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NEPEID TRILOBITES OF THE MIDDLE CAMBRIAN OF NORTHERN AUSTRALIA

BY

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SUMMARY

Twenty-five species of the Middle Cambrian Nepeidae of northern Australia are described; of these 10 are presented in open nomenclature, and 14 are named new. Four genera are recognized: *Nepea* Whitehouse and three new—*Penarosa, Loxonepea,* and *Folliceps.* Of these *Loxonepea* is reminiscent of some Menomoniidae. The stratigraphic distribution is uneven; *Nepea* dominates in the Zone of *Ptychagnostus nathorsti* and *Penarosa* in the earlier zones. It is, however, apparent that they represent concurrent stocks. The older form to appear belongs to the *Nepea* stock. The currently used Middle Cambrian scale is essentially the Scandinavian agnostid scale of zones; the name *Hypagnostus parvifrons* Zone is, however, replaced by the name *Euagnostus opimus* Zone. Collecting sites are described in superpositional order of strata. It appears that the nepeids lived in swarms floating most of the time in the surface waters, as inferred from the mode of embedding, from the occurrence in all kinds of sediments, the thin test, and the frontal boss—presumably a device to facilitate floating.

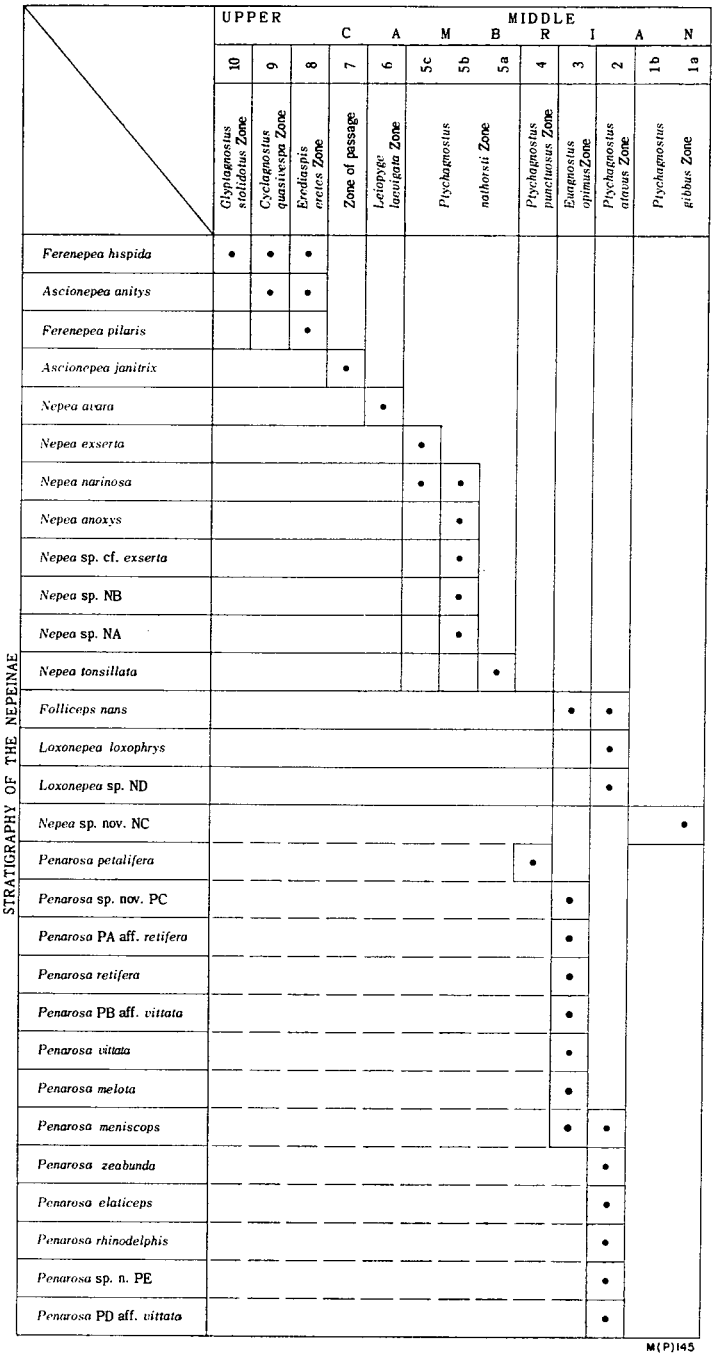


Fig. 1. Chart of stratigraphic distribution of species of the Nepeinae.

INTRODUCTION

The nepeid trilobites are a substantial ingredient of the Middle and the early Upper Cambrian faunas of Australia. The Upper Cambrian species and genera are already described (Öpik, 1967) and the present paper completes the record. Now described, the nepeids became a tool in stratigraphic dating of Cambrian faunas and sequences. Furthermore, they produced new information on the morphology and systematics of trilobites. Most of the described material (except for three forms from the Northern Territory sites H4 and the Ross River gorge) has been collected by me. The specimens are deposited in the type collection of the Bureau of Mineral Resources, Canberra; the catalogue numbers have the prefix CPC. The photographs were taken by Mr R. Miniotas and printed by Mr J. Zawartko.

The temporal succession of species

The stratigraphic succession of the known species of the Nepeidae is summarized in the accompanying chart (Fig. 1), which refers to north Australian Middle and Upper Cambrian forms. Published and unpublished fossil lists indicate the presence of Nepeidae in Tasmania (*Nepea,* late Middle Cambrian, gen. indet. in the early Upper Cambrian), Victoria (*Nepea,* Middle Cambrian); in South Australia, in the Gidgealpa wells (*Penarosa,* followed above by species of *Nepea*) and New South Wales, in the northwest (*Penarosa?,* in the Middle Cambrian).

In our chart the nepeid species are arranged in two separate sets: (1) the set topped by *Penarosa petalifera* shows the distribution of forms attributed to the genus *Penarosa,* and (2) the set starting with *Nepea?* sp. nov. NC contains species of all genera related to the genus *Nepea.* This arrangement demonstrates that the *Nepea* and *Penarosa* stocks existed as two independent and concurrent lineages and that the temporal continuity from *Penarosa petalifera* to *Nepea tonsillata* is not phyletic, but accidental. Otherwise the species are arranged in their superpositional order, which is primarily the order of strata and of the collecting sites.

The distribution of the species and genera as seen from the chart indicates a subsidiary stratigraphic scale of biostratigraphic operational units ('BSOU') roughly coinciding with the scale of agnostid zones (Öpik, 1956, 1960). Prominent are (1) the many species of *Penarosa* in the Zone of *Ptychagnostus atavus* (=*Penarosa rhinodelphis-zeabunda* zone or BSOU), followed above by (2) *Penarosa retifera* zone (BSOU); (3) the zone (BSOU) of *Nepea narinosa* and its allies coincident with the Zone of *Ptychagnostus nathorsti,* and (4) the Upper Cambrian Mindyallan zones. It is, however, evident that a full scale based only on species of the Nepeidae cannot be constructed yet.

In broad terms, *Penarosa* covers the interval of the *Ptychagnostus atavus, Euagnostus opimus,* and *Ptychagnostus punctuosus* Zones; *Nepea* (forms with intergenal spines) belongs to the *Pt. nathorsti-Leiopyge laevigata* interval of zones, and the quite distinctive genera *Ferenepea* and *Ascionepea* (described in Öpik, 1967a) mark the Mindyallan, including the Zone of Passage.

The species of the Nepeidae are assigned to the zones of the current scale on the basis of the associated trilobites. The agnostids, of course, are fundamental. Described and undescribed species of Ptychagnostinae and Diplagnostinae were instrumental in dating the collections and the strata. The zones (scale divisions) in the chart are enumerated; these numbers, however, are not zone symbols, but 'footnote' annotations directing the reader's attention to the comments that follow below.

(1) The division designated *'Ptychagnostus gibbus'* Zone as applied in the chart is composite and broad. In (1a) a *Xystridura* is associated with *Nepea?* sp. nov. NC, but its correct age is inconclusive: it may be an Ordian species or a contemporary of forms like *X. templetonensis* which belong in the early part of the *Ptychagnostus gibbus* Zone. (1b) designates the late part of the *Ptychagnostus gibbus* Zone, which is devoid of nepeid remains.

(2) The early part of the *Ptychagnostus atavus* Zone contains also a somewhat modified *Pt. gibbus,* and corresponds in part to the *Agnostus seminula* stage of Whitehouse (1939). This species itself is affiliated with *Pt. atavus.*

(3) *Euagnostus opimus* Zone is a substitute name for the zone of *Hypagnostus parvifrons,* a species probably lacking in Australia. *Euagnostus opimus* Whitehouse (1936) is now available even in complete specimens. The genus group *Euagnostus* consists of several species, some of which reach the *P. nathorsti* Zone.

(4) *Ptychagnostus punctuosus* is known from many sites and the material includes complete specimens as well.

(5a) indicates the lower part of the *Ptychagnostus nathorsti* Zone, which also contains *Ptychagnostus punctuosus* at several sites.

(5b) contains also *Leiopyge* sp. nov., whose early forms start in the *Pt. punctuosus* zone.

(6) the *Leiopyge laevigata* triple Zone is discussed in Öpik (1961).

(7), (8), (9), and (10) are discussed in detail in Öpik (1967).

Geographical and superpositional distribution of collecting sites

The collecting sites of the previously described Mindyallan Nepeidae are described in Öpik (1967) and will not be discussed further. The list that follows includes all sites of the Middle Cambrian specimens of the Nepeidae described in the present paper, and these are arranged in descending order of superposition, beginning with locality D95 of late Middle Cambrian. The adopted order of presentation disrupts somewhat the picture of the geographical distribution of forms between the political regions—Queensland and Northern Territory; but palaeozoogeographic unity is still maintained in the list.

The Queensland localities are entered in the maps of Noakes, Carter, & Öpik (1959), Öpik, Carter, & Noakes (1961), Carter & Öpik (1961), and Öpik,

Carter, & Randal (in press); the same maps are available in Carter, Brooks, & Walker (1961). The Northern Territory localities are described sufficiently by their co-ordinates or reference to the main geographical features. The locality H4 (Northern Territory) has been discussed by Casey & Tomlinson (1956).

LIST OF LOCALITIES

1. Localities of the Urandangi Sheet area:

D95. Lat. 21°56′S., long. 139°00′E. Steamboat Sandstone; Zone of *Leiopyge laevigata. Nepea avara* sp. nov. Also described (Öpik, 1967) are *Dipentaspis dipentas, Dipentaspis ratis, Quitacetra arenata, Leichneyella* sp. B, *Dolichoagnostus?* indet., *Linguagnostus* cf. *kjerulfi,* and *Peronopsis* aff. *fallax.*

D54. Lat. 21°57′S., long. 139°04′E. Early part of Steamboat Sandstone. Fossils same as in D95, Zone of *Leiopyge laevigata.*

D108. 1.5 mile south D54 (Quita Bore). Limestone with silicified fossils, including *Nepea avara.* It is a detrital limestone layer at the base of the Steamboat Sandstone. It rests on limestone of the Quita Formation, with a break in between; deposits of the Zone of *Ptychagnostus nathorsti* are missing. Zone of *Leiopyge laevigata.*

2. Split Rock Sandstone, Zone of *Ptychagnostus nathorsti,* Undilla Basin, Camooweal and Mt Isa Sheet areas.

M344. Lat. 19°57.5′S., long. 138°31′E., Camooweal area. Waterfall (intermittent), head of Waroona Creek. White friable quartzose sandstone set at base of the face; *Nepea exserta* (type), *N. narinosa,* and other trilobites. It is the highest known part of the Split Rock Sandstone and the highest horizon of the *Ptychagnostus nathorsti* Zone in the Undilla Basin.

M417. Lat. 19°57′S., long. 138°29.5′E., Camooweal area. Split Rock Rockholes on Waroona Creek. Type locality of the formation. *Nepea narinosa* (type), *N. anoxys* (type), and other trilobites and brachiopods.

M421. Lat. 19°48.5′S., long. 138°32′E., Camooweal area. Emu Soak, on Emu Creek. Same horizon and fossils as at M417.

M133. Lat. 19°35′S., long. 138°41′E., Camooweal area. Cluster of red sandstone buttes. *Nepea* cf. *exserta* and other trilobites; position within the formation inconclusive, but probably close to M417.

M141. Lat. 19°39.5′S., long. 138°48′E., Camooweal area. Red sandstone with *Nepea* sp. NB and other trilobites; horizon close to M417.

M226. Lat. 20°09.5′S., long. 138°30′E. Mount Isa area. Sandstone and silicified siltstone, west facing scarp. *Nepea narinosa* and other trilobites. Horizon and fauna same as M417.

M276. Lat. 19°59.2′S., long. 138°30.4′E., Camooweal area; one of several outcrops along the Barkly Highway. *Nepea narinosa* and other trilobites; probably the lowermost known fossiliferous horizon of the formation.

3. Mail Change Limestone, Undilla Basin.

A block of aphanitic limestone from the bank of the O'Shannassy River at Morstone (old site), Camooweal area, contains *Nepea narinosa* (Pl. 3, fig. 1) and other trilobites; the fauna is the same as in M417 and M226.

4. V-Creek Limestone, Undilla Basin.

M41. Lat. 19°27.5′S., long. 138°37′E., Camooweal area. Laminated hard limestone with chert pods. *Nepea* sp. NA (indet.) associated with *Papyriaspis lanceola, Asthenopsis,* and other trilobites. Zone of *Ptychagnostus nathorsti;* below this horizon *P. nathorsti* is associated with *P. punctuosus.*

M54. Lat. 19°37.3′S., long. 138°38′E., Camooweal area. Grey marly limestone; Douglas Creek stream bed, just south of Undilla. *Nepea tonsillata, 'Amphoton',* and other trilobites and brachiopods, Zone of *Ptychagnostus nathorsti.*

5. Currant Bush Limestone, Age Creek Formation, and Inca Formation, Camooweal Sheet area; Currant Bush Limestone, Lawn Hill (Queensland), and Mount Drummond (Northern Territory) Sheet areas.

Zone of Ptychagnostus punctuosus:

M130. Lat. 19°35.5′S., long. 138°48.5′E., Camooweal area. Shale and chert, top of Currant Bush Limestone.

Penarosa petalifera and agnostids.

M28. Lat. 19°27′S., long. 138°38.5′E., Camooweal area. Bituminous sandy limestone.

Penarosa petalifera (type).

M157. Lat. 19°25′S., long. 138°35′E. Camooweal area. Bituminous limestone in Age Creek Formation, with *Penarosa petalifera* and other fossils.

Zone of Euagnostus opimus:

M160. Lat. 19°23.5′S., long. 138°35.5′E. Chert interbed in dolomite of Age Creek Formation. Camooweal area. *Penarosa retifera* and other fossils.

M393. Lat. 18°38′S., long. 138°15′E., Lawn Hill area. Silty siliceous limestone.

Penarosa retifera.

M180. Lat. 18°38′S., and about 2.7 miles west of Queensland border (long. 138°E.), in the bed of Lancewood Creek, Mount Drummond area. Grey marly limestone.

Penarosa retifera (type), *Penarosa* sp., *P.* aff. *retifera,* and abundant other fossils.

M186. Lat. 18°38.5′S., long. 137°58′E., and about 0.5 mile west of M180, in the bed of Lancewood Creek, Mount Drummond area. Grey marly limestone.

Penarosa retifera, abundant and associated with numerous other fossils.

M123. Lat. 19°31′S., long. 138°47.6′E. Camooweal area. Limestone and chert. *Folliceps nans, Penarosa* sp. PB, aff. *vittata.*

M124. Lat. 19°31.6′S., long. 138°47.4′E. Camooweal area. Limestone and some chert.

Folliceps nans, Penarosa vittata, Penarosa melota.
Another site of the same bed is marked '124A'.

M412. Lat. 19°31′S., long. 138°53′E. Camooweal area (Chummy Bore, Thorntonia station). Inca Creek Formation, siliceous shale and chert.
Penarosa meniscops, Penarosa sp. nov. PC.

Zone of Ptychagnostus atavus:

M179. Lat. 18°38′S., long. 137°56.3′E., and about 3.5-3.8 miles west of Queensland border, Mount Drummond area. Grey nodular limestone interbedded with shale layers in lower part, and assigned to the Currant Bush Limestone.

Penarosa zeabunda, P. elaticeps, P. rhinodelphis, P. meniscops, and other fossils.

M393. Lawn Hill area, position given above. Shale with *Penarosa zeabunda,* below limestone with *P. retifera.*

M122. Lat. 19°30.7′S., long. 138°47.6′E. Camooweal area, silicified oolitic limestone and chert, an interbed in Age Creek Formation.

Loxonepea loxophyrys, Loxonepea sp. nov. ND.

H4. About 20 miles due east from Huckitta station, and close to the Arthur River, Northern Territory. Black bituminous limestone.
Penarosa sp. nov. PD (aff. *P. vittata* sp. nov.), *Penarosa* sp. nov. PE.
The age is inferred as the *Ptychagnostus atavus* Zone, but needs confirmation.

6. Early (or earliest) Middle Cambrian.
Ross River gorge, approx. Lat. 23°37′S., long. 134°28′E., east of Alice Springs, Northern Territory. Black hard limestone with *Nepea?* sp. nov. NC and *Xystridura* indet.

Ecology of Australian nepeids

The nepeids lived in swarms floating on, or near, the surface of the sea and probably also on shallow sea floors within reach of light and circulation. Observations supporting this picture are presented below.

Swarms are indicated in places and beds containing abundant remains of nepeids. Such places are locality M179 with *Penarosa zeabunda,* M180 and M186 with *Penarosa retifera,* and the Split Rock Sandstone at M417 with *Nepea narinosa.* Scattered pieces also occur sparsely in various sediments and places, left behind by itinerant swarms.

The fossils themselves are dismembered exuviae and dead bodies; undisturbed bodies retaining their free cheeks are rather rare — the whole record of such specimens consists of *Nepea narinosa,* Plate 2, figure 6, *Penarosa vittata,* Plate 15, figure 1, *Penarosa retifera,* Plate 9, figure 2, and *P. zeabunda,* Plate 10, figure 3. Such rarity of complete tests indicates a biotope with agitated water and life above the protective mud of the sea floor.

The breeding grounds of nepeids are unknown; the material available consists of holaspid individuals; meraspid specimens are very rare and protaspides are unknown. By contrast, at localities M180 and M186, where nepeids are abundant, the Dolichometopidae occur in all instars, including protaspides and complete holaspides. Hence, local conditions of fossilization were favourable to preservation of the early nepeid instars if present.

Nepeids occur in shale, siltstone, sandstone, current-bedded sandstone, calcareous sandstone, gypsiferous impure limestone, bituminous limestone, siliceous limestone and chert: hence, their distribution was not influenced by the character of the sediments, which should influence the dwellers on the sea floor. Nepeids are the only polymerid trilobites to share the Inca shale (locality M412) with the agnostids—a biotope inhospitable to other trilobites. Furthermore, nepeids lived in shelf, platform, and basin regions and in Tasmania and Victoria in a geosyncline. No phylogenetic unity is apparent among Australian nepeids; hence their record is as incomplete as can be expected from vagrant swarms in the relatively small Cambrian seaways of Australia.

The structure of a nepeid (see under *Nepea narinosa,* general aspect) provides no definite clues regarding its mode of life. It can be speculated, however, that the large frontal boss carried fat and served at once as a float and a container of emergency food.

The boss is absent in protaspides and early meraspides, whose small size and globose form were suited to a planktonic life in suspension in water; the larger and heavier breed, however, would have sunk to the floor of the sea unless prevented from gravitating down by a float.

The remains of nepeids are found in burial associations (taphocoenoses).

SYSTEMATICS

Superfamily NEPEACEA (Lochman in Harrington et al., 1959, ex Nepeidae Whitehouse)

Family NEPEIDAE Whitehouse, 1939

The Nepeacea are a superfamily of the order Ptychopariida, and probably of the suborder Ptychopariina. The concept of Nepeacea has been already discussed in Öpik (1967), and refers to the families Nepeidae and Menomoniidae Walcott, and the investigation history is discussed in Öpik (1963).

Genus NEPEA Whitehouse, 1939.

NEPEA NARINOSA Whitehouse, 1939.

(Pl. 1, figs 1-4; Pl. 2, figs 1-6; Pl. 3, fig. 1; Text-figs 2, 3).

Material. The illustrated and described material comprises six cranidia, four free cheeks, and a unique but worn cephalon with a larger part of the attached thorax. The Split Rock Sandstone at locality M417 has supplied hundreds of cranidia, but other parts are rare and no pygidia have been found yet. The selected specimens, however, allow of a reasonable description of the cephalon, and the whole collection indicates the existence of a single population of *N. narinosa* in a later part of *Ptychagnostus nathorsti* time in northwestern Queensland.

The holotype of *Nepea narinosa* is the cranidium plate 22, figure 15 in Whitehouse (1939). It is about 5-6 mm long; the base of its left intergenal spine is preserved; the left palpebral lobe lost its tip, but the shape of the preserved part indicates the same structure as, for example, in Plate 1, figures 2 and 3; the boss is circular, and the ocular ridges are horizontal. These characters of the holotype are sufficient for a specific identification of our material from Whitehouse's original locality and bed at Split Rock Rockholes (our locality M417) and prevent a possible confusion of *N. narinosa* with *N. anoxys* sp. nov. (q.v.) in collections from the same place.

The diagrammatic reconstruction (Öpik, 1963, fig. 2, p. 341) of *N. narinosa* is inaccurate:

(1) the boss and the oblique ocular ridges were taken from the holotype of *N. anoxys* sp. nov. (q.v.);

(2) the occipital spine is shown without the broad petaliform base of *narinosa,* but corresponds in structure to *N. tonsillata* sp. nov. Consequently, the reconstruction represents a synthesis of the genus *Nepea* and was prepared by lumping together information gained from specimens which at an early stage of study were presumed conspecific.

Diagnosis. Nepea narinosa Whitehouse has a semicircular cranidium (and cephalon), a circular boss, relatively wide interocular cheeks, and horizontal ocular ridges, and is distinguished by very long pointed palpebral lobes (as long as the glabella), and a marginal occipital spine with a triangular petaliform base.

Differential diagnosis. The difference of *N. narinosa* from the other, new, species of the genus is discussed in their differential diagnoses.

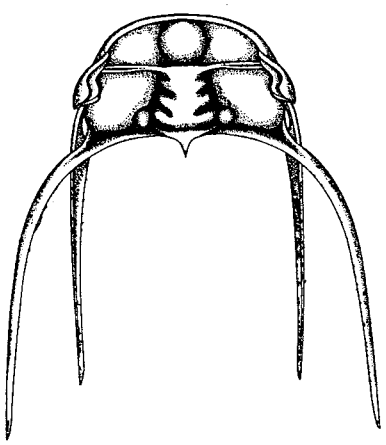


Fig. 2. *Nepea narinosa* Whitehouse, reconstruction of cephalon.

Fig. 3. *Nepea narinosa* Whitehouse, free cheek, lateral view; the doublure is shaded.

General aspect. Nepea narinosa is a small to medium sized trilobite, of about 40 mm in maximum length, with a compact and relatively voluminous test owing to the abruptly downsloping, almost vertical flanks, which are especially large in the cephalon; the furrows and lobes and the ocular ridges in the cephalon are strongly emphasized, the glabella is relatively small, and the frontal area with its boss large; the forward-placed eyes are large and far apart and roofed by the 'pixie ear'-like palpebral lobes; the genal spines are long blades, the intergenal spines long and slender, and the marginal occipital spine stands almost upright on its petal-like triangular base. The multisegmented semiovoid thorax, of about 30-35 segments,

and devoid of dorsal spines, has a narrow axis and wide pleural lobes, and terminates in a very small pygidium. *Nepea narinosa* was capable of spiral coiling, starting to involute the pygidium first.

