

RESULTS OF THE ARCHBOLD
EXPEDITIONS. NO. 59

STUDIES ON THE ANATOMY AND
PHYLOGENY OF THE MACROPO-
DIDAE (MARSUPIALIA)

G. H. H. TATE

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ERRATUM

Insert lines 30 through 50 (Subfamily Macropodinae), column 1, page 278, lines 1 through 53, column 2, page 278, and lines 1 through 4, column 1, page 279, after line 40, column 2, page 270 (before the paragraph beginning "The primitive permanent incisive series . . .").

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INTRODUCTION

THIS PAPER IS CONSTRUCTED primarily around the genera and species of Macropodidae contained in the Archbold collection. The important collection obtained by the late H. C. Raven in Australia and Tasmania and that of Miss G. N. Uhäuser in Queensland have also been employed. The work has been greatly aided and amplified by study of other collections in America. I am indebted to Miss Barbara Lawrence of the Museum of Comparative Zoölogy and to Drs. Remington Kellogg and David H. Johnson of the United States National Museum for allowing me unlimited access to the large and valuable collections of Macropodidae in their charge, and also to Mr. C. C. Sanborn of the Chicago Natural History Museum for the loan of certain species of *Potorous* and *Dorcopsis*. To Dr. Johnson, and to Mr. T. C. S. Morrison-Scott of the British Museum (Natural History), I express thanks for information on the genus *Peradorcas* in their collections. For access to the field records of the Harvard Australian Expedition I am further indebted to Miss Lawrence and to Dr. P. J. Darlington.

A map (fig. 1) gives, it is hoped, most of the localities alluded to in the paper.

Following the description of *Thylogale brunii* by Bruijn in 1714, the finding of *Protemnodon eugenii* by Pelsart in 1629, the discovery of the giant kangaroo by Captain Cook and its scientific recognition by Müller in 1776, and the description of the rat kangaroo, *Potorous tridactylus*, by Kerr in 1792, the earliest comprehensive account of the Macropodidae of importance seems to be the "Dissertation sur les animaux à bourse" by Etienne Geoffroy Saint-Hilaire (1796). This article probably forms the basis of Desmarest's work in "Nouveau dictionnaire d'histoire naturelle" (1804, and later editions).

From then onward additional genera and species of kangaroos and wallabies were recorded with increasing frequency by a large number of scientists. A climactic point in macropodid study was reached temporarily with the publication of J. Gould's "A monograph of the Macropodidae" (1841-1842) and Waterhouse's two books, "Marsupialia, or pouched animals," forming volume 24 in "The naturalist's library," and "Natural history of the Mammalia, Marsupialia."

During the next 20 years numerous

workers, among whom should be mentioned Garrod, Owen, Giebel, Flower, Schlegel, Müller, De Vis, and Krefft, contributed a wealth of further information to our knowledge of the family, and this was brought to a second climax by the appearance of Thomas' invaluable "Catalogue of the . . . Marsupialia and Monotremata in the . . . British Museum (Natural History)" (1888).

By that year almost all the living genera had been made known as well as a large proportion of the species, many of which were already threatened with extinction by the rapid settlement of Australia. Only the genera *Peradorcas* and *Wallabia* remained undifferentiated, although the species upon which each was founded were already well known.

Much of the work that has appeared since 1890 relates to the evolution of the marsupials (e.g., Dollo, 1898; Bensley, 1903) and to the anatomy, paleontology, physiology, and function of these animals.

Henry C. Raven, who studied the Macropodidae in Australia and Tasmania during the years 1921 and 1922, had commenced a phylogenetic study which was still incomplete at the time of his death. A condensation embodying his conclusions has since been published (Raven and Gregory, 1946). Those authors, after setting forth briefly the leading evolutionary characteristics of the kangaroos, divided the family Macropodidae into four subfamilies: the Hypsiprymnodontinae, the Potoroinae, the Sthenurinae (extinct), and the Macropodinae. Simpson, a year earlier (1945), had combined some of these subfamilies: he had placed *Hypsiprymnodon* in the Potoroinae and united the Sthenurinae and Macropodinae. He had left the extinct Pleistocene Burramyinae, which seems to stand quite close to *Hypsiprymnodon*, as a subfamily of the Phalangeridae. Much earlier, Bensley (1903) had divided the Macropodidae into three subfamilies: Macropodinae, Potoroinae, and Bettongiinae. He had thrown *Hypsiprymnodon*, *Bettongia*, and *Aepyprymnus* into the last named. From an investigation of the structure of their urogenital systems, Pearson has recently (1946) concluded that the Potoroinae plus the Hypsiprymnodontinae were derived independently of the Macropodinae from Phalangerioidea. He has proposed for them family rank.

PART 1. ANATOMICAL AND PHYLOGENETIC NOTES

THE TRUE MACROPODIDAE are usually considered to be the descendants of remote ancestors of the modern Phalangeridae. They can be distinguished from all Phalangeridae by the fact that both the upper and the lower third premolars, which are well developed and functional in the young (even though shed before or with the eruption of p_4^1), are morphologically very similar to the permanent fourth premolars. In all macropods except the extinct Sthenurinae, *Palorchestes*, and *Burramys*, p_{3-4}^2 are more or less narrowed and blade-like teeth. The fourth premolars in the Sthenurinae and *Palorchestes* possess the generally conical profile and ovoid or subtriangular appearance of p_4^1 of *Phalanger*. The third premolars of *Burramys* are apparently vestigial. The deciduous fourth premolars of all Macropodidae are so highly molarized as to be scarcely distinguishable from true molars. Deciduous fourth premolars of this markedly molariform type are not found among the Phalangeridae.

Extreme lengthening and narrowing of both p_3^2 and p_4^1 is characteristic of *Potorous* and its allies. Those teeth are further characterized in most potorine genera by regular vertical flutings present on both the lingual and the buccal faces of the teeth. Occlusion in this group produces a highly perfected shearing action capable of cutting off quite tough twigs. A weakly analogous development of p_3^2 and p_4^1 can be seen in *Dorcopsis* of the Macropodinae. The type of p_4^1 found in the Potorinae is carried to its optimum state of development in the case of the extinct *Thylacoleo*. However, in that animal the lateral vertical flutings are absent as in *Potorous*.

The shape of the high, fluted p_4^1 of *Hypsiprymnodon* and its extinct allies diverges from that of *Potorous*. The crown, instead of being elongate, low, and linear, is short, extremely high, and arched. This type of fourth premolar is closely matched by the fourth premolars of the extinct genera *Burramys* and *Propleopus* (= *Triclis*) and by those of the quite unrelated multituberculate *Plagiaulax*. Whether or not we place *Hypsiprymnodon* in the same subfamily with *Bettongia* and

Potorous, it nevertheless represents, probably with *Burramys* and *Propleopus*, a distinct division of macropodid genera.

Palorchestes, associated by Raven and Gregory (1946) with *Sthenurus*, presents such marked peculiarities of the palate, the first molar, and especially the fourth premolar that it is better placed in a subfamily by itself, the Palorchestinae.

The use of the tail as a balancing organ (as in *Dendrolagus* and *Petrogale*) instead of as a prop or third leg (*Macropus*, *Osphranter*, and most other genera) may show retention of a primitive function rather than a reversion to it. Although a modified tactile area of skin near the tip of the tail combined with active prehension is present in almost every genus of the Phalangeridae, and all the Phalangeridae are scansorial, such conditions are normally absent from the Macropodidae (weak prehension is reported in *Bettongia penicillata*), and only *Dendrolagus* is truly scansorial. Such being the case, one must exercise caution in assuming that the Macropodidae are derived from primitive Phalangeridae. Such an ancestral phalangerid had not then evolved the present prevalent system of caudal prehension.

It is clear that the Macropodidae exhibit other important and possibly fundamental characteristics not foreshadowed in any living Phalangeridae. Such new characteristics include partial or complete bilophodontism of the molars, increase in size of the posterior molars in proportion to the anterior ones, molarization of dp_4^1 , the special secant form of p_3^2 and p_4^1 , the masseteric foramen, the elongate macropod foot. Both the Phalangeridae and the Macropodidae show diprotodontism, syndactyly, and a forwardly opening pouch. The leaping type of hind foot, even the relatively unspecialized foot of *Hypsiprymnodon*, is already far removed both morphologically and functionally from the grasping phalangerid foot, even though the striated pads of *Hypsiprymnodon* may represent a hold-over from an earlier arboreal stage. This was discussed in detail by Bensley (1903).

CRANIAL CHARACTERS

In the Phalangeridae moderate brachycephaly with short, tapered muzzle seems to be normal (*Phalanger*, *Trichosurus*, *Cercartetus*, *Acrobates*, *Petaurus*, *Pseudocheirus*). Variations from this type of skull occur only as exceptional flattening (*Dactylopsila*, *Petro-pseudos*) or extreme secondary elongation of the muzzle (the aberrant *Tarsipes*). Moderate dolichocephaly, combined with considerable lengthening of the muzzle and diastema, must have become established very early in the evolutionary development of the kangaroos (*Hypsiprymnodon*; *Potorous* among the Potoroinae; most of the Macropodinae). It is uncertain whether or not the brachycephalic condition of *Bettongia*, *Caloprymnus*, *Aepyprymnus*, and *Dendrolagus* is secondary. The two divergent tendencies (1) towards extreme compression of the muzzle (*Petrogale*, *Peradorcas*, *Lagorchestes*) and (2) towards the relatively massive (though elongate) muzzle, sometimes with inflated sides (*Macropus*, *sensu stricto*, *Osphranter*, *Protemnodon* *bicolor*, and the extinct *Palorchestes*) are both new departures. The short, massive muzzles of *Dendrolagus* and of the fossil *Sthenurus* almost surely represent secondary changes.

In the mastoid-squamosal region of the skull, complete smooth union of the mastoid to the squamosal region of the zygoma, above the auditory meatus, is virtually universal in the Phalangeridae. The same is true only in very few of the Macropodinae (some *Petrogale*, *Dendrolagus*) and is generally untrue in the Potoroinae. In most of the large kangaroos and large wallabies the back of the squamosal root contains a large foramen which opens just above the meatus. The body of the parietal may also show a large perforation close to the root of the zygomatic process (*Wallabia dorsalis*, etc.), or there may be extensive fenestration at the junction of the squamosal and the parietal immediately anterior to the lambdoidal crest (*Wallabia bicolor*).

In the marsupial premaxilla the nasal process normally terminates posteriorly at the union of the maxillary and nasal bones. Most commonly wedge shaped, it may instead be truncated (some Dasyuridae and

Phalangeridae). But in the case of the tusk-bearing phalangerid genera *Dactylopsila* and *Dactylonax*, the premaxilla occupies nearly the whole genal area and, making broad contact with the frontal, lacrimal, and jugal bones, completely excludes the maxilla from its usual contact with the nasal. In the diprotodonts, a possible approach to this same condition can be inferred from published drawings of skulls, even though in those drawings the position of the maxillo-premaxillary suture is often either ill defined or omitted. In *Phascolarctos*, though only narrow contact occurs between the premaxilla and frontal, extreme enlargement of the premaxilla in proportion to the maxilla is not found. No condition such as that described above appears in the Macropodidae. Instead the naso-maxillary junction is invariably broad as in *Phalanger*.

Inflection of the angle of the mandible, a widespread marsupial character, occurs commonly in all the large families. In certain phalangerids secondary reversal of this condition is found: the angular process is scarcely at all inflected in *Phascolarctos*; it is virtually uninflected in *Dactylonax* and *Dactylopsila*; the same is true in *Nototherium* and its allies. In the Macropodidae, so far as known, the angle is invariably strongly inflected.

The macropodid mandible shows a further peculiarity that can be completely matched in no genus of the Phalangeridae. The masseteric fossa on the exterior face of the mandible is prolonged forward and downward through a large foramen and joins the canal of the mandibular nerve. This is the masseteric foramen and canal (Abbie, 1939). In the Potoroinae, including *Hypsiprymnodon*, this opening has become very much larger than the true mandibular foramen inside the mandible accommodating the inferior dental nerve. Its function is obscure. In some genera of Macropodinae it is less markedly developed than in the Potoroinae. In the Phalangeridae excavation of the masseteric fossa is rarely found, and its union with the nerve canal is either absent (*Phalanger*) or variably represented by a very small pore (some *Dactylopsila* and *Pseudocheirus*). It may be present in one jaw and not in the

other. On the contrary the masseteric fossa is always well excavated in the Macropodidae,

and the communication with the nerve canal is sometimes very large.

DENTAL CHARACTERS

INCISORS

The three upper incisor teeth of most marsupials (more are found in the Dasyuridae, the Peramelidae, and the American family Didelphidae) are usually so arranged that i^1 is the largest, while i^2 and i^3 play subsidiary roles. This is true throughout the Phalangeridae and many Macropodidae. The peculiar delayed eruption of i^1 found in the Dasyuridae, the Didelphidae, and in *Phalanger* is less marked in the kangaroos, and in both subfamilies secondary enlargement of i^3 occurs (*Aepyprymnus* in the Potoroinae, the large kangaroos and *Thylogale* in the Macropodinae). The unenlarged condition of i^3 in *Petrogale*, *Dorcopsis*, and *Dendrolagus* is here considered to be a less-specialized stage.

The first incisors of the Macropodidae usually appear to grow persistently, as do the incisors of rodents. In the Potoroinae they are tapered towards the tip and become slightly broader as their continuing eruption and accompanying abrasion progress. In the Macropodinae there comes in age a second narrowing of i^1 , which indicates that the very long enamel-bearing crown has worn down and that the narrower, enamelless root is appearing in its turn.

The crown lengths of the second and third incisors tend to become shorter as the crowns become abraded. The crown becomes less elongate in section as it wears down towards its more or less rounded root. Not only do the crowns become quickly worn, but their anterior and posterior portions are frequently chipped and broken soon after eruption by pressures exerted when the animals bite. The elongate premolars, which stand upon two or three roots, often considerably exceed them anteriorly. Their crown lengths also become shortened by attritional wear in much the same way as those of the incisors.

It is evident that a certain amount of movement takes place between tightly pressing contiguous cheek teeth. This movement results in shortening of the body in the long-erupted tooth by abrasion of the anterior and posterior shelves—the “prebasal” and

“postbasal” ridges of Owen (1874, p. 248). Because of such attrition the over-all lengths of the earlier erupted molars of old animals tend to be appreciably shorter than those of young animals. This wear must be allowed for when making comparisons for systematic purposes (Wood, 1938).

In polyprotodont marsupials i^1 differs in its mode of development from i^2 and i^3 . It is usually sharply distinct from those teeth morphologically and is erupted later in life, namely, at approximately the same growth stage as the canine and m^1 . The first upper incisors of the diprotodonts are not erupted so late. Both in the Phalangeridae and in the Macropodidae they include two distinct types. One form of i^1 is a straight, peg-like tooth, which may be either orthodont (*Potorous*, *Pseudocheirus*) or proödont (*Nototherium*, *Dactylopsila*). The other form of i^1 is a tooth weakly or strongly curved forward and downward (*Trichosurus*, *Phalanger*, *Hypsiprymnodon*, *Aepyprymnus*, *Macropus*, etc.). If these two types of i^1 really have phylogenetic significance, that significance obviously cuts across some of the currently established family divisions.

When working on other groups—Dasyuridae (Tate, 1947), *Phalanger* (1945a), and *Pseudocheirus* (1945b)—I pointed out that i^2 is the first tooth developed of the three incisors. It is normally flat crowned and may perhaps be employed by the pouch young to help hold the nipple. In *Phalanger*, *Trichosurus*, and *Petaurus* i^2 is opposed in the lower jaw by a minute, rounded, but (in the pouch stage) still functional i_2 . This lower tooth is not found in *Pseudocheirus*, *Dactylopsila*, or the Macropodidae. Its functional place is taken perhaps in the last mentioned by the tip of the newly erupting i_1 .

The third incisor in the Phalangeridae may serve either as a nipping tooth (*Trichosurus*) or a cutting tooth (*Phalanger*, *Pseudocheirus*, *Macropus*). Sometimes in the Macropodidae (*Aepyprymnus*, *Thylogale*, *Macropus*) it becomes exceptionally large. Usually it remains fairly small (*Hypsiprymnodon*, *Petrogale*, *Setonix*). It is erupted later than i^2 .

In the comparatively unspecialized phalangers (*Trichosurus*) although the ends of the crowns of all three incisors, i^{1-3} , wear against the tip of i_1 , i^3 remains little abraded. In *Phalanger celebensis* a rodent-like type of occlusion is found, the only upper incisor provided with a flat crown being i^2 , while i_1 cuts behind i^1 and seemingly fails to reach i^3 . The same condition prevails in *Pseudocheirus*. An unusual form of incisive occlusion may be seen in the tusk-bearing *Dactylopsila* and *Dactylonax*. In those genera the tip of i_1 wears against the inner face of the enlarged, proodont i^1 , while in turn the tips of i^2 and i^3 wear against the inner face of i_1 . Occlusion of a somewhat similar nature seems to have occurred in the incisors of the extinct Diprotodontidae. In the Macropodinae and allied genera extreme abrasion of i^1 and i^2 is usual and this soon extends to i^3 .

The existence and position of vertical grooves on the outer face of i^3 (and sometimes i^2) appear to be confined, among the kangaroos, to the Macropodinae. In most genera a single groove is seen on the labial face of the tooth halfway, or rather more, from its anterior edge. This position is regarded as typical. In *Thylogale* the position of the groove, almost or wholly at the back of the tooth, is considered a specialization. In *Macropus canguru* (= *giganteus*) there are two such grooves on the labial surface of i^3 . Thus the form of i^3 in the Macropodinae may be defined as characteristically unenlarged and provided with but one weak or incipient groove about halfway back on the labial surface (*Petrogale*, *Dorcopsulus*, *Dendrolagus*, etc.). Genera in which i^3 is enlarged, even though the groove is not at the back of the tooth, are also held to be specialized (some *Protemnodon*, *Macropus*, and *Osphranter*).

CANINES

The canines are large, functional teeth in the Didelphidae, Dasyuridae, and most Peramelidae. In most Phalangeridae (*Phalanger*, *Trichosurus*, *Eudromicia*, and *Petaurus*) the upper canines are large, but in *Dactylopsila* and *Pseudocheirus* they are small and seem to function as part of the incisive series. Lower canines are absent in all diprotodonts.

The upper canines of the Macropodidae have undergone considerable reduction in

size. In the Potoroinae (except *Caloprymnus*) and in *Hypsiprymnodon* this reduction is not extreme. In the Macropodinae, however, the upper canines are usually vestigial or obsolete (exceptions: *Dorcopsis*, *Dendrolagus*). The vestigial canines often come to lie pointing forward on either side of the palate and appressed to the lateral wall of the maxilla (*Onychogalea*). The canines are normally absent in those macropods that have i^3 enlarged, although minute alveoli that perhaps contained their germs can usually be described.

PREMOLARS

The premolars present special difficulties from the phylogenetic point of view. It is not only difficult to determine the character of the truly primitive premolars, but identification of the individual premolars may be uncertain. Is the macropod tooth, p^3 of this paper, homologous with p^3 of the Phalangeridae (often a disappearing structure), or is it in reality equal to the larger p^2 of the genus *Phalanger*? Is the massive, subconical p^4 of *Trichosurus* and *Phalanger* or the compressed blade-like p^4 of *Acrobates*, the Didelphidae, and the Phascogalinae the more primitive? In all marsupials in which p^4 is not obsolete (it is obsolete in some Dasyurinae and in *Acrobates* and *Distoechurus*) that tooth displaces a more or less molariform deciduous tooth, a tooth that in the Macropodinae has acquired the strongly bilophodont pattern of the true molars. For so long as dp^4 remains functional, p^3 , which in form is almost precisely a miniature of the still developing p^4 , functions as a secant or shearing organ in place of that tooth. This condition becomes untrue only when obsolescence has set in. Then, if either p^3 or p^4 has become non-functional, p^1 takes its place functionally (*Distoechurus* and some Dasyurinae).

The upper and lower third premolars in the dasyurid subfamily Phascogalinae are well-developed, compressed, triangular teeth, inferior in size as a rule to p^4 . In the Dasyurinae p^3 assume the function of the disappearing p^4 , ultimately achieving contact with m^1 (*Dasyurinus*, etc.). In most of the genera of Phalangeridae p^3 are already reduced to minute pegs or are obsolete (*Trichosurus*). In *Phalanger celebensis* p^3 is obsolete, and p_3 is a single-rooted, round-crowned peg. Es-

with m^1 . But in those Dasyuridae that still retain p^4 (*Murexia*, *Thylacinus*, juvenal not seen, *Sminthopsis*) the deciduous upper tooth is markedly phalangeroid and has but one anterior root and two posterior ones. Its crown pattern is wholly unlike that of m^1 . Its length is only one-fourth of that of m^1 , and it is probably almost functionless. The lower deciduous premolars are equally dissimilar. In *Didelphis*, dp_4 strikingly resembles m_1 , and likewise shows the characteristic anterior trigonid and posterior talonid portions of the latter. It possesses an anterior and a posterior root. In *Murexia* (Dasyuridae), on the contrary, the crown of dp_4 is reduced in size to a tiny narrow blade higher in front than behind, and its roots are diminished in number to one.

The deciduous fourth premolars of the Phalangeridae, so far as known, are not molariform. In *Phalanger* and *Trichosurus* they are considerably smaller than the permanent premolars, but in the case of *Dactylopsila* and *Dactylonax* dp_4 are vestigial, rounded, single-rooted structures.

In *Trichosurus* the deciduous teeth, although considerably smaller than m^1 , are undoubtedly functional. There is no molarization of dp_4 and, while dp_4 is bicuspid (with anterior and posterior cusps), dp_4 is often unicuspid. In both the upper and the lower deciduous teeth there is an anterior root and two (inner and outer) posterior roots (as in the upper jaw of *Murexia* but not as in *Didelphis*). Much the same condition is found in *Phalanger orientalis* and in *Trichosurus*, but dp_4 of the former is also bicuspid and weakly molariform. Both upper and lower teeth have three roots arranged as in *Trichosurus*.

In *Acrobates* evidence regarding dp_4 is lacking. In an anomalous specimen of *Petaurus b. papuanus*, adult (A.M.N.H. No. 101966), a triangular, compressed, two-rooted premolar (very similar to p^2 of that species) has been retained on either side, directly internal to the compressed-conical p^4 . On the other hand, in the very young *Petaurus*, A.M.N.H. No. 101969, the just-erupting p^4 is seen to be displacing a one-rooted vestigial tooth which for the present is assumed to be dp^4 .

The Phascolarctinae, although possessing

selenodont molars, have preserved the phalangerine characters of p^4 . In juvenals and pouch young of *Pseudocheirus cupreus* and *P. peregrinus*, I find no trace of dp^4 unless it be that the vestigial tooth commonly named p^3 is in reality a persisting dp^4 .

The deciduous premolar in the Macropodidae has become an almost exact, if slightly smaller, replica of m^1 . In the Potoroinae, which have quadritubercular molars dp^4 is also quadritubercular. In the Macropodinae the same tooth is bilophodont in conformity with the bilophodont structure of the macropodine molars. Nevertheless a slight difference between dp^4 and m^1 can be discerned owing to the presence of an extension of the external body of the tooth anterior to the paracone (and lack of such extension in front of the protocone) which makes functional continuity with p^3 . The root supporting the paracone, furthermore, stands well in advance of the root supporting the protocone. (This functional continuity is preserved after the substitution of p^4 for the combined p^3 and dp^4 by alinement of the blade of p^4 with the paracones and hypocones of m^1 .) Such very complete molarization of dp^4 as appears in the Macropodidae is wanting in the Phalangeridae (so far as shown by a limited number of juvenals representing various genera).

The permanent fourth premolars, which are singularly alike in both the Didelphidae and the Dasyuridae (when present), perhaps represent convergence due to carnivorous habits. In both, the teeth are high, more or less compressed, unicuspid, two-rooted shearing organs wholly unlike the molars. The over-all similarity of the permanent dentitions in these two families (Dasyuridae, part only) suggests a degree of affinity that is somewhat belied by the dissimilarity of the deciduous teeth.

I have pointed out (Tate, 1947) that in the Dasyuridae the fourth permanent premolars follow one of two courses: either they remain the dominant premolars (*Murexia*, *Thylacinus*) or, yielding their dominant position to p^3 , they tend to become obsolete (the Dasyurinae in general). I have also shown that the lower premolars are more reduced than the upper.

Somewhat similar behavior can be seen in

the fourth premolars of the Phalangeridae. In this family the lower tooth is sometimes very much smaller than the corresponding upper one: in *Trichosurus*, *Phalanger*, *Eudromicia*, *Pseudocheirus*, and *Phascogale* p_4 remains almost as large as p_4^1 ; in *Petaurus*, *Dactylopsila*, and *Dactylonax* p_4 is much the smaller tooth. Marked reduction in the size of the upper fourth premolar—the analogue of the condition found in the Dasyurinae—can be noted only in *Distoechurus*. In that genus p_4^1 is less than half as large as either p_1^1 or p_3^1 , and p_4 has disappeared. This corresponds to the *Myoictis* stage in the Dasyurinae.

In the Macropodidae there exists no instance of usurpation of the function of p_4^1 by p_3^1 , but cases of slight reduction in the size of p_4^1 (*Macropus*, *Onychogalea*) exist, and cases of enlargement of p_4^1 are not rare (some *Protemnodon*, *Dorcopsis*, the Potoroinae). As in the Dasyuridae and Phalangeridae the lower premolar is usually slightly smaller than the upper (except in *Aepyprymnus*).

The arrangement of the roots of the premolars in the Macropodidae is probably derived from the phalangerid pattern. In *Hypsiprymnodon* p_4^1 are three-rooted, having one anterior and two posterior roots (the body of the tooth being rotated somewhat as in *Phalanger gymnotis*). In *Bettongia* and *Aepyprymnus*, dp_4^1 are weakly four-rooted, p_3^1 three-rooted, and p_4^1 two-rooted; the posterior root is very large.

In *Dorcopsis* the molariform dp_4^1 remain three-rooted (developing only one internal root), p_3^1 remain three-rooted as in the Potoroinae, while the much elongated permanent premolars are three-rooted in the lower jaw and four-rooted (by addition of a supplementary internal root) in the upper jaw.

In *Dendrolagus* dp_4^1 is four-rooted (one anterior, three posterior roots), while dp_4 and p_3^1 are three-rooted. The massive, permanent p_4^1 develops a supplementary root in the same way as in *Dorcopsis*, while the corresponding lower tooth, perhaps owing to coalescence, appears to have but two.

In the higher wallabies and kangaroos the character of the roots of the premolars varies slightly with the size of those teeth. In *Protemnodon bicolor* the premolars, which

are quite large, are two-rooted, and their bilophodont dp_4^1 have either three or four roots while p_3^1 invariably have three roots. The same condition exists in *P. parryi*, in which the permanent premolars are considerably smaller. In it p_4^1 are actually very much smaller teeth than are their molariform predecessors. They are even slightly smaller than p_3^1 . Yet the arrangement of their roots is essentially the same as in *P. bicolor*.

Kreff (1875) pointed out the functional importance of two types of behavior of macropodine cheek teeth as represented in the kangaroos (*Macropus*, etc.) and the wallabies (*Protemnodon*). He showed that the long-faced kangaroos which have large diastemata and small-sized p_3^1 shed those teeth early in life and that they continue in age to shed true molars m_1^{1-2} and even m_3^1 . This is brought about by the molar teeth traveling forward in the toothrow. On the other hand Kreff pointed out that the short-faced wallabies (and here are included also the Sthenurinae), which have shorter diastemata, possess large-sized p_4^1 that commonly persist throughout life even though greatly worn. In this latter group little or no forward movement of the cheek teeth in the toothrow takes place.

The time of eruption of p_4^1 (to replace p_3^1 and dp_4^1) is closely linked with any forward motion of the molars. It is indicated for most of the genera and many of the species of Macropodidae in table 1.

The lower premolars of many Macropodidae, especially the Potoroinae, are essentially mirrors (in reverse) of the upper premolars. Important exceptions to this statement are found in the case of the Phalangeridae. The fourth lower molar and dp_4^1 in the majority of Phalangeridae are closely similar to their corresponding upper teeth after due allowance is made for occlusal adaptation. This is true in *Phalanger*, *Acrobates*, *Trichosurus*, and *Dromicia*. In *Pseudocheirus* p_4 corresponds essentially to p_4^1 . It is untrue in *Dactylopsila*, *Dactylonax*, and *Petaurus*, in which p_4 is very small. In genera such as *Petaurus*, in which p_4 is markedly reduced, the deciduous tooth, although extremely minute, develops and is regularly displaced by later eruption of the permanent tooth (e.g., A.M.N.H. No. 101969, right ramus). Although I have been unable to observe dp_4 or its replacement by p_4 in the

TABLE 1
ERUPTION OF P⁴ IN THE MACROPODIDAE IN TERMS OF M²⁻⁴

| | After m ² | After m ³ | After m ⁴ | Evidence |
|-------------------------------------|-------------------------|-------------------------|-------------------------|--|
| <i>Potorous tridactylus</i> | | | X | A.M.N.H. No. 66169 |
| <i>Caloprymnus campestris</i> | | X | | Finlayson (1932, p. 161) |
| <i>Bettongia cuniculus</i> | | | X | A.M.N.H. No. 65271 |
| <i>Bettongia p. ogilbyi</i> | | | X | M.C.Z. No. 27959 |
| <i>Bettongia gaimardi</i> | | | X | M.C.Z. No. 29206 |
| <i>Aepyprymnus rufescens</i> | | X | | A.M.N.H. Nos. 65283, 107390 |
| <i>Petrogale penicillata</i> | | X | | U.S.N.M. Nos. 237740, 38857 |
| <i>Petrogale lateralis hacketti</i> | | X | | U.S.N.M. No. 155377 |
| <i>Petrogale inornata</i> | | X ^a | | A.M.N.H. No. 107379, M.C.Z. No. 29296 |
| <i>Onychogalea unguifer</i> | | | X | M.C.Z. No. 29289 |
| <i>Onychogalea fraenata</i> | | | X | U.S.N.M. No. 219299 |
| <i>Lagorchestes conspicillatus</i> | | | X | U.S.N.M. No. 218468 |
| <i>Peradornas concinna</i> | | | X | U.S.N.M. No. 237690 |
| <i>Lagostrophus fasciatus</i> | | | X ^a | U.S.N.M. No. 218467 |
| <i>Dorcopsulus vanheurni</i> | | | X ^a | A.M.N.H. No. 151848 |
| <i>Dorcopsis hageni</i> | | X | | A.M.N.H. Nos. 109394, 109391 |
| <i>Dorcopsis mülleri</i> | | X | X ^a | A.M.N.H. Nos. 105990, 105995, 105997 |
| <i>Dendrolagus dorianus</i> | | | X | Genoa No. C.E. 1600 |
| <i>Dendrolagus lumholtzi</i> | | | X | A.M.N.H. No. 65245, M.C.Z. No. 7007 |
| <i>Protemnodon b. bicolor</i> | | X | X | A.M.N.H. No. 65122, U.S.N.M. Nos. 221189, 221195 |
| <i>Protemnodon agilis</i> | | X | X | A.M.N.H. No. 90295, U.S.N.M. No. 237636 |
| <i>Protemnodon e. binoë</i> | | | X | M.C.Z. No. 28036 |
| <i>Protemnodon e. decrex</i> | | | X | U.S.N.M. No. 236692 |
| <i>Protemnodon parma</i> | | X | | U.S.N.M. No. 38551/19557 |
| <i>Protemnodon parryi</i> | | | X ^a | A.M.N.H. No. 65059 |
| <i>Protemnodon r. banksiana</i> | | X | | U.S.N.M. No. 237660 |
| <i>Protemnodon r. fruticosa</i> | | X | | A.M.N.H. No. 6372, U.S.N.M. No. 124341 |
| <i>Protemnodon dorsalis</i> | | X | | A.M.N.H. No. 65084 |
| <i>Setonix brachyurus</i> | | | X | A.M.N.H. No. 35744, U.S.N.M. No. 238472 |
| <i>Thylogale thetis</i> | | | X ^a | U.S.N.M. No. 221185 |
| <i>Thylogale stigmatica</i> | | | X | A.M.N.H. No. 29292 |
| <i>Thylogale brunii</i> | | X | X | A.M.N.H. Nos. 79788, 104433, U.S.N.M. No. 268751 |
| <i>Thylogale billardieri</i> | | | X | A.M.N.H. No. 65217 |
| <i>Macropus robustus</i> | X | | | A.M.N.H. No. 65026 |
| <i>Macropus erubescens</i> | | X ^a | | A.M.N.H. No. 107374 |
| <i>Macropus antilopinus</i> | X ^b | | | U.S.N.M. Nos. 237614, 237654 |
| <i>Macropus major</i> | | X ^a | | U.S.N.M. No. 221169 |
| <i>Macropus melanops</i> | X | | | U.S.N.M. No. 236686 |
| <i>Macropus fuliginosus</i> | | X | | U.S.N.M. No. 236681 |
| <i>Macropus rufus</i> | | | X ^a | M.C.Z. No. 29368, A.M.N.H. No. 107694 |

^a Oris synchronous with.

^b Or slightly before.

cases of *Dactylonax* and *Dactylopsila*, I have noted that the small lower vestigial tooth adjoining m₁ is the last of its type to be erupted and in that sense conforms to the pattern of development of p₄. The third lower

premolar, if present, is reduced to an uncertainly identifiable vestige in every phalangerid genus known to me except *Acrobates* and *Distoechurus*.

MOLARS

The molars of the carnivorous marsupials are typically trituberculate. Here belong the molars of the Didelphidae, the Dasyuridae, and the Peramelidae. In the Phalangeridae the basic type of molar should be considered to be the bunodont quadrituberculate molar of *Phalanger*, etc. This may become modified into the wholly quadrituberculate molar of *Petaurus* or *Dactylopsila*, into the selenodont molar of *Phascolarctos* and *Pseudocheirus*, or become incipiently bilophodont, in which condition the molars of the rat kangaroos yet remain.

The molars in the Macropodinae are invariably bilophodont; those in the Potoroinae quadritubercular with incipient bilophodontism apparent in certain genera.

The dominant (widest and longest) molar of the series in the Phalangeridae is usually m^2 (m^1 in *Petaurus*, *Dactylopsila*, etc.), behind which the size becomes reduced to the small, terminal, sometimes obsolete m^4 . In the Potoroinae the same dominance of m^2 (sometimes m^1) can be observed, except in *Aepyprymnus* in which m^3 or m^4 are the largest teeth. In the Macropodinae this shift of size dominance to the third and fourth molars has become the rule. It is accompanied by delayed eruption of those teeth, m^4 often being cut only after animals have become quite aged (*Osphranter*, *Megaleia*, *Macropus*, *sensu stricto*, *Thylogale*, *Protemnodon*).

