded posterodorsally into well-rounded protrusion; S1 and S2 well impressed; L2 shorter than frontal lobe, which is shorter than L1; LO short and lower than L1; border furrow uniform throughout, may swing gently to posterior in midline; border narrow laterally, elongate sagittally, may bear up to three symmetrically arranged tubercles anteriorly. Pygidium with long, narrow axis of 10 rings reaching almost to posterior border; pleural areas smooth; border extremely narrow. *Lower Cambrian (Botomian)*: Mongolia, USA (New York).—FIG. 249, 1a, b. \**N. strobulatus*, Lower Cambrian (Egyngolskaya Suite), northwestern Mongolia; a, holotype, cranidium,  $\times 15$ ; b, pygidium,  $\times 10$  (Korobov, 1980).

**Oodiscus** RASETTI, 1966a, p. 28 [\**O. subgranulatus*; OD; holotype (RASETTI, 1966a, pl. 10, fig. 1–3), 146014, USNM, Washington, D.C.]. Cephalon tending towards subquadrate outline; glabella wide



1a



1b Ninadiscus



2a



2b Serrodiscus

FIG. 249. Weymouthiidae (p. 397–398)

(one-third cephalic width), strongly convex, completely unfurrowed except for shallow lateral depressions posteriorly as occipital furrow; preglabellar field short; border with 1 or 2 pairs of marginal spines laterally and a pair of small spines posteriorly (one species has a pair of tubercles anteriorly). Pygidium same shape as cephalon; axis tapered, unfurrowed, not reaching posterior border; border virtually flat, usually slightly wider laterally than long posteriorly. *upper Lower Cambrian*: USA (New York), Canada (Newfoundland).—FIG. 248, 6a, b. \**O. subgranulatus*, upper Lower Cambrian (*Acimetopus bilobatus* faunule), New York (Griswold

- Farm); *a*, holotype, cephalon,  $\times 5$ ; *b*, paratype, pygidium,  $\times 3$  (Rasetti, 1966a).
- Runcinodiscus** RUSHTON in BASSETT, OWENS, & RUSHTON, 1976, p. 635 [\**R. index*; OD; holotype (COBBOLD, 1931, pl. 38, fig. 17–18), 15360, SM, Cambridge]. Externally effaced; cephalon semielliptical; glabella long, tapering forward; border tuberculate, flat. Pygidium with long, conical axis of nine or more rings plus terminus; border distinct, level, short posteriorly, with ventral swellings or spines. [Questionably a synonym of *Serrodiscus*.] *upper Lower Cambrian*: England, Norway.—FIG. 247,3a–c. \**R. index*, *Protolenus* Zone, Comley Series (*Protolenus* Limestone), England (Shropshire); *a*, partly exfoliated holotype cranidium,  $\times 10$ ; *b*, mostly exfoliated pygidium,  $\times 6$ ; *c*, pygidium,  $\times 6$  (new).
- Semadiscus** E. V. ROMANENKO in REPINA & ROMANENKO, 1978, p. 109 [\**S. sollennis*; OD; holotype (E. V. ROMANENKO in REPINA & ROMANENKO, 1978, pl. 3, fig. 1), 1811/12, ZSGU, Novokuznetsk]. Glabella short, undivided except for well-impressed SO; long occipital spine present; border narrow throughout but tapering laterally. Pygidium unknown. [Questionably a synonym of *Serrodiscus*.] *Lower Cambrian (Botomian)*: Russia (Siberia, Gorno-Altayskaya), USA (New York), Canada (Newfoundland).—FIG. 246,3. \**S. sollennis*, Lower Cambrian (lower Botomian), Gorno-Altayskaya (Sema River); holotype, cranidium,  $\times 11$  (Repina & Romanenko, 1978).
