

COMMONWEALTH OF AUSTRALIA
DEPARTMENT OF NATIONAL DEVELOPMENT
BUREAU OF MINERAL RESOURCES, GEOLOGY AND GEOPHYSICS

BULLETIN 112

Late Upper Cambrian Trilobites from the Gola Beds, Western Queensland

BY

J. H. SHERGOLD

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MINISTER: THE HON. R. W. C. SWARTZ, M.B.E., E.D.

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DIRECTOR: N. H. FISHER

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SUMMARY

This Bulletin describes the trilobite fauna of the Gola Beds, an informally designated stratigraphical unit of late Upper Cambrian age outcropping along the Momedah anticline in the Boulia area, western Queensland.

On the basis of their trilobites the Gola Beds are provisionally considered correlatives of the late Franconian to early Trempealeauan interval of North America, and of the Fengshanian of north China, Korea, and Manchuria.

Of the 19 genera described below, 10 are new; and of the 25 species, 21 are described for the first time and four are left under open nomenclature owing to lack of material. New taxa are: *Pseudagnostus papilio* sp. nov., *P. clavus* sp. nov., *Connagnostus junior* sp. nov., *Distagnostus ergodes* gen. et sp. nov., *Rudagnostus avius* sp. nov., *Geragnostus* (*Micragnostus*) *acrolebes* sp. nov., *Richardsonella laciniosa* sp. nov., *R.(?) kainelliformis* sp. nov., *Sigmakainella translira* gen. et sp. nov., *S. longilira* sp. nov., *Kaolishania australis* sp. nov., *Mansuyites futiliformis* gen. et sp. nov., *Palacorona bacculata* gen. et sp. nov., *Lophosaukia torquata* gen. et sp. nov., *Eoshumardia cylindrica* sp. nov., *Dellea(?) laevis* sp. nov., *Lorrettina macrops* gen. et sp. nov., *Crucicephalus ocellatus* gen. et sp. nov., *Duplora clara* gen. et sp. nov., *Golasaphus momedahensis* gen. et sp. nov., and *Atopasaphus petasatus* gen. et sp. nov.

Although the fauna is largely new, about one-third of it has affinity with species previously described from North America, notably the pseudagnostinids, richardsonellinids, and the ptychoparioids *Dellea(?)* and *Lorrettina*. A further third has affinity with east Asian species, in this case the Kaolishaniidae, Saukiidae, and Shumardiidae. Only some agnostids show much affinity with trilobites from South America, Europe, and the USSR.

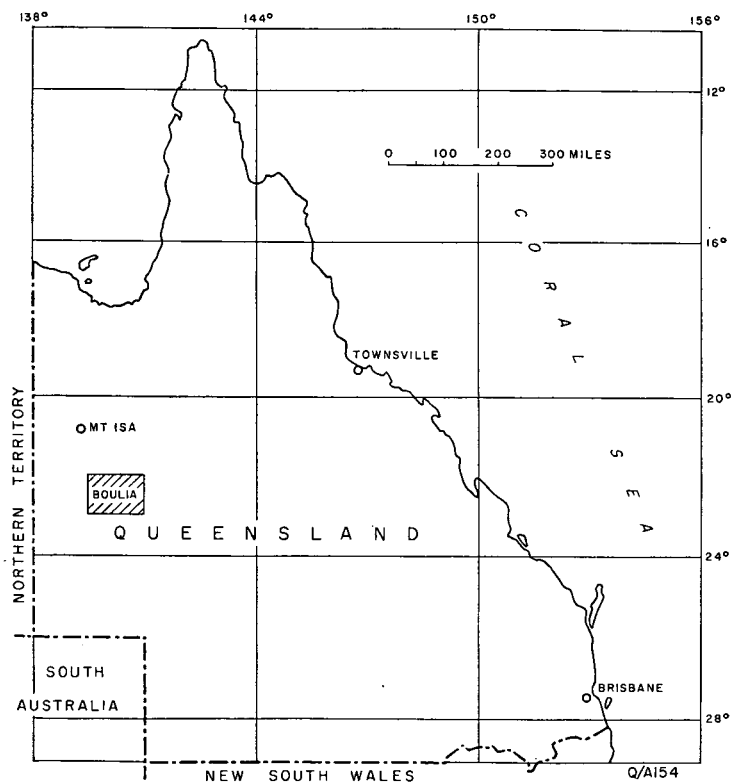
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INTRODUCTION

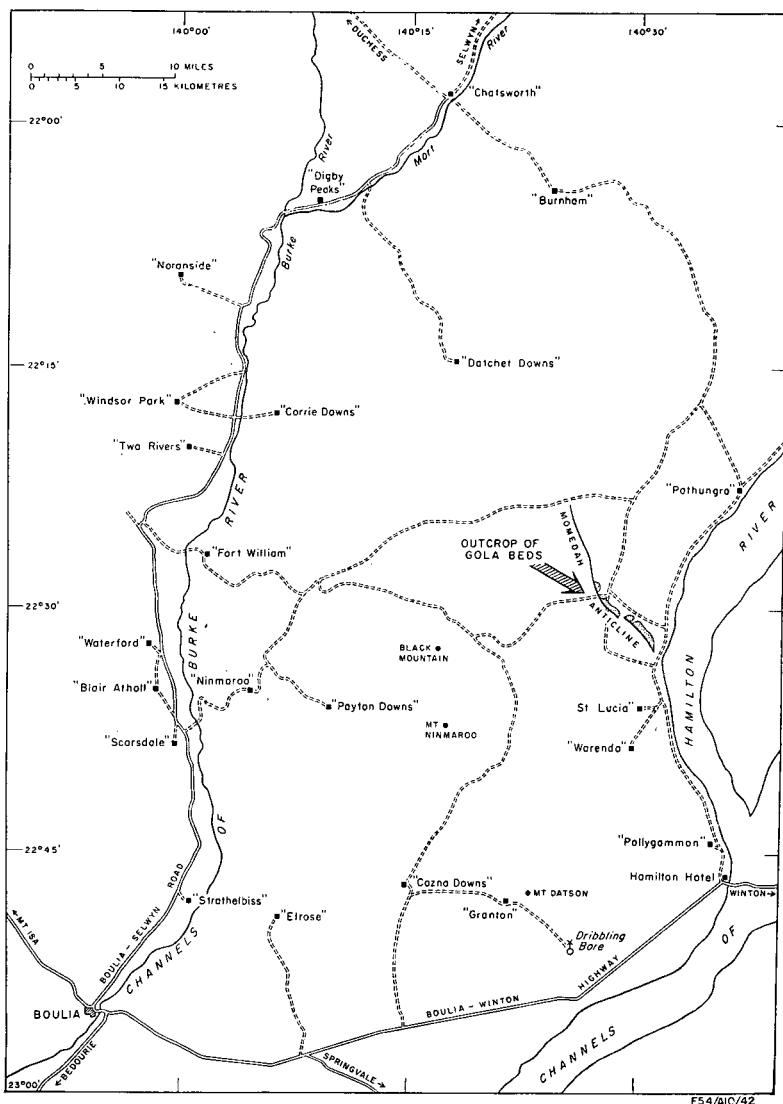
The trilobite faunas described in this paper are from collections assembled by the Bureau of Mineral Resources Georgina Basin Party in 1957, and by myself in 1967. They are from a sequence of calcilutites and calcarenites which crop out in a faulted anticline near Momedah Creek, in the Boulia area of western Queensland. These rocks have been informally designated as Gola Beds (Casey, 1959, p. 32; Öpik, 1960, p. 100).

The Gola Beds have been mapped on the Boulia 1:250,000 Geological Series Sheet (SF/54-10), whose location is shown on Text-figure 1. They occur as an isolated outcrop, straddling north-south and east-west boundary fences which separate the pastoral properties of St Lucia and Pathunga in the County of Gola (Casey, 1968).

From Boulia in the south access to the outcrop of the Gola Beds is readily gained via the Winton Highway, Hamilton Hotel, and the homesteads of Warenda and St Lucia (Text-fig. 2). From the north best access is from Duchess or Selwyn by way of Chatsworth, Burnham, and Pathunga homesteads. Tracks



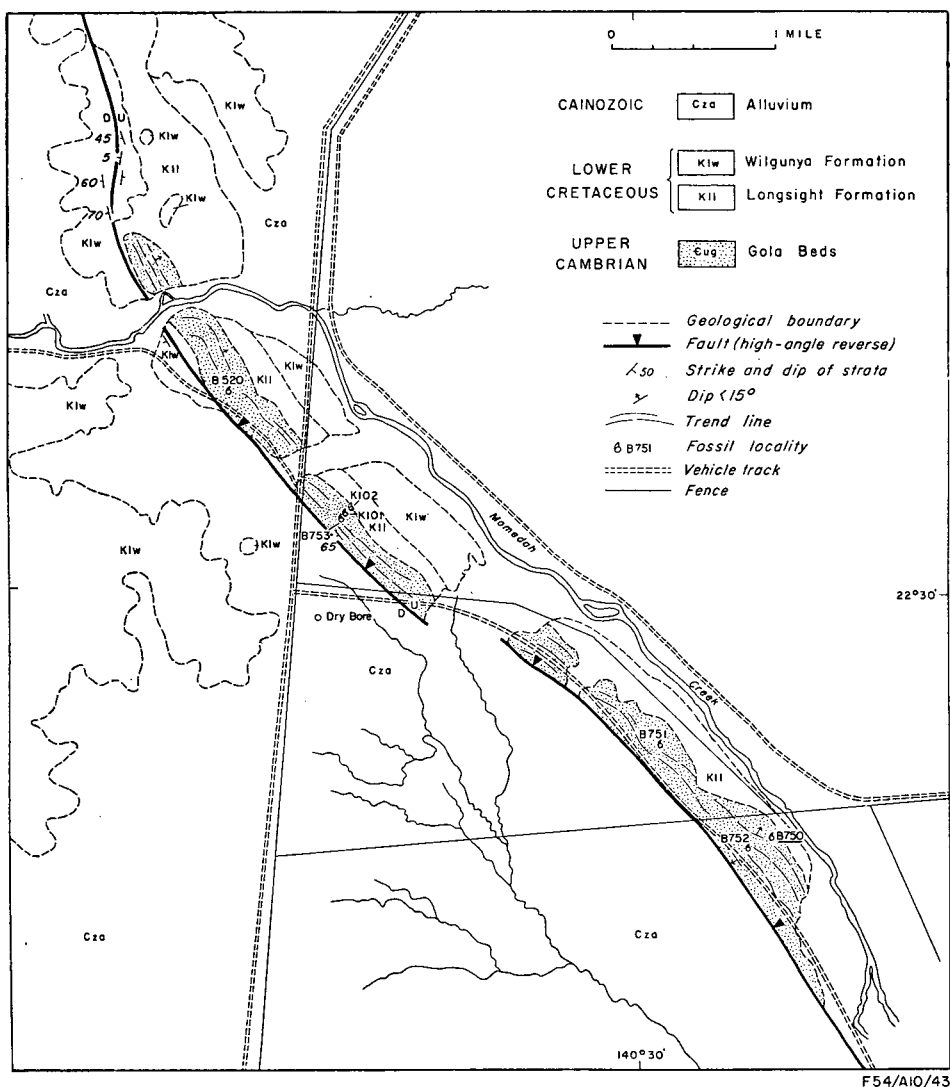
1. Position of the Boulia 1:250,000 Sheet.



2. Location of the Momedah anticline.

are rough and little used if the outcrop is approached from the Boulia-Selwyn road via Fort William or Ninmaroo, or from the Winton Highway by Cazna Downs. Boulia, the nearest town, lies 48 miles (77 km) by road from Momedah Creek.

Lithologically the Gola Beds are related to the Chatsworth Limestone, and especially to the part of the formation exposed in the faulted core of an anticlinal structure at Black Mountain, 12 miles (19 km) west-southwest of Momedah Creek. At the type section of the Chatsworth Limestone, at Lily Creek on Chatsworth Station, some 35 miles (56 km) west-northwest of Momedah Creek, calcarenite, calcilutite, and intraformational breccia have yielded faunas of mid-Upper Cambrian age, correlating with those of the Franconian Stage of North America. Gola Beds, of late Franconian to early Trempealeuan age on the basis of their trilobites, are younger than the Chatsworth of the type section. Exactly which interval of the Black Mountain section coincides with that of the



3. Outcrop of the Gola Beds.

Gola Beds remains to be established in detail. Conodont evidence (see below) suggests that the Gola Beds lie towards top of the Cambrian part of the Black Mountain succession.

The outcrop (Text-fig. 3) is a low, gently elevated belt of rocks, 6 miles (10 km) long by some 350 yards (310 m) wide, running in a northwesterly direction parallel to Momedah Creek, one of the many tributaries of the Hamilton River system. It is preserved by faulting as a window surrounded by Lower Cretaceous sediments. To the east and northeast the Gola Beds are overlain with angular unconformity by sandstone and conglomerate belonging to the Longsight Formation, the lowest division of the Lower Cretaceous in this region. The Longsight Formation is succeeded by claystone and siltstone of the Wilgunya Formation (*sensu* Casey, 1959, p. 34), which form a low plain that extends to the much braided system of the Hamilton River. To the west and southwest

the Gola Beds are terminated by faults which throw down the Wilgunya Formation. To the west and north members of the Wilgunya Formation form flat-topped mesas and small rounded buttes (Casey et al., 1960, pl. 7, figs 1-2), but to the south the country is again low, sloping gently to the Hamilton River.

Structurally the outcrop of the Gola Beds is a faulted anticline, the Momedah Anticline. The faulted southwestern limb dips strongly at angles of the order of 65° , and some bedding is contorted. Dips on Cretaceous sediments adjacent to the fault as high as 75° have been recorded. The northeastern limb dips at slightly lower angles. Different horizons within the Gola Beds are brought to the surface along the length of the outcrop: palaeontological evidence suggests that older horizons occur towards the northwestern and younger horizons to the southeastern end of the exposure. Further details of the Momedah Anticline, the faulting, and the relationships of these to the Burke River Structure are given in Casey et al. (1960, pp. 32, 77), and Casey (1968).

Trilobite faunas were obtained from all collected localities and horizons in the Gola Beds. Collections numbered B520, B750, B752, and B753 were originally assembled by the Georgina Basin Party in 1957. Collections K101 and K102 were made by me in 1967 during a brief visit to the Mobile Conodont Laboratory, from which E. C. Druce and P. J. Jones resampled all the original localities for conodonts. Jones measured three sections through the Gola Beds, as close as possible to the earlier collecting sites (see Text-fig. 3). At the southeastern end of the outcrop, along a line of section between B750 and B752, he calculated a total thickness of 180 feet for strata between the first and the last beds exposed. However, intervals of no outcrop accounted for 145 feet of this section. Farther to the northeast, on a line of section passing through B751, a total of 320 feet was estimated, intervals of no outcrop again accounting for 140 feet, and a similar total was assessed on a section through B753. The Gola Beds, therefore, achieve a minimum thickness of 320 feet (97 m). The total thickness is likely to be greater, however, as beds in the section between B750-B752 are palaeontologically younger than those along section B753-K101-K102. Five hundred feet would seem a reasonable total thickness, but even this may prove an underestimate. The base of the Gola Beds is nowhere exposed, and the top is concealed below Cretaceous sediments. Moreover, considerable faulting is apparent in this outcrop.

The Gola Beds were unknown prior to 1957 (Öpik, 1957, p. 8) and previous literature dealing with them is necessarily sparse. Extant literature includes the report of the Georgina Basin Party on the regional geology of the Boulia area (Casey, Reynolds, Dow, Vine, Pritchard, & Paten, 1960), and brief discussion by Casey (1959, 1968) and Öpik (1960). Conodonts from the Gola Beds have been recorded by Druce & Jones (1968, and in press).

INDEX OF LOCALITIES

Details of the localities and horizons given below have been accumulated from a locality index prepared by A. A. Öpik and mentioned by him in several recent publications (see for example 1961b). Use has also been made of the field notebooks of P. J. Jones to complement personal field observations.

Locality B520. Latitude $22^\circ 29.3'S.$, longitude $140^\circ 27.5'E.$ A layer of pale grey, white or greenish weathering, coarse-grained glauconitic calcarenite which

forms a low bench 0.6 miles (1 km) southeast from the intersection of the Momedah Anticline and Momedah Creek. A prolific fauna includes the following:

Trilobita: *Duplora clara* gen. et sp. nov., *Eoshumardia cylindrica* sp. nov., *Geragnostus* (*Micragnostus*) *acrolebes* sp. nov., *Golasaphus momedahensis* gen. et sp. nov., *Kaolishania australis* sp. nov., *Lophosaukia torquata* gen. et sp. nov., *Lorrettina macrops* gen. et sp. nov., *Mansuyites futiliformis* gen. et sp. nov., *Palacorona bacculata* gen. et sp. nov., *Pseudagnostus clavus* sp. nov., *Pseudagnostus papilio* sp. nov., *Pseudagnostus* sp. I, *Pseudagnostus* sp. II, *Pseudagnostus* sp. III, *Rudagnostus avius* sp. nov., *Sigmakainella longilira* sp. nov., *S. translira* gen. et sp. nov.

Brachiopoda: *Acrotreta* sp. indet., *Eoorthis*(?) sp., two genera of undetermined lingulelloids, one with affinity to *Westonia*.

Conodontophorida: *Coelocerodontus primitivus* (Müller), *C. tricarinatus* (Nogami), *Sagittodontus eureka* Müller, *S. furnishi* (Müller).

Locality B520A. Same locality and coordinates as B520, a different layer. Dark grey medium-grained glauconitic calcarenite. This contains:

Trilobita: *Geragnostus* (*Micragnostus*) *acrolebes*, *Golasaphus momedahensis*, *Richardsonella*(?) sp.

Conodontophorida: *Oneotodus gallatini* Müller.

Locality B520B. Same locality and coordinates as B520, a different layer. Pale grey or greenish coarse-grained ferruginized glauconitic calcarenite. Fauna:

Trilobita: *Connagnostus junior* sp. nov., *Duplora clara*, *Golasaphus momedahensis*, *Palacorona bacculata*, *Pseudagnostus* sp. indet., *Richardsonella*(?) sp. indet.

Brachiopoda: *Acrotreta* sp. indet., lingulelloid.

Locality B750. Latitude 22° 30.7'S., longitude 140° 30.8'E. This site lies 3 miles (5 km) north of Momedah Bore, approximately 5 miles (8 km) southeast of the intersection of Momedah Anticline and Momedah Creek. Exposed beds at this locality total 35 feet. They dip 13° northeast. The locality is shown on Druce & Jones, text-fig. 5A, 5B, as locality 5. A varied fauna was obtained from light to medium grey, or brownish grey, fine to medium-grained sandy calcilutite.

Trilobita: *Atopasaphus petasatus* gen. et sp. nov., *Crucicephalus ocellatus* gen. et sp. nov., *Distagnostus ergodes* gen. et sp. nov., *Eoshumardia cylindrica*, *Geragnostus* (*Micragnostus*) *acrolebes*, *Golasaphus momedahensis*, *Mansuyites futiliformis*, *Palacorona bacculata*, *Pseudagnostus clavus*, *P. papilio*, *Richardsonella laciniosa* sp. nov., *Richardsonella*(?) *kainelliformis* sp. nov., *Sigmakainella translira*, '*Tostonia*' sp.

Brachiopoda: *Acrotreta* sp. indet., two genera of lingulelloids, one similar to *Westonia*.

Conodontophorida: *Coelocerodontus burkei* Druce & Jones, *C. rotundatus* Druce & Jones, *C. tricarinatus*, *Oneotodus nakamurai* Nogami.

Locality B752. Latitude 22° 30.9'S., longitude 140° 30.6'E. This is Druce & Jones' locality 4, text-fig. 5A. It lies a similar distance from Momedah Creek and Momedah Bore as B750. The lithology is a light to dark grey medium to coarse-grained glauconitic calcarenite, with streaks and patches of medium grey fine-grained calcilutite. B752 lies 145 feet (44 m) lower in the succession than B750.

Trilobita: *Distagnostus ergodes*, *Duplora clara*, *Golasaphus momedahensis*, *Kaolishania australis*, *Lophosaukia torquata*, *Mansuyites futiliformis*, *Pseudagnostus* sp. indet., *Richardsonella laciniosa*, *Sigmakainella longilira*, *Sigmakainella* sp. indet.

Brachiopoda: *Acrotreta* sp. indet., two genera of lingulelloids (very common in this layer).

Conodontophorida: *Coelocerodontus tricarinatus*, *Sagittodontus furnishi*.

Locality B753. Latitude 22° 30.5'S., longitude 140° 29.6'E. A layer of pale grey coarse-grained ferruginized glauconitic calcarenite with patches of brownish-grey fine-grained calcilutite, forming a prominent bench 1.6 miles (2.5 km) southeast of the intersection of Momedah Anticline and Momedah Creek. The dip here is 40° northeast. This is locality 7 of Druce & Jones, text-fig. 5A.

Trilobita: *Connagnostus junior*, *Golasaphus momedahensis*, *Kaolishania australis*, *Lophosaukia torquata*, *Lorrettina macrops*, *Pseudagnostus* sp. II, *Pseudagnostus* sp. indet., *Sigmakainella* sp. indet.

Brachiopoda: *Acrotreta* sp. indet., lingulelloid.

Conodontophorida: *Oneotodus gallatini*.

Locality K101. Coordinates as for B753. The reference is Druce & Jones' section 7, horizon 4, 65 feet from the base of the section. Observed dip 30° northeast. A layer of medium grey medium to coarse-grained ferruginized calcarenite, with streaks of medium grey or brownish fine-grained calcilutite, and patches of medium-fine sand, with occasional ooliths. This layer forms a strong outcrop.

Trilobita: *Duplora clara*, *Geragnostus* (*Micragnostus*) *acrolebes*, *Golasaphus momedahensis*, *Kaolishania australis*, *Lophosaukia torquata*, *Mansuyites futiliformis*, *Palacorona bacculata*, *Pseudagnostus papilio*, *Pseudagnostus* sp. II.

Brachiopoda: *Acrotreta* sp., lingulelloids (two genera).

Conodontophorida: *Sagittodontus furnishi*.

Locality K102. Coordinates as for B753. Druce & Jones' section 7, horizon 24, 305 feet from the base of the section. A layer of brownish grey coarse-grained ferruginized sandy calcarenite which forms a marked bench after an interval of no outcrop. Fossils in shelly laminae. Dip 60° northeast.

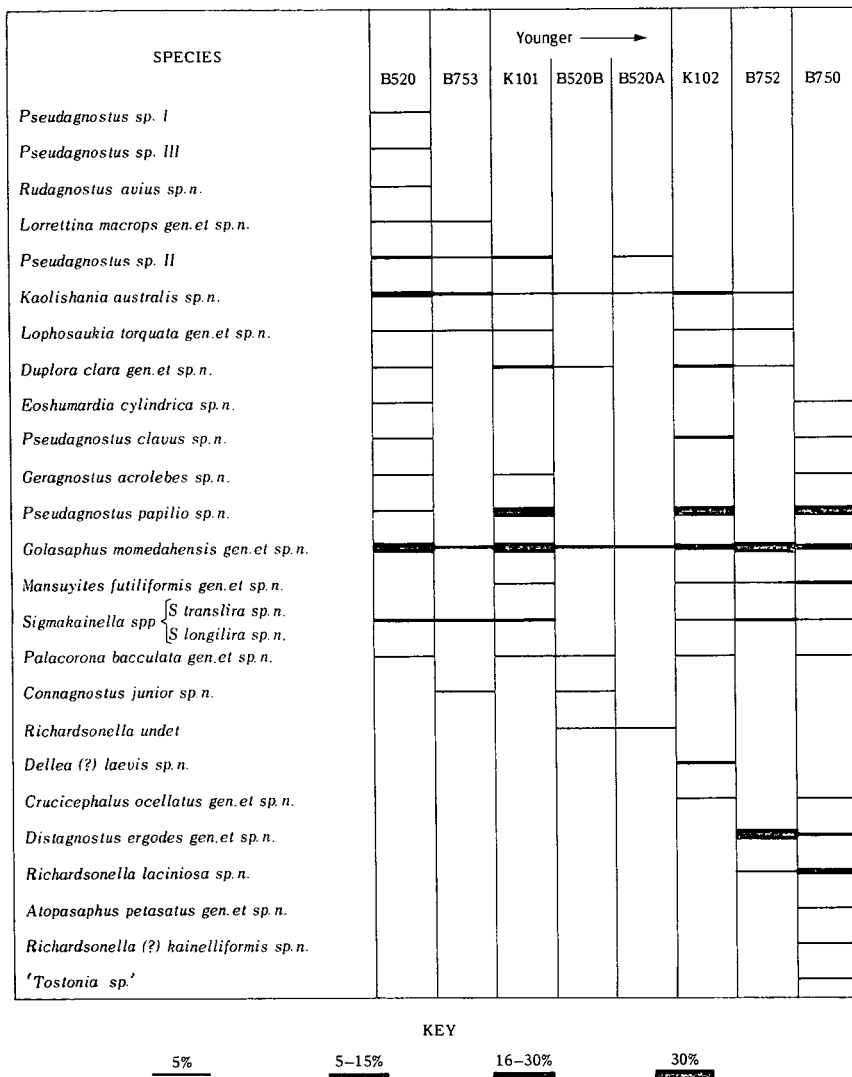
Trilobita: *Crucicephalus ocellatus*, *Dellea*(?) *laevis* sp. nov., *Duplora clara*, *Golasaphus momedahensis*, *Kaolishania australis*, *Mansuyites futiliformis*, *Palacorona bacculata*, *Pseudagnostus clavus*, *Pseudagnostus* sp. II, *Sigmakainella* sp. indet.

Brachiopoda: *Acrotreta* sp. indet., lingulelloid brachiopod, phosphatic brachiopod indet.

Conodontophorida: *Oneotodus nakamurai*, *Sagittodontus dahlmani* Müller.

THE FAUNA

The known trilobite fauna of the Gola Beds comprises 25 species distributed among 19 genera. Ten of the genera and 21 of the species are newly described, and four species remain under open nomenclature.



4. Range and relative abundance of trilobite species within the Gola Beds.

The chart, Text-figure 4, shows the distribution of these species among the sampled horizons, the width of line indicating the relative abundance of each. The Gola Beds, as a whole, are characterized by the common occurrence of the asaphid *Golasaphus momedahensis*. On the chart this is shown to range abundantly throughout the sampled horizons. Common at intervals is *Pseudagnostus papilio*. The gaps in the range of this species are probably due to both sampling and preservation. Species of *Pseudagnostus* do occur at B753, B520A, B520B, and B752, but their preservation prevents accurate determination.

On range and relative abundance the recognized taxa may be broadly differentiated into two overlapping faunal assemblages. Elements from B520, B520A, B520B, B753, and K101 together constitute a lower assemblage which is characterized by an abundance of Asian genera. This may be loosely termed a 'kaolishaniid assemblage.' Species from B750, B752, and K102 constitute a

higher assemblage in which Asian genera are subordinate to others with North American affinity. This younger fauna may be designated as a 'richardsonellid assemblage.' Although some elements range through both faunal assemblages, others are restricted to, or achieve notable acme in, one or the other. Until the late Upper Cambrian trilobite faunas of other areas in Australia are adequately described, and until the position of the Gola Beds can be established within the adjacent Cambro-Ordovician successions of Black Mountain, Mount Ninmaroo, and Mount Datson, discussion of the merits and status of these assemblages is deferred.

In terms of palaeozoogeography, approximately one-third of the trilobite genera of the Gola Beds are related to genera previously described from eastern Asia, notably Manchuria, Korea, China, and North Vietnam. A second one-third have North American affinity, being mainly related to trilobites of the western Cordilleran belt. The remainder of the fauna may be listed as cosmopolitan, European, or with uncertain affinity. Cosmopolitan describes trilobite genera occurring world-wide in more than one faunal province, e.g. *Pseudagnostus* and *Geragnostus* (*Micragnostus*); European refers to trilobites having some affinity with counterparts in the 'Baltic Province.' Apart from the cosmopolitan elements the fauna has no direct relationships with late Upper Cambrian trilobites from the USSR or South America, and very little in common with European faunas. Percentage affinities of species from selected horizons are listed below.

	B520	B753	K101	K102	B752	B750
Asian	30%	29%	40%	34%	37%	21%
North American	20	29	10	16	37	36
European	5					
Cosmopolitan	20		20	16		21
Uncertain affinity	25	42	30	34	26	21
	—	—	—	—	—	—
Total species	16	7	10	12	8	14
	—	—	—	—	—	—

← older ————— horizons ————— younger →

Strong Asian affinity is afforded by the Kaolishaniidae, Saukiidae, and Shumardiidae. The Kaolishaniidae, divided here into the subfamilies Kaolishaniinae, Mansuyiinae, and Tingocephalinae, occur most commonly in the lower part of the Gola Beds succession. Hitherto Kaolishaniid genera have been described and figured only from eastern Asia, where a Kaolishaniid assemblage is represented by the genera *Kaolishania*, *Mansuyia*, *Kaolishaniella*, *Paramansuyella*, and *Tingocephalus*. In varying combinations these characterize the Daizanian and lower Fengshanian Stages, and their correlatives. They are present in the Daizan and Yenchou Formations of Manchuria (Endo *in* Endo & Resser, 1937; Kobayashi, 1933, 1966); in the upper Tawenkou and lower Kaolishan Formations of Tawenkou, Taian, and Kaolishan districts of Shantung Province, northern China (Sun, 1924, 1935; Endo, 1939); the upper part of the lower Wolungshan Formation of the Huolu district, Hopei (Sun, 1935); and in the lower part of the Fengshan Limestone of the Kaiping Basin, Hopei (Sun, 1924; Kobayashi, 1966). Representatives of the family are found also in the Loung Co Beds of Tonkin, North Vietnam (Kobayashi, 1944; Saurin, 1956); in the middle and upper parts of the Kasetsu Formation of South Korea; and at a similar stratigraphical level in North Korea (Kobayashi, 1935c, 1960b, 1966). Öpik (1960, p. 100) has previously recorded *Kaolishania* from the Gola Beds, and (*in* Kaulback & Veevers, 1965, pp. 81-2) has noted the presence of *Paramansuyella* and another

Kaolishaniid in faunal units VIII-IX of the Clark Sandstone, Joseph Bonaparte Gulf, northeastern Western Australia. The first-mentioned is described here as *Kaolishania australis*. It is tempting to correlate the kaolishaniid fauna of the Gola Beds with the *Kaolishania*-bearing Daizanian of China, and to explain away the observed morphological differences between the Asian and Australian forms on environmental control. However, age determinations based on associated Pseudagnostidae and Richardsonellinae indicate rather that the Australian kaolishaniids of the Gola Beds are somewhat younger than those of the Daizanian of China, Manchuria, and Korea.

Saukiidae are represented in the Gola Beds by *Lophosaukia* gen. nov., a sauikiid with its anterior cranial border drawn into a spike or point. This type of sauikiid is confined in its known distribution to eastern Asia and Australia. It is present in the Yenchou Formation of Manchuria, where it has been varyingly described as *Saukia*(?) *orientalis*, *Prosaukia orientalis*, and *Prosaukia ulrichi*; in the Wolungshan Formation of Huolu, Hopei, and in the Kaolishan Formation of Shantung, where it is covered partially by *Sinosaukia pustulosa* and by *Ptychaspis angulata* var. *chinensis*. In the Loung Co Series of Tonkin it has been included in descriptions of *Ptychaspis angulata*. The genus also has a wide distribution in Australia. It is present in the Gola Beds and the Chatsworth Limestone of western Queensland; in the late Upper Cambrian of the Amadeus Basin and the Huckitta region of Central Australia (Casey & Gilbert-Tomlinson, 1956, p. 70: *Saukia*(?) (= *Sinosaukia*) *orientalis*); and in the Clark Sandstone of the Joseph Bonaparte Gulf Basin, northeastern Western Australia (Öpik in Kaulback & Veevers, 1965, p. 82). *Lophosaukia*, wide ranging both spatially and temporally, gives no fine age for the Gola Beds.

The Shumardiid of the Gola Beds again indicates affinity with Asia. It is best placed in the genus *Eoshumardia* Hupé, which is otherwise known with certainty from the Li Kouan Series of Tonkin, North Vietnam. There it is associated with *Calvinella walcotti*, which may indicate a Trempealeauan age. *Eoshumardia* as such has not been recorded from China, Manchuria, or Korea, although it may exist in those areas, as in Mexico, under the generic reference to *Koldinioidea*, e.g. *K. paiensis* Endo in Manchuria, and *K. aspinosa* Kobayashi (*sensu* Endo) in north China.

As successive horizons of the Gola Beds are traversed the affinities of the recorded faunas become increasingly North American in aspect. Richardsonellinae are represented in the youngest horizons of the Gola Beds by *Richardsonella*; a kainelloid trilobite described here as *Sigmakainella* gen. nov.; and pygidia referred to '*Tostonia*' sp. The true *Kainella*, as typified by *K. billingsi* (Walcott, 1924), is not represented; nor is *Apatokephalus*.

Richardsonella is known elsewhere mainly from North America, where it has been recorded from Alaska, Nevada, Vermont, and Quebec. A possible species of this genus is also known from Cambro-Ordovician rocks of Tonkin (Kobayashi, 1953 — *Kainella primigena*). A good many of the previously described species of *Richardsonella* are from the Lévis conglomerates of Quebec and as such their age is not absolutely certain. *Richardsonella* faunas recently described from Alaska (Palmer, 1968) range from beds which correlate with the higher levels of the Franconian Stage into beds correlated with the lower part of the Trempealeauan. *Richardsonella eurekensis* Kobayashi, 1935, occupies a similar horizon in Nevada, and several other species are known from the Gorge Formation of Vermont (Raymond, 1937).

Sigmakainella is represented in the late Franconian of Alaska by a pygidium described as *Richardsonella* sp. 3 (Palmer, 1968, pl. 14, fig. 6), and in Nevada possibly by '*Kainella*' *inexpectans* (Walcott, 1884).

The species described here as '*Tostonia*' sp. is also very closely related to North American species. *Richardsonella*(?) sp. 2 (Palmer, 1968), from the lower Trempealeauan of Alaska, and the pygidium which Walcott (1925, p. 117) referred to *Tostonia iole*, from the higher Catlin and Bullwacker Members of the Windfall Formation, Eureka district, Nevada, belong to the same genus as the Australian specimen. On the basis of its Richardsonellinae the upper part of the Gola Beds must be regarded as of late Franconian to early Trempealeauan age.

Two ptychoparioid trilobites indicating a Franconian age occur lower in the Gola Beds. The cranidium of *Lorrettina* has close morphological resemblance to that of *Kindbladia*, a trilobite with widespread distribution in the *Elvinia* Zone of Oklahoma, Texas, Missouri, Montana, northern Wyoming, Nevada, Dakota, Utah, and Pennsylvania. *Dellea*(?), if it does actually represent that genus, has an equally wide distribution, being found in the *Elvinia* and *Conaspis* Zones of Oklahoma, Texas, Wisconsin, Montana, Wyoming, Maryland, Pennsylvania, and New York.

Some of the agnostids from the Gola Beds are particularly valuable for dating and correlation, especially species of *Pseudagnostus*. The species of this genus named here fall into two well-defined groups. Most abundant is *P. papilio* sp. nov., a virtually effaced species with narrow cephalic and pygidial borders, and converging pygidial flanks. This is very closely related to species from the late Franconian and Trempealeauan of Nevada and Alaska, *P. convergens* Palmer and *P. clarki* Kobayashi. *P. papilio* is also readily compared to *P. obsoletus* Lermontova, a species from the highest Cambrian at Boshche-Kul, Kazakhstan. Less common, but of equivalent importance, is *P. clavus* sp. nov., a species with quadrate shields, well-defined glabella, effaced deuterolobe, and wide pygidial borders. Comparable species are *P. longicollis* Kobayashi, from the latest Cambrian of the Hungluohsien area, Jehol, north China; *P. simplex* Lermontova, from Kazakhstan (where it is associated with *P. obsoletus*); *P. cavernosus* Rosova and *P. vulgaris* Rosova, both from the late Cambrian Tolstochikha Suite of Salair; and an undescribed species from Oaxaca, Mexico, of presumed Tremadocian age (Robison & Pantoja-Alor, 1968). *Pseudagnostus vulgaris* is also reported from Alaska (Palmer, 1968), where it is associated with *P. clarki* Kobayashi in beds of Trempealeauan age.

Of the other agnostids *Geragnostus* (*Micragnostus*) has a very wide distribution — USSR, China, South America, and North America. The species described here, *G. (M.) acrolebes*, is most closely comparable to *G. (M.) chiushuensis* Kobayashi, from Cambro-Ordovician passage beds in southern Manchuria; to *G. (M.) brevispinus* (Lermontova) from Boshche-Kul, Kazakhstan, where it is associated with the *Pseudagnostus* described above; and to certain specimens from Mexico referred to *Geragnostus intermedius* Palmer by Robison & Pantoja-Alor (1968). Again, a very late Cambrian age is indicated.

The presence of the genus *Rudagnostus* in the Gola Beds is of interest, as European elements in the fauna are otherwise negligible.

Distagnostus gen. nov. is possibly derived from *Innitagnostus* Öpik, 1967, a genus previously known in Australia from the Georgina, Pomegranate, and Mungerebar Limestones of Queensland, of Mindyallan and Idamean age (Öpik

1963, 1967). *Innitagnostus* also occurs in North America (Nevada, Alabama, Texas, British Columbia) in beds of Dresbachian age. The species of *Distagnostus* described here is most closely related to, and may be congeneric with, the species described by Palmer (1955) as *Lotagnostus obscurus*. This species is another from the Catlin Member of the Windfall Formation, Eureka district, Nevada, where it is associated with partly effaced *Pseudagnostus* comparable with *Pseudagnostus papilio*.

Without obvious affinities are the asaphoids *Atopasaphus* and *Golasaphus*, although the latter seems to be on a phyletic line leading to *Asaphellus*; and the ptychoparioids *Duplora* gen. nov. and *Crucicephalus* gen. nov.

Concerning the ages and affinities of the conodonts of the Gola Beds, P. J. Jones writes the following notes.

'The conodonts from all localities of the Gola Beds consist of nine species distributed among three genera: these are — *Coelocerodontus burkei* Druce & Jones, *C. primitivus* (Müller), *C. rotundatus* Druce & Jones, *C. tricarinatus* (Nogami), *Oneotodus gallatini* Müller, *O. nakamurai* Nogami, *Sagittodontus eureka* Müller, *S. furnishi* (Müller), and *S. dahlmani* Müller. The distribution of these species among the sampled horizons is shown below.

	520	753	101	520B	520A	102	752	750
<i>Sagittodontus eureka</i>	*							
<i>Coelocerodontus primitivus</i>	*							
<i>C. tricarinatus</i>	*						⊙	*
<i>Sagittodontus furnishi</i>	*		*				*	
<i>Oneotodus gallatini</i>		*			*	*		
<i>Sagittodontus dahlmani</i>						*		
<i>Oneotodus nakamurai</i>						*		*
<i>Coelocerodontus burkei</i>								*
<i>C. rotundatus</i>								*

'Except for *Sagittodontus eureka* Müller, all are known from the Chatsworth Limestone of Black Mountain. *Coelocerodontus tricarinatus* (Nogami), the only species which ranges throughout the Gola Beds, occurs between 500 and 1240 feet above the base of the section at Black Mountain. For this reason Druce & Jones (in press) suggest that the Gola Beds may be equivalent to the upper rather than the lower part of the Chatsworth Limestone of that section.

'On the present state of knowledge four species (*Coelocerodontus primitivus*, *Oneotodus gallatini*, *Sagittodontus furnishi*, and *S. dahlmani*) are cosmopolitan, that is, they occur in Europe, China, and North America. Two have Asian affinities (*Coelocerodontus tricarinatus* and *Oneotodus nakamurai*); two are apparently endemic to Australia (*Coelocerodontus burkei* and *C. rotundatus*); and one (*Sagittodontus eureka*) occurs in North America, and possibly China (Nogami, 1966, 1967).

'In western Europe the cosmopolitan species *Coelocerodontus primitivus* ranges from Zone 5b to Zone 5e; in China it is present in the Yenchou Formation, but absent in the older Kushan Formation; and in the United States it occurs in the Deadwood Formation (Member 4) of the Black Hills, South Dakota. *Sagittodontus dahlmani* ranges from Zone 5c to 5e in Europe, and is recorded as *S. dunderbergiae* in both Kushan and Yenchou Formations of China (Nogami, 1966, 1967), and from the *Dunderbergia* Zone (Dresbachian) of the United States (Müller, 1959). Both Asian species, *Coelocerodontus tricarinatus* and *Oneotodus nakamurai*, are present in the Yenchou Formation, but absent from the Kushan Formation (Nogami, op. cit.).

