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RECORD 1975/86

CLASSIFICATION OF PSEUDAGNOSTUS JAEKEL, 1909 (TRILOBITA:AGNOSTINA)

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Shergold, J.H.: Classification of *Pseudagnostus* Jaekel, 1909 (Trilobita: Agnostina).

Eighty-eight species assigned or assignable to *Pseudagnostus sensu lato* are divided into two broad divisions based on the position of the glabellar node with respect to the anterior or anterolateral glabellar furrows and anterolateral lobes. A spectaculate division in which the node lies to the rear of the anterior furrow and to the rear of the anterolateral lobes, is divided into nine species groups which are recognised by degree of effacement of external morphology, shield shape, border morphology, glabellar morphology, pygidial spinosity, and metamerism. Three spectaculate species groups, *bulgosus*, *communis*, and *cyclopyge*, are referred to *Pseudagnostus* Jaekel, 1909, *sensu stricto*; one, *contracta*, to *Pseudagnostina* Palmer, 1962; and one, *securiger*, to *Sulcatagnostus* Kobayashi, 1937, these latter taxa being regarded as subgenera of *Pseudagnostus*. Four other spectaculate species groups, *araneavelatus*, *bilobus*, *canadensis*, and *clavus*, are classified with *Neoagnostus* Kobayashi, 1955, pending clarification of the taxonomic status and concepts of *Euplethagnostus* Lermontova, 1940, and *Pseudorhaptagnostus* Lermontova, 1940. *Hyperagnostus* Kobayashi, 1955 and *Machairagnostus* Harrington & Leanza, 1957 are synonymised with *Neoagnostus*. A *papilionate* division, in which the axial glabellar node lies between the anterolateral lobes and interrupts the course of the anterior furrow, consists of two species groups, *convergens* and *clarki*, which are assigned to *Rhaptagnostus* Whitehouse, 1936. The gneric name *Plethagnostus* Clark, 1923 is suppressed.

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INTRODUCTION

The genus Pseudagnostus was erected by Jaekel in 1909 for species of Agnostus possessing a short pygidial axis and an 'endolobe', currently termed a deuterolobe (see Öpik 1963, p. 31).

Jaekel (1909, p. 400) designated as type species Agnostus cyclopyge Tullberg (1880, p. 26; pl. 2, figs 15a, 15c, cephalon and pygidium respectively), which occurs in the Olenus Zone and the Zone of Parabolina spinulosa with Orusia lenticularis, at Andrarum, Skaane, and other localities in Sweden (Tullberg 1880, p. 26; Westergaard 1922, p. 117; 1944, pp 32-33; 1947, p. 22).

The type specimens, reported by Tullberg (1880, p. 26) to have been deposited in the Geological Museum, University of Lund, have not been identified. According to Dr Jan Bergström (letter, 10th August 1973), the specimens were numbered but there is no evidence that they were deposited in the type collections. Although they may not be lost, it might be difficult to differentiate them from other material in the collections from Andrarum. Until the specimens are positively located, the concept of Pseudagnostus cyclopyge is based on specimens collected from the type locality, figured by Westergaard (1922, pl. 1, figs 7, cephalon, Lund University Lo 3066t, and 8, pygidium, Lo 3067t), and reproduced here as Fig. 11. Westergaard's specimens were obtained from beds containing Orusia lenticularis.

Recent research (Öpik 1967; Shergold 1972, 1975) classifies the genus Pseudagnostus with Pseudagnostinae Whitehouse, 1936, which is regarded as a subfamily of Diplagnostidae Whitehouse, 1936, as emended by Öpik (1967).

When it was erected, a mere handful of species could be assigned to Pseudagnostus; but by now it is possible to assign no fewer than 88 species, listed in Appendix B. They are united by the possession of a deuterolobe similar to that seen in the type species. Excluding this characteristic, a wide range of forms has been included in *Pseudagnostus*, with the result that any original concept of the genus has been substantially diluted, and it has become necessary to discuss the genus in a *sensu lato* manner. This proliferation of species is directly responsible for the present review, as *Pseudagnostus sensu lato* is common in the Late Cambrian of northern Australia, currently under investigation by the author. There, a range of pseudagnostinid forms spans a wide interval of Late Cambrian time, and is potentially useful for the close zonation of Upper Cambrian strata (Shergold 1975).

AGE AND DISTRIBUTION OF *SENSU LATO* TAXON

The time span of *Pseudagnostus sensu lato* is long: it first appears in the earliest Late Cambrian (early Mindyallan *Erediaspis eretes* Zone in Australia; early Tuorian *Agnostus pisiformis*/*Homagnostus fecundus* Zone in Siberia; and early Dresbachian *Cedaria* Zone in North America) and continues into the earliest Ordovician (Canadian, *Symphysurina* and *Kainella* faunas in North America). Pseudagnostinid species are particularly common in correlatives of the late Mindyallan *Glyptagnostus stolidotus* Zone in Australia, in the late Dresbachian *Aphelaspis*/*Dunderbergia* Zones in North America, in the early Franconian and early Shidertan *Elvinia* and *Irvingella* Zones in North America and Siberia respectively, and in the late Shidertan *Lotagnostus trisectus*/*Peltura* Zone in Siberia and its equivalent post-Idamean/pre-Payntonian interval in Australia.

The genus is cosmopolitan, having lived in seas peripheral to Precambrian crustal masses now forming the nuclei of Europe, Eurasia, eastern Asia, North America, South America, Australia, and Antarctica. Within these seas, *Pseudagnostus* appears to have favoured habitats within ocean-facing environments (Palmer 1972), at the oceanic-neritic boundary (Robison 1972) which approximates the boundary between carbonate belt and outer detrital belt as interpreted by Palmer (1960, 1969, 1972, 1973) and Robison (1960a). Its species are commonly found in the deep subtidal (La Porte, 1971, for terminology) outer detrital belt dark shale, silt, and finely laminated limestone deposited on the oceanic margins of carbonate banks, in deep subtidal interbank channels, and other places with current connection to the open ocean. In such environments pseudagnosti presumably contribute to Late Cambrian equivalents of Agnostid Community Assemblages 1 and 2 of Jago (1973). Species of *Pseudagnostus* are also found in coarse calcarenite and debris layers, allochthonously deposited on beaches or in channels. Pseudagnosti are less commonly found in the sandstones and dolomites of the inner detrital belt (Palmer's (*op. cit.*) terminology). When found in inner detrital depositional environments they appear to retain a more or less constant morphology for an appreciable length of time, e.g. P. josepha (Hall), and are not repeatedly replaced in the biostratigraphical section by rapidly evolving taxa to the same extent as they appear to be in outer detrital and carbonate belt environments. Maximum species diversification is thus observed at the oceanic/neritic boundary, where warm shelf currents and cooler oceanic currents mingle.

MORPHOLOGY

In assessing morphology it is necessary to know if specimens are testiferous or moulds, as well as the nature of the matrix. Little information, other than the shapes of the cephalic and pygidial shields and a vague lobation and perhaps furrowing, can be gained from sandstone moulds, as is evident from the cotypes of Pseudagnostus josepha (Hall, 1863) (Fig. 1). By way of contrast, the species illustrated in Figs 2 and 3 demonstrate the range of morphological features shown by both tests and moulds preserved in limestone.

The distinction between morphology exhibited by moulds and by tests is basic to understanding both the reasons for the proliferation of species assigned to Pseudagnostus, and the difficulties in subdividing them at generic and subgeneric levels. Some species have been described from moulds alone, others from tests, both generally in an uncritical manner. Reference to Figs 2 and 3 will show that supposedly diagnostic differences may readily be found if preservation is ignored. When such differences become the basis for generic taxa, obvious problems arise.

In an earlier paper (Shergold 1975), and here, a major distinction is made between the morphology of the outer surface of the shell, and that of its internal surface. The latter can be observed directly on silicified or phosphatized shells; most commonly, however, it is interpreted from impressions on the surface of its mould. Such surfaces are here termed 'parietal surfaces', and their morphology, which is a negative of the inner surface of the shell, is termed 'parietal morphology'.

From the classificatory point of view, external testaceous morphology gives information on lobes and furrows, and the positions of nodes and spines. Parietal morphology, on the other hand, gives basic anatomical information relating to the internal musculature and the vascular and caecal systems of the organism, as deduced from the occurrence and distribution of various scrobiculations, muscle scar impressions, and pits.

Morphological terminology applicable to Pseudagnostinae (*inter alia*) has been defined exhaustively elsewhere (Öpik 1963, 1967; Shergold 1972, 1975). Terminology used in the classification presented here, and not readily evident from these papers or requiring further comment, is summarized in Appendix A.

LOCATION OF MATERIAL

Observations on personally collected Australian specimens have been supplemented by the acquisition of replicas of the types of most established taxa, and the study of museum materials in Europe, North America and Japan.

Located material is in the collections of repositories abbreviated as follows:

AMNH	American Museum of Natural History, New York, U.S.A.
BMNH	British Museum (Natural History), London, U.K.
BYU	Brigham Young University, Provo, Utah, U.S.A.
CPC	Commonwealth Palaeontological Collection, Canberra, A.C.T., Australia.
GMAN	Geological Museum, Kazakhstan Academy of Science, Alma Ata, USSR.
GSC	Geological Survey of Canada, Ottawa, Canada.
GSCh	Geological Survey of China, Peking, China.
GSM	Institute of Geological Sciences, London, U.K.
HAN	Cambrian Catalogue, Geological Survey, Hannover, Germany.
IGAL	Institute of Arctic Geology, Leningrad, USSR.
IGGN	Siberian Research Institute for Geology, Geophysics, and Mineral Raw Materials (SNIIGGIMS), Novosibirsk, USSR.
IGUT	Institute of Geology, University of Tokyo, Tokyo, Japan.
IPP	Institute of Palaeontology, Peking, China.
LU	Laval University, Quebec, Canada.
LULo	Lund University, Lund, Sweden.
MCZ	Museum of Comparative Zoology, University of Harvard, Cambridge, Massachusetts, U.S.A.
MNHU	Museum für Naturkunde, Humbolt University, East Berlin, D.D.R.
MSM	Manchurian Science Museum, Mukden, Manchuria, China.
NHMM	Natural History Museum, Mendoza, Argentina.
NUP	National University, Peking, China.
NZAR	Athropod Register, New Zealand, Geological Survey, Lower Hutt, New Zealand

OGM	Oklahoma Geological Survey, Tulsa, Oklahoma, U.S.A.
OUM	Oxford University Museum, Oxford, U.K.
RMS	Riksmuseet, Stockholm, Sweden,
SGU	Geological Survey of Sweden, Stockholm, Sweden.
THU	Tsing-hua University, Peking, China.
UBA	University of Buenos Aires, Buenos Aires, Argentina.
UQ	University of Queensland, St Lucia, Queensland, Australia.
USGS	United States Geological Survey, Washington, D.C., U.S.A.
USNM	United States National Museum, Washington, D.C., U.S.A.
UT	University of Texas, Austin, Texas, U.S.A.
YPM	Peabody Museum, Yale University, New Haven, Connecticut, U.S.A.
ZSGU	Museum of the West Siberian Geological Board, Novokuznetsk, USSR.

CLASSIFICATION

For the purposes of this review species assigned to the following closely related or synonymous genera and subgenera were considered: Pseudagnostus Jaekel, 1909, Plethagnostus Clark, 1923, Rhaptagnostus Whitehouse, 1936, Sulcatagnostus Kobayashi, 1937a, Pseudorhaptagnostus Lermontova, 1940, Euplethagnostus Lermontova, 1940, Neoagnostus Kobayashi, 1955, Hyperagnostus Kobayashi, 1955, Machairagnostus Harrington & Leanza, 1957 and Pseudagnostina Palmer, 1962. These species, together with others previously classified elsewhere, are listed in Appendix B. Three other pseudagnostinid genera were examined but are not considered further in the classification: Litagnostus Rasetti, 1944, because of the extreme difficulty in assessing this very effaced form; Xestagnostus Öpik, 1967, because of its uncharacteristically simple articulating device and different pygidial diverticular structure; and Oxyagnostus Öpik, 1967 because of its distinct deuterolobe morphology which cannot be confused with that of Pseudagnostus (see Öpik 1967, pp 159-161).

