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

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THE GEOLOGY AND PALAEONTOLOGY OF THE HEADWATERS OF THE BURKE RIVER, QUEENSLAND

BY

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SUMMARY

The headwaters of the Burke River are in the Selwyn Range, north-western Queensland. Exploration began in 1860; Cambrian fossils were discovered in 1931. Mapping by the Commonwealth Bureau of Mineral Resources (1952-1958) amplified the knowledge of the geology and palaeontology of the area.

Four formations (Roaring Siltstone, Devoncourt Limestone, Selwyn Range Limestone, and O'Hara Shale) and one unit of beds (Mount Birnie Beds) constitute the Cambrian of the Selwyn Range sequence. The Mount Birnie Beds (sandstone, arkose, regolithic clay) occurs as erosional residuals on the basement. Unconformably above follows the Roaring Siltstone with shale and sandstone interbeds; above it rests the Devoncourt Limestone, flaggy and bituminous; the next higher is the Selwyn Range Limestone, a calcilutite with chert and marly interbeds, overlain by the O'Hara Shale with interbeds of chert and sandstone. A Mesozoic conglomerate (erosional residuals) and alluvial deposits conclude the sequence.

The structure is a sunkland in the Precambrian basement. The Palaeozoic rocks were faulted and mildly folded late in the Ordovician. The Devoncourt Limestone and the Selwyn Range Limestone are jointed in diverse manner and the younger Selwyn Range Limestone has not inherited the joint-direction of the older Devoncourt Limestone.

The present erosional processes consist in slope retreat and development of pediments which are transitory, being dissected by streams. Dissection of jointed limestone consisting of hard beds and soft marly beds results in a terraced bastion topography. The surface of the Devoncourt Limestone is an undissected pediment of truncated gently dipping beds. Remnants of a pre-Cretaceous surface are present. A Tertiary land surface is still preserved, but is rapidly eroded owing to the late Tertiary or sub-Recent uplift of the Selwyn Range. No Davisian peneplain is apparent; pediplanation in the sense of L. C. King is prevalent, but stream erosion and wasting are active also, and the landscape can be described in terms of an 'old-land' in the sense of E. S. Hills.

The stratigraphy is presented as a succession of events in two charts. The Lower Cambrian Mount Birnie Beds cannot be dated accurately in the absence of diagnostic fossils. After a long interval (occupied by folding and erosion) the Roaring Siltstone and Devoncourt Limestone were deposited late in the Middle Cambrian. Their age is the span of *Leiopyge laevigata*, divided into three separate zones (*Ptychagnostus cassis, Proampyx agra,* and *Holteria arepo*). The correlation with the Swedish Zone of *Solenopleura brachymetopa* and *Leiopyge laevigata* is demonstrated. The unfossiliferous Selwyn Range Limestone is dated as basal Upper Cambrian. The lower part of the O'Hara Shale was deposited in the Zone of *Glyptagnostus stolidotus,* and the upper part in the Zone of *Glyptagnostus reticulatus,* followed by the '*Eugonocare* Stage'. These divisions, including an unnamed basal zone (pre-*stolidotus*), represent the Upper Cambrian Dresbachian stage in Australia.

The Middle Cambrian formations are marine, deposited in an epicontinental trough; the Selwyn Range Limestone indicates an almost evaporitic environment inimical to life. The O'Hara Shale was deposited in shallow water. Generally epicontinental 'cratontic' conditions prevailed. The 'biotectonic' criteria of Ch. Lochman-Balk and J. L. Wilson fail in the Selwyn Range Seqeuence, which contains no 'cratonic' but 64% of 'Euxinic-extracratonic eugeosynclinal' forms. Palaeoezoogeographically, Acado-Baltic fauna is dominant, and the Cathayan and Pacific provinces are well represented, especially in the Dresbachian.

The Middle Cambrian fauna of the Selwyn Range sequence, as described here, contains altogether 57 species, of which 23 are new; open nomenclature is applied to 20 forms.

Three species — *Grandagnostus imitans* sp. nov., *Papyriaspis lanceola* Whitehouse, and *Mapania angusta* (Whitehouse) — from the Undilla Basin are also described to facilitate the comparison with Selwyn Range forms.

Besides taxonomy the organization of trilobites (*Centropleura* and *Papyriaspis*) is discussed in detail.

Spongia are represented by *Pleodioria tomacis* gen. nov. et sp. nov., with pentacts and bifurcate tips of sclerites. Of brachiopods *Lingulella, Acroteta, Acrothele,* and *Micromitra* are present. Worms are indicated by rare burrows.

Agnostids are numerous. A simplified classification is suggested, and special attention is given to effaced forms. Quadragnostidae Howell 1935 is suggested for Peronopsidae Westergaard 1936, and Spinagnostidae is reserved for a single genus (*Spinagnostus*). *Peronopsis scaphoa* is a new species. *Hypagnostus* is represented by *H. brevifrons* (Angelin), and the new species *willsi, hippalus,* and *varicosus*. *H. hippalus* indicates relationship with *Grandagnostus,* which also is included in Quadragnostidae. Diplagnostidae are represented by *D. planicauda vestgothicus* (Wallerius) and *D. humilis* (Whitehouse), which also serves to illustrate the occipital (and pygidial) similarity in agnostids. Agnostidae are present with two subfamilies: Agnostinae (synonyms: Geragnostidae, Micragnostidae), and Glyptagnostinae (synonym: Hastagnostidae). *Agnostus* cf. *neglectus* Westergaard represents the Agnostinae.

Glyptagnostinae are: *Ptychagnostus* (*Ptychagnostus*) *cassis* sp. nov. and *aculeatus* (Angelin); *P.* (*Goniagnostus*) *fumicola* sp. nov. and *nathorsti* (Brogger); *Leiopyge laevigata* (Dalman) and *laevigata armata* (Linnarsson). Incertae familiae are *Delagnostus dilemma* gen. nov. et sp. nov., *Blystagnostus laciniatus* gen. nov. et sp. nov., and *Pseudaphalacroma dubium* (Whitehouse). *Agnostus* (*'Ciceragnostus'*) *cicer* Tullberg is probably a *Pseudophalacroma,* and unrelated to *Ciceragnostus barlowi* (Belt).

Polymerid trilobites are well represented. The Centropleuridae contain two new species, *Centropleura sonax* and *C. phoenix*. *C. phoenix* is rather well preserved and a complete reconstruction is given. Taxonomy of all known species is discussed. *Centropleura* was a pelagic trilobite. Dorypygidae are represented by *Holteria arepo* sp. nov., known from pygidia only; Corynexochidae by a single blind form — *Acontheus burkeanus* sp. nov; and Dolichometopidae by two new species of *Amphoton,* of which one (*bensoni*) is complete. Ellipsocephalids (Agraulidae) contain *Proampyx agra* sp. nov. (related to *difformis* Angelin), which is also complete. Agraulidae are removed from Solenopleuracea. Ptychopariacea (Papyriaspididae) contain *Tosotychia sors,* gen. nov. et sp. nov.; Papyriaspididae are removed from Olenacea, and considered to be related to *Chancia,* but *Rhodonaspis* is retained in Olenidae. *Papyriaspis lanceola* (not present in the Selwyn Range sequence) is re-described. Anomocarellidae occur as several new species of *Mapania*. *Mapania angusta* (Whitehouse) is re-described, although it is not present in the Selwyn Range sequence. The type, *Mapania striata* Resser & Endo (Manchuria), is discussed, and a reconstruction shows that the anterior sutures are divergent, and not convergent. Crepicephalidae produced a single pygidium (open nomenclature).

Two genera of Crustacea Bradoriida ('Conchostraca', Phyllocarida, Archaeostraca) occur: (1) *Svealuta* gen. nov., with *Leperditia primordialis* Linnarsson as type and (2) *Aristaluta gutta,* gen. nov. et sp. nov., which is trilobate, has a border with doublure, and a posterior gap. The affiliation of Bradoriida with ostracods seems to be probable. Misuse of the generic name *Aluta* Matthew is discussed.

Relevant localities are described in an Appendix, and the occurrence of the *Leiopyge laevigata* fauna outside the Selwyn Range is discussed in a separate chapter.

INTRODUCTION

The position of the area described here as the 'Headwaters of the Burke River' in the tropical zone of Australia is evident from the locality map, Figure 1. Topographically it is part of the Selwyn Range, which is a divide composed mainly of metamorphosed Precambrian rocks. These are described by Carter (1959), Carter & Brooks (1960), and Carter, Brooks, & Walker (1961). Structurally it is part of the Burke River Outlier, within which the Selwyn Range is built of Cambrian sediments, which are referred to as 'the Selwyn Range sequence'. This sequence is preserved here owing to post-Cambrian faulting that involves the whole Outlier; the Outlier itself is the northern segment of the Burke River Structural Belt, which extends south for another hundred miles.

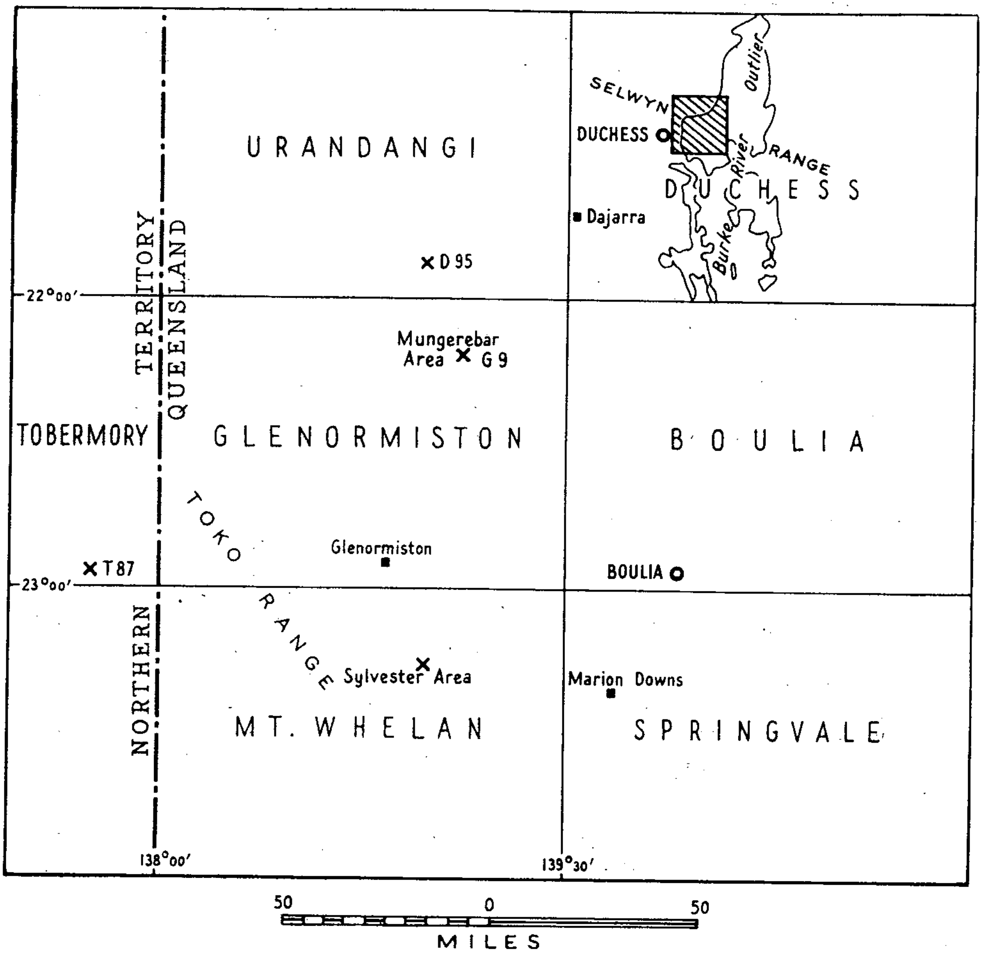


FIG. 1.—Locality map of the Headwaters Area of the Burke River, Queensland (see Fig. 2).

The fossils of the Selwyn Range sequence amplify the knowledge of the distribution of marine life of the Cambrian Period, because genera of diverse provinces are found here in one and the same formation. My claim that several agnostids of the Selwyn Range sequence belong to known Scandinavian species is a matter of special responsibility. With this in mind I studied in 1956 all specimens of Middle Cambrian agnostids (and other trilobites) in the collections of the U.S. National Museum in Washington, and in 1957 all Cambrian fossils in the Ricksmuseum and the Geological Survey in Stockholm, and in the Palaeontological Museum of the University of Oslo. I thank the Heads of these organizations for the assistance and hospitality received, and appreciated especially the meetings with Dr A. R. Palmer (Washington) and Dr G. Henningsmoen (Oslo), and the opportunity to meet again Dr A. H. Westergaard.

HISTORY OF EXPLORATION

Robert O'Hara Burke and William John Wills traversed the country in 1860, and the names of Burke River and O'Hara's Gap are the local memorials of their explorations.

The discovery of ore in the region in 1867 (see Carter, Brooks, & Walker, 1961) advanced subsequently the knowledge of the basement rocks. The lower Palaeozoic superstructure was discovered also, but not studied in any detail. The limits of the Burke River Outlier, however, were correctly mapped by Honman (1937), and Nye & Rayner (1941) describe it as a 'tongue of Middle Cambrian rocks', 50 miles long.

The Middle Cambrian age was already established by Whitehouse (1931) from fossils collected by C. Ogilvie in limestone about 8 miles north-east of Duchess. These fossils, altogether five species of agnostids, were described by Whitehouse (1936), and assigned to the *Phoidagnostus* Stage — the third and lowermost division of his *Phalacroma* Group of the Middle Cambrian Series. The limestone itself was regarded as belonging to the 'Georgina Limestones'. The locality is in the headwaters area of the Burke River, and the rock is the Devoncourt Limestone.

The mapping of the Mount Isa-Cloncurry Mineral Belt by the Commonwealth Bureau of Mineral Resources in 1950-1958 (see Carter, Brooks, & Walker (loc. cit.) required also a study of the Palaeozoic superstructure of the region. It is shown in the 10-mile map (Carter & Öpik, 1959), and in greater detail on the 4-mile sheets. One of these is the Duchess 4-mile Sheet (Carter & Öpik, in press), with its Burke River Outlier of lower Palaeozoic rocks.

The Outlier is relatively small (about 1400 square miles), but contains a fossiliferous Cambrian and Ordovician sequence previously almost unknown. Several large faunas are involved, and the present bulletin is concerned with a part of the Middle Cambrian fossils.

The structure of the Outlier has not been described in detail previously and is, therefore, illustrated here by the small 'sample' of the headwaters area of the

Burke River. Furthermore, the only published information concerning the geomorphology was the preliminary reports of Twidale (1956), and therefore observations made on that topic in the course of the work are included also.

I studied this area in 1952 and 1954, and published (1956, a, b) a brief account of the palaeontology, formations, palaeogeography, and structure of the Cambrian of the Outlier, including the Selwyn Range. In 1957 I once more visited the fossiliferous localities of the O'Hara Shale for collecting purposes. The stratigraphy is included in the correlation chart, and briefly discussed by Öpik (1960). Eighteen days were spent in the field in 1954 in the Selwyn Range part of the Burke River Outlier, and during this time the map (Fig. 2) was also prepared with the aid of air photographs.

The area of the Burke River headwaters is easily accessible from Duchess on the Mount Isa-Cloncurry-Townsville railway, as well as by the Mount Isa-Duchess-Cloncurry road, which crosses the area. Most of the relevant outcrops can be reached by that road, and local station roads and tracks. On these tracks, and cross-country traverses, a four-wheel-drive car is preferable.

ROCK UNITS

The five rock units that are described here as four formations and one unit of 'Beds' are listed in the Table, Figure 14. The names of these formations were first published by Öpik (1956a, p. 17) and were taken into formal use. Subsequently brief characteristics of the formations were published in Öpik (1960).

In the following descriptions the localities that are designated by geographical co-ordinates are meant to be the type localities or 'the sections selected as the types', in the sense of the Australian Code of Stratigraphic Nomenclature.

The rock-units described below in ascending order are: (1) Mount Birnie Beds, (2) Roaring Siltstone, (3) Devoncourt Limestone, (4) Selwyn Range Limestone, (5) O'Hara Shale, and (6) Mesozoic and younger rocks (unnamed). The fossils are listed in the Appendix (Description of Localities).

Mount Birnie Beds

The name Mount Birnie refers to the main occurrence of this sequence about 15 miles south from loc. D26. Mount Birnie Beds in the area described here occur only along the Pilgrim Fault and the Roaring Fault, as erosional residuals between the basement and the Roaring Siltstone.

The rocks are hard sandstone and arkosic sandstone. A regolithic purple clay with granite fragments (Öpik, 1956) found south-west of the Roaring Bore is also included in Mount Birnie Beds. The clay bed is in places 20 feet thick, and some of the sandstone wedges may exceed 100 feet. At the Roaring Fault in the interfluvium of the branches of Sandy Creek a small wedge of hard sandstone occurs. It is about 50-60 feet thick and dips 20 degrees east; above follows the Cambrian sequence, of which the Devoncourt Limestone is visible in the creek

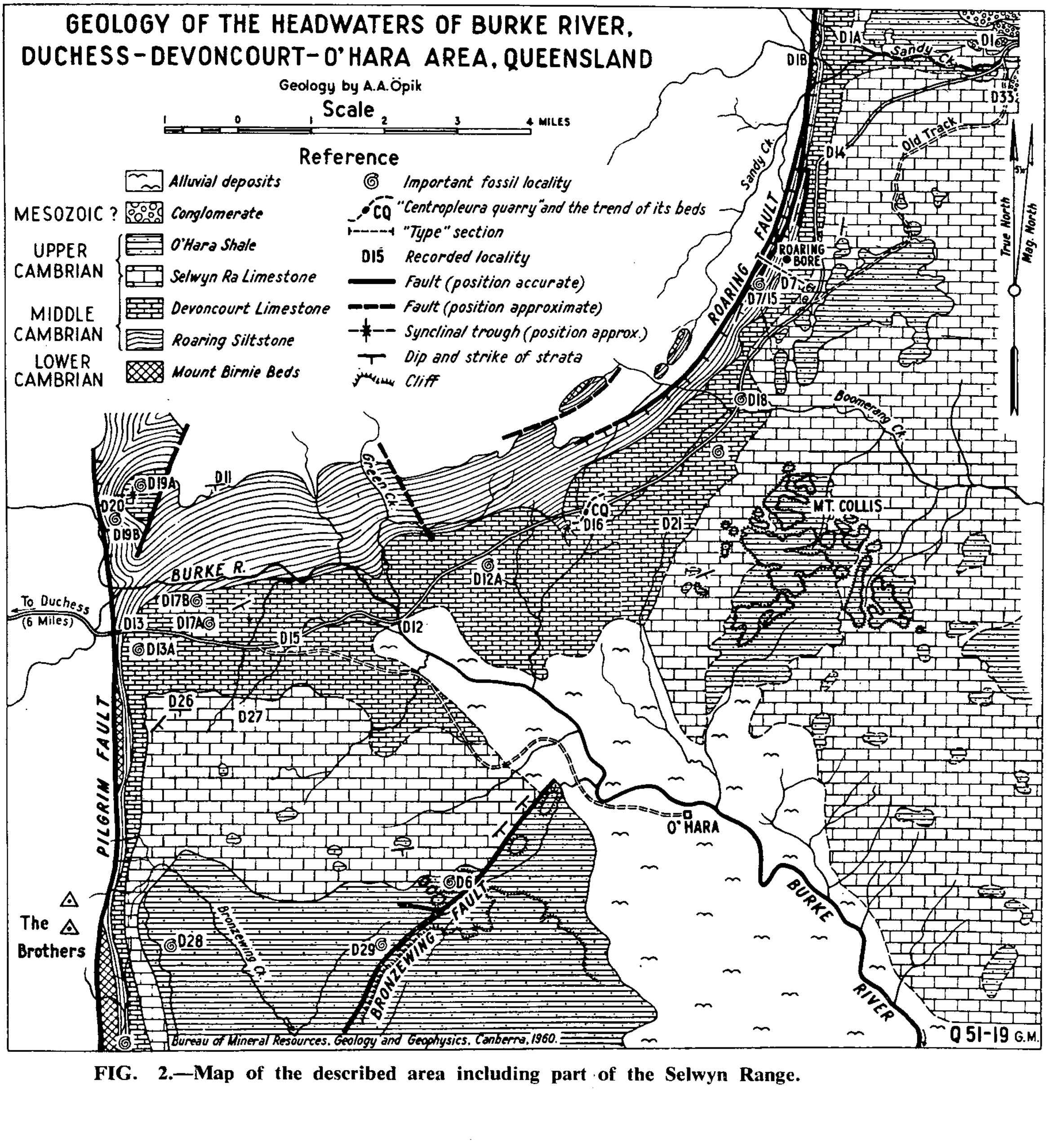


FIG. 2.—Map of the described area including part of the Selwyn Range.

bed. The limestone is on edge. The difference in the attitudes of the sandstone and the Cambrian suggests an unconformity. This is the 'Unconformity 5' (see chart, Fig. 14), which is also observable at Mount Birnie and farther south.

In the absence of conclusive evidence, Mount Birnie Beds were regarded previously as sub-Cambrian, but they are evidently of Lower Cambrian age, as indicated here in the chapter on stratigraphy.

Roaring Siltstone (*Roaring Bore Siltstone*)

The name is derived from the Roaring Bore; but, because no confusion will arise, the word 'bore' can be omitted from the name of the formation (Roaring Siltstone). The main outcrops occur immediately west from Roaring Bore (Lat. 20°17′ S., Long. 140°05′ E.). The thickness is 230 feet (see description of locality D7, p. 180).

The Roaring Siltstone rests on the basement or on residuals of Mount Birnie Beds. The upper contact against the Devoncourt Limestone is sharp, as discussed under that formation. The contact is observable at the Roaring Bore itself in a small stream-bed south of the Bore, and in several places along the right bank of the Burke River.

The formation is fossiliferous, and fossils occur in several bands in otherwise unfossiliferous rock. The age is upper Middle Cambrian (Figs. 14, 15).

Fresh rock occurs only in the stream-bed (running north) at the Bore itself, and is a friable, minutely laminated light grey siltstone with some calcareous matter in some of the laminae. In surface outcrops it is a leached and hardened white or coloured siliceous siltstone with interbeds of a similar shale and thin bands of fine-grained sandstone. The white (pallid) and mottled colours can be attributed to lateritization. The top of the profile (where preserved) consists of partly silicified siltstone and shale infiltrated by iron oxide, but no ferruginous laterite is present. The lateritization is consequently imperfect, because, with the exception of colour, no alteration is apparent, and the character of the rock, stratification, and fossils are preserved. All signs of lateritization are absent in the proximity of the overlying limestone, and below the limestone the rock is fresh. Consequently there must have been a time lag between the removal of the limestone cover and the onset of lateritization. Apparently erosion prevailed on the dip slope of the Roaring Siltstone, preventing the development of laterite, which requires horizontal surfaces that are protected from erosion. Lateritic cappings of clastic rocks resting on limestone are common in the region and sometimes interpreted in terms of decalcification and lateritization of limestone. In the present example the sequence is reversed: the clastic rock rests below the limestone, which remained intact, being incapable of lateritization. In all known outcrops the siltstone is contorted, apparently in conjunction with faulting. The relief is dominated by cuestas and homoclinal ridges facing west and north-west, where faulting and induration by lateritization hardened the rock. Farther north, however, and in the valley along the Pilgrim Fault the siltstone forms a part of the rubble-covered floor with occasional outcrops of soft, often fossiliferous, siltstone in breakaways.

The known geographical occurrence is confined to the western part of the northern end of the Burke River Outlier.

Hand specimens of Roaring Siltstone, in the absence of fossils, and without data regarding occurrence and superposition, cannot be identified, because its lithology can be confused with that of Mesozoic rocks and any Cambrian shale occurring in the region, and even in the whole of northern and central Australia.

Devoncourt Limestone

The name of the formation refers to the pastoral property 'Devoncourt'; almost the whole area covered by the limestone in the map (Fig. 2) is within the boundaries of the Devoncourt property. Whitehouse (1936, 1939) assigned the limestone to the *Phoidagnostus* stage and refers his collection to a position about 8 miles north-east of Duchess. Locality D15 (Lat. 21°21′ S., Long. 139°59′ E.) is the nearest to that position. The thickness is variable, but not less than 350 feet (see description of locality D7, p. 180). At Mount Mundi, 14 miles north from D7 (outside the area shown in the map, Fig. 2) it is 600 feet thick in the fault-zone of the Roaring Fault.

The Devoncourt Limestone rests conformably on the Roaring Siltstone. The contact is sharp, without interbedding, but no break is apparent. It appears that silt was continuously deposited, but was diluted by precipitation of calcite. Devoncourt Limestone is throughout impure, silty and sandy. The upper contact (with the Selwyn Range Limestone) is an interbedded passage, as described under the latter. Devoncourt Limestone is fossiliferous; its age is uppermost Middle Cambrian (see fossil lists, Figs. 14 and 15).

The rock is limestone in the sense that no dolomite or dolomitic limestone is present; the sequence in general consists of flaggy to medium-bedded hard beds (up to 6 inches), with partitions and interbeds of marly laminated limestone. Within the area these interbeds are sporadic, which has some effect on the topography, as discussed below. This litholigy is, however, not uniform as regards particular parts of the sequence. In the lower portion thick-bedded pink laminated beds occur, as well as dark bituminous varieties with pyrite. Two-toned limestone (pink laminated matrix with grey biscuits and layers) occurs near the base. The most common type is a grey fine-grained sandy bituminous limestone. It is laminated, but not fissile. In the upper portion of the formation in southern outcrops the limestone is even more bituminous, hard and splintery.

At locality 19A in dry wells grey laminated marl contains hard laminated ellipsoids. At locality D18 layers of crystalline calcite with drop-like grains of silica are present. Marly interbeds are fissile and contain minute mica flakes.

Main joints (Fig. 6) trend west-north-west at about 325°.

The formation's topographic expression is pediment (Figs. 6, 8, and 10), minutely ribbed by beds dipping at low angles. Within the described area, owing to paucity of marly interbeds, no bastion topography nor any hills are present. In the north, however, where soft interbeds occur at regular intervals, terraced bastions are common. In the valleys along the Pilgrim Fault and Roaring Fault, where the limestone is steeply dipping or even on edge, the limestone occurs as ribbed and rubble-covered floors.

Little is known about the former geographical distribution of the Devoncourt Limestone. It occurs only in the northern part of the Burke River Outlier, confined within the bordering faults. It is, however, a marine deposit and may have been of a regional extent. Far in the south, at Sylvester Creek, and in the south-west (west of Toko Range) limestone of a comparable lithology and of an identical age occurs (Öpik, 1956; see also also p. 48), which may be part of the Devoncourt Limestone—assuming (without any chance of proof) that it was originally a coherent body, and not scattered lenses of limestone.

Selwyn Range Limestone

The name Selwyn Range is taken from the part of the Range east of the Duchess-Cloncurry Road, and north-east of Roaring Bore, along the 'Old Track', and at locality D33 (Lat. 21°13′ S., Long. 140°10′E.) (Figs. 1 and 4). The visible thickness in a single outcrop in this area is about 20 feet; the total thickness is between 100 and 120 feet. The name cannot be abbreviated to 'Selwyn Limestone' because of the possibility of confusion with Selwyn Station in the same area.

The Selwyn Range Limestone rests on the Middle Cambrian Devoncourt Limestone, and below Upper Cambrian O'Hara Shale (see Figs. 14 and 15); its position in the sequence shows that its age is lowermost Upper Cambrian. The formation consists of hard, flaggy, light-coloured calcilutite beds with interbeds of softer marly limestone. Chert biscuits and layers are present. The beds are indistinctly banded and laminated; the marly rock is fissile, the calcilutite shows a conchoidal fracture. Pyrite occurs sporadically. The composition is calcite, with clay as impurity. In one place (locality D27) a dolomitic limestone is present.

Joints in the eastern part of the area are strong and open, and trend west to north (about 280°-285°). The outcrops consist here of pediments dissected by narrow and shallow streams, and a low bastion topography is prevalent. In the south-western area (localities D26-D27) the direction of the joints on air photographs is almost due west, because they appear as lines projected not on a horizontal, but on a surface dipping south at 5-10°; moreover, a fracture grid is superimposed, with north-west and north-east directions. These fractures are probably tectonic, because the whole area is a fault block, and faults with these trends (Bronzewing Fault, for example) are present in the Outlier.

The contact with the Devoncourt Limestone is gradual for a thickness of about 10-15 feet, because the marly interbeds have a similar appearance in both formations; but the harder beds are distinctive: they are sandy and have rough weathered surfaces in the Devoncourt Limestone, and are predominantly smooth calcilutite without sand in the Selwyn Range Limestone. The jointing is also distinct in both formations (Figs. 4 and 6).

The contact with the O'Hara Shale (above) is abrupt in the south. At locality D6 the top bed of the Selwyn Range Limestone bears ripple marks, and the surface of the Limestone in this area is uneven. The break thus disclosed is interpreted as a local diastem. In the north, at locality D1, the diastem is absent and the O'Hara Shale has near its base a thin interbed of limestone (calcilutite) of the same character as Selwyn Range Limestone.

The Selwyn Range Limestone peters out rapidly about 2-3 miles north from Sandy Creek and extends for about 8 miles south from O'Hara station; similar lithology in the same stratigraphical position is unknown elsewhere in the region.

O'Hara Shale

The name O'Hara refers to the O'Hara property (station) on the Burke River. The locality from which the first, and so far the most complete, fossil material was collected is D6 (Lat. 21°25′ S., Long. 140°00′ E.), four miles west-south-west of the station. The station is called on some maps 'O'Hara's Gap', after a gap between mesas of the O'Hara Shale, about five miles east of the station. The formation is about 200 feet thick, which is the preserved thickness. The original thickness is unknown, because no upper contact is preserved; it is the topmost formation in the area. For details of the section and structure see description of locality D6.

The formation is fossiliferous, and its age is Dresbachian (lower Upper Cambrian).

The lower contact against the Selwyn Range Limestone is marked here by a diastem and an abrupt change in lithology (see under Selwyn Range Limestone). In the north (outside the described area), where Selwyn Range Limestone is missing, O'Hara Shale rests directly on Devoncourt Limestone; in the south, on Chatsworth, it overlaps Pomegranate Limestone (Öpik, 1960).

The lithology is predominantly thinly laminated, fissile, pink and red shale with siltstone and sandstone interbeds and layers of chert. In northern outcrops silt with chert prevails. Fresh rock is not available. Presumably the original colour was light grey, and bands of limestone nodules and even thin laminae of limestone were, or are, present also in higher levels (see description of locality D6). The relief is dissected low plateau, tabletops and buttes, and, near the Pilgrim and Bronzewing Faults, cuestas. O'Hara Shale occurs as surface residuals over the whole length of the Burke River Outlier, and on Wills Creek south of Buckingham Downs in the Boulia Sheet area.

Mesozoic and Younger Rocks

Younger rocks in the area consist of alluvial deposits along the Burke River, and a conglomerate which occurs as cover on some mesas in the north.

Alluvial deposits are mainly sand, with pebbles in places. The sand consists of material originating in the Precambrian, at the extreme heads of the Burke River, but among the pebbles and cobbles are fragments of limestone and Roaring Shale. Alluvium forms flat grasslands, and the banks of the River are fringed by tall trees.

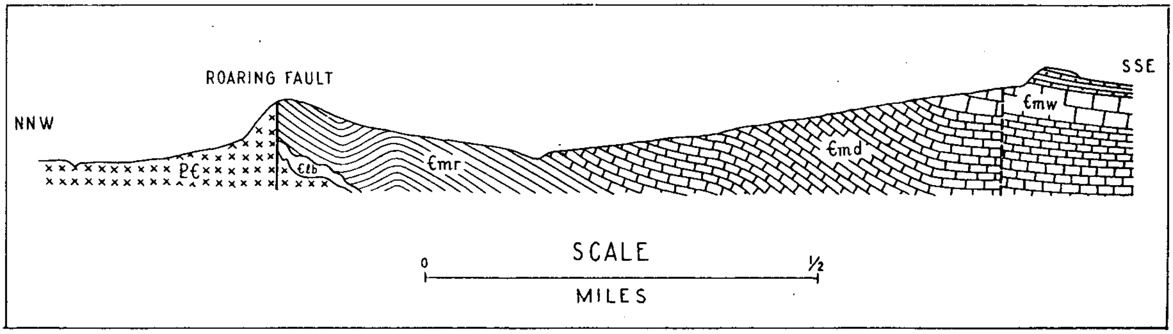


FIG. 3.—Section at Roaring Bore (see description of loc. D7). Topography and thicknesses exaggerated, attitude as exposed on the surface. Position of Precambrian/ Cambrian contact east of Roaring Fault estimated. PC—Precambrian basement; Clb—Mt Birnie Beds ((Lower Cambrian); Cmr—Roaring Siltstone; Cmd—Devoncourt Limestone; Cmw—Selwyn Range Limestone; Cuh—O'Hara Shale.

Outcrops of the conglomerate are seen at locality D1, and to the north and east. At locality D1 the conglomerate caps low mesas of O'Hara Shale, and is apparently deposited on an uneven erosional surface. The thickness ranges between 5 and 15 feet. It is an oligomict rock, with pebbles of quartz, quartzite, and chert derived from the O'Hara Shale. The conglomerate is silicified on the surface, but otherwise only moderately consolidated. The age is post-Ordovician, and, presumably, Mesozoic (Lower Cretaceous). Topographically the erosional residuals of the conglomerate are insignificant; but several residuals occur outside the described area on both sides of the eastern fault of the Burke River Outlier. These residuals rest on an uneven erosional surface the relief of which is less than one hundred feet. The displacement by faulting in the same place is not less than 700 feet; so the conglomerate is younger than the faulting and the erosion of the tectonic topography.

The conglomerate is unfossiliferous and provides no evidence of its own age. The Mesozoic age is, therefore, only an assumption based on the low degree of consolidation of the rock, and on geomorphological grounds.

STRUCTURE

The area here described is a part of a tongue-shaped graben 'bounded by post-Cambrian faults, which explains the preservation of the lower Palaeozoic sediments. The rocks are slightly folded, and a thrusting from the east is apparent' (Öpik, 1956, p. 11). The whole belt of these disturbed lower Palaeozoic strata is known as the Burke River Structural Belt, or briefly, Burke River Structures, visible on the surface between latitude 21° S. and the Tropic of Capricorn (Öpik, 1960). The part north of latitude 22°00'S. is surrounded by the Precambrian basement, and is, therefore, an outlier (Burke River Outlier). The southern part of the Burke River Outlier passes southward into a trough, but the northern part is a sunkland bounded by faults in the north, east, and west. The area described here is a part of that sunkland.

The deformation of Cambrian strata is mild, but quite general: in no outcrop do rocks preserve their original depositional attitude.

The angles of dip are steep along the Pilgrim Fault (from 70° to vertical) and along the northern part of the Roaring Fault, and decrease to east and south-east, and off the faults. The strike remains parallel to the faults for half a mile to a mile or even more. Farther away a general low dip to the south or south-south-west prevails, pointing towards the trough in the south. Small corrugations and rolls are ubiquitous in limestone, and the Roaring Siltstone is folded (Fig. 3).

The faults in the area are of three different degrees of magnitude: numerous small fractures with a negligible displacement occur in limestone (see Fig. 6), and will not be discussed further; the second magnitude is represented by the Bronzewing Fault, and the third—the largest—by the Pilgrim and Roaring Faults.

The Bronzewing Fault trends north-east, in a direction of lineament seen also farther south. A fault of similar magnitude is that at locality D19, which is indurated and topographically prominent. The Pilgrim Fault is near-meridional and almost straight, and the vertical displacement (opposite D28) is not less than 1000 feet. West of the Pilgrim Fault and parallel with it stands a Precambrian fault topographically manifested by trains of hogbacks (The Brothers). The Roaring Fault south-west of the Bore is of a small displacement and peters out rapidly. North of the Bore the fault takes a meridional course, and the displacement here is an estimated 7-800 feet; but it cannot be accurately determined because no Cambrian is preserved on the horst, and how much of basement rocks has been removed by erosion is also unknown.

Fracture cleavage occurs sporadically in the Roaring Siltstone, as, for example, locality D20. A similar but latent cleavage is also present in some places in the Devoncourt Limestone. At locality D16 it is meridional, dips about 70° east, and, although not immediately visible, must be taken into consideration in splitting the flags in search of fossils.

Everywhere limestone beds are cut by east-dipping slickensided fractures with a displacement of no more than a quarter of an inch each (see Pl. 11, fig.

7). The dip varies around 10° and is independent of the attitude of the beds. These slickensides indicate thrusting from the east and a pressure imposed on consolidated and already deformed rocks.

The age of the deformation is, according to Öpik (1960), Palaeozoic and, most probably, late Ordovician.

The limestones are strongly jointed. In the Devoncourt Limestone the direction of main joints is 325°, whereas in the younger Selwyn Range Limestone it is 285°. At one place (Fig. 6) the Selwyn Range joints are imposed on the Devoncourt Limestone below, but extend only to a shallow depth. But the younger Selwyn Range Limestone has not inherited the older joint direction from the underlying Devoncourt Limestone.

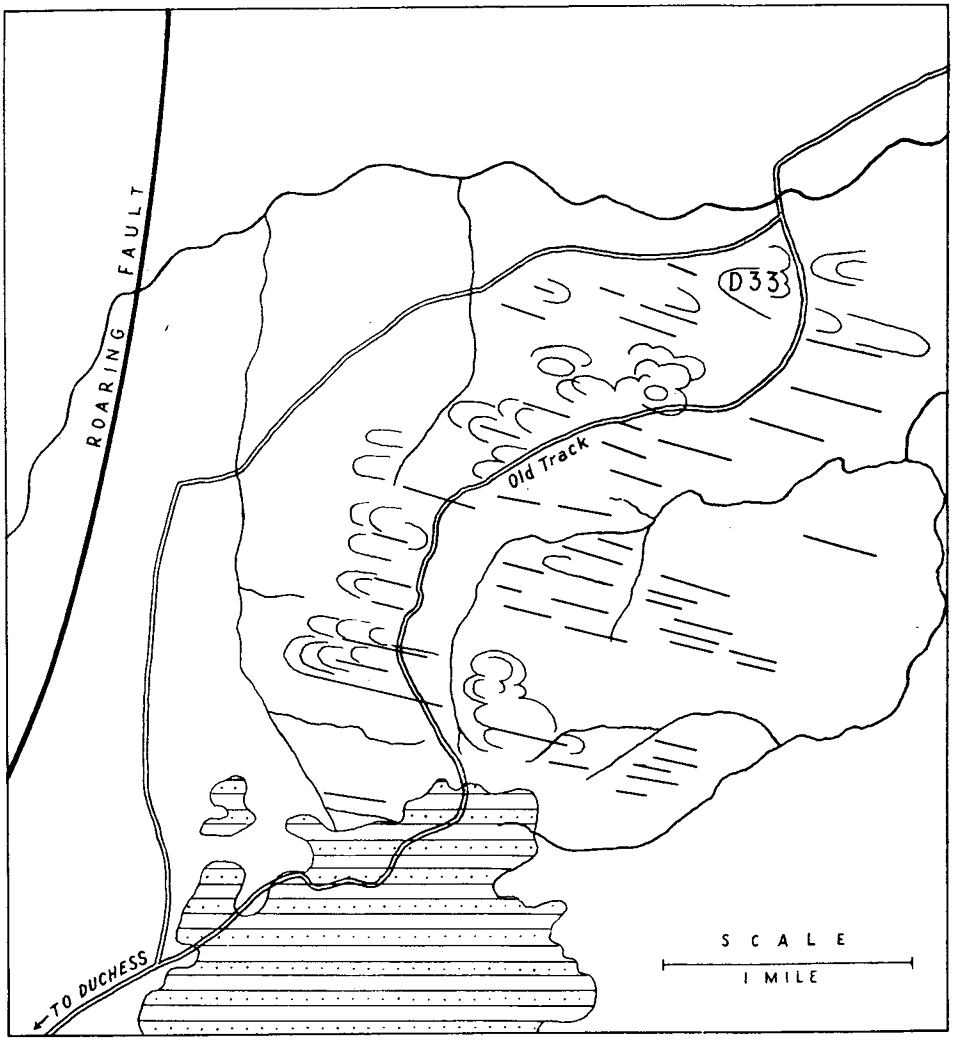


FIG. 4.—Joints and terraced slopes in Selwyn Range Limestone (adapted from air photograph); heads of creeks indicate highest place in Selwyn Range (compare Fig. 5; for position see Fig. 13).

GEOMORPHOLOGY

INTRODUCTION

The concepts of old (inherited) surfaces and landscapes, of transitory pediments, and of bastion topography of limestone, must be explained. It appears that the landscape of the Burke River headwaters area is an old and exhumed, and subsequently modified, pre-Cretaceous landscape, within which fragments of younger, but pre-Recent, surfaces are also present. The notion of transitory pediments is introduced to describe floors on Cambrian sediments formed during scarp retreat and shortly afterwards dissected by streams. They are distinct from undissected pediments of longer duration and from true pediments truncating Precambrian rocks of diverse composition and resistance that are present in the same area.

FIG. 5.—Bastion topography; limestone, Selwyn Range. Looking east from Old Track at 'highest place of Range' (see also Fig. 4; for position see Fig. 13).

The description *bastion topography* refers to the erosional landscape formed on limestone. The geomorphological theories prefer examples of topographic features developed on clastic rocks, but limestone serves only to elucidate karst phenomena. Carbonate rocks are in a minority with a 5 to 6 percent of the global total of sediments, and are therefore insignificant on a global scale. North-western Queensland, however, is a province of lower Palaeozoic carbonate rocks, which, depending on the attitude and lithology, produce three kinds of forms (Öpik, 1959): (1) cuestas and sierras in folded belts; (2) plains on horizontal beds of uniform lithology; and (3)bastion topography on horizontal sequences consisting of alternating hard bands and less resistant marly or sandy interbeds. Karst occurs sporadically, but is insignificant in the development of the bastion topography.

The term *bastion* has been used previously in geomorphology to designate fortress-like rock faces.

OLD SURFACES AND LANDSCAPES

The present land surface is naturally recent, but parts of it are now being modelled and parts have been modelled in the past, and at different times. Such inherited surfaces, however, are rarely intact, being subsequently degraded (or even aggraded) to some extent; but provided that the rocks, formations, and structures

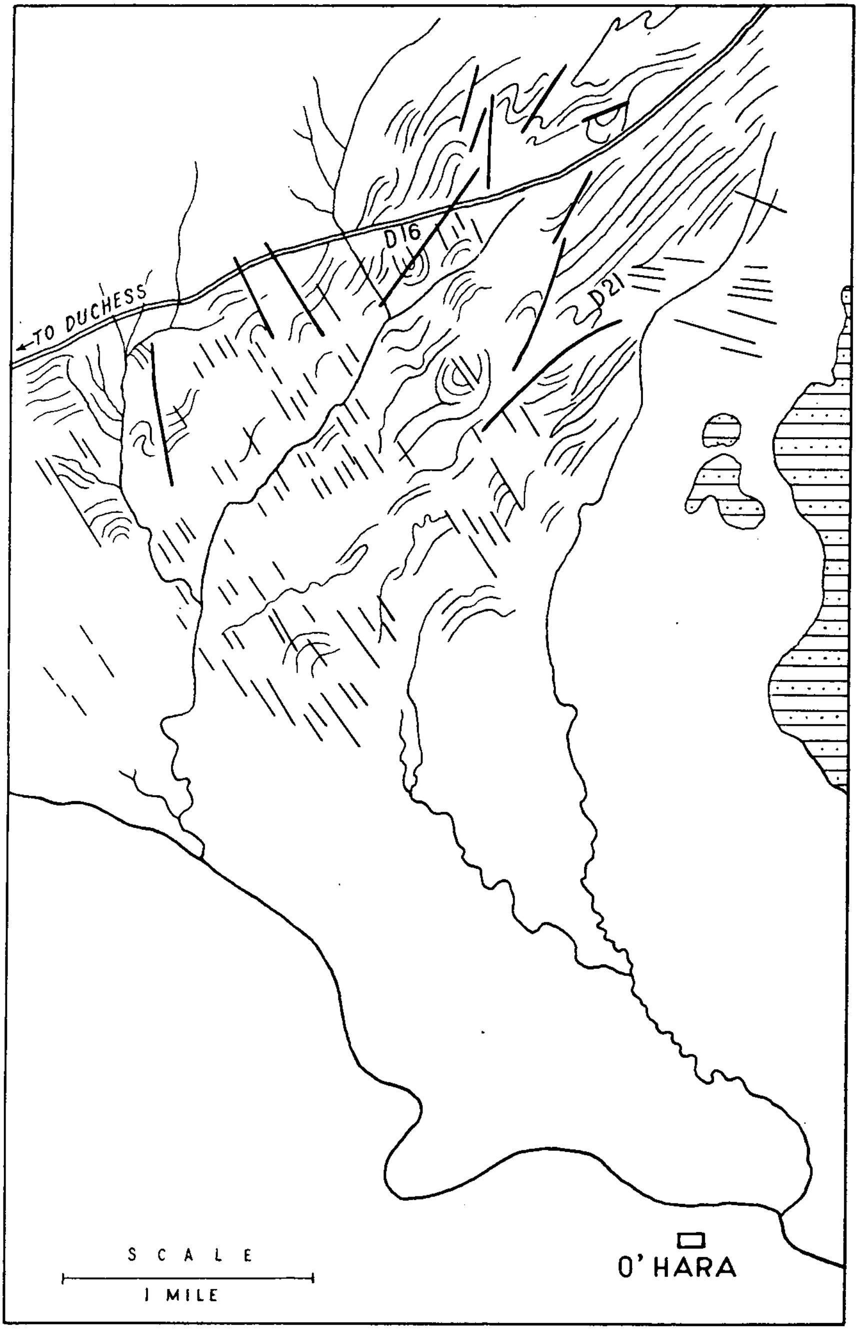


FIG. 6.—Pediment plain (Devoncourt pediment), adapted from air photograph. Minor faults, trends of truncated limestone beds, and joints indicated. East from D21 Selwyn Range Limestone joints are superimposed on Devoncourt Limestone. (For position see Fig. 13).

remain the same, they are supposed to be congruent with, and not far off from, the initial surfaces seen in outcrops of unconformities. A similar reasoning is applicable to a landscape, be it a simple plain, or a complex of topographic features. It is always recent, it exists now, but it may be congruent with forms of a preceding cycle.

To conclude, old land surfaces are preserved or exhumed features of relief and landscapes, and not exhumed 'exact surfaces'.

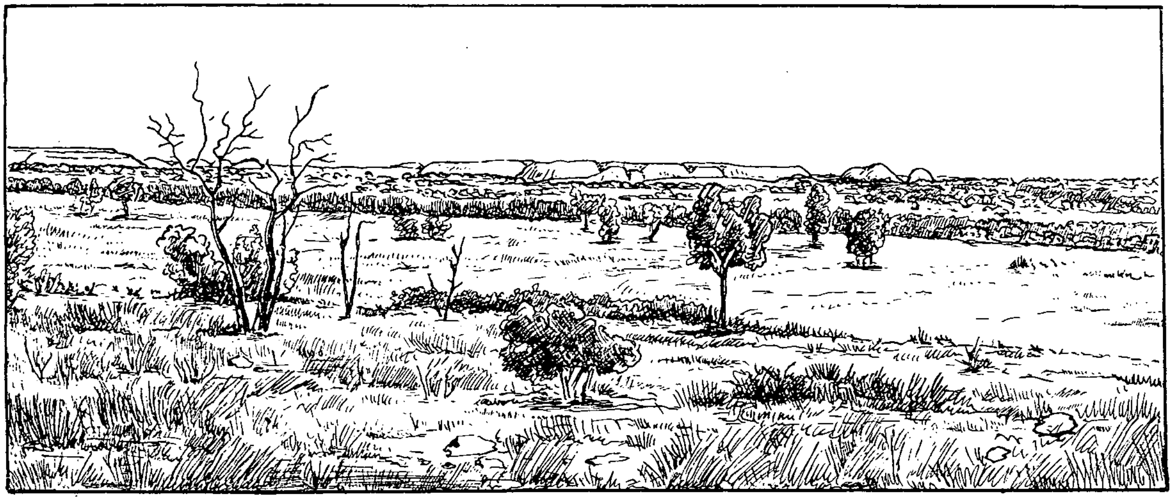


FIG. 7.—View from about southern bend of Old Track (about $\frac{1}{2}$ mile south from bend; for position see map, Fig. 13), looking south. Selwyn Range topography. Foreground: pebbly veneer of ferruginized O'Hara Shale; Boomerang Creek and dissected limestone pediment in the distance; sky line: Mt Collis group of mesas.

TRANSITORY PEDIMENTS

The term *pediment* when used without a particular qualification indicates rock floors that are, or are about to be, incorporated in a pediplain. These erosional surfaces develop regardless of the attitude and composition of the truncated rocks. Such pediments have a long duration when the base level of erosion remains essentially static. Stripped surfaces develop also above the erosional base in horizontal strata when a scarp of friable material retreats over a resistant floor. Such floors are also pediments, but transitory, because sooner or later they will be dissected by streams or be transformed into plateaux above another retreating scarp. In an arid climate erosion may be slow, however, and transitory pediments may persist over indefinitely long intervals of time, and if they become confluent over a large area constitute a structural plain.

A pediplain is related to the base level that existed during its formation, and a structural plain to the accident of a resistant bed in the sedimentary sequence. If the whole formation, however, is equally resistant and horizontal, discrimination between the two kinds of plain becomes inconclusive, because (1) a pediplain develops regardless of the attitude of rocks, which may be also horizontal, and horizontality excludes the application of the criteria of truncation; and (2) a structural plain can be identified only in the presence of a particular resistant bed which at the time of stripping has been above the base level. An illuminating example is the Camooweal Dolomite, which covers over 20,000 square miles of the Barkly Tableland. The surface of the dolomite is a perfect plain about 800 feet above sea level and all its beds are equally resistant to erosion. It is a stripped plain, and a plain of soil-covered pediments; but it may or may not be a pediplain.

Bastion Topography

The two limestone formations encountered in the area—the Devoncourt Limestone and the Selwyn Range Limestone—differ from each other in their topographic expression. The Devoncourt Limestone has a relatively uniform lithology and occurs as undissected pediment surfaces in plains and in gentle slopes of valleys. It is the older, and therefore also topographically the lower formation. Its low topographic position may be also a reason why its truncated surface remains almost undissected. The Selwyn Range Limestone differs by its bastion topography, which is controlled by alternation of hard and soft beds, and jointing. On an escarpment of such limestone intersecting joints produce a serrate edge with salient angles of bastions; the recesses that separate them are also formed by joint intersections and are sites of gullies. The same applies to isolated limestone hills, which even more resemble fortifications. Alternation of hard and soft beds results in terraced bastions, the benches of which are resistant beds. Dissection of transitory pediments results in a bastion topography, but slope erosion is the main factor in maintaining the bastion form, as well as in destroying the bastions. The edge (the free face) of a bench is vertical; the soft bed below is a rubble-covered slope, which is eroded and retreats, undercutting the hard bed. Thus, the reduction of the bastion is proceeding separately and simultaneously on a multitude of relatively low slopes, each of which is fringed by a narrow pediment—the surface of the hard bed. The summit is usually also a hard bed; but it may also be a gently sloping cap of soft-rock rubble, the hard-rock ceiling of which has been completely destroyed. Reduction of relief by the way of wasting of horizontal surfaces is testified by the rubble and skeletal soil that are crowning the bastions. In horizontal or subhorizontal strata bastion summits are tables and plateaux; they may be tilted, and with higher dips (ten degrees or more) cuestas, or only ribbed surfaces of low relief, are developed, to be finally transformed into pediments.

Some Geographical Nomenclature

Two names, the Burke Plain (Twidale) and the Burke River Plain (Öpik) have been applied to different features within the region under discussion, and their near-similarity may cause some confusion. Twidale (1956b, fig. 2) proposed for the area of the Burke River Outlier the name 'Devoncourt Upland', which is surrounded by the Burke Plain (in his nomenclature). However, only the Selwyn Range within the Outlier is an upland, and the country north of it is in parts a perched graben. The main part of the Outlier south of the Selwyn Range is a lowland—the Burke River Plain of this paper—and the River itself receives its tributaries from the Burke Plain (in Twidale's sense). 'The valley eroded in gneiss and granite', and shown in Figure 11, is also included in the Burke Plain by Twidale; it belongs to the watershed of the Cloncurry River. It is suggested that the later published name 'Burke River Plain' should not be abbreviated, and the name 'Burke Plain' should retain its form, which is apparently not derived from any geographical place, but refers to the explorer himself.

PHYSIOGRAPHY

The country of the headwaters of the Burke River, as described here, covers only about 120 square miles—less than one-tenth of the surface of the whole of the Burke River Outlier. Geomorphologically the headwaters area is an integral part of the Outlier (Fig. 1). Geographically the Burke River headwaters belong to the Selwyn Range, a low divide between the drainage of the Cloncurry River (discharging into the Gulf of Carpentaria) and the drainage of the Diamantina and Georgina Rivers of the Lake Eyre river system, which includes also the Burke River.

The altitudes of the Selwyn Range are low. The Burke River extreme headwaters, including Green Creek, are about 1200 feet above sea level. The Burke River Plain at O'Hara Homestead is about 1000-1030 feet, with a steady decline to the south of 4 feet in a mile. The highest place (Fig. 4)—estimated 1200-1250 feet—is along the 'Old Track', east of the Roaring Bore. Some six miles north the country drops to 900 feet on the Duchess-Cloncurry railway. The relief is low, as illustrated by Figure 3, which shows a valley about a mile wide and 200 feet deep. It is a limestone country, but karst is absent.

The annual rainfall (summer rain) of twenty inches is too small, in the subtropical continental climate, to keep the streams running: they are intermittent and their erosional effect is confined to a few weeks annually. Nevertheless, in the Selwyn Range erosion has been accelerated, probably by a late-Tertiary uplift, recognized from the tilt of Tertiary lake limestone along the Burke River within the Outlier (Öpik, 1960). Twidale (1956a, p. 2) describes the uplift as 'the low Pleistocene Selwyn upwarp' and rightly regards it as a geomorphologically significant event. This accelerated erosion is seen in the dissection of the transitory limestone pediments of the Selwyn Range Limestone, and the dissection of the superimposed O'Hara Shale plateaux. Of course, hand in hand with the accelerated stream erosion, slope retreat and pedimentation are in progress, and were prevalent before the late uplift of the Range.

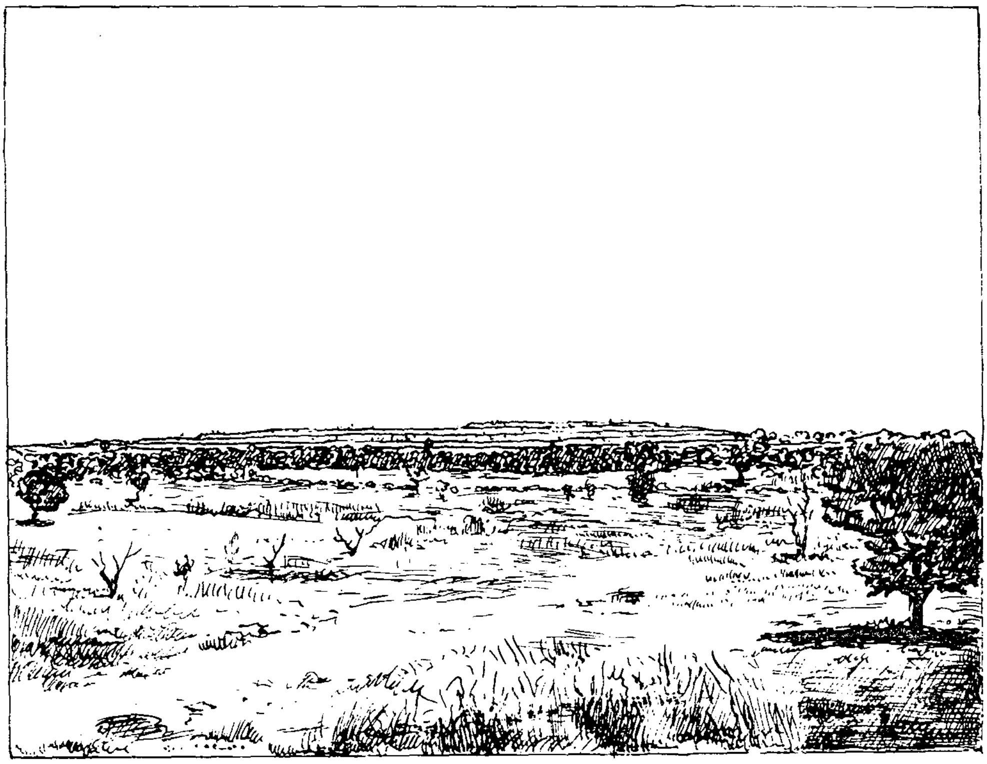


FIG. 8.—Terraced escarpment of Selwyn Range Limestone, facing north, between localities D26 and D27. Pediment of Devoncourt Limestone in foreground. For position see Fig. 13.

GEOMORPHOLOGICAL DIVISIONS

Seven morphological divisions (Fig. 13) can be recognized: (1) The Burke River Plain; (2) the dissected plateau of the O'Hara Shale in the south-west; (3) the terraced limestone country between localities D26 and D6; (4) the eastern limestone plateau; (5) the Devoncourt pediment between D13 and D18; (6) the marginal belt along the Roaring Fault and north of Burke River (to locality D20); (7) the western valley.

These seven divisions represent the following three geomorphological and structural classificatory units; (a) *depositional plains*—by (1) Burke River Plain; (b) *plateaux with subhorizontal rocks* — by (2) the plateau on O'Hara Shale, (3) the terraced limestone country, and (4) the eastern plateau; and, finally (c) *surfaces on deformed material*—by (5) the Devoncourt pediment, (6) the marginal belt, and (7) the western valley. This is a self-explanatory classification and a convenient generalization; but a small area is best described in respect of its morphological divisions, each of which belongs not only to a classificatory unit, but is also an individual geographical place.

The *Burke River Plain* is a flat depositional feature cut by shallow streams. Alluvial sand prevails in it, but north of O'Hara mud deposits occur, perhaps of lacustrine origin. At locality D12 rapids are present and upstream the Burke River has rocky outcrops in its bed and banks. This is the youngest part of the River, created by the Selwyn Range uplift. Downstream no rocks are seen and this part appears to be an old valley filled up with lake and stream deposits.

The *dissected plateau of the O'Hara Shale* is of a complex structure. The eastern part (south-east of the Bronzewing Fault) has a dissected, rolling surface bounded by cliffs 50-70 feet high. It is a down-faulted block, the northern extremity of which is a shale pediment covered by rubble. The cliff along the fault is dissected and is bordered by a valley with a narrow pediment strip. Erosion in the eastern area is active and consists mainly of slope erosion. The western area (localities D28—D26—D6) is the up-faulted block. The surface is of hills and small limestone pediments in many places; near the Bronzewing Fault small cuestas face north and north-west, and west-facing low-angle cuestas occur at the western edge of the plateau. The prevalent mode of erosion here is stream erosion. The rock itself is lateritized to a certain extent, as seen from widespread colours of the mottled zone. Silicified crusts occur, but are in process of destruction. A ferruginous and siliceous top layer covers the eastern portion; it is lateritic, but true laterite is not developed.

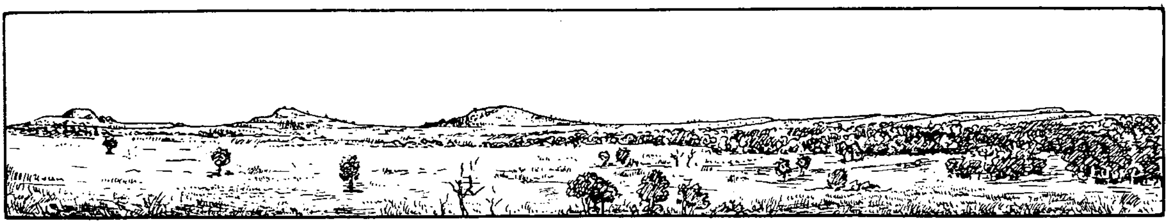


FIG. 9.—The terraced limestone country with O'Hara Shale residuals, and escarpment on right (north). Looking west from about northern end of Bronzewing Fault. For position see Fig. 13.

The *terraced limestone country* (Selwyn Range Limestone) has a north-facing escarpment (Fig. 8) and is dissected by streams running north. Bastion topography is well developed. The surface has a general decline to the south (Fig. 9) owing to the dip of the beds (of about 5°) in the same direction; the terraces face north; several small residuals of O'Hara Shale (Fig. 9) are preserved, even on salient angles of bastions, indicating that this surface developed from a dissected transitory pediment after the O'Hara Shale was stripped off. Locality D26 (Fig. 10) is a prominent terraced hill (estimated 120 feet above the plain) with bastions. Erosion in this area is relatively rapid and was initiated, presumably, on a surface of the O'Hara Shale cover before its destruction.

The northern part of the *eastern limestone plateau* (Fig. 7) along the 'Old Track', is the most elevated area of the Selwyn Range (Figs. 4, 5). There was formerly a continuous cover of O'Hara Shale, of which only cappings are preserved. The largest of them (Mount Collis) appears to be a mesa from a distance; it is, however, a cluster of small mesas, buttes, and ridges, resting on limestone. Slope erosion is active at these cappings and they are fringed by growing limestone pediments. These are transitory pediments, being dissected by streams and transformed into a bastion topography (Fig. 5). This topography is controlled by joints (Fig. 4) and by the dual lithology of soft marly interbeds and hard limestone bands. The cappings themselves are dissected clusters of hills, and even inside them limestone floors are exposed. The O'Hara Shale itself shows mottled lateritic colours, and ferruginous and siliceous crusts are preserved. To conclude: erosion here is in progress, and pre-Recent surfaces are destroyed; the flat summits of the O'Hara Shale cappings are fragments of such an old surface.

The cappings along the western fringe of the plateau, with dips up to 10°, are west-facing cuestas.

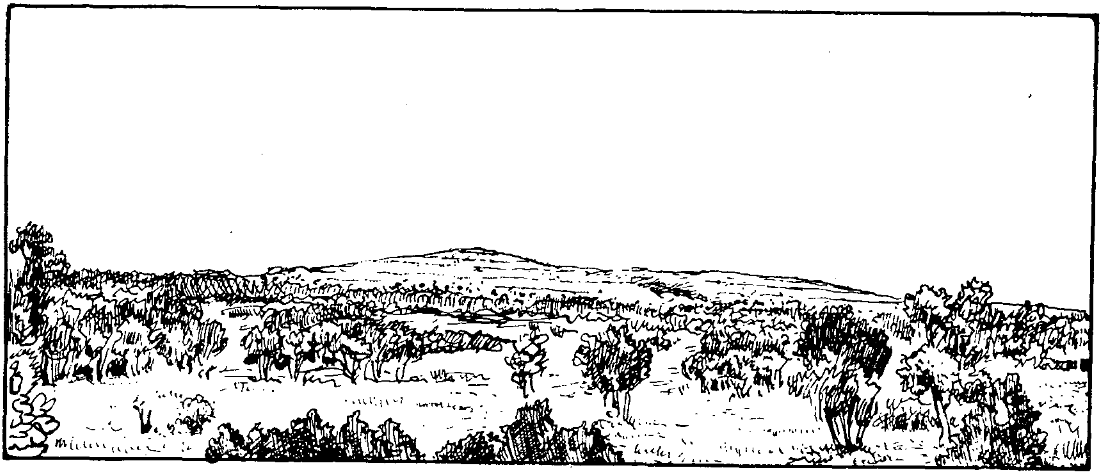


FIG. 10.—High limestone hill (bastions), loc. D26 ('Boundary Hill'), looking from north-west. Pediment of Devoncourt Limestone in foreground. For position see Fig. 13.

The *Devoncourt pediment* (Figs. 6, 8, 10) has an even surface truncating the Limestone beds, which dip south to south-east. The creeks on it are shallow and narrow channels just cutting into the rocks. The surface is ribbed with low edges of the truncated beds. It is a static pediment with a very slow loss of material to the Burke River. In spite of the Selwyn Range uplift its low topographical position protects it from speedy dissection. The Devoncourt pediment is an old surface; it is pre-Recent, and pre-uplift, but it is younger than the summit surface of the O'Hara Shale residuals.

To accomplish the Devoncourt pediment the cover of Selwyn Range Limestone and O'Hara Shale was removed, together with the prism of Devoncourt Limestone that stood above the present truncated plain. But considering the restricted areal extent of the Selwyn Range Limestone the probability remains that this formation was thinning out to the north and was already thin above the present Devoncourt pediment. If so, the main erosional event consisted in the removal of the thin shale cover and in truncation of the tectonically deformed Devoncourt Limestone, whereas in the south, where the Selwyn Range Limestone was thicker, an escarpment became established. North-east of locality D18 the outcrop of the Devoncourt pediment passes into the floor and slope of the marginal valley along the Roaring Fault, and extends also into the floor of the western valley. Thus, a confluence of the pediment with valley floors is apparent, but it cannot be interpreted in terms of panplanation. The present streams are too weak and the place is situated in the headwaters area where panplanation cannot be expected. Furthermore, no trace of an ancient stream is apparent to which the necessary lateral planation could be ascribed.

FIG. 11.—Cuestas of Roaring Siltstone (foreground) facing north-west, about 3 miles south-west from Roaring Bore. Valley eroded in gneiss and granite in the middle; ridges of Precambrian Argylla Formation (metasediments, lavas) in background. For position see Fig. 13.

The *marginal belt along the Roaring Fault* is composite: its northern part consists of a valley (Figs. 3 and 13), flanked by the indurated fault-ridge and the edge of the eastern limestone plateau; the remaining part, between the Boomerang Creek and the northern end of the Pilgrim Fault, includes the outcrop area of the Roaring Siltstone and its advanced outliers. Rubble-covered pediments, low cuestas, and rises constitute the main features here. The morphology of the whole belt reflects the tectonic structure and the lithology of the rocks. The Roaring Siltstone forms cuestas along the fault-line, and also west of it, because of the relatively high dip of the beds (Fig. 11). The Devoncourt Limestone (Fig. 3) forms valley slopes with almost smooth, or minutely ribbed, surfaces.

The Roaring Siltstone is lateritic, but the ironstone crust is destroyed. On its dip slopes stream erosion is active, and at the Roaring Bore the north-running stream has already cut into fresh rock. Northwards the dip increases, and the limestone becomes confined to the narrow valley floor. It appears that along this belt an older surface existed, protected by duricrust, but this surface is now being eroded.

The *western valley* (Fig. 12) is a narrow valley whose floor consists of pediments of steeply dipping (70°-90°) and truncated Middle Cambrian sediments, fringed in the east by low cuestas of O'Hara Shale. In the west it is defined by hogback ridges of the Precambrian faults. The Pilgrim Fault is prominent where it cuts the Mount Birnie Beds. Stream erosion prevails, but is slow. The morphology in this landscape is so controlled by the tectonic structure that the topography is not remodelled by erosion: advancing denudation is directed by the violent linear structures and will preserve the existing contrasts of the topography. Any subsequent landscape will be congruent with the preceding ones. The western valley is an old erosional feature, developed during the Ordovician-Cretaceous interval, and re-excavated subsequently more than once.

FIG. 12.—The western valley along Pilgrim Fault, looking south, from about one mile south of D13. Foreground: pediment of Devoncourt Limestone; on left (east): western escarpment of Selwyn Range Limestone; on right (west); two chains of steep hogbacks of indurated Precambrian faults; distant floor of the valley; steeply east-dipping Devoncourt Limestone and Roaring Siltstone, the Roaring Fault without topographic expression; skyline: Mt Birnie (cuesta on left)—Mt Alpin (highest summit) group of hills, 16 to 20 miles south. For position see Fig. 13.

HISTORY OF THE LAND SURFACE

The history of the present land surface and its forms covers a long interval of time. An uplift late in the Ordovician was followed by erosion of the horsts, and by the beginning of the Cretaceous the topographic contrast between the horsts and the graben was levelled out. The land subsided in the Cretaceous, erosion was arrested, and a blanket of marine sediments concealed the surface of the old land, as seen from the residuals of Cretaceous that are still present in the region (see Carter & Öpik, 1959).

In Upper Cretaceous time regression of the sea and uplift were followed by erosion of the sedimentary blanket, and the old topography became exposed and subjected again to destruction. The character of the pre-Cretaceous surface can be inferred from the fact that residuals of Mesozoic (Lower Cretaceous) conglomerates are resting on the same limestone floor side by side with residuals of the O'Hara Shale: only mesas and plateaux of the Shale were present at the beginning of the Cretaceous transgression, and before the conglomerate was deposited. The Tertiary passed without conspicuous events; the Cretaceous cover rocks were removed. The erosion was temporarily retarded by an episodic subsidence indicated by lake deposits in the Burke River Plain. At this time the Devoncourt pediment already existed at the foot of escarpments of the plateaux of the Selwyn Range Limestone with its O'Hara Shale cover. Finally, the Selwyn Range uplift accelerated once more the erosion of the plateaux, whereas the low-lying pediments, although tilted by the uplift, remained below the level of the accelerated erosion, and were conserved.

To sum up, the present landscape contains the following components: (1) the oldest and topographically the highest component, represented by the flat summits of the O'Hara Shale cappings. It was reduced in height and area once before, and after the Cretaceous; (2) the Devoncourt pediment that already existed in the Tertiary, and has remained unchanged ever since; it is topographically the lowest erosional surface; (3) the transitory, dissected, pediments on the Selwyn Range Limestone that are in an intermediate topographical position; they are formed by cliff retreat of the cappings and attacked by the concurrent stream erosion. These surfaces were initiated by the Selwyn Range uplift and their transformation is still in progress; (4) the late Tertiary to sub-Recent Burke River depositional plain, which is developed on a pre-existing valley.

Finally, the Precambrian rocks surrounding the Outlier are being rapidly eroded and deliver clastic matter to the streams, including the Burke River (Lake Eyre drainage) and Sandy Creek (Gulf of Carpentaria drainage), which are divided by the Selwyn Range; but the present rough and immature topography of the ridges of the basement rocks is older than the uplift. This is indicated by the small effect of the erosion on the less resistant Cambrian rocks, which have the same elevation as the basement, and have been lifted up to a similar height. The erosional impact of the Selwyn Range uplift on the resistant basement rocks could not, therefore, be stronger than on the Cambrian sediments.

The geomorphology of the small area of the Selwyn Range described here cannot be extrapolated over wider regions, but it is useful to contemplate it in the light of modern schools, as represented by L. C. King and E. S. Hills, in relation to the geomorphology of the plainlands of Australia.

