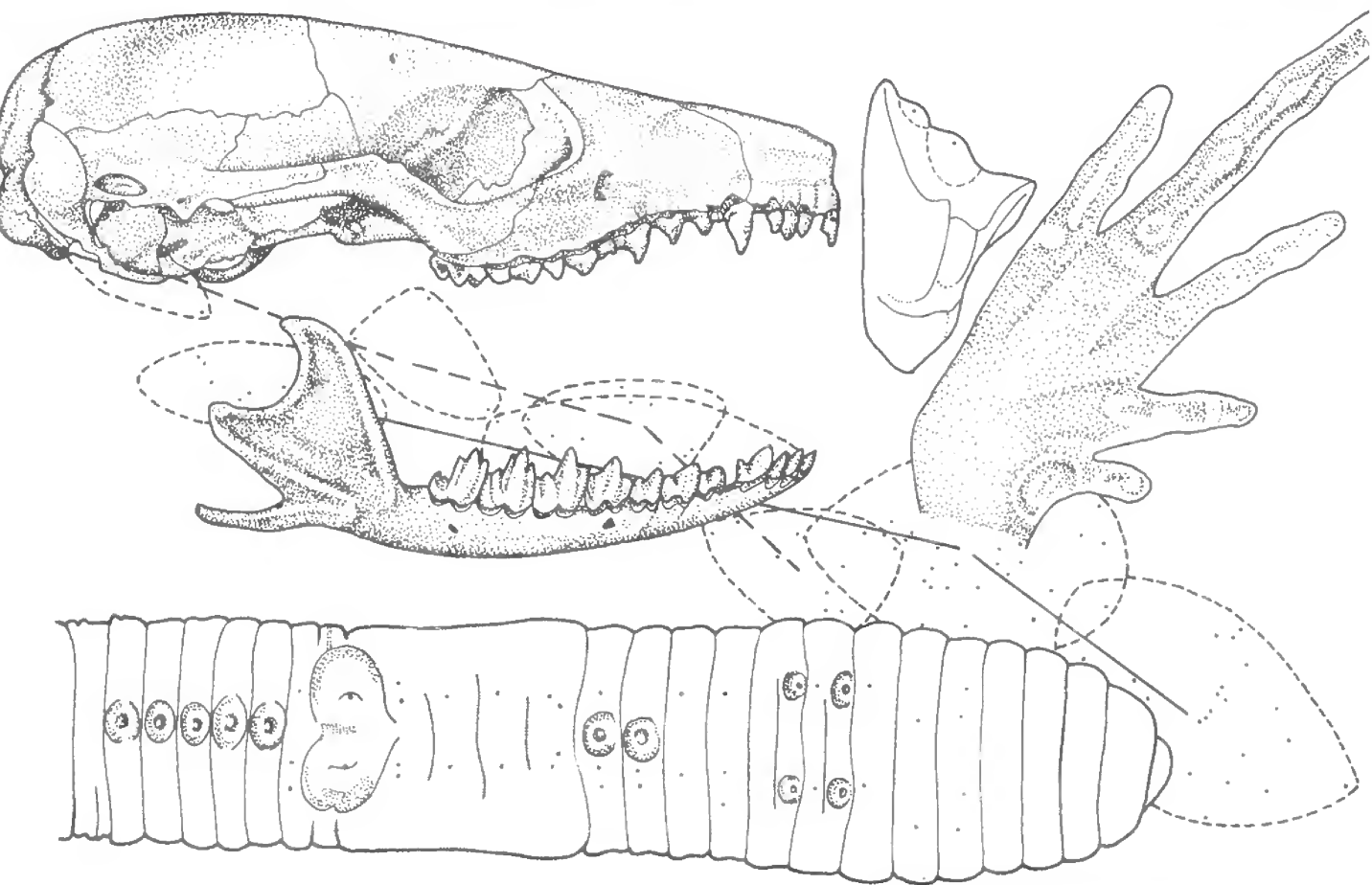


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THE GENUS *MACROPUS* SHAW (MARSUPIALIA: MACROPODIDAE) IN THE UPPER CAINOZOIC DEPOSITS OF QUEENSLAND

ALAN BARTHOLOMAI
Queensland Museum

ABSTRACT

The genus *Macropus* Shaw, 1790, is shown to comprise three subgenera, *M. (Macropus)* Shaw, *M. (Osphranter)* Gould, 1842, and *M. (Prionotemnus)* Stirton, 1955, on the basis of morphological and palaeontological evidence. *M. (Macropus)* is known only from Pleistocene sediments, whereas the other subgenera are also well represented in the late Pliocene Chinchilla Sand. Only two species of *M. (Macropus)* are recorded, the most commonly encountered being *M. titan*, while *M. rama* is described as a new species. Within *M. (Osphranter)*, four species are recognized, *M. altus* and *M. ferragus* from the Pleistocene deposits and *M. pan* and *M. woodsi* sp. nov. from the Chinchilla Sand. *M. (Prionotemnus)* possibly comprises six species, four of which, *M. agilis siva*, *M. gouldi*, *M. piltonensis* sp. nov., and *M. thor*, are restricted to Pleistocene sediments. *M. dryas* and *M. palankarinnicus* are present in the Chinchilla Sand. Palaeontological evidence suggests that *M. (Macropus)* was derived late in the geological history of the group and that within the other subgenera, general and occasionally particular relationships can be suggested for derivation of the recent fauna. Possible phylogenetic relationships within the *M. (Osphranter)* group are suggested back to the late Pliocene. In many species, statistical evaluation of most of the cheek teeth was possible, and comparisons with data from recent macropodids have been made.

Representatives of the genus *Macropus* Shaw are very abundant in the Upper Cainozoic sediments of Queensland. Although some specimens referable to the genus came from widespread localities in Queensland, most have been derived from the Pleistocene fluviatile deposits and the Chinchilla Sand of late Pliocene age, both in the Darling Downs area, southeastern Queensland.

Considerable diversity of opinion has existed regarding the generic limits of the genus *Macropus* and the taxonomy and temporal relationships of referred species. Bartholomai (1967, 1973a*, 1973b) has examined progressively aspects of the overall problem, and the present study clarifies the bulk of the remaining problems. Some of the results of the present study were foreshadowed in Bartholomai, 1972, while preliminary work on part of the older type material was included in a study by Bartholomai (1966). The availability of large samples now enables reassessment of the species to be made, especially aspects of intraspecific vari-

ation, utilizing evaluation of the populations by statistical and comparative morphological means. Results contribute to a better overall understanding of the taxonomy of the genus *Macropus*, and suggest that species are of potential value in correlation of Upper Cainozoic continental deposits.

Less detailed investigation has been made of the continental distribution of fossil species of *Macropus*, and until revisionary work has been completed on collections in other Australian museums, conclusions in this area are largely tentative. Exact temporal relationships are frequently difficult to establish away from the type areas.

All measurements are in millimetres.

Genus *Macropus* Shaw, 1790

TYPE SPECIES: *Macropus giganteus* Shaw, 1790 (validated under the plenary powers of the International Commission on Zoological Nomencla-

* Erratum: In Bartholomai (1973a) the illustrations of fossils comprising Plates 21 and 23, but not the captions to these plates, were inadvertently transposed during printing. Thus the caption to Plate 21 refers to the illustrations in Plate 23 and vice versa.

ture, Opinion 760, 1966, by monotypy, as interpreted by the neotype, Queensland Museum specimen, J10749, designated by Calaby *et al.*, 1962, and restated by Calaby and Ride, 1964).

The first large, modern macropodids were collected in 1770, some sixty years before the first fossil representatives of the family were discovered. A party from Captain James Cook's ship, the 'Endeavour' secured three specimens from the vicinity of the Endeavour River, near the present position of Cooktown, and from these Muller (1776) described *Macropus canguru*. The apparent holotype was destroyed during the Second World War through bombing of the Royal College of Surgeons. The identity of the species, however, was in doubt, and Iredale and Troughton (1925) had previously suggested that the specimen described may have been a wallaroo rather than a kangaroo. Further complication was added when these authors (Iredale and Troughton, 1937) suggested that the specimen may have been a Whiptail Wallaby (*Macropus parryi*). Both suggestions were based on unpublished work of Solander (1768-71). Raven (1939) contended that the first description was of a Grey Kangaroo, and this was strongly supported by Morrison-Scott and Sawyer (1950). In an attempt to stabilize the nomenclature, Calaby *et al.* (1962) also reaffirmed this position and selected a neotype, Queensland Museum specimen J10749. This specimen is a juvenile Grey Kangaroo collected from the Cooktown area. Ride (1963) commented further on the nomenclatural problem, and this was followed by a revised application by Calaby *et al.* (1963) which resulted in considerable comment. Kirkpatrick (1963) and Woods and Kirkpatrick (1964) indicated that the original specimen was a Wallaroo. Mayr (1964) and Lemche (1964) also commented on details of the case, numbered Z.N.(S.) 1584. New proposals were then outlined by Calaby and Ride (1964), and these were supported by Morrison-Scott (1964) and Finlayson (1964). Another complication was the designation by Troughton and McMichael (1964a, b) of an additional neotype, this being a Whiptail Wallaby. Voting on the case favoured the proposition by Calaby and Ride (1964) and involved the use of the plenary powers, stabilizing the nomenclature under Opinion 760, as indicated above.

Considerable diversity of opinion still remains regarding the generic limits to be applied to the genus *Macropus*, both in terms of its neontological and palaeontological usage. Ride (1962) concluded that 'no confusion would result from the perfectly valid action of any author who writes about a species of wallaby or kangaroo (living or extinct)

and prefers to remain non-committal about his generic concepts. Such an author may simply employ *Macropus* . . . or he may follow a stated taxonomic list'.

The problem is not a simple one and the species which may be referred to *Macropus* have been relegated to the following genera (or subgenera) depending on the limits placed by individual taxonomists—*Macropus*, *Halmaturus* (a junior secondary homonym of *Macropus* but used for the purpose of separation), *Osphranter*, *Fissuridon*, *Megaleia*, *Wallabia*, *Thylogale*, *Petrogale*, *Peradorcas*, *Lagorchestes*, *Onychogalea*, *Lagostrophus*, *Dorcopsis*, *Dorcopsulus*, *Dorcopsoides*, *Dendrolagus*, *Setonix*, *Synaptodon*, *Prionotemmus*, *Protemnodon* and *Troposodon*.

Ride (1962) has presented an historical summary of various usages suggested by major contributors to taxonomic interpretation of the group. Genera from the above list which are apparently nomenclaturally stable in recent literature include *Fissuridon*, *Thylogale*, *Petrogale*, *Peradorcas*, *Lagorchestes*, *Onychogalea*, *Lagostrophus*, *Dorcopsis*, *Dorcopsulus*, *Dorcopsoides*, *Dendrolagus*, *Setonix* and *Troposodon*.

Bartholomai (1973a) defined the generic limits of *Protemnodon*, indicating its distinction from other macropodids. Earlier work by Stirton (1963) was supported in the contention that *Protemnodon* is distinct from living kangaroos and wallabies, including the Swamp Wallaby, making available the generic name, *Wallabia*, for at least part of this group.

Progression of the cheek tooth row was considered by De Vis (1895) to be of extreme importance in separation of the Queensland fossil sample into the genera *Halmaturus* and *Macropus*. The process of progression is particularly evident in kangaroos, as shown by Kirkpatrick (1963, 1964) for *M. giganteus*, and later (Kirkpatrick, 1965) restated for this species, and shown for *Megaleia rufa* and *Macropus robustus*, where the extent of the progression has been employed in ageing of specimens. Information on molar progression in *M. rufa* has also been presented in Calaby (1968). Although rate of progression is less pronounced in brush wallabies it is nevertheless significant, as indicated for *M. rufogrisea* by Kirkpatrick (1965), and would appear to represent differences in function in the two groups rather than generic distinction. The degree of movement in *Wallabia bicolor* has not been investigated to the same extent but appears to be generally comparable with that in the brush wallabies.

Cytological investigation of recent macropodines by Sharman (1961) has shown the availab-

ility of characters previously disregarded and this has been followed by Kirsch (1968), who has examined marsupial haemoglobin and has presented preliminary information for many living macropodines. According to details provided by Sharman (1961), chromosome number and sex chromosome morphology indicate the generic distinctness of *Megaleia*, *Setonix* and *Lagostrophus*. In addition, middle-sized wallabies, kangaroos and wallaroos are diphyletic with the type species of *Wallabia*, *W. bicolor*, differing markedly from the rest of this group. Serological studies by Kirsch (1968) suggest that species of wallabies and kangaroos, including *W. bicolor*, *Megaleia* and *Lagorchestes* are closely associated, a conclusion which cannot be verified by the fossil record because of general deficiencies in fossil samples yet available. Sharman *et al.* (1966) have recently investigated reproductive physiology of *W. bicolor*, showing it to be unique among the Macropodidae. Further, Calaby (1966) states that this species differs in behaviour and has distinctive dental characters from the rest of the group. Calaby considers that *Wallabia* should be recognized as a monotypic genus, while the remainder of the wallabies, the Grey Kangaroo and the wallaroos should remain within *Macropus*. This action is supported by the present study.

All members of *Macropus* are characterized by 16 (2N) chromosomes. While differences are evident between species in this grouping, they are nowhere as marked as those enabling separation of *Wallabia*, which has a diploid complement of 10 in the female and 11 in the male. Ride (1970) applies this terminology, but Frith and Calaby (1969) again revert to use of *Macropus* for the Grey Kangaroo and wallaroos and *Wallabia* for all the brush wallabies.

Equal area grid diagrams, as proposed by Thompson (1959), have been shown by Bartholomai (1973a) to be of value in illustrating gross relative size and displacement differences present between skulls of species of *Macropus*, *Wallabia* and *Protemnodon*, based on a skull of *W. bicolor* as a standard. Apart from differences between the genera noted in Bartholomai (1973a), the figures indicate a remarkable uniformity in modification of the grid to *M. giganteus* and the brush wallabies which possess the diploid chromosome number of 16.

Separation of *Macropus* is further supported by the anatomy of the cheek teeth, particularly lower molars. All species referred to *Macropus* have high-crowned lower molars with strong links and with near vertical, lingual lophid margins and non-vertical labial margins. If ornamented, the strongly

curved, posterior hypolophid surface is, with rare exception, grooved or pocketed. *Protemnodon* has more rectilinear and generally relatively lower lophids, and has the posterior surface of the hypolophid considerably less curved. Ornamentation of this surface is restricted to development of a posterior cingulum. The permanent premolar is not lost through progression. *Wallabia* has low crowned molars with rectilinear lophids and low links. Lateral margins of the lophids are bulbous, while the posterior hypolophid surface is not ornamented. These characters are of paramount importance in consideration of the fossil material and support the generic distinction of these forms at least. The position of *Synaptodon*, described by De Vis (1889), cannot be resolved at this time, because it is based on inadequate and completely undiagnostic material. The holotype of its type species, *S. aevorum* De Vis, F811, from the late Pliocene Chinchilla Sand at Chinchilla, was stated by De Vis (1895) to be distinguished by peculiar anterior and posterior abutting processes of the molars. Examination has shown that crowns of the molars are almost totally devoid of enamel except for the 'processes' and a small patch on the trigonid basin of the posterior molar. This suggests that the 'processes' may have resulted from weathering, particularly as remaining enamel is soft and chalky, whereas the dentine is hard and mineralized. Certainly no other specimen in the Queensland Museum collections duplicates this condition and no adequate reason apart from abnormal weathering can be suggested for the state of preservation of the holotype.

Megaleia is not represented by fossil material in Queensland. Tedford (1967) records *Megaleia* in the Lake Menindee deposits in western New South Wales but applies the name in the subgeneric sense within *Macropus*. *Megaleia* is distinct from *Macropus* on the basis of modern species but this distinctness becomes difficult to apply to fossils because of general similarity in cranial morphology between species of both genera. The last molar in the cheek teeth series in *Megaleia* tends to be much larger than that preceding it, a feature not common in species of *Macropus*.

Although the description of the fossil genus *Prionotemnus* Stirton, 1955, is largely inadequate, an investigation of the referred sample in the University of California, Berkeley, indicates that the species is valid and that the name is available for use within the *Macropus* complex.

For the purpose of this study, the genera *Macropus*, *Megaleia*, *Wallabia* and *Protemnodon* are recognized. Within the *Macropus* group, several distinct species groups are apparent and these

are recognizable as far back as the late Pliocene. Broadly speaking, these correspond to the kangaroos (excluding *Megaleia*), the wallaroos and the brush wallabies (excluding *Wallabia*). These groups are regarded as subgenera.

GENERIC DIAGNOSIS: Medium to large macropodines; cranium with rostrum markedly deflected downwards; diastema relatively elongate; lower molars with high lophids, strong links and with lingual margin of lophids near vertical and labial margins markedly divergent; posterior hypolophid surface strongly curved, and where ornamented this comprises a groove, fossette, or very rarely a posterior cingulum.

Subgenus *Macropus* Shaw, 1790

TYPE SPECIES: *Macropus (Macropus) giganteus* Shaw, 1790 (validated under the plenary powers of the International Commission on Zoological Nomenclature, Opinion 760, 1966 by monotypy).

DIAGNOSIS: Medium to large macropodines with palate entire; foramen ovale unhooded and with alisphenoid only slightly grooved at margin of foramen; upper incisors form V-shaped series in occlusal view; I³ long with labial surface marked by two deep, vertical grooves; basioccipital slightly keeled; postglenoid foramen well-developed; diastema elongate; palate narrow anteriorly; permanent premolars reduced, rapidly lost during progression; upper molars with strong forelink; anterior ridge from paracone usually reduced or absent; infraorbital distance between foramen and anterior rim of orbit short; rostrum not greatly inflated; lower molars with strong posterior groove; mandible broad below anterior cheek teeth.

Subgenus *Osphranter* Gould, 1842

TYPE SPECIES: *Macropus (Osphranter) antilopinus* Gould, 1842 by monotypy.

DIAGNOSIS: Palate entire; foramen ovale hooded, with alisphenoid deeply grooved at margin of foramen; upper incisors form U-shaped series in occlusal view; I³ quadrangular with labial surface marked by one vertical groove at anterior one-third; basioccipital moderately keeled; postglenoid foramen very reduced; diastema variable but frequently short; palate broad anteriorly; permanent premolars relatively robust, but rapidly lost during progression; upper molars with negligible to weak forelink; anterior ridge from paracone usually reduced but occasionally stronger; infraorbital distance between foramen and anterior

rim of orbit long; rostrum moderately to greatly inflated; lower molars with strong posterior groove; mandible excavated and narrow below anterior cheek teeth.

Subgenus *Prionotemnus* Stirton, 1955

TYPE SPECIES: *Macropus (Prionotemnus) palankarinnicus* Stirton, 1955.

DIAGNOSIS: Palate with extensive post-palatine vacuities; foramen ovale hooded, with alisphenoid deeply grooved at margin of foramen; upper incisors form V-shaped series in occlusal view; I³ triangular with vertical lateral groove in median position or even in posterior moiety; basioccipital markedly keeled; postglenoid foramen well-developed; diastema moderately elongate; palate anteriorly narrow; permanent premolars robust, retained until very old age but occasionally lost through progression; upper molars with minimal forelink; anterior ridge from paracone strong; infraorbital distance between foramen and anterior rim of orbit long; rostrum not greatly inflated; lower molars lacking posterior groove but sometimes with reduced posterior cingulum; mandible broad below anterior cheek teeth.

Macropus (Macropus) titan Owen, 1838

(Plate 7, Figs. 1-2; Plate 8, figs. 1-4; Plate 9, figs. 1-4; Plate 10, figs. 1-3)

Macropus titan Owen, 1838, pp. 359-60, pl. 29, figs. 3-5; 1840-1845, I, p. 392, pl. 101, figs. 1-2; 1845a, p. 236; 1845b, pp. 324-5; 1873, p. 128; 1874a, pp. 248-60, pl. 21, figs. 6-17, pl. 22, figs. 10-8, pl. 23, figs. 2-3, 12-4, pl. 26, figs. 9-15; 1874b, pp. 783-4, pl. 76, figs. 1-6; 1876, pp. 204-9, pl. 25, figs. 1, 4, pl. 26, figs. 1-2; 1877, pp. 400-11, 435-9, pl. 76, figs. 1, 4, pl. 77, figs. 1-2, pl. 78, figs. 1-2, pl. 79, figs. 1-2, pl. 81, figs. 6-17, pl. 82, figs. 10-8, pl. 83, figs. 2-3, 12-14, pl. 86, figs. 9-15; Waterhouse, 1846, pp. 58-9; McCoy, 1862, p. 145; 1867, p. 191; Daintree, 1872, p. 274; Etheridge Jun., 1878, pp. 183-4; 1892, p. 673; Lydekker, 1887, pp. 225-30; Anderson, 1929, pp. 35-9, pl. 17, figs. 1-3, pl. 18, figs. 1-7; Simpson, 1930, p. 73.

Macropus magister De Vis, 1895, pp. 120-4, pl. 18, figs. 11-16; Bartholomai, 1966, pp. 123-4, pl. 19, figs. 1-3.

Macropus faunus De Vis, 1895, pp. 127-9, pl. 18, figs. 3-6; Simpson, 1930, p. 72; Bartholomai, 1966, pp. 122-3, pl. 18, figs. 1-3.

MATERIAL: F3738, cast of holotype, partial right mandibular ramus with M₁ broken, M₂, P₃ removed by fenestration, juvenile, original in British Museum (Natural History), No. 10777, Wellington Caves, N.S.W., from Pleistocene cave deposits (figd Owen, 1838, pl. 29, figs. 3-5; 1874a, pl. 22, figs. 17-8; 1877, pl. 82, figs. 17-18).

F2924, holotype *Macropus faunus* De Vis, partial right maxilla with P³-M³, juvenile, Darling Downs (figd in

part, De Vis, 1895, pl. 18, figs. 4-5; figd Bartholomai, 1966, pl. 18, figs. 1-3).

F645, lectotype *Macropus magister* De Vis, partial cranium containing P²-M², P³ removed by fenestration, juvenile, Ravensthorpe, Pilton, SE.Q., (figd in part, De Vis, 1895, pl. 18, figs. 13-14; figd Bartholomai, 1966, pl. 19, figs. 1-3).

Additional material referred to *Macropus titan* Owen comprises 74 juvenile mandibular rami, 126 adult mandibular rami, 4 isolated lower teeth, 11 cranial fragments, 25 juvenile maxillae and 84 adult maxillae from the following localities in the eastern Darling Downs: King Creek; King Creek, at M.R.045455 Clifton 1-mile map; King Creek, at M.R.037455 Clifton 1-mile map; King Creek, near M.R.039454 Clifton 1-mile map; King Creek, near M.R.047452 Clifton 1-mile map; King Creek, Manapouri, at M.R.099465 Liverpool Range 1-mile map; King Creek, at M.R.098465 Liverpool Range 1-mile map; King Creek, at M.R.048457 Clifton 1-mile map; King Creek, between Pilton and Nobby; Ravensthorpe, Pilton; Clifton; ?Pilton; Pilton; Spring Creek; Freestone Creek; Westbrook Creek, near Kingsthorpe; Hirstglen; Gowrie; Gowrie Creek; well at depth of c. 2 m, between Gowrie Creek and radio station 4AK, Oakey; in sewerage drain at c. 10 m, Dalby; near Dalby, Condamine River at Springvale; Jimbour Creek near Dalby; Jimbour Creek, about 3 km south of Jimbour; bank of Condamine River, at M.R.043426 Dalby 1-mile map; Jimbour District; Cambooya, and from the eastern Darling Downs (particular localities unspecified).

A juvenile mandibular ramus from Chinchilla is referred to *M. titan*, as is a juvenile mandible from the Nogoa River, near Rawbelle, mid E.Q., a mandible from Jimboomba, SE.Q., and an adult maxillary fragment from Rubyvale, near Anakie, C.Q.

SPECIFIC DIAGNOSIS: A large species. Diastema elongate. P² relatively small with longitudinal crest normally bifid and with strong, well-defined posterolingual cuspid, DP₃ and lower molars with high, slightly curved lophids and strong, high links and high anterior cingulum. Posterior surface of hypolophid with near vertical groove and well-defined posterior fossette. P₃ small, usually with bifid longitudinal crest, but occasionally trifid; posterolingual cuspid present, close to posterior cuspid of crest and united to this by high ridge. P² with well-defined cusps and high bifid longitudinal crest; protocone least well developed; cuspule present labiad to metacone. DP₃ and upper molars with high lophs and mid-links; forelink present, relatively well-defined. P³ small, with longitudinal crest normally bifid but occasionally trifid; hypocone well-defined but low; protocone absent.

DESCRIPTION: Mandible moderately deep, relatively thick; base of symphysis deflected at lower level than general base of ramus, near planar; symphysis very elongate, shallow, not ankylosed, rugose; geniohyal pit moderately deep, above

posterior symphyseal limit; diastema very elongate, with diastemal crest posteriorly acute, less acute anteriorly; ventral margin of ramus rounded between symphysis and extremely weak digastric ridge and process. Mental foramen moderately large, oval, usually set well below diastemal crest, well anterior to anterior root of P₃. Ramus with relatively shallow lateral groove extending posteriorly from just below posterior diastemal crest to below anterior root M₂, close to alveolar margin. Digastric process separated from base of angle by very shallow post-digastric sulcus, bounded above by shallow digastric fossa; this fossa separated above from broad depression opening posteriorly into pterygoid fossa. Post-alveolar shelf short, with angle not well-developed, leading to post-alveolar ridge, ascending posteriorly to disappear on mesial wall of coronoid process, above large mandibular foramen. Masseteric crest raised to about level of occlusion of cheek teeth; masseteric foramen moderately large, with masseteric fossa relatively deep. Angle of mandible markedly inflected. Anterior margin of coronoid process near vertical. Bulk of angle of mandible, coronoid process and condyle not preserved in any specimen.

I₁ elongate, lanceolate, deeply rooted; slightly curved in lateral view, markedly curved in occlusal view, developing subhorizontal facet of wear with upper incisors and mesial wear facet at tip by approximation with other lower incisor; root compressed, oval in section; crown subquadrantal in section, tapering and blade-like anteriorly, enamelled laterally, this produced dorsolabially and ventrolingually into flanges; crown also enamelled ventromesially; distally, subhorizontal dorsal wear facet develops rapidly, but tip is not rounded.

P₂ relatively small, short, approximately suboval in occlusal view, with lingual surface slightly convex and labial surface markedly convex. Anterior cuspid with well defined anterolingual and posterolabial ridges, the latter contributing to a poorly defined longitudinal crest; poorly developed cuspule present along anterolingual ridge; posterolabial cuspid with well-defined anterolingual ridge curving and descending to unite with ridge from anterior cuspid, as continuation of longitudinal crest; crest usually markedly bifid with well defined labial and lingual grooves present near mid-point; occasionally two, well-defined labial grooves are present, in close juxtaposition, corresponding with two lingual grooves, producing a trifid longitudinal crest; grooves sometimes reduced; strong, ornamented lingual ridge occasionally descends from posterior moiety of crest towards posterolingual cuspule; posterior ridge

from posterolabial cuspule curves into mesial posterior groove, sometimes uniting with labial ridge descending from posterolingual cuspule. Major posterior ridge from that cuspule curves anterolingually to terminate in slight basin formed between posterior cusps; anterior ridge from posterolingual cuspule descends slightly lingually to base of crown towards lingual groove from longitudinal crest. Lingual base of crown sometimes tumescent. Posterior of crown occasionally with angular ridge present at lingual margin.

DP₃ molariform, subrectangular in basal outline, slightly constricted across talonid basin, with lophids moderately high, convex posteriorly. Hypolophid much broader than protolophid. Trigonid basin relatively broad, its length being less than distance between lophids. Forelink high, strong, abruptly curving anterolingually from protoconid to point well labiad to mid-point of high anterior cingulum; cingulum more anteriorly extended at anterolingual margin than elsewhere. Trigonid slopes lingually, and more strongly labially and posteriorly from forelink and cingular margin; well-defined anterolabial fossette present while lingual moiety of trigonid somewhat broadly V-shaped. Slight ridges descend anteriorly and posteriorly from metaconid. Hypoconid with strong, high ridge curving anterolingually across talonid basin as midlink, uniting with strong posterior ridge from protoconid, close to protolophid, labiad to mid-line; weak anterior ridge from entoconid descends into talonid. Talonid slopes labially and lingually from midlink; basin broadly U-shaped in lingual moiety, sharply V-shaped labially; slight accessory ridges occasionally present near anterior of crest of hypolophid. Slight ridge descends posteriorly from entoconid, while stronger ridge descends from near mid-point of posterior surface of hypolophid, curving to posterolingual margin well above crown base, uniting with entoconid ridge to delimit well-defined posterior fossette; fossette emphasised by near vertical, broad groove in posterior surface of hypolophid. Labial bases of lophids much more expansive than lingual, giving crown appearance of flexure about labial limit of talonid; base of crown occasionally slightly tumescent at labial limit of talonid.

P₃ small, short, subtriangular in occlusal view, with crown somewhat constricted at anterior one-third; labial margin slightly convex, while lingual margin markedly concave; anterior cuspid well-defined, usually with moderately weak posterolabial ridge descending as longitudinal crest; anterior ridge poorly defined; posterolabial cuspid also well-defined with anterolingual ridge normally descending to unite with other portion of crest

above crown constriction; strong vertical labial and lingual grooves usually present at anterior one-third, giving crest a marked bifid appearance in labial view; grooves sometimes poorly developed with reduction in V-shaped appearance of crest; occasionally second set of vertical labial and lingual grooves present resulting in trifid appearance of crest; normally central area of crest depressed, but occasionally near planar where trifid condition prevails; broad, posterior ridge descends from posterolabial cuspid towards crown base, while high, well-defined lingual ridge unites cuspid with well-defined, but lower posterolingual cuspid; this posterior crest usually concave posteriorly, with broad, vertical, posterior groove present; slight anterior and posterior ridges descend from posterolingual cuspid. Base of crown normally unornamented.

M₁ < M₂ < M₃ < M₄; molars subrectangular in basal outline, slightly constricted across talonid basin; lophids high, with hypolophid crest more convex posteriorly than protolophid crest in unworn teeth, similar in worn examples; hypolophid broader than protolophid in M₁, approximately equal in M₂ and M₃, and narrower in M₄. Trigonid basin usually broad; length about equal to distance between lophids. Forelink high, curving anterolingually from protoconid to near mid-point of high anterior cingulum. Cingulum with central portion usually indented and squared in appearance at anterolingual and anterolabial margins; trigonid markedly sloped posteriorly from cingulum, and laterally from forelink; well-defined anterolabial fossette present; labial moiety of trigonid V-shaped, lingual portion sharply U-shaped. Strong, high ridge curves anterolingually from hypoconid across talonid as midlink, uniting with short ridge from labiad to mid-point of protolophid; junction frequently flexed in unworn teeth. Talonid basin descends labially and lingually from midlink; basin V-shaped labially; broadly U-shaped lingually; slight groove occasionally rises from near crown base, near posterolabial margin of base of protolophid; slight ridges usually descend anteriorly and posteriorly from metaconid. Posterior of hypolophid with broad, near vertical groove slightly lingual to mid-line, normally terminating basally in well-defined posterior fossette. Base of crown broadly extended posteriorly, occasionally tumescent at margins of talonid basin. Labial bases of lophids more expansive than lingual, giving crown appearance of flexure about labial margin of talonid.

Cranium known only from partial juvenile specimen and fragmentary supplementary material.

Maxilla laterally with infraorbital foramen opening above anterior margin of P² in juvenile cranium, with infra-orbital canal 29.0–40.5 (\bar{X} = 36.1; n = 7) in adult specimens; inferior process of anterior zygoma root moderately strong; palate entire, with palatine well-developed, fenestrated by anterior palatine foramen and posterior lateral foramen; jugal laterally excavated; zygomatic arch markedly sinuous, converging anteriorly; squamosal in narrow anterior contact with frontal, subsquamosal foramen anterodorsal to external auditory meatus, with postzygomatic foramen within meatus opening anteriorly into sinus of root of zygoma; postglenoid process of squamosal moderately well-developed. Ectotympanic deep, complete dorsally, poorly united with squamosal in roof of meatus. Alisphenoid not inflated, in slight contact with basioccipital, with foramen ovale bounded anterolaterally by deep groove. Paraoccipital process elongate.

Upper incisors not known.

P² relatively small, subrectangular in basal outline, unknown in unworn condition; crown constricted mesially in occlusal view. Paracone well-defined with strong ridges ascending anteriorly and posteriorly; anterior ridge from metacone ascends to unite with posterior paracone ridge forming bifid longitudinal crest; well-defined, broad vertical labial ridge present below basal constriction. Well-defined posterolabial cuspule present; protocone small, often separated, with slight curving anterolabial ridge developed below crown base; hypocone worn in all examples.

DP³ molariform, subrectangular in basal outline, slightly constricted across median valley; lophs high, moderately bowed anteriorly; metaloph broader than protoloph. Anterior cingulum moderately high, broad, short, with well-defined forelink linguad to mid-line, from base of protoloph to cingulum; slight anterolingual fossette present; slight ridge ascends anteriorly from paracone often reaching anterolabial limit of cingulum; anterior cingular shelf slopes labially and lingually from forelink. Well-defined, strong, high ridge curves posterolabially from protocone as midlink, uniting with ridge from near mid-point of metaloph, below median valley; weak ridge curves posterolingually from paracone into valley; median valley V-shaped labially and lingually, near planar transversely; lingual moiety often with low fold paralleling floor of valley; broad ridge ascends lingually from hypocone curving anteriorly at crown base, merging with general lingual basal swelling towards margin of median valley. Strong ridge ascends posteriorly from hypocone, curving labially to near posterolabial margin of crown,

uniting with slight posterior ridge from metacone; near centre of posterior surface of metaloph, strong groove ascends labially into posterior fossette. Slight grooves present, ornamenting strong ridge from hypocone. Base of crown somewhat swollen.

P³ moderately small, short, subtriangular in occlusal view, slightly constricted at anterior one-third, usually with well-defined, vertical labial and lingual grooves below constriction, subdividing longitudinal crest. Paracone with well-developed anterior and posterior ridges ascending from cusp; metacone also with ascending, well-defined ridges; anterior ridge from metacone and posterior ridge from paracone comprise longitudinal crest; occasionally two sets of vertical labial and lingual grooves present, giving crest trifid appearance; rarely crest nearly undivided; well-defined ridge connects metacone with lower hypocone; ridges from hypocone curve posterolabially and anteriorly; slight fossette formed well below posterior crown base, behind ridge connecting posterior cusps. Slight indication of basal style occasionally present below metacone.

M¹ < M² < M³ < M⁴; molars subrectangular in basal outline, slightly constricted across median valley; lophs high, with metaloph crest more convex anteriorly than protoloph crest in unworn teeth, but similar in worn examples; metaloph broader than protoloph in M¹, approximately equal in M² and M³, and narrower in M⁴. Anterior cingulum relatively high and broad, moderately short; well-defined, strong forelink ascends from protoloph, well linguad to mid-line, uniting with anterior cingulum near centre of anterior tooth margin; occasionally weak accessory links present paralleling forelink, particularly in labial moiety of anterior cingular shelf; shelf sloped labially and lingually from forelink, and posteriorly from cingulum, sharply U-shaped labially and V-shaped lingually; slight anterior ridge from paracone occasionally unites with labial extremity of cingulum, sharply U-shaped labially and V-present; posterior paracone ridge reduced; base of protoloph often broadly swollen labially, close to midlink. Midlink strong, high, curving posterolabially from protocone to unite with short ridge usually from point on metaloph, linguad to midline; junction often flexed; median valley near planar transversely, only slightly sloping labially and lingually from midlink, V-shaped labially and lingually; Midlink sometimes ornamented labially with accessory ridge to protoloph; low transverse fold in lingual base of valley sometimes present; slight ridges ascend anteriorly and posteriorly from metacone; strong, slightly flared ridge ascends posterolabially from hypocone to posterolabial

TABLE 1: SUMMARY OF MEASUREMENTS FOR *Macropus (Macropus) titan* OWEN

Character	Maxillae					Mandibles				
	n	O.R.	\bar{X}	s	V	n	O.R.	\bar{X}	s	V
P ₂ length	6	9.2- 9.8	9.5	0.249	2.62	20	7.3- 9.0	8.3	0.467	5.62
max. width	5	6.6- 7.3	6.9	0.308	4.47	19	3.6- 4.9	4.5	0.283	6.29
DP ₃ length	12	10.1-11.8	10.9	0.508	4.66	39	10.3-11.8	11.0	0.426	3.88
prot. width	9	7.9- 9.3	8.4	0.534	6.36		5.5- 6.6	6.0	0.260	4.33
P ₃ length	20	8.5-11.6	9.9	0.741	7.48	30	6.3- 9.2	7.4	0.577	7.80
max. width	17	4.8- 6.3	5.4	0.417	7.72	25	3.5- 5.0	4.0	0.325	8.13
M ₁ length	46	10.6-14.7	12.3	0.936	7.61	56	11.6-14.1	13.0	0.604	4.65
prot. width	32	8.2-10.7	9.7	0.644	6.64	47	6.9- 8.7	7.6	0.342	4.50
M ₂ length	77	12.4-16.7	13.9	0.869	6.25	59	12.9-17.0	14.5	0.888	6.13
prot. width	54	9.4-12.8	11.1	0.730	6.58	49	8.1-10.1	9.0	0.421	4.68
M ₃ length	88	13.7-18.3	15.4	0.827	5.37	111	13.3-18.3	16.5	0.912	5.60
prot. width	70	10.3-14.8	12.4	0.780	6.29	102	8.3-11.0	9.7	0.550	5.67
M ₄ length	69	14.8-18.9	16.6	0.742	4.47	109	15.5-19.6	17.5	0.941	5.38
prot. width	69	11.4-14.6	12.9	0.724	5.61	103	8.3-11.5	10.3	0.614	5.96

prot. = protoloph or protolophid.

margin below crown base, with production of posterior fossette; broad, near vertical groove in surface of metaloph often contributes to define this; sharp vertical groove frequently ornaments strong hypocone ridge linguad to mid-line. Base of crown often swollen, particularly at lingual extremity of median valley.

DISCUSSION: The partial right mandibular ramus which constitutes the holotype of *Macropus titan* Owen, was among the first marsupial fossils described from Australia (Owen, 1838), having been discovered by Major Sir T. L. Mitchell in cave deposits in the Wellington Valley, New South Wales and forwarded to England for determination by Sir Richard Owen. Although presenting few morphological characters apart from the unworn permanent premolar, later removed by fenestration, this tooth is sufficiently diagnostic to allow reference of subsequently obtained material. Similarity of the specimen to the living kangaroo, *M. major* was noted by Owen (1838, p. 359), but comparison was restricted to size only.

In later publications, Owen (1845b, 1874a) referred mandibular specimens from the Darling Downs to *M. titan*, and correctly assigned and described the upper dentition. Later, Owen (1876) described and figured a well-preserved cranium from King Creek.

McCoy (1879) and Lydekker (1887) considered *M. titan* Owen to be closely allied to *M. giganteus*, being distinguished only by its superior size and the occurrence of a groove or grooves on the posterior surface of the hypolophid. Lydekker indicated the probability that the two forms may pass imperceptibly into one another. No distinction was drawn between the sample from the Darling Downs and that from the type locality.

On the other hand, De Vis (1895) separated the Queensland material, describing *M. magister* and *M. faunus*, from the Pleistocene fluviatile deposits. Justification for naming *M. magister* was expressed in terms of supposed differences in proportions of M₂ between Queensland specimens and the holotype, the supposed lack of a groove in the posterior hypolophid surface of M₂ in *M. titan*, and minor differences in the structure of the trigonid basin and anterior cingulum. De Vis (1895) completely neglected the permanent premolar in his comparison, and gave no indication of knowing of the presence of such a tooth in the holotype, considering the holotype to present only 'a single perfect tooth, M₂'. This tooth, in fact, is fractured posteriorly and lacks the posterior hypolophid surface. *M. faunus* was separated largely because of the tricuspid crest of the upper and lower premolars. This feature is clearly derived from the normal bifid crest in *M. titan*, being achieved through observed intermediate stages in the large sample currently available.

Anderson (1929) considered the separation of the Queensland sample of *M. magister* from *M. titan* and concluded that there were no valid grounds for De Vis' (1895) suggestion, and relegated *M. magister* to synonymy. Anderson proposed that it is unlikely that *M. titan* and *M. giganteus* grade into one another, or that *M. giganteus* is a direct descendant of *M. titan*, but presented only the evidence of slightly more complex molars in the fossil material to support this.

Tedford (1967), gives statistical data for *M. titan* from Wellington Caves in the collections of the Australian Museum, Sydney, and presents population parameters for some tooth dimensions of fossil and living samples of species of *Macropus*. He

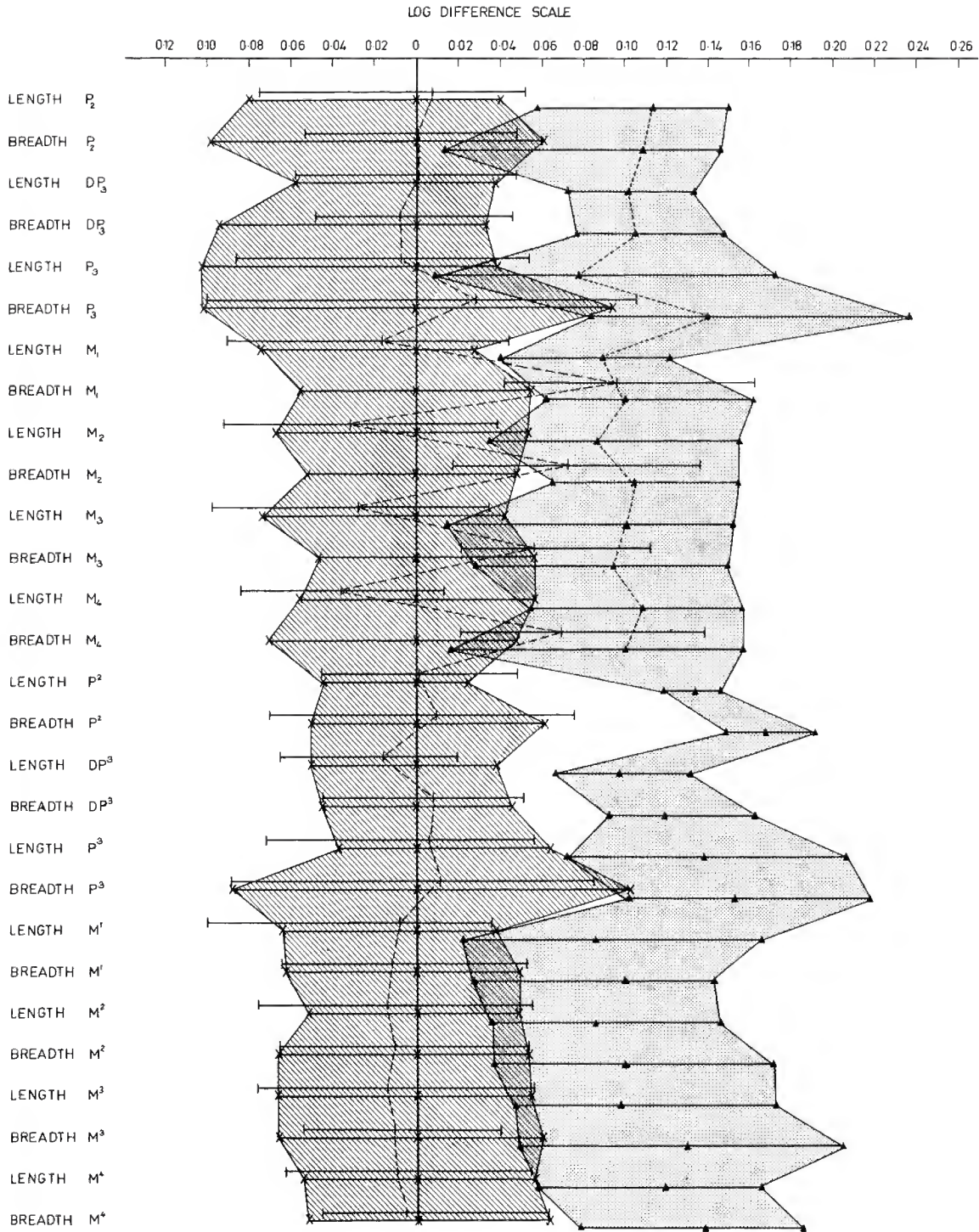


FIG. 1: Log Difference Diagram showing proportional relationships of cheek-teeth in *Macropus (Macropus) titan* (stippled) using mean values in the Queensland sample of *M. giganteus* (cross hatched) as standard. Data for Warwick sample of *M. giganteus* overlain.

TABLE 2: SUMMARY OF MEASUREMENTS FOR *Macropus (Macropus) giganteus* SHAW (QUEENSLAND SAMPLE)

Character	Maxillae					Mandibles				
	n	O.R.	\bar{X}	s	V	n	O.R.	\bar{X}	s	V
P ₂ ² length	35	6.3-7.7	7.0	0.326	4.63	34	5.3-7.0	6.4	0.339	5.32
max. width P ₂ ²	28	4.2-5.4	4.7	0.249	5.28	34	2.8-4.0	3.5	0.285	8.27
DP ₃ ³ length	45	7.8-9.5	8.7	0.468	5.39	42	7.8-9.5	8.7	0.398	4.60
prot. width	43	5.8-7.1	6.4	0.345	5.43	41	3.8-5.2	4.7	0.277	5.89
P ₃ ³ length	25	6.6-8.3	7.2	0.407	5.63	20	4.9-7.1	6.2	0.608	9.87
prot. width	25	3.1-4.8	3.8	0.390	10.31	20	2.3-3.6	2.9	0.323	11.19
M ₁ ¹ length	77	8.7-11.0	10.1	0.469	4.66	66	8.9-11.3	10.6	0.630	5.97
prot. width	75	6.7-8.6	7.7	0.411	5.35	60	5.4-6.8	6.0	0.293	4.86
M ₂ ² length	80	10.2-12.8	11.5	0.587	5.10	71	10.2-13.5	11.9	0.674	5.65
prot. width	78	7.4-9.7	8.6	0.482	5.59	71	6.3-7.9	7.1	0.345	4.86
M ₃ ³ length	61	10.6-14.0	12.3	0.711	5.79	50	10.9-14.2	12.9	0.675	5.26
Prot. width	58	7.9-10.7	9.2	0.558	6.06	48	7.0-8.7	7.8	0.461	5.95
M ₄ ⁴ length	37	11.4-14.7	12.9	0.776	6.03	34	12.2-15.2	13.6	0.828	6.10
prot. width	34	8.5-11.0	9.5	0.613	6.47	34	6.8-8.9	8.0	0.484	6.04

prot. = protoloph or protolophid.

also illustrates a log difference diagram comparing the juvenile cranium of *M. titan* described and figured by Anderson (1929) and previously figured by Ramsay (1882), with crania of recent species. Marked differences in proportions are indicated but, as suggested by Tedford (1967), some of the discrepancies may result from slight differences in maturity of the examples plotted. In juvenile specimens, such age differences could, in fact, result in marked proportional differences and the result of the comparison may not be entirely valid.

Certainly in other parameters, such as dimensions of cheek teeth, no outstanding discrepancies exist, particularly where the plotted values are derived from reasonably large living and fossil populations. In detail, however, different samples of the same species show some divergence.

The log difference diagram given here (Fig. 1) compares the relative proportions of the cheek teeth in *M. titan* with the standard provided by the mean values for Queensland *M. giganteus* (Table 2), and includes separate data for a geographically restricted sample of that species from the Warwick district, southeastern Queensland, published by Bartholomai (1971). Shading in the log difference diagram provides visual separation of comparisons of observed values for characters in two of the samples, and indicates those parameters where overlap occurs. Area have no significance. Presenting the diagram in this form reduces confusion resulting from incorporation of data from the number of samples considered. The diagram illustrates general overlap of the samples of *M. giganteus*, but shows the relatively broader nature of the lower molars in the Warwick sample, compared with the Queensland sample. On a

proportional basis, *M. titan* compares better with this latter material than with that from Warwick. This unexpected deviation within samples of the same species suggests that even with large samples of *Macropus* only generalised conclusions can be drawn from log difference diagrams.

M. birdselli, described by Tedford (1967), is very similar to *M. titan* in all of the characters presented, with the exception of the length of the diastema. In *M. titan*, Table 3 presents measurements for the length of the lower diastema, indicating that no overlap occurs with the *M. birdselli* sample. Dimensions of cheek teeth in *M. birdselli*, presented in Tedford (1967), fall well within the range of observed values for *M. titan*. Tedford (1967) has suggested a relationship between *M. birdselli* and *M. fuliginosus*, the Kangaroo Island and western mainland Grey Kangaroo and, on the basis of diastemal length and other morphological details, this is considered here to be a strong possibility. *M. birdselli* is maintained although, in most morphological features, considerable similarity exists with *M. titan*. Larger samples of *M. birdselli* will be required to ascertain whether variants of such features as diastemal length overlap with those in *M. titan*.

TABLE 3: LENGTH OF LOWER DIASTEMA IN *Macropus titan* OWEN

Specimen	F4198	F646	F4145	F3722	F4171	F4186
Diastema length	60.7	59.5	61.0	53.8	52.1	64.3

Summaries of measurements for lower and upper cheek teeth in *M. titan* are presented in Table

1. The size of the fossil samples is adequate for most characters considered. Only the deciduous upper dentition is poorly represented. As suggested by the Coefficient of Variation, the sample is likely to be homogeneous, and is in keeping with values for V provided from the Queensland and Warwick samples of *M. giganteus*. The generally high values for V associated with the permanent premolars indicate that the fossil sample in this case is somewhat less variable than *M. giganteus*.

Structurally, *M. titan* is very similar to *M. giganteus*, the most obvious difference being that of size. Grooving on the posterior surface of the hypolophid is less well-developed in *M. giganteus*, and the posterior fossette, usually present in *M. titan*, is normally absent in the recent species. In other features of the dentition and cranial morphology presented in the Queensland sample, no marked differences occur. Results of a statistical comparison of the fossil sample with the Warwick sample of *M. giganteus* are presented in Table 4 and show that whereas breadths of lower teeth are generally broader than in the Queensland sample, only the breadth of M_1 does not appear significantly different from that in *M. titan*. Using Student's t test, all other characters give probability values of 0.001. The Coefficient of Difference is generally larger than the 1.5 value considered by Ride (1964) as sufficient for the recognition of subspecific distinctness, usually being less than this only with respect to breadths of lower molar teeth. Comparison with the Queensland sample would provide much higher values for C.D. for breadths of lower molars, because of lower values for \bar{X} in that sample.

Because of the morphological differences noted, it is felt that the fossil sample is sufficiently distinct from the recent material to justify its separation at the specific level. Close relationship with the recent *M. giganteus* appears highly likely. No attempt has been made to associate post-cranial remains with the referred cranial remains.

In the Darling Downs, apart from one mandibular specimen, F4230, *M. titan* is currently restricted to the Pleistocene fluviatile deposits of the eastern Darling Downs. F4230 was collected from Chinchilla, but its preservation is not indicative of derivation from the Chinchilla Sand. It may have been recovered from one of the presumably younger terraces, possibly of Pleistocene age, which are associated with the Condamine River and Charley Creek, in the Chinchilla area. Lack of material referable to *M. titan* in the extensive collections from the Chinchilla Sand would support this suggestion. Other Queensland localities for the species are indicated in the list of material referred. Although probably widespread in eastern Australia, such occurrences as that indicated by Glauert (1912) from Western Australia, need to be checked against *M. birdselli* and *M. fuliginosus* before any synthesis is made of the Australian distribution for the species.

***Macropus (Macropus) rama* sp. nov.**
(Plate 11, figs. 1-4)

MATERIAL: F4773, associated left mandibular ramus with P_3 - M_4 , and right maxilla with P^3 - M^3 , adult, bend in King Creek, Pilton, at M.R.134444 Liverpool Range 1-mile map, eastern Darling Downs, SE.Q., in Pleistocene fluviatile deposits.

TABLE 4: COMPARISON OF THE WARWICK SAMPLE OF *M. giganteus* WITH THAT FOR *M. titan*

Character	Maxillae			Mandibles		
	t	P	C.D.	t	P	C.D.
P_2^2 length	20.7142	0.001	4.65	19.4400	0.001	2.20
max. width	15.1364	0.001	3.47	7.4582	0.001	2.09
DP_3^3 length	19.0282	0.001	2.70	28.4010	0.001	3.01
prot. width	14.7660	0.001	2.30	26.5232	0.001	2.91
P_3^3 length	16.3836	0.001	2.10	10.4586	0.001	1.25
max. width	13.7666	0.001	1.93	10.3157	0.001	1.33
M_1^1 length	21.2534	0.001	1.63	29.7851	0.001	2.45
prot. width	23.5865	0.001	2.06	1.4543	0.2-0.1	0.13
M_2^2 length	26.3636	0.001	1.84	9.2853	0.001	2.20
prot. width	30.4934	0.001	2.29	8.0134	0.001	0.68
M_3^3 length	32.1624	0.001	2.41	37.2105	0.001	2.72
prot. width	34.0161	0.001	2.68	13.3205	0.001	0.77
M_4^4 length	32.9439	0.001	2.96	36.7419	0.001	3.22
Prot. width	30.5746	0.001	2.79	9.3852	0.001	0.78

prot. = protoloph or protolophid.

SPECIFIC DIAGNOSIS: Relatively small species. Lower molars with trigonid basin widely spatulate in form and with hollowing of the posterior base of protolophid; lateral surfaces of lophids very narrow; hypolophid grooved at posterolingual base of crown. Upper molars lacking well-defined forelink.

DESCRIPTION: I_1 , P_2 and DP_3 unknown.

Mandible moderately shallow, robust and with moderately long post-alveolar shelf, but too incomplete for further description.

P_3 small, suboval in basal outline, being slightly constricted mesially. Longitudinal crest bifid, with well-defined anterior and posterior cuspids, separated mesially by prominent vertical labial and lingual grooves; posterior extension of crest descending directly to base of crown; lingual and anterior bases of crown slightly swollen.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline, considerably constricted across talonid basin; lophids moderately low, with protolophid broader than hypolophid in M_1 and M_2 and narrower in M_3 and M_4 ; hypolophid somewhat convex posteriorly, but protolophid nearly rectilinear and showing concave posterior surface in M_3 and M_4 ; lingual surfaces very narrow basally but with labial surfaces somewhat broader. Lateral surfaces of lophids moderately convex from base to crest. Trigonid basin extremely broad, spatulate, with moderately high, very broad anterior cingulum; length of trigonid approximates distance between lophids. Forelink moderately high, strong, curving anterolingually from protoconid to near mid-point of anterior cingulum. Trigonid gently descends ventrally in both labial and lingual moieties. Accessory link occasionally present near forelink, across lingual moiety of trigonid; slight fossette variably present near base of protolophid, at labial extremity of trigonid. Posterior surface of protolophid variably ornamented with a slight vertical ridge linguad to midlink. Midlink strong, moderately high, curving anterolingually from hypoconid to unite with extremely slight ridge from near mid-point of protolophid. Talonid basin V-shaped in labial and lingual moieties. Posterior surface of hypolophid broadly rounded, marked by relatively strong vertical groove towards posterolingual base of crown, and by variable, slight vertical grooves mesially.

I^{1-3} , P^2 , DP^3 and M^4 unknown.

P^3 moderately small, subovate in basal outline, being much broader posteriorly than anteriorly. Longitudinal crest subdivided mesially by well-defined vertical labial and lingual grooves giving crest a bifid appearance; anterior moiety transected by a pair of weak vertical labial and lingual ridges,

with production of cuspule at crest; posterior extension of crest ascending directly towards base of crown; crown worn posterolingually, but remaining ridges suggest presence of posterolingual cusp. Labial and anterior bases of crown slightly swollen.

$M^1 < M^2 < M^3$; molars subrectangular in basal outline, considerably constricted across median valley; lophids relatively low, moderately convex anteriorly, but apparently less so across protoloph; protoloph narrower than metaloph in M^1 and broader in M^2 and M^3 . Anterior cingulum moderately low, short, very broad ascending labially and lingually from axis of crown, worn mesially, with no trace remaining of forelink. Midlink moderately high, strong curving posterolabially from protocone to unite with short ridge from near mid-point of metaloph. Median valley V-shaped; posterolabial base of protoloph variably marked by transverse groove. Strong ridge ascends from hypocone towards base of crown, uniting posterolabially with posterior of metaloph with production of posterior fossette; slight, variable ridges ascend into fossette from metaloph.

DISCUSSION: The present material represents one of the few instances in the Pleistocene fluviatile deposits of the eastern Darling Downs of associated mandibular and cranial specimens. Although from different sides of the skull, the specimens were located together, and show morphological compatibility, similar stages of dental eruption, complementary wear patterns and similar size. Also located in the same isolated pocket of fossils were a partial right pelvis containing the acetabulum and remnants of the ilium, ischium and pubis, and the distal end of a left humerus. While it is possible that these macropodid post-cranial remains also belong to the same individual from which the skull remains were derived, no supplementary evidence can be presented to prove their association. Compared with modern macropodids, their size is in keeping with the size of the skull remains referred to *M. rama*.

The cranial remains show some morphological similarity to *M. giganteus* Shaw, but are considered to be specifically distinct. The permanent upper and lower premolars are similar to those in *M. giganteus*. P_3 shows no posterior incurving of the longitudinal crest, a feature observed rarely in *M. giganteus*. In *M. rama* the trigonid basin is widely spatulate in form, whereas that in *M. giganteus* is usually considerably narrower. Extreme variants of the modern species show some tendency towards broadening of the trigonid. The hollowing of the posterior base of the protolophid is seen in many

TABLE 5: MEASUREMENTS FOR *Macropus (Macropus) rama* SP. NOV.

Specimen	P ₃	M ₁	M ₂	M ₃	M ₄	P ³	M ¹	M ²	M ³
F4773	5.2 × 2.7	7.7 × 4.7	9.7 × 6.7	10.7 × 8.2	12.2 × 8.7	7.6 × 4.0	9.0 × —	9.9 × 8.1	11.2 × 8.7

examples in *M. giganteus*, but the narrowness of the lateral surfaces of the lophids is not duplicated to the same degree. The position of the posterior vertical groove at the posterolingual base of the crown is not usual for *M. giganteus*. In the upper molars, no trace remains of the presence of a forelink, a feature present in *M. giganteus*. The teeth are all well worn and traces of a forelink are frequently obliterated in similarly worn teeth in the modern species. Other differences in upper molars are within the range of variation for *M. giganteus*.

As can be seen from Table 5, the size of the fossil form is smaller than generally seen in *M. giganteus*, even in females of that species (Bartholomai, 1971), and is considerably smaller than *M. titan* (Table 1), the most commonly encountered species of *Macropus* in the Pleistocene fluvial deposits of the Darling Downs.

Macropus (Osphranter) altus (Owen, 1874)

(Plate 12, figs. 1–2; Plate 13, figs. 1–2; Plate 26, figs. 3–4)

?*Macropus titan* Owen, 1838, p. 360, pl. 29, figs. 4–5.

Osphranter cooperi Owen, 1874, p. 261, pl. 24, figs. 17–18.

Phascolargus altus Owen, 1874, pp. 261–4, pl. 22, figs. 1–2; 1877, pp. 413–6, pl. 82, figs. 1–2, pl. 111, ?figs. 1–6, pl. 117, ?figs. 1–6; Etheridge Jun., 1878, p. 187; 1892, p. 676.

?*Phascolargus altus* Owen, 1876, p. 218, pl. 30, figs. 1–5.

Macropus (Osphranter) cooperi (Owen): Owen, 1877, pp. 412–3, pl. 84, figs. 17–18.

Macropus altus (Owen): Lydekker, 1887, pp. 223–4; Simpson, 1930, p. 71.

Macropus cooperi (Owen): Lydekker, 1887, p. 224; Simpson, 1930, p. 71.

Halmaturus cooperi (Owen): De Vis, 1895 *partim*, pp. 116–8, pl. 17, figs. 24–7.

MATERIAL: F3399, cast of holotype of *Phascolargus altus* (Owen), British Museum (Natural History) specimen, juvenile palate with left P²–M², M³ exposed

laterally, right DP³–M², P³ and M³ exposed laterally, cave in Wellington Valley, New South Wales, from Pleistocene cave earth deposits (figd Owen, 1838, pl. 29, figs. 4–5; 1874, pl. 22, figs. 1–2; 1877, pl. 82, figs. 1–2).

F2849, juvenile right maxilla with P³ exposed by fenestration, M¹–M³, Bongee, Darling Downs.

F5608, cast of holotype *Osphranter cooperi* Owen, British Museum (Natural History) specimen number 32886, partial left mandibular ramus with I₁, broken, P₃–M₂, adult, Condamine River, Queensland, (figd Owen, 1874, pl. 24, figs. 17–8; 1877, pl. 84, figs. 17–8).

F5441, partial right mandibular ramus with M₂–M₄, eastern Darling Downs.

SPECIFIC DIAGNOSIS: Comparatively large species; P³ well-developed, moderately elongate with longitudinal crest straight, transected by two sets of ridges between paracone and metacone; hypocone low, with anterolabial ridge connecting to above metacone; lingual cingulum low, extending to above paracone; labial and anterior base of crown swollen. Upper molars with moderately high lophids; anterior cingulum low, slightly recurved, and with variable forelink, rarely strong; ridge from paracone usually links with labial limit of cingulum. P₃ relatively elongate with trifid longitudinal crest. Lower molars with moderately high lophids, links and anterior cingulum; posterior surface of hypolophid with deep, near vertical groove, flanked by slightly flared margins.

DESCRIPTION: Cranium known only from fragmentary palate and maxillary specimens. Palate entire.

I^{1–3} and M⁴ unknown.

P² moderately elongate, subovate in occlusal view, with longitudinal crest between paracone and metacone slightly concave labially, low; crest transected by two sets of vertical labial and lingual ridges with indication of cuspules on crest. Lingual cingulum low, but posterolingual portion of crown worn; cingulum extends anterolingual to paracone.

TABLE 6: MEASUREMENTS FOR *Macropus (Osphranter) altus* (OWEN) MAXILLA

Specimen	P ²	DP ³	P ³	M ¹	M ²	M ³
F3399, right*	9.1 × 5.1	9.8 × 7.0	—	11.1 × 9.4	12.9 × 10.0	—
F3399, left	—	—	10.0 × —	11.4 × 9.2	13.3 × 10.5	15.3 × —
F2849	—	—	9.8 × 5.0	10.7 × —	12.6 × —	— × 10.0

*Holotype *M. altus* (Owen)

DP³ molariform, subtriangular in occlusal view, very slightly constricted across median valley; loph moderately high, anteriorly convex with protoloph much narrower than metaloph. Anterior cingulum low, broad, with anterior cingular shelf moderately short; weak forelink present, uniting cingulum with protoloph base, linguad to mid-line; ridge from paracone connects with labial limit of cingulum. Midlink strong, high, curving posterolabially than lingually, nearly planar transversely. from near mid-point of metaloph above median valley; median valley more sharply U-shaped labially than lingually, near - planar transversely. Posterior ridge from metacone weak, ascending slightly lingually to unite with much stronger ridge from hypocone which curves posterolabially to margin of crown; posterior surface of metaloph excavated below ridges.

P³ relatively elongate and low-crowned, subovate in occlusal view with longitudinal crest between paracone and metacone straight, low; crest transected by two sets of vertical labial and lingual ridges with production of cuspules on crest. Paracone well-defined. Hypocone low, posterolingual to metacone; posterior ridge from hypocone curves labially to unite with posterolingually curving ridge from metacone: very shallow posterior fossette developed between these and anterolabial ridge connecting hypocone to above metacone. Anterior ridge from hypocone ascends sharply towards crown base, continuing anteriorly as low, swollen lingual cingulum to above paracone; lingual basin shallow, narrow. Labial and anterior base of crown swollen, delimited from rest of crown by well-defined groove.

M¹ < M² < M³; molars subrectangular in occlusal view with moderately high loph; loph convex anteriorly. Protoloph slightly narrower than metaloph in M¹ and M² and approximately equal in M³. Anterior cingulum low, broad, with anterior cingular shelf relatively short; cingulum slightly recurved, usually connected to mesial base of protoloph by variable, occasionally strong, forelink; shelf ascends slightly away from forelink; anterior ridge from paracone often well-defined, connecting with labial limit of anterior cingulum; posterior ridge from paracone weak. Midlink strong, high, ascending from protocone across

median valley to unite with slight ridge from near mid-point of metaloph; midlink lunate in unworn teeth; median valley sharply U-shaped, tending to be more V-shaped lingually, near planar transversely. Posterior ridge from metacone weak, ascending slightly lingually to unite with much stronger, slightly flared ridge curving posterolabially from hypocone; ridge from hypocone occasionally ornamented by slight accessory ridges; posterior surface of metaloph broadly excavated above junction, with production of posterior fossette.

Mandible known only from fragmentary rami; ramus moderately deep anteriorly, relatively broad, but markedly excavated laterally near alveolar margin below anterior cheek teeth and posterior of diastema; diastemal crest acute posteriorly. Symphysis rugose, not ankylosed, somewhat ventrally deflected, with geniohyal pit deep, positioned at posterior symphyseal limit. Ventral margin of ramus behind symphysis rounded, with digastric ridge and process very poorly developed, separated from base of angle by extremely weak post-digastric sulcus; process separated above by fossa with broad, shallow groove extending posteriorly into pterygoid fossa. Post-alveolar shelf short with shelf angle not developed, leading to post-alveolar ridge which ascends onto coronoid process, disappearing above large mandibular foramen; anterior wall of process near vertical, but angle of mandible, bulk of process and condyle not preserved.

I₁, P₂, DP₃ and M₁ are not known as yet.

P₃ relatively elongate, subovate in basal outline; longitudinal crest markedly trifid, with mesial cuspule as well-developed as posterior cuspid and better developed than anterior cuspid. Labial base of crown swollen, delimited from remainder of crown by slight longitudinal groove.

M₂ < M₃ < M₄; molars subrectangular in occlusal view, slightly constricted across talonid basin, with lophids relatively high, convex posteriorly; hypolophid much narrower than protolophid in M₄; anterior cingulum moderately high, broad, more expansive anterolingually than anterolabially, marked by vertical furrow slightly labial to mid-line; forelink descends from protoconid, curving anterolingually across trigonid

TABLE 7: MEASUREMENTS FOR *Macropus (Osphranter) altus* (OWEN), MANDIBLE

Specimen	P ₃	M ₁	M ₂	M ₃	M ₄
F5608*	6.7 × 3.0	—	—	—	—
F5441	—	—	13.2 × —	15.3 × —	17.4 × 9.0

*Holotype *M. cooperi* (Owen)

basin to unite with cingulum labiad to mid-line. Trigonid basin elongate, about as long as distance between lophids, sloping labially and lingually from forelink as well as posteriorly from cingulum; very slight anterolabial fossette present; slight ridges descend anteriorly and posteriorly from metaconid. Midlink strong, high, descending labiad to mid-line, anterolingually from hypoconid across talonid basin to unite with slight ridge from near protoconid; junction frequently flexed; talonid broadly U-shaped lingually, V-shaped labially, near planar transversely, sometimes with low transverse fold in floor of lingual moiety. Posterior hypolophid surface with deep, near vertical groove developed linguad to mid-line, bounded laterally by slight ridges. Labial lophid bases more expansive than lingual, with slight groove usually present near posterolabial margin of protolophid.

DISCUSSION: The holotype of *Phascolargus altus* Owen, 1874, was among material forwarded to Owen, following its collection by Major Sir Thomas Mitchell from caves in the Wellington Valley, New South Wales. It represents one of the first known fossil macropodid specimens. When figured by Owen (1838) it was doubtfully referred to *M. titan* Owen but its distinctness from that species was later confirmed (Owen, 1874) when it was described as *Phascolargus altus*. Lydekker (1887) relegated the genus *Phascolargus* to synonymy with *Macropus*, while both Iredale and Troughton (1934) and Tate (1948) indicated the belief that *Phascolargus* represented a junior synonym of *Osphranter*. This conclusion is here maintained on the basis of its cranial and dental morphology.

In addition to his description of *P. altus*, Owen (1874) defined *O. cooperi*. It was unfortunate that Owen chose to base this latter species on such inadequate, poorly preserved material. Uncertainty about the morphology of *O. cooperi* has led subsequent workers, particularly Lydekker (1887) and De Vis (1895), into error in interpretation of the limits and affinities of *O. cooperi*. It is likely that not one of the specimens referred by De Vis (1895) was *M. cooperi*. Not only is the permanent lower premolar the only tooth in the holotype sufficiently well preserved to be described, but also the mandible is not well preserved. This has led to incorrect assumptions regarding the diastemal slope (Lydekker, 1887). The specimen has been fractured and movement has occurred along an oblique line immediately anterior to P_3 , effectively reducing the anterior depth of the ramus and the diastemal slope. In

addition, the specimen has suffered some lateral crushing.

Maxillary and mandibular remains in *M. altus* have not, as yet, been located associated and synonymy of the mandibular remains of *O. cooperi* with the maxillary remains of *M. altus* has been undertaken on the basis of morphological compatibility and size.

The better preserved holotype of *M. altus* presents many features which enable reference of additional material to the taxon. Although the name *O. cooperi* has page priority over *M. altus* and has been more widely applied subsequently, Owen's application of the names has not been questioned. It is here considered that taxonomy can be better served by recognition of *O. cooperi* as a junior synonym of *M. altus*.

The dentition in *M. altus* is similar to that in *M. ferragus*, described below, and this supports the present association. *M. altus* differs from *M. ferragus* not only in its smaller size but also in the comparatively lower crown heights of its molars, the more longitudinal arrangement of the cuspids and cuspule of the longitudinal crest in P_3 , the generally stronger forelink in upper molars, the weaker posterolingual fossette in P^3 and the lack of an anterolingual extension of the lingual cingulum in that tooth.

Compared with living species, *M. altus* differs in being somewhat larger than *M. robustus* and *M. antilopinus*, but because of the small size of the fossil sample, no statistical evaluation and comparison of samples has been possible. P^3 in *M. altus* is more robust, being more strongly developed in its lingual cingulum than the living species. Forelinks in upper molars are generally stronger than in *M. robustus* and are similar to those in *M. antilopinus*. Both *M. robustus* and *M. antilopinus* have well-developed posterolingual cuspids on P^3 . Morphological variation is all but unknown in *M. altus* and this could account for some of the differences noted.

The status of the post-cranial material referred to the species by Owen (1877) is extremely doubtful. Until more complete, associated specimens are located, the identity of these specimens cannot be determined.

Eleven specimens in the collections of the British Museum (Natural History) were referred to *M. altus* by Lydekker (1887) and were listed as being derived from the Wellington Caves and Kerban, near Mendoran in New South Wales and from Eton Vale, Gowrie, and the Condamine River in Queensland. The status of these specimens is unknown. While additional specimens are present

in the collections of the Australian Museum, Sydney, which may be referred to *M. altus*, the species is one of the poorest represented in the Pleistocene deposits of the eastern Darling Downs. It is unknown from older sediments.

Macropus (Osphranter) ferragus Owen, 1874
(Plate 14, figs. 1-2; Plate 15, figs. 1-2)

Macropus ferragus Owen, 1874, p. 784, pl. 81, fig. 4, pl. 82, figs. 3-4, pl. 83, fig. 3; Lydekker, 1887, pp. 230-1; Simpson, 1930 p. 72.

Macropus (Leptosiaigon) gracilis Owen, 1874, pp. 785-6, pl. 76, figs. 11-15; 1877, pp. 450-1, pl. 89, figs. 11-15.

Macropus (Pachysiaigon) ferragus Owen, 1877, pp. 449-50, pl. 91, fig. 4, pl. 92, figs. 3-4, pl. 93, fig. 3.

Leptosiaigon gracilis Owen: Etheridge Jun., 1878, p. 182; 1892, p. 674.

Pachysiaigon ferragus Owen: Etheridge Jun., 1878, p. 186; 1892, p. 675.

Macropus ferragus Owen: Lydekker, 1887, pp. 230-1; Simpson, 1930, p. 72.

Macropus gracilis Owen: Simpson, 1930, p. 72.

?*Macropus (Macropus) ferragus* Owen: Tedford, 1967, pp. 127-43.

MATERIAL: F3865, cast of holotype *M. ferragus* Owen, British Museum (Natural History) number 32903, partial right mandibular ramus with M_2 shattered, M_3 - M_4 , adult, Condamine River, southeastern Queensland, apparently from Pleistocene fluviatile deposits (figd Owen, 1874, pl. 81, fig. 4; pl. 82, figs. 3-4; pl. 83, fig. 3; 1877, pl. 91, fig. 4; pl. 92, figs. 3-4; pl. 93, fig. 3).

F3867, cast of holotype *M. gracilis* Owen, British Museum (Natural History) number 40005, partial right mandibular ramus with M_2 - M_3 , juvenile, Queensland, apparently from Pleistocene fluviatile deposits (figd Owen, 1874, pl. 76, figs. 11-15; 1877, pl. 89, figs. 11-15).

Also referred to *M. ferragus* are 5 juvenile mandibular rami, 15 adult mandibular rami and 2 juvenile maxillae from the following localities in the Pleistocene fluviatile deposits: Ravensthorpe, Pilton; King Creek, Pilton, at M.R.098465 Liverpool Range 1-mile sheet; King Creek, near M.R.039454 Clifton 1-mile sheet; Macalister; Gowrie; and from the eastern Darling Downs (particular localities unspecified).

DIAGNOSIS: A large species, somewhat larger than *Macropus (Macropus) titan* Owen. Mandible narrow immediately below anterior cheek teeth and also deep in that area. P_3 small, with longitudinal crest trifid, with posterior cuspid and associated ridges offset and separated from anterior cuspid and mesial cuspsule which are united by longitudinal crest. Lower molars with very high lophids, with anterior moiety in occlusal view rotated labially relative to posterior moiety about a point approximately one-half distance along labial base, producing broadly U-shaped part of talonid basin lingually and sharply V-shaped part of basin

labially. Anterior cingulum very high, somewhat recurved, very broad; posterior of hypolophid with deep, moderately angled groove linguad to midline, flanked by ridges and reduced grooves; occasionally groove opens basally into strong posterior fossette. P_3 with longitudinal crest markedly concave labially and with one cuspsule intermediate between paracone and metacone along crest; hypocone strongly defined, united to below metacone by anterolabial ridge; lingual cingulum anteriorly convergent, markedly tuberculate in lingual view, extending to anterior of base of crown. Upper molars with very broad, moderately high anterior cingulum, somewhat recurved; forelink extremely reduced; anterior portion of midlink crescentic; labial moiety of median valley in anterior molars with reduced ridge connecting paracone and metacone; posterolabial ridge from hypocone widely flared.

DESCRIPTION: mandible deep below anterior molars and in diastemal area, relatively thick posteriorly; base of symphysis deflected, near planar; symphysis relatively elongate, shallow, not ankylosed, rugose; geniohyal pit relatively deep, above posterior symphyseal limit; diastema comparatively elongate, with diastemal crest posteriorly very acute, and with body of ramus very narrow below anterior cheek teeth; ventral margin of ramus rounded between symphysis and extremely weak digastric ridge and process. Mental foramen moderately large, oval, below diastemal crest, anterior to anterior root of P_3 . Ramus with very shallow lateral groove extending posteriorly to below anterior M_2 , close to alveolar margin. Digastric process separated from base of angle by shallow post-digastric sulcus, bounded above by shallow digastric fossa; this fossa separated above from broad depression leading posteriorly into pterygoid fossa. Post-alveolar shelf long, with angle not well-developed, leading to post-alveolar ridge, ascending posteriorly to disappear on mesial wall of coronoid process, above large mandibular foramen. Masseteric crest raised to about level of occlusion of cheek teeth; masseteric foramen moderately large, with masseteric fossa relatively deep. Bulk of angle of mandible, coronoid process and condyle not preserved in any specimen.

I_1 , P_2 and DP_3 not preserved.

P_3 small, short, subovate in occlusal view, with labial margin slightly convex, and lingual margin somewhat concave. Crest trifid in lateral view. Anterior cuspid well-defined, with anterior ridge descending to crown base; posterior ridge descends as longitudinal crest uniting with anterior ridge

TABLE 8: SUMMARY OF MANDIBULAR MEASUREMENTS FOR *Macropus (Osphranter) ferragus* OWEN

Character	n	O.R.	\bar{X}	s	V
P ₃ length	1	—	9.0	—	—
max. width	1	—	4.0	—	—
M ₁ length	—	—	—	—	—
prot. width	2	7.9-8.7	8.3	—	—
M ₂ length	8	16.0-17.8	16.9	0.7111	4.21
prot. width	8	9.1-10.1	9.7	0.3379	3.48
M ₃ length	18	17.0-19.9	18.8	0.8095	4.31
prot. width	16	10.2-12.1	11.1	0.5279	4.76
M ₄ length	13	19.4-22.4	20.8	0.8170	3.93
prot. width	13	10.4-12.6	11.4	0.6939	6.08

prot. = protolophid.

from well-defined mesial cuspule, above vertical labial and lingual ridges; posterior ridge from cuspule curves lingually to short groove at posterior one-quarter. Posterior cuspid with strong anterolabial ridge descending to strong groove at posterior one-third; a strong ridge descends posterolingually from posterior cuspid to base of crown; slight cuspule occasionally present along this ridge, just below cuspid. Labial base of crown slightly swollen.

M₁ < M₂ < M₃ < M₄; molars subrectangular in basal outline, somewhat constricted across talonid basin; lophids very high, with hypolophid crest more convex posteriorly than protolophid crest in unworn teeth, nearly similar in worn examples; hypolophid broader than protolophid in M₁, about equal in M₂ and M₃ and narrower in M₄. Trigonid basin very broad, its length being about equal to distance between lophids. Forelink very high, curving anterolingually from protoconid to point labiad to mid-line of very high somewhat recurved anterior cingulum. Cingulum with anterolabial indentation, very squared in appearance being inflated anterolingually and anterolabially; trigonid markedly sloping posteriorly from cingulum and descending slightly labially and lingually from forelink; slight anterolabial fossette usually present. Strong, high ridge curves anterolingually from hypoconid across talonid basin as midlink, uniting with short ridge from labiad to mid-point of protolophid; junction frequently flexed in unworn teeth. Talonid basin descends slightly labially and lingually from midlink; basin V-shaped labially, broadly U-shaped lingually, associated with strong labial flexure of crown about a point approximately mid-way along labial margin; slight groove usually present at crown base, near posterolabial margin of base of protolophid; slight ridges usually descend anteriorly and posteriorly from metaconid. Lingual moiety of talonid frequently

with transverse fold to tooth margin; fold occasionally ascends posterior surface of protolophid, near junction with midlink. Posterior of hypolophid with well-defined somewhat oblique groove, linguad to mid-line, very occasionally leading into well-defined posterolingual fossette. Slight ridges flank groove, and usually very slight grooves present beyond ridges; occasionally posterolabial crown base marked by several radiating grooves. Base of crown broadly extended posteriorly, sometimes slightly swollen particularly at margins of talonid base. Labial bases of lophids more expansive than lingual. Cranium known only from fragmentary maxillary remains.

I¹-I³, P², DP³, M⁴ not preserved.

P³ relatively small, subovate in occlusal view, with labial margin slightly concave, and with lingual margin convex. Paracone well-defined with strong anterior ridge ascending towards crown base where it curves lingually; posterior paracone ridge contributes to longitudinal crest. Crest trenchent, somewhat concave labially. Metacone reasonably well-defined, with anterior ridge extending as crest and with posterior ridge curving lingually above crown base to unite with labially curving ridge ascending from hypocone; metacone positioned at posterior one-third; longitudinal crest transected by one slight set of vertical labial and lingual ridges with production of cuspule at crest. Hypocone with low antero-labial ridge connecting with slight vertical ridge ascending from metacone, delimiting broad, shallow, posterior fossette; anterior ridge from hypocone ascends to above crown base as lingual cingulum; cingulum convergent anteriorly, marked by strong tuberculation where extension of ridge from crest cuspule unites; vertical ridge from paracone unites with cingulum at anterior tuberculation, but cingulum extends further, to unite with anterolingually curving ridge from paracone at anterior

TABLE 9: MEASUREMENTS FOR *Macropus (Osphranter) ferragus* OWEN, MAXILLA

Specimen	P ³	M ¹	M ²	M ³	M ⁴
F3720	13.0 × 6.4	—	15.1 × —	16.9 × 11.9	—
F1691	—	—	—	—	17.9 × 12.5

of crown. Lingual basin shallow, with transverse ridging slight. Base of crown somewhat swollen.

M¹ < M² < M³; molars subrectangular in occlusal view, slightly constricted across median valley; lophs high, with metaloph crest more concave posteriorly than protoloph crest in unworn teeth, but nearly similar in worn examples; metaloph broader than protoloph in M¹, approximately equal in M² and M³. Anterior cingulum relatively high, very broad, moderately short, overturned in unworn examples; forelink very weak, labiad to mid-line, frequently with no trace remaining in worn teeth; anterior cingular shelf less sloping lingually in labial moiety than lingual, strongly sloping posteriorly. Weak ridge ascends from paracone to labial extremity of anterior cingulum, separated from it by cleft. Midlink strong, high, ascending posteriorly from protocone in lunate form, uniting with slight ridge from near mid-point of metaloph, this ascending from near centre of metaloph crest; junction occasionally flexed; posterior ridge from paracone weak, ascending posteriorly to near base of median valley, then curving abruptly lingually before crossing valley to unite with equally weak, and similarly developed ridge from metacone; these ridges strongest in anterior molars; median valley slopes slightly labially and lingually from midlink, sharply U-shaped in labial moiety, V-shaped lingually; slight ridge usually delimits lingual extremity of median valley. Posterior ridge from hypocone strong, somewhat flared, ascending and curving labially to unite with much weaker ridge from metacone near posterolabial base of crown; well-developed posterior fossette present; posterolingually, broad groove normally descends from crown base, reaching hypocone ridge.

DISCUSSION: Tedford (1967) has very adequately presented evidence for the synonymy of *Macropus gracilis* Owen with *M. ferragus* Owen, a conclusion previously reached by Lydekker (1887). The mandible of the holotype of *M. ferragus* is poorly preserved. Excessive width of the ramus appears to be the result of fragmentation and wedging by calcite. This may have been combined with a primary abnormality in width. As a result, this character is of doubtful worth although Owen (1874) considered width of the mandible to be

diagnostic of the species. Morphologically, the molars of the holotypes of *M. gracilis* and *M. ferragus* are generally similar, differing mainly in the structure of the posterior surface of the hypolophid, a feature which shows some variation in the Queensland sample of *M. ferragus*. Grooving of the posterior hypolophid surface of the molars of the *M. gracilis* holotype is most commonly represented in the present sample. Owen (1874) stressed this feature in his description of *M. gracilis*, and regardless of some variation in this character, the synonymy is considered justifiable.

From Tedford's (1967) description and figures of *M. ferragus* it is evident that a mixed sample is involved in the Lake Menindee material. Tedford argued that high values for the Coefficient of Variation in that sample probably resulted from variable inter-tooth attrition, true variation patterns, and possibly sexual differences. Values of this order, up to $V = 13.26$ in the posterior width of M₄, are unknown in related fossil macropodines and are completely at variance with control statistical results reported by Bartholomai (1971) and with values for V for the present sample of *M. ferragus*. Further, while slight sexual differences are evident in the recent control samples, no marked separation occurs in the characters considered and only insignificant bimodality occurs in the histograms. Some overlap in measurements is evident in Tedford's (1967) sample with those of *M. titan* presented in the present study (Table 1). It would appear that material very similar morphologically to *M. titan* has contributed to Tedford's description of *M. ferragus*. This is supported by the morphology of premolars figured and described by Tedford.

Compared with the values presented in Table 8, a summary of mandibular measurements for *M. ferragus* from Queensland, Tedford's (1967) Lake Menindee sample overlaps considerably. These frequently exceed values for the present material in observed ranges of cheek teeth. Thus, while some Lake Menindee material may be referable to *M. ferragus* some may be separable from both *M. titan* and *M. ferragus*. For this reason, the specific identity of the post-cranial remains referred to *M. ferragus* by Tedford is uncertain, but they are undoubtedly referable to the genus *Macropus*.

Mandibular and maxillary remains of *M. fer-*

ragus have not been located together but the present association is considered correct. Occlusion is satisfactory and morphological features in upper and lower dentitions are compatible. *M. ferragus* is not common in the Darling Downs deposits and statistical evaluation has been limited to posterior lower molars. Measurements for referred maxillary remains are presented in Table 9.

Lydekker (1887) referred a partial palate and portion of a left maxilla from the Condamine River, Queensland, to this species, differentiating these from *M. titan* Owen by their slightly larger size and more complex molars. Lydekker also referred a partial mandible and maxilla from the Pleistocene of Kirban, Mendoran, New South Wales, stating that the molars of the mandible agree precisely with those in the holotype of *M. gracilis*.

M. ferragus is distinguished from *M. titan* by the structure of both molars and premolars, and to

some extent by the structure of the lower jaw. While P_3 in *M. titan* does achieve a trilobate appearance in extreme variants, the posterior lobe is never detached and angled to the general line of the longitudinal crest. Further, the lower molars are normally marked by a well-defined posterior fossette and a lower anterior cingulum, while the ramus is shallower in the diastemal area and is not so markedly compressed immediately below the anterior cheek teeth. Upper premolars in *M. titan* lack a lingual cingulum and have a cleft longitudinal crest, while upper molars in *M. titan* lack a recurved anterior cingulum and possess a strong forelink.

The log difference diagram presented in Fig. 2 indicates marked differences in relative proportions of mean values for cheek teeth in *M. ferragus* compared with those in *M. pan* from the Chinchilla Sand, described below. The permanent premolars are comparatively longer while the last lower molar

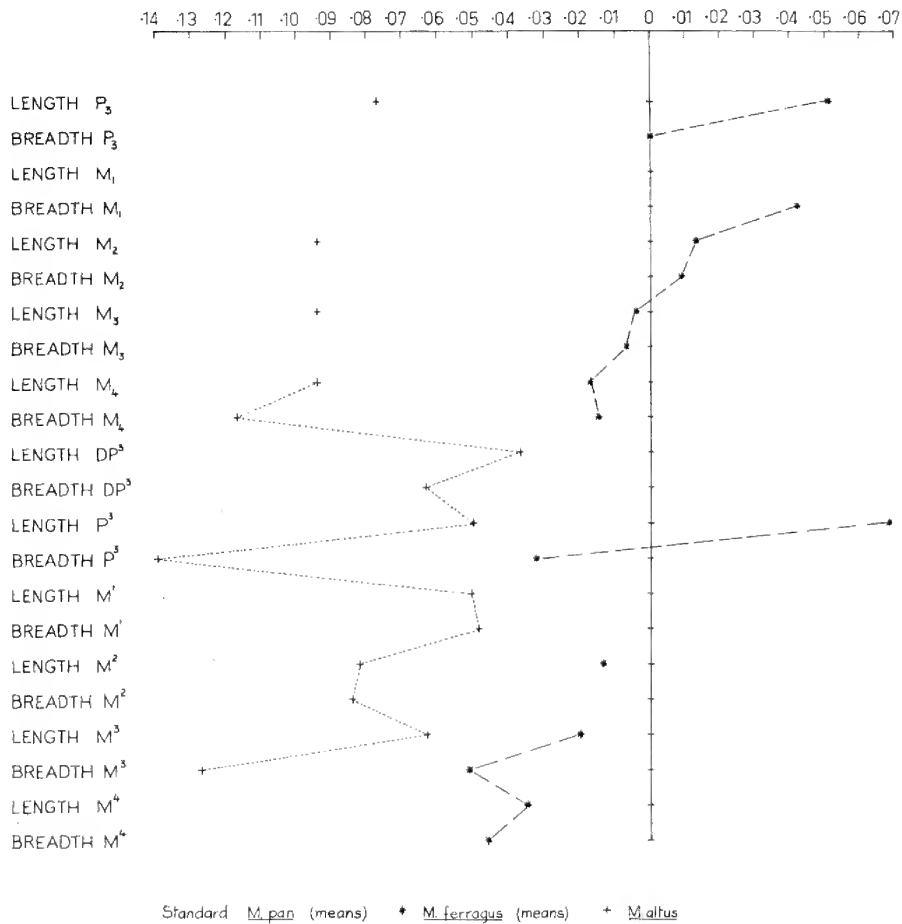


FIG. 2: Log Difference Diagram illustrating relative proportional differences in cheek-teeth in *M. ferragus*, *M. altus*, and *M. pan*.

is relatively smaller compared with M_3 . Comparison of the upper dentition is less conclusive, because it is based on a small sample in *M. ferragus*. This figure also presents details for *M. altus*, which compares more closely with *M. ferragus*, although again a very small sample is involved. *M. altus* is readily distinguished from *M. ferragus* by its much smaller size and by minor morphological details.