Description. The cephalon in plan (save the genal and intergenal spines) is semicircular; the cranidium without the free cheeks remains also semicircular because the cheeks stand on the marginal edge and are almost invisible from above.

The free cheek (Text-fig. 3) is large and divided into two parts by the deep and somewhat retral embayment of the posterior suture; the posterior part is essentially the long and falcate genal spine lined by the doublure; the anterior part (Pl. 2, fig. 3) is a trapezoidal piece carrying the low base of the eye, and apparently retains the visual surface after moulting. A thick convex marginal rim of the free cheeks is continuous all around; in front, it is cut by the equally continuous suture and a part of it is retained by the cranidium as the cranidial frontal rim. The lateral part of the anterior suture dives steeply down from the eye, and the posterior suture, diving less steeply, almost touches the rim of the cheek before climbing up and rearward; the doublure is exposed in the embayment of the isolated free cheek. In brief, the sutures are referable to the sagittal vertical plane of symmetry and cannot be described in the conventional terms of convergence, divergence, and parallelism.

In the cranidium of *N. narinosa* (and the Nepeidae in general) the posterolateral limbs are expanded and extended down into large flaps with a retral swing and set in the embayments of the free cheeks; it is therefore a 'superlative' cedariform structure. In other trilobites, however, the posterolateral limbs terminate at the points where the posterior suture intercepts the margin. At the points of interception and well abaxially from the fulcra the border carries a pair of slender rearward-rising and curved intergenal spines, of a unique length unknown in other trilobites. The posterior cranidial border is narrow and elevated, but has no extension on the upper edge of the free cheek. The posterolateral marginal furrow, deep and narrow at first, extends abaxially and peters out on the upper part of the flap.

The frontal area (in front of the ocular ridges and the glabella) is wide and long—in plan as long as, or slightly less (0.9) than, the glabella—and slopes steeply toward the rim; the frontal area consists of a circular, or even semiglobose, boss flanked by a pair of tumid subtriangular swellings. The boss is wider than the glabella and somewhat overhangs and even intrudes the rim. The rim itself is narrow, defined by the shallow frontal furrow, and not protruding forward, as seen in undeformed specimens (Pl. 1, fig. 1).

The interocular cheeks are horizontal, moderately tumid, about as wide as the glabellar length, and slightly wider (1.1) than the glabellar front. The ocular ridges are straight, horizontal, continuous, and prominent; they arise at the anterolateral corners of the glabella and are forked (double), but the branches remain close together.

The palpebral lobes, between their tips, are as long as the glabella, and about 0.7 of the glabella along the contact with the cheeks; the anterior tips bypass the ocular ridges and slope down; the posterior tips (see Pl. 2, fig. 2) are pointed; there is a deep adaxial and a shallow abaxial palpebral furrow; the lobes slope up abaxially and have been described as 'pixie ears'; the margin of the palpebral lobes is equipped with a narrow doublure. Thus, the structure of the palpebral lobes of *Nepea narinosa* is that of a falcate free pleura of the thorax. In internal casts the posterior tips are less prominent, as discussed in the 'Comment on illustrated specimens' below.

The glabella is relatively small, shorter than half the cephalon; its front is straight and defined by a deep furrow; the axial furrows are deep. The glabella tapers forward to about 0.7 of its rear width, which equals the glabellar length. There are three pairs of deep, oblique, and short glabellar furrows decreasing forward in size and emphasis; the lateral lobes are well defined by them. The occipital furrow is shallow in the middle, but the deep oblique pits at its ends repeat the structure of the posterior glabellar furrows. The occipital lobe is rather short, arched upward, and bears on its rear margin an upright and slightly curved spine arising from a triangular, flattened, petal-like base.

The bacculae ('alae' in Öpik, 1963), placed opposite, and close to, the posterior glabellar lobes, are low and circular.

In the thorax, the axial lobe is narrow and prominent; the segments are relatively short—about as short as the occipital lobe—and the pleural furrows are narrow and distinct.

As regards the ventral structure a rostral shield is absent; the free cheeks constitute an unbroken unit, and may have a furrow (Pl. 2, fig. 1) on the base.

The frontal area and the subocular part of the free cheek are venulose. The ornament consists of a dense granulation and the glabella carries three pairs of segmentally arranged tubercles; the rim of the palpebral lobe is granulated also, but the rest of the lobe is smooth.

Comment on illustrated specimens

The following three specimens come from the Split Rock Sandstone, locality M417—the place and the bed of the type material of *Nepea narinosa* Whitehouse.

The cranidium Plate 1, figure 1, CPC4740, is 5.0 mm long, and about as long as the holotype. The palpebral lobes are not preserved; the boss is circular; the bacculae are distinct. The posterolateral limb is seen in Figure 1a; the attitude of the intragenal spine is evident in frontal view, Figures 1d and 1c. It is an undeformed internal cast.

The cranidium Plate 1, figure 2, CPC7272, is 6.7 mm long; it is flattened, and is photographed with the upward-rotated front to allow for a better view of the occipital spine. The acute tip of the palpebral lobe is fractured. The test is not preserved.

The cranidium (rubber cast) Plate 1, figure 3, CPC7273, is 7.0 mm long; it is flattened, and a fragment of the phosphatic test of *Acrothele* adheres to its interocular cheek. The intergenal spine is there; the boss, 0.9 of glabellar length, is unusually large; the triangular occipital spine stands almost upright; the anterior tip of the palpebral lobe extends beyond the ocular ridge and slopes down; the acute point of the rear tip is lost.

The cranidium, Plate 1, figure 4, CPC7274, Split Rock Sandstone, locality M421, is 4.9 mm long; it is somewhat deformed (askew to right). The internal cast of the palpebral lobe is less acute than in the external cast, Plate 2, figure 2.

The next four specimens came from locality M226—a silicified siltstone bed of the Split Rock Sandstone.

The specimen (rubber cast), Plate 2, figure 1, shows in its upper left a free cheek (CPC7275) apparently retaining the ocular visual surface; the ventral side of another free cheek on the right has a furrow in its rear portion; this fragment is 18 mm long. Below: the cranidium, same Plate, figure 2.

The cranidium Plate 2, figure 2 (rubber cast), CPC7276, is 5.0 mm long. It represents the external features not seen in the internal casts in sandstone and siltstone. All the test is granulose; the ocular ridges are prominent and double; the bacculae are distinct; the triangular occipital spine is quite long (its tip is replaced by an air bubble); the palpebral lobes ('pixie ears') are long, about 0.7 of the glabella longitudinally, and from tip to tip as long as the glabella.

The fragment of a right free cheek (rubber cast), CPC7277, Plate 2, figure 3, is 4.0 mm high; it is the subocular part; beside the pustules veins are present also. The cranidium Plate 2, figure 4, CPC7278, is an internal cast, 4.4 mm long, associated with the specimen same Plate, figure 2. It is venulose in front of the ocular ridges and glabella; the glabella carries three pairs of segmentally arranged pustules; the rear palpebral tips are somewhat rounded, as seen also in a similar cast in sandstone. The drawn-out tip may have been hollow and filled with secondary calcite, or even solid; in either case a rounded edge is ascribable to leaching of the calcareous matter.

The left free cheek Plate 2, figure 5, locality M417, CPC4742, is 17.5 mm long; the upper margin of its spine lacks the thickening seen in *Penarosa,* Plate 10, figure 1.

The rather worn complete specimen (rubber cast) Plate 2, figure 6, CPC7279, in medium-grained sandstone, locality M276 (east from the site), is about 17 mm long. The cephalon retains the left free cheek, which on the flank stands in its original vertical position; the free pleurae also slope down steeply; the rubber cast shows some 20 segments; in the sandstone cast the rear of the thorax and the pygidium are curled under the thorax and unsufficiently preserved to show details.

The cranidium Plate 3, figure 1, CPC7280, from a block of aphanitic Mail Change Limestone at Morstone (Old Site), is 5.0 mm long; it preserves the proximal parts of the intergenal spines.

Occurrence and age. *Nepea narinosa* is very common in the Undilla Basin in the Split Rock Sandstone, especially in its lower part, and rare in the Mail Change Limestone below the Split Rock. Its age is the Middle Cambrian Zone of *Ptychagnostus nathorsti.*

NEPEA ANOXYS sp. nov.

(Pl. 3, figs 4a, b).

Material. *N. anoxys* is a rare species and found mostly as fragments; the best preserved cranidium, CPC4741, the holotype, is illustrated.

Diagnosis. *Nepea anoxys* is distinguished by (1) its very large subtrapezoidal boss, which is widest in front, (2) strongly oblique forked ocular ridges with divergent branches, (3) very wide interocular cheeks—as wide as 1.4 of the glabellar front, and (4) crescentic casts of the palpebral lobes.

Differential diagnosis. From *N. narinosa* the new species differs by all characters enumerated in the diagnosis. The large subtrapezoidal boss is somewhat similar in *N. avara* sp. nov., but in *avara* the ocular ridges are horizontal, the interocular cheeks narrow, and the palpebral lobes small. Furthermore, *avara* possesses other characters not seen in other species. *N. exserta* sp. nov. and *N. tonsillata* have a circular boss, narrow interocular cheeks, and shorter frontal area.

Description (abridged). The holotype cranidium is 8.5 mm long and quite large for a *Nepea.* The shape is subcircular to semielliptical, somewhat longer than half the rear width. The boss is as long as the glabella and the frontal area even slightly longer. The frontal marginal furrow is distinct and the rim as narrow as in *narinosa.* The base of the intergenal spine (Pl. 3, fig. 4b) is preserved, but the length of the spine is unknown. The casts of the palpebral lobes are 0.7 of glabellar length; in *N. narinosa* these casts have a different shape reflecting to some extent the shape of the palpebral test; the different shape in *anoxys,* however, is no indication that in its palpebral test posterolateral points and a peripheral doublure were absent; as seen from the illustration, the imprint of the doublure was carelessly removed with the needle. The bacculae are small. The glabella and its lateral furrows are the same as in *N. narinosa.*

Occurrence and age. *Nepea anoxys* has been found only in the Split Rock Sandstone, locality M417, in association with *N. narinosa.* The age is the Middle Cambrian Zone of *Ptychagnostus nathorsti.*

NEPEA EXSERTA sp. nov.

(Pl. 4, figs 1-3)

Material. A large number of cranidia have been examined; the rock is a fine-grained friable white quartzose sandstone with undistorted (not flattened) fossils.

Holotype. The best preserved and illustrated cranidium (CPC7284), an internal cast, is selected; it is 6.0 mm long.

Diagnosis. Nepea exserta sp. nov. refers to cranidia with a circular boss and horizontal ocular ridges distinguished by (1) the trapezoidal shape with straight flanks, (2) forward-protruding thick rim, (3) short boss—about 0.6 of glabella, (4) medium length of the casts of the palpebral lobes—about 0.65 of glabella, (5), a relatively long glabella and somewhat short frontal area of about 0.85 of glabellar length, and (6) almost subparallel flanks of glabella whose front is about 0.85 of its rear width.

Differential diagnosis. In the diagnosis the difference from all species with a circular boss is indicated; furthermore, in *anoxys* and *avara* the boss is subtrapezoidal and not circular; in *avara* the glabella also has subparallel flanks as in *exserta,* but other characters preclude any possibility of a confusion of *exserta* and *avara.*

Description (abridged). The palpebral lobes are pointed in the rear but remain shorter than in *N. narinosa;* the cast of the palpebral doublure is also preserved. The ocular ridges are double, with branches close together; the bacculae are small and low; the intergenal spines are curved, straddle the genal spines in plan, and are four times the glabellar length. The frontal area is weakly venulose. As seen in the frontal view (Pl. 4, figs 2 and 3), the interocular cheeks are flat and not as tumid as in *N. narinosa.*

Occurrence and age. Nepea exserta sp. nov. comes from the Split Rock Sandstone, locality M344; this site represents the highest known horizon in the Split Rock Sandstone, some 100-120 feet above the silty bed at locality M417; consequently, *N. exserta* is somewhat younger than *N. narinosa* but still belongs to the Middle Cambrian Zone of *Ptychagnostus nathorsti.*

NEPEA TONSILLATA sp. nov.

(Pl. 5, figs 1-3)

Material. Only the illustrated holotype cranidium, CPC7285, is available; it was damaged in a fire. Its test is preserved.

Diagnosis. Nepea tonsillata sp. nov. is distinguished by (1) a relatively short transverse elliptical boss, (2) triangular and angulate test of the relatively short palpebral lobe—as long as 0.7 of glabella, (3) a circular (not petaliform) base of the occipital spine, and (4) a relatively long and weakly carinate glabella. Furthermore, in the absence of the palpebral lobes, the combination of the following characters may serve in identifying this species: (5) the frontal area is

0.8 of glabellar length and therefore relatively short, or the glabella is relatively long; (6) the boss, 0.7 of glabellar length, is relatively short; (7) the interocular cheek, 1.2 of glabellar front, is wide, and (8) the glabella tapers forward to 0.7 of its rear width.

Differential diagnosis. The triangular and relatively short palpebral lobe prevents any confusion with *N. narinosa,* whose palpebral test is as long as the glabella; in *N. exserta* the boss is even shorter and circular, the glabella almost parallel-sided, and the interocular cheek much narrower than in *tonsillata;* in *N. anoxys* the frontal area is longer, the boss larger, the interocular cheek wider, and the ocular ridges oblique (horizontal in *tonsillata*); and *avara* is different in all characters listed above.

Description (abridged). The holotype cranidium is 5.1 mm long; the flanks behind the ocular ridges converge slightly forward and the margin of the frontal area is evenly arched forward. The rim is similar to *N. narinosa* (not forward protruding as in *exserta*); in frontal view, Plate 5, figure 3, its thickness is exaggerated because of the photographic perspective. The ocular ridges are broad, but indistinctly doubled. The palpebral lobe is almost imperceptibly drawn out at its posterolateral tip and divided by a deep central depression; its anterior tip extends forward beyond the ocular ridge and slopes down, as seen in Plate 5, figure 2, in frontal view. A weak notch is apparent in the front of the glabella; the occipital lobe is narrow, elevated, and arched upward, and the circular base of the spine is preserved. The proximal part of the intergenal spine is exposed. The interocular cheek is flat, the glabella is arched well above the cheek, and the bacculae are circular, large, and prominent. The ornament consists of scattered pustules on a background of a dense and relatively coarse granulation; the ornament on the glabella and probably on the rim of the palpebral lobe is worn owing to calcination in fire.

Occurrence and age. The holotype of *Nepea tonsillata* comes from the V-Creek Limestone, locality M54; rare fragments have been observed also in the same formation. Its age is the Middle Cambrian Zone of *Ptychagnostus nathorsti* —the beginning of that zone. It is the oldest species of *Nepea* yet known.

NEPEA sp. NA (indet.)

(Pl. 3, fig. 5)

Material. The material consists of a single silicified cranidium, CPC7283, with preserved test, partly immersed in chert. The palpebral lobes and the occipital lobe are missing and because of these defects the specific nomenclature is left open.

The intergenal spines were present (but only their bases are preserved)— hence a species of the genus *Nepea* is apparent.

Description. The cranidium is 6.3 mm long, and semicircular in plan. The frontal area is relatively short—0.7 of glabella; the boss is elongate elliptical and narrow; the rim is inconspicuous and only partly visible from above; the triangular frontal parts flanking the boss are quite large; the ocular ridges are horizontal, relatively narrow and their duplication is not apparent; the interocular cheek, 1.5 of glabellar front, is rather wide; the bacculae are elongate, reniform, and the palpebral lobe along the contact with the cheek is short—about 0.5 of glabella. The ornament consists of scattered pustules and dense granulation. The described characters and their combination in *Nepea* sp. NA prevent its inclusion in any of the named species of the genus.

Occurrence and age. *Nepea* sp. NA (indet.) comes from locality M41, from a higher level of the V-Creek Limestone; its age is the Middle Cambrian Zone of *Ptychagnostus nathorsti,* but predating *N. narinosa* within the span of that zone.

NEPEA sp. NB (indet.)

(Pl. 3, fig. 3)

Material. The illustrated cranidium, CPC7282, 6.6 mm long, has been selected from a larger number of specimens in sandstone whose specific identity cannot be established because of defective preservation.

The relatively long glabella and short frontal area (as long as about 0.7 of glabella) indicate a species different from *N. narinosa*; the casts of the retrally swinging palpebral lobes are insufficiently preserved, probably because of unsuccessful development from the matrix. The lateral view (Pl. 3, fig. 3b), illustrates the posterolateral limb characteristic of the genus.

Occurrence and age. The illustrated cranidium comes from the Split Rock Sandstone, locality M141; the matrix is a leached red quartzose sandstone. The position within the formation is unknown. The age is the Middle Cambrian Zone of *Ptychagnostus nathorsti.*

NEPEA cf. EXSERTA

(Pl. 3, fig. 2)

The illustrated cranidium, CPC7281, is 7.2 mm long; the matrix is red quartzose sandstone. The semielliptical shape of the cranidium and the relatively long and only slightly tapering glabella indicate *N. exserta;* but the rim is narrow and the boss relatively large, suggesting a variant or a subspecies of *exserta.* The cast of the palpebral lobe, a segment of a circle, attained this shape through loss of some sandgrains along its edge; the imprints of the palpebral doublure and of the posterior tip are preserved and the doublure dips adaxially, being represented by the hollow fissure around the cast of the palpebral lobe. The test of the palpebral lobes evidently possessed the structure characteristic of a *Nepea.*

Occurrence and age. The cranidium comes from the Split Rock Sandstone, locality M133; its age is the Zone of *Ptychagnostus nathorsti.*

NEPEA AVARA sp. nov.

(Pl. 6, figs 1-5; Text-fig. 4)

Material. Two cranidia with silicified test and three cranidial casts in sandstone are illustrated; the cranidia in sandstone are relatively common.

Holotype. The cranidium, Plate 6, figure 1, CPC7286, is selected; it is fragmentary but sufficient to illustrate the specific characters; it is supplemented by the associated cranidium, Plate 6, figure 2.

Diagnosis. Nepea avara sp. nov. possesses a large trapezoidal boss and a subrectangular, slightly tapering glabella, and is distinguished by (1) abaxially fading ocular ridges, (2) small palpebral lobes, 0.3 of glabellar length, (3) adaxially sloping interocular cheeks, (4) a rather weak frontal marginal furrow and (5) an inconspicuous rim coinciding with the steep slope of the boss.

Differential diagnosis. The boss is also trapezoidal in *N. anoxys* sp. nov. and *N. exserta* possesses a somewhat similar glabella; in their differential diagnosis, however, the differences from *avara* have been considered; from the remaining species *avara* differs by all its diagnostic characters.

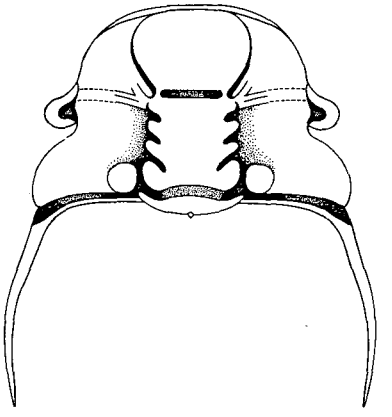


Fig. 4. *Nepea avara,* sp. nov., cranidium.

Description. The cranidium (and the cephalon) are somewhat elongate semielliptical, with an obtuse front. The posterolateral limbs are large, with a retral swing, and intergenal spines whose length is unknown. In sandstone casts the retral swing is less pronounced than in the silicified holotype. The posterolateral furrows fade out about the level of the intergenal spines. The frontal area is as long as the glabella; the boss is very tumid, prominent, as long as 0.9 of the glabella and well defined by furrows. The marginal furrow is weak; the rim is barely visible in plane but rather thick in frontal view. The interocular cheeks are about as wide as the glabellar front and tumid; at the palpebral lobes they are as high as the glabella and slope adaxially in a gentle arc. The ocular ridges are somewhat oblique and broad; they are prominent crossing the axial furrows; forked into two branches, they become inconspicuous on the interocular cheeks. Furthermore, they are connected with the boss by a pair of short ridges (ducts) arising almost at the glabellar corners. The palpebral lobes

are short (0.3 of glabellar length), with a weak posterolateral swing and depressed centrally. The subrectangular glabella tapers forward to about 0.8 of its rear width, and is well defined laterally by the axial furrows; the furrow in front is deep and broad. The three pairs of glabellar furrows are rather deep and so are the pits at the ends of the occipital furrow. The occipital lobe is short, arched upward, and may have possessed a tubercle or a short slender spine. The ornament consists of scattered pustules and a dense background granulation.

Comment on illustrated specimens

The two following specimens are silicified tests in limestone, locality D108. The holotype cranidium, Plate 6, figures 1a-1c, is 7.00 mm long (as preserved). The proximal part of the left palpebral lobe, the left posterolateral limb with the stump of the intergenal spine, and a small part of the occipital lobe are preserved; the short ducts connecting the glabella with the boss are visible; the marginal furrow (in Fig. 1b) is rather weak; the ocular ridges are almost fading out abaxially.

The cranidium, Plate 6, figure 2, is 6.5 mm long; its occipital lobe is preserved, thus supplementing the holotype.

The following specimens came from the Steamboat Sandstone, locality D95; these are decorticated casts.

The cranidium, Plate 6, figure 3 (right upper corner), and figure 4, is 4.6 mm long.

The cranidium, Plate 6, figure 3 (on the left) and figure 5, is 7.9 mm long. The casts of the palpebral lobes are preserved; note that the lobe in figure 3 is in an unconventional attitude.

Occurrence and age. *Nepea avara* is frequent in the Steamboat Sandstone, at localities D108, D54, and D95; its age is the Middle Cambrian Zone of *Leiopyge laevigata.*

NEPEA? sp. nov. NC

(Pl. 7, figs 4, 5; Text-fig. 5)

Material. The material consists of two fragmentary cranidia in black splintery limestone.

Nomenclature. *Nepea* appears the nearest genus; the name, however, is queried because some of the characters (shape of the palpebral lobes, the presence or absence of intergenal spines, the structure of the rim) are insufficiently preserved; for the same reasons open specific nomenclature is applied. It is, however, certain that the fragments represent a new species of the Nepeidae.

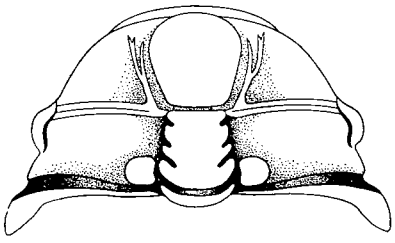


Fig. 5. *Nepea?* sp. nov. NC, reconstruction of cranidium.

Description. The better preserved cranidium, Plate 7, figure 4, CPC7293, is 4.0 mm long. It is semicircular in plan, with steeply down sloping posterolateral limb not visible from above; no intergenal spine is evident; the frontal area is rather long, the boss is longer than the glabella, very tumid, well defined and pyriform. The remnant of the rim in front of the boss is too small for a reliable reconstruction. The interocular cheek is tumid, and very wide (1.5 of glabellar front); the ocular ridge is horizontal, prominent and double, and a strong branching vein arises from its adaxial end and flanks the boss. The palpebral lobe, about 0.6 of glabella length, is indicated but its structure remains obscure. The bacculae are large and prominent; the tapering glabella bears three pairs of deep oblique lateral furrows. The ornament consists of a dense granulation.