King (1950) suggests that the Australian plainlands landscape is a creation of the processes of pedimentation and pediplanation. The area here described, with its pediments, low relief, and scattered inselbergs (mesas and buttes), has a pediplain appearance in the sense of King.

Pediplains originate by a gradual increase in number of pediments and by the growth of individual pediments in the wake of retreating slopes. Hence different parts of a land attain their pediplain character not simultaneously, but at different dates. Simultaneous erosion and wasting, and simultaneous reduction of relief, that are necessary in formation of a peneplain, should terminate in all parts of the land at a single geological date, or within a narrow interval of time.

These criteria are themselves generalizations and are applicable for the purpose of a generalized classification. This classification depends on the observed or deduced predominance of one process over another during the time of erosional activity, and may be at variance with some particular characters that contradict the decision, but are disregarded as being generally insignificant.

Relating to pediplanation an exclusive scarp retreat cannot be, and has never been, claimed. Ground-breaking incision by streams creates initial slopes and scarps and is a pre-requisite for the onset of scarp retreat, but incision itself works down from atop and is therefore not slope erosion itself. Further development of the drainage means increase in downward erosion which may or may not compete with the laterally directed erosion of slopes as regards the amounts of removed material. Marginal dissection (gullying) of plateaux is one of the main agents of slope retreat, and, strictly speaking, each of these gullies cuts down from above; but these gullies have no immediate effect on the remaining, intact surface of the plateau. Nevertheless the plateau is gradually reduced in area, inselbergs are left behind, the fringe of gullies migrates centripetally, and finally the residual is dissected into a cluster of mesas and buttes (as, for example, Mount Collis).

It appears now that a monistic approach to the problem of a genetic classification of plainlands is hardly justified because 'pure' pediplanation and 'pure' peneplanation cannot be expected. These kinds of geomorphological process have a 'borderland' within which they are inseparable: within this 'borderland' a duality of the process is evident, and where and when this duality has prevailed hybrid features of relief to the contention of the classifying minds may be expected. In classifying the plainlands the ambiguous element of the duality may not be considered, and the judgement is passed as regards the preponderance of pedimentation, or of downwasting and stream erosion.

In the Selwyn Range the observable, and not simply deduced, course of erosion consists of scarp retreat and gradual exposure of pediments that satisfy the main criteria of pedimentation. The element of duality is also recognizable in the dissection of the residuals of the plateaux. Wasting of the surface is apparent in the rubble-covered pediments and crowns of bastions, in the general skeletal character of the soils. The pediments are dissected and the drainage that develops on them cannot be dismissed as marginal gullying, even when some of the streams arise from gullies at the margins of the plateau residuals. Moreover older, inherited features are present that have been formed by stream erosion, as for example the tectonically controlled valley at the Pilgrim Fault and the now filled-up shallow Burke River valley. Nevertheless, pedimentation appears to be the dominant process in the area, and downwasting and stream erosion are also present; the 'element of duality' is evident, and it is probable that the bastion topography is its consequence.

Hills (1955) introduced the designation 'old land' to cover peneplains and pediplains in the Australian landscape, which bears the signs of both kinds of morphogenetic processes. But features of relief have been recorded that can be interpreted both ways, representing the outcome of the analytically inseparable interplay of scarp retreat and stream erosion.

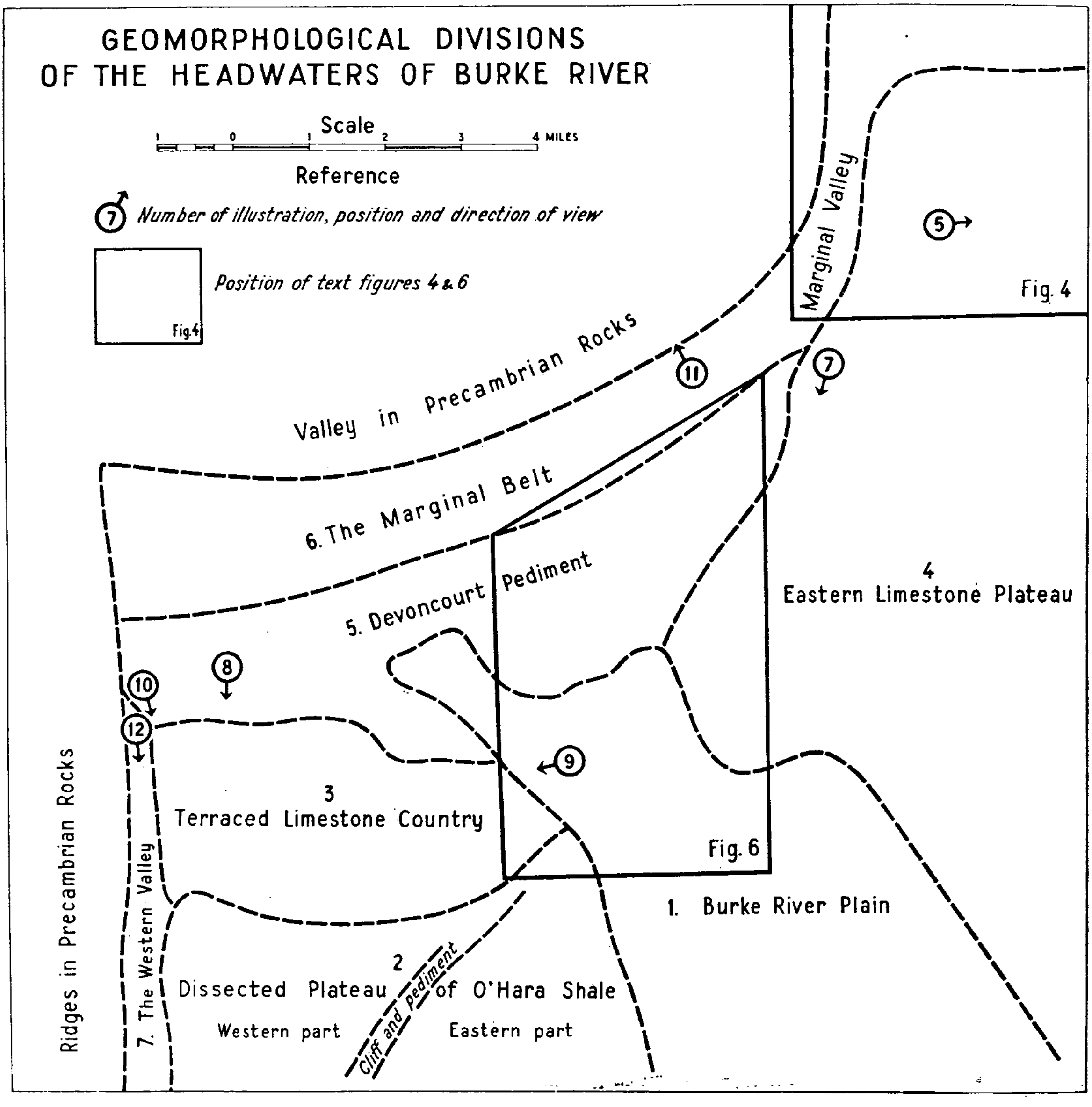


FIG. 13.—Geomorphological areas, Headwaters of the Burke River.

It is, perhaps, possible that pedimentation is prevalent in plainlands, and that in upwarps and uplifts the other kinds may gain in force; and that rainfall, lithology, and structure introduce further complications. In areas with horizontal or subhorizontal sediments, stripping of friable cover may expose very large surfaces consisting of a resistant rock and produce the appearance of a pediplain, or a plain of pediments, which may or may not be transitory. Landscapes of this kind cannot be called peneplains, to preserve the original meaning of the Davisian term. In the Selwyn Range pedimentation is at present the dominant process, but may be suppressed in future by stream erosion, and it appears that the future landscape will be an 'old-land' in the sense of Hills.

STRATIGRAPHY

The stratigraphy of the Cambrian sequence in the area of the Headwaters of the Burke River is summarized in the stratigraphic chart, Figure 14.

In the chart the lithological boundary between the Roaring Siltstone and the Devoncourt Limestone does not coincide with the *cassis/agra* zone boundary within the area of examined fossiliferous outcrops, but it cannot be taken for granted that this relationship will be the same elsewhere.

The Middle/Upper Cambrian boundary is important and critical, because on maps each series may have its own colour and its own letter symbol. A boundary is placed on the top of the Devoncourt Limestone; this boundary is a lithological passage and is assumed to be the series boundary for convenience, and in the absence of better criteria. It cannot be assumed, however, that the Devoncourt Limestone lithology is not continued above that boundary. At locality D6 the Selwyn Range Limestone is older than the *Glyptagnostus stolidotus* Zone, but north of Sandy Creek (see under Upper Cambrian stratigraphy) *G. stolidotus* is present in the Selwyn Range Limestone at a place where it is about to peter out to the north. It may mean that the Devoncourt/Selwyn Range Limestone contact does not coincide with the theoretical horizontal time-plane, between the series, but climbs or rises in places through it, and the climb may have started even below the series boundary. These are small irregularities if the scale of the maps and the accuracy of the charts (see below) are considered. Nevertheless they are present, and have enforced some generalizations in the following presentation of the stratigraphy of the Selwyn Range sequence.

The American name 'Dresbachian' (stage, age), in the absence of appropriate Australian nomenclature, is used in the chart as a brief designation for the lower third of the Upper Cambrian. The usage of this name is based on American customs and rules. Lochman & Wilson (1958), for example, intend to restrict the name Dresbachian to the lower half of the classical Dresbachian and give a new name for the upper half. Such procedure prevents the international application of a name loaded with homonymy. International usage will lag behind changes that are not controllable internationally, and the old and oldest usages will survive in the literature from which nothing can be deleted; furthermore, when

CAMBRIAN SELWYN RANGE SEQUENCE

Fig. 14

Period, epochs	Ages (stages)	Sequence of faunas (zones) and of tectonic events		Formations and breaks of the SELWYN RANGE sequence
UPPER CAMBRIAN	"DRESBACHIAN"	"EUGONOCARE stage" GLYPTAGNOSTUS RETICULATUS Zone (RETICULATUS Zone) GLYPTAGNOSTUS STOLIDOTUS Zone (STOLIDOTUS Zone) (Local repression) Unnamed Zone		O'HARA SHALE and lower chert bed of O'HARA SHALE DIASTEM SELWYN RANGE LIMESTONE
MIDDLE CAMBRIAN	No Stage names in use	LEIOPYGE LAEVIGATA Zone	LAEVIGATA III or AREPO Zone (= HOLTERIA AREPO Zone)	DEVONCOURT LIMESTONE
			LAEVIGATA II or AGRA Zone (= PROAMPYX AGRA Zone)	
			LAEVIGATA I or CASSIS Zone (= PTYCHAGNOSTUS CASSIS Zone)	ROARING SILTSTONE
			Uplift, erosion	Disconformity 4
			XYSTRIDURA Zone	BEETLE CREEK apparently, eroded
		Folding, uplift, erosion		Unconformity 5
LOWER CAMBRIAN	No subdivision	No diagnostic fossils		MT. BIRNIE BEDS
		Unconformity 6		
Basement				

FIG. 14.—Stratigraphic chart, Cambrian Selwyn Range sequence.

borrowing the name Dresbachian, for example, one should borrow also the American rules for this particular case. Consequently, a nomenclature based on national rules and customs is preferable.

LOWER CAMBRIAN STRATIGRAPHY

Little is preserved, and even less is known, of the Lower Cambrian history of the area. The only depositional episode is recorded as the Mount Birnie Beds. Their Lower Cambrian age is evident from their position between two breaks (Unconformities Nos. 5 and 6), and below the Middle Cambrian, and from fossils (*Diplocraterion, Protichnites, Crossochorda*) that have been found outside Selwyn Range (at Mount Birnie and Sylvester Creek; see Öpik, 1960). It appears that the Mount Birnie Beds were reduced to erosional remnants after a mild folding, and during an interval (Uncomformity 5) which comprises a large but undefined part of the Lower Cambrian, and of the basal zones of Middle Cambrian. The designations of the unconformities by numbers (Nos. 5 and 6) are taken from the chart in Öpik (1960).

MIDDLE CAMBRIAN STRATIGRAPHY

The Middle Cambrian depositional sequence of the Selwyn Range area is incomplete, but the intervals of non-deposition and erosion can be dated in terms of the scale of zones of the chart in Öpik (1960).

The lowermost part (with the *Redlichia* fauna) is missing, and was apparently never deposited at all: land conditions prevailed (Unconformity 5).

The first Middle Cambrian marine inundation arrived with the *Xystridura* fauna, whose age is upper *Paradoxides oelandicus* (in Scandinavian terms) and lower *gibbus* Zone (the Scandinavian and Australian terms). The *Xystridura* fauna is well represented in the area south and south-west of the Selwyn Range, in the Beetle Creek Formation. In the Selwyn Range itself, however, it appears to be present only as small silicified limestone blocks at the base of the Roaring Siltstone in the Roaring Bore area. These blocks were originally oolithic limestone, and contain only few and indeterminable fragments of fossils; so more evidence is needed as regards the presence of the *Xystridura* fauna in the Selwyn Range. If the area were inundated in *Xystridura* time, it could have been only an episode of brief duration, because after it comes a large interval (Disconformity 4), beginning with the upper *gibbus* and ending with the *nathorsti* Zone. Six of the twelve Australian subdivisions of the Middle Cambrian scale cover this interval, which records uplift and erosion after *Xystridura* time. But about 25 miles south this break is already small, because the Mount Merlin column in the chart (Öpik, 1960) indicates that the Inca Formation contains *Ptychagnostus punctuosus*, and only the *nathorsti* Zone remains unrecorded. The large interval of Disconformity 4 in the Selwyn Range reflects the uplift, and the persistence in Cambrian time of the Duchess Land (Öpik, 1956).

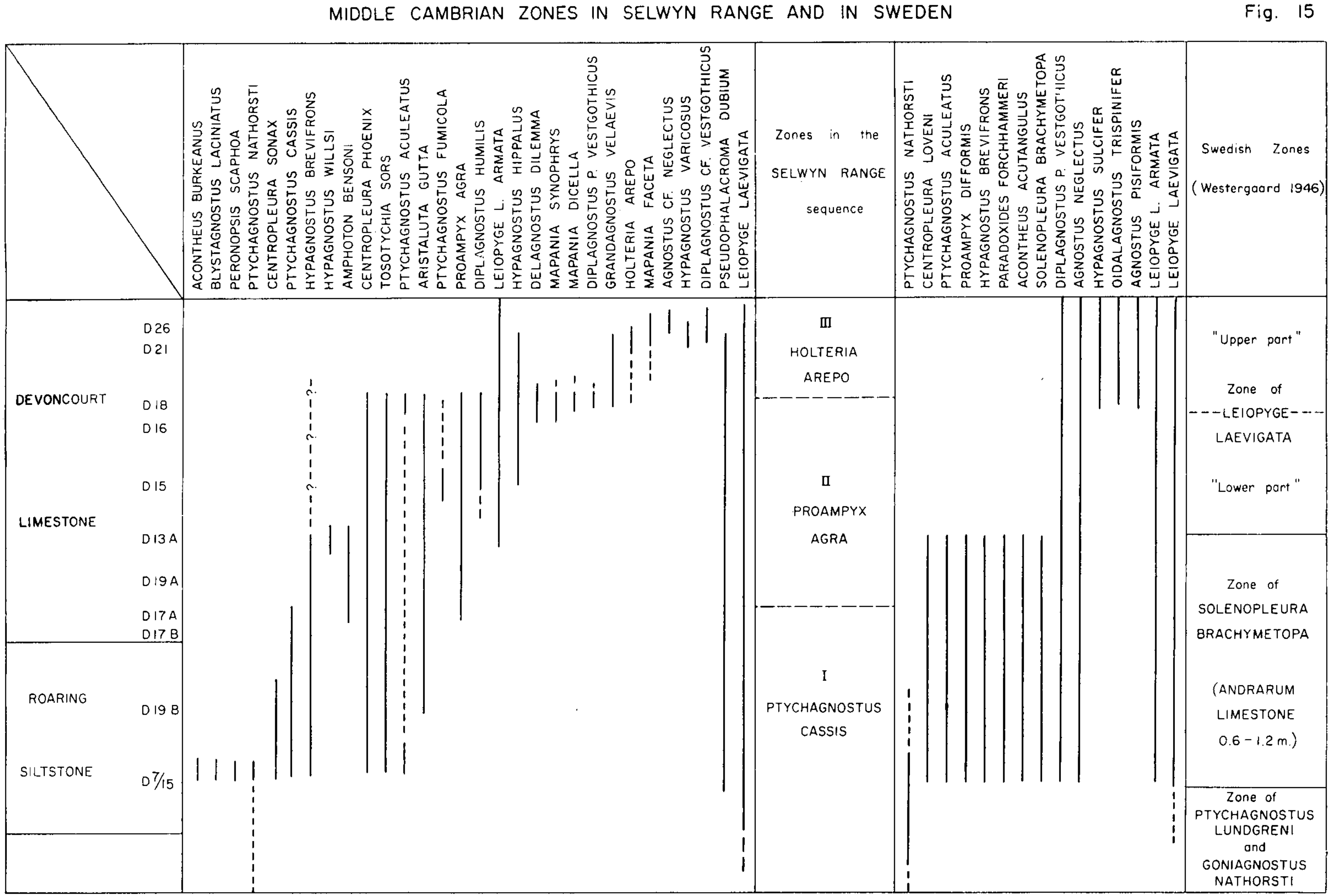


FIG. 15.—Biostratigraphic Chart of Middle Cambrian Zones (stratigraphic distribution of selected species in Selwyn Range and Sweden).

The southern portion of the Duchess Land was inundated again in *Ptychagnostus cassis* time, and the sea persisted in the headwaters area of the Burke River through the end of the Middle Cambrian and the 'Dresbachian' age of the Upper Cambrian. The end of the Middle Cambrian is known as the time of *Leiopyge laevigata*, whose biostratigraphic record is presented in the chart (Fig. 15).

THE BIOSTRATIGRAPHIC CHART (of *Leiopyge laevigata* time) (Fig. 15).

The chart presents (1) the distribution (order of superposition) of the relevant fossils through the Roaring Siltstone and Devoncourt Limestone sequence, (2) the resulting tripartition of the *Leiopyge laevigata* time scale in the Selwyn sequence, and (3) a correlation between that scale and the corresponding Scandinavian scale.

The chart was compiled as follows. Fossil lists were prepared for each of the numbered localities, which were entered in the left-hand column in their superpositional order and in positions according to field observation. Thirty species, considered to be verifiable, and therefore relevant, were selected from the lists and plotted against each of the localities in which they occur. These plots were, finally, connected by vertical lines representing the range of each species. Dashed lines indicate ranges that are apparent from localities outside the Selwyn Range; but the line of *P. aculeatus* is also dashed, to indicate a large gap in the records. The part of the chart referring to the Swedish sequence was compiled in a similar way. Only a selection of fossils which are relevant for this particular correlation was plotted. The ranges of the fossils are shown according to Westergaard's charts (1946; 1953), and the data given by him in the descriptive text of each species.

It should be noted that nowhere in the Selwyn Range can a continuous section be measured to show the positions of the fossils in the sequence. The superposition of the localities was found, however, with the aid of air photographs, which show also the attitude and the continuity of outcrops of the beds. Consequently, the position of each locality in the column is to some extent uncertain. Thus it is possible that D19B and D7/15 should be close together, and D15 and D13A. If so, the ranges of some of the fossils may change, but only slightly, without upsetting the tripartite subdivision or the correlation with the Scandinavian scale. For example, if D7/15 happens to have a higher position, only the range of *Ptychagnostus nathorsti* will be affected and extended higher up. This would correspond to Brögger's (1878) observation that at Krekling, in the type locality of *Agnostus nathorsti* Brögger, this species covers half of the range of *Paradoxides forchhammeri*, or half of the *S. brachymetopa* Zone.

The Accuracy of the Chart

The chart is imperfect, but the inaccuracies are small, if compared with the total range of *Leiopyge laevigata* or *Pseudophalacroma dubium*. The sources of the inaccuracies are: (1) absence of convincing evidence for the true time spans of the fossils; (2) inaccuracies in plotting the localities, as discussed above; (3) errors in identification of species from fragments which were used in compiling the fossil lists of single localities. No doubt, new collections and new occurrences will help to discover some of the inaccuracies and errors, and allow of improvements. This is illustrated by the following examples, especially by the collection from locality T87 (see p. 48).

The fossils of T87 are collected in a thin bed, which prevents an accurate determination of the age of the whole formation; its 'chart age' in Öpik (1960) is therefore an extrapolation up, and down, from this fossiliferous bed. But the accumulation of several species in a single bed is particularly useful for testing the time-marking power of single species and combinations of species that are, or may be, found scattered in a sequence of beds and in diverse localities.

Two species in that bed — *Hypagnostus hippalus* and *Delagnostus dilemma* — indicate an age of about the passage from *laevigata* II into *laevigata* III. *Holteria arepo* is also present, which in its other locality (D21) has a higher position. But at D21 only one specimen of *arepo* was found, and consequently no 'range' is indicated. From the evidence of locality T87 it is apparent, however, that it ranges as far down as *Delagnostus dilemma*. Hence, *H. arepo* appears to be indicative of the whole of *laevigata* III. In the same T87 *Hypagnostus ? brevifrons* has been noted. This is too high for this species, which elsewhere is confined to the *brachymetopa* Zone. So, the specimens may be wrongly identified as *brevifrons;* or the find belongs to the last surviving specimens; or the age of the T87 fossil bed is underestimated. It is unfortunate that the material of *H. brevifrons* so far recovered from T87 is insufficient to solve the problem, as only cephala, and no pygidia, have been recovered. The T87 list contains also the name of *H.* cf. *sulcifer*. The known range of *sulcifer* is given in the Scandinavian Chart and supports the age of the bed as the *laevigata* II/III passage.

Another example is the occurrence of *Oidalagnostus trispinifer* in Sweden, and of *O.* cf. *trispinifer* in our locality W36. It appears that the occurrence in W36 indicates an earlier appearance of *trispinifer*, or that the Australian form is another species. But whatever the case may be, *trispinifer* and cf. *trispinifer* both indicate a high position in the *L. laevigata* Zone.

The presence of *Agnostus pisiformis* in Scandinavia in the 'upper part of the Zone with *Leiopyge laevigata*' deserves a comment: if *pisiformis* is found in association with a Middle Cambrian species, it indicates the top of the Middle Cambrian; in association with an Upper Cambrian species it indicates the base of that series; but without a determinable association it marks only the Middle/Upper Cambrian passage sequence. The name *Agnostus pisiformis* Zone traditionally refers to the Upper Cambrian part of the sequence and is therefore misleading. The traditional name *'Paradoxides forchhammeri* stage' is also misleading. The chart illustrates the known fact that this species is confined to the Zone of *Solenopleura brachymetopa,* but its name covers three zones that are characterized by the occurrence of *Leiopyge laevigata.* This confused nomenclature has been a source of considerable misunderstanding of the stratigraphy and correlation of the Middle Cambrian.

Stratigraphic Subdivisions

Stratigraphic ('biostratigraphic') subdivisions are identifiable scale positions to which events of deposition, breaks, and biological events can be referred. The whole sequence of the Roaring Siltstone and Devoncourt Limestone falls into the life span (zone, stage) of *Leiopyge laevigata* or *Pseudophalacroma dubium* or both. Three subdivisions of this zone or stage are indicated and have been already operated with (Öpik, 1960). The lowermost subdivision has been designated as *'laevigata* I'; it coincides with the known range of *Ptychagnostus cassis* sp. nov., and can be referred to as the 'Zone with *Ptychagnostus cassis',* or, for brevity, *'cassis* Zone'. Five species occur only in this zone, and *Centropleura sonax* is one of them. The other species have a wider range and extend into the *agra* Zone. During the *cassis* Zone the Roaring Siltstone and the lower part of the Devoncourt Limestone (about 50 feet) were deposited; with the *cassis* Zone the sea inundated the Selwyn Range area; and *Ptychagnostus nathorsti* became extinct in *cassis* time. Several species (*Centropleura phoenix, Tosotychia sors, Hypagnostus brevifrons*) pass from the *cassis* Zone into the *'laevigata* II' subdivision, but none of them is known to reach into *'laevigata* III'. The *'laevigata* II' can be designated as the *Proampyx agra* Zone, because *P. agra* sp. nov. is confined to that Zone. The lower part of the *agra* Zone is marked by the presence of *Amphoton bensoni,* and the upper part by *Diplagnostus humilis.* Several species become extinct at the top of the *agra* Zone, and most conspicuous is the disappearance of *Centropleura. 'Laevigata* III' follows and concludes the Middle Cambrian Series. This zone is characterized by the absence of *Centropleura;* its most conspicuous species is *Holteria arepo,* which gives the name to the zone—*Holteria arepo,* or briefly *arepo* Zone.

It is evident from the chart that in the presence of a sufficient number of identifiable species each of these Zones can be recognized even where the nominate species are absent. The nominate species (*casis, agra,* and *arepo*) mark the scale positions and supply code names for contemporaneous faunas.

Correlation with the Swedish Scale

The Selwyn Range and the Swedish scales are mutually correlated by the occurrence of *Leiopyge laevigata;* the correlation of the lowermost and the uppermost portions of the time range of *L. laevigata* in Australia and Sweden, however, is somewhat uncertain, because these observed ranges cannot be compared by matching them against the unknown theoretical maximal life span of this species. But this uncertainty is small in comparison with the observed range and is here neglected, because it cannot be expressed even in terms of some other known shortlived species.

The correlation between the subdivisions of the scales, as presented in the chart, is not immediately evident and is in need of some comment. Consequently, datum levels had to be selected that are common to each of the scales. Such a datum level is the overlap of the ranges of *L. laevigata* and *Ptychagnostus nathorsti*, providing for the correlation of the base of the *S. brachymetopa* Zone with the base of the *cassis* Zone. Another is the top of the *Hypagnostus brevifrons* range, against which the range of the same species was plotted in the Scandinavian chart. Comparing the lists of fossils included between these two datum levels, some more similarities emerge: the occurrence of *Acontheus* and *Ptychagnostus aculeatus*, and the main distribution ranges of *Centropleura*, are also correlated.

The *Hypagnostus brevifrons* datum level is, by itself, not quite reliable, because it is possible that in T87 this species lived longer, and that in D18 a fragment of a pygidium (Pl. 21, fig. 3) of *Ptychagnostus aculeatus* upsets the known range of this species. The second datum level could be therefore lifted up to the level of D18, with the effect that the *Centropleura* ranges of both the charts coincide completely. This procedure, however, cannot be applied, because difficulties arise in correlation of two more datum levels of the Swedish Zone of *Leiopyge laevigata;* these are (1) the top level of the charts, assumed to be the level of the known uppermost occurrence of *Leiopyge laevigata*, and (2) the level marked in the Swedish chart as the base of the 'upper part' (Westergaard's phrase) of the Zone of *Leiopyge laevigata*. This 'upper part' conveniently correlates with *laevigata* III (*arepo* Zone), and the 'lower part' must be correlated with the upper portion of the *agra* Zone.

Some uncertainty in correlation of the scales depends also on the need of correlation of different lithologies and thicknesses. The Australian sequence is ten times as thick as the Scandinavian. The *Solenopleura brachymetopa* Zone, to which in the chart half of the *L. laevigata* span has been allotted, is confined to the four feet of the Swedish Andrarum limestone, an exclusive deposit within an otherwise shaly sequence. The Andrarum limestone appears to be an equivalent of a portion of the Selwyn Range sequence about 450 feet thick. In brief, the Swedish sequence is extremely condensed, as compared with the extended Selwyn Range suite of sediments.

The position of a fossil located in the Andrarum limestone with an accuracy of one foot, which is meaningless, would involve 110 feet in the Selwyn Range sequence, within which changes in faunal composition are observable.

To conclude, the correlation of the scales is accurate within small and undefinable limits, and the correlation of the subdivisions is accurate within the limits of a half of the span of one such subdivision (Selwyn Range zone).

UPPER CAMBRIAN STRATIGRAPHY

The Selwyn Range Limestone above the Devoncourt Limestone is almost unfossiliferous, except for rare finds of *Acrotreta*, and trilobite fragments found in the lowermost beds at locality D26, on the upper slope of the hill. Sedimentation between the *laevigata* III (*arepo*) Zone and the time of the Selwyn Range Limestone was however, continuous, which suggests that the bulk of the Selwyn Range Limestone should represent the lowermost Upper Cambrian. This is confirmed by the occurrence at D6, D28, and D29, above the Selwyn Range Limestone, of a fauna which belongs to the second lowest Upper Cambrian Zone. In the Mungerebar area (see Öpik, 1960) the equivalent of the Selwyn Range Limestone is fossiliferous. These fossils are not yet described and the name of this pre-*stolidotus* zone will refer to species of new genera as yet undescribed.

In April, 1960, Mr J. N. Casey of this Bureau collected a cephalon of *Glyptagnostus stolidotus* in the Selwyn Range Limestone, in a low terraced escarpment, about 3 miles north-east of the Sandy Creek crossing near locality D33. The co-ordinates of the discovery point are Latitude 21°14′ S., Longitude 140°10′ E., and it lies near the northern boundary of the Selwyn Range Limestone and near a low residual of O'Hara Shale (in the east). The presence of *G. stolidotus* indicates that this part of the Selwyn Range Limestone should correspond in age to the diastem at locality D6, and possibly also to the lowermost part of the O'Hara Shale at the same locality.

The stolidotus *Zone*

After the interval (the diastem) deposition started again, but instead of limestone, shale and chert were laid down. A single thin chert layer near the base of the O'Hara Shale (localities D6, D28, D29) contains a prolific fauna of trilobites, most of which are as yet undescribed. A provisional examination (Öpik, 1956) revealed its lower Dresbachian ('*Cedaria*') age. Subsequent study (Öpik, 1960) confirms this age and indicates that the fauna is Pacific, and partly American (*Catillicephala, Blountia, Meteoraspis,* Norwoodiidae, *Brassicicephalus*), and Kathayan (*Liostracina, Drepanura, Stephanocare, Blackwelderia*). So far described are *Rhodonaspis longula* Whitehouse, *Stephanocare richthofeni* Monke, and *Glyptagnostus stolidotus* Öpik (1960). This last species name designates the zone — *Glyptagnostus stolidotus* (or, abbreviated, *stolidotus*) Zone. It is a widespread and easily recognizable species.

The chert bed in the O'Hara Shale is, unfortunately, the only fossiliferous one in the lower sequence of that shale; but it is most valuable as an almost complete record of the fauna of the Zone, which helps in the dating of less complete faunas, even in the absence of *stolidotus* itself.

Deposition of the O'Hara Shale continued into the Zone of *Glyptagnostus reticulatus*, and the next higher '*Eugonocare* Stage'. *Glyptagnostus reticulatus* has not yet been found in the O'Hara Shale, and the sequence between the *stolidotus*-bearing chert below, and the '*Eugonocare* Stage' fauna above, which is of the *reticulatus* age, is locally unfossiliferous. For details see description of locality D6.

Mode of Occurrence of the Fossils

In the described sequences fossils occur (1) as bands—accumulations on a single bedding plane or in a single thin bed—and (2) scattered in the rock. Fossil bands are rare: examples are D 7/15 in the Roaring Siltstone, and D18 in the Devoncourt Limestone, and the chert bed near the base of the O'Hara Shale (D6, D29). It appears that each of these bands has a different mechanical origin, but they all represent thanatocoenoses. The D7/15 occurrence, containing a large number of fragments, is perhaps a concentration by removal of the fine-grained sediment by a sudden but small acceleration of currents. The D18 accumulation is not really rich; it is an accumulation only if compared with the general rarity of fossils in the Devoncourt Limestone. It marks, probably, a sudden decrease in supply of detrital matter and of precipitated fine-grained calcite that enabled the dismembered but otherwise unworn trilobite tests to settle on a bedding plane instead of being embedded in a greater volume of sediment. The bedding plane itself carries a thin layer of coarse-grained calcite, which appears to be the result of slow crystallization from a saturated solution. The chert bed in the O'Hara Shale with its 'lower O'Hara fauna' had a quite different origin: fragmentary fossils were embedded in colloidal silica together with quartz sand, and even with ooids, in a depression of the sea floor relatively close to land. These conditions were of brief duration, as seen from the absence of fossils in the shale below and above the chert bed; they were also local, because north and north-east of D6 the chert bed is episodic, and unifossiliferous. It has been found at locality D1, which is the most northern known occurrence, but yielded only a single and doubtful fragment of a trilobite. Farther south, at Pomegranate Creek, bituminous limestone was deposited instead of shale.

The second mode of occurrence—fossils scattered in the rock—is a characteristic of the Devoncourt Limestone. The first impression is that the limestone is unfossiliferous, because even fragments of trilobites are rare. Hammer work will reveal, however, that the brachiopods *Acrotreta* and *Lingulella* are scattered in almost every bed. Trilobites are rare and distributed unevenly, and a complete collection could not be obtained at a single site. Presumably the collection described here does not represent the whole fauna, which needs collecting over a longer period of time. The trilobites found are mostly dismembered exuviae, but complete specimens occur also, indicating quiet conditions and relatively rapid burial.

The absence of articulate brachiopods, echinoderms, and *Hyolithus* indicates a deficiency of the benthonic population. To sum up, a sparsely populated part of the Middle Cambrian Sea is represented in the sequence at the headwaters of the Burke River.

Environment of Deposition

The deposition of the Roaring Siltstone, Devoncourt Limestone, and Selwyn Range Limestone was an event of short duration, covering a fraction of the Middle

Cambrian Epoch and the very beginning of the Upper Cambrian. It was a marine episode of inundation of the fringe of the Cambrian Duchess Land, as indicated by the palaeogeography (Öpik, 1956).

The sequence, no doubt, extends south and should be present below the surface of the Burke River Structural Belt, perhaps in a changed lithological composition; it has been also observed (Öpik, 1960) that the Middle Cambrian becomes gradually more complete in the same direction. The Cambrian sediments in that belt were deposited in an epicontinental trough, and the water, as seen from the character of the rocks and their fossils, was persistently shallow.

The sedimentation began with the Roaring Siltstone; during the time of the Devoncourt Limestone the supply of fine-grained clastics was augmented by precipitation of calcite. The change from non-calcareous to calcareous sediments can be interpreted as a consequence of an influx of warm water, which does not necessarily imply that the non-calcareous siltstone is a cold-water sediment. Subsidence was in progress, but nothing indicates that these two formations were deposited in different depths.

The Selwyn Range Limestone, as seen from the description of that formation, indicates a shallowing of the sea, temporary emergence, and conditions inimical to life. It was almost an evaporitic environment, but of small extent and brief duration.

The Roaring Siltstone and the Devoncourt Limestone are both fossiliferous, and the number of species indicates that they are fully marine deposits. But, as indicated in the discussion of the mode of occurrence of the fossils, this part of the sea was only sparsely populated, and the benthos was deficient, consisting only of inarticulate brachiopods. The dominant inhabitants were pelagic agnostids and polymerid trilobites, as indicated in the discussion of the mode of life of *Centropleura*. The reason for the sparsity of the population was apparently a scarcity of food, but otherwise a healthy desert prevailed in the surface waters of the ocean.

The 'biotectonic' criteria of Lochman & Wilson (1958), when applied to the fossil list of the Roaring Siltstone and Devoncourt Limestone, enforce a classification of the environment as 'extracratonic Euxinic', and 'eugeosynclinal'. The count of species, or of genera, indicates that, by Lochman & Wilson's definition, 64% of them, including all agnostids, *Centropleura, Acontheus, Proampyx,* and *Svealuta,* are 'extracratonic Euxinic', and the rest is equally divided between new and indifferent forms, and forms of the 'intermediate' ('miogeosynclinal') realm. No genera of the 'cratonic realm' are present. Nevertheless, geological evidence proves that the environment of the deposition of the Roaring Siltstone and Devoncourt Limestone was 'cratonic' and epicontinental, which indicates that the biotectonic approach fails in Australia, and cannot be used even as a convenient form of presentation.

Of course, the concepts of what are eugeosynclinal and miogeosynclinal belts are not protected from liberal interpretations. Thus, Voisey (1959, p. 193) writes: 'the Upper Proterozoic and Cambrian limestones and shales of Western Queensland might well be regarded as comprising part of a miogeosynclinal belt to the north.' The only reason for such an interpretation is probably 'the current practice to call sedimentary sequences without volcanics, migeosynclinal' (loc. cit., p. 189). As regards facts, no 'Upper Proterozoic limestones and shales' exist in sequence with the Cambrian, and 'to the north' no Cambrian is known, and Öpik (1956) only postulates in his palaeogeographic maps of the Cambrian a seaway to the north-east to facilitate the understanding of the marine fauna in the narrows between the platform in the west and Duchess Land in the east. The outliers of the Cambrian sequences that are present in Western Queensland, in the absence of any suitable criteria, cannot be classed as miogeosynclinal or eugeosynclinal, but supply ample evidence of epicontinental deposition.

The zoogeographic provincial relationship and palaeogeographic significance of the Burke River Cambrian faunas has been discussed by Öpik (1956). In brief, the Acado-Baltic fauna is dominant; 'the great number of Acado-Baltic species of trilobites and their stratigraphic arrangement, which is identical with the arrangement in Sweden, renders any hypothesis of a confined and directed migration problematical.' The same applies to the Cathayan and American Pacific Provinces, which also have representatives in the Cambrian fauna on the Burke River, and especially in the Dresbachian.

PALAEONTOLOGY

Fossils Described in the Present Paper

Middle Cambrian Fossils from the headwaters of the Burke River

	Roaring Siltstone Localities	*Devoncourt Limestone Localities*
Spongia:		
Pleodioria tomacis gen. nov. et sp. nov.	D7/15	D13A
Spongia, spicules only (not described)	x	x
Vermes:		
Feeding burrows only		D17A
Brachiopoda:		
Acrotreta, two forms (not described)	x	x
Acrothele sp. *A*		D18
Lingulella (not described)	x	x
Micromitra sp. *C*		D18, D26
Arthropoda (Trilobita):		
(a) Polymerid trilobites		
Acontheus burkeanus sp. nov.	D7/15	
Amphoton ? arta sp. nov.		D18
Amphoton bensoni sp. nov.		D17, D19A, D13A,
Amphoton sp. *C* (not illustrated)		D26
Centropleura phoenix sp. nov.	D7/15	D13, D15, D16, D18
Centropleura sonax sp. nov.	D7/15	
Crepicephalus sp. *H*		D18
Holteria arepo sp. nov.		D21
?Mapania dicella sp. nov.		D18
Mapania faceta sp. nov.		D26
Mapania cf. *faceta*		D21
Mapania synophrys sp. nov.		D18
Proampyx agra sp. nov.		D17A, D13A, D16, D18
Proampyx sp. D	D7/15	
Tosotychia sors gen. nov. et sp. nov.	D19B, D7/15	D18

	Roaring Siltstone Localities	*Devoncourt Limestone Localities*
(b) Agnostids		
Agnostus sp. *C*, cf. *neglectus* Westergaard		D26
Blystagnostus laciniatus gen. nov. et sp. nov.	D7/15	
Delagnostus dilemma gen. nov. et sp. nov.		D18
Diplagnostus humilis (Whitehouse)		D15
Diplagnostus planicauda vestgothicus (Wallerius)		D18
Diplagnostus cf. *planicauda vestgothicus*		D21, D26
Diplagnostus sp. *I*	D7/15	
Grandagnostus velaevis sp. nov.		D18, D21
Hypagnostus brevifrons (Angelin)	D7/15	D13A
Hypagnostus hippalus sp. nov.		D18, D26
Hypagnostus cf. *hunanicus* Lu		D15
Hypagnostus varicosus sp. nov.		D21
Hypagnostus willsi sp. nov.		D13A
Hypagnostus sp. *F*		D18
Leiopyge laevigata (Dalman)	x	x
Leiopyge laevigata armata (Linnarsson)		D13A, D21, D26, D15, D11, D18
Peronopsis scaphoa sp. nov.	D7/15	
Peronopsis sp. *G*	D7/15	
Pseudophalacroma dubium (Whitehouse)	x	x
Pseudophalacroma sp. *K*		D18
Pseudophalacroma sp. *L*		D17B
Ptychagnostus aculeatus (Angelin)	D7/15	D18
Ptychagnostus cassis sp. nov.	D19B, D7/15	D17A
Ptychagnostus fumicola sp. nov.		D15
Ptychagnostus nathorsti (Brögger)	D7/15	
Ptychagnostus sp. *P* aff. *nathorsti* (Brögger)		D18
Ptychagnostus sp. *O*		D18
Crustacea (Bradoriina):		
Aristaluta gutta gen. nov. et sp. nov.		D17, D19A, D13A, D16, D18
Svealuta aff. *primordialis* (Linnarsson)		D13A

Middle Cambrian trilobites from localities outside the Burke River area and from other formations

Grandagnostus imitans sp. nov., Undilla Basin, V-Creek Limestone.
Mapania angusta (Whitehouse), Undilla Basin, V-Creek Limestone.
Papyriaspis lanceola (Whitehouse), Undilla Basin, V-Creek Limestone.
Ptychagnostus fumicola sp. nov., Smoky Creek, Glenormiston area.

Upper Cambrian trilobite from Australia, illustrated and mentioned in the text
Rhodonaspis longula Whitehouse.

Overseas trilobites illustrated for comparison

Centropleura belli Hutchinson (Canada)
Chancia odarayensis Rasetti (Canada)
Holteria problematica (Walcott) (Nevada)
Ptychagnostus (*Goniagnostus*) *nathorsti* (Brögger) (Sweden).

The list of the Middle Cambrian fossils from the headwaters of the Burke River contains some indeterminate forms (sponge spicules, worm burrows, two species of *Acrotreta*) that cannot be taxonomically described. Among them, the brachiopods referred to as *Acrotreta* are quite well preserved, but their description is postponed because practically all Middle Cambrian brachiopods of Queensland are undescribed as yet and should be treated as a special project.

A more definite open nomenclature is applied by indicating specific identities by letters of the alphabet. This lettering indicates that the corresponding forms are determinable within the Selwyn Range faunas, but the material is insufficient to diagnose these forms in relation to the already-described species of the named genera: for example *Agnostus* sp. *E* (cf. *neglectus* Westergaard).

FOSSILS PREVIOUSLY DESCRIBED FROM THE AREA

According to Whitehouse (1936) 'in the limestone at the margin of the basin eight miles north-east of Duchess' the following fossils occur:

Enetagnostus humilis Whitehouse (*Diplagnostus humilis*)
Leiopyge exilis Whitehouse (*Leiopyge laevigata* (Dalman))
Lisania
Phalacroma (?) *dubium* Whitehouse (*Pseudophalacroma dubium*)
Phoidagnostus limbatus Whitehouse (*Leiopyge laevigata*)
'Protospongia'
Solenagnostus acuminatus Whitehouse (*Ptychagnostus cassis* sp. nov.)
Brachiopods.

The names in parentheses are those adopted in the present paper. This nomenclature is suggested on the basis of collected material, and the illustrations and descriptions given by Whitehouse. I have not examined the material described by Whitehouse, but rely on published information.

Kobayashi (1939) and Westergaard (1946) have also commented on the generic position of some of these forms. *Enetagnostus* is, according to them, a synonym of *Diplagnostus,* and *Solenagnostus* a synonym of *Triplagnostus,* which is a *Ptychagnostus* according to the present author. Whitehouse (1939, p. 267) mentions also that 'only one rather indefinite polymerid fragment has been found'. It refers, presumably, to the occurrence of *Lisania,* mentioned in 1936.

The fossils described by Whitehouse were collected by C. Ogilvie not far from our locality D15 (8 miles east from Duchess), but north of it (north-east from Duchess) and relatively low in the Devoncourt Limestone, as seen from the presence of *Ptychagnostus cassis* (*cassis* zone).

No other Middle Cambrian fossils have been described from the Burke River Outlier. Whitehouse mentions also the occurrence of *Pseudagnostus vastulus, 'Solenopleura'* and *Anomocare* in the south, at Chatsworth, and suggests a correlation with the zone of *Agnostus laevigatus* (Whitehouse, 1936, p. 76). Whitehouse (1939, p. 265) deleted, however, the corresponding '*Solenopleura* Stage' from his list and correlation chart. Fossils occur in the vicinity of Chatsworth, but according to Öpik (1956d, 1960) the age is not Middle but Upper Cambrian.

Other Occurrences of the LEIOPYGE LAEVIGATA *fauna in Australia*

The distribution and palaeogeography of the *Leiopyge laevigata* fauna in Australia is seen from map 6 in Öpik (1956, p. 257). It is well documented in Tasmania (Banks, 1956, p. 188), and in Victoria an early *laevigata* fauna is represented by the '*Dolichometopus* band'.

In Queensland the fauna is not confined to the Selwyn Range alone. The map (Fig. 1) indicates all the known occurrences in that State, including a locality (T87) in Northern Territory. Several more localities have been found recently west of T87, and one was already recorded on the longitude of 136° (locality H11, Casey & Tomlinson, 1956).

The occurrences in Queensland and in the Toko Range are briefly discussed below. They occur within an area measuring about 180 miles between the Selwyn Range and T87; this area is about 100 miles wide, and it is only a small fragment of the former distribution area of the marine sediments of the *Leiopyge laevigata* time. The lithology, however, lacks uniformity, and several formations are indicated. In the Quita Creek Area ("D95", Fig. 1) the fauna occurs in the Steamboat Sandstone; south of it is the Mungerebar Limestone (G9, from which the type material of *Ptychagnostus fumicola* was collected), and the occurrences in the Sylvester Creek area and at T87 are limestones that are not yet assigned to any particular formation.

Steamboat Sandstone (D95; lat. 21°53′S., long. 139°00′E.)

The Steamboat is a leached calcareous sandstone with some limestone interbeds and interbeds of silty material with chert and silicified oolitic limestone.

In the sandstone, which yields most of the fauna, the fossils have lost their test and the identification of species is, therefore, difficult. For this reason the following list is only a selection.

The fossils are:

Leiopyge laevigata
Leiopyge laevigata armata
Hypagnostus brevifrons
Hypagnostus hippalus
Ptychagnostus fumicola
Pseudophalacroma dubium

and several more agnostids and other trilobites, including *Mapania, Nepea, Dorypyge,* and undescribed genera.

The list is compiled from identifications made for all known localities of the Steamboat Sandstone. It appears that the Steamboat Sandstone is of the same age as the Roaring Siltstone and Devoncourt Limestone taken together (see Chart in Öpik, 1960).

Mungerebar Limestone (G9; Lat. 22°10′ S., Long. 139°10′ E.)

The greater, upper part of the Mungerebar Limestone is lower Dresbachian. Its lower part on Smoky Creek interfingers with the Steamboat Sandstone and belongs to the top of the Middle Cambrian. Fossils are very rare in this part, but at one locality (G9) *Hypagnostus* cf. *brevifrons* and *Ptychagnostus fumicola* occur. This locality was found by J. N. Casey in 1957, and revisited later twice by the present author. The fossils occur in a single band at the base of the outcrop of about 60 feet of limestone. The pygidia of *H.* cf. *brevifrons* differ from *brevifrons* in having a postaxial median furrow.

The specimens of *Ptychagnostus fumicola* sp. nov. described below were found in this outcrop. The age could be the *laevigata* III Zone, but the presence of *Hypagnostus brevifrons* may indicate an older age, if the distribution of *H. brevifrons* in the Devoncourt area alone is considered. However, *H. ?brevifrons* occurs also in higher levels of the *laevigata* sequence, as seen in the fossil list of locality T87 below.

Sylvester Creek Area (Lat. 23°15′ S., Long. 139°00′ E.)

In the Sylvester Creek area pediments of a dark bituminous limestone are scattered in the gibber plain. This limestone has been referred to as 'Devoncourt' limestone (Öpik, 1960) informally, because its continuity with the Devoncourt Limestone itself is not apparent, and is impossible to establish. In one of these localities (W36)

Leiopyge laevigata
Leiopyge laevigata armata

Pseudophalacroma dubium
Hypagnostus brevifrons
Oidalagnostus sp. (cf. *trispinifer*)
Centropleura sp. nov.
Svealuta sp.

were collected. The *Centropleura* is distinguished by strong raised terraced lines, but only fragments are present. The age of this fauna is, presumably, lower part of *laevigata* III, or the top of *laevigata* II.

West flank of the Toko Range (locality T87; Lat. 22°54'S.; Long. 137°45' E.)

At locality T87 a steeply dipping limestone occurs, which has been referred to informally as 'Devoncourt' limestone (Chart, Öpik, 1960). It is a dark blue-grey flaggy limestone with numerous slickensided fractures. Fossils have been found as yet only in a single bed three to four inches thick. They are numerous and well preserved.

The collection contains:

Leiopyge laevigata
Pseudophalacroma dubium
Hypagnostus hippalus
Hypagnostus cf. *sulcifer* (Wallerius)
Hypagnostus ?brevifrons
Delagnostus dilemma
Agnostus cf. *neglectus*
Holteria arepo
Mapania synophrys
Mapania dicella

The age of the fauna is *laevigata* II/*laevigata* III, and *laevigata* III is indicated by the presence of *Holteria arepo* and *Agnostus* cf. *neglectus*. The majority of the species however are the same as in the middle part of the Devoncourt Limestone (for example locality D18), which is of *laevigata* II age.

Strictly, this age refers only to the thin bed in which the fossils are embedded. It is assumed that limestone below and above that bed together represent at least the full sequence of *laevigata* II and III.

The 'Devoncourt' limestone of locality T87 rests on a sequence of chert interbedded with a black and smelly bituminous limestone containing *Pagetia*, which is of a lower *gibbus* and *Xystridura* age. Consequently, a large break is here apparent in the middle of the Middle Cambrian, as already indicated (Öpik, 1956; Chart, Toko column, 1960), similar to the break in the Selwyn Range sequence.

DESCRIPTION OF FOSSILS

Depository: The fossils are kept in the Museum of this Bureau and the numbers (CPC) refer to the Commonwealth Palaeontological Collection.

SPONGIA

No Cambrian sponges have been described from Australia as yet, but they are nevertheless quite common. They occur mostly as isolated spicules or accumulation of spicules, that cannot be properly interpreted and named. Sponges are widespread in siliceous shales of Northern Australia. These shales and interbedded cherts are predominantly composed of sponge spicules and deserve the term spongiolites.

Spicules of the family Chancelloriidae Walcott have been identified in the Lower Cambrian of South Australia, in the Middle Cambrian of the Northern Territory and Queensland, and in the lower levels of the Upper Cambrian, also in Queensland. They can be referred to *Chancelloria* and, in one locality in the Northern Territory, in the Gum Ridge Formation, to *Eiffelia.*

Some of the spicules have been regarded as '*Protospongia*', which means only that simple crosses have been observed that may belong to a number of known and unknown genera.

Henningsmoen (1958) describes from the Upper Cambrian of Norway spicules of a sponge which 'apparently belong to a new species, probably also to a new genus'. He refers them provisionally to *Protospongia?* sp. 'The spicules are pentacts with four rays forming a cross and the fifth ray normal to these at their junction.' Similar spicules occur in *Pleodioria* and it seems probable that the Norwegian sponge belongs to the same genus.

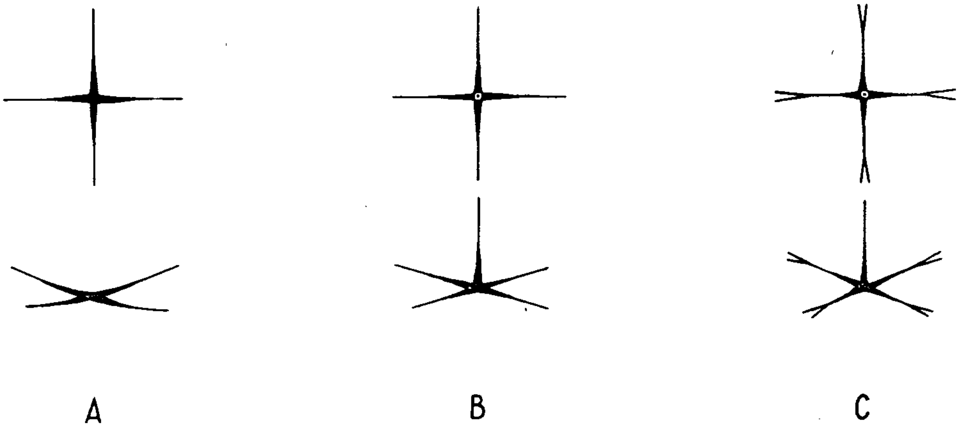


FIG. 16.—*Pleodioria tomacis,*—three kinds of spicules of holotype, Pl. 1, figs. 1a, 1b. Fig. A about x 6, B and C about x 12.

PLEODIORIA TOMACIS gen. nov. et sp. nov.

(Pl. 1, figs. 1a, 1b; Text-fig. 16)

Material: The material consists of a single specimen (CPC 3646) preserved as a void in siliceous shale. It was split in two and both halves have been recovered. During the splitting of the friable rock loose spicules were lost, but the inner wall of the void is still studded with them abundantly.

Description: The body of the sponge is about 25 mm. long and has the shape of an inverted cone. The wall is relatively thin, as seen in Plate 1, figure 1a. It consists of a friable, seemingly columnar silica layer with an uneven, probably porous internal surface.

Spicules are seen in the siliceous substance of the wall of the void. The spicules are displaced and their original arrangement cannot be observed. These spicules are illustrated in Text-figure 16. Three kinds of spicules are present:

(1) Simple rectangular crosses (Text-fig. 16A) with gently curved rays. These are the largest, measuring 3-4 mm. In specimens from the V-Creek Limestone of the Undilla Basin such stauracts are seen in a fenestrate diagonal arrangement. These spicules are interpreted as forming the framework of the walls. In some of the stauracts the tips are split in two.

(2) Rectangular pentacts (Text-fig. 16B) consisting of a simple cross with a vertical ray; they measure 2 mm., and are numerous.

(3) Pentacts (Text-fig. 16C) in which the tips of the cross-rays are split in two. They measure about 2 mm. from tip to tip.

Relationship: The simple structure with stauracts as the main type of sclerites indicates a genus of Protospongiidae Hinde. According to de Laubenfels (1955) pentact and hexact spicules had not yet evolved in Protospongiidae, which range from Lower Cambrian to the end of the Silurian. Pentact spicules have been observed in the Upper Cambrian by Palmer (1954); but they may belong not to the Protospongiidae, but to a different family. No spicules with split tips have been known as yet, but curved rays may have been present in *Protospongia*. The stauracts of *Protospongia* are believed to be crosses with rays in one plane; but *Protospongia* is mostly found in shale and the originally curved spicules may have been flattened secondarily. The spherical body of *Protospongia* anyway implies spherically curved sclerites.

The following definition serves the species and the genus, which are monotypical.

Definition: *Pleodioria tomacis* is a siliceous sponge, most probably a protospongiid, having a simple conical body with a thin wall and with sclerites consisting of stauracts and pentacts, some of whch have the tips of the cross rays split.

Occurrence: The described single specimen comes from the Roaring Siltstone, locality D7/15. Its age is the zone of *Ptychagnostus cassis*, or *Leiopyge laevigata* I. Spicules and coherent fragments of walls of a *Pleodioria* occur also in the Middle Cambrian V-Creek Limestone of the Undilla Basin, Queensland.

BRACHIOPODA

No calcareous brachiopods (Protremata) are found as yet in the Roaring Siltstone nor the Devoncourt Limestone. Only in the Upper Cambrian of the Burke River area have several forms of orthoid brachiopods, among them *Billingsella*, been collected.

The common brachiopod in the Middle Cambrian Devoncourt Limestone is a *Lingulella*. Specimens of *Acrotreta*-like brachiopods are numerous; examples are seen on Plate 18, figure 5, and Plate 19, figures 1-7. Two more brachiopods are described below, but their naming is reserved.

MICROMITRA (PATERINA) sp. B

(Pl. 1, figs. 3 and 4)

Two ventral valves are illustrated. The larger one, Plate 1, figure 3 (CPC 3644) is 3.1 mm. wide; the smaller, Plate 1, figure 4 (CPC 3645) is about 1.5 mm. long and 1.8 mm. wide.

The ornament consists of concentric irregular coarser and finer lines and coarser rounded radial ribs.

Occurrence: CPC 3644 was found in the Devoncourt Limestone at locality D18; CPC 3645 at locality D26 in the same limestone. The age is the Zones of *Proampyx agra* and *Holteria arepo.*

ACROTHELE sp. A

(Pl. 1, fig. 5)

A single ventral valve (CPC 3647), 3.1 mm. long, is illustrated. It is almost circular, with the apex slightly behind the centre. The ornament consists of irregular concentric raised lines and a very fine and dense granulation. About eight low radial ribs are present in the middle sector.

The illustration is made from a rubber cast, and the specimen itself is a partly exfoliated internal surface. It shows a ridge stretching from the apex half way to the posterior border; this ridge corresponds to a channel of the outer surface. The foramen is situated at the posterior end of the channel and well off the apex. The foramen appears to be a very short tube—a continuation of the outer channel.

In the Mail Change Limestone and Split Rock Sandstone of the Undilla Basin a similar *Acrothele* occurs abundantly.

Occurrence: The illustrated specimen was found in the Devoncourt Limestone at locality D18. Its age is the Zone of *Proampyx agra.*

VERMES

(Pl. 1, fig. 2)

Trails and tracks of worms are very rare in the Devoncourt Limestone and have as yet not been seen in the Roaring Siltstone.

The illustrated specimen (CPC 3648) was found in the Devoncourt Limestone at locality D17. The rock is an impure sandy laminated limestone—a thin interbed in darker, purer limestone. The tracks are interpreted as castings filling the burrow tunnels.

The age is the Zone of *Ptychagnostus cassis.*

AGNOSTID TRILOBITES

NOTES ON CLASSIFICATION AND NOMENCLATURE

About twenty-five agnostid generic names have been exploited to derive a suprageneric nomenclature beginning with subfamilies and ending with suborders, orders, and a subclass. It appears that the possibilities for creating new suprageneric names on the basis of the existing generic nomenclature should be nearly exhausted by now. According to Öpik (1959, 1961) the alimentary apparatus of agnostids is distinct from that of other trilobites, but resembles *Burgessia* and *Naraoia,* which have each been assigned by Stormer in Harrington et al. (1959) to a different subclass of the class Trilobitoidea. This similarity, however, is as yet no reason to transfer the agnostids from one class to another, because in their external morphology they remain trilobites. The affiliated eodiscids represent a link intermediate between the agnostids and all other trilobites. Still, two conclusions result from the comparison of the agnostids with *Burgessia* and *Naraioa*: (1) the cleft separating the trilobites from the Trilobitoidea has diminished, and (2) the agnostids indeed do deserve their subordinal and ordinal status within the class of trilobites.

The classification of agnostids on the family and subfamily levels, as presented by Howell in Harrington et al. (1959), is very elaborate, and is in need of simplification, as indicated below.

Two families, Clavagnostidae Howell and Condylopygidae Raymond, are valid: their genera are of unknown origin and they have given no derivatives. *Aspidagnostus* Whitehouse, as indicated bv Öpik (1956, p. 21), should be removed from the Agnostidae and included in the Clavagnostidae. *Mallagnostus desideratus* should be excluded from the Condylopygidae and transferred to the 'Spinagnostidae'. *Archaeagnostus* and *Eoagnostus* together are regarded here as a separate group of genera at the roots of the peronopsid stock: this is the oldest known (Lower Cambrian) group, but its genera are only inadequately known.

The families Geragnostidae Howell and Micragnostidae Howell are synonyms of Agnostidate McCoy, because *Geragnostus* and *Micragnostus* differ little from *Homagnostus* (Agnostinae), and can be regarded even as subgenera of *Agnostus. Homagnostoides,* however, is excluded from the Agnostidae, and its familial relationship is obscure: it represents an isolated 'appendix'-group of its own.

The family Cyclopagnostidae Howell 1937 is a synonym of the 'Spinagnostidae' because *Cyclopagnostus* is a synonym of *Hypagnostus*, or a subgenus of it. *Cyclopagnostus hesperius* Howell is a close relative of *Hypagnostus brevifrons* (Angelin) (p. 58). The genus *Spinagnostus* Howell itself, as illustrated and described by Howell in Harrington et al. (1959), is the only agnostid with true genal spines; hence, we still accept the separate family Spinagnostidae Howell 1935, which contains a single genus—*Spinagnostus*. *Hypagnostus denticulatus* Westergaard (1946, p. 49) resembles *Spinagnostus franklinensis* Howell in spinosity, but its cephalic spines are agnostoid, and not truly genal. Incidentally, the cephalon of *Hypagnostus denticulatus* resembles closely *Cyclopagnostus hesperius*, but its pygidium is quite different. It appears therefore that the name 'Spinagnostidae' Howell 1935, as amplified by Howell in Harrington et al. (1959, p. 184) covers two families, one of which requires a name. The substitute name is Quadragnostinae = Quadragnostidae Howell 1935, which has priority over the universally used Peronopsidae Westergaard, 1936 (not 1946, as indicated by Howell). I concur also with Kobayashi (1939) in regarding *Quadragnostus* as a junior synonym of *Peronopsis*. The following genera do not belong to the Quadragnostidae: *Sulcatagnostus* Kobayashi, which is a genus of Pseudagnostidae, as recognized already by its author, or even a synonym of *Pseudagnostus; Baltagnostus* Lochman, and *Oedorhachis* Resser, which appear to be related to the Diplagnostidae, but are in need of further inquiry; and *Ciceragnostus barlowi* Belt, which is apparently a pseudagnostid, and definitely Tremadocian (see below, under *Pseudophalacroma*, and also under Phalacromidae). But *Grandagnostus* Howell and *Phalagonstus* Howell should be included in the Quadragnostidae, as indicated below, under Phalacromidae.

The family Agnostidae McCoy should include also the 'Hastagnostidae' Howell, 1937. Howell (loc. cit., 1959) includes the genus *Glyptagnostus* Whitehouse in the family, but overlooked the family Glyptagnostidae Whitehouse, 1936, which has the priority over Hastagnostidae Howell, 1937. Thus, the family Agnostidae consist of two subfamilies: (1) the Agnostinae (including Geragnostidae and Micragnostidae) and (2) the Glyptagnostinae, which has a subjective priority over Triplagnostinae Kobayashi, 1939, Ptychagnostinae Kobayashi, 1939, and Leiopyginae Kobayashi, 1939.

The family Phalacromidae Hawle & Corda, 1847, contains effaced agnostid species with an obscure or disputable relationship with the diagnostic agnostids en grande tenure. This family is polyphyletic, and artificial because the accident of external effacement is not a unifying character.

Sdzuy (1955, p. 15) suggests that the names *Leiagnostus* and Leiagnostinae should be applied to all completely smooth species of the family Agnostidae, but admits the polyphyletic character of this and similar taxa. It is, however, apparent that suitable preservation reveals the relationship of effaced forms and disentangles them taxonomically. Of course, the known and additionally discovered characters may be evaluated as of generic or as only of specific significance, according to the experience or the taste of the taxonomist, but gross lumping is only postponement, rather than a solution of the problems.

Howell in Harrington et al. (1959) included in the Phalacromidae the following genera: (1) *Phalacroma,* (2) *Grandagnostus,* (3) *Phalagnostus,* (4) *Phoidagnostus,* (5) *Litagnostus,* (6) *Leiagnostus,* ((7) *Gallagnostus,* and (8) *Gallagnostoides;* Westergaard (1946) included (9) *Ciceragnostus.*

The status of the Phalacromidae, as discussed in the present paper, can be summarized as follows: (a) the family Phalacromidae is valid, but refers to a single genus — *Phalacroma;* (b) *Grandagnostus, Phalagnostus,* including *'Phoidagnostus' bituberculatus*), and *'Ciceragnostus' cicer* (without or with a new generic name) are not Phalacromidae, but Quadragnostidae; (c) *Litagnostus* belongs to Pseudagnostidae (because it is an effaced *Pseudagnostus;* Palmer, 1955). The remaining three genera in the list (*Leiagnostus, Gallagnostus,* and *Gallagnostoides*) cannot either be placed in a single known family, or distributed among several families, nor do they constitute a separate family. These forms are in need of further study and should be regarded as an 'appendix group' to the agnostids in general.

The name *Phoidagnostus* Whitehouse, 1936, is based on *Phoidagnostus limbatus* as the type species, I am of the opinion (see under *Leiopyge*) that *Phoidagnostus limbatus* is a synonym of *Leiopyge laevigata.* If this synonymy is accepted *Phoidagnostus* should be removed from the Phalacromidae. The concept of *Phoidagnostus* however, as applied in the literature, is solely based on *Agnostus bituberculatus* Angelin, 1851. *Agnostus bituberculatus* is a phalacromid with basal lobes, and is, therefore, a *Phalagnostus* in the amended sense of this genus. As a species *Phalagnostus bituberculatus* is distinct by its elongate glabellar node. If, however, *Phoidagnostus limbatus* Whitehouse, 1936, is interpreted as being congeneric with *Agnostus bituberculatus,* which is a species of *Phalagnostus* Howell, 1955, the latter becomes a junior synonym of *Phoidagnostus.*

Of all the genera mentioned above only *Grandagnostus* (and *'Phoidagnostus'*) have been found as yet in Australia. Within *Grandagnostus* two groups are present: (1) species without a cephalic marginal border (*G. velaevis* sp. nov.) and (2) species with a border (*G. imitans* sp. nov.). The type species of *Grandagnostus*—*G. vermontensis* Howell (1935)—'has little or no indication' of a cephalic border and its position within these two groups remains open.

CLASSIFICATION OF AGNOSTIDS DESCRIBED IN THE PRESENT PAPER

Superfamily Agnostacea (Agnostidea) of the suborder Agnostina Salter.
Family Quadragnostidae Howell (=Peronopsidae Westergaard). Genera: *Peronopsis, Hypagnostus, Grandagnostus.*
Family Diplagnostidae. Genus: *Diplagnostus.*
Family Agnostidae.

Subfamily Agnostinae. Genus: *Agnostus*.

Subfamily Glyptagnostinae. Genera: *Ptychagnostus* (subgenera *Ptychagnostus* and *Goniagnostus*), *Leiopyge*.

Incertae familiae. Genera: *Delagnostus, Pseudophalacroma, Blystagnostus*.

Most of the known agnostid species are 'non-effaced', displaying all their lobes and furrows. These 'non-effaced' agnostids are called here '*agnostids en grande tenure*, which term has been suggested by Mr K. A. Townley of this Bureau.

Within the families listed above, and several others, species en grande tenure are dominant, but effaced or partly effaced forms are also common. Diplagnostidae, however, are an exceptional example of absence of effacement. In some lineages, instead of effacement an accentuation of the relief is apparent.

Family QUADRAGNOSTIDAE Howell, 1955

The name Quadragnostidae Howell 1935 is here re-introduced to replace the name Spinagnostidae Howell 1935; the family Spinagnostidae remains valid but is restricted to a single genus, *Spinagnostus* Howell 1935. *Spinagnostus* is externally a *Hypagnostus*, and a possible synonym of the latter (Westergaard, 1946). But *Spinagnostus*, as illustrated and described several times by Howell, has true genal spines which are the extension of the lateral border. No other agnostid has such spines, and therefore *Spinagnostus* is in need of a separate family. In all other agnostids the spines are issued from the posterior margin at a clear distance from the posterolateral corners. The family Cyclopagnostidae Howell, 1937, is regarded here as a junior synonym of Quadragnostidae, and so is the name Peronopsidae Westergaard, 1936. *Quadragnostus*, however, is a junior synonym of *Peronopsis*, by which the concept of the family, as established by Westergaard, remains unchanged.

Genus PERONOPSIS Hawle & Corda 1847

PERONOPSIS SCAPHOA sp. nov.

(Pl. 18, figs. 1-3; Text-fig. 17)

Material: The two cephala and one pygidium illustrated constitute all material suitable for description. In the same formation (Roaring Siltstone) numerous fragments occur, indicating that *P. scaphoa* is not a rare species. The illustrated pygidium (Pl. 18, fig. 3), associated with the cephala, is assumed to belong to this species because (1) it is a pygidium of a *Peronopsis;* (2) by its size it matches the large cephala; (3) it has also a very wide, channel-like marginal furrow; and (4) no other agnostid is present to which such a pygidium can be attributed.

Measurements: Cephalon (holotype, CPC 3558)—7.2 mm. long; cephalon (CPC 3559)—6.5 mm. long and 6.8 mm. wide; pygidium (CPC 3560)—6.0 mm. long, 7.0 mm. wide; border 1.8 mm. wide; cephalon (CPC 3651, not illustrated)—3.3 mm. long.

Selection of holotype: The specimen CPC 3558 (Pl. 18, fig. 1) is fragmentary, but displays all characters necessary for the description of the cephalon, and shows even details that are not preserved in the other complete cephalon. Hence it was designated as the holotype.

Generic relationship: The pygidium is comparable with *Peronopsis fallax* (Tullberg), as seen, for example, in Westergaard (1946, pl. 3, figs. 5 and 6). The cephalon has no preglabellar furrow, the absence of which is diagnostic for most of the species of *Peronopsis*. The wide channel-like marginal furrow and the narrow border, and the very long basal lobes, are unusual in *Peronopsis*, but are not considered as being of a subgeneric significance.

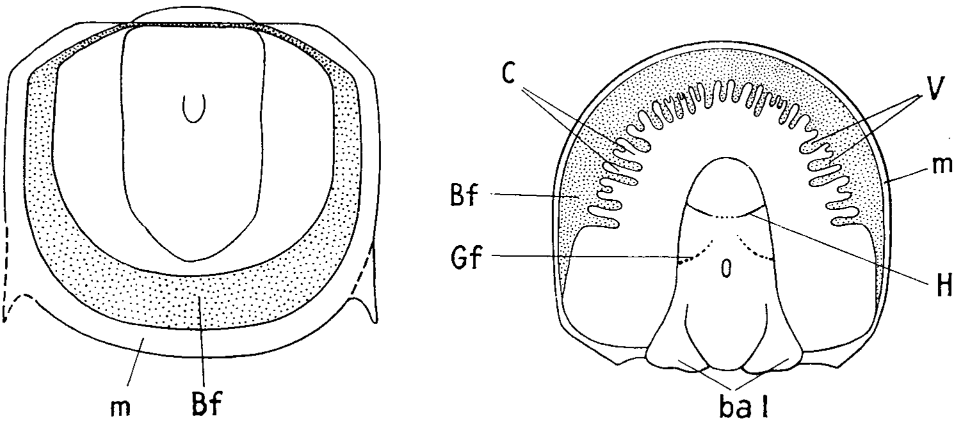


FIG. 17.—*Peronopsis scaphoa*, gen. nov. et sp. nov., cephalon and pygidium, restored. bal—basal lobes; Bf—marginal furrow; G—rugae; Gf—posterior glabellar furrow; H—transverse glabellar furrow; m—margin; V—scrobicule.

