

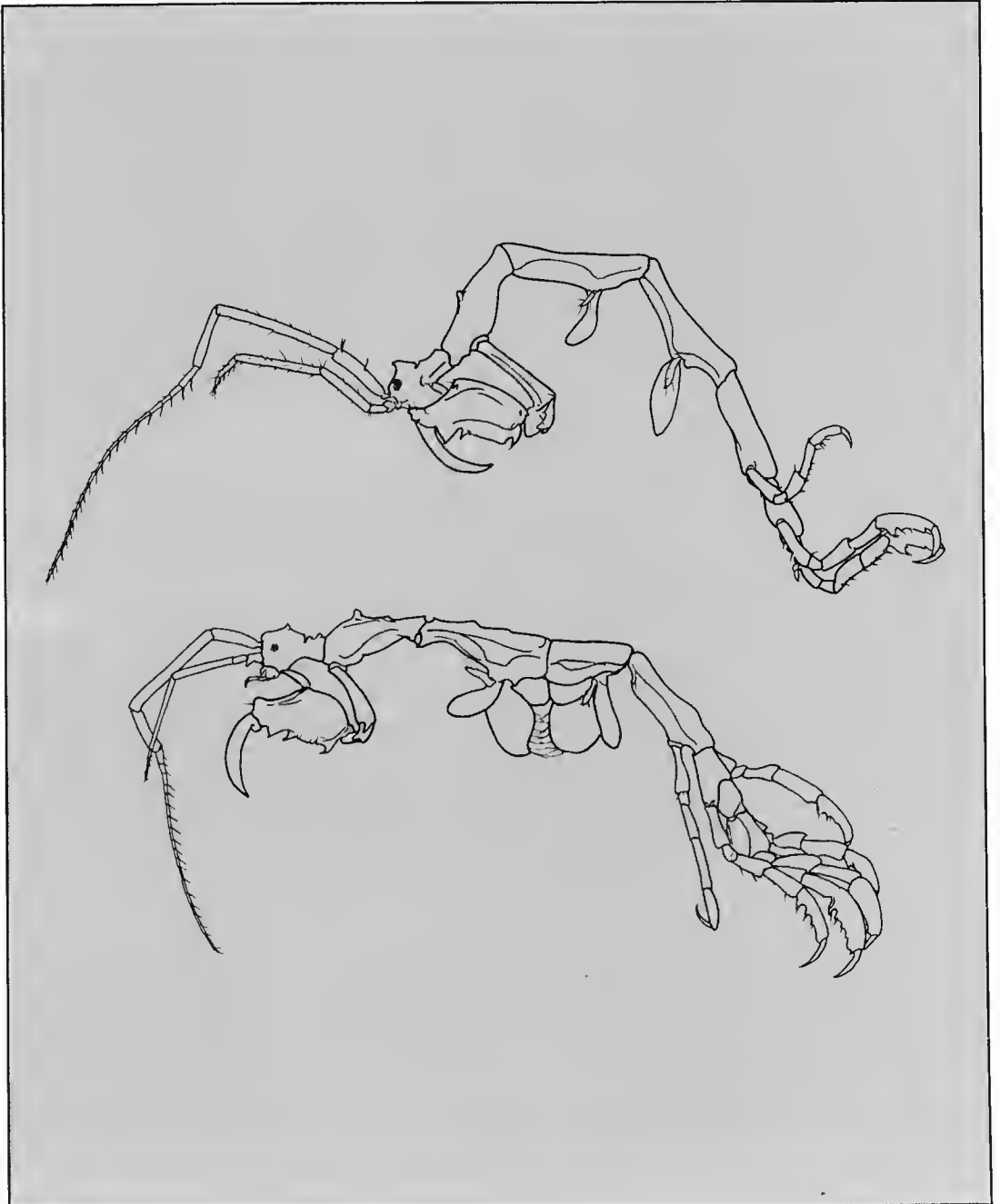
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Cover: *Paradicaprella brucei* gen. et sp. nov. Drawing by A. Hirayama.

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SCIENCES

A SECOND SPECIES OF *BRESILIA*, *B. PLUMIFERA* SP. NOV.,
NEW TO THE AUSTRALIAN FAUNA
(CRUSTACEA: DECAPODA: BRESILIIDAE).

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ABSTRACT

A new species of *Bresilia*, *B. plumifera* (Crustacea: Decapoda: Bresiliidae), is described and illustrated, increasing to four the number of species now known in this genus. The single specimen, the smallest in the genus (total length about 6 mm), was collected from the western Tasman Sea, at only 133 m, the most shallow depth from which this deep-sea genus has been recorded.

KEYWORDS: Crustacea. Decapoda, Bresiliidae, *Bresilia*, new species, Tasman Sea.

INTRODUCTION

The small genus *Bresilia* was first described by Calman (1896) from a single specimen collected off Ireland at 1372 m depth. Some ninety years passed before a further specimen of this genus was reported, when Forest and Cals (1977) described *B. corsicana*, again based on a single specimen from the western Mediterranean Sea, at a depth of 450 m. Recently, *B. antipodarum* has been recorded from off eastern Tasmania, at 800 m, by Bruce (1990). The discovery of a single specimen of another species of *Bresilia* in eastern Australian waters increases the size of the genus from three to four species, with two in the northern hemisphere and two at nearly the opposite pole of the southern hemisphere. All species are still known only from the single holotype specimens. All are very small shrimps and doubtless are easily overlooked in trawl or dredge catches.

Carapace length refers to the postorbital carapace length. Type material is deposited with the Australian Museum, Sydney (AM).

SYSTEMATICS

Genus *Bresilia* Calman
Bresilia plumifera sp. nov.
(Figs 1-4)

Type material. HOLOTYPE - AMP40086:
1 female, Taupo Sea Mount, western Tasman

Sea, 33° 14.21'S., 56° 10.68'E, 133 m, sled, 2 May 1989, coll. J.K. Lowry *et al.* F.R.V. *Franklin*, stn. FRO589-7.

Description. A small-sized, slenderly built shrimp, of generally subcylindrical body form, lacking parts of antennae, second to fifth pereopods, parts of pleopods, with distal caudal fan damaged.

Carapace slightly compressed, smooth; rostrum well developed, acute, about 0.3 of carapace length, straight, slightly shorter than proximal segment of antennular peduncle, dorsal carina distinct, shallow, with 4 small acute teeth, first tooth on carapace proximal to posterior orbital margin, second tooth over posterior orbital margin, distal teeth at about 0.4 and 0.8 of rostral length; ventral earina distinct, shallow, ventral border convex, unarmed, non-setose; lateral carinae distinct, broadened posteriorly, expanded to form orbital rim; inferior orbital angle acute, anterior margin of branchiostegite deeply convex, pterygostomial angle acutely produced; supraorbital, hepatic, and antennal spines absent.

Abdomen smooth; third segment strongly produced posterodorsally; sixth segment about 2.2 times length of fifth, 2.0 times longer than deep, compressed, posterolateral angle produced; acute, posteroventral angle small, subacute; pleura of first three segments expanded, broadly rounded; fourth posteriorly produced, rounded; fifth angular, with small posteroventral tooth. Caudal fan damaged,

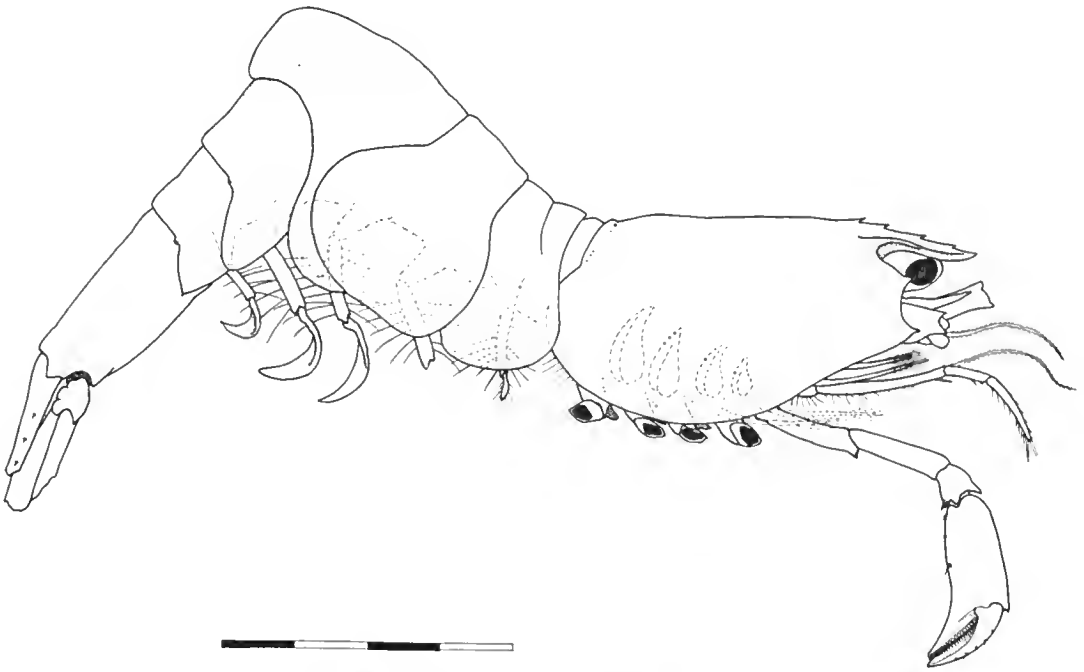


Fig. 1. *Bresilia plumifera* sp. nov., female holotype, Tasman Sea. Scale divisions in 0.5mm.

lacking distal telson and distal rami of uropods. Uropod with distolateral angle of protopodite acute.

Eye with rounded, pigmented cornea, obliquely hemispherical; stalk subcylindrical, slightly inflated proximally, without dorsal tooth.

Antennule with proximal segment of peduncle broad, about 1.3 times longer than wide, stylocerite broad, acute, not reaching distal margin of segment, medial border setose, with small ventral tooth; statoecyst obsolete; distal segments and flagella lacking.

Antenna with basicerite robust, with small distal dorsolateral tooth, larger ventrolateral tooth and strong ventral medial tooth; ischio-cerite bearing elongate plumose setae, mero-cerite normal; scaphocerites and flagella lacking.

Epistome with long slender, forwardly directed acute median process.

Mandible with feeble corpus; palp well developed, 2-segmented, proximal segment subcylindrical, distal segment suboval, flattened, with numerous short plumose or serrulate spiniform setae; molar process feeble, slender, slightly expanded and compressed distally, with numerous slender acute marginal teeth; incisor process broad, anterior margin with distinct knob-like process disto-

dorsally, cutting edge with 10 acute teeth, anteriormost tooth largest. Maxillula with slender, curved palp, with 2 unequal, pre-terminal setae; upper lacinia broad, with 12 stout, dentate marginal spines, largest ventrally, with submarginal row of 11 more slender serrulate spines and proximal row of 6 slender serrulate spines, dorsal and ventral margins with setulose setae; lower lacinia slender, with 5 long stout serrulate spines distally, setulose setae ventrally. Maxilla with elongate tapering palp, distal half subcylindrical, styloform, with few short proximomedial setae; basal endite bilobed, distal lobe subcircular, proximal lobe more elongate, both sparsely setose, with long finely setulose setae; coxal endite simple, similarly setose, with scaphognathite well developed, about 4.3 times longer than wide, posterior lobe narrow, with elongate posterior marginal setae, anterior lobe large, broad, 2.0 times longer than broad, rounded. First maxilliped with small simple palp, with about 6 plumose setae distomedially; basal endite small, broad, sparsely setose medially, coxal endite similar, smaller, exopod with small, narrow caridean lobe, with sparse stout plumose marginal setae, flagellum slender, with several short plumose setae distally; epipod bilobed, elongate, narrow. Second maxilliped with endopod stout, dac-

tylar segment terminal, about 1.6 times longer than wide, distally rounded, with numerous long serrulate marginal spines, oblique transverse row of similar submarginal spines; propod about 2.0 times dactyl length, 2.5 times

longer than wide, sparsely setose; carpus short, unarmed; ischiomerus 2.2 times longer than wide, 1.2 times longer than propod, sparsely setose medially; basis subequal to ischiomerus length, exopod with long slender

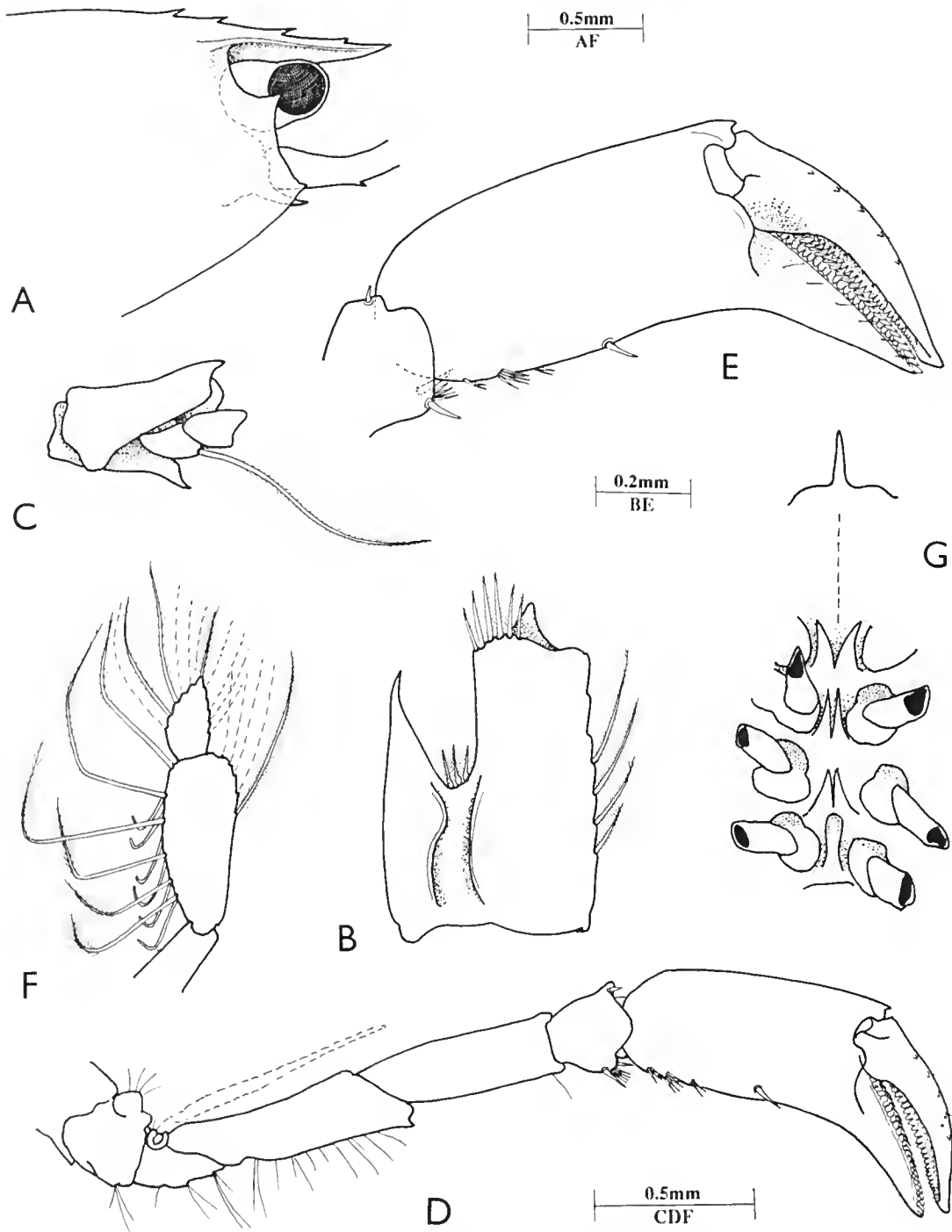


Fig. 2. *Bresilia plumifera* sp. nov., female holotype. A, anterior carapace, rostrum and eye, right antennae removed, epistome and epistomal spine indicated by dashed line. B, antennule, proximal segment of peduncle. C, basicerite, ventrolateral aspect. D, first pereiopod. E, same, chela. F, first pleopod. G, fifth to eighth thoracic sternites; above, epistomal spine.

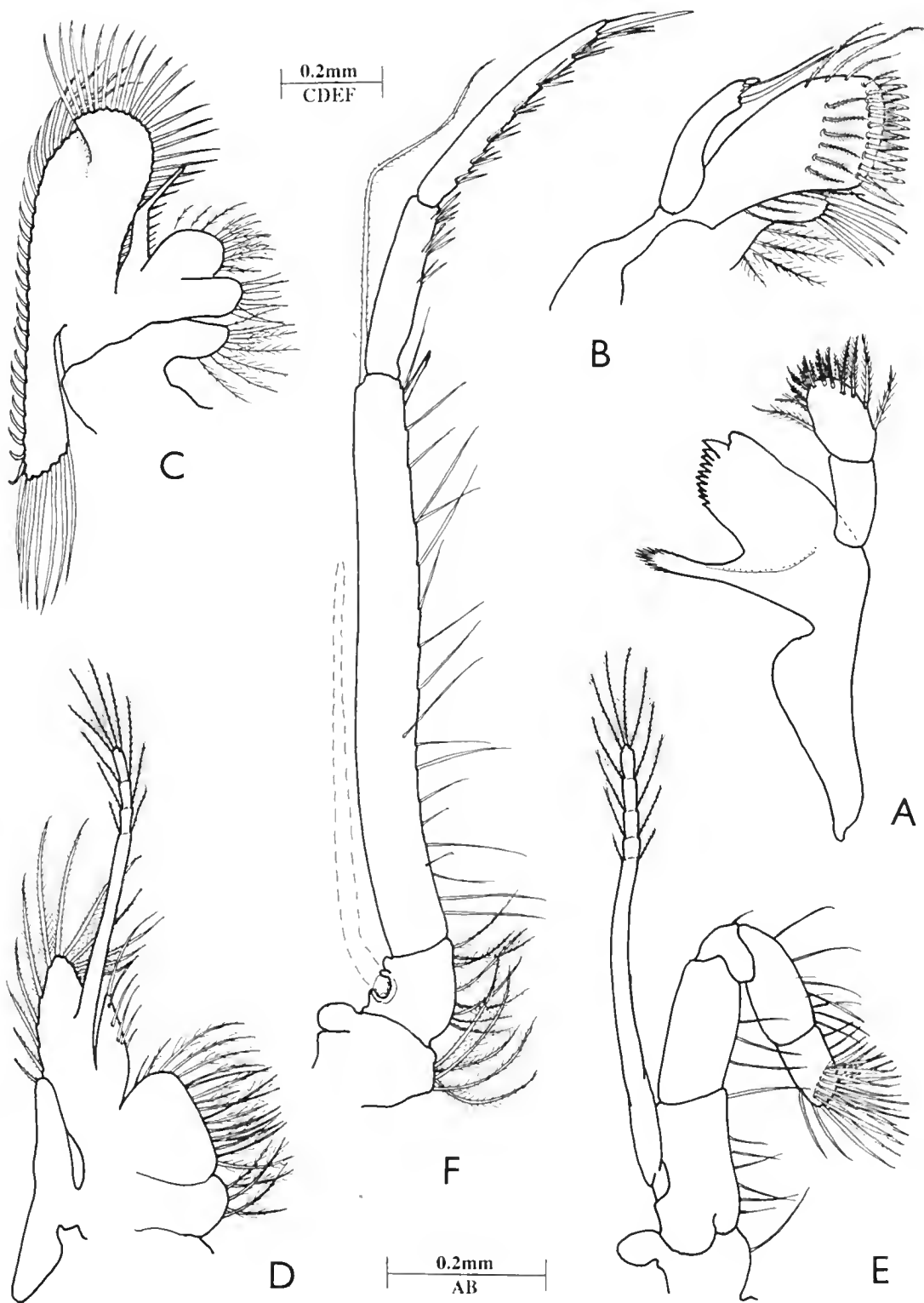


Fig. 3. *Bresilia plumifera* sp. nov., female holotype. A, mandible. B, maxillula. C, maxilla. D, first maxilliped. E, second maxilliped. F, third maxilliped.

flagellum with numerous short plumose setae distally; coxa medially rounded, with single seta, with reduced rounded epipod laterally. Third maxilliped with long slender endopod, exceeding proximal segment of antennular peduncle by length of distal segment; antepenultimate segment about 9.0 times longer than central width, tapering feebly distally, sparsely setose medially, with single elongate plumose seta at distodorsal angle, penultimate segment 0.3 of proximal segment length, 4.3 times longer than proximal width, feebly tapering distally, with 3 transverse rows of short serrulate spines along distal half of ventral border; terminal segment slender, tapering, about 9.0 times longer than proximal width, with stout subterminal distal spine, 0.4 of segment length, with 7 transverse rows of serrulate spines on ventral margin; basis distinct from ischiomerus, short, with slender plumose setae medially, exopod well developed, flagellum (lacking on right) slender, with short plumose setae distally, reaching to about 0.65 of ischiomerus length; coxa robust, with 5 long plumose setae medially, small globular epipod dorsolaterally.

Thoracic sternites narrow, first to fourth unarmed, fifth with submedian pair of large divergent triangular teeth, sixth and seventh with slender pairs of acute subparallel teeth, eighth with blunt median process, feebly dilated and flattened distoventrally.

First pereopod present on right side only, well developed, exceeding basicrite by carpus and chela; chela about 0.6 of carapace length, palm oval in section, smooth, about 2.0 times longer than central width, increasing slightly in width distally, distodorsal margin with small acute tooth, proximal ventral margin with three transverse rows of short serrulate spines with single larger stout simple spine at 0.5 of ventral border length; fingers strongly deflexed; dactyl about 0.75 of palm length, slightly exceeding fixed finger, with slightly upturned blunt tip, about 3.5 times longer than proximal depth, deeply concave laterally, dorsal margin convex, earinate, with 5 small acute denticles, ventromedial margin concave, with 9 small spinules, ventrolateral margin straight, strongly dentate, with about 40 strongly compressed teeth, largest centrally, decreasing strongly in size distally; fixed finger about 2.0 times longer than proximal width, deeply concave dorsolaterally, taper-

ing strongly distally, cutting edge straight, with series of deep fossae laterally for reception of dactylar teeth, medially with a row of stout simple spines, about 35, becoming shorter, stouter distally, extending to tip of fixed finger; carpus short, stout, as wide distally as long, slightly expanded, excavate distally, with small dorsal lobe with single short stout simple spine, rounded lateral lobe, small ventral lobe with strong simple medial and lateral spines, separated by four slender serrulate spines; merus about 0.8 of palm length, 3.4 times longer than central depth, unarmed; ischium obliquely articulated with merus, subequal to palm length, 3.5 times longer than distal width, tapering feebly ventrally, distoventral angle produced, with small acute tooth, ventral border sparsely setose; basis short, stout, without special features, exopod well developed, flagellum (lacking on right) slender, reaching to proximal merus, with numerous plumose setae distally; coxa normal, with rounded dorsolateral protuberance (epipod?).

Second of fifth pereopods lacking; well developed exopod on basis of second pereopod, (lacking on right) shorter than first pereopod exopod; posterior pereopods without exopods.

Pleurobranchs present on first four pereopods only, decreasing strongly in size anteriorly.

Pleopods damaged; first pleopod with basipodite 1.75 times longer than wide, with 6 elongate distally plumose setae medially, with inner row of 6 ovigerous setae; exopod lacking; endopod small, about 0.45 of basipodite length, tapering distally, with about 10-12 plumose marginal setae. Second pleopod lacking exopod and endopod. Posterior pleopods without special features, all lacking endopods.

Measurements (mm). Total length (approx.), 6.0 +; carapace and rostrum, 2.5; carapace, 1.8; first pereopod chela, 1.2.

Associated fauna. One small badly damaged hippolytid shrimp, unidentifiable at genus level.

Etymology. From *pluma*, Latin, a feather, and *fero*, Latin, to carry or bear.

Systematic Position. *Bresilia plumifera* is most closely related to the only other Australian species of the genus, *B. antipodarum* Bruce, which it particularly resembles in the presence of the postero-dorsally produced third abdominal segment, a feature not found

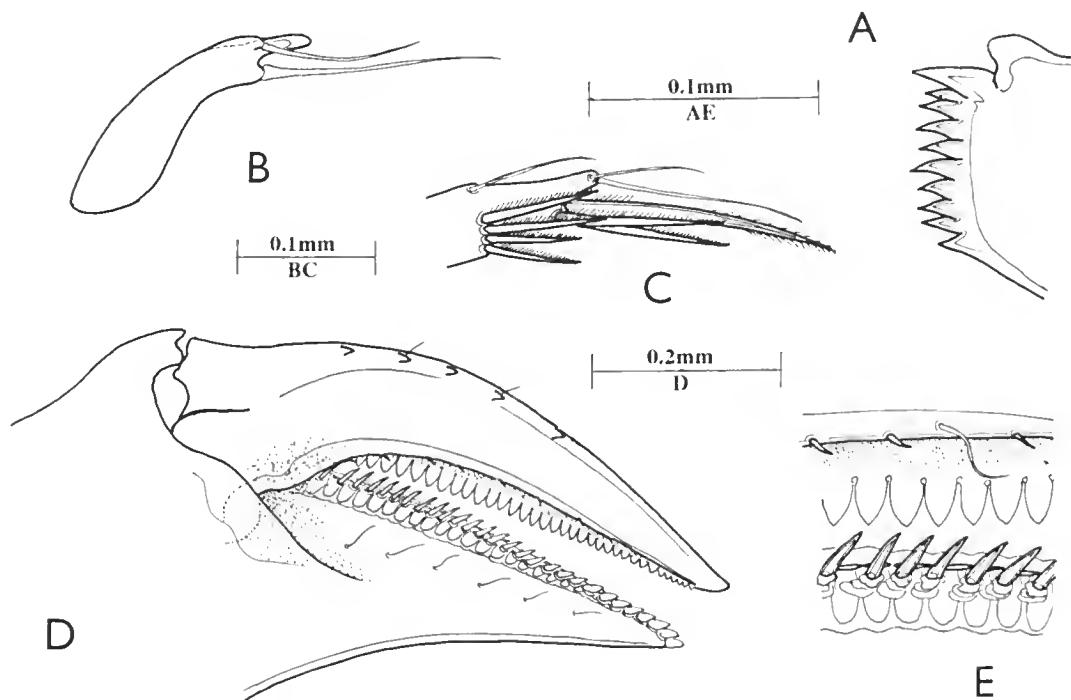


Fig. 4. *Bresilia plumifera* sp. nov., female holotype. A, mandible, incisor process. B, maxillula, palp. C, third maxilliped, tip of distal segment of endopod. D, first pereopod, chela, fingers. E, same, detail of cutting edges.

in the two other species of the genus. *Bresilia plumifera* may be distinguished from *B. antipodarum* by the presence of only four dorsal rostral teeth, with the ventral border of the rostrum unarmed, whereas the latter has nine dorsal rostral teeth and a small ventral tooth. The rostrum is also much shorter in *B. plumifera*, much less than half the carapace length, whereas it is well over half in *B. antipodarum*. *Bresilia antipodarum* also has the antennal tooth and pterygostomial angle more acutely produced than in *B. plumifera* and the posterodorsal enlargement of the third abdominal segment is larger and more compressed. In *B. plumifera* the proximal segment of the antennular peduncle is much broader than in *B. antipodarum*, with the stylocerite stouter, not reaching the level of the distal end of the segment. The mouth parts of the two species are essentially similar, but in *B. plumifera*, the incisor process of the mandible is much broader and more strongly dentate, the molar process more strongly provided with simple teeth and the distal segment of the palp with serrulate spiniform setae; the upper lacinia of the maxillula is also much more strongly dentate. The first pereopods of the two species are remarkably similar, but *B. antipodarum*

lacks the ventral palmar spine present in *B. plumifera*, and the small distodorsal palmar tooth. Also lacking is the distoventral tooth on the ischium. In *B. plumifera* the dorsal margin of the dactylus is carinate, with five small acute teeth, whereas in *B. antipodarum*, this surface is rounded and unarmed.

The features of *B. plumifera* that are without parallel in other species of *Bresilia* so far described, are the medial epistomal process and the long plumose setae on the ischiocrite and the distal antepenultimate segment of the endopod of the third maxilliped.

Both Australian species of *Bresilia* are characterized by the presence of a distinct flagellum on the exopod of the first maxilliped, a character in which they also resemble *Encantada*, and of a distinct posterodorsal carina on the third abdominal segment, features not present in the northern hemisphere species. It is possible that they should be considered as generically distinct, but this is best postponed until such time as intact specimens are available.

DISCUSSION

The posterior thoracic sternites of *Bresilia plumifera* show a great similarity to those of *B.*

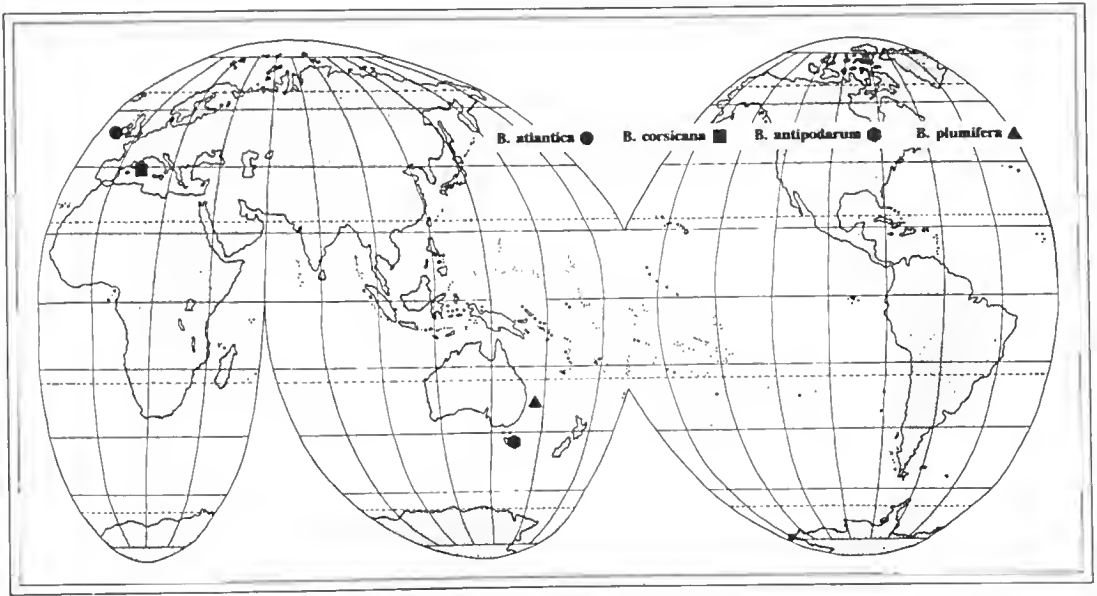


Fig. 5. The distribution of the species of *Bresilia* Calman.

corsicana (Forest and Cals 1977: fig. 20). Forest and Cals (1977) noted that the interpretation of these processes presented difficulties, and this applies equally to *B. plumifera*, at only half the size of *B. corsicana*, and cannot be elucidated further without destroying the unique specimen.

The function of the plumose setae on the antennular ischiocerite and the endopod of the third maxilliped, which probably functions as a complex in association with the median epistomal process, is not readily apparent. Apparently unique to *B. plumifera*, it seems unlikely that these setae would have been overlooked, particularly in the detailed study by Forest and Cals (1977), but it is possible that they could have been lost during capture of the specimens. This could not have happened in the case of the epistomal process.

The four species of the genus *Bresilia* are known only from the holotype specimens, incomplete in the case of *B. antipodarum* and *B. plumifera*. All are small shrimps, with *B. atlantica* the largest, with a total body length of 27 mm and *B. plumifera* the smallest, with a length of about 6 mm. Their small size probably contributes to the paucity of records of these species. Their zoogeography is clearly incompletely known (Fig. 5) and their bathymetric range is now known to extend from 1375 m to 133 m. *Bresilia antipodarum* is also known from the Tasman Sea, off Cape

Freycinet, eastern Tasmania (Bruce 1990). Most of the bresiliiform species of the Bresiliidae are deep-water species and the only other species so far reported from shallow waters is *Encantada spinoculata* Wicksten (1989) from 55-92 m depth.

The four species of *Bresilia* may be distinguished by the following key:

1. Third abdominal segment posterodorsally produced; first maxilliped endopod with flagellum 2
 Third abdominal segment not posterodorsally produced; first maxilliped endopod without flagellum 3
2. First pereopod with posteroventral angle unarmed; posterodorsal process of third abdominal segment compressed; rostrum with nine dorsal and one ventral tooth
 *B. antipodarum* Bruce
 First pereopod with posteroventral angle dentate, dactyl dorsally carinate, dentate; posterodorsal process of third abdominal segment not strongly compressed; rostrum with four dorsal teeth, ventrally unarmed
 *B. plumifera* sp. nov.
3. Posterior margin of telson truncate, with 6-7 pairs of spines *B. atlantica* Calman
 Posterior margin of telson with median notch, with four pairs of spines and four submedian spinules
 *B. corsicana* Forest and Cals

ACKNOWLEDGMENTS

I am most grateful to Dr. J.K. Lowry for the opportunity to examine this specimen from the collections of the Australian Museum.

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RECENT ADDITIONS TO THE PONTONIINE SHRIMP FAUNA OF AUSTRALIA.

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ABSTRACT

Recent additions to the pontoniine shrimp fauna of Australia are reviewed and data are provided on seven species not previously known from Australia: *Onycozaris spinosa* Fujino and Miyake, *Periclimenes mahei* Bruce, *Platypontonia brevirostris* (Miers), *Pontonia stylirostris* Holthuis, *Tuleariocaris holthuisi* Hipeau-Jacquotte, *Vir orientalis* (Dana) and *V. philippinensis* Bruce and Svoboda. Recent nomenclatural amendments are included. The number of species presently known is increased from 136 to 168 and their distributions and zoogeography are discussed.

KEYWORDS: Crustacea: Decapoda: Palaemonidae, Australian fauna, recent additions, new records, zoogeography, Indo-West Pacific.

INTRODUCTION

In 1983, Bruce (1983a) provided a review on the occurrence of 136 species of pontoniine shrimp in the seas around Australia, described up to 1980. Since that publication, three of the species, of the genus *Anchistoides*, have been transferred to the resurrected family Anchistoididae Borradaile, and two species, of *Gnathophylloides*, have been transferred from the family Gnathophyllidae Dana. Two of the species of *Periclimenaeus* have now been placed in separate monospecific genera. In addition, 21 new species of pontoniine shrimp have been described from Australian waters, including four new monospecific genera. Seven species previously recorded from the Indo-West Pacific have also been found in Australian waters, and a further seven species are reported here for the first time. The possible occurrence of *Coralliocaris macrophthalma* (H. Milne-Edwards) has been reported from Heron Island, Queensland (Bruce 1977), but because of its dubious status, it is not considered further in this review. These additions increase the total number of species known from Australia to 168.

Although a rich and diverse fauna is present in the seas around Australia, comparison with other regions is difficult as comparable studies in many areas have not yet been carried out.

Although detailed studies of the Indonesian fauna have been made through the activities of the *Siboga* and *Snellius* expeditions (1899-1900, 1929-1930), these were carried out before the common use of SCUBA equipment. Undoubtedly many of the recently discovered tropical Australian species will be found to also occur in Indonesian waters in due course, probably together with much that is completely new. The pontoniine fauna of the Philippines is not well known, and that of Papua-New Guinea even less. All these areas, with their extensive reef systems, the primary habitat for most pontoniine shrimps, may be expected to have a pontoniine fauna at least as diverse as that of Australia.

The enumeration of species follows the listing given in Bruce (1983a), after adjustment for the alterations mentioned above. Species with numbers represent new records; species without numbers (cited as -) represent nomenclatural changes.

ANNOTATED SPECIES LIST

Genus *Apopontonia* Bruce, 1976

134. *Apopontonia dubia* Bruce, 1981: This species was originally described from a single female specimen from 20m depth at Shag Roek, off North Stradbroke Island, Queensland, collected in 1979 in association with a

sponge, *Ircinia* cf. *echinata* (Keller) (Bruce 1981). It has subsequently reported from Heron Island, Queensland (Bruce 1983f); recently from 43 m depth, off New Caledonia. The genus contains only two other species, *A. falcistrostris* Bruce, known only from the type specimen from 73 m depth off Madagascar, and the following species.

135. *Apopontonia tridentata* Bruce, 1988: A single ovigerous female of this species was collected in 1983 from the Northwest Shelf from 54 m depth at 19° 41.9'S, 117° 57.15E (not 17° 57.15'E, as given in the original description (Bruce 1988b)). There have been no further reports of this species, whose host remains unidentified, but is most probably a sponge.

Genus *Cariopontonia* Bruce, 1988

136. *Carinopontonia paucipes* Bruce, 1988: The only known specimen of this unusual shrimp, unfortunately lacking many of its appendages, was collected from 83 m depth on the Northwest Shelf at 19° 04.4'S, 118° 47.55'E in 1983 (Bruce 1988b). The host of this species is unknown, but it is certainly a commensal species and a coelenterate association seems highly likely.

Genus *Chernocaris* Johnson, 1967

137. *Chernocaris placunae* Johnson, 1967: Twelve specimens were collected in 1981, from *Placuna placenta* from 27 m depth in the Arafura Sea at 12° 58.0'S, 132° 10.0'E (Bruce 1983d). This is only the second recorded occurrence of this species, otherwise known only from Singapore.

Genus *Conchodytes* Peters, 1875

- *Conchodytes kemp* Bruce, 1989e: This species was referred to in the list given by Bruce (1983a) under the name of *C. biunguiculatus* Paulson 1875. There is still doubt as to the distribution of Paulson's species and whether or not it occurs in Australian waters. *Conchodytes kemp* has been reported from the Andaman Islands and the Philippines, and it seems likely that Australian specimens will belong to this species. Further study of *Conchodytes* specimens from pinnid hosts will be necessary before the general distribution of these shrimps can be satisfactorily clarified.

138. *Conchodytes maculatus* Bruce, 1989: A pair of specimens and a single male speci-

men were first collected from pearl oysters, *Pinctada maxima*, from about 40 m depth in the Arafura Sea, at about 16° 33.5'S, 121° 25.75'E in 1985 (Bruce 1989c). There are no other known specimens of this species.

Genus *Dasella* Lebour, 1945

139. *Dasella ansoni* Bruce, 1990d. A male and ovigerous female were found together in an ascidian host, *Phallusia depressiuscula* Heller, from 27 m depth in the Arafura Sea, at 12° 58.0'S, 132° 10.0'E collected in 1981. (Bruce 1983b). No further occurrences have been reported.

- *Dasella brucei* Berggren, 1990: A specimen of this species was initially reported by Bruce (1981a), who recorded a single male in the ascidian *Herdmania momus* from Heron Island, Queensland, as *D. herdmaniae*, from 14 m depth. This species has been recently recognized as a distinct species, so far known from type material only, by Berggren (1990). *Dasella herdmaniae* is known only from southern India and Mozambique.

Genus *Epipontonia* Bruce, 1977

140. *Epipontonia anceps* Bruce, 1983: First described from four specimens from Heron Island, southern Great Barrier Reef from 18 m depth collected in 1979 from a sponge host, *Dysidea* sp. (Bruce 1983c). There have been no further records of this species. The genus contains one other species, *E. spongicola* Bruce, 1977 known only from Kenya.

Genus *Exopontonia* Bruce, 1988

141. *Exopontonia malleatrix* Bruce, 1988: A single ovigerous female specimen of this species was collected from pulverized coral rubble from intertidal reef flat at Ashmore Reef, Timor Sea in 1987 (Bruce 1988a). There are no other records of the species, whose host is unknown, but which may be an associate of sponges.

Genus *Gnathophylloides* Schmitt, 1933

142. *Gnathophylloides mineri* Schmitt, 1933: First recorded in Australian waters from the North Solitary Islands, New South Wales, from 12 m depth, in association with the urchin *Tripneustes gratilla* (L.) collected in 1988 (Bruce 1989a). Originally described from Caribbean specimens, this species is now also known from Malpelo Island, Colombia; Ha-

waii, Tonga, Zanzibar and the Seychelle Islands, and is therefore one of the few Australian shrimps that have a circumtropical distribution. The Australian records also represent the most southerly extent of the distribution of this species.

143. *Gnathophylloides robustus* Bruce, 1973: This species, known only from the type material, a male and three ovigerous females, was found on the sea-urehin, *Centrostephanus tenuispinus* H.L. Clark at 3 m depth off Point Moore, Geraldton, Western Australia (Bruce 1973). There have been no subsequent records of this shrimp.

Genus *Hamopontonia* Bruce, 1970

144. *Hamopontonia essingtoni* Bruce, 1987: Described from 13 specimens from Coral Bay, Port Essington, Cobourg Peninsula, in association with a coral host, *Stylophora pistillata* (Esper) collected in 1985 from 6 m depth (Bruce 1987a). No further records have been reported.

Genus *Miopontonia* Bruce, 1985

145. *Miopontonia yongei* Bruce, 1985: This species is known only from a male and an ovigerous female collected from 40 m and 80 m depth on the Northwest Shelf, by the FRV *Soela* in 1983, from stations at 19° 29.0'S, 118° 52.0'E and 19° 04.3'S, 118° 55.5'E respectively (Bruce 1985). The host animals were not identified but are considered most likely to be gorgonians or antipatharians. The genus *Miopontonia* is monospecific and most closely related to the Caribbean genera *Coutierea* Nobili and *Pseudocoutierea* Holthuis.

Genus *Onycocaridites* Bruce, 1987

146. *Onycocaridites anomodactylus* Bruce, 1987: The type material and only known specimens of this species, a damaged male and female, were obtained from an unidentified sponge from 60 m depth in the Arafura Sea, at 10° 40'S, 133° 50'E in 1986 (Bruce 1987e).

Genus *Onycocaris* Nobili, 1904

147. *Onycocaris spinosa* Fujino and Miyake, 1969: Not previously reported from Australian waters, a male and two ovigerous females were collected from a depth of 10 m depth in a blue sponge on the reef slope off Heron Island, Queensland, in 1980 by R. Boer. Originally described from Yoron-jima,

Ryukyu Islands, and subsequently from Okinawa, there have been no other records of this species.

Genus *Orthopontonia* Bruce, 1982

- *Orthopontonia ornatus* (Bruce, 1969): This species was referred to in the previous report (Bruce 1983a) under the name of *Periclimenaeus ornatus*. *Orthopontonia* is a monospecific genus and *O. ornatus* occurs from East Africa to Australia. The species is an associate of sponge hosts.

Genus *Periclimenaeus* Borradaile, 1915

148. *Periclimenaeus orontes* Bruce, 1987: Known only from a single ovigerous female specimen, collected on Orontes Reef off Port Essington, Cobourg Peninsula, from a sponge host *Jaspis stellifera* (Carter), from a depth of 3 m depth in 1982 (Bruce 1987a). There have been no subsequent records of this shrimp.

149. *Periclimenes agag* Kemp, 1922: Bruce (1990d) recently examined specimens of this species from Lizard Island, Queensland, from baited traps set at Coonut Beach, Watson's Bay and off Eagle Island at 1-17 m depth collected by S. Keable in 1988. There have been no previous records of this species from Australian waters. Originally reported from the Andaman Islands by Kemp (1922), and subsequently from the Red Sea, New Caledonia and the Marshall Islands, the species is probably a free-living micropredator.

150. *Periclimenes alegrias* Bruce, 1987: First found at Coral Bay, Port Essington, Cobourg Peninsula, and subsequently at North-West Vernon Island, this species is known from only four specimens, from 2-4 m and 8 m depth in association with erinoid hosts, *Stephanometra spicata* (Carpenter), *Lamprometra palmata* (Müller) and *Comanthina variabilis* (Bell) (Bruce 1987a). There have been no further reports of this species.

151. *Periclimenes anacanthus* Bruce, 1989: A dozen specimens of this species were first collected from *Zostera* beds in southern Moreton Bay, Queensland, in 1987 (Bruce 1989b). There have been no subsequent reports of this species, which is probably free-living.

152. *Periclimenes andamanensis* Kemp, 1922: Shrimps of a taxon resembling this species were reported from shallow-water sea-grass beds throughout Moreton Bay, Queensland, by Wadley (1978), as *Periclimenes* nr.

andamanensis. Some specimens also referred to this taxon by Wadley, from 3m depth over *Posidonia* beds from the South West Arm, Port Hacking, New South Wales, have also been examined, but unfortunately no second pereopods have been preserved, so the identification can not be fully confirmed.

153. *Periclimenes darwiniensis* Bruce, 1987: First discovered at Weed Reef, Darwin Harbour, Northern Territory, in 1985, this species is now known to be moderately common in intertidal pools in Darwin Harbour (Bruce 1987b) and also occurs in the Gulf of Carpentaria. The species is apparently free-living, and presumably a micropredator.