The second fragment, Plate 7, figure 5, CPC7294, is 4.5 mm long. The glabella is missing; the boss is somewhat outlined, and its flanking vein is well defined; the retral swing of the posterolateral limb is rather weak for a *Nepea;* the posterolateral marginal furrow is very deep, and the border prominent and narrow.

Occurrence and age. Nepea? sp. nov. NC comes from a limestone bed from the Ross River Gorge, Northern Territory. It is associated with fragments of a *Xystridura;* its age is, therefore, early Middle Cambrian—presumably early within, or older than, the zone of *Ptychagnostus gibbus;* even a late Ordian age is a possibility.

Genus FOLLICEPS nov.

The type of *Folliceps* is *F. nans* sp. nov.

Diagnosis. Folliceps refers to Nepeidae with a narrow rim and obtuse cranidial front similar to *Nepea,* but distinguished by simple, crescentic palpebral lobes, and by the absence of intergenal spines.

Differential diagnosis. The difference from *Nepea* is indicated in the diagnosis. *Penarosa* gen. nov. and *Folliceps* share the simple structure of the palpebral lobes and the absence of intergenal spines, but differ in the structure of the front: in *Penarosa* the cranidial front is upturned.

The difference from *Loxonepea* gen. nov. is discussed under the latter.

FOLLICEPS NANS sp. nov.

(Pl. 7, figs 1-3)

Material. Three cranidia are described and illustrated selected from less informative fragmentary material; it is a rare form.

Holotype. The cranidium Plate 7, figure 1, CPC7290, locality M123, is the best preserved and selected as the holotype.

Diagnosis. Folliceps nans sp. nov. is the sole representative of its genus; hence the generic diagnosis and differential diagnosis indicate the characters by which *F. nans* is distinguished from all other known species of its family—the Nepeidae.

Description. The holotype cranidium is 3.5 mm long; the illustration is prepared from a rubber cast of the external surface of the test and depicts correctly the structure of the rim and the palpebral lobes, and the absence of intergenal spines. The test is deformed (creased). The boss is subtrapezoidal, and about 0.9 of glabellar length; it is somewhat collapsed, exposing the narrow rim at its front. The interocular cheeks are as wide as the glabellar front; the palpebral lobes are relatively long (about 0.65 of glabella), narrow and crescentic; they are placed forward, with their midpoints almost level with the glabellar front. The bacculae are prominent; the test is granulose.

The fragmentary silicified cranidium, Plate 7, figure 2, CPC7291, locality M124, is 4.0 mm long; it is undeformed; the *Nepea*-like rim is indicated at the right corner of the boss and the boss is wider than the glabella; the interocular cheeks are tumid, and the ocular ridges are oblique; in the holotype these are obscured by secondary deformation.

The cranidium, Plate 7, figure 3, CPC7292, locality M123, is 6.1 mm long. It is a cast of the external surface of the test, showing the oblique ocular ridges, the narrow crescentic and advanced palpebral lobes, the *Nepea*-like boss, and the granulation; the left posterolateral limb is exposed and no intergenal spine is present.

Occurrence and age. Folliceps nans has been found in the Currant Bush Limestone and tongues of the Limestone extended into the Age Creek Formation; its age is the Middle Cambrian Zone of *Euagnostus opimus.*

Genus LOXONEPEA nov.

The type of the genus *Loxonepea* is *L. loxophrys* sp. nov.

Diagnosis. Loxonepea refers to Nepeidae distinguished by (1) rather oblique ocular ridges, (2) advanced, forward-placed palpebral lobes whose posterior tips are level, or almost level, with the glabellar front, and (3) diffuse or even obliterated transverse furrow in front of the glabella.

Differential diagnosis. Loxonepea is apparently related to *Penarosa,* whose species *petalifera* and *melota* have a somewhat similar aspect, but whose glabellar front and preglabellar furrow are well defined, ocular ridges and palpebral lobes only slightly oblique, in a normal, not advanced position. The frontal part of the cranidium of *Loxonepea* is insufficiently exposed, but a *Penarosa*-like upturned rim is still indicated and other structures mentioned in the description indicate *Penarosa,* and not *Nepea,* as the related genus. The ocular ridges are also oblique in *Folliceps,* but much less than in *Loxonepea,* and the rim, the large boss, and the well defined glabellar front and preglabellar furrow of *Folliceps* prevent confusion of these genera with each other. The forward position of eyes in *Loxonepea* is the same as in *Menomonia* (Menomoniidae, a family of the Nepeacea) which differs in the structure of the preglabellar area and the posterolateral limbs. The ptychoparioid design (glabella short, frontal area long) held a potentiality for a forward shift of the eyes independently in diverse lineages within the suborder.

LOXONEPEA LOXOPHRYS sp. nov.

(Pl. 17, fig. 1; Text-figs 6 and 7)

Material. Only one cranidium, 5.0 mm long, the illustrated holotype CPC7327, is sufficiently preserved to warrant description. It is embedded in a pod of silicified ooliths, in dolomitic limestone, locality M124A; the rock belongs to a tongue of the Age Creek Formation interfingering with the lower part of the Currant Bush Limestone.

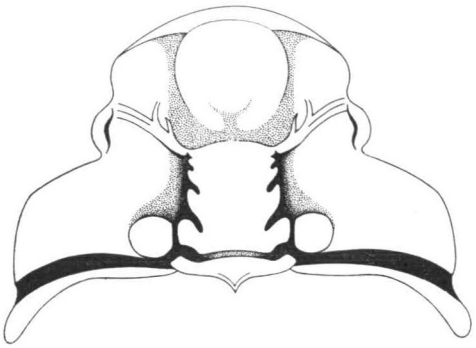


Fig. 6. *Loxonepea loxophrys* sp. nov., cranidium.

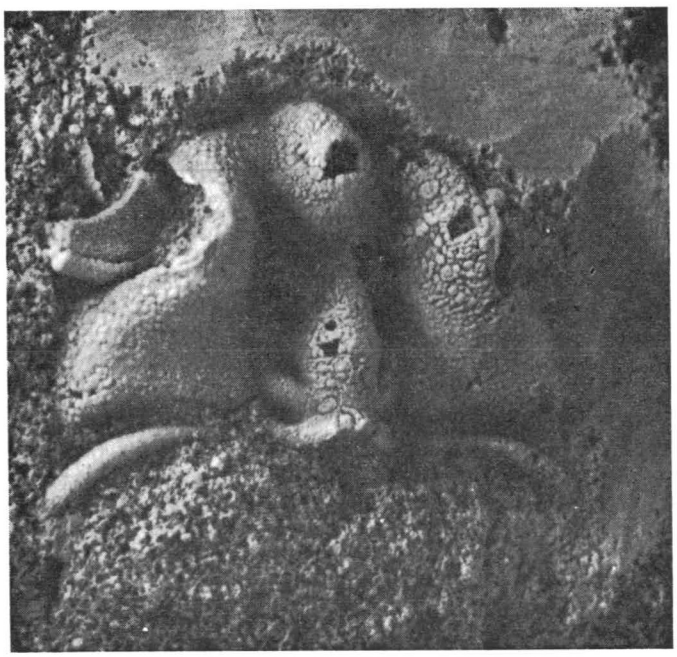


Fig. 7. *Loxonepea loxophrys* sp. nov., semi-lateral view of holotype illustrating its convexity.

Diagnosis. Characters of specific significance and differences from other forms are given in the generic diagnosis; the long frontal area (1.2-1.3(?) of glabellar length), the relatively narrow interocular cheek (0.55-0.6 of glabellar front), the well defined palpebral furrow, and the upsloping palpebral lobe are distinctive when compared with *Loxonepea* sp. nov. ND (q.v.).

Description. The cranidium is slightly longer than half its rear width; its rear part is broad and trapezoidal, but the front area narrows abruptly to 0.5 of the rear. The relief (Text-fig. 7) is very strong; the palpebral lobes are elevated on summits twice the height of the glabella and the boss, which themselves are quite prominent; the front is very steep and the abaxial flaps of the posterolateral limbs, as in all known Nepeidae, are hanging down. The posterolateral marginal border, generally narrow, is an abaxially widening ridge, and the posterolateral furrow is a wide and deep channel. No intergenal spines are apparent.

The frontal area (as far as it is preserved) is 1.25 of glabellar length, and consequently long; the boss, about as wide as the glabella in its middle, is quite tumid (more tumid than in *Penarosa*) and gains in tumidity forward. The rim buried in silica is only partly exposed; nevertheless a part close to the boss is exposed; it is flat, indicating a structure different from the rim of *Nepea.*

The interocular cheeks are bulging and slope steeply adaxially; behind the eyes the summits are defined by a sigmoidal and broad depression each running obliquely from the glabellar corners. The ocular ridges are oblique, at a right angle to each other; they are curved, widen and fork abaxially; forward directed branches are also apparent, flanking the rear of the boss. The palpebral lobe (seen on the right side) is defined by a palpebral longitudinal furrow and a steeply upsloping palpebral test; the palpebral internal cast of silicified ooliths is worn but retains its crescentic shape; the rear tips of the palpebral lobes are almost in line with the glabellar front.

The glabella is strongly convex transversely and slopes forward in a moderate curve; its front is defined by change of slope only; no furrow separates it from the frontal area. The glabellar furrows, including the pits of the occipital furrow, are oblique, short, and deep; three pairs are distinct, and a fourth, rather short, is discernible at the junction of the ocular ridges with the glabellar front. The occipital lobe is prominent, arched upward, and bears the base of a broken marginal, possibly petaliform, spine. The bacculae are large, but low.

The ornament consists of a dense granulation and scattered pustules.

Occurrence and age. The formation is indicated above, under 'material'; the age of *Loxonepea loxophrys* is the Middle Cambrian Zone of *Ptychagnostus atavus.*

LOXONEPEA sp. nov. ND

(Pl. 17, fig. 2)

Material. Only the illustrated cranidium, CPC7328, 9.0 mm long, is available; it is the mould of the internal surface of the test; the matrix is a thin layer of silicified oolites in dolomite.

The test is silicified and fragmentary, with the posterolateral limbs missing, and the front is immersed in the matrix; hence the open specific nomenclature became necessary.

The frontal area is wide, wider than in *Loxonepea loxophrys,* and venulose all over in a manner seen in the species of *Penarosa;* the boss is bulbous in front, low in the rear, and not separated from the glabella by a distinct transverse furrow. The ocular ridges are strongly curved and oblique, but the angle, about 110-120°, is much wider than in *L. loxophrys.* The palpebral lobe is low and smooth in cast—a structure not seen in other nepeids. The bacculae are small and distinct. The anterior glabellar furrows are developed as a pair of pits—observable also in some species of *Penarosa,* but not of *Nepea.* The test is minutely pustulose.

Occurrence and age. The described specimen comes from locality M122, Age Creek Formation; its age is the Middle Cambrian Zone of *Ptychagnostus atavus.*

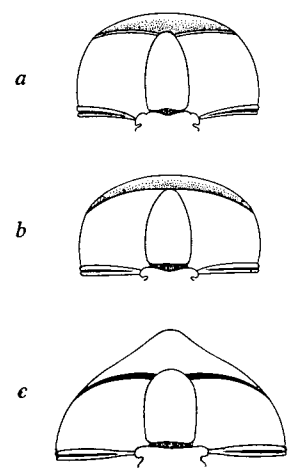
Genus PENAROSA nov.

The type species of *Penarosa* is *P. retifera* sp. nov.

Diagnosis. Penarosa refers to species of the Nepeidae having a very long frontal area, crescentic palpebral lobes, horizontal or slightly oblique ocular ridges arising from the anterolateral corners of the glabella, whose front is defined by a transverse preglabellar furrow, and having no intergenal spines; distinguished by the upward arched and upturned cranidial front and elongate narrow boss.

Differential diagnosis. In *Nepea* and *Folliceps* gen. nov. the front is horizontal, the margin is not upturned, and the boss is wide; in *Loxonepea* gen. nov., which is close to *Penarosa,* the ocular ridges are very oblique and the eyes are advanced forward; in the Upper Cambrian *Ferenepea* Ö. and *Ascionepea* Ö., the frontal area is relatively short, the boss circular, the ocular ridges arise behind the glabellar corners, and the cranidial margin has a different structure.

General aspect. The general aspect of *Penarosa* differs little from *Nepea narinosa* (q.v.); the main difference is the absence of intergenal spines in *Penarosa* and the concave border of its cephalon. The mode of life has been already discussed under the heading 'Ecology of the Australian nepeids'.



Figs 8a-8c. Structure of the front a.—in *Penarosa vittata,* with upturned border and transverse ridge; b.—in *P. zeabunda* with convex rim; and c.—in *P. rhinodelphis* with upturned and drawn out border.

Glabellar fronts and ocular ridges are also shown. In Text-figs 9 and 10 the boss is relatively short and the rimless front is upturned or even excavated.

PENAROSA RETIFERA sp. nov.

(Pl. 8, figs 1a-2b; Pl. 9, figs 1-4; Pl. 17, figs 7-9; Text-fig. 9-11)

Material. The illustrated and described material comprises four cranidia, one cephalon with a part of the thorax, one free cheek, one pygidium, and three small immature cranidia; *P. retifera* is a common species and a large number of mature cranidia have been examined.

Holotype. The cranidium, Plate 8, figures 1a-1d, CPC7297, is selected because of its relatively large size and excellent preservation.

Diagnosis. Penarosa retifera sp. nov. is distinguished by its concave cranidial border with reticulate veins, but without a rim and without a transverse ridge at the cranidial front; furthermore, its frontal area is very long (1.5-1.6 of glabellar length), the glabella is relatively plump, the ornament (granulation and pustules) is diversified, and the cephalon is strongly vaulted—more than in other species of the genus.

Differential diagnosis. The difference of *P. retifera* from the other new species of the genus is discussed in their differential diagnoses.

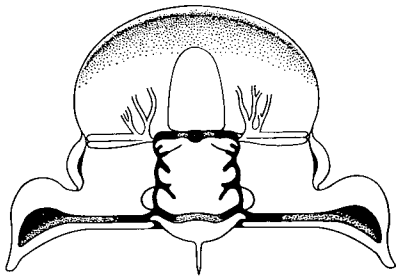


Fig. 9. *Penarosa retifera* sp. nov., cranidium.

Description. The cephalon in plan is semielliptical, slightly longer than half the width, with a moderately forward arched front. The relief of contrasting lobes and furrows is graphic; the large and steeply downsloping flanks with a concave flange produce a rather voluminous cephalic capsule as long as about 12 segments of the thorax. The free cheek is divided into two parts by the deep embayment receiving the flap of the posterolateral limb. The rear part is drawn out into a long curved spine with a thickened upper edge; the anterior, subocular part is large, trapezoidal, moderately tumid, separated from the marginal flange by a furrow, and conspicuously venulose. The principal vein is also present, running obliquely from the base of the eye down and rearward. The frontal doublure of the cheek, visible in Plate 10, figure 1, is about as wide as the concave

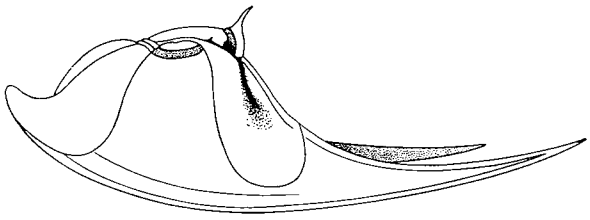


Fig. 10. *Penarosa retifera*, cephalon in lateral view, reconstructed.

cranidial front. A complete cheek unit as seen in *P. petalifera* (Pl. 16, fig. 2) is not available; but the broken end of the doublure in *retifera* indicates the absence of ventral sutures; so it is fair to assume that the free cheeks were united by the continuous subcephalic doublure.

As in *Nepea,* the posterior sutures dive down from the eye and rise again to intercept the rear cephalic margin at an acute angle, but remain invisible in plan view. The anterior sutures also descend steeply, and parallel to each other within the brim, then curve gently and meet on the ventral side, leaving a short part of the frontal doublure with the isolated cranidium.

The posterolateral limb expands distally, forming a spatulate retral flap, covered with a fan of osculating veins issuing from a strong duct which arises at the rear of the eye and runs along the suture. The posterolateral marginal furrow is rather deep, expands distally, and fades out well before reaching the border. The posterolateral border continues into the upper border of the genal spine.

The frontal area is very long, slightly variable around 1.5-1.6 of glabellar length; in larger cranidia this size is attained in specimens beginning with the length of about 5 mm. In smaller specimens (3.5-4.0 mm) it is less—1.3 to 1.4 of glabellar length. The boss is elongate, reaching the rear of the concave marginal border. The cranidial (and cephalic) frontal margin is strongly arched upward (Pl. 8, fig. 1d), and forward. There is no rim, but for a concave flange. The frontal area is graphically venulose, and its flange reticulate.

The interocular cheeks are tumid and sloping adaxially, and as wide as 1.0-1.15 of the glabellar front. The ocular ridges are straight in plan, conspicuous and forked. In some specimens (Pl. 8, fig. 2; Pl. 9, fig. 4) a pair of strong branching veins arising at the adaxial ends of the ocular ridges flank the boss. The palpebral furrows are well expressed; the palpebral lobes, as long as 0.6-0.65 of glabellar length, are crescentic and simple, lacking the doublure seen in *Nepea.*

The bacculae are small, reniform, and placed close to the posterior glabellar lobes. The axial furrows flanking the glabella are straight, deep, and V-shaped in section. The preglabellar transverse furrow is also straight, but unevenly deep; its adaxial ends are deep pits, and a median pit notches the glabellar front; between the pits the furrow is shallow, indicating the presence of a pair of ducts connecting the glabellar front with the rear of the boss. A similar structure occurs also in *Nepea* (*N. avara,* Pl. 6, fig. 1a).

The glabella is subrectangular, tapering forward to about 0.8 of its rear width, and relatively plump (the rear width is about 1.1 of the length). In the holotype the glabella is delicately carinate. The glabellar furrows, including the distal ends of the occipital furrow, are developed as short, deep, oblique pits, whose size decreases forward; four pairs of glabellar furrows, all connecting the axial furrows, are present; the two anterior furrows (see Pl. 8, fig. 2a) are rather short, close together, and separated from each other by a diminutive lobe. The occipital lobe is short, arched upward and carries a marginal needle-like slender reclined spine.

The thorax is incompletely known. About 24 segments are preserved in Plate 9, figure 2, and the total number is estimated as 34. The axial lobe tapers slowly and is rather narrow, about 0.22-0.23 of the width of flattened shields. The fulcra are weak and placed from the axial furrows at the distance of the width of the axial lobe, which, in the anterior part of the thorax, is the distance of the palpebral lobes from the glabella; the free pleurae originally sloped down steeply. The pleural tips are brevifalcate and drawn out into short retral spines. The pleural furrows are broad and deep channels bounded by narrow and elevated marginal ridges, each carrying a single row of pustules.

The pygidium is relatively small, estimated 0.2-0.25 of cephalic length and, therefore, hard to find; only three pygidia of *P. retifera* have been observed, and none of the remaining nepeids. The illustrated pygidium (Pl. 9, fig. 3, and Text-fig. 11) corresponds to a cephalon as large as the holotype, or even larger. The shield is semielliptical, longer than half its width; it has a concave marginal flange, five pairs of pleural ribs, and an axial lobe of about four annulations and a low rounded terminus extending to the flange.

The ornament is diversified, the whole test is granulose. In the cephalon the median part of the glabella is densely granulose, and coarser scattered tubercles may also occur; the glabellar flanks may be even smooth, or almost so; the occipital lobe is granulose and in the holotype the granules are arranged transversely. The cranidial cheeks are pustulose and the density of the ornament increases abaxially, but the posterolateral flaps are almost smooth; the frontal area is granulose and pustulose and the pustules are somewhat retrally reclined, and follow the trend of the veins. The ocular ridges are ornamented, but the palpebral lobes, the bacculae, and the occipital spine are smooth. The subocular part of the free cheek is pustulose, but the genal spine is smooth.

The axial lobe of the thorax is densely granulose, but pustules and axial spines are absent; the pygidial axis carries a pair of pustules on each annulation; as mentioned above, the marginal ridges of the pleurae and the ribs of the pygidium carry a row of pustules each.

Comment on illustrated specimens

All specimens, unless otherwise indicated, come from the Currant Bush Limestone of Northern Territory.

The holotype cranidium, Plate 8, figures 1a-1d, in limestone, locality M180, is 12.5 mm long; it is undeformed, with the posterolateral flaps hanging and parallel to each other; the parts missing in the illustration (the right palpebral lobe and a chip of the front) are preserved in the counterpart; the missing chip, however, or its scar reveals the presence of the frontal doublure. The ornament appears 'soft' because the pustules are somewhat decapitated. In the photograph Figure 1b, the specimen is tilted and specially illuminated to show the reticulate veins of the front; in Figure 1c (lateral view), the main vein along the rear suture is visible, fanning out into a reticulate system.

The cranidium, Plate 8, figures 2a-2b, CPC7298, locality M180, in limestone is 7.1 mm long; it is slightly deformed (the posterolateral flaps are displaced); the ornament is preserved better than in the holotype; the boss is quite tumid and flanked by conspicuous forward-directed branches of the ocular ridges.

The cranidium, Plate 9, figure 1, CPC7299, locality M180, in limestone (*Acrotreta* coquina), is 8.0 mm long; the test is collapsed, the palpebral lobe is distorted and defective; the ornament and the slender occipital spine are preserved; the frontal margin appears thicker than in the other specimens because the doublure is partly exposed.

The silicified fragmentary exoskeleton, Plate 9, figure 2, CPC7300, from about locality M393 of the Currant Bush Limestone (Queensland) is 32.0 mm long as preserved. The spine of the free cheek is longer than 10 segments; the pleural furrows are wide channels, the pleural margins are ornamented by a single row of pustules each.

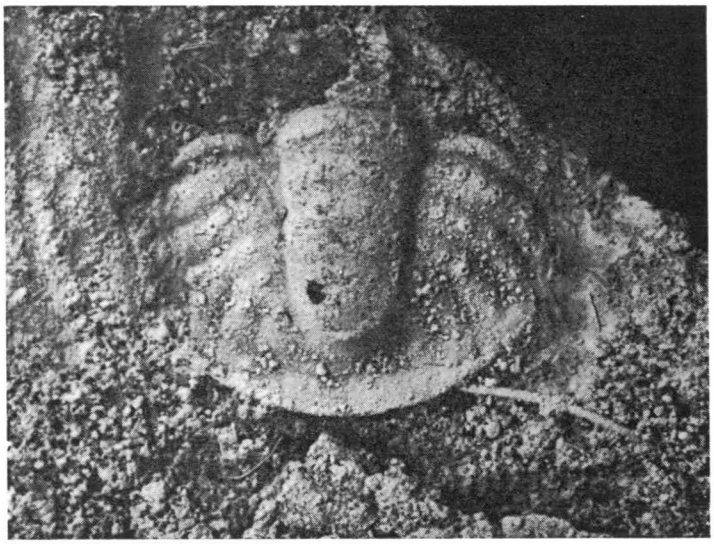


Fig. 11. *Penarosa retifera* sp. nov., pygidium x 7.2. Same specimen Plate 9, fig. 3.