Description: *P. scaphoa* is a large form. Complete specimens may have attained a length of 20 mm. The holotype cephalon corresponds to a specimen 17 mm. long.

The cephalon is suboval to subelliptical. The marginal furrow is a wide and shallow channel; the margin, which is slightly upturned and narrow, is only the slightly elevated edge of the test. The posterolateral spines are short and triangular, as usual in *Peronopsis*. The cheeks are scrobiculate along the border, with a pattern comparable with *Peronopsis quadrata sulcata* Westergaard (1946, pl. 4, fig. 1). The dorsal furrows are shallow. The glabella is about 2/3 of the length of the cephalon, with an evenly rounded front. The anterior lobe is small ($\frac{1}{4}$ of the glabella); the transverse furrow is curved, with the convexity directed rearward, as in *Peronopsis quadrata* (Tullberg) or *Quadragnostus solus* Howell (1935, 1937). The posterior glabellar furrows are directed inward and forward and mark a pair of quite large lobes. These furrows and lobes display a pattern usually seen in *Pseudagnostus*, but not in *Peronopsis*.

The pygidial axis is parallel-sided, and bluntly pointed in the rear. It is relatively short, but almost reaches the wide marginal channel. The axis is undivided and bears a low node. A postaxial median furrow is absent.

Differential diagnosis: *Peronopsis scaphoa* is a relatively large species related to *P. quadrata sulcata* and *P. fallax*. *P. quadrata sulcata* has also a scrobiculate cephalon, but almost straight posterior glabellar furrows and a preglabellar median furrow that is missing in *P. scaphoa*. *Peronopsis fallax* and all other species of *Peronopsis* have very short basal lobes, but a comparable pygidium with an undivided, parallel-sided axis. Thus, *P. scaphoa*, by its cephalon, is a '*Quadragnostus*', and by its pygidium is a *Peronopsis*. This should be interpreted as additional evidence that *Quadragnostus* is, in effect, a synonym of *Peronopsis*.

Diagnosis: *Peronopsis scaphoa* is a species with very wide marginal furrows in the cephalon and pygidium. It has scrobiculate cheeks, an extremely narrow cephalic margin, long and oblique, inward and forward directed posterior glabellar furrows, and long basal lobes fused by their tips to the glabella. The pygidial axis is parallel-sided and has no lobes or transverse furrows.

Occurrence: *Peronopsis scaphoa* is found only at locality D7/15 in the Roaring Siltstone. Its age is the Zone of *Ptychagnostus cassis*.

PERONOPSIS sp. G.

(Pl. 18, fig. 4)

Only one cephalon (CPC 3561) is available. It is laterally distorted, but otherwise almost intact. It cannot be referred to a particular species, but it is a *Peronopsis*, as seen from the following description.

The cephalon is 3.3 mm. long. The margin is convex, the marginal furrow deep. The cheeks are not scrobiculate. An incomplete preglabellar median furrow is present, but the frontal lobe of the glabella is not bilobed. The basal lobes are short, triangular, surrounded by furrows, and fused along the occipital margin by a very narrow connective band. The glabella bears a sub-central node, as is common in *Peronopsis*. No glabellar lateral furrows are present.

The specimen is, perhaps, related to '*Agnostus*' *damesi* Resser & Endo (1937, pl. 30, figs. 1 and 2) and '*Agnostus*' *chinensis* Dames, which also have the preglabellar median furrow. For the same reason it seems to be related also to the Australian *Euagnostus opimus* Whitehouse (1936).

The generic relationship of *Euagnostus* is, however, uncertain. Kobayashi (1939) regards it as a synonym of *Triplagnostus*, and Westergaard includes it in *Peronopsis*. For the time being *Euagnostus* can be regarded as a subgenus of *Peronopsis* that includes also '*Agnostus*' *damesi*. But it is still uncertain whether the specimen described here, in spite of its preglabellar furrow, is a *Euagnostus*.

Occurrence: The specimen is found in the Roaring Siltstone, at locality D7/15. Its age is the Zone of *Ptychagnostus cassis*.

Genus HYPAGNOSTUS Jaekel, 1909

Whitehouse (1936, 1939) described from Australia two species of *Hypagnostus* (*vortex* and *clipeus*). In Australia (in Queensland) *Hypagnostus* appears in the zone of *Ptychagnostus gibbus*, one zone earlier than in Sweden, and elsewhere. From here onward the genus persists with several undescribed species throughout the Middle Cambrian. One undescribed form occurs even in the Upper Cambrian Zone with *Glyptagnostus stolidotus*, and another Upper Cambrian species has been recorded by Thomas & Singleton (1956) in Victoria.

Hypagnostus can be described as a quadragnostid with the anterior glabellar lobe vestigial, or even effaced. According to Westergaard, *Hypagnostus* is derived from *Peronopsis*. *Kormagnostus* Resser 1938 is another genus with an effaced, or almost effaced, frontal lobe, but its relationship with *Hypagnostus* and with the Quadragnostidae is obscure. *Kormagnostus* has a large, wide, long and bulbous, pygidial axis, which can be interpreted as a smooth (partly effaced) axis of a *Homagnostus*-like form. If this is accepted, *Kormagnostus* is a genus of the Agnostinae.

It has been suggested (Öpik, 1961) that the effacement of the frontal lobe may be an external manifestation of a reduction of the oesophagus.

No doubt, *Hypagnostus* is polyphyletic in its origin, being derived from several different species of *Peronopsis*, as indicated by Westergaard. This is also illustrated by the fact that some of the described species (e.g. *H. parvifrons*) have no terminal axial node in the pygidium, whereas others have such a node (*H. hippalus*). Considering the polyphyletic composition of the genus, *Cyclopagnostus* Howell and *Tomagnostella* Kobayashi may represent subgenera.

HYPAGNOSTUS BREVIFRONS (Angelin)
(Pl. 18, figs. 6-10)

Westergaard (1946) gives the complete synonymy of the species.

H. brevifrons is characterized by its short, tapering glabella with a well-rounded front, and a relatively short pygidial axis without transverse furrows. The pygidial axis bears a small node.

The illustrated cephala are almost replicas of cephala illustrated by Westergaard, including the lectotype. The Australian pygidia are less variable than those from Sweden.

The cephalon, Plate 18, figure 6, is 7 mm. long, a size that is given as an upper limit for Swedish specimens.

Measurements: Cephalon (CPC 3563)—7.0 mm. long; cephalon (CPC 3564) —5.3 mm. long, 5.6 mm. wide; pygidium (CPC 3565)—5.6 mm. long and 5.6 mm. wide; pygidium (CPC 3566)—5.3 mm. long, 5.5 mm. wide; pygidium (CPC 3567)—5.3 mm. long, 5.5 mm. wide.

Occurrence: *Hypagnostus brevifrons* is found in the Roaring Siltstone and in the Devoncourt Limestone, in the zone of *Ptychagnostus cassis*. At locality D7/15, from which the illustrated specimens were collected, it is very abundant in one particular bed. It was originally described from Sweden, and, according to Brögger (1878), it occurs also in the Oslo Region.

Stratigraphic significance: In Scandinavia *Hypagnostus brevifrons* belongs to the Zone of *Solenopleura brachymetopa,* in which *Leiopyge laevigata* makes its first appearance. In the Roaring Siltstone it is associated with *Ptychagnostus aculeatus* and *L. laevigata* and is therefore of the same age as the Scandinavian representatives.

HYPAGNOSTUS WILLSI sp. nov.

(Pl. 18, figs. 11a, 11b)

Material: The material consists of a single complete specimen (CPC 3568), the holotype; its thorax is damaged.

Description: The specimen is 15.4 mm. long. The cephalon is 6.4 mm. long and 7.3 mm. wide; the pygidium is 6.7 mm. long and 7 mm. wide.

The glabella is short, shorter than half the cephalon; it is also narrow, less than one third of the cephalon, and truncated in front. The cheeks are faintly scrobiculate along the marginal furrow. The basal lobes are short and wide and connected along the neck. The posterolateral spines are very short, but are partly obscured by fragments of the first segment of the thorax that are accidentally in the position of spines.

The pygidium is suboval and evenly convex. The border is wide, the marginal furrow deep, the shoulders strongly inclined, forming together an angle of about 100 degrees.

The dorsal furrows are deep laterally, but quite shallow at the tip of the pygidial axis. The axis is broad; its anterior half is almost parallel-sided, its posterior half triangular. The anterior half consists of two lobes marked by a pair of short and deep lateral furrows and a transcurrent furrow. The second lobe carries an elongate node over its full length. The posterior half of the axis consists also of two lobes, which are indicated by a pair of lateral indentations. The tip of the axis is doubled by the duplication of the dorsal furrow at the axial terminus. The axis itself is long, about 5/6ths of the pygidium. It does not reach the marginal furrow, and no postaxial median furrow is present.

Comparison: The cephalon may be compared with that of *Hypagnostus brevifrons* (Angelin). But in *H. willsi* the glabella is truncated, or subtruncated, in front, and not rounded as in *brevifrons,* and the cheeks in *brevifrons* are not scrobiculate. The quadrilobate axis of the pygidium of *H. willsi* is unique.

Diagnosis: *Hypagnostus willsi* is a species with a short and narrow glabella, with scrobiculate cheeks, and with a quadrilobate, well divided pygidial axis. The second transverse axial furrow is transcurrent, the second lobe carries a long node, and the axial tip is doubled.

Occurrence: The described specimen has been found in the Devoncourt Limestone, at locality D13A. Its age is the Zone of *Proampyx agra.*

HYPAGNOSTUS HIPPALUS sp. nov.

(Pl. 19, figs. 1, 2, 5-10; Pl. 23, fig. 11; Text-fig. 18)

Material: The illustrated and described material consists of three cephala and five pygidia, which are all sufficiently preserved. More specimens are present in the collection, but they are mostly damaged and were, therefore, not considered in the present description.

Measurements: Cephalon, holotype (CPC 3583)—3.0 mm. long, 3.3 mm. wide; cephalon (CPC 3569)—3.5 mm. long; cephalon (CPC 3576)—2.4 mm. long; pygidium (CPC 3584)—about 3.5 mm. long; pygidium (CPC 3570), the smaller specimen—2.4 mm. long; two pygidia (CPC 3571)—4.6 mm. long each; pygidium (CPC 3573)—3.6 mm. long, 4.1 mm. wide; pygidium CPC 3581)—2.5 mm. long.

Holotype is the cephalon, Plate 19, figure 2, CPC 3583, from locality D18.

Selection of holotype: The selection of a cephalon in preference to a pygidium as the holotype needs some explanation. The cephalon of *H. hippalus* differs from *H. sulcifer* (Wallerius) and *H. sulcifer integer* (Wallerius) in minor details only and is, therefore, not quite appropriate as a holotype. If only cephala of *hippalus* were available they should be referred to as '*Hypagnostus* cf. *sulcifer*'. But these 'minor details' are, nevertheless, significant and serve as an illustration of the taxonomic usefulness of such differences when supported by other evidence, in the present case by the quite diverse structure of the pygidia. Moreover, the lectotype of *H. sulcifer* (vide Westergaard, 1946, p. 120) is also a cephalon. Pygidia and cephala attributed to *H. hippalus* occur in close association, as seen, for example, in Plate 19, figures 1 and 2; the cephalon, Plate 19, figure 5, is closely associated with the pygidia, Plate 19, figs. 6 and 7. On the same bedding plane a variety of agnostids is present and the cephala and pygidia of each species can be identified. It is, therefore, quite certain that the pygidia and cephala in question belong to the same species of *Hypagnostus*.

Comparison with Hypagnostus sulcifer *(Wallerius)*: *Hypagnostus sulcifer* (vide Westergaard, 1946) and *H. hippalus* have both sub-trapezoidal cephala with the glabella expanded in the middle. However, (1) in *sulcifer* the front of the glabella is pointed and angular, in *hippalus* it is rounded; (2) in *sulcifer* the glabella is consistently longer than half the cephalon, whereas in *hippalus* it is about half of the cephalon; (3) the preglabellar furrow is present in *sulcifer* and mostly missing in *hippalus;* (4) *sulcifer* is strongly scrobiculate, with a prominent rugose caecal pattern, but the caeca are indistinct in *hippalus;* (5) *H. sulcifer integer* is almost smooth, without rugae; but it has a subcentral node on the glabella, whereas in *hippalus* it is in the anterior third. The same differences are seen between *H. hippalus* and *H. exsculptus* (Angelin); but *exsculptus* is also different in shape: its cephalon is suboval and not subtrapezoidal. As regards the pygidia, *sulcifer* has (1) a shorter axis, (2) a postaxial furrow, (3) a deep dorsal furrow, (5) strong axial lobes and transverse furrows, and is, therefore, quite different from *H. hippalus*.

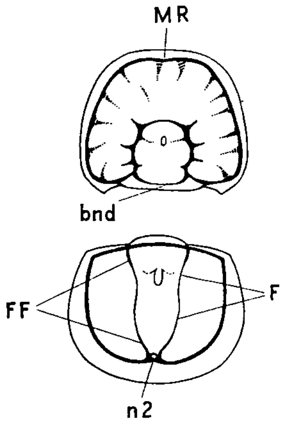


FIG. 18.—*Hypagnostus hippalus*, sp. nov., cephalon and pygidium, restored. Scrobicules are exaggerated. bud—connective band; F—dorsal furrow, effaced middle portion; FF—dorsal furrow, deep; n2—terminal node.

Comparison with Grandagnostus imitans *sp. nov.* (see Text-figs. 18 and 20): First, it should be noted that *Grandagnostus imitans* is not present in the Devoncourt Limestone, and that *Hypagnostus hippalus* has not yet been found associated with it in the V-Creek Limestone in the Undilla Basin. Secondly, *G. imitans* is about a zone older than *H. hippalus* and cannot be derived therefore from it.

The cephala of the two forms are strikingly different. The cephalon of *Grandagnostus* is effaced, but it still has a subcentral node almost in the same position as the glabellar node of *Hypagnostus hippalus.*

The pygidia, however, are of a similar design and, if compared on their own, could be regarded even as being congeneric. The main difference is that the axial furrows in *H. hippalus* are almost effaced, but not quite obsolete, whereas in *Grandagnostus* they are completely effaced and the pygidial axis appears as a vestigial elevation. The pygidia differ also in their shape: in *Grandagnostus imitans* the pygidium is subcircular, with short shoulders, in *H. hippalus* it is semioval, with broad shoulders. Both the pygidia have a wide border, the axis is long, reaching the marginal furrow, and in both of them the terminal node is present. This similarity of the pygidia cannot be accidental, and it is concluded that *Grandagnostus imitans* arose from a *Hypagnostus*—perhaps from an ancestor of *Hypagnostus hippalus.*

The pygidium of *Grandagnostus velaevis* (Text-fig. 21) is completely effaced, but in its general aspect corresponds to the pygidia of *H. hippalus* and *Grandagnostus imitans.* It seems, therefore, that both groups of *Grandagnostus,* one without and the other with the cephalic border, arose from the same stock.

A terminal axial node is seen also in pygidia of *Hypagnostus exsculptus* (Westergaard, 1946, pl. 6, figs. 4 and 5), and it is also present in the Upper Cambrian *Pseudagnostus* and *Kormagnostus* as demonstrated by Palmer (1954 and 1955). The presence of the terminal node may have a phylogenetic significance; but its absence, of course, may have no such significance, because it cannot be determined whether the absence is original or acquired.

Description: The cephalon is slightly wider than long, with forward converging sides and with rounded anterolateral angles, and is subtrapezoidal in shape. The border is narrow and convex, and has a gentle rearward retreat in the middle of the front. The posterolateral spines are triangular, short, upturned, and convex upward. No preglabellar furrow is present and the cheeks are, therefore, undivided in front of the glabella. Short and shallow scrobicules indicate simple and only moderately bifurcating caeca.

The dorsal furrows are deep all around the glabella, except for the middle of its front, where the furrow becomes shallow.

The glabella is about as long as wide and expanded in the middle, and about as long as half the cephalon. Two pairs of short lateral furrows indicate that the glabella consists of three lobes. A low elongate node is seen in the anterior third, at the junction of the anterior and middle lobes of the glabella. The basal lobes are prominent, short, and connected by the connective band along the occipital margin.

An immature cephalon (Pl. 19, fig. 10) is almost non-scrobiculate and seems to have a slightly narrower glabella than the adult specimens. The front of the glabella is bluntly rounded; the midline is subangular, but not quite carinate.

The pygidium is slightly larger than the cephalon, if the assumption is correct that the holotype cephalon (Pl. 19, fig. 2) and the pygidium associated with it (Pl. 19, fig. 1) are parts of a single exuvia. Its shape is suboval, with a rounded edge. The border is wide, gently convex, and slightly downsloping. The marginal furrow is deep. At the rear of the axis the border protrudes slightly forward, in accordance with the retreat in the cephalic front.

The axial furrows are distinct at the anterior, and at the terminal portion of the axis, whereas in the middle they are only mere lines. The axis is pointed, and cup-shaped, widest in front and constricted in its anterior third. Its rear protrudes into the marginal furrow, and has a rearward-directed terminal node at its tip.

The rear of the anterior axial lobe is elevated and bears a node, as seen in Plate 19, figure 1. In compressed pygidia the node may not be well visible.

Diagnosis: *Hypagnostus hippalus* is a species with a subtrapezoidal cephalon and suboval pygidium. The cephalon is slightly scrobiculate, with a trilobed glabella with bluntly rounded front and a node in its anterior third; the pygidium has a very wide border, and a pointed axis reaching the marginal furrow. The axial furrows are distinct anteriorly and at the axial terminus, but shallow or almost effaced in the middle.

Two small, immature pygidia (Pl. 18. fig. 6 and fig. 9) differ from larger, adult specimens in having the dorsal furrows developed evenly over their whole length.

Possibility of confusion: Pygidia of *Grandagnostus velaevis*, which occur in the same formation as *H. hippalus*, may be mistaken for it. However, these *Grandagnostus* pygidia are completely effaced and show no trace of axial furrows. The terminal node in them is an elevated node and not the extension of the axial tip. Nevertheless, the pygidium illustrated in Plate 19, figure 12, with its rounded outline and with a vestige of the axial node, may be interpreted as an exceptional *H. hippalus* pygidium, or a separate variation, although all other pygidia are quite stable and no intermediate forms have been found.

Occurrence: *Hypagnostus hippalus* occurs in the Devoncourt Limestone and is generally rare, except at locality D18, where it is numerous in a single bed. Its age is the Zone of *Proampyx agra* and lower part of the *Holteria arepo* Zone. It is numerous at locality T87, where it is associated with *Holteria arepo*.

HYPAGNOSTUS VARICOSUS sp. nov.

(Pl. 23, figs. 1, 2a, 2b; Text-fig. 19)

Material: The material consists of one complete specimen (Pl. 23, figs. 2a, 2b), the holotype, CPC 3626, and a fragmentary pygidium (Pl. 23, fig. 1), CPC 3625.

Description: The holotype is 5.5 mm. long, deformed by compression. The cephalon is evenly rounded, the marginal furrow is deep, the margin very narrow. The posterolateral spines are very short and abruptly upturned. The glabella is slightly longer than half the cephalon and has two pairs of lateral indentations. The basal lobes are exceptionally short. The cheeks are prominently rugose (varicose) and scrobiculate and the caeca arise in front of the transverse glabellar furrow. This furrow is interrupted in the middle. The caecal pattern is the same as described by Öpik (1961, fig. 2), with a single pair of diverticula.

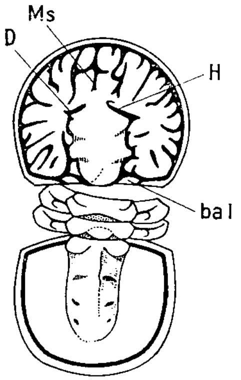


FIG. 19.—*Hypagnostus varicosus*, **sp. nov., reconstructed. bal—basal lobes; H—transverse glabellar furrow; D—diverticulum (ruga); Ms—median sulcus.**

The frontal lobe (which is in *Hypagnostus* mostly obsolete or vestigial) has the appearance of a pair of irregularly branching diverticles. The preglabellar furrow is irregular in shape and appears to be similar to the other scrobicules between the terminal caeca.

The pygidium is parallel-sided and evenly rounded in the rear. The marginal furrow is a narrow channel; the margin is narrow and convex and without spines. The shoulders appear non-geniculate. The dorsal furrows are distinct laterally and subparallel, but do not meet at the rear of the axis. The axis is only slightly elevated and about three-quarters as long as the pygidium. The first axial lobe is tripartite, and behind it are three pairs of disconnected transverse furrows that do not reach the axial furrows.

The thorax, as usual, consists of two segments. The axial lobe of the posterior segment is tripartite and similar to the first axial lobe of the pygidium. The axial lobe of the anterior segment has a pair of anterolateral lobules corresponding to the basal lobes of the cephalon. The pleurae are short, with deep, forward curving pleural furrows and angular tips.

The second specimen (Pl. 23, fig. 1), a large fragmentary pygidium, has an indistinctly granulate surface.

Specific relationship: Comparable species of *Hypagnostus* are as yet unknown; but '*Agnostus*' sp. No. 4 in Westergaard (1946, pl. 16, fig. 17) is a pygidium of a species probably related to *H. varicosus*. It has four pairs of disconnected transverse furrows not reaching the dorsal furrows, which, in turn, do not join posteriorly.

Diagnosis: *H. varicosus* is a species of *Hypagnostus* whose cephalic caeca are extremely prominent and varicose; the axial furrows of whose pygidium do not join at the rear; whose first axial lobe is tripartite; and whose axis has three pairs of disconnected transverse furrows.

Occurrence: Both the described specimens were found in the Devoncourt Limestone at locality D21. The age is the Zone of *Holteria arepo*.

HYPAGNOSTUS cf. HUNANICUS Lu

(Pl. 19, fig. 14)

Only one pygidium (CPC 3578), from locality D15, is available, in association with *Diplagnostus humilis* (Whitehouse). It is 3 mm. long, has a wide border, a long axis, and a short postaxial median furrow. The axis is trilobate and its first lobe is tripartite.

Among the species of *Hypagnostus* as yet described, *H. hunanicus* Lu (1957, pl. 137, figs. 9-11) seems to be the nearest.

The Australian specimen is not well enough preserved for specific identification, but the deep dorsal furrows, distinct division of the axis, and postaxial furrow exclude from consideration all other forms of the Middle Cambrian sequence in the Burke River area. *Hypagnostus clipeus* Whitehouse (1939, p. 263). which has an almost undivided axis, is also excluded.

Occurrence: Zone of *Proampyx agra*, Devoncourt Limestone.

HYPAGNOSTUS sp. F

(Pl. 19, fig. 11)

Only one pygidium (CPC 3575) is available. The precise locality is uncertain; the rock is Devoncourt Limestone, between 10 and 15 miles east of Duchess. Its age is the Zone of *Proampyx agra.*

The pygidium is only 2.1 mm. long. The axis is narrow, with an elevated node on the second axial lobe, deep dorsal furrows, and a wide short postaxial median furrow.

It is unlike any other Australian species of *Hypagnostus*, but is, perhaps, related to the Swedish *Hypagnostus exsculptus* (Angelin) as illustrated by Westergaard (1946, pl. 6. fig. 5).

Genus GRANDAGNOSTUS Howell 1935

The genus *Grandagnostus* is discussed above, p. 54.

GRANDAGNOSTUS IMITANS sp. nov.

(Not present in the Selwyn Range sequence)
(Pl. 23, figs. 12-15; Pl. 24, figs. 5-7; Text-fig. 20)

Phalacroma in Öpik (1956, p. 19) refers to this species. Whitehouse (1939, p. 262, pl. 25, figs. 23, 29) referred most probably the same species to *Phalacroma* cf. *nudum* (Beyrich). His illustrations allow of no comparison, but in the text Whitehouse states that the cephalon has a narrow rim.

Material: The material consists of one cephalon and three pygidia, all in one piece of limestone, and another pygidium from the same locality and bed. The cranidium and the pygidia are disconnected and doubt may be expressed as to their specific unity. Such a doubt is justified because the pygidia of *G. imitans* and *Hypagnostus hippalus* imitate each other and, if cranidia were absent, could be confused. Complete specimens of *G. imitans* are present, however, in collections, and display the combination of cephala and pygidia here illustrated.

The specimens here described were selected because of the exceptional preservation of the vestige of the axial lobe of the pygidium, which facilitates a comparison with *Phalacroma marginatum* Brögger and the discussion of the 'imitation' itself.

Measurements: Cephalon, holotype (CPC 3635)—3.4 mm. long, 3.6 mm. wide; pygidium (CPC 3636)—3.4 mm. long, border 0.4 mm. wide; pygidium (CPC 3638)—2.2 mm. long, border 0.3 mm. wide; 2.3 mm. wide.

Selection of the holotype: The cephalon Plate 23, figures 13, 13a (CPC 3635) is designated as the holotype because of its perfect preservation. However, the associated pygidium, Plate 23, figure 15, is equally important in diagnosing the species. It is probable (but, of course, not certain) that the holotype cephalon and this pygidium are parts of the exuvia of a single specimen.

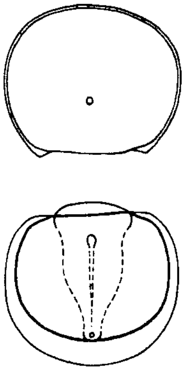


FIG. 20.—*Grandagnostus imitans* **sp. nov. The vestigial axial furrows and the outline of the median carina are indicated.**

Generic position: The species *imitans* has no cephalic basal lobes and belongs therefore to *Grandagnostus* Howell, 1935. The cephalic marginal border seen in *G. imitans* is also present in *Phalacroma nudum marginatum* Brogger, 1878 (pl. 6, fig. 3) which is also a *Grandagnostus*.

Differential diagnosis: The material of *G. vermontensis* is not preserved well enough for a proper comparison with other species. It appears, however, that this species differs in its narrow pygidial border and absence of an axial node. *Grandagnostus marginatus* (Brögger, 1878), as described also by Westergaard (1946), is very similar to *G. imitans*. In *G. marginatus* the axis of the pygidium is also vestigial, the terminal axial node is present (see Westergaard, pl. 14, fig. 27, and pl. 15, fig. 2), and the border is quite wide. *G. marginatus* and *G. imitans* differ, however, in the following characters: (1) the cephalic border (rim) is strong in *marginatus* and almost vestigial in *imitans;* (2) the axial pygidial node is almost obsolete in *marginatus*, but is consistently conspicuous in *imitans;* (3) the pygidial axis is slightly carinate in *imitans*, but not in *marginatus;* (4) the pygidial border of *imitans* is less convex than in *marginatus;* (5) the cephalon and the pygidium of *imitans* are consistently wider than long, whereas in *marginatus* they are almost as wide as long. This means that *imitans* is wider than *marginatus*.

Diagnosis: *Grandagnostus imitans* is a species of the group with a cephalic border (rim). It is distinguished by its faint cephalic marginal furrow and narrow, down-sloping border, by its carinate but vestigial pygidial axis, and by its conspicuous elongate to circular axial node, and, perhaps, relatively wide cephalon and pygidium.

Description: The cephalon is 3.4 mm. long, 3.6 mm. wide, and strongly convex. It is evenly rounded and slightly angular at its posterolateral angles. The marginal furrow is faint and separates a narrow border (rim) whose slope follows the general convexity of the shield. Small triangular posterolateral spines are present. A faint node is situated slightly behind the midpoint of the cephalon.

The adult pygidium (Pl. 23, fig. 15, pl. 24, fig. 5) is 3.4 mm. long, of which 0.4 mm. belongs to the border. It is about 4.1-4.2 mm. wide. The marginal furrow is distinct, the border is slightly convex, almost flat. The axis is vestigial and is indicated by a slight elevation. It tapers evenly rearward and is in touch with the marginal furrow in the rear. The terminal node is present. The axial node is prominent and a low crest (carina) extends from the node to the terminal node along the midline of the test. A young pygidium (Pl. 23, fig. 12a) is 2.2 mm. long and 2.3 mm. wide, and its border is 0.3 mm. wide. In another pygidium the axial node is quite long (elongate). The pygidium shown in Plate 23, figure 14 has a small axial node, and its border is more convex than in the other specimens.

Occurrence: *Grandagnostus imitans* has not been found as yet in the Devoncourt Limestone. In the Roaring Siltstone a *Grandagnostus* with a cephalic border occurs, but it cannot be determined because of defective preservation. The material described here is found in the V-Creek Limestone, in the Undilla Basin, at locality M41, east of Morstone. The age is the Zone of *Ptychagnostus nathorsti*.

GRANDAGNOSTUS VELAEVIS sp. nov.

(Pl. 19, fig. 12; Pl. 23, figs. 3, 4; Text-fig. 21)

The material consists of a cephalon (CPC 3630, the holotype) and two pygidia.

Generic position: *Grandagnostus* Howell (1935) (*Phalacroma* auctorum), seems to be the most appropriate genus. *Phalacroma*, with *Ph. bibullatum* as type, has axial furrows in the cephalon and the pygidium and is quite distinct, and *Phalagnostus* differs in having basal lobes.

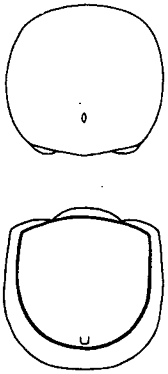


FIG. 21.—*Grandagnostus velaevis*, **sp. nov.**

Diagnosis: *G. velaevis* is a species of the *Grandagnostus* group without a marginal cephalic border, distinguished by its subquadrate cephalon and by the position of the cephalic median node in the posterior (third) quarter. The node is small and rounded.

Comparison: *G. glandiformis* (Angelin) has no border in the cephalon, but a suboval cephalon with a subcentral node.

Pokrovskaya (1958) described several new species of *Grandagnostus* under the genus *Phalacroma*. None of these species has a cephalic marginal border; but *G. velaevis* differs from all of them by the subangular shape of the shields. *Phalacroma 'laevis'* (=*laeve*) Pokrovskaya has no pygidial border at all, and its generic position is therefore doubtful. *Phalagnostus prantli* Šnajdr (1958) is a *Grandagnostus* (without basal lobes), and apparently has no cephalic border, but it differs from *velaevis* in the subcircular outline of its shields and in the convexity of its pygidial border. *Grandagnostus vermontensis* Howell is insufficiently known and therefore cannot be compared with other species.

Description: The cephalon, Plate 23, figure 3, is 4 mm. wide and long; its anterolateral and posterolateral angles are abruptly curved, justifying the description 'subquadrate'. It is evenly convex, without lobes and furrows. Short, inconspicuous cephalic spines are present. The test is smooth.

The pygidium CPC 3631, Plate 23, figure 4, is tentatively assigned to *G. velaevis*. It is not an associated pygidium, because it is found in a different locality and in a stratigraphically slightly lower level than the cephalon. It is 3.2 mm. long and 3.8 mm. wide. The border is 0.4 mm. wide at its widest (in the rear). Furrows, lobes and axial node are absent, but the axial terminal node is quite prominent. The outline is subquadrate and recalls the subquadrate outline of the cephalon.

The pygidium CPC 3674, Plate 19, figure 12, is associated with the holotype cephalon. It is 3.1 mm. long and 3.4 mm. wide and is not quite subquadrate in outline. The border is wide, and, but for the terminal axial node, the test is as smooth as in the pygidium CPC 3631. Both these pygidia may be mistaken for completely effaced pygidia of *Hypagnostus hippalus*, which also have a conspicuous axial terminal node. However, the most effaced pygidium of *H. hippalus* (Pl. 19, fig. 8) shows the outline of the axis and the median axial node and is quite distinct. In *H. hippalus* the marginal furrow is also deeper, and the border more convex, than in the pygidia assigned to *Grandagnostus velaevis*. As regards the axial terminal node, its presence has no generic significance as far as *Hypagnostus* and *Grandagnostus* are concerned.

Occurrence: Specimens CPC 3630 and 3574 were found in the Devoncourt Limestone, at locality D21. The pygidium CPC 3631 was found in another locality, probably D16, of the same Limestone; but it lost its identification number and label in a fire. The age is the Zones of *Proampyx agra* and *Holteria arepo*.

Family DIPLAGNOSTIDAE Whitehouse, 1936

Agnostids of the family Diplagnostidae have a collar-like external duplication of the posterior pygidial border, a wide cephalic marginal furrow, and a median sulcus in the frontal lobe of the glabella.

The cephalon appears to be conservative in its characters; it varies very little from one genus to another and is comparable to cephala of several species of *Peronopsis* and *Pseudagnostus*. *Tomagnostus*, however, with its narrow marginal furrow, is aberrant.

More variety is seen in the pygidia, especially in the structure of the axis.

Baltagnostus Lochman (*Proagnostus? centrensis* Resser, 1938, pl. 10, fig. 18) also has the collar-like duplication of the pygidial border and is therefore a diplagnostid; so is *Oedorhachis ulrichi* Resser (ibid., fig. 29). Still, the absence of the collar does not always disaffirm a diplagnostid classification: it is absent in most species of *Tomagnostus*, in *Dolichoagnostus* Pokrovskaya, 1958, and in *Linguagnostus Kjerulfi* (Brögger) Kobayashi (1939), as seen in Westergaard (1946, pl. 8, fig. 30). When the collar is absent the Diplagnostidae can be recognized from the characteristic pygidial axis; but the criterion is not applicable to forms like *Baltagnostus* and *Oedorhachis*. Doubt is cast by such instability on the validity of the family itself. One may concur therefore with Westergaard in regarding the group as the sub-family Diplagnostinae of the family Agnostidae, or of Quadragnostidae, as suggested by Kobayashi.

DIPLAGNOSTUS Jaekel, 1909

A summary on the genus *Diplagnostus* has been produced by Kobayashi (1939), who lists four described species, all of them from the Middle Cambrian.

According to Westergaard (1946, p. 100), in Scandinavia *Diplagnostus* appears first in the Zone with *Ptychagnostus punctuosus*, quite high in the Middle Cambrian. In Australia it is already present two zones earlier and is found from the upper part of the Zone with *Ptychagnostus gibbus* to the top of the Middle Cambrian. It is abundant in the Inca Formation of the Undilla Basin in north-western Queensland, but this material has not yet been described.

Westergaard (1946) assumes that *Diplagnostus* probably arose from *Tomagnostus;* but *Tomagnostus* in Scandinavia and *Diplagnostus* in Australia appear simultaneously at the time of *Ptychagnostus gibbus* and cannot be derived one from another. According to Kobayashi *Diplagnostus* is related to *Peronopsis*. It is indeed probable that *Diplagnostus* is a derivative of some early species of *Peronopsis*.

The characters of *Diplagnostus* are: (1) The median sulcus of the frontal lobe of the glabella; (2) the wide cephalic marginal furrow; (3) the broad, subdivided and pointed pygidial axis with the long node on the anterior lobes; (4) the 'duplication' of the posterior border of the pygidium. These characters are also familial, except for the structure of the pygidial axis. It is fairly long in *Diplagnostus*, short in *Linguagnostus*, and in *Oidalagnostus* (which is trispinose) the posterior portion of the axis is swollen and expanded as in *Pseudagnostus*. *Linguagnostus* is probably a synonym of *Diplagnostus*.

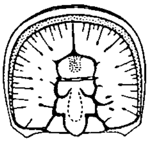


FIG. 22.—*Diplagnostus planicauda vestgothicus*, restored from Pl. 19, figs. 13a, 13b. See text-figures 23 and 25.

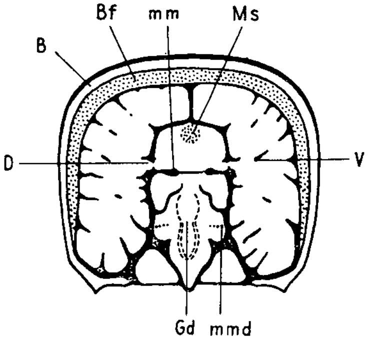


FIG. 23.—*Diplagnostus* cf. *planicauda vestgothicus*, restored from Pl. 19, fig. 17. The photograph does not show all details which are actually present. B—margin; Bf—marginal furrow; Du—anterior diverticulum; Gd—centre of posterior lobe of glabella (centre of the figure of "cross"); mm—muscle spots in transverse glabellar furrow; mmd—additional glabellar furrow; Ms—frontal salcus; V—scrobicule with pit.

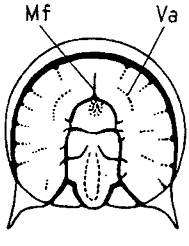


FIG. 24.—*Diplagnostus* cf. *planicauda vestgothicus*, restored from Pl. 20, fig. 3. Mf—preglabellar median furrow (incomplete); va—arcuate scrobicule; note the large spines.

DIPLAGNOSTUS PLANICAUDA VESTGOTHICUS
(Wallerius)
(Pl. 19, figs. 13a, 13b; Text-fig. 22)

Westergaard (1946, p. 62) gives the synonymy of *D. planicauda vestgothicus*.

For the terminology see Text-figures 23 and 25.

Description: The illustrated cephalon (CPC 3572) is 2.6 mm. long and 2.9 mm. wide. The marginal furrow is a wide channel, the margin is narrow and elevated. The posterolateral spines are triangular, short, upturned, and convex. The preglabellar median furrow is narrow and distinct. The dorsal furrows are deep. The cheeks are convex and densely scrobiculate; the scrobicules are straight and the longer ones have small pits at their adaxial ends. The anterior lobe of the glabella is subpentagonal and bears a wide shallow sulcus that is clearly separated from the preglabellar furrow. The transverse glabellar furrow is almost straight and bears a pair of spots (muscle scars). The posterior glabellar lobe is trilobate, as indicated by two pairs of disconnected lateral furrows. The first pair of these furrows turns inward and forward, separating a pair of rounded convex lobes just behind the transverse furrow. The posterior pair of the furrows is short, and separates the middle lobe from the posterior narrow lobe of the glabella rather incompletely. Along its midline the posterior portion of the glabella is high, convex. The shape of the lobes together is that of a stout cross. The surface seems to be minutely granulate.

Comparison: The illustrated cephalon is relatively small for an adult agnostid, but it corresponds by size and proportions to the Swedish specimens, especially to the specimen in Westergaard (1946, pl. 5, fig. 25). Some differences are present, of course. In Swedish specimens the frontal sulcus is, perhaps, deeper and the posterolateral spines shorter than in the specimen from Queensland. These characters are, however, variable.

Occurrence: The illustrated specimen was found in the Devoncourt Limestone at locality D18. From the same locality fragments of some more cephala have been collected. In Sweden *Diplagnostus planicauda vestgothicus* has been found in the Andrarum limestone (the zone of *Solenopleura brachymetopa*) and above it in the zone with *Leiopyge laevigata*. In Australia it is found in the Zone of *Proampyx agra*, above the *cassis* Zone, which is the equivalent of the *brachymetopa* Zone. Sweden and north-western Queensland are as yet the only places where this species has been recorded.

Stratigraphic and palaeogeographic significance: *Diplagnostus planicauda vestgothicus* occurs in Sweden in the two uppermost zones of the Middle Cambrian. It is, however, rare and its application in correlation is therefore limited. Palaeogeographically it is most significant, indicating that species, and even varieties, of Middle Cambrian agnostids may occur as far apart as 130 degrees of latitude.

DIPLAGNOSTUS cf. PLANICAUDA VESTGOTHICUS

(Pl. 19, fig. 17, and Text-fig. 23; Pl. 20, figs. 1 and 3, and Text-fig. 24)

Material: Three cephala are illustrated to show the range of variation. More, but rather fragmentary, material has been observed in the rock.

Measurements: Cephalon (CPC 3580)—2.5 mm. long; cephalon (CPC 3585)—1.6 mm. long; cephalon (CPC 3587)—1.9 mm. long.

Remarks: The largest of the cephala (Pl. 19, fig. 17, Text-fig. 23) differs from *D. planicauda vestgothicus* in the stronger convexity of each lobe and in a pair of additional glabellar furrows that produce an almost 'croix de Lorraine' shape of the posterior portion of the glabella. The cheeks are only moderately scrobiculate, and the posterior end of the glabella is acute and not rounded.

The specimen Plate 20, figure 3, Text-figure 24, is small and perhaps immature. It seems to have a different arrangement of caeca, a narrow marginal furrow, an incomplete preglabellar furrow, and very strong, broad posterolateral spines. The spines would appear large even in specimens twice the size.

The specimen Plate 20, figure 1 is small, and certainly immature. It has a narrow marginal furrow, extremely convex lobes, and a deep preglabellar furrow.

It is difficult to decide whether one or two species are represented. As all three cephala differ in size, and no more reasonably preserved material is present, they are considered provisionally as conspecific.

Occurrence: The described cephala are found in the uppermost levels of the Devoncourt Limestone, in the Zone of *Holteria arepo;* they are younger than *D. planicauda vestgothicus.*

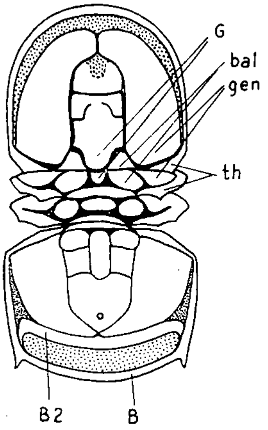


FIG. 25.—*Diplagnotus humilis* **(Whitehouse), from Pl. 19, figs. 15a, 15b. B—posterior margin of pygidium; B2—"collar", collarlike duplication of border (margin); similarity of anterior segment of thorax with posterior portion of cephalon indicated by similar lettering; Cal—basal lobes; G—glabella; gen—cheek; th—spine. Similarity of posterior segment with anterior portion of pygidium obvious.**

DIPLAGNOSTUS HUMILIS (Whitehouse, 1936)

(Pl. 19, figs. 15a, 15b, 16; Pl. 20, fig. 2; Text-fig. 25)

This species was originally described as the type of *Enetagnostus* Whitehouse. Kobayashi (1939), and later Westergaard (1946), have shown that *Enetagnostus* is a synonym of *Diplagnostus* Jaekel, 1909.

Material: A complete specimen, an isolated pygidium, and a cephalon are illustrated. They were collected at locality D15 in limestone in a creek bed, about 8.5 miles east of Duchess. No other species of *Diplagnostus* occurs at that place and it seems, therefore, that the specimens described here actually belong to *humilis*. The type material of Whitehouse is fragmentary and his diagnosis is incomplete.

Measurements: Complete specimen (CPC 3577)—4.7 mm. long; cephalon (CPC 3597)—2.8 mm. long; pygidium (CPC 3586)—1.6 mm. long.

Remarks: The cephalon differs very little from *Diplagostus planicauda* (Angelin) and *D. planicauda bilobatus* Kobayashi. From *vestgothicus* it differs in the absence of scrobicules. The pygidium, however, displays significant diagnostic characters: (1) its flanks are not subparallel as in other species, but converge rearward; (2) the axis tapers also and is shorter than in the other forms; (3) a small node is present on the posterior axial lobe of the pygidium; (4) the space between the rear margin of the pygidium and the collar is relatively wide.

The axis of the segments of the thorax is nodose. The distribution of the nodes on the anterior segment is that of the posterior edge of the cephalon (see Text-fig. 25). The pleural furrow corresponds to the marginal furrow of the cephalon. The opisthopleuron bears even a triangular projection (the posterolateral spine) and the propleuron is the posterior portion of the cheek. The median node of the axial lobe is the homologon of the posterior end of the glabella, and the large occipital connective band has its homologon along the rear border of the axial lobe of the segment. It is apparent that the anterior segment of the thorax is 'cephalic' in its structure. *Diplagnostus* is no exception with its occipital similarity, which is present in all agnostids. The posterior segment, however, is almost a replica of the anterior border of the pygidium, and a 'pygidial similarity' is apparent. In other agnostids, also, an even closer 'pygidial similarity' is observable. This arrangement indicates that the joint between the two segments of the thorax divides the agnostid into an anterior (cephalic) and a posterior (pygidial) tagma, and emphasizes the striking polarity of the organism.

Variation: The cephalon Plate 19, figure 16 differs in having a small and subtriangular frontal lobe.

Occurrence: *Diplagnostus humilis* occurs in the Devoncourt Limestone, in its lower half, and is a rare species. Its age is the Zone of *Proampyx agra*.

DIPLAGNOSTUS ? sp. I

(Pl. 18, fig. 5)

In a certain state of preservation cephala of *Diplagnostus* and *Peronopsis* may appear very similar and cannot be separated properly. This is, of course, understandable because the discrimination between these two genera depends on details that may easily become erased by accidents of preservation. The illustrated cephalon is an example of such a case and is placed in *Diplagnostus* only provisionally. Nevertheless, fragments of pygidia of a *Diplagnostus* are present in the same bed.

The cephalon (CPC 3562) is 3.9 mm. long. As in *Diplagnostus* (see Text-fig. 22) it has apparently slightly scrobiculate cheeks, and the scrobicules start as small pits. The marginal furrow is wide and the margin is narrow and convex; the posterior lobe of the glabella has lateral indentations and seems to be subdivided in the manner of a *Diplagnostus* (a cross-like median structure may be present, but is deformed); a faint glabellar median furrow is present.

The frontal lobe of the glabella is not, however, bilobed, there seems to be no frontal median sulcus, and the transverse glabellar furrow is not straight but curved. These characters, combined with the scrobiculation, the lateral glabellar furrows, and the preglabellar median furrow, may indicate a species of the group of *Peronopsis quadrata sulcata* Westergaard (1946). But, because the basal lobes are short and surrounded by furrows, and the glabella has lateral indentations, it is not related to *Peronopsis scaphoa,* with which it is associated.

Occurrence: The specimen was found in the Roaring Siltstone at locality D7/15. Its age is the Zone of *Ptychagnostus cassis.*

Family AGNOSTIDAE McCoy

The family Agnostidae consists of two large subfamilies, the Agnostinae and the Glyptagnostinae. The Agnostinae, as already indicated above, include also the genera of the families Geragnostidae and Micragnostidae. It should be noted that a rearrangement of the genera of the Agnostidae is possible. The Agnostinae contain the genus *Agnostus,* the type species of which, *A. pisiformis,* has a narrow and pointed pygidial axis, which is rather similar to the axis of the Glyptagnostinae, including *Ptychagnostus.* Other genera of the Agnostinae (for example *Homagnostus* and *Geragnostus*) have a somewhat bulbous axis with a rounded terminus. Hence, the subfamily Agnostinae may consist of *Agnostus* and the Glyptagnostinae, whereas the rest of the present Agnostinae (without *Agnostus*) may constitute another subfamily, which could bear the name of Geragnostinae Howell. No indisputable criteria however are available as yet to produce an objective subdivision of the Agnostidae, and no subjective subdivision is therefore erroneous.

Subfamily AGNOSTINAE McCoy

Genus AGNOSTUS Brongniart

The genus *Agnostus* is well known. It belongs to the uppermost Middle Cambrian, and lower levels of the Upper Cambrian.

It can be argued that *Homagnostus* Howell, and even *Geragnostus* Howell and *Micragnostus* Howell, are subgenera of *Agnostus,* and that *Geragnostus* and *Micragnostus* are probably synonymous. The distinction of these genera is based on the presence or absence of the preglabellar furrow, and the degree of effacement of the transverse glabellar furrow, as well as variations in length and width of the pygidial axis. These characters are of specific value, of course. The type of *Agnostus, A. pisiformis,* has a narrow, long, and pointed axis of the pygidium with incomplete transverse furrows; but the species also includes, according to Westergaard, forms with shorter, plumper and clearly trilobate axes. Such forms may be described as a separate species each, but they will remain within the genus *Agnostus.*

In Australia the genus *Agnostus* is represented also in the 'Dresbachian' of Queensland.

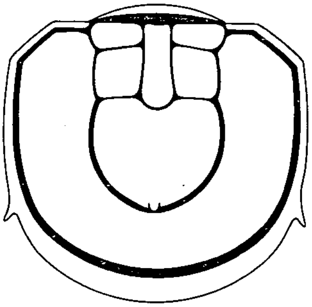


FIG. 26.—*Agnostus* sp. *e* (cf. *neglectus* Westergaard). A pygidium (CPC 3490), from loc. T87, to explain the fragmentary pygidium, Pl. 23, fig. 7.

AGNOSTUS sp. E. (AGNOSTUS cf. NEGLECTUS Westergaard, 1946)

(Pl. 23, fig. 7; Text-fig. 26)

Only the illustrated pygidium, CPC 3627, has been found in the Devoncourt Limestone. Its axial lobe is damaged, but it was relatively short and elevated. A pair of spines is present, a postaxial median furrow is absent.

The pygidium is 2.2 mm. long.

Occurrence: The specimen was found in the Devoncourt Limestone, at locality D26, almost at the top of the formation. The age is near the Zone of *Holteria arepo.* In the limestone at locality T87, western Toko Range, similar pygidia occur (Text-fig. 26), but with preserved axes. The axis is divided into two segments and a larger posterior lobe, with a blunt terminal node; a long median node is present also.

The pygidium in Text-figure 26 is about 2 mm. long and about 2.1 mm. wide. It can be compared with pygidia of *Agnostus neglectus* Westergaard, 1946 (1946, pl. 13, figs. 6 and 8), which have a slightly longer axis.

Subfamily GLYPTAGNOSTINAE Whitehouse

As already indicated above, the name Glyptagnostidae (—inae) Whitehouse, 1936, has priority over the name Hastagnostidae Howell, 1937, which is suggested by Howell in Harrington et al. (1959). *Hastagnostus* Howell is itself hardly related to any genus of this family. It can be described as an *Agnostus* without pygidial spines and should be transferred into the subfamily Agnostinae.

Doubt may be expressed as regards the subfamily relationship of *Glyptagnostus* and *Ptychagnostus*, and the subfamily could be split, therefore, into two subfamilies—the Glyptagnostinae, and the 'Triplagnostinae' or 'Ptychagnostinae', or 'Leiopyginae', whichever name may possess the page-priority of publication. *Glypnostus* and *Ptychagnostus* (*Goniagnostus*), however, appear to be closely related, as seen, for example, from a comparison of the pygidium of *P.* (*Goniagnostus*) *nathorsti* (Text-fig. 31) with the pygidium of *Glyptagnostus reticulatus* in Öpik (1961, Text-fig. 15).

Genus PTYCHAGNOSTUS Jaekel, 1909

The generic names *Ptychagnostus*, *Goniagnostus*, *Triplagnostus*, *Leiopyge*, and *Doryagnostus* appear justifiable when applied each to its type species. Intermediate forms exist, however, which can be placed at once in several of these genera. Phylogenetic considerations (which by themselves cannot replace morphology) may help in disentangling these nomenclatorial problems. So, *Leiopyge* and *Triplagnostus* constitute a lineage, which begins with an early form en grande tenure (*Triplagnostus*), and terminates with an effaced form (*Leiopyge*).

Ptychagnostus (*punctuosus, aculeatus, atavus, cassis*) differs very little from *Triplagnostus*, whose type is *T. gibbus* (Linnarsson). *Ptychagnostus* has the surface visibly granulose and the cheeks scrobiculate, whereas *Triplagnostus* is said to be smooth, non-granulate, and non-scrobiculate. I have examined Swedish specimens of *Triplagnostus gibbus* (courtesy of A. H. Westergaard) and found that its cephalon is not 'smooth', but minutely granulose, and that it differs, therefore, from *Ptychagnostus* in degree only, but not in principle. The same applies to the scrobiculation, because scrobiculate specimens are frequent in *gibbus* also. Furthermore, two of the above-listed species of *Ptychagnostus*, *punctuosus* and *aculeatus*, are scrobiculate and visibly granulose, *cassis* minutely granulose, and *atavus* only scrobiculate; finally, *Ptychagnostus lundgreni* is non-granulose, and mixed scrobiculate and non-scrobiculate. It is, therefore, only a matter of taste to consider which forms should be placed in *Triplagnostus* and which in *Ptychagnostus*.

Concurrently with the process of effacement, agnostids en grande tenure (*Ptychagnostus*, *Goniagnostus*) continue to exist, and forms evolve with accentuated relief (*P. fumicola*), manifesting a tendency opposed to effacement. Species which are listed as *Triplagnostus* must be classified with the bulk of forms en grande tenure, of course, because the classification with its descendant *Leiopyge* would mean a phylogeny 'in reverse'. It is already difficult to discriminate between *Triplagnostus* and *Leiopyge*, but a demarcation between *Triplagnostus* and *Ptychagnostus* would be even more difficult. *Triplagnostus* Howell, 1935, appears to be even a synonym of *Ptychagnostus* Jaekel, 1909, as indicated below.

The type of *Ptychagnostus* is *P. punctuosus* (Angelin). Besides being visibly granulose and scrobiculate, it displays one more character of importance. As seen, for example, in Westergaard (1946, pl. 12, fig. 4) its pygidial axis shows an incipient division of the posterior lobe, that corresponds to the posterior furrow (nf) in Text-figure 31 (*Ptychagnostus* (*Goniagnostus*) *nathorsti*). I assume that this incipient division in *P. punctuosus* is the beginning of a new character. In subsequent species (*nathorsti, fumicola*) this division has established itself as a deep furrow, which is regarded here as of generic significance.

To sum up, *Ptychagnostus* is a genus of Glyptagnostinae with (1) non-scrobiculate pygidia, and scrobiculate cephala, (2) pointed anterior glabellar lobe, (3) test in some species smooth, but mostly granulose, or visibly granulose, (4) trilobate, and secondarily quadrilobate, pygidial axis. It is divisible into two subgenera: (1) *Ptychagnostus* (*Ptychagnostus*), with the secondary division of the pygidial axis incipient, or absent, and commonly, but not always, without pygidial spines, and (2) *Ptychagnostus* (*Goniagnostus*), with the secondary division of the pygidial axis well developed, and with pygidial spines.

When these criteria are applied the genus *Triplagnostus* becomes a synonym of *P.* (*Ptychagnostus*), and *Doryagnostus* by the structure of its pygidial axis becomes *P.* (*Goniagnostus*).

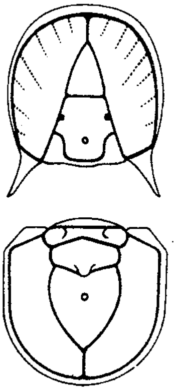


FIG. 27.—*Ptychagnostus cassis* **sp. nov., from Pl. 20, figs. 4b and 9.**

PTYCHAGNOSTUS (PTYCHAGNOSTUS) CASSIS sp. nov.

(Pl. 20, figs. 4a-13, Text-fig. 27)

Material: Ten specimens (five cephala and five pygidia) are illustrated to show the influence of slumping and tectonic distortion on the shape. Most of the specimens are selected from a sandstone interbed in the Roaring Siltstone. The fossil is even more abundant in shale, but is rather compressed and distorted. The cephalon Plate 20, figure 4 is in limestone and, therefore, almost undistorted.

The holotype cephalon, Plate 20, figures 4a, 4b, comes from the lowermost portion of the Devoncourt Limestone, locality D17A; all other specimens from a fine-grained sandstone locality, D19B (Roaring Siltstone).

Measurements: Cephalon, holotype (CPC 3588)—2.9 mm. long, 2.9 mm. wide; cephalon (CPC 3589)—3.1 mm. long, 3.1 mm. wide; cephalon (CPC 3590)—3.6 mm. long, 3.6 mm. wide; cephalon (CPC 3592)—3.4 mm. long, 3.4 mm. wide; pygidium (CPC 3593)—3.3 mm. long, 3.3 mm. wide; pygidium (CPC 3595)—3.0 mm. long, 2.5 mm. wide; pygidium (CPC 3597)—2.1 mm. long, 2.3 mm. wide.

Selection of the holotype: The cephalon Plate 20, fig. 4a, 4b (CPC 3588) is selected as the holotype because of its better preservation in limestone, and because limestone is more durable for safekeeping than the friable sandstone.

Previous record in literature: Whitehouse (1936, p. 86) described a new agnostid under the name of *Solenagnostus acuminatus* in which two different forms were included. The holotype of *Solenagnostus acuminatus*, by original designation, is a cephalon (op. cit., pl. 8, fig. 14) from the '*Dinesus* stage of Yelvertoft', of the Middle Cambrian of Queensland. Later Whitehouse (1939, p. 266) writes that it is asociated with *Triplagnostus gibbus* and *Agnostus seminula.* This corresponds to a horizon of the overlap of *Ptychagnostus gibbus* and *Ptychagnostus atavus,* or the '*atavus-gibbus*' Zone (Chart, Öpik, 1960), indicating that the holotype comes from a shale or a limestone interbed in the Inca Formation. The Inca Formation and the much higher Roaring Siltstone and Devoncourt Limestone have no species in common.

A cephalon (op. cit., pl. 8, fig. 13) and a pygidium (op. cit., fig. 15) from the '*Phoidagnostus* stage eight miles east of Duchess' were also illustrated by Whitehouse as *S. acuminatus.* These two specimens belong to *P. cassis*, and were found in the Devoncourt Limestone.

The fourth specimen illustrated by Whitehouse (op. cit., pl. 8, fig. 16) seems to be a fragment and its interpretation is, therefore, reserved.

Differences from other species: In the new *P. cassis* the preglabellar area, in all specimens, is one quarter (or slightly less) of the length of the cephalon, and the scrobicules are shallow straight lines; but in the holotype of *Solenagnostus acuminatus* the preglabellar area is one third (or slightly less) of the cephalon and the scrobicules seem to be grooves. These differences are specifically significant, and remain so even if *Solenagnostus acuminatus* should be found to have long posterolateral cephalic spines.

Ptychagnostus cassis itself has long posterolateral spines, a character that facilitates its differential diagnosis. Only three described species of *Ptychagnostus* have such spines: *Ptychagnostus gibbus* (Linnarsson), *P.* (*Goniagnostus*) *spiniger* (Westergaard), and *Ptychagnostus richmondensis* (Walcott).

Ptychagnostus gibbus (vide Westergaard, 1946) is distinguished by its high glabellar tubercle and by its median spine on the pygidial axis. *Ptychagnostus spiniger* is strongly scrobiculate, its glabella is deeply dissected, the pygidial axis is narrow, and it has also posterolateral pygidial spines, and cannot be confused with *P. cassis.*

Ptychagnostus richmondensis (Walcott), as described by Palmer (1954), and *P. cassis* are similar in several aspects. But in *richmondensis* the cephalic basal lobes are divided (they are entire in *cassis*) and the pygidial axis almost reaches the border and is, consequently, longer than in *cassis*.

Specimens of *P. cassis* with the posterolateral cephalic spines broken off may be confused with *Ptychagnostus lundgreni* (Tullberg) (vide Westergaard, 1946) as both have a pointed anterior glabellar lobe and similar scrobicules. But in *lundgreni* the basal lobes are short and the glabellar node is nearer to the centre than in *cassis*.

Description: The cephalon is about as wide as long. The border is narrow and convex, the marginal furrow is narrow and deep. The posterolateral spines are straight and about as long as the anterior glabellar lobe. The cheeks are evenly convex, with shallow linear scrobicules that are directed in a pennate arrangement forward and outward. A similar arrangement of the caeca is seen in *Ptychagnostus lundgreni nanus* (Grönwall), in *Ptychagnostus atavus*, and in *P. punctuosus*, but with a tendency toward a radiating arrangement. In other species, as a rule, the caeca are radiating. The preglabellar median furrow is deep and expands at its ends. The glabella is long, slightly more than three quarters of the cephalon. Its anterior lobe is pointed and almost triangular. The anterior transverse furrow is straight and distinct. The posterior glabellar lobe has a pair of lateral indentations, and a small node on its highest point between the anterior tips of the basal lobes. The basal lobes are relatively long, subangular, and simple (not split in two); the connective band is narrow, and depressed. The convexity of the glabella coincides with the general curvature of the cephalon. The surface is minutely granulate, almost smooth.

The pygidium is suboval, with slightly converging flanks, and an evenly rounded posterior margin. When undistorted it is almost as long as wide, but distorted specimens display a wide range of aberrations from the original form. The border is wider than in the cephalon and almost flat, the marginal furrow is deep and narrow. The shoulders are elevated, strongly geniculate at their middle, with a distinct rearward and downward slant. The pygidial axis is relatively short (about three-quarters of the pygidium) and slightly less than one-half of the width of the pygidium. The dorsal furrows are deep, and meet at the rear in a point, and the median postaxial furrow is distinct, though in distorted specimens (Pl. 20, fig. 13) it may be obliterated. In some specimens its posterior half may be shallow.

The pygidial axis is completely trilobate. The anterior lobe is tripartite and is distinctly wider than the rest of the axis. The middle lobe bears a relatively prominent node, and a small circular node is seen near the middle of the posterior lobe. Such a node occurs in several other species of *Ptychagnostus* (for example *punctuosus, nathorsti, fumicola*), in *Tomagnostus*, and in *Diplagnostus humilis*. It may or may not correspond to the terminal node of *Hypagnostus, Grandagnostus, Pseudagnostus*, and *Geragnostus*. Marginal spines are absent. It is not possible to point out characters that are particular to *Ptychagnostus cassis*, and its diagnosis is based on a combination of characters that occur in different combinations in related species.

Diagnosis: *Ptychagnostus cassis* is a species with long cephalic spines, weak pennate scrobicules, long subangular basal lobes, and a relatively short pygidial axis with a wide anterior lobe.

Occurrence: *Ptychagnostus cassis* is abundant in the Roaring Siltstone, at localities D7/15 and D19B; it is rare in the lower portion of the Devoncourt Limestone (locality D17A), and has not yet been found outside the Selwyn Range, Queensland. Its age is the Zone of *Ptychagnostus cassis*.

PTYCHAGNOSTUS (PTYCHAGNOSTUS) ACULEATUS (Angelin)
(Pl. 21, figs. 3, 4a, 4b)

Synonymy: See Westergaard (1946, p. 79).

Material: The material consists of several pygidia in one bedding plane of the Roaring Siltstone, locality D7/15; one of them (CPC 3605) and a fragment of a pygidium (CPC 3602) from the Devoncourt Limestone, locality D18, are illustrated.

Remarks: The pygidium CPC 3605 (Pl. 21, figs. 4a, b) is 2.9 mm. long and 3.6 mm. wide; it is flattened and distorted and appears to be shorter than it was originally. Another, undistorted, pygidium on the same bedding plane is 4.7 mm. long and 4.3 mm. wide, and appears to be longer than it was originally. Undistorted pygidia from Sweden are only slightly wider than long.

The following characters indicate that this specimen belongs to *Ptychagnostus aculeatus*, as seen from a comparison with the two pygidia in Westergaard (1946, pl. 12, figs. 9 and 10); (1) it is parallel-sided, evenly rounded in the rear, and has no marginal spines; (2) the axis is trilobate, and a long spine, arising from the second lobe, extends rearward over the posterior lobe; (3) the ornamental granulation is dense and coarse and consists of larger and smaller granules; (4) the granules are not confined to the pleural lobes alone, but cover also the axis and even the axial spine.

The specimen Plate 21, figure 3, represents a younger variation in which the spine is smooth and the border is angulate, indicating, perhaps, the position of an incipient spine. It is, however, too small a fragment for an accurate specific identification.

Occurrence: Specimen CPC 3605, Plate 21, figure 4a, b, together with some more fragments, was found in the Roaring Siltstone at locality D7/15. Its age is the Zone of *Ptychagnostus cassis*, as well as the Swedish *Solenopleura brachymetopa* Zone.

The second specimen (Pl. 21, fig. 3), a variation, was found in the Devoncourt Limestone at locality D18. It is younger than the previous specimen and belongs to the Zone of *Proampyx agra.*

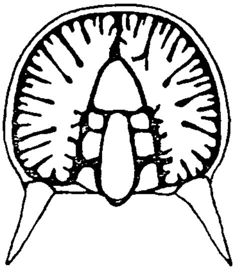


FIG. 28.—*Ptychagnostus (Goniagnostus) fumicola* **sp. nov. Cephalon, reconstructed from the three specimens, Pl. 20, figs. 15-17.**

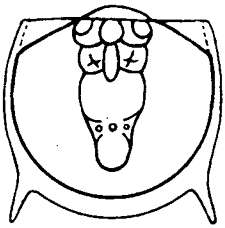


FIG. 29.—*Ptychagnostus (Goniagnostus) fumicola* **sp. nov. Holotype pygidium, from Pl. 20, figs. 9a, 9b.**

PTYCHAGNOSTUS (GONIAGNOSTUS) FUMICOLA sp. nov.

(Pl. 20, figs. 14a-17; Pl. 21, fig. 2; Text-figs. 28, 29)

Material: Only one fragmentary pygidium (Pl. 21, fig. 2, CPC 3604) has been found in the Devoncourt Limestone. It represents a new species, but is itself insufficient as a holotype. The species name refers primarily to better preserved specimens, here described, from another area (locality G9, Glenormiston 1:250,000 Sheet). They were collected by Mr. J. N. Casey in 1957.

Measurements: Pygidium, holotype (CPC 3598)—5.0 mm. long; axis 3.7 mm. long; and 1.5 mm. wide; total width 5.4 mm.; width of border 0.2 mm. Cephalon (CPC 3599)—4.1 mm. long.

Selection of the holotype: The pygidium CPC 3598, Plate 20, figures 14a, b, is selected because it is the best preserved specimen.

Specific unity of the material: The holotype pygidium and the three illustrated fragmentary cephala are considered as conspecific (1) because they are closely associated, (2) because the cephala and pygidia have the same coarse granulate ornament, and (3) because only one type of pygidium, and only one type of cephalon, both of *Ptychagnostus,* are present.

Specific relationship: In *Ptychagnostus fumicola* only the pleurae are covered with coarse granules and the axis is smooth. A similar coarse ornament is present also in *P. aculeatus*, where it covers also the axis; furthermore *P. aculeatus* has no pygidial spines, and its axis is trilobate, whereas *P. fumicola* has spines and its axis is quadrilobate. *Ptychagnostus punctuosus* has a finer granulation, a trilobate pygidial axis, no pygidial spines, and short cephalic spines. The cephalon of *P. spiniger* (Westergaard) is similar, but its test is smooth.

Ptychagnostus fumicola is related to *P. nathorsti*, and they both belong in the same group of species (subgenus *Goniagnostus*). Both have marginal pygidial spines and a quadrilobate pygidial axis with a tripartite anterior lobe. But *fumicola* differs from *nathorsti* by its coarse ornament, by the absence of the postaxial median furrow, by the greater length of the cephalic spines, and different proportions.

Description: No complete cephalon is available, but the three illustrated fragments allow of a fair reconstruction (Text-fig. 28). The cephalic border is narrow and convex, the marginal furrow is rather deep. The posterolateral spines are long, straight and divergent. The cheeks are moderately convex and slope outward, but also toward the deep dorsal furrows. The scrobicules are deeply incised and radiating, and the rugae produce a strong relief. The preglabellar median furrow is deep, but not straight, and has the appearance of a median scrobicule. The dorsal furrows are unusually deep, and only slightly shallower at the posterolateral corners of the anterior glabellar lobe, at the sites of the main caecal diverticula.

The glabella is almost triangular. Its anterior lobe is flat and pointed; the transverse furrow is deep and straight. The posterior lobe has two pairs of lateral subangular lobules separated by a pair of deep but disconnected furrows. The basal lobes are also subangular, simple, and surrounded by deep furrows. The glabella bears an elevated median crest. It is rounded on top, rises gradually rearward, and culminates as a blunt spine. The surface of the cheeks is granulate, but the glabella is smooth. The granules are smaller than in the pygidium.

The pygidium is wider than long, suboval, and strongly convex. The border is fairly wide and convex, and bears a pair of spines. The marginal furrow is deep and narrow, and continues to the anterolateral corners. The shoulders are elevated, their tips are far apart, and the geniculation is abrupt, almost vertical. The posterior margin between the spines is slightly angulate. The pleural lobes are covered with coarse granules, which are partly confluent, with pits in between. The border bears fine scattered granules. No postaxial median furrow is present.

The pygidial axis is about 0.7 of the length of the pygidium. It is bluntly pointed, constricted at the middle and the posterior transverse furrows, and is quadrilobate. The anterior lobe is tripartite, with a semi-globose middle lobule; the lateral lobules each are divided by a supplementary transverse shallow furrow.

The second axial lobe bears a prominent node terminating as a short blunt spine. Lateral parts of this lobe are nodose, a feature not seen in other species of

Ptychagnostus. The terminal part of the axis is divided into two convex lobes by a deep transverse furrow that widens outward. In the furrow there is a median node and a pair of small lateral nodes.

The prominently quadrilobate pygidial axis with the distinct posterior transverse furrow is a character of the *Ptychagnostus* (*Goniagnostus*) *nathorsti* group caused by the accentuation of the posterior transverse furrow. This furrow, however, occurs also in several other species (*P. elegans, P. punctuosus*) and even in *Tomagnostus,* but is shallow. Consequently, the presence or absence of this furrow is a matter of degree rather than quality, but can be conveniently used as a subgeneric distinction.

In its general appearance *P. fumicola* is distinguished by its coarse ornament and rough relief of lobes and furrows. This roughness of a very late species of *Ptychagnostus* is in contrast with the effacement of furrows and lobes that is so common within the same subfamily.

Variation: The pygidium CPC 3604 (Pl. 21, fig. 2), the only one found in the Devoncourt Limestone, differs in its less coarse ornament. The fusion of the granules is also more or less general, creating a vermiculate pattern. In all other respects it conforms to the holotype.

Diagnosis: *Ptychagnostus fumicola* is a species of the *nathorsti* group (*Goniagnostus*) with an extremely rough relief, coarsely granulate and pitted pleural lobes, and long cephalic spines, and without the median postaxial furrow in the pygidium. On the pygidium the ornamental granules tend to fuse into vermiculate ridges.

Occurrence: One specimen was found in the Devoncourt Limestone at locality D15. Its age is the Zone of *Proampyx agra.* The other specimens were collected from locality G9, in a limestone on the right bank of Smoky Creek, Glenormiston Sheet area. Here it is associated with *Hypagnostus brevifrons,* which indicates the Zone of *Solenopleura brachymetopa* of the Swedish Middle Cambrian scale, or our *Ptychagnostus cassis* Zone.

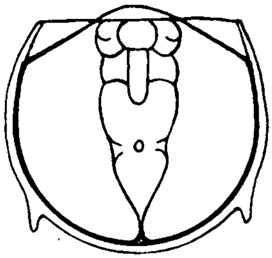


FIG. 30.—*Ptychagnostus (Goniagnostus)* **sp. aff.** *nathorsti.* **Pygidium, from Pl. 21, fig. 1, and its unpublished counterpart.**

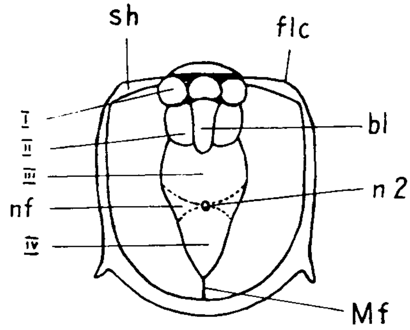


FIG. 31.—*Ptychagnostus (Goniagnostus) nathorsti* (Brogger). Adapted from Westergaard, pl. 12, fig. 13. I—anterior (first) segment of axis; II—second segment with spine; III—third segment; IV—terminal portion; bl—spine; n2—node; nf—posterior furrow (depression); Mf—post-axial furrow; fic—fulcral point (geniculation); sh—“shoulder”.