The form of m^1 in the rather generalized *Trichosurus* is bilophodont, and p^4 is a slightly compressed conical tooth with a somewhat shearing blade. In the lower jaw bilophodontism is confined to the posterior moiety of m_1 , the anterior half being unicuspid and "premolarized." This condition of m_1 is very widespread. However, a well-developed paraconid is retained in the Phascolarctinae, the selenodont division of the phalangerids comprising *Pseudocheirus*, *Phascolarctos*, and *Schoinobates*. Also, the anterior loph of m_1 of *Potorous*, although narrow, has distinct protoconid and paraconid cusps.

A process to be regarded more or less as a reversal of the molarization of dp_4 , found in greater or less development in the Phalangeridae, is absent or never more than incipient in the Macropodidae. This process may be termed the "premolarization" of

m_1 . It involves only the anterior moiety of m_1 and of dp_4 and consists of coalescence of the two anterior cusps of those teeth, to leave in each a single cusp which then is functionally coordinated with the premolar tooth immediately before it. Thus, in juvenals, p_3 plus the front half of dp_4 form a functional unit, and in adults p_4 combined with the anterior portion of m_1 also forms a functional unit (even though the premolar is obsolescent). This condition is imperfect in *Acrobates* and *Distoechurus*, well developed in *Petaurus*, *Trichosurus*, and *Phalanger*. In the Macropodidae premolarization of dp_4 and of m_1 is incipient in *Hypsiprymnodon*. It appears in dp_4 of *Potorous tridactylus* and of *Bettongia penicillata*, but not in m_1 .

In the lower jaw of *Hypsiprymnodon* a slight approximation of the protoconid and paraconid cusps of m_1 can be noted. The same is true of *Propleopus* (= *Trichis*), while complete confluence of those cusps has been reached in the case of *Burramys*. In all four of the living potoroinae genera both protoconid and paraconid of m_1 have been preserved, as well as in the strongly bilophodont Macropodinae. The paraconid in *Bettongia cuniculus* is well developed, but that in *B. gaimardi* is weaker. In the Macropodinae the paraconid is undiminished. In this last subfamily confluence of the two anterior cusps sometimes occurs in dp_4 (but not in m_1) among the forest genera *Dendrolagus* and *Dorcopsis*. The same condition, incipient in *Petrogale*, is expressed only by slight narrowing of the anterior loph of dp_4 in *Thylogale*, *Protemnodon*, and *Macropus*.

The molar gradient of the carnivorous marsupials Didelphidae and Dasyuridae is generally found to be arranged with the tooth sizes $m^1 < m^2 < m^3 > m^4$. The last tooth, m^4 , is abruptly reduced in size and modified to a subtriangular outline to conform with its terminal position in the toothrow. In the corresponding lower molars only the talonid of m_4 works against the much smaller upper tooth, the size of the anterior portion of m_4 being undiminished.

In the less-specialized genus *Phalanger* of the Phalangeridae the molar gradient has shifted to the condition $m^1 < m^2 > m^3 > m^4$, m^{1-3} being very nearly equal and m^4 slightly smaller and becoming subtriangular. In

Trichosurus the molar gradient is somewhat steeper, and m^1 is distinctly larger than m^2 . Both genera have bunolophodont molars. In their lower dentition the talonid of m_4 is but slightly smaller proportionally than the talonids of m_{1-3} . From this bunolophodont molar, modification in the direction of either purely bunodont or definitely lophodont structure is equally possible. In m_1^1 of *Trichosurus* and *Phalanger* the paracone remains distinct from the protocone, while the paraconid and protoconid are seen to be confluent. Exceptions to this confluent condition of the protoconid and paraconid can be noted in the selenodont Phascolarctinae (*Phascolarctos*, *Pseudocheirus*, *Schoinobates*).

In bunodont phalangerids such as *Eudromicia*, *Petaurus*, and *Dactylopsila* the emphasis of the molar gradient has shifted: $m^1 > m^2 > m^3 > m^4$. The order of diminution in size has become much greater, leading ultimately (*Cercartetus*, *Distoechurus*) to obsolescence of m^4 . The lower molars share quite largely in this group change, being arranged $m_1 < m_2 > m_3 > m_4$. The last lower molar is likely to become obsolete with the upper.

The molar gradient in the macropods remains phalangerine in *Hypsiprymnodon* and its extinct allies and somewhat less so in *Bettongia* and *Potorous*. But the condition seen in *Aepyprymnus* parallels the change to the moderate or pronounced hypsodontism and enlargement of m_4^1 resulting in the reversed size gradient $m^1 < m^2 < m^3 < m^4$ developed in the wallabies and kangaroos.

A similar progressive posterior enlargement of the strongly bilophodont molars can be noted in the case of the Diprotodontidae. In *Euryzygoma* and *Nototherium* p^4 is described as "subtriangular," while m_4^1 are invariably larger than m_3^1 , as in the Macropodinae. In this connection it should be pointed out that Owen seems to have misnamed the cheek teeth of both *Diprotodon*

and *Nototherium*. This means that under the system used in Owen's plates neither genus possesses m_4^1 . The teeth marked by him "d" and "d'" are actually m^1 and p^4 , respectively.

Increase in the number of the molars beyond four (excluding dp^4 , of course, which is unknown in the Phalangeridae) appears in both the Potoroinae and the Macropodinae. In the former, *Bettongia cuniculus* sometimes develops a small fifth molar. In the latter, *Peradorcas*, which may develop a total of seven or more molars, is a striking example. The increased number of molars in *Myrmecobius*, a possible derivative of the Dasyuridae, is very much better known.

It follows, in the case of *Peradorcas*, that the progressively erupting, forward moving series of molars will cause the displacement and loss of the permanent fourth premolar very soon after its eruption. Little wonder then that it is so seldom found in skulls or that Collett (1897) doubted whether it was ever developed.

"PRELACTEAL" TEETH

"Prelacteal" dentitions in marsupials have been demonstrated in a number of genera (Woodward, 1893, for Macropodidae; Dependorf, 1898, various; Engelhardt, 1932, for *Aepyprymnus*; and others). The identification of these teeth varied. Moreover, no agreement was reached on the number of dental series involved (Dependorf believed there were four series). During the present study I have found cleaned skulls of pouch young of *Thylogale brunii*, *Macropus robustus erubescens*, and *M. kanguru major* in which minute incisor teeth, evidently of the same character, can be seen present at the same time as the large, erupting, permanent incisors. Since as many as six upper and three lower prelacteal incisors have been reported, those seen by me are probably not identifiable.

EXTERNAL CHARACTERS

HAND AND FOOT

Little that is new can be added to what has already been published on the feet of the Macropodidae. Bensley's (1903) detailed analysis from the standpoint of evolution

should be consulted; and latterly a paper on the mechanical aspect of syndactyly has been published by Müller (1930).

In all recent kangaroos except *Dendrolagus* the arm and hand are reduced in size, and,

although they grasp food, they serve in only a subordinate way to aid the hind limbs, the primary organs of locomotion. In *Dendrolagus* the fore limbs, hands, and claws are large and strong. This is probably a secondary adaption which aids the animals to climb.

The foot, in all genera except *Hypsiprymnodon*, has become profoundly modified—lengthened and narrowed in conformity with the leaping type of locomotion usual in the family. Complete syndactyly is present, and the big toe is usually absent. In *Hypsiprymnodon*, which alone of all recent genera retains the big toe (essentially unopposable), a great advance has been made in the direction of the ricochet type of foot. But the foot is less narrowed and less elongated than in the typical kangaroos. The fact must not be lost to sight that even though friction ridges (found usually in scansorial mammals) are still present, the *Hypsiprymnodon* foot is already profoundly modified for leaping and already far removed structurally from the hand-like posterior organ, with its opposable first digit, found in the scansorial Phalangeridae.

TAIL

The normal macropod tail is thick at the base, tapered towards the tip. It is used as a prop or hind leg. This thick-based tail is widespread among the marsupials—in *Thylacinus* of the Dasyuridae, in *Lutreolina* and *Chironectes* of the Didelphidae, in the Phalangeridae, and the Peramelidae.

In the two kangaroo genera *Petrogale* and *Dendrolagus* the normal, tapered, prop-like type of tail gives place to a balancing type of tail of nearly uniform thickness, similar to the tails of such Old World monkeys as the langurs. I am inclined to connect this change of function and structure with change of habits. Both the rock kangaroos and the tree kangaroos are accustomed, at the end of a leap, to balance their bodies on narrow ridges and slender branches. Shift of the caudal center of gravity towards the tip might be advantageous in establishing such a balance.

Caudal prehension is also very widespread among the marsupials, especially among the Didelphidae and Phalangeridae. In the Macropodidae it is almost totally suppressed (or undeveloped?); the only instance of weak

prehension is that of *Bettongia penicillata*, which is reputed to pick up and carry nest materials with its tail. This behavior may bear no real relation to the truly prehensile tail, in which the under surface of the tip has modified bare skin.

Slight shortening or lengthening of the tail in proportion to the body size appears to have little functional meaning. The tails of some Potoroinae, of *Thylogale thetis* and *T. billyardieri*, of *Setonix*, and of *Dorcopsulus* are shorter than normal. The tails of *Protemnodon parryi* and *Dendrolagus* are unusually long.

PATTERN OF PELAGE

Aside from the usual dorsoventral contrast in color intensity, found in most mammals, and the commonplace development of post-auricular patches, several pattern features recur in comparatively unrelated marsupial genera.

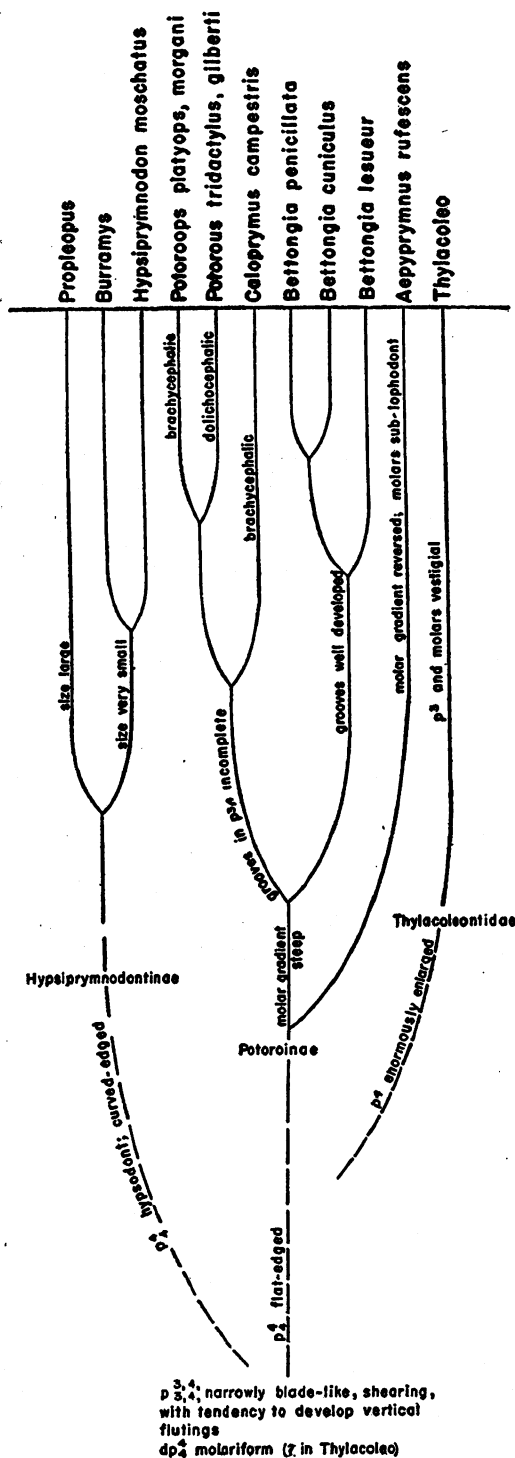
Transverse banding is seen in *Chironectes* and *Dromiciops* among the Didelphidae, in *Myrmecobius* and *Perameles* among the Peramelidae, and in *Thylacinus* among the Dasyuridae. No clear case of it is found in the Phalangeridae. Among the Macropodidae it appears rarely: *Lagostrophus*, *Petrogale xanthopus* (chiefly confined to the tail), and *Protemnodon greyi*.

A nuchal-scapular mark is characteristic of *Onychogalea*, *Peradarcas*, and (as a trace) some *Petrogale*. This pale mark, beginning behind the ears, extends backward along the upper side of the neck and bends downward to cross the posterior margin of the scapula.

A hip stripe is characteristic of many *Protemnodon*, some *Thylogale*, and *Onychogalea*. It may be faintly developed in some *Macropus*.

The side of the face sometimes bears a dark area running from eye to muzzle and a second, fainter dark line extending from the angle of the jaw to the chin. Between these lies a paler line. This pale area becomes relatively very intense in several *Protemnodon*, notably in *parryi* and its relatives. It is still well defined in *P. bicolor*, *P. agilis*, and *P. dorsalis* as well as in some *Petrogale* and in *Thylogale brunii*, but is indistinct or obsolete in *Macropus*, *Dendrolagus*, and the hare wallabies and rat wallabies.

PHYLOGENY



Whether the Potoroinae or the Macropodinae should be considered the more primitive and the less specialized is a question which I have not been able to decide. Accordingly, I have followed the customary method of treatment, which tends to place the latter subfamily higher than the former. The potorine premolars are, nevertheless, in my opinion much more specialized teeth than are the macropodine premolars. They represent a tooth form not even hinted at in existing Macropodinae.

It has been suggested by various writers (most recently by Pearson, 1946) that the Macropodidae comprise two families derived independently from phalangeroid stock. Then the ricochet type of locomotion, so well developed in both branches of the Macropodidae, would have to be explained as an outstanding example of convergence. Taken by itself it does not appear an impossibility, especially when we remember that the gliding membrane has twice been developed in the single family Phalangeridae. But in the present case we are compelled next to postulate a second, quite unrelated and very complex convergence, namely, the morphological similarity of p_3^3 to p_4^4 and the usual replacement of p_3^3 plus dp_4^4 by p_4^4 . No phenomena like these occur in the premolar series in any marsupial families other than the Macropodidae. The product of the two unrelated examples of morphological identity just referred to—foot structure and premolar structure—points much more strongly to real relationship than to convergence.

It would be difficult to indicate any one of the divisions of the recent phalangerids that could have given rise to either the Potoroinae or the Macropodinae. Regarding the latter subfamily I offer no suggestion; in the former case one may expect an ancestor provided with quadritubercular molars and a posteriorly diminishing molar gradient. Such conditions are still to be seen in *Eudromicia* and

FIG. 2. Suggested phylogenetic arrangement of the subfamilies Hypsiprymmodontinae and Potoroinae with the possible origin of *Thylacoleo*.

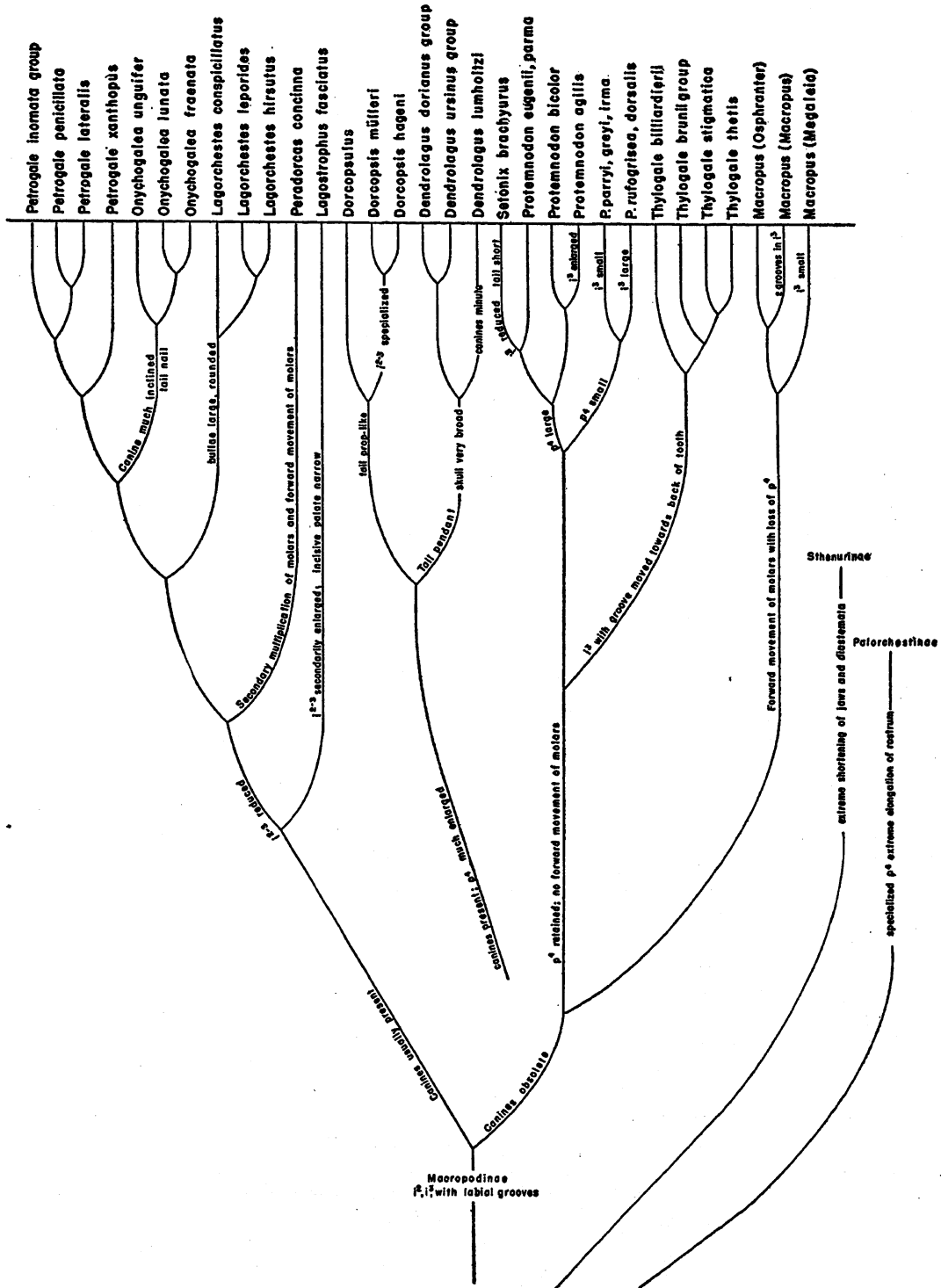


FIG. 3. Suggested phylogenetic arrangement of the subfamily Macropodinae and possible relationships of the extinct Sthenurinae and Palorchestinae.

its allies, and in *Petaurus*, *Acrobates*, *Distoechurus*, and *Dactylopsila*.

The potoroine division is without question much more diversified than the macropodine division. In figure 2 I have suggested the possible ancient convergence of three basal stems, the Hypsiprymnodontinae, the Potoroinae, and the Thylacoleontidae. In the last of these we may have an example of extremely rapid evolution (tachytely) away from a relatively stable origin, such as Simpson has discussed (1944, chap. 3, 4) and typified by the horse family (*tom. cit.*, p. 19). There exists no recent or fossil subfamily of marsupials other than the Potoroinae in which the fourth premolar in any way resembles that of *Thylacoleo*.

The hypsiprymnodonts, although their characters warrant them subfamily distinction, bear a much closer relationship to the potoroine than to the macropodine kangaroos.

The large complex of the Macropodinae is much more homogeneous than is the smaller potoroine complex. Numerous characters and trends seem to play genetic "hide-and-seek" in this subfamily, and my classification of the genera and generic groups (fig. 2) is provisional. Among important new characters found developing in the Macropodinae are the relatively early loss of p_4^1 , the forward movement of the molars in the molar toothrows (*Peradornas*, *Macropus*), brachycephaly (*Dendrolagus*, *Lagostrophus*), and uniform thickness of the tail and its use as a balancing organ (*Petrogale*, *Dendrolagus*). It will be noted that all four of these features occur in relatively unrelated genera.

Reexamination of Owen's illustrations of *Thylacoleo* (1859, 1866, 1872) in the light of the present discussion may be fruitful. The enormously developed blades of p_4^1 are most nearly reminiscent of those of the less exaggerated secant teeth found in the Potoroinae. A further specialized condition obtains in the almost total "premolarization" of m_1 , which provides functional continuity with p_4 . Yet another special character, unmatched in modern marsupials, is the extent of the obsolescence of the molar tooththrow from the back forward. Loss of m_4^1 is not a rare occurrence (*Distoechurus*, *Acrobates*, *Dromicia*), but the additional loss of m_3^1 and m^2 found in *Thylacoleo* is unique. The extreme shortening

of the face has caused retraction of the upper canine to the level of, and inward from, the anterior margin of p_4^1 . The extreme degree of obsolescence of the premolars anterior to p_4^1 may be regarded as a phalangerid character; it is certainly not normally macropodid but can be matched in the hypsiprymnodonts *Burramys*, *Propleopus*, and *Hypsiprymnodon*.

A study of the young stages, particularly of the character of dp_4^1 , would undoubtedly be highly rewarding. We should particularly inquire whether or not molarization of dp_4^1 occurs as in the Potoroinae.

In *Thylacoleo* the mandible has attained an extreme degree of shortening anteriorly, i_1 being separated from p_4 by a very small space containing the alveoli of two vestigial teeth. Obsolescence of lower premolars in advance of upper premolars is in accord with my findings in the Dasyuridae (Tate, 1947).

Anderson (1929) asserted that *Thylacoleo* possessed a postorbital bar (model, his pl. 23). I can find no fossil evidence in substantiation. Bensley (1903) considered this family to be very distantly related to the Phalangeridae.

Thylacopardus, a *nomen nudum* introduced by Owen (*vide* Palmer, 1904, p. 677), was validated by Anderson (1929). He believed it synonymous with *Thylacoleo* but held that the species *australis* might be distinct from *carnifex*.

Possibly the Thylacoleontidae, highly specialized as they obviously are, should be added to the Hypsiprymnodontinae and Potoroinae to form a triple group of bunodont, brachyodont diprotodonts, in contradistinction to the bilophodont, hypsodont Macropodinae. This idea would be strengthened if the feet of *Thylacoleo* should prove to be markedly syndactylous.

Among the marsupials, the extinct genera *Diprotodon*, *Nototherium*, and their allies take the place ecologically of the rhinoceroses of the placentals. Their strictly bilophodont molar teeth resemble only those of the Macropodinae among the recent marsupials. There is little sign of premolarization of the anterior loph of m_1 , as in the Phalangeridae and Potoroinae. However, p_4^1 (indicated in Owen's plates as " d_3^1 ") appear phalangerid rather than macropodid in form. The nearly parallel right and left incisive tooththrows can almost

be matched in both families, in *Dactylopsila* of the Phalangeridae and *Lagostrophus* of the Macropodidae, although possibly they are not especially significant phylogenetically. The condition of dp^4 was described by Glauert (1921, p. 110) for *Nototherium*. Its lack of molarization suggests phalangerid affinity. No trace has been found of a masseteric foramen, a character highly developed in the macropods but usually absent in the phalangerids.

Characters that probably indicate peculiar specialization include the exaggerated structure of the zygomata, which reaches a climax in *Euryzygoma*; the constriction of the middle part of the rostrum and development of the lateral nasal bosses; the extreme degree of shortening of the cerebral portion of the skull in proportion to the palatal portion; the highly ankylosed, spout-like mandibular sym-

physis; the very high articular process of the mandible; and the dominance of the fifth digit of the hind foot (Stirling and Zietz, 1899; Scott and Lord, 1921).

The lack of pronounced syndactyly in the Diprotodontidae, as in the Phascologyidae, seems to preclude close relationship either to the Phalangeridae or to the Macropodidae. However, as digits two and three are slightly reduced in size, the suggestion has been made (Bensley, 1903; and others) that syndactyly furnishes an instance of reversible evolution, in consequence of which the Diprotodontidae and the wombats could be derived from the otherwise fully syndactylous Phalangoidea. I cannot concur fully with this view. Yet the only alternative explanation lies in postulating separation of the Diprotodontidae¹ from the Phalangoidea before the general establishment of syndactyly in that superfamily.

DISTRIBUTION

The regional distribution of the recent Macropodidae is plotted in table 2. Only unmistakably distinct species have been shown.

The region of maximal species density is seen to be the eastern parts of the north, central, and southern districts of Queensland and eastern New South Wales. From 12 to 15 species are present in each of the three districts of Queensland; 16 species in New South Wales. This greater number is probably accountable by the much greater area of the last. Probably a maximum of 12 species represents the macropod fauna in any block of land 100 miles square within the regions named.

From the Queensland-New South Wales center of maximal concentration the number of species falls to nine in Cape York, 11 in Victoria, and eight in western Queensland and four in western New South Wales. North of Cape York, although eight species groups occur in New Guinea, their regional concentration falls lower: there are four species in south New Guinea, three in northern, and two in western, New Guinea, and three in the mountains. In Tasmania five species are found, a sharp drop from the 11 in Victoria.

South Western Australia is an important

second center of species concentration. If it northern and southern sections are combined no fewer than 14 species of kangaroos and wallabies can be tallied. These appear as 11 in the northern (Perth) section, eight in the southern (Albany) section. Only five are common to both. The southern section receives the greater amount of rain.

From this southwest center a tenuous connection is maintained along the south coast with southern South Australia, while northward a diminished fauna of six species in the northwest division with four only in the Kimberley (or northeast) division expands again to six species in Arnhemland.

The desert center of Australia has a very poor macropod fauna, and undoubtedly parts of it contain none at all. *Petrogale lateralis* and an occasional specimen of one of the races of *Macropus robustus*, or a stray of the *pallidus* race of the red kangaroo, probably indicate its total population.

Evidence from many sources has accumulated to show that the relatively high aridity of Australia today is comparatively new. In

¹ The distribution of the family in southern Australia has been investigated recently by Keble (1945).

TABLE 2
GEOGRAPHICAL DISTRIBUTION OF THE MACROPODIDÆ

| | New Guinea | | | | Eastern Queensland | | | | E. New South Wales | Victoria | Tasmania |
|---|-------------------|---------------------|-------------------|---------------------|--------------------|------------------|-----------------|------------------|--------------------|----------|----------|
| | Western; Vogelkop | Northern; Bismarcks | Eastern Mountains | Southern; Aru Isles | Cape York | Northern Portion | Central Portion | Southern Portion | | | |
| <i>Hypsiprymnodon moschatus</i> | | | | | | X | | | | | |
| <i>Potoroops platyops</i> | | | | | | | | | | | |
| <i>Potorous tridactylus, gilberti</i> | | | | | | | | | X | X | X |
| <i>Coloprymnus campestris</i> | | | | | | | | | | | |
| <i>Bettongia penicillata, gaimardi</i> | | | | | | X | X | X | X | X | |
| <i>Bettongia cuniculus</i> | | | | | | | | | | | X |
| <i>Bettongia lesueur</i> | | | | | | | | | | | |
| <i>Aepyprymnus rufescens</i> | | | | | | X | X | X | X | | |
| <i>Prolemnodon bicolor</i> | | | | | X | X | X | X | X | X | |
| <i>Prolemnodon agilis</i> | | | | X ^a | X | X | X | X | X | X | |
| <i>Prolemnodon eugenii, parma</i> | | | | | | | | X | X | X | |
| <i>Prolemnodon parryi</i> | | | | | | X | X | X | X | | |
| <i>Prolemnodon greyi</i> | | | | | | | | | | X | |
| <i>Prolemnodon irma</i> | | | | | | | | | | | |
| <i>Prolemnodon rufogrisea</i> | | | | | | X | X | X | X | X | X |
| <i>Prolemnodon dorsalis</i> | | | | | | | X | X | X | | |
| <i>Setonix brachyurus</i> | | | | | | | | | | | |
| <i>Petrogale inornata</i> and allies | | | | | X | X | X | | X | | |
| <i>Petrogale penicillata</i> | | | | | | | | X | X | | |
| <i>Petrogale lateralis</i> | | | | | | | | | | | |
| <i>Petrogale xanthopus</i> | | | | | | | | | | | |
| <i>Onychogalea unguifer</i> | | | | | | | | ? | | | |
| <i>Onychogalea fraenata</i> | | | | | X ^b | | | X | X | X | |
| <i>Onychogalea lunata</i> | | | | | | | | | | | |
| <i>Lagorchestes leporides</i> | | | | | | | | | | X | |
| <i>Lagorchestes hirsutus</i> | | | | | | | | | | | |
| <i>Lagorchestes conspicillatus</i> | | | | | | X | | | | | |
| <i>Peradornas concinna</i> | | | | | | | | | | | |
| <i>Lagostrophus fasciatus</i> | | | | | | | | | | | |
| <i>Dorcopsulus macleayi, vanheurni</i> | X | | X | | | | | | | | |
| <i>Dorcopsis mülleri</i> | | X ^c | | X ^a | | | | | | | |
| <i>Dorcopsis hageni</i> | | X ^c | | | | | | | | | |
| <i>Dendrolagus dorianus</i> | X | X ^c | X | | X | | | | | | |
| <i>Dendrolagus ursinus</i> | | X ^c | | | | | | | | | |
| <i>Dendrolagus lumholtzi</i> | | | | | X | X | | | | | |
| <i>Thylogale brunii</i> | | X | X | X | | | | | | | |
| <i>Thylogale stigmatica</i> | | | | X ^a | X | X | X | X | X | | |
| <i>Thylogale thetis</i> | | | | | | | | X | X | X | |
| <i>Thylogale billardieri</i> | | | | | | | | | | | X |
| <i>Macropus (Macropus)</i> | | | | | ? | X | X | X | X | X | X |
| <i>Macropus (Osphranter)</i> | | | | | X | X | X | X | X | ? | |
| <i>Macropus (Megaleia)</i> | | | | | X | X | X | X | X | X | |
| Total number of good species in each region | 2 | 3 | 3 | 4 | 9 | 14 | 12 | 15 | 16 | 11 | 5 |

^a Not in Aru.

^b Collected at Port Stewart by P. J. Darlington, Museum of Comparative Zoölogy.

^c Not in Bismarcks.

TABLE 2—Continued

| | North. Territory | | West. Queensland | W. New South Wales | South. Australia | | Western Australia | | | | | | |
|---|------------------|------------------|------------------|--------------------|------------------|------------------|-------------------|---------------------|---------------------|-------------------|-------------------|--------------------|--------------------|
| | Arnhemland | Southern Portion | | | Northern Portion | Southern Portion | Northeastern Div. | North of East. Div. | South of East. Div. | Southeastern Div. | Northwestern Div. | North of S.W. Div. | South of S.W. Div. |
| <i>Hypsiprymnodon moschatus</i> | | | | | | | | | | | | X | |
| <i>Potoroops platyops</i> | | | | | | | | | | | | X | |
| <i>Potorous tridactylus, gilberti</i> | | | | | | ? | | | | | | X | |
| <i>Caloprymnus campestris</i> | | | | | X | | | | | | | X | X |
| <i>Bettongia penicillata, gaimardi</i> | | | | | | X | | | | | | X | X |
| <i>Bettongia cuniculus</i> | | | | | | X | | | | | | X | X |
| <i>Bettongia lesueur</i> | | | | | | X | | | | | X | X | X |
| <i>Aepyprymnus rufescens</i> | | | | | | | | | | | | X | X |
| <i>Protemnodon bicolor</i> | | | | | | | | | | | | X | X |
| <i>Protemnodon agilis</i> | X | | X | | | | X | | | | | X | X |
| <i>Protemnodon eugenii, parma</i> | | | | | | X | | | | X | | X | X |
| <i>Protemnodon parryi</i> | | | | | | X | | | | | | X | X |
| <i>Protemnodon greyi</i> | | | | | | X | | | | | | X | X |
| <i>Protemnodon irma</i> | | | | | | | | | | | | X | X |
| <i>Protemnodon rufogrisea</i> | | | | | | | | | | | | X | X |
| <i>Protemnodon dorsalis</i> | | | | | | | | | | | | X | X |
| <i>Setonix brachyurus</i> | | | | | | | | | | | | X | X |
| <i>Petrogale inornata</i> and allies | X | | X | | | | | | | | | X | X |
| <i>Petrogale penicillata</i> | | | | | X | X | | | | | | X | X |
| <i>Petrogale lateralis</i> | | X | | | X | X | | | | | | X | X |
| <i>Petrogale xanthopus</i> | | | X | | X | X | | | | | | X | X |
| <i>Onychogalea unguifer</i> | X | | X | | | | X | | | | | X | X |
| <i>Onychogalea fraenata</i> | | | | | | | | | | | | X | X |
| <i>Onychogalea lunata</i> | | ? | | | | | | | | | | X | X |
| <i>Lagorchestes leporides</i> | | | | X | | | | | | | | X | X |
| <i>Lagorchestes hirsutus</i> | | | | | | | | | | | X | X | X |
| <i>Lagorchestes conspicillatus</i> | X | | X | | | | | | | | X | X | X |
| <i>Peradorchas concinna</i> | X | | | | | | X | | | | | X | X |
| <i>Lagostrophus fasciatus</i> | | | | | | | | | | | X | X | X |
| <i>Dorcopsulus macleayi, vanheurni</i> | | | | | | | | | | | X | X | X |
| <i>Dorcopsis mülleri</i> | | | | | | | | | | | X | X | X |
| <i>Dorcopsis hageni</i> | | | | | | | | | | | X | X | X |
| <i>Dendrolagus dorianus</i> | | | | | | | | | | | X | X | X |
| <i>Dendrolagus ursinus</i> | | | | | | | | | | | X | X | X |
| <i>Dendrolagus lumholtzi</i> | | | | | | | | | | | X | X | X |
| <i>Thylogale brunii</i> | | | | | | | | | | | X | X | X |
| <i>Thylogale stigmatica</i> | | | | | | | | | | | X | X | X |
| <i>Thylogale thetis</i> | | | | | | X | | | | | X | X | X |
| <i>Thylogale billardieri</i> | | | | | | | | | | | X | X | X |
| <i>Macropus (Macropus)</i> | | | X | | | X | | | | | X | X | X |
| <i>Macropus (Osphranter)</i> | X | | X | | X | X | X | | X | | X | X | X |
| <i>Macropus (Megaleia)</i> | | | X | X | X | X | | | | | X | X | X |
| Total number of good species in each region | 6 | 1 | 8 | 4 | 6 | 7 | 4 | 0 | 1 | 1 | 6 | 11 | 8 |

middle Pleistocene time in Queensland, Whitehouse (1940) shows increased rainfall accompanied by lower temperature. This was followed in late Pleistocene by less rainfall than today and by rising temperature. His curve shows for the "recent" (Quaternary?) a rainfall slightly heavier than the present rainfall. Many species of Macropodidae therefore may then have had different and probably more extensive ranges, and their present restricted ranges are thus explainable in terms of changes during the very recent past.

