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Co-occurrence of middle Miocene larger and planktic smaller foraminifera, New Ireland, Papua New Guinea

BY

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ABSTRACT

A fauna containing both larger and planktic smaller foraminifera has been found in two samples from New Ireland, Papua New Guinea. The planktic foraminifera indicate an age within the N.11-N.12 zonal interval; a new species, *Globigerina edita*, is proposed. The larger foraminifera consist mainly of lepidocyclinids, referred to the species *Lepidocyclina (N.) howchini howchini* Chapman & Crespin. Biometrical analysis of the lepidocyclinids has been made using two parameters: the degree of curvature and parameter *F* (the form number). The degree of curvature does not seem to be a reliable criterion for inter-regional correlation; more data are required for parameter *F*.

INTRODUCTION

The two samples containing the foraminifera discussed in this paper (7697–2010 and –2011) are in situ samples from the Lossuk River beds collected by C. M. Brown of the Papua New Guinea Geological Survey in January 1976; this formation, defined by Hohnen (1978), was not known previously to be younger than early Miocene. Sample 2011 is from a silty mudstone and 2010 from a calcareous sandstone layer within the mudstone. The sample locality, a road cutting along a timber track 1.8 km south-southwest of Lossuk, New Ireland, is shown in Figure 1. The samples are of interest in that they contain both larger foraminifera (mainly lepidocyclinids) and planktic foraminifera. The larger foraminifera are particularly well preserved; they have been abraded only slightly, and the chambers are empty. There is no reason to regard the specimens as redeposited, and the fauna has been examined in detail to compare the ages as given by both the larger and planktic foraminifera, and to relate the two biostratigraphic schemes based on each of the faunal groups.

Figured specimens are deposited in the Commonwealth Palaeontological collection at the Bureau of Mineral Resources, Canberra.

I wish to thank Dr C. G. Adams and Dr G. C. H. Chaproniere for constructive comments on the manuscript, and Mr C. M. Brown for locality information and geological data concerning the samples. The text-figures were drawn by G. Trott.

PLANKTIC FORAMINIFERA

In the following list only the original reference to each previously described species is given, followed by reference to illustrations in this paper and notes on some species.

Genus **Globigerina** d'Orbigny, 1826

Globigerina edita sp. nov.

(Pl. 1, figs. 1-10)

Material examined: 30 specimens.

Derivation of name: From the Latin *editus*, high, lofty, referring to the trochospiral test.

Diagnosis: A small species of the genus *Globigerina* characterised by a four-chambered high trochospiral coil and a reticulate test surface.

Description: Test small, trochoid, high-spired, chambers increasing only slowly in size as added, four chambers in last whorl. Chambers globular, sutures narrow, depressed, curved on dorsal side, radial on ventral side. Wall finely perforate, surface of test distinctly reticulate, except occasionally on last chamber, which may be finely pustulose. Umbilicus narrow, aperture small, arched, umbilical, no lip or thickened margin observed; final chamber on some specimens obscuring umbilicus, causing bulla-like appearance.

Dimensions:

	Max. Diameter	*Height*
Holotype	0.30	0.38
Paratype A	0.40	0.41
Paratype B	0.32	0.32
Paratype C	0.32	0.30

Occurrence: Holotype (CPC.18358) and paratypes A to C (CPC.18359 to 18361) from sample 7697-2010, Lossuk River beds in road cutting along timber track 1.8 km south-southwest of Lossuk, Kavieng 1:250 000 Sheet area, New Ireland, Papua New Guinea. Also occurs in sample 7697-2011 from this locality. Additional unfigured paratypes are deposited in the Commonwealth Palaeontological Collection under number CPC 18362, and in the ESCAP Fossil Reference Collection held at the Bureau of Mineral Resources under number E.811.

Remarks: G. edita sp. nov. is similar to *G. bradyi* Weisner in general test form, but differs from this species in having a distinctly reticulate rather than pustulose wall texture. The pustulose wall of *G. bradyi* is well shown by a specimen figured by Jenkins & Orr (1972, pl. 4, figs. 7, 8); another specimen figured by those authors (pl. 4, fig. 9) is not as strongly pustulose, but does not have a reticulate wall. *G. edita* sp. nov. also has a smaller, lower aperture than does *G. bradyi* and does not have an apertural lip.

Globigerina falconensis Blow, 1959, p. 177, pl. 9, figs. 40a–c, 41 (Pl. 1, figs. 11–15)

Specimens agree well with the original description and figures, and have the same surface texture as the specimens figured by Brönnimann & Resig (1971). Some smaller, slightly more tightly coiled specimens with a similar surface texture and a thickened apertural lip (see Pl. 1, figs. 14, 15) are also referred to *G. falconensis.* Other specimens (Pl. 2, figs. 1–3) are very similar to forms figured by Brönnimann & Resig (1971) as intermediate between *G. druyi* Akers and *G. falconensis.*

Globigerina praebulloides praebulloides Blow, 1959, p. 180, pl. 8, figs. 47a–c; pl. 9, fig. 48 (Pl. 2, 4–6)

Specimens of the *G. praebulloides* group are common in the Papua New Guinea samples; no attempt has been made to distinguish all the described subspecies. The figured specimen has the arched aperture of *praebulloides*, and is gradational to specimens with a more restricted aperture resembling the *praebulloides occlusa* morphotype.

Globigerina venezuelana Hedberg, 1937, p. 681, pl. 92, fig. 7 (Pl. 2, figs. 7, 8)

Occurs rarely in the present samples; some specimens lack the irregular final chamber obscuring the umbilicus.

Genus **Globigerinita** Brönnimann, 1951

Globigerinita sp. 1 (Pl. 2, figs. 9–12)

This small species, which cannot be referred to any described taxon, occurs commonly in sample 2011;

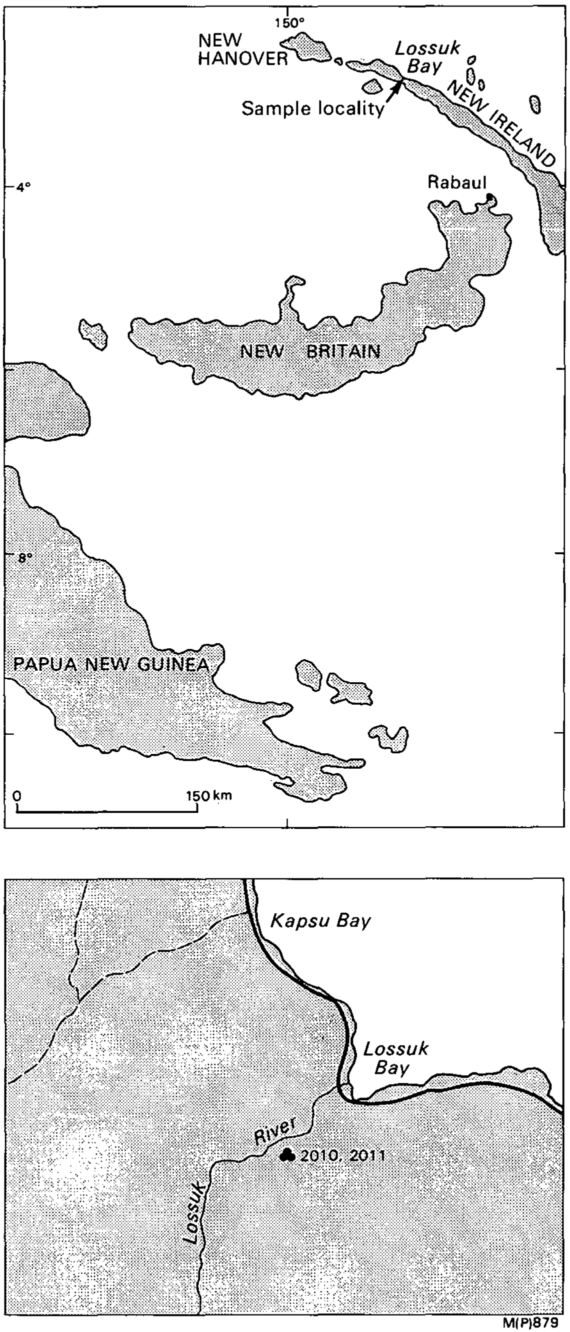

Fig. 1. Locality map showing collecting sites.

specimens have a bulla-like final chamber obscuring the umbilicus. Earlier chambers have a low small umbilical aperture. The last whorl has four chambers increasing only slowly in size. The test surface is pustulose, the pustules fusing on the early chambers of the last whorl to form irregular ridges or reticulations. The specimens resemble a specimen figured by Brönnimann & Resig (1971) as *G. glutinata glutinata* (Egger), but have a more strongly pustulose and reticulate test wall.

Genus **Globigerinoides** Cushman, 1927

Globigerinoides bollii Blow, 1959, p. 189, pl. 10, figs. 65a–c (Pl. 2, figs. 13–15)

Occurs commonly in the Papua New Guinea material.

Globigerinoides obliquus obliquus Bolli, 1957: *Globigerinoides obliqua* Bolli, 1957, p. 113, pl. 25, figs. 9a–c, 10a–c, text fig. 21, 5 (Pl. 2, figs. 16–18)

Rare specimens in sample 2010 show the compressed chambers and high arched primary aperture of *G. obliquus obliquus.*

Globigerinoides quadrilobatus quadrilobatus (d'Orbigny, 1846): *Globigerina quadrilobata* d'Orbigny, 1846, p. 164, pl. 9, figs. 7–10 (Pl. 3, figs. 5, 6)

The *G. quadrilobatus* group occurs commonly in the present material, specimens referable to *G. quadrilobatus quadrilobatus* being the most common.

Globigerinoides quadrilobatus irregularus LeRoy, 1944: *Globigerinoides sacculiferus* (Brady) var. *irregularus* LeRoy, 1944, p. 40, pl. 3, figs. 42–43 (Pl. 3, figs. 1–4)

Occurs only rarely in the present material.

Globigerinoides quadrilobatus triloba (Reuss, 1850): *Globigerina triloba* Reuss, 1850, p. 374, pl. 47, figs. 11a–e (Pl. 3, fig. 7)

A very rare component of the *G. quadrilobatus* group in the present material.

Globigerinoides subquadratus Brönnimann, 1954. *Globigerinoides subquadrata* Brönnimann, 1954, p. 680, pl. 1, figs. 5, 8a–c (Pl. 3, figs. 8–10)

A commonly occurring species in the planktic fauna from the present samples.

Genus **Globoquadrina** Finlay, 1947

Globoquadrina altispira altispira (Cushman & Jarvis, 1936): *Globigerina altispira* Cushman & Jarvis, 1936, p. 5, pl. 1, figs. 13a–c, 14 (Pl. 3, figs. 11, 12)

Occurs rarely in the present material.

Globoquadrina dehiscens (Chapman, Parr & Collins, 1934) group: *Globorotalia dehiscens* Chapman, Parr & Collins, 1934, p. 569, pl. 11, figs. 36a–c (Pl. 3, figs. 13–18; Pl. 4, figs. 1–9)

Specimens placed in this category include:

(a) forms with the quadrate outline of the holotype (Pl. 3, figs. 13–15); this form was figured by Quilty (1976) as *G. dehiscens dehiscens* form α.

(b) forms with a less distinctly quadrate outline and more globular chambers (Pl. 3, figs. 16–18). These specimens differ somewhat from the original concept of the species, but are considered to be referable to *G. dehiscens* s.s.; they are transitional to

(c) forms with more globular chambers and rounded umbilical shoulders resembling the *G. baroemoenensis* (LeRoy) morphotypes (Pl. 4, figs. 1–6), and

(d) large forms with 3–3½ chambers in the last whorl and a flat dorsal surface which resemble *G. dehiscens praedehiscens* Blow & Banner, particularly the specimen figured by Blow (1969) showing the '*Globigerina tripartita* early stage' of *dehiscens praedehiscens* (Pl. 4, figs. 7–9). These differ in having a more angulate umbilical shoulder, and resemble in this respect the phylogenetically advanced form of *G. baroemoenensis* figured by Blow (1969, pl. 28, fig. 4). These specimens differ from *Globigerina tripartita* Koch in their flatter dorsal surface.

Stainforth, Lamb, et al. (1975) placed *baroemoenensis* in the synonymy of the *G. dehiscens* group; the variation shown by the present specimens would support that view, but *baroemoenensis* could be retained at subspecific level.

Globoquadrina sp. 1 (Pl. 4, figs. 13–15)

Rare, very small specimens with 4–4½ chambers in the last whorl and a coarsely reticulate surface texture are placed here. They are possibly small specimens of the *baroemoenensis* morphotype, referred to under the *G. dehiscens* group.

Globoquadrina sp. 2 (Pl. 4, figs. 10–12)

Only one specimen of this form has been found; it is close to the *G. dehiscens praedehiscens* group, and probably should be included here. According to Blow (1969) *dehiscens praedehiscens* became extinct in Zone N. 6, so this record would represent a considerable extension of the recorded stratigraphical range.

This one specimen found may represent a reversion to a 'primitive' form within the *G. dehiscens* group.

Genus **Globorotalia** Cushman, 1927

Subgenus **Fohsella** Bandy, 1972

Globorotalia (Fohsella) peripheroacuta Blow & Banner, 1966, p. 244, pl. 1, figs. 2a–c; pl. 2, figs. 4–5, 13 (pl. 5, figs. 1–6)

Occurs commonly in the present material; the specimens show some variation in the degree of compression of the peripheral margin of the later chambers, ranging from specimens with the acute peripheral margin shown by the holotype to specimens with a narrowly rounded margin.

Subgenus **Hirsutella** Bandy, 1972

Globorotalia (Hirsutella) scitula scitula (Brady, 1882): *Pulvinulina scitula* Brady, 1882, p. 716 (figured Brady, 1884, pl. 103, figs. 7a–c as *Pulvinulina patagonica* (d'Orbigny)) (Pl. 5, figs. 7–9)

Rare specimens of this species occur in sample 2011.

Subgenus **Turborotalia** Cushman & Bermudez, 1949

Globorotalia (Turborotalia) mayeri Cushman & Ellisor, 1939, p. 11, pl. 2, figs. 4a–c (Pl. 5, figs. 10–12)

Abundant in the present material. The specimens have curved dorsal sutures, the main criterion disinguishing this species from *G. (T.) siakensis*. Stainforth, Lamb, et al. (1975) placed *mayeri* in the synonymy of *siakensis*.

Globorotalia (T.) obesa Bolli, 1957, p. 119, pl. 29, figs. 2a–c, 3 (Pl. 5, figs. 13, 14)

A long-ranging species occurring rarely in the present material.

Globorotalia (T.) sp. 1 (Pl. 5, figs. 15–17)

Only one specimen of this form has been found. It is a small trochospiral form with five chambers in the last whorl and a pustulose final chamber. It is intermediate in its morphological features between the *Globigerina praebulloides* group (e.g. *praebulloides pseudociperoensis* Blow) and *Globorotalia (T.) obesa.*

Genus **Globorotaloides** Bolli, 1957

Globorotaloides suteri Bolli, 1957, p. 117, pl. 27, figs. 9a–c, 10a–b, 11a–b, 12a–b, 13a–b (Pl. 5, figs. 18–20)

Frequent specimens from one sample (2010) are referred to this species. Stainforth, Lamb et al. (1975) discussed the problems of the taxonomy of *G. suteri.* Several of the present specimens lack a bulla and have a low slit-like aperture; many smaller specimens have a bullate final chamber. The test surface is not as coarsely reticulate as that of the specimens figured by Stainforth, Lamb et al. (op. cit.), particularly on the younger chambers.

Orbulina suturalis Brönnimann, 1951, p. 135, text-fig. 2, 1–2, 5–8, 10; text-fig. 3, 3–8, 11, 13–16, 18, 20–22; text-fig. 4, 2–4, 7–12, 14–16, 19–22 (Pl. 6, fig. 1)

Occurs abundantly in the present material.

Genus **Tenuitella** Fleisher, 1974

Tenuitella clemenciae (Bermudez, 1961): *Turborotalia clemenciae* Bermudez, 1961, p. 1321, pl. 17, figs. 10a–b (Pl. 6, figs. 2–8).

Specimens of this species in the present material show the thin, very finely perforate test wall and the small pustules, particularly on the ventral surface of the early chambers of the last whorl; four or five chambers are present in the last whorl.

LARGER FORAMINIFERA

Lepidocyclina (Nephrolepidina) howchini Chapman & Crespin group. (Pl. 6, figs. 9–16; Pl. 7, figs. 1–17)

External characters: Test small, discoidal, lenticular, diameter ranging from 1.5 to 2.8 mm, thickness from 0.5 to 0.9 mm; compressed, irregularly circular in outline, with thin flange, commonly broken; reticulate surface ornament, no pustules observed.

Internal characters: Embryoconch nephrolepidine to almost trybliolepidine; equatorial chambers spatulate to rarely hexagonal in outer part of test; arranged in circular concentric to stellate pattern, with the inter-ray areas slightly concave; six to nine layers of lateral chambers, elongate, subquadrangular; thin pillars sometimes developed, not forming pustules at test surface.

Remarks: The specimens from the present material are referred to the *L. (N.) howchini* Chapman & Crespin group. Chaproniere (1977; 1980) has made studies, including biometrical work, on populations of *Lepidocyclina (Nephrolepidina)* from Australia and New Zealand, and on his results the specimens would be referred to *L. (N.) howchini howchini.* This subspecies is distinguished from *L. (N.) japonica* Yabe in rarely having hexagonal equatorial chambers, which if developed appear only on the outer part of the equatorial layer.

Other groups

Apart from the lepidocyclinids, one specimen of *Miogypsina* referable to the *M. (M.) thecidaeformis* (Rutten) group has been found (Pl. 7, figs. 18, 19). Other forms recorded are *Operculina* sp., *Planorbulinella* sp., and *Amphistegina* sp.

BENTHIC SMALLER FORAMINIFERA

This group is abundant in the samples examined. A list of species identified, which is not exhaustive, is given in Table 1.

AGE OF THE FAUNA

Most of the species of planktic foraminifera in these samples are long-ranging; only two species give an age over a limited zonal interval. *Globigerinoides bollii* is shown by Blow (1969) as ranging from Zone N.11 to Zone N.21; the range of *Globorotalia (Turborotalia) peripheroacuta* is given as Zone N.10 to Zone N.12. The overlap of these two ranges indicates an age within the N.11–N.12 interval, that is, the middle part of the middle Miocene, and within the upper part of Tertiary lower *f* in the 'letter' classification of the Tertiary. This would be near the highest recorded level for *L. (N.) howchini howchini* and correlates closely with the level recorded by Palmieri (1973), who showed his A2 cluster, which included *L. (N.) howchini*, within the N.9–N.12 zonal interval. Chaproniere

TABLE 1
COMPOSITE LIST OF BENTHIC SMALLER FORAMINIFERA

Alabamina tubulifera (Heron-Allen & Earland)
Ammonia beccarii (Linne)
Anomalinella rostrata (Brady)
Astrononion sp.
Baggina indica (Cushman)
Bolivina robusta Brady
Brizalina alata (Seguenza)
B. cf. *semilineata* Belford
B. subreticulata (Parr)
B. tuberosa Belford
B. cf. *vescistriata* Belford
Bulimina striata d'Orbigny
Cassidulina delicata Cushman
Cassidulinoides inflatus (LeRoy)
Ceratobulimina pacifica Cushman & Harris
Chrysalidinella dimorpha (Brady)
Discorbinella bertheloti (d'Orbigny)
Elphidium spp.
'Eponides' subhaidingeri (Parr)
'E.' suturicrassus Belford
Euuvigerina crassicostata (Schwager)
E. flinti (Cushman)
E. schwageri (Brady)
Globocassidulina murrhyna (Schwager)
G. oblonga (Reuss)
Gyroidina cushmani Boomgaart
G. torulus Belford
Hoeglundina elegans (d'Orbigny)
Lamarckina ventricosa (Brady)
Neoeponides parantillarum (Galloway & Heminway)
Nonionella sp.
Pavonina flabelliformis d'Orbigny
Pararotalia sp.
Planulina ungeriana (d'Orbigny)
Plectofrondicularia interrupta (Karrer)
Protoglobobulimina pupoides (d'Orbigny)
Quinqueloculina spp.
Rectobolivina dimorpha (Parker & Jones)
R. cf. *limbata* (Brady)
R. papula Belford
R. tenuicostata Belford
Reussella spinulosa (Reuss)
Robertinoides cf. *oceanicus* (Cushman & Parker)
Siphouvigerina proboscidea (Schwager)
Textularia spp.
Tubulogenerina sp.
Valvulineria javana LeRoy

(1977 & in press) recorded *L. (N.) howchini* ranging from Zone N.6 to at least N.9 equivalents, and Carter (1964) from Zone N.8 equivalents.

ENVIRONMENT OF DEPOSITION

The organic remains in sample 2010 are dominated by algal fragments. Larger foraminifera are abundant; planktic and benthic smaller foraminifera also occur commonly, with a ratio of about 1:1. Rare mollusca (gastropoda) also occur.

Sample 2011 contains larger foraminifera, algal fragments, rare mollusca (bivalves, gastropoda), very rare bryozoans and ostracods. Planktic and benthic smaller foraminifera are common, with a ratio of about 1:1.5.

The larger foraminifera, together with other shallow-water genera such as *Amphistegina, Operculina, Elphidium, Anomalinella*, and miliolids, and also the algal fragments, indicate deposition within the photic zone, probably under either open shelf or fore-reef shoal conditions. *Operculina* was recorded by Graham & Militante (1959) from depths of 2 m to 32 m in the Philippines. In the Gulf of Elat, Leutenegger (1977) recorded microspheric specimens of *O. ammonoides* in relatively increasing numbers down to 100 m; Hottinger (1977) recorded *O. ammonoides* living directly on soft bottom between 30 m and 150 m; Fermont (1977) recorded the genus down to 150 m. *Amphistegina* is stenohaline, restricted to oceanic salinities; McKee et al. (1959) recorded *A. madagascariensis* in reefal areas to a depth of 8 m. Graham & Militante (1959) recorded this species down to 32 m in the Philippines. Lutze et al. (1971) recorded it from 15 m to 35 m in the Persian Gulf. Bandy (1954) found *A. lessonii* down to depths of 122 m and McKee et al. reported it as rare at less than 30 m, but abundant to about 65 m. Murray (1973) considered the principal range of *Amphistegina* to be from 5 m to 20 m. Hansen & Buchardt (1977) investigated the depth distribution of four species in the Gulf of Elat; the maximum depth at which living specimens were found was 120 m. *Elphidium* is a shallow-water genus found in association with sea-grass; *Anomalinella* was reported by Graham & Militante (1959) from 1.5 m to 27 m, and Brady (1884) recorded it at depths of 60 m.

The planktic/benthic ratio indicates deposition in somewhat deeper water on the shelf, and it is probable that there was some penecontemporaneous mixing of the faunas with the lepidocyclinids, miogypsinids, and other genera moving down the shelf or reef slope to deeper water. All specimens are well preserved and are not considered to have been redeposited.

BIOMETRICAL STUDIES

Methods and results

Several parameters have been used in biometrical studies of larger foraminifera; of these, Factor A introduced by van der Vlerk (1959) and the 'degree of curvature' (van der Vlerk, 1968; van der Vlerk & Gloor, 1968) have been widely used. Both parameters indicate the extent to which the protoconch is embraced by the deuteroconch. A modification of Factor A called the 'grade of enclosure' was used by van der Vlerk (1963; 1964; 1968), van der Vlerk & Postuma (1967), and van der Vlerk & Gloor (1968). As both this parameter and the 'degree of curvature' give analagous results van der Vlerk & Gloor (op. cit.) recommended that only the 'degree of curvature' be used; this value was said to lead to a more extended and reliable scale of values, and to be determined more accurately and more quickly. Only the 'degree of curvature' is used here; on forty-three specimens measured all except one specimen from sample 2010, the mean value obtained is 56.4% with a standard deviation of 11.3% (Text-fig. 2). This is within the range obtained by Chaproniere (1977; 1980) for *L. (N.) howchini howchini* from a level equivalent to planktic zones N.7 or N.8. A value of 48.3% ± 10.7% was obtained by Chaproniere for specimens of *L. (N.) japonica* from a level equivalent to planktic zone N.6.

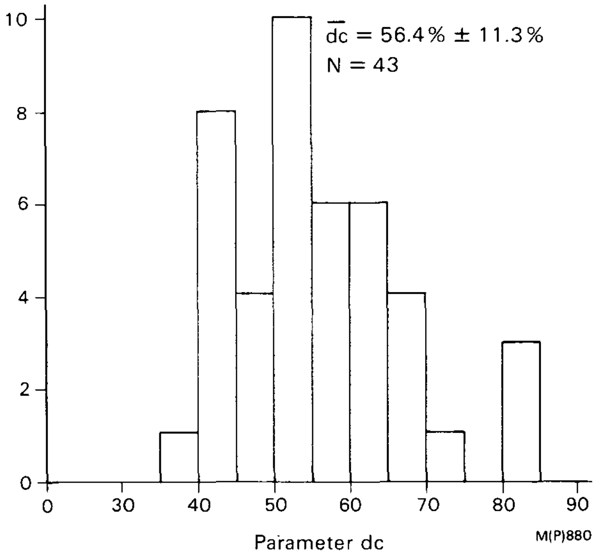

Fig. 2. Histogram of 'degree of curvature' dc for 43 specimens.

Chaproniere (op. cit.) introduced another parameter which he termed parameter F, or the form-number. This parameter expresses the phylogenetic stage of individual specimens, each of which is placed visually into one of five categories, depending on the overall pattern of the equatorial chambers; the category chosen is the result of a subjective judgement. This subjective judgement does not affect the accuracy of the method, and it appears to be the most reliable, although more results are needed to establish its suitability for interregional correlation. The most primitive category (1) includes all specimens in which 90% of the test consists of an 'engine-turned' chamber pattern. This is followed by specimens with chambers in a circular concentric pattern (category 2); those with a polygonal concentric pattern (category 3), in which a few elongate spatulate chambers form weak rays; those with the chambers in a stellate pattern and the inter-ray areas slightly concave (category 4), and the highest category, 5, in which the specimens have a strong stellate pattern, with very concave inter-ray areas. Values for parameter F found by Chaproniere for *L. (N.) howchini howchini* are greater than 3, compared to 2.48 for *L. (N.) japonica.* The mean value obtained for the Papua New Guinea material, based on observation of 37 specimens, is 3.13, again indicating a closer relationship to *L. (N.) howchini howchini* (Text–fig. 3).

Use in correlation

Statistical measurements on larger foraminifera have been proposed as a method of correlation (see, for example, van der Vlerk, 1968; van der Vlerk & Postuma, 1967; O'Herne & van der Vlerk, 1971; Ho Kiam Fui, 1976). In the case of the 'degree of curvature', it has been clearly demonstrated that the value of this parameter increases with time; it has not been demonstrated that the rate of change was the same in different areas, or that populations of the same age from different areas have the same or similar degree of curvature values. Van der Vlerk made no distinction between different morphotypes in his material; it is still not known if the mean degree of curvature for all species is the same at a particular level, for example in zone N.8. There is no reason why this should be the case; the statistical results for any one population would therefore be affected by the relative abundance of different morphotypes in the sample.

Ho Kiam Fui (1976) determined the degree of curvature for populations of *Lepidocyclina* from Sarawak, and plotted the results against a planktic time scale, using ages given by planktic species in the samples examined. On the diagram given by Ho Kiam Fui the value of 56.4% obtained for the present specimens would place them at the top of his *Globorotalia lobata/robusta Zone.* On the correlations given by Blow (1969) and Berggren (1971) this is equivalent to uppermost N.12 or basal N.13 in the zonation of Blow (1969); the age given by the planktic species in the Papua New Guinea material is slightly older, within the N.11–N.12 zonal interval.

Palmieri (1973) measured the degree of curvature in a group of lepidocyclinids from a level above the *Orbulina* datum. One group, consisting of specimens seemingly intermediate between the *L. (N.) angulosa-L. (N.) Howchini-L. (N.) japonica* group and *L. (N.) martini,* with others possibly referable to *L. (N.) sumatrensis* (Brady), has values ranging from 60% to 70%, and is within the N.9–N.12 zonal interval. Another group has values ranging between 65% and 75% and extends into Zone N.13. These values are considerably higher than that obtained from the Papua New Guinea specimens from within a similar zonal interval.

Van der Vlerk (1968) also plotted degree of curvature values against the planktic time scale; the value of 56.4% found for the Papua New Guinea specimens would on this scale fall within Zone N.8, a level below that indicated by the accompanying planktic species. An indication that the degree of curvature parameter does not give a high degree of resolution is shown by an example cited by van der Vlerk (op. cit.) in which forms not differing significantly in the degree of curvature ratio occur in samples referred to different

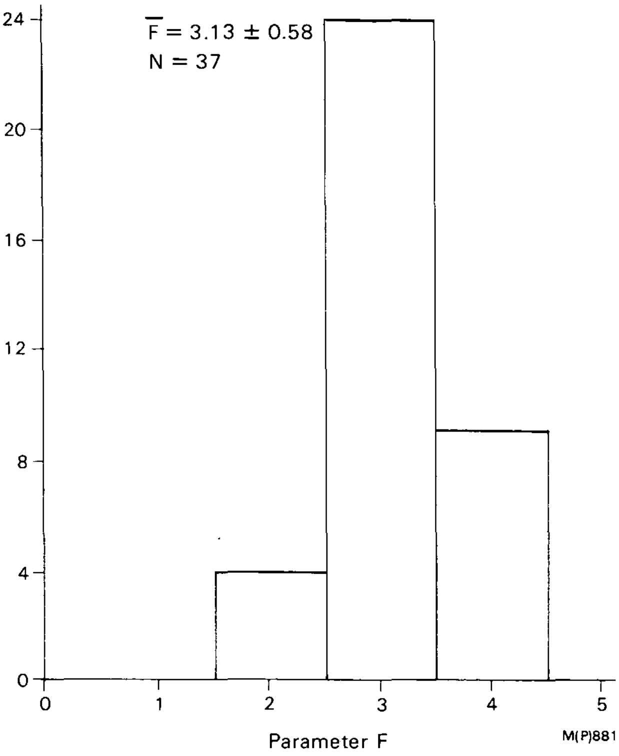

Fig. 3. Histogram of parameter F for 37 specimens.

planktic zones. The high standard deviation (11.3%) calculated for the Papua New Guinea specimens reflects the large range of the degree of curvature parameter, which militates against its use in correlation.

Another example of the range shown by the degree of curvature is given by Chaproniere (1977; 1980), who determined values ranging from 47.5% to 59.3% within the N.7–N.8 zonal sequence in northwestern Australia.

These few samples of the range of variation shown by the degree of curvature cast doubt on the validity of the method for inter-regional correlation. Its use may be restricted to local sequences; one indication that it can be used in a limited areas is given by the application of the method by Ho Kiam Fui (1976).

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PLATE 1

Figs.

1–10 **Globigerina edita**, sp. nov.

1–3, Holotype, CPC 18358, sample 7697–2010; 1, ventral view; 2, dorsal view; 3, side view; all x150.

4–6, paratype A, CPC 18359, same sample; 4, ventral view; 5, dorsal view; 6, side view; all x150.

7–8, paratype B, CPC 18360, same sample; 7, ventral view; 8, side view; both x150.

9–10, paratype C, CPC 18361, same sample; 9, ventral view; 10, side view; both x150.

11–15 **Globigerina falconensis** Blow

11–13, CPC 18363, sample 7697–2010; 11, ventral view; 12, dorsal view; 13, side view; all x150.

14–15, CPC 18364, same sample; 14, ventral view; 15, side view; both x150.

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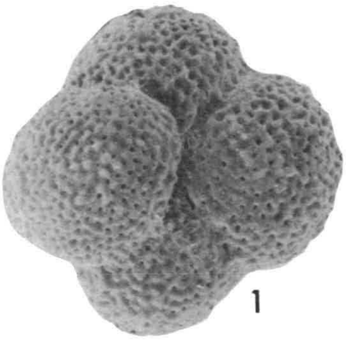
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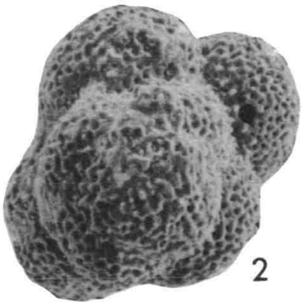
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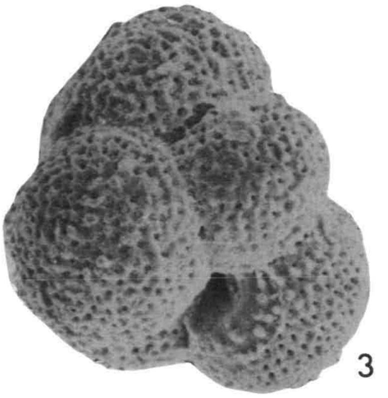
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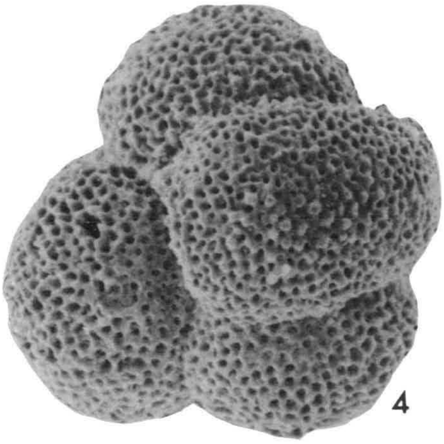
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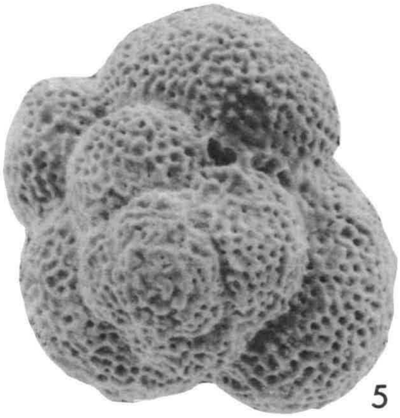
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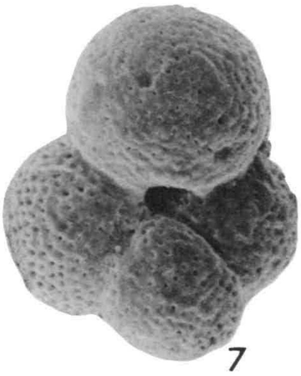
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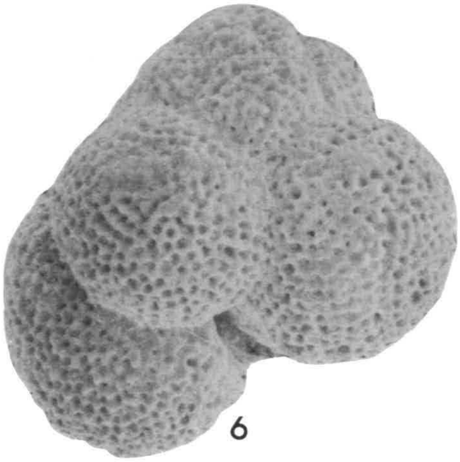
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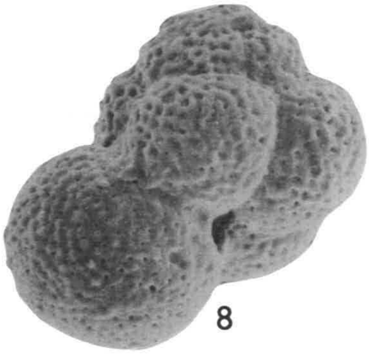
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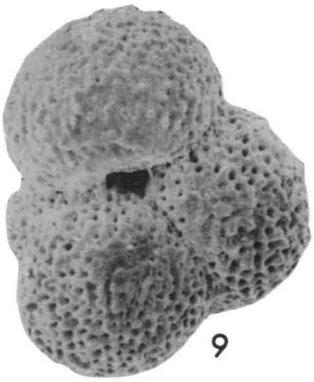
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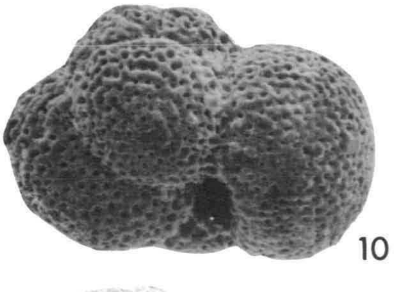
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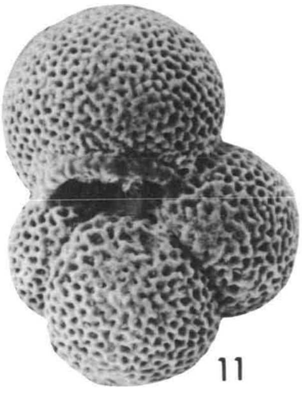
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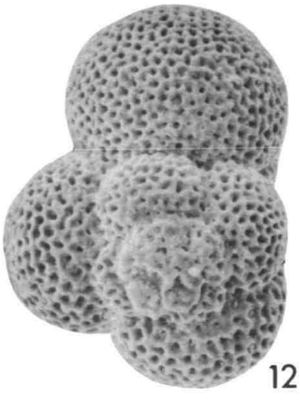
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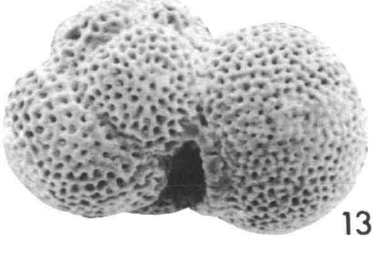
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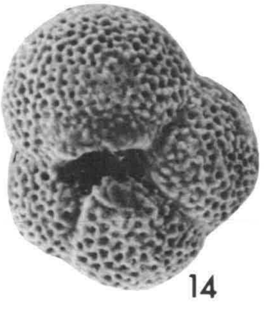
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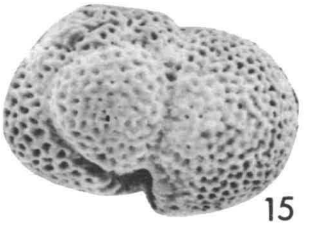
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PLATE 2

Figs.

1–3 Specimen intermediate between **Globigerina falconensis** Blow and **G. druyi** Akers.
CPC 18365, sample 7697–2011; 1, ventral view; 2, dorsal view; 3, side view; all x150.

4–6 **Globigerina praebulloides praebulloides** Blow
CPC 18366, sample 7697–2011; 4, ventral view; 5, dorsal view; 6, side view; all x200.

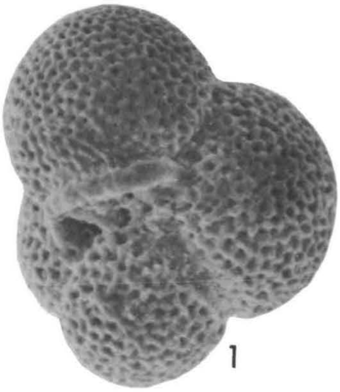
7, 8 **Globigerina venezuelana** Hedberg
CPC 18367, sample 7697–2010; 7, ventral view; 8, dorsal view; both x100.

9–12 **Globigerina** sp. 1
9, 10, CPC 18368, sample 7697–2010; 9, ventral view; 10, side view; both x150.
11, CPC 18369, same sample, ventral view; x150.
12, CPC 18370, same sample, ventral view; x150.

13–15 **Globigerinoides bollii** Blow
CPC 18371, sample 7697–2010; 13, ventral view; 14, dorsal view; 15, side view; all x150.

16–18 **Globigerinoides obliquus obliquus** Bolli
CPC 18372, sample 7697–2010; 16, ventral view; 17, dorsal view; 18, side view; all x100.

PLATE 2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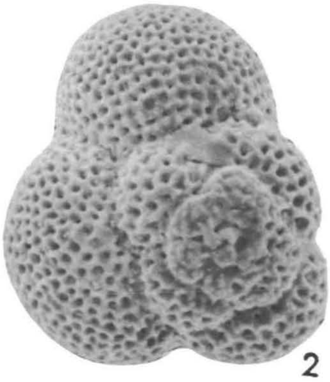
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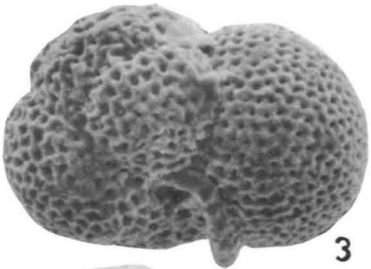
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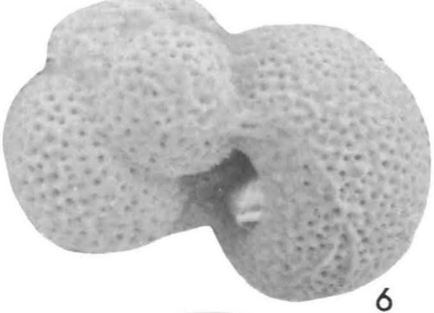
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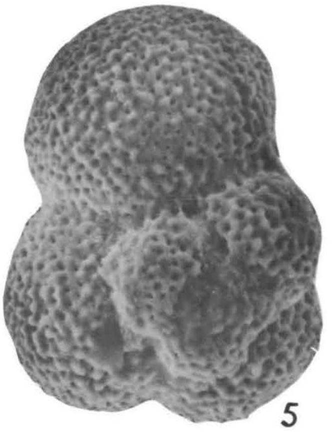
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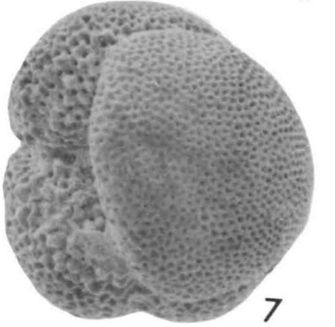
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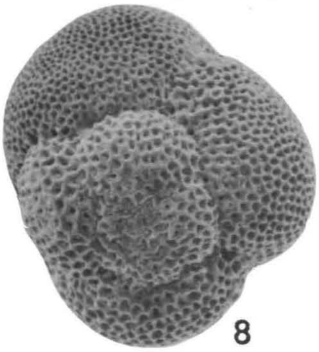
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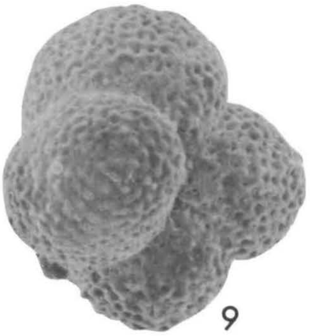
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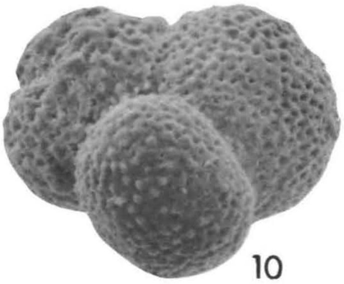
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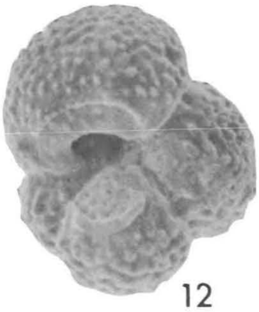
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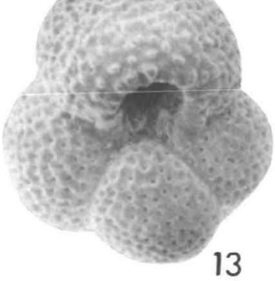
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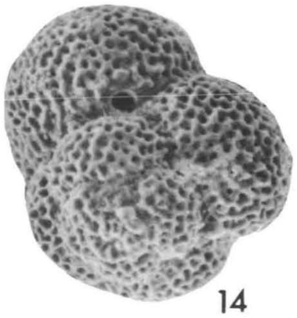
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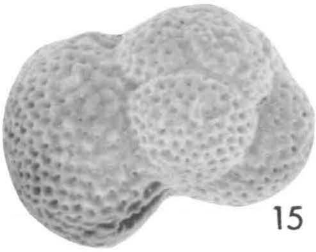
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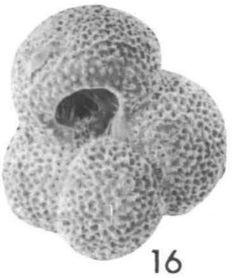
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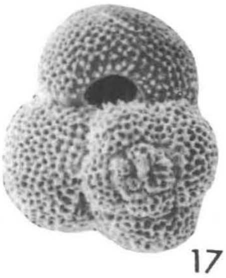
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PLATE 3

Figs.

1–4 **Globigerinoides quadrilobatus irregularus** LeRoy

1, 2, CPC 18373, sample 7697–2010; 1, ventral view; 2, dorsal view; both x80.
3, 4, CPC 18374, same sample; 3, ventral view; 4, dorsal view; both x80.

5, 6 **Globigerinoides quadrilobatus quadrilobatus** (d'Orbigny)

CPC 18375, sample 7697–2010; 5, ventral view; 6, dorsal view; both x80.

7 **Globigerinoides quadrilobatus triloba** (Reuss)

CPC 18376, sample 7697–2010; ventral view; x80.

8–10 **Globigerinoides subquadratus** Brönnimann

CPC 18377, sample 7697–2011; 8, ventral view; 9, dorsal view; 10, side view; all x100.

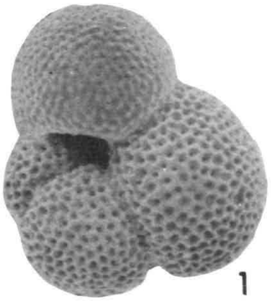
11, 12 **Globoquadrina altispira altispira** (Cushman & Jarvis)

CPC 18378, sample 7697–2010; 11, ventral view; 12, side view; both x80.

13–18 **Globoquadrina dehiscens** (Chapman, Parr & Collins) group: **Globoquadrina dehiscens dehiscens** (Chapman, Parr & Collins) morphotype

13–15, CPC 18379, sample 7697–2010; 13, ventral view; 14, dorsal view; 15, side view; all x150.
16–18, CPC 18380, same sample; 16, ventral view; 17, dorsal view; 18, side view; all x100.

PLATE 3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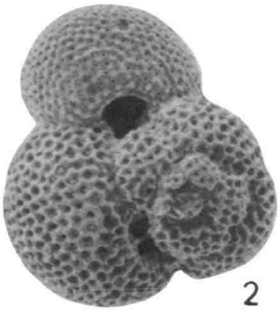
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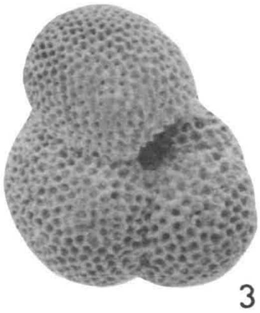
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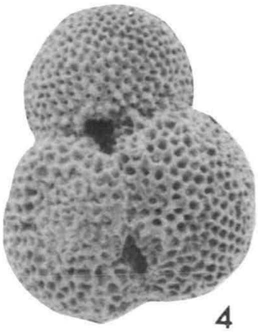
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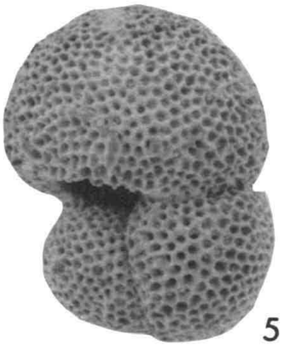
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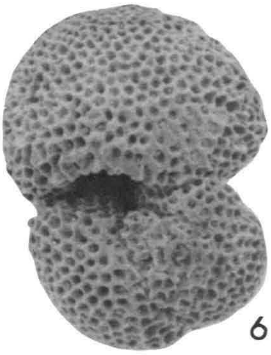
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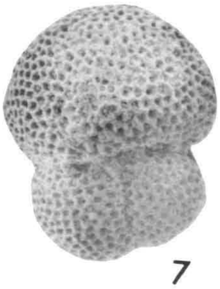
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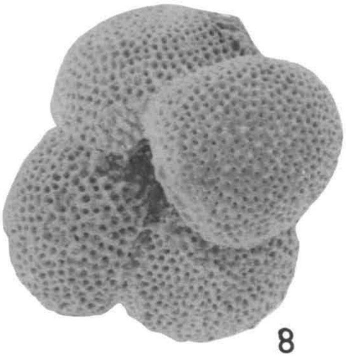
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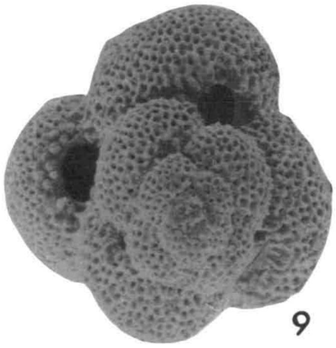
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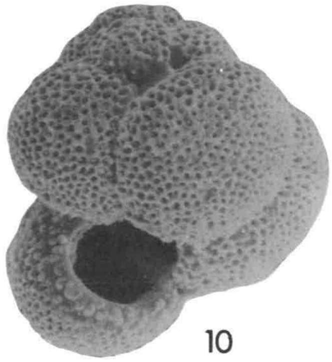
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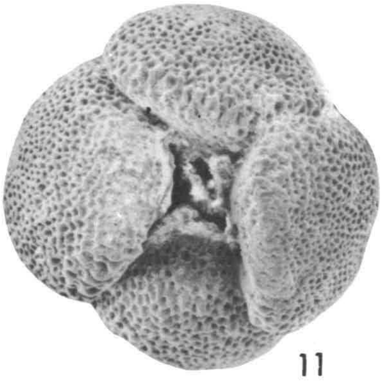
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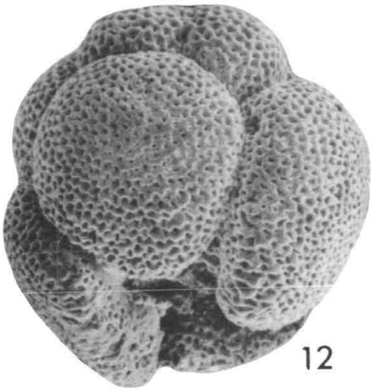
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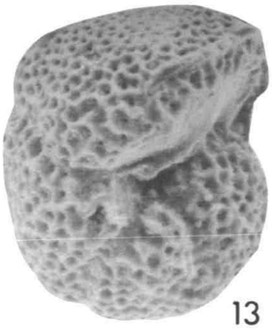
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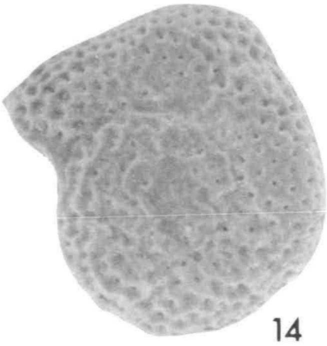
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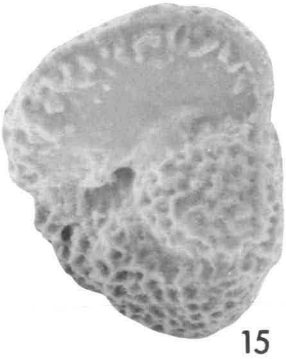
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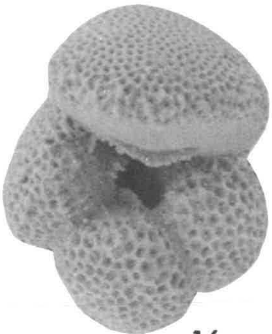
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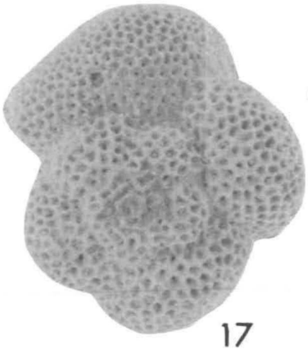
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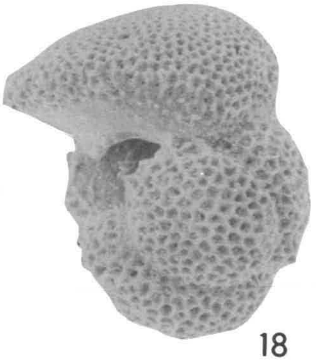
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PLATE 4

Figs.

1–9 **Globoquadrina dehiscens** (Chapman, Parr & Collins) group

1–6 **Globoquadrina baroemoenensis** (LeRoy) morphotypes

1–3, CPC 18381, sample 7697–2010; 1, ventral view; 2, dorsal view; 3, side view; all x100.

4–6, CPC 18382, same sample; 4, ventral view; 5, dorsal view; 6, side view; all x100.

7–9 **"Globigerina tripartita** early stage" of **G. dehiscens praedehiscens**

CPC 18383, sample 7697–2011; 7, ventral view; 8, dorsal view; 9, side view; all x100.

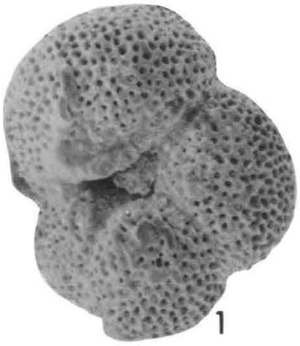
10–12 **Globoquadrina** sp. 2

CPC 18385, sample 7697–2010; 13, ventral view; 14, dorsal view; 15, side view; all x150.

13–15 **Globoquadrina** sp. 1

CPC 18384, sample 7697–2011; 10, ventral view; 11, dorsal view; 12, side view; all x200.

PLATE 4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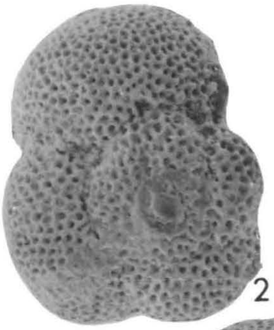
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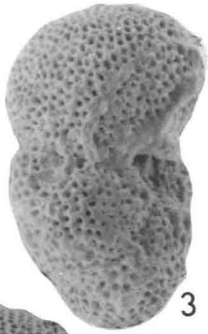
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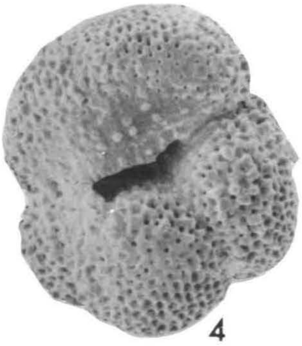
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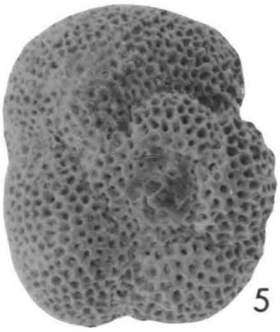
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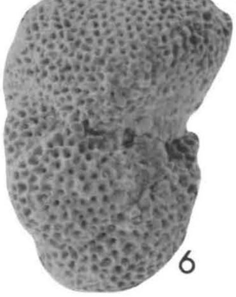
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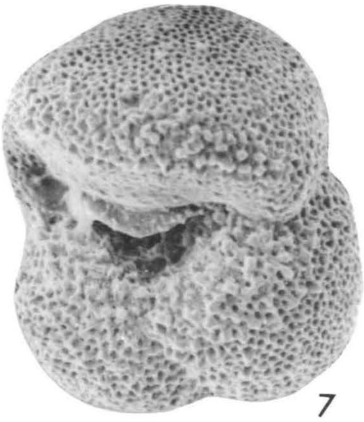
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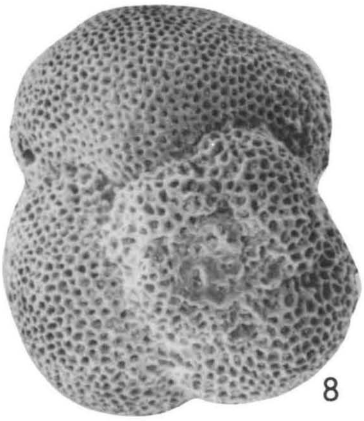
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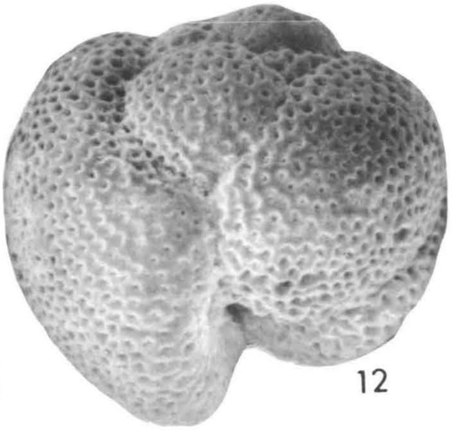
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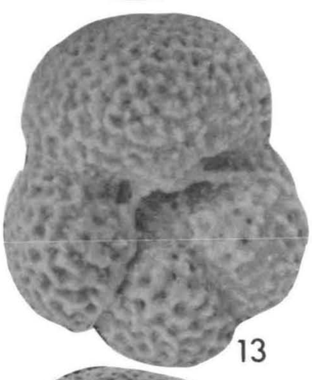
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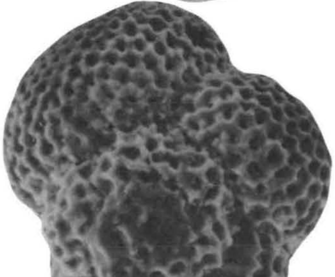
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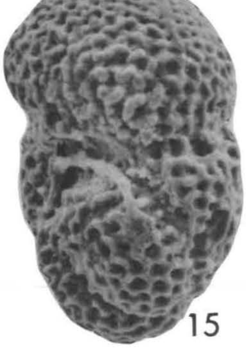
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PLATE 5

Figs.

1–6 **Globorotalia (Fohsella) peripheroacuta** Blow & Banner
1–3, CPC 18386, sample 7697–2011; 1, ventral view; 2, dorsal view; 3, side view; all x100.
4–6, CPC 18387, sample 7697–2010; 4, ventral view; 5, dorsal view; 6, side view; all x100.

7–9 **Globorotalia (Hirsutella) scitula scitula** (Brady)
CPC 18388, sample 7697–2011; 7, ventral view; 8, dorsal view; 9, side view; all x150.

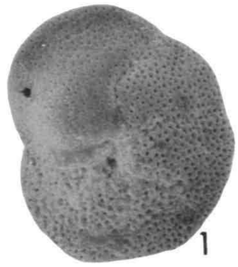
10–12 **Globorotalia (Turborotalia) mayeri** Cushman & Ellisor
CPC 18398, sample 7697–2011; 10, ventral view; 11, dorsal view; 12, side view; all x100.

13, 14 **Globorotalia (T.) obesa** Bolli
CPC 18390, sample 7697–2011; 13, ventral view; 14, side view; both x100

15–17 **Globorotalia (T.)** sp. 1
CPC 18391, sample 7697–2011; 15. ventral view; 16, dorsal view; 17, side view; all x150.

18–20 **Globorotaloides suteri** Bolli
CPC 18392, sample 7697–2010; 18, ventral view; 19, dorsal view; 20, side view; all x200.

PLATE 5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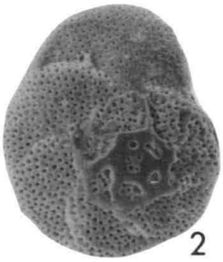
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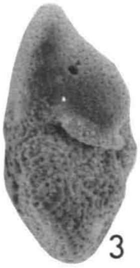
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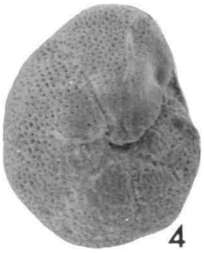
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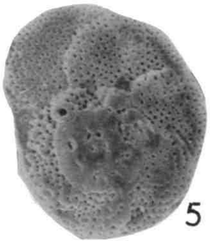
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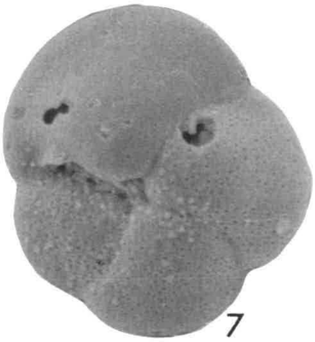
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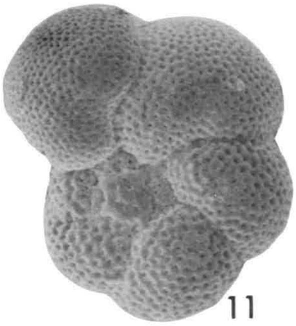
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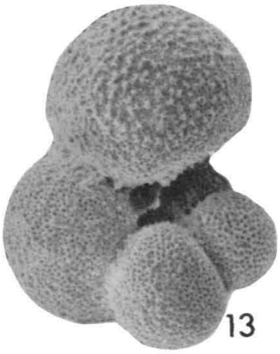
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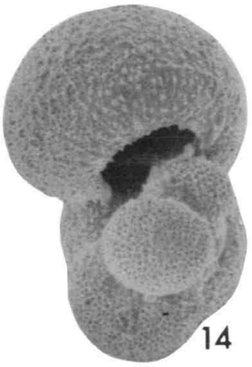
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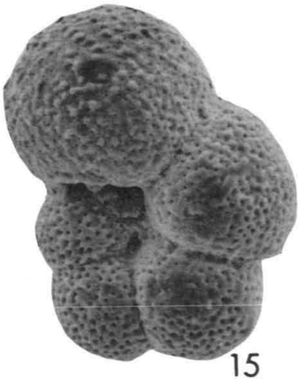
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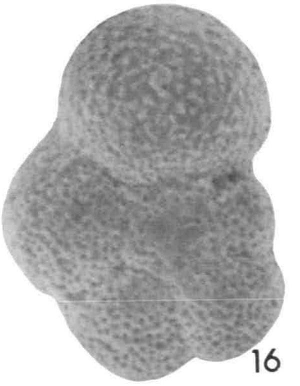
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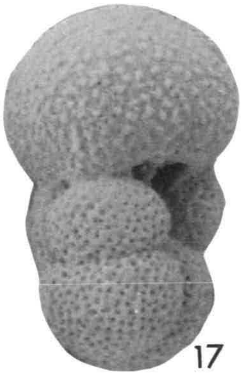
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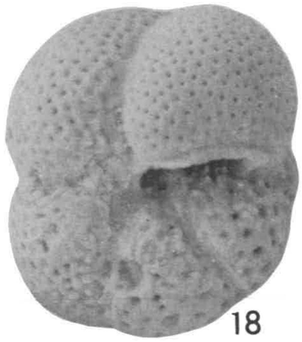
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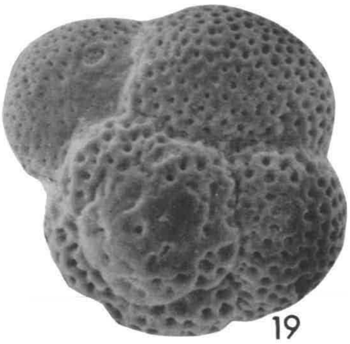
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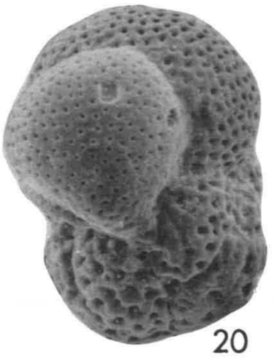
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PLATE 6

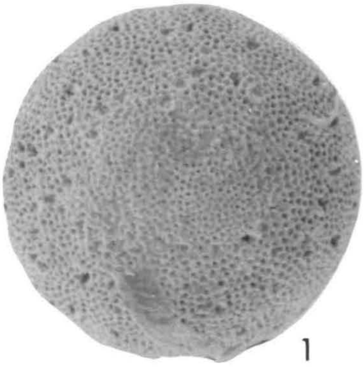
Figs.

1 **Orbulina suturalis** Brönnimann
CPC 18393, sample 7697–2011; x100.

2–8 **Tenuitella clemenciae** (Bermudez)
2–4, CPC 18394, sample 7697–2011; 2, ventral view; 3, dorsal view; 4, side view; all x150.
5–7, CPC 18395, same sample; 5, ventral view; 6, dorsal view; 7, side view; all x150.
8, CPC 18396, same sample; ventral view; x150.

9–16 **Lepidocyclina (Nephrolepidina) howchini howchini** Chapman & Crespin.
Equatorial sections.
9, CPC 18397, sample 7697–2010, category 2
10, CPC 18398, same sample, category 2
11, CPC 18399, same sample, category 2
12, CPC 18400, same sample, category 3
13, CPC 18401, same sample, category 3
14, CPC 18402, same sample, category 3
15, CPC 18403, same sample, category 4
16, CPC 18404, same sample, category 4
all x30.