154. *Periclimenes denticulatus* Nobili, 1906: A single male specimen from Lizard Island, Queensland, lacking both second pereopods, has been referred to this species. The specimen was caught in a trap at 37 m depth (Bruce, 1991a). The species was originally described from Gatawake, Gambier Islands, and subsequently reported only from the Tuamotu and Marshall Islands and the northern South China Sea.

- *Periclimenes goniopora* Bruce, 1989d: This species was included as a *nomen nudum* in Bruce (1983a). A description of this species has been recently published, thereby validating the use of this name (Bruce 1989d). *Periclimenes goniopora* is an associate of *Lobophyllia* and scleractinian corals (*Goniopora*, *Galaxea*, *Porites* and *Montipora*).

155. *Periclimenes franklini* Bruce, 1990b: A deep-water species, collected from about 300 m, at 17° 21'S, 146° 48.52'E in the Coral Sea in 1986. This species, whose host has not been identified, is thought to be probably a gorgonian associate (Bruce 1990b).

156. *Periclimenes laccadivensis* (Aleoek and Anderson, 1894): A single female specimen has recently been caught at 720 m depth off Cape Freycinet, Tasmania (Bruce 1991a), and represents one of the few deep-water and southerly components of the Australian pontonine fauna. Previously recorded from the Laccadive Islands, South China Sea, and off Hawaii, it is the most southerly occurrence of a pontonine shrimp with an otherwise Indo-West Pacific distribution. The species is possibly associated with gorgonians.

157. *Periclimenes* sp. nov. a - Bruce, 1991a: A single specimen of a new species has been recorded (currently in press) from a trap at

23 m depth from Chinaman's Ridge, Watson's Bay, Lizard Island, Queensland (Bruce 1991a). This species is known only from a single occurrence, and is thought to be of free-living habits.

158. *Periclimenes mabei* Bruce, 1969: Not previously reported from Australian seas, numerous specimens including ovigerous females were collected from a colony of *Pocillopora danicornis* from Point Quobba, Western Australia, in 1980. This species has been previously recorded only from the Seychelle Islands, Comoro Islands and Zanzibar.

159. *Periclimenes* sp. nov. b - Bruce, 1991a: This species (in press) known only from the holotype specimen collected in a trap at 3.5 m depth at Blue Lagoon, Lizard Island, Queensland (Bruce 1991a). It is probably a commensal species, possibly associated with echinoderms (echinoids?).

160. *Periclimenes venustus* Bruce, 1990d: Numerous examples of this species were collected from Port Essington, Cobourg Peninsula in 1985, mainly from unidentified anemones, but with two lots from *Heliofungia actiniformis*, mostly from unrecorded depths, but some from 2.5 - 3 m depth (Bruce 1991b). Except for its colour pattern, this species is closely similar to *P. holthuisi* Bruce, and it is likely that some of the specimens previously identified as *P. holthuisi*, particularly where the original colour patterns were not recorded, will prove to belong to *P. venustus* on re-examination. *Periclimenes venustus* is also known from Scott Reef, Western Australia and the Philippines (Bruce 1989e).

161. *Periclimenes yaldwyni* Holthuis, 1959: Known only at present from one male and three ovigerous females collected in 1983 from 16-28m depth in Mercury Passage, off Maria Island, Tasmania (Bruce and Kropp 1984). This species was first described from New Zealand material (as *Brachycarpus audouini* Bate 1888), and is one of the small number of carideans occurring in both southern Australian and New Zealand waters.

Genus *Periclimenoides* Bruce, 1990c

- *Periclimenoides odontodactylus* (Fujino and Miyake, 1968): This species was referred to in the species list given by Bruce (1983a) under the name of *Periclimenaeus odontodactylus*. The genus is monospecific, and *P. odontodactylus* has been reported from Japan,

Hong Kong and Australian waters only, in association with sponge hosts, (Bruce 1990c).

Genus *Platypontonia* Bruce, 1968

162. *Platypontonia brevirostris* (Miers, 1884): This species has not been recorded previously from Australian waters. A pair of specimens were collected by R. Boer from a specimen of *Lopha cristigalli* from 20 m depth on the reef slope of Heron Island, Queensland in 1980. This species was first described from specimens from the Seychelle Islands, collected by the H.M.S. *Alert* Expedition (1882), with further material subsequently also collected from the Seychelle Islands. There have been no reports of the species from other localities.

Genus *Pontonia* Costa, 1844

163. *Pontonia stylirostris* Holthius, 1952: This species has not been previously recorded from Australian waters. A single incomplete male specimen, with the characteristic rostrum and minor second pereopod, was found amongst coral rubble from 42 m depth off Townsville, Queensland, at 18° 42'S., 147° 1.0'E by R.A. Birtles in 1979. This species has only been previously reported from Indonesia, between Misool and New Guinea, at 32 m depth, and from Tanganyika and Oman. Its associations have not been identified, but are likely to be ascidians.

Genus *Tuleariocaris* Hipeau-Jacquotte, 1965

164. *Tuleariocaris holthuisi* Hipeau-Jacquotte 1965: Not previously recorded from Australian waters, a pair of specimens were found on *Diadema setosum* Leske, at Myora Light, North Stradbroke Island, at 0.5 m depth in September 1967.

Genus *Typton* Costa, 1844

165. *Typton dimorphus* Bruce, 1986: A male and ovigerous female, collected from coral rubble, although not necessarily a natural pair, were found in a sample from 5 m depth on Ashmore Reef, Timor Sea, at 12° 15.0'S, 123° 00.0'E in 1984 (Bruce 1986). No other specimens are known. Like other *Typton* species, *T. dimorphus* is likely also to be a sponge associate.

166. *Typton nanus* Bruce, 1988: *Typton nanus* is known only from the female holotype specimen, collected in 1985, from 40-46 m

depth on the Northwest Shelf (Bruce 1987c). Its host remains unidentified, but is presumably a sponge. This shrimp is one of the smallest pontiniine shrimps known, with a postorbital carapace length of only about 1.0 mm.

Genus *Vir* Holthius, 1952

167. *Vir orientalis* (Dana, 1852): A single example of this species, the first recorded from Australian waters, was collected by N. Coleman in 1979 from 10 m depth from Osprey Reef, Coral Sea, from an unidentified coral host. The species was first described from the Sulu Sea and was subsequently reported from Kenya, Zanzibar, Seychelle Islands, Andaman Islands, Mariana Islands and the South China Sea.

168. *Vir philippinensis* Bruce and Svoboda, 1984: This species has not been recorded previously from Australian waters. Two specimens were collected from *Pleurogyra sinuosa* from 8 m depth by J.E.N. Veron, from Fitzroy Reef, Queensland, in 1980. A further specimen was collected by T. Fromm, from *Euphyllia* sp., off Lizard Island, Queensland, in 1987. The species was first described from specimens from Cebu, Philippine Islands, and it has since been reported from Okinawa, Ryukyu Islands.

DISCUSSION

At present, 168 species of pontiniine shrimp, of 46 different genera, are known to occur in Australian waters. Four of these genera, all monospecific, are not yet known to occur outside Australian seas. Of the remaining 42 genera, 17 are also monospecific. As some 308 species have been reported from the Indo-West Pacific region as a whole, about half (54.2%) may be found in Australian waters, and 86% of the known genera are also represented in the Australian fauna.

Of the 168 Australian species, 141 occur on the eastern seaboard, with 49 on the northern and western, and only 6 on the southern coasts. The high figure for the eastern coasts is probably a reflection of the presence of the Great Barrier Reef combined with the increased scientific collecting effort that it has attracted over many years. Only one species, *Anchistus custos*, an associate of pinnid molluscs, occurs in all three regions. Twenty-four species (14.3%) have so far been found to occur in both eastern and north-western regions. Con-

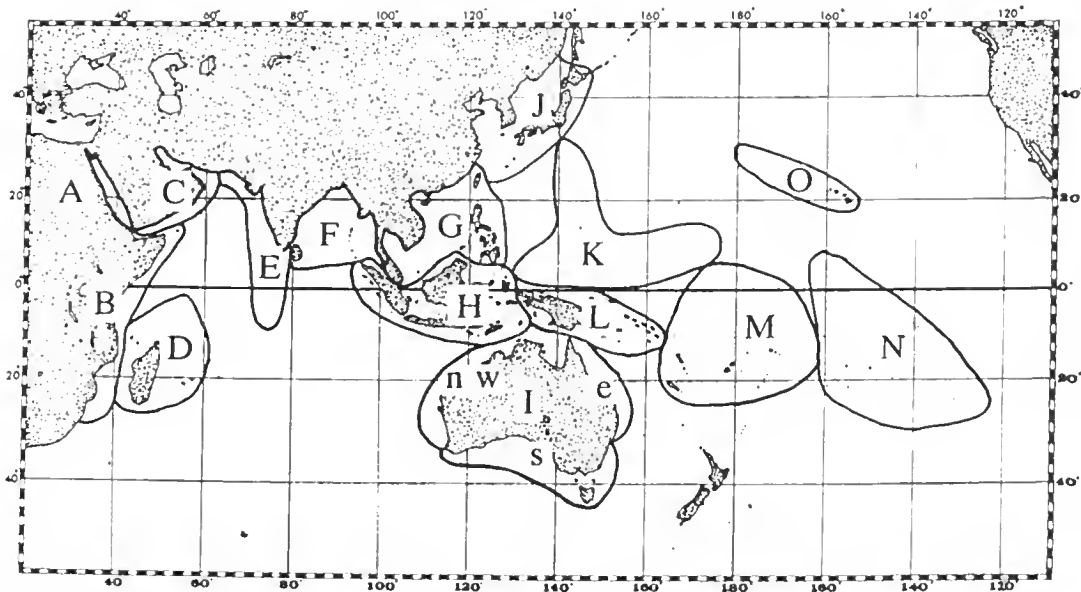


Fig. 1. Subdivision of Indo-Pacific zoogeographic zones, relating to areas described in Table I. A. Red Sea. B. East Africa. C. Southern Arabia, Arabian Gulf, Gulf of Oman. D. Madagascar, Comoro, Mascarene and Seychelle Islands. E. Western Indian peninsula, Maldiva, Laccadive and Chagos Islands. F. Sri Lanka, Bay of Bengal, Andaman and Nicobar Islands, Burma. G. Malaya, South China Sea, Taiwan, Philippines. H. Indonesia. I. Australia (e, eastern; nw, north-western; s, southern). J. east China, Japan, Ryukyu Islands, Korea. K. Marshall, Caroline and Marianas Islands. L. Papua New Guinea. M. New Caledonia, Fiji, Vanuatu, Tonga, Kiribati, Tuvalu, Samoan and Phoenix Islands. N. Tokelau, Cook, Line, Society, Austral, Tuamotu and Marquesas Islands. O. Hawaiian Islands. P. Eastern Pacific region.

versely, 115 species (168%), including 13 "endemics" (7.7%), are known from the eastern coasts only and 23 species, including 18 "endemics", occur only on the north-western coasts.

Many of the Australian species belong to taxa with very wide Indo-West Pacific distributions. Thirty two species are also known from the Red Sea, while 80 (48.2%) species are known from the east coast of Africa, with 82 (49.4%) from the combined Red Sea-East African region. The central East African region, principally Kenya and Tanzania, has a pontonine shrimp fauna of 134 species (Bruce 1976), of which 80 species (60%) have so far been found to occur around Australia. The pontonine fauna of the Pacific Ocean has not yet been adequately examined. The faunas of the extensive reef systems and deeper waters have not yet been generally studied in detail, except in the region of New Caledonia. Diversity appears to decrease in an easterly direction and only 19 species found in Australian waters occur also in the eastern parts of the Indo-West Pacific region (Fig. 1, zones N,O,) but several Indo-West Pacific species have ranges that extend to the eastern American

seaboard. Of the species presently known to do so, six occur in Australian waters (*Alloponotonia iaini*, *Fennera chacei*, *Gnathophylloides mineri*, *Harpiliopsis depressa*, *H. spinigera* and *Periclimenes soror*). These species, which are all commensal associates of other marine invertebrates, also occur in East African waters and therefore have ranges that extend across the whole Indo-Pacific region, but only *G. mineri* has so far been found in the Atlantic region, although *Palaemonella rotumana* has now extended its range through the Suez Canal into the eastern Mediterranean Sea (Holthuis and Gottlieb 1958). No free-living Indo-West Pacific species have yet been reported from the Eastern Pacific region.

As the pontonine shrimp faunas of Indonesia and New Caledonia have been studied in more detail than many of the adjacent regions, they may be conveniently compared with the fauna of Australia, although all must still be considered incompletely known. Such are the vagaries of field collections that even such an abundant and widely distributed species as *Periclimenes spiniferus* has not yet been formally recorded from New Caledonia, although it is inconceivable that it is absent from the

coral reefs there. The almost equally common *Harpiliopsis beaupresii* has also apparently not been collected. As further collecting is carried out, it is expected that the overlap between the faunas will increase, although all regions may be expected to have some indigenous species. At present, 204 species are known from the combined faunas of Indonesia, Australia and New Caledonia, about two-thirds of the number of species occurring in the whole Indo-West Pacific region, with 87 species from Indonesia (Holthuis 1952; Bruce 1983e; Fransen 1989) and 67 from New Caledonia (Bruce 1990a, 1991b). Eighty-seven of the 168 species found in Australia (49%) are also found in Indonesia or adjacent parts of Papua-New Guinea. The Siboga-Snellius collections in Indonesian waters and more recent collections in New Caledonian waters have indicated that a number of pontiniine shrimp occur in depths of over 100 m. These species are particularly poorly represented in the Australian fauna due to lack of deep-water sampling. At present only *Periclimenes alcocki*, *P. franklini*, *P. hertwigi*, *P. laccadivensis* and *Mesopontonia gorgonicola* are known from these depths, 2.8% of the Australian fauna, with *P. laccadivensis* reaching the greatest depth at about 720 m. In Indonesia, only four species occur in 100 m or over, representing 3.4 % of the pontiniine fauna but nine species, 15%, of the New Caledonian fauna have been found in these depths.

Of the 33 species that are presently known only from Australian waters, it is difficult to consider that many of these are truly endemic, that is, with a distribution limited to Aus-

tralian waters. Due to the small size and cryptic behaviour of most of species, it is probable that many have so far been merely overlooked in other parts of the Indo-West Pacific region. This applies particularly to the recently described taxa from the northern and eastern coasts of Australia, which seem highly likely to be components of the general Indo-West Pacific marine fauna. Species recently described from the Great Barrier Reef have already been found as far away as the Ryukyu Islands (*Periclimenes magnificus*: Bruce 1979; Nomura *et al.* 1988). Species from the south are more likely to be truly endemic and possibly members of an earlier marine Gondwana fauna. Species such as *Periclimenes aesopius*, the first pontiniine shrimp to be described from Australian waters (Bate 1863), is still only known from St Vincent Gulf, South Australia. It seems probable that it is restricted to this region, and may be a true relict. Another candidate as an endemic species is *Pontonia minuta*, first described by Baker (1907) from a single specimen from an unrecorded host, with a further occurrence at Meroo Point, New South Wales, indicating a rather less restricted distribution than *P. aesopius*. *Periclimenes aesopius* is a conspicuous associate of anemones. *Pontonia minuta* is undoubtedly a commensal species but probably not a true *Pontonia s. str.*, and its host remains to be identified; polychaete worms have been suggested. Once the host has been identified, the distribution of *P. minuta*, which is probably dependent on that of its host and closely related species, may be rapidly clarified.

Table 1. The Indo-West Pacific distributions of the Australian pontiniine shrimp fauna (+ = species present; O = species presently known only from Australian waters; ? = uncertain record)

SPECIES	LOCALITY															
	A	B	C	D	E	F	G	H	I nw e s	J	K	L	M	N	O	P
1. <i>Allopontonia iaini</i>	.	+	+	+
2. <i>Anapontonia denticauda</i>	.	+	.	+	.	.	.	+	.	+
3. <i>Anchistus australis</i>	+
4. <i>Anchistus custoides</i>	+
5. <i>Anchistus custos</i>	+	+	+	+	+	+	+	+	+	+
6. <i>Anchistus demani</i>	.	+	.	+	.	+	.	.	.	+
7. <i>Anchistus gravieri</i>	+
8. <i>Anchistus miersi</i>	+	+	.	+	+	+	+	+	.	+
9. <i>Anchistus pectinis</i>	.	+	.	.	.	+	.	.	.	+
10. <i>Apopontonia dubia</i>	+
11. <i>Apopontonia falcirostris</i>	.	.	.	+	+
12. <i>Apopontonia tridentata</i>	O
13. <i>Carinopontonia paucipes</i>	O
14. <i>Chernocaris placunae</i>	+	.	.	+
15. <i>Conchodytes kempii</i>	+	.	+	.	+
16. <i>Conchodytes maculatus</i>	O
17. <i>Conchodytes meleagrinae</i>	+	+	+	+	+	+	+	.	.	+	+	+	+	+	+	.

SPECIES	LOCALITY															
	A	B	C	D	E	F	G	H	I nw e s	J	K	L	M	N	O	P
18. <i>Conchodytes monodactylus</i>	+	+	+	+
19. <i>Conchodytes nipponensis</i>
20. <i>Conchodytes tridacnae</i>	+	+	.	+	+	+	+	+	+	.	+	+
21. <i>Coralliocaris brevirostris</i>
22. <i>Coralliocaris graminea</i>	+	+	.	+	.	+	+	+	+	+	+	+	.	.	.	+
23. <i>Coralliocaris superha</i>	+	+	.	+	+	+	+	+	+	+	+	+	.	+	.	.
24. <i>Coralliocaris venusta</i>	+	+	.	.	+	.	+	+	.	+	+	+
25. <i>Coralliocaris viridis</i>	.	+	.	.	+	+	.	+	.	+
26. <i>Dasella ansoni</i>	O
27. <i>Dasella hrucei</i>	O
28. <i>Dasycares ceratops</i>	.	+	+	.	+
29. <i>Dasycares zanzibarica</i>	.	+	+	.	.	.	+	.	.
30. <i>Epipontonia anceps</i>	O
31. <i>Exopontonia malleatrix</i>	O
32. <i>Fennera chacei</i>	.	+	.	+	+	+
33. <i>Gnathophylloides mneri</i>	.	+	.	+	+	+	+
34. <i>Gnathophylloides rabustus</i>	O	+	.	+
35. <i>Hamodactyloides incompletus</i>	+	+	.	+	+
36. <i>Hamodactylus aqahai</i>	+	+
37. <i>Hamodactylus buschmai</i>	.	+	.	+	.	.	.	+	+	+
38. <i>Hamodactylus noumeae</i>	.	+	+	+	+	.	.	.	+	.	.
39. <i>Hamopontonia corallicola</i>	+	+	+
40. <i>Hamopontonia essingtoni</i>	O
41. <i>Harpilopsis heaupresii</i>	+	+	+	+	+	+	+	+	.	+	.	+	.	.	.	+
42. <i>Harpilopsis depressa</i>	+	+	+	+	+	+	+	+	.	+	.	+	.	.	.	+
43. <i>Harpilopsis spinigera</i>	.	+	.	+	+	+	.	+	.	+	.	+	.	.	.	+
44. <i>Ischnopontonia lophos</i>	.	+	.	+	.	.	.	+	.	+	.	+
45. <i>Jocaste japonica</i>	+	+	+	+	+	.	.	+	.	+	.	+
46. <i>Jocaste lucina</i>	+	+	+	+	+	+	+	+	.	+	.	+	+	+	+	+
47. <i>Mesopontonia gorgoniophila</i>	+	.	+
48. <i>Miopontonia yongei</i>	O
49. <i>Onyccaridella monodoa</i>	.	.	.	+	+	.	+
50. <i>Onyccaridella prima</i>	O
51. <i>Onyccaridites anomodactylus</i>	+	.	+
52. <i>Onyccaridites amakusensis</i>	.	+	+
53. <i>Onyccaridites oligodentata</i>	+
54. <i>Onyccaridites quadratophthalma</i>	+	.	+	.	+	.	.	.	+
55. <i>Onyccaridites spinosa</i>	+
56. <i>Orthopontonia ornata</i>	.	+	+
57. <i>Palaemonella pottsi</i>	.	+	+	+	+	.	+	.	+	.	.
58. <i>Palaemonella rotumana</i>	+	+	+	+	+	+	+	+	+	+	.	+	+	+	.	+
59. <i>Palaemonella spinulata</i>	.	+	.	+	+	.	+
60. <i>Paranchistus armatus</i>	+	.	.	.	+	+	.	.	.
61. <i>Paranchistus pycnodontae</i>	O
62. <i>Parapontonia nudirostris</i>
63. <i>Paratypton siehenrocki</i>	+	+	.	+	.	.	.	+	.	+	.	+
64. <i>Periclimenaeus arabicus</i>	.	+	+	.	+	+	.	.	.	+	.	+
65. <i>Periclimenaeus ardeae</i>	.	+	+
66. <i>Periclimenaeus bidentatus</i>	+	+	+	.	.	+	.	.	.
67. <i>Periclimenaeus diplosomatus</i>	+
68. <i>Periclimenaeus djiboutensis</i>	+	+	.	+	O
69. <i>Periclimenaeus gorgonidarum</i>	+
70. <i>Periclimenaeus hecate</i>	.	+	+	+	+	.	.	+	.	+
71. <i>Periclimenaeus orbitospinatus</i>	O
72. <i>Periclimenaeus orontes</i>	O
73. <i>Periclimenaeus pachydentatus</i>	O
74. <i>Periclimenaeus rasterifer</i>	+	.	+	.	.	.	+	.	.
75. <i>Periclimenaeus rhadope</i>	.	+	+	+
76. <i>Periclimenaeus tridentatus</i>	.	+	+	.	+	+
77. <i>Periclimenaeus tuomotae</i>	.	+	+
78. <i>Periclimenaeus aesiopus</i>	O
79. <i>Periclimenaeus affinis</i>	+	+	.	?	.	.	+	.	.
80. <i>Periclimenaeus agag</i>	+	+	.	.	.	+	.	.	.	+	.	.
81. <i>Periclimenaeus alcocki</i>	.	.	.	+	+	.	+	.	.	+	.	.	.	+	.	.
82. <i>Periclimenaeus aegyptus</i>	O
83. <i>Periclimenaeus ambatensis</i>	+
84. <i>Periclimenaeus amymone</i>	+	+	.	.	+	.	.	+	+	.	.
85. <i>Periclimenaeus anacanthus</i>	O
86. <i>Periclimenaeus andamanensis</i>	.	.	.	+	.	+	.	.	.	+
87. <i>Periclimenaeus attenuatus</i>	+	.	+
88. <i>Periclimenaeus brevicarpalis</i>	+	+	+	+	+	+	+	+	+	+	.	+	+	+	.	.
89. <i>Periclimenaeus brockettii</i>	+	+
90. <i>Periclimenaeus cf. calmani</i>	+
91. <i>Periclimenaeus carinidactylus</i>	O
92. <i>Periclimenaeus ceratophthalmus</i>	.	+	.	+	+	.	.	+	.	+	.	+
93. <i>Periclimenaeus colemani</i>	O

Additions to Pontiniine shrimp fauna

SPECIES	LOCALITY															
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
									nw	e	s					
94. <i>Periclimenes commensalis</i>	.	+	.	+	.	.	+	+	.	+	.	+	+	.	.	.
95. <i>Periclimenes consobrinus</i>	.	+	.	+	.	.	.	+	.	+
96. <i>Periclimenes cornutus</i>	+	.	.	+	.	+
97. <i>Periclimenes cristimanus</i>	+	.	+
98. <i>Periclimenes darwiniensis</i>	O
99. <i>Periclimenes denticulatus</i>	+	.	+	.	+	.	.
100. <i>Periclimenes diversipes</i>	+	+	+	+	+	+	+	.	+	+
101. <i>Periclimenes elegans</i>	+	+	+	+	+	+	+	+	+	+	.	+
102. <i>Periclimenes franklini</i>	O
103. <i>Periclimenes galene</i>	.	+	+	.	+
104. <i>Periclimenes gonoporae</i>	.	+	.	+	+
105. <i>Periclimenes granulimanus</i>	.	.	.	+	+
106. <i>Periclimenes hertwigi</i>	+	.	+	.	.	.	+	.	.
107. <i>Periclimenes holthuisi</i>	+	+	.	+	+	+	+	+	+	+	.	+	+	+	.	.
108. <i>Periclimenes imperator</i>	+	+	.	+	+	.	+	+	.	.	.
109. <i>Periclimenes incertus</i>	.	+	+	+	+	+	+	+	+	+	.	+	+	.	.	.
110. <i>Periclimenes indicus</i>	+	+	+	.	+
111. <i>Periclimenes inornatus</i>	.	+	.	+	+	+	+	+	.	+	.	+	+	.	.	.
112. <i>Periclimenes investigatoris</i>	.	.	+	+	.	+
113. <i>Periclimenes kempfi</i>	+	+	.	.	.	+	+	+	+	+	.	.	.	+	.	.
114. <i>Periclimenes kororensis</i>	+	.	+	.	+
115. <i>Periclimenes laccadivensis</i>	+	.	.	+	.	+	+
116. <i>Periclimenes</i> sp. nov. a	O
117. <i>Periclimenes lanipes</i>	.	+	.	+	.	+	+	+	.	+	.	.	.	+	.	.
118. <i>Periclimenes longirostris</i>	+	+	.	+	+	+	+	+	.	+	.	.	+	+	.	.
119. <i>Periclimenes lutescens</i>	+	+	.	+	+	+	+	+	.	+	.	+	+	+	?	.
120. <i>Periclimenes madreporae</i>	.	.	.	+	+	.	+	+	.	.	.
121. <i>Periclimenes magnificus</i>	+	+	+	.	+
122. <i>Periclimenes mahei</i>	.	+	.	+	+	+
123. <i>Periclimenes nilandensis</i>	.	+	.	+	+	.	.	+	+	+	.	.	.	+	.	.
124. <i>Periclimenes ornatellus</i>	+	.	+
125. <i>Periclimenes ornatus</i>	+	+	+	+	+	.	+
126. <i>Periclimenes pectiniferus</i>	+	.	+
127. <i>Periclimenes platycheles</i>	+	.	+	.	.	+	+	.	.
128. <i>Periclimenes</i> sp. nov. b	O
129. <i>Periclimenes psamathe</i>	.	+	.	+	+	+	+	+	.	+	.	+	+	+	.	.
130. <i>Periclimenes ruber</i>	O
131. <i>Periclimenes seychellensis</i>	+	+	+	+	+	+	+	+	.	+	.	+	+	+	.	.
132. <i>Periclimenes soror</i>	+	+	+	+	+	+	+	+	.	+	.	+	+	+	+	+
133. <i>Periclimenes spiniferus</i>	.	.	.	+	+	+	+	+	+	+	.	+	+	+	+	+
134. <i>Periclimenes tenuipes</i>	+	+	.	+	+	+	.	.	+	+	.	+	+	+	+	+
135. <i>Periclimenes tenuis</i>	+	.	+	.	+	+	.	.	.
136. <i>Periclimenes toloensis</i>	.	+	+	.	+
137. <i>Periclimenes venustus</i>	+	.	+	.	?
138. <i>Periclimenes yaldwyni</i>	+
139. <i>Periclimenes zanzibaricus</i>	.	+	.	+	+
140. <i>Periclimenoides odontodactylus</i>	+	.	+	.	+
141. <i>Phylarius gerralchei</i>	+	+	+	+	+	+	+	+	.	+	.	+	+	+	+	+
142. <i>Phylarius imperialis</i>	+	+	.	+	.	.	.	+	+	+	.	+	+	.	.	.
143. <i>Phylarius lifuensis</i>	+	.	.	.	+	.	.
144. <i>Platycaris latirostris</i>	.	+	.	+	.	.	.	+	+	.	.	+	+	.	.	.
145. <i>Platypontonia brevirostris</i>	+
146. <i>Platypontonia furtiva</i>	.	+	+	+	.	.	+	.	+	.	.
147. <i>Pontonia ardeae</i>	O
148. <i>Pontonia katoi</i>	.	+	+	+	+	.	+	.	+	.	.
149. <i>Pontonia minuta</i>	O	O
150. <i>Pontonia okui</i>	.	+	+	.	.	+	+	+	.	+
151. <i>Pontonia sibogae</i>	.	.	+	+	.	.	.	+	.	+
152. <i>Pontonia stylirostris</i>	.	+	+	+
153. <i>Pontonides</i> sp.	+	+	.	+	+	.	+	.	.	+	.
154. <i>Pontoniopsis comanthi</i>	+	+	.	+	.	.	.	+	.	+	.	+	.	+	.	.
155. <i>Propontonia pellucida</i>	.	+	+
156. <i>Stegopontonia commensalis</i>	.	+	.	+	+	.	+	.	.	+	.
157. <i>Thaumastocaris streptopus</i>	+	+	.	+	.	.	.	+	+	.	+	+
158. <i>Tuleariocaris holthuisi</i>	.	+	.	+	+	+
159. <i>Typton anomalus</i>	O
160. <i>Typton australis</i>	O
161. <i>Typton bawii</i>	.	+	+
162. <i>Typton dentatus</i>	+	.	+
163. <i>Typton dimorphus</i>	O
164. <i>Typton nanus</i>	O
165. <i>Typton wasini</i>	.	+	.	+	+
166. <i>Vir orientalis</i>	.	+	.	+	.	+	+	+	.	+	.	+	.	.	.	+
167. <i>Vir philippinensis</i>	+	.	.	+
168. <i>Zenopontonia noverca</i>	.	+	.	+	+	.	.	.	+	.	.

Table 2. The pontonine shrimp faunae of Indonesia (I), Australia (A) and New Caledonia (NC). (+ = species present; O = not yet known outside designated areas; X = species occurring in depths of more than 100 m)

SPECIES	LOCALITY			SPECIES	LOCALITY		
	I.	A.	NC		I.	A.	NC
1. <i>Allapontonia iaini</i> Bruce, 1972	-	+	-	79. <i>P. diplosomatis</i> Bruce, 1980	-	O	-
2. <i>Altopontonia disparostris</i> Bruce, 1990	-	-	+	80. <i>P. djiboutensis</i> Bruce, 1970	-	+	-
3. <i>Anapontonia denticauda</i> Bruce, 1966	-	-	+	81. <i>P. gorgonidurum</i> (Bals., 1913)	-	+	-
4. <i>Anchistus australis</i> Bruce, 1977	+	+	+	82. <i>P. hecate</i> (Nobili, 1904)	+	+	-
5. <i>A. custoides</i> Bruce, 1977	+	+	-	83. <i>P. holthuisi</i> Bruce, 1969	O	-	-
6. <i>A. custos</i> (Forskål, 1775)	+	+	-	84. <i>P. minutus</i> Holthuis, 1952	+	-	-
7. <i>A. demani</i> Kemp, 1922	+	+	+	85. <i>P. nobilii</i> Bruce, 1974	+	-	-
8. <i>A. gravieri</i> Kemp, 1922	-	+	+	86. <i>P. orbitospinatus</i> Bruce, 1969	-	O	-
9. <i>A. miersi</i> (De Man, 1888)	+	+	+	87. <i>P. arontes</i> Bruce, 1986	-	O	-
10. <i>A. pectins</i> Kemp, 1925	-	+	+	88. <i>P. pachydentatus</i> Bruce, 1969	-	O	-
11. <i>Apopontonia dubia</i> Bruce, 1981	-	+	+	89. <i>P. rustriifer</i> Bruce, 1980	-	+	+
12. <i>A. falcicastris</i> Bruce, 1977	-	+	-	90. <i>P. rhodope</i> (Nobili, 1904)	-	+	-
13. <i>A. tridentata</i> Bruce, 1988	-	O	-	91. <i>P. spongicola</i> Holthuis, 1952	O	-	-
14. <i>Araopontonia odontorhyncha</i> Fujino and Miyake, 1970	+	+	+	92. <i>P. tridentatus</i> (Miers, 1884)	+	+	-
15. <i>Carinopontonia paucipies</i> Bruce, 1988	-	O	-	93. <i>P. truncatus</i> (Rathbun, 1906)	+	-	-
16. <i>Chernocaris placunae</i> Johnson, 1967	-	+	-	94. <i>P. tuamotae</i> Bruce, 1969	-	+	-
17. <i>Conchodytes kempii</i> Bruce, 1989	+	+	-	95. <i>Periclimenes aescopus</i> (Bate, 1863)	-	O	-
18. <i>C. maculatus</i> Bruce, 1989	-	O	-	96. <i>P. affinis</i> (Zehntner, 1894)	-	+	+
19. <i>C. meleagrinae</i> Peters, 1852	+	+	+	97. <i>P. agag</i> Kemp, 1922	-	+	+
20. <i>C. monodactylus</i> Holthuis, 1952	+	+	-	98. <i>P. alcocki</i> Kemp, 1922	-	O	-
21. <i>C. nipponensis</i> (De Haan, 1844)	-	+	-	99. <i>P. alegrais</i> Bruce, 1986	-	+	-
22. <i>C. tridacne</i> Peters, 1852	+	+	+	100. <i>P. amboinensis</i> (De Man, 1888)	+	+	+
23. <i>Corulliocaris brevis</i> Borradaile, 1898	-	+	-	101. <i>P. amyana</i> De Man, 1902	+	+	+
24. <i>C. graminea</i> (Dana, 1852)	+	+	+	102. <i>P. anacanthus</i> Bruce, 1989	-	O	-
25. <i>C. superba</i> (Dana, 1852)	+	+	+	103. <i>P. undamauensis</i> Kemp, 1922	+	+	-
26. <i>C. venusta</i> Kemp, 1922	+	+	-	104. <i>P. attenuatus</i> Bruce, 1971	+	+	-
27. <i>C. viridis</i> Bruce, 1974	+	+	-	105. <i>P. brevicarpalis</i> (Schenkel, 1902)	+	+	+
28. <i>Dasella ansoni</i> Bruce, 1983	-	O	-	106. <i>P. brockettii</i> Borradaile, 1915	-	+	-
29. <i>D. brucei</i> Berggren, 1990	-	O	-	107. <i>P. brocki</i> (De Man, 1888)	O	-	-
30. <i>Dasycares ceratops</i> Holthuis, 1952	+	O	-	108. <i>P. calmani</i> Tattersall, 1921	+	-	-
31. <i>D. symbiatus</i> Kemp, 1922	-	-	+	109. <i>P. carinidactylus</i> Bruce, 1969	-	O	-
32. <i>D. zanzibarica</i> Bruce, 1973	-	-	+	110. <i>P. veratophthalmus</i> Borradaile, 1915	+	+	-
33. <i>Epipontonia unceps</i> Bruce, 1983	-	O	-	111. <i>P. colemani</i> Bruce, 1975	-	O	-
34. <i>Exopontonia malleatrix</i> Bruce, 1987	-	O	-	112. <i>P. commensalis</i> Borradaile, 1915	+	+	+
35. <i>Fennera chacei</i> Holthuis, 1951	-	+	-	113. <i>P. consobrinus</i> (De Man, 1902)	-	+	-
36. <i>Gnathaphylloides mueri</i> Schmitt, 1933	-	+	-	114. <i>P. cornutus</i> Borradaile, 1915	-	+	-
37. <i>G. robustus</i> Bruce 1973	-	O	-	115. <i>P. cristimanus</i> Bruce, 1965	-	+	-
38. <i>Hamodactylodes incampletus</i> (Holthuis, 1953)	+	+	-	116. <i>P. darwiniensis</i> Bruce, 1987	-	O	-
39. <i>Hamodactylus aqaba</i> Bruce and Svoboda, 1983	-	+	-	117. <i>P. denticulatus</i> Nobili, 1906	-	+	-
40. <i>H. boschmai</i> Holthuis, 1952	+	+	+	118. <i>P. digitalis</i> Kemp, 1922	+	-	-
41. <i>H. noumeae</i> Bruce, 1970	-	+	+	119. <i>P. diversipes</i> Kemp, 1922	-	+	-
42. <i>Hamopontonia corallicola</i> , Bruce, 1970	+	+	-	120. <i>P. elegans</i> (Paulson, 1875)	+	+	-
43. <i>H. essingtoni</i> Bruce, 1986	-	O	-	121. <i>P. franklini</i> Bruce, 1990	-	xO	-
44. <i>Harpilopsis beaupresii</i> (Audouin, 1825)	+	+	-	122. <i>P. fujinoi</i> Bruce, 1990	-	+	xO
45. <i>H. depressa</i> (Stimpson, 1860)	+	+	+	123. <i>P. galene</i> Holthuis, 1952	+	+	-
46. <i>H. spinigeru</i> (Ortmann, 1890)	+	+	+	124. <i>P. gomporoe</i> Bruce, 1990	-	+	-
47. <i>Ischnapontonia lophos</i> (Barnard, 1962)	-	+	-	125. <i>P. grandis</i> (Stimpson, 1860)	+	-	-
48. <i>Isopontonia platycheles</i> Bruce, 1982	-	-	O	126. <i>P. gronulimanus</i> Bruce, 1978	-	+	-
49. <i>Jocaste japonica</i> (Ortmann, 1890)	+	+	+	127. <i>P. hertwigi</i> Bals., 1913	x	x	x
50. <i>J. lucino</i> (Nobili, 1901)	+	+	+	128. <i>P. holthuisi</i> Bruce, 1969	+	+	+
51. <i>Mesopontonia gorgoniophila</i> Bruce, 1967	-	x	-	129. <i>P. imperator</i> Bruce, 1967	-	+	+
52. <i>M. gracilicarpus</i> Bruce, 1990	-	-	x	130. <i>P. incertus</i> Borradaile, 1915	+	+	+
53. <i>Miopontonia yongei</i> Bruce, 1985	-	O	-	131. <i>P. indicus</i> (Kemp, 1915)	+	+	-
54. <i>Onyccaridella monodoa</i> Fujino and Miyake, 1969	-	+	-	132. <i>P. inornatus</i> Kemp, 1922	+	+	-
55. <i>O. prima</i> Bruce, 1981	-	+	-	133. <i>P. investigatoris</i> Kemp, 1922	-	+	-
56. <i>O. stenolepis</i> Holthuis, 1952	+	-	-	134. <i>P. ischiopsinosus</i> Bruce, 1990	-	-	O
57. <i>Onyccaridites anomodactylus</i> Bruce 1987	-	O	-	135. <i>P. jugalis</i> Holthuis, 1952	+	-	-
58. <i>Onyccaridites amakusensis</i> Fujino and Miyake, 1969	-	+	-	136. <i>P. kempii</i> Bruce, 1969	-	+	-
59. <i>O. longirostris</i> Bruce, 1980	-	-	O	137. <i>P. kororensis</i> Bruce, 1977	-	+	-
60. <i>O. aligdentata</i> Fujino and Miyake 1969	-	+	-	138. <i>P. laccadivensis</i> (Alcock and Anderson, 1894)	-	x	-
61. <i>O. quadratophthalma</i> (Bals., 1921)	-	+	-	139. <i>P. sp. nov. a</i> - Bruce, 1991a	-	O	-
62. <i>O. spinosa</i> Fujino and Miyake, 1969	-	+	-	140. <i>P. lanipes</i> Kemp, 1922	-	+	+
63. <i>Orthopontonia ornata</i> (Bruce, 1969)	-	+	-	141. <i>P. latipollex</i> Kemp, 1922	x	-	-
64. <i>Palaemonella lata</i> Kemp, 1922	+	-	-	142. <i>P. longirostris</i> (Borradaile, 1915)	-	+	-
65. <i>P. dolichodactylus</i> Bruce, 1990	+	-	O	143. <i>P. lutescens</i> auct.	+	+	-
66. <i>P. pottsi</i> (Borradaile, 1915)	+	+	-	144. <i>P. nadreporeae</i> Bruce, 1969	-	+	-
67. <i>P. rotumano</i> (Borradaile, 1898)	+	+	+	145. <i>P. magnificus</i> Bruce, 1979	+	+	-
68. <i>P. spinulata</i> Yokoya, 1956	-	+	-	146. <i>P. mahi</i> Bruce, 1969	-	+	-
69. <i>P. tenuipex</i> Dana, 1852	+	-	-	147. <i>P. nilandensis</i> Borradaile, 1915	+	+	-
70. <i>Paranchistus armatus</i> (H. Milne-Edwards, 1837)	+	+	-	148. <i>P. navucealedaniae</i> Bruce, 1968	-	+	+
71. <i>P. pycnodontae</i> Bruce, 1978	-	O	-	149. <i>P. ornateilus</i> Bruce, 1979	-	+	-
72. <i>P. serenei</i> Bruce, 1983	O	-	-	150. <i>P. ornatus</i> Bruce, 1969	+	+	-
73. <i>Parapontonia nudirastris</i> Bruce, 1968	-	+	+	151. <i>P. parvispinatus</i> Bruce, 1990	-	-	xO
74. <i>Paratypton siebenrockii</i> Bals., 1914	+	+	-	152. <i>P. parvus</i> Borradaile, 1915	+	-	-
75. <i>Periclimenaeus arabicus</i> (Calman, 1939)	-	+	+	153. <i>P. pectiniferus</i> Holthuis, 1952	+	+	-
76. <i>P. ardeae</i> Bruce, 1970	-	+	-	154. <i>P. platycheles</i> Holthuis, 1952	+	+	-
77. <i>P. arthroactylus</i> Holthuis, 1952	O	-	-	155. <i>P. sp. nov. h</i> - Bruce, 1991h	-	O	-
78. <i>P. bidentatus</i> Bruce, 1970	-	+	+	156. <i>P. psamathe</i> (De Man, 1902)	+	+	+
				157. <i>P. richeri</i> Bruce, 1990	-	-	xO

SPECIES	LOCALITY		
	I.	A.	NC
158. <i>P. ruber</i> Bruce, 1982	-	O	-
159. <i>P. seychellensis</i> , Borradaile, 1915	+	+	+
160. <i>P. sibogae</i> Holthuis, 1952	O	-	-
161. <i>P. soror</i> Nobili, 1904	+	+	+
162. <i>P. spiniferus</i> De Man, 1902	+	+	-
163. <i>P. tenuipes</i> Borradaile, 1898	+	+	+
164. <i>P. tenuirostris</i> Bruce, 1990	-	-	O
165. <i>P. tenuis</i> Bruce, 1969	+	+	-
166. <i>P. toloensis</i> Bruce, 1969	-	+	-
167. <i>P. unguiculatus</i> Bruce, 1990	-	-	xO
168. <i>P. vaubani</i> Bruce, 1990	-	-	xO
169. <i>P. venustus</i> Bruce, 1990	-	+	-
170. <i>P. yaldwyni</i> Holthuis, 1959	-	+	-
171. <i>P. zanzibaricus</i> Bruce, 1969	-	+	-
172. <i>Periclimenoides odontodactylus</i> (Fujino and Miyake, 1968)	-	+	-
173. <i>Philarius gerlachei</i> (Nobili, 1905)	+	+	-
174. <i>P. imperialis</i> (Kubo, 1940)	+	+	-
175. <i>P. lifuensis</i> (Borradaile, 1898)	-	+	+
176. <i>Platycaris latirostris</i> Holthuis, 1952	+	+	+
177. <i>Platypontonia brevis</i> Miers, 1884)	-	+	-
178. <i>P. hyotis</i> Hipeau-Jacquotte, 1971	+	-	-
179. <i>Pliopontonia futiva</i> Bruce, 1973	+	+	+
180. <i>Pontonia ardeae</i> Bruce, 1981	-	O	-

SPECIES	LOCALITY		
	I.	A.	NC
181. <i>Pontonia ascidicola</i> Borradaile, 1898	x	-	-
182. <i>P. latoi</i> Kubo, 1940	+	+	+
183. <i>P. minuta</i> Baker, 1907	-	O	-
184. <i>P. monioti</i> Bruce, 1990	-	-	xO
185. <i>P. okai</i> Kemp, 1922	+	+	-
186. <i>P. sibogae</i> Bruce, 1972	+	+	-
187. <i>P. styrostris</i> Holthuis, 1952	+	+	-
188. <i>Pontonides unviger</i> Calman, 1939	+	+	-
189. <i>Pontonides</i> sp.	-	+	+
190. <i>Pontoniopsis comanthi</i> Borradaile, 1915	+	+	-
191. <i>Propontonia pellucida</i> Bruce, 1969	-	+	-
192. <i>Stegopontonia commensalis</i> Nobili, 1906	-	+	+
193. <i>Thaunastacaris streptopus</i> Kemp, 1922	+	+	+
194. <i>Tuleariocaris holthuisi</i> Hipeau-Jacquotte, 1965	-	+	-
195. <i>Typton anomalus</i> (Bruce, 1979)	-	O	-
196. <i>T. australis</i> Bruce, 1973	-	O	-
197. <i>T. bawni</i> Bruce, 1972	-	O	-
198. <i>T. dentatus</i> Fujino and Miyake, 1969	-	+	-
199. <i>T. dimorphus</i> Bruce, 1986	-	+	-
200. <i>T. nanus</i> Bruce, 1987	-	O	-
201. <i>T. wasini</i> Bruce, 1977	-	O	-
202. <i>Vir orientalis</i> (Dana, 1852)	+	+	-
203. <i>V. philippinensis</i> Bruce and Svoboda, 1984	-	+	-
204. <i>Zenopontonia noverca</i> (Kemp, 1922)	-	+	+

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TWO NEW CAPRELLIDEAN (N. GEN.) AND KNOWN GAMMARIDEAN AMPHIPODS (CRUSTACEA) COLLECTED FROM A SPONGE IN NOUMEA, NEW CALEDONIA.