The silicified pygidium, Plate 9, figure 3, Text-figure 11, CPC7301, in chert, locality M160 of the Age Creek Formation, is 2.8 mm long; note the ribs carrying each a single row of pustules.

The silicified cranidium, Plate 9, figure 4, CPC7302, flattened in chert, is 10 mm long; it is associated with the pygidium above; the pygidium, however, belongs to a specimen with a larger cephalon.

The free cheek, Plate 10, figure 1, CPC7304, locality M180, is 21.0 mm long from tip to tip. The border is a concave flange; note the principal vein on the subocular part of the cheek.

The immature cranidium, Plate 17, figure 8, CPC7334, locality M180, is 0.55 mm long. The frontal area slopes down, and has a medium depression; there is no boss; the ocular ridges arise at the glabellar corners and are arcuate; the glabella bears three pairs of segmentally arranged tubercles.

The immature cranidium, Plate 17, figure 7, CPC7333, associated with the preceding, is 0.62 mm long.

The immature cranidium, Plate 17, figure 9, CPC7335, locality M180, is 0.75 mm long; the palpebral lobes are behind the glabellar front; there is a narrow and flat rim, but no boss; the glabellar front is notched.

Occurrence and age. *Penarosa retifera* occurs abundantly in the Currant Bush Limestone of Northern Territory and Queensland in outcrops along Lancewood Creek and the tributaries of the Mussellbrook River (northeast Drummond Sheet and Lawn Hill Sheet areas); it is sporadic in interbeds of the northern wing of the Age Creek Formation, and in the Currant Bush Limestone of the Camooweal Sheet area. Its age is the Middle Cambrian Zone of *Euagnostus opimus* (= Zone of *Hypagnostus parvifrons*).

PENAROSA sp. PA, aff. RETIFERA

(Pl. 9, figs 5a, 5b)

Material. A single fragmentary cranidium, CPC7303, is available; the species name is left open because the specimen is insufficient for a diagnosis.

Description. The cranidium is 4.5 mm long; its frontal area, 1.2 of glabellar length, is relatively short—shorter than in smaller cranidia of *P. retifera* (about 3.5-4.0 mm in length); but the palpebral lobes, 0.7 of glabella, are quite large; the glabellar front is peculiarly bilobed, and the glabella is relatively slender, its rear being about 0.9 of length. The concave rimless front indicates, however, a form close to *P. retifera.*

Occurrence and age. The specimen of *Penarosa* sp. PA comes from the Currant Bush Limestone, locality M180, where it is associated with *P. retifera* sp. nov. The age is the Zone of *Euagnostus opimus.*

PENAROSA VITTATA sp. nov.

(Pl. 10, fig. 2; Pl. 15, figs 1a-2; Text-fig. 8a)

Material. The illustrated and described material consists of a cranidium attached to a larger part of its thorax, another, deformed, cranidium, and fragments of several free cheeks in a piece of chert.

Holotype. The cranidium with its thorax, Plate 15, figure 1, CPC7318, is selected as the holotype.

Diagnosis. *Penarosa vittata* sp. nov. has a very long frontal area of about 1.5-1.6 of glabellar length and a concave cranidial front and no rim and is therefore related to *P. retifera* sp. nov.; *P. vittata* is, however, distinguished by (1) a moderately vaulted cephalon, (2) relatively small flaps of the posterolateral limbs, (3) wide interocular cheeks as wide as 1.35-1.7 of glabellar front, (4) absence of reticulate veins in the concave part of the cranidial front, and (5) the transverse ridge on the frontal part of the brim.

Furthermore, only three pairs of glabellar furrows are present, the foremost fourth pair being not discernible in the available material.

Differential diagnosis. The differences of *P. vittata* from *P. retifera* are indicated in the diagnosis; the other species of *Penarosa* have a frontal rim, or a much shorter frontal area, and cannot be confused with *P. vittata.*

Description. Descriptive data are included in the diagnosis and in the comment on illustrated specimens and are amplified briefly below. The moderate convexity of the cephalon (and cranidium) of *P. vittata* is apparent when the lateral view of its holotype (Pl. 15, fig. 1a) is compared with a specimen of *P. retifera* (Pl. 8, fig. 2b) of a similar size.

The glabella in *vittata* has slightly concave flanks in its anterior third, but its rear, of about 1.2 of glabellar length, is quite wide. The ocular ridges in uncompressed specimens are slightly oblique and curved. The cranidial ornament consists of a rather low and dense background granulation and widely spaced coarser pustules.

In the thorax the axial lobe is rather narrow, about 0.2 of the thorax as in other species of *Penarosa;* the pleural furrows are broad channels with elevated marginal ridges studded with pustules; the axial lobe is granulose and axial spines are absent.

Comment on illustrated specimens

All specimens come from the Currant Bush Limestone, locality M124.

The holotype cranidium with its thorax, in grey somewhat sandy limestone, is undeformed. It is 23 mm long; the cephalon is 8.8 mm long and as long as 12 anterior segments of the thorax. Twenty-eight segments of the thorax are preserved, the rear segments with the pygidium are lost; the thorax is estimated as 34-36 segments, judging from another (not illustrated) fragment. The pleural tips carry short retral spines.

The cranidium Plate 15, figure 2, CPC7319, associated with the holotype, is 12.3 mm long; it is flattened and fractured. Note the slender occipital spine and the transverse ridge on the frontal part of the brim.

The piece of chert, Plate 10, figure 2, CPC7305, contains numerous fragments of free cheeks; fragmentary cranidia attributable to *P. vittata* are also present. Frontal doublures are also visible, with ends broken beyond the midline; a median suture and a rostral shield are therefore absent.

Occurrence and age. Penarosa vittata comes from the Currant Bush Limestone and its interbeds at the margin of the Age Creek Formation; the age is the Middle Cambrian Zone of *Euagnostus opimus.*

PENAROSA sp. PB, aff. VITTATA

(Pl. 15, fig. 3)

A single cranidium, CPC7320, of this form is available. It is 9.00 mm long and flattened in limestone. Its front is concave, without a rim, and close to the margin a transverse ridge is weakly indicated—a structure suggesting affiliation with *Penarosa vittata* sp. nov. It differs, however from *P. vittata* by the

narrow interocular cheek a little wider than the glabellar front and somewhat longer and parallel-sided glabella, which has four pairs of lateral furrows. The frontal area is long, about 1.45 of glabellar length. The ornament is relatively coarse and dense.

Occurrence and age. The cranidium comes from the Currant Bush Limestone interbedded with the Age Creek Formation, locality M123; its age is the Zone of *Euagnostus opimus.*

PENAROSA ZEABUNDA sp. nov.

(Pl. 10, figs 3-5; Pl. 11, figs 1a-3; Pl. 12, fig. 1; Pl. 17, figs 5 and 6;

Text-figs 8b and 12)

Material. The illustrated and described material consists of one fragmentary exoskeleton, four mature and four immature cranidia; it is a common species and numerous cranidia have been identified.

Holotype. The cranidium, CPC7309, Plate 11, figures 2a-2b, and 3 (upper specimen) and Plate 12, figure 1, is selected as the holotype; it is the least deformed specimen.

Diagnosis. Penarosa zeabunda has a moderately long frontal area of about 1.3-1.4 of glabellar length, an evenly distributed granulose to pustulose ornament, suppressed veins on the frontal area, and a relatively slender annulated glabella, and is distinguished by its narrow and evenly convex rim and relatively wide glabellar furrows.

Differential diagnosis. The nearest species is *Penarosa elaticeps* sp. nov., which also possesses a convex rim, but with a retral recess in the middle not seen in *zeabunda;* also, in *P. elaticeps* the interocular cheeks are wider than in *zeabunda.* A rim is also present in *P. petalifera* and *melota,* but it is much narrower and the frontal area is much shorter in these species than in *zeabunda; P. retifera* and *P. vittata* cannot be confused with *zeabunda* because they are rimless.

Description. The cephalon and the cranidium of *P. zeabunda* are similar to *P. retifera* in general: the shape is semielliptical, the relief is rather strong, the front is arched up and forward, and upturned; the cephalon is as long as about 10 or 11 segments of the thorax and therefore slightly shorter than in *retifera.* The free cheek (see Pl. 10, fig. 3) is the same in both species, including the thickened upper border of the falcate genal spine. The frontal area in *zeabunda* is 1.3 to 1.35 of glabellar length and it may reach 1.4 in flattened specimens; it is therefore shorter than in *retifera.* A shallow but distinct frontal marginal furrow is present, defining the rear of a convex rim — structures not seen in *P. retifera*; the rim is upturned and different from the rim of *Nepea.* The veins on the frontal area are subdued and sporadic or may be absent altogether.

The interocular cheeks are tumid, sloping adaxially but also slightly toward the palpebral lobes, and as wide as 1.0 to 1.2 of the glabellar front. The ocular ridges are forked and horizontal, or almost so; the crescentic palpebral lobes are relatively long (0.65-0.7 of glabellar length). The bacculae are prominent and semicircular. The axial furrows flanking the glabella owing to the expansion of the frontal glabellar lobe are somewhat concave at the anterior part of the glabella; the preglabellar transverse furrow is distinct and bears three pits; the median pit notches the glabellar front.

The glabella is relatively slender, its rear being 0.9-1.0 of its length, and also subrectangular, tapering to 0.8-0.85 of its rear width. Four pairs of glabellar furrows are present, as seen best in Plate 10, figure 5. The glabellar furrows, including the pits of the occipital furrow, are quite wide and the lateral lobes are therefore narrow—a peculiar trait of the species; moreover, the glabella is annulated segmentally, more in immature (Pl. 17, fig. 6) and less in adult (Pl. 10, fig. 5; Pl. 11, fig. 1a) cranidia. The occipital lobe carries a short, slender, and reclined marginal spine.

In the thorax the axial lobe is very narrow—about 0.2 of the width of the flattened exoskeleton; the fulcra are distinct, the fulcral lines are far apart—in line with the eyes; the pleural furrows are wide channels bound by marginal ridges ornamented by a single row of pustules each; axial spines are absent.

The cranidial ornament consists of an even and dense granulation; the palpebral lobes, however, are smooth.

Comment on illustrated specimens

All specimens, unless otherwise indicated, come from the Currant Bush Limestone, locality M179, of Northern Territory.

The fragmentary exoskeleton, Plate 10, figure 3, CPC7306, from about locality M393 (Queensland), is 20.0 mm long; it is an external mould in siltstone, embedded dorsum down. Twenty segments of the thorax are preserved; in the left genal spine the thickened upper edge is visible. Note the convex rim and the slender glabella. The cephalon is as long as 11 segments.

The cranidium Plate 10, figure 4, CPC7307, is 5.5 mm long. The rim is fragmentary, but shows in section the narrow frontal doublure; no veins are visible. The associated fragmentary thorax belongs to the same specimen.

The cranidium Plate 10, figure 5, CPC7308, is 5.7 mm long; it is flattened in silty limestone. Veins are indicated on the left; on the right, the suture is convex, preserving its original structure.

The cranidium Plate 11, figures 1a, 1b, CPC7309, is 4.2 mm long. Its rim is wider longitudinally than in the previous specimens and the boss intrudes the rear of the rim. The occipital spine is preserved. The holotype cranidium, Plate 11, figures 2a-2b, and 3 (upper specimen) and Plate 12, figure 1, is 6.0 mm long. In Figure 3 it is associated with the holotype of *Penarosa elaticeps*. Some of the matrix still adheres to the rim and could not be removed.

Figures 2a and 2b are in somewhat different attitudes: in 2a the occipital margin is in line with the posterolateral margin, and in 2b the specimen is rotated front up and the occipital lobe is therefore arched rearward.

The immature cranidia, Plate 17, figure 6, CPC7332, are in silicified rock. The smallest (below) is 0.47 mm, the other (above) 0.5 mm, and the largest 0.8 mm long. The small cranidia belong apparently to earliest meraspides; the larger is an early meraspis, and shows the palpebral lobes and annulation of the glabella.

Fig. 12. *Penarosa zeabunda* sp. nov., immature cranidia, rubber cast of Plate 17, fig. 6, x 40. The smallest cranidium (below) belongs presumably to a meraspis degree O; compare the immature cranidia of *Bolaspidella* illustrated by Robison (1964).

The immature cranidium, CPC7371, Plate 17, figure 5, is 1.1 mm long; its convex rim is indicated.

Occurrence and age: Penarosa zeabunda occurs abundantly in the Currant Bush Limestone at locality M179 (Northern Territory); it is also present in the vicinity of locality M393 (Queensland) in a shale attributed to the same formation. Its age is the Middle Cambrian Zone of *Ptychagnostus atavus*.

PENAROSA ELATICEPS sp. nov.

(Pl. 11, fig. 3 (below); Pl. 12, figs 2a-2d)

Material. The description is based on the illustrated cranidium, the holotype, CPC7311. It is 8.0 mm long, and is associated with the holotype of *Penarosa zeabunda* sp. nov. Two more specimens of *P. elaticeps* have been identified.

Diagnosis. Penarosa elaticeps is distinguished by the retral recess in its convex rim, combined with wide interocular cheeks, about 1.3 of glabellar front, and its occipital lobe which is somewhat longer than in other species of the genus.

Differential diagnosis. Penarosa elaticeps is close to *P. zeabunda,* whose differential diagnosis refers also to *P. elaticeps.*

Description. The retral swing of the posterolateral limbs in *P. elaticeps* is of a lesser degree than in *P. retifera* and *zeabunda;* furthermore the limbs and their flaps slope abaxially and are not hanging down. It is possible, however, that the posterolateral limbs attained this attitude, unusual in a nepeid, accidentally; if so, I cannot explain why the limbs are still symmetrically disposed. The frontal area is wide and moderately long—about 1.3 of the glabellar length. The marginal furrow is distinct and the rim convex; a recess is apparent in the frontal margin, the median part of the rim is turned retrally and in frontal view shows the doublure which is slightly depressed. The front is moderately arched upward and subangulate at its tip. The interocular cheeks are wide, about 1.3 of the glabellar front, and the palpebral lobes are somewhat short—about 1.55 of glabellar length. The glabellar front is notched and there are four pairs of lateral glabellar furrows. The third furrows are elongate depressions not reaching the axial furrows. The occipital lobe is triangular, relatively long (longer than in other nepeids) and bears a delicate reclined marginal spine.

The ornament consists of a dense and evenly distributed granulation similar to *P. zeabunda,* but the veins on the frontal area are expressed better than in the last-named form.

Occurrence and age. Penarosa elaticeps is rare and comes from the Currant Bush Limestone, locality M179 (Northern Territory); its age is the Middle Cambrian Zone of *Ptychagnostus atavus.*

PENAROSA RHINODELPHIS sp. nov.

(Pl. 13, figs 1a-2c; Text-fig. 8c)

Material. Two cranidia are illustrated and described; eight cranidia have been identified altogether.

Holotype. The larger cranidium, Plate 13, figures 1a-1c, CPC7314, is selected as the holotype.

Diagnosis. *Penarosa rhinodelphis* sp. nov. has a cranidial rim, a frontal marginal furrow, a parallel-sided boss, a relatively slender glabella, large and prominent bacculae, narrow palpebral lobes, and a medium to short frontal area of 1.15-1.2 of glabellar length, and is distinguished by its snout-like drawn-out front, undercurled anterolateral cranidial corners, narrowness of its frontal arc, effacement of the frontal marginal furrow in the middle, and slightly depressed interocular cheeks between the ocular ridges and the bacculae.

Differential diagnosis. *P. rhinodelphis* cannot be confused with any other species of its genus; it is, however, close to *Penarosa meniscops* sp. nov., which is distinguished by its continuous frontal marginal furrow, snoutless front and wide span of the frontal arc.

Description. The cranidium of *P. rhinodelphis* is semicircular save for the drawn-out front and the retral posterolateral limbs. The posterolateral limbs are geniculated down quite abruptly at the fulcral points and the retral flaps are smaller than, for example, in *P. retifera.* The posterolateral marginal furrow expands abruptly past the geniculation, but its flare is less prominent than in *P. retifera* and *zeabunda.* The frontal area is relatively short, about 1.15-1.2 of glabellar length; the front is upturned, but the flanks are very tumid, bulging diagonally to left and right, and their anterolateral corners are curled under; the frontal margin is strongly arched upward but the span of the arc is short owing to the curls of the corners. The rim is relatively long and drawn-out into a 'snout' in the middle, but narrows rapidly, passing under the lateral bulges of the brim. The tip of the 'snout' has a short doublure.

The frontal marginal furrow is laterally well defined but rather shallow in the middle—indicated only by a change of slope from the boss to the rim. The boss is parallel-sided, and moderately tumid. The interocular cheeks, as wide as the glabellar front, are flat (not tumid), somewhat depressed between the ocular ridges and the bacculae, and slope abaxially in an even incline. The ocular ridges are horizontal, straight, and forked. The palpebral furrows are distinct, the palpebral lobes narrow, crescentic, and as long as 0.65-0.7 of the glabella. The bacculae are very large and prominent and impinge on the flanks of the posterior glabellar lobes. The axial furrows are straight and deep. The preglabellar transverse furrow is straight, and bears the usual three pits, of which the middle notches the glabellar front; passing between the pits short ducts connect the glabella with the rear of the boss, as seen also in *P. retifera* and some other species.

The glabella is as long as wide in the rear and tapers forward to about 0.75 of its rear width. Four pairs of glabellar furrows are present; the two anterior ones are diminutive and the third are, apparently, elongate pits; the others are wide, almost as wide as the lobes in between. In the holotype the glabella is weakly annulated—less than in *P. zeabunda*—and some effacement of furrows of the frontal area is apparent in Plate 13, figure 2.

The occipital lobe is equipped with a short triangular retral spine with a low median crest.

The ornament consists of an evenly distributed dense and relatively coarse granulation which on the brim follows the trend of the veins. The palpebral lobes are smooth.

Comment on illustrated specimens

All material available comes from the Currant Bush Limestone, locality M179 (Northern Territory). The matrix is a hard very fossiliferous limestone.

The holotype is 5.8 mm long. The frontal marginal furrow and rim disappear laterally under the forward bulging flanks of the brim (see Pl. 13, figs 1b and 1c).

The cranidium Plate 13, figures 2a-2c, CPC7315, is 4.5 mm long; as compared with the holotype, its furrows in the frontal area are slightly effaced.

Occurrence and age. *Penarosa rhinodelphis* is known only from the Currant Bush Limestone, locality M179 (Northern Territory); its age is the Middle Cambrian Zone of *Ptychagnostus atavus.*

PENAROSA MENISCOPS sp. nov.

(Pl. 12, figs 3a, 3b; Pl. 14, fig. 2)

Material. The illustrated material consists (1) of a cranidium, Plate 12, figures 3a, 3b, CPC7313, which is the holotype, and (2) a cranidium, CPC7317, flattened in shale. Two more cranidia have been identified in limestone, in association with the holotype.

Diagnosis. *Penarosa meniscops* sp. nov. is distinguished by its relatively flat crescentic rim, parabolic frontal margin, frontal marginal furrow well defined throughout, wide span of the frontal arc, and relatively broad palpebral lobes.

Differential diagnosis. In general aspect and proportions *P. meniscops* is close to *P. rhinodelphis,* which, however, is quite distinct with its frontal 'snout,' interrupted frontal marginal furrow, narrow span of the frontal arc, and relatively narrow palpebral lobes.

Description. The holotype is 7.0 mm long, and partly silicified. The frontal area is about 1.2 and the palpebral lobes 0.75 of the glabellar length. The front is upturned and arched upward, but the span of the arc is wide, and the brim is fully visible in plan, with its anterolateral corners not curled under as in *P. rhinodelphis.* The interocular cheek, as wide as the glabella, is flat and slopes gently adaxially. The palpebral lobes are broad and crescentic, with downsloping tips; owing to the slope the lobes have an obliquely truncate appearance in plan. The bacculae are very large (the largest known in the nepeids), conspicuously tumid, and almost confluent with the rear glabellar lobes; these, in turn, are connected across the glabella by a transverse swell (Pl. 12, fig. 3b)—a remnant of glabellar annulation seen also in *P. zeabunda.* The third glabellar furrows are pits, almost circular in outline. The ornament consists of a relatively coarse dense and evenly distributed granulation, but the palpebral lobes are smooth. The cranidium, Plate 14, figure 2, CPC7317, Inca Formation, locality

M412, is 3.8 mm long. It is flattened in shale and therefore the frontal area is somewhat longer than the holotype; the rim is flat and the marginal frontal furrow is well defined.

Occurrence and age. *Penarosa meniscops* occurs in the Currant Bush Limestone, locality M179 (Northern Territory), and in a shale of the Inca Formation, locality M412; its age is the Middle Cambrian Zones of *Ptychagnostus atavus* and *Euagnostus opimus* (at M412).

PENAROSA PETALIFERA sp. nov.

(Pl. 11, fig. 4; Pl. 16, figs 1-5; Text-fig. 13)

Material. Illustrated and described are five cranidia and one free cheek unit, from three separate localities. About 25 specimens altogether have been identified.

Holotype. The cranidium, Plate 16, figures 1a-1c, CPC7322, locality M28, is selected as the holotype because it is not distorted and displays its characteristic occipital spine; the palpebral lobes are missing but are seen in the associated cranidium Plate 16, figure 3b.

Diagnosis. *Penarosa petalifera* has a crescentic subtriangular cranidium with a relatively short frontal area (0.9-1.0 glabellar length), a concave front with a rather narrow marginal rim, and is distinguished by its triangular drawn-out petaliform occipital spine.

Differential diagnosis. *P. petalifera* has the shortest frontal area and the longest glabella within its genus; the front is also concave in *P. retifera,* but it has no rim and a much longer frontal area; in *P. zeabunda* and *P. elaticeps* the rim is longer and defined by a marginal furrow, and the frontal area is long; *P. melota* (q.v.) resembles *petalifera* in its frontal structure, but its marginal rim is fainter, its interocular cheeks are narrower, and its occipital spine is a slender needle. A petaliform occipital spine is unknown in all species of *Penarosa, P. petalifera* excepted, but is present in *Nepea narinosa,* which cannot be confused with *P. petalifera*—a species of another genus.

Description. The cranidium is slightly longer than half its width and subtriangular to semielliptical in plan. The free cheeks (Pl. 16, fig. 2) are united; neither a rostral shield nor a median suture is present; the genal spines extend rearward for a distance of about two lengths of the cephalon. The retral swing of the posterolateral limbs and flaps is quite strong; the posterolateral marginal furrow is deep, flares moderately, and peters out before passing into the flap. The anterior sutures (Pl. 16, fig. 1b) are straight in frontal view and converge downward. The frontal area, 0.9-1.0 of glabellar length, is rather short—the shortest known within the genus. The boss is narrow, elliptical, and moderately tumid. The front is concave but lacks a marginal furrow; the margin, arched forward in a parabolic curve, is strongly upturned and thickened into a narrow rim-like structure. It is also arched upward quite prominently, but the span of the arc is wide because the anterolateral corners are not curled under.