'To sum up, the conodont evidence suggests that the Gola Beds are equivalent to the upper part of the Chatsworth Limestone at Black Mountain, that is equivalent to the European Zones 5d-6a. Five, possibly six species are in common with those of the Yenchou Formation (uppermost Cambrian) of northeast China (Nogami, 1967). On the other hand, although four species occur in common with the North American Upper Cambrian, all are long ranging and cannot be used for correlation.'

NOTES ON MORPHOLOGICAL TERMINOLOGY

The bulk of the terminology employed here is defined by Harrington, Moore, & Stubblefield in Moore (1959). A number of terms have been coined by Öpik and used by him in publications postdating the Treatise on Invertebrate Paleontology. Some are used here, together with several new ones, and these are discussed briefly below.

Baccula (-ae). See Öpik (1967, p. 53). Bacculae are elevated swellings flanking the preoccipital glabellar lobes and lying in a homologous position to alae. The term is used here in a rather broad sense for swellings of any size or shape occupying this position. Bacculae may be connected to the glabella, as in *Tingocephalus* and *Palacorona*, becoming in the latter homologous to some extent with intervening lobes (see below), or they may be separated from the glabella by faint exsagittal furrows, e.g. in *Mansuyites*. Bacculae are most obvious in early holaspides; in late holaspides of some species they may appear depressed owing to the increased convexity of the surrounding glabella, and as such are indistinguishable from alae. Bacculae may be formed from intervening lobes when the intervening furrows are directed rearwards and contact the occipital furrow.

Border furrow. This is equivalent to marginal furrow; both terms have been used here indiscriminately.

Caecum (-a). Terminology associated with the caecal system is that of Öpik (1961a). Ramified caeca are very well developed on species described here of *Richardsonella*, *Sigmakainella*, and *Crucicephalus*. They are present also, but less well defined, on *Palacorona*.

En grande tenue. This term refers to agnostids having distinct furrows and lobes with obvious relief. The term was introduced by Öpik (1961b, p. 55) and redefined by him in 1967 (p. 56).

Eye index. Large and small eye indices were originally defined by Struve (1958, p. 167) and applied to dalmanitacean trilobites. The large eye index is the ratio of eye length to glabellar length, expressed as a percentage. The small eye index is the ratio of eye length to glabellar length plus the sagittal dimension of the occipital ring. The size of eye with respect to the length of the glabella may vary significantly during the morphogenesis of a single species or among species of a given genus (Shergold, 1966).

Intervening lobes and furrows. Intervening furrows are short, often faint, furrows interposed between the occipital furrow and the pre-occipital furrows. They are described here in connexion with *Kaolishania australis* (see Pl. 12, figs 5, 7). The intervening lobes lie between the occipital and intervening furrows. See also Shergold (1969) for similar structures in Oryctocephalidae.

Marginal gutter. The broad, overdeepened marginal furrow of either the

cephalon or pygidium. The term border gutter is used for the same. The terms are used here in the descriptions of *Connagnostus junior* and *Rudagnostus avius*.

Mucro (-onis). Latin, sharp point, hence mucronate, used as a homonym of spinose.

Occipital lobulae. Lobes developed at the anterolateral margins of the occipital ring. They are described for the Asaphidae of the Gola Beds.

Ocular striga. Öpik (1961a, p. 436) used this term to describe the faint furrow which divides the ocular ridge and extends into the palpebral lobe of *Papyriaspis*. The feature is present in *Kaolishania australis* (see Pl. 12, fig. 8) and in *Duplora clara* (Pl. 16, fig. 3).

Palpebral ledge. In some Saukiidae, e.g. *Lophosaukia*, a marked ledge or groove is situated on the palpebral lobe between the facial suture and the palpebral furrow (see Pl. 18, figs 3-4). In the descriptions which follow this is called a palpebral ledge.

Parafrontal band. This term was originally introduced by Hupé (1952, p. 105). The species of *Richardsonella* described here are observed to have a narrow (sag.) band lying between the frontal lobe of the glabella and the preglabellar furrow. The band (present on all the specimens figured on Pl. 6) appears to continue the anterior tips of the palpebral lobes around the front of the glabella, but the connexion is cut through by the axial furrows.

Plethoid. Species of *Pseudagnostus* with accessory furrows defining the deuterolobe clearly and continuing to the posterior marginal furrow are termed plethoid. Such species are invariably preserved *en grande tenue*. The term is derived from the Greek *plethos*, fullness, and from the discarded generic name *Plethagnostus*.

Posterolateral limb. The postocular part of the fixigena distal to the fulcrum or fulcral point.

Preglabellar area. This term is used for the preglabellar field, preocular areas, marginal furrow, and anterior border combined. It is frequently used here in the descriptions of the Asaphidae.

Preglabellar field. The area between the front of the glabella and the anterior border is the preglabellar field. It may be convex, as in the Richardsonellinae, or concave, in which case it merges anteriorly with the marginal furrow.

Prosopon. This term, originally introduced by Gill (1949), has been extensively used by Öpik (1961a and later papers), and by me in this paper. It is a term for the surface appearance of a fossil and replaces 'ornament.'

Pygidial bowl. This is a term of convenience applied to pygidia of Mansuyiinae. The bowl of the pygidium is that area enclosed by the lateral and posterior margins which lies between the bases of the two pygidial spines. The bowl of *Kaolishania* is shallow, the length of the pygidium being small compared to the width. In *Mansuyites* it is deep, the length being closer to the width.

Rhaptoid. Another term applied to species of *Pseudagnostus*, this refers to the presence of notular lines on the pygidial axis. Effaced Pseudagnostidae are frequently rhaptoid. The term is derived from the Greek, *rhaptos*, stitched or sewn, and from the discarded name *Rhaptagnostus*.

Rim. Marginal rim or border.

DEFINITION OF MEASURED PARAMETERS

The symbols used for the various measured parameters tabulated in the ensuing text are:

A. *Agnostid trilobites*

- L_c Length (sag.) of cephalon
- L_{bc} Length (sag.) of cephalic border
- L_{ac} Length (sag.) of cephalic acrolobe (i.e. the cephalic length minus the length of the anterior border)
- W_c Maximum width (tr.) of cephalon
- W_o Width (tr.) across the basal glabellar lobes
- L_p Length (sag.) of pygidium, from the transverse furrow immediately behind the articulating half ring to the posterior margin
- L_{bp} Length (sag.) of the posterior pygidial border
- L_{ap} Axial length (sag.) of pygidium, measured from the transverse furrow behind the articulating half ring
- W_p Maximum width (tr.) of pygidium
- W_{up} Width (tr.) across the first (anterior) segment of the pygidial axis

B. *Non-agnostid trilobites*

- L_c Length (sag.) of cranidium, often coinciding with the cephalic length
- L_{bo} Length (sag.) of cranial or cephalic border
- L_{pa} Length (sag.) of preglabellar area
- L_{pt} Length (sag.) of preglabellar field
- G Glabellar length (sag.), exclusive of the occipital ring
- G_n Length (sag.) of glabella plus occipital ring
- A Eye length (exsag.)
- W_{pl} Maximum cranial width (tr.)
- W_l Preoccipital glabellar width (tr.)
- P_p Posterior palpebral width (tr.)
- W_{pt} Width (tr.) of preglabellar field

SYSTEMATIC PALAEONTOLOGY

Order MIOMERA Jaeckel, 1909

Suborder AGNOSTINA Salter, 1864

Superfamily AGNOSTACEA M'Coy, 1849

Family AGNOSTIDAE M'Coy, 1849

Subfamily AGNOSTINAE M'Coy, 1849

Genus DISTAGNOSTUS nov.

Type Species. *Distagnostus ergodes* gen. et sp. nov., from the late Upper Cambrian, Gola Beds of Western Queensland.

Name. Latin, *disto*, stand apart, separate; a distinct 'agnostus.'

Diagnosis. A genus of Agnostinae with glabellar, prelabellar, and axial furrows largely effaced; obtusely angulate glabellar rear with anteriorly nesting basal lobes; narrow borders; simplicimarginate pygidium with laterally expanded posterior axial lobe; acrolobe constricted in the pygidium but not in the cephalon; pygidial articulating half-ring simple, of the agnostoid type; strongly concave articulating facets.

Discussion. The classification of *Distagnostus* is not facilitated by the effacement of the cephalic furrows. Using the tabular classification of Öpik (1967: between pp. 66 and 67) the genus is observed to display four out of the eight diagnostic characteristics of the Agnostidae: it is axiolobate, simplicimarginate, has an agnostoid-type articulating device and a smooth pygidium. The glabellar rear is obtusely angulate rather than rounded and the pygidial acrolobe is gently constricted, whereas that of the cephalon is unconstricted, these features being more commonly found in Diplagnostidae. Among the Diplagnostidae the last mentioned characteristic is typical of the Ammagnostinae, although Öpik (1967, p. 68) has noted that *Pseudophalacroma dubium*, which is assigned to the Agnostidae, also has faintly constricted acrollobes. *Distagnostus* is allied here to the Agnostinae on the affinities of a prevailing number of characteristics, and these become more apparent when the genus is compared to already described Agnostinae.

Comparisons and differences. The pygidium of *Distagnostus* is most similar to that of *Innitagnostus* Öpik, 1967. *I. inexpectans* (Kobayashi) in particular is comparable to *Distagnostus ergodes*. In both there is a similar shape and segmentation, although in *Distagnostus* the width (sag.) of the first axial segment is greater. The central portion of the annulation is constricted in *Innitagnostus*, but it is of equal width to that of the flanks in *Distagnostus*, in which characteristic there is some comparison with the condition of *Lotagnostus*. *Distagnostus* is further differentiated from *Innitagnostus* by its constricted pygidial acrolobe, and on glabellar characteristics. When visible, the glabella is anteriorly acutely rounded, posteriorly obtusely angled, whereas in *Innitagnostus* it is anteriorly blunt and posteriorly rounded. In both genera there are embayments on the posterolateral glabellar flanks to accommodate the anterior ends of the basal lobes.

Distagnostus has a well developed cephalic border which differentiates it from *Peratagnostus* Öpik, 1967, although otherwise the effaced cephalic shields of both are somewhat similar. The pygidium of *Peratagnostus nobilis* Öpik, 1967, is more

effaced than that of *Distagnostus ergodes*, the border is wider and more evenly so, and the whole outline more oval. *Peratagnostus* is placed by Öpik (1967) in the Quadratagnostinae (Agnostidae).

DISTAGNOSTUS ERGODES sp. nov.
(Pl. 4, figs 1-7; text-fig. 5)

Name. Greek, *ergodes*, irksome, troublesome: referring to the difficulty in classifying this effaced species.

Holotype. The pygidium CPC 9667, illustrated on Plate 4, figure 3, which shows more detail than is usual of the axial segmentation. A pygidium has been preferred because the cephalon is too greatly effaced to show constant detail.

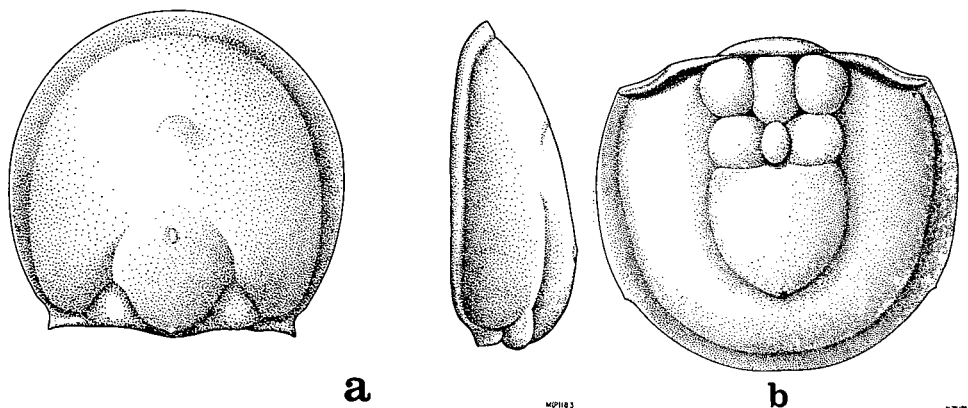
Material. About 25 specimens have been noted, of which 13 cephalae and 10 pygidia were prepared for more detailed examination. The former vary in length (sag.) between 2.25 and 4.45 mm and the latter between 2.60 and 4.25 mm. All specimens are preserved with some vestige of shell, the varying thickness of which influences the degree of visibility of surface details. Specimen CPC 9668, figured on Plate 4, figure 4, shows the underlying mould has more relief than the surface shell. The external cephalic mould (see the latex cast, CPC 9669, Pl. 4, fig. 2) is almost completely smooth.

Occurrence. The species is most common in the calcarenite layer recorded as locality B752, but it occurs also in sandy calcilutite at B750. The species apparently does not occur in the coarse calcarenite at B520.

Diagnosis. The specific diagnosis of *Distagnostus ergodes* is contained within that of the genus (above).

Description. The cephalic outline is evenly rounded, with a posterior width (tr.) a little over 75 percent of the length (sag.). The border is narrow, widest anterolaterally, anteriorly 5-7 percent of the cephalic length (sag.). The marginal furrow is merely a break in slope between the acrolobe and the border, the latter sloping outwards and downwards (adventrally) to the margin. Small intergenal spines are present.

The cephalic acrolobe is not perceptibly constricted; it is transversely moderately convex, sagittally gently convex. The preglabellar median furrow is completely



5. *Distagnostus ergodes* gen. et sp. nov.
(a) cephalon based on CPC 9671 and 9672, x15;
(b) pygidium based on CPC 9670, x10.

effaced. The axial furrows defining the glabella are extremely faint, as a rule only visible posteriorly. Similarly the glabella has little appreciable relief, save posteriorly. In the exceptional cases when it is visible the glabella is seen to taper forwards and to be acutely rounded anteriorly. The anterior glabellar lobe, when visible, occupies one-third the glabellar length, and is separated from the remainder of the glabella by a very faint transverse furrow. Lateral glabellar lobes are scarcely indicated, but the species appears nevertheless to have been derived from a stock in which there were at least three pairs of median lateral lobes. The glabellar rear is angulate with a minute terminal node. The basal glabellar lobes, which are comparatively small and triangular in shape, are accommodated at their anterior ends within slight flexures of the posterolateral glabellar outlines. A median glabellar node is situated a little less than one-half the way along the glabella from the rear.

The pygidium is less effaced than the cephalon. It has the same general outline and arrangement of the border, save that the latter is perhaps a little wider (sag.) posteriorly, 5-8 percent of the pygidial length (sag.). The anterior articulating half-ring is a simple bar, separated from the pygidial axis by a narrow transverse furrow, not appreciably overdeepened at any point. The articulating facets are strongly concave rearwards. The anterior border furrow is confluent with the peripheral marginal furrow.

The pygidial acrolobe has a similar convexity (tr. and sag.) to that of the cephalon, but is noticeably constricted laterally (see Pl. 4, fig. 7). Of the three axial segments the first (anteriormost) is widest (tr.), occupying 45-50 percent of the anterior pygidial width (tr.), and is longitudinally subdivided into three by shallow exsagittal furrows. The second (middle) segment is a compressed oval in shape, similar to the first in width. It is also longitudinally trilobed, the middle section developing a prominent median node. The third segment (the posterior one) is longer (sag.) than the first and second combined, attaining approximately one-third the total pygidial length (sag.). It is posteriorly acutely angled and culminates in a prominent terminal node. On some specimens (e.g. CPC 9670, Pl. 4, fig. 7) very faint notular lines are visible, but in the majority of specimens these are completely effaced. The posterolateral margins bear minute rounded spinules developed from the upper (dorsal) surface of the border and directed outwards and slightly downwards (Pl. 4, fig. 5).

No trace of prosopon has been observed on either cephalon or pygidium; neither scrobiculation nor reticulation. The surface appears to be quite smooth.

The table on the next page gives some idea of the cephalic and pygidial proportions of *D. ergodes*.

Comparisons and differences. Although *Distagnostus* is quite distinct from *Lotagnostus*, as typified by the type species *L. trisectus* (Salter, 1864), there are similarities between *Distagnostus ergodes* and the species described by Palmer (1955, p. 92) from the Bullwacker Member, Windfall Formation, Eureka district, Nevada, as *Lotagnostus obscurus*. Like that of *Distagnostus*, the pygidium of *L. obscurus* apparently lacks the very narrow (sag.) third pair of anterior axial segments found in *Lotagnostus*. *L. obscurus* and *D. ergodes* have similarly shaped pygidial axes, and the nature of their pygidial spines is indistinguishable. *L. obscurus* possesses a longitudinal tripartition of the pygidial axis which is wanting in *D. ergodes*. Neither species has the cephalic or pygidial scrobiculation so strongly developed in *Lotagnostus trisectus*, but this may vary within *Lotagnostus*, e.g., *L. asiaticus* Troedsson (1937, p. 25).

Cephala:

Specimen No.	L _c mm	W _c :L _c %	L _{ac} :L _c %	L _{bc} :L _c %	W _c :W _x %
CPC 9675	2.25	82.10	66.91	6.22	60.26
CPC 9672	3.20	76.70	64.45	6.95	67.28
CPC 9678	3.20	79.30	64.57	6.17	59.81
CPC 9673	3.40	80.67	67.07	6.58	61.31
CPC 9674	3.45	80.91	70.58	6.45	55.98
CPC 9677	3.59	80.54	68.53	5.64	63.24
CPC 9679	3.85	—	—	5.93	—
CPC 9671	4.30	77.78	68.92	7.32	64.58
CPC 9669	4.40	74.85	64.18	5.80	69.34
CPC 9676	4.45	77.49	64.69	5.92	67.57

Pygidia:

Specimen No.	L _p mm	W _p :L _p %	L _{ap} :L _p %	L _{bp} :L _p %	W _a :W _p %
CPC 9684	2.60	95.15	74.47	5.32	46.34
CPC 9683	2.90	80.85	71.78	8.31	—
CPC 9681	3.00	85.04	64.76	7.59	49.94
CPC 9668	3.10	90.26	77.71	7.16	48.96
CPC 9682	3.20	94.95	79.62	6.62	45.60
CPC 9685	3.20	—	71.63	—	—
CPC 9667	3.40	87.64	78.27	5.51	45.16
CPC 9680	3.85	94.79	75.04	8.41	48.78
CPC 9670	4.25	84.78	74.13	7.44	46.97

Agnostus innocens Clark *sensu* Raymond, 1924 (see Raymond, p. 390, pl. 12, fig. 1), from the Gorge Formation of Vermont, appears to lie morphologically between *Lotagnostus obscurus* and *Distagnostus ergodes*. The shape and segmentation of the pygidial axis, and the position of the pygidial spines, are characteristics comparable in the three species. Like *D. ergodes*, '*Agnostus*' *innocens* lacks the strong scrobiculation normally diagnostic of *Lotagnostus*. Like *L. obscurus*, the two anterior pygidial segments are each longitudinally trisected, the posterior one remaining undivided as in *D. ergodes*. Possibly all three species should be considered congeneric.

Genus RUDAGNOSTUS Lermontova, 1951

Type species. *Agnostus princeps*, β. *rudis* Salter, 1864b, p. 4, plate 1, figure 3. Salter figured two different trilobites under this name. Lake (1906, p. 21) restricted the term to Salter's figure 3, and raised the variety to specific rank. Salter's specimens were obtained from the Upper *Lingula* Flags of North Wales.

Other species. The following species are probably also referable to *Rudagnostus*:

Agnostus rudis Salter; Westergaard, 1922, p. 193, plate 1, figure 17, from Subzone 5c, *Peltura minor* with *P. acutidens*, of Andrarum, Sweden.

Agnostus rudis holmi Westergaard; Westergaard, 1922 pp. 118-9, plate 1, figures 13-16, from Subzones 5d-5e, *Peltura scarabaeoides* and *Parabolina longicornis*, from various localities, Västergötland and Öland.

Agnostus (Homagnostus) rudis Salter (?); Westergaard, 1947, pp. 4-5, plate 1, figures 13a, b, from Subzone 5c, *Peltura acutidens*, Sättra, Västergötland.

?*Micragnostus coreanicus* Kobayashi; Kobayashi, 1960a, p. 234, plate 13, figure 10, from the Lower Ordovician Bunkoku Formation of South Korea.

?*Geragnostus intermedius* Palmer; Palmer, 1968, p. B24, plate 12, figures 1-2, from the late Franconian, Hillard Peak, east-central Alaska.

Discussion. The genus was erected by Lermontova (1951, p. 7) with minimum discussion; neither types nor other materials were figured. Howell *in* Moore (1959) placed the genus questionably in his Micragnostidae alongside *Micragnostus*, *Anglagnostus*, and *Eurudagnostus*. *Rudagnostus* is a valid genus. It is comparable on the one hand with *Homagnostus* and on the other with *Geragnostus* and *Micragnostus*, forming a link between them. All four have been classified by Öpik (1967, tabular classification) as Agnostinae, a procedure followed here.

Little can be gained from study of Salter's original figures and discussion of *Rudagnostus princeps*; a good measure of reliance is therefore placed on Lake. The specimens figured by Lake (1906, pl. 2, figs 13-16) are all distorted and rather poorly preserved. They do, however, allow certain observations: that the posterior segment of the pygidial axis is shorter than in *Homagnostus* but longer than in either *Geragnostus* or *Micragnostus*; the median preglabellar furrow is externally absent and the anterior transverse furrow of the glabella well developed; the pygidial axial furrows are deep and allow the axis to 'nestle' within the acrolobe; the pygidium has stout spines; and the posterior axial lobe is swollen, as in *Homagnostus*, but unlike *Geragnostus*, in which it is parallel-sided, truncate posteriorly.

Westergaard (1922, pl. 1, fig. 17) figured a specimen from Andrarum having similarities to *Rudagnostus rudis*, and a variety called *rudis holmi* (pl. 1, figs 13-16) which has a long axis similar to that of *Homagnostus*. A specimen with shorter axis figured by Westergaard in 1947 (pl. 1, fig. 13) has greater affinity to the Australian material presented below. More recently a similar pygidium from the late Franconian of Alaska has been figured by Palmer (1968, p. B24, pl. 12, figs 1-2) under the name of *Geragnostus intermedius*.

Rudagnostus is quite distinct from *Eurudagnostus* Lermontova, 1951, which has a constricted cephalic acrolobe and decidedly tapering pygidial axis, flared out anteriorly but not swollen posteriorly. *Eurudagnostus* might possibly be classified with or near *Connagnostus* in the Diplagnostinae.

RUDAGNOSTUS AVIUS sp. nov.

(Pl. 5, figs 6-7)

Name. Latin, *avius*, remote, solitary: referring to the occurrence of *Rudagnostus* in Australia, remote from the Anglo-Baltic region from which it was first described.

Holotype. The designated holotype is CPC 9686 (Pl. 5, fig. 7). Though incomplete this pygidium shows all the diagnostic features of the axis.

Material. Only three pygidia are known and all are incomplete. Together, however, they give a good indication of all the major pygidial characteristics. Specimen CPC 9687 lacks the border with its spines but shows a complete axis. Of the other specimens, CPC 9688 lacks the anterior portion of the axis and acrolobe and a part of the border; CPC 9686 wants an articulating half-ring and posterolateral spines.

Occurrence. The available material is restricted in occurrence to a coarse-grained calcarenite layer at B520.

Diagnosis. A species of *Rudagnostus* based on the following pygidial characteristics: prominent marginal gutter, especially posteriorly; expansive lateral lobes on the anterior axial segment; and posterior axial lobe greater than one-half but less than two-thirds the total axial length (sag.).

Description. The border rim is narrow, posteriorly separated from the acrolobe by a distinct, narrow, but deep gutter (marginal furrow). Stout posterolateral spines are present on CPC 9688 (Pl. 5, fig. 6), whose bases lie rearwards of the posterior axial lobe, at or slightly in advance of a transverse line drawn across the rear of the acrolobe. The acrolobe is moderately convex (tr. and sag.), undivided posteriorly. Neither articulating facets nor articulating half-rings are preserved on the available material.

The axial furrows defining the axis are deep and wide, the acrolobe forming a definite step on joining these furrows. The axis occupies about 80 percent of the total pygidial length (sag.), of which the posterior lobe occupies 57 percent (on both CPC 9686 and 9687). The anterior segment is trilobate; a short central portion, poorly delimited by a shallow furrow from the second segment, is flanked by subtriangular lateral lobes which splay across the line of the axial furrows. These are separated from the second segment by diagonal furrows which isolate them from the remainder of the axis. Such furrows are also present in *Geragnostus* and *Micragnostus*. The second segment is a flattened ovoid, bearing a median node. The third (posterior) segment is expanded, evenly rounded or slightly angled posteriorly, where a small terminal node is evident.

Apart from a faint and irregular pitting on the holotype there is no visible surface marking.

Comparisons and differences. *Rudagnostus* appears to be the most convenient genus for the specimens illustrated here. They are essentially similar to Lake's (1906) specimens of *R. rudis* (Salter), especially as regards the nature of the axes and acrolomes. All Lake's specimens (1906, pl. 2, figs 13-16) are squashed or otherwise distorted, and it is impossible to make detailed comparisons with them. Noted with some certainty is that the pygidial axis of *R. avius* is shorter (sag.) than that of *R. rudis*. From *R. rudis* (Salter) *sensu* Westergaard (1922, p. 193, pl. 1, fig. 17) *R. avius* differs in having a shorter posterior axial segment and laterally more extensive anterior segment. Similar differences separate the Australian species from *R. rudis holmi* (Westergaard 1922, pp. 118-9, pl. 1, figs 13-16), which is a little reminiscent of *Homagnostus*. Fairly close comparison, however, may be made with the specimen figured by Westergaard (1947, pl. 1, fig. 13) as *Aagnostus* (*Homagnostus*) *rudis* Salter(?), but this species is differentiated from *R. avius* on the position of the node on the pygidial axis, well forwards in *A. (H.) rudis*, well backwards in *R. avius*. Comparison may also be made with one of the specimens figured by Shaw (1951, pl. 23, fig. 15) as *Micragnostus bisectus* (Matthew) *typica* Shaw, from late Upper Cambrian thrust strata at Highgate Falls, Vermont. This specimen differs from *R. avius* only in the relative proportions of the axial elements.

Genus GERAGNOSTUS Howell, 1935

Subgenus MICRAGNOSTUS Howell, 1935

Type species. *Aagnostus clavus* Lake, 1906, p. 23, plate 2, figure 18, from the Tremadocian of Nant Rhosddu, Arenig, North Wales.

Remarks. Howell (1935, pp. 231-3) erected separate families for *Geragnostus* and *Micragnostus*, but the only difference between them lies in the strength and orientation of the anterior transverse glabellar furrow and the position of the axial glabellar node. *Geragnostus* has a poorly developed anterior furrow, and an axial node which lies well forwards, touching the anterior furrow in the type species, *Agnostus sidenbladhi* Linnarsson. *Micragnostus*, however, has a well defined linear anterior transverse furrow, and its axial node lies considerably farther to the rear than in *Geragnostus*. In the pygidial axis the posterior segment appears to be slightly longer in *Geragnostus* than in *Micragnostus*, in which the three segments are more nearly equal in size. Harrington & Leanza (1957), however, illustrate species of *Micragnostus* with long axes similar to those of *Geragnostus*. They regard the differences between these taxa as of subgeneric rather than familial value, with which I concur. *Geragnostus* (*Geragnostus*) and *G.* (*Micragnostus*) appear to be related through *Rudagnostus* to *Homagnostus*, and all four should be classified within a single subfamily or family.

GERAGNOSTUS (MICRAGNOSTUS) ACROLEBES sp. nov.
(Pl. 5, figs 3, 5)

Name. Greek, *acrolebes*, pointed at the end: referring to the shape of the pygidial axis.

Holotype. The pygidium CPC 9689 (Pl. 5, fig. 4), though poorly preserved, is designated as the holotype.

Material. The two cephalae illustrated in Plate 5 are considered to be conspecific with the holotype pygidium. All are very small specimens; the pygidium CPC 9689 is 1.35 mm long and a second, CPC 9690, attains 1.20 mm. The cephalae vary in length between 1.30-1.80 mm.

Occurrence. *Geragnostus* (*Micragnostus*) *acrolebes* is most common in sandy calcilitite at B750, but is found also in coarse-grained calcarenite at B520, B520B, and K101.

Diagnosis. A species of *Geragnostus* (*Micragnostus*) with a glabella showing traces anteriorly of median lateral lobes. In the pygidium the axis is two-thirds the total length; the posterior lobe is small and acutely rounded, accounting for 45-50 percent of the total axial length; the pygidial border is wide, especially posteriorly.

Description. The cephalon has a subquadrate outline. The border is simple and narrow, accounting for 8 percent of the cephalic length anteriorly; the marginal furrow is shallow. Stout intergenal spines are present on the posterior cephalic border. The acrolobe is unconstricted and undivided in the preglabellar area, although there is a faint trace of a median preglabellar furrow proximal to the glabella.

The glabella is cylindrical, tapering very slightly forwards. There is a well developed anterior lobe which is isolated from the remainder of the glabella by a deep transverse furrow. Faint indications of median lateral lobes are present. The posterior lobe is rounded at the rear and a terminal node is apparently absent. The basal lobes are relatively small, flattened, and laterally extensive. A faint axial node is positioned well to the rear of the posterior lobe.

The pygidium has a quadrate outline, and is elevated in convexity. The border is wide, posteriorly about 15 percent of the pygidial length (sag.), but simple, with a shallow marginal furrow. Short, thorn-like posterolateral spines are present,

directed outwards and slightly downwards. The nature of the articulating half-ring and articulating facets is unknown. The acrolobe is appreciably convex (tr.), unstricted and undivided posteriorly. At the axial furrows it slopes strongly, forming an 'escarpment.'

The axis, occupying two-thirds of the pygidial length, is widest (tr.) at the first segment, drawn in a little at the second, and slightly expanded at the third. Posteriorly the axis culminates in a terminal node. The first segment is divided into three, the lateral lobes expanding across the line of the axial furrows. The second segment is broader (sag.) but narrow (tr.), and bears a median node. The third (posterior) segment is slightly expanded; it occupies 45-50 percent of the total axial length (sag.).

The surface of the cephalon is finely granulose, that of the pygidium apparently smooth.

Comparison and differences. *Geragnostus (Micragnostus) acrolebes* is related to those previously described species which have a short (sag.) posteriorly tapered posterior axial lobe in the pygidium. Among these the Australian species is most closely comparable to *G. (M.) chiushuensis* Kobayashi (1931, pl. 22, figs 1-4), a species from the Chiushukou Shale of the Hualienchai area, southern Manchuria, which is of late Cambrian or early Ordovician age. Both *G. (M.) acrolebes* and *G. (M.) chiushuensis* share common axial characteristics in the pygidium, and appear to have similar cephalae. They differ in the shape of the pygidium, and the size and orientation of its spines. In the Manchurian species, as illustrated by Kobayashi (1931), the pygidial margins are decidedly quadrate, and the spines, though short, are shown to be broad-based and strong, quite distinct from the delicate thorn-like spines of *G. (M.) acrolebes*.

Micragnostus subobesus (Kobayashi) (1936, p. 161, pl. 21, figs 1-2), from Jones Ridge on the Yukon-Alaska border, has a somewhat wider (tr.) pygidial axis, the posterior lobe being less acutely rounded than that of *G. (M.) acrolebes*, but it is otherwise similar. The pygidium from Frederick, Maryland, illustrated by Rasetti (1959, pl. 51, fig. 10) as *Agnostus* sp., has comparable axial elements, but differs in the width and extent of the acrolobe and narrowness of the lateral borders.

The pygidium from the Tremadocian Tiñu Formation of Oaxaca, Mexico, which Robison & Pantoja-Alor (1968, pl. 97, fig. 10) have regarded as a young holaspide of *Geragnostus intermedius* Palmer, is in every way compatible with *G. (M.) acrolebes* and may be conspecific.

Family DIPLAGNOSTIDAE Whitehouse, 1936

[as redefined by Öpik (1967, p. 80)]

Subfamily DIPLAGNOSTINAE Whitehouse, 1936

Genus CONNAGNOSTUS Öpik, 1967

Type species. *Connagnostus venerabilis* Öpik, 1967, from the Mindyallan Stage, *Glyptagnostus stolidotus* Zone, in northwest Queensland.

According to Öpik (1967, p. 131), *Proagnostus?* (Palmer, 1962), from a *Glyptagnostus stolidotus* assemblage in Alabama, also belongs to *Connagnostus*. The species *zonatus* Öpik, 1967, also from the Mindyallan of Queensland, was questionably placed in the genus (Öpik, 1967, p. 132).

The specimens at hand conform to the concept of *Connagnostus* in that the acrolobe of the cephalon is unconstricted, that of the pygidium narrow and strongly constricted. As far as can be judged from the disposition of the basal glabellar lobes the glabellar rear is subangulate. A preglabellar median furrow is not externally visible. The pygidium has wide borders bearing a pair of short spines. It is axiolobate, reminiscent of *Homagnostus* or *Geragnostus*, and simplicimarginate. The articulating device appears, however, to be agnostoid rather than glyptagnostoid.

CONNAGNOSTUS JUNIOR sp. nov.

(Pl. 5, figs 1 and 2)

Name. Latin, *junior*, younger: the species is the youngest yet assigned to the genus.

Holotype. The pygidium, CPC 9665, figured on Plate 5, figure 2.

Material. Only three specimens are known. The two figured specimens represent the better preserved material. Save for the loss of its spines the pygidium is complete. The cephalon, however, has lost a good proportion of the central portion of the glabella and a part of the preglabellar acrolobe. Head and tail occur within one inch of each other on the same piece of rock. The cephalon has a length of 2.05 mm and the pygidium measures 1.85 mm.

Occurrence. The species occurs in weathered calcarenite at localities B520B and B753.

Diagnosis. A species of *Connagnostus* with prominent cephalic border gutter and intergenal spines; pygidium with simple articulating device, mesially discontinuous anterior transverse axial furrow, short pygidial axis approaching two-thirds the total pygidial length, with short, bulbous posterior lobe, less than one-half the axial length.

Description. The cephalic outline is evenly rounded. The border consists of a narrow rim, bounded by a prominent gutter, which separates the rim from the acrolobe; anteriorly the border occupies 7 percent of the total cephalic length. Posteriorly the border is wide (exsag.), developing strong intergenal spines. The acrolobe is unconstricted, continuous in front of the glabella, there being no outward sign of a preglabellar median furrow.

The glabella, approximately two-thirds the total cephalic length (sag.), tapers forwards and is acutely rounded anteriorly. On the only cephalon available the greater part of the glabella is missing, but there seems to be only a faint indication of an anterior transverse furrow. The posterior lobe is mesially constricted. The position of the axial node remains uncertain. Posteriorly the glabella was possibly angulate, as is evident from the disposition of the basal lobes. The latter are pear-shaped, laterally extensive, and occupy 55-60 percent of the posterior cephalic width (tr.; including that across the rear of the glabella).

The pygidium has a subquadrate outline. Convexity is high and the specimen is preserved with full relief. The border is wide posteriorly — 7 percent of the pygidial length (sag.) — and posterolaterally. Short posterolateral spines (broken off) which continue the line of the lateral pygidial margins lie rearwards of the posterior end of the axis. The marginal furrow is wide but shallow. The articulating facets are very slightly concave, sloping strongly abaxially, bearing at the geniculation small fulcral points. The articulating device is a simple half-ring.

The acrolobe tapers posteriorly; it is strongly constricted but not divided posteriorly by a median furrow or extension of the axis.

The axis is prominent, attaining two-thirds the total pygidial length (sag.), but does not reach the marginal furrow posteriorly. The anterior segment is narrow (exsag.), laterally lobed; the first transverse furrows are mesially discontinuous, abaxially sloping backwards. The second segment, bearing a central node, is roughly barrel-shaped, defined posteriorly by a continuous but faint transverse furrow. The third (posterior) segment is evenly rounded posteriorly, attaining 45 percent of the total axial length. No posterior terminal node is visible. Muscle-scars are faintly visible on the axial segments of CPC 9665 (Pl. 5, fig. 2).

A faint prosopon of terrace lines remains on the rear of the posterior axial segment. The remainder of the pygidium is smooth. The cephalon is faintly scrobiculate.

Comparisons and differences. Because of its prominence, attention is first drawn to the pygidial axis of *Connagnostus junior*. This appears comparable to that found in species of the agnostid genera *Geragnostus*, *Geragnostus* (*Micragnostus*), *Homagnostus*, and *Rudagnostus*. In the last two the axis is more than three-quarters as long as the pygidium, and may reach the posterior marginal furrow. In *Micragnostus* it is about three-quarters of the total length, but in *Geragnostus* is less than two-thirds. A closer study, however, reveals the constricted pygidial acrolobe of *Connagnostus junior*, a feature differentiating it from all Agnostidae but allying it to the Diplagnostidae. Of the diplagnostid genera only *Connagnostus* is at all suitable for the reception of the species described here.

Large specimens of *Connagnostus venerabilis* Öpik, 1967, with cephalic or pygidial lengths in excess of 3.00 mm, are quite different from *C. junior*. Their pygidial axes are long and reach to the marginal furrow posteriorly. Öpik (1967, p. 131) has shown, however, that small specimens of *C. venerabilis* have short axes not reaching the marginal furrow, and that the posterior segment of the axis extends backwards during morphogenesis. Öpik's smallest specimen (1967, p. 130, text-fig. 36C, pl. 54, fig. 13) is only 1.30 mm long, and the posterior segment is less than one-half the axial length. The pygidium attributed here to *C. junior* has a length of 1.85 mm and the condition of the axis is similar to that in Öpik's text-figure 36B. It is suggested that *C. junior* may be neotenuously derived from *C. venerabilis*, retaining the immature condition of that species into later moults.

Other specimens figured in the literature under various names are comparable to *Connagnostus junior*. Attention may be called to the pygidium figured by Palmer (1955, pl. 20, figs 12, 15) as *Geragnostus tumidosus* (Hall & Whitfield) and later placed in *Homagnostus* (Palmer, 1960, 1968). Both Palmer's figure 12 of 1955, and the line drawing (fig. 15) have strongly constricted acrolobes. Their pygidial axes, however, are somewhat longer than that of *Connagnostus junior* and may indicate an earlier stage in the derivation from a form similar to *C. venerabilis*. Palmer's specimens are from the Dunderberg Shale (*Elvinia* Zone), Eureka district, Nevada. Similarly the pygidium with slightly constricted acrolobe figured by Palmer (1968, pl. 12, fig. 2) as *Geragnostus intermedius* Palmer, from the late Franconian of Alaska, may be another stage in the process. A specimen with constricted acrolobe and axial characteristics directly comparable to those of *Connagnostus junior* was figured by Rasetti (1959, pl. 51, fig. 17) as *Geragnostus* sp. undet. from the Frederick Limestone of Frederick, Maryland.

Subfamily PSEUDAGNOSTINAE Whitehouse, 1936

Genus PSEUDAGNOSTUS Jaeckel, 1909

Type species. *Agnostus cyclopyge* Tullberg, 1880, p. 27, plate 2, figures 15a, c, from the Zone of *Parabolina spinulosa* with *Orusia lenticularis* and the *Olenus* Zone of Andrarum, Sweden (Westergaard, 1922, pp. 116-7, pl. 1, figs 7-8).

The concept and organization of the genus *Pseudagnostus* has been noted by Jaeckel (1909), Whitehouse (1936), Kobayashi (1937, 1939), Ivshin (1956), Rosova (1960), and Palmer (1955, 1960, 1962). The ground has been covered more fully by Öpik (1963, 1967).

Regardless of synonymy, some 49 species' names have been applied to *Pseudagnostus*. Five further species are recorded below, two having been given names and three left under open nomenclature as insufficient material is available for their thorough description. With such a large number of species, each with its own combination of characteristics, some degree of subdivision of *Pseudagnostus* seems desirable. However, most previous attempts to split the genus have been unsuccessful owing to the difficulty of establishing characteristics which do not vary widely or grade from one condition to another. In this respect degree of effacement of morphological characteristics cannot be successfully utilized, for although there is obvious difference between effaced forms and those preserved en grande tenue, all degrees of variation exist between them. The strength of the prelabellar furrow or accessory furrows and the definition of the notular lines and furrows also fall into this category.

Several of the genera previously placed in the Pseudagnostinae are here considered synonymous with *Pseudagnostus*. These include:

Plethagnostus Clark, based on *P. gyps* (Clark, 1923, p. 124, pl. 1, fig. 9), revised by Rasetti (1944, p. 234), and considered in every way compatible with *Pseudagnostus*. Clark considered *Plethagnostus* distinct because the accessory furrows defining the deuterolobe continued to the pygidial marginal furrow. This is a common feature in early Upper Cambrian (Dresbachian, Mindyallan, and Idamean) species which are preserved en grande tenue, e.g. *P. ampullatus* Öpik, 1967, *P. bulgosus* Öpik, 1967, *P. boltonensis* (Resser, 1938), *P. canadensis* (Billings, 1860), *P. idalis* Öpik, 1967, *P. mesleri* (Resser, 1938), *P. mestus* Öpik, 1967, and possibly *P. cyclopyge* (Tullberg, 1880). Often it is a very subjective decision whether these furrows are well defined or not.