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ABSTRACT

Colomastix lunalilo J.L. Barnard and a new genus of caprellid amphipod were collected from a sponge, *Siphonochalina* sp., in Noumea, New Caledonia. *Colomastix lunalilo* is redescribed on the basis of mature specimens because only small and immature specimens have been previously observed. The new caprellid amphipod belongs to the subfamily Protellinae McCain and is clearly distinguished from other genera of this subfamily by a combination of unilobate abdomen with biarticulate abdominal appendages, of which the distal article is remarkably reduced, and unarticulate pereopods 3-4.

KEYWORDS: Crustacea, Amphipoda, *Colomastix lunalilo*, *Paradicaprella brucei* gen. et sp. nov., New Caledonia.

INTRODUCTION

Some amphipod specimens were collected by A.J. Bruce from a sponge, *Siphonochalina* sp., in Noumea, New Caledonia, in 1978, and consisted of two species, *Colomastix lunalilo* J.L. Barnard, 1979 (Barnard 1970) and a new caprellid species. *Colomastix lunalilo* has been recorded from coral, algae and other hosts in the tropical zone of the Indian and Pacific Oceans (Barnard 1970; Ledoyer 1978, 1979, 1982; Myers 1985). However, the previous specimens, including the type specimen, were all immature (shorter than 2.0 mm). On the other hand, the present specimens of this species are mature (10.2 mm - 4.0 mm), and morphological variations, which I consider due to growth, are observed between the previous and the present specimens. Therefore, I have redescribed *C. lunalilo* here on the basis of the present mature male and female specimens.

The new caprellid species clearly belongs to the subfamily Protellinae McCain (McCain 1970) with the following morphological characters: 1) mandible with molar process and palp; 2) pereonites 3-4 present but reduced; 3)

abdomen of single reduced segment. However, the abdomen of the male in the caprellid species is unique in this subfamily, with the distal segment of biarticulate appendages remarkably reduced and with an unilobe (maybe completely fused). I erect a new genus on the basis of these characters and discuss the relationships between the new genus and six other closely related genera, *Deutella* Mayer, 1890, *Luconacia* Mayer, 1903, *Monoliropus* Mayer, 1903, *Pseudoprotella* Mayer, 1890, *Triantella* Mayer, 1903 and *Triliropus* Mayer, 1903.

All the specimens are deposited in the collection of the Northern Territory Museum of Arts and Sciences, Darwin (NTM).

SYSTEMATICS

Order Amphipoda
Suborder Gammaridea
Family Colomastigidae
Colomastix lunalilo J.L. Barnard
(Figs 1-3)

Colomastix lunalilo J.L. Barnard, 1970:96, 100, figs 51-52; Barnard 1971:55, figs 24-25;

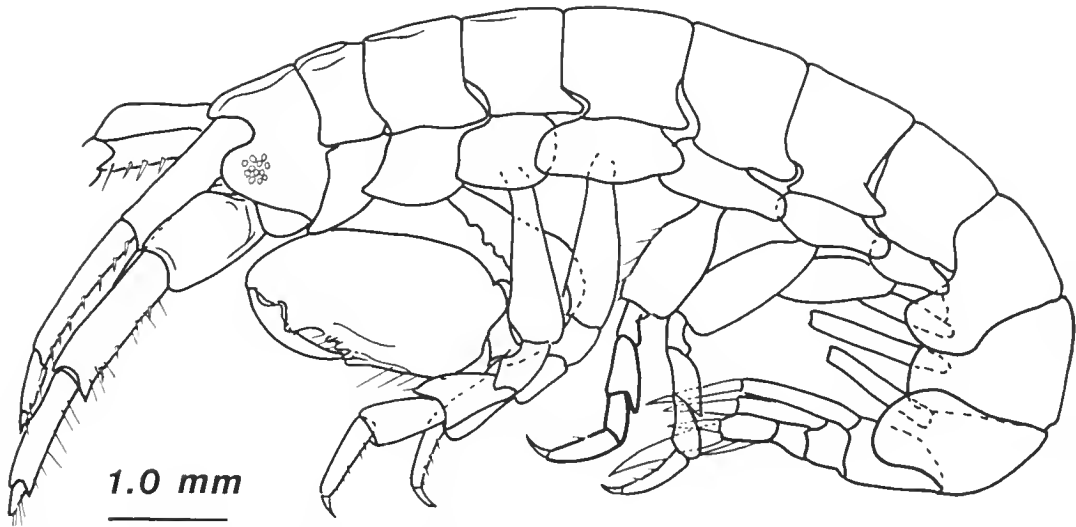


Fig. 1. *Colomastix lunalilo* J.L. Barnard. Male (no. 1, 10.2 mm).

Ledoyer 1978: 233, fig. 15; Ledoyer 1979:26, fig. 9; Ledoyer 1982:156-158, fig. 54; Myers 1985:56, fig. 57.

Material examined. NTM Cr.006944: Îlot Maitae, Noumea, New Caledonia. Stn. 203 (N.C. Amph. 1); male, nos. 1-3 (10.2 mm, 4.4 mm, 4.2 mm); female, nos. 4-6 (5.2 mm, 4.4 mm, 4.0 mm); collected from a sponge. *Siphonochalina* sp., by A.J. Bruce on 3 October 1978. A part of no. 1 (male) and no. 4 (female) are mounted on glass slides in gum-chloral medium.

Description of male (no. 1, 10.2 mm).

Body. Head broadly even and slightly concave dorsally; rostrum broad, central projection small, acute; anterocephalic lobe rounded, with eyes; anteroventral projection extending to midlength of peduncular article 1 of antenna 1, triangular, slender. At least pereonites 1-3 slightly ridged dorsally. Pleonal epimera 1-3 rounded. Gills present on pereonites 2-6.

Antennae. Subequal in length. Antenna 1: peduncular articles 1-3 in length ratios 8:9:4, acutely produced distoventrally; accessory flagellum absent; flagellum 3-articulate, proximal article projecting remarkably as hood-like process far beyond following articles. Antenna 2: peduncular articles 3-5 projecting acutely on both lateral ends of ventral side, length ratios almost 3:4:3; flagellum 2- or 3-articulate, both lateral projections reaching to ends of following articles.

Mouthparts. Upper and lower lips unknown (maybe absent). Maxilla 1: inner plate rather small, pubescent; outer plate broad,

provided with 5 small conical teeth and one inner-distal cusp; palp 1-articulate, with 4 apical setae. Maxilla 2: both inner and outer plates coalesced at base, setose. Mandibles similar, consisting of broad and quadrate plate and comb-like process, proximal tooth broadest, others slender. Maxilliped: inner plates completely fused, small; outer plates rectangular, with 2 small setae distally, distal end projecting; palp 4-articulate, penultimate article medially swollen, pubescent, with pair of setae at midlength.

Gnathopods. Gnathopod 1: coxa produced anteroventrally, lacking nipple-like anterior point; length ratios of segments from basis to propod almost 8:5:5:7:3; dactyl unknown (maybe absent), replaced by 6 finely pinnate setae. Gnathopod 2: coxa rectangular, with blunt nipple-like anterior point; anterior margin of basis tuberos; carpus provided with anterior lobe medially setose; palm oblique, defined by pair of cusps, with 2 teeth and distal triangular process; dactyl falcate, with blunt projection near base of grasping margin.

Pereopods 3-7. Homopodous except for coxae and basis; coxae 3-7 lacking nipple-like anterior point; basis of pereopods 3-4 slender, of pereopods 5-7 with thin hind plate; propod with 2 or 3 spines, without locking spines.

Pleopods. Peduncle stout, twice as long as rami, with 2 coupling spines on pleopod 1 and 1 spine on pleopods 2-3; rami broad, short, 4- or 5-articulate; swimming setae long.

Uropods. Uropod 1 extending slightly beyond uropod 2; rami equal in length, finely

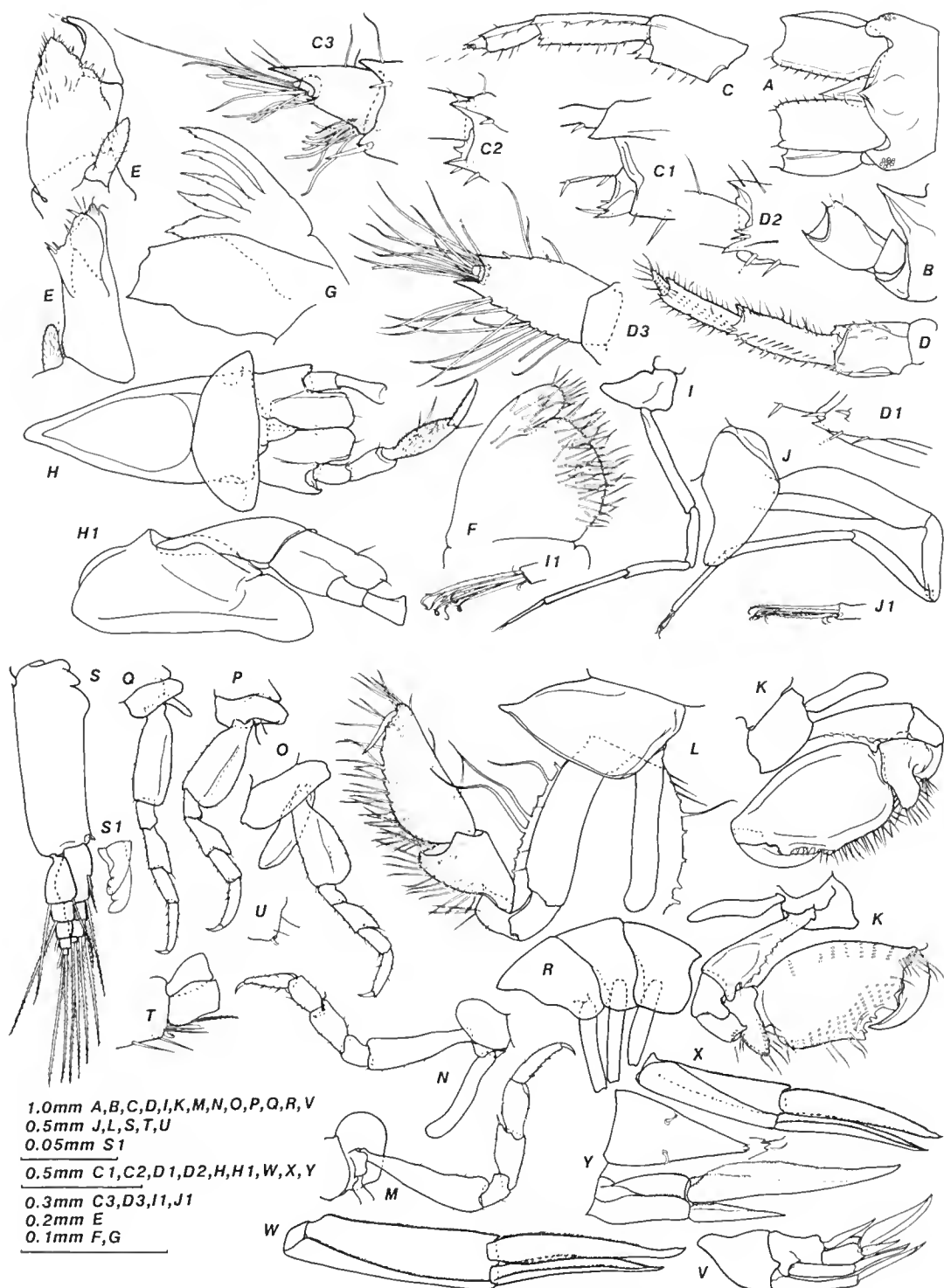


Fig. 2. *Colomastix lunalilo* J.L. Barnard. Male (no. 1, 10.2 mm) and female (no. 4, 5.2 mm: J, J1 and L). A. Head. B. Anteroventral projection of head. C, C1, C2, C3. Antenna 1. peduncular articles 1-2 and flagellum. D, D1, D2, D3. Antenna 2. peduncular articles 1-2 and flagellum. E. Maxilla 1. F. Maxilla 2. G. Mandible. H, H1. Maxilliped in dorsal and ventral views. I, I1. Male gnathopod 1 and distal part of propod. J, J1. Female gnathopod 1 and distal part of propod. K. Male gnathopod 2. L. Female gnathopod 2. M. Pereopod 3. N. Pereopod 4. O. Pereopod 5. P. Pereopod 6. Q. Pereopod 7. R. Pleon. S, S1. Pleopod 1 and coupling spines. T, U. Coupling spine of pleopods 2-3. V. Urosome. W. Uropod 1. X. Uropod 2. Y. Uropod 3 and telson.

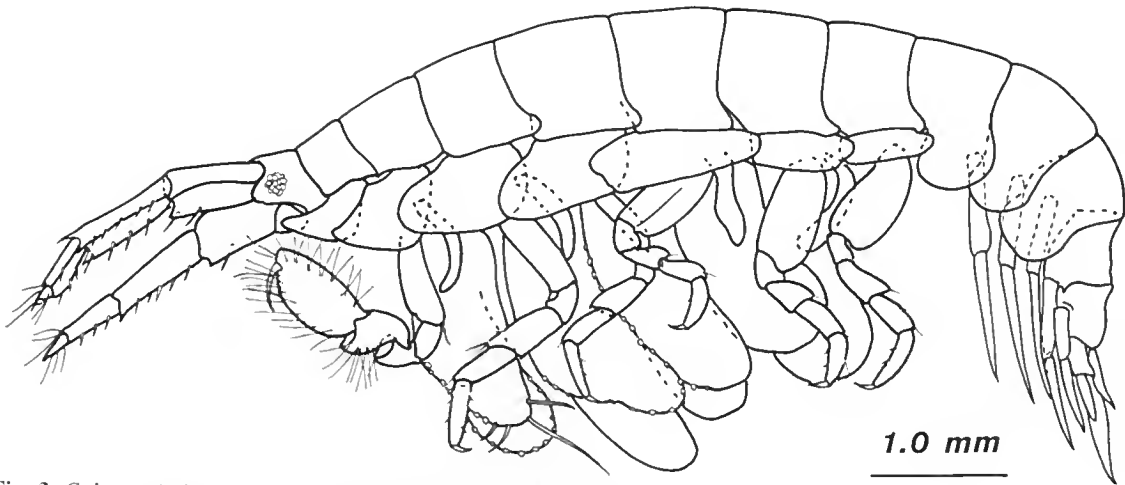


Fig. 3. *Colomastix lunalilo* J.L. Barnard. Female (no. 4, 5.2 mm).

serrate marginally. Uropod 2 similar to uropod 1, peduncle shorter. Uropod 3 distinctly extending beyond uropod 1; peduncle and outer ramus slightly shorter than half the length of inner ramus.

Telson. Triangular, slender with 2 opposing penicillate setae at midlength, apex with apicomedial tooth and 2 setae.

Description of female (no. 4, 5.2 mm).

Gnathopod 1: length ratios of segments from basis to propod almost 6:10:8:7:12; propod with 4 pinnate setae. Gnathopod 2: length ratios of carpus, propod and daetyl 7:12:4; propod gently rounded, setose posteriorly, palm undefined; daetyl slender.

Remarks. *Colomastix lunalilo* has been recorded from the Hawaiian Islands (Barnard 1979, 1971), Madagascar (Ledoyer 1979), Mauritius (Ledoyer 1978) and Viti Levu, Fiji (Myers 1985), in the tropical zone of the Indian and Pacific Oceans, and is easily distinguished from the other colomastigids by the following morphological characters: 1) in antenna 1, the first article of flagellum extends remarkably beyond the following articles; 2) in gnathopod 2 of the male, the daetyl is shorter than half the length of the propod; 3) the inner plates of the maxilliped are completely fused; 4) the outer ramus of uropod 3 is shorter than half the length of the inner ramus; 5) the telson is triangular and slender. These specific characters suggest that the present specimens are *C. lunalilo*. However, all the specimens collected from the above localities and previously described are small (less than 2.0 mm) and may be immature (see the

gnathopod 2), whereas the present specimens are large (10.2 mm to 4.0 mm) and mature. Therefore, although allometric variations of this species are not well known, the following morphological variations, which I estimate are due to growth, are observed between the present and previous material: **1**, eyes large (Barnard 1970; Myers 1985) (rather than medium or small in the new material); **2**, coxae 1-5 (Barnard 1970) or at least coxae 1-2 (Myers 1985) have nipple-like anterior points (absent from coxae 1 and 3-5 in the new material); **3**, in gnathopod 2 of the male, the palm is defined by large (Barnard 1970) or small (Myers 1985) cusps (in the new material, this is defined by a pair of small cusps, in addition to two teeth), the daetyl is slightly geniculate near the apex (not geniculate in the new material); **4**, in gnathopod 1, the propod and carpus are subequal in length (Barnard 1970; Ledoyer 1982; Myers 1985), (in the new material, the propod of the male is as long as the carpus and 0.75 times that of the female); **5**, in uropod 3, the outer ramus is about 0.25 times as long as the inner ramus (Barnard 1970; Ledoyer 1982; Myers 1985) (in the new material, it is nearly equal to half the length of the inner ramus); **6**, the head is smooth and rounded dorsally (Barnard 1970; Ledoyer 1982; Myers 1985) (in the new material, it is broadly even and slightly concave dorsally); **7**, the telson lacks penicillate setae (Barnard 1970; Ledoyer 1982; Myers 1985), the apex is truncate and serrate (Barnard 1970) (in the present material, it is provided with opposing penicillate setae midmarginally, and the apex has an apicomedial tooth).

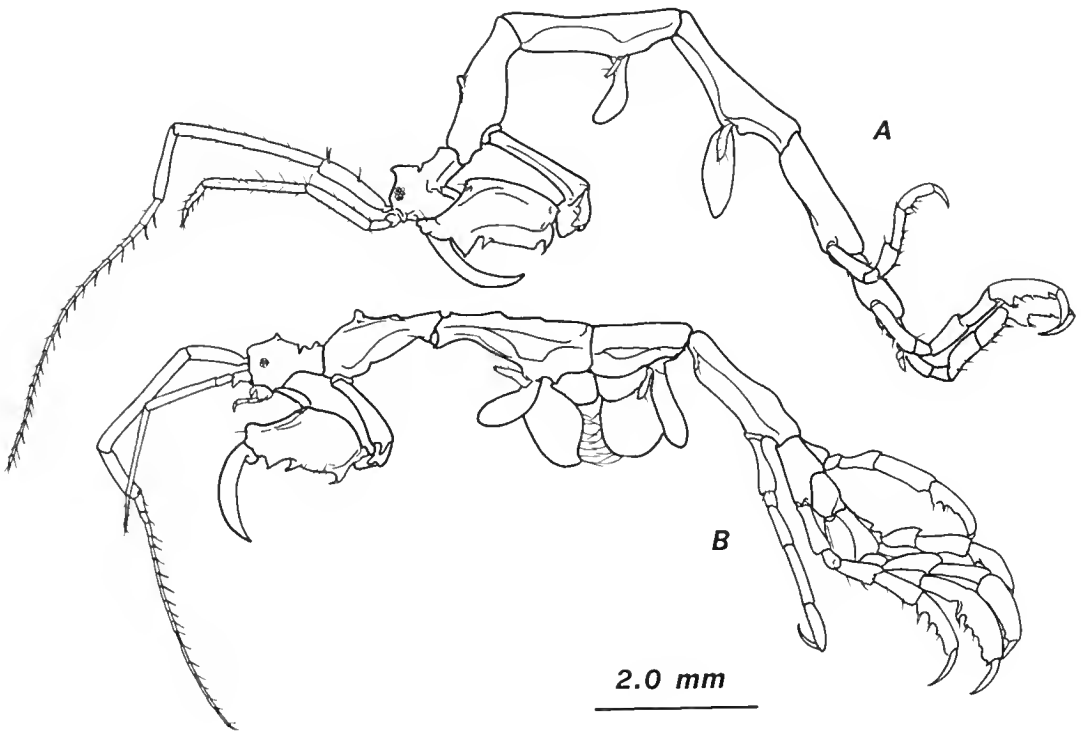


Fig. 4. *Paradicaprella brucei* gen. et sp. nov. A, Holotype, male, 10.4mm. B, Paratype no 3, female, 9.6 mm.

Suborder Caprellidea
Family Caprellidae
Subfamily Protellinae

Paradicaprella gen. nov.

Diagnosis. Antenna 2 lacking swimming setae; flagellum 2-articulate. Mandibular palp 3-articulate, not reduced, setae formula for ultimate article 1 - x (plumose setae) - 1; molar process developed. Inner lobe of maxilliped medium but smaller than outer lobe; both lobes less setose. Pereopod 5 6-articulate, inserted near posterodistal end of pereonite 5. Abdomen of male with single lobe and pair of biarticulate appendages, terminal article of appendages reduced; in female, without appendages. Gills present on pereonites 3-4.

Type species. *Paradicaprella brucei* sp. nov.

Etymology. A compound word is derived from "Paradi-" = paradise, an allusion to New Caledonia, and *caprella*. The gender is feminine.

Remarks. The new genus *Paradicaprella* is closely related to six other genera in the subfamily Protellinae: *Deutella* Mayer, 1890 (Cavedini 1981; Laubitz 1970; Mayer 1903;

McCain 1968), *Luconacia* Mayer, 1903 (Laubitz 1972; Mayer 1903; McCain 1968), *Monoliropus* Mayer, 1903 (Arimoto 1976; Griffiths 1973; Mayer 1903; Sivaprakasam 1967), *Pseudoprotella* Mayer, 1890 (Sars 1895; Chevreux and Fage 1925; Schellenberg 1942; Vassilenko 1974), *Triantella* Mayer, 1903 (Mayer 1903; Schellenberg 1931) and *Triliropus* Mayer, 1903 (Arimoto 1976; Mayer 1903). This group of genera has the following characters: pereopod 5 6-articulate, inserted near posterodistal end of pereonite 5; pererites 6-7 free; 3-articulate mandibular palp not reduced; abdomen of male with one pair of appendages (McCain 1970). However, *Paradicaprella* distinctly differs from these six genera in the abdomen of the male which has one lobe and the ultimate article of the male's abdominal appendages is greatly reduced. Paired lobes are present in these six genera, and perhaps in the whole subfamily. In *Monoliropus* and *Luconacia*, the ultimate article of the abdominal appendages is not reduced as observed in the new genus; the other four genera have uniaarticulate appendages. Further, *Paradicaprella*, *Triliropus* and *Monoliropus* have unisegmented pereopods 3-4, and these pereopods of the other genera

are biarticulate although the ultimate article of their pereopods 3-4 is remarkably reduced.

Paradicaprella brucei sp. nov.
(Figs 4-5)

Type material. HOLOTYPE - NTM Cr.006946: Male, 10.4 mm, taken from a

sponge, *Siphonochalina* sp., in Ilôt Maitae, Noumea, New Caledonia; 3 October 1978; coll. A.J. Bruce. PARATYPES - NTM Cr.006947: Two males (no. 1, 8.3 mm; no. 2, 8.1 mm) and one female (no. 3, 9.6 mm), collected with the holotype. The holotype and a part of the paratype no. 3 (female) are mounted on glass slides in gum-chloral me-

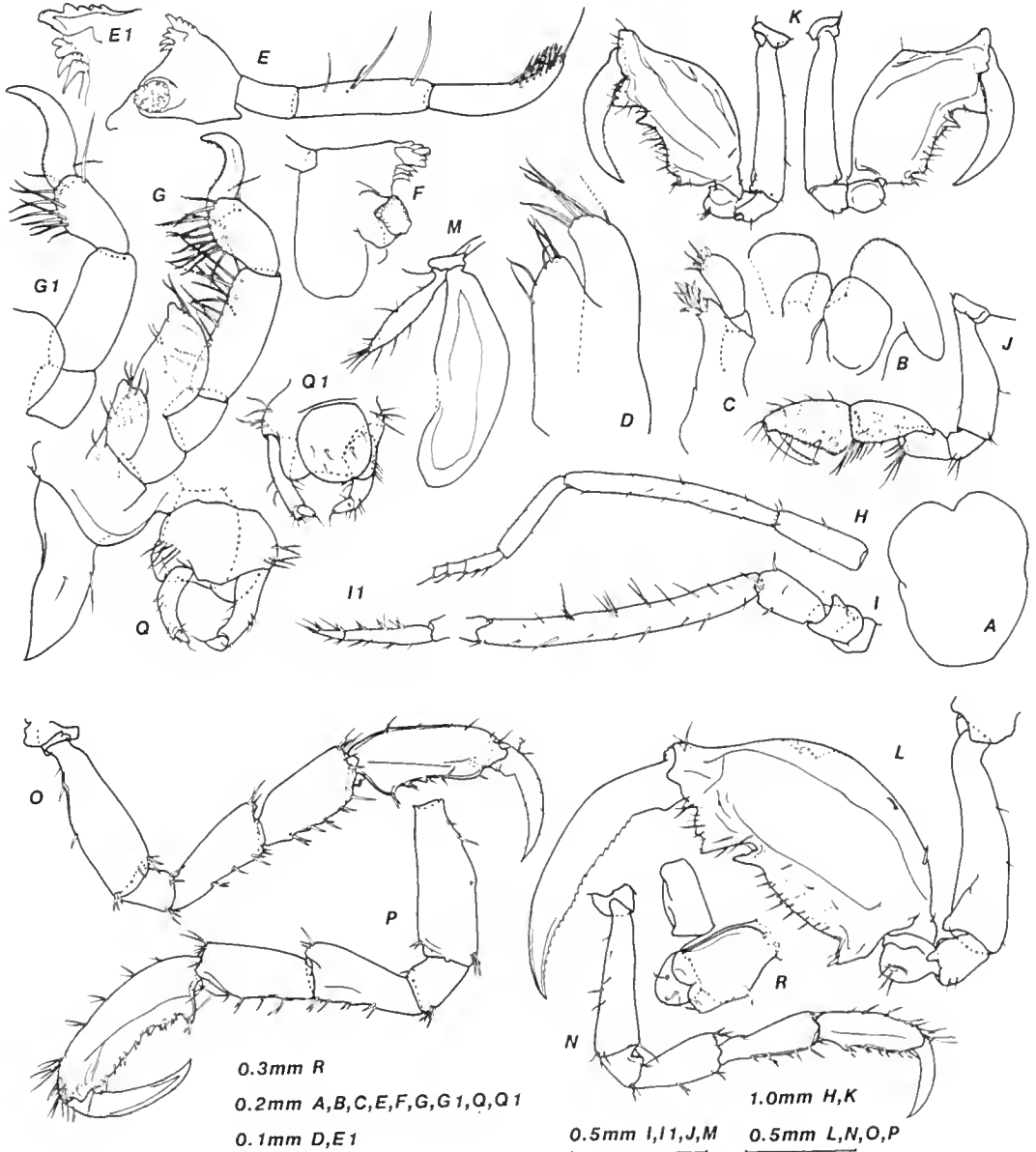


Fig. 5. *Paradicaprella brucei* gen. et sp. nov., male holotype (10.4 mm) and female paratype no. 3 (9.6 mm: L and R). A, Upper lip. B, Lower lip. C, Maxilla 1. D, Maxilla 2. E, E1, One mandible. F, the other mandible. G, G1, Maxilliped and palp. H, Antenna 1. I, I1, Antenna 2 and flagellum. J, Male gnathopod 1. K, Male gnathopod 2. L, Female gnathopod 2 (Para. 3). M, Pereopod 3. N, Pereopod 5. O, Pereopod 6. P, Pereopod 7. Q, Male pleon and penis in ventral view. Q1, Male pleon in dorsal view. R, Female pleon in ventral view (para. 3).

dium. Collection number: Stn. 203 (NC Amph. 2).

Description of the male holotype (10.4 mm). **Body.** Head armed with triangular process dorsally. Length ratios of pereonites 1-7 9:33:42:39:32:18:8. Pereonite 2 armed with pair of tubercles dorsomedially. Abdominal appendages not lobate, biarticulate, terminal segment with apical seta; abdominal lobe unilobate.

Antennae. Antenna 1: length ratios of peduncular articles 5:11:5; flagellum as long as peduncle, with aesthetases. Antenna 2: length ratios of peduncular articles 4-5 and flagellum 20:25:8; flagellum 2-articulate.

Mouthparts. Maxilla 1: outer plate armed with 7 tooth-like spines; ultimate article of palp with 4 spines and 3 setae apically. Maxilla 2: inner plate with 5 (right) and 7 (left) setae; outer plate with 6 (right) and 7 (left) setae. Mandibles similar; incisor with 5 teeth; laeina mobilis ornamented with 2 teeth; with 2 accessory blades in one mandible and 3 in the other; palp 3-articulate, middle article with 4 setae, setal formula for ultimate article 1 - 7 (plumose) - 1. Maxilliped: inner plate medium in size, with 3 apical setae; outer plate with 2 apical setae; palp rather slender, 4-articulate, penultimate article geniculate, pubescent on grasping margin.

Gnathopods. Gnathopod 1: propod as long as carpus, triangular, palm defined by spine and serrate margin. Gnathopod 2: carpus coalescent with propod; propod swollen, flattened or slightly concave on half of dorsal margin extending to well developed distal projection; palm gently curved, almost reaching base, defined by small protrusion with palmar spine, distal triangular process well developed, following poison tooth; dactyl reaching palmar protrusion when closed, provided with numerous pits on grasping margin.

Pereopods. Pereopods 3-4 1-articulate, with 4 setae distally. Pereopods 5-7 homopodous, becoming longer; propod with palmar protrusion armed with pair of spines, palm spinose; dactyl reaching palmar protrusion when closed.

Description of the female paratype no. 3 (9.6 mm). Small dorsal projection on head. Gnathopods 1-2 similar to those of male except distal dorsodistal process small. Abdomen without appendages.

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A NEW SPECIES OF SCINCID LIZARD FROM WESTERN ARNHAM LAND, NORTHERN TERRITORY.

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ABSTRACT

A new species of *Egernia* is described from the sandstone escarpment on the western edge of the Arnhem Land plateau. It is most similar in external morphology to the east Australian species *Egernia frerei*, but can be differentiated from this by significant differences in colouration and also by several scalation characters.

KEYWORDS: Scincidae, *Egernia*, Australia, taxonomy, new species.

INTRODUCTION

A large species of *Egernia* from the East Alligator Rivers region, bordering the western edge of Arnhem Land, Northern Territory, has been known since the fauna was initially listed by Cogger (1974) as *Egernia* cf. *frerei*. Further specimens have since been collected in that region, and the species has been figured by various authors (Cogger 1975 and subsequent editions; Swanson 1979, 1987; Wilson and Knowles 1988), but its status has never been investigated in detail. Cogger (1975 and subsequent editions) figured this species as *E. frerei* and included its distribution in the Northern Territory under the description of *E. frerei*. Swanson (1987) cited the photograph (pl. 106) of this species as *Egernia richardi*, but provided no explanation for doing so. Presumably, the basis for this action lies in the type locality for *Tropidolepisma richardi* Peters (1869) being "Alligator River ... North Australia." Reference to the description of *T. richardi* provided two characters which indicate that it could not be conspecific with the species described here: a flattened out (oblate) body and tail; and 30 mid-body scale rows. Further, Mr Glen Shea (pers. comm.) has examined the type specimen of *T. richardi* Peters, and he concluded it is conspecific with *Egernia carinata* Smith (1939) from south-west Western Australia, and that the cited type locality for *T. richardi* is most likely erroneous. Wilson and Knowles (1988) figure this species (Fig. 472) as *Egernia* sp. "a member

of the *E. frerei* group," but failed to give any diagnostic characters that would separate it from any other species of *Egernia*. In the species account of *E. frerei* they assign it to the *E. major* group. Apparent inconsistencies in group allocation and failure to define either the "*E. frerei* group" or "*E. major* group" have done little towards justifying their inclusion in the text. Similarly, the undiagnosed or unreferenced presentation of the Arnhem Land *Egernia* as an unassigned species has done little to clarify its status.

In this paper the Arnhem Land taxon previously allied to *Egernia frerei* is described as a new species.

MATERIALS AND METHODS

Measurements were made to the nearest millimetre and, other than maximum snout-vent length (SVL), are here expressed as a percentage of SVL.

Scalation characters discussed follow Taylor (1935: 11) for the headshields; 'midbody scale rows' are the number of longitudinal scale rows around the body counted at a point midway between the axilla and groin; 'paravertebral' scales are the number of scales in a paravertebral row posterior to the parietals to a point opposite the anus; fourth toe lamellae are the number of scales on the underside of the toe from its apex with the third digit to the nail.

Specimens of *E. frerei* (n = 175) held in the Australian Museum, Museum of Victoria,

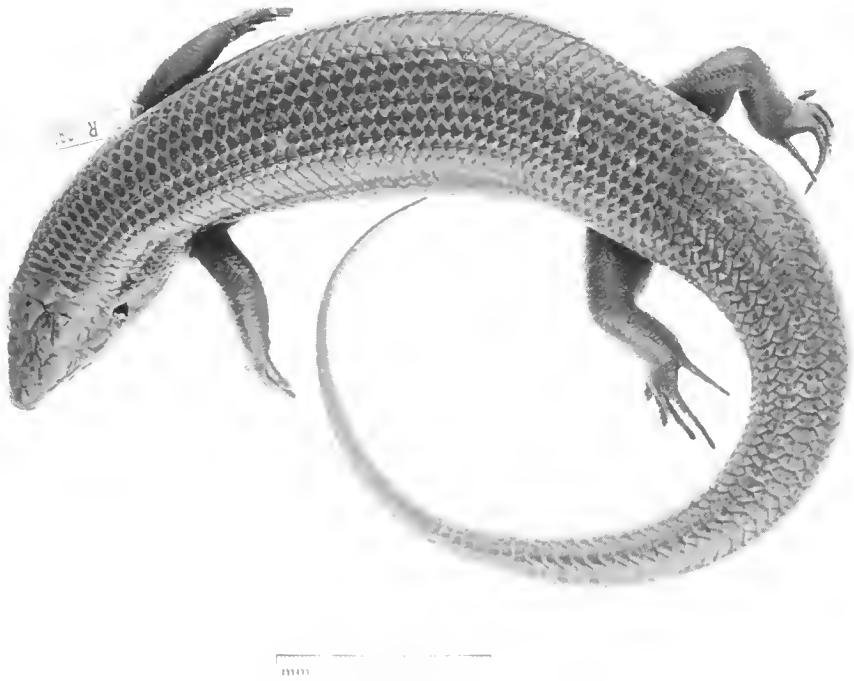


Fig. 1. Holotype (NTM R0809) of *Egernia arnhemensis* from Oenpelli, NT.

Queensland Museum, South Australian Museum and American Museum of Natural History were examined for comparison with known specimens of the new species described below. Abbreviations used in the text are as follows: AM, Australian Museum, Sydney; NTM, Northern Territory Museum.

Egernia arnhemensis sp. nov.
(Figs 1-3)

Type material. HOLOTYPE - NTM R0809: 6.1 km SW of Oenpelli, NT, 12°22'S, 133°02'E, collected by G. Gow and B. Jukes, 21 May 1975; adult (Fig. 1). PARATYPES - NTM R1190: 3 km SW of Oenpelli, NT, 12°21'S, 133°02'E; NTM R8032-34: R8181 Nourlangie Rock NT, 12°52'S, 132°50'E; NTM R8387-88: Little Nourlangie Rock, NT, 12°52'S, 132°47'E; AM R38384: Koongarra, Mt. Brockman Range, NT, 12°33'S, 132°56'E; AM R100018: SE corner of Jabiluka outlier, Magela Creek, NT, 12°33'S, 132°56'E.

Diagnosis. A large species of *Egernia* (maximum SVL 208 mm), distinguished from all other members of the genus by the following combination of scalation and colour characteristics: dorsal scales moderately smooth

with several longitudinal striations; enlarged subocular scale row complete, separating upper labials from contact with lower eyelid; nuchals usually 2 or 3 either side; midbody scale rows 44-48; paravertebral scale rows 59-65; colouration dark.

Details of holotype. Snout-vent length 192mm; tail length about 260mm, distal 42% reproduced; forelimb to snout length 68mm; axilla to groin length 120mm; hindlimb length 68mm. Prefrontals narrowly separated; supraeiliaries 8/7, 1st and 2nd enlarged, posteriormost present as 2 (1 upper and 1 lower) unenlarged subequal scales (lower similar in size to adjacent penultimate supraciliary); nuchals 3/3; primary temporal single; enlarged upper secondary temporals 1/1, each with 1 adjacent smaller temporal bordering the parietal; upper labials 7/8; enlarged auricular lobules 5/5.

Midbody scale rows 44; paravertebral scale rows 59; lamellae beneath the fourth toe 21/24

Description. Maximum SVL 208 mm; forelimb to snout length 35-38.9% of SVL (mean=36.1, N=9); axilla to groin length 57.9 - 62.5% of SVL (mean=60.3, N=9); hindlimb length 30.2 - 36.8% of SVL (mean=34.3, N=9); tail length approximately 135-140% of SVL (N=2).

Rostral in broad contact with frontonasal; prefrontals moderately to narrowly separated (44.4%), to narrowly to broadly contacting; supraciliaries 7(25%), 8(40%), 9(20%) or 10(15%); anterior supraciliaries variably enlarged with anteriormost 2(35%), or 3 larger; posterior supraciliaries variably enlarged or fragmented, with the posteriormost either larger(50%), or present as 2 (1 upper and 1 lower), unenlarged subequal scales (the lower similar in size to the adjacent penultimate supraciliary), and the penultimate occasionally similarly fragmented, or both the penultimate and last supraciliaries with a single large scale above (interdigitating between 3rd and 4th supraocular); nuchals 1-3 either side (mode 2, 75%), anteriormost pair occasionally separated by presence of large distinct internuchal; primary temporal single, large and distinct; enlarged upper secondary temporals 1 either side, with 1(90%) - 2 adjacent smaller temporals bordering the parietals; lower secondary temporal single large and distinct; nasals widely separated, each with a prominent postnarial groove; upper labials usually 8(65%), or 7(30%), rarely 9(5%); subocular scale row complete, separating upper labials from lower eyelid; ear opening large with 4(20%), 5(40%), 6(30%), or 7(10%), enlarged auricular lobules anteriorly.

Body scales with 3-4 faint striations, increasing in number towards the nape as scales broaden; midbody scale rows 44-48 (mean=45.3, sd=1.5, N=10); paravertebral scale rows 59-65 (mean=61.4, sd=1.9, N=10).

Lamellae beneath fourth toe 20-24 (mean=22, sd=1.1, N=9), basal portion broad (with a median division), distal portion compressed (undivided).

Colour and pattern. Dorsal surface grey to light brown, each scale with a mid to dark brown longitudinal streak medially, head and nape without dark streaking. Lateral surface grey-brown with dark streaking (similar to dorsal surface), becoming lighter ventrally; upper lateral surface between ear opening and forelimbs black (with occasional white flecking) interrupting continuity of the grey-brown dorsal and lateral colouration in this region. This dark colouration tends to break up posteriorly of forelimb to merge with dark longitudinal streaks of the upper to mid lateral surface respectively; facial surface grey-brown with marked dark flecking posterior to orbit. Venter anterior to forelimbs strongly marked with dark flecks, tending to form series of roughly transverse bars. Soles of feet and lamellae mid-dark brown. In life venter with a yellow flush posterior to forelimb.

Mr Keith Martin (pers. comm.) records the colouration of a juvenile individual (approx. 150 mm total length), as uniform dark brown-black marked with bands of yellow spots dorsally.

Etymology. The name "*arnhemensis*" has been chosen for the species to emphasise the restricted distribution of the species to a habitat associated with the Arnhem Land plateau.

Habits. Mr Keith Martin has collected and observed a number of specimens during the

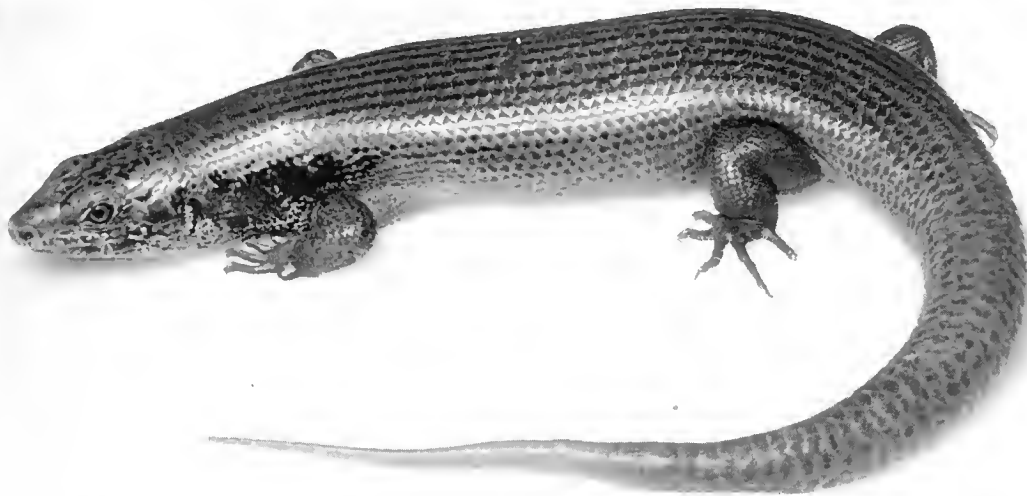


Fig. 2. Paratype (AM R100018) of *Egernia arnhemensis* from the Jabiluka outlier, Magela Creek, NT.

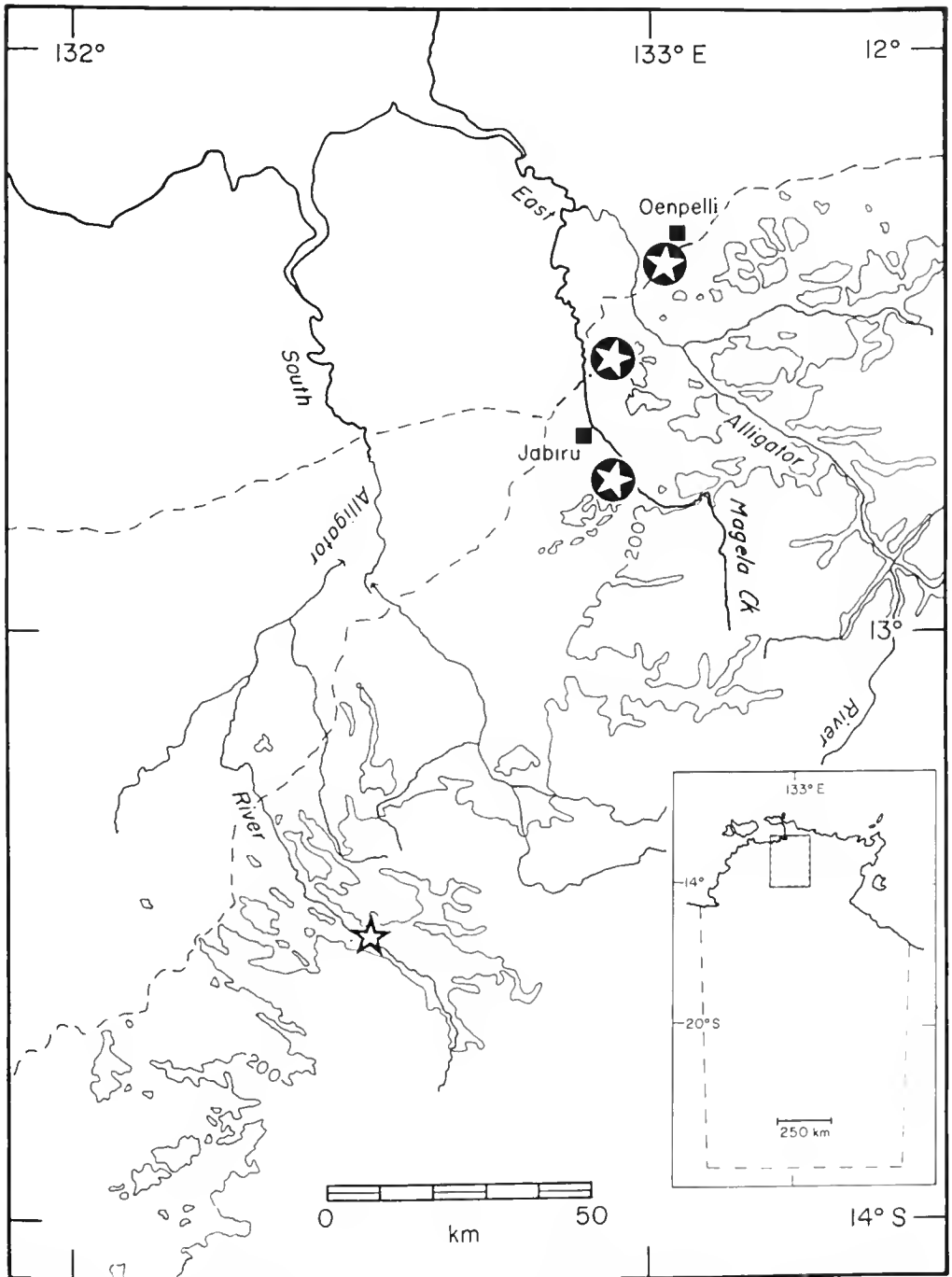


Fig. 3. Map showing the distribution of *Egernia arnhemensis* (specimen records indicated by closed stars, sight records indicated by open star) in the Alligator Rivers Region, NT.

course of field work in the Mt Brockman - Nourlangie region. In this region (K.Martin, pers. comm.) *E. arnhemensis* occurs in thickly vegetated, wet, rocky gorges with numerous deep crevices. The sites at which specimens were collected were "closed forest" and

"rocky crevice" habitats. Individuals were only observed to be active in the vicinity of deep crevices in the late afternoon and most specimens were collected in small mammal traps set in the very late evening and checked at first light. This pattern was also observed

for the specimen collected by Ms Anne Kerle on the Jabiluka outlier. Mr Grant Husband observed *E. arnhemensis* at El Sharana, some 95 km south of the Mt Broekman region.