Macropus (Osphranter) pan De Vis, 1895

(Plate 16, figs. 1–4; Plate 17, figs. 1–4; Plate 18, figs. 1–2)

Macropus pan De Vis, 1895 (*partim*), pp. 124–7, figs. 7, 9–10; *non* fig. 8; Simpson, 1930, p. 72; Bartholomai, 1966, pp. 124–5, pl. 18, figs. 4–6.

MATERIAL: F2925, holotype, partial right maxilla with DP^3 – M^2 , juvenile, Darling Downs (figd Bartholomai 1966, pl. 18, figs. 4–6); preservation indicates derivation from the late Pliocene Chinchilla Sand.

Also referred to *Macropus pan* from the collections of the Queensland Museum are a juvenile maxilla, 11 adult maxillae, 21 isolated upper molars, 34 juvenile mandibular rami, 23 adult mandibular rami and 23 isolated lower teeth from the following localities: Chinchilla, SE.Q.; Condamine River, 60 m east of eastern boundary of Chinchilla Rifle Range (Rifle Range No. 78, Par. of Chinchilla), SE.Q.; Condamine River, c. 5 km southeast of Chinchilla, SE.Q.; near M.R.363676 Chinchilla 4-mile sheet; and from the western Darling Downs (particular localities unspecified).

DIAGNOSIS: P_3 relatively large, with well-defined, short, low, lingual cingulum and with high, longitudinal crest transected by one vertical set of labial and lingual ridges; small posterolingual fossette present. Upper molars with high lophs, somewhat rotated; forelinks moderately well-defined and midlinks high. Labial portion of median valley with low accessory link, becoming weaker or absent in posterior molars. Mandible large; P_3 relatively small, usually presenting distinct posterolingual cuspid; longitudinal crest normally trifid, ascending posteriorly, usually transected mesially by set of vertical labial and lingual ridges. Lower molars with high, somewhat rotated lophs, and relatively high anterior cingulum and forelink; midlink high; posterior of hypolophid with slight oblique groove to base of crown; posterior fossette normally absent.

DESCRIPTION: I^1 – 3 , and P^2 unknown.

DP^3 molariform, too worn to be adequately described. Semblance of accessory link present in labial moiety of median valley.

P^3 relatively large, subovate in basal outline, broader posteriorly. High, relatively short longitudinal crest transected by median vertical set of

labial and lingual ridges, with production of cuspule at crest. Moderately high hypocone close to metacone, connected to above metacone by labial ridge; posterior ridge from hypocone curves posterolabially below base of crown to unite with posterior ridge from metacone, with production of well-defined posterolingual fossette; anterior ridge from hypocone ascends to unite with base of crown, linguad to paracone, as low lingual cingulum: cingulum with well-defined but low tuberculation; lingual basin narrow, moderately shallow. Low, broad ridge crosses lingual basin from tubercle on cingulum.

$M^1 < M^2 < M^3 < M^4$; molars subrectangular in basal outline, slightly constricted across median valley, particularly in posterior molars. Lophs very high in unworn teeth, anteriorly bowed, somewhat rotated in lateral and occlusal view; metaloph broader than protoloph in M^1 , almost equal in M^2 , and slightly narrower in M^3 and M^4 . Anterior cingulum relatively high and moderately narrow, short; forelink generally well-defined and strong but variable, passing posteriorly from near mid-point of anterior cingulum to point linguad to centre of protoloph. Lingual moiety of anterior cingular shelf ascending sharply; labial moiety ascending slightly from forelink with occasional production of shallow anterofabial fossette. Variable ridges ascend anteriorly and posteriorly from paracone. Midlink high, strong, ascending labially from protocone then posteriorly across median valley to unite with short ridge from near mid-point of metaloph; junction often marked by vertical grooves and flexure; median valley V-shaped, sometimes partially delimited labially by low, variable ridges on posterior surface of protoloph and anterior surface of metaloph. Anterior ridge from metacone weak, variable, generally ascending into median valley as accessory link across labial moiety of valley, this link becoming reduced or absent in posterior molars; accessory link often unites with weak posterior ridge from paracone; posterior surface of protoloph between midlink and ridge to accessory link broadly swollen. Well-defined ridge ascends posterolabially from hypocone to unite basally with slight variable posterior surface of diagonal ridge from hypocone generally grooved parallel to margin of ridge. Mandible elongate, strong, moderately deep and posteriorly broad. Symphysis relatively shallow, not ankylosed; geniohyal pit moderately deep. Diastema long, crest acute; ramus deep in diastemal area. Mental foramen relatively large, oval, set just below diastemal crest. Ramus narrow and grooved laterally from below anterior extent of

tooth row to position about one-half way along alveolar margin. Ventral margin of ramus broadly rounded posterior to symphysis, with digastric process weak; digastric fossa separated above from broad lingual depression opening posteriorly into pterygoid fossa. Post-alveolar shelf moderately long, leading to mesial surface of coronoid process. Most of coronoid process and angle of mandible not preserved.

I_1 and P_2 not preserved in any specimen.

DP_3 molariform, relatively small, much narrower anteriorly than posteriorly, only slightly constricted across talonid basin in some individuals. Lophids high, somewhat variably rotated forward. Trigonid basin relatively broad, its length almost equalling distance between lophids. Forelink strong, moderately high, descending across trigonid basin from protoconid to point well labiad of mid-point of moderately high anterior cingulum, almost at anterolabial margin of tooth. Talonid basin sharply U-shaped lingually and V-shaped labially. Midlink high, strong, descending from hypoconid across talonid to point well labiad to mid-point of posterior surface of protolophid. Moderately shallow diagonal groove descends from near hypoconid, to near posterolingual margin of crown.

P_3 relatively small, subtriangular in basal outline. Longitudinal crest secant, usually transected mesially by set of vertical labial and lingual ridges with the production of cuspule at crest; mesially, cuspule occasionally not developed; crest somewhat concave labially, variably ascending posteriorly. Small subsidiary cuspid developed posterolingually, close to crest, sometimes below and sometimes at same level as posterior cuspid of crest; separated from crest by anterior and posterior grooves, usually linked by short ridge. Base of crown slightly swollen.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline, somewhat constricted across talonid basin, particularly in posterior molars. Lophids very high, somewhat rotated in unworn teeth, with protolophid narrower than metalophid in M_1 and M_2 and slightly broader in M_3 and M_4 . Trigonid basin relatively broad but somewhat variable, its length almost equalling distance between lophids. Forelink high, strong, descending anterolingually from protoconid to point somewhat labiad of mid-point of moderately high anterior cingulum near mid-point. Forelink occasionally ornamented labially by low accessory fold. Labiad moiety of trigonid basin often with development of anterolabial fossette; trigonid descends variably on each side of forelink. Protolophid crest often distorted mesially in unworn teeth, while hy-

polophid crest often subdivided mesially by short vertical grooves. Midlink high, strong, descending anterolingually then anteriorly from hypoconid to unite above talonid basin with short ridge from near mid-point of protolophid; lingual moiety of talonid basin U-shaped, labial moiety V-shaped; low accessory link variably present in lingual moiety of talonid basin in M_1 . Posterior surface of hypolophid with shallow diagonal groove from near hypoconid to near posterolingual margin of crown. Posterior fossette normally absent.

DISCUSSION: *Macropus (Osphranter) pan*, described by De Vis (1895), was one of the few species for which he designated a holotype. This specimen, a juvenile maxilla, F2925, redescribed and figured by Bartholomai (1966), unfortunately lacks locality information other than Darling Downs. Preservation suggests it came from the Chinchilla Sand of late Pliocene age. The species appears to be restricted to that Formation. The material referred by De Vis (1895) to *M. pan* now appears to have also included *M. ferragus* Owen. Specimens referable to both species were figured by De Vis (1895, pl. 18, figs. 7–10). Of these, the subject of fig. 8, is the P^3 of F3720, here referred to *M. ferragus*.

M. pan and *M. ferragus* are morphologically similar, particularly in the permanent upper and lower premolars. P^3 in *M. ferragus* is a relatively more elongate tooth with a stronger lingual cingulum, while P_3 in *M. ferragus* is more definitely trifold, with the posterior lobe offset from the general line of the longitudinal crest. No well-defined internal cuspid is developed. Upper molars in *M. ferragus* lack well-defined forelinks but possess vestigial accessory links in anterior molars, a structure well-developed in *M. pan*. In lower molars, the main distinction occurs on the posterior surface of the hypolophid. *M. pan* normally has an oblique groove, while *M. ferragus* has a near vertical groove, flanked by accessory ridges. A posterior fossette is rarely present in both species but tends to be present more frequently in *M. ferragus*. Differences in relative proportions of cheek teeth between *M. pan* and *M. ferragus* are presented in Fig. 2.

Material exists in the Chinchilla Sand which is somewhat similar to *M. pan* but which possesses a widely flaring posterior fossette at the base of the posterior groove in the molars. These specimens, F5445 and F5449, could represent extreme variation in *M. pan*.

Although cranial remains have not been located together, the present association is considered correct. Occlusion is satisfactory and the basically similar morphology in the referred upper and lower

TABLE 10: SUMMARY OF MEASUREMENTS IN *Macropus (Osphranter) pan* DE VIS

Character	Maxillae					Mandibles				
	n	O.R.	\bar{X}	s	V	n	O.R.	\bar{X}	s	V
DP ₃ length	1	—	10.6	—	—	6	10.1–11.5	10.7	0.496	4.63
prot. width	1	—	8.1	—	—	6	5.1– 5.8	5.4	0.340	6.31
P ₃ length	1	—	11.1	—	—	8	6.5–10.1	8.0	1.104	13.80
max. width	1	—	6.9	—	—	8	3.3– 4.6	4.0	0.492	12.31
M ₁ length	4	11.7–13.8	12.8	—	—	20	12.4–14.5	13.5	0.542	4.01
prot. width	2	10.0–10.7	10.4	—	—	18	6.5– 8.1	7.5	0.418	5.58
M ₂ length	13	14.6–16.3	15.6	0.477	3.06	27	15.0–17.2	16.4	0.566	3.45
prot. width	12	11.6–13.6	12.5	0.566	4.53	25	8.1–10.7	9.5	0.591	6.22
M ₃ length	18	16.2–18.8	17.7	0.730	4.13	32	17.9–20.3	19.0	0.587	3.09
prot. width	17	12.5–14.3	13.4	0.488	3.64	30	10.2–12.5	11.3	0.552	4.88
M ₄ length	11	18.2–20.1	19.4	0.347	1.78	27	20.0–23.1	21.6	0.716	3.31
prot. width	9	13.0–14.5	13.9	0.475	3.42	26	10.8–12.7	11.8	0.515	4.36

prot. = protoloph or protolophid.

remains supports this. No post-cranial material has been referred from the Chinchilla Sand collections.

De Vis (1899b) recorded *M. pan* cranial material from Lake Colongulac, Victoria. As indicated previously, this is most likely *M. titan*. From De Vis' descriptions, the skull material is totally unlike that here referred to *M. pan*, and the anterior upper molars lack the characteristic accessory link present across the median valley. Similarly, the lower premolars are bifid, with a posterolingual cuspid, as in *M. titan*.

Of recent species, the wallaroos, *M. antilopinus* and *M. robustus* are morphologically similar to *M. pan*, with the same basic structure present in the cheek teeth and lower jaw. This similarity is less evident than that between *M. ferragus* and *M. altus* and these recent species. A strong lingual cingulum in P₃ is common to all, as are the relatively high, somewhat rotated molar lochs and lochids and grooved hypolophids.

Summaries of mandibular and maxillary measurements for the *M. pan* sample are presented in table 10. They indicate values for the Coefficient of Variation similar to those for other Queensland fossil and living macropodids. Only the size of P₃ shows excessive values for V. As in other species, this is believed to indicate true variation rather than mixing of samples or sexual differences.

M. pan represents the most common species of *Macropus* in the Chinchilla Sand and is the largest grazing macropodine recovered from that formation.

*Macropus (Osphranter) woodsi** sp. nov. (Plate 19, figs. 1–4; Plate 20, figs. 1–4)

MATERIAL: F3920, holotype, partial right mandibular ramus with P₃ erupting, M₁–M₂, M₃ erupting, juvenile, Condamine River end of Middle Gully system, Chinchilla Rifle Range (Rifle Range No. 78, Par. of Chinchilla), from the late Pliocene Chinchilla Sand.

Referred specimens in the collections of the Queensland Museum comprise F5460, partial right mandibular ramus with P₃–M₂, adult, Chinchilla; F40 partial right mandibular ramus with M₃–M₄, Warra; F5459, partial right mandibular ramus with M₄, adult, western Darling Downs; F5452, partial left mandibular ramus with P₃–M₄, adult, western Darling Downs; F5466, partial right mandibular ramus with M₁, P₃ removed by fenestration, upper limits of middle gully system, Chinchilla Rifle Range (Rifle Range No. 78, Par. of Chinchilla); F5453, partial left mandibular ramus with M₃–M₄, adult, western Darling Downs; F5454, partial right mandibular ramus with M₃, M₄ erupting, juvenile, western Darling Downs; F3631, partial right mandibular ramus with M₄, adult, Chinchilla; F5457, partial right mandibular ramus with M₃–M₄, adult, western Darling Downs; F5458, partial left mandibular ramus with M₄, adult, Western Darling Downs; F5451, partial left mandibular ramus with M₃–M₄, adult, western Darling Downs; F5461, partial left mandibular ramus with M₄, adult, Chinchilla; F5463, partial right mandibular ramus with M₄, adult, Chinchilla; F5464, partial right mandibular ramus with M₄ erupting, juvenile, Condamine River, at M.R.363675 Chinchilla 4-mile map; F5446, partial right mandibular ramus with M₂, P₃ removed by fenestration, juvenile, western Darling Downs; F5468, partial right mandibular ramus with all

* Named for Mr. J. T. Woods, in recognition of his contributions to the knowledge of the vertebrate fossils of Queensland.

teeth lost, adult, middle gully system, Chinchilla Rifle Range (Rifle Range No. 78, Par. of Chinchilla): F6090, isolated M_4 , juvenile, western Darling Downs: F6091, isolated M_4 , adult, western Darling Downs.

F5462, partial left maxilla with M^3 - M^4 , adult, Chinchilla: F5465, partial left maxilla with M^2 - M^4 , adult, Chinchilla Rifle Range, at M.R.363677 Chinchilla 4-mile map; F3718, partial right maxilla with M^2 - M^4 , adult, western Darling Downs; F5455, partial left maxilla with M^3 - M^4 , adult, western Darling Downs.

DIAGNOSIS: A small species, with ramus shallow, moderately wide; P_3 relatively elongate, having longitudinal crest transected mesially by broad, vertical set of labial and lingual ridges, and usually curving posterolingually in posterior one-third; crest ascends posteriorly. Lower molars with high, somewhat rotated lophids; links frequently labiad to mid-line, while posterior hypolophid surface marked by relatively strong, oblique groove, linguad to axis of crown. Upper molars with relatively strong links; labial moiety of median valley frequently crossed by low accessory link, this often well-developed even in posterior molars.

DESCRIPTION: Mandible shallow, relatively wide; base of symphysis inclined slightly at about 5° to base of mandible, somewhat deflected posteriorly; symphysis elongate, shallow, rugose, not ankylosed; geniohyal pit shallow, at posterior symphyseal limit; diastema elongate with crest acute; ventral margin of ramus rounded between symphysis and weak digastric process. Mental foramen small, ovate, situated below digastric crest, well anterior to P_3 . Ramus with shallow lateral groove developed from below P_3 to below posterior root M_3 , at some distance below alveolar margin. Digastric process separated from base of angle by very shallow post-digastric sulcus, bounded above from shallow depression opening posteriorly into pterygoid fossa. Post-alveolar shelf short, with angle poorly developed, leading to post-alveolar ridge, ascending posteriorly to disappear on mesial wall of coronoid process, above large mandibular foramen. Masseteric crest raised to slightly below level of occlusion of cheek teeth. Bulk of coronoid process, angle of mandible and condyle not preserved in any specimen.

I_1 and P_2 unknown; DP_3 known only in fractured state.

P_3 relatively elongate, subrescensitic to subovate in basal outline, frequently convex labially and concave lingually. Longitudinal crest trenchant, with anterior cuspid well-defined but with posterior cuspid less well-defined; crest ascends posteriorly, being transected mesially by broad set of vertical labial and lingual ridges, with production of cuspule at crest, giving crest trifid appearance in

lateral view; posterior one-third of crest usually curves posterolingually before descending to crown base, rarely offset and rarely with posterolingual cuspid developed. Base of crown slightly swollen.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline, slightly constricted across talonid basin; lophids high, convex posteriorly, somewhat anteriorly rotated in labial view, with hypolophid broader than protolophid in M_1 and M_2 , approximately equal in M_3 and narrower in M_4 . Trigonid basin relatively broad, its length approximately equalling distance between lophids. Forelink high, curving anterolingually from protoconid across trigonid basin to point labiad to mid-line on high, somewhat overturned anterior cingulum; trigonid slopes labially and lingually from forelink, and posteriorly from cingulum; anterior cingulum more expanded and angular anterolingually; slight ridge descends anteriorly from metaconid; slight anterolabial fossette developed in trigonid. Posterior ridge from metaconid very weak. Midlink high, strong, curving anterolingually from hypoconid to unite with short ridge from point labiad to mid-line, above talonid basin; junction often flexed; talonid basin sharply V-shaped labially, broadly U-shaped in lingual moiety; basin slopes labially and lingually from midlink, often ornamented by broad, low fold from hypolophid into lingual extremity; anterior and posterior ridges from entoconid weak. Posterior of hypolophid with moderate, oblique groove, developed linguad to axis of crown; M_4 often with posterior fossette developed at base of groove. Crown somewhat flexed about labial extremity of talonid, usually with subsidiary vertical groove developed at posterolabial base of protolophid; accessory vertical grooves occasionally present on labial portion of posterior of hypolophid.

TABLE 11: SUMMARY OF MAXILLARY MEASUREMENTS FOR *Macropus (Osphranter) woodsi* SP. NOV.

Character	n	O.R.	\bar{X}	s	V
M^2 length	1	—	14.0	—	—
M^3 length	4	14.1-16.1	15.2	0.787	5.18
prot. width	2	11.7-12.2	12.0	—	—
M^4 length	4	15.7-17.1	16.4	0.622	3.79
prot. width	4	12.1-12.7	12.3	0.264	2.15

prot. = protoloph.

Cranium known only from fragmentary maxillary specimens.

I^{1-3} , P^2 , DP^3 and M^1 unknown.

$M^2 < M^3 < M^4$; molars subrectangular in basal outline, slightly constricted across median valley;

lophs moderately high, anteriorly bowed, somewhat rotated anteriorly in labial view; metaloph slightly broader than protoloph in M^2 , approximately equal in M^3 and narrower in M^4 . Anterior cingulum relatively low, broad, short, nearly horizontal in labial moiety, descending lingually; forelink well-developed, near axis of crown; cingulum usually united to base of protoloph delimiting anterolabial fossette; anterior paracone ridge very slight. Midlink high, strong, curving posterolabially from protocone across median valley to unite with short ridge from near mid-point of metaloph; junction occasionally flexed. Median valley near horizontal transversely, sometimes excavated between midlink and limit of valley, V-shaped labially and lingually; posterior ridge from paracone and anterior ridge from metacone weak, usually uniting across median valley as accessory link, paralleling midlink; this often developed even in M^4 . Strong, flared ridge curves posterolabially from hypocone to posterolabial base of crown, uniting with slight ridge ascending posteriorly from metacone; well-defined posterior fossette developed between these and posterior, broadly grooved surface of metaloph.

DISCUSSION: At present, *Macropus woodsi* is recorded only from the late Pliocene Chinchilla Sand but it is reasonably well represented. Although incompletely known, enough is preserved to justify separation from *M. pan*, the dominant species of *Macropus (Osphranter)* in the Chinchilla Sand, which it resembles in general morphology. *M. woodsi* is the smaller of the two species, in both size of cheek teeth and dimensions of the mandibular ramus.

This size difference is not believed to represent sexual dimorphism in a single species, although it has been shown by Bartholomai (1971) that sexual dimorphism in the dentition of certain larger living macropodids may be significant. No comparable work, similar to that presented in Bartholomai (1971) has been undertaken for wallaroos but examination of sexed samples of *M. robustus* and *M. antilopinus* suggests that sexual dimorphism in the cheek teeth, if present, is not as great as size differences observed between *M. pan* and *M. woodsi*. Further, *M. woodsi* is considerably less well represented than *M. pan*. Should the differences comprise sexual dimorphism, approximately equal numbers of larger and smaller individuals would be expected in the sample because of approximately equal numbers of each sex in living species (Bartholomai, 1971). Size differences in lower molars between *M. woodsi* and *M. pan* are graphically represented in Fig. 3.

TABLE 12: SUMMARY OF MANDIBULAR MEASUREMENTS FOR *Macropus (Osphranter) woodsi* SP. NOV.

Character	n	O.R.	\bar{X}	s	V
P_3 length	5	7.5-9.1	8.1	0.592	7.30
max. width	4	4.1-4.9	4.3	0.387	9.00
M_1 length	5	10.4-12.3	11.4	0.973	8.53
prot. width	5	6.9-7.6	7.2	0.308	4.28
M_2 length	3	13.5-14.9	14.0	0.758	5.42
prot. width	5	8.1-9.1	8.5	0.331	3.89
M_3 length	5	15.2-16.5	16.0	0.570	3.56
prot. width	6	9.0-10.5	9.8	0.500	5.10
M_4 length	14	17.2-18.8	18.1	0.550	3.04
prot. width	14	9.6-10.8	10.0	0.404	4.04

prot. = protolophid.

A summary of mandibular measurements for *M. woodsi* is provided in Table 12. Coefficients of Variation are in keeping with those expected for a sample from a fossil species, taking into account the limited size of the sample examined. A summary of measurements for the small maxillary sample is provided in Table 11.

Mandibular and maxillary remains of *M. woodsi* have not been located together but occlusion and morphological compatibility of upper and lower dentitions indicate the correctness of the present association.

In addition to its smaller size, *M. woodsi* differs from *M. pan* in having a posterior fossette at the base of the oblique posterior hypolophid groove in M_4 , and in normally lacking a posterolingual cuspule in P_3 . The upper molars present in *M. woodsi* have similar accessory links in the lingual moiety of the median valley, but these are frequently well-developed in posterior molars as well as anterior molars. The occasionally offset posterior lobe of P_3 in *M. woodsi* is more like that developed in *M. ferragus* than in *M. pan*, but the posterior hypolophid groove in lower molars differs considerably from that in *M. ferragus*, where this groove is usually near vertical and flanked by lateral ridges.

Macropus (Prionotemnus) agilis siva (De Vis, 1895)
(Plate 21, figs. 1-4; Plate 22, figs. 1-3)

Halmaturus siva De Vis, 1895, pp. 113-4, pl. 17, figs. 21-22.

Halmaturus cooperi (Owen): De Vis, 1895 (*partim*), pp. 116-8.

Macropus siva (De Vis): Simpson, 1930, p. 73.

'*Halmaturus siva* De Vis: Bartholomai, 1966, pp. 118-9, pl. 16, figs. 4-6.

MATERIAL: F2926, holotype, partial right mandibular ramus with P_3 , M_2 - M_4 , adult, Darling Downs, south-eastern Queensland (re-described and figured by Bartholomai, 1966, pl. 16, figs. 4-6).

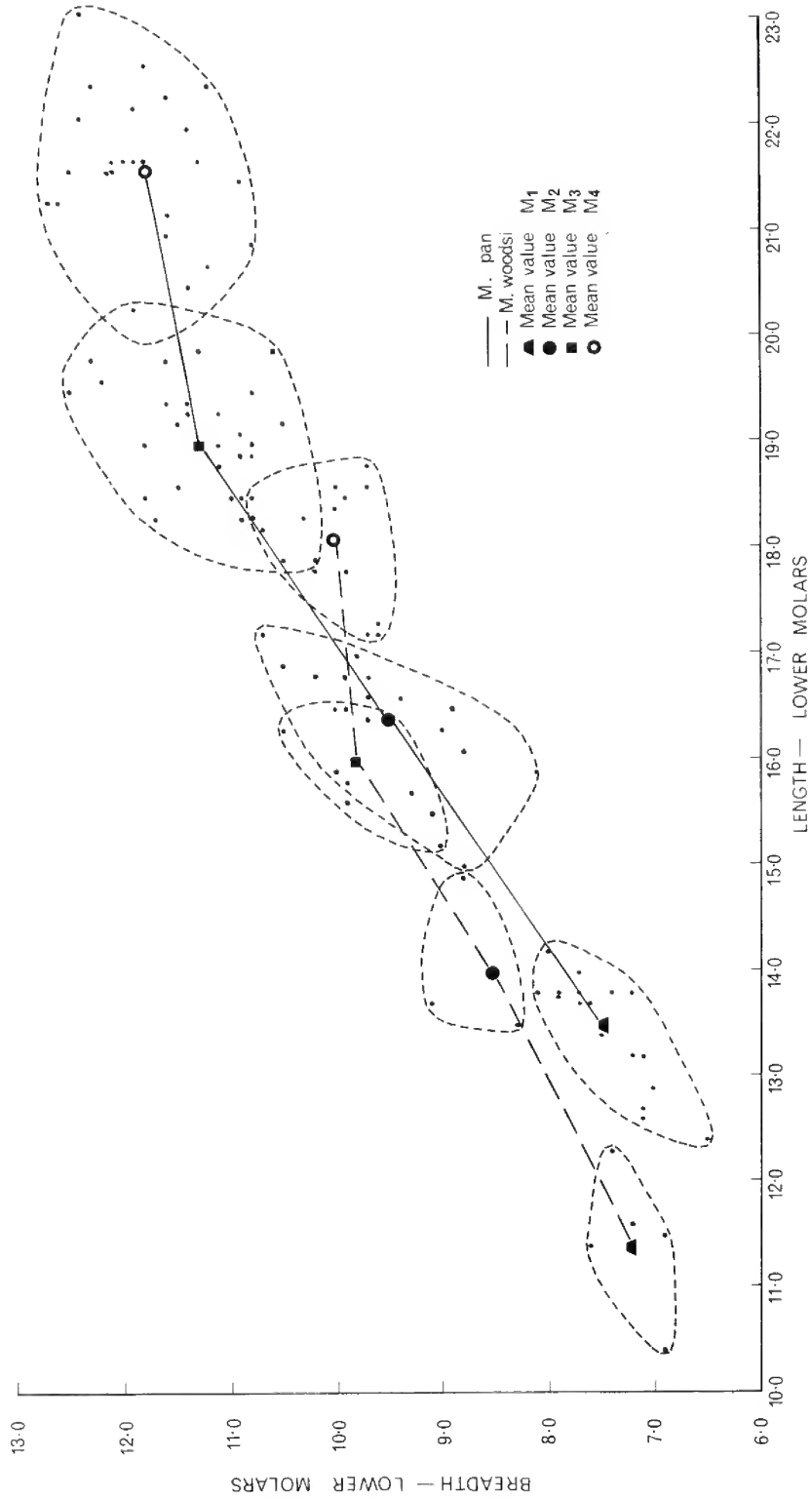


FIG. 3: Scatter diagram comparing lower molar teeth in *Macropus (Ospthrauter) woodsi* with *M. pan*. Lines have been added joining mean values.

In addition, 45 partial juvenile mandibular rami, 41 partial adult mandibular rami, one partial adult cranium, one premaxillary fragment, four juvenile maxillae and three adult maxillae have been referred to this subspecies from the following localities in the Pleistocene fluvialite deposits of the eastern Darling Downs: King Creek, near M.R.047452 Clifton 1-mile sheet; King Creek, Pilton; Ravensthorpe, Pilton; King Creek, near M.R.039454 Clifton 1-mile sheet; King Creek; ?Ravensthorpe, Pilton; King Creek, at bridge on Pratten road, at M.R.863331 Clifton 1-mile sheet; ?Pilton; Clifton; Freestone Creek; ?Freestone Creek; gravel below Freestone State School, Freestone Creek; Gowrie Creek; Gowrie; ?Gowrie; Jimbour Creek, near Dalby; Jimboomba; Spring Creek, Clifton; eastern Darling Downs, and from unspecified localities within the Darling Downs, but with specimens possessing preservation in keeping with derivation from eastern Darling Downs deposits.

One maxillary fragment is referred to *M. agilis siva* from 67 feet in a creek bed at Monto, southeastern Queensland.

DIAGNOSIS: Relatively large compared with living *Macropus agilis*. Ramus with elongate diastema, and with P_3 approximately as long as M_1 ; P_2 relatively elongate; lower molars with high lophids and moderately high links; posterior cingulum not developed.

Upper premolars elongate; upper molars with high lophids, slight forelink and moderately high midlink; ridge from paracone to labial extremity of anterior cingulum strong. Incisive foramina originate mid-way between I^3 and premaxilla-maxilla suture; posterior palatine vacuities originate opposite M^3 - M^4 at eruption of M^4 .

DESCRIPTION: Mandible moderately strong, being relatively wide but shallow, with longitudinal axis markedly concave laterally. Symphysis elongate, not ankylosed, set at low angle to base of mandible; geniohyal pit insignificant. Diastema long; ventral margin of ramus sharply rounded posterior to symphysis, becoming more broadly rounded posteriorly; mental foramen moderately large, ovate, situated close to diastemal crest, approximately mid-way between anterior root P_3 and limit of ramus; mandible usually with shallow labial groove present close to alveolar margin from above mental foramen to below anterior of M_3 . Digastric process extremely weak, separated from base of angle by slight post-digastric sulcus; shallow, broad depression present opening posteriorly into pterygoid fossa; post-alveolar shelf short, leading to post-alveolar ridge which disappears on mesial wall of moderately high coronoid process above large mandibular foramen; leading edge of process inclined at about 15° to vertical; condyle subtriangular, being moderately broad and long, slightly concave laterally. Tip of coronoid process and angle of mandible not preserved.

I_1 elongate, deeply rooted, slightly curved in lateral and occlusal views; wear facet with upper incisors sub-horizontal; mesial facet of wear present at tip by approximation with other lower incisor. Root compressed oval in section; crown subquadrantal in section, tapering and blade-like distally, enamelled laterally, this produced dorso-labially and ventrolingually into flanges.

P_2 relatively elongate, subcrescentic to subtriangular in basal outline. Longitudinal crest secant, curving lingually in its posterior extension and usually curving anterolingually but occasionally descending anteriorly from anterior cuspid. Crest transected by a major set of vertical, labial and lingual ridges at its anterior one-third and by a minor set of ridges at its posterior one-third, with production of cuspules at crest; anterior cuspule better defined. An accessory posterolingual cuspule occasionally present.

DP_3 molariform, subtriangular in basal outline; lophids high with hypolophid crest much broader than protolophid; both lophids markedly convex posteriorly in unworn teeth. Trigonid basin narrow, being particularly poorly developed labially, elongate, its length almost equalling distance between lophids. Forelink moderately high, strong, descending and slightly curving anterolingually then anteriorly or even anterolabially, from protoconid to point on moderately high anterior cingulum, well labiad to axis of crown. Variable accessory fold of enamel present in lingual portion of trigonid, usually close to and paralleling forelink; slight fossette formed in reduced labial moiety of trigonid. Moderately strong, short ridge descends posteriorly from protoconid to unite with moderately high midlink descending anterolingually from hypoconid. Talonid basin V-shaped in both labial and lingual moieties; labial portion much reduced. Anterior ridge from entoconid weak. Posterior of hypolophid rounded, unornamented.

P_3 elongate, its length approximately equalling that in M_1 , subtriangular in basal outline. Longitudinal crest secant, curving lingually moderately abruptly in its posterior extension; crest transected by two or three sets of vertical labial and lingual ridges, these decreasing in strength posteriorly; cuspules produced at crest and these also decrease in strength posteriorly; ridge from anterior cuspid of crest descends anteriorly or slightly anterolingually. Labial and anterior base of crown slightly swollen above roots, but only slightly swollen lingually.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline, slightly constricted across talonid

basin; lophids high, moderately convex posteriorly; hypolophid broader than protolophid in M_1 , usually broader in M_2 and M_3 but occasionally equal or slightly narrower, and frequently narrower in M_4 . Lateral surfaces of lophids nearly parallel, with labial surfaces only very slightly convex and diverging basally. Trigonid basin moderately broad, length almost equalling distance between lophids. Forelink moderately high, strong, descending anterolingually from protoconid then anteriorly across trigonid to near mid-point of moderately high anterior cingulum. Labial moiety of trigonid basin forming relatively deep anterolabial fossette. Slight, variable accessory ridge occasionally present close to and paralleling forelink in lingual moiety of trigonid in anterior molars. Strong, moderately high midlink descends anterolingually from hypoconid, curving anterolabially to unite with slight ridge from point labiad to axis of crown; midlink often puckered near junction. Lingual portion of talonid basin broadly U-shaped, labial portion V-shaped: slight, variable, accessory ridge occasionally present, close to midlink across lingual portion of talonid basin; a slight ridge descends anteriorly from entoconid towards talonid basin. Posterior of hypolophid broadly rounded, occasionally with weak median groove or variable slight ridges.

Cranium of moderate size, elongate. Nasals elongate, subparallel. Maxilla dorsally in moderate contact with frontals; infraorbital foramen opens above anterior root M^1 in specimens with M^4 just erupted. Inferior process of anterior zygoma root moderately developed; post-palatal vacuities large, originating opposite metaloph M^3 ; palatine extending along lateral margin of vacuity to opposite anterior root M^3 . Premaxilla with high to moderately high superior expansions at anterodorsal extremity of mutual suture; anterior palatine foramen originating posteromesial to posterior of I^3 , mid-way between this position and premaxillamaxilla suture. Diastema long. Jugals laterally excavated for insertion of superficial layer of masseter muscle. Lacrymal with lacrymal foramen opening large, at margin of orbit. Remainder of cranium not preserved or too incomplete to be described.

Upper incisors converging anteriorly to form V-

shaped series of teeth; I^1 large, axially curved, directed anteroventrally and somewhat mesially, approximated at tips; labial surface curved but lingual surface near planar; facet of wear ascending to I^2 . Second upper incisor with short, expanded crown, subrectangular in occlusal view; labial surface with minor groove at posterior one-third. I^3 elongate, spatulate, with well-defined mesial groove. Upper incisors unknown in unworn state. P^2 and DP^3 unknown.

P^3 elongate, subovate in basal outline, broader posteriorly. Longitudinal crest moderately high, slightly concave labially, transected by two sets of vertical labial and lingual ridges, with the anterior set being better developed; cuspules are produced at crest. Continuations of crest ascend anteriorly from paracone and posteriorly from metacone to unite with ridge curving posterolabially from relatively low hypocone; labial ridge ascending from hypocone unites with lingual ridge from metacone, confining extensive posterolingual fossette; anterior ridge from hypocone ascends to produce sinuous but generally anteriorly convergent lingual cingulum. Cingulum terminates ventrolingual to paracone; low cuspules present along cingulum. Lingual basin broader posteriorly, crossed by continuations of vertical ridges transecting longitudinal crest. Labial base of crown slightly tumid.

$M^1 < M^2 < M^3 < M^4$; molars subrectangular in basal outline, slightly constricted across median valley; lophids relatively high, moderately convex anteriorly, with metaloph broader than protoloph in M^1 , approximately equal in M^2 , and generally somewhat narrower in M^3 and M^4 . Anterior cingulum moderately low, short, relatively broad, descending labially and there united with paracone by well-defined ridge; this ridge generally becomes progressively weaker in posterior molars. Forelink short, variable and occasionally absent, but usually weakly developed from base of protoloph to anterior cingulum above axis of crown. Paracone with slight, variable posterior ridge ascending into median valley. Midlink moderately high, strong, ascending posterolabially from protocone to unite with short ridge from near centre of metaloph; midlink often puckered near junction. Slight ridge from metacone ascends anteriorly into median

TABLE 13: MEASUREMENTS FOR *Macropus (Prionotemnus) agilis siva* (DE VIS)

Specimen	P_3	M_1	M_2	M_3	M_4
F2926*	7.2 × 2.8	—	9.2 × 5.6	10.3 × 6.1	10.9 × 6.3

*Holotype

valley: valley V-shaped in labial and lingual moieties; slight, variable accessory ridge occasionally present close to midlink, in labial part of median valley in anterior molars. Strong posterolabial ridge ascends from hypocone, uniting with weaker ridge ascending posteriorly from metacone at posterolabial base of crown, with production of a posterior fossette; posterolabial ridge from hypocone plicated at fossette.

DISCUSSION: *Macropus (Prionotemnus) agilis* (Gould, 1841) is widespread throughout tropical northern Australia and is also represented in New Guinea. Three geographical subspecies have been recognized within Australia, these being *M. agilis agilis* (Gould) from the northern portion of the Northern Territory, *M. agilis nigrescens*, Lönnberg from the Kimberley area of Western Australia, and *M. agilis jardinei* (De Vis) from the northern and eastern parts of Queensland to about as far south as the Fitzroy River. This subspecies has also been recorded, however, from Stradbroke Island, Moreton Bay, southeastern Queensland, by Longman (1922). Recent work in Moreton Bay suggests that *M. agilis* may be more widespread in that area and may be present on Peel Island as well as on Stradbroke. A single subspecies, *M. agilis papuanus* (Peters and Doria), has been defined in New Guinea.

Distinctions between the recent subspecies have been summarized generally by Schwartz (1910), but are mainly restricted to variations in pelage colouration. He concluded that no cranial characters could be found to enable separation of the various subspecies. Lönnberg (1913), however, compared the crania of *M. agilis nigrescens* and *M. agilis aurescens* (Schwartz), this latter form having been placed subsequently in synonymy with *M. agilis agilis* by Tate (1948). Lönnberg's distinguishing characters relate largely to shape of the maxilla and amount of constriction of the cranium between the orbits and at the anterior of the palate. These areas are not normally preserved in fossils encountered in the Darling Downs deposits and are only poorly illustrated in a single specimen in the material here referred to *M. agilis siva* (De Vis).

Most of the fossil specimens referred to the successional subspecies, *M. agilis siva*, were included by De Vis (1895) within either *Halmaturus siva* De Vis or *Macropus cooperi* (Owen). The holotype of *M. agilis siva*, F2926, measurements for which are presented in Table 13, has been redescribed and refigured in Bartholomai (1966) as '*Halmaturus*' *siva*. De Vis (1895) considered that *H. siva* may be distinguished from *M. cooperi* mainly on the structure of the permanent lower premolars

and anterior lower molars. The longitudinal crest in P_3 in the holotype of *M. cooperi* is markedly tricuspidate, this feature being imitated in gross form, but not duplicated, in only a small proportion of the specimens here referred to *M. agilis siva*. Close examination reveals the presence of two major cusps and two or three cuspules along the longitudinal crest in *M. agilis siva*, but evidence of the presence of the cuspules is reduced by occlusion, producing the apparently unilobate P_3 of the holotype.

The other feature considered diagnostic by De Vis (1895) for *H. siva*, was the presence of an accessory ridge in the lingual moiety of the trigonid basin in anterior molars. This was absent in specimens he referred to *M. cooperi*. Presence of this structure was checked in a large sample of *M. agilis jardinei* from the Townsville area, indicating that this feature is present in a small proportion of specimens. It is suggested that presence or absence of this accessory ridge cannot be regarded as of even subspecific value in the fossil population. Extremely poor preservation of the molars in the holotype of *M. cooperi* prohibits close comparison. It is apparent that in *M. cooperi* all molars display the somewhat offset hypolophid typical of the wallaroo rather than kangaroo group. Size differences are not significant between De Vis' (1895) samples and there has been no hesitation in uniting most of his original material.

Table 14 provides a summary of mandibular and maxillary measurements for specimens of *M. agilis siva*. The Coefficients of Variation generally indicate a slightly more variable condition than in *M. agilis jardinei* investigated by Bartholomai (1971). This is the only living subspecies of *M. agilis* for which sufficient material was available for statistical consideration. Values of V exhibited in *M. agilis siva* are consistent with a single fossil population, as suggested by Simpson *et al.* (1960) for a sample drawn from slightly different stratigraphic levels. Where values for V are particularly low, the probability of inadequate sampling is indicated.

Specimens of *M. agilis siva* are very similar to those of *M. agilis jardinei*, but differ in the position of the anterior palatine foramen, the diastemal length, in the comparatively greater lengths of P_2 , DP_3 , M^1 , M^3 and M^4 , and the relatively shorter length of P_3 . The anterior palatine foramen is positioned posteromesiad to I^3 and about mid-way between I^3 and the maxilla-premaxilla suture in *M. agilis siva*, but is approximately level with the posterior of I^3 in *M. agilis jardinei*. This feature is present in only two specimens in the referred sample of *M. agilis siva*. Examination of cranial

TABLE 14: SUMMARY OF MAXILLARY AND MANDIBULAR MEASUREMENTS FOR *Macropus (Prionotemmus) agilis siva* (DE VIS)

Character	Maxilla					Mandible				
	n	O.R.	\bar{X}	s	V	n	O.R.	\bar{X}	s	V
P ₂ length	—	—	—	—	—	6	7.0-7.7	7.4	0.307	4.14
max. width	—	—	—	—	—	6	3.1-3.5	3.3	0.141	4.28
DP ₃ length	—	—	—	—	—	9	7.2-8.5	8.0	0.447	5.59
prot. width	—	—	—	—	—	8	4.0-4.6	4.3	0.200	4.65
P ₃ length	1	—	10.2	—	—	28	6.9-9.5	8.2	0.644	7.86
max. width	2	4.9-5.0	5.0	—	—	25	2.7-3.8	3.1	0.256	8.25
M ₁ length	6	8.7-9.1	8.9	0.173	1.95	35	6.9-9.3	8.2	0.745	9.09
prot. width	4	6.6-7.1	6.9	0.216	3.13	32	4.6-5.8	5.3	0.295	5.57
M ₂ length	8	9.6-11.1	10.3	0.534	5.19	49	8.4-10.7	9.7	0.620	6.39
prot. width	6	7.5-8.2	7.9	0.310	3.92	37	5.6-6.8	6.1	0.334	5.47
M ₃ length	7	10.9-11.8	11.4	0.355	3.11	55	9.5-12.0	10.9	0.640	5.87
prot. width	7	8.0-9.0	8.5	0.430	5.06	50	5.9-7.8	6.7	0.415	6.20
M ₄ length	4	11.4-12.4	12.0	0.424	3.54	38	10.9-13.3	11.9	0.509	4.28
prot. width	4	8.1-8.4	8.3	0.365	4.40	46	6.2-8.0	6.8	0.457	6.73

prot. = protoloph or protolophid.

remains of *M. agilis* in the collections of the Australian Museum, Sydney, suggests that the position of the incisive foramen varies between living subspecies. As suggested by De Vis (1895), the mandibular diastema appears to be slightly longer in *M. agilis siva* at equivalent stages in dental eruption, but this feature was not evaluated statistically.

Table 15 presents a comparison of the samples of *M. agilis siva* and *M. agilis jardinei* by Student's *t* test. This indicates significance at or approaching the 0.1% level in all dimensions except the length and breadth of P₃. The Coefficient of Difference has been calculated for these comparisons for statistical evaluation of subspecies, as outlined by Mayr *et al.* (1953). Ride (1964) has indicated that

values for C.D. should be 1.5 or larger to establish subspecies and this proviso is met only in the lengths of P₂, DP₃, M¹, M² and M⁴, all of which, however, are represented by small samples. Of these, it is likely that C.D. values for molars are incongruous, as similar results would be expected for lower molars if genuine differences are present.

The log difference diagram, Fig. 4, shows comparison of upper and lower dentitions of *M. agilis siva* and *M. agilis jardinei* based on mean values for the latter sub-species as a standard. This indicates general concordance of dental proportions of the fossil and living subspecies. Simpson (1941) states that such diagrams do not determine affinities directly, but that similarity of proportions is an important factor in determining

TABLE 15: COMPARISON OF SAMPLES OF *M. agilis siva* (DE VIS) AND *M. agilis jardinei* (DE VIS)

Characters	Maxilla			Mandible		
	t	P	C.D.	t	P	C.D.
P ₂ length	—	—	—	11.56	0.001	2.04
max. width	—	—	—	4.29	0.001	1.11
DP ₃ length	—	—	—	9.67	0.001	1.73
prot. width	—	—	—	5.08	0.001	0.95
P ₃ length	—	—	—	0.11	0.5	—
max. width	—	—	—	—	—	—
M ₁ length	8.30	0.001	2.41	7.89	0.001	0.74
prot. width	4.36	0.001	1.25	7.49	0.001	0.71
M ₂ length	4.57	0.001	1.36	9.71	0.001	0.80
prot. width	14.24	0.001	1.09	5.85	0.001	0.50
M ₃ length	8.12	0.001	1.66	10.36	0.001	0.80
prot. width	4.13	0.001	0.75	4.91	0.001	0.39
M ₄ length	5.90	0.001	1.54	10.80	0.001	1.07
prot. width	9.70	0.001	0.26	2.84	0.01-0.001	0.25

prot. = protoloph or protolophid.

relationships. The suggestion of close affinity between *M. agilis siva* and living forms of *M. agilis* is supplemented by overall cranial morphological similarity with *M. agilis jardinei*.

Mandibular remains of *M. agilis siva* have never been found associated with cranial specimens. Occlusion is good and morphological and proportional similarities of both upper and lower

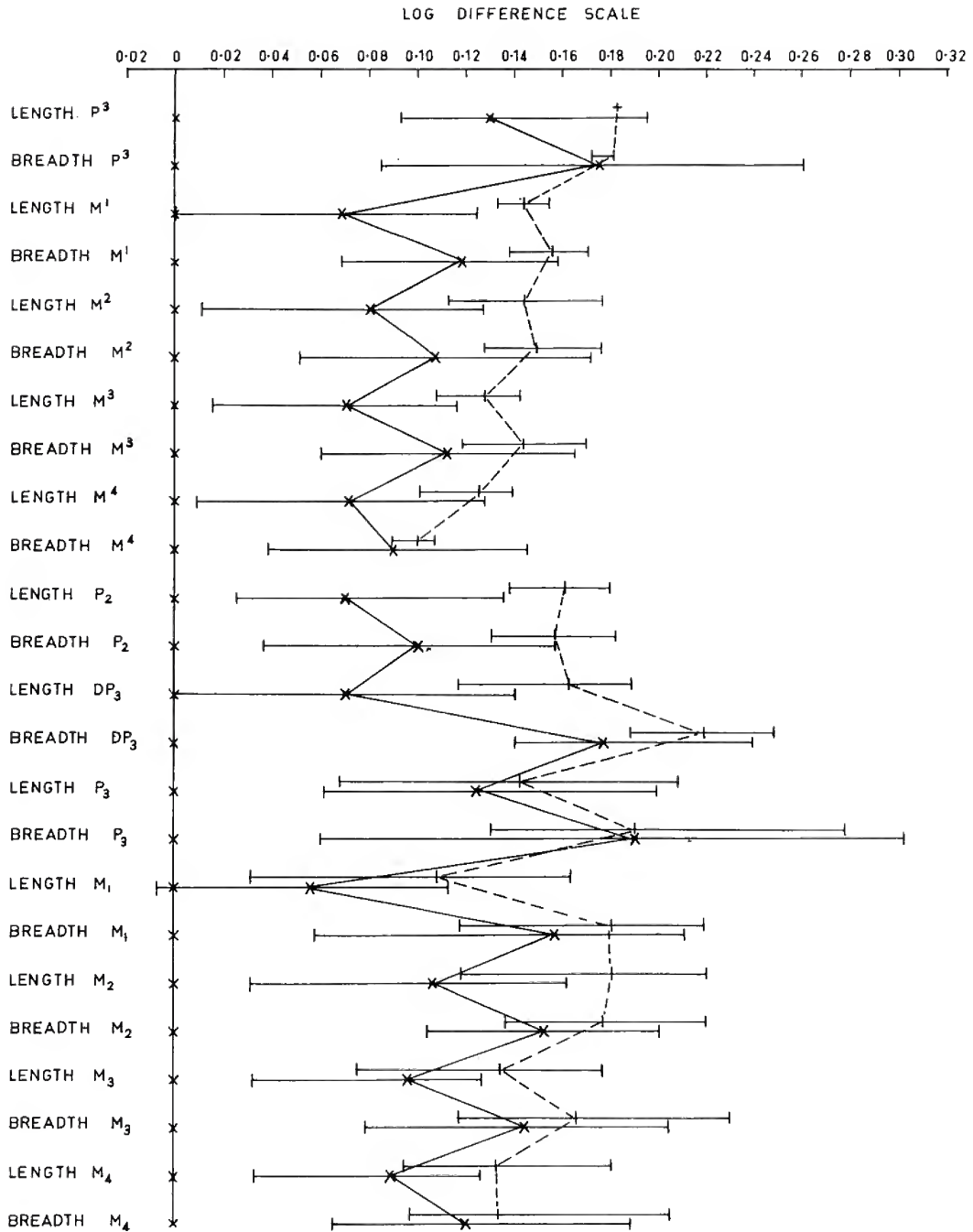


FIG. 4: Log Difference Diagram illustrating proportional relationships of *Macropus (Prionotemmus) agilis siva* (broken line) and *M. agilis jardinei* (solid line) using J4325, *M. dorsalis* as standard. Observed ranges have been included.

dentitions compared with those in *M. agilis jardinei*, indicate their correct association. Maxillary specimens are poorly represented in collections compared with mandibular remains, probably because of the more robust nature of the latter. Post-cranial remains are unknown.

As in the living subspecies, the permanent premolar is erupted before the last molar in both upper and lower dentitions and is reasonably worn by the time the last molar fully erupts.

Progression of the tooth row is moderate, although permanent premolars are retained throughout the life of all individuals encountered.

Material in the Queensland Museum collections indicates the presence of a form either identical with or close to *M. agilis siva* in the late Pliocene Chinchilla Sand. This comprises three mandibular specimens, F3598, F4733 and F4735 and a partial maxilla, F4734. Compared with the sample from the Pleistocene fluviatile deposits, this material is of similar size and, in general, is morphologically identical in the characters preserved. The single juvenile dentition, F3598, differs slightly in having the protolophid of DP₃ reduced to a greater degree than usual, with the lophid crest nearly rectilinear and with the labial portion of the trigonid basin very reduced. A slight ridge flanks the lingual margin of the trigonid, from the metaconid to the anterior cingulum. The posterior ridge from the protoconid is moderately strong. P³ is more trenchant, being less posterolingually curved than is usual in the Pleistocene sample. The midlink in the molars of this specimen is more direct than normal. It is believed, however, that the variation at present known in the Chinchilla Sand sample could well fall within the limits expected in *M. agilis siva*. On this basis, separation of the Chinchilla sample is not justifiable.

***Macropus* (?*Prionotemnus*) *gouldi* (Owen, 1874)**

Osphranter gouldi Owen, 1874, p. 261, pl. 23, figs. 15–6.

Macropus (Osphranter) gouldi Owen, 1877, p. 413, pl. 83, figs. 15–16; Simpson, 1930, p. 72.

Macropus parryi Bennett, 1834; Lydekker, 1887, pp. 220–1.

DISCUSSION: The holotype of the present species was described in very brief form by Owen (1874) and has since been apparently lost. The type locality was not indicated. From the evidence presented in the figures of this specimen (Owen, 1874, pl. 23, figs. 15–16), it is apparent that the specimen is not a juvenile, as suggested by Owen, but presents a fully erupted and ageing cheek tooth row. Lydekker (1887) previously expressed this view, and relegated the species to synonymy with

Macropus (Prionotemnus) parryi, the living Whip-tail Wallaby.

The structure of M₄, the only tooth well preserved in the holotype, is distinct and unlike any other specimens in the collections of the Queensland Museum. Lydekker (1887) suggested that British Museum (Natural History) specimen 43345a, a partial right mandibular ramus, presented by Dr. George Bennett and thus presumably from the fluviatile deposits of the Darling Downs, is indistinguishable from the holotype. M₄ in the holotype presents a much narrower hypolophid than protolophid, indicating its correct assignment in the cheek teeth series.

This tooth is broader across the trigonid basin than is normal in *M. parryi*, and has lower lophids. Its midlink is more direct and appears lower. The shape of the mandibular ramus, particularly the orientation of the symphysis, is in keeping with *Macropus* rather than *Wallabia*, but, on the basis of the morphological differences noted above, Lydekker's (1887) action cannot be supported. Its reference to *Prionotemnus* must remain questionable until more adequate material becomes available.

Thus the species is maintained as a distinct element of the Upper Cainozoic macropodid fauna, but it represents one of the least known taxa.

***Macropus* (?*Prionotemnus*) *piltonensis* sp. nov.** (Plate 23, figs. 3–4)

MATERIAL: F4576, a partial right mandibular ramus with I₁, P₂–DP₃, M₁ broken, P₃ unenamelled and not removed, juvenile, Ravensthorpe, Pilton, eastern Darling Downs, from Pleistocene Fluviatile deposits.

DIAGNOSIS: I₁ with lower margin, straight, and generally broadly rounded in section, but with labial and lingual surfaces meeting in slight ridge; upper enamelled flange broadly rounded to tip, giving rise to moderately blunted tip. P₂ with crest markedly curved lingually in its posterior extension, with slight separation of posteromesial cuspid. DP₃ with well-defined but slight posterior cingulum.

DESCRIPTION: P₃, M₂–M₄ and upper dentition unknown.

I₁ moderately large, deep, ascending at low angle, approximated ventrally at incurved tips, with crown subquadrangular in section becoming slightly less so anteriorly; crown flanged dorso-laterally, but generally broadly rounded ventro-mesially with lateral and mesial enamelled surfaces meeting in slight ridge; dorsolateral flange broadly

curving anteriorly to tip, producing rather blunt, round tip.

P_2 relatively short, robust, subtriangular in basal outline. Longitudinal crest secant, abruptly curving mesially in its posterior extension; crest subdivided into thirds by strong anterior set of vertical labial and lingual ridges and weak posterior set, with production of cuspules along crest; posterior extension of crest marked posteriorly by prominent vertical groove, giving slight separation of postero-mesial cuspid.

DP_3 molariform, subtriangular in basal outline, slightly constricted across talonid basin, with hypolophid much broader than protolophid; crests markedly convex posteriorly. Trigonid basin narrow, moderately well-developed labially, elongate, length being slightly less than distance between lophids. Forelink moderately high, slightly curving anterolingually then anteriorly from protoconid to near mid-point of high anterior cingulum; peaked dorsally at junction; lingual moiety of trigonid basin near planar, labial moiety markedly descending, leading to anterolabial fossette. Slight ridge descends anteriorly from metaconid towards trigonid. Midlink moderately high, curving anterolingually then anteriorly from hypoconid across talonid basin to unite with short ridge from protoconid; slight accessory ridge present across lingual portion of talonid, near lingual limit; moderate ridge descends from entoconid towards talonid. Talonid basin V-shaped. Base of hypolophid with moderately narrow, short, well-defined posterior cingulum.

M_1 known only from anterior moiety; protolophid, trigonid basin and anterior cingulum moderately broad. Protolophid crest only slightly convex posteriorly.

DISCUSSION: The present material represents a form quite distinct from other species described from Pleistocene deposits of the Darling Downs or elsewhere in Australia. Unfortunately, it is represented by only a single mandible.

In the structure of its deciduous dentition it is very similar to *M. agilis siva*. It differs in having the posterior extension of the longitudinal crest of P_2 more sharply inturned. It possesses a well-defined posterior cingulum on DP_3 and in this feature, it differs from material referable without question to *Prionotemnus*. It is not inconceivable that with extreme variation, at least the structure in P_2 could be duplicated in specimens of *M. agilis siva*. However, it is in the structure of I_1 that *M. piltonensis* is chiefly distinguished. If this tooth was taken alone, except for the presence of a slight ventromesial ridge, its generic position would be

difficult to reconcile. The blunt tip is particularly interesting, not being duplicated in any other species of *Macropus*.

TABLE 16: MEASUREMENTS OF *Macropus* (?*Prionotemnus*) *piltonensis* SP. NOV.

Specimen	P_2	DP_3	P_3	M_1
F4576*	7.1 × 3.5	9.3 × 4.6	—	— × 5.6

*Holotype.

Additional material, both mandibular and maxillary, will need to be located before possible relationships of this species with other fossil and living macropodids can be determined.

***Macropus* (*Prionotemnus*) *thor* (De Vis, 1895)**
(Plate 23, figs. 1–2; Plate 24, figs. 1–2)

Halmaturus thor De Vis, 1895, pp. 102–4, pl. 17, fig. 2.

Macropus thor (De Vis): Simpson, 1930, p. 73.

'*Halmaturus*' *thor* De Vis: Bartholomai, 1966, pp. 119–20, pl. 17, figs. 1–3.

MATERIAL: F3602, lectotype, partial right mandibular ramus with M_1 – M_3 , P_3 exposed from above, M_3 erupting, juvenile, Ravensthorpe, Pilton, Darling Downs, SE.Q., (fig in part, De Vis, 1895, pl. 17, fig. 2; figd Bartholomai, 1966, pl. 17, figs. 1–3).

In addition, one juvenile and 9 adult mandibular rami, together with a partial adult cranium have been referred to *M. thor* from the following localities in the Pleistocene fluviatile deposits of the eastern Darling Downs: Gowrie; Clifton; Ravensthorpe, Pilton; Freestone Creek; and from unspecified localities within the Darling Downs, but with specimens possessing preservation in keeping with the eastern Darling Downs deposits.

DIAGNOSIS: P_3 with longitudinal crest divided by prominent vertical grooves at its anterior third, and with posterior moiety transected by set of weak, vertical ridges with production of cuspule at crest; posterior extension of crest slightly curved mesially. Molars with moderately high links, and with posterior of hypolophid usually marked with near-mesial vertical groove and swollen base; base occasionally partially produced into weak posterior cingulum.

DESCRIPTION: Mandible strong, moderately wide and deep. Symphysis elongate, shallow, with moderately deep geniohyal pit. Diastema elongate, with diastemal crest broadly acute; mental foramen moderately large, oval, near diastemal crest. Ventral margin of ramus angular posterior to symphysis, but often acutely or even broadly rounded; base usually well-rounded posteriorly. Well-defined groove present labially, well below alveolar shelf, from between P_3 and mental foramen to

below anterior of M_2 ; digastric process slight; lingually, broad, shallow depression opens posteriorly into pterygoid fossa. Post-alveolar shelf moderately long, ascending as slight ridge onto mesial surface of coronoid process, above large mandibular foramen. Masseteric crest raised to below level of bases of molars. Anterior margin of coronoid process inclined at approximately 80° to base of mandible. Bulk of coronoid process, condyle and angle of mandible not preserved.

I_1 , P_2 and DP_3 unknown.

P_3 relatively short, subovate in basal outline. Longitudinal crest divided by prominent vertical grooves at its anterior third; posterior portion transected by a slight set of vertical labial and lingual ridges, with production of cusplule at crest. Posteriorly, extension of crest curves slightly lingually. Base of crown slightly swollen.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular, slightly constricted across talonid basin; lophids moderately high, somewhat convex posteriorly; hypolophid slightly broader than protolophid in M_1 , occasionally so in M_2 , but protolophid usually broader in M_3 and M_4 . Trigonid basin moderately broad, but somewhat variable, length almost equalling distance between lophids. Forelink high, strong, descending from protoconid curving anterolingually, then anteriorly to near mid-point of anterior cingulum; cingulum moderately high. Well-defined anterolabial fossette present in labial moiety of trigonid basin; extremely slight ridges descend anteriorly and posteriorly from metaconid towards trigonid and talonid basins, respectively. Mid-link from hypoconid moderately high, curving anterolingually then anteriorly to near mid-point of protolophid. Talonid basin V-shaped with minor, variable, accessory ridges occasionally across lingual moiety in some molars, close to midlink. Very slight anterolabial ridge descends from entoconid towards talonid. Posterior surface of hypolophid curved, usually with shallow, variable, near median, vertical groove near base; base of crown swollen but variable in this feature, occasionally partially produced into weak, posterior cingulum.

Anterior of cranium unknown; cranium large, about 100.0 mm posterior to line between anterior of orbits; inferior process of zygoma root moderately strong; palate posteriorly with large vacuities; palatines apparently moderately developed behind vacuities; jugals laterally excavated for insertion of superficial layer of masseter; zygomatic arches laterally expanded, slightly converging anteriorly; roof of braincase gently arched with weak temporal ridges nearly confluent posteriorly; squamosal and extension of jugal with broad, elongate,

slightly convex condyle; postglenoid process of squamosal moderate; ectotympanic deep, complete dorsally; alisphenoid not inflated with foramen ovale bounded anterolaterally by weak groove.

I^{1-3} , P^2 , DP^3 , P^3 and M^1 not represented.

$M^2 < M^3 < M^4$; molars subrectangular in basal outline, slightly constricted across median valley, with protoloph approximately as broad as metaloph in M^2 but broader in M^3 and M^4 . Lophs moderately low, anteriorly bowed. Anterior cingulum moderately high, broad, relatively elongate mesially; subdued forelink extends from near base of protoloph to anterior cingulum, labiad to axis of crown; well-defined ridge ascends from paracone to labial limit of anterior cingulum while slight ridge ascends posteriorly from paracone; cingulum near planar in labial moiety, but descending to moderate degree in lingual moiety. Midlink moderately high, curving posterolabially from protocone then posteriorly to unite with short ridge from near mid-point of metaloph, above median valley; median valley V-shaped. Strong ridge from hypocone and weaker ridge from metacone ascend posteriorly to unite near base of crown, labiad to axis of crown, with production of fossette.

TABLE 17: MEASUREMENTS FOR *Macropus (Prionotemnus) thor* (DE VIS), MAXILLA

Specimen	M^2	M^3	M^4
F4550 rt.	10.4 × 8.8	12.0 × —	13.4 × 10.0
F4550 lt.	—	12.3 × 9.7	13.2 × 10.0

DISCUSSION: In his original description of *Macropus (Prionotemnus) thor*, De Vis (1895) omitted to nominate a holotype. Bartholomai (1966) selected F3602 as lectotype from De Vis' original series of referred specimens, this being one of the best preserved of the series and the specimen figured (De Vis, 1895, pl. 17, fig. 1).

While the structure of P_3 is regarded as highly variable in macropodines, it can be extremely useful taxonomically, particularly if used in conjunction with other characters. Occasionally it can be used by itself, if no overlap with other taxa occurs. De Vis (1895) placed great importance on the morphology of the permanent lower premolar in distinguishing *M. thor*. Although De Vis was justified in the conclusion that the species is distinct, it is known from too few individuals to be distinguished by premolar structure alone. Referred specimens are somewhat variable in molar structure but this variation is not inconsistent with that observed within better known fossil and recent macropodine populations.

Table 18 presents a summary of mandibular measurements for *M. thor*. The sample is small, this having influenced all values for the Coefficient of Variation. The summary by no means expresses the characteristics of the population, but does provide a guide to the attributes of the species.

Figure 5, a Log Difference Diagram, compares *M. thor* with the standard provided by measurements for living *M. dorsalis*. It also incorporates data from other living wallabies, notably *M. parryi* and *M. rufogriseus*. The figure shows a comparatively greater correspondence in proportions between *M. thor* and *M. parryi* than with other wallabies considered. In molar proportions, some similarity is evident between *M. thor* and *M.*

rufogriseus or *M. dorsalis* at this time. However, from an examination of material referable to these species, it is probable that the Log Difference Diagram will not be greatly altered by use of statistical data, especially mean values, for cheek teeth in these species.

Cheek teeth in *M. thor* have more in common with those of *M. parryi* than with other wallabies, and it may be that these species are related. Based on size alone, the differences between these species appear to be much broader than between the fossil *M. agilis siva* and the recent *M. agilis jardinei* discussed above.

The permanent lower premolar in *M. parryi* is of similar proportions to that of *M. thor* and usually

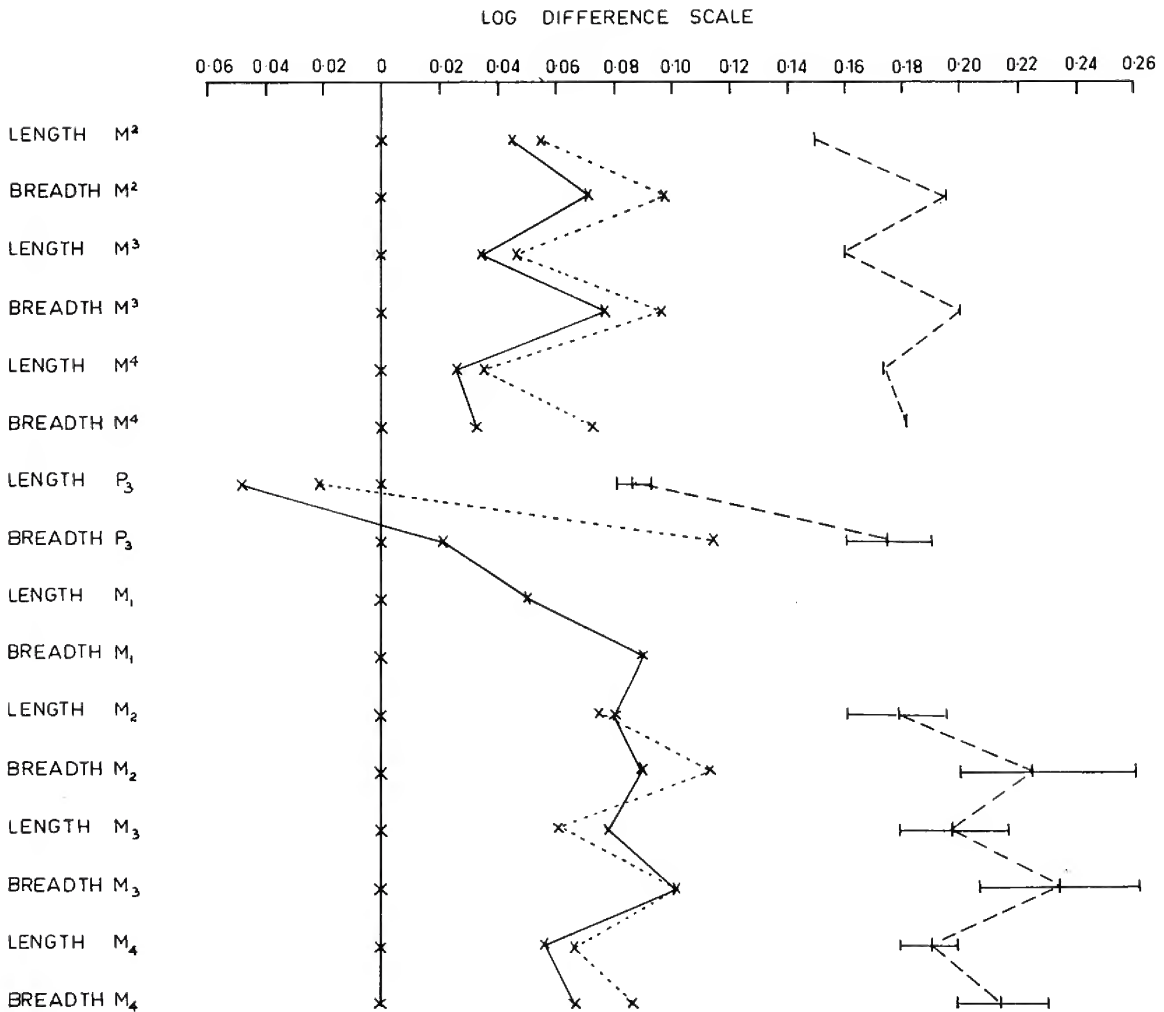


FIG. 5: Log Difference Diagram illustrating proportional relationships of *Macropus (Prionotemnus) thor* (broken line), J10756, *M. parryi* (solid line) and J8128 *M. rufogriseus* (dotted line) using *M. dorsalis* (J4325) as standard. Observed range for *M. thor* has been plotted.

has its longitudinal crest divided by vertical grooves near the anterior cuspid, but has two, or occasionally three, weak sets of ridges transecting the crest posteriorly. Lower molars are basically similar to those in *M. thor*, but the posterior surface, while usually bearing a slight, near median groove, is only very slightly swollen basally, or not swollen at all. Swellings of any kind have not been observed in lower molars in either *M. rufogriseus* or *M. dorsalis*.

TABLE 18: SUMMARY OF MEASUREMENTS FOR *Macropus (Prionotemnus) thor* (DE VIS), MANDIBLE

Character	n	O.R.	\bar{X}	s	V
P ₃ length	2	7.1-7.3	7.2	—	—
max. width	2	2.9-3.1	3.0	—	—
M ₁ length	—	—	—	—	—
prot. width	—	—	—	—	—
M ₂ length	3	10.0-10.8	10.4	—	—
prot. width	3	6.5-7.4	6.9	—	—
M ₃ length	6	12.1-13.2	12.6	0.438	3.48
prot. width	6	7.4-8.4	7.9	0.326	4.12
M ₄ length	8	13.3-13.9	13.6	0.203	1.50
prot. width	8	7.9-8.5	8.2	0.207	2.53

prot. = protolophid.

De Vis (1895) did not refer any maxillary specimens to *M. thor*. Measurements for the single cranial specimen here referred are presented in Table 17. These have also been plotted in the Log Difference Diagram (Fig. 5), indicating basic proportional similarity in the characters considered to both *M. parryi* and *M. rufogriseus*, but showing greater similarity to *M. parryi* in the breadth of M¹. As for lower dentition, this is unsupported by statistical data to indicate comparative proportions in tooth dimensions of the populations but is sufficient to support association of the cranial fossil with the mandibular specimens. Occlusion is satisfactory, and morphological comparison with recent specimens shows greater similarity with *M. parryi* than with *M. rufogriseus* or *M. dorsalis*. This is particularly true of the more elongate nature and breadth of the anterior cingulum, development of a weak forelink in most molars, and the possession of large posterior palatine vacuities in *M. parryi*.

Macropus (Prionotemnus) dryas (De Vis, 1895)
(Plate 25, figs. 1-4)

Halmaturus dryas De Vis, 1895, pp. 109-11, pl. 17, figs. 11-15.

Macropus dryas (De Vis): Simpson, 1930, p. 71.

'*Halmaturus*' *dryas* De Vis: Bartholomai, 1966, p. 116, pl. 15, figs. 1-3.

MATERIAL: F3582, lectotype, partial right maxilla with P³-M³, adult, ?Chinchilla, SE.Q., ?Chinchilla Sand of Late Pliocene age (figd in part, De Vis, 1895, pl. 17, figs. 13, 15; figd Bartholomai, 1966, pl. 15, figs. 1-3).

Other referred specimens include 2 adult maxillae, an isolated P³, 17 juvenile mandibular rami, and 39 adult mandibular rami from the following localities in the Chinchilla Sand: Chinchilla; ?Chinchilla; Chinchilla, at M.R.363677 Chinchilla 4-mile map; Chinchilla Rifle Range (Rifle Range No. 78, Par. Chinchilla), in side gully leading into middle gully; and from the western Darling Downs (particular localities unspecified).

DIAGNOSIS: Moderately large species; P³ elongate, with longitudinal crest nearly straight, and with lingual cingulum low, reduced anteriorly to basal tuberculations; lingual basin narrow. Upper molars with well-defined forelink, lacking strong anterior ridge from paracone. Mandible with labial groove only slightly developed, and with symphysis only slightly elevated to base of mandible. P₂ relatively elongate with posterior extension of longitudinal crest in addition to posterolingual extension. DP₃ with well-defined anterolabial fossette and moderately strong posterior ridge from entoconid to crown base. P₃ elongate, with crown height decreasing somewhat anteriorly; crest nearly straight, only slightly flexed posterolingually. Lower molars high, with moderately low, narrow anterior cingulum and well-defined anterolabial fossette; links high, with accessory ridges occasionally present in lingual moiety of talonid basin; posterior of hypolophid rounded, slightly grooved linguad to crown axis, and with posterior cingulum absent.

DESCRIPTION: Cranium known only from fragmentary maxillary remains.

Upper incisors, P² and DP³ unknown.

P³ elongate, subtriangular in basal outline, broader posteriorly. Crown with high longitudinal crest, only very slightly concave labially, transected by three sets of vertical labial and lingual ridges,

TABLE 19: MEASUREMENTS FOR LECTOTYPE OF *Macropus thor* (DE VIS)

Specimen	P ₃	M ₁	M ₂	M ₃	M ₄
F3602	7.1 × 3.1	—	10.4 × —	12.3 × 7.8	—

TABLE 20: MEASUREMENTS FOR *Macropus (Prionotemmus) dryas* (DE VIS), MAXILLA

Specimen	P ³	M ¹	M ²	M ³	M ⁴
F3582*	13.2 × 6.6	9.7 × 8.2	12.1 × 9.3	13.8 × 10.1	—
F3584	—	—	10.7 × 8.8	12.7 × 9.8	—
F3583	14.6 × —	—	— × 9.2	12.1 × 9.5	13.7 × 9.5
F4655	13.8 × 6.7	—	—	—	—

*Lectotype *M. dryas* (De Vis).

with production of cusps at crest; strength of ridges decreases posteriorly; apex of paracone about one-quarter distance along crown from anterior limit of crown. Hypocone moderately high, being about three-quarters as high as metacone, united to metacone by high, strong, anterolabial ridge; posterior ridge from hypocone curves labially to unite with posterior ridge from metacone, delimiting well-defined posterior fossette; anterior ridge from hypocone ascends towards crown base, with resultant lingual egingulum low, nodular, discontinuous anteriorly, marked by three or four well-defined tubercles, occasionally extending to above paracone. Lingual basin very narrow. Anterolingual crown base swollen, while labial base swollen and nodular.

M¹ < M² < M³ < M⁴; molars subrectangular, slightly constricted across median valley; loph moderately high, anteriorly bowed; metaloph broader than protoloph in M¹, but narrower in M²–M⁴. Anterior egingulum relatively low, narrow, moderately short; well-defined strong forelink passes posteriorly from near mid-point of egingulum to centre of protoloph; extremely slight ridge ascends anteriorly from paracone; posterior ridge from paracone into median valley stronger. Midlink high, strong, ascending posterolabially from protocone then posteriorly across median valley to mid-point of metaloph; slight ridge occasionally ascends anterolingually from metacone into median valley; lingual moiety of median valley V-shaped, labial portion sharply U-shaped. Strong posterolabial ridge ascends from hypocone across mid-line of crown, meeting posterolingual ridge from metacone below tooth base, delimiting posterior fossette. Posterior surface of metaloph occasionally ornamented by very slight vertical ridges.

Mandible moderately shallow, relatively thick; base of symphysis elevated slightly to base of mandible; symphysis elongate, shallow, not ankylosed, rugose; geniohyal pit shallow, near posterior symphyseal limit; diastema moderately elongate with crest broadly acute, more rounded anteriorly; ventral margin of ramus rounded between symphysis and weak digastric process and ridge. Mental foramen moderate, oval, positioned close

to diastemal crest, somewhat anterior to P₃. Ramus with moderately shallow, often ill-defined labial groove extending to below posterior of M₂, about one-third distance from alveolar margin to base of mandible. Digastric process separated from base of angle by shallow post-digastric sulcus, bounded above by shallow digastric fossa; this fossa leads to depression opening posteriorly into pterygoid fossa. Post-alveolar shelf short, leading to post-alveolar ridge, ascending to disappear on mesial wall of coronoid process, above large mandibular foramen. Masseteric crest raised to about level of bases of crowns of cheek teeth; masseteric foramen moderately large, with deep masseteric fossa. Angle of mandible markedly inflected, but bulk of angle, condyle and coronoid process not preserved.

I₁ known only in fractured and worn condition.

P₂ relatively elongate, semi-lunate in occlusal view, with labial surface markedly convex and lingual surface somewhat concave. Longitudinal crest secant, nearly straight, extending posteriorly beyond posterior cuspid, as well as presenting a posterolingual extension; anteriorly, slight lingual curvature evident below anterior cuspid; crest transected by two sets of vertical labial and lingual ridges with production of cusps at crest; strength of ridges decreases posteriorly. Base of crown somewhat swollen labially.

DP₃ molariform, subtriangular in basal outline, unconstricted across talonid basin, with lophids moderately high, posteriorly convex. Hypolophid much broader than protolophid. Trigonid basin moderately narrow, its length being slightly less than distance between lophids. Forelink high, strong, curving anterolingually from protoconid to point labial to mid-point of high anterior egingulum; strong ridge descends anteriorly from metaconid across lingual margin of trigonid to unite with anterior egingulum, with production of pocket-like lingual moiety of trigonid; labial moiety reduced, descending rapidly, with well-defined anterolabial fossette present. Midlink moderately high, strong, curving anterolingually from hypoconid across talonid basin to near mid-point of protolophid; moderate ridge descends posteriorly from metaconid into talonid; lingual

moiety of talonid basin sharply U-shaped, labial moiety more broadly U-shaped. Moderate ridge descends posteriorly from entoconid to base of crown, giving posterolingual crown margin an angular appearance. Posterior cingulum not developed.

P_3 elongate, robust, with crown higher posteriorly than anteriorly; suboval in basal outline; longitudinal crest secant, slightly convex labially, slightly curving lingually in its posterior and anterior extensions; crest transected by three sets of vertical labial and lingual ridges with production of cuspules at crest; strength of ridges decreases posteriorly. Anterior cuspid of crest well-defined, posterior cuspid less well-defined. Base of crown swollen labially and lingually.

$M_1 < M_2 < M_3 < M_4$; molars subrectangular in basal outline, slightly constricted across talonid basin; lophids high, convex posteriorly, with hypolophid broader than protolophid in M_1 and M_2 and slightly narrower in M_3 and M_4 . Trigonid basin relatively narrow, its length approximately equalling distance between lophids. Forelink high, strong, curving anterolingually from protoconid to near mid-point of moderately high, narrow anterior cingulum; slight ridge descends anteriorly from metaconid towards trigonid basin. Trigonid basin descends labially and lingually from forelink, with anterolabial fossette well-defined. Midlink high, strong, curving anterolingually from hypoconid across talonid basin, to unite with short ridge from near mid-point of protolophid; slight ridge ascends posteriorly from metaconid into talonid, as does slight anterior ridge from entoconid. Talonid basin sharply U-shaped, descending labially and lingually from midlink. Posterior surface of hypolophid generally broadly rounded, usually with poorly defined, broad, vertical groove linguad to axis of crown. Posterior cingulum not developed.

DISCUSSION: Remains of *Macropus* (*Prionotemmus*) *dryas* (De Vis) are at present known only from the Chinchilla Sand of late Pliocene age. The lectotype, F3582, was selected from De Vis' (1895) original series of referred specimens and illustrated by Bartholomai (1966).

Reference of the species to the subgenus *Prionotemmus* has been made, although the species differs from others of this group in possessing a well-defined forelink in upper molars and in the presence of some slight grooving on the posterior hypolophid surface in lower molars. In all other preserved features, the species conforms with other members of the subgenus *Prionotemmus*. It is considered that this type of overlap is to be expected in rapidly evolving groups reacting to

basically similar evolutionary pressures.

M. dryas is reasonably common in collections from the Chinchilla Sand. It is better represented by mandibular remains than by maxillary. Association of upper and lower jaw fragments has not been observed in the field and reference of mandibular remains is by size and morphological similarity. Occlusion is satisfactory and the present association is considered correct. Post-cranial skeletal elements have not been recorded for *M. dryas*.

The mandibular premolars figured by De Vis (1895, pl. 17, figs. 11–12) are morphologically identical with material here referred to *M. dryas* but it has not been possible to determine the specimen or specimens which formed the subject for these illustrations. Because of the poor illustration, the identity of the M_3 figured by De Vis (1895, pl. 17, fig. 14), is doubtful. The apparent ornamentation of the anterior surface of the protolophid suggests that the specimen may not represent *M. dryas*. De Vis (1895) assigned 73 specimens to *M. dryas*, apparently including some material which is now known to be referable to other species. The only evidence for this is provided by the labels in De Vis' handwriting affixed to individual specimens, but it cannot be confirmed whether these were written at the time of his revision or subsequent to it.

M. dryas is readily distinguished from other Chinchilla Sand species by morphology, but in very worn specimens of this and *Protemnodon chinchillaensis*, the lower molars are difficult to separate. Thus a number of very worn mandibles are doubtfully assigned here, and statistical evaluation of the variation exhibited by the population has been undertaken excluding these specimens.

The summary of mandibular measurements presented in Table 21 indicates Coefficients of Variation similar to those of other fossil macropodids considered in this study. All characters, with the exception of breadth of P_3 , show only slight to moderate variation. However, samples of P_2 and DP_3 are inadequate for consideration. As for other species, values are consistent with those from a single species from slightly differing stratigraphic levels (Simpson *et al.*, 1960). The high value for V for breadth of P_3 expresses the relatively more variable nature of this character. Upper tooth parameters, presented in Table 20, are derived from a sample too small for statistical evaluation.

M. dryas represents the most common species of *Macropus* (*Prionotemmus*) in the Chinchilla Sand. Its relationships with other fossil species are obscure.

TABLE 21: SUMMARY OF MANDIBULAR MEASUREMENTS FOR *Macropus (Prionotemnus) dryas* (DE VIS)

Character	n	O.R.	\bar{X}	s	V
P ₂ length	3	8.0- 8.9	8.3	—	—
max. width	3	3.4- 3.8	3.6	—	—
DP ₃ length	3	8.5- 9.3	9.0	—	—
prot. width	2	4.4- 4.8	4.6	—	—
P ₃ length	7	10.2-11.7	11.0	0.5582	5.07
max. width	5	3.6- 4.2	3.9	0.2958	7.58
M ₁ length	10	9.7-11.4	10.4	0.5415	5.21
prot. width	9	6.1- 6.9	6.5	0.3724	5.73
M ₂ length	19	10.4-12.7	11.6	0.5691	4.91
prot. width	20	7.0- 8.5	7.6	0.3912	5.15
M ₃ length	22	11.9-14.0	13.2	0.5515	4.18
prot. width	18	7.1- 9.2	8.3	0.5173	6.23
M ₄ length	21	13.8-15.7	14.7	0.6168	4.20
prot. width	23	7.7- 9.6	8.7	0.4953	5.69

prot. = protolophid.

Macropus (Prionotemnus) palankarinnicus Stirton, 1955

(Plate 26, figs. 1-2)

Prionotemnus palankarinnicus Stirton, 1955, pp. 252-8, figs. 3-5.

MATERIAL: F3285, cast of holotype, University of California number 44381, partial right mandibular ramus with P₃-M₄, adult, west side of Lake Palankarina, east of Lake Eyre, c.29 km S.75°W. of Etadunna Station Homestead (figd Stirton, 1955, fig. 3), of Pliocene age.

F3589, partial right mandibular ramus with P₃-M₄, adult Darling Downs (but preservation indicates derivation from the Chinchilla Sand of late Pliocene age). F6869, very worn right mandibular ramus with P₃-M₄, aged, base of Chinchilla Sand type section, Condamine River, Chinchilla Rifle Range (Rifle Range No. 78, Par. Chinchilla), from the Chinchilla Sand.

DIAGNOSIS: A relatively large species. Mandible with lateral groove descending obliquely and symphysis not greatly downflexed. P₃ relatively elongate with base of crown swollen. Lower molars with comparatively more rectilinear lophids, low links, somewhat convex lateral lophid surfaces, and posterior cingulum.

DESCRIPTION: Mandible relatively large, strong moderately deep; symphysis elongate, elevated at only very low angle to base of mandible, shallow, not ankylosed; geniohyal pit shallow, towards posterior symphyseal limit; diastemal crest broadly rounded, except for area immediately anterior to P₃ where crest becomes less rounded. Mental foramen relatively large, oval, set just below diastemal crest, slightly in advance of P₃. Base of mandible broadly rounded posterior to symphysis with extremely weak digastric process; very slight post-digastric sulcus separating process from angle; digastric fossa weak separated above by weak ridge from

broad depression opening posteriorly into pterygoid fossa. Moderately weak lateral groove present from P₃ posteriorly to below anterior of M₄, descending from near alveolar margin to slightly above base of mandible. Post-alveolar shelf short, with slight angle, leading to post-alveolar ridge ascending lingual surface of coronoid process. Bulk of angle, process and condyle lacking.

I₁, P₂ and DP₃ not preserved.

P₃ relatively elongate, with longitudinal crest trenchant, transected by three very weak sets of vertical labial and lingual ridges with production of slight cuspules at crest; anterior cuspid well-defined, at slightly higher level than rest of crest; crest posterolingually curved, otherwise approximately straight. Anterior tooth margin very steep. Base of crown labially and lingually swollen, this separated from rest of crown by slight groove; swelling continues around anterior margin.

M₁ < M₂ < M₃ < M₄; molars subrectangular in basal outline, slightly constricted across talonid basin in anterior molars, becoming more constricted in posterior molars. Lophids relatively low, nearly rectilinear with slight wear, slightly laterally swollen in anterior view; protolophid slightly narrower than hypolophid in M₁, approximately equal in M₂ and M₃ and broader in M₄. Anterior cingulum relatively low, with trigonid basin broad, moderately elongate, about as long as distance between lophids; cingulum rather squared anterolabially and anterolingually; forelink curves anterolingually from protoconid across trigonid to near mid-point of anterior cingulum; forelink rather low; lingual moiety of trigonid near horizontal, labial portion descends at moderately low angle from forelink. Anterior and posterior ridges from metaconid weak. Midlink descends almost directly from hypoconid across talonid to near mid-point

TABLE 22: MEASUREMENTS FOR *Macropus* (*Prionotemmus*) *palankarinnicus* STIRTON, MANDIBLE

Specimen	P ₃	M ₁	M ₂	M ₃	M ₄
F3285*	9.7 × 4.1	—	10.8 × —	13.3 × —	— × 8.3
F3589	9.5 × 3.7	8.2 × —	9.9 × 7.4	12.5 × 8.2	12.9 × 8.4

*Holotype *M. palankarinnicus* Stirton

of protolophid; midlink rather low. Talonid broadly U-shaped labially and lingually and descends slightly labially and lingually from midlink. Anterior ridge from entoconid weak. Posterior surface of hypolophid with well-defined posterior cingulum.

Upper dentition unknown from Queensland deposits.

DISCUSSION: Although only two specimens referable to this species have been recorded from the Darling Downs area, these are morphologically so similar to the holotype, a cast of which, F3285, is held in the Queensland Museum, that no doubt exists regarding their identification. Stirton (1955) states that the basal swellings on P₃ are not continuous around the anterior margin. However, the holotype cast indicates that this is present, although not as strongly developed as in the Queensland specimen, F3589. P₃ is very slightly longer in the holotype, and other cheek teeth are generally larger. However, compared with the variation exhibited by better known species, these differences are not believed to be significant. The cheek tooth row is straighter in occlusal view in the Queensland specimen than in the holotype.

A second specimen, F6989, with very worn dentition has recently been collected from the Chinchilla Sand. Although less complete than the holotype, reference of this specimen to *M. palankarinnicus* is undertaken with confidence.

Macropus palankarinnicus is the most common macropodid recovered from the Mampuwordu Sands at Lake Palankarina, in the Tirari Desert of South Australia (Stirton *et al.*, 1961). Stirton (1963) compared it with *Wallabia* (*sensu lato*) and *Protetnodon* showing its distinctness from the latter. Examination of the extensive sample in the collections of the University of California, Berkeley, was made and while the possibility of a mixed sample exists, it is certain that the material referable to the species is clearly related to the living *Macropus* wallabies.

Ride (1962) suggests that *L. palankarinnicus* does not appear to differ greatly from the Sandy Wallaby, *M. agilis*. However, compared with that species, the molars possess a well-defined posterior cingulum, have more rectilinear lophid crests, lower links and more laterally convex lophid

surfaces. The symphyseal region of the ramus is not as markedly downflexed.

It is unfortunate that the referred specimen, F3589, is not adequately localised. However, its preservation is wholly consistent with derivation from the Chinchilla Sand of late Pliocene age. This specimen was part of the series referred to *Halmaturus odin* by De Vis (1895), a species regarded as a *nomen dubium* by Bartholomai (1966). It does not present any of the characters considered diagnostic by De Vis (1895) for '*H. odin*'.

Measurements for the available sample of *M. palankarinnicus* are presented in Table 22.

DISCUSSION

At present, 12 species of *Macropus* Shaw are recorded from the Upper Cainozoic deposits of Queensland, 8 from the Pleistocene fluvialite deposits and 4 from the late Pliocene Chinchilla Sand. Bartholomai (1972) has drawn attention to the apparent disproportionate number of macropodid species present in the Pleistocene fluvialite deposits of the eastern Darling Downs and this observation is also true of the number of species of *Macropus* represented. It has been suggested by Bartholomai (1972) that this diversity probably reflects, in part, faunal shifts associated with the fluctuating climatic conditions of the Pleistocene. It probably also relates to the assumption that the Pleistocene fluvialite sediments represent approximately similarly aged deposits, whereas this is quite obviously an over-simplification of the temporal relationships within the deposits. However, insufficient information is available to permit more precise resolution of Pleistocene stratigraphy at this time.