- Serrodiscus** RICHTER & RICHTER, 1941a, p. 23 [\**Eodiscus (Serrodiscus) serratus*; OD; holotype (RICHTER & RICHTER, 1941a, pl. 1, fig. 1), 1234, SMF, Frankfurt am Main] [= *Paradiscus* KOBAYASHI, 1943, p. 38 (type, *Microdiscus speciosus* FORD, 1873, p. 137; OD; lectotype, NYSM 4588)]. Cephalon semielliptical; glabella long, conical or parallel sided, usually weakly furrowed or unfurrowed (but S2 and S3 may be better impressed); LO generally short, with or without a spine; cheeks joined anteriorly in short preglabellar field or separated by a depression; border convex, with up to eight pairs of tubercles laterally. Thorax with three segments. Pygidium with wide, subconical axis of more than eight rings; pleural area unfurrowed or extremely weakly furrowed on internal mold; border narrowing posteriorly, usually with ventral spines. *Lower Cambrian*: USA (New York, Massachusetts, Alaska), Canada (Newfoundland, New Brunswick, Northwest Territories), Greenland, Spitsbergen, England, Wales, Spain, Germany, Poland, Morocco, Russia (Mt. Altay), China (Gansu), Australia (South Australia, New South Wales).—FIG. 249,2a,b. \**S. serratus*, Herrerías-Mergel Formation (*serratus*-Band), Spain (Cala); *a*, cephalon,  $\times 2$ ; *b*, holotype, pygidium,  $\times 2.5$  (Richter & Richter, 1941a).
- Stigmatiscus** RASETTI, 1966a, p. 35 [\**S. stenometopus*; OD; holotype (RASETTI, 1966a, pl. 12, fig. 1–2), 146029, USNM, Washington, D.C.]. Cephalon semielliptical; glabella parallel sided, anteriorly pointed; S1 and S2 as deep pits close to the axial furrow in the posterior half of the glabella with area adaxial from them considerably inflated; SO with pair of deep pits laterally; LO bearing a spine or node; border narrow, with pair of small spines posteriorly. Assigned pygidium semielliptical, of low convexity; axis tapering, with 12 axial rings, the first ring shorter medially than laterally; pleural areas bearing well-impressed, oblique pleural furrows; border narrow, with five pairs of downwardly directed marginal spines. [Assignment of the pygidium (RASETTI, 1967, p. 53) is not certain due to difference in outline from that of the cephalon, lower convexity of shield, and style of furrows on axis.] *upper Lower Cambrian*: USA (New York), Canada (Newfoundland), Russia (Gorno-Altayskaya).—FIG. 248,4a–c. \**S. stenometopus*, *upper Lower Cambrian (Acimetopus bilobatus* faunule), New York (Griswold Farm); *a*, holotype, cranidium,  $\times 3$  (Rasetti, 1966a); *b*, partial pygidium,  $\times 3$  (Rasetti, 1967); *c*, partial pygidium,  $\times 3$  (Rasetti, 1967).
- Tannudiscus** POKROVSKAYA, 1959, p. 177 [\**T. tannuolaicus*; OD; holotype (POKROVSKAYA, 1959, pl. 11, fig. 20), 3536/98, VNIGNI, Moscow]. Glabella long, wide, bilobed; posterior lobe lacking furrow or spine but may be roundly inflated posteriorly; LO short, low at rear of inflated rear of glabella; border convex, moderately wide, elongate sagittally and extending back to anterior of glabella in some species. Thorax with three segments. Pygidial axis conical, of seven or eight rings, may or may not reach posterior border furrow; ring furrows indistinct or obsolete; border almost flat, similar in width to cephalic border. *Lower Cambrian (Toyonian)*: England, Canada (Newfoundland), Russia (Gorno-Altayskaya, Tuva), China (Gansu).—FIG. 248,3a. \**T. tannuolaicus*, Toyonian (Shivelikskaya Suite), Tuva (Shivelik-Khem River, eastern Tannu-Ola Mountains); holotype,  $\times 10$  (Pokrovskaya, 1959).—FIG. 248,3b,c. *T. balanus* RUSHTON, 1966, Lower Cambrian (Purley Shales), England (Warwickshire); holotype, cranidium in dorsal and lateral views,  $\times 12$  (Rushton, 1966).