Comparison with other species. *Egernia arnhemensis* is unlikely to be confused with any other member of the genus apart from *E. frerei*, which is similar in size and superficial morphology. It is not the purpose of this paper to document variation in *E. frerei* in Eastern Australia and New Guinea, but rather to point to the distinct differences in features of scalation and colouration between *E. arnhemensis* and *E. frerei*. Those characters which readily distinguish *E. arnhemensis* from *E. frerei* include the following: more numerous midbody scale rows (44-48 vs. 30-36); more numerous paravertebral scales (59-65 vs. 44-56); and a lack of differentiation in colour between the dorsal and lateral surfaces in contrast to a variety of colour patterns in *E. frerei*, most of which feature not only dorsal and lateral differentiation, but also a distinct laterodorsal zone (if in *E. frerei* the dorsal and lateral zones are poorly differentiated, then there is generally an accompanying lack of the dark flecking that is a feature of the colour pattern of *E. arnhemensis*).

ACKNOWLEDGMENTS

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arnhemensis; Mr F. Parker and Dr R. Zwiefel for their observations on *E. frerei*; and Mr G. Shea for use of his transcription of Peters' (1869) description of *T. richardi*, and comments on the status of the type specimen of this species. Dr A. Greer provided the photo for Figure 2; Mr T. Farr the photo for Figure 1; and P. Koshland the artwork for Figure 3. I thank Ms K. Havansky and Ms J. Nancarrow for typing the various drafts of this manuscript.

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A NEW SPECIES OF *NEMIPTERUS* (PISCES: NEMIPTERIDAE) FROM THE SOUTH-WESTERN PACIFIC

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ABSTRACT

A new species of *Nemipterus* from Fiji and Vanuatu is described and figured. The new species appears most closely related to *N. aurifilum* (Ogilby) and *N. bathybius* Snyder, but differs principally in colour pattern: *N. aurifilum* has a single yellow stripe from beneath the origin of the lateral line to the caudal peduncle; *N. bathybius* has two yellow stripes, the first from beneath the origin of the lateral line to the peduncle and the second from behind the pectoral fin to the caudal fin base; whereas the new species has a single indistinct pale yellow stripe from above the pectoral fin base to the peduncle.

KEYWORDS: *Nemipterus*, new species, Fiji, Vanuatu.

INTRODUCTION

In the course of revisionary studies of the Indo-West Pacific fish genus *Nemipterus*, presently being undertaken by the author, numerous specimens were received for identification. Amongst the material obtained were several specimens of an undescribed species of *Nemipterus* sent from Fiji by Dr A.D. Lewis. Additional specimens from Vanuatu (New Hebrides) were found also in the Australian Museum. These specimens are described herein as a new species of *Nemipterus*.

Methods of counting and measuring specimens follows Russell (1986). Lengths of specimens are standard length (SL) unless otherwise indicated, and all measurements are expressed in millimetres rounded to the nearest 0.1 mm. In the description, measurements and counts for the holotype are given first; those for the paratypes, where different from the holotype, are enclosed in parentheses.

Specimens are deposited in the Australian Museum, Sydney (AMS) and Northern Territory Museum, Darwin (NTM).

SYSTEMATICS

Family Nemipteridae

Nemipterus vitiensis sp. nov.

(Fig. 1, Tables 1-2)

Type material. HOLOTYPE - NTM S.11744-001: 170 mm SL, male, Vatutotolu

Reef, Viti Levu, Fiji, 17°10'S, 177°38'E, hook and line, 273 m depth, coll. P. Mead, 16 March 1984. PARATYPES - AMS I.12012: 140.9 mm SL, Efati I., Vila, Vanuatu, 17°45'S, 168°18'E. AMS I.12013: 161.7 mm SL, Vila, Vanuatu, 17°45'S, 168°18'E, 27.3 m depth. AMS I.26907-001: 2 specimens, 142.5-159.0 mm SL, Suva market, Viti Levu, Fiji, coll. A.D. Lewis, May 1984. NTM S.11140-001: 2 specimens, 190.5-218.5 mm SL, Suva market, Viti Levu, Fiji, coll. A.D. Lewis, 17 February 1984.

Diagnosis. Pectoral-fin rays ii,14-16; gill rakers 12-14; body moderately elongate, depth 3.2-3.8 in SL; head length about equal to body depth, depth 1.0-1.1 in head length; diameter of eye equal to snout length, 1.0 in snout; lower margin of eye tangent to a line from tip of snout to upper pectoral fin base; suborbital shallow, its lower edge emarginate, least depth 2.0-3.0 in eye diameter; imaginary line extended upward from posterior edge of suborbital reaching dorsal profile about 3-7 scale rows before origin of dorsal fin; pectoral and pelvic fins moderately long, both reaching to or beyond level of vent; upper lobe of caudal fin with long, trailing filament.

Description. Dorsal-fin rays X,9; anal-fin rays III,7; pectoral-fin rays ii,14 (left) or 15 (right) (ii,14-16); lateral-line scales 46 (46-48); transverse scale rows 3/11 (3/10-11); gill rakers 14 (12 in New Hebrides paratype only; gills removed in Fiji paratypes).

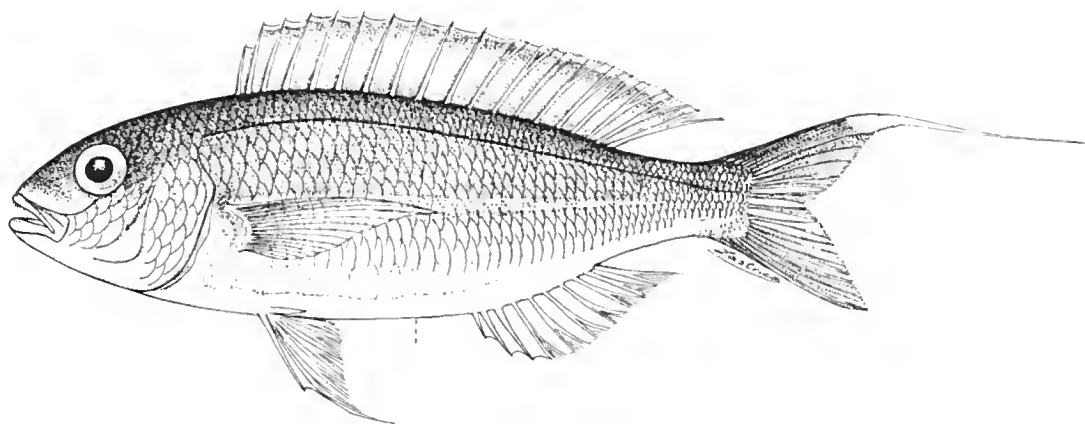


Fig. 1. *Nemipterus vitiensis*, drawing based on paratype (NTM S.11140-001, 190.5 mm SL).

Depth 3.2 (3.4-3.8) in SL; head 3.2 (3.2-3.5) in SL; head length about equal to body depth, depth 1.0 (1.0-1.1) in head; snout short, bluntly rounded in profile, 3.2 (3.0-3.3) in head; eye 3.1 (3.0-3.2) in head; diameter of eye equal to snout length, 1.0 in snout; lower margin of eye tangent to line from tip of snout to upper pectoral fin base; interorbital width 1.7 (1.6-1.8) in eye; least depth of suborbital 2.5 (2.0-3.0) in eye; ventral margin of suborbital emarginate, its posterior edge rounded; an imaginary line extended upward from posterior edge reaching dorsal profile about 3-7 scale rows before origin of dorsal fin; naked width of preopercle 2.3 (1.8-2.3) in scaly width; margin of preopercle finely denticulate; caudal peduncle depth 1.3 (1.3-1.4) in

peduncle length; dorsal fin length 1.9 in SL; dorsal spines 8-10 longest, 1.8 (1.5-1.9) times length of first dorsal spine; dorsal rays 6-8 longest, 1.3 (1.4-1.6) times length of longest dorsal spine; anal fin length 5.6 (5.6-5.9) in SL; first anal spine 2.2 (1.7-2.2) in second; second anal spine 1.3 (1.2-1.3) in third; pectoral fins moderately long, reaching to or beyond level of vent, length 1.1 (1.0-1.2) in head; pelvic fins moderately long, reaching almost to or just beyond vent, length 1.5 (1.3-1.4) in head; pectoral fins length 0.7 (0.7-0.9) in pelvic fins length; caudal fin forked, upper rays produced into long, trailing filament.

Maxillary reaching to below anterior margin of pupil; jaw teeth small, pointed, in narrow tapering bands in both jaws; upper jaw

Table 1. Measurements (mm) of type specimens of *Nemipterus vitiensis*.

Measurement	Holotype	Paratypes		AMS 1.26907-001	AMS 1.26907-001	NTM S.11140-001	NTM S.11140-001
	NTM S.11744-001	AMS 1.12012	AMS 1.12013				
Standard length	170.0	140.9	161.7	142.5	159.0	190.5	218.5
Depth	52.4	39.2	46.0	38.0	45.7	56.3	62.0
Head length	53.4	44.6	50.5	41.7	45.5	54.8	64.0
Snout length	16.9	13.8	15.3	13.0	15.0	17.4	20.3
Eye diameter	17.1	15.0	16.0	13.3	15.0	18.0	20.0
Interorbital width	10.2	8.5	9.1	8.0	9.1	11.6	12.5
Suborbital width	6.8	4.8	5.4	5.3	6.1	8.0	10.2
Peduncle depth	17.9	13.8	16.2	14.4	15.0	20.0	21.7
Peduncle length	24.0	19.0	22.1	20.7	20.0	28.3	31.4
Dorsal fin length	91.7	72.2	85.1	74.3	83.7	99.1	112.3
Anal fin length	30.4	23.8	28.9	25.5	28.5	32.4	37.9
Pectoral fin length	48.6	39.3	49.0	35.5	43.8	54.5	63.3
Pelvic fin length	35.9	30.2	35.6	32.4	35.0	41.0	49.8
First dorsal spine length	12.0	10.3	9.7	11.4	12.5	12.4	14.1
Longest dorsal spine length	21.2	18.0	18.8	16.8	16.5	23.1	26.7
Longest dorsal ray length	27.2	20.8	25.2	24.4	27.1	32.2	42.1
First anal spine length	6.0	5.0	6.0	5.6	6.1	6.0	9.0
Second anal spine length	12.9	10.2	11.9		12.9	13.2	14.9
Third anal spine length	17.4	12.8	14.9	14.2	15.5	17.2	19.4
Preopercle scaly width	12.9	9.3	9.5	9.0	10.1	13.0	13.7
Preopercle naked width	5.7	5.1	4.7	4.5	5.6	5.7	7.2

with anterior outer row of 4 pair of small, recurved canines.

Colour in alcohol: body pale brown, with traces of silvery white on opercle and ventral surface. Faint dusky submarginal band along dorsal fin.

Colour in life (from colour transparencies): head and body silvery white, dusky blue on dorsum; indistinct, pale yellow stripe from above pectoral fin to caudal peduncle; broad lemon-yellow band on either side of ventral midline; eye silvery; dorsal fin light dusky, upper margin of fin yellow-edged, with dusky mauve submarginal band; anal fin transparent; caudal fin dusky pink, caudal filament yellow; pelvic fins transparent; pectoral fins pink, with dusky base.

Etymology. Named *vitiensis* after the main Fiji island, Viti Levu, where the holotype and 4 of the 6 paratypes were collected.

Remarks. *Nemipterus vitiensis* appears to be most closely related to *N. aurifilum* (Ogilby, 1910), a species that is restricted to tropical and subtropical eastern Australia, and *N. bathybius* Snyder, 1911, which ranges from southern Japan to northwestern Australia. All three species are characterised by having a long caudal filament and a yellow band on either side of the midventral line. However, the position of stripes on the sides of the body readily distinguishes fresh specimens of *N. vitiensis* from *N. bathybius* and *N. aurifilum*: *N. vitiensis* has a single, indistinct pale yellow stripe from above the pectoral fin to the caudal peduncle; *N. bathybius* has two yellow stripes, one from beneath the origin of the lateral line to the peduncle, and the other from behind the pectoral fin to the caudal base; and *N. aurifilum* has a single yellow stripe from beneath the origin of the lateral line to the peduncle. In preserved specimens all traces of striping on the body are lost.

Meristic data are not useful in separating species of *Nemipterus*, and proportional measurements do not provide complete separation of the taxa. Selected meristic and morphometric data for *N. vitiensis*, *N. aurifilum* and *N. bathybius* are given in Table 2. Only a narrower interorbital width (1.6-1.8 in eye diameter) clearly separates *N. vitiensis* from *N. aurifilum* (interorbital width 1.3-1.5 in eye diameter), although *vitiensis* also tends to have a slightly longer snout (3.0-3.3 in head length, versus 3.3-3.9) and somewhat broader naked

Table 2. Selected counts and proportional measurements (mm) of *Nemipterus vitiensis*, *N. aurifilum* and *N. bathybius*.

	<i>N. vitiensis</i>	<i>N. aurifilum</i>	<i>N. bathybius</i>
Pectoral branched rays	14-16	13-15	13-15
Lateral line scales	46-48	46-49	46-49
Transverse scale rows			
above lateral line	3.5-3.5	3.0-3.5	3-4
Transverse scale rows			
below lateral line	10-11	9-10	9-11
Gill rakers (total)	12-14	14-20	13-16
Depth in SL	3.2-3.8	3.2-3.8	2.9-3.6
Head in SL	3.2-3.5	3.1-3.6	2.9-3.5
Depth in head length	1.0-1.1	1.0-1.2	0.9-1.1
Snout in head length	3.0-3.3	3.3-3.9	3.1-3.9
Eye in head length	3.0-3.2	2.6-3.4	2.7-3.6
Eye in snout length	0.9-1.0	0.7-1.0	0.7-1.2
Interorbital width in eye diameter	1.6-1.8	1.3-1.5	1.3-1.9
Suborbital width in eye diameter	2.0-3.1	2.2-4.7	1.9-4.7
Peduncle depth in peduncle length	1.3-1.4	1.2-1.6	1.0-1.4
Dorsal fin length in SL	1.9-2.0	1.8-2.1	1.8-2.1
Anal fin length in SL	5.6-5.9	5.4-6.1	5.0-6.0
Pectoral fin length in head length	1.0-1.2	1.0-1.3	1.0-1.4
Pelvic fin length in head length	1.3-1.5	1.3-1.6	1.1-1.6
Pectoral fin length in pelvic fin length	0.7-0.9	0.6-1.0	0.7-1.0
First dorsal spine length			
in longest dorsal spine	1.5-1.9	1.5-2.9	1.3-2.4
Longest dorsal spine length			
in longest dorsal ray	1.3-1.6	1.1-1.4	1.0-1.6
First anal spine length in second anal spine	1.7-2.2	1.7-2.3	1.6-2.4
Second anal spine length in third anal spine	1.2-1.3	1.2-1.4	1.1-1.4
Preopercle scaly width in naked width	1.8-2.3	1.4-1.9	1.5-2.2

preopercle (preopercle scaly width 1.8-2.3 in naked width, versus 1.4-1.9) than *aurifilum*. In *Nemipterus vitiensis* and *N. bathybius* the angle of the posterior edge of the suborbital is more acute, and a line drawn upwards from the posterior edge of the suborbital reaches the dorsal profile before the origin of the dorsal fin; while in *N. aurifilum* the angle of the posterior margin of the suborbital is distinctly obtuse, and a line drawn upwards from it reaches the dorsal profile at or behind the origin of the dorsal fin. *Nemipterus vitiensis* may also have a lower gill raker count (12-14) than *N. aurifilum* (14-20) or *N. bathybius* (13-16), but only two of the specimens examined had intact gill arches and further material needs to be examined.

Nemipterus vitiensis is so far known only from Fiji and Vanuatu (New Hebrides). Specimens were collected in depths ranging from 27-273 m.

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PRIMITIVE MARSUPIAL TAPIRS (*PROPALORCHESTES NOVACULACEPHALUS* MURRAY AND *P. PONTICULUS* SP. NOV.) FROM THE MID-MIOCENE OF NORTH AUSTRALIA (MARSUPIALIA: PALORCHESTIDAE).

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ABSTRACT

The upper molar dentition of *Propalorchestes novaculacephalus* demonstrates a transitional state between the bilophodont marsupial tapirs and the selenodont wynyardiids. Although *Propalorchestes* had developed bilophodont crowns, the metacone and stylar cusp D remained sufficiently differentiated to verify the development of bilophodonty in diprotodontoid (vombatimorphian) marsupials from a selenodont condition, in which the primary buccal cusp is formed by stylar cusp D rather than the metacone.

KEYWORDS: Palorchestinae, Wynyardiidae, molar evolution, diprotodontoid systematics, Bullock Creek Local Fauna, Riversleigh "Systems" Fauna.

INTRODUCTION

A cranial fragment from the Bullock Creek Local Fauna indicated that tapir-like marsupials (Palorchestinae) were already highly modified forms by mid-Miocene times and that they differed in many significant respects from the palorchestid *Ngapakaldia tedfordi* Stirton (Murray 1986). Several years had elapsed since the cranium of *Propalorchestes* was described before any palorchestine dentitions from the Camfield Beds came to light. What was thought to be the first to be recovered, a right maxillary fragment containing one and a half molars, was actually preceded several years by a dentary collected by Dr Thomas Rich in 1982, from the Horseshoe West locality of the Camfield beds. The dentary and maxilla fragment are well-matched and of the correct proportions to belong to the same species as the edentulous cranium. Casting further afield, Dr Mike Archer and Ms Sue Creagh assembled a small assortment of isolated teeth and dentary fragments from Riversleigh which have palorchestid features.

The total collection of late Oligocene to mid-Miocene palorchestine material consists of only eight specimens: three dentary frag-

ments, a maxilla, a cranial fragment and three isolated teeth. Despite the sparseness and fragmentary condition of the sample, it substantially improves our resolution of the systematics of the marsupial tapirs and moreover, adds a previously unknown transitional element to the interpretation of the phylogeny of bilophodont dentitions within the Vombatimorphia.

The "diprotodontoid" (vombatimorphian) affinity as opposed to a macropodoid (Owen 1874; Raven and Gregory 1946) affinity of palorchestids was first noted by Woods (1958). Since then, palorchestid *affines* possessing vombatimorphian character complexes were diagnosed by Stirton (1967) (*Ngapakaldia*, *Pitikautia*). However, the molar crown morphology of these genera showed few synapomorphic features to unite them with members of the genus *Palorchestes*. *Ngapakaldia* is usually treated as a plesiomorphic sister group of the apparently more derived Palorchestinae (Stirton *et al.* 1967). However, Archer (1984) correctly observed that there is very little to support an even monophyletic union of the two groups or the state of the morphocline for their dental and cranial characters.

Evidence is presented indicating that the distinctive upper molar morphology of *Propalorchestes* more closely resembles that of a wynyardiid than any other described, potentially antecedent, vombatimorphian group. Moreover, if the transitional state of the dentition is taken as an indication of the polarity of the morphoeline, the Subfamiliae Incertae palorchestids (*Ngapakaldia*, *Pitikan-tia*) must represent a more derived state, indeed, if they are even to remain within the Family Palorchestidae.

The following abbreviations are used in the text: NTM, Northern Territory Museum; NMV, Museum of Victoria (formerly National Museum of Victoria); AR, Palaeontology Laboratory University of New South Wales; CPC, Commonwealth Palaeontological Collection.

SYSTEMATICS

Family Palorchestidae Archer and Bartholomai Subfamily Palorchestinae Tate Genus *Propalorchestes* Murray

Propalorchestes Murray, 1986:195.

Type species. *Propalorchestes novaculacephalus* Murray, 1986:195.

Additional species. *Propalorchestes ponticulus* n. sp.; *Propalorchestes* cf. *ponticulus*.

Diagnosis. To the diagnostic features given in Murray (1986) I add the following: dentary shorter, thicker, more massive relative to size of dentition than in *Palorchestes painei*; intercoronoid sulcus absolutely and relatively wider and deeper, forming a definite crest extending to below M_2 , defining a deep subalveolar fossa. Horizontal ramus deepens anteriorly in contrast to attenuated depth of ramus in *Palorchestes painei*. Lower molars absolutely smaller and much smaller relative to the size of the horizontal ramus. Crowns lower, interloph valleys less steeply inclined toward the buccal and lingual sides than in *Palorchestes painei*. Anterior cingulum thicker, buccal cingulum more clearly defined than in *Palorchestes painei*. Maxilla relatively shorter, wider and deeper than in *Palorchestes* spp., zygomatic root of maxilla thicker and projects laterally perpendicular to the tooth row in contrast to a definite posterior slant of the process in *Palorchestes* spp. Anterior surface of infraorbital fossa flat; infraorbital fo-

ramen higher and relatively larger than in any *Palorchestes* species. Upper molars trapezoidal in outline shape, metaloph markedly narrower than protoloph. Buccal cingulum absent. Styler cusp E well developed; styler cusp D forming primary buccal cusp of metaloph, metacone reduced to a swelling between the metaconule ("hypocone") and styler cusp D. Conspicuous postmetacrista slants buccally from the metacone to the base of styler cusp E.

Propalorchestes novaculacephalus Murray (Figs 1-2, 3A-B)

Propalorchestes novaculacephalus Murray, 1986:195-211, figs 1-6.

Type material. HOLOTYPE - NTM P8552-10: left and part of the right side of neurocranium including most of the zygomatic arch and latex endocast (Murray 1986: figs 1-6). PARATYPES - NTM P862-27: right maxilla with M^{2-3} (Fig. 1A-B). NMV P187282: right dentary, containing $M_{3,5}$ (Fig. 2A-B), Camfield Beds, Northern Territory. AR 9682: isolated right M^3 , damaged on the buccal side, Riversleigh Queensland (Fig. 3B).

Type locality: Camfield Beds "...16 miles Southeast of Camfield Homestead in the north central Northern Territory" (Plane and Gatehouse 1968).

Formation. Camfield beds, light coloured calcareous sandstone, siltstone and limestone with basal ferruginization and silification at the top.

Age. Mid-Miocene, determined on the basis of the stage of evolution of diprotodontid species (Woodburne *et al.* 1985).

Description. Lower molars: $M_{2,5}$ essentially homomorphic; lower molars rectangular, shallowly waisted at the midvalley and equidistant between the trigonid and talonid (Fig. 2A-B). Relatively long and narrow (length to width proportions about 1.5: 1.0). Molar gradient a very slight increase from front to back, (M_3 is 98% of the length of M_5). Molars are about 15% shorter than *Palorchestes painei* and much smaller than in other *Palorchestes* species.

Breached lophids have crescentic, slightly oblique cementum exposures with basinlike expansions on the protoconid and hypoconid. Protoconid large, offset anterolabially and divided anteriorly from the metaconid by a deep sulcus originating from a fossette developed in the lingual margin of the precingulid.

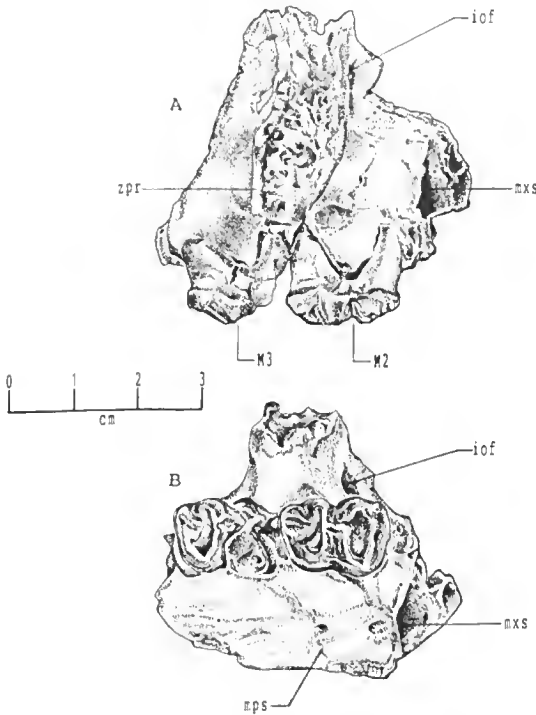


Fig. 1. Maxilla fragment of *Proplorchestes novaculacephalus*, paratype NTM P862-27. A, lateral aspect; B, ventral aspect. Abbreviations: iof, infraorbital foramen; mxs, maxillary sinus; zpr, zygomatic process; mps, maxillopalatine suture.

In worn molars this sulcus results in a narrowing of the lophid by an invaginated crescent of enamel similar to the neomorphic cuspid described in *Muramura williamsi* (Pledge, 1987).

Precingulid extends from labial side of anterior portion of protoconid, ascending and expanding slightly to the midline of the crown then descending abruptly before reaching the lingual side of the crown. The area of maximum expansion and height of the precingulid forms a small cuspid (paraconid). Cristid obliqua (midlink) broad, low, complete, situated near the longitudinal midline of each molar.

Faint, rounded labial cingulid present on all molars; interlophid valley on either side of the midlink broad, shallow and gently tilted towards the margins of the crown. Anteroposteriorly deep, rounded postcingulid extending slightly higher up the crown lingually than labially; connected to the middle of the hypolophid by a stout post-link demarcated on either side by deep, crescentic sulci. (Measurements approximate; M_3 length 16.6; anterior width 10.6; posterior width 10.0; M_4

length 16.5, anterior width 10.0; posterior width 11.0;

M_5 length 17.1; anterior width 11.0; posterior width 11.2).

Upper molars: M^2 broad, bilophodont, low crowned and trapezoidal in occlusal outline with the protoloph markedly wider than the metaloph (Figs 1A-B, 3A). Labial side of the crown composed of four stylar cusps. Moieties deeply divided labially by a sulcus extending from the midlink down to the cementoenamel contact of the crown. Protoloph broader and wider than metaloph; precingulum wide and deep anteroposteriorly, merging anterolabially with a short postparastylar crest terminating in a small paraconal facet.

Stylar cusp C, separated from the paracone by a shallow labial sulcus, forms the largest and buccal-most cusp of the protoloph. The posterior enamel crest of the breached loph curves sharply mesiad to form a short remnant of the centrocrista. The interloph valley is narrow and V-shaped, slightly expanded lingually behind the protocone to terminate at a well-developed lingual eingulum (postproto-crista). Within the interloph valley, slightly labial to the midline of the crown, a small rhomboidal fossa separates two enamel bulges at the base of each loph lingually and the remnant centrocrista labially, forming a double midlink-like structure.

The posterior moiety of the crown retains a strong triangular outline due to the prominence distobuccally of stylar cusp E. The labial cusp of the metaloph is composed of stylar cusp D which is separated from stylar cusp E by a deep sulcus. The metacone is represented by an enamel thickening about midway along the metaloph, and is connected to stylar cusp E by a long, obliquely oriented postmetacrista. The posterior surface of the metaloph angles anterolingually towards the metaconule ("hypocone") presenting a smooth, steeply angled face, emarginated by a well-developed postcingulum, situated low on the crown.

M^3 is similar to M^2 , with a slightly narrower metaloph and a less obliquely oriented and less prominent, though still remarkably robust, postmetacrista. (Measurements: M^2 length 16.8; anterior width, 13.2; posterior width, 12.0; M^3 estimated length, 15.7; posterior width, 11.6).

A possible M^4 is represented by a system C Riversleigh specimen (AR9682, paratype). This isolated, lightly worn crown (16.0 mm

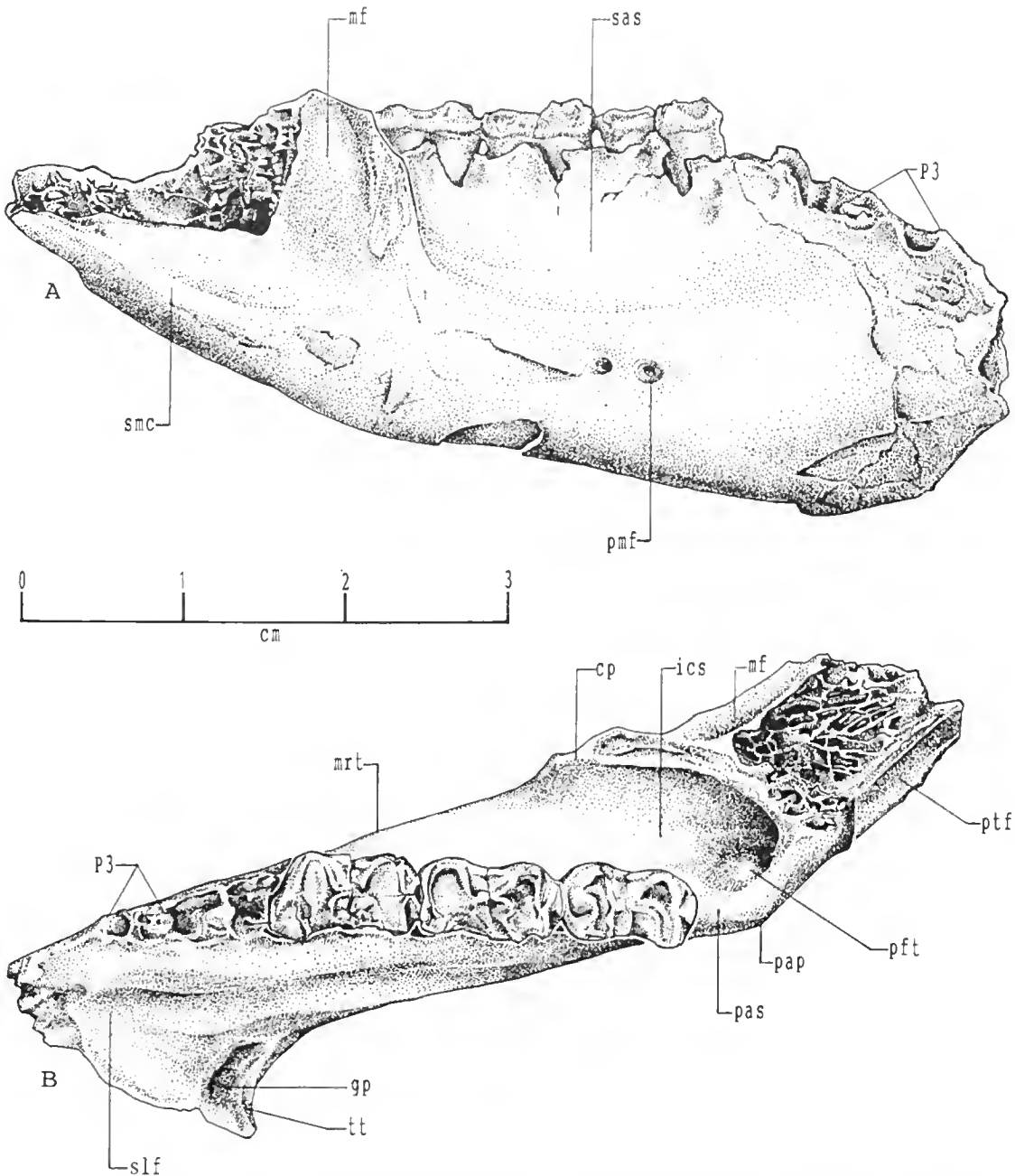


Fig. 2. Right dentary of *Propalorchestes novaculacephalus*, paratype NMV P187282. **A**, lateral aspect; **B**, dorsal aspect. Abbreviations: mf, masseteric fossa; sas, subalveolar sulcus; smc, submassteric crest; pmf, posterior mental foramen; ics, intercoronoid sulcus; cp, coronoid process; mrt, mid-ramal torus; pft, pit for fleshy temporalis muscle; ptf, pterygoid fossa; pap, postalveolar process; pas, postalveolar shelf; slf, sublingual fossa; tt, transverse torus; gp, genial pit.

long) shows all of the previously noted features in a slightly more suppressed form than the M^3 of the holotype. Because the M^3 of NTMP862-27 shows a similar reduction of its features, a gradient along the molar row is likely. However, AR9682 could also be interpreted as a slightly more derived M^3 of *Propalorchestes novaculacephalus*.

Dentary: The right horizontal ramus of *Propalorchestes novaculacephalus* (NMV P187282) is distinctive in its robustness and strong angularity. Compared to *Palorchestes painei*, *P. novaculacephalus* is slightly shorter, but significantly thicker (23.8 mm thick below $M_{3,4}$), and markedly triangular in section. In contrast to *P. painei*, the dentary

slightly increases in depth towards the symphysis, rather than tapering forward (42.0 mm deep below P_3 ; 40.0 mm below M_3). Relative to the length, depth and thickness of the horizontal ramus, the cheek teeth of *P. novaculacephalus* are proportionally much smaller than in *P. painei*. The 18.0 mm wide furrow-like intercoronoid sulcus, which is a conspicuous feature of palorchestines, is exceptionally broad in *P. novaculacephalus* and is continued forward to form a wide, sloping, shelf-like crest extending 25.0 mm from the molar alveoli to the mid region of the dentary. In other *Palorchestes* species a notable, though less distinguished (due to the weakness of the coronoid crest) subalveolar fossa is likewise present. In *P. novaculacephalus*, the coronoid crest is prominent and sharp; grading into a definitive mid-ramal torus below M_3 .

The lower portion of the ascending ramus is more produced laterally, and more confined dorsoventrally than in other palorchestines. Consequently, the masseteric fossa is deeper and the submasseteric crest ascending to the posterior masseteric eminence is thicker and more prominent. The pterygoid fossa is relatively deeper and more confined than in *P. painei*. As in other palorchestines, the digastric fossa is shallow and indistinct.

The postalveolar shelf is significantly shorter than in other palorchestine species. The postalveolar crest is higher, more robust and more laterally deflected. A distinct 10.0 mm diameter fossa for the fleshy temporalis insertion in the posterior end of the intercoronoid furrow in *P. novaculacephalus* is absent or indistinct in *Palorchestes* species.

Propalorchestes novaculacephalus has large, deep genial pits in the lower mid-posterior surface of the dentary symphysis, and a thick, though short transverse torus. *Palorchestes painei* has small genial pits located relatively higher on the posterior surface of the symphysis. No transverse torus is present. The dentary symphysis of *P. novaculacephalus* is shorter, more rounded, relatively deeper than in *P. painei* and apparently slightly less decurved.

Relative to the posterior margin of the symphysis and in combination with its less horizontal inclination, the diastema was perhaps shorter in *P. novaculacephalus* than in *P. painei*. The diastemal crest descends towards the incisor alveolus less steeply than in *P.*

painei, but overall, the dentaries of the two species appear to have been very similar.

Maxilla: The maxilla (paratype NTM P862-27) containing previously described M^{2-3} , corresponds in size and robusticity to the dentary (Fig. 1A-B). The oclusal surfaces and theotics of the assigned upper and lower dentitions match closely. Although there are no contact points with the cranium (holotype, NTM P8552-10) the maxilla readily corresponds to the projected missing proportions in relation to its shape and the thicknesses of its broken margins.

Compared to the same region in other *Palorchestes* species, the mediolateral thickness of the maxilla above M_2 is much greater in *Propalorchestes novaculacephalus* due to the formation of a large sinus. This sinus is not present in *P. parvus* and is either reduced or absent in *P. painei*. The expanded maxillary antrum creates a conspicuous swelling beneath the infraorbital foramen in *P. novaculacephalus*, and a deep groove for the emergent infraorbital nerve is inscribed on its external surface. Unlike *P. parvus*, in which the facial plane slants posteriorly, the anterior surface of the zygomatic root abruptly projects at a right angle to the surface of the maxilla. In some respects, *P. novaculacephalus* more closely resembles *P. painei*, in which the zygomatic roots and jugals must have presented a broad, flat facial plane extending around the orbits and nearly up to the corresponding lateral expansions of the frontal crests. However, the entire facial plane of *P. painei* also retreats more than in *P. novaculacephalus*. The relatively large diameter of the infraorbital nerve canal and foramen (10.0 mm by 8.0 mm) and its slightly elevated position compared to *P. parvus*, are also common to *P. painei*.

Judging from the more anterior position of the maxillopalatine suture, which transects the palate between M^2 and M^3 , the palate must have been proportionally different from *P. painei*. This could, of course, indicate that the molar series is M^{3-4} , but relative to the zygomatic root, the position of the molars correspond closely to M^{2-3} in *Palorchestes painei*. However, assuming that a more primitive condition was manifest, similar to that of *Muramura williamsi* (Pledge, 1987), the position of the molars relative to the maxillary process of the zygoma in *P. novaculacephalus* might eventually be found to differ substan-

tially from that of *Palorchestes* species. In any case, I have taken the least speculative course, and await the resolution of the problem from a more complete specimen.

The internal surface of the maxilla preserves the contour of the internal nares, which was relatively more expanded than in the corresponding regions of *P. parvus*.

Palorchestes painei appears to show an intermediate condition between *P. novaculacephalus* and *P. parvus*. Overall, the maxillary fragment indicates that the midfacial region in *P. novaculacephalus* was relatively more laterally expanded and deeper than in any species of *Palorchestes* and perhaps that the palate was shorter. The large infraorbital foramen and deep, broad, perpendicular facial plane of the zygoma, ostensibly for the attachment of nasolabialis musculature, strongly suggest the presence of a trunk-like appendage in this species.

There is however, an indication that the narial aperture may have been much wider transversely and perhaps relatively shorter than in *P. painei*. In all *Palorchestes* species, the plane of the zygoma slopes posteriorly about 10 degrees relative to the occlusal line, whereas in *Propalorchestes novaculacephalus* it slopes to about the same extent anteriorly, as in more typical diprotodontoid marsupials. This indicates that the nasofrontal region projected more anteriorly than in *Palorchestes painei*, which would result in a greater overhang of even highly reduced nasal bones. As no portion of the rostrum of this species has been recovered, I can only conclude that while *Propalorchestes novaculacephalus* probably had a well-developed tapir-like trunk, its proportions and perhaps its extent of mobility differed somewhat from the more evolved *Palorchestes* species.

In conjunction with its cranial morphology (holotype NTM P8552-10), *Propalorchestes novaculacephalus* had a deep cranium, with a high, narrow braincase and robust, wide zygomatic arches which terminated abruptly in a wide, flat facial platform for the attachment of the facialis muscles of the trunk. The rostrum was probably relatively broader, shorter and less downturned than in *Palorchestes painei*. The fragmentary remains of this species indicate that the more primitive palorchestines had fully developed, by mid-Miocene times, a characteristic masticatory complex which is distinctive for the subfamily (Murray 1986).

Indeed, no other species within this lineage shows this constellation of characters as conspicuously, relative to the size of its dentition and braincase. Presumably, as palorchestines increased in size, an allometric adjustment of the adductor complex resulted in the moderation of some of these features in later forms.

***Propalorchestes ponticulus* n.sp.**
(Fig. 3C)

Type material. HOLOTYPE - AR1802: isolated right M_2 (Fig. 3C), D-site (System A, Archer *et al.* 1989) Riversleigh, Queensland.

Provisionally referred material. AR11302: ? M_5 (Fig. 3E,F), Wayne's Wok Locality (System B, Archer *et al.* 1989) Riversleigh Queensland. AR1779: dentary fragment (Figs. 3D; 4A-C), fully fused symphysis with portion of M_2 , no site designated, Riversleigh, Queensland. SGM1008: fragment of dentary, hemimandibles fully fused at the symphysis with P_3 - $M_{2,3}$ crowns sheared off (Fig. 4D-F), Sticky-Beak locality (System A, Archer *et al.* 1989), Riversleigh Queensland.

Type locality. "D-Site", northern tip of Carl Creek Limestone exposures, 2.4 km South of Verdon Creek (Tedford, 1966).

Formation. Carl Creek Limestone: mottled, vuggy cream and yellow limestone.

Age. Late Oligocene or early Miocene (Tedford 1966; Archer *et al.* 1989).

Diagnosis. Smallest palorchestine, with cheek teeth similar in size to *Pitikantia*; characteristic, nearly equal-sized, narrow lophids and anterior displacement of the protoconid; low, centrally divided and labially situated cristid obliqua, weaker than in other palorchestines, deep, tapering postcingulid and hindlink. Differs from other palorchestines but resembles *Pitikantia dailyi* in having a more labially situated cristid obliqua, deeply notched in the interlophid valley and traversing a narrower declivity between the lophids; differs from *Pitikantia dailyi* in having a secondary swelling on the anterolingual side of the hypolophid, in having a clearly defined preproto-cristid immediately mesial to the protoconid and a broad shallow sulcus in the middle of the anterior surface of the protolophid of M_2 .