The several habitats that I suggested when dealing with the Dasyuridae (Tate, 1947) reappear recognizably in the case of the Macropodidae: the New Guinea mountains (*Dorcopsulus*, *Thylogale brunii keysseri*); Torresia (*Protemnodon agilis*); northern Australia from west to east, south of Torresia (*Petrogale inornata*, *Lagorchestes conspicillatus*); humid eastern Australia (*Thylogale stigmatica*, *Protemnodon bicolor*, *parryi*, *rufogrisea*) and the more restricted Queensland-northern New South Wales area (*Hypsiprymnodon*, *Aepyprymnus*, *Protemnodon dorsalis*, *Thylogale thetis*, *Onychogalea fraenata*); and south Western Australia (*Potoroos platyops*, *Potorous gilberti*, *Protemnodon irma*, *Onychogalea lunata*, *Lagorchestes hirsutus*, *Lagostrophus*, *Setonix*). Animals with much more

extensive ranges in southern Australia and west to east include *Bettongia penicillata*, *Protemnodon eugenii* (with *parma*), and *Macropus canguru*. Those with equally extensive range but crossing north instead of south of the central desert are *Petrogale inornata*, *Lagorchestes conspicillatus*, *Osphranter*, and *Megaleia* (?).

The Macropodidae appear to be primarily animals of the lowlands. But in New Guinea, where there are very high mountains, wallabies occur at 10,000 feet and higher. In those high ranges *Dorcopsulus* is endemic, and the long-haired mountain representative of *Thylogale brunii* is found between 7000 and 11,000 feet. The New Guinea tree kangaroos normally live at altitudes between 2000 and 8000 feet, but the north Queensland species *lumholtzi*, doubtless limited by the relative lowness of the mountains available, is found between 1000 and 4000 feet.

In the southeast of Australia also, where heights of land in combination with seasonal cold can produce comparatively frigid climates, certain of the macropods are found quite high, e.g., *Macropus robustus* and *Protemnodon rufogrisea*. Troughton (1941, p. 204) indicates that the latter occurs as high as 4000 feet in Tasmania, where there is an appreciable winter.

PART 2. TAXONOMY

FAMILY MACROPODIDAE

THE MACROPODIDAE are diprotodont marsupials having a leaping type of locomotion and unreduced tails. Their diprotodont dentition comprises: incisors, three upper, one lower; upper canines obsolete or obsolescent; strongly specialized upper and lower premolars, third permanent and fourth deciduous, the latter and sometimes both displaced by the fourth permanent; and molars, four upper and four lower.

Here are included the subfamilies Hypsiprymnodontinae (including Burramyinae Simpson), Potoroinae, Palorchestinae, Sthenurinae, and Macropodinae.

Among the principal characters that serve to distinguish the subfamilies from one another are: various modes of specialization of the third and fourth premolars; development of molar bilophodontism and hypsodontism (Palorchestinae, Sthenurinae, Macropodinae) in contradistinction to quadrituberculy (Potoroinae, Hypsiprymnodontinae); and development of upward instead of downward molar size gradients (later-erupting molars becoming successively smaller as in most Potoroinae, or larger as in most Macropodinae).

Appearance in the upper incisors of size dominance (or else of extreme reduction) of one or two teeth and variability of the size of the bullae seem usually to be merely of generic systematic value. This is usually true, too, of changes in length and breadth of the skull and of individual cranial bones, although an exception may be seen in the Sthenurinae in which shortening and thickening of the bones of the skull have been carried to an extreme. Even so, the Sthenurinae must be coderived with the Macropodinae.

The peculiarities of the palatal foramina and of the premolars in the Palorchestinae (very imperfectly known) may well have subfamily significance.

It is questionable whether any one family can be treated as "most primitive" or another as "most specialized." All possess varied combinations of primitive and specialized characters. The retained posterior fifth digit

in *Hypsiprymnodon* is primitive, its fourth premolar is highly specialized, its urogenital system (Pearson, 1946) is regarded as specialized. In the Potoroinae the prevalently quadrituberculate molars are probably less specialized than the bilophodont molars of the Macropodinae, but the third and fourth premolars are more specialized in the Potoroinae than in the Macropodinae. Pearson (*ibid.*) indicates for the Potoroinae a condition of the urogenital system equally specialized with *Hypsiprymnodon* and more specialized than in the Macropodinae.

The subfamilies are presented in the order Hypsiprymnodontinae, Potoroinae, Macropodinae, Sthenurinae, and Palorchestinae.

SUBFAMILY HYPsiprymnodontinae

Collett (1887) accorded the genus *Hypsiprymnodon* full family rank, and Thomas (1888) placed it in a separate subfamily, an opinion opposed by Bensley (1903) but endorsed by Raven and Gregory (1946). Simpson's (1945) treatment of it as a divergent genus of the Potoroinae suggests that it is more closely related to the Potoroinae than to the Macropodinae.

Furthermore *Hypsiprymnodon*, *Burramys*, and *Propleopus* (= *Triclis*) are more closely related to one another than the present systems of classification indicate. All three genera share in having p_4^1 extremely high, short (longitudinally in the toothrow), and marked by numerous vertical flutings. Because of imperfect preservation their further distinction rests mainly upon the extent to which vestigial lower incisors, anterior premolars, and m_4^1 have disappeared.

The second lower incisor is present as a remnant in *Hypsiprymnodon* and in *Propleopus* but is apparently absent in *Burramys*. A vestigial upper premolar is present in *Burramys*, and a well-developed one in *Hypsiprymnodon*. In *Propleopus* the characters of p_3^2 remain unascertained. A small upper canine is present in *Hypsiprymnodon* and in *Burramys*. Vestigial lower premolars anterior to p_4 are found in *Burramys* but not in *Hypsiprymnodon* or in *Propleopus*. In *Hypsiprymnodon* p_3^2 are developed teeth in the pouch stage but are lost either during or

after it. Sharp accentuation in the size gradient (m_1 largest, m_4 much smaller) similar to the condition in *Petaurus* and other Phalangeridae is seen in *Hypsiprymnodon* but not in *Propleopus* (De Vis, 1888, pl. 1). In *Burramys* this condition is again apparent (Broom, 1896, pl. 7). Outward rotation of p_4 has reached approximately 30 degrees in *Hypsiprymnodon* and 15 degrees in *Burramys*, but has scarcely commenced in *Propleopus*. The deciduous premolars of *Hypsiprymnodon* are quadritubercular; p_3^3 although sectorial, are sharply different from p_4^4 . The diastemata are long in all three genera.

Hypsiprymnodon and *Burramys* are subequal in size, while *Propleopus* is as large as a large wallaby. The proportional length of the crown of p_4 to the length of m_{1-3} is 13.5:33.2, or 31 per cent in the large *Propleopus*; it is 44 per cent in *Hypsiprymnodon* and as high as 60 per cent in *Burramys*. The depth of the mandibular ramus beneath m_1 and p_4 is far greater in *Propleopus* than in either *Hypsiprymnodon* or *Burramys*. It is approximately three times the height of p_4 in *Propleopus*, equal to that height in *Hypsiprymnodon*, and one and one-half to two times that height in *Burramys*.

Of these three genera, the much larger *Propleopus* appears to be the most generalized in spite of the fact that it seems to have retained no vestigial premolars. Neither i_1 nor p_4 has yet attained a great degree of enlargement in proportion to the sizes of the molars, nor can there be discovered in *Propleopus* any tendency for reduction of the size or number of the posterior molars.

PROPLEOPUS LONGMAN

Triclis DE VIS, 1888, Proc. Linnean Soc. New South Wales, ser. 2, vol. 3, p. 5.

Propleopus LONGMAN, 1924, Mem. Queensland Mus., vol. 8, p. 20 (new name; *Triclis* preoccupied).

TYPE: *Triclis oscillans* De Vis.

The generic characters have been pointed out in the early part of this paper in the comparison of this marsupial with *Hypsiprymnodon* and *Burramys*. The most noteworthy characters are the considerable depth of the ramus, the small, fluted, high-crowned premolar which appears annectant between the potoroine p_4 and that of *Hypsiprymnodon*,

and the equality of size of the quadrituberculate molars.

Propleopus oscillans (De Vis)

Triclis oscillans DE VIS, 1888, Proc. Linnean Soc. New South Wales, ser. 2, vol. 3, p. 8.

The description of this fossil was based upon a mandible, of which the parts behind the toothrow were missing (De Vis, 1888, pl. 1).

BURRAMYS BROOM

Burramys BROOM, 1896, Proc. Linnean Soc. New South Wales, ser. 2, vol. 10, p. 563; 1896, *ibid.*, ser. 2, vol. 11, p. 51; 1898, *ibid.*, ser. 2, vol. 13, p. 63.

TYPE: *Burramys parvus* Broom.

The genus *Burramys* as figured by Broom (1896, *ibid.*, ser. 2, vol. 11, pl. 7) has much the appearance of *Hypsiprymnodon* but retains one upper and at least two lower vestigial antemolar teeth. The vestigial characters of p_3^3 should be contrasted with the still well-developed p_3^3 reported in *Hypsiprymnodon* by Carlsson (1915).

The structure of p_4^4 is remarkably like that of *Hypsiprymnodon*, as is the steeply graded quadritubercular molar complex. The maseteric canal was not shown by Broom, perhaps because still filled with matrix. If it were absent, such absence might be adduced as taking *Burramys* closer to the phalangers and removing it farther from *Hypsiprymnodon*.

Burramys parvus Broom

Burramys parvus BROOM, 1896, Proc. Linnean Soc. New South Wales, ser. 2, vol. 10, p. 564; 1896, *ibid.*, ser. 2, vol. 11, p. 51; 1898, *ibid.*, ser. 2, vol. 13, p. 63.

This species is known only from a part of a mandible containing i_1 , a vestigial i_2 , p_4 , and m_{1-4} . The angular, coronoid, and articular processes are absent. Drawings were published by Broom (1896, *ibid.*, ser. 2, vol. 11, pl. 7).

HYPSIPRYMNODON RAMSAY

Hypsiprymnodon RAMSAY, 1876, Proc. Zool. Soc. New South Wales, vol. 1, p. 33.

Pleopus OWEN, 1877, Ann. Mag. Nat. Hist., ser. 4, vol. 20, p. 542.

TYPES: Of *Hypsiprymnodon*, *moschatus*. Of *Pleopus*, *nudicaudatus*.

This remarkable genus was discussed by

Owen (1879) soon after its discovery. Bensley (1903) thought it to be closely related to *Bettongia*. Although he discussed the dp_4^4 of the marsupials generally (pp. 190–191), he was apparently unfamiliar with those of the present genus. The morphology of *Hypsiprymnodon* was well investigated by Carlsson (1915), who figured (pl. 2, figs. 12–15) the very early deciduous p_3^3 and dp_4^4 , which she discovered to be present in pouch young. As was to be expected, the quadritubercular pattern of the molar series was found to be reflected in dp_4^4 . Contrary to the case in the Macropodinae and Potoroinae, however, p_3^3 proved to be unlike p_4^4 . Seen from the labial side these premolar teeth are tricuspid; also, the occlusion surface of p_3^3 reveals two smaller internal cusps and that of p_4^4 one internal cusp. These premolars are not narrowly sectorial teeth as p_4^4 are. Instead, although their anterior portions may have a slicing function, their posterior portions are essentially molariform and appear to function as extensions of the molariform dp_4^4 .

Hypsiprymnodon moschatus Ramsay

Hypsiprymnodon moschatus RAMSAY, 1876, Proc. Linnean Soc. New South Wales, vol. 1, p. 34.

Pleopus nudicaudatus OWEN, 1877, Ann. Mag. Nat. Hist., ser. 4, vol. 20, p. 542.

TYPES: Of *moschatus*, at Sydney. Of *nudicaudatus*, B.M. Nos. 78.1.12.1 (skin) and 1694a (skull), adult female from Herbert River, Queensland.

Two male specimens exist in the Archbold collection and two others in the American Museum general collection. One of the Archbold specimens is from Lake Barrine, 2400 feet, the other from Mount Spurgeon, 3600 feet. The two in the American Museum general collection, male and female, were taken by the late H. C. Raven at Atherton Tableland, 9 miles southeast of Ravenshoe, northern Queensland, in November, 1921 (A.M.N.H. Nos. 65339, 65340). At the United States National Museum are three adults (Nos. 238443, 238444, 238445), two males and one female, all also from Atherton Tableland, and a pouch juvenile, U.S.N.M. No. 238654, female, preserved in alcohol. At the Museum of Comparative Zoölogy there are five specimens: one from Mount Spur-

geon, three from Lake Barrine, and one from near Cairns—all collected by P. J. Darlington and all adults with p_4^4 and m_4^4 in place.

The rostrum is greatly elongated, the interorbital region not narrowed. The posterior palate has large openings; the bullae, although quite small, are slightly inflated (their length, ± 6.5 mm.). The mastoid processes are narrow and laterally expanded; the paroccipital processes are extremely short as in *Bettongia* of the Potoroinae.

The dental dimensions are: width across tip of i^1 , 1.8 mm.; crown length of i^2 , 2.3; of i^3 , 1.8 (i^2 flat crowned, i^3 simply compressed).

The compressed canine, measured longitudinally in the toothrow, 1.6 mm.

The deciduous teeth were not present in any specimens studied by me. The length, anterior and posterior widths of the quadrituberculate molars are: m^1 , 3.0 by 2.7 and 2.5; m^2 , 3.0 by 2.9 and 2.6; m^3 , 2.7 by 2.5 and 2.1; m^4 , 2.4 by 2.2 and 1.6 mm. In the second individual m^4 has the anterior width only 2.0, the posterior width 1.3 mm.

The extraordinarily hypsodont p^4 , with five grooves, is broad behind and at the middle of its base, tapered or wedge shaped in front. Its crest is sectorial throughout. There is no cingulum and only a trace of a postero-internal cusp. Its length is 4.3; its greatest width (basal), 2.9.

All three of the specimens in the United States National Museum have a white area on the throat which extends as a narrow line to the chest. These marks, although present in the Archbold specimens, are much less prominent. The female (U.S.N.M. No. 238445) was recorded as having four nipples and two young in the pouch.

SUBFAMILY POTOROINAE

The Potoroinae may be defined as Macropodidae having a long, dagger-like i^1 ; usually simple i^{2-3} (exception, *Aepyprymnus*); canine not greatly reduced (exception, *Caloprymnus*) and never absent; premolars slightly to complexly vertical grooved, low crowned (not high as in *Hypsiprymnodon*), and lacking an internal cingulum; molars quadrituberculate (except *Caloprymnus* and *Aepyprymnus* which tend to bilophodontism); molar gradient usually pronounced, i.e., sharply dimin-

ishing backwards (exception, *Aepyprymnus* and, in part, *Bettongia cuniculus*). This type of gradient is commonly to be observed in certain Phalangerinae such as *Petaurus* and *Eudromicia*.

The skull is normally very short, broad, and shallow (but is elongate and narrow in *Potorous*). The dolichocephaly developed in *Potorous* (e.g., *P. apicalis*) is sharply different in character from that of *Hypsiprymnodon*, in which the outline of the skull is superficially similar. In the former the frontals, lacrimals, and jugals extend far in front of the orbit, and the infraorbital foramen is placed slightly behind the posterior part of p^4 . The premaxillary part of the muzzle is also elongated so that the canine is farther from i^1 than it is from p^4 . All this is contrary to the conditions present in *Hypsiprymnodon*. The bullae of the Potoroinae are considerably to greatly inflated in *Bettongia* and *Potoroops morgani*, relatively flat in the remaining genera. The posterior palatal foramina are large in all genera except *Aepyprymnus*.

Bensley (1903, pp. 143-144) distinguished two divisions of this subfamily (including *Hypsiprymnodon*), to each of which he gave subfamily rank. These distinctions were based upon the number and relative prominence of the ridges and grooves on p_3^3 and p_4^4 . By this means he associated *Potoroops*, *Potorous*, and *Caloprymnus* in one group, and *Bettongia*, *Aepyprymnus*, and *Hypsiprymnodon* in the other. He thought the Potoroinae had "originated independently from the Macropodinae from phalangerine forms."

Bensley's system, although excellent for a classification founded on the degree of premolar specialization, ignored such conflicting characters as widening or narrowing of skull, which also attains extremes. *Potorous* and *Hypsiprymnodon* are markedly dolichocephalic. *Potoroops*, *Caloprymnus*, *Bettongia*, and *Aepyprymnus* are markedly brachycephalic.

Finally, *Hypsiprymnodon*, *Potorous*, *Potoroops*, and *Bettongia* have quadrituberculate molars, while the molars of *Caloprymnus* and *Aepyprymnus* are incipiently bilophodont. A number of other dichotomous characters suggest still other groupings of the potoroine genera. Although *Hypsiprymnodon* is placed in a separate subfamily in this paper, it

should be regarded as generally closer to the Potoroinae than to the Macropodinae.

POTOROOPS MATSCHIE

Potorous MATSCHIE, 1916, Mitt. Zool. Mus. Berlin, vol. 8, p. 264, footnote (as a subgenus).

TYPE: *Hypsiprymnus platyops* Gould.

Matschie distinguished *Potoroops* by its short broad head, which did not exceed 62 mm. in length, its long hind foot, and its unlengthened muzzle.

Potoroops, if the type of *platyops* is used as a basis, may be rediagnosed as follows: skull brachycephalic as in *Bettongia*, not dolichocephalic as in *Potorous*; third and fourth premolars with few and shallow grooves as in *Potorous*, not with many and deep grooves as in *Bettongia*.

The bullae are not present in the broken type skull of *platyops*.

The subfossil *Potorous morgani* from a cave on Kangaroo Island, as stated by Finlayson (1938), is probably closely related to *platyops*. The bullae (in Finlayson's illustration) have about the degree of inflation to be seen in *Bettongia cuniculus*.

Potoroops platyops (Gould)

Hypsiprymnus platyops GOULD, 1844, Proc. Zool. Soc. London, p. 103.

TYPE: B.M. No. 46.4.25.11 (283a, female) from Walyema Swamps, 40 miles northeast of Latham, Victoria County, Western Australia.

I have seen only the type specimen of this probably extinct species. Troughton (1941, p. 163) cites a record of a specimen living in 1908. The type lacks most of the teeth and the hinder part of the skull. The skin has short ears. The pelage consists of brown wool hairs and long, black-tipped, whitish guard hairs. The fur of the underparts is buff, with dark gray bases. The feet and hands are brownish gray; the tail is dark brown above, buff beneath.

The skull is very short and broad; the nasals are also short and broad. Crown lengths measure: i^1 , 1.8 mm.; i^2 , 1.2; i^3 , 1.6; c, 1.8; width of lower incisor, 2.9.

Concerning the bullae of *platyops* Thomas (1888, p. 122) wrote "bullae apparently distinctly inflated." In his table (p. 125) he indicated the measurements of an "adult" male

(the type being a female). The length of "p⁴" of the male was indicated as 4.9 mm. The fact that this tooth had "two broad shallow grooves externally and internally" suggests that both of Thomas' specimens were juvenals and that his "p₄⁴" were in reality p₃³, his "m¹" thus being dp₄⁴. This few-grooved condition removes the possibility that this animal is after all a *Bettongia*, despite the indication offered by the marked molar gradient [length of "m⁴" (=m³) 2.1 mm.] the breadth of its skull, and the "apparently" (see Thomas above) large size of its bullae (actually the bullae are missing, as indicated by my photograph of the type skull).

Additional measurements of type: hind foot, s.u. 61 mm., c.u. 68; zygomatic breadth, 39.6; interorbital breadth, 16; breadth of braincase, 27; greatest length of nasals, 10.7; height of muzzle behind incisors, 8.9; palatal length, 31.4; posterior palatal foramina, 7.0; breadth of mesopterygoid fossa, 7.4; width inside m¹⁻¹, 9.0; length of mandible, 36.0; m¹⁻³, 8.0; p⁴, 4.2 by 1.8¹; m¹, 3.0 by 3.0¹; (m² missing); m³, 2.25 by ?; m⁴, 2.0 by 2.3; m¹⁻³, 8.6.

Potoroos morgani (Finlayson)

Potorous morgani FINLAYSON, 1938, Trans. Roy. Soc. South Australia, vol. 62, p. 135.

Finlayson described two seemingly adult skulls of this extinct animal, which he designated (p. 139) as cotypes.

The general appearance of the skulls is strikingly like that of the type of *platyops*. In one specimen p⁴⁻⁴ are present; in the other only the two alveoli for the anterior and posterior roots of those teeth can be seen. The length of the crown, 5.0 mm., obviously exceeds the length of m¹ (pl. 5, fig. c). The quite small size of the last molar in each skull indicates a marked molar gradient. The crown length (estimated) of m¹ is ± 3.7 ; of m⁴, ± 2.0 .

POTOROUS DESMAREST

Potorous DESMAREST, 1804, Nouveau dictionnaire d'histoire naturelle, 1st ed., vol. 34, Tabl. Meth. Mamm., p. 20.

¹ I suspect that this animal was juvenal. If so, the first two teeth are p³ and dp⁴, respectively, and the identities of the other molars should be shifted correspondingly.

Hypsiprymnus ILLIGER, 1811, Prodrum systematis mammalium et avium, p. 79 (new name for *Potorous*).

TYPE: *Didelphis murina* Cuvier = *Didelphis tridactyla* Kerr.

As here restricted, *Potorous* contains the two recent species *tridactylus* and *gilberti*. The fossil form *morgani* Finlayson belongs to *Potoroos*. The genus is characterized by pronounced dolichocephaly in combination with elongation of the muzzle, by relative lack of inflation of the bullae as in *Aepyprymnus*, and by the weak, almost ungrooved p₃³ and p₄⁴ as in *Potoroos* and *Caloprymnus*. In *Potorous* i¹ is strongly orthodont, not proödont, and i² and i³ are compressed and unspecialized. The canine is normal for the subfamily. The molars form a moderate gradient (considerably steeper in *gilberti* than in *tridactylus*).

Potorous tridactylus (Kerr)

This species differs significantly from the Western Australian *gilberti* by its reduced molar gradient, m⁴ being considerably larger. There are other characters which are pointed out beyond.

Potorous tridactylus tridactylus (Kerr)

Didelphis tridactyla KERR, 1792, The animal kingdom . . . of . . . Linnaeus, p. 198.

Didelphis murina CUVIER, 1798, Tableau élémentaire de l'histoire naturelle des animaux, p. 126.

TYPES: "Not in existence" (Thomas, 1888, p. 119). I have not examined either of Thomas' two individuals from New South Wales. The United States National Museum collection contains a specimen, U.S.N.M. No. 237718, female, taken by Hoy at Ebor, New South Wales; a second specimen, U.S.N.M. No. 124641, without precise locality, obtained by Dr. F. W. Goding, United States Consul stationed at Newcastle, New South Wales; and a third specimen, U.S.N.M. No. 22468, marked *Hypsiprymnus murinus*, New Holland, received from Dr. Beauregard (his number 1017), of the Bureau of Arts, Paris, 1886. At the Museum of Comparative Zoölogy a skin without skull, M.C.Z. No. 6447, is labeled "New South Wales." These four specimens are apparently the sole representa-

tives of the mainland race in American museums. The first two only have good skulls. Both are adults, the deciduous teeth shed. The following notes are founded upon the wild-caught specimen from Ebor:

Crown length of i^1 , 2.3 mm.; i^2 , 2.0 (worn); i^3 , 3.2 (worn); in the Newcastle specimen worn to 2.8 mm.).

Molars: m^1 , 3.8 by 3.7 (posterior); m^2 , 4.0 3.9 (posterior); m^3 , 4.2 by 3.6 (anterior) and 3.1 (posterior); m^4 , 3.3 by 3.0 (anterior) and 2.3 (posterior).

The lengths of m^{1-4} (15.0) and of m^{1-3} (11.7 mm.) indicate a slightly smaller form than the Tasmanian race (U.S.N.M. No. 38798, 17.3 and 13.2 mm., respectively). Moreover, the nasals are much wider at the base (13.2) in the Ebor specimen than in the Tasmanian specimen listed above (only 9.8 mm.).

The skin of the Ebor specimen has the white of the inner side of the leg coming out on the dorsal surface of the foot at the base of the metacarpals. The pouch, with four nipples, contained only one young.

Finlayson (1935) records localities in Victoria at which this animal can still be found.

Potorous tridactylus apicalis (Gould)

Hypsiprymnus apicalis GOULD, 1851, The mammals of Australia, vol. 2, pl. 68.

Potorous rufus HIGGINS AND PETTERD, 1884, Proc. Roy. Soc. Tasmania, for 1883, pp. 181, 196.

Types: Not seen; *apicalis* from New Norfolk, near Hobart, southern Tasmania; *rufus* from Launceston, northern Tasmania.

A large series of skulls without skins of this animal was obtained by H. C. Raven at Moonah, near Hobart, southern Tasmania, in 1922. There are three specimens from Arthur River, northern Tasmania, at the United States National Museum, Washington, D. C. The discussion following relates to the larger south Tasmanian form, *apicalis*.

The crown lengths of i^2 and i^3 are ± 2.2 mm. and ± 3.2 , respectively, wearing to 2.0 and 2.8 in age. The left and right tooththrows are almost parallel.

The third premolar, weakly two- to three-grooved, is 4.0 mm. in length; its anterior and posterior widths are 1.8 and 2.1. The deciduous fourth premolar, much narrower than m^1 , measures 3.5 mm. in length, 2.5 and 2.7 in

anterior and posterior widths. The lengths and anterior and posterior widths of m^{1-4} are: m^1 , 4.4, 3.8, 3.7; m^2 , 4.5, 4.0, 3.8; m^3 , 4.6, 3.8, 3.5; m^4 , 3.7, 3.3, 2.7 mm. The abrupt diminution and modification of the posterior loph of m^4 indicate that it is the terminal tooth of the tooththrow. There is no indication of a fifth molar such as appears in *Bettongia cuniculus*. The fourth premolar (in A.M.N.H. No. 65328), weakly four-grooved, is 7.8 mm. in length, 3.0 and 3.1 in anterior and posterior widths. The anterior and posterior cusps of the secutor ridge are much larger than the intervening cuspules. The lingual side of the tooth is much abraded in most specimens.

The larger size of the teeth, compared with those of the almost extinct Australian race *tridactylus*, is obvious.

While acknowledging the possible distinctness of the smaller north Tasmanian form named *rufus*, Thomas (1888, p. 120) found himself unable to reach a decision. The measurements which I made of one of the specimens in Washington (U.S.N.M. No. 238449, juvenal male) indicate a somewhat smaller size: crown length of i^2 , 2.4; i^3 , 2.7; p^3 , 4.0 by 1.7; dp^4 , 3.1 by 2.3 (anterior) and 2.4 (posterior); m^1 , 4.1 by 3.1 (posterior). The dimensions are not so small as those of the true *tridactylus* from New South Wales, which I have shown previously. I have tentatively left *rufus* in the synonymy of *apicalis*.

Potorous gilberti (Gould)

Hypsiprymnus gilberti GOULD, 1841, Proc. Zool. Soc. London, p. 14.

TYPE: B.M. No. 46.4.447 (282b), skull, with B.M. No. 41.1152, skin, female, collected by Gilbert at King George Sound, Western Australia.

The rostrum of this rare species, which is relatively broad and low, is more massive than that of *tridactylus*. The back of the skull of the type is broken, and i^1 is very high (5.9 mm.). The premolar complex of the type (as shown in my photograph) suggests that the deciduous dentition is still present; the premolar (5.1 by 2.7) is short and its maximum thickness occurs before the middle, while the first molariform tooth (dp^4 ?) is considerably narrower than the second (m^1 ?). The lengths of the incisive crowns are: i^1 , 2.0; i^2 , 2.0; i^3 ,

2.2; but while i^1 is massive, i^{2-3} are markedly compressed.

The molar gradient is steeper than that of Tasmanian *P. tridactylus*: m^1 , 4.0 by 3.6; m^2 , 4.0 by 3.9; m^3 , 3.7 by 3.3; m^4 , 2.7 by 2.6 mm. The small size of the last tooth suggests that it is really m^4 , not m^3 . On the other hand there is an appearance of still another tooth erupting in my photograph.

The zygomatic width is decidedly narrower than in *apicalis* (41 mm. compared with 49 mm.). On the other hand the braincase and the nasals are wider (32 and 14 mm. compared with 28 and 9 mm.).

A specimen at the Museum of Comparative Zoölogy, M.C.Z. No. 1869 from "Melbourne," received from Prof. J. McCoy, has the back of the braincase broken. The cheek teeth are greatly worn, and all the molars are present. The number of grooves in p^4 is two to four, in p_4 , four. Dimensions: p^4 , 6.0 by 2.4 (postero-internal cusp probably worn away); m^1 , 3.8 by 3.1; m^2 , 4.4 by 3.8; m^3 , 4.2 by 3.5; m^4 , 3.2 by 2.8 (the posterior loph, 2.3).

The first incisors are very elongate as are those of *tridactylus*. The crown lengths of i^{2-3} are 2.3 and 2.7. Both of these teeth have compressed, elongate crowns without infoldings of enamel. The crown length of the canine is 1.6 mm. The anterior palatal foramina measure 2.6; the posterior palatal foramina, ± 9 mm. The length of the anteorbital canal is 11.2 mm. There is considerable facial exposure of the lacrimal bone. The zygomatic width is 33.5 mm.; the nasals measure 31 by 9.8 mm. The mandible is shallow (5.7 mm. beneath m_1), and the coronoid process is very low and straight.

CALOPRYMNUS THOMAS

Caloprymnus THOMAS, 1888, Catalogue of the Marsupialia and Monotremata in the . . . British Museum, p. 114.

TYPE: *Bettongia campestris* Gould.

The rediscovery of this remarkable genus by Finlayson (1932) has provided a wealth of facts of which Thomas (1888) was ignorant. The outstanding characters of *Caloprymnus* are its extraordinarily great nasofrontal breadth, the infrazygomatic process, the extreme degree of canine reduction, the few, weak grooves on the premolars, the incip-

iently bilophodont condition of the molars as in *Aepyprymnus*, and the slight molar gradient. In other respects the skull conforms rather closely to that of *Bettongia*. The posterior palate and bullae resemble those of *B. cuniculus*. The incisors show none of the specialization to be seen in *Aepyprymnus*.

Caloprymnus campestris (Gould)

Bettongia campestris GOULD, 1843, Proc. Zool. Soc. London, p. 81.

TYPE: B.M. No. 46.4.4.44, adult male, studied and photographed.

From the standpoint of dentition, Finlayson's specimen (1932, p. 161, figs. A, B) is clearly only subadult, since, although p^4 appears in the left tooththrow, p^3 and dp^4 are still shown in the right; also the last molars shown are m^{3-3} . The dimensions of the teeth of the premolar area are shown in his table 2 (p. 166): p^3 , 3.0 to 3.5 mm.; p^4 , 5.5 to 6.0 (p^4 of type, 6.1 by 2.9). He omits the measurements of dp^4 . The grooves of p^3 and p^4 , ill developed according to Bensley (1903), are not mentioned by Finlayson. The length of the bulla (not given by Finlayson) is 12.5 mm. in the type. The molar gradient is relatively slight, although m^4 is small; m^{1-4} in the type, 3.8 by 3.9; 4.4 by 4.2; 4.2 by 3.9; 3.2 by 3.0. The crown lengths of the incisors of the type are: i^1 , 2.2; i^2 , 1.1; i^3 , 2.5. The cuspidate "canine" similarly measures only 1.1 mm.

In M.C.Z. No. 37651, a juvenal female, p_3^3 , dp_4^4 , and m_{1-2}^{1-2} are present. The measurements of the upper teeth are: p^3 , 6.2 by 3.4; dp^4 , 4.4 by 4.4; m^1 , 4.8 by 4.7; m^2 , 4.2 by 4.0; of the lower teeth, p_3 , 5.5 by 2.4; dp_4 , 4.0 by 3.9; m_1 , 4.5 by 4.3; m_2 , 4.2 by 4.2. Thus the molar gradient falls sharply from the large m^1 (compare with Finlayson's illustration).

The third upper premolar shows the customary broadening of the hind end of the tooth (anterior width, 2.5 mm.). It has about five weak external and internal grooves along the main sectorial ridge. There is also a weak internal cingulum with two or three ill-defined cuspules just anterior to the middle of the cingulum.

The incisors of this young specimen are relatively unworn: i^{2-3} show wear only at their anterior tips. All incisors are wholly ungrooved. The crown length of i^2 is 2.6; that

of the forwardly inclined i^3 taken at right angles to the axis of the tooth, 1.7; along the surface of occlusion, ± 2.6 . The crown length of i^1 is 2.3, which will increase as the tooth lengthens.

In the type skin there appears a well-defined neck gland, and the tail is untufted. The range, as shown by Finlayson, is east of Lake Eyre and then north for 250 miles.

BETTONGIA GRAY

Bettongia GRAY, 1837, Mag. Nat. Hist. (Charlesworth), vol. 1, p. 584.

Bettongiops MATSCHIE, 1916, Mitt. Zool. Mus. Berlin, vol. 8, p. 264.

TYPES: *Bettongia cuniculus* Ogilby, designated by Thomas in 1888 (*Bettongia*); *Hypsi-prymnus lesueur* Quoy and Gaimard (*Bettongiops*).

A combination of three rather artificial characters is generally held to distinguish this genus from others, namely: upper premolars with six or more vertical grooves, large palatal vacuities, and inflated bullae. The skull is broad and pear shaped, the rostrum short and pointed. The molar gradient is steep in *lesueur* and *penicillata*. If it appears to be little developed in *cuniculus* that is because size reduction appears only in a rarely developed fifth molar.

It appears that the Tasmanian *B. cuniculus* is the most primitive of living *Bettongia*. Its bullae, although much more inflated than the bullae of *Potorous*, are smaller than those of *B. lesueur* and do not become coalesced with the paroccipital processes. Its permanent fourth premolar, smaller also than that of *lesueur*, has from seven to eight grooves compared with the nine grooves of *lesueur*. Yet in regard to the development of its anomalous fifth molar *cuniculus* is specialized.

On the contrary, *B. lesueur* may be considered specialized because of its greatly swollen bullae which unite with the paroccipitals. Its molar gradient is very steep, and its muzzle is shortened and somewhat pinched in at the sides.

Upper and lower p^{3-4} in many *Bettongia* tend to be secondarily thickened at the anterior middle; p^3 in young *Bettongia penicillata* are short, thick teeth; p^4 are often broadened at the middle almost to the thickness of the

posterior end. This is less noticeable in *B. lesueur*.

Bettongia penicillata of Western Australia, which is smaller in size but has larger bullae than *cuniculus*, appears to be intermediate in relationship. *B. gaimardi* is not surely known to me (but see p. 268).