PTYCHAGNOSTUS (GONIAGNOSTUS) sp. *P.* aff. NATHORSTI

(Pl. 21, fig. 1; Text-fig. 30)

Material: The material consists of a single pygidium (CPC 3603), of which the mould and the cast have been recovered, permitting the reconstruction shown in Text-figure 30.

Remarks: The specimen can be well compared with *Ptychagnostus nathorsti* (Brögger) (Text-fig. 31). The Australian specimen is relatively wider, with wider pleural lobes, and with curved flanks. Its shoulders are also wider and more abruptly geniculate than in *nathorsti.* The test of the Australian specimen is granulate, whereas, according to Westergaard (1946, p. 81), in *nathorsti* it is smooth in Norwegian forms and ‘faintly shagreened’ in Swedish specimens. Our specimen is 3.5 mm. long, 4.2 mm. wide; its axial lobe is 3 mm. long and 1.1 mm. wide.

Ptychagnostus nathorsti occurs in the Zone of *Ptychagnostus lundgreni* and *P. nathorsti*, and above it in the Zone of *Solenopleura brachymetopa*, and is slightly older than the Australian‘*p*’ form. According to Westergaard (1946, p. 81) ‘this characteristic species is remarkably constant from its appearance to its extinction’.

Occurrence: The only available specimen was found in the Devoncourt Limestone at locality D18. Its age is the zone of *Proampyx agra.*

PTYCHAGNOSTUS (GONIAGNOSTUS) NATHORSTI (Brögger)

(Text-fig. 31)

Fragmentary pygidia of *Ptychagnostus nathorsti* occur in the Roaring Siltstone, at locality D7/15. The age is the Zone of *Ptychagnostus cassis*, which corresponds essentially to the *Solenopleura brachymetopa* Zone of Sweden, in which *P. nathorsti* makes its last appearance.

PTYCHAGNOSTUS sp. O

(Pl. 11, fig. 8)

Only one pygidium (CPC 3582), a mould, is available. It is 2.3 mm. long, and 2.6 mm. wide. The border is narrow and apparently flat. It bears a pair of tiny lateral spines, on the level of the tip of the axial lobe. One of the spines is preserved on the right flank. The axial furrows are distinct, but rather shallow. The axial lobe is not elevated and follows the curvature of the test. The tip of the axis is pointed; the anterior third of the axis is constricted slightly and the two anterior lobes are indicated by shallow transverse furrows. The second lobe bears an elongate node. A postaxial median furrow is present.

The pygidium is that of an almost effaced *Ptychagnostus,* with the lateral spines. It cannot be placed in *Leiopyge laevigata,* because all furrows and lobes are still discernible, and because the lateral spines are placed more forward than in *Leiopyge laevigata armata.*

Occurrence: The specimen is found in the Devoncourt Limestone, at locality D18, in close association with *Hypagnostus hippalus, Delagnostus dilemma,* and *Mapania synophrys,* in the piece of rock illustrated on Plate 19, figs. 1-4. It is also present in the limestone at locality T87. The age is the Zone of *Proampyx agra.*

Genus LEIOPYGE Hawle & Corda, 1847

Leiopyge was the first described genus of the *Ptychagnostus* group of forms. When the genera *Ptychagnostus, Goniagnostus, Triplagnostus, Doryagnostus,* and *Leiopyge* are interpreted as subgenera of a single genus, then by priority the valid name of that genus is *Leiopyge.* Westergaard (1946, p. 75) established that *Ptychagnostus* (*Triplagnostus*) *elegans, P. elegans laevissimus,* and *Leiopyge laevigata* 'constitute an evolutionary series with very small intervals'. Hence, *Leiopyge* is an effaced *Triplagnostus,* and *Triplagnostus* is a *Leiopyge* en grande tenure. At the same time, *Triplagnostus* Howell can be regarded as a synonym of *Ptychagnostus* (*Ptychagnostus*), as discussed under that genus.

LEIOPYGE LAEVIGATA (Dalman)

(Pl. 21, figs. 5-9b.)

Synonymy: See Westergaard (1946, p. 87).

Material: One specimen (Pl. 21, fig. 5) illustrates the preservation in the Roaring Siltstone; the mode of preservation in limestone is illustrated by the specimens collected from the Devoncourt Limestone, locality D15. Most of the better preserved collected specimens are illustrated here.

Measurements: Cephalon (CPC 3606)—2.5 mm. long; cephalon (CPC 3607)—2.6 mm. long, 2.3 mm. wide; pygidium (CPC 3608)—2.2 mm. long, 2.1 mm. wide; pygidium (CPC 3609)—1.7 mm. long; pygidium (CPC 3610)—4.0 mm. long, 4.1 mm. wide.

Remarks: Westergaard illustrated a number of specimens to show the great variability of this species. In identification of the Australian specimens, however, the complete specimen in Westergaard, plate 16, figure 9, was consulted the most. Westergaard selected his specimens from an abundant material, whereas only about twenty specimens were collected in the Devoncourt Limestone; therefore not all the variations shown by Westergaard could be reproduced here. Thus, specimens with a scrobiculate test are absent. Moreover the cephalic front in Australian specimens has a slightly stronger curvature than in the Scandinavian specimens. This difference is very small, and may be an expression of the geographical separation.

It appears also that in the illustrations of these Australian specimens some characters (lobes and furrows) are expressed differently than is seen in Westergaard's illustrations. This is merely the result of the different modes applied in preparation of the illustrations. The illustrations in this paper are photographs of specimens coated with chlorammonia, whereas Westergaard photographed his specimens without coating, and retouched them later. Moreover, applications of chlorammonia exaggerates the effect of relief (convexity) in photographs.

It is most probable that the holotype cephalon of *Leiopyge exilis* Whitehouse (1936, pl. 9, fig. 9) is a cephalon of *Leiopyge laevigata;* but it could be also a cephalon of *Leiopyge laevigata armata.* Only specimens with preserved posterolateral angles and spines can establish the distinction.

Phoidagnostus limbatus Whitehouse (1936, pl. 9, figs. 10, 11) seems to be two compressed specimens of *L. laevigata* or *L. laevigata armata,* in which the basal lobes are shifted from their original position and become exposed. Whitehouse himself (p. 97) remarks that there is a tendency to confuse *Leiopyge exilis* and *Phoidagnostus limbatus.*

The pygidium in Whitehouse (pl. 9, fig. 12) that was tentatively assigned to *Leiopyge exilis* belongs apparently to a variety of *Phalacroma? dubium* Whitehouse, or to *Hypagnostus hippalus,* but not to *Leiopyge exilis* or *L. laevigata.*

According to Westergaard, *Leiopyge laevigata* can be confused with *Ptychagnostus elegans* (Tullberg) and probably with some of the other effaced, or almost effaced, species. Such forms occur also in the Middle Cambrian of Queensland in rocks older than the Devoncourt Limestone and Roaring Siltstone. Most of them occur in the Zones of *Ptychagnostus atavus, P. punctuosus,* and *P. nathorsti,* and *P. elegans* itself is probably present.

Brief description: *Leiopyge laevigata* is an effaced *Ptychagnostus.* In the cephalon only the posterior sections of the dorsal furrows, the basal lobes, and the connective band are preserved (Pl. 21, fig. 6c). The cephalic border is narrow and down-sloping, and may not be seen from above; but it is illustrated in *L. laevigata armata* (Pl. 22, fig. 1b). The posterolateral spines are short. In larger pygidia the anterior section of the axial furrows is preserved (Pl. 21, fig. 9a), but its posterior part is vestigial. In young specimens (Pl. 21, figs. 7 and 8) and, especially, in exfoliated ones, the axis is complete and even the vestige of the median postaxial furrow may be visible. The pygidial border is wider than the cephalic and, therefore, visible from above. It is slightly down-sloping in uncompressed specimens.

A low node is present in most of the specimens on the posterior part of the glabella, and an elongate node on the second axial lobe of the pygidium.

The test is smooth and shiny to the naked eye; but coating with chlorammonia brings up a very fine granulation in some specimens. Without coating it escapes observation. It may be, however, only the granulosity of the sediment imprinted on the test.

Occurrence: *Leiopyge laevigata* is found in the Roaring Siltstone and the whole of the Devoncourt Limestone. It occurs also in the upper levels of the Steamboat Sandstone in the Quita Creek area (Öpik, 1956) and in Tasmania. It is the nominate species of its own zone in Sweden, and in Queensland it covers the range of three zones (*Ptychagnostus cassis, Proampyx agra,* and *Holteria arepo* Zones).

LEIOPYGE LAEVIGATA ARMATA (Linnarsson)

(Pl. 21, fig. 10a, b; Pl. 22, figs. 1-4)

Synonymy: See Westergaard (1946).

Material: The illustrated specimens are selected to show the appearance of the fossils in a compressed and non-compressed state. Altogether about twenty specimens were collected.

Measurements: Cephalon (CPC 3611)—1.3 mm. long; cephalon (CPC 3612)—3.9 mm. long, 3.6 mm. wide; pygidium (CPC 3616)—2.5 mm. long, 2.6 mm. wide.

Remarks: *L. laevigata armata* differs from *L. laevigata laevigata* in having long cephalic and pygidial posterolateral spines. It appears that the illustrated pygidia are more effaced than those of *L. laevigata.* This is, however, only apparently so, because the illustrated pygidia of *armata* retained their test, whereas the others are more or less exfoliated.

Occurrence: *Leiopyge laevigata armata* occurs in the Devoncourt Limestone in every locality and over the full extent of the formation. It is also present in Tasmania (Öpik, in Banks, 1956, p. 188, 192). In Sweden it is widespread in both the uppermost zones of the Middle Cambrian. Its age in Queensland is the Zones of *Proampyx agra* and *Holteria arepo.*

AGNOSTACEA INCERTAE FAMILIAE

Three genera, *Delagnostus, Pseudophalacroma,* and *Blystagnostus,* are included in the group of *incertae familiae.* Most probably each of these genera belongs to a different family, but even this cannot be established with certainty. *Delagnostus* is, probably, a quadragnostid, or an agnostid related to *Ptychagnostus; Pseudophalacroma* may be a quadragnostid; and *Blystagnostus* may be even *suae familiae.*

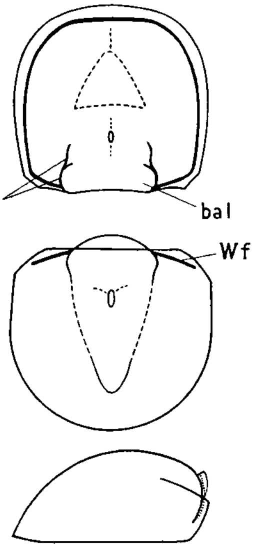


FIG. 32.—*Delagnostus dilemma,* **gen. nov. et sp. nov. Cephalon after Pl. 23, figs. 8a and 10; pygidium, dorsal and lateral views after Pl. 23, fig. 9. Lateral view of cephalon. Pl. 23, fig. 8b. bal—basal lobe; F—dorsal furrow; Wf—anterior lateral furrow.**

DELAGNOSTUS gen. nov.

Type species: *Delagnostus dilemma,* sp. nov.

Delagnostus is a monotypical genus, and its generic diagnosis coincides with the diagnosis of the type species.

DELAGNOSTUS DILEMMA sp. nov.

(Pl. 19, figs. 3, 4; Pl. 23, figs. 8a-10; Text-fig. 32)

Material: The described material consists of two cephala (Pl. 23, figs. 8 and 10) and one pygidium (Pl. 23, fig. 9), all found in close association. The pygidium and the cephala coincide in their shape, convexity, proportions and size. It is even probable that the cephalon Plate 23, figure 10, and the pygidium figure 9 are parts of the same exuvia.

Measurements: Cephalon (CPC 3632)—4.1 mm. long and 4.5 mm. wide; cephalon (CPC 3633)—3.9 mm. long and 4.2 mm. wide; pygidium (CPC 3634)—4.6 mm. long, 4.6 mm. wide.

Slection of the holotype: The pygidium CPC 3633 (Pl. 23, fig. 9) is selected because of its many peculiarities. The selection of a cephalon is inappropriate because it imitates *Phalacroma.*

Generic relationship: The cephalon of *Delagnostus* recalls *Phalacroma bibullatum*: if only cephala were available they could be placed in *Phalacroma.* The common characters are the retention of the marginal furrow and the narrow border, the well marked posterior sections of the dorsal furrows, and the fact that the basal lobes are incorporated in the glabella. Less similar is *Ciceragnostus cicer* (Tullberg); as seen in Westergaard (1946, pl. 14, fig. 5 and 7) the vestiges of its basal lobes remain outside the dorsal furrows and are not confluent with the glabella. In *Cotalagnostus* Whitehouse (1936), as seen in Westergaard (1946), the dorsal furrows are as short as in *Phalacroma* and *Delagnostus,* but the basal lobes are preserved and remain outside the dorsal furrows.

The pygidium of *Delagnostus* has no marginal furrow, and no border, and the test slopes down evenly to the edge of the shield. The effacement of the pygidial marginal furrow is altogether an exceptional character. In effaced agnostids these furrows are commonly retained and combined with a wide pygidial border. The vestige of the axial lobe of *Delagnostus* recalls the axis of a *Ptychagnostus,* or a *Peronopsis,* or a *Hypagnostus* (including *Cotalagnostus*), but certainly not that of *Phalacroma bibullatum,* which has a very wide pygidial axis and extremely narrow pleural lobes.

Skryjagnostus pompeckji Šnajdr, 1957 (see Šnajdr, 1958), has also a borderless pygidium which can be confused with that of *Delagnostus.* But the cephalon of *Skryjagnostus* is quite different: it has no external border, its dorsal furrows are close to the midline, and pass not outside, but at the adaxial side of the basal lobes, in a manner different from *Delagnostus.*

The *Peronopsis — Hypagnostus — Cotalagnostus — 'Phoidagnostus' bituberculatus* lineages of effaced agnostids retain their basal lobes or their vestiges outside the dorsal furrows, and it is, therefore, improbable that *Delagnostus* arose from this lineage. But in the Australian Middle Cambrian (in the Inca Formation and in the Currant Bush Limestone of the Undilla Basin) in association with *Ptychagnostus atavus,* undescribed forms of *Ptychagnostus* occur in which the basal lobes fuse with the glabella. From such forms, or in such a manner of effacement, *Delagnostus* may have originated. Of course, no evidence is available that *Delagnostus* arose in Australia or that its ancestors are some particular Australian species of *Ptychagnostus,* but it is as yet the only probable explanation.

Delagnostus could be regarded as a subgenus of *Ptychagnostus,* or of *Hypagnostus,* or even of *Phalacroma.* Such procedure will be based on disputable phylogenetic considerations and involve considerable changes in the concept of the genus that will be selected by chance and taste and not by morphological evidence. Thus, for the time being, *Delagnostus* is proposed here as a genus *incertae familiae.*

The following diagnosis is at once generic and specific because only one species is known as yet.

Diagnosis: Agnostids with a cephalon imitating *Phalacroma* and a pygidium without a marginal furrow and border. The cephalon has a narrow convex border, a deep marginal furrow, and short, posteriorly preserved, dorsal furows. The glabella and the basal lobes are fused together. In the pygidium the dorsal furrows are distinct anteriorly. There is a tiny subcircular node on the glabella in its posterior third, and an elongate low node on the axis of the pygidium, presumably on the second axial ring.

It is, perhaps, possible to distinguish between the cephala of *Delagnostus* and *Phalacroma*: in cephala of *Delagnostus* the anterior ends of the dorsal furrows turn slightly inward, but in *Phalacroma* outward; the node is elongate in *Phalacroma* and circular in *Delagnostus*. In well preserved specimens of *Delagnostus* the vestiges of the transverse glabellar furrow and of the frontal lobe can be discerned (Text-fig. 32), which have not yet been observed in *Phalacroma*.

Description: The cephalon is subcircular, slightly wider than long, the ratio of length/width being about 0.85-0.9. The convexity is slightly more than a third of its width. Short triangular posterolateral spines are present. The vestige of the transverse furrow is quite clear. The frontal lobe may have been triangular. The trace of the preglabellar furrow is indicated, and the glabella is slightly carinate. The test is smooth.

The pygidium is as wide as long. It is more convex than the cephalon and has its highest point in the middle (behind the node). The dorsal furrows are distinct anteriorly and just discernible at the rear of the axis. The axial lobe (mostly vestigial) is long and triangular, with a rounded terminal point. The shoulders are prominent, narrow and geniculate. The anterolateral furrows end before reaching the edge. The pygidium has no border.

Variation: Numerous specimens of *Delagnostus*, most probably of *D. dilemma*, were collected in a limestone in western Toko Range (loc. no. T 87) after the plates of the present paper were printed. These specimens indicate (1) that the specimens described here are adults, with a relatively thick test; (2) that the outlines of the axial lobes as interpreted in Text-figure 32 are correct; (3) that a terminal node is present on the pygidial axis; (4) that some of the pygidia have a faint marginal 'flange' but still no marginal furrow; and (5) that the young specimens are less effaced than the large ones. The presence of the terminal node at the very termination of the axis is not in favour of a ptychagnostid interpretation, and may indicate a derivation from *Hypagnostus*.

Occurrence: Devoncourt limestone, locality D18, high in the Zone of *Proampyx agra;* very abundant at T87, in the zone of *Holteria arepo*.

Genus PSEUDOPHALACROMA Pokrovskaya, 1958

The genus *Pseudophalacroma*, with the species *crebra* Pokrovskaya (the correct form should be *crebrum*) as the type, refers to forms related to *Phalacroma? dubium* Whitehouse, 1936. The genus is based on the following characters: (1) the furrows and lobes of the test are almost effaced; (2) the cephalic border is narrow, the pygidial border relatively wide and widening posteriorly; (3) the pygidial axis is outlined in its anterior portion only. In the type species cephalic basal lobes and the glabellar node are said to be absent.

Phalacroma? dubium Whitehouse differs from the type in the presence of a median glabellar node, distinct basal lobes, and segmentation of the anterior part of the pygidial axis, which itself is vestigial.

Pseudophalacroma is placed by Pokrovskaya in the subfamily Leiopyginae Kobayashi, 1939, of the family Peronopsidae. The subfamily Leiopyginae is, however, not applicable because *Leiopyge* itself is a genus of Glyptagnostidae Whitehouse, 1936.

The genus *Pseudophalacroma,* according to Pokrovskaya, contains only one species--*P. crebrum;* it appears, however, that *Phalacroma? dubium* is another species of it, distinct by its lesser degree of effacement. In other words, it is assumed that the presence of basal lobes in *dubium,* and their absence in *crebrum,* is a difference in the degree of effacement without generic significance. However *Pseudophalacroma crebrum* and *dubium* are regarded here as *incertae familiae,* because the effacement of their external characters is well advanced and prevents a satisfactory comparison with other genera. The survey that follows indicates also that *Pseudophalacroma* cannot be regarded as a synonym of any of the following genera: *Phalacroma, Grandagnostus, Cotalagnostus, Ciceragnostus, Leiopyge,* and *Skryjagnostus.*

Whitehouse (1936) himself queried the assignment of his species *dubium* to *Phalacroma.* At that time the concept of the genus *Phalacroma* was rather obscure, and the generic position of many effaced agnostids was uncertain. Now it is evident that *Phalacroma* should be restricted to forms related to *P. bibullatum* with a wide and non-effaced pygidial axis; consequently *crebrum* and *dubium* cannot be species of that genus. *Grandagnostus,* as described in the present paper, has a wide pygidial border, but otherwise is so dissimilar that even a comparison is difficult. *Cotalagnostus* Whitehouse, however, can be compared with *P. dubium;* the pygidium of *C. confusus* (Westergaard) has an even wider border than *dubium,* and only the anterior portion of its axial furrows is developed. The cephalon, however, is that of a *Hypagnostus* and much less effaced than in *crebrum* and *dubium.* Still, it is possible that *Pseudophalacroma* and *Cotalagnostus* are genera of a common family (Quadragnostidae).

The cephala of *P. dubium* (Pl. 22, figs. 8a, b and 9) and of *Leiopyge laevigata* (Pl. 21, fig. 6) are very similar, but the pygidia are so different that they are probably not closely related. The similarity of the cephalic structure may be only an expression of a similar degree of effacement in otherwise dissimilar species. It should be noted that Kobayashi (1939) placed *Cotalagnostus confusus* in *Leiopyge,* and regarded the genus *Cotalagnostus* as a member of his Leiopyginae, apparently being guided by the similar degree of effacement of these forms.

Some similarity is apparent between *P. crebrum* and *dubium* and some forms referred to as *Ciceragnostus* Kobayashi. For example *Ciceragnostus* (?) sp. in Westergaard (1946, pl. 16, fig. 7) is a pygidium comparable with *P. dubium* but with a very wide axis. *'Ciceragnostus' cicer* (Tullberg) is based on a pygidium with a broad axis (lectotype, vide Westergaard), but contains also pygidia with narrow axis, comparable with *Pseudophalacroma.* The cephalon of *cicer* (Westergaard, 1946, pl. 14, fig. 7) with its short dorsal furrows and vestigial basal lobes is comparable with that of *dubium,* and appears to be congeneric with the latter.

It is even probable that *'Ciceragnostus' cicer* should be transferred into *Pseudophalacroma,* or into the genus to which the species *dubium* may belong, because the species *cicer* has been erroneously placed in *Ciceragnostus.* The type of *Ciceragnostus* Kobayashi is *Agnostus barlowi* Belt, but all commentators refer not to *barlowi,* but to the better preserved *cicer.*

Agnostus cicer is a Middle Cambrian Scandinavian species, and Kobayashi, following Lake, assumed the same age for *Agnostus barlowi.* Belt (1868) however states that *Agnostus barlowi* occurs 'in the Lower Tremadoc beds', and lists Tremadoc fossils found in its association. Lake (1906), believing that *Agnostus cicer* is a junior synonym of *A. barlowi,* assumed that Belt made a mistake assigning a Tremadocian age to an 'indubitable' Middle Cambrian species. Forty years later Lake (1946) admitted that the mistake was made by himself and not by Belt.

Agnostus barlowi and *Agnostus cicer* both are semi-effaced agnostids preserving the anterior section of the dorsal furrows in the pygidium and their posterior section in the cephalon. This mode of effacement appears in a number of disconnected agnostid stocks. It has a taxonomic significance, but taken alone it cannot serve to lump such species into a generic or family unit. It is also unlikely that a genus persisted from the Middle Cambrian into the Ordovician and retained its degree of effacement unchanged. In effect, *Agnostus barlowi* in Lake (1906, pl. 2, fig. 7) has retained the vestigial outline of the glabella and seems, consequently, to be less effaced than the much older *Agnostus cicer.* It is even possible that *Agnostus barlowi* is an effaced offspring of a species of *Pseudagnostus.*

Finally, *Skryjagnostus* Šnajdr, 1957 (see Šnajdr, 1958) appears to be related to *P.? dubium* and *Pseudaphalacroma crebrum.* The cephalon of *Skryjagnostus* with its basal lobes resembles *P. dubium,* but the glabellar node is absent as in *P. crebra. Skryjagnostus,* however, has no marginal furrows, and therefore no external borders.

Distribution of the genus and its stratigraphic and palaeogeographic significance: *Pseudaphalacroma* outside Australia is known from Sibera (Yakutia), where it occurs in the upper Middle Cambrian (Pokrovskaya, 1958, p. 89). In Australia, in north-western Queensland, undescribed species of the genus are present in the Zone of *Ptychagnostus punctuosus* and younger zones, and one species (*P. dubium*) persists through the whole span of *Leiopyge laevigata.* It appears, therefore, that the genus is indicative of the upper half of the Middle Cambrian. Palaeogeographically a communication between Australia and the subarctic Siberia is indicated.

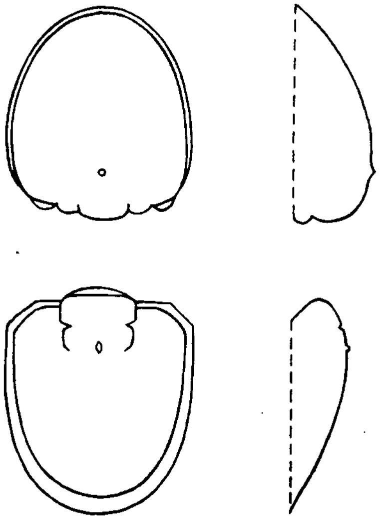


FIG. 33.—*Pseudophalacroma dubium* **(Whitehouse).**

PSEUDOPHALACROMA DUBIUM (Whitehouse)
(Pl. 22, figs. 5-10; Text-fig. 33)

Material: The six illustrated specimens represent all available material sufficiently well preserved to elucidate the species.

Measurements: Pygidium (CPC 3617)—4.0 mm. long, 3.8 mm. wide; cephalon (CPC 3618)—4.9 mm. long, 4.2 mm. wide; pygidium (CPC) 3623—4.4 mm. long, 4.1 mm. wide; pygidium (CPC 3621)—4.5 mm. long, 4.2 mm. wide; cephalon (CPC 3619)—3.1 mm. long, 2.5 mm. wide; cephalon (CPC 3620)—4.5 mm. long, 3.9 mm. wide.

Status of the species dubium *Whitehouse* (1936, p. 25): The cephalon figured in Whitehouse (pl. 9, fig. 13) is the holotype, and it agrees with the cephala shown in Plate 22, figures 8 and 9. In the illustration the holotype appears to be oval, because it was apparently photographed with the front slightly tilted up to show the border. One pygidium (Whitehouse, plate 9, fig. 15) is correctly assigned to *dubium* by Whitehouse. The other pygidium (fig. 14), however, seems to be too fragmentary for a proper interpretation from an illustration.

The best support for the interpretation of the 'associated pygidium' is produced by the specimens Plate 22, figures 5 and 6. They are together on a single piece of rock, a sandstone bed in the Roaring Siltstone; more such pygidia and cephala are found associated in a similar manner, and there is no other agnostid present to which the pygidia could be attributed.

Furthermore, about 150 miles south-south-west of the Selwyn Range, in the Sylvester Creek area (see below, locality W36) an almost complete specimen was found showing the combination of cephalon and pygidium of the kind assigned here to *P. dubium*.

Description: The cephalon is almost egg-shaped, semi-oval and truncated in its rear. Its convexity is slightly less than its width, with the highest point slightly in front of the median node. The marginal furrow is faint but distinct, the border is very narrow and convex. The glabella is outlined only in its rear and the dorsal furrows are confluent with the furrow separating the glabella from the connective band. The basal lobes are swellings separated from the cheeks by faint furrows, and confluent with the connective band, as seen in Plate 22, figure 8b. The median node is small, circular, and placed in the rear of the glabella. Its position is slightly variable, as seen from comparison of Plate 22, figure 8a with figure 9. The posterolateral spines are small, short and triangular. The cephalon of *dubium* recalls that of *Leiopyge*, but differs from it by (1) a more salient front, (2) considerably shorter residuals of the dorsal furrows, and (3) the effacement of the furrows surrounding the basal lobes.

The pygidium is oval and truncated in front. It is slightly, almost imperceptiblv. constricted in the middle, as seen in the specimen Plate 22, figure 7a. A similar constriction seems to be present in the cephalon Plate 22, figure 9, just in front of the middle.

The pygidial marginal furrow is deep, the border is relatively wide (up to 0.5 mm.) and slightly convex. In all specimens the dorsal furrows are distinct at the first axial lobe; at the second axial lobe they are vestigial, as seen in Plate 22, figure 7a, or are missing. A small node may or may not be present at the posterior margin of the second axial lobe.

Except for the two anterior lobes no trace of the remaining part of the axis is indicated.

The pygidium is less convex than the cephalon (Text-fig. 33).

Occurrence: *Pseudophalacroma dubium* occurs in the Roaring Siltstone at localities D19B and D7/15, and in the Devoncourt Limestone in all localities and over its full vertical extent. Outside the Selwyn Range it has been recorded in the Steamboat Sandstone, in the Sylvester Creek area (locality W36), and in the Northern Territory at locality T87. Its age (vertical range) is the same as of *Leiopyge laevigata*.

PSEUDOPHALACROMA sp. K.

(Pl. 22, fig. 11)

Only one specimen, a pygidium (CPC 3622), of this form has been found. It is distinguished by its triangular shape, very wide border, and acute angular posterior extremity. It is 3.8 mm. long (3.5 mm. without the articulating half-ring), and 2.9 mm. wide. The border at its widest is 0.9 mm. wide.

The specimen was found in Devoncourt Limestone, locality D18, at the road crossing Boomerang Creek, right bank, in the Zone of *Proampyx agra*.

PSEUDOPHALACROMA sp. L.

(Pl. 22, fig. 12)

Only one specimen, a pygidium (CPC 3624), has been found. It is large, and is distinguished by its evenly curved flanks. The surface appears to be minutely granulated, and muscle spots are indicated in the anterior portion of the axis delineated by the dorsal furrows. The pygidium is 5.7 mm. long (without articulating half-ring), and 5.3 mm. wide (4.5 mm. without border); the border at the rear is 1.1 mm. wide.

The specimen was found in Devoncourt Limestone, locality D17B, low in the sequence, in the Zone of *Ptychagnostus cassis*.

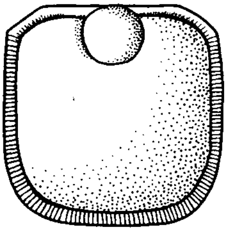


FIG. 34.—*Blystagnostus laciniatus*, **gen. nov. et sp. nov.**

Genus BLYSTAGNOSTUS nov.

BLYSTAGNOSTUS LACINIATUS sp. nov.

(Pl. 23, figs. 5 & 6; Text-fig. 34)

The material consists of two pygidia. The larger specimen, Plate 23, figure 5 (CPC 3628), is the holotype. The genus is monotypical, and the type species is *B. laciniatus* sp. nov.

Description: The holotype pygidium is 1.8 mm. long and about 1.7 mm. wide, and evenly and only slightly convex. It is parallel-sided and the posterior edge is evenly rounded. The marginal furrow is distinct, the border is flat and narrow, slightly more than 0.1 mm. wide. The border is a frill covered with radiating ridges. The axis is very short, about a quarter of the total length, and consists of a single semiglobose elevation. The shoulders are prominent, and slant abruptly at the fulcra. The surface is minutely and densely granulate. Figure 6 shows the frill and the surface granulation well preserved.

The narrow axial lobe of the pygidium indicates that the axial lobe of the thorax was also very narrow, and the pleurae relatively long.

B. laciniatus is an unusual agnostid that cannot be compared with any known genus or species. The short semiglobose axial lobe, the frill-like border, and the granulated surface are its diagnostic features.

Occurrence: *Blystagnostus* was found in a rock sample of the Roaring Siltstone, from locality D7/15. Its age is the Zone of *Ptychagnostus cassis*.

POLYMERID TRILOBITES

Family CENTROPLEURIDAE Angelin 1854

COMPARISON WITH PARADOXIDIDAE AND PROTOLENIDAE

A revision of the current taxonomy of the families Paradoxididae and Protolenidae is here suggested, and the erroneous belief that the Paradoxididae are indicative of the Middle Cambrian and the Protolenidae of the Lower Cambrian is discussed. Protolenidae and *Protolenus* itself occur also in the Middle Cambrian.

Howell (1937), Whitehouse (1939), Westergaard (1950), Hupé (1952), and Poulsen in Harrington et. al. (1959) regard the subfamily Centropleurinae as a subdivision of the Paradoxididae Emmrich 1839. Öpik (1958a) however indicated that the assumption of a close relationship between *Paradoxides* and *Centropleura* cannot be supported. Centropleuridae therefore are regarded here as a family independent from the Paradoxididae.

Paradoxides and *Centropleura* have in common an expanded glabella and transcurrent posterior glabellar furrows, but are dissimilar in other characters. Even in the mode of the expansion of the glabella they are different: in *Centropleura* the greater width is across the L4 lobes (Fig. 37), whereas in *Paradoxides* the frontal lobe is the widest.

The characters of the family Centropleuridae are as follows:

(1) Hypostoma (Fig. 39) without maculae; (2) anterior glabellar furrows longitudinal; (3) anterior branches of facial sutures retrodivergent; (4) glabella divided into an anteroglabella and a posteroglabella (Fig. 37) which includes also the occipital lobe; (5) thorax multisegmented; (6) pygidium large, fused; (7) posterior segments of the thorax and the pygidium form a pygidial unit.

For a comparison some comment is needed concerning the family Paradoxididae and related genera.

The subfamily Xystridurinae was included by Whitehouse in the Paradoxididae as an intermediate link between the latter and the Centropleurinae. This view arose from a certain similarity of the pygidia of *Xystridura* and *Centropleura.* In both genera the pygidium is a shield consisting of three or more segments with falcate pleurae, but this is not necessarily evidence for a close relationship of these genera: any trilobite with falcate pleurae may attain such a pygidium in the process of caudalization. It is to be noted that in *Xystridura* the anterior articulating pleural edge of the pygidium is normal, linear, whereas in *Centropleura* (Fig. 43) the articulation was mechanically prevented by the structure of the pygidial unit with its lateral joints. This difference should be evaluated taxonomically higher than the general resemblance of the pygidia.

The derivation of the pygidium of *Xystridura* from the fusion of a *Paradoxides*-like pygidium with the posterior segments of the thorax can be assumed without difficulty. The cephala of *Xystridura* and *Paradoxides* are also very much alike externally. Moreover, the ontogeny of *Xystridura* (unpublished) is very similar to that of *Paradoxides.* Consequently, these two genera appear to be related and can be regarded as members of a single family, the Paradoxididae. But *Xystridura* differs from *Paradoxides* by having a constant number of thirteen segments in the thorax and a large rostral shield that extends almost to the genal spines, and a dorsal rostral suture. Thus, a separate subfamily Xystridurinae seems to be appropriate. The first appearance of *Xystridura* coincides roughly with the earliest appearance of *Paradoxides,* which may indicate that the one is not a direct derivate of the other. It is possible that *Xystridura* is even closer to *Bergeroniellus* Lermontova, as discussed below.

The origin of *Centropleura* is unknown. *Centropleura, Anopolenus,* and *Clarella* appear soon after the extinction of *Xystridura,* and disappear simultaneously with the last species of *Paradoxides.* This succession of genera is however no evidence that *Xystridura* or *Paradoxides,* or an unknown intermediate form of the Middle Cambrian, was an ancestor of *Centropleura.*

Xystridura is so much like *Bergeroniellus* Lermontova (see Suvorova, 1956) that a close relationship of the two genera can be assumed. *Bergeroniellus* is older and differs from *Xystridura* by its non-fused, *Paradoxides*-like, pygidium, and is probably the ancestor of *Xystridura.*

The specimen of *Bergeroniellus asiaticus* Lermontova (1940, pl. 38, fig. 1) can be easily confused with a compressed specimen of *Xystridura* Whitehouse. Another related genus is *Bergeroniaspis* Lermontova, 1951 (vide Suvorova, 1956, p. 107). It differs little from *Bergeroniellus* and may be regarded as a subgenus of the latter. Suvorova correctly indicates that the ontogeny of these forms is very similar to the ontogeny of *Paradoxides,* and the same is true of *Xystridura.* Suvorova includes *Bergeroniellus* and *Bergeroniaspis* in the subfamily Protoleninae Hupé (Protolenidae Richter). It seems, however, that *Bergeroniellus* et al. constitute a separate subfamily of the Paradoxididae. The ventral cephalic structure of *Bergeroniellus* is as yet unknown, except for the hypostoma, which is comparable with that of *Paradoxides* and *Xystridura.* Suvorova mentions also (p. 28) that in the hypostoma of *Bergeroniellus asiaticus* a pair of small anterolateral spines is present, which is a character seen also in *Paradoxides* and *Xystridura.*

Two species of *Bergeroniaspis, B. procera* and *B. nitens,* both described by Suvorova, may, however, constitute a separate group (subgenus or genus) distinguished by their tapering glabellae. The family position of *Olekmaspis* Suvorova remains open: by its relatively large posterolateral limbs and the almost *Redlichia*-like position of the eyes it is not a paradoxidid, and hardly a protolenid.

The genus *Lermontovia* Suvorova (subfamily Lermontoviinae Suvorova) differs from *Bergeroniellus* in its multisegmented thorax and cephalic characters, but its ontogeny is like that of *Paradoxides* or *Xystridura.*

In my opinion the Lermontoviinae are not protolenids, but should be included in the Paradoxididae, or, considering its many peculiarities, regarded as a separate family of the Paradoxidacea. Small pygidia, short posterolateral limbs, and divergent anterior sutures occur also in the Protolenidae, but these characters are too general to be regarded as paradoxidid or protolenid in structure. So is also the shape of the glabella, which in the Paradoxidacea is expanded in front, but also conical and tapering; and in *Xystridura, Bergeroniellus,* and *Lermontovia* moderately expanding, but in protolenids tapering and seldom parallel-sided.

The expanded frontal lobe in *Paradoxides* deserves a special comment. In immature specimens the glabella is only slightly expanded, as in mature *Bergeroniellus* or in mature *Xystridura,* and, consequently, an expanded frontal lobe may not be diagnostic of Paradoxididae.

To sum up, the family Paradoxididae contains the subfamilies (1) Paradoxidinae, (2) Lermontoviinae (=idae), (3) the *Bergeroniellus* group, and (4) Xystridurinae.

Of course, the Paradoxididae and the Protolenidae may be regarded as two related families in the sense that, early in the Lower Cambrian, forms existed referable at will to one or the other of these families, but the known protolenids are regarded as Ellipsocephalacea, which should not be merged with Paradoxidacea.

The problem of the geological age of the Paradoxididae and Protolenidae deserves some comment. At the present state of knowledge of the time distribution of the Paradoxididae, and in the absence of other time markers, they are taken as Middle Cambrian ('Paradoxidian'). But such a decision is not commonly made by a reference to the family, but to the genus *Paradoxides* itself, because the 'axiom' that all Paradoxididae are of the same Middle Cambrian age is a bare assumption only. Similarly, the occurrence of Protolenidae is considered as indicative of the Lower Cambrian. This is a traditional and recurrent error, because protolenid trilobites, including *Protolenus,* do occur in the Middle Cambrian, as demonstrated, for example, by Sdzuy (1957, 1958). Hence, disputable protolenids (*Bergeroniellus, Lermontovia*) are not indicative of a Lower Cambrian age, no do they by themselves indicate a Middle Cambrian age, when transferred into the Paradoxididae.

Thus, *Paradoxides* and the Paradoxidinae are Middle Cambrian, but they do not mark the beginning of the series. The oldest known *Paradoxides* occurs in the Swedish *oelandicus* stage, which has a break at its base corresponding to at least two Middle Cambrian zones of the American Pacific sequence. *Xystridura,* according to Öpik (1956), occurs in the lower half of the Middle Cambrian and corresponds approximately to the upper part of the *oelandicus* stage and the lower part of the zone with *Ptychagnostus gibbus* of the Swedish scale of zones.

According to Suvorova (1956, chart, p. 10/11) *Bergeroniellus, Bergeroniaspis,* and *Lermontovia* occur in the Lena (Lenaic) Stage on the middle reaches of the

River Lena and on the River Olenek. This stage is regarded by Russian authors as the upper division of the Lower Cambrian.

Assuming that the sequence is continuous and that no break exists between the Middle and the Lower Cambrian in this region, the Lower Cambrian age of the Lena Stage cannot be substantiated. The upper part of it is Middle Cambrian and the lower part is probably Middle Cambrian or uppermost Lower Cambrian. This is borne out by the age and correlation of the fauna just above the Lena Stage. This fauna, considered by Suvorova to be basal Middle Cambrian, contains *Oryctocephalus*, *Oryctocephalops* (=?*Oryctocephalites*), *Olenoides*, *Peronopsis*, and *Pentagnostus;* it is a fauna correlated by Lermontova (1940) with the American 'Mt Stephen' or Spence fauna, for obvious paloeontological reasons. Its oldest possible age is the lower half of the *Ptychagnostus gibbus* zone, or uppermost part of the *Paradoxides oelandicus* stage (with *Ptychagnostus praecurrens*) in terms of the Swedish scale of zones, or the *Xystridura-Dinesus* fauna of Australia (Öpik, 1956, p. 18). Below follows in Europe the main part of the *oelandicus* stage and the break separating it from the top of the Lower Cambrian. Consequently, if the assumption of continuity is correct (and the Russian authors describe the sequence in terms of continuity), a substantial upper part of the Lena stage is certainly Middle Cambrian. The stage below the Lenaic sequence—the Aldan Stage—is Lower Cambrian, as indicated by the occurrence of the olenellid *Paedeumias*.

Among all the fossils listed by Suvorova in her chart as found in the Lena Stage none definitely indicates a Lower Cambrian age. Most of the genera and species are endemic and are themselves in need of dating by means of non-endemic forms. Non-endemic, but still stratigraphically inconclusive, are *Solenopleurella*, *Bathynotus*, and *Kootenia*. *Solenopleurella*, according to Rasetti (1951, p. 240), 'is common in some of the Middle Cambrian formations of the Appalachian and Cordilleran provinces'. *Bathynotus* is known to occur in the Lower Cambrian, but also in the Middle Cambrian (Öpik, 1956, p. 43). *Kootenia* appears first in the Lower Cambrian and is most abundant in the Middle Cambrian.

It appears that the abundance of previously unknown genera and species regarded as protolenids was the main reason for regarding the Lena Stage as Lower Cambrian.

CENTROPLEURA Angelin, 1854

Westergaard (1950) gives a full account of the history of *Centropleura* and related forms, and describes the Swedish species of the genus. Howell (1933) earlier proposed the subdivision of the genus into the three separate genera *Centropleura* Angelin, *Anopolenus* Salter, and *Clarella* Howell.

The independence of *Anopolenus* is doubtful. Howell re-established the genus, believing that the even curvature of its long palpebral lobes reaching to the rear corners of the cranidium is generically significant. According to Westergaard, *Anopolenus heinrici* Salter (the type species) has a definite border in the pygidium, whereas *Centropleura loveni* Angelin (the type of *Centropleura*) has no border.

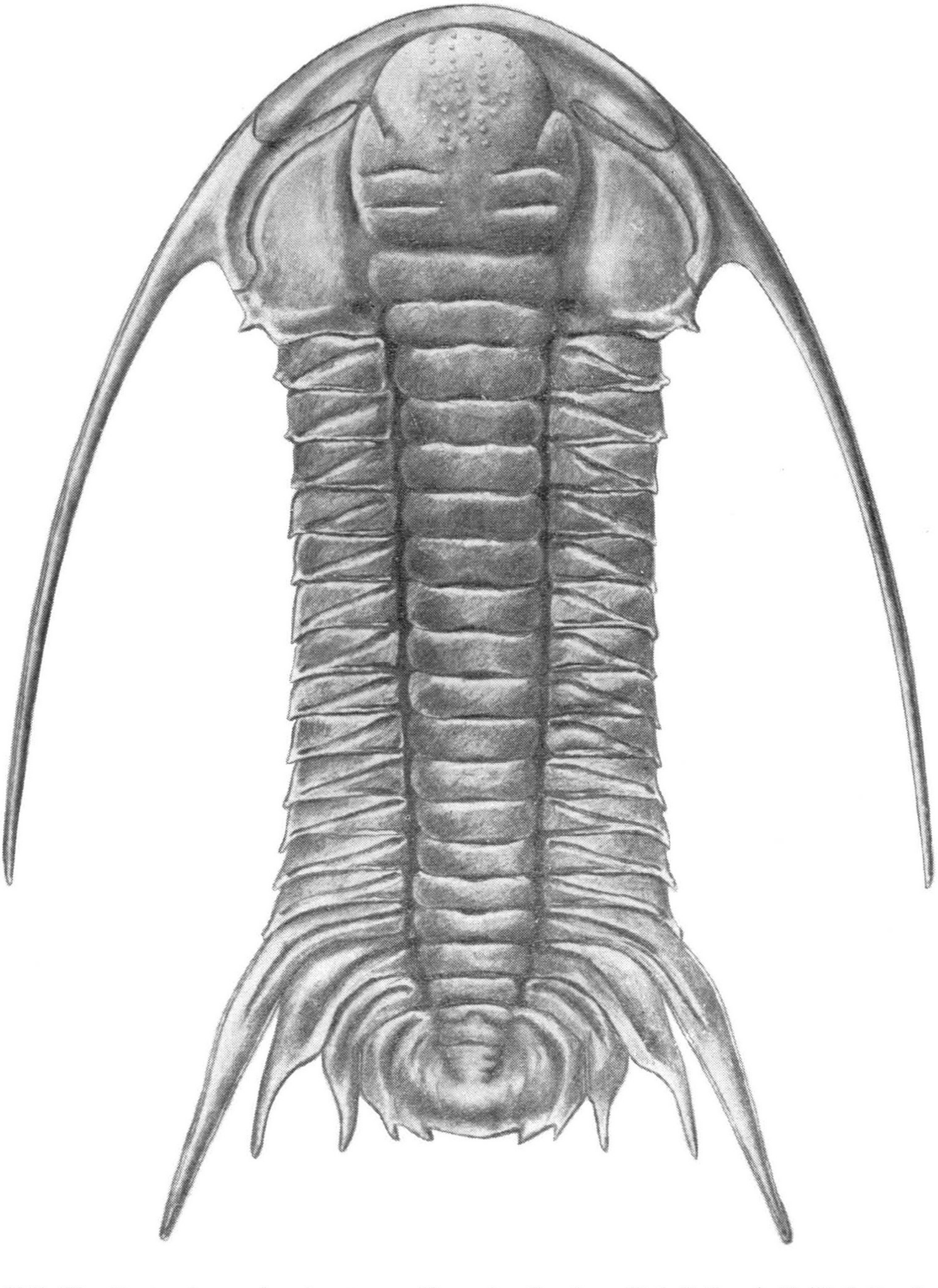


FIG. 35.—*Centropleura phoenix,* **sp. nov. Reconstruction from Plate 2, figs. A, B; Pl. 3, figs. 1, 2 and 5; Pl. 7, fig. 6; Pl. 8, figs. 3a, 3b.**

The Swedish species *Centropleura angelini* Westergaard, 1950, has palpebral lobes like *Anopolenus* in their length, but like *C. loveni* in their uneven curvature and a borderless pygidium. The new species *C. phoenix* and *C. sonax* have relatively short palpebral lobes, and *phoenix* has a depressed pygidial border, whereas *sonax* has no border. It appears now that the only real distinction between *Centropleura* and *Anopolenus* is the difference in the curvature of the palpebral lobes, as already indicated by Howell (1933); and *Anopolenus*, having only one distinctive character, should be regarded therefore only as a subgenus of *Centropleura*.

Clarella Howell, 1933, has a sinuous curvature of the palpebral lobes, and these lobes are as long as in *Anopolenus*. The type of *Clarella* is *Anopolenus venustus* Billings from the Middle Cambrian of Newfoundland, where it occurs in association with *Ptychagnostus punctuosus*.. *Anopolenus venustus* has been described from a cranidium only. However, judging from material kept in the U.S. National Museum, its thorax and pygidium are identical with a *Centropleura*. If Lake (1932, p. 189) is right in counting only fourteen segments in the thorax of *Centropleura* (*Clarella*) *impar*, then *Clarella*, with its peculiar shape of the palpebral lobes, could be regarded as a good subgenus of *Centropleura*.

A *Centropleura* was also described by Öpik (1949) from Australia. This *Centropleura neglecta* was compared with the British species *pugnax* Illing which was erroneously placed by Howell in his genus *Clarella*. *Centropleura neglecta* has a coarsely granulate surface that is not seen in specimens from Queensland.

All the forms mentioned so far are older than the species of *Centropleura* from Queensland, and are also quite distinct and will not be discussed any further.

The *Centropleura* species from Queensland have (1) unevenly curved palpebral lobes not reaching the posterior corners of the cranidium, and (2) a non-granulate test. Most of the described species of *Centropleura* belong in this group (subgenus *Centropleura*); they are: *Centropleura loveni* (Angelin 1851), *C. angustata* Westergaard (1950), *C. sibirica* Lermontova (1940), *C. oriens* Tschernyscheva (1953), *C. vermontensis* Howell (1932), *C. belli* Hutchinson (1952). The position of *Centropleura angelini* Westergaard (1950) is doubtful, and is discussed below.

Because all these species are described from incomplete material, and pygidia are known only in four of them (*loveni, angelini, oriens,* and *vermontensis*), a complete diagnostic key cannot be compiled, but a rough grouping is possible and follows below.

I. Anterior glabellar furrows do not reach the third glabellar furrows: all species as listed above.

II. Anterior glabellar furrows (S4) reach the third glabellar furrows (S3); *Centropleura sonax* sp. nov.

III. Cranidial rim indistinctly defined and anterior marginal furrow obsolete or very shallow: *C. vermontensis, C. belli.*

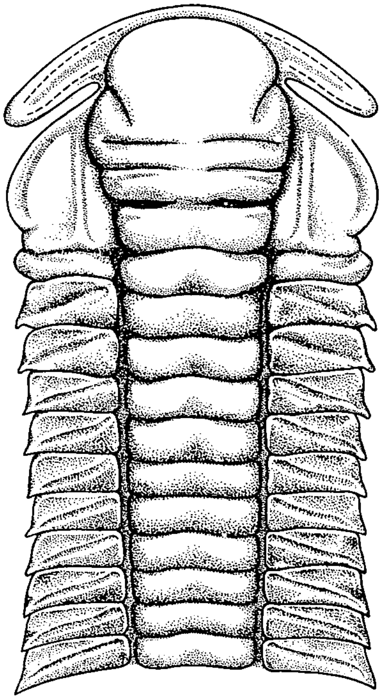


FIG. 36.—*Centropleura belli* **Hutchinson. Reconstruction from Hutchinson (1952).**

IV. Pygidium bell-shaped: *C. vermontensis, C. sonax* sp. nov. (compare VI).

V. Pygidium elliptical, transverse: *C. loveni, C. phoenix* sp. nov.

VI. Palpebral lobes reach the marginal furrows (but not the posterolateral corners) of the cranidium; pygidium bell-shaped, trapezoidal: *C. angelini.*

The species whose pygidia are known can be arranged as follows: (1) Pygidium elliptical, transverse—*C. loveni, C. phoenix;* (2) Pygidium bell-shaped—*C. angelini, C. vermontensis, C. sonax.*

The three Swedish species (*loveni, angelini,* and *angustata*) are known in sufficient detail and are based on diagnostic characters that warrant their validity. The validity of some of the remaining species is, however, not immediately clear from their descriptions and a discussion of them is called for.

Centropleura sibirica Lermontova is established on a fragmentary cranidium. It has a salient front not seen in any other *Centropleura.* The possibility that this peculiar curvature is accidental has not been discussed by the author. Until a confirmation is produced subsequently described species cannot be cleared of potential synonymy, and *sibirica* itself is a potential synonym of *C. loveni.* Consequently, *sibirica* is in need of further study and no further reference will be made to this species in the description of the *Centropleura* species from Queensland.

Centropleura vermontensis has been described briefly but is amply illustrated. According to Howell (personal communication) its pygidium is bell-shaped as in *Centropleura angelini,* and not transverse elliptical as in *C. loveni. C. vermontensis* differs from *angelini* in the shortness of the palpebral lobes. It seems also that in *vermontensis* the anterior glabellar furrows (S4) do not join the third pair of furrows, although this is not quite certain. The *vermontensis* rock is sheared shale and all specimens are greatly distorted.

It is also apparent from Howell's illustrations (1937) that *vermontensis* has relatively wide anterolateral limbs of the cranidium and a weak or even obsolete marginal furrow. In this respect *C. belli* should be compared with *vermontensis.*

The pygidium of *C. belli* is unknown. The glabella is flattened and it is difficult to decide whether the glabellar furrows are transcurrent across the glabella, as assumed by Hutchinson, or remain separate as shown in our reconstruction, Figure 36. *C. belli,* therefore, is related to *vermontensis,* but their possible synonymy still remains inconclusive.

The extension of the two posterior pairs of glabellar furrows in *C. vermontensis* and in *C. belli* deserves one more comment. Two cranidia of a *Centropleura* illustrated by Walcott (1910, p. 225, figs. 10 and 11) and attributed to *C. vermontensis* by Howell (1937) show the second pair of furrows continuing across the glabella. Walcott's specimen, figure 10, shows also a distinct marginal frontal furrow and a prominent rim which is not seen in Howell's material. It is, therefore, quite possible that the material described as *Centropleura vermontensis* belongs, in effect, to two species, as was suggested by Howell (1937, p. 1171). The diagnostic characters of *C. vermontensis* are by no means well established.

Centropleura oriens has unusually narrow pleurae (transversely) and should be compared in this respect with *C. angustata* Westergaard. Minor differences seem to be apparent in the form of the glabella: in *angustata* its frontal part is pyriform, whereas in *oriens* the front of the glabella is evenly rounded and expanded. The pygidium of *angustata* is unknown; *oriens* has well defined pleural furrows in the pygidium and four rings plus the terminus in the axis. It is of some significance that *C. angustata* (*punctuosus* Zone) and *oriens* (*Paradoxides davidis* — lower *P. forchhammeri* Zone) are contemporaneous or almost so, and are older than all other known species of *Centropleura. C. oriens* is possibly a synonym of *C. angustata.*

Paradoxides expectans Barrande, a Bohemian Middle Cambrian form, has a *Centropleura*-like pygidium. The cranidium, however, is no *Centropleura,* but rather like a *Paradoxides.* Šnajdr (1958) established his new genus *Luhops* with *Paradoxides expectans* as the type species, and selected a pygidium as the lectotype. This pygidium, and the thorax with pygidium (loc. cit., pl. 31, figs. 3 and 4) are of a centropleurid structure, and even the presence of a 'pygidial unit' is evident. The species is distinguished by longer pygidial spines and slightly recurved falcate pleural tips. As indicated below, a similar structure is possibly present also in *Centropleura loveni*, the type of the genus. Consequently *Luhops* should be regarded as a junior synonym of *Centropleura*, and the cranidia attributed to it ought to be transferred into *Paradoxides* or *Hydrocephalus*.

Finally, the British species, *Centropleura pugnax* Illing (see Lake, 1932), is based on an immature specimen and therefore cannot be compared with the others. Its pleurae are even narrower than in *C. angustata*. Westergaard placed it correctly in *Centropleura*, and not in *Clarella* as Howell (1933) did.

The generic concept of *Centropleura* is clear as far as the structure of the cranidium and the pygidium is known, but some problems arise concerning the structure of the segments of the thorax. All species of *Centropleura* the thorax of which is known (*Centropleura angustata*, *C. belli*, *C. oriens*, and *C. phoenix*) have very short pleurae with small spines that become larger and falcate in the rear segments. According to Westergaard (1950, p. 5), in an otherwise undescribed thorax attributed to *C. loveni*, the pleurae 'terminate in broad and short recurved spines'. I have seen Westergaard's specimens, and indeed, one of them has eleven segments all with falcate and slightly recurved pleural spines. In the same piece of rock another, overturned, thorax shows similar terminations. These fragments undoubtedly belong to a *Centropleura*. No such pleurae however are seen in the species listed above, in which the first ten segments have no falcate terminations, except for the thorax of *Paradoxides expectans* Barrande (1872, pl. 14, fig. 35) or *Luhops* Šnajdr (1958).

According to Westergaard 'the specimens depicted by Angelin cannot be identified' and, consequently, a lectotype cannot be designated; Westergaard (pl. 1, fig. 1) illustrates 'one of Angelin's specimens', a fragmentary immature cranidium, but it was not depicted by Angelin and cannot be regarded as the type. Thus, for the time being, and following Westergaard's tentative conclusions, the status of the genus *Centropleura* is as follows: (1) the type species is *Centropleura loveni;* (2) a type specimen has not yet been designated for *C. loveni;* (3) provisionally it is assumed that the cranidium in Westergaard (1950, pl. 1, fig. 3) is a cranidium of *C. loveni;* it was illustrated by Holm & Westergaard (1930) as *loveni* and subsequent authors in describing new species have referred to it in their differential diagnoses; (4) this cranidium is distinguished by its short palpebral lobes not reaching the marginal furrow; (5) following Westergaard (pl. 1, fig. 4, and p. 5) a transversely elliptical pygidium is regarded as that of *C. loveni*.

The thorax with the falcate pleurae (see above) was referred tentatively to *C. loveni* by Westergaard. However, another interpretation is possible if the position of the intergenal spines in the cranidium is also considered. In *Centropleura loveni* the intergenal spines are advanced, and this suggests that at least in the anterior segments of the thorax the pleural spines were also advanced, and small. Such a correlation of advanced cranidial spines and advanced pleural spines is a rough 'rule' in Cambrian trilobites. It is valid in *Centropleura phoenix* also. Consequently it is not likely that *C. loveni* had, as an exception to the rule, falcate anterior pleural terminations.

The other Swedish species, *C. angelini*, has relatively strong intergenal spines that are only slightly advanced, or not at all advanced, as seen in Westergaard (pl. 1, figs. 5 and 6). Applying the 'rule' as above, it is suggested that the pleural spines also were not advanced, but falcate, with slightly recurved spines. If this rule holds, then *Centropleura angelini* is quite different from *loveni*: *C. angelini* (1) has curved longitudinal bars on fixed cheeks, (2) long palpebral lobes reaching the marginal furrow, (3) almost not advanced intergenal spines, (4) falcate anterior pleural spines, and (5) a bell-shaped, trapezoidal pygidium.

Also, Westergaard (pl. 1, fig. 5) illustrates an almost complete cranidium of his *C. angelini* and explains that it is 'one of Angelin's specimens of *C. loveni* (RM. No. Ar. 32355)'. Angelin's own reconstructions correspond in some respect to *C. angelini* as interpreted above. The original (rejected) reconstruction has a bell-shaped trapezoidal pygidium, whereas the amended one has the transversely elliptical pygidium. In both reconstructions the palpebral lobes do not reach the marginal furrows, but the cranidial spines are not advanced and the longitudinal bars are curved. Thus, in describing his *Centropleura loveni* Angelin used predominantly material belonging to *C. angelini*, but incorporated in the original reconstruction some characters of what now is believed to be *C. loveni.*

To conclude, Angelin described as *C. loveni* two distinct species without realising that they were distinct. Westergaard described one of these species as new (*C. angelini*) and in doing so he restricted also the concept of *C. loveni* to the other form. One hopes that a neotype for *C. loveni* will be designated, and the nomenclature finally fixed in accordance with Westergaard's decision.

CENTROPLEURA PHOENIX sp. nov.

(Pls. 2-8; Pl. 14, fig. 6; Text figs. 35, 37-43)

In the present description taxonomics are given first, followed by detailed morphology and discussion of organization, degree of specialization, and mode of life.

Centropleura phoenix has been mentioned previously as *Centropleura* new species, by Öpik (1956, p. 20; 1958, p. 204).

The material described consists of twenty specimens, or fragments of twenty specimens. About the same number more was examined. The studied collection does not represent a population because: (1) the collecting sites are far apart; (2) the specimens collected come from different beds within a thickness of strata of about 300 feet; and (3) the species is rare and fragments are scattered. Nevertheless, the morphology is uniform, which leads to the conclusion that the species persisted for the time interval of about two zones.

Measurements

Complete specimen: Holotype, CPC 3484 (Pl. 2):—Length, total, as preserved—88 mm.; cephalon, length—30.0 mm.; three anterior segments together, length—14.0 mm.; three posterior segments together, length—8.3 mm.; transverse width of pleurae: first pleura—9.9 mm.; third pleura—9.4 mm.; thirteenth pleura —about 11.5-12.0 mm.

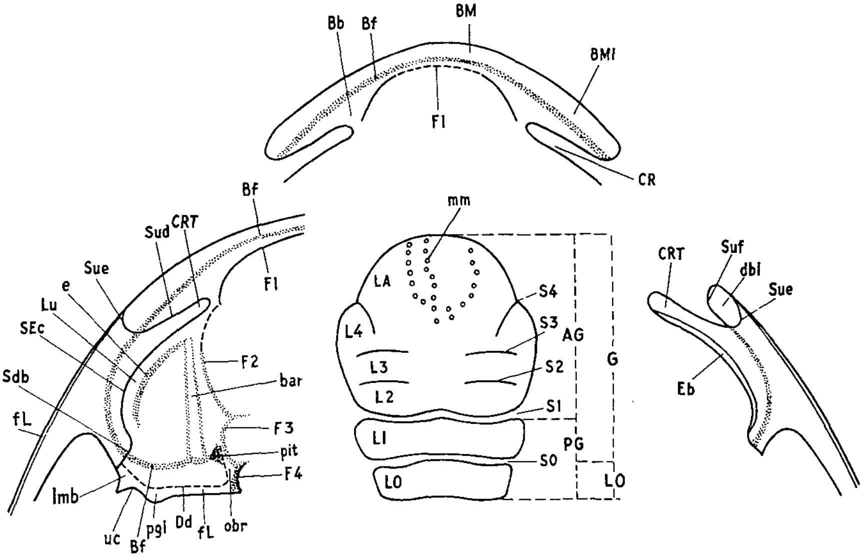


FIG. 37.—Cephalon of *Centropleura phoenix*, explanatory diagram. Centre—axial lobe; top—frontal limb; left—pleural lobe; right—free cheek.

***Axial lobe*: SO—occipital furrow; S1-S4—glabellar furrows; LO—occipital lobe, L1-L4—glabellar lobes, LA—frontal glabellar lobe; G—glabella; AG—anteroglabella, PG—posteroglabella; mm—muscle spots.**

***Frontal (anterior) limb*: Bb—"brim" of anterolateral limb; Bf—frontal marginal furrow; BM—frontal border, preglabellar; BM1—frontal border (of anterolateral limb); CR—crena; F1—preglabellar (axial) furrow.**

***Pleural lobe*: Axial furrow: F1—preglabellar section; F2—anteroglabellar section; F3—preoccipital section; F4—occipital section. Suture: Sda—see Text-figure 40; Sdb—postocular section; SEc—ocular section; Sud—preocular (retrodivergent) section; Sue—dorsal intramarginal section; Suf—submarginal section (connective suture). Other characters: Dol—opisthopleural vein; e—palpebral furrow; fL—flange (of spine, and of posterior margin); lmb—posterolateral limb; lu—palpebral lobe; obr—occipital bridge; pgl—posterolateral angle; pit—lateral pit; uc—intergenal spine with "undercut" b.**

***Free cheek*: CRT—crenal tongue; dbl—ventral doublure (internal side); Eb—base of the eye; Sue—dorsal intermarginal section of suture; Suf—ventral intramarginal suture (connective suture).**

Cranidium and thorax: CPC 3485 (Pl. 3, fig. 1):—Length, total, as preserved—52.2 mm.; cephalon, length—20.3 mm.; three anterior segments together—9.1 mm.; width of third segment—21.4 mm., its axial lobe—8.9 mm. Width of cranidium; anterior—25 mm.; between palpebral lobes—26.5 mm.; posterior margin (between sutures)—27.0 mm.

Free cheeks, length as preserved: CPC 3487 (Pl. 3, fig. 2):—45.5 mm.; CPC 3486—34.5 mm (Pl. 3, fig. 3).

Hypostoma: CPC 3489 (Pl. 3, fig. 4):—length 13.0 mm.

Cranidium: CPC 3493 (Pl. 4, figs. 3a, 3b)—length 23 mm.; width (anterior)—24.8 mm. and (palpebral) 27.2 mm; CPC 3494 (Pl. 4, fig. 2; Pl. 5; Pl. 6; Pl. 7, fig. 4)—length, 34.1 mm.; width (palpebral) 38.1 mm.; occipital lobe, length, 5.3 mm.; palpebral lobe, length 15.5 mm.; CPC 3496 (Pl. 7, fig. 3)—length 26.1 mm.; width 24.8 mm. and (palpebral) 27.2 mm.; CPC 3494 (Pl. 4 fig. 2; Pl. 5; Pl. 6; Pl. 7, fig. 4) length, preglabellar border—1.6 mm.

Pygidial unit: CPC 3498 (Pl. 7, fig. 6); length, total 8.5 mm.; pygidium 5.0 mm.; width between tips of spines 18.5 mm.

Pygidium: CPC 3500 (Pl. 8, fig. 2b): length with articulating half -ring 16.4 mm. CPC 3491 (Pl. 8, fig. 3): width 21.5 mm. CPC 3502 (Pl. 14, fig. 6): length, total 8.0 mm.

Selection of the holotype: The specimen CPC 3484 (Pl. 2) is selected because it produced most information, even regarding the delicate ornament. It is, however, damaged by fire.

Diagnosis: *Centropleura phoenix* displays no unique features by which it could be readily identified, but is based on a combination of characters that are present in other known species in different combinations. The other species, in their turn, are described from fragments but are not described in sufficient detail. For this reason the information now available for *C. phoenix* cannot be exploited diagnostically in full, although it probably contains material for a satisfactory diagnosis.

Centropleura phoenix is a species (1) with eyes not reaching the marginal furrows (and, therefore, distinct from *Clarella, Anopolenus,* and *Centropleura angelini,* and related to *C. loveni*); (2) with a transversely elliptical pygidium (and, therefore, distinct from *C. angelini, C. vermontensis,* and *C. sonax,* sp. nov.); (3) with very short spines of the anterior pleurae (and, therefore, distinct from *C. belli*); (4) with a notch on the first axial ring of the pygidium (and, therefore, distinct from *C. loveni*); (5) with a ratio of 2.5 of the width of the first segment and the axial lobe of the first segment (and, therefore, distinct from *C. oriens* and *C. angustata*); (6) with a distinct marginal furrow and rim (and, therefore, distinct from *C. vermontensis* and *C. belli*); (7) with relatively strong and well advanced intergenal spines in the late holaspis; (8) with relatively narrow fixed cheeks; and (9) with the front of the glabella rounded.

A separate differential diagnosis is omitted, because it is contained (in parenthesis) in the diagnosis above. Moreover, the general description contains comparisons with other species. The possibility of confusion with *C. sonax* is discussed under the latter.

Occurrence: *Centropleura phoenix* has been found as yet in the lower two-thirds of the Devoncourt Limestone in the Selwyn Range area. The most prolific locality is D16, in the lower half of the Limestone. Fragments occur also in the Roaring Siltstone, locality D 7/15.

Age: The Zones of *Ptychagnostus cassis* and *Proampyx agra.*

Reconstruction of *Centropleura phoenix* (Text-figs. 35 to 40)

The reconstruction is based essentially on the specimens, Plate 2, Plate 3, figure 1, and Plate 7, figure 6. The rear of the pygidium, which is missing in the complete specimen, Plate 2, and the posterior segments were restored according to the specimens, Plate 7, figure 6, and Plate 8, figure 2. All these specimens differ in size but not in proportions. Therefore, when magnified to the same size they complemented one another.

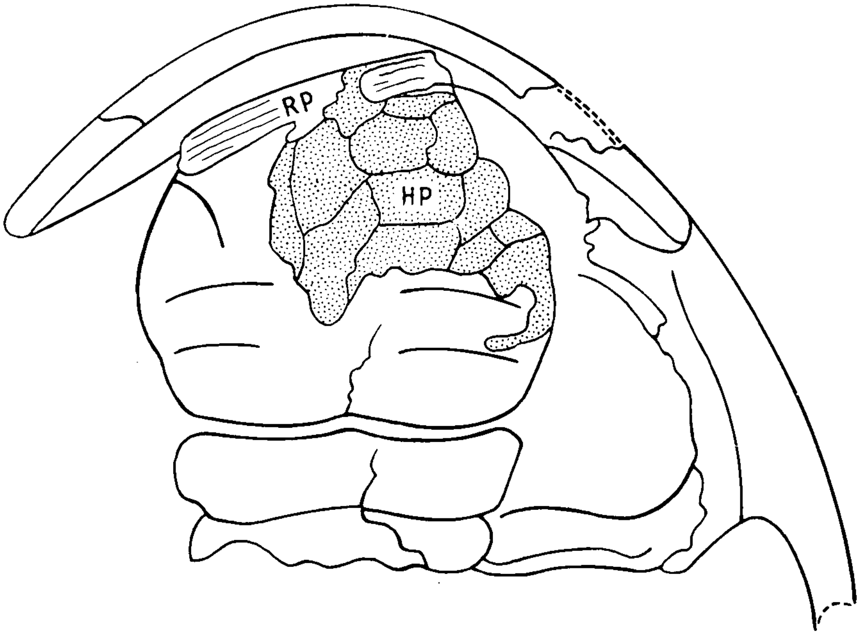


FIG. 38.—*Centropleura phoenix* : **explanatory diagram for Pl. 2, fig. C. RP—rostral shield, HP—hypostoma.**

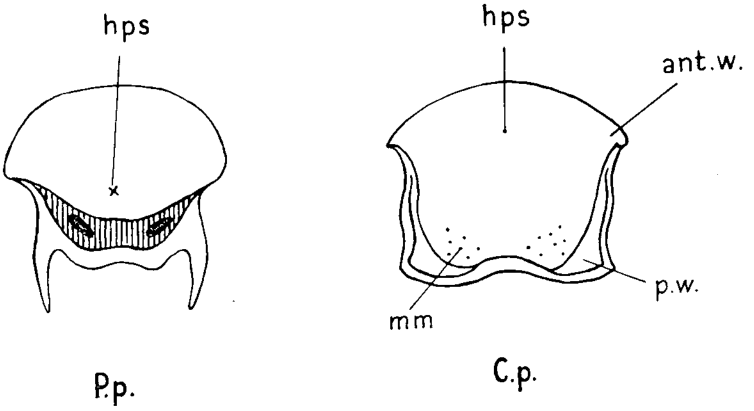


FIG. 39.—Pp—Hypostoma of *Paradoxides pinus* **(adapted from Westergaard, 1936); Cp—hypostoma of** *Centropleura phoenix* **(Pl. 3, fig. 4). ant. w.—anterior wing; p.w.—posterior wing; lip—lip and median sinus; mm—muscle spots; hps—hapsidium position of centre; shades—posterior lobe with maculae, not discernible in** *Centropleura.*

In the specimen, Plate 2, the tips of the genal spines reach almost to the level of the pygidium. The free cheeks in this specimen are, however, displaced backward and the spines rotated toward the axis. In the same specimen two segments are partly overlapping and the whole thorax is twisted out of line. This was all corrected with the aid of the specimen, Plate 3, figure 1, including the position of the free cheeks, which is determined by the course of the facial sutures.