Description. Considered to be an M_2 on the basis of its narrow interproximal facet and less expanded protoconid (Fig. 3C); it is also pos-

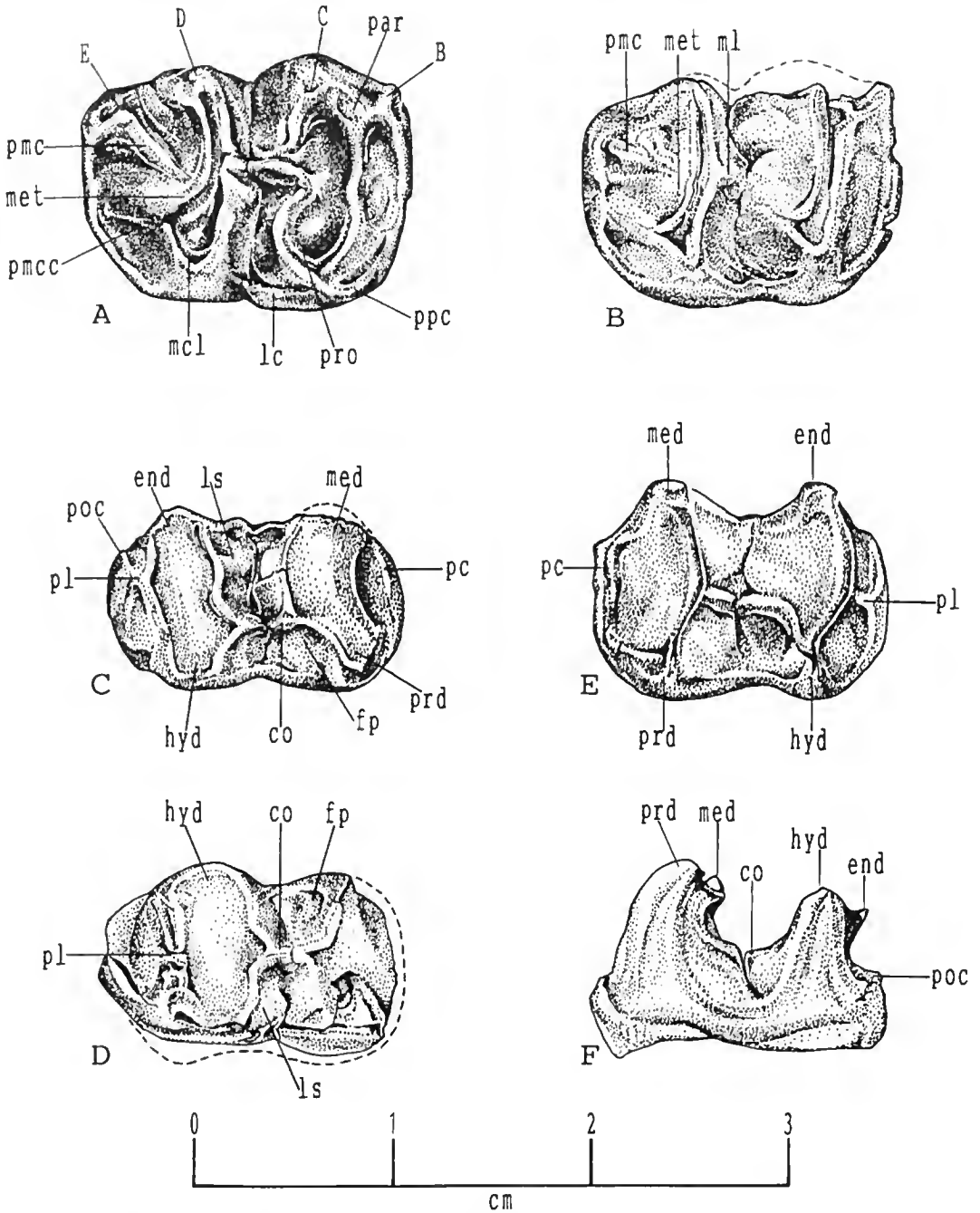


Fig. 3. Upper and lower molars of *Propalorchestes* species. A, upper right second molar of *Propalorchestes novaculacephalus*, paratype NTM P862-27; B, upper right third or fourth molar of *Propalorchestes novaculacephalus*, paratype AR9682; C, lower right second molar of *Propalorchestes ponticulus* sp. nov., holotype AR1802; D, lower left second molar of *Propalorchestes* cf. *ponticulus*, SGM 1008; E, occlusal aspect of left lower ?fifth molar of *Propalorchestes* cf. *ponticulus*, AR11302; F, labial aspect of left lower ?fifth molar of *Propalorchestes* cf. *ponticulus*, AR11302. Abbreviations: E, styler cusp E; D, styler cusp D; C, styler cusp C; B, styler cusp B; par, paracone; ppc, preprotocrista; pro, protocone; lc, lingual cingulum (postprotocrista); mcl, metaconule ("hypocone"); pmcc, postmetaconulecrista; met, metacone; pmc, postmetaconulecrista; ml, "midlink"; end, entoconid; ls, lingual swelling of the base of the hypolophid; mcd, metaconid; pc, precingulid; prd, protoconid; fp, fossa behind protoconid; co, cristid obliqua; hyd, hypoconid; pl, postlink; poc, postcingulid.

sible that the more prominent preprotocristid is a gradient-related feature, as no complete *Propalorchestes novaculacephalus* cheek-tooth series is known. Compared to *P. novaculacephalus*, the roots are small relative to the crown and less divergent from one another anteroposteriorly.

Judging from the narrower interloph valley, and depth of the breached lophids, the lophids were relatively high and steep. The crown base lacks the distinctive narrow swellings above the cemento-enamel junction in *P. novaculacephalus*. Although the protoconid is offset anterobuccally as in other palorchestines, it is not conspicuously hypertrophied. This feature may also relate to the molar gradient, but extrapolating from the condition in *P. novaculacephalus*, the condition is adduced to be a characteristic of the entire molar series.

The cristid obliqua is divided in the mid-valley rather than continuous as in *P. novaculacephalus*. It is situated in the buccal third of the interlophid valley rather than traversing the longitudinal midline of the tooth. This feature is also present on the M_2 of *Pitikantia dailyi*. The anterior surface of the protolophid is concave due to a shallow sulcus commencing immediately above the precingulum. This concavity is accentuated by a distinct but low, broad and steep preprotocristid (forelink) and a low, broad swelling emanating from the base of the metalophid on the lingual side.

The anterior surface of the hypolophid is analogous to the protolophid. The labially situated cristid obliqua delineates a shallow concavity in the middle third of the tooth, accentuated lingually by a distinct swelling of the enamel on the anterior surface of the lingual third of the hypolophid. The lingual swelling, resembling a faint mid-link, was a low bulge in the enamel that only becomes an obvious feature of the hypolophid structure after advanced attrition of the crown.

The labial interlophid valley is more distinctively concave behind the protolophid than in *P. novaculacephalus*. This indicates that the posterior surface of the protolophid was more hollowed-out and probably more posteriorly recurved on the labial protolophid apex than in *P. novaculacephalus*. Like *P. novaculacephalus*, the interloph surface was less cambered labially and lingually than in other palorchestines. A short, weak lingual cingulum is present. (Measurements: length, 14.5; anterior width 9.2; posterior width, 10.5).

Etymology. Latin, *ponticulus* "little bridge" in reference to the weaker, shorter, partially divided midlink and alluding to its apparent phyletic position relative to other palorchestids.

Propalorchestes cf. ponticulus
(Figs 3D-F, 4)

Material. ARI1302: a perfectly preserved lower molar crown of a palaorchestine marsupial from the Wayne's Wok Locality, Riversleigh, Queensland (Fig. 3E,F). According to Archer *et al.* (1989) Wayne's Wok is a system B (provisionally early-Miocene) equivalent.

Remarks. The specimen may represent an encrypted M_5 in which the enamel surface was only just completed and was perhaps slightly dehydrated before fossilization. However, the specimen preserves, in a conservative way, some of the key features of *Propalorchestes ponticulus* and is therefore assigned provisionally to that species. These characters are: protolophid offset as in typical palorchestines, but not greatly enlarged at the base, well developed preprotocristid, which however, becomes faint as it reaches the precingulid; a shallow sulcus on the anterior surface of the protolophid; a somewhat hollow posterior surface of the protolophid immediately below the protolophid; a swelling at the base of the anterior surface of the hypolophid; crown base not swollen above the cemento-enamel junction; divided cristid obliqua confined to the labial side of the interloph valley, though stronger, higher and not situated as labiad as in the holotype of *Propalorchestes ponticulus* (ARI802).

The crown is slightly longer (0.3mm) and relatively broader anteriorly (0.8mm) than the holotype, although the slight front to back molar size increase in palorchestines could easily account for this. The primary differences are that the protolophid is slightly wider than the hypolophid (characteristic of the M_5 of *Palorchestes* species), and that the floor of the interloph valley is more cambered on either side of the midlink. (Measurements: length 15.1, anterior width, 10.0, posterior width, 9.6).

Though slightly smaller and otherwise less derived than other palorchestine species, the lophids of *P. ponticulus* are high, sulcate anteriorly and recurved posteriorly as in the later palorchestines. Because all of the *P. novacu-*

lacephalus specimens are heavily worn, it can only be inferred that they were similarly high-crowned but larger, thicker, with a wider interloph valley and a relatively larger protoconid.

The provisionally referred specimen AR1779 is a dentary fragment with both hemimandibles fully fused at the symphysis.

The anterior portion of the protolophid and the lingual sides of both lophids of M_2 are broken and the lophids are severely worn. Based on the size of the crown base and roots, the Riversleigh M_2 is slightly smaller than the M_2 of the Camfield *P. novaculacephalus* (Figs 3D, 4A-C).

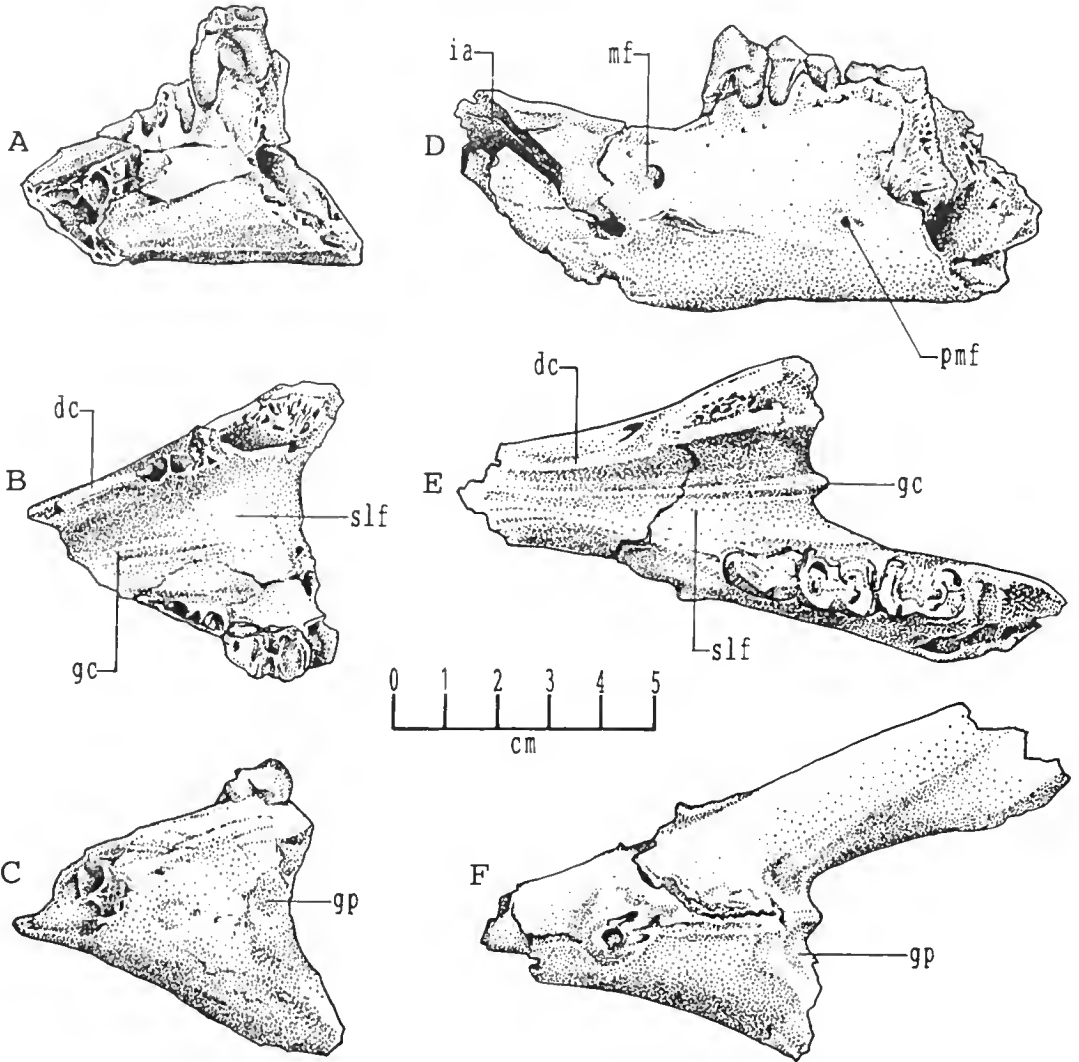


Fig. 4. Dentary fragments of *Propalorchestes* cf. *ponticulus*. These specimens share a variety of features with *Pitikantia*, *Ngapakaldia* and *Propalorchestes*. A, anterior portion of the dentary of AR1779, lateral aspect; B, dorsal aspect of AR1779; C, ventral aspect of AR1779; D, lateral aspect of SGM 1008. Abbreviations: dc, diastemal crest; gc, genial crest; gp, genial pit; slf, sublingual fossa; ia, incisor alveolus; pmf, posterior mental foramen. The profile of the dentaries more closely resemble those of the genera *Ngapakaldia* and *Pitikantia* than the genus *Palorchestes*; like the former genera, there is an apparently greater front-to-back molar gradient and the incisor implantation is more like that of *Ngapakaldia* than *Palorchestes*. Like *Propalorchestes* and *Palorchestes*, the dentary symphysis is fully ankylosed, with a long, deep sublingual fossa, but the genial pits are located on the ventral surface rather than posterior to the symphysis. Because A-C (AR1779) retains a lower second molar that resembles the holotype of *P. ponticulus*, and because the dentary morphology of D-E (SGM 1008) closely resembles AR1779, I have provisionally included them in the species *P. ponticulus*. These fragments support a close relationship of *Pitikantia*-like forms to the palorchestines and may represent a stage of evolution close to their divergence.

The remnants of the crown reveal a narrower, steeper interloph valley than in *P. novaculacephalus* and the presence of an enamel bulge on the anterior surface of the base of the entoconid is only just apparent. The midlink is short, though well-developed and situated immediately labial of the midline of the tooth. The dentary fragment is more informative. The portions in common with *P. novaculacephalus* indicate that AR1779 was not as deep or thick transversely through each hemimandible.

The symphysis is shallower posteriorly and less steeply inclined. The genial pits are located on the ventral surface of the symphysis rather than comparatively high up on the posterior surface. As in later palorchestines, the diastemal crests are prolonged anteriorly to form a deep, U-shaped sublingual trough.

The provisionally referred specimen SGM1008 is a more complete dentary fragment, but lacking cheek tooth crown details (Fig. 4 D-F). It is therefore aligned with the formerly described specimen on the basis of its overall morphological similarity and the comparison of the sizes of the cheek tooth alveoli. Although the P_3 crown is damaged on the lingual side, the occlusal and lateral profile of the tooth, combined with its size and proportions, the steepness and breadth of the anterior cuspid and the indication of a sulcus just lingual to the preprotoeristid all favour an incipiently palorchestine morphology.

The proportions of the crown bases of the molars and their alveoli indicate that the molar gradient was very slight, as in all palorchestines. The lateral surface of the anterior portion of the horizontal ramus is flat, moderately deep with a broad, rounded inferior border. The gently upturned symphysis is long, and narrows gradually towards the incisor alveoli. The incisor alveoli are large, vertically oriented, oval cavities separated throughout their considerable depth by a thin bony septum. The implantation angle of the incisors was shallow, but due to a lack of symphyseal deflection, typical of *Palorchestes* species, SGM1008 had only moderate procumbency of the incisors, comparable to that of *Pitkantia dailyi* (Stirton, 1967). As in all known palorchestines, the diastema is exceptionally long and forms a narrow trough extending to the base of the incisor crowns.

In contrast to *P. novaculacephalus*, the genial pits are located on the ventral surface of

the symphysis as in AR1779. These are separated by a prominent genial crest that extends anteriorly within the sublingual sulcus to below the P_3 . A remnant of this crest is visible in AR1779, immediately anterior to the level of P_3 , and as the posterior portion of the symphysis is severely weathered, the genial crest must have been equally well developed.

Although the fossil material is fragmentary, I am confident that the presence of these two palorchestine species in the lower Oligocene and mid-Miocene of Australia will eventually be confirmed by more complete specimens. *Propalorchestes ponticulus* is a less robust form, that could be ancestral to *P. novaculacephalus* as the specimens appear to be confined to system B and A faunas at Riversleigh. Experience with other genera from Camfield, Riversleigh and Wipajiri (*Wakaleo* spp., *Neohelos tirarensis*) has shown that such species distinctions as I have just made become blurred when larger samples are obtained. It is therefore with the same reservation that Murray and Megirian (1990) place upon the distinction of *W. vanderleueri* from *W. oldfieldi* that I designate *P. ponticulus* as distinct from *P. novaculacephalus*. A closer relationship of SGM 1008 to the genus *Pitkantia* cannot be ruled out. However, that Riversleigh specimen differs from *Pitkantia dailyi* in being more robust, in possessing a posterior mental foramen, in having an apparently more strongly ankylosed symphysis and in showing some differences in the cheektooth crown proportions and morphology.

CONCLUSIONS

Tedford *et al.* (1977) first noted that wynyardiid upper molars show a transitional stage in the development of bilophodont molars in which the labial side of the lophs are composed of stylar cusps B, C and D, with the metacone and paracone taking up a median position within gradually evolving transverse crests. This evidence supported the observations of Winge (1941), Ride (1971) and Archer (1976) that a selenodont pattern resembling phaseolaretids and peramelids, gave rise to the highly developed, albeit superficially uncomplicated bilophodonty characteristic of, for example, the nototherine and zygomatic Diprotodontidae. The traditional descriptive nomenclature (Stirton *et al.* 1967) applied to the Diprotodontidae assumed that the hy-

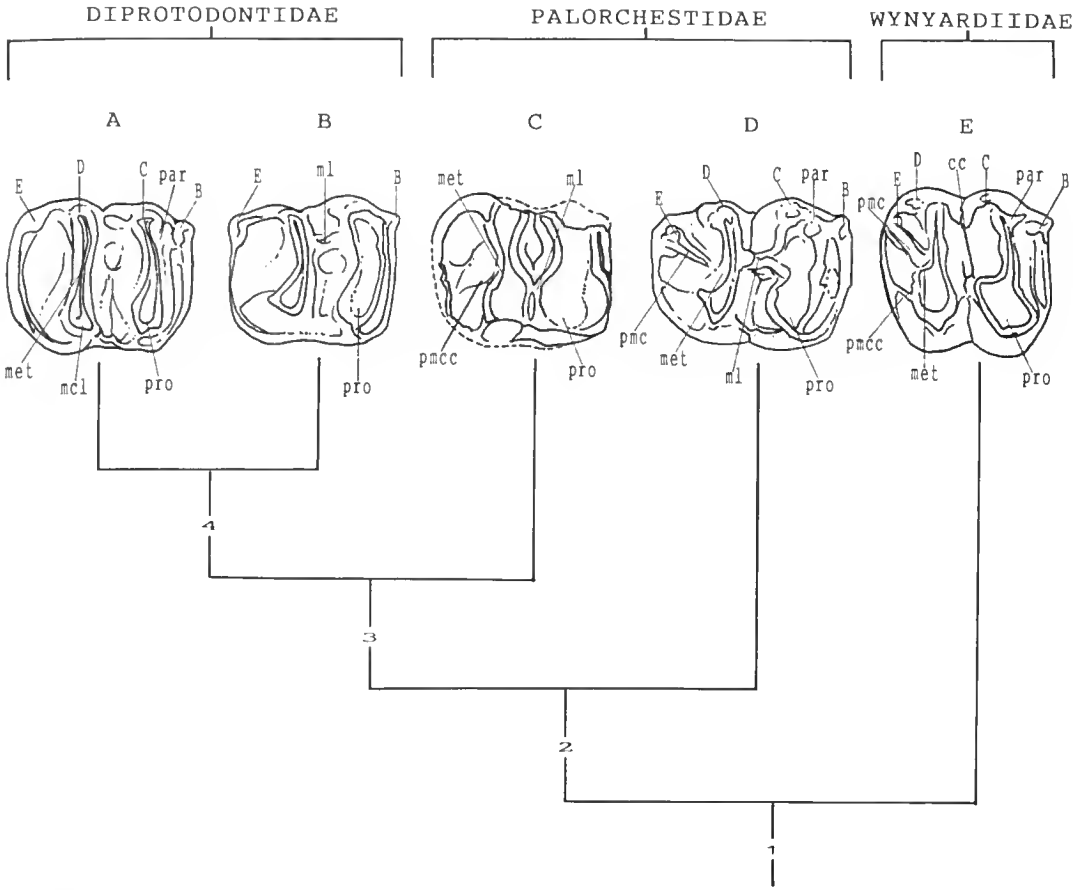


Fig. 5. Phenogram depicting a hypothesis of the evolution of bilophodont "diprotodontoids" from a selenobilophodont ancestor partially based on the morphology of the second upper molar. **A**, *Neohelos* (Zygomaturinae); **B**, *Pyramios* (Diprotodontinae); **C**, *Ngapakaldia* (Subfamily Incertae); **D**, *Propalorchestes* (Palorchestinae); **E**, *Muramura* (Wynyardiidae, Subfamily Incertae). **1**, (synplesiomorphic) expression of "posterobuccal triangle"; **2**, (synapomorphic) loss of "posterobuccal triangle"; **3**, (synapomorphic) suppression of the metacone; **4**, (synapomorphic) widening of interloph valley and transverse expansion of lophs. The postulated connection between *Propalorchestes* and wynyardiids is deduced from phenetic resemblances; possible synapomorphies include the robust, elongated postmetacrista and the distinct swelling in the middle of the proto-loph that could have been a precursor to the double midlink complex (?centrocrista + postparacrista) in *Propalorchestes*. These resemblances are more compelling than with other selenodont vombatimorphians or phascolarctomorphians.

pocone and the metacone formed the respective lingual and buccal cusps of the metaloph.

Tedford *et al.* (1977: fig. 3A-D) illustrated a series of second upper molars of a wynyardiid, two vombatoids and a phascolarctid from the Pinpa Local Fauna. This series clearly demonstrated the cusp homologies from a selenodont phascolarctid in which the hypocone was not present, to an incipiently bilophodont wynyardiid, that unambiguously demonstrated the intraloph position of the metacone, absence of the hypocone and labial position of stylar cusp D, to form the metaloph of the molar, with the metaconule as the proxy "hypocone".

Although wynyardiids such as *Muramura williamsi* Pledge (1987) and *Namilammeta snideri* (Rich and Archer, 1979) are incipiently bilophodont, they retain a predominately selenodont pattern. The possibility of paraphyletic bilophodonty could not be ruled out, particularly with respect to the diprotodontids, among which no clear representation of the conspicuous posterobuccal triangle of cusps (D, E and metacone) remains.

Propalorchestes novaculacephalus is fully bilophodont but retains the "posterobuccal triangle" of the wynyardiids and demonstrates the reduction of the metacone and hypertrophy of the metaconule to form the metaloph

(Fig. 5). Moreover, a hypso-bilophodont pattern, in which the postmetacrista and discrete expression of the metaconule and styler cusp D, obscured by the development of the loph, had developed in parallel among the Palorchestinae. Among species of the more derived genus *Palorchestes*, a fully bilophodont pattern is present, and only by tracing the specific details of its transformation can the homologous structures relating to the obfuscated selenodont heritage of the lineage be understood.

It is by close analogy to this subtle transition, that I consider the characteristic bilophodonty of the Diprotodontidae to have occurred. By association with synapomorphic features in the basicranium (the large epitympanic fenestra) and the dentition (P^3 morphology) we can assume a close relationship between the fully bilophodont genus *Ngapakaldia* and the Palorchestinae. Because *Ngapakaldia* has further suppressed its selenodont heritage, it represents a state, too derived to be directly ancestral (e.g. absence of a postmetacrista), but immediately post-transitional, to the diprotodontidae (Zygomaturinae, Diprotodontinae).

SUMMARY

The genus *Propalorchestes* was initially diagnosed on the basis of a cranial fragment representing a primitive palorchestine. Dentitions assigned to this genus are likewise plesiomorphic, and show the transition between selenodont wynyardiid or wynyardiid-like dentitions and the fully evolved bilophodont dentitions that characterize members of the family Diprotodontidae. Derived palorchestids paralleled the diprotodontids by also incorporating styler cusp D into the metaloph while suppressing the metacone; therefore little, if any, indication of this state is evident in the later Tertiary genus *Palorchestes*.

Palorchestine palorchestids were present in the late Oligocene as evinced by *Propalorchestes ponticulus*. In retaining a remnant metacone and a large postmetacrista, *Propalorchestes novaculacephalus* from the mid-Miocene (post-Wipajiri) Camfield beds appears be less derived than the Riversleigh system C specimen. The distinctive features of the upper molar crowns observed for *P. novaculacephalus* from Camfield are obviously pres-

ent, though suppressed in the Riversleigh example. Although this could be attributed to changes along the molar gradient, the possibility of a chronological difference has not been eliminated.

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ALKWERTATHERIUM WEBBI, A NEW ZYGOMATURINE
GENUS AND SPECIES FROM THE LATE MIOCENE
ALCOOTA LOCAL FAUNA, NORTHERN TERRITORY
(MARSUPIALIA: DIPROTODONTIDAE).

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ABSTRACT

Alkwertatherium webbi, gen. et sp. nov., possesses characteristics structurally intermediate between the diprotodontine genus *Pyramios* and the zygomaturine genus *Plaisiodon* of the family Diprotodontidae. In its expression of a clearly differentiated and well-developed parastyle on the P³, *Alkwertatherium* is aligned with the Subfamily Zygomaturinae. In its absence of a hypocone on the P³ and its markedly constricted diastemal palae, *Alkwertatherium* resembles the members of the Subfamily Diprotodontinae. *Alkwertatherium* was derived from diprotodontines at a structural grade similar to that of *Pyramios*. It may have shared ancestry with the primitive zygomaturines *Plaisiodon* and *Nimbadoron*. *Pyramios*, *Alkwertatherium* and *Plaisiodon* exemplify a gradual structural succession in cheek tooth and cranial morphology from the Diprotodontinae to the Zygomaturinae.

KEYWORDS: Late Miocene marsupials, Alcoota Local fauna, Diprotodontidae, zygomaturinae, zygomaturine origins, Diprotodontinae, nototheriines, *Pyramios*, *Plaisiodon*.

INTRODUCTION

Primarily a description of a new taxon, this study also attempts to address the character states of the Diprotodontidae in relation to *Alkwertatherium*, which is compared with other Cheltenhamian-Mitchellian equivalent forms in considerable detail, incorporating a brief review of the mid- to late Miocene diprotodontid genera.

At least three large genera and one smaller diprotodontid genus are present in the Alcoota Local Fauna. The molar dentitions of the three largest genera: *Pyramios alcootense* Woodburne, *Plaisiodon centralis* Woodburne and *Alkwertatherium webbi*, gen. et sp. nov., overlap in size and morphology. Isolated molars of these genera are difficult to discriminate without the associated third premolar. It is possible, judging from the size distributions, that the tables of measurements provided by Woodburne (1967a) may contain an admixture of these forms. Sampling of the Alcoota site between 1985 and 1989 indicates that *Pyramios* and *Alkwertatherium* are un-

common and therefore the inclusion of the odd molar of these species would not seriously influence the statistical definition of *Plaisiodon*.

The upper third premolars of three of the four Alcoota genera are readily distinguishable.

The P³ of *Pyramios alcootense* is characterized in having a weakly expressed or absent parastyle, absence of a hypocone and presence of a faint posterobuccal cingulum. Its broadly trilobate occlusal profile, large, conical protocone and equally large triangular, undivided parametacone with a short, steeply descending postparametacrista are associated with diprotodontine (Diprotodontinae) diprotodontids. The large size of the P³ relative to the molars is more in proportion with the condition in zygomaturines. In Plio- Pleistocene diprotodontines, (eg. *Euryzygoma*, *Nototherium* and *Diprotodon*) the P³ is reduced relative to the molars.

Plaisiodon centralis permanent upper premolars are elongated, with a prominent, posteriorly curved parastyle and a long, blade-

like postparametacrista. The posterobuccal cingulum is absent. The hypocone is at least incipiently present, sometimes budding off the posterior side of the protocone. In some individuals the parametacone is weakly differentiated into two conjoined cusps, but the conspicuous vertical buccal sulcus that accompanies such a division in the zygomaticurines *Kolopsis torus* Woodburne and *Zygomaturus* species is less distinct. *Kolopsis torus* has a broad, low molariform, 5-cusped P³ with a divided parametacone, well-developed anterobuccal and posterobuccal cingulae and a low, but distinct mesostyle.

While these three genera cannot be mistaken for any other diprotodontid. *Alkwertatherium webbi* upper third premolars have a large parastyle combined with a *Pyramios*-like absence of the hypocone; steep, triangular undivided parametacone and large conical protocone. A weak posterobuccal cingulum is present. An indistinct mesostyle is confluent at its apex with the parametacone, as in *Pyramios*. The premolar is similar to that of *Pyramios*, but larger relative to the molars, and distinctive in its possession of a massive, strongly differentiated parastyle.

The apparent absence of unambiguous discriminative features in the upper molar dentitions and the diprotodontine-zygomaturine continuity in the premolar morphology resulting from the discovery of *Alkwertatherium* raises some issues in diprotodontid systematics. On the basis of cranial characters, *Alkwertatherium* is very similar to *Plaisiodon*, but otherwise expresses affinities with *Pyramios*.

Abbreviations of museum accession numbers: NTM, Northern Territory Museum; NMV, Museum of Victoria (formerly National Museum of Victoria); CPC, Commonwealth Palaeontological Collection (BMR); SGM, Spencer and Gillen Museum (NTM Alice Springs); VCMP, University of California Museum of Paleontology.

SYSTEMATICS

Family Diprotodontidae Gill Subfamily Zygomaturinae Stirton, Woodburne and Plane

Genus *Alkwertatherium* gen. nov.

Type species. *Alkwertatherium webbi* sp. nov.

Diagnosis. Cranium narrower (relatively longer in proportion to width) than *Pyramios*, *Plaisiodon*, *Kolopsis* or *Neohelos*; dorsal profile forming a distinct vertex, with weak frontal and low sagittal crests resembling the type *Plaisiodon centralis* (CPC 6784). Constricted and elongated postsquamosal lamina, similar to, but more extreme than in *Neohelos* or *Plaisiodon*; occiput lower and narrower than any similar-sized diprotodontid. Rostrum narrower than in *Pyramios*, *Plaisiodon* and *Neohelos*, constricted at the level of the infraorbital foramen; diastemal palate similar to, though longer and more narrowly constricted immediately anterior to P³ than in *Pyramios*; laterally expanded premaxillary palate, as in *Pyramios*, but with a shallow, wide, as opposed to a narrow, deep, interincisival fossa. Nasals elevated slightly and expanded anteriorly as in *Plaisiodon* and *Neohelos*, not downturned and pointed as in *Pyramios*. Zygomatic arch long, as deep anteriorly as posteriorly, contrasting with the short, anteriorly narrowing zygomatic arches of *Pyramios*. Squamosal-jugal suture long, squamosal process extends to beneath the orbit as in *Pyramios*; contour of arch relatively flat as in *Plaisiodon* and in contrast to the strongly-bowed zygomatics of *Pyramios*; masseteric processes broad and short as in *Neohelos*, in contrast to long, robust processes in *Pyramios*; dccp, well-defined nasolabialis fossa similar to *Plaisiodon* and *Neohelos*, but differing from *Pyramios* in which the fossa is poorly developed. Trilobate, posteriorly broad P³ composed of a large, slightly buccally offset parastyle, pyramidal, undivided parametacone and conical protocone; hypocone absent, weak posterobuccal cingulum present, differing from *Pyramios* in having a well-developed parastyle as large or larger than that of *Plaisiodon*. Upper molars more similar to *Pyramios* than to *Plaisiodon* with gradual progression in molar width from M²⁻⁴; wide interproximal contact between P³ and M², but differing from *Pyramios* in having a more distinct, thicker lingual cingulum, wider mouth of the lingual side of the interloph sulcus, more concave posterior surface of the hypoloph, more distinct "midlink", large metastyle on M¹ and much narrower hypoloph on M⁵. A conspicuous obliquity of the lophs of M²⁻³ resembles the condition of later diprotodontines, but *Plaisiodon* among the zygomaticurines, has similarly obliquity of the lophs. Dentary hori-

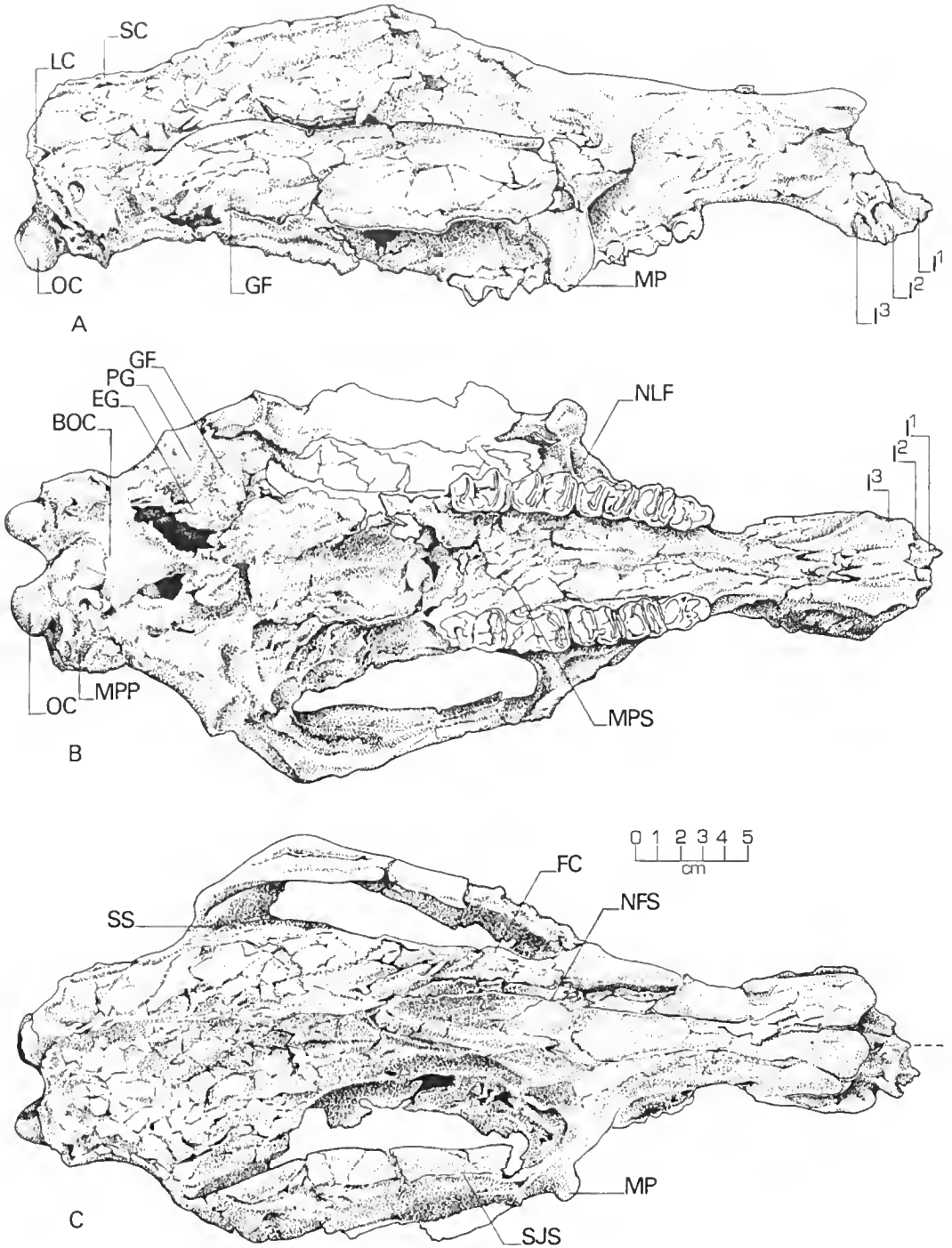


Fig. 1. *Alkwertatherium webbi* gen. et sp. nov. (holotype, SGM 888). **A**, lateral aspect of cranium; **B**, ventral aspect of cranium; **C**, dorsal aspect of cranium. Abbreviations: LC, lambdoid crest; OC, occipital condyle; GF, glenoid fossa; MP, masseteric process; In, incisors; BOC, basioccipital; EG, entoglenoid swelling; PG, postglenoid process; NLF, nasolabial fossa; MPP, mastoid/paroccipital process; MPS, maxillo-palatine suture; FC, frontal crest; NFS, nasofrontal suture; SC, sagittal crest; SS, squamosal sulcus; SJS, squamosal-jugal suture.

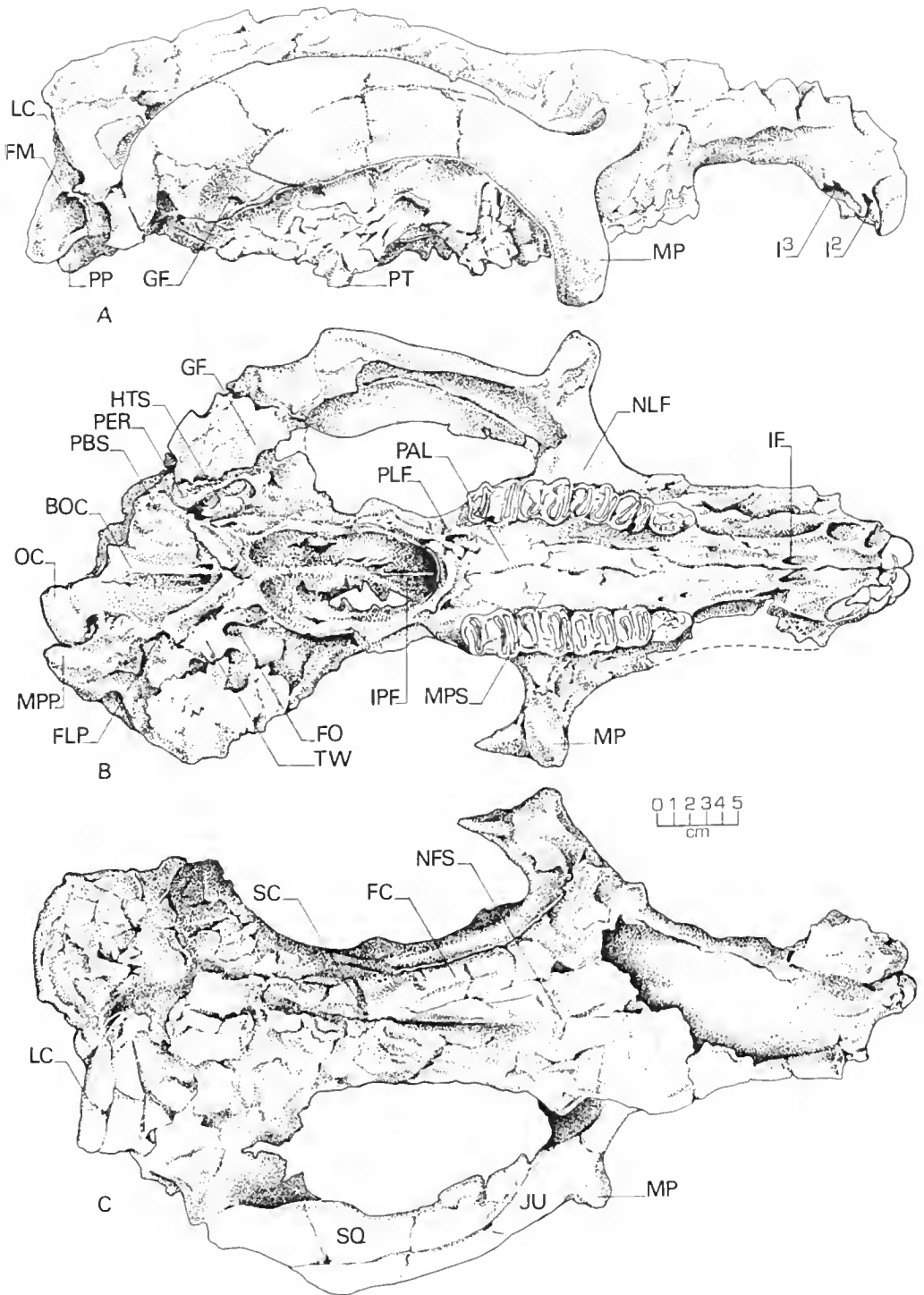


Fig. 2. *Plaisiodon centralis* Woodburne, 1967 (SGM 871) for comparison with *Alkwertatherium webbi*. A, lateral aspect of cranium; B, ventral aspect of cranium; C, dorsal aspect of cranium. Abbreviations not included in Fig. 1: FM, foramen magnum; PP, paroccipital process; PT, pterygoid; HTS, breached hypotympanic sinus; PER, periotic; PBS, paroccipital-basioccipital suture; FLP, foramen lacerum posterior; TW, vestigial squamosal tympanic wing; IPF, interpterygoid fossa; PLF, posterolateral palatine foramina; PAL, palatine; IF, incisive foramina; SQ, squamosal; JU, jugal.

zontal ramus deep but relatively thin in section, inferior border straight and proportionally similar to *Plaisiodon*; differing from the short, deep, thick-sectioned ramus with convex "rocker" inferior border profile of *Pyramios*; straight, strong, high diastemal crests expanded into wide, flattened surfaces anteriorly and elongated diastema resembling *Plaisiodon* proportionally but more similar to *Pyramios* in its expression: dentaries unankylosed at the symphysis as in *Plaisiodon* and in contrast to *Pyramios*; symphysis extremely long and horizontal, extending to posterior M_2 , as opposed to *Pyramios* in which the symphysis is short and steeply inclined. Sublingual fossa long, narrow and horizontal, similar to *Plaisiodon*, much longer and more horizontal than in *Pyramios*; lower incisors wide, thick, and spatulate, resembling those of *Pyramios* and the New Guinea Pliocene zygomaturine, *Kolopsoides*.

Etymology. *Alkwerta* (= *Alcoota*) means "native shield" in Eastern Arrente or Iliaura language. *Alkwerta* is the accepted Arrente orthography of *Alcoota*. The area around Alcoota Homestead was named after a rocky landmark resembling a shield. As this object is similar in shape to the parastyle of the upper third premolar, reference is made to the prominence of the cusp which appears to stand up in front of the tooth like a shield. The generic name *Alkwertatherium* also emphasizes the uniqueness of the Alcoota Local Fauna by designating a form with the locality name.

Alkwertatherium webbi n.sp
(Figs 1-13)

"*Plaisiodon*" *webbi* Murray, 1989:12 (nomen nudem).

Type material. HOLOTYPE - SGM 888: nearly complete, slightly crushed and asymmetrically distorted eranium missing the incisors, paroccipital processes and portions of the basicranium. PARATYPES - SGM 883: associated dentaries missing third premolars and posterior portion of the ascending rami. SGM P892: right dentary fragment with complete cheek dentition (P_3 - M_3).

Comparative material. *Plaisiodon centralis* - SGM 887: maxillary palate; SGM 881: right dentary; SGM 772: right dentary fragment; SGM 885: left maxillary fragment with complete cheek dentition; SGM 884: cast of holotype (CPC 6784); SGM 871: cranium.

Pyramios alcootense - SGM 872: palate with complete right cheek dentition. *Neohelos tirarensis* - SGM 891: right and left dentaries from cranium of NTM P8695-38. *Kolopsis torus* - SGM 889: eranium. Supplementary specimens referred to are noted in the text and figures.

Diagnosis. As for the genus.

Type Locality. Alcoota, Flinders Quarry, "...Waite Formation, 4 miles [6.4 km] southwest of Alcoota Station, 2.1 miles [3.4 km] southwest of junction of Waite and Ongeva Creeks, Northern Territory, Australia" (Woodburne 1967b).

Age. The Alcoota Local Fauna is probably Cheltenhamian Stage equivalent or slightly older (Woodburne *et al.* 1985). *Kolopsis* sp. and *Zygomaturus gilli* are reported from Beaumaris, Victoria which is considered to be Cheltenhamian Stage (Stirton *et al.* 1967). A *Kolopsis* species (*Kolopsis rotundus* Plane) is described from the radiometrically dated Otibanda Formation of New Guinea, at between 7.6-5.7 million years B.P. (Everenden *et al.* 1964; Stirton *et al.* 1967). That age has subsequently been adjusted to between 3.5 and 2.5 myBP (Page and McDougall 1972; Hock and Holm 1986). Stirton *et al.* (1967) consider the Awe Fauna to be a relict of mid-Tertiary Australian faunas and therefore not amenable to an overall stage of evolution correlation. On the basis of the presence of *Zygomaturus* at Beaumaris, the Alcoota Local Fauna is provisionally considered to be older than the Beaumaris Local Fauna.

Description and comparison. General comparison: The eranium of *Alkwertatherium webbi* (Fig. 1) is more similar in overall appearance to *Plaisiodon centralis* (Fig. 2) and some morphs of *Neohelos tirarensis* than it is to either *Pyramios alcootense* or *Kolopsis torus*. The *Alkwertatherium webbi* eranium is smaller, more elongated and laterally compressed, more gracile and more prognathic than any known example of *Plaisiodon centralis* or *Pyramios alcootense* (Fig. 3). The upper incisor arcade is broader and more procumbent (Figs 4-5; Tables 1-2); the rostrum is narrower and more elongated. The palate is narrower and the cheektooth row is straighter, narrower and shorter (Fig 6).

The gracile, elongated *Alkwertatherium webbi* cranium is proportionally dissimilar to the type *Pyramios alcootense* (CPC 6749), (Fig. 6), which has a broad, relatively short

Table 1. Measurements (mm) of A, upper incisors, B, lower incisor, including implantation angles, and C, dentary dimensions.