Of species of *Macropus* represented in the Tertiary deposits in Queensland, only *M. palankarinnicus* has been recorded elsewhere, having been described from the Pliocene Mampuwordu Sands of the Tirari Desert sequence from central Australia. Restriction of other species to the Chinchilla Sand suggests that these may prove useful in correlation of Tertiary continental deposits.

The origins of *Macropus* are obscure. It is apparent from both morphological and stratigraphic considerations that *Macropus* (*Macropus*) represents a reasonably recent offshoot from the

earlier developed *M. (Osphranter)* or *M. (Prionotemmus)*. Both these latter subgenera appear to retain features which could have been present in ancestral stock, including better developed, more functional permanent premolars. As in other macropodid genera, there appears to have been a genuine, marked radiation in *Macropus* dating from an origin in the Miocene at the earliest, this regardless of the fact that the late Tertiary and Pleistocene species have been more accessible for collection and study.

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PLATE 7

FIG. 1: *Macropus (Macropus) titan* Owen. Lateral view of partial right adult mandibular ramus, F4193, Ravensthorpe, Pilton, Darling Downs, natural size.

FIG. 2: *Macropus (Macropus) titan* Owen. Stereopair of occlusal view of F4193, natural size.

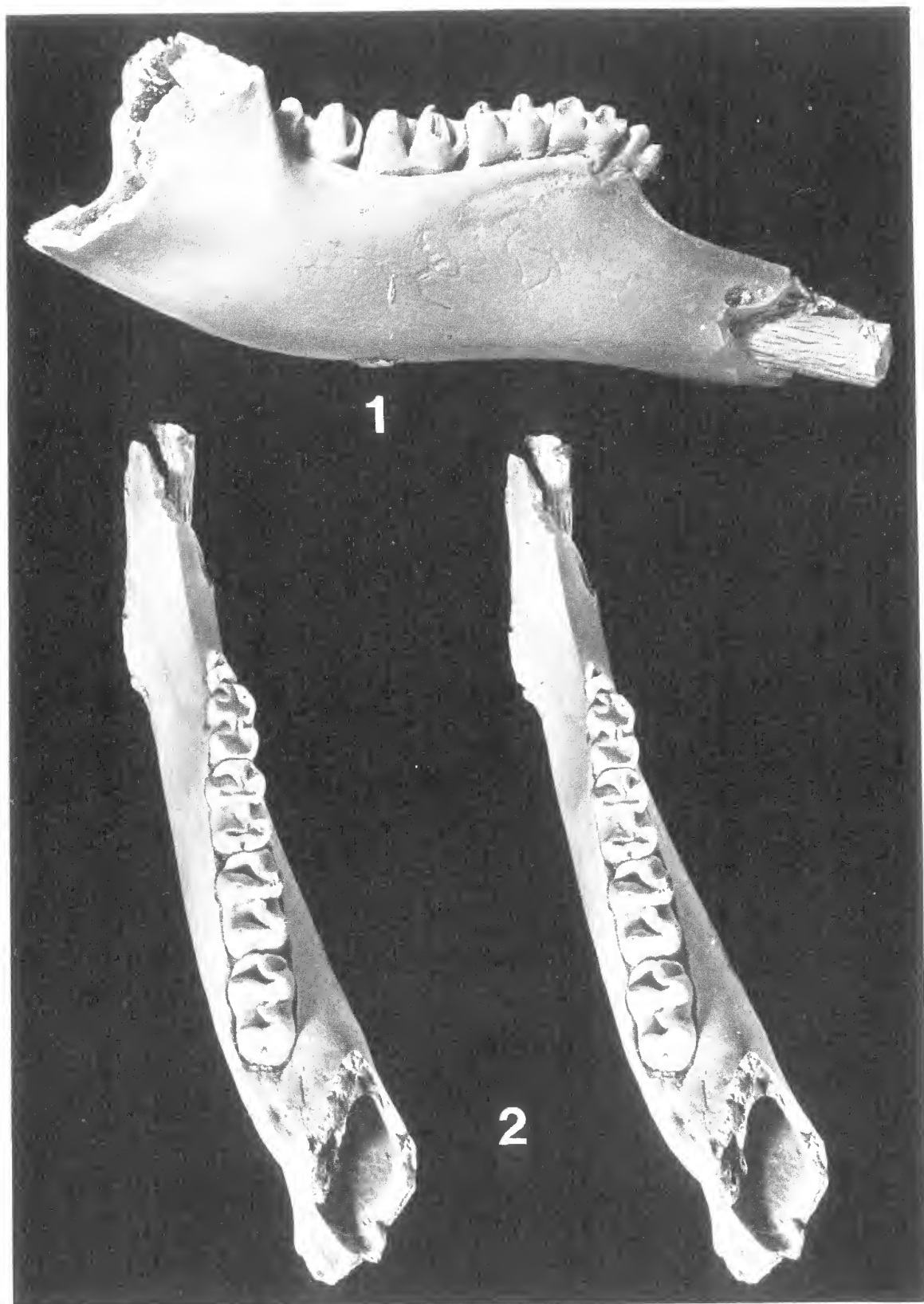


PLATE 8

FIG. 1: *Macropus (Macropus) titan* Owen. Lateral view of juvenile, partial right mandibular ramus, F3740, Darling Downs, natural size.

FIG. 2: *Macropus (Macropus) titan* Owen. Stereopair of occlusal view of F3740, natural size.

FIG. 3: *Macropus (Macropus) titan* Owen. Lateral view of juvenile partial right maxilla, F5716, Dalby, at 30 feet in sewerage drain, Darling Downs, natural size.

FIG. 4: *Macropus (Macropus) titan* Owen. Stereopair of occlusal view of F5716, natural size.

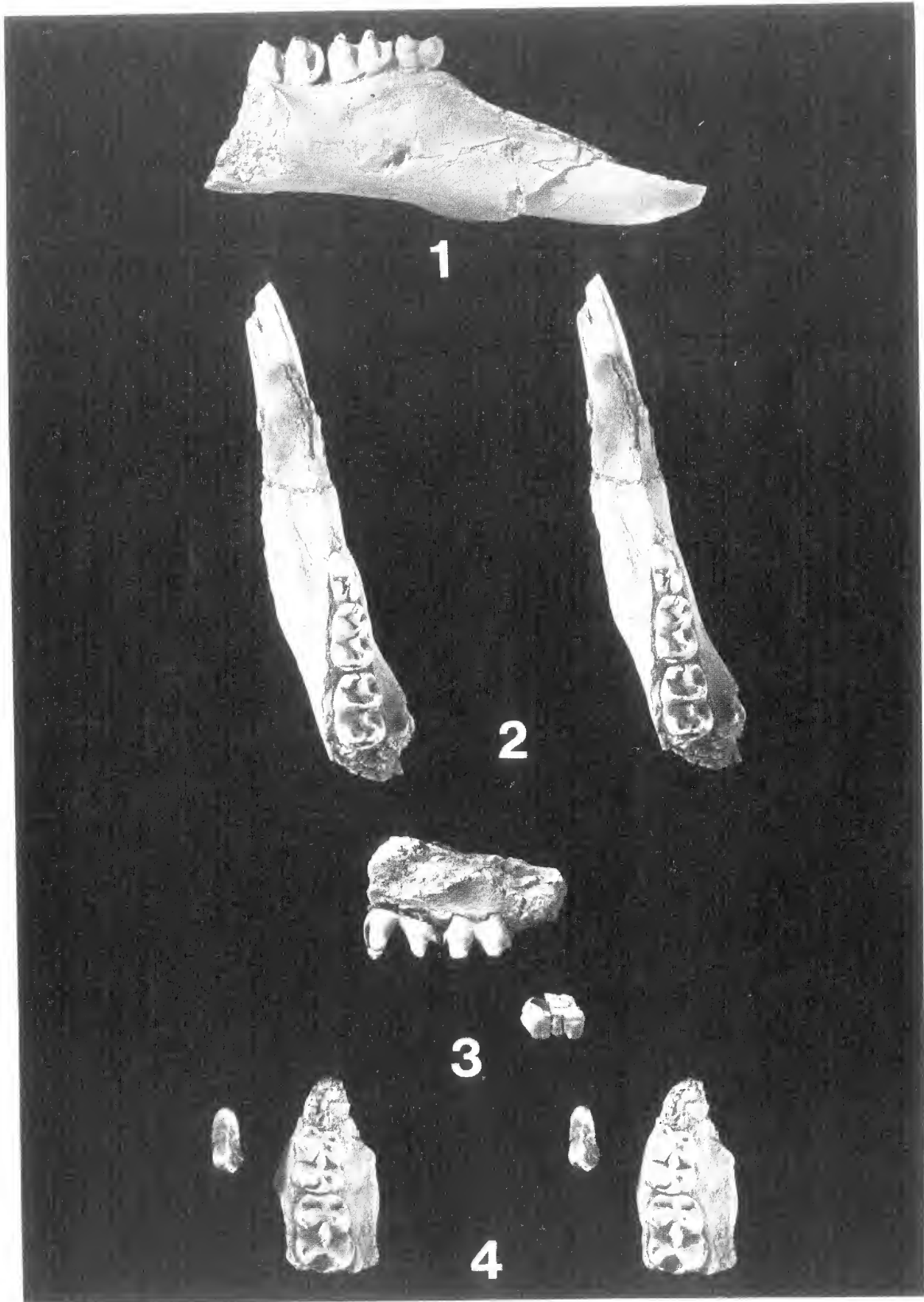


PLATE 9

- FIG. 1: *Macropus (Macropus) titan* Owen. Lateral view of juvenile partial left maxilla, F4321, Darling Downs, natural size.
- FIG. 2: *Macropus (Macropus) titan* Owen. Stereopair of occlusal view of F4321, natural size.
- FIG. 3: *Macropus (Macropus) titan* Owen. Lateral view of juvenile partial left maxilla, F3924, Darling Downs, natural size.
- FIG. 4: *Macropus (Macropus) titan* Owen. Stereopair of occlusal view of F3924, natural size.

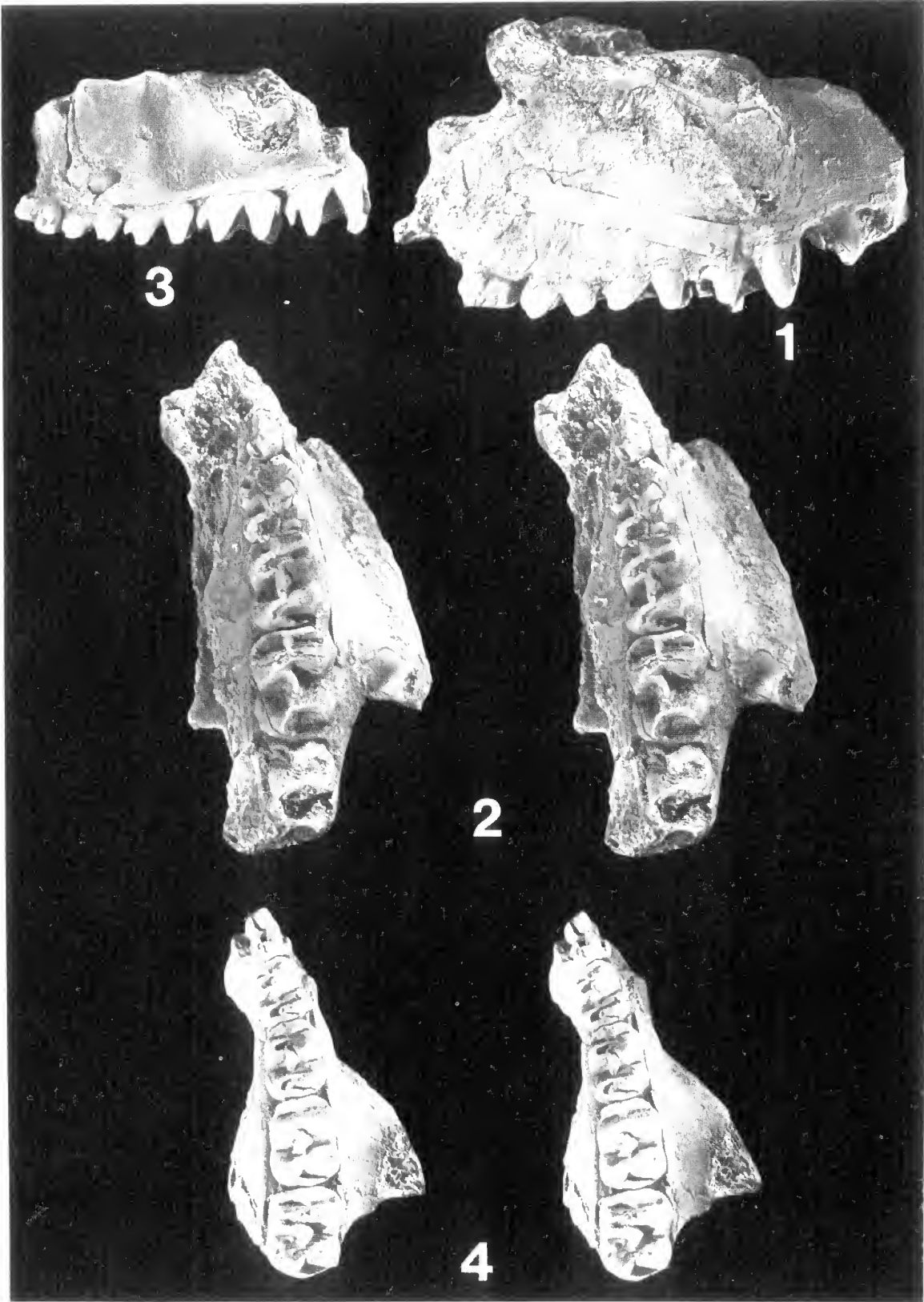


PLATE 10

FIG. 1: *Macropus (Macropus) titan* Owen. Lateral view of juvenile left maxilla of partial palate, F4326, Pilton, Darling Downs, natural size.

FIGS. 2, 3: *Macropus (Macropus) titan* Owen. 2, occlusal view of F4326; 3, stereopair of occlusal view of left maxilla of F4326, natural size.

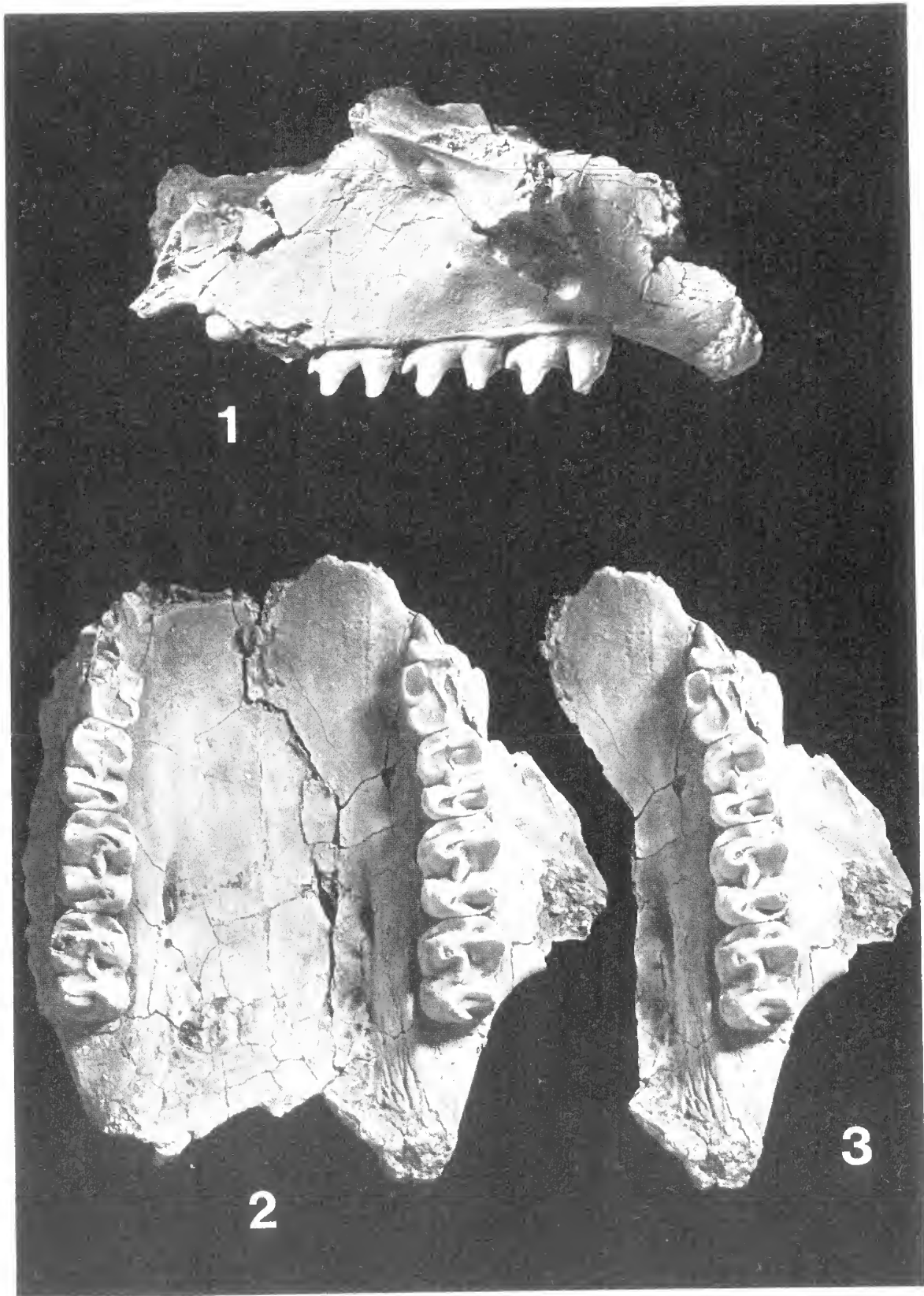


PLATE 11

- FIG. 1: *Macropus (Macropus) rama* sp. nov. Lateral view of adult partial left mandibular ramus, F4773, at M.R. 134444 Liverpool Range 1-mile sheet, Pilton, Darling Downs, natural size.
- FIG. 2: *Macropus (Macropus) rama* sp. nov. Stereopair of occlusal view of mandible, F4773, natural size.
- FIG. 3: *Macropus (Macropus) rama* sp. nov. Lateral view of associated partial right maxilla, F4773, natural size.
- FIG. 4: *Macropus (Macropus) rama* sp. nov. Stereopair of occlusal view of maxilla, F4773, natural size.

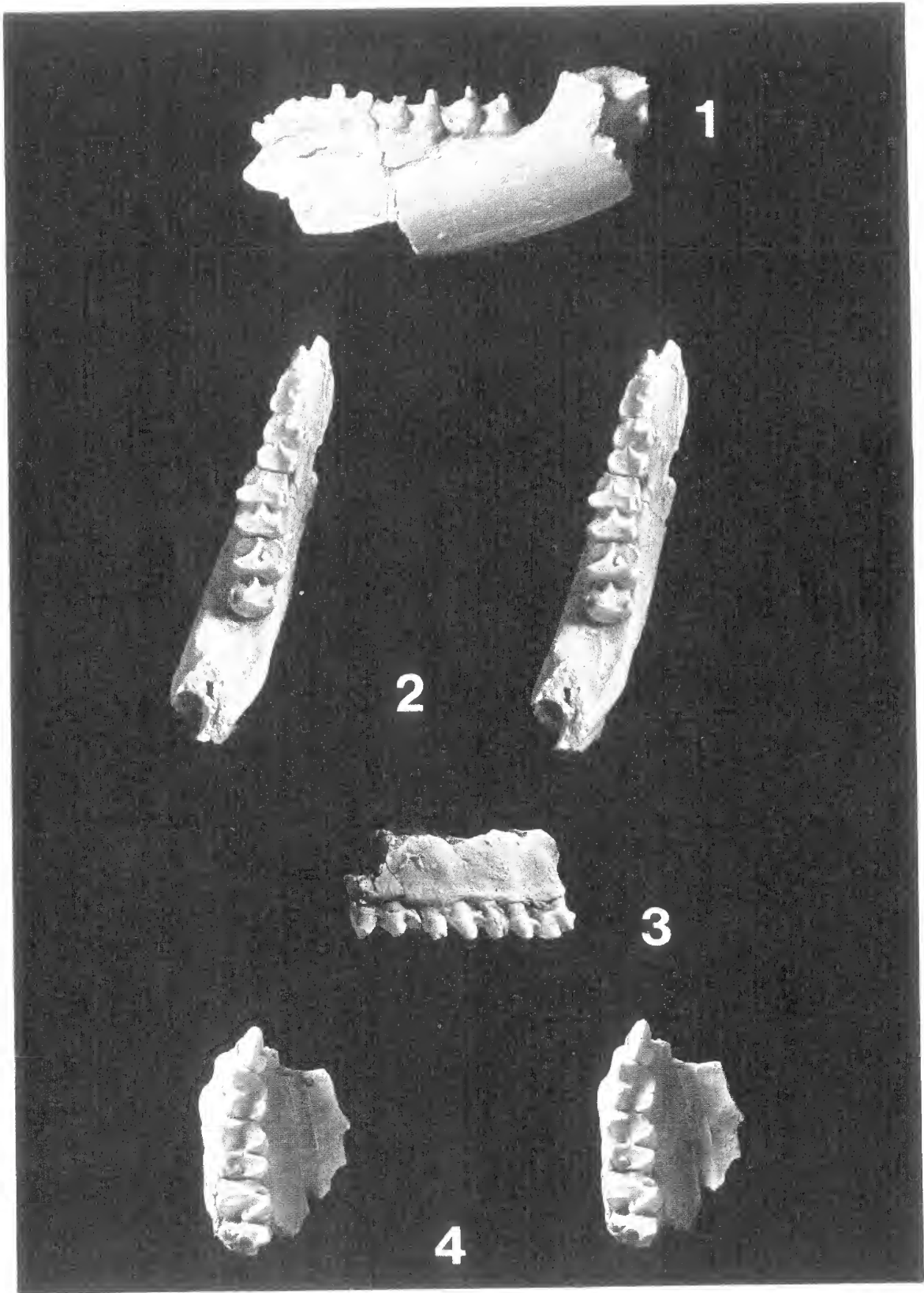
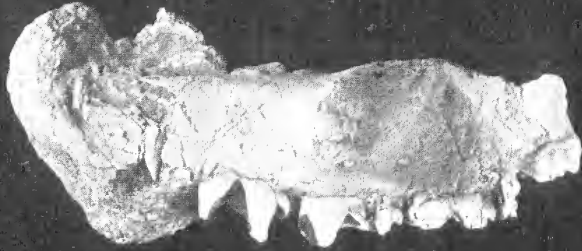


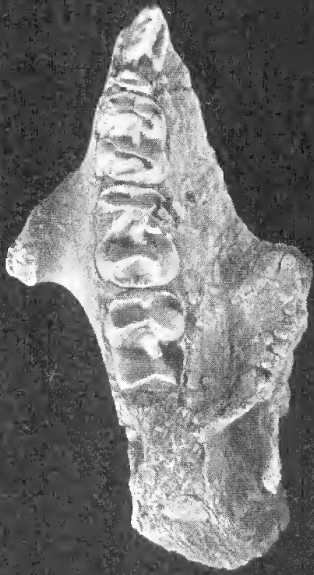
PLATE 12

FIG. 1: *Macropus (Osphranter) altus* (Owen). Lateral view of juvenile partial right maxilla, F2849, Bongeen, Darling Downs, natural size.

FIG. 2: *Macropus (Osphranter) altus* (Owen). Stereopair of occlusal view of F2849, natural size.



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PLATE 13

FIG. 1: *Macropus (Osphranter) altus* (Owen). Lateral view of adult partial right mandibular ramus, F5441, Darling Downs, natural size.

FIG. 2: *Macropus (Osphranter) altus* (Owen). Stereopair of occlusal view of F5441, natural size.

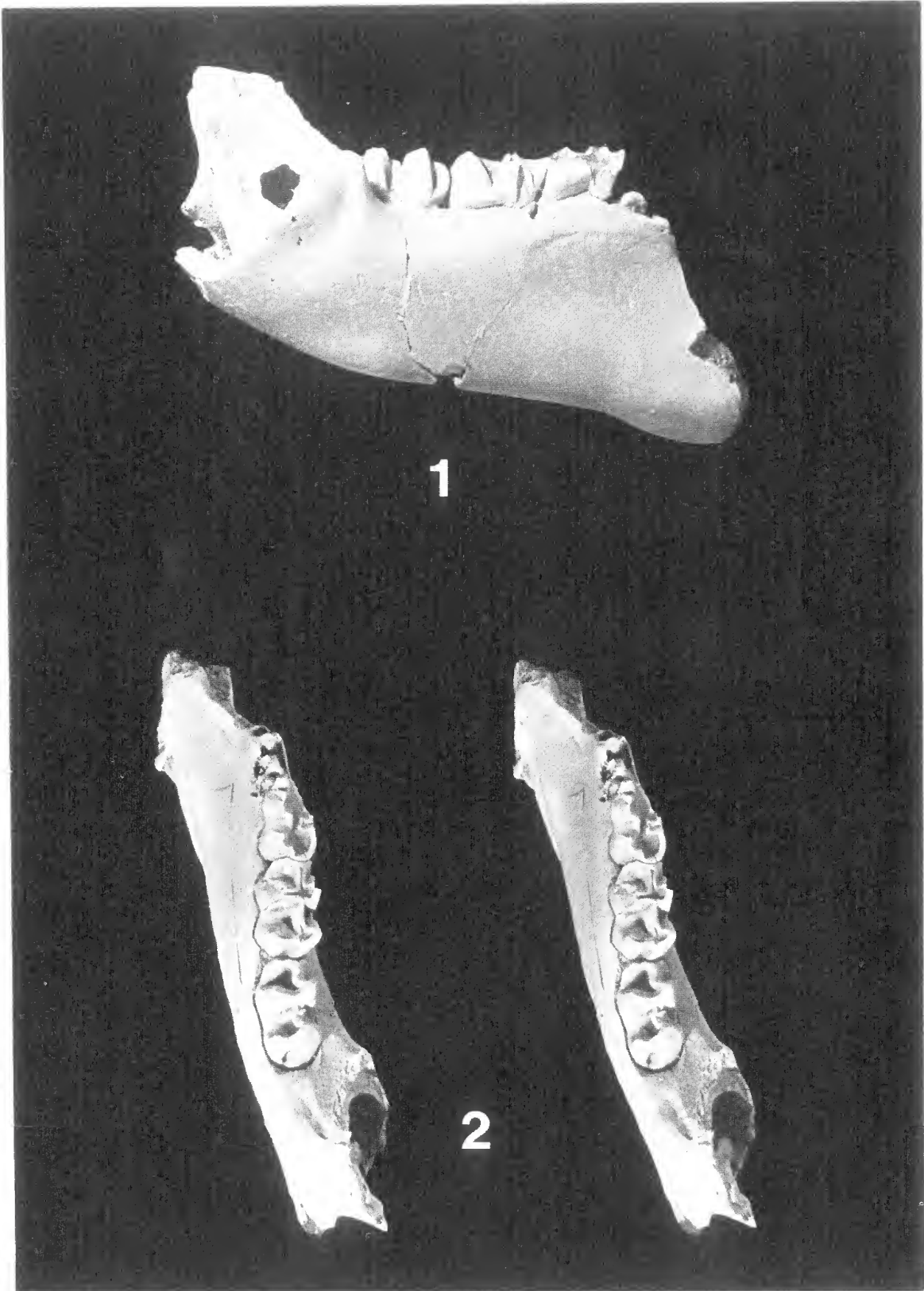


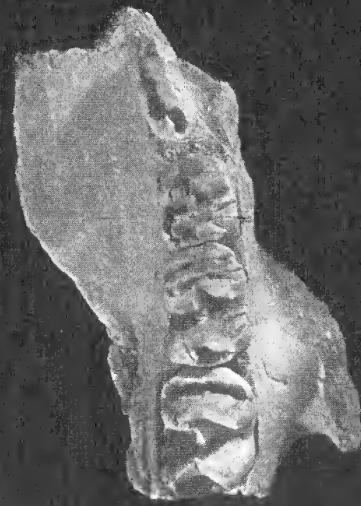
PLATE 14

FIG. 1: *Macropus (Osphranter) ferragus* Owen. Lateral view of adult partial left maxilla, F3720, Ravensthorpe, Pilton, Darling Downs, natural size.

FIG. 2: *Macropus (Osphranter) ferragus* Owen. Stereopair of occlusal view of F3720, natural size.



1



2

PLATE 15

FIG. 1: *Macropus (Osphranter) ferragus* Owen. Lateral view of juvenile partial left mandibular ramus, F3974, Darling Downs, natural size.

FIG. 2: *Macropus (Osphranter) ferragus* Owen. Stereopair of occlusal view of F3974, natural size.

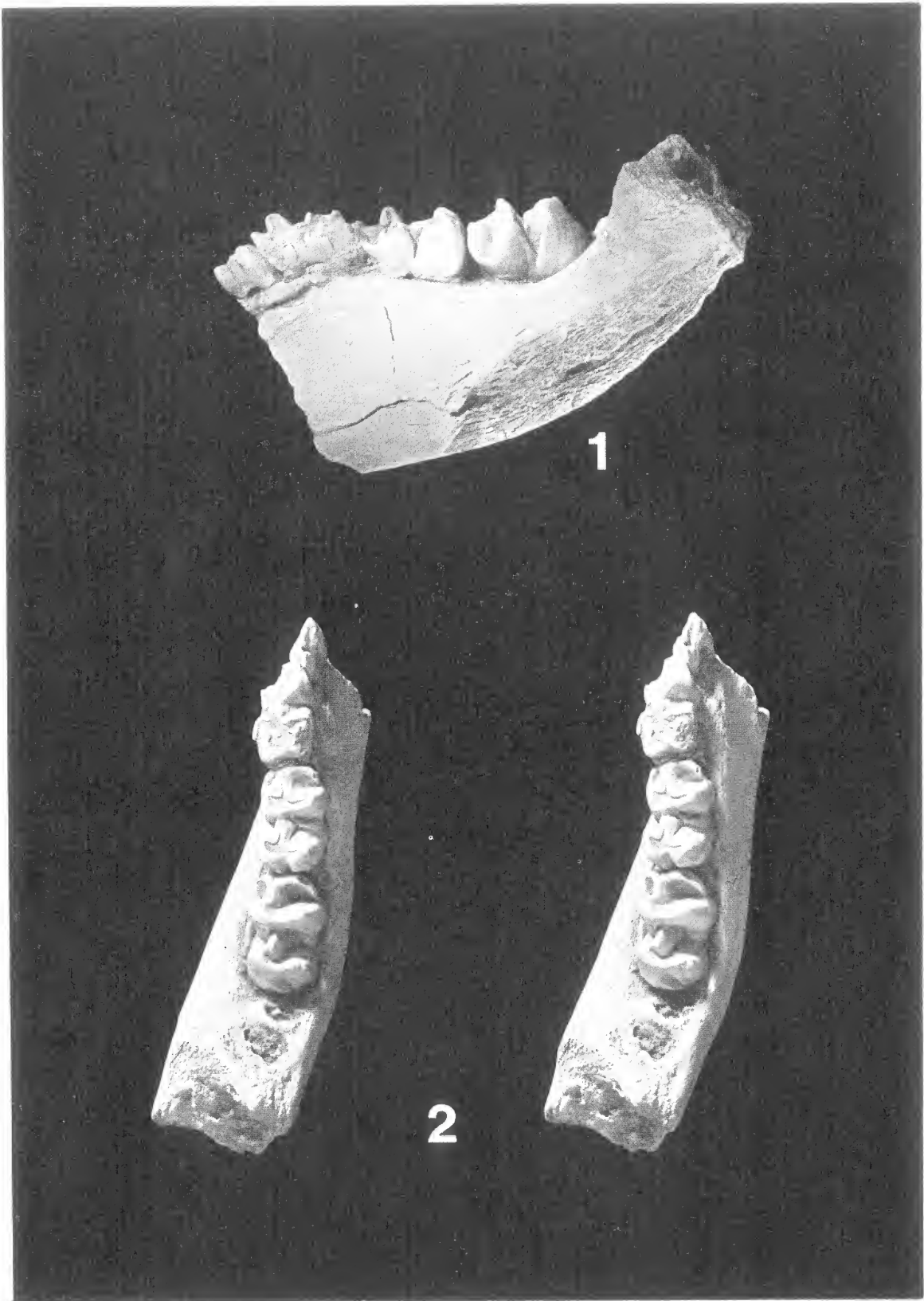


PLATE 16

- FIG. 1: *Macropus (Osphranter) pan* De Vis. Lateral view of adult partial left maxilla, F3713, Chinchilla, Darling Downs, natural size.
- FIG. 2: *Macropus (Osphranter) pan* De Vis. Stereopair of occlusal view of F3713, natural size.
- FIG. 3: *Macropus (osphranter) pan* De Vis. Lateral view of adult partial right maxilla, F3714, Chinchilla, Darling Downs, natural size.
- FIG. 4: *Macropus (Osphranter) pan* De Vis. Stereopair of occlusal view of F3714, natural size.

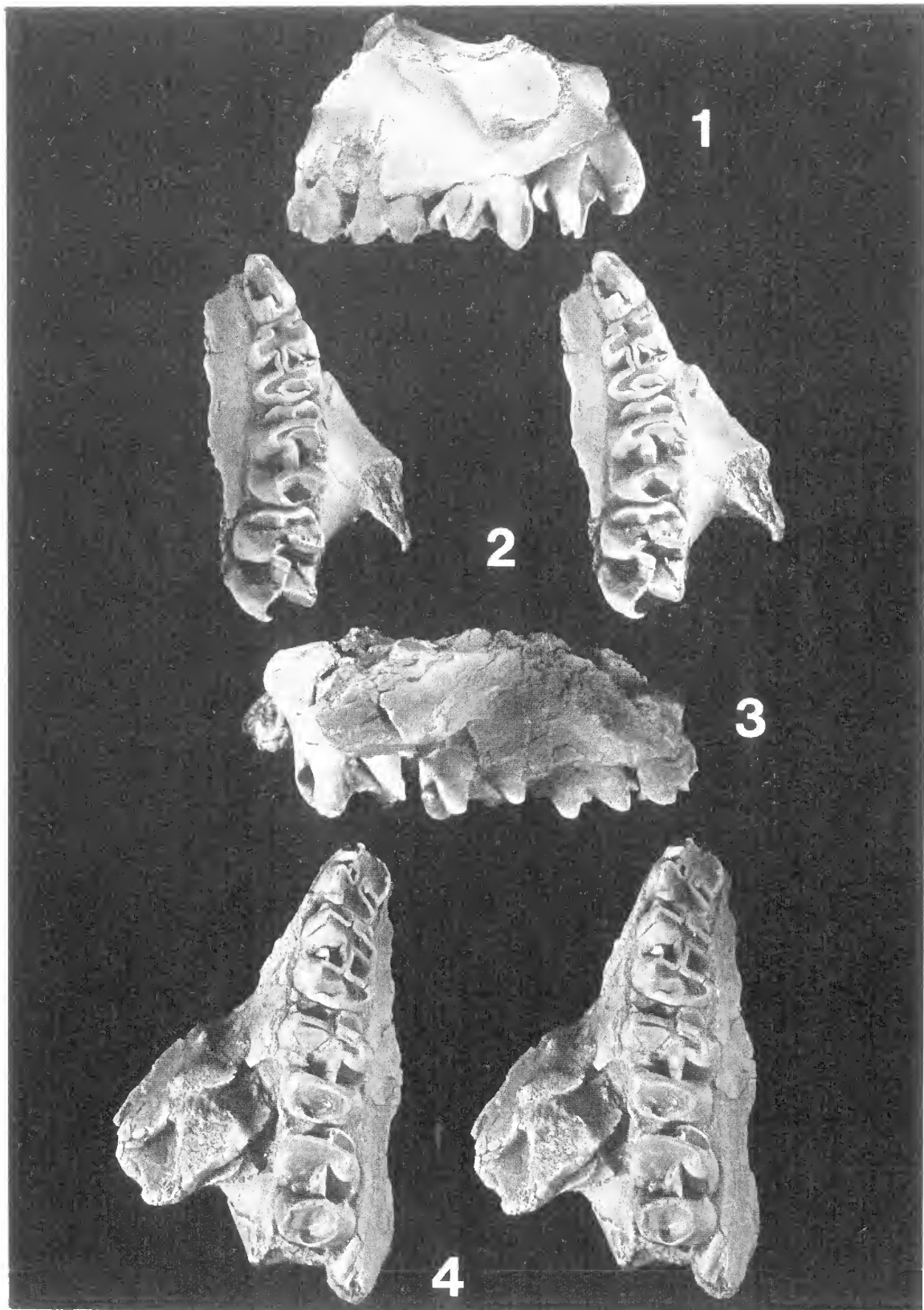


PLATE 17

FIG. 1: *Macropus (Osphranter) pan* De Vis. Lateral view of adult partial left mandibular ramus, F3715, Chinchilla, Darling Downs, natural size.

FIG. 2: *Macropus (Osphranter) pan* De Vis. Stereopair of occlusal view of F3715, natural size.

FIG. 3: *Macropus (Osphranter) pan* De Vis. Lateral view of juvenile partial left mandibular ramus with P₃ removed by fenestration, F3717, Condamine River, near top of bank, 60 metres east of eastern boundary of Chinchilla Rifle Range (Rifle Range No. 78, Par. Chinchilla), Darling Downs, natural size.

FIG. 4: *Macropus (Osphranter) pan* De Vis. Stereopair of occlusal view of F3717, natural size.

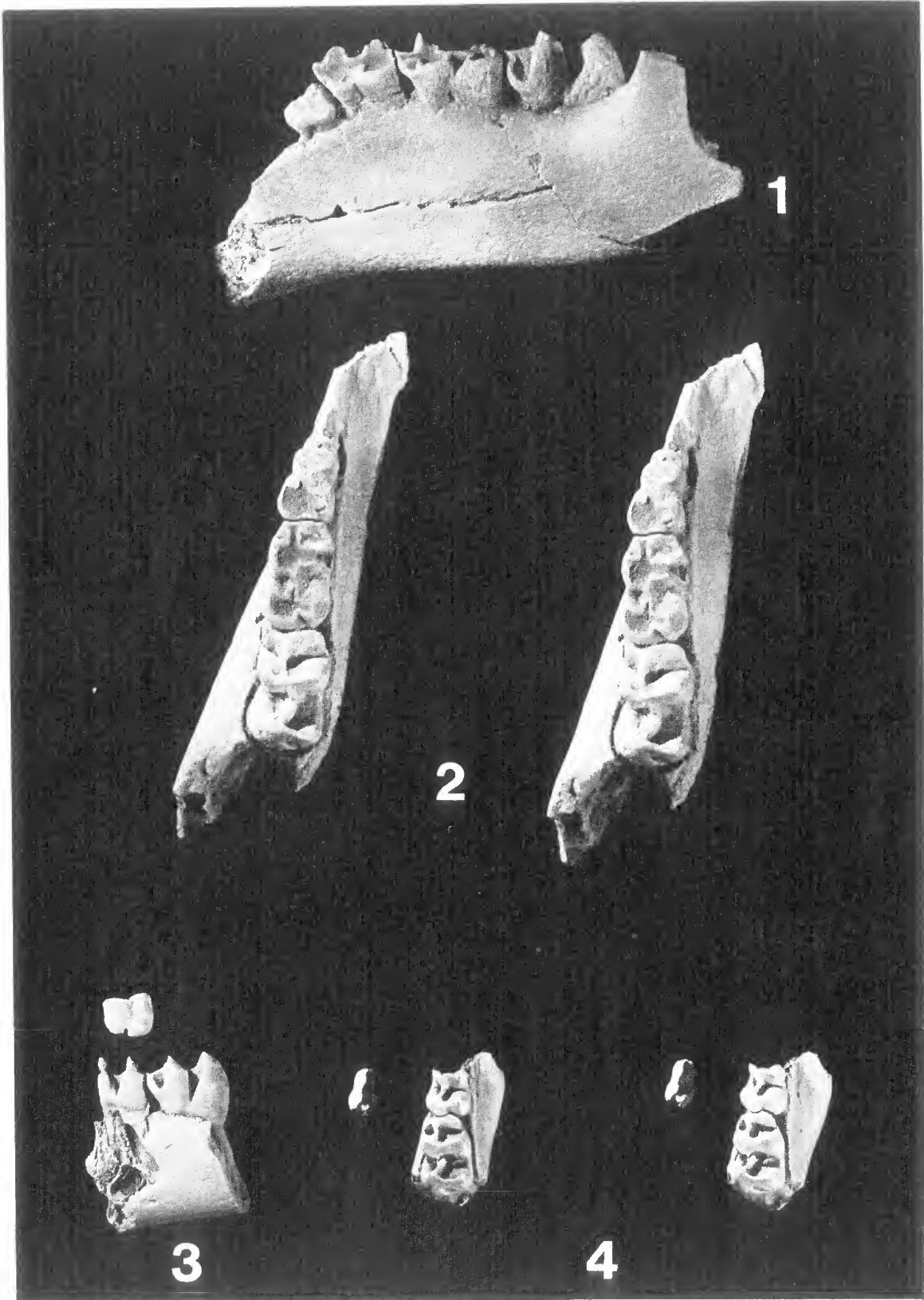


PLATE 18

FIG. 1: *Macropus (Osphranter) pan* De Vis. Lateral view of adult partial left mandibular ramus, F3611, western Darling Downs, natural size.

FIG. 2: *Macropus (Osphranter) pan* De Vis. Stereopair of occlusal view of F3611, natural size.

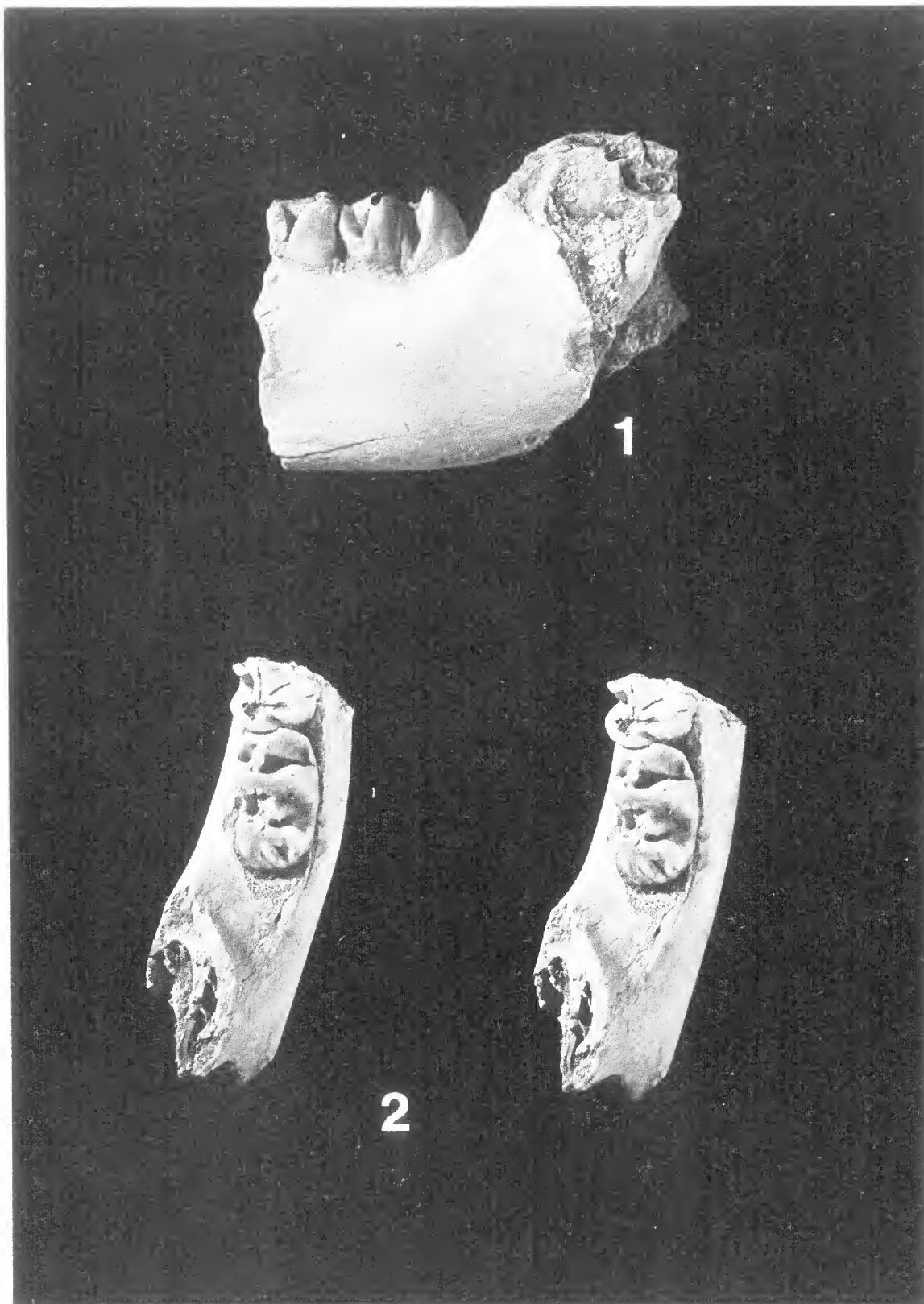


PLATE 19

- FIG. 1: *Macropus (Osphranter) woodsi* sp. nov. Lateral view of holotype, juvenile partial mandibular ramus, F3920, Condamine River end of middle gully system, Chinchilla Rifle Range (Rifle Range No. 78, Par. Chinchilla), Darling Downs, natural size.
- FIG. 2: *Macropus (Osphranter) woodsi* sp. nov. Stereopair of occlusal view of F3920, natural size.
- FIG. 3: *Macropus (Osphranter) woodsi* sp. nov. Lateral view of adult partial right mandibular ramus, F5460, Chinchilla, Darling Downs, natural size.
- FIG. 4: *Macropus (Osphranter) woodsi* sp. nov. Stereopair of occlusal view of F5460, natural size.

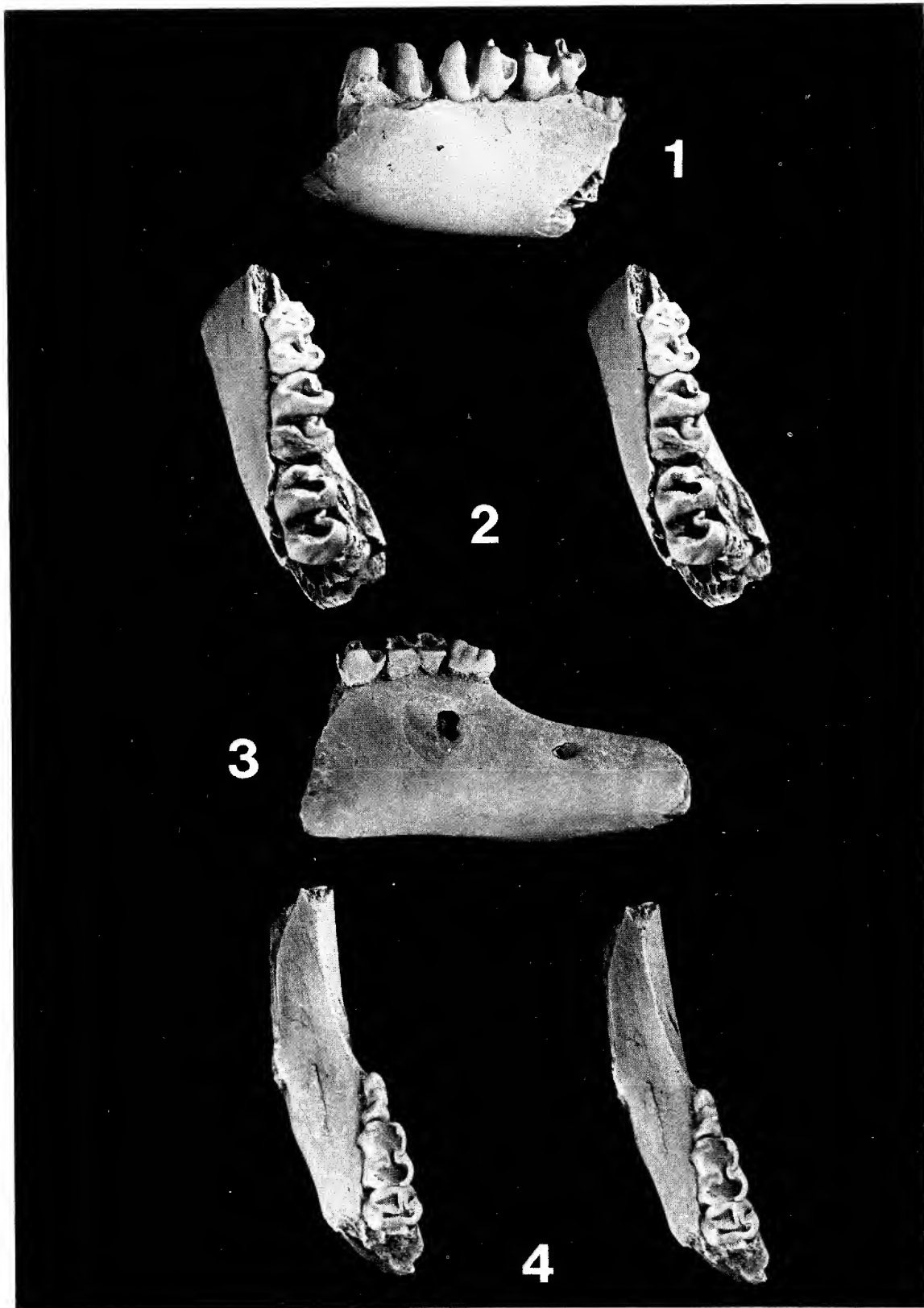


PLATE 20

- FIG. 1: *Macropus (Osphranter) woodsi* sp. nov. Lateral view of adult partial right mandibular ramus, F40, Warra, Darling Downs, natural size.
- FIG. 2: *Macropus (Osphranter) woodsi* sp. nov. Stereopair of occlusal view of F40, natural size.
- FIG. 3: *Macropus (Osphranter) woodsi* sp. nov. Lateral view of adult partial right maxilla, F3718, western Darling Downs, natural size.
- FIG. 4: *Macropus (Osphranter) woodsi* sp. nov. Stereopair of occlusal view of F3718, natural size.

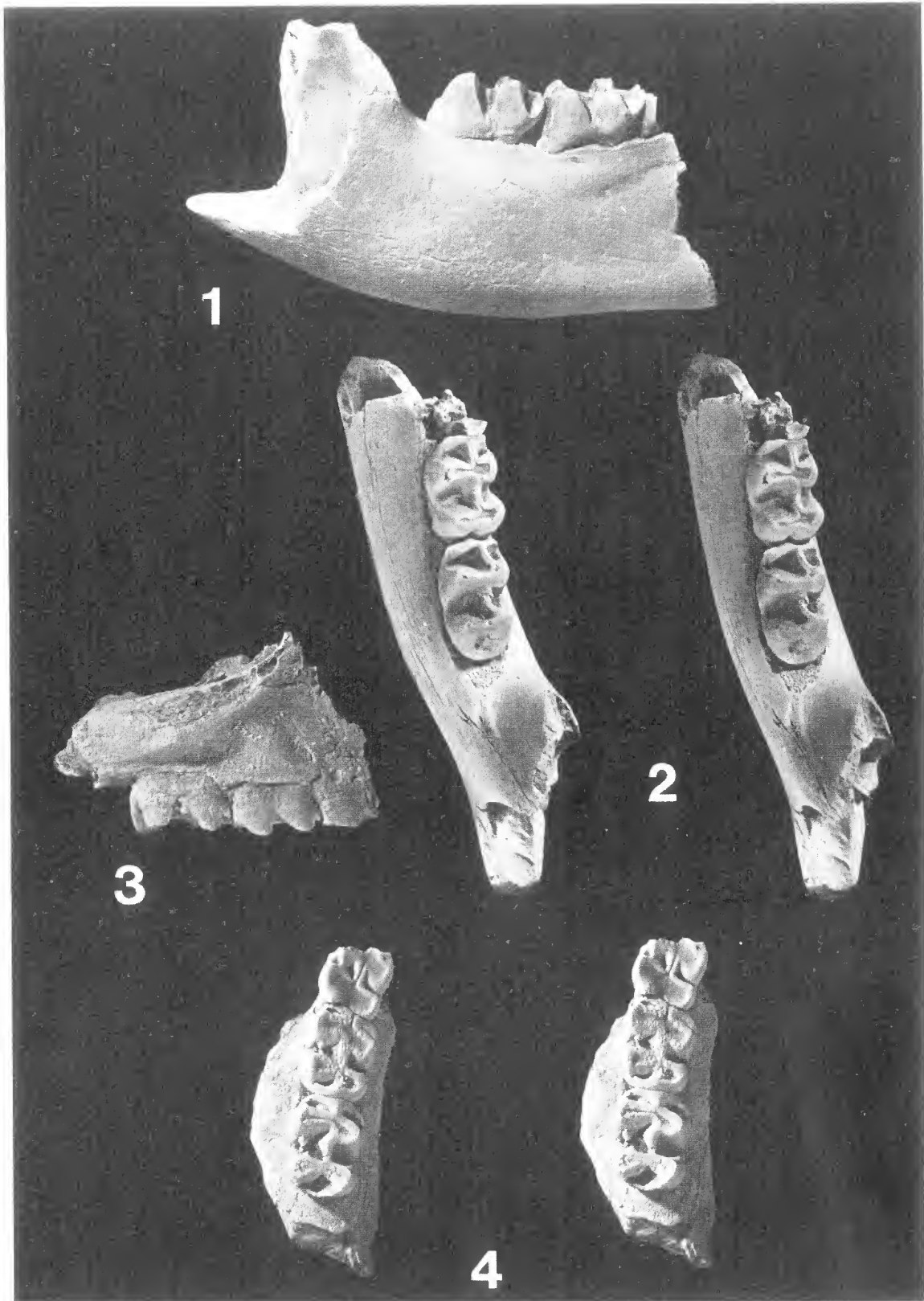


PLATE 21

FIG 1: *Macropus (Prionotemnus) agilis siva* (De Vis). Lateral view of adult partial left mandibular ramus, F4492, Gowrie, Darling Downs, natural size.

FIG. 2: *Macropus (Prionotemnus) agilis siva* (De Vis). Stereopair of occlusal view of F4492, natural size.

FIG. 3: *Macropus (Prionotemnus) agilis siva* (De Vis). Lateral view of juvenile partial right mandibular ramus with P₃ removed by fenestration, F4483, ?Gowrie, Darling Downs, natural size.

FIG. 4: *Macropus (Prionotemnus) agilis siva* (De Vis). Stereopair of occlusal view of F4483, natural size.

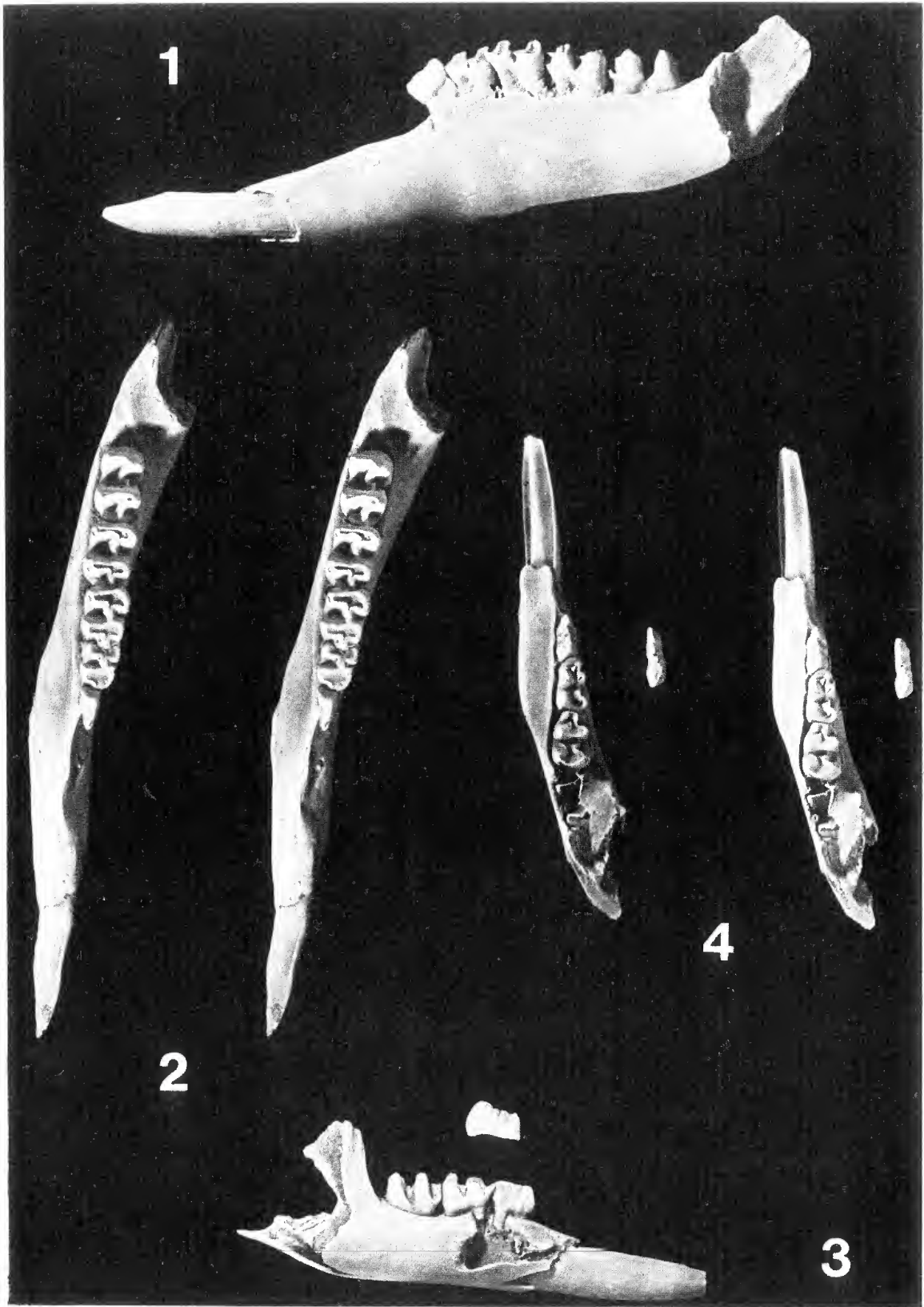


PLATE 22

FIG. 1: *Macropus (Prionotemnus) agilis siva* (De Vis). Lateral view of adult partial cranium, F652, Gowrie, Darling Downs, natural size.

FIG. 2: *Macropus (Prionotemnus) agilis siva* (De Vis). Stereopair of occlusal view of F652, natural size.

FIG. 3: *Macropus (Prionotemnus) agilis siva* (De Vis). Stereopair of occlusal view of juvenile partial left maxilla with P³ exposed by fenestration, F4541, Darling Downs, natural size.

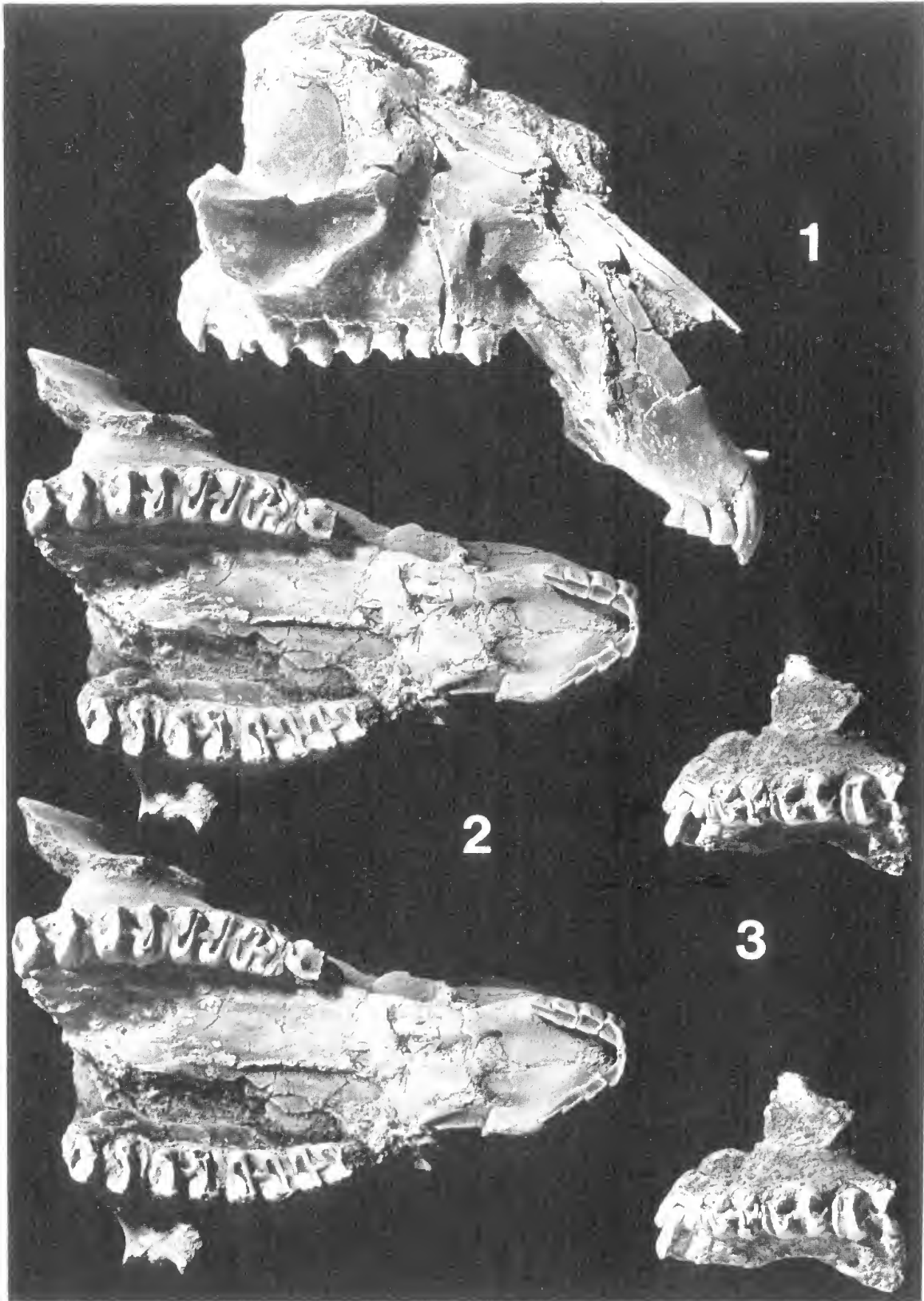


PLATE 23

- FIG. 1: *Macropus (Prionotemnus) thor* (De Vis). Stereopair of occlusal view of adult partial left mandibular ramus, F4553, Clifton, Darling Downs, natural size.
- FIG. 2: *Macropus (Prionotemnus) thor* (De Vis). Lateral view of F4553, natural size.
- FIG. 3: *Macropus (?Prionotemnus) piltonensis* sp. nov. Stereopair of occlusal view of juvenile partial right mandibular ramus, F4576, Ravensthorpe, Pilton, Darling Downs, natural size.
- FIG. 4: *Macropus (?Prionotemnus) piltonensis* sp. nov. Lateral view of F4576, natural size.

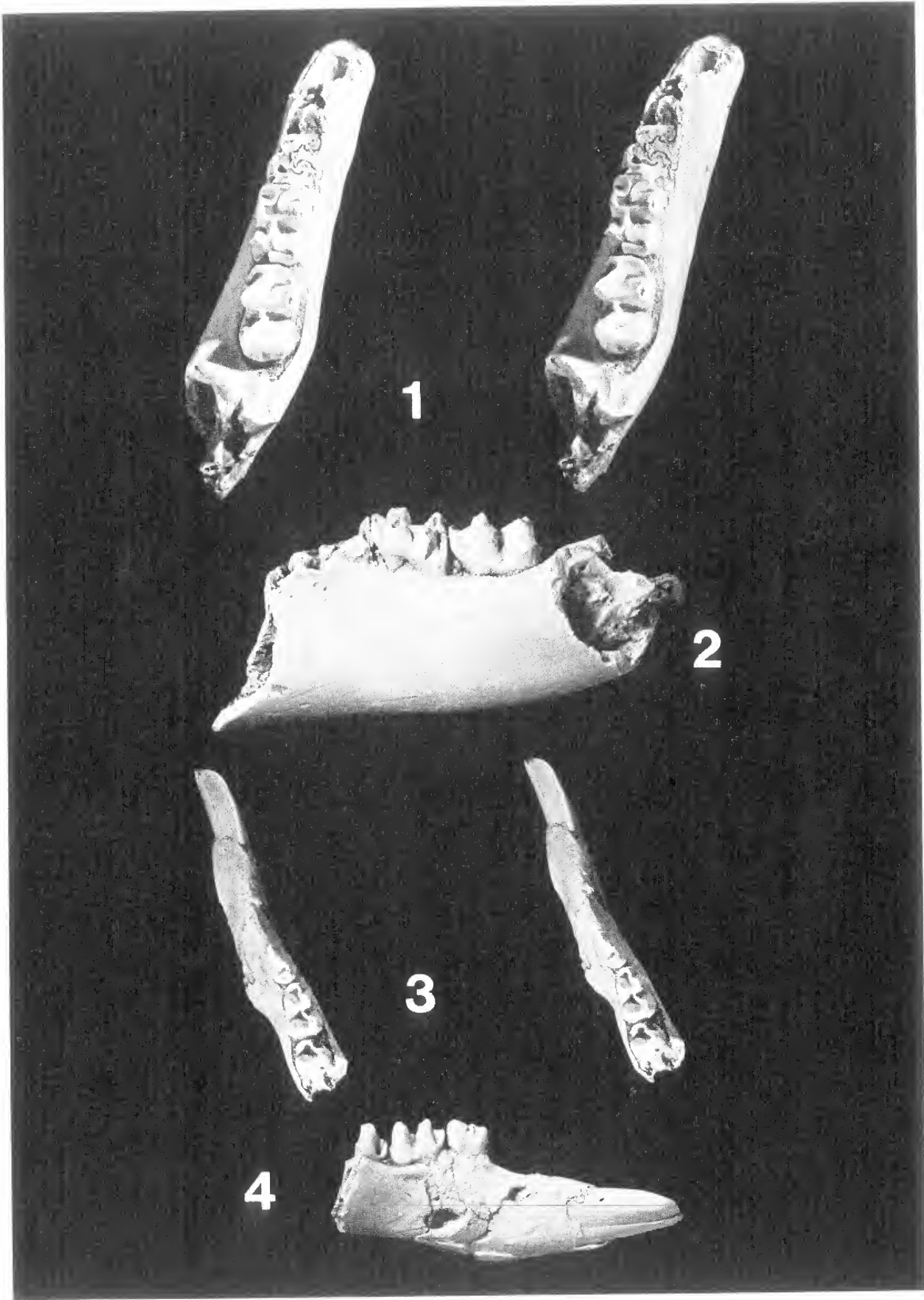


PLATE 24

FIG. 1: *Macropus (Prionotemnus) thor* (De Vis). Stereopair of palate of partial adult cranium, F4550, eastern Darling Downs, natural size.

FIG. 2: *Macropus (Prionotemnus) thor* (De Vis). Lateral view of partial cranium, F4550, natural size.

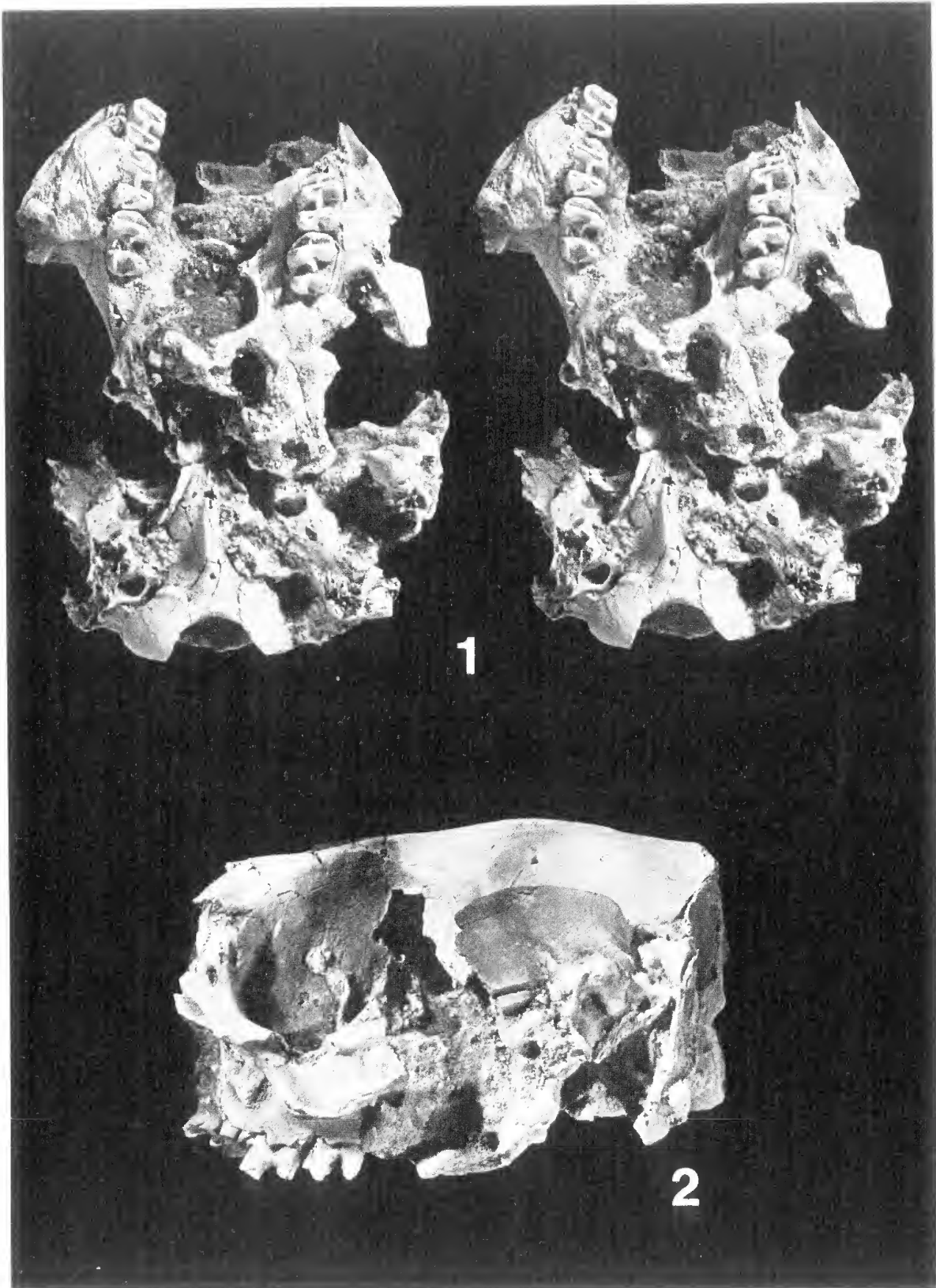


PLATE 25

- FIG. 1: *Macropus (Prionotemnus) dryas* (De Vis). Lateral view of juvenile partial right mandibular ramus, F2508, Chinchilla, Darling Downs, natural size.
- FIG. 2: *Macropus (Prionotemnus) dryas* (De Vis). Stereopair of occlusal view of F2508, natural size.
- FIG. 3: *Macropus (Prionotemnus) dryas* (De Vis). Lateral view of adult partial right mandibular ramus, F4590, Chinchilla, Darling Downs, natural size.
- FIG. 4: *Macropus (Prionotemnus) dryas* (De Vis). Stereopair of occlusal view of F4590, natural size.

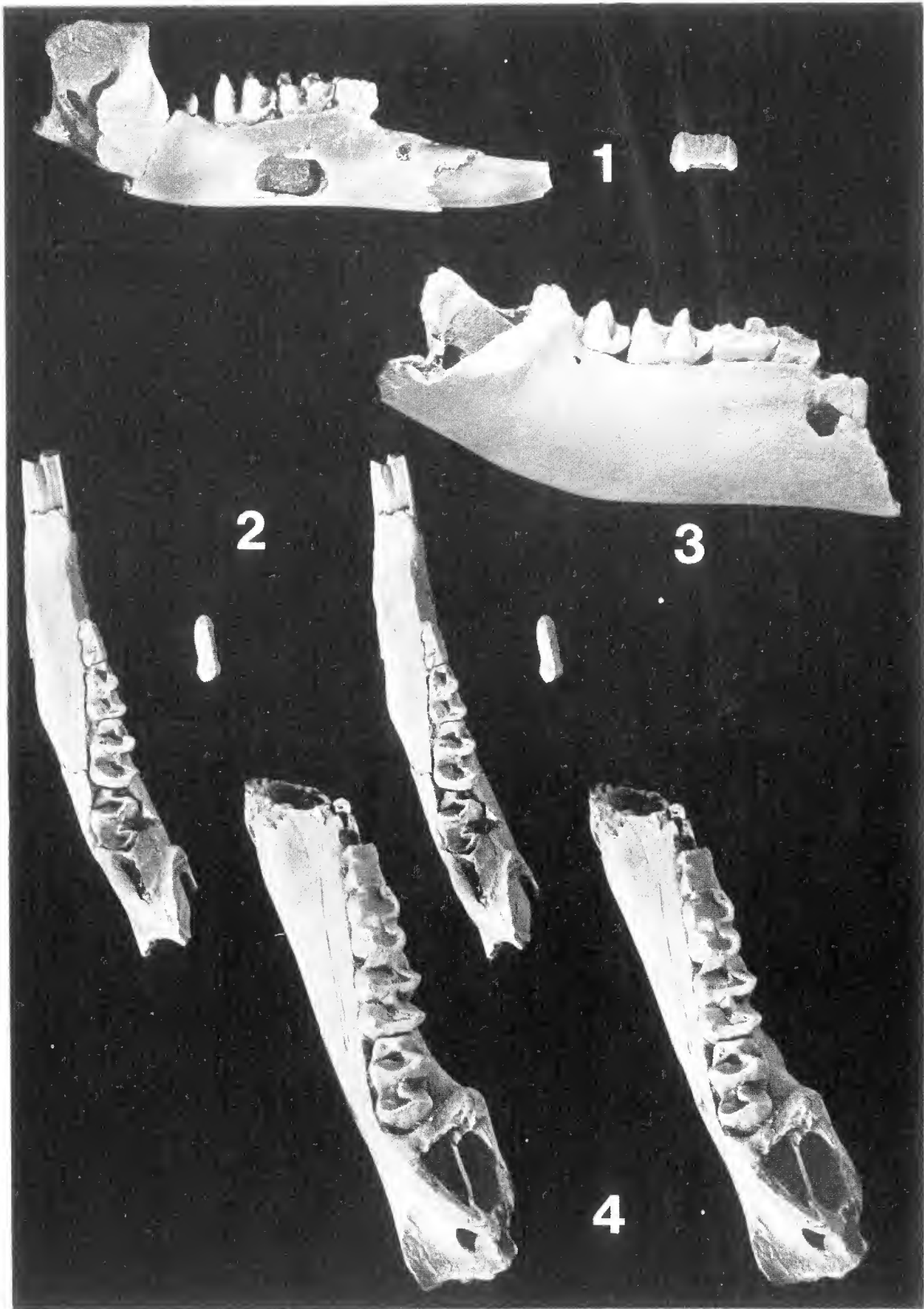
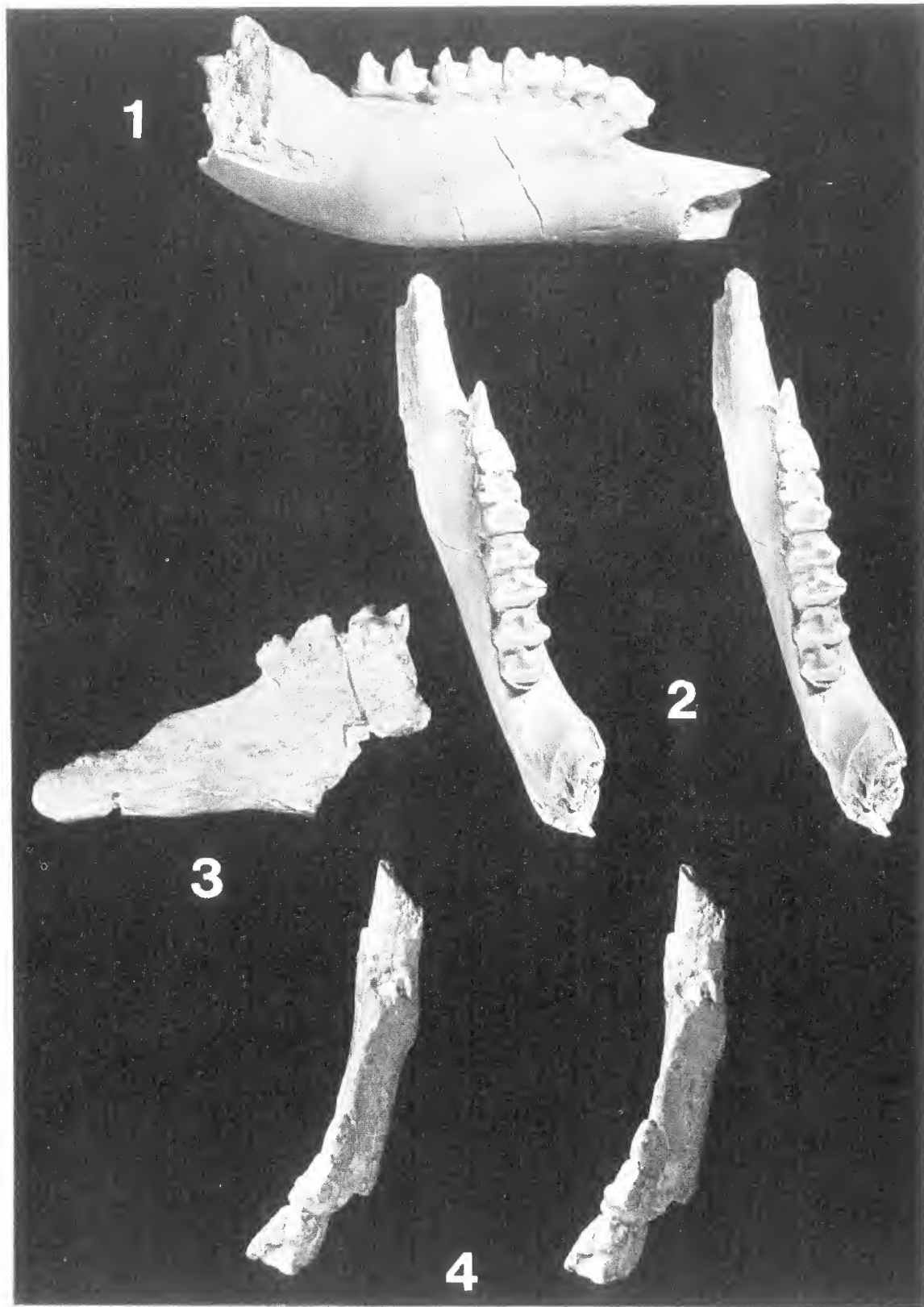


PLATE 26

- FIG. 1: *Macropus (Prionotemnus) palankarinnicus* (Stirton). Lateral view of adult partial right mandibular ramus, F3589, western Darling Downs, natural size.
- FIG. 2: *Macropus (Prionotemnus) palankarinnicus* (Stirton). Stereopair of occlusal view of F3589, natural size.
- FIG. 3: *Macropus (Osphranter) altus* (Owen). Lateral view of cast of holotype of *Macropus cooperi*, F5608, Queensland, natural size.
- FIG. 4: *Macropus (Osphranter) altus* (Owen). Stereopair of occlusal view of F5608, natural size.





NINGAUI, A NEW GENUS OF TINY DASYURIDS (MARSUPIALIA) AND TWO NEW SPECIES, *N. TIMEALEYI* AND *N. RIDEI*, FROM ARID WESTERN AUSTRALIA

MICHAEL ARCHER
Queensland Museum*

ABSTRACT

Ningau is described as a new genus of small dasyurids with two new species, *N. timealeyi* and *N. ridei*. The similarities of species of the genus *Ningau* are greatest with species of *Sminthopsis*, but differ from these in construction of the lateral wall of the skull, structure and relative width of the hind foot, more reduced protocone and paracone, and smaller size. Cranial and dental differences also distinguish species of *Ningau* from those of other similar genera such as *Planigale*, *Antechinomys* and *Antechinus*. *N. timealeyi* from northwestern Western Australia is better-known than *N. ridei* from central Western Australia. Both species occupy relatively arid habitats. Some cranial and dental characteristics are interpreted as arid adaptations. The two species differ from one another in degree of development of the alisphenoid tympanic wing, morphology and size of the post-interdigital hind foot pads, nipple number, and possibly morphology and size of P₁ and P₄.

Some of the small dasyurids were first recognized as a separate group when Gray (1843) transferred six species (*apicalis*, *minimus*, *affinis*, *leucogaster*, *flavipes*, and *leucopus*) from *Phascogale* and *Dasyurus* to the genus *Antechinus*, which has been erected by Macleay (1841) for a single species, *A. stuartii*. Waterhouse (1846) agreed with this grouping and included six additional species, but regarded *Antechinus* as a subgenus of *Phascogale*. Gould (1845) recognized *Antechinus* but separated two of the species (*macrourus* and *crassicaudata*), proposing the name *Podabrus*. As this name was preoccupied by *Podabrus* Westwood, 1840, Thomas (1888) replaced it with *Sminthopsis* in which he included an additional three species (*virginiae*, *murina*, and *leucopus*).

In 1928 a further dasyurid genus, *Planigale*, was proposed by Troughton to receive three of the smallest forms (*ingrami*, *subtilissima*, and *tenuirostris*). *Planigale* Troughton has been universally adopted (except Simpson 1945). Tate (1947) recognizes four species, *P. ingrami*, *P. subtilissima*, *P. tenuirostris* and *P. novaeguineae*.

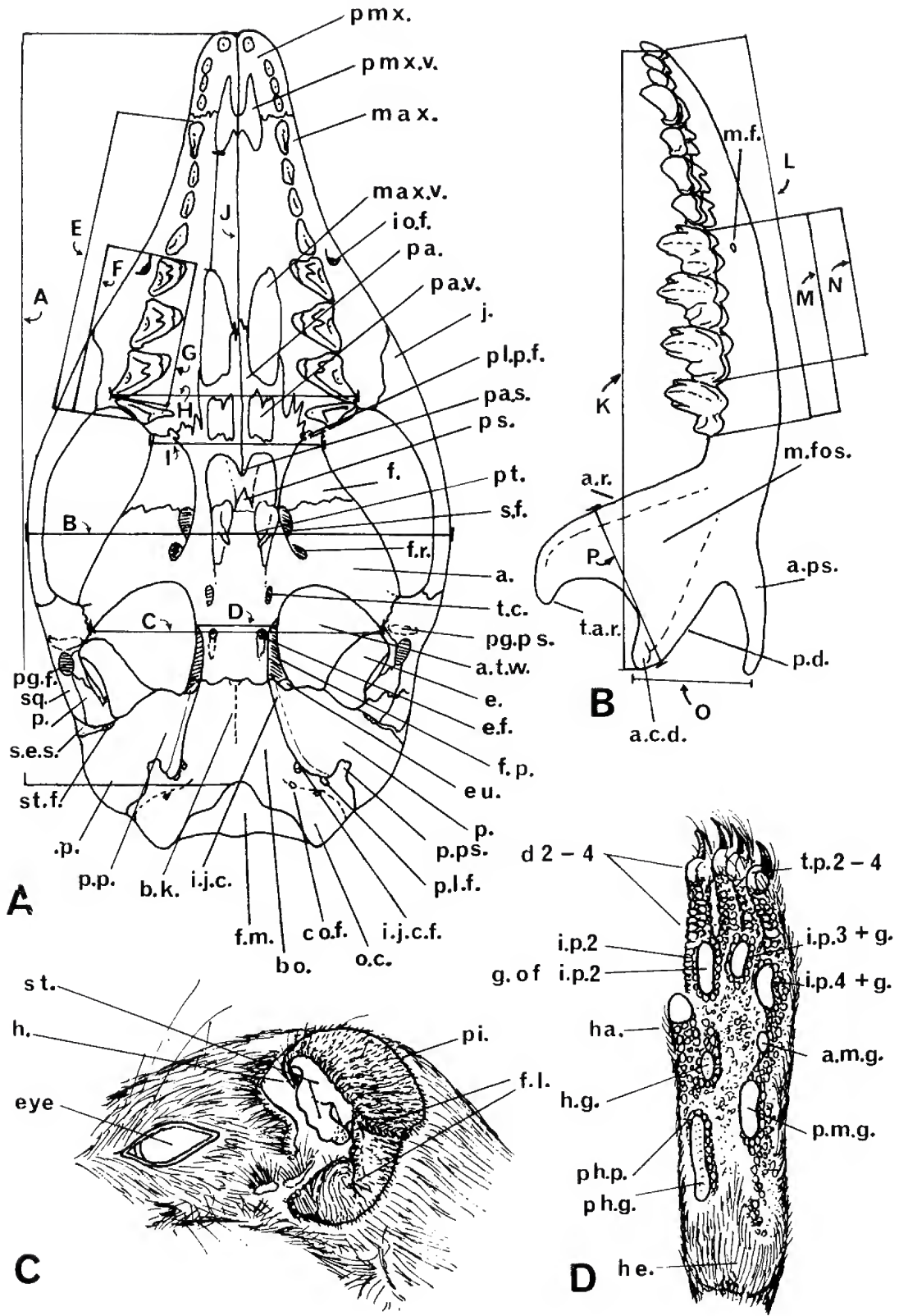
Ride (1970, p. 119) in discussing the Australian species of *Planigale* (i.e. the species not including *P. novaeguineae*) together with *Antechinus maculatus* commented that 'The three ... species ... are commonly put together in one genus, *Planigale*. The fourth species (*maculatus*) is conventionally

placed with other *Antechinus*. The relationships of these minute marsupials is largely a matter of conjecture at present. The flat-headed nature of the group is not absolute and I only follow the usual convention in the generic names with considerable reservation. In addition careful examination of the specimens in collections reveals that there are probably more species than the four usually recognized.'

The specimens studied comprise two new species which are sufficiently distinct from all known genera to warrant the erection of a new genus, *Ningau*. The genus *Planigale*, to which the species had been tentatively assigned by Ride (1970), is re-examined and re-defined.

All catalogue numbers used in this paper unless otherwise indicated are those of the modern mammal collections in the Western Australian Museum. The nomenclature of teeth, hind feet, ears, and basicranial foramina is illustrated in Figs. 1-2. Nomenclature of tooth number follows Archer (1974). Nomenclature of basicranial structures has been determined as part of a broader study of the auditory region of marsupicarnivorans (in preparation).

* Much of this work was carried out at the Western Australian Museum, Perth.



Family DASYURIDAE

Genus *Ningai* nov.TYPE SPECIES: *Ningai timealeyi* sp. nov.

DIAGNOSIS

Dasyurids differing from *Sminthopsis* in being smaller and in having relatively broader pentadactyl hind feet with enlarged apical granules, namely the inner, anterior and posterior metatarsal granules and the hallucal granule; protocone and paracone of M^{1-3} reduced; and no contact between the squamosal and frontal on the outside of the braincase; size as in *Planigale* but differing from these in possessing a relatively narrow hind foot; a curled external edge on the supratragus of the ear; large palatine vacuity; and no posterior cingulum on M^{1-3} .

DESCRIPTION

TAIL: Thin; without brush or crest; approximately equal to or longer than nose-vent (anus) length.

HIND FOOT (Fig. 1D; Plate 28C-D): Apical granules of interdigital and post-interdigital pads* either elongate or round, with or without visible striae or physically expressed striae; pads themselves small; ventral surface of foot without hair except on heel and postero-mesial corner; hallux without claw; and terminal pads of digits smooth.

EAR (Fig. 1C; Plate 27): Supratragus folds back on itself postero-dorsally; helix curls beneath root of supratragus; tragus covered on its anterior edge with short hairs; in pinna, distance between antero-dorsal and antero-ventral points of contact between pinna and head greater than distance from

midpoint of line joining those points and postero-external rim of pinna; one to two fold lines present for retraction of pinna; and no conspicuous notch on external rim of pinna.

NOSE: (Terminology as in Pocock 1926.) Median groove pronounced and to top of rhinarium; pronounced groove demarcating whole of external rim of rhinarium; and nostrils centrally placed on each side.