Euplethagnostus Lermontova, based on *E. subangulatus* Lermontova (1940, p. 126, pl. 49, figs 15, 15a), is said to be similar to *Plethagnostus* but additionally possesses pygidial spines. As these are in fact present in the type species of *Plethagnostus*, *P. gyps* (see Rasetti, 1944, pl. 36, figs 20-22), *Euplethagnostus* loses its value.

Sulcatagnostus was erected by Kobayashi (1937, p. 451) to accommodate *Agnostus securiger* Lake (1906, p. 20, pl. 2, fig. 11). The species is strongly deuterobate and is clearly comparable to the 'plethoid' species of *Pseudagnostus*.

Rhaptagnostus was based by Whitehouse (1936, p. 97) on *Agnostus cyclopygeformis* Sun (1924, p. 26, pl. 2, figs 1a-h). Whitehouse considered the presence of notular lines and the (presumed) absence of pygidial spines diagnostic of this genus. These characteristics have been subsequently reported, separately or in combination, for a number of species which can be referred to *Pseudagnostus*. Recorded without spines are *P. clarki* Kobayashi, 1935b, *P. semiovalis* Kobayashi, 1937, *P. primus* Kobayashi, 1935c, *P. josepha* (Hall, 1863), and *P. acutifrons*

(Troedsson, 1937). With notular lines are a variety of species, including all those formerly referred to *Pseudorhaptagnostus*, e.g. *P. simplex* Lermontova, 1951, *P. punctatus* Lermontova, 1940, *P. cavernosus* Rosova, 1960, *P. vulgaris* Rosova, 1960, and in addition *P. ampullatus* Öpik, 1967, *P. communis* (Hall & Whitfield, 1877) *sensu* Bell & Ellinwood (1962, pl. 51, fig. 18), *P. prolongus* (Hall & Whitfield, 1877) *sensu* Lochman & Hu (1959, pl. 57, figs 10, 11), *P. semiovalis* Kobayashi, 1937, and the species described here as *P. papilio* and *P. clavus*. Notulae are also present in the related genus *Xestagnostus* Öpik, 1967. The diagnostic characteristics of *Rhaptagnostus* seem insufficient to differentiate it from *Pseudagnostus*.

Placed in synonymy with *Pseudagnostus* with some reserve is *Pseudorhaptagnostus* Lermontova, which was first introduced in 1940 (p. 126), ascribed to Lermontova, 1937. Ivshin (1956, pp. 12, 14) dates the genus as Lermontova 1938 MS, but I am unaware of these early publications by Lermontova. In 1940 the type species is quoted by Lermontova as *Pseudorhaptagnostus simplex* Lermontova, but no description or illustration of this species was given until the posthumous publication of 1951. *P. punctatus* Lermontova was, however, both described and illustrated in 1940.

As defined by Lermontova (1951, p. 12), *Pseudorhaptagnostus* is diagnosed by a wide pygidial border, well developed pygidial spines, and the presence of notular lines behind the second axial segment. As discussed above, neither of the last two characteristics can be considered diagnostic alone. There are, however, others which might eventually justify *Pseudorhaptagnostus*, but they ought to be verified from the original material. The pygidium is subquadrate in outline, generally wider than long; the border is posteriorly widened (sag.); the deuterolobe may be poorly defined; the spines are direct continuations of the lateral pygidial margins or deflected very slightly outwards, lying on a transverse line across the rear of the deuterolobe; the first axial segment is formed by two narrow (exsag.) lobes which overlap the axial furrows and the anterolateral edges of the second segment; a third segment is represented by a pair of gently convex swellings. The cephalic shield is also subquadrate; a preglabellar furrow may be present or absent, strongly or weakly incised. The characteristics of the glabella, which if it is like that of *Pseudagnostus clavus* described below are important, have not been discussed for the type series.

Pseudorhaptagnostus covers *P. simplex* Lermontova, 1951, *P. punctatus* Lermontova, 1940, *P. vulgaris* Rosova, 1960, *P. cavernosus* Rosova, 1960, and the Australian species described here as *Pseudagnostus clavus* sp. nov. *Pseudagnostus bilobus* Shaw, 1951, is possibly also related to this group of species.

For all its apparent distinctiveness, *Pseudorhaptagnostus* is here classified with *Pseudagnostus*, until the type material has been adequately re-examined.

PSEUDAGNOSTUS PAPILIO sp. nov.
(Pl. 1, figs 1-8; Pl. 2, figs 1-2; Text-fig. 6)

Name. Latin, *papilio*, a butterfly: referring to the shape of the arrangement of the anterior and median lateral glabellar lobes.

Holotype. Although small, the cephalon CPC 8442, illustrated on Plate 1, figure 3, has been selected as the type on account of its completeness.

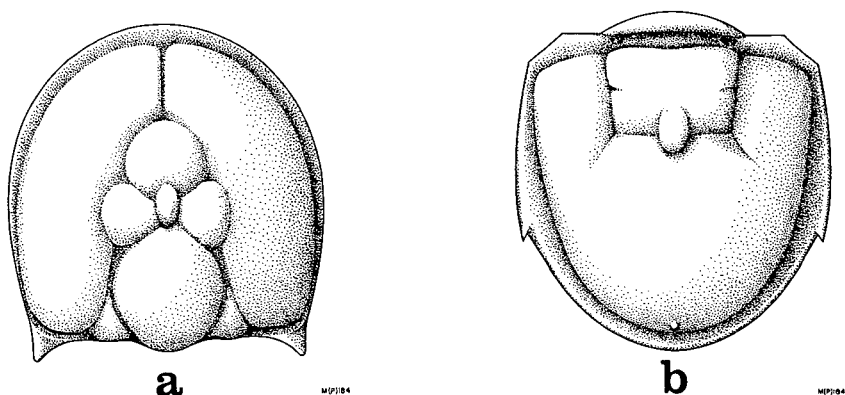
Material. Disarticulated cephalae and pygidia are known from a large number

of specimens. No complete articulated specimen is known, and nothing is known of the thorax. All specimens are preserved as limestone moulds, although some retain vestiges of shell. Measured cephalon have lengths varying between 2.25-3.10 mm; associated pygidia have lengths between 2.30 and 3.60 mm.

Occurrence. *Pseudagnostus papilio* occurs in all the sampled horizons of the Gola Beds. It is most common in sandy calcilutite layers at B750 and K101, and in coarse-grained calcarenite layers at B520 and K102. A suite from some of these localities is illustrated on Plates 1 and 2.

Diagnosis. A species of *Pseudagnostus* with ovoid cephalon and pygidium, each with a narrow border rim. On the exterior surface the cephalon is paucifurrowed and weakly scrobiculate. The pygidium has small posterolateral spines placed well forwards, flanks which converge rapidly to the rear, a poorly defined deuterolobe, and nearly completely effaced accessory and transverse furrows.

Description. The cephalon is moderately convex (tr. and sag.) and has an ovoid outline; the width (tr.) is approximately 85-95 percent of the length (sag.). The border, although narrow overall, is widest anteriorly (sag.) where it occupies 4-10 percent of the cephalic length, and is narrowest posterolaterally. The border slopes outwards and downwards (adventrally). The posterolateral corners are angled and lie below the convexity of the acrolobe. The intergenal processes appear to be very small. The axial furrows and the median preglabellar furrow are generally weak and incised with varying degrees of clarity.



6. *Pseudagnostus papilio* sp. nov. reconstruction (a) based on cephalon CPC 8447, x12; (b) pygidium based on CPC 8448, x14.

The glabella is subcylindrical in shape, with slight anterior tapering. The posterior glabellar lobe, which is clearly defined only at the rear, is bulbous and elevated, posteriorly rounded or very obtusely angled; anteriorly it is effaced. The anterior and median lateral lobes are partly effaced and arranged in the shape of a clover leaf. The rhomb-shaped anterior lobe is separated from the median lateral lobes by faint furrows which converge on the anterior end of the glabellar axial node. The median lateral lobes flank the axial node as low swellings differentiated from the posterior lobe by faint forward directed furrows. As far as can be judged the axial node lies a little to the rear of the midpoint of the cephalon. The basal glabellar lobes are conspicuous, triangular, and emphasized by the strong convexity of the posterior lobe. On some specimens they are indistinct anteriorly. Lightly impressed muscle scars are visible on CPC 8443 (Pl. 1, fig. 2) occupying similar positions to those of *Pseudagnostus*

prolongus (cf. Lochman & Hu, 1959, p. 412, text-fig. 1) and *P. convergens* Palmer (1955, pl. 20, fig. 13).

Short, faint, disconnected scrobicules are evident around the periphery of the acrolobe on latex casts taken from the external moulds of many specimens (see CPC 8444, Pl. 1, fig. 1). Otherwise the cephalic surface is smooth or has a very faint granulosity which probably reflects the texture of the enclosing matrix.

The pygidial outline is ovoid, like that of the cephalon. In small specimens, having a maximum pygidial length (sag.) between 2 and 3 mm, the postero-lateral flanks appear to converge rapidly towards the posterior, but this is not quite so evident in larger specimens. The pygidial border is narrow, sagittally 5-10 percent of the pygidial length. It is slightly upturned (addorsal) in contradistinction to that of the cephalon, which slopes downwards (adventral). In most specimens the acrolobe is distinctly constricted, certainly more so than that of the cephalon. The axis is fairly well defined, the enclosing axial furrows tapering slightly backwards. The transverse furrow between the first and second axial rings is generally obliterated, although traces may be observed abaxially (e.g. CPC 8445, Pl. 1, fig. 8). The pygidial axial node lies on the second axial segment and extends backwards on to the front part of the deuterolobe. No third axial segment has been observed, nor any trace in the form of vestigial lobes. The accessory furrows which define the deuterolobe are very faint, especially abaxially, and are altogether effaced on large specimens. The deuterolobe itself is depressed, posteriorly rounded, and differentiated from the anterior pleural lobes by a faint change in surface convexity. Faint notular lines are preserved on the deuterolobe of some specimens. A terminal axial node is, however, invariably present. The posterolateral margins bear a pair of very small spines which are easily destroyed during preparation. These are thorn-like and are projected outwards from the margins and slightly downwards (see CPC 8446, Pl. 1, fig. 6). They are placed well in front of the posterior termination of the deuterolobe. The pygidial surface is smooth or very faintly pitted (CPC 8445, Pl. 1, fig. 8).

Comparisons and differences. In many species of *Pseudagnostus* the furrows of the cephalon and pygidium are virtually effaced externally, although they may be present on the internal mould, a fact well illustrated by Bell & Ellinwood (1962, pl. 51, figs 7, 11). *Pseudagnostus papilio* is such an effaced species, but the dorsal furrows are faint even on the internal mould. As such this species is readily differentiated from the species listed above that are preserved en grande tenue. Degree of effacement distinguishes *P. papilio* from such species as *P. cyclopyge* (Tullberg), *P. communis* (Hall & Whitfield), *P. josepha* (Hall), and *P. chinensis* (Dames), in which the dorsal furrows are less distinct than in species en grande tenue. The degree of effacement of *P. papilio* is most comparable to that of *P. obsoletus* Lermontova, 1951, *P. convergens* Palmer, 1955, *P. clarki* Kobayashi, 1935, and *P. prolongus* (Hall & Whitfield) *sensu* Palmer, 1960.

Pseudagnostus obsoletus, known from the latest Upper Cambrian of Boshche-Kul, Kazakhstan, is similar to *P. papilio* in its cephalic and pygidial outlines and in its narrow borders. Specimens preserved with the test (Lermontova, 1951, Pl. 2, fig. 9) are similarly nearly completely effaced. The pygidium assigned to *P. obsoletus* (loc. cit., fig. 8) may be very closely compared to those figured here on Plates 1 and 2. *Obsoletus* and *papilio* may eventually prove conspecific, but it is not possible to be absolutely sure from study of Lermontova's text and illustrations. As I have no access to the type specimens of *P. obsoletus* I have considered the species better separated.

Pseudagnostus convergens, isolated by Palmer on account of its pygidial shape, the flanks strongly converging to the posterior, is in its outlines and in the position and size of its spines identical with *P. papilio*. The pygidial furrows, however, are somewhat less effaced; there are constant traces of the first transverse furrow on the axis. *P. convergens* is from the highest fauna of the Catlin Member of the Windfall Formation, which crops out in the Eureka district, Nevada, USA (Palmer in Nolan, Merriam, & Williams, 1956).

When preserved with the shell, *Pseudagnostus clarki* Kobayashi (= *Pseudagnostus laevis* Palmer, 1955) is a very smooth pseudagnostinid, but the internal mould has somewhat greater relief (Palmer, 1955, pl. 19, figs 8, 11; 1968, pl. 15, figs 10, 13, 14). The cephalic outline is rather more subcircular than that of *P. papilio*, and the pygidium, which is similar to those figured on Plate 2, figures 6, 7, is more strongly effaced. *P. clarki* is present in the fauna of the Bullwacker Member of the Windfall Formation, Nevada, and also occurs in rocks of Trempealeauan age described by Palmer (1968) from east-central Alaska.

As figured by Palmer (1960, pl. 4, figs 5, 6) *Pseudagnostus prolongus* (Hall & Whitfield) is also similar to *P. papilio*. The former, however, apparently lacks pygidial spines, whereas, though small, they are present in the Australian species. The specimens figured as *P. prolongus* by Lochman & Hu (1959, pl. 57, figs 7-16) have decidedly more quadrate outlines than *P. papilio*, but the pygidia do bear small spines. A specimen referred to *P. prolongus* by the same authors in 1960 (pl. 96, fig. 36) cannot be adequately assessed. Bell & Ellinwood (1962, p. 389), in discussing *P. communis* (Hall & Whitfield), recognized a gradation between species with readily visible dorsal furrows and those partly effaced. They placed *P. convergens* Palmer, *P. prolongus* (Hall & Whitfield) *sensu* Palmer, 1955, and Lochman & Hu, 1959, and *P. josepha* (Hall) *sensu* Fredrickson, 1949, all in the synonymy of *P. communis* (Hall & Whitfield).

PSEUDAGNOSTUS CLAVUS sp. nov.
(Pl. 3, figs 1-8; Text-fig. 7)

Name. Latin, *clavus*, a nail: referring to the studded or nailed appearance given by the notular lines of the pygidium.

Holotype. The internal mould of a pygidium (CPC 8453), which has an external counterpart (CPC 8452). This specimen, the most complete showing the diagnostic characteristics of the species, is illustrated on Plate 3, figures 5-7.

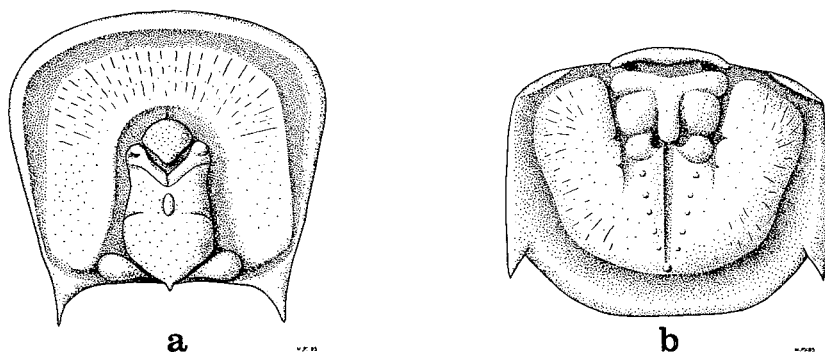
Material. Twenty-six specimens are known from three horizons in the Gola Beds; all are preserved as limestone moulds. Measured pygidia vary in total length (sag.) between 2.70 and 3.25 mm. The measured cephalae which are assigned to this species have lengths (sag.) between 2.60 and 4.00 mm.

Diagnosis. A species of *Pseudagnostus* with the following combination of characteristics: cephalon en grande tenue; with weakly constricted acrolobes; no preglabellar furrow; and small nodes on the anterolateral edges of the median lateral glabellar lobes. Pygidium with three axial segments; an axial node arising from the first axial segment; well defined notular lines and traces of both intra- and extra-notular areas; very wide posterior border; and spines which continue the line of the lateral pygidial margins.

Description. The cephalae assigned to *Pseudagnostus clavus* have subquadrate outlines, with sides diverging forwards from the posterolateral corners; posteriorly

their width (tr.) is 90-95 percent of the length (sag.), but anterolaterally the dimensions are very nearly equal. On this type of cephalon the border is narrow posterolaterally, becomes widest (exsag.) anterolaterally, and is as wide as 7-11 percent of the total cephalic length (sag.) anteriorly. The border consists of a narrow upturned rim and a shallow, but wide, concave marginal furrow. The cephalic acrolobe is visibly constricted; it has moderate convexity (tr. and sag.) and slopes strongly to the marginal furrow. There is no preglabellar median furrow, either on the mould or on the latex cast of the exterior. The axial furrows, however, are strongly defined.

The glabella is cylindrical, with a marked constriction near the middle (see CPC 8454, Pl. 3, fig. 3). The anterior lobe is small, rhomb-shaped, resting within strongly defined chevron-shaped anterior furrows which meet sagittally some way in front of the glabellar axial node. The median lateral lobes are poorly defined, subtriangular, and are bisected mesially by a short furrow leading backwards from the apex of the chevron of the anterior furrows. The furrows separating the median lateral lobes from the posterior lobe are indistinct. At the antero-lateral end of each median lateral lobe there is a small node, separated from the remainder of the lobe by an indistinct and shallow furrow. The posterior lobe is strongly elevated, especially at the rear, where it is strongly angled, culminating in a small node. The basal lobes are rather conspicuous flattened triangles, well separated from the glabella and spread out laterally. They are confluent below (ventral to) the posterior glabellar node. The glabellar axial node lies midway along the length of the glabella but only one-third the way along the cephalic length. The glabella is two-thirds the cephalic length (sag.) and two-thirds to three-quarters the length of the acrolobe (sag.).



7. *Pseudagnostus clavus* sp. nov., reconstruction of (a) cephalon based on CPC 8454, x10; (b) pygidium based on CPC 8453b, x11.

The surface of the acrolobe is faintly but densely scrobiculate. In addition a fine punctation is visible on limestone moulds blackened before coating with ammonium chloride (CPC 8454, Pl. 3, fig. 3).

The pygidium also has a quadrate outline; it is 10-20 percent wider (tr.) than long (sag.). The margins are straight, diverging backwards to the tips of the spines; the posterior margin is nearly square. The border is wide, posteriorly up to 17 percent of the total pygidial length (sag.), and flat; the marginal furrow is represented merely by a break in slope between the acrolobe and the margin, except anterolaterally where it narrows and deepens. The pygidial acrolobe is quite visibly constricted (see CPC 8452, Pl. 3, fig. 7). The margin of the acrolobe adjacent to the axial furrows is scalloped.

The axis is well defined anteriorly, three segments being clearly visible. The abaxial extremities of the first segment slightly overlap those of the second, and are quite strongly lobate. The first transverse furrows are curved forwards abaxially but are interrupted mesially by an axial node which originates on the first axial ring. The second axial ring is represented by swellings on either side of the axial node. The second transverse furrow is wide, shallow, and well defined compared with the faint first one. A pair of vestigial swellings, low and obscure, but nevertheless visible, represent the third pygidial segment. Strong axial furrows define the first two axial segments. Though they peter out at the level of the vestigial third they can be partly traced as extranotular furrows backwards from this level. The extranotular furrows enclose faintly convex areas delimited adaxially by two rows of notular lines, each apparently containing five notulae, which converge on the posterior terminal node at the extreme end of the deuterolobe. The notular lines start immediately behind the swellings of the vestigial third axial segment (Pl. 3, fig. 5) and enclose a depressed intranotular area, readily visible on CPC 8452 and 8451 (Pl. 3, figs 7, 8) as a longitudinal groove upon the sagittal line. The deuterolobe is weakly developed, the accessory furrows being extremely faint or absent altogether. The anterior axial node lies across the second axial segment. Its origin, however, appears to be from the first segment, because a forward directed tongue from the node bisects this ring (Pl. 3, fig. 7). In profile (Pl. 3, fig. 6) the node is highest where it posteriorly overlaps the second transverse furrow.

A pair of spines is present on the posterolateral margins of the pygidium. They are small and delicate and rise from the dorsal surface of the rim, projecting directly the line of the lateral pygidial margins backwards and very slightly upwards. The ends of the spines lie in advance of a transverse line drawn across the rear of the deuterolobe.

The surface of the pygidial acrolobe is scrobiculate; faint scrobicular pitting is seen especially on the lateral and posterolateral flanks.

Comparisons and differences. *Pseudagnostus clavus* belongs to the group of *Pseudagnostus* species with quadrate cephalic and pygidial shields. The cephalon is preserved with relief, the pygidium partly effaced.

Pseudagnostus canadensis (Billings, 1860), from Lévis, Quebec, as refigured by Rasetti (1944, p. 234, pl. 36, figs 8-13), has similarly shaped dorsal shields, but considerably greater surface relief. A preglabellar median furrow may be discerned in the cephalon, and the chevron-shaped anterior glabellar furrows are not developed. The pygidium has more extensive pleural acrolobes and the marginal spines extend farther rearwards.

The cephalon of *Pseudagnostus vulgaris*, from the Tolstochikha suite, Orlinaya Mountain, Salair, figured by Rosova (1960, pp. 14-6, pl. 1, figs 5-13), are insufficiently preserved to allow detailed comparison. They do, however, possess a preglabellar median furrow which is not present in *P. clavus*. A specimen from Alaska figured under *P. vulgaris* by Palmer (1968, B30, pl. 12, figs 5, 6) lacks the deep chevron-shaped anterior glabellar furrows characteristic of *P. clavus*. Pygidia of *P. vulgaris* are quite similar to those of the Australian species, being differentiated most readily by their posteriorly drawn out deuterolobes. In Alaska *P. vulgaris* is associated with *P. clarki*.

Pseudorhaptagnostus simplex Lermontova (1951, pp. 12-3, pl. 2, figs 11-17), from Boshche-Kul, Kazakhstan, has been attributed with two types of cephalon. One of these, that with the quadrate outline (Lermontova, 1951, pl. 2, fig. 15),

is possibly similar to that of *P. clavus*, but the illustration leaves much to be desired. Pygidia of *P. simplex* are more effaced than those of *P. clavus*, but nevertheless morphologically close. The axial node is shorter and the marginal spines possibly further forwards. *P. simplex* is associated with *P. obsoletus*, a species which may prove conspecific with *P. papilio*.

Euplethagnostus subangulatus Lermontova (1940, p. 126, pl. 49, figs 15, 15a) and *Pseudorhaptagnostus punctatus* Lermontova (1940, p. 126, pl. 49, figs 14, 14a), both from Orlinaya Mountain, Kuznets Basin, Salair, though poorly illustrated, are obviously morphologically related to *P. clavus*. Preglabellar median furrows are present in the cephalon of each, but their pygidia are quite similar. Not a great deal distinguishes *Euplethagnostus subangulatus* Lermontova from *Pseudagnostus vulgaris* Rosova, or *Pseudorhaptagnostus punctatus* Lermontova from *Pseudagnostus cavernosus* Rosova.

Pseudagnostus quadratus Lazarenko (1966, pp. 46-7, pl. 1, figs 24-9), from the Irvingella-Cedarellus felix and Plicatolina perlata Zones of the Olenek River, north Siberian Platform, has a cephalon with anteriorly tapered glabella lacking glabellar furrows. As such it is quite distinct from that of *P. clavus*. The accessory furrows in its pygidium are clearly defined, and the marginal spines sited well to the rear of the back of the deuterolobe.

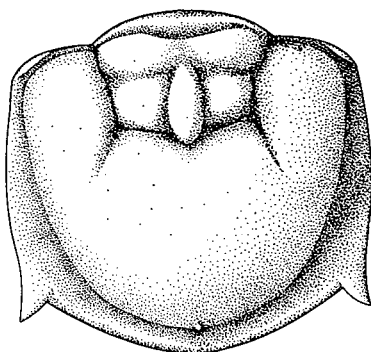
Pseudagnostus longicollis Kobayashi (1966, p. 283, fig. 7), from Cambro-Ordovician strata of Hungluohsien, Jehol, north China, is similar to *P. clavus* in both cephalic and pygidial characteristics. Glabellar features cannot be satisfactorily determined from Kobayashi's figure, but the pygidium is readily distinguished from that of *P. clavus* by its unusually long marginal spines.

An even closer example, however, is the Tremadocian species from the Tiñu Formation of Oaxaca, Mexico, described by Robison & Pantoja-Alor (1968, p. 780, pl. 97, fig. 23) as 'undetermined pseudagnostid.' This species has the quadrate cephalic shield, with wide upturned borders, nearly an exact replica of *P. clavus*. The glabellar and preglabellar median furrows are strongly incised, however, and the median lateral glabellar lobes are wider (sag.) at their junction on the sagittal line. In addition, the prominent basal lobes differentiate the Mexican species. Notwithstanding the obvious differences due to relief and degree of effacement the Mexican and Australian species must be closely related.

PSEUDAGNOSTUS sp. I (Pl. 2, figs 3-5; Text-fig. 8)

Pseudagnostus sp. I is described from a single pygidium (CPC 8457) which was prepared from coarse-grained calcarenite at locality B520. The length of this pygidium is 3 mm. Although it is distinct from other species of *Pseudagnostus* described here, insufficient material is available for proper treatment and accordingly the species is left under open nomenclature.

Pseudagnostus sp. I is undoubtedly related to *P. papilio*. It is readily differentiated, however, by the nature of its posterolateral spines. These are quite prominent and sited farther to the rear than those of *P. papilio*. Their position and size give rise to a straighter posterior margin, which comes to a decided culmination sagittally. The borders are somewhat broader; the transverse furrow between the first and second axial segments is completely absent; and the axial node does not overlap to the same extent on to the anterior edge of the deuterolobe.



8. *Pseudagnostus* sp. I, reconstruction based on CPC 8457, x15.

PSEUDAGNOSTUS sp. II
(Pl. 2, figs 6, 7)

This species is known from several imperfectly preserved pygidia which are rather larger than the majority of pseudagnostinids found in the Gola Beds. Specimen CPC 8458 has a length of 5.10 mm and CPC 8459 attains an estimated 5.60 mm. Both specimens figured here are from the coarse-grained calcarenites of B520. Others occur at K101 and K102.

Pseudagnostus sp. II is noted for its strongly constricted acrolobe, almost completely effaced furrows, and wide borders which are about 12 percent of the total length posteriorly. Faint axial furrows flanking the anterior part of the axis are the only traces of furrows preserved. Even the axial node is nearly effaced.

These features serve to differentiate *Pseudagnostus* sp. II from *P. papilio*, although it is conceivable that the former are merely large specimens of the latter. In that event trends operating during morphogenesis in the pygidium are towards complete effacement of the furrows and axial node, and the widening of the borders.

PSEUDAGNOSTUS sp. III
(Pl. 2, fig. 8)

Pseudagnostus sp. III is known from three indifferently preserved pygidia. That illustrated here on Plate 2, figure 8 (CPC 8460) is a large specimen with a length of 4.90 mm. It is characterized by an unconstricted pygidial acrolobe, wide borders, and completely effaced axial, transverse, and accessory furrows. The deuterolobe is completely undifferentiated from the anterolateral pleural lobes, and the axial node has nearly disappeared. Small spines are situated in advance of the rear of the acrolobe (see left hand side of the illustrated specimen).

Rasetti would no doubt include this species in his genus *Litagnostus*. Palmer (1955, p. 92) has discussed the relationship between effaced species of *Pseudagnostus* and those of *Litagnostus*. *Pseudagnostus* sp. III is comparable with his *Litagnostus expansus* from the Bullwacker Member of the Windfall Formation, Eureka district, Nevada. Attention is drawn to the faintness of the axial node

in *Pseudagnostus* sp. III and to the pygidial spines. In *Litagnostus*, no spines are recorded on any of the known species, and the axial node is generally prominent. I feel that sufficient characteristics are observable to retain this species in *Pseudagnostus* in spite of its severe effacement.

Pseudagnostus sp. III was obtained from locality B520.

Order PTYCHOPARIIDA Swinnerton, 1915

Suborder PTYCHOPARIINA Richter, 1913

Superfamily REMOPLEURIDACEA Hawle & Corda, 1847

Family REMOPLEURIDIDAE Hawle & Corda, 1847

Subfamily RICHARDSONELLINAE Raymond, 1924

Genus RICHARDSONELLA Raymond, 1924, emend. Rasetti, 1944

Type species. *Dikelocephalus megalops* Billings, 1860, p. 311, fig. 9, from the Lévis conglomerates of Lévis, Quebec.

Other species. A second species described by Billings (1860, p. 312, fig. 10) as *Dikelocephalus cristatus* was referred to *Richardsonella* by Raymond (1924, p. 440). This, and the type species, were refigured by Rasetti (1944, pl. 39) along with several new taxa: *Richardsonella convexa*, *R. elongata*, and *R. unisulcata*. All the species handled by Billings and Rasetti were from the Lévis conglomerates of Lévis, Quebec. A suite from the Gorge Formation of Highgate Falls, Vermont, described by Raymond (1937), included the species *R. arctostriata*, *R. granulata*, and *R. spiculata*. *Richardsonella subcristata* was described by Rasetti (1959, pl. 55, figs 15-18) from a loose block of Grove Limestone found near Frederick in Maryland. In the western Cordillera species of *Richardsonella* have been described by Kobayashi (1935a, p. 55, pl. 9, fig. 9) — *R. eurekaensis* — from the Eureka district, Nevada, and by Palmer (1968) from localities in east-central Alaska. Palmer's species include *R. nuchastria*, *R. quadrispinosa*, *R. cf. quadrispinosa*, and *Richardsonella* spp. 1-4. Of the last *Richardsonella*? sp. 2 is comparable to the species described here as '*Tostonia*' sp., and the pygidium attributed to *Richardsonella* sp. 3 probably belongs to the new genus *Sigmakainella*, which is described further below. *Richardsonella variagranula* has been described by Robison & Pantoja-Alor (1968, pp. 794-5, pl. 104, figs 5-11) from the Tiñu Formation of Nochixtlán, Oaxaca district, Mexico. Described below are *Richardsonella laciniosa* and *R.(?) kainalliformis*, from western Queensland. Several undescribed species are present in the section at Black Mountain, also in western Queensland. The species described under *Richardsonella* and noted above range in time from the Franconian into the Trempealeauan/Tremadocian.

Comments. Rasetti (1944, p. 255) has examined plastotypes of species of *Protapatocephalus* Raymond, 1937, and *Richardsonella* Raymond, 1937, and declared these genera to be synonymous. In emending the generic diagnosis of *Richardsonella*, Rasetti (1944) restricted the specific content of the taxon, but in spite of these modifications a considerable amount of variation remains within *Richardsonella*, and the concept of the genus is far from clear. The last is aggravated by the incomplete nature of the types of *R. megalops* (Billings), and

by a total absence of articulated specimens. As refigured by Rasetti (1944, pl. 39, figs 48, 49) the types of *R. megalops* are two incomplete cranidia. Neither the full extent of the prelabellar area, nor the posterolateral limbs, can be deduced from either, and no pygidium was included in the type series. Discernible characteristics include: a subparallel-sided glabella, tapering only slightly forwards; three pairs of glabellar furrows, the anteriormost being very faint; a long (sag.) prelabellar field flanked by an evenly narrow (sag.) anterior border; long palpebral lobes, extending backwards to the occipital furrow, close to the glabella posteriorly but apparently not contacting the axial furrows; and narrow palpebral areas.

Rasetti and Palmer have included in *Richardsonella* cranidia with very short prelabellar fields, thickened anterior cranidial borders, and with varyingly shaped and furrowed glabellae. The absence of articulated specimens has led to the assignment of a wide selection of pygidia, variously shaped and segmented, but invariably spinose. Similarly, librigenae with advanced and non-advanced genal spines have both been placed in the genus. I concur with Palmer (1968, B78) in regarding as distinct a generic group based on *R. unisulcata* Rasetti. This would include species with forward-tapering glabella, posteriorly convex (sag.), narrow (sag.) prelabellar field, and thickened anterior cranidial border. The pygidium which probably belongs to this type of cranidium has four or five axial segments, and four pleural segments, the latter terminating in stout free spines, all directed rearwards. Such species may be considered referable to the genus *Pseudokainella* Harrington, 1938, being comparable to the type species *P. keideli* from the Upper Tremadocian of Argentina. *Richardsonella unisulcata*, *R. convexa*, *R. cristata*, from Lévis, and *R. nuchastria*, *R. quadrispinosa*, *R. cf. quadrispinosa*, from Alaska, might be accommodated within *Pseudokainella*.

Of the Australian material described below, *R. laciniosa*, the most common species, has a prelabellar area similar to that of *R. megalops*, *R. elongata*, or *R. eurekensis*, a parallel-sided glabella most similar to *eurekensis*, and rather widely spaced palpebral lobes which differentiate it from all other described species of the genus. This type of cranidium is associated with pygidia similar to those assigned by Raymond (1937) to *R. arctostriata* and *R. spiculata*. These are wider than long, with three to five axial segments and three to five pleural ones which terminate in saw-tooth spines, and quite distinct from those referred to, say, *R. quadrispinosa*, which have long free spines.

RICHARDSONELLA LACINIOSA sp. nov.
(Pl. 6, figs 1-5; Pl. 7, figs 1-4; Text-fig. 9)

Name. Latin, *laciniosa*, indentate or jagged: referring to the nature of the pygidial margin.

Holotype. The pygidium (CPC 9702), illustrated on Plate 7, figure 1.

Material. *Richardsonella laciniosa* occurs commonly in the higher levels of the Gola Beds, but is rarely well preserved. One hundred and twenty-one identifiable fragments were recovered from locality B750; of these twelve cranidia and eight pygidia were assessed for descriptive purposes. Heads and tails were matched on relative abundance within the same deposit (B750). The specimens selected for figuring show the complete range of morphological variation discussed in the ensuing description.

The preserved remains have been well sorted; few very small specimens and no definite thoracic materials have been observed. The range of cephalon noted varies in length between 5.00 and 6.26 mm; pygidial lengths range between 2.80 and 4.25 mm. Selected measurements and proportions are included in Table 2.

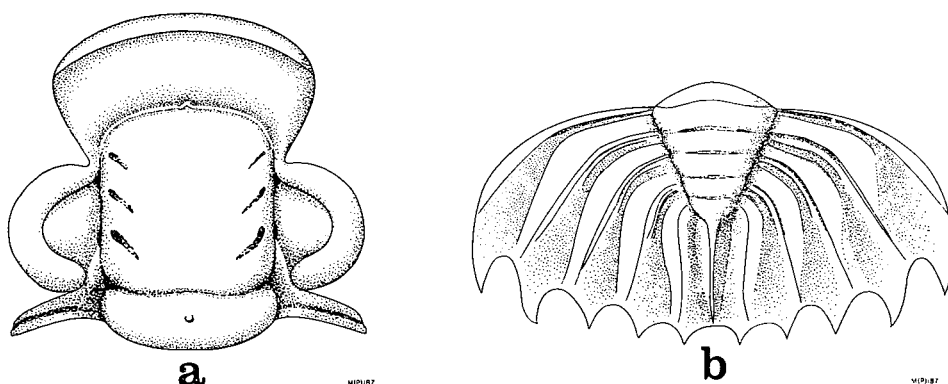
Occurrence. *Richardsonella laciniosa* appears to be confined to sandy calcilititic sediment, occurring commonly at B750 and much less so at B752. Fragments of a species of *Richardsonella* were also recovered from horizons B520B and 520A.

Diagnosis. A species of *Richardsonella* with the following cranial characteristics: glabella rectangular; large eyes, extending backwards across the postero-lateral limbs, terminating anteriorly as eye lines, close to but not contacting the axial furrows posteriorly; baculate; a sagittally placed glabellar median node on the anterior glabellar contour; a parafrontal band similarly placed; 'fingerprint' prosopon; the pygidium is spinose.

Description. The glabella is rectangular, anteriorly very gently rounded, bearing two faint pairs of glabellar furrows, obliquely directed to the posterior, which do not reach the axial furrows. The axial furrows defining the sides of the glabella are constricted at the base of the glabella, at the median lateral lobes, and at the point where they are joined by the eye lines. At these points the floor of the axial furrows is pitted (see CPC 9699, Pl. 6, fig. 1). Anteriorly and sagittally the glabella bears a small node (see same specimen). Running concentric to the anterior contour is a narrow rim (CPC 9700, Pl. 6, fig. 5), the parafrontal band. The glabella occupies 54-60 percent of the total cephalic length (sag.).

The occipital furrow is well-defined, deepened abaxially. The occipital ring is decidedly wider (tr.) than the base of the glabella; it bears a small indistinct median node.

The palpebral lobes are large and crescentic in plan, extending from near the anterior edge of the occipital ring to a point lying in front of the median lateral glabellar furrows; so the small eye index lies between 57 and 66 percent and the large eye index between 67 and 78 percent. Anteriorly the palpebral lobes fade into poorly defined eye lines which cut the axial furrows a short way behind the antero-lateral corners of the glabella. A narrow parafrontal band may continue the eye lines around the front of the glabella, but there is no directly visible confluence between band and lines. Posteriorly the palpebral lobes overlap the narrow posterolateral limbs, and are separated from the glabella and axial furrows by low baculae (Pl. 6, figs 1, 2, 3). The palpebral furrows are ill defined, and the palpebral areas have low convexity (tr.). The posterolateral limbs are narrow and apparently short (tr.), but in none of the available specimens has the distal end been definitely observed. The anterior sections of the facial suture diverge at angles between 70 and 90 degrees. This angle becomes less as they curve inwards on approaching the anterior border. The preglabellar field and border together occupy 27-31 percent of the total cephalic length (sag.), the border alone being 5-9 percent. The length of the preglabellar field is 32-41 percent of the width (tr.). It is gently convex (sag.) and bears, in all specimens, a radiating network of ramified caeca which branch just before they reach the anterior marginal furrow. A series of punctae lies along the length of this furrow, each embraced within the arms of a branching caecum. An indistinct dark patch around the anterior frontal node of the glabella may be interpreted as a parafrontal band (after Öpik, 1961, p. 436). The anterior border is gently curved, and the border itself bears a series of anastomosing striae which are divorced from the caecal system, being a part of the prosopon.



9. *Richardsonella laciniosa* sp. nov., reconstruction of (a) cranidium based on CPC 9695, x8; (b) pygidium based on CPC 9703, x8.

The glabella and occipital ring carry a coarse 'fingerprint' prosopon.

The pygidia assigned to *Richardsonella laciniosa* (Pl. 7, figs 1-4) are moderately large, twice as wide as long. The axis, moderately convex (tr.), is composed of four clearly defined segments, together with a bluntly rounded terminal piece which is projected to the posterior margin by a postaxial ridge corresponding to the line of fusion of the fifth pair of pleurae. The five pleural segments are delicately fluted. Each pleuron widens slightly distally and each possesses an articulating band which occupies the greater part of the propleuron. The pleural furrows are deep proximal to the axial furrows, but at the geniculation sweep steeply backwards to the margin, rapidly narrowing the opisthopleuron and correspondingly widening the propleuron. The interpleural furrows are indistinct, their presumed courses being indicated on Text-figure 9. The margin is serrate: the spines are short and broad-based. The prosopon is of raised terrace lines around the periphery of the pygidium, including the spine bases, and irregular hieroglyph-like raised lines may be present on the posterior axial segments.

The nature of the thoracic segments and the hypostome is unknown.

Selected measurements and cephalic proportions are presented on Table 2. Measurements on the solitary specimen which represents *Richardsonella(?) kainelliformis* sp. nov. are also included.

Comparisons and differences. The combination of parallel-sided glabella and widely spaced palpebral lobes serves to differentiate the cranidium of *Richardsonella laciniosa* from other species assigned to the genus. Otherwise the cranidium is comparable with that of *R. megalops* (Billings, 1860). *R. laciniosa* is also similar to *R. elongata* Rasetti in the nature of its preglabellar area and disposition of the preocular branches of its facial suture. *R. eurekaensis* has comparable glabellar tapering, but its palpebral lobes (as illustrated by Kobayashi, 1935a, pl. 9, fig. 9) are closer to the glabella. *Kainella primigena* Kobayashi (1953, pl. 4, figs 9, 9b), a species from the Cambro-Ordovician of the Yunnan-Tonkin border, differs in essentially similar characteristics. The cranidium figured by Palmer (1968, pl. 14, fig. 5) as *Richardsonella* sp. 3 has a similar small amount of glabellar tapering, but it has a shorter (sag.) preglabellar field and longer (sag.) border.