For the purposes of classification the most obvious differences between species are carapace shape and degree of effacement. Less obvious, but seemingly more important from the anatomical point of view, is the position of the axial glabellar node with respect to the anterior furrow and anterolateral glabellar furrows. Species fall broadly into two divisions:

1. Spectaculate pseudagnosti are those in which the glabellar node lies to the rear of the anterolateral lobes. Two groups are discernible: (a) those in which the anterior furrow is transverse, straight or gently curved backwards and the anterolateral lobes are distinctly separated sagittally, e.g. Pseudagnostus communis (Hall & Whitfield), as refigured by Palmer (1955) (see here Fig. 9); (b) those in which the anterior furrow is V-form, and the anterolateral lobes meet, and may fuse, sagittally, e.g. Neoagnostus bilobus (Shaw, 1951) (Fig. 5).

2. Papilionate pseudagnosti are those in which the node interrupts the course of the anterior furrow, dividing it into V-form anterolateral furrows, and lies between the anterolateral lobes as for example in Rhaptagnostus clarki (Kobayashi, 1935) (Fig. 13).

An intermediate condition, in which the node interrupts the course of the anterior furrow, dividing it into V-form anterolateral furrows, but still lies slightly behind the anterolateral lobes, is included within the spectaculate division of this classification, but could possibly be regarded as a distinct category. The condition appears to be gradational, but the observed differences could be interpreted as the result of preservation.

The spectaculate condition embraces the bulk of species assigned to Pseudagnostus sensu lato. Spectaculate pseudagnosti occur earlier, being first found in the earliest Late Cambrian of Australia, North America and Siberia, and disappear later, in the Early Ordovician of North America. The intermediate forms occupy a relatively narrow time interval during the Late Cambrian, in the Elvinia and Conaspis Zones and their correlatives in Europe, North America, Siberia, and Australia. Papilionate pseudagnosti arise during this time interval, at least in Australia (Shergold, in prep.), and continue into the earliest Ordovician (in Mexico). Thus there appears to be a time-related forward migration of the axial glabellar node.

The function of the axial glabellar node is not known: nor is the reason for its apparent migration. Some speculation may, however, be offered. Parietal surfaces of some pseudagnostinid cephala show the axial and terminal glabellar nodes connected by an axial carina which itself bears a longitudinal sulcus (Shergold 1975, pl. 3, fig. 5; text-fig. 15), structures which can be interpreted as having supported the gut and a dorsal tubular heart. The high spot of the axial glabellar node is frequently perforated, particularly in limestone moulds. Ruedemann (1916) interpreted the cephalic node of Cryptolithus as a dorsal median eye containing a single fluid lens, and such lenses may have occupied the perforated regions of both cephalic and pygidial nodes in agnostids, their function being to assess the intensity and direction of light and orient the animal within the water column. Harris & Mason (1956) have shown that experimentally blinded Daphnia are 'more sensitive to light than normal ones and show a greater capacity for adaptation to light during the cycle of vertical migration' (p. 285). Thus the lack of a compound eye, also lacking in agnostids, is no bar to photokinesis. Harris & Mason (op. cit.) have suggested for Daphnia an interrelationship of the photosensitive system, the nervous system, and reflex control of the heart rate. The cephalic and pygidial nodes of pseudagnosti may well, therefore, be connected with photosensitive systems in direct connection with the blood vascular system, the combination facilitating orientation and migration of the animal in the water column.

Öpik (1961a, p. 417) has considered that the agnostid stomach consists of anterior and posterior sacs connected by a constricted passage beneath the anterior transverse glabellar furrow. In pseudagnosti, however, the lateral portions of this furrow merely represent the internally raised anterior margins defining the anterolateral muscle attachment areas which, depending on the length of muscle, would not necessarily constrict the stomach. Any interruption or modification of the course of the anterior furrow, as is apparent, is therefore more likely to reflect a modification of the muscle attachment areas. The positioning of the axial glabellar node between the anterolateral muscle attachment areas in papilionate pseudagnosti may have resulted in the lateral separation of the bases of the appendages attached there, and/or restricted the area of attachment of such appendages, which would presumably be restricted in size. This situation may be contrasted with that seen in the spectaculate species here assigned to Neoagnostus, in which the attachment areas may meet axially. The anterolateral muscle scars are generally the largest of the pseudagnostinid cephalon, and are thought to represent the areas of attachment for mandibular appendages.

Thus modification of the shape and position of the mandibular attachment areas could reflect difference in feeding habit. Hence this classification is based on anatomical features fundamental to the animal.

While the position of the axial node and its relationship to the anterolateral muscle scars is regarded here as basic in the classification of Pseudagnostinae, other factors are of considerable value in recognizing species groups. Some can be recognized by degree of effacement, whereas in others this characteristic varies presumably in response to environmental conditions. Ideally species groups should comprise taxa in which the condition of effacement is relatively constant, and in practice this is difficult to attain owing to the differing preservation exhibited by established species. Ideally genera should embrace effaced, partially effaced, and en grande tenue species groups.

Degree of effacement influences observation on the condition of other characteristics used in this classification. Although all pseudagnosti are deuterolobate, as deduced from parietal morphology, the degree of tumidity of the deuterolobe and degree of incision of its associated bounding accessory furrows vary considerably. Externally effaced and partially effaced pseudagnosti are generally weakly deuterolobate and non-plethoid parietally. Species externally en grande tenue are usually strongly denterolobate and plethoid, but there are exceptions, e.g. the <u>bilobus</u> species group described below. In similar manner degree of deliquiation is related to effacement. Externally effaced and partially effaced species are non-deliquiate or subdeliquiate: their moulds are likely to have subdeliquiate and deliquiate marginal furrows. En grande tenue species are deliquiate, and their moulds strongly so; generally cephala are more strongly deliquiate than their assigned pygidia.

Carapace shape, which may be subcircular, subovoid, subquadrate, or subrectangular, is relatively constant in some, but not all, species groups. Pygidial segmentation, which can be assessed from the number of muscle scars and apodemes on the internal surface of the test, or the number of muscle-scar impressions and notulae on the parietal surface, may be related to shield shape. As a generalization, elongated pygidia have more segments than subquadrate ones. Similarly, the position of the posterolateral pygidial spines may be related the shield shape: elongate pygidia have anteriorly situated spines with respect to the termination of the deuterolobe, whereas subquadrate pygidia have retrally sited spines. Shield shapes, and consequently spine positions, may change during morphogenesis. Most species in which meraspid pygidia have been observed have a subquadrate shield with retrally positioned spines. Change in shape occurs with the development of the deuterolobe during late meraspid morphogenesis (see Palmer 1955, pp 94-6, pl. 20 for Pseudagnostus communis).

DELINEATION OF SPECIES GROUPS

Species are grouped here on the combinations of characteristics listed above. Considerable variation occurs in some of the groups recognized whereas others are quite homogeneous. The groups are not species, although synonymous species may exist within them. Groups of species groups are united into the genera and subgenera discussed below.

Of the species listed those marked with an asterisk signify that type or subsequently figured material has been examined in museum collections, or from silicone replicas.

A SPECTACULATE PSEUDAGNOSTI

ARANEAVELATUS GROUP (Fig. 4)

Nominal species. *Pseudagnostus araneavelatus Shaw, 1951, p. 113, figs 12-16, holotype pygidium USNM 124466, paratypes USNM 124467, remainder untraced, Early Ordovician, Missisquoia Zone, Vermont, U.S.A.

Diagnosis. Cephalon subcircular, en grande tenue to partially effaced, non-deliquiate to subdeliquiate, spectaculate, tendency to develop prominent furrows to the rear of the anterolateral lobes, anterolateral furrows generally externally effaced, median preglabellar furrow absent. Pygidium subcircular, partially effaced, non-deliquiate, non-plethoid, weakly deuterolobate, spines posteriorly situated close to a transverse line drawn across the rear of the deuterolobe, possibly 8 late holaspid metameres.

Other species.

* Pseudagnostus coronatus Shergold, 1975, pp. 85-7, pl. 6, figs 1-6, holotype cephalon CPC 11692, paratypes CPC 11693-11697.

  Pseudagnostus cyclopygeformis (Sun) sensu Kobayashi, 1960, p. 341, pl. XIX, fig. 6, IGUT no number, non fig. 7 (clarki group), IGUT no number.

* Phalacroma cyclostigma Raymond, 1924, p. 397, pl. 12, fig. 4, holotype pygidium YPM 4747.

* Pseudagnostus denticulatus Shergold, 1975, pp. 87-9, pl. 8, figs 1-5, holotype cephalon CPC 11705, paratypes CPC 11706-11709.

* Pseudagnostus sp. C Shergold, 1975, pp. 91-2, pl. 7, figs 5-7, CPC 11714-11716.

Age & distribution.

Late Cambrian: pre-Payntonian/post-Idamean, Rhaptagnostus clarki patulus with Caznaia squamosa through Rhaptagnostus bifax with Neoagnostus denticulatus Assemblage-Zones (Shergold, 1975), western Queensland, Australia; late Changshanian; Kaolishania Zone, Tanggok, South Korea.

Early Ordovician; Missisquoia Zone, Vermont, U.S.A.

Comments. The Australian species listed here as constituting the avaneavelatus group were previously placed in the clavus group (Shergold, 1975). They are nevertheless distinguishable from the clavus and bilobus groups (below) by their rounded shield shapes and proportions. The arrangement of glabellar lobes and furrows shown is common to all groups.

BILOBUS GROUP (Shergold, 1975, p. 92,) (Fig. 5)

Nominal species. *Pseudagnostus bilobus Shaw, 1951, pp. 112-3, pl. 24, figs 17-22, holotype pygidium USNM 124468, paratypes USNM 124469-124471, Early Ordovician, Missisquoia Zone, Vermont, U.S.A.

Diagnosis. Cephalon subquadrate, generally en grande tenue, deliquiate to subdeliquiate, spectaculate, tendency to over-deepen furrows both in front and behind the anterolateral glabellar lobes; a median preglabellar furrow is generally present. Pygidium subcircular to subquadrate, partially effaced, deliquiate to subdeliquiate, non-plethoid, weakly deuterolobate, spines generally sited on a transverse line across the rear of the deuterolobe or behind it; a third pair of muscle scar impressions is incorporated into the axis behind and adjacent to the pygidial axial node.

Other species.

* Neoagnostus aspidoides Kobayashi, 1955, pp 473-4, pl. VII, fig. 5, holotype cephalon GSC 12745, non fig. 4, geragnostoid pygidium GSC 12746, pl. IX, fig. 5 (line drawing).

* Hyperagnostus binodosus Kobayashi, 1955, p. 475, pl. VII, fig. 2, holotype cephalon GSC 12747, non fig. 3, geragnostoid pygidium GSC 12748, pl. IX, fig. 4 (line drawing).

Agnostus cyclopyge Tullberg sensu Sun, 1939, p. 30, pl. 1, figs 1-3, repository and numbers not known.

* Pseudagnostus longicollis Kobayashi, 1966, p. 283, fig. 7, IGUT no number.

* Trinodus priscus Kobayashi, 1955, p. 476, pl. VII, fig. 6, holotype pygidium GSC 12751.

* Pseudagnostus quasibilobus Shergold, 1975, pp. 94-5, pl. 12, figs 1-7, holotype cephalon CPC 11717, paratypes CPC 11718-11723.