### Family YUKONIIDAE S. Zhang, 1980

[*nom. transl. et emend.* JELL, herein, ex Yukoniinae S. ZHANG in W. ZHANG, LU, & others, 1980, p. 21]

Glabella narrow, usually parallel sided and anteriorly rounded. SO a pair of pits low on sides of glabella and angling back beneath median cranial spine; LO extremely short, overridden by cranial spine. Large spine arising from L1 medially and directed back almost horizontally to pointed tip. Preglabellar area usually long, with smooth anterior border. Pygidium variable with axis of three to seven rings. *Lower Cambrian–Middle Cambrian*.

**Yukonia** PALMER, 1968, p. 38 [\**Y. intermedia*; OD; holotype (PALMER, 1968, pl. 2, fig. 14), 146674,



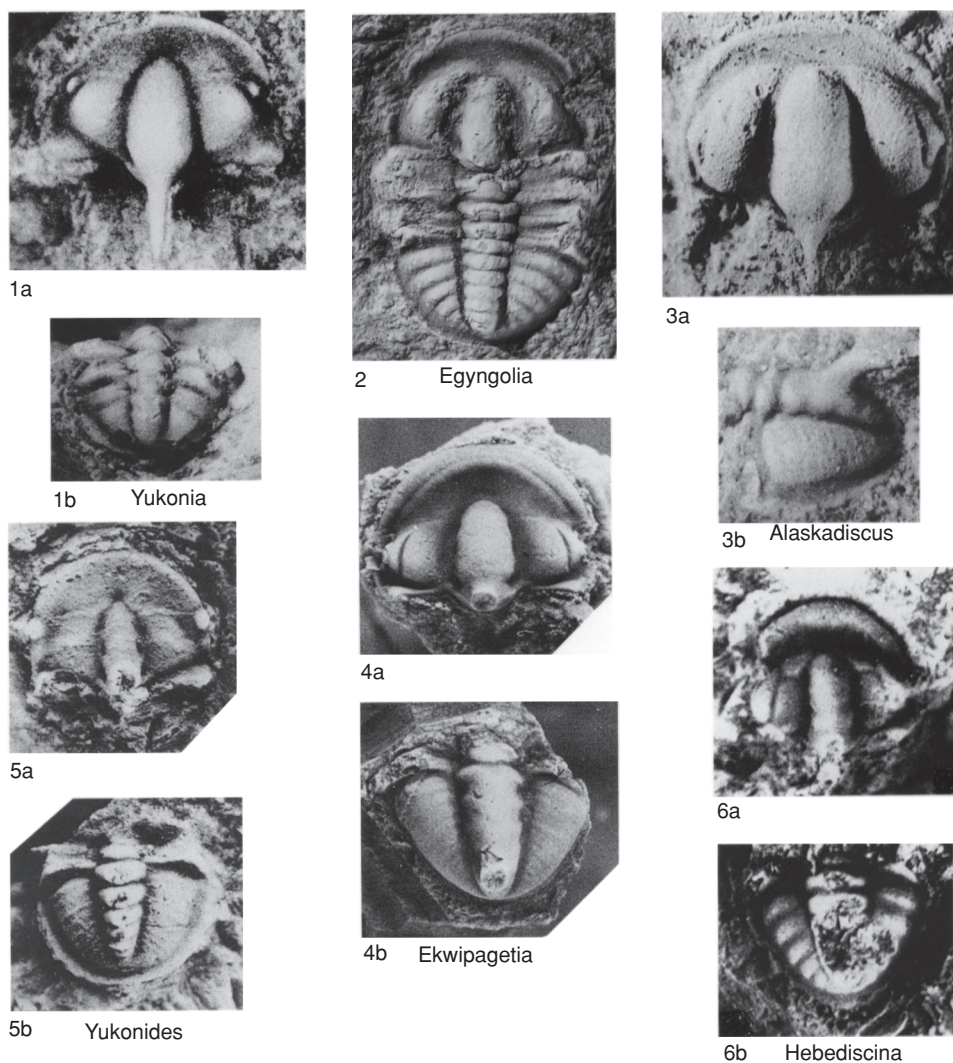


FIG. 250. Yukoniidae (p. 398–400)

USNM, Washington, D.C.]. Glabella relatively wide, unfurrowed, strongly tapered into cranial spine; eye tubercles situated laterally just above the border furrow. Thorax with three segments. Pygidium transverse, with narrow, poorly segmented axis; border narrow, with irregular (possibly weakly spinose) margin. *Lower Cambrian*: USA (Alaska).

—FIG. 250, 1a, b. \**Y. intermedia*, Lower Cambrian (Adams Argillite), Alaska (Water Level area, Yukon River); a, holotype, cranidium,  $\times 20$ ; b, paratype, pygidium,  $\times 15$  (Palmer, 1968).

*Alaskadiscus* S. ZHANG in W. ZHANG, LU, & others, 1980, p. 31 [\**Neocobboldia spinosa* PALMER, 1968, p. 34; OD; holotype (PALMER, 1968, pl. 2, fig. 9–10), 146670, USNM, Washington, D.C.]. Glabella

unfurrowed except for SO low on sides at rear, reaching rear of long border furrow; SO running up to cranial spine just behind greatest tapering of the cranial spine; LO short, overlain by slender, horizontal cranial spine (much narrower than glabella); border uniformly short; palpebral furrows well impressed; librigena short, small. Thorax with two segments. Pygidium transverse; axis of five or six rings, with large geniculate spine on third and fourth; border narrow, with several pairs of marginal spines. *Lower Cambrian*: USA (Alaska).

—FIG. 250, 3a, b. \**A. spinosa* (PALMER), middle Lower Cambrian (Adams Argillite), Alaska (Yukon River); a, holotype, cranidium,  $\times 15$ ; b, left lateral view of pygidium,  $\times 15$  (Palmer, 1968).

**Egyngolia** KOROBV, 1980, p. 83 [*\*E. obtusa*; OD; holotype (KOROBV, 1980, pl. 7, fig. 1), 102, coll. 4251, PIN, Moscow] [= *Mongolodiscus* KOROBV, 1980, p. 99 (type, *M. zaicevi*; OD; PIN 137, coll. 4251)]. Glabella wide; SO to S3 impressed as deep circular pits isolated or almost isolated from axial furrow; S1 and S2 may continue faintly across the axis; palpebral lobes short but prominently raised; librigena tiny; anterior border usually a short rim marginal to long border furrow. Thorax with three segments. Pygidium with axis of six or seven rings and tiny terminal portion, with small tubercle on each ring, and no terminal spine; pleural areas usually with pleural furrows; border narrow, usually with six pairs of small marginal tubercles. *Lower Cambrian (Atdabanian)*: Russia (Siberian Platform, Dzhangy Mountains), Mongolia, South Australia.—FIG. 250, 2. *\*E. obtusa*, Lower Cambrian (Botomian, Egyngolskaya Suite), northwestern Mongolia; holotype,  $\times 7.5$  (Korobov, 1980).

**Ekwipagietia** FRITZ, 1973, p. 9 [*\*E. plicofimbria* FRITZ, 1973; OD; holotype (FRITZ, 1973, pl. 6, fig. 7–9), 33214, GSC, Ottawa]. Large; glabella relatively short, wide, with much narrower occipital spine; anterior border bearing epiborder furrow; palpebral furrows well impressed. Pygidium with narrow, poorly furrowed axis bearing posterodorsally directed spine towards its posterior; border thin, with fine marginal spines. *Lower Cambrian*: USA (New York), Canada (Northwest Territories), Greenland, “Nevadella” Zone.—FIG. 250, 4a, b. *\*E. plicofimbria*, “Nevadella” Zone, Sekwi Formation, Northwest Territories (Mackenzie Mountains); *a*, holotype, cranidium,  $\times 7.8$ ; *b*, paratype, pygidium,  $\times 7.8$  (Fritz, 1973).