The interocular cheeks, as wide as 1.0-1.1 of glabellar front, slope steeply and axially and their summits carrying the palpebral lobes are elevated above the level of the glabella. The ocular ridges are oblique and high crossing the axial

furrows, but become horizontal and loose in expression, climbing up the slope of the cheeks. The palpebral lobes are crescentic and relatively wide, and about as long as 0.7 of glabellar length. The bacculae are small, inconspicuous, and separated from the posterior glabellar lobes by narrow crescentic swellings. The axial furrows flanking the glabella are straight and deep; the preglabellar transverse furrow shows a median elongate pit moderately notching the glabellar front; the lateral pits are shallow. Between the pits ducts connect the glabella with the boss. The glabella is subrectangular, tapering forward to about 0.8 of its width in the rear, and its front is only slightly expanded laterally. Four pairs of glabellar furrows are apparent; the posterior furrows are slightly forked; the third furrows, close to the front, are developed as pits, best seen in the holotype (Pl. 16, fig. 1); the frontal fourth pair is diminutive. The margin of the occipital lobe is extended into a flat petaliform, and drawn-out, spine which may exceed 0.7 of glabellar length.

Fig. 13. *Penarosa petalifera* sp. nov., cranidium, CPC 7321, immersed in chert, x 7.2. Locality M130. The associated pygidia, of a different trilobite, will be described on another occasion.

The veins on the brim are prominent and wavy; the ornament consists of irregularly distributed granulation and pustules; the rim is minutely granulose; the occipital lobe shows retrally convex lines; the palpebral lobes are smooth.

Comment on illustrated specimens

The cranidium, Plate 11, figure 4, CPC7312, locality M130, is 4.5 mm long; it is decorticated; the matrix is a pod of chert from a silty shale with chert layers. The occipital spine is missing, but is preserved in an associated cranidium, CPC7321, Text-figure 13; owing to a pair of oblique fractures and partial collapse, the retral swing of the posterolateral limbs, which is in any case strong in this species, became accentuated excessively, imitating a proparian condition with falcate genal spines; the tips of these quasi-spines, however, are cut by the suture, as can be seen on the right limb.

The following three specimens come from the Currant Bush Limestone.

The holotype cranidium is 6.2 mm long to the tip of the occipital spine. The granulation on the cheeks is subdued. Note the pits of the third pair of glabellar furrows. The matrix is a bituminous dark limestone with chert pods and drops.

The free cheeks unit, Plate 16, figure 2, locality M28, CPC7323, is 20.0 mm long; it is partly silicified and the limestone is interwoven irregularly with silica. The ventral side is exposed; the collapse of the frontal arch resulted in an irregular longitudinal fracture; a median suture and a rostral shield are absent. At the left lower corner the cranidium Plate 16, figure 3, is visible.

The cranidium, Plate 16, figures 3a-3b, CPC7324, locality M28, is 5.8 mm long; its cast (fig. 3b) shows the ornament and the right palpebral lobe.

The two next cranidia come from locality M157—a fossiliferous limestone interbed in the Age Creek Formation.

The cranidium Plate 16, figure 4, CPC7325, is 7.0 mm long. Its triangular occipital spine is preserved.

The cranidium Plate 16, figure 5, CPC7326, is 6.0 mm long; it is fragmentary and distorted; the marginal rim is accentuated.

Occurrence and age. *Penarosa petalifera* occurs in the Currant Bush Limestone, and in its interbeds in the Age Creek Formation; and at locality M136 it is found in a local shale topping the Currant Bush Limestone. Its age is the Middle Cambrian Zone of *Ptychagnostus punctuosus.*

PENAROSA MELOTA sp. nov.

(Pl. 14, figs 1a, 1b)

Material. The available material consists of a single cranidium, the holotype, CPC 7316.

Diagnosis: Penarosa melota is a species with a concave cranidial front and a thickened rim-like marginal upturned border, related to *Penarosa petalifera,* and distinguished by (1) its narrow interocular cheeks, about 0.8 of glabellar front, (2) a relatively wide glabella, with a rear as wide as 1.2 of its length, and (3) a slender (not petaliform) occipital spine.

Differential diagnosis. The main differences from *P. petalifera* are indicated in the diagnosis; furthermore, in *P. melota* the frontal margin is less strongly arched forward than in *P. petalifera,* the frontal area is longer (about 1.13 of glabella), and the third glabellar furrows are connected with the axial furrows, and not isolated pits as in *P. petalifera.* The relatively short frontal area of *melota* prevents any confusion with any of the other species of its genus.

Description. The holotype cranidium is 8.5 mm long. The palpebral lobes are almost lost, but adaxial parts are preserved, indicating a length of about 0.7 of the glabella. A median notch is absent in the glabellar front. The veins are very conspicuous, osculating and wavy; on the boss they are finer than on the flanks.

The ornament consists of scattered conspicuous pustules on the veins of the frontal area and the median part of the glabella; the interocular cheeks and the posterolateral limbs are densely covered by smaller pustules.

Occurrence and Age. Penarosa melota comes from locality M124 of the Currant Bush Limestone; its age is the Middle Cambrian Zone of *Euagnostus opimus.*

PENAROSA sp. nov. PC

(Pl. 17, figs 3, 4; Text-fig. 14)

Material. The illustrated material consists of one mature and one small immature cranidium in shale; numerous less well preserved specimens are associated in the same sample. The material is insufficient for a definite specific nomenclature.

The mature cranidium, Plate 17, figure 3, CPC 7329, is 7.8 mm long and is distinct in having a flat, upturned, and transversely narrow frontal border, and a relatively narrow elliptical boss. Its glabella is relatively broad and large, the frontal area is about 1.2 of the glabellar length, and the ornament consists of evenly distributed coarse pustules. The immature cranidium, Plate 17, figure 4, CPC 7330, is 1.2 mm long; it shows a narrow convex rim, narrow palpebral lobes and a triangular occipital spine; the boss is already outlined. Its structure is the same as that of *P. zeabunda,* Plate 17, figure 5.

Occurrence and age. *Penarosa* sp. nov. PC comes from a shale of the Inca Formation, locality M412; its age is the Middle Cambrian Zone of *Euagnostus opimus*.

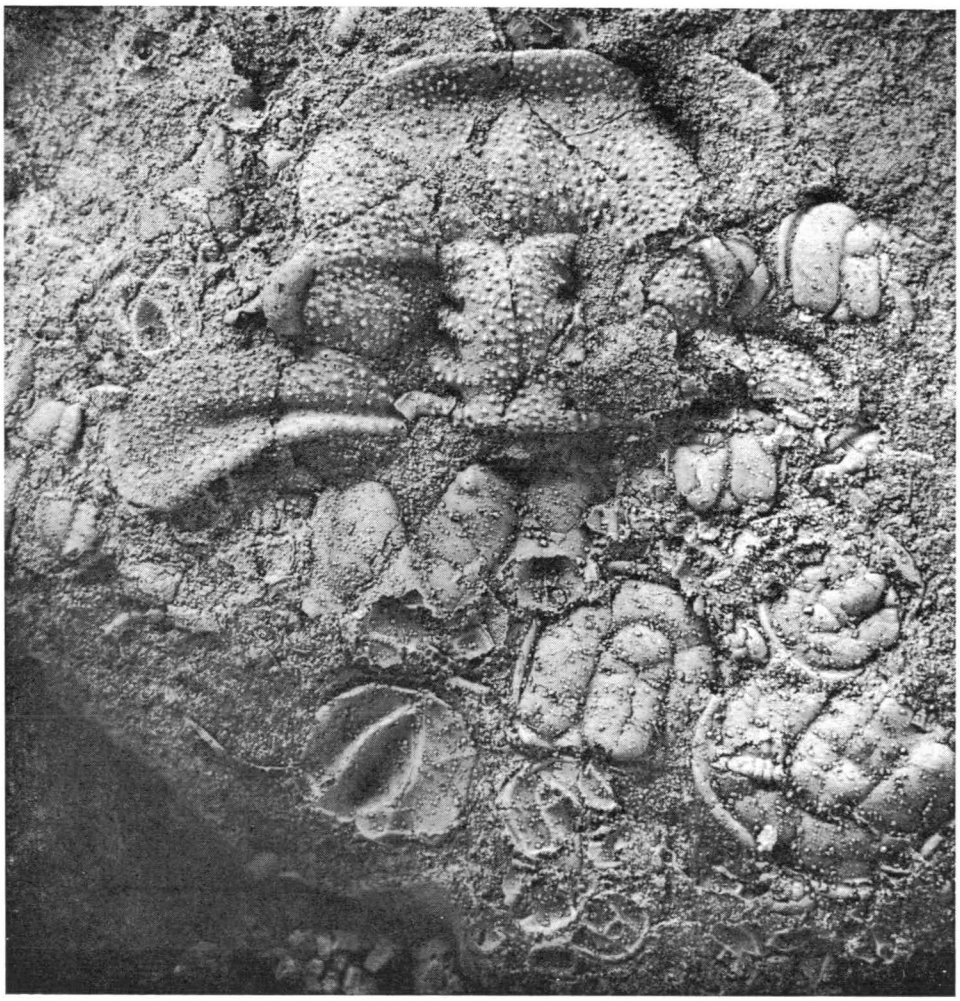


Fig. 14. *Penarosa* sp. nov. PC, x 8; same in Plate 17, fig. 3. *Peronopsis* and *Pagetia* are associated.

Fig. 15. *Penarosa zeabunda* immature cranidium, rubber cast of Plate 17, fig. 5; x 25.

PENAROSA sp. nov. PD, aff. VITTATA

(Pl. 7, fig. 6)

The illustrated fragment, CPC 7295 — the anterior half of a cranidium — is 8.0 mm wide and 6.5 mm long as preserved. The transverse ridge in the frontal part reminds one of *Penarosa vittata* but is placed much more rearward than in this species; furthermore, a rim defined by a marginal furrow is apparent and the boss is relatively short; the ornament consists of pustules which are quite prominent in the space between the rim and the transverse ridge.

These characters are sufficiently diagnostic for a new species, but open nomenclature is still applied because of the fragmentary state of the specimen.

Occurrence and age. *Penarosa* sp. nov. PD comes from a black bituminous limestone, locality H4, Huckitta area, Northern Territory; the associated agnostids indicate a Middle Cambrian age about the Zone of *Ptychagnostus atavus*.

PENAROSA sp. nov. PE

(Pl. 7, fig. 7)

The illustrated fragment CPC 7296 — the right half of a cranidium — is 7.0 mm long. It has a concave frontal border, but no transverse ridge nor a rim, and may belong therefore to the group of *P. retifera;* it differs, however, by its slender glabella, shorter frontal area, as long as 1.3 of glabellar length, and lofty palpebral lobes placed on the summits of the cheeks well above the level of the glabella. Furthermore, only two pairs of glabellar furrows are present, and not three or four pairs as seen in other nepeids.

Occurrence and age. *Penarosa* sp. nov. PE comes from locality H4, Huckitta Sheet area, Northern Territory, where it is associated with *Penarosa* sp. nov. PD aff. *vittata* (q.v.).

MORPHOGENESIS OF THE NEPEIDAE

(Pl. 17, figs 4-9; Text-figs 12 and 15)

Nepeid protaspides, and early instars of *Nepea,* are unknown; *Penarosa* supplies some morphogenetic information, but only regarding the cranidium.

In *Nepea* the intriguing problem is the morphogenesis of its exceptionally long intergenal spines. Only a small number of trilobites (for example *Olenellus, Redlichia, Centropleura, Zacanthoides*) retain the intergenal spines in maturity and in others (for example *Paradoxides, Xystridura, Leptoplastus*) these spines are relatively long in early instars but disappear before completion of the holaspis. It appears therefore that in the rather small number of trilobites whose morphogenesis is known the intergenal spines are a morphogenetically recessive part of the meraspid equipment. Obviously the opposite happened to *Nepea* with its hypertrophic intergenal spines.

In *Penarosa* no intergenal spines are evident at all, not even in its earliest meraspides.

The cranidial meraspid and holaspid specimens of *Penarosa* (*P. zeabunda, P. retifera,* and *P.* sp. nov. PC) are listed below as a sequence of size (instar) groups, and the morphology of the groups is discussed.

Group A: Cranidia 0.46-0.6mm long. Plate 17, figure 6, lower specimen, is 0.46 mm long; same figure, upper specimen, is 0.5 mm long; these are attributed to *Penarosa zeabunda;* same Plate, figure 8, 0.5 mm long, and figure 7, 0.6 mm long, belong to *Penarosa retifera.*

Instars filling the interval of 0.15 mm between Groups A and B are missing.

Group B: Cranidia 0.75-0.8 mm long. Plate 17, figure 9, of *Penarosa retifera,* is 0.75 mm long; same Plate, figure 6, central specimen, attributed to *Penarosa zeabunda,* is 0.8 mm long.

Instars filling the interval of 0.3 mm between Groups B and C are missing.

Group C: Cranidia 1.1-1.2 mm long. Plate 17, figure 5, and Text-figure 15, attributed to *Penarosa zeabunda,* is 1.1 mm long; same Plate, figure 4, attributed to *Penarosa* sp. nov. PC, is 1.2 mm long.

The three specimens of Group A are cranidia of early meraspides. The glabella is very long, notched in front and annulated; the frontal area is short, slopes down steeply, and possesses a flat rim in *P. penarosa.* The retral swing of the posterolateral limbs is well expressed, and an occipital node or spine is present. The ocular ridges arise not at, but a short distance behind, the glabellar corners and are curved, convex forward. The palpebral lobes are invisible in a low position in relation to the top level of the cheeks. The brim is venulose (veins are not visible in the photograph) and no trace of a boss is present. The frontal boss 'begins to develop in an early meraspid stage and is therefore a morphogenetically late and, within a given stock, a phylogenetically novel character' (Öpik, 1967, p. 57); the evidence is given below (Group C). Consequently, protaspides have no boss. The

smallest cranidium of Group A, 0.46 mm long, of an instar of a meraspis degree 0 illustrates the protocranidial structure of metaprotaspides, which may have been also brimless. This specimen is about the size of, and structurally similar to, the meraspid 0 cranidium of *Bolaspidella housensis* (Walcott) illustrated by Robison (1964, pl. 89, fig. 5) side by side with its anaprotaspis. In passing, *Bolaspidella* is a bossless nepeid having a rostral shield.

The two cranidia of Group B represent meraspides of an early, but compared with Group A advanced, morphogenetic step. The posterolateral retral swing gained in emphasis and in *P. retifera* (Pl. 17, fig. 9) the flaps are preserved. A rim is present, convex in *P. zeabunda* and flat in *P. retifera;* the palpebral lobes have migrated upward and are visible, placed well behind the glabellar front in a position not seen in holaspides; the lobes are very narrow and oblique; a boss is still absent, but its position is indicated by a pair of longitudinal lines on the brim; the glabella is strongly annulated and an occipital spine (seen in the mould of the cranidium of *zeabunda*) has gained in prominence.

The cranidia of Group C belong to meraspides in which the main nepeid traits (forward placed eyes, long frontal area, equidimensional glabella) are not evident yet; only the retral swing of the posterolateral limbs indicates a nepeid *in statu nascendi,* but the general design of the cranidium is ptychoparioid. The rim is distinct and convex, indicating species different from *P. retifera;* a circular boss is now apparent; the palpebral lobes are lifted up and levelled with the glabella but retain their position behind the glabellar front; the long and narrow glabella is also immature. The occipital spine is somewhat triangular, but more like *P. rhinodelphis* than *petalifera.* Specimens of Group C are relatively common and include instars up to 1.4 mm.

Instars of the size interval 1.5-2.5 mm are not available; within this interval the transformation, however, is complete. The palpebral lobes take the position opposite the frontal part of the glabella, the glabella itself grows in width and attains its somewhat equidimensional shape, and the frontal area overtakes the length of the glabella. In a cranidium of *P. zeabunda* 2.0 mm long (associated with Pl. 10, fig. 5, but not illustrated) the frontal area is about as long as the glabella, and at a length of 3.0 mm holaspid proportions are attained.

Summing up, (1) the earliest and most persistent character of *Penarosa* (and the Nepeidae) is evident in the retrally swinging posterolateral limbs with the flap, (2) the boss appears in larger meraspides, which are of a ptychoparioid design, followed by (3) the development of the large frontal area, the transformation of the glabella from elongate to equidimensional, and the eyes reaching the holaspid, advanced position in relation to the glabellar front. The glabellar frontal lobe is rather slow in growing and remains therefore diminutive throughout the morphogenesis.

Phylogeny within the Australian Nepeidae

It has been stated already (Öpik, 1963, p. 340) that no phylogenetic unity is apparent among the Australian nepeids and that the absence of such unity indicates that the Australian nepeids, of a single subfamily, cannot be regarded as the sole representatives of the family itself. The conclusion is in accordance

with the mode of life of the nepeids as floating itinerants, with the sudden appearance of their species in the Australian Cambrian, and with the comparative morphology which indicates several independent stocks each of an unknown parentage.

For the purpose of a discussion of the phyletics of the Nepeinae the following four morphological groups can be distinguished:

Group 1. Nepea? sp. nov. NC and *Folliceps nans* sp. nov. These forms have a *Nepea*-like cranidial front but no intergenal spines.

Group 2. Nepea narinosa, exserta, tonsillata, and *avara,* distinguished by hypertrophic intergenal spines.

Group 3. Ferenepea hispida Ö. and *pilaris* Ö., *Ascionepea janitrix* Ö., and *anitys* Ö., distinguished by the small size of the boss, forward projection of the glabella beyond the ocular ridges, relatively slender glabella, and absence of intergenal spines.

Group 4. Penarosa gen. nov., distinguished by its upturned front and absence of intergenal spines. Within this group three subgroups are apparent: (a) the species with a cephalic rim — *P. zeabunda, elaticeps, rhinodelphis,* and *meniscops;* (b) the rimless *retifera* and *vittata;* and (c) with a short frontal area — *petalifera* and *melota.*

Loxonepea loxophrys sp. nov. may belong also to group 4; but the peculiar organization of this species suggests a separate nepeid stock whose phyletic connexions are obscure and are in no need of further comment.

In group 1 *Nepea?* sp. NC is the oldest known nepeid, morphologically close to *Nepea* itself; it may have been coeval with the ancestor of *Nepea* and the forms of group 2, but is not itself an ancestor; it belongs to a stock which earlier lost its intergenal spines, which are still present in the much later *Nepea. Folliceps nans,* however, may be a descendant of *Nepea?* sp. NC, but both are separated from each other by a temporal gap of about two zones as yet devoid of nepeids.

Group 2 consists of all known species of *Nepea;* of these *N. avara* ranges through the three zones of *Leiopyge laevigata*—a remarkable longevity for a species of nepeid; it may have arisen from *N. narinosa* or another species of the same group which all are concentrated in the zone of *Ptychagnostus nathorsti;* no older species of the genus are known — hence it is a group of newcomers whose ancestors never managed to outlive their intergenal spines. The palpebral lobe of *Nepea narinosa* preserving the structure of a pleural tip may be regarded even as a conserved feature of an ancestral 'pre-trilobite'.

The species of group 3, of the genera *Ferenepea* and *Ascionepea,* all Mindyallan (early Upper Cambrian), are the youngest known nepeids. They could be derived from a species of *Nepea* by reduction of the intergenal spines and decrease of the size of the eyes; the forward protruding glabella, however, is less modified than in others which all have a diminutive frontal glabellar lobe; *Ferenepea hispida* compares, therefore, with the larger meraspides of *Penarosa* (q.v.); but a comparison with *Nepea,* whose morphogeny is unknown, is unattainable yet. So, a neotenic origin of *Ferenepea* and *Ascionepea* is a possibility, but what the ancestral

stock was, and where, and when it existed, remain to be answered. Considering, however, that the reduction of the frontal glabellar lobe of the Middle Cambrian nepeids is a secondary acquisition derived from a normal glabella of a ptychoparioid design one may conclude that this regular glabella remained unmodified in *Ferenepea* throughout its phyletic past. If this is accepted the Upper Cambrian nepeids of Group 3 have no ancestors among the known Middle Cambrian nepeids.

The nepeids of group 4, consisting of all known species of *Penarosa,* are concentrated in the short span of two zones (*Ptychagnostus atavus* and *Euagnostus opimus*); only one species (*Penarosa petalifera*) survived into the zone of *Ptychagnostus punctuosus.* Presumably at this time *Penarosa* expired in Australia and elsewhere altogether and the stock of *Nepea* gained in diversification and arrived in Australian seaways.

Penarosa arrived in Australia quite suddenly about the turn from the zone of *Ptychagnostus gibbus* to *P. atavus;* its geographic provenance and ancestors are totally unknown yet. The first arrivals belong to Group 4a of four concurrent species (*zeabunda, elaticeps, rhinodelphis,* and *meniscops*) distinguished each by a characteristic frontal rim; being contemporaneous they cannot be arranged in a phyletic order. This group is followed immediately by the species of group 4b represented by the rimless *Penarosa retifera* and *P. vittata.* The morphogenesis of *retifera* differs little from *P. zeabunda* because the meraspides of both possess a rim; this rim disappears, however, completely in the holaspides of *retifera;* it is fair to assume therefore that *P. retifera* and probably *vittata* arose from *zeabunda* or a species close to it. In the other rimmed species, especially in *P. rhinodelphis,* not reduction but modification of the rim is apparent; hence, such forms, in the presence of *P. zeabunda,* cannot be considered ancestors of *P. retifera.* The two species of subgroup 4c (*P. petalifera* and *melota*) represent a stock separate from both the *P. zeabunda* and the *retifera* groups; morphologically these species are, however, rather close to each other, and the younger *P. petalifera* could be even a derivate of the older *P. melota.*

Nepeidae outside Australia

The superfamily Nepeacea includes the Menomoniidae, as already mentioned; of these *Bolaspidella* Resser may belong to the Nepeidae rather than the Menomoniidae, or even to a separate subfamily of the Nepeidae; the Australian forms belong to the subfamily Nepeinae, which is not represented elsewhere. Furthermore, the Periomellinae Rasetti, 1955, believed to be a subfamily of the Ptychopariidae, should be placed also in the Nepeacea. Its only genus, *Periomella* Resser, 1938, as seen from Rasetti (1955, p. 28-30, pl. 5, figs 1-8; *P. yorkensis* Resser) has forward-arched ocular ridges arising at the anterolateral corners of the glabella, wide interocular cheeks, a circular boss, indistinct bacculae, and deep posterolateral marginal furrows petering out before reaching the sutures. Its posterolateral limbs are, however, short without flaps and without a retral swing, and the upturned rim is rather thick for the Nepeinae, or even Nepeidae. Furthermore, forms like *Alokistocare lobatum* Rasetti, 1963, provided with bacculae, and even *Kochiella? declivis* and *K.? tumida* Rasetti, 1963, also may be affined in some way with the Nepeacea.

GLOSSARY

(Explanation of names of taxa)

avara, Nepea: Lat., 'greedy', referring to the voluminous frontal boss.

elaticeps, Penarosa: Lat., 'uplifted head', front.

exserta, Nepea: Lat., 'forward protruding', in reference to its front.

Folliceps: neuter, Lat., 'windbag head'.

Loxonepea: fem., Greek, 'oblique, and generic name *Nepea*'.

loxophrys, Loxonepea: Greek, 'with slanting eyebrows'.

melota, Penarosa: fem., Lat. and Greek; 'sheepskin, unshorn'.

meniscops, Penarosa: Greek, 'crescent front'.

nans, Folliceps: Lat. 'floating'.

narinosa, Nepea: Lat. 'broad-nosed'.

Nepea: Greek, 'childish' (Whitehouse, 1939, p. 211).

Penarosa: artificial combination of syllables from *Nepea* and *narinosa*.

petalifera, Penarosa: Lat., 'petal carrier', in reference to the shape of the occipital spine.

retifera, Penarosa: Lat., 'net carrier', in reference to the frontal ornament.

rhinodelphis, Penarosa: Greek, 'nose' and 'dolphin'.

tonsillata, Nepea: Lat., 'with tonsils' — the large bacculae.

vittata, Penarosa: Lat. 'with a band or ribbon' on its front.

zeabunda, Penarosa: Lat., 'covered with grain' (zea); refers to the granulose ornament.