Machairagnostus tmetus Harrington & Leanza, 1957, p. 64, figs 6-7, holotype (complete specimen) UBA 1297, paratypes UBA 1195, 1292-4, 1298.

* Undetermined pseudagnostid, Robison & Pantoja-Alor, 1968, p. 780, pl. 97, fig. 23, USNM 158886.

Age & distribution.

Late Cambrian: Payntonian, Neognostus quasibilobus with Tsinania nomas Assemblage-Zone (Shergold, 1975), western Queensland, Australia; Fengshanian, Yunnan; Wanwanian, Jehol Block, China.

Early Ordovician: Oaxaca Province, Mexico; Missisquoia Zone, Vermont, U.S.A.; Tremadocian, Parabolina argentina Zone, Argentina; Missisquoia, Symphysurina, and Kainella-Evansaspis faunas, British Columbia, Newfoundland, Canada.

Comments.

Like the clavus group from which it is possibly derived, the bilobus group represents an assemblage of species linked through the orientation of their glabellar furrows. Cephala are, in general, preserved en grande tenue, whereas pygidia have depressed deuterolobes and effaced accessory furrows. The retral position of the pygidial spines is constant among the spiecies cited.

BULGOSUS GROUP (Fig. 6)

Nominal species. *Pseudagnostus bulgosus Öpik, 1967, pp. 156-8, pl. 38, fig. 8; pl. 62, figs 1-4, Mindyallan Zones of Erediaspis eretes and Glyptagnostus stolidotus, western Queensland, Australia. Designated holotype pygidium CPC 5901, paratypes CPC 5902-4, 5656.

Diagnosis. Cephalon subovoid, en grande tenue, spectaculate, deliquiate, anteriorly converging acrolobe, transverse rectilinear anterior furrow, median preglabellar furrow absent, Pygidium subovoid, en grande tenue, convergent flanks, subdeliquiate, plethoid, deuterolobate, restricted pleural lobes, very small spines in advance of a transverse line drawn across the rear of the deuterolobe in holaspides.

Other species.

* Oedorhachis boltonensis Resser, 1938, p. 50, pl. 10, figs 19, 20, cotypes USNM 94869.

Pseudagnostus levatus E. Romanenko in Romanenko & Romanenko, 1967, pp. 75-6, pl. 1, figs 18-19, holotype pygidium ZSGU 133/5, paratype ZSGU 133/6.

* Oedorhachis mesleri Resser, 1938, p. 50, pl. 10, figs 13-14, cotypes USNM 94864.

* Pseudagnostus nganasanicus Rosova, 1964, pp. 27-28, pl. 16, figs 3-4, holotype pygidium IGGN 113/875, paratype IGGN 113/928.

Possibly also included in the bulgosus group is:

Pseudagnostus mestus Öpik, 1967, pp. 155-6, pl. 62, figs 5-6, holotype pygidium, CPC 5906, paratype cephalon, CPC 5905.

Age & distribution.

Late Cambrian: Mindyallan, Erediaspis eretes and Glyptagnostus stolidotus Zones, western Queensland, Australia; Dresbachian, Cedaria Zone, Virginia and Tennessee, U.S.A.; Tuorian, Zones of Agnostus pisiformis with Homagnostus fecundus and Glyptagnostus stolidotus, Kulyumbe River, Katun River and Lena River, Siberian Platform, USSR.

Comments.

This is the earliest species group referable to *Pseudagnostus sensu lato*, homogeneous in content and character.

CANADENSIS GROUP (Fig. 7)

Nominal species. Agnostus canadensis Billings, 1860, p. 304, figs 3a-b, lectotype pygidium (designated Rasetti, 1944), GSC 858b, paratype cephalon GSC 858, refigured as Pseudagnostus canadensis (Billings), (Rasetti, 1944, p. 234, pl. 36, figs 8-13, GSC 858, 858b, LU 1104a-d), Late Cambrian, Lévis Conglomerate, Quebec, Canada.

Diagnosis. Cephalon subquadrate, en grande tenue, wide borders with deliquiate marginal furrows, spectaculate, anterolateral glabellar furrows effaced, but those to rear of anterolateral lobes prominent, median preglabellar furrow present parietally. Pygidium subquadrate, en grande tenue, wide borders with deliquiate marginal furrows, strongly deuterolobate, strongly plethoid, restricted pleural areas, retral spines.

Other species. Rasetti (1944) has synonymized Agnostus janei Clark, 1923, p. 124, fig. 8; 1924, p. 19, fig. 5, MCZ 1696.

Age & distribution.

Late Cambrian. Lévis Conglomerate, Quebec, Cow Head Group conglomerates, Newfoundland (Kindle, pers. comm.).

Comments. The canadensis group is readily recognized by its strongly en grande tenue condition and fused anterior and anterolateral glabellar lobes. Most probably it has been derived from the same ancestral stock as the araneavelatus group.

CLAVUS GROUP (Shergold, 1975, p. 82) (Fig. 8).

Nominal species. *Pseudagnostus clavus Shergold, 1972, pp. 31-4, pl. 3, figs 1-8, holotype pygidium CPC 8453, paratypes CPC 8451, 8454-8456; also Shergold, 1975, pp. 84-5, pl. 8, figs 6-12, CPC 11689-11704, Late Cambrian, Rhaptagnostus bifax with Neoagnostus denticulatus and R. clarki maximus with R. papilio Assemblage-Zones (Shergold, 1975), western Queensland, Australia.

Diagnosis. Cephalon subquadrate, en grande tenue to partially effaced, wide borders with subdeliquiate to deliquiate marginal furrows, spectaculate, prominent V-form anterolateral glabellar furrows, weakly chevronate furrows to rear of anterolateral lobes, rhomboid anterior lobe, median preglabellar furrow absent, proximally present or present. Pygidium subquadrate to subovoid, en grande tenue to partially effaced, non-deliquiate to subdeliquiate, non-plethoid or subplethoid, generally weakly deuterolobate, retral pygidial spines, 7-8 metameres in late holaspides.

Other species.

* Rhaptagnostus acutifrons Troedsson, 1937, pp. 22-24, pl. 1, fig. 9, RMS number not known.

* Pseudagnostus cavernosus Rosova, 1960, pp. 12-14, pl. 1, figs 1-4, holotype pygidium IGGN 76/557, paratype 74/556; holotype refigured Rosova in Khalfin 1960, p. 165, pl. Cm-XVIII, fig. 4.

Pseudorhaptagnostus punctatus Lermontova, 1940, p. 126, pl. 49, figs 14, 14a, repository and numbers not known.

Pseudorhaptagnostus simplex Lermontova, 1951, pp. 12-13, pl. 2, figs 11-15, non figs 16-17, designated holotype is pygidium fig. 11, repository and numbers not known; also Pseudagnostus simplex (Lerm.) in Nikitin, 1956, pl. XIV, fig. 5, non fig. 4.

Euplethagnostus subangulatus Lermontova, 1940, p. 126, pl. 49, figs 15, 15a, repository and numbers not known.

* Pseudagnostus vulgaris Rosova, 1960, pp. 14-16, pl. 1, figs 5-13, holotype pygidium IGGN 76/645, paratypes, 74/524, 76/578, 75/582, 76/647, 76/653, 76/654, 76/656, 79/633; refigured Rosova in Khalfin, 1960, p. 165, pl. Cm-XVIII, figs 5a-c.

* Pseudagnostus sp. A Shergold, 1975, pp. 89-90, pl. 7, figs 1-2, CPC 11710-11711.

* Pseudagnostus sp. B Shergold, 1975, pp. 90-91, pl. 7, figs 3-4, CPC 11712-11713.

Questionably belonging to this group are:

* Homagnostus cf. acutus Kobayashi, 1938, pp. 173-4, pl. XV, fig. 4, cephalon, GSC 11979.

Pseudagnostus bituberculatus Ivshin in Khalfin, 1960, p. 165, pl. Cm-XVIII, figs 6a-b, repository and numbers not known.

Pseudagnostus quadratus Lazarenko, 1966, pp. 46-7, pl. 1, figs 24-29, holotype cephalon IGAL 36/8907, paratype numbers not known.

Age & distribution.

Late Cambrian: post-Idamean/pre-Payntonian, Rhaptagnostus clarki patulus with Caznaia squamosa through R. clarki maximus with R. papilio Assemblage-Zones (Shergold 1975), western Queensland, Australia; Shidertan, Zones of Irvingella to Lotagnostus trisectus/Peltura (Ivshin & Pokrovskaya 1968), Kazakhstan, Sayan Altai, Olenek River, USSR: early Franconian, Elvinia Zone, British Columbia, Canada; Changshanian, Kaolishania Zone, South Korea. Late Cambrian, Tienshan, China.

Comments.

As presently constituted, this is a heterogeneous group that varies considerably in degree of effacement and deliquiation, and somewhat in shield shape. Species are presently linked in possessing a V-form anterior glabellar furrow, rhomboidal anterior lobe, and seven or eight pygidial metameres. Many Russian species are, however, inadequately known and may be wrongly classified within this group. Possibility exists for further dividing the group on presence or absence of a median preglabellar furrow. As far as is known only Australian representatives lack a well defined median preglabellar furrow externally.

COMMUNIS GROUP (Palmer 1968, p. 30) (Fig. 9).

Nominal species. *Agnostus communis Hall & Whitfield, 1877, pp. 228-9, pl. 1, figs 28-29, Late Cambrian, Dunderberg Shale, locality unknown, Nevada; sensu Palmer (1955, pp. 94-96, pl. 19, figs 20-21, USNM 24557).

Reglardless of synonymy, many specimens have been referred to Pseudagnostus communis (Hall & Whitfield), viz:

* Palmer, 1954, pp. 720-1, pl. 76, figs 1-3, UT 32205, USNM 123309 UT 32169.
* Palmer, 1960, p. 61, pl. 4, figs 3-4, USNM 136832a-b.
* Robison, 1960b, p. 14, pl. 1, figs 2, 5, BYU 10911-0-975a-b.
* Rasetti, 1961, p. 109, pl. 23, figs 13-17, USNM 143054-5.
Bell & Ellinwood, 1962, p. 389, pl. 51, figs 7-21, UT 34842-56.
* Lochman, 1964, pl. 47, pl. 9, figs 32-36, USNM 140664a-e.
* Rasetti, 1965, p. 39, pl. 10, figs 23-25, USNM 144547.
* Palmer, 1968, pp. 29-30, pl. 7, figs 5, 10, USNM 136832a-b.

Diagnosis. Cephalon subcircular to subovoid, partially effaced, narrow borders with non-deliquiate to subdeliquiate marginal furrows, spectaculate, anterior glabellar furrow usually transverse rectilinear, median preglabellar furrow invariably present. Pygidium subcircular to subovoid, partially effaced, subplethoid, weakly to strongly deuterolobate, narrow borders with subdeliquiate marginal furrows, spines well in advance of a transverse line drawn across the rear of the deuterolobe, 8 late holaspid metameres.

Other species.

* Agnostus coloradoensis Shumard, 1861, p. 218, cephalon, USNM 26928.
* Pseudagnostus convergens Palmer sensu Lochman & Hu, 1959, p. 412, pl. 57, figs 1-6, USNM 1 37088a-f.
* Agnostus josepha Hall, 1863, p. 178, pl. 6, figs 54-55; 1867, p. 169, pl. 1, figs 54-55; refigured in Shimer & Shrock, 1944, pl. 251, figs 5-6 cotypes AMNH 311.

* Pseudagnostus josephus (Hall) /sic 7 sensu Grant, 1965, p. 108, pl. 13, figs 13-14, USNM 142409-10.

* Pseudagnostus cf. P. laevis Palmer sensu Grant, 1965, p. 108, pl. 14, figs 34-35, USNM 142319.