In the reconstruction of the ventral side of the cranidium an outline of the dorsal side was prepared first. The specimen, Plate 2, provided the form of the rostral shield (Text-fig. 38) and the hypostoma. The proper size of the rostral shield was found by tracing the subcephalic doublure of a free cheek (Text-fig. 37) cut by the connective suture. The accurate size of the hypostoma, however, was difficult to assess because in the specimen, Plate 2, it is flattened and its edges are not preserved. But it was observed that the lateral wings of the hypostoma should meet the dorsal furrows at the ends of the crenae; so a controlling measurement was obtained and the outline of the hypostoma (Text-fig. 39) was magnified to fit it.

The colour or colour pattern of the shield of *Centropleura* will remain unknown; but it is not impossible that such a pattern was actually present. For example, the 'bald spots' arranged in pairs on each axial ring of the thorax and of the posterior segments of the cephalon (Text-figs. 41, 42), and the hapsidia on the axial lobes, and in pairs on the pleural tips, may have been colour spots.

External Habit

The body is slender, multisegmented and long, and has a greatly expanded cephalon, and a posterior pygidial unit consisting of three macropleural hind segments and the pygidium. The thorax has concave and serrate flanks, with a 'waist' at the sixth to seventh segment, and an hour-glass shape. The cephalon is large, as long as seven anterior segments, with a parabolic outline accentuated by the diverging, long, curved genal spines, which are advanced and as long as the thorax itself.

The axial lobe is convex and elevated, with an expanded glabella and tapering short pygidial axis, whereas the pleural lobe, including the cheeks, pleurae, and pygidial pleural platform, is flat, and the three posterior pairs of pleurae are flattened blades.

The pygidium is relatively small, as long as about three anterior segments, and with short marginal spines.

It is a relatively large trilobite, exceeding 10 cm. in length.

The Cephalon

The dorsal side of the cephalon of *Centropleura phoenix* is schematically represented in Text-figure 37, and the ventral side in Text-figure 40. As in most

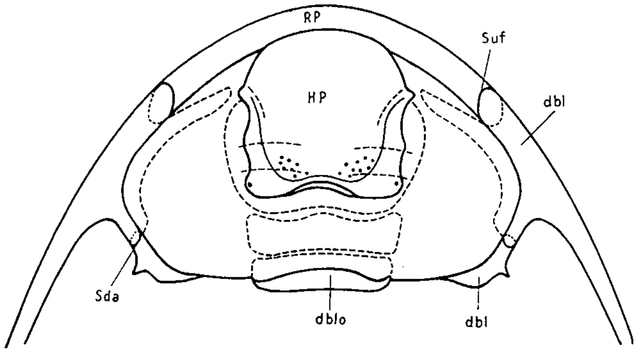


FIG. 40.—*Centropleura phoenix,* **cephalon, in ventral view, RP—rostral shield; HP—hypostoma; dbl—doublure marginal and posterolateral; dblo—occipital doublure (articulating doublure); Sda—ventral posterior section of suture; suf—ventral anterior section of suture (connective suture).**

of the trilobites the cephalon may be divided into: (1) shields—the cranidium, with the rostral plate, and the free cheeks effectuated by the facial sutures, and (2) lobes—the axial lobe, and the surrounding pleurae (pleural lobe, pleural region) defined by the joined axial and preglabellar furrows. These two kinds of division are in principle quite different, but still supplement one another, and are considered in the following description.

Facial sutures: The facial sutures of *Centropleura phoenix* are of generic but not of specific significance. Their course is the same as in *C. loveni* and other species, but *phoenix,* owing to its superior preservation, allows of a complete description. The most conspicuous character of the sutures of a *Centropleura,* including *C. phoenix,* is the retrodivergent (Hupé, 1952, p. 269) course of the pre-ocular sutures (Text-fig. 37). Trilobites with retrodivergent sutures are extremely rare, and are not related.

The sutures are best seen in Plate 3, figure 1, Plate 7, figure 3, and Text-figures 37, 38 and 40. Each suture can be described as consisting of seven sections. (1) The postocular ventral section, cutting the doublure of the posterior margin outside the intergenal spine. Its direction is not visible, but it forms an acute angle with the marginal part of the dorsal postocular suture. (2) The postocular section, or simply postocular suture, which is short and almost straight, but may be curved abaxially, as seen in Plate 4, figure 3a. (3) The ocular section, defined by the edge of the palpebral lobe. With an abrupt hairpin bend it passes into (4) the preocular suture, or anterior section, or anterior branch of the facial suture; the preocular sutures are retrodivergent. (5) The dorsal intramarginal section, cutting the margin in an abrupt curve. (6) The so-called connective suture, intramarginal, ventral, and adaxially convex. The pair of 'connective sutures' disconnects the rostral plate and the remainder of the ventral doublure. (7) The rostral suture, which is marginal; it disconnects the rostral plate and the cranidium.

At three separate points the facial suture in its course effects special characters. Firstly, the short postocular sutures, combined with the great abaxial distance of the palpebral lobes, produce only very small posterolateral limbs of the cranidium; secondly, the retrodivergent anterior sutures combined with the ocular sutures produce the deep cranidial crenae, interlocking with the crenal tongues of the free cheeks; and, thirdly, the connective sutures, as seen in the free cheek (Text-fig. 37), being placed well adaxially from the dorsal intramarginal sutures, produce a rostral plate shorter (transversely) than the cranidial front, and expose a part of the doublure of the free cheek, when the latter is isolated.

The sutures for the purpose of moulting disconnect the cephalon into three kinds of 'shields': the cranidium, the rostral plate, and a pair of free cheeks. As described below, the rostral shield and the hypostoma form a unit, and a hypostomal suture is absent. It may be absent for one of two reasons: it was present, but disappeared through a secondary anchylosis of the shields; or, it never existed. In early morphogenetic stages the hypostoma was, probably, not in touch with the doublure, but was connected with it by a stalk; in the course of growth the space between the hypostoma and the doublure diminished and both merged in a meraspid instar, without passing through a stage with a functional suture. The ontogeny of *Centropleura* is unknown, but for a single immature specimen—the type of *Centropleura pugnax* Illing (Lake, 1932, p. 195, pl. 24, fig. 13). It has a brim, which may indicate separation of the hypostoma from the doublure, and the brim has a median ridge to be interpreted as the external manifestation of a connective stalk. For analogy with olenellids, see Palmer (1957).

The axial (dorsal) furrows of the cranidium: As is best seen in Plate 3, figure 1, Plate 7, figure 3, and Text-figure 37, the axial furrows of the cranidium are not evenly impressed: four different sections of the furrows are indicated. The anterior section known as the preglabellar furrow surrounds the frontal lobe of the glabella, from crena to crena, and is narrow and shallow. The second (paired) section is deep and wide, begins at the anterior end of the palpebral lobe, and persists almost to the outer end of the first (S1) glabellar furrows, with which it merges. The third section is the pair apparently flanking the preoccipital (L1) lobe. These furrows are shallow and mark a change of slope from the cheek to the elevated glabella, and they terminate in the lateral pits. At the pits (Text-fig. 37) the axial furrows are interrupted by the occipital bridges. The fourth sections of the axial furrows flank the occipital lobe; they are out of the line of the third section of the axial furrows, because the occipital lobe is narrower than the lobe anterior to it. But these 'axi-occipital' furrows are well in line with the axial furrows of the thorax and have a similar depth. Thus, the axial furrows of the thorax extend into the posterior, occipital segment of the cranidium unchanged.

The lateral pits of *Centropleura* are in a position comparable with that of the alae (Hupé, 1953, p. 103) or the '*Pharostoma* markings' (Öpik, 1937b). But a complete coincidence in position of the alae and the lateral pits is not evident and for this reason the terminology remains different. The lateral pits are discussed once more below, under the heading 'fixed cheeks'.

The occipital bridge is seen best in Plate 3, figure 1, and Plate 6, figure A, and Text-figure 37. It is a swelling at a right angle to the posterior margin and joins the enlarged preoccipital lobe. The occipital bridge appears to be a part of the opisthopleural diverticulum, and the junction of the bridge and the L1 lobe may indicate the diverticular orifice of the stomach.

The Cranidium

The axial lobe of the cephalon: It is customary to describe the axial lobe of the cephalon of trilobites as consisting of the glabella and the occipital lobe. This division is, of course, applicable for most of the trilobites, and *Centropleura* also can be described in a similar manner. But in *Centropleura* another organization is apparent, which cannot be adequately described by the 'glabella and occipital lobe' terminology only, and which is in need of such subsidiary terms as anteroglabella and posteroglabella.

In *Centropleura* (Text-fig. 37) the cephalic axial lobe consists of an anterior division (the anteroglabella) and two posterior parts, the occipital lobe and the preoccipital lobe, which both together are referred to as the posteroglabella.

The anteroglabella is completely surrounded by the preglabellar and axial furrows, and the transcurrent first glabellar furrow. It is expanded, its furrows are discontinuous in the middle and do not reach the dorsal furrows: briefly, if compared with the remaining part of the axial lobe, the anteroglabella of *Centropleura* is a well-fused piece of the tergite. The anteroglabella is the positional antagonist of the hypostoma (Text-fig. 40) and both together form the capsule that encases the proventriculum.

The posteroglabella consists of two axial lobes and two transcurrent articulating furrows, the occipital and the first glabellar furrows (S1), the outer ends of which served as appendiferi, and the median parts of which are the rudiments of the transverse articulating furrows and the articulating half-rings. The ornament on both lobes of the posteroglabella (Text-figs. 41 and 42) is the same as on the axial rings of the thorax, whereas the ornament on the anteroglabella (Pl. 7, figs. 4, 5) is a simple network.

To sum up, the anteroglabella of *Centropleura phoenix* and any other *Centropleura* consists of four fused and modified mesotergites, and has its own distinct ornament; it is the antagonist of the hypostoma and both together served as the exoskeleton of the proventriculum. The posteroglabella consists of two separate mesotergites that preserve the axial ornament of the thorax and the segmental dividing furrows of the thorax, and are fused among themselves and with the anteroglabella only by absence of articulation, but otherwise preserve the rudiments of the articulation apparatus.

The occipital and the preoccipital lobes, forming the posteroglabella, have the appearance of axial lobes of the thorax and display an 'occipital similarity' as described in *Redlichia* (Öpik, 1958 b).

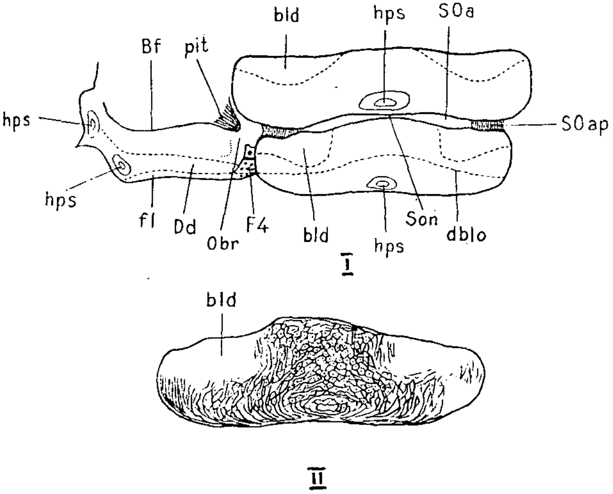


FIG. 41.—*Centropleura phoenix*, structure and ornament of posterior part of cephalon. I. Posteroglabella with its macropleura (posterior fixed cheek); II. Ornament of occipital lobe (LO), from Pl. 5, fig. D. bld—bald spots; Bf—marginal furrow; dblo—inner edge of occipital doublure; Gd—opisthopleural vein; F4—occipital section of axial furrow; fl—flange; hps—hapsidium; obr—occipital bridge; pit—lateral pit; occipital furrow: SOap—appendifer. SOa—lateral widening (almond shaped); SOn—transcurrent part (narrow).

The pleural lobes of the cranidium: The pleural lobes of the cranidium (Text-fig. 37) contain (1) the anterior limb with its two anterolateral limbs and (2) the fixed cheeks, separated from the anterior limb by the preocular sutural crenae. These parts are discussed separately. Of course, the free cheeks are included in the pleural lobe of the cephalon. The pleural lobes of the cephalon include all parts of the test outside the axial furrows and the preglabellar furrow. The anterior limb, including its doublure and rostral shield, is also made up from pleural elements, as inferred by Öpik (1958b, 1961), and includes no mesotergite.

The anterior limb: The anterior limb consists of the moderately convex border defined by the well-marked marginal furrow. There is no brim in front of the glabella, which is almost in touch with the border. Laterally a pair of triangular narrow areas are seen separated from the glabella by the preglabellar furrow. These areas are brim, and, together with the portions of the border adjacent to them, are also parts of the anterolateral limbs. In *Centropleura phoenix, C. loveni, C. angelini,* and *C. angustata* the border, the brim, and the marginal furrows are distinct. In *Centropleura belli* (Text-fig. 36) and *C. vermontensis,* however, the border and the brim seem to be more or less confluent.

The ornament of the anterior limb consists of fine raised lines parallel to the margin (Pl. 5, fig. E). They differ by their fineness from the coarse lines of the other parts of the test. At the outer ends of the anterolateral limbs these lines have an oblique course, backward and outward from the margin, as seen in Plate 4, figure 3a. In one specimen (Pl. 7, fig. 3) two or three coarser lines are seen on the border in front of the glabella.

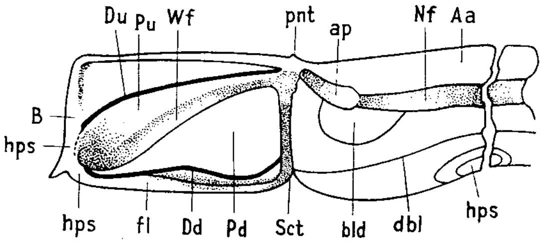


FIG. 42.—*Centropleura phoenix,* **anterior segment, Pl. 4, fig. 1. Aa—articulating half-ring; ap—appendifer; B—border with doublure; bld—bald spot; dbl—edge of axial doublure (articulating doublure); Dd—opisthopleural vein; Du—propleural vein; fl—flange; hps—hapsidia (on pleura only centres indicated); Nf—articulating furrow; Pd—opisthopleuron (with triangular cushion); Pn—propleuron; put—articulating process; Sct—articulating socket; wf—pleural furrow.**

The fixed cheeks: The term 'fixed cheek' has a variable meaning, depending on the character of the material that is in need of description. Thus, in sutureless trilobites the fixed and the free cheeks cannot be separated; and there is no clear division between posterolateral limbs (where present) and the fixed cheeks or interocular cheeks. For the present purpose (of description of *Centropleura*) the fixed cheek is the area behind the crena, comprising the ocular and postocular portion of the pleural lobe of the cranidium, including the palpebral lobes and the posterior border. It is homologous with that part of the cephalic pleural lobe posterior to the ocular ridge, where a ridge is present, or its position can be inferred.

The fixed cheek of *Centropleura* (Text-fig. 37; Pl. 3, fig. 1; Pl. 4, fig. 3a; Pl. 6, fig. A) includes the following features: the palpebral lobe and the palpebral furrow, the interocular area with the genal bar, the marginal furrow, the border with the intergenal spine and the opisthopleural vein, and the lateral pit.

The fixed cheeks are almost flat and horizontal, as seen in Plate 7, figure 1b, 1c: they are as flat and horizontal as the pleural lobes of the thorax. The general shape is that of a square sector of an ellipse, but distorted, of course, by the particular structure of its border. It is widest at the posterior end of the suture, where the ratio of length to width is about 5/3. The palpebral lobe is a narrow flat band, separated by a shallow furrow. The interocular area shows an almost straight genal bar parallel to the axial furrow. The surface of the interocular area is covered by scattered pinpoint tubercles (Pl. 5, fig. E; Pl. 6, fig. A). The marginal furrows are broad, widen even more at their adaxial ends, and follow the curvature of the posterior margin. The posterior border is convex and shows a median crest interpreted as the opisthopleural vein. The crest of the border (the vein) makes a rectangular bend forward and passes into the occipital bridge.

The posterior margin of the cranidium has a narrow flange similar to the flanges of the pleurae of the thorax. The adaxial end of the flange is in touch with the occipital lobe (Pl. 6, fig. A), and at their junction is seen the small axial pit to accommodate the axial articulating process of the first segment of the thorax. The abaxial end of the flange fades out at the posterolateral angle. The posterolateral angle is rounded and slightly swollen. From this point the border 'advances', turns forward and sidewise, and continues as a straight line to the base of the genal spine. Half-way between the posterolateral angle and the posterior end of the suture the intergenal spine is situated. As seen in Plate 4, figure 3a, the spine is undercut at its posterior base, indicating, perhaps, an incomplete hooked or advanced falcate pleural tip. Small triangular posterolateral limbs are only slightly indicated: each is defined by an imaginary line between the posterior end of the eye and the posterolateral angle, and by the advanced border and the posterior branch of the suture. They would deserve no special description were it not for the statement that posterolateral limbs are undeveloped or almost missing in *Centropleura.*

The lateral pits are a pair of deep depressions outside the axial furrows, but on the inner surface the pits are a pair of bosses. Details of the structure of the boss are seen in Plate 6, figure B. The boss has a distinct parietal summit from which strong lines radiate along the crests (=furrows) that meet at the boss (pit). The whole structure should be interpreted as a fortified spot to which strong muscles were attached.

The posterior half of the fixed cheek is ornamented by irregular netting and by raised lines (Pl. 2, fig. C; Pl. 4, fig. 2; Pl. 6, fig. A), which are arranged on the border obliquely to roughly parallel to the margin.

The genal bar: The genal bar is a feature known only in *Centropleura* and its allies. It is a linear, low narrow longitudinal ridge on the fixed cheek between the anterior end of the palpebral lobe and the posterior marginal furrow just outside the lateral pit (Text-figure 37; Pl. 3, fig. 1; Pl. 6, fig. A; Pl. 7, fig. 2). The function of the bar is unknown; but, beside other possibilities, it served to add some extra rigidity to the thin test of the flat cheeks. In *C. phoenix* the bars are straight or almost so, in *C. angelini* they are curved, and in *C. sonax* (Pl. 9, fig. 1) the bars are connected with the convex posterior border.

At the intergenal spine and at the posterolateral corner (Pl. 4, fig. 2, and Text-fig. 41) a hapsidium is seen, similar to the two pleural hapsidia, one above the pleural tip, and the other at the posterolateral corner of the pleura (Pl. 3, fig. 6). A hapsidium is a concentric cluster of closed ornamental or terraced lines, or loops of lines. Pleural hapsidia occur near pleural tips, and axial hapsidia on the mesotergites (Text-figs. 41, 42).

The glabella: The following description refers to the conventional division of the cephalic axial lobe into the glabella and the occipital lobe to facilitate comparison with other trilobites. It is unfortunate that all available cranidia are more or less damaged and permit no accurate description of the convexity. The best preserved specimen for this purpose (Pl. 7, figs. 1-1e) has a median fracture and is depressed in the middle. The glabella is pyriform, with the greatest width across the L4 lobes. It is elevated above the almost flat fixed cheeks, with the greatest convexity (Pl. 7, fig. 1b) in the middle of the frontal lobe. In the lateral view it appears that the convexity decreases rearward, that the lobes are slightly inclined in the same direction, and that the posterior border of the occipital lobe has a slightly overhanging edge.

The frontal lobe of the glabella of *C. phoenix* (Pl. 5; Pl. 7, fig. 4) has several irregular longitudinal rows of small nodes or swellings. They are interpreted as muscle attachments and are homologous to similar nodes in *Chasmops* and some other proparian trilobites (Öpik, 1937b). Similar nodes are developed on the hypostoma of *Centropleura phoenix* (Pl. 3, fig. 4 and Text-figs. 39 and 40).

The glabellar furrows and the occipital furrow: The occipital furrow and the first glabellar furrow (S1, preoccipital furrow) have a similar structure. Both are transcurrent and have depressed outer ends—corresponding to the appendiferi. The connexion between the outer depressions is a pair of elongate amygdaloidal and depressed, smooth areas which are connected in the middle by a narrow furrow. This structure of the occipital furrow is best seen in Plate 5, figure D. In the preoccipital furrow this structure is less clearly developed (Pl. 2, fig. A) because the outer depressions are more or less confluent with the almond-shaped floor of the furrow.

The three pairs of the anterior glabellar furrows are disconnected in the middle. The S2 are slightly curved and fade out at their outer ends before reaching the dorsal furrows. The S3 furrows are more curved than S2, and do not reach the dorsal furrows. They are almost in the middle of the anteroglabella. In one specimen (Pl. 5) the left S3 furrow is bifurcate. The S4 (the anterior glabellar furrows) are slightly curved or almost straight, as seen in Plate 5, figure E. They join the dorsal furrows at the crenae and are directed rearward and inward. This particular direction of the anterior glabellar furrows is a distinctive character of *Centropleura.*

The occipital lobe: The occipital lobe (LO, Text-fig. 37) is of the same shape and size as the axial lobe of the first segment of the thorax. One specimen (Pl. 4, fig. 3b) has a tiny node near the anterior border of the occipital lobe. The occipital lobe is definitely narrower (transversely) than the preoccipital lobe as seen in the figured specimens.

The glabellar lobes: The preoccipital lobe (L1) is relatively large and swollen at its outer ends. The L2 lobes have slightly forward-turned outer ends, whereas the L3 lobes turn their ends rearward. The lobes L3 and L4 are confluent at their flanks and seem to be a single pair of lobes, each split in the middle by the S3 furrows. The L4 lobes are almost triangular and relatively small. The frontal lobe is large, evenly rounded in front, is convex, and higher than the L4 lobes; it slopes steeply down at the front.

Some taxonomic significance may be attributed to the evenly rounded front of the glabella, and to the large size of the preoccipital lobe as compared with the occipital. The preoccipital lobe overhangs abaxially the ends of the occipital lobe.

The axial ornament of the cephalon: The ornament of the anteroglabella is seen in Plate 7, figures 4, 5. It consists of an irregular fine network of raised lines. In the centre of each mesh a tiny pit is present. Rearward this ornament gains in strength, but its arrangement remains the same.

The occipital and the preoccipital lobes both have the same ornament, which differs in several aspects from the ornament of the anteroglabella, but coincides with the ornament of the axial rings of the anterior part of the thorax (Text-fig. 41; Pl. 5, fig. D; Pl. 6, fig. C). On these lobes the raised lines are arranged concentrically around the axial hapsidia with centres near the posterior border. The meshes in the frontal part of the lobes are angular and bear tiny pits in their centres. Each lobe has a pair of bald spots near the anterolateral corners. These spots are almost smooth, with faint traces of ornamental lines visible only in exceptionally well preserved material.

The free cheeks (Pl. 3, figs. 2, 3; Pl. 2; Text-fig. 37): The structure of the free cheek of *Centropleura phoenix* is characteristic for the genus. A similar structure is present in all other known species, as indicated by the course of the facial sutures. Variations of specific and subgeneric significance are seen in the shape of the crenal tongue, which is triangular in *Clarella* and *Anopolenus*, and also in the degree of the advancement of the genal spine.

The free cheek is narrow, a quarter of the width of the glabella. Most of the surface of the cheek consists of the border and the genal spine. The anterior part of the ocular platform is a narrow piece—the crenal tongue. The genal spines are curved, divergent, and as long as the thorax; but because of their advanced position their tips reach only the level of the thirteenth segment. The ornament consists of raised lines running on the border parallel to its edge. On the spine, on both its dorsal and ventral side, the lines run diagonally; the spine has also a depressed narrow flange on its outer margin on which the lines turn abruptly backward and outward, producing a chevron pattern.

The specimen Plate 3, figure 3, shows an elevated ridge along the base of the eye. The upper edge of this ridge carried the very low visual surface of the eye. The doublure is wide (Pl. 2), reaching almost to the base of the eye, and its outer border is covered with terraced lines.

The hypostoma and the rostral shield (Pl. 2; Pl. 3, fig. 4; Text-figs. 38, 39, 40): A completely preserved hypostoma has not been found as yet, owing, perhaps, to the thin test, easily broken even during moulting; nor is a specimen available that exposes the outer surface of the hypostoma. The outer surface is rough, with concentric lines, and adheres firmly to the matrix, whereas the inner surface is smooth and opens up easily.

The ornamental lines on the hypostoma are arranged concentrically around a median point (a hapsidium) situated about one-third of the length of the hypostoma from its anterior border. The lines are, perhaps, weaker than in the Swedish forms as illustrated by Westergaard (1950, pl. 2, figs. 2 and 3). The lines of *C. phoenix* are seen in Plate 2, figure C, but are very weak indeed.

Similar lineate hypostomal ornaments are common in a number of unrelated trilobites from Cambrian to Devonian and cannot therefore serve as an indication of a close relationship of forms in which they are developed. For instance, a similar lineate ornament is present in *Paradoxides*, but it cannot be taken as a proof that *Centropleura* and *Paradoxides* are close relations.

It is a functional ornament, a 'prosopon' in the sense of Gill (1949), which served to strengthen the test of the hypostoma without making it too thick. The recurrence of the ornament is the indication of its mechanical value.

The hypostoma of *Centropleura* is almost square; its anterior border is strongly curved, the flanks are sub-parallel, slightly cuspate, and with a pair of small prominences in the middle. The anterior wings are short. The posterior, free wings are separated by a shallow sinus. At the tips of each free wing a small pit (Text-fig. 40) indicates an inward-directed node. There is a narrow 'lip', a crescentic depression in the deepest part of the hypostomal sinus. Most of the hypostoma consists of the strongly convex central body. Maculae are absent, but a pair of clusters consisting of rounded nodes (muscle spots) is seen on the posterior slope of the hypostoma.

No characters of a specific significance are seen in the hypostoma of *Centropleura phoenix*, when compared with the Swedish material illustrated by Westergaard.

The rostral shield is seen in specimen Plate 2, figures B and C, and Text-figures 38 and 40. It is a short piece cut out of the doublure by the rostral and the pair of connective sutures, and is of a similar relative size, as in some species of *Paradoxides* and in *Redlichia* (Öpik, 1958b), and ornamented by terraced lines. The rostral shield and the hypostoma are fused into a hypostomal unit.

The position of the hypostoma is seen in the reconstruction, Text-figure 40. Most of its frontal border is fused with the rostral shield; the tips of the anterior wings are braced against the dorsal furrow at the anterior ends of the palpebral lobes. The frontal lobe of the glabella and the hypostoma are provided with clusters of similar nodes, which may have been the ligament insertions of muscles controlling the activity of the proventriculum. This is a well-known interpretation by R. Richter.

The hypostomata of *Centropleura* and *Paradoxides* are superficially similar in the sense that both are wide and convex shields of contemporaneous Middle

Cambrian trilobites. In detail they are, however, so different (Text-fig. 39) that only a remote relationship can be assumed. The main difference is seen in the fact that the central body in the hypostoma of *Centropleura* extends almost to the posterior border and has the clusters of nodes, whereas in *Paradoxides* this body is short and without the clusters; but there is a special crescentic lobe in the hypostoma that bears the maculae not seen in *Centropleura.*

The Thorax

The thorax of *Centropleura phoenix* has sixteen segments, a number that was also given by Angelin to his *C. loveni.* The thorax of *C. phoenix* is divided into two parts, an anterior part of thirteen segments with short pleurae, and a posterior one of three segments that are macropleural or hypertrophic. A similar structure was already known in *Anopolenus salteri* (Hicks, 1865; 1872); Lake (1934) regarded it as almost an impossibility. He assumed that the pleural terminations of the anterior segments 'are buried in the matrix, and, because the change of level is sudden, the pleurae usually appear to be abruptly truncate'. Hutchinson (1952, p. 280) applies the same reasoning to *C. belli,* although in his specimen the posterior hypertrophic pleurae are not preserved.

That the shortness of the anterior pleurae in a *Centropleura* is not accidental 'truncation' but a real structure was already indicated by Westergaard's (1950) description of *C. angustata.* The same structure is seen in the specimens Plate 2 and Plate 3, fig. 1, of *Centropleura phoenix.* The two specimens of *Centropleura impar* (Lake, 1934, pl. 25, figs. 1 and 2) are insufficiently preserved and allow no definite interpretation. But when *Anopolenus salteri* is compared now with the specimens of *C. phoenix* one should conclude that Hicks interpreted the two kinds of pleurae in the thorax correctly. The shape of the thorax, and even more so of the whole exoskeleton, is hourglass. The thorax of *C. phoenix* narrows slightly toward the middle, and from here it gradually expands toward the rear, whereas the axial lobe tapers consistently. Hence, the expansion is effected by an increase in transverse length of pleurae that is greater than the gradual tapering of the axial lobe. The anterior pleurae are truncated and have short advanced spines, which, beginning with the third segment, shift to the posterior corners; from here the pleurae become gradually truncato-falcate (thirteenth segment). The posterior three segments have developed long and falcate pleural terminations and are discussed separately below, as are particulars of the structure of the anterior segment.

The pleural lobes are flat, horizontal, and not geniculate. The axial lobe is convex, but the convexity cannot be measured because of deformation. It can be described as moderate to strong. The axis tapers only slightly within the first thirteen segments; from the fourteenth segment it tapers more abruptly and peters out in the pygidium without forming a clear terminus.

The axial furrows are distinct, deep, and relatively wide. The test in the furrows is smooth. The articulating half-rings are narrow, less than a third of a segment (longitudinally) and convex, allowing for a considerable amplitude of movement. The appendiferi (Text-fig. 42) are elongate shallow depressions without a marked prominence on the ventral side of the test.

Articulation: The segments of the thorax are linked together along the axial furrows by the common axial point-and-socket device, with axial processes in front of the segment fitting in the corresponding sockets on the next segment. The pleurae have narrow depressed flanges and fit flange to flange together. In at least ten anterior segments no fulcral joints are present and thus the articulation is based only on the two-point hinges of the axial joints.

The thirteenth segment (Pl. 7, fig. 6) shows small fulcral processes at the anterolateral corners of the pleurae. It is fair to conclude that in the posterior falcate segments (eleventh to thirteenth) fulcral point-and-sockets, and consequently four-point hinges, were present.

Comparison: The anterior part of the thorax is known in *C. angustata* Westergaard, *C. oriens* Tschernyscheva, and *C. belli* Hutchinson. It was indicated above that *C. angustata* and *C. oriens* are perhaps synonyms. In both these species the pleurae are shorter (transversely) than in *phoenix*. Moreover a difference is indicated by the prominent swellings of the opisthopleura of *C. angustata*. These swellings are low in *phoenix*. The hourglass shape is more distinct in *C. oriens* than in any other species, including *phoenix*. *C. belli* (Text-fig. 36) has a wider thorax than *C. phoenix*, and the pleural spines of *belli* are much stronger. The following figures, showing the proportion of the width of the thorax to the width of the axial lobe, indicate for *C. phoenix* a position intermediate between *angustata* and *belli*.

	oriens	*angustata*	*phoenix*	*belli*
First segment	2.0	2.3	2.5	2.7
Sixth segment	2.0	2.0	2.5	2.6

It is mentioned above that one of the Swedish species (*loveni* or *angelini*) has falcate anterior pleurae. Using figures given by Westergaard (1950, p. 5), its ratio should be for the fourth segment 3.3, indicating a quite different species.

The anterior segments: Details of the structure of the anterior segments are seen in Plate 3, figure 6, Plate 4, figure 1, and Text-figure 42. The specimen Plate 3 shows the surface of the test and in the specimen Plate 4 the internal surface is seen.

The structure of the axial lobe is seen in Text-figure 42. The articulating furrow is broad and deep and on each of its abaxial ends an elongate and shallow depression marks the appendiferi. The axial furrow is deep and is confluent with depressions of the flanges and with the pleural furrow.

The articulating half-ring is well elevated and convex; the extent of the articulating doublure on the rear of the axial lobe cannot be exposed. It is an extremely thin lamella, perhaps less than 0.05 mm. thick.

The pleura is almost rectangular and slightly less than half a square. It is bordered by narrow and depressed flanges; the outer margin has a narrow doublure, which is about 0.5-0.7 mm. wide in Plate 3, figure 6. A short slightly advanced terminal spine is seen just opposite the end of the pleural furrow. The pleural furrow cuts the pleura diagonally in two subequal parts, a propleuron and an opisthopleuron (Öpik, 1961). The furrow has a slight curvature and its abaxial end is hooked, as seen in Plate 4, figure 1, and Text-figure 42. The anterior slope of the furrow is steep, the posterior one is gentle.

The surface of the pleura is covered by raised lines. On the opisthopleuron the lines are vertical at the posterior flange, and turn in a curve toward the pleural furrow. Having crossed the furrow, they resume on the propleuron the general sagittal trend. On the outer border two hapsidia are present, one just above the spine and the other on the posterolateral corner of the pleura (Pl. 3, fig. 6). Hapsidia are arranged exactly the same on the posterolateral limbs (Pl. 4, fig. 2).

The internal surface of the pleura (Pl. 4,. fig. 1, and Text-fig. 42) shows two veins, one on the opisthopleuron and the other on the propleuron. According to Öpik (1961) these veins are imprints of intestinal appendages (diverticula).

The pleura with its two veins and ornamental lines has some superficial resemblance to an insect wing.

The thirteenth segment, the last of the 'anterior segments', is seen in Plate 7, figure 6. The pleural termination is here already falcate and the elliptical clusters of veins on its outer margin are missing. A fulcral process is visible on its anterolateral corner.

On all the thirteen anterior pleurae the opisthopleuron bears a triangular cushion or swelling. This feature was first described by Westergaard (1950) in *Centropleura angustata.* In *angustata* it is short and very prominent, in *phoenix* it is longer and less high. It seems that the character of this opisthopleural cushion is a specific distinction between the two species of *Centropleura.*

The axial lobes of each segment are covered by raised lines that are arranged generally parallel to the anterior margin. In the anterior segments a concentric arrangement of the lines is present around a central point, a hapsidium, on the posterior margin, as it is seen also on the occipital ring (Text-figs. 41 and 42); and also a pair of extended anterolateral bald spots is present. No definite hapsidia are observable in the posterior segments.

The three posterior segments: The three posterior segments (numbers fourteen, fifteen, and sixteen) are partly preserved in Plate 2, but complete in Plate 7, figure 6; in the specimens Plate 8, figures 1, 2 and 4, fragments of the fifteenth and sixteenth segments are preserved in situ. The specimen Plate 3, figure 5, shows the ventral side of pleura number fourteen. Each of the three segments has its own shape and size, but they possess also a number of common features not seen in the anterior pleurae. These features are: (1) the large, hypertrophic size; (2) the curved commissures between the segments; (3) the wide doublure; and (4) the thickness of the space between the doublure and the dorsal test.

The fourteenth segment is the largest, with its free pleural ends extending beyond the rear of the trilobite. The anterior commissure of this segment is straight and was consequently a normal hinge-line. The posterior commissure is curved, and prevented any articulation. The shape of the free pleura is that of a slightly curved double-edged blade. The free edges are narrow depressed flanges. The ornamental lines on the ventral side are directed upward, but on the external outer face (Pl. 7, fig. 6) they are arranged in a chevron pattern similar to that of the free cheek (Pl. 3, fig. 2). The inflated space between the doublure and dorsal test is seen in Plate 3, figure 5. By its shape and large size this fourteenth segment differs completely from any other segment and it is assumed to be genuinely macropleural.

The two last segments are of a similar shape, but the fifteenth is slightly larger than the sixteenth (the last). The pleural spines are extenuated and falcate. The commissures are all curved, and are provided with the lateral fulcral flanges and the point-and-socket devices already described. The shape of the two posterior pairs of pleurae is the same as the shape of the anterior pleurae of the pygidium (Text-fig. 43). Hence, a pygidial similarity, as distinct from the occipital similarity of the foremost segments of the thorax, is indicated.

The extent of the doublure is seen in Plate 7, figure 6. The inner edge of the doublure is marked by the ends of the pleural furrows. The doublure narrows rapidly forwards, and in the thirteenth segment is reduced to the pleural tips.

The Pygidium

The pygidium of *Centropleura phoenix* is a transversely elliptical shield with the ratio of length/width variable between 0.55-0.6. The axis tapers posteriorly, and consists of two to three annulations and a vestige of a terminus, the end of which reaches the middle of the pygidium. The axial and the dorsal furrows are shallow. A shallow notch is present in the rear of the anterior annulation. Two pairs of pleurae are indicated by pleural furrows and vestigial pleural grooves. The posterior margin bears two pairs of backward and adaxially directed spines; a third pair of tiny spines may be present also. The lateral margins are straight depressed flanges with a fulcral process each, and the anterior margin is an evenly curved commissure line with a narrow flange. The posterior border between the ends of the flanges is the 'free margin'; the flanges themselves and the anterior margin constitute the intersegmental commissure. The pleural platform is almost flat, with a slight convexity in its posterior portion and a depressed broad border along the free margin. The doublure is wide, with a curved anterior edge running from the anterior ends of the lateral flanges towards the end of the axis. The doublure is covered with slightly irregular terraced lines parallel to the free margin. The pygidium (including the articulating half-ring) is as long as three segments of the thorax, or slightly less than half of the length of the cephalon, and half as wide as the cranidium: it is a large pygidium for a Cambrian trilobite.

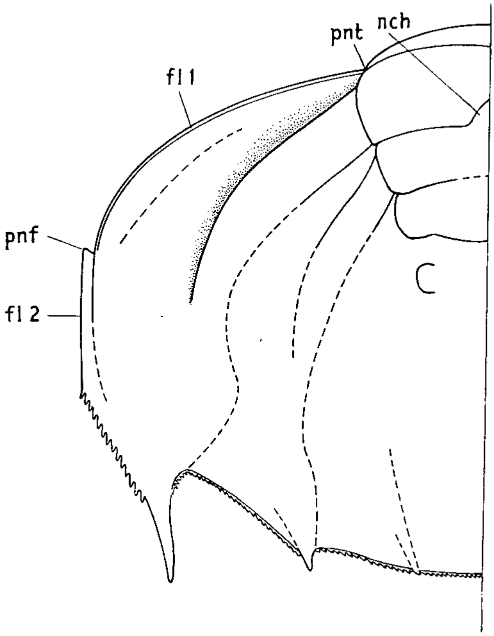


FIG. 43.—*Centropleura phoenix*, **pygidium, Pl. 8, fig. 3b. fl1—flange of intersegmental commissure; fl2—flange, lateral; nch—notch on axial ring; pnf—fulcral process; pnt—articulating process (visible in Pl. 8, figs. 2a, 2b).**

The ornament (Pl. 8) consists of irregular raised lines on the middle part of the axis and on the peripheral parts of the pleural platform, with an indistinct network in the space in between. The free margin is minutely denticulate.

Only *C. loveni* and *C. oriens* Tschernyscheva have pygidia of the same transversely elliptical shape as is seen in *C. phoenix*. *C. oriens* has four annulations and a terminus in the pygidial axis (*phoenix* has two or three), and well defined furrows on the pleural platform, and is, therefore, distinct. *C. loveni*, as seen in Westergaard (1950, pl. 1, fig. 4) has also deep furrows, no notch on the first axial ring, weak ornamental lines, and proportions different from the pygidium of *C. phoenix*. The length/width ratio in *C. loveni* is 0.48, whereas in *phoenix* it is 0.55-0.6. The length is measured between the upper end of the axial furrow and the inner base of the inside (second) spine, and the width between the posterior ends of the lateral flanges. A comparison of the ornament, however, remains inconclusive. Westergaard's illustration shows no ornament, but he mentions that it is 'more pronounced on the pygidium' than on the cranidium of *C. loveni*, which is 'smooth to the naked eye but under a lens it sometimes displays a faint network'. The pygidial axes of *phoenix* and *loveni* have the same number of annulations.

Variations: The number of axial annulations of the pygidium is not constant. The specimen Plate 8, figure 1, has two annulations; the specimen Plate 8, figure 4, has a third annulation indicated; the specimens Plate 7, figure 6, and Plate 14, figure 6, have three annulations, but the third is not sharply defined in the rear. The specimen Plate 8, figure 3, has three well defined annulations. And the largest available pygidium (Pl. 8, fig. 2) has three annulations and two more vestigial segments indicated by pairs of low swellings. The number of annulations does not correlate with the length/width ratio. The third (innermost pair) of spines is present in small specimens and absent in the largest. The external ornament shows no variation.

Ornamentation: The ornament is similar to that of the two posterior segments of the cephalon and the thorax. It consists of raised wavy lines on the peripheral part of the pygidium and the median part of the axis. The lines are arranged transversely, more or less parallel to the posterior margin. On the inner part of the pleural platform the lines are very weak and form an indistinct network. Every mesh has a faint knob in its centre.

Marginal denticulation: The free margin of the pygidium is minutely denticulate or serrate, as partly seen in Plate 8, figure 36, and indicated in Text-figure 43. Two sizes of denticulations are apparent. The flanks behind the flanges have coarser denticles, whereas on the margin between the spines the serration is minute. They sit here on a depressed, very narrow border of the test that is seldom exposed to observation. A similar but more prominent denticulation occurs on the pygidia of all species of the Australian lower Middle Cambrian genus *Xystridura.*

The pygidial unit: The pygidial unit consists of the pygidium and the three posterior segments linked together along curved commissures. Curves have replaced straight hinge-lines, without which articulation between the tergites is impossible. The difference in mechanics of straight hinge-lines and curved commissures is apparent from a comparison of the normal segment (Text-fig. 42), with the pygidia (Text-figs. 43 and 44).

The commissures between the three posterior segments are of the same structure as the commissure between the last segment and the pygidium, and it suffices to discuss only the latter.

The commissure line of the pygidium (Text-fig. 43) consists of a pair of curved anterior edges with flanges, on each side of the axis, with the ball-and-socket device at the ends of the axial furrows, as seen in Plate 8, figures 2a and 2b. The fl 1 flanges pass rearward into the lateral flanges (fl 2), which have also fulcral processes (pnf), indicating a second ball-and-socket device. Thus, there are two potential hinge-lines, one with the pnt points, the other with pnf points; these two parallel transverse lines are, however, far apart, the four ball-and-socket points are on a single plane, articulation is eliminated, and the tergites together form a firm and rigid unit.

The commisures, however, remained open without any trace of anchylosis or fusion of the tergites. Still, some interlocking occurs along the commissures, and thus the pygidial unit may have been also a moulting unit shed off as a whole. After moulting it could easily distintegrate into its components. During life the pygidial unit was a rigid mechanical structure, a single piece articulated as a whole along the hinge of the commissure between the thirteenth and fourteenth segments. The unit is part thorax and part pygidium. The hypothesis of caudalization is applicable to the pygidium itself, but it is doubtful whether it is applicable to the pygidial unit of *Centropleura*. Still, it may be assumed that the ontogenetically youngest, hindmost segments of the thorax were not completely separated from the pygidium and that the non-articulated commissures were developed only to facilitate the moulting. If so, the pygidial unit may be regarded as an example of unfinished caudalization.

The structure of the thorax and pygidium of Centropleura *compared with those of olenellids*: The thorax of *Centropleura* consists of three or even of four kinds of segments. The first 10-11 segments have reduced tips and even the fulcra are missing; segments 11-13 are fully developed, with falcate pleurae; the fourteenth is a macropleural segment. Behind it follow two hypertrophic segments and a large, fused pygidium. It is important to note that the anterior segments are shortened (reduced) in *Centropleura*. In *Olenellus* all the anterior 13-14 segments are unreduced, with well developed pleural tips and doublure. The fourteenth or fifteenth segment is macropleural, with a dorsal spine. Behind it the segments are reduced, the pleurae become gradually free and the fulcral joint is missing, and no caudalization is apparent. Thus, pleurae of both *Centropleura* and *Olenellus* are reduced; but the reduction is totally different: it shows in anterior pleurae in *Centropleura*, but posterior ones in *Olenellus*.

The occipital similarity in Centropleura phoenix

Under the heading 'the axial lobe of the cephalon' the similarity between the axial lobes of the anterior segments of the thorax and the posteroglabella was summarized as an example of occipital similarity. This similarity in *Centropleura* is also present as a homology of the posterior part of the pleural lobe of the cranidium and pleurae of the thorax (Pl. 4, fig. 2, and Pl. 3, fig. 6). Thus, the intergenal spine is homologous with the advanced pleural spine of an anterior segment of the thorax; at the posterolateral angle of the pleura, and of the cranidium, and in front of the pleural spine and of the intergenal spine, similar hapsidia are present, and the outer free edge of the pleura and the posterolateral free edge of the cranidium are of the same shape. The marginal furrow of the cranidium is the modified pleural furrow, its posterior border is the opisthopleuron with its diverticular vein. It seems that in the cranidium the pleura of the occipital segment has preserved its free edge and its opisthopleuron with its diverticular vein almost unchanged. But the occipital bridge and the lateral pit, both missing in the thorax, are cephalic modifications of the pleura. It is also significant that the occipital pleura underwent the same reduction as the anterior pleurae of the thorax, because both are deprived of the originally falcate or advanced-falcate tips with a wide doublure. The diagram, Text-figure 41, indicates also that the two posteroglabella mesotergites have a single pair of pleurae in common, a combination which is also possible in the thorax of trilobites.

The occipital similarity decreases forwards, and little of it is seen in the anteroglabella. It is assumed that the occipital similarity and its decrease reflect the gradual incorporation of the preoccipital segment and the occipital segment into the pre-existing cephalon of the ancestral arthropod.

Raw (1953, p. 87) attributes the likeness of the occipital segment and the segments of the thorax 'to the muscular connexion and movement between the two'. But this argument is applicable neither to the similarity of the occipital and preoccipital lobes that are not articulate, nor to the homology of the ornamental hapsidia, which have nothing in common with the muscles and articulation. Some more arguments against Raw's interpretation are given by Öpik (1958b).

The distribution of the hapsidia deserves a special comment. They occur on the axial lobes in a position where in many trilobites axial spines are present. On the pleurae hapsidia are placed above and below a spine. But in the same position on fully developed falcate pleurae (Pl. 7, fig. 4) only a chevron pattern of lines, but no hapsidia, is developed. One may conclude therefore that the hapsidia indicate positions of potential spines. But it is even more likely that they indicate the positions of vanishing and already vanished spines in *Centropleura*.

Primitiveness and specialization

The problem of primitiveness and specialization in trilobites has been often discussed. For example, the absence of facial sutures in olenellids is regarded by one school of palaeontologists as a primitive and fundamental character, whereas another school of thought maintains that it is a specialization, that olenellids have lost these sutures and cannot therefore be regarded as ancestral to trilobites provided with facial sutures. The facial or ocular lines of olenellids are regarded by the first school as sutures *in statu nascendi,* whereas the second school would regard them as non-functional vestiges of vanished sutures (see Hupé, 1952, p. 275).

This second school is now generally accepted (Harrington, 1959). It is, indeed, most probable that after the sutures became non-functional their vestiges disappeared gradually; but it is rather improbable that 'lines' appeared first, then were developed gradually, and finally started to perform their function in moulting.

Primitiveness and specialization have no absolute meaning. These terms refer to an evaluation of the general morphology of a species or of some of its particular characters in relation to its probable ancestors and progeny, and to the environment. The terms 'primitiveness', 'primitive', as applied to a species refer to an assumed potential capability to produce a chain of new species which are able to specialize, to adapt themselves to a variety of environments. In this sense 'primitive', 'ancestral', and 'progressive' are related terms. The term 'primitive' may describe also a single character or a particular set of characters less variable than the rest. Once established, such characters may appear as 'primordial' and 'simple' and therefore conservative and stable. Such characters, however, may be, in effect, early specializations.

Specialization in general means the development or loss of characters that is assumed to result in a restricted adaptivity of the species, fixing it and its descendants to a particular environment. Specialization may also imply that the species is less likely to be ancestral to a chain of new species. However, successful specializations may persist and contribute to the longevity of the phylogenetic lineage.

The degree of primitiveness and specialization of *Centropleura* should be evaluated in relation to Lower Cambrian and Middle Cambrian trilobites, but no immediate—or remote—ancestors of the Centropleurinae have been discovered as yet. Hupé (1952, p. 270) suggests that *Centropleura* doubtless arose quite abruptly from a *Paradoxides* of the group of *P. harlani* Green because in this species the anterior facial sutures are greatly divergent (about 70°). The same angle in *Centropleura* is about 120° (retrodivergent), but these figures, large or small, substantiate nothing. *Paradoxides harlani* is an early species (about the age of the *oelandicus* Stage) and there is a gap of about three zones between *P. harlani* and the first appearance of Centropleuridae (about the time of *Ptychagnostus punctuosus*).

Primitive characters of Centropleura

1. The presence of sutures is a primitive character antedating the appearance of olenellids. The majority of trilobites preserved the facial sutures; they were an advantage in moulting. But the deep preocular crenae are, perhaps, correlated with the large size of the eyes in *Centropleura*, and were irrelevant in moulting.

2. The intergenal spines are primitive in the sense of displaying an ancestral feature. They are not functional and their final loss is no specialization.

3. The advanced position of the genal spines is most probably ancestral, but no important function can be attributed to the position of the spines.

4. The occipital similarity is a primitive character inherited from ancestors of the trilobite class. It is a conservative character inherent in many independent lineages of trilobites. In post-Cambrian trilobites it is preserved only in the occipital segment itself, but in *Centropleura* and, for example, in *Redlichia* it is visible also in the pre-occipital lobe.

5. The multisegmented thorax is primitive, and is subject to specialization by the reduction of the number of segments.

6. The presence of a macropleural segment in the thorax (the fourteenth) is a primitive character; its preservation so far away from the cephalon may be explained by the accident of the development of the pygidial unit.

7. The large eyes are primitive in the sense of a potentiality to be reduced, or modified.

8. The redlichoid (narrow) rostral shield is a simple piece of the doublure and cut out by the sutures. It is a conservative character, when compared with the rostral shield of olenellids and *Xystridura*, which extends to the posterolateral angles of the cephalon.

The external reticulate ornament is a conservative character seen in many Lower Cambrian trilobites. Its function is purely mechanical (increase of strength of the test) and its acquisition or loss cannot be regarded as specialization.

Specialization in Centropleura

1. The hypostoma is simplified by the reduction of maculae.

2. The frontal part of the glabella is expanded and it is assumed that such a glabella developed from a tapering glabella. The expanded glabellas of *Olenellus* and of *Paradoxides* are independent acquisitions.

3. The longitudinal position of the anterior pair of glabellar furrows is an indication of a specialization of corresponding appendages.

4. The lateral pits of the cranidium may indicate strengthening of muscles controlling the occipital appendages; it may be deduced that these appendages were large, compared with the rest of the legs of the thorax.

5. The reduction of the pleural tips of the anterior segments of the thorax, the reduction of the doublure, and the loss of fulcra, are together an important specialization decreasing the effectiveness of the protective coiling. The flatness of the pleural lobes means the complete absence of the protective 'semi-ovoid form of the body' (Raw, 1953). But these modifications may have been an advantage in a pelagic environment.

6. The large fused pygidium is a specialization if compared with olenellids, *Redlichia*, and *Paradoxides*, all of which are micropygous. But caudalization is a prevalent trend in trilobites and a fused pygidium by itself is not, therefore, an exclusive centropleurid character.

7. The pygidial unit, eliminating any articulation between the three posterior tergites and the pygidium, is a unique specialization. The loss in flexibility that resulted was, most probably, compensated for by some advantage provided by the pygidial unit in the pelagic environment.

8. The axial hapsidia may indicate the positions of vanished axial spines. The loss of spines was, perhaps, an advantage, because surface friction of the tergum became reduced, and the body streamlined.

It is now possible to conclude that the ancestors of *Centropleura* were trilobites with (1) well developed facial sutures, (2) a tapering glabella and transcurrent posterior glabellar furrows, (3) large arcuate eyes, (4) a wide frontal limb, (5) a multisegmented thorax with falcate pleurae, (6) a macropleural segment (about the fourteenth), (7) axial spines on the anterior segments, (8) a small pygidium, and (9) a reticulate ornament. It is a vague deduction, recalling a trilobite with the appearance of a *Redlichia*-like form. But it is improbable that *Redlichia* or any known Lower Cambrian trilobite is the actual ancestor of *Centropleura.*

No known Upper Cambrian or younger trilobites can be regarded as descendants of *Centropleura.*

Compared with other Cambrian trilobites *Centropleura* was highly specialized and adapted to a pelagic mode of life. After the Ordovician the trilobites trend towards development and perfection of the protective ability of coiling, which was, perhaps, an advantage in the benthonic environment, because the pelagic space became a domain of nautiloids, for example.

Mode of life

Wherever *Centropleura* has been found as yet it is rare and its tests are dismembered. The only known complete specimen, even with its hypostoma almost *in situ,* is the one illustrated in Plate 2. This specimen is embedded dorsum up and this was presumably its position at the moment of death. The undisturbed embedding indicates quiet water, absence of scavengers, and almost total absence of an animal population at this place and time. In the same bed but not necessarily on the same bedding plane the specimens of *Proampyx agra,* Plate 12, figures 3 and 5, were found. One of them (fig. 3) is not an exuvia but a complete specimen subsequently slightly dismembered. Associated with these bodies scattered parts of several more specimens of *Centropleura* were found, which may have been moults or subsequently disintegrated bodies. Agnostids are rather rare at this site. Thus, it appears that locality D16 was neither a feeding ground nor a moulting station of trilobites. Consequently these individual trilobites left their habitat to die on the bottom of the sea. It is assumed, therefore, that *Centropleura phoenix* was in its adult form a pelagic animal. Palaeogeographical, environmental, and biological evidence supports this assumption.

The widespread geographical distribution of *Centropleura,* the rarity of sites, the small number of specimens found at any site, and the small number of species that are all closely related, indicate a habitat of great uniformity and global extent —the surface waters of the open sea. Littoral and benthonic modes of life, so often assumed for trilobites, are indicated by a greater diversity of local forms and local abundance of fossils, including immature specimens. No immature specimen of *Centropleura* has been collected: only the adults (of various sizes, of course) are known. One should assume that the breeding grounds of *Centropleura* are as yet unknown.

Centropleura shows no preference for a special kind of rock: it is found in limestone, shale, and sandstone, deposited in diverse benthonic environments and at various depths of water. The facies of the sediments, therefore, in which the fossils were found has not influenced their distribution. This is possible in the case of pelagic animals, the remains of which can be embedded in any sediment and at any depth of water. In exceptional cases the dying animal settled down on the floor of the sea.

The most common associates of *Centropleura* are agnostids. Several species of Middle Cambrian agnostids, some of which are described in the present paper, have a world-wide distribution that can be explained only by a pelagic mode of life. Consequently, the agnostid-*Centropleura* association may have been pelagic and universal. If this is correct the organization of *Centropleura* should indicate an adaptation to the pelagic environment — which does not mean that the trilobite could not walk on its legs on the floor of the sea and even visit the shallow grounds.

Several peculiarities in the body of *Centropleura* were most suitable for free floating and swimming, but may have been a handicap on the floor of the sea. The first is the reduction in length of the anterior thirteen pleurae and the flatness of the pleural lobes of the thorax: when coiled the flanks of the trilobite remained gaping open and unprotected. This is a disadvantage when resting on the ground, but a floating trilobite was, perhaps, in no need to protect itself by coiling because the three dimensions of the surface waters offered a better chance of escaping enemies. The second is the large size of the rigid pygidial unit. It provided a good balance for the cephalon, which was of about the same size, and both together may have been an advantage in gliding or passive floating. The third is the strength of the occipital appendages, as deduced from the combination of the usual appendiferi with the lateral pits. These legs were, perhaps, larger and more powerful than the others. They were useful in any environment, of course, but not quite suitable for walking. But a pair of excessively large legs is good for active swimming and, especially, for sudden acceleration. A floating animal could use them best. Of course, the great number of segments was suitable for motion by body waves, walking or swimming alike.

Centropleura was too small and not strong enough to be a long-distance swimmer, nor a traveller by its own power. Carried by currents, it caught its prey in short cruises and dashes.

To conclude, *Centropleura* was a pelagic hunter.

Pathology

Two pathological specimens of *Centropleura phoenix* have been found (Pl. 2 and Pl. 5). This is unusual in view of the small number of the specimens collected and the exceptional rarity of pathological specimens among trilobites. In one of the specimens (Pl. 2) a notch, subsequently healed, is seen on the left margin of the occipital lobe. In the other specimen a similar scar is seen on the left anterolateral limb. In both the specimens the wound was inflicted before the secretion of the test when the animals were unprotected by armour. The wounds were healed and seemingly were no hindrance to successful moulting afterwards.

CENTROPLEURA SONAX sp. nov.

(Pl. 9; Pl. 10, fig. 10; Text-fig. 44)

Material: The fragments were found close together in a single bed in the Roaring Siltstone at locality D 7/15.

Measurements: Cranidium, holotype (CPC 3504)—10.6 mm. long (as preserved); cranidium (CPC 3505)—3.5 mm. long (without border), 4.5 mm. wide (palpebral); pygidium (CPC 3506)—12.5 mm. long (including half-ring), 18.0 mm. wide; pygidium (CPC 3507)—7.4 mm. wide.

Selection of the holotype: The cranidium CPC 3504, Plate 9, figure 1, is selected (1) because all other species of *Centropleura* are based on cranidia, and (2) because it shows the junction of the furrows assumed to be unique.

Mode of preservation: Articulate specimens have not been found: in the absence of other species it is assumed that the two available pygidia belong to the same species as the cranidia. The rock is a friable siliceous siltstone, almost a shale. It is completely leached, and no tests are preserved.

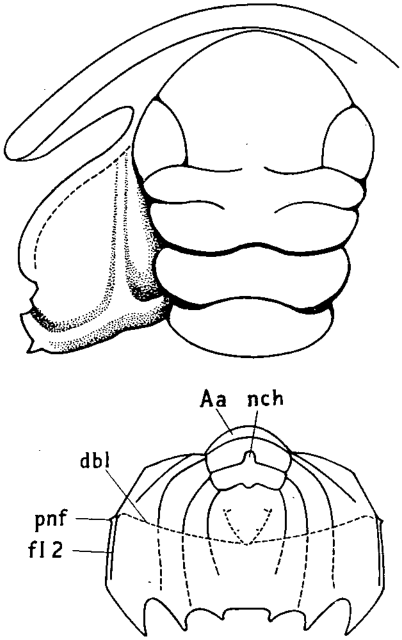


FIG. 44.—*Centropleura sonax*, cephalon, Pl. 9, fig. 1, pygidium, Pl. 9, fig. 4.Aa—articulating half ring; dbl—inner edge of doublure; fl2—flange, lateral; nch—notch on axial ring; pnf—fulcral process.

Description: The cranidium (Pl. 9, fig. 1), a fragment without test, combined with some more, otherwise undescribed, fragments, allows for the reconstruction, Text-figure 44. The palpebral lobes are 'short' in the sense that they do not reach the posterior margin of the cranidium. If the distortion is eliminated the posterior ends of the palpebral lobes should be on the middle level of the first glabellar lobe. The glabella is evenly rounded in front and does not protrude forward. The anterior glabellar furrows (the fourth pair of glabellar furrows) join the third furrows, and the anterior glabellar lobes are thus completely enclosed by furrows. All glabellar furrows join the axial furrows. The genal bars on the fixed cheeks are almost straight, well apart from the glabella, and connected with the posterior margin. The frontal border is only slightly convex and the marginal furrow is shallow but distinct, as observed on fragments. Unfortunately the posterolateral corner of the holotype is damaged, but an intergenal spine in an only slightly advanced position is indicated. The small cranidium (Pl. 9, fig. 2) has an almost flat frontal border, apparently no marginal furrow and no brim in front of the glabella, and is, consequently, quite different from the immature *Centropleura pugnax* Illing (Lake, 1934, Pl. 24, fig. 13).

From the description of the cranidium it appears that the structure of the frontal margin recalls *C. vermontensis* and *C. belli;* that the position of the intergenal spine may be compared with *C. angelini* Westergaard (1950, pl. 1, fig. 8), though the genal bar of *angelini* is curved; and that the size of the palpebral lobes is average.

The pygidium (Pl. 9, fig. 4a-4c) is bell-shaped, almost parallel-sided, and widest in the rear. Its posterior margin (disregarding the spines) is straight. The grooves and furrows on the pleurae are almost obsolete and only the anterior furrows on the pleurae are distinct, but short: it is a well fused pygidium. Three pairs of slightly upturned spines are present; the adaxial pair is quite short. The axis is conical with two annulations indicated by shallow furrows. On the terminus two more segments are indicated by vestigial depressions. The anterior axial ring has a shallow notch in the middle of its rear border. The floor of the indentation may be the rudiment of the articulating half-ring of the second segment. The doublure is very wide (longitudinally), reaching the fulcral processes and the axis, and bears regular terraced lines parallel to the posterior margin. The lateral flanges are long; the fulcral processes are small and indicated by crowding of terraced lines of the doublure.

Two species, *C. angelini* Westergaard and *C. vermontensis* Howell, have bell-shaped pygidia. The pygidium of *C. angelini* is, however, trapezoidal in outline, and has distinct furrows on the pleurae, and three distinct annulations of the axis, as seen in Westergaard (1950, pl. 1, fig. 10a). Only one very small pygidium of *Centropleura vermontensis* is known as yet (Howell, 1937, pl. 3, fig. 14; see also Howell, 1932). It has two pairs of spines, and its outline is rounded. Still, it reminds one of *C. sonax,* because 'the ribs and furrows on the pleural lobes are only weakly developed' (Howell, 1937, p. 1171). Its 'bell shape' has been confirmed by Professor B. F. Howell (personal communication).

Little is known of other parts of the trilobite. On Plate 10, figure 10a, a genal spine and two pleurae are seen. The larger pleura is the second from the pygidium. Its blade is wide, wider than in any other known *Centropleura*. As seen from scattered fragments, the pleurae of the segments of the thorax were as short or almost as short as in *C. phoenix*.

The ornament consists of raised lines and netted lines, whose arrangement cannot be established because of poor preservation.

It follows from the description above that the diagnosis of the species refers both to unique characters and to a new combination of characters already known in other species of *Centropleura*. Since the material is incomplete and fragmentary, the diagnosis is also incomplete, and is subject to amendment in the future.

Diagnosis: *Centropleura sonax* is a species of the genus in its strictest sense (that is, with the palpebral lobes not reaching the posterior margin), with the anterior glabellar furrows continued into the third glabellar furrows, a bell-shaped almost parallel-sided pygidium with three pairs of marginal spines, and pleural grooves and furrows preserved as vestiges only.

Differential diagnosis: *C. sonax* seems to be related to *Centropleura vermontensis* Howell, but *vermontensis* has a pygidium with two pairs of spines, and cranidia in which. as far as can be seen, the fourth and the third glabellar furrows remain separated. Generally, the described specimens of *C. vermontensis* allow of no definite comparison of significant details.

Possibilities of confusion: *C. sonax* cannot be confused with *C. phoenix* when cranidia or pygidia are available; but the two species occur together, and dismembered parts of the thorax, free cheeks, and hypostomata, cannot be safely referred to either.

Occurrence: *Centropleura sonax* has been found as yet only in the Roaring Siltstone, at localities D 7/15 and D19.

Age and palaeogeographic significance: The age is the Zone of *Ptychagnostus cassis*. The associated fauna indicates a correlation with the *Solenopleura brachymetopa* Zone of the Middle Cambrian of the Swedish scale. The resemblance with *C. vermontensis* should not be used for correlation with the St Albans Shale of Vermont because the species are not identical and may have a different range.

Family DORYPYGIDAE Kobayashi, 1935

Genus HOLTERIA Walcott, 1924

HOLTERIA AREPO sp. nov.

(Plate 14, figs. 5a, 5b; Text-fig. 45)

The occurrence of this species of *Holteria* has been mentioned by Öpik (1956, p. 20). It is not related to the trilobite referred to as *Holteria?* (ibid., p.

22) from the Upper Cambrian of the O'Hara Shale, which belongs to a different genus.

The genus, and its only known species, *H. problematica* (Walcott), were revised by Palmer (1954).

Only one specimen was found in the Selwyn Range — a pygidium (holotype, CPC 3546). Scattered fragments have been also observed, but are too small for interpretation. The pygidium is 4 mm. wide at its front and 2.2 mm. long.

Comparison of the pygidia of *Holteria problematica* and *H. arepo* (Text-fig. 45) reveals that they are congeneric but represent two distinct species. *Holteria arepo* has pygidial spines directed abruptly rearward, a wide axis with three annulations, and a thick convex rear border between the posterior spines. The anterior spines are short. In *H. problematica* the pygidial spines are directed rearward and outward, and it has a slender axis with four annulations. The anterior spines of *H. problematica* are long. The number of spines (two pairs), their shape, and the character of the pleural furrows and interpleural grooves, are the same in both species.

Occurrence: Locality D21, in the upper third of the Devoncourt Limestone, associated with *Leiopyge laevigata armata*. Its age is the Zone of *Holteria arepo*. It is relatively abundant at locality T87, north-western Toko Range, Northern Territory, where it occurs in association with *Hypagnostus hippalus*.

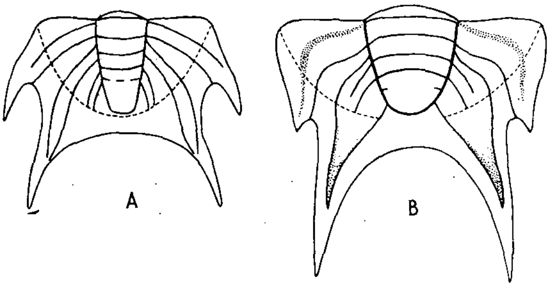


FIG. 45.—Pygidia of *Holteria*. **A—***Holteria problematica* **(Walcott); B—***Holteria arepo*, **sp. nov., Pl. 14, fig. 5b.**

Palaeogeographical and stratigraphical significance: In assessing the stratigraphical significance of the occurrence of *Holteria* in Australia, Öpik (1956, p. 20) wrote: '*Holteria* is known only from the Secret Canyon shale of the Eureka District, Nevada, U.S.A., which is placed by Howell and others (1944) in the *Deissella/Centropleura vermontensis* Zone at the top of the Middle Cambrian and correlated accurately with the *Leiopyge laevigata* Zone of Sweden'.

Palmer (1954) refers the occurrence of *Holteria problematica* to a shaly limestone in the lower part of the Hamburg limestone resting on the Secret Canyon shale. The reasons for this re-assignment are explained in Nolan, Merriam, &

Williams (1956): Secret Canyon shale grades into the Hamburg dolomite, and the revising authors selected a boundary for convenience of mapping.

Two occurrences, each with a distinct species of *Holteria,* are now known in the world. The contemporaneity of the two species results from their position in the sequence and the associated fossils rather than from their generic identity. It is, however, improbable that the time range of both species is restricted to few bedding planes only.

The palaeogeographic significance (Öpik, 1956b, p. 270) of the occurrence of two species of the same genus separated by a distance of 12,000 kilometres is obvious: the seaways were open in the Middle Cambrian at least for the immediate ancestors of these species, which probably arose not in Australia, nor in America in the highest Middle Cambrian, but somewhere else, and earlier. Lochman-Balk & Wilson (1958, p. 322), however, regard *Holteria* as a late genus, indigenous to North America. The same authors (ibid., p. 321) regard *Holteria* as a genus of their 'Intermediate Realm', confined to the 'miogeosynclinal environment'. The Australian *Holteria* is embedded in sediments of an epicontinental sea. Thus, the presence of *Holteria* provides no clues as to the tectonics of its habitat.

Family CORYNEXOCHIDAE Angelin, 1854

Subfamily ACONTHEINAE Westergaard, 1950

Genus ACONTHEUS Angelin, 1851

ACONTHEUS BURKEANUS sp. nov.

(Pl. 10, figs. 1-7; Text-fig. 46)

Material: About twenty specimens have been found at localities D 7/15, and all the better preserved ones are illustrated. The rock is a leached friable siliceous shale, a bed of the Roaring Siltstone.

Measurements (length only): Cephalon (CPC 3523)—3.2 mm.; cephalon (CPC 3525)—0.78 mm.; pygidium, holotype (CPC 3526)—2.5 mm.; pygidium (CPC 3527)—3.4 mm.

Selection of the holotype (Pl. 10, fig. 4, CPC 3526): All material available is fragmentary, but the cranidia are especially so. In conformity with the genotype, *Acontheus acutangulus* Angelin, a cranidium ought to be selected. As no doubt exists, however, in the correctness of the identification of the pygidia of *A. acutangulus* and *burkeanus,* a pygidium is selected here as the holotype of the latter.

Diagnosis: *Acontheus burkeanus* is a species with three distinct, and a fourth indistinct, axial annulations of the pygidium and with all glabellar furrows developed only as lateral indentations.

Differential diagnosis: Only one species of *Acontheus* (*A. acutangulus*) was known previously. *A. burkeanus* differs from it by the characters given in the diagnosis. In *acutangulus* the posterior glabellar furrows are transcurrent, but in *burkeanus* they are disconnected. Moreover, *acutangulus* is less angular at the anterolateral corners of the cranidium (*burkeanus* has prominent corners, as seen in Pl. 10, fig. 1), very short genal spines, and a less expanded glabellar front.

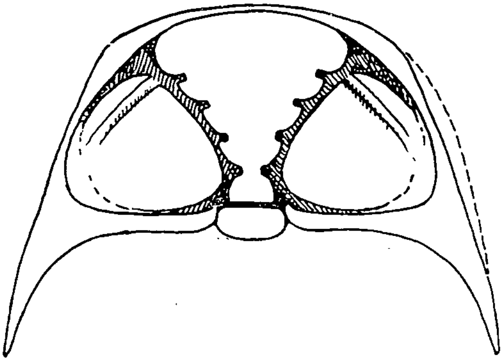


FIG. 46.—*Acontheus burkeanus* **sp. nov., reconstruction of cephalon, Pl. 10, fig. 1.**

Acontheus is a blind corynexochid, as demonstrated by Westergaard. It has no eyes, and Westergaard assumes that it has no facial sutures. The straight flanks of the cephalon of *A. burkeanus*, however, suggest that this species had narrow marginal free cheeks and straight facial sutures. This may explain also the absence of a lateral border in *A. burkeanus*. The probable free cheeks are indicated in Text-figure 46. If this reconstruction is correct the illustrated specimens are not cephala but cranidia, with a proparian structure.

Occurrence and age: *Acontheus burkeanus* is common in the Roaring Siltstone, at locality D 7/15, but has not been found elsewhere. It is contemporaneous with the genotype, *A. acutangulus* Angelin, from the Swedish Andrarum limestone, and the Zone of *Solenopleura brachymetopa.*

The age of *A. burkeanus* is the Zone of *Ptychagnostus cassis*.

Subfamily DOLICHOMETOPINAE Walcott, 1916
Genus AMPHOTON Lorenz, 1906
AMPHOTON BENSONI sp. nov.
(Pl. 11; Text-fig. 47)

Material: The illustrated seven specimens are selected from about fifteen collected fragments, all in limestone.