**Hebediscina** RASETTI, 1972, p. 46 [*\*H. sardoa*; OD; holotype (RASETTI, 1972, pl. 7, fig. 5–6), 69, SG, Rome] [= *Szechuanaspis* CHIEN & YAO in LU & others, 1974, p. 84 (type, *S. longispinus*; OD; NIGP 20456); *Zhenbadiscus* S. ZHANG in W. ZHANG, LU, & others, 1980, p. 36 (type, *Z. typicalis*; OD; NIGP 37336)]. Preglabellar field usually depressed, particularly at glabellar anterior; cranial spine short, often slender; anterior border convex in section, without radial markings; palpebral lobes large; palpebral furrows well impressed. Pygidium with axis of four to seven rings tapering posteriorly almost to border furrow; pleural furrows variable but generally impressed; border narrow, with several (commonly five) pairs of marginal or dorsomarginal spines. *Lower Cambrian*: Sardinia, Mongolia, China (Sichuan), South Australia.—FIG. 250, 6a, b. *\*H. sardoa*, Lower Cambrian (Nebida Formation), Sardinia (Monte Cuccurinu); *a*, holotype, cranidium,  $\times 12$ ; *b*, paratype, pygidium,  $\times 12$  (Rasetti, 1972).

**Lenadiscus** REPINA in KHOMENTOVSKII & REPINA, 1965, p. 109 [*\*L. unicus*; OD; holotype (KHOMENTOVSKII & REPINA, 1965, pl. 1, fig. 9), 265/1269, CSGM, Novosibirsk]. Glabella narrowed near anterior just behind eye ridges; eye ridges prominent, palpebral lobes teardrop-shaped. Frontal area long

and flat, with prominent caecal network in some specimens. Pygidium subsemicircular; wide axis of three rings plus terminal portion. Pair of long, slender posterolateral marginal spines; four prominent ridges on pleural lobe occurring intersegmentally at the axis and converging on base of marginal spines. *Lower Cambrian (Botomian)*: Russia (Siberian Platform), Mongolia.—FIG. 251a–d. *\*L. unicus*, Lower Cambrian (Botomian), Siberia (Lena River); *a*, cranidium,  $\times 20$ ; *b*, partial cranidium,  $\times 20$ ; *c*, holotype, pygidium,  $\times 10$ ; *d*, pygidium,  $\times 20$  (Repina & Pereladov, 1988).

**Yukonides** FRITZ, 1972, p. 10 [*\*Y. lacrinus*; OD; holotype (FRITZ, 1972, pl. 8, fig. 1–2), 27278, GSC, Ottawa]. Glabella narrow; with marked preglabellar depression; eye ridge, when elevated, extending to eye tubercles on lateral margin; librigenae absent. Pygidium with axis of five to seven rings; border bearing inconspicuous marginal spines or nodes. *middle Lower Cambrian*: USA (New York), Canada (Northwest Territories), Russia (Siberian Platform).—FIG. 250, 5a, b. *\*Y. lacrinus*, “Nevadella” Zone, Sekwi Formation, Northwest Territories (Mackenzie Mountains); *a*, holotype, cranidium,  $\times 8.7$ ; *b*, pygidium,  $\times 10.8$  (Fritz, 1972).

### Family EODISCIDAE Raymond, 1913

[Eodiscidae RAYMOND, 1913b, p. 102, *emend.* JELL, 1975a, p. 29 and herein] [= Dawsoniidae RESSER, 1937, p. 9; Pagetidae KOBAYASHI, 1935, p. 112; Aulacodiscidae HUPE, 1954, p. 59; Opsidiscidae HUPE, 1953b, p. 170; Pagetiellinae S. ZHANG in W. ZHANG, LU, & others, 1980, p. 23]

Same as Yukoniidae, but anterior border scrobiculate. Pygidial axis of four to ten rings. *upper Lower Cambrian–Middle Cambrian*.

**Eodiscus** HARTT in WALCOTT, 1884b, p. 24 [*\*E. pulchellus*; OD; syntypes (RASETTI, 1952a, pl. 54, fig. 10–11), 3794, CU, Ithaca; = *Microdiscus scanicus* LINNARSSON, 1883, p. 29; lectotype (LINNARSSON, 1883, pl. 4, fig. 17), 5602, SGU, Uppsala] [= *Spinodiscus* KOBAYASHI, 1943, p. 39 (type, *Microdiscus punctatus* SALTER, 1864c, p. 237; OD; lectotype BMNH 42646); *Deltadiscus* KOBAYASHI, 1943, p. 39 (type, *Microdiscus punctatus precursor* MATTHEW, 1886, p. 75; OD; ROM 47; = *Microdiscus scanicus* LINNARSSON, 1883, p. 29)]. Glabella may be anteriorly acuminate; S1 and S2 discontinuous lateral indentations only; frontal area relatively long, with median preglabellar furrow; border short, uniform; scrobicules may be effaced; eyes and facial sutures absent. Thorax with three segments. Pygidium with long, narrow axis of 10 or more rings; border narrow. Surface ornament variable between species. *Middle Cambrian*: Canada (Newfoundland, New Brunswick), Sweden, Spain, Wales, England, Norway, Russia (Siberian Platform).—FIG. 252, 1a–c. *\*E. scanicus* (LINNARSSON), Middle Cambrian (*Psychagnostus atavus* Zone), Sweden; *a*, whole specimen,  $\times 6$ ; *b*, lectotype, cranidium, SGU 5602,  $\times 6$ ; *c*, cranidium,  $\times 6$  (Westergård, 1946).