* Pseudagnostus latus Kobayashi, 1938, p. 171, pl. XVI, figs 23-24, cotypes GSC 11989-11990, ? non figs 40-41, GSC 1191-2.

* Agnostus neon Hall & Whitfield, 1877, pp. 229-230, pl. 1, figs 26-27, cotypes USNM 24568; refigured Palmer 1955, pp. 94, 96, pl. 19, figs 16, 19, and synonymized with communis.

* Pseudagnostus orientalis Kobayashi, 1933, pp. 98-99, pl. IX, figs 20-22, IGUT unnumbered /holotype fig. 22 7; 1935 b, pp. 110-111, pl. III, figs 7-11, 23, IGUT unnumbered.

* Agnostus prolongus Hall & Whitfield, 1877, pp. 230-231, pl. 1, figs 30-31, cotypes USNM 24637; refigured Palmer, 1955, pp. 98-99, pl. 19, figs 17, 22.

* Pseudagnostus prolongus (Hall & Whitfield) sensu Lochman & Hu, 1959, pp. 412-3, pl. 57, figs 7-16, USNM 137089a-k.

* Pseudagnostus cf. prolongus (Whitfield)/sic 7 sensu Lochman & Hu, 1960, p. 812, pl. 95, fig. 36, USNM 138218.

Pseudagnostus rotundatus Lermontova, 1940, p. 125, pl. 49, figs, 12, 12a-c, repository and numbers not known.

Pseudagnostus rotundatus Lermontova sensu Pokrovskaya in Tchernysheva et al., 1960, p. 464, pl. 2, fig. 7, repository, numbers and location (apart from Siberia) unknown.

* Pseudagnostus sentosus Grant, 1965, pp. 108-9, pl, 9, figs 2-3, 5, holotype pygidium USNM 142284, paratypes USNM 142283, 142434.

* Pseudagnostus vulgaris Rosova sensu Palmer, 1968, p. 30, pl. 12, fig. 5, USNM 146845, ? non fig. 6, USNM 146661.

* Pseudagnostus spp., Palmer, 1962, p. 21, pl. 2, figs 16, 21, 26, USNM 143147a-b, 143148.

* Pseudagnostus sp., Robison & Palmer, 1968, pp. 169-170, photo 3, USNM 158031.

Questionably included in the communis group are also:

* Pseudagnostus gyps (Clark) sensu Rasetti, 1959, p. 381, pl. 51, figs 13-14, USNM 136929.

Pseudagnostus cyclopygeformis (Sun) (pars) sensu Endo in Endo & Resser, 1937, p. 316, pl. 65, figs 19-22, non pl. 68, figs 8-16, MSM 1080, 1157, 1249, 1260, 2582 (unplaced).

Age & distribution

Late Cambrian: late Dresbachian Zones of Aphelaspis, Dicanthopyge, and Dunderbergia, Franconian Zones of Elvinia, Conaspis (Taenicephalus), Ptychaspis (Idahoia), and Saukia (Illaenurus), Nevada, Utah, Texas, Idaho, Montana, Wyoming, Alabama, Wisconsin, Minnesota, Maryland, Tennessee, Alaska, U.S.A., Elvinia Zone, British Columbia, Canada; late Tuorian, Zone of Glyptagnostus reticulatus; Shidertan, Zone of Plicatolina perlata, Yakutia, Olenek River, USSR, (Lazarenko, 1966; Ivshin & Pokrovskaya, 1968); Paishanian, Chuangia Zone, Liaotung and Taitzuho, Manchuria, South Korea.

Comments.

A Pseudagnostus communis species group initially was recognized by Palmer (1968, p. 30), although no unifying or diagnostic characteristics were listed. The assignment of species made here differs from those listed by Palmer.

As constituted here, the communis group exhibits variation in shield shape and to some extent the position of the axial glabellar node. Species intermediate between spectaculate and papilionate exist, e.g. P. communis sensu Rasetti, 1961, P. neon (Hall & Whitfield), and the specimens ascribed to P. prolongus by Lochman & Hu (1959), which appear to link the communis group morphologically to that of Rhaptagnostus clarki (following). Within a single paradigm there is a more or less constant degree of effacement.

CONTRACTA GROUP (Fig. 10)

Nominal species. *Pseudagnostina contracta Palmer, 1962, p. F21, pl. 2, figs 18-20, 22-25, holotype pygidium USNM 143150, paratypes USNM 143149a-b, 143151-2, 143153a-b, Late Cambrian, Dresbachian, Cedaria Zone, Nevada, Alabama, U.S.A.

Diagnosis. Cephalon subovoid to subquadrate, effaced and partially effaced, deliquiate and subdeliquiate marginal furrows, strongly spectaculate, rectilinear transverse anterior furrow, median preglabellar furrow absent. Pygidium subovoid to subquadrate, effaced and partially effaced, subdeliquiate marginal furrows, non-plethoid, weakly deuterolobate, spines variable but usually posteriorly positioned close to the rear of the deuterolobe.

Other species.

* Pseudagnostina vicaria Öpik, 1967, pp. 158-9, pl. 55, fig. 4, pl. 63, figs 8-9, holotype pygidium CPC 5918, paratypes CPC 5816, 5919.
* Pseudagnostina ?sp. indet. (aff. vicaria sp. nov.) Öpik, 1967, p. 159, pl. 63, fig. 10, CPC 5920.

Öpik (1967, p. 150) has noted that species described as Agnostus douvillei Bergeron by Walcott (1913, p. 100, pl. VII, figs 3, 3a-b; pl. XI, figs 6-7) and Resser & Endo (in Endo & Resser, 1937, p. 162, pl. 49, figs 25-28) may belong to Pseudagnostina. Agnostus koerferi Monke (1903, pp. 111-114, pl. 3, figs 1-9, pl. 9; Woodward, 1905, pp. 211-215, 251-255, pl. 13, fig. 5) synonymized with douvillei by Walcott (1913, p. 100), thus may also belong to Pseudagnostina. Wolfart (1974, p. 90) has synonymized other references to Agnostus douvillei (Mansuy, 1916, Kobayashi 1935b, Lu et al., 1957, 1965), with his Pseudagnostus kobayashii, which is tentatively included here in the cyclopyge group. The type cephalon of Agnostus douvillei Bergeron (1899, p. 503, pl. XIII, fig. 3, repository and number unknown), cannot be readily interpreted. The species Oedorhachis boltonensis Resser, which Palmer (1962, p. 21) regarded as belonging to Pseudagnostina, is here placed in the bulgosus species group.

Age & distribution.

Late Cambrian: Mindyallan; Glyptagnostus stolidotus Zone, western Queensland, Australia; Dresbachian, Cedaria Zone, Alabama, Nevada, U.S.A.; Kushanian, Drepanura-Stephanocare interval, Vietnam, China (Shantung), Manchuria (Liaotung), South Korea.

Comments.

This group may represent an effaced derivation from the bulgosus group.

CYCLOPYGE GROUP (Fig. 11)

Nominal species. *Agnostus cyclopyge Tullberg, 1880, p. 26, pl. II, figs 15a, c, as intepreted by Westergaard, 1922, pp. 116-7, pl. 1, figs 7-8 (LU Lo 3066t-3067t), Late Cambrian, Zones of Olenus and Parabolina spinulosa with Orusia lenticularis, Andrarum, Skaane, Sweden [see discussion in introduction to this paper]. Of other specimens which have been assigned to this species, the following have been traced:

* Agnostus cyclopyge Tullberg sensu Lake, 1906, pp. 27-8, pl. II, figs 21-22, OUM number not known and BMNH 58494 respectively; also * Pseudagnostus cyclopyge (Tullberg) sensu Rushton (in Taylor & Rushton, 1971, p. 26, pl. VIII, figs 1-2, GSM Ru 1202, 1042).

Diagnosis. Cephalon subovoid to rounded subquadrate, en grande tenue, wide borders with strongly deliquate marginal furrows, spectaculate, subovoid to subcircular acrolobe, transverse rectilinear anterior furrow in early representatives becoming curved or V-form in later ones, median preglabellar furrow present. Pygidium subovoid to rounded subquadrate, en grande tenue, wide borders with strongly deliquiate marginal furrows, plethoid, deuterolobate, spines generally well forwards of a transverse line across the rear of the deuterolobe.

Other species.

* Pseudagnostus ampullatus Öpik, 1967, p. 150, pl. 61, figs 7-11, holotype pygidium CPC 5896, paratypes CPC 5897-5900.

Pseudagnostus angustilobus Ivshin, 1956, pp. 19-21, pl. 9, figs 11-15, 18-23, holotype cephalon GMAN 69/926, paratypes GMAN 73/926, 68/926, 72/926, 78/926, 79/926, 85/926, 84/926, 83/926, 123/926, 84/926.

Agnostus chinensis Dames, 1883, pp. 27-8, pl. 2, figs 18-19; Kobayashi 1973b, p. 434, pl. 17, figs 14a-b, material destroyed; Schrank, 1974, pp. 622-3, pl. 1, figs 1-7, MNHU K302, T893.2, 893.3, 894.1, 895.1; non Agnostus chinensis sensu Walcott, 1913, pp. 99-100, pl. 7, figs 4-5;

non Pseudagnostus chinensis (Dames) sensu Lu et al., 1965, p. 41, pl. 4, figs 3-5 = Peronopsis rakuroensis (Kobayashi) fide Kobayashi (1937b, p. 434).

Pseudagnostus communis (Hall et Whitfield) sensu Lu et al., 1965, pp. 41-2, pl. 4, figs 6-8, repository and numbers not known.

Homagnostus convexus Chu, 1959, pp. 88-89, pl. 1, figs 3-4, non figs 1-2, 5-7, also in Lu et al., 1965, p. 20, pl. 1, fig. 10, non figs 8-9, IPP 9411-9412.

* Pseudagnostus cf. cyclopyge (Tullberg) sensu Whitehouse, 1936, p. 100, pl. X, fig. 8, UQF 3188; probably equivalent to Pseudagnostus cf. vastulus Whitehouse sensu Öpik, 1963, pp. 50-53, text fig. 13, CPC 4302.

* Pseudagnostus idalis Öpik, 1967, p. 153, pl. 62, figs 8-9, pl. 63 figs 1, 3, holotype pygidium CPC 5908, paratypes CPC 5909-5911, 5913.

* Pseudagnostus cf. idalis Öpik, 1967, p. 154, pl. 63, fig. 4, CPC 5914.

* Plethagnostus jarillensis Rusconi, 1953, p. 4 [nom. nud.]; 1954, pp. 19-20, fig. 6, holotype pygidium NHMN 16674.

* Pseudagnostus leptoplastorum Westergaard, 1944, p. 39, pl. 1, fig. 1, holotype pygidium SGU C459; also Pseudagnostus leptoplastorum Westergaard sensu Ivshin, 1962, pp. 16-18, pl. 1, figs 8-18, GMAN 646/105-107, 110, 113-117, 120, 124.

* Pseudagnostus marginisulcatus Kobayashi, 1962, p. 32, pl. III, figs 10-11, holotype cephalon, paratype pygidium IGUT, unnumbered.

* Pseudagnostus nuperus Whitehouse, 1936, p. 100, pl. X, figs 5-7, holotype cephalon UQ F 3199, paratypes UQ F 3200-1.

* Agnostus obtusus Belt, 1868, pp. 10-11, pl. II, figs 15-16 [fig. 15, not located, fig. 16 BMNH 58494].

* Pseudagnostus primus Kobayashi, 1935b, pp. 108-9, pl. XIV, figs 6-10, IGUT, unnumbered (fig. 6 designated holotype cephalon); also Kobayashi, 1962, pp. 31-32, pl. III, figs 15-17, pl. V, figs 8-12, IGUT, unnumbered.