Measurements: Complete specimen (CPC 3516): total length 35.4 mm.; thorax 17.0 mm. long; pygidium 7.9 mm. long (without half-ring), 18.5 mm. wide. Cranidium, holotype (CPC 3517) 13.6 mm. long, 20.5 mm. wide between tips of posterolateral limbs. Pygidium (CPC 3522), length: total 9.1 mm.; articulating half-ring 0.9 mm.; of axis 6.8 mm.; width: total 18.5 mm., of axis 4.7 mm (anterior) and 3.6 mm (posterior), of border 2.3 mm.

Selection of the holotype: A complete specimen (Pl. 11, fig. 2) is available and demonstrates that all the described fragments are conspecific. This complete specimen is, however, too damaged to serve as the type. Diagnostic characters are present in the cranidium, free cheek and pygidium, but the cranidium (Pl. 11, figs. 1a, b) is selected because the holotypes of related species also are cranidia.

External habit: The complete body is oval, and widest across the eyes; the width is about two-thirds of the total length. The cephalon is almost as long as the thorax, and the pygidium is half as long. There are seven segments in the thorax. The pleural lobes are strongly geniculate, and so are the posterior margin of the cranidium and the anterior margin of the pygidium. The pleurae and the pygidium have long narrow facets beginning at the fulcra. The occipital ring and the thorax bear long axial spines, and the pleurae are extended into slightly recurved blade-like spines. The genal spines are short, slightly advanced, and deflected; the test is smooth to the unequipped eye. In its general aspect *Amphoton bensoni* is very similar to *Amphoton deois* (Walcott) as described by Kobayashi (1942); the shape, the proportions of the tagmata, and the number of segments in both species are identical. *Amphoton deois*, has, however, no genal or axial spines. *Amphoton deois* and *Amphoton bensoni* are the only species of the genus (including all its subgenera) that are known as complete specimens, one in each species. All others, numbering about ten, are known as fragments only.

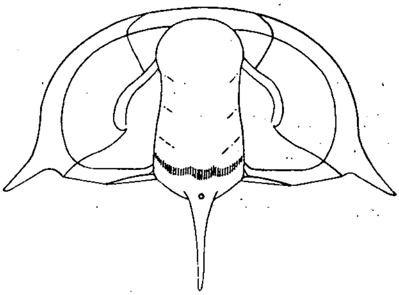


FIG. 47.—*Amphoton bensoni* sp. nov., reconstruction of cephalon from Pl. 11, fig. 1b and 3b.

The cephalon: The outline of the cephalon is seen in Text-figure 47. This reconstruction is not accurate because the free cheeks and the posterolateral limbs are shown in horizontal plan. Actually the abaxial parts of the posterolateral limbs slope down from the fulcra and the free cheeks follow that slope. The degree of the slope is, however, unknown because the specimens themselves are flattened. The shape of the cephalon is almost a half-circle, or an ellipse truncated parallel to its longer axis. The frontal border is flat, and slightly curved. No brim is present and the glabella even intrudes the rim slightly; it is a common structure among other species of *Amphoton*. The anterior sutures are straight, diverge slightly, and remain within the surface of the rim for a short distance. The anterior sutures pass into the eyes a short distance from the glabella (about a quarter to a fifth of the width of the glabella), as in *Fuchouia*, but in *Sunia* this distance is even narrower. The posterior sections of the sutures diverge greatly, are slightly sinuous or even straight, and cut the posterior margin at an acute angle close to the base of the genal spines. In other species, as far as can be ascertained, the sutures curve rearward when crossing the marginal furrow. The posterolateral limbs are large with pointed tips. Such large triangular posterolateral limbs are not seen in any other species. The posterior marginal furrows are wide and distinct. The fulcra are opposite the posterior ends of the eyes and at the adaxial third of the posterolateral limbs. The eyes are set obliquely, as in *Dolichometopus* and *Fuchouia*, and not sub-parallel as in *Amphoton deois*. The palpebral lobes are short, about three-fifths of the width of the glabella at its midlength. They are shorter than in any other related species except *Fuchouia manchuriensis* (Walcott), which, as seen in Kobayashi (1942, pl. 3, fig 7) has similar short eyes. The palpebral furrows are distinct and continue along the ocular ridges, and these ridges are the continuation of the palpebral lobes. The glabella has a rounded front and a constriction on the level of the anterior ends of the eyes. The middle of the glabella is constricted in *Amphoton*, but not in *Fuchouia*, whose dorsal furrows are subparallel, or even slightly convex abaxially.

Glabellar furrows are absent, except for three pairs of short vestiges on the sides of the glabella, visible only under chlorammonia. A slight keel is seen in the specimen shown in Plate 11, figure 4. In *Amphoton* only the posterior furrows are present; these are distinct in *Sunia*, and *Fuchouia* has up to three pairs of glabellar furrows. The occipital furrow is distinct but evenly shallow, as seen in other Dolichometopinae, including *Amphoton*. *Amphoton deois* is shown by Kobayashi (1942, pl. 3, fig. 6) erroneously without an occipital furrow, which is seen in his plate 1, figure 10. Near the posterior margin of the occipital lobe a strong spine is always present and on the base of the spine there is a small occipital node. Evidently, the 'occipital spine' and the 'occipital node' are not always identical.

The free cheek is evenly convex and down-sloping, and has a strongly curved edge. The marginal furrow is shallow, the margin slightly convex. The genal spine is advanced and strongly deflected sideways. A similarly shaped free cheek is seen in *Amphoton deois*, but without a spine. All other species of *Amphoton*, *Sunia*, and *Fuchouia* have long backward-directed spines, which may be only slightly deflected and not, or very slightly, advanced.

The test is minutely punctate.

The thorax: The thorax is described above The abaxial ends of the axial lobes protrude only slightly into the pleural furrows. The axial spines are long and stout. Similar axial spines are present in *Sunia* and also in the Australian *Amphoton spinigerum* Whitehouse.

The pygidium: The pygidium is almost triangular, with a rounded posterior margin, and acute anterolateral tips. The axis tapers slightly and extends to the border. It has four distinct annulations and a terminus. The furrows between the annulations are not straight, as in all other species, but are double-curved, with a rearward directed median peak, as is seen in the specimen, Plate 11, figure 6. The pleural platform is almost flat, with four pairs of pleural furrows and vestigial interpleural grooves. The pleural furrows extend to the border (but not to the margin) and become wider and deeper at their outer ends, as in *Fuchouia*. The border is flat and narrower than in *Amphoton* but wider than in *Fuchouia*. *Fuchouia manchuriensis* (Walcott) has four axial annulations and five pairs of pleural furrows, and *F. quadrata* Resser & Endo (1937) has five annulations and four pairs of pleural furrows. The general aspect of the pygidium of *Amphoton bensoni* is *Fuchuoia*-like, flat, but with too wide a border for a *Fuchuoia*. It can also be compared with the pygidium of *Amphoton* (*Sunia*) Kobayashi (1942). which is also subtriangular in outline, but has narrower pleural platforms. None of the discussed forms has such a wide pygidium and acute tips as *A. bensoni*.

Generic position: Three generic names are mentioned above in connexion with *Amphoton bensoni*: *Amphoton* Lorenz, *Fuchouia* Resser & Endo, and *Sunia* Kobayashi. For completeness, one more genus, *Dolichometopus* Angelin, is also discussed below. All these genera and their species are discussed exhaustively by Kobayashi (1942). The following comment is a discussion of the interrelationship of these genera, to facilitate the compilation of the diagnosis and the differential diagnosis of *Amphoton bensoni*.

Dolichometopus Angelin, 1854, is the oldest known genus, revised by Westergaard (1948). *Dolichometopus* has a thick test and for this reason its relief is externally somewhat effaced. On account of its smooth pygidium it differs from *Amphoton* Lorenz, 1906, which has a pygidium with well-developed furrows. Westergaard (1948, pl. 3, fig. 15) illustrates an exfoliated pygidium of *Dolichometopus suecicus* Angelin that shows the otherwise invisible pleural furrows and axial annulations. This pygidium is, in principle, of the same structure as that of *Amphoton deois* (Walcott), the type species of *Amphoton*, as shown in Kobayashi (1942, pl. 1, fig. 10). The glabella of *Dolichometopus suecicus* is variable, with concave flanks as in *Amphoton*, or slightly convex, as in *Fuchouia*. Thus *Amphoton* differs from *Dolichometopus* essentially by the thickness of its test only. The thick test of *Dolichometopus* is, however, a secondary development, indicating that *Dolichometopus* arose from an *Amphoton* or *Fuchouia*-like ancestor. But *Dolichometopus* is not known sufficiently and its interrelation with *Amphoton* cannot be studied in all respects. It is convenient, therefore, to retain both as separate genera, as an expression of the deficiency of our knowledge.

Fuchouia is an *Amphoton* with a parallel-sided or abaxially convex glabella and without, or almost without, a pygidial border. Other differences between the two (absence or presence of genal and axial spines, convexity, shape of the pygidium, etc.) have a specific value only. So Kobayashi rightly regards *Fuchouia* as a subgenus of *Amphoton*. At this point it should be mentioned that *Amphoton bensoni* has almost a *Fuchouia*-like pygidium and a glabella that resembles *Amphoton;* thus it is a generically intermediate species endangering the validity of *Fuchouia.*

Sunia is an *Amphoton* with long genal and axial spines. Of course, there are several valid species of *Sunia* that differ one from another in various ways. For the time being *Sunia* should be regarded as a synonym of *Amphoton*. The axial and genal spines of *A. bensoni* are also *Sunia*-like, although the genal spines are shorter.

For completeness it should be mentioned that Kobayashi (1942) established one more subgenus, *Amphoton* (*Amphotonella*) with *Dolichometopus alceste* Walcott as the type. The type material is, however, very fragmentary. *Amphotonella*-like forms are as yet unknown in Australia, and a discussion is, therefore, reserved.

To sum up, the species *bensoni* is an *Amphoton,* and, depending on what characters are considered as significant, it can be placed in any one of the subgenera *Amphoton* (*Amphoton*), *A.* (*Fuchouia*), or *A.* (*Sunia*), or regarded even as a separate subgenus. Our present preference is *Amphoton* (*Amphoton*), but if the concept of *Fuchouia* is restricted to peculiarities of the pygidium alone (pleural furrows almost reaching the pygidial margin; border absent or very narrow) it may be an aberrant *Fuchouia.*

Diagnosis: *Amphoton bensoni* is a species intermediate between *A.* (*Amphoton*), *A.* (*Fuchouia*), and *Amphoton* (*Sunia*), with a glabella constricted in its anterior third, without glabellar furrows, with large triangular posterolateral limbs with acute tips, with short and obliquely set eyes, and with advanced short and strongly deflected genal spines. The pygidium is wide and subtriangular, and has almost flat pleural lobes and a narrow flat border. There are four pairs of pleural furrows reaching the border, and vestigial interpleural grooves. The pygidial axis has four annulations and a terminus separated by double-curved transverse furrows. The thorax consists of seven segments with strong axial spines.

Differential diagnosis: No species has been described as yet with which *Amphoton bensoni* may be confused. Whitehouse (1939) described two upper Middle Cambrian species from Queensland: *Amphoton spinigerum* from the Split Rock Sandstone and *Amphoton serotinum* from the V-Creek Limestone. Both these species are older than *Amphoton bensoni.* They both have long eyes and pygidia with wide border. *A. spinigerum* has also long genal spines, three segments in the pygidium defined by furrows, and glabellar furrows, and is quite distinct, although it has axial spines as seen in *A. bensoni.* Kobayashi placed *A. spinigerum* in his subgenus *Sunia.* *Amphoton serotinum* has, according to Whitehouse, three annulations and two pairs of ribs in the pygidium, and long eyes situated close to the glabella, whereas *A. bensoni* has a different pygidium and obliquely set short eyes.

About ten undescribed species of Dolichometopinae are present in the Middle Cambrian of the Undilla basin in north-western Queensland. Some of them have *Amphoton*-like pygidia and others have pygidia of the *Fuchouia* design. A species with a thick, *Dolichometopus*-like test is also present.

Occurrence: *Amphoton bensoni* has been found only in the Devoncourt Limestone in Queensland, at localities D17 and D19. The age is the lower part of the Zone of *Proampyx agra.* It is, perhaps, the youngest known species of an *Amphoton.*

AMPHOTON? ARTA sp. nov.

(Pl. 13, fig. 10; text-fig 48)

Material: Only one incomplete cranidium, the holotype, CPC 3540, has been found. The photograph does not show the left posterolateral limb, which remains in the shadow, although it is preserved. It is shown in the reconstruction, Text-figure 48. The specimen was damaged by fire.

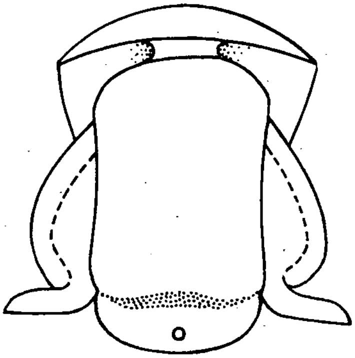


FIG. 48.—*Amphoton ? arta* sp. nov., Pl. 13, fig. 10.

Description: The cranidium is 5.5 mm. long. The anterior border is almost flat, elevated, and slightly upturned. The brim is very short, with a pair of shallow depressions. Between the depressions the marginal furrow appears to be shallow, indicating perhaps the presence of a vestigial plectrum. The anterior sections of the facial sutures are divergent and straight. They cut the marginal furrow abruptly, turn inward, and remain dorsal for a third of the width of the cranidial front each.

The palpebral lobes are long, about two-thirds of the length of the glabella. They are flat, and the palpebral furrows are vestigial. The ocular ridges are broad and slanting, and form with the midline an angle of 33 degrees each. The fixed cheeks are very narrow, about a third of the glabella. The eyes are placed opposite the posterior half of the glabella; the rear ends of the eyes are almost on the level of the occipital furrow and very close to the axial furrow. Such position of the eyes is common in dolichometopids. The posterolateral limbs are narrow bands, small, and, apparently, without the posterior marginal furrow.

The occipital lobe is relatively short, with its outer ends turning forward. It bears a low node. The occipital furrow is broad, and evenly shallow.

The axial furrows are distinct but shallow. The glabella is rounded in front, almost parallel-sided, but has a slight constriction in the middle. No glabellar furrows are present.

Generic relationship: The position of the eyes opposite the posterior half of the glabella and the straight divergent anterior sutures indicate a genus of the Dolichometopinae. The almost parallel-sided glabella constricted in the middle recalls the glabella of *Amphoton deois*, as illustrated by Kobayashi (1942).

Specific relationship: *Dolichometopus derceto* and *D. dirce*, as described by Walcott (1913), have narrow cranidia comparable with *Amphoton? arta*. *D. derceto* has, however, well developed glabellar furrows not seen in *arta*. In *D. dirce* glabellar furrows are absent and the posterolateral limbs are narrow; but the eyes are much shorter than in *arta*. *Amphoton deois* also has shorter eyes.

Diagnosis: *Amphoton? arta* is a species with very long eyes almost reaching the occipital furrow, with a parallel-sided constricted glabella without furrows, with small unfurrowed posterolateral limbs and vestigial palpebral furrows.

Occurrence and age: *Amphoton? arta* was found in the Devoncourt Limestone at locality D18. Its age is the Zone of *Proampyx agra*.

Family ELLIPSOCEPHALIDAE Matthew, 1887

Subfamily AGRAULINAE Raymond, 1913

The new species *Proampyx agra* and its close relationship with *Agraulos* necessitate a discussion of the systematic position of the Agraulidae (or Agraulinae).

If *Agraulos* and related forms are retained in the Solenopleuracea (see Harrington et. al., 1959), then Agraulidae should stand as an independent family whose solenopleurid affinity would be still a matter of contention. Hupé's (1955, p. 139) suggestion would be acceptable as regards a separate superfamily Agrauloidae or Agraulacea, with the inclusion of *Proampyx*, which was misplaced in the family Acrocephalitidae of the superfamily Solenopleuroidae. The erratic frontal cusp in *Proampyx* and its occurrence in *Acrocephalites* is, apparently, the only reason why *Proampyx* became separated from the agraulids.

A much simpler classification results when the ellipsocephalid affinities of *Agraulos* and *Proampyx* are considered: the rank of a superfamily will be unnecessary and that of a family can be supported by the elaborateness of the system of the Ellipsocephalacea rather than by morphological considerations.

Agraulos is close to *Ellipsocephalus* and *Ellipsostrenua,* and the differences can be conveniently evaluated as being of a subfamilial rank.

Howell (1937) first summarized the cranidial characters of the Agraulidae and Agraulinae as distinct from the ptychopariids, but omitted a comparison with the Ellipsocephalidae. Howell's definition of the Agraulidae is almost coincident with a general description of an *Ellipsocephalus.* Being distinct from the ptychopariids, they must be excluded also from the solenopleurids, because *Solenopleura, Parasolenopleura,* and *Asthenopsis* are themselves closely affiliated with *Ptychoparia.*

Hupé (1955, p. 112) in establishing the superfamily Agrauloidae indicated its affiliation with the Protolenidae, and especially with the Strenuellinae, which themselves are related to the Ellipsocephalidae.

The trilobite *Crassifimbra,* as described by Palmer in great detail from the Lower Cambrian of Nevada, displays characters that may be ancestral to *Agraulos* and *Proampyx.* Palmer (1958, p. 159) admits that *Agraulos ceticephalus* has a cranidium superficially similar to that of *Crassifimbra walcotti;* but *Ptychoparia striata* and *Crassifimbra* are not even superficially similar.

The agraulid characters in *Crassifimbra* are the effacement of furrows, a narrow free and a wide fixed cheek, a double curved marginal frontal furrow, and short (transversely) posterolateral limbs. Palmer refers *Crassifimbra* to 'ptychoparioid trilobites', a non-committal term that is useful to designate a superfamily or a suborder, as well as a particular design of trilobite organization. Ellipsocephalidae include forms of a similar design, hence *Crassifimbra* can be described as an 'ellipsocephaloid' as well.

Crassifimbra Lochman (1947) was established without being referred to a definite family. Rasetti (1951) refers it, together with some definite Ptychopariidae, to the superfamily Ptychoparioidae, and finally (Rasetti, 1955) to Ptychopariidae, subf. Antagminae Hupé. It seems, however, that in the Lower Cambrian of America the generalized ptychoparioids can be clearly differentiated. One lineage consists of the generalized ptychopariids, and the other is the ellipsocephalid-agrauline kind, equally generalized, but nevertheless distinctive. Genera like *Crassifimbra* have not yet been compared with ellipsocephalids, as if the occurrence of ellipsocephalids in the Pacific realm of America is an *a priori* impossibility.

I note that text-figure 3 in Palmer's paper conforms to the text description of *Crassifimbra,* showing the flush relief of the cranidium, and that the photographs display non-existing contrasts. If I am right the contrasts in photographs may mask the general ellipsocephaloid appearance of the cranidium of *Crassifimbra.*

Hupé (1953), and Harrington (in Harrington et al. 1959) have included the ellipsocephalids 'in the second group of the Redlichioidae,' and the suborder

Redlichiina respectively. But the Ellipsocephalacea have so little in common with the Redlichiacea that they cannot be placed even 'artificially' in the same order or suborder, as is done in recent classifications.

To conclude, the ptychoparioid and the ellipsocephaloid trilobites can be regarded as two related superfamilies.

Genus PROAMPYX Frech, 1897

According to Stubblefield in Harrington et al. (1959, p. 287), *Proampyx* is a junior subjective synonym of *Anomocare* Angelin, 1852, by the type designation of the latter by Vogdes, 1890. However, a decision by the I.C.Z.N. to replace *Proetus difformis aculeatus* Angelin (Vogdes' selection) by *Anomocare laeve* as the type of *Anomocare* is expected; *Proampyx* will gain, therefore, full validity because it refers primarily not to the species *difformis aculeatus*, but to *difformis acuminatus* Angelin as its type.

The nomenclature of *Proampyx* and its synonymy are discussed by Westergaard (1953). Westergaard, however, preferred to use the generic name *Agraulos* for these forms. Only cranidia of *Agraulos acuminatus* are known. Hence, the concept of the genus *Proampyx* is incomplete and the difference between *Proampyx* and *Agraulos* is not quite apparent, although *Agraulos* itself is a well-known genus.

Agraulos ceticephalus (Barrande) has sixteen segments in the thorax and a minute pygidium with two axial rings, a terminus, two pairs of pleurae, and no border. In the cranidium the eyes are very small, smaller than in any species of the Scandinavian *acuminatus-difformis* group. A British species, *Agraulos longicephalus* (Hicks), known from complete specimens, has according to Lake (1932) also sixteen segments, small eyes, and a minute pygidium. It seems, therefore, that these characters should be regarded as significant for the genus *Agraulos*. Lake mentions also that in *Agraulos* the fixed cheeks are wide and the free cheeks narrow, and that the genal spine is deflected from the even curve of the cephalic border.

Proampyx (=*Agraulos*) *acuminatus* (the type of *Proampyx*) has a punctate test, wide fixed cheeks, and perhaps narrow free cheeks with deflected spines. The anterior facial sutures diverge slightly. The eyes of *acuminatus* are large (larger than half the length of the glabella), the palpebral furrows are deep, and the front is extended into a long cusp. By these characters *Proampyx acuminatus* differs from *Agraulos*. The presence or absence of the cusp has apparently no generic significance, because in different specimens of a single species (*Agraulos difformis*, vide Westergaard, 1953), the cranidial front may be quite variable. The large eyes, however, are not seen in any species of the *Agraulos ceticephalus* group (with sixteen segments in the thorax). *Agroulos ceticephalus* has been recently re-described by Šnajdr (1958).

Cranidia of another species — *Agraulos aculeatus* (Angelin)—are associated in Sweden with *Proampyx acuminatus*. *A. aculeatus*, according to Westergaard, has no cusp, but its front is extended, tongue-like, and it has a long occipital spine, not seen in *acuminatus*. Otherwise it is like *acuminatus*, and it is reasonable to assume that these species are congeneric. Westergaard confirms also that the form described by Brögger (1878) from Norway as *Arionellus difformis* (Angelin) is conspecific with *Agraulos aculeatus*. According to Brögger (p. 60) it has twelve to thirteen segments in the thorax, axial spines on the thorax, and a quite large pygidium. Such a form is difficult to place in *Agraulos* and the application of the name *Proampyx* is therefore justified.

The generic status of *Agraulos difformis* (Angelin) results from a comparison with *aculeatus* and *acuminatus*, from both of which it differs in minor characters. Moreover, the Australian *Proampyx agra* described here is close to *difformis* itself, and has fourteen segments in the thorax (and not sixteen as *Agraulos* has) and a relatively large pygidium. It seems to be congeneric with *Arionellus difformis* in the sense of Brögger and should be placed in the same genus, *Proampyx*.

To conclude, the generic name *Proampyx* is applied for the Australian species *agra* (1) because *agra* cannot be regarded as being an *Agraulos*, and (2) because the congeneric relationship of *agra* and *Proampyx acuminatus* and *P. difformis* is most probable.

In two papers Wilson (1954, 1956) describes a new genus *Nasocephalus* from Cambrian exotic boulders in an Ordovician shale of Texas. *Nasocephalus* is regarded by its author as a crepicephalid trilobite, and believed to be closely related to the Swedish Middle Cambrian *Agraulos difformis, A. anceps, A. acuminatus,* and *A. aculeatus*.

Nasocephalus Wilson is, nevertheless, a valid genus, unrelated to *Proampyx*, as seen from the following comment. In *Nasocephalus* the dorsal furrows of the cranidium are deeply cut and surround the glabella completely; the posterolateral limbs are long; the eyes are small, as seen from the free cheeks; the genal spine is not deflected; the free cheek has a distinct marginal furrow; the eyes are close to the glabella, and the fixed cheek is much too narrow (0.25 to 0.3 of basal glabellar width) for a *Proampyx* (0.75 and over); the free cheek is wide; the test is tuberculate and not punctate. Of course, *Nasocephalus nasutus* (the type species) has a cusp, but several unrelated cusp-bearing genera occur in the Upper Cambrian, and *Nasocephalus flabellus* Wilson has no cusp: the cusp is not even significant within the genus *Nasocephalus* itself.

Skrejaspis Ružička, 1944 (see Šnajdr, 1958) is another Bohemian agraulid related to *Proampyx*. It also has fourteen segments in the thorax, but its pygidium is smaller and the cranidial furrows are deeper than in *Proampyx*. In the reconstruction of *Skrejaspis* by Šnajdr (loc. cit., p. 180) the glabella is shown to be conical and the genal spines in line with the margin. It appears, however, that the glabella is in effect almost parallel-sided and the spines are deflected.

Diagnosis of Prompyx *Proampyx* is a genus of the ellipsocephalid subfamily Agraulinae with divergent anterior facial sutures, large eyes, and punctate test. Its thorax contains twelve to fourteen segments; the pygidium is relatively large and has no border and no marginal furrow.

PROAMPYX AGRA sp. nov.

(Pl. 12)

Proampyx agra was previously listed (Öpik, 1956, p. 20) as *Agraulos* cf. *difformis* (Angelin), but not described.

Material: The material consists of several cranidia, three pygidia, and two articulate specimens, one of them almost complete; all in limestone.

Measurements: Crandium, holotype (CPC 3510), lengths: cranidium 13.1 mm.; axial lobe 8.9 mm.; palpebral lobe 3.8 mm.; widths: frontal margin 13.1 mm.; palpebral lobe 16.4 mm.; posterior margin, 17.4 mm.; glabella 5.4 mm. Complete specimen (CPC 3512) 30 mm. long. Incomplete specimen (CPC 3513): cephalon 14.2 mm. long, axial lobe 9.5 mm. long. Pygidium (CPC 3514) 3.1 mm. long, 6.2 mm. wide; pygidium (CPC 3515) 6.0 mm. long, 11.7 mm. wide.

Selection of holotype: The cranidium Plate 12, figure 1 (CPC 3510) is selected as the holotype, in preference to the more complete specimens. It is measurable and allows of a comparison with *Agraulos difformis*, which also is based on cranidia only.

Related species: The nearest described species is *Agraulos difformis* (Angelin) Westergaard, 1953. All other known species of *Proampyx* are quite different and a comparison with them is unnecessary. *Proampyx difformis* is a variable form, and especially variable are the size of its brim and the shape of the frontal margin.

A similar but smaller variability is apparent also in *Proampyx agra*. The main difference between the cranidia of *difformis* and of *agra* is seen in the width of the fixed cheeks between the edge of the palpebral lobe and the dorsal furrow. In *P. agra* the fixed cheek is as wide as the glabella; in *P. difformis* the fixed cheek is 0.75 of the width of the glabella, and this proportion is constant in all specimens of *difformis*.

Cephalon: The test is fairly thick, and minutely punctate all over. The outer ventral side of the genal spine is also punctate (Pl. 12, figs. 1 and 5c). The cranidium is as long as nine thoracic segments. It is subtrapezoidal in outline with its greatest width along the posterior margin. The anterior sutures are straight and slightly divergent (in *Agraulos* convergent); the posterior sutures are also straight. The frontal border is parabolic and protrudes forward, but to a different extent in different specimens. A rim is present; it is wide in the middle, with an indistinct plectrum in the form of a peak directed rearward, and is bordered by a slightly depressed brim, which is narrower than the rim. The fixed cheeks are wide, as wide as the glabella, with a globose convexity, and an abaxial slope. The palpebral lobes are set out obliquely to the median line, strongly arched, and show a shallow palpebral furrow. The eyes are central, placed almost against the middle of the glabella. The ocular ridges are double, low and slanting. The test makes a 'step down' in front of the ocular ridges, as is common in ellipsocephalids. The posterolateral limbs are short and triangular, the posterior marginal furrow is broad and shallow.

The axial furrows are shallow, almost vestigial, but the preglabellar furrow is distinct (in *difformis* all the furrows around the glabella are distinct).

The glabella is parallel-sided (in *difformis* it tapes slightly) and slightly convex, with a vestigial median carina. The glabella is almost rectangular at the anterolateral corners, as in *Proampyx acuminatus,* and *Kingaspis* Kobayashi. Three pairs of almost effaced glabellar furrows are indicated. The occipital furrow is deep at its outer ends and vestigial in the middle. A very small occipital node is sometimes present, but *difformis* always has the node and it is quite prominent.

The free cheek is narrower than the fixed cheek, with a short deflected genal spine. It has a relatively wide doublure and an angular ventral border.

The relief of the cranidium in general is very low, and all its furrows tend to be effaced. Howell's description of the agraulids: 'the glabella is almost or quite flush with the fixed cheeks in convexity' is here applicable.

Thorax: In contrast with the almost effaced relief of the cranidium the thorax exhibits a strong relief and deep furrows suggesting a relationship with *Ellipsocephalus* and *Agraulos.*

The test is fairly thick and punctate, like the cephalon. Fourteen segments are present (Pl. 12, fig. 3); the first ten segments are almost of even width, the posterior four narrow gradually rearward. The axial lobe is prominent, the dorsal furrows are distinct but shallow. The axis is about a third of the total width in non-flattened specimens. The pleural furrows are broad and distinct, the pleural terminations are obliquely truncate and slightly rounded and seemingly without spines. The thorax is strongly geniculate along the fulcral lines. The doublure is narrow, not reaching in the middle of a pleura beyond the external end of the pleural furrow. Each pleura bears an opisthopleural and a propleural vein.

Pygidium: The test of the pygidium is impunctate and bears scattered tubercles. On the two anterior annulations of the pygidial axis six or seven tubercles are arranged in a single transverse row. A combination of a punctate cranidium and thorax with an impunctate pygidium is surprising. Isolated pygidia were expected also to be punctate, and without the complete specimen the identification of the correct pygidium would have been uncertain.

The pygidium is relatively large, its length being about that of two anterior segments of the thorax. Its shape is subtriangular, with a rounded rear. No border and no marginal furrow are present and the margin is bent down abruptly. The axis is parallel-sided and long, almost reaching the posterior margin, and less than a third of the width of the pygidium. The axial furrows are shallow but quite distinct. Two distinct annulations, followed by two vestigial annulations and a short rounded terminus, are the divisions of the axis. Two pairs of pleurae with wide and distinct pleural furrows and two pairs of weak interpleural grooves are present. The anterior border is strongly geniculate at the fulcra.

The pygidium of *P. agra* resembles pygidia of some species of *Bailiella* and *Solenopleura.*

Specific diagnosis: *Proampyx agra* is a species of the *difformis* group, that is, without a frontal cusp. It is a species with wide fixed cheeks which are as wide as the glabella; a parallel-sided glabella; indistinct cranidial axial furrows and a distinct preglabellar furrow; an almost obsolete or missing occipital node; and double ocular ridges.

The characters of the thorax and the pygidium are not included in the specific diagnosis because they are not yet known from any other species of the *difformis* group. They are mentioned above, in the diagnosis of the genus.

Occurrence and age: *Proampyx agra* occurs in the Middle Cambrian Devoncourt Limestone of Queensland and has not yet been found elsewhere. The age is the Zone of *Proampyx agra.*

PROAMPYX sp. D.

(Pl. 10, figs. 8 and 9.)

Fragments of a *Proampyx* occur in the Roaring Siltstone, at locality D 7/15, but are insufficient for a description on a specific level.

The cranidium Plate 10, figure 9 (CPC 3530) is punctate, and its front is, perhaps, of a shape suggesting a similarity with *P. agra.* It seems, however, that the glabella is tapering and the axial furrows are more distinct than in *agra.* The fixed cheeks are not as wide as in *P. agra.*

The associated pygidium (CPC 3531), although much distorted, is of a similar structure to the pygidium of *P. agra.* A border is absent and two anterior segments are indicated by the annulation and the pleurae. The interpleural grooves are stronger than in *P. agra.*

The cranidium (fragment) is 7.5 mm. long, and the pygidium is 9.4 mm. wide. The pygidium evidently belongs to a much larger specimen than the cranidium.

Family PAPYRIASPIDIDAE Whitehouse, 1939

Summary: Papyriaspididae are a family of the Ptychopariacea represented in Australia by the genera *Papyriaspis* and *Tosotychia.* The genus *Rhodonaspis,* however, remains with the Olenidae.

Diagnosis: Papyriaspididae are Ptychopariacea with a multisegmented thorax (with more than sixteen segments) which is the only character separating this family from the Ptychopariidae.

Discussion: According to Whitehouse (1939, p. 216) the genera of the Papyriaspidinae 'are characterized particularly by the flatness of the test and by the relatively narrow axis'. But the test of *Papyriaspis* is, in reality, convex, and a narrow axis is most common in Ptychopariidae as well. The diagnosis of the family Papyriaspididae in Harrington et al. (1959) refers to a heterogeneous group of genera. The diagnosis of Papyriaspididae (Ptychopariacea with a multisegmented thorax) is applicable only to genera whose thorax is known, and the full significance of this criterion as applied to the Ptychopariacea remains to be demonstrated. Because no other criteria common to all genera of the family can be detected the Papyriaspidinae can be regarded as a subfamily of the Ptychopariidae.

The name Alokistocaridae Resser, October 1939 postdates the name Papyriaspidinae Whitehouse, March 1939; considering that the Alokistocaridae are multisegmented Ptychopariacea, and that *Alokistocare* itself is also multisegmented, the nomenclatorial priority of the Papryiaspidinae becomes apparent. The list of the Alokistocaridae in Harrington et al. (1959) includes also genera with a small number of segments in the thorax (up to 14), which should be transferred to the Ptychopariidae.

Papryiaspididae (synonym: Alokistocaridae) are: *Papyriaspis, Tosotychia, Chancia, Alokistocare, Alokistocarella, Amecephalus, Inglefieldia? birdsalli* Howell, *Kochina, ?Elrathina,* and *?Mexicella.* The two last-mentioned genera are multisegmented, but otherwise not readily comparable with the Ptychopariidae and Papyriaspididae, nor are they mutually related.

Ptychopariidae (excluded from the Alokistocaridae) are: *Elrathia, Elrathiella, Ehmania, Parehmania, Periura, Bythicheilus. Annamitia,* however, may represent a separate family.

The trilobite described below as *Tosotychia* gen. nov. has been previously (Öpik, 1956, p. 20) listed as *Papyriaspis* aff. *lanceola* Whitehouse. It is regarded here as a genus of the subfamily Papyriaspidinae, the meaning of which adheres to its type species—*Papyriaspis lanceola* Whitehouse. Hence the necessity arose to describe the species *lanceola* in greater detail, without which *Tosotychia* could not be properly described—or, at least, only by references to such characters of *Papyriaspis* as are not available in the literature. *Papyriaspis* however is not present in the Selwyn Range sequence, and is described here from material from the Undilla Basin, 140 miles north-west of the Selwyn Range.

The Papyriaspidinae were originally established by Whitehouse as a subfamily of the Olenidae. Harrington et al. (1959) changed the ranking into Papyriaspididae of the superfamily Olenacea, by which the problem of the affilia-

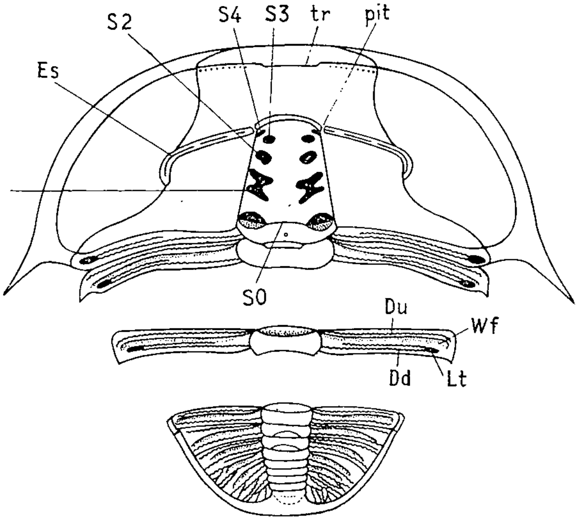


FIG. 49.—*Papyriaspis lanceola* after Pl. 16 and 17, fig. 3. Cephalon, first segment, ninth segment and pygidium with last segment. Dd—opisthopleural diverticular vein (intestinal appendage); Du—propleural diverticular vein; Es—ocular striga; Lt—opisthopleural (terminal glandular) swelling; pit—anterior pit; S1-S4—glabellar furrows; SO—occipital furrow (transcurrent, with double muscle scars); tr—plectrum; wf—pleural furrow. Pleural furrows and interpleural grooves—straight lines; diverticular veins—exaggerated wavy.

tion of *Papyriaspis* with the family Olenidae became shelved. The reasons for this procedure are found in Henningsmoen (1957).

The erection of the family Papyriaspididae leaves open the question of the division of this family into subfamilies. Whether all its genera still belong to the single nominate subfamily, the Papyriaspidinae, or some of them may constitute another subfamily, has not yet been discussed. All that has been achieved so far is a purification of the family Olenidae. The present author concurs with Henningsmoen (1957, p. 21) who doubts that these genera listed below are closely related to each other.

Six genera are included in Harrington et al. (1959) in the Papyriaspididae: *Papyriaspis, Hedinaspis, Rhodonaspis, Pianaspis, Proaulacopleura* and *Prohedinia*.

Proaulacopleura Kobayashi is not a papyriaspidid at all; it is so distinct that a discussion can be omitted. *Prohedinia* Lermontova has *Prohedinia attenuata* Lermontova as the holotype; but this species has not been described, and it must be deduced from the generic diagnosis and the description of another species, *Prohedinia solida* Poletaeva in Halfin (1955). *Prohedinia* has a subrectangular glabella with deep furrows, a wide brim with a low preglabellar boss, large eyes on a triangular elevation of the fixed cheeks, a narrow upturned rim, subparallel and anteriorly converging sutures, and relatively small posterolateral limbs. It is

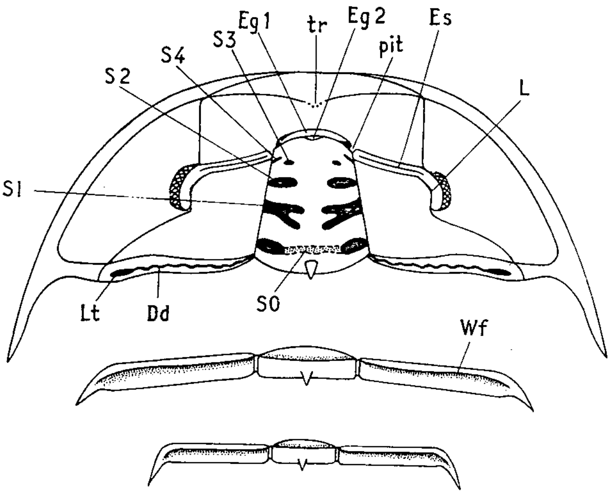


FIG. 50.—*Tosotychia sors*, cephalon, an anterior and posterior segment of thorax, from Pl. 15, figs. 2, 3, 6 and 7. Dd—opisthopleural diverticular vein (exaggerated wavy); Eg1—parafrontal band (anterior); Eg2—posterior parafrontal band; Es—ocular striga; L—angularity of palpebral lobe; Lt—opisthopleural (terminal glandular) swelling; pit—anterior pit; S1-S4—glabellar furrows; SO—occipital furrow (transcurrent); tr—plectrum; Wf—pleural furrow. Veins on pleurae of thorax omitted.

a distinctive cranidium, and ptychoparioid, but cannot be assigned to a definite superfamily.

Pianaspis Saito & Sakakura was included in the Papyriaspidinae by Whitehouse, who compared it with the ptychopariid *Lyriaspis*. It may have affinities with Olenacea. According to Henningsmoen, 'it is the most olenid-like of these genera' and should be examined therefore once more. I myself have no first-hand knowledge of *Pianaspis*.

Whitehouse (1939) in describing the Papyriaspidinae as a division of the family Olenidae followed Troedsson (1937), who placed *Hedinaspis* in the Olenidae, and even in the Oleninae. Troedsson (p. 60), in discussing the olenid nature of *Hedinaspis*, regarded this genus as linking together the Olenidae and "*Arethusina*" (= *Aulacopleura*), and considered no other possibilities. Hupé (1955) included the Papyriaspidinae and the Aulacopleurinae Angelin in the Olenidae.

According to Henningsmoen (1957) the Papyriaspidinae are not olenids. He writes (pp. 21-22): '*Papyriaspis* itself clearly differs from the olenids in the type of glabella, glabellar furrows, and thoracic segments'. Henningsmoen's diagnosis of the family Olenidae is a schedule of about 140 characters that may or may not occur in an olenid trilobite. But his 'Remarks' (p. 95) give a condensed diagnosis of the family for which the combination of the following characters is considered to be significant: (1) 'facial sutures meeting in front'; (2) 'narrow border and doublure'; (3) 'simple and well defined glabella'; (4) 'pleurae with oblique pleural furrows'; (5) 'small pygidium'. It should be also noted that the classification of the Olenidae by Henningsmoen (p. 17) is 'based on the assumed phylogeny'. This phylogeny, in its turn, is presented (p. 303) in the form of a chart. In this chart the Olenidae are depicted as a tree of three main branching limbs, of which the genus *Olenus* forms the trunk. It is quite certain that the Papyriaspidinae have no place in this 'phylogenetic family Olenidae'. In other words, if placed in the Olenidae, the whole family will appear polyphyletic. But it is perhaps already polyphyletic and its branches may each have arisen from a different ptychopariid.

The Papyriaspidinae can be tested from a morphological point of view, as regards the five tenets of the 'Remarks' above:

1. 'Facial sutures meeting in front'. In other words, the free cheeks form a unit together, and a rostral shield is not cut out of the doublure by the subcephalic sutures; the hypostoma is not fused to the doublure. This is the most important item of the diagnosis, but has not yet been established in all genera of the Olenidae. Considering that *Papyriaspis* has a wide brim and a narrow rim it is probable that it has a similar organization. It is almost certain that the free cheeks of *Papyraspis* are not separated by a suture, or a rostral shield. In this sense *Papyriaspis* is 'olenid', and so is *Tosotychia.*

2. 'Narrow border and doublure'. This is also so in *Papyriaspis,* in *Hedinaspis* and *Tosotychia.* But the narrowness of the doublure and the border is not only an 'olenid' but also a ptychopariid character.

3. 'Simple and well defined glabella'. This must be considered in connexion with the statement (loc. cit., p. 22) that *Papyriaspis* differs from olenids in the type of glabella and glabellar furrows. Henningsmoen, of course, had to consider the incomplete material published by Whitehouse (1939, pl. 23, and text-figure, p. 218). But the similarity of the pattern of glabellar muscle-marks of *Acerocare* (Henningsmoen, p. 92) and of *Papyriaspis* (Text-fig. 49) is obvious. *Papyriaspis* has a simple and well defined glabella.

4. 'Pleurae with oblique pleural furrows'. In all olenids, ptychopariids, paradoxidids, etc., these furrows are 'oblique', because they start at the anterior adaxial corner and fade out toward the posterior abaxial tip. In forms with relatively long (transversely) and narrow pleurae the 'angle of obliquity' is small, of course. In olenids and in *Papyriaspis* the pleural furrows are long, reaching almost to the tips of the pleurae.

5. 'Small pygidium'. The small size of the pygidium is hardly a diagnostic character. All genera in question have small pygidia, but similar pygidia occur in several genera of ptychopariοids. Isolated pygidia of this kind cannot be assigned to a family or superfamily, when their specific or generic name is unknown.

The comments above indicate that *Papyriaspis* satisfies all single diagnostic characters of the Olenidae, and has also the correct combination of characters. But these characters and their combination are too general, and too common, to be used in a differential diagnosis of Olenidae against 'non-Olenidae'. A diagnosis of Olenidae remains elusive, if it exists at all. Evidently no distinction exists between the ptychopariids and the Oleninae, but such a distinction is apparent between the ptychopariids and the remaining subfamilies and genera of the Olenidae (without the Oleninae).

The inclusion of *Papyriaspis* and the related *Tosotychia* in the Olenidae and Olenacea is possible but cannot be enforced on morphological grounds. These genera are, however, conveniently accommodated in the Ptychopariacea if their morphological similarity with *Chancia* Walcott, 1924, is accepted as being significant at a familial level.

The following sources are illuminating to compare *Chancia* with *Papyriaspis* and *Tosotychia*: (1) *Chancia palliseri* (Walcott), as described by Rasetti (1951); (2) the diagram of *Chancia ebdome* Walcott in Hupé (1955, p. 124, fig. 9); and (3) *Chancia odarayensis* Rasetti, the cranidium of which (Text-fig. 51) has the same proportions as *Papyriaspis* (Text-fig. 49) or especially *Tosotychia* (Text-fig. 50).

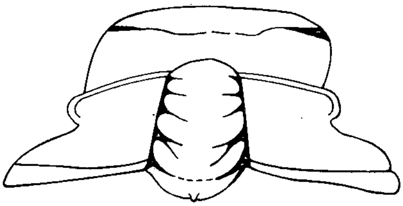


FIG. 51.—*Chancia*, **cranidium, after** *Ch. odarayensis* **Rasetti, adapted from Rasetti (1951, pl. 33, fig. 15).**

Chancia ebdome is the type species of the genus, described in detail by Walcott (1925). Resser (1939a, p. 4, fig. 12-14) illustrated some more specimens of *Ch. ebdome,* but without any explanatory text. His figure 12 represents an almost undistorted cranidium which could be even confused with a cranidium of *Tosotychia.*

Chancia is a multisegmented ptychopariid, with a narrow axial lobe and very wide pleural lobes, but without axial spines. The cranidium has a wide brim, wide fixed cheeks, and almost central eyes; the posterolateral limbs are large and triangular. The anterior facial sutures are in most species slightly divergent and almost straight. The glabella has two or three pairs of lateral furrows. The genal spines are not deflected.

Chancia differs from *Papyriaspis* and *Tosotychia* by its simple glabellar furrows connected with the dorsal furrows; from *Papyriaspis* it differs also by its smaller pygidium. *Papyriaspis, Tosotychia,* and *Chancia* are generically distinct, but are hardly separable on a familial level.

Two more genera, *Hedinaspis* Troedsson and *Rhodonaspis* Whitehouse, must be discussed. *Hedinaspis* is known in great detail. It is the only ptychoparioid known that has a subcentral glabellar tubercle. Its organization is so peculiar that it cannot be accommodated in any known family of the Ptychopariacea or Olenacea, and should be considered as *suae familiae*, and *incertae superfamiliae.*

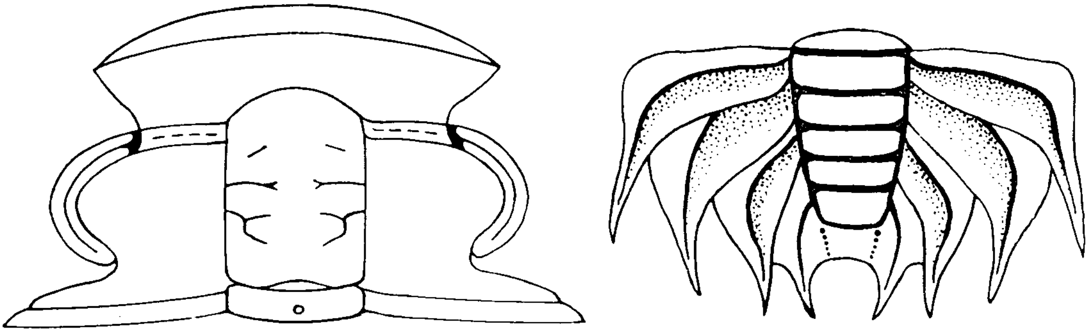


FIG. 52.—*Rhodonaspis longula* Whitehouse. Upper Cambrian Georgina Limestone, lower part; zone of *Glyptagnostus stolidotus*. Cranidium, W20, Mt Whelan 4-M Sheet; pygidium Loc. G48, Glenormiston, Queensland. Palpebral lobes and ocular ridges double, but separated by depression (black).

Rhodonaspis, as described by Whitehouse (1939), is a valid genus, but is not yet known sufficiently to be placed in a family. A full description is reserved, but the new material allows for the following amplifications (Text-fig. 52): (1) the pygidium is identical with that of a *Parabolina,* for example *P. ancanthura* (Angelin) in Westergaard (1922, pl. 7, fig. 14); and (2) the cranidium has long posterolateral limbs and diverging anterior sutures (the reconstruction by Whitehouse, 1939, p. 220, indicates short posterolateral limbs and abaxially convex sutures). *Rhodonaspis* is older than *Glyptagnostus reticulatus* and occurs in the Upper Cambrian zone of *Glyptagnostus stolidotus.* In the Selwyn Range it occurs in the lower part of the O'Hara Shale (localities D6, D28, and D29).

For the time being *Rhodonaspis* should be regarded as a genus of the family Olenidae, distinguished by its large eyes, elongate glabella, multisegmented thorax, and *Parabolina*-like pygidium.

Genus PAPYRIASPIS Whitehouse, 1939

The genus *Papyriaspis* is monotypical and it consists at present of a single species, *P. lanceola* Whitehouse.

Diagnosis: Papyriaspididae with abaxially concave anterior facial sutures, with the three posterior pairs of glabellar furrows developed as muscle markings, with deflected and advanced genal spines, without axial spines on the thorax and a relatively large and fused pygidium.

The following description of this species amplifies the diagnosis of the genus.

PAPYRIASPIS LANCEOLA Whitehouse, 1939

(Pls. 16, 17; Text-fig. 49)

Papyriaspis lanceola has been partly redescribed (Öpik, 1961) as regards its alimentary apparatus (caeca) and other details of its organization; the present description is intended to serve taxonomic purposes.

A large quantity of material of *Papyriaspis* has been accumulated in recent years in the collections of the Bureau of Mineral Resources in Canberra from many localities and several horizons of the higher Middle Cambrian beds of the Undilla Basin of Queensland. The oldest specimens are found in the Currant Bush Limestone, in the Zone of *Ptychagnostus punctuosus.* The type specimens were collected by Whitehouse in the V-Creek Limestone in the lower levels of the Zone of *Ptychagnostus nathorsti.* Ample material from this formation and stratigraphic level is now available. *Papyriaspis* is also found above the V-Creek Limestone, in the Mail Change Limestone, and at one locality at the base of the Split Rock Sandstone.

It is already evident that all these specimens referred to *Papyriaspis lanceola* display variations of several kinds. It is, however, not yet evident whether a single species is present, or whether the material is specifically heterogenous: it is a problem to be studied statistically in the future. The specimens described here have been collected from the same horizon and formation as the original material of Whitehouse.

General aspect: Complete specimens of *Papyriaspis lanceola* have not yet been found: the free cheeks are always missing. Specimens between 4 and 6 cm. in length are common; but it is estimated from fragments that the largest specimens were about 10 to 12 cm. long. The smallest specimens are around 2 cm. in length, and are adults (holaspis stage), because they show the complete number of segments.

The body is subovate or oval, with almost straight edges of the thorax, moderately convex, and slightly geniculate along the fulcra. The test is thin and almost translucent.

The general appearance is that of a *Ptychoparia* or *Elrathia* (but for the larger number of segments and straight flanks), or of a *Chancia.*

Measurements (in mm.):

	CPC 3557 Pl. 17, Fig. 5	CPC 3554 Pl. 16
Cranidium:		
Length, total	16.3	16.3
,, , axial lobe	10.8	10.1
,, , frontal border	1.7	1.3
,, , brim	3.8	4.9

Width, frontal	16.0	17.0
,, , brim, minimal	15.0	15.9
,, , across palpebral lobes	21.1	21.0
,, , posterolateral tips	33.1	33.8
,, , glabella, anterior	4.9	5.3
,, , glabella, posterior	8.1	8.4
Pygidium:		
Length, total	8.4	8.4
,, , without articulating half-ring	8.1	7.7
,, , axis	6.5	6.0
Width	18.2	17.9
Thorax:		
Width, axis, anterior	8.3	8.4
,, , axis, posterior	4.3	4.1
Length	30.2	31.4
Body:		
Length	54.6	55.4
Number of segments:	19	18

Whitehouse (1937, figure on p. 318) gave a restoration of *Papyriaspis lanceola* which needs some amendments and amplification.

Thus, (1) the anterior branches of the facial sutures are shown as straight and converging, as, for example, in *Elrathina*. In reality they are outwardly concave. No other ptychoparioid trilobite has such sutures. (2) The genal spine is shown as continuous with the border, but in reality it is deflected and slightly advanced, as in many ptychopariids and in the Leptoplastinae. (3) The fixed cheeks are shown as smooth, but in reality they are venose and reticulate. (4) The pleural tips are shown as angular and the edge of the pleural lobe appears serrate. In reality only the two anterior segments have faint terminal pleural spines, and the remaining pleural tips are truncate and form an even, unbroken edge of the thorax. (5) The test is very thin, but not flat, as assumed by Whitehouse. The flatness is the result of the compaction of the sediment. The cranidium in Plate 17, figure 1 shows a gently down-sloping frontal area, and the free cheek in Plate 17, figure 3 has preserved some of its original convexity. It is evident that the cephalon was gently and evenly convex with the free cheeks and the brim sloping downward. The thorax was geniculate along the fulcral line, as seen in the specimen Plate 17, figure 5. The free parts of the pleurae were, consequently, bent down along the fulcra, but the adaxial part was, of course, flat. (6) The outline of the glabella is less conical than the reconstruction by Whitehouse shows; in younger specimens the glabellar furrows are lateral 'notches', but in well developed specimens they are depressions combined with 'muscle markings'.

The pygidium: Two pygidia (Pl. 16 and Pl. 17) are illustrated. The pygidium of the second specimen is flattened and slightly worn. It is also slightly asymmetrical and the two anterior left-side pleurae are less fused than the pleurae on the right. This pygidium has five annulations in the axis and a posterior (sixth) indicated by lateral indentations of the terminus. It is, perhaps, slightly larger than the pygidium of the specimen Plate 16. The pygidium Plate 16 is perfectly preserved. The axis has six annulations and a short and blunt terminus; there is a narrow border with an equally narrow doublure. The border widens rearward at the axial terminus. The two anterior pairs of pleurae are well defined by the interpleural grooves, and have regular pleural furrows and veins (pleural caeca). The posterior part of the pygidium, slightly reniform in shape, is well fused and the otherwise linear caecal veins are changed here into a reticulation (see Öpik, 1961). On the anterior part of the axis the articulating half-rings are exposed, indicating that not only the pleurae but also both the anterior segments are loosely fused.

The pygidium is about one-seventh, whereas its posterior fused part (without two anterior segments) is about one-twelfth, of the total length of the whole specimen. The latter proportion is about the same as in *Chancia palliseri* (Walcott) (vide Rasetti, 1951, p. 215).

According to Whitehouse, the pygidium of *P. lanceola* has four annulations and a long terminus in the axis. Such forms are also present in our collection.

Ornament (other than pleural caeca): The surface of the pleural lobes is smooth, without any granulation or lines. The axial lobe, especially its median portion, is minutely and densely granulate. This ornament is sometimes obscure on the thorax, but stronger on the glabella and the pygidium. The granulation is arranged in closely spaced transverse wavy lines. On the occipital lobe and on the glabella the granules merge to form short intermittent lines.

The thorax: The thorax contains eighteen segments in the specimen Plate 17 and nineteen in the specimen Plate 16. The maximum observed number is twenty. Immature specimens below 20 mm. have seventeen, but small specimens with eighteen and nineteen segments have been collected. The thorax tapers gradually rearward and the last segment is only about 0.6 of the width of the first. The taper of the axis is, perhaps, slightly less than that of the pleurae. The axial lobe is convex and elevated; the inner portions of the pleurae are flat, and the outer, free ends (outside the fulcra) are convex and down-sloping. The width of the free ends decreases rapidly rearward: the free pleura of the posterior segment is only about 0.3 of the width of the free pleura of the first segment. The line of the fulcra is well seen on the left side of the specimen Plate 17. The pleural furrows in large specimens are broad channels reaching almost the inner edges of the doublure. These furrows are oblique, starting at the anterior inner corner of the pleura and terminating near the posterior outer corner. The slant in the adaxial part and on the free pleura is steeper than in the middle, and in small specimens the pleural furrows are narrow and visibly oblique. The posterior tips of the anterior two or three segments bear minute outwardly deflected spines. The remaining pleurae have straight truncate edges all in one line; each has a tiny, backward-directed spine at the posterolateral corner. The axial rings are angular and protrude slightly into the pleural furrows. The dorsal furrows are very shallow but distinct, and, because of the angularity of the axial rings, they appear as a pair of wavy lines.

The cephalon: Text-figure 49 explains the structure of the cephalon of *P. lanceola*. The free cheeks are taken from Plate 17, figure 3, and the outline of the cranidium from the specimen Plate 16. The reconstruction is that of a flattened cephalon. In reality the downsloping and convex free cheeks and anterior area would produce a slightly different projection.

The cephalon is semi-elliptical in outline. It is almost as wide as the length of the thorax and pygidium taken together, and as long as about nine segments, or half of the length of the thorax. Its axial lobe (the glabella and the occipital ring) is small in comparison with the wide cheeks and frontal area.

The free cheeks are wide, slightly wider than the fixed cheeks including the palpebral lobes. Their marginal furrow is distinct, the border is narrow and convex, the genal spine short, deflected, and slightly advanced. The caecal veins of the free cheek are described in Öpik (1961). The free cheeks of *P. lanceola* are easily recognized by their curved anterior inner edge (the anterior branch of the facial suture) and cannot be confused, therefore, with cheeks of other associated ptychopariids which also have radial veins and deflected spines.

The posterior sutures are widely divergent, as in *Hedinaspis, Rhodonaspis, Chancia,* and the alokistocarids. The anterior branches, however, are concave outward; they remain for a short distance dorsal when cutting the border and join into a single suture along the margin. The doublure of the free cheeks is continuous in the front and no rostral shield is cut out of it. This is borne out by fragments of free cheeks in which the submarginal frontal doublure is seen to continue for a distance greater than half the width of the brim, and to have broken and not clean-cut ends.

The cranidium is twice as wide as long. Its front is slightly curved, almost linear, the rim is rounded, convex, and not upturned. The marginal furrow is deep and narrow and has a bow-like course, around the short median plectrum. The length of the frontal area (including the brim and rim) and its width are variable as seen in the illustrated specimens. The specimen Plate 16 has a larger frontal area than the specimen Plate 17, as seen from the following comparison:

	Length (L)	Width (W)	L/W ratio
	of the frontal area in relation to the length of segments of the thorax		
Specimen Plate 16	3½ segments	9 segments	0.4
Specimen Plate 17	3 segments	8 segments	0.4

The length of the rim is a third or slightly less of the length of the brim.

The palpebral lobes are about a third of the length of the glabella and are situated opposite its middle. The distance from the midpoint of the glabella to the palpebral lobe equals the distance from that midpoint to the frontal margin of the cranidium.

The ocular ridges slant at an angle of 70 to 75 degrees to the midline. They are slightly curved, but may be almost straight (Pl. 3). The ridges are strong, elevated, narrow and well defined. They are double, with a faint dividing furrow (striga) running on the crest and extending into the palpebral lobe as a second palpebral furrow. The external, anterior bands of the ocular ridges may join in front of the glabella in a parafrontal band.

The axial lobe of the cephalon: The cephalic axial lobe consists of the occipital lobe and the glabella. The occipital lobe is slightly wider than the axis of the thorax and the glabella, narrows laterally and bears a very small node. In smaller specimens, however, the node is quite prominent. The occipital furrow is shallow and only slightly depressed at its outer ends. The glabella is subconical, with the outline of a flower pot. The width at its base equals its length. The front of the glabella is sub-truncate. The preglabellar furrow and the dorsal furrows are shallow but distinct all around the glabella. Pits are present, one at each of the adaxial ends of the ocular ridges.

Four pairs of glabellar furrows are discernible in not too much compressed or collapsed specimens. The three posterior pairs are shallow depressions and have the appearance of muscle scars. They do not reach the dorsal furrows, are constant in their position, but vary in shape according to the specimen. The anterior pair of furrows (S4) is situated just behind the ocular ridges. These furrows are short and reach the dorsal furrows. At the outer ends of the occipital furrow ‘muscle scars’ are always present. In some specimens these markings are halved by the occipital furrow. In one specimen (Pl. 17, Fig. 2) the outer ends of the occipital furrow are bifurcated and enclose a lateral lobule each. In ptychopariids four pairs of glabellar furrows represent a ‘full set’, as seen for example in *Chancia* (Text-fig. 51). In some of them, as for example, *Kochiella? maxeyi*, and *Onchocephalus skapta* Rasetti (1957, Pl. 120) the S3 and S4 furrows have the same arrangement as in *Papyriaspis*, where the S3 furrows are pits not reaching the axial furrows. In these early forms all glabellar furrows are normal furrows, whereas in *Papyriaspis* the posterior ones are converted into scars.

The frontal rim is relatively narrow and slightly convex with a broad and short plectrum, in a corresponding median recess of the marginal furrow.

Variation: The variability of *Papyriaspis lanceola* can be illustrated by a comparison of the two complete specimens Plate 16 and Plate 17. Both these specimens are of the same size (54.6 mm. and 55.4 mm.). They were selected as representative adults, for completeness of their preservation and for the differences they display.

The specimen Plate 16 has nineteen segments in the thorax, six annulations in the pygidial axis, a wide and long frontal area, a smaller pygidium, and straight ocular ridges. The specimen Plate 17 has eighteen segments in the thorax, five annulations in the pygidial axis, a narrower and shorter frontal area, a larger pygidium and straight ocular ridges.

Each of these brief descriptions is probably a diagnosis of a separate species. However, they do not exhaust all the variations seen in the collection and it is difficult without a complete survey to decide which characters are specifically significant. It seems that the specimen Plate 17 is the nearest to the holotype of *Papyriaspis lanceola* Whitehouse (1939, pl. 23, fig. 1).

Pathology: The cranidium, Plate 17, Figure 2, is asymmetrical, the left and the right anterior sutures are slightly different, and the glabellar furrows are also asymmetrical. It is as yet the only monstrosity found among *P. lanceola*.

Genus TOSOTYCHIA nov.

Tosotychia is a monotypical genus, with *T. sors* sp. nov. as its type. A separate generic diagnosis is unnecessary because it would coincide with the specific diagnosis as given below.

TOSOTYCHIA SORS sp. nov.

(Pl. 15; Text-fig. 50)

Tosotychia sors has been listed previously by Öpik (1956, p. 20) as *Papyriaspis* aff. *lanceola* Whitehouse.

Material: Besides the seven illustrated specimens, a fragment of a thorax, two free cheeks, several cranidia, and isolated segments have been examined. All material (with the exception of Pl. 15, Fig. 1) has been damaged in a fire.

Measurements: Cranidium (CPC 3547), 9.0 mm. long as preserved; cranidium, holotype (CPC 3548), lengths: total 9.5 mm.; axial lobe, 7.0 mm.; frontal area, 2.5 mm.; rim, 1.1 mm.; widths: glabella, anterior, 3.9 mm.; glabella, posterior, 5.3 mm.; palpebral, 12.7 mm.; cranidium (CPC 3549), 6.8 mm. long; pygidium (CPC 3550), 2.5 mm. long; thorax (CPC 3551), as preserved, 11.1 mm. long.

Selection of holotype: The largest cranidium (CPC 3548), Plate 15, Figure 2, is selected for its size.

External habit: *Tosotychia sors* is a trilobite with a semi-elliptical cephalon as wide as the total length of the thorax and much wider than the anterior segment of the thorax; with a slender multisegmented thorax gradually narrowing rearward, and a small pygidium. The edges of the pleural lobes are spinose and serrate. The oval body is moderately convex, and gently geniculate along the fulcra. The narrow axial lobe is elevated above the flat inner parts of the pleural lobes, and adorned with short axial spines.

The pygidium: Only one pygidium (Pl. 15, figs. 5a, b) is available, associated with numerous fragments of *Tosotychia.* Because of this association, and absence of other fragments of other trilobites in this association, and because it suits no other trilobite known in the Devoncourt Limestone, this pygidium is assigned to *T. sors.* Attached to this pygidium is also a segment similar to the posterior segments of the thorax (Pl. 15, fig. 7). The axis of the pygidium reaches almost to the border and consists of two annulations and a long, bluntly rounded terminus. The pleural lobes have two pairs of pleurae sharply divided by the grooves and the pleural furrows into four pairs of ribs. All the furrows reach the border, indicating that the doublure was very narrow. The pygidial border is narrow and flat, and may have been provided with two pairs of backward-directed spines in conformity with the pleural spines of the thorax. The pygidium is about twice as wide as long. Considering that the pygidium was not wider but even slightly narrower than the last segment of the thorax the length of the pygidium was about one seventh (or less) of the thorax and one eleventh (or less) of the total length of the trilobite. In *Papyriaspis* it is one seventh, in *Chancia palliseri* Walcott (Rasetti, 1951, p. 215) it is about one twelfth, in *Rhodonaspis* about one tenth. Consequently the pygidium of *T. sors* is small, comparable in size with the pygidium of *Chancia.*

The thorax: The thorax Plate 15, figure 7, certainly belongs to *T. sors.* This is borne out by its general papyriaspid structure, by the similarity of the proportion of the axial and pleural lobes of its first segment and of the posterior margin of the cranidium, and by the fact that isolated segments of similar structure and one more fragment of the thorax have been found in association with cranidia, and that the axial lobes and occipital lobe have similar spines.

In the illustrated thorax the sixth segment is missing and at least one more segment remained attached to the pygidium; as twenty segments are present the total number of segments must have been twenty-one or twenty-two, but not much more. It is slightly more than in *Papyriaspis* and about the same number as in some species of *Chancia* and *Alokistocare* Lorenz (Palmer, 1954).

The axial lobe is narrow, its width being about one-quarter of the width of a segment in the anterior part of the thorax; but in the posterior segment it is slightly wider than its pleura. The thorax, as a whole, decreases in width quite rapidly and evenly; the last segment is only a third as wide as the first. The fulcra are indistinct and the free pleural ends are about one-third of the whole pleura. The pleural furrows are oblique and long, almost reaching the spines. The pleural tips are spines which in anterior segments are directed almost outward, but become gradually falcate posteriorly (Text-fig. 50). The edges of the pleural lobes are serrate, and not unbroken lines as in *Papyriaspis*. Short, backward-directed axial spines are present.

Each segment bears two pairs of simple pleural caeca. They are slightly wavy raised ridges running along the anterior and posterior borders of each pleura. They have the same appearance as the opisthopleural caeca of the cranidium.

The free cheek: The free cheek (Pl. 15, fig. 6) is a slightly convex shield with a narrow border and doublure, with a genal spine that is continuous with the border and not deflected, and covered with caeca radiating out from the base of the eye. The veins are more anastomosing than, for instance, in *Papyriaspis*. It differs from *Papyriaspis* also by the direction of the spine, which is deflected in *Papyriaspis*.

The cranidium: The cranidium (Text-fig. 50) is half as long as wide, with a wide frontal area (brim and rim), a conical glabella, medium-sized eyes, slanting ocular ridges, wide fixed cheeks, and large posterolateral limbs. The proportions and the distribution of these features are very similar to the arrangement seen in *Papyriaspis lanceola* (Text-figure 49) and *Chancia* (Text-fig. 51).

The facial sutures are characteristic in two respects. The posterior branches are almost straight, beginning at the rear ends of the palpebral lobes. In *Papyriaspis* and *Chancia* these sutures are directed rearward at the eye, but turn outward in a curve in some distance from the eye. In *Tosotychia* the anterior sutures are parallel, but on the rim they turn abruptly toward the middle. The sutures cut the frontal margin about midway between the median line and the corners of the brim. In several species of *Chancia*, including the type, *Ch. ebdome*, the anterior sutures are divergent, but also convex outward (*Chancia stenometopa* Rasetti, 1951).

The palpebral lobes are quite large for a ptychopariid. They are about 0.4 of the length of the glabella, angular, elevated, and steeply sloping inward, and from an angle of 20° with the median line. The palpebral furrows are distinct but shallow, and are not duplicated. The eyes are as far apart as in *Papyriaspis* and placed almost opposite the midpoint of the glabella. The ocular part of the fixed cheeks is almost as wide as the glabella.

The ocular ridges are elevated and strong. Their abaxial ends merge with the palpebral lobes; their adaxial ends, before touching the glabella, are curved forward. The ridges are double, divided by a rather deep striga. In front of the glabella the parafrontal band, although disconnected from the ocular ridges by the anterior pits, is regarded as the extension of the anterior bands of these ridges.

Between the parafrontal band and the glabella a small short band is seen (Pl. 15, fig. 2, and Text-fig. 50), which can be regarded as a portion of the posterior ocular ridge and a culmination of the connective caeca of the posterior ocular ridges. The ocular ridges are almost horizontal in Plate 15, figure 3. In other illustrated cranidia they are slanting at an angle of 82-85° to the median line.

The brim is slightly convex and about a third of the length of the glabella. The rim is slightly shorter than the brim, slightly convex and upturned, and has a narrow plectrum that almost interrupts the marginal furrow. The plectrum of *Tosotychia* is much narrower than in *Papyriaspis* and *Chancia.* The marginal furrow is quite distinct except for the short distance at the plectrum, where it is shallow or even obsolete. The fixed cheeks are slightly narrower than the glabella (about 0.8 of its width). The posterolateral limbs are wide and triangular and, immediately below the eye, as long as half the glabella. The posterolateral marginal furrows are wide and deep. The posterior borders are narrow and bear each a prominent, slightly wavy, caecal vein with a low terminal glandular swelling.

The axial lobe of the cranidium: The occipital lobe is relatively short and is almost pointed abaxially. It bears a low, backward-directed node or spine. The occipital furrow is broad and transcurrent, with deeply depressed lateral appendiferi, best seen in Plate 15, Figure 3. The glabella is slightly longer than wide and tapers anteriorly: its width in the front is about three-quarters of the width at its base. The glabellar front is bluntly rounded and has an indentation. Four pairs of deep and distinct glabellar furrows are present. The first furrows (S1) are bifurcate: the second furrows (S2) are simple and also deep. The third furrows (S3) are small pits not reaching the axial furrows. The anterior furrows (S4) are short and narrow, and reach the dorsal furrows just at the ocular ridges. The three posterior pairs are combined with muscle scars, but these are smaller than in *Papyriaspis.* The arrangement of the furrows recalls *Kochiella,* and to a lesser degree *Chancia.* The test is minutely granulate.

The caeca on the cranidium are arranged in the same manner as in *Papyriaspis* (Öpik, 1960), but some differences in details are seen. Thus, on the brim the veins are relatively low in front of the glabella, but are stronger in front of the ocular ridges. On the fixed cheeks caecal nodes are present at the posterior ends of the palpebral lobes and at the outer ends of the occipital furrows, but not along the palpebral lobes and the posterior edge of the ocular ridges. The caeca of the fixed cheeks are reticulate rather than radiate veins. The reticulation is even stronger than in *Ptychoparia striata* (Hupé, 1953, p. 82).

Diagnosis: *Tosotychia sors* is a papyriaspidid with subparallel anterior sutures and straight posterior facial sutures, angular palpebral lobes, upturned rim, deep glabellar furrows, border-continuous, not deflected genal spine, axial spines, and a small pygidium.