TABLE 2

Specimen	L _c	G _n :L _c	G:L _c	L _{pf} :L _c	L _{pf} :W _{pf}	L _{bo} :L _c	A:G	A:G _n
<i>Richardsonella laciniosa</i>								
CPC 9699	5.05	69.56	58.42	27.89	40.68	5.71	78.12	65.61
CPC 9695	5.10	69.61	54.68	28.74	32.11	7.43	76.35	59.96
CPC 9706	5.10	71.47	57.29	30.18	34.03	5.48	77.61	62.22
CPC 9707	5.40	70.37	55.55	31.48	39.53	8.33	75.01	59.21
CPC 9708	5.45	70.08	57.33	30.54	36.02	7.22	71.20	58.25
CPC 9696	5.50	70.09	56.44	36.51	34.46	8.84	75.11	60.47
CPC 9701	5.50	72.61	56.61	26.68	32.86	6.30	74.16	59.17
CPC 9709	5.90	69.61	58.68	29.07	33.38	9.29	67.42	56.83
CPC 9710	5.90	71.09	57.73	28.24	33.11	8.35	71.90	58.38
CPC 9694	6.05	72.43	56.87	27.38	34.77	7.14	74.60	58.66
CPC 9711	6.25	70.74	59.89	30.38	36.00	7.90	—	—
<i>Richardsonella</i> (?) <i>kainelliformis</i>								
CPC 9712	13.80	68.58	59.53	29.80	24.89	—	67.14	58.28

Richardsonella cristata Rasetti, *R. unisulcata* Rasetti, and *R. convexa* Rasetti, all from Lévis, Quebec, have distinctly forward tapering glabellar flanks, short preglabellar fields, and thickened anterior borders. These, together with *R. quadrispinosa* Palmer, and *R. nuchastria* Palmer, might be better placed in the genus *Pseudokainella*.

The pygidium of *Richardsonella laciniosa* is most similar to that of *R. arctostriata* Raymond (1937, pl. 1, fig. 7). In both species the pleura are delicately fluted and the serrated pygidial margins have five pairs of short, triangular spines. Whereas the pygidium of *R. laciniosa* has four axial segments, there are only two in *R. arctostriata*. These pygidia are quite different from that ascribed to *R. unisulcata* by Rasetti (1944, pl. 39, fig. 55), which has three pairs of backward free spines. The orientation of the marginal spines of *R. laciniosa* is similar to that shown by *Apatokephalus serratus* (Boek), a Lower Ordovician trilobite from Scandinavia; to that of *Elkia nasuta* (Walcott, 1884) from the Trempealeauan of the Eureka district, Nevada; and to that referred by Palmer (1960, pl. 10, fig. 3) to *Sigmocheilus serratus* Palmer, a species from the Dunderberg Shale of the same area.

RICHARDSONELLA (?) KAINELLIFORMIS sp. nov.
(Pl. 7, figs 5, 6; Text-fig. 10)

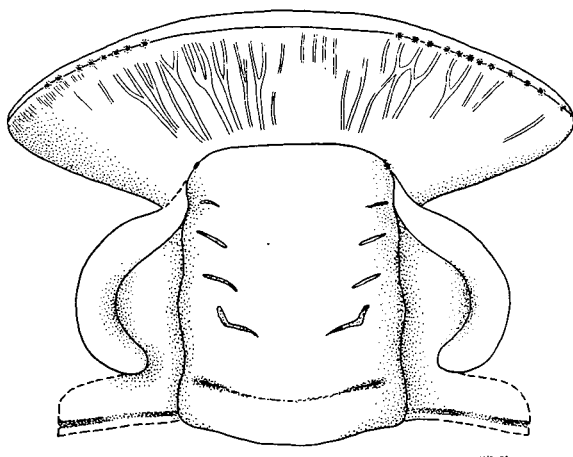
Name. Latin, *forma*, shape, suffixed to generic nomen *Kainella*: referring to the similarity of this species to those of *Kainella*.

Holotype. CPC 9712a, a cranium, with counterpart CPC 9712b, illustrated on Plate 7, figures 5 and 6.

Material. The species is known from a single limestone mould, with counterpart, of a cranium. A latex impression from the external mould is figured alongside the internal. The specimen is large: its sagittal length is 13.80 mm. Selected measurements and proportions are included in Table 2.

Occurrence. The species occurs in sandy calcilutite at locality B750.

Diagnosis. A species questionably assigned to *Richardsonella* with very broad (tr.) preglabellar field but narrow (sag.) anterior border; preocular sections of



10. *Richardsonella*(?) *kainelliformis* sp. nov., reconstruction based on CPC 9712a, x4.

the facial suture diverging forwards at an angle approaching 140 degrees; eyes large but not reaching the axial furrows or the posterior border furrow; glabella parallel-sided.

Description. The glabella is similar to that of *Richardsonella laciniosa* sp. nov., parallel-sided and bluntly rounded anteriorly. The preoccipital and median lateral glabellar furrows are faint, obliquely directed rearwards, and isolated from the axial furrows. Short, very faint anterior lateral furrows are present close to the axial furrows. The glabellar outline is constricted at the preoccipital lobes, the median lateral lobes, and at the confluence of the anterior lateral furrows with the axial furrows. At the last level the axial furrows are overdeepened, and additional pits may be present at the anterolateral corners of the glabella. A faint median glabellar node is just visible on the anterior contour of the frontal lobe on the latex cast (Pl. 7, fig. 5), as is a faint parafrontal band. The glabella is 60 percent of the total cephalic length (sag.).

The occipital furrow is as faint as the glabellar furrows and does not reach the axial furrows laterally. The occipital ring is wider (tr.) than the base of the glabella, low in lateral profile.

The palpebral lobes are large and subcrescentic in plan, extending from the level of the anterior glabellar furrows to the occipital furrow. Posteriorly they are separated from the axial furrows by a measurable extent of fixigena, and similarly from the posterior border furrows. Anteriorly the palpebral lobes merge into faint eyelines which cut the axial furrows in front of the anterior glabellar furrows. The palpebral furrows are well-defined; the palpebral lobes, lacking convexity, slope gently to the axial furrows. The small eye index for the holotype is 58 percent and the large eye index 67 percent.

The nature of the posterolateral limbs is not known, that on the right hand side being broken off below the back of the eye, and that on the left being altogether absent. Those shown on Text-figure 10 are tentatively reconstructed. The anterior sections of the facial suture are straight proximally, distally slightly curved, diverging forwards at an angle of about 140 degrees. The preglabellar field is long (sag.) and wide (tr.), the length being 25 percent of the breadth.

The anterior border is narrow (sag.); the marginal furrow pitted. Ramified caeca crossing the preglabellar field are clearly visible. They radiate outwards from the preglabellar furrow, branching and braiding about one-half to two-thirds the way along the preglabellar field; the branches so formed pass between the pits of the marginal furrow.

No surface prosopon is visible.

Comparisons and differences. *Richardsonella*(?) *kainelliformis* resembles species of *Kainella* in its wide (tr.) preglabellar field and its widely divergent preocular facial sutures. In particular it resembles *K. meridionalis* Kobayashi (1945b, pl. 11, figs 5-7), from the lower Tremadocian of Argentina, and *K. primigena* Kobayashi (1953, pl. 4, fig. 9a), from Cambro-Ordovician strata on the Tonkin-Yunnan border, North Vietnam. It is differentiated from *Kainella* species on its longer (sag.) preglabellar field, very narrow border (sag.), and eyes set farther from the axial furrows. In the length of its preglabellar field *Richardsonella*(?) *kainelliformis* approaches species of *Richardsonella* and its glabellar characteristics are essentially similar to those of *R. laciniosa*. The width (tr.) of the preglabellar field is greater than any other described species of *Richardsonella*. As it appears to bridge the gap between the latter and *Kainella* a new genus could conceivably be erected for it. At the present time, however, insufficient material is available.

RICHARDSONELLA sp.
(Pl. 19, figs 5, 7)

Two librigenae are figured on Plate 19 as *Richardsonella* sp. They could be assigned to either *R. laciniosa* or *R? kainelliformis*; probably they both belong to *laciniosa*.

The cheeks are relatively narrow (tr.), but bear strongly imprinted marginal furrows. The long spines which carry the lateral margins backwards are not advanced. These and the lateral borders bear anastomosing striae similar to those found on the anterior cranial border of *R. laciniosa*. Additionally, specimen CPC 9726 (Pl. 19, fig. 7) has a readily visible caecal network which radiates from the vicinity of the palpebral lobe.

Both specimens are from locality B750.

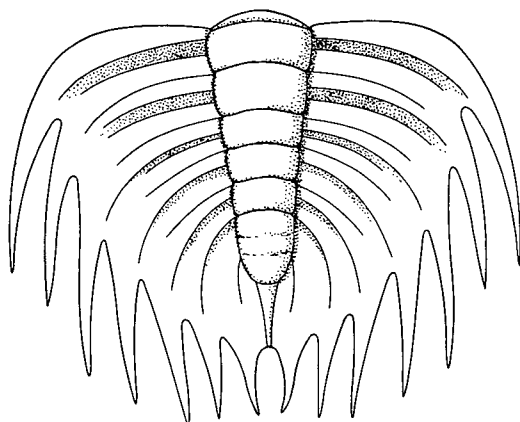
Genus TOSTONIA Walcott, 1924

‘TOSTONIA’ sp.

(Pl. 9, fig. 4; Text-fig. 11)

Three fragmentary pygidia from sandy calcilutite at locality B750 allow the pygidium of this richardsonelloid species to be reconstructed with some certainty.

Description. The axis is long (sag.) and narrow, reaching to the posterior marginal furrow. It is composed of an estimated seven axial rings, and an indistinct terminal piece. A strong postaxial ridge runs from the axial termination to the posterior margin of the pygidium. There are six flat pleural segments, and a possible seventh may be inferred. Each pleural segment bears a pair of shallow furrows which extend nearly to the pygidial margins, and each has additionally a pair of long delicate marginal spines derived entirely from the anterior pleural



M(P)189

11. '*Tostonia*' sp., reconstruction based on CPC 9713, x6.

bands. In all there are seven pairs of spines, those at the rear of the pygidium being very short. The interpleural furrows are very weak, and there is a poorly defined marginal furrow which is traversed by the distal ends of the pleural furrows. The only visible prosopon is represented by raised lines on the edges of some of the spines.

Comments. *Tostonia* is based on *Dicellosephalus iole* Walcott (1884, pp. 43-4, pl. 10, figs 19, 20), and is known from both Catlin and Bullwacker Members of the Windfall Formation of the Eureka district, Nevada (Palmer *in* Nolan et al., 1956). *Tostonia iole* (Walcott) was originally described from a cranidium, but later Walcott (1925, p. 117, pl. 18, figs 13, 14) referred associated pygidia to the species. Palmer (1968, p. B78) considers the head and the tails incorrectly matched, and would assign the latter to *Richardsonella*. Though I agree with Palmer on the matter of Walcott's assignments I cannot readily accept, at the present time, the inclusion of these pygidia in *Richardsonella*, which I consider to have a pygidium of the *R. laciniosa* type.

The Australian material is very close to those pygidia described by Walcott (*loc. cit.*), differing in having an additional pair of marginal spines (seven pairs); those illustrated by Walcott (1925) have only six pairs. The specimens at hand are also comparable to the pygidium from the early Trempealeauan of Alaska which Palmer (1968, p. B79, pl. 14, fig. 16) describes as *Richardsonella*(?) sp. 2.

In view of the uncertainty surrounding the correct generic status of pygidia of the '*Tostonia*' type I retain the original reference of Walcott (1925). I place the generic nomen in inverted commas to distinguish the species from those of *Tostonia sensu stricto*, and the nomenclature is left open. It is possible that the pygidium described here as '*Tostonia*' sp. may match the cranidium figured as *Richardsonella*(?) *kainelliformis* (Pl. 7, figs 5, 6). In this event the combined species would be referred to a new genus of Richardsonellinae.

Genus SIGMAKAINELLA nov.

Type species. *Sigmakainella translira* gen. et sp. nov., from the late Upper Cambrian Gola Beds of western Queensland.

Name. Greek, *sigma*, the letter 'S,' whence sigmoid: this prefixing the generic nomen *Kainella* refers to the sigmoidal courses of preocular sections of the facial suture.

Diagnosis. A genus of Richardsonellinae with cephalon similar to that of *Kainella*, but with a pygidium similar to *Hungaia*. The cephalon is distinguished by the following character complex: short (sag.) preglabellar field; thick anterior border (sag.); strongly sigmoidal preocular branches of the facial suture; glabella tapering forwards, gently rounded anteriorly; eyes large, close to the glabella, with narrow (tr.) palpebral areas. The pygidium has strongly swept back pleurae running parallel to the sagittal line; a short axis; and four pairs of fringe spines.

Comparisons and differences. The cephalon of *Sigmakainella* is very similar to that of *Kainella*, but few species of the latter possess the strongly sigmoidal preocular branches of the facial suture. Only one, referred by Walcott (1884, p. 90, pl. 1, fig. 10) to *Dicellosephalus inexpectans*, and by Kobayashi (1953, p. 44) to *Kainella*, is at all comparable. This is yet another species from the late Upper Cambrian of the Eureka district, Nevada, having affinity with Australian material. It may well be an American representative of *Sigmakainella*, but as Walcott's original illustration is a rather indistinct line drawing the species requires re-examination for generic confirmation.

The pygidium of *Sigmakainella* has strongly swept-back pleurae and morphologically lies between *Kainella* and *Hungaia*. It possesses four pairs of marginal spines, however, somewhat similar to those of *Pseudokainella lata* (Kobayashi, 1935b) *sensu* Harrington & Leanza (1957, fig. 53), but farther extended posteriorly. The specimen figured by Palmer (1968, pl. 14, fig. 6) as *Richardsonella* sp. 3, from the late Franconian of Alaska, possesses all the characteristics of *Sigmakainella*, and in particular those of *S. translira*, the type species of the new genus.

SIGMAKAINELLA TRANSLIRA gen. et sp. nov.
(Pl. 8, figs 1-6; Pl. 9, figs 3, 6; Text-fig. 12)

Name. Latin, *lira*, ridge: *translira* refers to the transversely ridged prosopon of the pygidium.

Holotype. The cranidium CPC 9715a, with counterpart CPC 9715b, illustrated on Plate 8, figures 1, 2.

Material. Eight fragmentary cranidia and three fragmentary pygidia are referred to this species. The available material is preserved in calcilutite and calcarenite; both limestone moulds and counterparts are present. The three most complete cranidia vary in length (sag.) between 5.05 and 10.90 mm. The associated pygidia are too fragmentary to measure.

Occurrence. *Sigmakainella translira* is recorded from four localities within the Gola Beds: B520, B750, B752, and K101. It is possibly present also at K102, but in the absence of pygidia the cranidia of *S. translira* may be confused with those of *S. longilira* sp. nov.

Diagnosis. A species of *Sigmakainella* gen. nov. with prosopon of coarse anastomosing raised ridges — *lirae*. In the pygidium these run approximately across the surface, more or less normal to the sagittal line.

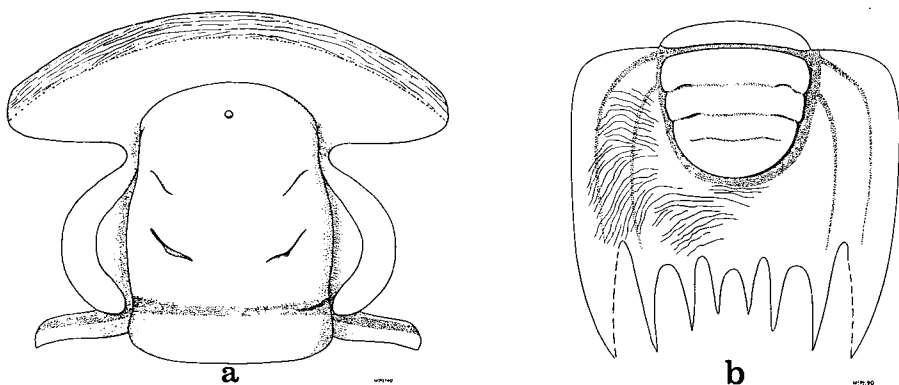
Description. The glabella tapers forwards and is evenly rounded anteriorly.

It bears two pairs of glabella furrows of which only the preoccipital ones are well-defined. If anterior glabellar furrows are present they are extremely faint. A median node is present sagittally on the frontal lobe, some distance from the anterior margin. The axial furrows are overdeepened adjacent to the anterolateral corners of the glabella. On measured specimens the glabella occupies 64-67 percent of the total cranial length (sag.).

The occipital ring is as wide (tr.) as the maximum glabella width (tr.), opposite the midpoint of the palpebral lobes. In lateral profile it rises no higher than the level of the glabellar lobes.

The palpebral lobes are well-defined, elevated, and subcrescentic in plan. They extend from the anterior glabellar furrows to the occipital furrow, which they nearly contact posteriorly, and embrace very narrow (tr.) palpebral areas. The small eye index varies between 60 and 63 percent and the large eye index between 74 and 78 percent.

The posterolateral limbs are not preserved on any of the specimens. The anterior sections of the facial suture commence at the anterior edge of the eye and initially run almost parallel to the sagittal line, but rapidly swing outwards to run nearly transversely before turning sharply inwards once more just before the marginal furrow. The preglabellar field is relatively short, occupying 17-24 percent of the total cranial length (sag.) and 15-20 percent of its width (tr.). There is a slight roll immediately in front of the preglabellar furrow and a slight depression adjacent to the marginal furrow. The last bears a row of some 34-36 pits as in *Kainella* and other Richardsonellinae. The anterior border is wide (sag.): 10 percent of the cranial length (sag.). Ramified caeca are visible on the preglabellar field.



12. *Sigmakainella translira* gen. et sp. nov.
reconstruction of (a) cranidium based on CPC 9715a and b, x4.
(b) pygidium based on CPC 9718, x4.

The surface of the glabella, occipital ring, palpebral lobes and areas, and anterior border is covered with a coarse 'fingerprint' prosopon, consisting of roughly concentric raised ridges. On some specimens (Pl. 9, figs 3, 6) these are particularly coarse. On others they intersect the caeca to form a reticulate prosopon (Pl. 8, fig. 3).

The hypostome and the thorax are unknown.

The pygidium is known from three fragments, all from locality B750. If the spines are included it has a broadly rectangular shape. The axis is short, posteriorly drawn out into a short triangular postaxial ridge, comprising only

three segments, the third being rather indistinct. The articulating half-ring is a simple bar. The first transverse furrow is wide (sag.) and shallow; the second and third are interrupted mesially and curve gently backwards. The axis is elevated prominently above the pleurae which are strongly swept back to lie parallel to the axis. The segmentation is vague and only two pleural furrows are visible. The first interpleural furrows are seen only adjacent to the axial furrows, the second not at all. The bases of four marginal spines are discernible on one specimen, CPC 9719 (Pl. 8, fig. 5). There is no caudal spine. The pygidial surface is covered with more or less transverse raised ridges, trending backwards around the end of the axis or into the spine bases. A reverse pattern is seen on the ventral surface of the doublure (Pl. 8, figs 4, 5). Similar raised ridges are present on the axis where they are again more or less transverse.

Comparisons and differences. These have been considered on p.

SIGMAKAINELLA LONGILIRA sp. nov.
(Pl. 9, figs 1-2; Text-fig. 13)

Name. *Longilira*: the species name alludes to a prosopon of longitudinal raised lines, which are distinct from those running transversely.

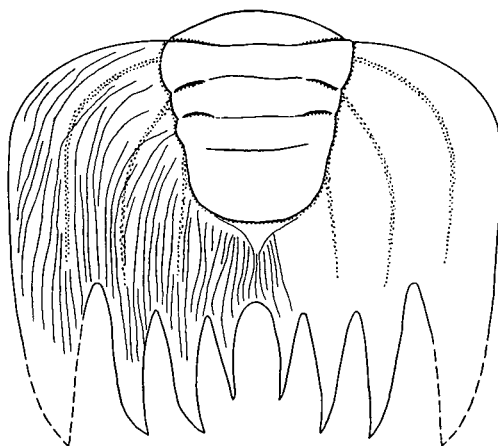
Holotype. The pygidium CPC 9723 figured on Plate 9, figure 1.

Material. Only two pygidia are known; both are figured on Plate 9. The holotype retains most of its shell, lacking only that from the axis.

Occurrence. Both specimens are from locality B520, where they are preserved in coarse grained calcarenite.

Diagnosis. A species of *Sigmakainella* gen. nov. with prosopon of raised lines following the courses of the pleural furrows, and arranged longitudinally in the posterior part of the pygidium.

Description. The axis is short, composed of three segments, the third being indistinct. The postaxial ridge is not strongly developed. The pleurae are swept



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13. *Sigmakainella longilira* sp. nov., reconstruction based on CPC 9723 and 9724, x12.

back more sharply than in *S. translira*, and the geniculation is weaker. Two pleural furrows are visible but no interpleural furrows. The furrows pass into the bases of the marginal spines. These, numbering four pairs, are broad-based, long and all extend distally to approximately the same level. There is a deep embayment between the fourth pair of spines, behind the axis. The prosopon of *S. longilira* is of a coarse network of raised ridges, as in *S. translira*, but they follow the courses of the pleural furrows rather than cutting across them as they do in the latter. The lirae run along the pleurae and into the spines. Behind the axis they radiate almost parallel to the sagittal line. The lirae of the axis are mesially transverse, but abaxially they curve sharply into the axial furrows. The prosopon of the ventral surface of the doublure is as in *S. translira*.

SIGMAKAINELLA sp.
(Pl. 19, figs 1, 4)

Ventral aspects of two librigenae are figured on Plate 19. One of these (Fig. 1) is certainly referable to *Sigmakainella*; the generic assignment of the other (Fig. 4) may be queried.

Specimen CPC 9725 (Pl. 19, fig. 1) has the prosopon of the dorsal surface imprinted on the ventral. This is a reticulate pattern caused by the intersection of the caecal system and the lirae. It matches well the prosopon of the preglabellar field of *S. translira*, e.g. the cranidium illustrated on Plate 8, figure 3. The genal spine is long, stout, and in an advanced condition. It bears raised lines similar to those seen on the anterior cranial border of *S. translira*. A faint raised articulating node is just visible at the junction of spine and cheek.

Specimen CPC 9728 (Pl. 19, fig. 4) does not show the prominent prosopon of CPC 9725. The spine, while remaining advanced, is more delicate. It nevertheless probably belongs to *Sigmakainella*.

Specimen CPC 9725 is from calcarenite at B520; specimen CPC 9728 from calcilutite at B750.

The cranidium of *S. longilira* is not definitely known. In all probability it is very similar to that of *S. translira*. As a result these librigenae cannot be accurately specifically determined.

Superfamily LEISTEGIACEA Bradley, 1925

Family KAOLISHANIIDAE Kobayashi, 1935

The family Kaolishaniidae is here considered in a broad sense to include three subfamilies related by the structure of the preglabellar area, characteristics of the glabella, and, where known, the nature of the pygidial shape, axis, and spines. The subfamilies recognized are Kaolishaniinae Kobayashi, 1935, Mansuyiinae Hupé, 1955, restricted, and Tingocephalinae Hupé, 1955.

Subfamily KAOLISHANIINAE Kobayashi, 1935

The subfamily Kaolishaniinae is restricted to include the single genus *Kaolishania* Sun, 1924. *Kaolishaniella* Sun, 1935, which was placed in this subfamily by Kobayashi (1960b, p. 356), is here transferred to Mansuyiinae.

Genus KAOLISHANIA Sun, 1924

Type species. *Kaolishania pustulosa* Sun, 1924, pp. 53-54, plate 3, figures 8a-h, from the Kaolishan Formation of Tawenkou, near Taian, Shantung, and Wolungshan, near Huoluh, Hopei, north China.

Other species. Apart from the type species the following have been described to date:

Kaolishania cf. *pustulosa* Sun (Kobayashi, 1933, pp. 103-4, pl. 11, figs 17, 18, partial cranidia), from Hsishan, Wuhutsui basin, Liaotung, southern Manchuria.

Kaolishania granulosa Kobayashi (1933, p. 104, pl. 11, figs 19, 20, partial cranidium) = *Paramansuyella granulosa* Endo (in Endo & Resser, 1937, p. 359, pl. 70, figs 1, 2, 4-6, ?9, non figs 3, 7, 8), from Paichiashan, Wuhutsui basin, Liaotung, southern Manchuria; and also recorded from Doten, South Korea (Kobayashi, 1935c, pp. 175-7).

Kaolishania(?) obsoleta Kobayashi (1933, p. 104, pl. 11, fig. 15, non fig. 16, partial cranidium), from Sanki-rei, Sosan, North Korea.

Kaolishania(?) latiura Kobayashi (1960b, p. 356, pl. 21, fig. 19, pygidium), from 350 metres southwest of Sodo-ri, South Korea.

Kaolishania sp. [= *Chuangia nais* Walcott *sensu* Mansuy (1915, p. 20, pl. 2, figs 14a-h, cephalae and pygidia), = *Kaolishania* sp. b of Kobayashi (1944, p. 116)], from Dong-van, North Vietnam — Yunnan/Tonkin border.

In China, Manchuria, and North Korea *Kaolishania* gives its name to a 'Zone' near the middle of the Chaumitien Series, which forms the bulk of the Daizan Stage (= Paishanian of Endo, 1944). A possible species of *Kaolishania* occurs in the *Dictyites* 'Zone' of South Korea (Kobayashi, 1935c, p. 179). That from Vietnam is said to occur in association with *Prosaukia angulata* (Mansuy, 1915, p. 20).

KAOLISHANIA AUSTRALIS sp. nov.

(Pl. 12, figs 1-8; Pl. 19, figs 2, 3; Text-figs 14, 15)

Name. Latin, *australis*, southern: the first occurrence of *Kaolishania* in the southern hemisphere is acknowledged in this name.

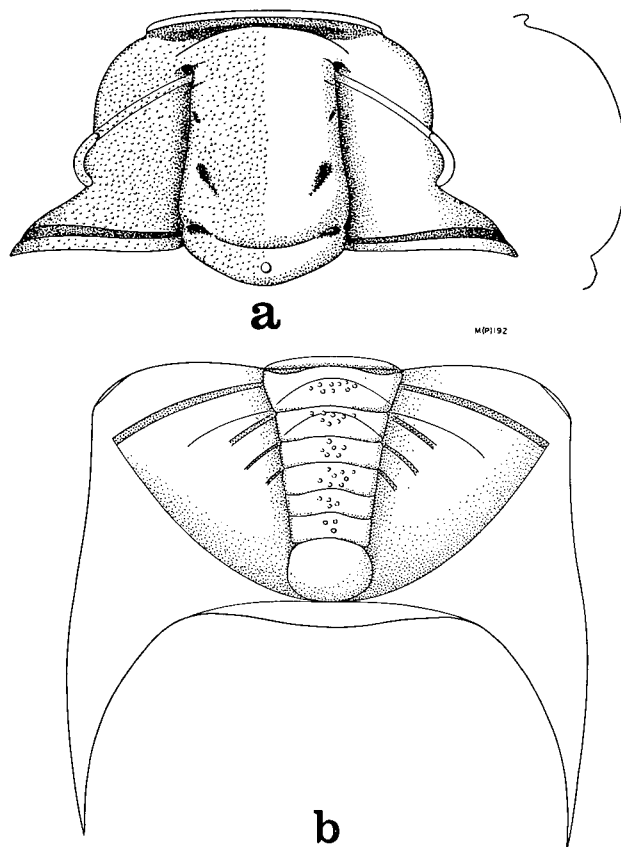
Holotype. The cranidium CPC 9729, illustrated on Plate 12, figure 5. A cranidium is preferred owing to uncertainty surrounding the correct assignment of the pygidium.

Material. Twenty-three cranidia belonging to this species were examined and measured (Table 3). They vary in cranidial length (sag.) between 1.95 and 4.55 mm. Two reasonably large pygidia and three meraspid pygidia are also assigned to the species, but with some reservation (see below). The meraspids, varying in pygidial length (sag.) between 1.40 and 1.70 mm, have comparable proportions to the larger pygidia, the largest of which is 5.50 mm long. In addition several genae are known.

Occurrence. *Kaolishania australis* occurs at localities B520, B752, B753, K101 and K102, in a coarse calcarenite matrix. It is significantly absent from locality B750.

Diagnosis. A species of *Kaolishania* Sun, 1924, with the following complex of cranial characteristics: no preglabellar field, the marginal furrow lying immediately anterior to the glabella and passing into a narrow upraised anterior border; ocular strigae; eyes situated posteriorly on the cheeks; distance between back of eye and posterior border furrow equivalent to total eye length (exsag.); intervening glabellar furrows and lobes; low ridges connecting anterolateral margins of frontal lobe to preocular genal areas; deep 'antennary' pits situated between adaxial ends of eye ridges and anterolateral glabellar connecting ridges; nuchal node; densely granulose prosopon.

Description. The glabella is long (sag.), occupying 75-90 percent of the total cranial length (sag.), and tapers slightly to the anterior, where it is bluntly rounded. The maximum width (tr.) is across the preoccipital glabellar lobes. In all there are five pairs of glabellar furrows, but only the preoccipital ones are deeply impressed. Lying immediately in front of the occipital furrow, and running more or less parallel to it, is a pair of shallow, scarcely visible, intervening furrows (Text-fig. 14). The preoccipital furrows are deep, linear or slightly sigmoidal, running obliquely inwards and not reaching the axial furrows. The median lateral furrows are short, faint, linear, transverse, and are confined to the flanks of the glabella. The anterior lateral furrows are likewise faint and situated, but they are anteriorly directed. An additional very faint pair of furrows lies at the level of the 'antennary' pits. In lateral profile the glabella is strongly convex (sag.).



14. *Kaolishania australis* sp. nov. reconstruction based on (a) cranidium CPC 9729, x9; (b) pygidium CPC 9733, x6.

The occipital furrow is well-defined, shallow and transverse mesially, over-deepened abaxially, confluent with the axial furrows. The occipital ring is slightly expanded sagittally; in profile it rises to the level of the glabellar side lobes. It bears a nuchal node, but this is eroded away in many specimens.

The palpebral lobes are arcuate in plan, small, 21-30 percent of the glabellar length (sag.), and extending from the posterior end of the preoccipital furrows to the middle of the median lateral lobes. An area of fixigena equivalent to the eye length separates the back of the eyes from the posterior border furrow. Palpebral furrows are present but shallow. The palpebral areas are wide (tr.), posteriorly 53-65 percent of the preoccipital glabellar width (tr.). Well-defined ocular ridges, with faint strigae, intersect the axial furrows at angles between 50 and 60 degrees, just in front of the anterior glabellar furrows.

TABLE 3

Cranidial proportions of *Kaolishania australis*

Specimen No.	L _c	G _n	G	A:G	A:G _n	P _D :W ₁
CPC 9743	1.95	2.00	1.85	27.86	23.70	58.62
CPC 9746	3.10	2.95	2.45	27.71	23.85	56.48
CPC 9745	3.15	3.00	2.55	28.18	21.90	59.10
CPC 9732	3.35	3.10	2.55	22.39	19.05	59.64
CPC 9744	—	3.15	2.55	27.13	21.86	55.13
CPC 9741	—	3.30	2.75	23.34	19.32	65.07
CPC 9731	3.40	3.20	2.85	22.11	18.95	57.81
CPC 9742	—	3.60	3.15	18.51	16.14	52.84
CPC 9739	4.00	3.75	3.15	29.86	26.02	60.27
CPC 9740	—	—	—	—	—	62.95
CPC 9729	4.10	3.75	3.25	26.33	21.91	56.72
CPC 9738	4.20	3.90	3.10	20.84	16.74	60.63
CPC 9730	4.55	4.30	3.70	25.59	21.91	55.98
CPC 9737	4.55	4.30	3.70	23.88	20.00	57.65

The axial furrows converge slightly forwards, and cause a constriction of the glabella about the median lateral glabellar lobes. Immediately in front of their confluence with the ocular ridges lie a pair of deepened pits. In front of these the courses of the axial furrows are blocked by low ridges connecting the preocular areas with the anterolateral margins of the glabella.

A deep preglabellar furrow lies anterior to the frontal glabellar lobe, and an upraised preglabellar ridge forms the anterior cranidial border. This lies well below the level of the glabellar surface in lateral profile.

The preocular sections of the facial suture run parallel from the front of the eyes, then curve inwards near the anterolateral margins of the cranidium, coursing across the convexity of the preocular areas. The postocular sections of the facial suture diverge rapidly to the posterior cranidial margins, enclosing triangular posterolateral limbs. The posterior border furrow widens distally and becomes shallower. The posterior cranidial borders are evenly narrow (exsag.).

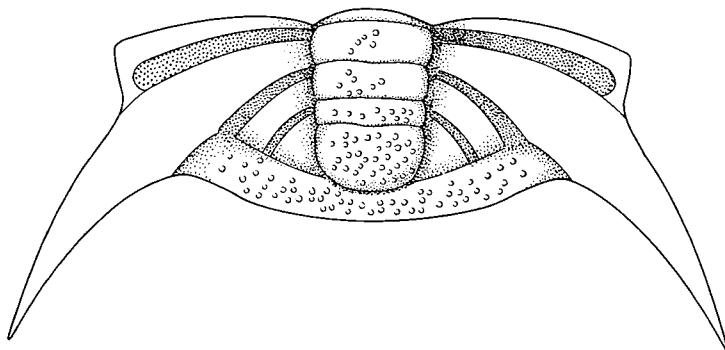
The surface of the cranidium is densely granulose. On some specimens the granules are considerably finer on the cheeks flanking the intervening glabellar furrows, and in the posterior border furrows.

The librigenae (Pl. 19, figs 2, 3) are small and relatively convex with marginal furrows well developed around the complete periphery. The genal spines are

long, advanced, and distally incurved. These librigenae are quite different from those shown on the reconstruction of *Kaolishania pustulosa* offered by Kobayashi (1956a, pl. 2, fig. 4a).

Hypostome and thorax are unknown.

Four pygidia are figured as belonging to *K. australis*, but may not belong to the figured cranidia. Three of the illustrated specimens are meraspides (Pl. 12, figs 1, 3, 4), the fourth a large holaspid. All are from the same deposit, B520, preserved in coarse calcarenite.



15. *Kaolishania australis* sp. nov., meraspid pygidium based on CPC 9734 and 9735, x12.

The three meraspides are wider than long, their lengths (sag.) varying between 39 and 44 percent of their widths (tr.). Their axes, 89-91 percent of the total pygidial length (sag.), are parallel-sided, with slightly expanded terminal pieces. They have additionally four strongly convex (tr.) axial rings. Three pleural segments are indicated, the posterior bands of the first and the anterior bands of the second combining distally to form stout lateral pygidial spines. Marginal furrows are weakly defined posteriorly. Scattered granules on the border and axis form the observed prosopon.

The holaspid pygidium (Pl. 12, fig. 2) has a length:width ratio of 1:2, and the axis occupies 89 percent of the pygidial length. Six axial rings are observed, together with a bulbous terminal piece. The axis tapers slightly rearwards. Again only three pleural segments are indicated. The marginal spines are strong and appear to be developed from the whole of the lateral borders, but this condition is evidently emphasized by the removal of the shell. The posterior margin is straight and passes directly into the spine bases. On the axis a prosopon of coarse granules is present but the pleural segments are smooth.

Comparisons and differences. The cranidium of *Kaolishania australis* is comparable to that of *K. pustulosa*, the type species, *K. obsoleta* Kobayashi, and *K. granulosa* Kobayashi, but it is differentiated as follows:

Kaolishania pustulosa Sun (1924, pl. 3, figs 8a-b) has narrower (tr.) palpebral areas, eyes situated farther forward, and wider (sag.) anterior border. The preglabellar furrow is not overdeepened and the glabellar furrows are stronger. The preoccipital furrows of Sun's specimens connect with the axial furrows. The specimen of *K. pustulosa* figured by Lu (1957, pl. 143, fig. 14) has a more closely comparable glabellar situation. The prosopon of both *K. pustulosa* and

K. australis is similar. The two species differ markedly in their assigned librigenae, and the point of correct matching must be raised. Those referred by Kobayashi (1956a, pl. 2, fig. 4a) to *K. pustulosa* are large, not advanced, and drawn out at the spines, which themselves are long and deflected outwards from the outline of the cephalic margins.

Kaolishania obsoleta Kobayashi, 1933 (see 1935c, pl. 9, figs 17, 18, ?16) has a smooth surface. Again its eyes are sited farther forward, and the preglabellar furrow is shallow and wide, approaching the condition of *Mansuyia*.

Kaolishania granulosa Kobayashi (1933, pl. 11, figs 19, 20) has a similar prosopon, especially Kobayashi's figure 19. Specimens attributed to this species by Kobayashi in 1935 (1935c, pl. 8, figs 9-11; pl. 9, fig. 15) belong to different species. *K. australis* is similar to the cranidium figured on plate 9, figure 15, but that specimen has a wider preglabellar furrow and stronger glabellar furrowing, the preoccipital furrows reaching the axial furrows.

The pygidia which Sun (1924, pl. 3) figured as *Kaolishania pustulosa* are subparallel-sided, having spines developed from the posterior bands of the first and the anterior bands of the second pairs of segments. The bases of these spines extend from the level opposite the rear of the axis to the posterior bands of the first pleural segment. They are aligned along the margins of the pygidium and continue them backwards. The axis, composed of six segments and a terminal piece, is long, reaching nearly to the posterior pygidial margin. There are four pleural segments. The posterior margin of the pygidium is only very gently rounded, thus contrasting with that of *Mansuyia* which is otherwise similar.

The holaspid pygidium illustrated here on Plate 12, CPC 9733, is quite comparable to the pygidium of *Kaolishania pustulosa* in its general structure, differing only in the straighter posterior margin, and the number of observed pleural segments. It is also similar to the specimen figured by Lu (1957, pl. 143, fig. 16) as *K. pustulosa*. The meraspid pygidia discussed above differ from the holaspid specimen in the position and orientation of the spines, which are deflected outwards from the pygidial margins. In this respect they are essentially similar to the specimen which Kobayashi (1935c, pl. 9, fig. 14) has attributed to *K. granulosa*, and to pygidia which he (*op. cit.*, pl. 10, figs 6, 7) has referred to *Prochuangia mansuyi*. Pygidia similar to these occur at the base of the exposed Chatsworth Limestone section at Black Mountain, Queensland. There they are associated with cranidia of the *Mansuyites* type.

Subfamily MANSUYIINAE Hupé, 1955, restricted
nom. correct. Shergold, herein (*pro* Mansuyinae Hupé, 1955)

Mansuyiinae, envisaged by Hupé (1955, p. 179) as a subfamily of Leiostegiidae, is here placed in the family Kaolishaniidae and restricted to cover *Mansuyia*-like genera. Rejected from the subfamily are *Chosenia* Kobayashi, 1934, *incertae familiae*, and *Prochuangia* Kobayashi, 1935c, Leiostegiidae. Included are *Mansuyia* Sun, 1924, *Paramansuyella* Endo in Endo & Resser, 1937, *Kaolishaniella* Sun, 1935, and *Mansuyites* gen. nov. As considerable confusion surrounds some of these genera and their type species a brief review of each is given below.

Genus MANSUYIA Sun, 1924

Type species. *Mansuyia orientalis* (Grabau) Sun [Sun, 1924, pp. 50-2, pl. 3,

figs 7i-j only *non* figs 7a-d = *Taishania taianensis* Sun, 1935; *non* figs 7f-h = *Mansuyia chinensis* (Endo, 1939)], from the Fengshan Stage of Yehli, Machiakou, and Chihli, eastern Hopei, China.

Other species are:

Mansuyia tani Sun (1935, p. 59, pl. 5, figs 12-15), Tawenkou Formation, Kaolishan and Tawenkou, Shantung, China; *non* *Mansuyia tani* Sun *sensu* Kobayashi, 1952 = *Mansuyia chinensis* (Endo, 1939).

Mansuyia trigonalis Kobayashi (1960b, pp. 364-5, pl. 21, fig. 18, text-fig. 5c), Fengshanian part of the Hwajeol Formation, between Sodo-ri and Hyol-li, South Korea.

Mansuyia manchurica Kobayashi (1952, p. 148, based on *Hysterolenus* sp. undet. of Endo *in* Endo & Resser, 1937), Fengshanian of Paichiashan, Liaotung Peninsula, southern Manchuria; Machiakou, Hopei; and Chaumitien, Shantung, China.

Paramansuyella planilimbata Endo *in* Endo & Resser (1937, pp. 359-60, pl. 70, figs 16-19), Daizan Formation, Paichiashan, southern Manchuria.

Paramansuyia chinensis Endo (1939, pp. 9-10, pl. 2, figs 3-10, ?35), Tawenkou and Kaolishan Formations, Tawenkou, near Tianfu, Shantung, China, and from Saisho-ri, Sosan, North Korea. An extensive probable synonymy is associated with this species:

Mansuyia orientalis (Grabau) Sun; Sun, 1924, pl. 3, figs 7f-h.

Chuangia batia Walcott; Sun, 1924, pp. 58-9, pl. 4, figs 4a-e *non* *Chuangia batia* Walcott, 1913.

Kaolishania orientalis (Grabau); Kobayashi 1935c, p. 178, pl. 8, fig. 12.