PLATE 6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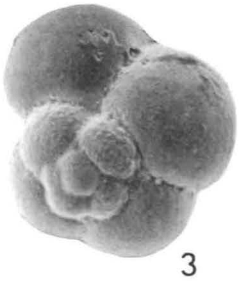
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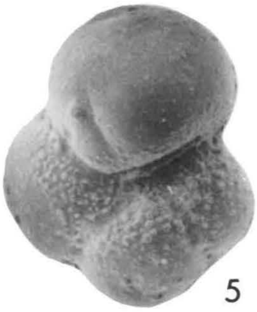
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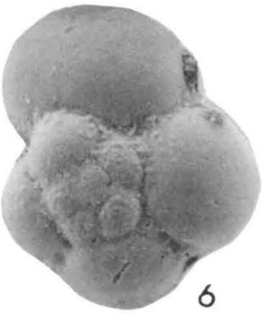
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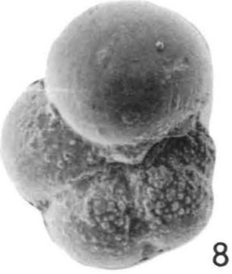
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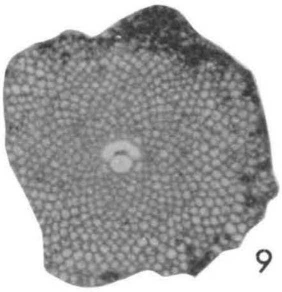
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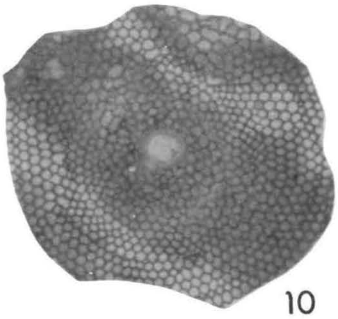
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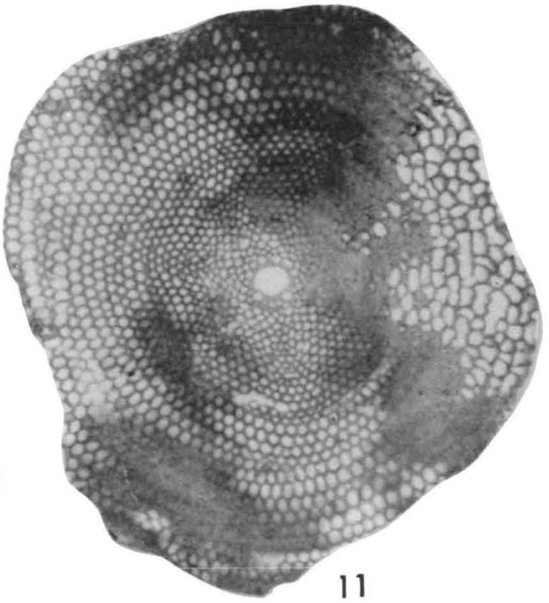
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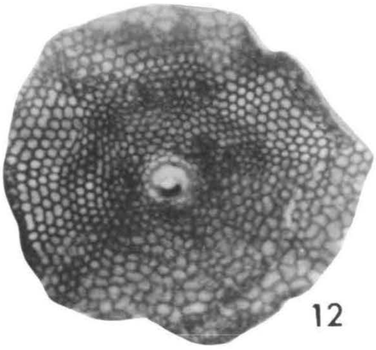
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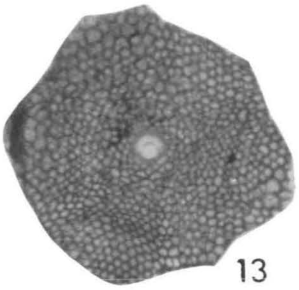
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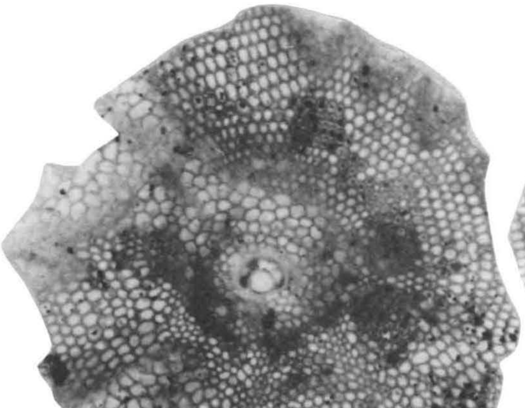
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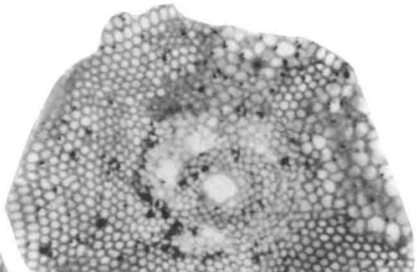
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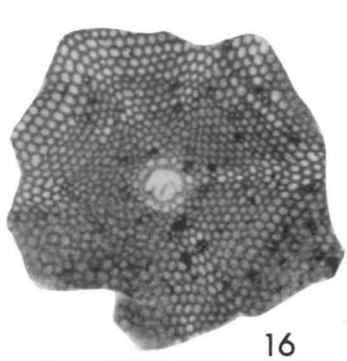
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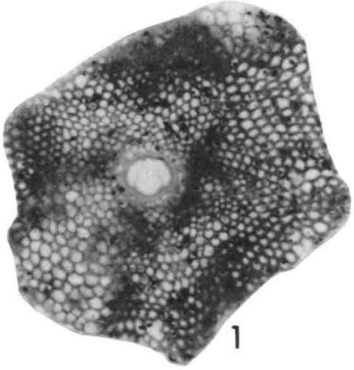
PLATE 7

1–17 **Lepidocyclina (Nephrolepidina) howchini howchini** Chapman & Crespin
1, equatorial section, CPC 18405, sample 7697–2010, category 4; x30.
2–4, vertical sections
2, CPC 18406, sample 7697–2010
3, CPC 18407, same sample
4, CPC 18408, same sample; all x30.
5–17, details of embryoconch, showing degree of embracing of protoconch by deuteroconch, all from sample 7697–2010; all x110.
5, CPC 18397 (see Pl. 6, fig. 9)
6–10, CPC 18409–18413
11, CPC 18400 (see Plate 6, fig. 12)
12, CPC 18414
13, CPC 18405 (see Pl. 7, fig. 1)
14, CPC 18415
15, CPC 18401 (see Pl. 6, fig. 13)
16, 17, CPC 18416, 18417

18, 19 **Miogypsina (M.) thecidaeformis** (Rutten) group
CPC 18418, sample 7697–2010
18, x30; 19, x110.

PLATE 7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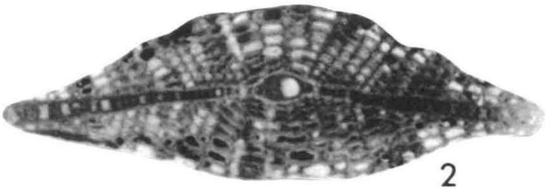
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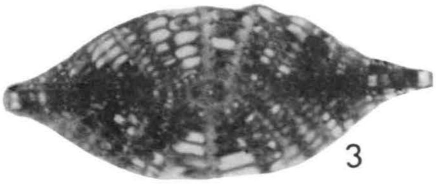
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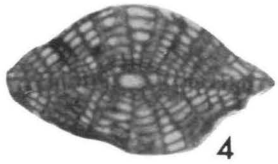
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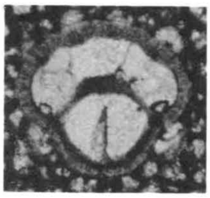
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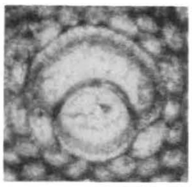
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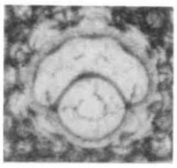
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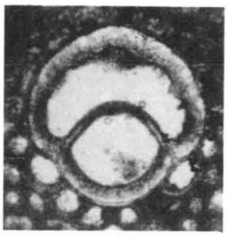
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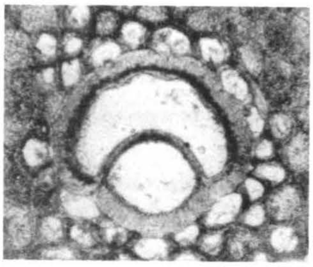
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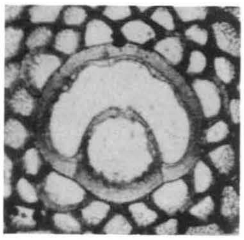
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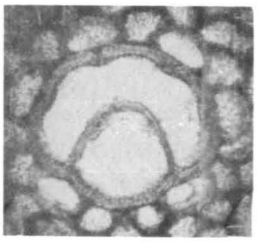
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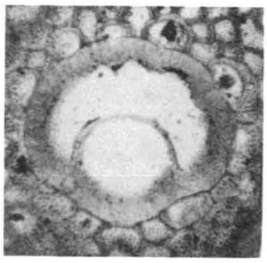
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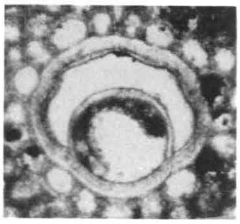
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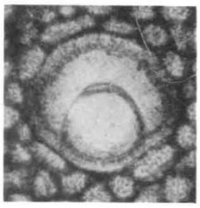
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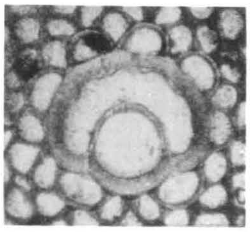
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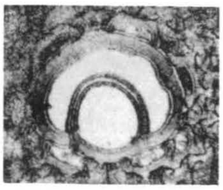
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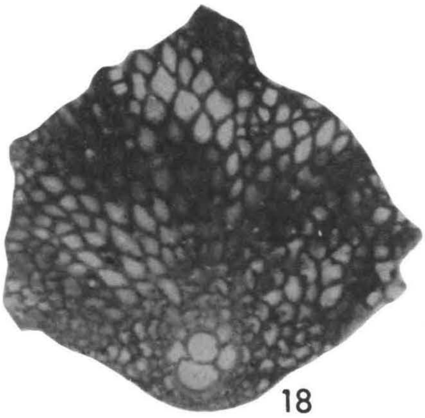
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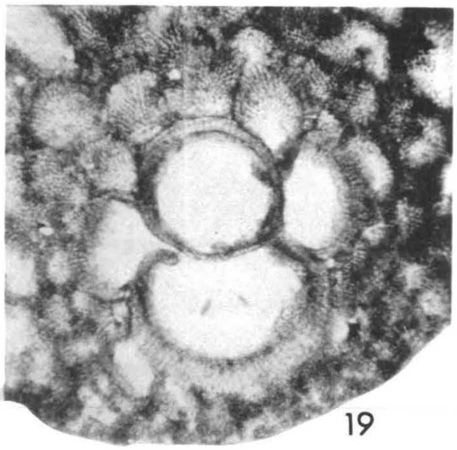
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A Permian invertebrate fauna from the Warwick area, Queensland

BY

J. M. DICKINS

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ABSTRACT

A fauna of Permian marine invertebrates comprising 18 species of pelecypods, gastropods, and brachiopods from 13 genera is described from the Eight Mile and Tunnel Blocks, south of Warwick, Queensland. One new name *Myonia olgersi* sp. nov. is introduced. It is concluded that right valves of *Aviculopecten planoradiatus* McCoy, 1851, the type species, have been placed in *Aviculopecten tabulatus* McCoy, 1844, and this affects the understanding of the characters of the genus. Specimens of *Stutchburia farleyensis* Etheridge Jnr, 1900, are figured. No information has been added on this species since its original description. Type speciments of *Peruvispira elegans* (Fletcher) 1958 are figured and the type designated. The fauna is regarded as equivalent in age to Fauna IIIA of the Bowen Basin, the fauna of the Ulladulla Mudstone of the southern part of the Sydney Basin, and the *Fenestella* Zone of the Hunter Valley of the northern part of the Sydney Basin. The fauna is therefore of early Baigendzhinian age. i.e. mid-Artinskian of the Russian standard sequence, Leonardian of the United States. The ranges of some of the species are found to differ from those found in the Sydney and Bowen Basins (the fauna is situated in a geographically intermediate position between the two) and this is attributed mainly to differences in water temperature.

INTRODUCTION

The Permian fauna from the Eight Mile and Tunnel Blocks south of Warwick, Queensland, was identified according to localities by Dickins *in* Olgers, Flood & Robertson (1974), where the geology is discussed. That report concluded that the fauna represents a limited time span and for correlation can be regarded as a single fauna. The fauna was regarded as younger than Fauna II of Dickins (see Dickins & Malone, 1973) and older than Fauna IIIB of the Bowen Basin and closely equivalent in age to the fauna of the Ulladulla Mudstone and the *Fenestella* Zone of the Sydney Basin and Fauna IIIA of the Bowen Basin. Differences between the ranges of some of the species in the Sydney Basin, the Warwick area, and the Bowen Basin were regarded as indicating differences in water temperature. This fauna is described here, and the correlation and the differences in water temperature are discussed further.

CORRELATION

The following fauna is described:

Pelecypods
- *Vacunella* cf. *etheridgei* (de Koninck) 1876
- *Myonia* cf. *corrugata* (Fletcher) 1932
- *Myonia olgersi* sp. nov.
- *Merismopteria* cf. *imbricata* (Dana) 1847
- *Etheripecten tenuicollis* (Dana) 1847
- *Etheripecten fittoni* (Morris) 1845
- **Deltopecten limaeformis* (Morris) 1845
- *Deltopecten multicostatus* (Fletcher) 1929
- **Astartella* cf. *obliqua* Dickins 1963
- **Stutchburia randsi* (Etheridge Jnr) 1892

Gastropods
- *Keeneia?* sp.
- *Peruvispira* sp.
- *Platyteichum* sp.

Brachiopods
- *Terrakea* cf. *dickinsi* Dear 1971
- **Echinalosia preovalis* (Maxwell) 1954
- *Martiniopsis (Ambikella) ingelarensis* (Campbell) 1960
- *Notospirifer extensus tweedalei* Campbell 1961
- *Neospirifer* sp.

* Species characteristic of Fauna II of Bowen Basin.

Of the eighteen species, four do not provide information on the age, including the one species given a new name. The four forms marked above with an asterisk are conspecific with, or closely related to, species not found in beds younger than Fauna II in the Bowen Basin. Two of the species, however, apparently appear in beds close to the base of Fauna III—*Terrakea* cf. *dickinsi* and *Martiniopsis (Ambikella) ingelarensis*. In the fauna, however, *Vacunella* cf. *etheridgei*, *Myonia* cf. *corrugata* and *Platyteichum* are younger than Fauna II. *V.* cf. *etheridgei* and *M. corrugata* are confined to Fauna III. *Platyteichum* is not known in the Bowen Basin below Fauna III and the forms of *Martiniopsis (Ambikella) ingelarensis* are more advanced than those known from Fauna II. The specimens of *Notospirifer extensus tweedalei* are closest to those from the type locality, which is referable probably to Fauna IIIA rather than Fauna II.

The absence from this fauna of species characteristic of Faunas IIIB and IIIC, the presence of *M. (A.). ingelarensis* and *N. extensus tweedalei*, and the overall composition of the fauna suggest a correlation with Fauna IIIA of the Bowen Basin. This conclusion is strengthened by a comparison with the fauna of the Sydney Basin. The fauna of the Ulladulla Mudstone of the southern part of the Sydney Basin (Dickins, Gostin & Runnegar, 1969) has similar features to that of the Eight Mile and Tunnel Blocks. In addition to species rcorded from Fauna II of the Bowen Basin, the Ulladulla Mudstone contains species suggestive of a younger age—in particular *M. corrugata* and *Martiniopsis (Ambikella)* with more advanced characters than those found in Fauna II. It shares in common with the Eight Mile and Tunnel Blocks the occurrence of *Deltopecten limaeformis* and *Deltopecten multicostatus*. In the Bowen Basin *Deltopecten* is not known in Fauna III. The Ulladulla Mudstone has been correlated with the *Fenestella* Zone of the Branxton Formation of the Hunter Valley Sequence by Dickins, Gostin & Runnegar (1969) and further evidence for this is afforded by the fauna of the Eight Mile and Tunnel Blocks, where similar forms of *Echinolosia* and *Martiniopsis (Ambikella)* are found.

It is concluded, therefore. that the fauna of the Eight Mile and Tunnel Blocks is equivalent in age to Fauna IIIA of the Bowen Basin, the Ulladulla Mudstone, and the *Fenestella* Zone of the Branxton Formation. This appears to be in general agreement with the correlations of McClung (1978, p. 38) and presumably the fauna from the Eight Mile and Tunnel Block is equivalent to the upper part of the *brevis* zone of McClung.

It corresponds, apparently also, to Faunizone 6 of Clarke & Banks (1975, p. 462).

Faunal Range and Water Temperature

On the basis of the correlation considered above, the differences in ranges of some of the species in New South Wales and Queensland become apparent. Dickins, Gostin & Runnegar (1969) indicated that in the southern part of the Sydney Basin some species, which in the Bowen Basin were confined to Fauna II, had longer ranges and extended into the part of the sequence which in age was equivalent to Fauna III. The same feature has already been indicated for the fauna of the Eight Mile and Tunnel Blocks (Dickins *in* Olgers, Flood & Robertson, 1974). Some of the species with longer ranges are adapted to cold water, therefore indicating that water was colder in the Sydney Basin than at the same time in the Bowen Basin. This has also been discussed elsewhere (Dickins, 1968; Dickins, 1978a). The fauna in the Eight Mile and Tunnel Blocks is apparently intermediate in character. The cold-water forms *D. limaeformis* and *D. multicostatus* are found in Fauna IIIA equivalent, as in the Sydney Basin, whereas *V.* cf. *etheridgei* and *Platyteichum* of Fauna III of the Bowen Basin are present in the Eight Mile and Tunnel Blocks but are not known from the Sydney Basin. Both *Eurydesma* and the gastropod *Keeneia* may be present in the Eight Mile and Tunnel Blocks, which could add further information on the question, but the specimens possibly referable to these genera are fragmentary.

Information on the present north-south water temperature trend can also be obtained from recent work in Tasmania (Clarke & Banks, 1975). In Tasmania, cold-water genera and species range through the whole marine sequence, indicating that conditions colder than in New South Wales persisted in Tasmania throughout the sequence.

Class Pelecypoda

Superfamily Pholadomyacea (= Grammysiacea)

Family Megadesmidae

The classification of Upper Palaeozoic burrowing genera has undergone considerable change in the last decade, accompanying a rapid development in the understanding of this group. Runnegar (1974) has reviewed the classification. He uses the superfamily Pholadomyacea in essentially the same sense as the use of Grammysiacea by Dickins (1963), considering Pholadomyacea has priority. Astafieva-Urbaitis (1973) has considered the characters and position of the family Megadesmidae and has proposed that the Megadesmidae and the Edmondiidae should be grouped together in the superfamily Edmondiacea as distinct from the Pholadomyacea. Agreement is general on the close relationship of the Edmondiidae and the Megadesmidae (Dickins, 1963; Waterhouse, 1969a; Astafieva-Urbaitis, 1973; Runnegar & Newell, 1974; Runnegar, 1974). On the basis of the information provided by Runnegar & Newell (1974), that the posterior thickening of the inner part of the hinge plate of *Edmondia* has a role in supporting the viscera and does not indicate an important difference in the ligament structure, possibly it is not necessary to recognise a separate superfamily, the Edmondiacea. Recent examination by N. J. Morris and the author of Lower Carboniferous faunas at the British Museum (Natural History) London confirms that close relationship of *Edmondia, Cardiomorpha,* and *Scaldia* with the Pholadomyacea. The internal thickening (plate) does not seem to be of significance in the ligament structure, which is a similar type to megadesmid forms. The ligament in *Edmondia* is lodged in a narrow groove behind the umbo. The nymph is slender, and this together with the internal thickening can be used to distinguish the Edmondiidae from the Megadesmidae.

Astafieva-Urbaitis (1973) has argued for the separation of *Myonia* and *Vacunella* from the Megadesmidae into another family, the Vacunellidae. She considers that *Vacunella* was derived from *Myonia.* Runnegar (1967, 1974) also concludes that *Vacunella* is derived from *Myonia.* That *Vacunella* was derived from the Megadesmidae by progressive adaptation to deeper burrowing can be accepted, and therefore it would be consistent to place the Megadesmidae (together with the Edmondiidae) and the Vacunellidae in a single superfamily, the Pholadomyacea. Certainly *Myonia* and *Vacunella* represent a separate group, but I would prefer to recognise the grouping at the subfamily level to indicate relationship within the Megadesmidae.

Subfamily Vacunellinae Astafieva-Urbaitis 1973

Genus **Vacunella** Waterhouse 1965

Type species: Allorisma curvatum Morris 1845, p. 270, pl. 10, fig. 1, by original designation of Waterhouse 1965, p. 377

Vacunella cf. **etheridgei** (de Koninck) 1876

Pl. 1, fig. 1

Type specimens: Runnegar (1967, p. 67) indicates that the syntypes are destroyed. He refrained from choosing a lectotype, as specimens from the type locality are not available. Until a lectotype is chosen the characters of this species are subject to review.

Discussion: The figured specimen is longer than any described by Runnegar (1967). It resembles the specimens from the Gebbie Subgroup of the Bowen Basin (including the Ingelara Formation) in its overall shape and particularly in the distinct sulcus running from the umbo to the ventral margin and in the thickening of the shell along the posterior umbonal ridge.

Dimenions (mm):	Height	Length	Max. width
CPC 20146	74	149 approx.	30

Occurrence: Locality TH 198

Genus **Myonia** Dana 1847

Type species: Myonia elongata Dana 1847, p. 158, by subsequent designation of Fletcher 1932, p. 398

Synonym: Maeonia Dana, 1848, variant spelling of *Myonia*

Myonia cf. **corrugata** Fletcher 1932,

p. 404, pl. 1, figs. 3, 4

Pl. 1, figs. 2, 3

Description: Shells are large with a very distinct posterior carina and the umbo turned towards the front. The external ornament is composed of prominent concentric rugae. A shallow sulcus runs down from the umbo to the ventral margin in front of the carina. The anterior part of the pallial line is shown with a distinct oval anterior adductor muscle. The impressions of three pedal sets of muscles are visible; the first is slightly above the anterior adductor and possibly joined to it and represents the pedal protractor of Runnegar (1967); the second is slightly higher on the umbonal ridge, and separate, and represents the anterior retractor; the third, the umbonal retractor, is suitated on the anterior side of the umbo.

Discussion: It is not possible to fully reconstruct the original shape of the shell, but in shape and internal ornament it appears to be close to *Myonia corrugata* Fletcher. Apparently it is the same as the form from the Gebbie Subgroup (Fauna IIIA) of the Bowen Basin referred to by Runnegar (1967, p. 55, pl. 4, figs. 6, 7) as *Myonia* sp. nov.? and earlier referred to by me as *Pachymyonia* sp. nov.

The type and closely related specimens of *Myonia corrugata* are found in the Ulladulla Mudstone and the equivalent Wandrawandrian Siltstone of the southern part of the Sydney Basin. Runnegar (1967, p. 57) also records as belonging to the species, specimens from the Branxton Subgroup of the northern part of the basin. The specimens from Fauna IV which have been referred by Dickins (1964; 1966) as *Myonia* cf. *corrugata* Fletcher 1932 and which Runnegar (1967) has referred to *Myonia corrugata* should be separated specifically and require a new name. This species from Fauna IV is distinguished by the very strong inflection of the umbo towards the front and the thickening of the anterior part of the shell. The shells are thicker and the overall shape is accordingly different. The specimen from Member E Malbina Formation, Kangaroo Bay, Cygnet Peninsula, southeast Tasmania (Runnegar, 1967, pl. 6, fig. 2) also belongs to the new species.

Myonia corrugata therefore seems to be found in Fauna III, whereas another younger species, yet to be named, occurs in Fauna IV in Tasmania and in the Bowen Basin, Queensland.

Dimensions:	Height	Width
CPC 20147 (possibly crushed)	80	44
CPC 20148 (external)	95+	32

Occurrence: Locality TH 198

Myonia olgersi sp. nov.

Pl. 1, figs. 4-11

Diagnosis: Moderately elongate, upturned slightly towards the back of the shell, development of carina variable, slight gape at the rear.

Description: The holotype is partly an internal impression which nevertheless shows the external concentric ornament. Apparently there is a slight gape at the rear. A distinct carina is perhaps amplified by compaction or crushing, but seems to be an original feature. The musculature is poorly preserved, but apparently the anterior adductor is oval and the posterior adductor circular and situated largely behind the carina.

The other specimens show variation of the carina from rounded to moderately sharp as in the holotype. The shape shows considerable variation which is partly caused by crushing.

Dimensions:	Length	Height	Thickness
Holotype, CPC 20149	110+	66	29
Paratype A, CPC 20150	78	48	20
Paratype B, CPC 20151	82+	56	15
Paratype C, CPC 20152	93+	56+	27
Paratype D, CPC 20153	62	40	20

Occurrence: Holotype and paratypes A-D, Locality TH 198; other specimens, TH 171, 202.

Discussion: The specimen appears distinct from any already described. It is similar in shape to species of *Australomya* Runnegar (1969, p. 285) but because of the carina is referred to *Myonia.*

The species is named after F. Olgers, formerly of BMR, who together with P. G. Flood carried out the geological field work during which the fossils now described were collected.

Superfamily *PTERIACEA* Gray 1847
Family PTERINEIDAE Miller 1877
Genus **Merismopteria** Etheridge Jnr 1892

Type species: Pterinea macroptera Morris 1845, p. 276, pl. 13, fig. 3, (by original designation of Etheridge Jnr, 1892, p. 211)

Discussion: Although *Merismopteria* may be present in some localities in large numbers, only a few, poorly differentiated species have been described.

The genus has been discussed by Dickins (1960). Although the internal characters of *Leiopteria* remain obscure, it seems that *Merismopteria* can be separated by its more laterally elongated shape, its imbricate external shell surface, and its rounded anterior margin without a strong indentation (sinus).

The nature of the anterior musculature and the anterior 'clavicle' (buttress) continue to present difficulties. A left valve, TMF 442011, forwarded by M. J. Clarke from Flowerpot Point, South Blackmans Bay, near Kingston, Tasmania, about 40 m below the top of the Ferntree Mudstone Faunizone 10 (Clarke & Banks, 1975) shows some additional details (Pl. 2, fig. 16; Text-fig. 1). Two positions of the pallial line are possible. The first is that the pallial line may be represented by the distinct line on the flattened anterior ear, running to the front of the 'clavicle' to the base of the assumed anterior adductor muscle; an alternative explanation of this line is that it represents the extent of the internal nacreous layer. The second possible position of the pallial line is represented by the line of more or less well developed elongate pits along the anterior rounded umbonal ridge behind the anterior ear and running apparently to the base of the large rounded muscle behind the 'clavicle'.

If this rounded muscle represented the anterior adductor muscle the reason for the 'clavicle' or buttress and the muscular-like area in front of the 'clavicle' forming a hollow in the shell would be difficult to explain. The large rounded muscle behind the 'clavicle' would seem consistent with the presence of a strong byssus which would be required to anchor a shell of this size.

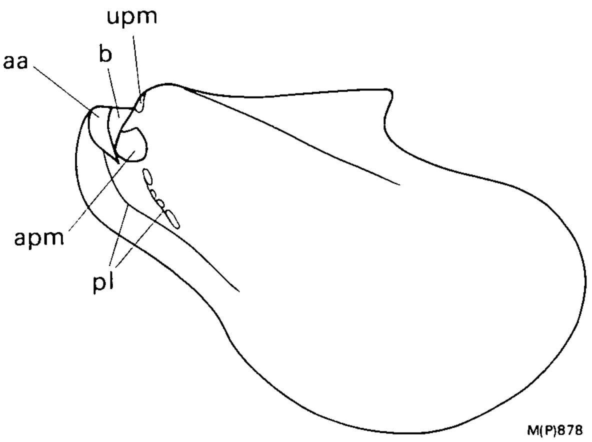

Fig. 1. Merismopteria sp., TMF442011 from Flowerpot Point, South Blackmans Bay near Kingston, Tasmania, showing internal structure of a left valve: aa, anterior adductor muscle?; apm, anterior pedal muscle?; upm, umbonal pedal muscle; b, 'clavicle' or buttress ridge; pl, alternative positions of pallial line.

Merismopteria cf. **imbricata** (Dana) 1847, p. 109; 1849, p. 702, pl. 8, fig. 5

Pl. 2, figs. 14, 15

Description: Shell rather elongate and moderately thick—these features, however, have probably been accentuated by squashing. Anterior buttress or 'clavicle' well preserved with muscle impressions apparently in front and behind the buttress.

Dimensions (mm):	Length	Height	Thickness
CPC 20154	39	23	8
CPC 20155	42	32	4

Occurrence: Locality TH 198

Superfamily Pectinacea Rafinesque 1815

Family Aviculopectinidae Etheridge Jnr

Subfamily Aviculopectiniae Meek & Hayden

Genus **Etheripecten** Waterhouse 1963

Type species: Etheripecten striatura Waterhouse 1963, p. 195, figs. 1-5 by original designation of Waterhouse, 1963, p. 193

Discussion and characters of *Aviculopecten:* Waterhouse (1969b) re-examined and figured the type specimens of *Aviculopecten planoradiatus* McCoy (1851, p. 171), the type species of *Aviculopecten.* He recorded the growth lamellae on the left valve as swinging ventrally on the interspaces between the costae, not dorsally as stated by Newell (1938). My examination of these specimens at the Sedgwick Museum, Cambridge confirms the variations in this feature described by Waterhouse—in some places the growth lines are relatively straight as in the specimens in the Sedgewick Museum identified as *Aviculopecten interstitialis* (Phillips) 1836, in other places they swing ventrally, and in others again dorsally. I agree with Waterhouse's conclusion, therefore, that *Aviculopecten* is related to *Limipecten* and that *Etheripecten* should be regarded as a separate genus.

The right valve of *A. planoradiatus,* important for generic comparison, has never been definitely identified, which is rather puzzling as substantial collections of left valves are held in the British Museum (Natural History), London, in the Sedgwick Museum, Cambridge, and in the Institute of Geological Sciences, Leeds. In these collections, however, right and left valves are held under the name *Aviculopecten tabulatus* McCoy, 1844. The left valves do not seem to differ in any important way from those of *A. planoradiatus.* Some of the right valves show a chondrophore. The ribbing is of a single order—the manner of rib subdivision is not clear in the specimens I have examined.

It is interesting that Hind (1903, p. 67) regarded *A. planoradiatus* as a synonym of *A. tabulatus.* I am grateful to Dr W. H. C. Ramsbottom for discussion of his work on this matter. The specimen of *A. tabulatus* figured by Hind (pl. 12, fig. 1) as the type of *A. tabulatus,* which is held at Leeds, does not appear to be McCoy's figured specimen. Unfortunately McCoy's collection in Dublin is apparently lost or unavailable for examination, but his figure of *A. tabulatus* (1844, pl. 16, fig. 12) shows little resemblance to the British specimens included under the name *A. tabulatus.*

It seems likely, therefore, that right valves of *A. planoradiatus* are being held under the name *A. tabulatus.*

Etheripecten tenuicollis (Dana) 1847 p. 160; 1848 p. 705, pl. 9, figs. 7-7a

Pl. 2, figs. 12, 13

Discussion: The relationship between *E. tenuicollis* (Dana) 1847 and *E. subquinquelineatus* is discussed by Dickins (1957, pp. 45, 46). Most of the present specimens show relatively simple ribbing and therefore can be referred to *E. tenuicollis.* The material from TH 201 and TH 203, however, has been compared to *E. subquinquelineatus* which is larger and has more complicated ribbing.

Dimensions (mm):	Length	Height	Thickness
CPC 20156	34	ca 28	5
CPC 20157	42	38	8

Occurrence: CPC 20156, 7—Locality TH 198; other specimens TH 202, TH 411.

Etheripecten fittoni (Morris) 1845, p. 277, pl. 14, fig. 2

Pl. 2, fig. 17

Discussion: Specimens referred to *E. fittoni* have a very distinctive rib pattern which is shown in the specimen CPC 20170, figured here (Pl. 2, fig. 17). In outline the ribs form a wave-like pattern and are covered by fine parallel riblets. The furrows contain a single distinct rib. In the Sydney Basin the species has been recorded only from the lower part of the Permian sequence (apparently no higher than the Snapper Point Formation) and in the Bowen Basin only from Fauna II. In the Eight-Mile Block it occurs with a fauna here regarded as Fauna IIIA. In Tasmania *E. fittoni* has an even longer range. It appears in Fauna II and persists apparently into the lower part of Fauna IV (Clarke & Banks, 1975). Apparently *E. fittoni* is adapted to colder water and its range reflects the persistence of cold water conditions.

Family Deltopectinidae Dickins 1957

Genus **Deltopecten Etheridge** Jnr 1892

Type species: Pecten illawarensis Morris 1845, p. 277, pl. 14, fig. 3, by original designation of Etheridge Jnr 1892, p. 269

Deltopecten limaeformis (Morris) 1845, p. 277, pl. 13, fig. 1

Holotype: Morris figured two shells which make up a bivalved specimen held at the British Museum (Natural History) London, No. PL 3886. This specimen, the locality of which Morris gave as Eastern Marches, Van Diemen's Land (i.e. Tasmania), is, therefore, the holotype.

Discussion: Although only two shells occur in the material, their assignment to *D. limaeformis* seems clear. The primary ribs are regularly rounded and with some intervening secondary ribs. The left valve (CPC 20172) has more than 30 ribs and the right valve (CPC 20171) more than 28. These characters fit within the range of *D. limaeformis.*

Occurrence: Locality TH 411

Deltopecten multicostatus (Fletcher) 1929, p. 8, pl. 2, figs. 1-3

Pl. 2, fig. 11

Holotype: Australian Museum specimen F 19097, St Georges Basin, New South Wales, by original designation of Fletcher, 1929, p. 9.

Paratypes: Australian Museum specimens F 19513 and F 19377 from Kangaroo Point, St Georges Basin, New South Wales (Fletcher, 1929, pl. 2, figs. 2, 3).

Discussion: A single fragmentary specimen (CPC 20173) seems to belong to *D. multicostatus.* The ribbing corresponds to what might be expected in the outer part of a large valve, but the determination is open to confirmation.

Occurrence: Locality TH 411

Family ASTARTIDAE d'Orbigny 1844

Genus **Astartella** Hall 1858

Type species: Astartella vera Hall 1858, p. 715, pl. 29, figs. 1a-e, by subsequent designation of Miller 1889—Fide Treatise on Invertebrate Paleontology

Astartella cf. **obliqua** Dickins 1963, p. 104, pl. 16, figs. 2-9

Pl. 2, figs. 1-4

Description: Specimens rather variable in size but characterised by the oblique appearance of the shell. External ornament of distinct growth lines with a slight tendency to form lamellae. The growth lines also tend to be denticulate. Anterior and posterior lateral teeth present and two cardinal teeth in the right valve. A slight lunule apparently present—none of the specimens preserve the details dorsally behind the umbo.

Dimensions (mm):	Length	Height	Width
CPC 20158, TH 411	16	12	2
CPC 20159, TH 199	ca 17	15	12*
CPC 20160, TH 411	8	8	2
CPC 20161, TH 198	7	9	2

*2 valves

Occurrence: Localities TH 171, 198, 199, 202, 406, 411

Discussion: The specimens from the Eight Mile and Tunnel Blocks seem related to *Astartella obliqua* from the Fossil Cliff and Callytharra Formations, the Nura Nura Member of the Poole Sandstone, and age equivalents in Western Australia. These specimens also seem to resemble those from Fauna II in the Bowen Basin (Hill & Woods, 1964, pl. P XII, fig. 8). All these are similar in their oblique shape and their ornament. Whether all these specimens represent a single species or a number of closely related species it not clear.

Superfamily CARDITACEA Fleming 1820

Family PERMOPHORIDAE Van der Poel 1959

Genus **Stutchburia** Etheridge Jnr 1900

Type species: Orthonota? costata Morris 1845, p. 273, pl. 11, fig. 1, by original designation.

Stutchburia randsi (Etheridge Jnr) 1892, p. 275 pl. 14, fig. 14

Pl. 3, figs. 12-16

Description: Subrectangular with a distinct posterior umbonal ridge. Several radial ribs running from the umbo towards the posterior ventral margin in the middle of the back part of the shell.

Dimensions (mm):	Length	Height	Thickness
CPC 20162, TH 411	48	18	3
CPC 20163, TH 411	26	14	2
CPC 20164, TH 198	42	21	5
CPC 20165, TH 411	ca 33	22	3

Occurrence: Localities TH 198, 411, 414

Discussion: The posterior radiating ribs are poorly developed on some specimens but they do appear to be present. Although *S. randsi* is poorly known (see Dickins 1963, p. 97, pl. 15, figs. 14, 15) the present specimens seem sufficiently close to be referred to the same species. On the other hand the specimens do not seem close to any other described species. A comparison has been made with *Stutchburia farleyensis* Etheridge Jnr (1900, p. 183, pl. 32, figs. 3–6) to which no information has been added from the time of Etheridge's original description. Additional specimens all from the Farley Formation at Farley are figured here (Pl. 3, figs. 1–11). *S. farleyensis* differs from the Warwick specimens and is characterised by considerable thickening of the width of the shell in the mid region along the posterior umbonal ridge. In front of this ridge is a distinct sulcus running down to the mid part of the dorsal margin. The shell is expanded more at the back than at the front. A few radiating posterior ribs are shown in some specimens.

Class GASTROPODA

Superfamily PLEUROTOMARIACEA Swainson 1840

Family SINUOPEIDAE Wenz 1938

Genus **Keeneia** Etheridge Jnr, 1902

Type species: Keeneia platyschismoides Etheridge Jnr 1902, p. 199, Plate 32; Plate 33, figures 3-5, by original designation of Etheridge Jnr 1902, p. 198

Discussion: A single fragment, CPC 20166, is part of an outer whorl (Pl. 2, fig. 9). The cross-section shows that almost certainly *Keeneia* is present. Assignment to a species is hardly possible.

Occurrence: Locality TH 411.

Family PLEUROTOMARIIDAE Swainson 1840

Genus **Peruvispira** Chronic 1949

Type species: Peruvispira delicata Chronic *in* Newell, Chronic & Roberts, 1949, p. 147; 1953, p. 139, pl. 28, figs. 9-12, by original designation

Discussion: The characters of this genus are discussed in Dickins (1961) where a close relationship with *Ptychomphalina* is suggested. Information justifying the separation of *Ptychomphalina* and *Mourlonia* is referred to in Dickins (1978b).

Peruvispira sp.

Pl. 2, figs. 7, 8; Pl. 3, figs. 17-21

Description: Spire moderately high; upper whorl surface flat or slightly concave and lower whorl surface rounded. Selenizone let down between the two bounding lirae. The third lira is visible only on one of the specimens in which the concave area below the selenizone is about twice as wide as the selenizone. The collabral (transverse) ornament is well developed. The shell has no umbilicus and a thin callus is present on the inner lip.

Dimensions (mm):	Height	Width	Apical angle
CPC 20167, TH 406	16	10	40°
CPC 20168, TH 198	12+	11	49°

Occurrence: Localities TH 198, 406

Discussion: The specific relationships of the specimens are not clear. They are apparently similar in age to *Peruvispira elegans* (Fletcher) (1958, p. 112, pl. 12, fig. 1). *P. elegans* seems to differ, however, in having a less angular cross-section and a narrower groove between the selenizone and the third (lowest) lira.

Specimens of *P. elegans* including those illustrated by Fletcher (1958, pl. 12, fig. 1) are figured here to allow a more satisfactory understanding of the species. Fletcher did not indicate which of the specimens on the piece of rock he figured was the holotype and the specimen refigured here (Pl. 3, figs. 20, 21) is now chosen as the lectotype. This specimen corresponds to the dimensions given by Fletcher. The only number mentioned by Fletcher, Australian Museum No. 46587, is on the reverse side of the piece of rock to that he figured, next to a specimen which does not correspond to the dimensions given by Fletcher. This specimen is also figured here (Pl. 3, fig. 18). It cannot be a valid holotype as it was not figured by Fletcher in his original description.

Genus **Platyteichum** Campbell 1953

Type species: Platyteichum costatum Campbell 1953, p.23, pl. 7, figs. 11-14, by original designation

Platyteichum sp.

Pl. 2, fig. 10

Discussion: A single rather poorly preserved specimen is attributed to *Platyteichum* because of its even triangular shape and poorly preserved revolving ornament. On shape the specimen appears to be close to *Platyteichum costatum* Campbell 1953 from the Lower Permian Ingelara Formation of the Bowen Basin.

Dimensions (mm):	Height	Width	Apical angle
CPC 20169	30	28 (approx)	77°

Occurrence: Locality TH 171

BRACHIOPODA

Superfamily PRODUCTACEA Gray 1840

Family LINOPRODUCTIDAE Stehli 1954

Genus **Terrakea** Booker 1930

Type species: Productus brachythaerus Morris 1845, p. 284, pl. 14, fig. 4c, by original designation of Booker, 1930, p. 68 and subsequent opinion of International Commission on Zoological Nomenclature

Discussion: The problem of the recognition of the name *Terrakea* has been discussed by Dorothy Hill (1950, p. 18). Booker nominated *'Terrakea brachythaera* G. B. Sowerby, 1844 (sp.)' as type. Booker had not seen Sowerby's unfigured syntypes and interpreted *T. brachythaerus* from Morris (1845, pl. 14, fig. 4c). Dorothy Hill's examination showed that the only syntype of Sowerby remaining was a strophalosiid.

Dear (1971, p. 15) and Waterhouse (1964, p. 63) provide the information that the International Commission on Zoological Nomenclature has approved an application by Maxwell to nominate the specimen figured by Morris (pl. 14, fig. 4c) as lectotype, validating the name *Terrakea*. Dear clearly refers to fig. 4c and not fig. 40 as shown in his text.

Terrakea cf. **dickinsi** Dear 1971, p. 15, pl. 4, figs. 2-9

Pl. 4, figs. 6-10

Discussion: Only a few specimens are present. Their resemblance in shape and external character to *T. dickinsi* Dear 1971 seems apparent. The geniculation is similar, umbonal thickening is absent, and scars are similar.

Dimensions (mm):	Length	Width	Height
CPC 20174, TH 406	28	32	18
CPC 20175, TH 198	32	34	22

Occurrence: Localities TH 198, 201, 203, 406, 411

Superfamily STROPHALOSIACEA Muir-Wood & Cooper 1960

Family STROPHALOSIIDAE Schuchert 1913

Genus **Echinalosia** Waterhouse 1967

Types species: Strophalosia maxwelli Waterhouse 1964, p. 32, pl. 4, figs. 6-11, pl. 5, pl. 6, pl. 7, figs. 1-3, pl. 36, figs. 5, 6, by original deignation of Waterhouse, 1967, p. 167

Discussion: Wyndhamia Booker 1929 is distinguished from *Echinalosia* by its thickened brachial valve. Both have spines on the brachial and pedicle valves. This relationship has recently been discussed by Clarke (1970) who regards the thickening of the brachial valve as unsatisfactory for generic separation. The importance of the absence of spines from the brachial valve on which the separation of *Wyndhamia* (and *Echinalosia*) from other genera is based, may also be doubted, but for the present, *Echinalosia* is retained as a generic grouping separate from *Wyndhamia* and *Strophalosia.*

Echinalosia preovalis (Maxwell) 1954, p. 542, pl. 54, figs. 1-11

Pl. 4, figs. 1-5

Discussion: The specimens appear to fit in most respects within the limits of *E. preovalis.* The shape, dimensions, and musculature are similar to the specimens figured by Maxwell (1954). Earlier (Dickins *in* Olgers, Flood & Robertson, 1974, p. 99) I had considered that the muscle platform in the pedicle valve was higher than in *E. preovalis*, but re-examination of these specimens from the Bowen Basin suggests the Warwick specimens are not greatly different from *preovalis* (see Pl. 4, fig. 3).

Dimensions (mm):	Width	Length	Height
CPC 20176, TH 199	26	26	10
CPC 20178, TH 199	16	18	8
CPC 20179, TH 199	23	23	10
CPC 20180	20	20	9

Occurrence: Localities TH 199, 201, 203

Superfamily RETICULARIACEA Waagen 1883

Family MARTINIIDAE Waagen 1883

Genus **Martiniopsis** Waagen 1883

Subgenus **Ambikella** Sahni & Srivastava 1956

Type species: Ambikella fructiformis Sahni & Srivastava 1956, p. 207, pl. 35, figs. 6-10, by original designation

Synonym: Ingelarella Campbell 1959, p. 340

Discussion: Which generic name should be used for this group is not clear. Runnegar (1969, p. 293) and Waterhouse (1965, p. 160) considered that *Ingelarella* was a synonym of *Ambikella*. Waterhouse (1971, p. 68) however, considered that *Ambikella* (and *Ingelarella*) might be synonymous with *Tomiopsis* Benedictova 1956 which had priority. The name *Tomiopsis* was published on 10 April 1956, whereas *Ambikella* was published in an unspecified month of 1956, and therefore regarded as December 1956 (Waterhouse, 1971, p. 69). Pitrat (1965, p. H718) apparently accepts the separation of *Ambikella* from *Ingelarella* (and *Tomiopsis*) because it has a fold in the pedicle valve and a sulcus in the brachial valve. Waterhouse (1965, p. 160), however, indicates that the fold and sulcus were reversed in the original description, and this is confirmed by my examination of Sahni and Srivastava's collection at the Geological Survey of India in Calcutta.

Ambikella possibly differs from *Tomiopsis*, the type species which is of Lower Carboniferous age, in the median septum of the brachial valves and in the micro ornament. The name *Martiniopsis* Waagen 1883 has been used for *Ambikella* by Runnegar & McClung (1975) and Clarke & Banks (1975). The type species of *Martiniopsis*, however, lacks a sulcus and a fold (see Browne, 1953) and differs considerably from the forms with a distinct sulcus and fold for which the name *Ambikella* (and *Ingelarella*) was proposed. McClung (1978, p. 40) has reservations about the relationship between *Ambikella* and *Ingelarella* and retains the generic name *Ingelarella*. My examination, however, of the Indian type material of *Ambikella* convinces me that *Ingelarella* is a synonym of *Ambikella*. I propose, therefore, to retain the name *Ambikella* but at the subgeneric level to indicate, on one hand, differences with *Martiniopsis (Martiniopsis)* and, on the other hand, the close relationships between the two groups of forms.

Martiniopsis (Ambikella) ingelarensis (Campbell) 1960

Pl. 4, figs. 20-24; Pl. 5, figs. 1-17

?1924 *Martiniopsis subradiata* (Sowerby) Richards & Bryan pl. 19, fig. 4

Discussion: The present collection contains numerous specimens, and a large collection has been examined at the Geology Department at the University of Queensland, St Lucia, Brisbane. The specimens show a wide variation without any sharp division lines and either a number of species must be recognised with vague and gradational limits or the whole collection can be referred to a single variable species.

Pedicle valve: specimens vary from those showing a broad shallow sinus to those showing a moderately deep V-shaped sinus. Plication seems to be absent in some specimens but in others several moderately well but not strongly developed plicae are present. The umbo also varies in sharpness.

Brachial valves: Shape and plication correspond to those described for pedicle valves. The adminicula are of moderate length and vary from straight to moderately curved. The commissure of some specimens is uniplicate whereas in others it appears slightly parasulcate. Some specimens show a shallow sulcus in the fold.

Conclusions: The specimens could be referred to *Ambikella plana* (Campbell, 1960, p. 1112, pl. 136, figs. 1–7), *A. ingelarensis* (Campbell, 1960, p. 1115, pl. 135, figs. 1–3; pl. 138, fig. 4) and *A. undulosa* (Campbell, 1961, p. 180, pl. 26, figs. 4–9). The specimens seem to vary around the features characteristic for *A. ingelarensis,* particularly in length of the adminicula, and it is proposed here to regard the variable plexus under a single species name *A. ingelarensis.*

Taking into consideration the length of the adminicula and the presence of specimens related to *A. ingelarensis* and *A. undulosa* it seems likely the species postdates the Sirius shale with *A. plana* and *A. plica* and antedates the Ingelara Formation with *A. ingelarensis* and *A. angulata.* It can most readily be related to localities referred in the Bowen Basin to Fauna III A.

Dimensions (mm):	Length	Width	Height
Pedicle valves			
CPC 20181, TH 198	39	60	21
CPC 20182, TH 198	49	ca 54	18
CPC 20183, TH 406	ca 35	44	14
CPC 20184, TH 406	34	38	12
CPC 20185, TH 198	40	58	14
Brachial valves			
CPC 20186, TH 198	33	ca 46	8
CPC 20187, TH 411	58	72	18
CPC 20188, TH 198	42	50	12
CPC 20188, TH 198	28	32	7
CPC 20190, TH 198	ca 30	ca 45	8

Occurrence: Localities TH 198, 406, 411

Genus **Notospirifer** Harrington 1955

Type species: Spirifer darwini Morris 1845, p. 279, by original designation. For further information and designation of lectotype see Campbell (1959, p. 342, pl. 56, figs. 1a-c).

Notospirifer extensus tweedalei Campbell 1961

Pl. 4, figs. 11-19

Description: The specimens are consistently small and on this basis may be referred to *N. extensus tweedalei* Campbell (1961, p. 188, pl. 28, figs. 5–8) rather than to *N. extensus* Campbell (1961, p. 187, pl. 28, figs. 1–4). The plicae are perhaps stronger than might be regarded as characteristic for *N. extensus* sensu stricto. Four plicae are present in the specimens in which they can be counted. The width of the sulcus and the strength of the plicae are somewhat variable and may reflect the influence of compaction. A faint groove is visible in one of the brachial folds (Pl. 4, fig. 13). The micro-ornament is poorly preserved.

Conclusions: The specimens seem closest to those from the type locality of *N. extensus tweedalei* in Oaky Creek near Homevale homestead. The fauna from this locality is probably referable to Fauna III A.

Apart from the size, the features used by Campbell (1961) in distinguishing *N. extensus* and *N. extensus tweedalei* are not readily discernible in these specimens.

Dimensions (mm):	Length	Width	Height
Pedicle valves			
CPC 20194, TH 198	ca 20	33	10
CPC 20195, TH 198	ca 25	32	12
CPC 20196, TH 198	12	ca 18	8
CPC 20198, TH 411	13	23	—
Brachial valves			
CPC 20191, TH 198	19	26	5
CPC 20192, TH 411	18	30	6
CPC 20193, TH 411	17	ca 25	6
CPC 20197, TH 411	14	26	8

Occurrence: Localities TH 198, 406, 411

Superfamily SPIRIFERACEA King 1846

Family SPIRIFERIDAE King 1846

Genus **Neospirifer** Fredericks 1924

Type species: Spirifer fasciger Keyserling, 1846, by monotypy, Fredericks, 1924

Discussion: The position of species to be referred to *Neospirifer* is very much an open question. The material from the Eight Mile Block is very limited, and a detailed discussion of the problem is not warranted here as the material throws no light on the matter.

Maxwell (1951, p. 14) has pointed out the difficulty in understanding the characters of *Neospirifer.* Keyserling figured three syntypes of *Spirifer fasciger* which could all be different. I am grateful to N. W. Archbold of the Department of Geology of the University of Melbourne for making part of his unpublished M.Sc. thesis on *Neospirifer* available to me as well as a copy of Keyserling's figures. Cooper & Grant (1976, p. 2174) have designated Keyserling's 1846, pl. 8, fig. 3b as lectotype. On this basis *Neospirifer* can be regarded as characterised by having fascicles or bundles of fine ribs on the lateral plicae. Armstrong (1968) has suggested that *Neospirifer* is a synonym of *Trigonotreta* Koenig 1825, but this conclusion is not acceptable as *Trigonotreta* has coarser ribbing. The name *Aperispirifer* has been proposed by Waterhouse (1968, p. 35) for *Neospirifer* which lack a delthyrial plate at juvenile and early mature growth stages and have internal thickening in the pedicle umbonal area, but the consistency of these characters is not clear.

Neospirifer sp.

Pl. 5, fig. 18

Discussion: The material is rather fragmentary and is not referred to any species. The sulcus is moderately deep, V-shaped in the younger part of the shell and U-shaped in the older part, and has about 8 costae which are evenly developed as distinct from the bundles of ribs on the flanks of the shell.

Dimensions (mm):	Length	Width	Height
Pedicle valve			
CPC 20199	38	52	11

Occurrence: Locality TH 199

LOCALITIES AND SPECIMENS

TH 171	2.2 km north-northeast of Oaklands homestead
TH 198	4 km east-northeast of Silverwood siding
TH 199	3 km north of Silverwood siding
TH 201	1.9 km north-northeast of Oaklands homestead
TH 202	1.4 km north-northeast of Oaklands homestead
TH 203	1.2 km north-northeast of Oaklands homestead
TH 406	3 km northeast of Silverwood siding
TH 411	3 km northeast of Silverwood siding

The localities are shown on the Warwick 1:250 000 geological sheet accompanying the Report on the sheet area by Olgers, Flood & Robertson (1974) and in Figure 17 of that Report.

The prefix CPC refers to the Commonwealth Palaeontological Type Collection, AMF to Australian Museum Fossil specimens, and TMF to Tasmania Museum Fossil specimens.

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PLATE 1

Vacunella cf. **etheridgei** (de Koninck) 1876

1 CPC 20146, side view of right valve; x½.

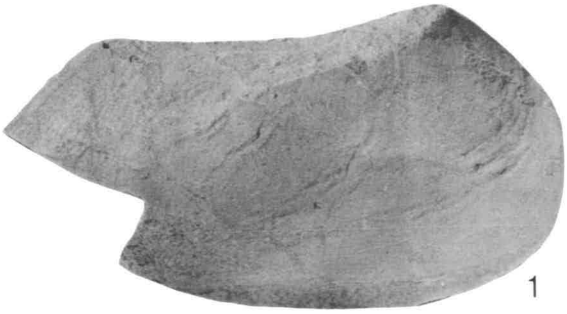
Myonia cf. **corrugata** Fletcher 1932

2 CPC 20148, latex cast of external impression of left valve; x½.
3 CPC 20147, left valve; x½.

Myonia olgersi sp. nov.

4–6 Paratype A, CPC 20150—front, side, and top views of left valve; x1.
7 Holotype, CPC 20149, side view of left valve; x½.
8, 9 Paratype C, CPC 20152—top and side views of left valve; x1.
10 Paratype B, CPC 20151, side view of left valve; x1.
11 Paratype D, CPC 20153, side view of left valve; x1.

PLATE 1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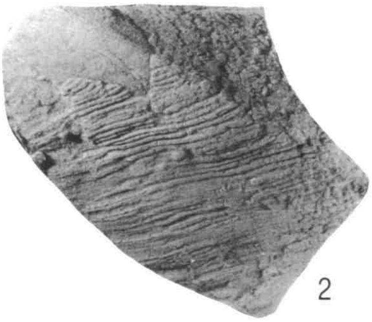
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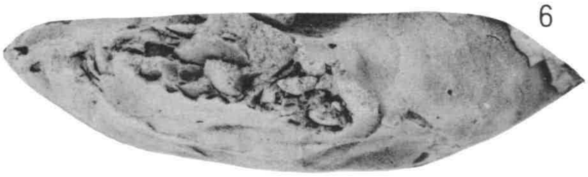
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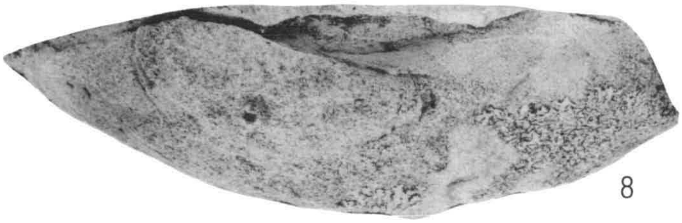
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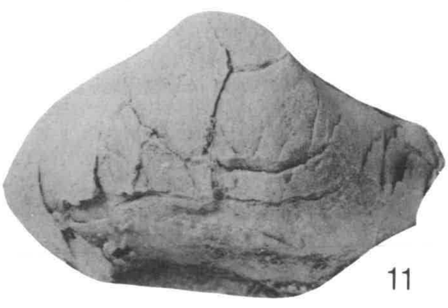
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PLATE 2

Astartella cf. **obliqua** Dickins 1963
1 CPC 20158, side view of internal impression of left valve; x2.
2 CPC 20159, latex cast of external impression of left valve; x2.
3 CPC 20161, side view of internal impression of right valve; x4.
4 CPC 20160, latex cast of internal impression of right valve; x4.

Deltopecten limaeformis (Morris) 1845
5 CPC 20172, latex cast of external impression of left valve; x1.
6 CPC 20171, latex cast of external impression of right valve; x1.

Peruvispira sp.
7 CPC 20167; x2.
8 CPC 20168; x2.

Keeneia? sp.
9 CPC 20166; x1.

Platyteichum sp.
10 CPC 20169; x1.

Deltopecten multicostatus (Fletcher) 1929
11 CPC 20173, latex cast of external impression of left valve; x1.

Etheripecten tenuicollis (Dana) 1847
12 CPC 20156, left valve; x1.
13 CPC 20157, left valve; x1.

Merismopteria cf. **imbricata** (Dana) 1847
14 CPC 20154, left valve; x1.
15 CPC 20155, right valve; x1.

Merismopteria sp.
16 TMF 442011, internal impression of left valve, to show anterior musculature; x1.

Etheripecten fittoni (Morris) 1845
17 CPC 20170, latex cast of external impression of left valve; x1.

PLATE 2


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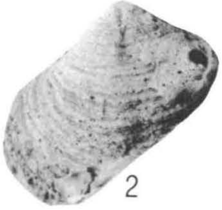
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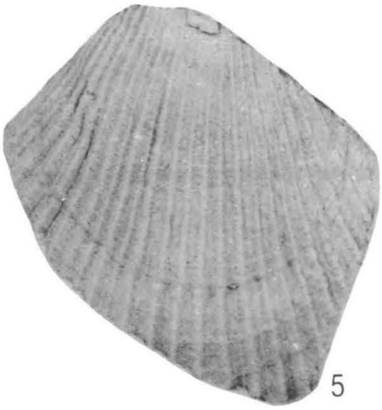
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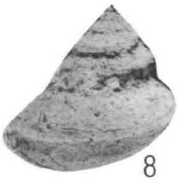
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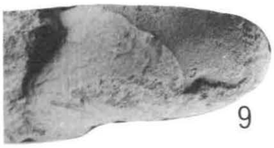
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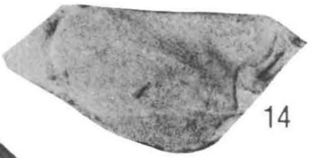
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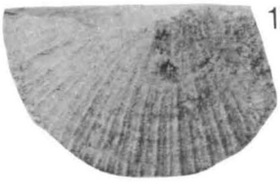
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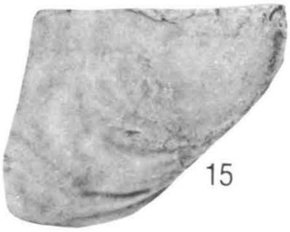
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PLATE 3

Stutchburia farleyensis Etheridge Jnr 1900
(all specimens from Farley, NSW)

1	AMF 38295, internal impression of left valve; x1.
2, 9, 10	AMF 6596, internal impression of left valve; side, top, and front views; x1.
3–5	AMF 38301, top view, side view of right valve, and front view; x1.
6–8	AMF 35430, front view, side view of left valve, and top view; x1.
11	AMF 38303, internal impression of left valve; x1.

Stutchburia randsi (Etheridge Jnr) 1892

12	CPC 20162, left valve (Note radiating ornament, rear posterior dorsal margin); x1.
13	CPC 20163, right valve; x1.
14, 15	CPC 20164, top and side views of internal impression of right valve; x1.
16	CPC 20165, right valve (Note radiating posterior ornament); x1.

Peruvispira elegans (Fletcher) 1958

17	AMF 1174, Richmond Vale Colliery, Maitland, NSW; Elderslie Formation of Branxton Subgroup; x4.
18	AMF 46587, Richmond Vale, Hunter River valley, NSW, Elderslie Formation of Branxton Subgroup; x4.
19	AMF 46587, locality as for Fig. 18; x4. The specimen in Figure 19 is on the same side of the piece of rock as that figured by Fletcher; the specimen in Figure 18 is on the reverse side.
20	Lectotype, AMF 46587. Lectotype is specimen at bottom right; x4.
21	Lectotype, AMF 46587. Lectotype is specimen at right; the shell to the left of the lectotype has dropped out; x2.

PLATE 3


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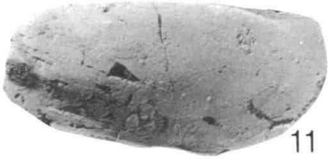
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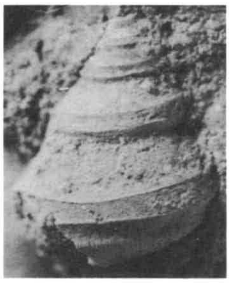
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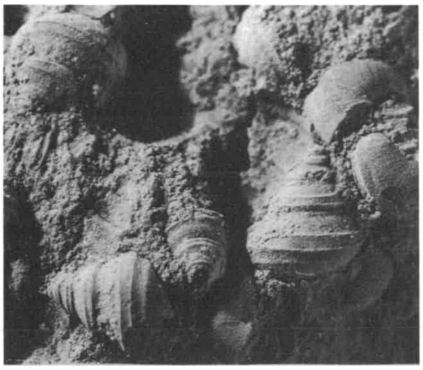
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PLATE 4

Echinalosia preovalis (Maxwell) 1954

1 CPC 20180; x2.
2 CPC 20179; x1.
3 CPC 20177, locality MC 485, 2.5 km upstream from Turrawalla-Eungella road crossing of Hazelwood Creek, Tiverton Formation, Bowen Basin, Queensland; x1.
4 CPC 20176; x1.
5 CPC 20178; x1.

Terrakea cf. **dickinsi** Dear 1971

6, 7 CPC 20175; x1.
8–10 CPC 20174; x1.

Notospirifer extensus tweedalei Campbell 1961

11 CPC 20191; x1.
12 CPC 20192; x1.
13 CPC 20193; x1.
14 CPC 20194; x1.
15 CPC 20197; x1.
16 CPC 20195; x1.
17, 18 CPC 20196; x1.
19 CPC 20198; x1.

Martiniopsis (Ambikella) ingelarensis (Campbell) 1960

20–22 CPC 20181; x1.
23, 24 CPC 20182; x1.

PLATE 4


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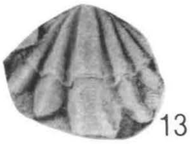
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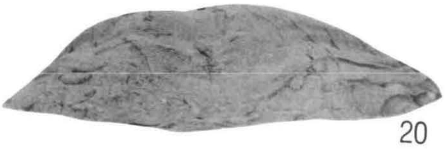
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PLATE 5

Martiniopsis (Ambikella) ingelarensis (Campbell) 1960

1	CPC 20189; x1.
2, 3	CPC 20183; x1.
4, 5	CPC 20186; x1.
6, 7	CPC 20184; x1.
8, 9	CPC 20187; x½.
10–12	CPC 20188; x1.
13, 14	CPC 20190; x1.
15–17	CPC 20185; x1.

Neospirifer sp.

18	CPC 20199; x1.

PLATE 5


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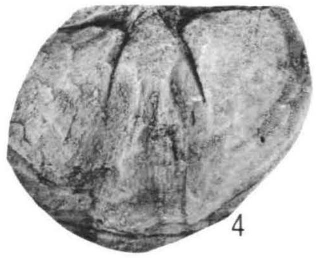
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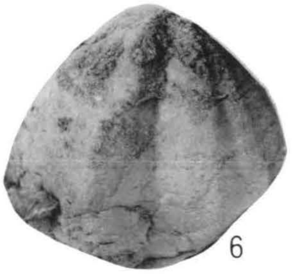
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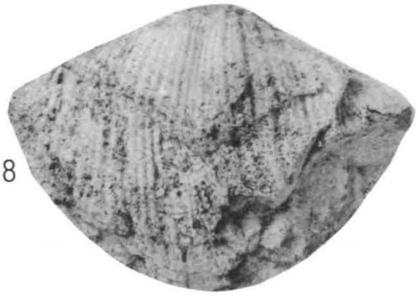
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Six short papers on Mesozoic bivalves

BY

S. K. SKWARKO

1. Neocomian (Lower Cretaceous) bivalves from northern Queensland.
2. A new upper Mesozoic trigoniid from western Papua New Guinea.
3. First report of MEGATRIGONIINAE (BIVALVIA, Cretaceous) from Papua New Guinea.
4. *Nototrigonia cinctuta* (BIVALVIA, mainly Lower Cretaceous) from northern Queensland and Papua New Guinea.
5. *Spia,* a new Triassic bakevellid bivalve from Papua New Guinea.
6. On the TRIGONIINAE, NOTOTRIGONIINAE, and AUSTROTRIGONIINAE.

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Neocomian (Lower Cretaceous) bivalves from northern Queensland

BY

S. K. SKWARKO

ABSTRACT

Bivalves described in this paper are from a small outcrop of sandstone at Normanby River crossing in northern Queensland. Some, like *Iotrigonia (Zaletrigonia) normanbyia, Sphenotrigonia queenslandica,* and *Tatella? woodsi* are new, some others are similar to previously described species, and the rest are too poorly preserved for positive identification. The age of the assemblage is regarded as Neocomian, shown by the trigoniid *Sphenotrigonia* hitherto known only from the Neocomian of South Africa, and implied by *Hatchericeras,* an ammonite similar to related forms of probable Neocomian age in Patagonia.

INTRODUCTION

Fossils described below are from a small outcrop of grey-weathering to greenish brown calcareous sandstone which crops out in Normanby River between the homesteads of Lakefield and Kalpowar, south of Princess Charlotte Bay, north Queensland (Text-fig. 1). The outcrop forms the Normanby Crossing, a source of *Hatchericeras lakefieldense* Woods, 1962, the only known representative of the presumably Neocomian ammonite *Hatchericeras* outside Patagonia.

Ammonites were in fact the first fossils to be found at the Normanby Crossing, by the geologists of the New Consolidated Gold Fields (Australasia) Pty Ltd, who presented them to the University of Queensland, which subsequently passed them to J. T. Woods for study. Woods recorded a preliminary determination (Denmead, 1960) before describing the new species in detail (Woods, 1962).

Bivalves were first collected at the crossing by K. G. Lucas and J. T. Woods in August 1961; then by L. G. Cutler, K. G. Lucas, and J. T. Woods in July 1962, in the course of the geological mapping of the Cape Melville 4-mile Sheet area (Woods, 1963, unpubl.); and in 1973 by R. W. Day (Lucas was an officer of the Bureau of Mineral Resources; Woods, Cutler, and Day, of the Geological Survey of Queensland). All the three collections are housed at the Geological Survey of Queensland. The material which forms the basis for this paper is that of Lucas, Cutler, and Woods, supplemented by some new trigoniids collected by the author in 1974.