Differential diagnosis: *Tosotychia* differs from *Papyriaspis* in so many characters of all parts of the tergum that it seems unnecessary to refer to them once more. The nearest genus, however, is *Chancia* Walcott, which has not been considered previously a member of this family. *Chancia* has divergent anterior and sinuous posterior sutures, less impressed glabellar furrows, curved palpebral lobes and no axial spines.

Occurrence and age: *Tosotychia sors* occurs in the Roaring Siltstone and in the lower half of the Devoncourt Limestone. Its age is uppermost Middle Cambrian, Zones of *Ptychagnostus cassis* and *Proampyx agra*.

Family ANOMOCARELLIDAE Hupé, 1955

(ANOMOCARELLINAE Hupé)

Anomocarellidae and Anomocarellinae are not accepted by Harrington et al. (1959), wherein *Anomocarella* is included in Asaphiscidae Raymond. Most probably Anomocarellidae (and/or Anomocarellinae) are a division of the Asaphiscacea, within which their rank is a subjective matter. *Mapania*, however, which is also an anomocarellid, has been placed in another superfamily—the Anomocaracea—a procedure which cannot be substantiated.

The distinction between the asaphiscid and anomocarid trilobites, however, may not be of a superfamilial rank because forms are known that can be freely redistributed without much changing the familial concepts. For example *Anomocare ephori* Walcott, which was included by Resser & Endo in *Proasaphiscus*, and appears to be affiliated with the anomocarellids, is considered by Westergaard (1950, p. 13) to be an *Anomocare*, related to *A. laeve* Angelin. According to Resser & Endo (1937, p. 269) the anomocarellid *Psilaspis* has certain resemblances to *Asaphicus*.

Genus MAPANIA Resser & Endo, 1937

(Text-fig. 53)

The occurrence of *Mapania* in Australia was mentioned by Öpik 1956a, p. 20; 1956b, p. 270). *Anomocare? angustum* Whitehouse (1939, p. 224) was also transferred by Öpik into *Mapania* (Öpik, 1956a, p. 19). This species, although absent in the Selwyn Range sequence and in the Roaring Siltstone, is re-described below to be used in comparison with forms of the Devoncourt Limestone.

In the meantime Chang (1957, 1959) has established two more genera, *Luia* and *Poshania*, that seem to be related to *Mapania*. *Poshania*-like forms occur also in the upper levels of the Middle Cambrian of Queensland and were included under *Mapania* by Öpik (1956).

Luia is an anomocarellid reminiscent of *Mapania* in the shape of the tapering glabella, but it has small eyes and four pairs of glabellar furrows. *Luia typica* has no plectrum, but *Luia yaochiayuensis* has a short plectrum. The pygidium of *Luia* is fused and has a flat border. *Poshania* recalls *Mapania synophrys* sp. nov. in the

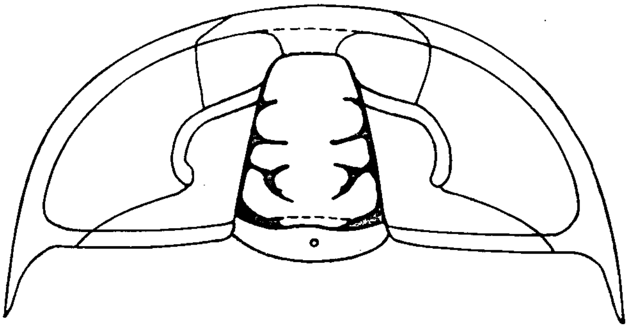


FIG. 53.—*Mapania striata* **Resser & Endo. Reconstructed from Endo & Resser, 1937, p. 252 and pl. 35, figs. 10, 16, 17 (posterior glabellar furrows only) and 18.**

absence of a brim in front of the glabella and in having a conspicuous plectrum, which is, however, much stronger than in any species of *Mapania.* In one species (*Poshania transversa*) four pairs of glabellar furrows are indicated, and the preoccipital furrows are complex (trifid?). The pygidium of *Poshania* is, however, *Anomocarella*-like, with a flat or even slightly excavated border. Thus, *Luia* and *Poshania* are distinct genera and these names are not applicable to the species of the Devoncourt Limestone.

Mapania angusta (Whitehouse) is a distinct species related to the type, *Mapania striata* Resser & Endo. The three other Australian species which are here described (*synophrys, faceta,* and *dicella*) have relatively large eyes and small posterolateral limbs, as are common in *Anomocarella* Walcott. These characters, however, are correlated and not independent features, because an increase in the size of eyes is by necessity accompanied by a decrease in the size of the posterolateral limbs. The more or less tapering glabella, the distinct marginal furrow in the pygidium, the narrow convex pygidial border with its extremely narrow doublure, and the interpleural gooves, exclude *Anomocarella,* but indicate an affiliation with *Mapania striata. Mapania angusta* is older than the species of the Selwyn Range, and intermediate undescribed forms occur also in the Middle Cambrian sequence in the Quita Creek area (Öpik, 1956, p. 20; Öpik in Noakes et al., 1959). The description of these forms is postponed, and so is a revision of the whole group on a familial and generic level. This group includes undescribed Australian forms as well as described Manchurian genera which can be taken together as *Anomocarella* and its affiliates: *Anomocarella* Walcott itself, and Resser & Endo's *Psilaspis, Eymekops,* and *Manchuriella.*

All cranidia of *Mapania* described by Resser & Endo are fragmentary, flattened in shale, and somewhat distorted by shearing. Some of these cranidia show converging anterior facial sutures, but this convergence is only apparent and is produced by the mode of preservation and imperfect exposure of the specimens on the bedding planes. Subsequent authors have been misled by illustrations of such cranidia, and an erroneous reconstruction of *Mapania* with sutures converging in frontal direction is found in Hupé (1955, p. 121, figs. 103-7).

The illustration of *Mapania striata* in Harrington et al. (1959, fig. 213, p. 289) is also misleading. Kobayashi (1960) gives a better reconstruction of the cephalon, but in the pygidium the pleural furrows are too short.

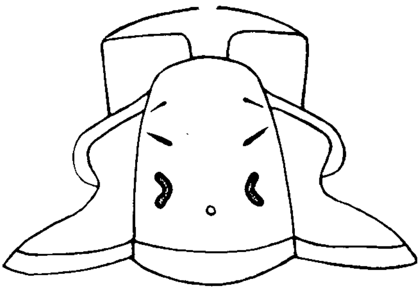
Resser & Endo (1937, p. 252) correctly describe the anterior sutures of *Mapania* as diverging and note the apparent convergence as the result of flattening and incomplete exposure. I have examined all the specimens of *Mapania*, published and unpublished, preserved in the collection of the Smithsonian Institution in Washington, and confirm the observations of Resser & Endo.

The proper, diverging, course of the sutures is visible in one of Walcott's specimens (1913, pl. 12, fig. 14a), and in a free cheek (ibid., fig. 14b), and in the free cheeks in Resser & Endo (1937, pl. 35, figs. 10 and 16).

Three species, all from eastern Asia, have been described as yet: (1) *Mapania striata* (the type) and (2) *M. liaotungensis*, both by Resser & Endo, and (3) *M. beichoensis* Kobayashi (1935). *M. beichoensis* was referred to *Mapania* before the genus itself was established.

Conocephalites typus Dames (1883) may or may not be a *Mapania*. Kobayashi (1935) placed *Mapania* apparently provisionally in the Ptychopariidae. According to Hupé (1955) *Mapania* belongs to the family Anomocarellidae Hupé. This corresponds in principle to the interpretation of Resser and Endo, who discussed *Mapania* as related to *Anomocarella*.

The cranidia of *Mapania* (Text-figure 53) and of *Proceratopyge* (Text-figure 54) are rather similar. *Proceratopyge* has less divergent sutures, smaller eyes and a median glabellar node; both have plectra, about the same number of segments in the thorax, and large pygidia, but *Proceratopyge* has a wider doublure, and lateral pygidial spines. It is hardly an accidental similarity, although their relationship cannot be evaluated as yet taxonomically.



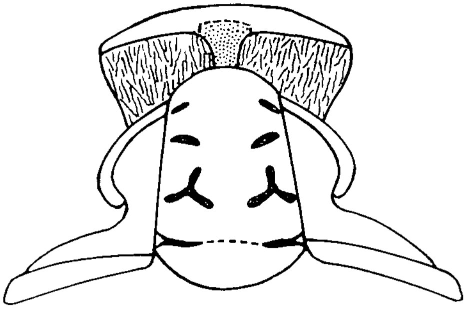


FIG. 54.—Cranidium of *Proceratopyge*, **after** *P. conifrons* **Wallerius, adapted from Westergaard, 1948, pl. 1, fig. 11.**

FIG. 55.—*Mapania angusta* **(Whitehouse), Pl. 14, fig. 1.**

MAPANIA ANGUSTA (Whitehouse)

(Pl. 14, fig. 1-4; Text-fig. 55)

Mapania angusta is not found in the Selwyn Range sequence; it occurs only in the V-Creek Limestone, Undilla Basin.

The species was described by Whitehouse (1959, p. 224, pl. 23, fig. 21) under the name *Anomocare? angustum.* His material consisted of a single fragmentary and distorted cranidium. The diagnosis of Whitehouse is, however, adequate, and in his illustration the plectrum, the shape of the glabella, and the glabellar furrows are recognisable.

Material: Four selected specimens are described here to amplify the knowledge of this species. These specimens are more or less flattened in limestone.

Measurements: Cranidium (CPC 3542), lengths: total 12.0 mm., frontal area 2.9 mm.; axial lobe 9.1 mm.; glabella 7.6 mm.; occipital lobe 1.5 mm.; widths: frontal 11.0 mm., in front of eyes 8.4 mm., palpebral, 11.4 mm., posterior 20.1 mm., glabella at base 6.4 mm. Pygidium (CPC 3544), lengths: total, including half ring 6.6 mm., axis 4.7 mm. (without half-ring); widths: maximal 13.0 mm., of axis 3.2 mm.

Mapania angusta differs from all other described species in the following characters: (1) its brim is slightly concave; (2) the rim is upturned and flat; (3) the frontal marginal furrow is an angularity only; (4) the glabella is slightly carinate; (5) the pygidium has five axial annulations as in *M. striata,* but it has six pairs of furrowed pleurae, whereas *striata* has only four pairs. Other species of *Mapania* have fewer pygidial divisions.

Remarks: Comparing the cranidia Plate 14, figures 1 and 2, it appears that the plectrum varies slightly in shape, having a blunt or a pointed end. The occipital furrow is vestigial in the middle, but deep on its flanks, and has the appearance of the transverse furrows of the pygidial axis. The preoccipital furrow is trifid, and not connected with the axial furrow. The adaxial branches of these furrows are distinct and vary in length. The caecal veins in the brim are delicate, and even faint on the plectrum. The anterior sutures are divergent and slightly convex outward. The posterolateral limbs are large, indicating wide free cheeks. The free cheeks (not illustrated) are striate, with a slightly curved, undeflected genal spine. The test of the glabella and the occipital lobe is densely and minutely granulate.

The thorax (Pl. 14, fig. 4) is incompletely preserved. The number of segments is estimated at about ten to twelve, as seen also in *Anomocarella.* Its axis is narrow and moderately convex. The pleurae expand distally slightly, are truncated, and have very short spines on the posterolateral corners. The pleural tips are in line and the edges of the pleural lobes are non-serrate, unbroken. The pleural furrows are narrow and oblique, and almost reach the tips. The doublure is extremely narrow.

The pygidium is subtriangular, and half as long as wide. The border is convex, very narrow, corresponding to the narrow doublure; the marginal furrow is distinct. The rear of the pygidium is slightly upturned in the middle and provided with a shallow sinus. The axis is bluntly rounded in the rear. Its transverse furrows are shallow in the middle, and the posterior furrows do not reach the axial furrows.

The pygidium is large; it is as long as six segments of the thorax and apparently only slightly shorter than the cranidium.

Occurrence: *Mapania angusta* occurs only in the Middle Cambrian of the Undilla Basin, Queensland, in the uppermost part of the Zone of *Ptychagnostus punctuosus* and the next higher Zone of *Ptychagnostus nathorsti*. The formation is the V-Creek Limestone. The specimens Plate 14, figures 1-3, were found at the V-Creek Crossing (locality M409), where Whitehouse collected the holotype. The specimen fig. 4 was collected at locality M25, about three miles east of Morstone Homestead.

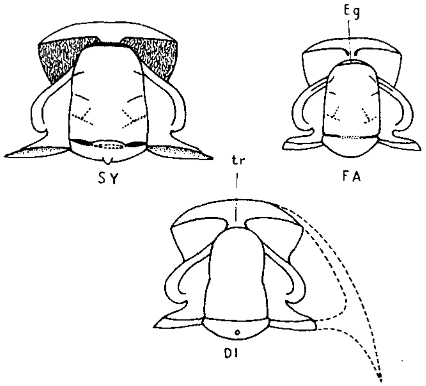


FIG. 56.—Diagrams of cranidia of *Mapania synophrys* (SY) *faceta* (FA) and *dicella* (Di), Pl. 13, figs. 1, 2, 4, 7, and 8.—Eg—parafrontal band; tr—plectrum.

MAPANIA SYNOPHRYS sp. nov.

(Pl. 13, figs. 1-3; Text-fig. 56)

Material: The illustrated specimens, two cranidia and one pygidium, are found in a single bed. Abundance of fragments indicates that it is a fairly common species.

Measurements: Cranidium, holotype (CPC 3532), lengths: total 6.5 mm.; glabella 4.6 mm.; cranidium (CPC 3533) 6.3 mm. long; pygidium (CPC 3535) 9.7 mm. wide.

Selection of holotype: The cranidium Plate 13, figure 1 (CPC 3532) is selected because the anterior sutures and the palpebral lobe are preserved; the other cranidium (Pl. 13, fig. 2). with its preserved posterolateral limb supplements the holotype.

Generic position: It seems at first that this species cannot be regarded as a *Mapania,* because its glabellar furrows are indistinct, the palpebral lobes are relatively large, and there is almost no brim in front of the glabella. These characters, however, vary from species to species, and are of specific significance, as can be recognized by comparing *M. synophrys* with *M. angusta, M. striata,* and *M. faceta.*

Differential diagnosis: *Mapania synophrys* differs from all other species in having a relatively short brim; furthermore, it has larger eyes and smaller posterolateral limbs than *M. striata* and *M. angusta,* and a wider cranidium than *M. faceta.* No confusion is possible with *M. dicella.* which has a peculiar, constricted glabella.

Description: The cranidium is almost square, but for the laterally extended posterolateral limbs. The fixed cheeks, including the palpebral lobes, are slightly wider than half the glabella. The posterolateral limbs are wide but short (longitudinally), with a deep and wide marginal furrow. The posterior border is narrow and elevated, and has a slight fulcral geniculation. The anterior border is narrow, convex, and evenly curved, with a short but wide and prominent plectrum. The brim is very short and replaced by the plectrum in front of the glabella. The marginal frontal furrow is deep. The anterior sutures are divergent, and almost straight; they cut the border abruptly and turn inward for about a third (or slightly less than a third) of the anterior width of the cranidium. The posterior sutures are greatly divergent and slightly sinuous.

The palpebral lobes lie somewhat behind the midpoint of the glabella. They are arcuate, wide, and slightly less than half the length of the glabella. The ocular ridges are slanting, relatively broad, and elevated. The palpebral furrows are distinct and continue along the posterior border of the ocular ridges. The brim is covered with fine veins, the fixed cheeks are smooth.

The occipital lobe is short and bears a prominent node. The occipital furrow is shallow in the middle, and narrow and deep at its ends. In one of the specimens (Pl. 13, fig. 2) this furrow is widened in the middle and its floor appears to be the vestige of the articulating half-ring of the occipital lobe.

The dorsal furrows are distinct, surround the glabella, and seem to be deepest at the front, between the glabella and the plectrum. The glabella tapers anteriorly, and has rounded anterior corners and a slight frontal recess. There are three pairs of very shallow and erratic discontinuous glabellar furrows, of which the preoccipital ones are trifid. The surface is minutely and densely granulate.

The associated pygidium has a narrow border and upturned rear (like *M. angusta*), and broad pleurae (here damaged) with pleural furrows and interpleural grooves reaching the border. The axis has five annulations and a terminus. The transverse furrows are continuous, but remain shallow in the middle. The surface is minutely granulate. The pygidium differs from that of *angusta* by its longer axis, which reaches the border, and by the continuity of the transverse axial furrows.

Diagnosis: *Mapania synophrys* is a species with a very short brim, a short and wide plectrum, large eyes, and indistinct glabellar furrows.

Occurrence: *M. synophrys* is widespread in the middle part of the Devoncourt Limestone; its age is the Zone of *Proampyx agra.* It occurs also in the Northern Territory at locality T87.

MAPANIA FACETA sp. nov.

(Pl. 13, fig. 4; Text-fig. 56)

The material consists of a single cranidium, the holotype, CPC 3538.

Description: The cranidium is 4.3 mm. long, and it is very narrow, if compared with the other species of *Mapania.* The brim is as wide as the rim (without the plectrum). The palpebral lobes are long, longer than half the length of the glabella, and placed behind its midpoint. The plectrum is short and narrow, and does not reach the glabella. The anterior sutures are moderately divergent and almost straight, the posterior sutures are strongly sinuous and diverge almost diametrically. The ocular ridges are prominent, slanting, and apparently double; the vestige of a parafrontal band is present. The occipital lobe is relatively long and triangular. The occipital furrow is shallow in the middle, and deep and very narrow at its outer ends.

The glabella tapers anteriorly, is evenly rounded in front, and bears three pairs of distinct and short furrows, of which the preoccipital ones are indistinctly trifid. The surface of the glabella is minutely granulate, the fixed cheeks are apparently smooth; the brim is densely covered with faint, delicate radial veins.

Diagnosis: *Mapania faceta* is a species with a narrow cranidium, with large eyes close to the glabella, a long triangular occipital lobe, and a short plectrum.

Differential diagnosis: Although it displays all essential characters of a *Mapania, M. faceta* cannot be confused with any other species of the genus.

Occurrence: The specimen has been found at locality D26, in the lower limestone terrace at Boundary Hill. It is about the uppermost fifty feet of the Devoncourt Limestone. It is associated with *Leiopyge laevigata armata,* and its age is the Zone of *Holteria arepo.* It occurs also in the Northern Territory, locality T87.

MAPANIA cf. FACETA

(Pl. 13, fig. 6)

The illustrated pygidium (CPC 3537) belongs to the genus *Mapania* for the following reasons: (1) it has a narrow and convex border; (2) the pleurae reach the border; (3) the axis is long; (4) the general appearance corresponds to the pygidia of *M. angusta* and *M. striata*; (5) pleural furrows and grooves both are present; (6) the ornament consist of minute and dense granulation of the same kind as seen in the cranidia of *M. synophrys,* and, especially, of *M. faceta;* (7) the marginal furrow is quite distinct.

The pygidium is 2.8 mm. long measured along the dorsal furrow, and 5 mm. wide. The axis consists of six annulations and a terminus, and the flanks of five pairs of pleurae. The interpleural grooves are shallow, indicating that the fusion is more advanced than in other species of *Mapania,* but less than in *Anomocarella* and *Manchuriella.* The transverse furrows on the axis are transcurrent, and not interrupted, or shallow in the middle, as in *M. angusta* and *M. synophrys.*

Seeing that the axis in this pygidium is as wide as the pleural lobe, one concludes that this pygidium belongs to a narrow and slender trilobite, probably to *M. faceta,* which also has a granulate test.

Occurrence: The illustrated pygidium is found at locality D21, in the upper third of the Devoncourt Limestone. It is about the same level in which *M. faceta* is found at locality D26. Its age is the Zone of *Holteria arepo.*

MAPANIA? DICELLA sp. nov.

(Pl. 13, figs. 5, 7 and 8; Text-fig. 56)

The material consists of two cranidia and a free cheek, all found almost on the same bedding plane.

The cranidium Plate 13, figure 7 (CPC 3539) is selected as the holotype because it has most of the characters preserved. It is 3.5 mm. long. It is damaged by fire.

Generic position: The structure of the rim with the prominent plectrum, the large eyes close to the glabella, and the divergent anterior sutures, are characters of *Anomocarella* and *Mapania.* The total absence of glabellar furrows and the evenly transcurrent occipital furrow are not seen in the other species of *Mapania,* but occur in *Anomocarella* and *Manchuriella.* The oblique set of the palpebral lobes and the pyriform shape of the tapering glabella are unique. These characters are specifically significant, but they may also indicate that this species represents a new genus of Anomocarellidae. It is, however, placed provisionally in *Mapania,* of which it may represent a separate subgenus.

Description: The anterior border is elevated and flat, with a prominent plectrum, which is in touch with the front of the glabella. The glabella has no furrows, is constricted in the middle, and is widest in its posterior half. The palpebral lobes are situated opposite the midpoint of the glabella, are wide, and set at an angle to the midline. Their length is slightly less than half the glabella. The ocular ridges are broad and distinct, and slanting at an angle of 45 degrees to the midline. The occipital ring bears a node. The anterior sutures are divergent, almost straight, or slightly convex outward. The posterolateral limbs are triangular and relatively small.

The free cheek (Pl. 13, fig. 8) is identified from the oblique set of the eye and the course of the posterior branch of the suture, which indicates a small triangular posterolateral limb. The free cheek is about as wide as the fixed cheek and the palpebral lobe together, or as about three-quarters of the width of the glabella. A genal spine with flange-like flattened edges is undeflected. The surface is covered with delicate radiating lines arising at the base of the eye.

A diagnosis is unnecessary, because the description above refers to all particular characters or their combination not seen in any other species.

Occurrence: The illustrated specimens are found at locality D18 in the middle part of the Devoncourt Limestone. They are associated with *Mapania synophrys, Centropleura phoenix, Leiopyge laevigta,* etc. The age is the Zone of *Proampyx agra.*

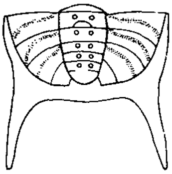


FIG. 57.—*Crepicephalus* **sp.** *H,* **Pl. 13, fig. 9.**

Family CREPICEPHALIDAE Kobayashi

CREPICEPHALUS? sp. H.

(Pl. 13, fig. 9; Text-fig. 57)

Only a single pygidium (CPC 3541) has been found. No cranidia, or even fragments of cranidia, are present to support the generic position. But the generic interpretation results from comparison with the restored specimen of *Crepicephalus coosensis* Walcott (1916, p. 206, pl. 32, fig. 3), and with *C. iowensis* (ibid., p. 207, pl. 29, fig. 1). They differ in the degree of fusion of pygidial pleurae: *C. coosensis* (restored), has the less fused pleurae.

Description: The pygidium is small, only 3 mm. long, not counting the spines. The ratio of the width of its axis to its total width is 0.3. The axis is short, not quite reaching the border. It has five annulations provided with a pair of low knobs each, and a short terminus. The pleural furrows and interpleural grooves are distinct, and there are four pairs of pleurae. The border is flat, its posterior margin (between the spines) is straight, and it bears a pair of slightly curved and only slightly divergent spines. The anterolateral corners of the pygidium are rectangular. The pleural furrows and interpleural grooves reach the border.

Comparison: The nearest described species is *Crepicephalus coosensis* Walcott (reconstructed). It has a slightly wider (the ratio is 0.35) and longer axis reaching the border, no knobs on the axial rings, and rounded anterolateral corners. The number of axial rings and pleurae is the same as in *C.* sp. H. The pleural furrows in *C. coosensis* seem to be, however, shorter than in *C.* sp. *H.*, but its preservation is unsatisfactory for a comparison.

To conclude, *Crepicephalus* sp. *H.* is a species with a pygidium in which the pleural furrows and interpleural grooves are distinct and reaching the border, with a pair of knobs on each axial ring, with rectangular anterolateral corners, and with curved and only slightly divergent marginal spines.

Occurrence and age: Devoncourt Limestone, locality D18. It is associated with *Leiopyge laevigata, Centropleura phoenix,* etc., and its age is the Zone of *Proampyx agra.*

Remarks: Resser (1938, p. 84, pl. 9, figs. 1 and 2) assigns *Crepicephalus coosensis* to the genus *Kochaspis* Resser, 1935. The pygidium of this *Kochaspis* differs clearly from *C.* sp. *H.* in having the pleurae extending into the lateral spines. A similar pygidium is also illustrated by Walcott (1916, pl. 32, fig. 3b) as *C. coosensis.* Walcott's reconstructed specimen displays, however, a pygidium different from *Kochaspis,* but similar in outline to that of *C. iowensis.* But as no holotype or a lectotype has been selected as yet, the question of what actually is *C. cooensis* remains open. The stratigraphic significance of sp. *H.* is small. If it is a *Kochaspis* it is within that known range of genus, which is Middle Cambrian; if it is a *Crepicephalus,* it is an early forerunner of the Upper Cambrian forms, and its occurrence in the Middle Cambrian renders the name of the '*Crepicephalus* Zone' of the Dresbachian somewhat illusory.

Class CRUSTACEA

Order BRADORIIDA Raymond 1935

(BRADORINA Raymond)

Roger in Piveteau (1953) indicates that the name of the order Archaeostraca Claus, 1889, is a junior synonym of Phyllocarida Pacard, 1879. Shimer & Shrock (1949) use the name Archaeostraca for a sub-class, and include in it the order Bradorina Raymond (1935), comprising Cambrian genera like *Bradoria, Hipponicharion, Beyrichona,* which probably are affiliated with our new genera *Aristaluta* and *Svealuta.* The same bivalved Crustacea have been traditionally and tentatively regarded as Conchostraca (Ulrich & Bassler, 1931) and classified as such by Deschaseaux in Piveteau (1953).

Conchostraca are living and fossil bivalved Crustacea in which the shell grows by apposition and is retained, and no moulting is known to occur in them. The Cambrian forms, however, had to moult, as indicated below under *Aristaluta,* and consequently are not Conchostraca.

The name Phyllocarida as revised in Ulrich & Bassler (1931) cannot be readily applied because it refers in the first place to forms like *Ceratiocaris* and *Echinocaris,* but not to the less well known Cambrian genera, most of which were described after the concept of Phyllocarida was established. These forms were regarded originally as ostracods, an interpretation that can be supported for forms with a moulting habit.

Thus, the name Archaeostraca could be applied, but provisionally, because it is not free of synonymy and homonymy. The new material described here is also insufficient to warrant the creation of a new name for forms which finally may turn out to be related to Ostracoda. An ordinal valid name, the Bradorina Raymond, is already available, but it should be transcribed into Bradoriida, for the sake of conformity of spelling as applied in the 'Treatise on Invertebrate Palaeontology'. According to Raymond, it is an order of the subclass Archaeostraca.

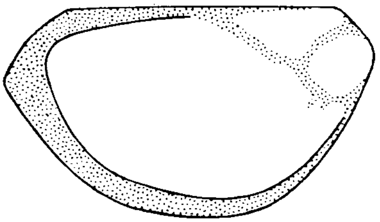


FIG. 58.—*Svealuta primordialis* (Linnarsson), diagram to show the flattened border and the posterior angularity.

Genus SVEALUTA nov.

The new name and genus *Svealuta* is established to clarify some nomenclatorial and taxonomic problems that arose through the use of the generic name *Aluta* Matthew, which should be restricted to its type species only. The meaning of *Aluta* is discussed below, under *Svealuta* aff. *primordialis*.

The type species of *Svealuta* is *Leperditia primordialis* Linnarsson, 1863.

It is a genus of the Bradoriida (Archaeostraca) with articulating valves, without gaps in the commissure, and with a smooth test. It has a wide flat ventral, posterior, and dorsal border and is angulate posteriorly (as in the type species), or posteroventrally or even ventrally. Its anterior extremity carries two subglobose nodes that may be surrounded by sulci.

The age of known species is upper Middle Cambrian.

SVEALUTA sp. M. aff. SVEALUTA PRIMORDIALIS (Linnarsson)

(Pl. 24, figs. 1a-1e)

Material: The material consists of a single fragmentary valve (CPC 3640). It is damaged at its anterior extremity, where nodes and sulci are expected as in *Svealuta primordialis*, Text-figure 58. Because of this fragmentary preservation open nomenclature is applied, although it is evident that the fragment represents a new species.

Generic relationship: The fossil is congeneric with the Swedish species *primordialis* Linnarsson, originally described as *Leperditia* or *Isochlina* (ostracods) and referred to also as *Aristozoe* or *Callizoe* (phyllocarids). Ulrich & Bassler (1931) compiled the generic synonymy of *primordialis*, and regarded it as an *Aluta*.

The genus *Aluta* itself has a doubtful meaning because its type species, *Aluta flexilis* Matthew, is based on a distorted and imperfect specimen, which was figured by Matthew upside down. For this reason, Ulrich & Bassler, in amending the generic concept, designated *Leperditia troyensis* Ford as the 'second genotype'. It is evident that the name *Aluta* is legitimate, and adheres to *A. flexilis,* but should be restricted only to this species. The rest of the forms that were placed in *Aluta* by Ulrich & Bassler should be referred to a new generic name. It is not compulsory to base the new genus on the 'second genotype' of *'Aluta'* (*Leperditia troyensis*), and it is even advisable to select a new species (not *troyensis*) as the type. It is also evident that the family name Alutidae Huo (1956) follows the fate of the name *Aluta* and will remain without a proper definition.

Leperditia primordialis Linnarsson differs from *Aluta exilis, 'Aluta' troyensis* and other species placed in *Aluta* so much that it deserves a generic name (*Svealuta*) on its own. This genus includes more than one species.

Description: The specimen is a right valve, 7 mm. high and between 3 and 4 mm. deep. Its anterior extremity is broken off. Its flat border fades out on the anteroventral margin, but is continuous along the dorsum. The border forms two angles: (1) in the middle of the ventral margin, and (2) at the posterolateral corners. The test is smooth. It differs from *Svealuta primordialis* by having two angulations of the border, and no angularity of the posterior extremity (see Text-fig. 58). Moreover in *primordialis* the border fades out at about the mid-point of the dorsum, whereas in our specimen it is continuous along the dorsum.

Occurrence and age: The illustrated specimen was found in the Devoncourt Limestone at locality D13A. Its age is the Zone of *Proampyx agra,* and it is slightly younger than the Swedish species *primordialis,* which is abundant in the Zone with *Solenopleura brachymetopa.*

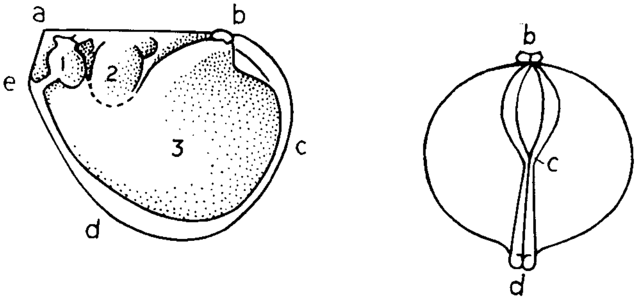


FIG. 59.—*Aristaluta gutta*, **Pl. 24, figs. 2a-3d, a—anterodorsal angle; b—posterodorsal angle with articulating (?) knobs; c—posterior midpoint; d—ventral border; e—anterior extremity; a-b—hinge line; b-c—gap; 1—anterior, 2—middle, 3—posterior lobe.**

Genus ARISTALUTA nov.

(Text-fig. 59)

The type of *Aristaluta* is *A. gutta,* new species.

Aristaluta is a bivalved crustacean with valves articulated along the dorsal hinge, with a gap at its posterior upper extremity, and with a complete closure but for the gap. Both valves have a border with a doublure. The carapace is leperditoid and trilobate, with two pairs of sulci in the anterodorsal portion. The test is probably punctate.

It differs from the contemporaneous *Svealuta* in the dorsal position of the lobes (or nodes) and the presence of the posterior gap.

Discussion: Ulrich & Bassler (1931) found that a gaping carapace is present in several Cambrian 'Conchostraca'. Gaping carapaces were included in the families Bradoriidae Matthew and Indianidae Ulrich & Bassler. In some forms the valves gape at both ends, in others along the ventral edge. Moreover, these authors (loc. cit., p. 3) had 'some reason for believing that the valves were always tightly joined along the back, often perhaps by fusion of the cardinal edges'. This assumption is based on the fact that Cambrian bivalved crustacea are found very often with both valves open on the bedding plane, but in complete juxtaposition and joined along the hinge. But this cannot be interpreted as an indication of fusion and absence of articulation: it merely indicates that the cardinal ligament or ligaments were strong and durable. Such mode of embedding occurs in shale and can be seen in Palaeozoic ostracods also. It is less common in limestone, but even from limestone ostracods with valves in juxtaposition have been described (Öpik, 1937, pl. 8, fig. 9). It seems, therefore, that the valves of Bradoriida and Ostracoda had a similar articulating mechanism, but the former had, probably, stronger ligaments. The gaping valves in Bradoriidae and Indianidae, for example, cannot enforce the conclusion that these forms were in no need of articulation with a carapace that could not be closed tightly anyway. A gap in the commissure of a closed carapace, and articulation along a dorsal hinge, are not mutually exclusive devices, as can be seen in *Aristaluta*.

Ulrich & Bassler described also a genus, *Mononotella*, as probably consisting 'either of firmly united (ankylosed) valves or of a single plate bent so as to simulate the bivalved forms'. If so, it is an organization seen in *Ribeiria* and its allies that are placed by Ulrich & Bassler in Notostraca and not in 'Conchostraca', and consequently *Mononotella* should be excluded from the Bradoriida. Ulrich & Bassler (loc. cit., p. 42) define the family Beyrichonidae as follows: 'Carapace bivalved with valves apparently fitting close together all around the edges, leaving no gap'. This is also so in *Svealuta primordialis*. The complete closure of the carapace excludes primary and secondary fusion of the hinge and is the evidence for articulation along the hinge. Such forms are truly 'bivalved'.

To conclude, it is improbable that in most of the forms referred to in the literature as Cambrian Conchostraca the valves were fused at the cardinal edges in a manner eliminating articulation.

The carapace of *Aristaluta* shows no signs of growth by accretion, which is characteristic in Conchostraca. The posterior gap, the distinct border, the doublure, the lobes and sulci can be produced and maintained only when growth proceeded by moulting. Moulting, for similar reasons, was also the rule for *Svealuta*, and the Bradoriidae. No growth lines are observed in them that could indicate the growth of the valves by accretion. Of course, it can be also assumed that the carapace was formed at the last stage of growth, after the completion of a larval development without a carapace. In this case, there was no growth after the secretion of the test.

Measurements given for some of the species (e.g. Matthew, 1903, p. 164), however, indicate that a variation in size exists, and Ulrich & Bassler (1931, pl. 6, figs. 8-10) illustrate larger and smaller valves of a species of *Beyrichona*. This is in support of moulting and growth, and it should be expected that in *Bradoria, Beyrichona* and so forth, moulting instars will be finally identified. Raymond (loc. cit., p. 228) describes his new order Bradorina as 'leading to Ostracoda'.

Huo (1957) follows Raymond in regarding the order Bradorina Raymond as being ancestral to the Ostracoda, and he describes the alutids from this point of view. Huo concurs, however, with Ulrich & Bassler in assuming a fusion of the alutid valves at the dorsal edges, and regards it as one of the many differences between the ostracods and Archaeostraca. Huo also assumes that the retral swing of the carapace, its lesser height in the anterior part, and the stronger prominence of the anterior extremity, if compared with the posterior part, are fundamental in orientation of fore and aft, left and right, and should be considered in ostracods before all other criteria. This particular shape of the carapace, is, however, not peculiar to ostracods, because it is too general and is present also in *Hymenocaris*, in the Phyllocarids, and even in the modern crayfish and prawn. Moreover the orientation of ostracods is still a matter of dispute. To conclude, if an affiliation of Bradoriida and Ostracoda exists, it is indicated by the common habit of moulting, the presence of an articulating dorsal hinge, and similarities in the morphology of the carapace.

ARISTALUTA GUTTA sp. nov.

(Pl. 24, figs. 2a-2c, 3a-3d, 4; Text-fig. 59)

Material: *Aristaluta gutta* is a rare species and most of the specimens collected are damaged and distorted to an extent preventing specific description. The specimen Plate 24, figure 4, is for example completely flattened and adds nothing to the diagnosis, but it is still useful for a comparison with other Bradoriida, most of which are also shale specimens.

Measurements:

	Length	*Height*	*Depth*	*Locality*
Pl. 24, figs. 3a-3d CPC 3641	4.4 mm.	3.4 mm.	2 mm.	D13A
Pl. 24, figs. 2a-2c CPC 3642 (holotype)	4.4 mm.	3.5 mm.	2 mm.	D(6-8)
Pl. 24, fig. 4 CPC 3643	6.5 mm.	9 mm.	—	D19A

Selection of holotype: The specimen CPC 3642 is selected as the holotype in preference to CPC 3641, which is a calcite void and in danger of disintegration because of the cleavage of the crystals.

Description: The carapace (for terms see Text-fig. 59) is leperditioid in lateral view. The hinge-line (a-b) is straight and visible from the side. The anterodorsal corner (a), and the anterior extremity (e) are angular. A slightly convex border (a-e-d-c-b) marks the free margin and is widest at the ventral mid (d) and the posterior upper edge (c-b), at the gap; but the border is quite narrow between the anterior extremity and the ventral middle (e-d). The border has a doublure seen in Plate 24, figures 3b, 3c, and 4. The borders fit together and the commissure is closed between a-e-d-c, but remains gaping open from b to c, evidently as a passage for the abdomen and telson. At the posterior end of the hinge (b) a pair of knobs may indicate the position of an interlocking mechanism.

Laterally the valves are trilobate, and the lobes are separated by short sulci. The anterior lobe (1) is the smallest, but rather convex.

The surface is, probably, punctate, as seen in Plate 24, figure 2b, and the test is thin and shiny.

The shape of *A. gutta* is quite similar to some species of *Beyrichona*, as for example, *B. gevalensis* Wiman (vide Ulrich & Bassler). But in *Beyrichona* the distribution of lobes is different and a gap is absent.

Occurrence: *A. gutta* has been found only in the lower half of the Devoncourt Limestone. Its age is the Zones of *Ptychagnostus cassis* (upper part) and *Proampyx agra* (whole range).

DESCRIPTION OF LOCALITIES

The data below are extracted from a register of localities (card catalogue) of north-western Queensland and Northern Territory that contains the observations made in the field, supplemented by entries of subsequent laboratory investigations. These localities are marked also on the 4-mile geological maps published by this

Bureau. The same numbers are marked also on fossil collections and rock specimens. The number of cards already exceeds 1000, and is steadily increasing by new contributions. The card catalogue is an unofficial enterprise initiated by the present author, who takes here the opportunity to thank his colleagues for the most valuable collaboration and ample supply of information. The catalogue is located in the office of this Bureau in Canberra.

The term locality has several meanings. It may refer to a single point of observation, or a point of sampling, or fossil collecting, or a 'field station', or site, or section, that may be larger than a point; the meaning is apparent from the description.

The geographical co-ordinates are taken from the 4-mile-to-an-inch geological sheets.

D1. Lat. 21°15'S., Long. 140°05'E. Left bank of Sandy Creek, at the crossing. Low hills, dissected tabletops. Cambrian subhorizontal or with local dips (0°—5°—10°) in various directions.
(1) Cappings of conglomerate (rounded pebbles of quartz, quartzite, and chert fragments from O'Hara Shale) up to 15 feet; rests on an uneven, eroded surface of (2) O'Hara Shale, silty siliceous, laminated, leached, with chert; a thin lutitic limestone interbed near base; thickness 15 to 20 feet; rests on (3) Selwyn Range Limestone, flaggy, pale calcilutite with a chert bed 2-3 feet thick; 10 feet exposed. In limestone are slickensided fractures, dipping 10° to east. On right bank of Sandy Creek, and east of crossing, a prominent hill with conglomerate rests direct on tilted Selwyn Range Limestone.

D1A. Lat. 21°15'S., Long. 140°05'E. Left bank of Sandy Creek, and about 2 miles west from crossing. Dissected tabletops of O'Hara Shale, silty, and with chert; conglomerate as capping on an eroded surface. The west-facing cliffs of O'Hara Shale are partly cuesta; dip of the underlying limestone increases to west (towards Roaring Fault).

D1B. Lat. 21°15.5'S., Long. 140°05' E. Interfluvium at Roaring Fault. Fault indicated by a train of north-trending rocky crests. Sandstone (hard, almost quartzite) of Mount Birnie Beds cut by fault, and dips east 20° to 30°. East of it Devoncourt Limestone in creek bed on edge (dip 90°); thus an angular unconformity between Middle Cambrian and Mount Birnie Beds.

D6. Lat. 21°25'S., Long. 140°00'E. 3 miles west (south of west) from O'Hara Station. Access cross-country. Five hills, cuestas, facing north-west. Main information collected from outcrops of the eastern hill. Cliffs of shale in south-west and south. Base: Selwyn Range Limestone, light coloured flaggy calcilutite with conchoidal fracture; pyrite concretions; uppermost surface with ripple marks. Dip variable between south and south-west, and between 6° and 15°, rolling. O'Hara Shale rests with an abrupt contact on the Limestone as follows: (1) shale, with chert layers and nodules, 15-20 feet; above follows (2) a bed of chert, few inches thick, variable, discontinuous, apparently with slumps; consists of translucent silica and porous white silica, in irregular contact; in parts abundantly fossiliferous ("lower O'Hara fauna", Öpik, 1956; 1960); above follows (3) shale, with rare fragments of trilobites, about 70 feet, dipping 15°; (4) interbed of fine grained sandstone, 3-5 inches thick, very fossiliferous (*Eugonocare, Proceratopyge, Pseudagnostus,* etc.). Off the foot of the dip slope of cuesta, a pediment outcrop with a thin layer of silicified oolitic limestone (fossiliferous: *Pseudagnostus, Idamea*). The dip of the beds of the pediment outcrop increases towards south-west (Bronzewing Fault); fresh rock (shale with a band of limestone nodules, friable sandstone interbeds), all steeply dipping, in a small creek. Subhorizontal shale in the cliff, on the other side of fault, Ferruginous and siliceous duricrust on top. Mottled colours, but red prevails.

D7. Lat. 21°18'.5S., Long. 140°05'E. Section at Roaring Bore, Text-figure 3. The section was paced, and observations of eighteen points recorded as D7/1-D7/18. Selwyn Range Limestone and Devoncourt Limestone were visible 80% of their total thickness, Roaring Siltstone 90%. Devoncourt Limestone is seen in a stream bed; the stream is not quite linear, and blanks in the stream were only partly covered by pediment outcrops along its banks. No fossils were found in the Devoncourt Limestone; parts of it cannot be therefore assigned to zones. The Figure shows the mode of deformation: Devoncourt Limestone rolling, dips between 12° and 40°; Roaring Siltstone asymmetrically folded, dips 20°, 40° and 32°. Several small strike faults in Devoncourt Limestone affect the thickness figure. The order below is descending.

D7/1. O'Hara Shale, lateritic, dip east-south-east 10°, rapidly decreasing to 3°.

D7/2-D7/3. Selwyn Range Limestone and upper part of Devoncourt Limestone, partly covered by rubble and soil; a small strike fault seems to intervene. Dip of limestone 10°.

D7/4. Creek bed, grey, flaggy, sandy limestone with marly interbeds;

D7/5. Dip increases to 40°; grey and varicoloured limestone, with shaly and marly interbeds.

D7/6-D7/10. Dip decreasing to 12° and increasing to 20°; laminated pink two-toned beds appear and become gradually prominent downward.

D7/11. Contact of Devoncourt Limestone (pink, and two toned, laminated, thick bedded) and Roaring Siltstone (grey, friable, non-calcareous); dip 20°; exposed in stream bed just south of Bore.

D7/12-D7/14. Roaring Siltstone, with shale and sandstone interbeds. Dip 20°, but rolls present.

D7/15. A point, marked on map by fossil symbol, about ¼ of a mile south-south-west from section traverse. A sandstone interbed, apparently slumped, seen only in the bed of a small stream, on a distance of about 10 feet only. Fossils very abundant. Its position is about 150-180 feet below the top of Roaring Siltstone.

Acontheus burkeanus sp. nov.

Acroteta sp. indet.

Blystagnostus laciniatus gen. nov. et sp. nov.

Centropleura sonax sp. nov.

Centropleura phoenix sp. nov. (fragments)

Diplagnostus sp. *I*

Grandagnostus sp. (one imperfect cephalon, 10 mm. long)

Hypagnostus brevifrons (Angelin), very abundant.

Leiopyge laevigata (Dalman)

Peronopsis scaphoa sp. nov.

Peronopsis sp. G.

Proampyx sp. *D.*

Pseudophalacroma dubium (Whitehouse), common.

Pleodioria tomacis gen. nov. et sp. nov.

Ptychagnostus aculeatus (Angelin), rare

Ptychagnostus cassis sp. nov., abundant

Ptychagnostus (*Goniagnostus*) *nathorsti* (Brogger), rare

Svealuta sp. (fragments)

North of section traverse a similar, but very corrugated (slumped) bed occurs with fragmentary fossils, including *Tosotychia sors.*

D7/16, D7/17. Reversal of dip from 20° east to 40° west, and to 32° east again. Banded (pink and yellow) shale and siltstone.

D7/18. Crest of cuesta, representing the fault line. Well laminated, hard (indurated), banded siltstone with numerous fractures (minute 'faults' with ¼ of an inch of displacement), dip 32° east. Steep slope of cuesta facing west, covered with rubble.

At its foot, and sloping to west, outcrops of basement rocks (pink granite, nearest to fault; pink, apparently crushed pegmatitic granite; about half a mile west—purplish porphyry and quartzite in creek bed).

The displacement along Roaring Fault decreases rapidly to south-west but the fault line (broken line on map) remains a train of cuestas; purple to brown regolithic clay with rock fragments, up to 20 feet thick, appears between the base of the Roaring Siltstone and basement, especially in outliers north-west of fault line. It is regarded as part of Mount Birnie Beds (Lower Cambrian). Along fault line in vicinity of Roaring Bore lenticular boulders (some feet in length) occur of presumably silicified oolithic limestone with fossil fragments, perhaps dragged up in the fault. The Roaring Fault as seen from the map is a fault zone parts of which are not yet studied in detail. Roaring Siltstone is 250 feet thick; it is more than 200 feet, because the Bore is 200 feet deep in siltstone and stands some hundreds of feet west from siltstone/shale contact. Variability of thickness is present on account of topography of the Precambrian subsurface. Devoncourt Limestone is not less than 350 feet, but calculation from attitude indicates 400-450 feet. Selwyn Range is estimated 100 feet.

D11. Lat. 21°20′.5S., Long. 139°58′E. A summit of cuesta (and a group of low ridges), about 50 feet above plain; Roaring Siltstone (with chert), dip 10° south. Rests direct on basement rocks. On older maps its name is 'Boundary Hill'; in local usage this name refers to the hill at loc. D26.

D12. Lat. 21°22′S., Long. 140°00′E. Road crossing Burke River. High sandy banks. In river bed flaggy blue impure laminated limestone; dip low, 2-3° south-south-east.

D12A. Lat. 21°21′S., Long. 140°01′E. Pediment outcrops along road. Grey sandy flaggy limestone, low dip to south-south-east.

Lingulella sp., common.

D13. Lat. 21°22′S., Long. 139°57′ E. Plain, partly with dense scrub and pediment outcrops. Pilgrim Fault exposed in creek sixty yards west of fence. Roaring Siltstone vertical at fault; with dip decreasing to 25° off fault. Lower part of Roaring Siltstone not on surface. Roaring Siltstone and Devoncourt Limestone together form a belt of contorted beds 150 yards wide. East of it 5-10 degrees of dip in limestone. Slickensided fractures dipping east abundant. Fossils in Devoncourt Limestone; *Centropleura phoenix* sp. nov., and agnostids (fragmentary).

D13A. South of road, within half a mile of loc. D13. 13A marks a fossil collecting ground, recorded as points '6.3 miles', 6.75 miles', '6.7 miles', and '6.8 miles' east of Duchess. Pediment outcrops in scrub ('Turkey bush'). Devoncourt Limestone, rolling attitude, dips low 2-5°).

Acroteta sp.

Amphoton cf. *bensoni* sp. nov.

Centropleura phoenix sp. nov.
Aristaluta gutta gen. nov., sp. nov.
Hypagnostus brevifrons (Angelin)
Hypagnostus willsi sp. nov.
Leiopyge laevigata (Dalman)
Lingulella sp. (Dalman)
Pleodioria ? sp.
Proampyx agra sp. nov.
Pseudophalacroma dubium (Whitehouse)
Svealuta sp. *M* aff. *primordialis* (Linnarsson)
Leiopyge laevigata armata (Linnarsson)

D14. Lat. 21°16′.5S., Long. 140°06′E. Creek crossing, rocky gully. Impure, sandy limestone with softer marly interbeds containing limestone ellipsoids and pyrite. Marly limestone bed contains small brown or red fragments, probably of hydroids.

D15. Lat. 21°21′.5S., Long. 139°59′E. Creek crossing 8.5 miles east of Duchess. Plain with small limestone pediment outcrops. In creek bed hard laminated flaggy smelly limestone interbedded with grey marly limestone.

Acroteta sp.
Centropleura phoenix sp. nov. (fragments)
Diplagnostus humilis (Whitehouse)
Hypagnostus cf. *hunanicus* Lu
Leiopyge laevigata (Dalman)
Leiopyge laevigata armata (Linnarsson)
Ptychagnostus fumicola sp. nov.

D16. Lat. 21°20′S., Long. 140°03′E. Plain with pediment outcrops of limestone (see Text-fig. 6). Grass plain near the road, scrub ('turkey bush') in the south. Trend of beds shown on map, dip variable (2-3°) to south-east. Fracture cleavage becomes apparent under the hammer; it dips south-east about 70°. Hard, grey, sandy, smelly, flaggy limestone. Complete specimens of *Centropleura* just south of road (shallow pit where fossils were quarried).

Centropleura phoenix sp. nov.
Aristaluta gutta gen. nov., sp. nov.
Proampyx agra sp. nov.

D17A. Lat. 21°22′S., long. 139°58′E., about 7 miles east of Duchess. Grass plain sloping gently to north. Large pediment outcrops of limestone, dipping south 2-3°. At the road a low rocky step (2-3 feet high) trending north of east. Hard pink and grey laminated limestone with *Acrotreta.* Some hundred yards north, flaggy, hard, smelly dark grey limestone interbeds with

Amphoton bensoni sp. nov.
Sponge spicules
Worm burrows
Acrotreta sp.
Lingulella sp.
Proampyx agra sp. nov. (one pygidium)

and in a deeper bed (marly limestone interbed)

Ptychagnostus cassis sp. nov.

D17B. As 17A, but about half a mile north.

Pseudophalacroma sp. *L*
in sandy limestone

D18. Lat. 21°19′.5S., Long. 140°04′E. Road crossing Boomerang Creek. Small pediment outcrops of Devoncourt Limestone. West of crossing the limestone contains small and thin lenticular chert layers—the only known occurrence of chert in Devoncourt Limestone. East bank: in 1952 road work ploughed up a fossiliferous bed covered again in 1954. It is dark, flaggy limestone with silicified flat dipping (10°) slickensided fractures; lamellar interbeds of calcite with fossils; small calcite lenses with granules of silica. It is the only known occurrence of Devoncourt Limestone with fossils accumulated on a bedding plane. Usually they are scattered in the rock.

Acrothele sp. *A*
Acroteta (two forms)
Amphoton arta sp. nov.
Aristaluta gutta gen. nov., sp. nov.
Centropleura phoenix sp. nov.
Crepicephalus ? sp. *H*
Delagnostus dilemma gen. nov., sp. nov.
Diplagnostus planicauda vestgothicus Westergaard
Grandagnostus velaevis sp. nov.
Hypagnostus hippalus sp. nov.
Hypagnostus sp. *F*
Leiopyge laevigata (Dalman)
Micromitra sp. *B*
Mapania dicella sp. nov.
Mapania synophrys sp. nov.
Proampyx agra sp. nov.
Pseudophalacroma dubium (Whitehouse)
Pseudophalacroma sp. *K*
Ptychagnostus (*Goniagnostus*) sp.*P*, aff. *nathorsti*
Ptychagnostus aculeatus (Angelin)
Ptychagnostus sp. *O*
Tosotychia sors, gen. nov., sp. nov.

Traverse to north-west: Roaring Siltstone/Devoncourt Limestone contact mostly covered by soil and rubble; Roaring Fault appears as a shattered line without displacement; the basement is gneiss; at the base of outliers the 'basal purple clay and arkose' passes into the decomposed gneiss at its base.

D19-20. The fault block at the northern end of Pilgrim Fault.

D19A. Lat. 21°20′S., Long. 139°57′E. Plain with scrub, savannah; low limestone terraces; the eastern fault is an elevated indurated ridge. Outcrops on surface and in two dry wells (fresh rock). Displacement on eastern fault about 200 feet; limestone fills a shallow syncline or basin. Limestone (on surface) laminated, grey, fine grained, splintery, with two or more marly interbeds (terraced topography).

Acroteta sp., flattened specimens cover bedding plane in marly bed from well.
Amphoton bensoni sp. nov.
Aristaluta gutta gen. nov., sp. nov.

In wells: laminated, dark, smelly limestone, some beds with alternating black and grey laminae; marly limestone interbeds with circular limestone ellipsoids 5-6 inches thick; ellipsoid material limestone, minutely laminated, grey, with thin black laminae.

D19B. Roaring Siltstone, pediment of siltstone with sandstone interbeds; sandstone as floaters arranged in strike lines; fossils in sandstone:

Acroteta sp.
Centropleura (fragments)
Leiopyge laevigata (Dalman)
Pseudophalacroma dubium (Whitehouse)
Ptychagnostus cassis sp. nov. (abundant)
Tosotychia sors, gen. nov., sp. nov.

D20. Lat. 21°21'S., Long. 139°56'.5E. Cuesta facing west. Roaring Siltstone — with chert, contorted, dips east 20-40 degrees; Pilgrim Fault visible, Burke River almost coincides with fault line.

D21. Lat. 21°20'.5S., Long. 140°03'E. See Text-figure 4. Plain, in parts apparently swampy; pediment outcrop, ribbed. Flaggy, bituminous, smelly, dark grey limestone with numerous flat dipping slickensided fractures.

Acroteta sp.
Diplagnostus cf. *planicauda vestgothicus* Westergaard
Grandagnostus velaevis sp. nov.
Holteria arepo sp. nov.
Hypagnostus varicosus sp. nov.
Leiopyge laevigata armata (Linnarsson)
Lingulella sp.
Mapania cf. *faceta* sp. nov.
Mapania sp.
Pseudophalacroma dubium (Whitehouse)

D26. Lat. 21°23'S., Long. 139°58'E. Text-figures 8 and 10. High (estimated 150 feet) terraced hill on the corner of east, and south trending terraced escarpments; at its foot pediment plain with scrub ('turkey bush'). Locally known as Boundary Hill (see D11). Lower terraces (about 20 feet) Hard, grey, smelly, flaggy splintery limestone (top of Devoncourt Limestone), with fossils; recorded as 'D26, lower bench'.

Agnostus sp. *E.*, cf. *neglectus* Westergaard
Amphoton sp.
Diplagnostus cf. *planicauda vestgothicus* Westergaard
Hypagnostus cf. *hippalus* sp. nov.
Leiopyge laevigata armata (Linnarsson)
Mapania faceta sp. nov.
Mapania (fragments)
Micromitra sp. *B*

Above, with a passage, follows lutitic limestone (calcilutite) with marly interbeds—Selwyn Range Limestone. Dip east, and south, about 5°.

D27. Lat. 21°23'S., Long. 139°59'E. On Trekelano track. Terraced escarpment with salient angles facing north and flanked by ravines (bastion topography). Dip 7-8° south (see Text-fig. 9). In the south dissected pediment plateau with residuals of O'Hara Shale capping some of the salients. Hard calcilutite with conchoidal fracture and laminated marly interbeds. Beds of dolomitic limestone are present. Selwyn Range Limestone.

D28. Lat. 21°26′.5S., Long. 139°57′.5E. Eastern flank of the valley along Pilgrim Fault. Dissected shale cuestas facing west; valley floor of steeply dipping limestone. Considerable lateritization of O'Hara Shale; in breakaways and gullies soft, well laminated shale and siltstone with thin sandstone interbeds. Chert layers are present. Chert and silicified shale litter abundant. Near the base of shale a chert layer (poorly exposed) with the 'lower O'Hara fauna' (see Opik, 1956, 1960).

D29. Lat. 21°26′S., Long. 139°59′.5E. O'Hara Shale country; ferruginous and siliceous duricrust cappings of rolling low hills with deep gullies in between; more to the west the top of the Selwyn Range Limestone is exposed in streams and as small pediments. Overall colour of rocks is red. The point D29 is, however, a white butte (about 60-70 feet high), the only white in the landscape, visible from a distance, and on air photographs. Silty siliceous shale with chert layers. At the western foot of the white butte in a small stream bed, and at a distance of 2-3 yards the only chert bed, 4-5 inches thick, with 'lower O'Hara fauna' present. A young gum tree blazed with 'D29' and chert chips on creek bank indicate the spot. Access very rough (on wheels along the fault cliff from D6).

D33. Lat. 21°16′S., Long. 140°07′E. Near the junction of main road with 'Old Track' and along Old Track across Selwyn Range. Terraced limestone hills (bastions) (Text-figs. 5 and 7). Small tilt blocks; joints trending west to north with heads of streams. Dissected transitory pediment, with lateritic (ferruginous) shale, and chert rubble on highest tops. Aphanitic limestone (calcilutite), flaggy, in some layers laminated, limestone with chert beds and biscuits, interbedded with laminated marly limestone. Estimated (and visible) thickness 100 to 120 feet.

Numberless localities

In the south-western corner of the map the fossil locality sign indicates an outcrop of Roaring Siltstone in breakaway in creek, near Trekelano track crossing. Shale is corrugated, dips steeply east, and contains agnostids (*Ptychagnostus cassis* sp. nov.).

Between D18 and D21, and east of main road agnostids have been noted in Devoncourt Limestone.

GLOSSARY

(Explanation of new names of fossils)

agra (*Proampyx*): Abbreviated from *Agraulos* (Greek, fem. name, also a name of genus of trilobites); alludes to the affiliation of the genera *Proampyx* and *Agraulos*.

Amphoton: Generic name of a trilobite (Lorenz, 1906), Greek, 'with ears on both sides', traditionally feminine, gender originally not indicated.

arepo (*Holteria*): Lat., the meaningless word from the known magic square of Pompeii.

Aristaluta: Combined from generic names *Aluta* and *Aristozoe*.

arta (*Amphoton*): Lat., narrow.

bensoni (*Amphoton*): After the late W. N. Benson, the Australian and New Zealand geologist.

Blystagnostus: Greek, blyst—bubble, allusion to the shape of the pygidial axis.

burkeanus (*Acontheus*): Refers to the explorer R. Burke, and to the Burke River.

cassis (*Ptychagnostus*): Lat., snare, trap, alluding to the difficulties in identification of this species.

Delagnostus: Lat., delere, to efface; abbreviated from 'Del (et) agnostus'.

dicella (*Mapania*): Greek, dikella, double pick; allusion to the shape of the border with plectrum.

dilemma (*Delagnostus*): Allusion to the uncertainty of its relationship.

faceta (*Mapania*): Lat., elegant.

fumicola (*Ptychagnostus*): Lat., smoke dweller, allusion to the occurrence at Smoky Creek.

gutta (*Aristaluta*): Lat., drop.

hippalus (*Hypagnostus*): Hippalus, a navigator of antiquity.

imitans (*Grandagnostus*): Lat., imitating, alluding to its pygidial structure.

laciniatus (*Blystagnostus*): Lat., fringed.

phoenix (*Centropleura*): Greek, after the mythological bird. The specimen Plate 2 was burned in fire and recovered from the cinders.

Pleodioria: Greek, full with double points (tips).

scaphoa (*Peronopsis*): Greek, hollow hem; with a channelled border.

sonax (*Centropleura*): Lat., noisy, roaring, allusion to the occurrence at the Roaring Bore.

sors (*Tosotychia*): Lat., a share, e.g., in booty.

Svealuta: From 'Svea' Sweden, and the generic name *Aluta*.

synophrys (*Mapania*): Greek, with joined brows.

tomacis (*Pleodioria*): Greek, 'with split tips' of sclerites.

Tosotychia: Fem., Greek, so much of chance; alludes to the genus *Chancia*.

varicosus (*Hypagnostus*): Lat., with swollen veins.

velaevis (*Grandagnostus*): Lat., very smooth.

willsi (*Hypagnostus*): After the explorer W. J. Wills.

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PLATE 1.

Pleodioria tomacis gen. nov. et. sp. nov. .... Page 50

Figs. 1a, 1b.—Two views (x 3, 7) of holotype CPC 3646.
Roaring Siltstone, loc. D 7/15.

Worm burrows.

Fig. 2—x 1, CPC 3648. Devoncourt Limestone, loc. D17.

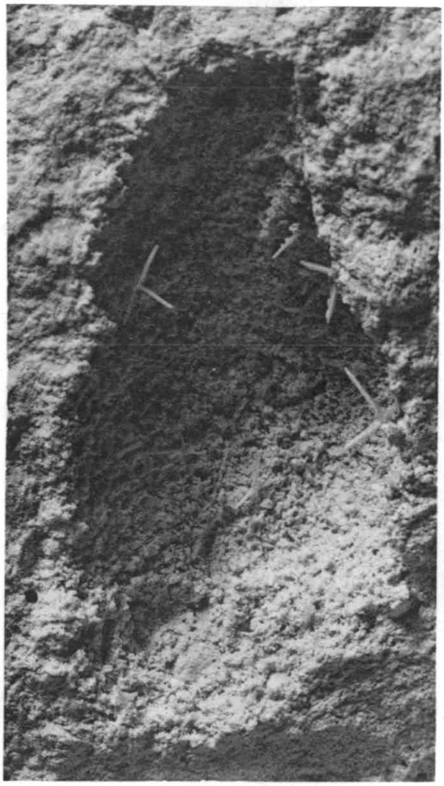
Micromitra (*Paterina*) sp. *B* .... Page 51

Fig. 3.—Ventral valve (x 3), CPC 3644. Devoncourt Limestone, loc. D18.

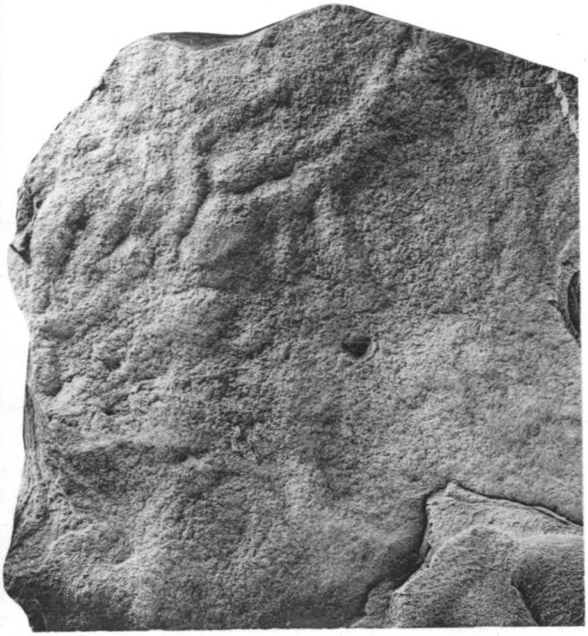
Fig. 4.—Ventral valve (x 7), CPC 3645. Devoncourt Limestone (uppermost beds), loc. D26. (at the foot of hill).

Acrothele sp. *A* .... Page 51

Fig. 1—Ventral valve (x 6), rubber cast of CPC 3647. Devoncourt Limestone, loc. D18.



1a



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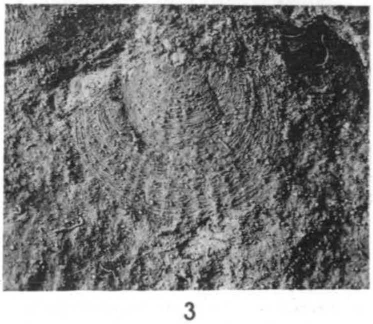

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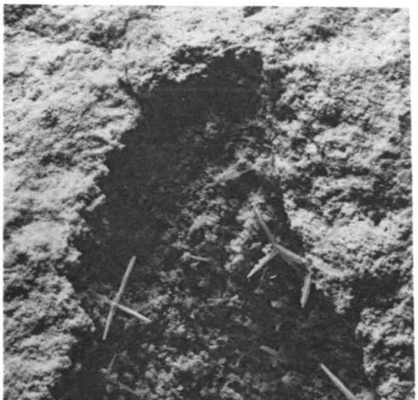

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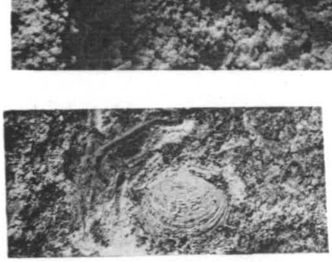

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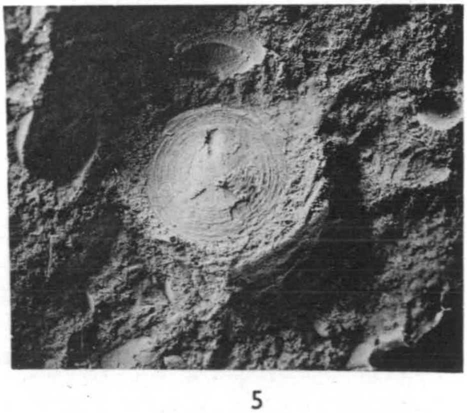
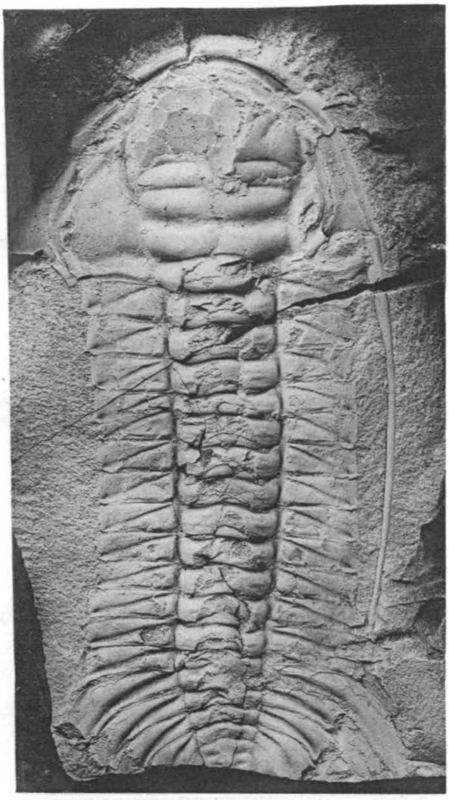


5

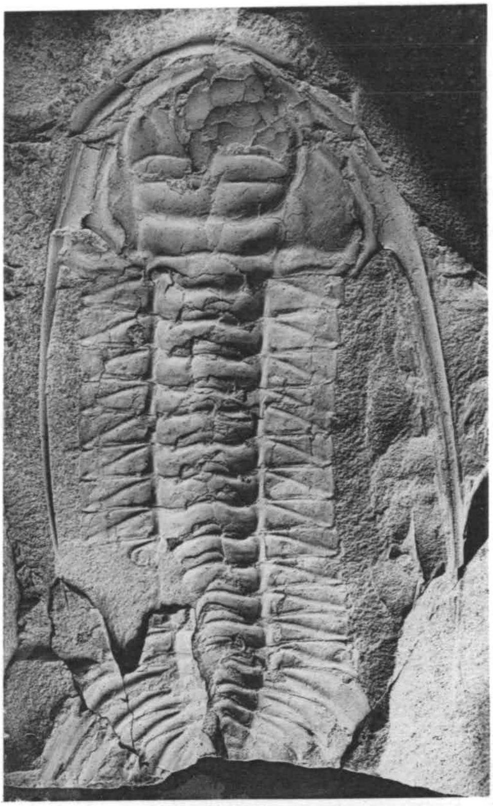
PLATE 2.

Centropleura phoenix sp. nov. .... **Page 105**

Three views of holotype, CPC 3484. Figs. A and B (external mould) x 1; Fig. C x 2.3. Devoncourt Limestone, loc. D16.



A



B

C

PLATE 3.

Centropleura phoenix sp. nov. .... Page 105

Fig. 1.—Crandium and part of thorax, partly decorticated (x 2), CPC 3485. Devoncourt Limestone, loc. D13A.

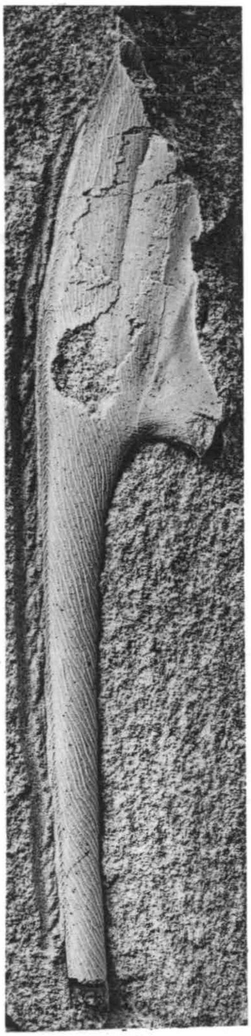
Fig. 2.—Left free cheek, fragmentary (x 3), CPC 3487. Outer flange preserved. Devoncourt Limestone, loc. D16.

Fig. 3.—Left free cheek, a fragment (x 2), rubber cast of CPC 3486. Devoncourt Limestone, Loc. D16.

Fig. 4.—Hypostoma (x 3), rubber cast of CPC 3489. Devoncourt Limestone, loc. D16.

Fig. 5.—Free pleura of fourteenth segment, ventral view (x 2.3), CPC 3488.

Fig. 6.—Pleura of first segment (x 10), CPC 575. Devoncourt Limestone, loc. D16.



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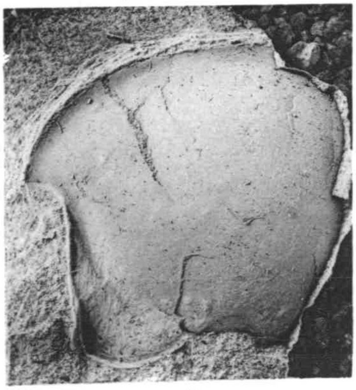

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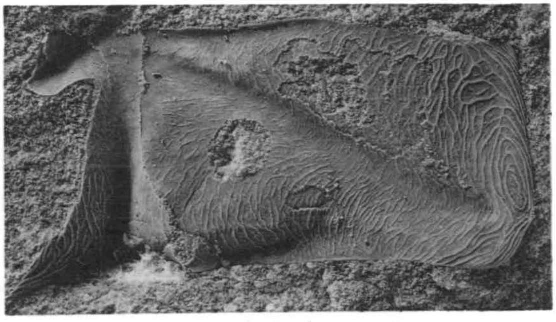

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PLATE 4.