Mansuyia orientalis Sun; Sun, 1935, p. 58, pl. 2, figs 20-4.

Paramansuyia taianensis, new species; Resser, 1942a, p. 38.

Mansuyia orientalis Sun; Kobayashi, 1952, p. 147, pl. 13, figs 13-15.

Mansuyia tani Sun; Kobayashi, 1952, pl. 13, figs 16-18.

Mansuyia orientalis Sun; Lochman-Balk *in* Moore, 1959, p. 0319, text-fig. 236.2.

Mansuyia tani Sun; Kobayashi 1960b, p. 364, text-fig. 5b.

Mansuyia is confined in its distribution to northern Australia and eastern Asia (Daizanian and Fengshanian of northern China, southern Manchuria, North and South Korea).

Mansuyia is a problematic genus which has been extraordinarily confused by previous writers. Its type species, *M. orientalis* Sun, 1924, has been equally confused. Grabau (MS) originally mentioned the species *Ceratopyge orientalis* in 1922, but the species remained *nomen nudum* until Sun (1924, pl. 3, figs 7a-j) figured a suite of specimens, which included two of Grabau's pygidia, under the name *Mansuyia orientalis*. Later, Sun (1935, 58) removed the four cranidia (figs 7a-d) from the original suite and placed them in *Taishania* Sun. In the same paper Sun figured further pygidia (pl. 2, figs 23-24) and two substitute cranidia (pl. 2, figs 20-21), modifying the original generic diagnosis to accommodate them.

Resser (1942a, p. 30) has stated that *Mansuyia orientalis* should be typified by the 'types of *Ceratopyge orientalis* Grabau' (Sun, 1924, p. 10), these being Sun's pygidia, figures 7i-j. With *Mansuyia orientalis* thus restricted, Resser then proposed a new name, *Mansuyia endoi*, for Sun's remaining pygidia, figures 7f-h. Unfortunately, however, Resser seems to have confused Sun's figure numbers, as he quotes in synonymy Sun's figures 7a-d, which had already been justifiably referred to *Taishania taianensis* Sun, 1935.

Kobayashi (1952), taking an opposing standpoint, considered that Sun's figures 7f-h should typify *Mansuyia orientalis* Sun, arguing that the original descriptions and localities of Sun (1924) were given with these specimens in mind. He then considered (1960b, p. 364) a new name, *Mansuyia hopeiensis* (loc. cit., fig. 5a), appropriate for the specimens 7i-j which are, in fact, the types of *Ceratopyge orientalis* Grabau. In view of the fact that Sun (1924) actually figured specimens used by Grabau, that the species nomen *orientalis* was taken from Grabau's manuscript, and that Sun quite obviously knew the concept of Grabau's species, *Mansuyia orientalis* must unquestionably be based on Grabau's specimens, the two pygidia figured by Sun (1924, pl. 3, figs 7i-j). Hence the synonymy of *Mansuyia orientalis* Sun, 1924, includes:

Ceratopyge orientalis; Grabau (MS), 1922 *nom. nud.*

Mansuyia orientalis (Sun); Resser 1942a, p. 31.

Mansuyia orientalis (Grabau) Sun; Lu 1957, pl. 145, fig. 5.

Mansuyia hopeiensis Kobayashi, new species; Kobayashi 1960b, p. 364, fig. 5a.

Mansuyia hopeiensis Kobayashi; Kobayashi 1966, p. 275.

The subsequent treatment of Sun's remaining pygidia, figs 7f-h, is considered under the synonymy of '*Paramansuyia*' *chinensis* above.

As a working diagnosis that of Lochman-Balk *in* Moore (1959, p. 0319) is accepted with the provision that the statement that there is no preglabellar field be corrected. The preglabellar field of *Mansuyia* is a concave depression with a length (sag.) of approximately 12 percent that of the cranidium. It rises anteriorly into a well-defined anterior cranial border. The posterolateral limbs are triangular and blade-like.

Genus PARAMANSUYELLA Endo *in* Endo & Resser, 1937

Type species. *Paramansuyella puteata* Endo *in* Endo & Resser (1937, pp. 357-8, pl. 70, figs 10-15), Daizan Formation, Paichiashan, near Chinchichengtzu, southern Manchuria.

Paramansuyella is restricted to its type species. It is a poorly known genus which has been considered by Kobayashi (1952) and Lochman-Balk *in* Moore (1959) as synonymous with *Mansuyia*. As Hupé (1955, p. 179) has pointed out, however, *Paramansuyella* may be readily distinguished by its considerably narrower (tr. and sag.) preglabellar field. The pygidia assigned by Endo & Resser (1937) to *Paramansuyella puteata* are rather obscure and difficult to assess. They may not be congeneric.

Several of the species originally described under *Paramansuyella* have been transferred elsewhere. *P. chinensis* Endo, 1939, and *P. planilimbata* Endo *in* Endo & Resser, 1937, are now referred to *Mansuyia*. *P. granulosa* Endo *in* Endo & Resser, 1937, has been considered by Kobayashi (1960b, p. 355) as synonymous

with *Kaolishania granulosa* Kobayashi, 1933. *Paramansuyella glabra* Endo in Endo & Resser, 1937, is now placed by Kobayashi (1960b, p. 398) in the genus *Taipaikia* Kobayashi, 1960.

Genus KAOLISHANIELLA Sun, 1935

Type species. *Kaolishaniella transita* Sun (1935, pp. 64-5, pl. 3, figs 1-15), from the Lower Wolungshan Formation, Huolu district, Hopei, China.

One other species is known:

Kaolishaniella westergaardi Sun (1935, p. 65, pl. 3, figs 16-18), from the same formation and locality as the type species. The diagnosis of Lochman-Balk in Moore (1959, p. 0319) sufficiently covers this genus.

Genus MANSUYITES nov.

Type species. *Mansuyites futiliformis* gen. et sp. nov., late Upper Cambrian Gola Beds, Momedah Creek, western Queensland.

Name. Derived from the generic nomen *Mansuyia* and referring to its close relationship.

Diagnosis. A genus similar to *Mansuyia* Sun, 1924, with the following diagnostic characteristics: anteriorly pointed cranidial outline; broad (tr. and sag.), concave preglabellar field with poorly defined anterior cranidial border; paucifurrowed glabella; posteriorly sited eyes, distant from the glabella; narrow, band-like posterolateral limbs; long pygidial axis, reaching near to the posterior margin, with bulbous terminal piece; strongly curved posterior pygidial margin.

Comparisons and differences. The broad (tr. and sag.) preglabellar field of *Mansuyites* prevents confusion with cranidia of *Paramansuyella*. It is also proportionately longer (sag.) and wider (tr.) than that of *Mansuyia chinensis* (Endo, 1939), the only species of *Mansuyia* known adequately from cranidial characteristics. In *Mansuyites* the anterior sections of the facial suture diverge at considerably larger angles; the border is less well-defined; the eyes placed farther to the rear of the cephalon; and the posterolateral limbs narrower (exsag.), band-like rather than blade-like. *Mansuyia* and *Mansuyites* are comparable in their glabellar characteristics, and in the relationship of the glabella to the anterior margins of the preocular areas.

The pygidium of *Mansuyites* has more axial rings than that of *Mansuyia*, but approximately the same as that of *Kaolishaniella*. The overall appearance of the pygidium is reminiscent of *Mansuyia chinensis*, but the margin is more convex between the rear of the spine bases, i.e. the 'bowl' of the pygidium is deeper.

MANSUYITES FUTILIFORMIS sp. nov.

(Pl. 13, figs 1-7; Pl. 14, figs 1-6; Text-fig. 16)

Name. Latin, *futile*, a vessel broad above and pointed below; and *forma*, shape: the combination describing the shape of the pygidium.

Holotype. The pygidium CPC 9749, illustrated on Plate 13, figure 1.

Material. The species is known from about 60 fragments; 23 fragmentary

cranidia and 10 pygidia were prepared. These are preserved largely as limestone moulds, but often retain vestiges of shell. The pygidia vary in length (sag.) between 1.25 and 9.30 mm. The majority of the cranidia are anteriorly incomplete. The smallest complete cranidium has a length of 1.45 mm, and the largest complete one 8.60 mm. However, larger cranidia with lengths, excluding the preglabellar field and anterior border, up to 8.45 mm, would give an estimated maximum length of 12 mm or more.

Occurrence. About two-thirds of the total number of fragments referred to this species are from sandy calcilitite at locality B750. The majority of the remainder are from coarse calcarenite at B520. Four specimens occurred in the sample from K102, and one each in those from K101 and B752.

The specimens appear to have been well sorted for size. Cranidia at B750 range in length between 1.45 and 6.00 mm, while the smallest of those observed at B520 has an estimated length in excess of 8.00 mm. Similarly the pygidia at B750 range in length between 2.15 and 4.85 mm; that at B520 measures 9.30 mm.

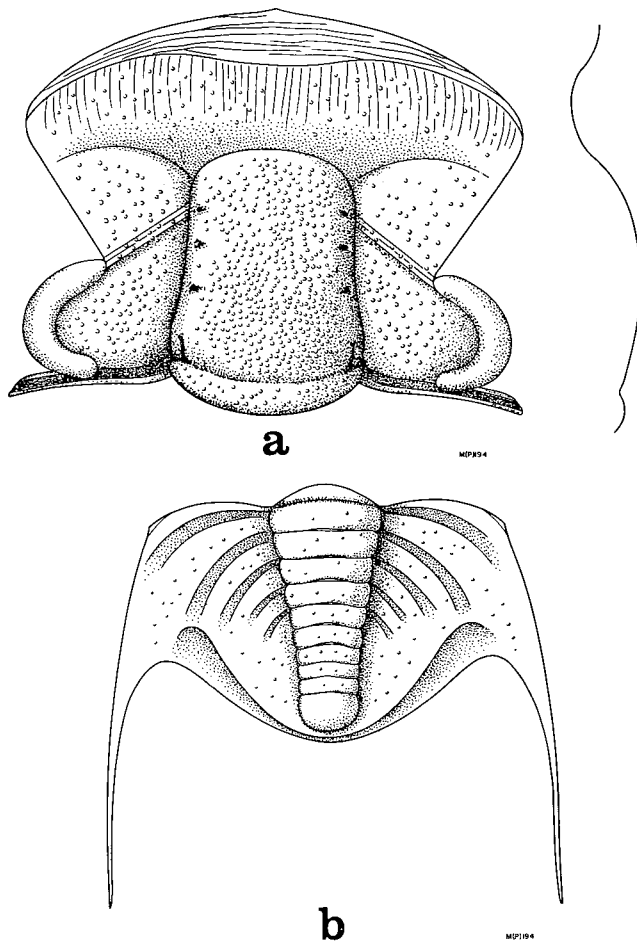
Diagnosis. The generic diagnosis covers that of the type species.

Description. The glabella is subrectangular, tapers slightly forwards, and is anteriorly rounded, with low profile convexity (sag.). It occupies 55-66 percent of the total cranidial length (sag.). Three pairs of glabellar furrows are represented by pits, all equally shallow, and located on the glabellar flanks. The glabellar is widest (tr.) at the preoccipital lobes.

The occipital furrow is transverse, linear, shallow, and narrow (sag.). The occipital ring rises to the level of the glabellar side lobes in profile. It is narrow (sag.), but as transversely wide as the preoccipital lobes and bacculae combined. Small specimens (CPC 9758, Pl. 14, fig. 3) are strongly bacculate. The bacculae are small elongated raised patches lying along the flanks of the preoccipital lobes and separated from them by faint furrows running exsagittally. In some specimens they appear to be joined to the glabella at their anterior ends. Large specimens tend to be alate rather than bacculate: the alae are similarly situated to the bacculae described above, but are well depressed below the level of the glabella and give rise to a prominent constriction in the axial furrows. During morphogenesis the difference between alae and bacculae becomes obliterated, the former deriving from the latter.

The palpebral lobes are crescentic in plan view; large, extending from the middle of the occipital ring to the middle of the median lateral glabellar lobes; and posteriorly situated, abutting against the posterior border furrows of the cranidium. They occupy 50-66 percent of the total glabellar length. The palpebral furrows are shallow, but the lobes are elevated. The palpebral areas are gently convex (tr.), and wide (tr.), posteriorly 30-50 percent of the preoccipital glabellar width (tr.). The palpebral lobes are connected anteriorly to duplicated ocular ridges which intersect the axial furrows at angles of approximately 50-55°. They are rather faint, and wide.

The postocular sections of the facial suture diverge strongly from the back of the eyes and enclose narrow, band-like posterolateral limbs. In line with the palpebral furrows, at the midlength of the eyes, are small fulcral processes; frequently the limbs are broken off at this geniculation. At this point the backs of the eyes overhang the narrow (exsag.) posterior marginal furrows. The posterior cranidial border is narrow (exsag.), and straight. The preocular sections of the facial suture also diverge strongly. They enclose a broad (tr. and sag.)



16. *Mansuyites futiliformis* gen. et sp. nov. reconstruction of (a) cranidium based on CPC 9758, x8; (b) pygidium based on CPC 9749, x8.

preglabellar field and anterior border, and meet on the sagittal line to form a small apex. The enclosed preocular areas are moderately convex (exsag.), terminating abruptly in line (tr.) with the front of the glabella, as in Damesellacea. The preglabellar field is concave and wide (sag.), occupying 25-30 percent of the cranial length (sag.). It curves upwards into a gently convex (sag.), poorly differentiated border.

The ventral surface, hypostome, librigena, and thorax remain unknown.

The cranial prosopon, when completely preserved (usually on specimens in a calcilutite matrix), is of a dense granulation, especially on the glabella. Specimens preserved in calcarenite show a varying degree of granulation. One such (CPC 9760, Pl. 14, fig. 6) has perforated granules.

The pygidium is approximately triangular: wide (tr.) anteriorly, drawn out (sag.) posteriorly, and 56-72 percent as long as wide. The axis, tapering gently to the posterior, is moderately convex (tr.). It is composed of nine axial segments and a bulbous terminal piece, occupying 95-98 percent of the pygidial length (sag.), and anteriorly 32-33 percent of the width (tr.). There are four pleural

segments with wide and shallow pleural furrows, and obliterated interpleural furrows; the furrowing dies out posteriorly, giving an unfurrowed posterior pleural field.

Two long spines, longer than the pygidium, are derived from the posterior bands of the first and the anterior bands of the second pleural segments. They are placed well forwards, the spine bases extending from opposite the second to the sixth axial segments. These spines are deflected outwards from the pygidial margins, but not greatly. Immediately behind each spine base is a narrow flange representing the lateral border, which dies out rapidly posteriorly. The posterior margin is strongly rounded in holaspides, giving depth to the 'bowl' of the pygidium, but less so in meraspides (see Pl. 13, fig. 5).

The surface of limestone moulds is covered with sparsely distributed granules of two sizes. They are roughly aligned along the pleural bands and across (tr.) the axial segments. When the shell is preserved (Pl. 13, fig. 3, right flank) the granules have an apparent greater density. This same specimen shows that the granules are perforated on the mould (left flank). In addition it shows a narrow and smooth ventral doublure, and features interpreted here as anterior pleural veins (Öpik, 1961a, p. 426).

Morphogenesis. The most striking observed change during morphogenesis is the rapid increase in length of the pygidium. The length:width ratio, expressed as a proportion, varies from 46 percent in the smallest to 72 percent in the largest specimens. The number of segments incorporated into the axis also increases, from seven to nine. Variation shown by the bacculae and alae is noted above.

Comparisons and differences. *Mansuyites futiliformis* may be compared with *Mansuyia chinensis* (Endo, 1939). The latter, however, has a shorter (sag.) preglabellar field, anteriorly placed eyes and broader, triangular posterolateral limbs. The pygidia of the two species are quite similar, but that of *M. chinensis* has fewer axial rings in its late holaspid condition; only seven are visible on the specimens figured by Sun (1924, pl. 3, figs 7f-h), and Sun's specimens are all larger than the majority of those of *Mansuyites futiliformis*. They also have less bulbous terminal pieces.

Mansuyia orientalis Sun (see section on *Mansuyia* above), which is known only from pygidia, cannot be directly compared because of poor preservation. Pygidia of this species have the long axis characteristic of *Mansuyites*, but their spines appear to have wider bases. *Mansuyia tani* Sun, 1935 (*non* Kobayashi, 1952) may actually represent *Mansuyites*. It is known only from pygidia, which have the same number of axial segments, nine, as *M. futiliformis*. However, I cannot offer further comparison, being unable to interpret some of Sun's illustrations.

Subfamily TINGOCEPHALINAE Hupé, 1955

Hupé (1955) placed Tingocephalinae in the Dikelocephalidae, and Kobayashi (1960b) referred the subfamily to the Damesellidae. Although its members are known only from cranidia, and although further morphological information seems desirable for accurate familial classification, nevertheless the genera already known exhibit most similarity to the Kaolishaniidae. Tingocephalinae is classified here alongside Kaolishaniinae and Mansuyiinae.

Genus PALACORONA nov.

Type species. *Palacorona bacculata* gen. et sp. nov., from the late Upper Cambrian Gola Beds, Momedah Creek, western Queensland.

Name. *Palacorona* is derived from L., *pala*, f., shovel, and L., *corona*, crown, rim or border: the name refers to the shovel-shaped area of the cranium.

Diagnosis. *Palacorona* is a tingocephalinid genus with strongly pointed triangular anterior cranial outline; broad (sag.), shallow, concave preglabellar field; bacculae incorporated into the glabella as lateral preoccipital lobes; glabellar front on the same transverse line as, or slightly in front of, the anterior margins of the preocular areas.

Comparisons and differences. *Palacorona* is most closely comparable to *Tingocephalus*, as interpreted by Kobayashi (1960b, pp. 357-8). Although both may have an anteriorly angled anterior cranial outline, and eyes positioned posteriorly on the cheeks, there are sufficient other differences to separate them. In *Tingocephalus* the front of the glabella is situated behind the anterior margins of the preocular areas. Furthermore, the glabella of *Tingocephalus* is proportionately narrower (tr.), and the palpebral areas proportionately wider (tr.). The large reniform lobes, attached laterally to the flanks of the preoccipital lobes, which are characteristic of *Tingocephalus*, are not so greatly exaggerated in *Palacorona*.

Kobayashi (1960b, p. 357) has noted the glabellar resemblances of *Tingocephalus* with certain species of *Kaolishania* and *Blackwelderia*, and these hold also for *Palacorona*. With regard to the position of the frontal glabellar lobe relative to the adjacent preocular areas, *Tingocephalus* may be compared to *Teinistion*(?), *sensu* Öpik (1967, pp. 334-5) and *Histiomona* Öpik (op. cit., pp. 335-6) from the Mindyallan Stage of Queensland. In *Palacorona* the glabella extends forwards to the margins of the preocular areas.

Lateral lobes derived from the preoccipital glabellar lobes are characteristic of *Tingocephalus*, *Teinistion*, *Histiomona*, and several species of *Blackwelderia*. Öpik (1967) has used the term bacculae to describe them. As they occur in several other, unrelated, genera their taxonomic usefulness appears to be limited.

PALACORONA BACCULATA sp. nov.

(Pl. 15, figs 1-5; Text-fig. 17)

Name. *Baccula* is derived from L., *bacca*, berry: referring to the bacculate condition of the cranium.

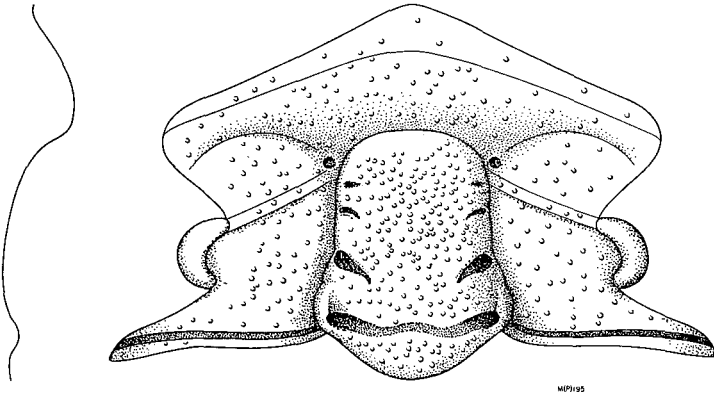
Holotype. The cranium, CPC 9761, figured here on Plate 15, figures 1, 3. Both internal and external moulds are present in the collection.

Material. Eight cranial fragments — all the available material — were prepared. No complete cranium is known, but the fragments enable most of the relevant features to be observed. The largest specimen from which the cranial length can be assessed measures 5.95 mm. In other specimens, however, the glabella is larger than this: the glabellar length of one, excluding the occipital ring, is in excess of 7.50 mm.

Occurrence. *Palacorona bacculata* was collected, in both coarse calcarenite and sandy calcilutite, from four horizons in the Gola Beds: B520, K101, K102, and B750.

Diagnosis. See the generic diagnosis, which is based on this species.

Description. The glabella is subrectangular, anteriorly obtusely rounded, tapering forwards, occupying 55-58 percent of the cranial length (sag.); in lateral profile having a low to moderate convexity (sag.). It is widest at the preoccipital lobes, constricted a little at the level of the median lateral furrows. Three pairs of lateral glabellar furrows are visible on most specimens. The preoccipital furrows are deep, oblique, sloping adaxially backwards, and are not confluent with the axial furrows, being separated from them by a low threshold. The median lateral furrows are less deep, and shorter, sited on the flanks of the glabella; in some examples they break the threshold and merge with the axial furrows. The anterior lateral furrows are faint pits, situated some distance from the margins of the glabella, about half-way towards the sagittal line (Pl. 15, fig. 5, CPC 9763). The preoccipital glabellar lobes have faint swellings at their posterolateral corners which run confluent with the abaxial extremities of the occipital ring. In *Tingocephalus* these lateral preoccipital lobes extend laterally on to the postocular fixigenae, forming large reniform swellings or bacculae. In *Palacorona* they remain confined within the limits of the axial furrows.



17. *Palacorona bacculata* gen. et sp. nov., cranial reconstruction based on CPC 9761, x8.

The occipital furrow is wide, arched forward mesially, very deep abaxially, but not joining the axial furrows. The occipital ring is of similar transverse width to the preoccipital glabellar lobes; sagittally narrow. In profile it does not rise appreciably above the level of the glabellar side lobes.

The palpebral lobes are raised high above the palpebral areas, and are differentiated by strong palpebral furrows. They are crescentic in plan, small, and extend from the posterior edge of the preoccipital lobes to the middle of the median lateral lobes in the smaller specimens (Pl. 15, fig. 1), or from the middle of the preoccipital lobes to the median lateral furrows in larger specimens (Pl. 15, fig. 5); they occupy about 30 percent of the glabellar length (exag.). The palpebral areas are wide (tr.), 62-74 percent of the preoccipital glabellar width (tr.), and slightly convex. The palpebral lobes are connected to the frontal glabellar lobe by ocular ridges which intersect the axial furrows at angles of approximately 60°.

The postocular sections of the facial suture diverge sharply from the back of the eyes and pass obliquely to the posterior margins of the cranidium, intersecting them at angles of approximately 30°. They enclose long triangular posterolateral limbs. The posterior border furrows are wide (exsag.), but not deep; the posterior

cranial margins narrow (exsag.), and slightly sinuous. The preocular sections of the facial suture diverge outwards to a point opposite the anterolateral margins of the glabella, then curve inwards to meet anteriorly at right angles. The preglabellar field is a shallow concave depression into which slope the preocular fixigenal areas and the frontal lobe of the glabella. The margins of these morphological areas lie on roughly the same transverse line. Anteriorly the preglabellar furrow turns upwards, and passes without appreciable differentiation into a triangular cranial border.

Two types of prosopon are visible. One is represented by a mixture of coarse and fine granules, perforated when eroded down (Pl. 15, fig. 5). These granules are more thickly distributed on the glabella than on the cheeks, preglabellar field or border. The second type of prosopon is of raised caeca, well seen on the preglabellar field in Plate 15, figure 5.

Comparisons and differences. *Palacorona bacculata* can be satisfactorily compared only to species of *Tingocephalus*. *T. granulosus* Sun (1935, pp. 62-3, pl. 3, figs 26-27), from the Tawenkou Formation of Taian, Shantung, and the Lower Wolungshan Formation of Huolu, Hopei, is difficult to interpret owing to the very poor illustrations of Sun. His text-figure (p. 62) and comments, however, indicate that the anterior cranial border is only slightly angled, but otherwise similar to that of *Palacorona bacculata*. The bacculae are more extensive, and the posterolateral limbs are apparently longer. The glabella lies posterior to the margins of the preocular areas.

Tingocephalus magnus Kobayashi (1960b, p. 358, pl. 20, fig. 17), from *Kaolishania*-bearing strata south of Tanggok, South Korea, has a cranial outline and arrangement of glabella to preocular areas similar to *T. granulosus*. The bacculae are more laterally extensive, and the palpebral areas wider than those of *Palacorona bacculata*. The test of *T. magnus* is smooth.

Tingocephalus concavolimbatus (Endo) (*in* Endo & Resser, 1937, p. 330, pl. 70, figs 20-22), from the Daizan Formation of Paichiashan, southern Manchuria, is reminiscent of the smallest available specimens of *Palacorona bacculata*. It has a similar preglabellar field and cranial outline, but is differentiated by the position of the frontal lobe of the glabella and its extensive bacculae.

Superfamily DIKELOCEPHALACEA Miller, 1889

Family SAUKIIDAE Ulrich & Resser, 1930

Genus LOPHOSAUKIA nov.

Type species. *Lophosaukia torquata* gen. et sp. nov., from the late Upper Cambrian Gola Beds, Momedah Creek, western Queensland.

Name. Greek, *lophos*, crest or comb, prefixing the generic name *Saukia*. *Lophosaukia* is named from its prominently protruded anterior cranial border.

Diagnosis. A saukiid genus with the anterior cranial border reduced to a triangular area, either strongly sloping adventrally, or lying in a nearly horizontal plane; and a deep preglabellar furrow which undermines the frontal lobe.

Comparisons and differences. *Lophosaukia* is an unusual saukiid with restricted anterior border. Anterolaterally the preocular sections of the facial suture are subparallel, enclosing narrow strips of fixigenae. Anteriorly they border the

preglabellar furrow, and converge in a decided apex which encloses a small mesially downsloping, triangular cranial border. These characteristics distinguish *Lophosaukia* from other Saukiidae. *Sinosaukia* Sun, 1935, the closest relative, has a wider preglabellar furrow, and laterally more extensive cranial border, less steeply inclined and only slightly angled (Sun, 1935, p. 52).

Other species. Several other species described in the literature have the generic attributes of *Lophosaukia*. These are:

Prosaukia(?) *orientalis* Kobayashi (1933, p. 126, pl. 13, fig. 10), *Tsinania* 'Zone,' Paichiashan, Wuhutsui basin, southern Manchuria. This species becomes *Lophosaukia orientalis* (Kobayashi, 1933).

Saukia(?) *orientalis* Resser & Endo (in Endo & Resser, 1937, p. 285, pl. 55, figs 14-16; ? pl. 71, figs 24-28), Yenchou Formation, Paichiashan, near Chinchichengtzu, southern Manchuria. This species may be synonymous with *Prosaukia*(?) *orientalis* Kobayashi, 1933, which is from the same locality. If not, then a new name is required for the Resser & Endo species.

Prosaukia ulrichi Kobayashi (1933, p. 125, pl. 13, fig. 11), *Tsinania* 'Zone,' Paichiashan, southern Manchuria. This species becomes *Lophosaukia ulrichi* (Kobayashi, 1933).

Sinosaukia pustulosa Sun *pars* (Sun, 1935, pp. 52-53, pl. 5, figs 2a, b, 5a, b; non figs 1, 3, 4, 6 = *S. pustulosa* Sun *sensu stricto*), from either the Upper Wolungshan Formation, *S. pustulosa* Zone, of Huolu, or the Kaolishan Formation, *Quadricephalus walcotti* Zone, of Kaolishan, Taian, Shantung, China. Sun does not specify which of his localities his individual specimens come from. A new species name appears to be required for the specimens in question.

Ptychaspis angulata Mansuy var. *chinensis* Sun (1924, pp. 67-68, pl. 5, figs 1a, b), Kaolishan Formation, conglomeratic limestone of Taian Shantung, China. This species becomes *Lophosaukia chinensis* (Sun, 1924).

Ptychaspis angulata Mansuy *pars* (Mansuy, 1916, p. 34, pl. 6, figs 1a, b; non figs 12a, b = ?*Sinosaukia pustulosa* Sun; non *Ptychaspis angulata* Mansuy, 1915, p. 25, pl. 3, figs 2a-v, a mixture of saukiid cranidia being figured here), horizon with *Tsinania ceres* (Walcott), Luong Co, North Vietnam. If they are not equivalent to other species described above, a new name is required for Mansuy's specimens.

LOPHOSAUKIA TORQUATA gen. et sp. nov.

(pl. 18, figs 1-6; Text-fig. 18)

Name. Latin, *torquata*, adorned with a collar: alluding to the collar-like anterolateral fixigenae.

Holotype. The cranium, CPC 9765, figured here on Plate 18, figures 1-3.

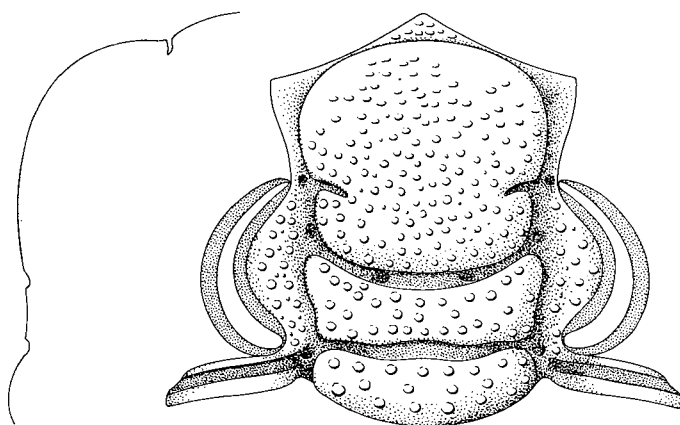
Material. The species is known from nine cranial fragments. They range in cranial length (sag.) between 4.55 and 6.00 mm.

Occurrence. *Lophosaukia torquata* occurs in coarsely crystalline calcarenite layers at K102, B520 and B753. It is notably absent from locality B750.

Diagnosis. The generic diagnosis sufficiently covers the species.

Description. The glabella is more or less cylindrical, widening a little anteriorly

across the frontal lobe, anteriorly rounded. It is strongly convex (sag.), the frontal lobe being strongly curved anteriorly and bent under to the extent that the anterior margin lies at an angle of 180° to the dorsal surface of the lateral side lobes. Two pairs of glabellar furrows are visible on all specimens. The preoccipital furrows are abaxially deep, and continue across the sagittal line as a shallow groove, dividing the glabella into two parts. The anteriormost furrows are short shallow grooves lying on the glabellar flanks. The glabella is widest (tr.) across the median lateral lobes. When the dorsal surface of the preoccipital lobes is mounted in a horizontal plane the glabellar length occupies 75 percent of the cranial length.



18. *Lophosaukia torquata* gen. et sp. nov., cranial reconstruction based on CPC 9765, x9.

The occipital furrow is deep abaxially, shallow mesially, relatively wide (sag.). The occipital ring has nearly the same width (sag.) as the mesial width (sag.) of the preoccipital lobes, and it is equally wide (tr.). In lateral profile the occipital ring rises slightly above the level of the glabellar side lobes. The axial furrows defining the occipital ring and the glabella are deep, and bear paired pits at their confluence with the occipital and glabellar furrows. Another pair of pits lies at the anterolateral margins of the glabella.

The palpebral lobes are well defined by deep palpebral furrows; they are gently convex and rise appreciably above the palpebral areas. Deep palpebral ledges run around the abaxial margins of each palpebral lobe and the facial suture runs along the outer edge of these. The palpebral lobes occupy approximately 55-60 percent of the glabellar length (sag.) and extend from the occipital furrows to the confluence of the anterior glabellar furrows and the axial furrows. Posteriorly the palpebral lobes abut against the posterior cranial border furrow and come close to the occipital ring. The palpebral areas are narrow (tr.), gently convex, and gently sloping to the deep axial furrows.

The postocular sections of the facial suture diverge sharply from the back of the eyes and enclose moderately long (tr.), blade-like posterolateral limbs, which bear wide marginal furrows. The preocular sections diverge forwards slightly; then follow close to the line of the axial furrows as far as the anterolateral margins of the glabella, enclosing narrow (tr.) strips of preocular fixigenae. Opposite the anterolateral corners of the glabella they swing through a near right angle and pass obliquely to the anterior, intersecting at an obtuse angle in front of the glabella. The anterior cranial border is restricted to a small triangular

area, placed sagittally, which slopes strongly adventrally, in fact lying nearly normal to the dorsal surface of the glabellar side lobes (Text-fig. 18). The preglabellar furrow is deep sagittally, undercutting the frontal lobe. Anterolaterally it is bounded by the preocular sections of the facial suture, and anteriorly by the anterior cranial border.

The cranidium of *Lophosaukia torquata* has a pustulose prosopon; pustules are present on the glabella, occipital ring, palpebral lobes, and anterior cranial border. On the preoccipital glabellar lobes these pustules are arranged in two major transverse rows, three on the occipital ring, but as far as can be ascertained they are randomly distributed on the frontal lobe and palpebral areas. The pustules are much larger on testiferous specimens; when the shell is removed they are no larger than granules (Pl. 18, fig. 4).

Comparisons and differences. The strongly downslipping triangular anterior cranial border of *Lophosaukia torquata* is closely comparable to that seen on some specimens figured by Sun (1935, pl. 5, figs 2a, 5b) as *Sinosaukia pustulosa*, and additionally these specimens show the strong convexity (sag.) of the frontal glabellar lobe. Judging from the tilting of the illustration, the specimen figured by Mansuy (1916, pl. 6, fig. 1a) as *Ptychaspis angulata* also has the adventrally sloping cranial border. That of *Saukia* (?) *orientalis* Resser & Endo (in Endo & Resser, 1937, pl. 55, figs 14, 15) has the cranial border raised into the plane of the glabella and the frontal lobe has appreciably less sagittal convexity. *Ptychaspis angulata* Mansuy var. *chinensis* Sun (Sun, 1924, p. 67, pl. 5, figs 1a, 1b), *Prosaukia* (?) *orientalis* Kobayashi (1933, pl. 13, fig. 10), and *Prosaukia ulrichi* Kobayashi (loc. cit., fig. 11), all of which have a similar cranial border to that of *Lophosaukia torquata*, cannot be adequately compared for want of lateral profile illustrations.

Apart from the anterior border, and morphological features associated with it, *L. torquata* is in general comparable with species of *Saukia*. The strongly defined palpebral ledge, for instance, is found in other sauikiid trilobites: *Saukia separatoidea* Ulrich & Resser (1933, pl. 30, fig. 10), *S. subrecta* Ulrich & Resser (1933, pl. 28, fig. 12), and *Saukia* (?) *orientalis* Resser & Endo (in Endo & Resser, 1937, pl. 55, fig. 16).

Superfamily INCERTAE SEDIS

Family SHUMARDIIDAE Lake, 1907

Genus EOSHUMARDIA Hupé, 1953

Type species. *Shumardia orientalis* Mansuy (1916, p. 18, pl. 1, figs 28a-e) from an horizon with *Calvinella walcotti*, of Fengshanian age (Kobayashi, 1944), Li-kouan-keu, Tonkin-Yunnan border, North Vietnam.

Comment. Kobayashi (1944, p. 119) and Saurin (1956, p. 399) have previously referred *Shumardia orientalis* Mansuy to *Koldinioidea* Kobayashi, 1931. As, however, *S. orientalis* lacks genal spines and eyes, which are present in the type species *Koldinioidea typicalis* Kobayashi (1931, p. 187, pl. 22, figs 8, 9b), Hupé (1953) erected a new genus, *Eoshumardia*, to accommodate it. His diagnosis is as follows: 'glabella subconical; glabellar furrows present, a pair of intercalating furrows; an occipital spine; pericephalic rim absent; pygidium relatively large with five axial rings' (Hupé, 1955, p. 154).

Name. Latin, *cylindrica*, cylindrical; describing the shape of the glabella.

Holotype. The cephalon CPC 9768, illustrated on Plate 18, figure 8.

Material. The species is not common. Five cephalons were prepared, two of which are illustrated on Plate 18. They are very small, ranging in length (sag.) from 0.95 to 1.35 mm.

Occurrence. *Eoshumardia cylindrica* occurs in both calcarenite and calcilutite matrices, at horizons B750 and B520A. It is most abundant at B750, from which ten determinable fragments were obtained.

Diagnosis. *Eoshumardia cylindrica* is characterized by: a semicircular cephalic outline; cylindrical glabella, anteriorly depressed and rounded, not expanded laterally; two pairs of glabella furrows; and an apparent absence of eyes.

Description. The cephalon is convex (tr. and sag.), with semicircular outline. The glabella is cylindrical, defined by nearly parallel axial furrows which become faint anteriorly. Two pairs of short faint discontinuous furrows lie on either flank of the glabella. The frontal lobe is anteriorly rounded and depressed. A pair of swellings is present laterally but these do not expand across the courses of the axial furrows as they do in species of *Shumardia*.

The occipital furrow is faintly impressed. The occipital ring is as wide (tr.) as the basal glabellar lobes, and in lateral view is not appreciably elevated. A faint nuchal node is present.

The preglabellar field, which occupies about 15 percent of the cephalic length, is gently convex (sag.). The posterolateral corners of the cephalon (?) are non-spinose and the posterior marginal furrows appear to terminate distally before reaching them. Eyes and facial sutures are apparently absent.

The hypostome, thorax, and pygidium are unknown.

Comparisons and differences. The specimens at hand are not so well preserved that I can be sure that cephalons of *Eoshumardia cylindrica* are not in actual fact cranidia. No trace of a facial suture has been seen on these specimens and there are apparently no eyes. Whittington (1965, p. 329, pl. 16, fig. 17) has demonstrated the presence of a facial suture in *Shumardia granulosa* Billings, showing that many specimens originally illustrated as cephalons are probably cranidia. For this reason the term cephalon might be queried in the descriptions.

Eoshumardia cylindrica is differentiated from *E. orientalis* (Mansuy, 1916) notably by the absence of a nuchal spine and by the less pronounced lateral swellings of the frontal lobe; but in other respects they are very similar. *E. cylindrica* is differentiated from species of *Shumardia* by the less expanded lateral swellings of the frontal lobe, which in *Shumardia* may form large eye-like lobes, e.g. *S. granulosa* Billings (see Whittington, 1965, pl. 16). The anteriorly rounded frontal lobe of species of *Eoshumardia* differentiates them further from species of *Shumardia*, from *Shumardops* Hupé, 1953, and *Leioshumardia* Whittington, 1965, all of which have anteriorly pointed frontal lobes. The large raised eye spots of species of *Shumardops* and *Koldinioidea* Kobayashi, 1931, are not found in those of *Eoshumardia*. Species of *Hospes* Stubblefield, 1927, *Koldinioidea*, and *Leioshumardia* have anteriorly tapering glabellae.

Several species which have been described under *Koldinioidea*, however, have close morphological relationship to *Eoshumardia cylindrica*. *Koldinioidea paiensis* Endo (in Endo & Resser, 1937, p. 329, pl. 71, fig. 5) and *K. aspinosa* Kobayashi (*sensu* Endo, 1939, p. 9, pl. 1, fig. 23), from the Yenchou Formation of Manchuria and the highest Tawenkou Formation of Shantung, north China, are closely comparable. The more recently described *Koldinioidea sulcatus* from the Tiñu Formation of Nochixtlán, Oaxaca, Mexico (Robison & Pantoja-Alor, 1968, 796-7, pl. 104, figs 20-23) must, however, be considered the closest adequately described species.

Superfamily and family INCERTAE SEDIS

Genus DELLEA Wilson, 1949

Type species. *Dellea wilbernensis* Wilson (1949, pl. 11, figs 1-2, 4-7, 12), from the Morgan Creek Member, Wilberns Limestone, Elvinia Zone, basal Franconian, Texas, USA.

Comment. *Dellea* is a genus described previously from the Franconian of North America, where it is known from central Texas (Wilson, 1949, 1951), Oklahoma (Frederickson, 1949), Maryland (Wilson, 1951), Pennsylvania (Wilson, 1951), and New York (Resser, 1942a). Because the species described below is known from such a small number of specimens it is placed in this typical North American genus with some reserve.

DELLEA(?) LAEVIS sp. nov. (Pl. 17, figs 5-7)

Name. Latin, *laevis*, smooth, polished: describing the smooth cranidial test.

Holotype. The cranidium CPC 9770, illustrated on Plate 17, figs 5-7 (three views).

Material. The species is known from a suite of five incomplete cranidia. The maximum observed cranidial length is 3.75 mm.

Occurrence. *Dellea(?) laevis* is confined to coarse-grained calcarenite at locality K102.