VIBRISSAE: Mystacial vibrissae on each side in five to six ill-defined rows with three to five vibrissae in each row; three to six genal vibrissae; one supra-orbital vibrissa; and two to three carpal vibrissae.

SKULL AND DENTARY: (Figs. 1A-B, 3-4; Plate 29) Nasals parallel or only slightly widened posteriorly, about as in *Sminthopsis*; premaxillary-nasal contact generally longer than nasal-maxillary contact; very slight medial depression in skull between antero-dorsal corners of frontals; no postorbital process on frontal; interorbital constriction narrow and this region distinctly not tubular; lacrimal canal (either one or two on each side) inside or on rim of orbit; infraorbital foramen very large and opens onto surface of maxilla without contact with jugal; lacrimal large but without postero-dorsal spine; venous foramen of frontal conspicuous on dorsal rim of orbit; lack of contact between squamosal and frontal and broad contact between parietal and alisphenoid; premaxillary palatal vacuity does not extend posteriorly beyond alveolus of canine; maxillary vacuity does not extend anteriorly beyond level of M^1 ; palatine vacuity large; incomplete to absent postero-lateral palatal foramen; conspicuous posterior palatal spine; no obvious interdental fenestrae perforating palate; pterygoid with spinous hamular process; alisphenoid tympanic wing large;

*The term post-interdigital is used to include the hallucal and metatarsal granules collectively.

FIG. 1: A, B. Terminology and mensuration of the skull and dentary of *Ningai* spp., based on WAM M8041 and WAM M6181. *a.*, alisphenoid; *a.t.w.*, alisphenoid tympanic wing (or bulla); *a.c.d.*, articular condyle of dentary; *a.p.s.*, angular process; *a.r.*, anterior face of ascending ramus; *bo.*, basioccipital; *b.k.*, basioccipital keel; *co.f.*, condylar and/or hypoglossal foramen; *e.*, ectotympanic; *e.f.*, entocarotid foramen; *eu.*, eustachian canal opening; *f.m.*, foramen magnum; *f.p.*, foramen pseudovalve; *i.o.f.*, infraorbital foramen; *j.*, jugal; *i.j.c.*, internal jugular canal; *i.j.c.f.*, internal jugular canal foramen; *max.*, maxilla; *max.v.*, maxillary vacuity; *m.f.*, mental foramen; *m.fos.*, masseteric fossa; *o.c.*, occipital condyle; *p.*, periotic; *pa.*, palatine; *pa.s.*, palatine spine; *pa.v.*, palatine vacuity; *p.d.*, posterior border of dentary; *pg.f.*, postglenoid foramen; *pg.ps.*, postglenoid process; *p.l.f.*, posterior lacerate foramen; *pl.p.f.*, postero-lateral palatal foramen; *pmx.*, premaxilla; *pmx.v.*, premaxillary vacuity; *p.p.*, petrosal tympanic wing of periotic; *ps.*, presphenoid; *pt.*, pterygoid; *s.e.s.*, squamosal epitympanic sinus; *s.f.*, sphenorbital fissure or foramen; *st.f.*, stylomastoid foramen; *sq.*, squamosal; *t.a.r.*, tip of ascending ramus; *t.c.*, transverse canal. A-P indicate measurements given in Table 2.

C. Terminology of the left ear based on WAM M8041. *f.l.*, fold lines of pinna; *h.*, helix; *pl.*, pinna; *st.*, supratragus.

D. Terminology of the left hind-foot, based on WAM M6181. *a.m.g.*, anterior metatarsal granule; *d2-4*, digits 2 through 4; *g. of i.p.2*, apical granule of 2nd interdigital pad; *ha.*, hallux; *he.*, heel; *h.g.*, hallucal granule; *i.p.2*, 2nd interdigital pad; *i.p.3 + g.*, 3rd interdigital pad and apical granule; *i.p.4 + g.*, 4th interdigital pad and apical granule; *ph.g.*, post-hallucal granule; *ph.p.*, post-hallucal pad; *p.m.g.*, posterior metatarsal granule; *t.p.2-4*, terminal pads 2 through 4.

periotic tympanic wing (from petrosal part) well-developed; mastoid tympanic wing only just developed; ectotympanic develops very small tympanic wing in forms with smallest alisphenoid tympanic wing (*N. timealeyi*); paroccipital does not develop a tympanic wing although it encloses a small non-auditory sinus; squamosal develops small epitympanic sinus continuous with postglenoid cavity; an abrupt break occurs in the periotic's lateral surface at the level of the horizontal semicircular canal; the mastoid part of the periotic is swollen laterally, the result of a grossly enlarged floccular fossa; foramen pseudovale long and narrow; no true foramen ovale ever develops; entocarotid foramen large, mesial to foramen pseudovale, and leads via short canal to endocranium; no direct ventral observation through entocarotid foramen possible; transverse canal large and pierces basisphenoid mesial to anterior ends of alisphenoid tympanic wings; transverse canal foramen leads directly into endocranial sulcus for entocarotid artery and does not appear to pass transversely through basisphenoid; postglenoid foramen pierces postglenoid cavity immediately posterior to postglenoid process and is separated by thin transparent bone from the much enlarged subsquamosal foramen; entire roof of postglenoid cavity thin, transparent, and functions solely to floor large postglenoid canal; posterior surface of postglenoid process almost horizontal and continuous with roof of postglenoid cavity; rim of postglenoid foramen penetrated anteriorly by postzygomatic foramen which leads into zygomatic arch; small branch of postzygomatic penetrates external surface of zygomatic arch; internal jugular canal very well-developed between basioccipital and periotic with a very steep to vertical basioccipital wall; internal jugular canal actually penetrates basioccipital at anterior end; posterior lacerate foramen passes between paroccipital and periotic dorso-mesially to paroccipital process; complete stylomastoid foramen bordered anteriorly by periotic with small slip of squamosal on ventro-lateral rim; small foramen rotundum floored by variably enlarged shelf of alisphenoid; large sphenorbital fissure; basisphenoid with median ventral keel; ectotympanic wide with marked sulcus and crest associated with pars tensa of tympanic membrane; anterior (dorsal) end of ectotympanic helps enclose mesial wall of postglenoid canal; anterior end of ectotympanic pointed, posterior end blunt; incus as in *Sminthopsis* and other small dasyurids, articulates (not fused) with malleus, with short incudal and long stapedial processes, latter with oval lenticular process at distal end; malleus with pronounced orbicular

apophysis, small anterior dorsal spine on head, pronounced capitular crest and lamina, and non-expanded distal tip on manubrium; tubular periotic hypotympanic sinus and almost total lack of development of mastoid epitympanic sinus; incudal fossa of epitympanic recess of periotic large, with well-developed lateral squamosal wall; no sulcus or canal connects facial nerve canal or sulcus with postglenoid canal; periotic horizontal antero-lateral projection from epitympanic recess contacts postglenoid foramen and almost excludes squamosal from roof of postglenoid cavity; facial nerve canal large and sulcus well-developed; small foramina sometimes (e.g. WAM M6181) pierce mastoid tympanic wing; fenestra ovalis subrounded rather than oval; endocranial structure of periotic largely unknown because specimens intact but clear that floccular fossa very large and deep, internal auditory meatus divided into widely separate passages for facial and auditory nerves; squamosal reduced in all directions by surrounding bones and squamosal hypotympanic sinus also small; stapes as in other dasyurids, imperforate, columnar, and with small posterior process for attachment of stapedial muscle and tendon; dentary shallow ventral to teeth; lateral surface of ascending ramus wide; angular process long and slender; mental foramen beneath M_1 or M_2 .

DENTITION: (Fig. 2; Plate 28A, B). I^1 tallest upper incisor and set off from I^2 by diastema; I^2 taller-crowned or subequal to I^3 which is taller-crowned than I^4 ; I^2 - I^4 subequal in crown length; slight buccal cingula developed I^1 - I^4 ; I^4 lacks posterior cingular cusp or lobe; diastema separates I^4 from C^1 ; C^1 taller-crowned than any premolar except sometimes P^4 which may be subequal in size; C^1 - P^4 not crowded in adult condition, small spaces separating all teeth; in adult condition P^1 just shorter-crowned than P^3 which is markedly shorter-crowned than P^4 ; buccal cingula complete C^1 - P^3 but incomplete P^4 and sometimes incomplete C^1 ; lingual cingula complete P^1 - P^3 but incomplete C^1 and P^4 ; posterior and anterior cingular cusps present P^1 - P^4 but only posterior cusp present C^1 ; anterior cingular cusps may be small on C^1 , P^1 and P^4 ; P^4 blade-like with convex postero-buccal flank; DP^4 (WAM M8081) small with two very closely approximated cusps, paracone and metacone, a very small and low protocone, and no styler cusps; all cusps except protocone linked by longitudinal buccal crest; M^1 narrower than M^2 which is subequal to M^3 which is wider than M^4 ; M^1 longer than M^2 which is longer than M^3 which is longer than M^4 ; paracone increases in size posteriorly but is reduced overall relative to most other dasyurids;

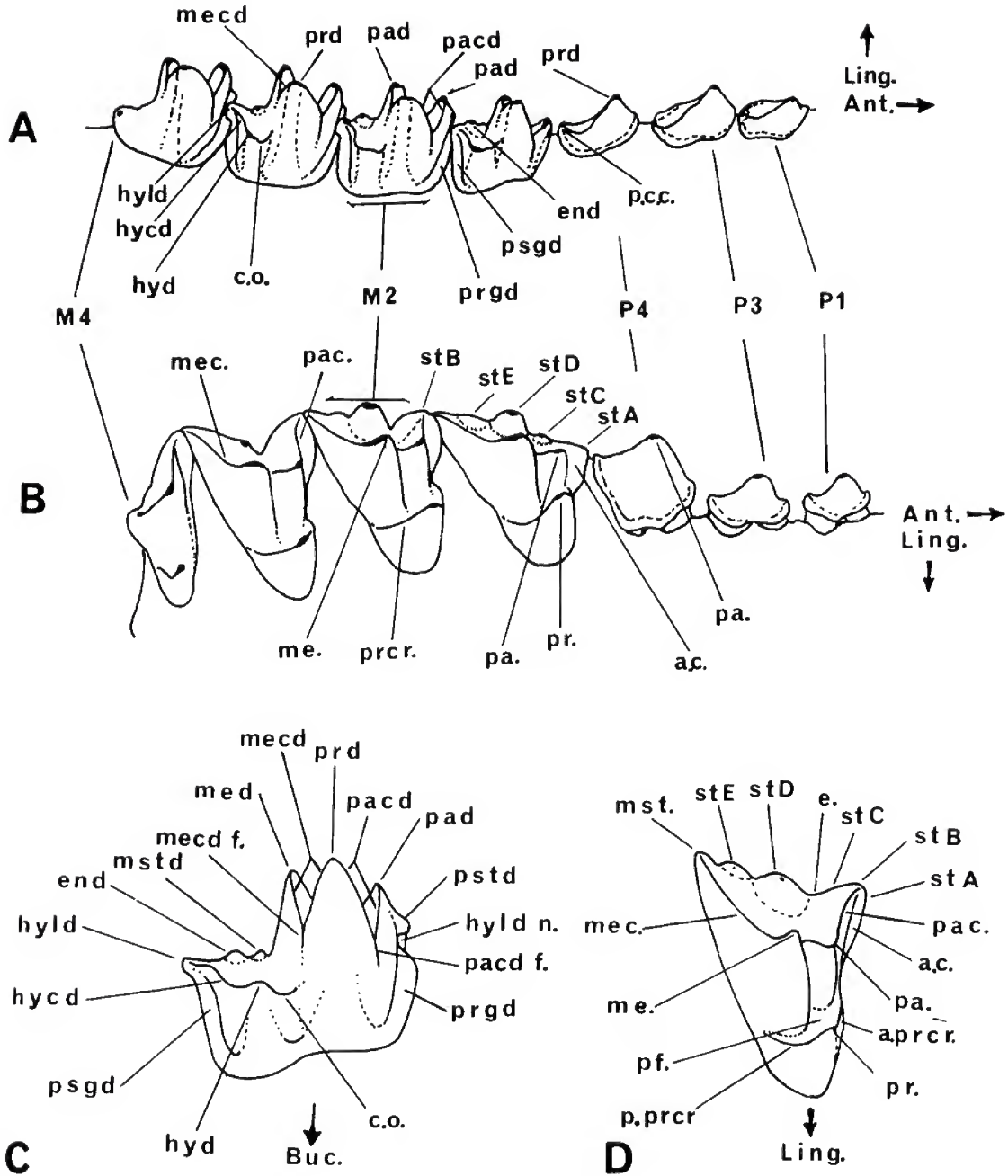


FIG. 2: The terminology of the dentition of *Ningaui* spp. A, lower right P₁-M₄. B, upper right P¹-M⁴. C, lower right M₃. D, upper right M₃.

a.c., anterior cingulum; *a.prcr.*, anterior protoerista or preprotoerista; *c.n.*, carnassial notch; *c.o.*, crista obliqua; *e.*, ectoflexus; *end*, entoconid; *hycd*, hyporistid; *hyd*, hypoconid; *hyld*, hypoconulid; *hyld.n.*, hypoconulid notch; *me.*, metacone; *mec.*, metaerista; *mecd*, metaeristid; *mecd.f.*, metaeristid fissure or cranassial notch; *med*, metaconid; *mst.*, metastylar corner of tooth; *mstd*, metastylid; *pa.*, paracone; *pac.*, paracrista; *pacd.*, -aracristid; *pacd.f.*, paracristid fissure or cranassial notch; *pad*, paraconid; *p.c.c.*, posterior cingular cusp; *pf.*, prefossa; *p.prcr.*, posterior protoerista or postprotoerista; *pr.*, protocone; *prd*, protoconid; *prgd*, precingulid or anterior cingulum; *psgd*, posteingulid or posterior cingulum; *pstd*, parastylid; *stA*, stylar cusp A or position of stA; *stB*, stylar cusp B; *stC*, stylar cusp C or position of stC; *stD*, stylar cusp D; *stE*, stylar cusp E.

paracone and metacone approximated; metacone M^2 taller than subequal metacones M^1 and M^3 ; metacone M^4 absent; protocone small overall and decreases in size posteriorly; very slight protoconule development M^{1-3} ; no metaconule development; protocone basin opens posteriorly; anterior cingulum complete M^1 only antero-buccal cingula well-developed M^{1-4} ; no posterior cingula; stD present M^{1-3} and decrease in size posteriorly; stB present or position at end of paracrista clear M^{1-4} ; stB M^1 variably developed and may even be absent in some specimens (e.g. WAM M6181) where stB and stA may be indistinguishable; stE variably present M^{1-3} and if present tiny; stA indistinguishable M^{2-3} and sometimes M^1 ; paracrista increases in size posteriorly M^{1-4} ; metacrista M^1 just shorter than that of M^2 which is longer than that of M^3 ; ectoflexus increases posteriorly from M^1 to M^3 ; I_1 taller-crowned and longer than I_2 which is taller-crowned and larger than I_3 ; I_{1-3} with slight postero-buccal cingula; poorly-developed posterior cingulum I_3 ; no diastema between I_3 and C_1 ; C_1 with buccal and lingual cingula; C_1 premolariform but just taller-crowned than any premolar; P_1 shorter-crowned than P_3 which is longer-crowned than P_4 ; C_1-P_3 wide and contrast with relatively narrow P_4 ; small anterior but well-developed posterior cusps present P_{1-4} ; well-developed buccal but slightly-developed lingual cingula P_{1-4} ; premolars contact one another antero-posteriorly but are not crowded; dP₄ two-rooted with one main cusp, the protoconid, and possibly a very small posterior cingular cusp; M_{2-4} subequal in length and just longer than M_1 ; talonid M_1 wider, M_2 subequal to, and M_{3-4} narrower than talonid; protoconid increases in height posteriorly from M_1 to M_3 ; protoconid M_4 subequal to that of M_1 ; metaconid M_1 just shorter than subequal metaconids M_{2-4} ; paraconid M_{1-4} increases in height posteriorly; hypoconid subequal in height M_{1-3} but just shorter in M_4 ; entoconid miniscule M_{1-4} and variably absent M_4 ; extremely tiny metastylid sometimes present (e.g. WAM M8080) M_{2-3} ; notch for hypoconulid or its homologue in P_4 occurs in anterior cingulum M_{1-4} ; anterior and posterior cingula well-developed M_{1-4} ; slight buccal cingula formed only on M_1 ; no lingual cingulum M_{1-4} or posterior cingulum M_4 ; paracristid M_1 shorter than and directed more anteriorly than that crest in M_{2-4} ; paracristid M_4 shorter than subequal paracristids M_{2-3} ; metacristids M_{1-3} increase in length posteriorly; metacristid M_4 shorter than that of M_3 ; carnassial notch metacristids well lingual to midpoint of crest; hypocristid longest in M_2 , subequal in M_1 and M_3 , and shortest or absent in M_4 ; crista obliqua longest

in M_4 and subequal in M_{1-3} ; crista obliqua intersects trigonid well buccal to point below metacristid carnassial notch on all molars except M_4 where this crest intersects trigonid below metaconid; hypocristid links hypoconid and hypoconulid and does not contact very small entoconid; metacristid and hypocristid M_{2-4} almost transverse to long axis of cheek-tooth row; difference in height of smaller paraconid and larger metaconid decreases posteriorly from M_1 to M_4 , two cusps being subequal in M_4 ; hypoconulid locks into gap (hypoconulid notch) of antero-lingual cingulum of each posterior molar; no cristid links hypoconulid and entoconid; well-developed fissure in paracristid and slight fissure in metacristid M_{2-4} ; these fissures in M_1 very small; tiny parastylid variably developed on M_{1-4} .

DISCUSSION

In diagnosing *Ningau* comparison has been made with *Sminthopsis* and *Planigale*. There is little risk of confusion with larger forms such as *Antechinus* or *Phascogale*, or with the long-limbed form *Antechinomys* which in a number of characteristics is very similar to some species of *Sminthopsis*. The species of *Antechinomys* share the same characters with species of *Sminthopsis* that enable those species to be distinguished from species of *Ningau*, i.e. long narrow hind feet (in *Antechinomys* there is additionally a total loss of the hallux) without enlarged post-interdigital granules, and a broad contact on the outside of the skull between the squamosal and frontal bones.

The characters used in the diagnosis of *Ningau* are not all absolute because some are not expressions of exclusive presence in or absence from *Ningau*. *Ningau* must be related to other taxa and it is to be expected that even the diagnostic characters of the genus will reflect these relationships.

The use of the character of the post-interdigital enlarged granules in the diagnosis should not be taken to imply that these granules are invariably small in *Sminthopsis*. Some species of *Sminthopsis* possess slightly or variably enlarged post-interdigital granules, but none have all four post-interdigital granules conspicuously enlarged. For example in the four known specimens of *S. longicaudata*, the three which have feet preserved show an enlarged hallucal and a single enlarged metatarsal granule. However, this species is at once distinguishable from species of *Ningau* by its possession of the other *Sminthopsis* characters noted above as well as by the extremely long tail (twice the length of the head and body). *Sminthopsis murina* and *S. leucopus* are species which do not

normally possess enlarged metatarsal granules, but one and even two metatarsal granules, as well as a hallucal granule, sometimes occur in abnormal specimens. For example, WAM M1854 *S. murina* has an enlarged hallucal, post-hallucal and slightly enlarged posterior metatarsal granule. Some specimens (e.g. Macleay Museum M1183) of *S. rufigenis* from the Herbert River in Queensland have a slightly enlarged oval posterior metatarsal granule and an enlarged hallucal granule. These species of *Sminthopsis*, however, are otherwise unlike species of *Ningai*.

In considering the diagnostic dental characters of *Ningai*, *Sminthopsis ooldea* (= *Sminthopsis murina ooldea* Troughton, 1965) demonstrates some of the dental characters of species of *Ningai*. For example WAM M8077 has slightly reduced paracones and talonids, although the degree of reduction is not as great as that in species of *Ningai*. In all other respects *S. ooldea* possesses *Sminthopsis* characters and is easily distinguished from specimens of species of *Ningai*.

Because of the blurring of these diagnostic characters between *Ningai* and *Sminthopsis* it is tempting to regard *Ningai* as a possible derivative or ancestor of that genus. Many of the characters of *Ningai* occur in *Sminthopsis* as well, where they occur as arid-adaptations of the structurally more generalized form. For example, a detailed study of *Sminthopsis* (in preparation) reveals that there are several species-groups which probably have achieved arid-adaptation independently. Characters involved in such arid-adaptation include small body size, relatively short premolar rows, well-evacuated palates, and high-crowned teeth. Some of these characters can possibly be interpreted as mechanical rather than physiological specializations demanded by thick cuticles of prey species of that environment. In the case of these very small mammals, prey species are likely to be insects with hard cuticles and small vertebrates such as skinks. To masticate such foods it is necessary to have teeth mainly adapted to shear; this may be the reason for the relatively enlarged metacones and trigonids. However, some characters cannot, at present, be understood as mechanical adaptations, such as the lack of contact between the squamosal and frontal. The presence of a squamosal-frontal contact has a peculiar distribution among marsupials. It is present in some *Autechinus macdonnellensis*, *Neophascogale* and *Phascosorex* spp., some *Phascolarctos cinereus* (Ride 1957), Vombatids, all *Sminthopsis* spp., *Thylacinus* spp., at least some borhyaenids (those whose condition can be determined from figures of Sinclair 1906), hypsiprimnodontine and potoroine macropodids

(Pearson 1950), peramelids (*ibid*, and all living genera checked by the present author), zygomaturine, palorchestine and nototheriine diprotodontids (Stirton 1967, Woodburne 1967). It is not present in other dasyurids, macropodine macropodids (Pearson 1950), didelphoids (*ibid* and absence confirmed in this study in *Didelphis*, *Marmosa*, *Monodelphis*, *Metachirus*, and *Philander*), caenolestoids (*ibid* and confirmed in this study in *Caenolestes*), and all other phalangeroids. The absence of this character from all didelphoids and caenolestoids does not suggest that, among marsupials in general, the character is primitive. Moreover, among Australian marsupials it is absent from generalized phalangeroids. If the presence of a squamoso-frontal contact is primitive it would seem that a number of marsupial phyla have achieved it independently from more primitive forms.

I would suggest that the characters of *Sminthopsis* are a derivation from a non-arid-adapted *Ningai*-like ancestor.

ORIGIN OF GENERIC NAME

The generic name *Ningai* is here given masculine gender. It is an Aboriginal name given to tiny mythological beings that are hairy, have short feet, and only come out at night to hunt for food all of which is eaten raw (Roberts and Mountford 1969). The allusion to these dasyurids involves their very tiny size, hairy and (compared with the related dasyurid *Sminthopsis* spp.) short feet, and nocturnal habits.

SPECIES

The genus *Ningai* contains two species: *N. timealeyi* and *N. ridei*.

Ningai timealeyi sp. nov. (Figs. 1–3; Plates 28A–C, 29A)

Planigale tenuirostris: Ride, 1970, pp. 120, 200 (in part) (*nec* Troughton 1928).

HOLOTYPE: Western Australian Museum specimen WAM M6181, young adult female, skull, dentaries, and carcase in spirit, collected by Mr A. Snell, 7 July 1963, 32.2 km southeast of Mt. Robinson, northwestern Western Australia. Specimen 'caught while escaping burning Spinifex'.

PARATYPES: WAM M5076, male collected 1957 (E. H. M. Ealey, *in litt.*, 19 September 1972) by Dr E. H. M. Ealey from aerodrome of Abydos Station, W.A. (21°25'S 118°54'E). WAM M8041, male, collected July 1969 by Mr T. Fletcher at Kangan Station, W.A. (21°09'S 118°30'E). WAM M8042, male, collected June 1969 by Mr T. Fletcher from Pilbara Townsite, W.A. (21°15'S 118°18'E).

REFERRED SPECIMEN: WAM M8729, female, found by Messrs A. Baynes and M. K. Youngson 15 December 1968, in small cave in breakaway about 30 m above sea level, on North West Cape near lighthouse (21°48'S 114°6'E). Found freshly killed with head missing, presumably removed by predator. Specimen referred to *N. timealeyi* on basis of foot structure and general appearance.

DIAGNOSIS

This species differs from *N. ridei* as follows: Inner and outer posterior metatarsal granules of hind feet elongate; distal end of hallux extends to level of or beyond posterior edge of interdigital pads; hind foot relatively short (HF/NV ratio between 0.17 and 0.20); supratragus of ear relatively long antero-posteriorly; tail exceeds nose-vent length; alisphenoid tympanic wing relatively less well-developed (M^{1-3} /outside bullar distance—inside bullar distance value 0.69); I^2 length approximately equals I^4 ; nasals may be slightly expanded posteriorly; uninflated ventral portion of periotic larger than periotic tympanic wing; paracrista M^4 considerably larger than that of M^3 .

DESCRIPTION

PLAGE: Ridgeway (1912) colours for holotype (spirit specimen) are as follows: side of face Salmon Colour to Bister; mid-back near Blackish Brown (3) to Chaetura Black; belly near Massicot Yellow to Pale Chalcedony Yellow.

TAIL: All specimens have thin tails which exceed nose-vent length (TV/NV ration between 1.13 and 1.36).

HIND FEET: Pads somewhat variable. In holotype, posterior metatarsal granule shorter than post-hallucal granule; in WAM M5076 posterior metatarsal granule present. Hallucal granule also varies in similar manner. WAM M5076, left foot, post-hallucal granule entire; right foot with divided but small separate granule at anterior end. Granules barely striate (when held in incident light some striae reflect light demonstrating very slight surface expression; in others striae are visible, but without surface expression, e.g. as in holotype).

EAR: Supratragus of ear relatively long antero-posteriorly (St/E ratio between 0.25 and 0.29).

NIPPLE NUMBER: Six (holotype and referred specimen WAM M8729).

SKULL AND DENTITION: Table 1 gives absolute measurements and ratio values. Dorsal, ventral and lateral views of holotype shown in Fig. 3. Characters of teeth shown in Plate 28 where they are accurately illustrated by use of scanning electron microscope. In Fig. 3 damaged areas illustrated unrestored. For example, portion of left jugal, both hamular processes of pterygoid, both

alisphenoid tympanic wings and right ectotympanic missing or broken. Also portion of right tympanic wing displaced towards basicranial midline and minor depressed fracture of right alisphenoid. Mild asymmetry of basicranium accurately illustrated. Some basisphenoid foramina of holotype not prepared sufficiently for illustration and as result condition in WAM M8042 shown in Plate 29. In Fig. 3C dentary slightly tilted such that tip of ascending ramus rotated buccally. This shortens apparent distance between tip of angular process and articular condyle. Nasals as shown in Fig. 3A appear to expand posteriorly slightly more than they actually do in holotype. In Figs. 3B and 3C teeth only approximations and their characters should be examined in Plate 28. Figs. 2A and 2B have been made using a camera lucida.

HABITAT

Burbidge (1959) and Ealey (1967) give habitat information for Abydos—Woodstock area which includes locality of paratype WAM M5076. Burbidge (1959) describes flat plain areas as spinifex (*Triodia*) steppe with *Acacia pyrifolia*, *Grevillea pyramidalis* and *Eucalyptus dichromophloia*. Although *Triodia* dominates the grasses, other small plants and bushes occur sporadically. Ealey (1967) describes area as one of erratic summer rainfall (between ten and twelve inches per annum) in which driest months are September to November. He notes that since 1915 number of native grasses in area severely reduced as result of stocking with sheep. Paratype WAM M5076 collected by Ealey amongst *Triodia pungens* and *T. lanigera*. Ealey (*in litt.* 19 September 1972) adds that habitat was shallow sand overlying hard pan with very sparse corkbark trees. Collection area about half mile from water and granite outcrops.

REPRODUCTION

Holotype has relatively undeveloped nipples. WAM M8041 and WAM M8042 juvenile males collected June and July. Referred specimen WAM M8729 collected in middle December and probably lactating. Has very well-developed pouch with six large nipples.

ORIGIN OF SPECIFIC NAME

The specific name is in honour of Dr E. H. M. ('Tim') Ealey, of Monash University, who besides collecting the first known specimen of a species of *Ningau* while an officer of the Wildlife Survey Section of CSIRO, was also responsible for the collection of specimens of rare and little-known species such as *Antechinus rosamondae* from

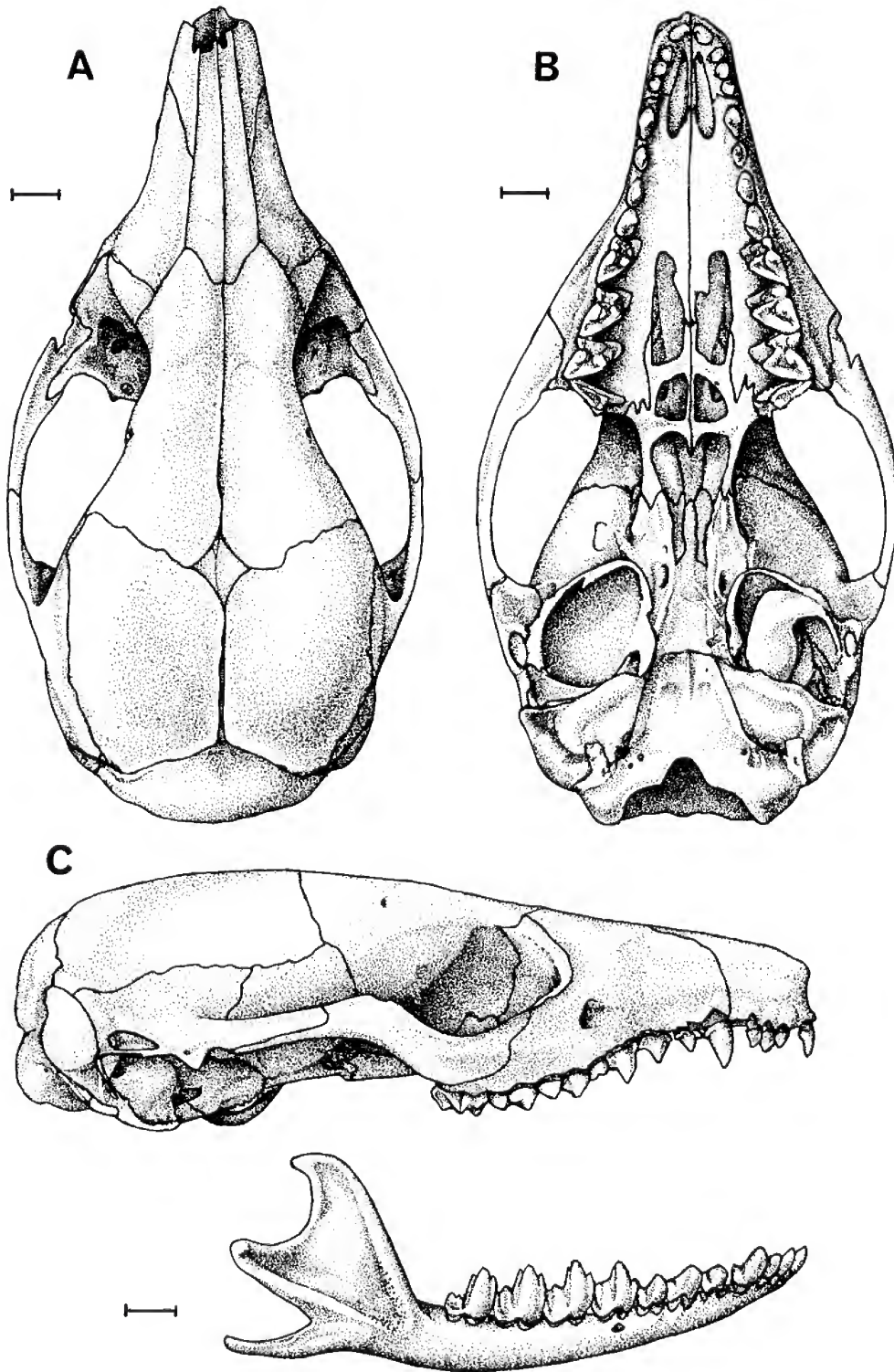


FIG.3: Holotype *Ningai timealeyi* sp. nov. (WAM M6181). A, dorsal; B, ventral; C, lateral skull and dentary. Nasals, left jugal and parts of basicranium damaged. Right ectotympanic and most of left and right alisphenoid tympanic wings missing. See text for comments. Line represents one mm.

northwestern Western Australia from 1953 to 1962.

***Ningai ridei* sp. nov.**
(Fig. 4; Plates 27, 28D, 29B)

Planigale ingrami: Ride, 1970, pp. 120, 238, pl. 35 (as *Planigale*, close to *P. ingrami*), (in part) (*nec* Thomas 1906).

HOLOTYPE: Western Australian Museum WAM M8080, very young adult female with P4 erupting, skull, dentaries and spirit carcase, caught by Dr and Mrs E. Pianka, February 1967, 38.6 km along White Cliffs Road East-northeast of Laverton, Western Australia (28°30'S 122°47'E).

PARATYPE: WAM M8081, juvenile male with dP4 in place, same collection locality as holotype WAM M8080.

DIAGNOSIS

N. ridei differs from *N. timealeyi* as follows: Post-hallucal and metatarsal granules generally more oval than elongate; distal end of hallux does not reach base of interdigital pads; supratragus outer edge of ear relatively short; tail-vent length just less than nose-vent length; alisphenoid tympanic wing well-developed; periotic tympanic wing relatively large; I² just larger than I⁴ and somewhat recurved; nasals do not appear to expand posteriorly; paracrista M⁴ subequal to paracrista M³.

DESCRIPTION

PELAGE: Ridgway (1912) colours for holotype (spirit specimen) as follows: side of face near Salmon Colour to Buffy Brown; mid-back near

Fiscous-Black to Chaetura Black; belly near Ivory Yellow to Pale Russian Blue.

TAIL: All specimens have thin, relatively short tails (TV/NV ratio 0.96 and 0.97).

HIND FEET: All hallucal and metatarsal granules on hind feet of holotype oval. However, hallucal and posterior metatarsal granules of paratype more elongate than oval; interdigital pad granules either long, partially fused series of small median granules, or shorter somewhat oval apical granule; left foot of holotype shows questionably fused median granules on 2nd and 4th interdigital pads and smaller but isolated apical granule on 3rd interdigital pad; in paratype, situation similar with 3rd interdigital pad having unfused but enlarged oval apical granule; 4th interdigital pad appears to have fused elongated apical granule; 2nd interdigital pad has elongate apical granule but margins indented halfway along to suggest incomplete fusion of median granules; some suggestion of slightly enlarged granule between hallucal and apical granule of 2nd interdigital pad of left foot of paratype; as result, three conspicuous but smaller inner post-interdigital pad granules present; in holotype only two, a hallucal granule and one between it and apical granule of 2nd interdigital pad.

EAR: All specimens have relatively short outer edge of supratragus (St/E ratio 0.20 and 0.22).

NIPPLE NUMBER: The holotype is a young female with seven barely distinguishable nipples. The referred specimen is a juvenile male.

SKULL AND DENTITION: Holotype just barely adult (P4 practically fully erupted); paratype

TABLE 1: EXTERNAL MEASUREMENTS (MM) OF *Ningai timealeyi* AND *N. ridei* GEN. ET SPP. NOV.

Species	TV	NV	HF	E	St	TV/NV	HF/NV	St/E
<i>N. timealeyi</i>								
WAM M6181	62.0	55.0	10.0	10.6	3.0	1.13	0.18	0.28
WAM M8041	68.0	?	10.0	11.7	3.4	1.36	0.20	0.29
WAM M8042	79.0	?	10.0	—	—	1.32	0.17	—
WAM M5076	65.0	57.0	11.0	11.5	2.9	1.14	0.19	0.25
WAM M8729	65.0	—	9.0	—	—	—	—	—
\bar{x}	67.8	56.0	10.0	11.3	3.1			
s	6.61	1.41	0.71	0.59	0.27			
v	9.75	2.52	7.10	5.22	8.71			
<i>N. ridei</i>								
WAM M8080*	50.6	53.0	11.6	10.9	2.2	0.96	0.21	0.20
WAM M8081*	48.0	49.7	11.3	11.3	2.5	0.97	0.23	0.22
\bar{x}	49.3	51.4	11.5	11.1	2.4			

*Indicates juvenile or very young adult specimens whose absolute body measurements are probably not indicative of adult body measurements. Abbreviations: TV = tail tip to cloacal vent; NV = nose tip to cloacal vent; HF = hind foot from heel to toe tips not including claws; E = ear from base of notch to tip of pinna; St = supratragus maximum length.

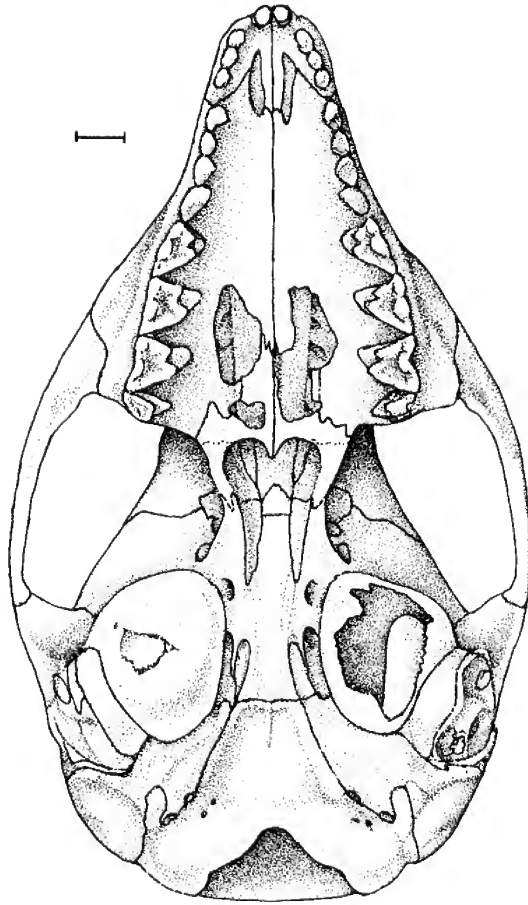


FIG. 4: Holotype *Ningai ridei* sp. nov. (WAM M8080). Damage described in text. Line represents one mm.

juvenile (dP4 in place). Absolute and relative ratio values given in Table 1. As noted above, the periotic and alisphenoid tympanic wings of *N. ridei* are more enlarged than those of *N. timealeyi* (Plate 29). It is possible that in older individuals of *N. ridei* this difference may become even greater.

HABITAT

The only two specimens were caught by Dr and Mrs Pianka in February 1967. The holotype was caught in a pit trap dug for lizards. The paratype was collected in spinifex (*Triodia*). Pianka and Pianka (1970) describe the area within which the holotype and paratype were collected, as open savannah woodland with gently rolling red sand plains, and low lying *Triodia* meadows. The woodland consists in part of mallee eucalypt and *Eucalyptus gongylocarpa*, some of which grow to 15 m in height, as well as *Acacia* sp. and a ground cover of *Triodia*.

TABLE 2: CRANIAL AND DENTAL MEASUREMENTS (MM) OF *Ningai timealeyi* AND *N. ridei* GEN. ET SPP. NOV.

Species	A.	B.	C.	D.	E.	F.	G.	H.	I.	J.	K.	L.	M.	N.	O.	P.
	basiramaial length	max. skull width	outside bullae distance	inside bullae distance	C ¹ -M ⁴	M ¹ -M ⁴	M ¹ -M ³	LM ³ -RM ³	min. interorbit.	interpatal vacuity	dentary condyle to I ₁	I ₁ -M ₃	M ₁ -M ₄	M ₁ -M ₃	angle-condyle	condyle-ramus
<i>N. timealeyi</i>	WAM M6181	9.1	6.3	—	6.5	3.6	3.1	5.3	3.0	2.8	12.0	7.3	4.0	2.9	3.7	3.1
	WAM M8041	—	6.9	2.0	7.4	3.9	3.6	5.8	3.6	3.9	14.0	8.2	4.4	3.3	3.7	3.9
	WAM M8042	16.2	9.2	6.8	6.6	3.8	3.5	5.5	3.5	3.3	—	—	3.5	3.2	3.9	3.4
	WAM M5076	17.5	10.0	—	7.2	3.8	3.3	5.6	3.5	4.0	13.6	8.2	4.3	3.1	4.0	3.8
	\bar{x}	16.5	9.5	6.7	6.9	3.8	3.4	5.6	3.4	3.5	13.2	7.9	4.1	3.1	3.8	3.6
	s	0.93	0.42	0.33	0.17	0.44	0.39	0.22	0.21	0.27	0.56	1.50	0.52	0.40	0.17	0.14
v	5.64	4.42	4.93	9.4	6.4	10.26	6.47	3.75	7.94	16.0	11.36	6.58	9.76	5.48	3.68	10.28
<i>N. ridei</i>	WAM M8080	15.4*	9.8*	7.2*	6.2*	3.8	3.4	5.7*	3.3*	3.1*	12.1*	7.4*	4.2	3.1	—	3.2*
	WAM M8081	—	9.7*	7.0*	6.4*	4.0	3.7	6.0*	3.5*	3.3*	12.1*	7.5*	4.4	3.3	4.0*	3.2*
	\bar{x}	15.4	9.8	7.1	6.3	3.9	3.6	5.9	3.4	3.2	12.1	7.5	4.3	3.2	4.0	3.2

*Indicates measurements made on juvenile or very young adult specimens which are probably smaller than corresponding measurements made on adult specimens. For example, antero-posterior growth of rostrum and dentary increases A, E, K and L. Similarly, growth of cranium in lateral direction increases B, C, D, H, and I.

Ningau *ridei* IN CAPTIVITY

The holotype was kept in captivity until 13 April 1967, during which time it was photographed. It was also drawn by Mrs E. Fry and forms the basis of plate 35 in Ride (1970). The photographs (Plate 27) reveal that in some respects the living animal does not clearly resemble species of either *Sminthopsis* or *Planigale*. The body is covered with guard hairs which give the animal a bristly appearance, not unlike that of *Antechinus apicalis*, but markedly unlike that of any *Sminthopsis* I have seen. It does resemble the pelage condition of *Planigale gilesi* as suggested by photographs in Aitken (1972). The photographs show that the foot width is broader than that of *Sminthopsis* but distinctly narrower than the feet of *Planigale*. The animal has been photographed while eating a large grasshopper (*Austracris guttulosa*, in litt. J. H. Calaby, 1973). Although the initial seizing of the grasshopper's head is made with the front of the mouth, appendages and projecting body parts are subsequently shifted to the molar region of the dentition where they are sheared off by the large metacristae and paracristids. Dr W. D. L. Ride (pers. comm.) noted that the jumping legs of the grasshopper were quickly severed, perhaps as a way of immobilizing the animal.

DISCUSSION

The holotype of *N. ridei* is a young adult animal and the paratype a juvenile. All of the specimens representing *N. timealeyi* are adult. Because of this age difference, many of the cranial ratios given in Table 1 are not directly comparable between the two species of the genus.

There are other characters of the canine and premolar region which, when more specimens referable to *N. ridei* are available and the degree of variation is better understood, may prove to be diagnostic. For example, in the only specimen of *N. ridei* in which P_4 is visible, it considerably exceeds in length the crown of P_1 . In *N. timealeyi* on the other hand, the P_4 crown is approximately the same length as that of P_1 .

There also appears to be a difference in the shape of the premolars. In *N. ridei* P^1 appears to be broader and more massive in appearance than P^1 of *N. timealeyi*. Similarly, C_1 and P_1 of *N. timealeyi* appear relatively more elongate and narrower than those teeth in *N. ridei*.

The difference in nipple number may, when more specimens of both species are known, prove to be diagnostic. At the moment these characters are not listed in the diagnosis because it is not clear how much variation will be demonstrated by larger samples.

ORIGIN OF SPECIFIC NAME

The specific name is in honour of Dr W. D. L. Ride, who recognized the complexity and possibly polyphyletic nature of the small marsupials earlier referred to *Planigale*, including the forms described here as species of *Ningau*.

RE-DIAGNOSIS OF *PLANIGALE*

The recognition of the difference between species of *Ningau* and those of *Planigale* enables the genus *Planigale* to be re-diagnosed as follows:

Dasyurids smaller than *Antechinus* and differing from these in having an extremely reduced maxillary vacuity; very small paracone; and small talonid on M_{1-3} . Generally smaller in size than *Sminthopsis* and *Antechinomys* and differing from these in possessing a straight external edge on the supratragus of the ear; short broad pentadactyl hind feet; enlarged metatarsal granules; broadened nasals; lack of squamosal-frontal contact on the outside of the skull; posterior cingula on M^{1-3} ; reduced paracone, protocone, and talonid on M_{1-3} ; single-rooted or absent P_4 ; and lack of a palatine vacuity.

Under this concept, *Planigale* contains *P. ingrami*, *P. maculata*, *P. subtilissima*, *P. tenuirostris*, *P. novaeguineae* and *P. gilesi* (discussed as part of a revision of *Planigale*, in preparation).

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PLATE 27

Holotype (WAM M8080) *N. ridei* photographed live shortly after capture. A and B show bristly appearance, relatively broad hind foot, fold line of ear, curled supratragus, and use of anterior molar region (presumably large metacones) to cut locust's leg (photographs, W. D. L. Ride).



PLATE 28

A, B. Scanning electron microscope photographs (composite overlays) of teeth of *N. timealeyi* (WAM M8041). Line is 1 mm in length. A, RI₁-M₄. B, RP¹-M⁴.

C, D. Left hind foot of *Ningau* spp. C, Holotype (WAM M6181) *N. timealeyi*. D, Holotype (WAM M8080) *N. ridei*. Ruled lines are 1 mm apart.



PLATE 29

A. B. Ventral view of skulls of *Ningauia* gen. nov. A, *N. timealeyi* sp. nov. (WAM M8042). B, *N. ridei* sp. nov. (WAM M8080). Outlines show differences in basicranial region of two species, and in particular, relative development of alisphenoid tympanic wings. Line represents one cm.





ABNORMAL DENTAL DEVELOPMENT AND ITS SIGNIFICANCE IN DASYURIDS AND OTHER MARSUPIALS

MICHAEL ARCHER
Queensland Museum

ABSTRACT

Abnormal dental developments in dasyurids and other marsupials are described, including supernumerary and lost teeth, divided and fused crowns, abnormal molar crown morphology, and accidents of development including abnormal tooth positions or postures and malocclusion. Instances of ephemeral teeth are also given although these are not regarded as abnormal dental developments. The literature of abnormal dental development in non-marsupials as well as marsupials is briefly reviewed. Premolar number variation is not considered a valid means for determining the position of a possibly suppressed fourth premolar in marsupials. P5 and M5 occurrences are regarded as indications of the proliferative potential of the posterior end of the dental lamina. Some supernumerary teeth are regarded as atavisms. Evidence is given that supernumerary teeth may originate as divided tooth crowns. Fused crowns are probably the result of damage to crowded, developing tooth germs. Some abnormal molar crown variations are also probably the result of antero-posterior compression of the developing tooth germ. Examples are given of abnormal tooth shape and number which may be the result of disease. Some abnormal developments in tooth crown shape and occlusion are more frequent among inbred individuals. Many examples of ephemeral teeth noted are regarded as normal, representing rarely noted vestigial milk-teeth or canine teeth in the process of phylogenetic suppression. Although most abnormal dental developments occur in one tooth only, some occur with occlusal and/or bilateral counterparts. These facts suggest that most single-tooth abnormalities are not genetically determined, in contrast to bilateral and occlusal pair abnormalities which may develop under the influence of a dental morphogenetic field.

Skulls and dentitions of 2990 individuals of dasyurids have been examined, representing many stages of dental development. Observations on non-dasyurids have been more limited. Abnormal developments (i.e. those outside limits given with taxonomic descriptions, as noted for example by Archer 1975) in dasyurids and other marsupials may be placed in three categories: (1) supernumerary or lost teeth, loss not obviously being the result of accident or physical disturbance; (2) morphological abnormalities including misshapen tooth crowns, extra cusps, and composite odontomas; (3) developmental accidents including teeth erupting in unusual positions or postures, tooth loss resulting from physical disturbance or disease, and malocclusion. These categories are not mutually exclusive. For example, a supernumerary molar may also have a morphologically abnormal crown.

This review is based (a) on personal observations of specimens housed in collections throughout

Australia, in the British Museum, and in the American Museum of Natural History, and (b) on literature references. For each abnormality, records from these two sources are listed in separate paragraphs. Literature citations are by author and date except that references to Bateson (1894) are so numerous that they are given only as the case number listed by Bateson (e.g. case no. 366). Catalogue numbers are prefixed by letters as follows: Australian Museum, e.g. AM M4343; American Museum of Natural History, e.g. AMNH109524; British Museum (Natural History), e.g. BM No. 2.9.8.7; Butler collection housed in the Western Australian Museum, e.g. B1944; National Museum of Victoria, e.g. C1009; Fisheries and Wildlife Department of Victoria, e.g. D966; Queensland Museum fossil collection, e.g. F4713; Queensland Museum modern mammal collection, e.g. J23087 or JM169; South Australian Museum modern mammal collection, e.g. SAM M7536; Northern Territory Museum, e.g.

NTM274; Western Australian Museum modern mammal collection, e.g. WAM M2477; Western Australian Museum fossil vertebrate collection, e.g. WAM 68.3.43; Queen Victoria Museum and Art Gallery modern mammal collection, e.g. QVM 1964.1.33.

Literature references to non-erupting teeth or teeth so small they have usually escaped detection in description are mentioned here and although these are not abnormal developments, some further examples are given.

The purposes of this study are twofold. Firstly, to attempt to discover whether 'atavisms' occur at any regular positions suggesting sites of earlier evolutionary losses from a toothrow. Secondly, to describe abnormal structural developments in various populations so that abnormal individuals (e.g. unique fossils like the Fromm's Landing Thylacine, Archer 1971) can be more easily evaluated.

Molar cusp terminology is that used by Archer (1974, 1975). Tooth nomenclature is that used by Thomas (1888). Australian marsupial names are those employed by Ride (1970) and Archer (1975). *Sminthopsis* sp. (a) and (b) refer to two species which will be described elsewhere. New Guinean marsupial names are those employed by Laurie and Hill (1954).

DASYURIDAE

MATERIAL EXAMINED AND NUMBER OF ABNORMAL DEVELOPMENTS: Incidence (in brackets) of abnormalities, other than ephemeral teeth, follows the number of individuals examined in the samples listed below.

Sarcophilus harrisi 17 (3); *Dasyurus hallucatus* 64 (2); *D. maculatus* 33 (1); modern *D. geoffroii* 45 (2); fossil *D. geoffroii* 17 (0); *D. viverinnus* 11 (1); *D. albopunctatus* 3 (0); *D. dumalli* 4 (0); *Murexia longicaudata* 2 (0); *Myoictis melas* 3 (0); *Neophascogale lorentzii* 3 (1); *Phascosorex dorsalis* 5 (0); *P. doriae* 4 (0); modern *Dasyercus cristicauda* 24 (2); fossil *D. cristicauda* 574 (4); *Dasyuroides byrnei* 46 (6); modern *Antechinus flavipes* 41 (5); fossil *A. flavipes* 252 (0); modern *A. apicalis* 5 (1); fossil *A. apicalis* 77 (2); *A. stuartii* 10 (0); *A. swainsonii* 10 (0); *A. bellus* 14 (2); *A. macdonnellensis* 38 (0); *A. rosamondae* 10 (0); *A. godmani* 3 (0); *Phascogale tapoatafa*, (in access of) 50 (5); modern *P. calura* 19 (1); fossil *P. calura* 31 (0); *Planigale maculata* 43 (11); *P. ingrani* 33 (1); *P. subtilissima* 7 (0); *P. tenuirostris* 14 (1); *P. gilesi* 5 (0); modern *Sminthopsis murina* 140 (7); fossil *S. murina* 615 (0); *S. ooldea* 13 (1); *S. leucopus* 69 (9); *S. crassicaudata* 143 (7); modern *S. granulipes* 6 (1); fossil *S.*

granulipes 207 (0); *S. psammophila* 4 (0); *S. longicaudata* (modern and fossil) 8 (0); *S. hirtipes* 7 (0); *S. virginiae* 37 (1); *S. macroura* 100 (6); *S. sp.* (a) 7 (1); *S. sp.* (b) 3 (2); modern *Antechinomys spenceri* 30 (1); fossil *A. spenceri* 170 (1); *A. laniger* 12 (0); *Ningaui ridei* 2 (0); and *N. timealeyi* 4 (0).

The number of abnormal dental developments recorded above is certainly an underestimate of the true number because many specimens examined have worn teeth and wear obliterates some morphological abnormalities. Also because fossil specimens examined are generally incomplete, likelihood of detecting abnormal dental developments in individuals is markedly reduced.

TOOTH NUMBER: Adult tooth formula of $\frac{5}{3} \frac{1}{1} \frac{3}{3} \frac{4}{4}$ is regarded as structurally ancestral for marsupials in general. In living dasyurids the maximum adult tooth formula is $\frac{4}{3} \frac{1}{1} \frac{3}{3} \frac{4}{4}$. In most juvenile dasyurids there is also a molariform tooth, dP4, displaced from the tooth row by the erupting P4. Normally non-erupting tooth rudiments (of milk teeth) also develop ontogenetically, lingual to the incisors and canine in dasyurids (Archer 1974).

In *Mrymecobius* (a dasyuroid considered below with dasyurids) there are eight cheek-teeth in the adult dentition. Tate (1947) suggests that one of these is dP4 which persists together with P4.

SUPERNUMERARY TEETH

INCISORS: *Mrymecobius fasciatus*: Two teeth in position of LI³ (case no. 366); extra incisor on lower right side (case no. 367 and noted by Bensley 1903). *Dasyurus* spp.: Swellings interpreted as tooth germs between I² and I³, in front of I₁, and between I₁ and I₂ in sectioned specimens of *D. maculatus* and *D. viverinnus* (Woodward 1896). *Antechinus* sp.: Supernumerary tooth positions in sectioned specimens between I² and I³, between I₁ and I₂, and in front of I₁ and these positions were distinguished from deciduous tooth germs (Woodward 1896). Deciduous teeth associated with all incisors (Archer 1974).

CANINES: *Antechinus flavipes* WAM M7111 small accessory LC¹; *A. minimus* D966 small accessory LC¹; *Sminthopsis crassicaudata* J14376 two teeth at LC¹ position. Supernumerary canines observed in this study may be abnormally enlarged deciduous canine tooth rudiments, such as in *Antechinus* (Woodward 1896, Archer 1974).

PREMOLARS: *Dasyurus geoffroii* WAM M4464 tooth between RP¹ and RP³; *Phascogale calura* WAM M8069 tooth either anterior to LP¹ or between LP¹ and LP³; *Antechinus flavipes* WAM

M7107 tooth posterior to L and RP⁺; WAM M6785 extra RP_x, homology uncertain, appears to be anterior to RP₁; *A. bellus* NTM274 two teeth in LP³ and RP³ positions; *A. apicalis* J1741 tooth antero-lingual to LP¹; WAM 64.10.47 extra P, homology uncertain; *Sminthopsis leucopus* C891 tooth posterior to RP₄.

Dasyurus spp.: Swelling of dental lamina in sectioned specimens of *D. maculatus* and *D. viverinnus*, between P1 and P3, interpreted as rudiments of P2 (Woodward 1896). *Phascosorex dorsalis*: Premolar between LP¹ and LP³ (case no. 386). *Antechinus* sp.: Swelling of dental lamina in sectioned specimen between P1 and P3 interpreted as rudiments of P2 (Woodward 1896).

DP4: *Sminthopsis leucopus* D524 spicule between RdP⁺ and RM¹.

MOLARS: *Sarcophilus harrisii*: Possible occurrences of M⁵ discussed below as divided teeth. Fifth molar (Green 1967). *Dasyurus maculatus*: Five upper left molars and five molars on both sides of lower jaw (case no. 385). Bateson (1894) interprets these as LM⁵ and L and RM₅. I agree with Bateson's interpretation. Thomas (1888) describing same specimen, notes that besides being very small, specimen has asymmetrical squamosal bone.

MISSING TEETH

PREMOLARS: *Dasyurus hallucatus* J16753 missing RP³; *Dasyercus cristicauda* J23101 missing RP₃; *Antechinus minimus* D968, D967 missing RP₄; *Planigale maculata* J10989 missing L and RP³; *Sminthopsis* sp. (a) B1939 missing LP¹ and possibly RP₃.

Antechinus flavipes: In sample of seven specimens, one lacked P₁ (case no. 387).

MOLARS: *Sarcophilus harrisii* WAM 71.10.209 missing all LM².

DIVIDED CROWNS

INCISORS: *Sminthopsis crassicaudata* BM No. 2.9.8.7 L and RI⁺ crowns bicuspid. Roots partly divided.

PREMOLARS: *Dasyurus geoffroii* WAM M4464 RP₃ partly divided. LP₃ has transverse groove; *Dasyercus cristicauda* WAM 68.9.91 LP₃ divided and tooth has three roots; J23098 RP₃ crown tip divided; *Phascogale tapoatafa* WAM M7453 LP³ crown divided and tooth has three roots; WAM M1338 RP³ crown divided; *Sminthopsis crassicaudata* J11388 RP₃ tip of crown divided; *S. murina* WAM M1642 RP₄ crown partially divided.

S. leucopus AM M4343 LP³ partially divided; D793 LP⁴ partially divided and has three roots; D741, D458, C10019 RP₃ has partially divided crown.

Dasyurus geoffroii RP₄ partly divided along plane transverse to long axis of jaw (case no. 383).

DP4: *Sminthopsis leucopus* D524 spicule between RdP⁺ and RM¹ may represent split portion of RdP⁺; *S. rufigenis* AM M6562 LdP⁺ crown tip divided.

MOLARS: *Sarcophilus harrisii* QVM 1964.1.201 LM⁴ may be completely divided producing two small teeth.

FUSED CROWNS

PREMOLARS: *Dasyercus cristicauda* WAM 69.6.269 P¹ and P³ crowns fused (an isolated maxilla); *Dasyuroides byrnei* J11510 RP¹ and RP³ crowns fused, sharing one root; *Antechinus bellus* CSIRO (Canberra) CM1141 LP¹ and LP³ fused on point of contact; *Planigale maculata* J10989 RP⁴ and RP³ almost completely fused; *Planigale* sp. J14089 LP¹ and P³ fused at base of crowns; *Sminthopsis murina* WAM M2046 LP₁ and P₃ fused.

ABNORMAL CROWN AND ROOT MORPHOLOGY

INCISORS: *Sminthopsis crassicaudata* BM No. 2.9.8.7 bilobed L and RI⁺.

PREMOLARS: *Sarcophilus harrisii* WAM 71.10.209 grossly abnormal tooth in position of LP³; *Phascogale tapoatafa* WAM M7951, WAM M1338 RP₄ has one root; *Dasyercus cristicauda* WAM 68.9.91 LP₃ has three roots; *Antechinus flavipes* B1814 RP¹ caniniform and also tallest premolar; *Planigale tenuirostris* AM M5438 P₄ two-rooted; *P. ingrami* J7656 LP1*3 have buccal notches or imperfections in cingula; *P. maculata* WAM M420 RP⁴ has extra large cusp posterior to paraconid; *Sminthopsis leucopus* D793 LP⁴ resembles enlarged and divided dP⁺; *S. macroura* AM M4403 RP⁴ has very large antero-lingual cingular shelf; *S. sp.* (a) B1939 tooth posterior to LP₁ (topographic homologue of P₃) morphologically resembles molarized protoconid such as occurs on M₄; *S. murina* WAM M6998 L and RP₃₋₄ possess small postero-lingual cuspids.

DP4: *Sminthopsis leucopus* D524 RdP⁺ mildly deformed, possibly result of split-off corner.

MOLARS: *Sarcophilus harrisii* QVM 1964.1.134 M⁴ very small; *Dasyurus geoffroii* WAM M4464 talonids very reduced, trigonids enlarged, particularly M₃; *D. maculatus* J16744 LM⁴ either part of

composite dental odontoma or grossly abnormal; *Dasyuroides byrnei* J11509 L and RM³ ectolophs compressed antero-posteriorly; *Planigale maculata* J16721 small buccal cusp on talonid near base of protoconid; *Antechinus apicalis* unregistered LM¹ paracone slightly displaced, paracrista absent, and extra cusp present anterior to displaced paracone; *A. flavipes* WAM M8092 M² has prominent antero-lingual cusp on flank of protocone; *Sminthopsis macroura* WAM M6903 L and RM¹⁻³ ectolophs compressed antero-posteriorly; J7407 L and RM¹⁻² have conspicuous protoconules; WAM M5701 very large entoconid M₄; WAM M5411 M₄ talonid has lingual cusplets and M₁ has tiny cusp between paraconid and metaconid; J23555 R and LM³ ectolophs compressed antero-posteriorly with buccally displaced parastyles; *S. ooldea* WAM M5888 LM₁ has cusp between paraconid and metaconid and tiny cusp in position of entoconid RM₁₋₃; *S. murina* WAM M2477 L and RM₁₋₃ have large entoconids; SAM M7536 LM₁ has cusp anterior-buccal to paraconid; *S. leucopus* C6343 M¹⁻³ ectolophs compressed antero-posteriorly; C1009 M₁₋₄ have tiny metastylids; AM M4343 M₁₋₃ have tiny entoconids; C9566 L and RM⁴ abnormally shaped; *S. crassicaudata* WAM M373 M₄ talonid tricuspid; *S. sp.* (b) J5459 RM₃ entoconid split transversely; *Antechinomys spenceri* WAM 68.2.265 RM₂ with small entoconid; WAM M2860 M₃ has two tiny cusps in topographic position of entoconid.

Dasyurus spp.: RM⁴ of *D. viverinus* larger than normal sized LM⁴ (case no. 384). Specimen of *D. maculatus* with supernumerary molars (case no. 384, see above). Bateson interprets (I believe correctly) supernumerary molars as LM₅, LM₅ and RM₅. LM⁴ and L and RM₄ enlarged and morphologically abnormal. Tooth in position of LM⁴ more closely resembles normal M³, and teeth in positions of L and RM₄ both resemble normal M₃.

Abnormal Molar Styler Cusps: *Dasyurus hallucatus* WAM M8085 styler cusp B distinct on L and RM¹; *D. viverinus* J20413 styler cusp B distinct on L and RM¹; *Phascogale tapoatafa* WAM M2855 styler cusp C occurs between B and D on M¹; WAM M1338 styler cusp C large on anterior flank of D on L and RM¹; WAM M6390 styler cusp anterior to D on L and RM¹; *Neophascogale* sp. AMNH109524 styler cusp D divided transversely on RM¹; *Planigale maculata* WAM M420 prominent styler cusp A on RM¹; J19668 styler cusp C on L and RM¹⁻³; J16722 tiny styler cusp E on M¹⁻³ (uncommon but occurs also in three other specimens); *Sminthopsis* sp. (b) J5173 extra styler cusps between B and D on L and RM¹

and LM²; *S. granulipes* WAM M6062 styler cusp D divided transversely on L and RM¹⁻²; *S. murina* WAM M8652 styler cusp D unusually enlarged on L and RM¹, projecting buccally; *S. leucopus* C6343 styler cusp A on M¹, extra styler cusps between B and D on RM³, and extra styler cusp on M⁴; C9566 L and RM⁴ have two styler cusps each.

ERUPTION AND OCCLUSION

Sminthopsis crassicaudata: WAM M4503 has what appears to be reversed (antero-posteriorly) LP₄. Tooth slightly smaller than RP₄. WAM M4497 shows abnormal occlusion resulting from very short lower jaw. RC₁ bites behind RC¹ and RC¹ occludes with RI₃. LC₁ just passes anterior to LC¹. Upper incisors do not occlude. *Planigale maculata*: J8070 has lower canines, premolars and molars heavily worn, while upper cheek-teeth almost unworn. Reasons unknown. Possible that specimen includes wrongly associated dentary. *Phascogale calura*: WAM M8069 maloccluded. RM¹ rotated out of position. Result is hypoconid of RM₁ opposes, rather than shears anterior to, metacone of RM¹ and protoconid of RM₁ bites into protocone basin of RM¹, rather than anterior to protocone. Specimen also possesses supernumerary left premolar (see above). *Dasyuroides byrnei*: J11433 missing LM¹ while spaces set RM¹ and RM⁴ off from RM²⁻³. Left and right lower molar rows crowded antero-posteriorly so that lower molars on both sides distorted out of position. Teeth maloccluded. J10935 has maloccluded RI² which bites lingual to lower incisors. J11509 maloccluded. LM¹ deflected posterolingually and hypoconid of LM₁ passes over tip of metacone producing abnormal wear facet. LM₂ also distorted. LM₂ protoconid occludes with LM² protocone basin, rather than shearing past it with very large wear facet across LM² protocone and paracone. Series of thirty *Dasyuroides byrnei* specimens (including all noted above) in Queensland Museum were bred in captivity. Comparison of measures of brachycephaly (maximum skull width/maximum skull length) in wild-caught and laboratory-bred individuals indicates higher incidence of brachycephaly in latter. Concurrently, much higher incidence of dental abnormalities such as malocclusion, tooth loss, supernumerary premolars, and antero-posteriorly compressed molars evidenced in laboratory-bred samples (Archer and Vernon in preparation).

DISEASE OR TRAUMA

Dasyurus maculatus: J16744 has complex LM⁴ which may be either composite odontoma or

teratoma, possibly result of disease. *Dasyercus cristidauda*: WAM 69.6.165 dentaries fused at symphysis. *Antechinomys spenceri*: J23103 isolated right dentary has RI_{1-3} , C_1 and M_{2-4} with alveoli for M_1 . No trace of any premolar. Dentary in area where premolars missing has roughened surface. Large abscesses occur beneath M_1 and below posterior root of M_4 . Abscess below M_1 has perforated buccal surface of dentary below alveolar margin of M_1 . Case may be example of partial anodontia following disease. *Sminthopsis crassicaudata*: WAM M8082 missing LI_3 , C_1 and P_1 . These possibly lost during life, with alveoli then overgrown by bone.

NORMALLY NON-ERUPTING OR EPHEMERAL TEETH

Dasyurus geoffroi: WAM M6370 rudimentary spicule-like tooth in position of normally absent RP^4 ; *Dasyuroides byrnei* J11435 tiny calcified rudimentary tooth adhering to postero-lingual corner LP_3 . *Dasyurus*, *Myrmecobius*, *Antechinus*: Calcified rudiments or positions for milk-teeth associated with incisors of *Dasyurus* spp., *Myrmecobius fasciatus*, and *Antechinus* (species not given) in sectioned material (Woodward 1896). Milk-tooth rudiments associated with C_1 in *Dasyurus maculatus*, *D. viverinus*, *Antechinus* sp., and *Myrmecobius fasciatus* in sectioned material (Woodward 1896). *Dasyurus hallucatus*: DP^4 (Tate 1947). DP^4 and P^4 normally absent *Dasyurus* (except *D. dumalli*). *Antechinus flavipes*: Milk-canine tooth rudiments and non-erupting milk-tooth rudiments in association with incisors in sectioned material (Archer 1974). Examples noted above of supernumerary canines may represent abnormal development of normally non-erupting milk-canines.

THYLACINIDAE

Abnormal molar cusps, supernumerary stylar cusps, enlarged basal cingula and proximation of paracone and metacone of upper molar in *Thylacinus* spp. (Archer 1971). *Thylacinus cynocephalus* with four lower premolars (Röse 1892). Calcified but rudimentary tooth in *T. cynocephalus* interpreted as dP^4 (Flower 1868).

PERAMELIDAE

Suggestion of undeveloped incisor tooth position between I^3 and I^4 (Woodward 1896). Similar tooth rudiments in *Perameles* (Wilson and Hill 1897). *Echymipera*: In 22 per cent of skulls, supernumerary upper incisor present (Ziegler 1971). Ziegler interprets this as I^5 which normally present in most other peramelids. In series of six

skulls of *Echymipera rufescens* (J123063-8), no examples of supernumerary incisors or other dental abnormalities. *Isoodon obesulus*: J23082 shows morphologically abnormal L and RM_1 . RM_1 has normal talonid. Anterior to this are five principal cusps. Anterior three may represent trigonid. Two large accessory cusps also present on tooth, one (normal on some specimens of *I. obesulus*) anterior to hypoconid on buccal edge of crown and other posterior to possible homologue of protoconid. LM_1 identical except that last mentioned accessory cusp less well-developed. LdP_4 has enlarged antero-buccal cusp, usually homologous with protoconid of molars. This cusp less well-developed in RdP_4 . *Isoodon macrourus*: J13743 with RP_3 missing. Position marked by pebbly knobs of calcified tissue not extending above oral epithelium. Much more complex pebbly knobs occur near base of P^4 , surrounding P^3 and surrounding posterior margin of P^1 . L and RP^3 partially resorbed at points around crown. Eroded pit in anterior root of LP^4 . LI^1 missing although reason not clear. J8765 has four upper right premolars. Extra tooth apparently between RP^1 and RP^3 . J21908 has no teeth posterior to R and LC^1 , no right upper incisors, rudiments only of two left upper incisors, and no lower teeth. Gum lines irregular and all post-canine alveoli (if they existed) filled with bone.

PHALANGERIDAE

Trichosurus vulpecula: Variation in occurrence of small teeth between C^1 and P^4 and between I_1 and P_4 (Kingsmill 1962). P^1 variably present (case no. 378). 'Premilk' teeth in association with I^3 in sectioned material (Woodward 1896). J23083 isolated left maxilla without normal P^1 . J23070 isolated right maxilla with abnormal tooth in RdP^4 position. Tooth much larger than normal dP^4 and has unusual lingual cusp. Tooth with unclear morphology projecting buccally. J23080 has RP^4 erupting out of alignment antero-buccal to M^1 . *Phalanger* spp.: *P. orientalis* with LI^3 imperfectly bifid, crown almost completely divided, but root single (case no. 368). Individuals of *P. orientalis*: four upper premolars on one side; one premolar absent; two teeth occur in place of P^1 ; and tooth present between normal P^4 and P^3 (case no. 372-275). *P. maculatus* lacking L and RI^3 (case no. 369). 'Premilk' teeth in incisor and canine region sectioned specimens of *Phalanger* sp. (Woodward 1896).

PETAURIDAE

Pseudocheirus spp.: *P. forbesi* has I^3 and no P^1 (case no. 371). In present study, *P. peregrinus* skulls

(including 23 dentaries) from caves in Western Australia show following abnormalities and variations: J23076 has incipiently two-rooted RP¹; J23078, left maxillary fragment, shows same P¹ condition; J23075 has four left upper premolars, extra premolar either first or second in row, both being simple peg-like teeth. Teeth posterior to I₁ and anterior to P₄ lost but alveoli vary in number from one (J23072) to two (J23074) to three (J23073). J11427 has small calcified tooth adhering to postero-buccal corner of RP⁴. Long posterior root present on this tooth and appears that anterior root broken off. Tooth probably dP⁴, not previously recorded in this group because either lost very early in development or not normally developed to stage of calcified crown. *Schoinobates volans*: J22083 has tiny calcified tooth adhering to antero-lingual tip of RM₁. No roots apparent. This rudiment may represent dP⁴, previously unrecorded in genus. *Petaurus* sp.: In 25 skulls, two show variations in number of post-I₁-pre-P₄ teeth (case no. 380). One has four on left side. *Hemibelideus leadbeateri*: J9294 has slightly abnormal L and RM₄. Entoconids and postero-lingual corners of teeth reduced.

PHASCOLARCTIDAE

Phascolarctos cinereus: In sectioned specimen, small calcified incisor present in front of I₁ and another uncalcified incisor present behind I₁. Toothgerms for lower canine, two lower premolars, and additional upper premolar present; none attain functional maturity (Woodward 1896). Rudimentary dP₄ (Thomas 1887b). Tooth rudiments noted by Woodward and Thomas probably best regarded as uncommon observations of normally occurring structures. J10023 has two incisors in place of RI³. Both resemble normal LI¹. J8811 has very tiny hypocones on L and RM¹⁻⁴. Size of protoconule varies in this species, being absent to miniscule in R and LM¹⁻³ (e.g. J8811) to conspicuous in same teeth (e.g. J10023). J13278 shows two tiny calcified teeth in shallow sockets on right lower side between erupting RI₁ and RP₄. First of these immediately posterior to I₁. Second adpressed to antero-lingual corner of P₄ crown. On left side, same two teeth present but anterior one lost, perhaps during preparation of specimen. J7209 has no L or RM⁴ but has L and RM₄. J5749 has mildly twisted L and R dentary, resulting in malocclusion and abnormal resting position of incisors.

MACROPODIDAE

SUPERNUMERARY TEETH

INCISORS: *Macropus giganteus* J23087 small tooth anterior to LI³.

PREMOLARS: *Macropus giganteus* J23089 RP⁵ erupting beneath RP⁴; J23108 LP^x present anterior to P⁴; J23105 RP^x present anterior to P⁴.

MOLARS: *Macropus giganteus* J23110, J23151, J23135, J23150, J23137, J23120, J23125, J23083, J23085 L and RM⁵; J23107 L and RM⁵ and LM₅; J23128 L and RM⁵ and ?LM⁶; J23109, J23129, J23130 LM⁵; J23140, J23134 RM⁵; *Macropus robustus* J23122 L and RM⁵; J23117 RM⁵; *Megaleia rufa* J23091 supernumerary between RM³ and RM⁴; J23086, J23084, J23152 LM⁵; *M. sp.* J23115, J23147 RM⁵; J23136 LM⁵; *Potorous tridactylus* WAM 70.7.242 LM₅; *Bettongia lesueur* WAM 68.10.2 M₅.

Supernumerary molars in *Peradorcas concinnus* common (Tate 1948, Troughton 1967). *Macropus* spp.: Supernumerary molars, premolars, presence of rudimentary canines, and absence of P₄ (Kirkpatrick 1965). Kirkpatrick (1965) notes frequency of some abnormalities (e.g. presence of paired M₅ on maxillae) to be as high as seven per cent in one species. *Bettongia* spp.: M₅ in *B. penicillata* (case no. 390) and *B. lesueur* (Waterhouse 1846, Thomas 1888). L and RM⁵ in two other specimens *B. lesueur* and L and RM⁵ and L and RM₅ in *B. gaimardi* (as *B. cuniculus*) (Thomas 1888).

MISSING TEETH

Macropus giganteus J23114 L and RM₄ missing; J23119 L and RM⁴ missing; J23133 L and RM₄ missing; J23126 all lower molars missing R side only; J23134 RM₄ missing; *M. robustus* J23117 L and RM₄ missing; *M. sp.* J23123 RM₄ missing; J23144RM_x missing; J23145RM₄ missing; J23149 RM₄ missing.

Bettongia spp.: *B. penicillata* molar formula was M₁₋₃¹⁻³ (Bateson 1894). LM₄ missing (case no. 389). M⁴ . . . is itself often aborted in *Bettongia*, there being then only three molars' (Thomas 1888, p. 105).

ABNORMAL TOOTH MORPHOLOGY

INCISORS: *Macropus giganteus* J23092 L and RI² show two pronounced lingual grooves and crowns deflected buccally; J23087 RI³ has large buccal projection from walls of crown adjacent to incisive groove; J23090, J23153, J23111 RI³ distorted shape; J23112 L and RI³ shape abnormal.

MOLARS: *Macropus giganteus* J23083 LM⁵ horseshoe-shaped, RM⁵ similar but more complex; J23085 LM⁵ horseshoe-shaped but RM⁵ molariform; J23139 RM⁴ peg-shaped, LM⁴ mildly abnormal; J23109 LM⁵ submolariform with one loph and one cusp; J23131 possible odontoma in crypt buccal to LM: *M. robustus* J23117 prominent

mesostyles on L and RM³; *Megaleia rufa* J23088 RM² with one major transverse loph, RM⁴ may also be peg-shaped (tooth gone); J23091 abnormal supernumerary tooth between RM³ and RM⁴, three-rooted and tricuspid; J23084 LM⁵ metaloph appears complexly folded; J23068 LM⁵ simple conical cusp surrounded by cingulum; Macropodid, indet., F4713 LM₄ lacks clear homologue of hypolophid.

In macropodids, abnormally shaped teeth relatively more common than in other marsupial families. Abnormalities in shape also different from those found in other groups in that divided cusps and crowns, fused crowns, and buccally compressed crowns extremely rare.

Normal morphological variation in premolars of several modern and fossil species of large macropodids described (Bartholomai 1973, 1974), with view to interpreting variation in fossil species.

VARIATIONS IN ERUPTION AND OCCLUSION

INCISORS: *Macropus giganteus* J23087 RI³ on premaxilla-maxilla boundary; J23092 RI³ positioned near maxilla boundary; J23104 skull distorted and RI₁ occludes with LI³.

PREMOLARS: *Macropus fuliginosus* WAM M6956 R and LP⁴ erupting near buccal wall of maxilla.

MOLARS: *Macropus giganteus* J23132 L and RM⁴ erupted abnormally high in tooth row; J23113 RM³ erupted abnormally high; J23126 all upper R molars erupted abnormally, lower molars missing.

NORMALLY NON-ERUPTING OR EPHEMERAL TEETH

INCISORS AND POSSIBLY CANINES: *Macropus irma* WAM M8127 (basicranial length 44.3 mm) two tooth rudiments, one antero-buccal to unerupted I¹, other on premaxilla-maxilla boundary; *M. robustus* WAM M6976 (51.4 mm) one tooth rudiment on premaxilla-maxilla boundary; WAM M6137 (62.9 mm) no rudimentary teeth, but socket only just resorbed; *M. fuliginosus* WAM M6588 (50.4 mm) shallow socket present on premaxilla-maxilla boundary; *M. giganteus* J23087 (adult) spicule-like tooth immediately anterior to LI³.

These teeth undoubtedly normal in developing dentitions of many species and no examination of sectioned macropodid material fails to mention them, although not commonly observed in gross skeletal preparations.

Many cases cited of normally non-erupting teeth in macropodids (e.g. Flower 1868, Woodward 1893, Hopewell-Smith and Tims 1911, Tate 1947a, Johnson 1964, Berkovitz 1968c, Bartholomai

1973). Incisors of macropodids normally have deciduous predecessors that resorb without erupting (Kirkpatrick 1969). Normally non-erupting canine develops ontogenetically (Kirkpatrick 1969).

DIDELPHIDAE

Bensley (1906) presented comprehensive analysis of normal and abnormal variations in stylar cusp morphology in species of *Monodelphis* (as *Peramys*), *Marmosa*, *Caluromys*, *Metachirus*, *Chironectes*, and *Didelphis*. *Didelphis marsupialis*: Six right upper incisors (case no. 363). Four right lower incisors (case no. 364). Upper incisor missing from left and right sides (case no. 365). One out of 79 had no R or LM⁴ (case no. 388). RM⁴ larger than LM⁴ (also case no. 388).

STAGODONTIDAE

Didelphodon padanicus: Type specimen (dentary fragment) of this Cretaceous didelphid may have had four premolars (Clemens 1966).

CAENOLESTIDAE

Garzonia patagonica: Specimen of Tertiary *Garzonia* may have supernumerary number of antemolar teeth (Sinclair 1906, Ride 1962, Ziegler 1971).

VOMBATIDAE

Extra calcified (but rudimentary) teeth reported in vombatids (Owen 1840-45, Röse 1893).

EUTHERIANS

Abnormal dental developments in human teeth have received considerable attention. The most important general treatise on the subject is Stones, Farmer and Lawton (1966). Several other papers (not noted in Stones *et. al.*) dealing with general dental abnormalities are: Black (1902), Kraus, Jordon and Pruzansky (1966); to papers dealing with specific abnormalities such as shovel-shaped incisors, Carbonell (1963); double-rooted lower canines, Alexandersen (1963); carabelli's tubercle, Meredith and Hixon (1954); abnormal cusp development in addition to carabelli's tubercle, Kallay (1966); dens in dente, Swanson and McCarthy (1947); and to papers dealing with the genetic nature of dental abnormalities such as Brothwell, Carbonell and Goose (1963), and Hopewell-Smith (1913).

Minor dental abnormalities in some placentals are documented, for example by Allow (1971), Bateson (1894), Berkovitz (1968), Berkovitz and

Musgrave (1971), Chasson (1955), Churcher (1959), Fish and Whitaker (1971), Forsten (1973), Frisch (1963), Garn and Lewis (1963), Hooper (1955), Jones (1960), Hooper (1955), Jones (1960), Mech, Franzel, Karns and Kuehn (1970), Miller and Tessier (1971), Peterson and Fenton (1970), Schitoskey (1971), Spinage (1971), Van Valen (1966, 1964), Wolfe and Layne (1968), Zakrzewski (1969), Ziegler (1971).

Several studies have been made using dental abnormalities in eutherians to interpret factors controlling tooth development. These include Berkovitz (1969), Butler (1963), Gaunt (1967), Grunenburg (1951, 1965), Hitchin (1966), Johnson (1952), Kurten (1955, 1957, 1963, 1967), Stockard *et. al.* (1941), Van Valen (1962, 1970) and Wallace (1968).

DISCUSSION

SUPERNUMERARY TEETH

PREMOLAR NUMBER: Diversity of position in abnormally occurring teeth noted in the present study indicates that some interpretations attempting to clarify the marsupial premolar dental formula are probably unjustified. For example, Thomas (1887) concludes that appearance of a premolar between the first and third premolars represents an atavistic reappearance of a lost marsupial second premolar. This view is not held by Owen (1840-5) or by Ziegler (1971). Ziegler concludes (p. 240) that 'The premolar position vacant in all marsupials is . . . most logically homologized with that of the retained first milk premolar of placentals . . . accordingly, the first three metatherian post canines are . . . designated the second, third and fourth premolars.' Owen (*op. cit.*) believes that premolar teeth are normally lost from the front of the premolar row. However, Bateson (1894 p. 249) after an examination of dental variations in marsupials in general concludes that '. . . the system elaborated by Thomas breaks down; not because there is any other system which can claim to supersede it, but because the phenomena are not capable of this kind of treatment'. Considering cases noted in the present study, it seems that extra premolars may occur at almost any position in the tooth row, as well as anterior and posterior to the first premolar. In addition, recent ontogenetic studies by Archer (1974), Berkovitz (1968) and others have not supported the suggestion of Woodward (1896) that there is clear evidence for a suppressed premolar position between P1 and P3 in marsupials, nor the view held by Owen (1840-45) or Ziegler (1971) that a similar premolar position has been lost in marsupials anterior to P1.

P5: Development of P5 in dasyurids and macropodids invariably results in a premolariform tooth, clearly indicating that potential for premolar production exists posterior to P4. Production of P5 presumably occurs later than P4 since it erupts later than and posterior to P4. Archer (1974) demonstrates that even before P4 is calcified in *Antechinus*, the dental lamina connections between it and adjacent teeth are already breaking down. Prior to normal breakdown of dental lamina, this tissue is continuous posterior to the canine. For this reason, the extra premolar probably could not result simply from an abnormal posterior extension of the premolar part of the dental lamina. It appears that the P5 tooth family position is established well before the tooth actually develops, posterior to the P4 position and anterior to the dP4 position on the continuous band of dental lamina.

M5: Molars sometimes occur posterior to M4 in macropodids but rarely in other marsupials. However, one case noted above of a *Dasyurus maculatus* specimen with L and RM⁵ and LM₅ is of this kind. It differs in that L and RM₄ resemble a normal L and RM₃. This specimen was, in part, the basis for Bateson's (1894) formulation of the concept of homoeosis in meristic series. This concept is that particular teeth in a series may vary in shape, and come to resemble aspects of adjacent teeth. In macropodids with more than four molars, homoeosis is not clearly evident because the normal macropodid M4 closely resembles the normal M3, and homoeotic variation in M4 would not be as obvious as in dasyurids.

M5 probably develops as an extra tooth family position at the posterior end of the dental lamina (Kirkpatrick 1969). In *Peradorcas*, production of additional molars is the normal condition (see Tate 1948). Obstructions to addition of teeth at the posterior end of the tooth row result from lack of space. This crowding may be, in part, responsible for abnormal shape of many supernumerary teeth. Butler (1956), Grunenberg (1937), and Lefkowitz, Bodecker and Mardfin (1953) have suggested that distortion of tooth germs can produce abnormally shaped teeth. Sofair, Bailit and MacLean (1971) and Stein (1943) note that this is most likely to be the case with posterior teeth of a particular tooth series. 'Normality' of supernumerary molars in macropodids may be due to forward progression of molars and consequent relative freedom from crowding.

PROBABLE ATAVISMS

In some taxa with a dental number reduced below that possessed by close relatives, teeth

occasionally occur in the position of the 'missing' tooth family. Such occurrences appear to be rather regular and should be regarded most probably as atavisms. These would include appearances of teeth in some dasyurids (e.g. *Dasyurus*) at the P4 position, and in some peramelids (e.g. *Echymipera*) at the I⁵ position.

EUTHERIANS

Berkovitz (1969), Johnson (1969), Kurten (1963) and others have presented interpretations regarding supernumerary teeth in various eutherians. Berkovitz (1969) demonstrates the existence of dI⁴ in a eutherian carnivore. He suggests this is evidence for the presence of four incisors in primitive eutherians. Johnson (1969) notes the appearance of M⁴ in a murid rodent and considers that this may be the homologue of the normal eutherian M³ and that in murid rodents the so-called M¹ is actually a persistent dP⁴. Kurten (1963) believes that in one lineage of felids, so-called supernumerary molars at the rear of the dentition represent an atavistic reappearance of a molar previously lost through evolution.

Although many Mesozoic mammals had more than seven molariform teeth (e.g. *Peramus* and *Amphitherium*), there is no particular reason for believing that the abnormal marsupial M5 noted in the present study is an atavistic reappearance of a lost tooth. More probably, these teeth are simply the result of abnormal activation of a potential tooth-producing structure, the posterior end of the dental lamina.

MISSING TEETH

Missing teeth, partial anodontia, or hypodontia noted in the present study occur mostly in the premolar region and only rarely in the molar region. Some instances are presumably due to trauma, others perhaps to disease, while others seem likely to be caused by genetic defects. Stones, Desmond and Lawton (1966) note that anodontia in humans is frequently due to a gene mutation in the X chromosome. Brekhuis, Oliver and Montelius (1944) note that there are often clear correlations between tooth absences. For example, loss of M1 is usually correlated with absence of other molars. In the only instances of non-traumatic molar loss noted in the present study, there were other teeth missing including premolars as well as molars. However, the great majority of cases of premolar loss do not involve molar loss.

ABNORMAL TOOTH MORPHOLOGY

DIVIDED TEETH: Divided teeth were found in the present study only among ante-molar teeth. Bate-

son (1894) notes that when teeth are divided, the plane of division is usually transverse to the long axis of the tooth row. This was invariable in examples considered here. A tendency for the divided tooth to be a RP₃ among dasyurids is present. There is also evidence for correlation of divided teeth and supernumerary premolars among dasyurids. In *Dasyurus geoffroii* (WAM M4464) an extra premolar occurs on the upper right side and the RP₃ has a divided crown. Division of single tooth germs in various stages of development may be one way in which supernumerary teeth are produced.

Concepts of tooth development, as discussed by Butler (1956), do not provide a mechanism for actually dividing established cusps. Rather, a divided crown tip could develop from two centres of suppressed mitosis in the developing tooth germ.

FUSED TEETH: Fused, geminated or connated teeth were found in the present study only among premolars. Fusion may involve only roots or anything up to and including the whole crown. Hitchin and Morris (1966) suggest that actual teeth do not become fused by any other means than by cementum after tooth formation is complete. They present reasons (p. 575) why fusion of tooth germs is unlikely to occur after epithelial contact between teeth is broken and follicles develop around each germ. They suggest (p. 583) that '... primary developmental abnormality in connation is persistence of the dental lamina between the teeth germs.' However, it seems equally plausible that physical trauma could result in ruptured follicles and subsequent fusion of previously separated portions of epithelium. Some fused teeth noted in the present study are also abnormally shaped. Combinations of abnormal features might result from fusion of previously ruptured and adjacent tooth germs. These developmental accidents certainly have no evolutionary significance.

OTHER ABNORMAL MORPHOLOGY: Mis-shapen molars noted in the present study are also often supernumerary teeth. In some cases they may be sub-molariform with part of the tooth, such as a protoloph, resembling a serially homologous structure in an anterior molar. M5 is commonly a tooth of this sort. Horseshoe-shaped and peg-like M5s are also known. Supernumerary molars occurring between other molar teeth are generally not molariform.