The tail, which is crested in *penicillata*, is reported to be partly prehensile.

Bettongia penicillata Gray

Three races of this rat kangaroo are recognized in the check list of Iredale and Troughton (1934): true *penicillata* of New South Wales, *gouldii* of South Australia, and *ogilbyi* of Western Australia. The first two have been reputed to be extinct, but the specimens from Queensland listed beyond appear to be referable to the first. I have seen no example of *gouldii*. One wonders whether *gaimardi* from Port Jackson, New South Wales, and *penicillata* were not synonymous.

Bettongia penicillata penicillata Gray

Bettongia penicillata GRAY, 1837, Mag. Nat. Hist. (Charlesworth), vol. 1, p. 584.

TYPE: B.M. No. 50.11.22.47 (skull No. 279f, skin No. 298c), adult male, "New South Wales."

Skull short, pear shaped, with short, heavy rostrum. Nasals exceeding the premaxillae; bulla large, well inflated; paroccipital process knob-like.

Length of skull, 76.1 mm.; condylobasal length, 69.1; zygomatic width, 41.5; breadth of braincase, 30.0; mastoid width, 28.3; length of nasals, 30.5; their width at base, 14.0; palatal length, 42; length of anterior and posterior foramina, 2.2 and 11.0; length of bulla, 13.7. I give these details of the type skull of a now extinct race.

The teeth of this specimen have the following crown dimensions: i^1 , 2.4 mm.; i^3 , 3.2; c, 2.5; p^4 , 7.0 by 2.9; m^1 , 4.2 by 4.5; m^2 , 4.2 by 4.7; m^3 , 3.5 by 3.6; m^4 , 2.3 by 2.1.

The tail of the type skin is brush tipped as in the western Australian race, and the tail hairs are ± 20 mm. in length.

I suspect that the following four specimens from north Queensland represent true *penicillata*:

A juvenal, A.M.N.H. No. 65280, collected by Raven at Ravenshoe, northern Queens-

land, shows essentially the same general structure of the bulla (length, 13 mm.) as our *lesueur*. Its nasals and the palate anterior to the canines are broken away. The molars m^{1-2} measure 4.5 by 4.0 and 4.6 by 4.3 mm., respectively. The posterior palatal foramina extend only to the back of m^{1-1} . The premolar (p^3) has six external grooves.

Three specimens in the Museum of Comparative Zoölogy, collected by P. J. Darlington at Mount Spurgeon in July, 1932, No. 29206, juvenal, and Nos. 29205 and 29207, adults, are also referable to the above. In each case the molar toothrow curves inward at the back slightly less than in three *lesueur* from "Victoria" in the Museum of Comparative Zoölogy. Inner width of m^{4-4} is ± 13 mm.; in south Australian *lesueur*, ± 11 mm. The connection of the masseteric canal with the nerve opening, although large, lies deep and is almost concealed in the above-mentioned specimens. It is large and exposed in *lesueur*. In all these characters the animals closely resemble the Western Australian *B. p. ogilbyi*.

The dental dimensions of the three specimens from the Museum of Comparative Zoölogy are:

| | M.C.Z. No. 29206 JUVENAL MALE |
|--------|----------------------------------|
| p^3 | 5.4 × 2.7 |
| dp^4 | 3.7 × 3.3 (ant. loph) |
| m^1 | 4.0 × 4.2 |
| m^2 | 4.2 × 4.4 |
| m^3 | 3.9 × 4.0 |
| m^4 | Just visible |
| p^4 | Not erupted |

The third premolar has six grooves: p^4 , eight to nine grooves: m^4 is exceptionally small (see No. 29205). The maximum size in the molar gradient is located in m^2 .

The anterior widths of the bullae are 9.3 mm., 8.9, 10.7. The pelage consists of long, thin, rather coarse hair. It is not woolly.

The type of *peron* from New South Wales (Paris No. A 2650) has permanent p^4 with seven external grooves and measuring 7.1 by 3.4 mm. The premolars diverge slightly in front as in *B. penicillata*. The molar gradient is steep as in *Bettongia*, the length of m^{1-3} being 3.6, 3.5, and 2.9. The smallness of the

alveolus of the missing m^4 as well as the much inflated bulla conforms also to *Bettongia*. The specimen is thus to be regarded as synonymous with *B. gaimardi* and *B. penicillata*, both of which come from southeastern Australia.

Bettongia penicillata ogilbyi (Waterhouse)

Hypsiprymnus ogilbyi WATERHOUSE, 1841, Naturalists library, marsupials and monotremes, p. 185.

TYPE: Not seen; from Swan River, Western Australia.

Two specimens from Chicago Natural History Museum, a juvenal male from Pinjelly, and an adult male from King River (Albany), have been lent me for study. I have also examined six at the Museum of Comparative Zoölogy and nine at the United States National Museum.

The incisive crown lengths are nearly equal, although i^1 becomes heavier as most of it is erupted, and i^2 is thicker and more oval in outline than the compressed i^3 . In the young Chicago Museum specimen i^3 and c are scarcely worn. Lengths: i^2 , 2.8 mm.; i^3 , 3.0. In U.S.N.M. No. 237720, juvenal female, the incisors measure: i^1 , 2.4; i^2 , 2.9; i^3 , 3.9. A

| | M.C.Z. No. 29205 FEMALE | M.C.Z. No. 29207 MALE |
|--|----------------------------|--------------------------|
| | Shed | Shed |
| | Shed | Shed |
| | 4.2 × 4.2 | 4.3 × 4.1 |
| | 4.5 × 4.5 | 4.3 × 4.3 |
| | 4.1 × 3.9 | 3.8 × 3.7 |
| | 2.6 × 2.4 | 2.8 × 2.8 |
| | 8.4 × 3.0 | 8.6 × 3.0 |

trace of a labial groove appears at 0.8 mm. from the front of the tooth.

Both p^3 and p^4 show the partial outward rotation of the anterior end indicated by Jones (1923-1925, fig. 158). The deciduous p^4 is (characteristically of the subfamily) much smaller than m^1 . An increasingly sharp backward size reduction in the molars leads to the very small-sized m^4 in the adult.

The third premolar is short and thick and has five external grooves. Its length is 4.5 mm.; width, anterior, 2.2, posterior, 2.7. There is no trace of the circulum of the Macropodinae.

The dimensions of dp^4 are: length, 3.3 mm.; anterior and posterior widths, 2.9 and 3.4. The lengths of m^1 to m^4 are approximately: 3.9 to 4.2, 4.1 to 4.2, 3.6 to 3.7, 2.4 mm. Their anterior and posterior widths are: m^1 , 4.0 and 4.2; m^2 , 4.2 and 4.2; m^3 , 3.7 and 3.3; m^4 , 2.8 and 2.1 mm. The molar gradient is thus normally steep for the genus. The last molar is often fully in place before p^3 and dp^4 are shed.

The permanent premolar has eight external grooves. After a slight narrowing immediately in front of the hind end of the tooth it swells again at its middle to the same breadth. Length is 7.7 mm.; anterior, middle, anteposterior, and posterior widths are, respectively, ± 2.3 , 2.9, 2.4, 3.0 mm.

The anterior palatal foramina are ± 2.5 mm., the posterior openings 9 to 11 mm. in length. The lengths of the bulla are (juvénal) 14.0, (adult) 15.4; their greatest width, 9.5 and 11.2. The bases of the nasal bones run about at right angles to the median sutural axis.

The skins of these specimens show the crested terminal parts of the tails characteristic of the species. The tail is slightly tapered.

[*Bettongia gaimardi* (Desmarest)]

Kangurus gaimardi DESMAREST, 1822, *Mammalogie ou description des espèces de mammifères*, Suppl., p. 542.

TYPE: Paris No. 79, a mounted skin, labeled "La tête et une portion du squelette au Cabinet d'Anatomie." This specimen also bears the erroneous label *Potorous tridactylus*.

The foot of the type is 108 mm. in length (s.u.), 116 (c.u.). The skull, numbered Paris A-2650, a young adult from the voyage of the "Uranie," has the bulla only 9.4 mm. in length. The premolar is seemingly adult, as it is provided with seven grooves and measures 7.1 by 3.4, yet on the other hand its comparative thickness and the small size of the molariform tooth next to it (3.6 by 3.7), compared with the succeeding true molar (3.5 by 4.0), combine to suggest that the tooth is a complex p^3 . I cannot clear up this situation at present, partly because the Paris skull and skin may not belong together and partly because I am uncertain whether this specimen is a juvenal or a young adult. The molar gradient of the three visible molariform

teeth is: 3.6 by 3.7, 3.5 by 4.0, 2.9 by 3.2. A quite small alveolus marks where a fourth molar stood. The molar pattern is markedly divergent from that of *B. cuniculus* and most nearly resembles that of *B. penicillata*.

Although I suspect that *gaimardi* is actually a synonym of *B. p. penicillata*, I hesitate for the present to place it in synonymy.

Bettongia cuniculus (Ogilby)

Hypsiprymnus cuniculus OGILBY, 1838, *Proc. Zool. Soc. London*, p. 63.

TYPE: Not seen; probably from Tasmania (Thomas, 1888, p. 108 and footnote).

Three skulls and three complete skeletons were collected at Moonah, near Hobart, Tasmania, by H. C. Raven; two others are in the United States National Museum, Washington, D. C.; at the Museum of Comparative Zoölogy there is one specimen from the Macquarie River, Tasmania.

The bullae of this species (length, ± 12.2 mm.) are substantially smaller than those of *B. penicillata* and very much smaller than in *lesueur*. The premaxillary-maxillary suture descends from the nasals only slightly in front of p^3 , and then bends forward to the canine, whereas in *penicillata* the suture descends well in front of p^3 and directly to the canine.

The molar gradient, pronounced in *penicillata* and *lesueur*, is inconspicuous in *cuniculus*; m^4 , as in *Aepyprymnus*, is only slightly smaller than m^3 . However, this may be illusory, because of the fifth molar erupting behind m^4 (in A.M.N.H. No. 65267), which is sharply smaller than that tooth. This development of a supernumerary molar is reminiscent of the multiple production of molars in *Peradorcas*. An accessory incisor (apparently of the same cusp form as i^3) may also be present (i.e., in A.M.N.H. No. 65276).

The first incisors are nearly as deep as those of *Potorous*. The lengths of the crowns of i^2 and i^3 are (in M.C.Z. No. 29753), 3.0 mm. and 3.1. In A.M.N.H. No. 65276 (see above) the incisors posterior to i^2 have crown lengths 2.5 and 3.0. From this it appears that the first of these is the supernumerary tooth.

The canine (crown length 2.3 mm.) stands close to i^3 .

In three American Museum of Natural History specimens p^3 measures 5.1 by 2.7, 5.4 by

2.8, and 4.8 by 2.4. The early shed p^3 is proportionately thicker and shorter than p^4 and very little wider behind than in front. The number of grooves is six (A.M.N.H. No. 65276).

The molar gradient is moderate: the lengths of m^{1-4} are 4.2 mm., 4.5, 4.2, 3.8 (A.M.N.H. No. 65267). Rarely (as in the foregoing specimen), a fifth molar is developed, its crown length approximately 3.0. This unusual occurrence is substantiated by the fact that the molariform dp^4 is much smaller and narrower than m^1 (4.0 by 3.4 in A.M.N.H. No. 65270, juvenal male; 4.0 by 3.5 in No. 65269, juvenal female; 3.6 by 3.1, No. 65276, juvenal male). The identity of the fifth molar is further attested to by the presence of the permanent premolar (length, 7.4 mm.).

The number of grooves in p^4 is seven. This tooth is longer and much more compressed than p^3 . Its length varies from 7.4 to 8.4 (M.C.Z. No. 29753). Its anterior and posterior widths are ± 2.4 and ± 2.5 mm. The posterior end of the tooth is abruptly widened.

Bettongia lesueur (Quoy and Gaimard)

Hypsiprymnus lesueur QUOY AND GAIMARD, 1824, Voyage autour du monde sur . . . l'Uranie et la Physicienne, 1817-1820, Zoologie, p. 64.

TYPE: Not seen. Type locality: Dirk Har-

antero-externally and coalesce behind with the paroccipital processes. It is also distinguished by the extreme compression of p^4 (which have nine external grooves) and the very steep molar gradient (especially of the posterior molars): m^{1-4} , 4.8 by 4.2; 4.5 by 4.4; 4.2 by 3.9; 2.4 by 2.3.

The rostrum, compared with that of *B. cuniculus*, is short and pinched in just anterior to p^4 . The palatal openings are very large, reaching the middle of m^{1-1} . The length of the bulla is 17 mm. (in the largest adult *cuniculus*, only 12 mm.). The mandible is generally more massive than that of *cuniculus*.

The mainland race (Western Australia) has received the name *graii* Gould, but it is very doubtful whether this can be maintained; and while the South Australian race *harveyi* Waterhouse was probably valid, I have seen no material that I can identify with it geographically. The three specimens marked "Melbourne" sent the Museum of Comparative Zoölogy by J. McCoy may actually be *harveyi*.

Those three specimens all have the rear of the braincase broken away and lost. The crown lengths of the incisors of the two younger specimens are: M.C.Z. No. 1863, i^{2-3} , 2.9 mm., 3.0; No. 1876, i^{2-3} , 2.0, 3.2. The canine, which is close to i^3 , is 2.0. Their cheek teeth have the following characteristics:

| | M.C.Z. No. 1876 YOUNG ADULT (p_3 still present on one side of mandible) | M.C.Z. No. 1878 ADULT | M.C.Z. No. 1863 YOUNG ADULT |
|-------|---|--------------------------|--------------------------------|
| m^1 | 4.0×4.0 | 3.9×4.2 | 4.0×3.7 |
| m^2 | 4.0×4.1 | 4.2×4.6 | 4.1×4.1 |
| m^3 | 3.9×3.8 | 4.0×4.0 | 3.9×3.7 |
| m^4 | 2.7×2.8 | 2.6×2.7 | 2.7×2.6 |
| p^4 | 8.2×3.1 | 9.1×3.1 | 7.7×2.7 |

tog's Island, Shark's Bay, mid-Western Australia.

We have one complete "zoo" skeleton, A.M.N.H. No. 119489, and a female "zoo" skin and skull, A.M.N.H. No. 6364/8007. Both are adults. There are three at the Museum of Comparative Zoölogy from Victoria.

This species is characterized outstandingly by the extreme degree of inflation of the bullae which encroach upon the glenoid fossa

The number of grooves in p^4 in these specimens is nine, nine, and eight. In M.C.Z. No. 1876, right p_3 measures 4.5 by 2.3, compared with left p_4 , 6.7 by 2.4; and in No. 1863, right p_3 , 3.9 by 2.4, left p_4 , 6.5 by 2.3. The bulla of M.C.Z. No. 1876 is destroyed; the anterior width of the bulla of M.C.Z. No. 1878 is 12.5 mm. The lengths of the bullae cannot be determined. The mandibular nerve canal leading into the masseteric fossa is large. The skins of these animals are soft and densely

woolly, in marked contrast to the series of *penicillata* from Mount Spurgeon, northern Queensland.

AEOPYPRYMNUS GARROD

Aeopyprymnus GARROD, 1875, Proc. Zool. Soc. London, p. 59.

TYPE: *Bettongia rufescens* Gray, designated by Thomas in 1888.

This monotypic genus reveals a mixture of specialized and primitive characters. The second and third incisors are enlarged. The second incisor, although very large, retains the flat crown common to so many phalangeroidea. The cutting edge of i^2 is rotated inwardly so that it presents a stop for the lower incisors. In old specimens it becomes worn off. The canine is not greatly reduced in size but is compressed. Both p^3 and p^4 are large strong teeth. Five grooves appear in p^3 , seven to eight grooves in p^4 . As is usual in the subfamily, dp^4 is considerably narrower than m^1 . Its antero-external tubercle is compressed and functions in continuity with p^3 . The molars show a trend towards bilophodontism. The molar gradient, unlike that of the species of *Bettongia* and other Potoroinae, is almost reversed (m^1 , 5.0 by 4.5; m^4 , which is erupted quite late in life, 5.5 by 4.3). Accompanying the modification of the premaxillary teeth, the premaxilla itself becomes so much shortened that it occupies relatively little of the face, and the incisive foramina are greatly shortened. The nasals also are short and extend to i^2 . The bullae are small and flat. The skull is broad and generally pear shaped in outline. The palate is unfe-nestrated.

Here, apparently, is a case of a genus of the Potoroinae pursuing a course commonly followed by the Macropodinae, a course leading to increasing hypsodontism, and to enlargement and late eruption of the hinder molars.

Engelhardt (1932), dissecting very small pouch young, discovered a "prelacteal" dentition comprising: incisors $\frac{1-4}{1-3}$; canines $\frac{1}{0}$; premolars $\frac{3-4}{3-4}$, and molars $\frac{1-3}{1-3}$. This dentition is strongly reminiscent of the polyprotodont permanent dentition. Many of these minute teeth are "bell-shaped," their crowns having raised edges and depressed centers.

Aeopyprymnus rufescens (Gray)

Bettongia rufescens GRAY, 1837, Mag. Nat. Hist. (Charlesworth), vol. 1, p. 584.

TYPE: Not seen.

A considerable number of specimens from Queensland collected by H. C. Raven and by Gabriele Neuhäuser are in the American Museum of Natural History, six more are in the Museum of Comparative Zoölogy, and a further 19 at the United States National Museum. The localities of specimens in the Museum of Comparative Zoölogy include Molloy, Yungaburra, and Mount Coolon. Most of those at the United States National Museum are from Atherton Tableland, and one (doubtfully) is from "New South Wales." Finlayson (1931) records *rufescens* as common in the Dawson and Fitzroy valleys.

The narrowly tapered i^1 is only 2.5 mm. in juvenals, widening in adults to 2.8. The length of the labial face of i^2 , ungrooved, is 4.0. The labial face of i^3 is 3.0, but its transversely placed cutting edge amounts to ± 4.5 mm.

The canine is substantial, the anteroposterior distance of its crown being 2.7 mm.

The third premolar, with five to six grooves, is ± 7.4 mm. in length. Its width, nearly uniform throughout, is 3.2 mm.

The deciduous fourth premolar is 5.3 mm. in length, 3.8 and 4.2 in anterior and posterior widths. These three dimensions in m^{1-3} are: 5.1 mm., 4.4, 4.5; 6.2, 5.0, 4.8; 7.0, 5.2, 4.5. The fourth molar similarly measures 6.0, 4.3, 3.5. Thus, m^3 is the longest, m^2 the widest, of the molars. Reduction of m^4 is only slight compared to that in *Bettongia*.

The permanent premolar has seven to eight grooves and measures ± 9.0 in length, 3.3 and 3.4 in anterior and posterior widths.

The primitive permanent incisive series of the Macropodinae is composed of a large, slightly compressed hypsodont i^1 , a flat-crowned, subtriangular i^2 , and a compressed, unenlarged i^3 , having a groove on its labial face which extends forward along the crown of the tooth. This condition is met in the large and moderately variable genus *Protemnodon*. Modification of the same condition, combined with other special characters, results in other genera. Enlargement of the i^3 (incipient in *P.*

agilis) leads to *Thylogale* and to *Macropus*. Shift of the labial groove almost to the back of i^3 results in *Thylogale*. Simple enlargement of i^3 , added to great body size and the previously mentioned forward march of the molars, gives us *Macropus*. Reduction in size of i^3 , added to increase in the size of p^4 —the latter found in *Protemnodon bicolor*, *agilis*, and *eugenii*—produces also the short-tailed quokka, *Setonix*.

In another direction a strong trend towards reduction in size of both i^2 and i^3 gives *Petrogale* and its derivatives *Onychogalea* and *Lagorchestes*. In *Onychogalea* i^3 is both quite small and strongly slanted, and the well-known "nail" is developed on the tail. *Lagorchestes* is heavy skulled, has large bullae, and (in one species) less reduced canines. The second and third incisors are less reduced. *Peradornas*, in many respects like *Petrogale*, develops more than the usual number of molars (as does *Myrmecobius* in another marsupial family). *Lagostrophus* has probably sprung independently from the *Protemnodon* stem and is specialized though its narrowly Δ -shaped incisive outline.

The relationship of *Dorcopsulus* (including *Dorcopsis*) and *Dendrolagus* depends in part on the importance of their respective protype and pendant-type of tails. *Dorcopsis* could be derived from the *Protemnodon* stem, if p^3 and p^4 were greatly enlarged. In it i^{2-3} are small. *Dendrolagus* may come either from the pendant-tailed rock kangaroos, by a long series of modifications, or from *Dorcopsulus*, or from an ancestral *Protemnodon* by an equally long series of modifications. It should be remembered that *D. ursinus* is considerably less brachycephalic than the commoner Australian *D. lumholtzi*.

PETROGALE GRAY

Petrogale GRAY, 1837, Mag. Nat. Hist. (Charlesworth), vol. 1, p. 583.

TYPE: *Kangurus penicillatus* Griffith (by monotypy).

The rostrum, particularly that part anterior to the molars, is slender, narrow, and shallow. Typically, the bullae are slightly inflated. There is no postglenoid foramen, and a tendency exists for contact to be made between the mastoid and the squamosal process

of the zygoma immediately above the meatus (fully attained in *P. inornata*). A well-developed lacrimal process exists. The anterior palatal foramina vary from small to very small. The posterior palatal openings are quite large, and the bony palatal area behind them is reduced to a fragile, X-like structure similar to that in *Thylogale stigmatica*.

In the upper incisive series i^1 is much larger and stronger than either i^2 or i^3 . The third incisor, in which the fold is lateral as in *Protemnodon*, tends towards marked reduction in size as compared with the same tooth in either *Thylogale* or typical *Protemnodon* or *Macropus*. In the type species, *penicillata*, and in *P. xanthopus* this reduction of i^3 is somewhat less advanced than in other species.

A minute right canine is preserved in *inornata*, A.M.N.H. No. 107377.

Heavy wear of the anterior cheek teeth is apparent in quite young animals in *Petrogale*. Typically, the anterior root of p^4 projects strongly lateral to the general level of the face of the maxilla. The fourth premolar is erupted early, replacing p^3 and dp^4 , at, or immediately after, the time of the eruption of m^3 (A.M.N.H. No. 107379). I have evidence to this effect in all important species except *xanthopus*.

In all species except *P. xanthopus* a hair whorl occurs at the withers from which the hairs of the dorsal surface of the neck lie pointing forward.

The skull of *Petrogale xanthopus*, the most aberrant of the species as its unusual color pattern suggests, not only has i^3 comparatively little reduced; it also exhibits to only a minimal degree the confluent tendency of the mastoid and the zygomatic process of the squamosal, and in it the lacrimal process is much less developed than in more characteristic species. This is the only species in which the hairs of the dorsal surface of the neck are not reversed.

In some species of *Petrogale*, including *inornata* and *penicillata* (but not *xanthopus*), a tendency exists for the maxillonasal suture to remain rather widely open along a few millimeters anterior to the frontal.

Jones (1923-1925, p. 230) writes of the presence of the bregmatic bone in *P. pearsoni*

and *P. xanthopus*. It is present in our *xanthopus*. We have no specimens of *brachyotis* Gould from north Western Australia. I suspect it will be found allied to the Queensland *inornata* group.

It appears to me that *Petrogale herberti* from just north of Brisbane is more nearly related to the southern *penicillata* than to the northern *inornata*. My reasons are founded partly upon the skin pattern but chiefly upon features of the skulls. In both *penicillata* and *herberti* the foramen ovale is not floored beneath with bone but in combination with the carotid foramen forms an exceptionally large opening (A.M.N.H. No. 6265/7917). In *inornata* the foramen ovale is smaller, is floored beneath, and there is no obviously open fissure. In the race *inornata purpureicollis*, which otherwise is almost indistinguishable from *inornata puella*, this flooring of the foramina ovals is extraordinarily broad, the openings of those two foramina being 22 mm. apart compared with ± 17 mm. in *puella*. In the two first-mentioned forms the crown length of i^3 varies in little worn specimens from 4.3 mm. (*penicillata*) to 4.0 mm. (*herberti*) but reaches only ± 3 mm. in *inornata*. In *penicillata* the space between the mastoid and the squamosal process of the zygoma is open. It is partly closed in *herberti* and almost completely closed in *inornata*. I am inclined to regard *herberti* as the warm-country representative of *penicillata*.

Photographs of the type skulls of *P. longmani* and *P. venustula* indicate rock wallabies having the characteristics of *inornata* rather than *penicillata* but show a greater proportional degree of broadening of the bases of the nasals than is found in either.

Petrogale penicillata (Griffith)

This, the typical species of the genus *Petrogale*, is characterized by its large size, brownish gray dorsal fur, buffy underparts, and all-black tail. In the typical race the hairs of the body and of the tail are long and almost shaggy, but in our specimens from southern Queensland the pelage is decidedly shorter. In the skulls the suprameatal fissure between the mastoid and squamosal is partly open, and the area marking the union of the two above-mentioned bones with the parietal is

markedly fenestrated; also i^3 is considerably less reduced than in other species seen by me, except *P. xanthopus*.

In spite of the difference in color pattern between *penicillata* and *lateralis* (with its allies), differences chiefly of degree, I have linked the two together specifically because of their very close cranial and dental resemblance. Moreover, as there appear to be no geographical overlaps, they may well constitute local representative forms. All are considerably larger than any race of *inornata* of the northeastern part of Australia.

Petrogale penicillata penicillata (Griffith)

Kangurus penicillatus GRIFFITH, 1827, The animal kingdom . . . by . . . Cuvier, Mamm., vol. 3, plate facing page 49; vol. 5, p. 204.

Heteropus albogularis JOURDAN, 1837, Compt. Rendus Acad. Sci., Paris, vol. 5, p. 522.

TYPES: Of *penicillatus*, not in existence (Thomas, 1888). Of *albogularis*, in Paris.

This museum possesses only two old faded examples of this wallaby. In one the lower jaw is missing. The other is mismatched with a skull of *Protemnodon rufogrisea*. At the United States National Museum there are two from Tamworth, one from Cambawama, one from Ebor, 52 miles east of Arvondale, one from Coombie, two from Wandandian, 19 miles southwest of Nowra, New South Wales, also one from Farina, South Australia.

The width of the cutting edge of i^1 , slightly narrowed when first erupted (U.S.N.M. Nos. 38856, 237711), 3.7 to 4.0, becomes broadened to 4.2 to 4.3 mm. (U.S.N.M. Nos. 221200, 221201). In this tooth the condition in *Pseudodorcas* is foreshadowed. The internal (mesial) thickness is 1.5 mm.; the external thickness (adjoining i^2), 2.1. An internal cuspule is at first present but is speedily worn away.

The external lamina of i^2 exceeds the internal lamina, 4.1:3.8 (U.S.N.M. No. 237711). The labial face of the tooth is speedily shortened by abrasion to 3.1 to 3.3 mm.

The small i^3 in the unworn juvenile has the crown length 5.4; that of the external lobe is 4.0 mm. This tooth by chipping and wear becomes shortened to ± 4.3 .

The third premolar measures: length, 5.0 to 6.1; anterior width, 2.6 to 3.0; posterior width, 3.0 to 3.4.

In U.S.N.M. No. 237711, juvenal male, the main cutting ridge of p^3 is divided by two grooves into three cusps, the middle one of which is quite small. A trace of an external cingulum shows at the outer base of each groove. Interiorly a strong cingulum extends the length of the tooth with the postero-internal cusp, as usual, well developed but the anterior, internal, and median cusps small. The tooth is only slightly narrowed at the front.

The lengths of the molariform teeth are: dp^4 , 5.0 to 5.9; m^1 , 5.4 to 6.1; m^2 , 5.7 to 7.0; m^3 , 7.4 to 7.7; m^4 , 7.6 to 8.6 mm.

The fourth premolar is substantially larger than p^3 : length, 7.1 to 7.5; anterior width, 3.0 to 3.2; posterior width, 3.6 to 3.8 mm.

***Petrogale penicillata herberti* Thomas**

Petrogale herberti THOMAS, 1926, Ann. Mag. Nat. Hist., ser. 9, vol. 17, p. 626.

TYPE: From Eidsvold, Burnett River, southern Queensland; not examined by me.

Henry C. Raven collected six specimens of this rock wallaby at Lochaber Station, Mundubbera District, southern Queensland, in July, 1922. M.C.Z. No. 6431, an adult from the Queensland Museum, appears to fit our New South Wales specimens very closely and is probably of southern (not northern Queensland at least) origin. In it m^1 , length 4.6 mm., is much worn; m^4 measures 7.9 by 6.7 (anterior loph); p^4 , worn, is 6.7 mm. in length.

The comparatively large size of i^3 and other characters induce me to place this form with *penicillata* rather than with *inornata* as was done by Iredale and Troughton (1934).

***Petrogale penicillata lateralis* Gould**

Petrogale lateralis GOULD, 1842, A monograph of the Macropodidae, pt. 2, pl. 24.

TYPE: In British Museum (Thomas, 1888) but not seen by me; from Liverpool Plains, New South Wales. Lectotype (Thomas, 1922, p. 128), B.M. No. 42.5.26.3, male.

Two specimens, an old male and an adult female, both with worn teeth, from near Barrow Creek on the Overland Telegraph at about latitude 22° S., are in the Museum of Comparative Zoölogy. In these the crown length of i^3 (chipped) is 3.2, of its external lobe, 2.0 mm.; the length of m^1 is 5.2 and 4.5;

of m^4 , 7.5 and 6.7. The fourth premolar is 6.8 to 7.0 in length, with the anterior width, ± 2.6 (worn), posterior width, 3.5 (worn).

***Petrogale penicillata hacketti* Thomas**

Petrogale lateralis hacketti THOMAS, 1905, Ann. Mag. Nat. Hist., ser. 7, vol. 16, p. 425.

TYPE: Not seen; B.M. No. 5.4.1.5, collected by J. T. Tunney at Mondrain Island, Recherche Group, south coast of Western Australia.

Two topotypes in the United States National Museum were taken in April, 1906: juvenal male, U.S.N.M. No. 155377; adult female, No. 155376.

The skins have the blackish lateral bands of *lateralis*, and there are strong white scapular and face marks. The arms and a narrow ventral stripe are buffy white.

The incisors, lost in the juvenal and worn in the adult, have dimensions: i^1 , 3.5; i^2 (labial face), 2.3; i^3 (crown length), 3.5, with external lobe, 2.5 mm.

In the juvenal p^3 is 5.3 mm. in length; its anterior width, 2.9, posterior width, 3.4. The lengths of the molariform teeth are: dp^4 , 5.1; m^1 , 5.5 to 5.7; m^2 , 5.5 to 6.4; m^3 , 6.5 to 7.0; m^4 (in adult only), 7.6 mm. The anterior loph of dp^4 and m^1 are unusually narrow.

The fourth premolar is 7.7 mm. in length; its anterior width, 3.3, posterior width, 3.5 (worn) mm.

***Petrogale inornata* Gould**

Petrogale inornata is distinguished from *penicillata* by its much reduced i^3 , the tendency for the fissure dorsal to the meatus between the mastoid and the squamosal root of the zygoma to close, its smaller size, and relatively unpatterned pelage. In the majority of races the tail is gray brown or at least brown beneath, and only black dorsally. In a very few examples from the neighborhood of Atherton Tableland, central Queensland, wholly black tails similar to the tail in *penicillata* are encountered.

As previously indicated, the form *herberti* is now transferred to *penicillata*. Also, *purpureicollis*, provided that our specimen from Quamby, near Dajarra, is truly of that race, may be regarded as specifically distinct.

This species, highly variable in local color

forms, has been divided into several races. The forms of *inornata* seem to be merely color phases, unaccompanied by significant cranial characters.

The following dental measurements characterize *P. inornata*:

The first incisor (unworn), 3.4 mm., rapidly wearing to 3.9 to 4.0. The crown length of the second incisor (unworn), 3.3, (worn), 3.2 to 3.0. The crown length of i^3 , 4.0 to 4.5; its outer lobe, 3.0 to 3.5; in worn condition only, 2.5 mm.

The third premolar is usually shed in American Museum specimens. Its length: 4.5 mm. (Coen), 4.5 to 4.6 (Carbine), 4.6 to 4.7 (Hughendon area). Anterior width, 2.4 to 2.6, posterior width, 2.8 to 3.0.

The lengths of the molars: m^1 , 5.1 to 5.5 (wearing to 4.8), m^4 , 6.8 to 7.1 mm.

The fourth premolar is rather variable in length but always substantially larger than p^3 : length, 6.2 to 7.1; anterior width, 2.8 to 3.0; posterior width, 3.7 to 4.0. The newly erupted tooth is strongly secant but soon becomes flattened by abrasion. It is erupted with or immediately following m^3 .

Petrogale inornata inornata Gould

Petrogale inornata GOULD, 1842, A monograph of the Macropodidae, pt. 2, pl. 25.

Petrogale assimilis RAMSAY, 1877, Proc. Linnean Soc. New South Wales, vol. 1, p. 360.

TYPES: Thomas (1888, p. 70) was unable to identify the type locality of *inornata*, but, as Troughton (1941, p. 179) points out, Thomas did not have all the facts. The type locality of *inornata* was Cape Upstart, near Townsville, northern Queensland; of *assimilis*, Palm Island, north of Townsville.

Of *inornata* Gould wrote, "basal half of the tail sandy brown, the remainder black, the former color extending along the sides of the tail for some distance towards the tip." Ramsay's more detailed account of *assimilis* agrees essentially with that of Gould.

Iredale and Troughton give the range as between latitudes 18° and 21° S. or approximately from the Herbert River to Mackay. This coastal extent includes Townsville and Bowen. The range inland from the coast is not determined but probably stops at the main divide, along the slopes of which this race may extend farther to the north. To the

north *inornata* is replaced by the considerably paler *godmani*, and beyond the divide to the west by *puella*.

Petrogale inornata godmani Thomas

Petrogale godmani THOMAS, 1923 (Feb.), Proc. Zool. Soc. London, Abstr., no. 235, p. 13; 1923 (April), Proc. Zool. Soc. London, p. 177.

TYPE: In British Museum; not seen by me.

This most northern race of *inornata*, described from Black Mountain, 16 miles southwest of Cooktown, is paler and more buffy than *inornata* and has the terminal part of the tail colored drab instead of black.

Two specimens (one juvenal) taken by Miss Neuhäuser from Mount Carbine between Cairns and Cooktown are unquestionably referable to *godmani*. But four others from the same locality, although their body pelage is equally pallid, have the dorsal surface of the tail blackish brown and perhaps are better referred to *inornata* (= *assimilis*). Four specimens in the Museum of Comparative Zoölogy from Coen and one from Mount Carbine (two of them juvenals) are likewise referred here.

Petrogale inornata puella Thomas

Petrogale puella THOMAS, 1926, Ann. Mag. Nat. Hist., ser. 9, vol. 17, p. 627.

TYPE: In British Museum; not seen by me.