Diagnosis. A species of *Dellea* (?) with narrow (tr.) prelabellar area; long posterolateral limbs; convex glabella (sag.) and prelabellar field (sag.); small eyes, close to the glabella; steeply inclined palpebral areas; smooth test.

Description. The glabella is subrectangular, anteriorly gently rounded, tapering very slightly forwards. It occupies about 60 percent of the total cranidial length (sag.). Three pairs of glabellar furrows are present but are extremely faintly impressed. Of these, the preoccipital furrows, the most readily discernible, are long, projected inwards and backwards. The median lateral furrows are similarly oriented but very faint. The anterior lateral furrows are scarcely visible; they lie as short depressions on the flanks of the glabella. In lateral profile the glabella obtains a moderate sagittal convexity (Pl. 17, fig. 6).

The occipital furrow is shallow and broad mesially, arching a little to the anterior. The occipital ring is narrow (sag.) and in profile lies below the level of the glabella. It is slightly wider (tr.) than the preoccipital glabellar lobes.

The palpebral lobes are poorly defined, small, occupying 57 percent of the

glabellar length, and sited between the confluence of the axial furrows with the preoccipital glabellar furrows and the middle of the anterior lateral glabellar lobes. Between the back of the eyes and the posterior marginal furrows are areas of fixigenae approximately equivalent to 52 percent of the eye-length. The palpebral areas are narrow, posteriorly 40 percent of the preoccipital glabellar width (tr.), and steeply inclined to the axial furrows.

The preocular sections of the facial suture diverge forwards at low angles to the sagittal line, enclosing moderately convex (sag.) preglabellar and preocular areas, which occupy 16 percent of the cranial length. These slope evenly to a well marked anterior marginal furrow flanked anteriorly by a border which occupies some 12 percent of the cranial length (sag.). The ocular ridges are very faint. The postocular sections of the facial suture enclose laterally extensive posterolateral limbs which have shallow border furrows. The axial furrows are well impressed, but shallow. Two pits lie in these furrows at the anterolateral margins of the glabella.

Apart from the anterior border the surface of the cranium is smooth. The border bears a faint prosopon of raised lines.

Comparisons and differences. Although extending the higher range of *Dellea*, the present species fits well into the concept of that genus. It differs from the type species, *D. wilbernensis* Wilson from the Wilberns Limestone of central Texas, *D. suada* (Walcott) *sensu* Wilson (1951, pp. 636-7, pl. 91, figs 4-10, 18, 20-23, 25, 26), from the Ore Hill Limestone of Pennsylvania, and *D. sarotogensis* (Resser) (see 1942a, p. 91, pl. 15, figs 22-25), from the Potsdam Sandstone of New York, in having narrower (tr.) limbs, and a more rectangular glabella.

Dellea juvenalis Frederickson (1949, p. 351, pl. 69, figs 8-15), from the Honey Creek Limestone of the Arbuckle and Wichita Mountains of Oklahoma, and *D. butlerensis* Frederickson (loc. cit., figs 16-18), from the same formation and State, are essentially similar to *Dellea(?) laevis*. Particularly comparable are those specimens illustrated by Frederickson (pl. 69, fig. 18) and Wilson (1951, pl. 91, figs 1-3). *D.(?) laevis* differs from these in having a lower sagittal convexity, shorter (sag.) preglabellar field, and somewhat varying glabellar proportions.

The cranium figured by Bell, Feniak, & Kurtz (1952, p. 188, pl. 34, fig. 2a) as *Monocheilus anatinus* (Hall), from the *Ptychaspis granulosa* and *P. striata* teilzones of Minnesota, differs from *D.(?) laevis* mainly in its smaller, forward placed eyes, but in other respects is similar.

GENUS LORRETTINA NOV.

Type species. *Lorrettina macrops* gen. et sp. nov., from the late Upper Cambrian Gola Beds, of Momedah Creek, western Queensland.

Name. The name *Lorrettina* is derived from the homestead called Lorrett Downs, on the eastern bank of the Hamilton River, approximately nine miles northeast of the main Gola Beds outcrop.

Diagnosis. A genus of uncertain familial classification with the following distinguishing cranial characteristics: three pairs of glabellar furrows; narrow (sag.), convex preglabellar field; narrow (tr.), downsloping, and extended anterior cranial border; large anteriorly placed eyes, close to the glabella; narrow (tr.) palpebral areas.

Comparisons and differences. *Lorrettina* is a ptychoparioid trilobite most closely related to certain genera which Lochman (1959) has placed in the Dokimocephalidae. As interpreted by Lochman this family is largely indicative of the Franconian; in fact only one of the genera which Lochman included in it, *Heterocaryon* Raymond, 1937 (*H. platystigma*), ranges into the Trempealeauan, and this is atypical of the family.

Lorrettina is morphologically most closely comparable to *Kindbladia* Frederickson, 1949, a genus originally described from the Honey Creek Limestone of Oklahoma, but subsequently recorded from South Dakota, Missouri, and Nevada. *Kindbladia* exists within the basal Franconian, *Elvinia* Zone. *Lorrettina* and *Kindbladia* are related by common glabellar shape and furrowing, and similarly convex preglabellar fields. They differ in the size, and to some extent position, of the eyes. *Lorrettina* has a narrower (tr.) anterior cranial border, more or less transverse rather than bowed forwards. In this last respect *Lorrettina* is comparable with *Taenicephalus* Ulrich & Resser in Walcott, 1924, and *Glyptometopsis* Rasetti (1961, p. 113) as illustrated by *G. tumida* (see Clark & Shaw, 1968, pl. 54, figs 20-25).

LORRETTINA MACROPS gen. et sp. nov.

(Pl. 17, figs 1-4; Text-fig. 19)

Name. Greek, *macrops*, large eyes.

Holotype. The cranidium, CPC 9771a, figured here on Plate 17, figure 1. A latex mould from the counterpart of the holotype is also figured (specimen CPC 9771b, Pl. 17, fig. 4).

Material. The species is represented by six incomplete cranidia. No pygidia are known. It has been found impossible to prepare out the posterolateral limbs on the illustrated specimens owing to the nature of the matrix, large plates of calcite adhering to the thick granular test. Three measurable specimens have cranial lengths (sag.) ranging between 6.35 and 7.00 mm.

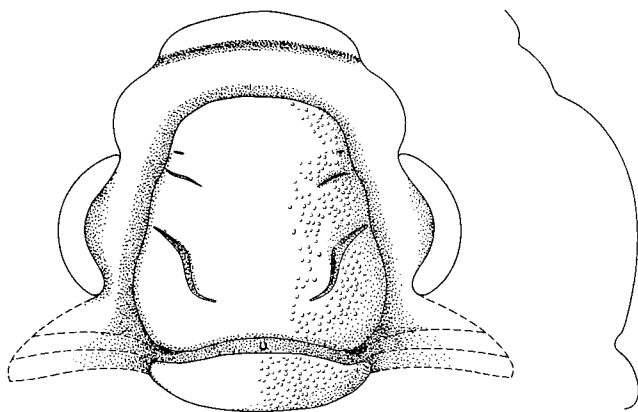
Occurrence. *Lorrettina macrops* occurs in coarse calcarenite layers at localities B520 and B753.

Diagnosis. See the generic diagnosis, which is culled from this species.

Description. The glabella is appreciably convex (tr. and sag.), is broad-based, tapers forwards, and is anteriorly rounded. Three pairs of glabellar furrows are present on all specimens, the anteriormost being often very faint. The preoccipital furrows are deeply impressed, sigmoidal in shape, and curve sharply to the posterior; they reach and join the axial furrows. The median lateral furrows, also deeply incised, are short, gently curved inwards and slightly backwards; they are confluent with the axial furrows. The anterior lateral furrows are short, faint, transversely oriented or gently curved. The preoccipital glabellar lobes are abaxially rather narrow (tr.). The glabella occupies 60-63 percent of the total cranial length (sag.).

The occipital furrow is wide (sag.) and shallow. The occipital ring is raised a little above the glabella in lateral profile. Its transverse width is equivalent to that of the preoccipital glabellar lobes. There is no nuchal node.

The axial furrows are deep and very wide (tr.), uniting anteriorly to form a shallow but wide (sag.) preglabellar furrow. The preglabellar field is narrow (sag.), amounting to 12-14 percent of the cranial length (sag.), and moderately



MPV 92

19. *Lorrettina macrops* gen. et sp. nov., cranial reconstruction based on CPC 9771a, x8.

convex, falling to a shallow, wide marginal furrow. The anterior border is widest sagittally, and drawn out a little anteriorly.

The palpebral lobes are elevated above the surrounding areas, delineated by strong palpebral furrows. They are arcuate in plan, placed forwards on the cheeks, between the anterior edge of the preoccipital glabellar lobes and the middle of the anterior lateral lobes, occupying 50-57 percent of the total glabellar length. The palpebral areas are convex (tr.), narrow (tr.), sloping both to the palpebral and axial furrows. Wide areas of fixigenae are presumed to lie between the back of the eyes and the posterior marginal furrows of the cranidium. Ocular ridges are extremely faint or absent altogether.

The preocular sections of the facial suture curve outwards across the convexity of the preocular areas, thence rapidly inwards towards the sagittal line to restrict the width (tr.) of the anterior cranial border.

The surface of the whole cranidium is covered with fine granules.

Genus CRUCICEPHALUS nov.

Type species. *Crucicephalus ocellatus* gen. et sp. nov., from the late Upper Cambrian, Gola Beds, Momedah Creek, western Queensland.

Name. *Crucicephalus*, literally cross-head; its name is derived from the association of glabella, preglabellar boss, and ocular ridges in the form of a cross.

Diagnosis. A genus of uncertain familial status with: a narrow (sag.) pitted anterior border; a preglabellar boss; long, straight, transverse ocular ridges; very small, pin-head eyes; distally extended posterolateral limbs which culminate in intergenal spines; alae and bacculae; a straight transverse posterior cranial border.

Comparisons and differences. At first sight *Crucicephalus* appears to be morphologically similar to two genera described by Rasetti, *Pareuloma* and *Zacompsus*, from Newfoundland and Quebec. *Pareuloma brachymetopa* Rasetti (1954, pp. 584-5, pl. 60, figs 1-8), from the early Ordovician of Broom Point, Newfoundland, and Cap des Rosiers, Quebec, has a similar pitted border, preglabellar boss, long, transverse ocular ridges, small eyes, and similar glabellar

furrowing. It is, however, distinguished from *Crucicephalus* by lacking bacculae and intergenal spines. Furthermore, its glabella tapers forwards, the preocular sections of the facial suture diverge, rather than converge, forwards, and the posterolateral limbs are decidedly shorter.

Crucicephalus also shares some morphological characteristics with a second eulominid, *Euloma cordilleri* Lochman (1964, pp. 464-5, pl. 63, figs 27-38) from Zone A, basal Ordovician, of Montana. This also has a pitted anterior border and preglabellar boss, but Lochman's specimens are insufficiently preserved to carry detailed comparison further.

?*Zacopsus*, as typified by ?*Z. levisensis* Rasetti (1944, p. 258, pl. 39, fig. 6; 1945, p. 475, pl. 62, figs 18, 19) from the Lévis conglomerates of Quebec, also has characteristics in common with *Crucicephalus*. However, this trilobite lacks boss, bacculae, pitted border, and intergenal spines. Although the eyes of both *Pareuloma* and ?*Zacopsus* are small, they are not the pin-head eyes of *Crucicephalus*. All three genera, however, have a decided ptychoparioid appearance, although the straight ocular ridges, extended posterolateral limbs, small eyes, and glabellar shape are reminiscent also of Olenidae. More than one of the diagnostic features of *Crucicephalus* indicates morphological resemblance with Nepeidae. On the other hand several features indicate possible relationship with Harpididae. In both *Crucicephalus* and *Loganopeltoides*, for instance, the posterior cephalic margin has a distinct geniculation. This in combination with the probable arrangement of the facial sutures at the pin-head eyes looks forwards to the situation found in Harpididae and Entomaspidae in general. Alae, and often bacculae, are also common features in the suborder Harpina.

CRUCICEPHALUS OCELLATUS gen. et sp. nov.
(Pl. 16, figs 1, 2, 8; Pl. 19, fig. 6; Text-fig. 20)

Name. Latin, *ocellatus*, having small eyes.

Holotype. The cranidium, CPC 9775, figured here on Plate 16, figure 1.

Material. Five incomplete cranidia and a possible free cheek are all that is known of this species, but enough is preserved to allow the cranidial characteristics to be interpreted in some detail. The cranidial lengths (sag.) vary between 3.50 and an estimated 4.70 mm.

Occurrence. The species occurs in a matrix of coarse calcarenite at locality K102, and a single fragment was recovered from sandy calcilutite at B750.

Diagnosis. *Crucicephalus ocellatus* has all the attributes listed in the generic diagnosis.

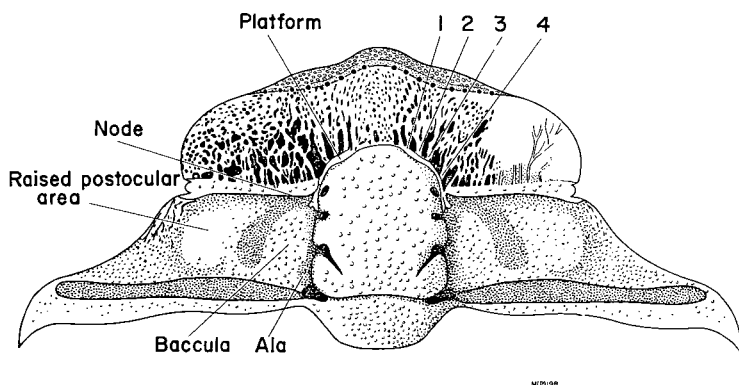
Description. The cranidium of *Crucicephalus ocellatus* is characterized by a median preglabellar boss and extensive posterolateral limbs.

The glabella is subrectangular, elevated, anteriorly rounded, and occupies a little over half the total cranidial length (sag.). It bears three pairs of glabellar furrows. The preoccipital furrows are deeply incised, sigmoidal, with posterior median deflection, opening out abaxially and becoming confluent with the axial furrows. The median lateral furrows are short (tr.) deep grooves lying on the flanks of the glabella, a little over half-way along its length from the rear. The anterior lateral furrows are pits, lying on the glabellar flanks somewhat to the anterior of the median lateral furrows; these pits are isolated from the axial furrows.

The occipital furrow is shallow, save abaxially, where it passes into deep apodemal pits. The occipital ring appears to have been long (sag.), but it is not preserved in entirety on any of the available specimens. Laterally it does not rise appreciably above the glabellar side lobes.

Unusually long ocular ridges, straight and transversely projected parallel to the posterior cranial margins, originate from a point on the axial furrows opposite the anterior glabellar pits. They are expanded distally into small button-like palpebral lobes which are damaged on all the available specimens.

The preglabellar and preocular fields are long (sag.), occupying about one-third of the total cranial length. They are appreciably convex (tr. and sag.); the preglabellar field is raised into a convex boss and the anterior border and anterior cranial margins are bowed forwards around it. The border itself is narrow and restricted to a small area sagittally. The marginal furrow is a shallow ledge carrying pits, five on each side of the sagittal line (Pl. 16, fig. 2). The preocular sections of the facial suture curve forwards from the eyes and around the convexity of the preocular areas, cutting in sharply towards the sagittal line on reaching the marginal furrow, and restricting the width (tr.) of the anterior cranial border. The postocular sections of the facial suture curve gracefully backwards and outwards to enclose long, but narrow, posterolateral limbs. These excluded, the fixigenae are essentially rectangular. They comprise several morphological elements. Adjacent to the preoccipital glabellar lobes lie depressed rounded alae which blend into the axial furrows. Adjacent to the remainder of the glabella, and extending from the ocular ridges to the posterior marginal furrows, are crescentic raised areas, termed bacculae. These in turn are flanked by shallow depressions whose relief is accentuated by gently convex 'cushions' lying between the midpoint of the ocular ridges and the posterior marginal furrows. Lying in the floor of the axial furrows at their junctions with the ocular ridges are small sac-like swellings whose function and morphological significance are uncertain.



20. *Crucicephalus ocellatus* gen. et sp. nov., cranial reconstruction based on CPC 9775, x8, showing caecal network and selected morphological elements.

The posterior cranial margins are straight proximally, parallel to the ocular ridges, but directly below the eyes they become gently sigmoid and distally drawn out into stout intergenal spines. The posterior marginal furrows are shallow but wide, widening distally.

Associated on the same piece of rock as the two cranidia figured on Plate 16 is a free cheek, the three specimens lying within the same square inch of surface.

This librigena is illustrated on Plate 19, figure 6. Its assignment to *Crucicephalus ocellatus* is open to some dispute as it is incomplete where it would fit against the palpebral lobes.

The prosopon is formed of granules and caeca, the former often overlying the latter to give a maze-like surface texture (seen on the postocular areas, Pl. 16, fig. 2). Ramified caeca are exceedingly well preserved on the preglabellar, preocular and postocular areas (in the case of the last, just below the eyes). Four pairs of main veins (Text-fig. 20) give rise to a densely branching network across the preglabellar area. These caeca have their origins in a smooth, shadowy parafrontal band which lies laterally in the axial furrows at the anterolateral margins of the glabella, and anteriorly in the preglabellar furrow. One pair of veins is initiated at the point where the anterior edges of the ocular ridges and preglabellar furrow coincide, this pair radiating outwards anterolaterally across the preocular areas. The other three pairs of caeca have their origins close together on the base of the boss, which they effectively define. These give rise to the caecal network on the highest point of the boss, in front of the glabella. The caeca of the preocular areas are derived largely from veinlets arising from the ocular ridges whence they branch finely to give a second large area of reticulation. A major caecal system is connected with the palpebral lobes, and this gives rise to the highly reticulate network of the postocular areas.

The surface of the glabella bears coarsely granular prosopon. Similar granules are found elsewhere on the anterior and posterior borders, and superimposed on the caecal capillary network in various places, but particularly on the postocular areas.

Genus DUPLORA nov.

Type species. *Duplora clara* gen. et sp. nov., from the late Upper Cambrian Gola Beds, Momedah Creek, western Queensland.

Name. *Duplora* is compounded from the Latin, *duplus*, double or twofold, and Latin, *ora*, edge or margin: this name refers to the apparently duplicated anterior cranial border.

Diagnosis. A genus of doubtful familial classification with the following complex of cranial characteristics: anterolateral edges of preglabellar field upraised into a narrow (exsag.) rim, which fades out along the sagittal line; preglabellar field separated from an upraised anterior cranial border by a deep and wide (sag., exsag.) marginal furrow which is impressed as a 'gutter'; preglabellar field slightly swollen mesially; well-defined palpebral lobes and furrows; posterolateral glabellar margins truncated.

Comparisons and differences. Few trilobite genera have the peculiar arrangement of marginal furrow and anterior preglabellar field observed in *Duplora*. *Bellaspidea* Rasetti (type *B. resseri* Rasetti, 1945, p. 466, pl. 60, figs 20-22), however, has a similar overdeepened marginal furrow, and this type of feature seems also to be present in *Paraolenus papilionaceus* Lermontova (1951, pl. 4, figs 4, 5), a species from Kazakhstan. The anterior rim of the preglabellar field appears to be comparable to a similar morphological condition seen in *Ctenopyge neglecta* Westergaard (see 1922, p. 150, pl. 10, figs 10, 14) from Zone 5a of Sweden, but in that species it is continuous across the margin of the preglabellar field and not, as here, interrupted mesially.

The general arrangement of the glabellar furrows, the size and position of the eyes and ocular ridges, and the course of the facial suture, are similar to those seen in *Proteuloma* Sdzuy, 1958. Weathered specimens of *Duplora*, which have widened glabellar furrows, are particularly similar to those of *Proteuloma geinitzi* (Barrande) (see Sdzuy, 1955, pl. 3, figs 77, 79, 81a), from the Tremadocian, Leimitz-Schiefer of Germany, and to some extent also to those of *P. monile* (Salter, 1873) (see Lake, 1940, p. 303, pl. 43, figs 2-9), a species from the Tremadocian Shineton Shale of Salop and Bronsil Shale of the Malvern Hills, British Isles. *Euloma* Angelin, characterized by *E. laeve* Angelin and *E. ornatum* Angelin, differs from *Duplora*, and from *Proteuloma*, by its larger eyes and overdeepened glabellar furrows. *Duplora* could possibly be interpreted as an early representative of Eulominae Kobayashi, 1955.

DUPLORA CLARA gen. et sp. nov.
(Pl. 16, figs 3-7; Text-fig. 21)

Name. Latin, *clarus*, clear, distinct: referring to the sharpness of definition of the preglabellar rim.

Holotype. CPC 9777, the cranidium figured here on Plate 16, figures 3-4.

Material. The figured specimens were selected from a paradigm of ten cranidia. The pygidium remains unknown. Generally the preservation is poor and few specimens are complete, most lacking the anterior border and the posterior part of the glabella and occipital ring. Measured specimens range in cranial length (sag.), estimated or true, between 3.00 and 4.00 mm.

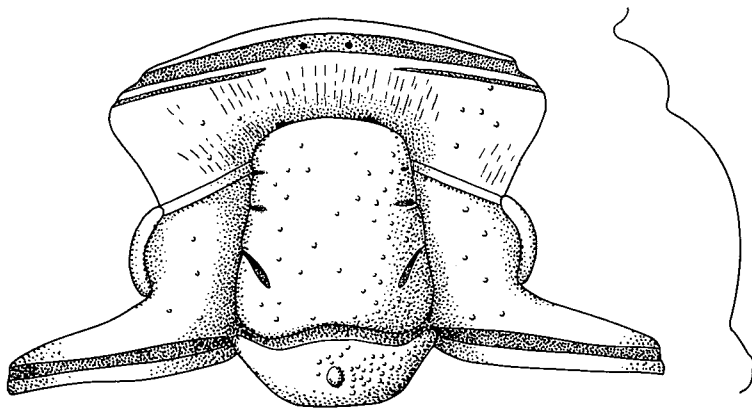
Occurrence. *Duplora clara* occurs at five localities in the Gola Beds, but is most common at K102, where fourteen fragments were recovered from coarse-grained ferruginized calcarenite.

Diagnosis. The generic diagnosis is based on *Duplora clara*.

Description. The glabella is subrectangular, tapering slightly forwards, and occupies approximately two-thirds of the total cranial length (sag.). Two pairs of glabellar furrows are generally visible, and a third, anterior, pair is sometimes seen. The preoccipital glabellar furrows are deep, sloping inwards and backwards. When the shell is preserved they do not reach the axial furrows, but on exfoliated specimens these are confluent. The median lateral furrows are faint short linear grooves or pits, lying on the flanks of the glabella. The anterior lateral furrows, when preserved, are extremely faint and oriented similar to the median furrows.

The posterolateral margins of the glabella are truncated by occipital apodemal pits running parallel to the preoccipital glabellar furrows. Mesially the occipital furrow is wide (sag.) and shallow. The occipital ring is a little wider (tr.) than the preoccipital glabellar lobes, and is often confluent with the posterior border of the cranidium. Mesially the occipital ring is wider (sag.) and bears a nuchal node. In lateral profile it does not rise appreciably above the level of the glabella.

The palpebral lobes are well-defined, arcuate in plan, and strongly raised above the palpebral areas. They extend from the middle of the preoccipital lobes to the level of the median lateral furrows, and occupy approximately 60 percent of the glabellar length. The ocular ridges are well defined proximal to the glabella, but on some specimens become faint near their junction with the palpebral lobes. They intersect the axial furrows at angles of approximately 60 degrees. The palpebral areas are wide (tr.), at their maximum about half as wide (tr.) as the



21. *Duplora clara* gen. et sp. nov., cranidial reconstruction based on CPC 9777a, x15.

preoccipital glabellar lobes, and gently convex. Between the back of the eyes and the posterior marginal furrows are areas of fixigenae amounting to 40-45 percent of the eye length.

The postocular sections of the facial suture diverge rapidly from the back of the eyes and enclose long blade-like posterolateral limbs. The preocular sections diverge outwards as far as the anterior marginal furrow, then slightly inwards to cut across the anterior border.

The preocular areas are gently convex (exsag.), sloping into a slight marginal depression which is flanked anterolaterally by an upraised rim. The rim delimits the anterior extent of the preocular areas. In many specimens the true anterior cranial border is broken off and the rim assumes the appearance of a border. The preglabellar area is also gently convex (tr. and sag.), but is raised slightly above the preocular areas. The anterolateral rim is not present at the anterior margin of the preglabellar area. When preserved the marginal furrow is deep and wide (sag.), with a prominent elevated floor in front of the preglabellar area. On this platform are situated two pits, one on each side of the sagittal line. The true anterior border rises sharply from the marginal groove and rises, in profile, to the level of the preglabellar area.

The surface of the glabella, occipital ring, palpebral areas, and lobes is covered with a finely granular prosopon. The preocular and preglabellar fields bear faintly indicated caeca radiating from the ocular ridges and frontal glabellar lobe.

Comparisons. Only a single previously described species is comparable to *Duplora clara*. This was figured by Westergaard (1909, p. 51, pl. 1, figs 21, 22; 1922, p. 180, pl. 2, figs 21, 22) as *Euloma primordiale*, and is from the *Acerocare* Zone (probably Subzone of *Cyclagnathus*, 6b) of South Öland. It is known from a single fragmentary cranidium and a librigena. The former is surprisingly similar to *Duplora clara*. It lacks an anterior border, as do many specimens of *D. clara*, which perhaps indicates that it had a similar arrangement of marginal groove and border.

Suborder ASAPHINA Salter, 1864

Superfamily ASAPHACEA Burmeister, 1843

Family ASAPHIDAE Burmeister, 1843

Subfamily ISOTELINAE Angelin, 1854

Genus GOLASAPHUS nov.

Type species. *Golasaphus momedahensis* gen. et sp. nov., from the Upper Cambrian Gola Beds, Momedah Creek, western Queensland.

Name. *Golasaphus*: the prefix is derived from the Gola Beds, a late Cambrian stratigraphical unit mapped on the Boulia 1:250,000 Geological Series Sheet.

Diagnosis. An isotelinid genus with the following character complex: anteriorly tapering glabella; occipital lobulae and posterior occipital band; faint palpebral lobes; distally expanded posterolateral limbs; marginal librigenal furrow; short genal spines; semicircular pygidium with entire margin and largely effaced segmentation; narrow axis; wide doublure; paradoublural lines, but no pygidial marginal furrow; hypostome with entire posterior margin; posterior lobe drawn out rearwards; anterior lobe with median cleft; thoracic doublure relatively narrow (tr.).

Comparisons and differences. The diagnostic characteristics of *Golasaphus* are sufficient to distinguish it from all other Asaphidae. Only two other genera are in any way comparable. The most closely related on cranidial characteristics appears to be *Plesiomegalaspis* (*Plesiomegalaspis*) Thorax as interpreted by Tjernvik (1956). Jaanusson (1959 in Moore) questionably includes this genus in synonymy with *Megalaspidella* Kobayashi, 1937, but as there seems to be considerable difference between them in the courses of the preocular sections of the facial suture they are considered here as distinct genera. *P.* (*Plesiomegalaspis*) and *Golasaphus* have similarly shaped cranidia, with preglabellar fields of similar length (sag.) and width (tr.). Their eyes are similarly shaped and of similar size, and there are equivalent features in the glabella and librigena of both genera. They differ in the shape of their posterolateral limbs, in most of their pygidial characteristics, and in some of those of the hypostome.

Asaphellus Callaway, the other comparable genus, has a more rectangular glabella, shorter preglabellar field, wide (exsag.) posterolateral limbs, and smaller eyes, placed farther forward. The pygidia of *Asaphellus* and *Golasaphus* are similar in shape and segmentation, but the former has a marginal pygidial flange.

GOLASAPHUS MOMEDAHENSIS gen. et sp. nov.

(Pl. 10, figs 1-8; Pl. 11, figs 1-9; Text-figs 22-25)

Name. Derived from Momedah Creek, a tributary of the Hamilton River, Boulia 4-mile Sheet, western Queensland. *Golasaphus* is particularly characteristic of the Gola Beds in the Momedah Creek exposures.

Holotype. The large cranidium CPC 9781, figured here on Plate 10, figures 1 and 2.

Material. Fragments of *Golasaphus momedahensis* are common in the Gola Beds and allow much of the species to be fairly accurately reconstructed. No complete specimens are known. Measurements were taken on 10 cranidia, 25

pygidia, and 5 hypostomata. Several librigenae are also known, and one fragment of the ventral surface of a thoracic segment.

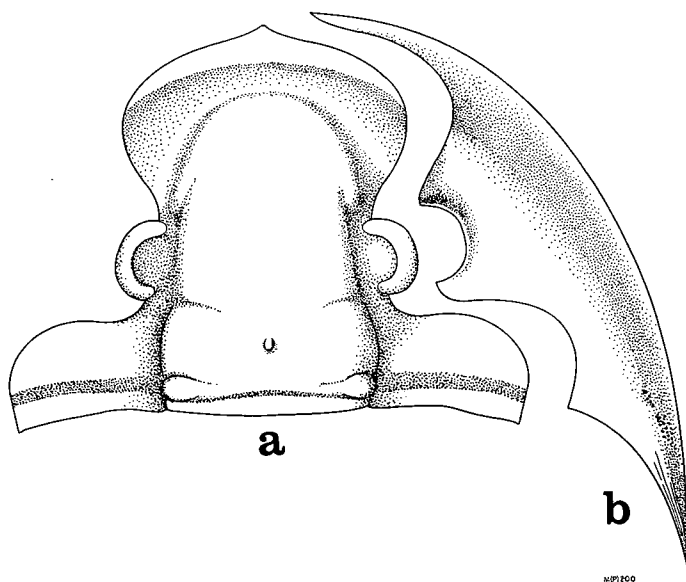
The observed cranidia vary in length between 3.05 and 12.95 mm; only one specimen, the holotype, is longer than 5.80 mm. The pygidia vary in length between 1.55 and 6.25 mm; the majority of specimens (22) fall between 2.25 and 4.55 mm. The hypostomata, measured for width (tr.) rather than length, fall between 2.70 and 7.30 mm.

Occurrence. The species occurs in all the rock types of the Gola Beds, from calcilutite to calcarenite. It has been identified in collections from B750, B752, B753, B520, K101, and K102. One hundred and sixteen determinable fragments were recovered from B750, and 69 from B520.

Diagnosis. The diagnostic characteristics of *Golasaphus momedahensis* are listed under the generic diagnosis.

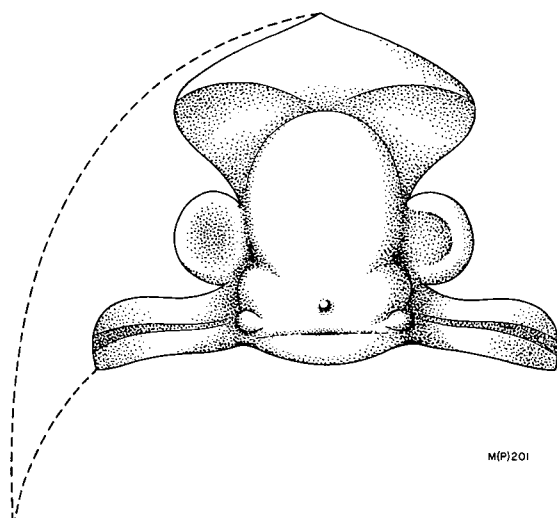
Description. The axial furrows defining the glabella are indistinct laterally, but become more obvious anteriorly. The glabella tapers forwards and anteriorly is acutely rounded. In lateral profile its convexity (sag.) is low. The furrowing is largely effaced, but opposite the midpoint of the palpebral lobes there is a faint constriction of the axial furrows, and shadows indicate the presence of a pair of furrows running adaxially and posteriorly towards the glabellar median node. This node is sited between one-fifth and one-seventh of the way along the cranidium from the rear (15-18 percent of the total length from the rear). On the holotype cranidium (CPC 9781) a pair of furrows seems to run inwards and forwards from a point near the confluence of the palpebral and axial furrows, but these may reflect hypostomal structures impressed by crushing.

Low swellings lie on the posterolateral flanks of the glabella besides the confluence of the posterior cranidial marginal furrows and the axial furrows. These are considered to represent occipital lobulae. A shallow and faint furrow



22. *Golasaphus momedahensis* gen. et sp. nov.
reconstruction of (a) cranidium based on CPC 9781, x4;
(b) librigena CPC 9786, x4.

which cuts across the posterior of the axis of the cranium separates a posterior occipital band from the remainder of the occipital ring, which is confluent with the glabella.



23. *Golasaphus momedahensis* gen. et sp. nov., reconstruction of early holaspid cranium based on CPC 9783, x12.

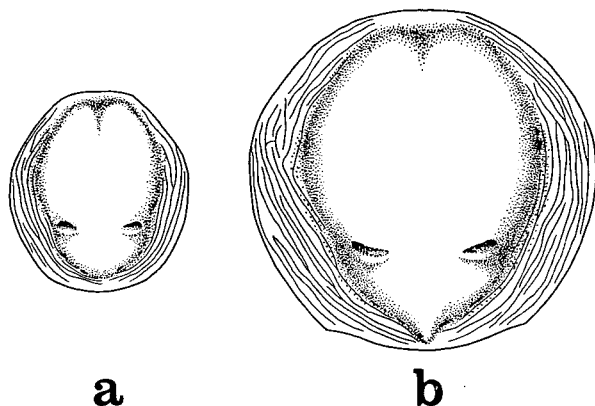
The palpebral lobes are separated from the palpebral areas by weak, but nonetheless visible, palpebral furrows. The lobes are crescentic in plan, and occupy between 22 and 31 percent of the total cranial length (sag.). The areas are narrow (tr.), and slightly inclined to the axial furrows.

The preocular sections of the facial suture curve sigmoidally to the anterolateral border, thence inwards very sharply, uniting on the sagittal line marginally. The anterior cranial border is only slightly elevated above the preglabellar field. The marginal furrow (=preglabellar furrow) is wide and extremely shallow, occupying the entire preglabellar field between the front of the glabella and the border (sag.). Exsagittally the marginal furrow is separated from the axial furrows by gently convex ridges on either side of the glabella, possibly formed as paradoublural lines (Text-fig. 22). Where the preocular sections of the facial suture unite sagittally the cranium is drawn into a short but prominent apex. In length the preglabellar area occupies 16-28 percent of the total cranial length (sag.) and 51-63 percent of the maximum cranial width (tr.) across the posterolateral limbs. The postocular sections of the facial suture curve slightly forwards, expanding slightly the fixigenal length (exsag.). The posterior marginal furrows are shallow and wide (exsag.).

The surface of the glabella, fixigenae, and occipital lobe is smooth.

The librigena is provided with a shallow, wide marginal furrow which passes into the base of the genal spine. The latter is short and carries raised lines running along its length.

In some specimens (Pl. 10, figs 4, 9) a longitudinal keel runs the length of the glabella along the sagittal line and terminates at the median glabellar node. This would be regarded by Harrington (1959) as the impression of the ligament suspensor of the heart and paired muscle scars. Other specimens (Pl. 10, fig. 1) show it associated with muscle scars.



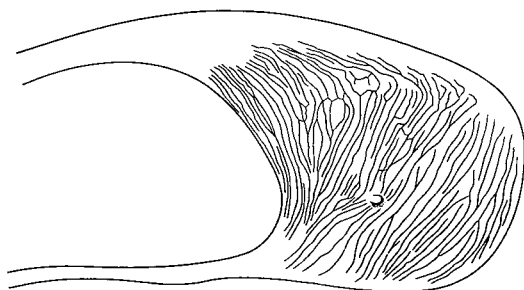
MPI202

24. *Golasaphus momedahensis* gen. et sp. nov., reconstruction of small and large hypostomata, (a) CPC 9788, x9; (b) CPC 9789, x6.

The hypostome is ovoid in outline with very wide lateral borders. Anteriorly the wings are bent under (dorsally) very strongly and are not seen in normal ventral aspect. The posterior margin is entire and non-bifurcated, although the posterolateral corners are decidedly angled. The posterior border is very narrow (sag.), and the anterior border is confluent with the anterior lobe of the median body. The latter, which forms the main part of the hypostome, is more or less heartshaped, being cleft by a median sulcus anteriorly. The maculae are prominent, lying immediately behind short, overdeepened grooves which divide the median body exsagittally. The posterior lobe is triangular in shape, posteriorly drawn out into a blunt point, reaching almost to the posterior margin. Five pairs of pits lie in the marginal furrow at intervals along its length (Text-fig. 24). The lateral borders carry a prosopon of anastomosing raised lines.

The ventral surface of the thorax is known from the distal end of a single thoracic pleuron (Pl. 11, fig. 7, Text-fig. 25). This shows a relatively narrow (tr.) distal doublure, the position of the panderian protuberance and the prosopon of the surface. The panderian organ (opening) is not preserved on this specimen.

The pygidium is twice as wide (tr.) as long (sag.), the length being 45-65 percent of the width. The margin is entire, non-spinose. The axis is relatively narrow, the width (tr.) at the first segment being 22-31 percent of the total width, and relatively long (sag.), 66-80 percent of the total length. The segmentation



MPI203

25. *Golasaphus momedahensis* gen. et sp. nov., panderian protuberance and ventral thoracic doublure, CPC 9787, x8.

is obscure on both axis and pleurae. However, faint transverse axial and pleural furrows show up on some deeply weathered and ferruginized specimens (Pl. 11, fig. 6) permitting six axial and six pleural segments to be discerned. Paradoublural lines are observed on some of the material but on none is a marginal furrow present. The articulating half ring is a simple half segment, and the articulating facet is a mere downturning of the anterolateral corners. The doublure (Pl. 11, fig. 5) is wide, ornamented by concentric raised lines which closely follow the pygidial margin. There is a deep notch in the ventral edge of the doublure to accommodate the posterior end of the axis.

Morphogenetic variation. Enough specimens of *Golasaphus momedahensis* are available to observe some morphological change with increase in size during the holaspis stage of growth. In the cranium the palpebral lobes are larger in small specimens than in large ones, their length, expressed as a proportion of the total cranial length, being about 30 percent in the smallest (cranial length 3.00 mm) and 25 percent or less in the larger ones (6.00-12.00 mm) (Table 4). The preglabellar area increases in length (sag.) at a slower rate than the glabella. In the smallest specimens (length 3 mm) the length of the preglabellar area, expressed as a proportion of the cranial length, is around 28 percent, but in the largest specimens this has decreased to 16 percent. Little change is evident in the pygidial proportions, length to width of axis to width of pygidium, although Henningsmoen (1960, p. 224) reports that pygidia of *Ogygiocaris sarsi* Angelin become relatively wider and the axis shorter, during morphogenesis. Change is, however, observed in the hypostome of *Golasaphus momedahensis*. In small hypostomata the posterior lobe of the median body is obtusely rounded at the back and the posterior border is wider. With growth the posterior lobe becomes pointed and encroaches backwards, restricting the width of the posterior border. This rearward migration of the median body is accompanied by a rearward movement of the posterior two pairs of pits, which lie in the marginal furrow.

TABLE 4

Cranial proportions of *Golasaphus momedahensis* and *Atopasaphus petasatus*.

For symbols see p. 16

Specimen No.	Lc	A:Lc	W _{pa} :Lc	L _{pa} :Lc	W _{pa} :W _{pl}
<i>Golasaphus momedahensis</i>					
CPC 9798	3.05	31.15	78.68	28.13	62.96
CPC 9783	3.60	29.17	80.56	27.48	60.42
CPC 9785	3.95	—	—	23.03	—
CPC 9796	4.05	29.56	83.95	25.84	61.27
CPC 9784	4.70	29.79	76.60	24.61	59.50
CPC 9782	4.95	25.20	71.71	26.45	57.25
CPC 9797	5.05	23.97	68.31	23.56	51.11
CPC 9799	5.80	22.42	81.91	24.85	61.69
CPC 9781	12.95	25.09	74.50	16.47	56.26
<i>Atopasaphus petasatus</i>					
CPC 9714	4.40	22.73	115.90	29.73	86.64

Comparisons and differences. Satisfactory comparison may be made with only three previously described species: *Plesiomegalaspis* (*Plesiomegalaspis*) *planilimbata* (Angelin) *sensu* Tjernvik (1956, pp. 235-8, pl. 6, figs 1-9), from the

planilimbata Zone, early Arenigian, of Sweden; *Asaphellus homfrayi* (Salter) *sensu* Lake (1942, pp. 321-6, pl. 45, figs 1-9; pl. 46, fig. 1), from the Tremadocian of North Wales and Shropshire, British Isles; and *Asaphellus communis* Robison & Pantoja-Alor (1968, p. 782, pl. 98, figs 12-22), a species recently described from the Tifú Formation of Nochixtlán, Oaxaca, Mexico, again of Tremadocian age.