Pseudagnostus pseudocyclopyge Ivshin, 1956, pp. 17-19, pl. 1, figs 1-8, 10, 16-17, holotype cephalon GMAN 74/926, paratypes 64/926, 66/926, 121/926, 70/926, 75/926, 83/926, 80/926, 77/926, 87/926, 86/926; Ivshin, 1962, p. 18, pl. 1, figs 19-22, GMAN 646/217, 646/125, 646/123.

* Pseudagnostus sericatus Öpik, 1967, pp. 152-3, pl. 62, fig. 7, holotype cephalon CPC 5907.

* Pseudagnostus sp. undet., Shergold in Shergold et al. (in press), pl. 4, figs 9-11, NZ AR 601-3.

The cyclopyge group possibly also includes;

Pseudagnostus kobayashii Wolfart, 1974, pp. 90-93, pl. 10, fig. 8; pl. 11, figs 3-7, HAN 82/1, 82/2, 83/1. 84/2 (synonymy given).

* Oedorhachis tennesseensis Resser, 1938, p. 50, pl. 10, figs 24-26, cotypes USNM 94871.

* Pseudagnostus vastulus Whitehouse, 1936, pp. 99-100, pl. X, figs 3-4, holotype pygidium UQ F 2303, paratype UQ F 3202.

Pseudagnostus sp., Lu, 1956b, pp. 367-8, pl. 1, figs 1-2, ?IPP 8643-8644; also in Lu et al., 1965, p. 43, pl. 4, figs 18-19, same repository and numbers.

Age & distribution

Late Cambrian: Zones of Parabolina spinulosa, P. brevispina, Leptoplastus rhaphidophorus and Peltura scarabaeoides, United Kingdom, Sweden; late Tuorian, Glyptagnostus reticulatus Zone; early Shidertan, Irvingella Zone, central Kazakhstan (Ivshin & Pokrovskaya 1968); Kushanian, Blackwelderia paronai fauna, Manchuria; late Kushanian, Afghanistan; Paishanian, Chuangia Zone, China (Kweichow), Eochuangia Zone, South Korea; late Mindyallan Glyptagnostus stolidotus Zone, Idamean Zones of Glyptagnostus reticulatus with Proceratopyge nectans, Corynexochus plumula, Erixanium sentum, and Irvingella tropica with Agnostotes inconstans (Öpik, 1963, 1967), western Queensland, Australia. Species of the group also occur in South America (Argentina), where the age is uncertain; in Antarctica (northern Victoria Land) of probable late Idamean age (Shergold et al., in press); and possibly in North America (Tennessee), early Dresbachian, Blountia Zone (Resser 1938).

Comments.

The *cyclopyge* group is heterogeneous and probably capable of further division. Its members exhibit some variation in shield shape, degree of effacement, orientation of anterior glabellar furrow, extent of pygidial pleural lobes, and strength, shape, and orientation of the pygidial spines. Early species are distinctly spectaculate, but later Cambrian ones may begin to approach the papilionate condition, in that the axial glabellar node migrates forwards and begins to interfere with the anterior furrow without actually coming to rest between the anterolateral lobes. The *cyclopyge* group grades with effacement into the *communis* group.

SECURIGER GROUP (Fig. 12)

Nominal species. *Agnostus securiger Lake, 1906, p. 20, pl. II, fig. 11, GSM 57650, Late Cambrian, Olenus Zone, Outwood Shales, Chapel End, near Nuneaton, Worcestershire, U.K.

Diagnosis. Cephalon subovoid to subquadrate, en grande tenue, spectaculate, deliquiate marginal furrows, subovoid acrolobe, transverse rectilinear anterior glabellar furrow, median preglabellar furrow present. Pygidium subovoid to subrounded, en grande tenue, deliquiate marginal furrows, strongly deuterolobate, plethoid, posterolateral spines in advance of a line drawn across the rear of the deuterolobe plus a third sagittal spine developed from the posterior margin.

Other species.

No other species are described, although a trispinose pygidium of pseudagnostinid type is present in the Elvinia Zone assemblages of Cherry Creek, Egan Range, Nevada, U.S.A., USGS collection C02527 (A.R. Palmer, pers comm.).

Age & distribution.

Late Cambrian: late Olenus Zone, Worcestershire, U.K., early Franconian, Elvinia Zone, Nevada, U.S.A.

Comments.

The generic name Sulcatagnostus was erected by Kobayashi (1937a, p. 451) for Agnostus securiger (see below). Apart from its possession of a third, sagittal pygidial spine, Sulcatagnostus securiger (Lake) compares well with members of the cyclopyge group such as Pseudagnostus ampullatus Öpik and P. idalis Öpik, both of which have similar overall morphology.

[B] PAPILIONATE SPECIES GROUPS

CLARKI GROUP (Shergold, 1975, p. 60) (Fig. 13).

Nominal species. *Pseudagnostus (Plethagnostus) clarki Kobayashi, 1935a, p. 47, pl. IX, figs 1-2, holotype pygidium USNM 93062, paratype USNM 146887, Late Cambrian 'Briscoia' fauna, Hard Luck Creek, Alaska; refigured Palmer, 1968, 29, pl. 15, figs 10, 13-14.

Diagnosis. Cephalon subovoid to subcircular, effaced, wide borders with non-deliquiate marginal furrows, papilionate, V-form anterolateral glabellar furrows, median preglabellar furrow externally effaced, present parietally. Pygidium subovoid, effaced, wide borders with non-deliquiate marginal furrows, non-plethoid, weakly deuterolobate, small posterolateral spines sited well in advance of a transverse line drawn across the rear of the deuterolobe, 9-10 axial metameres.

Other species.

* Pseudagnostus clarki maximus Shergold, 1975, pp. 70-71, pl. 5, figs 1-2, holotype cephalon CPC 11587, paratype CPC 11588.

* Pseudagnostus clarki patulus Shergold, 1975, pp. 62-4, pl. 1, figs 1-6, pl. 2, figs 1-2, holotype cephalon CPC 11524, paratypes 11525-11531.

* Pseudagnostus clarki prolatus Shergold, 1975, pp. 64-9, pl. 3, figs 1-6, pl. 4, figs 1-6, holotype cephalon CPC 11532, paratypes CPC 11533-11542.

* Pseudagnostus cyclopygeformis (Sun) sensu Kobayashi, 1933, pp. 97-8, pl. IX, figs 19, 23-24, pl. X, fig. 7; 1935b, pp. 111-2, pl. III, figs 12-14, IGUT, no numbers.

* Pseudagnostus elix Shergold, 1975, pp. 71-3, pl. 2, figs 3-7, holotype pygidium CPC 11688, paratypes CPC 11689-11691.

* Pseudagnostus laevis Palmer, 1955, pp. 97-8, pl. 19, figs 8-9, 11-12, holotype pygidium USNM 123559, paratypes USNM 26990, 123560-61.

* Pseudagnostus orbiculatus Shergold, 1975, pp. 73-4, pl. 12, figs 8-13, holotype cephalon CPC 11591, paratypes CPC 11592-11595.

* _Pseudagnostus papilio_ (_pars_) Shergold, 1972, pp. 28-31, pl. 1, fig. 2, CPC 8443, _non_ pl. 1, figs 1, 3-8, pl. 2, figs 1-2 [_convergens_ group].

* _Peronopsis planulata_ Raymond, 1924, p. 395, pl. 12, fig. 9, holotype pygidium MCZ 1729.

* _Pseudagnostus_ cf. _prolongus_ (Hall & Whitfield) _sensu_ Kindle & Whittington, 1965, p. 686, pl. 1, figs 17-20, Kindle Collection.

* _Pseudagnostus_ sp. _II_, Shergold, 1972, p. 35, pl. 2, figs 6-7, CPC 8458-8459.

* _Pseudagnostus_ sp. _III_. Shergold, 1972, pp. 35-6, pl. 2, fig. 8, CPC 8460.

* _Pseudagnostus_ sp., Robison & Pantoja-Alor, 1968, p. 780, pl. 97, figs 17-18, USNM 158884-85.

Possibly also belonging to this species group are:

Pseudagnostus α sp., Kobayashi, 1935a, p. 41, plus plate explanation, p. VIII, fig. 3, repository and number not known.

Pseudagnostus β sp., Kobayashi, 1935a, p. 41, plus plate explanation, p. VIII, fig. 4, repository and number not known.

Age & distribution

Late Cambrian: pre-Payntonian and Payntonian, _Rhaptagnostus clarki patulus_ with _Caznaia squamosa_ through _Neoagnostus quasibilobus_ with _Tsinania nomas_ Assemblage-Zones (Shergold, 1975), western Queensland, Australia; Trempealeauan _Saukia_ Zone, _Saukiella pyrene_? and _S. serotina_ Subzones, Nevada, Montana, Vermont, Alaska, U.S.A.; Trempealeauan?, Oaxaca Province, Mexico; late Changshanian, _Kaolishania_ Zone, Shantung, China; Fengshanian, _Tsinania_ Zone, North and South Korea.

Comments.

The _clarki_ group is a homogeneous association of taxa exhibiting specific and subspecific variation in shapes and proportions, and border parameters.

CONVERGENS GROUP (Shergold 1975: 74) (Fig. 14)

Nominal species. *Pseudagnostus convergens Palmer, 1955, pp. 96-7, pl. 19, figs 14-15, holotype pygidium USNM 123562, paratype USNM 123563, Late Cambrian, Trempealeauan, Saukia Zone, Saukiella pyrene Subzone, Nevada, U.S.A.

Diagnosis. Cephalon subovoid to subcircular, effaced, and partially effaced, narrow borders with non-deliquiate marginal furrows, papilionate, V-form anterolateral furrows, median preglabellar furrow externally effaced, present parietally. Pygidium subovoid, with rearwards converging flanks and acrolobe, narrow borders with non-deliquiate marginal furrows, subplethoid, weakly deuterolobate, very small posterolateral spines well in advance of a transverse line drawn across the rear of the deuterolobe, 10 late holaspid metameres.

Other species.

* Pseudagnostus bifax Shergold, 1975, pp. 75-9, pl. 9, figs 1-7, holotype cephalon CPC 11596, paratypes CPC 11597-11602, 11649, 11656, 11662, 11667-68.

Agnostus cyclopygeformis Sun, 1924, pp. 26-28, pl. II, figs 1a-h, GSCh 501-4, 507-510; 1935: 16, pl. III, figs 29-32, NUP 1194-1197; also

* Pseudagnostus cyclopygeformis (Sun) sensu Endo, 1939, p. 6, pl. 1, figs 14-15, USNM 96092b-c, non fig. 13, USNM 96092a; Pseudagnostus cyclopygeformis (Sun) sensu Lu et al., 1957, pl. 137, figs 20-21, repository and numbers not known; 1965, p. 42, pl. 4, figs 9-12, repository and numbers not known.

Pseudagnostus obsoletus Lermontova, 1951, pp. 10-11, pl. 2, figs 8-10, repository and numbers unknown.

Pseudagnostus cf. obsoletus Lerm. (MS), Lermontova, 1940, p. 125, pl. 49, fig. 11, repository and number not known.

* Pseudagnostus papilio Shergold, 1972, pp. 28-31, pl. 1, figs 1, 3-8, non fig. 2 [clarki group], pl. 2, figs 1-2, holotype cephalon CPC 8442, paratypes CPC 8443-8450, also 1975, pp. 79-82, pl. 11, figs 1-8, CPC 11669-11677.

Possibly also belonging to this group are:

* Pseudagnostus sp. I, Shergold, 1972, p. 34, pl. 2, figs 3-5, CPC 8457.

Age & distribution.