REFERENCES

CASEY, J. N., and GILBERT-TOMLINSON, JOYCE, 1956—Cambrian geology of the Huckitta-Marqua region, Northern Territory. *In* EL SISTEMA CAMBRICO, SU PALEOGEOGRAFIA Y EL PROBLEMA DE SU BASE, 2, 55-74, *20th int. geol. Cong., Mexico.* Reprinted in Öpik, A.A., and others, 1957, *Bur. Miner. Resour. Aust. Bull. 49.*

CARTER, E. K., BROOKS, J. H., and WALKER, K. R., 1961—The Precambrian mineral belt of north-west Queensland. *Bur. Miner. Resour. Aust. Bull.* 51.

CARTER, E. K., and ÖPIK, A. A. 1961—Lawn Hill 4-mile geological series. *Bur. Miner. Resour. explan. Notes* 21.

HARRINGTON, H. T., et al., 1959—Treatise on Invertebrate Paleontology: O(1) Trilobita. *Univ. Kansas Press* and *Geol. Soc. Amer.*

NOAKES, L. C., CARTER, E. K., and ÖPIK, A. A., 1959—Urandangi 4-mile geological series. *Bur. Miner. Resour. explan. Notes* 1.

ÖPIK, A. A., 1956—Cambrian geology of Queensland. *In* EL SISTEMA CAMBRICO, SU PALEOGEOGRAFIA Y EL PROBLEMA DE SU BASE, 2, 1-24. *20th int. geol. Cong. Mexico.* Reprinted in Öpik, A. A., and others, 1957, *Bur. Miner. Resour. Aust. Bull.* 49.

ÖPIK, A. A., 1960—Cambrian and Ordovician geology (of Queensland). *J. geol. Soc. Aust.,* 7, 91-103.

ÖPIK, A. A., 1961—Cambrian geology and palaeontology of the headwaters of the Burke River, Queensland. *Bur. Miner. Resour. Aust. Bull.* 53.

ÖPIK, A. A., 1963—*Nepea* and the nepeids (trilobites, Middle Cambrian, Australia). *J. geol. Soc. Aust.,* 10(2), 313-316.

ÖPIK, A. A., 1967—The Mindyallan fauna of north-western Queensland. *Bur. Miner. Resour. Aust. Bull.* 74, 2 vols.

ÖPIK, A. A., CARTER, E. K., and NOAKES, L. C., 1961—Mt Isa 4-mile geological series. *Bur. Miner. Resour. Aust. explan. Notes* 20.

ÖPIK, A. A., CARTER, E. K., and RANDAL, M. A., 1969, in press—Camooweal 4-mile geological series. *Bur. Miner. Resour. explan. Notes.*

RASETTI, F., 1955—Lower Cambrian ptychopariid trilobites from the conglomerates of Quebec. *Smith. misc. Coll.,* 128(2).

RASETTI, F., 1963—Middle Cambrian ptychoparioid trilobites from the conglomerates of Quebec. *J. Paleont.,* 37(3), 575-594.

ROBISON, R. A., 1964—Late Middle Cambrian faunas from Western Utah. *J. Paleont.,* 38(3), 510-566.

WHITEHOUSE, F. W., 1936—The Cambrian faunas of north-eastern Australia, Part 1, stratigraphic outline; Part II, Trilobita (Miomera). *Mem. Qld Mus.,* 11, 59-112.

WHITEHOUSE, F. W., 1939—Idem, Part III: the polymerid trilobites. *Ibid.,* 11 (3), 179-282.

PLATE 1

Page

Nepea narinosa Whitehouse 9

All specimens from the Split Rock Sandstone.

Figs 1a-1d. Cranidium, CPC4740, x 5 and (fig. 1d) x 10.

Fig. 2. Cranidium, CPC7272, x 4.

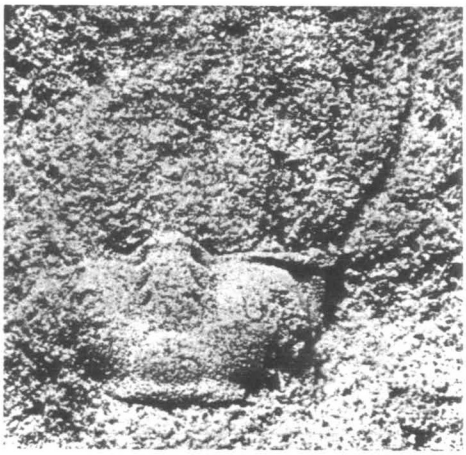
Fig. 3. Cranidium, rubber cast of CPC7273, x 3. Figs 1-3 from loc. M417, at Split Rock on Waroona Creek, east of Camooweal.

Fig. 4. Cranidium, CPC7274, x 7, loc. M421, Emu Soak, east-northeast of Camooweal.

1a

1b

1c



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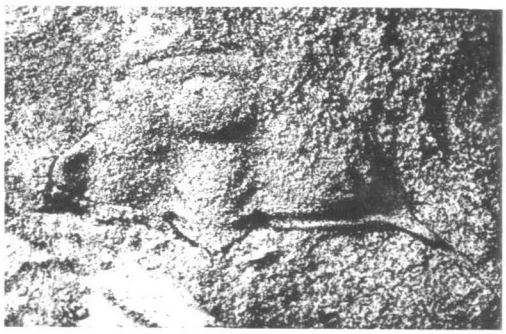

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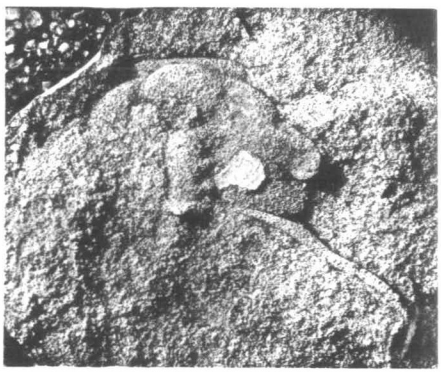

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4

PLATE 2

Fig. 1. Free cheeks, rubber cast of CPC7275, x 2.2.

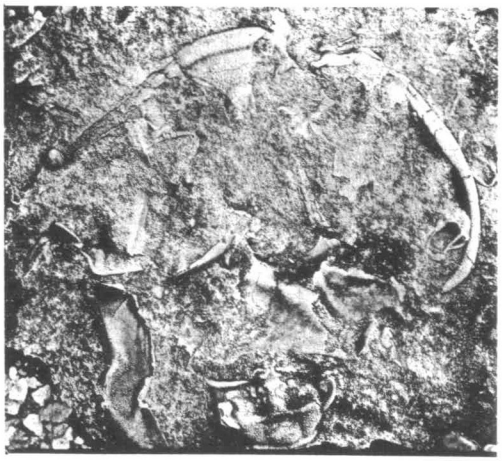
Fig. 2. Cranidium, rubber cast of external surface of CPC7276, x 8.5. Same cranidium in Fig. 1, at lower edge.

Fig. 3. Fragment of free cheek (ocular part), rubber cast of CPC7277, x 8.

Fig. 4. Cranidium, CPC7278, x 3. Figs 1.4 in chert (silicified Split Rock Sandstone), loc. M226, northeastern part of Mt Isa Sheet area.

Fig. 5. Left free cheek, CPC4742, x 4. Split Rock Sandstone, loc. M417.

Fig. 6. Partly coiled exoskeleton, rubber cast of CPC7279, x 3. Split Rock Sandstone, loc. M276.



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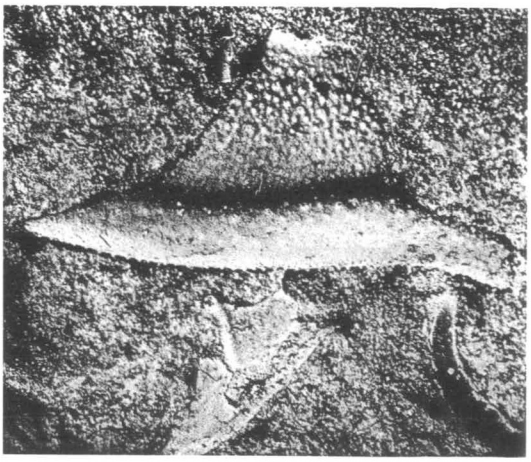

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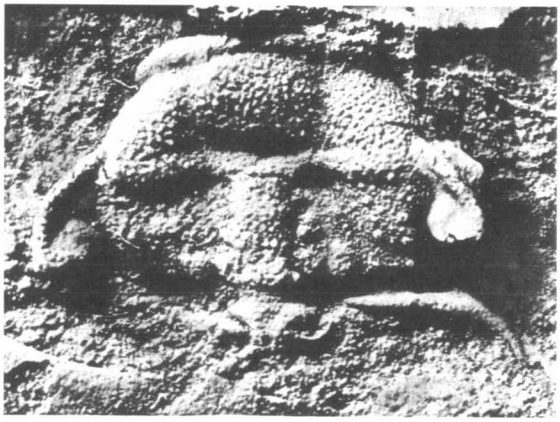

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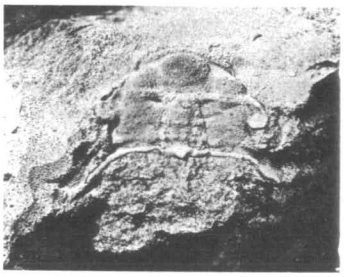

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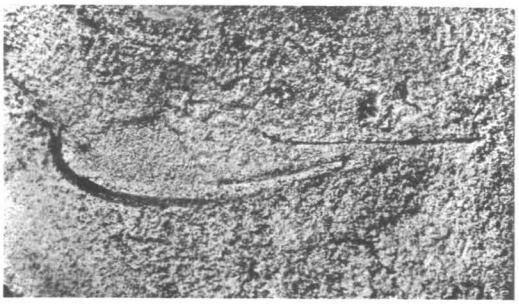

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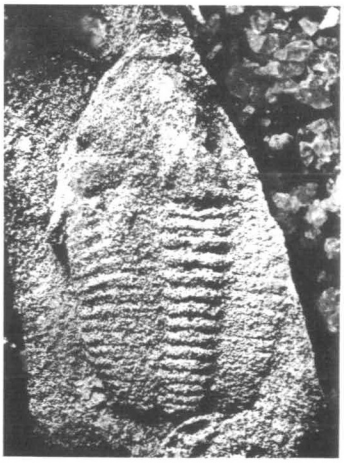

6

PLATE 3

Page

Nepea narinosa Whitehouse 9

Fig. 1. Cranidium, CPC7280, x 6. Aphanitic limestone (? Mail Change Limestone), O'Shannassy River at Morstone (old site).

Neapea sp., cf. *exserta* sp. nov. 15

Fig. 2. Cranidium, CPC7281, x 3. Split Rock Sandstone, loc. M133, 4 miles northeast of Undilla.

Nepea sp. NB (indet.) 17

Figs 3a, 3b. Cranidium, CPC7282, x 3. Split Rock Sandstone, loc. M141. Fig. 3b is left lateral view.

Nepea anoxys sp. nov. 14

Figs 4a, 4b. **Holotype** cranidium, CPC4741, x 3 Split Rock Sandstone, loc. M417.

Nepea sp. NA (indet.) 16

Fig. 5. Cranidium, CPC7283, x 4.5, loc. M41. Chert at base of Split Rock Sandstone.

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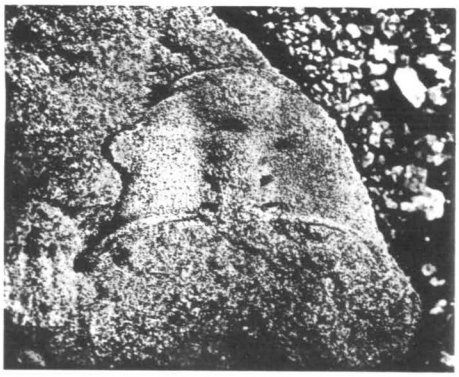

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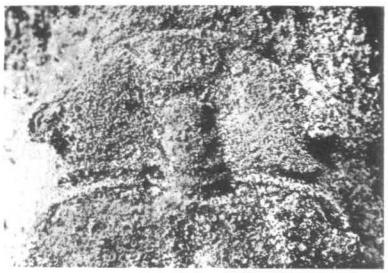

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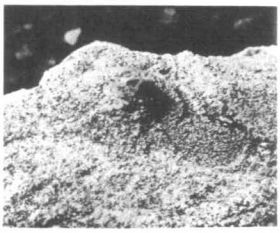

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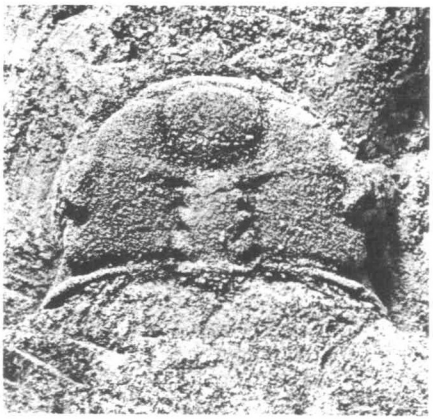

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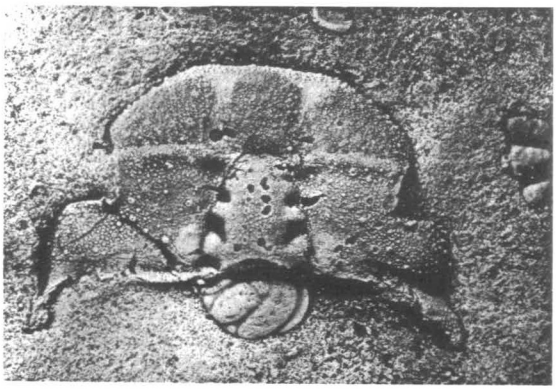

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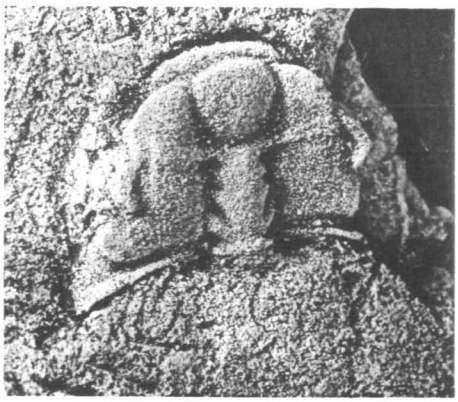
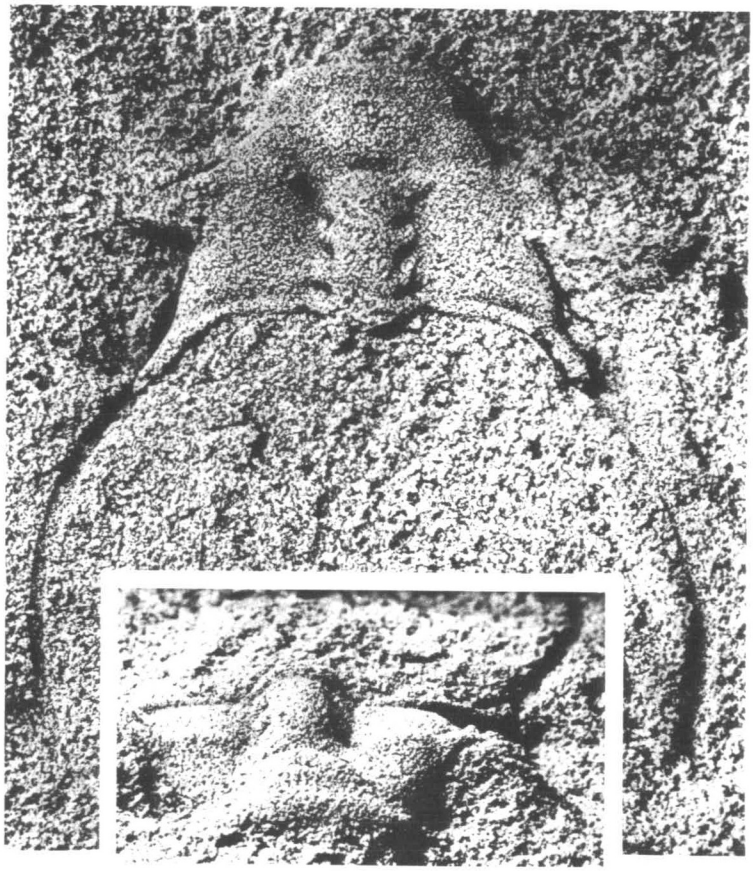


4b

PLATE 4

Holotype, CPC7284, about x 6. Split Rock Sandstone, loc. M344, at heads of Waroona Creek.



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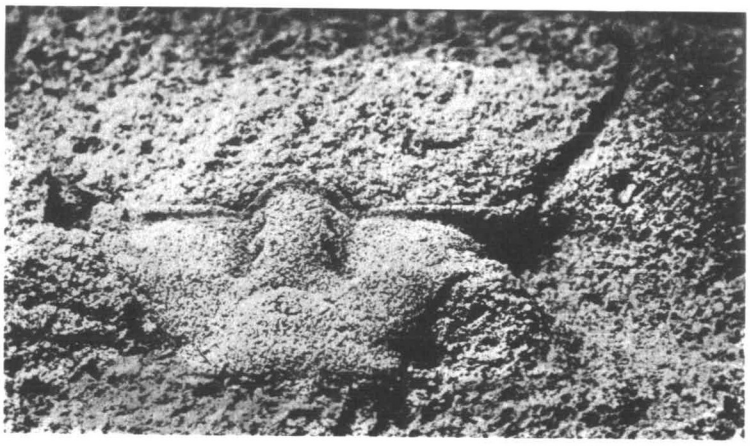

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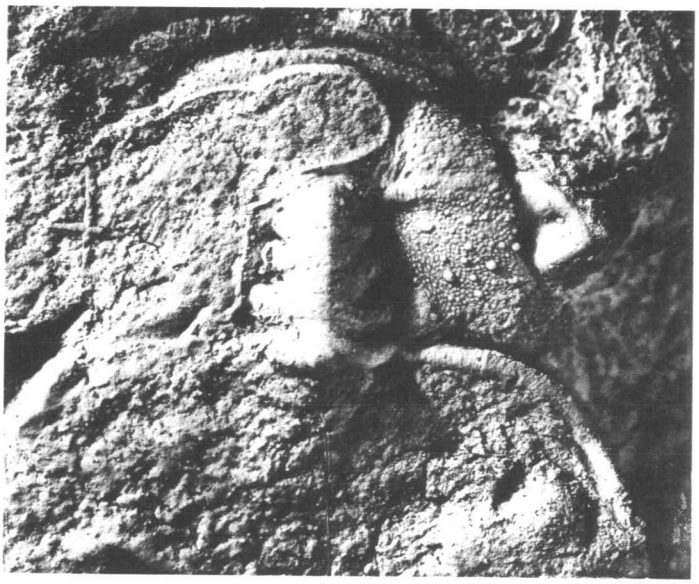
PLATE 5

Page

Nepea tonsillata sp. nov. 15

Holotype cranidium, CPC7285; Figs 1 and 3—x 10; Fig. 2—x 12. V-Creek Limestone, loc. M54, Undilla.



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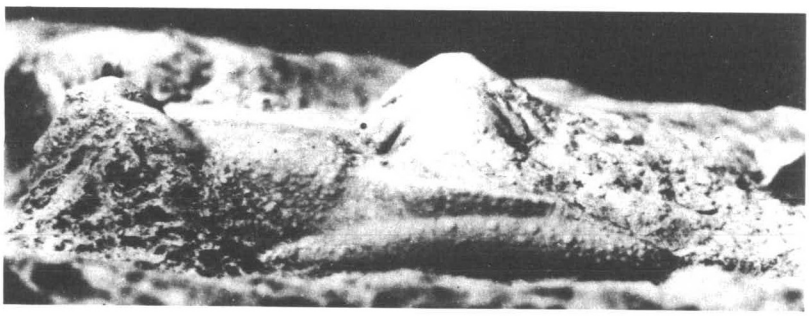

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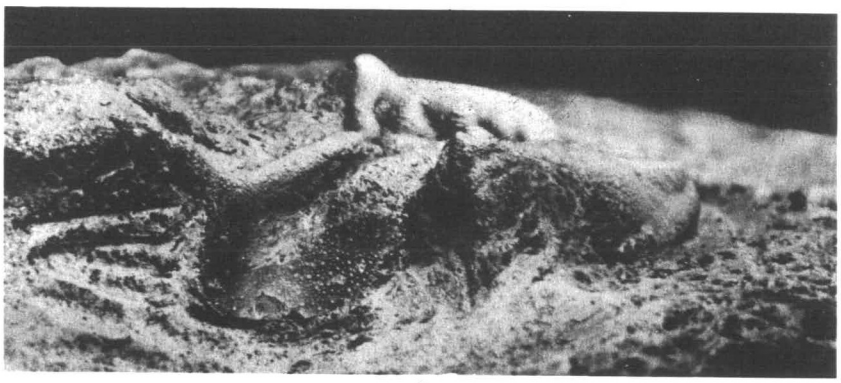

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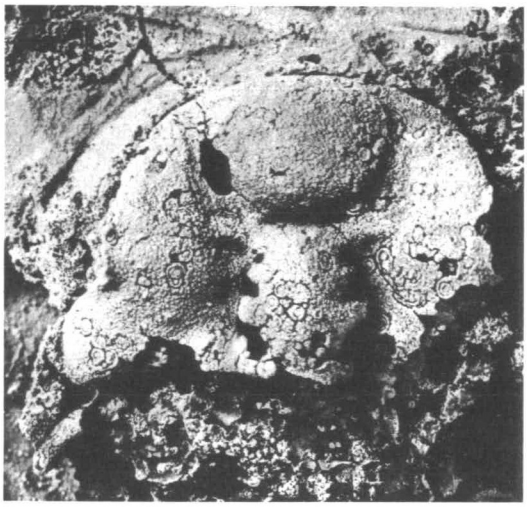
PLATE 6

Figs 1a-1c. **Holotype** cranidium, CPC7286, x 6. Silicified, in limestone.

Fig. 2. Cranidium, CPC7287, x 6.5. Figs 1 and 2—Quita Formation, loc. D108, Urandangi Sheet area.

Figs 3-5. Two cranidia in sandstone. Fig. 3.—x3; Fig. 4, CPC7288, x 6; Fig. 5.—CPC7289, x 3. Loc. D95, Steamboat Sandstone, Urandangi Sheet area.