**Dawsonia** HARTT in DAWSON, 1868, p. 655

[\**Microdiscus dawsoni*; OD; types not traced] [= *Aculeodiscus* ŠNAJDR, 1950, p. 201 (type, *A. bohemicus*; OD; NMP 32028); *Metadiscus* KOBAYASHI, 1943, p. 39 (type, *Microdiscus sculptus* HICKS in HARKNESS & HICKS, 1871, p. 400; OD; SM A1088)]. Coarsely granulose; glabella poorly furrowed laterally; anterior border convex; blind. Thorax with two segments. Pygidium with axis of six rings plus terminus; pleural furrows deeply incised; border extremely narrow. *Middle Cambrian*: Canada (Newfoundland, New Brunswick), Sweden, Wales, Czechoslovakia, Russia (Siberian Platform).—FIG. 253,2. \**D. dawsoni*, Middle Cambrian (Fossil Brook Formation), New Brunswick (Fossil Brook); latex cast of whole specimen,  $\times 8$  (Rasetti, 1952a).

**Helepagetia** JELL, 1975a, p. 82 [\**H. bitruncula*; OD; holotype (JELL, 1975a, pl. 29, fig. 1), 27793, ANU, Canberra]. Small species; like *Pagetia* except that eyes are present and facial sutures are absent. Pygidium with few axial rings and a terminal or subterminal axial spine. Ornament of dense, fine pustules with larger granules sparsely interspersed. *Middle Cambrian*: Australia (Queensland, Tasmania), *P. punctuosus* to *L. laevigata* Zones.—FIG. 252,5a,b. \**H. bitruncula*, Middle Cambrian (Currant Bush Limestone), western Queensland; *a*, holotype, cephalon,  $\times 15.6$ ; *b*, paratype, pygidium,  $\times 12.5$  (Jell, 1975a).

**Kiskinella** ROMANENKO & ROMANENKO, 1962, p. 24 [\**K. cristata*; OD; holotype (ROMANENKO & ROMANENKO, 1962, pl. 3, fig. 3), 1328/1958, ZSGU, Novokuznetsk]. Glabella not reaching border furrow, unfurrowed except for SO; median preglabellar furrow separating fixigenae; librigenae extremely small; palpebral lobe small, low on side of fixigenal elevation. Pygidium with parallel-sided axis of four rings (plus terminal portion) finishing well before border furrow; pleural furrows deep; border extremely narrow. *Middle Cambrian (Amgaian)*: Russia (Gorno-Altyskaya).—FIG. 252,6a,b. \**K. cristata*, Middle Cambrian (Amgaian), Gorno-Altyskaya (Kiska River); *a*, holotype, cranidium,  $\times 9$ ; *b*, pygidium,  $\times 9$  (Romanenko & Romanenko, 1962).

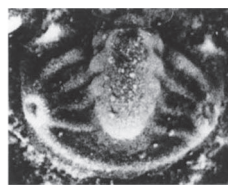
**Macannaia** JELL, 1975a, p. 71 [\**Pagetia maladensis* RESSER, 1939, p. 25; OD; holotype (RESSER, 1939, pl. 2, fig. 5, right), 98491a, USNM, Washington, D.C.]. Small; similar to *Pagetia*; glabella narrow, occupying small part of cranidium, may be anteriorly truncated; preglabellar field short, depressed immediately in front of glabella; palpebral lobes usually highly elevated. Thorax with two segments, with geniculate spine on axis of second segment. Pygidial axis narrow, reaching posterior border furrow, usually expanded dorsally at rear, with spine varying from minute node to long horizontal spine; border widest in midlength of pygidium. *Middle Cambrian*: Spain; USA (Idaho), *Glossopleura* Zone; Australia (New South Wales), *Peronopsis longinqua* Zone; Russia (Siberian Platform), upper Toyonian—



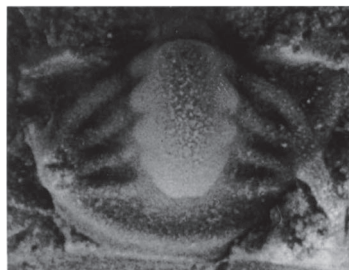
a



b



c



d

#### Lenadiscus

FIG. 251. Yukoniidae (p. 400)

Amgaian.—FIG. 252,3a,b. \**M. maladensis* (RESSER), Middle Cambrian (Langston Limestone), Idaho; *a*, holotype, cranidium,  $\times 12$ ; *b*, pygidium,  $\times 12$  (Rasetti, 1966b).