Some grossly abnormal molars suggest structurally ancestral cusp patterns. Examples of this may be cited among abnormal macropodid molars which show isolated cusps rather than crests. However, an equivalent number of abnormal

crowns do not suggest structurally ancestral shapes, such as the horseshoe-shaped or peg-like supernumerary molars. Stein (1934, p. 1817) notes that '... from a reasonably large collection of human third molars, different specimens could be selected and arranged in such order as to prove almost any theory of the evolution of the human dentition'. Abnormally shaped non-supernumerary molars are also noted above. Compression is a common abnormality of this kind. This was also noted by Archer (1971) in thylacine teeth. Probably this results from compression of the tooth germ follicle. Gruneberg (1937) and Lefkowitz, Bodecker and Mardfin (1953) have stressed the importance of the follicle in production of normally-shaped teeth. Osborn (1902) notes that increasing brachycephaly of rhinocerotids is correlated with antero-posteriorly shorter but wider molars. Butler (1956) suggests the possibility that this is the result of antero-posterior compression of the tooth germ follicles. In most of the examples given in the present study, antero-posterior molar compression is correlated with brachycephaly, shortening of the molar row, and sometimes malocclusion.

Number of stylar cusps present in dasyurid molars is clearly variable within species, although these variants are generally uncommon and their significance is unclear. Except in *Neophascogale* and *Phascolosorex*, there are normally only two conspicuous stylar cusps, st.B and st.D. St.A is not usually distinguishable from st.B. Sometimes, a stylar cusp (or pair) is developed between st.B and st.D, and it has been called here st.C. Stylar cusps may appear posterior to st.D. Some didelphids (considered structurally ancestral to dasyurids) have five stylar cusps. Other didelphids have practically no stylar cusps. Bensley (1906) has demonstrated considerable variation in didelphid stylar cusps. He concludes (pp. 12-13) that although these '... relatively small and subsidiary structures in the molar crown are certain to exhibit signs of variation, they are surprisingly constant in their relations... they show throughout the family indications of a general type...'. The same can be concluded for the stylar cusp area of dasyurids. Despite intra-specific variation and even inter-specific modification, the dasyurid basic pattern described above is clear. However, more information about the Tertiary record of dasyurid stylar cusp development is required before the structurally ancestral dasyurid condition can be defined.

ERUPTION AND OCCLUSION ABNORMALITIES

Malocclusion is rare among marsupials but several instances have been described. An example

of exaggerated overbite noted above is similar to examples presented by Stockard et al. (1941) among dogs. They suggest that upper and lower jaw development is under separate genetic control because, for example, in a cross between a Saluki Dog and a Bassethound, the hybrid had a skull of a Saluki-type in length and a dentary of a Bassethound-type in length, resulting in gross malocclusion with the C_1 biting behind the C^1 .

Another case of malocclusion noted in the present study, involves *Dasyuroides byrnei*. A large series of these animals were trapped and lodged in the Queensland Museum's collection (e.g. J10226). Some bred in captivity (Mack 1961) through several generations. Comparison of 30 skulls of animals bred in captivity and the 9 animals caught in the wild indicates that problems of malocclusion and missing teeth occurred only among animals bred in captivity. In addition there was occurrence of abnormally compressed molars and brachycephaly in some animals bred in captivity. Reasons for this are not clear but factors such as diet and inbreeding are likely to have been involved.

ABNORMALITIES AND DISEASES

Examples of morphological variation, tooth loss, and bony accretion around the tooth roots noted in the present study may be the result of disease. In other instances, some teeth show abnormal dentine accretions around roots, and one specimen may possibly represent a composite odontoma. The difference between composite odontomas and congenital teratomas such as ovarian dermoid cysts (Stones, Farmer and Lawton 1966) seems to be one largely of position. The case noted in the present study involves an abnormal M^4 with apparently several surrounding and related calcified structures. There is, however, no evidence that these calcified structures and M^4 were fused.

EPHEMERAL TEETH

Ephemeral teeth observed in sectioned material or carefully prepared juvenile specimens, do not really represent abnormal dental developments in the sense outlined in the introduction. However, they have been considered here either because they are not commonly observed or because they represent teeth previously unobserved.

Observations of the occurrence of small calcified incisors are reported in this paper and by others (e.g. Berkovitz 1967, Woodward 1896), particularly among macropodids. They rarely persist in adults. These teeth probably represent true deciduous teeth related to the incisors (as suggested by Kirkpatrick 1969). Clear embryological evid-

ence for them is known (e.g. Archer 1974, Berkovitz 1968c, Rose 1892, Woodward 1896) for many marsupial groups and they are generally assumed to be rudimentary deciduous teeth. This may not be true for rudimentary canines in macropodids. These may represent rudimentary non-deciduous teeth, which in other macropodids (e.g. potoroines) are parts of the functional adult dentition.

It has been noted that some ephemeral teeth occurring in the position of a 'missing' tooth family in some closely related forms should be interpreted as atavisms. Tate (1947) notes a case of a dental rudiment in the P⁴ region of a specimen of *Dasyurus hallucatus* and considers this a dP⁴. However, its actual identity is doubtful, since it could be either a rudimentary dP⁴ or a rudimentary P⁴. Reduction of size in these teeth is not necessarily correlated. For example, it has been noted above that while the *Phascolarctos* P⁴ is large, dP⁴ is a mere rudiment (Thomas 1887). In macropodids, while dP⁴ is as large as a molar, P⁴ may be (in some species) a rudiment. This is clearly so in thylacinids (Flower 1868), adding support to the idea (Archer 1974, Berkovitz 1966) that the two teeth do not belong to the same tooth family and hence development of one may not depend on development of the other.

Bateson (1894) concludes that meristic variation in teeth is discontinuous, and that a structure was either a tooth or not a tooth. However, ephemeral teeth in the incisor and canine regions clearly present exceptions to this concept. These have been found in all stages of development from mere lingual growths of dental lamina to calcified and even erupted teeth. Commonly, even after calcification, the teeth are resorbed. Sometimes they persist into the adult dentition as do the small canines in some species of macropodine and most potoroine macropodids.

DENTAL ABNORMALITIES AS INDICATORS OF PATTERN IN DEVELOPMENT

Value of dental abnormalities in general in understanding factors controlling development of teeth is doubtful. There have been many attempts to interpret the nature of controlling factors by analysis of the kinds and incidence of dental abnormalities.

Butler (1967) concludes, after noting studies of abnormal conditions of human jaws, that disturbances in migration of mesenchyme from the neural crest may account for abnormal developments of teeth and their supporting bones. In cases where the tongue is doubled, a median series of teeth may develop between the two tongues. Similarly in unilateral hypertrophy of the face,

teeth are enlarged on the affected side. It is therefore interesting to consider the possible significance of unilateral and bilateral dental abnormalities. Bateson (1894) finds that dental abnormalities sometimes occur simultaneously on both sides of the head but rarely occur simultaneously in upper and lower dentitions. Nevertheless, he cites examples of extra molars on both upper sides only (e.g. case nos. 178, 179 and 194), on both lower sides only (e.g. case nos. 171 and 251), on upper and lower right sides only (e.g. case nos. 190 and 196), on both lower sides and only one upper side (e.g. case nos. 182 and 385), on both upper sides and only one lower side (e.g. case nos. 166 and 167), and on both upper and both lower sides (e.g. case 189). Similar examples of correlated variations are given for other tooth series and for missing teeth. Apparently all combinations of this sort are possible. In specimens noted in the present study, particularly among macropodids, L and RM⁵ may be grossly different (e.g. J23085) or mirror images of one another (e.g. J23083). The case given of a grossly abnormal L and RM₁ in *Isoodon obesulus* shows that complex bilateral abnormalities may occur, without abnormal occlusal counterparts.

Butler (1961, p. 122) considers that 'If the mutation of teeth (upper, lower and adjacent) were fortuitous, variability of pattern would result so frequently in malocclusion that natural selection would operate to reduce that variability to a minimum. Yet molar teeth show a high degree of individual variation.' Accordingly he proposes that genes controlling tooth shape (and presumably number) may have a dual or pleiotropic effect, producing mirror image structures on surfaces of teeth which contact. This idea relates to the concept of dental morphogenetic fields (Butler 1937, and discussed by Butler 1961, Van Valen 1962, 1970, Wallace 1968, *et. al.*). The concept is based on the belief of the equipotential nature of all tooth germs of a particular species (suggested by Bolk 1922). This potential is modified by other factors such as heredity, position in the tooth row, chemical imbalances, disease, trauma, and available room. Many of these factors have been analyzed (e.g. Stones, Farmer and Lawton 1966). However, the way in which position in the tooth row controls tooth shape is not clearly understood. Butler (1967), notes that Remane (1926) figures a specimen of *Colobus* whose first and second permanent molars are dwarfed and premolariform. Stein (1934) notes a specimen of a human M³ which corresponds cusp for cusp, ridge for ridge, and groove for groove with a normal P². These examples suggest that position in the tooth row is

not always the most important factor in development. Butler (1963) regards such variation in dP^3 as evidence for slight shifts in dental morphogenetic field at the molar-premolar boundary, and this may also apply to Remane's (1926) specimen but not to Stein's (1934).

The present study offers no additional examples among marsupials which bear on the question of developmental importance of position in the tooth row. It does provide examples (e.g. bilaterally symmetric abnormal L and RM_1) of abnormal molars that have not been correlated with abnormal occlusal counterparts. It may be that composition of dental morphogenetic fields, if they exist, is much more complex than has been visualized (e.g. by Wallace 1968 and Van Valen 1970).

CONCLUSIONS

Abnormal dental developments do not appear to provide a basis for interpreting position of a supposedly phylogenetic lost premolar tooth in marsupials other than $P4$ of some dasyurids. It has been concluded elsewhere (Archer 1974) that ontogeny in some dasyurids similarly fails to reveal a 'lost' premolar position in structurally ancestral marsupials. There does not appear to be any sound reason for believing that marsupials phylogenetically suppressed a particular premolar position.

In some dasyurids with only two premolars on each side, there is evidence from dental variations that the $P4$ position has been suppressed. Such dental variations should be referred to as atavisms.

Abnormal production of $P5$ and $M5$ in marsupials suggests that the dental lamina may remain proliferative at its posterior end even after the normal complement of tooth families has been established. This is particularly evident in the macropodid *Peradorcas* where continuous production of supernumerary molars may occur.

Abnormal crown morphology occurs most commonly among premolars. These often exhibit fused or divided crowns. Fused crowns may result from damage to adjacent developing teeth. Divided crowns, because they are sometimes related occlusally to supernumerary teeth, may be one stage in a process in which supernumerary teeth are produced. Abnormal variations are also common on the styler shelf of molars. Grossly abnormal molar crowns are uncommon in marsupials in general but are more common in supernumerary macropodid molars. Distorted molar crowns may result from crowded tooth germs. Among dasyurids, antero-posteriorly compressed molars are among the most commonly encountered molar abnormalities.

Malocclusion and abnormal molar crown morphology appear, among some dasyurids, more common among inbred than among trapped individuals, suggesting some abnormalities may have a genetic basis.

From ontogenetic studies, many ephemeral teeth developing in canine and incisor positions appear to represent short-lived milk-teeth (e.g. macropodid incisors) or small vestiges of teeth in the process of phylogenetic reduction (e.g. macropodine canines). These are sometimes found in dry skulls representing very juvenile individuals, if the skulls are carefully prepared.

Most abnormal dental developments appear to be of little or no significance in interpreting phylogeny, while others do appear significant and suggest that mechanisms determining tooth shape are complex. Dental morphogenetic fields do not always ensure that abnormalities occur with occlusal counterparts and the majority of dental abnormalities occur in one tooth row only. Other examples do involve occlusal or bilateral counterparts, and add support to the concept of dental morphogenetic fields. The apparent inconsistency may be resolved if the majority of dental abnormalities lack a genetic basis.

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PLATE 30

- A. *Antechinus flavipes* (WAM M6785) with extra right lower premolar anterior to P₁.
- B. *Sarcophilus harrisii* (WAM 71.10.209) with abnormal tooth posterior to LP¹ and otherwise missing posterior left upper teeth. Specimen from cave deposit.
- C. *Phascogale tapoatafa* (WAM M7453) with three-rooted partially divided LP³.
- D. *Dasyurus maculatus* (J 16744) with abnormal LM⁴, possibly part of composite dental odontoma.

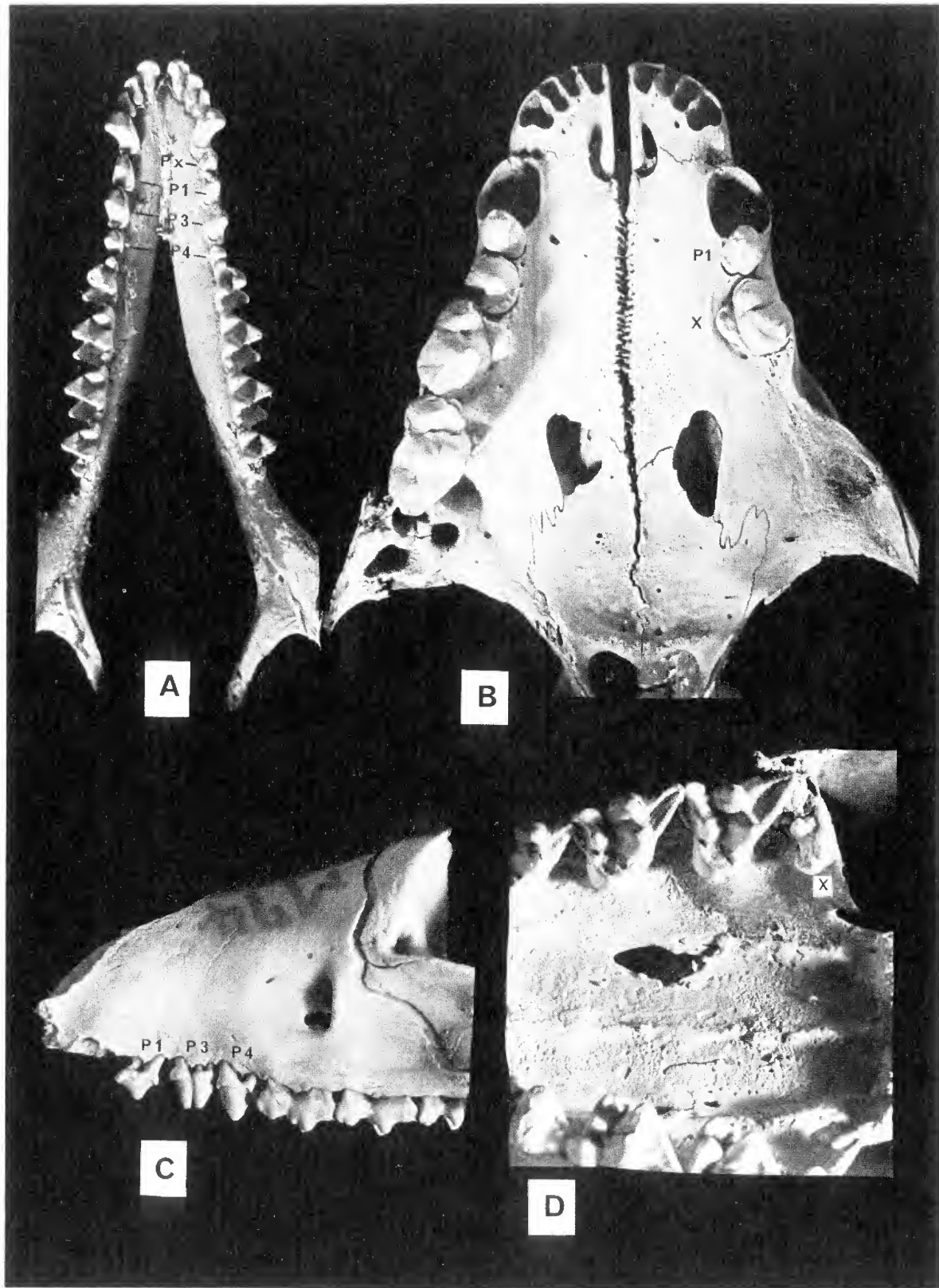


PLATE 31

- A. *Sminthopsis* sp. (b) (J5459) with divided entoconid on RM₃.
- B. *Sminthopsis* sp. (b) (J 5173) with bifid stylar cusp C on RM¹.
- C. *Sminthopsis granulipes* (WAM M6062) with stylar cusp C on RM¹ or split stylar cusp D.
- D. *Neophascogale* sp. (AMNH 109524) with divided stylar cusp C and possibly also divided stylar cusp D on RM¹.
- E. *Dasyuroides byrnei* (specimens in Queensland Museum). E1, captured live, presents normal skull form. E2, inbred in captivity, shows extreme brachycephaly and related distortions of 'wild' condition.

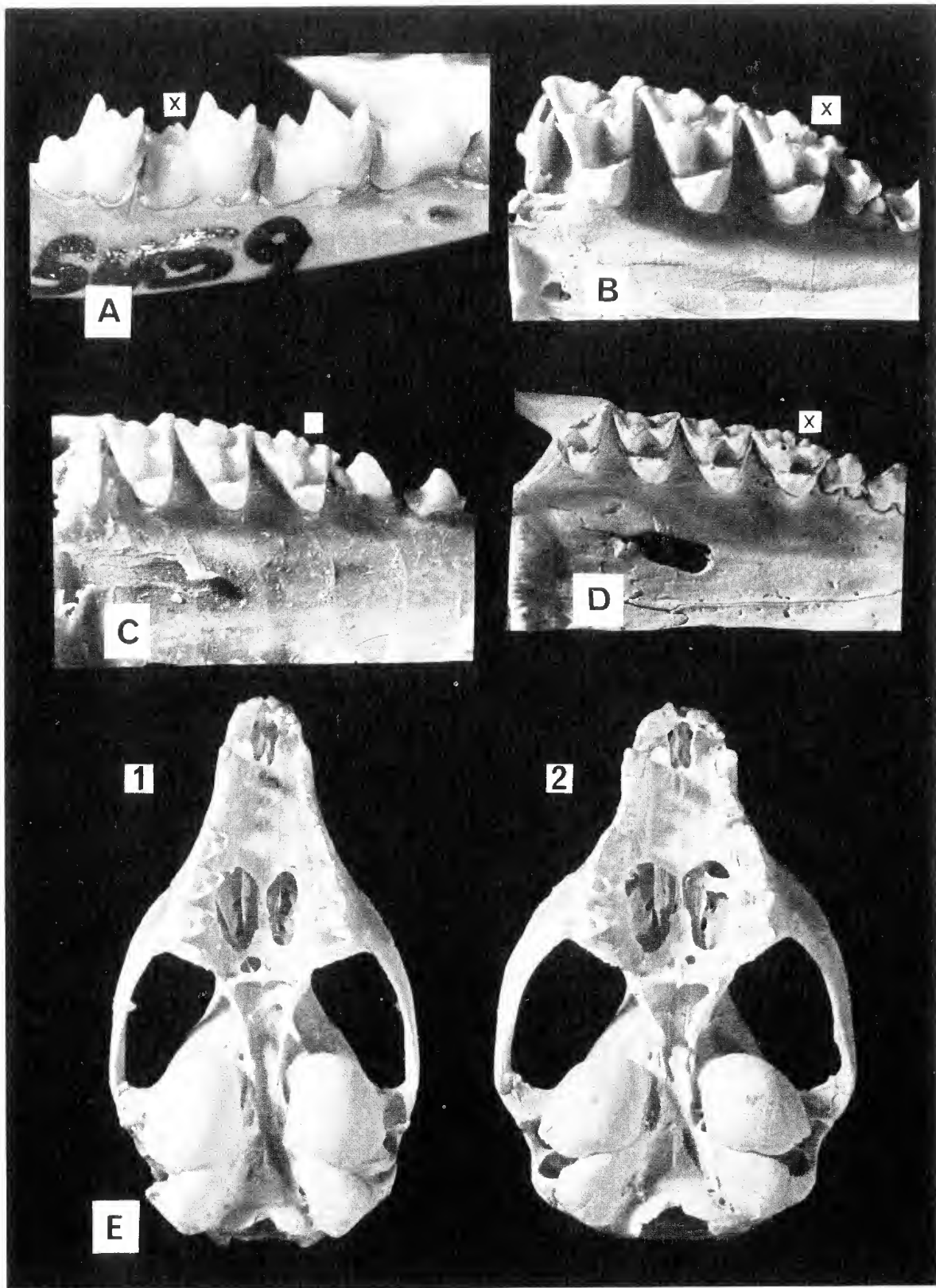


PLATE 32

- A. *Isoodon obesulus* (J 23082) with grossly abnormal L and RM₁.
- B. *Isoodon macrourus* (J 21908) showing almost total anodontia.
- C. *Trichosurus vulpecula* (1, J 23071; 2, J 23070). C1 shows normal RdP⁴. C2 shows abnormal ?RdP⁴ erupting above this tooth through side of maxilla.

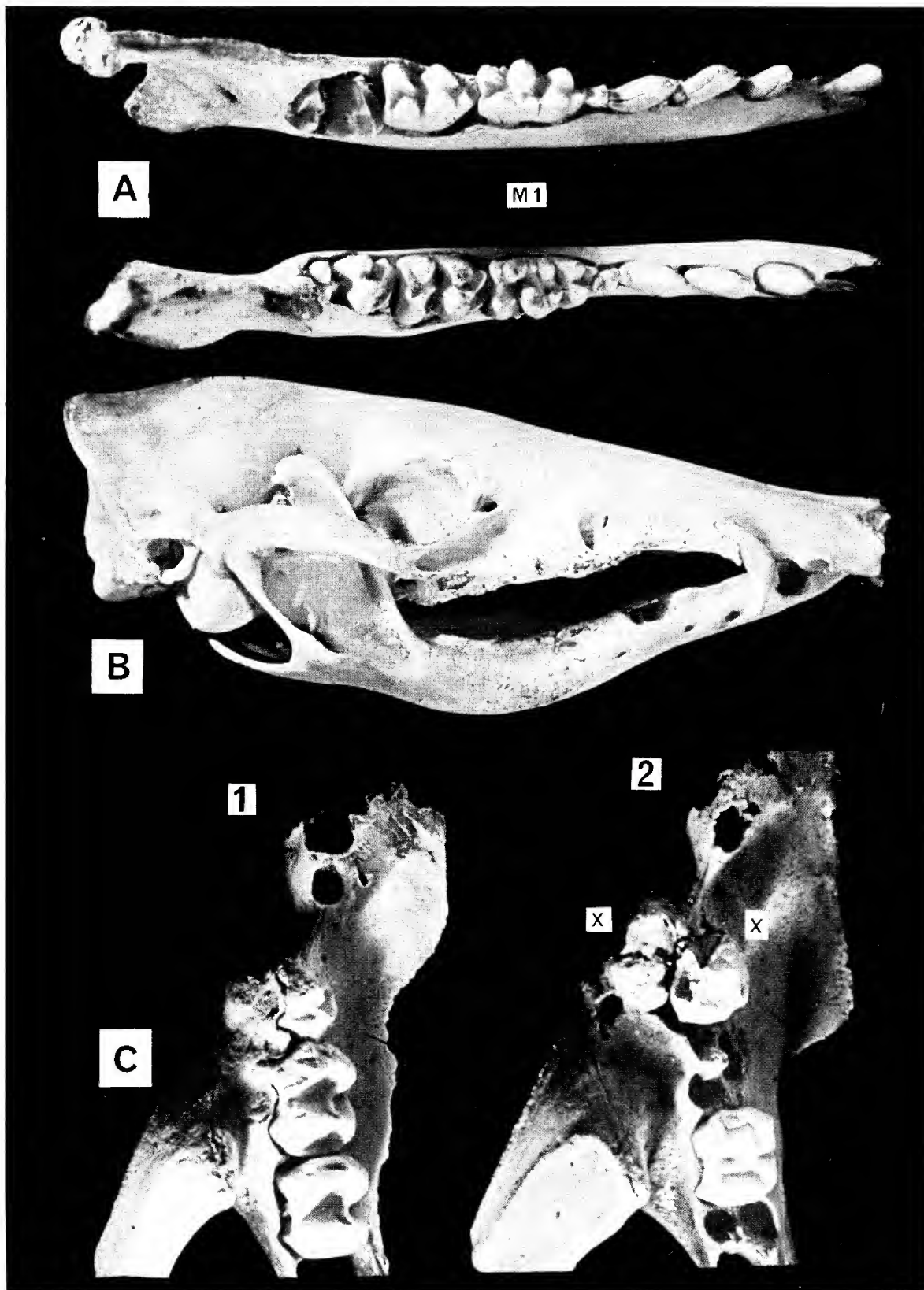


PLATE 33

- A. *Pseudocheirus peregrinus* (J 11427) with calcified ?RdP⁴ adhering to buccal side of RP⁴.
- B. *Phascolarctos cinereus* (1, J 8811; 2, J 10023). B1 shows reduced hypocones on RM¹⁻⁴. B2 shows extra right incisor and unreduced hypocones on RM¹⁻⁴.
- C. *Macropus irma* (WAM M8127) showing calcified ?LC¹ with maxillary-premaxillary crypt and calcified ?L and RdI¹ anterior to unerupted L and RI¹.

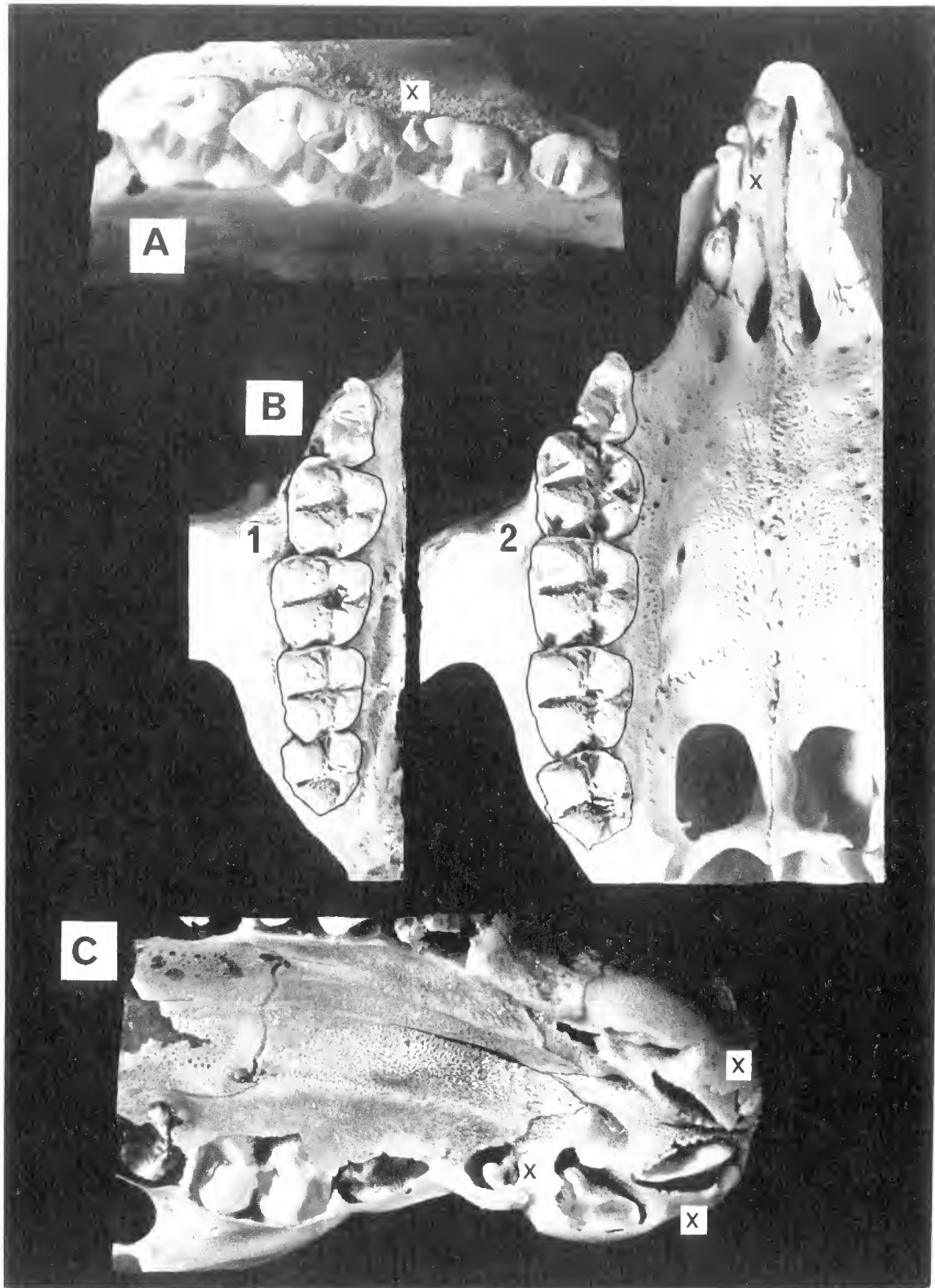


PLATE 34

- A. *Macropus robustus* (1, WAM M6976; 2, WAM M6137). A1 shows ?LC¹ in maxillary-premaxillary crypt formed by anterior extension of maxillary bone. A2 shows older individual in which anterior projection of maxillary bone has been resorbed (former position indicated by arrow) and ?RC¹ lost.
- B. *Macropus giganteus* (J 23092) with abnormal L and RI² and RI³ erupting in abnormal position.
- C. *Macropus giganteus* (J 23087) with RI³ abnormal in structure and position, and supernumerary incisiform tooth anterior to LI³.

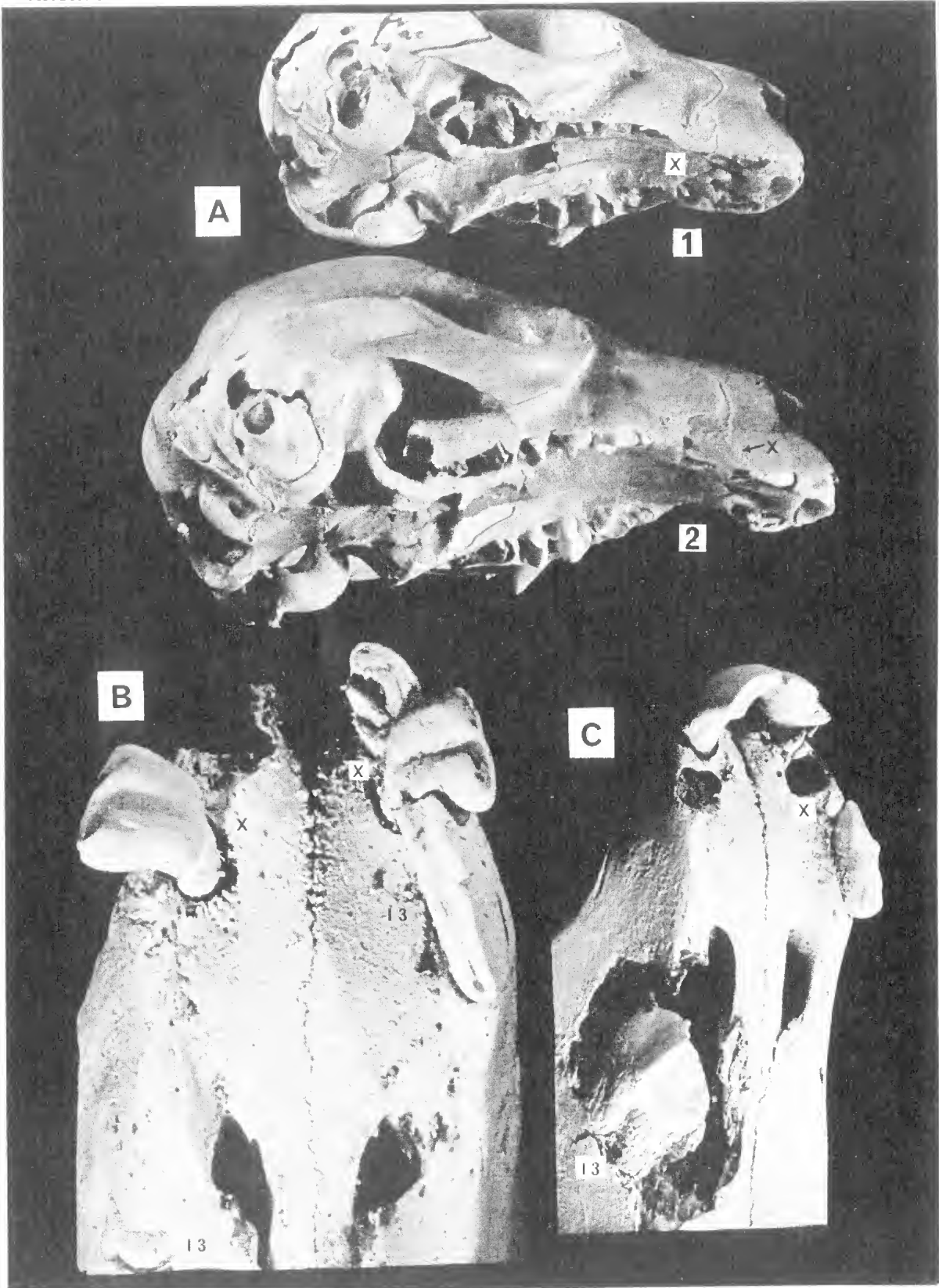
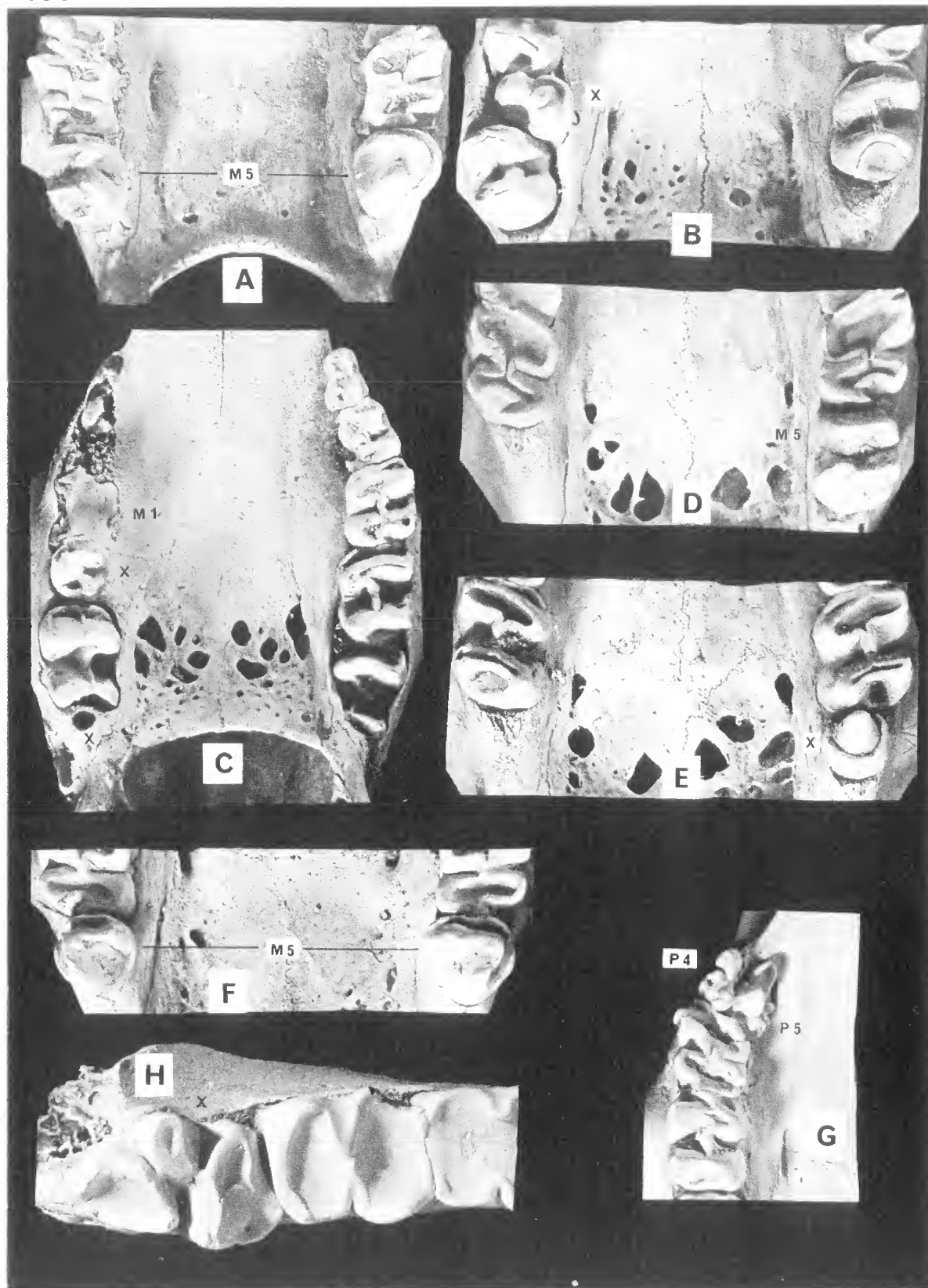


PLATE 35

- A. *Macropus giganteus* (J 23083) with abnormal L and RM⁵.
- B. *Megaleia rufa* (J 23091) with abnormal supernumerary tooth between RM³ and RM⁴.
- C. *Megaleia rufa* (J 23088) with supernumerary abnormal tooth posterior to RM¹ and alveolus for another posterior to ?RM³.
- D. *Megaleia rufa* (J 23084) showing abnormal LM⁵.
- E. *Megaleia rufa* (J 23086) showing abnormal conical LM⁵.
- F. *Macropus giganteus* (J 23085) showing abnormal but bilaterally symmetric L and RM⁵.
- G. *Macropus giganteus* (J 23089) showing RP⁵ replacing RP⁴ anterior to RM¹.
- H. Macropodid (F 4713) from Pliocene Chinchilla Sands Formation, showing abnormally shaped LM₄ or M₅.





THE GENUS *DIGASTER* (MEGASCOLECIDAE: OLIGOCHAETA) IN QUEENSLAND

B. G. M. JAMIESON
Department of Zoology, University of Queensland

ABSTRACT

Digaster is here emended to exclude *Perissogaster excavata* and *P. nemoralis* but to retain *P. queenslandica*. The redefined genus is limited, as previously, to the montane coastal province of the Eastern Subregion of Australia. It consists of 17 species: 13 in southern Queensland, 2 in New South Wales and 2 species shared between the two states. Evidence given suggests that the genus has originated locally from holonephric species with a pair of combined male and prostatic pores on XVIII, or from meronephric monogastric descendants of these, and that origin, or at least major speciation, of the genus has been relatively recent. It is deduced that the digastric or trigastric condition of the genus is derived from the monogastric condition and that this multiplication of gizzards has occurred in Australia independently of other regions. A new generic definition and a key to all species are given together with descriptions of 5 new species, 2 new subspecies and of new material of 5 previously known species.

The genus *Digaster* was erected by Perrier (1872) for a single species, *D. lumbricoides*, from the vicinity of Port Macquarie in northern New South Wales. This remained the only known Australian oligochaete with two gizzards (the digastric or digiceriate condition) until Fletcher (1887) erected the genus *Didymogaster* for *Didymogaster sylvatica* from further south in New South Wales. The latter genus remained monotypic until Jamieson and Bradbury (1972) added the geographic replacement species *Didymogaster prothecata* and validated generic distinction from *Digaster*. The first additions to *Digaster* were *D. armifera* Fletcher, 1887 and *D. perrieri* Fletcher, 1889, also from New South Wales. Subsequently, Spencer (1900) added three species and Michaelsen (1916) and Boardman (1932) each added one species, all from Queensland. Three further Queensland species were added by Jamieson (1970, 1972). The present paper is devoted to description of 5 new species and 2 new subspecies of *Digaster* recorded in intensive collecting for oligochaetes in Queensland, from its southern border, at approximately 29°S., northwards along its eastern seaboard to Cooktown, at approximately 15°30'S., on Cape York Peninsula. A single, brief collecting foray on the Peninsula from its east coast at 15°30'S. to Normanton, near its west coast, at approximately 18°S. was unproductive, presumably because conditions were dry. The oligochaete fauna of the northern half of the

Peninsula and of its Carpentaria catchment thus remains unknown. The map of localities sampled will be limited to southern Queensland as the most northerly record for *Digaster* is 25°S.

The new additions bring the generic complement to sixteen digastric species and evidence will be given for the inclusion of a seventeenth species, the trigastric *Perissogaster queenslandica* Fletcher, 1889.

Perissogaster was first placed in the synonymy of *Digaster* by Beddard (1895) who included its three species and also *Didymogaster*. Michaelsen (1900, 1907) separated the three genera but Sweet (1900) and Jamieson (1963) again included the three species of *Perissogaster*, but excluded *Didymogaster*. Jamieson (1970) presented evidence in support of exclusion of the type-species of *Perissogaster*, *P. excavata* Fletcher, 1888 and of *P. nemoralis* Fletcher, 1889 and retention in *Digaster* of *P. queenslandica* but these changes were deferred pending examination of *Digaster lumbricoides*. The latter species was redescribed in Jamieson (1971b), in which a *lumbricoides* species-group was defined, and it will be appropriate in the present work to redefine the genus.

Genus *Digaster* Perrier, 1872

Digaster Perrier, 1872, pp. 94-6; Michaelsen, 1900, p. 196; 1907, p. 162; Stephenson, 1930, p. 839.

Digaster (part.); Beddard, 1895, p. 484; Jamieson, 1963, pp. 85-6; Jamieson, 1971a, pp. 74-5; Jamieson, 1971b, pp. 1307-8.

DIAGNOSIS: Setae lumbricine. Gizzards 2, in V and VI or VI and VII, or 3, in V, VI and VII; extramural calciferous glands absent though poorly differentiated oesophageal pouches may be present. Intestine commencing in or behind XVII; typhlosole absent. Meronephric; the medianmost nephridium in caudal segments exonephric with preseptal funnel. Combined pores of a pair of racemose or tubuloracemose prostates and the vasa deferentia in XVIII or rarely in XVII. Testisacs absent. Spermathecal pores intersegmental or at the anterior margins of their segments.

DETAILED DEFINITION: Small to large terrestrial worms (28 mm to more than a metre long). Prostomium zyglobous to tanylobous. Circular in cross section throughout, with terminal anus. First dorsal pore in 3/4-11/12 (rarely far posterior?). Setae 8 per segment, in straight or irregular longitudinal rows; fairly closely paired; *cd* significantly wider than *ab* (minimally 1.2 *ab*); *dd:u* 0.2-0.8 in the forebody. Nephropores scattered, only sporadically visible. Clitellum annular, occupying 4-8 segments, the first segment occupied usually being XIII or XIV. Combined male and prostatic pores a pair on XVIII varying from median to *a* to *b* lines. Accessory genital markings present or absent. Female pores paired or, rarely, single; anteromedian to setae *a* of XIV. Spermathecal pores 2 or, rarely, 3 pairs, intersegmental or at the anterior borders of their segments, the last in or immediately behind 8/9, varying from median to *a* to *b* lines.

Dorsal blood vessel single, continuous onto the pharynx; last hearts in XII or XIII; supra-oesophageal vessel present but often poorly differentiated; the last hearts in and posterior to X latero-oesophageal; dorsoventral commissurals present anteriorly to the hearts. Subneural vessel absent. Gizzards 2, in V and VI or VI and VII or (*queenslandica* and rare individual variation) 3, in V, VI and VII; contiguous or separated by unmodified oesophagus. Oesophagus vascularized and internally folded and often dilated, in a few to most segments occupied, but extramural calciferous glands absent; intestine commencing in XVII to XIX; typhlosole, muscular thickening and caeca absent.

Wholly meronephric; micromeronephridia in anteriormost segments aggregated in bands or usually forming bucco-pharyngeal or exonephric tufts; succeeding nephridia exonephric astomate micromeronephridia; in the hindbody the medianmost nephridium on each side possessing a pre-

septal funnel which usually (and typically) is enlarged as an exonephric megameronephridium. Holandric (testes and funnels a pair in each of X and XI) or metandric (these in XI only); testisacs absent; seminal vesicles in IX and XII, XI and XII or XII only. Prostates 1 pair, racemose or (*queenslandica*) tending to tubuloracemose; unipartite or bipartite; the vasa deferentia (always?) joining the junction of gland and duct. Penial setae present or, more commonly, absent. Ovaries 1 pair, in XIII; ovisacs absent. Spermathecae 2 or 3 pairs, with 1 or 2 often multiloculate diverticula. All structures sometimes (*D. lumbricoides* and *D. anomala*) displaced one segment anteriorly by suppression of an anterior metamere but gizzards never anterior to V).

DISTRIBUTION: New South Wales (Port Macquarie and Kyogle areas and the Sydney Basin); Queensland (South of 25° S., coastal to as far west as 151° E.).

TYPE SPECIES: *Digaster lumbricoides* Perrier, 1872.

SPECIES: (NSW = New South Wales; Q = Queensland).

- | | |
|---|--------|
| 1. <i>D. anomala</i> Jamieson, 1970 | Q |
| 2. <i>D. armifera</i> Fletcher, 1887 | NSW |
| 3. <i>D. binnaburra</i> sp. nov. | Q |
| 4. <i>D. bradburyi</i> Jamieson, 1970 | Q |
| 5. <i>D. brunneus</i> Spencer, 1900 | Q |
| 6. <i>D. gayndahensis</i> Spencer, 1900 | Q |
| 7. <i>D. gwongorellae</i> Jamieson, 1972 | Q |
| 8. <i>D. lamingtonensis</i> Michaelsen, 1916 | Q |
| 9. <i>D. longmani</i> Boardman, 1932 | NSW, Q |
| 10. <i>D. lumbricoides</i> Perrier, 1872 | NSW, Q |
| 11. <i>D. minima</i> sp. nov. | Q |
| 12. <i>D. minor</i> Spencer, 1900 | Q |
| 13. <i>D. nothofagi</i> sp. nov. | Q |
| 14. <i>D. perrieri</i> Fletcher, 1889 | NSW |
| 15. <i>D. pseudoperichaeta</i> sp. nov. | Q |
| 16. <i>Perissogaster queenslandica</i> Fletcher, 1889 | Q |
| 17. <i>D. sexpunctata</i> sp. nov. | Q |

REMARKS: Jamieson (1970) showed that the type-species of *Perissogaster*, *P. excavata* (see also Bage, 1910), and *P. nemoralis* had only astomate micromeronephridia posteriorly. The third known species, *P. queenslandica*, was shown to have the dichogastrin condition, with the medianmost nephridium enlarged and stomate. Demonstration (Jamieson, 1971b) that the dichogastrin condition was typical of *Digaster* supported the contention in the previous paper that *P. queenslandica* could be accommodated in *Digaster* while *Perissogaster*

should be revived for *P. excavata* and *R. nemoralis*. *Perissogaster* is here formally re-instated although it must be stated that existing material of the genus is not in sufficiently good condition to allow full characterization of the genus.

With the re-instatement of *Perissogaster* as an independent genus, the number of di- or tri-gastric genera in the Megascolecinae is raised to thirteen of which only *Digaster*, *Didymogaster* and *Perissogaster* are Australian. The fact that all thirteen genera have the advanced (meronephric) condition of the nephridia, all holonephric megascolecines being monogastric or agastric, suggests that multiplication of gizzards is a secondary condition, at least in the Megascolecinae. Ten of the genera with multiplied gizzards (*Benhamia*, *Dichogaster*, *Eudichogaster*, *Eutrigaster*, *Lennogaster*, *Millsonia*, *Omodeona*, *Pellogaster*, *Rillogaster* and *Trigaster*) differ from the three Australian genera in lacking the megascolecine of the male terminalia (pores of a pair of prostates and of the vasa deferentia combined on XVIII). This difference, in addition to its diagnostic value, is of interest in suggesting that multiplication of the gizzards has occurred in Australia independently of replication in groups in other regions. This inference is supported by the fact that the primitive (that is, holonephric, monogastric) Australian genera have the same, megascolecine condition of the male pores, a fact which suggests that they are ancestral to the di- or tri-gastric Australian genera and contraindicating descent of the latter from allopatric genera with non-megascolecine male pores whether with one or more gizzards.

The five new species of *Digaster* and two new subspecies are all assignable to the very homogeneous *lumbricoides* species-group defined by Jamieson (1971b). Inclusion of the remaining species, *D. armifera*, *D. perrieri* and *D. queenslandica*, in the genus confers greater heterogeneity on the genus but their exclusion cannot on present evidence be justified. The displacement of the gizzards in the *lumbricoides* group from VI and VII to V and VI in *D. lumbricoides* and *D. anomala* by deletion or suppression of an anterior metamere, together with occurrence of gizzards in V, VI and VII in the morphologically close *D. queenslandica* and (Jamieson, 1963) a variant in *D. perrieri*, do not allow convincing subdivision on the basis of distribution of the gizzards.

Perissogaster s. strict., now limited to *P. excavata* and *P. nemoralis*, from New South Wales, is diagnosed from all other megascolecids by the combination of three gizzards, megascolecine male pores and non-dichogastrin (megascolecine) nephridia. *Didymogaster*, also from New South Wales,

is distinguished by the combination of two gizzards, in VI and VII, megascolecine male pores, the segmental (not intersegmental) location of the spermathecal pores and the suboesophageal testis-sacs.

While the tribes Perionychini and Dichogastrini, characterized by holonephric and dichogastrin nephridia respectively, are acceptable groupings by virtue of their homogeneity, the tribe Megascolecini, diagnosed by non-dichogastrin meronephridia, which includes *Perissogaster*, is less satisfactory, being more heterogeneous in morphology and probably in origin. Relegation of *Perissogaster* s. strict. to the Megascolecini still leaves the possibility of close relationship of this genus with *Digaster*.

The distribution of *Digaster* (like that of *Didymogaster* and *Perissogaster*) conforms with the montane coastal province of the Eastern Subregion of Australia recognized for the avifauna by Kikkawa and Pearse (1969; see Jamieson, 1974). In view of the large number of very similar species in the genus, this limited geographical distribution does not appear to be evidence, as might have been thought, that *Digaster* is a relict genus with a former wide distribution in Australia. If it were taken to be a relict with a much-contracted distribution it would be necessary to explain why the similarly digastric *Didymogaster* and the tri-gastric *Perissogaster* also survived only in this province. Nor can the limited distribution be explained in terms of recent introduction from outside Australia for this would require either concomitant introduction of all its species and, presumably, of *Didymogaster* and *Perissogaster*, or massive speciation since introduction. It seems more acceptable that *Digaster* (and the clearly related *Didymogaster* and the less certainly related *Perissogaster*) originated locally from monogastric holonephric worms, or their meronephric descendants, sufficiently long ago for considerable speciation but not long enough ago for colonization of other parts of Australia. Part of the restriction in range must be due to ecological preferences and not to lack of time for dispersion but it must be reiterated that the digastric condition suggests relatively recent, and local, origin of the genus for reasons given above.

KEY TO THE SPECIES AND SUBSPECIES OF *Digaster*

1. 3 oesophageal gizzards present
 *D. queenslandica**
2. 2 oesophageal gizzards present 2
2. Male pores in XVII 3
 Male pores in XVIII. 4
3. Accessory genital markings a pair of oval

- glandular areas in front of and behind the male pores, posteriorly in XVI and anteriorly in XVIII. Other accessory genital markings absent
- . . . *D. lumbricoides lumbricoides*, Fig. 9F
- Accessory genital markings midventral, unpaired transverse pads in 19/20 and 20/21; sometimes also in varying numbers of intersegments 18/19, 21/22–24/25, and in 8/9–10/11 *D. anomala*, Fig. 9B
4. Gizzards in V and VI. 5
Gizzards in VI and VII 6
5. A square glandular pad midventral in each of XI and XII. At maturity, 2 elliptical genital markings, one behind the other, lateral of the male pores. A pair of ellipses often present in each of XVII and XIX
. *D. armifera**, Fig. 9C
- Genital markings absent from XI and XII. 3 transverse ventral ridges typically present, in 17/18, XVIII and 18/19 *D. perrieri**
6. Dorsal setal couples (*cd*) in caudal segments displaced far dorsally, the 4 setae in 4 equispaced lines 7
Dorsal setal couples not displaced far dorsally; significantly further apart than the setae of each couple 8
7. Accessory genital markings a midventral pad in X, XVI and XVII, and a pair of white tumescences presetally in XIX
. *D. pseudoperichaeta*, Fig. 7
- Accessory genital markings a midventral circular papilla in XIII, XX, XXI and in varying numbers of segments XII, XV, XVI, XIX, and XXII–XXIV. A paired marking sometimes present in X
. *D. minima*, Fig. 6A
8. One or more midventral unpaired genital markings (papillae or transverse pads) in or within a segment or two of IX 9
Midventral unpaired genital markings absent or, if present, not in the vicinity of IX 13
9. 3 pairs of small disc-like markings located between the male porophores on XVII
. *D. sexpunctata*, Fig. 8
- No genital markings between the male porophores 10
10. Metandric (testes and funnels in XI, seminal vesicles 1 pair, in XII only). First dorsal pore in 5/6 or 6/7 *D. longmani* (part.)
Holandric (testes and funnels in X and XI, seminal vesicles 2 pairs, in IX and XII or XI and XII). First dorsal pore in 4/5 11
11. Seminal vesicles in XI and XII. First dorsal pore in 5/6 *D. longmani* (part.)
Seminal vesicles in IX and XII. First dorsal pore in 4/5 12
12. Midventral unpaired papillae transversely elongate on segments following the spermathecal pores; intersegmental in the vicinity of the male pores where there may be paired papillae also *D. nothofagi*, Fig. 6B
Midventral unpaired papillae circular or longitudinally extended on segments following and often including the spermathecal pores; not present in the vicinity of the male pores where there are usually paired segmental markings *D. binnaburra*, Fig. 2
13. A midventral circular, oval or almost bifid pad on XVIII between or including the male pores 14
No midventral pad in XVIII. Genital markings usually present elsewhere 15
14. Female pore unpaired. No genital markings present in addition to that on XVIII
. *D. gwongorellae*, Fig. 9E
Female pore paired. Typically with an additional genital marking on XIX
. *D. minor**, Fig. 9D
15. Metandric (testes and funnels in XI, seminal vesicles in XII only) 16
Holandric (testes and funnels in X and XI, seminal vesicles 2 pairs, in IX and XII or XI and XII) 18
16. Unpaired transverse midventral pads intersegmental on the clitellum. First dorsal pore in 9/10–12/13
. *D. brunneus* (part.), Fig. 4B
Clitellar pads absent. First dorsal pore in 5/6–12/13 17
17. First dorsal pore in 9/10 or further posteriorly *D. brunneus* (part.), Fig. 3B
First dorsal pore in 5/6 or 6/7
. *D. longmani* (part.)
18. A pair of glandular patches present in the vicinity of 17/18 in front of the male pores. Other genital markings present or absent 19
No paired glandular patches anterior to the male pores. Male pores in *ab* of XVIII on small papillae within a common lip-like ridge. Midventral unpaired transverse pads extending to *ab* in 19/20, 20/21 and 21/22
. *D. gayndahensis**, Fig. 9G
19. A pair of genital markings in or just anterior to 17/18 and a similar, unilateral (left) marking in or just anterior to 18/19. First dorsal pore in 5/6. Spermathecal ducts not dilated
. *D. lamingtonensis**, Fig. 9H
Paired markings in or near 17/18; markings if present near 18/19 paired. First dorsal pore in 4/5 or 8/9–10/11. Spermathecal ducts not

dilated 20	areas but paired markings behind the pores indistinct or absent. 21
20. First dorsal pore in 4/5. Male pores preceded at 17/18 and succeeded at 18/19 by a pair of oval glandular areas	21. Body approximately 90–140 mm long and 4–5 mm wide . . . <i>D. bradburyi bradburyi</i> , Fig. 9A
. <i>D. lumbricoides kondalilla</i> , Fig. 5	Body approximately 185–265 mm long and 8–10 mm wide
First dorsal pore in or behind 8/9. Male pores preceded at 17/18 by a pair of glandular <i>D. bradburyi bunyaensis</i> , Fig. 3A

* Asterisked species have not been recorded, and are therefore not described, in this study. Published illustrations of their genital fields are, however, reproduced. The fields of *D. perrieri* (see Jamieson, 1963) and *D. queenslandica* (see Fletcher, 1889) on available specimens do not merit illustration.

Digaster anomala Jamieson, 1970

Figs. 1, 9B; Table 1

Digaster anomala Jamieson, 1970, pp. 40–3, figs. 1B, C; 2D, E.

MATERIAL EXAMINED: *Or* 3, 152°50'E. 27°15'S., Kobbie, rocky hillside covered by Lantana, E. Bradbury, 10 Jul 1970 and 10 Aug 1970, BM(NH) 1973.10.1-5, 6-15; rocky hillside by road, E. Bradbury, 8 Oct 1970, BM(NH) 1973.10.16-21. *Or* 5, 152°45'E. 27°21'S., 6 miles from Mt. Nebo on Mt. Glorious road, on side of eucalypt-covered hill by ferns and nettles, E. Bradbury, 12 Jun 1970, BM(NH) 1973.10.22-23; Mt. Glorious, rainforest, E. Bradbury, 12 Jun 1970, BM(NH) 1973.10.24; 8 Oct 1970 BM(NH) 1973.10.25; I. Naumann, 13 Sep 1971, BM(NH) 1973.10.26. *Or* 7, 152°47'E. 27°23'S., Mt. Nebo road Mt. Nebo, in loamy soil in gully in eucalypt area, E. Bradbury, 12 Jun 1970, 3, Jamieson collection; 1 mile from Mt. Nebo on road, E. Bradbury, 10 Aug 1970, BM(NH) 1973.10.27-28. *Or* 11, 152°54'E. 27°28'S., Gold Creek Road, Brookfield, in loose damp soil in leaf mould near creek, E. Bradbury, 24 Apr 1970, BM(NH) 1973.10.29-44, 45. *Or* 12, 152°54.5'E. 27°30'S., Willunga Street, Brookfield, on dirt road surface after heavy rain, B. Jamieson, 9 Dec 1970, BM(NH) 1973.10.46-55; Brookfield, E. R. Johnson, no date, BM(NH) 1973.10.56. *Or* 13, 152°51'E. 27°32'S., banks of Kholo Creek, Mt. Crosby Road, near Brisbane, B. Jamieson and/or E. Bradbury, 13 Mar 1970, 24 Apr 1970, 2 Feb 1970, 4 Mar 1970, 2 Jun 1966, BM(NH) 1973.10.57, 58-59, 60-65, 66-67, 68-70. *Or* 14, 152°53'E. 27°35'S., Moggill, near Brisbane, E. R. Johnson, no date, BM(NH) 1973.10.71-72. *Or* 16, 152°58'E. 27°28'S., Eastern part of Mt. Coot-tha, Brisbane, in sandy *Lantana* soil, L. Lyndon, 5 Sep 1971, BM(NH) 1973.10.73-74. *Or* 18, 152°58'E. 27°33'S., Fig Tree Pocket, Brisbane, cleared land near river bank, Mrs C. C. Wallace, 27 Oct 1969, QM G8316-24. *Or* 20, 152°49'E. 27°49'S., Mt. Flinders, H. Mayne, no date, BM(NH) 1973.10.75-77, 78.

The following account is abstracted from Jamieson (1970). New material is listed under 'Material Examined' and is discussed under 'Genital Field Variation', below.

l = 69–105 mm, w (midclitellar) = 3–4 mm, s = 103–146. Unpigmented excepting the brick red clitellum. Prostomium epilobous. First perforate dorsal pore 4/5. Setae in 8 longitudinal rows

throughout; commencing on segment I; *aa:ab:bc:cd:dd* in XII averaging 2.9:1.4:3.3:0.19:6; *dd:u* = 0.47–0.55. Clitellum annular, XIII–XVII. Male pores on XVII in *a*. Accessory genital markings midventral unpaired transverse pads in 19/20 and 20/21 and sometimes also in 18/19, 21/22, 23/24 and 24/25; sometimes with slight ventral epidermal elevations in some or all of intersegments 8/9–10/11. Female pores antero-medial of seta *a* in XIII. Spermathecal pores 2 pairs, well median of *a* lines, in 6/7 and 7/8.

Last hearts in XII. Gizzards in V and VI; calciferous glands absent; intestinal origin XVII. Nephridia meronephridia with exonephric tufts in III and, caudally, an exonephric stomate megameronephridium median to astomate micromeronephridia in each segment. Holandric; testes in IX and X; seminal vesicles racemose in VIII or VIII and XI. Ovaries in XII; ovisacs absent. Prostates bipartite, in XVII. Spermathecae 2 pairs, in VII and VIII; diverticulum large, ovoid-subspherical, internally multiloculate, almost sessile on the ectal end of the duct; length of a spermatheca = 3.0 mm; ratio of length: length duct = 3.5; ratio of length: length diverticulum = 4.7.

GENITAL FIELD VARIATION: Specimens from the type-localities (including the new material from *Or* 12, Willunga Street, and *Or* 13, Kholo Creek) differ from material from all other recorded localities in having the spermathecal pores median to setal lines *a*, not in or lateral of *a*. These two alternative conditions may, for convenience in discussion, be said to characterize a typical and an atypical population, respectively. Table 1 lists the distribution of transverse genital markings in 31 typical specimens, including the holotype and 11 paratypes as described by Jamieson (1970), and in 30 atypical specimens from all localities sampled. It is seen that in the typical population transverse genital markings are present in a few to most of intersegments 6/7–11/12, 15/16, 16/17–24/25. The distribution in the atypical population agrees with this except for absence in 11/12, 16/17 and 22/23–24/25. These absences in atypical specimens

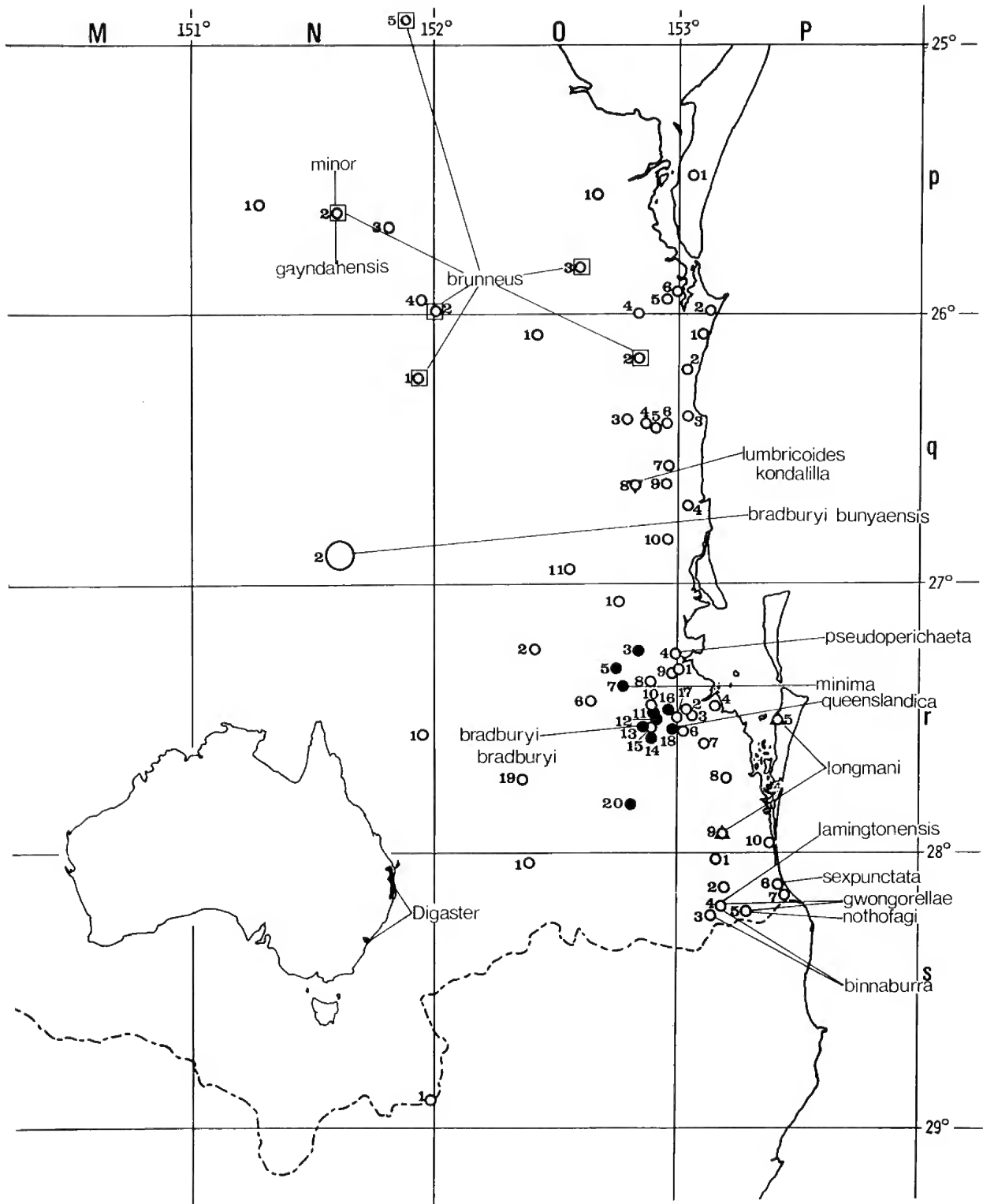


FIG. 1: Queensland records of *Digaster*. ● = *D. anomala*. Other species shown by labelled symbols. Unlabelled blank circles indicate sampled localities which did not yield *Digaster*. Localities are referred to in the text by co-ordinates and number (e.g. Or 3). The inset shows the Australian distribution of this endemic genus.

may not represent a significant difference as the frequency of markings at these sites is low in the typical specimens. In both populations the genital markings are most frequent in 19/20–20/21, being virtually constant in 19/20 and very frequent in 20/21. Good agreement between the two populations is seen in the frequency of 23–26% in the occurrence of a marking in 21/22 but a major difference is seen in the frequency in 17/18 and 18/19, for in the typical population the marking is more frequent in 17/18 (55%) than in 18/19 (19%) whereas in the atypical population the frequency is reversed, 13% in 17/18 against 83% in 18/19. A further difference is that the marking in 18/19 when present is always simple in the typical specimens while it is usually composed of a pair of more or less conjoined ellipses in the atypical specimens. Penial setae have not been observed in typical specimens whereas in the atypical population in 19 specimens examined for penial setae they were present in 13 specimens (BM(NH) 1973.10.1, 6, 7, 16, 17, 25, 27, 30, 45, 74. Jamieson collection, Mt. Nebo), though absent in 6 specimens (BM(NH) 1973.10.22, 23, 56, 71, 75, 78). All specimens show the *anomala* condition, apparent suppression of the first metamere so that segment I is setigerous and structures including the ovaries and prostates are displaced one segment anteriorly relative to their position in most Megascolecinae.

TABLE 1: DISTRIBUTION OF GENITAL MARKINGS IN THE *Digaster anomala* COMPLEX.

Intersegment occupied	Number of specimens			
	Typical population (of 31)	%	Atypical population (of 30)	%
6/7	17	54.8	11	36.6
7/8	17	54.8	11	36.6
8/9	10	32.3	1	3.3
9/10	10	32.3	1	3.3
10/11	6	19.4	1	3.3
11/12	3	9.7	0	0
12/13	0	0	0	0
13/14	0	0	1	3.3
14/15	0	0	1	3.3
15/16	1	3.2	2	6.7
16/17	6	19.4	7	23.3
17/18	17	54.8	4	13.3
18/19	6	19.4	25	83.3
19/20	31	100	29	96.7
20/21	28	90.3	24	80.0
21/22	8	25.8	7	23.3
22/23	1	3.2	0	0
23/24	3	9.7	0	0
24/25	2	6.5	0	0

TYPE-LOCALITY: Brisbane (Gap Creek Road and Willunga Street, Or 12; Kholo Creek, Or 13).

REMARKS: The anomalous segmentation, with male pores on XVII, together with the presence of a transverse genital marking in 19/20 and usually in 20/21, distinguish *D. anomala* from all other species of *Digaster*, though the same segmental anomaly occurs in the nominate subspecies of *D. lumbricoides*. The term '*D. anomala* complex' is here proposed for the combined typical and atypical populations as defined above. That the two populations are conspecific remains to be confirmed but they are clearly very closely related and if specifically distinct would have to be considered sibling species.

***Digaster binaburra* sp. nov.**

Figs. 1; 2; 10A, B; 11A; Table 2, 3

MATERIAL EXAMINED: Lamington National Park, South Queensland: *Ps* 4, 153°11'E. 28°12'S; 3 miles from Binna Burra, in rainforest with Casuarinas, B. Jamieson and E. Bradbury, 25 Mar 1970, Holotype(H) QM G7382, Paratypes (P) 1-6 (clitellate), P7-11 (with genital markings but acitellate), QM G7383-93; Binna Burra, in *Tristania-Casuarina* and mixed broadleaf forest, with tree ferns and palms, B. Jamieson and E. Bradbury, 25 Mar 1971, P14-17, 29, BM(NH) 1973.10.79-82, 83; Binna Burra, rainforest, B. Jamieson and E. Bradbury, 24 Mar 1971, P19, 20 (clitellate), 21-25 (with genital markings but acitellate), BM(NH) 1973.10.84-85, 86-90. *Ps* 3, 153°09'E. 28°14'S., in park near O'Reilly's Guest House: at Elbana Falls, B. Jamieson, 3 May 1970, P18, BM(NH) 1973.10.91; in rainforest, B. Jamieson and T. Walker, 18 Mar 1972, P12, 13, BM(NH) 1973.10.92-93; B. Jamieson, 19 Mar 1972, P26-28, BM(NH) 1973.10.94-96.

l = 62–65 mm. w (midclitellar) = 3 mm, s = 188,185 (H,P1). Form circular in cross section throughout; moderately slender; lacking strong secondary annulation. Pigmentless, excepting the brick-red clitellum, in alcohol. Prostomium propilobous; no canaliculi present dorsally or ventrally on it or the segments. First dorsal pore 4/5; pores inconspicuous. Setae in 8 regular longitudinal rows, commencing on II; setae *a* and *b* absent in XVIII. Nephropores not externally visible. Clitellum annular, XIV–XVII(H), $\frac{1}{2}$ XVIII(P1), with weak extension to $\frac{1}{2}$ XIII; intersegmental furrows and dorsal pores obscured excepting at 13/14 and 17/18; setae retained. Male pores minute in *ab* of XVIII, each at the centre of a small, low, circular porophore which at maximum development (P1) fills the segment longitudinally. Accessory genital markings small inconspicuous transversely oval pads paired postsetally in XVII, XIX (H,P1) and XX(H), in *ab*; the markings and

the male porophores contained within a ventral glandular area. Unpaired low boss-like accessory genital markings present anteriorly, a postsetal marking in each of VIII(H), IX and X(H,P1) and a presetal marking in IX and XI (H) or X (P1). Female pores small but distinctly visible antero-medial of *a* of XIV, about $\frac{1}{3} qa$ apart. Spermathecal pores 2 pairs, in 7/8 and 8/9, in *a* lines on small papillae (H), or in *a* and *ab* respectively (P1).

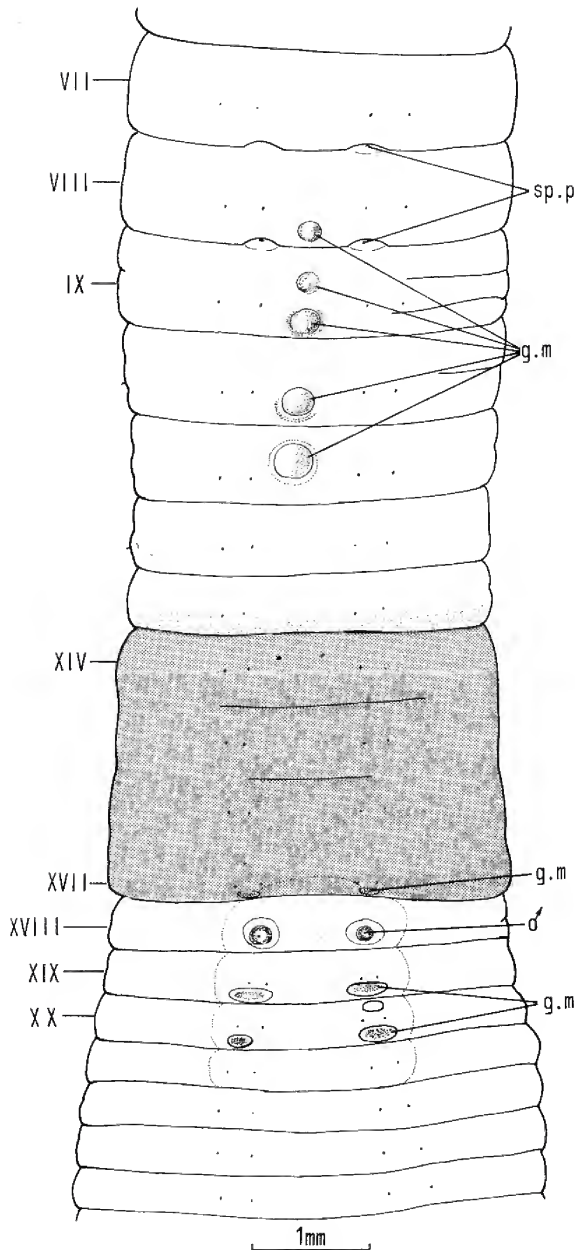


FIG. 2. *Digaster binnaburra* sp. nov. Genital field of holotype. For key to abbreviations, see Fig. 9.

Some preclitellar septa thickened; 10/11 the thickest, moderately strongly thickened. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XII, those in X–XII latero-oesophageal, each with a connective from the dorsal and the supra-oesophageal vessel. Supra-oesophageal vessel present but extent indeterminate as it is indistinctly delimited from the roof of the oesophagus. Subneural absent. Oesophagus in V thinwalled but fusiform and glossy and therefore gizzardlike in appearance, hidden by septal glands. Two strong slightly elongate spherical gizzards, each with anterior rim, in VI and VII, separated by a short region of unmodified oesophagus. Oesophagus almost suppressed, by backward extension of the gizzards, in VIII and IX; short in X–XII; swollen and vascularized in XIII–XVII, especially in XIV(P1), XV and XVI(H,P1) in each of which it has a reniform but not separate dilatation on each side which is slightly bilobed owing to a circumferential vessel which arises from the closely adherent dorsal vessel. Parallel sinuous rugae present on the internal wall of the oesophagus in XV and XVI but no true extramural calciferous glands present. Intestinal origin XIX; typhlosole, caeca and muscular thickening absent. Nephridia meronephridia: small tufts in II, III and IV sending a common composite duct on each side to the peristomium near the mouth; large tufts in V sending a composite (exonephric) duct to the region of segment II(H,P1) where (P1) it appears to continue to the wall of the pharynx. Thereafter with lateral bands of numerous astomate, exonephric micromeronephridia. In the anterior intestinal region with 8 such nephridia on each side; caudally with the medianmost nephridium enlarged as an exonephric megameronephrium with preseptal funnel. Holandric; gymnorchous (sperm funnels iridescent in X and XI); seminal vesicles racemose, in IX and XII. Prostates racemose, tongue-shaped, that on the left in the holotype consisting of adpressed dorsal and ventral halves; vas deferens joining the short, muscular medianly directed duct at its junction with the gland. Penial setae absent. Metagynous; ovaries, consisting of several strings of oocytes, and funnels in XIII; ovisacs not recognizable. Spermathecae 2 uniform pairs; ampulla elongate ovoid; duct cylindrical, bearing an iridescent rounded multiloculate diverticulum at its ectal extremity; length of right spermatheca of VIII (H) = 1.7 mm; ratio of length spermatheca: length duct = 2.4; ratio of length spermatheca: length diverticulum = 5.8.

REMARKS: The midventral anterior genital markings which, like the paired markings in the male

TABLE 2: GENITAL MARKINGS IN 18 SPECIMENS OF *Digaster binnaburra*.

		Specimen*	Total
Midventral markings			
VI	Presetal	—	0
	Postsetal	P13, 18	2
VII	Presetal	—	0
	Postsetal	P12-14, 17-20, 26, 28	9
VIII	Presetal	P3, 13-14, 17-20, 26	8
	Postsetal	H, P12-15, 17-20, 26, 28	12
IX	Presetal	H, P3, 12-15, 17-20, 26-28	13
	Postsetal	H, P1-5, 12-15, 18-20, 26-28	16
X	Presetal	P1-5, 12-15, 17-20, 26-28	16
	Postsetal	H, P1-5, 12-20, 26-28	18
XI	Presetal	H, P1-5, 12-15, 17-20, 26-28	17
	Postsetal	P2-5, 12-20, 26-28	16
XII	Presetal	P5, 19	2
	Postsetal	—	0
Paired markings in <i>ab</i>			
XVIII	Postsetal	H, P1-4, 12-13, 16-20, 26	13
XIX	Postsetal	H, P1-4, 12-20, 26-28	17
XX	Presetal	H (left), P17, 26	3
	Postsetal	H, P12-13, 16, 18, 27, 28	7
XXI	Presetal	P26	1
	Postsetal	P26	1

*H = Holotype, P = paratype.

field, are present in partly mature a clitellate and in clitellate specimens, permit ready diagnosis of *D. binnaburra*. The postsetal markings in X are constant in the type sample and are almost invariably accompanied by markings postsetally in IX, presetally in X, and pre- and post-setally in XI. Some fusion of presetal and postsetal markings is common.

Digaster bradburyi Jamieson, 1970

Digaster bradburyi Jamieson, 1970, pp. 35-40, figs. 1A, 2A-C, 3.

The following account is based on Jamieson (1970) and new material, comprising a new subspecies, from Bunya Mountains.

l = 88-265 mm, w (midclitellar) = 4-10 mm, s = 116-269. Body slender, circular in cross section throughout, pigmentless or pale brown, clitellum pigmented purplish brown. Prostomium epilobous (or sometimes prolobous?). First dorsal pore 8/9, 9/10 or 10/11. Setae in eight longitudinal rows throughout, commencing on II; minute and not, or only sporadically visible in the forebody, conspicuous on the clitellum owing to pale encircling fields; *aa:ab:bc:cd:dd* in XII (measured for nominate subspecies only) averaging 3.9:1.3:3.2:7:13.5;

dd:u = 0.41-0.45; *c* and *d* not especially dorsal posteriorly. Nephropores not externally recognizable. Clitellum annular, XIII, $\frac{1}{2}$ XIII, XIV-XVIII, $\frac{1}{3}$, $\frac{1}{2}$ XIX (= 5 $\frac{2}{3}$ -6 $\frac{1}{3}$ segments) but its pigmentation may reach XII-XX. Male pores on XVIII in *a* or *ab*. Accessory genital markings an approximately oval glandular marking occupying the postsetal portion of XVII and extending over intersegment 17/18 slightly median or slightly lateral of the male pores. One or two pairs of less distinct markings present behind the male pores, in XVIII and/or XIX, or absent. Female pores anteromedian to setae *a* of XIV. Spermathecal pores 2 pairs, in 7/8 and 8/9, in *a* lines.

Dorsal blood vessel continuous onto the pharynx. Last hearts in XII; those in X-XII latero-oesophageal, each receiving a connective from the dorsal vessel and from a poorly or well defined supra-oesophageal vessel; subneural vessel absent. Gizzards in VI and VII, not separated by unmodified oesophagus. Extramural calciferous glands absent. Intestinal origin $\frac{1}{2}$ (or anterior?) XVIII; typhlosole, caeca and muscular thickening absent. Nephridia meronephridia: tufts in II-VI; those in IV-VI, at least, enteronephric. Holandric; testes in X and XI; seminal vesicles racemose, in IX and XII. Ovaries in XIII; ovisacs absent. Prostates

bipartite, in XVIII; penial setae absent though follicles *a* and *b* may be present in the male porophores. Spermathecae 2 approximately equisized pairs, in VIII and IX, though the ampullae may be displaced into the preceding segment, each with an approximately ovoid ampulla and a well demarcated, dilated duct which is widest slightly ectal of its midlength and bears, at or ental of its widest part, 1 or sometimes 2 bulb-shaped, externally simple diverticula; length of a spermatheca 2.4–4.0 mm; ratio of length spermatheca: length duct = 1.9–2.8; ratio of length spermatheca: length diverticulum = 4.9–6.2.

TYPE-LOCALITY: Kholo Creek, near Brisbane (Or 13).

WIDER DISTRIBUTION: Bunya Mountains (Nq 2).

***Digaster bradburyi bradburyi* Jamieson, 1970**
Figs. 1; 9A

Digaster bradburyi Jamieson, 1970, pp. 35–40, figs. 1A, 2A–C, 3.

MATERIAL EXAMINED. *Or* 13, 152°51'E. 27°32'S., Kholo Creek at Ugly Gully, E. Bradbury, 10 May 1970, 4 specimens, BM(NH) 1973.10.112–115.

For detailed account see Jamieson (1970). Characters as for specific description, above, with *l* = 88–140 mm, *w* (midclitellar) = 4–5 mm. Body, excepting clitellum, pigmentless. Prostomium epilobous $\frac{1}{5}$ – $\frac{1}{3}$. Clitellum $\frac{1}{2}$ XIII, XIV–XVIII, $\frac{1}{3}$, $\frac{1}{2}$ XIX (= 4–6 segments). Male pores in *ab*. Accessory genital markings a pair of approximately

oval, sunken, translucent markings occupying the postsetal portion of XVII and intersegment 17/18 only; slightly median to the male pores.

Supra-oesophageal very well developed. Intestinal origin $\frac{1}{2}$ XVIII. Nephridial tufts in IV sending a composite duct on each side to the lateral extremity of the mouth; those in V and VI to pharynx behind brain. Ectal portion of spermathecal duct dilated and joined entally by diverticulum; length spermatheca = 2.4–3.6 mm; ratio length: length duct = 1.9–2.8; ratio length: length diverticulum = 4.9–7.8.

TYPE-LOCALITY: Kholo Creek, near Brisbane (Or 13).

REMARKS: Of the above characters, the only significant differences from the second subspecies appear to be the smaller size, perhaps effluence of the tufted nephridia of V and VI into the pharynx and not into the buccal cavity into which those in III–VI discharge in the Bunya specimens, and possibly the unpigmented body.

***Digaster bradburyi bunyaensis* subsp. nov.**
Figs. 1; 3A; 10C, D; 11B.

MATERIAL EXAMINED: *Nq* 2, 151°35'E. 26°57'S., Bunya Mountains National Park, in mixed rainforest at c.1000 metres, B. Jamieson and E. Bradbury, 20 Feb 1971, Holotype (H), QM G8333; Paratype (P) 1, BM(NH) 1973.10.97; P2, QM G8334; P3, Jamieson collection.

l = 185 (P1), 265 (H) mm, *w* (midclitellar) = 8.0 (P1), 9.6 (H) mm, *s* = 231 (P1), 237 (H). Secondary

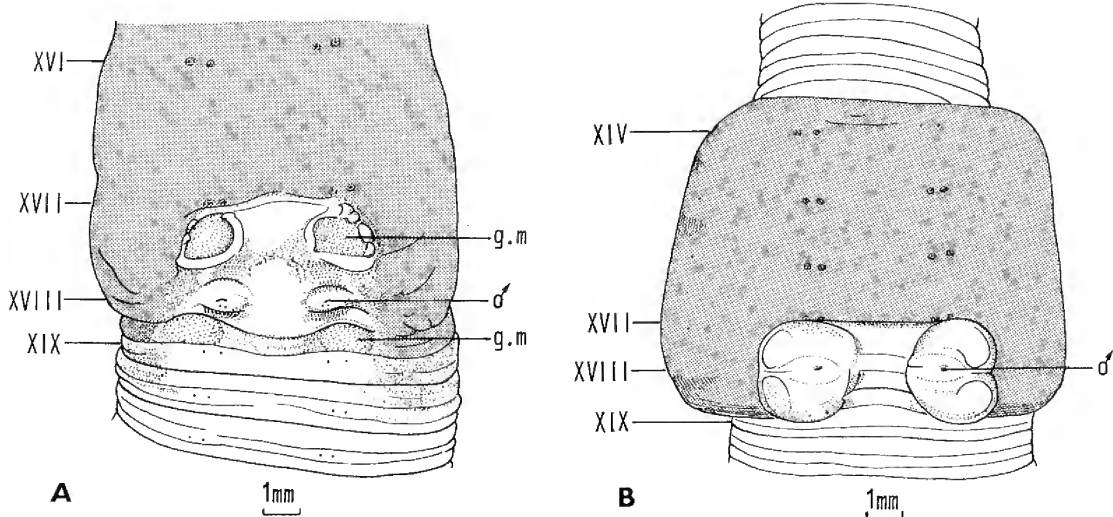


FIG. 3: A, *Digaster bradburyi bunyaensis* subsp. nov. Genital field of holotype. B, *D. brunneus* Spencer, 1900, specimen from Wolvi, BM(NH) 1973.10.105; the clitellum is shown widened owing to dorsal incision. For key to abbreviations, see Fig. 9.

TABLE 3: INTERSETAL DISTANCES IN SEGMENT XII IN *Digaster*

Species	Intersetal distance, mm								Standardized as % of periphery							
	aa	ab	bc	cd	dd	dc	cb	ba	aa	ab	bc	cd	dd	dc	cb	ba
<i>D. binnaburra</i>																
Holotype	0.9	0.3	1.3	0.7	3.4	0.7	1.2	0.3	10.1	2.8	14.2	8.5	39.7	8.5	13.4	2.8
Paratype 1	0.8	0.3	1.2	0.8	3.0	0.8	1.1	0.3	9.3	3.1	14.9	9.9	36.5	9.3	13.6	3.4
Mean									9.7	3.0	14.5	9.2	38.1	8.9	13.5	3.1
Interval/ab									3.3	1.0	4.9	3.1	12.8	3.0	4.5	1.1
<i>D. lumbricoides kondalilla</i>																
Holotype	1.1	0.3	1.1	0.9	4.2	1.1	1.1	0.4	10.9	3.1	11.1	9.0	40.8	10.2	11.1	3.9
Interval/ab									3.6	1.0	3.6	2.9	13.3	3.3	3.6	1.3
<i>D. minima</i>																
Holotype	0.5	0.2	1.3	0.2	1.0	0.2	1.3	0.2	10.8	3.4	26.9	4.0	20.6	4.0	26.9	3.4
Interval/ab									3.2	1.0	7.9	1.2	6.0	1.2	7.9	1.0
<i>D. nothofagi</i>																
Holotype	1.3	0.3	1.3	0.7	2.1	0.7	1.3	0.2	16.3	3.4	16.5	9.2	26.4	8.8	16.3	3.1
Interval/ab									4.8	1.0	4.8	2.7	7.7	2.6	4.8	0.9
<i>D. pseudoperichaeta</i>																
Holotype	0.8	0.3	1.0	0.3	2.3	0.3	1.3	0.3	12.9	4.0	15.3	4.8	34.5	4.4	19.3	4.8
Paratype 1	1.1	0.3	1.4	0.4	1.4	0.3	1.5	0.3	15.6	4.7	21.1	6.3	21.1	4.7	21.9	4.7
Mean									14.2	4.4	18.2	5.5	27.8	4.6	20.6	4.8
Interval/ab									3.3	1.0	4.2	1.3	6.4	1.1	4.7	1.1
<i>D. sexpunctata</i>																
Holotype	1.2	0.4	1.3	0.7	6.8	0.8	1.1	0.3	9.5	3.0	10.0	5.8	54.1	6.0	9.0	2.5
Paratype	1.2	0.4	1.0	0.8	7.4	0.8	1.1	0.4	9.2	3.1	7.7	5.8	57.0	5.8	8.2	3.1
Mean									9.4	3.1	8.9	5.8	55.6	5.9	8.6	2.8
Interval/ab									3.1	1.0	2.9	1.9	18.1	1.9	2.8	0.9

annulation strongly developed but not obscuring the primary segmentation. Pigmented pale brown with the clitellum deep purplish brown. Prostomium epilobous $\frac{1}{2}$, closed (H); or appearing prolobous with lateral borders continued to $1/2$ but not more conspicuous than the numerous longitudinal peristomial grooves (P1). First dorsal pore $9/10$. Postclitellar setae visible with some difficulty; setae *a* and *b* in XVIII represented by two follicles behind each male pore (only a single, left, follicle in P1). Clitellum annular, XIII- $\frac{1}{3}$ XIX but continued as rosy pigmentation throughout XII and XX; interrupted in *bb* behind the setal arc of XVII; only intersegmental furrow 13/14 complete; dorsal pores occluded; setae visible. Male pores transverse slits equatorially in XVIII in *a*, on elliptical porophores. Accessory genital markings a pair of oval unelevated glandular patches posteriorly in XVII and apparently extending slightly on to XVIII (intersegmental furrow 17/18 obscured) in *ab* (all specimens), each patch (H) with a whitish laterally papillated border; a further pair of

patches presetally in XIX centred in *b* but indistinctly delimited; in P2 a pair of glandular depressions situated posteriorly in XVIII and similarly placed in XIX; each slightly extending onto the succeeding segment. Midventral and other accessory genital markings absent. Female pores approximately $\frac{1}{2}$ *aa* apart. Spermathecal pores 2 pairs of conspicuous slits in *a* on small papillae.