This gray race, from the highlands west of the range of *inornata*, has the tail black above, brown beneath. The type locality is Glendower Station, Torrens Creek, upper Flinders River. The Archbold collection contains four specimens from Pentland, on the railroad out from Cairns, only a few miles west of the type locality.

Raven's series of 10 specimens (all adults) from Kaban, Atherton Tableland, and near Ravenshoe, places a short way south of Cairns, include both buff-tailed and black-tailed individuals. Four from the Hughendon area and one from Mount Hedlow are in the Museum of Comparative Zoölogy. Two specimens from Atherton Tableland are in the collection of the United States National Museum.

This is probably the most widely ranging of the races, extending over all the western slopes of the Queensland coastal mountains.

***Petrogale inornata purpureicollis* Le Souef**

Petrogale purpureicollis LE SOUEF, 1924, Australian Zool., vol. 3, p. 274.

TYPE: Probably at Sydney. Not seen.

This race, provided our specimen from Quamby, only a few miles from Dajarra, the type locality, is correctly identified, differs rather sharply from the race of *inornata* from farther east on account of its short diastema and the extensive bony flooring of the foramen ovale. The skin, on the contrary, is gray and very similar to the skins of the adjoining race *puella*.

I am unable because of lack of material to discuss *longmani*, *wilkinsi*, *brachyotis*, and *rothschildi*, although I have photographs of the type skulls of *longmani* and *l. venustula*.

***Petrogale xanthopus* Gray**

Petrogale xanthopus GRAY, 1885, Proc. Zool. Soc. London, for 1854, p. 259.

TYPES: Thomas (1888) records the co-types as being in the British Museum.

The most aberrant in regard to color pattern and the least specialized as regards the character of i^3 , this species stands isolated from all other species of *Petrogale*. Jones (1923-1925, p. 225) considers it one of the largest species, although *penicillata* is almost as, if not quite so, large.

There are five species in the American Museum collection, all received from the New York Zoological Society, three without skulls, and one having the skull so young that dp^4 is still present. The fifth skull, although adult, is greatly marred by malformations probably caused by dietary deficiencies. A juvenal, No. 238717, in the United States National Museum, was also received from a "zoo." The bullae are moderately enlarged. That part of the palate caudal to the posterior palatal foramina contains a few pore-like openings quite unlike the same region in other rock wallabies of the genus. The mandibular foramen is rather small, 4.0 by 2.5 mm., and the external wall of the mandibular fossa is so low as to be virtually obsolete.

In the dentition, the incisors measure (U.S.N.M. No. 238717): i^1 , 4.5; i^2 , inner lamina, 4.1, outer lamina 3.9 (chipped); i^3 (unworn), crown length, 5.0, external lobe, 3.0 mm. The fourth premolar is relatively

massive; its length is 7.5 mm., its anterior and posterior widths are 3.4 and 4.5 mm. In the juvenal, the length of p^3 is 5.4 to 5.5; the anterior and posterior widths are 2.6 and 3.5 mm. The lengths of the molariform teeth are: dp^4 , 5.7 to 6.3; m^1 , 6.1 to 6.7; m^2 , 7.3 to 7.8; m^3 , ± 8.0 ; m^4 , ± 7.7 . In the United States National Museum specimen p^3 and dp^4 are still in place while m^3 is partly erupted. Note that m^4 is shorter than m^3 in our single adult specimen.

The brownish yellow feet, the barred base of the tail, and strong shoulder marks are highly distinctive.

Like so many other wallabies, this rock species has a northern and a southern form. The northern race is *P. x. celeris* Le Souef. The species inhabits the eastern half of Australia inland from the coastal mountains, from South Australia to southwestern Queensland.

ONYCHOGALEA GRAY

Onychogalea GRAY, in Grey, 1841, Journals of two expeditions . . . in . . . Australia, vol. 2, App., p. 402.

TYPE: *Macropus unguifer* Gould, by subsequent designation (Thomas).

Onychogalea is probably derived from the line which led to *Petrogale*. Compression of the anterior part of the rostrum and palate in *Onychogalea* has been carried to a greater extreme (less in *unguifer*) than can be found in *Petrogale*, and there is a deep depression on either side of the diastema. Except in *O. unguifer*, which has small, multiple, posterior palatal foramina, those openings are essentially as in *Petrogale*, the anterior ones very short, the posterior ample. The bullae, variably inflated, are especially large in *O. lunata*. Contrary to the condition in *Petrogale*, the interorbital region and braincase are considerably broadened, but the zygoma is rather weak and shallow, and the anteorbital foramen is placed only slightly in front of the orbit.

Small canines are ordinarily retained in *O. unguifer*. They may also be found occasionally as minute structures in *O. fraenata* (none in our skulls), and more commonly in *O. lunata*. (I detected a vestigial canine in one specimen of *Petrogale inornata*.)

Reduction of i^3 has been carried further

than in any rock wallaby, and that tooth, as well as i^2 , is strongly inclined forward. (Compare with *P. xanthopus*.) As in *Petrogale*, the groove of i^3 (except in *O. unguifer*) has the *Protemnodon* pattern. That is to say, it lies slightly behind the middle of the labial face of the tooth. The second incisor is grooved (not in *unguifer*). The fourth premolar is unusually short and subtriangular. It is divided into well-defined anterior and posterior cusps, the posterior one compound.

In *Onychogalea*, an important character is the exceptionally small size and subtriangular outline of p^3 and p^4 in proportion to the lengths of the molariform teeth and the shapes of the premolars of other genera.

The specialized shoulder pattern in skins of *Onychogalea* is vaguely forecast by the pattern found in *Petrogale xanthopus*. The banded tail pattern of *P. xanthopus* is sometimes weakly repeated in *O. unguifer* (see *annulicauda* De Vis).

Onychogalea unguifer (Gould)

Macropus unguifer GOULD, 1840, Proc. Zool. Soc. London, p. 93.

Onychogalea annulicauda DE VIS, 1884, Proc. Roy. Soc. Queensland, vol. 1, p. 157. (Possibly a good race.)

Types: Of *unguifer*, B.M. No. 41.1108 (1852a), a young male (p^4 present but m^4 not completely in place), collected by Bynoe on the northwest coast of Australia. Of *annulicauda*, perhaps near Brisbane.

There are three specimens of this rare marsupial, one from Broome and a female and young from 32 miles southeast of Derby, in the United States National Museum; and in the Museum of Comparative Zoölogy, a single rather young animal (representing *annulicauda*) from Queensland. I have also seen British Museum material from the Fitzroy River, Kimberly district, north Western Australia.

The skin of this species, unlike that of the two other species, is light tan, and the pale marks are confined to a hip stripe and a short scapular stripe. Another adult skin is pale sandy brown with a darker stripe from withers to mid-tail, the face is white, the ears, feet, and hands are white, the distal half of tail is black, and the underparts are buffy white, becoming smoky on the body either

side of the white median area. The hair of very small specimens is very short, of females and young longer and softer. U.S.N.M. No. 237646 (803) was marked by Hoy, "4 nipples, 1 young in pouch." The nail on the tail is long and narrow (8 by 3 mm.).

The frontal area of the skull is inflated. The rostrum is elongate, considerably heavier, and less compressed than that of *fraenata*. It is of considerable depth (21 mm. anterior to p^3). A very sharp downward bend (angle) occurs at the point marking the posterior end of the diastema. The posterior palatal foramina are small, with few supplementary pores. The bullae are rounded, more swollen than in *fraenata*, less so than in *lunata*. The length of the bulla in the type specimen is 12.2 mm. The length of the anteorbital canal is 9.0 mm. The opening from the mandibular nerve canal to the masseteric fossa is very large, its diameter approximately 5.8 mm.

The dental wear in this species is very great. In the United States National Museum specimens, adults, the lophs of the two anterior molariform teeth have been quite worn away, and the third molariform teeth are substantially abraded.

The first incisor is a tapered tooth which, unlike that of *Peradorcas*, becomes thicker in section with age. The crown length varies from 2.9 (juvenile male) to 3.4 to 3.5 in adults.

The second incisor, unworn, has the inner lamina 2.7, outer (labial) lamina 2.4, the latter reduced in old specimens to 2.2, 2.0, and 1.8 mm.

The third, much inclined incisor in unworn state has the crown length 2.9 (the anterior lamina 1.5). In worn specimens this crown length is reduced to 2.5, 2.6, 3.0 mm.

All three incisors are worn to a nearly uniform abrasion level, only the internal portions of i^{1-3} descending, beak like, slightly below that level.

The narrow, forwardly inclined i^3 is subequal to i^2 , and both are much smaller than i^1 . A mere trace of a groove of *Protemnodon* type is present on i^3 .

The extraordinarily slender canines (crown length, only 1 mm.) are one of the characteristics of this wallaby. In the United States National Museum material the canines are present in the juvenile only.

The third and fourth premolars are both

simple and very small. They are composed of two parts, anterior and posterior enlargements with a deep groove between them. Their external faces parallel those of the bilophodont true molars. The very small p^4 is more compressed than p^3 and in age may become partly rotated outwards.

The dimensions of p^3 are: length, 3.6 mm.; anterior width, 2.1; posterior width, 2.7 (U.S.N.M. No. 237643, male). The lengths of the crowns of the molariform teeth are: dp^4 , 5.0 to 5.1; m^1 , 5.8 (wearing to 5.4 and 4.8); m^2 (worn), 5.5 to 6.1; m^3 , 7.6 (wearing to 7.0); m^4 , 6.5 to 7.5. The permanent fourth premolar, present in two United States National Museum specimens, is: length, 4.0 to 4.2; anterior width, 1.8 to 1.9; posterior width, 2.4 to 2.6 mm. It is thus slightly longer and more compressed than p^3 .

Onychogalea fraenata (Gould)

Macropus fraenatus GOULD, 1841, Proc. Zool. Soc. London, for 1840, p. 92.

TYPE: B.M. No. 41.1130 (272a), a young adult male labeled New South Wales.

At the American Museum of Natural History are six "zoo" specimens without localities, and two obtained by H. C. Raven: one in exchange from Sydney Museum, A.M.N.H. No. 65244, Raven's No. 1189, Sydney Mus. No. M. 1649, from southern Queensland; the other, A.M.N.H. No. 66171, Raven's No. 1197, from Tallong, southern New South Wales. Four more may be seen in the Museum of Comparative Zoölogy and another four at the United States National Museum, all lacking precise localities.

This gray wallaby is easily distinguished from the other two species by its small size and by the fact that the scapular stripes run along the back of the neck to the head. The bullae are rather low and flat, the posterior palatal foramina proportionately larger than in either *lunata* or *unguifer*. The rostrum is much more compressed laterally in *fraenata* than in *unguifer*. Thomas gives the length of p^4 as 3.5 mm.

The incisive crowns of the type measure: i^1 , 3.6 mm.; i^2 , 2.1; i^3 , 2.1. The dimensions of the cheek teeth are: p^4 , 3.7 by 3.1; m^1 , 4.8 by 4.1; m^2 , 5.6 by 4.7; m^3 , 6.6 by 5.9; m^4 , 6.5 by 5.0. The length of the bulla is 12.4.

The first incisor is a stout tooth (width, 3.4

mm.), much stronger than i^2 or i^3 , and i^2 slightly exceeds i^3 in thickness (2.5:2.2), taken at right angles to the axis of each tooth. The inclination of these two teeth gives crown lengths of ± 2.9 and 2.5 mm. The external lamina of i^2 is ± 2.0 , of i^3 , ± 1.3 mm.

Canines can be seen in U.S.N.M. No. 122614 (one side) and A.M.N.H. No. 66171 (both sides). They are splint-like teeth closely appressed to the side of the rostrum and lying nearly parallel to the surface of the anterior palate.

Two specimens at the Museum of Comparative Zoölogy, Nos. 1877 (with skin) and 1880 (without skin), are animals much smaller than a second pair, M.C.Z. Nos. 1865 and 1879, but all are believed to be truly referable to *fraenata* of Australia.

The bulla is moderately inflated; it descends to about half the length of the paroccipital process. The opening for the mandibular nerve is variable (2.2 to 4.0 by 7.0 mm.). One skull (M.C.Z. No. 1877) is juvenal, the other adult, with freshly erupted p^4 (and m^3 in place but broken). This fourth premolar is sharply larger than p^3 of the juvenal (lengths, 4.5:2.9). The usual triangular form of the latter is shown by its anterior and posterior widths: 1.5, 2.2. The lengths of dp^4 and m^1 are, respectively, 3.9 and 4.3 to 4.4 mm.

These dimensions are confirmed and expanded by the series at the United States National Museum, comprising two juvenals, a subadult, and a fully adult specimen. In these: p^3 , length 3.2 to 3.4 mm., widths, 1.5 and 2.5 to 2.7; lengths of dp^4 , 4.0 to 4.2; m^1 , 4.0 to 4.9; m^2 , 4.8 to 5.7; m^3 , 5.8 to 6.4; m^4 , 6.4. In both adults p^4 is smaller than in the Cambridge specimen: length, 3.6 to 3.7; anterior and posterior widths, 1.8 to 2.1, 2.3 to 2.8 mm.

The premolars are evidently subject to considerable individual variation. In A.M.N.H. No. 70395 the right p^4 is normally tricuspid or provided with a postero-internal cusp (linked to the secant ridge by a well-developed commissure) and a secant ridge divided into strongly differentiated anterior and posterior cusps by a deep transverse groove. But the left p^4 is five-cusped; its secant ridge is divided into three cusps by two transverse grooves, and the anterior end of the internal

cingulum, obsolete in the right tooth, rises to form a distinct auxiliary cuspule. This latter tooth is considerably larger than its opposite (lengths, 3.2:4.2). One naturally suspects that these teeth are respectively p^3 and p^4 , yet each stands in front of three uniformly developed molariform teeth, presumed to be m^{1-3} . There is no equivalent difference between the right and left inferior premolars.

Of this species Krefft writes (1865, p. 19), "... female producing one young at a time, generally in the beginning of May; pouch containing four teats."

Onychogalea lunata (Gould)

Macropus lunatus GOULD, 1840, Proc. Zool. Soc. London, p. 43.

TYPE: In British Museum (not seen by me); a juvenal male from Swan River, Western Australia, collected by Gilbert. Its measurements were given by Thomas (1888, p. 79). The permanent (?) fourth premolar, not measurable in the type, is quite small in another specimen at the British Museum: length of p^4 , ± 2.8 mm. The bulla, according to Thomas, is much more inflated than in *fraenata*. The enlarged bulla is well shown by Jones (1923-1925, fig. 166) to descend to approximately the same depth as the paroccipital process (compare with *fraenata*).

SUBFAMILY MACROPODINAE

The members of the Macropodinae are distinguished from the Potoroinae and Hypsiprymnodontinae by their relatively simple, unfluted premolars; by their lophodont and hypsodont instead of bunodont and brachyodont molars (some Potoroinae have incipiently lophodont molars); by the usually extero-internally compressed, instead of laterally compressed, i^1 , the grooved crown of i^3 , and the more diminished and often obsolete condition of the canines.

In the skull dolichocephaly is the rule, although secondary brachycephaly does occur (*Dendrolagus*). The reverse is the case in the Potoroinae (excluding *Potoroops*). Rostral attenuation and lateral compression are likewise usual in the Macropodinae, less usual in the Potoroinae. In the Macropodinae the mastoid process tends to coalesce with the zygomatic squamous process (incompletely in

Petrogale, *Dendrolagus*, etc.), whereas in *Bettongia* of the Potoroinae the two remain well separated. Bullae are usually uninflated in the Macropodinae (exceptions occur), usually inflated in the Potoroinae (except in *Aepyprymnus*). The paroccipital process in the Macropodinae is normally elongate. In *Bettongia* it is a short, stump-like structure. The coronoid process of the mandible rises steeply in most Macropodinae. It is low and inclined at a narrower angle in most Potoroinae. Pearson (1946) just lately pointed out differences of importance in the reproductive systems of these subfamilies.

The relationships to one another of the many genera of the subfamily Macropodinae are not easily worked out. Latent or new trends, presumably of recessive genetic character, become apparent in otherwise rather widely separated genera. A good example of this phenomenon can be noted in the behavior of the cheek teeth in the specialized rock wallaby, *Peradorcas*, and in the large kangaroos, *Macropus*. In each example forward travel of the molars quickly thrusts out the premolars and the anteriormost of the molars at the front of the molar tooththrow. In the case of *Peradorcas* the remarkable ability to continue to form new molars behind m^4 is further superimposed. In near relatives of both of these genera, i.e., in *Petrogale* and *Protemnodon*, p^4 remains firmly in place throughout most of the life of the animal, and the molars line up behind it in a relatively immovable series.

The same may be true regarding the form and function of the tail in *Petrogale* and *Dendrolagus*. In most genera, including *Dorcopsis*, the tail is thick at the base and tapered to the tip, and is used as a prop or third hind leg. In the rock and tree kangaroos the tail is of uniform thickness and is employed as a balancing organ. Is this a case of convergence or does it show true phyletic relationship? It is clearly held to represent convergence by those who believe that *Dorcopsis* and *Dendrolagus* are close relatives. Again, is the untapered, balancer type of tail an ancestral character that has persisted in the few genera that possess it, or is it in each case a new modification derived from the prop-like tail prevalent in the family?

The discovery in *Macropus* of deciduous

vestigial i^2 and i^3 , in an otherwise rather specialized genus, serves apparently as an instance of retention of an exceedingly primitive character.

The range in Western Australia was mapped by Shortridge (1909, p. 815). It occurred formerly in South Australia also (Jones, *tom. cit.*, p. 232). Spencer (1896, p. 16) recorded it from Alice Springs and the Everard Ranges.

LAGORCHESTES GOULD

Lagorchestes GOULD, 1841, A monograph of the Macropodidae, pt. 1, text to pl. 12.

TYPE: *Macropus leporides*.

The type species of *Lagorchestes* and the western hare wallaby, *L. hirsutus*, are markedly distinct from the heavier-built third species, *L. conspicillatus*. In the former the muzzle is slender as in *Petrogale* (though short) and the canines are very small; in the last the muzzle is much broader and the canines rather heavy. The bullae are large, rounded, well inflated. The palate is little fenestrated. The second and third incisors are unreduced, and p^4 is large, rather narrow, and unprovided with a postero-internal cusp.

We have no representative of this genus at the American Museum, and of the three species I have photographs of *leporides* only. There are specimens of *L. conspicillatus* in the United States National Museum and in the Museum of Comparative Zoölogy.

Lagorchestes leporides (Gould)

Macropus leporides GOULD, 1841, Proc. Zool. Soc. London, for 1840, p. 93.

TYPE: Cotype, B.M. No. 41.11.28, an adult female, "interior of New Holland." Iredale and Troughton (1934, p. 40) have restricted it to the interior of New South Wales.

The long, shaggy pelage of the type is mixed dark brownish gray and straw colored. The legs and sides are reddish; the slender limbs black; the underparts with the tips of the hairs white, their bases gray.

In the type skull i^3 is grooved at about the middle of its labial face. The length of its crown equals that of i^2 . The canine is exceedingly slender. The fourth premolar is slightly longer than m^1 , and is narrow, blade like, and of equal thickness front and back.

The muzzle is narrow in front as in *Petrogale*, but the back of the skull is wide. The bullae and mastoids are full and well inflated, while the paroccipital processes are shorter even than in *Peradorcas*. The posterior palate is weakly and irregularly fenestrated.

The skull, as figured by Jones (1923-1925, p. 223), in many respects resembles his figure of *Onychogalea lunata*, but the third incisor is much less specialized and p^4 is obviously a much larger tooth.

The length of the incisive crowns of the type is: i^1 , 3.3 mm.; i^2 , 2.4; i^3 , 2.3. Its cheek teeth measure: p^4 , 5.4 by 2.2; m^1 , 4.5 by 3.8; m^2 , 5.2 by 4.1; m^3 , 5.9 by 4.5; m^4 , 6.0 by 4.5. The length of the bulla is 12.4.

Lagorchestes hirsutus Gould

Lagorchestes hirsutus GOULD, 1844, Proc. Zool. Soc. London, p. 32.

TYPE: Not seen; from York, Western Australia. According to Thomas, this species must be much more nearly related to *leporides* than to *conspicillatus*. The muzzle is narrow, the canine minute. The length of p^4 (in another specimen, not the type) was given by Thomas as 5.7 mm.

Two island forms, *bernieri* Thomas and *dorreae* Thomas, respectively from the adjacent Bernier and Dorre Islands, have been recognized. The species, virtually extinct, is shown by Shortridge (1909, p. 820) to have extended over much of Western Australia.

Lagorchestes conspicillatus Gould

Thomas (1888, p. 80) distinguished *conspicillatus* from *leporides* and *hirsutus* by its broad, heavy muzzle and comparatively large canines. The ears were shorter than in those two species and white lateral bands were present. Troughton (1941, pl. 12) shows a white hip mark and a second white mark on the flank just before the thigh.

Three races are currently recognized, stretching interruptedly across the northern part of Australia from Barrow Island and northwest Western Australia to Queensland, and apparently absent from Arnhemland.

Lagorchestes conspicillatus conspicillatus Gould

Lagorchestes conspicillatus GOULD, 1841, Proc. Zool. Soc. London, p. 82.

TYPES: Not seen (Thomas lists two cotypes from Barrow Island).

Thomas described the skull as heavily built and provided with well-developed canines. The posterior palate, in comparison with that of the other two species, had few vacuities. The large, swollen bullae were flatter and rougher than in other species. The notch of i^3 was nearly obsolete, and p^4 , larger and broader than in related species, measured 6.9 to 7.8 mm.

This island race, having been discovered before the mainland race of northern Australia (*leichardti*), bears the specific name. Thomas indicated that the insular race was duller in coloration than the mainland race. The race *pallidior* Thomas and Dollman from mid-northern Queensland was recognized by Iredale and Troughton (1934).

A single topotypical specimen of this rare Barrow Island wallaby is contained in the collection of the United States National Museum (U.S.N.M. No. 218468, young adult male), collected by P. Jack. In it p^3 is retained in one side of the jaw (dp^4 shed), and the newly erupted p^4 is present in the opposite side. The third molar is present and m^4 visible in its alveolus.

The width of i^1 is 3.1 mm. The second incisor, slightly worn, has the inner lamina 3.4, the labial lamina 2.2. The unworn i^3 has the crown length 3.4 and that of the external lamina only 1.5. The groove is thus placed well forward. The canine is fairly substantial, its thickness 2.9.

The third premolar, possibly abraded, reaches its greatest thickness, 1.5 mm., a little before its center, and tapers posteriorly to 1.3. A weak vertical groove is visible on the labial face just posterior to the greatest thickness. Its crown length is 3.1.

The lengths of m^{1-3} are 5.2 mm., 6.4, 7.0; their greatest widths, 5.0, 5.6, 5.8.

The fourth premolar is a large, rather compressed tooth, provided with four grooves separating five cusps along the secant blade. The first and last cusps are the largest, the next to last the smallest. The postero-internal cusp is prominent. The internal cingulum is rather weak and provided with four small cusps, the most anterior of which is longer and slightly bigger than the others. Length of p^4 , 7.1 mm.; anterior

width, 2.8; posterior width, 3.3 mm. The lower p^4 has four external grooves.

In this specimen a pair of large openings (4.5 mm.) lie just above and behind the squamosal root of the zygoma.

The body hair is grizzled gray brown; the tail, hands, and hind limbs are pale straw, and the underparts are dull reddish laterally, buffy white mesially. An area of orange brown hairs surrounding each eye is especially conspicuous.

Lagorchestes conspicillatus pallidior
Thomas and Dollman

Lagorchestes conspicillatus pallidior THOMAS AND DOLLMAN, 1909, Proc. Zool. Soc. London, for 1908, p. 693.

TYPE: Not seen; from Inkerman, Burdekin River, Queensland.

M.C.Z. No. 29319 from Richmond, north Queensland, some 200 miles west of the type locality, is fully adult, with m^4 in place and p^4 already somewhat worn. The skull, taken as a whole, is heavily built, and the breadth of the frontal area and rostrum (with the nasals) is somewhat reminiscent of *Caloprymnus* of the Potoroinae. The nasals are short (36 mm.) and very broad (combined width, 19 mm.). The opening between the mandibular nerve canal and the masseteric fossa, although large, lies deep within the fossa. The coronoid process is upright and high. The articular process, in response to the enlargement of the bulla, stands high above the crowns of the lower molars.

The first incisors are by far the strongest teeth of the incisive series. The forwardly inclined i^3 is not quite reduced to the same size as i^2 ; it has a weak posterior groove possibly analogous to the posterior groove in *Thylogale*. No grooves appear on i^{1-2} . Three to four grooves are present on the outer face of p^4 . The molars are strongly bilophodont.

The crown lengths of the incisors are: i^1 , 3.8 mm.; i^2 , 2.5; i^3 , 2.9; of the canine, 2.4. The deciduous premolars have been shed. The lengths of m^1 and m^4 are 4.8 and 6.7; their greatest width, 4.5 and 5.6. The length of p^4 is 6.8; its greatest (posterior) width, 3.4.

PERADORCAS THOMAS

Peradorcas THOMAS, 1904, Novitates Zool., vol 11, p. 226.

TYPE: *Petrogale concinna*.

The second and third incisors are relatively small as in *Onychogalea*. The canine is absent. The third premolar is lost very early. The permanent replacing tooth is very much larger than the deciduous tooth and apparently is not erupted until after m^4 is fully in place. Supplementary molars behind m^4 are developed.

The anterior palate of *Peradorcas* is narrowed much as in *Onychogalea* (but i^3 in the latter is much more reduced and is set at an extreme forward angle). The back of the palate is almost precisely as in *Petrogale inornata* (which species is perhaps the most generalized of *Petrogale*). But *Peradorcas* differs in the virtual non-reduction of i^3 (as in *Petrogale xanthopus*). The bullae are small, little developed. The monotypic *Peradorcas concinna*, originally placed in *Petrogale*, is probably derived from a *Petrogale*-like ancestor.

Although this museum has no example of *Peradorcas*, examples at the British Museum and at the United States National Museum have been studied.

A review of various observations on the dentition of *Peradorcas* may be helpful. Thomas (1888, p. 71) called attention to the fact that the type (and at that time the only known specimen) of *Petrogale concinna* (of which I have photographs) had five molariform teeth in one side of the jaw and four in the other.

Collett (1897, pp. 325-326), with half a dozen specimens before him, had few delusions regarding the dentition of *concinna*: "... the last molar has in no case reached its full growth ... the skulls ... seem as if they had five molars and no premolars. The anterior of the teeth is, however, the milk p^4 , which has exactly the shape of a true molar." He distinguished three immature growth stages: young stage, with p^3 and dp^4 present; middle stage, with p^3 in course of being lost, its loss coinciding with the eruption of m^3 ; nearly adult stage, showing m^4 not yet fully developed. He remarked, "The perfectly

molar-like p^4 [dp^4] is present in all; most likely it is changed at a very late period, and it may even be open to question whether it is ever changed at all." Collett made no suggestion that supplemental molars behind m^4 might be developed.

In his original characterization of the genus *Peradorcas*, Thomas (1904, p. 226), having before him the type and four additional specimens, pointed out that the anterior one of the five "square" cheek teeth was indeed dp^4 , because the true, blade-like p^4 could now be located in and extracted from the juvenal jaw. In one place he contented himself with an expression of doubt as to the possible total number of erupted true molars (but actually he never recorded more than four). He gave the lengths of p^4 and p^3 as 5.0 and 4.1 mm., respectively.

Again, under *concinna canescens*, Thomas wrote, "... this fresh specimen of *concinna*, although very old, with the incisors worn down, is still continuing to produce additional molars at the back of its toothrow."

The same vagueness is seen in Thomas's remarks on *concinna monastria*. Although he wrote, "... not one of these specimens is so old that it has ceased to produce additional molars at the hind end of the tooth series ...," he failed again to indicate which molars or how many were present.

It was probably on the basis of Thomas' diagnosis of, and Jones' key (1923-1925, p. 219) to, *Peradorcas* that Troughton (1941, p. 184) wrote: "It was found that the molars increased to at least double the normal four, the usually permanent narrow premolar being shed soon after eruption, and the molars gradually sliding forward, falling out in front and being renewed at the back of the jaws, somewhat in the style of a slot machine."

Mr. T. C. S. Morrison-Scott has kindly examined the four specimens of *Peradorcas* in the British Museum collection and reports the following molariform tooth counts (I saw only the types in 1937):

| | UPPER JAW | LOWER JAW |
|------------------------|---------------------|---------------------|
| B.M. No. 26.3.11.13, ♀ | 4+1 (just erupting) | 6+1 (unerupted) |
| B.M. No. 26.3.11.12, ♀ | 4 (5)+1 (unerupted) | 4+1 (unerupted) |
| B.M. No. 9.10.3.4, ♂ | 4+1 (unerupted) | 5+1 (unerupted) |
| B.M. No. 10.12.25.4, ♀ | | 5 (4)+1 (unerupted) |

In the above, parentheses indicate a greater (or lesser) number of teeth in the opposite side of the jaw.

In comparison with the above, the specimens (four adults, two juvenals) at the United States National Museum from "rocky hill," 100 miles south of Port Darwin show:

| | UPPER JAW | LOWER JAW |
|-----------------------------|----------------|-----------------------------------|
| U.S.N.M. No. 237691, ♂ | 5+1 (erupting) | 4+1 (erupting) |
| U.S.N.M. No. 237693, ♀ | 4+1 (erupting) | 4+1 (erupting) |
| U.S.N.M. No. 237692, ♀ | 4+1 (erupting) | 4+1 (erupting) |
| U.S.N.M. No. 237690, ♂ | 4+1 (erupting) | 5 (right), 4 (left) +1 (erupting) |
| U.S.N.M. No. 237712, juv. ♂ | 2+1 (erupting) | 2+1 (erupting) |
| U.S.N.M. No. 237713, juv. ♂ | 2+1 (erupting) | 2+1 (erupting) |

The two juvenal specimens are important because they demonstrate the early loss of the short, thick p_3^3 , while in U.S.N.M. No. 237690 the large, narrowly secant p^4 is to be seen. This controverts Collett's suggestion that dp^4 may never be replaced.

As may be surmised, the largest of these skulls is the one with the highest number of molariform teeth—six; its total length is 77.0 mm., its palatal length, 43.8. This specimen is the only one of the series at the United States National Museum which proves the increase in molars numerically. All the other specimens can be explained by supposing the anterior molariform tooth to be dp^4 .

Identification of the individual molariform teeth in terms of size has been attempted in the following table (table 3). It is necessarily subjective, for we do not know the degree of size variation in those teeth. However, the table suggests that as many as nine molars may be successively erupted. It shows also that seldom more than five are in place at any one time, and that the size is independent of sex.

Peradorcas concinna (Gould)

The range of the single known species of *Peradorcas* is northwestern Australia. The three local races proposed by Thomas are retained provisionally, even though I doubt their validity. This is because I lack evidence to show that they are synonymous.

The adult skins at the United States National Museum (mentioned earlier) are reddish; the tail is long and slightly tufted.

The underparts are white with gray bases to the hairs. The young are rather darker, grayer, and less red. U.S.N.M. No. 237692, female, had four teats and one young in the pouch. U.S.N.M. No. 237693 had also one young. (Both pouch young are preserved in alcohol, U.S.N.M. Nos. 237865–237866.)

The skulls of the United States National Museum specimens show a swelling in the lateral wall of the maxilla over the position of p^4 , as in *Petrogale*. The diastema is rather short (± 15 mm.), only 8 mm. in juvenals with dp^4 present. The coronoid process of the mandible is inclined and pointed. The masseteric canal is small (2.2 mm.), and its opening is well concealed by the exterior wall of the masseteric fossa.

In i^1 (juvenal, unworn) considerable thickening of the exteroposterior half of the tooth in contrast to the intero-anterior half can be seen. This thickened portion is terminated by a small cusp as in some *Petrogale*. The length (along the occlusal surface) is 3.3 mm. The thickness of the anterior half is 1.4 mm., of the posterior half (including the above mentioned cusp), 1.8 mm. These conditions, which can be observed only in very young animals, change quickly with age, and, because of the intense wear to which i^1 is subjected, the small cusp disappears. The tooth, however, does not become broader but becomes strongly recurved. Its crown length is 3.0 to 3.3 mm.

In i^2 the long external cutting blade (2.9 mm.) is nearly paralleled by a somewhat shorter (2.3) inner blade, the two fusing at the front. The lengths of these blades become reduced by wear.

The third incisor is of *Protemnodon* type in its proportions; crown length, 2.8 to 3.0 mm.; external lamina, ± 2.0 (in worn specimens, 1.8).

In U.S.N.M. No. 237712, juvenal, p^3 is seen

TABLE 3

MEASUREMENTS OF SKULL AND DENTITION OF *Peradarcas concinna* AND *P. c. monastria*

| | U.S.N.M. No. 237712 Male | U.S.N.M. No. 237713 Male | U.S.N.M. No. 237692 Female | U.S.N.M. No. 237690 Male | U.S.N.M. No. 237693 Female | U.S.N.M. No. 237691 Male | Type of <i>concinna</i> Male | Type of <i>monastria</i> Female |
|-----------------|-----------------------------------|-----------------------------------|-------------------------------------|-----------------------------------|-------------------------------------|-----------------------------------|------------------------------------|---------------------------------------|
| Skull | | | | | | | | |
| Total length | 51.8 | 52.5 | 69.0 | 68.0 | 73.0 | 77.0 | 74.7 | 78.8 |
| Palatal length | 25.8 | 27.0 | 38.2 | 40.0 | 41.0 | 43.8 | 41.6 | 45.0 |
| p ³ | | | | | | | | |
| Length | 4.0 | 4.0 | | | | | | |
| Anterior width | 2.3 | 2.0 | | | | | | |
| Posterior width | 2.4 | 2.5 | | | | | | |
| dp ⁴ | | | | | | | | |
| Length | 3.9 | 4.0 | | | | | | |
| Anterior width | 2.8 | 2.6 | | | | | | |
| Posterior width | 3.0 | 2.9 | | | | | | |
| m ¹ | | | | | | | | |
| Length | 4.0 | 4.0 | 3.8 | | | | | |
| Anterior width | 3.1 | 3.0 | | | | | | |
| Posterior width | 3.3 | 3.2 | 3.4 | | | | | |
| m ² | | | | | | | | |
| Length | | | 4.4 | 4.2 | 4.6 | | | |
| Posterior width | | | 3.6 | 3.8 | 3.8 | | | |
| m ³ | | | | | | | | |
| Length | | | 4.8 | 4.8 | 4.8 | | | |
| Anterior width | | | 3.7 | 3.9 | 3.9 | | | |
| m ⁴ | | | | | | | | |
| Length | | | 4.9 | 5.0 | 5.1 | 5.2 | 5.3 | |
| Posterior width | | | 3.9 | 3.9 | 3.8 | 3.9 | 4.0 | |
| m ⁵ | | | Visible | | | | | |
| Length | | | | 5.1 | 5.3 | 4.9 | 5.3 | 5.4 |
| Posterior width | | | | 3.9 | 3.8 | 3.9 | 4.2 | 4.4 |
| m ⁶ | | | | Visible | Visible | | | |
| Length | | | | | | 5.0 | 5.4 | 5.5 |
| Posterior width | | | | | | 4.0 | 4.2 | 4.5 |
| m ⁷ | | | | | | | | |
| Length | | | | | | 5.1 | 5.6 | 5.6 |
| Posterior width | | | | | | 3.9 | 4.4 | 4.4 |
| m ⁸ | | | | | | | | |
| Length | | | | | | 4.9 | | 5.5 |
| Posterior width | | | | | | 4.0 | | 4.1 |
| m ⁹ | | | | | | Visible | | |
| p ⁴ | | | | | | | | |
| Length | | | | 4.6 | | | | |
| Anterior width | | | | 1.9 | | | | |
| Posterior width | | | | 2.6 | | | | |

to be almost as broad anteriorly as posteriorly. Its main crest is divided into four cusps by three external grooves, the anterior and posterior cusps being much larger than the two inner ones. The internal cingulum, well developed both anteriorly and posteriorly, bears three cusps, the largest being the large postero-internal cusp characteristic of the Macropodinae. The second largest is the antero-internal cusp. The third cusp is considerably smaller and stands on the cingulum slightly closer to the anterior of the two large cusps.