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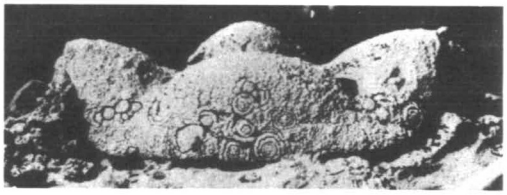

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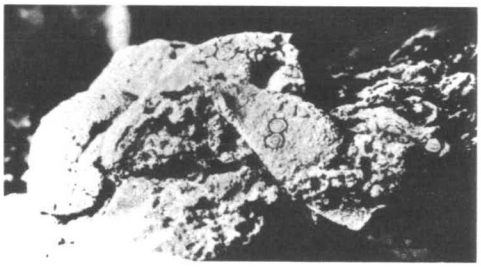

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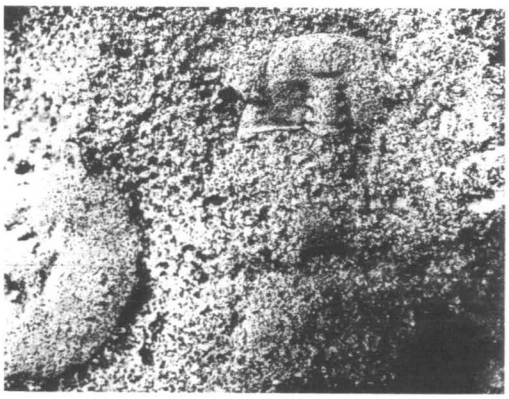

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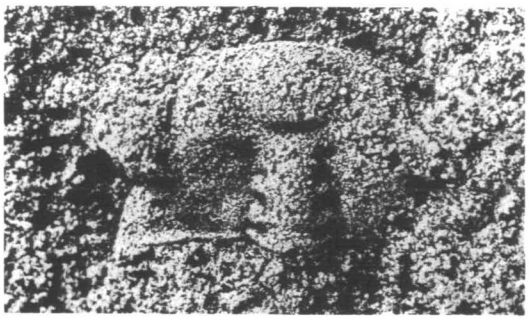

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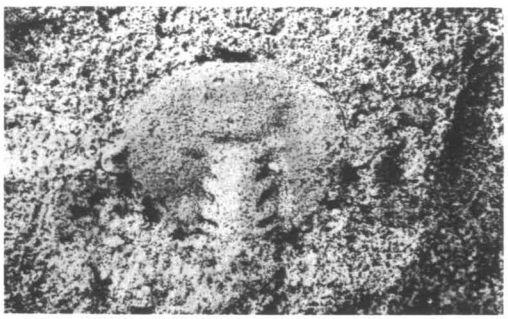

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PLATE 7

Page

Folliceps nans gen. nov., sp. nov. 20

Fig. 1. **Holotype** cranidium, rubber cast of CPC7290, x 6. Currant Bush Limestone (chert layer in limestone), loc. M123.

Fig. 2. Cranidium, CPC7291, x 6. Currant Bush Limestone, loc. M124(A) (a silicified layer in limestone).

Fig. 3. Cranidium, rubber cast of external surface of CPC7292, x 3. Currant Bush Limestone, loc. M123.

Nepea ? sp. nov. NC. 19

Fig. 4. Cranidium, CPC7293, x 10.

Fig. 5. Cranidial fragment, CPC7294, x 7. Figs 4 and 5 in black limestone, Ross River gorge, east of Alice Springs, Northern Territory.

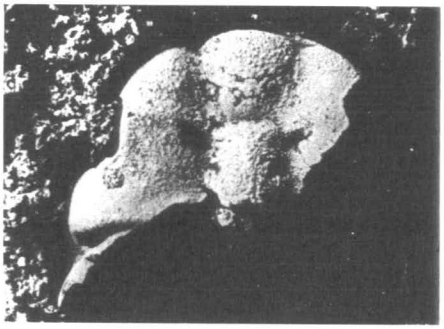
Penarosa sp. nov. PD (aff. *Penarosa vittata* sp. nov.) 29

Fig. 6. Cranidial fragment, rubber cast of CPC7295, x 6.

Penarosa sp. nov. PE. 42

Fig. 7. Cranidium, CPC7296, x 6. Figs 6 and 7 in black limestone, loc. H4, Huckitta Sheet area, Northern Territory.

1



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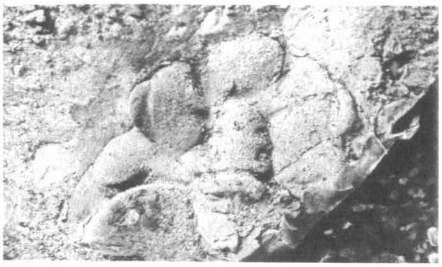

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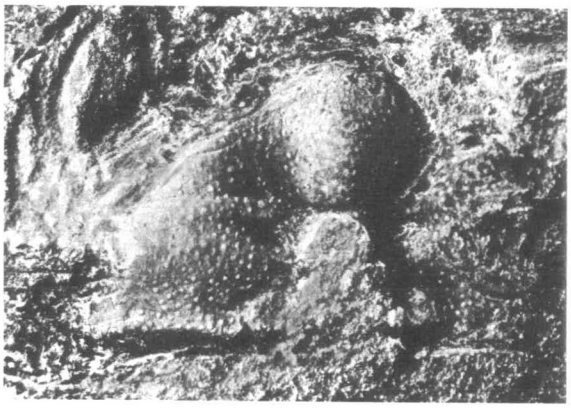

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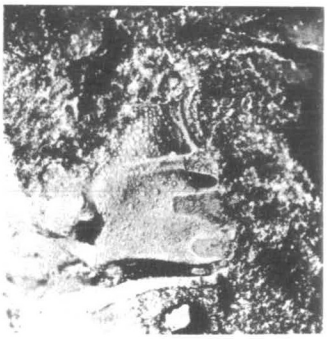

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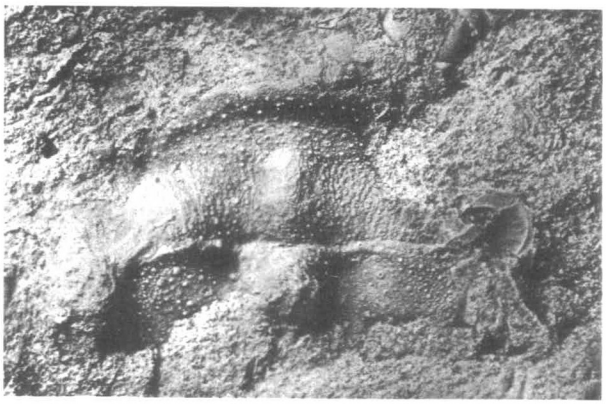

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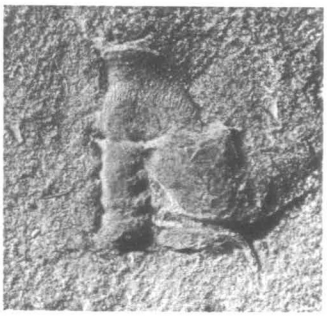

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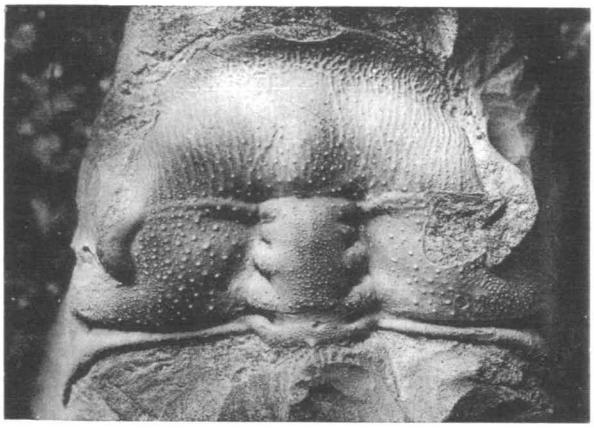
PLATE 8

Figs 1a-1d. **Holotype** cranidium, CPC7297, x 3.5. Loc. M180.

Figs 2a-2b. Cranidium, CPC7298, x 7. Loc. M186. Currant Bush Limestone, Lancewood Creek, eastern fringe of Drummond Sheet area, Northern Territory.



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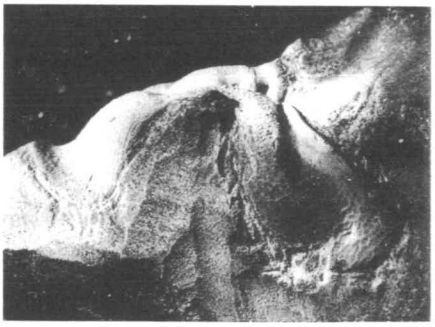

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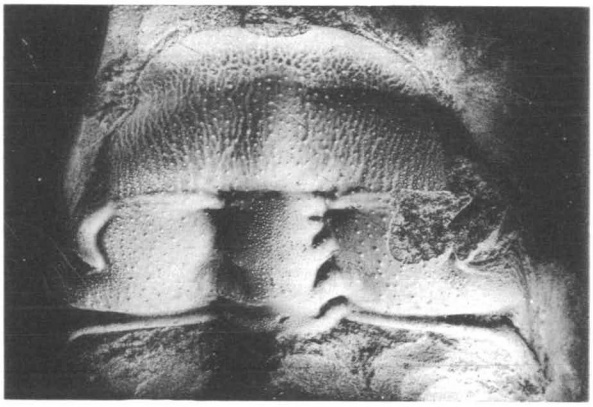

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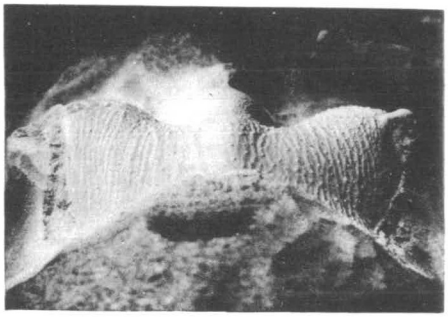

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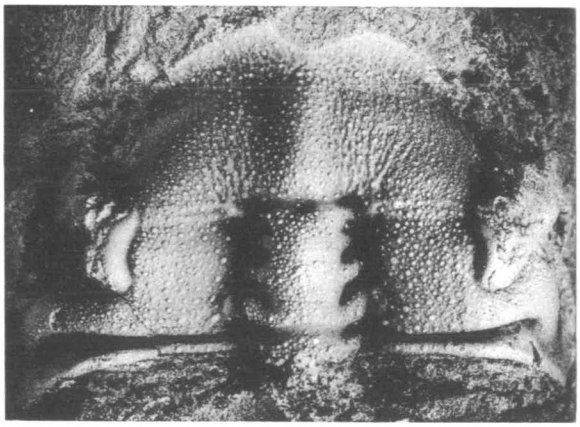


2a

2b

PLATE 9

Page

Penarosa retifera sp. nov. 25

Fig. 1. Cranidium, CPC7299, x 7. Currant Bush Limestone, loc. M180, Lancewood Creek, eastern fringe of Mt Drummond Sheet area, Northern Territory.

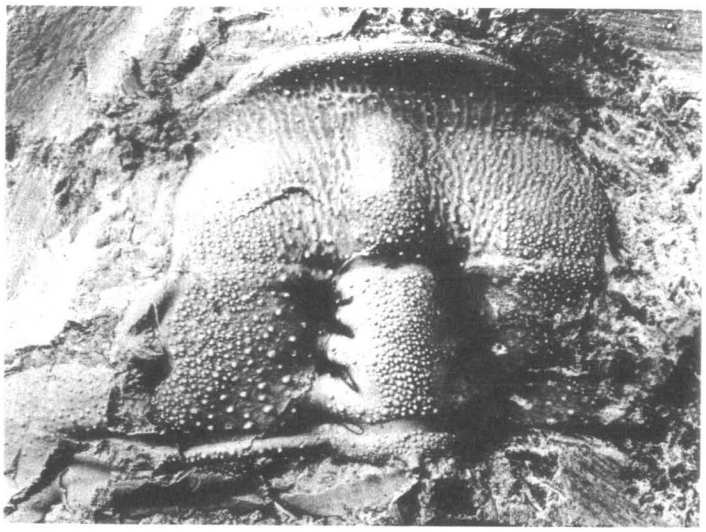
Fig. 2. Exoskeleton, CPC7300, x 2.2. Currant Bush Limestone (calcareous siltstone), close to loc. M393, southwestern part of Lawn Hill Sheet area, Queensland.

Fig. 3. Pygidium, CPC7301, x 7.2.

Fig. 4. Cranidium, CPC7302, x 3.5. Figs 3 and 4 associated in a chert layer, loc. M160, Age Creek Formation, Camooweal Sheet area, Queensland.

Penarosa sp. PA, aff. *Penarosa retifera* 25

Figs 5a, 5b. Cranidium, CPC7303, x 3 and x 6.5 respectively. Currant Bush Limestone, loc. M180, Lancewood Creek, eastern fringe of Mt Drummond Sheet area, Northern Territory.



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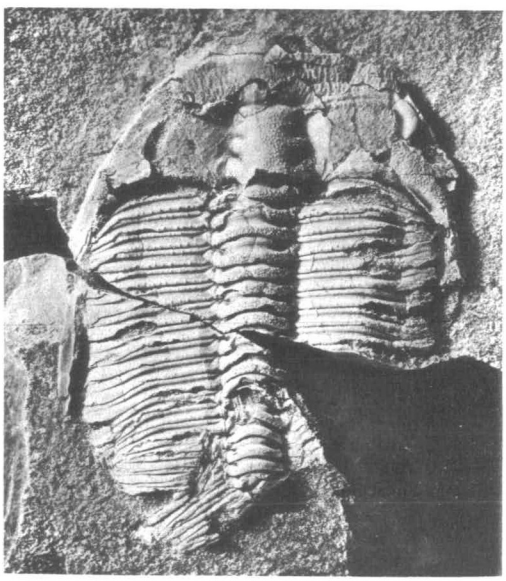

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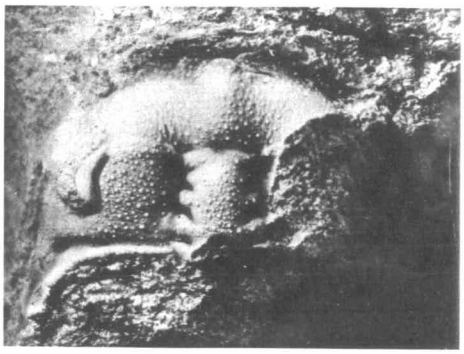

5b

3

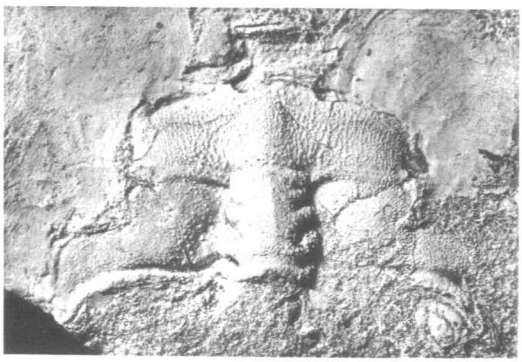

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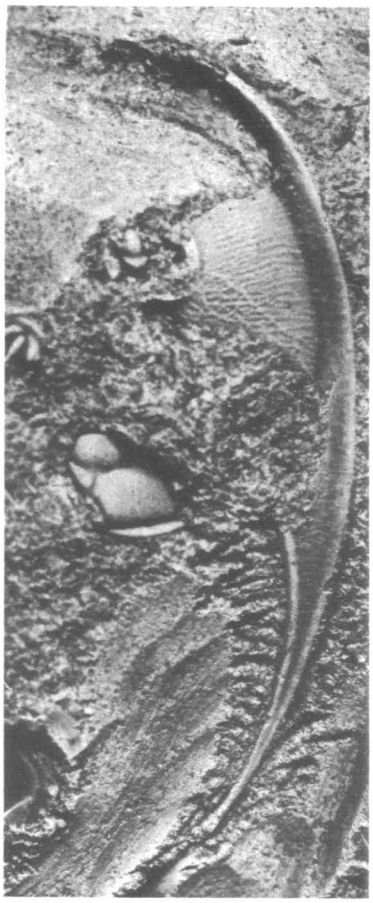
PLATE 10



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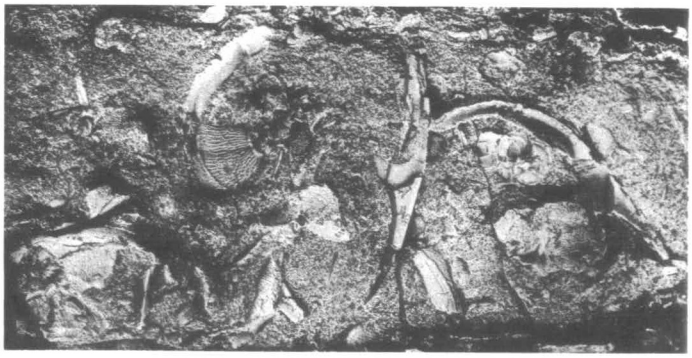

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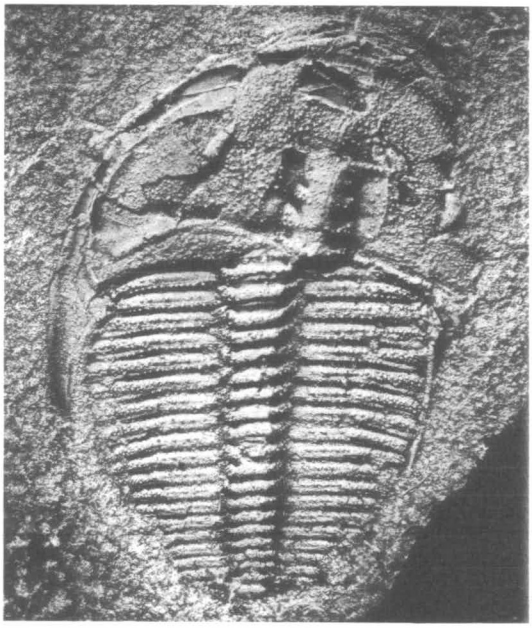

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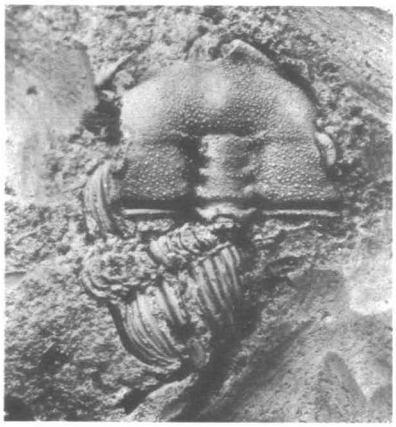

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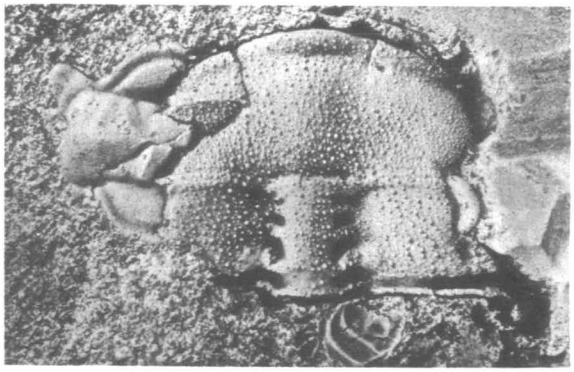


5

PLATE 11

Page

Penarosa zeabunda sp. nov. 31

Figs 1a, 1b. Cranidium, CPC7309, x 8 and x 6 respectively.

Figs 2a, 2b. and upper back to front cranidium in Fig. 3. **Holotype** cranidium, CPC7310. Fig. 2a—x 6, 2b—x 4, and Fig. 3—x 4.8.

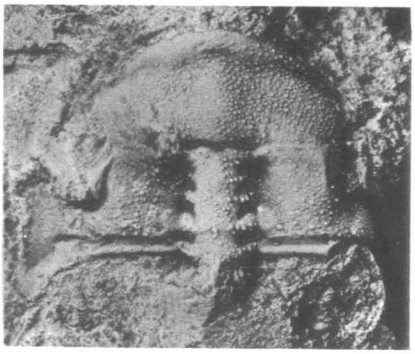
Fig. 3. See above explanation of Figs 2a, etc.

Penarosa elaticeps sp. nov. 34

Fig. 3 (lower cranidium). **Holotype** cranidium, CPC7311, x 4.8. Figs 1-3 from Currant Bush Limestone, Lancewood Creek, loc. M179, western fringe of Mt Drummond Sheet area, Northern Territory.

Penarosa petalifera sp. nov. 37

Fig. 4. Cranidium, CPC7312, x 6. Internal cast in chert, Currant Bush Limestone, loc. M130.



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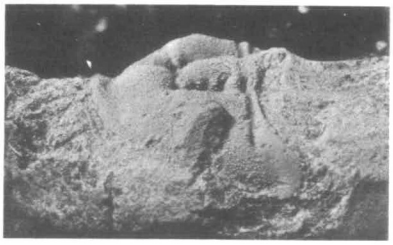

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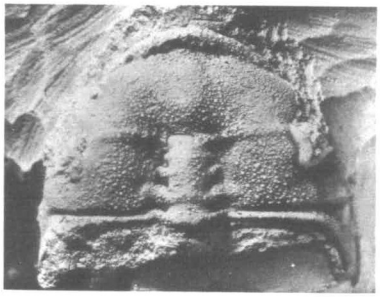

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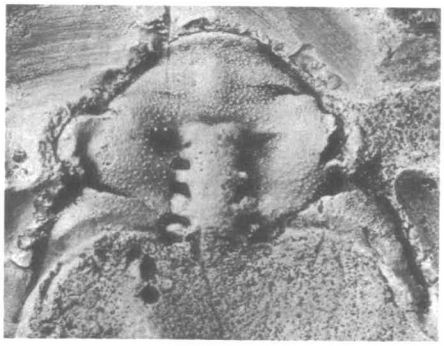

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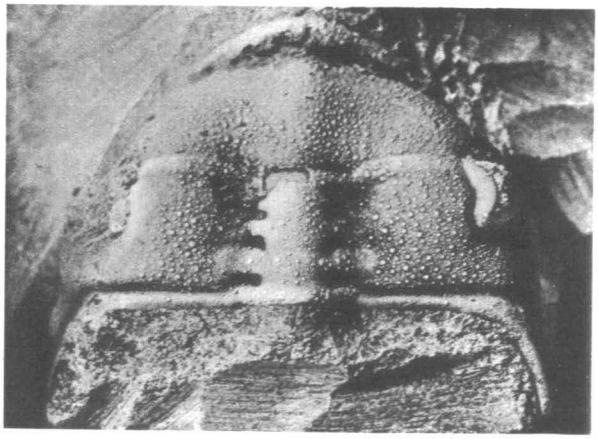

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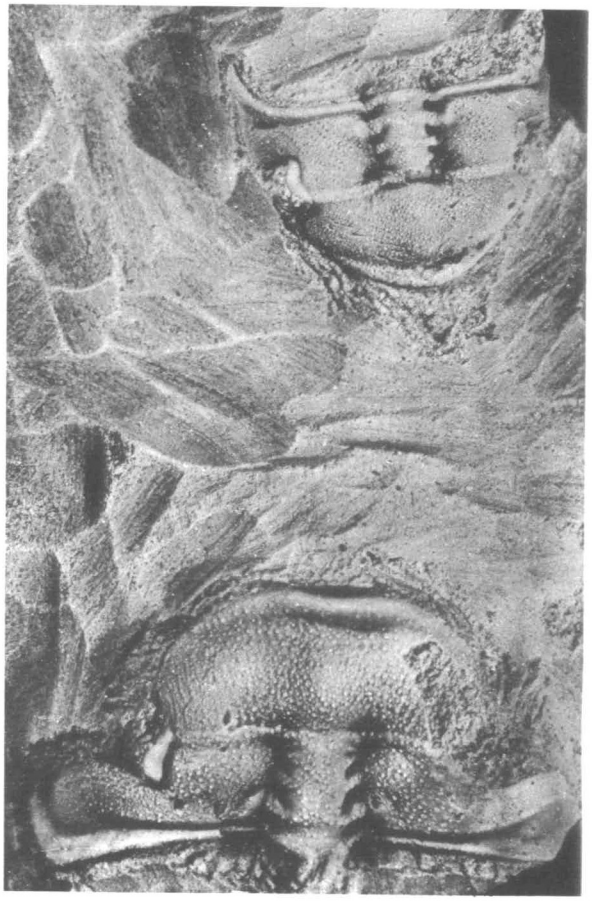

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PLATE 12

Page

Penarosa zeabunda sp. nov. 31

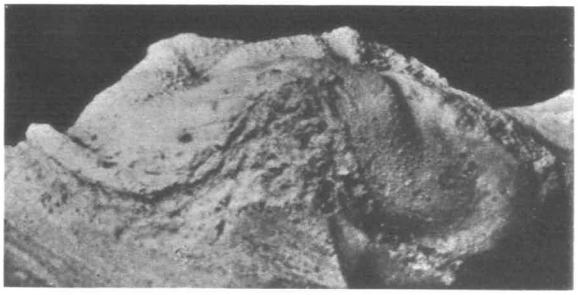
Fig. 1. Cranidium, lateral view of **holotype** (see Pl. 11). x 8.