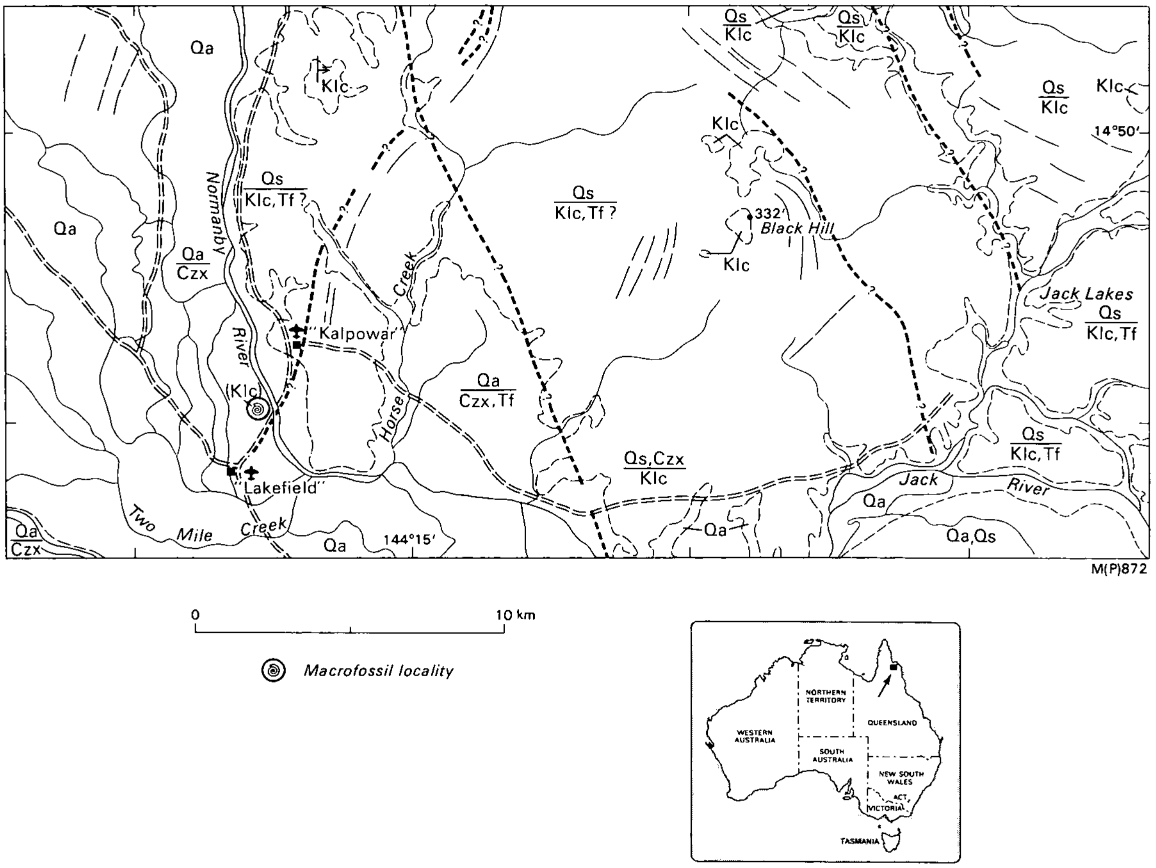

Fig. 1. Locality map. For detail see Cape Melville 4-mile geological Sheet, 1963.

I wish to thank the Director, Geological Survey of Queensland, for making available material from the Survey's collections.

THE AGE OF THE NORMANBY CROSSING SANDSTONE

The assemblage of fossils from the Normanby Crossing discussed below consists of

Bivalves:

'Nuculana' sp.
?Meleagrinella cf. *superstes* (Spitz, 1914)
Meleagrinella sp. indet.
Entolium cf. *argentinus* (Stanton, 1901)
Iotrigonia (Zaletrigonia) normanbyia sp. nov.
Sphenotrigonia queenslandica sp. nov.
Panopea (Panopea) sp. indet. aff. *gurgitis* Brongniart, 1909
Tatella? woodsi sp. nov.
Modiolus (Modiolus) sp.

Ammonite:

Hatchericeras lakefieldense Woods, 1962

The Neocomian age was originally proposed for the sandstone on the basis of the presence of *Hatchericeras*, an ammonite represented by several species in the presumably Neocomian (lower Hauterivian?) fauna of the Belgarno beds, Patagonia (Woods, 1962). The dating now finds additional support through the demonstrated presence in the Normanby Crossing assemblage of the South African Necomian genus *Sphenotrigonia* Rennie, and the Patagonian Necomian species *Entolium* cf. *argentinus*.

Within Australia, the Normanby Crossing fauna possibly shares *?Meleagrinella* cf. *superstes* with the Neocomian Stanwell bed near Rockhampton (Skwarko, 1968), and at subgeneric level the *Iotrigonia (Zaletrigonia) hoepeni* Skwarko, 1963 with both the upper Neocomian strata of Northern Territory and the Neocomian Nanutarra Formation in Western Australia (Skwarko, 1966).

DESCRIPTION OF SPECIES

The 'F' and 'W' numbers used below are the fossil and locality numbers of the Geological Survey of Queensland; the 'CPC' numbers are the Commonwealth Palaeontological Collection numbers of the Bureau of Mineral Resources, Canberra.

BIVALVIA

Family NUCULANIDAE Adams & Adams, 1958

Genus **Nuculana** Link, 1807

Type species: *Arca rostrata* Chemnitz, 1774, by original designation.

'Nuculana' sp.

Pl. 1, fig. 3

Material: Internal impression of left valve.

Description: Shell 10 mm long, fairly inflated, attenuated and produced to rear, with about 10 short parallel post-umbonal teeth. Umbo somewhat anterior, obtuse, ill-defined in front but with high post-umbonal shoulder in rear. Beak incurved. Maximum tumidity about middle of shell, decreasing rapidly only near ventral periphery of shell and at post-umbonal shoulder.

Discussion: Unsatisfactory preservation of our specimen precludes verification of the presence of the resilifer. The specimen is different from the previously described Australian isodont bivalves, whilst insufficient detail is preserved to enable comparison with overseas specimens.

Family OXYTOMIDAE Ichikawa, 1958

Genus **Meleagrinella** Whitefield, 1885

Type species: *Avicula curta* Hall, 1852, by subsequent designation of Cox, 1941, p. 134

?Meleagrinella cf. **superstes** (Spitz, 1914)

Pl. 1, fig. 2

?1946 *Pseudomonotis* sp., Whitehouse, *Proc. Roy. Soc. Qld*, 57(2), 13, pl. 1, figs. 7, 8
?1960 *?Meleagrinella* cf. *superstes* (Spitz); Brunnschweiler, *Bur. Miner. Resour. Aust. Bull.* 59, pp. 20-21, pl. 1, figs. 20, 22, 25, 26, text-fig. 15
?1968 *?Meleagrinella* cf. *superstes* (Spitz); Skwarko, *Bur Miner. Resour. Aust. Bull.* 80(10), pp. 171, 180, pl. 14, figs. 1, 2

Material: One left valve abraded proximally.

Description: Shell small, acline or slightly prosocline, generally circular in outline, 7 mm high, well and evenly inflated. Posterior ear obtuse, probably subangular. Exterior with fine linear radial riblets of two orders, including up to 20 secondary riblets, separated by wider flat interspaces.

Discussion: The single valve may be conspecific with *'Pseudomonotis'* sp. from the Neocomian (Valanginian?) marine beds at Stanwell, but poor preservation does not allow a definite comparison. Brunnschweiler (1960) regarded the Stanwell form as conspecific with the Western Australian form from the lower Neocomian Jowlaenga Formation. The detail of ribbing on our specimen certainly seems to resemble that of the Stanwell specimens, but the umbo of the latter may be somewhat more inflated.

Meleagrinella sp. indet.

Pl. 1, figs. 1, ?6

Material: Three left valves, and two right valves probably of the same species. In all specimens the shell material is at least partly exfoliated.

Description: Left valve almost 12 mm high, 11 mm long, acline, moderately inflated, ovate with narrow, sharply defined, strongly inflated umbo, moderately incurved beak and regularly curved distal margins. Auricles not visible, possibly due to unsatisfactory preservation. Some concentric, irregularly spaced growth rugae and very faint radial riblets discernible.

Right valve circular in outline, weakly inflated, with small inconspicuous umbo and evenly arched distal shell margin. Posterior ear obtuse, moderately developed, possibly angular; front ear small, placed above narrow and shallow subauricular notch. No surface lineation discernible; shell material partly exfoliated.

Family ENTOLIIDAE Korobkov, 1960

Genus **Entolium** Meek, 1865

Type species: *Pecten demissus* Phillips, 1858.

Entolium cf. **argentinus** (Stanton, 1901)

Pl. 1, fig. 5

cf. 1901 *Pecten argentinus* Stanton, *Rep. Princeton Univ. Exped.* 4, pp. 13-14, pl. 4, fig. 5

Material: Three complete valves, two left, one right.

Description: Shell about 29 mm high and 27 mm long, very weakly inflated, vertically ovate, subequilateral. Posterodorsal shell margin slightly concave, meets the longer and straight or very slightly convex anterodorsal margin at right-angles; distal shell margin broad and apparently evenly arched. Auricles subequal, right-angular, extending beyond beak at outer angles.

Surface of main body of shell partly exfoliated particularly proximally where fine regular concentric lineation exposed; surface of distal part of shell lined with equally fine concentric irregular and interrupted lamination and very fine straight and uninterrupted radial threads.

Remarks: The specimen illustrated by Stanton (1901) is not bilaterally symmetrical, possibly as a result of postdepositional distortion. The description of the shell in Stanton's text, however, brings out its very close resemblance to our specimens.

Family TRIGONIIDAE Lamarck, 1819

Subfamily MEGATRIGONIINAE van Hoepen, 1929

Genus **Iotrigonia** van Hoepen, 1929

Type species: *Iotrigonia crassitesta* van Hoepen, 1929, by original designation.

Subgenus **Zaletrigonia** Skwarko, 1963

Type species: *Iotrigonia (Zaletrigonia) hoepeni* Skwarko, 1963

Iotrigonia (Zaletrigonia) normanbyia sp. nov.

Pl. 3, figs. 2, 3, 5, 6

1963 *Iotrigonia sp.* cf. *I. (Zaletrigonia) hoepeni* Skwarko, *Bur. Miner. Resour. Aust. Bull.* 67, p. 20, pl. 1, fig. 9

Material: Holotype: QGS F5562 (Pl. 3 figs. 5, 6) anteroventrally incomplete left valve and its almost-complete internal cast, steinkern (QGS F3614).

Paratypes: QGS F3613 (W189) (Pl. 3, fig. 3) proximal portion of the left valve. Two small impressions of small part of proximal portion of the left valve and the right valve showing part of oblique ribbing pattern (QGS F5563 and F5556).

Diagnosis: Combination of the overall considerable elongation of the shell and the thickness of the shell wall with radial ribbing consisting of a set of fine short anterior posteroventrally directed riblets parallel to each other in the anterodorsal part of the flank, and a set of more robust ribs a little to the rear of the umbo, the proximal-most of which form a V-pattern with the anterior set of riblets.

Separation from other species: Z. hoepeni Skwarko, 1963 from the Necomian of the Northern Territory has similar ornament to that of the new species, though its posterior radial ribs seem to persist farther to the rear of the shell. Its overall shape is subquadrate, and its shell wall thinner, allowing the concentric ornament to persist onto the inside surface of each valve.

Description: Shell of size about average for genus, more than 12 cm long, 6.5 cm high, and 5 cm thick. Shell wall more than 5 mm thick in mature specimens.

Anterior of shell truncated. Umbo probably orthogyrous, sharply defined, slightly incurved. Post-umbonal carina clearly defined close to umbo.

Shell lined with concentric growth-lines and strong and fairly regular growth-rugae over most of surface. On proximal part of umbo concentric lineation obscured with two sets of diagonal ribs. Anterior set of thin parallel to subparallel short riblets oriented posteroventrally, mildly convex in cross-section, separated by linear interspaces. Posterior set slightly longer, initially narrow but broadening rapidly distally, convex in cross-section, separated from each other by narrow interspaces directed ventrally with tendency for slight curving to front of shell.

Anterior and posterior riblets form V-pattern in proximal part of umbo. More distally, posterior ribs form L-pattern with concentric rugae.

Remarks on Zaletrigonia: Megatrigoniinae, a subfamily of the Trigoniidae, was erected by van Hoepen in 1929 to include his *Megatrigonia* and *Iotrigonia.* Since then its concept and content were the basis for discussion by Crickmay, Cox, Kobayashi & Mori, Kobayashi, and Saveliev, a discussion which was summarised by Nakano (1965) who concluded the matter as it had started, namely by restricting its content to two genera, *Megatrigonia* and *Iotrigonia.*

More recently, however, Levy (1967) included in Megatrigoniinae not only her *Anditrigonia* but also *Apiotrigonia* Cox, 1952, which Nakano previously excluded. So presumably the discussion is not finished and will go on, though probably not in relation to *Iotrigonia,* a genus whose place in the Megatrigoniinae has never been seriously questioned. *Iotrigonia* is but of indirect interest in the present discussion, and only by virtue of the fact that some time ago I referred to it my then new subgenus *Zaletrigonia.*

Zaletrigonia was erected in 1963 (type series *Z. hoepeni* Skwarko, 1963) for a shell which is '. . . broadly trigonal to subquadrate in shape, and in which two sets of subradial ribs on the flank are inconspicuous in the early growth stages of mature specimens and are quite independent of each other in the later growth stages' (Skwarko, 1963, p. 18). Apart from *normanbyia* discussed above and the type species, two other species of *Iotrigonia* may be referable to this subgenus. These are *Z.? telefominiana* Skwarko (see this volume paper 3) and the little known *I. nanutarraensis* Cox, 1961 from the Neocomian strata of Western Australia. All four species come from one limited part of the globe, and none of the remaining thirty or so known species of *Iotrigonia* share their morphological peculiarity—a fact regarded as justification for their separation under a distinct subgeneric name.

Subfamily NOTOTRIGONIINAE Skwarko, 1963 em.

Genus **Sphenotrigonia** Rennie, 1936

Type species: *Trigonia (Sphenotrigonia) frommurzei,* by original designation.

Sphenotrigonia queenslandica sp. nov.

Pl. 1, figs. 4, 7; Pl. 2, figs. 1-3

Material: Two mature, almost complete bivalves, each with opposed valves; internal impression of right valve; numerous fragmentary material.

Holotype: CPC 16498 (Pl. 1, fig. 4; Pl. 2, figs. 1, 2)

Paratypes: CPC 16499 (Pl. 2, fig. 3; Pl. 1, fig. 7)

Specific diagnosis: The combination of convexity of anterior and ventral shell margins, subrostrate overall shape, and very slightly opisthogyrous umbones.

Description: Shell up to 14 cm long, 9 cm high, and 6.5 cm thick, with walls up to 5 mm thick; equivalve, gently subrostrate, well inflated, very inequilateral, strongly produced to rear with umbones slightly opisthogyrous and positioned in anterior quarter of shell.

Anterior and ventral shell margins gently and regularly convex, meeting in anteroventral part of shell in tight arch. Posterodorsal margin straight in front, then flexed little dorsally and ventrally, and then tightly turned down to meet ventral margin.

Maximum tumidity in front-central portion of shell from where it decreases gradually in all directions, but plunges vertically into commissure in front and in posterodorsal part of shell, and fairly steeply in ventral part.

Flank large, concentrically striated with irregular ribs and growth-lines similar to those in the type species in front and middle part, but persistence of ribs to rear not clearly visible. Ribbing apparently absent from escutcheon and posterior and ventral parts of flank.

Preumbonal carina tightly rounded; postumbonal carina sharply defined only near umbo, and indistinguishable from escutcheon carina. Escutcheon concave in transverse section, weakly concave in longitudinal seciton. Marginal carina not clearly observed but possibly follows broad flexure to commissure in posterior part of shell.

Ligament strong, at least 23 mm long.

Remarks: The calcareous sandstone from which the currently described fauna was collected is weathered on the surface. Shells exposed on surfaces of boulders have been at least partly weathered away, but those inside the rock still retain their calcareous matter. In *S. queenslandica* described above some additional chemical reaction seems to have taken place between the shell's surface and the enclosing matrix, with some transfer of matter, so that in the course of technical preparation it is difficult to pinpoint the boundary between the shell surface and the matrix. There is as a result some uncertainty regarding the detail of the external ornament of the new species. Ribbing as seen in the holotype (Pl. 2, fig. 1) may have been exaggerated in the course of technical preparation, both in relief and in the breadth of the interspaces. One shell fragment freed of matrix by weathering shows concentric ribs on at least a part of a shell to be low, broad, slightly convex in cross-section and separated from each other by linear interspaces.

Family HIATELLIDAE Gray, 1824
Genus **Panopea** Menard, 1807

Type species: *Panopea faujasi* Menard, 1807, by subsequent designation of Fleming, 1818

Panopea (Panopea) sp. indet. aff. **gurgitis** Brongniart, 1909
Pl. 3, fig. 1

Material: Single right valve with shell wall mostly exfoliated. F5569 (W189).˙

Description: Shell 33 mm long, 14 mm high, strongly inflated, inequilateral, produced to front and more strongly to rear.

Cardinal margin and dorsal shell margin almost straight, anterior margin evenly and tightly rounded, ventral margin slightly and unevenly convex, rear margin with greatest convexity in posteroventral part.

Umbo slightly forward, broad but well defined, incurved, with broad anterior shoulder.

Surface of valve ornamented with low irregular growth rugae and growth striae.

Remarks: It has not been possible to expose for scrutiny the dentition of our specimen. The rather median position of the umbo is reminiscent of *Panopea,* a genus represented in the Australian Lower Cretaceous by some ten species, all of which can be readily distinguished from our valve. The South African *gurgitis* associated with *Sphenotrigonia frommurzei* appears to be closely similar, but our material is unsuitable for positive comparison.

Family Uncertain
Genus **Tatella** Etheridge, 1901

Type species: *Corbicella? maranoana* Etheridge, 1892

Tatella woodsi sp. nov.
Pl. 3, fig. 4

Material: Almost complete internal cast of right valve (holotype) with but little shell material preserved (F5588, W189). Several internal impressions of both valves in various stages of growth and variously incomplete.

Holotype: F5588 (W189) (Pl. 3, fig. 4).

Diagnosis: Combination of size of shell large for genus with shape governed by cardinal and ventral margins subparallel to each other, and vertical rather than oblique rear truncation.

Separation from other species: T.? woodsi is larger than both *T. aptiana* Whitehouse, 1925, and *T. maranoana* (Etheridge Jnr, 1902). In addition, *T. maranoana* has a more convex ventral shell margin.

Description: Shell up to about 70 mm long and 26 mm high, thin walled and moderately inflated.

Dorsal shell margin straight for most of length, but curves downwards near extremities, gently at first and then rapidly to merge with gently arched ventral margin.

Umbo very broad and ill-defined. Tumidity greatest in dorsal third of shell, decreasing fairly rapidly dorsally, less rapidly ventrally.

Surface of shell lined with very fine concentric growth striae.

Remarks: The generic affinity of our specimens cannot be proven because of their obscured hinges.

The shell is named in honour of Mr J. T. Woods, former Director, Geological Survey of Queensland.

Family MYTILIDAE Rafinesque, 1815
Subfamily MODIOLINAE Keen, 1958
Genus **Modiolus** Lamarck, 1799

Type species: *Mytilus modiolus* Linne, 1758

Modiolus (Modiolus) sp.

J. T. Woods (1963, unpubl.) in his report mentions a few small specimens of *Modiolus* sp., one of which displays minute radial striae.

The best specimen available measures 9 mm by 5 mm, is well inflated, but because its shell wall is almost entirely missing, the presence of radial striae cannot be verified.

CEPHALOPODA
Family BERRIASELLIDAE Spath, 1922
Subfamily NEOCOMITINAE Spath, 1924
Genus **Hatchericeras** Stanton, 1901

Type species: *Hatchericeras patagonense* Stanton, 1901

Hatchericeras lakefieldense Woods, 1962
Pl. 3, fig. 7

1962 *Hatchericeras lakefieldense* Woods, *J. geol. Soc. Aust.,* 8(2), pp. 240-242, pl. 1, figs. 1-4

The best of the several recently collected specimens of *H. lakefieldense* is illustrated in Plate 3 (fig. 7) for the sake of completeness of presentation of the faunal assemblage. Our specimens add little to the original description of the species, which was, however, rather poorly illustrated.

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A new upper Mesozoic trigoniid from western Papua New Guinea

BY

S. K. SKWARKO

ABSTRACT

Richly fossiliferous sandstone river boulders from near Olsobip, western Papua New Guinea yielded abundant *Eselaevitrigonia tyna* sp. nov., a single specimen of *Bakevellia* s. str., and almost equally rare Bivalve gen. et sp. nov? The stratigraphic position of these bivalves in the local sequence, and their age, are not known. However, on overall appearance the new trigoniid seems to be closely related to *E. trapeziformis* from the Upper Jurassic part of the Oomia beds of Cutcch, India, and is the only age indicator of the fauna.

This is the first report of the Upper Jurassic to 'middle' Cretaceous genus *Eselaevitrigonia* from Papua New Guinea.

INTRODUCTION AND ACKNOWLEDGEMENTS

Large river-rounded boulders of hard, cream-pink, richly fossiliferous sandstone from which the currently described fauna was extracted were collected in 1972 by the author in the course of mapping of the Blucher Range 1:250 000 Sheet area, western Papua New Guinea. The collecting site was a helicopter touch-down point on a bank of Wok Wunik, a few hundred metres upstream from its junction with Wok Feneng, south of the Olsobip Patrol Post (Text-fig. 2). Limited time and trackless jungle frustrated attempts at tracing the boulders to their source, so it is not known from what stratum they were derived. The only known Mesozoic rocks in the area are the Middle?-Upper Jurassic Kuabgen Group, and the Cenomanian-Campanian Ieru Formation, but in this difficult terrain the boulders could equally well have shed from some hitherto unknown stratum of a different age. Possible age of the contained trigoniids would suggest, however, source strata from the Kuabgen Group.

Though numerous, the fossils represent only three genera and species—all bivalves, the trigoniids being most numerous. Extraction of shells from matrix by

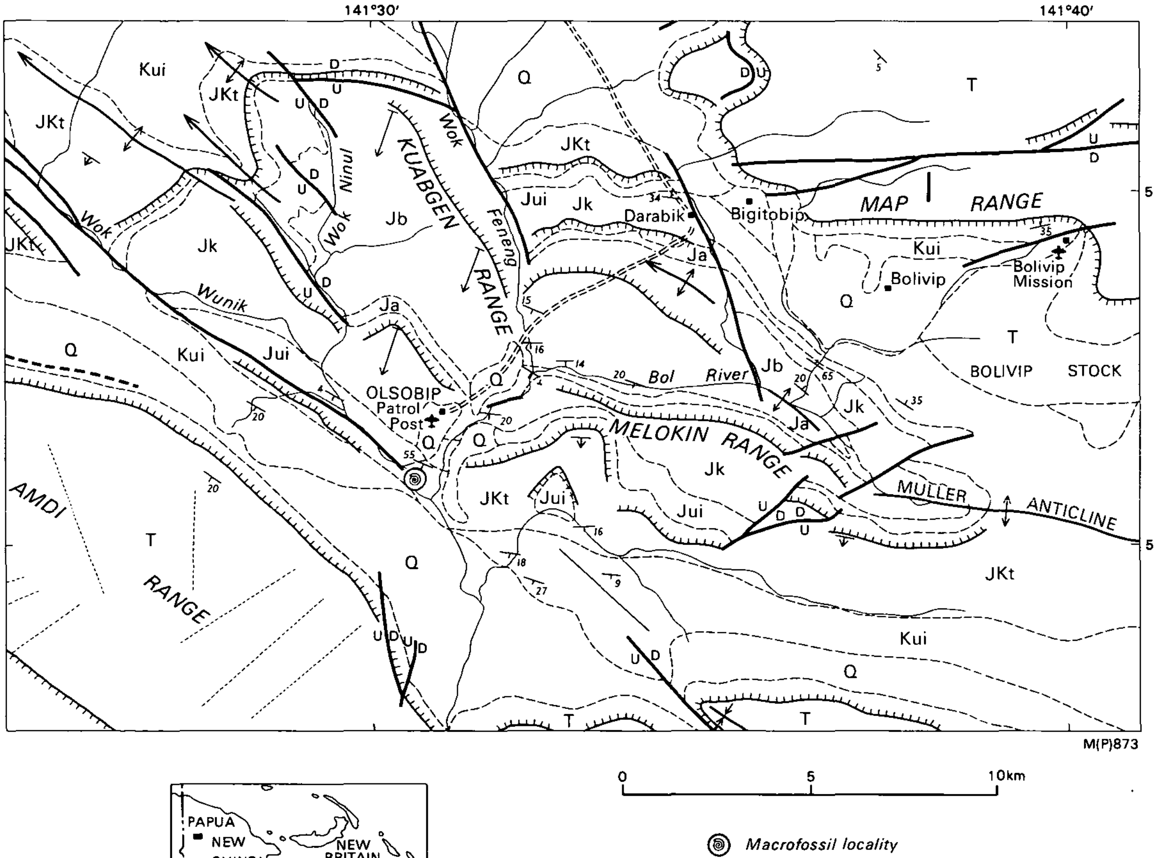

Fig. 2. Locality map. For detail see Blucher Range 1:250 000 Geological Sheet.

mechanical means proved impossible because of the hardness of the enclosing matrix. The boulders were consequently immersed in dilute hydrochloric acid which dissolved the calcareous shells, and the original shape of the leached out bivalves was then reproduced by means of a latex compound.

All the three genera and species encountered are described below for the sake of completeness of presentation of fossil record.

I wish to thank Professor Mitsuo Nakano, Hiroshima University, for helpful discussion and suggestions on the phylogeny of *tyna*.

Description of Species

Family Trigoniidae Lamarck, 1819

Subfamily Nototrigoniinae Skwarko, 1963, em.

Genus **Eselaevitrigonia** Kobayashi & Mori, 1954

Type species: *Trigonia meridiana* Woods, 1916

Eselaevitrigonia tyna sp. nov.

Pl. 4, figs. 1-6, 8

Material: Three external impressions of the left valve and two of the right valve; two internal impressions of the right valve and three of the left valve; numerous fragments and unextracted specimens.

Holotype: CPC 15806 (Pl. 4, fig. 1)

Paratypes: CPC 15807 (Pl. 4, fig. 2); CPC 15808 (Pl. 4, figs. 3, 8); CPC 15809 (Pl. 4, fig. 4); CPC 15810 (Pl. 4, fig. 5)

Specific diagnosis: The diagnostic feature of the new species is the combination of its small size, subquadrate shape produced posteriorly with diagonally to concentrically ribbed disc, rather shallow and narrow precarinal sulcus, marginal carina of uneven strength and tuberculation, and wide, weakly tuberculate area concentrically striated with growth-striae or rugae-like continuations of cardinal tubercles, and very faint radial threads close to the umbo.

Separation from other species: The new species can be distinguished from its apparently close relative, *T. trapeziformis* Kitchin, 1903 from the Oomia beds of Cutcch by its finer, more interrupted and more diagonally oriented disc ribs, and by its sparser radial threads on the area practically limited to its proximal part. *Trigonia tealei* Cox, 1937, from the Callovian beds of Tanzania is a larger species, with stronger and concentric ribbing on the disc, and with almost equally strong and concentric ribbing on the area to the almost complete exclusion of radial ribbing.

Description: The shell is small, the largest specimen being 27 mm high and 29 mm long. It is moderately to weakly but evenly inflated, subquadrate in shape, somewhat produced posteriorly, and with a broad orthogyrous umbo.

The disc is large in proportion to the rest of the shell, lined with concentric growth-lines and with diagonal and concentric ribs. The ribs are narrow and sharp-ridged, possibly concentric in the proximal-most and the distal-most parts of the shell, but elsewhere progressing somewhat sinuously—separated from each other by flat broad interspaces—from the anterior shell margin diagonally in the posteroventral direction. There is a marked tendency towards interruption and offsetting of the ribs in the posteroventral part of the disc; in some specimens ribs curve dorsally near their end, becoming concentric and somewhat raised and thickened near the pre-carinal sulcus.

The pre-carinal sulcus is narrow and moderately-to-weakly incised with its concave-to-flat surface lined with growth-lines. In one left valve disc ribs seem to continue with reduced relief across the pre-carinal sulcus in the distal part of the shell.

The marginal carina is angular and usually carries some iregularly spaced tubercles in some specimens, but is obtuse and diffuse in others.

The area is moderately wide and inclined to the commissure, lined with concentric growth-lines and rugae. On some specimens the area carries small tubercles apparently joined by very fine and poorly defined radial riblets. A median radial groove can be distinguished in most specimens.

The escutcheon carina is obtuse and ill-defined; the escutcheon narrow and difficult to observe, probably lined with growth-lines only.

The dentition is of trigoniid type. On the left valve 2 and inner walls of 2a and PII are ribbed, and on the right valve 3a and 3b are ribbed on both sides; in the right valve, however, 3a and 3b are not in contact, being fairly widely separated from each other.

Discussion: Tyna seems to be only the fifth bivalve to be referred to *Eselaevitrigonia.* The previously referred species are the already mentioned type species *meridiana* (Woods, 1916) from the 'middle' Cretaceous of New Zealand, and the three Upper Jurassic Indian species *cardinioformis, spissicostata,* and *trapeziformis* Kitchin, 1903 (Nakano, 1961, p. 90). As already elaborated, the *trapeziformis* resembles *tyna* most closely and in many respects; the remaining Indian species also bear reasonable similarity to it as well as to each other; it is only the type species which, possibly because of considerably younger age, is somewhat disturbingly distinct. I do not think that the age of the new species differs substantially from that of *trapeziformis.* I name it after my daughter, Krystyna.

Family Bakevellidae King, 1850

Genus **Bakevellia** King, 1848

Type species: *Avicula antiqua* von Münster *in* Goldfuss, 1836

Bakevellia sp.

Pl. 4, fig. 7

Material: Right valve, CPC 15812.

Description: The shell is about 43 mm long and 22 mm high, strongly produced to the rear and moderately inflated. The cardinal margin is broadly angular at the umbo located in the anterior one-fifth of the shell.

The posterior shell margin is gently concave, dorsally, becoming gently, and then probably strongly, convex lower down. The anterior shell margin is fairly convex dorsally and broadly flexed to the rear ventrally.

On the inside surface of the valve the front ear is marked off from the main body of the shell by a weak pre-umbonal carina; the posterior ear is not discrete, as viewed from the inside of the shell.

The ligament area is narrow and broadly triangular, widest beneath the umbo; inclined to the commissure at about 60°, it carries beneath and behind the umbo five flat, shallow, mainly squarish ligament pits which seem to increase in distance from each other posteriorly; in front of the umbo it is transversely grooved with five extensions of the anterior teeth on the cardinal area.

The cardinal area, widest anteriorly, is generally narrow; it carries in front seven very short and small transverse teeth; in the rear there is certainly one, possibly two thin elongate longitundinal teeth, somewhat sinuous, subparallel and very close to the cardinal margin.

Only the anterior-most part of the pallial line can be seen, and it is fairly deeply but rather unevenly incised.

Remarks: The outside of the only available valve is obscured by matrix, a limitation reflected in the description of the shell. The material is insufficient to allow specific identification.

Bakevellia s. str. is a cosmopolitan subgenus which ranges in age from Permian to Cretaceous.

Bivalve gen. et sp. nov.?

Pl. 4, figs. 9-11

Material: Three impressions of interior of right valves, two mature and incomplete, and one immature and complete.

Description: Shell at least 80 mm long and 47 mm high, produced to the front and much more strongly to the rear, fairly evenly inflated, fuller in front and somewhat attenuated in the back.

Umbo situated in the anterior quarter of the shell apparently fairly sharply defined proximally and with its beak incurved.

Hinge plate robust. Resilifer pit deep, and guarded in the front and back by two prominent subtriangular teeth protruding into the commissure. Anterior lateral teeth not distinct from the hinge plate; rear lateral teeth bifid posteriorly.

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First report of Megatrigoniinae (Bivalvia, Cretaceous) from Papua New Guinea

BY

S. K. SKWARKO

ABSTRACT

Iotrigonia (Zaletrigonia?) telefominiana sp. nov., the first known representative of the bivalve subfamily Megatrigoniinae van Hoepen, 1929 in Papua New Guinea, is described from possibly Neocomian strata of the western part of the country.

INTRODUCTION

A collection of fossils from a large gravitational slide, the Digiam landslide, west-northwest of Telefomin, northern Blucher Range 1:250 000 Sheet area, west-central Papua New Guinea (Text-fig. 3) contains, among others, two trigoniid genera. One is *Nototrigonia,* a genus hitherto known only from the Australian continent, represented by a variant of the well-known Australian species *N. cinctuta* (Etheridge Jnr, 1902); it is discussed in a separate paper below. The other is *Zaletrigonia,* a subgenus of *Iotrigonia* van Hoepen, 1929, of the Megatrigoniinae, described for the first time from Papua New Guinea in the current paper below.

The *Nototrigonia* and the *Zaletrigonia* occur together in the landslide. The assemblage, which also includes a few belemnites and rare foraminifers, was collected in 1971 by the author in the course of regional mapping of the Sheet area. The trigoniids were found in loose boulders in scree derived from some 180 m of section (Text-fig. 4), whose top 36 m is of unknown age; the age of the next 144 m is Cretaceous as shown by the rare belemnites in the upper part, and presumably the trigoniids in the lower part. The 40 m of dark siltstone which underlies this Cretaceous sequence has shed boulders composed almost entirely of the Jurassic genus *Pronoella* s.l.

The hitherto known age of *N. cinctuta* is Aptian, but the Papua New Guinea variant need not necessarily be of the same age. The Digiam *Iotrigonia* is a new species but of Cretaceous age as *Iotrigonia* is confined to strata of that age in Antarctica, Asia, New Zealand, South Africa and South America. In Australia *Iotrigonia* is represented by a subgenus *Zaletrigonia* which seems to be confined to the Neocomian. Though *telefominiana* may be a *Zaletrigonia* it is not a typical representative of that subgenus. Still, *telefominiana* may indeed be of Neocomian age, and so would consequently be by inference the variant of *N. cinctuta.* In fact the age of

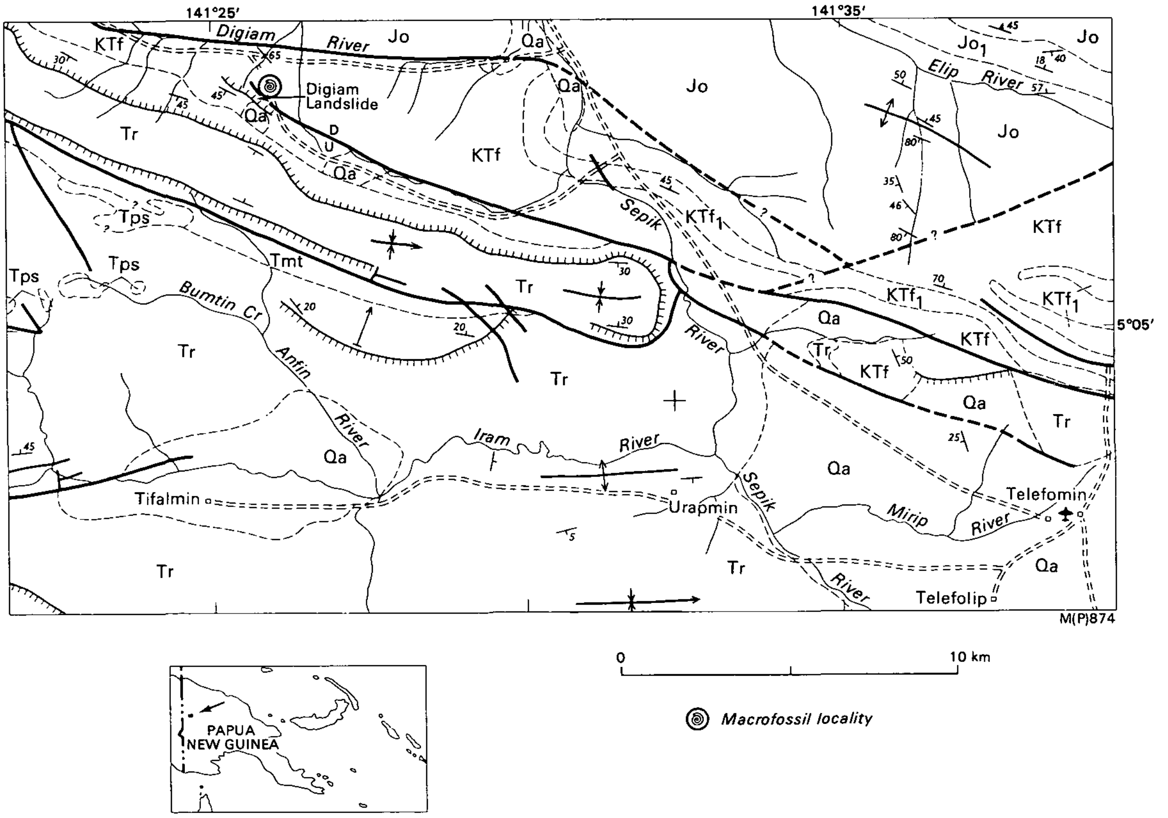

Fig. 3. Locality map. For detail see Blucher Range 1:250 000 Geological Sheet.

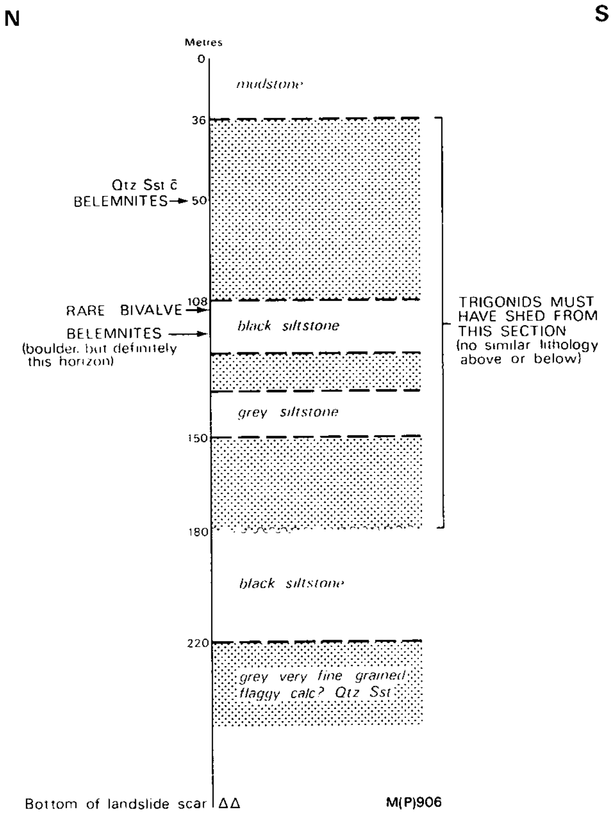

Fig. 4. Digiam landslide scar.

this variant may range even into Jurassic, as indicated by a single incomplete but almost unmistakable imprint of its valve in the *Pronoella* shell bed underlying the *Iotrigonia-Nototrigonia* horizon.

DESCRIPTION OF SPECIES

Family TRIGONIIDAE Lamarck, 1819

Subfamily MEGATRIGONIINAE van Hoepen, 1929

Genus **Iotrigonia** van Hoepen, 1929

Type species: *Iotrigonia crassitesta* van Hoepen 1929

?Subgenus **Zaletrigonia** Skwarko, 1963

Type species: *I. (Z.) hoepeni* Skwarko, 1963

Iotrigonia (Zaletrigonia?) telefominiana sp. nov.

Pl. 5, figs. 1-7; Pl. 6, figs. 8, 11

Material: Five incomplete external impressions of the left valve and two of the right valve; two complete internal impressions of the right valve and one incomplete impression of the left valve. About a dozen additional fragmenary impressions.

Diagnosis: The diagnostic feature of the new species is the combination of the fine, parallel, diagonal, anterodorsal riblets with robust rear ribs of the type normal for the genus, and the tendency for the fine riblets to form in the anteroventral part of the shell an inverted V-pattern with the rapidly thickening rear ribs.

Separation from other species: The tendency for the anterodorsal riblets to form an inverted V-pattern is not very common in *Iotrigonia*, as only four out of 30 or so known species exhibit it. In all four, however, the anterior ribs are robust and the new species can be readily distinguished from them through the thinness of its front thin, parallel riblets, a characteristic of *Zaletrigonia*. Such thin riblets occur also in *hoepeni* Skwarko, 1963, *recurva* Kitchin, 1903, and possibly *nanutarraensis* Cox, 1961, none of which, however, show any tendency to form an inverted V-pattern, and thus can be readily distinguished from the new species.

Description: Shell of about normal size for genus, of average tumidity, and with broad orthogyrous umbo.

Anterior shell margin of greatest convexity in anteroventral part, gently sinuous posterodorsally; ventral margin broadly and evenly curved; posteroventral margin unevenly but gently convex; dorsal flank margin concave; rear shell margin fairly tightly flexed.

Flank ornamented in front with set of riblets anterior to set of heavier posterior ribs. Front riblets fine, equal in size, parallel or almost parallel to each other in antedorsal part of flank, but in anteroventral part either absent or forming inverted V-pattern with anteriormost extremities of inverted V which thicken rapidly in antero ventral direction. Rear ribs thick, robust, convex in cross-section and separated by concave narrower or equal interspaces; sinuous in front, rapidly attaining maximum thickness which in case of rear-most ribs continues undiminished to ventral shell margin, but in case of frontal ribs tapers off rapidly near terminations of anterior riblets. Growth-rugae particularly prominent in ventral portion of shell and interrupt posterior ribs imparting semitubercular appearance. Rear of flank free of ribbing in most specimens, narrow triangular in shape, striated with growth-lines.

Marginal carina and escutcheon carina indistinct; both area and escutcheon narrow and apparently lined with growth-lines only.

Remarks: The new species is not a typical *Zaletrigonia*, but seems to have valve ornament intermediate between that in *Zaletrigonia* and *Iotrigonia* s. str. With *Zaletrigonia* it shares the attenuation and the sub-parallel orientation of the anterodorsal riblets; with *Iotrigonia* s. str. it shares the ventral persistence of the posterior ribs, the foremost ones of which reach the ventral shell margin, and in the front part of the disc the inverted V-pattern hitherto unobserved in *Zaletrigonia*.

Nototrigonia cinctuta (Bivalvia, mainly Lower Cretaceous) from northern Queensland and Papua New Guinea

BY

S. K SKWARKO

ABSTRACT

Two new variants of the Australian Aptian bivalve *Nototrigonia cinctuta* (Etheridge Jnr, 1902) are described, one from northern Queensland, and the other from Papua New Guinea.

Previously *N. cinctuta* s.l. was reported only from South Australia, central and north-central Queensland, and the Northern Territory, associated with Aptian molluscs. The recent discovery of one of its variants in Papua New Guinea extends the known geographic range of the species to 22 degrees of latitude, and the stratigraphic range possibly into the Jurassic.

INTRODUCTION

One of the two new variants of *N. cinctuta* described below was collected by the author in 1973 at Emu Creek, a tributary of Coen River near Boyds Lagoon, 3 km north of Jabiru Outstation west-northwest of the township of Coen, Coen 1:250 000 Sheet area, Cape York Peninsula (Text-fig. 5). Fossils associated with it in outcrop are well known, and indicate Aptian age (see below).

The second variant was collected by the author two years earlier in the course of the regional mapping of Papua New Guinea, from the Digiam landslide near Digiam River, west-northwest of Telefomin, northwest Blucher Range 1:250 000 Sheet area, western Papua New Guinea (Text-fig. 3). In the landslide, specimens of the variant of *N. cinctuta* are associated with specimens of *I. (Z.?) telefominiana* described in the previous paper, which implies Neocomian rather than Aptian age. A single incomplete specimen was found associated with numerous shells of *Pronoella* s.l. which form a layer immediately below the *Iotrigonia-Nototrigonia* horizon. Hitherto, *Pronoella* has been identified only from Jurassic strata of Europe.

The new occurrences of *N. cinctuta* increase the known range of geographical distribution of this obviously very adaptable and successful species to 22 degrees of latitude (Text-fig. 6).

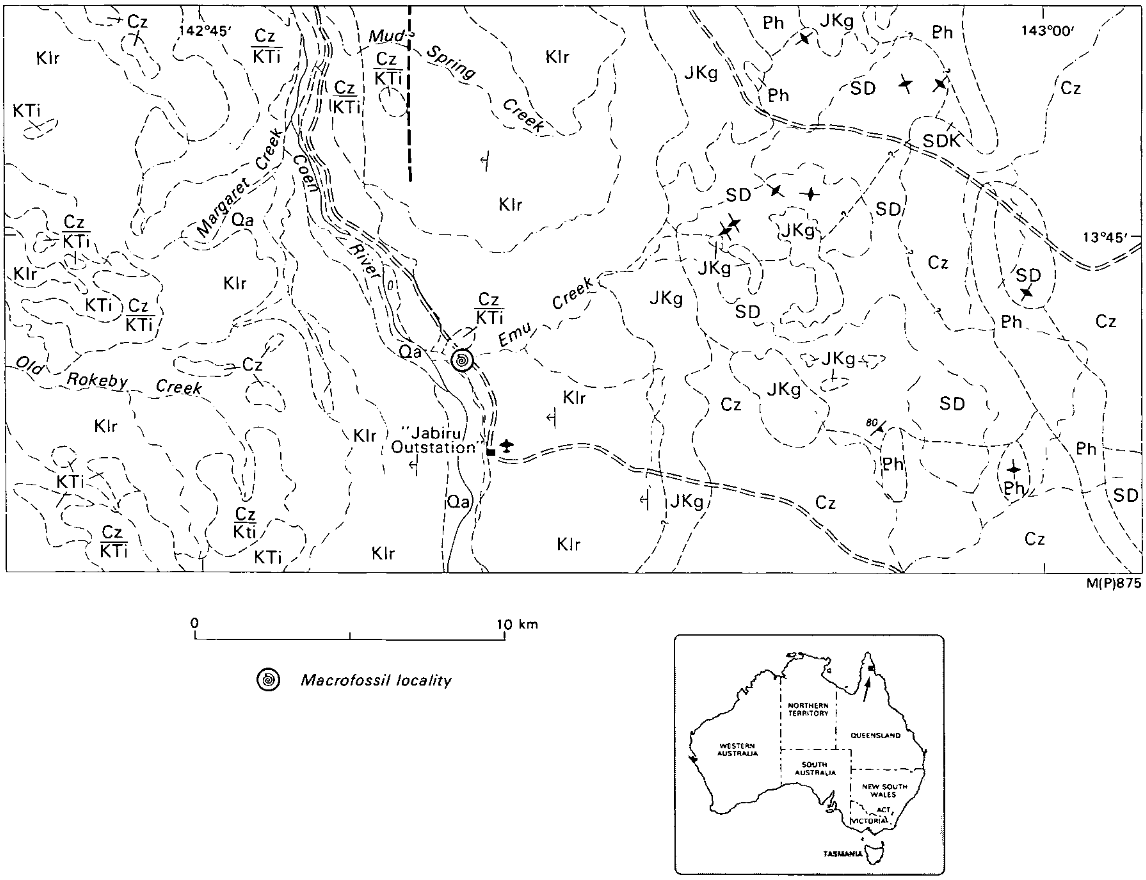

Fig. 5. Locality map. For detail see Coen 1:250 000 Geological Sheet.

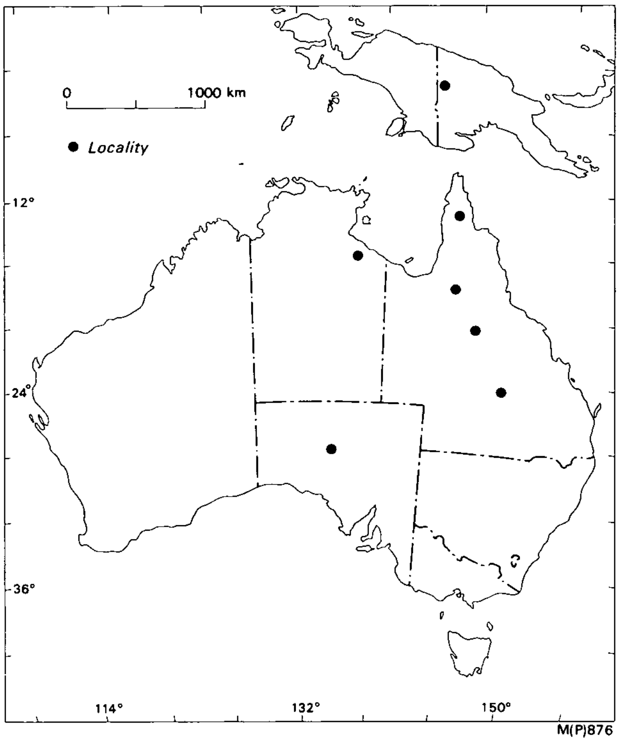

Fig. 6. Distribution of Nototrigonia cinctuta.

DISTRIBUTION, FAUNAL ASSOCIATIONS, AND AGE OF N. CINCTUTA

Hitherto, the Australian Lower Cretaceous bivalve *N. cinctuta* (Etheridge Jnr, 1902) has been reported from five localities: one in South Australia, one in the Northern Territory, and three in central Queensland. It is now reported for the first time from north-central Queensland, from northern Queensland, and from outside Australia, viz., from Papua New Guinea.

In Australia *N. cinctuta* is confined to sediments of Aptian age. It was first described from the Peake area, South Australia, where it is associated with bivalves *Eyrena tatei* (Etheridge Jnr, 1902), *Panopea sulcata* Etheridge Snr, 1872, *P. maccoyi* (Moore, 1870), *Fissilunula clarkei* (Moore, 1870), *Cyrenopsis australiensis* Newton, 1914 and *C. meeki* (Etheridge Jnr, 1892) and a gastropod *Euspira ornatissima* (Moore, 1870). Apart from *C. australiensis,* which may range from Aptian to Albian, all the species in this assemblage are of Aptian age.

In the Northern Territory, somewhat distorted shells identified by the author (Skwarko, 1966) as *N.* cf. *cinctuta* almost certainly belong to this species and seem to be confined to strata which are probably of Aptian age. Their associates are bivalves *Nuculana?* sp., *Maccoyella* sp. indet., Genus et sp. nov., Bivalvia indet., and a belemnite, *Peratobelus? bauhinianus* Skwarko, 1966.

In Central Queensland the age of *N. cinctuta* only appears to be less clear. Day (1968, p. 235, unpubl.) described *cinctuta* as an Aptian shell, yet at one of the three source localities (GAB 1933) it is reputedly associated with such key Albian fossils as *Pseudavicula papyracea* and *Dimitobelus diptychus.* The full faunal list for the three localities is: *'Nuculana'* sp. indet., *Leionucula quadrata* (Etheridge Snr, 1872)*, *Maccoyella corbiensis* (Moore, 1870)*, *Pseudavicula anomala* (Moore, 1870)*, *P. papyracea* Etheridge Jnr, 1907, *Tancredia (Corburella)* aff. *trigoniformis* Day, 1967*, *Fissilunula clarkei* (Moore, 1870)*, *Cyrenopsis* cf. *meeki* (Etheridge Jnr, 1892), *Barcoona trigonalis* (Moore, 1870); gastropods *Anchura?* sp. and *Euspira reflecta* (Moore, 1870)*; scaphopod *Laevidentalium wollumbillaense* (Etheridge Jnr, 1892)*; and belemnites *Peratobelus australis* (Phillips, 1870)*, *P. oxys* (Tenison Woods)*, *P. robustus* Day (MS name)* and *Dimitobelus diptychus* (M'Coy, 1867). The collection from locality GAB 1933 almost certainly represents two distinct faunas, one Aptian and the other Albian, and fossils marked above with an asterisk are those which are associated with *N. cinctuta* at the other two, uncontaminated, localities (i.e. GAB 699 and GAB 2101).

40 km southeast of Croydon, in central-northern Queensland, *N. cinctuta* is associated with *Maccoyella* aff. *reflecta* (Moore, 1870), *?Tancretella plana* (Moore, 1870), *?Thracia primula* Hudleston, 1890, and *Natica variabilis* Moore, 1870—a presumably Aptian assemblage.

At Emu Creek, in northern Queensland, fossils associated with *N. cinctuta* are clearly of Aptian age, the evidence from bivalves being additionally strengthened by the presence of an ammonite and a belemnite (R. Day, pers. comm.): *?Tropaeum leptum* (Etheridge Jnr, 1909), *Peratobelus oxys* (Tenison Woods), *Maccoyella corbiensis* (Moore, 1870), *Trancretalla plana* (Moore, 1870), *Panopea maccoyi* (Moore, 1870), *Thracia primula* Hudleston, 1890, *Maranoana etheridgei* Day (MS name). There is nothing to suggest that in Australia the stratigraphic range of *N. cinctuta* extends beyond Aptian.

In Papua New Guinea, however, at the Digiam landslide, *N. cinctuta* is associated with *Iotrigonia (Zaletrigonia?) telefominiana* sp. nov. (see above), indicating that its age is not limited to Aptian as the Australian subgenus *Zaletrigonia* is confined to Neocomian strata. Furthermore, one incomplete specimen which almost certainly belongs to *N. cinctuta* was identified from an underlying horizon, associated with numerous specimens of the European Jurassic bivalve *Pronoella* Fischer, 1887. It would seem, therefore, that the stratigraphic range of *N. cinctuta* has to be extended downwards.

DESCRIPTION OF SPECIES

Family TRIGONIIDAE Lamarck, 1819
Genus **Trigonia** Bruguiere, 1789

Type species: *Venus sulcata* Hermann, 1781; ICZN opinion 327 (1955)

Subfamily NOTOTRIGONIINAE Skwarko, 1963
Genus **Nototrigonia** Cox, 1952 em.

Type species: *Nototrigonia cinctuta* (Etheridge Jnr, 1902)

Nototrigonia cinctuta (Etheridge Jnr, 1902) subsp. nov. A

Pl. 6, figs. 1-6

Material: Three external impressions of the right valve, one of which is juvenile and only one nearly complete; two incomplete external impressions of the left valve, some fragmentary internal impressions of both valves.

Locality: Low ridge on old track from Coen to 'Rokeby' via 'New Yard', 0.8 km north of Emu Creek Crossing. Grid reference 616248. Coen 1:250 000 Sheet area, Cape York Peninsula, northern Queensland.

Discussion: The *Nototrigonia* from Emu Creek west of Coen has many similarities to the type *N. cinctuta* (Etheridge Jnr, 1902) from South Australia, yet it is not an identical shell, the difference being seen in:

1. The disc, which in the northern form is somewhat more inflated, with a more sharply defined rear margin and a tendency in mature valves to lose their diagonal ribbing in favour of concentric growth-lines and rugae.
2. The sulcus, which is possibly a little narrower and certainly more deeply incised, particularly in the front.
3. The area, which is more curved and narrow, with the longitudinal groove dividing it into uneven parts, the ventral being the wider one with two fine longitudinal striae.
4. The overall shape of the shell, which is a little narrower posteriorly, and somewhat more graceful and elegant.

Despite these differences the Cape York Peninsula form is still *Nototrigonia,* basically *N. cinctuta.* Rather than obscure its close relationship to *N. cinctuta* by giving it a new specific name or camouflage the differences between them by simply referring it to *N. cinctuta,* it is thought best to differentiate them at the subspecific level.

Nototrigonia cinctuta (Etheridge Jnr, 1902) subsp. nov. B

Pl. 6, figs. 7, 9, 10

Material: Two external impressions of the left valve, both incomplete; fragment of internal impression of left valve.

Locality: Digiam landslide, about 17 km west-northwest of Telefomin, Blucher Range 1:250 000 Sheet area, western Papua New Guinea.

Discussion: The *Nototrigonia* from the Digiam landslide is very similar to the type specimen of *N. cinctuta* (Etheridge Jnr, 1902) from South Australia, the only differences being in the disc, which is in the northern form proportionally somewhat smaller and ornamented with diagonal riblets somewhat thinner and more interrupted than in the type species, and the area, which in the northern form seems to be unevenly divided by a longitudinal groove into two parts, the larger or the ventral part being striated with up to four thin, hairlike longitudinal threads criss-crossed by similarly thin but equally prominent growth striae.

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Spia, a new Triassic bakevellid bivalve from Papua New Guinea

BY

S. K. SKWARKO

ABSTRACT

Spia janeki subgen. et sp. nov., a new bakevellid bivalve and a new subgenus of *Bakevellia* King, is described from the Upper Triassic Jimi Greywacke, west-central Papua New Guinea.

Only two known species are referable to *Spia*, and both are from the Carnian-Norian strata of Papua New Guinea.

INTRODUCTION

The regional mapping of Papua New Guinea at the 1:250 000 scale which is nearing completion, is currently accompanied by a more detailed mapping of select areas at 1:100 000 scale. Some of this mapping has recently focused on areas which several years ago yielded the first Triassic fossils to be found in Papua New Guinea, with the result that a second wave of Triassic fossils has become available for study. However, because of past research the number of species new to science coming to light is becomnig fewer and the excitement of their discovery gradually gives way to the increasing usefulness of the already known species in correlation and dating.

The material described below is from locality P5699 east of Mount Oipo, in the bed of Kanel River, Ramu 1:250 000 Sheet area (Text-fig. 7). The collection was made in 1977 by C. J. Pigram, Papua New Guinea Geological Survey.

Some years ago I described from the same area a similar but smaller shell which I called *simbaiana*, and which because of the extreme posterior direction of the shell's elongation, as well as its bakevellid hinge, I referred to *Gervillia* s. str. (Skwarko, 1967). The bivalve described below, like *simbaina*, is from the Jimi Greywacke, and consequently of Carnian-Norian age. It belongs to a new species, and helps to illustrate the strong persistence of supra-specific morphological characters in the two species. These characters, because of the current status of subgenus *Bakevelloides*, are justification for erecting a new subgenus, here named *Spia*. *Spia* is closely related to both *Bakevellia* and *Bakevelloides* as shown by internal structures, but differs from them by the posteriorly directed elongation of the body.

Spia is a Pidgin word for spear, and reflects the overall elongate and narrow shape of the shell. I named the species after Janek, my son.

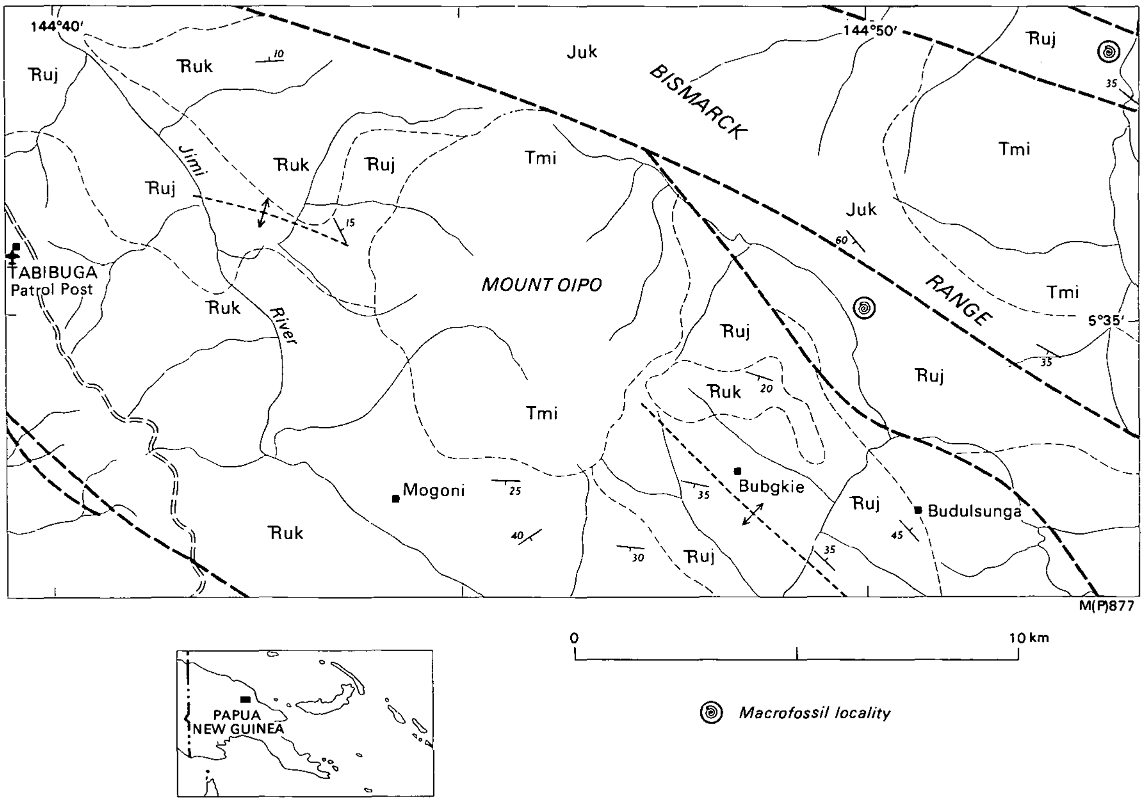

Fig. 7. Locality map. For detail see Ramu 1:250 000 Geological Sheet.

Family BAKEVELLIDAE King, 1850

Genus **Bakevellia** King, 1848

Type species: *Avicula antiqua* von Münster in Goldfuss, 1836

Subgenus **Spia** nov.

Type species: *Bakevellia* (*Spia*) *janeki* subgen. et sp. nov.

Diagnosis: Shell of variable size, posteriorly alate, equivalve, very inequilateral with anteriorly placed umbo and main body strongly produced to the rear. Ornamentation concentric and limited to growth striations and rugae. Hinge with multiple ligament pits, anterior short transverse teeth, and several elongate posterior teeth. Anterior pedal retractor muscle scar small and close to small pedal elevator muscle scar; posterior pedal retractor muscle scar large.

Additional included species: Gervillia (Gervillia) simbaiana Skwarko, 1967.

Comparison with related forms: In the new subgenus the hinge is virtually identical with that of *Bakevelloides* Tokuyama, 1959—a subgenus of *Bakevellia*; the strongly posteriorly produced shape is reminiscent of *Gervillia* Defrance, 1820.

Spia janeki subgen. et sp. nov.

Pl. 7, figs. 1-8

Material: Seven specimens, some almost complete, from locality P5699: outcrop in Kanel River, a tributary of Jimi River at its junction with Kana River. Ramu 1:250 000 Sheet area.

Holotype: CPC 19073 (Pl. 7 figs. 2, 7, 8)

Paratypes: CPC 19072 (Pl. 7, figs. 1, 3, 6); CPC 19074 (Pl. 1, figs. 4, 5)

Diagnosis: Shell possibly large for subgenus. Hinge plate broad, with upper part inclined to commissure and with five—possibly six—large and shallow ligament pits. Lower part of hinge plate parallel to commissure, with about 18 short transverse anterior teeth in front and three—possibly four—oblique posterior teeth. Anterior pedal retractor muscle scar deep and small, close to and beneath hinge plate in umbonal region, and close to slightly larger but equally deep pedal elevator muscle scar. Posterior pedal retractor muscle scar large, moderately deep, near and under rear end of hinge plate.

Description: The holotype is almost 130 mm long, 38 mm high, and 26 mm.thick. The posteriorly incomplete paratype is 42 mm high.

The cardinal margin—the dorsal margin of the posterior wing—is straight and extends for almost 2/3 of the length of the shell. The umbo is broad and well defined only on its posterodorsal side by the post-umbonal carina which is sharp-ridged near the umbo and which persists for most of the length of the shell.

The shell is fairly well inflated, with tumidity decreasing gradually back from the centre of the shell, more rapidly to the front and downwards, and quite suddenly across the post-umbonal carina—particularly close to the umbo.

The anterior shell margin is tightly curved, particularly in the upper part, with convexity decreasing gradually downwards so that the ventral margin is tightly convex, and the posterodorsal margin—behind the wing—probably straight.

The surface of the shell is lined with fine concentric striae, and with coarse and irregularly spaced and ill-defined rugae.

There is no gape, but the upper, wider portions of hinge plates are inclined to the commissure forming a narrow V-shaped gape along the dorsal part of the shell. These inclined portions of the hinge plate are up to 1 cm wide under the umbo, but taper gradually to the back and a little more suddenly to the front. Each carries five, possibly six ligament pits of about the same depth but of size proportional to the width of the hinge plate. The lower part of the plate meets the upper part along a straight line. It is parallel to the commissure, up to about 5 mm wide in the front, tapering to about 1 mm beneath the umbo and increasing again to about 10 mm in breadth posteriorly.

The short transverse teeth are located in the front lower part of the hinge plate. They number possibly as many as 14 and are preceded by a single robust oblique tooth.

The longitundinal rear teeth originate in the lower part of the hinge plate a little behind the umbo. They number three, possibly four, are directed posteriorly, and are separated from each other by deep or shallow interspaces.

On the right valve the anterior pedal retractor muscle scar is small and fairly deep and situated under the anterior part of the hinge plate and close to and a little in front of a similarly deep but somewhat larger pedal elevator muscle scar. The posterior pedal retractor muscle scar is large and moderately deep and situated underneath and close to the rear end of the hinge plate.

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On the Trigoniinae, Nototrigoniinae, and Austrotrigoniinae

S. K. SKWARKO

The history of classification of family Trigoniidae is a long and tortuous one, and is a reflection of its complexity resulting from the extraordinary diversity of shape and ornament exhibited by the group. Three approaches to classification have been used by generations of palaeontologists: into sections, into genera and subgenera, and into subfamilies.

Grouping into sections was originated by Agassiz, who in 1841 referred all the then known species of *Trigonia* to one or other of his eight sections, viz. Scaphoideae, Clavallatae, Quadratae, Scabrae, Undulatae, Costatae, Glabrae, and Pectinatae. These sections were later modified or added to by Lycett (1872-1879) who proposed Byssiferae; by Stainmann (1882) who established Pseudoquadratae; by Bigot (1893) who divided Glabrae into Semiaeves, Gibbosae, and Excentricae; by Kitchin (1903) who recognised certain groups subordinate to the main sections which could not acommodate trigoniids from India and Africa; and by Packard (1921) who subdivided Scabrae into Pennatae and the 'Aliformis'. This type of grouping later fell into disfavour, but was rejuvenated more recently, though in a modified form, by Kobayashi & Mori (1954) who subdivided Kobayashi's Trigoniinae into *Laevitrigonia* section, *Trigonia* section, and *Indotrigonia* section.

The trend of splitting up of the very broad and unwieldly genus *Trigonia* into genera and subgenera was started by Bayle who in 1878 separated from it *Lyrodon* and *Myophorella.* It was continued by Cossman (1912) who named *Eotrigonia* and *Neotrigonia*; by Deecke (1925a, b) who first erected the subgeneric names *Laevitrigonia, Scaphotrigonia,* and *Scabrotrigonia* to three sections of Agassiz; by van Hoepen (1929), who proposed ten new genera; and later by Crickmay (1930a, b) and many others including Krumbeck, Marwick, Dietrich, Rennie, Kobayashi, Leanza, Nakano, Saveliev, Freneix, Tamura, Skwarko, Fleming, and Levy.