A. UPPER INCISORS				
	Alveolar length		implantation angle	
	<i>A. webbi</i>	<i>P. centralis</i>	<i>A. webbi</i>	<i>P. centralis</i>
I ³	14.5	20.6	145°	130°
I ²	10.6	10.8	145°	115°
I ¹	15.0	16.5	175°	150°

B. LOWER INCISOR				
	Thickness	Width	Implantation angle (frontal, from horizontal)	
<i>A. webbi</i>	11.0	29.0	20°	
<i>P. centralis</i>	12.0	12.9	55°	
<i>P. alcootense</i>	11.0	28.0	40°	

C. DENTARY MEASUREMENT				
	<i>P. centralis</i>	<i>A. webbi</i>	<i>P. alcootense</i>	
Length I ₁ to P ₃	80.0	85.0	67.5	
Length tooth row	148.5	117.0	112.2	
Depth at M ₁	70.0	55.5	60.0	
Depth M ₂ /M ₁	74.5	68.3	80.5	
Depth at P ₁	53.5	60.0	65.0	
Length ramus	315.0	276.0	270.0	
Length symphysis	121.0	117.0	88.0	
I ₁ above inferior border	52.0	23.0	50.0	

cranium, long robust masseteric processes and lacks the postorbital and postsquamosal constrictions conspicuous in *A. webbi* and to a lesser extent *P. centralis*. However in certain specific features, principally those relating to the trophic complex, *Pyramios alcootense* shows some striking similarities to *Alkwertatherium*. These are seen in the narrowly constricted diastemal palate, strongly developed diastemal crests, flared premaxillary palate, broad, spatulate lower incisors and length of cheek tooth rows. There are no specific similarities to *Kolopsis torus* expressed in the cranium and dentaries of *Alkwertatherium*.

Cranium: The lateral profile of the cranium of *Alkwertatherium webbi* is long and relatively low, but with a definite vertex, unlike that of the holotype of *Plaisiodon centralis* (CPC 6784) (Fig. 1). A subsequently recovered specimen of *P. centralis* (SGM 871) also differs from the holotype in this respect (Fig. 2). It is possible that the holotype represents an extreme condition for the genus *Plaisiodon*. The basiscranial axis of *Alkwertatherium* is however, less upward-flexed relative to the occlusal plane than either the type specimen or SGM 871 *Plaisiodon centralis*. *Alkwertatherium webbi*'s cranium is approximately the same length and has the same state of tooth wear as the *P. centralis* type, which has the

advantage of neutralizing the considerable allometric distortions encountered in this family in relation to size, growth stage, and sexual dimorphism (Table 2).

The rostrum of *Alkwertatherium webbi* is narrower, more uniformly tubular and about the same length as *P. centralis*, CPC 6784, but differs in being constricted bilaterally at the level of the infraorbital foramen, and the nasals are narrowest, about 30 mm across at this point, in relation to the arcing dorsal margin of the maxilla. Each nasal termination of *A. webbi* is gently rounded and widest there (46 mm) in contrast to *P. centralis* in which the widest point of the combined nasal bones is immediately anterior to the jugal eminence. *Pyramios* nasals are narrowest distally and combine to form a pyriform, decurved, overhanging nasal process.

Table 2. Measurements (mm) of the A, upper, and B, lower cheek dentitions of *Alkwertatherium webbi* compared with *Pyramios alcootense* and *Plaisiodon centralis*.

A. UPPER CHEEK DENTITION						
	<i>Alkwertatherium</i>		<i>Pyramios</i>		<i>Plaisiodon</i>	
	L888	R888	L872	R872	L887	R887
P ¹ L	18.7	19.2	—	18.0	24.0	23.3
W	17.7	17.6	—	17.1	17.6	17.7
M ² L	23.3	22.5	—	20.0	23.5	23.5
AW	19.2	18.8	—	18.2	20.0	20.0
PW	18.1	18.2	—	18.0	20.0	21.0
M ¹ L	27.1	25.2	—	25.2	27.1	26.5
AW	21.5	—	—	21.0	23.0	22.5
PW	—	19.7	21.2	19.0	21.6	21.1
M ⁴ L	28.7	27.7	26.0	26.7	32.0	30.1
AW	22.5	24.1	23.9	22.5	25.5	25.5
PW	18.3	—	20.5	21.0	22.2	—
M ³ L	27.7	—	—	28.5	—	32.0
AW	20.1	—	—	24.9	—	27.2
PW	17.0	—	—	21.0	—	19.8

B. LOWER CHEEK DENTITION						
	<i>Alkwertatherium</i>		<i>Pyramios</i>		<i>Plaisiodon</i>	
	R892	L883	R883	L891	R891	R881
P ₁ L	13.8	—	—	16.5	15.5	19.5
W	9.5	—	—	11.0	10.6	13.5
M ₁ L	21.5	19.9	18.3	20.6	20.3	24.0
AW	14.5	14.0	—	14.3	15.2	15.2
PW	15.0	15.1	13.7	15.0	14.4	17.0
M ₂ L	26.2	23.9	22.1	—	—	30.5
AW	19.0	17.3	15.5	17.0	18.5	19.0
PW	—	—	14.8	—	—	19.8
M ₃ L	28.2	25.5	25.8	28.0	27.5	35.0
AW	20.2	18.7	—	20.5	20.0	23.0
PW	18.3	—	18.3	18.8	19.0	23.0
M ₄ L	26.2	27.5	27.4	30.0	30.0	33.2
AW	19.5	20.5	20.3	20.4	21.0	24.9
PW	16.6	17.8	18.2	19.2	19.0	21.5

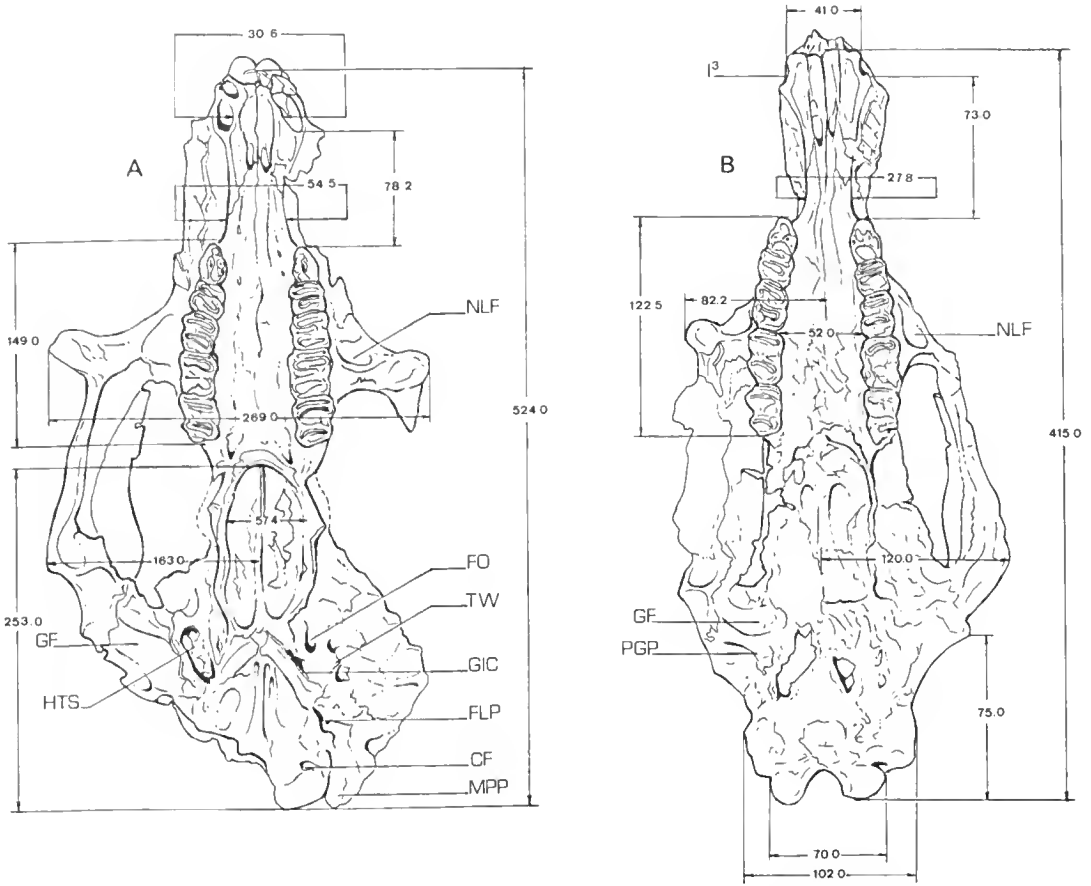


Fig. 3. Dimensions and comparison of the ventral aspect of *Alkwertatherium webbi* with *Plaisiodon centralis*. A, *Plaisiodon centralis* (SGM 871); B, *Alkwertatherium webbi* (SGM 888). Key to abbreviations (see Figs 1-2), plus: GIC, groove for internal carotid artery; FO, foramen ovale; CF, condylar foramen. Scaled to equivalent condylobasall length.

In lateral view, the profile of the diastema is slightly more elongated and less curved downwards along with the profile of the incisors than in *P. centralis* (Fig. 5). As in *P. centralis*, the premaxillary-maxillary suture is nearly vertical. The dorsal profile of the nasals is gently concave. Though slightly crushed, a natural-looking depression located about 30 mm behind the end of the nasals indicates that they were weakly elevated. A small premaxillary-nasal notch appears to have been present. The narial aperture is trapezoidal, the nasals lying almost horizontal to the frontal plane. Posteriorly, the nasal bones are gabled resulting in a low, oval elevation situated immediately anterior to the frontal depression. *Alkwertatherium* and *P. centralis* are similar in this respect, and strong resemblances to *Neohelos* are also present in the dorsolateral

contours of the rostrum and particularly in the basic shape of the nasal bones.

Alkwertatherium differs substantially from *Plaisiodon* and *Pyramios* in the width of the base of the rostrum at the nasofrontal contact. In *A. webbi*, the width of this region, 50 mm, is little more than half the width of the similar-sized *Plaisiodon*, CPC 6784, and considerably less than half the width of that of *Plaisiodon*, SGM 871. Immediately behind the rostrum, *Alkwertatherium* resumes its proportional similarities with CPC 6784, in which the interorbital width is only slightly greater than that of the new genus.

The frontal region of *Alkwertatherium* retains the narrow aspect of the base of the rostrum as it ascends into the frontal crests. The frontal depression is shallow and flat compared to the deeply clefted fossae in CPC

6784 and SGM 871, *Plaisiodon centralis*. In *Pyramios alcootense* the frontal crests are large, rounded swellings in marked contrast to the long narrow, crisply delineated and straight crests of *Plaisiodon* and *Alkwertatherium*. As in *P. centralis*, the frontal crests converge in a low sagittal crest and the flat lateral wall of the braincase descends steeply towards a long, narrow squamosal sulcus. In *Pyramios* the frontal crests do not converge into a sagittal crest, remaining as separate temporalis crests for the length of the neurocranium. The basic shape of the neurocranium of *Alkwertatherium* differs little from that of *P. centralis*, except for its greater length and narrowness posterior to the squamosal root, and the extent to which it is elevated above the tooth row. The latter difference however, amounts to only about ten degrees.

A larger discrepancy in cranial shape between *Alkwertatherium webbi* and *Plaisiodon centralis* is the nasofrontal angle, which, as measured at the nasofrontal suture, registers a difference of about twenty degrees (Fig. 6). As in *P. centralis* the parietals of *Alkwertatherium* are long and narrow and the squamosal lamina is broad. The postsquamosal arch in *Alkwertatherium* is considerably longer and more deeply concave than in comparable *P. centralis* specimens.

The zygomatic arch of *Alkwertatherium webbi* is deep and long. The contour of the undistorted left zygomatic arch is flatter than in *P. centralis*, closely resembling the condition in *Neohelos tirarensis* (Fig. 6). The squamosal process is long and sustains a considerable width, extending anteriorly to lie beneath the orbit. The squamosojugal suture also contributes to the posterior orbital margin in *Pyramios*. Both CPC 6784 and SGM 871 have much shorter squamosal processes that terminate 30 mm or more posterior to the distal orbital margin. Consequently, in *Alkwertatherium*, the zygomatic arch is at least as deep anteriorly, immediately posterior to the orbit, as it is immediately anterior to the glenoid fossa.

In *P. centralis* and *Pyramios alcootense*, the zygomatic arch is narrower anteriorly than it is posteriorly. Although the squamosal process does not extend as far anteriorly in *Neohelos* as in *Alkwertatherium*, the anterior depth of the arch is approximately the same as the posterior depth, and the squamosal process is

relatively longer than in either *Plaisiodon* or *Pyramios*. The masseteric process in *A. webbi* is relatively delicate and short, not extending more than a few millimetres below the occlusal line. The processes are missing from the holotype of *P. centralis* but its broken surface indicates that a much more robust process was present. The extent to which the masseteric process was developed in *P. centralis* is demonstrated by SGM 871. The masseteric processes of *Pyramios* are also much longer and more robust than in *Alkwertatherium*. The nasolabial fossa is deeper, more inferiorly directed and more sharply delineated in *Alkwertatherium* than in *Plaisiodon* or *Pyramios*, more closely resembling that of *Neohelos tirarensis*.

Palate: The diastemal palate of *Alkwertatherium webbi* is markedly constricted immediately anterior to the P³ and attains a minimum width of only about 28 mm at 15 mm anterior to the tooth. Anterior to the P³, at 25 mm, the palate begins to flare laterally to attain a maximum width of 52 mm immediately posterior to the I³ alveoli. In *P. centralis*, the diastema is moderately narrow, relatively more constricted than in most *Neohelos tirarensis* and *Kolopsis torus* crania in which the maximum interincisive width is approximately the same as the interdiastemal minimum (Figs 5-6; Tables 1-2). In conjunction with the anteriorly expanded premaxillary palate, the incisor alveoli open more laterally than ventrally and the implantation angles of the incisor roots are closer to horizontal. A more graphic expression of this complex is seen in the position of the I³ alveolus immediately in line with I² in *Plaisiodon centralis*, *Neohelos tirarensis* and *Kolopsis torus* in contrast to the laterally offset I³ alveoli in *Alkwertatherium*. In the morphology of the diastemal and premaxillary palate, *Alkwertatherium* is a bit different from zygomaturnines, more closely resembling the notothere *Pyramios alcootense*. However, in *Pyramios*, the interincisive fossa is a deep, spoon-shaped depression. In *Alkwertatherium*, the interincisive region is a shallow, wide concave surface.

Although no upper incisors have been identified for the species, the implantation angles of the teeth indicate that the crowns were more procumbent than in *P. centralis*, *Neohelos tirarensis* or *Kolopsis torus*. The diastemal palate is also relatively longer than in *P. cen-*

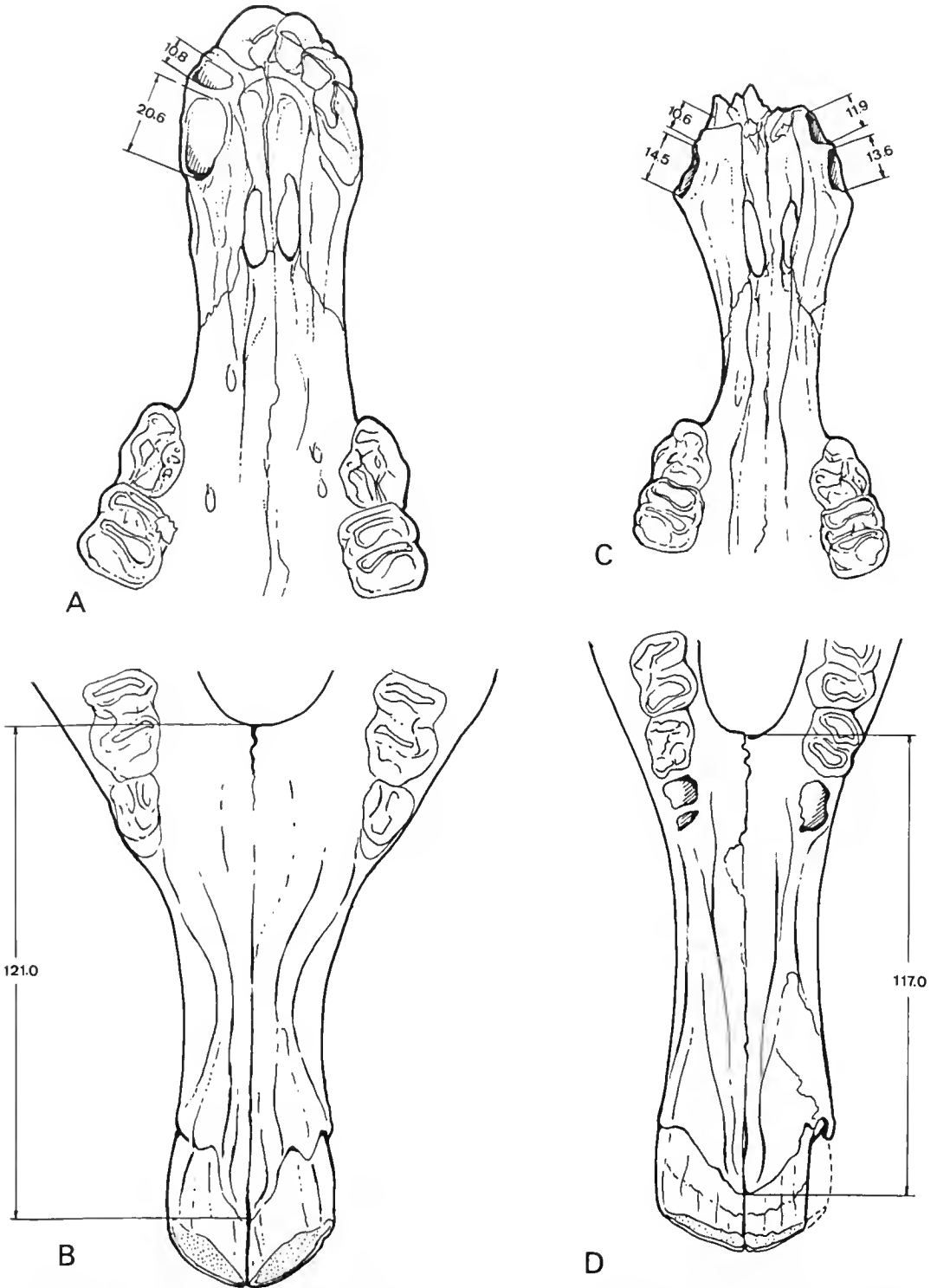


Fig. 4. Comparison of the anterior palatal and dentary diastemal regions in *Alkwertatherium webbi* and *Plaisiodon centralis*. A, ventral aspect of anterior palatal region of *P. centralis* (SGM 871); B, ventral aspect of symphyseal region of the dentary of *P. centralis*; C, ventral aspect of anterior palatal region of *A. webbi* (SGM 888); D, ventral aspect of the symphyseal region of the dentary of *A. webbi*. Not to scale.

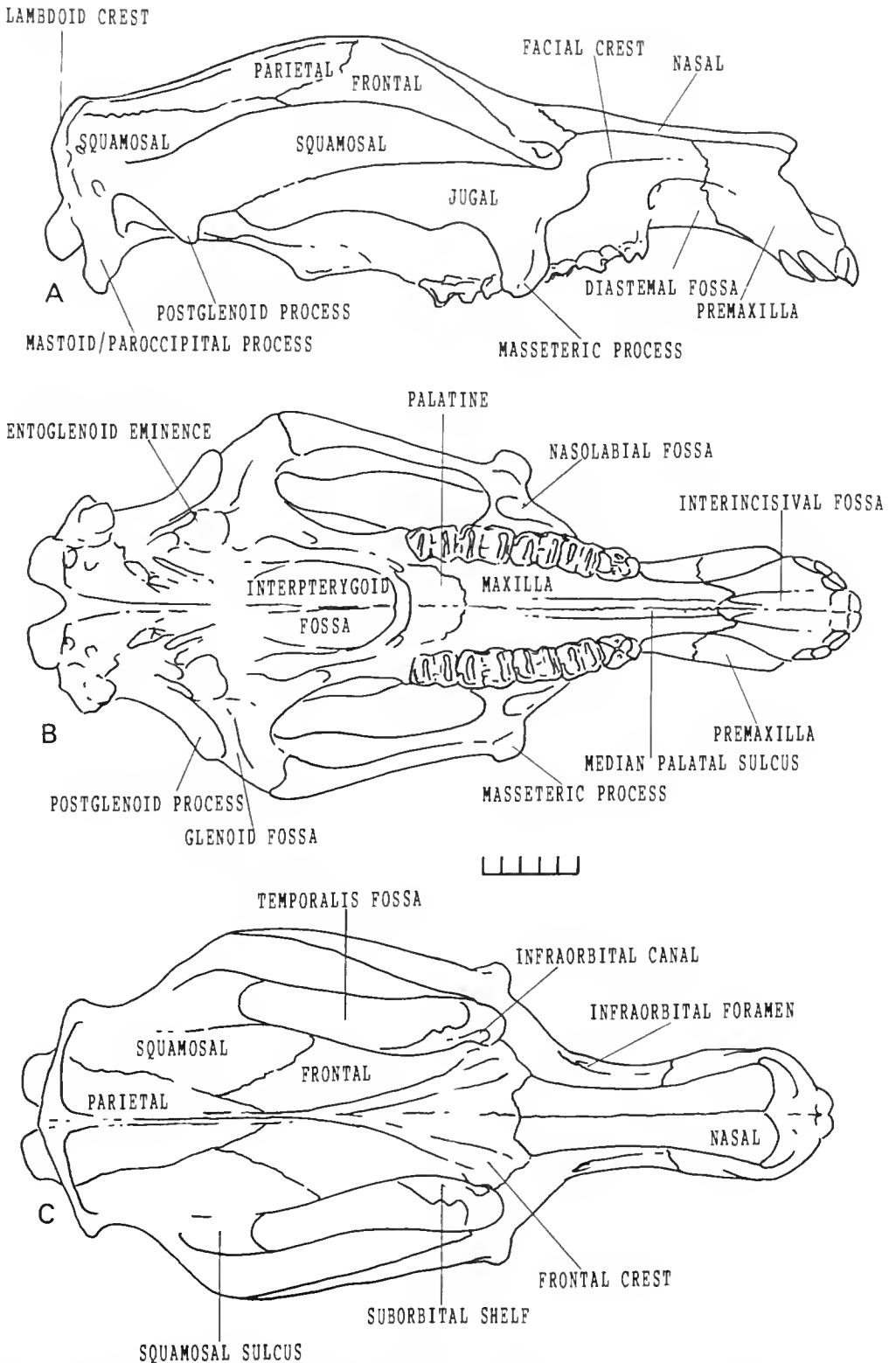
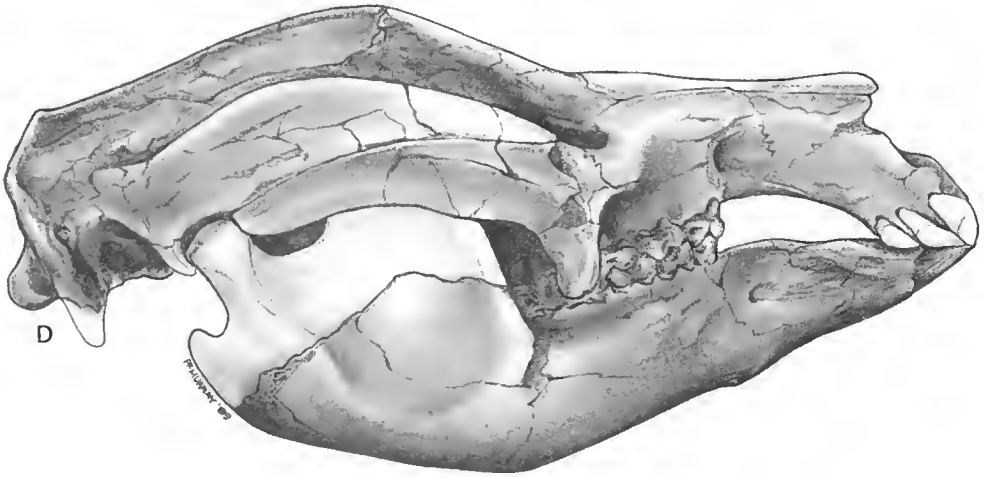


Fig. 5. Restorations of *Alkwertatherium webbi* gen. et. sp. nov. **Opposite**, restorative sketch of lateral aspect of skull, scale 50mm; A-C, diagrammatic restorations of cranium.



tralis. The incisor implantation in *Pyramios* is more similar to that of *Alkwertatherium*, though also less procumbent.

The maxillary palate of *Alkwertatherium* is slightly narrower than in *P. centralis*, made less visually apparent perhaps, by the narrower and shorter cheek tooth rows (Figs 1-3, 6). The palate is otherwise similar to that of *Plaisiodon*, particularly in the shape of the cheektooth arcade and moderate extent of posterior divergence. *Pyramios alcootense* has a relatively broader, shorter, more domed palate with more posteriorly divergent tooth rows (Fig. 6).

Cranial base: The internal nares and interpterygoid fossa appear to be shallower in *Alkwertatherium* than in *P. centralis*, in which an exceptionally deep, cavernous excavation is a conspicuous feature of SGM 871. The cranial base is poorly preserved in *Alkwertatherium*. Sufficient surface contour is present to define the extremely wide, obliquely oriented glenoid fossae, ventrolaterally directed pterygoid fossae and low, wide, but apparently thin, delicate postglenoid processes. SGM 871, *Plaisiodon centralis*, preserves many basicranial features of the genus and the majority of those portions visible in *Alkwertatherium* appear to correspond closely to it. In *Pyramios*, exceptionally wide glenoid fossae are oriented at right angles to the axis of the cranium. There is, moreover a highly distinctive lateral profile of the glenoid notch which is narrowly V-shaped, as opposed to the broadly U-shaped profile of *Alkwertatherium*. An interesting similarity between *Pyramios*

and *Alkwertatherium* is the shared feature of thin postglenoid processes.

The occipital region of *Alkwertatherium* is conspicuously narrower than in *Plaisiodon*, *Pyramios* and *Kolopsis*, but is similar in width though lower than in some *Neohelos* specimens (eg. NTM P8695-38). The occipital condyles, which are the most posterior structures of the cranium, are comparatively small, transversely elongated and narrow, in contrast to the large, widely separated occipital condyles of *Pyramios*. The condyles are separated ventrally by a deep, V-shaped inter-

Table 3. Cranial measurements (mm) of *Alkwertatherium webbi* (888) compared with *Plaisiodon centralis* (884, 871) and *Pyramios alcootense* (872).

Cranial measurements	SGM888	872	884	871
Length-II to occipital condyle	415.0	-	-	520.0
Length-lambdoid crest to outer I ¹	-	-	-	525.0
Length-zygomatic arch	204.0	-	195.0	243.0
Length-temporalis fossa	122.0	-	125.0	155.0
Length-diastemal palate	73.0	-	52.0	78.0
Length-upper cheek tooth row	122.5	120.0	-	149.0
Length-interpterygoid fossa	-	-	-	138.0
Length-masseteric process	65.2	-	-	104.5
Length-lambdoid crest to nasals	395.0	-	-	-
Height-basioccipital-sagittal crest	70.0	-	122.0	121.0
Depth-vertex to pterygoid	145.0	-	-	175.0
Depth-posterior zygomatic arch	50.0	-	52.4	84.5
Depth-anterior zygomatic arch	50.0	-	-	56.6
Distance-molars above masseteric pr	<5.0	-	-	35.0
Depth-maxilla above P ¹	57.0	-	54.0	-
Depth from M ² to top of frontal	110.0	-	104.0	115.0
Width-occiput	98.0	-	-	130.0
Width-across mid point of orbits	95.0	-	110.0	140.0
Width-frontal above orbits	58.0	-	88.0	127.0
Width-cranium at frontal converg.	60.0	-	61.0	60.0
Width-PMX across narial aperture	69.0	-	60.0	92.0
Width-zygoma to sagittal crest	120.0	-	90.0	167.0
Width-anterior to lambdoid crest	102.0	-	-	190.0
Width-premaxillae between I ¹	41.0	-	26.0	30.0
Width-palate anterior to P ¹	27.8	39.0	37.7	54.5
Width-maxillae labial sides P ¹	67.0	72.0	75.5	91.4
Width-palate lingual M ¹ *	52.0	62.0	-	64.0
Width-maxillae labial sides M ²	87.0	100.0+	-	111.0
Width-interpterygoid fossa	47.0	-	-	54.0

condylar notch. The foramen magnum is transversely wide and distinctly oval in shape. Immediately above the foramen magnum, the

Table 4. Summary of characters of *Alkwertatherium webbi* gen. et sp. nov. and key to comparisons shown in Figures 6, 8, 11, 13.

Summary of characteristics of <i>Alkwertatherium webbi</i>	
1.0 Dorsum cranii	<ul style="list-style-type: none"> 1.1 high steep frontal 1.2 constricted preorbitally 1.3 constricted postsquamosally 1.4 upward basicranial flexion 1.5 high, thin narrow frontal crests 1.6 anteriorly expanded nasals 1.7 trapezoidal nasal aperture 1.8 low, narrow occiput 1.9 wide, oval foramen magnum
2.0 Zygomaticofacial	<ul style="list-style-type: none"> 2.1 long, deep squamosal process of zygomatic arch 2.2 zygomatic arch flattened in lateral aspect 2.3 zygomatic arch deep anteriorly 2.4 short, delicate masseteric processes 2.5 deep, well-defined nasolabial fossa 2.6 high, distinct sinusoidal facial crest 2.7 long, well defined buccinator sulcus 2.8 long squamosal sulcus 2.9 shallowly arcing diastemal profile
3.0 Palate	<ul style="list-style-type: none"> 3.1 flat, narrow and long 3.2 nearly straight arcades, slight posterior divergence 3.3 diastemal palate markedly constricted 3.4 flaring premaxillary palate, shallow IC fossa 3.5 I¹ lateral to I², alveoli open anterolaterally
4.0 Basis cranii	<ul style="list-style-type: none"> 4.1 Narrow, shallow interpterygoid fossa 4.2 small, shallow pterygoid fossae 4.3 wide oblique glenoid fossae 4.4 deep, V-shaped intercondylar notch
5.0 Upper third (permanent) premolar	<ul style="list-style-type: none"> 5.1 large parastyle 5.2 hypocone absent 5.3 undivided parametacone 5.4 buccal cingulum present 5.5 high clearly expressed mesostyle 5.6 wide, deep posterior fossa, distinctively worn
6.0 Upper molars	<ul style="list-style-type: none"> 6.1 weak parastyle, strong postparaconal crest 6.2 strong, short, rounded lingual cingulum 6.3 small protostyle M² 6.4 M¹ in line with M² lingually 6.5 P¹ widely contacts M² interproximally 6.6 metalophs sharply reduced M^{1,2} 6.7 metastyles low on PMC, strong on M⁴ 6.8 labial cingulae short, thick, rising confined to MV
7.0 Dentary	<ul style="list-style-type: none"> 7.1 body deep, tapers anteriorly 7.2 diastemal crests, long high, anteriorly expanded 7.3 near horizontal symphysis, terminates behind M₂ 7.4 short, shallow digastric fossa 7.5 genial pits in ventral border of symphysis
8.0 Lower incisors	<ul style="list-style-type: none"> 8.1 wide, thick crowns 8.2 nearly horizontal implantation 8.3 enamel on all surfaces 8.4 thick cementum base raised above enamel
9.0 Lower third premolar	<ul style="list-style-type: none"> 9.1 small relative to molars 9.2 narrow, oval crown 9.3 weak buccal cingulum present 9.4 large central cuspid, short posterior moiety
10.0 Lower molars	<ul style="list-style-type: none"> 10.1 parolophid crest weak, protolophid face steep 10.2 protolophids M_{2,3} high relative to hypolophids 10.3 midvalleys V-shaped 10.4 lingual offset of P₃-M₁ 10.5 weak, short precingulid 10.6 reduced size of M₁

proportionally small occipital surface was deeply excavated for the attachment of nuchal musculature.

Upper cheek dentition: The P³ is a short, broadly trilobate tooth composed of a large, high, transversely oval-sectioned parastyle with a slight buccal offset of the apex, a high, pyramidal, undivided parametacone and a robust, conical but slightly lower protocone (Figs 7-9; Table 4). The hypocone is absent. The apex of the parastyle is set closer to the parametacone than in *Plaisiodon*, but closely resembles it proportionally. The buccal groove separating the parastyle from the parametacone is deeper, longer and more cleft-like than in any other zygomaticurine genus. The anterolingual basin is deeper, more confined and forms a more definitive horizontal shelf than in *Neohelos* or *Plaisiodon*. The anterolingual eingulum is short but distinct, commencing from the mid-lingual base of the parastyle to ascend the anterolingual aspect of the protocone, forming near its base, a minute protostyle. A distinct secondary basin, slightly elevated above the parastylar basin, lies immediately anterior to the base of the protocone. This preprotoconal basin is incipient in *Neohelos*, distinct but small in *Kolopsis* and variably expressed in *Plaisiodon*, in which its presence is associated with a reduction of the parastylar basin. A protostyle is present in some *Neohelos* and *Kolopsis* specimens, but appears to be absent in *Plaisiodon*. The protocone is large, though slightly smaller than the parametacone and higher, relative to the parametacone than in *Neohelos*, *Plaisiodon* and *Kolopsis*.

In section, the protocone of *Alkwertatherium* approximates a rounded trapezoidal shape compared to the distinctly rounded section of the cusp in *Plaisiodon* and *Pyramios*. A short, thick postprotoerista ascends the cusp near vertically, becoming indistinct immediately short of the lingual portion of the posteingulum. The posteingulum is well-developed lingually, becoming indistinct interproximally and distobuccally. The posterior surfaces of the parametacone and protocone are steep and delineate the sides of a deep, oval distal basin, exaggerated to some extent perhaps, by wear. Although there is ample room on the posterolingual shelf for a hypocone, not so much as a thickening of the cingulum can be found to betray a phenotypic expression of the structure.

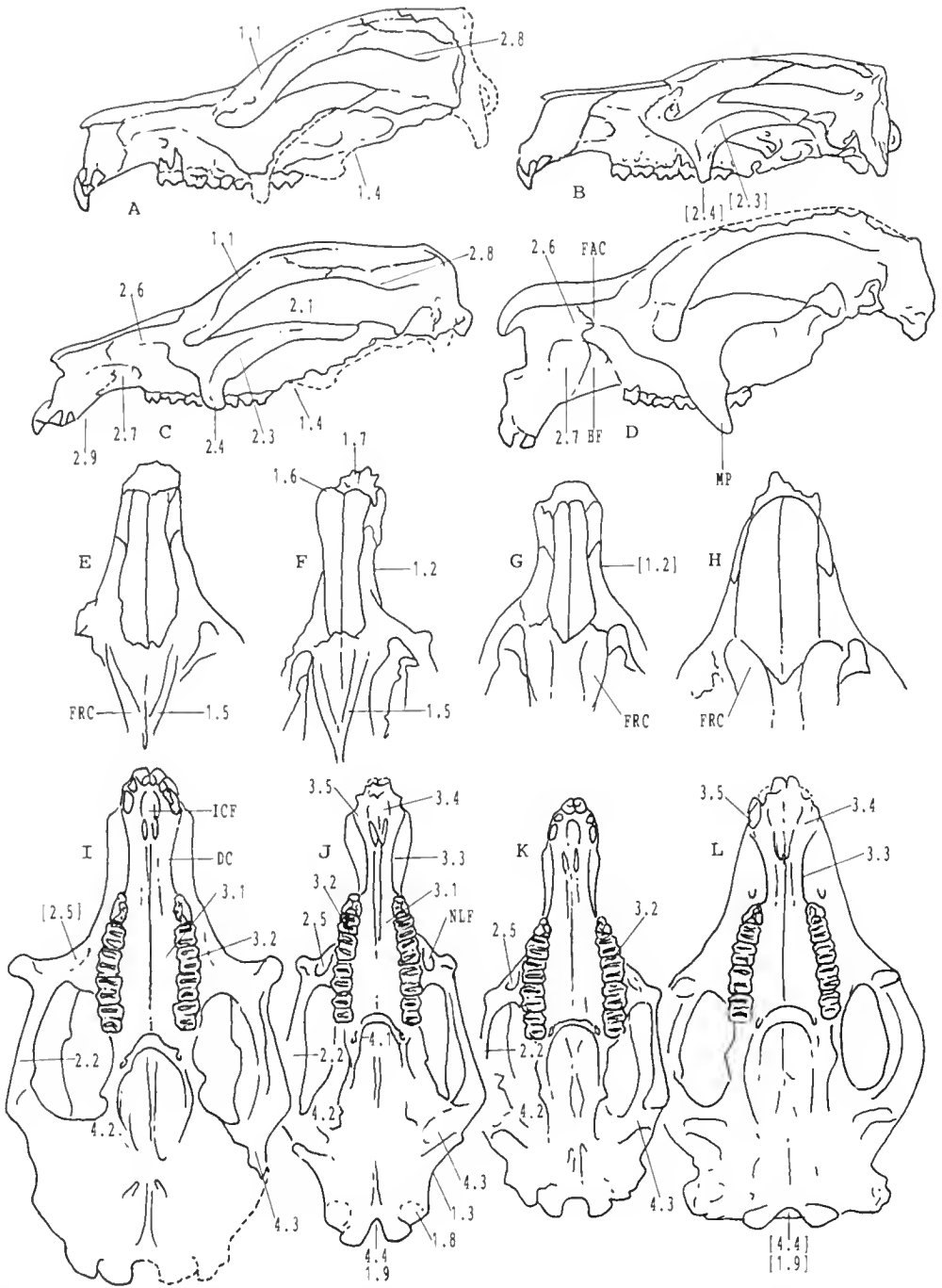


Fig. 6. Character distribution comparison of the cranium of *Alkwertatherium webbi* with crania of the larger mid- to late Miocene diprotodontid genera. **A**, *Plaisiodon centralis*, (holotype CPC 6784, restored from cast SGM 884); **B**, *Neohelos tirarensis* (NTM P8695-38); **C**, *Alkwertatherium webbi*, (SGM 888) restored; **D**, *Pyramios alcootense* (holotype cranium CPC 6749, partially restored) (after Woodburne 1967); **E**, dorsal aspect of snout of *P. centralis* (from cast SGM 884); **F**, *A. webbi*; **G**, *N. tirarensis*; **H**, *P. alcootense* (after Woodburne 1967); **I**, ventral aspect of *P. centralis* SGM 871 (restored); **J**, *A. webbi* (restored); **K**, *N. tirarensis*; **L**, *P. alcootense*, (restored) (after Woodburne 1967). Numerical references to characters are given in Table 4. Corresponding numbers indicate a strong similarity; brackets indicate a variable condition or less distinct, though similar features. Abbreviations: FRC, frontal crest; FAC, facial crest; BF, buccinator fossa; MP, masseteric process; ICF, Interincisive fossa; DC, diastemal constriction; NLF, nasolabial fossa.

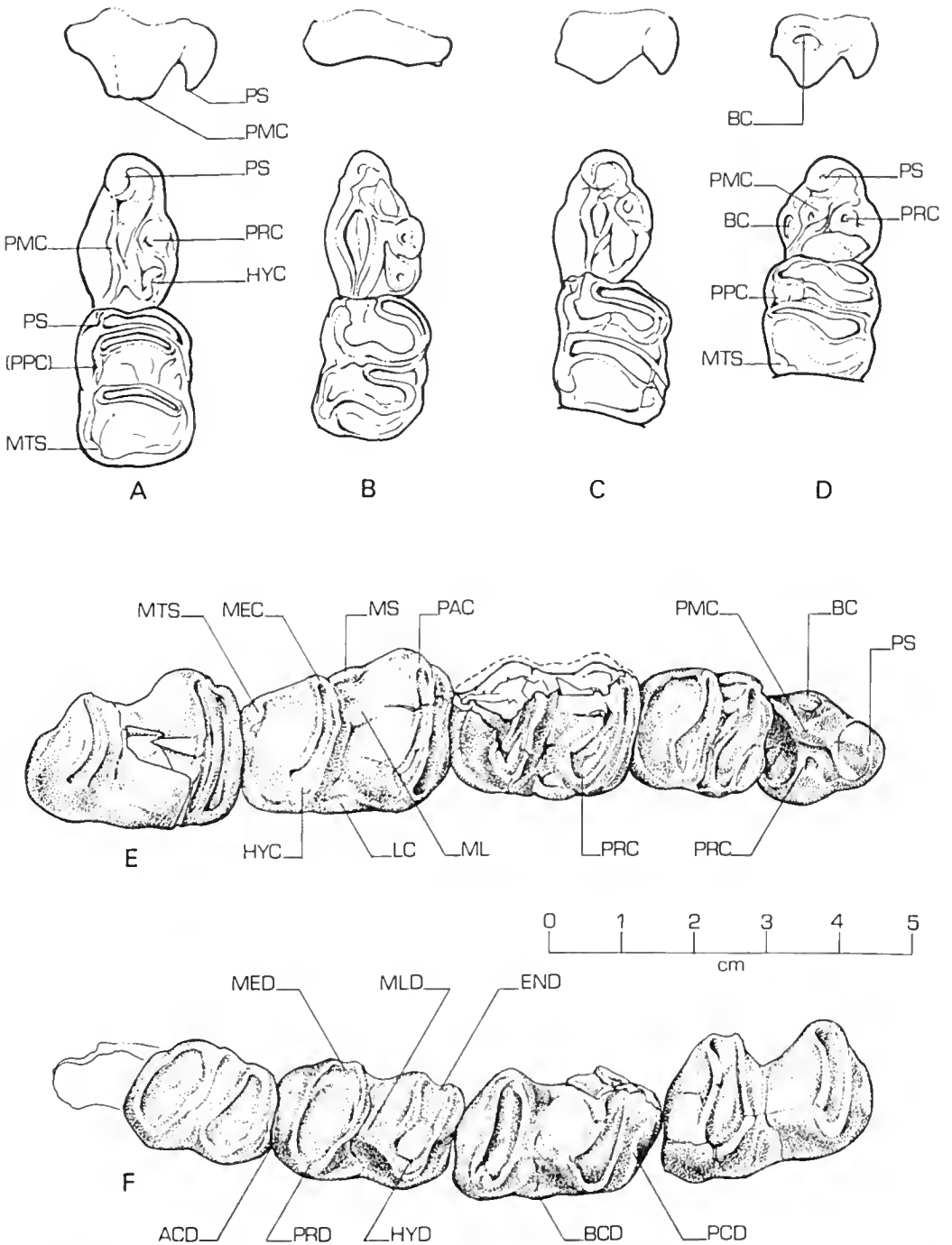


Fig. 7. Upper cheek dentition of *Alkwertatherium webbi*. (A-C) comparison of P¹-M² of *Plaisiodon centralis* with (D) *Alkwertatherium webbi*. A-C, range of morphological variation in cusp morphology of *Plaisiodon centralis*; C, "hypoconeless variant" which has a thickening in the lingual cingulum; in B, the parastyle is exceptionally worn. Note the narrow labiad interproximal contact of the P¹ with M² in *Plaisiodon*; E, upper cheek tooth row of *Alkwertatherium webbi*; F, lower cheek tooth row of *Alkwertatherium webbi*. Abbreviations: PS, parastyle; PMC, parametacone; PRC, protocone; HYC, hypocone; PPC, postparaconal crest; MTS, metastyle; BC, buccal cingulum; MEC, metacone; MS, mesostyle; PAC, paracone; LC, lingual cingulum; ML, midlink; MED, metaconid; END, entoconid; ACD, anterior cingulid; PRD, protoconid; HYD, hypoconid; BCD, buccal cingulid; PCD, postcingulid; MLD, metalophid or cristid obliqua.

Apparently "hypoconeless" variants of *Neohelos* usually show a thickening of the cingulum in the position of the hypoconc. The posterior portion of the tooth is more similar to that of *Pyramios*, both structurally and thegotically, except that the posterolingual portion of the posteingulum is more generous in *Alkwertatherium*. The low, interproximally indistinct posteingulum commences on the distobuccal corner of the parametacone after which it ascends the posterolabial margin of the cusp in the form of a steep, thick, slightly irregular postparametaerista, narrowing gradually as it approaches the apex of the cusp. The parametacone is steep and triangular in section with the anterior face presenting a transversely flattened, apically tapering surface. A distinct cusplule is present immediately lateral to and below the apex of the parametacone. This mesostyle (possibly homologous with stylar cusp C of primitive vombatiform molars) is continuous with the posterobuccal cingulum, which in *Alkwertatherium* defines a distinct, oval fossette on the distobuccal flank of the parametacone.

The P³ of SGM 872, *Pyramios alcootense*, is similar to *Alkwertatherium* in the shape of the parametacone and the degree of development of the postparametaerista. A posterobuccal cingulum is present but does not establish a fossette. The mesostyle is larger but less distinctly delineated. There is a faint postparastylar sulcus separating a small parastyle from the parametacone and defining the anterior extent of the mesostyle. None of the *Pyramios* third premolars show a tendency to develop more than an incipient parastyle, although the anterior crown base is more generous than in other nototheriines, being more comparable to that of zygomaturines, and a faint buccal crease, delineating the base of the parastyle, is present on some specimens. The large size of the P³ and the incipient parastyle development gives the impression that *Pyramios* is structurally intermediate to nototheriines (Diprotodontinae) and zygomaturines.