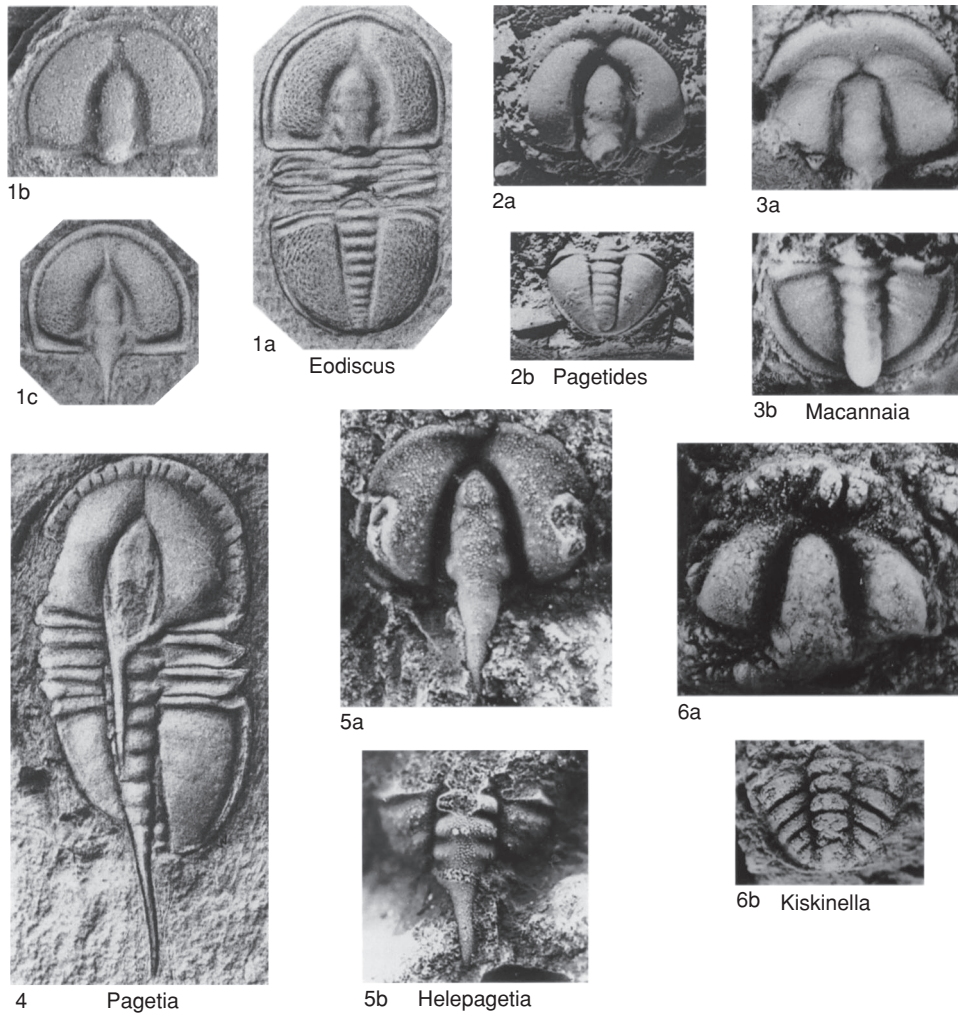


FIG. 252. Eodiscidae (p. 400–403)

*Opsidiscus* WESTERGÅRD, 1950b, p. 606, *nom. nov. pro Aulacodiscus* WESTERGÅRD, 1946, p. 26, *non* DOUVILLE, 1921 [*Aulacodiscus bilobatus* WESTERGÅRD, 1946, p. 26; OD; holotype (WESTERGÅRD, 1946, pl. 1, fig. 21), 4702, SGU, Uppsala]. Small species; like *Pagetia*, but has small abathochroal eye and fused facial suture. Thorax with two segments, the second segment bearing small, geniculate median spine. Pygidium with axis of two to six rings plus terminal portion but no terminal spine. *upper Middle Cambrian*: Sweden, Russia (Siberian Platform, Gorno-Altayskaya), Australia (Queensland, Tasmania), India, Antarctica.—FIG. 253, 1a, b. \**O. bilobatus*, upper Middle Cambrian (*Lejopyge laevigata* Zone), Sweden; a, holotype, cranidium, Östergötland, ×8;

b, pygidium, Västergötland, ×8 (Westergård, 1946).

*Pagetia* WALCOTT, 1916b, p. 407 [\**P. bootes*; OD; syntypes (WALCOTT, 1916b, pl. 67, fig. 1), 62855–62861, USNM, Washington, D.C.] [= *Eopagetia* KOBAYASHI, 1943, p. 40 (type, *Microdiscus significans* ETHERIDGE, 1902, p. 3; OD; lectotype chosen WHITEHOUSE, 1936, p. 83, AMF 9138A); *Mesopagetia* KOBAYASHI, 1943, p. 40 (type, *Pagetia clytia* WALCOTT, 1916b, p. 408; OD; syntypes USNM 62862–62867)]. Glabella may taper forward, usually with furrows poorly impressed laterally; preglabellar field of variable length, usually depressed; border tapering laterally; abathochroal eye present; facial suture proparian. Thorax with two or

three segments, with geniculate, posteriorly directed median spine on second. Pygidium with axis of three to six rings plus terminal portion bearing spine of variable length; axis not reaching border furrow. *upper Lower Cambrian*: USA (New York), Canada (Yukon Territory). *Middle Cambrian*: USA (Idaho, New York), Canada (Quebec, British Columbia), India, Russia (Siberian Platform), Korea, China (Guizhou, Yunnan), Antarctica, Australia (Queensland, New South Wales, Northern Territory, South Australia).—FIG. 252.4. \**P. bootes*, *Bathyriscus-Elrathina* Zone, Burgess Shale, British Columbia; articulated syntype,  $\times 8$  (Rasetti, 1966b).

**Pagetides** RASETTI, 1945b, p. 311 [\**P. elegans*; OD; holotype (RASETTI, 1945b, pl. 1, fig. 1), 304a, LU, Montreal] [= *Discomesites* ÖPIK, 1975b, p. 32 (type, *D. frugum*; OD; AGSO 13177)]. Like *Pagetia*, but with well-developed palpebral furrows. Pygidium without axial spine. *upper Lower Cambrian*: Scotland, USA (Alaska, New York, Vermont), Canada (Northwest Territories, Quebec), Russia (Siberian Platform), Australia (New South Wales), Antarctica. *lower Middle Cambrian*: Canada (Newfoundland).—FIG. 252,2a,b. \**P. elegans*, upper Lower Cambrian (Sillery Formation), Quebec (Levis); a, holotype, cranidium,  $\times 6$ ; b, pygidium,  $\times 6$  (Rasetti, 1945b).