The third approach to subdivision, into subfamilies, originated much more recently than the other two, with separation from the family Trigoniidae of van Hoepen's (1929) Megatrigoniinae, Pterotrigoniinae (later amended by Kobayashi & Nakano, 1957), Rutitrigoniinae, and Pleurotrigoniinae, followed by Kobayashi's (1954) Trigoniinae, Minetrigoniinae, Myophorellinae, and Vaugoniinae; Saveliev's (1958) Laevitrigoniinae; Fleming's (1962) Praegoniinae; and Skwarko's (1963, 1968) Nototrigoniinae and Austrotrigoniinae.

Today all the workers on the Trigoniidae subdivide into genera and subgenera, most subdivide also at the subfamily level, one or two lump some genera into sections below the subfamily level, and a few—perhaps not surprisingly—seem to refrain from using any kind of grouping between the genus and family level (Cox, 1969; Poulton, 1976).

Now to turn to the three subfamilies, the Trigoniinae, Nototrigoniinae and Austrotrigoniinae, which are the topic of the present discussion.

As originally defined (Skwarko, 1963) the Nototrigoniinae was to include *Nototrigonia* Cox, *Pleurotrigonia* van Hoepen, *Opisthotrigonia* Cox, *Eselaevitrigonia* Kobayashi & Mori, *Pacitrigonia* Marwick, *?Austrotrigonia* Skwarko, and *?Sphenotrigonia* Cox. The Austrotrigoniinae established later (Skwarko, 1968) was to include *Austrotrigonia* Skwarko and *Prototrigonia* Cox.

During the nineteen-sixties, however, the number of known trigoniid genera and subgenera increased considerably through the work of Fleming (1962, 1963: *Praegonia* and *Agonisca*), Cox (1964: *Actinotrigonia, Climacotrigonia,* and the subgenera *Callitrigonia* of *Nototrigonia,* and *Malagasitrigonia* of *Laevitrigonia*); and Skwarko (1967: *Guineana*). Consequently, when Nakano in 1970 (a, b) revised the three subfamilies in question, there were these additional genera to be considered. Nakano's grouping was as follows:

Subfamily Trigoniinae s. str.: *Trigonia* Bruguiere, 1789, *Guineana* Skwarko, 1967, *Pleurotrigonia* van Hoepen, 1929, *?Praegonia* Fleming, 1962, and *?Pseudomyophorella* Nakano, 1961.

Subfamily Nototrigoniinae Skwarko, 1963 em.: *Nototrigonia* Cox, 1962 em. (including its subgenus *Callitrigonia* Cox, 1964), *Actinotrigonia* Cox, 1964, *Pacitrigonia* Marwick, 1932 em., and *?Heterotrigonia* Cox, 1952.

Subfamily Austrotrigoniinae Skwarko, 1968 em.: *Indotrigonia* Dietrich, 1933, *Eselaevitrigonia* Kobayshi & Mori, 1954, *Opisthotrigonia* Cox, 1952, *Austrotrigonia* Skwarko, 1963, and *Sphenotrigonia* Rennie, 1936.

In 1973 Nakano also included in the Trigoniinae his new genus *Arabitrigonia.*

New genera aside, the differences between Nakano's and Skwarko's placings are fairly obvious. It may be opportune, therefore, before discussing them to outline principles accepted by and guiding the present author. These are: i. The morphology of the juvenile part of the shell is regarded as the critical criterion for determining the shell's sub-family classification; ii. The morphology of both the immature and the mature portions of the shell is the guide to its generic placing; iii. In the specific case of differentiation between members of Nototrigoniinae and Austrotrigoniinae the critical factor is the presence or absence of radial ribbing on the area (Skwarko, 1968, pp. 177, 179).

There is no disagreement regarding the placing of *Guineana* in the Trigoniinae.

The reason for the original placing of *Pleurotrigonia* in Nototrigoniinae rather than in Trigoniinae (Skwarko, 1963) was its elongate, strongly inequilateral shape combined with a broad and distinct antecarinal depression, viz. features similar to those found in *Nototrigonia* and absent from *Trigonia.* However, it would seem that both the antecarinal depression and the elongate shape are absent in the juvenile forms (Nakano, 1970a, p. 101), and consequently its placing in Trigoniinae is justified.

The monotypic *Praegonia* lacks structures associated with *Trigonia* s. str., being distinguished from it by non-triangular shape, lack of prominent marginal carina, and lack of transverse grooving on the main teeth. These features probably outweigh those shared with *Trigonia* s. str. such as surface sculpture, which though weak is nonetheless concentric on the flank and radial over most of the area. The apparent absence of radial ribbing on the proximal part of the area has not been encountered in *Trigonia* s. str. and Fleming is right in placing *Praegonia* in a distinct subfamily.

It is easy to agree with Nakano (1973, p. 65) regarding the aberrant nature of his *Pseudomyophorella* and *Arabitrigonia*, as shells which otherwise have all the morphological features of *Myophorella* in the one case and *Pterotrigonia* in the other have 'unexpectedly' developed radial ribbing on the area. As it is this radial ribbing—weak when compared with the flank ribbing—which is aberrant, and not the flank ribbing itself or the remaining shell structures, the idea suggests itself that these two genera should perhaps more naturally fit in Myophorellinae and Pterotrigoniinae respectively rather than in the Trigoniinae. One is here reminded of three species of subgenus *Callitrigonia* Cox 1964—viz. *minima, nimbosa,* and *yeuralba*—which alone out of some ten known species of *Nototrigonia* developed radial ribbing on the antecarinal depression, and then only on one valve. Cox (1964) saw fit to regard this, which may also be regarded as a kind of morphological aberration, as worthy of no more than subgeneric status.

There does not seem to be any disagreement regarding the placing of *Actinotrigonia* and *Pacitrigonia,* as well as the subgenera of *Nototrigonia* in the Nototrigoniinae. However, though members of *Pacitrigonia* such as *hanetiana* d'Orbigny have well-developed radial ribbing on the area, it is well to remember that through lack of new material it has not been possible to this day to demonstrate the suspected presence of this structure in the type species *P. sylvestri.*

Heterotrigonia should also be excluded from Nototrigoniinae as it lacks a marginal carina as well as the antecarinal depression; in addition, the ornament on the flank is in part radial and is neither concentric nor oblique in the sense of the nototrigoniids discussed in this paper.

There is no obvious reason for the removal of *Opisthotrigonia* from the Nototrigoniinae. It cannot be placed with the Austrotrigoniinae because of the radial ribbing on the area, and despite the fact that in both *A. prima* and *A. secunda* the dorsal margin of the sulcus is somewhat concave, the genus is not sickle-shaped (cf. Nakano, 1970a, pp. 95, 96) but produced straight to the rear, as borne out by both their descriptions and illustrations (Skwarko, 1963, p. 33; 1968, pp. 176–178).

Similarly, it is the presence of radial ribbing on the proximal portion of the area of *Eselaevitrigonia*—in combination with other nototrigoniid features—that has prompted its placing with the Nototrigoniinae.

Indotrigonia is excluded from Austrotrigoniinae because of the presence of radial costae on at least the proximal part of the area, and from Nototrigoniinae by the absence of an antecarinal depression. The placing, in this paper, of this elongate shell without a well-defined marginal carina in Trigoniinae is made easier by the fact that near the umbo the shell is much less produced and is distinctly tripartite (Nakano, 1961, p. 89).

There is less doubt regarding *Sphenotrigonia,* which can be retained in the Nototrigoniinae since the presence of radial ribbing on the proximal part of its area has been demonstrated (Nakano, 1970b, p. 12).

Prototrigonia shares with *Austrotrigonia* concentric ribbing on the disc and lack of a defined marginal carina. In both *P. seranensis* and *A. prima* the portion of the shell between the disc and the area is smooth and devoid of ribbing. However, in *Prototrigonia* the area is strongly curved and the whole shell is subrostrate in the rear—both features absent from *Austrotrigonia.* As suggested by Nakano (1970a, p. 96) *Prototrigonia* should probably be removed from Austrotrigoniinae, though there seems to be even less justification for placing it with *Prosogyrotrigonia.*

In summary, tht subdivision of Trigoniinae sensu lato proposed here is as follows:

- Subfamily Trigoniinae s. str.:
  - Genus *Trigonia* Bruguiere, 1879
  - Genus *Guineana* Skwarko, 1967
  - Genus *Pleurotrigonia* van Hoepen, 1929
  - Genus *Indotrigonia* Dietrich, 1933
- Subfamily Praegoniinae Fleming, 1962
  - Genus *Praegonia* Fleming, 1962
- Subfamily Nototrigoniinae Skwarko, 1963, em.
  - Genus *Nototrigonia* Cox, 1952, em.
    - Subgenus *Nototrigonia* s. str.
    - Subgenus *Callitrigonia* Cox, 1964
  - Genus *Actinotrigonia* Cox, 1952
  - Genus *Opisthotrigonia* Cox, 1952
  - Genus *Eselaevitrigonia* Kobayashi & Mori, 1954
  - Genus *Sphenotrigonia* Rennie, 1936
  - Genus *Pacitrigonia* Marwick, 1932, em.
- Subfamily Austrotrigoniinae Skwarko, 1968
  - Genus *Austrotrigonia* Skwarko, 1968

Recent evidence (this volume, p. 60) suggests that *Nototrigonia* appeared in Papua New Guinea earlier—in the Upper Jurassic—than in Australia. However, it was in the south, in the Australia-New Zealand region, that it found the most favourable breeding and evolving conditions, giving rise in Australia to *Callitrigonia* in the Aptian, and *Actinotrigonia* in or before the Cenomanian; and in New Zealand to *Pacitrigonia* in the Campanian, possibly via the Cenomanian 'N. Gen. aff. *Nototrigonia*' (for illustrations of this undescribed species see Fleming, 1964).

The origin of *Nototrigonia* is uncertain. Whether it evolved from *Trigonia* s. str. (Nakano, 1970a, p. 94) or *Guineana* (whose detail of structure in the juvenile part of shell is not known) or, more likely, from one or other of the Indo-African genera such as *Indotrigonia* or *Opisthotrigonia* is not known. It seems likely, however, that the Indo-African region was an area of origin and radiation of a number of late Mesozoic genera, including the Australian *Sphenotrigonia* and *Opisthotrigonia* and the Papua New Guinean *Eselaevitrigonia* (see above).

I wish to thank Professor Mitsuo Nakano, Hiroshima University, for the critical reading of the manuscript and for his helpful suggestions, a number of which were followed in the above paper.

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PLATE 1

All specimens coated with ammonium chloride and photographed in lateral view unless stated to contrary.

Meleagrinella sp. indet.
1 Left valve F5570 (W189); x3.
?6 Right valve F5568 (W328); x3.

?Meleagrinella cf. **superstes** (Spitz, 1914)
2 Proximally abraded left valve. F5565 (W328); x3.

'Nuculana' sp.
3 Internal cast of left valve. F5599A (W328); x3.

Entolium cf. **argentinus** (Stanton, 1901)
5 Left valve. F5697 (W189); x1.

Sphenotrigonia queenslandica sp. nov.
4 HOLOTYPE, CPC 16498. Anterior view; x1.
7 PARATYPE, F3614. Internal cast of right valve; x1.

Normanby River crossing, south of Princess Charlotte Bay, north Queensland. Neocomian.

PLATE 1

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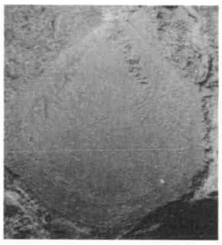

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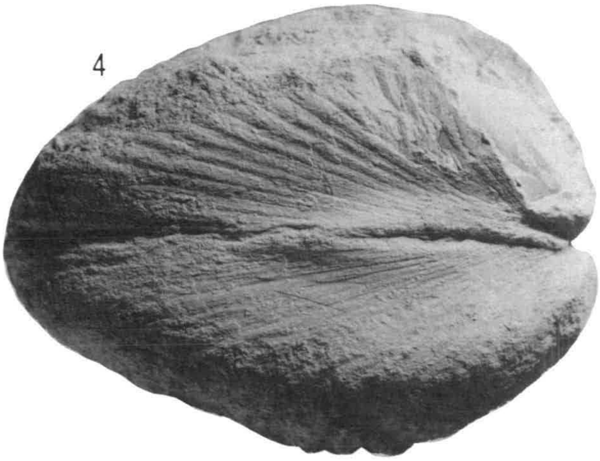

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PLATE 2

All specimens coated with ammonium chloride and photographed in lateral view unless stated to contrary.

Sphenotrigonia queenslandica sp. nov.

1, 2 HOLOTYPE, CPC 16498. View of left valve, and dorsal view; x0.8.

3 PARATYPE CPC 16499. Left valve; x0.8.

Normanby River crossing, south of Princess Charlotte Bay, north Queensland. Neocomian.

PLATE 2

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PLATE 3

All specimens coated with ammonium chloride and photographed in lateral view unless stated to contrary.

Panopea (Panopea) sp. indet. aff. **gurgitis** Brongniart, 1909

1 Right valve. QGS F5569 (W189); x1.

Iotrigonia (Zaletrigonia) normanbyia sp. nov.

2 Latex copy of ornament on proximal-most part of the right valve; x1.
3 PARATYPE QGS F3613 (W189). Proximal part of left valve; x1.
5, 6 HOLOTYPE QGS F5562. Latex copy of anteroventrally incomplete mould of mature left valve and its steinkern (QGS F3614); x0.77.

Tatella? woodsi sp. nov.

4 HOLOTYPE. Posteriorly incomplete internal cast of right valve QGS F5588 (W189); x1.

Hatchericeras lakefieldense Woods, 1962

7 Incomplete specimen CPC 16500 showing tubercles on immature part of shell and detail of pattern of most of penultimate suture; x1.

Normanby River crossing, south of Princess Charlotte Bay, north Queensland. Neocomian.

PLATE 3

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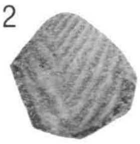

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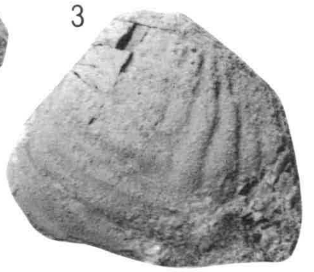

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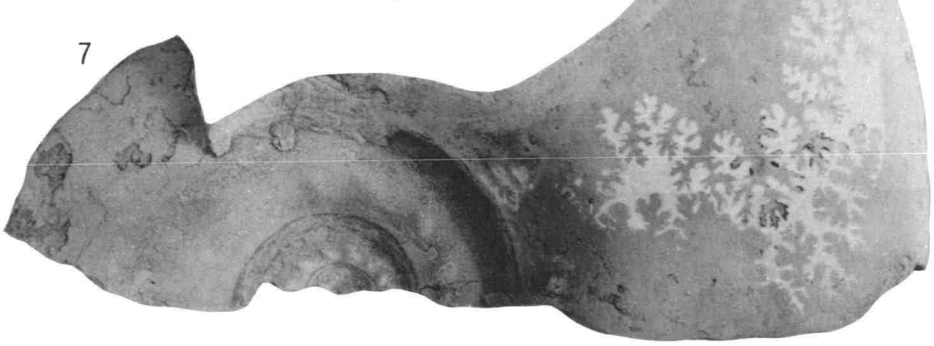

PLATE 4

All figures latex copies in natural size, coated with ammonium chloride and photographed in lateral view unless stated to contrary.

Eselaevitrigonia tyna gen. et sp. nov.

1 HOLOTYPE, CPC 15806. External impression of left valve. Note exfoliated surface of most of area.

2 PARATYPE, CPC 15807. External impression of left valve. Note fine tubercles on area; radial threads on area not readily discernible.

3, 8 PARATYPE, CPC 15808. External and internal impressions of left valve. Sulcus broad and shallow.

4 PARATYPE, CPC 15809. Internal impression of left valve.

5 PARATYPE, CPC 15810. External impression of right valve.

6 Internal impression of left valve. CPC 15811.

Bakevellia sp.

7 Internal impression of right valve. CPC 15812.

Bivalve gen. et sp. nov?

9 Cardinal area and proximal-most part of right valve. CPC 15813.

10 Posteriorly incomplete right valve. CPC 15814.

11 Internal impression of immature right valve. CPC 15815.

Wok Wunik, upstream from Wok Feneng near Olsobip Patrol Post, western Papua New Guinea. Upper Mesozoic.

PLATE 4

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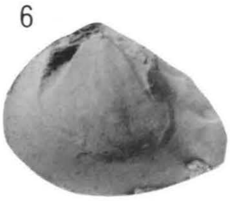

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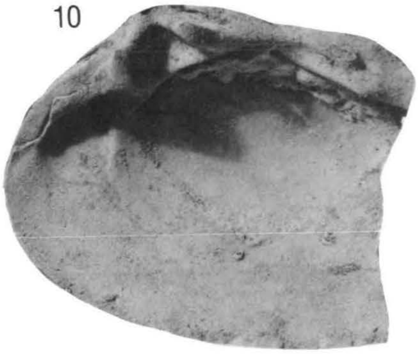

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PLATE 5

All figures are latex copies at natural size, coated with ammonium chloride and photographed in lateral view unless stated to contrary.

Iotrigonia (Zaletrigonia?) telefominiana sp. nov.

1 HOLOTYPE. CPC 16060. Anterior part of left valve.

2 PARATYPE. CPC 16062. Anteroventrally incomplete right valve.

3 PARATYPE. CPC 16059. Left valve.

4 PARATYPE. CPC 16064. Rear part of left valve showing distal part of area and ribbing on posteroventral part of flank.

5 Almost complete left valve; inverted V-pattern on front of flank barely discernible because of direction of illumination. CPC 16057.

6 PARATYPE. CPC 16058. Right valve with most of diagonal ribbing missing.

7 Ornament of proximal portion of right valve of probably large specimen showing well developed but rare V-pattern. CPC 16061.

Digiam landslide, Papua New Guinea. ?Neocomian.

PLATE 5

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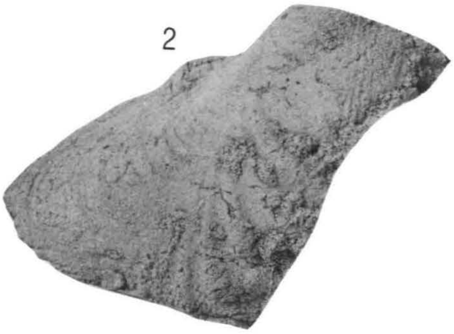

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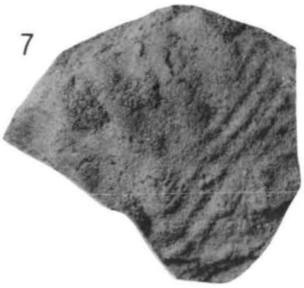

PLATE 6

All of figures latex copies of natural size, coated with ammonium chloride and photographed in lateral view unless stated to contrary.

Nototrigonia cinctuta (Etheridge Jnr, 1902) subsp. nov. A

1 Disc of immature right valve showing oblique and concentric ribbing. CPC 16054.
2 Most of left valve showing diagonal ribbing almost completely absent. CPC 16055.
3 Disc of right valve with concentric lineation only. CPC 16056.
4 Partly obscured view of interior of left valve. CPC 17107.
5 Almost complete disc of immature left valve with only diagonal ribbing developed. CPC 16068.
6 Nearly complete right valve and dorsal part of left valve. CPC 16069.
Emu Creek, Cape York Peninsula, Aptian.

Nototrigonia cinctuta (Etheridge Jnr, 1902) subsp. nov. B

7 Left valve, partly obscured, with radial ribbing on area indiscernable because of direction of illumination. Locality 4107. CPC 16063.
9 Incomplete disc of left valve from *Pronoella* layer.
10 Left valve with obscured detail of radial sculpture on area. CPC 16065.
Digiam landslide, Papua New Guinea. ?Neocomian-Upper Jurassic.

Iotrigonia (Zaletrigonia?) telefominiana sp. nov.

8 Incomplete proximal portion of left valve showing part of dentition. CPC 16066.
11 View of interior of nearly complete right valve. CPC 16067.
Digiam landslide, Papua New Guinea. ?Neocomian.

PLATE 6

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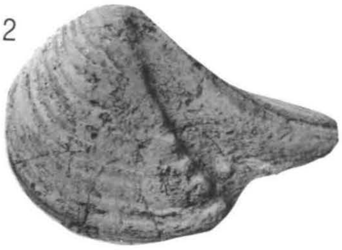

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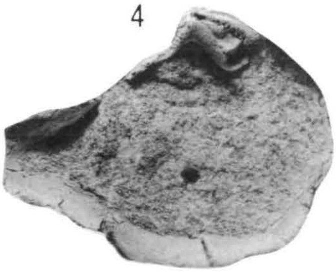

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PLATE 7

All figures of natural size, coated with ammonium chloride and photographed in lateral view unless stated to the contrary.

Bakevellia (Spia) janeki subgen. et sp. nov.

1, 3, 6 PARATYPE: exterior of posteriorly incomplete left valve; lateral cast of internal impression of left valve; latex cast of internal impression of right valve. CPC 19072.

2, 7, 8 HOLOTYPE: anterior, dorsal and lateral views. CPC 19073.

4, 5 PARATYPE: Both valves. CPC 19074.
Locality P5699 in Kanel River, a tributary of Jimi River at its junction with Kana River. Ramu Sheet area, central Papua New Guinea. Upper Triassic.

PLATE 7

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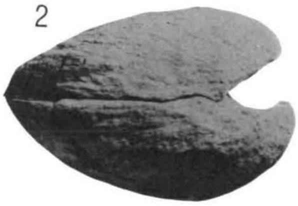

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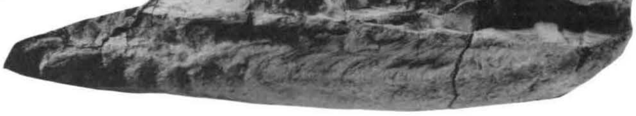

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A new fish fauna of Middle Devonian age from the Taemas/Wee Jasper region of New South Wales

BY

G. C. YOUNG & J. D. GORTER

CONTENTS

ABSTRACT

A new fish fauna has been discovered some 1900 m above the base of the Hatchery Creek Conglomerate, a thick sequence of fluvial and lacustrine sediments overlying Lower Devonian marine limestones of the Murrumbidgee Group. The following taxa are described and figured: *Turinia?* cf. *hutkensis* Blieck & Goujet (agnathan thelodont scales); *Bothriolepis verrucosa* sp. nov. and *Sherbonaspis hillsi* gen. et sp. nov. (bothriolepidid and pterichthyodid antiarchs); *Denisonosteus weejasperensis* gen. et sp. nov. (phlyctaeniid euarthrodire); Euarthrodira *incertae sedis*; Placodermi *incertae sedis; Gyroptychius? australis* sp. nov. (osteolepidid rhipidistian); and climatiid and ?ichnacanthiform acanthodian spines and scales (gen. et sp. indet.). New definitions for the antiarchan suborders Bothriolepidoidei and Asterolepidoidei are formulated on the assumption that the long obstantic margin in the former is a primitive feature, as indicated by the absence of a processus brachialis in the pectoral fin articulation of yunnanolepids. A new generic definition for *Bothriolepis* Eichwald is based on the shape and overlap relations of the anterior median dorsal and mixilateral plates, and *B. verrucosa* sp. nov. is interpreted as a primitive early representative of the genus. The holotype of *B. gippslandiensis* Hills is refigured to demonstrate the presence of orbital facets on the nuchal plate, which indicates that this species is properly referred to the genus. *Hillsaspis* Stensiö is therefore redundant. A modified definition for the family Pterichthyodidae permits the inclusion of *Stegolepis* Malinovskaya, in which the anterior median dorsal plate is narrow anteriorly, and *Sherbonaspis* gen. nov., which has three mesial marginal plates in the distal pectoral fin segment. Euarthrodiran relationships within the suborder Phlyctaenioidei are discussed, and it is concluded that the family Phlyctaeniidae is a grade group. *Denisonosteus* gen. nov. is distinguished from other phlyctaeniids by nuchal shape and the convex posterior margin of the skull-roof. The latter character was acquired independently in *Groenlandaspis* and *Holonema* on the assumption that *Arctolepis* is a primitive holonematid with a straight posterior skull-roof margin. The trunk-shield of *Denisonosteus* gen. nov. has similar proportions to that of *Phlyctaenius* Traquair. *Gyroptychius? australis* sp. nov. differs from other species in the short broad fronto-ethmoidal shield. The two acanthodians are represented only by a few incomplete spines and scales.

A maximum age for this fauna is provided by the underlying limestones (probably Emsian). The association of pterichthyodid antiarchs and osteolepidid rhipidistians in the fauna suggests broad correlation with European Middle Devonian assemblages, and an Eifelian age is proposed on the occurrence of *Turinia* cf. *hutkensis* in the Eifelian of Iran, and the fact that the earliest species of *Bothriolepis* previously reported (*B. tungseni* Chang) is also of Eifelian age. It is suggested that the *Wuttagoonaspis* fauna from the Mulga Downs Group of western New South Wales and the Cravens Peak beds in the Georgina Basin is probably older than the Hatchery Creek fauna, whilst two probably younger Middle Devonian vertebrate faunas occur in the Broken River Formation (Broken River Embayment, Queensland), and the Bunga beds (south coast of New South Wales).

INTRODUCTION

In this paper we describe a new fish fauna of probable Middle Devonian age from the Devonian sequence near Wee Jasper, New South Wales, discovered during revision of the Brindabella 1:100 000 Geological Sheet by the Bureau of Mineral Resources Tantangara Field Party in 1975 (Owen & Wyborn, 1979). The presence of a diverse fish fauna in Lower Devonian marine limestones of the Murrumbidgee Group around Burrinjuck Dam has long been known (e.g. Etheridge, 1906; Woodward, 1941; White, 1952, 1978; Schultze, 1968; Thomson & Campbell, 1971; White & Toombs, 1972; Young, 1978, 1979, 1980). However, the new fauna described here comes from a thick probably non-marine sequence of shales, sandstones, and conglomerates which overlies the western limestone outcrop in the Goodradigbee valley (Pedder, Jackson & Philip, 1970), and from which no fossil remains have previously been reported. There is little doubt however that the 'Antiarchan from Taemas' referred to by Hills (1958, p. 88) comes from this fauna, although locality information for that specimen is not available.

Numerous Devonian fish localities have previously been recorded in the literature from probable non-marine rocks in eastern and central Australia (see Hills, 1932, 1936, 1958; Tomlinson. 1968; Marsden, 1976), but except for the work of Hills (1929, 1931), Ritchie (1973), and Thomson (1973), the faunas themselves remain largely undescribed. They have generally been regarded as Late Devonian in age, although Ritchie (1973) has assigned an Early or Middle Devonian age to a fauna from the Mulga Downs Group of western New South Wales. The new fauna described here is of special interest in being the first Middle Devonian fish fauna of European aspect to be described from the southern hemisphere. In recognising the urgent need for systematic study of Devonian fish occurrences in Australia before their biostratigraphic potential is realised, our intention in the present study has been to make the faunal diversity of this occurrence known by providing a preliminary systematic account based on six collecting trips to the locality (there is ample opportunity for further collecting and a good chance that other localities will be discovered in the region). In view of the large amount of Devonian fish material from various parts of Australia at present awaiting description, we believe this to be the most practicable way of providing basic taxonomic data for use in biostratigraphic studies.

The classification of fishes adopted here generally follows Moy-Thomas & Miles (1971). Certain standard abbreviations are used in the text for dermal bones of the placoderm head and trunk-shields; these are incorporated in the list on pp. 128–9. Proportions of antiarch dermal bones are expressed in terms of a breadth/length (b/l) or length/breadth (l/b) index, as defined and used by Stensiö (1948) and Miles (1968). In the description of osteolepid remains the dermal bone terminology of Jarvik (1948) is followed. All new material described herein is deposited in the Commonwealth Palaeontological Collection (prefix CPC), housed in the Bureau of Mineral Resources, Geology & Geophysics, Canberra, Australia. Other specimen number prefixes referred to are: MUGD (type collection of the Department of Geology, University of Melbourne, Parkville, Victoria), and NMP (palaeontological collection, National Museum of Victoria, Melbourne, Victoria).

STRATIGRAPHIC OCCURRENCE

Except for the specimen mentioned above (see Hills. 1958), which was collected by H. S. Edgell some 30 years ago from an unknown locality, all material described herein comes from locality GR 469199 (1:100 000 topographic sheet 8627, Brindabella, NSW), from a horizon some 1900 m above the base of a thick succession of clastic sediments which overlies the Taemas Limestone of the Murrumbidgee Group, northwest of Wee Jasper village (Fig. 1). This succession was named the Hatchery Creek Conglomerate by Joplin et al. (1953), and has now been formally defined by Owen & Wyborn (1979). As described by these authors, its lower 1500 m is made up of conglomerate-sandstone-siltstone cycles, probably deposited in a meandering streams environment, which are overlain by a finer-grained sequence, some 1100 m thick, of mainly buff sandstone and red siltstone cycles. These are interpreted as indicating a lower energy environ-

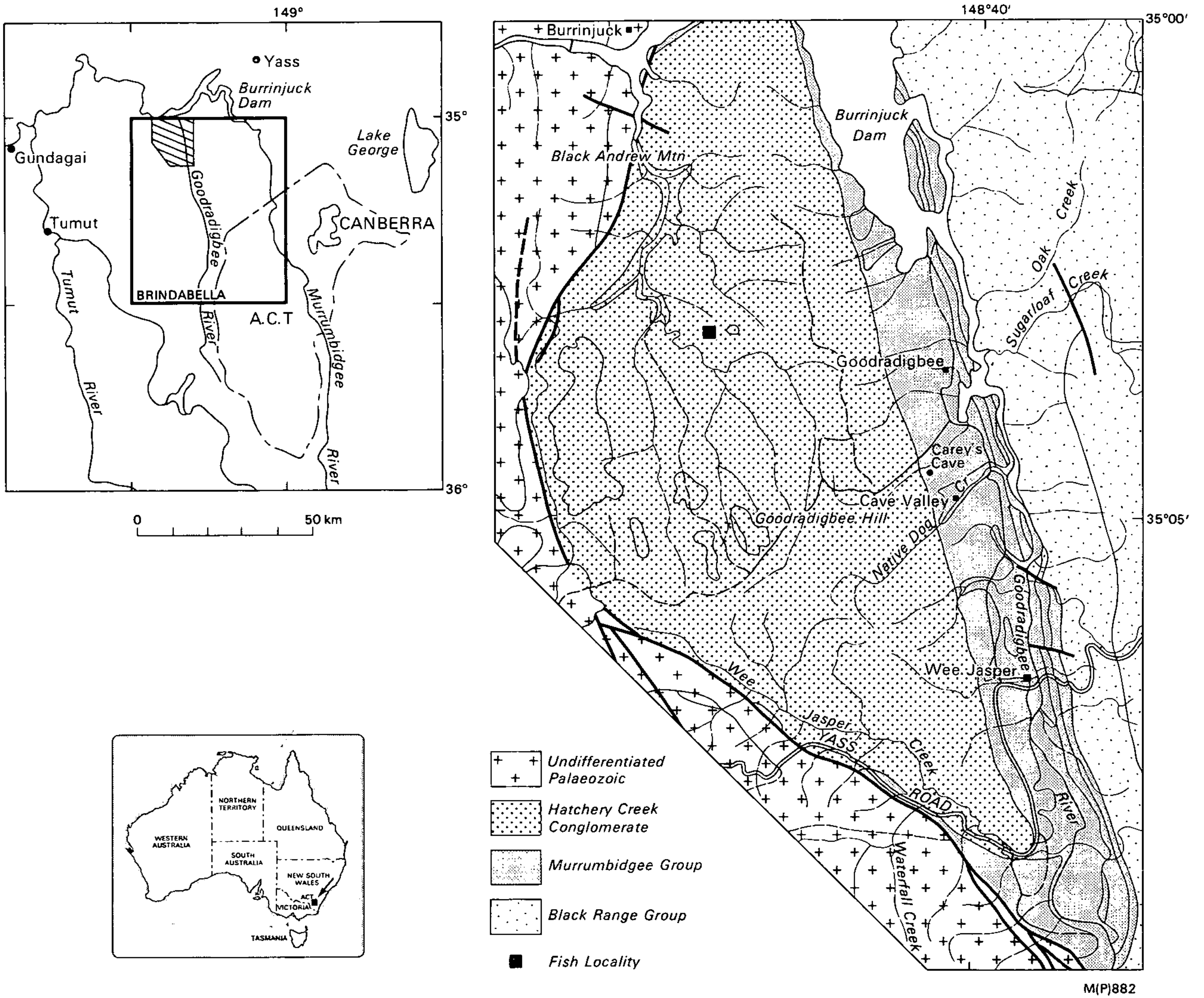

Fig. 1. Locality map for the Brindabella 1:100 000 Sheet Area in southeastern New South Wales, with a generalised geological map of Devonian rocks in the Burrinjuck Dam area.

ment, perhaps resulting from more subdued relief. Above this is another series of cycles containing basal conglomerates, of which about 300 m thickness is preserved, the top being faulted out. The relation between the Hatchery Creek Conglomerate and the underlying Taemas Limestone is uncertain, since the boundary is not marked by any obvious structural discontinuity. However the complete lithological change, and the supposed considerable difference in age between the two formations (see below), has previously been taken to indicate a disconformable relation (e.g. Pedder et al., 1970; Owen & Wyborn, 1979).

Within the middle unit of buff sandstones and red siltstones are several medium to dark grey, fine-grained cycles, each less than 30 m thick and of limited lateral extent, which have been interpreted as lacustrine deposits. From one of these darker units comes the fish fauna described here, associated with vascular plant stems (unidentified) and a few highly carbonised indeterminable spores (E. M. Truswell, pers. comm.). Some small limestone nodules have been digested in acid for conodont extraction, but have yielded only fish remains (R. S. Nicoll, pers. comm.). Most of the fish material occurs in the associated grey and red sandstones, siltstones, and dark mudstones, generally as disarticulated plates, scales and spines, although in a few instances several plates from one individual are closely associated. The bone is well preserved, dark grey except when weathered, and shows little or no sign of abrasion by current action.

FAUNAL CONTENT AND AGE

A maximum age limit for the Hatchery Creek Conglomerate is provided by the underlying Taemas Limestone, which has been dated as Emsian, with its uppermost beds possibly extending into the early Eifelian (for discussion see Pedder et al., 1970; Thomson & Campbell, 1971; Strusz, 1972; Savage, 1973; Weddige & Ziegler, 1977). However, the putative disconformity between the two formations was previously assumed to represent a considerable break in sedimentation, and in the absence of palaeontological data the Hatchery Creek Conglomerate was tentatively correlated on lithological grounds with the Late Devonian Hervey Group farther north (Pedder, 1967; Packham, 1969; Pedder et al., 1970). The fish fauna described below now indicates a Middle Devonian age for the formation. The vertebrate fauna may be listed as follows:

AGNATHA
  thelodontid:
    Turinia? cf. *hutkensis* Blieck & Goujet
GNATHOSTOMATA
  antiarchs:
    Bothriolepis verrucosa sp. nov.
    Sherbonaspis hillsi gen. et sp. nov.
  euarthrodire:
    Denisonosteus weejasperensis gen. et sp. nov.
  other placoderms:
    Euarthrodira *incertae sedis*
    Placodermi *incertae sedis*
  rhipidistian:
    Gyroptychius? australis sp. nov.
  acanthodians:
    climatiid, gen. et sp. indet.
    ?ischnacanthiform, gen. et sp. indet.

These forms provide conflicting evidence of age, with the difficulties compounded by the presence of new genera and species, and by the paucity of comparable data from other Australian Devonian fish localities. On their Old World stratigraphic distribution (e.g. Turner, 1973; Karatajūtė-Talimaa, 1978), the presence of thelodont scales referable to *Turinia* would indicate an Early Devonian age. The scales described below compare with *T. hutkensis* from the Devonian of Iran, which was dated by Blieck & Goujet (1978, p. 367) as no younger than Siegenian on the presence of an undescribed species of *Turinia* in the Kapp Kjeldsen Formation of the Wood Bay Group in Spitsbergen (see Turner, 1973, fig. 11), previously regarded as the youngest known representative of the genius (cf. Karatajūtė-Talimaa, 1978, table 1). In higher horizons of the Spitsbergen sequence thelodonts are represented by species of *Amaltheolepis*, which probably ranges into the Eifelian (Ørvig, 1969b,c; Turner, 1976). However Blieck & Goujet (1978) admitted the possibility of a younger (Emsian) age for their species, and subsequently Turner & Janvier (1979) have described similar material from north-eastern Iran, which they regard as Middle Devonian (Eifelian), as in suggested below for the Hatchery Creek fauna. Also described below are scales which in certain respects resemble species of the Emsian/Eifelian form *Amaltheolepis*, and the somewhat older *Nikolivia* (Gedinnian according to Karatajūtė-Talimaa, 1978, table 1). These associations are not easily interpreted using previously accepted stratigraphic ranges for thelodonts based on northern hemisphere occurrences. In addition thelodonts occur much more widely in Australia than the published record indicates, and although the occurrences reported by Johnstone et al. (1967; see Turner, Jones, & Draper, 1980) and Gross (1971) have been dated as Early Devonian, Eifelian and Givetian/?Frasnian thelodonts are reported by Turner & Janvier (1979, p. 892; see Turner & Dring, 1981) from limestones in New South Wales, and the Gneudna Formation of the Carnavon Basin in Western Australia. Until these Middle/?Late Devonian forms are studied in detail any biostratigraphic conclusions based on thelodonts must be regarded with caution.

The Hatchery Creek thelodonts are associated with various placoderms including a species of the genus *Bothriolepis*, a widely represented form in Australian Late Devonian sediments (e.g. Tomlinson, 1968). The earliest well dated occurrence of *Bothriolepis* in Australia prior to this work is in the early Frasnian Gogo Formation (Gardiner & Miles, 1975), and on present evidence the genus appears to be restricted to the Late Devonian in Europe and North America (e.g. Young, 1974; Lyarskaya, 1978; but cf. Westoll, 1979). In China however, it occurs as early as Eifelian (e.g. Wang et al., 1978; P'an, 1979), where it is associated with species referred to other bothriolepid genera (e.g. Chang, 1965). Of possible significance in this respect is the fact that *B. verrucosa* sp. nov. differs in several important (probably primitive) features from all other well-known species of the genus. *Sherbonaspis hillsi* gen. et sp. nov. is an asterolepid antiarch included in the family Pterichthyodidae, other representatives of which have not previously been reported from Australia, although they are well known in Middle Devonian sediments in Europe and Russia. *Byssacanthus* occurs in the Pärnu, Narova, and Lower Tartu (Aruküla) Beds in the Baltic Province (Karatajūtė-Talimaa, 1960), which were previously dated as Givetian (e.g. Westoll, 1951; Tarlo, 1964), although Russian workers now regard them as Eifelian (Obruchev, 1973; Lyarskaya, 1978). *Stegolepis* is associated with a Givetian floral assemblage in the Taldysay Suite in central Kazakhstan (Malinovskaya, 1973), and *Gerdalepis* is represented by several species in the Eifelian and Givetian of Germany and possibly the Frasnian of Belgium (Gross, 1933b; Andrews et al., 1967; Denison, 1978). In its morphology *Sherbonaspis hillsi* gen. et sp. nov. shows closest resemblance to species of these three genera. Of other pterichthyodids, *Pterichthyodes* is associated with osteolepids in the Middle Old Red Sandstone fish beds of Scotland, Orkney and Shetland (Eifelian; see Westoll, 1979), and Ørvig (1969b, p. 303) has mentioned undescribed antiarch remains in the Wood Bay Group of West Spitsbergen (Emsian/Eifelian), which may belong to a spine-bearing pterichthyodid.

The euarthrodire *Denisonosteus weejasperensis* gen. et sp. nov. is placed in the family Phlyctaeniidae, which again is a well-known group in rocks of Siegenian to Frasnian age in the northern hemisphere. Important phlyctaeniid faunas have been described by Heintz (1929) from Spitsbergen, and Pageau (1969a,b) from Canada. The Spitsbergen fauna comes mainly from the Kapp Kjeldsen and Lykta Formations of the Wood Bay Group (Siegenian/Emsian), with *Huginaspis* occurring in the slightly younger Grey Hoek Formation (Eifelian). The Canadian fauna occurs in the Gaspé Peninsula area of Quebec and New Brunswick. *Phlyctaenius acadica* (Whiteaves) was originally described from these beds, the age of which is uncertain, although they are generally regarded as being either Emsian or Eifelian (see also Denison, 1958, fig. 104). Other phlyctaeniids occur in Siegenian and Emsian strata in the Rhineland of Germany (Gross, 1933b, 1937, 1962). The youngest known phlyctaeniid, *Neophlyctaenius* from the Frasnian of New York State, retains a relatively primitive morphology (Denison, 1950, 1978). From Australia Ritchie (1969, figs. 3, 4) has figured undescribed material from the Mulga Downs Group of western New South Wales, which shows 'a close resemblance to Northern Hemisphere genera such as *Huginaspis, Heterogaspis* and *Arctolepis*' (Ritchie, 1973, p. 70). Similar forms have recently been collected in the Georgina Basin (see below). The new phlyctaeniid described here resembles several Early Devonian forms in retaining an elongate Nu plate in the skull-roof (but this feature is not known in *Neophlyctaenius*), whilst its trunk-shield morphology is unspecialised, and generally similar to that of *Phlyctaenius acadica.* For the present we regard it as indicating an Emsian/Eifelian age.

The Hatchery Creek rhipidistian is tentatively referred below to the osteolepidid genus *Gyroptychius* McCoy, and represents another well studied northern hemisphere family previously very poorly known in Australian Devonian rocks (see Hills, 1958, p. 90). Fragmentary rhipidistian remains from the Upper Devonian in the Parkes/Forbes area of New South Wales were described by Hills (1932), but they all show surface ornament. and probably belong in part to eusthenopterids or holoptychiids. (*Canowindra grossi* Thomson, 1973, from the Upper Devonian Manadery Sandstone, shows holoptychoid affinities, although Ritchie (1975) notes that some of Hills's figured material belongs to the euarthrodire *Groenlandaspis.*) Other crossopterygian remains have been reported from the Late Devonian of Victoria (Marsden, 1976, p. 122), and from several horizons on the New South Wales south coast (Young, in Fergusson et al., 1979). For the most part these remains also comprise ornamented bones and scales, and do not belong to members of the Osteolepididae. However, the New South Wales material includes a single cosmoid scale which compares well with the osteolepid scales described below, although such isolated remains are not generically determinable (see Jarvik, 1948, p. 106), and from the South Blue Range near Mansfield, Victoria, other cosmine-covered remains have been collected. (One specimen, NMP47820, an osteolepid frontoethmoidal shield from Ovens Creek in the South Blue Range, was borrowed for comparative purposes, but has quite different proportions to the material described below. In all probability it is Late Devonian in age.) In contrast the osteolepid record from the northern hemisphere is much more completely known, the earliest reported species being *Thursius macrolepidotus* from the Wick Beds of the Middle Old Red Sandstone sequence in Scotland (Andrews et al., 1967; for a stratigraphic revision of this area, see Donovan et al., 1974). Species of *Osteolepis* and *Gyroptychius* occur slightly higher in the Scottish sequence in the well known Achanarras fish band, which has a diverse fish fauna including the antiarch *Pterichthyodes milleri,* as mentioned above. In the overlying John O'Groats Sandstone osteolepids are replaced by the eusthenopterid *Tristichopterus.* The Achanarras horizon and equivalent fish beds in the Scottish Middle Old Red Sandstone (see Miles & Westoll, 1963, p. 206) have been broadly correlated with the Pärnu and Narova Beds of the Baltic sequence (see Nilsson, 1941, p. 50; Gross, 1942; Jarvik, 1950a, table 7; Westoll, 1951, table 3). Hemmings (1978; also Jarvik 1950c, p. 40) has argued against this correlation on the grounds that the antiarch remains from the Baltic previously referred to *Pterichthyodes* were wrongly determined, and belong either to *Asterolepis* or *Byssacanthus* species. Nevertheless, the latter genus is a pterichthyodid, and in the absence of contradictory evidence from other groups the correlation proposed by earlier workers must stand as a best approximation. As noted above, the most recent Russian work indicates that this part of the Baltic sequence is Eifelian in age (Obruchev, 1973; Lyarskaya, 1978).

Finally the few small spines in the Hatchery Creek fauna tentatively referred to an ischnacanthiform acanthodian are insufficiently known for any biostratigraphic inference to be drawn, as similar remains occur widely in Upper Silurian to Middle Devonian strata in Europe (see Ørvig, 1957, p. 338; Andrews et al., 1967). The same applies to the climatiid spines described below, which do, however, show special morphological features also seen in the Baltic form *Nodocosta pauli,* which according to Lyarskaya (1978) is known from both Eifelian and Frasnian levels in the sequence. Other members of the Climatiidae occur in rocks of Late Silurian to Middle Devonian age in Europe and North America (Miles, 1966; Pageau, 1969a). From the Australian Devonian, isolated acanthodian spines have been described by Hills (1929, 1931), and articulated remains reported by Warren (1971; also in Marsden, 1976, p. 122), and Young (in Fergusson et al., 1979). That the group was widespread is indicated however by numerous other reports of isolated spines and scales from southeast, central, and northwest Australia (Hills, 1932, 1958; Tomlinson, 1968; Gross, 1971; Ritchie, 1973; Turner et al., 1980), in rocks ranging in age perhaps from the Late Silurian (the occurrence near Canberra recorded by Tomlinson, 1968, p. 211) to the end of the Devonian. At present however these remains have not been studied in sufficient detail for their considerable biostratigraphic potential to be realised.

Synthesising these remarks, it can be seen that the Hatchery Creek fauna is made up of associations either not previously recorded, or not properly documented (e.g. thelodont scales with bothriolepid and asterolepid antiarchs; *Bothriolepis* with a pterichthyodid, and a small osteolepid), and an age assessment based on straightforward comparison with European vertebrate zones is therefore not possible. However, broad comparisons with certain European occurrences (for example the association of pterichthyodid antiarchs and osteolepidid rhipidistians in the Achanarras fish band of the Scottish sequence) would point to a Middle Devonian age for the fauna, and this is supported by the absence of certain forms (e.g. the placoderm *Phyllolepis*) which are widespread in Frasnian and younger Devonian deposits in Australia (Hills, 1959; Tomlinson, 1968; Young, in Fergusson et al., 1979). It has previously been suggested (e.g. Hills, 1958; Tomlinson, 1968; Young, 1974) that the long-established vertebrate zones for the Late Devonian of Europe are not applicable to Australian sequences, and it now seems that this also applies to Middle Devonian continental deposits in Australia. There are however clear indications that more relevant comparisons should be possible with the vertebrate faunas of south China on the one hand, and those currently being studied in the Middle East (e.g. Janvier, 1974, 1978; Blieck & Goujet, 1978; Turner & Janvier, 1979) on the other. On this basis we would put forward the following evidence as indicating an Eifelian age for the Hatchery Creek fauna: 1) the revised assessment of the Iranian occurrence of *Turinia hutkensis* as Eifelian; 2) the fact that the earliest known species of *Bothriolepis* (*B. tungseni* Chang) is also Eifelian; and 3) the fact that *Bothriolepis verrucosa* sp. nov. displays various primitive characters consistent with it being an early representative of the genus. An Eifelian age is not contradicted by other elements of the Hatchery Creek fauna (pterichthyodids, phlyctaeniids, osteolepids, acanthodians), but it should be pointed out that since the fauna occurs some 1900 metres above the base of the formation and the underlying (Emsian/?Eifelian) limestones, the suggested age would imply a rate of sedimentation of the same order as that recorded by Friend & House (1964, table 1) as a maximum for this part of the geological column (almost 4,000 metres for the whole Middle Devonian sequence of East Greenland). We would conclude therefore that a late Eifelian age is more likely for the Hatchery Creek fauna, and that the deposition of the Hatchery Creek Conglomerate continued probably into Givetian time.

FAUNAL COMPARISONS

Accepting this tentative age determination for the Hatchery Creek fauna, some of the differences to contemporaneous assemblages in European sequences may be further considered in a closer analysis of faunal changes across the Eifelian/Givetian boundary in Europe. In some instances these have been documented in considerable detail, and no doubt reflect only local features of little biostratigraphic relevance to elucidating the Devonian vertebrate succession in Australia. However the absence of various taxa which were abundant and diverse in Europe is of potential biogeographic and ecological interest. By comparison with the well known Achanarras fish band of Scotland for example (see Rayner, 1963; Saxon, 1975), the Hatchery Creek fauna is impoverished, lacking such major groups as brachythoracid and ptyctodontid placoderms (*Coccosteus, Homostius, Rhamphodopsis*), holoptychoid rhipidistians (*Glyptolepis*), dipnoans (*Dipterus*), palaeoniscoids (*Cheirolepis*), and the enigmatic *Palaeospondylus.* In addition, the osteolepids and acanthodians at Achanarras are each represented by several genera and species. Similar differences are evident in comparisons with the lower (Pärnu) horizon in the Baltic sequence. Gross (1942, p. 376) presented faunal lists for this sequence which were updated by Obruchev (1973), with details of the Latvian succession provided by Lyarskaya (1978). Obruchev's list for the Pärnu again includes species of *Homostius* and *Glyptolepis*, and also *Porolepis* (not known from Scotland). Dipnoans, coccosteids, and palaeoniscoids first appear higher in the sequence, whilst placoderms are further represented in the Pärnu by the dolichothoracid *Actinolepis.* Although *Dipterus* sp. indet. was listed by Gross (1942) and Obruchev (1958, p. 45), in subsequent lists it is shown first appearing in the overlying Narova. Lyarskaya (1978) omits *Glyptolepis*, but also records *Heterostius* from the Pärnu, although this form is again more characteristic of the overlying Narova Beds (e.g. Obruchev, 1951). The significant resemblance between the Pärnu assemblage and the Hatchery Creek fauna is in the association of the pterichthyodid antiarch *Byssacanthus* with osteolepids (*Thursius talsiensis* and *Gyroptychius latvicus* according to Lyarskaya). A further significant difference however is the presence of psammosteid heterostracans in the Baltic fauna. This major agnathan group has yet to be discovered in the Australian Devonian. It should also be noted that in the Scottish sequence psammosteids do not appear until the Late Devonian (see Tarlo, 1964; Miles, 1968).

In the overlying beds of the Baltic sequence *Byssacanthus dilatatus* ranges through the Narova and Lower Tartu (Aruküla) horizons (see Young, 1974, fig. 1), in both formations being associated with the first *Asterolepis* species (*A. estonica* Gross). According to Lyarskaya, *Thursius* and *Gyroptychius* are represented by different species in each horizon, the palaeoniscoids *Orvikuina* and possibly *Moythomasia* (see Obruchev, 1973) are recorded, and the small brachythoracid *Millerosteus orvikui* makes its appearance in the Narova, with species of *Coccosteus* and *Holonema*, and the acanthodian *Nodocosta pauli*, appearing in the Aruküla. There are significant changes in the psammosteids, which have proved to be one of the most useful index fossil groups for this succession (e.g. Tarlo, 1964). The overlying Burtnieck (Upper Tartu) beds, now regarded as Givetian (Obruchev, 1973; cf. Young, 1974), contain new species of psammosteids, *Actinolepis, Coccosteus, Holonema, Asterolepis* and *Gyroptychius.* According to Lyarskaya this *Gyroptychius* species is the highest osteolepid occurring in the Baltic sequence, whilst *Byssacanthus* possibly also extends into the Burtnieck, but no higher. In general terms, the influx of a variety of brachythoracids, and species of *Asterolepis*, *Glyptolepis*, and palaeoniscoids in the Narova, Aruküla, and Burtnieck beds, would seem to indicate increasing dissimilarity to the Hatchery Creek fauna, and it could be suggested therefore that the Hatchery Creek fauna represents a broadly equivalent or perhaps slightly older fauna than preserved in the lowermost Baltic horizon (the Pärnu Beds). Conversely, certain other well-known vertebrate occurrences from the northern hemisphere would appear to be slightly older than the fauna described here. Of the assemblages containing phlyctaeniid euarthrodires from the German Rhineland, Spitsbergen, and eastern Canada mentioned above, none is known to contain osteolepid rhipidistians. Antiarchs have been reported from the Wood Bay Group in Spitsbergen but remain undescribed (see above), whilst the Rhenish phlyctaeniid faunas are Siegenian/Emsian in age, and the slightly younger *Gerdalepis* occurrences in the Eifelian Mühlenberg Sandstone are not associated with other vertebrate remains (Gross, 1937; 1941). Not to be overlooked, furthermore, is the strong likelihood that facies control and perhaps provinciality due to migration barriers between Laurasia and Gondwana during the Devonian have markedly accentuated these faunal differences. Until they are better understood, such factors stand in the way of well supported correlations based on Devonian vertebrates between Australia and the northern hemisphere.

Finally some remarks should be made regarding possible biostratigraphic relationships between the Hatchery Creek fauna and other vertebrate occurrences in Australia which have been assigned a Middle Devonian age. Three of these are now known: the *Wuttagoonaspis* fauna of Ritchie (1969, 1973), the small fauna from the Bunga beds briefly described by Young (in Fergusson et al., 1979), and a newly discovered marine fauna from the Broken River area of northeast Queensland. The identification of *Asterolepis* (?Middle Devonian) from Gilberton in Queensland by Hills (1958, p. 89) is doubtful, and probably represents another Late Devonian occurrence of *Bothriolepis*.

Ritchie (1973) has suggested an Emsian/Eifelian age for the fauna from the lower part of the Mulga Downs Group of western New South Wales, which includes *Wuttagoonaspis fletcheri* Ritchie, a placoderm of uncertain affinity (Miles & Young, 1977; Denison, 1978; Young, 1980) and not known from outside Australia, and also various undescribed phlyctaeniid euarthrodires said to resemble northern hemisphere genera such as *Huginaspis*, *Heterogaspis*. and *Arctolepis*. Subsequently, Ritchie (1975, p. 570) has also reported plates displaying 'features approximately intermediate between those of *Tiaraspis* and *Groenlandaspis*.' In addition Ritchie (1973) noted the presence of a *Wuttagoonaspis* species in the Cravens Peak beds of the Toko Syncline, Georgina Basin, from which thelodont scales had previously been reported (Johnstone et al., 1967; Tomlinson, 1968). Much additional thelodont material has since been obtained from a small limestone outcrop in the southern Toomba Range of the Georgina Basin, which evidently differs at least at specific, and possibly at generic level from the thelodonts described herein (Turner, Jones, & Draper, 1981). According to these authors the calcareous thelodont-bearing unit at the new locality forms a gradational, conformable upper contact with more typical sandstones and conglomerates of the overlying Cravens Peak beds, from which an abundant fauna with *Wuttagoonaspis* sp., various other placoderms (including phlyctaeniids), acanthodians, crossopterygians, and other undetermined remains is now known. In addition, from the small limestone outcrop just mentioned one of us (GCY) has collected acanthodian spines, fragmentary plates of large placoderms and a small (pterichthyodid) antiarch, and teeth and scales probably belonging to an onychodontid crossopterygian.

These substantial collections of Devonian vertebrates from the Georgina Basin will be fully described at a future date, and for the present it can be assumed that they represent a contemporaneous fauna to the *Wuttagoonaspis* fauna from the Mulga Downs Group. Until other elements in these faunas are adequately described, detailed comparisons with the Hatchery Creek fauna cannot be made but there is other evidence that the latter fauna may be somewhat younger. Glen (1979) has recently reported wuttagoonaspid fish plates in upper beds of the Amphitheatre Group, which underlies the Mulga Downs Group in western New South Wales, and contains a marine invertebrate fauna indicating a late Early Devonian (Pragian) age. In addition, Turner et al. (1981) have determined the thelodonts from the Cravens Peak beds as *Turinia* cf. *pagei* and *Turinia australiensis*, which are Dittonian zone fossils in Europe (Turner, 1973). This is consistent with the invertebrate evidence from the Amphitheatre Group just cited. We tentatively suggest therefore that the *Wuttagoonaspis* fauna may be somewhat older (Emsian/?Eifelian) than the fauna described below.

Conversely, the Bunga beds fauna from the New South Wales south coast probably represents a younger Middle Devonian occurrence. Preliminary determinations (Young, in Fergusson et al., 1979) include a holoptychoid rhipidistian, various acanthodians, and elasmobranchs of uncertain affinity with diplodont teeth and ctenacanth-like spines (previously determined as a possible dolichothoracid placoderm). This fauna is dated as no younger than early Frasnian, and probably Givetian, and on present information it has no elements in common with the new fauna described below. Finally the recently discovered placoderm material from the Broken River Embayment in Queensland comes from several horizons in the Broken River Formation, and associated invertebrates indicate both Eifelian and Givetian ages (J. S. Jell, personal communication). Both euarthrodires (a large brachythoracid) and antiarchs are represented, the latter including a pterichthyodid-like form suggesting a possible broad correlation with the Hatchery Creek fauna. The biostratigraphic relationships between these faunas should be clarified when the Broken River assemblage has been described.

In summary, at least four distinct vertebrate faunas are now known from the Middle Devonian of Australia. In approximate order of decreasing age they are the *Wuttagoonaspis* fauna (?Emsian/early Eifelian), the Hatchery Creek fauna (?late Eifelian), the Broken River fauna (?Eifelian/Givetian) and the Bunga beds fauna (?Givetian/early Frasnian). It is to be expected that systematic description of these faunas should provide a basis for more detailed correlation of marine and non-marine Middle Devonian strata within Australia.

SYSTEMATIC DESCRIPTIONS

Superclass	AGNATHA
Class	PTERASPIDOMORPHI
Subclass	THELODONTI
Order	THELODONTIDA
THELODONTIDA	incertae sedis

Remarks: In two recent classifications of the Order Thelodontida, Turner (1976) has recognised three families (Thelodontidae, Turiniidae, and Apalolepididae), and Karatajūtė-Talimaa (1978) five (Coelolepididae, Turiniidae, Apalolepididae, Nikoliviidae, and Palaeodontidae). The material dealt with below shows closest resemblance to scales described by Blieck & Goujet (1978) as a new species of *Turinia* (Family Turiniidae of Turner, 1976, and Karatajūtė-Talimaa, 1978), but in certain morphological features some scales also resemble those referred to the genera *Apalolepsis, Amaltheolepis,* and *Nikolivia* (Families Apalolepididae and Nikoliviidae of Karatajūtė-Talimaa, 1978; cf. Turner, 1976, p. 15). Nevertheless there are morphological consistencies in the available small sample which suggest that a single species is involved, thereby indicating that these proposed familial groupings may be unreliable. In view of the considerable intraspecific variation known in thelodont scales (e.g. Gross, 1967), and the paucity of articulated remains, we consider the erection of familial groupings based on only one scale morphology and histology to be premature at this stage, and the material described below has therefore been left in open nomenclature.

Genus **Turinia** Traquair, 1896

Type species: T. pagei (Powrie, 1870)

Remarks: Other species referred to this genus have been described by Gross (1971; *T. australiensis*), Karatajūtė-Talimaa (1978; *T. polita*) and Blieck & Goujet (1978; *T. hutkensis*). *Turinia? oervigi* (Karatajūtė-Talimaa, 1968) has been referred to the new genus *Nikolivia* (Karatajūtė-Talimaa, 1978). As noted above, the new material described here shows closest overall resemblance to *T. hutkensis* Blieck & Goujet, and it is tentatively included in *Turinia* on the assumption that the latter species has been correctly assigned. However, *T. hutkensis,* like most of the scales described here, differs mainly from other *Turinia* species (e.g. Karatajūtė-Talimaa, 1978, pls. 38-41) in lacking a distinctly flattened central area on the crown. Whether this warrants generic separation is at present unclear, but other possibly significant characters of the genus, for example the elongation of the base into a prominent anterior process, are well developed in both *T. hutkensis* (see Blieck & Goujet, 1978, p. 364, Turner & Janvier, 1979) and this new material. *T. hutkensis* has not been studied histologically, but one scale here has been sectioned, and although poorly preserved shows a simple pulp cavity of *Thelodus*-type (see Gross, 1967, p. 6), developed similarly to that figured for *Turinia pagei* by Gross (1967, fig. 7C), with numerous side branches emanating from the central pulp cavity. It is possible however that the dentine tubules were more densely distributed, as is apparently also the case in *Amaltheolepis winsnesi* Ørvig (Karatajūtė-Talimaa, 1978, figs. 39-41). Other resemblances to *Amaltheolepis* are the greater elongation of body scales and the apparent predominance of elongate or thorn-shaped scale types in the sample. However this new material can be distinguished from the *Amaltheolepis* species so far described (Ørvig, 1957, 1969b,c; Karatajūtė-Talimaa, 1978) by the apparent absence of tricuspate scale forms, by the presence of flat-topped or grooved ridges on the crown, often bearing prominent lateral projections, and by the common elongation of the base to form a prominent anterior process. These features never occur in *Amaltheolepis* (Ørvig, 1957, p. 293), but are commonly developed in species of *Turinia.*

Turinia? cf. **hutkensis** Blieck & Goujet, 1978

Fig. 2; Pl. 1; Pl. 2, figs. 1, 2

Material: 19 disarticulated scales separated from the matrix (CPC 17015-17032), one of which has been sectioned (CPC 17030), and 47 scales in hand specimen (CPC 17033-17040).

Remarks: T. hutkensis was erected by Blieck & Goujet (1978) on the basis of some 20 scales said to differ from those of other species in the following characters: the less elongate tear-shaped crown on the flank scales; the more convex central region of the crown; and the presence of minor grooves on the coronal ridges. It is suggested below that a further distinguishing feature from the type species may be the larger proportion of the body covered by navicular trunk scales.

The present material includes a wider variety of scale morphologies than described by Blieck & Goujet, but this is to be expected in a larger sample. This material is regarded as closely comparable to *T. hutkensis* primarily on the morphology of typical body scales, which in both instances have a very similar disposition of ridges and major and minor grooves on the crown.

Description: The three characters specified by Blieck & Goujet are each displayed in some of the material described here, although taking the sample as a whole the new scales appear to be more elongate than either *T. hutkensis* or other *Turinia* species. A predominance of elongate thorn-like scales is also seen in *Amaltheolepis* (Ørvig, 1957; 1969b, c; Karatajūtė-Talimaa, 1978), but. as noted above, the ridges and grooves on the crown in *Amaltheolepis* have quite a different morphology, and the base never develops an anterior process. On the other hand, the navicular body scales which form a a large proportion of this new collection (e.g. Fig. 2L, M) normally have a strong anterior process, and show a coronal sculpture which corresponds well with that figured by Blieck & Goujet (1978, pl. 61, figs. 3, 5, 7, 10; also Turner & Janvier, 1979, fig. 1E). Characteristic are fairly prominent paired lateral grooves converging toward the posterior, and separated by a tear-shaped central region carrying a number of subsidiary grooves near its anterior margin (e.g. Pl. 1, fig. 7). A slight variation is seen in CPC 17034, which has a similar spur on the base but a shorter broader crown with a fairly flat dorsal surface, and only the paired lateral grooves well developed. Such scales are of similar size to those figured by Blieck & Goujet (1–1.5 mm long), and in both occurrences there are also occasional larger scales, up to 2 mm long (e.g. Fig. 2N; Pl. 1, fig. 13; cf. Blieck & Goujet, 1978, pl. 61, fig. 10). As previously illustrated the neck in these scales forms a distinct trough separating crown and base. In CPC 17023 (Fig. 2N) the base was apparently extended anteriorly in two prongs on an asymmetrical scale in which the lateral ridges on the crown are expanded to form flanges or short processes, as are also evident in the examples of Blieck & Goujet (1978, pl. 61, figs. 6, 7, 8). Similar flanges have been reported in *T. pagei* (Turner et al., 1981), and are also well displayed in CPC 17024 (Pl. 1, fig. 2), which has a symmetrical crown with five paired ridges and again a broader median ridge with minor longitudinal grooves. CPC 17015 is another body scale with a blunt posterior margin, a less prominent neck, and fine grooves on some of the lateral ridges (Fig. 2A; Pl. 1, fig. 1; cf. Blieck & Goujet, 1978, pl. 61, fig. 7). Again lateral protuberances can be seen on some of the ridges.