Septa 8/9-11/12 very thick (6/7, 7/8 and 12/13 moderately strongly thickened). Latero-oesophageal hearts, in X-XII, each arising from the dorsal vessel and receiving a slender connective from an imperfectly differentiated supra-oesophageal vessel. Pharynx ending in IV; oesophagus narrow in V; gizzards firm but only moderately large, tubular. Oesophagus almost suppressed in VIII by backward extension of the gizzards. Nephridia (H): tufts in II-VI, increasing in size posteriorly to large in VI; those in II apparently (but not certainly) exonephric; those in II-VI enteronephric, sending composite ducts to the anterior region of the buccal cavity. Dense

lateral bands of nephridia on the posterior septum of VII are exonephric by numerous ducts which enter the body wall anteriorly in the segment; nephridia in succeeding segments less numerous, exonephric micromeronephridia on the body wall posteriorly in their segments; nephridia in anterior intestinal segments equatorial on the body wall, approximately 10 per side in each segment; caudally with a slightly enlarged exonephric megameronephridium, with preseptal funnel, median to astomate, exonephric micromeronephridia on each side. Prostate ducts bound by a muscular and fibrous covering, on each side, to the ventral body wall. Spermathecae each with an ovoid though asymmetrical ampulla and a well demarcated broadly fusiform duct which bears dorsolaterally, at its widest point, 1 or (H, right VIII) 2 bulb-shaped diverticula which are externally simple but internally have complex lumina; length of right spermatheca of VIII (H) = 4.0 mm; ratio length: length duct = 2.0; ratio length: length diverticulum = 6.2.

REMARKS: The large size of the specimens of this taxon and general morphological similarity (including location of the first dorsal pore in the vicinity of 9/10) to those specimens of *D. brunneus* which lack transverse genital markings at first suggested their close relationship, if not conspecificity with *D. brunneus*. However, it differs from *D. brunneus* but conforms with *D. bradburyi*, in dilatation of the spermathecal ducts, holandry, in the bipartite form of the prostates and in the form of the genital markings in 17/18. Though the body size is much greater than that of *D. bradburyi*, the dimensions and proportions of the spermathecae are strikingly similar, though also similar to those of *D. brunneus*. Dilatation of the spermathecal ducts and bipartite prostates are also seen in the closely similar *D. lumbricoides kondalilla* but the latter differs in location of the first dorsal pore in 4/5. It is possible that the Kondalilla specimens are closer to *D. bradburyi* than to *lumbricoides* but the uncertainty in this respect is a reflection of the especially close relationship, within the genus, of *lumbricoides* and *bradburyi* and, less closely, *brunneus* and *lamingtonensis*.

The validity of placing *bunyaensis* in *D. bradburyi* as a subspecies in the sense of a geographical race is questionable. The Bunya Mountains are geographically somewhat isolated but whether the Bunya and typical populations could interbreed if in contact is doubtful owing to their great difference in body size. If reproductively and geographically isolated they would have to be considered

separate, though very similar (sibling?) species. If, on the other hand, gene exchange is possible through as yet unknown intervening populations, with specimens intermediate in size, the grounds for separation into distinct subspecies or species might be considered lost. Taxonomic recognition of the large mountain forms seems desirable, however, on present evidence and similarities with *D. bradburyi* warrant inclusion in this species as a distinct subspecies.

***Digaster brunneus* Spencer, 1900**

Figs. 1; 3B; 4A, B; 10E-G; 11C.

Digaster brunneus Spencer, 1900, p. 66, pl. 12, figs. 103-5.

MATERIAL EXAMINED: *No* 5, 151°53'E. 24°55'S., 10 miles from Gin Gin, in very damp clay soil, Mrs C. C. Wallace, 7 Dec 1969, QM G8325-6. *Np* 2, 151°35'E. 27°37'S., Burnett River, Gayndah: in loam covered by weeds on river bank, E. Bradbury, 11 Mar 1970, BM(NH) 1973.10.98-99; orange orchard on river bank, E. Bradbury, 11 Mar 1970, BM(NH) 1973.10.100. *Nq* 1, 151°57'E. 26°94'S., Murgon, in shallow soil, collector and date not known, BM(NH) 1973.10.101. *Op* 2, 152°01'E. 25°59'S., 5 miles N. of Tansey, on road covered with water, E. Bradbury, 7 Feb 1971, BM(NH) 1973.10.102-104. *Op* 3, 152°36'E. 25°50'S., 1 mile south of Bauple, in dry clay soil in grassy area near creek, Mrs C. C. Wallace, 6 Dec 1969, 2 Jamieson collection, QM G8327-31. *Oq* 2, 152°50'E. 26°10'S., Wolvi, C. A. Scarlett, no date, BM(NH) 1973.10.105.

The following account is based on two Gayndah specimens, BM(NH) 1973.10.98 and 100, with some additional data from other specimens where indicated. Spencer's brief account is in agreement except where noted.

l = 210+430 mm (150 mm, Spencer); w (midclitellar) = 10-11 mm (6 mm, Spencer); s = 161+397 (Specimen 98 is a posterior amputee). Form slender, circular in cross section throughout; secondary annulation strongly developed, obscuring the primary segmentation. Pigmentless in alcohol excepting the pale chocolate-brown clitellum. Prostomium prolobous; peristomium with numerous longitudinal grooves. First dorsal pore 10/11 (with a rudiment at 9/10, specimen 100) or 11/12 (specimen 98); location not given by Spencer. Setae minute, only sporadically visible; *a* and *b* absent in XVIII. Nephropores not recognizable. Clitellum annular, $\frac{1}{2}$ XIII(?), XIII-XIX; interrupted ventrally between and behind the male pores; intersegmental furrows weakened and laterally interrupted and other annulations well marked; dorsal pores faint; setae not visible. Male pores transverse slits equatorially in *ab* of XVIII, on elliptical porophores. Accessory genital markings

in 7 specimens (2 from No 5, 2 from Np 2 and 3 from Op 3): unpaired, midventral transverse pads in intersegments 12/13 (4 Gayndah specimens); 13/14 (7 specimens); 14/15, 15/16 and 16/17, with a similar pad posteriorly in XVII and a callus-like pad posterior to and confluent with each male porophore and crossed near its posterior border by intersegmental furrow 18/19 (6 specimens). Transverse unpaired equatorial pads illustrated in XVII, XIX and (partial) in XX by Spencer. Female pores only slightly anterior of the equator of XIV, almost contiguous medianly (specimen 98) or well separated though median to *a* (specimen 100). Spermathecal pores 2 pairs of stellate apertures, each on a small rounded tubercle, in 7/8 and 8/9, in *ab* approximately; seen to lie nearer *a* than *b* in specimen 100 where ventral setal couples are here visible; (apparently in *a* lines, Spencer).

Septa 4/5–11/12 very thick (12/13 moderately strongly thickened). Dorsal blood vessel single,

continuous onto the pharynx. Last hearts in XIII (or XII according to Spencer and in a specimen from Op 3 examined); hearts in X posteriorly latero-oesophageal, each arising from the dorsal vessel and receiving a connective from a thin supraoesophageal vessel. Commissurals in V–IX valvular, like the latero-oesophageal hearts, but differing from the latter in being dorsoventral only and in giving off a lateral branch shortly before joining the ventral vessel. Subneural vessel absent. Racemose, fatbody-like masses present in XIII and XIV lateral of the dorsal vessel in XIII and XIV (specimen 98 only). Pharynx ending in IV; oesophagus in V dilated but thin-walled; gizzards, in VI and VII, large, globose, thin-walled anteriorly, the musculature thick only in the posterior half; closely abutting; not separated by unmodified oesophagus. Oesophagus wide, moniliform and very thin-walled in VIII–XVI; narrow in XVII; lacking calciferous glands but more vascularized in

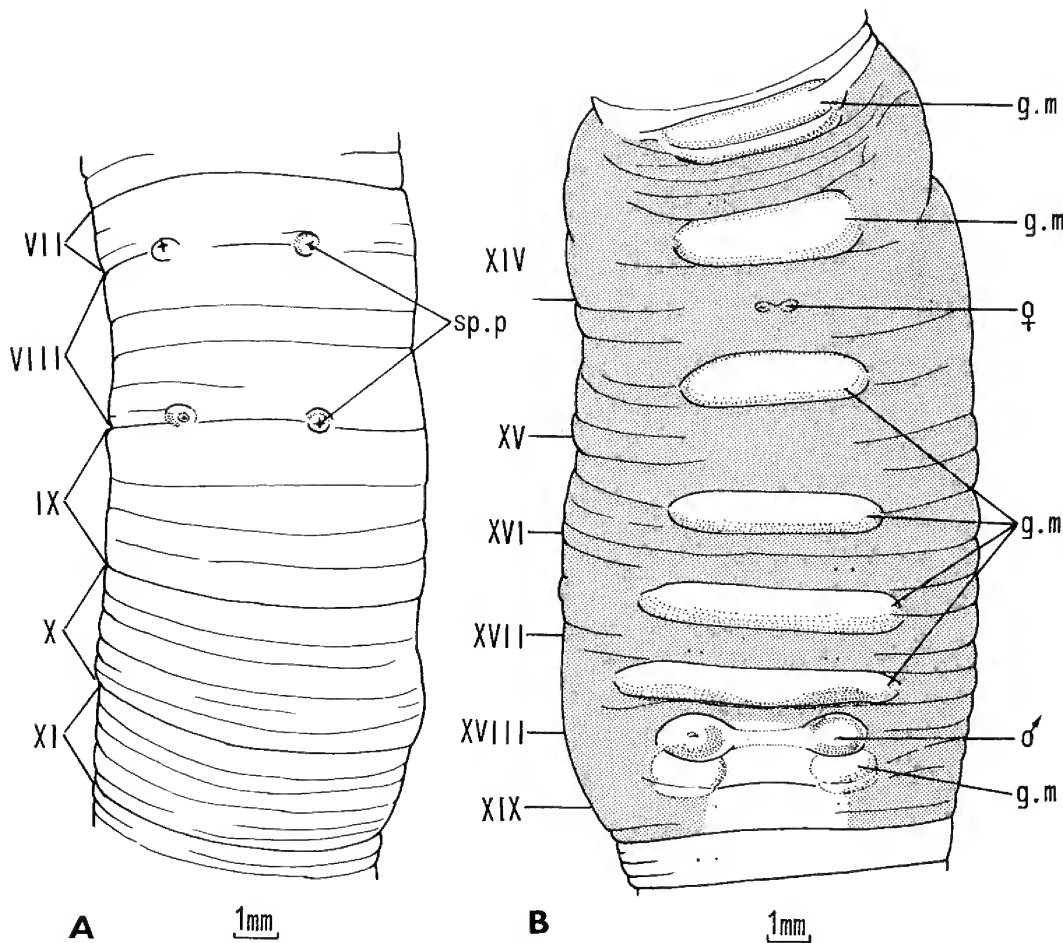


FIG. 4. *Digaster brunneus* Spencer, 1900, Gayndah specimen, BM(NH) 1973.10.98. A, Spermathecal field; B, Male genital field. For key to abbreviations, see Fig. 9.

XII–XVI than elsewhere. Intestine originating in XVIII but not greatly widening until XIX; typhlosole, caeca and muscular thickening absent. Nephridia meronephridia: tufts in II, III and IV, increasing in size posteriorly to very large in IV, adherent dorsally and laterally to the pharynx (specimens 98 and 100). The tufts in IV divisible into a dorsolateral mass discharging by several ducts directly into the pharynx and by composite ducts directly into the pharynx in III and a dorsal mass sending a composite duct forward to the wall of the buccal cavity in II (specimen 100). Thick bands of nephridia on the posterior septa of V and VI show no close association with the gut and from their peripheral position, near the body wall, may be exonephric; parietes lacking nephridia in V and VI except where a few nephridia impinge on the body wall near the septum in VI. Scattered parietal and septal exonephric micromeronephridia in VII. Nephridia in VIII–XI (specimen 98) or –XII (specimen 100) on the posterior septum and adjacent parietes with ventral aggregations; thereafter with numerous minute exonephric micromeronephridia scattered on the parietes. Caudally with numerous moderately large astomate micromeronephridia on each side all of which, in a segment, discharge into a common transverse duct which is traceable to the midline below the intestine, though enteronephry, if present, is not demonstrable; the medianmost nephridium enlarged as a stomate megameronephridium with preseptal funnel (specimen 100). Metandric (sperm funnels iridescent in XI); seminal vesicles racemose, in XII only. Metagynous, bushy ovaries, and funnels, in XIII; ovisacs not observable. Prostates racemose, not bipartite, restricted to XVIII the medianly directed duct weakly developed so that, in specimen 100 especially, the gland is almost sessile on the body wall. Penial setae absent. Spermathecae 2 uniform pairs, each with an elongate ovoid ampulla reflexed on or in line with the externally poorly differentiated slightly shorter, thicker walled duct; the duct bearing a rounded multiloculate diverticulum dorsolaterally near its ectal extremity (A very small double diverticulum reported by Spencer). Length of right spermatheca of IX = 4.0–6.2 mm; ratio length spermatheca: length duct = 2.5–2.8; ratio length spermatheca: length diverticulum = 5.3–5.9.

TYPE-LOCALITY: Gayndah (Np 2).

REMARKS: An extensive search of the Gayndah area, the type-locality, has yielded only one species which could be identified with *D. brunneus*, though, owing to the brevity of the type-description and loss of the types (Jenz and Smith, 1969), the

identification cannot be entirely certain. Spencer did not mention accessory genital markings but transverse pads are illustrated on the clitellum, on which they occur in the new material from Gayndah. The latter material agrees closely with Spencer's account in other respects including metandry which is known elsewhere in the genus only in the allopatric *D. longmani*. The distribution of the genital marking noted by Spencer, segmental in XVII, XIX and XX, differs from that in the new material in which markings are not present in XIX and XX and in which those anterior to the one in XVII are intersegmental but the fact that Spencer did not mention the markings in the text suggests that they were not closely observed and might have been overlooked anteriorly to XVII. Transverse genital markings are absent from material from Murgon (Nq 1), Tansey (Op2) and Wolvi (Oq 2) which is here identified with *D. brunneus* on general anatomy and this variation suggests that absence of markings anteriorly to XVII in the types, if real, would not necessarily exclude the new Gayndah material from the species. The specimens lacking transverse markings, although listed in 'Material Examined' above, have been excluded from the specific description pending further elucidation of their status. All are metandric with dorsal pores in 9/10–10/11, as in the new Gayndah material; hearts are in XII (Wolvi) or XIII (Tansey); and the spermathecal ducts are narrow, not dilated. Lengths vary from 152–250 mm, and widths from 6–9 mm.

The specimens from Bauple (with transverse pads) have a suggestion of a genital marking on each side of the transverse pad in XVII and the male porophore has a callus-like extension into XVII and XIX. This extension supports identity with the Wolvi material which is illustrated in Fig. 3B.

Identity of the new material listed above with the similarly metandric *D. longmani* is ruled out on the grounds that in *D. longmani* the transverse genital markings are preclitellar and the first dorsal pore is more anterior.

***Digaster gwongorellae* Jamieson, 1972**

Figs. 1; 9E

Digaster gwongorellae Jamieson, 1972, pp. 261–4, figs. 1A–C.

MATERIAL EXAMINED: *Ps* 4, 153°11'E, 28°21'S., Binna Burra, Lamington National Park, in rainforest, B. Jamieson and E. Bradbury, 24 Mar 1971. QM G8332, BM(NH) 1973.10.106.

1 > 110 and 75 mm (specimens 1 and 2, posterior amputees) w (midclitellar) = 5 mm, s = ?

Prostomium tanylobous. First dorsal pore 5/6 faint but perforate; larger but inconspicuous from 6/7. Clitellum annular, $\frac{1}{2}$ XIII– $\frac{1}{3}$ XIX but circumscribed by deep furrows at 13/14 and 18/19 (extent XIV–XVIII in syntypes). Setae in 8 regular longitudinal rows. Setae *a* and *b* absent in XVIII. Male genital field an almost circular though transversely somewhat widened flat topped conspicuous pad in XVIII extending almost to the setal arcs of XVII and XIX and laterally almost to *c* lines; no median porelike marking present on this pad. In both specimens two minute white points are included within the margin of the pad at *a* and *b* on each side. That in *b* is the larger and has been taken (Jamieson, 1972) to be the male pore but the two markings are possibly the follicles of the absent setae *a* and *b* for, as noted in the type-description, the prostate ducts enter the body wall internally in *a* lines. The muscular ducts are straight and converge medianly so that it is possible that the male pores are shortly median of *a* lines (specimen 1). In specimen 2 the genital pad is narrower longitudinally and is depressed medianly so that an impression of a pair of medianly conjoined papillae is produced. Female pore moderately conspicuous, midventral and presetal in XIV. Spermathecal pores 2 inconspicuous pairs, in 7/8 and 8/9 very slightly lateral of *a* lines (in *a* lines in the types).

Last hearts in XII. Gizzards in VI and VII. Calciferous glands absent. Intestine commencing in XVIII but pushing septum 17/18 forwards so as to appear to commence in XVII. Meronephric. Holandric (sperm funnels iridescent in X and XI); gymnorchous; seminal vesicles racemose, in IX and XII. Prostates restricted to but expanding XVIII, rounded tongue shaped with a deep lateral incision but (unlike the type-specimens) not bipartite. Penial setae absent. Metagynous; ovisacs absent. Spermathecae 2 pairs, in VIII and IX; each with elongate-ovoid ampulla, a slightly shorter well demarcated duct and ectally a multiloculate diverticulum as in the types, (specimen 1).

TYPE-LOCALITY: Gwongorella National Park (Ps 5).

REMARKS: The above brief description confirms identity of this material with the type-series, agreeing with the type-description in almost all respects. The greater extent of the clitellum is attributable to the very mature condition of the new material and inclusion of the points (male pores?) at *b* in XVIII on the protuberant genital marking and not, as in the holotype, on each side of it with an encircling rim, is ascribable to greater elevation of the marking. The very slightly more lateral position of the spermathecal pores and the

form of the prostate glands in the new material are very minor differences.

Digaster longmani Boardman, 1932

Digaster longmani Boardman, 1932, pp. 125–7, fig. 1.
Jamieson, 1963, pp. 101–5, fig. 5.

The following account is abstracted from the type description and that of Jamieson, 1963. Some features of a specimen from Stradbroke Island, Queensland, which is tentatively identified with *D. longmani*, are appended to the account.

l = 520–1025 mm, w (preclitellar) = 20–25 mm, s = 309–382. Body (pigmented?) brown; clitellum dark brown. Prostomium zygalobous, prolobous or proepilobous. First dorsal pore 5/6, or sometimes 6/7. Setae 8 per segment, difficult to discern or only sporadically visible; typically, in the forebody, $aa:ab:bc:cd = 4:1:3:1.7$; $dd:u > 0.5$; means in the Kyogle specimens, in IX, $cd:ab = 1.6$ (1.3–1.8); $bc:aa = 0.4$ (0.4–0.5); $dd:u = 0.7$ (0.7–0.8). Clitellum annular, $\frac{1}{2}$ XIII, $\frac{1}{3}$ XIII, XIV to XVIII, $\frac{1}{4}$ XIX– $\frac{1}{2}$ XIX (= 5–6 segments). Male pores equatorial or just presetal in XVIII, in *ab*, from *a* to *b*. Accessory genital markings if present, a postsetal, unpaired midventral transverse strip extending laterally to $\frac{1}{2} bc$ in each of segments VIII–XII. Female pores presetal in XIV, transversely or diagonally placed. Spermathecal pores 2 pairs, at anterior borders of VIII and IX or 2 or 3 pairs in 6/7 to 8/9, in or just dorsal of *a*.

Last hearts in XII or, typically, XIII. Gizzards in VI and VII; calciferous glands absent (an unpaired, dorsal oesophageal structure reported as a gland in the holotype was probably a fixation artefact). Intestinal origin XVIII. Nephridia meronephridia; septal bands present but no definite tufts observed; caudally with a median (stomate?) megameronephridium on each side. Metandric; gymnorchous; seminal vesicles in XII only. Prostates racemose, tongue-shaped or discoidal, incised but unipartite in XVIII. penial setae absent. Metagynous; ovisacs unknown. Spermatheca 2 or 3 pairs, tubular to tapering sacciform with the ectal portion forming a poorly demarcated duct; diverticulum typically single, elongate-ovoid, obliquely placed near the pore, extending almost across the flattened side of the duct, containing several sperm masses; duct also bearing 1 or 2 conspicuous obliquely placed sacculations at midlength; if 2, on opposite sides and convergent ectally; the pair of sacculations the only diverticula in the Kyogle specimens.

TYPE-LOCALITY: Tamborine Mountain, South Queensland (Pr. 9).

WIDER DISTRIBUTION: near Oaky Creek, Richmond Range State Forest, and near Kyogle, New South Wales.

STRADBROKE ISLAND SPECIMEN

MATERIAL EXAMINED: *Pr* 5, 153°25'E. 27°30'S., Stradbroke Island, in deep sand, V. Pattemore, 13 Aug 1971, BM(NH) 1973.10.107.

Postclitellar amputee with *w* (midclitellar) = 8 mm. Pigmentless in alcohol excepting light brown clitellum. Prostomium probolous but peristomium much grooved. First dorsal pore 5/6. Setae 8 per segment; dorsal couples varying significantly in width and ventral couples slightly irregular, in the forebody; both couples very irregular in width behind the clitellum. Clitellum annular, dorsally XIII–XX. Male pores transverse slits in *a*, porophores not developed. Accessory genital markings very faint transverse pads filling the posterior annulus, and including the setal arc, in IX, X, XI and XII. Female pores not certainly recognisable, possibly unpaired. Spermathecal pores 2 pairs, in 7/8 and 8/9, in *a*.

Last hearts in XII. Gizzards in VI and VII; calciferous glands absent. Intestinal origin(?) Meronephric. *Holandric*; gymnorchous; seminal vesicles in XI and XII. Prostates racemose, tongue-shaped, unipartite. penial setae absent. Metagynous. Spermathecae 2 pairs, duct tapering; ?diverticulum single, small and caplike on the ectal end of the duct.

REMARKS: Typical specimens of *D. longmani* are distinguished from the only other metandric species in the genus *D. brunneus*, by location of the first dorsal pore in 5/6 or 6/7 (not 9/10–11/12), location of transverse accessory genital markings segmentally in the region of VIII–XII (not intersegmentally in 12/13–16/17) and in possessing an elongate diverticulum sessile over its length or a pair on each side of the duct (not rounded and multiloculate or small and double). Conspecificity of the material from the environs of Kyogle, in New South Wales, with *D. longmani* is not entirely certain as it lacks accessory genital markings and has spermathecal diverticula restricted to the pair of convergent sacculations reported, in addition to a diverticulum, by Boardman but erection of a separate species for its reception is not warranted on present evidence. The identity of the single Stradbroke Island specimen with *D. longmani* is based primarily on the large body size and presence of segmental preclitellar bands which are so faint that positive recognition of them as accessory genital markings must await discovery of further material. The holandric gonads are otherwise un-

known in *D. longmani* though known in *D. bradburyi bunyaensis*, a subspecies of large worms of closely similar morphology. The Stradbroke Island specimen can be excluded from *D. bradburyi*, however, because the latter has its first dorsal pore in 9/10, bipartite prostate glands and dilated spermathecal ducts. The *brunneus-longmani* complex and its relationships with *D. lumbricoides kondalilla* requires further elucidation.

Digaster lumbricoides Perrier, 1872

Digaster lumbricoides Perrier, 1872, pp. 94–96, pl. 1, fig. 24, pl. 4, figs. 64, 65. Fletcher, 1887, pp. 559–60; 1889, pp. 1531–2. Beddard, 1895, p. 485. Michaelsen, 1900, p. 197. Jamieson, 1971b, pp. 1303–6, figs. 1, 1–K.

The following account is based on the redescription of the type-specimens by Jamieson, 1971b and on new material, comprising a new subspecies, from Kondalilla.

l = 82 mm, *w* (midclitellar) = 3.3–3.5 mm, *s* = 158. Form moderately stout, circular in cross section throughout; pigmentless buff in alcohol. Prostomium probolous. First dorsal pore 4/5 but may not be perforate until 5/6 or 6/7. Setae small, in 8 regular longitudinal rows, commencing in II; setae *a* and *b* present or absent on the segment bearing the male pores; *aa:ab:bc:cd:dd* in XII averaging 2.3–3.6:1.3–6.4:2.1–8.3:3.12–6–13.3; *dd:u* = 0.40–0.48; *c* and *d* not especially dorsal posteriorly. Clitellum annular, typically XII– $\frac{1}{2}$ XVII. Male pores on XVII or XVIII in *ab* or *b* in an approximately rectangular tumid field which extends to the equators of the adjacent anterior and posterior segment, an oval glandular genital marking located near each corner of the field, posteriorly in XVI and anteriorly in XVIII (where male pores are in XVII) or at intersegments 17/18 and 18/19 (where male pores are in XVIII). Female pores shortly anteromedian of setae *a* of XIII or XIV. Spermathecal pores 2 pairs, in 6/7 and 7/8, or 7/8 and 8/9, in *a* or *ab*.

Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XI or XII; the last 3 pairs latero-oesophageal, each receiving a connective from the dorsal vessel and from the roof of the oesophagus, no discrete supra-oesophageal vessel being recognisable. Subneural vessel absent. Gizzards in V and VI or VI and VII, intervening unmodified oesophagus short or inappreciable; calciferous glands absent though the oesophagus is dilated and vascularized in some of the segments XIII–XVI; intestinal origin $\frac{1}{2}$ XVI or XVIII; typhlosole, muscular thickening and caeca absent. Nephridia meronephridia, enteronephry not obser-

ved; caudally with a stomate megameronephridium on each side median to astomate micromeronephridia. Holandric; gymnorchous; seminal vesicles racemose in X and XI or XI and XII, accompanied below the oesophagus in XI or in XI and XII by an unpaired seminal vesicle. Prostates racemose unipartite or bipartite. Penial setae absent. Ovaries in XIII (or XII[?]); ovisacs unknown. Spermathecae 2 uniform pairs; duct cylindrical with small subspherical ectal diverticulum or duct pyriform, ectally widening, with a small rounded more or less bifid diverticulum on the ectal dilatation; length of a spermatheca 2.2–3.9 mm, ratio of length spermatheca: length duct = 1.6–2.0; ratio length spermatheca: length diverticulum = 5.3–7.9.

TYPE-LOCALITY: Port Macquarie, New South Wales.

WIDER DISTRIBUTION: Kondalilla National Park, Queensland (Oq 8).

***Digaster lumbricoides lumbricoides* Perrier, 1872**

Figs. 1; 9F

For detailed account see Jamieson, 1971b. Characters as for specific description, above, with: l = 82 mm, w (midclitellar) = 3.3 mm, s = 158. In XII, *aa:ab:bc:cd:dd* averaging 2.3:1.4:2.1:8:12.6; *dd:u* = 0.40–0.48. Male pores in XVII, in *ab*; paired genital markings posteriorly in XVI and anteriorly in XVIII, in and lateral of *b* lines. Spermathecal pores in 6/7 and 7/8 in *ab*.

Septa 6/7 or 7/8 the thickest, strongly thickened. Last hearts in XI. Gizzards in V and VI; intestinal origin $\frac{1}{2}$ XVI. Seminal vesicles in X and XI, accompanied below the oesophagus in XI by an unpaired seminal vesicle. Prostate glands unipartite. Spermathecae each with a subspherical ampulla and a wide cylindrical duct; diverticulum ectal on the duct; length of a spermatheca 2.2 mm, ratio of length:length duct = 1.6; ratio of length:length diverticulum = 5.3.

TYPE-LOCALITY: Port Macquarie, New South Wales.

***Digaster lumbricoides kondalilla* subsp. nov.**

Figs. 1; 5A, B; 10H, I; 11D

MATERIAL EXAMINED: Oq 8, 150°50'E. 26°40'S., Kondalilla National Park, in black soil under boulder on creek bank, in rainforest, T. Walker, 2 Jun 1972, Holotype, QM G7396.

l = 60+ mm (posterior amputee at 71st. segment), w (XV) = 3.5 mm. Peristomium with several dorsal longitudinal grooves though not

grooved ventrally. First dorsal pore 4/5. Setae small but distinctly visible; setae *a* and *b* persisting in XVIII in the vicinity of the male pores. Clitellum not developed. Male pores transverse slits in XVIII shortly anterior to setae *b*, each on a low oval tumescence which bears setae *a* and *b*; the male porophores preceded at 17/18 and succeeded at 18/19 by a pair of oval glandular areas, in *ab*, each of the posterior areas accompanied by and partly continuous with a similar glandular marking lateral of *b* lines in the same intersegment. The male porophores and these genital markings lying in an approximately tumid quadrangular field which extends to the setal arcs of segments XVII and XIX and laterally almost to *c* lines. Female pores shortly anteromedian of setae *a* of XIV on a common transverse presetal protrusion. Spermathecal pores 2 pairs of partially concealed transverse slits at the anterior limit of small knoblike swellings, in 7/8 and 8/9, centred in *a* lines.

Septa 8/9–11/12, the thickest, strongly thickened. Last hearts in XII; those in XII (and X–XI?) latero-oesophageal. Pharynx ending in IV; in V the oesophagus is dilated and gizzard-like in appearance though not thickwalled and little more than half the diameter of the gizzards. Gizzards large and firm, in VI and VII; globose though with an anterior rim which is weakly developed in the posterior but is well developed in the anterior gizzard; the gizzards filling their segments; and not separated by an appreciable length of unmodified oesophagus though the oesophagus is narrowly constricted between them. Oesophagus longitudinally constricted and lacking special modification in IX–XIII; in each of XIV, XV and XVI dilated and vascularized, with a pair of circumferential vessels which join the dorsal vessel, and internally with many high clavate villi; slender in XVII and XVIII. Intestinal origin XIX. Nephridia in IV–VI aggregated into loose tufts; no enteronephry demonstrated but certain elucidation of the excretory system not feasible as preservation unsatisfactory; in the anterior intestinal region with seven astomate exonephric parietal micromeronephridia on each side from setal line *a* to above *d* and an aggregation of similar but smaller nephridia median to *a*; these median aggregations not present further posteriorly. No stomate nephridia detectable anterior to the amputation. Sperm funnels iridescent in X and XI; small paired seminal vesicles racemose in XI and XII, accompanied below the oesophagus by a large unpaired racemose seminal vesicle in each segment. Prostate glands large but restricted to XVIII, racemose and bipartite, the muscular duct branching entally to the two major lobes, then the branches in turn showing limited

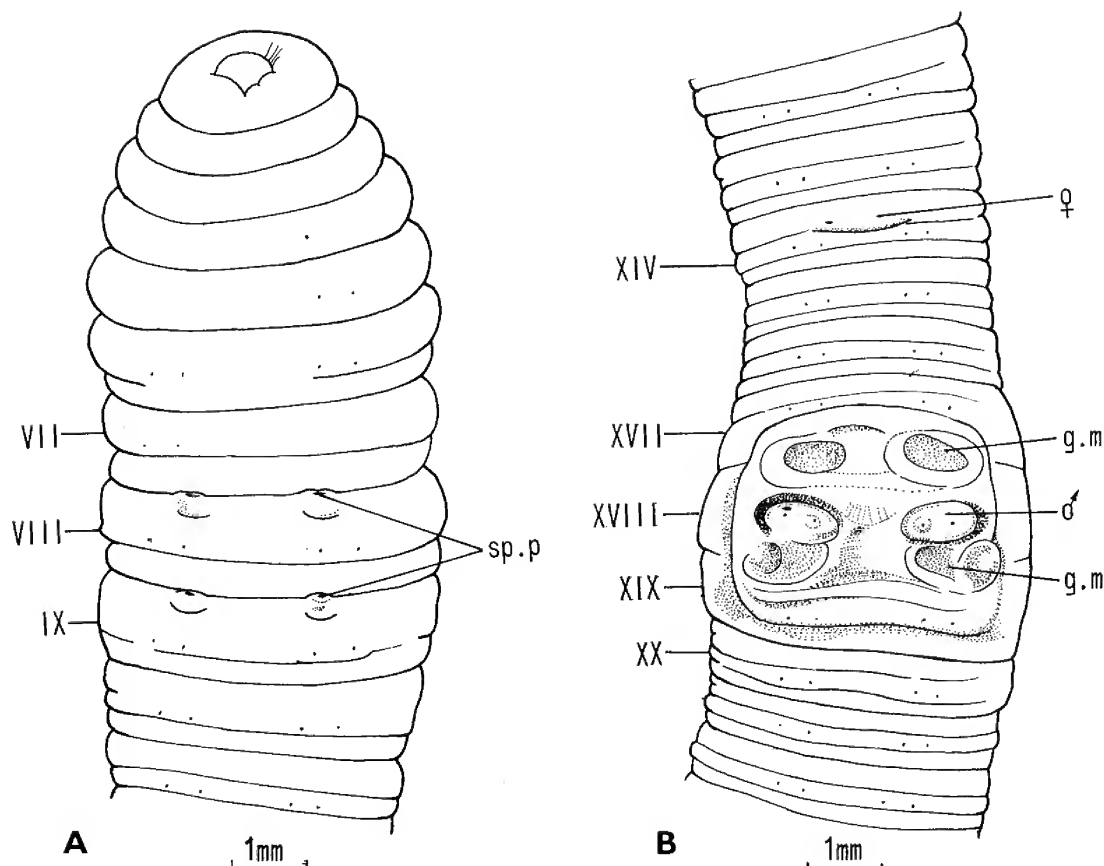


FIG. 5: *Digaster lumbricoides kondalilla* subsp. nov. A, Spermathecal field; B, Male genital field of holotype. For key to abbreviations, see Fig. 9.

branching; the branching visible when the prostatic lobes are separated. Penial setae absent, though *a* and *b* follicles are externally visible. Ovaries (diffuse webs with small oocytes) and funnels in XIII. Spermathecae each with an ovoid-sacciform ampulla and an elongate pearshaped, ectally widening duct of similar length which bears a small rounded sessile more or less distinctly bifid (iridescent) diverticulum dorsally on the ectal dilatation; length of right spermatheca of VIII = 3.9 mm; ratio of length spermatheca: length duct = 2.0; ratio of length spermatheca: length diverticulum = 7.9.

REMARKS: *Digaster lumbricoides*, the type-species of the genus was previously known only from material collected at Port Macquarie in 1846 (Jamieson, 1971b). Although erection of a new subspecies on a single specimen is undesirable, it is preferable to total identification of this distinctive specimen with *D. lumbricoides* as represented by the earlier material. Some differences from the nominate subspecies are: location of male pores on XVIII; origin of the intestine in XIX (not $\frac{1}{2}$ XVI);

the more strongly bipartite condition of the prostates and (significantly?) the ectal widening of the spermathecal ducts; location of the male pores in *b* and of spermathecal pores in *a* lines, rather than *ab*, and the intersegmental, not postsetal location of the genital markings with lateral duplication of the posterior markings. These are minor differences of doubtful importance.

Dilatation of the spermathecal ducts and the bipartite form of the prostate glands are shared with *D. bradburyi* with which affinities are close. On the other hand, the quadrangular raised genital field with genital markings on the corners, post-testicular paired and median seminal vesicles and anterior dorsal pores strongly indicate conspecificity with *D. lumbricoides*. It is possible that *D. bradburyi* consists of populations of the earlier named *D. lumbricoides* but elucidation of the *lumbricoides-bradburyi* complex and of relationships of these with *D. brunneus* and *D. longmani* requires further studies of morphology and reproductive isolation of the constituent populations.

***Digaster minima* sp. nov.**

Figs. 6A; 10J; Table 3

MATERIAL EXAMINED: *Or* 7, 152°47'E. 27°23'S., Mt. Nebo Road, Mt. Nebo, Queensland, in loamy soil in gully in eucalypt area, E. Bradbury, 12 Jun 1970, Holotype (H) QM G7397, Paratypes (P) 2, 3, QM G7398-9. P1, BM(NH) 1973.10.108. 1 mile from Mt. Nebo on road, E. Bradbury, 10 Aug 1970, P4, BM(NH) 1973.10.109.

1 = ? (H, posterior amputee), 28 (P1), 41 (P2) mm, w (midclitellar) = 1.7 mm, s = 122 (P2). Form slender, circular in cross section; pigmentless in alcohol. Prostomium proepilobous, slightly (P1, 2) to $\frac{2}{3}$ peristomium (H), peristomium with or without slight dorsal furrows. First dorsal pore 9/10 (H, P1, 2) with possibly some imperforate preceding this. Setae visible with difficulty anteriorly where they lie in 8 longitudinal rows, commencing on II; shortly behind the clitellum they are recognisable only with the greatest difficulty until in the last approximately 30 caudal segments where the dorsal pair on each side is enlarged and is shifted dorsally so that the 4 setae *cd* are approximately equidistant from each other; *c* and *d* are also displaced dorsally in anterior segments though not so markedly; setae *a* and *b* absent in XVIII. Clitellum annular, XIV- $\frac{2}{3}$ XVIII; (H, P2) setae visible; dorsal pores obliterated; intersegmental pores represented only ventrally. Male pores in longitudinal crescentic grooves equatorially in *ab* of XVIII on broad, low, medianly widely conjoined (H) or just contiguous porophores (P1, 2) which almost reach the setal arcs of XVII and XIX or (P1, 2) are less extensive. Accessory genital markings midventral unpaired circular segmental papillae with porelike centres in each of segments XII and XIII and XX-XXIV (H). A paired marking sometimes present in the setal arc and bearing setae *ab* on its posterior aspect in X (P1, unilateral left only; P2, 4 bilateral). Median marking in XII (P1, 3, 4), XIII (P1-4); XV (P2, 4); XVI (P4); XIX (P2, 3); XX and XXI (P1-4) and XXII (P2, 3). Female pores a pair shortly anteromedian of setae *a* of XIV. Spermathecal pores 2 pairs, near the anterior margins of VIII and IX in *ab*, nearer *a* (H) or in *a* lines, on small rounded papillae.

Septa 6/7 and 7/8 the strongest, those to 10/11 moderately strong. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XII. Pharynx ending in IV; oesophagus wide and thinwalled in V; gizzards well developed, globose, not separated by unmodified oesophagus but a narrow anterior part of the posterior gizzard relatively unthickened. Calciferous glands absent. Origin of intestine indefinite, apparently $\frac{1}{2}$ XVII in P1; caeca and muscular thickening absent; definite

typhlosole absent but a very low dorsal ridge present from approximately XXIV posteriorly. Meronephric: no tufts present; nephridia few micromeronephridia; in the anterior intestinal region 3 on each side in longitudinal rows, one row in *ab*, the second at mid *bc*, the third in *cd*. Metandric; sperm funnels strongly iridescent in XI; gymnorchous; seminal vesicles racemose in XII (H, P1) a spermatheca-like iridescent sac (accessory seminal vesicle?) extends below the gut from septum 12/13 into XIII (H only). Metagynous; ovaries flattened laminae with numerous oocytes in XIII; ovisacs absent. Prostates racemose, squarish bifid lobes, occupying about four segments; vas deferens joining the muscular anteromedianly directed duct at its junction with the gland. Penial setae absent. Spermathecae 2 uniform pairs, each with ovoid ampulla and well demarcated fairly slender duct; a single (inseminated) subspherical diverticulum joining the duct by a narrow very short stalk at midlength; the diverticulum externally simple but with several internal sperm masses; length of right spermatheca of IX (H) = 1.7 mm; ratio of length spermatheca: length duct = 1.8; ratio of length spermatheca: length diverticulum = 5.6.

REMARKS: Only *D. pseudoperichaeta* shares with *D. minima* the extreme dorsal displacement of the dorsal setal couples in caudal segments. Both have the metandric condition of the male gonads seen elsewhere in the genus only in *D. brunneus* and *D. longmani*. It appears likely that the two species are more closely related one to the other than to other species. They are clearly interdistinguishable by the male genital fields.

D. minima is the smallest known species of *Digaster*.

***Digaster nothofagi* sp. nov.**

Figs. 1; 6B; 10K; 11F; Table 3

MATERIAL EXAMINED: *Ps* 5, 153°17'E. 28°13'S., Springbrook, Best of All Lookout, under *Nothofagus* (Antarctic beeches), B. Jamieson and E. Bradbury, 22 Apr 1971, Holotype, QM G7400.

1 = 81 mm, w (midclitellar) = 5.2 mm, s = 196. Form moderately stout, circular in cross section; pigmentless buff in alcohol. Prostomium epilobous $\frac{2}{3}$ open, dorsally bisected by a longitudinal groove. Peristomium with numerous faint longitudinal grooves but not bisected. First dorsal pore 4/5. Setae small but visible, in 8 regular longitudinal rows throughout, commencing on II. Setae *a* and *b* absent.

Nephropores not externally recognisable. Clitellum hardly appreciable externally but seen from the

dorsal incision to extend from XIV–XVII with some very weak development in the adjacent halves of XIII and XVIII; apparently annular. Male pores minute, in *ab* of XVIII, on small papillae. Accessory genital markings: an unpaired midventral papilla posteriorly in IX, X and XVII and in 18/19, 19/20 and 20/21, all well within *aa* excepting that in IX which extends laterally into *ab*; paired papillae postsetal in *ab* in XVII and lateral to *b* in XVIII; segments VII and VIII with an indistinct tumid

band postsetally connecting the spermathecal pores. Female pore unpaired, presetal in XIV. Spermathecal pores 2 pairs in 7/8 and 8/9, immediately lateral to *a* lines on minute papillae.

Septa 6/7–10/11 strongly thickened. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XII; those in X–XII latero-oesophageal, taking their main origin from the supra-oesophageal vessel but with very slender connectives from the dorsal vessel. Supra-

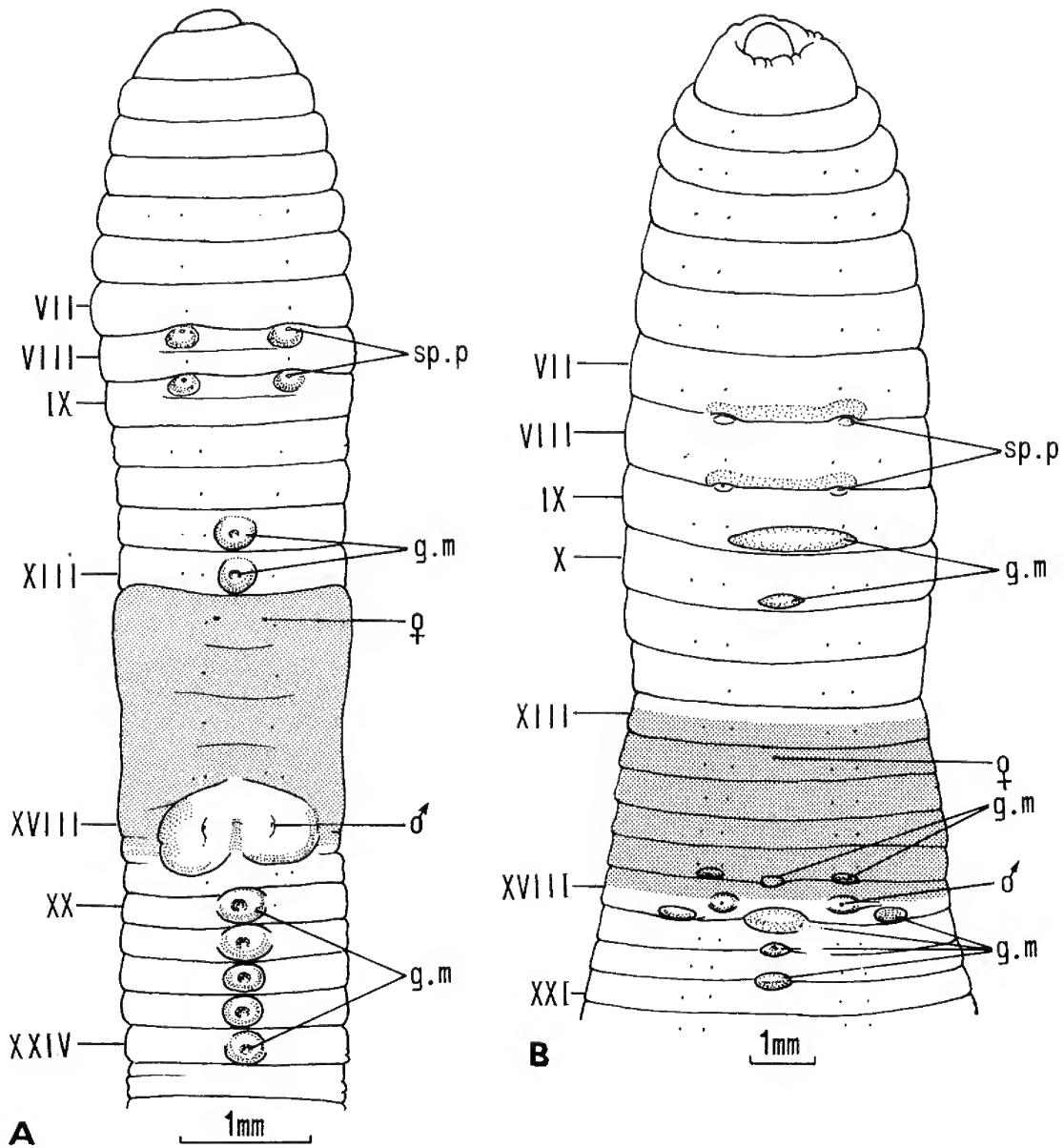


FIG. 6: A, *Digaster minima* sp. nov. Genital field of holotype. B, *D. nothofagi* sp. nov. Genital field of holotype. For key to abbreviations, see Fig. 9.

oesophageal ill-defined, limits indeterminable. Subneural vessel absent. Oesophagus in V slightly dilated, thin-walled, hidden by septal glands. Two strong subspherical gizzards with slightly developed anterior rims, in VI and VII, the oesophagus between them strongly constricted but very short. Oesophagus almost suppressed, by backward extension of the gizzards, in VIII and IX; short and simple in X–XIII; swollen and vascularized in XIV–XVII, where a paired circumferential vessel joins the dorsal vessel, with low, sinuous internal rugae especially dilated in XV and XVI; oesophagus narrow in XVIII. Intestinal origin XIX; typhlosole, caeca and muscular thickening absent. Nephridia meronephridia: masses of spiral loops in IV, V, VI and VII, on the posterior septa of these segments, those in V–VII apparently but not certainly exonephric, those in IV with connections to the pharynx which may be ducts. Sparse lateral parietal bands of exonephric micromeronephridia in II and III and in VIII posteriorly; in the anterior intestinal region 8 or 9 on each side and a small group median to these; caudally with the median-most nephridium enlarged as an exonephric megameronephridium with preseptal funnel. Holandric, gymnorchous (sperm funnels iridescent in X and XI); seminal vesicles racemose, in IX and XII. Prostates racemose, tongue-shaped, each entally divisible into a dorsal and a ventral lobe; vas deferens joining the straight medianly directed muscular duct near its junction with the gland. Metagynous (ovaries not seen; oviducal funnels in XIII); ovisacs absent. Spermathecae 2 uniform pairs; ampulla elongate ovoid; duct cylindrical bearing an iridescent multiloculate diverticulum near its ectal extremity; length of right spermatheca of IX = 2.6 mm; ratio of length spermatheca: length duct = 2.6; ratio of length spermatheca: length diverticulum = 4.1.

REMARKS: *D. nothofagi*, from a spur on the escarpment of the Macpherson Range, closely resembles *D. binnaburra* from neighbouring parts of the same range. The two taxa are clearly distinguished by the genital fields which are sufficiently different to suggest reproductive isolation, one from the other.

***Digaster pseudoperichaeta* sp. nov.**

Figs. 1; 7; 10L; 11G; Table 3

MATERIAL EXAMINED: *Or* 4, 152°59'E. 27°16'S., Y.M.C.A. Camp Warrawee, near Petrie, in sandy loam under *Catospermum* in riverine vine forest, B. Jamieson, 17 Feb 1969. Holotype (H) QM G7401, Paratypes (P) 2, 3 QM G7402–3, P1, BM(NH) 1973.10.110.

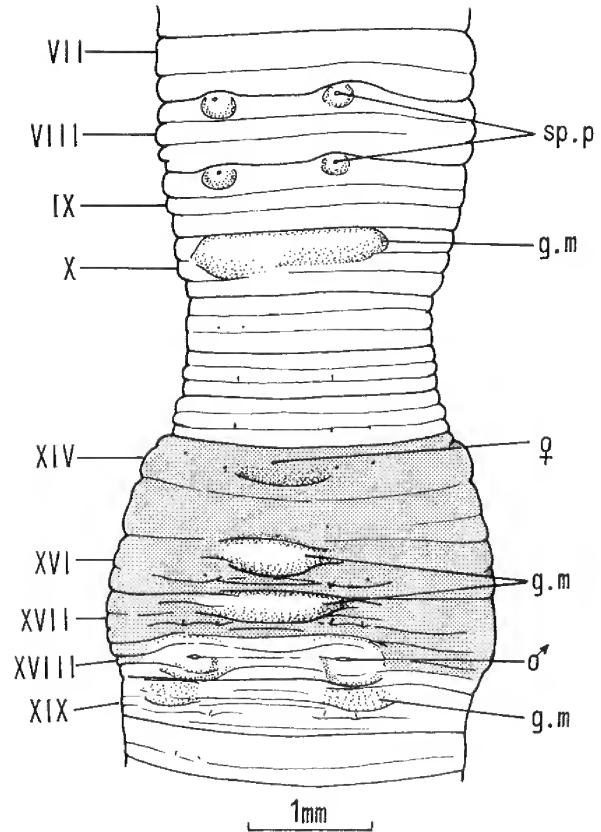


FIG. 7: *Digaster pseudoperichaeta* sp. nov. Genital field of holotype. For key to abbreviations, see Fig. 9.

l = 36 (P1)–45 mm(H), w (midclitellar) = 2.7 (P1)–3.3(H) mm, s = ? (not countable owing to maceration). Form circular in cross section, moderately slender. Pigmentless in alcohol. Prostomium epilobous $\frac{1}{2}$, open, faintly canalliculate. Dorsal pores minute, commencement indeterminable. Setae commencing on II, in 8 regular longitudinal rows throughout but the dorsal couples (*cd*) caudally moving to a dorsal situation so that by approximately 15 (P1) or 25(H) segments from the posterior end the four setae of the two dorsal couples are equispaced, and are large and readily seen, whereas the more anterior setae, and all ventral couples, are minute and inconspicuous. Setae *a* and *b* absent in XVIII. Clitellum annular, XIV–XVII well developed and protuberant; setae visible, dorsal pores occluded; intersegmental furrows almost obscured. Male pores a pair of transverse slits in *ab* on low whitish porophores which fill the segment longitudinally. Accessory genital markings: a midventral transverse, strongly protuberant pad occupying the anterior two thirds of X and extending laterally beyond *b*; a further

midventral pad anterior to but overlapping the setal arc of XVI and XVII, anteriorly impinging very slightly on the preceding segment, and extending laterally to *a* and *ab* respectively; and a pair of white tumescences on XIX anterior to the ventral setal couples which latter are themselves on a white glandular transverse ridge on each side (H, P1-3). Spermathecal pores 2 pairs, near the anterior borders of VIII and IX, in *ab* on circular prominences:

Septa 6/7 and 7/8 the thickest, strongly thickened. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XII (vascular system macerated).

Oesophagus wide and very thin walled in V; two relatively very large, strong, globular gizzards, in VI and VII, separated by a deep constriction where the oesophagus is unthickened though of negligible length. Oesophagus suppressed by backward extension of the gizzards in VIII; moniliform and vascularized but lacking calciferous glands, in IX-XII; narrowly tubular and sinuous in XIII-XVII; intestinal origin XVIII; typhlosole, caeca and muscular thickening absent. Meronephric, with a few rows of fairly large meronephridia on each side in the oesophageal and intestinal regions of which the medianmost nephridium in caudal segments has a preseptal funnel but is not appreciably enlarged; nephridia in pharyngeal and buccal segments more numerous but no tufts detectable. Metandric (sperm funnels, iridescent, XI); gymnorchous; seminal vesicles racemose in XII only. Metagynous (ovaries with several chains of large oocytes); ovisacs absent. Prostates racemose, tongue-shaped but entally bifid; restricted to XVIII; vas deferens joining the junction of the gland with the short muscular duct. Penial setae absent. Spermathecae 2 uniform pairs, ampulla very slender and elongate, almost tubular, lacking a distinct duct though the widened ectal fourth may be considered one; diverticulum (inseminated) consisting of several distinct loculi, sessile near its ectal limit; length of right spermatheca of IX (H) = 2.27 mm; ratio of length spermatheca: length diverticulum = 4.1.

REMARKS: *D. pseudoperichaeta* is closest to *D. minima* from which it is distinguished on p. 285.

***Digaster sexpunctata* sp. nov.**

Figs. 1; 8; 10M; 11H; Table 3.

MATERIAL EXAMINED: *Ps* 6, 153°27'E. 28°05'S., 2 miles along Austinville Road, near Burleigh, South Queensland, E. Bradbury, 10 Apr 1970, Holotype (H) QM G7404, Paratype (P) BM(NH) 1973.10.111.

l = 55 mm, w (midclitellar) = 5 mm, s = 142 (H; paratype is posterior amputee). Form circular in cross section throughout, moderately stout. Pigmentless. Prostomium indistinctly tanylobous, faintly canaliculate, but almost indistinguishable from other longitudinal furrowing of the peristomium. First dorsal pore 4/5 (H) or 5/6 (P). Setae in 8 regular longitudinal rows, commencing on II; setae *a* and *b* absent in XVIII. Nephropores not externally visible. Clitellum (developed in H only, though not fully) annular, XIV- $\frac{2}{3}$ XVIII; intersegmental furrows and dorsal pores present though weaker, setae present. Male pores in

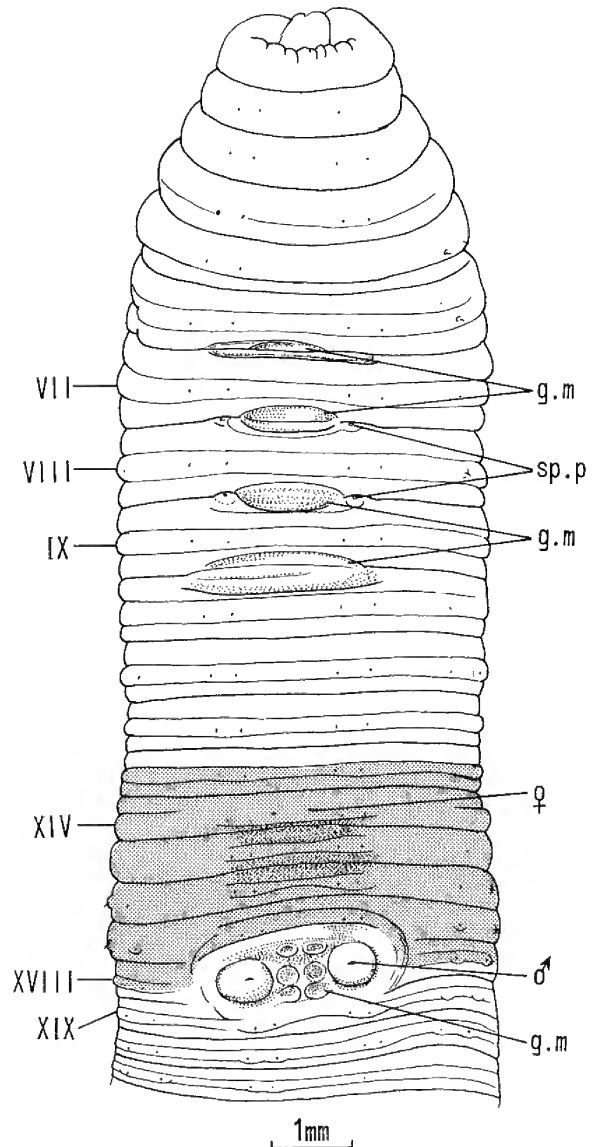


FIG. 8: *Digaster sexpunctata* sp. nov. Genital field of holotype. For key to abbreviations, see Fig. 9.

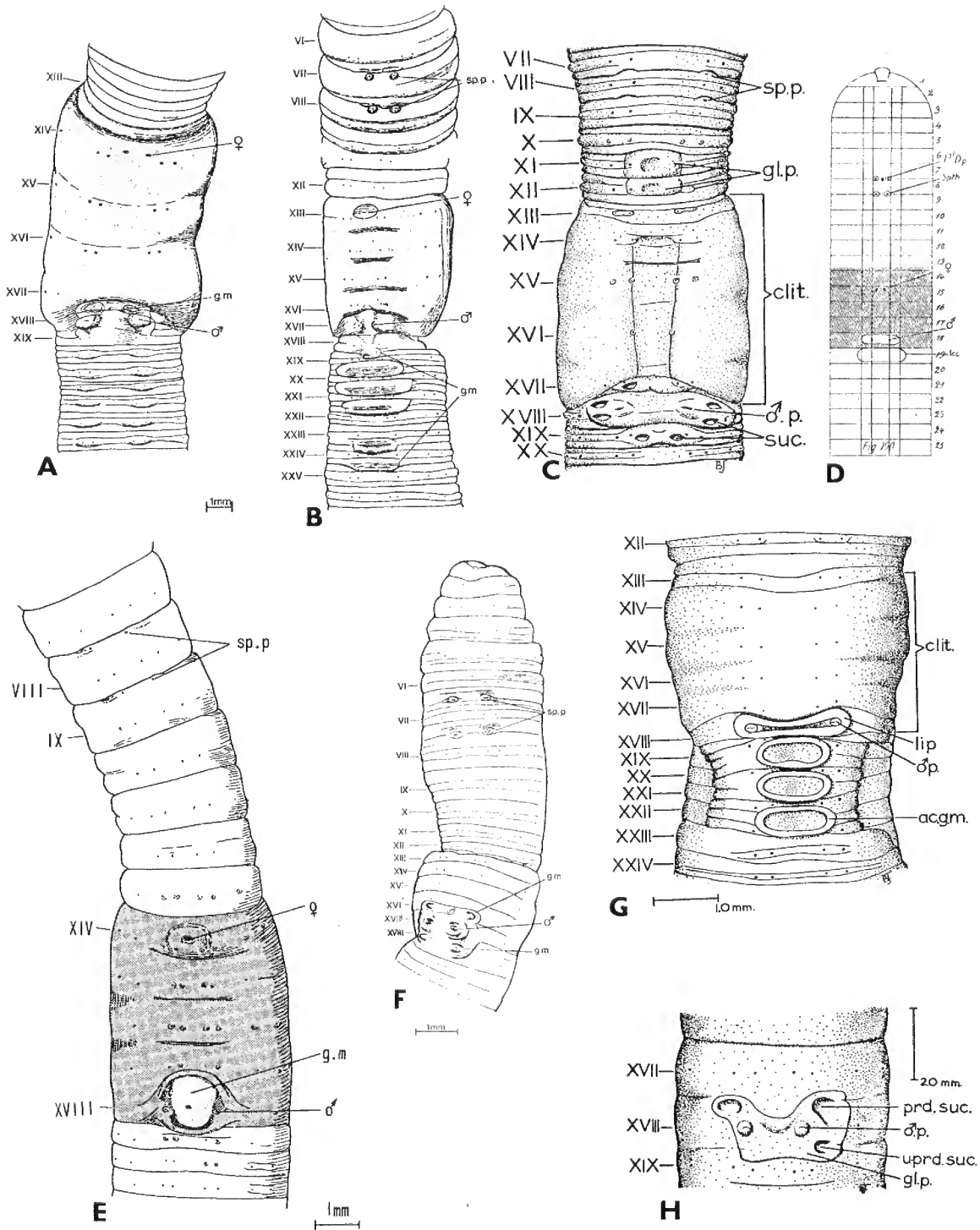


FIG. 9: Genital fields of: A, *Digaster bradburyi bradburyi*; B, *D. anomala*; C, *D. armifera*; D, *D. minor*; E, *D. gwongorellae*; F, *D. lumbricoides lumbricoides*; G, *D. gayndahensis*; H, *D. lamingtonensis*. (A and B from Jamieson, 1970; C, G and H from Jamieson, 1963; D from Spencer, 1900; E from Jamieson, 1972; F from Jamieson, 1971).
 ac.g.m, accessory genital marking; clit, clitellum; ♀, female pore; g.m, accessory genital marking; gl. p, glandular pad; ♂, male pore; prd. suc, paired suckerlike genital marking; sp.p, spermathecal pore; suc, suckerlike genital marking; uprd. suc, unpaired suckerlike genital marking.

XVIII in *ab* near *b* on hemispheroidal papillae surrounded by a common prominent rim which extends at least to the setal arcs of XVII and XIX and laterally to mid *bc*; the male porophores separated by a pair of very small disc-like equatorial genital markings which are preceded and succeeded by a similar pair of markings which are intersegmental in 17/18 and 18/19 (H, P); additional genital markings on a transverse pad in each of intersegments 6/7, 7/8, 8/9 (H, P) and 9/10 (H); those in 6/7 and 9/10 filling *bb* (H) or that in

6/7 median to *a* (P); those in 7/8 and 8/9 filling the interval between the spermathecal pores. Female pores anteromedian to setae *a* of XIV, about $\frac{1}{4}aa$ apart, on a common elliptical tumescence. Spermathecal pores 2 pairs, at the anterior borders of VIII and IX, on small papillae (H, P).

Septa 10/11 and 11/12 the thickest, strongly thickened. Dorsal blood vessel single, continuous onto the pharynx. Last hearts in XII; those in X–XII latero-oesophageal, each receiving a connective from the dorsal vessel and the weakly

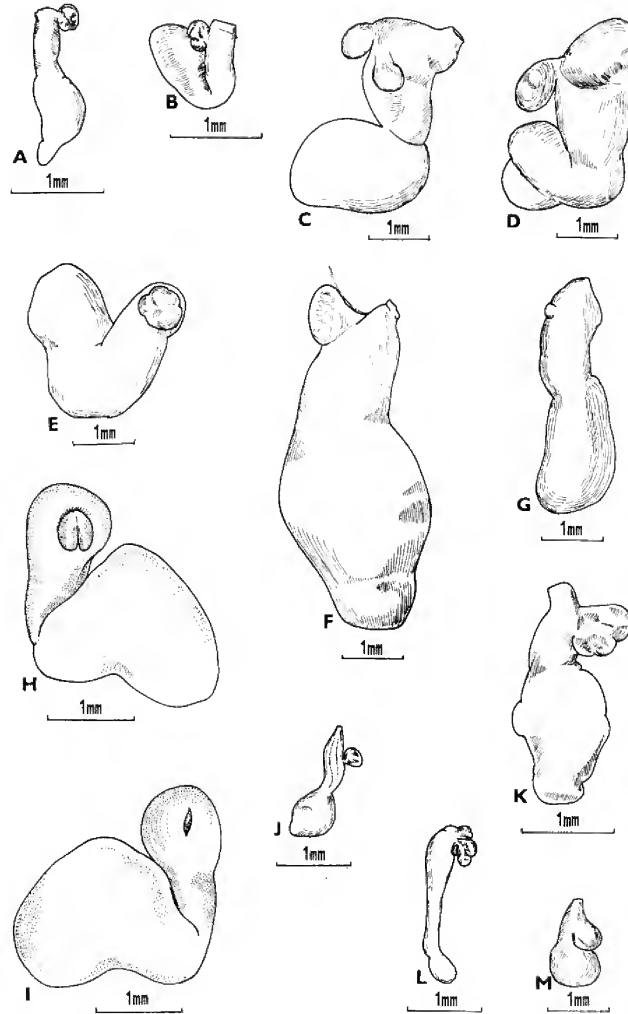


FIG. 10: Spermathecae in *Digaster*: A, B, *D. binnaburra* sp. nov., holotype, A, right VIII, B, right IX; C, D, *D. bradburyi bunyaensis* subsp. nov., holotype, C, left VIII, D, right IX; E–G, *D. brumeus* Spencer, 1900, right IX, E, BM(NH) 1973.10.98; F, BM(NH) 1973.10.100, G, Wolvi specimen, BM(NH) 1973.10.105; H, I, *D. lumbricoides kondalilla* subsp. nov., holotype, right VIII, H, dorsal, I, ventral; J, *D. minima* sp. nov., holotype, right IX; K, *D. nothofagi* sp. nov., holotype, right IX; L, *D. pseudoperichaeta* sp. nov., holotype, right IX; M, *D. sexpunctata* sp. nov., holotype, right IX.

developed supra-oesophageal vessel. Subneural vessel absent. Pharynx ending in III; oesophagus in IV and V segmentally dilated and very thin walled. Two strong subspherical gizzards, in VI and VII, separated by a short region of unmodified oesophagus. Oesophagus almost suppressed in VIII by backward extension of the gizzards; moniliform and vascular in IX–XIII; in XIV, XV and XVI with longitudinally striated lateral outpouching but not cut off from the oesophageal lumen and with only low internal rugae, not forming definite calciferous glands. Oesophagus narrow in XVII; intestinal origin XVIII; muscular thickening, caeca and typhlosole absent. Nephridia meronephridia (H, P); large tufts in IV, V and VI sending ducts to a common composite duct on each side which joins the anterior aspect of the buccal cavity dorso-

laterally; II, III and VII posteriorly, with parietal micromeronephridia which form dense lateral bands in VII; approximately 10 on each side by the anterior intestinal region. Posteriorly with moderately enlarged exonephric megameronephridium, with preseptal funnel, median to astomate, exonephric micromeronephridia (H). Holandric (iridescent sperm funnels in X and XI); gymnorchous; large racemose seminal vesicles in IX and XII. Metagynous, ovaries with numerous united strings of large oocytes (H, P); small ovisacs (?) in XIV in H, not observable in P. Prostates racemose, tongue-shaped, restricted to but enlarging XVIII; vas deferens joining the straight medianly directed duct where this joins the gland. Penial setae absent. Spermathecae with widely ovoid to subspherical ampulla; the mod-

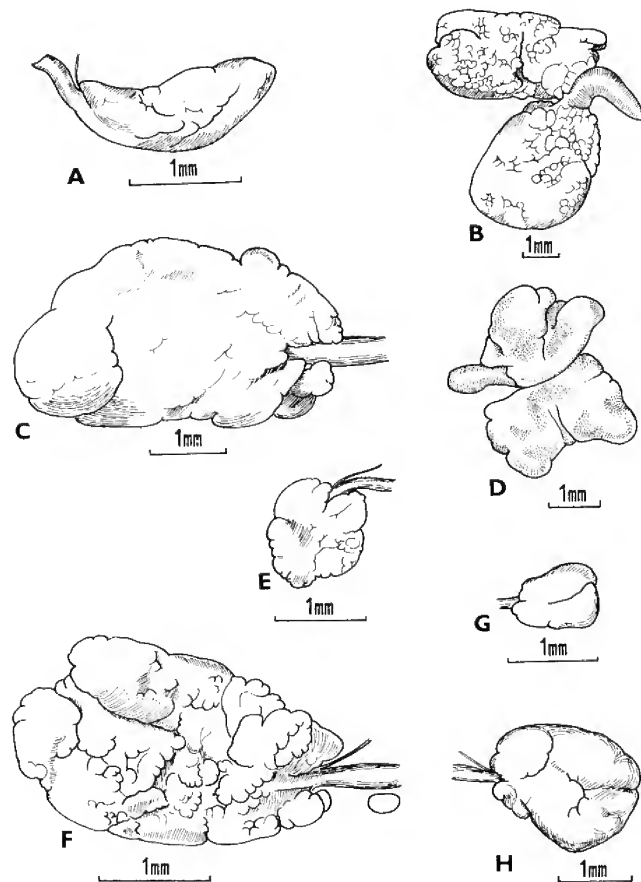


FIG. 11: Prostates in *Digaster* (L = left; R = right). A, *D. binnaburra* sp. nov., holotype, R; B, *D. radburyi bunyaensis* subsp. nov., holotype, L; C, *D. brunneus* Spencer, 1900, BM(NH) 1973.10.98; L; D, *D. lumbricoides kondalilla* subsp. nov., holotype, R; E, *D. minima* sp. nov., holotype, L; F, *D. nothofagi* sp. nov., holotype, L; G, *D. pseudoperichaeta* sp. nov., holotype, R; H, *D. sexpunctata* sp. nov., holotype, R.

erately narrow, well demarcated duct joined at or shortly ectal of midlength by a subspherical internally multiloculate (inseminated) broadly sessile diverticulum; the ampulla packed with nematodes (H, P); length of right spermatheca of IX (H) = 1.5 mm; ratio of length: length duct = 1.8 ratio of length: length diverticulum = 3.0.

REMARKS: The spermathecal and male genital fields of this species are highly distinctive.

ACKNOWLEDGMENTS

I am deeply indebted to Mr R. W. Sims, the authorities of the British Museum (Natural History), and Professor R. P. Dales of Bedford College, for providing facilities for this study. Mr E. Bradbury and Mr T. Walker are thanked for their assiduous collecting and Mr Walker for aid in mapping. The work was made possible by Royal Society Nuffield and Australian Research Grants Committee grants.

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A REVIEW OF THE GENUS *PHYLLURUS* (LACERTILIA: GEKKONIDAE)

JEANETTE COVACEVICH
Queensland Museum

ABSTRACT

Two new species of *Phyllurus* (*P. caudiannulatus* and *P. salebrosus*) are described from mid-eastern Queensland and the other two species of this genus, which is confined to eastern Australia, are redescribed. A key to their identification is provided and distribution of the species is discussed.

The genus *Phyllurus* Schinz, 1822, is defined in detail by Kluge (1967, p. 1017) to include four species—*P. platurus* (White, 1790), *P. milii* (Bory de St. Vincent, 1825), *P. cornutus* (Ogilby, 1892), and *P. sphyrurus* (Ogilby, 1892). Two distinct groups are recognisable within the genus as it is defined by Kluge. The first comprises *P. milii* and *P. sphyrurus*. These deep-headed species, covered in rounded tubercles, with robust moderately depressed tails, are referred to *Underwoodisaurus* by Wermuth (1965, p. 47). Species of the second group (*P. platurus* and *P. cornutus*) have extremely depressed heads, very broad, depressed, 'leaf-like' tails, and are covered in conical tubercles.

Two new species described here are referred to *Phyllurus* (*sensu stricto*) because both have extremely depressed heads and are covered with conical tubercles. Only one species (*P. salebrosus* sp. nov.) has the characteristic 'leaf-like' tail of *Phyllurus* species. The other (*P. caudiannulatus*), has a tail that is long, slender, and round in cross-section or slightly leaf-shaped. As *P. caudiannulatus* is very similar to *P. platurus* (the only obvious differences are in tail shape and distribution) and as *U. sphyrurus* and *U. milii* form an easily recognised separate group, Kluge's definition of the genus *Phyllurus* must be modified to exclude *P. sphyrurus* and *P. milii* (following Wermuth, 1965) and to include *P. caudiannulatus*. This can be done by describing the tail of *Phyllurus* as moderately long, cylindrical or extremely depressed, not prehensile, without modified terminal subcaudal lamellae.

The four species here referred to *Phyllurus* are confined to eastern Australia between mid-eastern New South Wales and northeastern Queensland. Only one species (*P. salebrosus*) is found far from

the coast. Two species (*P. cornutus*, *P. caudiannulatus*) are apparently usually confined to closed forests and the other two species (*P. platurus* and *P. salebrosus*) inhabit drier rocky areas with sparser vegetation cover.

METHODS

All specimens of *Phyllurus* in the reference collections of the Queensland Museum (QM), the Australian Museum (AM), and the National Parks Branch (Department of Forestry) Museum (RG) have been examined. The following body measurements and morphological characters have been used in separating the species.

Snouth to vent length (SVL): From tip of snout to anterior margin of vent.

Tail length (T): Taken in two ways (a) in species with 'leaf-like' tails, because almost all tails have been cast posterior to the vent where the leaf begins, as shown in Fig. 1; (b) in *P. caudiannulatus* which has a 'conventional' tail, from posterior margin of cloaca to tip of tail.

Attenuated tip of tail (TT): As shown in Fig. 1.

Head length (HL): Between tip of snout and posterior margin of ear.

Head width (HW): Greatest width of head.

Snout (S): Tip of snout to anterior margin of eye.

Labials: Counted to exclude granular scales towards angle of mouth.

Number of rows of spines across attenuated portion of tail: Counted from first complete row across the tail, usually corresponding with the posterior end of the 'leaf' (see Fig. 1a).

Rows of tubercles on eyelid: Counted to exclude the row forming the 'eyelash' and the orbital row (see Fig. 2).

KEY TO *Phyllurus* SPECIES

- 1 Throat completely covered with calcareous deposits *P. salebrosus*
 Throat almost smooth, calcareous deposits only in skin covering bones of lower jaw *P. cornutus*
 Throat and skin covering bones of lower jaw smooth 2
 2(1) Specimen with original tail 3
 Specimen with regenerated tail or no tail 4
 3(2) Tail with distinct white bands, cylindrical or slightly leaf-shaped . . . *P. caudiannulatus*
 Tail without distinct white bands, leaf-shaped *P. platurus*
 4(2) Specimen from mid-eastern Queensland *P. caudiannulatus*
 Specimen from mid-eastern New South Wales *P. platurus*

***Phyllurus platurus* (White)**

(Figs. 3, 4; Plates 37B, 38C, 39C, 40D)

Lacerta platura White, 1790, p. 246, pl. 32, fig. 2. (Australia—presumed to be near Sydney, N.S.W.; ?holotype BM xxii98a).

Agama discosura Merrem, 1820, p. 51. (Australia; type(s) presumed lost).

[?] *Phyllurus australis* Swainson, 1839, p. 370.

Phyllurus inermis Gray, 1845, p. 176. (Australia; holotype BM xxiii00a).

MATERIAL EXAMINED

QM Blue Mts., J160; Buladelah J9054; AM no data, 5241, A1237, R959, R966, R992, R1550, R1575, R3588, R3601, R3666, R5182, R11587; Bondi, R1124; Kiama, R2306; Balmain, R2531; Hawkesbury, R3143; Woolwich, R3182; Brooklyn, R3392; Sackville, near Windsor, R3582; near Sydney, R3583, R8305; Callan Park, R3585; Greenwich, Lane Cove R., R3793; Darling Point, R4396; North Sydney, R4404, R12209; Gosford, R4814; Bradley's Head, R5181; Sydney, R5520, R8087; Linfield, R6141; Terrace Falls, Hazelbrook, R6728; Freshwater, Manly, R7087, R7189, R8036; Pennant Hills, R7294; Double Bay, Sydney, R7747; Woodford, Blue Mountains R7987; Coalcliff, R8037; Mittagong, R8125, R8126; Hunters Hill, R8271; Mosman, near Sydney, R8277, R8918; North Sydney, R8595; Lithgow, R8980; Cremorne, R9274; Northbridge, R9826; Epping, R1005, R10377; Lane Cove R., R10066; Annandale, R10068; Watson's Bay, R10220; Croydon Park, R10374; near Gosford, R10384; Harbord, R10387; Sydney, R10412, R21047; Tuggerah Lakes, R10429; Edgecliffe, R10504; Longueville, R11733; Northbridge, R11889; Northmead, R12907; Punchbowl, R13105; Giruan, via Stroud, R15412; Jannali, Sydney, R19084; Jenolan Caves, R20381; Mangrove Creek, via Spencer, R25891, R25912; Saratoga, R26208; Miranda, Sydney, R27324; Faulconbridge, R27325; St. Ives, Sydney, R27330; Castle Hill, Sydney, R27334; Hunters Hill, Sydney, R27940; Baulk-

ham Hills, Sydney, R28308; North Shore, Sydney, -4942, A11701; Double Bay, Sydney, A9615; Wallis Lake, Tuncurry, R8253; Buladelah, R8103. All localities are in New South Wales.

DIAGNOSIS

A small leaf-tailed *Phyllurus* very similar to *P. caudiannulatus* from which it may be distinguished readily by tail shape (depressed, broad, leaf-like original and regenerated tail vs conventional cylindrical original and regenerated tail*). Specimens without tails virtually indistinguishable although *P. caudiannulatus* is usually more spinose, especially on the head, than *P. platurus* and the two species occur in widely separated localities (mid-eastern N.S.W. vs mid-eastern Queensland). Distinguished from *P. cornutus* from southeastern Queensland and northeastern New South Wales, with which it has been confused, by size (SV 95.9 (max) vs 140.0), absence of calcareous deposits on throat (present on skin covering bones of lower jaw in *P. cornutus*) and, less reliably, tubercles at flank (very small vs larger, rounded or flattened and strongly hooked in northern specimens).

DESCRIPTION

White's type description of this species is very brief and, although it is accompanied by an illustration, is hardly adequate for distinguishing the species. J. E. Gray (1845, p. 176) examined two specimens he referred to *P. platurus* from 'New Holland' (= Australia). G. R. Gray (1845, p. 17, fig. 2) referred material from 'Sydney' and 'Macquarie River' to *P. platurus*. His illustration shows typical specimens of *P. platurus* with original and regenerated tails (as *P. inermis*). It seems reasonable to assume that White's type specimen was included in those examined by Gray and, in any case, the specimen on which the type description is based almost certainly came from near Sydney because in 1790 there were no other settlements in New South Wales. The only other species of *Phyllurus* which occurs in Sydney (and this is based on a slightly doubtful record) is *P. salebrosus* sp. nov., a very large species which has the attenuated portion of the tail less than $\frac{1}{3}$ total length of the tail. White's type specimen measured $4\frac{1}{2}$ " (114.3 mm) and his illustration is of a specimen with the attenuated portion of the tail equal to almost half the total length of the tail, a feature typical of *P. platurus*.

Boulenger (1885, pp. 49–50) gives a detailed description of *P. platurus* but this is certainly based on several specimens (p-r, Queensland; s, Pt. Curtis

*See footnote on p. 298.

(Gladstone area, Queensland)) which are not *P. platurus* if present distributions have any significance. The measurements given are of a specimen much larger than any examined in this study and the description may be a composite based on specimens of at least *P. platurus*, *P. salebrosus* and possibly *P. cornutus*, highlighting similarities in some of the external morphological features of these species. Examination of specimens of *P. platurus* makes the following elaboration of Boulenger's description possible. Features common to all *Phyllurus* (e.g. head large, very depressed, distinct from neck . . . covered with small granules, intermixed with conical, spinose tubercles . . .) and which do not serve to distinguish the species have been omitted from this description.

SIZE: *P. platurus* is a small species, similar in size to *P. caudianmulatus*. The largest specimen examined is R6728. Dimensions of this specimen are SVL 95.9, HL 29.3, HW 22.3, (tail regenerated). The largest specimen with an original tail (R8980) has the following dimensions SVL 85.5, T 69.0, TT 36.5, HL 27.3, HW 22.2.

FLANK TUBERCLES: Invariably minute if present, and rounded; absent in some specimens (e.g. R25912, R1550).

ORIGINAL TAILS: Few specimens ($\frac{26}{84}$) have original tails. The length of the attenuated tip is close to half the total length of the tail (0.40–0.56). There are 6–9 rows of spines across the attenuated tip of the tail, the posterior half of which is smooth. In most specimens the whole 'leaf' is dotted with conical tubercles but in some the central thickened portion of the tail is smooth. The tubercles at the edges of the tail are long and slender or short, almost conical. The anterior portion of the 'leaf' may be strongly heart-shaped or have almost parallel sides.

REGENERATED TAILS: Smooth both ventrally and dorsally; fringe broad or narrow and usually terminating in a well defined tip which may be very short or long and tapering.

ROWS OF TUBERCLES ON EYELIDS: Usually one row, but may be none or two or the tubercles may be irregularly arranged. All are very small.

COLOUR: Live specimens of *P. platurus* have not been examined for this study. Green (1973, p. 21) notes that this species is 'usually light brown or grey, similar to the sandstone in which it lives'. Preserved specimens are light brown or grey and most bear darker brownish flecks or striations all over the dorsal surface. Ventrally specimens are pale cream to grey.

HABITAT

Green (1973) has discussed the habitat of this species in detail. *P. platurus* is almost invariably confined to sandstone areas.

DISTRIBUTION

P. platurus occurs only in mid-eastern New South Wales and is confined to the 'Sydney-Hawkesbury Sandstone' as it is defined by Bredeen (1972, p. 6). Queensland records of this species (e.g. Museum of Comparative Zoology, Harvard specimen 10259, Mt Tamborine, S.E.Q. of Loveridge 1935, p. 298 and the small specimen of Lönnberg and Anderson (1915, p. 3), also from Tamborine) are almost certainly based on specimens of the southern form of *P. cornutus*.

Phyllurus cornutus (Ogilby)

(Figs. 1, 3, 4; Plates 36A, 37D, 38D, 39D, 40C)

Gymnodactylus cornutus Ogilby, 1892, p. 8. (Bellenden Ker Ranges, northeastern Queensland; syntypes AM R748–50, R752–3, R1094).

Phyllurus lichenosus Gunther, 1897, p. 405, pl. 12. (Mount Bartle Frere, northeastern Queensland, holotype presumed lost).

Gymnodactylus sphyrrus Barrett, 1950, p. 31. (non *G. sphyrrus* Ogilby).

MATERIAL EXAMINED

SYNTYPES: Bellenden Ker, NE.Q., AM R748–50, R752–3, R1094.

OTHER SPECIMENS: QM (NE.Q.): Shipton's Flat, via Cooktown, J17801; 14.4 km SW. Mossman, J7936; Atherton, J5704; Walsh Camp, via Atherton, J9532; Millaa Millaa, J5508; Bellenden Ker, J3021; Innisfail, J5323; Ingham, J3429; AM (NE.Q.): Millaa Millaa R11375; Bartle Frere, R4769; Evelyn, approx. 14.4 km from Ravenshoe, R26117–23. QM (SE.Q., NE.NSW.): Tamborine J8183, J12257; Mt. Tamborine (= Tamborine Mt.) J398, J2409, J2933–4, J3254, J4439, J8359, J8861, J10440; Eagle Heights, (?) J4819; Mt. Cluny J8074–5, J8099; Binna Burra J8646; Mudgeeraba J4198, J5690; Canungra J148, J3215; Mt. Ballow J23937; Beechmont J5649; Tallebudgera J3313, Mt. Lindsey J10565; Lamington J5382; Tweed R. J1143; N.S.W. J730. AM (N.S.W.) Murwillumbah R2409, A233; Bulga Tableland R6247, R11860; Huonbrook R2315; Nambucca R. R6792; Nimbin R11553; Wauchope, R11621. Queensland. R11844. Girraween, near Stanthorpe RG10.

DIAGNOSIS

A large leaf-tailed *Phyllurus*, distinguished from *P. salebrosus* in having calcareous deposits only in the skin covering the bones of the lower jaw (vs calcareous deposits all over throat) and by length of attenuated tip of tail (greater than one third total length of tail vs less than one third total length of tail). *P. cornutus* is distinguished from the small species *P. platurus* with which it has been confused

in some areas by tubercles at flank (long hooked spines surrounded by smaller spines (*P. cornutus* NE.Q. specimens) or shorter, unhooked, but slender spines usually surrounded by smaller spines (*P. cornutus* SE.Q.–NE.N.S.W. specimens) vs very small, rounded tubercles without smaller tubercles (*P. platurus*). Specimens with original tails are further distinguished by the presence of spines for the full length of the tail tip (absent towards the tip in most specimens of *P. platurus* examined).

DESCRIPTION

SIZE: *P. cornutus* is a large species being smaller than only *P. salebrosus*. The largest specimen examined, a northern specimen (J5704), has the

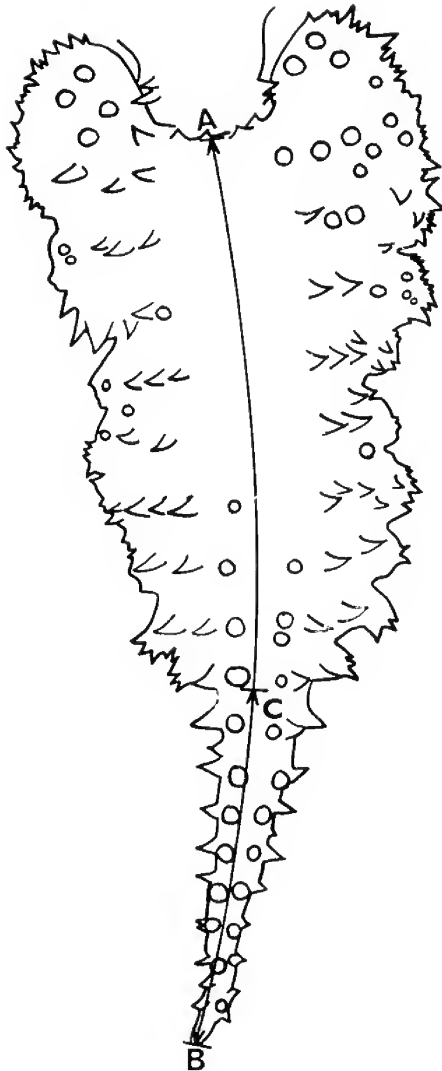


FIG. 1. *Phyllurus cornutus*. A–B, tail length; B–C, length of attenuated tip of tail.

following dimensions SVL 140.0, HW 30.9, HL 40.5, tail missing. The dimensions of the largest specimen with an original tail (R12935, also a northern specimen) are SVL 140.0, T 89.4, TT 38.4, HW 30.1, HL 41.6. Specimens from southeastern Queensland and northeastern N.S.W. are apparently slightly smaller (dimensions of largest specimen, R11860, SVL 128.0, HW 26.0, HL 35.6, tail regenerated). Only two specimens of the Girraween, near Stanthorpe, SE.Q., population have been examined (RG10; QM live specimen: SVL 96.9–100.2, T (QM live specimen) 70.0, TT 30.0, HW 22.5–23.4, HL 27.8–28.0).

FLANK TUBERCLES: All northern specimens have long, slender, hooked, closely adjacent spines surrounded by smaller hooked spines. In southern specimens the flank tubercles range from long, hooked spines surrounded by smaller hooked spines (J2126) through weakly developed spines (RG10) to small rounded or flattened, widely spaced spines which occur in about half the specimens examined. The absence of long hooked spines in southern specimens has apparently led to some of the confusion of *P. cornutus* with *P. platurus* which has weakly developed flank tubercles.

ORIGINAL TAILS: Length of attenuated tip of tail/total length of tail is shown in Fig. 1. The length of the tip of the tail is approximately half its total length. There are normally 12 (9–14) complete rows of spines across the tail and the spines occur along the total length of the tail tip.

REGENERATED TAILS: Very broad (J3021), or relatively narrow (J5690, J2409) depending on the width of the fringe. The tail is smooth, parallel sided, and usually terminates in a well defined tip.

ROWS OF TUBERCLES ON EYELID: usually 2 rows, rarely 1 or 3.

COLOUR: Very few live specimens have been examined but both greenish and greyish specimens with the typical 'lichen' pattern have been seen. Spirit specimens vary from plain dark brown to very light grey, and are patterned with fine brown lines.

HABITAT

P. cornutus is an inhabitant of closed forests, areas formerly covered in closed forest, and adjoining wet sclerophyll forests. It is believed to be a tree-dweller as specimens are frequently found where trees are being felled. *P. cornutus* is very common in some areas of northeastern Queensland (China Camp, approximately 80 km S. of Cooktown) (J. James, pers. comm.) and southeastern

Queensland (Lamington National Park), specimens being found sitting on trees at night, apparently feeding on insects. The Stanthorpe population is common in granite boulder country, an area with rather sparse, open vegetation cover. In the Girraween National Park 30 specimens were observed in 2½ days. The bulk of these were seen under exfoliations on the boulder sites and the remainder in deep cracks in the boulders. A single young specimen was found under an isolated rock on a large flat boulder. Usually the specimens were solitary but up to three adults were found in several 'suitable' crevices (T. Low, pers. comm.).

DISTRIBUTION

P. cornutus occurs in northeastern Queensland, southeastern Queensland, and north- and mid-eastern New South Wales. No *P. cornutus* have been collected or reported between Ingham and Tamborine although it is likely that the species will be found here with more intensive collecting, especially in the closed forests of the ranges of Mackay, mid-eastern Queensland. With only three exceptions (Mudgeeraba, SE.Q; Ingham, NE.Q.; Innisfail, NE.Q.) the localities from which Queensland *P. cornutus* have been collected are above 300 metres, so it appears that this species has a preference for elevated, cool areas.

DISCUSSION

Three forms of *P. cornutus* are recognisable in the specimens examined—from northeastern Queensland, southeastern Queensland—northeastern New South Wales, and from the Stanthorpe area—but, until more specimens are available especially from mid-eastern Queensland, despite differences in size, flank tubercles and habitat preference, it seems preferable to regard them as a single, rather variable species rather than three distinct taxa.

The detailed description of this species by Ogilby (1892, pp. 8–10) is adequate to enable easy recognition of northern specimens upon which it was based but, although he noted this species to be 'very distinct from *G. platurus*, its nearest ally' Ogilby did not elaborate on his reasons for this. He regarded one unspecified specimen, apparently collected at the same time and place as the syntypes of *P. cornutus*, as being specifically inseparable from *P. platurus*. All northern *P. cornutus* in the collection of the Australian Museum have all the features regarded as diagnostic of the species.