The deciduous fourth premolar is distinguished from the true molars by development (as in many other macropods) of a forward extension of the external moiety of the tooth to form functional continuity with p^3 indicated by me (p. 246) as "premolarization." This gives the anterior end of the unworn tooth a slightly pointed or wedge-shaped outline.

The true molars, apart from their multiplication in number, have no distinctive characters. They remain nearly uniform in width throughout the series. Table 3 represents a probably inaccurate attempt to name them serially on the basis of the United States National Museum series. However, even though the identities of the molars in the adults may remain in doubt, there is no question concerning those of the two juvenals in which p^3 are still present. This attempted identification naturally rests upon the assumption that m^1 is invariably a much shorter tooth than m^2 , etc., and that in various individuals m^1 , m^2 , m^3 , and m^4 do not vary in size to any great degree.

The permanent p^4 can be seen in only one specimen, U.S.N.M. No. 237690. Its dimensions are: length, 4.6 mm.; anterior width, 1.9; posterior width, 2.6 mm. It is thus much more elongate and compressed than is p^3 . From my attempt to correlate the molariform teeth in my series of measured skulls (see above) it appears, from the absence of p^4 in old, large-sized, large-toothed skulls, that p^4 is either developed at about the time of m^4 and is then speedily thrust out of the jaw by the advancing series of new molars, or is rarely developed at all, as inferred by Collett (1897, p. 326). I lean towards the former hypothesis. From the relatively good condi-

tion preserved by the incisors (in a sandy environment) it is clear that the molars must succeed each other with considerable rapidity. A premolar erupting in front of the forward moving molars would be speedily swept away.

In the lower teeth p^3 is tricuspid, the three cusps separated by two external grooves. There is no internal cingulum. In dp^4 the anterior loph is narrower than the posterior (2.0:2.4 mm.). The permanent p^4 is narrow, blade like, and lacking in peculiarities.

Peradorcas concinna concinna (Gould)

Petrogale concinna GOULD, 1842, Proc. Zool. Soc. London, p. 57.

TYPE: B.M. No. 42.5.26.20, young male, from "N.W. coast of Australia." Restricted to Wyndham (Iredale and Troughton, 1934, p. 42).

The type, of which I have photographs, has i^3 fully erupted but unworn. In this genus i^3 is larger than i^2 . Its deep groove is of the usual *Protemnodon* type. It can be likened somewhat to i^3 in *Petrogale xanthopus*. The crown lengths of the incisors are: i^1 , 3.2 mm.; i^2 , 1.9; i^3 , 2.7.

The color of the skin of *concinna* is bright russet, not grayish rufous as in *canescens*.

Peradorcas concinna monastria Thomas

Peradorcas concinna monastria THOMAS, 1926, Ann. Mag. Nat. Hist., ser. 9, vol. 17, p. 630.

TYPE: B.M. No. 10.2.25.4, young female collected by G. F. Hill of Perth Museum at Napier Broome Bay, north of Kimberley and Drysdale River, north Western Australia. As in true *concinna*, i^3 is longer than i^2 : 2.7:1.9 mm. I have photographs of the skull.

The dimensions of the subequal molariform teeth are: 5.4 by 4.4 mm.: 5.4 by 4.5; 5.5 by 4.5; 5.6 by 4.4; 5.5 by 4.1.

The skin of the type is silvery gray on the neck and shoulders, turning to brownish posteriorly; limbs and face are buffy brown; underparts are white with gray-based hairs; pouch hairs are russet. The tail is gray with its tip blackish. A blackish shoulder stripe is followed by a pale buff mark.

Peradorcas concinna canescens Thomas

Peradorcas concinna canescens THOMAS, 1909, Ann. Mag. Nat. Hist., ser. 8, vol. 4, p. 198.

TYPE: "Brit. Mus. No. 4.1.3.58, adult male" (not seen by me), from Nellie Creek, Arnhemland, collected by J. T. Tunney in February, 1903.

LAGOSTROPHUS THOMAS

Lagostrophus THOMAS, 1887, Proc. Zool. Soc. London, for 1886, p. 544.

TYPE: *Kangurus fasciatus*.

The peculiar condition of the incisors, including their very narrow inverted-V arrangement (which slightly resembles that of the phalangerid genus *Dactylopsila*), the size dominance of i^2 over i^3 , and the reduction of i^1 set this genus apart from all other Macropodinae. There is a groove at the middle of the outer face of i^3 as in *Protemnodon*. The canine is absent. Thomas (1888, p. 101) states that p^3 , equal in length to m^1 , is scarcely smaller than p^4 and has three or four external grooves, and that p^4 has four or five such grooves. The measurements in his table (p. 85) are not those of a cotype but of an adult in which the length of p^4 is 4.8. My notes on, and photograph of, the young cotype of *albipilis* from Wongan Hills show that p^3 measured 4.7 by 3.0 mm.; dp^4 , 4.4 by 4.1; m^1 , 4.5 by 4.5. In the even younger cotype from York, p^3 still present, measures 4.3 by 3.0.

The anterior part of the rostrum and palate in *Lagostrophus* is greatly narrowed as in *Onychogalea*. The bullae are enlarged and inflated. The coronoid process is very high and is set nearly at right angles to the ramus.

Lagostrophus fasciatus (Péron and Lesueur)

Kangurus fasciatus PÉRON AND LESUEUR, 1807, Voyage... aux terres Australes, Atlas, pl. 27; PÉRON, 1807, *op. cit.*, vol. 1, p. 114.

Lagorchestes albipilis GOULD, 1842, Ann. Mag. Nat. Hist., ser. 1, vol. 10, p. 2.

TYPES: Type of *fasciatus* not seen but possibly in Paris. Cotypes of *albipilis*: B.M. No. 46.4.25.13-14, young adult female and male, respectively from York and from Wongan Hills, Western Australia, each with the back of the skull badly broken. The skins of these two skulls are, respectively, B.M. Nos. 44.9.30.1 and 44.9.30.2. My remarks on this species are partly based upon a specimen from Dorre Island, Western Australia, U.S.N.M. No. 218467, young adult female. In this p^3 - p^4 have been shed, dp^4 is retained on

one side, and p^4 is visible and measurable on the other side.

The ears are rather short. The posterior half of the body is banded transversely (12 bands in 200 mm.). The long guard hairs are black but have white subterminal bands 10 to 15 mm. in extent. Underparts buffy white, with the hair bases gray. Hands, feet, and tail gray. The pads of the feet in juvenal B.M. No. 44.9.30.2 are densely hairy. This is not always the case, as in *fasciatus* from Dorre Island.

The first incisor has the cusp and root much better differentiated than in other Macropodinae. The cusp is relatively short, and growth of the tooth is apparently not long-persistent. Its crown width varies from 1.7 to 1.9 mm. The labial face of i^2 is ± 3.1 . The anterior edge of i^3 fits the posterior notch of i^2 . Its crown length is 2.9, or, in the slightly chipped American specimen, 2.7. The external lamina is 1.4 mm. in length.

In the deciduous premolar the anterior loph is not narrower than the posterior loph (as is usual in macropods). The lengths of those molariform teeth visible are: dp^4 , 4.2; m^1 , 4.2; m^2 , 4.6; m^3 , 5.0 mm. The fourth molar is visible in the alveolus of our specimen, and the length of the incompletely erupted p^4 can be determined as ± 4.5 mm. Thomas gave this measurement from his "specimen d" as 4.8.

The bullae, only slightly inflated, are ± 9 mm. in length. The length of the anteorbital canal is 6.3 mm. The nasal notch is very short. The greatest length of the skull is ± 71 mm., the zygomatic width 40 mm.

The original range of this peculiar animal is shown by Shortridge (1909, p. 817) to have covered a large part of Western Australia.

The interrelationships of *Dendrolagus*, *Dorcopsulus*, and *Dorcopsis* are possibly not so close as suggested by Raven and Gregory (1946). This fact is brought out clearly by the differences existing in i^2 and i^3 and in p^3 and dp^4 of young specimens, in spite of the resemblance due to considerable lengthening of p^4 of *Dorcopsis* and *Dendrolagus*; and by the fact that the tail functions in *Dendrolagus* as a balancing organ, as in *Petrogale*, whereas in *Dorcopsulus* and *Dorcopsis* it is used, as is

that of *Protemnodon* and *Macropus*, as a prop or third hind limb.

In *Dorcopsulus* i^2 is subtriangular, and its crown when unworn is cleft in such a way as to present a dominant cutting edge along the labial margin of the tooth which terminates externally in a distinct cuspule, and a secondary, less trenchant edge along the lingual face. Those two edges converge anteriorly, and the valley between them opens broadly towards i^3 . This condition of i^2 is only imperfectly matched in *Dendrolagus*, as the valley is less accentuated. In *Dorcopsis*, on the contrary, the same tooth is more or less oval in section (the lingual side flattened), and the crown surface is excavated into two cells, a large anterior cell and a smaller posterior one, both surrounded by enamel.

The third incisor in *Dorcopsulus* is formed much as that of *Protemnodon*. It has a short labial cutting edge and a long internal one, the groove between the two edges appearing at about the middle of the labial face of the tooth (nearer the back in *Dorcopsulus rothschildi*). This condition is not even approximated in *Dendrolagus*, in which the crown surface of i^3 consists of a single, cup-like cell surrounded by enamel. In *Dorcopsis* the same cell is narrower and more elongated, while the enamel at the rear edge is less developed, allowing a suggestion of a groove to appear well back on the labial face of the tooth.

In *Dorcopsulus* the third premolar, behind which stands the molariform dp^4 , is a fairly symmetrical secant tooth not very greatly compressed (in fact less so than p^4 of *Petrogale*). It has four vertical grooves, separated by three ridges, both internally and externally. It is scarcely longer than dp^4 . On the other hand, *Dendrolagus dorianus* has p^3 short, thick, unsymmetrical, only slightly longer than dp^4 ; and its posterior width equals two-thirds of its length. The same is not true of *Dorcopsis*, in which the narrow, slightly curving juvenal secutor (p^3) is considerably longer than dp^4 . Thus, while p^3 in both *Dorcopsulus* and *Dorcopsis* is substantially a miniature of p^4 , in *Dendrolagus* it is short and thick compared with the lengthened and (except at its posterior end) considerably narrowed p^4 . Eruption of p^4 is synchronous with m^4 in *Dorcopsulus* and *Dorcopsis*; in

Dendrolagus it follows that of m^4 , at least in *ursinus* and *lumholtzi*.

In adults of *Dendrolagus dorianus* and *lumholtzi* considerable frontal swelling (much as in *Phalanger maculatus*) is found, while almost no such swelling occurs in *Dorcopsis* or *Dorcopsulus*. Large posterior palatal vacuities are seen in the two last; none or only minute openings, in *Dendrolagus*. The rostrum is not extremely elongated in *Dorcopsulus*. It is much elongated in *Dorcopsis* but is short and massive in *Dendrolagus*. The anteorbital canal in *Dendrolagus* is shorter than in *Dorcopsulus*; in *Dorcopsis* it is longer. There is a pronounced interorbital constriction and supraorbital notch in *Dorcopsis* which remains undeveloped in *Dorcopsulus* and *Dendrolagus*. The postglenoid process is weakly developed in *Dorcopsulus*, *Dorcopsis*, and some *Dendrolagus*, strongly developed in *D. lumholtzi* of Australia.

DORCOPSULUS MATSCHIE

Dorcopsulus MATSCHIE, 1916, Sitzber. Gesellsch. Naturf. Fr. Berlin, p. 57.

TYPE: *Dorcopsis macleayi*.

I have pointed out that the members of this genus (or subgenus) have p^3 (but not p^4) less compressed and attenuated than have the species of true *Dorcopsis*. The skull, also, is less narrow and less elongate. In other respects *Dorcopsulus*, despite its dense, soft pelage and small size, closely resembles *Dorcopsis*. It is to be regarded as generally less specialized than that lowlands genus.

Three forms have been described: *macleayi* from the central mountain chain behind Port Moresby, *vanheurni* from the central mountains (Doormanpad) in Netherlands New Guinea, and *rothschildi* from the mountains of the Huon Peninsula.

Now that several specimens from the Bele River and Lake Habbema, 7000 to 8000 feet (near the type locality of *vanheurni*), have been added to our collection, the supposed difference between the highlands form and the mid-mountain form (true *macleayi*) becomes substantiated.

In males of *macleayi* not only are the teeth larger than those of *vanheurni* but the entire rostrum is much more massive, being substantially wider and deeper than that of *vanheurni*, while the anterior palatal foramina

are short (3 mm.) compared with those of *vanheurni* (5 mm.). In all essential particulars except its smaller size the Huon mountain race, *rothschildi*, is found to agree with the

list these specimens by altitude, month of capture, sex, and age. Only three males and one female are old enough to have p_4^1 fully in place.

| | METERS | MONTH COLLECTED | MALES | | FEMALES | |
|------------------------------------|--------|--------------------|-------|-------|---------|-------|
| | | | JUV. | ADULT | JUV. | ADULT |
| 4 km. southwest of Idenburg River | 850 | Mar.-Apr. | 5* | — | 3 | — |
| 6 km. southwest of Idenburg River | 1200 | Feb.-Mar. | — | — | 2 | 1 |
| 10 km. southwest of Idenburg River | 1500 | Mar. | — | — | 1 | — |
| 15 km. southwest of Idenburg River | 1800 | Jan. | — | 1 | — | — |
| Bele River, 18 km. from Habbema | 2200 | Nov. | 2 | 1 | 2 | — |
| Bele River, 9 km. from Habbema | 2700 | Oct. | — | 1 | — | — |

* One subadult (p_4^1 changed on one side).

upland race, *vanheurni*, which spreads along the central mountain chain of New Guinea. In consequence, *Dorcopsulus* is here held to comprise only two species, *macleayi* and *vanheurni*, with *rothschildi* a local race of the latter.

Dorcopsulus macleayi (Miklouho-Maclay)

Dorcopsis macleayi MIKLOUHO-MACLAY, 1885, Proc. Linnean Soc. New South Wales, vol. 10, p. 149.

TYPE: In Sydney (not seen). The type locality as given by Miklouho-Maclay was "inland from Hanuabada" (= Port Moresby). Therefore, the several specimens taken by Archbold at Mafulu (Tate and Archbold, 1937); Berlin No. 22726, male, collected by Weiske on the Astrolabe Range; and Genoa No. C.E. 10449, female, from the Vanapa River obtained by Loria, may be regarded as virtual topotypes.

Dorcopsulus vanheurni Thomas

Dorcopsulus vanheurni vanheurni Thomas

Dorcopsulus vanheurni THOMAS, 1922, Ann. Mag. Nat. Hist., ser. 9, vol. 9, p. 264.

TYPE: B.M. No. 22.2.2.64, a young adult female, taken by W. C. van Heurn at Doormanpad, a few miles north of Mount Wilhelmina, 4500 feet.

The type has dense, soft fur. Most of the incisors have been lost, and p_4^1 is very narrow (length, 9.0 mm.: posterior width, 3.1).

The series of 19 *Dorcopsulus vanheurni* secured by the Third Archbold Expedition in the region between the Idenburg River and Mount Wilhelmina probably is the largest known. It has been considered valuable to

The ventral pelage in the foregoing series is in general nearly white in juvenals, but exceptions with smoky ventral pelage occur. In only one instance (a male) is white ventral fur seen in an adult.

No very significant differences between the skulls of highland and foothills animals can be detected. The anterior palatal foramina tend to be elongate and slit-like in high-country specimens (in the adult male from 2700 meters, 5 mm. long; in that from 2200 meters, 4.5 long; in the one from 1800 meters, 4.0 long; and in the adult female from 1200 meters, 3.8 long). I find no corresponding gradation in tooth sizes.

Our two males and one female of *macleayi* from the Central Division (Mafulu, 1250 meters) have much heavier teeth, while the lengths of their anterior palatal foramina range from 3.0 to 3.4 mm.

Our one adult and two juvenal males from Mount Tafa, 2400 meters, referred earlier (Tate and Archbold, 1937) to *rothschildi*, and a single adult male of *rothschildi* from Huon Peninsula, 1700 meters, have the light skull structure and dentition of the western *vanheurni*. They are distinguished from both *macleayi* and *vanheurni* by the position of the notch in i^3 , which comes nearer the back of the tooth instead of at the middle of the labial face.

Dorcopsulus vanheurni rothschildi Thomas

Dorcopsulus rothschildi THOMAS, 1922, Ann. Mag. Nat. Hist., ser. 9, vol. 9, p. 672.

TYPE: B.M. No. 28.10.1.10, adult female collected by Keysser in the Saruwaged Mountains, Huon Peninsula.

Besides our single adult male from Sevia, 1700 meters, Huon Peninsula, there is an adult female topotype at Tring, No. R.M. 15 (with mismatched mandible). The dimensions of p^4 in the type are: length, 7.3 mm.; posterior width, 3.1. That tooth in our Huon male measures 8.1 by 3.7.

DORCOPSIS SCHLEGEL AND MÜLLER

Dorcopsis SCHLEGEL AND MÜLLER, in Temminck, C. J., 1839–1844, *Verhandelingen over de Natuurlijke Geschiedenis der Nederlandsche overzeesche bezittingen, Zoologie*, vol. 1, p. 130. (For rejection of *Conoyces* Lesson, see p. 312).

TYPE: *Dorcopsis brunii* Schlegel and Müller (not *Didelphis brunii* Schreber) = *Dorcopsis mülleri* Schlegel.

The present scope of this genus is restricted. *Dorcopsulus*, originally employed subgenerically, is here considered to represent a full genus. The interrelationships of these two genera and *Dendrolagus* have been discussed elsewhere (p. 285). A comparison of freshly killed *Dorcopsis mülleri* and the similar appearing *Thylogale brunii* appears on page 317.

A captive juvenal *D. luctuosa* in our camp on the Fly River used its tail as a prop in much the same way as the wallabies and the large kangaroos use their tails.

Dorcopsis, as may be inferred from marked differences in the color pattern, is primarily divisible into two groups: the unornamented *mülleri* group of New Guinea south of the central mountain chain, and the *hageni* group from northern New Guinea, in which a narrow white dorsal stripe is present. This division is supported by a number of cranial and dental characters.

The posterior palatal vacuities are relatively small in *mülleri*, very large and subrectangular in *hageni*. The alisphenoid process which forms the outer wall of the ectopterygoid fossa is weakly developed in *mülleri*, while in *hageni* it is a strong deep lamina descending in males 7 mm. below the basis cranii. The foramen ovale in *mülleri* is floored by a portion of the alisphenoid, so that it emerges laterally, its opening being ± 5 mm. from the base of the pterygoid. In *hageni*, the same foramen is larger and, because scarcely floored by the alisphenoid, opens ventrally.

Its opening lies only ± 3 mm. from the base of the pterygoid. The tympanic bone of *mülleri* containing the auditory meatus, although rugose, is only moderately enlarged in that portion lying between the alisphenoid bulla and the glenoid process. In *hageni* that same part of the tympanic (anterior to the meatus) has become considerably more enlarged. The lacrimal processes in *mülleri* are less prominent than those of *hageni*. The anteorbital canal in *mülleri* is often shorter than in *hageni*.

The dentition of *mülleri* is distinctly weaker than that of *hageni*. In juvenal males the notch of i^2 is posterior in *mülleri*, lateral (near the back of the labial surface) in *hageni*, and in that species the internal lamina is expanded into a flat cusp. In i^3 the notch between the inner and outer lamina emerges slightly to the rear of the center of the labial surface in *mülleri*, almost exactly at the center in *hageni*. In the latter the crown length of the unworn canine is almost equal to that of i^3 . The narrow-bladed p^3 and p^4 are invariably smaller in *mülleri* than in *hageni*: length of p^3 in *mülleri*, ± 7.4 mm., in *hageni*, ± 8.5 ; length of p^4 in *mülleri*, ± 13.2 , in *hageni*, ± 14.0 . The toothrow, m^{1-4} , in *mülleri* is ± 23 ; in *hageni*, ± 26 . In both species the replacement of p^3 and dp^4 by p^4 is completed before m^4 is fully erupted. I have found no instance in which dp^4 and m^4 are in place at the same time, so as to give a row of five molariform teeth.

The skulls of females of *Dorcopsis mülleri* and *D. hageni* scarcely differ from the males. In the former the female grows almost as large as the male, but in the latter it remains more definitely smaller. The larger canines of males of *hageni* are reproduced in the female, so that the canine in female *hageni* is somewhat heavier than in male *mülleri*. Other characters, such as the large ectopterygoid wings of the alisphenoid in *hageni*, are as strongly developed in females as in males.

The named forms related to *mülleri* extend virtually throughout New Guinea south of the central chain of mountains. They begin in the extreme west with the insular form *mysoliae* on Mysol, Waigeu, and Salawatti. They occupy (*mülleri*) the Vogelkop: Sorong, Dorei (=Manokwari), Andai, Lobo Bay (on

the south coast), the Weyland Mountains at 1000 feet (Stein), and the Lorentz and Noord River area (Lorentz). As *luctuosa* they occur in the Fly River basin, and as *beccarii* they are recorded from Yule Island, Port Moresby, and the lower Kemp Welch (Willis collection). Under the name *chalmersii* one specimen was described from the mainland opposite Samarai at the extreme eastern end of New Guinea.

The species *hageni* occupies an extensive portion of northern New Guinea between the Huon Peninsula and Geelvink Bay.

***Dorcopsis mülleri* Schlegel**
***Dorcopsis mülleri mülleri* Schlegel**

Kangurus veterum LESSON, 1826, Voyage autour du monde . . . sur . . . La Coquille, Zoologie, vol. 1, p. 164.

Dorcopsis brunii SCHLEGEL AND MÜLLER, in Temminck, C. J., 1839-1844, Verhandelingen over de Natuurlijke Geschiedenis der Nederlandsche overzeesche bezittingen, Zoologie, vol. 1, p. 131.

Hypsiprymnus dorsocephalus OWEN, 1839, Proc. Zool. Soc. London, p. 16 (a virtual *nomen nudum*).

Dorcopsis mülleri SCHLEGEL, 1866, Nederlandsch Tijdschr. Dierk., vol. 3, p. 353.

Halmaturus luctuosus D'ALBERTIS, 1874, Proc. Zool. Soc. London, p. 110.

Dorcopsis chalmersii MIKLOUHO-MACLAY, 1884, Proc. Linnean Soc. New South Wales, vol. 9, p. 570.

Dorcopsis beccarii MIKLOUHO-MACLAY, 1885, Proc. Linnean Soc. New South Wales, vol. 10, p. 146.

Dorcopsis rufolateralis ROTSCCHILD AND ROTSCCHILD, 1898, Novitates Zool., vol. 5, p. 512.

Dorcopsis lorentzii JENTINK, 1909, Nova Guinea, vol. 9, p. 10.

TYPES OR COTYPES: Of *veterum*, not in existence; procured at Dorei, but lost overboard from the "Coquille." Of *brunii*, based on Bruijn (1714, pl. 213 and p. 374), no locality. Of *dorsocephalus*, unknown. Of *mülleri*, from Lobo Bay. Specimens a, b, c, of Jentink (Cat. Syst. des Mamm.). Of *luctuosus*, B.M. No. 75.4.16.1, young adult female, originally in a "zoo." Of *chalmersii*, Dinner Island (=Samarai), extreme east end of New Guinea; not seen, but probably at Sydney; juvenal. Of *beccarii*, not seen; from Port Moresby. Of *rufolateralis*, at Tring, adult

male, from the "zoo" at Regents Park; skull apparently lost. Of *lorentzii*, Leiden Mus. Nos. 125, 126, 127, from Van Weil's Camp and Alkmaar, 300 meters, Noord River.

The American Museum collection contains a large series from the middle Fly River (Sturt Island Camp, and Lake Daviumbu) representing *luctuosus*; the two specimens earlier recorded (Tate and Archbold, 1937) from Kabuna, near Port Moresby; and two others taken by L. A. Willis from the Kemp Welch River, east of Port Moresby. The last four represent *D. beccarii* Miklouho-Maclay. In addition, I have examined a female specimen from Panaman, Mimika River, at the Museum of Comparative Zoology (M.C.Z. No. 14759), which perhaps can be regarded as representing *lorentzii*. At Brisbane Museum is a specimen (No. 4231) from the Edrich River, near the mouth of the Digul River, Netherlands New Guinea.

Dorcopsis mülleri is thus seen to be distributed throughout the forested lowlands of New Guinea south of the central range of mountains from Vogelkop to Samarai (*chalmersii*), a distance of more than 1000 miles. It has not yet been discovered in northern Queensland, but in view of the presence there of other mammals characteristic of New Guinea, it may well be discovered sooner or later in suitable habitats.

***Dorcopsis mülleri mysoliae* Thomas**

Dorcopsis mysoliae THOMAS, 1913, Ann. Mag. Nat. Hist., ser. 8, vol. 11, p. 507.

TYPE: B.M. No. 61.12.11.22, adult male from Mysol Island, off Vogelkop, collected by A. R. Wallace, 1860. This specimen, although slightly smaller, is virtually identical to *mülleri* of the mainland. I have left it provisionally as an island race of inferior size pending the appearance of further information.

***Dorcopsis hageni* Heller**

Dorcopsis hageni HELLER, 1897, Abhandl. Ber. K. Zool. Anthropol. Ethnogr. Mus. Dresden, vol. 6, no. 8, p. 7.

Dorcopsis hageni caurina THOMAS, 1922, Ann. Mag. Nat. Hist., ser. 9, vol. 9, p. 264.

TYPES: Of *hageni*, not seen; taken at

Stefansort, near Astrolabe Bay, northern New Guinea. Of *caurina*, B.M. No. 22.2.2.63, adult male, collected by Van Heurn, 1921, at Pionier Bivak, Mamberano River.

Other specimens seen by me are a male topotype of *hageni* taken by Förster in 1906 (Berlin Mus. No. 22368 with skull No. 22369); a large series secured by the Third Archbold Expedition near Hollandia and the Cyclops Mountains and also in the middle Idenburg River; a number of specimens from various parts of the Sepik Valley (three taken by Bürgess, in Berlin; two collected by Wonder at Marienburg, in the Chicago Natural History Museum).

I find no valid distinction between *caurina* and *hageni*.

So far as now indicated, *D. hageni* occurs only in north central New Guinea. There is no evidence yet of its presence either in the Vogelkop to the west or in the Huon area to the east. I have not seen an example of *D. hageni eita*pe Troughton.

DENDROLAGUS SCHLEGEL AND MÜLLER

Dendrolagus SCHLEGEL AND MÜLLER, in Temminck, C. J., 1839-1844, *Verhandelingen over de Natuurlijke Geschiedenis der Nederlandsche overzeesche bezittingen*, Zoologie, vol. 1, p. 130.

TYPE: *Dendrolagus ursinus* Schlegel and Müller.

Dendrolagus is one of the few macropodid genera that have been formally revised in recent years (Rothschild and Dollman, 1935). Some additional species have been subsequently described by Troughton. Raven and Gregory (1946, pp. 8-10) have briefly indicated their views on the relationships of *Dendrolagus* to other Macropodidae.

Changes relating to the proportions of the limbs, modification of the feet, enlargement of the claws, etc., are to be regarded as secondary adaptations to the arboreal environment of this genus. The shortening and thickening of the head may also well be secondary.

Certain characters remain which seem to have escaped this secondary modification. These include size and functional dominance of i^1 coupled with reduction of i^2 and i^3 (the notch of i^3 when present is lateral) in the incisive series; retention of weak canines; non-reduction of p^3 and p^4 (the enlargement

of p^4 may be secondary and in agreement with the general shortening and strengthening of the skull); the late eruption of p^4 (in *D. ursinus*, M.C.Z. No. 7007, m^4 is in place before p^3 and dp^4 have been lost); and the total lack of inflation of the bullae.

Dendrolagus exhibits certain features in common with *Petrogale*: the marked reduction in size and function of i^3 mentioned above and the coalescence of the convex mastoid surface with the squamosal portion of the zygoma. It differs from *Protemnodon* and *Thylogale* by precisely these characters. The tail is long and of nearly uniform thickness, as in *Petrogale*, and shows no basal thickening such as appears in the tails of those genera of large kangaroos that use their tails for support. The tail of *Dendrolagus*, like that of *Petrogale*, is a balancing organ. No tactile surface exists. There is no area near the tip where the hairs show exceptional wear. From the functional viewpoint the anatomy of the rock-climbing wallabies, *Petrogale*, should be rather readily adaptable to the tree-climbing habitus of *Dendrolagus*.

One other characteristic of the skins of *Dendrolagus*, namely, the reversed hair of the nape, should be kept in mind. This appears also in *Dorcopsis*, *Petrogale* (except *P. xanthopus*), and *Thylogale* (*thetis* only). It was suggested by Wallace and by Darwin (*vide* Miklouho-Maclay, 1885), that the reversed pelage of the dorsum of the neck may be related to some characteristic attitude, perhaps holding the head very low. They thought that when such a posture was assumed the hair whorl near the withers or elsewhere would automatically be at the highest part of the body and rain would be readily thrown off over the head. However, that explanation is not generally accepted.

It is necessary to state at once my unproved suspicion that *Dendrolagus ursinus* and *D. inustus* are not distinct species but color phases of a single species. Both forms come from Lobo Bay, on the southern side of Vogelkop. In my discussion of species groups, *ursinus* will be found to include the latter and its races.

The revisionary work on *Dendrolagus* by Rothschild and Dollman (1935) dealt only with the interrelationships of species and

subspecies. Three primary species groups based upon the positions of the hair whorls in the skins were adopted. Such use of a single character is usually open to criticism; besides, the positions of the hair whorls are rather less definite than appears in the monograph cited. Rothschild and Dollman state of *D. dorianus* that the hair whorl is near the root of the tail but neglect to add that there is also a whorl at the withers in substantially the same position as that in the majority of the species. In fact, in a young specimen (A.M.N.H. No. 104080), the parting of the hairs occurs slightly anterior to the withers, and the whorl on the rump is obsolete. These facts weaken the conclusions reached by Rothschild and Dollman. Their observations on the middorsal position of the hair parting in *D. matschiei* is substantiated by our two specimens of that species. Characters other than the positions of hair whorls that may either fortify or contradict the conclusions of Rothschild and Dollman have been sought in the present study.

The second and third incisors, although invariably much smaller and less important than i^1 in all species, are proportionately the least reduced in *D. dorianus*. Both are actually and proportionately smaller in *ursinus*. They attain maximum reduction in *lumholtzi*. The canine in *ursinus* shows sexual dimorphism; it is still a substantial structure in males but is considerably smaller in females. It is equally substantial in both sexes in *dorianus*, but is reduced to a slender rudiment in both males and females of *lumholtzi*.

Owing to its frequent loss early in the life of species in this genus, the third premolar has been seen by me rarely, and then only in *dorianus*, *ursinus*, and *lumholtzi*. In *dorianus* it is much broadened by development of a cingulum on the labial side. In *lumholtzi* it is more nearly symmetrical, approaching that of *Dorcopsulus*. (Although p^3 is shed early, dp^4 is persistent.)

The molars reach maximum size in *Dendrolagus dorianus* (width of m^3 , ± 6.5 mm.). In *ursinus* and *lumholtzi* they are narrowed (width of m^3 , ± 6.0).

In *Dendrolagus lumholtzi* m^4 is erupted before p^3 and dp^4 are replaced by p^4 . This often results in a tooththrow of five molariform teeth. I have rarely observed the same condi-

tion in other species, perhaps only because so few juvenals are included in our material.

The fourth premolar shows the fewest peculiarities in the case of Australian *lumholtzi*. In that species it is elongate and possesses an anterior cusp and an interoposterior cusp, with an incipient exteroposterior cusp. In *ursinus* the interoposterior cusp becomes enlarged and emphasized, and a weak internal cingulum is found. In *dorianus* these characters are further developed, the enlarged exteroposterior cusp extending laterally and the internal cingulum becoming more pronounced. In *dorianus* p^4 reaches maximum proportional size, while, on the contrary, in *ursinus* the anterior two-thirds of that tooth is scarcely half as wide from side to side as the posterior third (which carries the supplementary cusps).

The skull of fully adult *Dendrolagus ursinus* is slender (although strongly built) compared with the broader skull of *dorianus* and the still more brachycephalic *lumholtzi*. Females of *ursinus* have substantially smaller skulls than males. This sexual disparity is less perceptible in *lumholtzi*, and evidence on this same point is lacking in *dorianus* and *matschiei*. The greater length of the skull of *ursinus* causes it to resemble superficially that of *Dorcopsis*.

Moderately developed postorbital processes of the frontal are present in *D. ursinus*, immediately beneath which is a small but well-developed foramen. Postorbital processes in *dorianus* are weak or obsolescent, and the said foramen is either absent or merely a minute pore; in *lumholtzi*, accompanying the broadened and swollen condition of the frontals, the postorbital processes may be regarded as obsolete. The inferior foramen is minute or absent.

The lacrimal foramina in *ursinus* are quite large openings about 2 mm. in diameter, and the anteorbital canal opens from 10 to 12 mm. anterior to the orbit. In *dorianus* the superior lacrimal foramen (situated above the lacrimal process) is much the smaller, 1 mm. or less in diameter, and the mouth of the anteorbital canal is found only 7 to 8 mm. from the orbit. In *lumholtzi* both foramina are small, 1.0–1.4 mm. in diameter, and the anteorbital canal is also short, 7 to 8 mm.