Late Cambrian: pre-Payntonian, Rhaptagnostus bifax with Neoagnostus denticulatus and R. clarki maximus with R. papilio Assemblage-Zones (Shergold, 1975), western Queensland, Australia; late Changshanian, Kaolishania Zone, Shantung, Hopei, China; Trempealeauan, Saukiella pyrene Subzone, Saukia Zone, Nevada, U.S.A.; Shidertan, Lotagnostus trisectus/Peltura Zone, Kazakhstan, USSR.

Comments.

As for clarki group.

PSEUDAGNOSTINID SPECIES UNASSIGNED

* Pseudagnostus cf. P. convergens Palmer sensu Lochman, 1964, p. 51, pl. 13, fig. 10, USNM 140686.

Agnostus cyclopyge Tullberg sensu Sun, 1935, pp. 15-16, pl. III, figs 33-36, THU 1198-1201; sensu Lu et al., 1965, pp. 40-41, pl. 4, figs 1-2 [reproductions of Sun's figures].

Pseudagnostus cyclopyge (Tullberg) sensu Wilson, 1954, p. 284, pl. 25, fig. 19, pl. 26, fig. 13.

*?Hypagnostus empozadensis Rusconi, 1953, p. 6 [nom. nud.]; 1954, p. 34-5, pl. II, fig. 11, NHMM 16872, an effaced papilionate subquadrate cephalon.

* Leiopyge empozadense Rusconi, 1953, pp. 5-6 [nom. nud.]; 1954, pp. 33-4, pl. 11, fig. 10, NHMM 16856, an incomplete pygidium.

* Oedorhachis greendalensis Resser, 1938, p. 51, pl. 10, fig. 9, USNM 94861.

* Plethagnostus gyps Clark, 1923, p. 124, pl. 1, fig. 9, holotype pygidium MCZ 1700; refigured Clark, 1924, p. 16, pl. 3, fig. 2; sensu Rasetti 1944, p. 234, pl. 36, figs 20-22, LU 1105a-c [may represent a distinct en grande tenue papilionate species group].

Pseudagnostus impressus Lermontova, 1940, p.125, pl. 49, figs 13, 13a, repository and numbers not known.

* Pseudagnostus jeholensis Kobayashi, 1951, pp. 76-7, pl. 7, figs 13-14, IGUT no numbers; reproduced in Lu et al., 1965, p. 43, pl. 4, figs 16-17.

Pseudagnostus j sepha (Hall) as illustrated by:

Frederickson, 1949, p. 362, pl. 72, fig. 17, OGM 105-16F-53.

Lochman, 1950, pp. 329-330, pl. 46, fig. 14.

Nelson, 1951, p. 776, pl. 107, fig. 5.

Bell, Feniak & Kurtz, 1952, pp. 196-7, pl. 32, figs 4a-b, pl. 33, fig. 1.

Ellinwood, 1953, p. 65, pl. 4, figs 9-10.

Wilson, 1954, p. 284, pl. 25, figs 5, 22.

* Agnostus maladensis Meek 1873, p. 464, USNM 24597 [a medley of taxa].

* Pseudagnostus mesleri (Resser) sensu Lochman, 1940, pp. 26-7, pl. 2, figs 38-43, USNM 98703.

Microdiscus paronai Airaghi, 1902, p. 23, pl. 2, figs 24-25, repository and numbers not known.

* Spinagnostus pedrensis Rusconi, 1951, p. 8, fig. 9, NHMN 9963 [referred to Leiopyge by Rusconi, 1953, p. 6, originally illustrated as a cephalon, this specimen is actually an indeterminate pseudagnostinid pygidium].

Agnostus pii Airaghi, 1902, p. 19, pl. 1, fig. 28, repository and number not known.

* Pseudagnostus prolongus (Hall & Whitfield) sensu Palmer, 1960, p. 61, pl. 4, figs 5-6, USNM 136833a-b.

Pseudagnostus (Rhaptagnostus?) semiovalis Kobayashi, 1973a, pp. 452-3, pl. II, figs 8-9, repository Freiburg, types destroyed (Kobayashi pers comm., October 1972).

? Pseudagnostus sp. Lu, 1956a, pp. 282-3, pl. 1, figs. 8; Lu et al., 1965: 44, pl. 4, fig. 20, repository and number not known.

PSEUDAGNOSTI NOMINA NUDA

Pseudagnostus ovatus Rusconi, 1950, p. 94 [plate explanation error, fig. 6, for P. parabolicus].

Pseudagnostus huangluoensis Kobayashi, 1951, p. 75.

Pseudagnostus mirus Pokrovskaya in Vasilenko, 1963, p. 22, Chart 3 [listed].

Pseudagnostus solus Endo in Endo & Resser, 1937, p. 304 [listed].

DEFINITION OF GENERIC GROUPS

Since Jaekel erected Pseudagnostus in 1909 several attempts have been made to subdivide the genus, e.g. Clarke 1923, Whitehouse 1936, Kobayashi 1937a, 1955, Lermontova 1940, inter alia. Accordingly there is a proliferation of generic and subgeneric names, some of which have doubtful taxonomic validity. These are briefly reviewed below in discussing the generic classification of pseudagnosti.

In this classification Pseudagnostus Jaekel 1909, type species Agnostus cyclopyge Tullberg (1880, p. 26, pl. II, figs 15a, 15c), is restricted to include only the cyclopyge, communis, and bulgosus species groups as documented above.

Plethagnostus, erected by Clark (1923, p. 124), originally differentially diagnosed from Pseudagnostus by having 'divergent dorsal [accessory] furrows continued to the border of the pygidium' as in Plethagnostus gyps Clark (loc. cit., pl. I, fig. 9), its type species, is suppressed. This action is taken because:
[1] many pseudagnostinid species are plethoid, the courses of the accessory furrows continuing to the marginal furrows, particularly in en grande tenue and partially effaced species groups, e.g. the cyclopyge and communis group referred above to Pseudagnostus; [2] the type species is based on a single incomplete pygidium (MCZ 1700) which lacks a posterior margin; [3] usage of the name Plethagnostus has been confused by Kobayashi (1935a, pp. 46-7), who utilised Clark's taxon in a subgeneric sense for the species Pseudagnostus clarki, which has a papilionate cephalon and non-plethoid pygidium with effaced accessory furrows! Subsequent usage of Plethagnostus appears to have followed Kobayashi's interpretation. It is recommended that this practice be discontinued because the type specimen of Plethagnostus gyps quite obviously does not belong to the same species group as Pseudagnostus clarki, and because of its incompleteness cannot be adequately classified anyway. Plethagnostus gyps Clark is left unclassified with respect to species groups and is referred to Pseudagnostus sensu lato.

Rhaptagnostus Whitehouse (1936, p. 97), based on Agnostus cyclopygeformis Sun, 1924, was differentiated from Pseudagnostus by possessing 'an elliptical arrangement of foramina [notulae] in the post-axial region' of the pygidium, and a 'simple, non-spinose brim'. Sun's specimens (1924, pl. II, figs 1a-h) appear to be parietal surfaces, and such surfaces of many pseudagnosti display notular lines given the right medium of preservation. The absence of pygidial spines in any pseudagnostinid species is greatly doubted. Very often these spines are extremely small and readily destroyed by certain modes of preservation, e.g. in arenaceous matrices, and by negligent preparation. Cephala matched by Sun with the pygidia which Whitehouse chose to differentiate from Pseudagnostus, are papalionate and thus different from those of Pseudagnostus cyclopyge (Tullberg) which is spectaculate. Pseudagnostus cyclopygeformis (Sun) is here included within the convergens species group. Rhaptagnostus is used herein to distinguish the two closely related papilionate species groups, clarki and convergens, from spectaculate ones at the generic level. This name is preferred to the previously and erroneously used Plethagnostus Clark sensu Kobayashi 1935a.

Sulcatagnostus was erected by Kobayashi (1937a, p. 451) for Agnostus securiger Lake (1906, p. 20, pl. II, fig. 11), and distinguished by possessing 'irregular divergent furrows on the side lobes' (Kobayashi, op. cit., 450-451). This was later redefined as 'Pseudagnostinae with reticulated furrows on side lobes' (Kobayashi 1939, p. 159). The reticulation described (Fig. 12) refers to the caecal network of the cephalic acrolobe and pygidial pleural lobes. The presence of a caecal display, common on exfoliated specimens under certain conditions of preservation, is itself insufficient to justify differentiation from Pseudagnostus. Overlooked by Kobayashi, however, is the fact that Agnostus securiger Lake also possesses a trispinose pygidium (Rushton in Taylor & Rushton 1971, p. 20), which certainly is a significant characteristic. In view of the otherwise similar morphology to spectaculate pseudagnost, Sulcatagnostus is retained as a subgenus of Pseudagnostus.

Euplethagnostus Lermontova (1940, p. 126), based on E. subangulatus Lermontova (loc. cit., pl. XLIX, figs 15, 15a), was compared to Plethagnostus Clark, 1923, but distinguished by the possession of posterolateral pygidial spines, sometimes an intranotular axis [lanceolate ridge], and the presence of a posterior pygidial terminal node. Such characteristics are emphatically not diagnostic in generic classification because: [1] the type specimen of Plethagnostus gyps, type species of Plethagnostus, is damaged and it is not possible to ascertain whether it possessed spines - Clark (1923) assumed that their traces were still apparent, and Rasetti (1944, pl. 36, figs 20-22) has illustrated material possessing pygidial spines which can be assigned to P. gyps; [2] the presence of terminal nodes and intranotular axes is commonly observed on a multiplicity of pseudagnostinid parietal surfaces; [3] Lermontova's specimens are poorly illustrated and inadequately described, no type specimen was selected for E. subangulatus and the repository of material is unknown. E. subangulatus appears most similar to species classified herein with the clavus group. Its type specimens require redescription and reillustration if the name Euplethagnostus is to be retained.

Problems associated with the taxonomic validation of Pseudorhaptagnostus Lermontova (1940, p. 126) have been previously discussed (Shergold 1972, p. 28). These problems remain unresolved. The name Pseudorhaptagnostus was introduced by Lermontova in 1940, P. simplex Lermontova (1951, pp. 12-13, pl. 2, figs 11-17) being designated as type species. Although a second species, P. punctatus Lermontova, was illustrated in 1940, P. simplex was neither illustrated not described until 1951. At this time a heterogeneous collection of cephala and pygidia was figured. While the pygidia (Lermontova, 1951, p. 2, figs 11-14) show morphological consistency, two types of cephalon were figured: one (fig. 15) is probably that associated with the pygidia, whereas the others (figs 16-17) belong to a species of the convergens group. Nikitin (1956, p. XIV, figs 4-5) reillustrated this combination of convergens group cephalon with Pseudorhaptagnostus pygidium. Such mismatching appears to result directly from Lermontova's failure to designate a holotype. According to Lermontova

(1940), Pseudorhaptagnostus is differentiated from Rhaptagnostus Whitehouse in possessing a thickened pygidial rim and well developed posterolateral spines. A lanceolate field [intranotular axis] is stated to be present on pygidial internal casts [parietal surfaces]. None of these characteristics is considered to justify separation from Pseudagnostus, either separately or in combination. Others, exhibited by Pseudarhaptagnostus simplex, can however be utilised if the name is to be retained (Shergold, 1972, p. 28).

These characteristics, which can only be verified from examination of the actual material on which Pseudorhaptagnostus is based, involve the cephalic and pygidial shapes, nature of their borders and pygidial spines, and pygidial segmentation. Although it appears that P. simplex has much in common with the clavus species group recognized above, judgement on the validity of the genus must await clarification of the concept of the taxon. It is very likely that Pseudorhaptagnostus and Euplethagnostus Lermontova are synonyms. If so, Pseudorhaptagnostus has priority, being first listed.