In his description of *P. lichenosus* from Bartle Frere (the mountain adjoining Bellenden Ker, the type locality of *P. cornutus*) Gunther separated *P. lichenosus* from *P. cornutus* because it lacked the

'strong spinate knob surmounted by a conical tubercle behind the eye' and from *P. platurus* largely because it had the 'series of slender tubercles which flanks the abdomen' and which are not present in *P. platurus*. The conical tubercles on the knob behind the eye of *P. cornutus* and the other species of *Phyllurus* occur in a variety of sizes and the size and pattern of tubercles on *Phyllurus* specimens vary greatly. Gunther's illustration shows a definite cluster of spines, if not a knob, behind the eye. This feature is not diagnostic of the species. The original tail of the specimen illustrated has the attenuated tip greater than ⅓ total length of tail—a feature diagnostic of *P. cornutus*. No specimens of *P. cornutus* from mid-eastern Queensland are known and the unnumbered specimen from Port Curtis, mid-eastern Queensland, referred to *P. cornutus* by Gunther is probably *P. salebrosus* sp. nov. the only large *Phyllurus* which occurs in the area. Garman (1901, p. 2) briefly described *P. cornutus*, again from northern material, and noted for the first time the difference in the lateral spines of this species and *P. platurus*.

Only two other reptiles have a recorded distribution similar to that of *P. cornutus*. These are *Tropidechis carinatus* Krefft 1863 (Trinca, Graydon, Covacevich and Limpus, 1971, pp. 803–4) and *Leiopisma challengerii* (Queensland Museum reference collection). Two frogs have similar distributions—*Lechriodus fletcheri* (Boulenger) 1890, *Litoria chloris* (Boulenger) 1893 (Queensland Museum reference collection). Several genera of reptiles with different northern and southern closed forest species have been noted—*Goniocephalus*, *Cacophis* (Queensland Museum reference collection) and *Mixophyes* (Liem and Hosmer, 1973, p. 455). Specimens of species of these genera from the intervening closed forests of mid-eastern Queensland are not known.

Phyllurus caudiannulatus sp. nov.

(Figs. 2, 3, 4; Plates 36B, 37C, 38A, 39A, 40A)

MATERIAL EXAMINED

HOLOTYPE: Queensland Museum J15619, ♂ (with original tail), Bulburin State Forest, via Many Peaks, ME.Q. Coll. 3rd Sept., 1968, J. Covacevich, T. P. Tebble.

PARATYPES: J22286, ♀ (with original tail) and J22287, ♀ (with regenerated tail), both from Granite Creek, Bulburin State Forest, via Many Peaks, ME.Q. Coll. 1st April, 1972, G.B. and S.R. Monteith; J24132, ♂ (with regenerated tail), Forest Station, 700 m, Bulburin State Forest, via Many Peaks, ME.Q. Coll. S.R. Monteith, 29th April, 1974; J25411, ♂ (with original tail), Eungella National Park, via Mackay, ME.Q. Coll. Feb, 1975, K. McDonald.

DIAGNOSIS*

A small *Phyllurus* which differs from other *Phyllurus* in having distinct white bands on the original tail, which may be cylindrical or slightly leaf-shaped. Regenerated tails are cylindrical (*vs* leaf-shaped in all other species of *Phyllurus*). Specimens without tails are very similar in size and shape to *P. platurus*. They differ only in being slightly more spinose and in being restricted to closed forest of mid-eastern Queensland (*vs* more open forest in rocky, especially sandstone areas of mid-eastern New South Wales).

DESCRIPTION OF HOLOTYPE

SVL 74.2, TL 138.4, T 64.2, HL 22.0, HW 17.5. Head large, depressed, elongate, triangular, very distinct from neck; skin of the head more or less confluent with cranial ossification; ear opening elliptical, less than half as large as eye. Body moderate. Limbs long; digits strong; subcylindrical at base, compressed distally. Head covered in small granules, intermixed with larger rounded to conical tubercles; a distinct row of small conical tubercles across the head midway between ear and eye, one distinct row of tubercles on eyelid which also bears another row of smaller, irregularly placed tubercles; labials $\frac{14}{14}$. Body and limbs covered dorsally and ventrally with small granules; dorsally these are intermixed with larger conical tubercles which are largest laterally on the body and quite small along the dorsal mid-line and on limbs close to digits. Tail not depressed, slender, tapering, covered dorsally and ventrally by fine granules intermixed dorsally with large, conical tubercles; tubercles in regular rows, smaller towards tip. In spirit, basically fawn (between Tilleul-Buff and Pale-Olive Buff of Ridgway, 1912) dorsally and cream (close to Ivory Yellow of Ridgway) ventrally darker, brownish (Close Brown of Ridgway) blotches irregularly over head, back and limbs. Tail bears six distinct creamish (Cartridge Buff of Ridgway) bands.

VARIATION IN PARATYPES

Variation is very slight. The flank tubercles in the four specimens of *P. caudiamulatus* are similar. The first row is very small, rounded at the base and

TABLE 1: DIMENSIONS OF PARATYPES OF *P. caudiamulatus*

Specimen	SVL	TL	T	HL	HW
J22286*	75.8	139.0	53.2	21.5	17.6
J22287†	76.5	122.6	46.1	21.5	17.1
J24132†	81.8	133.8	52.0	23.7	18.9
J25411*	84.8	145.0	60.0	23.4	18.0

*original tail †regenerated tail

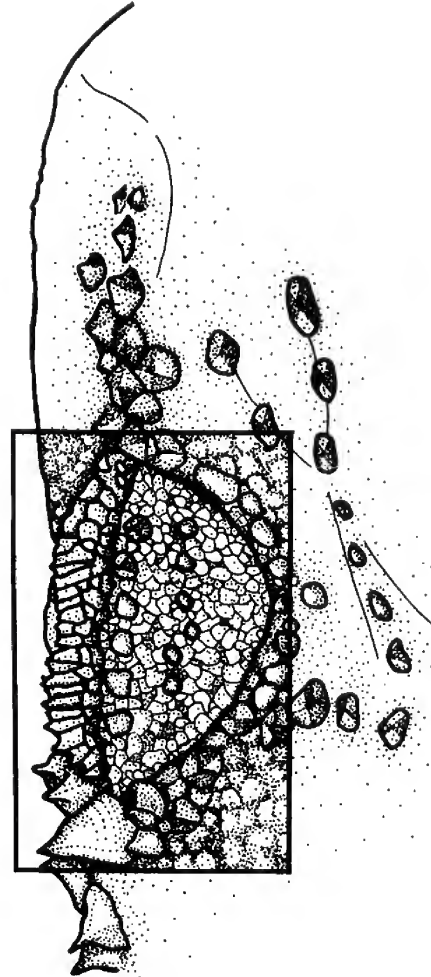


FIG. 2: *Phyllurus caudiamulatus* (J15619), showing two rows of tubercles on the eyelid.

*Since this paper went to press a large series of *Phyllurus* has been collected in the Eungella area by the Australian and Queensland Museums supported financially by the Australian Biological Resources Survey.

Although these specimens have slightly flared to distinctly leaf-shaped original and regenerated tails unlike *P. caudiamulatus* previously described, they resemble *P. caudiamulatus* in size, body proportions, colour pattern (including the presence of light bands on the tail), and spination. Like *P. caudiamulatus* previously described, specimens from Eungella without tails are difficult to distinguish from *P. platurus* although light tail bands are not present in any *P. platurus* examined and *P. caudiamulatus* and the Eungella specimens are generally more spinose than *P. platurus*.

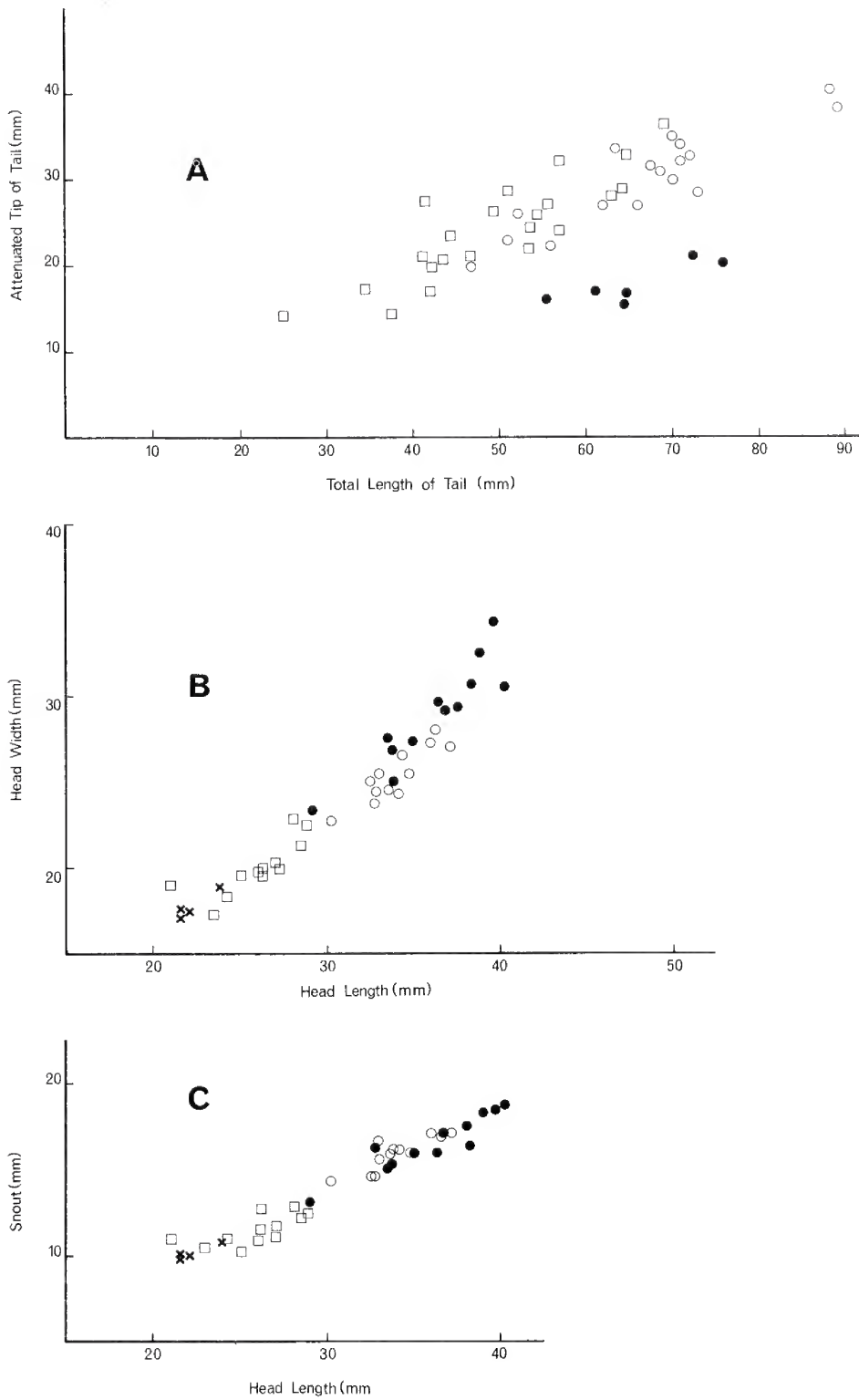


FIG. 3: Head and tail measurements in *Phyllurus* spp.
 ● *P. salebrosus*; ○ *P. cornutus*; □ *P. platurus*; X *P. caudiammulatus*

sharp. Dorsally they are larger and very spinose. Tubercles on the eyelids of all specimens are very small and are irregularly placed. On J22286 the dark blotches of the dorsum form distinct striations on the head, giving an impression of a slightly darker specimen. The tail bands on this specimen were white in life. The regenerated tails of J22287 and J24132 taper conventionally and are covered in small granules which form uniformly small tubercles dorsally and which are smooth ventrally. The regenerated tails lack the distinct light bands of the original tails of J15619 and J22286 but are marked with fine dark lines forming an irregular pattern. The original tail of J25411 is slightly expanded to form a 'leaf' and bears three white bands and one white blotch instead of the 5-6 distinct light bands of the tails of J15619 and J22286.

HABITAT, DISTRIBUTION

P. caudiannulatus is known only from closed forest in two localities in mid-eastern Queensland—Bulburin State Forest, via Many Peaks and Eungella National Park, via Mackay. The holotype (J15619) was collected during the day under the bark of a lichen-covered dead tree stump. Two of the paratypes (J22286-7) were collected at night on a dead tree. The third paratype (J24132) was found at night on the buttress of a live tree. J25411 is one of six specimens seen at night by spotlight approximately 12m above the ground on trees in the Broken River area of the Eungella National Park. *P. caudiannulatus* and *P. salebrosus* are sympatric in the Bulburin State Forest but apparently occupy different niches here. One specimen of *P. salebrosus* (J22288) collected at the same time and in the same place as two paratypes of *P. caudiannulatus* (J22286-7) was found on granite rocks close to the ground.

Phyllurus salebrosus sp. nov.

(Figs. 3, 4; Plates 36C, 37A, 38B, 39B, 40B)

MATERIAL EXAMINED

HOLOTYPE: Queensland Museum J8142, ♂ (with original tail), Monto, SE.Q.

PARATYPES: J2879, ♀ (with original tail), Roma, SC.Q.; J4474 ♀ (with original tail), Coongoola, SC.Q.; J4897, ♀ (with original tail) Coomoooolaroo, via Duinga, ME.Q.; J9770, ♂ (with original tail) Lowmead, ME.Q.; J5390, ♂, J6198, ♀ (with regenerated tails), Goodnight Scrub, Wallaville, SE.Q.; J8377, ♂ (with regenerated tails); Injune, SE.Q.; J22288, ♀ (with regenerated tail), Bulburin State Forest, via Many Peaks, ME.Q.; J6328, ♀ (tail missing), roof of cave, Cracow Creek, Cracow, ME.Q.

OTHER MATERIAL: AM Pt Lincoln [?], R5586; Sydney [?], R300. QM Goodnight Scrub, Wallaville J25360.

DIAGNOSIS

A large (the largest) *Phyllurus*, *P. salebrosus* is distinguished from all other species of *Phyllurus* by its extremely rough throat. Tubercles are present all over the chin, not only on the scales below the jaw bones as in *P. cornutus*, the species it resembles most. The original tail of *P. salebrosus* further distinguishes it from *P. cornutus* (attenuated tip of tail $> \frac{1}{3}$ total length of tail vs $< \frac{1}{3}$ total length of tail).

DESCRIPTION OF HOLOTYPE

SVL 139.1, TL 242.7, T 75.7, TT 20.1, HL 40.4, HW 30.6. Head large, depressed, triangular, very distinct from neck; skin of head almost confluent with cranium; ear opening elliptical, vertical, less than half as large as the eye. Body moderate. Limbs long; digits strong; subcylindrical at base, compressed distally. Head covered with small granules, intermixed with larger, rounded to conical tubercles; one and a half rows of tubercles on eyelid; labials $\frac{14}{13}$; body and limbs covered with small granules, intermixed with conical, almost spinose larger tubercles which are surrounded by smaller conical tubercles towards the sides. Chin, throat and ventral surfaces covered with flat granules intermixed with larger, but still small tubercles. Tail depressed, very broad, leaf-like, contracted at the base, attenuated at the tip; fringed with larger, hooked tubercles; very large conical tubercles in a cluster near contracted base of tail, irregularly towards fringes of leaf, and in eight regular rows over posterior one third of tail; ventral surface of tail smooth. In spirit, basically gray (between Pearl Gray and Light Gull Gray of Ridgway) dorsally and cream (close to Ivory Yellow of Ridgway) ventrally. Dorsally there is a series of brown (close to Burnt Umber of Ridgway) lines forming roughly shaped hexagons. The ventral surface is flecked with a lighter brown (close to Road's Brown of Ridgway) which forms a series of irregular transverse lines on the chin.

TABLE 2: DIMENSIONS OF PARATYPES OF *P. salebrosus*

Specimen	SVL	TL	T	TT	HL	HW
J2879*	119.0	183.8	64.5	16.6	34.5	27.4
J4474*	120.4	196.7	64.4	15.2	33.8	26.7
J4897*	93.5	167.2	55.3	16.0	29.1	23.4
J9770*	115.0	198.4	61.2	17.0	32.8	24.1
J5390†	133.0	187.2	47.8	—	36.7	29.1
J6198†	133.2	173.3	39.6	—	38.0	29.2
J8377†	125.4	194.0	47.6	—	35.0	27.4
J22288†	141.0	197.3	53.2	—	38.8	32.0
J6382 ‡	128.5	—	—	—	39.0	34.5

* original tail † regenerated tail ‡ tail missing

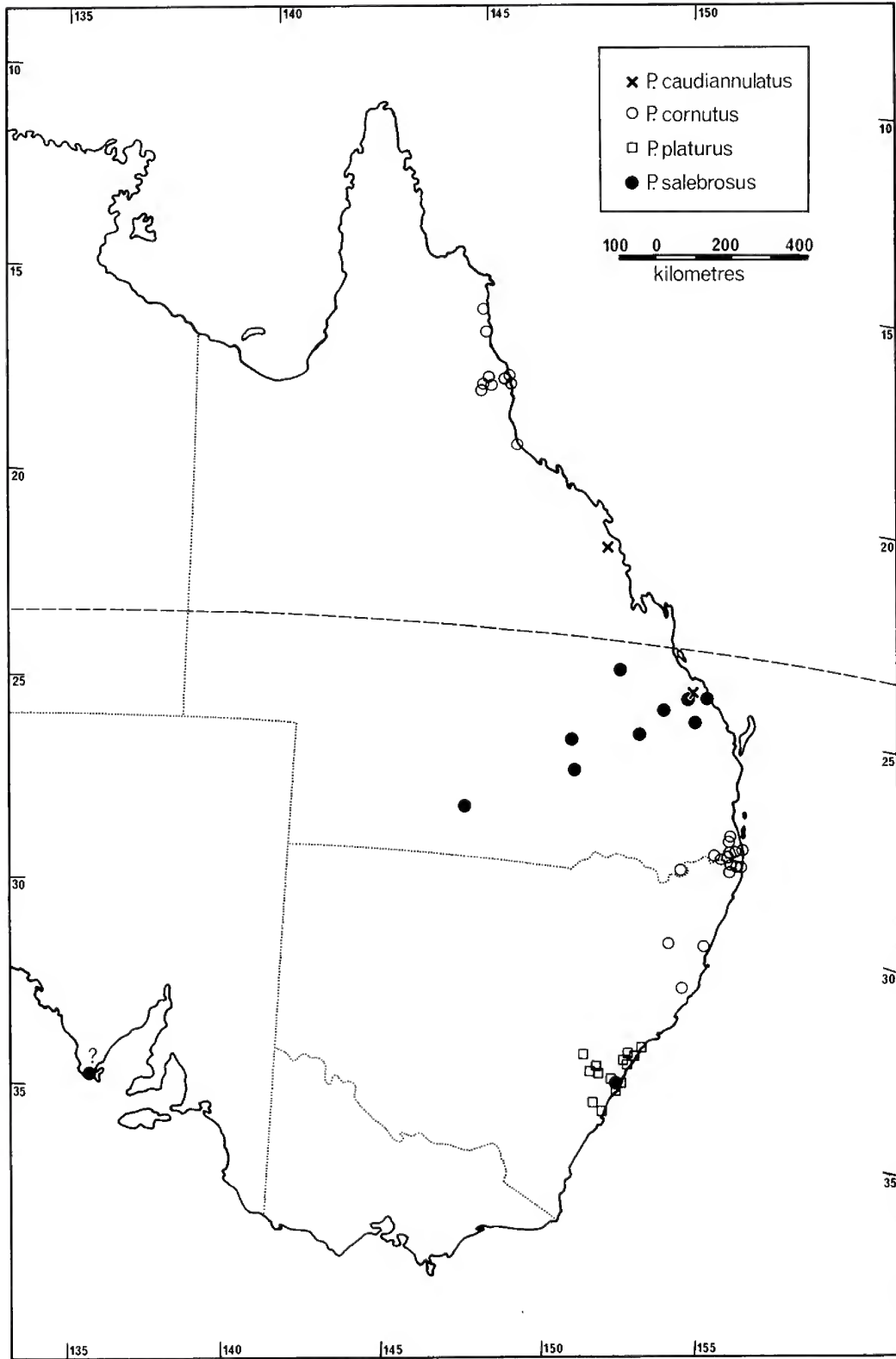


FIG. 4: Distribution of *Phyllurus* spp.

VARIATION OF PARATYPES

Variation is slight. Flank tubercles may be quite long, rounded at the base and surrounded by smaller tubercles (J4474, J6198) or smaller, narrow, and without smaller tubercles (J8377). The calcareous deposits in the throat may be large and well developed (J22288) or smaller and less obvious (J8377). There are two rows of tubercles on the eyelid in five specimens, one is present in two specimens (J22288, J9770), and in J4897 and J6198 there are one and a half rows. Rows of spines across tail in specimens with normal tails vary between 6 (J2879, J4897) and 9 (R5586). Four of the paratypes have regenerated tails, two of which are illustrated. These differ from the regenerated tails of *P. cornutus* in lacking the tip which is usually present in this species and gives the regenerated tail a true 'leaf' shape.

DISTRIBUTION

All *P. salebrosus* examined are from mid-eastern and south-central Queensland, with the exception of two specimens, R5586 (a completely faded specimen with original tail from Pt. Lincoln, S.A.) and R300 (a tailless specimen from Sydney). Although these could be reliable records of a species which is apparently uncommon wherever it occurs, these localities are 1200 and 900 km respectively from the nearest Queensland locality in which *P. salebrosus* is known, and there are no other records of this species outside Queensland.

Detailed collection data is available for only a few specimens of *P. salebrosus*. J6328 was collected from the roof of a cave adjoining Cracow Creek, Cracow, mid-eastern Queensland and J22288 was found at night on granite rocks in closed forest of the Bulburin State Forest, via Many Peaks, mid-eastern Queensland. With the exception of the Bulburin State Forest the localities from which this species has been collected are generally quite dry and rocky. Most are sandstone or granite areas. J22288 was collected at the same time and in the same place as two of the paratypes of *P. caudimaculatus* in the Bulburin State Forest, a moist area bounded on either side by drier granite ridges in which *P. salebrosus* has been collected (J8142, Monto and J9770, Lowmead). Three specimens (J5390, J6198, J25360) have been collected in the Good Night Scrub, near Wallaville, southeastern Queensland. The last, one of two specimens seen by spotlight in similar situations, was found eight metres above the ground on a Bottle Tree (*Brachychiton rupestris*). The Good Night Scrub where these specimens were found is an Araucarian Vine Thicket (Wcbb 1968, p. 308) on 'stony, light to medium clay with many quartzite fragments'

(Cannon *et. al.* 1962 p. 121). The only other specimen collected recently (held live in the collection of Mr T. Low) was found in Robinson Gorge, via Taroom, southeastern Queensland on the wall of a small open sandstone cave. The species is either uncommon or difficult to find in both areas.

ACKNOWLEDGMENTS

Mr A. Easton prepared the plates and Miss S. Hiley prepared the map. Mr T. Low, Mr J. James, Mr G. Monteith and Mr K. McDonald provided data on *Phyllurus* populations. Mr B. Campbell and Dr H. Cogger have given helpful advice and criticism throughout this work. Dr H. Cogger and Mr P. Rawlinson have provided data on type specimens and supplied obscure references. Mr J. Tracey and Mr E. Zillman supplied data on the Good Night Scrub.

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PLATE 36

Queensland species of *Phyllurus*.

- A. *Phyllurus cornutus* Girraween (released)
- B. *P. caudiamulatus* Bulburin State Forest (J22286)
- C. *P. salebrosus* Robinson Gorge (released)

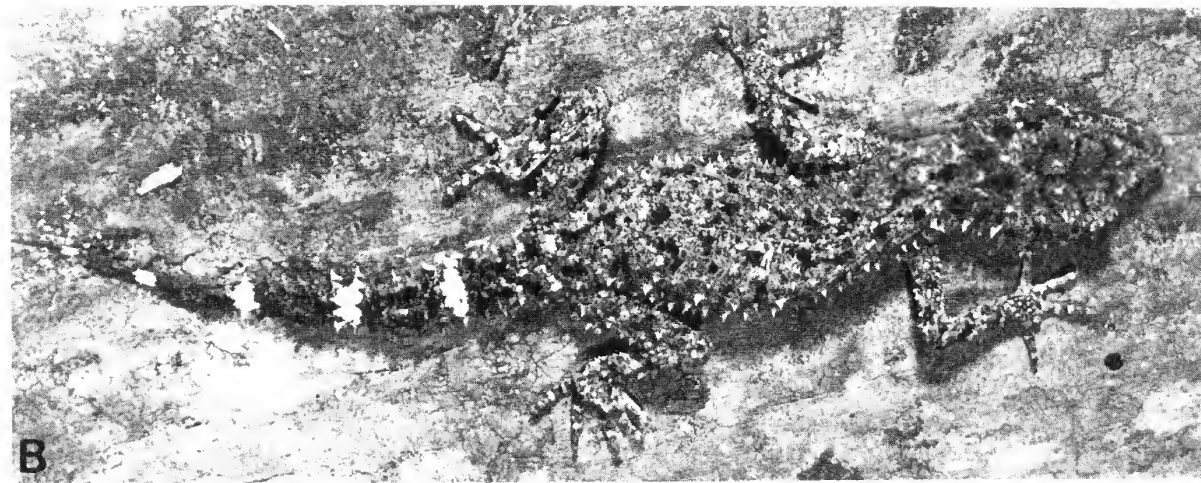
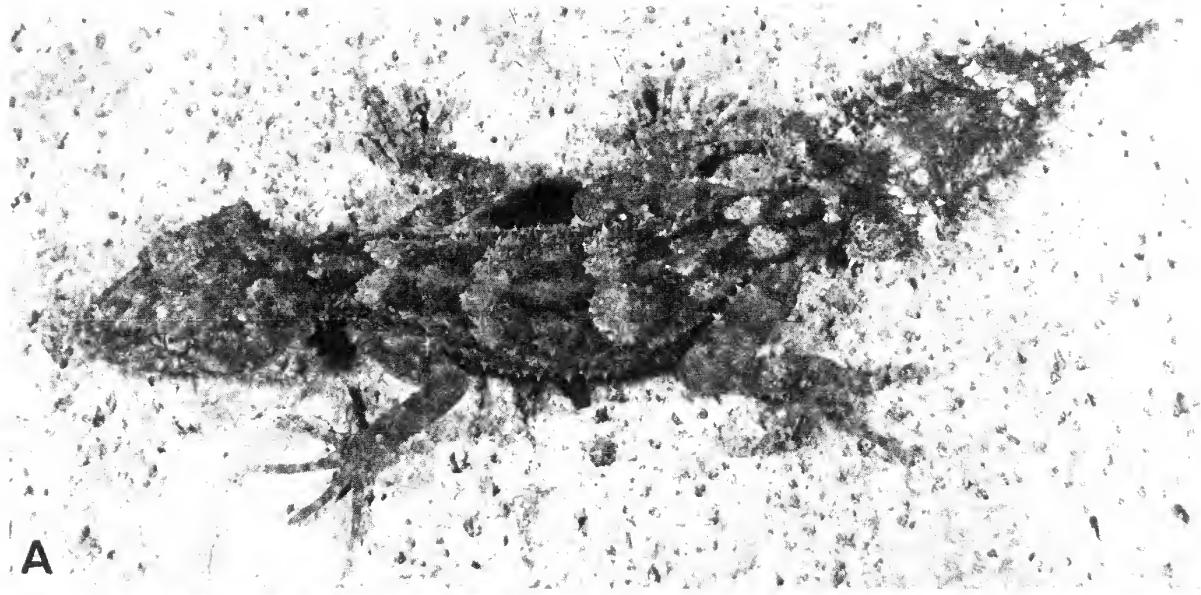


PLATE 37

Variation in flank tubercles of *Phyllurus* spp.

A. *Phyllurus salebrosus* J22288, J8377, J2879

B. *P. platurus* R10220, R10387

C. *P. caudiannulatus* J22287

D. *P. cornutus* R26119, R12935, R2126, R4769, R26118, J2934,
J5690, A233

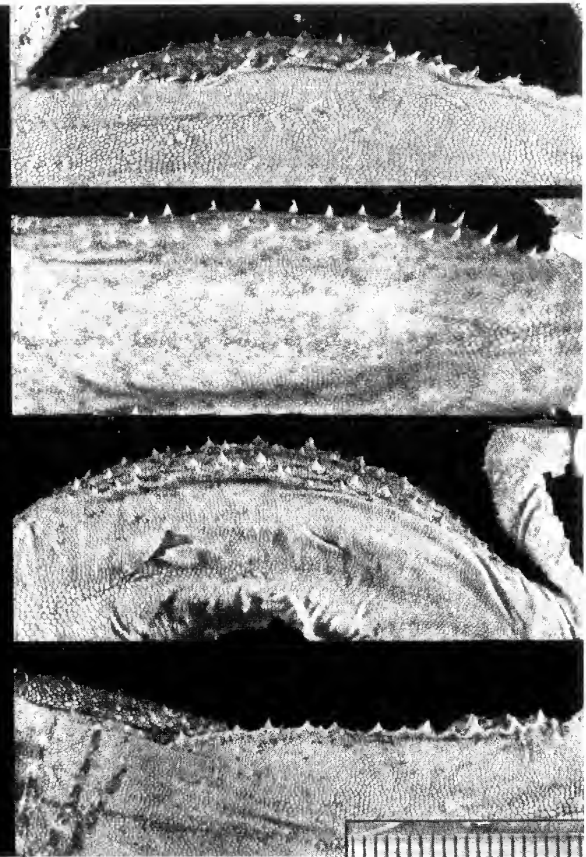
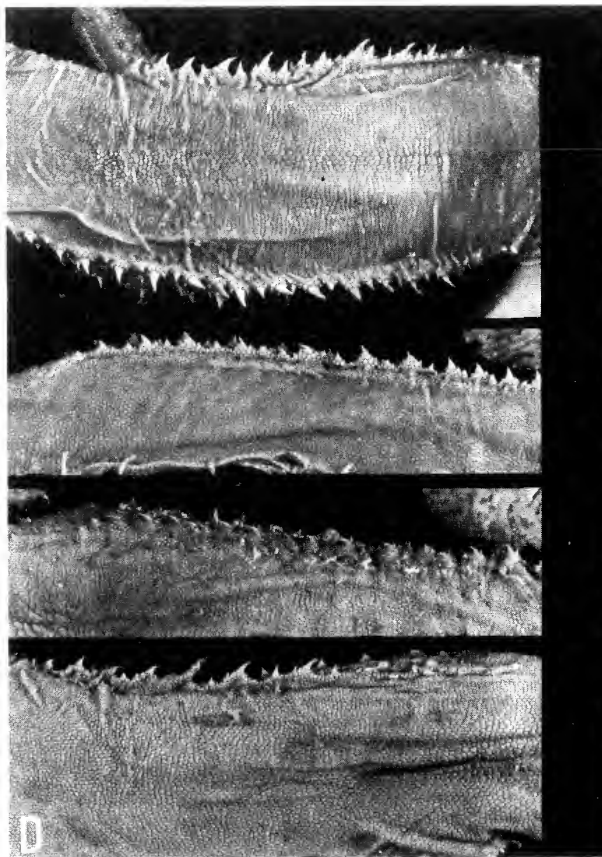
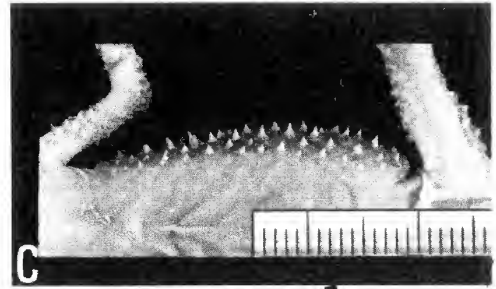
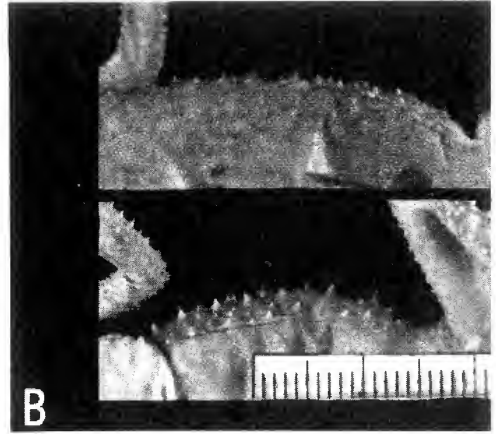
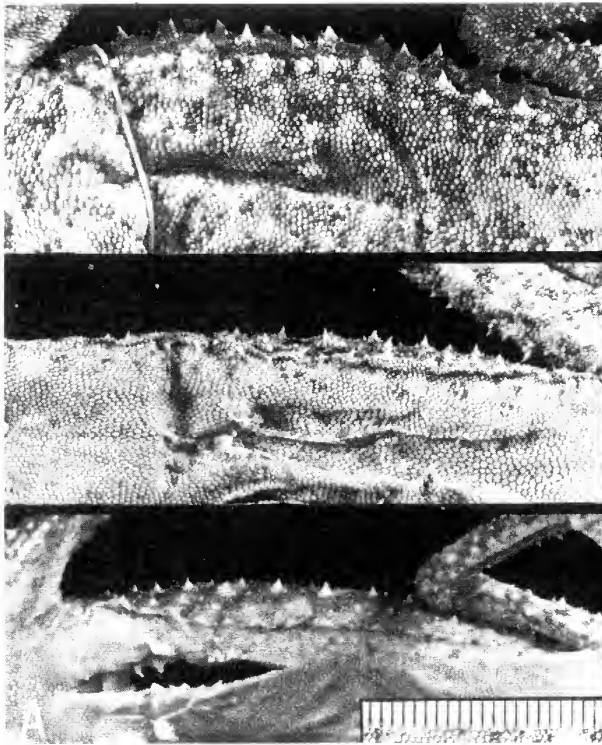


PLATE 38

Variation in original tails of *Phyllurus* spp.

- A. *Phyllurus caudiannulatus* J22286, J25411
- B. *P. salebrosus* J4474, J8142
- C. *P. platurus* R10387, R9274, R27324, R19084, R3793
- D. *P. cornutus* J8075, J8099, R12935, J8359

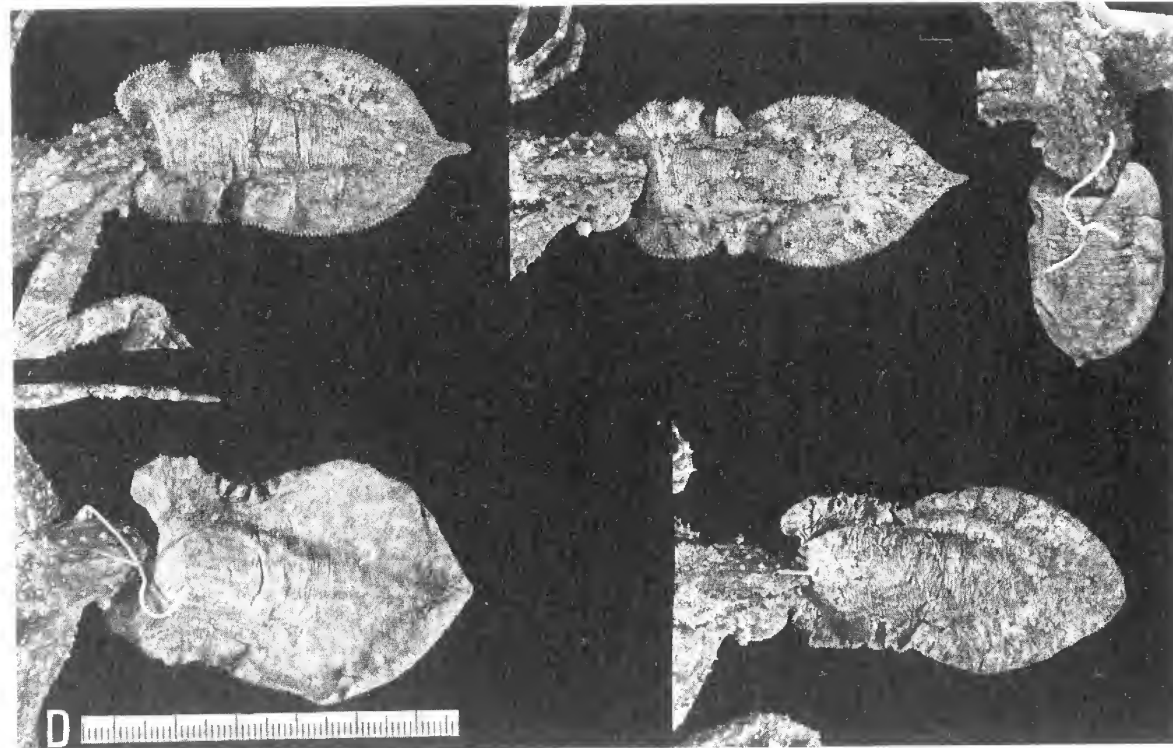
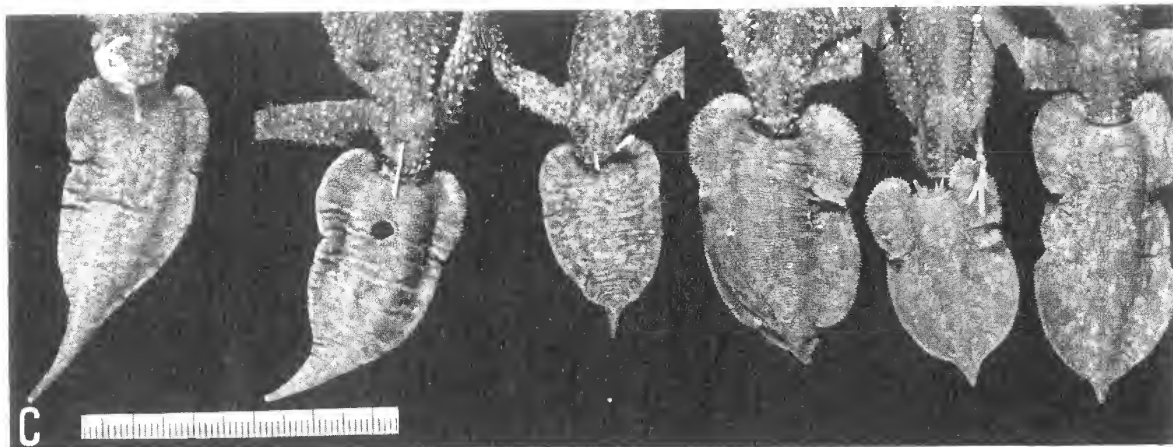
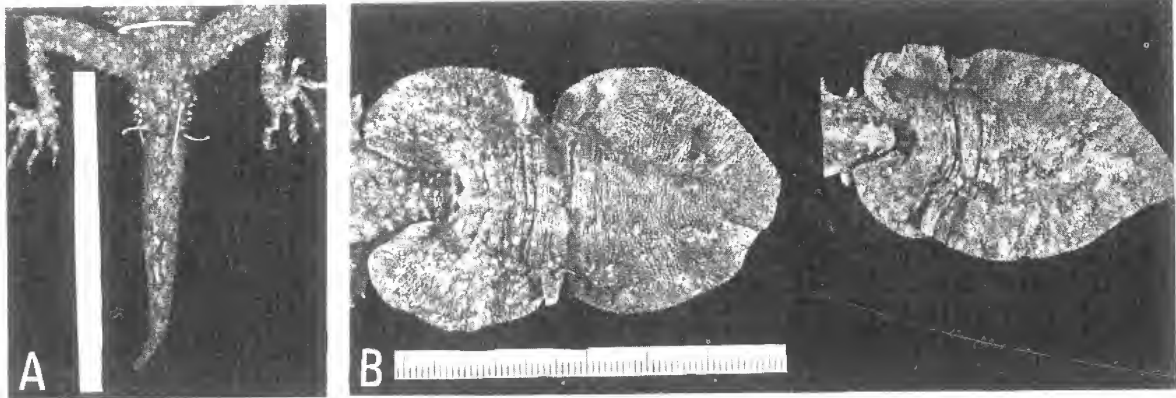


PLATE 39

Variation in regenerated tails of *Phyllurus* spp.

A. *Phyllurus caudiannulatus* J22287

B. *P. salebrosus* J22288, J8377

C. *P. platurus* R4814, R10220, R28308, R11621, R6284, R8253

D. *P. cornutus* J5690, R2409, A233, R4769, R26117

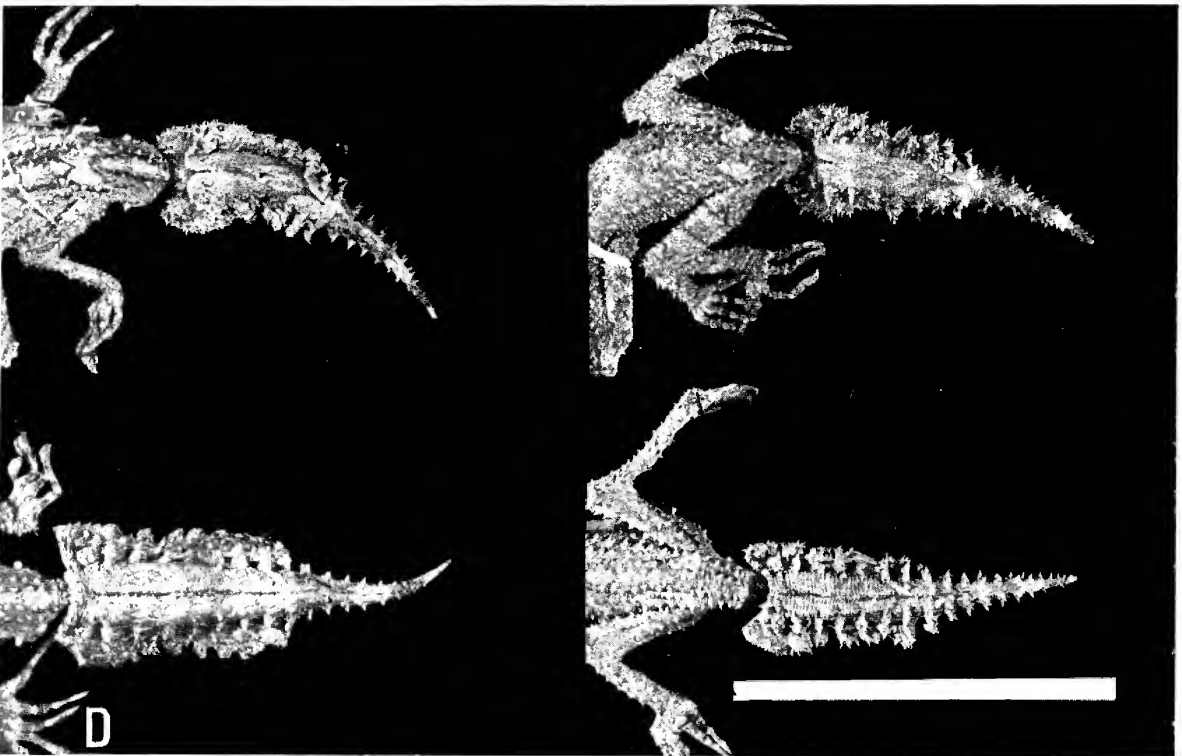
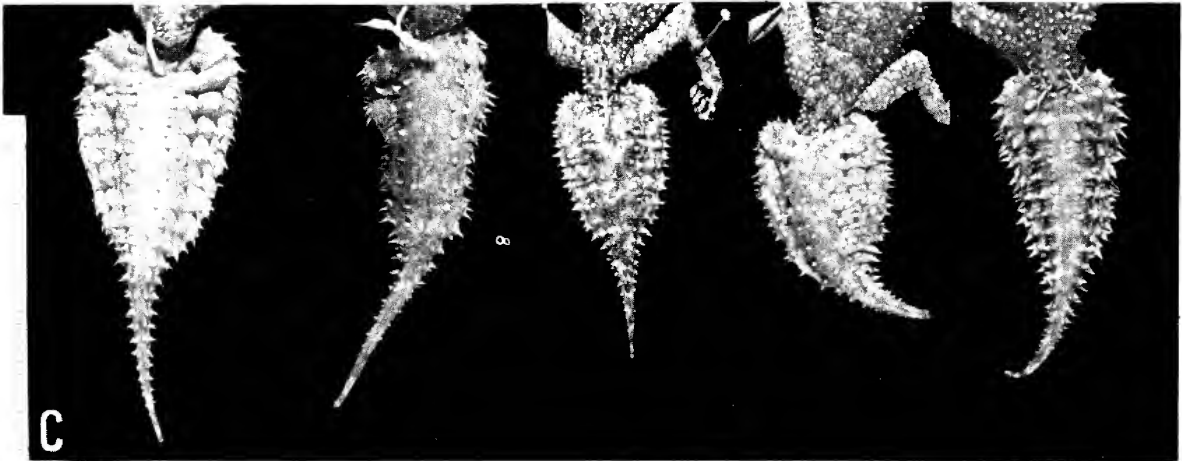
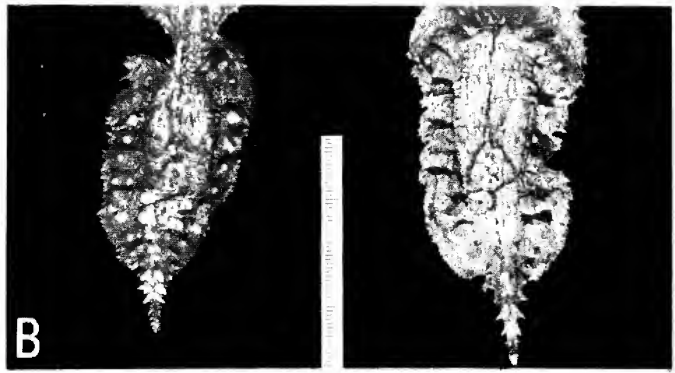
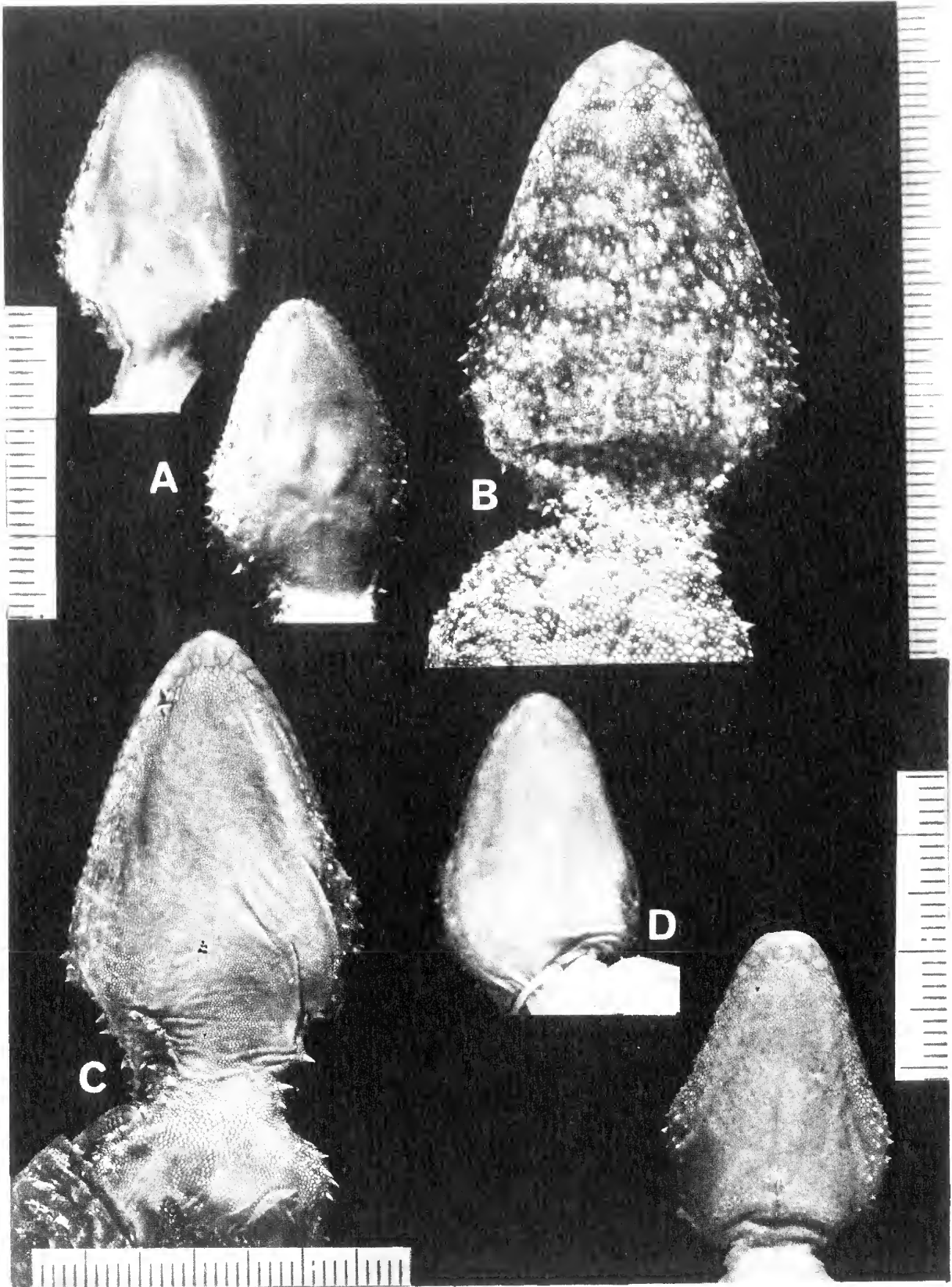


PLATE 40

Throats of *Phyllurus* spp.

- A. *Phyllurus caudiannulatus* J15619, J22286
- B. *P. salebrosus* J22288
- C. *P. cornutus* R11375
- D. *P. platurus* R4814, R28308





THE DISTRIBUTION OF THE CANE TOAD, *BUFO MARINUS*, IN AUSTRALIA AND ITS EFFECTS ON INDIGENOUS VERTEBRATES

J. COVACEVICH
and
M. ARCHER
Queensland Museum

ABSTRACT

Bufo marinus was released in cane growing districts of Bundaberg, Mackay, and northeastern Queensland in 1935 and 1936. At present this species occurs in eastern Queensland and northeastern N.S.W. between Coen and Ballina, across Cape York Peninsula south of Coen, and widely in northwestern Queensland. It is highly toxic to several native vertebrates and the results of mouthing or ingestion of *Bufo marinus* by thirty-three native species are summarised.

Bufo marinus occurs naturally in North and South America between southern Texas and central Argentina (Mungomery 1936, p. 72). It has been used as a biological control of insects, snails and rats (Honegger 1970, p. 453) and has been introduced to southern Florida and Louisiana, most islands of the Caribbean, Hawaii, and many western Pacific islands. A consignment of *Bufo marinus* from Hawaii was released in sugar cane growing districts of northeastern Queensland in June, 1935' . . . giving definite promise of yielding some permanent measure of relief in many of the (cane growing) areas stricken by 'white grubs' (larvae of the Grey back Beetle, *Dermolepida albobirtum* Waterhouse and the Frenchi Beetle, *Lepidiota frenchi* Blackburn) . . .' (Mungomery 1936, p. 63). In late 1935 the introduction of the species beyond the Cairns-Tully area, northeastern Queensland was banned briefly but *B. marinus* was soon released in other sugar cane growing districts between Mossman, northeastern Queensland and Isis, southeastern Queensland (Mungomery 1937, p. 12).

Although some local protests were made prior to the introduction of *Bufo marinus* into Australia, it was not until 1938 that doubts about the wisdom of this introduction were published. Kinghorn (1938, p. 411) suggested that ' . . . it would . . . have been wiser to postpone liberation of the toads until more searching inquiries . . . had been made.' Such caution was countered by other views and it was seriously suggested that *B. marinus* should be protected to enable it to adapt to its

new environment and control insects, especially pests to sugar cane, as planned. By 1941 it was apparent that the role *B. marinus* was playing in controlling Greyback and Frenchi Beetles in Queensland was a minor one. Greyback Beetles are only rarely in contact with the ground (and hence with *B. marinus*). Contact occurs when a few adults fall from trees after mating, or when females move into cane fields to oviposit. *B. marinus* does not frequent the cane fields at the time of the Frenchi Beetles flights owing to lack of cover in the fields.

In early 1974, following repeated press reports of the spread and potential danger of *Bufo marinus*, we decided to examine the distribution of this animal and some of its effects on the native fauna. Our own observations were supplemented with information gathered from associates, veterinarians, and the return of 2,500 circulars sent, with the cooperation of the Department of Education, to Primary Schools, Secondary Schools, and Primary Correspondence Schools. Other circulars were distributed through the National Parks Branch of the Forestry Department.

DISTRIBUTION

The present known distribution of *Bufo marinus* in Queensland and northeastern New South Wales is shown in Fig. 1. Circulars reporting the presence of *B. marinus* in particular areas were assessed with regard to the possibility of identity confusion with the native Giant Burrowing Frog, *Cyclorana aus-*

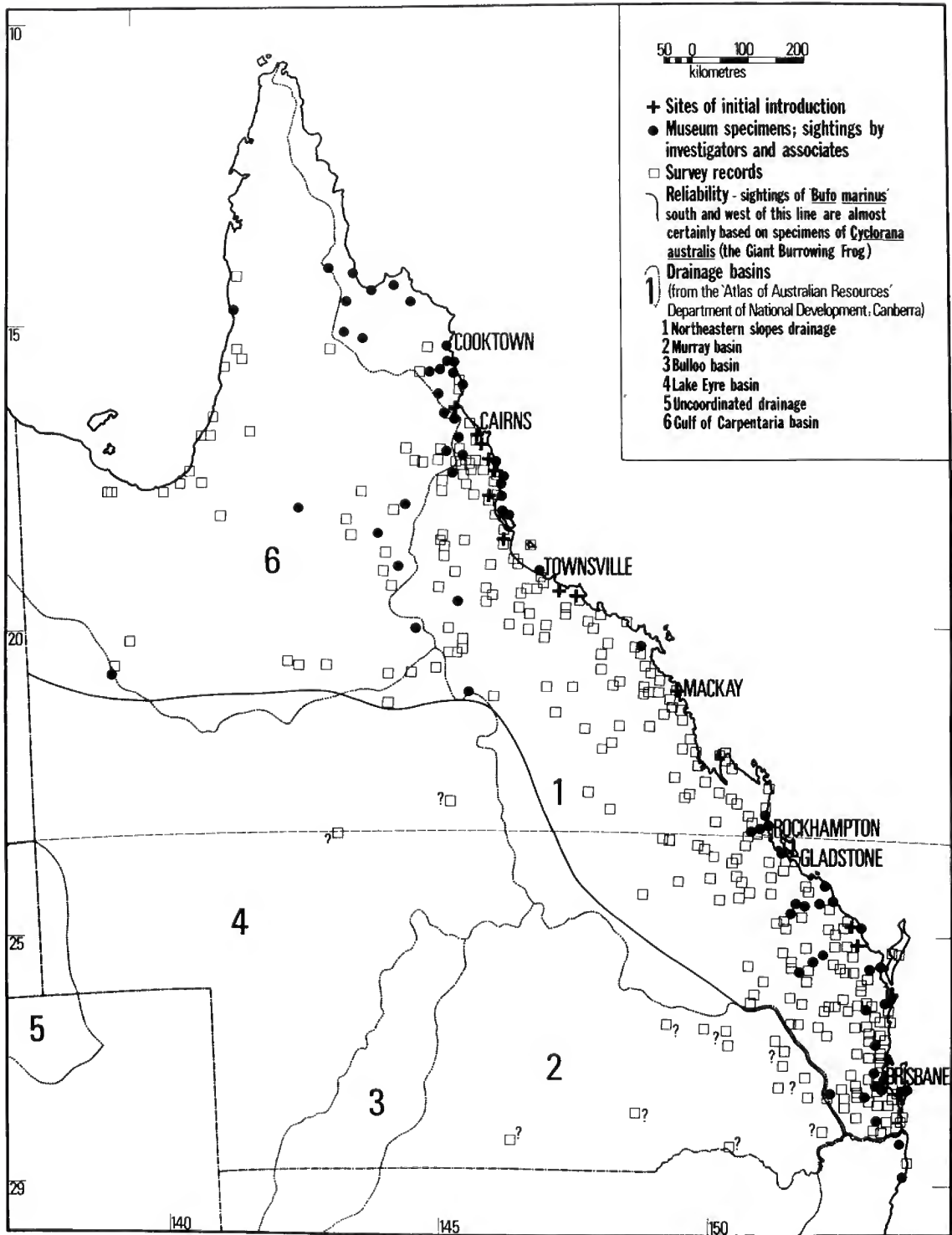


FIG. 1: Distribution of *Bufo marinus* in Queensland.

tralis, which is a large species known as a 'toad' in many western areas of Queensland. This assessment has resulted in the reliability line in Fig. 1. Without specimens to confirm extreme western reports of *Bufo marinus*, we assume these reports probably refer to *Cyclorana australis*. *Bufo marinus* and *Cyclorana australis* are compared in Plate 41.

Small numbers of the species have recently been released accidentally ('Time', August 5th, 1974) in the Northern Territory (Darwin) and in Western Australia (Perth). It is not yet known whether these unfortunate introductions will result in the establishment of *B. marinus* in these areas.

It is probable that the spread of *B. marinus* as shown in Fig. 1 was aided by accidental or deliberate transportation by humans. It was used by medical practitioners in pregnancy tests, and was believed to eradicate many species of insects and snakes. Many universities use these animals in large numbers, importing them into areas where they have not yet been established. Private collectors also maintain live *B. marinus* in many cities. Reports of deliberate introductions of *B. marinus* to Nambour SE. Q., Fraser Island SE. Q., and Normanton NW. Q. have been received although most correspondents could provide no information on how or when the species first appeared in their areas.

The precise factors controlling the spread of *B. marinus* are not understood. There can be no doubt, however, that temperature, water, food, and availability of shelter, especially during dry periods, are controlling factors. Straughan (1966, p. 230) reports that mating will not occur unless the water temperature reaches 25.6° C. There is no information about minimal water temperature requirements to enable *B. marinus* tadpoles to develop to the stage of metamorphosis but this normally occurs in water 25.6° C and above.

The success of *B. marinus* in establishing itself in Australia is attributable to its adaptability, resilience, high breeding potential, and relative freedom from predators. It has been found in every vegetation zone excluding very high altitude closed forests and extremely arid districts of the far west. Specimens have been observed recently in the following varied habitats—frontal dunes of ocean beaches (Mon Repos, via Bundaberg, SE. Q.; Walker Bay, via Cooktown, NE. Q.); the inland border of coastal mangroves (Amos Bay, via Cooktown); highly acidic areas of coastal wallum (Cooloola, SE. Q.); *Melaleuca* swamps (Cooktown, NE. Q.); open grassland (Marina Plains, near Princess Charlotte Bay, NE. Q.); open sclerophyll forest (Lily Creek, via Cooktown and Mt. Molloy, NE. Q.); highland closed forest (Mt.

Glorious, SE. Q. and Dawes range, ME. Q.); dry, sparse open plains adjoining Mitchell and Morland Rivers, N. Q.; wet or dry creek beds, and towns and cities between Cooktown, NE. Q. and Ballina, NE. N. S. W.

Almost any water is used by *B. marinus* for egg deposition and fertilization. Queensland Museum slide MF321 shows a pair in amplexus and a string of freshly laid eggs in the salt water of Rainbow Beach, Cooloola, SE. Q. No data is available on the survival potential of such eggs but eggs, tadpoles, and newly metamorphosed young have been observed on a tidal flat at Amos Bay, 30km S. of Cooktown (J.C. early 1973; January, 1974). Here water from heavy rain drains across the flat and accumulates in tyre tracks. The whole flat is regularly covered in salt water. *B. marinus* has apparently used the hot, shallow, slightly brackish pools to breed successfully in great numbers although adults have been seen only rarely in the surrounding area. Schultze-Westrum (1970, p. 37) has reported the ability of *B. marinus* in New Guinea to breed in brackish water and to survive water temperatures of 40° C in the larval stage. Straughan (1966, p. 230) notes that *B. marinus* will utilize '... any waterhole, transient pool, ditch, or sluggish creek backwater ...' irrespective of whether the water is clear or muddy, whether water weeds are present or absent, and whether the substrate is of sand, mud or rock. This remarkable adaptability as far as breeding sites is concerned contrasts sharply with the habits of many species of native frogs which are highly selective in their choice of breeding sites.

The high breeding rate of *B. marinus* has also assisted its spread in Queensland. J.H.B. (1936, p. 25) reported the production of 125,000 eggs by nine females in one morning and notes that females may breed more than once in a season. At Barrett's Lagoon 8 km west of Cooktown, NE. Q., at the height of the breeding season in 1970, the shallow edges of the lagoon appeared to be 'alive' with pairs of *B. marinus* in amplexus for several successive nights. Many of the millions of eggs produced in such permanent water presumably develop, metamorphose, and grow to adulthood because they have few predators. In some areas (e.g. Endeavour R., Cooktown, NE. Q.) teeming thousands of newly metamorphosed *B. marinus* have been observed leaving the water and gradually moving into the shelter of grass or flood debris on the banks.

Similarly, its catholic choice of shelter sites indicates that this requirement for establishment is only a minor one. We have seen or collected *B. marinus* from shallow depressions, in logs, drain

pipes, debris, hollows at ends of well constructed burrows (greater than 25cm deep) in soft stony and clayey soils, under cement slabs, rocks, and sheets of roofing iron. Presumably by using these shelters they are able to survive prolonged hot and dry periods in areas of relatively low rainfall (e.g. Laura, Charters Towers, and Mt. Garnet). The remarkable endurance of *B. marinus* to extremes of temperature is demonstrated by individuals which were observed moving slowly away from a bushfire, having survived massive burning (D. Crossman, pers. comm.).

B. marinus also exhibits catholic food habits. Several studies have shown that the major part of the diet of *B. marinus* in Queensland is insects, largely beetles (Mungomery 1936, pp. 63-74; Straughan 1966, p. 322; van Tets and Vestjens 1973, p. 52) but survey circulars indicate that small snakes of several species (including *Amphiesma mairii*), lizards, and frogs are also eaten and recently a small marsupial (*Planigale maculata*) was found in the gut of a toad collected near Samford, SE.Q. (C. Limpus, pers. comm.). These tastes, which include its only known common predator (*Amphiesma mairii*), ensure a food supply for *B. marinus* in any Australian habitat where cold or extreme aridity do not prevent its survival.

Another adaptation facilitating the spread of *B. marinus* is its relative freedom from predation. With the possible exception of the freshwater Snake (*Amphiesma mairii*), which has been reported as eating young *B. marinus* regularly (Lyon 1973, p. 4) and observed eating tadpoles, *B. marinus* has no major predators in Australia. It is a highly toxic species (Meyer and Linde 1971, p. 522). The bulk of the venom is contained in the parotid glands and the skin but much of the remainder of the animal is also apparently toxic to Australian vertebrates.

EFFECTS ON ENDEMIC VERTEBRATES

The effect *B. marinus* has had on endemic vertebrates since its introduction forty years ago cannot be assessed in detail from the data presented here and may never be completely known because little information is available on species populations before 1935 and because so many other possibly detrimental changes have taken place in the environment since *B. marinus* was introduced. Schultze-Westrum (1970, p. 37) in reviewing the effects of *B. marinus* on native New Guinean vertebrates has examined its detrimental effects in terms of (1) predation, (2) food competition, (3) competition for resting places.

Many of the reports of predation upon toads are

inconclusive because the subsequent fate of the predator was not or could not be determined. In the case noted of the Western Native Cat (*Dasyurus geoffroii*), death was not immediate, and it is conceivable that such a predator could be seen to attack a toad, and leave without apparent upset. There is no substantiated evidence that any endemic mammal can prey successfully upon *B. marinus*. We regard *B. marinus* as a potential threat to the existence of some terrestrial endemic predators such as frog-eating snakes and native cats (*Dasyurus* spp.) with which it is sympatric. One of us (M.A.) kept a Western Native Cat (*Dasyurus geoffroii*) in captivity for three years. During this time it was never observed to hesitate in attacking any small vertebrate. Although it often exhibited caution in the method of killing these prey, it never hesitated to bite. It was the result of a single bite (an accidental encounter) on an individual *B. marinus* that caused its death. We have no reason to believe that other individuals of *Dasyurus* spp. would behave any differently if confronted by a toad. It is of interest to note that the only recent undoubted reports of the common occurrence of *D. viverrinus* and *D. maculatus* coming to the attention of the Queensland Museum are from areas where toads are known not to occur (e.g. the Lamington Plateau and the Wyberba district near Stanthorpe).

Predation by toads on some native vertebrates is noted above. The instance of a whole *Planigale maculata* being found in the stomach of a *B. marinus* is not a positive indication of predation. The toad may conceivably have found the animal dead. However, considering that *B. marinus* normally (we have no evidence to the contrary) eats live prey, this record strongly suggests predation.

Competition involving toads concerns food and living space. It is now common, when searching for reptiles and small mammals in some areas of eastern Queensland, to find only *B. marinus*, sometimes in groups, in niches occupied by small native vertebrates in adjoining toad-free areas. *B. marinus* is probably the most common small vertebrate in eastern Queensland and apparently survives where native vertebrates cannot. In late 1973 a search for reptiles on a small island in the partly constructed North Pine Dam near Petrie, southeastern Queensland, was unsuccessful. With the exception of a single *Litoria fallax* there were no native vertebrates on the island. Every log and grass-shaded depression housed numerous adult and young *B. marinus* all of which appeared to be in excellent condition. Competition for and domination of breeding grounds have probably been instrumental in reducing populations of some native frogs along with

clearing of habitats. Reports of the disappearance of certain species of frogs (*Limnodynastes peroni*) and snakes (*Pseudechis porphyriacus*, *Acanthophis antarcticus*, and *Pseudonaja textilis*) following the arrival of *B. marinus* in several areas are too numerous to be ignored although it is impossible to prove *B. marinus* responsible.

EFFECTS OF MOUTHING OR INGESTING *B. marinus**Kuhlia rupestris* (Jungle Perch)

Ingesting; no ill effects. (Remains of *B. marinus* found in gut; observed feeding, Daintree R., NE.Q.—J. Grimes, pers. comm.)

'Jew (= Cat) Fish'*

Ingesting eggs, young; no ill effects.

'Eel' (probably *Anguilla* sp.)*

Ingesting eggs, young; no ill effects. (Populations reported to have been affected adversely initially.)

'Perch'*

Ingesting eggs, young; no ill effects.

Chelodina sp. (Long-necked Tortoise)

Ingesting; no ill effects. (Specimen observed feeding on dead *B. marinus*, Gunn et al. 1972, p. 110.)

Egeria bunganana (Land Mullet)

Mouthing; death. (*B. marinus* entered cage and was apparently bitten on hind leg—R. Latcham, pers. comm.)

Varanus spp. (Goannas)

Ingesting whole; death. (*Varanus* populations reported repeatedly to have declined in numbers. Captive specimen died within a few minutes—P. Douglas, pers. comm.)

Crocodylus porosus (Estuarine Crocodile)

Mouthing whole; no ill effects. (One 2m wild specimen found near Edward R., NW.Q. with *B. marinus* in mouth; *B. marinus* released when specimen captured—J. Bredl, pers. comm.)

Ingesting whole; no ill effects. (Hungry captive specimens have eaten many *B. marinus* reluctantly on several occasions; well-fed specimens refused them—C. Tanner, pers. comm.)

'Carpet Snake' (probably *Morelia spilotes variegata*)*

Ingesting whole; effects not reported. (Reported frequently, but doubtful because *M. spilotes variegata* is normally a mammal and bird eater.)

'Black-headed Python' (probably *Aspidites melanocephalus*)*

Ingesting whole; effects not reported. (Doubtful, normally a reptile and mammal eater.)

Stegonotus cucullatus (Slatey Grey Snake)

Mouthing whole; death. (One specimen found dead with *B. marinus* only partly ingested, near Cairns, NE.Q.—C. Tanner, pers. comm.)

Anphiesma mairii (Common Keelback)

Ingesting eggs, tadpoles, young; no ill effects. (Lyon 1973, p. 4. *A. mairii* thrives in captivity on diet of *B. marinus*—C. Tanner, pers. comm. Only species known to utilize *B. marinus* regularly as food source.)

'Green Grass Snake' (probably Green Tree Snake, *Dendrelaphis punctulatus*)

Ingesting tadpoles, young; no ill effects. (Captive specimen—R. Latcham, pers. comm.)

Boiga irregularis (Brown Tree Snake)

Ingesting whole, whole minus skin; death. (Two adult specimens were force-fed on *B. marinus* minced whole and minus skin; both died overnight—C. Tanner, pers. comm.)

Pseudechis porphyriacus (Red-bellied Black Snake)

Ingesting whole; death. (Populations reported repeatedly to have declined in several areas since arrival of *B. marinus*; Covacevich, 1974, p. 23.)

Acanthophis antarcticus (Death Adder)

Mouthing; death.

Ingesting; death. (Two adults found dead with *B. marinus* partly ingested, Deighton R., NE.Q.—F. Woolston, pers. comm. Populations reported to have declined since arrival of *B. marinus*; Shipton's Flat, via Cooktown, NE.Q.—J. Roberts, pers. comm.; Mt. Molloy, NE.Q.—F. Little, pers. comm.)

Pseudonaja textilis (Brown Snake)

Ingesting; death. (Dead adult found in Bauple State Forest, SE.Q., with *B. marinus* in gut.—D. Crossman, pers. comm. Young *P. textilis* from McIvor R., NE.Q. refused young *B. marinus* in captivity. Populations reported to have declined in some areas following arrival of *B. marinus*. McIvor R., NE.Q.—C. Tanner pers. comm.)

Notechis scutatus (Tiger Snake)

Mouthing; death.

Ingesting; death. (J24594 captive juvenile, died suddenly with *B. marinus* only partly ingested. Clutch of approximately 30 captive young were fed young *B. marinus*; all died overnight, some with 2 *B. marinus* in gut but most with only 1 partly ingested—C. Tanner, pers. comm.)

'Ducks'*

Ingesting young; no ill effects. (Domestic ducks not affected according to survey reports and fowls reported with no ill effects following ingestion. No indication of whether ducks are native or domestic.)

'Ibis'*

Ingesting intestine only; no ill effects.

'Crane'*

Ingesting; no effects reported.

'Swamp Hen'*

Ingesting tongue only; no ill-effects.

'Pheasant'*

Ingesting young; no ill effects.

Corvus sp. (Crow)

Mouthing; death.

Ingesting stomach, tongue, old road killed specimens; no ill effects. Frauca, 1974, p. 112-4. (Pet *Corvus* sp. died suddenly after pecking *B. marinus*—R. Latcham, pers. comm. Two circulars report the eating of *B. marinus* tongues and stomachs; many report pecking at old road-kills.)

Dacelo gigas (Kookaburra)

Mouthing; death.

Ingesting freshly killed young adults; no im-

mediate ill effects. (O15549, *D. gigas* with *B. marinus* in mouth found dead with no apparent injuries on roadside, Woodgate State Forest, SE.Q. Young freshly killed adult *B. marinus* consumed readily by *D. gigas* at Mt. Nebo, SE.Q.—F. Dale, pers. comm.)

'Owl'*

Ingesting tongue only; no ill effects.

Podargus strigoides (Tawny Frogmouth)

Ingesting; no ill effects. (Filmer 1974, p. 2).

'Kite Hawk'*

Ingesting; no ill effects. (Observed following tractor and eating disturbed *B. marinus*.)

'Whistling Kite'*

Ingesting gut only; no ill effects.

Koel

Ingesting gut only; no ill effects. (Cassels 1970, p. 16).

Hydromys chrysogaster (Water Rat)

Ingesting possibly stomachs only; no ill effects. (Carcasses of *B. marinus* minus stomachs have been found in several areas along river banks. *H. chrysogaster* believed to be predator along Endeavour R., NE.Q.—C. Tanner, pers. comm.; many survey reports.)

Dasyurus geoffroyi (Western Native Cat)

Mouthing; death. (Captive individual observed to bite *B. marinus* and drop it. Panting, rapid pulse, tetanic contractions, convulsions, and death in 30 minutes.)

Sarcophilus harrisi (Tasmanian Devil)

Mouthing; death. (Captive specimen—P. Douglas, pers. comm.)

*Reported only in survey circulars.

DISCUSSION

B. marinus has not eradicated the pests it was introduced to control; it is still actively spreading in Australia, and it is not clear what limiting factors will eventually control this spread. It has a deleterious effect on some native vertebrate fauna, which may result in the regional extinction of native terrestrial predators, although several species can apparently ingest *B. marinus* or its remains without ill effects.

At present there is no effective biological control of the species here despite the fact that the snake *Amphiesma mairii* regularly consumes *B. marinus* larvae and young and is common in many of the areas supporting *B. marinus*. Prolonged cold temperatures and frost and, to a lesser extent, dryness may restrict its spread much further into inland Queensland and southern New South Wales. While *B. marinus* has thrived in all the areas to which it has been introduced, there are no records of successful large scale eradications.

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PLATE 41

FIG. A: *Bufo marinus* (Brisbane)

FIG. B: *Cyclorana australis* (Cooktown)





THE WOLF SPIDERS OF AUSTRALIA (ARANEAE: LYCOSIDAE): 5.
TWO NEW SPECIES OF THE BICOLOR GROUP

R. J. MCKAY
Queensland Museum

ABSTRACT

Two new species *Lycosa snelli* and *Lycosa duracki* from north Western Australia are added to the bicolor group of Australian Wolf Spiders.

McKay (1973) defined the 'bicolor group' of lycosid spiders as being similar in coloration, form of epigynum, and internal genitalia. Two new species found on open gravel areas in the Pilbara and Kimberley regions of Western Australia are described and are placed in the bicolor group of species. The concept of this species group was originally morphological in nature, but the species are also characterised by a number of behavioural and ecological parameters. An expanded definition of the bicolor group can be given:

1. The carapace is uniformly coloured and lacks median or lateral stripes.
2. All species are robust with heavy legs and well developed eyes.
3. The female epigynum and internal genitalia are similar in morphology in all species (McKay 1973, figs. 2, 3).
4. Capture of prey is made at the burrow entrance and females rarely if ever leave the immediate vicinity of the burrow; the characteristic positions are: straddling above, straddling to one side with a leg in contact, or draping over the mouth of the burrow. All species rapidly retreat into the burrow when disturbed, and appear highly sensitive to ground vibrations or movement.
5. The burrow is usually vertical with an open entrance flush with the soil surface; more rarely closed with a pebble, a silk and sand-grain lid, or a well constructed hinged door.
6. The habitat is always open, largely un-vegetated areas, with compact soils, usually in arid or semi-arid regions.

In most details these spiders agree well with the American species of the genus *Geolycosa*. Their behaviour is remarkably similar (see Kaston 1948,

p. 316). All the American species lack dorsal spines on tibia 4 of females, this is considered by most authors to be important in the diagnosis of the genus *Geolycosa*. 1 + 1 dorsal spines are present on tibia 4 of females of Australian species as on the males of Australian and American *Geolycosa*, so the generic significance of such spines is open to doubt. The genus *Geolycosa* can be defined by using behavioural data, but not yet in a completely satisfactory manner by using morphological characters. A redefinition of the genus *Geolycosa* is considered to be premature at this stage of our knowledge of the Australian Lycosinae.

The male palpal organs of *Lycosa snelli* and *Lycosa duracki* have been figured but the structure of the palpal organs of other members of the bicolor group is unknown. I have placed these new species in the older genus *Lycosa* pending a generic revision of the Australian lycosid spiders.

***Lycosa snelli* sp. nov.**

(Figs. 1 a-g)

MATERIAL EXAMINED

HOLOTYPE: Western Australian Museum, WAM 69-797, ♀ M, C.L. 12.0 mm, Towera Station, north of Lyndon River, W.A., collected by Mr A. Snell, January, 1952. In spirit.

PARATYPES: Western Australia; Barradale 18 km south, 29.v.1972, RJM, 1 ♀ P, 1 ♂ P, QM W4021; Barrow Island, 18.vi.1964, HB, 1 ♀ M, WAM 71-1716, 20.ii.1969, A. R. Main, 2 ♂ M, WAM 74-498-9; Carnarvon 14.5 km north, 22.v.1969, JG, 1 ♀ M, WAM 69-1035; Lyndon Station, i.1952, A. Snell, 1 ♀ P 1J, WAM 69-798-9, vii.1951, A. Snell, 1 ♀ M 2 ♀ P, WAM 69-803-5; Manberry 11 km towards Wandagee, 9.iv.1969, G. W. Kendrick, T. A. Darragh, 1 ♀ P 11J, WAM 73-117-28; Mardie Station, 23.v.1962, W. D. L. Ride, 1 ♀ P, WAM 71-1718; Marilla Station, 29.v.1972, RJM, 1 ♀ P 1 ♂ P

3J, QM W4022; near Marilla Station turnoff, 4.ii.1970, JG, RH, 1 ♀ M 1J, WAM 70-163-4; Yannarie River, 13.xi.1953, A. R. Main, 1 ♀ M, WAM 71-1717, 13.v.1952, RJM, JG, 1 ♀ M 2 ♂ P, QM W4023.

DESCRIPTION: (Based on the holotype)

Carapace fawn to buff without lateral or median stripes, but becoming light brown with slightly darker brown stripes radiating from the fovea after preservation in alcohol; face brown with fawn hair; paturon dark brown with the anterior surface fawn or buff; lateral condyle orange-red; fangs dark brown; labium and maxillae brown; sternum light brown. Abdomen fawn to buff with vague slightly darker lanceolate stripe reaching almost to the mid-length of the dorsal surface, and becoming more conspicuous after preservation; ventral surface fawn to buff with a darker brown transverse crossbar behind the epigynum; spinnerets fawn. Legs with coxae buff above, darker below, remainder of legs buff to light brown, the joints slightly darker, spines dark brown; palpi buff.

TABLE 1: MEASUREMENTS OF LEG SEGMENTS OF HOLOTYPE OF *L. snelli* IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	8.5	4.3	5.9	6.2	3.2
2	7.7	4.3	5.5	6.2	3.2
3	6.9	4.0	4.8	6.7	3.2
4	8.8	4.3	7.2	8.0	4.0
Palp	4.5	2.3	2.6	—	3.3

Anterior row of eyes with the upper tangent procurved, AM larger than AL, PM very large and protruding, more than twice the diameter of the AM and about half their diameter apart, the AL are situated close to the PM, PL eyes about twice the diameter of the AM. Ratio of eyes AM:AL:PM:PL = 17:11:42:38; distance AM:AM 6, AM:AL 5, AM:PM 4, AL:PM 3, PM:PM 26.

Ocular quadrangle 103 × 118. Clypeus to AM 8. PM to PL 32. Width of the first row of eyes 71; width of second row 104.

Chelicerae with three promarginal teeth, the middle one largest; three retromarginal teeth of equal size (all specimens examined). Labium slightly longer than broad.

VARIATION: Juveniles are orange-buff to sandy brown and resemble the adults in coloration. On dark red substrates the adults may become dark orange-buff to pale brown, sometimes with a faint golden tinge. The brown cross-bar behind the epigynum is sometimes lacking in juveniles, may be almost absent in some adults, or may be a well defined black bar.

The eye measurements of 10 specimens are expressed as a percent of the total width of the first eye row in Table 2.

Variation in the shape of the epigynum is shown in Fig. 1c, g, the male palpal organ in Fig. 1b, and the internal genitalia of a female in Fig. 1e.

SIZE RANGE: Mature females 11.1 to 12.0 mm.

DIAGNOSIS: *Lycosa snelli* differs from all other Australian species of the genus *Lycosa* in having the following combination of characters: no median or lateral stripes on the carapace; venter of abdomen fawn or light brown with a dark transverse bar usually situated behind the epigynum in females, and present or absent in males; large protruding PM eyes; epigynum with the anterior part of the median guide expanded; male palp with a long tapered embolic guide.

LIFE HISTORY

Mature females may be collected throughout the year, but appear to be most abundant during the late summer months. Two mature males were collected at Barrow Island in February. Juvenile specimens are common during April and May, and

TABLE 2: EYE DIAMETERS AND INTERSPACES OF *Lycosa snelli* CONVERTED TO PERCENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM
Holotype	♀M	12.0	24	15	59	53	8	7	37	6
WAM 69.798	♀P	11.2	23	14	63	55	9	9	35	5
WAM 69.799	♀J	9.0	21	14	60	50	10	10	34	5
WAM 71.1716	♀M	11.5	22	15	60	53	8	8	33	7
WAM 71.1717	♀M	11.1	23	13	61	50	11	9	33	7
QM W4022	♂P	11.5	23	15	60	52	9	9	36	6
QM W4022	♀J	8.3	22	13	60	53	9	7	31	8
QM W4022	♀P	11.3	22	15	59	51	10	9	32	6
QM W4021	♀P	11.7	23	14	61	54	9	11	36	8
QM W4021	♂P	10.0	22	13	60	55	12	8	32	3

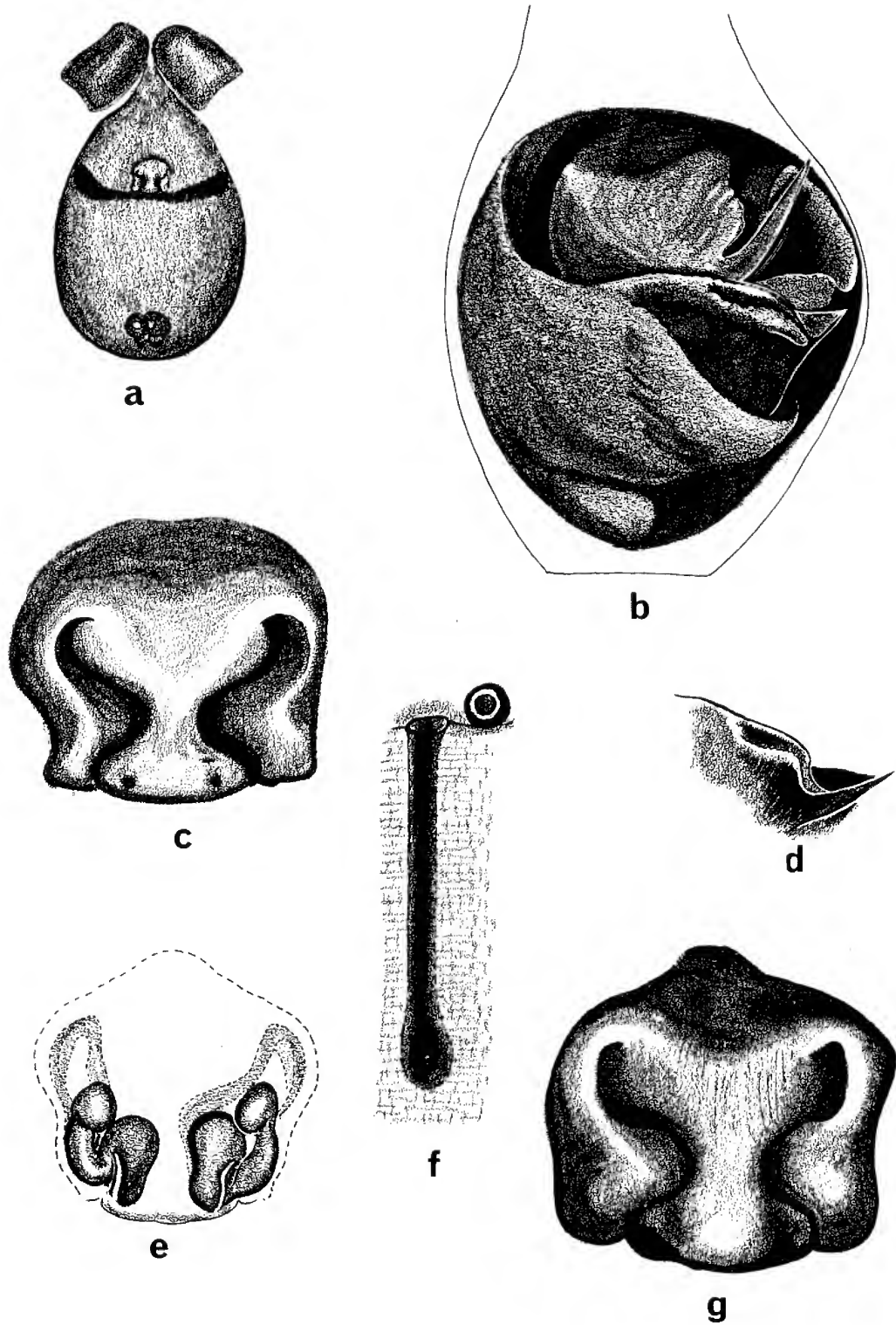


FIG. 1: a-g, *Lycosa snelli*. a, ventral surface of abdomen; b, male palpal organ; c, epigynum of holotype; d, median apophysis of male palp; e, internal genitalia of WAM 71-1717; f, burrow and pebble door showing silk seal; g, epigynum of female from Barrow Island WAM 71-1716.

penultimate males and females are found during May, June, July, and possibly through to August.

HABITAT

Open areas of spinifex, low acacia bushes, or bare gravel slopes without vegetation. The soils are always well compacted red to brown clay-loams, usually in sheet-washed gravel areas covered with small pebbles and rounded stones. Occasional specimens may be found on light clay-loams near clay pans or clay depressions in rocky areas. Most mature specimens are found at night on bare open gravel slopes well away from vegetation.

BURROW

Lycosa snelli has a very characteristic burrow up to 16 mm in diameter and 12–24 cm in depth. The burrow is normally vertical with or without a slightly cone-shaped entrance, and always sealed securely during the day with a round pebble, piece of wood, or on many occasions the dung pellet of introduced rabbits or sheep. The pebble 'door' is rolled back at dusk when a thick ring of silk betrays the door stone: the door is sealed shut late at night when the temperature drops to about 6°C., or at the first light of day on warm nights. Repeated sealing of the burrow occurs on the same side of the stone where a ring of silk builds up; no doors, even the lighter doors of sheep dung, had more than one ring of silk, suggesting that the door was juggled into position on top of the burrow (Fig. 1f).

At night *Lycosa snelli* straddles the burrow usually with the tarsus of at least one posterior leg in contact with the burrow entrance, and retreats rapidly head-first into the burrow if disturbed. This species appears to be highly sensitive to any movements or vibration near the burrow, and on still nights is very difficult to approach without the spider retreating into the burrow, frequently leaving the 'door' upturned some 1 to 2 cm from the entrance. The spider is then very reluctant to be enticed from the burrow by careful teasing with a straw or insect prey. If the disturbed spider is left in the burrow it may emerge some time later to seal the burrow with the door or resume its stance over the burrow entrance. Some disturbed females may sit just below the burrow entrance for 10 to 20 minutes before re-emerging. I have collected *L. snelli* quite successfully by approaching the spider with great stealth and then striking just before the burrow with the blade of a spade to dislodge the spider from above the entrance; once removed from the burrow the spider appears quite disoriented and makes a somewhat circular search for the entrance.

DISCUSSION

In the form of the burrow, the robust size of the spider, coloration, shape of the epigynum, and behaviour, *Lycosa snelli* is very similar to members of the bicolor group (McKay 1973) and is assigned to that group of species. *L. snelli* like other members of the bicolor group may belong to the genus *Geolycosa* but all species examined (*L. bicolor*, *L. storri*, *L. forresti*, *L. errans* and *L. snelli*) have 1 + 1 dorsal spines on the tibiae of the fourth leg. American species of the genus *Geolycosa* lack dorsal spines on tibia 4 in mature females, although these are present in males.

DISTRIBUTION

Arid regions of northwest Western Australia. Possibly common throughout the Gascoyne, Ashburton and Pilbara regions.

DERIVATION

Named after Mr A. Snell who collected many interesting insects, spiders, and fishes for Australian Natural History Museums.

Lycosa duracki sp. nov.

(Figs. 2, a–e)

MATERIAL EXAMINED

HOLOTYPE: Western Australian Museum, WAM 74 494, ♀ M, C.L. 11.9 mm, Old Argyle Downs Station, Ord River, W.A., collected by R. J. McKay and W. H. Butler, October 23, 1971. In spirit with young spiderlings removed from holotype.

PARATYPES: Old Argyle Downs Station, Ord River, W.A., 5.x.1971, RJM, J. Dell, 2♀ M, 1♂ M, WAM 74-495–7.