The zygomata of *Dendrolagus*, as is frequently the case in mammals, are subject to sexual variation. But, discounting this, the zygomata of *dorianus* are decidedly the most massive, while those of *lumholtzi* are somewhat weaker than those of *ursinus*. Both the descending process of the maxilla and the glenoid process are most strongly developed in males of *dorianus* and *ursinus* but are considerably weaker in females of the latter. In *lumholtzi* they are generally smaller in both sexes. The depth of the molar below the orbit in females is: *dorianus*, 11 mm.; *ursinus*, 8-9 mm.; *lumholtzi*, 7-8 mm. The depth of the zygomatic process of the squamosal at the level of the frontoparietal suture in females is: *dorianus*, 18 mm.; *ursinus*, 13-15 mm.; *lumholtzi*, 10-11 mm.; in males: *dorianus*, ?; *ursinus*, ± 18 mm.; *lumholtzi*, 14-15 mm.

The auditory portion of the alisphenoid (when enlarged, named the alisphenoid bulla) is quite broad in *dorianus* (± 7 mm.): narrower in *ursinus* (4 to 5 mm. in males, 2 to 3.5 in females); and ± 4 mm. in *lumholtzi*.

The paroccipital processes in *dorianus* are thick and relatively smooth, and the mastoid processes descend only level with the bottom of the condyles. In *ursinus* the paroccipital processes are more slender and more rugose, and the mastoid processes descend below the bottoms of the condyles. In *lumholtzi* the paroccipital processes are still more slender, and the mastoid processes descend as far as 3 mm. below the lower level of the condyles.

The frontoparietal suture in *ursinus* is characterized by considerable development of minute indentations. In *lumholtzi* the same suture is, so far as I can discover, perfectly simple. In *dorianus* and allies slight sinuities may be found. Bregmatic bones occur not infrequently in *Dendrolagus* (sometimes also in *Petrogale*). They are seen in *D. ursinus* (Rothschild and Dollman, 1935, pl. 54), *D. inustus* (Rothschild and Dollman, pl. 56), and *D. bennettianus* (Rothschild and Dollman pl. 57).

From evidence drawn from the foregoing observations I suggest the following classification of the tree kangaroos:

1. *D. dorianus* and allies: canines comparatively unreduced in both sexes; frontoparietal suture weakly sinuate; teeth large; skull broad.

2. *D. ursinus* and allies: canines unreduced in males, reduced in females; suturae dentatae usually between the frontal and parietal bones; outline of male skull relatively narrow and superficially similar to that of *Dorcopsis*.

3. *D. lumholtzi*: canines rudimentary in both sexes; suturae simplices in frontoparietal area. Skull broad. Teeth relatively small.

Dendrolagus bennettianus, the second species known from Australia, is probably an offshoot of the *dorianus* group. This view is confirmed not only by cranial and dental similarities but even by the pattern of the pelage; a pale area surrounding the base of the tail is present in both *bennettianus* and *dorianus*.

I have not had actual skulls of either *goodfellowi* or *matschiei*, or even of *ursinus* before me when doing the present work, although I studied and photographed the types of the first two in 1937. Yet because of the numerous similarities found in their skulls and the general similarity of the skin patterns and even though the colors vary widely, I regard *goodfellowi* and *matschiei* and the several races referred to each as close allies of *dorianus*.

The *Dendrolagus dorianus* group thus contains:

dorianus
bennettianus
aureus
notatus
mayri
profugus
spadix
goodfellowi
shawmayeri
deltae
matschiei
flavidior
xanthopus
bürgersi

The *Dendrolagus ursinus* group contains:

maximus
schoedei
sorongensis
leucogenys
keiensis
inustus
finshi

The *Dendrolagus lumholtzi* group includes, besides *lumholtzi*, only the synonymous *fulvus*.

Of these three groups *dorianus*, to judge from the number of described forms, is dominant and actively evolving. It occupies suitable altitudes in central and eastern New Guinea and extends (as the race *bennettianus*) into northern Queensland. The *ursinus* group is essentially indigenous to western New Guinea but extends east to Hollandia and Eitape along the northern coast. The *lumlholtzi* group occurs only in Queensland.

The American Museum collection of the *dorianus-goodfellowi-matschiei* group has not increased since I reported on *Dendrolagus* previously (Tate and Archbold, 1937), but from Australia both H. E. Raven and Gabriele Neuhäuser obtained good series of *lumlholtzi*, and the Third Archbold Expedition obtained a small series of topotypical *D. ursinus finschi* from the Cyclops Mountains, near Hollandia.

Dendrolagus ursinus Schlegel and Müller

The distribution of this species, if we assume the synonymy of *inustus*, extends from the Vogelkop through New Guinea north of the central mountain ranges as far east as the Finsch coast. There is no evidence to show that it occurs south of the mountains or east of the Huon Peninsula. If, on the contrary, it is proved that *ursinus* and *inustus* are full species, they will be found to be virtually sympatric.

Dendrolagus ursinus finschi Matschie

Dendrolagus finschi MATSCHIE, 1916, Sitzber. Gesellsch. Naturf. Fr. Berlin, art. 4, p. 163.

TYPE: Berlin Mus. No. 45060, a tail only, from Tami, Humboldt Bay, 5.5 kilometers from the Dutch border. The use of such a specimen for a type represents one of those unfortunate cases in which the author's good judgment was exceeded by his zeal to propose a new race. The color of the tail in question is fairly uniform grayish white, with a slight admixture of gray hairs. Its length is ± 390 mm.

Rothschild and Dollman (1935) accepted Ernst Mayr's specimen from the Cyclops Mountains as equal to *finschi*, although one might well conclude from their plate 46 that its tail was perfectly white.

The Third Archbold Expedition obtained

five skins and four skulls from near Hollandia (at the eastern end of the Cyclops Mountains). These comprise three adult males, one adult female, and one rather young female. Although the black dorsal patch shown by Rothschild and Dollman is present in all, there is elsewhere considerable variation. The underparts of the three males are grayish white. The tail of one is substantially as in the Berlin type, those of the others being darker or even blackish dorsally. The inner sides of the limbs of the female are perfectly white; the brownish flanks shown by Rothschild and Dollman appear only in the young female. Although I have no material representing other races of *ursinus* with which to compare *finschi*, the considerable degree of color variation in the series from the Cyclops area lying before me suggests possible wide variation in color throughout the species.

Dendrolagus ursinus keiensis Matschie

Dendrolagus keiensis MATSCHIE, 1916, Mitt. Zool. Mus. Berlin, vol. 8, no. 2, p. 297.

Dendrolagus schoedei MATSCHIE, 1916, Mitt. Zool. Mus. Berlin, vol. 8, no. 2, p. 300.

TYPES: Of *keiensis*, Berlin Mus. No. 11362, collected in German New Guinea by Rolle, a dealer, according to Dr. E. Stresemann. Of *schoedei*, Berlin Mus. No. 22641, taken by Schoede at Eitape, Finsch coast.

This is treated provisionally as a separate race. There are apparently no *Dendrolagus* on Kei Island.

Dendrolagus ursinus ursinus Schlegel and Müller

Dendrolagus ursinus SCHLEGEL AND MÜLLER, in Temminck, C. J., 1839-1844, Verhandelingen over de Natuurlijke Geschiedenis der Nederlandsche overzeesche bezittingen, Zoologie, vol. 1, p. 131.

Dendrolagus inustus SCHLEGEL AND MÜLLER, in Temminck, C. J., 1839-1844, loc. cit.

Dendrolagus maximus ROTHSCILD, 1898, Novitates Zool., vol. 5, p. 511.

Dendrolagus sorongensis MATSCHIE, 1916, Mitt. Zool. Mus. Berlin, ser. 8, vol. 2, p. 300.

Dendrolagus leucogenys MATSCHIE, 1916, Mitt. Zool. Mus. Berlin, ser. 8, vol. 2, p. 293.

TYPES: Of *ursinus*, cotypes, Leiden, skin a and skull c, and skin b with skeleton a, also skull d (without skin), collected by Müller

and Macklot at Lobo Bay, south shore of Vogelkop, 1828. Of *inustus*, Leiden, d with skeleton a, collected by Müller and Macklot, August, 1828, at Triton (=Lobo) Bay. Of *maximus*, in Tring Museum, no locality, procured from Brün. Of *sorongensis*, Berlin Mus. No. 5122 (22467), collected by D'Alberty at Sorong. Of *leucogenys*, Berlin Mus. No. 21968, no locality, from Berlin "zoo."

The specimens of *ursinus* and *inustus* figured by their describers were both juvenals, as the position of p^4 was dotted in each sketch.

I have examined two animals from the northern part of Vogelkop: M.C.Z. No. 7007, female, from Manokwari; and M.C.Z. No. 7008, female, from Dorei. Considered alone, one would scarcely hesitate to treat them as separate species, and they bear on their labels the names *ursinus* and *inustus*, respectively. The differences between them do not agree with those of the skulls shown in Rothschild and Dollman (1936, pls. 54, 55). They do agree with the typical skulls figured by Schlegel and Müller to the extent that the nasofrontal sutures form a V in *inustus* and are drawn much straighter in *ursinus*. More evidence is needed to prove whether these are two full species or simply a highly variable race. In this paper they are treated as the latter.

In both specimens in the Museum of Comparative Zoölogy, p^4 has three external grooves, the canine stands close to i^3 , and the canal for the mandibular nerve is very large.

In two of the cotypes, *ursinus* skeleton a and *inustus* skull d, both juvenals, m^3 is present, and p^3 and dp^4 are still in place. The third premolar of *ursinus* cotype a is much smaller (6.1 by 4.0 mm., greatest width, and in a specimen from Arfak, Genoa C.E. No. 1602, 5.4 by 4.0) than that of *inustus* cotype d (6.5 by 4.9, greatest width). The same is true in regard to the widths of the molars: 5.4 in m^{1-3} of *ursinus*, 5.9, 6.3, 6.0 in m^{1-3} of *inustus*. In the case of the adult cotype of *ursinus*, skull c, this narrowness of the molars is even greater: m^{1-3} , 5.1, and m^4 , 4.6 mm. The size of p^4 in this cotype is: length, 9.0; greatest (posterior) width, 5.5 mm.

The two specimens in the Museum of Comparative Zoölogy, checked for width of molars, confirm the above: the width of m^1 of "*ursinus*," 5.2; of "*inustus*," 5.5 mm. This

is not borne out in m^4 , which shows, respectively, 5.2 and 5.4 mm. (anterior loph).

Dendrolagus dorianus Ramsay

Dendrolagus dorianus dorianus Ramsay

Dendrolagus dorianus RAMSAY, 1883, Proc. Linnæan Soc. New South Wales, vol. 8, p. 17 (skin).

TYPE: A cotype is in the Australian Museum, Sydney; not seen by me. The skull of this species was described by Miklouho-Maclay (1885, p. 1154).

Since reporting our two specimens (Tate and Archbold, 1937), I have examined a young male, Genoa No. C.E. 1600, collected by Loria on the upper Vanapa River. In it p^3 and dp^4 are both functional, and m^4 is partly erupted. Its molars form a well-marked curve converging slightly at the back. An adult, M.C.Z. No. 29680, from Mount Misim, near Morobe, northeast Papua, has shed p^3 and dp^4 . The lengths of m^1 and m^4 are 5.5 and 6.2, respectively; the posterior width of m^1 is 5.1; the anterior and posterior widths of m^4 are 5.0 and 4.5 mm. The fourth premolar is 9.6 in length, 4.5 and 5.8 in anterior and posterior widths.

No new material representing the *dorianus-matschiei* group has been received recently. But it may be well to set forth certain dental measurements of type specimens examined in Europe during 1937 (see table 4).

Dendrolagus lumholtzi Collett

Dendrolagus lumholtzi COLLETT, 1884, Proc. Zool. Soc. London, p. 387.

Dendrolagus fulvus DE VIS, 1887, "Evening Observer," Brisbane, Oct. 17; 1888, Proc. Roy. Soc. Queensland, vol. 4, p. 132.

TYPES: Cotypes of *lumholtzi*, B.M. No. 84.4.18.2, juvenal female, collected by Lumholtz in Herbert Vale, northern Queensland; (B.M. No. 84.4.18.3, a topotypical skull, may belong to skin No. 84.4.18.2, the skull of which was not found). Type of *fulvus* possibly at Brisbane.

The American Museum has a considerable series of this species. Nearly all are field-taken specimens, either from Atherton Tableland or nearby Evelyn. There are also a few "zoo" specimens. In the Museum of Comparative Zoölogy there are three from Millaa, one from Ravenshoe, and one from Mount Spurgeon.

As pointed out under my discussion of the species groups, this animal is notable for its full, rounded rostrum, inflated frontal region, and for the extreme reduction of the canines in both sexes. Its characters were fully discussed by Collett (1887).

premolar, which is at the fore part, is but half the anteroposterior diameter; the utmost thickness (at the back part of the crown) is less than the height. . . . A feeble indication of a cingulum runs along the outer side . . . and is more dubiously represented by a slight

TABLE 4

| | | p ³ | | dp ⁴ | m ¹ | m ⁴ | p ⁴ | |
|--------------------|---------|----------------|----------------|-----------------|----------------|----------------|----------------|----------------|
| | | Length | Greatest Width | Width | Width | Width | Length | Greatest Width |
| <i>aureus</i> | Juv. ♀ | 5.5 | 4.3 | 5.0 | 6.0 | — | — | — |
| <i>mayri</i> | Ad. ♂ | — | — | — | 6.0 | 6.0 | 10.3 | 5.9 |
| <i>goodfellowi</i> | Ad. ♂ | — | — | — | 6.1 | 6.3 | 10.0 | 5.8 |
| <i>notatus</i> | Ad. ♂ | — | — | — | 6.0 | 6.3 | 9.8 | 6.0 |
| <i>shawmayeri</i> | Ad. ♂ | — | — | — | 5.5 | 5.5 | 9.9 | 5.3 |
| <i>flavidior</i> | Young ♀ | 5.1 | 4.0 | 4.4 | 5.3 | — | — | — |
| <i>bürgersi</i> | Ad. ♂ | — | — | — | 5.1 | 5.4 | 9.6 | 5.4 |

PROTEMNODON OWEN

Protemnodon OWEN, 1874, Phil. Trans. Roy. Soc. London, vol. 164, pp. 274–281.

Wallabia TROUESSART, 1905, Catalogus mammalium tam viventium quam fossilium, Suppl., p. 834, footnote.

TYPES: Of *Protemnodon*, *Macropus anak* (by subsequent designation, Tate and Archbold, 1937). Of *Wallabia*, *Macropus ualabatus* Lesson and Garnot (by tautonymy) = *Kangurus bicolor*.

Owen (1874) wrote: "The genus *Protemnodon* is allied to *Sihenurus* [a statement no longer regarded as particularly true], but distinguished therefrom by the more simple trenchant shape of the crown of the premolar. . . . The upper molars of *Protemnodon* are more like those of *Sihenurus atlas* than of *Macropus tilan*; they have a narrow prebasal ridge without link . . . the lower premolar [marked "p³" in all Owen's figures], in its relative anteroposterior extent to the molars which follow, rather exceeds that tooth in *Sihenurus atlas*. The proportion of p³ in *Protemnodon* is much the same as in the Bettongs . . . the lower premolar of *Protemnodon* shows no indication of the three-lobed division which is marked on the outer surface of the crown of that premolar of *Dendrolagus*. . . . The greatest height of the crown of the

smooth out-swelling along the base of the inner surface. The tooth is implanted by two antero-posterior, slightly divergent fangs."

All recent wallabies of the genus *Protemnodon* have prop-like tails, like those of *Macropus* but unlike those of *Dendrolagus* and *Petrogale*.

A primary distinction between the wallabies, *Protemnodon*, and the kangaroos, *Macropus*, pointed out by Krefft (1875) lies in the behavior of p⁴. In the wallabies p⁴, erupted after m³, are retained in the tooth-row long after the eruption of m⁴ and are only rarely shed (in species in which they are exceptionally small, such as *parryi* and *rufogriseus*). In *Macropus* p⁴, sometimes erupted after m², are usually shed after the development of m³ and before that of m⁴. Combined with this difference in behavior of p⁴ is the relative lack of forward movement in the tooth-row of the molars of the wallabies and the pronounced forward movements of the molars of the kangaroos, accompanied by their successive loss at the front of the tooth-row. So far as one can judge, the first of these patterns of behavior of the cheek teeth is present in *P. anak*.

When the inferior dental characteristics of the type of *P. anak* are checked with those of related recent wallabies the following situation appears:

| | <i>anak</i> | <i>agilis</i> A.M.N.H. No. 108046 NEW GUINEA | <i>bicolor</i> (= <i>ualabatus</i>) A.M.N.H. No. 65125 QUEENSLAND |
|--------------------|--------------------------|---|---|
| p_4-m_4 | 66 | 45.5 | 37.9 |
| p_4 | 14.5×6.5 (max.) | 8.9×3.5 | 8.5×4.2 |
| m_1 (post. loph) | 9.2×8.0 | 7.0×5.7 | 6.0×6.2 |
| m_2 (post. loph) | 12.8×10.5 | 8.1×6.4 | 6.8×6.5 |
| m_3 (post. loph) | 13.9×10.9 | 9.8×6.8 | 8.0×6.8 |
| m_4 (post. loph) | 17.0×10.7 | 10.3×6.7 | 8.1×6.0 |

In no species of those normally referred to *Protemnodon* (or *Wallabia*) other than *bicolor* and *agilis* is p_4 so outstandingly more elongate than m_1 . The most likely candidate otherwise for this distinction would be the big wallaby *rufogrisea*, but the proportion of the length of p_4 to that of m_1 in *rufogrisea* is 6.0:7.5 mm., and in *parryi* p_4 is even smaller.

From the foregoing table the percentage ratio of the length of p_4 to the lengths of the several molars works out as follows:

| | <i>anak</i> | <i>agilis</i> | <i>bicolor</i> |
|-------|-------------|---------------|----------------|
| m_1 | 157 | 127 | 142 |
| m_2 | 114 | 100 | 125 |
| m_3 | 105 | 90 | 106 |
| m_4 | 81 | 86 | 105 |

This shows p_4 to be relatively longer in *anak* and *bicolor* than in *agilis*. On the other hand m_4 is longer than m_3 in *agilis*, much longer in *anak*, and approximately equal in *bicolor*. *Protemnodon agilis* is actually the largest of the living wallabies referable to *Protemnodon* and in this respect most nearly approaches *anak*.

From the point of view of dental structure no generic incompatibility between *bicolor*, *agilis*, and *anak* can be found. The greatest width of the fourth lower premolar proportional to its length occurs in *bicolor* (49 per cent), next comes *anak* (45 per cent), and last *agilis* (40 per cent). The processes in front of the anterior loph of each molar are developed in *bicolor* and *agilis* precisely as in *anak*. The lack of even a semblance of a talon in m_4 in the type of *anak* is also duplicated in both. Therefore, despite Troughton's (1937, p. 118) protest, I must support Raven's conclusion that *anak*, *bicolor*, and *agilis* are congeneric (although I have placed *anak* in a separate section of the genus).

In addition to the species of wallabies that agree closely with *P. anak* in having large p_4 , there are others, notably *irma*, *parryi*, *rufogrisea*, and *dorsalis*, in which p_4 are considerably reduced. These agree with the large-toothed *agilis* and *bicolor* in other respects, namely, in replacing the deciduous teeth after the eruption of m^3 and in the possession of a marked fold in the labial surface of i^3 (not very close to the back of that tooth as in *Thylogale*). Among these, *irma* and *parryi* have not enlarged the blade of i^3 . The small wallabies *eugenii* and *parma*, which also have i^3 small, have only partly reduced p_{3-4} . Thus, *Protemnodon* may be considered to comprise one group of extinct and four groups of living wallabies, as follows:

- A. *Protemnodon* of great size (extinct) in which p_4 attains a length of 14 mm. or more. *anak*
- B. *Protemnodon* in which p_4 is longer than m_1 :
 1. In which the crown length of i^3 is almost equal to the combined crown lengths of i^1 and i^2 ; size large. *bicolor* (= *ualabatus*) with *agilis*
 2. In which the crown length of i^3 is little more than one-half of the combined lengths of i^1 and i^2 ; size medium to small. *eugenii*, with *parma* and *bedfordi*
- C. *Protemnodon* in which p_4 is shorter than m_1 :
 3. In which the crown length of i^3 is almost equal to the combined crown lengths of i^1 and i^2 *rufogrisea*, with the smaller *dorsalis*
 4. In which the crown length of i^3 is about one-half of the combined crown lengths of i^1 and i^2 *parryi*, with *greyi* and *irma*

This arrangement leaves the short-tailed *Setonix*, in which i^3 has undergone extreme reduction, a probable derivative of group B (above).

THE *Protemnodon anak* GROUP*Protemnodon anak* Owen

Protemnodon anak OWEN, 1874, Phil. Trans. Roy. Soc. London, vol. 164, p. 275.

TYPE: A left mandibular ramus from Darling Downs, collected by Henry Hughes; figured in Owen, 1874 (pl. 25, figs. 1, 2). It was then in the Natural History Museum of Worcester, England. The identification of this mandible of *Macropus anak* had been recorded by Owen much earlier as a *nomen nudum* (1858, Quart. Jour. [and Proc.] Geol. Soc. London, vol. 15, pl. 185).

The crowns of m_1 , m_2 , and m_3 show very considerable but progressively less wear. That of m_4 shows little wear, and the crown of p_4 shows wear only of the topmost posterior part of the blade. As stated by Lydekker (1887, p. 214), "no talon exists behind m_4 ." Subject to confirmation it is suggested that M-1895 (Lydekker, p. 217), "presented by Sir R. Owen," is either the true type or a cast of the same. The history of its transfer from Worcester to the British Museum is probably a matter of record.

The association of other large fossil mandibles in Owen's monograph with the type of *P. anak* may well be correct but, as pointed out by Lydekker, Owen's attempt to harmonize certain maxillary tooththrows with the type was less fortunate. Lydekker suggested that not only *P. og* but several specimens referred by Owen to *Sthenurus* were instead equal to *P. anak*.

I will not now discuss the identities of those fossils that Owen referred to *anak*, and others that he identified as members of the genus *Sthenurus* (Lydekker, 1887, pp. 214-218), beyond remarking that certain of his other mandibles (pl. 25, figs. 3, 5, 6, 8, 9, 10, 14), which possess long diastemata and weak symphyses, as in *agilis*, must be accepted as *Protemnodon* (probably *anak*), and that the skull portion comprising the maxillary and premaxillary (pl. 27, fig. 1) may well be *Protemnodon (mimas)*. On the other hand, as indicated by Lydekker, the mandibular cheek teeth (Owen, 1874, pl. 24, fig. 4, etc.), in which the large secant p^4 is essentially similar to that of *agilis*, probably belong to *Protemnodon* and not to *Sthenurus* as suggested by

Owen. The form of p^4 in *Sthenurus* is roughly oval and double crested.

The validity of the names *P. og* Owen and *P. minor* Owen (Lydekker, 1887, p. 218) will not be examined at this time.

THE *Protemnodon bicolor-agilis* GROUP

This group is characterized by its large premolars and by having the groove of i^3 much closer to the front than to the back of the tooth. There are large posterior palatal openings. The opening for the mandibular nerve is extremely large (in old specimens, 8 mm.). The subequality in length of m^3 and m^4 (9.9:10.2 in *agilis*) may serve to keep the present forms in a group distinct from the *anak* group (same lengths from Owen's plate, 15.8:17.0 mm.).

Protemnodon bicolor (Desmarest)

Of the several living species currently placed in *Protemnodon* (= *Wallabia*), *bicolor* (= *ualabatus*) can be accepted as the recent generic prototype, not only because it is the designated type of *Wallabia* but because its lower premolar structure is in close accordance with that of the fossil *Protemnodon anak*. The upper premolar is more complex than the lower, having a pronounced postero-internal cingulum cusp, which descends almost to the level of the blade. The cingulum is well developed anteriorly with several minute cuspules. In the milk dentition a repetition of the foregoing is found in the structures of p_3^3 and dp_1^4 . The constant similarity of p_3^3 to p_4^4 and of dp_1^4 to m^1 is a striking phenomenon throughout the macropods.

Compared with *agilis*, *bicolor* is constantly smaller, the frontal portion of the skull is less arched, the anteorbital canal is shorter, a large hiatus exists between the mastoid and the squamosal root of the zygoma (somewhat as in *Petrogale*), the posterior palatal foramina are divergent anteriorly, and p^4 is less compressed anteriorly. The pelage of *bicolor* contains much black, even in the pale form *ingrami*, and is never clear sandy brown as in *agilis*. The tail is blackish in the southern forms.

The range of *bicolor* includes a relatively narrow strip of eastern Australia adjoining the coast, from the northern tip of the Cape

York Peninsula to New South Wales and Victoria. This range overlaps that of the nearest related species *agilis* in many parts of Queensland.

***Protemnodon bicolor bicolor* (Desmarest)**

Kangurus bicolor DESMAREST, 1804, Nouveau dictionnaire d'histoire naturelle, 1st ed., vol. 12, p. 357.

Kangurus ualabatus LESSON AND GARNOT, 1827, Voyage autour du monde... sur... La Coquille, Zoologie, vol. 1, p. 161, pl. 7 (1826).

TYPES: Not seen; probably non-existent but should be in Paris.

Desmarest's (1804) original description of *bicolor* reads: "...commoner than '*giganteus = kanguru*' in the interior of New South Wales. Its form absolutely as in the giant kangaroo except that its muzzle is less elongate and its ears shorter; it is smaller; the body hairs are gray-brown, tipped with fawn, those around the ears clear red, those of the four feet blackish; tail brown tipped with a few fawn hairs. The underparts of the body lighter than the upper..." In a later article (1817, p. 44) Desmarest was inclined (mistakenly) to synonymize *bicolor* with the Aru Island wallaby, *Thylogale brunii*.

The discussion (although not the plate) of *ualabatus*, "very common in the Cumberland district of New South Wales," by Lesson and Garnot agrees well with the present concept of *ualabatus*, and *bicolor* is shown in synonymy. "The ears are oval, pointed, bare within, ... black at the tips and clear red at the base..." No description of the skull was given. Their colored plate, on the contrary, lacking the rufous patches normally present at the bases of the ears, more nearly resembles *Macropus kanguru* or *robustus*.

Jones (1923-1925, p. 247) seems to have been the first to point out the synonymy of *ualabatus* with *bicolor*.

The American Museum series of true *bicolor* is very defective: two faded skins from the Verreaux collection; one skin from Glen Ferneigh, New South Wales (Raven); one skin with skull and one skin only from Ebor, New South Wales (Raven); one juvenal skin and skull and one skin only, both without localities, from Ellis Joseph (dealer); one skull only without locality from the New York

Zoological Society. I have also examined at the United States National Museum a series of nine specimens collected in various places: Gloucester, Wandandian, and Milton in New South Wales, and three collected by Dr. D. H. Johnson 50 miles northwest of Sydney.

Compared with the skins of northern races of *bicolor*, these from New South Wales are quite dark reddish gray, with the underparts russet and with russet around the bases of the ears. The pelage is long and lax. This wallaby is known locally as the "swamper" (D. H. Johnson).

From the same valuable series in the United States National Museum it has been possible to obtain notes of the structure and measurements of the unworn (and worn) teeth of the typical race.

The first incisor is 4.7 to 4.8 mm. in width, abruptly tapered at the tip of the newly erupted tooth to 4.3.

The labial face of i^2 , usually flat, may occasionally be slightly concave (U.S.N.M. Nos. 221173, 221188, 221193). The tooth becomes chipped at an early age. The length of the external lobe is 5.2 mm. in the juvenal females, Nos. 221188 and 277377. In old specimens, No. 221193, female, from Wandandian, and No. 221190, female, from Milton, wear has reduced this dimension to 4.0 and 3.9 mm.

The large i^3 has the crown length from 8.5 to 8.8, with the external lobe 5.3 to 5.6. In this tooth also wear greatly shortens the crown, to 6.5 and 6.9, with the external lobes ± 4.0 mm.

The third premolar is a large, relatively thick tooth, with its anterior portion but little compressed. The length varies from 6.7 to 7.3, the anterior width from 3.5 to 4.0 (wearing to 2.7), the posterior width from 3.9 to 4.7. The postero-internal cusp is united (not divided by a groove) to the main secant edge of the tooth.

The deciduous premolar, considerably shorter than p^3 , has the length 6.1 to 6.4 (wearing to 6.0), the anterior width 5.1 to 5.7, and the posterior width 5.5 to 6.2.

The lengths of m^{1-4} are: 6.3 to 6.7, 7.3 to 8.0, 7.8 to 8.8, and 8.0 to 9.0 mm. The widths of the anterior and posterior lophs of m^4 are 7.0 to 7.5 and 5.8 to 6.2.

The permanent premolar, erupted after m^2 , has a length of 9.3 to 10.3, an anterior width of 3.9 to 4.3 (wearing to 3.6), a posterior width of 5.0 to 5.2 (wearing to 4.6).

***Protemnodon bicolor wellsbyi* (Longman)**

Macropus wellsbyi LONGMAN, 1922, Mem. Queensland Mus., vol. 7, p. 298.

TYPE: At Brisbane (not seen by me), a juvenal with p^3 and dp^4 still present. The type locality, Stradbroke Island, is less than 160 miles south of that of the race *mastersii* of the Burnett River.

Protemnodon wellsbyi, which has p^4 large, "of the massive *ualabatus* type" (approximately 9 mm. in length in *ualabatus*) is undoubtedly a member of the *bicolor* group. Finlayson (1927, p. 363) alluded to "the remarkable *M. wellsbyi*." Longman continued, "it is quite distinct from *M. ualabatus apicalis*." He did not compare it with *mastersii*. The pelt is reported to be strongly reddish.

***Protemnodon bicolor mastersii* (Krefft)**

Halmaturus mastersii KREFFT, 1871, The mammals of Australia, text to Great Kangaroo, p. 3.

TYPE: Of *mastersii* possibly at Brisbane, specimen from Burnett River, 100 miles north of Brisbane, southern Queensland.

A single specimen, M.C.Z. No. 29420, adult female, from Dorman Gulley, 2500 feet, in the Bunya Mountains, collected by W. E. Schevill in February, 1932, is apparently referable to *mastersii*.

Krefft's description, under *ualabatus*, is fragmentary. He writes: "An allied species to which the name *Halmaturus mastersii* has been given, occurs in some of the Queensland districts at the Burnett and other rivers. This variety is lighter in color . . ." In a footnote he adds, "Mr. Masters has lately collected a fine series of these wallabies on the Burnett River . . . though skull and teeth differ little, except in the smaller third upper incisor [my italics] from those of the black wallaby, the reduced size of the fore limbs proves it a distinct species. The color is iron gray, with rusty hairs interspersed, a rusty colored belly, and a black short bridle mark behind the shoulder."

While not employing the name *mastersii*, Finlayson (1931) believed that the *ualabatus* he encountered in the rather dry Dawson Valley was equal to *mastersii*. The Dawson River, although only a little more than 100 miles from the Burnett, lies to the west of a considerable range of hills (the Bunya). Finlayson was not convinced that *mastersii* and *ingrami* were distinct, and he recorded his material under the latter name. Keeping in mind the climatic differences between the two localities, it may be that the dry-country *ingrami* does extend, as *agilis* does, along the dry inside of the coastal ranges to the Dawson, while *mastersii* inhabits the more humid areas east of the ranges.

In the Museum of Comparative Zoölogy specimen, i^2 (worn) has a slight vertical groove on the labial face and its crown measures 3.4 mm.; i^3 , 6.0 (the anterior lobe, 3.5); m^1 (shortened by wear), 5.9 by 6.9; m^4 , 8.9 by 6.9 (anterior loph) and 5.9 (posterior loph). The worn p^4 , length 8.8; anterior width, 4.1; posterior width, 4.2.

***Protemnodon bicolor ingrami* (Thomas)**

Macropus ualabatus ingrami THOMAS, 1909, Proc. Zool. Soc. London, for 1908, p. 792, pl. 42.

TYPE: B.M. No. 8.8.8.25, subadult female (not seen by me), from Inkerman, Burdekin River, southeast of Townsville, north Queensland. "Most nearly related to *apicalis* but smaller and much grayer . . . length of p^4 , 8.3 . . ."

This is the palest known race of *bicolor*. Its northern distributional limit would seem to be just south of the latitude of Cairns, as Raven collected three fine examples, two at Ravenshoe and one at Kaban. The color of *apicalis* from Cape Grafton, just east of Cairns, is much more saturate.

The range of *ingrami* probably extends, inland from the coast, between Inkerman and Atherton Tableland.

This race is quite well represented in American collections: from the neighborhood of Atherton, Hoy took three for the United States National Museum; H. C. Raven took his three for the American Museum of Natural History; Darlington took one at Millaa Millaa for the Museum of Compara-

tive Zoölogy. I refer three dark, long-haired specimens of *bicolor* taken by Miss Neuhäuser at Somerset and Lake Barrine to *apicalis*. Shevill also took one at Lake Barrine.

The pelage of our specimens of undoubted *ingrami* are pale reddish gray, much lighter than the colors of either true *bicolor* or the race from northern Cape York. The color about the base of the ears is yellow tawny. In two of the three male specimens of this gray brown wallaby taken by Raven at Atherton Tableland, the crown length of i^1 is 4.0, 4.0; i^2 , 3.0, 2.6; i^3 (worn), 5.1, 5.5. The second incisor is reduced and grooved on the labial face just as in specimens of *apicalis*. Its crown length is somewhat less than in true *bicolor* (3.2:3.6-4.0).

In a pouch specimen, U.S.N.M. No. 238334, female, the width of i^1 is 3.8 mm. This is probably due to slight tapering at the cutting edge of the unworn tooth because in an adult female (No. 238333) the width of i^1 equals 4.0 mm. In an aged specimen wear has reduced the width to 3.3. The lateral side is much thicker than the mesial side, as in *Petrogale*.

The second incisor (in a pouch female) has the outer crown length 4.9 mm. (the inner lamina, 3.8). This becomes reduced after wear to 4.5, 2.9, 2.7.

The crown length of the third incisor (unworn) varies from 6.0 to 8.0, the external lamina ± 4.6 . Worn teeth measure as little as 4.4 and 3.6 mm.

The deciduous premolar can be measured only in the pouch young: length, 6.2; anterior width, 4.5; posterior width, 4.9. The largest m^1 (M.C.Z. No. 29416, male) is 7.5 in length, with posterior width 6.4. In the much worn female, M.C.Z. No. 29284, the length is reduced to 6.2 and in two old specimens in the United States National Museum to 6.3 and 6.5 mm.

The lengths of m^{2-4} are 6.9 to 7.3, 7.5 to 8.4, and 7.9 to 8.3. The anterior and posterior widths of m^4 are 6.4 to 7.1 and 5.8 to 6.4 mm.