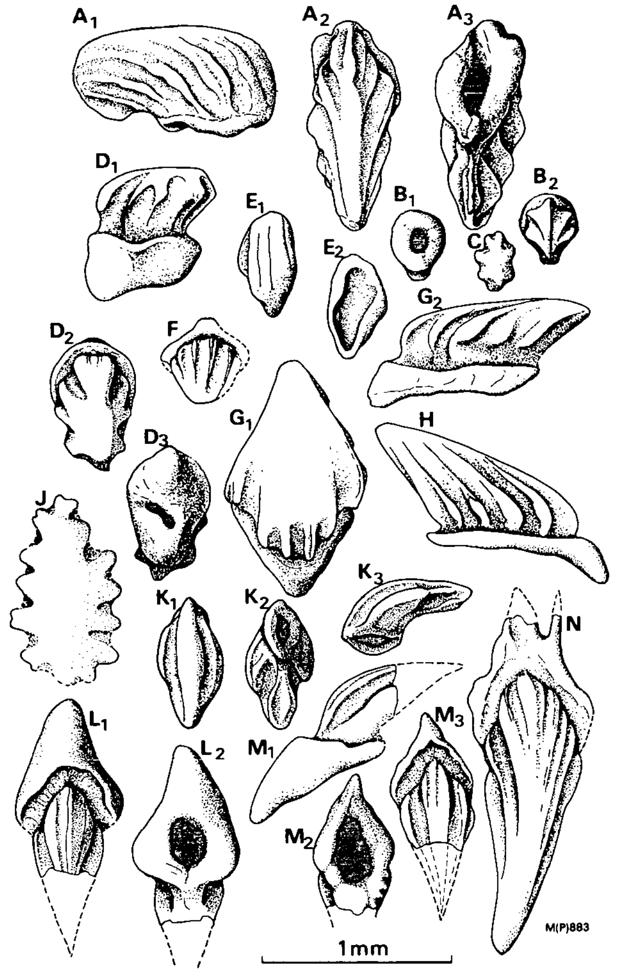

Fig. 2. ***Turinia?* cf. *hutkensis* Blieck & Goujet. A1-3, body scale in lateral, dorsal, and ventral views, CPC 17015; B1,2, head scale in ventral and dorsal views, CPC 17019; C, head scale in dorsal view, CPC 17921; D 1-3, head scale in lateral, dorsal, and ventral views, CPC 17016; E1,2, scale in dorsal and ventral views, CPC 17017; F, scale in dorsal view, CPC 17022; G1,2, scale in dorsal (inverted) and lateral views, CPC 17020; H, scale in lateral view, CPC 17035; J, scale in dorsal view, CPC 17038; K1-3, scale in dorsal, ventral, and lateral views, CPC 17018; L1,2, incomplete body scale in dorsal and ventral views, CPC 17025; M1-3, incomplete body scale in lateral, ventral and dorsal views, CPC 17028; N, body scale in dorsal view, CPC 17023.**

These scales can be regarded as fairly typical body scales, but there are other morphological variants apparently not represented in the material described by Blieck & Goujet. CPC 17033 is a hand specimen on which 12 scales are exposed. Most are typical body scales, but in several the crown is flattened and expanded on either side of the paired lateral grooves. This flattened area is fringed posterolaterally by a row of cusps to give a morphology somewhat similar to some *Amaltheolepis* scales figured by Ørvig (1957, fig. 3M), and Karatajūtė-Talimaa (1978, pl. 53). However, the raised central portion in the scales described here is essentially the same as on the associated normal body scales, with a number of subsidiary grooves along its anterior margin. This suggests that this is a special scale type from some limited region of the trunk. It is noteworthy that more extreme development of this flattened and expanded crown morphology is characteristic of the genus *Apalolepis* (Karatajūtė-Talimaa. 1978, pls. 49, 50). CPC 17018 is a different type of small scale (length about 0.5 mm), which is less pointed posteriorly with a raised central portion lacking intermediate grooves (Fig. 2K; Pl. 2, fig. 1), and has an asymmetrical base (Pl. 2, fig. 2). In the anterior position of base, and the generally less pronounced coronal ornament than in the other scales just described, this specimen compares well with certain scales of *Nikolivia oervigi* (e.g. Karatajūtė-Talimaa, 1978, pl. 46, fig. 4). In some respects it also resembles the scale compared by Turner & Janvier (1979, fig. 1B) with *Skamolepis*. In an associated immature scale whose pulp cavity has not closed in (Fig. 2E), the ornament is further reduced to give a fairly simple crown morphology again similar to that in species of *Nikolivia* (e.g. Karatajūtė-Talimaa. 1978, pl. 42, fig. 7), in which, however, the pulp cavity is generally less extensive. Another scale, with a fairly high posterodorsally-directed conical crown ornamented with a smooth median and five lateral ridges (Fig. 2H), resembles a different scale type referred to *Nikolivia* (Karatajūtė-Talimaa, 1978, pl. 43, figs 1, 11). This crown morphology is also reminiscent of some *Amaltheolepis* scales (e.g. Ørvig, 1969b,c) but unlike *Amaltheolepis* the specimen described here shows an incipient anterior spur on the base. This scale bears no resemblance to the single tricuspid scale from the Cravens Peak beds tentatively referred to the family Nikoliviidae and compared also to *Amaltheolepis* scales by Turner et al. (1980, fig. 13).

Other scales closely resemble figured examples of *Turinia pagei*, in which most of the body surface was covered with scales with a fairly flat crown and crenulate margins (see Ørvig, 1969a, fig. 2). CPC 17038 (Fig. 2J) is a scale of this type about 1 mm long with a slightly convex crown carrying some 13 crenulations (cf. Turner, 1973, fig. 8a). Its base is not exposed. Other examples of this scale type are CPC 17026 and 17031. CPC 17016 (Fig. 2D, Pl. 1, figs 5, 6) is a high-crowned scale with a cushion-like base closely resembling those named *Turinia* sp. by Ørvig (1969a, fig. 2B-D), or the head scale of *T. pagei* figured by Turner (1973, pl. 2B). Other scales resembling some previously referred to *T. pagei* may also come from the head region (Fig. 2B, C; Pl. 1, figs 3, 4; cf. Karatajūtė-Talimaa, 1978, pl. 35). Similar small scales have been referred to *T. australiensis* (Gross, 1971. pl. 12, fig. 5), and Turner et al. (1981, p. 58) have commented that 'In some instances, it is difficult to decide whether a scale belongs to *pagei* or *australiensis*'. Finally CPC 17020 (Fig. 2G; Pl. 1, fig. 10) and CPC 17027 are large scales probably from a zone of transition, with a fairly flat crown showing in dorsal view two lateral grooves and three subsidiary mesial grooves on the anterior margin. The sides of the crown are ornamented with three flange-like ridges. In these examples the crown is wider than the base, in contrast to the transitional scale of *T. hutkensis* figured by Blieck & Goujet (1978, pl. 61, figs. 9, 11), which does however have a fairly flat central region to the crown (cf. Remarks above). The scales described here show some resemblance to the *T. pagei* scales figured by Gross (1967, pl. 7, figs. 1, 2).

These illustrations and descriptions give some idea of the morphological variation encountered in this material, but no indication of relative abundance. Of the 66 scales examined, almost 60% were elongate navicular scales from the body. This is in contrast to what might be expected of *T. pagei* remains, in which, as noted above, elliptical scales with a flat crown and crenulate margins cover much of the body surface (Ørvig, 1969a; Turner et al. 1981). Clearly any sample could be strongly modified by current sorting, but in the present case the finest surface detail is always preserved, with no indication of abrasion on any of the scales examined. It is tentatively suggested therefore that a greater proportion of the body surface was covered by elongate or pointed scales, with the elliptical or transition scales restricted to a much smaller area than in *T. pagei*. A larger sample is required before this feature can be demonstrated in the type material of *T. hutkensis*.

Superclass	GNATHOSTOMATA
Class	ELASMOBRANCHIOMORPHI
Subclass	PLACODERMI
Order	ANTIARCHA
Suborder	BOTHRIOLEPIDOIDEI Miles, 1968

Definition: Antiarchs with a small PP plate separated from the LA plate by the Nu, which forms part of the posterior margin of the orbital fenestra. AMD plate with a broad anterior margin; processus obstans strongly developed; PDL and PL plates replaced by a single MxL; semilunar plate unpaired. Adducted pectoral appendage reaching back beyond trunk-shield; dorsal central plate 2 small, and separated from doral central plate 1 by lateral and mesial marginal plates 2.

Family BOTHRIOLEPIDIDAE Cope, 1886

Definition: as for suborder (only family).

Remarks: This definition is modified after Miles (1968, p. 21), who placed the genera *Bothriolepis*, *Grossilepis*, and *Dianolepis* in a single family within the suborder and also tentatively included *Wudinolepis*. Denison (1978) has proposed a similar grouping, but has followed Gross (1965) in including also *Yunnanolepis* (see below). In *Dianolepis liui* Chang however, the PP plate excludes the Nu from the margin of the orbital fenestra, and the obstantic margin is apparently short (Chang, 1965), and this form may therefore not properly belong in the family. (For supposed similarities between *Dianolepis* and *Bothriolepis gippslandiensis* Hills see further remarks below). On the other hand, in *Wudinolepis weni* Chang there is probably a small PP, and Nu of bothriolepid form (see Chang, 1965, pl. 1 (labelled 3), fig. 2), an elongate pectoral fin in two segments, and an MxL plate in the trunk-shield. The absence of a preorbital recess and the form of the otico-occipital depression are probably primitive characters, and like Denison (1978) we therefore regard *Wudinolepis* as properly referred to this family. The head-shield of *Wudinolepis* also displays a long obstantic margin, with the posterolateral angles anteriorly placed, to give a hexagonal shape characteristic of all bothriolepids and previously incorporated in definitions at subfamilial to subordinal level (e.g. Stensiö, 1948, p. 19; Miles, 1968; Denison, 1978). Similarly, a short obstantic margin facing posteriorly has been regarded as a distinctive feature of all asterolepidoids (see below), although on the grounds of parsimony alone one or other condition must in the first instance be regarded as symplesiomorphic. New evidence discussed below now indicates that the long obstantic margin of bothriolepids may be primitive, and this character has therefore been excluded from the above definition.

Miles (1968) recognised only one bothriolepidoid family, but Hemmings (1978) has since proposed that the families Microbrachiidae and Sinolepididae be also included in the suborder, for which she has presented a diagnosis (1978, p. 42). However, the basis for this rearrangement is unclear, since in neither *Sinolepis macrocephala* Liu & P'an (1958) nor *Microbrachius dicki* Traquair (see Hemmings, 1978, p. 44) is the 'posterolateral angle of the head-shield situated well in front of the posterior margin', as is specified in her subordinal diagnosis. Although the pectoral fin in *Sinolepis* is apparently of advanced structure, we regard the exclusion of the Nu from the orbital fenestra by the PP plate in both forms as a more significant character, indicating asterolepidoid rather than bothriolepidoid affinities.

Genus **Bothriolepis** Eichwald, 1840

Type species: Bothriolepis ornata Eichwald, 1840, subsequently designated by Woodward (1891).

Definition: Bothriolepididae in which the AMD plate is broadest across its lateral corners, and normally overlaps the ADL and is overlapped by the MxL plate; and the MxL is broadest through its dorsal corner, with its lateral lamina of similar extent to the lateral lamina of the ADL plate, and not forming extensive contact with the AVL plate.

Remarks: Miles (1968, p. 21) modified Stensiö's longer diagnosis (1948, p. 222) in order to distinguish *Bothriolepis* from *Grossilepis* on their differences in ornament. However, we regard plate proportions and overlap relationships as more important characters, and the above definition has been modified from Stensiö (1948) to emphasise such characters; this allows inclusion of the new species described below, which in most respects is typical of the genus. In addition we retain in this genus the species *B. gippslandiensis* Hills, for which Stensiö (1969, p. 508) erected the new genus *Hillsaspis* on the basis that the Nu plate was excluded from the orbital margin by the PP (see Hills, 1929, 1931). This is one of several features in which *B. gippslandiensis* has been reported as resembling *Dianolepis liui* Chang (see Chang, 1965, p. 8; Miles, 1968, p. 63; Denison, 1978, p. 112). However, a reexamination of the holotype of *B. gippslandiensis* (MUGD 776; see Hills, 1929, pl. 18, fig. 8) has established the presence of orbital facets on the Nu plate (the 'peculiar bevelling' of Hills, 1931, p. 218), which proves that this plate participated in the orbital margin (obm, Pl. 2, fig. 3) as in all other species of the genus. The sutural margin with the PP is clearly shown, and there is no contact with the LA plate either internally or externally (cf. Hills, 1931). In addition, a short, broad PP is a well-established juvenile characteristic in other *Bothriolepis* species (e.g. Stensiö, 1948, p. 212), and since there are no other features which justify exclusion from the genus, *Hillsaspis* Stensiö becomes redundant.

Bothriolepis verrucosa sp. nov.

Figs. 3-10A, 10D; Pl. 2, figs. 4-10; Pl. 3; Pl. 4, figs. 1-5

Name: from *verrucosus* (L.) — covered with warts, with reference to the coarse tubercular ornament along the ridges of the trunk-shield.

Holotype: CPC 17053, comprising disarticulated AMD, ADL, and semilunar plates.

Other material: 6 Nu plates (CPC 17041-17046); 6 AMD plates (CPC 17047-17052); 11 PMD plates (CPC 17054-17061, 19401-19403); 11 ADL plates (CPC 19404-19414); 16 MxL plates (CPC 17055, 19415-19429); 18 AVL plates (CPC 19430-19447); 1 MV plate (CPC 19448); 6 PVL plates (CPC 19472-19477); and 35 pectoral fin elements (CPC 17049, 17052, 19413, 19418, 19421, 19425, 19435, 19437, 19439, 19440, 19442, 19449-19471).

Diagnosis: A *Bothriolepis* with a mid-dorsal length of head and trunk-shields reaching about 60 mm. Nu plate strongly arched with a deeply impressed obtected nuchal area and l/b index of 70–78. Other plates of head-shield unknown. Trunk-shield fairly high with dorsal wall enclosing an angle of at least 105° at the median dorsal ridge, and meeting the lateral wall at about the same angle. AMD with b/l index of 81–85, and the tergal angle anteriorly placed about 0.25 of total length from anterior margin. Harmonic suture with ADL for some distance in front of lateral corner. Levator fossa delineated posteriorly by transverse crescent-shaped ridge; anterior ventral pit poorly developed. PMD with b/l index of 73–82, and the posteroventral pit close to the posterior margin. ADL with b/l index of 59–75, and with a dorsal lamina as broad or slightly broader anteriorly than posteriorly. MxL with l/b index for the dorsal lamina of 170–214, and for the lateral lamina of 210–255. Ventral lamina of AVL with l/b index of 175–205, with a subcephalic division comprising 25–30% total length, and with a relatively long posterior division of the mesial margin. Lateral lamina of AVL of fairly uniform height, with l/b index of about 225, and a small axillary foramen. PVL with l/b index of about 135, a ventral lamina just over twice as long as broad, a lateral lamina 2.25 times as long as high, and subanal division about 20% total length of plate. Lateral lamina with distinct dorsal corner but otherwise of fairly uniform height throughout its length. Proximal segment of pectoral fin about 4 times as long as broad; Cd_1 normally just over twice as long as broad, Cv_1 about 2.5 times as long as broad, Mm_1 at least 3 times as long as broad, Cd_2 about 1.5 times as long as broad, and Cv_2 at least 3.4 times as long as broad. Mesial and lateral spine rows developed; Mm_1 and Cv_2 may be completely separated by sutural contact between Cv_1 and Mm_2. Sensory grooves on Nu plate not clearly defined; posterior oblique abdominal pitline groove apparently absent. Ornament of scattered tubercles superimposed on network of anastomosing ridges; tubercles sometimes in radial rows, dense over ossification centres and along median dorsal, dorsolateral, and ventrolateral ridges, but tending to be sparse near bone margins in the dorsal wall of the trunk-shield.

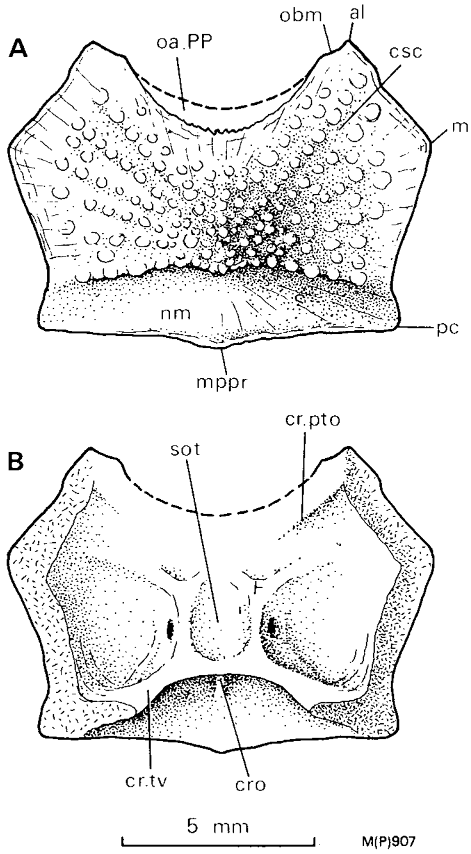

Fig. 3. *Bothriolepis verrucosa* **sp. nov. Nu plate restored in dorsal (A), and ventral (B) views. After CPC 17042, 17043, 17045, 17046. For explanation of lettering see list of abbreviations.**

Remarks: B. verrucosa sp. nov. is readily distinguished from other species of the genus by the transverse crescentic ridge on the visceral surface of the AMD, the small size of the axillary foramen, the poor development of the central sensory groove on the Nu and the absence of a posterior oblique abdominal pitline groove on the trunk-shield, the fairly uniform height of the lateral laminae on the AVL and PVL, the uniform breadth of the ADL, the relatively large size of the MV plate, and the tubercular ornament. In the last three of these characters *B. verrucosa* sp. nov. resembles *Grossilepis tuberculata* (Gross; see Stensiö 1948, pp. 525-34); but it differs in the presence of pronounced lateral corners on the AMD, the fairly narrow anterior margin of the PMD, which carries a ventral tuberosity, the small axillary foramen, the development of sensory grooves on the head and trunk-shields, the shorter, broader pectoral fin, the consistently developed dorsal corner on the MxL, and in details of the ornament. Another species of *Grossilepis* described by Miles (1968) also differs in ornament, in the more slender Cv_2, and in the broad and shallow central sensory groove on the Nu plate. *Dianolepis liui* Chang resembles *B. verrucosa* sp. nov. in its tuberculate ornament and its very small axillary foramen (Chang, 1965, p. 8), but the connection between the PP and LA plates in *Dianolepis* shows they are not closely related.

In the shape of its AMD and MxL, *B. verrucosa* sp. nov. is typically developed for the genus, and since the head-shield is still very incompletely known, we consider that at this stage this new species is best referred to *Bothriolepis*. One other species (*B. tungseni* Chang) is known from Eifelian rocks, and resembles *B. verrucosa* sp. nov. in the proportion of various trunk-shield plates and of the proximal pectoral fin segment (Chang, 1965, p. 9). However, in addition to the differences listed above, *B. tungseni* apparently had a lower trunk-shield, with dorsal and lateral walls meeting at about 90°, and with proportionately longer and lower lateral laminae of the flank plates. It also probably attained a greater size.

Description: There is a limited size range in the material, and following reconstructions in Miles (1968), a total length for head and trunk-shields of about 60 mm would appear to be fairly typical, making this a relatively small species of *Bothriolepis*. The *head-shield* is not represented by articulated examples, and of isolated dermal bones only the Nu plate has been identified in the collection. Three examples of this plate (CPC 17042, 17045, 17046) were sufficiently complete to be measured, giving l/b indices within the range of many species of *Bothriolepis*. Ornament on the plate tends to be radially arranged (Fig. 3), dense near the ossification centre and sparse or absent around the margins and behind the postpineal notch. No specimen shows the endolymphatic openings, nor are sensory canals evident, although a slight notch along the anterior division of the lateral margin suggests that the central sensory line groove ran anterolaterally between tubercle rows (csc, Fig. 3A). The orbital margin is short but distinct (obm); the anterior division of the lateral margin is 2/3 to 9/10 as long as the posterior, and posterolateral corners are only slightly developed (pc). The obtected nuchal area (nm) is fairly flat, and deeply depressed relative to the ornamented surface of the plate, from which it is sharply delineated. Its posterior margin is well preserved in

CPC 17042, which shows a slight posterior median process (mppr). The overlap area for the PP is not well shown, but is partly visible in CPC 17043, which also shows part of the visceral surface. The transverse nuchal crista (cr.tv) is strongly developed with a deep median notch. A slight median occipital crista is indicated (cro). In posterior view these structures resemble those figured for species of *Asterolepis* (e.g. Stensiö, 1931, fig. 15; Karatajūtė-Talimaa, 1963, fig. 29). The supraotic thickening (sot) carries a shallow median depression and is continued anterolaterally as indistinct paired ridges. The anterior part of the visceral surface is not well exposed, but part of the right postorbital crista is visible along the broken edge of the bone in CPC 17043, and was apparently well developed and presumably of normal extent. Behind the postpineal notch the surface is concave, suggesting an increase in bone thickness around the margin of the notch. In posterior view the plate is quite strongly arched across the midline (about 110°), with an angular rather than curved profile.

Disarticulated dermal bones of the *trunk-shield* are much better represented. The proportions of the AMD (see diagnosis) are based on four fairly complete specimens (CPC 17047-17049, 17053). The anterior division of the plate comprises 64–68% of total length. The plate is strongly arched transversely, the angle between laminae being measured at 125° in CPC 17051. Total length varies from 13.8 to 22.6 mm. Some specimens (e.g. CPC 17049) lack a postnuchal notch, but this region is not well known, since only the thickened part of the postlevator process is preserved in most specimens (pr.pl, Fig. 4). The length of the contact face for the ADL is uncertain. Only in CPC 17049 is it well preserved; here it is probably at its most extensive, but still terminates some distance in front of the lateral corner. The available material indicates that a harmonic suture with the ADL was normally developed for some distance in front of the lateral corner. The same feature occurs, but is less strongly developed, in *Grossilepis tuberculata* and *B. cellulosa* (Stensiö, 1948, p. 121), and *B. leptocheira* (Miles. 1968, p. 78).

The levator fossa (f.retr, Fig. 4A) is deep and narrow. The postlevator thickening (pl.th) tends to be more sharply delineated near the anterolateral corner of the plate, but there is otherwise no sign of a postlevator crista. The levator fossa is delineated posteriorly by a transverse crescent-shaped ridge (r.cr), not previously described in species of *Bothriolepis*, which can be assumed to incorporate the anterior ventral process of other forms (see Stensiö, 1948, p. 113). If there was an ossified floor to the levator fossa (Stensiö, p. 112), it presumably originated from the top of this ridge. When developed (CPC 17053), the anterior ventral pit (pt_1) lies immediately in front of the transverse crescentic ridge, and is continued anteriorly as a short median ventral ridge (mvr). Typically however a pit as such is not developed, being replaced by an indistinct roughened area at the posterior end of the median ventral ridge. Behind the crescentic ridge is a flattened area of thickened bone with a somewhat coarser surface texture (tb_1), resembling the tuberosity on the visceral surface of the PMD (Fig. 5B). Farther back a faint median groove may be developed. One specimen (CPC 17047) shows a fine groove symmetrically placed on both sides, running posterolaterally off the postlevator thickening as shown on the right side in Figure 4A. These grooves are irregular or indistinct in other specimens.

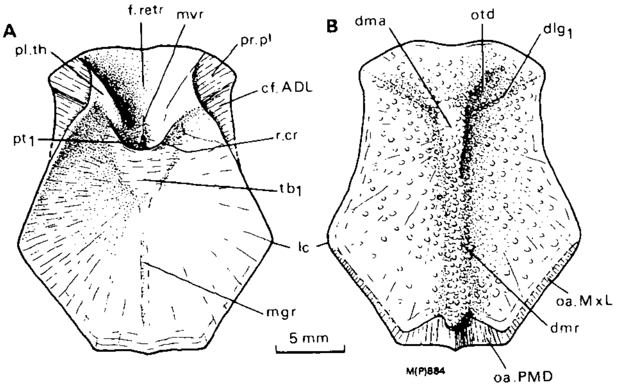

Fig. 4. ***Bothriolepis verrucosa*** **sp. nov. AMD plate restored in visceral (A), and dorsal (B) views. After CPC 17047-17053. For explanation of lettering see list of abbreviations.**

The external surface of the AMD (Fig. 4B; Pl. 2, fig. 5) carries a broad low dorsal median ridge (dmr), formed as a zone of crowded tubercles which increases in width in the region of the tergal angle (dma). This angle is anteriorly placed in the anterior third of the plate, and is rounded in lateral view. The oblique transverse depressions (otd) are clearly developed, and an alignment of tubercles suggests the presence of an anterior oblique dorsal pitline groove (dlg_1), but on this specimen there is no sign of the posterior oblique groove which normally occurs in all previously described species of *Bothriolepis* (see Stensiö, 1948, p. 186). The MxL confirms that this is characteristic of *Bothriolepis verrucosa* sp. nov. (see below). As shown in Figure 4B, the posterior end of the dorsal median ridge in CPC 17051 apparently occupied a notch in the PMD, although other material indicates that the overlap area for this plate was typically more extensive and triangular in shape (see Fig. 5B).

Three measurable PMD plates (CPC 17056, 17058, 19041) gave b/l indices of 75, 73, and 82 respectively, the last value being larger as a result of better developed posterolateral processes. Apart from its fairly elongate proportions the plate is normally developed for *Bothriolepis* (Fig. 5). A rounded posterolateral process seems to be typical (prl), and the anterolateral corners vary in form, being slightly more rounded in CPC 17057 than shown in Figure 5. Typically there is a rounded posterior median angle (pa), but one specimen (CPC 19401) exhibits instead a shallow median concavity similar to but less strongly developed than that known to occur in *B. canadensis* (see Stensiö, 1948, fig. 137). The external surface resembles that of the AMD, with a broad low dorsal median ridge carrying crowded tubercles which are also concentrated around the ossification centre and along the posterior margin, but are sparsely distributed elsewhere (Pl. 2, fig. 8). To some extent in CPC 17057, and especially in CPC 17054 and 17060, these tubercles are superimposed on a network of anastomosing ridges of the type forming the typical ornament of most other *Bothriolepis* species. The two laminae of the plate enclose an angle of about 105°. On the visceral surface (Fig. 5B) the posterior ventral pit (pt_2) is bounded behind by a posterior ventral process developed as a thickening on the anterior face of the crista transversalis interna posterior (cr.tp). CPC 17055 has a distinct groove between this crista and the posterior margin (gr, Fig. 5B), but in other specimens the

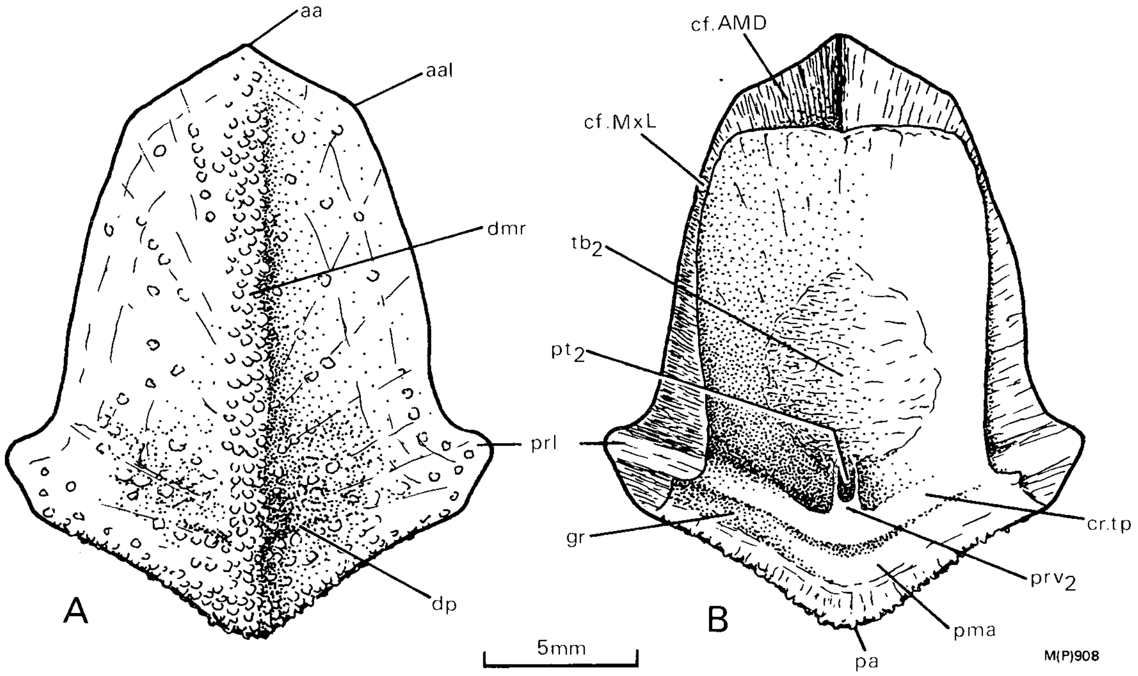

Fig. 5. *Bothriolepis verrucosa* **sp. nov. PMD plate restored in dorsal (A), and visceral (B) views. After CPC 17055, 17059, 19401. For explanation of lettering see list of abbreviations.**

posterior marginal area is normally developed. The ventral tuberosity (tb_2) is present in all specimens showing the ventral surface (e.g. Pl. 2. fig. 10).

The ADL plate is fairly common in the material but the two antiarch species are not easily differentiated. Of the twelve plates included here, six (CPC 19404, 19407-19409, 19412, 19413) were measurable, the remaining incomplete or isolated specimens being only tentatively referred to the species. All are preserved in visceral view (Pl. 3, fig. 2), and plate proportions given in the diagnosis compare only in a general way with those detailed by Stensiö (1948, p. 13); length was measured at the level of the dorsolateral ridge from the posterior margin to the edge of the crista transversalis interna anterior (which approximates the position of the processus obstans), and compared with maximum total breadth (breadth of dorsal and lateral laminae could not be measured). The more elongate proportions distinguish this plate from the ADL of *Sherbonaspis hillsi* (see below). CPC 19412 gave the highest b/l index, and is also the only measured ADL which is broadest near its posterior margin, all others being slightly broader anteriorly. In this respect *B. verrucosa* sp. nov. differs from all other described species of *Bothriolepis* (see Stensiö, 1948. p. 126). Bone was removed from CPC 19407 and 19408 to partly expose the external surface. In neither is the processus obstans clearly seen. The two laminae enclose an angle of about 125°. The overlap area for the AMD is short (oa.AMD, Fig. 6), and the lateral line sensory groove lies at a fairly constant distance beneath the dorsolateral ridge, which is densely ornamented with crowded tubercles (Pl. 3, fig. 1). Ornament is sparsely distributed on the dorsal lamina, but remains fairly dense on the lateral lamina. On the visceral surface of the plate the contact face for the MxL is deeply impressed; out of six specimens with the posteroventral region exposed, three (CPC 19406, 19409, 19413) had also a short contact face for the PVL inside the posteroventral margin.

The MxL is also commonly preserved in visceral view. Proportions given in the diagnosis for the dorsal and lateral laminae were approximated from measurement of the visceral surface in six specimens (CPC 17055, 19416, 19417, 19423, 19424, 19426). Similar proportions are seen in many other *Bothriolepis* species, although in some (e.g. *B. maxima, B. gigantea, B. groenlandica*) the lateral lamina is much narrower (see Stensiö, 1948, p. 132). The l/b index for the plate as a whole varies between 120 and 146. The visceral surface of the plate shows the normal features (Pl. 3, fig. 4). In several specimens (e.g. CPC 19424) there is a roughened area in the region of the ossification centre, although in others this part is quite smooth. The contact face for the AMD would appear to have been quite narrow, and is often poorly preserved or absent. In CPC 19419 it is clearly preserved only along the posterior part of the anterodorsal margin, and possibly the plate was also overlapped anteriorly by the AMD.

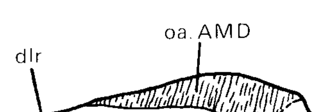

Fig. 6. *Bothriolepis verrucosa* **sp. nov. Right ADL plate restored in lateral view. After CPC 19404, 19407, 19408. For explanation of lettering see list of abbreviations.**

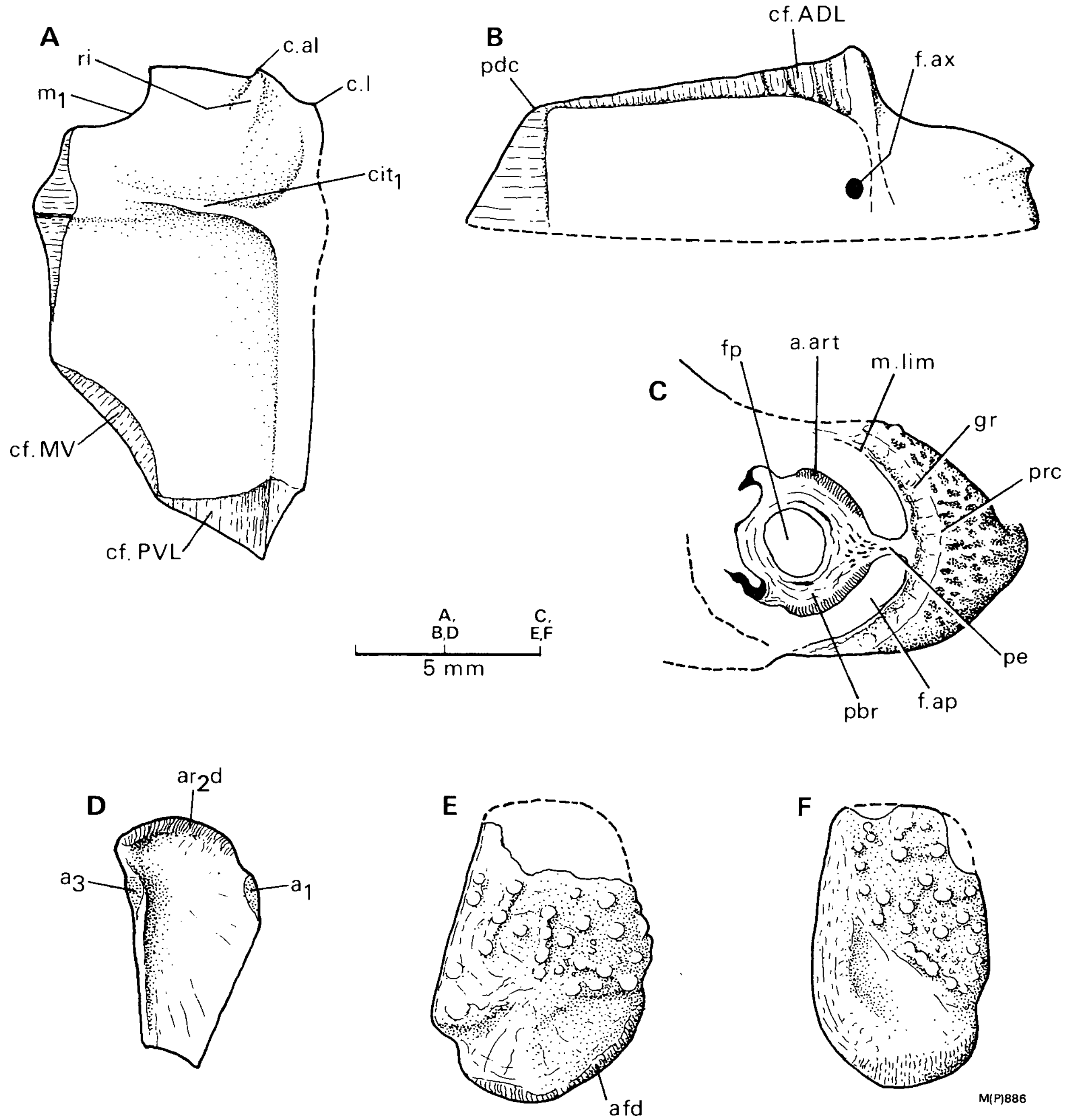

Fig. 7. ***Bothriolepis verrucosa*** **sp. nov. A, part reconstruction of a right AVL in dorsal view. After CPC 19431, 19432; B, lateral lamina of left AVL in visceral view. After CPC 19441; C, posterolateral view of fracture surface through the processus brachialis of a right AVL (CPC 19438); D, left Cd_1 in visceral view (CPC 19461); E, F, two incomplete Cd_2 plates in dorsal view (CPC 19455, 19462). For explanation of lettering see list of abbreviations.**

This type of overlap is commonly observed in other species and genera (see Stensiö, 1948, p. 121). Bone was removed in CPC 19425 to expose the external surface as an impression (Pl. 3, fig. 3). The two laminae meet at an angle of about 105°. The dorsolateral ridge is narrower than on the ADL, and there also appears to be a faint ridge running towards the anterodorsal corner. Like the AMD, this specimen shows no sign of a posterior oblique pitline groove.

AVL plates of the two antiarch species have proved difficult to distinguish. In a few instances diagnostic remains of the pectoral fin are associated, and for the remainder it is assumed that the presence or absence of a contact face for the MxL at the posterodorsal corner is a reliable character for separating the two species. Proportions given above for the ventral lamina are based on measurement of CPC 19430, 19431, 19433 and 19441. The breadth of this lamina is fairly constant throughout the length of the middle division of the mesial margin (Fig. 7A), but this is also the case with *Sherbonaspis hillsi* gen. et sp. nov. (see below), and it is not a useful character (cf. Stensiö, 1948, p. 134). The subcephalic division generally comprises 25–30% of the length of the ventral lamina. The anterior margin is variably developed, but normally shows a distinct anterolateral, and sometimes a slight lateral corner (Fig. 7A). The anterolateral corner may be supported by a low ridge on the visceral surface (ri), which in CPC 19445 has a corresponding groove on the external surface (Pl. 3. fig. 7). The notch for the semilunar plate may be distinct (m_1, Fig. 7A), but the only disarticulated semilunar identified in the collection is a broad subtriangular plate with a curved posterior margin, as indicated by the more shallow notch in CPC 19445 and 19447 (Pl. 3, fig. 7). Similar variability is shown by *B. canadensis* and other species (e.g. Stensiö, 1948, figs. 167, 168). The posterior division of the mesial margin of the AVL is extensive (cf.MV, Fig. 7A), and the middle division is relatively shorter than in most other species (e.g. Stensiö, 1948, figs. 41, 51, 160–166; cf. *B. maxima*, fig. 242). A relatively large MV plate is seen in the bothriolepid *Grossilepis* (Stensiö, 1948, fig. 41D), but the incomplete MV preserved here (CPC 19448) suggests a shorter, broader form, as seen for example in some pterichthyodids (e.g. Hemmings & Rostron, 1972; Malinovskaya, 1973). The crista transversalis interna anterior on the AVL is well marked laterally, but forms a low ridge mesially. There is no clear subdivision into anterior and posterior ridges as is seen in *Pterichthyodes* (Hemmings, 1978, fig. 13).

The lateral lamina (Fig. 7B) is not well preserved, but was probably about 2–2.25 times as long as broad (CPC 19430, 19441). It is highest anteriorly, except in CPC 19438 (which lacks a mixilateral contact face), where it is higher at the posterodorsal corner. Stensiö (1948, p. 133) has regarded this character as generically diagnostic for other antiarchs. In CPC 19441 the contact face for the ADL carries four prominent ridges behind the dorsal corner (Fig. 7B).

The axillary foramen is preserved in five antiarch AVL plates in the collection (CPC 19434, 19436, 19441, 19447, 19518). On the presence or absence of a mixilateral contact face CPC 19436 and 19441 can be referred to *B. verrucosa* sp. nov., and CPC 19518 to the other species, yet in all five examples the foramen is relatively small, much smaller than in *Asterolepis* and other *Bothriolepis* species, *Grossilepis,* and even *Microbrachius* (Stensiö, 1931, 1948; Hemmings, 1978), but comparable to the foramen in *Remigolepis* (e.g. Stensiö, 1931, p. 96, fig. 81), *Dianolepis* (see Chang, 1965, p. 8), or *Pterichthyodes* (see Hemmings, 1978, fig. 13). The processus brachialis is preserved in CPC 19445, and a broken section through it in the region of the pars pedalis is exposed in CPC 19438 (Fig. 7C). Both show a prepectoral corner normally developed for the genus, which in CPC 19438 is separated posteriorly by a broad shallow unornamented groove (gr, Fig. 7C) from the margo limitans (m.lim). The exposed section through the processus brachialis shows dorsal and ventral pads of bone with a columnar internal structure, which must represent areas of articulation for the pectoral fin (a.art). Irregular dorsal and ventral processes project from the posterior border of the processus brachialis. They are assumed to enclose pits corresponding to those in the groove surrounding the funnel pit in other species (Stensiö, 1948, p. 136; Watson, 1961). Except for the small foramen axillare there are no preserved features suggesting that the pectoral fin articulation differed appreciably from that in other *Bothriolepis* species.

The PVL is poorly represented and most specimens are very incomplete. The proportions given in the diagnosis are based on only one specimen (CPC 19477; Pl. 3, fig. 9), which on the presence of an overlap area for the ADL may be definitely referred to this species. The morphology of the ADL shows, however, that this overlap was not always developed (see above). Plate proportions are similar to those in *B. canadensis* (Stensiö, 1948, p. 331), except that the subanal division was probably somewhat shorter, being only about 20% of total length of the plate. Another difference is the shape of the lateral lamina (Fig. 8E), which shows no appreciable decrease in height towards the anterior. The two laminae enclose an angle of about 100°. The ventrolateral ridge is similarly developed to the median dorsal and dorsolateral ridges, as a rounded zone of closely packed tubercles. The margins of the plate are normally developed except in the region of the anterodorsal corner. In *B. canadensis* the AVL may abut against the ADL over a short section of the anterodorsal margin (Stensiö, 1948, fig. 174E), but overlap has not previously been reported. Similar overlap is shown by CPC 19472. The mesial margin of the ventral lamina has a prominent posterior corner (cm_3). The visceral surface of this lamina is partly exposed as an impression (Pl. 3, fig. 9), which shows depressions for the crista transversalis interna posterior and a transverse thickening, as in other species (e.g. Stensiö, 1948, fig. 172C). Four other incomplete PVL plates are tentatively referred to the species on the basis of the fairly constant height of the lateral lamina.

Pectoral fin remains are associated with the AVL in CPC 19435, 19437, 19439, 19440 and 19442; in CPC 19435, 19437, 19440, 19453, and 19454 partly articulated proximal segments are preserved (Pl. 3, figs. 8, 10). As restored (Fig. 8A, B) this segment seems to have been about 4 times as long as broad, which is fairly normal for the genus (Stensiö, 1948, p. 151). Traces of both mesial and lateral spine rows are preserved. The configuration of plates on the ventral surface is displayed in CPC 19437, some of the mesial plates are shown in CPC 19453, and some of the dorsal plates are shown in CPC 19454. This information is supplemented by a number of disarticulated plates. The Cd_1 (Fig. 7D; Pl. 7, fig. 1) could be measured in CPC 19418, 19461, 19466, and 19469, giving l/b indices of 208, 215, 200 and 202 respectively. A mesial row of about 15 enlarged turbercles is present in CPC 19469. The Cv_1 is longer and narrower, as in other species; CPC 19442 (Pl. 4, fig. 2), 19463, and 19471 gave l/b indices of 2.7, 2.5, and 2.7 respectively. Both plates are therefore relatively shorter and broader than in *B. canadensis* or *B. cellulosa* (Stensiö, 1948, pp. 367, 421). The Mm_1 is preserved as an impression in CPC 19450 (Fig. 10D), and is about 3 times as long as broad, although the corresponding plate is considerably more elongate in CPC 19453. This specimen (Fig. 10A) shows the sutural connections to surrounding bones, with the Mm_2 in contact with Cv_1 and widely separating the Mm_1 and Cv_2. In *B. canadensis* (Fig. 10B) the latter two plates normally meet only at a point, although this is occasionally developed as a short common suture (Stensiö, 1948, p. 372). In *Asterolepis*, on the other hand, the Mm_1 and Cv_2 are in broad contact, and widely separate the Cv_1 and Mm_2 (Fig. 10C). CPC 19450 is tentatively interpreted as a left Mm_1, and its shape suggests a different arrangement again (Fig. 10D). There are two short sections of the posterior margin which presumably were in contact with Mm_2 and Cv_1 (c.Mm_2, c.Cv_1, Fig. 10D), to give a somewhat similar configuration to that shown by *B. maxima* (Gross, in Stensiö, 1948, fig. 244D). A very short intervening section (c.Cv_2) suggests a ventro-distal process in contact with the Cv_2, similar to that figured for *B. canadensis* (Stensiö, 1948, fig. 190C).

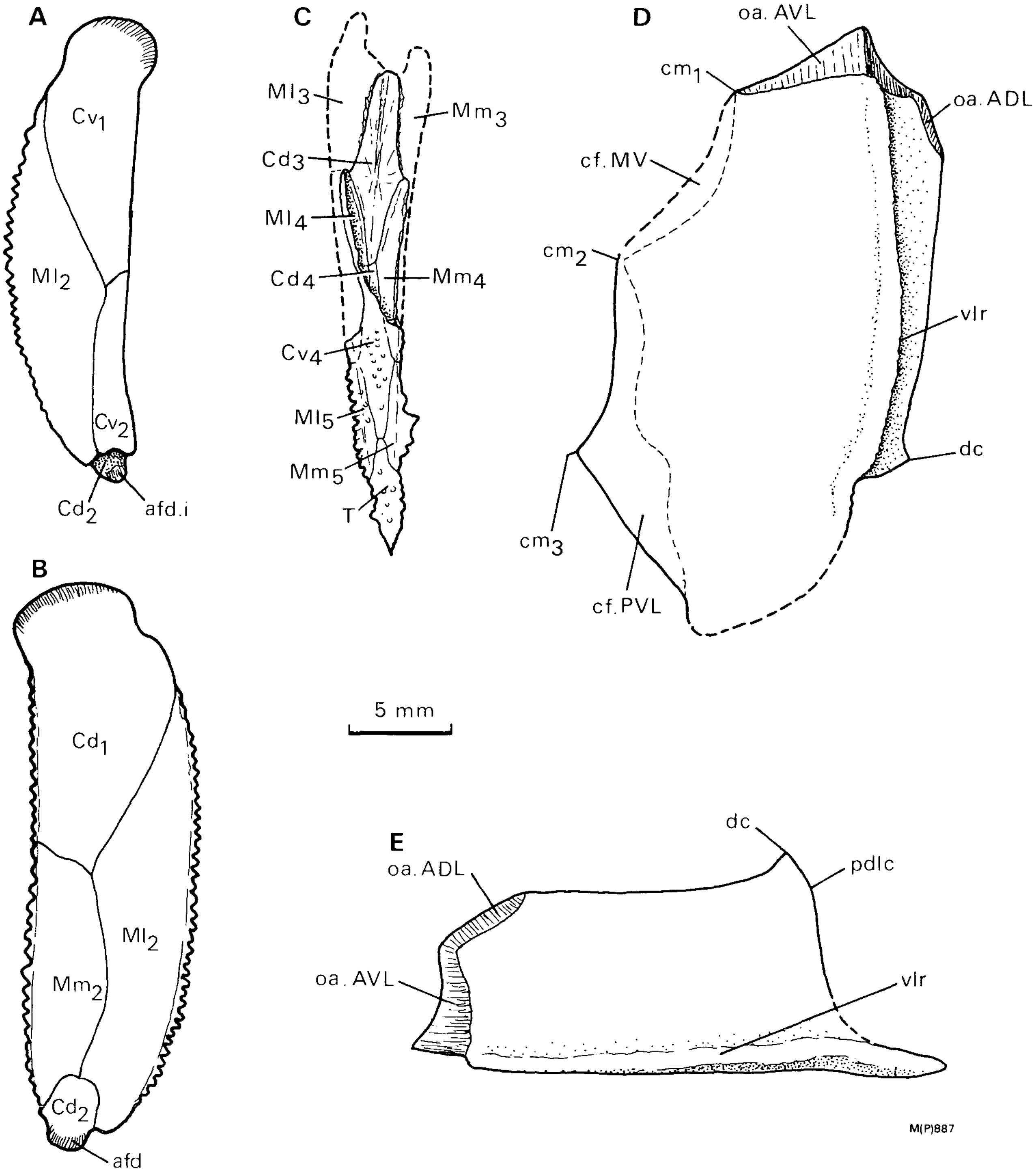

Fig. 8. ***Bothriolepis verrucosa*** **sp. nov. A, B, outline restoration of the proximal segment of a right pectoral fin; A, ventral surface, after CPC 19425, 19437, 19442; B, dorsal surface after CPC 19454, 19455, 19461, 19462; C, right distal segment of pectoral fin in ventral view, the Cd_3, and part of the Cd_4, Ml_4 and Mm_4 showing their internal surfaces, and the remaining plates preserved in external view. After CPC 19413; D, E, left PVL in ventral and lateral views. After CPC 19477. For explanation of lettering see list of abbreviations.**

The Cv_2 is preserved as an impression in CPC 19425 (Fig. 9C), and gives a l/b index of 34. Two other incomplete Cv_2 plates are identified on the basis of their elongate shape and the presence of internal articular surfaces at their distal ends (afv.i, Fig. 9A, B; cf. Gross, in Stensiö, 1948, fig. 244C). These articular areas, associated ridges and the surrounding bone margins are differently developed in each, but the taxonomic significance of this is unknown. A third specimen (Fig. 9D) lacks a well-defined internal articular area, although part of the inner surface is not exposed, and it may have been of more limited extent. In shape this plate differs considerably from the other examples, but it possesses an external articular area and has a convex distal margin, and can only be interpreted therefore as an atypical Cv$_2$. It bears no resemblance to the Cd$_2$ or Cv$_2$ in *Sherbonaspis hillsi* (see below).

The Cd$_2$ in *B. verrucosa* sp. nov. is represented by two disarticulated specimens, both from fairly large individuals (Fig. 7E, F). It is of somewhat quadrilateral shape, and up to 1.5 times as long as broad. This shape is also indicated by the embayment for the Cd$_2$ as preserved on the Ml$_2$ in CPC 19454 (Fig. 8B). The latter plate is represented by several disarticulated specimens (e.g. Pl. 2, fig. 7). CPC 19449 and 19454 are fairly complete, and show the length of the plate to be respectively 3.33 and 3.75 times the breadth of the dorsal lamina. CPC 19449 is smaller, although in *B. canadensis* the plate tends to be broader in larger individuals (Stensiö, 1948, p. 372). The dorsal lamina of the Mm$_2$ is also preserved in CPC 19454, and in CPC 19451 and 19456 (Pl. 3, fig. 6); it varies between 3.9 and 4.6 times as long as broad. Again the largest specimen (Pl. 3, fig. 6) is the most elongate, contrary to the trend reported for *B. canadensis* (Stensiö, 1948, p. 372).

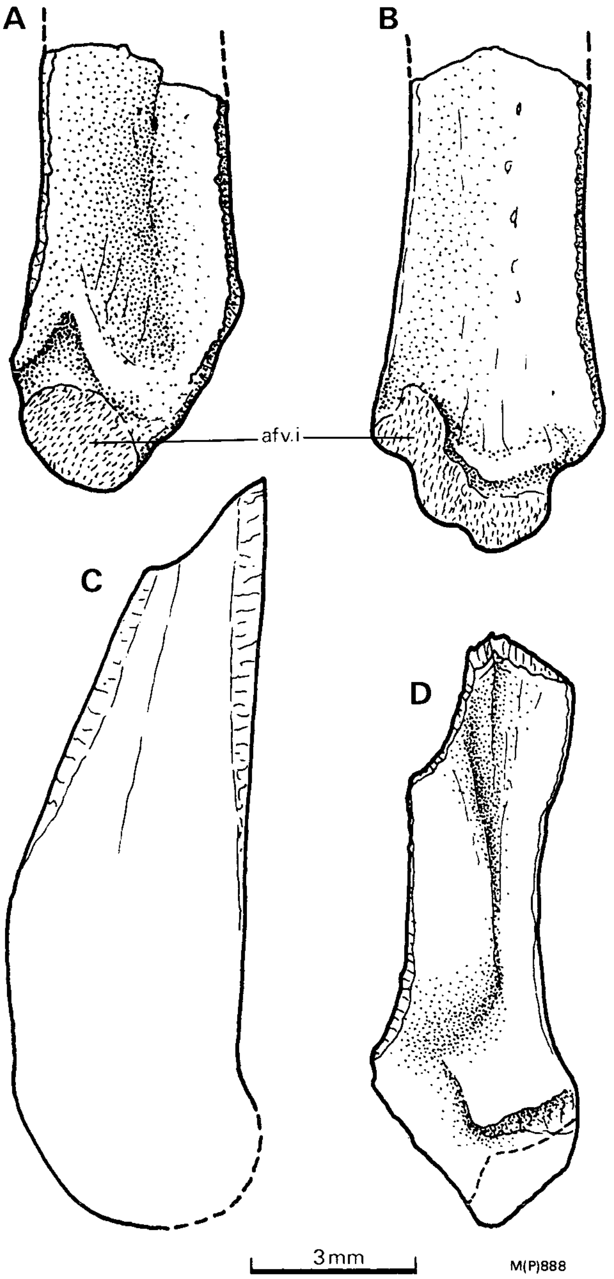

Fig. 9. *Bothriolepis verrucosa* **sp. nov. A, incomplete right Cv$_2$ in internal view. CPC 19452; B, incomplete right Cv$_2$ in internal view. CPC 19467; C, outline of the impression of the internal surface of a right Cv$_2$. CPC 19425; D, possible left Cv$_2$ in internal view. Area of internal surface not preserved delimited by broken line. After CPC 19457. For explanation of lettering see list of abbreviations.**

The distal segment of the pectoral fin is represented by one incomplete articulated specimen (CPC 19413), and two isolated central plates (CPC 19459, 19470). CPC 19413 (Fig. 8C; Pl. 2, fig. 9) is interpreted as a right distal segment in ventral view, since the T plate lacks lateral processes (see Stensiö, 1948, fig. 58). The Ml$_3$ and Mm$_3$ are missing, but the form of the other plates suggests that the distal segment was normally developed for *Bothriolepis*. Only the more distal sections of the lateral and mesial spine rows are preserved, and individual spines tend to be irregularly fused (Fig. 8C). The exposed external surface is ornamented with scattered tubercles, and longitudinal ridges are not conspicuously developed. Assuming similar relative sizes of proximal and distal segments to that given for *B. canadensis* (Stensiö, 1948, p. 361), this specimen probably comes from a somewhat larger individual than represented in Figure 8B.

Suborder ASTEROLEPIDOIDEI Miles, 1968

Definition: Antiarchs with the posterolateral angle of the head-shield situated at or just in front of the posterior margin, a short subobstantic area facing posteriorly, a PP plate much shorter than broad, and forming simple sutural contact with the LA plate, and the Nu plate with distinct anterolateral corners, no orbital facets, and a wide postpineal notch. Prelateral plate absent. Processus obstans low. Pectoral appendage broad, primitively with a distal joint, and not reaching back beyond the posterior border of the trunk-shield in adducted position; dorsal central plate 1 always suturing with dorsal central plate 2.

Remarks: This definition has been modified after Hemmings (1978, p. 7). At present the interrelationships of those genera included by Gross (1965, p. 12) in his order Asterolepiformes are poorly understood, and it is not yet well established that the group is defined on the basis of specialised characters only. Few issues raised by Gross have been clarified by more recent contributions, although Miles (1968), Hemmings (1978), and Denison (1978) have followed him in incorporating *Remigolepis* with other asterolepidoids on the assumption that the absence of a distal joint in the pectoral fin is secondary (cf. Stensiö, 1931, 1948). Zhang (1978) has now reported an unjointed pectoral fin in the yunnanolepid *Phymolepis*, which he reasonably interprets as a primitive character state, but Hemmings (1978, p. 2) has stressed the close morphological similarity between *Remigolepis* and *Asterolepis*, especially in the preobital region of the skull, where both genera exhibit an anterior unornamented shelf, premedian notch, and visceral rostrocaudal groove (see Stensiö, 1931, pp. 31-34). These structures have not been observed in yunnanolepids (Zhang, 1978), nor any other antiarch. If, as this distribution suggests, these peculiarities indicate shared specialisation in mouth position and function in *Asterolepis* and *Remigolepis* (see Stensiö, 1948, p. 217), then the unjointed pectoral fin in *Remigolepis* must still be interpreted as secondary. This is tentatively accepted here.

The length of the obstantic margin and position of the posterolateral angle on the head-shield are widely recognised distinguishing features between asterolepidoid and bothriolepoid genera, and the fact that this angle in *Yunnanolepis* is anteriorly placed was used by Gross (1965) to suggest affinity with *Bothriolepis* (see also Denison, 1978). Zhang's (1978) account now demonstrates that in yunnanolepids the proximal joint of the pectoral fin comprises

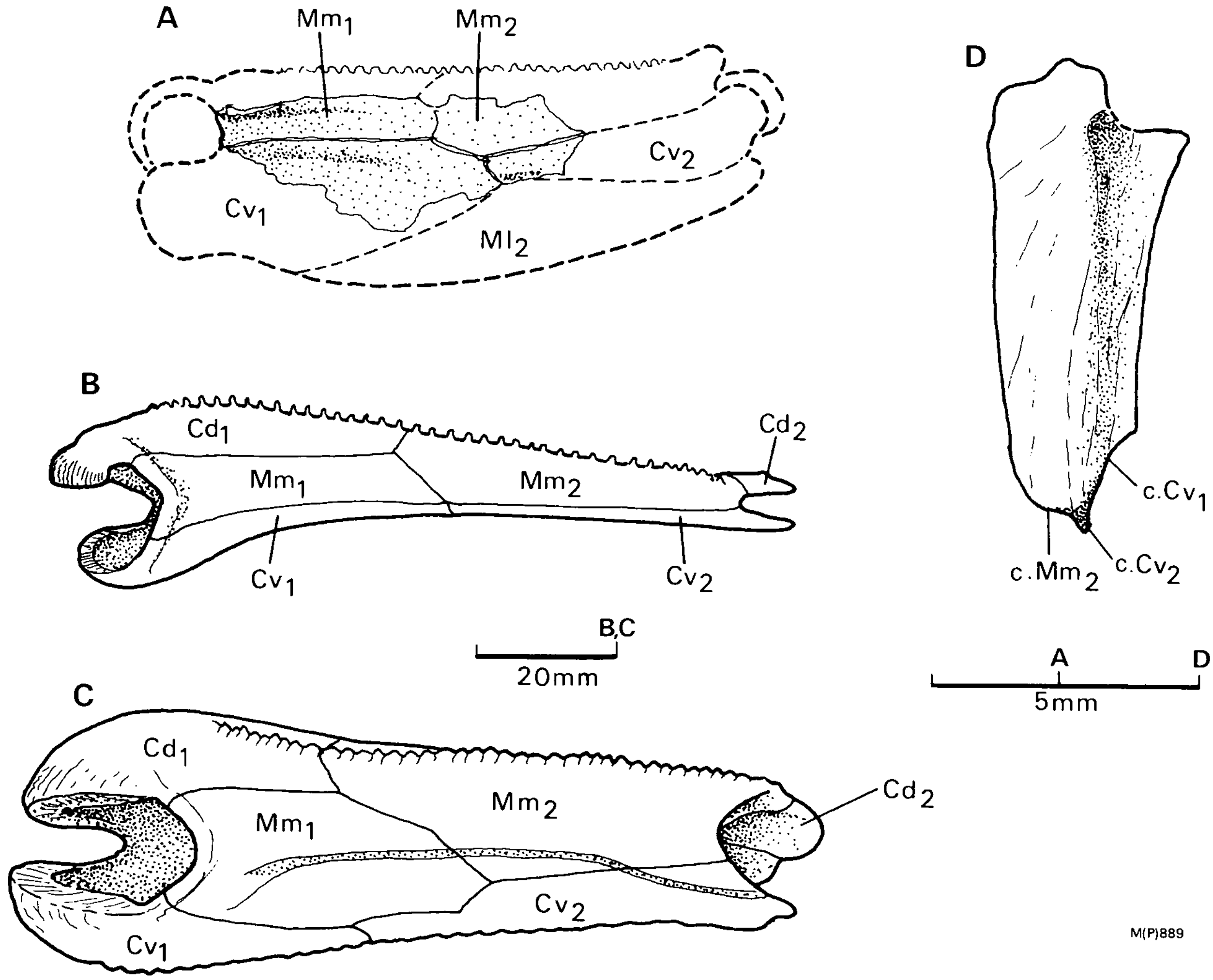

Fig. 10. A, *Bothriolepis verrucosa* sp. nov. Proximal segment of right pectoral fin in ventromesial view, showing the area preserved in CPC 19453 (cf. Pl. 3, fig. 10); B, *Bothriolepis canadensis* (Whiteaves). Proximal segment of right pectoral fin in mesial view, after Stensio (1948, fig. 196B); C, *Asterolepis ornata* Eichwald. Proximal segment of right pectoral fin in mesial view, after Gross (1931, pl. 6, fig. 2); D, *Bothriolepis verrucosa* sp. nov. Impression of internal surface of Mm_1. CPC 19450. For explanation of lettering see list of abbreviations.

a simple fossa axillaris and lacks a brachial process, which implies that the typically developed brachial process in all asterolepidoid and bothriolepidoid genera is a shared specialisation. It follows that either the similar skull-roof shape in yunnanolepids and bothriolepids has developed in parallel, or else this shape is a primitive antiarchan feature. The latter possibility is supported by the occurrence of a well developed obstantic margin in euarthrodires, which have been proposed as the sister group of antiarchs (Miles & Young, 1977; Denison, 1978; Young, 1980). It may also follow therefore that the short obstantic margin facing posteriorly is an advanced character for asterolepidoids, and it has been retained in the above definition. In yunnanolepids and *Sinolepis* Liu & P'an (1958) the PP plate excludes the Nu from the orbital fenestra, and this is also likely to be primitive for antiarchs. However, the crown-shaped Nu and short, broad PP again are typical asterolepidoid features (e.g. Gross, 1965, fig. 3), which may also be regarded as advanced. Finally, the likely homology between the antiarch prelateral plate and the postsuborbital of euarthrodires (Miles, 1971, p. 135) suggests that its absence in asterolepidoids is a secondary (advanced) feature, as was proposed by Stensiö (1948, p. 206).

Family PTERICHTHYODIDAE Stensiö 1948

Definition: Asterolepidoids with a high and short trunk-shield, the component plates being broad in proportion to their length. Distal segment of pectoral fin with two dorsal central and two ventral central plates.

Remarks: This definition has been shortened from the diagnosis proposed by Hemmings (1978, p. 8), who failed to take account of Malinovskaya's (1973) descriptions of *Stegolepis*, in which the AMD plate has a narrow anterior margin. Diagnostic characters for the pectoral fin have been modified on the basis of new information provided below. Hemmings recognised two pterichthyodid subfamilies (Pterichthyodinae and Gerdalepidinae), and presented a further diagnosis for the Pterichthyodinae (*Pterichthyodes*, *Byssacanthus*) using head-shield proportions, the presence of internal ridges on the trunk-shield, and paired semilunar plates. However, the anterior region of the skull-roof in *Gerdalepis* is not known, there is no information on the form of the skull in *Grossaspis* and *Lepadolepis*, and both internal ridges and paired semilunar plates also occur in *Asterolepis* (Karatajūtė-Talimaa, 1963). Previously Karatajūtė-Talimaa (1960, 1963; also Obruchev, 1964) had included *Gerdalepis* with *Pterichthyodes* and *Byssacanthus* in a family Pterichthyodidae, whilst Gross (1965) suggested that *Gerdalepis*, *Grossaspis*, and *Lepadolepis* be united in a subfamily Gerdalepidinae on the similar nature of the spongiose layer in the dermal bone of the trunk-shield (cf. Denison, 1978, p. 118). None of these proposals is based on strong evidence, and we prefer at this stage not to attempt a formal subfamilial grouping of the Pterichthyodidae.

Genus **Sherbonaspis** nov.

Type species: Sherbonaspis hillsi sp. nov.

Diagnosis: Pterichthyodid with a mid-dorsal length of head and trunk-shields reaching at least 90 mm. Nu plate with l/b index of 60, PrM plate with pronounced lateral corners and about 1.2 times as broad as long, and LA plate about twice as long as broad. Other plates of head-shield unknown. SM plate longer than broad. High trunk-shield with flat ventral wall; dorsal wall enclosing an angle of about 75° in the region of the tergal angle, and meeting the lateral wall at about 140°–150°. Lateral and ventral walls enclosing an angle of about 100°–110°. AMD with b/l index of 54–60, the anterior division slightly longer than the posterior, the tergal angle placed just behind the level of the lateral corners, and the anterior margin of the plate considerably shorter than the posterior. PMD high and short, and conical in shape. b/l index for ADL 86–114, and for MxL 130–138. MxL may be separated into PDL and PL components, and may overlap AMD with remigolepid suture. Ventral lamina of AVL with b/l index of 183–224; lateral lamina about 2.5 times as long as high, with a short posterodorsal contact face for the MxL. Ventral lamina of PVL with a subanal division 20–25% of total length; lateral lamina with l/b index of about 185. MV plate relatively large. Foramen axillare very small, and subcircular in shape. Proximal segment of pectoral fin about 0.75 times as long as the distal segment, and about 2.3 times as long as broad; distal segment with three lateral marginal and mesial marginal plates, and a terminal plate with a proximal process separating the most distal lateral and mesial marginal plates. External ornament of tubercles tending to form radiating rows. Low median dorsal crest on PMD, and on AMD behind the tergal angle; no median dorsal spines; dorsolateral ridge formed by a single row of coalesced tubercles; additional anteroventral ridge beneath lateral line sensory groove on MxL.

Remarks: This diagnosis includes both generic and specific characters. *Sherbonaspis* may be distinguished from all other known pterichthyodids by the short, broad Nu, the shape of the PrM, and the number of plates in the distal segment of the pectoral fin. From *Pterichthyodes* it differs in such characters as the shape and proportions of various trunk-shield plates, the separate PDL and PL, the larger MV plate, the restriction of the internal dorsal oblique ridge to the MxL plate, the proportions of the pectoral fin, and the radially arranged ornament. It shows closer resemblance to *Byssacanthus*, but differs in the notched SM plate, the absence of a spine on the MD, the shape of the lateral lamina of the AVL, with a shorter contact face for the MxL; the proportions of the PVL, and differences in ornament. There are certain resemblances between *Sherbonaspis* and *Stegolepis*: *Stegolepis jugata* has radiating ornament (Malinovskaya, 1973), but the ridges are more strongly developed, and this species attained a much greater size. *Stegolepis asiatica* (= *S. tuberculata* Malinovskaya; see Dennison, 1978, p. 117) is a smaller species, but the ornament is finer and more tuberculate. In addition, in both species of *Stegolepis* the LA plate is broader and the Nu narrower, the dorsal wall of the trunk-shield is less steep, with a much flatter AMD in which the tergal angle is closer to the posterior margin and carries a dorsal spine, the PMD also carries a spine, the MxL is broader, the lateral lamina of the AVL higher and shorter, and the PVL more elongate with probably a longer subanal division. By these and other characters *Stegolepis* is readily distinguished from *Sherbonaspis*. *Gerdalepis* has somewhat similar ornament, but differs in the smaller MV and shape of the semilunar notch on the AVL (Gross, 1941, fig. 9), the proportions of the AMD, MxL, and AVL plates (e.g. Gross, 1941, pl. 23, fig. 1), and the presence of an apical chamber (Gross, 1965). Both *Grossaspis* and *Lepadolepis* are poorly known, but exhibit highly distinctive trunk-shield morphologies (Gross, 1933b, pls. 1-3), by which they are easily distinguished from *Sherbonaspis.*

Sherbonaspis hillsi sp. nov.