**Sinopagetia** W. ZHANG & YUAN, 1981, p. 162 [\**S. neimengguensis*; OD; holotype (W. ZHANG & YUAN, 1981, pl. 2, fig. 1), 62248, NIGP, Nanjing; = *Pagetia jinmanensis* LIN & WU in W. ZHANG, LIN, & others, 1980, p. 47; holotype (W. ZHANG, LIN, & others, 1980, pl. 1, fig. 1), 51075, NIGP, Nanjing]. Glabella wide at base, tapering forward; L1 expanded posteriorly but not spinose; anterior border elongate medially; librigena subquadrate; palpebral furrow not impressed. Pygidial axis of five rings and terminal portion, lacking posterior spine, not reaching posterior border furrow; ring furrows not well impressed; border extremely narrow, smooth. *lower Middle Cambrian*: Inner Mongolia, China (Shaanxi).—FIG. 253,3a,b. \**S. jinmanensis*, lower Middle Cambrian (Hsuehuang Formation), Inner Mongolia (Gangdeershan); a, holotype, cranidium,  $\times 20$ ; b, pygidium,  $\times 18$  (W. Zhang & Yuan, 1981).

**GENERA PREVIOUSLY ASSIGNED  
TO EODISCOIDEA BUT HERE  
CONSIDERED DOUBTFUL OR  
EXCLUDED**

**Dipharus** CLARK, 1923a, p. 478 [\**D. insperatus*; OD; holotype (SHAW, 1950, pl. 79, fig. 18), 1693, MCZ, Cambridge] [= *Pseudodipharus* KOROBOV, 1980, p. 91 (type, *P. privus*; OD; PIN 128, coll. 4251)]. Glabella subconical, narrow, extending to anterior border furrow, with slightly expanded frontal lobe and up to three pairs of poorly impressed lateral glabellar furrows; LO medially elongate, without a spine; fixigenae with a prominent tubercle behind eye

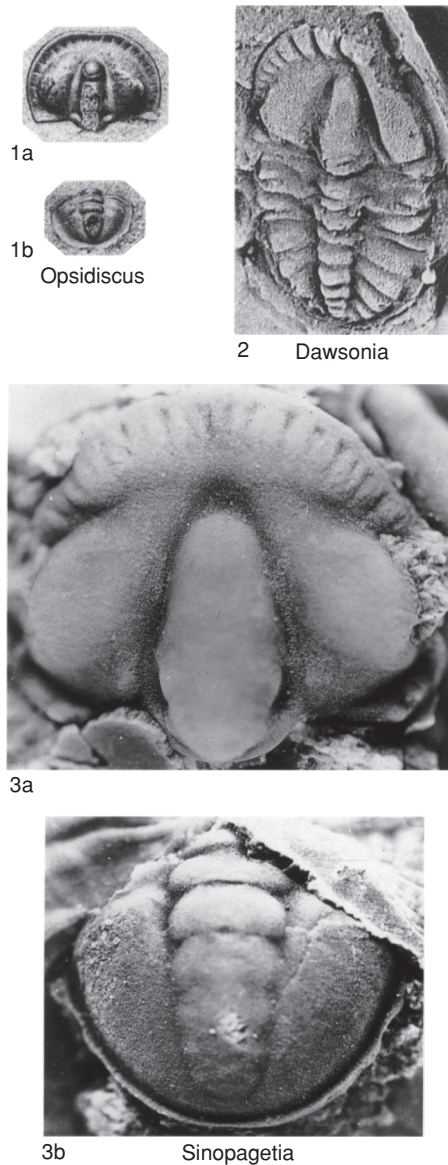


FIG. 253. Eodiscidae (p. 400–403)

ridge; palpebral lobe long, curved, defined by well-impressed palpebral furrow, and continuing into eye ridge and meeting axial furrow at level of anterior of glabella; border extremely short; librigena long and narrow. Pygidium with posteriorly tapering axis of six rings plus terminal portion, finishing just forward of border furrow; pleural areas with pleural and interpleural furrows extending across border area so that pleural ribs extend into