The upper molars of *Alkwertatherium*, in comparison with similar-sized CPC 6748, *Plaisiodon centralis*, are smaller relative to the splanchnocranium, particularly M⁴⁻⁵, which do not abruptly widen behind the third molar as in *P. centralis*. This marked transition in the molar gradient in *P. centralis* is a distinctive and consistent feature of the spe-

cies, and indeed among zygomaturines in general. There are two other consistent differences in the morphology of the arcade: in *Alkwertatherium* the interproximal contact between the P³ and M² is wide and centered, and the M⁵ is aligned with the M⁴ on the lingual side. In *Plaisiodon centralis* the P³ is offset buccally leaving a large V-shaped gap between the teeth on the lingual side, and the M⁵ is offset lingually creating a step-like contour of the occlusal profile on the lingual side. The primary differences in molar morphology between *Alkwertatherium* and *P. centralis* are in the degree of development in the buccal and lingual cingulae and crests related to the posterior margins of the lophs.

The second molar in *Alkwertatherium* is distinctive in having a wider mid-valley buccally and in possessing a well-developed buccal cingulum, continuing anteriorly into a short postparaconal crest. The parastyle is poorly developed on all molars. The molar crown morphology is otherwise very similar in the two species and the determination of isolated molars is complicated by a high degree of morphological variability.

The M² of *Alkwertatherium* has a weakly developed parastyle, but a distinct, short, postparastylar crest. A short postparaconal crest ascends the base of the paracone and is continuous with a thick buccal cingulum which spans the mouth of the interloph valley to the base of the hypocone, where it is transected by a faint sulcus. The cingulum bulges slightly as a presumptive mesostyle. The protoloph is slightly wider and more massive than the metaloph. A low, short, midlink is present and a second, faint crest transects the interloph valley just lingual to the longitudinal midline of the crown. The posteingulum is wide and rounded. Buccally it ascends the metacone as a distinct postmetaerista, at the base of which is developed a low, indistinct metastyle. Lingually, the posteingulum terminates near the base of the hypocone and is separated by the lingual side of the metaloph from a short lingual cingulum that flares out around the mouth of the interloph sulcus. At its anterior extreme, a small protostyle is present. The anterior cingulum is wide lingually and slightly thickened on the midline.

The M³ is larger than the M² with a distinctly wider lingual interloph sulcus and correspond-

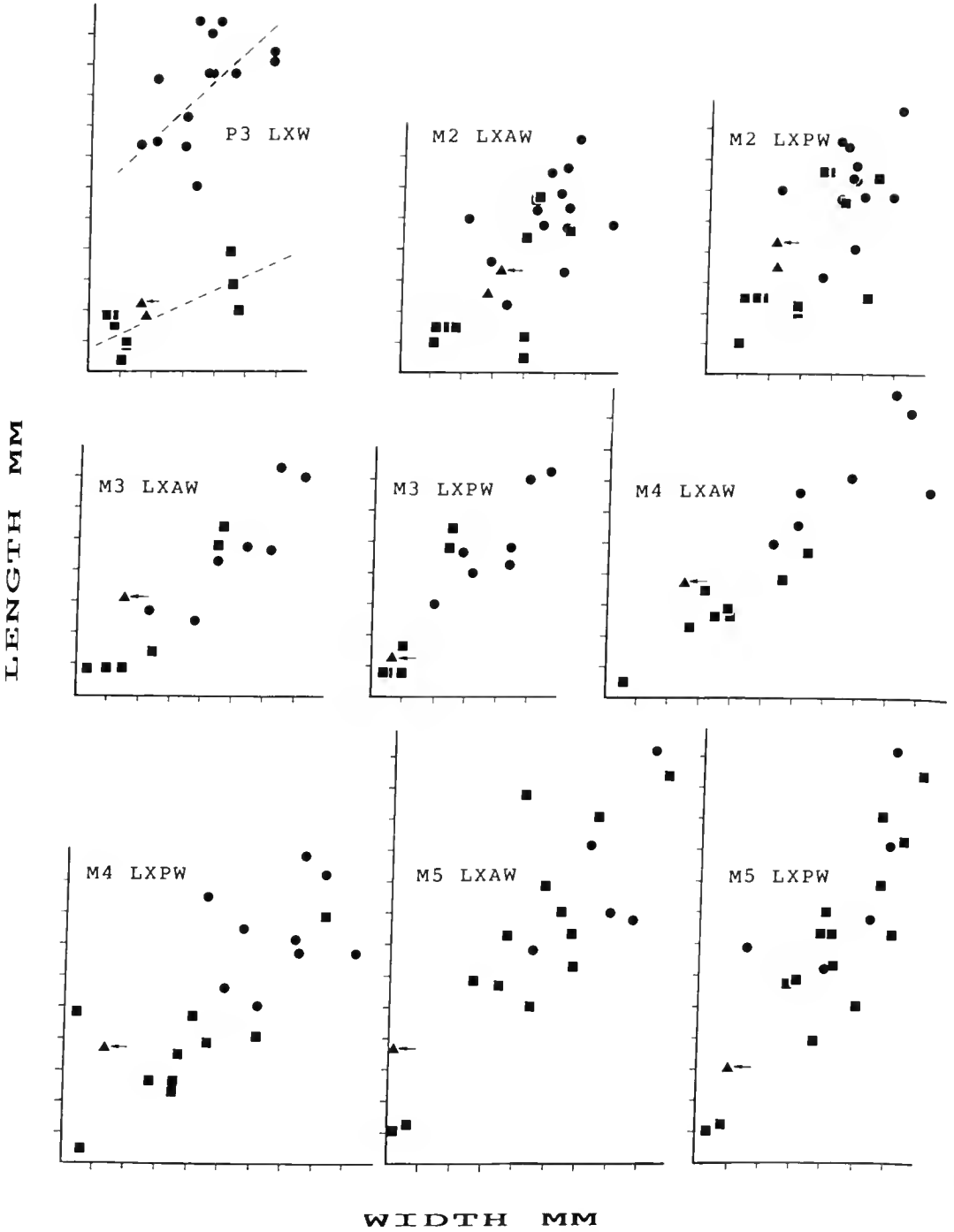


Fig. 8. Scatter diagram of the dimensions of upper cheek teeth comparing *Alkwertatherium* (triangles) with *Plaisiodon* (dots) and *Pyramios* (squares); data from Woodburne (1967a) with the addition of new specimens listed under Comparative Material of *A. webbi*. Note the relatively clear separation of genera with the premolar compared to the large degree of overlap with the molar dimensions. *Alkwertatherium webbi* aligns with *Pyramios alcotense*. Scale is in millimetres, X axis = width, Y axis = length; regressions were not calculated due to to small sample size.

ingly longer lingual cingulum. The protostyle is reduced to a low bulge. The "midlink" (which does not appear to be homologous with a crista obliqua), is a teardrop-shaped enamel boss developed on the base of the paracone side of the protoloph. The interloph valley is sinuous, deep and narrow. Both moieties are approximately equal-sized. The postmetacrista is indistinct. The postcingulum is reduced lingually but remains wide and low on the posterobuccal corner of the metaloph, where a low metastyle is present.

The M^4 is larger than M^3 and is distinguished by its narrower metaloph, wide protoloph and buccally expanded paracone, wider midvalley, less well-developed postcingulum and less distinct though broader "midlink". The M^5 closely resembles M^4 in size and shape, but the metaloph is relatively narrower, the postcingulum is confined to the posterobuccal side of the crown, the midlink is reduced to a faint swelling and the buccal cingulum is absent.

Although the molars are indeed distinctive, there are no individual characters of the crown morphology that can invariably separate them from *Plaisiodon centralis* or from *Pyramios alcootense*. Except for their smaller size, slightly greater apparent obliquity of the lophs of M^{2-3} and the difference in the molar gradient, the degree of variability in *Plaisiodon* crown morphology, and indeed, even the differences between the right and left sides of the *Alkwerthatherium* cheek dentition, render the distinction of isolated teeth somewhat dubious, given that the size range of *Alkwerthatherium* is unknown. Worn molars, particularly M^2 , have a distinctive thegotic character which will be discussed in conjunction with the lowers. The molar gradient, dimensions, and the low disposition of the metastyle on M^2 of *Alkwerthatherium* more closely resembles *Pyramios*, but the proportional widths of protoloph to metaloph for each molar, the occlusal contours, particularly M^{4-5} , with a marked reduction of the width of the metaloph, are more similar to *Plaisiodon*.

Dentary: The associated dentary of *Alkwerthatherium* superficially resembles that of *Palorchestes* in having an extremely long, kangaroo-like, horizontally disposed symphysis, containing broad, spatulate, procumbent lower incisors (Figs 10-11). The molars are typical of diprotodontids and most closely resemble those of the nototheriine, *Pyramios*

alcootense. Although the dentary was found in association with the cranium of *Alkwerthatherium*, which was isolated from other fossil concentrations, direct association of fossils in the Alcoota assemblage is no guarantee that the remains represent a single individual.

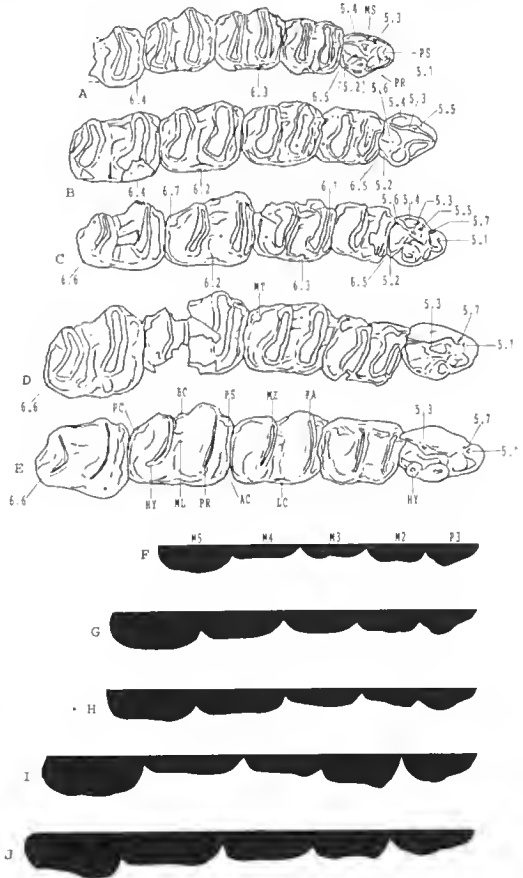


Fig. 9. Comparisons of the upper cheek dentitions of larger mid- to late Miocene diprotodontid genera with *Alkwerthatherium webbi*. A, *Neohelos tirarensis* (NTM P8690) "hypoconeless variant"; B, *Pyramios alcootense* (SGM [R]872); C, *Alkwerthatherium webbi* (SGM [R]888); D, *Plaisiodon centralis* (SGM [R]887); E, *Plaisiodon centralis* (SGM 885); F, lingual occlusal profile of *Neohelos tirarensis* (NTM P8690) compared with G, *Pyramios alcootense* (SGM [R]872); H, *Alkwerthatherium webbi* (SGM 888); I, *Plaisiodon centralis* (SGM [R]887); J, *Plaisiodon centralis* (SGM 885). Abbreviations: MS, mesostyle; PS, parastyle; PR, protocone; MT, metastyle; PC, postcingulum; HY, hypocone; BC, buccal cingulum; ML, midlink; AC, anterior cingulum; LC, lingual eingulum; ME, metacone; PA, paracone. Numerical references to the characters are listed in Table 4. The lingual profiles of the molars show the step-like offset of M^3 in *Plaisiodon*, in comparison to the other genera. There is a tendency towards this condition in some *Neohelos* and some *Pyramios* (F, G); but the trait is apparently not present in *Alkwerthatherium webbi*.

However, there are occasionally isolated pockets in which partially articulated material is recovered. *Alkwertatherium* occurred in one of these situations. The dentary lay slightly above and at the posterior end of the cranium with the dentitions of both facing upwards. As the excavation around the dentary progressed, the cranial base of SGM P888 was partially exposed immediately beneath the posterior end of the inferior border of the dentary, the anterior ends of the jaws and cranium pointing away from one another, as though the dentary had been dislodged backward from the skull.

To the extent that the somewhat distorted lower tooth rows can be physically occluded with the uppers, they match closely in terms of occlusal surface angles of the similarly worn lophs and lophids, the distance between them, and in terms of the individual variations of each tooth in the degree of wear, pattern of attrition and thegotic correspondence.

The dimensions of the individual molar teeth are also within the expected tolerances for the same individual which ranges normally between 0.85 and 1.0. The length of the right uppers from front to back are: 23.3, 27.1, 28.7,

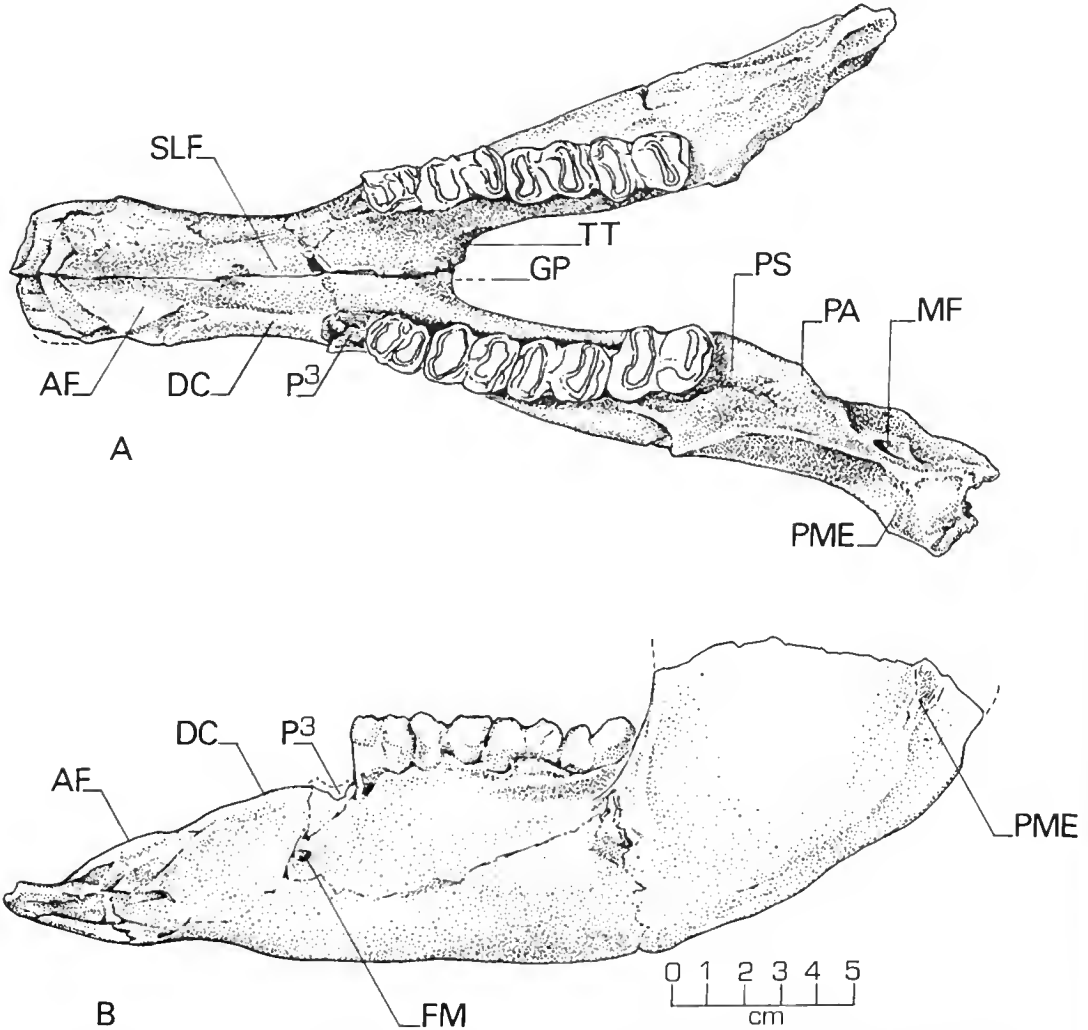


Fig. 10. Dentary of *Alkwertatherium webbi* gen. et sp. nov. (SGM 883, paratype). A, occlusal aspect; B, lateral aspect. Note the extreme procumbency of the lower incisors, anteriorly tapering horizontal ramus, high long diastemal crests and their bony expansions, long deep, sublingual fossa and short, weak transverse torus penetrated by genial pits. The symphysis, which is unused, extends to the posterior moiety of M₂. Abbreviations: SLF, sublingual fossa; DC, diastemal crest; AF, anteriorly flattened surfaces of diastemal crests; GP, genial pit; TT, transverse torus; PS, postalveolar shelf; PA, postalveolar process; MF, mandibular foramen; PME, posterior masseteric eminence; FM, mental foramen.

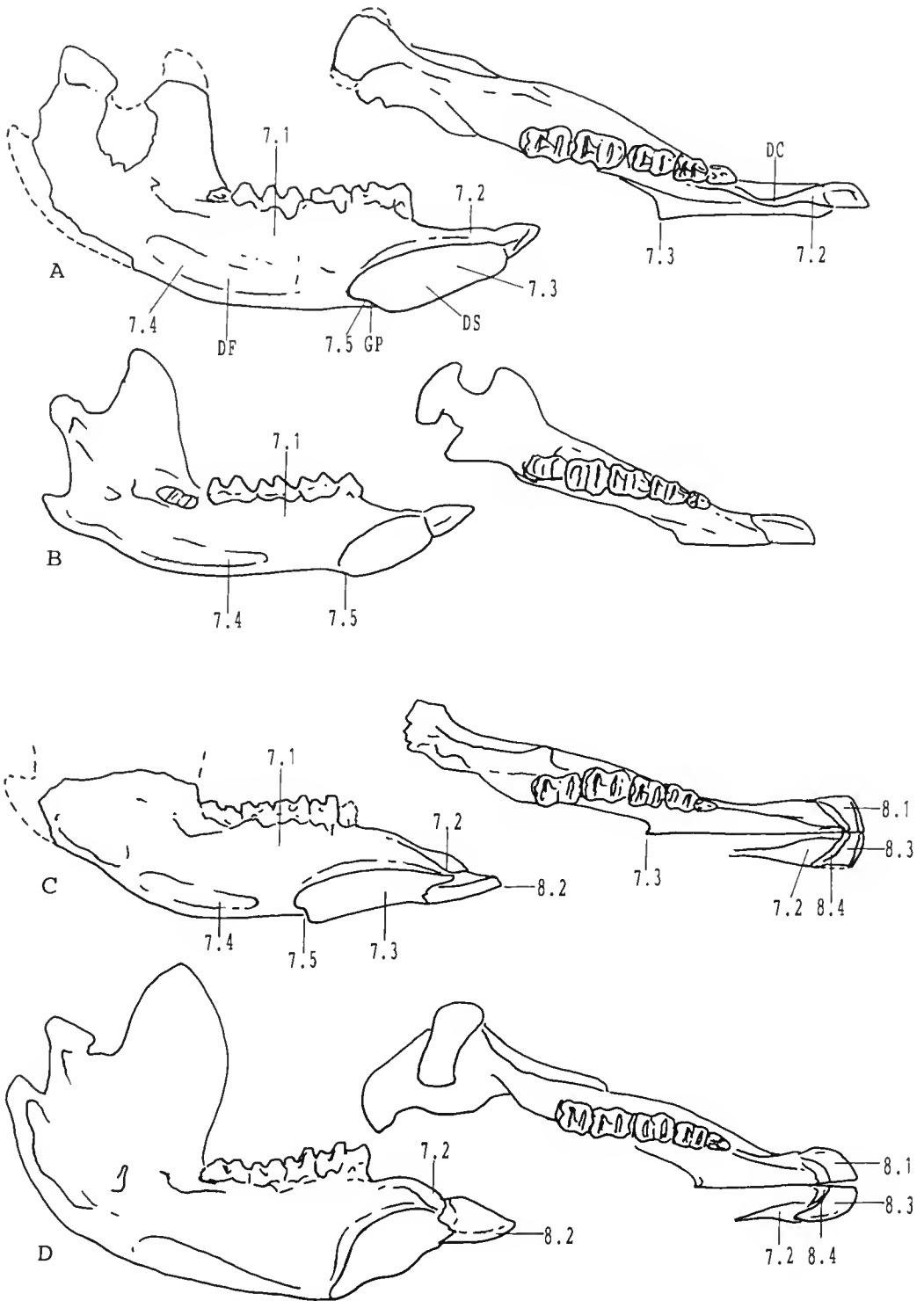


Fig. 11. Comparison of the dentaries of larger mid- to late Miocene diprotodontids with *Alkwertatherium webbi*. A, *Plaisiodon centralis* (SGM 881); B, medial aspect (left) and occlusal aspect (right) of *Neohelos tirarensis* (CPC 22530); C, *Alkwertatherium webbi* (paratype SGM 883); D, *Pyramios alcootense*, (SGM 891). Numerical character definitions are given in Table 4. Abbreviations: DC, diastemal crest; DF, digastric fossa; DS, dentary symphysis; GP, genial pit.

27.7. The right lowers are 18.3, 22.1, 25.8, 27.4; resulting in a proportional congruence of 0.87. The distance between the lophs and lophids for each occluding pair are as closely matched as can be determined by simple measurements. The congruence of the lower incisors with the upper incisor sockets appears to be close. Presumably the low angulation and buccal offset of the empty upper incisor sockets is disposed to the accommodation of the broad, procumbent lower incisors.

The dentary of *Alkwertatherium* differs from that of the nototheriid *Pyramios alcootense* in having a nearly straight inferior border of the horizontal ramus, an anteriorly tapering and more slender as opposed to a more massive, anteriorly deep, posteriorly tapering body; much shorter and vertically narrower, more horizontal diastemal portion, and a much longer and more horizontally disposed symphysis that extends to behind M_2 as opposed to behind the P_3 . In *Pyramios alcootense*, the dorsal contour of the symphysis (sublingual sulcus) is nearly vertical in SGM P891. Ventrally, in *Pyramios*, a distinct mental eminence is developed immediately below the incisor alveoli. This is also evident in the paratype UCMP 69784. The dentary is similar to, though much smaller than any mature specimen of *Plaisiodon centralis*, differing principally from that genus in the more procumbent incisor alveolus and relatively longer diastemal portion of the jaw. The symphyseal outline is more similar to *Plaisiodon* than it is to *Pyramios*.

The horizontal ramus is relatively deeper in proportion to length than in *Plaisiodon*, but it is also proportionally less thick in section below the molar alveoli. The diastemal crests of *Alkwertatherium* are much thicker, higher and less sinuous than in *P. centralis*. Anteriorly, the diastemal crests become laterally expanded, flat surfaces paralleling the sub-horizontally implanted incisor crown bases. The diastemal crests of *Pyramios* are similar, though more arched dorsally, much shorter and less expanded anteriorly than in *Alkwertatherium*. Internally, the digastric sulcus is slightly deeper than in either *Pyramios* or *Plaisiodon* and extends further anteriorly than in the latter but not as far anteriorly as in the former genus. The position of the genial pits is also intermediate between *Pyramios*, in which they are on the posterior surface of the sym-

physis and *Plaisiodon*, in which they are situated on the ventral surface. In *Alkwertatherium*, the genial pits penetrate the ventral surface of the symphysis, but extend onto the posterior surface as well.

Lower dentition: The lower incisors are extremely wide, thick, spatulate horizontally implanted teeth that repose with the lateral margin of the crown at about ten degrees from horizontal (Figs 5, 10-11; Table 1). *Plaisiodon centralis* incisors are only moderately spatulate, with the crowns oriented about 55 degrees from horizontal in frontal aspect, and lying at about 35 degrees from horizontal in lateral aspect, being considerably less procumbent than in *Alkwertatherium*. The lower incisor implantation of *Pyramios* is nearly horizontal, as in *Alkwertatherium*, but the symphyseal angle is substantially more steeply inclined and extends far deeper below the alveoli. The frontal implantation angle of the incisor crowns in *Pyramios* is acute. The internal angle of the paired incisors of *Pyramios* is V-shaped at between 80 and 85 degrees. In *Alkwertatherium* the internal angle (dorsal surfaces) of the paired incisors presents an obtuse surface of approximately 120 degrees.

The enamel extends entirely around the crown of the lower incisors of *Alkwertatherium*, as in *Pyramios*, in contrast to its being confined to a narrow strips on either side of the dorsal surface of the crown as in the zygomatic *Plaisiodon centralis*. The severely worn tips of the crowns of *Alkwertatherium* lower incisors precludes a description of their original shape, but there can be little doubt that they were very similar to those of *Pyramios alcootense*. The transverse width of the crown is at least 28 mm and about 10 mm thick medially, near the base of the crown. The crowns are thicker medially, tapering towards the external margins. The cementum is raised above the enamel on the dorsal surfaces forming a continuation with the broad, bony diastemal platform.

The P_3 of the paratype dentary SGM P883 was broken off, then placed in a small box which was subsequently mislaid during transportation of the specimens from the field. It was exceptionally small relative to the molars. Fortunately it is well preserved on SGM P892, a right dentary fragment of *Alkwertatherium* (Figs 12-13). The P_3 has a small, oval crown

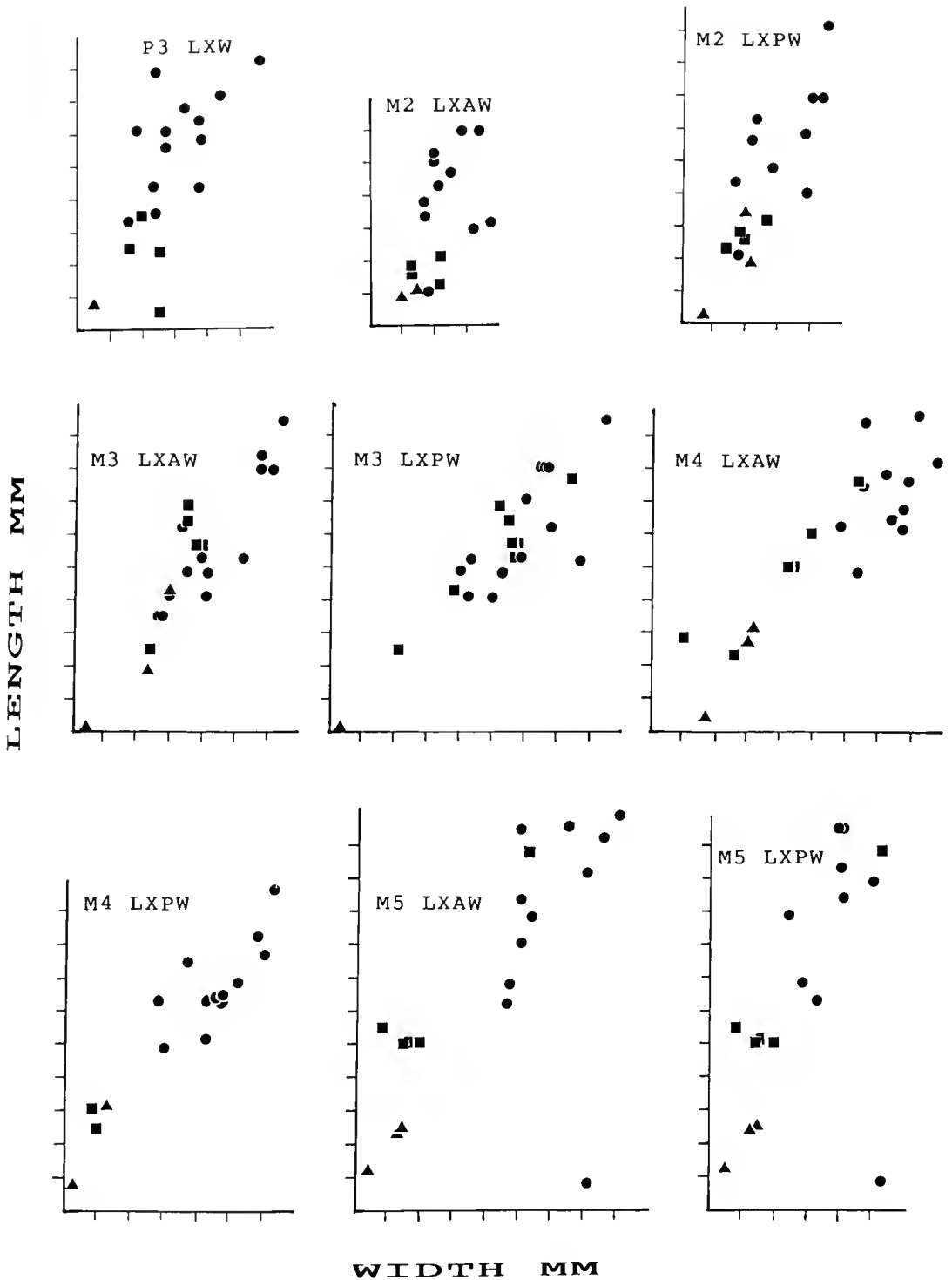


Fig. 12. Scatter diagram of the dimensions of lower cheek teeth of *Alkwertatherium webbi* (triangles), *Plaisiodon centralis* (dots) and *Pyramios alcootense* (squares). As with the upper dentitions, *Alkwertatherium* is more closely aligned with *Pyramios alcootense*. Data from Woodburne (1967a) and new specimens given in materials list. Regressions were not calculated due to small sample of *Alkwertatherium*.

composed of a large central cuspid and a median cristid which extends back to the interproximal contact with M_2 and is conjoined by a weak buccal and a more distinct lingual cingulum. The buccal cingulum trends obliquely towards the anterior edge of the posterior root, then faintly ascends the flank of the central cuspid to define a shallow, U-shaped fossa. The posterolingual cingulum surrounds a kidney-shaped basin. Structurally the P_3 crown is more similar to that of a zygomaturine (e.g. *Plaisiodon centralis*) and differs from that of *Pyramios* in being smaller, relatively narrower, shorter posterior to the central cuspid, in possessing a buccal cingulum and in lacking a clearly defined transverse crest from the central cuspid.

The lower molars are similar to those of *Pyramios alcootense* (Fig. 13). *Alkwertatherium* has a distinct but low paralophid crest and a steep, high protolophid on the M_2 . This high protolophid relates thegotically to the correspondingly low protoloph of the upper and the deeply worn posterior fossa of the P_3 and anterior cingulum of M_2 . With the exception of M_2 , the protolophids are wider than the hypolophids. The M_2 is relatively small, and the gradient is that of a gradual front to back increase in size. The lophids of $M_{2,3}$ are more obliquely oriented than the other molars. The protolophid of M_3 is also much higher than the hypolophid. The interlophid valleys of the first two molars are more sinuous and steeply V-shaped than in the last two. A short, low precingulum is present on the lingual side of the anterior base of the protolophid. Its expression diminishes gradually from front to back. A low cristid obliqua is present on all molars, extending from the hypoconid down the anterior face of the hypolophid to the base of the posterior face of the protolophid in the approximate longitudinal midline of the tooth. Weak cingulae occur in the buccal and lingual mouths of the interlophid sulcus. The postcingulum is thick, relatively deep and rounded. It is elevated slightly near the longitudinal midline of the tooth, commencing on the labial side proximally and swinging gradually toward the lingual side distally.

Etymology. The species designation "*webbi*" is made in gratitude to Thomas and Wendy Webb of Alcoota Station, Northern Territory, for their valued support in palaeontological research at Alcoota.

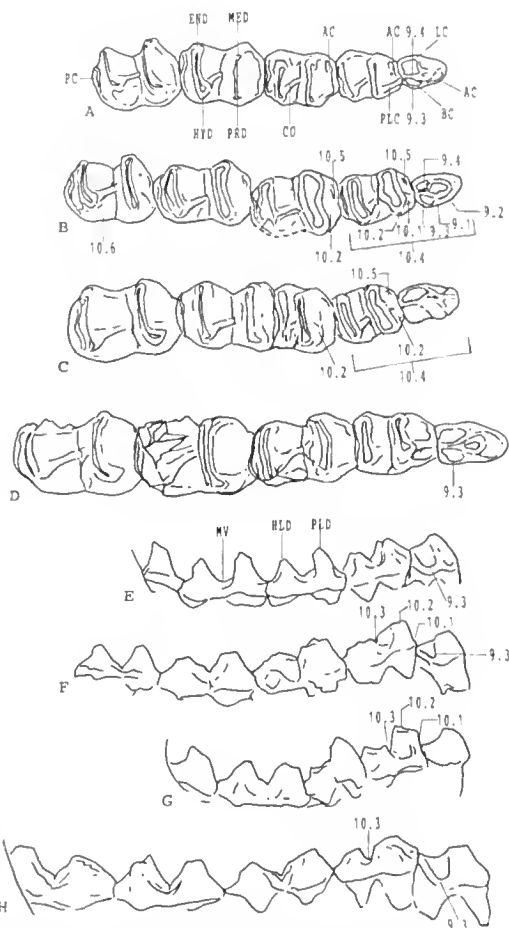


Fig. 13. Comparison of the lower cheek dentitions of the larger mid- to late Miocene diprotodontid genera with *Alkwertatherium webbi*. **A**, *Kolopsis torus* (SGM 893); **B**, *Alkwertatherium webbi* (paratype SGM 892); **C**, *Pyramios alcootense* (SGM 891); **D**, *Plaisiodon centralis* (SGM 881); **E**, labial aspect of dentition of *Kolopsis torus* (SGM 893); **F**, *Alkwertatherium webbi* (SGM 892); **G**, *Pyramios alcootense* (SGM 891); **H**, *Plaisiodon centralis* (SGM 881). Numerical references to character definitions are given in Table 4. Abbreviations: **END**, entoconid; **MED**, metaconid; **HVD**, hypoconid; **PRD**, protoconid; **CO**, cristid obliqua; **PLC**, paralophid crest; **BC**, posterobuccal cingulid; **AC**, anterobuccal cingulid; **MV**, midvalley (U-shaped in *Kolopsis torus*, as considered typical of zygomaturines); **HLD**, hypolophid; **PLD**, protolophid.

Analysis of characters. The morphological description of *Alkwertatherium webbi* broadly samples comparable morphological features, of which only a few are specifically useful in diprotodontid systematics (Tables 3, 5; Figs 6, 8, 11, 13). Many important features (suture configurations, upper incisor morphology etc.) could not be considered due to the poor

state of preservation of the specimen. Though incomplete, this constellation of characters is adequate to formulate an hypothesis of the approximate systematic position of *Alkwertherium*.

Based primarily upon the work of Stirton *et al.* (1967) and subsequently Archer and Bartholomai (1978), Aplin and Archer (1987), the Diprotodontidae can be divided into two subfamilies, the Zygomaturinae and the Nototheriinae or Diprotodontinae. Recent revisions have sunk the Nototheriinae. Consensus purports that the two groups of diprotodontids, the Zygomaturinae, with a well-developed parastyle on the upper third premolar and the Diprotodontinae which either lack or have small parastyles, are monophyletic. It is assumed that the large zygomaturine parastyle is a synapomorphic character. However, in the case of the Diprotodontinae, the absence or small size of the parastyle is a symplesiomorphic state.

Diprotodontines are also descripted from zygomaturines on the basis of tighter, more V-shaped interlophid valleys; "cleaner", less complex internal loph faces; high, steep protolophid of the M_2 ; suppression of the paralophid crest; weak anterior cingulid; strong postparaconal crest on the upper molars; reduced size of the upper and lower premolars relative to the size of the molars, and a greater obliquity of the molar loph and lophids. In derived forms (*Diprotodon*), the loph (-ids) of the molars are hypsodont.

This character complex may succeed in distinguishing the later Tertiary Diprotodontinae from the Zygomaturinae, but *Pyramios alcootense* variably expresses zygomaturine-like midlinks, complex interloph shapes and cingulum configurations, as well as possessing an upper third premolar that is consistently as large relative to M^2 , as in for example, the zygomaturine, *Neohelos*.

Pyramios alcootense aligns with diprotodontines in having a steep, high protolophid on the M_2 , a suppressed, practically nonexistent, paralophid crest; in the molar gradient of the uppers, in which there is a simple front-to-back enlargement and in which the metaloph is not as reduced relative to the protoloph as in zygomaturines, and of course, the upper third premolar, which lacks a well-developed parastyle. In cranial characters, *Pyramios* resembles *Euryzygoma* in its diastemal constriction, deep, broad cranium and short, pos-

teriorly divergent molar arcades. However, the I^3 's in *Euryzygoma* and *Diprotodon* are in line with the I^2 's and the zygomatic processes are flat-sided.

The lower incisor morphology, relatively wide though V-shaped interlophid valleys, weak cristid obliquae and comparatively low

Table 5. Distribution of characters in representatives of four diprotodontoid families. 1, wynyardiid (*Muramura williamsi*); 2, "palorchestid" (*Ngapakaldu*) and 3, palorchestine (*Propalorchestea*) examples represent the outgroup; 4, diprotodontine (*Pyramios alcootense*); 5, zygomaturine (*Alkwertherium webbi*); 6, zygomaturine (*Neohelos tirarensis*); 7, zygomaturine (*Plasiodon centralis*); 8, zygomaturine (*Kolopsis torus*). Symbols: 0=absent; +=present; ±=more or less present; -=not observed; ?=unsure of homology; AP=apomorph, PL=plesiomorphy.

	1	2	3	4	5	6	7	8	CHARACTER DISTRIBUTION AND STATE
1.1	0	0	0	0	+	+	+	0	long, high steep frontal (AP)
1.2	0	0	0	0	+	+	0	0	constricted preorbitally (AP)
1.3	+	0	0	0	+	+	+	0	postsquamosal constriction (PL)
1.4	0	±	0	0	+	+	0	+	upward BC flexion (AP)
1.5	+	+	0	+	0	+	+	0	thin frontal crests (PL)
1.6	0	0	0	0	+	+	+	+	nasals expand anteriorly (AP)
1.7	0	0	0	0	+	+	+	0	trapezoid narial aperture (AP)
1.8	+	0	0	0	+	+	0	0	low, narrow occiput (PL)
1.9	0	+	+	+	+	+	+	+	wide, oval foramen magnum (PL)
2.1	0	0	+	+	+	0	0	0	long squamosal process (AP)
2.2	0	+	+	0	+	+	+	+	flattened zygomatic arch (PL)
2.3	0	0	0	0	+	0	0	0	zygomatic deeper anteriorly (AP)
2.4	+	+	0	0	+	+	+	+	short masseteric processes (PL)
2.5	+	+	0	+	0	+	+	+	deep nasolabial fossa (PL)
2.6	0	0	0	+	+	0	0	0	distinct facial crest (AP)
2.7	0	0	0	+	+	0	0	0	distinct buccinator fossa (AP)
2.8	+	+	+	0	+	+	+	0	long squamosal sulcus (PL)
2.9	0	+	?	+	+	0	0	0	shallow diastemal profile (AP)
3.1	0	0	+	+	0	+	0	0	long, narrow palate (AP)
3.2	+	+	+	0	±	+	+	+	arcades parallel, straight (PL)
3.3	0	0	+	+	+	0	+	0	constricted diastema (AP)
3.4	0	+	0	+	+	0	0	0	flared premaxillary palate (AP)
3.5	0	0	+	+	0	0	0	0	I^1 lateral to F (AP)
4.1	+	0	0	0	+	0	0	0	narrow, shallow IP fossa (PL)
4.2	-	+	+	+	+	+	+	+	small pterygoid fossae (PL)
4.3	0	0	0	0	+	+	+	+	oblique glenoid fossae (AP)
4.4	0	0	±	0	+	0	0	0	deep, V-shaped condylar notch (AP)
5.1	?	0	0	0	+	+	+	+	large parastyle on P^3 (AP)
5.2	+	+	+	+	+	0	0	0	hypocone absent (PL)
5.3	+	+	+	+	+	+	+	0	undivided parametacone (PL)
5.4	0	0	0	+	+	+	0	+	buccal cingulum present (PL)
5.5	?	±	+	+	0	0	0	0	high, large mesostyle (PL)
5.6	0	0	+	+	+	0	0	0	functional posterior basin (AP)
6.1	+	+	+	+	0	0	±	0	weak parastyle, strong PPC (PL)
6.2	0	0	0	±	0	±	0	0	thick, short, rounded LC (AP)
6.3	0	0	0	0	+	0	±	0	protostyle on M^2 (AP)
6.4	+	+	+	±	+	0	0	0	M_2 - M_1 in line lingually (PL)
6.5	+	+	+	+	0	0	0	0	P^3 widely contacts M^2 (PL)
6.6	0	0	0	0	±	+	+	+	Metaloph reduction $M^{4,5}$ (AP)
6.7	0	0	0	0	+	0	0	0	large metastyle low on M_1 (AP)
6.8	0	0	0	+	0	+	0	+	short, thick buccal cingulum (AP)
7.1	+	+	+	0	+	+	+	+	deep ramus tapers anteriorly (PL)
7.2	0	0	+	+	0	+	0	+	strong diastemal crests (AP)
7.3	0	0	+	0	+	0	±	0	long, horizontal symphysis (PL)
7.4	0	0	+	+	0	0	0	0	short, weak digastric fossa (AP)
7.5	+	+	+	±	±	+	+	+	genal pits ventral surface (PL)
8.1	0	0	+	+	+	0	0	0	spatulate I_1 crown (AP)
8.2	0	+	+	+	0	0	0	0	horizontally implanted I_1 (AP)
8.3	0	0	+	+	0	0	0	0	enamel all surfaces I_1 crown (AP)
8.4	0	0	0	+	0	0	0	0	cementum raised above enamel (AP)
9.1	0	+	0	0	0	0	0	0	P_2 small relative to molars (PL)
9.2	0	+	0	0	0	0	0	0	narrow, oval crown of P_1 (PL)
9.3	0	0	0	0	+	+	+	+	buccal cingulum present on P_1 (AP)
9.4	0	0	+	0	+	+	0	+	short posterior moiety P_3 (PL)
10.1	0	0	+	+	0	0	0	0	steep protolophid, weak crest (AP)
10.2	0	+	+	+	0	0	0	0	protolophids higher (AP)
10.3	+	+	+	+	0	0	0	0	V-shaped mid valleys (PL)
10.4	0	0	+	+	0	0	0	0	lingual offset P_1 (AP)
10.5	0	0	+	+	0	0	0	0	weak, short precingulid (AP)
10.6	0	0	0	0	±	+	+	+	reduced M_1 (AP)

lophs and lophids of *Pyramios* are not suggestive of a close relationship to *Euryzygoma* or any other later Tertiary notothere (Woodburne 1967a, 1967b).

Having noted these discrepancies in combination with the geologically late occurrence of *Pyramios*, Woodburne (1967a, 1967b) characterized *Pyramios* as a primitive notothere residing near the base of subsequent diprotodontine radiations. Although Woodburne (1967a) does not make the point explicit, the odontological similarity of *Pyramios* with certain Alcoota zygomaturines is difficult to ignore, and some of the ambiguities in differentiating *Pyramios* from the zygomaturines are implicit in his conclusions.

Among the zygomaturines, some *Plaisiodon centralis* specimens have strong postparaconal crests, as in *Alkwertatherium*. The molar parastyles of both *Alkwertatherium* and *Plaisiodon* are relatively small; and the interloph valleys are proportionally similar in these genera. The thick, short labial cingulae that arise along the anterior ends of the midvalleys are also present in some *Plaisiodon* specimens and are especially prominent in *Alkwertatherium*.

Assuming monophyly for the Diprotodontidae, *Pyramios* and *Alkwertatherium* could represent remote descendants of the two respective subfamilies (Fig. 14). An alternative hypothesis is that *Pyramios*, *Alkwertatherium*, *Plaisiodon* and perhaps *Kolopsoides* represent an intermediate clade of diprotodontids into which a degree of parallel evolution (i.e. independent development of the parastyle and hypocone) must be introduced. The reality is, given the degree of morphological variability (i.e. absence of hypocone in some *Neohelos* specimens) and difficulty in establishing clear complementary distributions in character complexes in these genera (correlation of the presence or absence of a feature with another), combined with the extraordinarily long period of time since their inferred divergence from a parent clade or their respective parent clades, that few "pristine" character states of a precisely comparable nature are present for comparison.