Figs. 11-21; Pl. 4, figs. 6-13; Pl. 5, figs. 1-7

1958 'an Antiarchan from Taemas' Hills, p. 88.
1974 cf. *Pterichthyodes* Young, pp. 251, 254.
1978 cf. *Pterichthyodes* sp. Denison, p. 116.

Name: After Professor E. Sherbon Hills FRS, in honour of his pioneering work on Australian Devonian fishes.

Holotype: CPC 19478, comprising left AVL and right MxL plates, and a distal pectoral fin segment, presumably from one individual.

Other material: 3 Nu plates (CPC 19479-19481); 1 PrM plate (CPC 19482); 1 LA plate (CPC 19483); 5 SM plates (CPC 19484-19488); 6 AMD plates (CPC 19489-19494); 5 PMD plates (CPC 19491, 19495-19498); 10 ADL plates (CPC 19499-19508); 9 MxL plates (CPC 19501, 19509-19516); 5 AVL plates (CPC 19517-19521); 3 PVL plates (CPC 19522-19524); and 15 pectoral fin elements (CPC 19492, 19515, 19519, 19525-19536).

Diagnosis: as for genus (only species).

Description: Sherbonaspis was a small pterichthyodid, the available material indicating a similar maximum size to *Gerdalepis rhenana, Pterichthyodes milleri,* or *Stegolepis asiatica* (Gross, 1941; Malinovskaya, 1973; Hemmings, 1978). *Byssacanthus dilatatus, Stegolepis jugata,* and *Gerdalepis dohmi* were somewhat larger species (Karatajūtė-Talimaa, 1960; Denison, 1978).

Of the dermal bones of the *head-shield* only the Nu, PrM, LA, and SM plates are known. One Nu plate is fairly complete (Pl. 4, fig. 6), and is proportionately shorter and broader than in *Pterichthyodes, Byssacanthus, Gerdalepis, or Stegolepis* (Gross, 1941; Karatajūtė-Talimaa, 1960; Malinovskaya, 1973; Hemmings, 1978), but of similar proportions to some species of *Asterolepis* (e.g. *A. ornata, A. radiata*; Gross, 1931; Karatajūtė-Talimaa, 1963). Other features of the plate are the great breadth across the lateral corners (1.5 times the breadth across the posterolateral corners), the fact that the postpineal notch is almost as wide as the posterior breadth, and the relatively short anterior division of the lateral margin (Fig. 11). In *Asterolepis sinensis* and *Stegolepis jugata* (P'an, 1964; Malinovskaya, 1973) the anterior division is also short, but in the former the posterior margin is strongly convex, and in the latter very narrow. In other respects

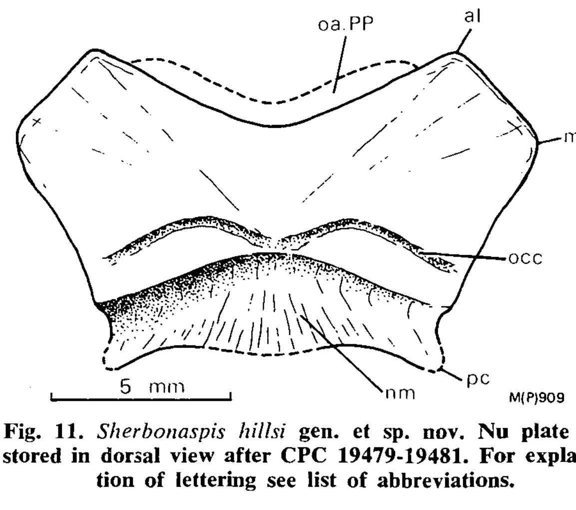

Fig. 11. *Sherbonaspis hillsi* **gen. et sp. nov. Nu plate restored in dorsal view after CPC 19479-19481. For explanation of lettering see list of abbreviations.**

this plate resembles that of *Asterolepis estonica* (Gross, 1940, fig. 8), which is, however, proportionately longer than the specimen described here. The obtected nuchal area is deeply impressed (nm, Fig. 11), and the occipital cross commissure is clearly seen on the left side, but is obscure on the right. There is no sign of external openings for the endolymphatic ducts on any of the available specimens. The posterior margin is incompletely known, but appears to have been gently concave laterally and convex mesially. In posterior view the plate is strongly arched.

One specimen (Fig. 12; Pl. 4, fig. 7) is tentatively identified as a PrM plate. It is of unusual structure, and bears some resemblance to the PP plate of *Sinolepis macrocephala* in its possession of lateral angles, and in the configuration of grooves and ridges on its external surface (see Liu & P'an, 1958, pls. 3, 5, 6). This resemblance is not regarded as significant however, since the other head-shield plates described here show none of the highly characteristic features of *Sinolepis*. The orientation of the plate as figured (Fig. 12) is based on comparison with the PrM in *Asterolepis radiata* (Karatajūtė-Talimaa, 1963, pl. 11, fig. 1), which is somewhat similar in shape. Special features are the more posterior position of the lateral angles (la), and the presence of slight anterolateral and posterolateral ridges (alr, plr) and an anterior median depression (dep). The plate is only slightly broader than long, and is therefore more elongate than in other asterolepids. The groove for the infraorbital sensory line (ifc_1) is not deeply defined; a transverse median section (soc) may represent the anterior section of the supraorbital groove. As in *Remigolepis* and *Asterolepis*, and in contrast to *Bothriolepis* and *Pterichthyodes* (Stensiö. 1931, p. 31; Hemmings, 1978, p. 15), the anterior margin of the plate is concave, although there is no sign of an unornamented anterior shelf. The convex posterior margin is also seen in some other genera (e.g. Gross, 1965, fig. 3).

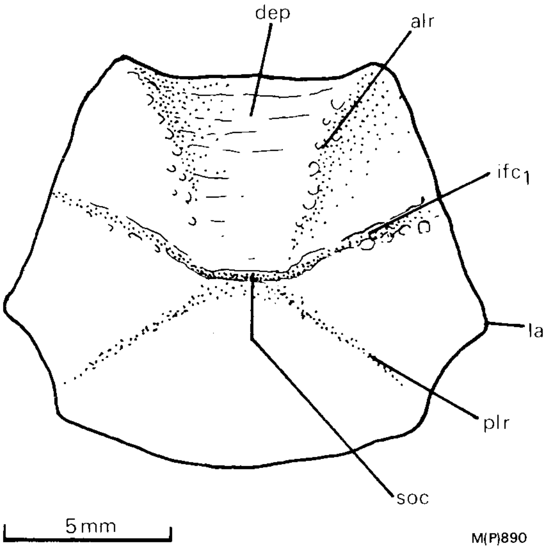

Fig. 12. ***Sherbonaspis hillsi*** **gen. et sp. nov. PrM plate restored in dorsal view after CPC 19482. For explanation of lettering see list of abbreviations.**

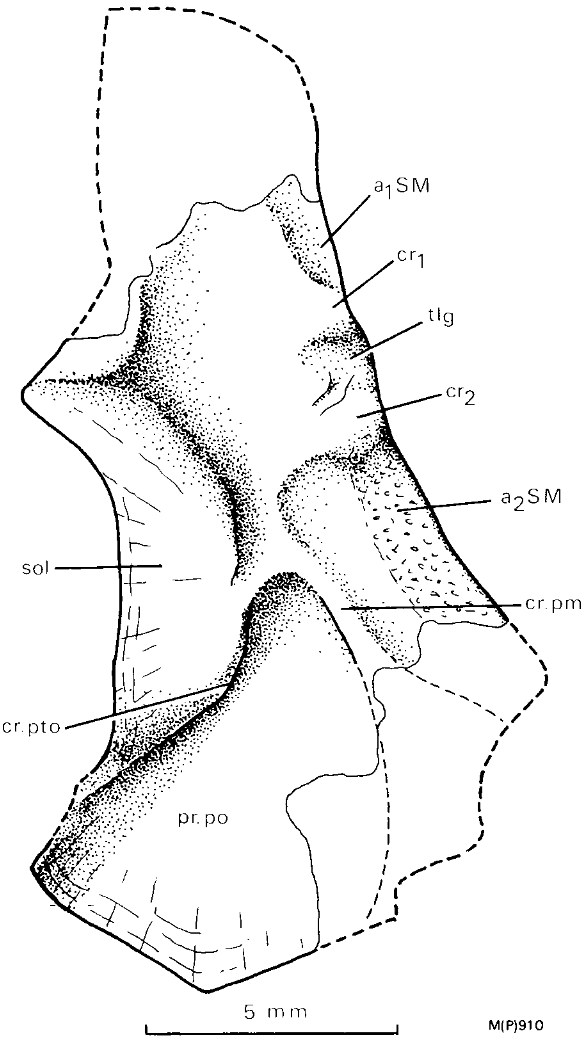

Fig. 13. ***Sherbonaspis hillsi*** **gen. et sp. nov. Left LA plate in visceral view. After CPC 19483. For explanation of lettering see list of abbreviations.**

The single LA plate is exposed in visceral view, with part of its external surface preserved as an impression. Its posterolateral and anteromesial parts are incomplete, but the orbital and lateral margins are well preserved, and as reconstructed (Fig. 13) the plate is about twice as long as broad. The preserved part of the paramarginal crista (cr.pm) is so placed as to suggest a fairly lateral position for the infraorbital sensory canal, with a correspondingly narrow lateral division of the bone, as is characteristic of all asterolepidoids (Stensiö, 1948, p. 82). In its elongate form the specimen resembles the LA plate of *Asterolepis* or *Pterichthyodes* rather than *Bothriolepis*, although in some other asterolepidoids (e.g. *Stegolepis jugata*; Malinovskaya, 1973, p. 191) the plate is much broader. The prominent postorbital crista (cr.pto) is continued beneath the orbital cavity as an extensive suborbital lamina (sol), but there is no indication of a lateral division to the preorbital recess, as is characteristic of *Bothriolepis* (Stensiö, 1948, p. 49). It is assumed that the postorbital crista extended posteriorly directly onto the PP plate, and not onto the Nu as it does in bothriolepids and *Pterichthyodes* (see Hemmings, 1978, p. 13), although there is no preserved conclusive evidence that this region of the margin formed a suture with the PP. In *Pterichthyodes* the PP overlaps the LA along a short section of its margin, which is normally separated from the orbital margin by a slight angle on the LA plate (Hemmings, 1978, figs. 1, 2). A similar arrangement occurs in *Asterolepis* (e.g. Stensiö, 1931. fig. 8). This region in CPC 19483 is unfortunately fractured and obscured by the suborbital

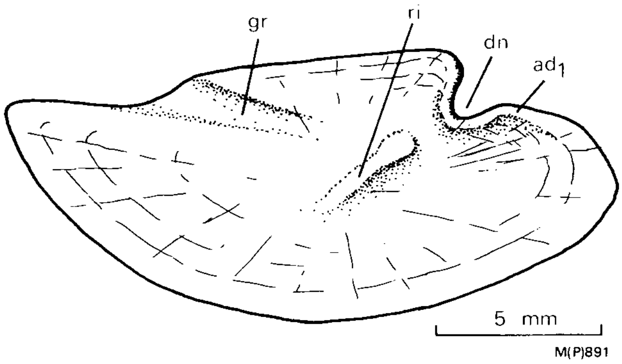

Fig. 14. *Sherbonaspis hillsi* **gen. et sp. nov. Left SM plate in visceral view. After CPC 19484. For explanation of lettering see list of abbreviations.**

lamina (sol). The short preserved section of the paramarginal crista is thick and high, and generally asterolepid in form (see Stensiö, 1948, p. 53). Two slightly roughened areas inside the lateral margin presumably represent attachment areas for the SM (a_1SM, a_2SM); they are separated by a shallow depression and two slight elevations (tlg, cr_1, cr_2), which presumably corresponds to the transverse lateral groove and pre- and post-lateral cristae as described in *Bothriolepis* (Stensiö, 1948; terminology of Miles, 1968, p. 18). These structures are similarly developed in *Asterolepis* (Karatajūtė-Talimaa, 1963, fig. 7), and *Pterichthyodes* (Hemmings, 1978, p. 15).

The SM plate is well represented by five examples (Fig. 14; Pl. 4, fig. 8), which closely resemble the corresponding plate of *Pterichthyodes* in shape (see Hemmings, 1978, fig. 5E-I). The dorsal margin has a distinct notch (dn, Fig. 14), which has been homologised by Hemmings with the dorsal ('infraspiracular') notch in *Bothriolepis* (see Stensiö, 1948, fig. 32; Miles, 1968, p. 19). However Watson (1961, p. 219) referred to the SM in *Pterichthyodes* as having 'a long, straight dorsal border' with a 'conical pit' in the thickened dorsal edge towards its hinder end. Whether this pit corresponds to the dorsal notch is unclear, but in any case a specimen figured by Hemmings (1978, pl. 3, fig. 1) shows unequivocally that in *Pterichthyodes* the notch lies towards the anterior end of the plate, and this is assumed also for *Sherbonaspis hillsi.* In *Asterolepis ornata* the notch is placed about midway along the dorsal margin (Gross, 1931, pl. 4, fig. 11; 1933a, fig. 16). It is apparently absent in *Asterolepis scabra* (see Nilsson, 1941, fig. 3), *Remigolepis* (e.g. Stensiö, 1931, pl. 4, fig. 2), and *Byssacanthus* (see Karatajūtė-Talimaa, 1960, p. 295), but well developed in *Gerdalepis* (e.g. Gross, 1941, p. 196) and *Stegolepis asiatica* (see Malinovskaya, 1973, p. 195).

The visceral surface of the plate is concave, with a centrally placed ossification centre crossed by a low ridge (ri); Nilsson (1941, p. 19) has described a groove in an equivalent position in *Asterolepis scabra.* Unlike *Pterichthyodes*, the areas of attachment are not clearly developed along the dorsal margin, although there is a slight thickening in front of the dorsal notch (ad_1). Posterodorsally there may be a shallow groove associated with the concave posterior part of the dorsal margin (gr).

Dermal bones of the *trunk-shield* are much more common than skull remains, and most plates are well represented by disarticulated examples. Only the semilunar and median ventral plates remain unknown. An attempted reconstruction of the trunk-shield in lateral view is presented in Figure 21 (cf. Gross, 1941, fig. 2; Karatajūtė-Talimaa, 1960, fig. 3; Malinovskaya, 1973, fig. 3; Hemmings, 1978, fig. 7). Of the six available AMD plates, two (CPC 19489, 19490) were measurable (see diagnosis). The posterior division is 0.85 to 0.95 times the length of the anterior, and the anterior margin is considerably shorter than the posterior (Fig. 15A). The visceral surface of the plate is well known in CPC 19489 (Pl. 4, fig. 9), with a distinct supranuchal area (sna), and low anterolateral ridges enclosing a long narrow depressed area corresponding to the levator fossa in *Bothriolepis* (f.retr). The visceral surface is deeply concave in the region of the tergal angle, which lies just behind the level of the lateral corners (lc). In the anterior half of the plate a slight median ventral ridge is developed. The contact face for the ADL is normally developed, terminating posteriorly at or just in front of the lateral corner (lc); in no specimen is there any sign of a contact face for the MxL (but see below). The external surface of the plate is not well known, but in CPC 19490 and 19493 a low rounded median dorsal crest is exposed (Fig. 21), reaching its maximum height behind the position of the deepest concavity on the visceral surface. Unlike *Byssacanthus* and *Stegolepis*, there was no dorsal spine.

The PMD is normally preserved as an external impression of a single (left or right) lamina (Pl. 4. fig. 10), although in CPC 19497 both laminae are present. This mode of preservation suggests that the plate was high and short, with a somewhat conical shape, like the PMD in *Gerdalepis*, *Byssacanthus*, and *Stegolepis* (Gross, 1941; Karatajūtė-Talimaa, 1960; Malinovskaya, 1973). The median dorsal ridge is developed as a low crest (cr.d, Fig. 15B, C), presumably continuous with that on the AMD. In all specimens a single prominent row of tubercles (dp) runs down to the lateral corner (1), and marks the position of the transverse posterior crista on the internal surface. The PMD in *Stegolepis* carries a groove in this position (Malinovskaya, 1973). The lateral margin is variably developed, being concave in CPC 19498 (Fig. 15B), but fairly straight in other specimens. The posterior margin is gently convex, and the apex of the plate is blunt, and does not carry a spine (cf. *Stegolepis*).

ADL plate proportions given above are based on six specimens (CPC 19499, 19501-19505; see the description of *Bothriolepis verrucosa* for measurement details). The plate is generally much shorter and broader than the ADL of *B. verrucosa.* Its external surface is not well known, but in CPC 19505 the anterior portion of the overlap area for the AMD is preserved, with the adjacent region of the dorsal lamina projecting forwards as a slight post-nuchal ornamented angle (pnoa, Fig. 16A). The processus obstans (pro) is poorly preserved, and the precise position of the lateral line sensory groove (lcg) is not shown by any specimen. CPC 19504 (Fig. 16B) is a high, short ADL preserved in visceral view, with the articular fossa for the dermal neck-joint shown as an impression (f.art). The anterodorsal corner in this specimen is more rounded, resembling some of the plates figured for *Pterichthyodes* (see Hemmings, 1978, fig. 11). In most specimens the contact face for the MxL (cf. PDL + cf. PL) is well exposed, either as a single area (Fig. 16A), or subdivided into two in association with a notch (n) in the posterior margin of the lateral lamina (CPC 19506; Fig. 16B). These overlap the PDL and PL com-

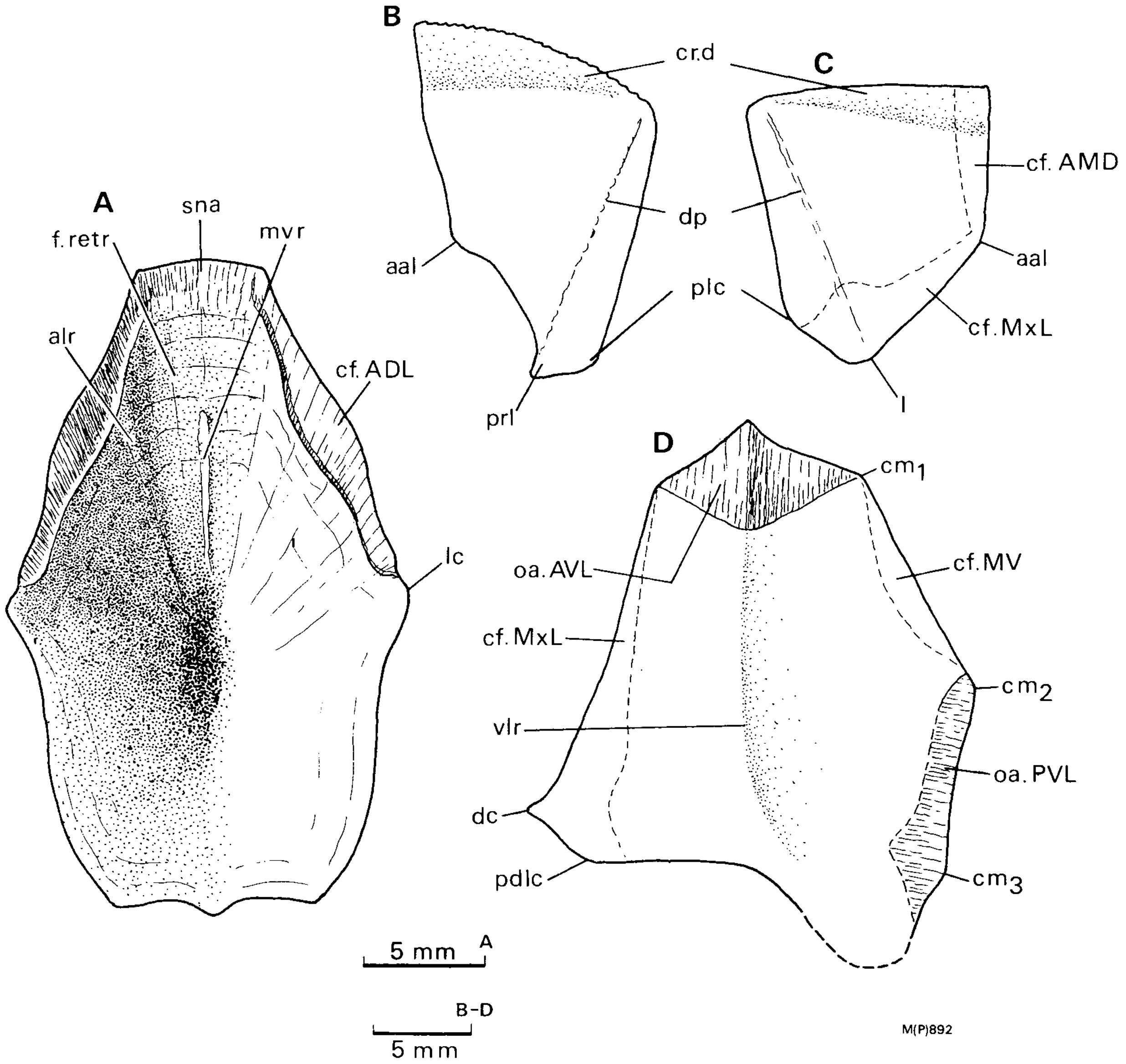

Fig. 15. ***Sherbonaspis hillsi*** **gen. et sp. nov. A, AMD plate in visceral view. After CPC 19489; B, C, two PMD plates in left lateral and right lateral views (CPC 19498 and 19496); D, right PVL plate restored in ventrolateral view after CPC 19524. For explanation of lettering see list of abbreviations.**

ponents of the MxL. A ventral overlap area for the AVL may be inferred (see Fig. 18B; cf. *Pterichthyodes*, Hemmings, 1978).

Proportions of the MxL plate are based on two specimens (CPC 19509, 19513; measured as in Karatajūté-Talimaa, 1963, fig. 53). The plate is slightly less broad than in *Gerdalepis* and *Byssacanthus*, but broader than in *Pterichthyodes*, *Stegolepis*, and various species of *Asterolepis* (Karatajūté-Talimaa, 1963, p. 164; Malinovskaya, 1973, Hemmings, 1978). In CPC 19478 (Pl. 5, fig. 1) there is a remigolepid overlap area for the AMD (Fig. 17A), but in CPC 19509 the plate apparently overlapped the AMD over the length of their common suture. The MxL is ornamented in a radial pattern, with more prominent tubercle rows running towards the dorsal (d), anterodorsal (adc), and anterior (arc) corners. The latter row in CPC 19513 forms a low keel, as in *Byssacanthus* (e.g. Karatajūté-Talimaa, 1960, pl. 2 fig. 8), and possibly *Pterichthyodes* (see Hemmings, 1978, fig. 12D). There is no clear indication of the presence of the posterior oblique sensory groove on the plate (cf. *Stegolepis*; Malinovskaya, 1973). The dorso-lateral ridge (dlr) is low but distinct, and the overlap areas for the PMD, ADL, AVL, and PVL are normally developed. The visceral surface of the plate (Pl. 5, fig. 2) carries dorsal oblique and horizontal ridges (tdr, tlr, Fig. 17B), as figured for *Byssacanthus* by Karatajūté-Talimaa (1960, pl. 2, figs. 5, 6). There is no indication that the anterodorsal ridge extends onto the AMD, as it does in *Asterolepis* (e.g. Karatajūté-Talimaa, 1963) and *Pterichthyodes* (see Hemmings, 1978, p. 23). The horizontal ridge carries the PDL/PL suture, which can be traced back as far as the crista transversalis interna posterior (cr.tp). In two specimens (CPC 19501, 19514) the plate lacks the PL component, and in CPC 19514 the separation apparently occurred along the lateral line groove. The suture and groove are also coincident in *Gerdalepis* (Gross, 1965, fig. 2). No suture was observed in other specimens exposed in external view.

In addition to the holotype, three examples of the AVL may be referred with confidence to *Sherbonaspis* *hillsi.* CPC 19517 and 19518 show posterodorsal contact faces for the MxL, the holotype includes an associated distal pectoral fin segment and an MxL plate which is clearly referable to this species (Pl. 5, figs. 1, 5), and CPC 19519 comprises left and right plates, one showing the MxL contact face, associated with a complete pectoral fin. The proportions of the ventral lamina in these specimens suggest slightly broader development than in *Bothriolepis verrucosa* sp. nov. (cf. diagnoses). In its squarish outline the ventral lamina resembles that of *Byssacanthus* or *Stegolepis* (Karatajūtė-Talimaa, 1960; Malinovskaya, 1973) rather than *Asterolepis* (e.g. Karatajūtė-Talimaa, 1963), whereas it is less elongate with a proportionately smaller MV in *Gerdalepis* (Gross, 1941, fig. 9). The subcephalic division comprises 20–30% of its length. The anterior margin is well preserved only in CPC 19518, which shows a distinct anterolateral corner (c.al, Fig. 18A) associated with a low ridge on the visceral surface, as described above for *Bothriolepis verrucosa* sp. nov. The configuration of the notch for the semilunar plate (m$_1$) suggests a less quadrilateral shape for this plate than in some other asterolepidoids (e.g. Malinovskaya, 1973; Hemmings, 1978). The crista transversalis interna anterior (cit$_1$) forms a high rounded ridge laterally, and is not subdivided mesially. The ventral lamina was apparently fairly flat, as in *Byssacanthus* and *Stegolepis*, and in contrast to *Gerdalepis* (see Malinovskaya, 1973, fig. 2).

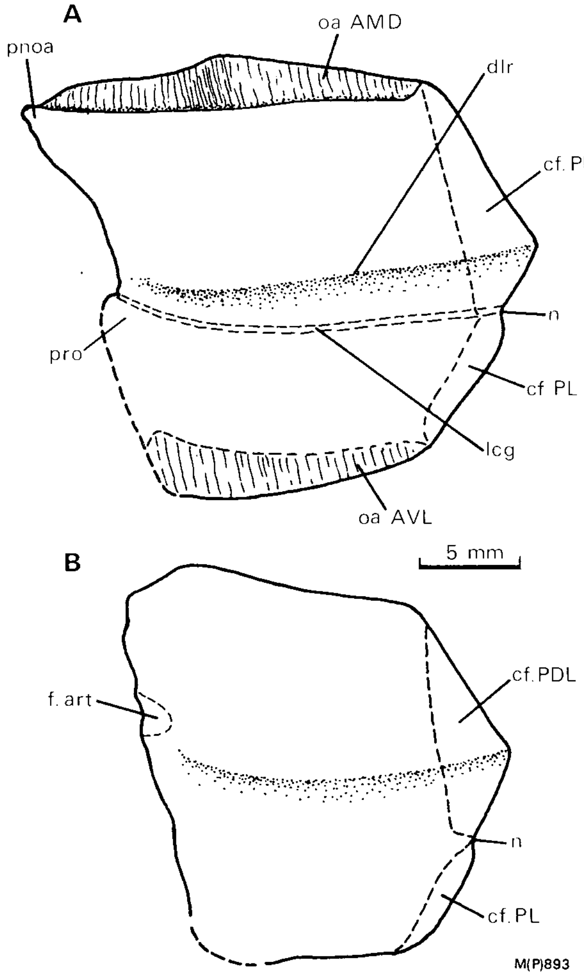

Fig. 16. *Sherbonaspis hillsi* **gen. et sp. nov. Two left ADL plates in lateral view; A, after CPC 19505; B, after CPC 19504. For explanation of lettering see list of abbreviations.**

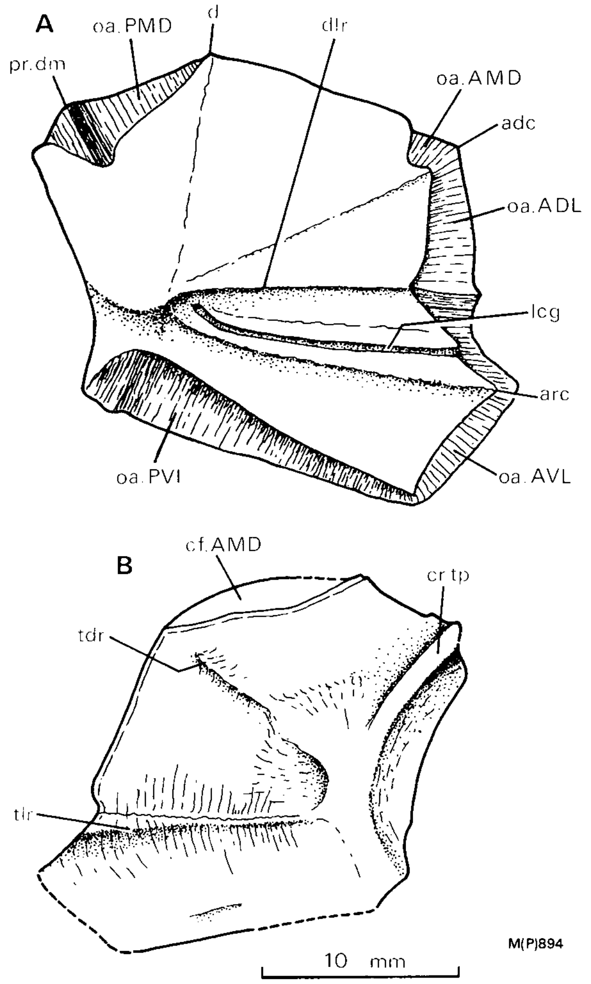

Fig. 17. *Sherbonaspis hillsi* **gen. et sp. nov. Right MxL plates; A, in lateral view, restored after CPC 19478 (holotype) and 19514; B, in visceral view, after CPC 19509. For explanation of lettering see list of abbreviations.**

The lateral lamina in CPC 19518 (Fig. 18B) is about 2.5 times as long as high, its height being about 0.6 the width of the ventral lamina (cf. *Stegolepis*; Malinovskaya, 1973, p. 194). The lateral lamina in *Byssacanthus* is proportionately higher (Karatajūtė-Talimaa, 1960, pl. 3, fig. 2). In *Sherbonaspis* it is highest at the posterodorsal corner, at which a distinct contact face for the MxL is developed (cf.MxL, Fig. 18B). However, this contact face is shorter than in *Byssacanthus* or *Pterichthyodes*. The angle between laminae measured in two specimens was 100° and 110°. As noted above the foramen axillare (f.ax) is very small, and unlike *Pterichthyodes* it is subcircular rather than oval in shape (cf. Hemmings, 1978, p. 31). The pectoral fin articulation is not preserved and comparisons cannot be made with the peculiarities of structure reported for *Byssacanthus* (see Karatajūtė-Talimaa, 1960, p. 297). However, the bone partitions described on the inner surface around the rostrocaudal canal in *Byssacanthus* are clearly absent (Fig. 18A).

Two further examples of the AVL are only tentatively referred to this species. CPC 19520 (Fig. 18C) is a ventral lamina preserved in visceral view, which differs from other plates in the collection in its more elongate shape, shorter subcephalic division, larger semilunar notch, and the configuration of its anterolateral and lateral corners. Similar proportions are indicated on another very incomplete specimen (CPC 19521).

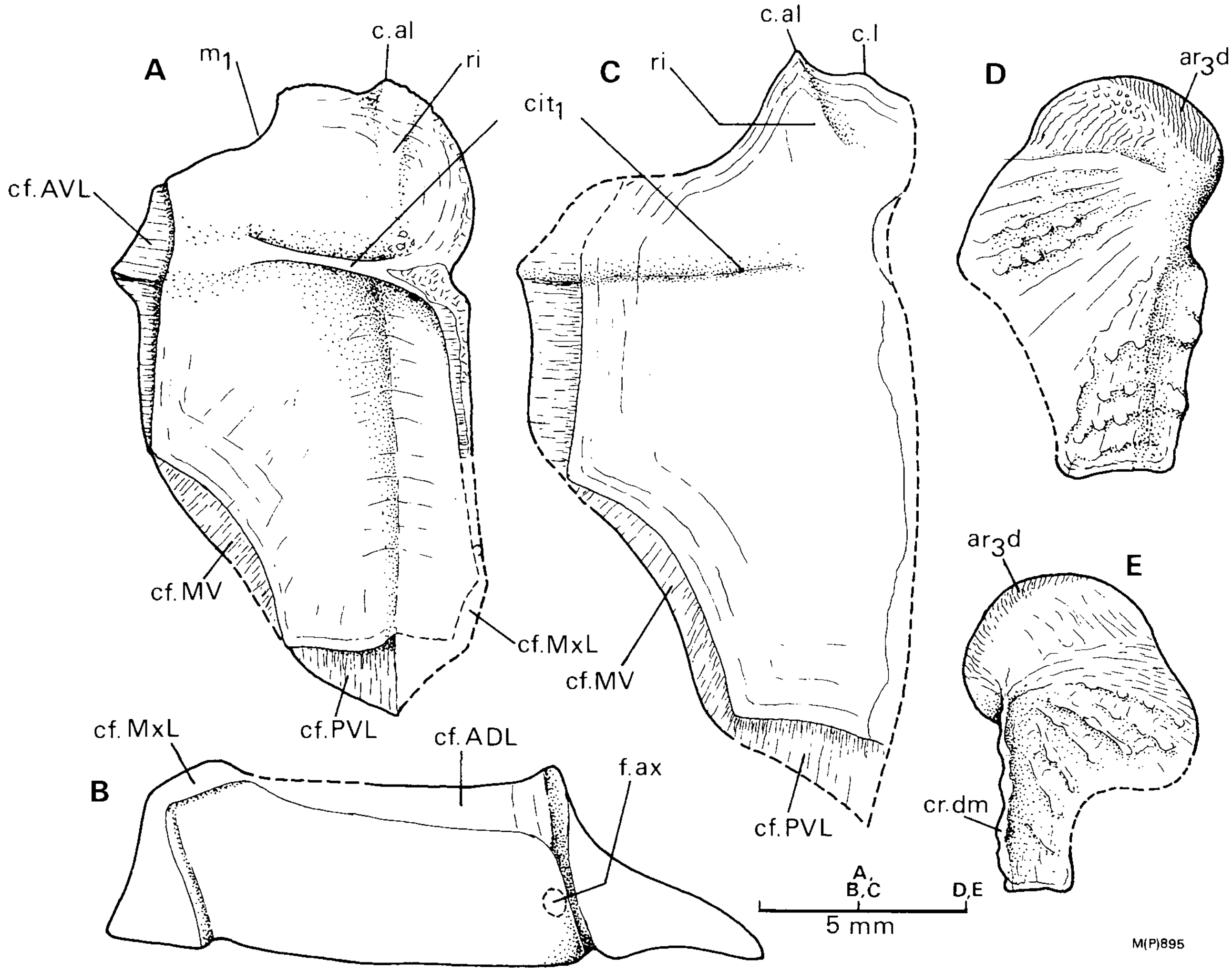

Fig. 18. ***Sherbonaspis hillsi*** **gen. et sp. nov. Right AVL plates; A, restored in dorsal view after CPC 19518; B, impression of lateral lamina, lateral view (CPC 19518); C, ventral lamina in dorsal view (CPC 19520). D, left Cd_1, dorsal view (CPC 19526); E, right Cd_1, dorsal view (CPC 19529). For explanation of lettering see list of abbreviations.**

The PVL of *Sherbonaspis* is distinguished by the shape of its lateral lamina, which decreases considerably in height in front of the dorsal corner (Pl. 5, fig. 3; cf. Fig. 8E). Two fairly complete examples are available. The ventral lamina in CPC 19524 (Fig. 15D) is considerably broader than that of *Pterichthyodes* (e.g. Hemmings, 1978, p. 31), *Byssacanthus* (e.g. Karatajūtė-Talimaa, 1960, pl. 3, fig. 3), or *Stegolepis* (e.g. Malinovskaya, 1973, fig. 3b). The corresponding lamina in CPC 19522 is more elongate, with a longer subanal division (20–25% of total length for the two specimens), which is still less than the corresponding proportion in *Stegolepis* (about 33% of total length). The l/b index for the lateral lamina is 185 in CPC 19522. Other features of the plate are the prominent dorsal and low anterior corners (Fig. 21), the latter being just more than one third the height of the former (see Hemmings, 1978, p. 31), and the long anterior division of the mesial margin of the ventral lamina, indicating a relatively large MV, as in *Stegolepis*, and in contrast to *Gerdalepis* (e.g. Gross, 1941) and *Pterichthyodes* (e.g. Hemmings & Rostron, 1972). The angle enclosed by the two laminae is estimated at about 95° in CPC 19522 and 115° in CPC 19524. Most of the external surface has been lost in the latter specimen, but the impression of the visceral surface indicates a broad transverse thickening. The extension of the transverse posterior crista onto the ventral lamina is not preserved.

The *pectoral fin* is represented by one fairly complete specimen (CPC 19519, Pl. 5, fig. 6), two incomplete distal segments (CPC 19478, 19533), and various disarticulated plates. The joint between proximal and distal segments in CPC 19519 is somewhat crushed, but this specimen gives an approximate idea of overall proportions of the fin (see diagnosis). The proximal segment is relatively longer than the distal segment, but otherwise of similar proportions to the proximal segment in *Pterichthyodes* (see Hemmings, 1978, p. 34). The Cd_1 is somewhat variable in shape (Fig. 18D, E); three specimens (CPC 19526, 19529, 19530) gave l/b indices between 156 and 175, and are therefore relatively shorter and broader than in *Pterichthyodes* (Hemmings, 1978). Another example (Pl. 4, fig. 13) is more elongate, and closely resembles the corresponding plate in *Asterolepis* or *Pterichthyodes* (Stensiö, 1931, fig. 59; Hemmings, 1978, fig. 20A). The dorsomesial crista is quite distinct (cr.dm), and the mesial lamina of the plate lacks ornament, again as in *Asterolepis*. Two examples (Fig. 19A) show the Cv_1 to be shorter and broader (l/b index 189), but otherwise similar in shape to the corresponding plate in *Asterolepis* (Stensiö, 1931, fig. 60). Other disarticulated plates are two left Cd_2 plates (Fig. 19B; Pl. 5, fig. 4) and right Cv_2

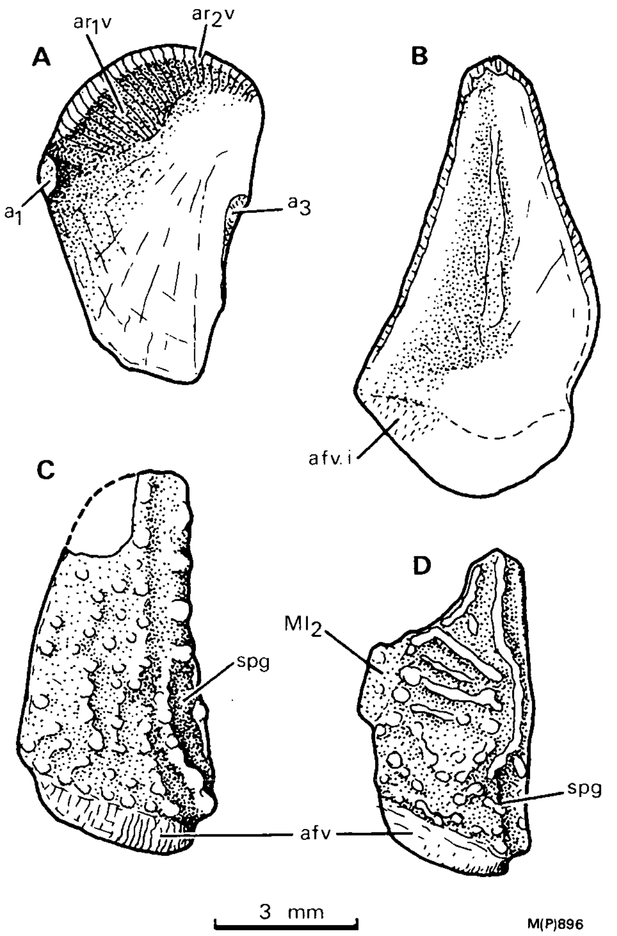

Fig. 19. *Sherbonaspis hillsi* **gen. et sp. nov. A, left Cv$_1$ in internal view (CPC 19527); B, left Cd$_2$ in internal view (CPC 19531); C, D, right Cv$_2$ plates in external view (CPC 19532, 19527). For explanation of lettering see list of abbreviations.**

plates (Fig. 19C, D), which again show normal asterolepid development. A fragment of the Ml$_2$ may be fused to the lateral margin of CPC 19527. The Ml$_2$ in CPC 19519 is somewhat crushed, but was evidently short and broad, as is also indicated by another incomplete disarticulated example (CPC 19534). Part of the Mm$_1$ is also exposed in CPC 19519, but its margins cannot be discerned. The Mm$_2$ in this specimen is obscured by the distal segment.

In addition to the three articulated examples (CPC 19478, 19519, 19533), the distal segment is represented by two detached T plates (CPC 19525, 19528) from somewhat larger individuals, which show that this plate was an asymmetrical bone with a proximal process which separated the most distal lateral and mesial marginal plates (Fig. 20C, D). It is therefore of the type characteristic of *Asterolepis* (e.g. Gross, 1931, pl. 6, figs. 3, 4), and occasionally developed also in *Bothriolepis canadensis* (see Stensiö, 1948, p. 158). On the other hand the T plate in *Pterichthyodes* has quite a different shape (Hemmings, 1978, figs. 18, 19). The two figured distal segments are incompletely exposed, with indistinct sutures, and the reconstructions (Fig. 20A, B) must be regarded as tentative. The T plate appears to vary in shape, and in CPC 19519 there is possibly a common suture between the Mm$_5$ and Ml$_5$, which has not previously been reported in antiarchs. Both specimens demonstrate however that there were two bones in each central series and three in each marginal series of the distal segment; that is, one more central series plate than in *Asterolepis*, and one more

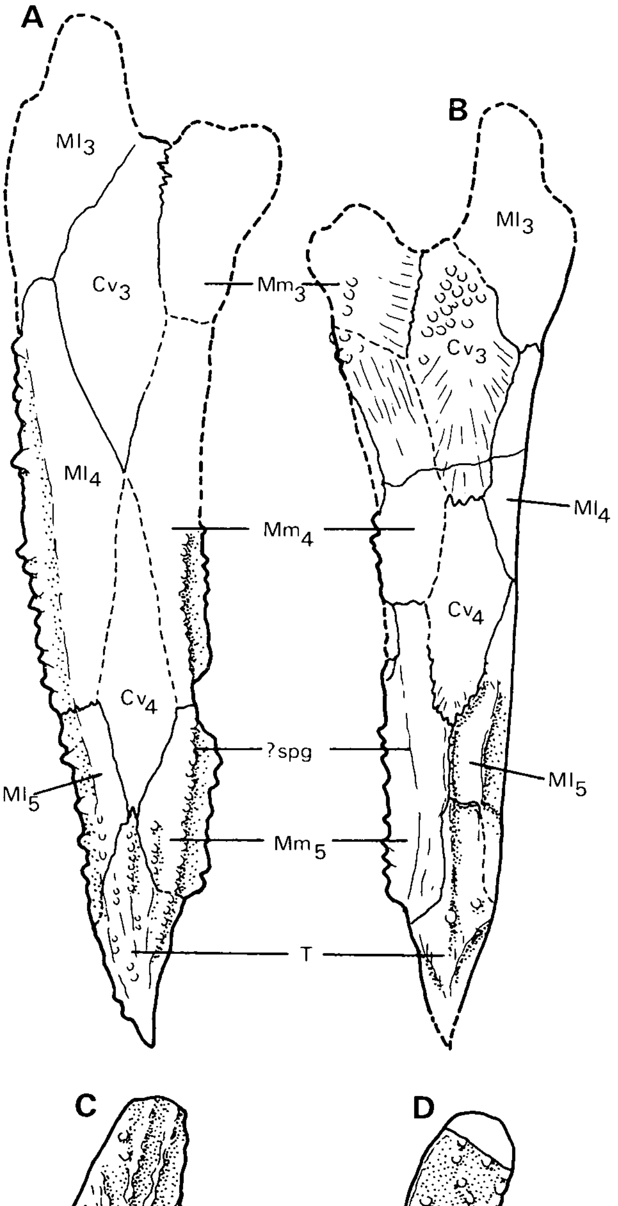

Fig. 20. *Sherbonaspis hillsi* **gen. et sp. nov. A, B, attempted reconstructions of the distal segment of the pectoral fin; ventral view. After CPC 19478 (holotype) and 19519; C, D, two T plates (CPC 19525, 19528); missing portions are preserved as impressions. For explanation of lettering see list of abbreviations.**

mesial marginal plate than in *Pterichthyodes*, to give an arrangement otherwise only recorded atypically in *Bothriolepis* (see Stensiö, 1948, fig. 58C). The distal segment is ornamented with scattered tubercles which tend to form longitudinal rows on and near the T plate. The strong ridging seen in *Byssacanthus* (e.g. Karatajūtė-Talimaa, 1960, pl. 3, fig. 8) is not developed.

Order EUARTHRODIRA

Definition: see Young (1979, p. 344).

Remarks: Denison (1978, fig. 10) has provided an alternative definition to the one cited, based on two supposed euarthrodiran (= arthrodiran) specialisations: 'Two pairs of supragnathals; sliding or ginglymoid dermal craniothoracic articulation, latter with condyles on anterior dorsolaterals'. However, the possession of a sliding dermal neck-joint may be primitive for all dolichothoracomorphs (Young, 1980, p. 69), so it cannot be regarded as a euarthrodiran specialisation. Other characters included in the cited definition are based on new morphological information (Young, 1979), and it is therefore retained here.

Suborder PHLYCTAENIOIDEI Miles, 1973a

Definition: see Young (1979, p. 345).

Remarks: This suborder is a cladal grouping of all euarthrodires possessing a hinged dermal neck-joint, and as such is equivalent to the combined suborders Phlyctaeniina, Heterosteina, Coccosteina, and Pachyosteina in Denison's (1978, fig. 30) scheme of relationships. An equivalent grouping is embodied but not formally named in the cladograms of Miles & Dennis (1979) and Dennis & Miles (1979a, b), but these authors propose an additional specialisation of this group, namely the presence of a ventral ridge on the MD plate. However, a corresponding ventral ridge also occurs in some actinolepids, for example in *Aethaspis* (e.g. Denison, 1958, p. 481), *Sigaspis* (see Goujet, 1973, fig. 1B), and *Actinolepis* (see Mark-Kurik, 1973, pl. 11). This character may therefore be discounted as a phlyctaenioid specialisation. Young (1979) proposed specialisations of the cheek to define the Brachythoraci, but no attempt was made at phylogenetic analysis of the remaining phlyctaenioid groups. However, Denison (1978, fig. 30) has put forward a scheme whereby the long narrow MD is a shared specialisation of two phlyctaenioid families (Phlyctaeniidae, Holonematidae), with the relationships of a third (Williamsaspidae) left open. Denison has characterised the Phlyctaeniidae by a tendency to elongate the SP plates, but since in some actinolepids and phlyctaeniids these are of similar length (e.g. Denison, 1958, fig. 112H, K), this would appear to be unreliable. Included with *Holonema* in the second family are *Groenlandaspis* and *Tiaraspis*, with *Arctolepis* presumably as an early member, since the stated holonematid specialisations include the presence of a large P plate separating the PrO plates in the skull-roof (Denison, 1978, p. 60). An alternative scheme has been proposed by Dennis & Miles (1979a, b), in which *Holonema* is regarded as more closely related to brachythoracids than to *Groenlandaspis* on the premise that the presence of a pre-endolymphatic thickening and a long pectoral fin base are shared specialisations.

Here we propose to follow Denison's scheme in part, and tentatively to accept the suggested synapomorphies between *Arctolepis*, *Groenlandaspis*, and *Holonema*. (*Arctolepis* should therefore be removed from the Phlyctaeniidae, and placed in the Holonematidae). However, the presence of a long narrow MD in some brachythoracids (e.g. *Gemuendenaspis*; Miles, 1962) invalidates Denison's basis for defining the suborder Phlyctaeniina (1978, fig. 30). This means that the family Phlyctaeniidae can at present be defined only on the basis of primitive characters, and therefore must still be regarded as a grade group.

Family PHLYCTAENIIDAE Fowler, 1947

Definition: Phlyctaenioids in which the PrO plates meet behind the P plate, the supraorbital sensory canals do not extend onto the C plates, the lateral lines are not sinuous on the trunk-shield, the overlap of skull-roof plates is minimal, the Nu is not posteriorly expanded and lacks a ventral thickening, and the PNu lacks a postnuchal process and a differentiated para-articular process on the subobstantic area. In many forms the spinals may be elongate.

Remarks: As just noted, most or all of these characters may be primitive for phlyctaenioids, making the Phlyctaeniidae a paraphyletic group. Within the group, subgroups are not readily defined; Dennis & Miles (1979a, p. 3) have proposed the course of the occipital cross-commissure as a means of separating primitive and advanced phlyctaeniids, but this would seem to be totally inadequate (for example in the brachythoracid *Buchanosteus* this sensory groove has the supposed primitive position; see White & Toombs, 1972, fig. 3). We have not attempted a subdivision into suprageneric groupings.

Genus **Denisonosteus** nov.

Name: After Dr R. H. Denison, Lincoln, Massachusetts.

Type species: *Denisonosteus weejasperensis* sp. nov.

Diagnosis: A phlyctaeniid with the dermal armour (head and trunk-shields) attaining a mid-dorsal length of at least 115 mm; skull-roof with a convex posterior margin, an elongate Nu plate reaching the level of the C ossification centres, and deeply notched by the PNu plates behind its ossification centre; PNu notching and overlapping the M plate lateral to the lateral line sensory groove, the M notching the PNu mesial to the lateral line sensory groove, and considerably larger than the PtO, the PM projecting from the skull-roof margin to form a distinct posterior postorbital notch, and the PtO forming a fairly distinct dermal postorbital process. R, P, and PN plates probably forming a separate rostral capsule. Trunk-shield with the MD plate about 1.85 times as long as broad, and with a slightly convex anterior margin and posterior median process; ADL with a convex dorsal margin and reaching maximum breadth at the level of the posteroventral angle; AL with a postbranchial lamina ornamented with ridges and a fairly short ventral margin; PDL slightly higher than long, with straight dorsal, and gently convex posterior margins, and the lateral line groove terminating near the anterior margin; PL high posteriorly with a convex posterior margin, and an anterior margin sloping posteroventrally; SP of moderate length, with a free mesial margin bearing curved denticles; AMV with a median embayment in the anterior margin; PMV with concave anterolateral margins. Ornament typically of scattered tubercles, but possibly aligned in concentric rows in some individuals.

Remarks: In Denison's comprehensive revision (1978, pp. 54-60), fifteen genera are included in the family Phlyctaeniidae (but see the above remark regarding *Arctolepis*). *Denisonosteus* gen. nov. may be distinguished from all of these by the shape of its Nu plate, and by the convex posterior margin of the skull-roof. In the latter character it resembles the holonematids *Holonema* and *Groenlandaspis*, but as mentioned by Denison (1978, p. 60; see Remarks above), *Arctolepis* may be interpreted as a primitive holonematid on the size and position of its P plate. This implies that the convex posterior margin in *Denisonosteus* gen. nov. must have evolved in parallel, since *Arctolepis* has a straight posterior skull-roof margin. *Denisonosteus* gen. nov. resembles *Aggeraspis*, *Cartieraspis*, *Pageauaspis*, and *Gaspeaspis* in Nu length, other genera tending to have shorter, broader Nu and PNu plates. Of the genera just listed however, only *Pageauaspis* has proportionately similar PtO and M plates, but may be distinguished by Nu and PNu shape, the coarser ornament, and the development of skull-roof margins (Pageau, 1969b, pl. 27, fig. 1; pl. 28, fig. 3). *Denisonosteus* gen. nov. resembles *Arctolepis* and *Dicksonosteus* and differs from *Phlyctaenius*, in the

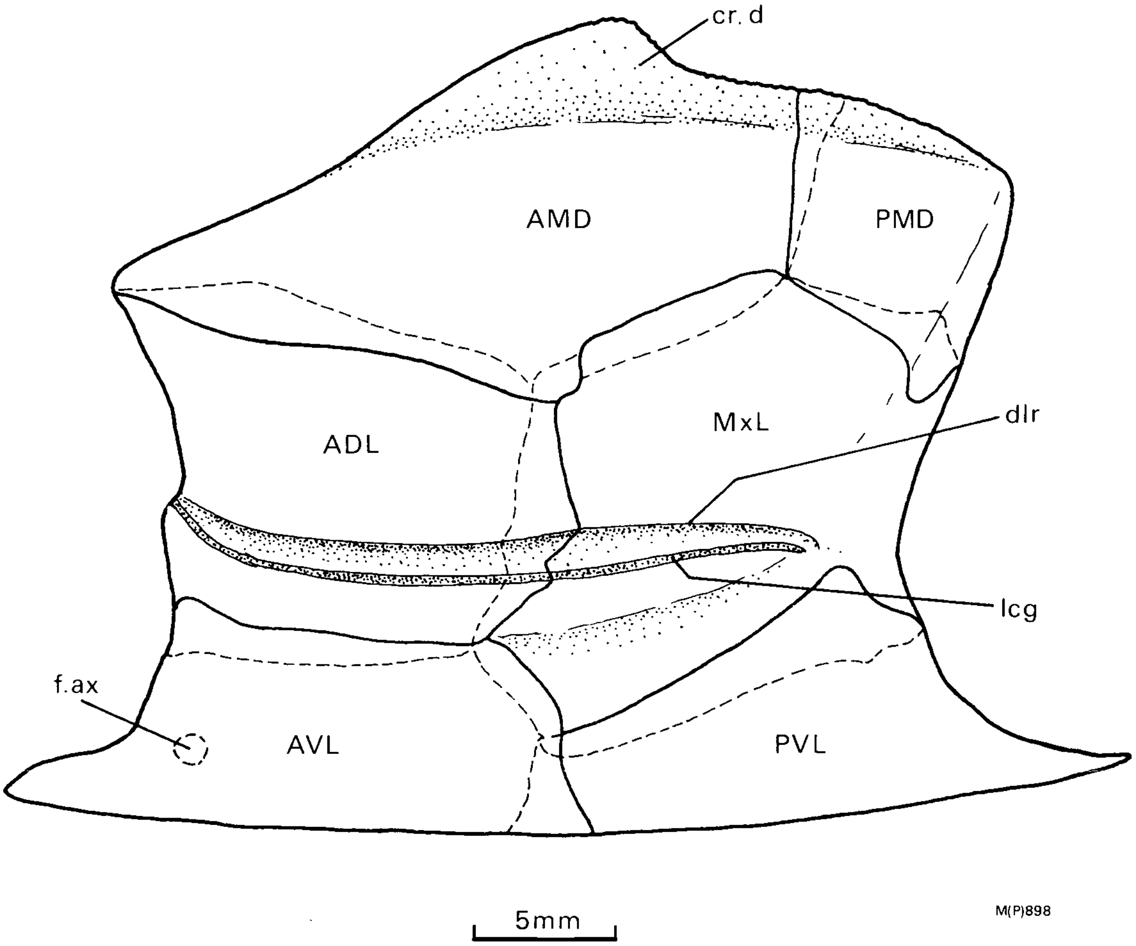

Fig. 21. *Sherbonaspis hillsi* **gen. et sp. nov. Attempted restoration of the trunk-shield in left lateral view. For explanation of lettering see list of abbreviations.**

shape and size of the PM plates (e.g. Goujet, 1975, fig. 1); it may be distinguished from the former two genera by the narrower width across the PN plates, and the relatively smaller PtO and larger M. In trunk-shield morphology *Denisonosteus* gen. nov. may be readily distinguished from most other genera by the shape and proportions of the MD (e.g. Denison, 1978, figs. 39, 41E), from *Aggeraspis, Dicksonosteus, Cartieraspis,* and *Diadsomaspis* by its higher, shorter dorsolateral plates, from *Elegantaspis* and *Heterogaspis* by SP length and ornament (Heintz, 1929), from *Huginaspis* which has a high trunk-shield with a median dorsal crest, and from *Neophlyctaenius* in which the trunk-shield plates are generally longer. There is a closer resemblance in trunk-shield morphology to *Phlyctaenius*, but the following distinguishing features may be listed: in *Denisonosteus* the MD is shorter and broader with a convex anterior margin, the ADL differs in shape, the PDL has a slightly convex posterior margin, the AL has a less extended posterodorsal corner, the AMV has an embayed anterior margin, the PMV has concave anterolateral margins, and the SP plate carries curved denticles along its free mesial margin.

Denisonosteus weejasperensis sp. nov.

Figs. 22, 23C, 24; Pl. 5, fig. 8; Pl. 6; Pl. 7, figs. 1-3, 7

Name: After Wee Jasper village.

Holotype: CPC 19537, an incomplete skull-roof in part and counterpart, associated with an incomplete left AL and a complete MD plate.

Other material: 2 head-shields (CPC 19538, 19539), PNu (CPC 19540), SO (CPC 19541), SM (CPC 19542, 19579), M (CPC 19544) and PN (CPC 19543) plates, ADL plates (CPC 19545-19547), 6 AL plates (CPC 19551-19556), 1 SP plate (CPC 19560), 9 AVL plates (CPC 19561-19569), 1 PDL plate (CPC 19558), 1 PL plate (CPC 19559), 9 PVL plates (CPC 19571-19579), AMV and PMV plates (CPC 19549, 19570), and a few fragmentary remains (CPC 19580, 19581).

Diagnosis: as for genus (only species).

Description: Denisonosteus weejasperensis was a phlyctaeniid of medium size, the holotype indicating a mid-dorsal length for head and trunk-shields of about 120 mm. The holotype includes a *skull-roof* of medium size (Pl. 6, fig. 1), with a post-pineal length of about 66 mm. CPC 19538 (Pl. 7, fig. 2) is a smaller example (post-pineal length about 30 mm), and CPC 19539 is larger than the holotype, but too crushed and incomplete for measurement. The skull-roof reconstruction given in Figure 22 is based mainly on these specimens. The strongly convex posterior margin is clearly shown in the holotype, and in this respect *Denisonosteus* resembles *Holonema* and *Groenlandaspis* (see Miles, 1971; Ritchie, 1975). In most other phlyctaeniids and actinolepids the posterior skull-roof margin is fairly straight or concave (e.g. Denison, 1978, figs. 31, 38). The posteromesial angle of the skull-roof (pmaa) is well marked, and in front is a distinct embayment, with a rostrocaudally aligned unornamented lamina projecting ventrally in a corresponding position to the 'para-articular process' in *Dicksonosteus* (see Goujet, 1975). As described and figured by Goujet, this lamina in *Denisonosteus* takes the form of a thickened truncated

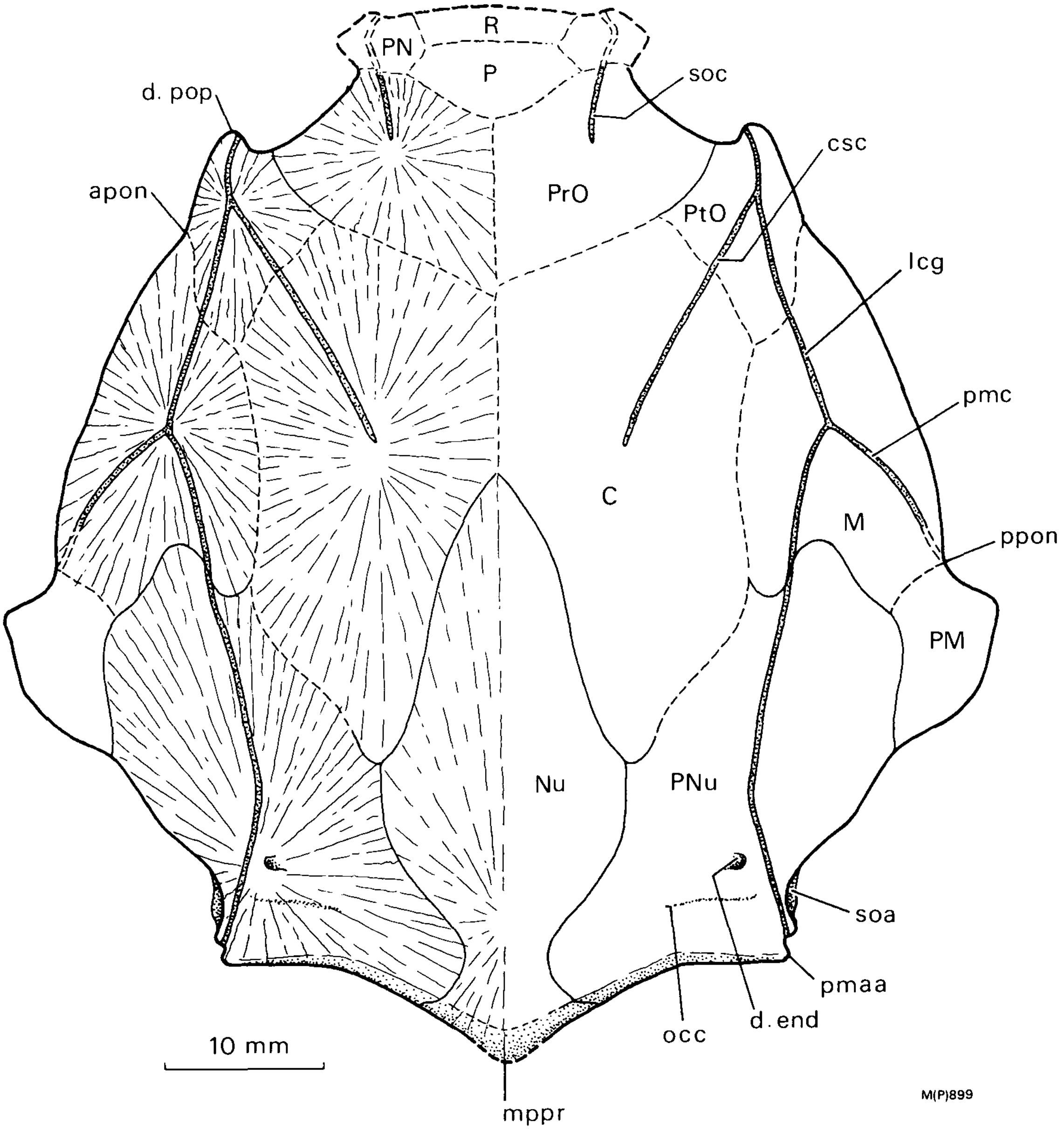

Fig. 22. ***Denisonosteus weejasperensis*** **gen. et sp. nov. Skull-roof in dorsal view, after CPC 19537 (holotype), 19538, 19539. For explanation of lettering see list of abbreviations.**

edge to the skull-roof margin. It is here termed the subobstantic area (soa), since a distinct para-articular process, as seen for example in *Holonema* (Miles, 1971, fig. 29), is not developed. No other structures relating to the dermal neck-joint are preserved in this specimen. The posterolateral angle of the skull-roof is well preserved in CPC 19538, and is generally similarly developed to *Baringaspis*, *Dicksonosteus*, or *Arctolepis* (Miles, 1973a, fig. 2; Goujet, 1975, fig. 1), with a distinct posterior postorbital notch (ppon) in front of the PM plate. There is a slight anterior postorbital notch at the PtO/M suture (apon), and a short dermal postorbital process (d.pop). The margins in the preorbital region are not well shown in these specimens, but bone sutures and ossification centres are in general clearly displayed. Noteworthy is the deep lateral embayment of the Nu plate just behind its ossification centre, as is well shown on the right side of the holotype (Pl. 6, fig. 1; cf. *Aethaspis*; Denison, 1958, p. 474). The Nu is a fairly elongate bone, extending anteriorly to the level of the C ossification centres (cf. *Cartieraspis* or *Pageauaspis*; Denison, 1978. fig. 38). The PNu is longer and narrower than in many genera, resembling most closely that of *Aethaspis major* (e.g. Denison, 1958, fig. 105B) or *Dicksonosteus arcticus* (see Goujet, 1975). On the right side of the holotype the anterior margin of the PNu is convex on the lateral side of the lateral line canal, where it overlaps the M plate. A corresponding overlap area is shown on the right M plate in CPC 19539, which also shows a posterior process notching the PNu margin on the mesial side of the sensory groove. In contrast, other phlyctaeniids and some actinolepids have a fairly straight transverse PNu/M suture, and in most actinolepids the PNu has an anterior process on the mesial side of the sensory groove, which may extend as far forward as the PtO (e.g. Denison, 1978, fig. 31A-F, I, J). *Denisonosteus* resembles other phlyctaeniids in having extensive contact between C and M plates. However, the M is relatively larger and the PtO relatively smaller than in most genera, although similar proportions are seen in *Pageauaspis russelli* (e.g. Denison, 1978, fig. 38E). The C/PrO suture is not preserved, but the ossification centre of the right PrO and the PrO/PtO suture are clearly seen in visceral view in the holotype. In CPC 19538 the impression of the visceral surface shows a shallow transverse groove (cr.seth, Pl. 7, fig. 2), similar to that in *Kujdanowiaspis* (e.g. Stensiö, 1942, fig. 6), which indicates the presence of a crista supraethmoidalis (the 'ventral lamina of the preorbital plate' of Stensiö, 1945, fig. 8B). This suggests that the PrO was short and broad, and that the bones of the rostral region (P, R, PN) had a similar disposition to those in *Kujdanowiaspis* and many other phlyctaenioid genera. Unlike *Arctolepis*, *Groenlandaspis,* and *Holonema* therefore, the rhinocapsular and postethmo-occipital bones of the endocranium were presumably separately ossified.

The sensory canal pattern as preserved in these specimens was apparently normally developed. In the holotype the occipital commissure and posterior pitline are very indistinct. The external surface of the C plate is not preserved, but grooves on the impression of the visceral skull-roof surface (gr.csc, Pl. 6, fig. 1) indicate that the central sensory canal extended back to the ossification centre of the C plate. A similar groove beneath the PrO (gr.soc, Pl. 7, fig. 2) shows the presence of the supraorbital canal on this plate (soc, Fig. 22). A groove for the postmarginal canal on the right side of CPC 19538 terminates at the posterior postorbital notch, so it is not clear whether this canal extended onto the PM plate. Ridges on the visceral surface beneath these sensory grooves are also well displayed in CPC 19544. Various other structures developed on the visceral surface of the skull-roof are also represented by impressions (Pl. 6, fig. 1; Pl. 7, fig. 2). There was a rounded ventral process behind the Nu ossification centre (if.r), a median ridge (mvr) on the Nu, and an endolymphatic thickening (th.end) on the PNu. Ridges beneath the C plate marked the position of the labyrinth cavity (r.scc). Similar structures are seen in many other euarthrodires (e.g. Stensiö, 1945, 1963; Miles, 1973a; Young, 1979).