Penarosa elaticeps sp. nov. 34

Figs 2a-2d. Cranidium, **holotype,** CPC7311, x 5, x 3.5, x 3.5 and x 2.5 respectively.

Penarosa meniscops sp. nov. 36

Figs 3a, 3b. **Holotype** cranidium, CPC7313, x 7 and x 5 (Fig. 3b. rubber cast). All specimens from Currant Bush Limestone, loc. M179; Lancewood Creek, eastern fringe of Mt Drummond Sheet area, Northern Territory.



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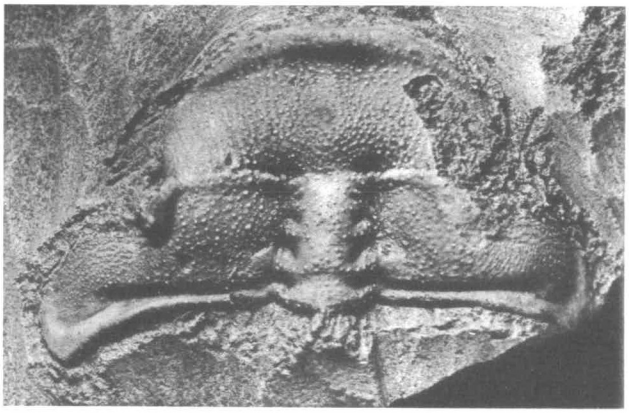

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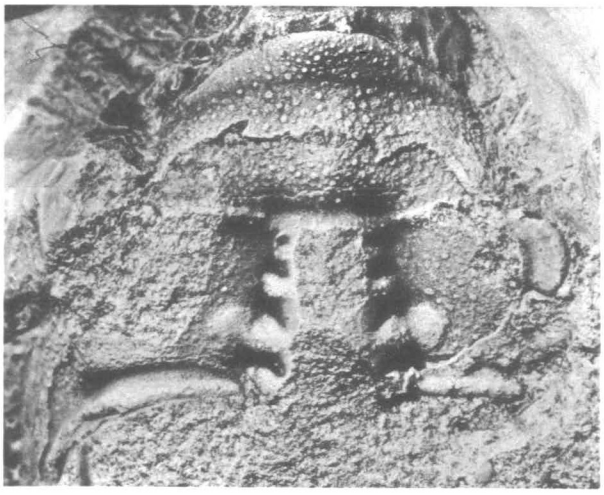

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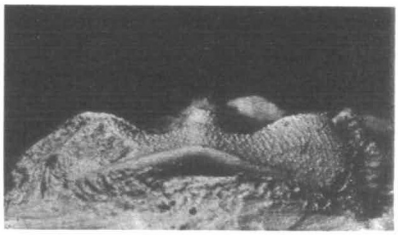

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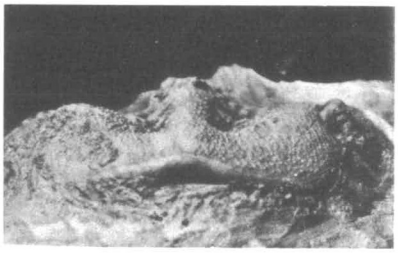

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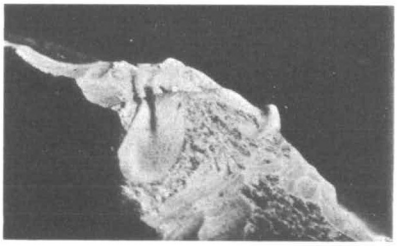

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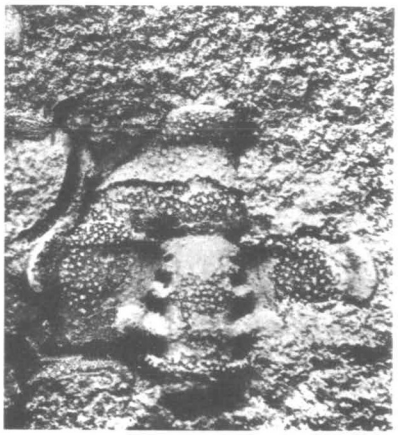
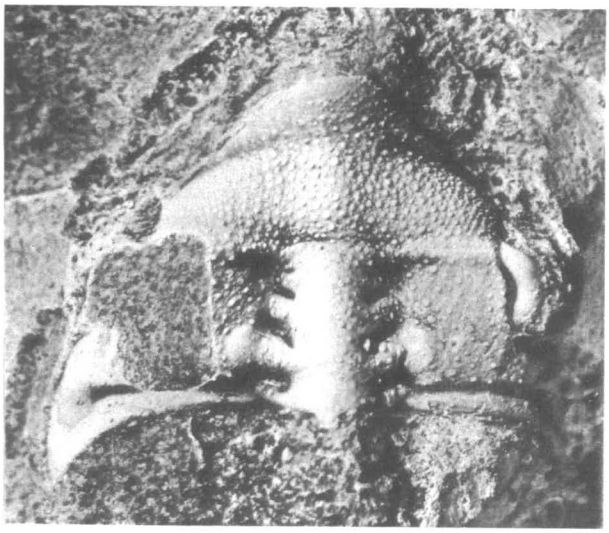


3b

PLATE 13

Figs 1a-1c. **Holotype** cranidium, CPC7314, x 8.

Figs 2a-2c. Cranidium, CPC7315, x 8. Currant Bush Limestone, loc. M179, Lancewood Creek, eastern fringe of Mt Drummond Sheet area, Northern Territory.



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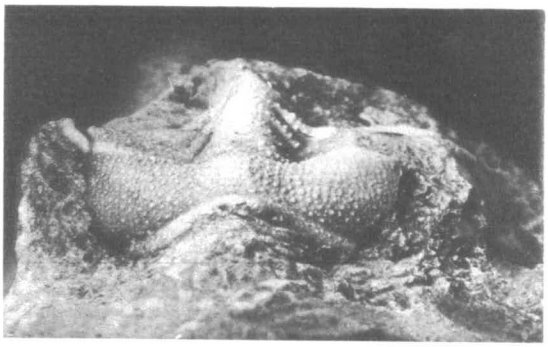

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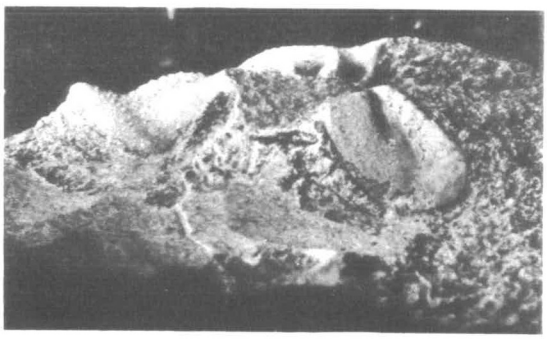

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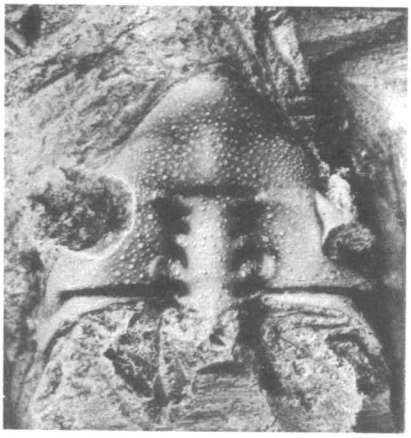

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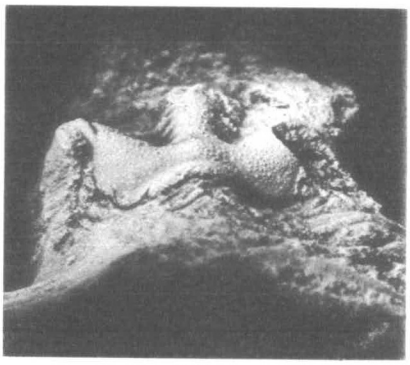

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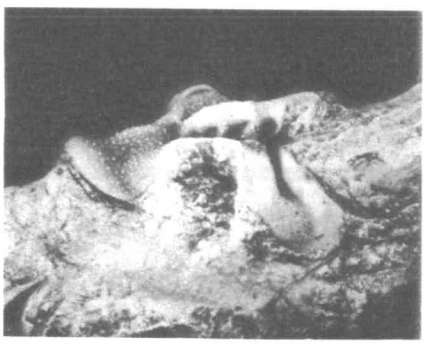


2c

PLATE 14

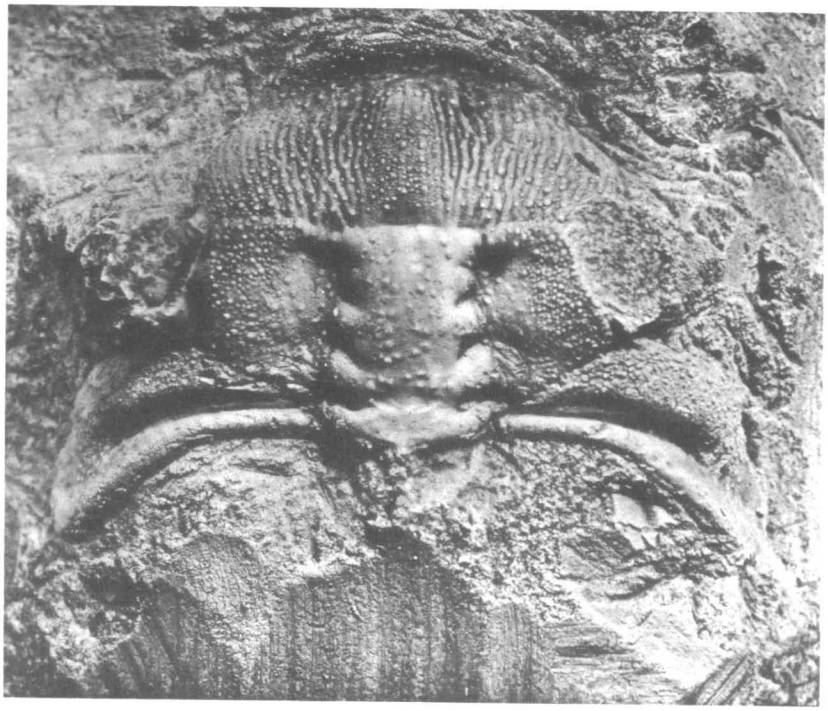
Page

Penarosa melota sp. nov. 40

Figs 1a, 1b. **Holotype** cranidium, CPC7316, x 8 and 3.8 respectively. Currant Bush Limestone, loc. M124.

Penarosa meniscops sp. nov. 36

Fig. 2. Cranidium, CPC7317, associated with a fragment of *Ptychagnostus,* x 11. Loc. M412, shale of Inca Formation.



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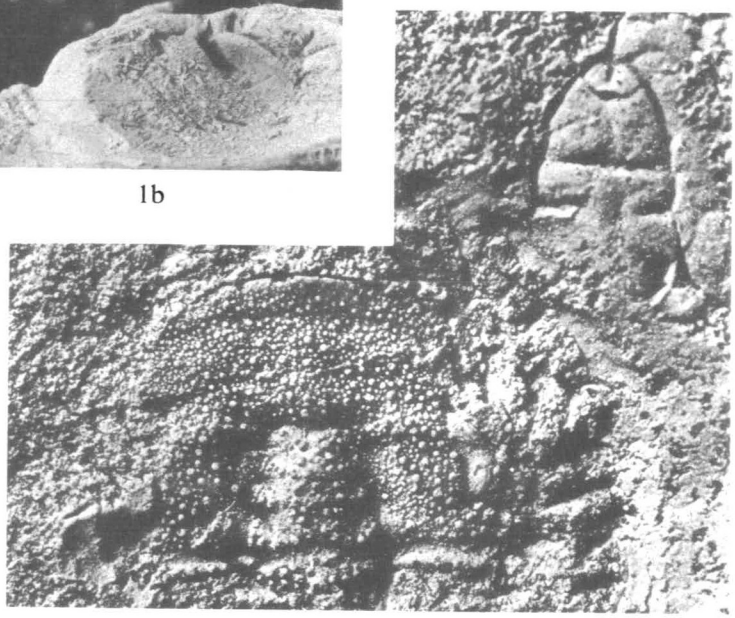

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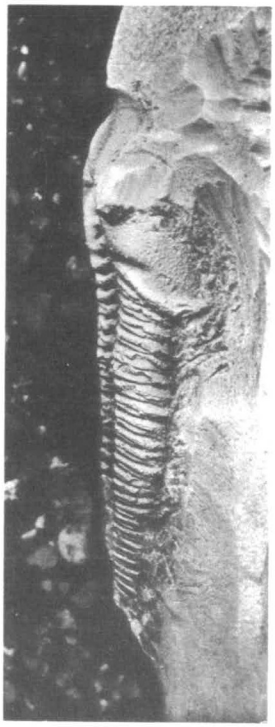
PLATE 15



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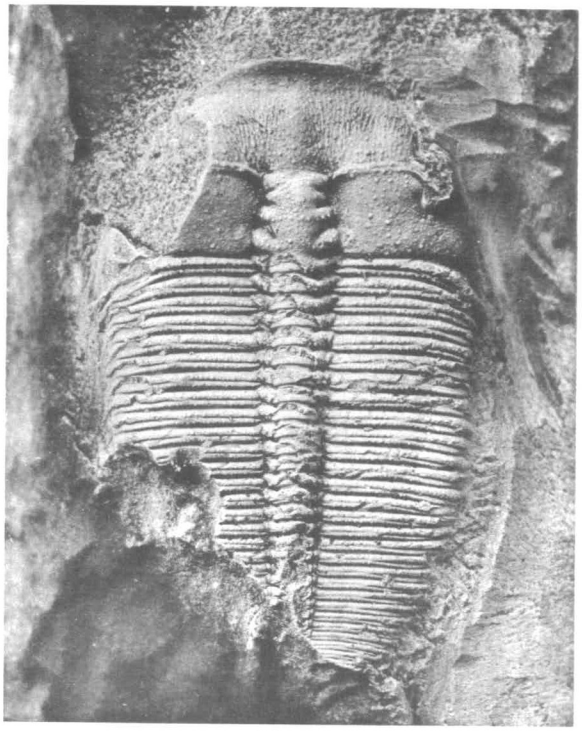

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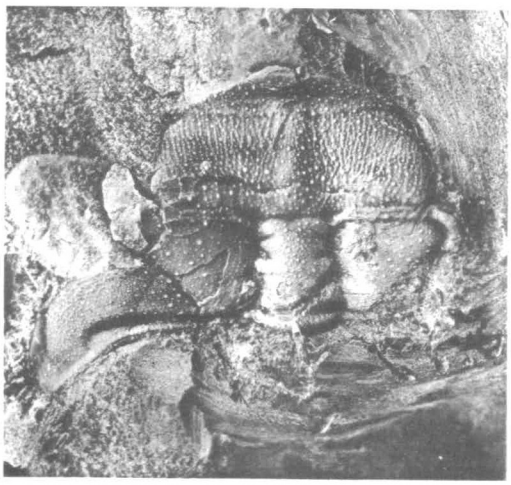

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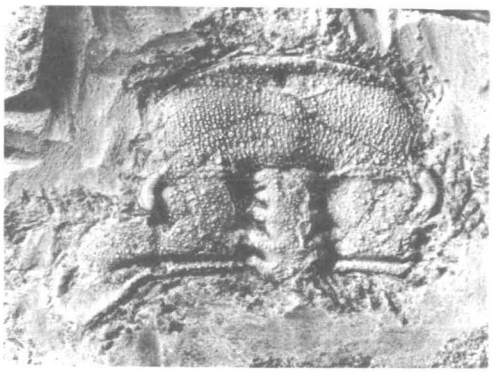

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PLATE 16

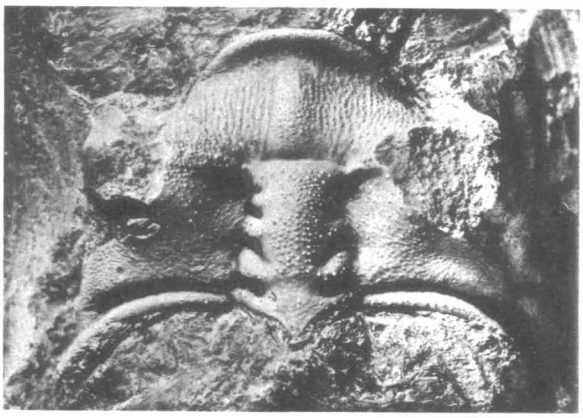
Figs 1a-1c. **Holotype** cranidium, CPC7322, x 7, x 5 and 3.5 respectively.

Fig. 2. Free cheeks unit, CPC7323, x 3. Ventral view.

Figs 3a-3b. Cranidium, CPC7324, x 5 and x 3 (rubber cast). Currant Bush Limestone, loc. M28.

Fig. 4. Cranidium, CPC7325, x 3.

Fig. 5. Cranidium, CPC7326, x 4. Figs 4 and 5 from loc. M157, limestone (Currant Bush) interbedded in Age Creek Formation.

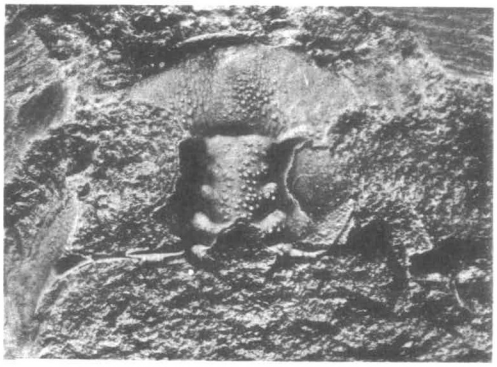


1a

1b

1c

2



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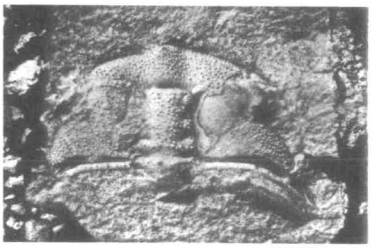

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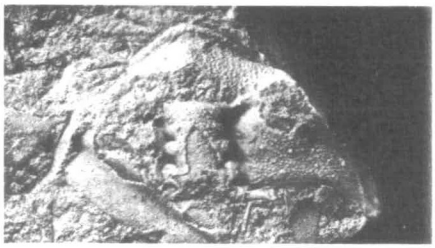

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PLATE 17

Page

Loxonepea loxophrys gen. nov., sp. nov. 22

Fig. 1. **Holotype** cranidium, CPC7327, x 7. Currant Bush Limestone (oolitic and silicified), loc. M124(A). See also Text-fig. 7.

Loxonepea sp. nov. ND 23

Fig. 2. Cranidium, rubber cast of CPC7328, x 6. Loc. M122, interbed in Age Creek Formation.

Penarosa sp. nov. PC 40

Fig. 3. Cranidium, rubber cast of CPC7329, x 4.

Fig. 4. Immature cranidium, CPC7330, x 12. Shale of Inca Formation, loc. M412.

Penarosa zeabunda sp. nov. 31

Fig. 5. Immature cranidium, rubber cast of CPC7331, x 20.

Fig. 6. Three immature cranidia, CPC7332, x 18. Currant Bush Limestone, Lancewood Creek, loc. M179, eastern fringe of Mt Drummond Sheet area.

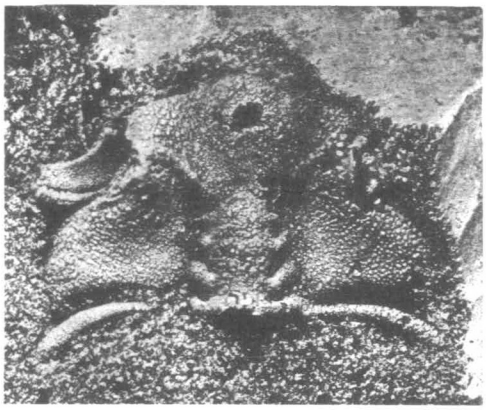
Penarosa retifera sp. nov. 25

Fig. 7. Immature cranidium, CPC7333, x 30.

Fig. 8. Immature cranidium, CPC7334, x 30.

Fig. 9. Immature cranidium, CPC7335, x 30.

Currant Bush Limestone, Lancewood Creek, loc. M180, near M179.



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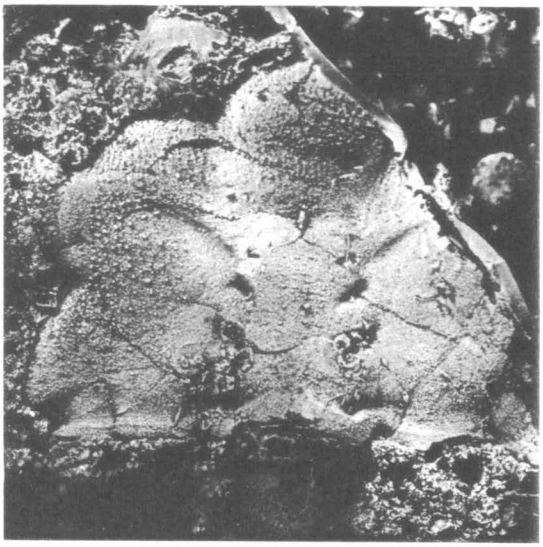

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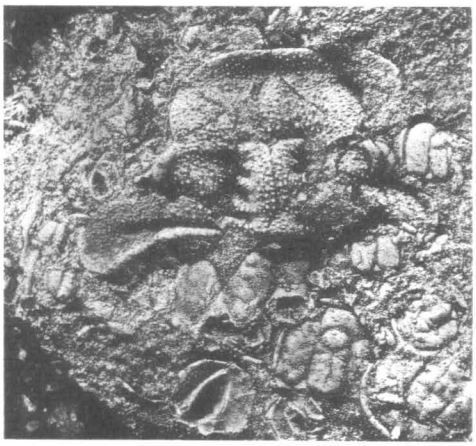

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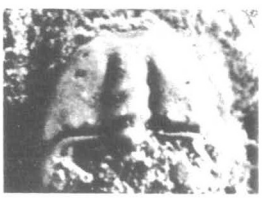

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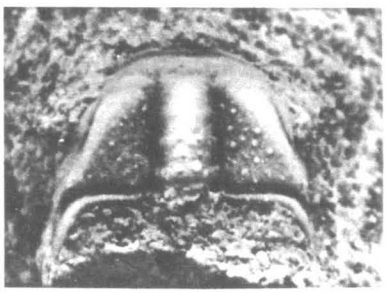

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