Centropleura phoenix sp. nov. .... Page 105

Fig. 1.—First segment (x 6), rubber cast of CPC 576, parietal surface of test. Devoncourt Limestone, loc. D13A.

Fig. 2.—Right posterolateral extremity of cranidium (x 6), rubber cast of CPC 3494. Same specimen Plates 5, 6 and 7. Devoncourt Limestone, loc. D16. For correct orientation compare with fig. 3a.

Figs. 3a, 3b.—Cranidium, CPC 3493.

3a.—Left fixed cheek, rubber (x 6).

3b.—Cranidium (x 2).

Devoncourt Limestone, loc. D13A.

1

3a

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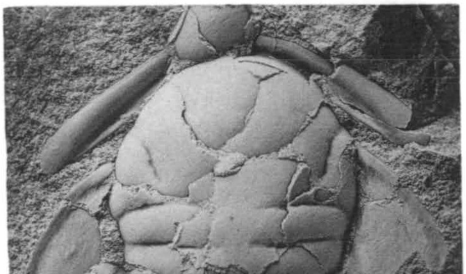

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PLATE 5.

Centropleura phoenix sp. nov. .... Page 105

Cranidium, CPC 3494. (Same specimen Plates 4, 6, and 7)

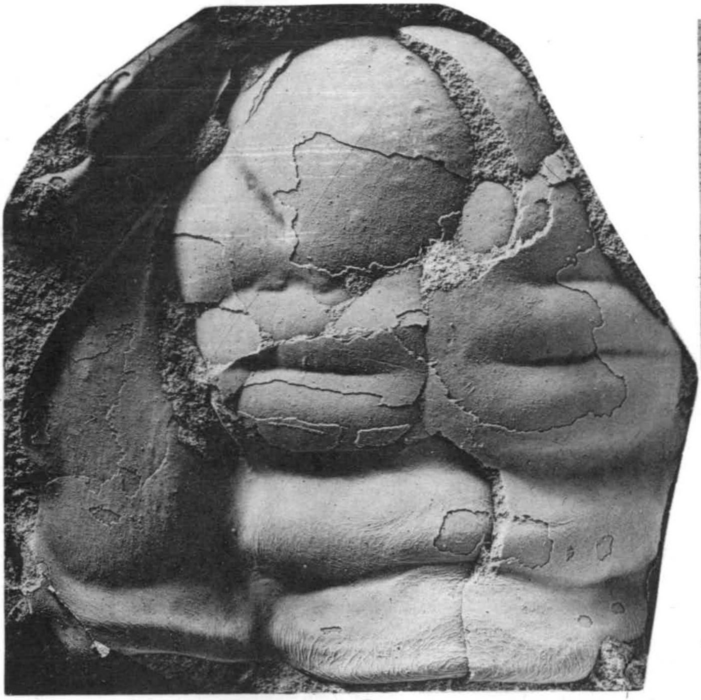
Fig. A.—Cranidium (nat. size).

Fig. B.—Rubber cast (slightly reduced).

Fig. C.—Rubber cast (x 2.5).

Fig. D.—Rubber cast of occipital lobe (x 4).

Fig. E.—Rubber cast of anterolateral limb (pathological), frontal lobe (with muscle spots), and part of cheek and palpebral lobe (x 4). Devoncourt Limestone, loc. D16.



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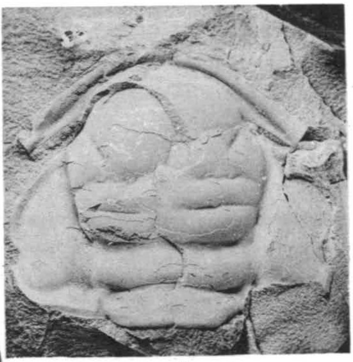

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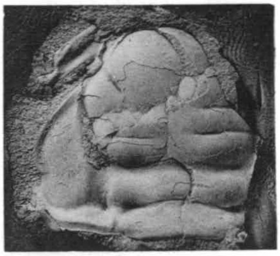

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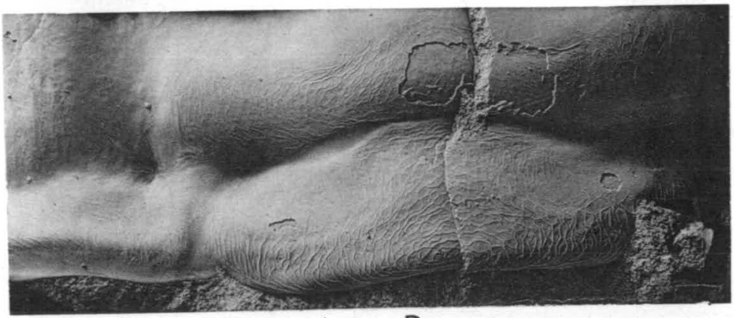

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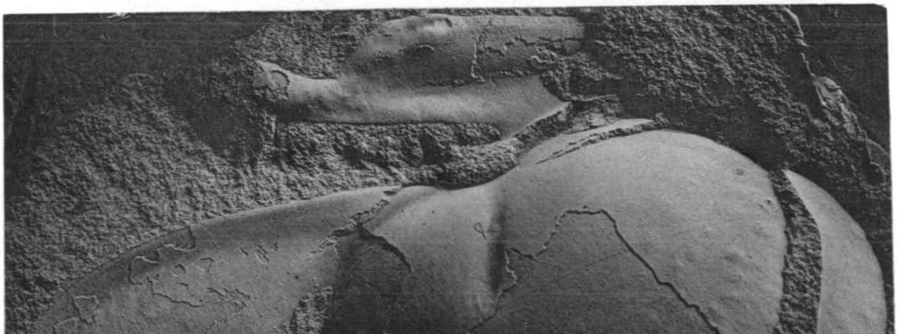

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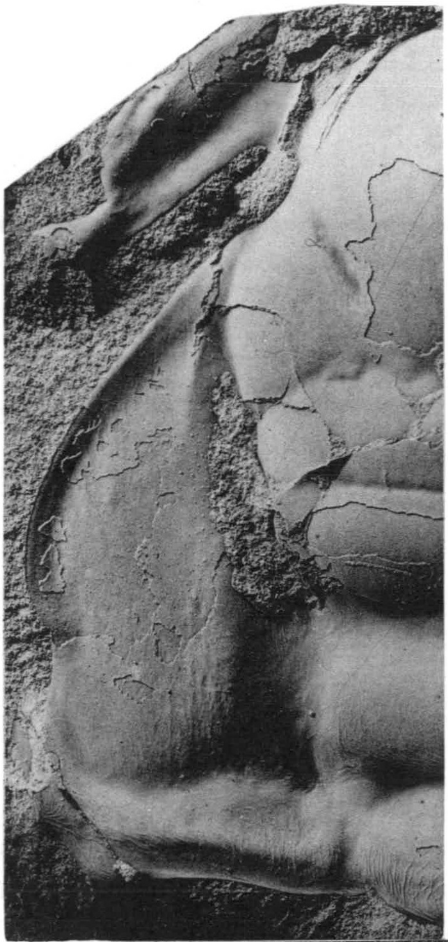
PLATE 6.

Centropleura phoenix sp. nov. .... Page 105
Cranidium, CPC 3494.
Same specimen Plates 4, 5, and 7.

Fig. A.—Left side, rubber (x 4).
Fig. B.—Parietal surface of junction of dorsal and occipital furrows (x 11).
Fig. C.—Occipital lobe, rubber (x 11). Devoncourt Limestone, Loc. D16.



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B

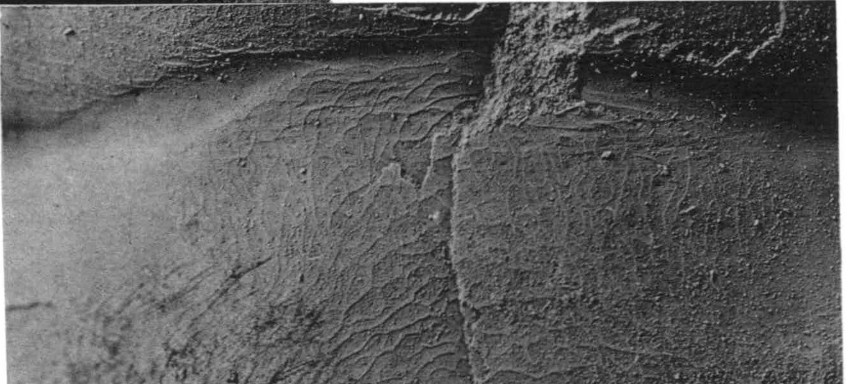

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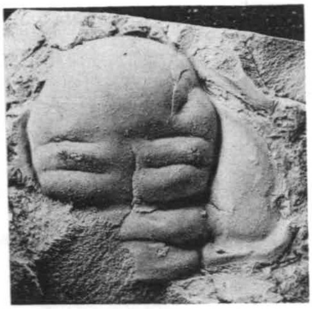
PLATE 7.

Centropleura phoenix sp. nov. .... Page 105
Devoncourt Limestone, loc. D16

Figs. 1a-1e.—A cranidium in five different views (x 2.5). CPC 3495.
Fig. 2.—A cranidium, rubber cast (x 1), from CPC 3503.
Fig. 3.—An almost complete cranidium (x 1), CPC 3496.
Fig. 4.—Frontal lobe, detail, rubber (x 8), of CPC 3494. Same specimen Plates 4, 5, and 6.
Fig. 5.—Frontal lobe of glabella (a fragment) (x 8), CPC 3497.
Fig. 6.—Pygidium and four posterior segments (x 4), rubber cast of CPC 3498.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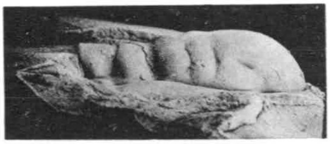
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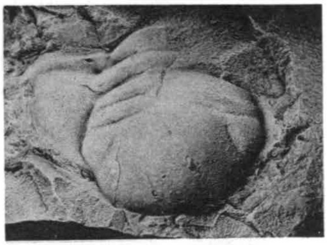
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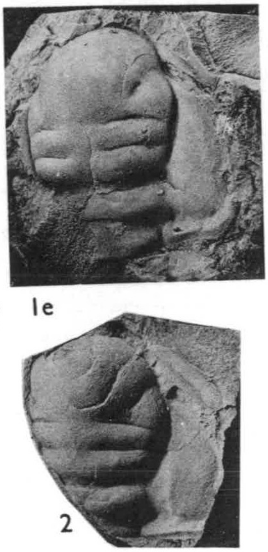
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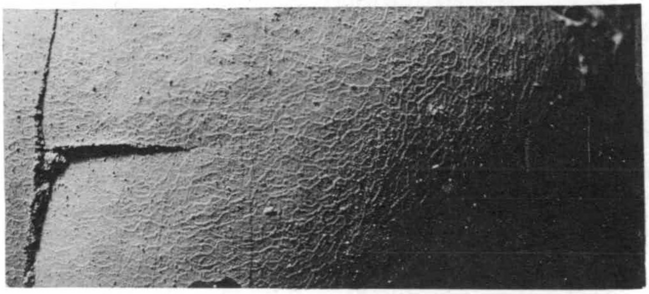
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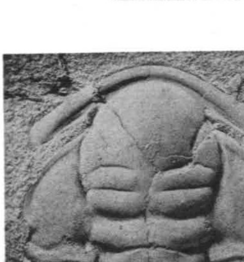
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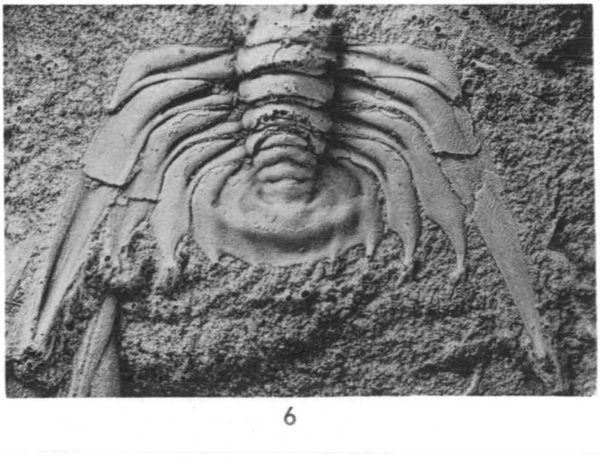
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PLATE 8.

Centropleura phoenix sp. nov. .... Page 105

Devoncourt Limestone, loc. D16.

Fig. 1.—Pygidium and posterior segment (x 2), rubber cast of CPC 3499.

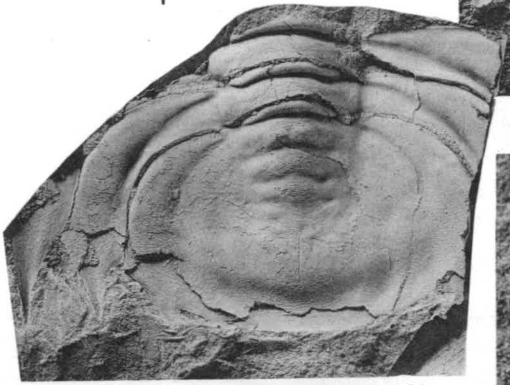
Figs. 2a, 2b.—Pygidium with two posterior segments (2b. is rubber cast) (x 2), CPC 3500.

Figs. 3a, 3b.—A pygidium. Fig. 3a x 2.2, Fig 3b. x 10. CPC 3491.

Fig. 4.—Pygidium and parts of thorax (x2). An exuvia. CPC 3501.

1

2a



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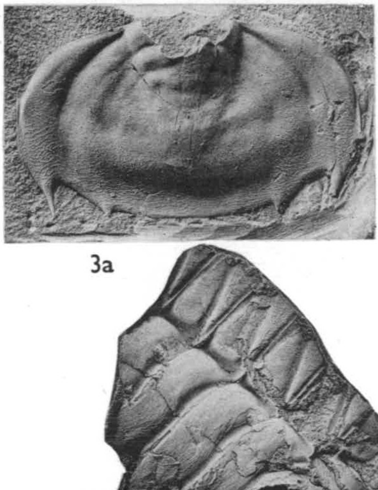

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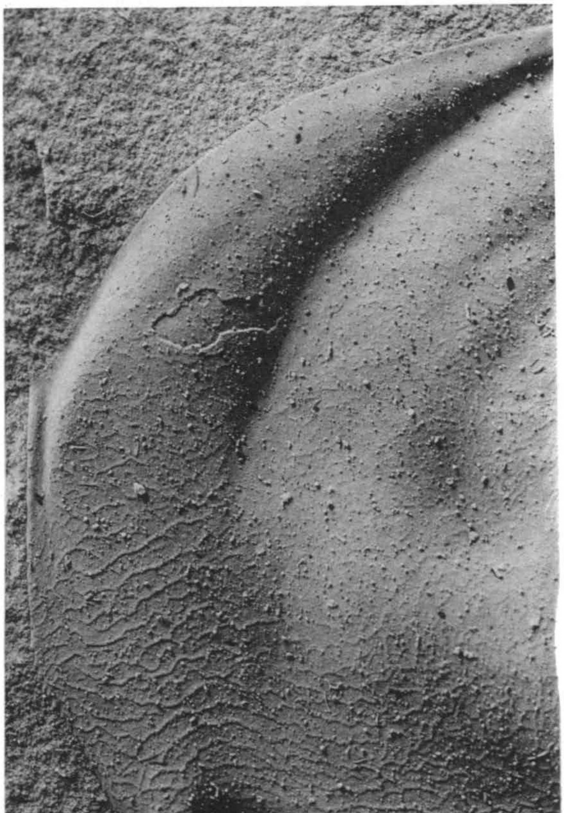

3b

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Plate 9.

Centropleura sonax sp. nov. .... **Page 131**

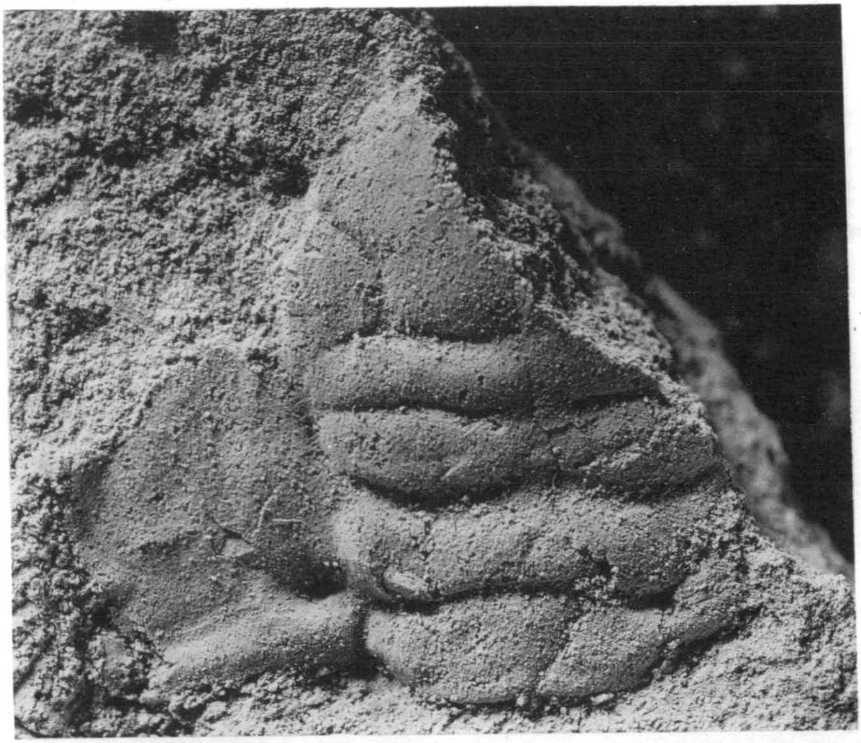
Roaring Siltstone, loc. D 7/15

Fig. 1.—Cranidium (x 8), holotype, CPC 3504.

Fig. 2.—Small cranidium (x 4), CPC 3505.

Fig. 3.—Small pygidium (x 4), CPC 3507.

Figs. 4a-4c.—A larger pygidium, CPC 3506; figs. 4a, and 4c.—x 2; fig. 4b. (rubber) — x 4.



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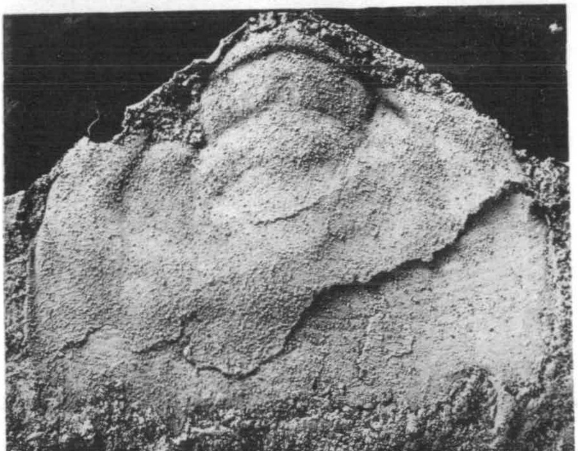


4b

4c

PLATE 10.

Roaring Siltstone, loc. D 7/15.

Acontheus burkeanus sp. nov. .... Page 135

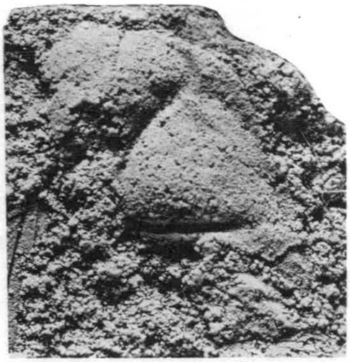
Fig. 1.—Fragmentary cranidium (x 9), CPC 3523.
Fig. 2.—Small cranidium (x 9), CPC 3524.
Fig. 3.—Immature cranidium (x 8), CPC 3525.
Fig. 4.—Pygidium (x 6), holotype, CPC 3526.
Fig. 5.—A larger pygidium (x 8), CPC 3527.
Fig. 6.—Small pygidium (x 4), CPC 3528. Its counterpart in left lower corner of fig. 9.
Fig. 7.—Pygidium (x 8), CPC 3529.

Proampyx sp. *D*. .... Page 148

Fig. 8.—Fragmentary pygidium (x 3), CPC 3531.
Fig. 9.—Fragmentary cranidium (x 3), CPC 3530.

Centropleura sonax sp. nov. .... Page 131

Fig. 10.—Pleura of fifteenth segment, and a cheek spine (x 3), CPC 3508.



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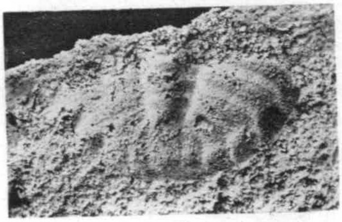

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PLATE 11.

Amphoton bensoni sp. nov. .... Page 136

Figs. 1a, 1b.—Cranidium, holotype CPC 3517; fig. 1a—x 2.2, fig. 1b— x 4. Devoncourt Limestone, loc. D17.

Fig. 2.—Complete specimen (x 1), CPC 3516. Devoncourt Limestone, loc. D19.

Figs. 3a, 3b.—Right free cheek, CPC 3519. Fig. 3a— x 2; fig. 3b—x 4. Devoncourt Limestone, loc. D19.

Fig. 4.—Fragmentary cranidium (x 2), CPC 3518. Devoncourt Limestone, loc. D19.

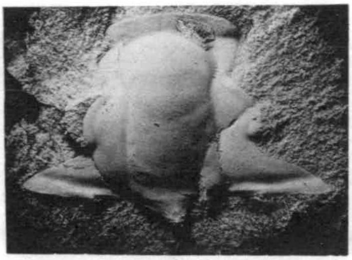
Fig. 5.—Pygidium (x 2), CPC 3520. Devoncourt Limestone, loc. D19.

Fig. 6.—Pygidium (x 2), CPC 3521. Devoncourt Limestone, loc. D19.

Fig. 7.—A pygidium (x 2), CPC 3522. The pygidium is disrupted and its parts displaced by a flat dipping slickensided fracture. Devoncourt Limestone, loc. D19.

Ptychagnostus sp. *O* .... Page 85

Fig. 8.—Pygidium (x 6), CPC 3582. Devoncourt Limestone, loc. D18.



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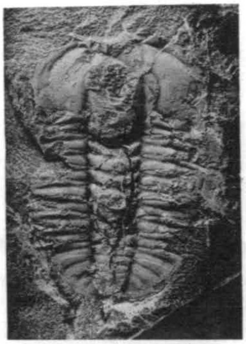
3a



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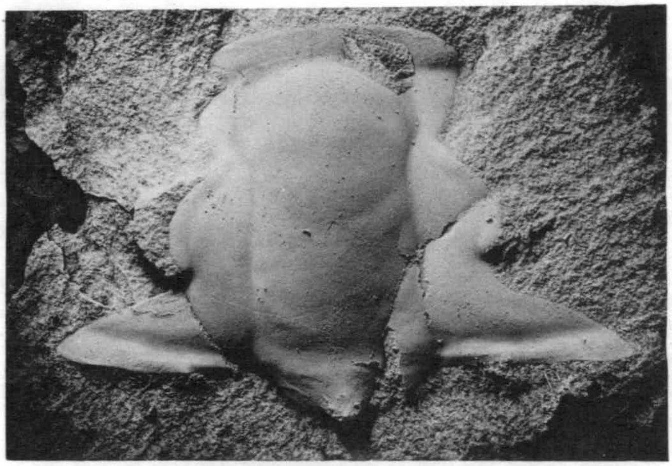

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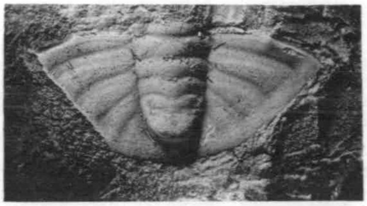

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PLATE 12.

Proampyx agra sp. nov. .... Page 146

Fig. 1.—Cranidium (x 3), Holotype CPC 3510. Devoncourt Limestone, loc. D18.

Fig. 2.—Pygidium (x 3), CPC 3514. Devoncourt Limestone, loc. D13A.

Fig. 3.—Complete specimen (x 1.8), rubber cast from CPC 3512. Devoncourt Limestone, loc. D16.

Fig. 4.—Cranidium, damaged, but palpebral lobes well preserved (x 2), CPC 3511. Devoncourt Limestone, loc. D18.

Figs. 5a, 5c.—Cephalon and thorax, CPC 3513. Fig 5a — x 2; fig. 5b (rubber) — x 2; fig. 5c (rubber) — x 6. Devoncourt Limestone, loc. D16.

Figs. 6a, 6b.—A pygidium (x 3), CPC 3515. 6b is rubber cast. Devoncourt Limestone, probably loc. D14.


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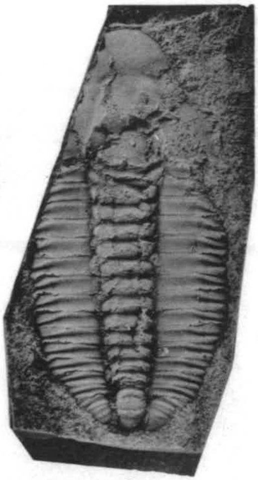
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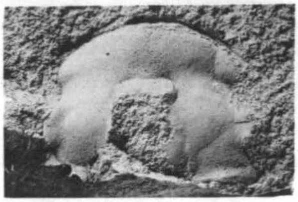
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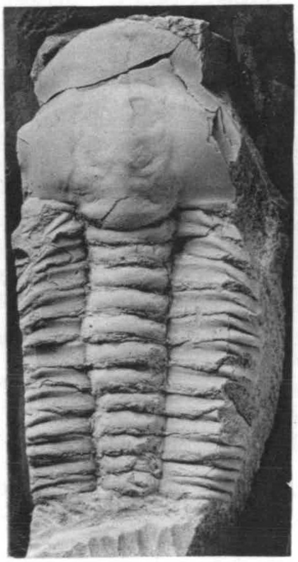
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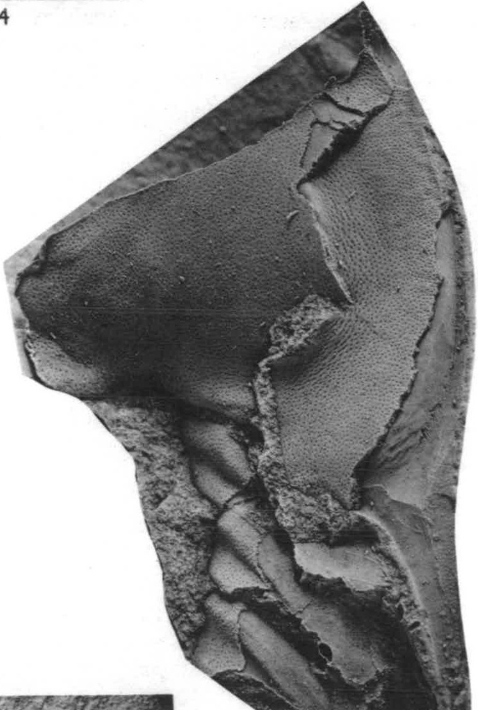
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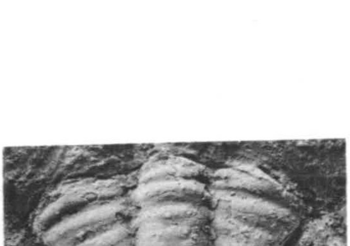
6a


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PLATE 13.

Mapania synophrys sp. nov. .... Page 168

Fig. 1.—Cranidium (x 5.7), holotype CPC 3532. Devoncourt Limestone loc. D18.
Fig 2.—Cranidium (x 5.7), CPC 3533. Devoncourt Limestone, loc. D18.
Fig. 3.—Pygidium (fragment) (x 3.5), CPC 3535. Devoncourt Limestone, loc. D18.

Mapania faceta sp. nov. .... Page 170

Fig. 4.—Cranidium (x 8), holotype, CPC 3538. Devoncourt Limestone. loc. D26.

Mapania ?dicella sp. nov .... Page 171

Fig. 5.—Crandium (x 2.5), CPC 3534. Devoncourt Limestone, loc.?

Mapania cf. *faceta* .... Page 170

Fig. 6.—Pygidium (x 6), CPC 3537. Devoncourt Limestone, loc. D21.

Mapania ?dicella sp. nov. .... Page 171

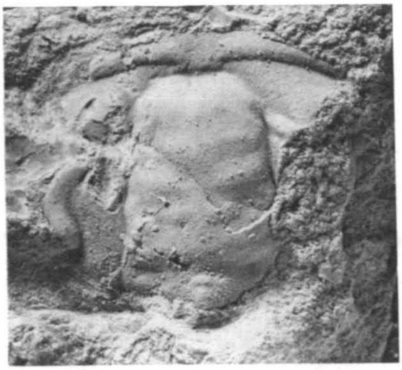
Fig. 7.—Crandium (x 10), holotype, CPC 3539. Devoncourt Limestone, loc. D18.
Fig. 8.—Free cheek (x 3), CPC 3536. Devoncourt Limestone, loc. D18.

Crepicephalus? sp. *H* .... Page 172

Fig. 9.—Pygidium (x 8), CPC 3541. Devoncourt Limestone, loc. D18.

Amphoton arta sp. nov. .... Page 141

Fig. 10.—Cranidium (x 9), holotype, CPC 3540. Devoncourt Limestone, loc. D18.



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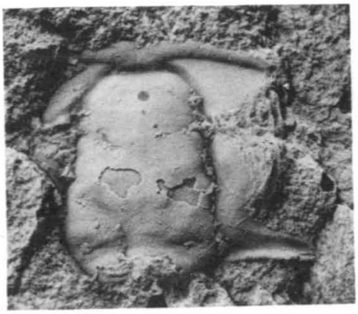

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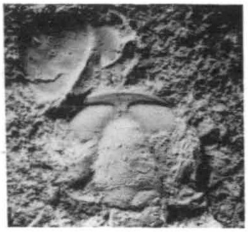

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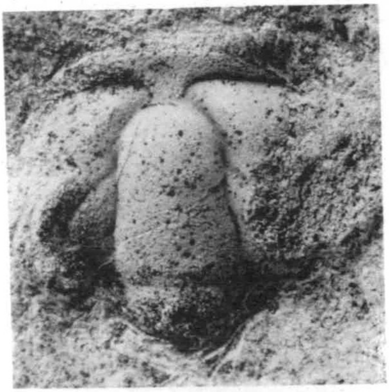

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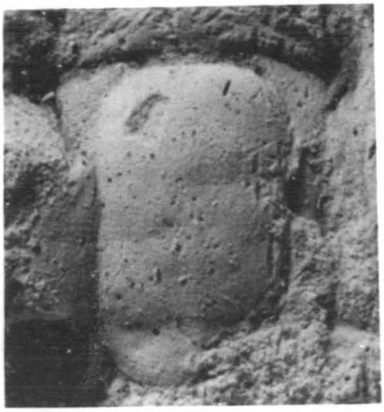

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PLATE 14.

Mapania angusta (Whitehouse) .... Page 167

Fig. 1.—Cranidium (x3), CPC 3542. V-Creek Limestone, Undilla Basin, loc. M409.

Fig. 2.—Cranidium (x3), CPC 3543. V-Creek Limestone, Undilla Basin, loc. M409.

Fig. 3.—Pygidium (x 3), CPC 3544. V-Creek Limestone, Undilla Basin, loc. M409.

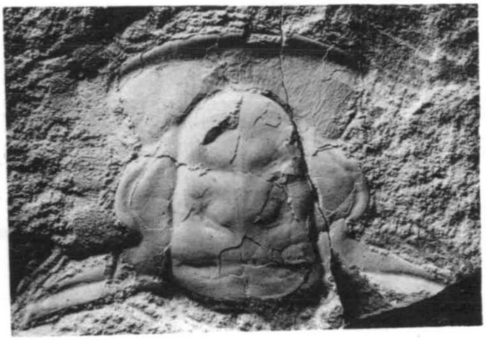
Fig. 4.—Thorax and pygidium (x 2), rubber cast of CPC 3545. V-Creek Limestone, Undilla Basin, loc. M25.

Holteria arepo sp. nov. .... Page 133

Figs. 5a, 5b.—Pygidium (x 6 and x 18), holotype, CPC 3546. Devoncourt Limestone, loc. D21.

Centropleura phoenix sp. nov. .... Page 105

Fig. 6.—Pygidium (x 2), CPC 3502. Devoncourt Limestone, loc. D13A.



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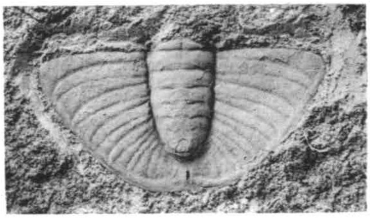

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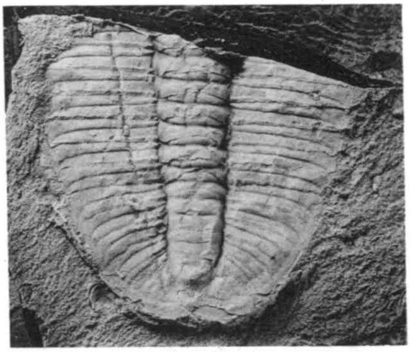

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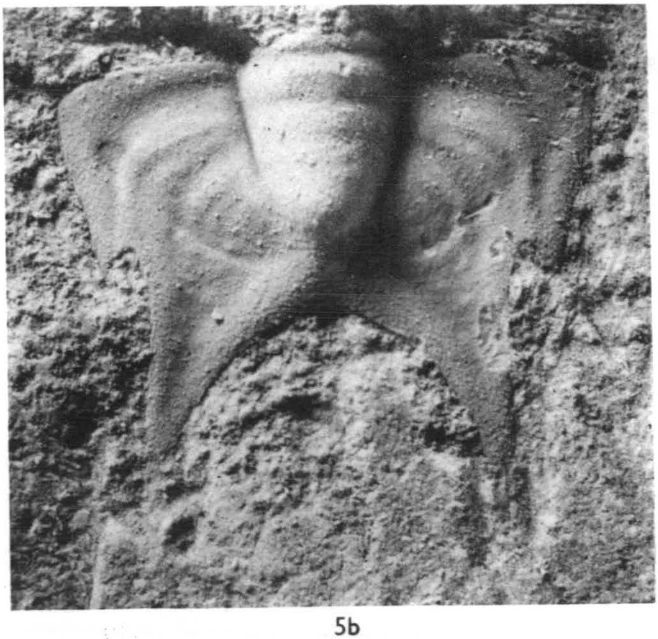

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PLATE 15.

Tosotychia sors gen. nov., et sp. nov. .... Page 160

Fig. 1.—Fragmentary cranidium (x 3) CPC 3547. Roaring Siltstone (sandstone interbed) loc. D19.

Fig. 2.—Cranidium (x 5), rubber cast of holotype, CPC 3548.

Fig. 3.—Cranidium (x 3), CPC 3549.

Fig. 4.—Fragmentary cranidium (x 3), CPC 3550.

Figs. 5a, 5b.—Pygidium and posterior segment (Fig. 5a x 5; fig. 5b x 10), CPC 3552.

Fig. 6.—Free cheek (x 8), CPC 3553.

Figs. 7a, 7b.—Thorax (fig. 7a x 3, fig 7b x 6), CPC 3551. Devoncourt Limestone, loc. D18?

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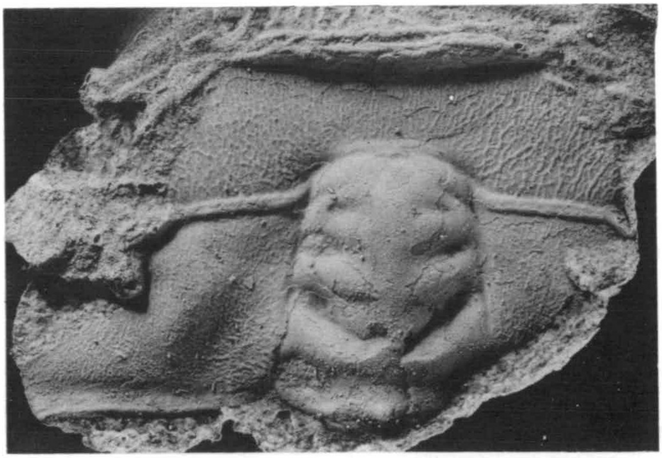

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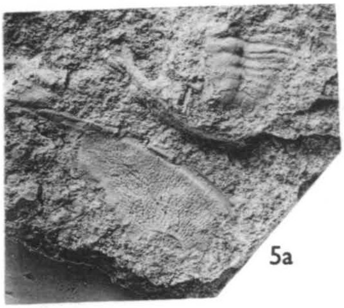

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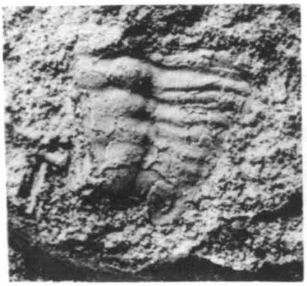

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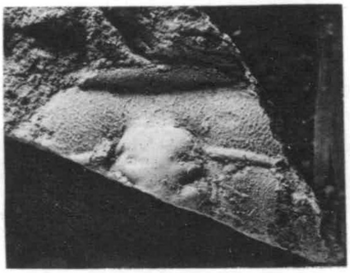

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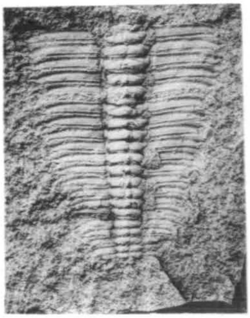

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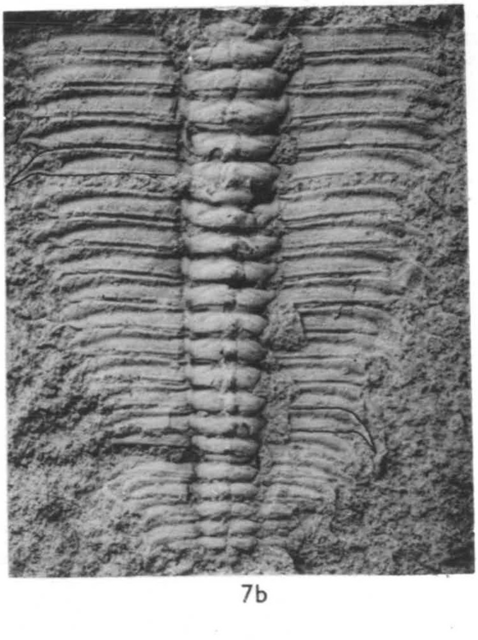


7b

PLATE 16.

Papyriaspis lanceola Whitehouse . ... **Page 155**

Complete specimen and fragment of a cranidium (x 3.2), CPC 3554.
V-Creek Limestone, Undilla Basin, loc. M418.

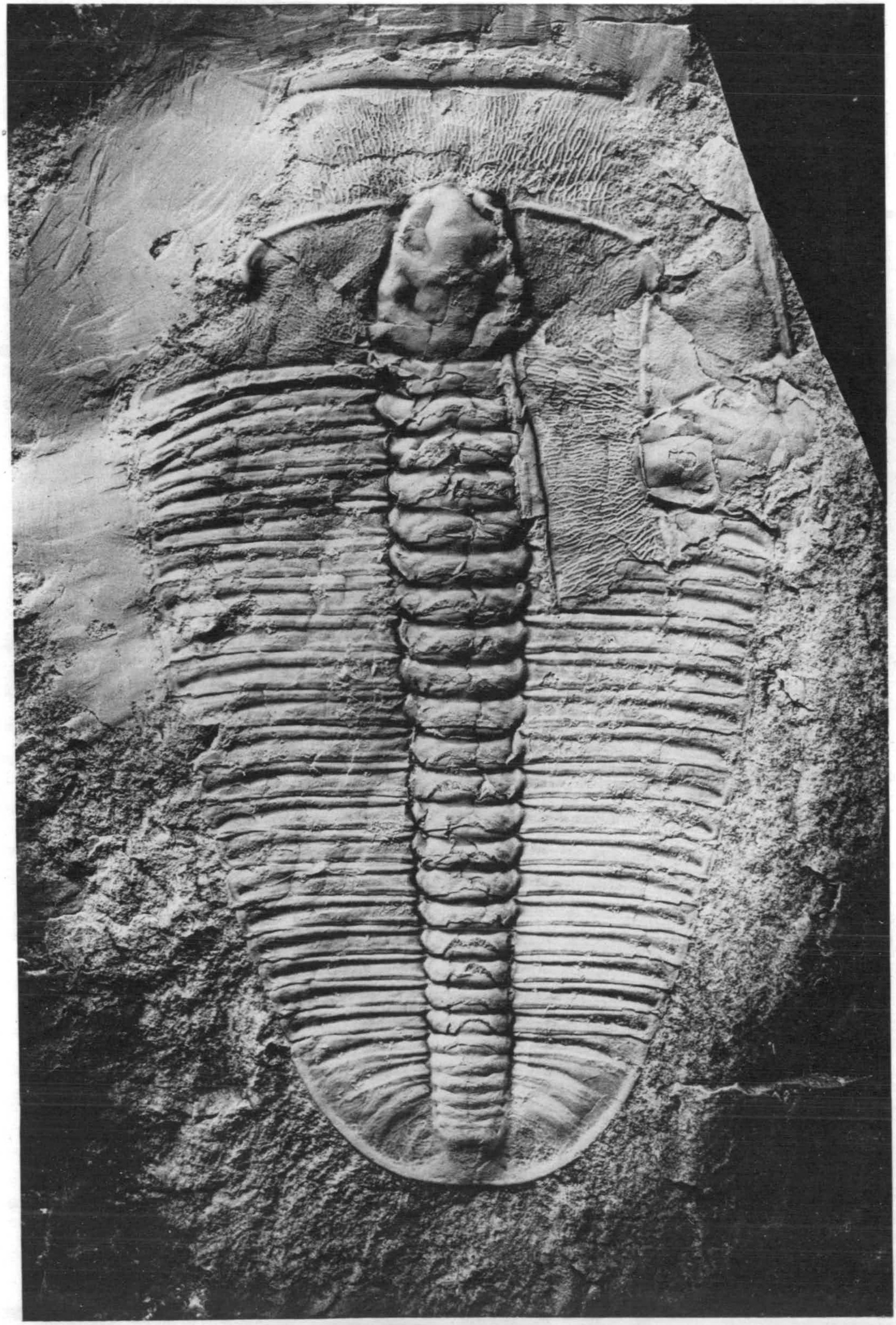
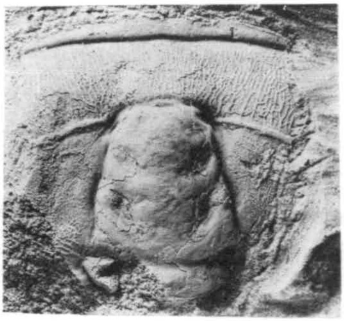


PLATE 17.

Papyriaspis lanceola Whitehouse .... Page 155
V-Creek Limestone, Undilla Basin

Fig. 1.—Fragmentary (but not flattened) cranidium (x 2), CPC 3555. Loc. M409.
Fig. 2.—Cranidium (x 3), rubber cast of CPC 3556. Loc. M409.
Fig. 3.—Free cheek (x 3), CPC 574. Loc. M418.
Fig. 4.—Cranidium and part of thorax (x 2), CPC 573. Loc. M418.
Fig. 5.—Complete specimen (x 2), CPC 3557. Loc. M410.



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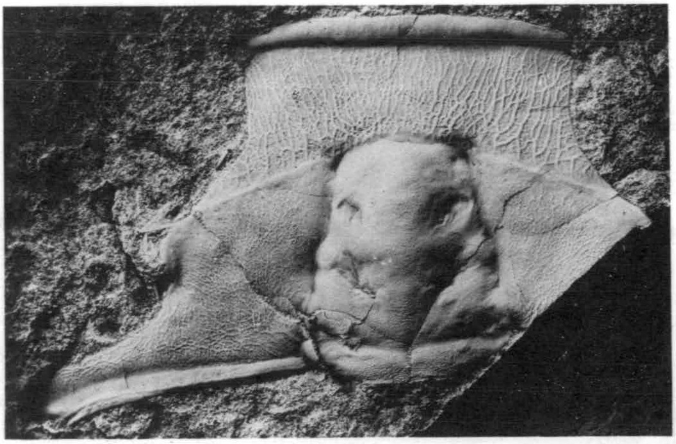

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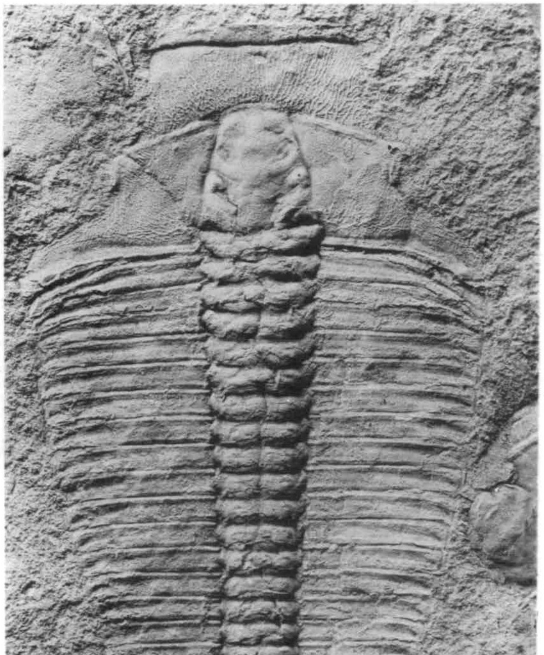

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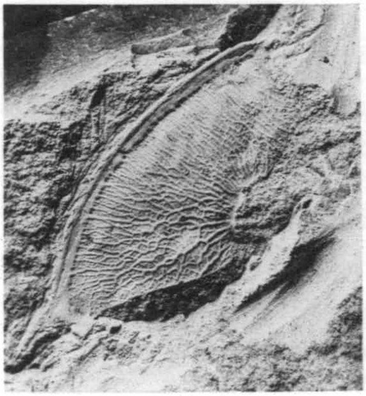

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4

PLATE 18.

Peronopsis scaphoa sp. nov. .... Page 55

Fig. 1—Cephalon (fragmentary) (x 4), holotype, CPC 3558.
Fig. 2.—Cephalon (x 4), CPC 3559.
Fig. 3.—Pygidium (x 4), CPC 3560.

Peronopsis sp. *G.* .... Page 57

Fig. 4.—Cephalon (x 4), CPC 3561.

Diplagnostus sp. *I* .... Page 73

Fig. 5.—Cephalon (associated with *Acroteta,* dorsal valve) (x 4), CPC 3562.

Hypagnostus brevifrons (Angelin) .... Page 58

Fig. 6.—Cephalon (x 4), CPC 3563.
Fig. 7.—Cephalon (x 4), CPC 3564.
Fig. 8.—Pygidium (x 4), CPC 3565.
Fig. 9.—Pygidium (distorted) (x 4), CPC 3566.
Fig. 10.—Pygidium (x 4), CPC 3567. Roaring Siltstone, loc. D 7/15.

Hypagnostus willsi sp. nov. .... Page 59

Figs. 11a, 11b.—Complete specimen (x 3.5 and x 4), holotype. CPC 3568. Devoncourt Limestone, loc. D13A.


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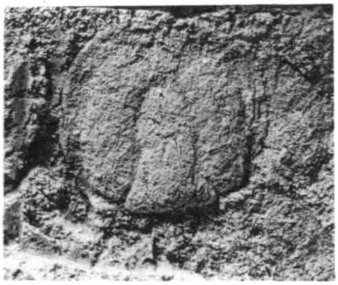
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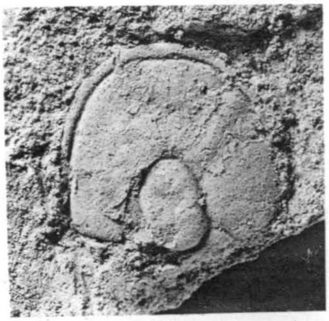
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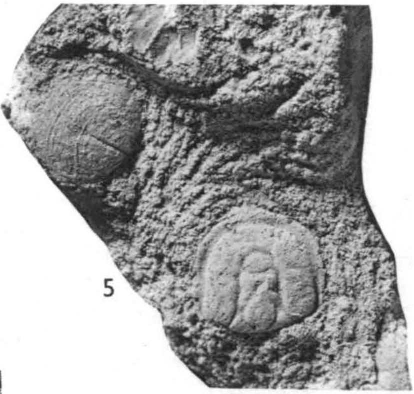
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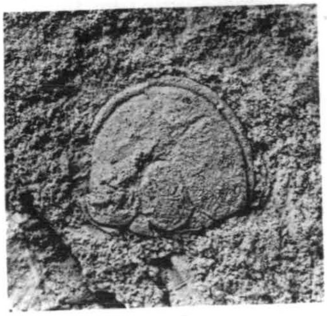
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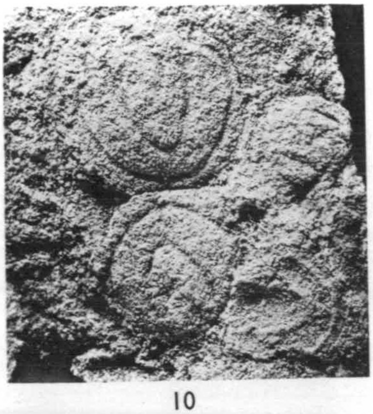
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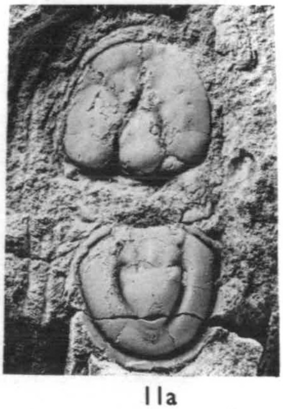

11a

PLATE 19.

Hypagnostus hippalus sp. nov. .... Page 60

Fig. 1.—Pygidium (x 4), rubber cast of CPC 3584.

Fig. 2.—Cephalon (x 4), rubber cast of holotype CPC 3583 (same specimen Plate 23, fig. 11).

Delagnostus dilemma gen. nov. et sp. nov. .... Page 88

Fig. 3.—Cephalon (x 4), rubber cast of CPC 3634; see plate 23, fig. 10.

Fig. 4.—Pygidium (x 4), rubber cast of holotype, CPC 3633; see plate 23, fig. 9.

Hypagnostus hippalus sp. nov. .... Page 60

Fig. 5.—Cephalon (x 7), rubber cast of CPC 3569. Photographed back to front to show the occipital structure.

Fig. 6.—Two pygidia (x 4); small pygidium, CPC 3570.

Fig. 7.—Two larger pygidia (x 4), CPC 3571, associated with a pygidium of *Diplagnostus*.

Fig. 8.—Pygidium (x 4), CPC 3573.

Fig. 9.—Pygidium (immature) (x 4), CPC 3581. Devoncourt Limestone, loc. D18.

Fig. 10.—Cephalon, immature (x 6), CPC 3576. Devoncourt Limestone, loc. D26.

Hypagnostus sp. *F* .... Page 65

Fig. 11.—Pygidium (x 6), CPC 3575. Devoncourt Limestone, loc. D18?

Grandagnostus ? velaevis sp. nov. .... Page 67

Fig. 12.—Pygidium (x 8), rubber cast of CPC 3574. Devoncourt Limestone, loc. D21.

Diplagnostus planicauda vestgothicus (Wallerius) .... Page 70

Figs. 13a, 13b.—Cephalon (x 8.5 and x 7), CPC 3572. Fig. 13b is rubber cast. Devoncourt Limestone, loc. D18.

Hypagnostus cf. *hunanicus* Lu .... Page 64

Fig. 14.—Pygidium (x 8), CPC 3578.

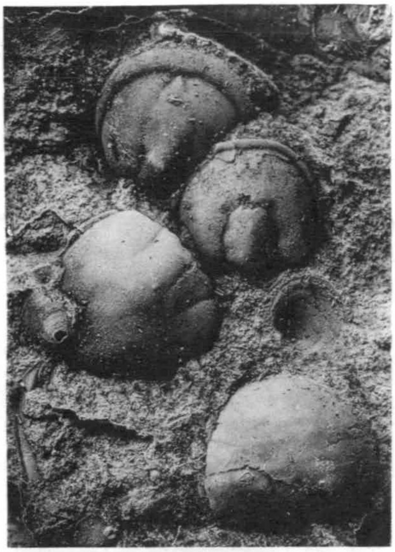
Diplagnostus humilis (Whitehouse) .... Page 72

Fig. 15a, 15b.—Complete specimen (x 8 and x 6), CPC 3577. Fig. 15a is rubber cast.

Fig. 16.—Cephalon (x 6), CPC 3579. Devoncourt Limestone, loc. D15.

Diplagnostus cf. *planicauda vestgothicus* .... Page 71

Fig. 17.—Cephalon (x 6), CPC 3580. Devoncourt Limestone, loc. D21.



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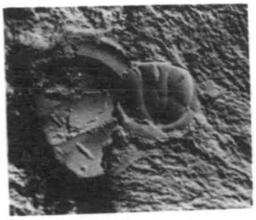

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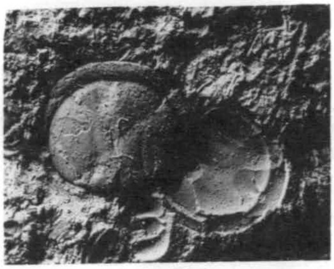

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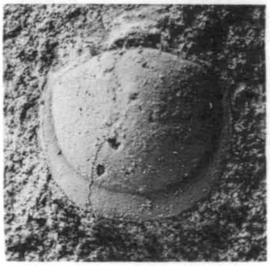

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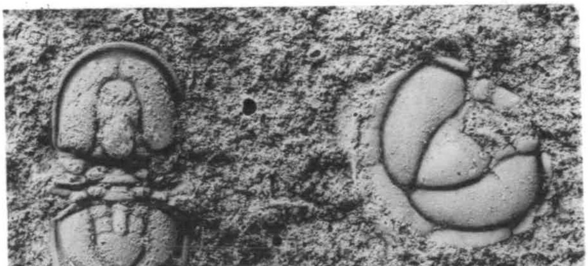

15a

14

13b

15b

17

16

PLATE 20.

Diplagnostus cf. *planicauda vestgothicus* .... Page 71

Fig. 1.—Cephalon (x 5), CPC 3585. Devoncourt Limestone, Loc. D26.

Diplagnostus humilis (Whitehouse) .... Page 72

Fig. 2.—Pygidium (x 6), CPC 3586. Devoncourt Limestone, Loc. D15.

Diplagnostus cf. *planicauda vestgothicus* .... Page 71

Fig. 3.—Cephalon (x 6), CPC 3587. Devoncourt Limestone, Loc. D26.

Ptychagnostus cassis sp. nov. .... Page 77

Figs. 4a, 4b.—Cephalon (x 4 and x 7), holotype, CPC 3588. Fig. b is rubber cast. Devoncourt Limestone, Loc. D17.

Figs.. 5a, 5b.—Cephalon (x 7 and x 6), CPC 3589. Fig. a is rubber cast.

Fig. 6.—Cephalon (x 6), CPC 3590.

Fig. 7.—Cephalon (x 6), CPC 3591, slightly distorted.

Fig. 8.—Cephalon (x 6), CPC 3592.

Fig. 9.—Pygidium (x 6), CPC 3593.

Fig. 10.—Pygidium (x 6), CPC 3594. Slightly deformed.

Fig. 11.—Pygidium (x 6), CPC 3595. Deformed.

Fig. 12.—Pygidium (x 6), CPC 3596. Deformed.

Fig. 13.—Pygidium (x 6), CPC 3597. Deformed (shortened). Roaring Siltstone (sandy interbed) loc. D19.

Ptychagnostus fumicola sp. nov. .... Page 81

Figs. 14a, 14b.—Pygidium (x 5), holotype, CPC 3598. Fig. b. is rubber cast

Fig. 15.—Cephalon (x 6), CPC 3599.

Fig. 16.—Cephalon (x 6), CPC 3601.

Fig. 17.—Cephalon (x 6), CPC 3600.

Mungerebar Limestone (lower portion) loc. G9.


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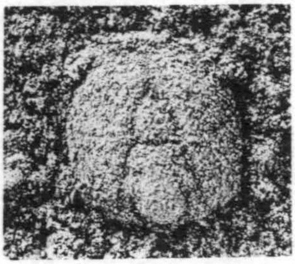
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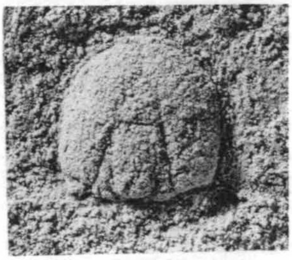
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4b


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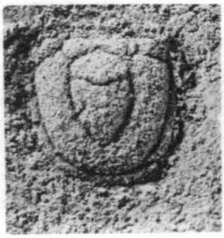
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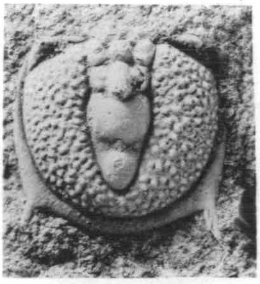
14a


14b


15


17

PLATE 21.

Ptychagnostus sp. *P* aff. *Nathorsti* .... Page 84

Fig. 1.—Pygidium (x 8), rubber cast of CPC 3603. Devoncourt Limestone, Loc. D18.

Ptychagnostus fumicola sp. nov. .... Page 81

Fig. 2.—Pygidium (x 6), rubber cast of CPC 3604.

Ptychagnostus aculeatus (Angelin) .... Page 80

Fig. 3.—Fragmentary pygidium (x 6), CPC 3602. Devoncourt Limestone, Loc. D18.

Figs. 4a, 4b.—Pygidium (x 6.5 and x 6), CPC 3605. Fig. b is rubber cast.
Roaring Siltstone, Loc. D 7/15.

Leiopyge laevigata (Dalman) .... Page 85

Fig. 5.—Cephalon in sandstone (x 6), CPC 3606. Roaring Siltstone, Loc. D19.

Figs. 6a, 6b, 6c.—Cephalon (x 12 and x 6), CPC 3607. Figs. a. and b. horizontal; fig c tilted to show occipital structure.

Figs. 7a, 7b.—Pygidium (x 6 and x 14), CPC 3608.

Figs. 8a, 8b.—Pygidium (x 4 and x 5), CPC 3609.
Axis short, post-axial furrow present.

Figs. 9a, 9b.—Pygidium flattened (x 6), CPC 3610. Fig. c. tilted to show spineless border.
Devoncourt Limestone, Loc. D15.

Leiopyge laevigata armata (Linnarsson) .... Page 87

Figs. 10a, 10b.—Cephalon (x 6.5 and 13), CPC 3611.
Devoncourt Limestone, Loc. D13A.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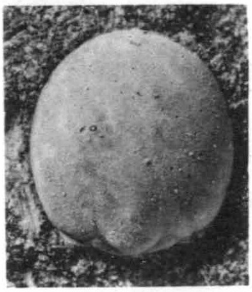
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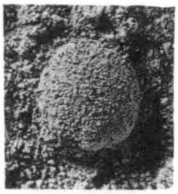

5


4a

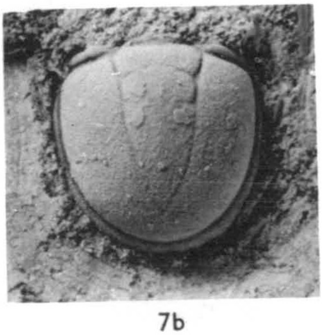

4b


6c


6a


7a


8a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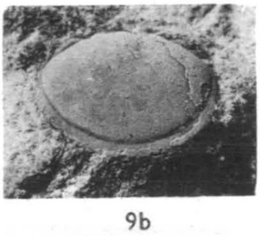
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10a

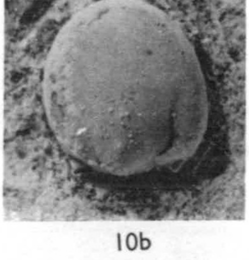

10b

PLATE 22.

Leiopyge laevigata armata (Linnarsson) .... Page 87

Figs. 1a, 1b.—Cephalon (x 6 and x 11), CPC 3612. Left genal spine visible in fig. 1b.
Figs. 2a, 2b.—Pygidium (x 6 and x 14), CPC 3616. Devoncourt Limestone, Loc. D26.
Figs. 3a, 3b.—Pygidium (x 6), CPC 3614.
Fig. 4.—Pygidium (x 6), CPC 3615. Devoncourt Limestone, Loc. D15.

Pseudophalacroma dubium (Whitehouse) .... Page 93

Fig. 5.—Pygidium (x 6), CPC 3617.
Fig. 6.—Cephalon (x 6), CPC 3618. Roaring Siltstone (sandstone interbed) Loc. D19.
Figs. 7a, 7b.—Pygidium (x 4.3), CPC 3623. Devoncourt Limestone, Loc. D18?
Figs. 8a, 8b.—Cephalon (x 6), CPC 3619. Devoncourt Limestone, Loc. D18
Fig. 9.—Cephalon (x 7), CPC 3620.
Fig. 10.—Pygidium (x 4), CPC 3621. Devoncourt Limestone Loc. D13A.

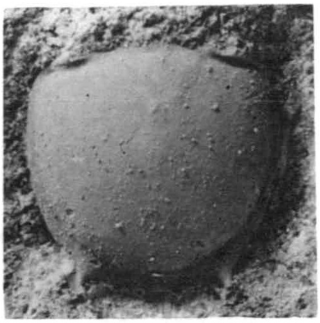
Pseudophalacroma sp. *K.* .... Page 94

Fig. 11.—Pygidium (x 2.5), CPC 3622. Devoncourt Limestone, Loc. D18.

Pseudophalacroma sp. *L.* .... Page 95

Fig. 12.—Pygidium (x 8), rubber cast of CPC 3624. Devoncourt Limestone, Loc. D17.


1a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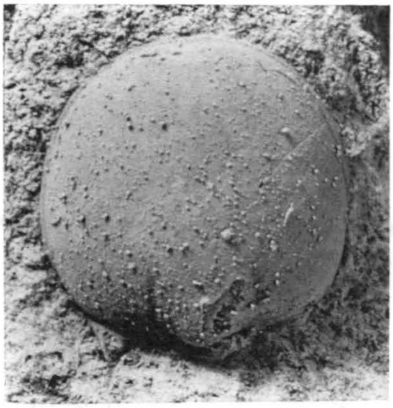
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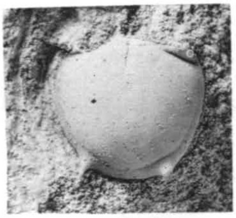
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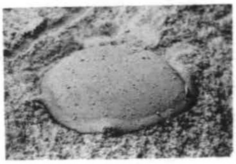
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8b


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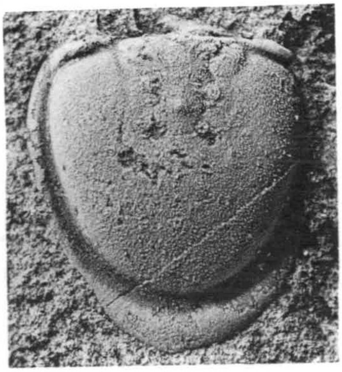
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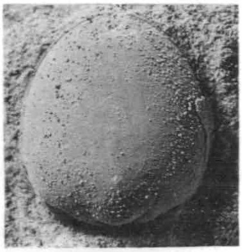
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7b

PLATE 23.

Hypagnostus varicosus sp. nov. .... Page 63

Fig. 1.—Pygidium (x 6), CPC 3625.

Figs. 2a, 2b.—Complete specimen (x 8), holotype, CPC 3626. Fig. b. is rubber cast. Devoncourt Limestone, Loc. D21.

Grandagnostus velaevis sp. nov. .... Page 67

Fig. 3.—Cephalon (x 6), holotype. CPC 3630. Devoncourt Limestone, Loc. D21.

Fig. 4.—Pygidium (x 6), CPC 3631. Devoncourt Limestone, Loc. D18? or D21?

Blystagnostus laciniatus gen. nov. sp. nov. .... Page 95

Fig. 5.—Pygidium (x 8.5), holotype, CPC 3628.

Fig. 6.—Pygidium (x 7), CPC 3629. It is photographed back-to-front. Roaring Siltstone Loc. D 7/15.

Agnostus sp. *L* cf. *neglectus* Westergaard .... Page 75

Fig. 7.—Pygidium (x 5), CPC 3627. Devoncourt Limestone, Loc. D26.

Delagnostus dilemma gen. nov. sp. nov. .... Page 88

Figs. 8a, 8b.—Cephalon (x 4), CPC 3632.

Fig. 9.—Pygidium (x 6), holotype, CPC 3633. Same specimen Plate 19, fig. 4.

Fig. 10.—Cephalon (x 6), CPC 3634. Same specimen Plate 19, fig. 3. Devoncourt Limestone, Loc. D18.

Hypagnostus hippalus sp. nov. .... Page 60

Fig. 11.—Cephalon (x 6), holotype, CPC 3583. Same specimen (rubber cast), Plate 19. fig. 2. Devoncourt Limestone, Loc. D18.

Grandagnostus imitans sp. nov. .... Page 65

Figs. 12, 12a.—Small pygidium (x 4 and 10), CPC 3638.

Fig. 13, 13a.—Cephalon (x 4 and x 6), holotype, CPC 3635. Same specimen Plate 24, fig. 7.

Fig. 14.—Pygidium (x 4), CPC 3637.

Fig. 15.—Pygidium (x 4), CPC 3636. Same specimen plate 24, fig. 6.
V-Creek Limestone, Undilla Basin, Loc. M41.


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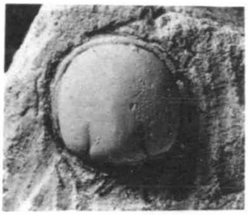
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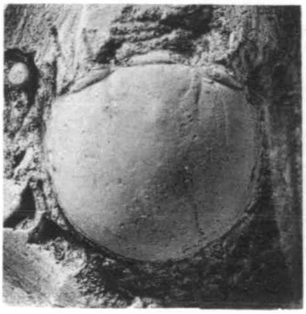
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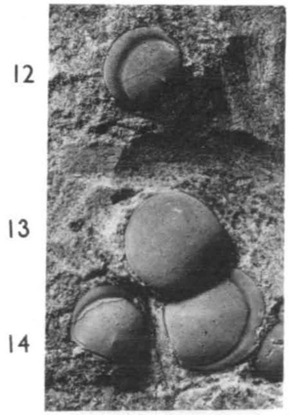
13a



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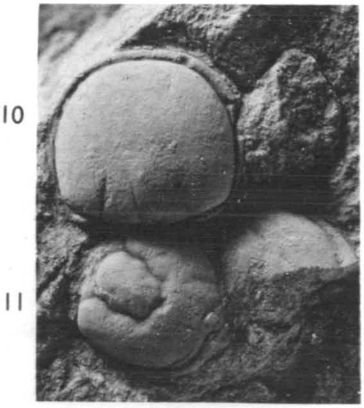



12a

PLATE 24.

Svealuta sp. nov. aff. *primordialis* (Linnarsson) .... **Page 174**

Figs. 1a-1e.—Right valve (x 4), CPC 3640.

Aristaluta gutta, gen. nov. sp. nov. .... **Page 177**

Figs. 2a-2c.—Left valve (x 4; fig. c -x 8), holotype, CPC 3642.

Figs. 3a-3d.—Complete carapace, right valve still in rock (x 6; gg. c -x 8), CPC 3641. Devoncourt Limestone, Loc. D13A.

Fig. 4.—Flattened right valve (x 2.3), CPC 3643. Devoncourt Limestone, Loc. D19.

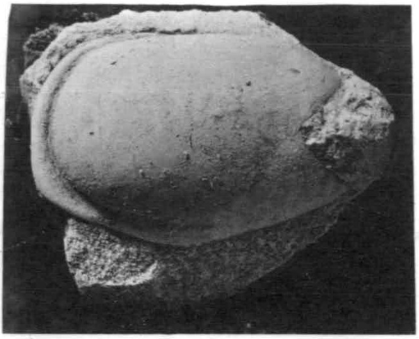
Grandagnostus imitans sp. nov. .... **Page 65**

Fig. 5.—Pygidium (x 7), rubber cast of CPC 3639.

Fig. 6.—Pygidium (x 10), CPC 3636. Same specimen Plate 23, fig. 15.

Fig. 7.—Cephalon (x 10), holotype, CPC 3635. Specimen tilted to show border and glabellar node. Same specimen Plate 23, figs. 13, 13a.

V-Creek Limestone, Undilla Basin, Loc. M41.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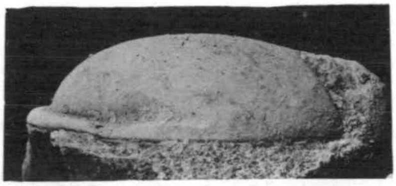
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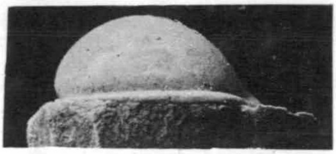
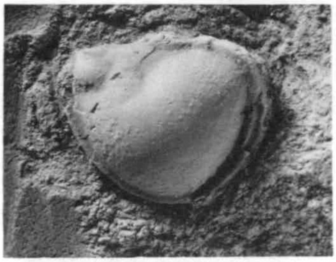
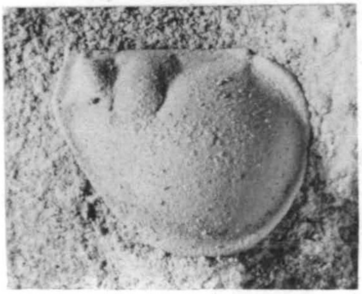

1d


2a


2b


3a


3d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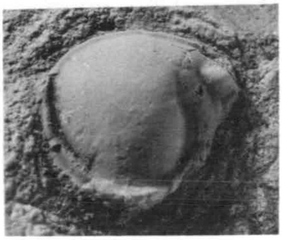
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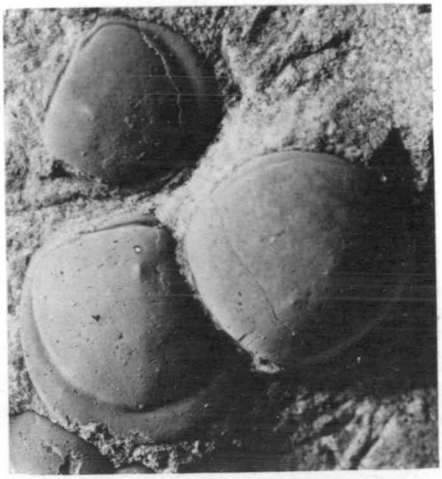
4


3c


5


6 7

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