Several other disarticulated plates from the head have been identified. CPC 19541 (Pl. 6, fig. 6) is a right SO plate from a small individual (preserved total length of plate 11 mm), preserved mainly as an impression of its visceral surface. The suborbital process shows a section of the groove for the suborbital division of the infraorbital sensory line (ifc.sb), and another possible sensory groove near the posterior margin may be part of the postsuborbital or horizontal sensory lines, although neither is seen on the SO of *Dicksonosteus* (Goujet, 1975, fig. 2A). In overall proportions this plate is similar to that of *Dicksonosteus* or *Phlyctaenius* (e.g. Denison, 1958, fig. 106D), but with a lower and longer postorbital lamina. In addition two incomplete SM plates are referred to this species. One of these (Pl. 5, fig. 8) is associated with a left PVL, and is assumed also to be from the left side, with the shallow notch near the anterior end of its dorsal margin corresponding in position to the notch and groove for the epihyal as identified on the SM by Goujet (1972, pl. 1). In *Denisonosteus*, however, the plate was evidently more ovate than those described by Goujet (1972, 1975). In *Holonema* the SM plate is of similar shape, although Miles (1971, fig. 36) has interpreted the shallow dorsal notch as a posterior embayment for the PM plate. It is possible that left and right plates in *Holonema* have been misidentified. The second specimen included here (CPC 19542) is also preserved in visceral view, and again shows a notch in the dorsal margin. It is assumed to be from the right side. Finally a small bone crossed by a sensory canal (Fig. 23C) is provisionally identified as a PN plate of *Denisonosteus.*

Plates of the *trunk-shield* are again fairly well represented in the collection, and only the anterolateral plate has not been identified. The MD plate as preserved in the holotype (Pl. 6, fig. 2) resembles in shape the corresponding plate of *Phlyctaenius acadicus* (see Heintz, 1933), with a rounded posterior median process (mppr, Fig. 24A). However, it is proportionately broader, being about 1.85 times as long as broad (total length 44 mm), with a convex rather than concave anterior margin. Only the visceral surface is exposed, showing short, broad anterior and more elongate posterior contact faces (cf. ADL, cf. PDL) for the dorsolateral plates. A median ventral ridge (mvr) is developed in the most concave region of the visceral surface, which probably approximates to the position of the ossification centre of the plate. Anteriorly are paired shallow grooves (gr), and posteriorly is a slightly thickened protuberance flanked by paired depressions (dep). These last structures may be compared with the 'posterior keel' in *Holonema* (see Miles, 1971, fig. 66). The ADL plate as reconstructed (Fig. 24B; cf. Pl. 6, fig. 4) resembles that of *Phlyctaenius acadicus* (e.g. Denison, 1958, fig. 108), or *Groenlandaspis antarcticus* (see Ritchie, 1975, fig. 2). From the former it differs mainly in the shape of the dorsal margin and in the more prominent posteroventral angle on the lateral lamina. From the latter it may be distinguished by the more dorsal position of the lateral line sensory groove (indicated by a notch in the posterior margin of CPC 19547). Only the visceral surface of the plate is exposed, but the shape of overlap areas may be inferred from the morphology of adjacent plates (Fig. 24A, C). The contact face for the PL plate is weakly developed in CPC 19547 (Pl. 6, fig. 4), and unlike *Groenlandaspis* it extends beneath the level of the lateral line canal (see also below).

The external surface of the AL plate is poorly known, but it displays normal tubercular ornament in the holotype (Pl. 6, fig. 2), whilst two other specimens (CPC 19553, 19555) show impressions of ridged ornament on the postbranchial lamina. This lamina is fairly well developed as a mesial inflection of the anterior quadrant of the plate. On the visceral surface of the plate conspicuous ridges pass from the ossification centre to the posterodorsal and posteroventral corners (Fig. 24C; Pl. 6, fig. 3). The contact faces for surrounding plates are generally clearly defined, except in the region of the posterodorsal corner, where they are indistinct, but presumably had a similar configuration to the contact faces for the PDL and PL plates in *Phlyctaenius* as figured by Denison (1958, fig. 110B). In overall shape the AL resembles that of several other forms (e.g. Denison, 1958, fig. 110; White, 1969). The pectoral embayment is more pronounced than in *Phlyctaenius*, whilst the ventral margin is proportionately shorter than in *Aggeraspis* or *Tiaraspis* (Gross, 1962). The PDL plate (Fig. 24D) is represented by a single specimen preserved as part and counterpart (CPC 19558) which again shows resemblance to *Phlyctaenius* in its overall proportions and broad, fairly straight dorsal margin (cf. Denison, 1958, fig. 109A). It differs however in its slightly convex posterior margin, in the relative extent of the overlap areas for the AL and PL plates, and in the restriction of the lateral line sensory groove to a short section near the anterior margin. The PL plate is also represented by a single fairly complete specimen preserved showing its visceral surface (Fig. 24E). In shape it differs in minor details from the PL in other forms (Denison, 1958, fig. 111). Its orientation is fixed by the presence of a contact face for the PDL along its dorsal margin. The visceral surface is crossed by a low ridge (th), presumably continuous with ridges on the PVL plate (see below).

The single incomplete SP plate (Pl. 6, fig. 5) has an ornament of fine tubercles, and was probably of similar proportions to the SP of *Phlyctaenius acadius* (e.g. Heintz, 1933, fig. 3). Along its free mesial margin is a smooth zone bearing a row of curved denticles, as has been described in some other forms (Denison, 1958, fig. 112B, E, I), but not in *Phlyctaenius* (e.g. Heintz, 1933, p. 138). The AVL is represented by several specimens, of which CPC 19566 is a fairly complete example (Pl. 7, fig. 1), again showing general similarity in shape and proportions to the AVL of *Phlyctaenius acadicus* (e.g. Heintz, 1933, fig. 6). It has no special features. There are single specimens of the AMV and PMV plates both again preserved in visceral view. The AMV (Pl. 6, fig. 8) is more elongate than in *Phlyctaenius acadicus* (cf. Denison, 1978, fig. 42), with a median embayment in the anterior margin, and a broad low median ridge on the anterior half of the visceral surface. The PMV is incompletely preserved, but probably was of similar proportions to that of *Phlyctaenius acadicus* (see Denison, 1958, fig. 113). Unlike this and other forms, however, the anterolateral margins are distinctly concave (Pl. 6, fig. 7). Finally, of the 9 PVL plates available for study, one (CPC 19579) is fairly complete, (Pl. 7, fig. 3), and shows a similar short broad form to the PVL of *Phlyctaenius* (e.g. Denison, 1958, fig. 114A). Of interest in this specimen are impressions of elongate plates abutting against the posterior and lateral margins of the subanal lamina, which may indicate the presence of enlarged dermal elements around the ventral part of the pelvic girdle, as described in *Sigaspis* by Goujet (1973, fig. 2B). In this and another specimen (CPC 19573), an associated ridge and groove run down the posterior border of the lateral lamina and onto the subanal division of the ventral lamina. Similar grooves have been noted in other dolichothoracids (Miles, 1964, figs. 9, 11). Two other specimens (CPC 19572, 19578) show part of the external surface of the plate, with the overlap area for the AVL normally developed.

The *dermal ornament* of *Denisonosteus weejasperensis* seems generally to comprise fine tubercles, sometimes with stellate bases, irregularly distributed without any obvious alignment in rows (e.g. Pl. 6, figs. 1, 2, 5; Pl. 7, fig. 1). However, in several indeterminable specimens (e.g. CPC 19580, 19581) the tubercles show a marked concentric arrangement, and may fuse more or less completely to form continuous ridges (Pl. 7, fig. 7). It is possible that these remains represent another species, since Pageau (1969b) has used such differences to erect new species and genera of phlyctaeniids in the Gaspé Sandstone fauna of Quebec (but see Denison, 1978, p. 60). However, a skull-roof specimen designated *'Phlyctaenaspis' acadica* (Whiteaves) in the National Museum of Victoria (NMP13267; see Chapman, 1916, pl. 21, fig. 6) shows no alignment of tubercles, in marked contrast to the specimen figured by Woodward (1892, pl. 1, fig. 7), and it is possible therefore that this character varied within the species. Since most of the remains of *Denisonosteus weejasperensis* just described are exposed only in visceral view, so that variations of ornament in adequately determined plates cannot be assessed, it seems prudent for the present to regard those indeterminate specimens showing concentric ornament as examples of intraspecific variation.

EUARTHRODIRA incertae sedis

Fig. 23A, B, D; Pl. 7, figs. 5, 6

Material: a possible left PrO (CPC 19582) and left SM (CPC 19583), an undetermined plate carrying a sensory groove (CPC 19584), and an incomplete left PDL (CPC 19557).

Remarks: The specimens included here are sufficiently well preserved to show different morphology from the corresponding plates described above, and it is clear that there were several euarthrodires in the fauna. However, further material is required before the one or more additional species can be properly determined.

Description: CPC 19582 is preserved partly as an impression of its visceral surface, with a central portion of the bone remaining. It is crossed by a sensory groove, and carries two cristae on its visceral surface. One crista lies inside an embayed margin of the plate (om, Fig. 23D), and resembles a supraorbital vault, so the plate is tentatively determined as a PrO. It is restored as a left plate, with the supraorbital canal (soc) passing anteromesially from the plate's posteriorly placed ossification centre. Across its broadest dimension (a-a) the plate is strongly arched, so the inflected postorbital part (preserved only as an impression) would have lain over the dorsolateral curvature of the skull-roof. (An alternative interpretation, with this inflected region representing the preorbital part of a right petalichthyid PrO, has been rejected because the sensory canal is developed as a continuous open groove). A second ventral crista (la.v) lies beneath the central section of the sensory canal, and bifurcates distally around a shallow groove preserved as an impression near the anteromesial margin (tg). The preserved part of the external surface is ornamented with radiating rows of tubercles.

The affinities of this plate are very uncertain, but only in *Holonema* does the supraorbital canal have a somewhat similar course across the PrO (e.g. Miles, 1971, figs. 4, 10), whilst the ventral crista and groove just described may be compared with the less strongly developed 'ventral lamina' and 'transverse groove' illustrated by Miles for *H. westolli* (1971, figs. 10B, 53). There is less similarity in overall shape, but this varies considerably in *H. westolli*, and in one figured example (Miles, 1971, fig. 52) the PrO forms a deep angular notch in the P plate, as is suggested by the prominent anterolateral angle in CPC 19582 (ala, Fig. 23D).

The second plate carrying a single sensory groove (Pl. 7, fig. 5) is conceivably also from the head, but may be incomplete, and at present cannot be determined. It is ornamented with stellate tubercles, which are somewhat coarser than the typical ornament of *Denisonosteus*. The third specimen is a SM plate exposed in visceral view (Fig. 23A, B), which differs considerably from the corresponding plate of *Denisonosteus* (Pl. 5, fig. 8), but shows some resemblance to an isolated SM from the Water Canyon Formation of Utah described and figured by Denison (1958, fig. 103E, F). The position of the epihyal groove (gr.eh) indicates that it is from the left side (cf. Goujet, 1972,

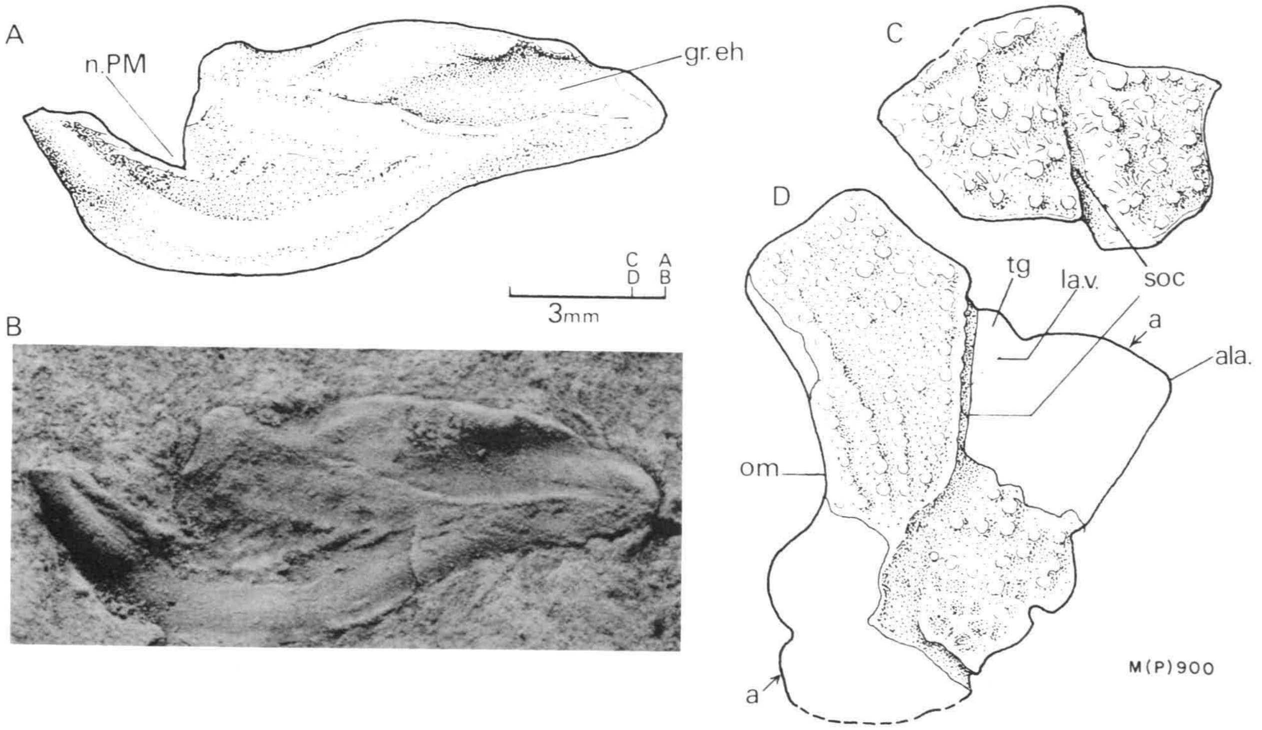

Fig. 23. A, B. Euarthrodira ***incertae sedis*****. Left SM plate in visceral view (CPC 19583); C,** ***Denisonosteus weejasperensis*** **gen. et sp. nov. Possible left PN plate in dorsal view (CPC 19543; D, Euarthrodira** ***incertae sedis*****. Possible left PrO, restored after CPC 19582. Missing portions preserved as impressions. For explanation of lettering see list of abbreviations.**

pl. 1. fig. 2). Noteworthy is the deep notch in the dorsal margin (n.PM), which is much more pronounced than in previously figured euarthrodiran SM plates, and presumably conformed with the configuration of the lateral margin of the skull-roof. It may be significant that the position and shape of the notch approximate to the area of the SM shown overriding the PM in reconstructions of *Arctolepis* and *Dicksonosteus* (Goujet, 1972, fig. 2; 1975, figs. 4, 6; but cf. 1975, pl. 1), and this plate may therefore have belonged to a form with a more flexible cheek, in which the SM could be contracted inside the postmarginal corner of the skull-roof. Finally, the fragmentary PDL included here (Pl. 7, fig. 6) differs clearly from the corresponding plate of *Denisonosteus* in that the lateral line groove passes anteriorly off the plate at the junction of the overlap areas for the ADL and AL plates. This condition is otherwise seen only in *Groenlandaspis* (see Denison. 1958, fig. 109C; Ritchie, 1975). However, the specimen may be distinguished from the PDL of *Groenlandaspis* by the course of the sensory groove across the plate, the configuration of the anteroventral corner, and the shape of the overlap areas. In addition, it appears to be much shorter ventrally than the PDL of other primitive phlyctaenioids, but in contrast to the condition in advanced brachythoracids (and *Holonema*; see Miles, 1971, p. 160), the contact with the AL plate was retained.

There is no way at present of determining whether the specimens just described are conspecific, and until their affinities are clarified with additional better material they are left in open nomenclature.

PLACODERMI incertae sedis

Pl. 7, figs. 4, 9

Material: 4 ADL plates (CPC 19548-19550, 19585), all incompletely preserved.

Remarks: Each of these specimens displays a similarly developed prominent articular condyle, and there is little doubt that they belong to a single species, which was probably a phlyctaenioid euarthrodire. However the morphology of the condyle as preserved and exposed does not preclude the possibility that instead they represent another antiarch species, and they are therefore described here as Placodermi *incertae sedis*.

Description: These plates were initially determined as phlyctaenioid ADL plates which could be differentiated from the corresponding plates of *Denisonosteus* by their more slender and pointed articular condyles. Only CPC 19548 is fairly complete (Pl. 7, fig. 9), and shows in addition the lower and longer dorsal lamina, with a more elongate, slightly convex dorsal margin, and the more fully developed ventral lamina (cf. Pl. 6, fig. 4). They are also smaller (length of CPC 19548, including condyle, is about 23 mm), and the external surface, as partly preserved in CPC 19585 and exposed by removal of bone from CPC 19548 and 19550, is ornamented with radiating rows of tubercles, and lacks any clear indication of a sensory groove in the expected position.

This ADL shows some resemblance to the holotype of *Aggeraspis heintzi* (see Denison, 1958, fig. 108C) in overall shape, in the configuration of the posterior margin, and in the high position of the articular condyle, but there is less similarity to other ADL plates subsequently referred to the species (Gross, 1962, fig. 9). Another very similar plate was earlier figured by Gross (1940, pl. 3, fig. 2) and provisionally referred to *Asterolepis estonica*, and it is therefore relevant that broken sections through the end of the condyle in CPC 19548 and 19585 seem to indicate that the anterior articular surface was concave. In view of the poor preservation, however, and bearing in mind the likelihood that such articular surfaces were in-

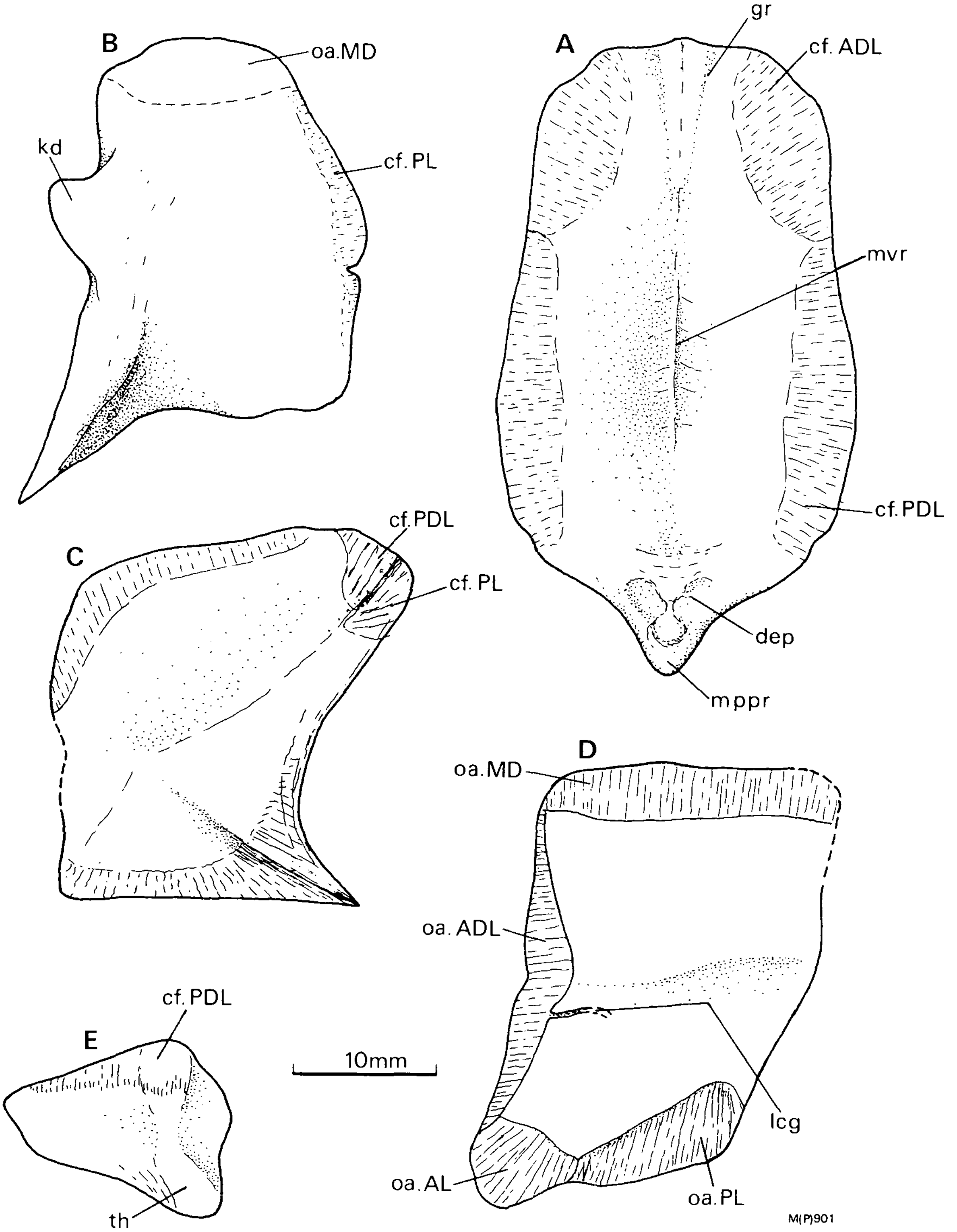

Fig. 24. *Denisonosteus weejasperensis* **gen. et sp. nov. A, MD plate in visceral view after CPC 19537 (holotype); B, right ADL in visceral view, restored after CPC 19545, 19547; C, right AL in visceral view, restored after CPC 19552-19556; D, left PDL in lateral view (CPC 19558); E, right PL in visceral view (CPC 19559). For explanation of lettering see list of abbreviations.**

vested with cartilage during life (see Miles & Young, 1977, p. 185), we do not at present regard this as unequivocal evidence that the neck-joint was of antiarchan type. The specimen originally figured by Gross showed a distinct posterior contact face for the posterior dorsolateral plates of the trunk-shield, but this is weakly developed or absent in the material described here. In addition Gross (1940, p. 20) noted that his plate had an outline reminiscent of the ADL in the *Pterichthyodes,* but the most recent description of *Pterichthyodes milleri* (see Hemmings. 1978, fig. 11) shows its ADL to be essentially similar to that of *Sherbonaspis* as described above (Pl. 4, figs. 11, 12). It is clear therefore that this additional type of placoderm ADL represents another species over and above the two new antiarchs and the new euarthrodire already described, but until other plates of the trunk-shield become available its affinities within the subclass must remain uncertain. Finally there is no good evidence of conspecificity with the various plates described above as Euarthrodira *incertae sedis,* although CPC 19582 does show some similarity in ornament.

Class	TELEOSTOMI
Subclass	OSTEICHTHYES
Superorder	RHIPIDISTIA
Order	OSTEOLEPIDIDA
Family	OSTEOLEPIDIDAE Cope, 1889
Genus	**Gyroptychius** McCoy, 1848

Diagnosis: see Jarvik (1948, p. 236).

Remarks: The Middle Devonian osteolepid material from Scotland studied by Jarvik is preserved mainly as fairly complete remains of whole fish, and in the fragmentary and disarticulated material dealt with here information on many of the characters used by Jarvik is not available. Jarvik (1948, p. 5; 1950a, p. 13) has noted the difficulty in determining isolated osteolepid scales and cranial remains, and in addition Thomson (1964a) has commented on the limited number of specimens on which Jarvik's diagnosis of the genus *Gyroptychius* was based. Taking these points into consideration, and until the generic status of the new osteolepid described below is clarified with better material, we propose to erect for it a new species which is tentatively referred to the genus *Gyroptychius* on the basis of the following characters (cf. Jarvik, 1948, pp. 141, 198, 236): the fenestra exonarina is ventrally placed and was probably not visible from above, whereas in *Osteolepis* it was dorsally placed, and in *Thursius* was probably partly visible from above; the orbital notch is relatively small and deep, whereas in both *Osteolepis* and *Thursius* it is relatively long and shallow; the estimated length of the postorbital notch relative to the length of the parietal shield is much greater than in *Osteolepis* or *Thursius* (although this condition is approached in *Th. moythomasi*); the pineal foramen lies behind the postorbital corner (again approached in *Th. moythomasi*); and individuals of the new species may have attained a total length of some 470 mm, and were therefore of moderate size, whereas species of *Osteolepis* and *Thursius* were generally less than 300 mm in total length. Of the other genera assigned to this family, *Latvius* Jarvik is distinguished by its numerous sensory canal pores, the more elongate skull-roof with nasal openings dorsally placed, and its smaller size (see Jarvik, 1948; Gross, 1956; Jessen, 1966, 1973; Greiner, 1977); and the post-Devonian forms *Megalichthys* Agassiz and *Ectosteorhachis* Cope differ in numerous characters such as their larger size, the unfused dermal bones of the snout, the absence of a pineal foramen and of a median extrascapular, and the shape and proportions of the skull-roof (see Thomson, 1964b).

Gyroptychius? australis sp. nov.

Figs. 25-28; Pl. 8; Pl. 9, figs. 1-7, 10, 11

Holotype: CPC 19586, a fairly complete but slightly compressed and distorted fronto-ethmoidal shield from the skull-roof.

Other material: 3 fronto-ethmoidal shields (CPC 19587-19589); 1 parietal shield (CPC 19590); 1 possible left lateral extrascapular (CPC 19591); a left preopercular and squamosal (CPC 19592); 3 operculars (CPC 19593-19595) and 1 subopercular (CPC 19596); 3 incomplete canal-bearing bones, probably from the head (CPC 19597-19599); 9 mandibles (CPC 19592, 19600-19607); 1 isolated tooth (CPC 19608); 4 branchiostegals (CPC 19609-19612); 7 principal gulars (CPC 19613-19619); 2 cleithra (CPC 19620-19621); 4 clavicles (CPC 19622-19625); various isolated scales (CPC 19626-19645); and a possible epineural or epihaemal spine (CPC 19646).

Diagnosis: An osteolepid in which the fronto-ethmoidal shield is short and broad, with breadth between the orbits equal to its length, and about 1.13 times as long as the parietal shield; lachrymo-maxillary notch deep and angular and of similar length to the orbital notch, which lies in the anterior half of the fronto-ethmoidal shield; preorbital corner almost right angular; frontal pitline long or short; lower jaw short and deep, about 4.5 times as long as high with pitlines variably developed; principal gular narrow anteriorly; cleithrum short and broad; clavicle with long ascending process, and interclavicle probably large.

Remarks: In view of the comments made above regarding the assignment of this species to *Gyroptychius*, it is clear that some of the listed features may prove to be generic rather than specific characters when this form is better known. *G.? australis* sp. nov. is readily distinguished from other species of the genus on the proportions and shape of the fronto-ethmoidal shield, and in view of the disarticulated nature of the material there is little point in attempting a comprehensive specific diagnosis at this stage.

Description: All the crossopterygian material from this locality is assumed for the present to belong to one species. The few available skull-roof remains are of similar size, and using the relative proportions obtained by Jarvik for *Gyroptychius agassizi* (1948, table 9), a typical total length of about 300 mm is indicated for the species. However, some individuals evidently attained a greater size, and a large gular plate described below (CPC 19613), by comparison with the holotype of *G. agassizi* (Jarvik, 1948, p. 243), suggests a fish some 470 mm in length.

Remains of the *skull-roof* include four examples of the fronto-ethmoidal shield, of which only the holotype is fairly complete, although somewhat crushed and distorted (Pl. 8, figs. 1, 2). The parietal shield is represented by a single fairly complete specimen (Pl. 8, fig. 3). Using the system developed by Jarvik (1948, fig. 12, table 1), the following measurements have been made, and ratios calculated. It is stressed however that these are derived from a small number of incomplete specimens which have been flattened or otherwise distorted, and they should be regarded as only approximate values permitting general comparisons:

Measurements (in millimetres)

	a	b	c	d	e	f	g	h	l.io	dp.io	r	s	t	v	w
CPC 19586	—	17.5	5.4	19.5	17.5	9.5	—	—	4.4	2.7	6.7	4.4	6.4	8.0	9.5
CPC 19588	16	—	—	—	—	10	14.7	19	—	—	—	—	—	—	—
CPC 19590	—	18.5	—	18.4	—	11.6	—	—	5.3	—	6.5	5.5	6.5	8.5	10.0

Proportions

	$\frac{d}{b}$	$\frac{e}{b}$	$\frac{f}{a}$	$\frac{g}{a}$	$\frac{c}{b}$	$\frac{l.io}{b}$	$\frac{l.io}{dp.io}$	$\frac{r}{s+t}$	$\frac{t}{r+s}$	$\frac{v}{w}$
CPC 19586	1.11	1.00			.31	.25	2.3	.62	.58	.84
CPC 19588	—	—	.625	.92	—	—	—	—	—	
CPC 19590	1.03	—	—	—	—	.29	—	.65	.42	.85

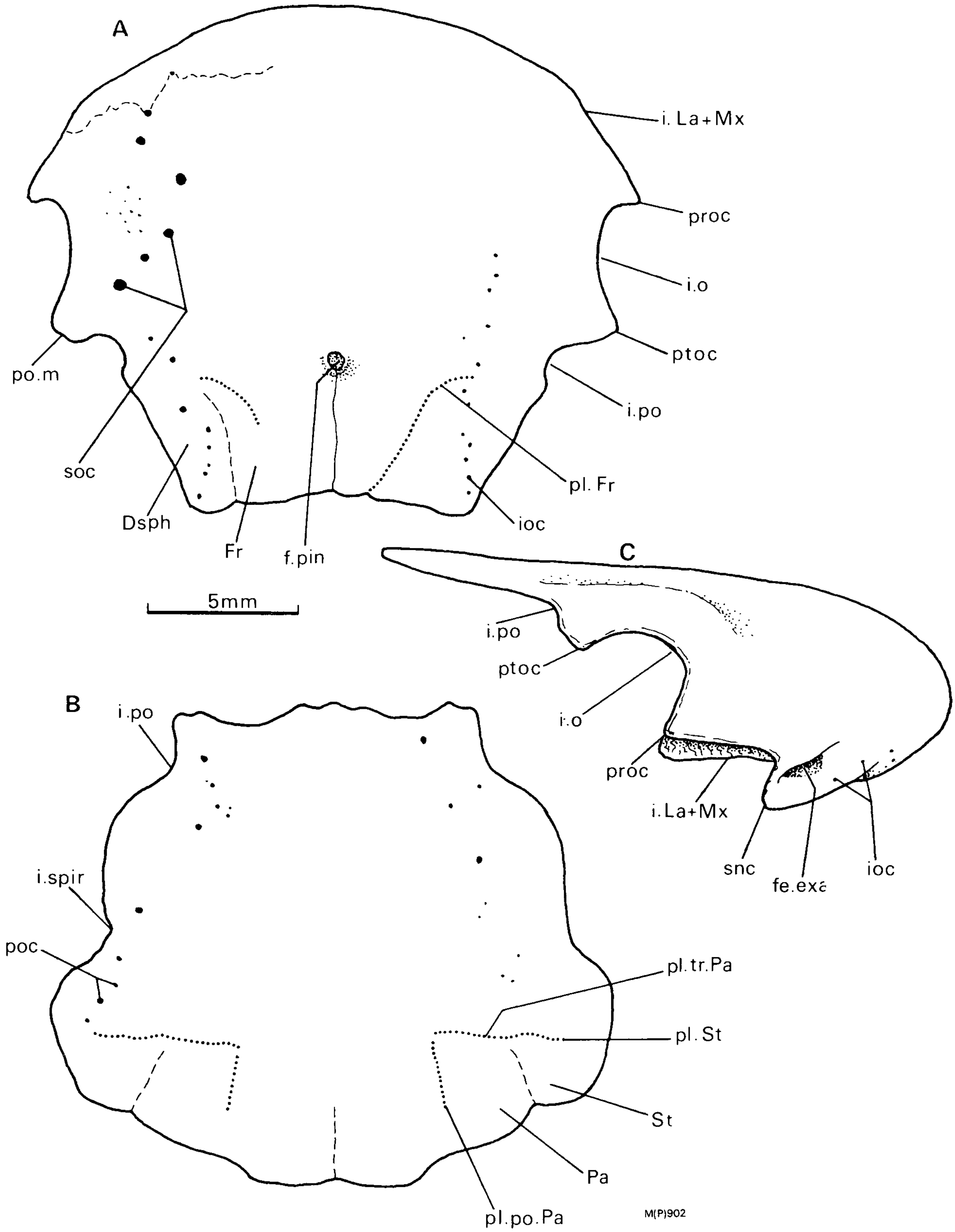

Fig. 25. *Gyroptychius? australis* **sp. nov. A, C, fronto-ethmoidal shield in dorsal and right lateral views. After CPC 19586 (holotype); B, parietal shield in dorsal view. After CPC 19590. For explanation of lettering see list of abbreviations.**

As reconstructed (Fig. 25A), the fronto-ethmoidal shield is unusually short and broad, its relative proportions (d/b) being approached only in *Thursius pholidotus*, *Gyroptychius milleri* and *'Gyroptychius sp. inc.* 2' as studied by Jarvik (1948, table 1), whilst its great breadth between the orbits (e/b) is not matched by any previously described species (see also Jarvik, 1950a, p. 99; Jessen, 1968, p. 67; Janvier, 1978, fig. 1). The pineal foramen in the holotype is placed about one third of the length of the shield from the posterior margin (c/b); that is, within the range of variation for *Osteolepis macrolepidotus*, *O. panderi*, and *Thursius pholidotus,* but relatively farther forward than in *Th. macrolepidotus*, *Th. moythomasi*, and *Gyroptychius* spp. In *Th. moythomasi* and *Gyroptychius* spp. however, although the prepineal region is proportionately longer (Jarvik, 1948, table 1, column 18), the pineal foramen has a postorbital position, as in the material described here, and in contrast to the remaining *Thursius* and *Osteolepis* species (Jarvik, 1948, fig. 13). The dorsal surface in the holotype is fairly flat, probably with a slight median depression behind the pineal foramen, which is open, and surrounded by a small elevation (cf. *G.? taylori* Jessen, 1968). Anterior and anterolateral extremities of the shield are strongly folded downwards and inwards (Pl. 8, fig. 2), probably obscuring the fenestra exonarina in dorsal view. (The left nasal opening is visible in CPC 19588, but this specimen is much compressed). The lachrymo-maxillary notch is well displayed on both sides of the holotype (i.La+Mx, Fig. 25C); it is deeper and more angular than in the Scottish Middle Devonian osteolepids (Jarvik, 1948, fig. 13), although its form is approached in *Gyroptychius milleri*, *G. groenlandicus*, and *G.? taylori* (Jarvik, 1948, fig. 79; 1950a, fig. 13B; Jessen, 1968, fig. 8B). The preorbital corner (proc) is almost right angular, and the configuration of the orbital notch (i.o) resembles that in other *Gyroptychius* species (Jarvik, 1948, fig. 13P) in being short and deep. The lachrymo-maxillary and orbital notches are of similar length. The middle part of the orbital notch is situated within the anterior half of the length of the fronto-ethmoidal shield ($\frac{v}{w} < 1$), and in this respect *Gyroptychius? australis* differs from all the Scottish Middle Devonian species (see ratios in Jarvik, 1948, p. 40). The postorbital corner (ptoc) is prominent, and the postorbital notch (i.po) deeply embayed. This section of the margin may be variably developed; on the right side of the holotype the corner is somewhat acute (Fig. 25C), but on the left side it is obtuse with a short postorbital margin (po.m) lying in front of the postorbital notch. The latter is divided into anterior and posterior sections, separated by a short process as in other forms (Jarvik, 1948, p. 40), but the anterior section is unusually short and deep, suggesting an anterodorsal process on the postorbital plate. (The distribution of sensory pores confirms that the dermosphenotic has not been lost.) This condition is approached in *Latvius niger* (e.g. Jessen, 1973, pl. 20, fig. 1). A similar configuration of the postorbital notch is shown along the right margin of CPC 19588 (Pl. 8. fig. 7).

The parietal shield as preserved in CPC 19590 is normally developed, with embayments in its lateral margin for the posterior part of the postorbital notch and the spiracular notch (i.po, i.spir, Fig. 25B). Its breadth/length index is 92, making it broader than in *Osteolepis macrolepidotus*, fairly similar to species of *Thursius* and *Gyroptychius agassizi*, and somewhat narrower than in *Osteolepis panderi* and *Gyrotchius milleri* (Jarvik, 1948, fig. 12, table 1, column 16). This specimen and the holotype come from different individuals, and there are minor differences in the configuration of their margins at the parietal/frontal suture, but they are approximately the same width at this level, and taken together give some indication of overall proportions. Thus the fronto-ethmoidal shield may be estimated at about 1.13 times as long as the parietal shield; this is well below the range of variation in certain species (e.g. *Osteolepis panderi, Thursius moythomasi,* and *Gyrotychius* spp.; see Jarvik, 1948, table 1, column 9).

As is normal in osteolepids the bone sutures in the available skull material tend to be obscured by cosmine. On the left side of the holotype a possible suture runs mesially from the lachrymo-maxillary notch, but it lies dorsal to the fenestra exonarina, and therefore does not represent the junction of anterior tectals and the premaxillary (naso-rostro-premaxillary of Jarvik, 1948, fig. 14). Behind the pineal foramen the suture between frontal bones is clearly shown (Pl. 8, fig. 1), and on the right side of CPC 19588 (Pl. 8, fig. 7) the frontal/dermosphenotic suture is developed from a notch in the posterior margin of the shield (left side of Fig. 25A). In CPC 19590 sutures between the two parietals, and between parietals and supratemporals, are indicated near the posterior margin, which is notched at the bone junctions (Fig. 25B). Similar notches are developed in the anterior margin but no bone sutures are apparent.

Sensory pores for the lateral line system are displayed in the holotype and CPC 19590. A single irregular row for the postotic (poc) and infraorbital (ioc) sections of the lateral line canal crosses the supratemporal, intertemporal, and dermosphenotic, and larger pores form a more conspicuous row on the left side of the holotype for the supraorbital canal (soc). On the ventral surface of the snout between the nasal openings are scattered pores of the ethmoid commissure (ioc, Fig. 25C). In general the sensory pores are less conspicuous (smaller and fewer) than in the Scottish Middle Devonian osteolepids, and much less prominent than those of *Latvius* (e.g. Gross, 1956, pls. 1, 2). Jarvik (1948, p. 123) has suggested that relatively few pores and unbranching sensory canal tubes are primitive for osteolepids. The frontal pitline (pl.Fr) is well developed in the holotype and on the right side of CPC 19588. Jarvik (1948, pp. 131, 132) has described differences in its development in Scottish species; *Gyroptychius? australis* sp. nov. differs from both Scottish species of *Osteolepis,* in which the pitlines of each side normally meet at the median suture between frontals and extend anteriorly past the level of the postorbital corner (e.g. Jarvik, 1948, fig. 38). On the right side of the holotype and in CPC 19588 (Pl. 8, figs. 1, 7) the pitline reaches the posterior margin of the frontals, as in species of *Thursius,* but on the left side it is much shorter, and as in *Thursius moythomasi* and species of *Gyroptychius* (Jarvik, 1948, p. 132; 1950a), it does not reach the posterior margin. Supratemporal, transverse, and posterior parietal pitlines are clearly seen on both sides of CPC 19590 (pl.St, pl.tr.Pa, pl.po.Pa, Fig. 25B), and show normal osteolepid development.

Several fragmentary plates are tentatively identified as disarticulated skull remains. CPC 19591 (Pl. 8, fig. 6) may be a left lateral extrascapular with part of the median extrascapular attached. Its angular anterior margin resembles that displayed in a specimen of *Thursius macrolepidotus* (Jarvik, 1948, pl. 17, fig. 3). A short pitline near the anterior margin is assumed to correspond to that noticed by Jarvik in one specimen of *Osteolepis panderi*, and in the holotype of *Gyroptychius agassizi* (1948, p. 133). In addition CPC 19597-19599 are small plates carrying sensory pores or pitlines, which conceivably come from the skull-roof or possibly the cheek but are too fragmentary for positive identification.

Apart from the fragmentary plates just mentioned, only one example of the *cheek unit* has been identified.

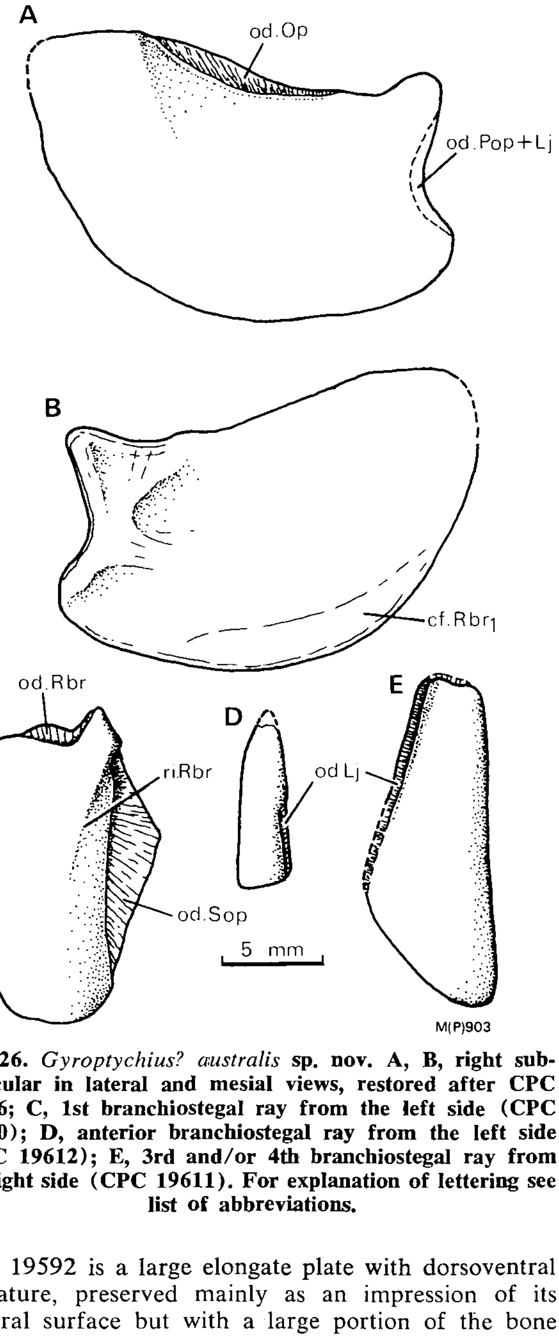

Fig. 26. ***Gyroptychius? australis*** **sp. nov. A, B, right subopercular in lateral and mesial views, restored after CPC 19596; C, 1st branchiostegal ray from the left side (CPC 19610); D, anterior branchiostegal ray from the left side (CPC 19612); E, 3rd and/or 4th branchiostegal ray from the right side (CPC 19611). For explanation of lettering see list of abbreviations.**

CPC 19592 is a large elongate plate with dorsoventral curvature, preserved mainly as an impression of its visceral surface but with a large portion of the bone remaining in its posterior half. A short section of suture is preserved, crossed by a row of sensory pores (juc, p.mcp, Pl. 8, fig. 5), and this specimen is therefore interpreted as part of a left preopercular and squamosal (cf. Jarvik, 1948, fig. 21). A slight overlap area along the ventral border suggests that the maxillary bone has been lost. The proportions of the cheek unit in other species have been utilised taxonomically (see Jarvik, 1948, pl. 86), but this specimen is too incomplete for dimensions to be determined.

Bones from the *operculum* are represented by several specimens, of which CPC 19593–19595 are large incomplete plates with the dorsal margin inflected mesially, a feature of the opercular in other osteolepids (Jarvik, 1948, p. 95). They are too incomplete for a reliable estimate of shape and proportions, so it cannot be established that the plate was short and high, as is characteristic of *Gyroptychius* (Jarvik, 1948, p. 95). The suborpercular is represented by a single fairly complete specimen (CPC 19596), showing the normal dorsal overlap area for the opercular plate (od.Op, Fig. 26A). The anterior margin is preserved only in visceral view, and the overlap area for the preopercular is not exposed. Inside the anterior margin are several low ridges (Fig. 26B), and part of the contact face for the first branchiostegal ray is faintly shown near the ventral border (cf.Rbr$_1$). The opercular and subopercular plates are known to vary considerably in shape and size in other osteolepids (Jarvik, 1948, p. 95).

The *lower jaw* is represented by nine examples, of which only one (CPC 19592) is fairly complete. Its length is 52.5 mm, this being about 4.5 times its height, and suggesting a shorter broader lower jaw than in Scottish species (cf. Jarvik, 1948, p. 94). CPC 19602 is a larger incomplete specimen (Fig. 27D) whose length is estimated at about 62 mm, and CPC 19600 is an anterior fragment from a lower jaw of about the same size. As previously described by Jarvik (1948), all bone sutures in these specimens are obscured by cosmine. A posterior depression for the quadratojugal is well displayed in CPC 19592, 19602, and 19606 (od.Qj, Fig. 27C; cf. Pl. 9, fig. 1), but the pars articularis of the meckelian bone is not shown (cf. Jarvik, 1948, fig. 23). There is some variation in the shape of the anterior end of the jaw (Fig. 27A, B, E), and also in the arrangement of pitlines. CPC 19601 shows both horizontal and vertical pitlines, as are normally developed in other species (plh.Id, plv.Id$_2$, Fig. 27A), and also a possible additional line near the anterior margin (plv.Id). Assuming similar overall proportions to CPC 19592, the vertical pitline for the second infradentary has a fairly posterior position ($k/m = 1.82$), comparable with that of *Osteolepis macrolepidotus* (Jarvik, 1948, table 1, column 34). In CPC 19607 the horizontal pitline extends right to the anterior margin, and the vertical pitline is probably absent (Fig. 27B), whilst CPC 19592 is apparently devoid of pitlines altogether (Pl. 9, fig. 1). In CPC 19606 the horizontal pitline is broken into a short posterior and a longer anterior section. This range of variation is not normally seen in other species (see Jarvik, 1948, p. 134). All specimens show an irregular scattering of pores for the ventrally placed mandibular sensory canal (p.mcp), which posteriorly moves round onto the ventral margin of the jaw (Fig. 27C, D, E). Groups of pores for cutaneous sense organs have not been observed, and in no specimen is the dentition exposed, although the collection includes one example of an isolated tooth which may be tentatively referred to the species. (On their own, however, such remains are normally indeterminable—see Jarvik, 1948, p. 283). CPC 19608 (Pl. 8, fig. 4) is a conical slightly curved tooth about 6.5 mm long, round in section, and striated near its base. It is shorter and stouter, with coarser striations, than the similar tooth from Greenland described by Jarvik (1950a, pl. 23, fig. 7).

The *branchiostegal* and *gular* series of bones are moderately well known. CPC 19610 (Pl. 9, fig. 4) is a first branchiostegal ray from the left side, which shows the normal overlap areas for the subopercular and second branchiostegal (od.Sop, od.Rbr, Fig. 26C), and has a moderately developed rostrocaudal ridge (ri.Rbr). This element is known to be variable in other species, but CPC 19610 is fairly high and broad, with a distinct anterodorsal corner in contact with the lower jaw, as in *Gyroptychius agassizi* (Jarvik, 1948, fig. 75H, J). CPC 19609 (Pl. 8, fig. 8) is a quadrilateral plate carrying a curved pitline, which is tentatively identified

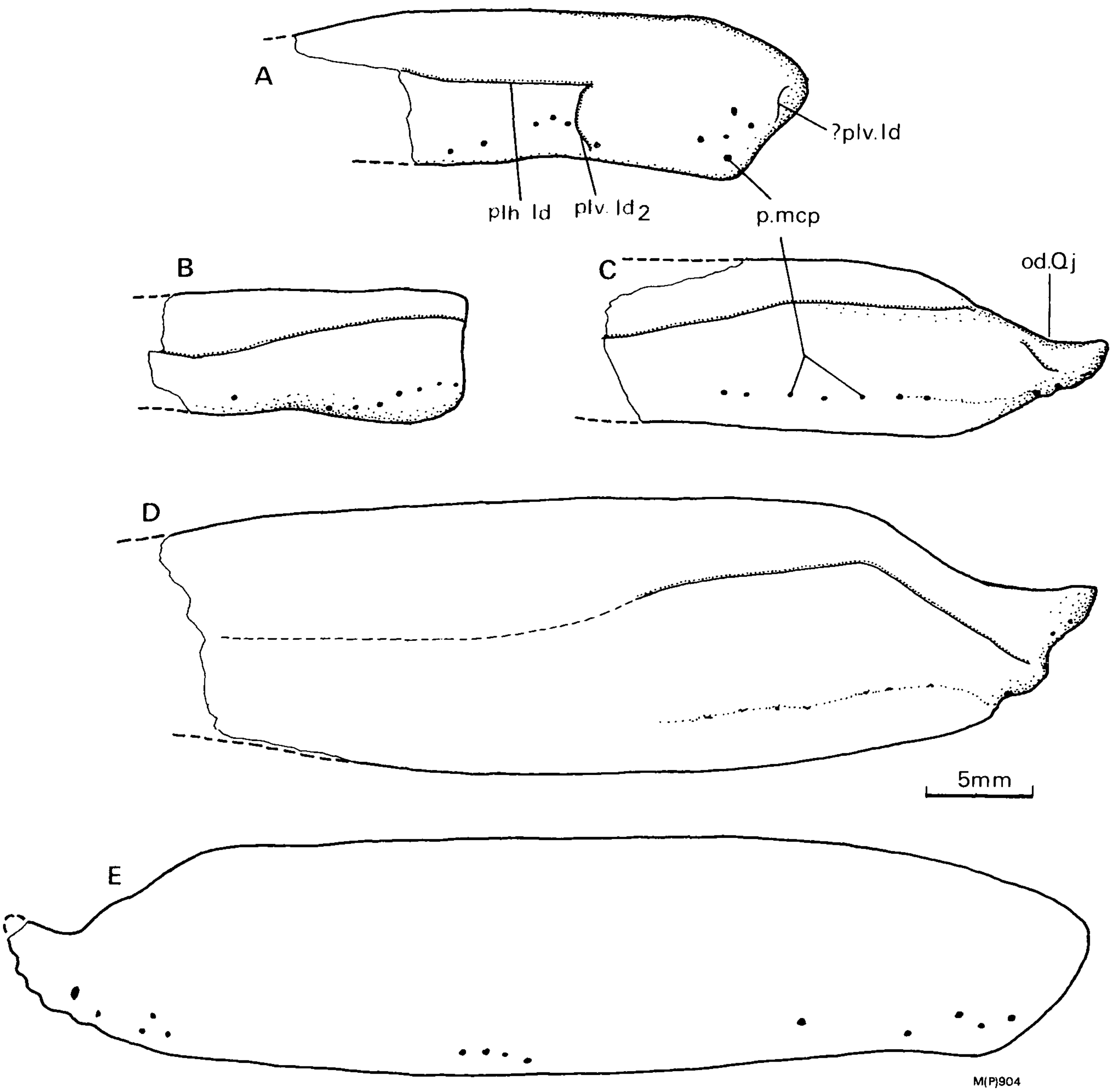

Fig. 27. *Gyroptychius? australis* **sp. nov. Various lower jaws. A, CPC 19601; B, CPC 19607; C, CPC 19606; D, CPC 19602; E, CPC 19592. For explanation of lettering see list of abbreviations.**

as a second branchiostegal from the left side. CPC 19611 is an elongate bone lacking a pitline but carrying a narrow overlap area along its shorter longitudinal margin (Fig. 26E), which may be identified as a third and/or fourth branchiostegal from the right side. It is just over 2.5 times as long as broad, and is therefore more elongate than figured examples for *Osteolepis, Thursius macrolepidotus,* and *Gyroptychius* (Jarvik, 1948, figs. 44, 56U, 60M, 71C, 80H), but similar to the combined third and fourth branchiostegal shown for *Thursius pholidotus* (Jarvik, 1948, fig. 69A). Finally CPC 19612 is tentatively identified as an anterior branchiostegal from the left side, since it also shows an overlap area along part of its presumed lateral margin (od.Lj, Fig. 26D).

Only one of the principal gulars is sufficiently complete for measurement (Pl. 9, fig. 11). It comes from a large individual, with gular length estimated at 48 mm, and the bone about 2.6 times as long as broad. This proportion is similar to that for some Scottish species, but the plate is less slender than in *Osteolepis macrolepidotus* and *Gyroptychius agassizi,* and broader than in *Gyroptychius milleri* (Jarvik, 1948, table 1). The mesial margin behind the notch for the median gular is slightly concave, and the anterior part of the plate is generally narrower than in the Scottish osteolepids, and in this respect shows some similarity to the gular of *Tristichopterus* figured by Jarvik (1950a, fig. 26). In contrast the gular of *Gyroptychius groenlandicus* is much more ovate (e.g. Jarvik, 1950a, pls. 19, 20; 1950b, fig. 1D). Along its lateral margin CPC 19613 has a distinct inner ridge, and a similar ridge is seen in CPC 19615, a smaller left gular incompletely preserved in visceral view. CPC 19614 is preserved in external view, and shows a slightly developed overlap area for the branchiostegal rays along

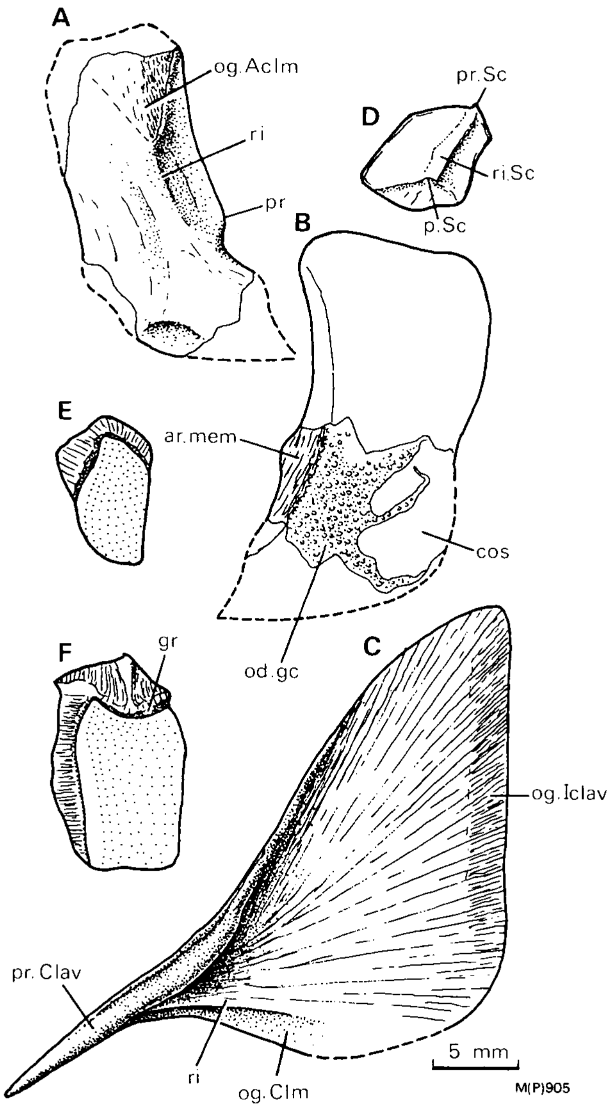

Fig. 28. *Gyroptychius? australis* **sp. nov. A, left cleithrum in visceral view, after CPC 19620; B, left cleithrum in lateral view, the dorsal part preserved as an impression (CPC 19621); C, left clavicle in visceral view, restored after CPC 19623; D, scale, inner surface (CPC 19627); E, F, scales, external surface (CPC 19632, 19645). For explanation of lettering see list of abbreviations.**

its lateral margin. The median gular has not been recognised in the material, but judging from the configuration of the principal gular it was much the same as the corresponding bone in other osteolepids.

Of the dermal bones of the *pectoral girdle* only the cleithrum and clavicle are represented. CPC 19620 is an incomplete left cleithrum preserved in visceral view (Fig. 28A). The bone is thick, and running up the visceral surface is a prominent ridge (ri), which appears to be broader and more heavily developed than the corresponding ridge figured for *Gyroptychius groenlandicus* (Jarvik, 1950a, pl. 21, fig. 2). A dorsal roughened area possibly overlapped the anocleithrum (og.Aclm). The anterior margin carries a blunt process (pr), but this does not correspond to the anterior process of the cleithrum of *Eusthenopteron* (Jarvik, 1944, fig. 3D) because of its more dorsal position relative to the overlap area for the clavicle. A corresponding process is seen on a second specimen (Fig. 28B), in which the middle part of a left cleithrum is preserved in lateral view, with the dorsal margins of the bone indicated by an impression. The external surface is ornamented with fine tubercles anteriorly, which are covered by cosmine layer (cos) near the posterior margin. The ornamented zone (od.gc) was presumably covered by the operculum and branchiostegal membrane (Jarvik, 1948, p. 99). As in *Osteolepis* (Jarvik, 1948, p. 98) there is a mesially inflected lamina along the anterior margin of the bone (ar.mem), which lacks ornament and is considerably broader than the corresponding structure in *Eusthenopteron.* In these respects therefore the two specimens described here show typical osteolepid development, although CPC 19621 would appear to have been proportionately broader than the cleithrum of *Osteolepis* or *Gyroptychius agassizi* (see Jarvik, 1948, fig. 25, pl. 27). However, a short, broad cleithrum also occurs in *Thursius pholidotus* (e.g. Jarvik, 1948, fig. 68R), although for the present this resemblance is not assumed to have taxonomic significance. The cleithrum of *Latvius* (e.g. Gross, 1956, fig. 4) is readily distinguished by its more slender form and various differences in shape (cf. Greiner, 1977, fig. 5c).

The clavicle (Fig. 28C) is represented by two nearly complete specimens from larger individuals exposed mainly in visceral view, and two fragmentary examples (CPC 19622, 19624). In CPC 19623 the ascending process is separated by a fracture from the ventral lamina (Pl. 9, fig. 5), and has probably been crushed and flattened. As restored (Fig. 28C) the process (pr.Clav) has a similar orientation to that of *Osteolepis* (Jarvik, 1948, fig. 25E; cf. *Eusthenopteron,* Jarvik, 1944, fig. 4E), but is slightly longer. The visceral surface of the ventral lamina exhibits strong radiating striations (Pl. 9, fig. 5) which are densely distributed in a zone along the mesial margin (og.Iclav). If this zone represents a contact face for the interclavicle, it must have been a more extensive bone than in *Osteolepis* (Jarvik, 1948, fig. 25F), resembling more closely the larger interclavicle of *Eusthenopteron* (Jarvik, 1944, fig. 3H). The contact face for the cleithrum (og.Clm) is indistinct, but was presumably delineated anteriorly by a ridge running down the inside of the ascending process and across the ventral lamina (ri, Fig. 28C).

Finally, remains of the *axial skeleton, squamation,* and *fins* may be briefly described. Except for the occurrence of small scale-like elements and larger units comparable respectively to the basal fine scales and scutes in other osteolepids (CPC 19644; cf. Jarvik, 1948, fig. 30, pl. 10), the structure of the fins is unknown. However, cosmine-covered scales of various shapes and sizes occur scattered throughout the material, and in some specimens are abundant and closely grouped (e.g. CPC 19626, 19629), suggesting only minor post-mortem disturbance or bioturbation (Pl. 9, fig. 10). Jarvik (1948, p. 106) has noted considerable variation in shape and size of scales in the Scottish osteolepids, and this is also evident in the material described here (Fig. 28D, E, F). A non-overlapped part about 5 mm across is a typical scale size, ranging up to a height of about 9 mm as a maximum (e.g. Fig. 28F). Comparing the measurements given by Jarvik (1948, tables 1, 2), scales of similar size may occur in *Osteolepis macrolepidotus, Thursius pholidotus* and *Gyroptychius agassizi,* whilst those of *Osteolepis panderi, Thursius macrolepidotus* and *Th. moythomasi* are somewhat smaller. Scale morphology is typically osteolepid (Fig. 28E, F), with the overlapped areas clearly differentiated from the non-overlapped part by distinct grooves (see Jarvik, 1948, p. 106; 1950a, p. 92). The non-overlapped part is normally covered by smooth cosmine, with the cosmine pores randomly distributed, and lacking the peripheral ridges or fluting seen in porolepid scales (see Ørvig, 1957, p. 400). In some cases however the cosmine has a finely pustulose surface texture (Pl. 9, figs. 2, 6), but scales lacking the cosmine layer have not been observed. A number of scales are exposed in visceral view (e.g. Pl. 9, fig. 7), and show an inner ridge, pit, and process (ri.Sc, p.Sc, pr.Sc, Fig. 28D) which are directly comparable with those of previous descriptions (e.g. Jarvik, 1948, fig. 28D; 1950a, pl. 22, figs. 7, 8). Finally a single specimen (CPC 19646) is tentatively identified as an epineural or epihaemal spine. It is a symmetrical tube of bone about 3 mm in diameter, with a thickened end showing a slight flexure which may represent the proximal articulation with the corresponding neural or haemal arch, as has been previously described in rhipidistians (e.g. Andrews & Westoll, 1970, p. 471).

Subclass ACANTHODII

Order CLIMATIIFORMES

Suborder CLIMATIOIDEI Miles, 1966

Family CLIMATIIDAE Berg, 1940

Remarks: Although the determination of isolated acanthodian spines is of limited reliability, the specimens described here can be readily distinguished from the fin spines of *Diplacanthus* and *Rhadinacanthus* (suborder Diplacanthoidei of Miles, 1973b, p. 116) and *Euthacanthus* (suborder Climatioidei, family Euthacanthidae of Miles, 1973b) by their ornament of tuberculate ribs, and from the gyracanthids (suborder Climatioidei, family Gyracanthidae of Miles, 1973b) by the absence of a chevron pattern in the ornament. On the other hand, in typical representatives of the family Climatiidae, in which tuberculate or nodose longitudinal ribs on the fin spines are characteristic, the spines had a superficial position in the skin, whereas in one of the new spines included here a base of insertion is clearly preserved. Superficially placed fin spines are, however, widely regarded as being the primitive condition in acanthodians (e.g. Obruchev, 1964; Miles, 1966), and *Nodocosta pauli* Gross (1940) indicates that inserted spines had evolved within the Climatiidae at least by Middle Devonian time (see Miles, 1966, p. 171; Pageau, 1969a). The two spines described below may therefore be referred to the Family Climatiidae with some confidence, primarily on the detailed similarity in the form of the nodes developed along the ribs of the spine (see below).

climatiid gen. et sp. indet.

Pl. 9, fig. 8

Material: Two incomplete fin-spines (CPC 19647, 19648), and possibly a sectioned scale (CPC 19652).

Remarks: Acanthodians were apparently rare in the fauna, being represented in the whole collection by five incomplete spines of two different types, and a few broken scales extracted from limestone nodules by acid digestion. One of these has been sectioned, but shows no histological detail other than concentric zones of growth, so it is therefore not possible to determine to which spine type the scale belongs. Furthermore the two climatiid spines described here may represent a new form, but until better material is found the erection of new specific or generic names does not seem justified. By comparison with other species referred by Miles (1973b) to the Climatiidae, the following differences in spine morphology may be noted. In *Brachyacanthus* and *Climatius* the spines are much shorter and broader (e.g. Watson, 1937, figs. 2, 6), whilst the considerably longer anterior dorsal spine in *Parexus* (see Watson, 1937, fig. 7) has less curvature. The pectoral spine of *Erriwacanthus* (e.g. Ørvig, 1967; Miles, 1973b) is ornamented with higher ridges and deeper grooves, and is more curved, and the spines of *Ptomacanthus* have fewer ribs (Miles, 1973b). In *Vernicomacanthus* the tubercles on the spines are more pronounced and there is apparently a greater number of ribs, and in *Sabrinacanthus* the spines are broader with greater curvature and have fewer, more widely spaced ribs. In addition, as already noted, in all these forms the fin spines were superficially placed in the skin, and lacked a base of insertion (but cf. Pageau, 1969a). One isolated spine with a base of insertion described by Gross (1940) as *Nodocosta pauli* was however previously referred by Miles (1966, p. 166) to the Climatiidae. This spine differs from the new specimens in being less curved, and having fewer ribs ornamented with more prominent nodes (Gross, 1940, pl. 1, figs. 8, 9).

Description: CPC 19647 (Pl. 9, fig. 8) is a curved, laterally compressed spine which when complete was probably about 35 mm long. Maximum preserved width is 4 mm. It is ornamented with longitudinal nodose ribs which number 12–13 on one side at the most proximal preserved portion, reducing to about 5 near the tip of the spine. Distally the anterior rib is separated from the others by a slightly wider groove, and the posterior border of the spine carries at least 3 fairly prominent curved denticles pointing proximally. The ornament varies in different regions of the spine. Posteriorly the ribs are less pronounced, and carry fairly high rounded tubercles, regularly spaced along their length. On the coarser anterior ribs the nodes have paired ridges runing down each side of the longitudinal rib and directed slightly distally, to give an ornament of the 'cone-like climatioid type with each node appearing to fit into the adjacent proximal node' (Miles, 1973b, p. 122). At the proximal end of the preserved portion the spine cavity appears to have been open posteriorly, but this may be due to crushing and requires confirmation with better material. In any event the cavity appears in the broken section to be bilobed or possibly double, as is reported for *Nodocosta pauli* (Gross, 1940; Obruchev, 1964). In the second very fragmentary specimen part of the base of insertion is preserved. Again it was probably of similar extent to that of *Nodocosta pauli* (see Gross, 1940, pl. 1, figs. 8, 9), and as in that form it is ornamented with fine longitudinal striations. A base of insertion of similar proportions has also been figured for *Climatius latispinosus* (Whiteaves), which has been ascribed a Middle Devonian age (Pageau, 1969a, fig. 16E, p. 457). The taxonomic significance of these resemblances cannot be assessed until further material becomes available for study.

Order ISCHNACANTHIFORMES Berg, 1940

?ischnacanthiform gen. et sp. indet.

Pl. 7, fig. 8; Pl. 9, fig. 9

Material: 3 incomplete fin-spines (CPC 19649-19651), and possibly a sectioned scale (CPC 19652; see previous remarks).