Neoagnostus Kobayashi (1955, p. 473), type species N. aspidoides Kobayashi (op. cit., 473-4), possesses a cephalon with trilobed glabella and median preglabellar furrow (Fig. 15). The holotype cephalon (loc. cit., pl. VII, fig. 5) is a parietal mould preserved en grande tenue. The associated pygidium (loc. cit., fig. 4), labelled paratype, is geragnostoid.

Hyperagnostus Kobayashi (1955, p. 474), based on H. binodosus Kobayashi (op. cit., 475), also has a trilobed glabella, but is said to differ from Neoagnostus in not possessing a median preglabellar furrow (Fig. 15). The holotype cephalon (loc. cit., pl. VII, fig. 2) is partially exfoliated, somewhat distorted, and incomplete, the anterior portion of the cephalon having been lost. A thin veneer of shell lies across the position in which the median preglabellar furrow would be expected and its presence or absence cannot be absolutely verified; it appears not to be present on the external test, but may be weakly present on the parietal surface. The assigned pygidium (loc. cit., fig. 3) is agnostoid rather than pseudagnostoid.

Although Neoagnostus and Hyperagnostus occur at different localities and are of slightly different ages, they are temporarily synonymized herein, Neoagnostus taking priority.

Machairagnostus Harrington & Leanza (1957, p. 63), based on M. tmetus Harrington & Leanza (op. cit., 64, fig. 7), is represented by parietal surfaces. The glabella is faintly trisegmented, but the cephalic acrolobe is scrobiculate. The pygidium is weakly deuterolobate, and the muscle scar impressions of the third axial segment are incorporated into the anterior portion of the axis which is delineated by axial furrows. M. tmetus has the glabellar morphology of members of the araneavelatus species group, and pygidial characteristics of the bilobus group with which it is classified here. The scrobiculation of the cephalic acrolobe is non-diagnostic under the conditions of this classification, and so Machairagnostus is synonymized with Neoagnostus.

Pseudagnostina Palmer (1962, pp. 20-21), type species P. contracta Palmer (1962, pp. 20-21, pl. 2, figs 18-20, 22-25), was coined for pseudagnosti having 'Peronopsis-like cephalon and Pseudagnostus-like pygidium'. The concept of the taxon is broadened somewhat here by the inclusion of some Asian species previously referred to Agnostus douvillei Bergeron, 1899. Because of overall basic similarity of the pygidium to that of other pseudagnosti, Pseudagnostina is regarded here as a subgenus of Pseudagnostus, covering the effaced and partially effaced, strongly spectaculate, weakly deuterolobate species constituting the contracta species group.

SYNOPSIS

Spectaculate species groups fall readily into two larger groupings:

[1] The bulgosus-communis-contracta-cyclopyge-securiger grouping whose morphology differs by degree and which can largely be encompassed within a concept of Pseudagnostus based on its type species P. cyclopyge (Tullberg, 1880). Effaced variants are differentiated as the contracta group regarded as a distinct subgenus, Pseudagnostina Palmer, 1962; and the securiger group, with three pygidial spines, likewise is separated at the subgeneric level as Sucatagnostus Kobayashi, 1937.

[2] The araneavelatus-bilobus-canadensis-clavus grouping is united by an arrangement of glabellar lobation and furrowing different from that of Pseudagnostus. The anterolateral lobes are closer together and may meet adaxially so that the glabellar furrows intersect as a cross. Within this division species group are differentiated by shield shape, and degree of effacement, particularly which glabellar furrows are effaced and which are not. Five generic names appear to be available for classifying these groups: Pseudorhaptagnostus Lermontova, 1940, Euplethagnostus Lermontova, 1940, Neoagnostus Kobayashi, 1955, Hyperagnostus Kobayashi, 1955, and Machairagnostus Harrington & Leanza, 1957. As indicated above, Pseudorhaptagnostus and Euplethagnostus may be synonymous, the former taking priority; and Hyperagnostus and Machairagnostus are regarded as synonyms of Neoagnostus.

Although Pseudorhaptagnostus and Euplethagnostus have priority over Neoagnostus, their concepts are very poorly understood, and it has been found not possible to obtain adequate information to verify their characteristics. Accordingly, Neoagnostus is temporarily adopted in this classification, in preference to either of the Russian genera, for the araneavelatus-bilobus-canadensis-clavus grouping.

The papilionate species groups, clarki and convergens, are placed here in Rhaptagnostus Whitehouse, 1936, because its interpretable type species is representative of the convergens group.

Thus the following classification is adopted:

Family Diplagnostidae Whitehouse, 1936, emend. Öpik, 1967.

Subfamily Pseudagnostinae Whitehouse, 1936.

Genus Pseudagnostus Jaekel, 1909

Type species: Agnostus cyclopyge Tullberg, 1880, designated Jaekel, 1909. Pseudagnostinae with long (sag.) anteriorly rounded or pointed anterior glabellar node, axial node lying behind anterolateral lobes and anterior furrow which is straight or curved rearwards sagittally. Shields are subcircular to subovoid, effaced to en grande tenue, non-deliquiate to deliquiate, weakly and strongly deuterolobate. Up to eight late holaspid pygidial metameres.

Subgenus Pseudagnostus Jaekel, 1909

Type species and diagnosis as above

Group bulgosus, based on Pseudagnostus bulgosus Öpik, 1967

Group communis, based on Agnostus communis Hall & Whitfield, 1877.

Group cyclopyge, based on the type species.

Subgenus Pseudagnostina Palmer, 1962

Type species: Pseudagnostina contracta Palmer, 1962 (by original designation)

Spectaculate pseudagnostinae with subquadrate shields and with effaced median preglabellar furrow, accessory furrows and deuterolobe.

Group contracta, based on the type species.

Subgenus Sulcatagnostus Kobayashi, 1937

Type species: Agnostus securiger Lake, 1906 (designated Kobayashi, 1937a).

Spectaculate en grande tenue pseudagnostinae with trispinose pygidium.

Group securiger, based on the type species.

Genus Neoagnostus Kobayashi, 1955.

Type species: Neoagnostus aspidoides Kobayashi, 1955 by original designation.

Spectaculate pseudagnosti with anterolateral glabellar lobes close together or meeting adaxially, and a tendency to efface or overdeepen either the furrows in front of or behind the anterolateral lobes; anterior lobe small and rhomboid. Pygidium with distinct tendency to incorporate a third segment into that portion of the axis defined by axial furrows; retrial spines. Generally, species have subquadrate shields, whose external morphology may be effaced, partially effaced or en grande tenue, non-deliquiate to deliquiate, weakly to strongly deuterolobate. Up to eight late holaspid pygidial metameres.

Group araneavelatus based on Pseudagnostus araneavelatus Shaw, 1951.

Group bilobus based on Pseudagnostus bilobus Shaw, 1951.

Group canadensis based on Agnostus canadensis Billings, 1860.

Group clavus based on Pseudagnostus clavus Shergold, 1972.

Genus Rhaptagnostus Whitehouse, 1936.

Type species: Agnostus cyclopygeformis Sun, 1924, designated Whitehouse, 1936.

Papilionate pseudagnosti with subovoid shields, externally generally effaced or partially effaced. Pygidia with 10 late holaspid metameres; spines advanced with respect to the rear of the deuterolobe, and minute.

Group clarki, based on Pseudagnostus clarki Kobayashi, 1935a.

Group convergens, based on Pseudagnostus convergens Palmer, 1955.

Non-investigated genera of Pseudagnostinae are Litagnostus Rasetti, 1944, Xestagnostus Öpik, 1967, and Oxyagnostus Öpik, 1967.

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APPENDIX A.

MORPHOLOGICAL CONDITIONS APPLICABLE TO PSEUDAGNOSTI

Constricted/unconstricted acrolobes. If the lateral margins of the acrolobe are curved slightly inwards, then the condition is known as constricted. Where a constant curvature of the flanks of the acrolobe is maintained the condition is said to be unconstricted. Most species of Pseudagnostus have constricted pygidial acrolobes, the condition being most readily observed on parietal surfaces. Some species also have constricted cephalic acrolobes.
Deliquiate/non-deliquiate marginal furrows. Marginal furrows which are deeply grooved or channel-like are described as deliquiate (Shergold, 1975). If the marginal furrow is merely a break in convexity at the junction of the acrolobe and border the condition exhibited is non-deliquiate. Gradations exist, for which the term subdeliquiate is introduced to permit the description of degrees of deepening of furrows. Degree of deliquiation is related directly to degree of effacement. Shell and mould of the same specimen will have differing degrees of deliquiation, the mould having deeper wider furrows.

Deuterolobate. All pseudagnosti are deuterolobate. Degree of elevation of the deuterolobe, however, varies. En grande tenue species generally have a tumid deuterolobe well defined by accessory furrows. For this condition the term strongly deuterolobated is used here. Species with depressed deuterolobes are described as weakly deuterolobate.

Effaced/effacement/partial effacement. An effaced condition is one in which furrows and lobes with visible convexity are obliterated to give a smooth or nearly smooth surface. In Pseudagnostinae all conditions of partial effacement exist, from highly effaced to en grande tenue.

En grande tenue. Introduced by Öpik (1961b, p.55), this term was redefined (Öpik 1967a, p. 56) to categorize agnostids having distinct lobes and furrows.

Papilionate. Pseudagnostinae in which the axial glabellar node lies between the anterolateral lobes are termed papilionate. The term is derived from the butterfly-like appearance of these lobes and furrows.

Plethoid. Pseudagnostinae with accessory furrows clearly encircling the deuterolobe or continued posteriorly to the marginal furrow exhibit a plethoid condition.

Retral. This term refers to the siting of the posterolateral pygidial spines at the rear of the shield, behind or at the level of the rear of the deuterolobe.

Simplicimarginate/zonate borders. Simplicimarginate agnostids have a basic unmodified border. Those having a duplicated posterior margin are said to be zonate (Öpik, 1967a).

Spectaculate. A term introduced for pseudagnosti in which the axial glabellar node lies to the rear of the anterolateral glabellar lobes, and is therefore also to the rear of the anterior glabellar furrow. The resulting appearance resembles a bespectacled face - hence the term.

APPENDIX B. CLASSIFICATION OF SPECIES ASSIGNABLE TO PSEUDAGNOSTUS sensu lato

	SPECIES/AUTHOR/DATE	ORIGINAL GENERIC ASSESSMENT	SPECIES GROUP	REVISED GENERIC ASSIGNMENT
1.	acutifrons Troedsson, 1937	Rhaptagnostus	clavus	Neoagnostus
2.	cfr. acutus Kobayashi, 1938	Homagnostus	clavus?	Neoagnostus
3.	ampullatus Öpik, 1967	Pseudagnostus	cyclopyge	Pseudagnostus (Pseudagnostus)
4.	angustilobus Ivshin, 1956	Pseudagnostus	cyclopyge	Pseudagnostus (Pseudagnostus)
5.	araneavelatus Shaw, 1951	Pseudagnostus	araneavelatus	Neoagnostus
6.	aspidoides Kobayashi, 1955	Neoagnostus	bilobus	Neoagnostus
7.	bifax Shergold, 1975	Pseudagnostus	convergens	Pseudagnostus (Rhaptagnostus)
8.	bilobus Shaw, 1951	Pseudagnostus	bilobus	Neoagnostus
9.	binodosus Kobayashi, 1955	Hyperagnostus	bilobus	Neoagnostus
10.	bituberculatus Ivshin, 1960	Pseudagnostus	clavus?	Neoagnostus
11.	boltonensis Resser, 1938	Oedorhachis	bulgosus	Pseudagnostus (Pseudagnostus)
12.	bulgosus Öpik, 1967	Pseudagnostus	bulgosus	Pseudagnostus (Pseudagnostus)
13.	canadensis Billings, 1860	Agnostus	canadensis	Neoagnostus
14.	cavernosus Rosova, 1960	Pseudagnostus	clavus	Neoagnostus
15.	chinensis Dames, 1883 (pars)	Agnostus	cyclopyge	Pseudagnostus (Pseudagnostus)
16.	clarki Kobayashi, 1935A	Plethagnostus	clarki	Pseudagnostus (Rhaptagnostus)
17.	clarki patulus Shergold, 1975	Pseudagnostus	clarki	Pseudagnostus (Rhaptagnostus)
18.	clarki prolatus Shergold, 1975	Pseudagnostus	clarki	Pseudagnostus (Rhaptagnostus)
19.	clarki maximus Shergold, 1975	Pseudagnostus	clarki	Pseudagnostus (Rhaptagnostus)