The cladogram (Fig. 14) is based primarily upon dental morphology, particularly the upper third premolar. The family Diprotodontidae is distinguished from the Palorchestidae on the basis of the synapomorphic loss,

incorporation or suppression of styler cusps C and D into the lophs (Fig. 14 [1]). The absence of the parastyle on the P³ is plesiomorphic. A symplesiomorphic diprotodontid character is the presence of a large epitympanic fenestra, which decreases in size in the derived diprotodontids, but remains more highly expressed in the zygomaturines than in the nototheres. In *Pyramios* the epitympanic fenestra is small and simple (Woodburne 1967b) whereas in *Neohelos*, the fenestra is usually large, though sometimes subdivided and narrowed transversely. The ventral squamosal tympanic wing is virtually absent in plesiomorphic diprotodontids so that the tympanic cavity is a mere hollowing of the posterior wall of a bulla-like hypotympanic swelling that also forms the entoglenoid eminence. In *Pyramios*, a secondary ventral tympanic process is derived from the mastoid (Woodburne 1967b). The polarity of this morphological complex appears to be a progressive reduction of the alisphenoid tympanic process, present in *Propalorchestes* (Murray 1986) to a short, entirely squamosal tympanic process (e.g. Vombatidae). The diprotodontid condition is accompanied by a hypertrophy of a hypotympanic sinus immediately anterior to the tympanic cavity and the tympanic process is further reduced. In *Pyramios*, the reduced anterior processes are replaced by a mastoid tympanic wing. In *Diprotodon* the tympanic cavity is partially floored by fusion and hypertrophy of other surrounding elements. In all known zygomaturines, except perhaps, *Zygomaturus*, in which secondary bony fusions are evident, the tympanic cavity is open ventrally.

The derived diprotodontids show a more distinct front to back molar gradient than in palorchestids and primitive diprotodontids (Fig. 14 [2]), (Rich *et al.* 1978). Plesiomorphically a strong paraeristid (paralophid crest of Stirton *et al.* 1967) is present.

The synapomorphic basis for clade stem [3] is inferred to be the reduction of the paralophid crest on M². There is a plesiomorphic retention of the small parastyle, high mesostylar cusp and simple, undivided parametacone on the P³.

Pyramios alcootense retained or developed a P³ of large size relative to the molars [4] with a small, though in some individuals (SGM P872) an incipiently zygomaturine-like, parastyle. Symplesiomorphically the upper mo-

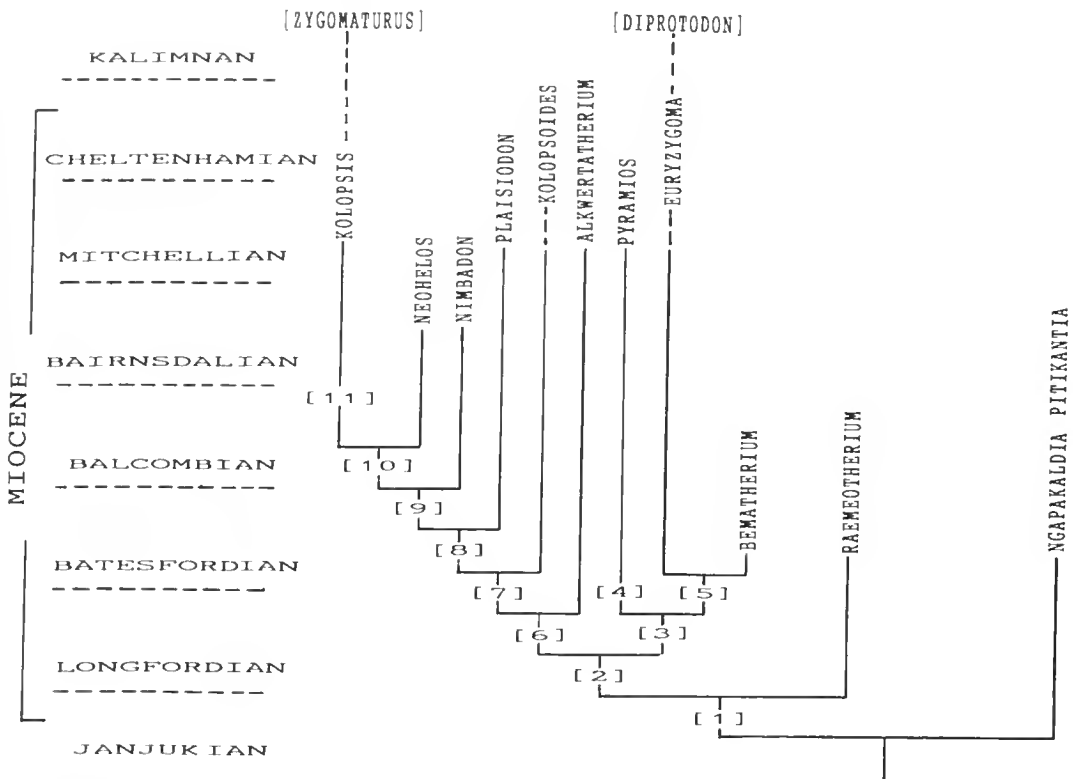


Fig. 14. Hypothesis of phylogenetic branching in Miocene diprotodontids based primarily upon a cladistic assessment of odontological characters (Table 5), depicted with minimum circuitry. The approximate Lyellian equivalency of the included genera is related to pan-continental stages (Woodburne *et al.* (1985). The discussion contains a more detailed interpretation. [1] loss, incorporation or suppression of styler cusps C and D in relation to the lophis; [2] distinct front to back molar gradient; [3] reduction of paralophid crest; [4] P³ large relative to molars; [5] reduction of size of permanent premolars relative to molars; [6] large parastyle, separated from the parametacone by a deep cleft; [7] development of a hypocone on the P³; [8] "hook-like" parastyle on P³ (Hand *et al.*, in preparation); [9] basic proportional similarity of the P³ in *Nimbadon* and *Neohelos* (narrow posterior fovea of P³, etc); [10] mesostyle retracted towards egingulum; [11] parametacone in *kolopsis* divided into two distinct cusps.

lars develop midlinks to the extent of *Plaisiodon* and *Alkwertatherium*. The paralophid crest is weak or absent and the protolophid of M² is high and steep.

Character complex [5] sets the other nototheriines apart from *Pyramios*: synapomorphic reduction of the size of the permanent premolars relative to the molars and tendency towards higher, steeper lophis and lophids.

The development of a large parastyle on the P³ [6] unites all zygomatuline diprotodontids. Plesiomorphically it lacks a hypocone, is broad posteriorly and retains a high styler cusp on the labial side of the apex of the parametacone. A marked narrowness of the metaloph relative to the protoloph on M⁴ and especially M⁵ is also characteristic.

Subsequent zygomatulines are united by the development of a hypocone on the P³ [7].

Plesiomorphically the genus *Kolopsoides* retains a poorly differentiated parastyle, though interpreted by Plane (1967) to be a derived feature. Autapomorphically, the hypocone is as large or even larger than the protocone in *Kolopsoides*. *Kolopsoides* and *Plaisiodon* appear to be united by a lengthening of the parametacone in which however, the paracone and metacone remain essentially undifferentiated, the mesostylar cusp remains high and poorly defined labially, and a posterobuccal egingulum is absent in these two genera. Phenetic similarity in the long, nearly horizontal dentary symphysis of *Plaisiodon*, *Kolopsoides* and *Alkwertatherium* combined with the large, deep, almost fully enamelled lower incisors in (young only) *Kolopsoides* (Plane 1967) suggest a minor clade grouping, but evidence is thin.

Nimbadon and *Plaisiodon* are tenuously united by a "hook-like" shape of the parastyle of P³ (Hand *et al.* personal communication) [8]. The shape and proportions of the cusps the P³ are also similar in *Neohelos* and *Nimbadon* [9]. However, *Neohelos* usually has a prominent buccal cingulum with a small but fully differentiated mesostyle located well below the apex of the parametacone [10]. In *Kolopsis* the parametacone is divided into two distinct cusps [11] and an anterobuccal in addition to a posterobuccal cingulum, sometimes with a defined mesostyle, is usually present.

DISCUSSION

The similarities between *Alkwertatherium* and *Pyramios* on the one hand and *Alkwertatherium* and *Plaisiodon* on the other, are not easy to reconcile because of discontinuities in some of the character complexes and the continuously varying nature of others. My initial impression of *Alkwertatherium* was that it might belong to the genus *Plaisiodon*, (Murray 1989), impetuously resulting in a *nomen nudem* status for the name "*Plaisiodon webbi*". Although the type *Pyramios* description seemed more remote relative to *Alkwertatherium* than that of *Plaisiodon*, there are also both general and specific similarities to *Pyramios*. In order to include *Alkwertatherium* within one or the other genus, either generic diagnosis would have to be revised to accommodate the specimen. If the differences among *Plaisiodon*, *Pyramios* and *Alkwertatherium* were to be sunk to the specific level, the subfamilial diagnoses as well as the generic diagnoses would require revision due to the higher level systematic emphasis placed upon the presence of a large, differentiated parastyle on the P³ of *Alkwertatherium* and all other zygomaturines. The least disruptive option is to differentiate the new form at the generic level.

Alkwertatherium shows divisions of certain character complexes that are perceived as interrelated characters in other Alcoota genera. For example, the protolophid of M₂ is steep in *Alkwertatherium* but the paralophid crest is more differentiated than in *Pyramios*, suggesting that the two characters are genetically independent. The long, horizontal symphyseal profile in *Alkwertatherium* is more similar to that of *Plaisiodon* than to the nearly

vertical profile of *Pyramios*, yet the procumbent incisor implantation and morphology of the incisors suggest a closer relationship between *Pyramios* and *Alkwertatherium*. Conversely, the deep, spatulate lower incisor crowns of the zygomaturine *Kolopsoides* are more similar to those of *Alkwertatherium* and *Pyramios* than to those of other zygomaturines.

The constricted diastemal palate in *Alkwertatherium* is very similar to the condition in *Pyramios* and other nototheres. It is one of a few consistent apomorphic features that could unite the diprotodontinae (nototheres) and, were it not for the prominent parastyle-bearing *Alkwertatherium*, a monophyletic grouping might be supported with this character. *Plaisiodon centralis* also has a more extreme constriction of the diastemal palate than in other zygomaturines, except perhaps for *Zygomaturus*. The condition varies continuously from *Pyramios* to *Alkwertatherium* to *Plaisiodon* (Fig. 6). A number of other features (Table 5) align the cranium of *Alkwertatherium* to the zygomaturines, especially to that of *Plaisiodon*.

The zygomaturines *Nimbadon*, *Neohelos* and *Kolopsis* appear to form a distinct subclade, largely through a retention of plesiomorphic zygomaturine features. I surmise that they separated from the *Alkwertatherium-Plaisiodon-Kolopsoides* subclade at the point of the expression of the hypocone on the P₃. In order to express this phenomenon on a cladogram, I would be compelled to postulate a series of dichotomies for which there is no concrete evidence. A similar series of dichotomies would be entailed to resolve the relationship between *Pyramios* and *Alkwertatherium*. I have not expressed these palaeontologically unsupported branchings on the cladogram.

It has not been directly demonstrated in the fossil record that the zygomaturines arose from a parastyle-less ancestor. The condition is inferred from the plesiomorphic alignment of palorchestids with the diprotodontids. The earliest recognizable diprotodontids (e.g. *Ngapakaldia*) lack the prominent parastyle of zygomaturines (Murray in press; Murray and Wells, in press).

The preferred hypothesis is that zygomaturines arose from a notothere-like form in which the parastyle was reduced, as in primitive palorchestids. It is therefore more compelling to view *Pyramios* as a structural intermediate

between the diprotodontines and zygomaturines, than to place the genus in a position ancestral to later diprotodontines. The morphology of *Alkwertatherium* is resolved as being largely symplesiomorphic with *Pyramios*, but in possession of the zygomaturine apomorphy of a large, differentiated parastyle.

As yet, there are no recognizable annectent forms for either *Alkwertatherium* or *Pyramios* in any of the pre-Cheltenhamian local faunas. The Bullock Creek *Neohelos tirarensis* appears to be closely related to *Kolopsis torus* (Stirton *et al.* 1967). *Nimbadon* spp could represent basal zygomaturines with some specific affinity to *Plaisiodon* and *Neohelos* (Hand *et al.*, in preparation) but there is no firm evidence to support this observation. It is not likely however, that the apomorphic character complexes in *Alkwertatherium* and *Pyramios* evolved entirely within the intervening period between the mid- and late Miocene. It is reasonable to assume that the ancestors of both of these distinctive genera will eventually be recognized in one of the early to mid-Miocene faunas.

The presence of *Alkwertatherium*, *Plaisiodon*, *Pyramios* and other unique non-diprotodontid forms such as the primitive macropodid *Hadronomas puckeridgei*, sets the Alcoota Local Fauna apart from the mid-Miocene and early to mid-Pliocene faunas. It appears to represent an assemblage of plesiomorphic relicts, the ancestors of some of which must antedate the Bullock Creek Local Fauna and which must have evolved in relative isolation. Of the diprotodontids, only *Kolopsis* is suggestive of later annectents (*Zygomaturus*). I suspect therefore, that a significant portion of the Alcoota Local Fauna may represent a relict of early to mid-Miocene radiations analogous to the New Guinea Pliocene local faunas. Although there is no obvious geographic feature that would explain such an isolation, it may be that the isolation of drainage patterns and associated habitats occurred earliest in the centre, severely limiting population movements by mid-Miocene times.

CONCLUSIONS

Alkwertatherium webbi gen. et sp. nov. establishes a close relationship between diprotodontines (= nototheres) and zygomaturines, if

it is accepted that *Pyramios* is a diprotodontine rather than a primitive zygomaturine. The Alcoota form, *Plaisiodon centralis*, appears to be more closely related to *Alkwertatherium* than to any other known zygomaturine. It is postulated that there were two minor zygomaturine lineages, one represented by *Nimbadon*, *Neohelos* and *Kolopsis*, and the other represented by *Alkwertatherium*, *Plaisiodon* and *Kolopsoides*. The two minor lineages could be united through the ancestor of *Nimbadon*.

This assumes, of course, that I have not described one of the extreme ends of two highly variable generic clines (*Plaisiodon* and *Pyramios*) as a new genus. I justify the generic distinction of *Alkwertatherium* on the basis of its possession of a character that is also employed to distinguish the two subfamilies of the Diprotodontidae. The systematic emphasis of this character depends upon the assumption that *Alkwertatherium* is more derived than *Pyramios* and more primitive than *Plaisiodon*. Should it eventually be shown that *Alkwertatherium* is an extreme variant of either genus, this account would be no less informative, because it will have drawn attention to a degree of morphological variability sufficient to seriously question current diprotodontid systematics.

Meanwhile, I submit that *Alkwertatherium* accounts for some of the anomalies in the cheek tooth measurements of *Pyramios* and *Plaisiodon* provided by Woodburne (1967a). Its morphology, though derived, provides a glimpse of the antecedents of the two subfamilies of diprotodontids and gives some indication of the polarity of certain characters as well as documenting structurally, the stages transitional between diprotodontines and zygomaturines.

SUMMARY

Alkwertatherium webbi exhibits a unique combination of diprotodontine (= nototheriine) and zygomaturine characters in its cranium, dentition and dentary morphology. Although the upper third premolar had developed a large parastyle as in the zygomaturine diprotodonts, it retains a weak posterobuccal cingulum, lacks a hypocone and otherwise resembles the P₃ of the notothere, *Pyramios alcootense* Woodburne. The cranium of *Alkwertatherium* is basically similar to that of the

zygomaturine *Plaisiodon centralis* Woodburne, differing principally from that genus in having an extremely constricted diastemal palate, expanded interincisival fossa and incisor angulation more characteristic of nototheriines. The dentary resembles some nototheriines and especially palorchestines in having a long, narrow sublingual fossa and spatulate incisors, but is more similar to the zygomaturine *Plaisiodon* in overall shape and proportions. *Alkwertatherium* can be explained as a relict form which evolved from an ancestral clade structurally intermediate between zygomaturines and nototheriines. It is concluded that *Alkwertatherium webbi* is a late surviving representative of a plesiomorphic zygomaturine clade ancestral to *Plaisiodon centralis* and *Neohelos tirarensis*.

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HUMANITIES

A BRIEF NOTE ON THE MALAGAN *CURVUNAVUNGA* FROM TABAR, NEW IRELAND PROVINCE, PAPUA NEW GUINEA.

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ABSTRACT

A type of malagan sculpture previously used for peace-making is described and placed within its current cultural context on Tabar, New Ireland.

KEYWORDS: Papua New Guinea, New Ireland, Tabar, malagan, art, peace-maker.

INTRODUCTION

Malagan traditions of New Ireland first came to notice of the outside world through the work of Richard Parkinson in the late 19th century (Meyer and Parkinson 1895; Parkinson 1907). Parkinson, followed by Krämer (1925), Peckel (1910, 1926-7, 1928, 1929, 1931, 1932) and Walden (Walden and Nevermann 1940) developed the rudiments of the western understanding of malagan: that it is a series of rites accompanied by an outstanding art tradition concerned with honouring and maintaining the memory of the dead. Powdermaker (1931a, 1931b, 1932, 1933), Groves (1934, 1934-5, 1936, 1936-7) and then Bühler (1933) extended descriptive knowledge with detailed studies at the village level, but it was not until Lewis's work in 1953-4 (Lewis 1969) that the social contextual meaning of malagan was explicated. More recently Brouwer (1980), Heintze (1969), and Kuchler (1985, 1987) gave detailed analysis of malagan symbolism in three locations on mainland New Ireland. Most recently Lincoln (1987) edited a body of work by Bodrogi, Clay, Heintze, Gunn, Lincoln, and Wagner that covered aspects of some of the still active malagan traditions in New Ireland.

Despite this relatively intensive documentation, there is no record of those items of malagan sculpture which were used by antagonistic clans at major peace ceremonies. This paper documents the last of these old *Curvunavunga* peace-making malagans on Tabar, the traditional home of malagan. The

original function of the malagan type is described, followed by a discussion of the subsequent use of the *Curvunavunga* sculpture found at the Obun village site.

DISCUSSION

In June 1982, on behalf of the National Museum of Papua New Guinea, the author purchased the last known remaining example of a *Curvunavunga* malagan on Tabar from Daniel Kariets of Vutigamgam clan (*matabu*) at Manggavur village, southern Tatau Island. It is now registered with the National Museum of Papua New Guinea as 82.50.7.1.

The four metre horizontal hardwood *Curvunavunga* malagan sculpture was in a badly weathered condition, but still resting on its support posts on Tirodan clan land in the centre of the old village site of Obun, 2 km east of Manggavur (Plate 1). Obun was last occupied before the Second World War, then abandoned when the inhabitants moved to Manggavur.

Although four people were able to give the author information about the *Curvunavunga* type malagan, only two locations for this malagan type were recorded and the example under discussion was the only one sighted. Around Mapua and southern Tatau Island (central in the Tabar Group) informants referred to the malagan type as *Curwunawunga* or *Curwunawungga*. In central and southern Big Tabar it was referred to variously as *Surwunawunga*, *Suruniwunawungga* or *Suruwunawungga*. These glosses reflect

dialect variants based upon *cur-* = reproducing or cloning malagan (lit. bed, from which many spring); and *vunavunga* = ridge-pole of a house. At Tatau village, north Tatau Island, the *Curvunavunga* type of malagan was remembered as *Watirewong* by Lomlom, now an old man over 70 years old. Other associations for this name were not known by Lomlom or any other informants.

On the basis of data provided in 1982 by informants at Manggavur village and 1983-4 at Wang village, it seems that the *Curvunavunga* malagan type was used in two phases: initially as a peace malagan, and later as a woman's malagan used to mark the completion of the initiation of young adult women into "big-woman" status.

Up until the end of 1884 Tabar was perceived as hostile to all foreigners and the inhabitants were apparently at war with the people of mainland New Ireland (Romilly 1886:42) as well as with one another. Shortly after the German annexation of New Ireland in 1884, the warships "Elisabeth", "Albatros", "Hyane", and "Marie" made the Imperial German Government's presence known in the area (see Sack and Clark 1979) and the people of Tabar were persuaded to cease fighting.

As a peace-making malagan the *Curvunavunga* assumed a significance above all other malagan types. From oral traditions recorded from Lapan Landavak at Wang village, south-

ern Big Tabar, I understand that after initial peace negotiations had taken place the necessary gardens prepared and pigs were located and counted, then the *Curvunavunga* malagan sculpture was made by sculptors commissioned by both sides. Upon completion of the sculpture, the malagan ceremony for the *Curvunavunga* was jointly operated by the two disputing clans. During the ceremony, each clan exchanged a number of lengths of *re* shell discs in order to "buy the war-dead" of the opposing clan. Both sides then brought out the heads of all those who had been killed and placed them on top of the *Curvunavunga*. This action was termed "*vavunga kita pi a mu koa ni rivirua*" [this one is to finish for all time the heads of all those killed in the fighting].

After the peace was made the *Curvunavunga* malagans remained in village centres until they disintegrated or were sold to foreigners. If sold, the support posts would be left in the ground. One immense old fig tree near Datava village on Big Tabar Island still has a pair of posts amongst its roots, firmly planted in the ground. Local people said that these support posts were placed in the ground and consolidated by using strong magic associated with *koravar* (*Zingiber* sp.) and lime. This consolidation had the effect of placing a taboo on the posts so that the relics would remain as evidence of the reconciliation for future generations.



Plate 1. A horizontal *Curvunavunga* malagan sculpture from Tabar, four metres long, hardwood.

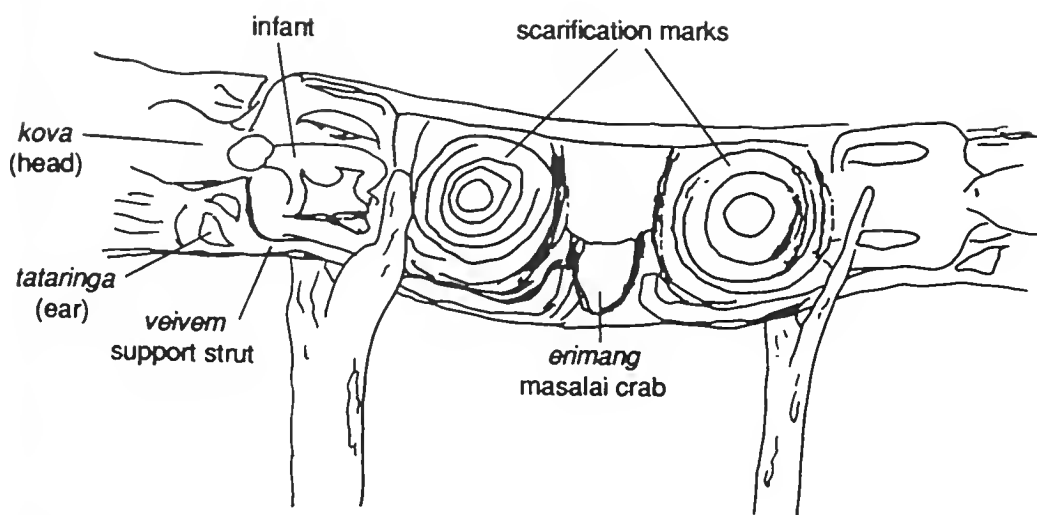


Fig. 1. Reconstructed sketch of *Curvunavunga*.

SUBSEQUENT USE OF THE OBUN *CURVUNAVUNGA*

Those malagans which remained in the village centres became subject to the processes of transfer of ownership which affect all property on Tabar. Traditions of inheritance for the *Curvunavunga* were quite different to those for normal malagans on Tabar, for the *Curvunavunga* appear to have been permanent fixtures in village centres. Normal malagan sculpture is ephemeral, for it is made according to inherited prescription which changes owners at a malagan ceremony held in graveyards. An example of the sculpture is made and displayed at the ceremony as part of the change of ownership of normal malagans, and is rarely reused (see Gunn 1987:78-83). Malagan sculpture is today either thrown into the *vuotung* "cold house" part of the graveyard after use, or else wrapped in pandanus spathe and kept in the roof of the men's house to be sold to a passing foreigner.

According to oral traditions recorded from Daniel Kariets at Manggavur, the *Curvunavunga* was owned by the first born woman of each generation and passed from one woman owner to the next (Appendix 1). The first-born girl of the next generation was confined for a period in a separate building inside the men's house area in the graveyard. She resided with 10 to 20 other children, both male and female, who were undergoing a period of seclusion (*davan*) prior to the end of puberty, a process which made them into potential community leaders. Confinement of young women has

been reported elsewhere in the literature from other parts of New Ireland. Krämer (1925:27) noted a very similar system in the Madak language area, where the confinement house was called *eandavan*. Parkinson (1907:272) reported the practice from south-western New Ireland, and Bell's report (1936) on *dafal* from the Tanga Group indicates the geographic spread of this custom. Reports of the confinement of young men as well as women on Tabar was recorded from two unrelated informants and suggests a Tabar variation on the practices found elsewhere.

When a girl who was to inherit the *Curvunavunga* malagan was about to "come out", she was escorted to the centre of the village and placed on a platform underneath the big malagan. She would then be given a piece of taro to hold in her hand and her father's classificatory sisters would come and eat from the taro. Those who ate the taro would then drape the initiate with *re* (strings of shell discs). After this section of the ceremony was completed, the shell lengths would then be draped over the malagan above her.

Following the initiation, women of the father's clan would "play" with the initiate's mother's brothers. A similar "play" between clans during initiation is still carried out today in the *beriber* cycle of ceremonies for a first-born child. In one such "play" witnessed by the author in Monun village, north Simberi Island, a large group of singing women from the child's clan climbed over the entrance into the men's house enclosure and graveyard where the men were solemnly feasting, picked

up handfuls of food and rubbed it into the faces and hair of the men from the child's father's clan. This "play" culminated with the women flogging the men with twigs and then throwing them into the sea. *Beriber* women's ceremonies today often have an attached malagan component, where there is a need to hand a malagan onto the next generation before the original owner dies. Ownership of the rights to produce malagan sculpture can only be transferred to the next generation through public display of the sculpture. If the owner dies without passing on his rights to the next generation, then the malagans he owns die with him. Consequently, when an owner approaches death, every opportunity is taken to display and transfer malagan sculpture. Opportunities include *beriber* ceremonies, a person returning home from a long absence and malagan ceremonies held by distant kinsmen.

According to the oral traditions received by the current owner of the *Curvunavunga*, the images on the malagan found at Obun (Fig. 1) are of two women lying opposed, their genitalia joined by the crab *erimang*. In this context *erimang* is one of a group of ancestral concepts called *tadar* (or variously *tandar*, *tandaro*, *tendar*) on Tabar. *Tadar* are spirit images linked to clans and strongly associated with land ownership. *Tadar* concepts will be discussed in a later paper. The author recorded a further example of *Erimang* on Tabar as *Erimang Porpor Merik*, a *tadar* crab belonging to Betet clan. This *tadar* is located close to the sea in a creek to the north near Maragat village on the north west part of Tatau Island. *Porpor merik* literally means "red flower" and is a reference to the red decoration or hair on the crab's chest. It is not known whether Betet or any related clan had a connection with the malagan, the clans, or with the land involved with the *Curvunavunga* under discussion.

An infant (sex now indeterminate) lies on the breast of the woman to the left, but due to the deteriorated condition of the carving it was not possible to determine whether a similar infant lay on the other woman's breast. Another example of *Curvunavunga* which was burnt in earlier times was described by an informant from Wang village, southern Big Tabar Island, as featuring a woman giving birth.

According to a Daniel Kariets the concentric circles surrounding the women's navels

on the *Curvunavunga* are indicative of the scarification traditions of earlier times, when each woman had her own personal design. *Veivem* side rails found top and bottom on the malagan also occur on many current types of malagan sculpture, and often are said to indicate the spears previously used to support the dead in the *bo*, the chair on which corpses were previously displayed.

Although the antecedents of the *Curvunavunga* malagan traditions are not known, smaller malagan types are still used today to terminate clan separations and disputes. In the one example of a dispute termination recorded at Pekinberiu village by the author, both sides came together to "work a malagan" as part of a larger ceremony which both of the clans operated. The conciliatory ceremony was termed *vedega* "looking at one another", and for this ceremony *kupkup ci malaga* "fountain of malagan" sculptures was used. *Kupkup ci malaga* are a quick-to-work type of malagan and are generally small figure sculptures, although other styles can also have this classification. Two malagan sculptures, together with *re* shell disc strings and pigs, were exchanged between the two big-men. The final action of *vedega* culminated with the two big-men each holding one end of a piece of pandanus, a ritual master *minguc* then cut the pandanus in two with a knife, signifying that "the argument was broken".

ACKNOWLEDGEMENTS

I would like to thank the people of Tabar for their work in documenting their traditions; and Nick Nani, Fr Bernie Miller, and Barry Craig for their help in securing the old malagan for the National Museum.

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APPENDIX 1

Although the mechanism for the establishment of the original ownership of the Obun *Curvunavunga* is not clear, the malagan is understood by the current owner to have been passed to the first-born daughter for four generations. However, the pattern of ownership gives more exceptions than the norm. Maso, the first owner in the second generation, had no children, so she passed it to her sister Melul. Melul had three children, two boys and a third

born girl, who unfortunately was born deaf mute and did not marry. So the *Curvunavunga* was passed out of the clan to Lagase, the first born son, to pass to his first daughter when she came of age. But Lagase fathered two sons and no daughters, so the pattern was again interrupted when he was forced to pass it out of the clan to his eldest son, Daniel Kariets. Kariets had intended to pass the ownership of this *Curvunavunga* to his eldest daughter, Matse in Katobi clan, but decided it would be better kept in the National Museum.

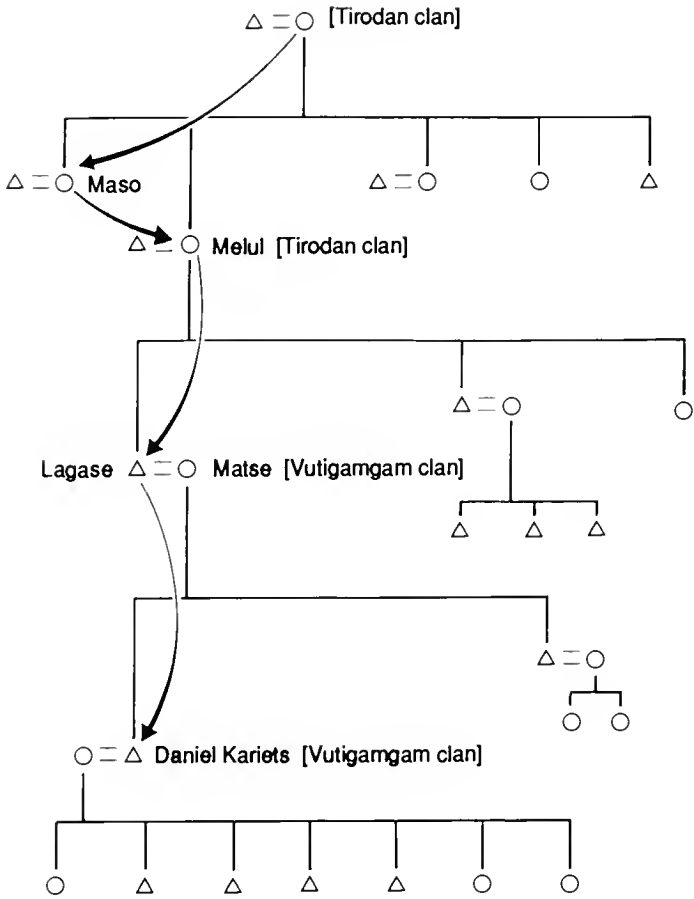


Fig. 2 Ownership history of the Obun Curvunavunga

WEHIRIYA - A MISSING GRAVE AND A LOST TOWN

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ABSTRACT

The discovery and identification of the grave of a Buginese princess near Dili, East Timor, indicates a closer nexus between South Sulawesi and Timor than previously thought, and a Bugis/Makassan settlement predating Portuguese occupation.

KEYWORDS: Bugis, Dili, graves, Hera, history, historic site, Islam, Makassans, Timor.

INTRODUCTION

This contribution is part of my ongoing research into the Makassan voyages to Australia since the 16th century, and the expansion of Islam to the Kingdoms of Gowa and Tallo in South Sulawesi and Waihalu in Timor.

Whilst working in Makassar, Zainuddin Daeng Pabetta, a descendant of the Kings of Tallo, recounted traditional legends relating to the expeditions to Timor by the Kings of Tallo in the 16th, 17th and 18th centuries at the behest of the Solorese in a bid to oust the Portuguese.

DISCUSSION

In April 1989, I took the opportunity to visit East Timor to carry out a survey of archival and library holdings in Dili as well as to conduct interviews with people who might have knowledge of Makassan contact with the area.

Following from a radio interview on the purpose of my visit to East Timor, I received a phone call from Ronny Sjamsuddin, a Makassan reporter with Antara Newsagency. He had something to show me. Would I go and talk with him? It turned out to be a small publication produced by the Department of Education & Culture which contained illustrations of historic buildings and objects in East Timor together with brief texts.

My attention was drawn to a dark photograph of a carved stone on which were some barely discernible characters. The caption suggested that from the shape of the stone, it

was possibly part of an Islamic grave but the decoration was more in keeping with classic Hindu, not East Timor culture. The inscription could not be identified.

We discussed the characters and came to the conclusion that there were two distinct scripts and two languages. The first were Arabic numerals which we deciphered as the year 1052 of the Hijrah. The other appeared to be either Lontara; Makassar or Lontara; Bugis. (Arabic is written from right to left, and Lontara is written from left to right). Apparently the stone had been found by a resident of Dili in the jungle.

I made a number of enquiries as to whom the finder of the 'Nisan' (Muslim gravestone) was, or where it was deposited, but without success.

On a later visit to Makassar I consulted with Drs Muttalib and Drs Bahru of the Department for the Protection and Conservation of Historical and Archaeological Remains and they confirmed the Arabic date as A.D. 1632. The Lontara' is Lontara' Bugis which reads - WEHIRIYA. "WE" is an honorific indicating a Buginese princess and "Hiriya" her personal name. The Christian year is based on the calculation for year 1052 Hijrah plus 580.

This was an exciting find. It was not what I was searching for but could be an indicator. I sent the news to Sjamsuddin in Dili and asked him to check further but unfortunately I had no further contact with him.

In September 1989, I returned to Dili and made further enquiries regarding the identity of the finder of the grave stone and its location.



Fig. 1. Headstone from the grave of Wehiriya.

tion. It was only when I contacted the Director of the East Timor Museum, Drs Paulus Susilo, that I at last had some results.

He told me that he now knew who the finder of the gravestone was and where it was located. When I told him of the translation of the inscription he immediately became interested in it and agreed to my request to interview the finder and to visit the site where it was found, since he had not previously visited the site.

It was important that we endeavoured to locate the grave site as this could be an indicator to a cemetery and possibly a village of considerable age. We met with the Camat and the Kepala Desa, Francisco Da Silva, the finder of the stone.

Da Silva explained that an area of land was being cleared to make way for development of a new Kampung, when the stone was knocked over. He had removed it to a safe place since he suspected that it was of some importance although he knew nothing about it.

We were driven to the place where the stone was kept and a quick inspection showed that the inscription shown in the photograph was identical (Fig. 1). This object was quite definitely an Islamic grave post made of locally quarried stone.

From the Camat's office we drove to the small town of Hera, some 20 km from Dili by road (but no more than 3 km by sea). From the road we walked inland a few hundred metres, passing by two very old Beringin trees which probably indicate the presence of a former Kampung. We came to a place in an overgrown area amidst scrub land and gathered at a small low mound covered with grass and stones, possibly indicators of other graves.

I questioned Da Silva as to the orientation of the head stone because being an Islamic burial, as I suspected, the grave would be oriented north-south with the head to the north, and with the body lying on its right side, facing towards Meeea (in this case to the west). He

could not remember clearly but indicated an east-west orientation. I explained that it is normal in Islamic burial for there to be one headstone for a male person and a headstone and a footstone, which is usually smaller, for a female person.

He could not remember ever seeing a footstone. It was rather disappointing and inconclusive.

We discussed the situation and searched the area around for signs of other graves, but apart from the slightly elevated ground and the small rocks which were spread around there was nothing else. I then decided to take some photographs of the site and the headstone. The grass was beaten flat and, so that I could get a better view, I asked the men to pull aside a small thick bush atop the mound.

Everyone was astounded to find, *in situ*, below the bush, a small carved stone (Fig. 2). The footstone was small, made of the same material as the headstone, but with no inscription or decoration. But what was most impor-

tant was that on matching the headstone with the foot-stone, the grave was found to have a north-south orientation, thus indicating it to be an Islamic burial.

As a result of these findings further research is now being conducted on the toponymy of the area and its local history, in an endeavour to determine the history of what may quite well be the earlier village of Hera.

The two Beringin trees are 'keramat', that is, sacred to the local people, and are situated on the eastern side of a small silted-up river about 100 m away and the grave of Wehiriya is approximately 200 m to the east. The name of the grave site is called Makirate, the place of the dead, and the name of the kampung nearest the site is Manuroni. The name of the suku or tribe of this area is Mantarlidu, a part of the Kingdom of Hera which also holds authority over the island of Atauro.

From an unidentified, mid-17th century Dutch map of Timor (Fig. 3), which shows a distorted geography of the eastern part, there



Fig. 2. Gravesite of Wehiriya, showing footstone.

is shown a river named "Macassars River", which is approximately where one would expect to find Hera.

CONCLUSION

Further research should reveal the history of the site; but what will it be? The town and kingdom of Hera appear to be older than the city of Cioli. Are we searching for the ancient town of Hera or Kampung Makassar where the King of Tallo died? What was a Buginese princess doing in East Timor before the advent of the Portuguese in Dili, being an Islamic

princess when Islam was only accepted by the Kingdom of Bone in 1611? Hera Hira Hiriya??

ACKNOWLEDGEMENTS

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BOOK REVIEW

Dragonflies (Naturalists' Handbooks; 7)

Peter L. Millar

Cambridge University Press 1987, ISBN 0521 317657
paperback, pp. 84; RRP. \$21.50

This volume is the seventh in a series designed to aid people without a university education in biology who may be interested in studying local natural history. The editors' preface states "The books in this series offer... the information and ideas needed to plan an investigation and the practical guidance needed to carry it out. They draw attention to regions on the frontiers of current knowledge where amateur studies have much to offer."

The book is divided into 6 chapters, each of which offers information under various sub-headings. While other dragonfly faunas are mentioned the emphasis is on the British fauna.

The Introduction contains four sections Evolution; The aesthetic appeal and economic importance of dragonflies; The British fauna; Dragonflies are very good animals for field work.

Chapter two is titled Eggs and Larvae and provides a good summary of the types of eggs and larvae produced by dragonflies. Other topics discussed in this chapter include habitat specificity, different modes of feeding, locomotion, territorial behaviour and respiration.

The third chapter entitled simply "The adult" is by far the largest in the book. There are 21 subheadings covering a wide range of topics which are logically arranged beginning with Emergence, then progressing through such topics as Flight, Thermoregulation, Vision, Feeding behaviour, to Reproduction, Courtship, and Oviposition.

This chapter is particularly well written. In concise, easy to understand text each of the topics is examined. The reader quickly becomes aware of the diversity of dragonfly biology and of the complexity of dragonfly

behaviour. It also becomes apparent that dragonflies are one of the better known groups of insects.

At every opportunity the author highlights where there are significant gaps in our knowledge of dragonflies and suggests research which could be undertaken by the reader.

The fourth chapter provides keys to larvae and adults of British species. The key to larvae was prepared by Graham Viek and the key to adults by David Chelmick.

Any key to species usually contains a lot of specialist terminology and a poor understanding of the terminology often leads to errors in identification. Both of the keys presented here are profusely illustrated. Definitions of many terms are provided and important structures are clearly labelled on the illustrations.

Chapter five is a brief examination of the status of the British dragonfly fauna which notes that 11 of 39 breeding species are currently under threat. Drainage of wetlands for land reclamation and pollution from agricultural, industrial or sewage disposal are responsible.

Attempts to preserve habitats or create new ones are documented, and descriptions of ideal dragonfly habitats are provided.

The dragonfly recording scheme, which seeks to update records of dragonfly species in Britain, is described at the end of the chapter.

Chapter six describes some techniques for studying dragonflies and includes some useful tips on experimental design and how to write up the findings of research so that it may be published. Several journals which publish short papers on insect biology are listed and there is also a list of useful addresses, including several dragonfly societies, entomological

suppliers and the headquarters of the dragonfly recording scheme.

An excellent bibliography of important works on dragonflies is provided under the heading Further Reading.

There are two appendices, the first is a checklist of the British species and the second documents the months of the year when adults of the British species appear.

The final part of the book is a small index.

The volume is well illustrated throughout with line drawings and there are four good colour plates in the centre of the book.

As the subject of this work is the dragonflies of Britain, it could be said that it is of limited use outside the British isles or western Europe. While it is certainly true that most of the species mentioned are more or less endemic to that region, the general description of dragonfly biology provided would be useful anywhere.

The volume is a very handy size for field studies and is printed on good quality paper. One minor fault with the paperback version is the use of two staples to bind the pages together; one of the staples fell out not long after I began reading.

In conclusion, I enjoyed reading this book which I found informative and stimulating. It is well written and illustrated. Perhaps the most endearing quality of the book is the obvious fascination of the author for all things dragonfly. I have no hesitation in recommending this volume to anyone who is interested in dragonflies or general natural history.

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GUIDE TO AUTHORS

Authors are advised to follow the layout and style in the most recent issue of *The Beagle*.

Three copies of typewritten manuscripts should be submitted. Manuscripts should be in English, double-spaced throughout and have a margin of at least 4cm on the left-hand side. Text should be on one side of good quality A4 bond paper. If available, a computer file of the manuscript (on 5" or 3" MS/IBM DOS floppy disk) should be submitted together with the printed version. Where appropriate, articles should conform to the sequence: Title, Abstract, Keywords, Introduction, Materials and Methods, Text, Discussion, Acknowledgements, References.

The Title should be concise and informative. An abridged title (not exceeding 50 letter spaces) should be included for use as a running head.

The Abstract should not exceed 150 words, and should state concisely the scope of the work and give the principal findings.

Keywords, to facilitate information retrieval, of up to 15 in number should be chosen to outline the main subjects covered.

The Introduction, including a review of literature, should not exceed what is necessary to indicate the reason for the work and the essential background. Abbreviations used throughout the text may be explained at the end of the introductory material, or placed separately in the Materials and Methods section.

Footnotes are to be avoided, wherever possible, except in papers dealing with historical subjects.

The International System of units should be used.

In the descriptive text numbers from one to nine should be spelt out and figures used for numbers over nine. For associated groups, figures should be used consistently, e.g. 5 to 10, not five to 10.

Systematic papers must conform with the International Code of Zoological Nomenclature and, wherever possible, with their recommendations.

Synonymies should be given in the short form (*taxon* author, date:page) and the full reference cited at the end of the paper. Full citations of taxa used in the text (i.e. *taxon* author, date) must also be included in the references, whereas the short citation (i.e. *taxon* author) need not be included. Subsequent citations of taxa given in synonymies should be separated from bibliographical details by a dash (-).

TABLES

Tables should be numbered with arabic numerals and accompanied by a title. Horizontal rules are inserted only above and below column headings and at the foot of the table. Footnotes on tables should be kept to a minimum and be reserved for specific items in columns. All other explanatory material should be incorporated with the title.

ILLUSTRATIONS

Line drawings, maps, graphs and photographs are generally regarded as "figures" and are to be numbered consecutively for interspersing through the text. Drawings must be on drafting film or good quality board with appropriate lettering inserted. Black and white photographs must be sharp, of high contrast on glossy paper, and mounted on board. The author's name, title of paper and figure number must be indicated on the reverse side of all illustrations. Captions or legends should be typed together on pages at the end of the text.

Colour illustrations may be accepted for larger papers, such as substantial revisions, and only where colour contributes significantly to the descriptive or scientific merit of the paper.

CITATIONS AND REFERENCES

Citations of sources within the body of the text should include the author, year of publication and page reference (where appropriate), e.g. Roth (1896); (Roth 1896); (Roth 1896, 1898); (Roth 1896; Smith 1915). Note that commas are not used to separate bibliographical citations (e.g. Roth 1896), whereas they should be included for taxonomic citations; for the original citation (e.g. *Dasyurus* Geoffroy, 1796), but not for subsequent citations (e.g. *Dasyurus* - Gould 1842).

References should be arranged alphabetically and chronologically at the end of the paper. Titles of all references must be given in full and wherever possible citations given in BIOSIS format. Where an author has published more than one work referred to in the same year, the references should be appended with the letter (a), (b), etc. The following examples show the style to be followed:

- Brake, B., McNeish, J. and Simmons, D. 1979. *Art of the Pacific*. Oxford University Press: Wellington.
- Cogger, H.G. 1981. A Biogeographic Study of the Arnhem Land Herpetofauna. In: *Proceedings of the Melbourne Herpetological Symposium*: 148-155. Zoological Board of Victoria: Melbourne.
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