Remarks: The spines included here are similar to some of the ichthyodorulites referred to the genus *'Onchus'* (e.g. Gross, 1947, pl. 27), which are currently regarded as probably belonging to an ischnacanthiform acanthodian (see Ørvig, 1957, p. 338; Miles, 1966), although similar longitudinally ribbed spines occur in many other acanthodians (e.g. Watson, 1937; Obruchev, 1964; Miles, 1966; Pageau, 1969a). These very fragmentary remains may be tentatively referred here to the Ischnacanthiformes for the purposes of description.

Description: As far as can be determined the spines were slender, longitudinally ribbed, and laterally compressed. Only one (CPC 19650) shows a slight curvature. They vary in width from 1.1 to 1.4 mm, with a longest preserved portion of 9.5 mm (CPC 19649).

There are 4 fairly coarse longitudinal ribs on one side in CPC 19651, 1 coarse and 6 finer ribs in CPC 19650, and 10 fine ribs in CPC 19649. All ribs are smooth, and there appears to have been an unornamented zone along the posterior spine surface. The central cavity was moderately large. Other information (e.g. the presence and form of insertion areas and posterior denticles) is not provided by these examples, and further material is required before they can be more meaningfully determined.

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ABBREVIATIONS USED IN TEXT, FIGURES, AND PLATES

ADL	anterior dorsolateral plate
AL	anterior lateral plate
AMD	anterior median dorsal plate
AMV	anterior median ventral plate
AVL	anterior ventrolateral plate
$a_{1,3}$	lateral and mesial areas of connection between Cd_1 and Cv_1
aa	anterior angle of PMD
aal	anterolateral angle of PMD
a.art	articular area on processus brachialis of AVL
ad_1	anterior attachment area of SM plate
adc	anterodorsal corner of MxL plate
afd	external articular area on Cd_2 plate
afd.i	internal articular area on Cd_2 plate
afv	external articular area on Cv_2 plate
afv.i	internal articular area on Cv_2 plate
al	anterolateral angle of Nu plate
ala	anterolateral angle of PrO plate
alr	anterolateral ridge
apon	anterior postorbital notch
arc	anterior corner on PL component of MxL plate
ar_2d	marginal articular area of Cd_1 plate
ar_3d	external articular area of Cd_1 plate
ar.mem	area on cleithrum probably for membraneous attachment
ar_1v	internal articular area of Cv_1 plate
ar_2v	marginal articular area of Cv_1 plate
a_1SM	anterior attachment area for SM plate
a_2SM	posterior attachment area for SM plate
C	central plate
$Cd_{1\text{-}5}$	dorsal central plates 1-5
$Cv_{1\text{-}5}$	ventral central plates 1-5
c.al	anterolateral corner of subcephalic lamina of AVL
$c.Cv_1$	section of margin in contact with Cv_1 plate
$c.Cv_2$	section of margin in contact with Cv_2 plate
cf.ADL	contact face for ADL
cf.AMD	contact face for AMD
cf.AVL	contact face for AVL
cf.MV	contact face for MV
cf.MxL	contact face for MxL
cf.PDL	contact face for PDL
cf.PL	contact face for PL
cf.PVL	contact face for PVL
$cf.Rbr_1$	contact face for first branchiostegal ray
cit_1	postbranchial crest (anterior division of crista transversalis interna anterior)
c.l.	lateral corner of subcephalic lamina of AVL
$c.Mm_2$	section of margin in contact with Mm_2 plate
cm_1	anteromesial angle of ventral lamina of PVL
cm_2	middle angle of ventral lamina of PVL
cm_3	posteromesial angle of ventral lamina of PVL
cos	area covered by cosmine
$cr_{1,2}$	pre- and post-lateral cristae of transverse lateral groove of head-shield
cr.d	dorsal median crest of trunk-shield
cr.dm	dorsomesial crest of pectoral fin
cro	median occipital ridge of head-shield
cr.pm	paramarginal crista of head-shield
cr.pto	postorbital crista of head-shield
cr.seth	crista supraethmoidalis
cr.tp	crista transversalis interna posterior
cr.tv	transverse nuchal crista of head-shield
csc	central sensory canal groove
d	dorsal corner of MxL
dc	dorsal corner of lateral lamina of PVL
d.end	external opening of endolymphatic duct
dep	depression
dlg_1	anterior oblique dorsal sensory line groove
dlr	dorsolateral ridge of trunk-shield
dma	tergal angle of trunk-shield
dmr	dorsal median ridge of trunk-shield
dn	dorsal notch in SM plate
dp	external groove above crista transversalis interna posterior on PMD
d.pop	dermal postorbital process
Dsph	dermosphenotic
Fr	frontal
f.ap	fossa articularis pectoralis
f.art	articular fossa of ADL
f.ax	foramen axillare of AVL
fe.exa	fenestra exonarina anterior
fp	funnel pit of processus brachialis
f.pin	pineal foramen
f.retr	levator fossa of AMD
gr	groove
gr.csc	groove for ridge beneath central sensory canal
gr.eh	groove, possibly for epihyal
gr.soc	groove for ridge beneath supraorbital sensory canal
ifc_1	principal section of infraorbital sensory line on head-shield
if.r	infranuchal ridge
ifc.sb	suborbital part of infraorbital sensory line
i.La+Mx	lachrymo-maxillary notch
i.o	orbital notch
ioc	pores of infraorbital sensory canal
i.po	postorbital notch
i.spir	spiracular notch
juc	jugal sensory canal
kd	articular condyle on ADL
LA	lateral plate
l	lateral corner of PMD
la	lateral corner of PrM
la.v	ridge along transverse groove of preorbital plate
lc	lateral corner of AMD
lcg	main lateral line sensory groove
M	marginal plate
MD	median dorsal plate
$Ml_{2\text{-}5}$	lateral marginal plates 2-5
$Mm_{1\text{-}5}$	mesial marginal plates 1-5
MV	median ventral plate

MxL	mixilateral plate
m_1	anterior division of mesial margin of ventral lamina of AVL (in contact with semilunar plate)
mc	lateral corner of Nu plate
mgr	median groove
m.lim	margo limitans of AVL
mppr	posterior median process
mvr	median ventral ridge
Nu	nuchal plate
n	notch
nm	obtected nuchal area
n.PM	notch, possibly for PM plate
oa.ADL	overlap area for ADL
oa.AL	overlap area for AL
oa.AMD	overlap area for AMD
oa.AVL	overlap area for AVL
oa.MxL	overlap area for MxL
oa.PL	overlap area for PL
oa.PMD	overlap area for PMD
oa.PP	overlap area for PP
oa.PVL	overlap area for PVL
obm	orbital facet of Nu plate
occ	occipital cross-commissural pitline groove
od.gc	ornamented area probably lying beneath gill-cover
od.Lj	area overlapped by lower jaw
od.Op	area overlapped by opercular
od.Pop+Lj	area overlapped by preopercular and lower jaw
od.Qj	area overlapped by quadratojugal
od.Rbr	area overlapped by branchiostegal ray
od.Sop	area overlapped by subopercular
og.Aclm	area overlapping anocleithrum
og.Clm	area overlapping cleithrum
og.Iclav	area overlapping interclavicle
om	orbital margin
otd	oblique transverse depression on AMD
P	pineal plate
Pa	parietal
PDL	posterior dorsolateral plate
PL	posterior lateral plate
PM	postmarginal plate
PMD	posterior median dorsal plate
PMV	posterior median ventral plate
PN	postnasal plate
PNu	paranuchal plate
PP	postpineal plate
PrM	premedian plate
PrO	preorbital plate
PSO	post-suborbital plate
PtO	postorbital plate
PVL	posterior ventrolateral plate
pa	posterior angle of PMD
pbr	processus brachialis
pc	posterolateral corner of Nu
pdc	posterodorsal corner of AVL
pdlc	posterodorsal corner of lateral lamina of PVL
pe	pars pedalis of processus brachialis
plc	posterolateral corner of PMD
pl.Fr	frontal pit-line
plh.Id	horizontal pit-line of infradentary
pl.po.Pa	posterior oblique parietal pit-line
plr	posterolateral ridge
pl.St	supratemporal pit-line
pl.th	postlevator thickening
pl.tr.Pa	transverse parietal pit-line
plv.Id	possible vertical pit-line
plv.Id$_2$	vertical pit-line of infradentary 2
pma	posterior marginal area of PMD
pmaa	posteromesial angle of skull-roof
pmc	postmarginal sensory groove
p.mcp	pores of (preoperculo-) mandibular sensory canal
pnoa	postnuchal ornamented angle of ADL
poc	postotic sensory canal
po.m	postorbital margin
ppon	posterior postorbital notch
pr	process
prc	prepectoral corner
pr.Clav.	ascending process of clavicle
pr.dm	median dorsal process of MxL
prl	lateral process of PMD
pro	processus obstans on ADL
proc	preorbital corner
pr.pl	external postlevator process of AMD
pr.po	anterolateral angle of otico-occipital depression of head-shield
pr.Sc	articular process of scale
prv$_2$	posterior ventral process of dorsal wall of trunk-shield
p.Sc	articular pit of scale
pt$_{1,2}$	anterior and posterior ventral pits of dorsal wall of trunk-shield
ptoc	postorbital corner
R	rostral plate
r.cr	tranverse crescentic ridge
ri	ridge
ri.Rbr	rostrocaudal ridge on posterior branchiostegal ray
ri.Sc	ridge on inner face of scale
r.scc	ridge over semicircular canals of labyrinth cavity
SM	submarginal plate
SO	suborbital plate
SP	spinal plate
St	supratemporal
sna	supranuchal area
snc	subnarial corner
soa	subobstantic area
soc	supraorbital sensory groove
sol	suborbital lamina
sot	supraotic thickening
spg	pectoral pit-line groove
T	terminal plate
tb$_{1,2}$	anterior and posterior ventral tuberosities of dorsal wall of trunk-shield
tdr	internal dorsal oblique ridge on MxL
tg	transverse groove on visceral surface of PrO
th	thickening
th.end	endolymphatic thickening
tlg	transverse lateral groove of head-shield
tlr	internal horizontal ridge on MxL
vlr	ventrolateral ridge of trunk-shield

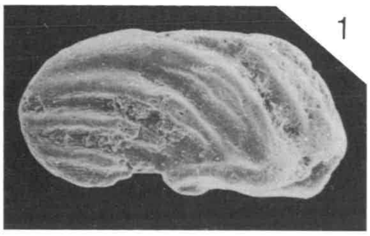
EXPLANATION OF PLATES

PLATE 1

Turinia? cf. **hutkensis** Blieck & Goujet

Figs.	
1	CPC 17015; right lateral view; x40.
2	CPC 17024; left lateral view; x40.
3, 4	CPC 17019; dorsal and left lateral views; x100.
5, 6	CPC 17016; left lateral and ventral views; x60.
7, 8	CPC 17028; dorsal and ventral views; x60.
9	CPC 17025; ventral view; x40.
10	CPC 17020: dorsal view; x40.
11, 12	CPC 17017; dorsal and ventral views; x100.
13, 14	CPC 17023; dorsal and left ventrolateral views; x33.

PLATE 1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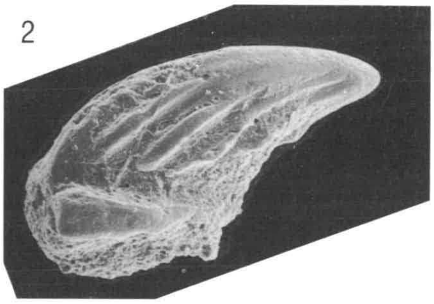
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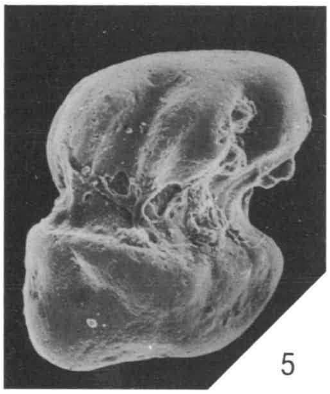
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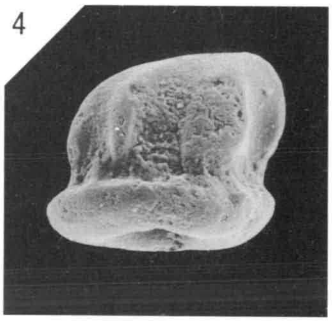
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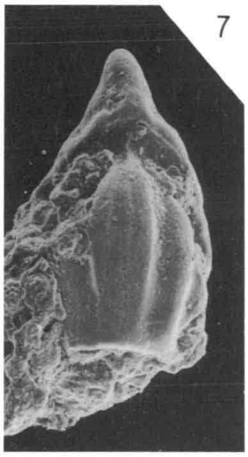
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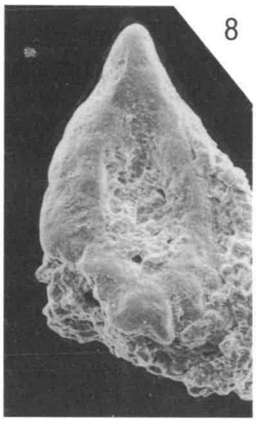
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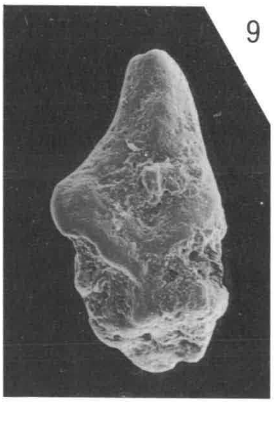
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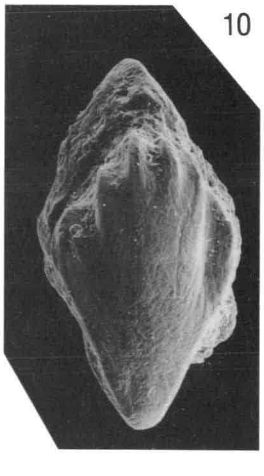
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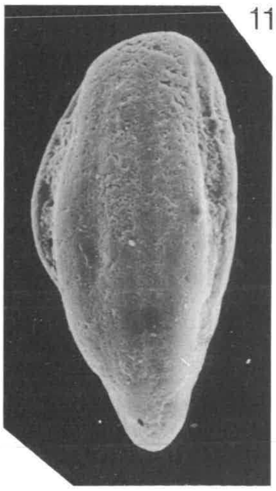
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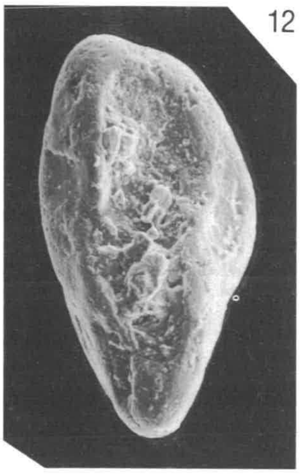
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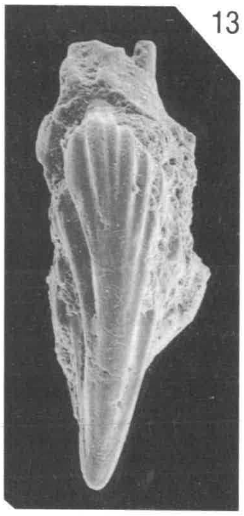
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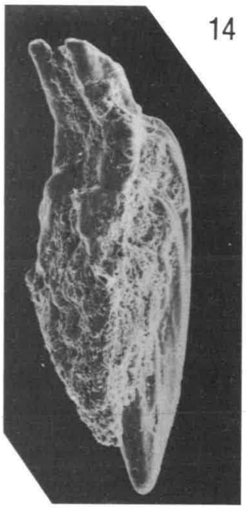
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PLATE 2

Turinia? cf. **hutkensis** Blieck & Goujet

Figs.
1, 2 CPC 17018; dorsal and ventral views; x60.

Bothriolepis gippslandiensis Hills

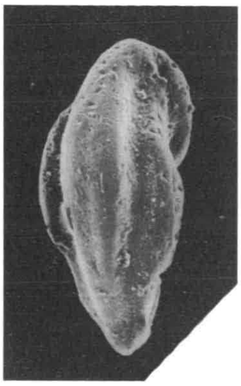
3 incomplete skull-roof in dorsal view. Holotype, MUGD776; x2.

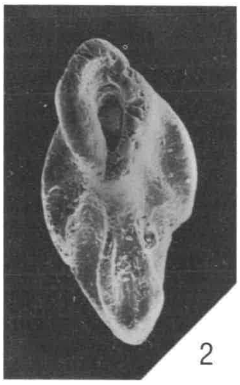
Bothriolepis verrucosa sp. nov.

4 Nu plate; dorsal view. CPC 17046; x4.
5 AMD; dorsal view. CPC 17051; x3.
6 AMD; ventral view. Holotype, CPC 17053; x2.
7 AMD, Ml_2; internal view. CPC 17049; x3.
8 PMD, Cd_1; external view. CPC 17060; x3.
9 distal segment of right pectoral fin; ventral view. CPC 19413; x3.
10 PMD; visceral view. CPC 19401; x3.

For explanation of lettering see p. 128.

PLATE 2





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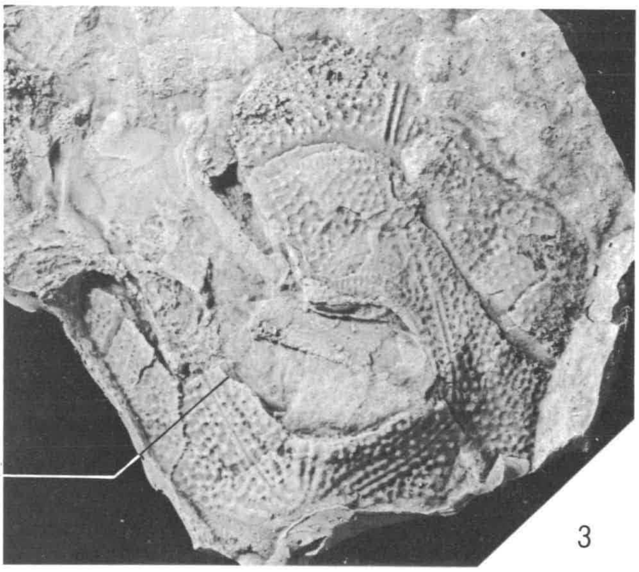

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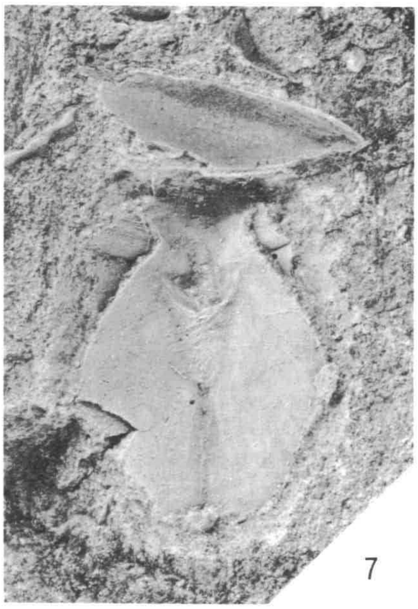

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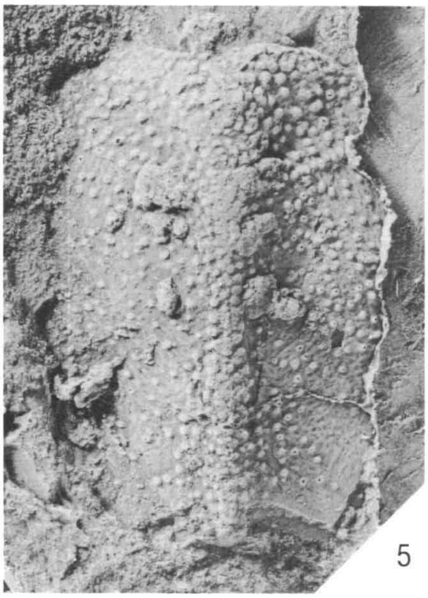

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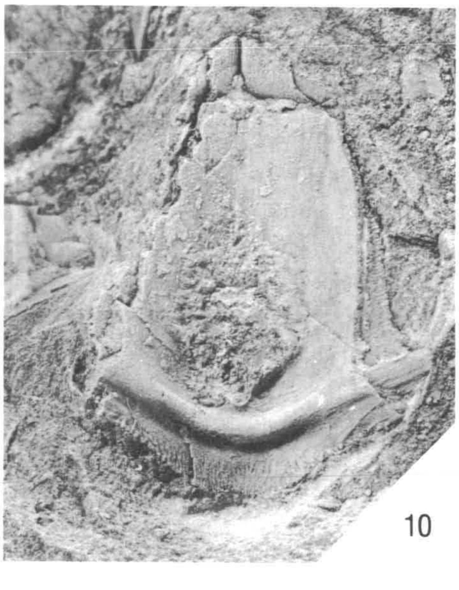

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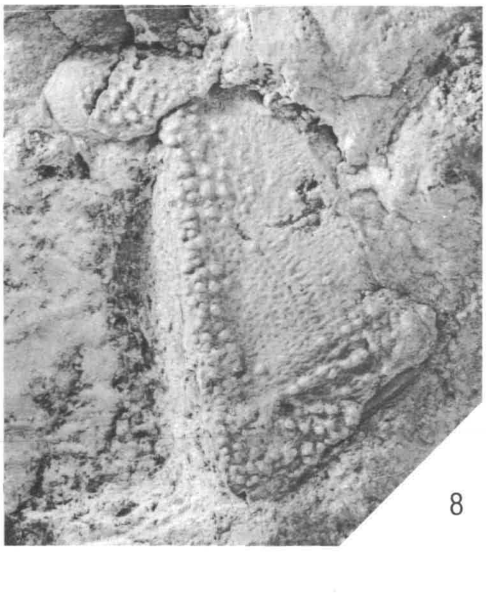

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PLATE 3

Bothriolepis verrucosa sp. nov.

Figs.

1 left ADL; lateral view. CPC 19407; x3.

2 left ADL; visceral view. CPC 19404; x3.

3 left MxL; lateral view. CPC 19425; x3.

4 left MxL; visceral view. CPC 19424; x3.

5 central plate (Cd_3 or Cv_3) from distal segment of pectoral fin; internal view. CPC 19459; x3.

6 Mm_2 of pectoral fin; dorsal lamina preserved as impression. CPC 19456; x3.

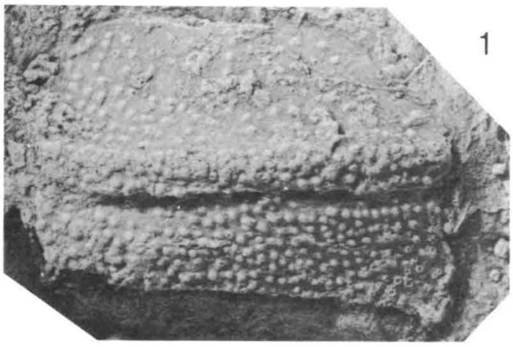
7 right AVL; ventral view, with part impression of the visceral surface. CPC 19445; x3.

8 incomplete proximal segment of left pectoral fin, showing internal surface of dorsal plates. CPC 19454; x3.

9 left PVL; ventrolateral view with ventral lamina preserved mainly as an impression of the visceral surface. CPC 19477; x3.

10 mesial plates of the proximal segment of a left pectoral fin, incompletely preserved; internal view. CPC 19453; x3.

PLATE 3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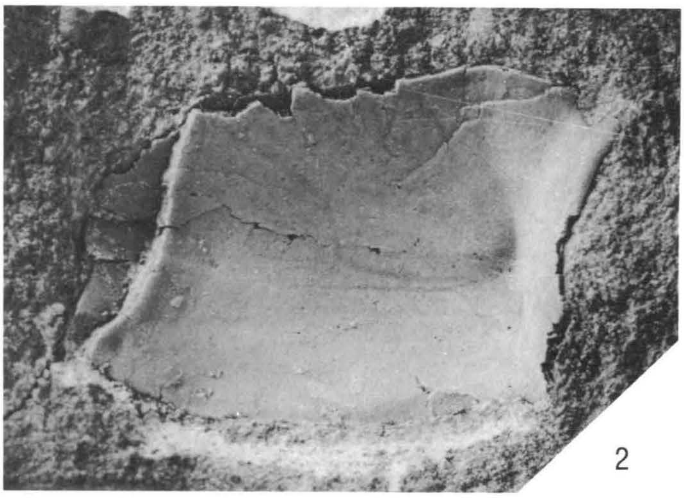
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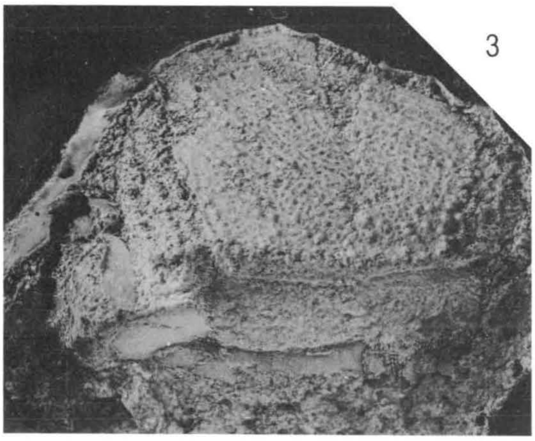
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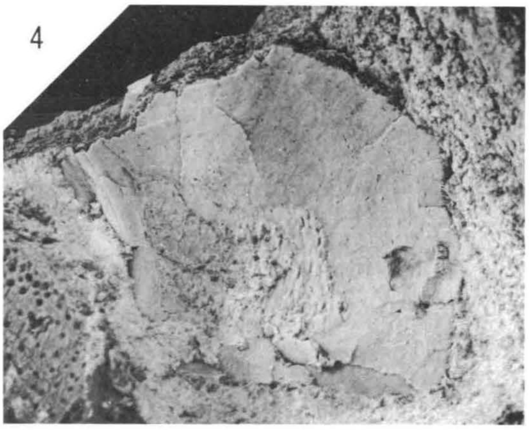
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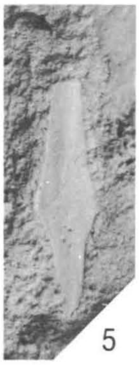
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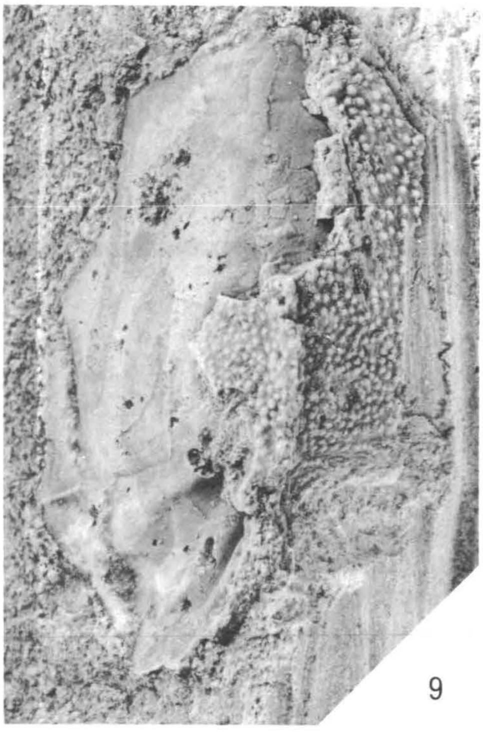
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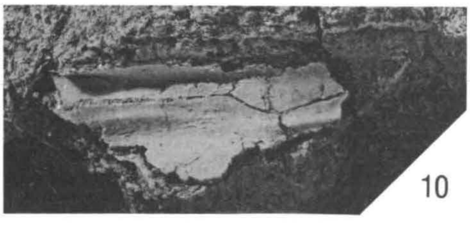
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PLATE 4

Bothriolepis verrucosa sp. nov.

Figs.

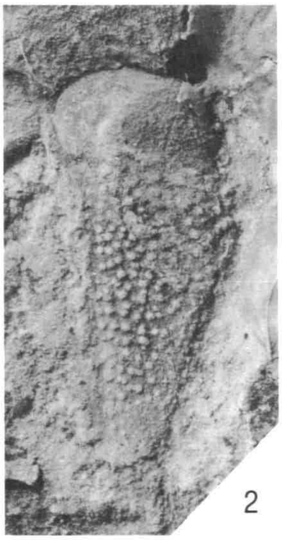
1 right Cd$_1$ of pectoral fin; dorsal view. CPC 19469; x4.
2 left Cv$_1$ of pectoral fin; ventral view. CPC 19442; x4.
3 incomplete Cv$_2$ of pectoral fin; visceral view. CPC 19452; x6.
4 internal surface of Mm$_1$ of pectoral fin, preserved as an impression. CPC 19450; x6.
5 incomplete Cd$_2$ of pectoral fin; dorsal view. CPC 19462; x4.

Sherbonaspis hillsi gen. et sp. nov.

6 Nu plate, dorsal view. CPC 19479; x3.
7 PrM plate; dorsal view. CPC 19482; x3.
8 SM plate; visceral view. CPC 19485; x4.
9 AMD; visceral view. CPC 19489; x2.
10 PMD; right lateral view. CPC 19496; x3.
11 incomplete left ADL, preserved mainly as an impression of the visceral surface. CPC 19499; x3.
12 right ADL; visceral view. CPC 19501; x3.
13 left Cd$_1$ of pectoral fin; ventral view. CPC 19515; x4.

PLATE 4


1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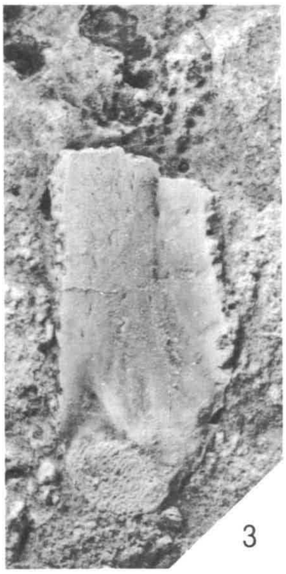
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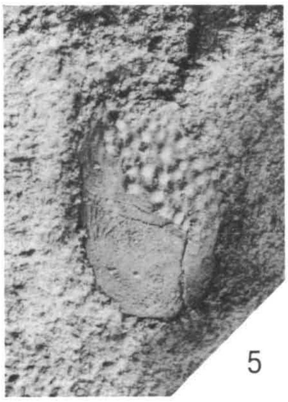
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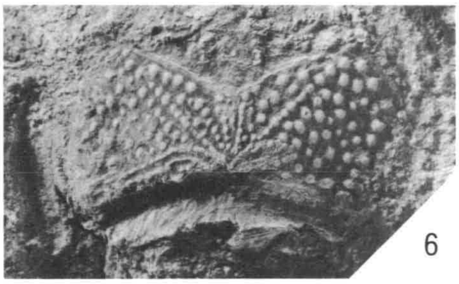
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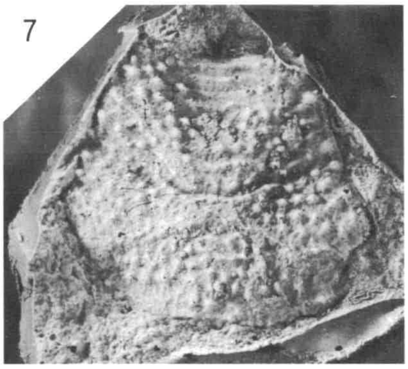
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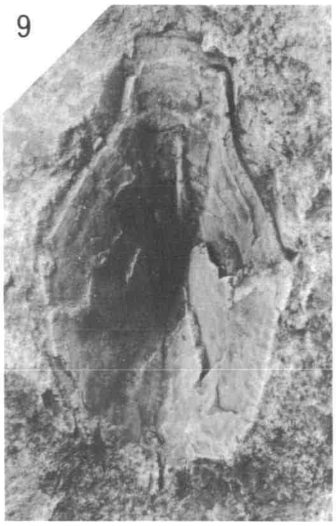
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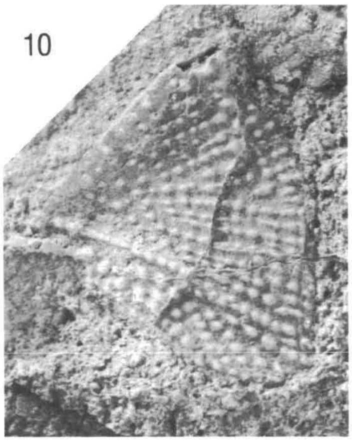
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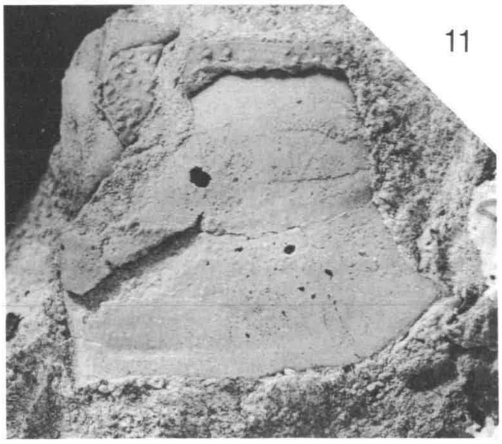
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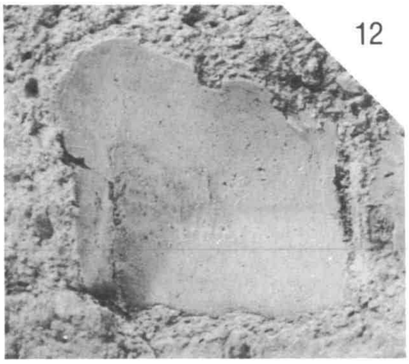
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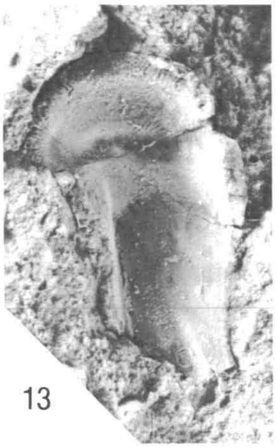
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PLATE 5

Sherbonaspis hillsi gen. et sp. nov.

Figs.

1 incomplete right MxL in lateral view. Holotype, CPC 19478; x3.

2 fairly complete right MxL in visceral view. CPC 19509; x3.

3, 7 right PVL in lateral and ventral views. CPC 19522; x3.

4 left Cd_2 of pectoral fin; dorsal view. CPC 19492; x6.

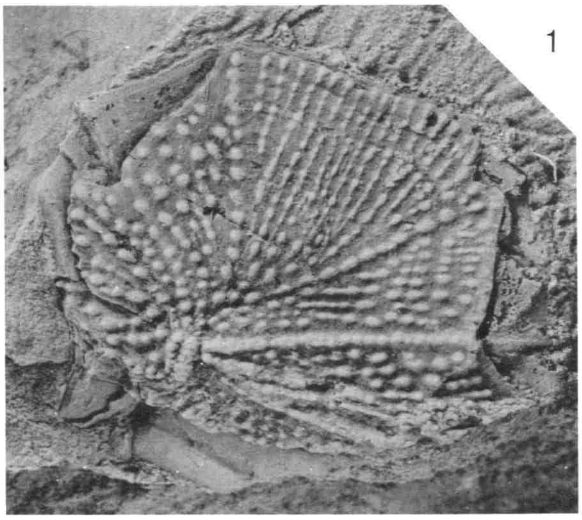
5 left AVL in visceral view with a distal segment of the pectoral fin. Holotype, CPC 19478; x3.

6 left pectoral fin; ventral view. CPC 19519; x3.

Denisonosteus weejasperensis gen. et sp. nov.

8 incomplete left SM plate; visceral view. CPC 19579; x3.

PLATE 5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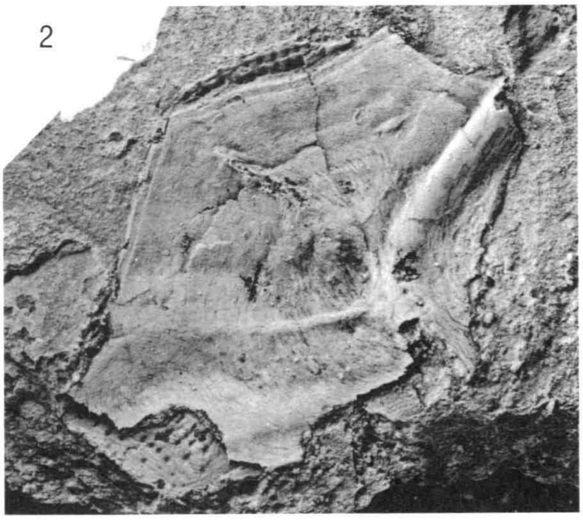
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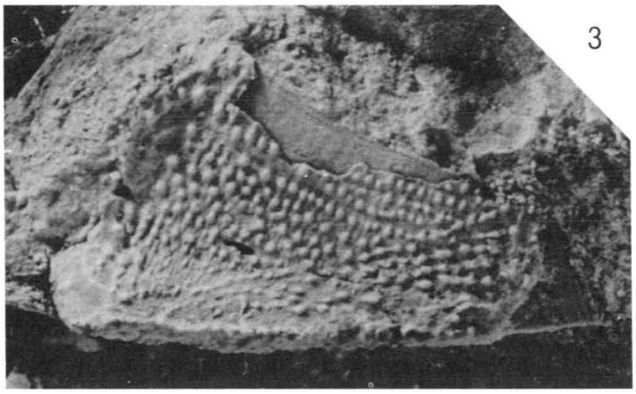
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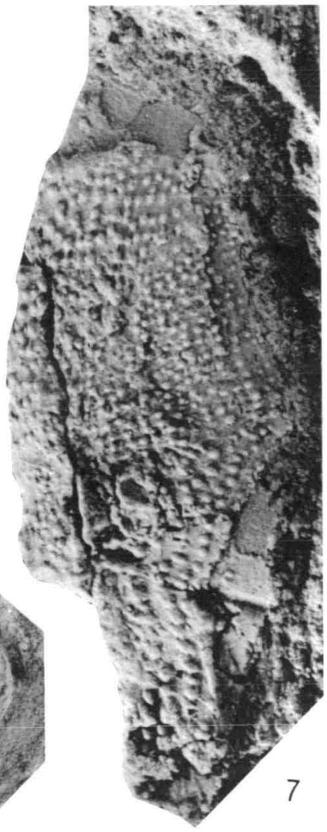
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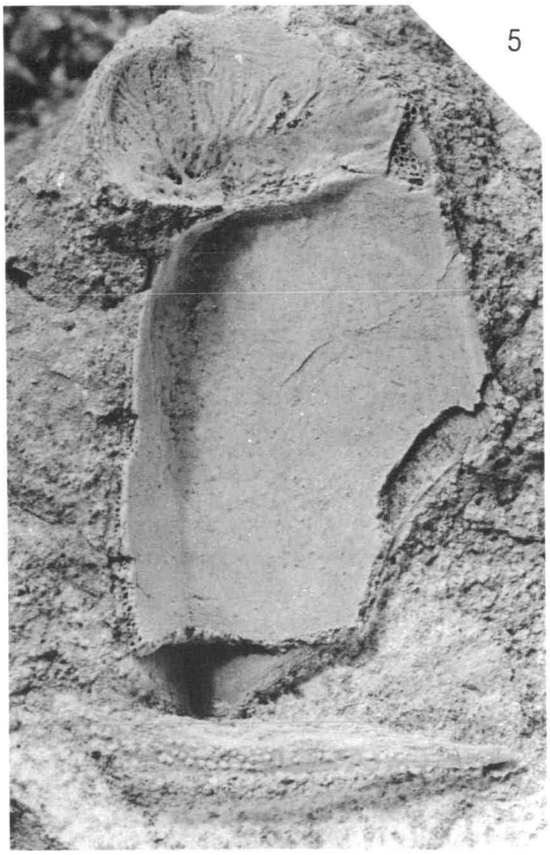
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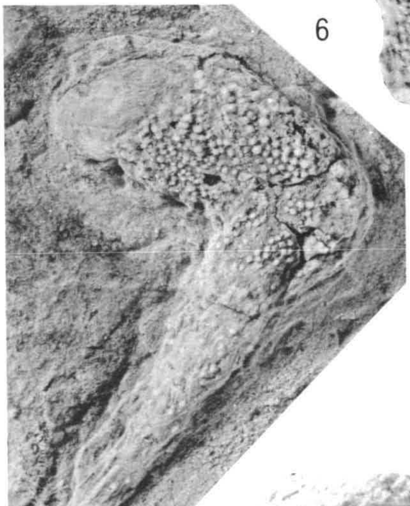
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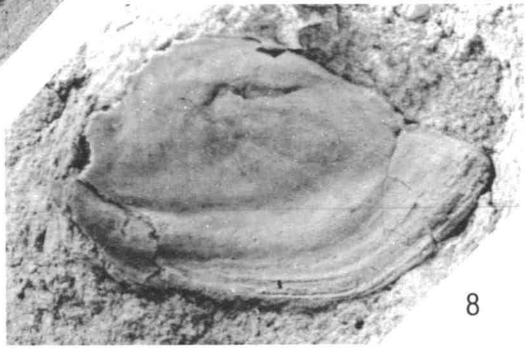
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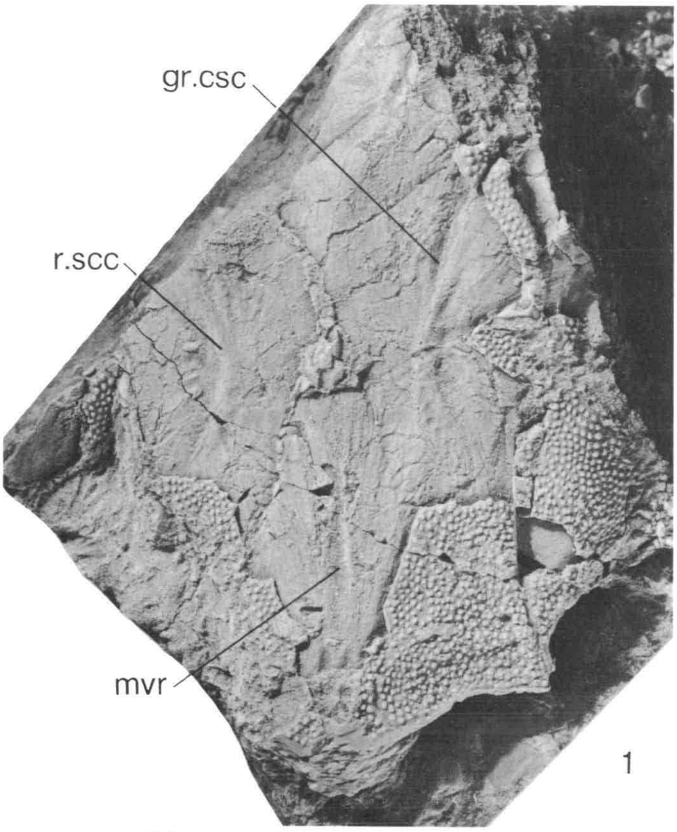
PLATE 6

Denisonosteus weejasperensis gen. et sp. nov.

Figs.	
1	incomplete skull-roof in dorsal view, preserved largely as an impression of the visceral surface. Holotype, CPC 19537; x1.5.
2	MD in visceral view, with portion of the left AL. Holotype, CPC 19537; x1.5.
3	left AL; visceral view. CPC 19553; x2.
4, 8	ADL and AMV plates in visceral view. CPC 19547; x2.
5	incomplete SP plate. CPC 19560; x3.
6	right SO; lateral view with much of the postorbital lamina preserved as an impression of the visceral surface. CPC 19541; x4.
7	PMV in visceral view. CPC 19570; x2.

For explanation of lettering see p. 128.

PLATE 6



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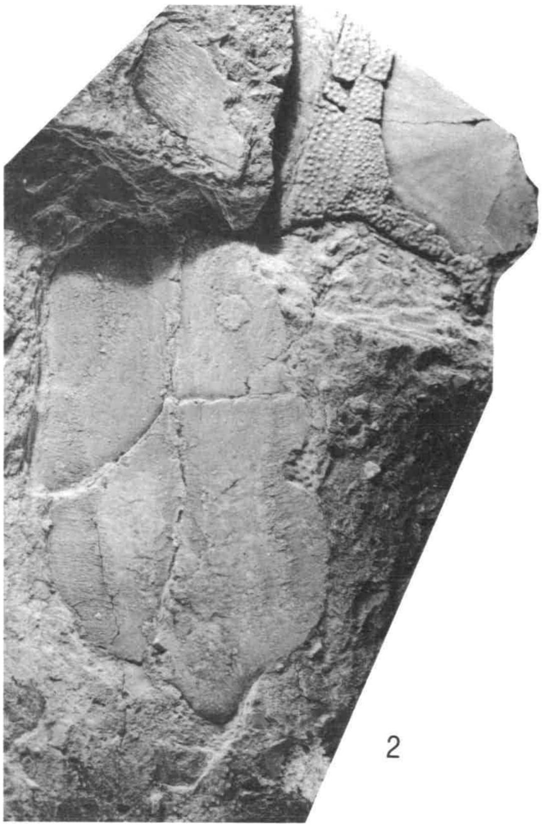

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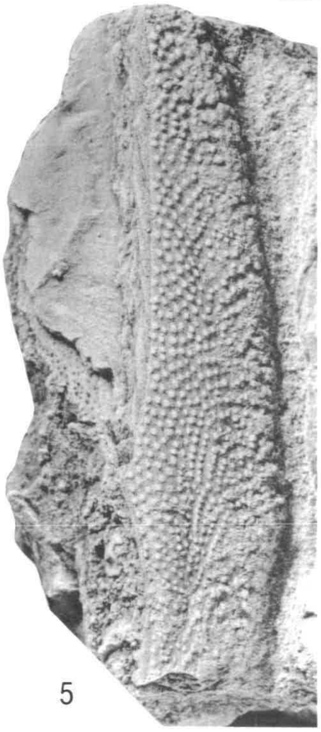

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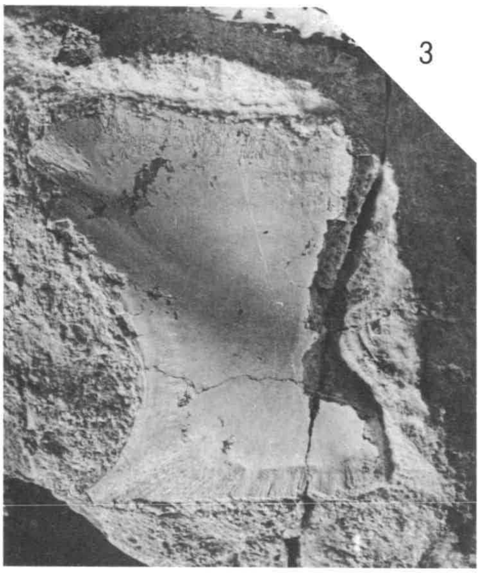

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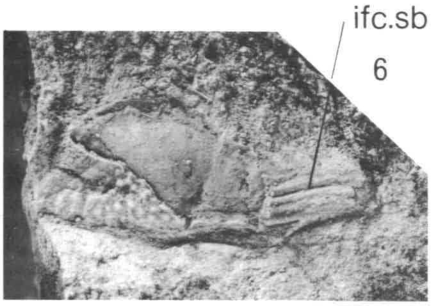

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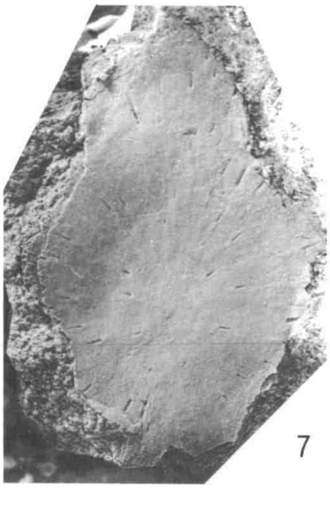

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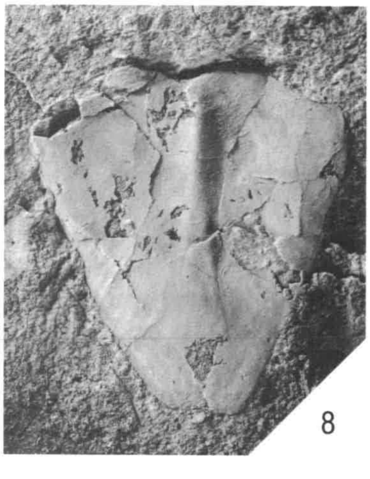

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PLATE 7

Denisonosteus weejasperensis gen. et sp. nov.

Figs.

1 right AVL, preserved mainly as an impression of the visceral surface (CPC 19566), associated with a left Cd_1 of *Bothriolepis verrucosa* sp. nov. (CPC 19466) preserved in visceral view; x1.5.

2 incomplete skull-roof in dorsal view, preserved mainly as an impression of the visceral surface. CPC 19538; x2.

3 left PVL in visceral view. CPC 19579; x2.

7 undetermined incomplete plate, probably from the ventral wall of the trunk-shield, showing alignment of tubercles into concentric rows. CPC 19581; x1.5.

EUARTHRODIRA incertae sedis

5 undetermined plate carrying a sensory groove, possibly from the head. CPC 19584; x3.

6 ventral portion of a left PDL; lateral view. CPC 19557; x3.

PLACODERMI incertae sedis

4 incomplete left ADL in visceral view. CPC 19549; x3.3.

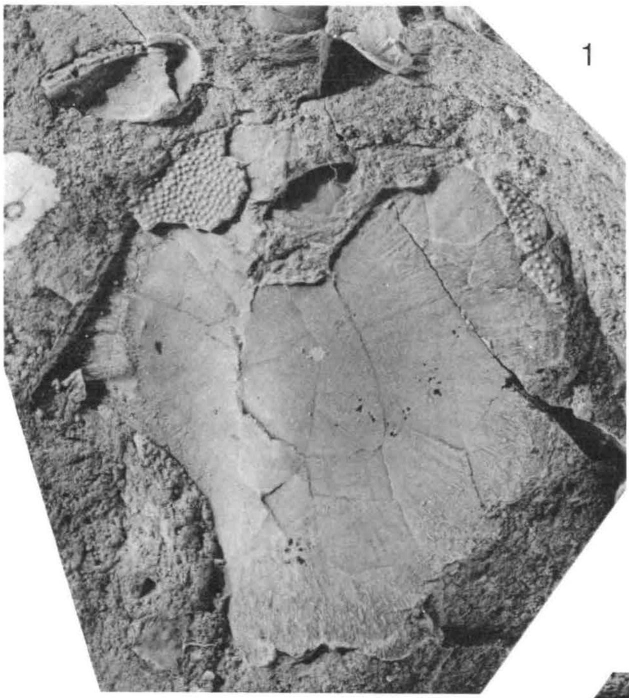
9 incomplete right ADL in visceral view. CPC 19548; x3.

?ischnacanthiform gen. et sp. indet.

8 incomplete spine. CPC 19649; x6.

For explanation of lettering see p. 128.

PLATE 7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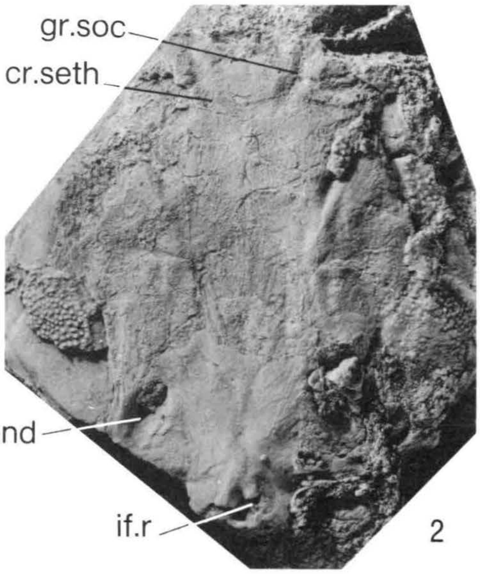

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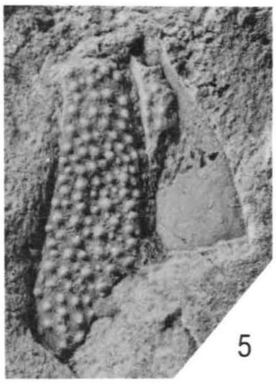
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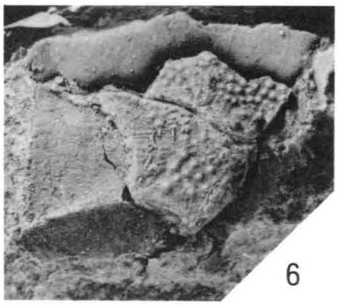
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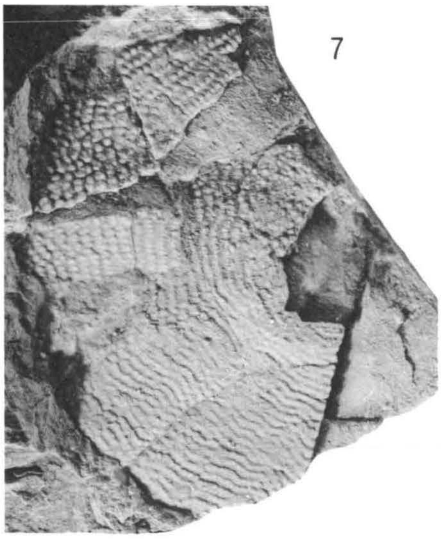
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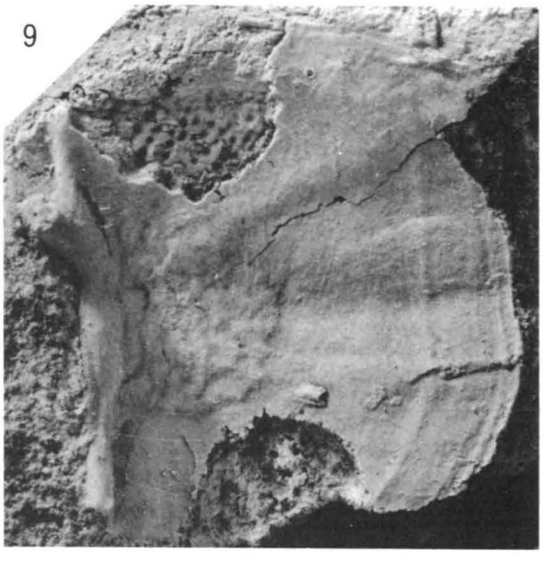
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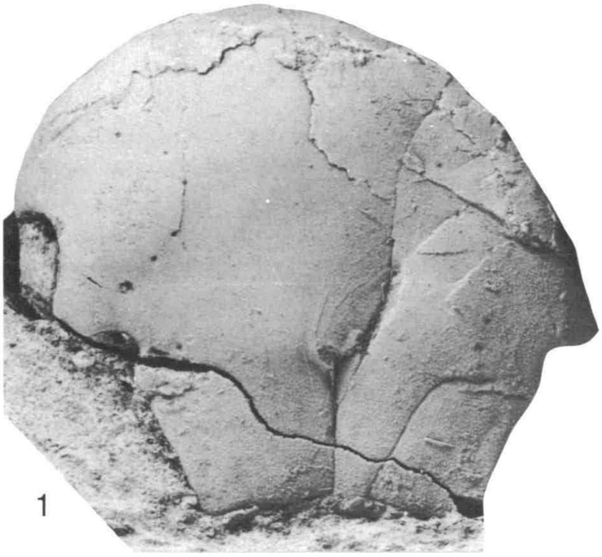
PLATE 8

Gyroptychius? australis sp. nov.

Figs.	
1, 2	fronto-ethmoidal shield in dorsal and ventral views. Holotype, CPC 19586; x4.
3	parietal shield in dorsal view. CPC 19590; x4.
4	isolated tooth. CPC 19608; x5.
5	incomplete left preopercular and squamosal; lateral view. CPC 19592; x2.
6	possible left lateral extrascapular with part of the median extrascapular attached. CPC 19591; x4.
7	incomplete fronto-ethmoidal shield in dorsal view. CPC 19588; x4.
8	possible second branchiostegal ray from the left side; ventral view. CPC 19609; x4.

For explanation of lettering see p. 128.

PLATE 8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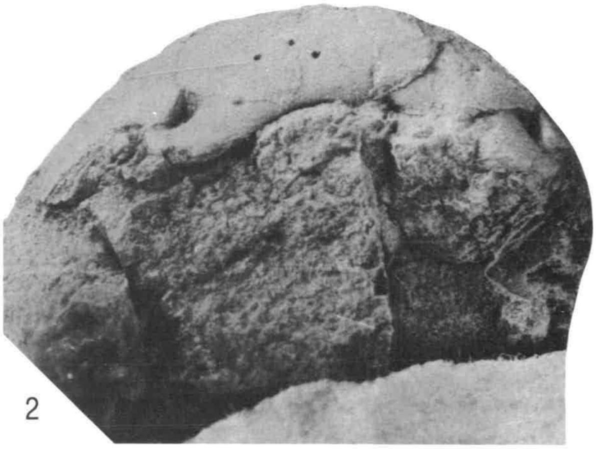
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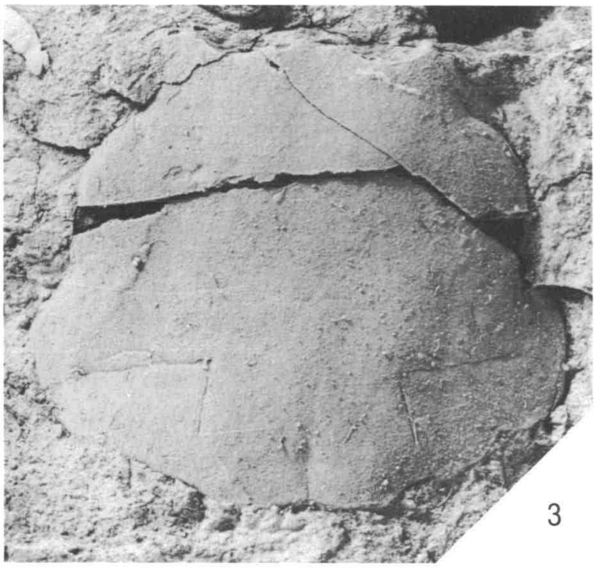
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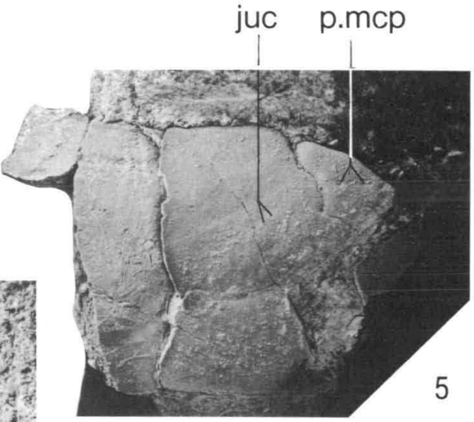

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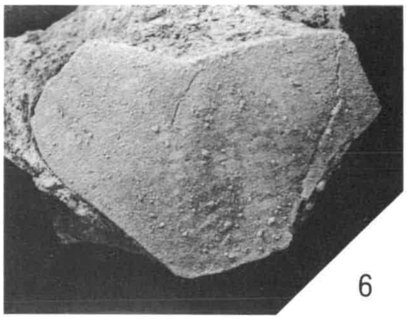
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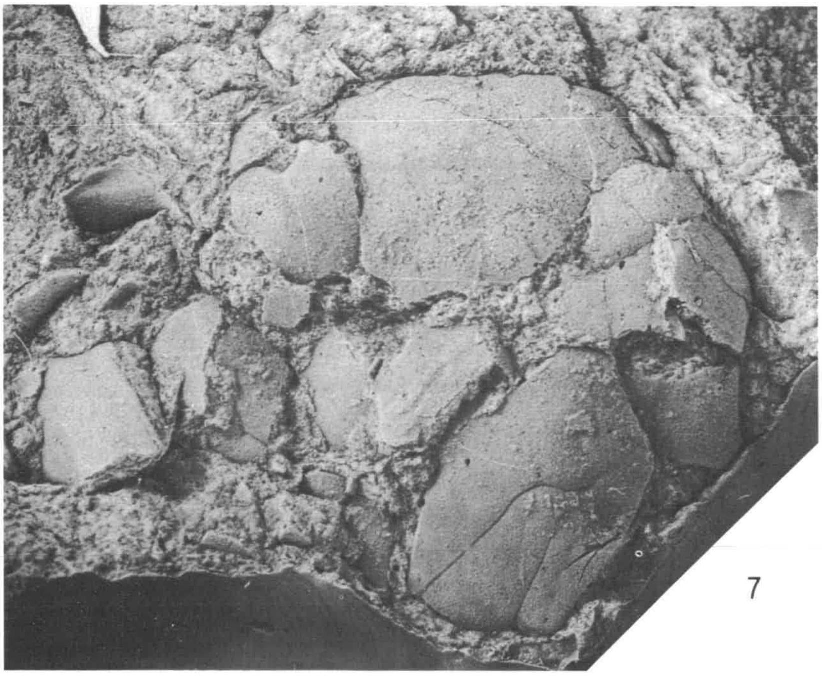
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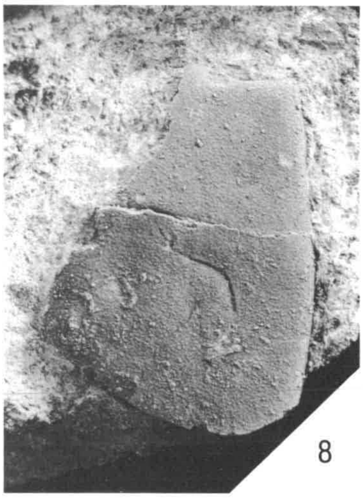
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PLATE 9

Gyroptychius? australis sp. nov.

Figs.

1	right lower jaw in lateral view. CPC 19592; x2.
2	scale in external view. CPC 19645; x4.
3	scale in external view. CPC 19632; x6.
4	first branchiostegal ray from the left side; ventral view. CPC 19610; x4.
5	left clavicle; visceral view. CPC 19623; x3.
6	scale in external view. CPC 19634; x6.
7	scale in internal view. CPC 19633; x4.
10	scales in various orientations. CPC 19629; x1.5.
11	right principal gular; visceral view. CPC 19613; x2.

climatiid gen. et sp. indet.

8	incomplete spine. CPC 19647; x4.

?ischnacanthiform gen. et sp. indet.

9	incomplete spine. CPC 19650; x9.

PLATE 9


1


2


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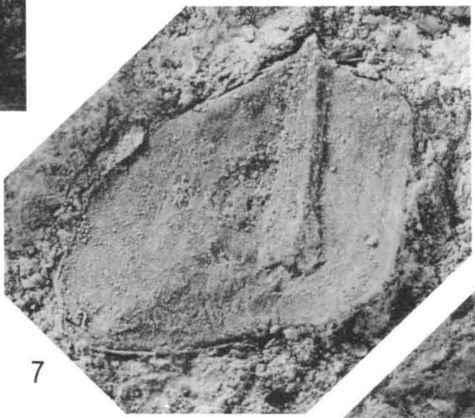
4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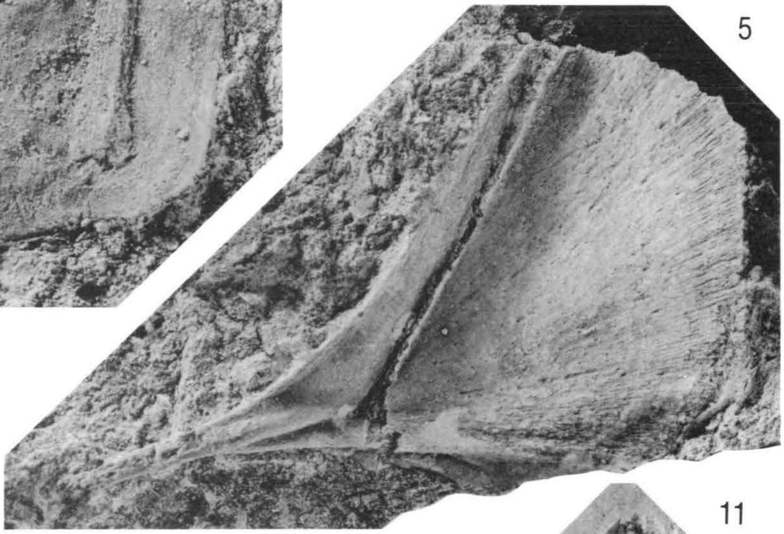
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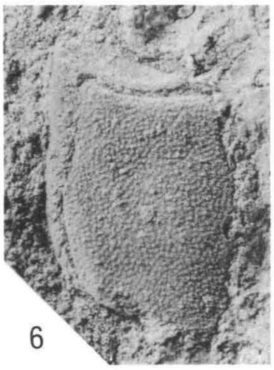
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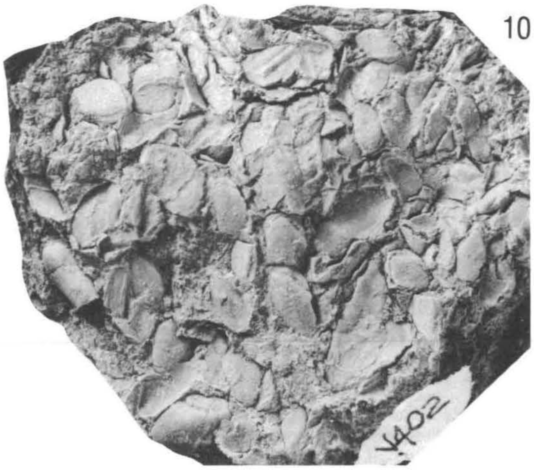
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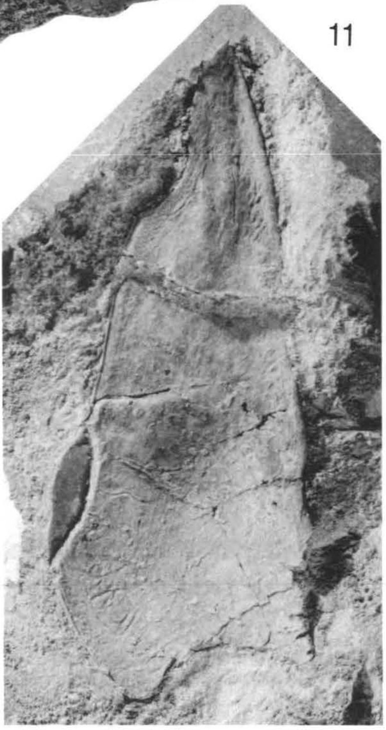
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