SPECIES/AUTHOR/DATE	ORIGINAL GENERIC ASSESSMENT	SPECIES GROUP	REVISED GENERIC ASSIGNMENT
20. clavus Shergold, 1972	Pseudagnostus	clavus	Neoagnostus
21. coloradoensis Shumard, 1961	Agnostus	communis	Pseudagnostus (Pseudagnostus)
22. communis Hall & Whitfield, 1877	Agnostus	communis	Pseudagnostus (Pseudagnostus)
23. contracta Palmer, 1962	Pseudagnostina	contracta	Pseudagnostus (Pseudagnostus)
24. convergens Palmer, 1955	Pseudagnostus	convergens	Pseudagnostus (Rhaptagnostus)
25. convexus Chu, 1959 (pars)	Homagnostus	cyclopyge	Pseudagnostus (Pseudagnostus)
26. coronatus Shergold, 1975	Pseudagnostus	araneavelatus	Neoagnostus
27. cyclopyge Tullberg, 1880	Agnostus	cyclopyge	Pseudagnostus (Pseudagnostus)
28. cyclopygeformis Sun, 1924	Agnostus	convergens	Neoagnostus
29. cyclostigma Raymond, 1924	Phalacroma	araneavelatus	Neoagnostus
30. denticulatus Shergold, 1975	Pseudagnostus	araneavelatus	Neoagnostus
31. douvillei Bergeron, 1899	Agnostus	contracta	Pseudagnostus (Pseudagnostina)
32. elix Shergold, 1975	Pseudagnostus	clarki	Pseudagnostus (Rhaptagnostus)
33. empozadense Rusconi, 1954	Lejopyge	?	?
34. empozadensis Rusconi, 1954	Hypagnostus?	?	?
35. greendalensis Resser, 1938	Oedorhachis	?	?
36. gyps Clark, 1923	Plethagnostus	?	?
37. huangluoensis Kobayashi, 1966	Pseudagnostus	nomen nudum	
38. idalis Öpik, 1967	Pseudagnostus	cyclopyge	Pseudagnostus (Pseudagnostus)
39. impressus Lermontova, 1940	Pseudagnostus	communis	Pseudagnostus (Pseudagnostus)

SPECIES/AUTHOR/DATE	ORIGINAL GENERIC ASSESSMENT	SPECIES GROUP	REVISED GENERIC ASSIGNMENT
40. janei Clark, 1923	Agnostus	canadensis	Neoagnostus
41. jarillensis Rusconi, 1953	Plethagnostus	cyclopyge	Pseudagnostus (Pseudagnostus)
42 jeholensis Kobayashi, 1951	Pseudagnostus	?	?
43. josepha Hall, 1863	Agnostus	communis	Pseudagnostus (Pseudagnostus)
44. kobayashii Wolfart, 1974	Pseudagnostus	cyclopyge?	Pseudagnostus (Pseudagnostus)
45. koerferi Monke, 1903	Agnostus	contracta	Pseudagnostus (Pseudagnostus)
46. laevis Palmer, 1955	Pseudagnostus	clarki	Pseudagnostus (Rhaptagnostus)
47. latus Kobayashi, 1938	Pseudagnostus	communis	Pseudagnostus (Pseudagnostus)
48. leptoplastorum Westergaard, 1944	Pseudagnostus	cyclopyge	Pseudagnostus (Pseudagnostus)
49. levatus Romanenko, 1967	Pseudagnostus	bulgosus	Pseudagnostus (Pseudagnostus)
50. longicollis Kobayashi, 1966	Pseudagnostus	bilobus	Neoagnostus
51. maladensis Meek, 1873	Agnostus	?	?
52. marginisulcatus Kobayashi, 1962	Pseudagnostus	cyclopyge	Pseudagnostus (Pseudagnostus)
53. mesleri Resser, 1938	Oedorhachis	bulgosus	Pseudagnostus (Pseudagnostus)
54. mestus Öpik, 1967	Pseudagnostus	bulgosus	Pseudagnostus (Pseudagnostus)
55. mirus Pokrovskaya, 1963	Pseudagnostus	nomen nudum	
56. neon Hall & Whitfield, 1977	Agnostus	communis	Pseudagnostus (Pseudagnostus)
57. nganasanicus Rosova, 1964	Pseudagnostus	bulgosus	Pseudagnostus (Pseudagnostus)
58. nuperus Whitehouse, 1936	Pseudagnostus	cyclopyge	Pseudagnostus (Pseudagnostus)
59. obsoletus Lermontova, 1951	Pseudagnostus	convergens	Pseudagnostus (Rhaptagnostus)

SPECIES/AUTHOR/DATE	ORIGINAL GENERIC ASSESSMENT	SPECIES GROUP	REVISED GENERIC ASSIGNMENT
60. obtusus Belt, 1868	Agnostus	cyclopyge	Pseudagnostus (Pseudagnostus)
61. orbiculatus Shergold, 1975	Pseudagnostus	clarki	Pseudagnostus (Rhaptagnostus)
62. orientalis Kobayashi, 1933	Pseudagnostus	communis	Pseudagnostus (Pseudagnostus)
63. ovatus Rusconi, 1950	Pseudagnostus	nomen nudum	
64. papilio Shergold, 1971	Pseudagnostus	convergens	Pseudagnostus (Rhaptagnostus)
65. paronai Airaghi, 1902	Microdiscus	?	?
66. pedrensis Rusconi, 1951	Spinagnostus	?	?
67. pii Airaghi, 1902	Agnostus	?	?
68. planulata Raymond, 1924	Peronopsis	clarki	Pseudagnostus (Rhaptagnostus)
69. primus Kobayashi, 1962	Pseudagnostus	cyclopyge	Pseudagnostus (Pseudagnostus)
70. priscus Kobayashi, 1955	Trinodus	bilobus	Neoagnostus
71. prolongus Hall & Whitfield, 1977	Agnostus	communis	Pseudagnostus (Pseudagnostus)
72. pseudocyclopyge Ivshin, 1956	Pseudagnostus	cyclopyge	Pseudagnostus (Pseudagnostus)
73. punctatus Lermontova, 1940	Pseudagnostus	clavus	Neoagnostus
74. quadratus Lazarenko, 1966	Pseudagnostus	clavus?	Neoagnostus
75. quasibilobus Shergold, 1975	Pseudagnostus	bilobus	Neoagnostus
76. rotundatus Lermontova, 1940	Pseudagnostus	communis	Pseudagnostus (Pseudagnostus)
77. securiger Lake, 1906	Agnostus	securiger	Pseudagnostus (Sulcatagnostus)
78. sentosus Grant, 1965	Pseudagnostus	communis	Pseudagnostus (Pseudagnostus)
79. sericatus Öpik, 1967	Pseudagnostus	cyclopyge	Pseudagnostus (Pseudagnostus)

SPECIES/AUTHOR/DATE	ORIGINAL GENERIC ASSESSMENT	SPECIES GROUP	REVISED GENERIC ASSIGNMENT
80. semiovalis Kobayashi, 1937A	Rhaptagnostus	?	?
81. simplex Lermontova, 1951	Pseudorhaptagnostus	clavus	Neoagnostus
82. solus Endo, 1937	Pseudagnostus	nomen nudum	
83. subangulatus Lermontova, 1940	Euplethagnostus	clavus	Neoagnostus
84. tennesseensis Resser, 1938	Oedorhachis	cyclopyge?	Pseudagnostus (Pseudagnostus)
85. tmetus Harrington & Leanza, 1957	Machairagnostus	bilobus	Neoagnostus
86. vastulus Whitehouse, 1936	Pseudagnostus	cyclopyge?	Pseudagnostus (Pseudagnostus)
87. vicaria Öpik, 1967	Pseudagnostus	contracta	Pseudagnostus (Pseudagnostus)
88. vulgaris Rosova, 1960	Pseudagnostus	clavus	Neoagnostus

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EXPLANATION OF FIGURES

Figures 1 - 15 have been omitted from the hardcopy of Record 1975/86.

FIG. 1 Pseudagnostus josepha (Hall, 1863); [A] and [B] replicas of cotypes, AMNH 311, preserved as sandstone moulds, X10.

FIG. 2 Pseudagnostus ampullatus Öpik, 1967; [A] paratype cephalon, CPC 5899, X16; [B] holotype pygidium, CPC 5896, X16; an en grande tenue species preserved in limestone.

FIG. 3 Rhaptagnostus bifax (Shergold, 1975); [A] paratype cephalon, CPC 11597, X13.5; [B] paratype pygidium, CPC 11667, X10; [C] holotype cephalon, CPC 11596, X14; [D] paratype pygidium, CPC 11656, X14; specimens [C] and [D] preserved with shell are compared with the exfoliated [A] and [B].

FIG. 4 Neoagnostus araneavelatus (Shaw, 1951); [A] replica of paratype cephalon, USNM 124467, X20; [B] replicas of holotype pygidium, USNM 124466, X21.

FIG. 5 Neoagnostus bilobus (Shaw, 1951); [A] replica of paratype cephalon, USNM 124470, X20; [B] replica of holotype pygidium, USNM 124468, X20.

FIG. 6 Pseudagnostus bulgosus Öpik, 1967; [A] paratype cephalon, CPC 5904, X13; [B] holotype pygidium, CPC 5901, X12.

FIG. 7 Neoagnostus canadensis (Billings, 1860); [A] replica of paratype cephalon, GSC 858, X11.5; [B] replica of lectotype pygidium, GSC 858b, X11.5.

FIG. 8 Neoagnostus clavus (Shergold, 1972); [A], [B] paratype cephalon, CPC 8454, X12; [C], [D] paratype pygidium, CPC 8451, X14.

FIG. 9 Pseudagnostus communis (Hall & Whitfield, 1877); [A] replica of hypotype cephalon (Palmer 1955), USNM 24557e, X11; [B] replica of hypotype pygidium (Palmer 1955), USNM 24557d, X13.

FIG. 10 Pseudagnostina contracta Palmer, 1962; [A] replica of paratype cephalon, USNM 143149b, X22; [B] replica of holotype pygidium, USNM 143150, X20.

FIG. 11 Pseudagnostus cyclopyge (Tullberg, 1880); [A], [B] holotype cephalon (Westergaard, 1922), LU Lo 3066, X9; [C], [D] holotype pygidium (Westergaard, 1922) LU Lo 3067, X9.5. The concept of Pseudagnostus currently rests on these specimens.

FIG. 12 Sulcatagnostus securiger (Lake, 1906); replica of holotype, GSM 57650, X6.

FIG. 13 Rhaptagnostus clarki (Kobayashi, 1935); [A] paratype cephalon, USNM 146887, X12; [B] holotype pygidium, USNM 93062, X6.

FIG. 14 Rhaptagnostus convergens (Palmer, 1955); [A] paratype cephalon, USNM 123563, X12; [B] holotype pygidium, USNM 123562, X12.

FIG. 15 [A] Hyperagnostus binodosus Kobayashi, 1955, replica of holotype, GSC 12747, X10; [B] Neoagnostus aspidoides Kobayashi, 1955, replica of holotype, GSC 12745, X10; [C] Trinodus priscus Kobayashi, 1955, replica of holotype, GSC 12751, X8.