DESCRIPTION (Based on the holotype)

Carapace light buff without lateral or median stripes, uniformly coloured in life, but with faint slightly darker brown stripes radiating from the fovea after preservation in alcohol; face light brown with buff hair; paturon dark brown with the anterior surface and sides with buff hair; lateral condyle dull red-brown; fangs dark brown; labium and maxilla brown; sternum brown. Abdomen pale brown to buff above and below; anterior slope of

TABLE 3: MEASUREMENTS OF LEG SEGMENTS OF HOLOTYPE OF *L. duracki* IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	8.1	4.2	6.1	6.3	3.5
2	8.0	4.0	5.6	6.3	3.5
3	7.1	3.9	5.0	6.2	3.5
4	8.6	4.1	6.8	8.3	4.3
Palp	4.8	2.3	2.6	—	3.5

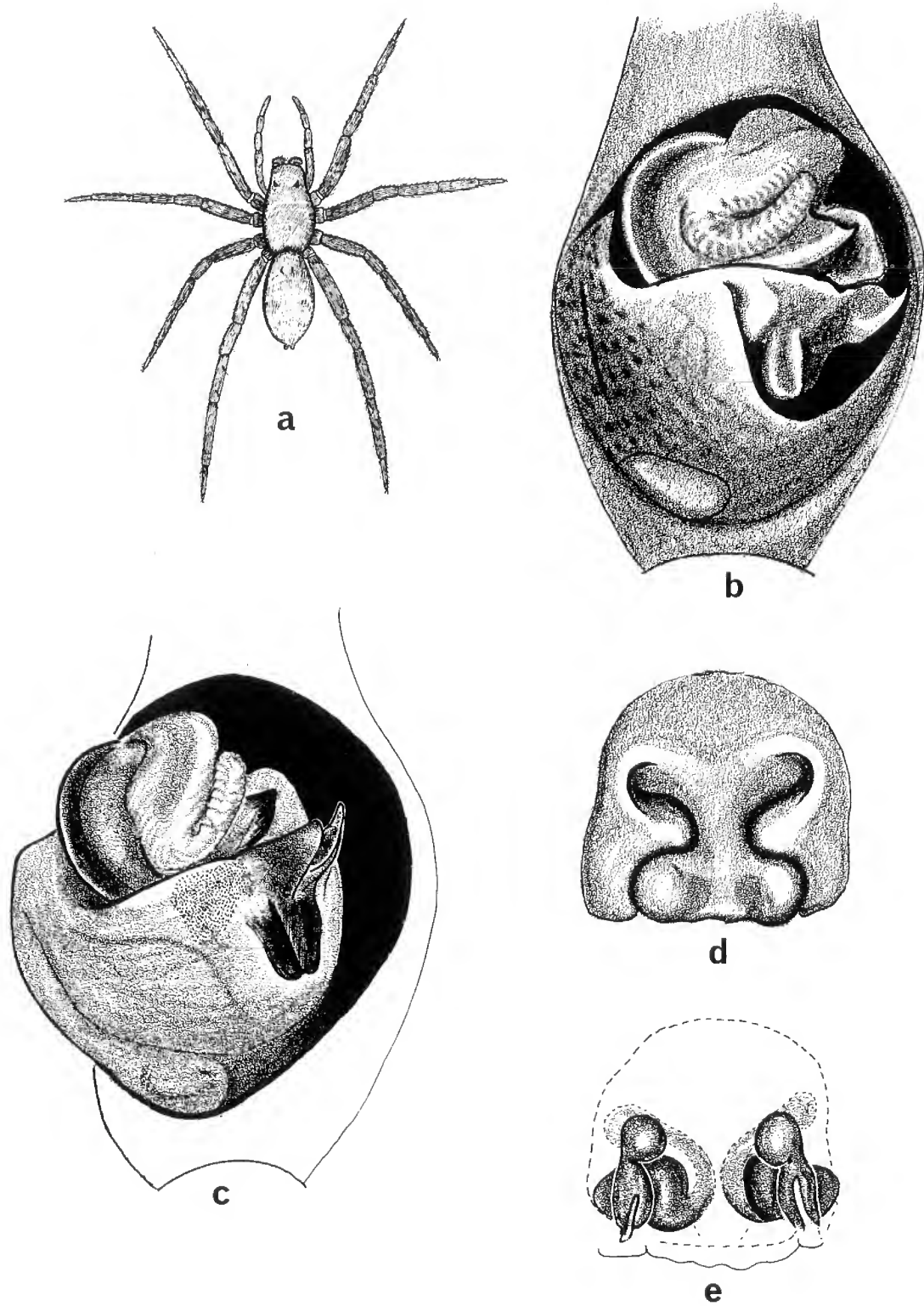


FIG. 2: a-c, *Lycosa duracki*. a, holotype; b-c, male palpal organ; d, epigynum of holotype; e, internal genitalia of female paratype.

TABLE 4: EYE DIAMETERS AND INTERSPACES OF *L. duracki* CONVERTED TO PERCENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM
Holotype	♀M	11.9	24	15	54	47	10	7	30	5
WAM 74-495	♀M	11.0	24	16	54	46	11	6	32	9
WAM 74-496	♀M	10.7	23	13	56	49	10	8	30	7
WAM 74-497	♂M	10.3	26	15	57	50	11	5	30	8

abdomen brown and two semicircular brown marks on anterior one third of dorsal surface (Fig. 2a); ventral surface without markings; spinnerets brown. Legs pale brown covered with pale buff hair; patellae slightly darker; ventral surface of tibiae, metatarsi and tarsi ash-grey.

Anterior row of eyes with the upper tangent procurved, AM larger than AL, PM large and protruding, more than twice the diameter of the AM and a little less than half their diameter apart, the AL are situated close to the PM, PL eyes about twice the diameter of the AM. Ratio of eyes AM:AL:PM:PL = 21:13:46:40; distance AM:AM 9, AM:AL 6, AM:PM 4, PM:PM 26. Clypeus to AM 8. Width of first row of eyes 86; width of second row 111.

Chelicerae with three promarginal teeth, the middle one largest; three retromarginal teeth of equal size. Labium slightly longer than broad.

The epigynum is shown in Fig. 2d.

VARIATION: Newly hatched spiderlings are orange in colour with slightly darker radiating stripes on the carapace. Abdomen orange with a well defined dark serrated mark on the anterior dorsal surface of the abdomen which extends over the anterior slope of the abdomen and connects posteriorly to three dark transverse chevrons; venter pale.

Adults may have radiating dark brownish or greyish stripes on the carapace after preservation in alcohol but these are not present in life. The abdomen may have the anterior slope buff or darker brown, in one paratype female two vertical brown marks are present; the dorsal surface of the abdomen may have a pair of semicircular marks on the anterior one third, with three brown or faint grey transverse chevrons on the posterior third of the abdomen. No transverse dark bar behind the epigastric furrow as in *L. snelli*.

The eye measurements of the holotype and three paratypes are expressed as a percent of the total width of the first eye row in Table 4.

SIZE RANGE: Mature females 10.7 to 11.9 mm.

DIAGNOSIS: *Lycosa duracki* is very similar to *L. snelli* but differs in lacking a dark bar behind the epigastric furrow; the male palp has a very short,

broad embolic guide, and a more robust median apophysis (Fig. 2b, c). The burrow entrance is sealed with a hinged door, not a loose pebble.

LIFE HISTORY

Three mature females and one mature male were collected in October. The holotype female was carrying young, and was dug from the burrow at night.

HABITAT

Bare pebble-strewn gravel slopes and ridges bare of vegetation.

BURROW

A vertical burrow up to 14 mm in diameter and 15–20 cm in depth is constructed in heavy clay-gravel. One burrow (♀M) was simply an open hole and did not appear to have a lid although this may have been overlooked as the spider was dislodged by striking the ground with a spade. The other three burrows had a well constructed hinged lid and were not sealed with a pebble 'door' although pebbles similar to those used by *L. snelli* were present. The behaviour of *L. duracki* is remarkably like *L. snelli*.

DISCUSSION

Lycosa duracki is assigned to the bicolor group of species (see discussion under *L. snelli*) and may belong to the genus *Geolycosa* although 1 + 1 dorsal spines are present on tibiae 4 in mature females.

DISTRIBUTION

Kimberley region of Western Australia.

DERIVATION

Named after the Durack family that settled the Kimberley region in 1884 and founded Argyle, Lissadel, and Rosewood stations.

LITERATURE CITED

- KASTON, B. J., 1948. Spiders of Connecticut. *Bull. Conn. Geol. Nat. Hist. Surv.* **70**: 1–874, pls. 1–144.
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THE WOLF SPIDERS OF AUSTRALIA (ARANEAE: LYCOSIDAE): 6
THE LEUCKARTII GROUP

R. J. MCKAY
Queensland Museum

ABSTRACT

Lycosa leuckartii is redescribed with notes on the life history. *Lycosa christopheri* is a synonym of *Lycosa leuckartii*. *Lycosa gilberta* and *Lycosa molyneuxi* are morphologically similar species.

Thorell described *Lycosa leuckartii*, the first of the Australian wolf spiders, in 1870. His holotype female was redescribed by Koch in 1877. Hogg (1905) described *Lycosa gilberta* and *Lycosa molyneuxi*, two species of *Lycosa* that are morphologically similar to *L. leuckartii* and may prove to be synonyms. Simon in 1909 recorded *Lycosa leuckartii* from Western Australia and described *Lycosa christopheri*, here considered a junior synonym of *Lycosa leuckartii* that lacked the characteristic coloration of the ventral surface of the abdomen. Extensive collecting in Western Australia and an examination of specimens from other Australian Museums showed that *Lycosa leuckartii* may have the venter of the abdomen with a well developed median yellow-orange spot, a faint or much reduced yellow spot, or a completely black venter.

Lycosa leuckartii was placed into the genus *Scaptocosa* by Roewer (1954) but as *Scaptocosa* is a subjective-objective synonym of *Geolycosa* (Guy, 1966), all species referred to *Scaptocosa* are *Geolycosa*'s. Roewer's (1954) concept of *Scaptocosa* is closer to Guy's (1966) concept of *Schizocosa* and by using Guy's key such species would fall into *Schizocosa*. *Lycosa christopheri* was placed into the genus *Avicosa* by Roewer (1954), but as Guy (1966) treats that genus as a subgenus of *Schizocosa*, both *L. leuckartii* and *L. christopheri* were placed in the genus *Schizocosa* by McKay (1973). *Schizocosa* was proposed by Chamberlin (1904, p. 177) to include those species with the transverse guide of the epigynum double or divided. The epigynum of *Lycosa leuckartii* is quite unlike that of the species now contained within *Schizocosa* by American authors. Gertsch and Wallace (1937, p. 14) state 'With each addition it is becoming more and more evident that *Schizocosa*, like most of the genera of the Lycosidae will grade

gradually into *Lycosa* as this genus is used in the American sense'. I have placed *Lycosa leuckartii* into the genus *Lycosa* until a complete generic revision of the Australian Lycosinae is made.

Chamberlin (1904) wrote a classic paper on the difficulty of subdividing the family Lycosidae. His introductory remarks are even more pertinent today 'Scarcely any two men who have studied the Lycosidae have interpreted or defined the genera of the family wholly in the same way. The purely relative nature of the characters most frequently used in separating the species into genera leaves room for much diversity in opinion and usage; and, in consequence, it is not surprising to find that genera used without question by one arachnologist are by others unhesitatingly relegated to synonymy.

'Various genera that have been proposed in this family are clearly artificial, having been erected on single characters without reference to the existence or non-existence of correlated differences. That is, the species in such cases are grouped with a view to convenience rather than with the intent to express generic relationship. There can be little doubt, however, that some of the more commonly accepted genera represent in the main natural associations of species, the difficulty here being encountered in the choice of characters for definition and diagnosis.'

Part of the confusion in the choice of generic characters is undoubtedly due to the lack or complete neglect of a study of the individual and geographic variation encountered within species. Such studies are of paramount importance in the choice of specific and generic characters. The use of eye diameters and interspaces, relative proportions of leg segments, chaetotaxy, cheliceral teeth, coloration, and genitalic differences are clearly impor-

tant in a study of the Lycosinae, but all such characters are variable to some degree and in order to assess their worth as taxonomic characters, this variation should be studied more fully. In later papers in this series I propose to discuss the variation encountered in the characters most commonly employed in the systematics of the family Lycosidae. It is hoped that the initial papers will allow students of the Australian Lycosinae to correctly identify the Wolf Spiders now under review and act as an incentive to further collecting and research. Some of the problems outlined in the present paper may be clarified by a study of the reaction of mature males to the pheromone of mature unmated females of morphologically similar species. Such studies, including the mating of males and females, have been undertaken for some species by the author. These preliminary studies on courtship and behaviour, whilst in themselves not completely conclusive, have added another dimension to the systematic study of the Australian wolf spiders.

***Lycosa leuckartii* (Thorell, 1870)**
(Figs. 1 A–E, 2 A–I, 3 E–F)

Tarentula leuckartii Thorell, 1870, p. 388.

Lycosa leuckartii: L. Koch, 1877, pp. 896–99, pl. 77, figs. 3, 3a (Peak Downs, Queensland); Simon, 1909, p. 182 (Wooroloo, Guildford, Fremantle, Donnybrook, Gooseberry Hill, York, Beverley, Western Australia); Rainbow, 1911, p. 269, Bonnet, 1957, p. 2649.

Lycosa christopheri Simon, 1909, p. 182 (Fremantle, Western Australia); Rainbow, 1911, p. 266; Bonnet, 1957, p. 2638; Rack, 1961, p. 37.

Scaptocosa leuckartii: Roewer, 1954, p. 291.

Avicosa cristopheri [sic]: Roewer, 1954, p. 236.

Schizocosa leuckartii: McKay, 1973, p. 381.

Schizocosa christopheri: McKay, 1973, p. 381.

MATERIAL EXAMINED

Lycosa leuckartii: Western Australia: BM 92.6.12.4–20, three females from Darling Range. B. H. Woodward, examined by Dr Barbara Main; (WAM specimens) Broomhill, Hambg.S.W. Austral. Exp. 1905. 158, 24–25. viii, WAM 4299, dried and pinned; Aldersyde, Albany Highway at 76 mile peg, Albany Highway at 110 mile peg, Applecross, Arthur River, Armadale, Attadale, Bakers Hill, Balingup, Bayswater, Belmont, Bickley, Boya, Bridgetown, Broome Hill 29 km east, Bruce Rock at Nangeen Hill, Brunswick Junction, Bullsbrook East, Bullsbrook, Bunbury, Bunbury Highway 51 mile peg, Bungulla 14 km north, Burngup, Byford, Cannington, Cannington East, Churchmans Brook, Collie, Collie 43 km east, Collie 48 km east, Collie 67 km east at Hillman River, Congelin on abandoned railway, Coorow 14 km south-southwest, Corrigin, Crossman, Cunderin, Darkan, Darkan East, Darkan 11 km north,

Darkan 19 km east, Darlington, Dedari, Desperate Bay near Snag Island, Dulbelling, Dunsborough at beach, Fitzgerald River, Geraldton 16 km east, Gin Gin, Gooseberry Hill, Great Eastern Highway 59 mile peg, Great Northern Highway, 58 mile peg, 70 mile peg, 77 mile peg, 87 mile peg, 92 mile peg, Green Head at 170 mile peg, Guildford, Harvey, Hyden, Hyden 32 km east, Israelite Bay, Jandakot, Jarrahood, Jennacubbine, Kalgarin, Kalgoorlie at 24 km west of Randells, Kelm-scott, Kojonup 27 km east, Kojonup 29 km east, Koorda, Lake Moore south end, Margaret River, Marvel Loch 16 km east-south-east, Merredin 32 km east, Merredin, Mingenew, Mogumber 29 km west at Moore River, Molpar, Moora 8 km south, Mount Helena, Mullalyup, Mundaring Weir, Murchison River at Gee Gee Camp, Narembeen, National Park, New Norcia 11 km north, New Norcia 13 km north-west, Northam, Northcliffe, Ongerup 3 km east, Ongerup 70 km east, Pingelly East, Pinjarra, Point Peron, Red Hill, Rossmoyne near Canning River, Tammin, Toodyay, Wagin, Wagin West, Walyunga National Park, Wickepin, Woodanilling, Wubin 16 km northeast, Yellowdine 29 km south, Yellowdine 61 km south, Yorkrakine.

South Australia: Brown Hill Creek, i.1936, SAM; Claire, 7.xii.1952, BYM, WAM 68-844; Eucla, 96 km east, M. Archer, B. Muir, 2.xii.1969, WAM 71-467; Hammond, 21.iii.1949, V. H. Mincham, AM; Horrocks Pass near Port Augusta, 8.xii.1952, BYM, WAM 70-33; Moonarie Gap Wilpena Pound Range, 22.viii.1970, HB, W. D. L. Ride, WAM 71-209–10; Port Lincoln, 77 km west, 19.xii.1952, BYM, WAM 69-926; Quorn north, 8.xii.1952, BYM, WAM 68-839. (Note: Most specimens have a black venter).

Victoria: Cardross, 10.vi.1953, E. J. Dean, NM; Lake Hattah, ix.1928, NM; Nyah, 28.x.1913, C. French, NM; Oakleigh, 8.vi.1950, E. F. Murnane, NM; Red Cliffs, ii.1956, NM; Western District Mallee scrub, NM.

ACT: Canberra, 6.iv.1929, G. F. Hill, AM K58918; 14.iv.1929, G. F. Hill, AM K58904; ix.1968, J. T. Dare, WAM 70-170.

New South Wales: Bathurst, AM K26746; Broken Hill 140 km east, 21.x.1952, BYM, WAM 69-995–1001; Byrock 24 km west, 5.xi.1959, R. Mackay, AM; Cooma, 19.i.1953, N. Lambert, NM; Harden, 3.ii.1931, E. G. Larkin, AM K63625; Leeton, iv.1928, K. McKeown, AM K58304; McAlister, 28.iii.1939, O'Connolly, QM W293.

Queensland: BM. 1919. 9.18.526, a male from Peak Downs; Glenmorgan, 27.ii.1939, Mrs Doran, QM W1026; Goondiwindi, 7.i.1957, E. J. Lindsay, QM W3855.

Lycosa christopheri: Holotype female, Hamburg Zool. Mus. Inst. No. 488 labelled 'Sudwest-Australien. E. Simon publ. 1909', 'Fremantle, W. Australien. W. Wolting leg. 1907. H. Christopher ded. i.vii.1907'. The holotype has the abdomen rather extensively damaged, and only the anterior part of the venter remains; the epigynum is intact.

DESCRIPTION (after L. Koch, 1877)

Female, C.L. 12.0 mm (Holotype of the species). Carapace red-brown with yellow-brown hair and

with a white stripe on the lateral margin that gradually tapers anteriorly; a whitish median longitudinal band commences near the posterior margin and continues to the head; between the head and the thorax is a narrow white stripe edged posteriorly with black; three white lines edged in black radiate onto the lateral slope of the thorax; mandibles black with the upper half yellow-grey; maxillae and labium dark red brown; sternum red-brown with grey-brown hair. Abdomen yellow-brown above with white hair on the sides and numerous brown spots above; anteriorly on the dorsal surface is a darker longitudinal stripe, which is serrated and broader at the posterior corners with white spots on the tips of the serrations; behind this longitudinal spot is a black angular stripe with black spots on each end, followed by a curved stripe, and more posteriorly, two curved transverse black stripes with a white hind margin; venter black-brown with a large yellow-grey spot in the middle; spinnerets yellow-brown. Legs red-brown with grey-yellow hair.

Anterior row of eyes slightly procurved, the eyes equidistant by their radius; AM larger, a little more than their diameter from the clypeus, and not further from the PM than from the AL.

Chelicerae with two promarginal teeth and three retromarginal teeth.

Male C.L. 9.0 mm. Carapace red-brown, a narrow white marginal band, the remaining hair pale yellow; on either side of the head is an angular white spot; mandibles red-brown covered anteriorly with pale yellow hair; maxillae labium and sternum reddish-brown, the latter covered with white to yellow hair. Abdomen with the middle of the dorsal surface pale yellowish and the sides with light brown to yellow hair; the dorsal surface has at the anterior end two black spots surrounding a small yellowish-white spot, behind these in a longitudinal spot with black borders inside which is yellowish hair rounded at the posterior end, and on either side of its posterior end is a yellowish-white spot; on the posterior half of the dorsum is a row of yellowish-white spots bordered with black anteriorly, the sides and the posterior curve covered with white hair; the epigaster covered with yellow-brown hair, and at its posterior margin a brownish-yellow field surrounded by deep black hair; spinnerets yellow-brown. Palpi and legs reddish-brown with yellowish-white hair.

Anterior row of eyes slightly procurved and not as broad as the second; AM larger than AL and not quite a radius from the AL, the PM, and each other; PM very large, slightly less than their radius apart, and not quite a diameter from the PL.

Chelicerae with two promarginal teeth and three

retromarginal teeth.

VARIATION: Although mature males and females have a pale yellowish, brown, or buff coloured area in the middle of the ventral surface of the abdomen, some specimens, particularly those collected on sandy substrates, have the venter completely black, but may show the typical coloration after long preservation in alcohol. The holotype of *Lycosa christopheri* was described by Simon as having a completely black venter but a re-examination of this specimen shows the venter to have a light-coloured area in the middle as does *Lycosa leuckartii*. The epigynum of *Lycosa christopheri* agrees with that of *Lycosa leuckartii* and the two nominal species are synonymous.

Koch (1877) described a male from Peak Downs, Queensland. This male (BM. 1919.9.18.526 in the British Museum) has the coloration and pattern of the female and is quite unlike the illustration of the male of '*Lycosa leuckartii*' given by Koch (1877, pl. 81, figs. 1, 1a) which is undoubtedly of a different species. An illustration of a male *Lycosa leuckartii* is provided in Fig. 1, A-B. The undersurface of the anterior pairs of legs and the anterior surface of the paturon may be covered with bright orange-yellow to gold hairs.

The epigynum varies in the depth of the depression on each side of the median guide, and specimens from Canberra, A.C.T., and Victoria, have these depressions markedly deeper than those from Western Australia, New South Wales, and Queensland. In some examples the median guide may almost disappear anteriorly and resemble the epigyna of *Lycosa gilberta*. The few specimens from South Australia have the venter almost completely black and have a rather deep epigynum. Further collecting in South Australia and Victoria may establish that *Lycosa gilberta* is a junior synonym of *Lycosa leuckartii*. The male palpal organ is now figured (Fig. 1, C-E) and the variation in the shape of the epigynum and internal genitalia of the female is provided in Fig. 2, A-I.

The promarginal cheliceral teeth are 3+3 in all specimens listed above but some variation may occur in the size and spacing of these teeth as illustrated in Fig. 3E. The retromarginal teeth are equal in size and number 3+3.

The eye diameters and interspaces of 12 specimens are given as a percent of the total width of the first row of eyes (Table 1).

SIZE RANGE: Mature females C.L. 7.4 to 14.8 mm. Mature males C.L. 9.1 to 12.5 mm.

DIAGNOSIS: *Lycosa leuckartii* is one of a group of Australian species with a 'Union Jack' pattern of

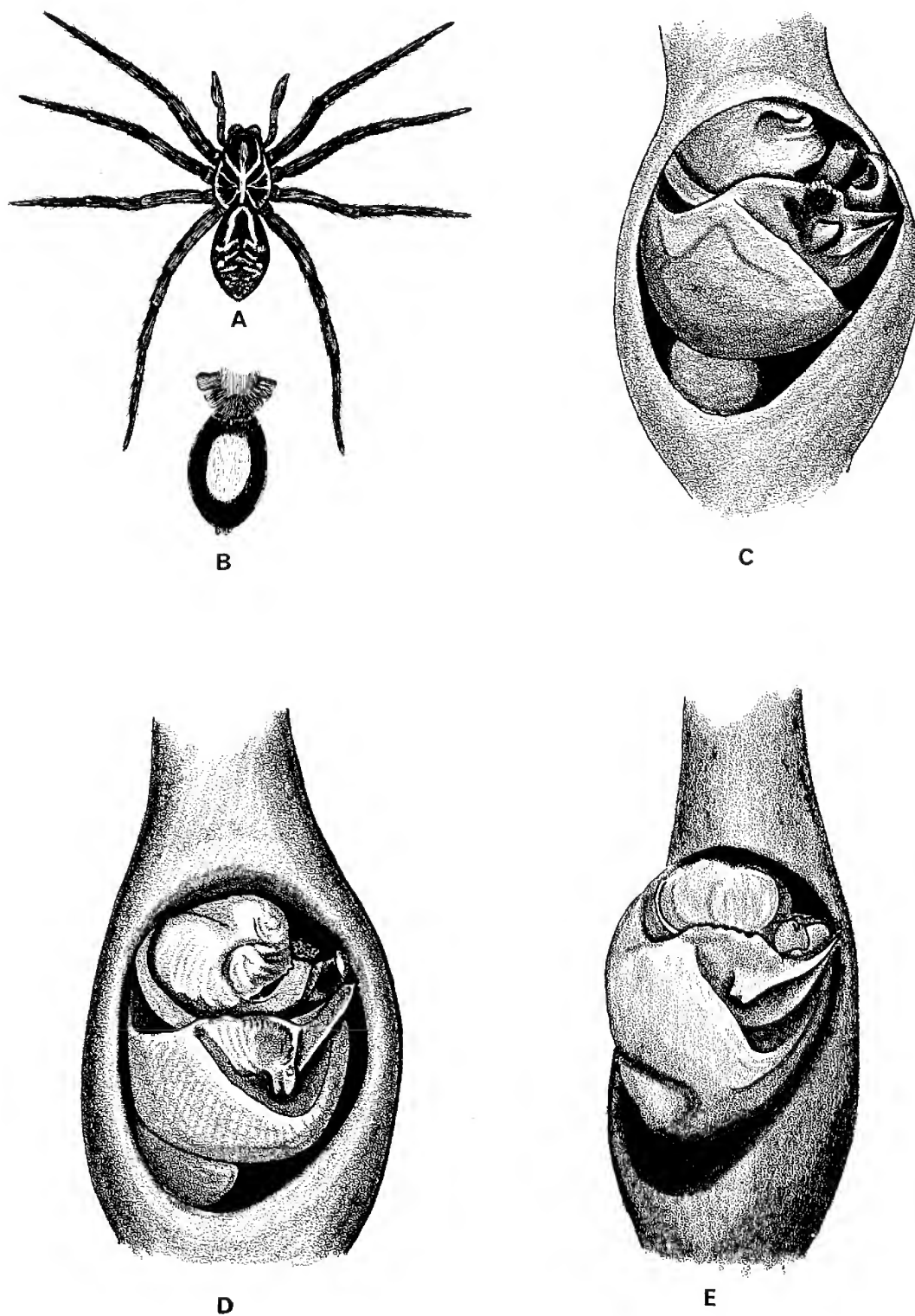


FIG. 1: A–E. *Lycosa leuckartii*. A, mature male from Western Australia; B, undersurface of abdomen; C–E, male palpal organs of WAM 71-1573-4, from Bullsbrook, Western Australia.

TABLE 1: EYE DIAMETERS AND INTERSPACES OF *L. leuckartii* CONVERTED TO PERCENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM
BM 1919.9.18.526	♂	9.4	24	17	57	47	9	7	26	5
QM W3855	♀	12.7	22	16	49	42	8	7	29	14
QM W293	♀	11.0	22	15	51	43	8	6	29	12
QM W1206	♂	10.7	22	17	52	39	9	4	28	11
SAM Brown Hill Ck	♂	10.9	21	17	50	42	10	8	29	13
WAM 68.844	♀	12.3	22	15	53	40	9	7	25	14
AM Northam W.A.	♂	13.6	21	17	47	40	9	6	31	13
WAM 68.409	♂	12.0	21	17	54	39	8	8	27	12
WAM 69.838	♀	14.2	21	16	52	41	11	8	31	11
WAM 71.1236	♂	8.3	21	15	49	41	10	7	30	11
WAM 71.1573	♂	12.3	21	15	51	40	10	8	29	10
WAM 71.1574	♂	11.9	22	16	50	39	10	8	32	14

radiating black-edged white lines on the carapace and a black mark on the anterior dorsal surface of the abdomen. The ventral surface of the abdomen is usually black with a pale yellowish-brown centre. The epigynum is of characteristic shape; the median guide is narrow with moderately deep to very deep lateral furrows, and a well developed transverse guide posteriorly. Specimens without a yellowish spot on the venter would key down to *Lycosa hasseltii* using Koeh's (1877) key to species but the epigynum is of different shape (median guide of *L. hasseltii* is wider, and lateral furrows not markedly deep) and *L. hasseltii* has a pale longitudinal stripe on the carapace as wide as the distance between the PL eyes whereas in *L. leuckartii* this stripe is much narrower.

LIFE HISTORY

Mature females may be collected throughout the year but are most common from October to March. Mature males are uncommon during the winter months but are abundant from November to March. Females carrying egg cocoons have been taken from October to April. In Western Australia females bearing young are common during April but have been collected in February, May, and June. The young are released just prior to the early winter rains, and immature specimens are common throughout the winter months. Two females with young were collected in Victoria during February and April. At Goondiwindi in southeast Queensland one female was captured with young in January.

Mature males commence courtship in November and continue to court females throughout the summer months in Western Australia. The male commences courting behaviour immediately the female pheromone is sensed. A male from Wickipin, Western Australia was placed on filter paper

with a mature female from Kelmscott, some 160 km northwest, and the following response was observed: the male drummed the palps slowly on the surface of the paper then held the forelegs at an angle of 45° to 50° for approximately three minutes without moving the body. A short run towards the female ended with the forelegs held at 45° as if to ward off an attack; short cautious moves towards the female terminated in brief pauses, and then the male commenced to jerk the forelegs in an up and down fashion whilst approaching with rather jerky movements of the body. At no time did the male retreat from the female. The female did not allow the male to copulate, and would not copulate with mature males collected at Kelmscott.

One female from Jarrahwood C.L. 11.6 mm had a cocoon measuring 11.5 mm containing 376 ova of 1.2–1.3 mm, another female from Gingin, W.A., C.L. 9.0 mm had a cocoon measuring 11.2 × 13.5 mm containing 512 ova with a diameter of about 1.2–1.25 mm. Four females from Western Australia C.L. 9.3–11.6 mm were found to be carrying 292–511 young in April and June.

HABITAT

Lateric gravels, loam, or clay soils, especially on alluvial clay soils near swamps, streams, and on river banks. Stony clay soils in damp forested areas where the undercover of vegetation is sparse frequently supports a large population of *Lycosa leuckartii*. In less favourable habitats this species may be collected on stone ballasted railway lines, in suburban gardens, occasionally on loose sand substrates, and around the margins of sandy swamps. *Lycosa leuckartii* may be associated with *Lycosa godeffroyi*, but gives way to the latter species in the drier areas. Open areas free of dense vegetation appear to be preferred.

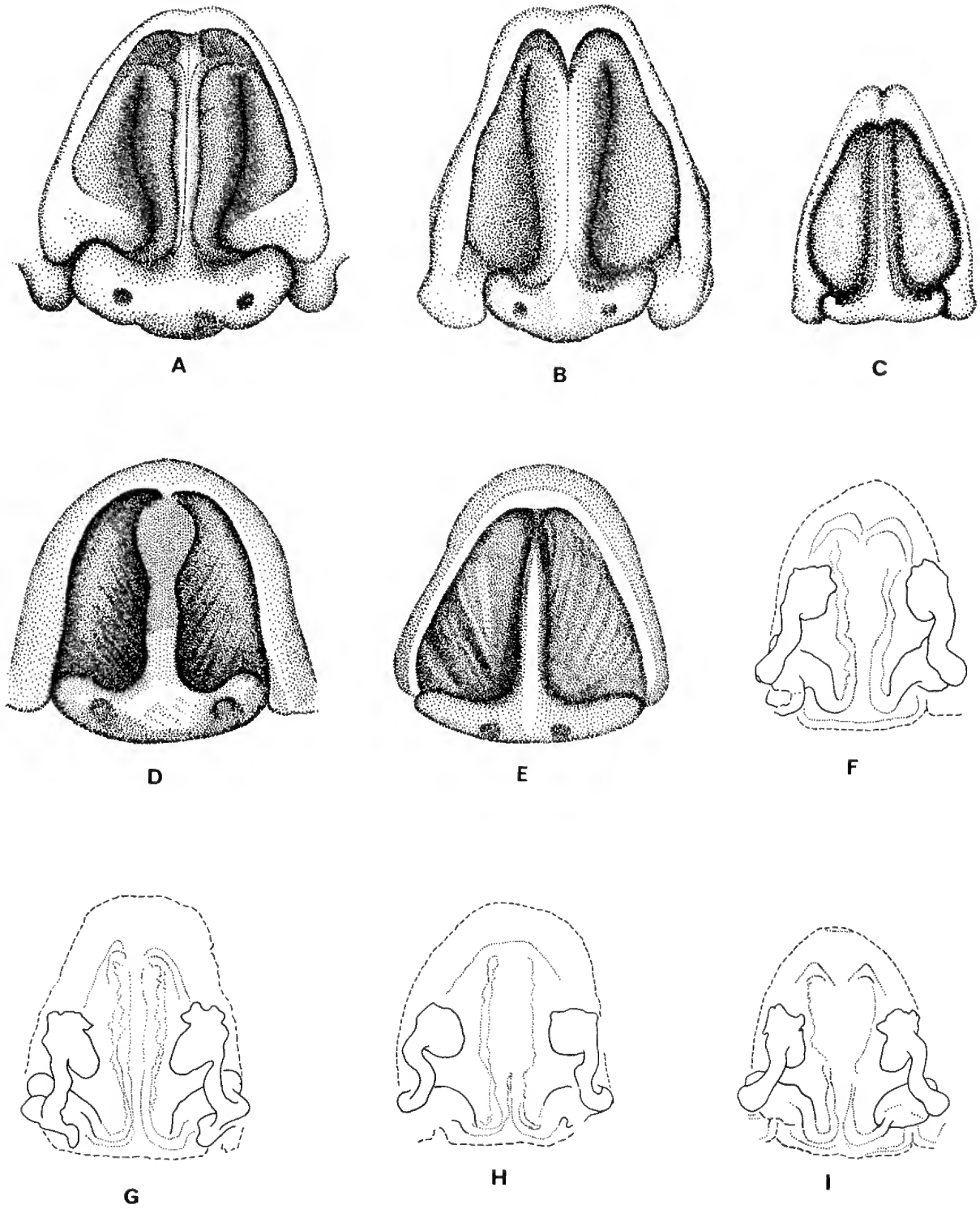


FIG. 2: A-I, *Lycosa leuckartii*. A-C, epigyna of three females from National Park, Western Australia, WAM 68-846-52; D, epigynum of female from Red Cliffs, Victoria; E, epigynum of female from Bathurst, AM K26746; F-I, internal genitalia of WAM 68-409, WAM 68-838, WAM 71-1573, WAM 71-552.

BURROW

Lycosa leuckartii constructs an open burrow in clay loam soils. The burrow may be excavated adjacent to stones, granite boulders, or logs, and extend beneath such objects in a more or less horizontal fashion with one or two sinuous curves. Vertical burrows may have a large funnel-shaped opening that becomes constricted some 3–5 cm down the burrow, and then expands again into a terminal chamber some 15 cm down. The burrow entrance may have the surrounding grass, leaves, or twigs silk bound into a crude barricade. In areas of cracking clay soil this species may occupy the fissures and build a rough chamber-like retreat some distance down the crack. Some examples of typical burrows are given in Fig. 3F. The female normally enters the burrow entrance head first.

DISTRIBUTION

Western Australia, South Australia, Victoria, New South Wales and southern Queensland within the region receiving more than 250 mm annual rainfall.

***Lycosa gilberta* Hogg 1905**
(Figs. 3A–D)

Lycosa gilberta Hogg, 1905, pp. 582–4, fig. 86 (Gilbert River, Riverina, New South Wales); Rainbow, 1911, p. 268; Bonnet, 1957, p. 2643; McKay, 1973, p. 379.

Venonia gilberta: Roewer, 1954, p. 307.

Hogna gilberti: Roewer, 1960, p. 975.

Hogna gilberta: Roewer, 1961, p. 13.

MATERIAL EXAMINED

SYNTYPES: 5, SAM, CL 12.8, 14.0, 11.2, 11.3, and 10.5 mm. The two large females are together in one tube labelled 'LYCOSA GILBERTA HOGG. GILBERT R. RIVERINA, S.A. MUS. COLL.' in ink, 'F 172' in pencil, '*Lycosa gilberta* F 172. Type—Gilbert R. Riverina' in pencil, and a printed label 'PARATYPES'; the three smaller females are together in another tube labelled '*Lycosa gilberta* Hogg. A. Molineux. Gilbert R. Riverina ♀', in ink and '*Lycosa gilberta* H. R. Hogg, F. 174. Gilbert River, Molyneux, females (Small) types' in pencil and on the reverse side 'S.A. Mus. Coll.', and a small printed label 'paratypes'.

LECTOTYPE: As the 12.8 mm C.L. female has the abdomen attached (the 14.0 mm female has the abdomen detached and is in poor condition) I designate this specimen as lectotype, but have retained it in the tube with the 14.0 mm C.L. female as there are a number of detached legs in the tube; the remainder have been labelled paralectotypes.

OTHER MATERIAL: South Australia: Adelaide, 1937, 3 ♀ M, SAM; Hack's Bridge, Onkaparinga, xi.1896, Tepper, 2 ♀ M, 5 ♂ M, SAM; Stenhouse Bay, Rivers Head, Dr Pulleine, 1 ♀ M, SAM; Ceduna, 21.xii.1952, BYM, WAM 68-861.

Victoria: Baldwin, Mr Chapman, 1 ♀ M, NM; Mount

Duboulay, 5.iii.1883, 1 ♀ M, NM; North Carlton, 3.vi.1902, G. A. Keartland, 1 ♀ M, NM; Victoria, no locality, W. Duboulay, 1 ♀ M, NM; Victoria, no locality, 19.vi.1911, A. S. Kenyon, 1 ♀ M, NM; Western District mallee scrub 2 ♀ M, 23.ii.1914, C. French, 1 ♀ M, NM.

New South Wales: Jerilderie, 29.iii.1959, Pinchen, 1 ♀ M, NM.

DESCRIPTION (After Hogg, 1905)

Female. Cephalothorax brown with yellow-grey hair; a paler yellow-grey median, marginal, and four side-streaks on each side, the latter backed by darker brown; mandibles black-brown with thick yellow hair and long erect brown bristles; labium, maxillae, and sternum dark red-brown, with dark yellow-brown hair; coxae with rather browner hair. Abdomen yellow or grey-brown above and almost orange to paler yellow-brown on sides. Under-surface from base to spinnerets of a dull dingy brown, about the same colour as the coxae. Legs and palpi red-brown with pale yellow-grey hair somewhat darker below. Three retromarginal chelicerae teeth of equal size. Anterior row of eyes straight along the lower edge, the AM 1.5 times the AL, and a radius apart. $PM\frac{2}{3}$ of their diameter apart. Clypeus as broad as an AM. Epigynum horseshoe-shaped, slightly broader than long; the median ridge broad at the base and tapers to a narrow ridge anteriorly.

Legs with two spines above on tibiae III and IV none on I and II.

VARIATION: The ratio of the eye diameters and their interspaces is given for three specimens from South Australia.

Adelaide, mature female C.L. 11.2 mm; ratio of eyes AM:AL:PM:PL = 9:7:19:15; distance AM:AM 4, AM:AL 2, AM:PM 6, AL:PM 4, PM:PM 12. Clypeus to AM 8. Width of first eye row 41, width of second eye row 48. Ocular quadrangle 50 × 62.

Adelaide, mature female C.L. 11.0 mm; ratio of eyes AM:AL:PM:PL = 9:7:19:16; distance AM:AM 4, AM:AL 2, AM:PM 6, AL:PM 4, PM:PM 11. Clypeus to AM 8. Width of first eye row 42, width of second eye row 49. Ocular quadrangle 49 × 63.

Onkaparinga, mature female C.L. 10.5 mm; ratio of eyes AM:AL:PM:PL = 9:7:19:14; distance AM:AM 4, AM:AL 1.5, AM:PM 6, AL:PM 4, PM:PM 11. Width of first eye row 40, width of second eye row 48. Ocular quadrangle 49 × 58.

The coloration of *Lycosa gilberta* appears indistinguishable from that of *Lycosa leuckartii*. No *L. gilberta* examined by me have a lighter brown or yellow spot on the ventral surface of the abdomen, however.

The epigynum is deeply recessed and may show little trace of the median guide. The epigynum of the lectotype is refigured (Fig. 3A) and the epigynum of a female misidentified by Hogg as *Lycosa obscura* from Hacks Bridge, Onkaparinga (Fig. 3, B). Two epigyna from specimens intermediate in form between *Lycosa leuckartii* and *Lycosa gilberta* are illustrated in Fig. 3C, D. A number of specimens collected in South Australia and identified by me as *Lycosa leuckartii* without a pale spot on the venter have epigyna very like *Lycosa gilberta* but grade imperceptibly into the typical *L. leuckartii* epigynum. The close similarity of both species would suggest that *Lycosa gilberta* is a synonym of *Lycosa leuckartii* or merely a local form of the latter. One typical *Lycosa leuckartii* was collected in association with *Lycosa gilberta* from the mallee scrub, Western District, Victoria (NM). A study of both forms from western Victoria would be necessary to resolve the identity of *Lycosa gilberta*.

SIZE RANGE: Mature females C.L. 7.4 to 13.30 mm. Mature males C.L. 9.0 to 11.3 mm.

LIFE HISTORY

Mature females have been collected during March, April and June in Victoria, and March in New South Wales.

DISCUSSION

Roewer (1954) placed *Lycosa gilberta* into the genus *Venonia* within the subfamily Hippasinae but later (1960, 1961) transferred this species to *Hogna* now considered to be a subgenus of *Lycosa* (Guy, 1966).

DISTRIBUTION

South Australia, Victoria, and New South Wales.

Lycosa molyneuxi Hogg 1905

Lycosa molyneuxi Hogg, 1905, pp. 575-7, fig. 82 (Gilbert River, Riverina, New South Wales); Rainbow, 1911, p. 270; Bonnet, 1957, p. 2653; McKay, 1973, p. 379.

Allocosa molyneuxi: Roewer, 1954, p. 206.

MATERIAL EXAMINED

The location of the holotype of *Lycosa molyneuxi* is unknown to me, and no additional material has been collected from the type locality.

DESCRIPTION (After Hogg, 1905)

Cephalothorax red-brown with pale to darker yellow-brown flattened hair intermixed with dark brown erect hair; a paler marginal and median stripe with side streaks the same; mandibles black-brown, with yellow-brown hair; labium, maxillae,

sternum and coxae reddish-brown with yellow-brown hair. Legs and palpi yellow-brown; the ventral surface of the femoral joints much paler than the dorsal surface.

Abdomen yellow-brown above with a small darker patch at the base and two pairs of darker spots near the middle; sides pale. Ventral surface bright rich brown anteriorly, with two broad stripes of the same curving inwards and joining in front of the spinnerets which are of the same colour; the space so enclosed is pale buff.

First row of eyes clearly procurved and shorter than the second row; AL not quite $\frac{2}{3}$ the diameter of the AM; AM half a diameter apart, the same distance from the PM, and slightly less from the AL. The clypeus is broad, the distance to the root of the mandibles being twice the diameter of the AM, but a transverse edge marking runs across at more than half the distance away from the eyes. PM more than half their diameter apart. Labium less than half the length of the maxillae. Palpi longer than the cephalothorax.

'In colouring, pattern, and size this spider is very like *L. leuckartii* Thor. from Peak Downs, Queensland, as described by L. Koch, but differs in having the pattern of the under side of the abdomen bright brown instead of black-brown. The clypeus is much wider, instead of slightly only, than the front median eyes, which are rather wider apart than they are from the side eyes instead of equidistant. The palpi are longer instead of shorter than the cephalothorax, and the lip less instead of more than half the length of the maxillae. The epigynal ridge of *leuckartii* is drawn by L. Koch widest in the middle, while here it certainly widens from the middle anteriorly.' (Hogg, 1905, p. 576).

DISCUSSION

Many of the characters reported by Hogg to distinguish *L. molyneuxi* from *L. leuckartii* are clearly within the range of variation found in the latter species. In *L. leuckartii* the ventral surface of the abdomen varies from pale yellowish, buff, or brown, surrounded by light brown, dark brown or black, to a completely dark brown or black venter; the clypeus is frequently wider than the AM eyes, the variation encountered in 5 specimens was 5:9, 8:7, 9:8, 11:8, 12:8; the distance AM-AM is normally wider than AM-AL (Table 1); the lip may vary from about half length of maxillae to more than half, none had the labium less than half the length of the maxillae; the palpi are normally about equal to the length of the carapace; a few specimens have the median guide of the epigynum widening anteriorly.

The Gilbert River area is of special significance

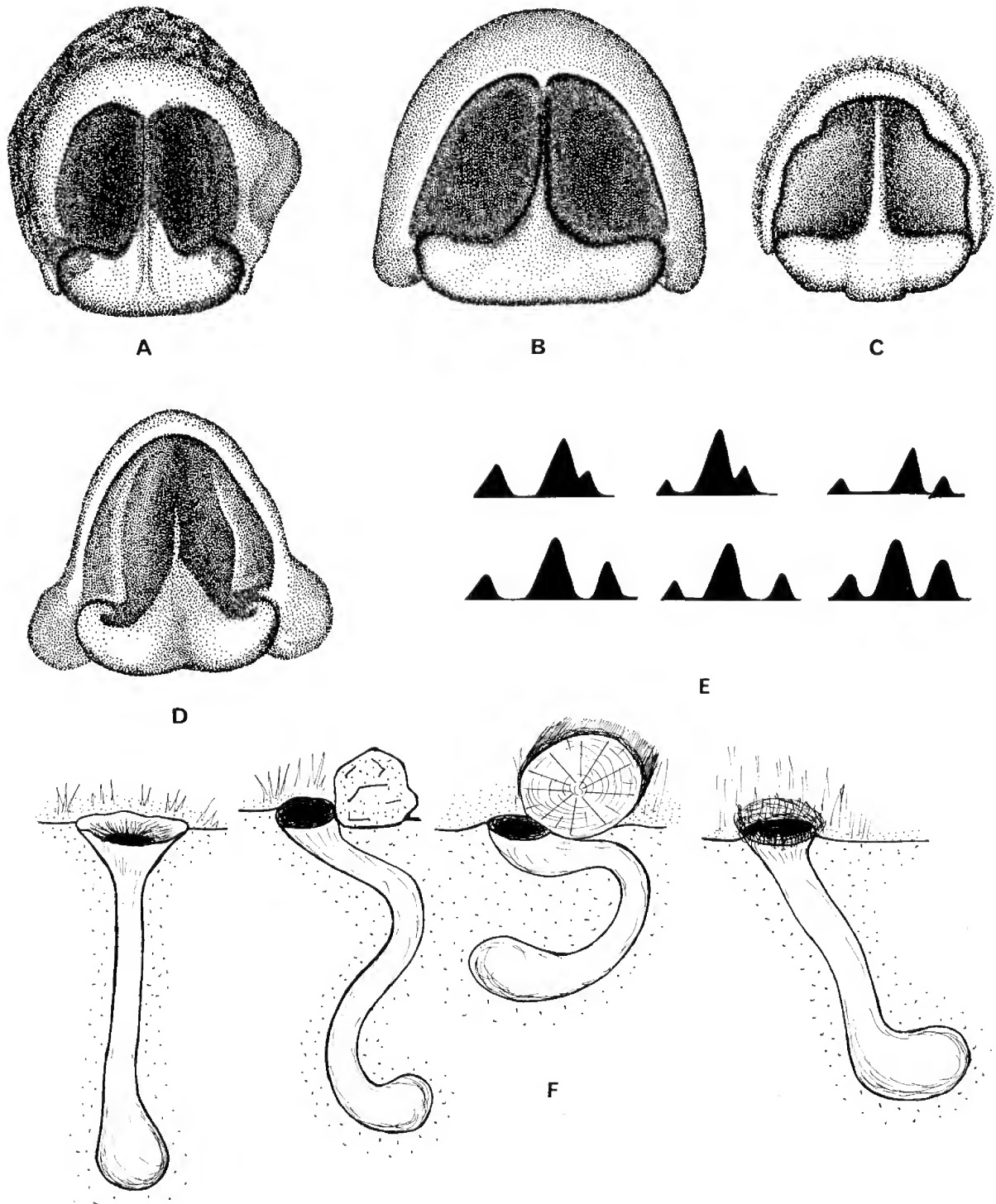


FIG. 3: A–D, *Lycosa gilberta*. A, epigynum of lectotype; B, epigynum of female from Onkaparinga, South Australia; C, epigynum of female from Mt. Douboulay, Victoria; D, epigynum of WAM 68-861, a female from Ceduna, South Australia.

E–F, *Lycosa leuckartii*. E, promarginal cheliceral teeth from the left side of six mature females from National Park, WAM 68-846–52; variation in the burrows of Western Australian specimens.

in the clarification of species within the 'leuckartii group' as both *L. gilberta* and *L. molyneuxi* were described from this locality; further collecting may show all three species to be synonymous.

DISTRIBUTION

Gilbert River, New South Wales.

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BIRDS OF MORETON ISLAND AND ADJACENT WATERS

D. P. VERNON
Queensland Museum
and

J. H. D. MARTIN
Fauna Branch,
Department of Primary Industries

ABSTRACT

One hundred and twenty birds are listed from Moreton Island and adjacent waters, southeastern Queensland. This list includes the first specimen record from Queensland of the Fleshy-footed shearwater, *Puffinus carneipes*.

Moreton Island, situated at Lat. 27° 10' S and Long. 153° 25' E., forms with Stradbroke Island a natural eastern boundary protecting the waters of Moreton Bay.

The island (18615 hectares) is composed predominantly of siliceous sand which forms massive dunes, the highest being Mount Tempest at 282 metres. These present a low to hilly terrain, while the only older rocks are Ipswich coal measures in the northeastern tip of the island. Acidic peats overlay most of the wetlands, which consist of many inland and coastal freshwater lakes and swamps.

Dominant vegetation is eucalypt open forest and wallum with mangroves and associated vegetation on tidal mudflats, and strand vegetation on coastal dunes. Unlike Fraser Island and North and South Stradbroke Islands, Moreton Island has no rain forest flora (L. Durrington, pers. comm.).

Moreton Island receives a high rainfall (average 1448 mm per annum at Cape Moreton) and during the wet season numerous streams drain from the freshwater swamps into the sea. Elsewhere, water is absorbed quickly, leaving a porous soil deficient in organic material.

Weatherill and Tryon (1908) published a list of 29 species of birds from Moreton Island after a short visit to the settlement of Bulwer, and Geissmann, (1924), added 13 species in her list of 27 species noted in the Cowan Cowan area. Straw, (1968), by the addition of 12 species, brought the island total to 54. This paper brings the current number of species recorded to 120, including those

listed by the previous authors. This compares with 254 species recorded for Stradbroke, (Vernon and Martin 1975), and 200 recorded for Fraser (Vernon and Barry 1972).

Moreton Island is approximately 26 km from the mainland and closely adjoins North Stradbroke and Peel Islands which are situated somewhat closer to the mainland. Many species recorded from the former by Vernon and Martin (1975), and from the latter by Agnew (1913, 1921), also occur on Moreton Island. However, 134 species recorded from Stradbroke are not yet recorded from Moreton Island. The present relatively low number of recorded species can be explained in terms of reduced habitat diversity, lack of trained observers and the moderately difficult access to, and on, the island.

The most common bush birds on Moreton Island are the resident Brown honeyeater, *Lichmera indistincta* and the Noisy friarbird, *Philemon corniculatus*, and these are the most common on Stradbroke Island (Vernon and Martin, 1975). Their prevalence could be attributed to the ready availability of nectar from the flowering Banksias (*Banksia aemula*, *B. integrifolia* and *B. serrata*), which are well distributed throughout the coastal fringes and inland. Three pigeons, the Brown pigeon, *Macropygia phasianella*, the Green-winged pigeon, *Chalcophaps indica*, and the Purple-crowned pigeon, *Ptilinopus superbus* occur in the more densely wooded areas of open forest. They probably migrated from the mainland via Stradbroke Island as all three have been observed on that

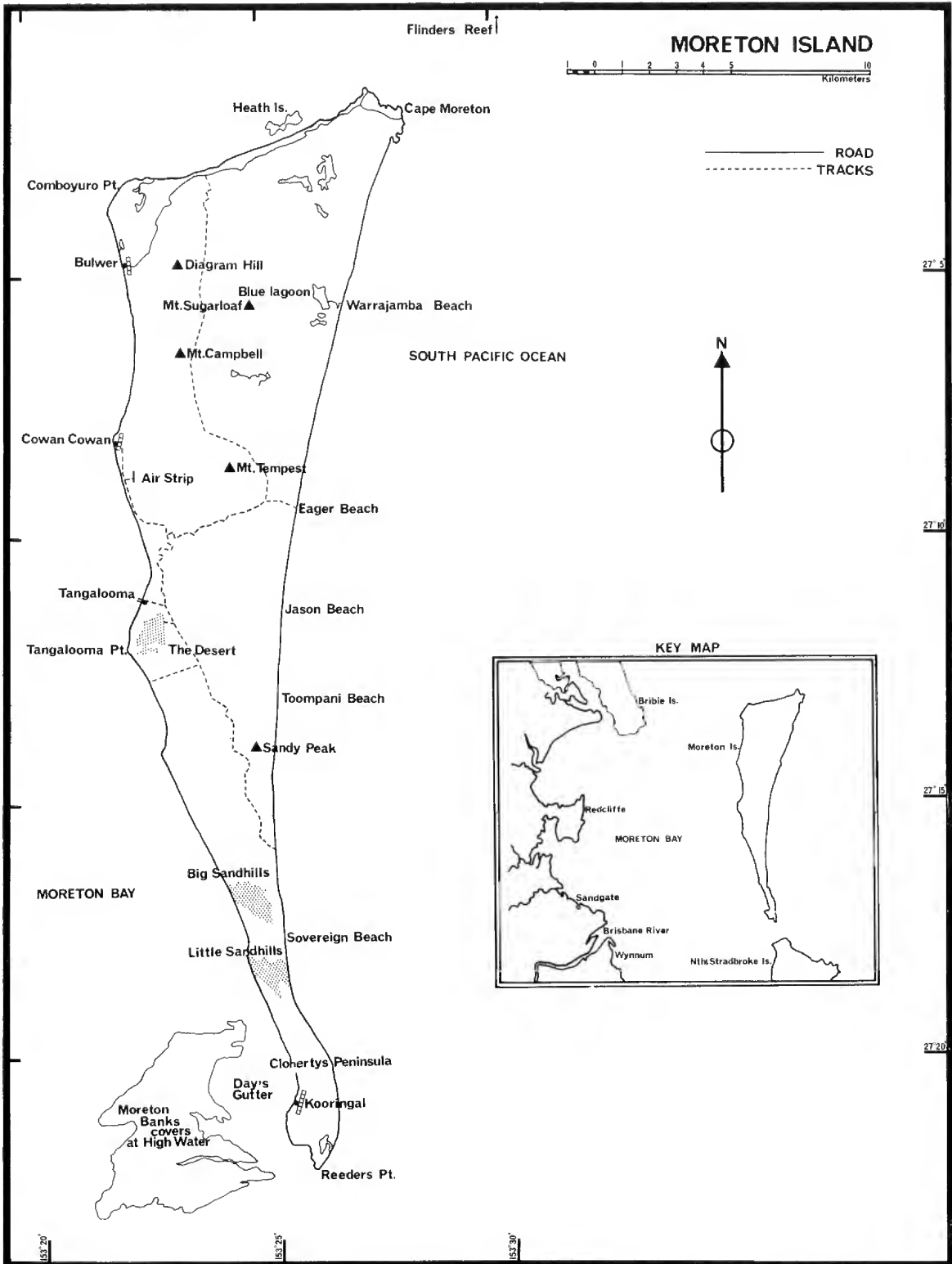


FIG. 1: Moreton Island, showing localities mentioned in the text.

island intermittently. The occurrence of *M. phasianella*, usually a rain forest inhabiting species, is surprising here.

A specimen of the Fleishy-footed shearwater, *Puffinus carneipes*, is recorded for the first time from Queensland. This was found as a beach-washed specimen and confirms sightings of this species in coastal waters (Elks 1966, Hindwood 1945, McKean and Hindwood 1964).

Many of the species which occur on the nearby mainland have not been observed to date. Although no insular forms have been found on Moreton Island, continued work is justified and should proceed in conjunction with the study of all major off-shore islands from Fraser Island to South Stradbroke Island.

The nomenclature used in the list follows Lavery (1969). Where records are based on Queensland Museum specimens, registration numbers (e.g. O11531), locality, and date collected are listed. References to previous records are given in full or abbreviated as follows: W.W. and H.T. = Weatherill and Tryon, 1968; H.G. = Geissmann, 1924; P.S. = Straw, 1968. Where neither registration number nor reference is given, the record is based on sighting by the authors. Prevalence of a species on the island is listed as abundant, common, moderately common, uncommon, or rare; other brief annotations regarding specimens are included where necessary.

SYSTEMATIC LIST

- Diomedea exulans* Wandering Albatross. O11531, east coast, 1.iv.1971. (Uncommon).
- Diomedea melanophris* Black-browed albatross. Flinders Reef. Oct. 1970. G. Ingram pers. comm. (Uncommon).
- Macronectes giganteus* Giant petrel. O11812, Cape Moreton, 12.vii.1971. (Uncommon).
- Fulmarus glacialisoides* Silver-grey petrel. O14802, Eager Beach, 9.x.1973. Vernon and Martin 1974. (Rare).
- Daption capense* Cape petrel. O15679, Cape Moreton. 23.viii.1974. (Rare).
- Pterodroma rostrata* Tahiti petrel. 2 km E. of Tangalooma Point. 8.x.1973, D.P.V. (Rare).
- Puffinus carneipes* Fleishy-footed shearwater. O14803, Eager Beach, 11.x.1973. (Rare, first specimen record for Queensland).
- Puffinus pacificus* Wedge-tailed shearwater. O14830, Eager Beach, 9.x.1973. (Uncommon).
- Puffinus tenuirostris* Short-tailed shearwater. O14912, O14913, Ocean Beach, Dec. 1973. (Uncommon).
- Puffinus gavia* Fluttering shearwater. O15439, Eager Beach, Jan. 1974. (Uncommon).
- Puffinus huttoni* Huttons shearwater. 1 km E. of Reeders Point, 12.viii.1973., Corben, Roberts and Ingram 1974. (Rare).
- Morus serrator* Australian gannet. O14914, Warrajamba Beach. Nov. 1973; O15490, Warrajamba Beach, 14.iv.1974. (Moderately common).
- Phalacrocorax carbo* Black cormorant. (Uncommon).
- Phalacrocorax sulcirostris* Little black cormorant. W.W. and H.T. (Uncommon).
- Phalacrocorax varius* Pied cormorant. O15449, 6 km S. of Tangalooma Point, W.W. and H.T. (Moderately common).
- Phalacrocorax melanoleucos* Little pied cormorant. O14162, Blue Lagoon, 28.iii.1973; O15451 Reeders Point, 11.iv.1974; W.W. and H.T. (Common).
- Ardea pacifica* White-necked heron. W.W. and H.T. (Uncommon).
- Ardea novae-hollandiae* White-faced heron. O15440, 8 km S. of Tangalooma Point, 16.iv.1974; P.S. (Moderately common).
- Butoroides striatus* Mangrove heron. (Moderately common).
- Egretta alba* White egret. (Uncommon).
- Egretta intermedia* Plumed egret. O15436, Heath Island, 16.iv.1974. (Moderately common).
- Egretta sacca* Reef heron. (Uncommon).
- Ixobrychus minutus* Little bittern. (Uncommon).
- Threskiornis molucca* White ibis. (Common).
- Platalea regia* Royal spoonbill. (Moderately common).
- Anas superciliosa* Black duck. W.W. and H.T. (Uncommon).
- Anas gibberifrons* Grey teal. O14822, Clohertys Peninsula, 9.x.73. (Uncommon).
- Biziura lobata* Musk duck. (Moderately common).
- Haliaeetus indus* Red-backed sea eagle. W.W. and H.T. (Moderately common).
- Haliaeetus sphenurus* Whistling eagle. W.W. and H.T., H.G.; P.S. (Uncommon).
- Accipiter fasciatus* Australian goshawk. O15435, 6 km N. of Mount Tempest, 17.iv.1974. (Uncommon).
- Aquila audax* Wedge-tailed eagle. (Uncommon).
- Haliaeetus sphenurus* White-breasted sea eagle. W.W. and H.T.; H.G.; P.S. (Moderately common).
- Pandion haliaetus* Osprey. O15434, 6 km S. of Tangalooma Point, 14.iv.1974. P.S. (Moderately common).
- Falco ceenchoides* Nankeen kestrel. O15437, Cape Moreton, 16.iv.1974. (Uncommon).
- Falco berigora* Brown falcon. (Uncommon).
- Coturnix ypsilophorus* Brown quail. W.W. and H.T. (Uncommon).
- Turnix varia* Painted quail. O15450, 3 km N. of Mount Tempest, 30.iv.1974. (Uncommon).
- Rallus philippensis* Banded landrail. P.S. (Uncommon).
- Haematopus ostralegus* Pied Oystercatcher. O14142, Eager Beach, 27.iv.1973; O14791, O14799, Eager Beach, 8.x.1973; O14142, Jason Beach, 6.iv.1973; P.S. (Common).
- Vanellus novaehollandiae* Spur-winged plover. O14817, 4 km S. of Tangalooma Point, 9.x.1973. W.W. and H.T. (Common).
- Pluvialis squatarola* Grey plover. Moreton Banks, 12.viii.1973, C. Corben pers comm. (Uncommon).
- Charadrius ruficapillus* Red-capped dotterel. O14173, Sovereign Beach, 27.iii.1973; O14789, O15469, Eager Beach, 8.x.73. (Common).
- Charadrius mongolus* Mongolian sand dotterel. O14166, O14167, Sovereign Beach, 29.iii.1973; O14798, Eager

- Beach, 8.x.1973; O15466, Eager Beach, 8.iv.1974. (Common; summer migrant).
- Numenius minutus* Little whimbrel. (Uncommon; summer migrant).
- Numenius phaeopus* Whimbrel. O15438, 6 km S. of Tangalooma Point, 16.iv.1974. (Moderately common; summer migrant).
- Numenius madagascariensis* Eastern curlew. O14165, Sovereign Beach, 29.iii.1973. (Common; summer migrant).
- Limosa lapponica* Bar-tailed godwit. O15462, 6 km S. of Tangalooma Point, 16.iv.1974. (Common; summer migrant).
- Tringa nebularia* Greenshank. (Moderately common; summer migrant).
- Tringa brevipes* Grey-tailed tattler. O15463, O15464, 8 km S. of Tangalooma Point, 16.iv.1974. (Common; summer migrant).
- Tringa incana* Wandering tattler. O14792, 4 km S. of Tangalooma Point, 10.x.1973. (Uncommon; summer migrant).
- Arenaria interpres* Turnstone. O15473, Sovereign Beach, 11.iv.74. (Uncommon; summer migrant).
- Calidris alba* Sanderling. O14800, 2 km S. of Cape Moreton, 11.x.1973. (Uncommon; summer migrant).
- Calidris ruficollis* Little stint. O14221, Sovereign Beach, 29.iii.1973. (Common; summer migrant).
- Calidris acuminata* Sharp-tailed sandpiper. O14789, Clohertys Peninsula, 9.x.1973. (Uncommon; summer migrant).
- Calidris ferrugineus* Curlew sandpiper. (Uncommon; summer migrant).
- Burhinus magnirostris* Southern Stone Curlew. W.W. and H.T. (Uncommon).
- Esacus magnirostris* Beach stone curlew. O14776, Eager Beach, 11.x.1973. W.W. and H.T. (Uncommon; summer migrant).
- Stercorarius skua* Southern skua. (Uncommon).
- Stercorarius parasiticus* Arctic skua. (Uncommon).
- Larus novaehollandiae* Silver gull. O14156, 3 km N. of Tangalooma Point, 28.iii.1973. W.W. and H.T.; H.G.; P.S. (Common).
- Chlidonias leucoptera* White-winged black tern. O15443, Sovereign Beach, 11.iv.74. (Uncommon).
- Gelochelidon nilotica* Gull-billed tern. (Uncommon).
- Hydroprogne caspia* Caspian tern. (Uncommon).
- Sterna hirundo* Eastern common tern. O15445, Sovereign Beach, 11.iv.1974; O15446, Sovereign Beach, 11.iv.1974. (Moderately common).
- Sterna albifrons* Little tern. O14163, Sovereign Beach, 29.iii.1973. H.G. (Moderately common).
- Sterna bergii* Crested tern. O14145-7, Eager Beach, 27.iii.1973; O15444, Sovereign Beach, 11.iv.1974; W.W. and H.T.; H.G. (Common).
- Ptilinopus superbus* Purple-crowned pigeon. O15743, Cape Moreton, 28.xi.1974. (Rare).
- Columba livia* Feral pigeon. (Uncommon).
- Macropygia phasianella* Brown pigeon. O14793, 3 km N. of Tangalooma Point, 11.x.1973. (Rare).
- Geopelia humeralis* Bar-shouldered dove. O13771, Bulwer, 22.viii.1972; O14174, O14175, 2 km S. of Mount Tempest, 27.iii.1973; O14780, O14818, O14819, 2 km W. of Warrajamba Beach, 8.x.1973. W.W. and H.T.; H.G. (Common).
- Chalcophaps indica* Green-winged pigeon. O14784, O14785, 4 km SE. Tangalooma Point, 9.x.1973. (Uncommon).
- Trichoglossus chlorolepidotus* Scaly-breasted lorikeet. P.S. (Moderately common).
- Trichoglossus haematodus* Rainbow lorikeet. W.W. and H.T.; H.G. (Common).
- Cuculus saturatus* Oriental cuckoo. Reeders Point, 10.iv.1974, D.P.V. (Rare).
- Cacomantis pyrrhophanus* Fan-tailed cuckoo. O13774, Bulwer, 22.viii.1972; O15546, Reeders Point, 18.iv.1974. (Moderately common).
- Chrysococcyx lucidus plagosus* Golden bronze cuckoo. O15460. Reeders Point, 11.iv.1974. (Uncommon).
- Centropus phasianinus* Pheasant coucal. O14164, Bulwer, 28.iii.73; O15461, 2 km E. Bulwer, 11.iv.74; O15532, Reeders Point, 18.iv.74; W.W. and H.T.; H.G. (Moderately common).
- Ninox novaeseelandiae* Boobook owl. O14152, 4 km N. of Tangalooma Point, 26.iii.1973; O14788, SE. of The Desert, 8.x.73. W.W. and H.T. (Moderately common).
- Podargus strigoides* Tawny frogmouth. (Uncommon).
- Dacelo gigas* Laughing kookaburra. O14161, 10 km SE. Tangalooma Point, 28.iii.1973; W.W. and H.T.; H.G.; P.S. (Moderately common).
- Halcyon macleayi* Forest kingfisher. O13773, Bulwer, 22.viii.1972; O14157, O14160, Blue Lagoon, 27.iii.1973; O14158, 3 km N. of Tangalooma Point, 28.iii.1973; O14777, 7 km S. of Tangalooma Point, 8.x.1973; O14831, 2 km N. Mount Tempest, 11.x.1973; O15529, 3 km N. Mount Tempest, 18.vi.1974; W.W. and H.T.; H.G.; P.S. (Moderately common).
- Halcyon australasiae* Sacred kingfisher. O15470, Koorringal, 11.iv.1974. (Uncommon).
- Merops ornatus* Rainbow-bird. O14783, Eager Beach, 8.x.1973; H.G. (Moderately common).
- Eurystomus orientalis* Eastern broad-billed roller. (Moderately common).
- Hirundo tahitica* Welcome swallow. O14795, 4 km N. of Tangalooma Point, 8.x.1973; O14796, 3 km S. Tangalooma Point, 9.x.1973; W.W. and H.T.; H.G.; P.S. (Common).
- Petrochelidon nigricans* Tree martin. P.S. (Uncommon).
- Anthus novaeseelandiae* Australian pipit. O14155, Jason Beach, 28.iii.1973, O14826, Toompani Beach, 9.x.1973. O15472, Eager Beach, 10.iv.1974; W.W. and H.T. (Common).
- Coracina novaehollandiae* Black-faced cuckoo-shrike. O15524, 3 km S. Mount Tempest, 18.iv.1974; P.S. (Moderately common).
- Lalage sueurii* White-winged triller. (Uncommon).
- Cisticola exilis* Golden-headed fantail-warbler. O14143, O14144, O14821 Blue Lagoon, 27.iii.1973; O14827, O14832, Eager Beach, 9.x.1973; W.W. and H.T. (Moderately common).
- Acanthiza pusilla* Brown thornbill. (Uncommon).
- Dicaeum hirundinaceum* Mistletoe-bird. O13776, Bulwer, 22.viii.1972. H.G. (Uncommon).
- Pardalotus punctatus* Spotted pardalote. (Uncommon).
- Rhipidura fuliginosa* Grey fantail. O13775, Bulwer,

22.viii.1972; O15467, 3 km S. of Mount Tempest, 8.iv.1974; O15468, 3 km E. Tangalooma Point, 17.iv.1974; H.G. (Moderately common).

Rhipidura leucophrys Willie wagtail. O15471, Reeders Point, 10.iv.1974; H.G. (Moderately common).

Myiagra rubecula Leaden flycatcher. O13777, Bulwer, 22.viii.1972; O15477, Mount Tempest, 10.iv.1974; O15441, 8 km S. Tangalooma Point, 16.iv.1974; W.W. and H.T. (Uncommon).

Myiagra cyanoleuca Satin flycatcher. O15442, Mount Tempest, 8.iv.1974. (Rare).

Petroica cucullata Hooded robin. H.G. (Rare).

Pachycephala pectoralis Golden whistler. O13778 Bulwer, 22.viii.1972; O14786, 3 km S. of Mount Tempest, 8.x.1973; O14829, Mount Tempest, 11.x.1973. (Uncommon).

Pachycephala rufiventris Rufous whistler. O13779, Bulwer, 22.viii.1972; O14456, O14787, O15454-7, O15685, Mount Tempest, 9.iv.1974; H.G. (Moderately common).

Zosterops lateralis Grey-breasted silvereve. O13772, Bulwer, 22.viii.1972; O15453, 5 km N. Tangalooma Point, 9.iv.1974. (Moderately common).

Lichmera indistincta Brown honeyeater. O13782, O14360, Bulwer, 22.viii.1972; O14149, O14151, 3 km N. of Tangalooma Point, 29.iii.1973; O14781, 4 km NW. Tangalooma Point, 8.x.1973; O14782, O14824, O14825, Koorringal, 9.x.1973; O14823, Mount Tempest, 11.x.1973; W.W. and H.T.; H.G. (Abundant).

Myzomela dibapha Scarlet honeyeater. O13781, Bulwer, 22.viii.1972; O15680, O15681, O15683, 5 km NE. of Tangalooma Point, 18.iv.1974. (Moderately common).

Meliphaga fasciogularis Mangrove honeyeater. O14794, O14828, 1 km N. Day's Gutter, 9.x.1973. (Uncommon).

Meliphaga chrysops Yellow-faced honeyeater. W.W. and H.T. (Uncommon).

Phylidonyris novaehollandiae New Holland honeyeater. H.G. (Uncommon).

Phylidonyris niger White-checked honeyeater. O13780, Bulwer, 22.viii.1972; O14148, O14790, Eager Beach, 27.iii.1973; O15452, 5 km NW. Tangalooma Point, 9.iv.1973; W.W. and H.G.; H.G. (Common).

Philemon corniculatus Noisy friarbird. O14141, 3 km SE. Tangalooma Point, 29.iii.1973; O14779, 6 km NE. Tangalooma Point, 8.x.1973; W.W. and H.T.; H.G. (Abundant).

Philemon citreogularis Little friarbird. H.G. (Uncommon).

Manorina melanocephala Noisy miner. (Uncommon).

Artamus leucorhynchus White-breasted woodswallow. O14797, Koorringal, 10.x.1973; O15474, 3 km SW. Cape Moreton, 17.iv.1974. (Moderately common).

Carduelis carduelis Gold finch. (Uncommon).

Passer domesticus House sparrow. (Uncommon).

Oriolus sagittatus Olive-backed oriole. O15458, 3 km N. of Mount Tempest, 10.iv.1974. (Uncommon).

Dicrurus hottentottus Spangled drongo. O14778, Mount Tempest, 11.x.1973; O15459, Bulwer, 10.iv.1974; H.G. (Moderately common; summer migrant).

Grallina cyanoleuca Magpie lark. (Moderately common).

Cracticus torquatus Grey butcher-bird. O14361, Bulwer, 22.viii.1972. (Moderately common).

Gymnorhina tibicen Black-backed magpie. (Uncommon).

Corvus orru Crow. O14153, O14154, 4 km N. Tangalooma Point, 26.xi.1973; W.W. and H.T.; H.G. (Common).

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A NEW SPECIES OF *KYARRANUS* (ANURA: LEPTODACTYLIDAE) FROM QUEENSLAND, AUSTRALIA

GLEN J. INGRAM
Queensland Museum
and
CHRISTOPHER J. CORBEN
Wildlife Research Group, P.O. Box 867, Fortitude Valley

ABSTRACT

Kyarranus kundagungan sp. nov, a ground-dwelling rainforest frog from the Great Dividing Range of southeast Queensland, is characterised by its robust pear-shaped body, bright red to black dorsal surface, and immaculate yellow surface with a red patch on the throat. Notes are provided on its habitat, call, ova, and larvae.

In the course of studying frogs of southeastern Queensland, the authors discovered an undescribed species near Cunningham's Gap, on the Great Dividing Range. The species is a member of the montane genus, *Kyarranus* Moore. Further searching located it 20 kilometres north at Mistake Mountains, and 19 kilometres south at Teviot Falls.

Abbreviations used in text are: EN = eye to naris distance; IN = internarial span; HW = head width; TL = tibia length; SV = snout to vent length. Institutions in which specimens are deposited are: QM = Queensland Museum, AM = Australian Museum, NMV = National Museum of Victoria, SAM = South Australian Museum, WAM = West Australian Museum, QVM = Queen Victoria Museum.

Kyarranus kundagungan sp. nov.

MATERIAL EXAMINED

HOLOTYPE: Adult female, QM J23944, from Mistake Mountains (Lat. 27°53'S, Long. 152°21'E), about 800 metres above sea level, and 83 kilometres southwest of Brisbane, SE. Queensland, collected by C. J. Corben and A. K. Smyth, 3 January 1974.

PARATYPES: QM J23945, SAM R13921-2, WAM R45071, QVM 1974/4/1, collected 3 January 1974 by C. J. Corben and A. K. Smyth at type locality. QM J22677-81, AM R38193-4 (1 December 1972), NMV D33826 (26 June 1973), collected by G. J. Ingram and C. J. Corben at Lat. 28°04'S, Long. 152°24'E. QM J23946, collected 3 January 1974 by G. J. Ingram at Teviot Falls (Lat. 28°14'S, Long. 152°29'E.).

OTHER MATERIAL: D. S. Liem collection 6817, Cunningham's Gap, Qd.

DEFINITION

A small squat frog (SV 23.8-29.9) of montane rainforests, characterised by its robust, pear-shaped body, bright red to black dorsal surface, immaculate yellow ventral surface with red patch on throat, unwebbed fingers and toes, concealed tympani, first finger shorter than second, and vomerine series behind level of choanae.

DESCRIPTION OF HOLOTYPE

Body robust, pear-shaped; in profile, snout slopes anteriorly to a blunt tip; canthus rostralis distinct and concave; pupil horizontal; tympanum concealed; tongue large, posterior edge free; vomerine teeth in two straight series, posterior to, and extending to medial edges of, choanae.

No webbing on fingers or toes; fingers in decreasing order of length are $3 > 2 > 4 > 1$; inner and outer palmar tubercles small but distinct. Large flange along inside edge of second finger. Hind limbs short; toes cylindrical, with small tubercles at proximal joints; toes in decreasing order of length are $4 > 3 > 5 > 2 > 1$; inner metatarsal tubercle small and at base of first toe; no outer metatarsal tubercle. Skin smooth.

Dimensions: SV 25.0; TL 11.0; HW 8.1; EN 2.0; IN 2.9; TL/SV = 0.44; HW/SV = 0.32; EN/IN = 0.70.

Colouration in life: On body, dorsal surface bright purplish-red (Pompeian red of Ridgway

1912), with two black (Dull violet black of Ridgway) V-shaped markings on back originating medially, and extending posteriorly towards inguinal regions; lips edged yellow, with fine black barring; heavy black band extends from nostrils to eye, and from eye towards arm; black patch on lateral surface between arm and leg; ventral surfaces bright yellow (Strontian yellow of Ridgway), with an extensive diffuse red patch on throat; cloaca, inguinal and axillary regions yellow. On forelimbs, dorsal surface black with yellow round base of arm; ventral surface yellow; palm brown and fingers yellow with black bands on third and fourth. On hindlimb, dorsal surface black; ventral surface yellow; posterior surface of tarsus and sole of foot black. In alcohol all yellow regions have turned white.

VARIATION

Female paratypes (AM R38194, NMV D33826, QM J23945) do not differ much from holotype in dimensions and proportions: SV 23.8–25.4 (mean 24.5); TL 9.8–10.4 (10.0); HW 8.6–9.2 (8.8); EN 1.8–1.9 (1.9); IN 2.8–3.1 (2.9); TL/SV 0.34–0.43 (0.39); HW/SV 0.36–0.39 (0.38); EN/IN 0.61–0.68 (0.64). Dimensions of male paratypes are similar to those of females: SV 23.8–29.9 (26.2); TL 9.9–11.9 (10.8); HW 7.8–9.9 (9.0); EN 1.6–2.2 (1.9); IN 2.6–3.4 (3.0); TL/SV 0.38–0.44 (0.41); HW/SV 0.31–0.39 (0.34); EN/IN 0.53–0.74 (0.63).

In most specimens the vomerine series do not extend to the medial edges of the choanae. Males in breeding condition show extensive dark brown nuptial pads on the dorsal surfaces of the first fingers. (Fig. 1B). Breeding females show flanges on second fingers, as in holotype (Fig. 1A). Fingers of males in decreasing order of length are $3 > 2 = 4 > 1$. The head stripe is variable in extent and intensity. The dorsal colouration varies from one extreme where the entire dorsal surface is bright red, to the other where the red is replaced by black. J22680–1 and J23945–6 have turned brown from preservation.

In most individuals the red colouration on the throat is confined to a small diffuse patch, but in some the throat is entirely red and sharply delimited from the rest of the under-surface.

LARVAL MORPHOLOGY

The following description applies to typical larvae in stages 31 to 33. Eight such larvae had total lengths between 16.6 and 19.0 mm (mean 18.0).

The body is widest across the mid-region of the abdomen, and at this point it is slightly wider than deep. The snout is evenly rounded from both dorsal

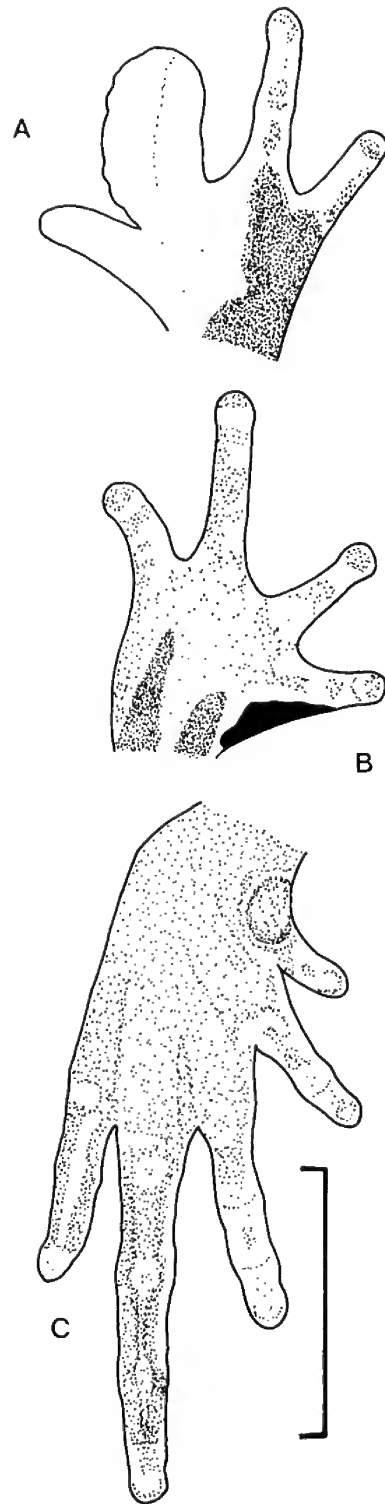


FIG. 1: A. Ventral view of hand of female in breeding condition (AM R38194). B. Ventral view of hand of breeding male. C. Ventral view of foot of female (AM R38194). (Scale line 5 mm).

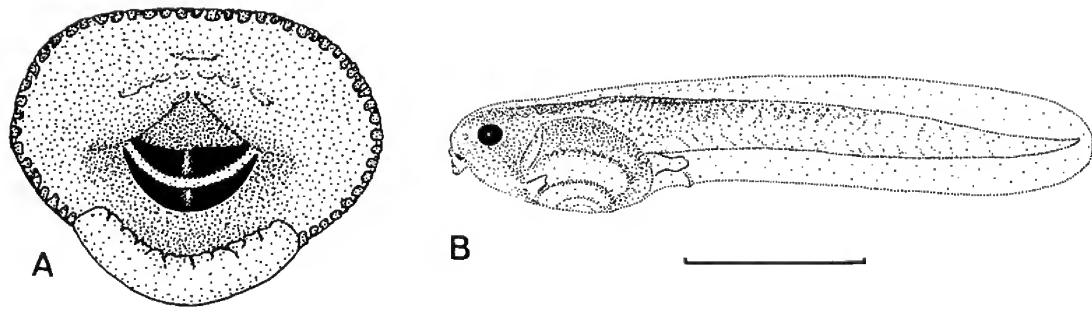


FIG. 2: A, Mouthparts of stage 31 larva. B, Lateral view of stage 31 larva (Scale line 5 mm).

and lateral views. The nares are widely spaced, being positioned dorso-laterally in line with the eyes. They open in an antero-lateral direction. The eyes are dorso-lateral in position and variable (in diameter) from quite small to fairly large. The spiracle is sinistral, lateral in position and visible from above. It opens posteriorly and increases in diameter from the opening to the origin. The anal tube is median and quite prominent, opening well out from the body at the edge of the ventral fin.

The mouth is antero-ventral in position and opens anteriorly. There is a single row of peripheral papillae around all but the upper median two-thirds of the disc where a partially involuted flap of skin forms a pocket (Fig. 2A). There are no labial tooth rows. In some specimens, the lower labium bears broken papillae-like ridges arranged somewhat in rows.

The curved beaks both have fine serrations. The upper beak is a little less massive than the lower.

In preserved specimens, the dorsal surface is lightly pigmented, the density increasing over the brain and spinal cord regions and over parts of the intestinal mass. In lateral view, the pigment partly extends over the gill region and the intestinal mass. The ventral surface is clear. The dorsal surface of the tail musculature is lightly stippled over most of its length, the pigment decreasing posteriorly. Laterally it scatters over the anterior half of the musculature. The dorsal fin is sparsely stippled while the ventral fin is clear or with occasional flecks. The iris appears black.

FIELD NOTES

Kyarranus kundagungan is a ground-dwelling frog of sub-tropical rainforest in mountainous areas. It is known only from very damp situations, particularly saturated leaf-litter and mud in soaks or small creek beds. In such sites, males call from water-filled cavities covered with rocks or leaf-litter. Calling takes place from late August to mid-February.

Egg masses have been found in late November and early December. The foam mass resembles that described by Moore (1961) for *K. loveridgei*. The albumen is very wet and sticky with air bubbles mainly at the top and the large cream-coloured eggs concentrated at the bottom. The eggs are about 3.1 mm in diameter and are contained in individual jelly capsules of approximately 4.9 mm diameter.

Tadpoles have been found in typical water-filled cavities, and groups of newly metamorphosed larvae in drier hollows. Juvenile frogs have been located in January and late August, the latter presumably being progeny from the previous season. Very young individuals are blackish with variable amounts of white speckling on the ventral surfaces.

Vertebrates found synchronosympatric with *K. kundagungan* were: *Lechriodus fletcheri*, *Mixophyes fasciolatus*, *M. balbus*, *Litoria pearsoni*, *Lampropholis challengerii* (Challenger Skink), *Tropidechis carinatus* (Rough-scaled Snake), and *Melomys cervinipes* (Mosaic-tailed Rat) at Cunningham's Gap; *Adelotus brevis*, *Lechriodus fletcheri*, *Mixophyes fasciolatus*, *Litoria pearsoni*, *L. leseurii*, and an undescribed *Litoria* belonging to the *ewingi* group, and *Anomalopus truncatus* at Teviot Falls; *Adelotus brevis* at Mistake Mountains.

COMPARISON WITH OTHER SPECIES*

Kyarranus kundagungan is markedly different from *K. sphagnicolus* and *K. loveridgei* in exhibiting the distinctive red, black and yellow colouration. *Kyarranus sphagnicolus* has a more rounded, wider head and longer tibia (TL/SV 0.45–0.50), the dorsal ground colouring is grey to reddish brown, the

*Based on examination of 29 specimens of *K. loveridgei* in the Queensland Museum collections (from Lamington Plateau, 35 km S. of Boonah, and Mt. Warning) and 2 specimens of *K. sphagnicolus* (from Pt. Lookout).

ventral surface white to brown and the throat darkly mottled. Breeding females have flanges on both first and second fingers. The call of *K. sphagnicolus* is described by Moore (1961) as a soft growl 'gurr-r-r', quite different from that of *K. kundagungan*, which is a deep guttural 'ork'. It is difficult to distinguish between the calls of *K. loveridgei* and *K. kundagungan*.

Kyarranus loveridgei and *K. kundagungan* are similar in shape, size and habitat. *Kyarranus loveridgei* has SV 21.7–30.2 (26.4), TL/SV 0.35–0.46 (0.41), HW/SV 0.31–0.39 (0.35) and EN/IN 0.50–0.83 (0.63). However, *K. kundagungan* is more robust and pear-shaped, and the canthus rostralis is usually less defined than that of *K. loveridgei*. The dorsal colouring of *K. loveridgei* is grey to brown, the ventral surface is whitish to grey with darker speckling, and the throat has brown mottling, while *K. kundagungan* has a dorsal ground colouring of bright red to black, the ventral surface is immaculate yellow, and the throat has a diffuse red patch or is completely red. Male *K. loveridgei* may be found calling from cavities anywhere on the forest floor, especially along creeks, whereas *K. kundagungan* is confined to wet patches in creeks and soaks. The cavities of *K. loveridgei* are smooth-walled, in moist earth, and contain no water. The eggs are placed in these, and the tadpoles when present, are in liquified jelly. (Moore, 1961, reports similar observations). The cavities of *K. kundagungan* are filled with water which can freely seep in and out, and in which the eggs are laid and the tadpoles swim during development.

Moore (1961) suggests that *K. loveridgei* could lack nuptial pads, however breeding males of both it and *K. kundagungan* possess similar nuptial pads on the dorsal surfaces of the first fingers.

ETYMOLOGY

The name *kundagungan* is derived from the words 'kunda', mountain, and 'gungan', frog, from the dialect of the Kabi tribe, that once lived in south-east Queensland.

DISTRIBUTION

Currently known from Mistake Mountains (the type locality) in the north, south along the Great Dividing Range to Teviot Falls.

DISCUSSION

Spencer (1901) named *Phyloria frosti* from Mt. Baw Baw, Victoria. Parker (1940) described *Phyloria loveridgei* from the McPherson Range, SE Queensland. Moore (1958) concluded that *loverid-*

gei was generically distinct from *P. frosti* and referred the former and a new species (*sphagnicolus*, from Pt. Lookout, near Ebor, New South Wales) to a new genus, *Kyarranus*.

The status of *Kyarranus* has been the subject of controversy. The similarity between *Kyarranus* and *Phyloria* in adult and larval morphology, and ecology has been commented on by several authors. Brattstrom (1970) indicated his intention to synonymise these two genera, (a move which Watson and Martin, 1973, supported by evidence from life histories). However, Lynch (1971) considered the two genera to be superficially similar, reflecting parallel adaptation to a montane environment, and suggested that they represent the result of independent divergence from a *Limnodynastes*-like ancestor. Tyler (1972) recognised both genera when describing the superficial mandibular musculature and vocal sacs, and reviewing the phylogeny of Australo-Papuan leptodactylids. As currently recognised, *Kyarranus* consists of two species groups, one containing *K. sphagnicolus*, the other including *K. loveridgei* and *K. kundagungan*. These groups resemble each other considerably more than either resembles *Phyloria*. The authors consider that with the data presently available it is best to recognise *Kyarranus* as a distinct genus.

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PLATE 42

Kyarranus kundagungan, live specimen, Cunningham's Gap.







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