The cranium of *Golasaphus momedahensis* is most similar to that of *Plesiomegalaspis planilimbata*, the similarities being noted in the generic comparisons above. In fact only the narrower posterolateral limbs differentiate the crania of the two species. The specimen figured by Tjernvik (1956, pl. 6, fig. 1) is especially similar. The hypostome which Tjernvik attributed to *P. planilimbata* differs in having anterolateral wings less strongly curved addorsally. The pygidium, however, is quite different in shape, and it possesses a marginal furrow which is not present in *Golasaphus momedahensis*.

The pygidium of *G. momedahensis* is possibly most similar to that of *Asaphellus homfrayi*. Although it is somewhat shorter (sag.), the segmentation is similarly obscure. The hypostomata are essentially the same, both having the strongly curved anterolateral wings, and the anterior portion of the median body mesially cleft (see Lake, 1942, pl. 45, fig. 5).

The cranium of *Asaphellus communis* has longer (sag.) prelabellar area and narrower (exsag.) posterolateral limbs, but otherwise it is similar to that of *Golasaphus momedahensis*. The pygidium has comparable segmentation (cf. Robison & Pantoja-Alor, 1968, pl. 98, fig. 21), but is proportionally longer, and like *Plesiomegalaspis planilimbata* possesses a marginal furrow. The hypostoma figured by Robison & Pantoja-Alor (pl. 98, figs 18-19) is most strikingly similar to the juvenile form figured here on Plate 11, figure 9. Other Mexican species of *Asaphellus* are quite different from either *Golasaphus momedahensis* or *Asaphellus communis*.

Subfamily INCERTAE SEDIS

Genus ATOPASAPHUS nov.

Type species. *Atopasaphus petasatus* gen. et sp. nov., from the late Upper Cambrian Gola Beds, Momedah Creek, western Queensland.

Name. Compounded from the Greek, *atopos*, odd, strange, or unusual, and the generic nomen *Asaphus*: an unusual asaphid.

Diagnosis. An asaphid genus of uncertain subfamily displaying the following combination of characteristics: glabella anteriorly tapering, with median sulcus in the anterior outline; bacculae; occipital lobulae; widely divergent preocular sections of the facial suture; prelabellar area nearly as wide (tr.) as the cranial width (tr.) across the posterolateral limbs; small eyes, close to the glabella.

Comparisons and differences. *Atopasaphus* cannot be readily classified with any of the subfamilies recognized by Jaanusson (1959). The anteriorly tapering glabella is reminiscent of the Isotelinae and is not greatly different from that of *Golasaphus* discussed above. Bacculae are not commonly found in Isotelinae, however, and are doubtfully present in Asaphinae. They are occasionally seen in members of the Niobinae. The forward placed median glabellar node is uncharacteristic of Asaphinae, Isotelinae, and Ogyiocarinae, but is again present

in the Niobinae, the Symphysurinae, and possibly the Promegalaspidinae. Only the asaphinid genera *Basiliella*, *Pseudobasilicus*, and *Lachnostoma* have preglabellar areas of equivalent width (tr.) to that of *Atopasaphus*. The shape of the posterolateral limbs is comparable to that of *Borogothus* Tjernvik, although the posterior marginal furrows are not so sharply defined.

ATOPASAPHUS PETASATUS gen. et sp. nov.

(Pl. 9, fig. 5; Text-fig. 26)

Name. Latin, *petasatus*, with hat or helmet on: alluding to the helmet-shaped preglabellar field.

Holotype. CPC 9714, the cranidium figured on Plate 9, figure 5.

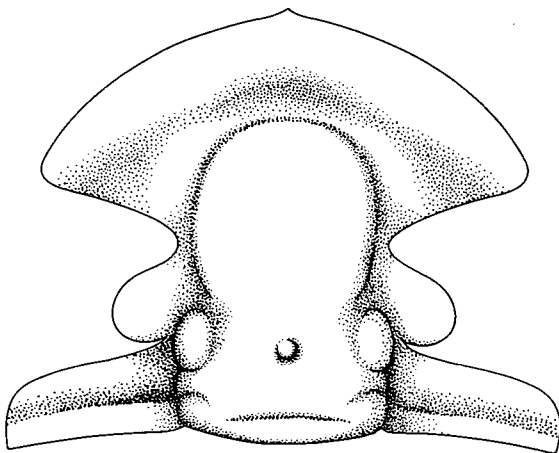
Material. A single cranidium is known. It is preserved with its shell in sandy calcilutite and apart from damage to the eyes is complete. The specimen is small, attaining a cranial length of 4.40 mm. The width (tr.) of the preglabellar area is 5.10 mm and the width (tr.) across the posterolateral limbs 5.90 mm.

Occurrence. The species occurs at locality B750.

Diagnosis. The generic diagnosis is based on that of *Atopasaphus petasatus*.

Description. The glabella of *Atopasaphus petasatus* tapers forwards and is anteriorly rounded. The glabellar furrowing is obsolete, apart from faint shadows leading inwards and backwards from a point near the middle of the palpebral lobes. A pair of bacculae lie adjacent to the rear of the glabella, behind the palpebral areas. A median glabellar node is situated between these bacculae. A faint median crest or ridge extends from the node forwards to the anterior margin of the glabella terminating in a shallow cleft in the anterior contour of the frontal glabellar lobe.

The glabella and occipital ring are confluent. Occipital lobulae are indicated by faint swellings, and there is also a faint posterior occipital band.



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26. *Atopasaphus petasatus* gen. et sp. nov., cranial reconstruction based on the holotype, CPC 9714, x12.

The palpebral lobes are crescentic and sited opposite the mid-length of the glabella. Palpebral furrows are weakly impressed, and the palpebral areas narrow, and slightly inclined to the axial furrows. Between the back of the palpebral lobes and the glabella are interposed the anterior ends of the bacculae. The palpebral lobes occupy approximately 23 percent of the total cranial length.

The anterior sections of the facial suture diverge strongly at an angle of 145 degrees. Anteriorly they meet in a right angle, forming a definite cranial apex. The cranial border is indistinct, and the prelabellar marginal furrows wide and shallow. A narrow ridge runs along the sagittal line from the apex of the facial suture to the front of the glabella. *Hunnebergia retusa* Tjernvik and *Golasaphus momedahensis* sp. nov. have similar structures. Paradoublural lines are only faintly impressed. The width (tr.) of the prelabellar area exceeds the total cranial length (sag.), and is 80 percent of the width (tr.) across the posterolateral limbs. Its length (sag.) is 30 percent of the cranial length. The postocular sections of the facial suture deviate sharply from the back of the eyes and curve evenly to the posterior cranial margins. The posterolateral limbs are narrow and blade-like, not distally expanded. The posterior marginal furrows are indistinct.

The surface of the cranium appears to be completely smooth.

Comparisons and differences. Some account of the relationships of *Atopasaphus petasatus* has been given in the generic comparisons. The species is not closely comparable to any other asaphid species, but it does have points of similarity with the following. The shape of the glabella is reminiscent of that of *Plesiomegalaspis* (P.) *planilimbata* (Angelin), as figured by Tjernvik (1956, pl. 6, fig. 1). The posterolateral limbs are similar not only to *P. planilimbata*, but also to those of *Borogothus stenorhachis* (Angelin), from the late Tremadocian of Sweden and the *Ceratopyge* Limestone of Norway (cf. Tjernvik, 1956, p. 256, fig. 41A). Similarly the forward-placed glabellar node, lying a little more than one-fifth of the way along the cranium from the rear, is comparable to that of *B. stenorhachis*. Some similarity also exists with *Hunnebergia retusa*, another species from the early Arenigian of Sweden.

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PLATES

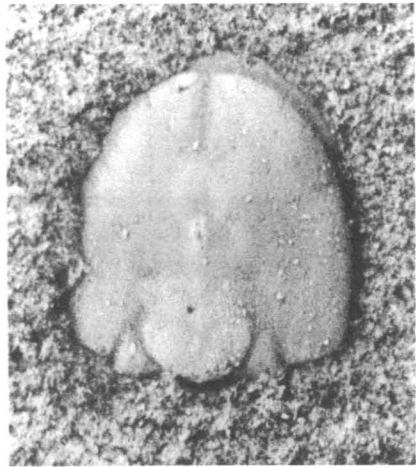
All the illustrated specimens have been whitened with either ammonium chloride or magnesium oxide prior to photography. Specimens preserved in calcarenite matrix were initially blackened with indian ink before whitening, so as to cut down surface reflection and give a matt surface. As some of the quoted magnifications are not quite accurate, a measured parameter is quoted to give the reader some idea of the true size of the specimen.

The illustrated specimens were prepared by H. M. Doyle, J. E. Zawartko, and the author.

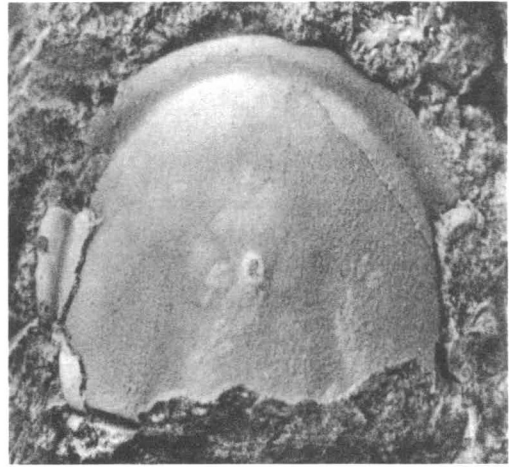
PLATE 1

Pseudagnostus papilio sp. nov.

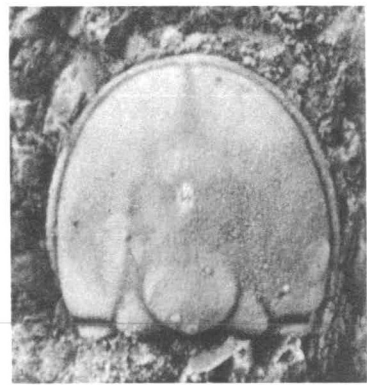
- Fig. 1 CPC 8444, latex mould of cephalon, length 2.95 mm, x16, locality B750.
- Fig. 2 CPC 8443, incomplete exfoliated cephalon, x16, locality B520.
- Fig. 3 CPC 8442, **holotype**, limestone mould of cephalon, length 2.70 mm, x14, locality K102.
- Fig. 4 CPC 8447, limestone mould of cephalon, length 2.60 mm, x15, locality B750.
- Fig. 5 CPC 8447, lateral aspect of cephalon, x15.
- Fig. 6 CPC 8446, nearly complete exfoliated pygidium, length 2.35 mm, x15, locality B750.
- Fig. 7 CPC 8448, limestone mould of pygidium, length 2.30 mm, approx. x14, locality B750.
- Fig. 8 CPC 8445, exfoliated pygidium, length 2.95 mm, x14, locality B750.



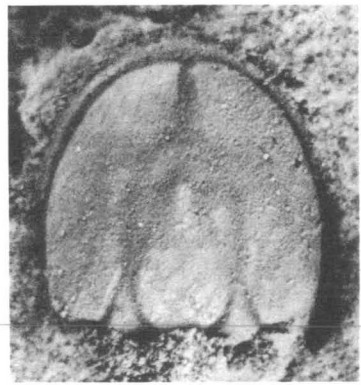
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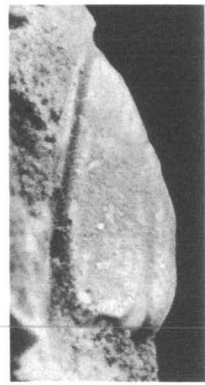
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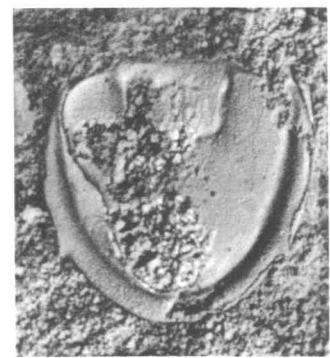
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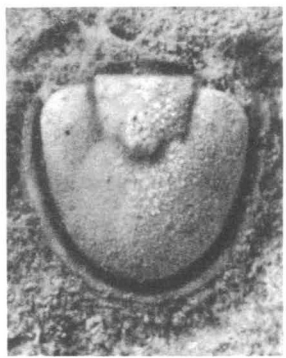
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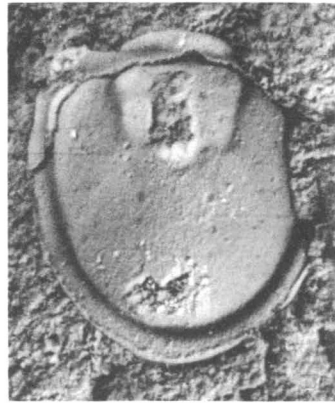
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PLATE 2

Pseudagnostus papilio sp. nov.

Fig. 1 CPC 8449, limestone mould of pygidium, length 2.30 mm, x14, locality B750.

Fig. 2 CPC 8450, limestone mould of pygidium, length 2.95 mm, x12, locality K102.

Pseudagnostus sp. I

Fig. 3 CPC 8457, limestone mould of pygidium, posterior view, approximately x12, locality B520.

Fig. 4 CPC 8457, lateral view, x12.

Fig. 5 CPC 8457, dorsal aspect, length 3.00 mm, x14.

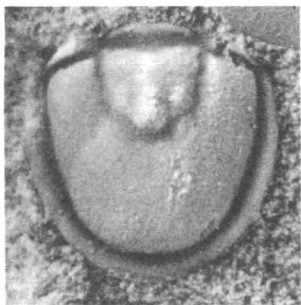
Pseudagnostus sp. II

Fig. 6 CPC 8458, limestone mould of pygidium, length 5.10 mm, x10, locality B520.

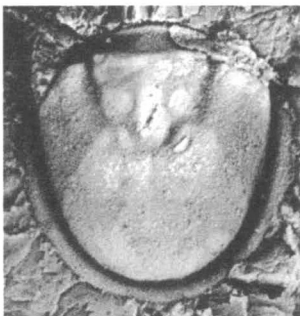
Fig. 7 CPC 8459, limestone mould of pygidium, estimated length 5.60 mm, x11.5, locality B520.

Pseudagnostus sp. III

Fig. 8 CPC 8460, limestone mould of pygidium, with vestiges of shell, length 4.85 mm, x11.5, locality B520.



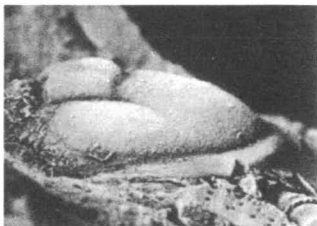
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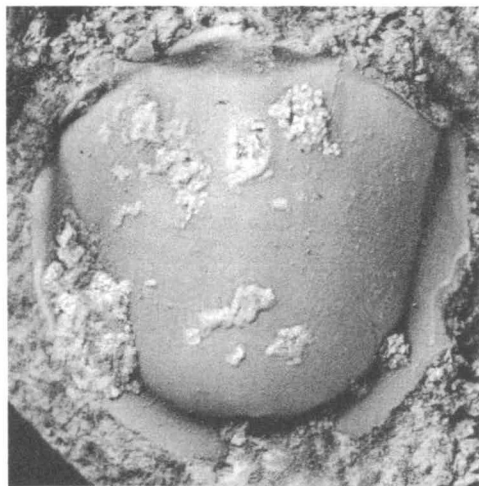
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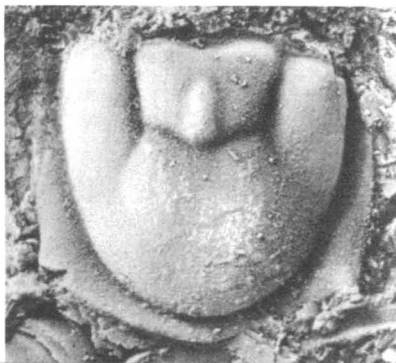
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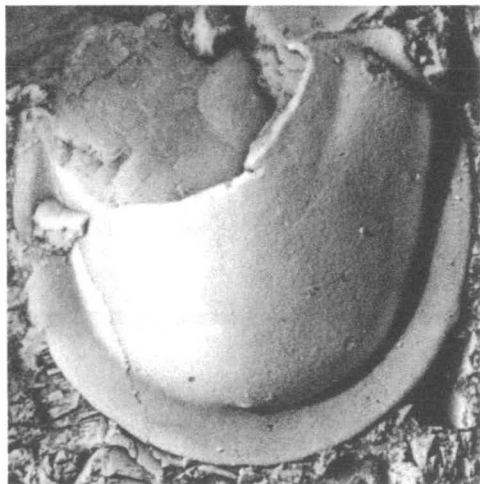
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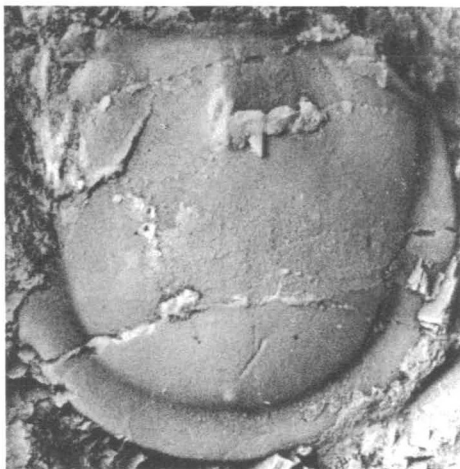
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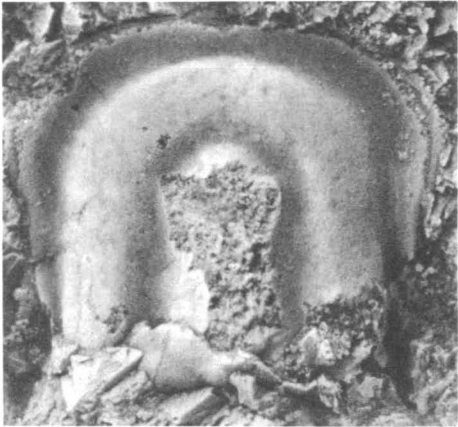
PLATE 3

Pseudagnostus clavus sp. nov.

- Fig. 1 CPC 8455, latex mould of cephalon, length 2.95 mm, x15, locality B750.
- Fig. 2 CPC 8456, exfoliated cephalon, length 4.20 mm, x12, locality B520.
- Fig. 3 CPC 8454, limestone mould of cephalon, length 4.00 mm, x11, locality B520.
- Fig. 4 CPC 8454, lateral aspect, x11.
- Fig. 5 CPC 8453a, **holotype**, limestone mould of pygidium, oblique posterior view, length 3.05 mm, x12, locality B750.
- Fig. 6 CPC 8453a, **holotype**, lateral view, x12.
- Fig. 7 CPC 8453b, latex cast from external mould of the **holotype**, x14.
- Fig. 8 CPC 8451, limestone mould of pygidium, length 3.15 mm, approximately x12, locality B750.



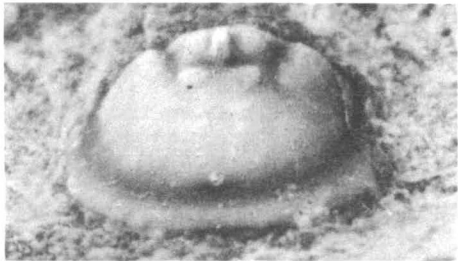
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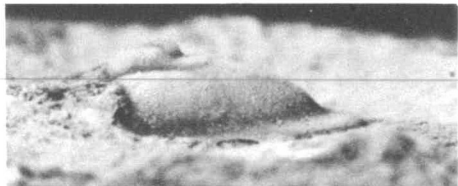
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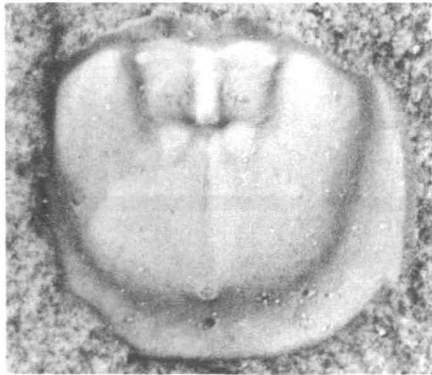
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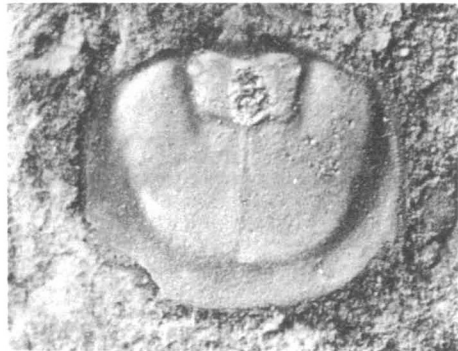
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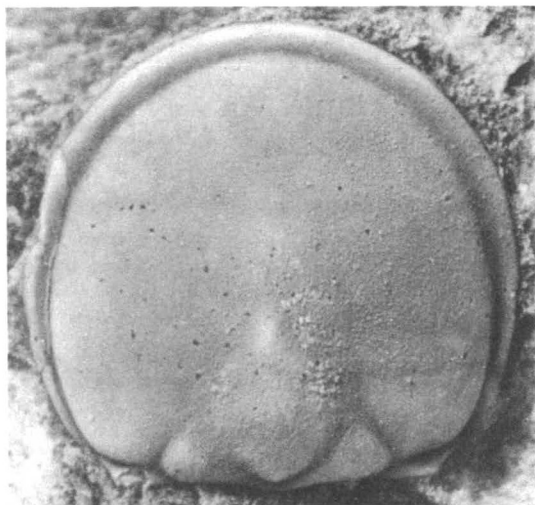


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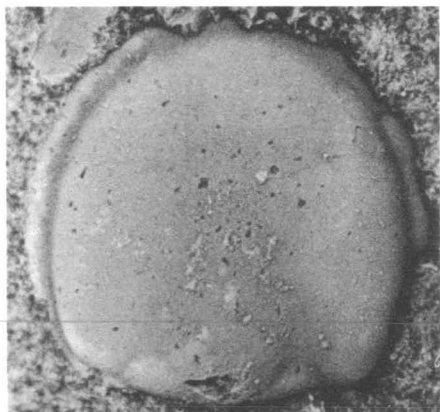
PLATE 4

Distagnostus ergodes gen. et sp. nov.

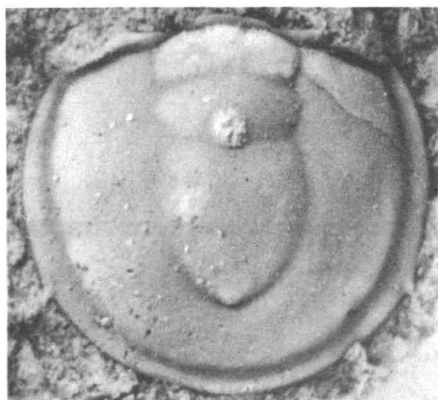
- Fig. 1 CPC 9671, cephalon with shell, length 4.30 mm, x14.5, locality B752.
- Fig. 2 CPC 9669, latex cast from external mould of cephalon, length 4.40 mm, approximately x12, locality B752.
- Fig. 3 CPC 9667, **holotype**, internal mould of pygidium, length 3.40 mm, approximately x15, locality B752.
- Fig. 4 CPC 9668, partially exfoliated pygidium, length 3.10 mm, x13, locality B750.
- Fig. 5 CPC 9668, lateral aspect, x13.
- Fig. 6 CPC 9672, cephalon with shell, lateral aspect, length 3.20 mm, x13, locality B750.
- Fig. 7 CPC 9670, internal mould of pygidium, length 4.25 mm, approximately x13, locality B752.



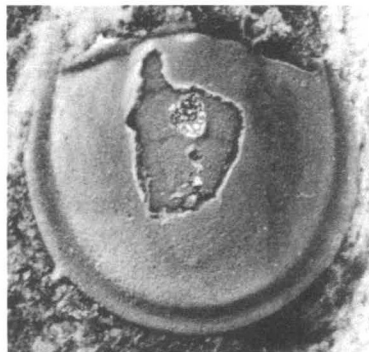
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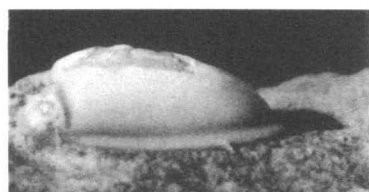
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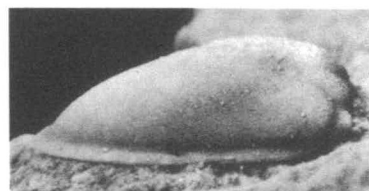
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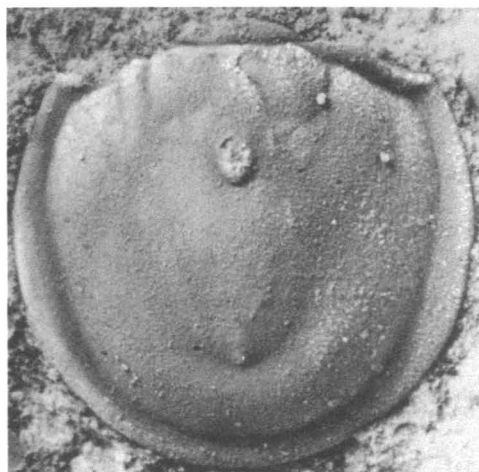
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PLATE 5

Connagnostus junior sp. nov.

Fig. 1 CPC 9666, limestone mould of cephalon, length 2.05 mm, approximately x23.5, locality B520B.

Fig. 2 CPC 9665, **holotype**, limestone mould of pygidium, length 1.85 mm, x29, locality B520B.

Geragnostus (*Micragnostus*) *acrolebes* sp. nov.

Fig. 3 CPC 9693, latex mould from cephalon, length 1.80 mm, approximately x18, locality B520A.

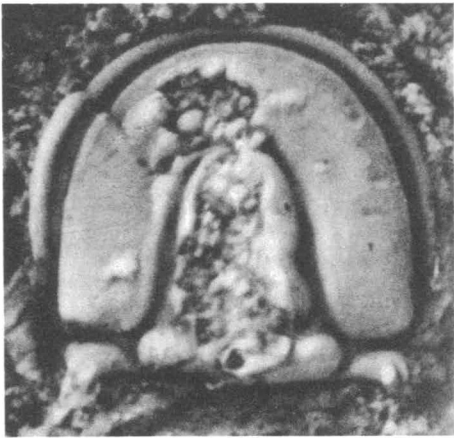
Fig. 4 CPC 9689, **holotype**, limestone mould of pygidium, length 1.35 mm, x19, locality B750.

Fig. 5 CPC 9692, limestone mould of cephalon, length 1.40 mm, x23, locality B750.

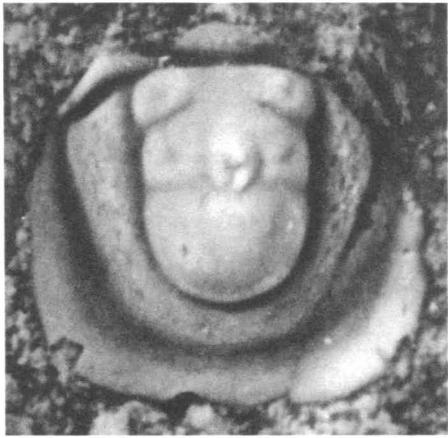
Rudagnostus avius sp. nov.

Fig. 6 CPC 9688, limestone mould of pygidium, length 1.70 mm, approximately x20, locality B520.

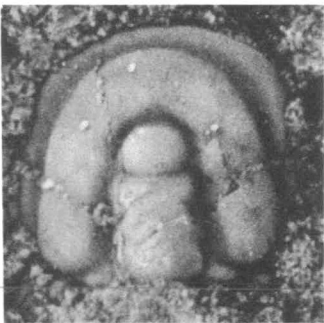
Fig. 7 CPC 9686, **holotype**, limestone mould of pygidium, estimated length 1.70 mm, approximately x26, locality B520.



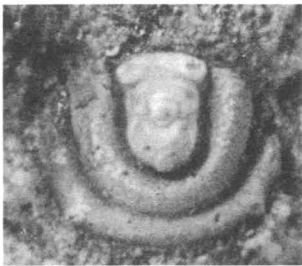
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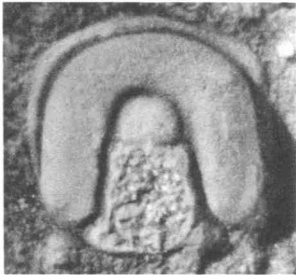
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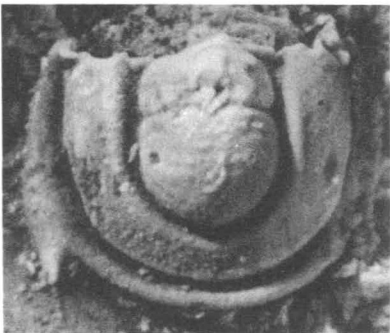
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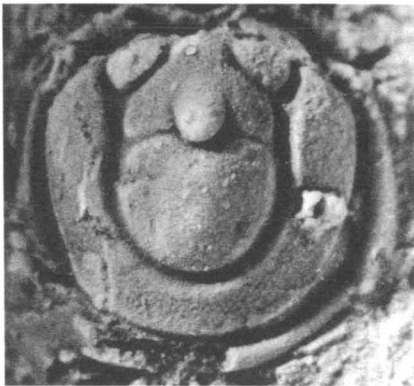
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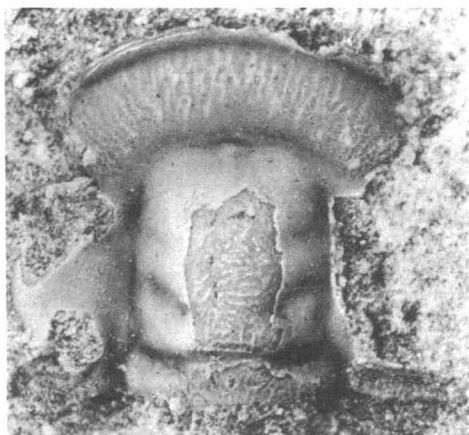


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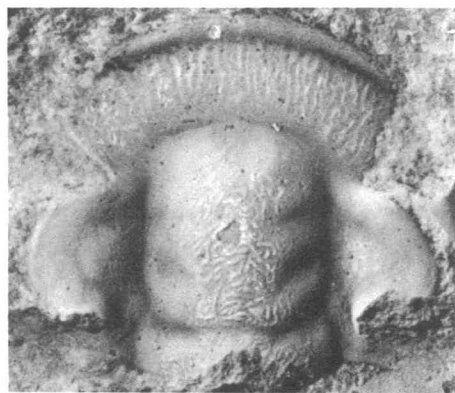
PLATE 6

Richardsonella laciniosa sp. nov.

- Fig. 1 CPC 9699, partially exfoliated cranidium, length 5.05 mm, x10, locality B750. Note anterior node on frontal glabellar lobe flanked by preglabellar rim.
- Fig. 2 CPC 9695, cranidium with shell, length 5.10 mm, x10, locality B750.
- Fig. 3 Block showing association of three cranidia with cephalon of *Pseudagnostus papilio* sp. nov. Fig. 3a, CPC 9696; Fig. 3b, CPC 9697; Fig. 3c, CPC 9698; all x6, locality B750.
- Fig. 4 CPC 9701, detail showing preglabellar area (cranidial length 5.50 mm) and preglabellar rim, x8, locality B750.
- Fig. 5 CPC 9700, detail of cranidium showing anterior glabellar node and preglabellar rim, x8, locality B750.



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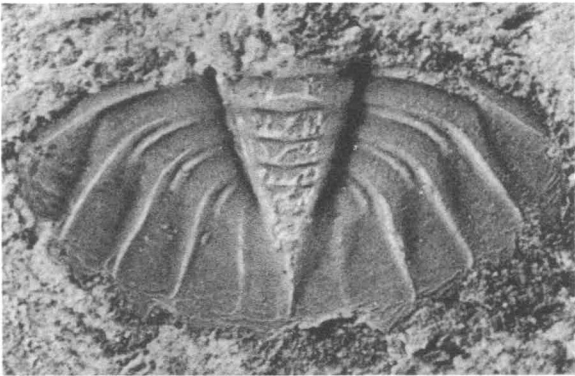
PLATE 7

Richardsonella laciniosa sp. nov.

- Fig. 1 CPC 9702, **holotype**, pygidium with shell, length 4.25 mm, x8, locality B750.
- Fig. 2 CPC 9703, latex cast from external mould of pygidium, length 3.60 mm, x9, locality B750.
- Fig. 3 CPC 9705, limestone mould of pygidium, x8, locality B750.
- Fig. 4 CPC 9704, latex cast from external mould of pygidium, length 3.35 mm, x9, locality B750.

Richardsonella (?) *kainelliformis* sp. nov.

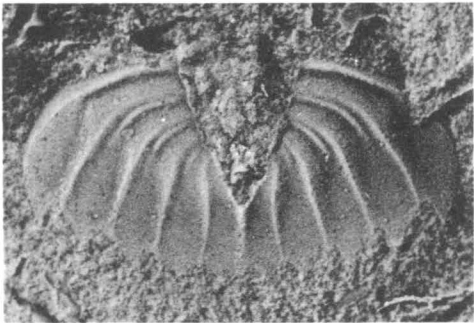
- Fig. 5 CPC 9712b, latex cast from external mould of **holotype** cranidium, x3.5, locality B750, counterpart to CPC 9712.
- Fig. 6 CPC 9712a, **holotype**, limestone mould of cranidium, length 13.80 mm, x3.5, locality B750.



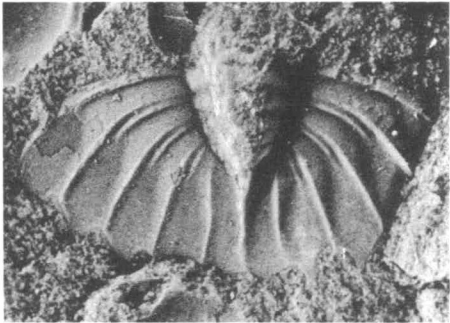
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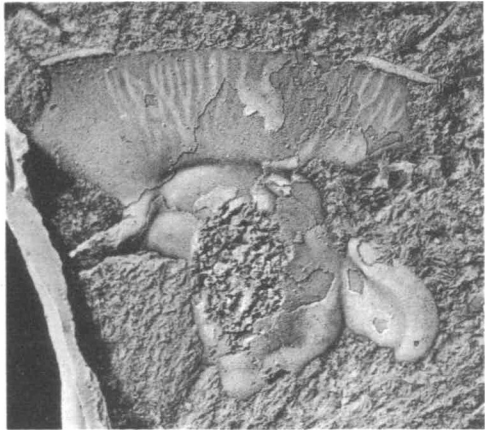
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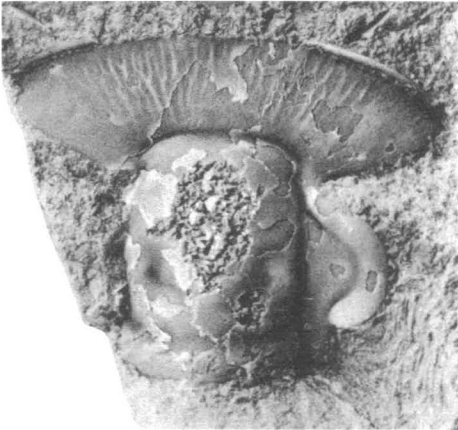
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PLATE 8

Sigmakainella translira gen. et sp. nov.

- Fig. 1 CPC 9715a, **holotype**, incomplete exfoliated cranidium, with counterpart CPC 9715b, estimated length 10.90 mm, x6, locality B750.
- Fig. 2 CPC 9715b, latex cast from **holotype** cranidium, x6, locality B750. Note the median glabellar node placed some distance from the anterior margin of the frontal lobe.
- Fig. 3 CPC 9717, incomplete cranidium with shell, estimated length 6.95 mm, x7, locality B750.
- Fig. 4 CPC 9719, latex cast from external mould of pygidial axis and portion of doublure, x8, locality B750.
- Fig. 5 CPC 9718, latex cast from external mould of pygidial fragment, showing portion of doublure and spine bases, x8, locality B750.
- Fig. 6 CPC 9720, exfoliated pygidium, x8, locality B750.

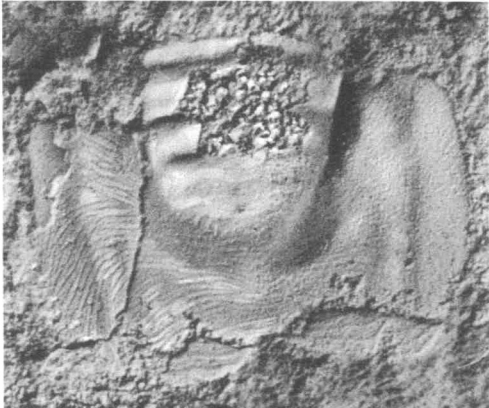
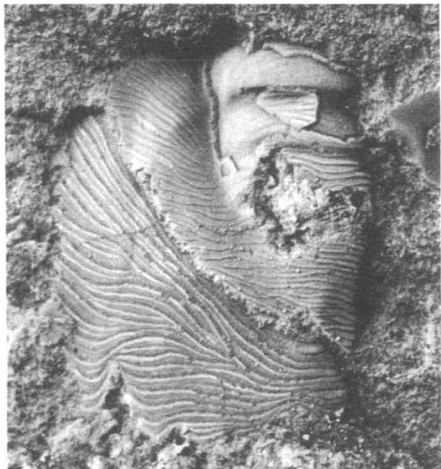
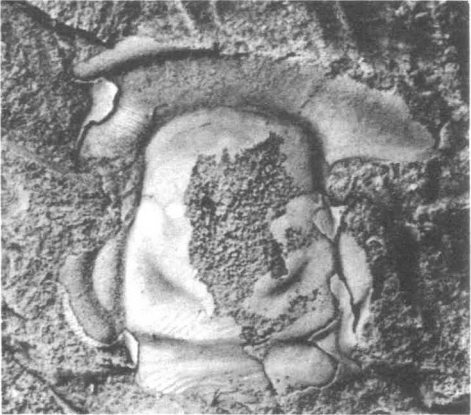
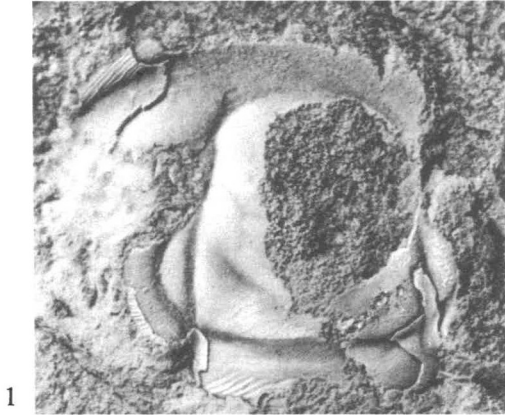
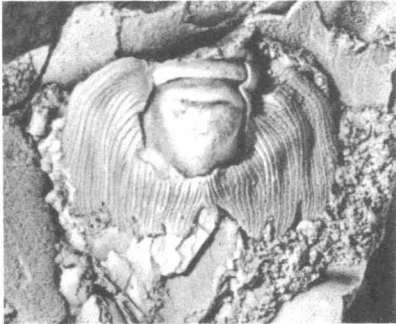


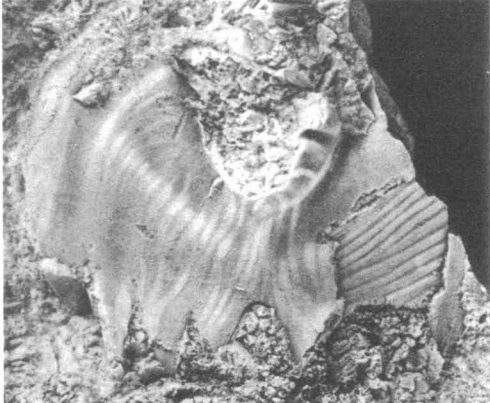
PLATE 9

Sigmakainella longilira sp. nov.

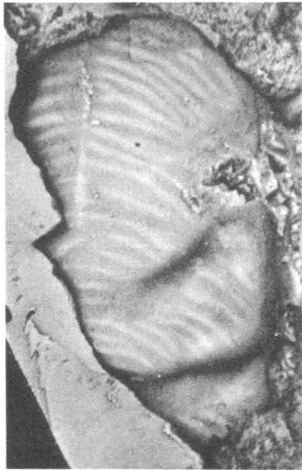
- Fig. 1 CPC 9723, **holotype** pygidium with shell, axis exfoliated, x8, locality B520.
- Fig. 2 CPC 9724, incomplete pygidium showing fragment of doublure, x6, locality B520. Note postaxial prosopon.
Sigmakainella translira(?)
- Fig. 3 CPC 9721, latex cast from external of cranidial fragment, x8, locality B520.
'Tostonia' sp.
- Fig. 4 CPC 9713, limestone mould of incomplete pygidium, x6, locality B750.
Atopasaphus petasatus gen. et sp. nov.
- Fig. 5 CPC 9714, **holotype**, limestone mould of cranidium, length 4.40 mm, x8, locality B750.
Sigmakainella translira(?)
- Fig. 6 CPC 9722, limestone mould of early holaspid cranidium, length 5.05 mm, x9, locality B520.