- exsagittal marginal spines. [Probably the juvenile form of a Redlichiida; too imperfectly known.] *Lower Cambrian*: USA (Massachusetts), Mongolia.
- Discagnostus** ÖPIK, 1963, p. 55 [\**D. spectator*; OD; holotype (ÖPIK, 1963, pl. 2, fig. 14–15), CPC 4262, AGSO, Canberra]. Glabella short, with continuous glabellar furrow dividing short anterior glabellar lobe, with rear of glabella roundly expanded posterodorsally; border with closely spaced, radial scrobicules; two pairs of prominent genal tubercles situated anteriorly and posteriorly. [SHERGOLD and others (1990) assigned this genus to the Eodiscoidea. If this genus is a derivative of the *Pagetia-Opsidiscus* lineage, one of the pairs of genal tubercles would be a new feature; if it is an Agnostina, both pairs of tubercles are new features. Its assignment, which is doubtful, must await further knowledge, particularly of the cephalothoracic area and pygidium.] *Upper Cambrian*: Australia (Queensland), *Glyptagnostus stolidotus* Zone.
- Glabella** LERMONTOVA, 1940, p. 120 [\**G. ventrosa*; OD; syntypes (LERMONTOVA, 1940, pl. 35, fig. 9, 9a–d), 64, 74, 77, TsGM, St. Petersburg]. Probably belongs to Kingstoniidae or Corynexochida. *Middle Cambrian (Amgaian)*: Russia (Tian-Shan, southern Fergama).
- Mendodiscus** RUSCONI, 1950a, p. 74 [\**M. tuberculatus*; OD; holotype (RUSCONI, 1956, fig. 4), 2644, MHN, Mendoza]. The holotype and only figured specimen is a trilobite pygidium, probably belonging to the Corynexochidae; it is not an eodiscoid, much less a cranidium. *lower Middle Cambrian*: Argentina.
- Miraculaspis** ROMANENKO in ROMANENKO & ROMANENKO, 1967, p. 72 [\**M. picta*; OD; holotype (REPINA & ROMANENKO, 1978, pl. 7, fig. 14–15), 1329/18, ZSGU, Novokuznetsk]. Cephalon unknown. Pygidium subquadrate; axis wide, parallel sided to slightly narrowed at rear of first ring, bluntly rounded posteriorly at border furrow, with 3 pairs of pits laterally but isolated from axial furrow; pleural areas narrow, shorter than axis, with widely spaced tubercles; border furrow and border forming wide flange tapering forward and crossed by numerous dividing radial ridges. [Style of furrows laterally on axis and caecal network suggest a cephalon, but structure of the transverse margin, particularly the oblique lateral sections, suggest a pygidium. Similar furrows on the pygidial axis are known on pygidia of the Condylropygidae (Agnostina). Moreover, an expanded border region is common in the Condylropygidae. Assignment of this genus must await a cephalon.] *Lower Cambrian (Botomian)*: Russia (Gorno-Altayskaya).
- Shivelicus** POKROVSKAYA, 1959, p. 180 [\**S. parvus*; OD; holotype (POKROVSKAYA, 1959, pl. 10, fig. 15), 3536/99, VNIGNI, Moscow]. Probably belongs to Corynexochida. *Lower Cambrian (Botomian)*: Russia (Tuva, Transbaikal, Gorno-Altayskaya, western Sayan, Kuznetsk Altay).
- Triangulaspis** LERMONTOVA, 1940, p. 120 [\**Ptychoparia meglitzkii* TOLL, 1899, p. 22; OD; holotype (LERMONTOVA, 1940, pl. 35, fig. 5), 21/5156, TsGM, St. Petersburg] [= *Angusteva* HUPE, 1953a, p. 114 (type, *Ptychoparia? annio* COBBOLD, 1910, p. 24; OD; syntypes Cobbold Nos. 401–403); *Acutaspis* REPINA in REPINA, BELYAEVA, & SOBOLEV, 1976, p. 151 (type, *A. facilis*; OD; IGGN 509/51)]. Pygidium not known with certainty as markedly different forms have been assigned to different species apart from the type. [Probably belongs to Ellipsocephaloidea, especially after SDZUY (1962b) showed the Spanish species *T. fusca* (pl. 22, fig. 13) with at least five thoracic segments.] *Lower Cambrian (Atdabanian, Botomian)*: Russia (Siberian Platform), England, Spain, Morocco, Canada (Newfoundland).
- Triangullina** REPINA in KHOMENTOVSKII & REPINA, 1965, p. 107 [\**T. parvula*; OD; holotype (KHOMENTOVSKII & REPINA, 1965, pl. 1, fig. 11), 265/1608, CSGM, Novosibirsk] [= *Plenudiscus* KOROBOV, 1980, p. 74 (type, *P. crassus*; OD; PIN 71, coll. 4251)]. Probably belongs to Ellipsocephaloidea; closely related to *Triangulaspis*. *Lower Cambrian (Atdabanian)*: Russia (Siberian Platform), Mongolia.

## Order REDLICHIIA

### Richter, 1932

[*nom. transl.* FORTEY & WHITTINGTON, herein, ex suborder Redlichiida RICHTER, 1932, p. 852]

Ocular lobe attached to glabella in front of S3, prominent throughout development; eye ridge may be subdivided. Many-segmented thorax, with pleural spines; may be subdivided into prothorax and opisthothorax. *Lower Cambrian–Middle Cambrian*.

The systematic arrangement of this section follows recent practice, but these views were questioned by GEYER (1996), who gave arguments for placing the Fallotaspidioidea in Suborder Redlichiina.

## Suborder OLENELLINA

### Walcott, 1890b

[*nom. correct. et transl.* PALMER & REPINA, 1993, p. 20, *pro* Olenellidae WALCOTT, 1890b, p. 635] [= Mesonacidae WALCOTT, 1890b, p. 635; WALCOTT, 1910, p. 236; Mesonacida SWINNERTON, 1915, p. 538; C. POULSEN, 1927, p. 315; Olenellidea RICHTER & RICHTER, 1941a, p. 33; Protoparia STORMER, 1942, p. 59, *non* SWINNERTON, 1915; Olenellacea HENNINGSMOEN, 1951, p. 184; BERGSTRÖM, 1973a, p. 39; BERGSTRÖM, 1973b, p. 284; Olenelloidea HUPE, 1953a, p. 116; Olenellida BERGSTRÖM, 1973a, p. 39; BERGSTRÖM, 1973b, p. 284; AHLBERG, BERGSTRÖM, & JOHANSSON, 1986, p. 40; Olenelloidea REPINA, 1979, p. 27; Olenellina PALMER & REPINA, 1993, p. 20]

No facial suture; wide (tr.) rostral plate extending between genal angles, perrostral suture. Hypostome probably conterminant in holaspides in which preglabellar area was