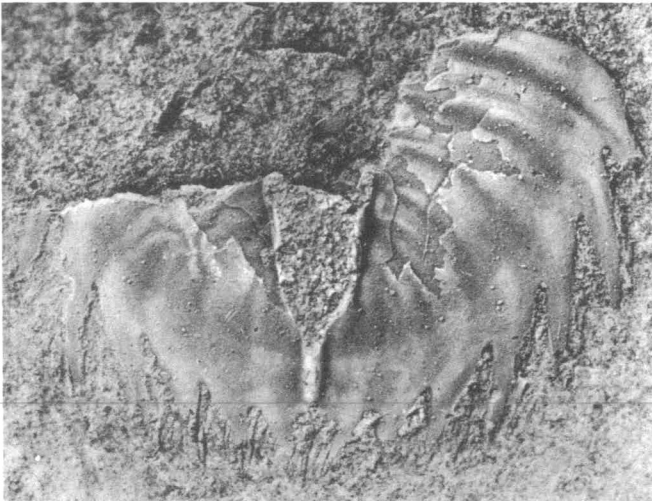
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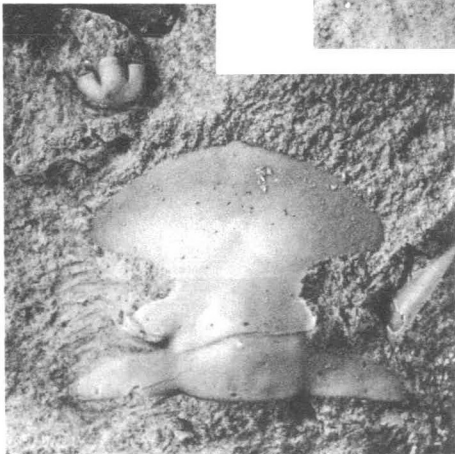
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PLATE 10

Golasaphus momedahensis gen. et sp. nov.

- Fig. 1 CPC 9781, **holotype**, cranidium with shell, length 12.95 mm, x6, locality B520.
- Fig. 2 CPC 9781, lateral view of **holotype** cranidium, x6.
- Fig. 3 CPC 9783, limestone mould of cranidium, length 3.60 mm, x7.5, locality B750.
- Fig. 4 CPC 9785b, latex cast from external mould of cranidium, estimated length 3.95 mm, x8, locality B750.
- Fig. 5 CPC 9786, latex cast from external mould of librigena, x8, locality B750.
- Fig. 6 CPC 9782, limestone mould of cranidium, length 4.95 mm, x8.5, locality B750.
- Fig. 7 CPC 9784, limestone mould of cranidium, anterior view, x8, locality B750.
- Fig. 8 CPC 9784, dorsal aspect, length 4.70 mm, x9, locality B750.

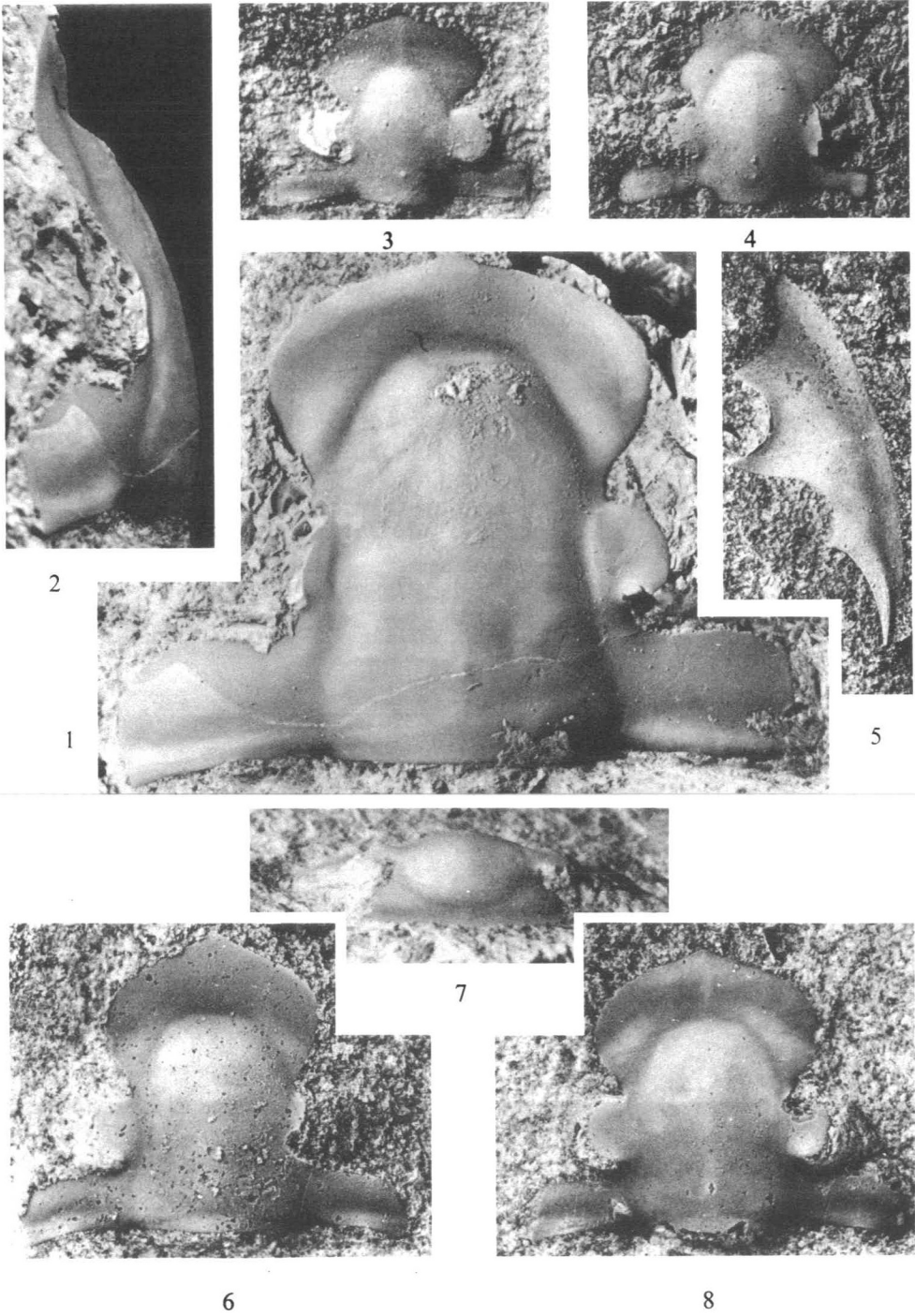


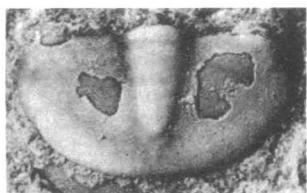
PLATE 11

Golasaphus momedahensis gen. et sp. nov.

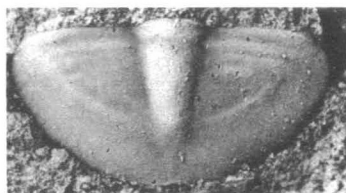
- Fig. 1 CPC 9795, limestone mould of pygidium, length 2.40 mm, x8, locality B752.
- Fig. 2 CPC 9794, partly exfoliated pygidium, length 2.65 mm, x8, locality B750.
- Fig. 3 CPC 9793, limestone mould of pygidium, length 2.36 mm, x10, locality B750.
- Fig. 4 CPC 9792, latex cast from partly exfoliated pygidium, length 3.15 mm, x8, locality B750.
- Fig. 5 CPC 9791, limestone mould of pygidium showing doublure, length 4.20 mm, x8, locality B750.
- Fig. 6 CPC 9790, ferruginized internal mould of pygidium, showing segmentation, x8, locality B750.
- Fig. 7 CPC 9787, ventral surface of thoracic segment showing width of doublure, prosopon, and panderian organ, x6, locality B753.
- Fig. 8 CPC 9789, latex cast from external mould of large hypostome, maximum width (tr.) 7.30 mm, x7, locality K101.
- Fig. 9 CPC 9788, latex cast from mould of small hypostome, maximum width (tr.) 2.70 mm, x15, locality B752.



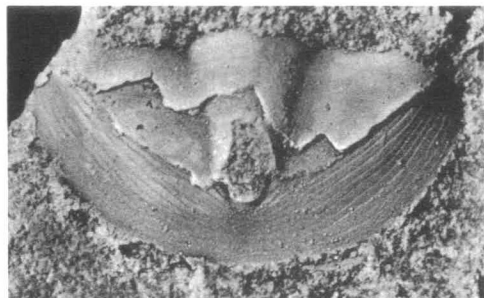
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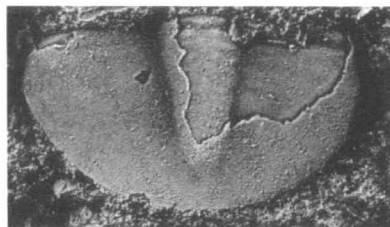
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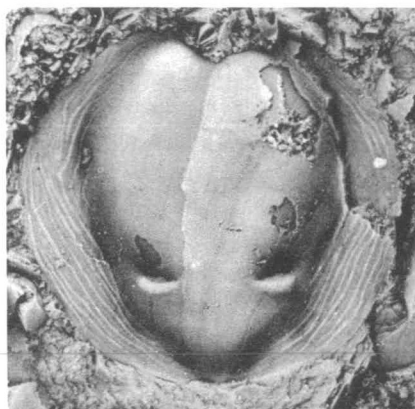
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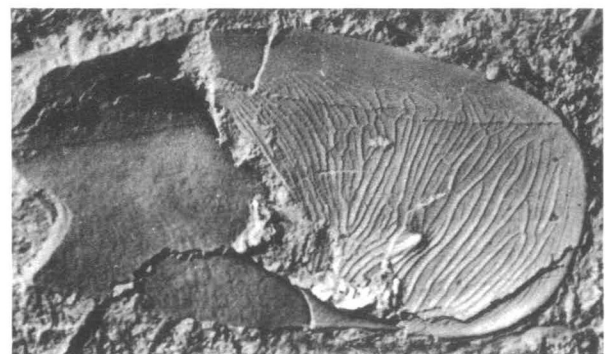
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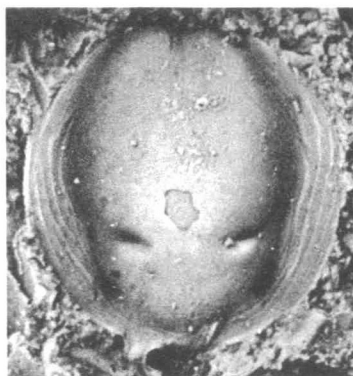
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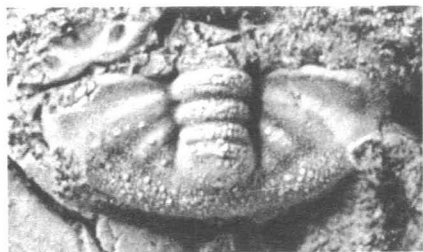


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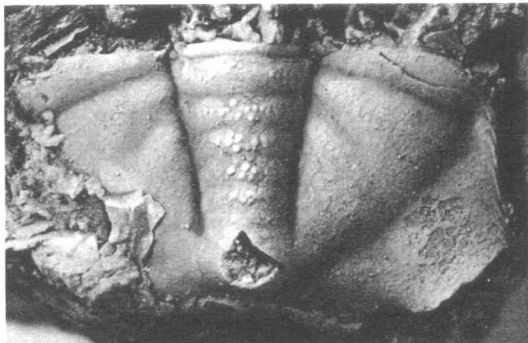
PLATE 12

Kaolishania australis sp. nov.

- Fig. 1 CPC 9736, limestone mould of meraspid pygidium, length 1.40 mm, x15, locality B753.
- Fig. 2 CPC 9733, limestone mould of pygidium, length 5.50 mm, x6, locality B520.
- Fig. 3 CPC 9735, limestone mould of meraspid pygidium, length 1.65 mm, x15, locality B520.
- Fig. 4 CPC 9734, limestone mould of meraspid pygidium, length 1.70 mm, x15, locality B520.
- Fig. 5 CPC 9729, **holotype**, limestone mould of cranidium, length 4.10 mm, x8, locality B520, showing the connecting ridges bridging the frontal lobe and preocular areas.
- Fig. 6 CPC 9731, latex cast from external mould of cranidium, estimated length 3.40 mm, locality B520.
- Fig. 7 CPC 9730, limestone mould of cranidium, length 4.55 mm, x8, locality B520, showing intervening lobes and furrows.
- Fig. 8 CPC 9732, limestone mould of cranidium, length 3.35 mm, x8, locality B520.



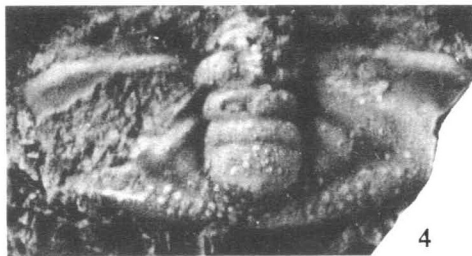
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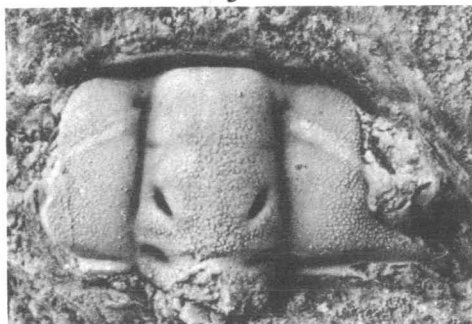
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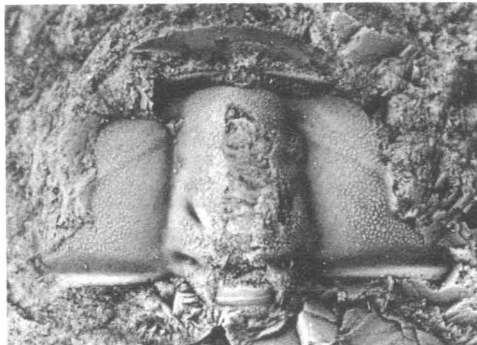
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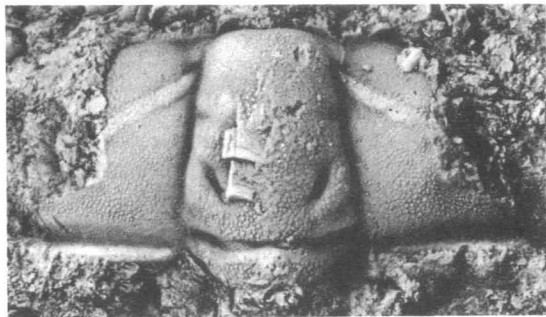
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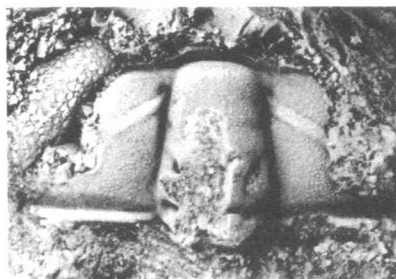
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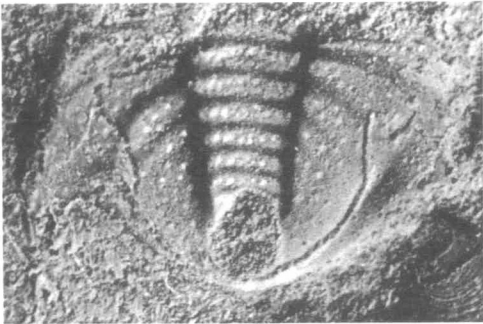


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PLATE 13

Mansuyites futiliformis gen. et sp. nov.

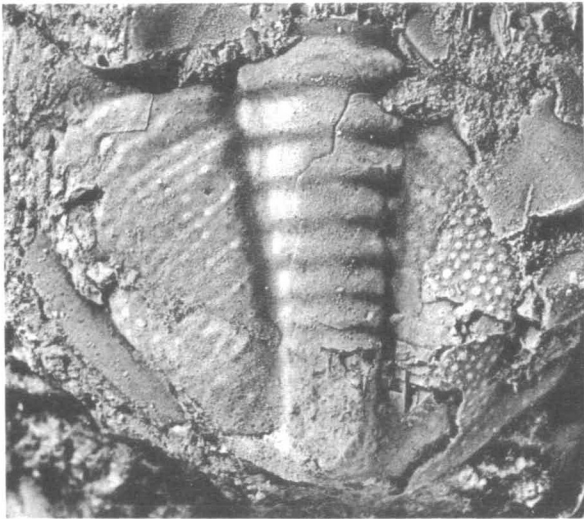
- Fig. 1 CPC 9749, **holotype**, partly exfoliated pygidium, length 3.95 mm, x8, locality B750.
- Fig. 2 CPC 9750, limestone mould of pygidial fragment emphasizing the convexity of the pleural field and the extent of the border, length 4.10 mm, x8, locality B750.
- Fig. 3 CPC 9751, latex cast from the external mould of a partly exfoliated pygidium, length 9.20 mm, x6.8, locality B520, showing the pleural caecal system.
- Fig. 4 CPC 9752, latex cast from the external mould of a pygidial axis, length of pygidium 3.75 mm, x8, locality B750.
- Fig. 5 CPC 9753, limestone mould of an early holaspid pygidium, length 2.15 mm, x8, locality B750.
- Fig. 6 CPC 9754, limestone mould of pygidium, length 2.75 mm, x12, locality B750.
- Fig. 7 CPC 9755, limestone mould of damaged pygidium, estimated length 4.85 mm, x8, locality B750.



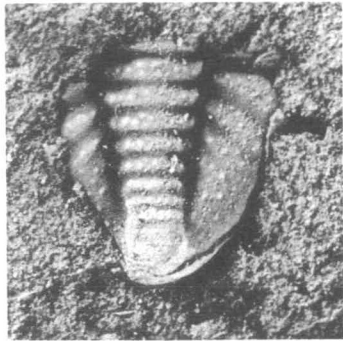
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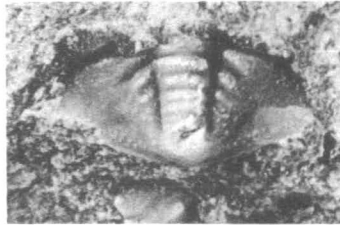
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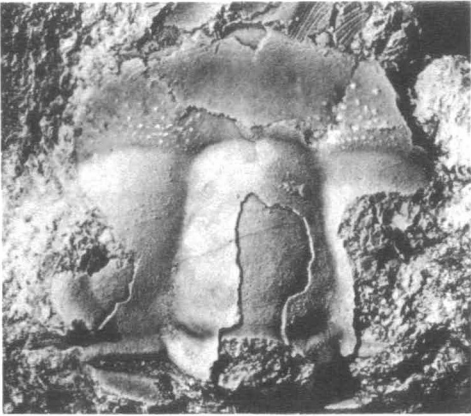


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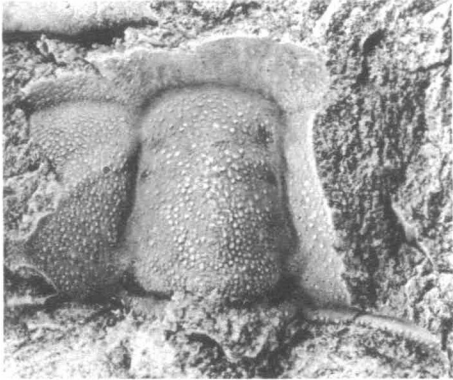
PLATE 14

Mansuyites futiliformis gen. et sp. nov.

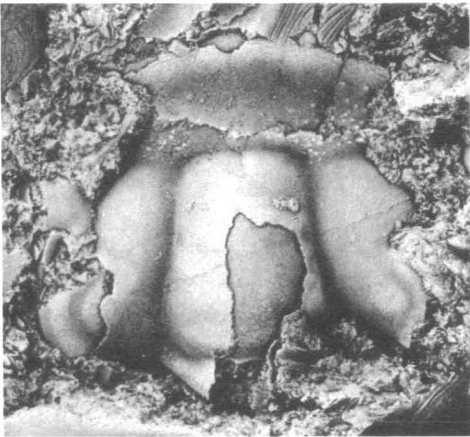
- Fig. 1 CPC 9756a partly exfoliated cranidium, length 8.60 mm, x6, locality B752.
- Fig. 2 CPC 9756b, counterpart of CPC 9756a, latex cast, x6.
- Fig. 3 CPC 9758, limestone mould of cranidium, glabellar length 3.80 mm, x8, locality B750, showing the presence of bacculae.
- Fig. 4 CPC 9759, incomplete limestone mould of cranidium, glabellar length 3.55 mm, x8, locality B750.
- Fig. 5 CPC 9758, lateral aspect, x7.
- Fig. 6 CPC 9760, limestone mould of cranidium, glabellar length 6.70 mm, x6, locality B520, showing the presence of alae.



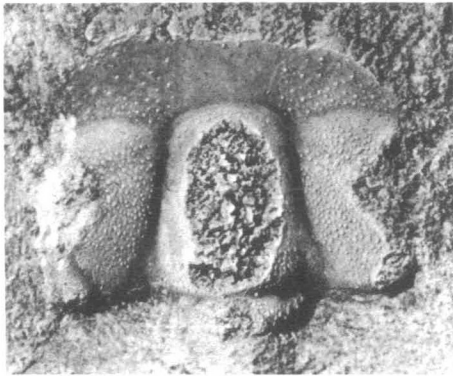
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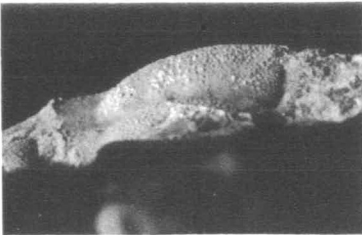
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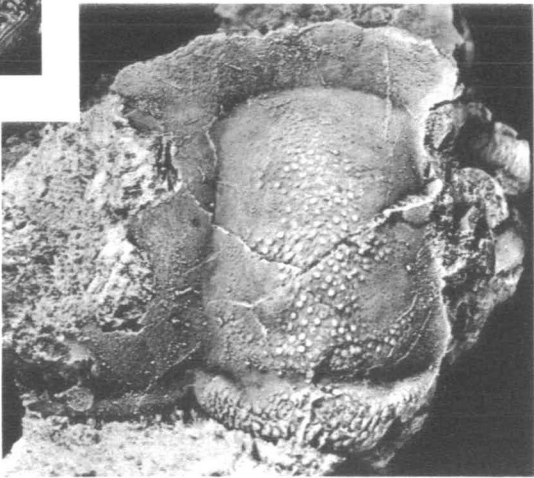
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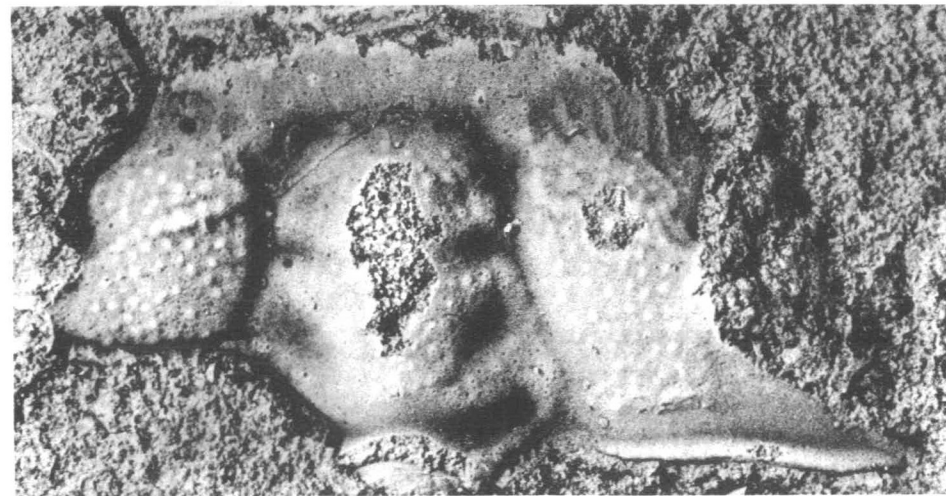
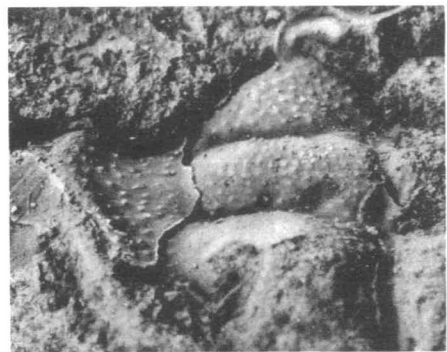
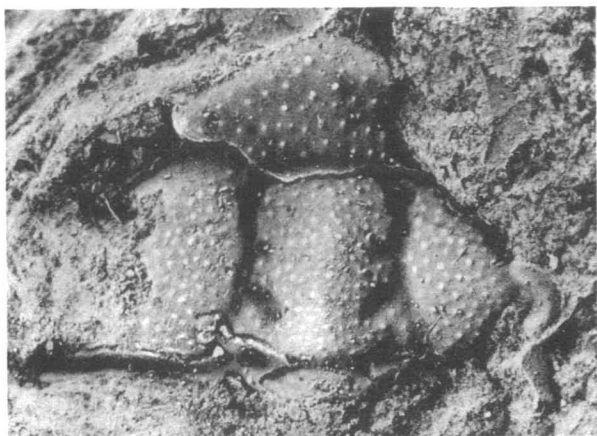


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PLATE 15

Palacorona bacculata gen. et sp. nov.

- Fig. 1 CPC 9761b, **holotype**, latex cast from external mould of
 cranium, length 5.95 mm, x8, locality B750.
- Fig. 2 CPC 9762, lateral aspect of cranidia limestone mould,
 estimated length 5.45 mm, x8, locality B750.
- Fig. 3 CPC 9761b, **holotype**, lateral aspect, x8.
- Fig. 4 CPC 9762, dorsal aspect, x8.
- Fig. 5 CPC 9763b, latex cast from external mould of cranium,
 x6, locality B750.



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PLATE 16

Crucicephalus ocellatus gen. et sp. nov.

Fig. 1 CPC 9775, **holotype**, limestone mould of cranidium, glabellar length 2.50 mm, x12, locality K102.

Fig. 2 CPC 9776, limestone mould of cranidium, length 3.50 mm, x8, locality K102.

Duplora clara gen. et sp. nov.

Fig. 3 CPC 9777a, **holotype**, limestone mould of cranidium, glabellar length 2.50 mm, x7.5, locality K102.

Fig. 4 CPC 9777b, latex cast from external mould of **holotype**, x8.

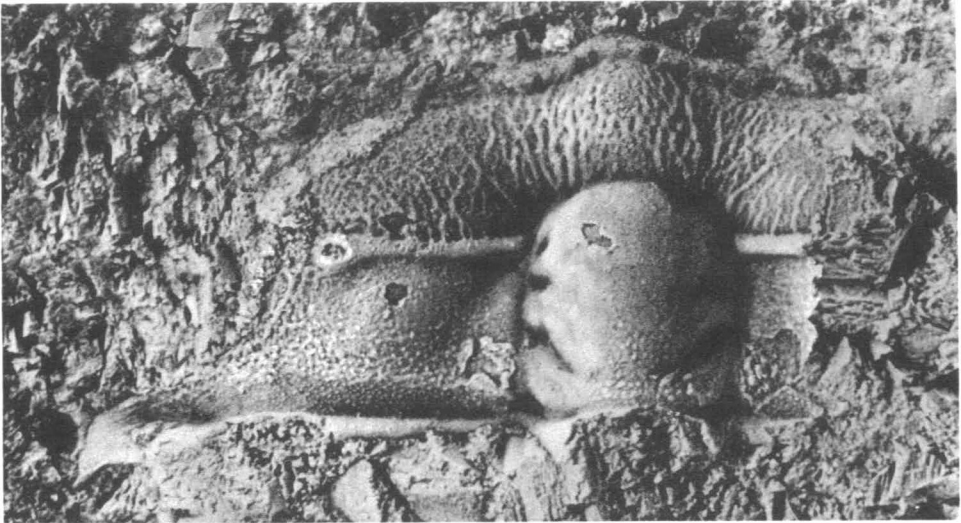
Fig. 5 CPC 9779, limestone mould of cranidium, glabellar length 2.10 mm, x8, locality K102.

Fig. 6 CPC 9780, limestone mould of cranidium, glabellar length 2.05 mm, x8, locality K102, showing duplicated anterior border.

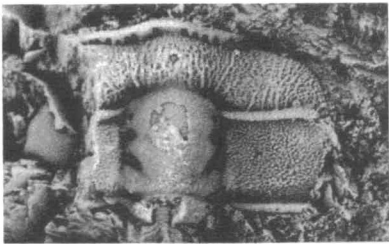
Fig. 7 CPC 9777a, **holotype**, lateral aspect, x7.5.

Crucicephalus ocellatus gen. et sp. nov.

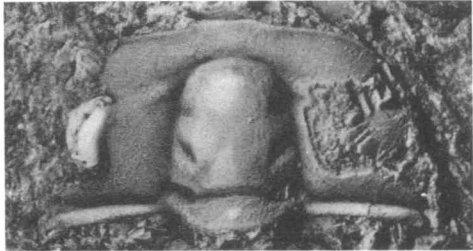
Fig. 8 CPC 9776, lateral aspect, x4.5.



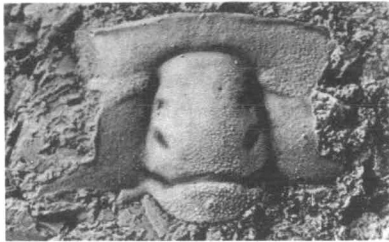
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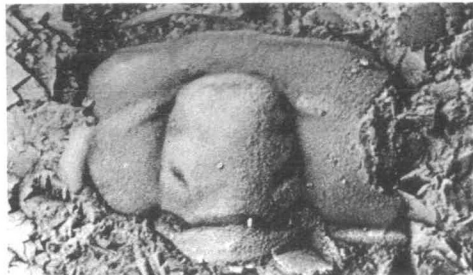
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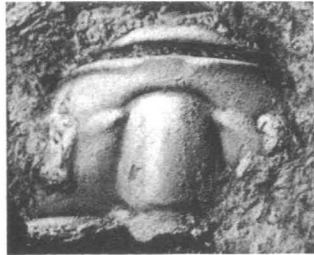
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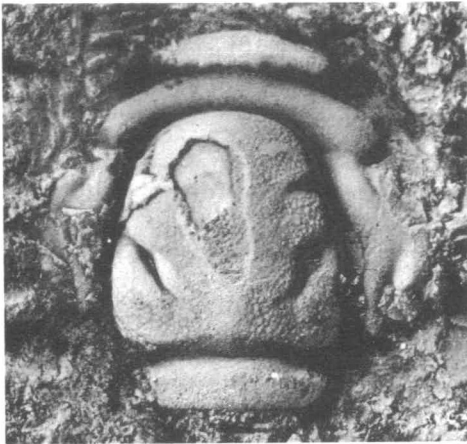


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PLATE 17

Lorrettina macrops gen. et sp. nov.

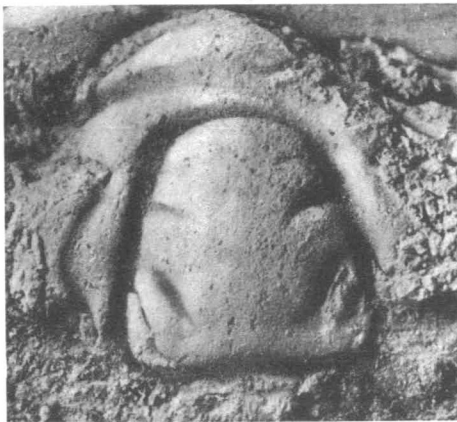
- Fig. 1 CPC 9771a, **holotype**, incomplete cranidial mould, length 6.60 mm, x7.6, locality B520.
- Fig. 2 CPC 9774, limestone mould of cranidium, length 6.35 mm, x7.6, locality B753.
- Fig. 3 CPC 9773, limestone mould of cranidium, glabellar length 4.35 mm, x8, locality B520.
- Fig. 4 CPC 9771b, latex cast from external mould of **holotype**, x7.5.
Dellea(?) laevis sp. nov.
- Fig. 5 CPC 9770, **holotype**, cranidium with shell, length 3.75 mm, x10, locality K102.
- Fig. 6 CPC 9770, **holotype**, lateral aspect, x10.
- Fig. 7 CPC 9770, **holotype**, anterior view, x10.



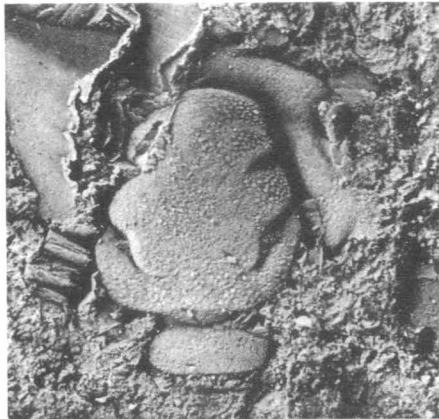
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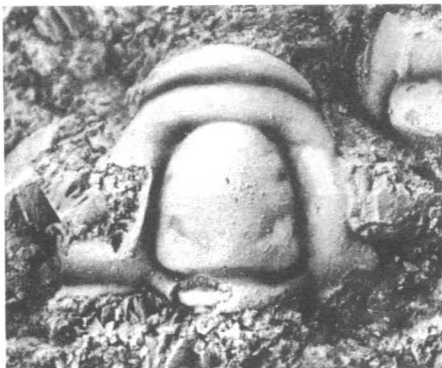
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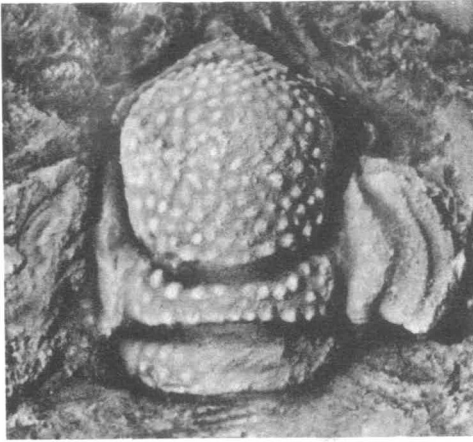


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PLATE 18

Lophosaukia torquata gen. et sp. nov.

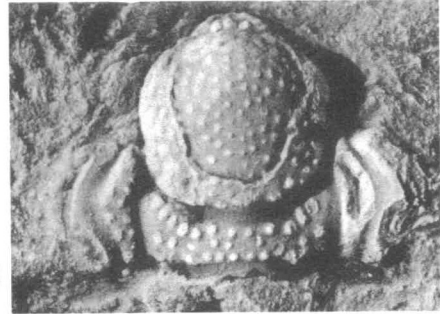
- Fig. 1 CPC 9765, **holotype**, limestone mould of cranium, glabellar length 3.40 mm, approximately x10, locality B520.
- Fig. 2 CPC 9765, **holotype**, lateral view, approximately x10, showing the undercutting preglabellar furrow and the downsloping anterior border.
- Fig. 3 CPC 9765, **holotype**, anterior view, approximately x10, showing the palpebral ledge and triangular anterior border.
- Fig. 4 CPC 9766, limestone mould of cranium, glabellar length 4.40 mm, x7.2, locality B520.
- Fig. 5 CPC 9766, anterior view, x7.2.
- Fig. 6 CPC 9767, limestone mould of cranium, glabellar length 5.50 mm, x8.2, locality B753.
- Eosumardia cylindrica* sp. nov.
- Fig. 7 CPC 9769, limestone mould of cephalon (?), length 0.95 mm, x23, locality B750.
- Fig. 8 CPC 9768, **holotype**, limestone mould of cephalon (?), length 1.35 mm, x23, locality B750.



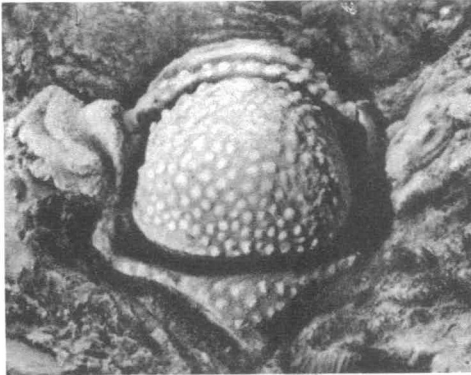
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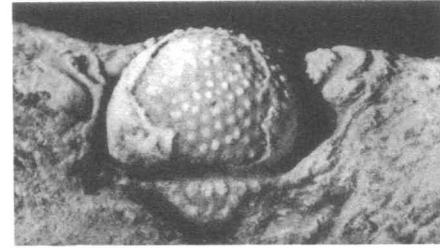
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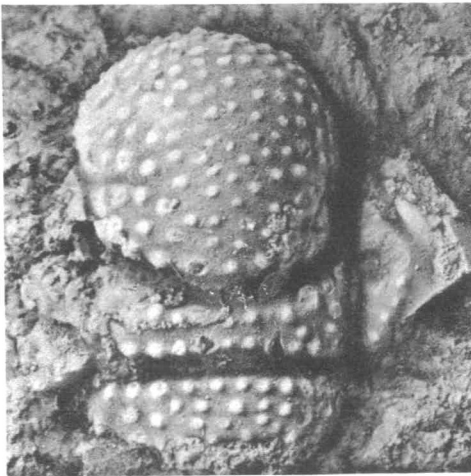
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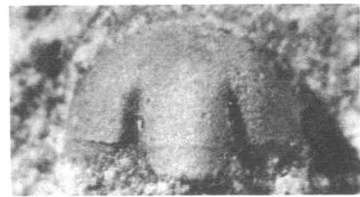
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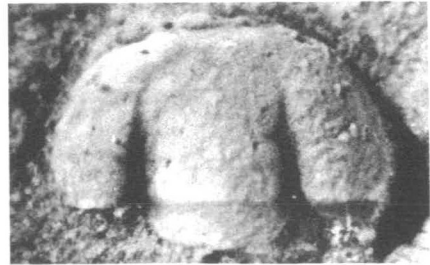
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PLATE 19

Sigmakainella sp.

- Fig. 1 CPC 9725, ventral surface of right librigena showing reticulate prosopon, and advanced genal spine, x8, locality B520.

Kaolishania australis sp. nov.

- Fig. 2 CPC 9747, limestone mould of left librigena, genal spine not advanced, x8, locality B520.

- Fig. 3 CPC 9748, limestone mould of right librigena, x8, locality B520.

Sigmakainella sp.

- Fig. 4 CPC 9728, ventral aspect of left librigena, x6, locality B750.

Richardsonella sp.

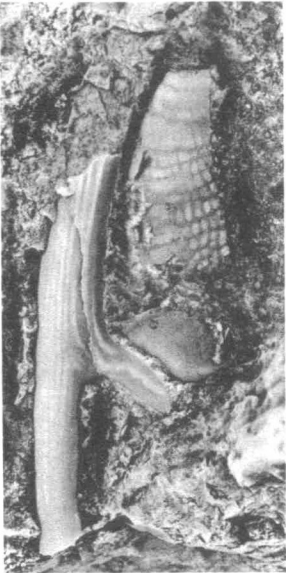
- Fig. 5 CPC 9727, limestone mould of right librigena, x8, locality B750.

Crucicephalus ocellatus gen. et sp. nov.

- Fig. 6 CPC 9778, limestone mould of right librigena, x10, locality K102.

Richardsonella sp.

- Fig. 7 CPC 9726, limestone mould of right librigena, x8, locality B750.



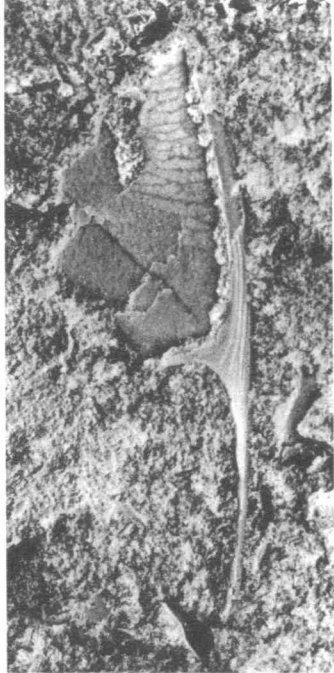
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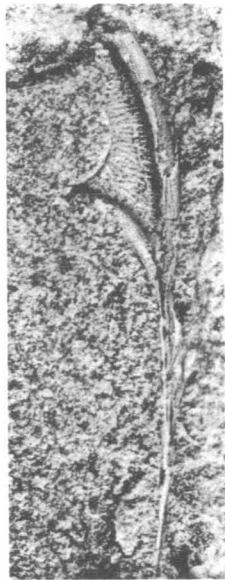
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