The fourth premolar has: length, 8.0 to 8.8; anterior width, 3.0 to 3.7; posterior width, 3.9 to 4.2 mm. Malocclusion in p_4^{4-4} has produced abnormal wear in U.S.N.M. Nos. 238332 and 238333.

Protemnodon bicolor apicalis (Gunther)

Halmaturus apicalis GUNTHER, 1874, Proc. Zool. Soc. London, p. 653.

TYPE: Probably in British Museum, from Cape Grafton, east of Cairns, northern Queensland. A skin only.

This race is the northernmost of the named forms of *bicolor* (= *ualabatus*). It had the tip of the tail white, a condition not present in our specimens.

A specimen, U.S.N.M. No. 19559, from Bellenden Ker Range, a few miles southeast of Cape Grafton, is a virtual topotype.

The American Museum possesses two specimens (one without skull) from the northern tip of Cape York, Queensland, in one of which i^2 is very small and bears a distinct external longitudinal groove. Two others from Lake Barrine seem to match these exactly.

The skins are dull grayish brown, the tail tipped with blackish; the ears lack the red or yellowish brown circumaural color patch which normally characterizes *bicolor* and which is distinctly shown in Gunther's plate of *apicalis*.

The distribution of this relatively dark race seems to be mainly coastal, east of the divide. It appears to extend from the tip of the Cape York Peninsula southeast at least to the Bellenden Ker Range. In the neighborhood of Cairns it reaches inland as far as Lake Barrine, where both Neuhäuser and Schevill took specimens. On the open parts of Atherton and along the western side of the divide its place is occupied by the pallid, short-haired race, *ingrami*.

The youngest specimen I have seen is A.M.N.H. No. 107385, juvenal male, from Lake Barrine, in which p^3 is 7.0 in length by 4.3 (posterior width) and dp^4 measures 6.1 by 5.8 (posterior loph). An older specimen is M.C.Z. No. 29416, young male (skull only), from Lake Barrine. In it m^1 is 7.5 mm. in length by 6.4 in width (posterior loph). In quite old specimens the length is reduced by wear to 6.3 to 6.5; the width (posterior loph) varies from 5.8 to 6.8.

The fourth molar is 9.0 mm. long by 7.7 (anterior loph) in the Lake Barrine specimen, A.M.N.H. No. 107386, male; 10.5 by 8.6 in

the Somerset specimen, A.M.N.H. No. 108902, female.

The fourth premolar, on the contrary, is shorter in the Somerset animal (8.5) than in the Lake Barrine animal (9.5). The posterior width is 4.9 to 5.0 mm.

In all the old specimens the incisors are much worn, and the vertical grooving of i^2 is much in evidence.

Protemnodon agilis (Gould)

Although Thomas (1888) placed *agilis* in a position remote from *bicolor* (= *ualabatus*) on the basis of his color key (p. 12), he brought them close together in his key to cranial characters (pp. 13-14). In my opinion *agilis* does belong fairly close to *bicolor*. In it p_4 are proportionately larger than in *bicolor*, an extreme condition seen in no other of the recent species currently assigned to *Protemnodon* (= *Wallabia*). Structurally, too, the p_4 of *agilis* are very like those of *bicolor*. *P. agilis* is readily distinguished from *bicolor*, however, by its larger size, by the angled (instead of rounded) outline of the posterior lobe of unworn i^3 , and by the much narrowed posterior ends of the anterior palatal foramina. Compared with *bicolor*, the proportion of the length of crown of p_4 to the length of crown of m^1 is $\pm 10.0: \pm 7.4$ mm. The crown lengths of p^3 and of the molariform dp^4 are, respectively, ± 7.0 and ± 7.1 mm.

Schwarz, who briefly reviewed the wallabies allied to *agilis* (1910b), recognized four races, one in New Guinea and three in northern Australia. Iredale and Troughton (1934) admit a fifth race, *nigrescens* Lonnberg, from near Broome, north Western Australia.

Protemnodon agilis agilis (Gould)

Halmaturus agilis GOULD, 1842, Proc. Zool. Soc. London, for 1841, p. 81.

Macropus agilis aurescens SCHWARZ, 1910, Ann. Mag. Nat. Hist., ser. 8, vol. 5, p. 166.

Types: Of *agilis*, B.M. No. 44.2.15.2, male, from Port Essington, Northern Territory (Thomas, 1922, p. 128 and footnote). Of *aurescens*, Fitzroy River. The United States National Museum has nine specimens taken by Hoy 100 miles south of Port Darwin.

In a male and a female with slightly worn incisors from Brooklyn Station, Mount Car-

bine (the dry side of the mountains), northeast of Cairns, collected by Gabriele Neuhäuser, the lengths of the incisive teeth measure: i^1 , 5.1, 4.8; i^2 , 4.5, 4.1; i^3 , 8.2, 7.0. The notch in i^2 is posterior, in i^3 slightly before the center of the labial face. Reference of these two specimens to typical *agilis* is made partly on the basis of their pale, sandy coloration. *P. a. aurescens* seems merely to be *agilis* in fresh pelage. Finlayson (1931) records *agilis* as far south as the Dawson Valley.

The unworn incisors of *agilis agilis* can be measured in juvenal male, A.M.N.H. No. 65039, and juvenal male, M.C.Z. No. 29288. The width of i^1 , 4.6 to 4.8; i^2 (slightly chipped), 4.9 to 5.2 (internal lobe, 5.3 to 5.9); i^3 , 8.4 to 8.8 (external lobe, 4.4 to 4.6).

The third premolar has the internal cingulum well developed but the postero-internal cusp much reduced. A trace of an external cingulum bearing two cusps appears at the middle of the outer face of the tooth. The length is 6.4 to 7.6; the anterior width, 3.5 to 4.1; the posterior width, 4.0 to 4.7 mm. The deciduous premolar (7.0 to 7.2) is only slightly shorter than p^3 .

The fourth premolar (in Coen material) is ± 10.0 mm. in length (but in one specimen only, 8.6); its anterior width, 4.2 to 4.5; its posterior width, 4.9 to 6.3 mm. The corresponding p_4 , with its two massive roots, is extraordinarily like p_4 of the type of *anak*. Its anterior point is slightly less elevated and is set off by only a trace of a lateral valley.

Protemnodon agilis nigrescens (Lonnberg)

Macropus agilis nigrescens LONNBERG, 1913, K. Svenska Vetensk. Akad. Handl., vol. 52, art. 1, p. 8.

TYPE: Probably at Stockholm (not seen), from near Broome, north Western Australia. A series of between 20 and 30 animals has been examined; taken by Hoy for the United States National Museum in 1920 near Derby.

This race seems to be consistently very slightly darkened by the addition of a few blackish hairs to the prevailing sandy pelage of typical *agilis*. It is the most westerly of the races of the species.

Unworn incisors were not found in this series: i^1 , 4.1 to 4.6; i^2 (much worn), 3.3 to

4.5; i^3 , 6.8 to 7.4, with external lobe 3.0 to 3.3 mm. The third premolar in juvenals: length, 7.0 to 7.2; anterior width, 3.0 to 3.4; posterior width, 3.9 to 4.3. The largest p^4 measured 9.2 mm. in length.

Protemnodon agilis jardinei (De Vis)

Halmaturus jardinei DE VIS, 1884, Proc. Roy. Soc. Queensland, vol. 1, p. 109.

TYPE: At Brisbane; not seen by me. Discussing the type, Longman (1922, p. 299) mentioned "the large type specimen of *Macropus jardinei*, now somewhat faded."

De Vis described this form, which came from open forest within 30 miles of Somerset, extreme tip of Cape York, very fully. Noteworthy were "the feet, blackish above, towards the toes, and on the middle of the great toe . . ." The skull has never been described.

Schwarz (personal communication) has recently assured me that *jardinei* is unquestionably a form of *agilis*.

Protemnodon agilis papuanus

(Peters and Doria)

Macropus papuanus PETERS AND DORIA, 1875, Ann. Mus. Civ. Genova, vol. 3, p. 544.

Halmaturus crassipes RAMSAY, 1876, Proc. Linnean Soc. New South Wales, vol. 1, p. 162.

Dorcopsis aurantiacus ROTHSCHILD, 1898, Novitates Zool., vol. 5, p. 513.

TYPES: Of *papuanus*, Genoa No. C.E. 1580, mounted skin, with skull No. C.E. 1581, juvenal female with p^3 , dp^4 , and m^1 alone in place, collected by D'Albertis in 1875 on mainland near Yule Island, Papua. Of *crassipes*, probably at Sydney Museum, collected near Port Moresby. Of *aurantiacus*, skin without skull, from New Guinea, subadult female, at Tring Museum. In addition to the material from New Guinea listed by me previously (Tate and Archbold, 1937, pp. 410-411), the American Museum now has the following: Tarara, Wassi Kussa, one; Gaima, lower Fly River, four; Lake Daviumbu, middle Fly River, 15; Kemp Welch River (east of Port Moresby), 12. There is a juvenal specimen, M.C.Z. No. 23126, female, from Merauké, received from P. T. L. Putnam, 1926, in which p^3 measures 7.5 by 4.5. U.S.N.M. No. 38578, juvenal, is from Port Moresby.

The incisive crowns of unworn specimens from the Port Moresby area measure: i^1 , 5.0; i^2 , 5.3; i^3 , 9.0. A deep groove is found near the back of i^2 and another two-fifths from the front of i^3 . South New Guinea specimens are essentially similar, but they seem slightly larger and the groove of i^2 is virtually at the back of the tooth.

I can see no reason for Schwarz' (1910) removal of *aurantiacus* from the synonymy of *papuanus* to that of *agilis agilis* of north Australia. The hind foot of the type measures ± 170 mm. s.u.; 190 c.u.

Extension of the range of *papuanus* to the Trobriand Islands is indicated by two juvenal specimens at Tring Museum, taken at Kiriwina Island by A. S. Meek in 1895. The ears of these are not white tipped, and the hip stripes are rather indistinct. In the skull of one, i^2 carries a well-defined labial notch, i^3 being but partly erupted; p^3 , dp^4 , and m^1 (partly). The crown length of i^1 is 5.0 mm.; of i^2 , 6.0.

THE *Protemnodon eugenii*-*parma* GROUP

Perhaps because Thomas (1888, p. 14) merged the three wallabies above mentioned with *Thylogale* (*sensu stricto*) under the heading "small wallabies" it became usual to treat *eugenii* and *parma* as *Thylogale*. Thomas' action may have been due in part to Krefft's lumping of all the foregoing under "padymelons or small kangaroos" (Krefft, 1871, p. 4 of Great Kangaroo). Iredale and Troughton (1934, pp. 46-47), following Thomas, also left these species in *Thylogale*. It remained for Jones (1924) and later for Raven and Gregory (1946, p. 11) to show that *eugenii*, etc., are merely small members of *Protemnodon*, as is shown by the character of i^3 (the groove of the labial surface not at the back of the tooth).

Although the third incisors are relatively small, p^4 remains equal in length to, or slightly longer than, m^1 .

I suspect that this present group is the ancestor from which *Thylogale* arose. Its small size and moderately large premolars are in agreement, although the special nature of the *Thylogale* incisors is but weakly foreshadowed.

Protemnodon eugenii (Desmarest)

This, the smallest-sized species in the

genus *Protemnodon*, is distributed in south Western Australia, South Australia, and islands off their coasts. The skull has subparallel zygomata, giving the posterior portion a subrectangular appearance, and the rostrum is moderately to considerably compressed. It is related to *parma* of New South Wales.

I have recognized four races: a western and an eastern mainland race, and a western and an eastern island race.

Probably, from a genetic viewpoint, the Western Australian *derbianus* gave rise independently to the strains occupying the various rather widely separated islands off the coasts. It is only possible to picture the Rottnest and Abrolhos strains as genetically identical if the strains on the mainland opposite each island, whence they came, were also genetically identical. So, too, with the Recherche Islands wallabies. Yet the name *binoë* is employed for the Rottnest as well as for the Abrolhos strain. And as one can only imagine the Recherche wallabies coming from the nearby mainland it appears wrong to call them after one of the eastern races (*eugenii*).

Protemnodon eugenii eugenii (Desmarest)

Kangurus eugenii DESMAREST, 1817, Nouveau dictionnaire d'histoire naturelle, nouv. ed., vol. 17, p. 38.

Thylogale flindersi JONES, 1924, Proc. Roy. Soc. South Australia, vol. 48, pp. 12-14.

TYPES: Of *eugenii*, not in existence, from Ile Eugene, Josephine Archipelago (=St. Peter's Island, Nuyt's Archipelago), western South Australia. Of *flindersi*, probably at Adelaide, from Flinders Island, Investigator Group. The proximity of Flinders Island to Nuyt's Archipelago (110 miles southeast of it) and the much greater distance from Nuyt's Archipelago of Kangaroo Island (300 miles southeast) make it more probable that the Flinders Island wallaby rather than the Kangaroo Island wallaby equals the original *eugenii*. This leaves for the broad-snouted race on Kangaroo Island the name *decre* Troughton.

Troughton believes that *eugenii* still exists on the Eyre Peninsula. If so it will be interesting to learn whether those survivors on the mainland are closer to *flindersi* or to *decre*.

I have seen no example of the narrow-

snouted *flindersi* in American collections. Naturally the above synonymy is provisional.

Protemnodon eugenii derbianus (Gray)

Halmaturus derbianus GRAY, 1837, Mag. Nat. Hist. (Charlesworth), vol. 1, p. 583.

Halmaturus dama GOULD, 1844, Proc. Zool. Soc. London, p. 32.

Macropus gracilis GOULD, 1844, Proc. Zool. Soc. London, p. 103.

TYPES: Of *derbianus*, B.M. specimen j of Thomas (1888) from Swan River (Waterhouse, 1846, p. 155, lists Swan River; Iredale and Troughton, 1934, give no exact locality). Of *dama*, B.M. specimen d of Thomas (1888) from Moore River (Gould, giving no locality on the mainland, wrote, "It is very numerous on the islands of the Houtmann's Abrolhos, and also inhabits Western Australia . . .," but Thomas must have had good reason for indicating Moore River. Of *gracilis*, B.M. specimen f of Thomas (1888) from Walyema Swamps, northeast of Northam.

Two of these three names were considered synonymous by Iredale and Troughton (1934), who placed *dama* in the synonymy of the island form *binoë*, disregarding Thomas' designation of Moore River. In any case, *derbianus* must be employed for the mainland race of Western Australia.

It seems possible that the animals found on the Recherche Group of islands, assigned by Iredale and Troughton (1934, p. 46) to the race *eugenii*, may be derived from the opposite mainland and should, therefore, be referred to *derbianus*.

I have seen no material from the mainland of Western Australia.

Protemnodon eugenii binoë (Gould)

Halmaturus binoë GOULD, 1842, Proc. Zool. Soc. London, p. 57.

Halmaturus houtmanni GOULD, 1844, Proc. Zool. Soc. London, p. 31.

Halmaturus emiliae WATERHOUSE, 1846, A natural history of the Mammalia, vol. 1, p. 157.

TYPES: Of *binoë*, probably B.M. specimens n and o of Thomas (1888) from Wallaby Island, erroneously given by Gould as Port Essington but corrected (Gray, 1843, "List of the specimens of Mammalia in . . . the British Museum, p. 90) to Wallaby Island; "lectotype," B.M. No. 44.2.15.10 (specimen

l), indicated by Thomas (1922, p. 128). Of *houtmanni*, B.M. specimens l and m (cotypes) of Thomas (1888) from Wallaby Island, Houtmann's Abrolhos.

A good series of *binoë* from West Wallaby Island to be seen at the Museum of Comparative Zoölogy comprises eight specimens of various ages (but no pouch young). The animals (and their skulls) are distinctly smaller than the Kangaroo Island *deces*. The rostrum, although slightly more compressed in *binoë* than in *deces*, is not nearly so much narrowed as in *flindersi* (as figured by Jones).

The length of the lacrimal canal is ± 7 mm. Secondary posterior palatal openings are present in all specimens. The paroccipital process is very heavy, its thickness as much as 5 mm. The mandibular nerve opening is large, 5 mm., and deeply placed. Uniform abrasion occurs in the three upper incisors.

The width of i^1 is 3.5 to 3.6 mm.; that of i^2 in young specimens, 3.0, wearing in old animals to 2.5–2.7. The third incisor has the crown length 4.6 to 4.8 mm. and that of the outer lamina 3.2 to 3.3. Moderate wear reduces these dimensions to 4.5 and 3.0. In an extremely old animal (M.C.Z. No. 28072) the crown length of i^3 is reduced to 3.9.

The deciduous dentition is still present in five specimens, p^4 in three. The length of p^3 varies from 4.4 to 4.7, its width (quite variable), anteriorly from 2.8 to 3.2, posteriorly from 2.4 to 3.0. The deciduous tooth, subequal in length, varies from 4.5 to 4.8, its posterior loph from 3.5 to 4.1.

The first molar: length, 4.8 to 5.2, sometimes wearing to 4.6; width of posterior loph, 4.0 to 4.5 mm.

The fourth molar: length, 6.2 to 6.6 (shorter in the one female, 4.6); anterior loph, 4.9 to 5.0; posterior loph, 4.2 to 4.7 (in the female, 4.0).

The fourth premolar, also somewhat larger in males than females: length, 4.6 to 5.0; anterior width, 2.1 to 2.2; posterior width, 2.8 to 3.0. It is to be noted that the anterior width of p^4 is considerably less than the anterior width of p^3 .

Protemnodon eugenii decres (Troughton)

Thylogale eugenii decres TROUGHTON, 1941, Furred animals of Australia, p. 194.

TYPE: Presumed to be at Sydney, from Kangaroo Island.

A series at the United States National Museum, taken by C. M. Hoy on Kangaroo Island, has been studied. These animals are relatively large, and their skulls do not exhibit the extreme of rostral compression that one sees in the race *binoë* (= *houtmanni*) of Houtmann's Abrolhos of Western Australia. The nasals have broad bases somewhat as in *Lagorchestes*. In these respects the Kangaroo Island wallaby appears to be somewhat transitional between the western *binoë* and the species *parma* of Victoria and New South Wales.

Jones (1923–1925, p. 240) figured the rhinarium, feet, and skull (figs. 167–170) of this race when comparing it with his *flindersi*.

The proximity of Flinders Island to, and remoteness of Kangaroo Island from, Nuyt's Archipelago suggest that *flindersi* was more probably equal to the original *eugenii* than was the form on Kangaroo Island, *deces*.

The race *deces* has the following dental characters: the width of i^1 in juvenal males is ± 4.0 , wearing to 3.8; in juvenal females, 3.7 to 3.8 mm. Unworn i^2 has the crown length 3.6 to 3.8, but this may be reduced by wear to 2.8 to 3.0. The crown length of unworn i^3 varies from 5.6 to 5.7, with the external lamina 3.6 to 3.7. Wear reduces these amounts to 4.4 and 2.9.

The third premolar, constant in length, varies in width. Length, 4.8 to 4.9; anterior width, 2.6 to 2.7; posterior width, 3.0 to 3.4. As in *binoë*, dp^4 is almost equal in length to p^3 , 4.7 to 5.0; the anterior loph, 3.8 to 4.0; the posterior loph, 4.0 to 4.2.

The first molar: length, 5.3 to 5.6 by (posterior loph) 4.5 to 4.9; m^2 , 6.1 to 6.4 by (posterior loph) 4.8 to 5.6; m^3 , 7.0 to 7.2 by (anterior) 5.7 to 6.0, (posterior) 5.1 to 5.6; m^4 (present in only one specimen), 7.3 by (anterior) 5.5, (posterior) 5.1.

The fourth premolar (cut after m^3): length, 5.1 to 5.2 by (anterior) 2.3 to 2.7, (posterior) 3.0 to 3.3.

The over-all greater size of the teeth in *deces* compared with *binoë* is obvious.

A single specimen in the American Museum, No. 881, collected by A. H. Helme in 1888 (no locality) bears a strong general re-

semblance to *decreas* but may be a mainland animal.

Protemnodon bedfordi (Thomas)

Macropus bedfordi THOMAS, 1900, Proc. Zool. Soc. London, p. 112.

TYPE: B.M. No. 0.2.19.1, juvenal female, from "north Australia."

The very distinct groove on the outer face of i^3 makes it reasonably certain that *bedfordi* is a *Protemnodon*. The relationships are likely to be with the *eugenii-parma* section of the genus.

The dental dimensions are: p^3 , 4.1 by 2.6 (maximum); dp^4 , 4.8 by 4.7; m^1 , 5.8 by 4.8; m^2 , 6.1 by 4.9; m^3 , 6.5 by 4.8; (m^4 not erupted).

Thomas compared this mainly fawn-colored wallaby with *eugenii*, mentioning a faint nuchal stripe. The small size of the premolar was mentioned.

The maximum width of any of the molari-form teeth in the type was 4.9 mm. This suggests the relationship can be only with the small *eugenii* section and not with the *parryi* section or with *dorsalis*, the smallest of the *rufogrisea* section. The width of the molars in *parma* reaches 5.5, which leaves only those small *Protemnodon* of the *eugenii* group as possible relatives.

Protemnodon parma (Waterhouse)

Macropus (Halmaturus) parma WATERHOUSE, 1846, A natural history of the Mammalia, vol. 1, p. 149.

TYPE: B.M. No. 41.1116, old male, marked "New South Wales." I have a photograph of the skull.

The type of *parma* is an extremely old male. The fourth premolars have disappeared, and their alveoli are almost closed. The present dorsal color is dark brown with some paler guard hairs, becoming reddish on the shoulders. The underparts have gray-based buffy hairs. There is a trace of a dark dorsal line, and the hands and feet are brownish buff. The present length of head and body is ± 600 mm.; tail, 530; hind foot (c.u.), 150; (s.u.), 130. In the skull, the length of the nasals is 43, width, 17.7; height of muzzle behind incisors, 19.8. The anterior palatal foramina are sharply narrowed behind by

encroachment of the side walls. There are well-marked posterior palatal openings.

The American Museum of Natural History collection contains the faded skin and skull of a specimen of a wallaby, A.M.N.H. No. 882, from the Verreaux collection, without locality, which agrees closely with the description of *parma*.

Besides the Verreaux specimen we have a pouch young, A.M.N.H. No. 66164, skull only, taken by H. C. Raven at Point Lookout Gorge, near Ebor and Moseley's Ranch. At the Museum of Comparative Zoölogy are two adult specimens from Dorriggo, Cascade, New South Wales; and in the United States National Museum is an adult from Sassafras, Mawarra, New South Wales.

This extraordinarily rare wallaby, which Troughton (1941, p. 195) regards as virtually extinct, is apparently a relative of *eugenii* to the west. I think it likely that *bedfordi* was a member of this same group.

The groove in i^3 lies just behind the middle of the blade, and i^3 itself is relatively small, as is the case of *greyi* of South Australia, but p^3 and p^4 are not markedly cleft, as in *greyi*.

The dimensions for the unworn anterior teeth are taken from A.M.N.H. No. 66164. The width of its first incisor is 4.0 mm.; in our old specimen, A.M.N.H. No. 882, 4.1; in M.C.Z. Nos. 29301, 29302, 3.8, 4.1; and in U.S.N.M. No. 38551/19557, 3.8. The combined i^{1-1} together form a mesial, beak-like structure.

The second incisor (juvenal) has the outer and inner lobes subequal, each 3.8 mm. In all other specimens the tooth is chipped and worn, the labial face measuring 3.2, 2.5, 2.5, 3.5.

The crown length of the third incisor (also juvenal) is 5.8 mm., with the anterior (external) lobe 3.3. Wear has reduced this in old specimens to 5.0 and 3.0. In the old female, M.C.Z. No. 29301, the crown length is only 4.4.

A minute, bead-like tooth rooted in the maxilla in the position of the left canine can be seen in the juvenal specimen.

The third premolar and dp^4 have been replaced in all but the pouch specimen. In the last, p^3 has a well-developed cingulum raised anteriorly and medially to form small cusps. The postero-internal cusp is large and almost

separate, but connected to the main secator cusp by a narrow ridge. The tooth is nearly as wide in front as behind. Length, 4.8 mm.; anterior width, 2.4; posterior width, 2.8. The length of dp^4 , 5.0, slightly exceeds that of p^3 . The width of its anterior loph is 3.7; posterior loph, 3.9. It is considerably smaller than the newly erupted m^1 : length, 5.9; anterior loph, 4.3; posterior loph, 4.5. The dimensions of m^1 in the older animals from Dorriggo and Sassafras are: length, 5.7 to 6.4 (wearing to 5.2); width, posterior loph, 4.4 to 5.0. The remaining molars and p^4 are as follows:

and by the relatively complete palate . . . reduction of the fore limbs and manus . . . caudal crest . . . details of ornamentation . . . especially marked in the common possession of a system of loin bands [transverse across the dorsum; see Finlayson's pl. 17, fig. 2]. The eastern *parryi* is much more divergent. It agrees with *irma* and *greyi* in the small size of p^3 and p^4 and in the intensity of the facial markings. However, it has large posterior palatal openings, has much larger i^{3-5} , no crest on the tail, and it lacks the transverse dorsal bands. Perhaps *irma* and *greyi*

| | M.C.Z. No. 29301 | M.C.Z. No. 29302 | U.S.N.M. No. 38551/19557 |
|-----------------|---------------------|---------------------|-----------------------------|
| | OLD FEMALE | ADULT MALE | ? |
| m^2 | | | |
| Length | | | 6.4 |
| Posterior width | | | 4.8 |
| m^3 | | | |
| Length | | | 7.4 |
| Anterior width | | | 5.0 |
| Posterior width | | | 4.5 |
| m^4 | | | Visible |
| Length | 8.0 | 8.2 | |
| Anterior width | 6.1 | 5.8 | |
| Posterior width | 5.3 | 5.2 | |
| p^4 | | | |
| Length | 4.8 | 5.9 | 5.1 |
| Anterior width | 2.3 | 3.2 | 2.1 |
| Posterior width | 2.2 | 2.7 | 2.7 |

The foregoing suggests that in the male p^4 is substantially larger than in the female. It also shows that p^4 is erupted with m^3 and before m^4 , as in other *Protemnodon*.

THE *Protemnodon parryi-greyi-irma*
GROUP

Medium to large wallabies with p^4 reduced. Basic color of pelage gray. The relationship of *greyi* and *irma* is anticipated by Finlayson (1927), who wrote of *greyi*: "Within the limits of the subgenus *Wallabia* its relationships are undoubtedly closest to *M. irma* . . . evinced by the diminutiveness of the second and third incisors, retention of broad unconstricted interorbital region throughout life,

are conspecific and *parryi* is a related full species.

Protemnodon irma (Jourdan)
Protemnodon irma irma (Jourdan)

Halmaturus iri a JOURDAN, 1837, Compt. Rendus Acad. Sci., Paris, vol. 5, p. 523; 1837, Ann. Sci. Nat., Paris, ser. 2, vol. 8, p. 371.

Macropus (Halmaturus) manicatus GOULD, 1841, Proc. Zool. Soc. London, p. 127.

TYPES: I have not seen the types of either *irma* or *manicatus*. Thomas (1888, p. 41) listed the type of *manicatus* from Swan River. He wrote that the type of *irma*, also from Swan River, was not traceable. Jourdan's description of the skin is very detailed, but no mention is made of the skull.

The American Museum possesses a single young specimen, A.M.N.H. No. 891, male, without locality from the Verreaux collection. The skin is greatly faded, and the posterior palate and basis cranii are destroyed. However, the dentition as far as erupted is complete. In addition, there is a pair in a fine state of preservation in the United States National Museum (U.S.N.M. Nos. 155372, 155373), but unfortunately the skull matched with No. 155372 is that of *eugenii*. They are, respectively, from Katanning (1899) and Gracefield (1908), Western Australia.

The length of p^4 (in the type ?) was given by Waterhouse as $2\frac{1}{2}$ lines, or approximately 5.3 mm., a dimension that approximates the small size of the same tooth in *parryi* and diverges strongly from the large-toothed species *bicolor*. The extreme breadth of i^1 is not quite reached in *parryi*, although the position of the lateral groove in i^3 is the same (Waterhouse, 1846b, p. 122).

The coal black color of the hands and feet of the "black-gloved wallaby" contrasts amazingly with the sandy buff metacarpal and metatarsal areas. The body and proximal part of the tail are grizzled gray, except for a vague sandy shade on the side between thigh and shoulder. The ears and crown (the hairs of the crown reversed) are dark brown, the tips of the ears black, their posterior edges, interior and posterior auricular patches white. The penciled tail bears both dorsal and ventral crests. The dorsal crest is somewhat darker than the dorsal body color. The ventral crest is black. The male wallaby is considerably larger than the female.

In the skull the nasals are comparatively unwidened behind; their total width at the frontomaxillary suture (American Museum specimen), 15.4 mm.; (United States National Museum specimen), 18 mm. Total length of United States National Museum skull, 118 mm.; zygomatic width, 58.

The dental dimensions of the younger American Museum specimen are given first: width of i^1 , 4.8 mm., 4.8; width of labial face of i^2 , 3.2, 2.9 (worn); crown length of i^3 , 4.9, 4.5, of external lamina of i^3 , 3.5, 2.8 (both worn).

The size of p^3 and dp^4 (American Museum specimen only): p^3 , length 5.0 mm.; anterior width, 2.5; posterior width, 3.9; dp^4 , 6.0 (length), by 5.8 (greatest width). The milk

p^3 is short, very thick at the posterior, has the postero-internal cusp closely fused to the secant ridge, and virtually lacks the antero-internal cingulum.

The lengths of the molars m^{1-3} are: 6.6 and 6.4; 7.0 and 7.0; 7.4 and 7.5. The fourth molar and p^4 are present only in the United States National Museum specimen: m^4 , length, 7.5; anterior width, 5.4; posterior width, 5.3; p^4 , length, 6.2; anterior width, 2.8; posterior width, 4.1. The postero-internal cusp of p^4 , although greatly enlarged, is not confluent with the secant ridge. The cingulum appears to be obsolete as in p^3 . The main crest is divided in two by a shallow external groove one-third from the front of the tooth. The crown of p^4 , higher than long, is remarkably small.

The species was recorded from Moore's River (Jentink), Mount Barker, Southern Cross, and from Stockpool, Dwaladine, Way-aline, and Dale River (Thomas), Albany District (Alexander), near Geraldton east to near No. 3 rabbit-proof fence (Glauert).

Protemnodon irma greyi (Waterhouse)

Macropus (Halmaturus) greyi WATERHOUSE, 1846, A natural history of the Mammalia, vol. 1, p. 122.

COTYPES: Thomas (1888, p. 37) listed male and female cotypes from South Australia and figured the skull and incisor teeth (not seen by me). In 1922 (p. 128) he indicated specimen a, B.M. No. 43.1.4.42, male, as "lectotype." Finlayson (1927, pp. 366-377) has dealt with *greyi* intensively. It was also discussed by Jones (1923-1925, p. 244). Troughton has since (1932, p. 187) pointed out that it is nearing extinction.

This rare animal is apparently represented in American collections by a single specimen, U.S.N.M. No. 236782, an adult skull picked up near Port Lincoln by C. M. Hoy. The zygomatic spread is wide, the rostrum is narrow and compressed, the width across the base of the nasals is 16.8 mm. A long slender process from the maxilla almost separates the frontal from the lacrimal (possible anomaly).

All three incisors are much worn, their crown lengths being, i^1 , 3.5; i^2 , 2.4; i^3 , 4.2, with external lamina, of which only a trace is left, 2.8 mm.

The length of m^{1-3} and their greatest

widths are: m^1 , 5.3 by 4.5 (worn); m^2 , 5.5 by 5.1 (slightly worn); m^3 , 6.4 by 5.6; m^4 , 6.4 by (anterior) 5.4, (posterior) 4.4.

The fourth premolar is short, 4.9 mm., and newly erupted. Its anterior width is 2.6; posterior width, 3.0. It is divided by an external groove into subequal parts, the anterior smaller. The tooth is broadened by the internal cingulum which surrounds a basin. The postero-internal cusp is confluent with the secant ridge.

This wallaby occurred "between the Albert Sea and the Glenelg River" (Wagner, *in* Schreber, 1855, "Die Säugethiere," Suppl.); and in Victoria (Le Souef).

Protemnodon parryi (Bennett)

Macropus elegans LAMBERT, 1807, Trans. Linnæan Soc. London, vol. 8, p. 381 (and pl. 16). ? Not certainly determinable.

Macropus parryi BENNETT, 1835, Proc. Zool. Soc. London, p. 151; 1835, Trans. Zool. Soc. London, vol. 1, p. 295 (pl. 37).

TYPE: In British Museum (Thomas, 1888, p. 40), but not seen by me. The type locality is Stroud, near Port Stephens, New South Wales.

Lambert's account of *M. elegans*, supported by a figure which lacks any trace of the distinctive white facial mark of *parryi*, is not satisfactory. The principal characters given relate to its silver gray color, solitary habits, and proportions (tail, 26 inches; head and body, 36 inches; length of skull, $5\frac{1}{8}$ inches; length of ear, $3\frac{1}{8}$ inches; length of hind leg from claw to knee, 10 inches). No closer locality than "New South Wales" was given. On the other hand Bennett's description of *parryi* is clear and unmistakable. Waterhouse (1846b, pp. 115-116) discussed this same problem and reached the conclusion that *elegans* was probably equal to *parryi*. Although Thomas (1888, p. 33, footnote) considered *elegans* undeterminable, Iredale and Troughton (1934) revived it.

This is the "whiptail wallaby" or "pretty-face wallaby," which Troughton attempted to show was the true "Captain Cook's kangaroo," a contention that was more or less refuted by Raven (1939).

Material representing this species is ample: Raven collected a good series from the Mundubbera District, southern Queensland,

and there is one from Bunya Mountains in the Museum of Comparative Zoölogy. Hoy procured two at Atherton, Neuhausser two at Mount Carbine, northern Queensland, and Raven took still others at Ravenshoe, Kaban, and Evelyn. Raven also collected two at Glen Ferneigh, northern New South Wales. It has been recorded at Inkerman, Burdekin River, northern Queensland.

The frontal region of the skull of *parryi* is low and flat, sometimes depressed, and the rostrum, although considerably compressed, has the nasals rather short. The molar tooth-rows are strongly arched around the ample posterior palatal foramina, but anteriorly the palate is very narrow, only expanding slightly to accommodate the incisors. The anterior palatal foramina are often greatly narrowed in the back by encroachment of bone from the outer sides and occasionally (as in A.M.N.H. No. 65097) are shortened through the complete closing of their posterior parts by this means. The back of the palate is strongly downturned.

My description of the unworn incisors is based upon a pouch female (U.S.N.M. No. 238316) and a juvenal male (U.S.N.M. No. 238312), both from Atherton Tableland, and upon A.M.N.H. No. 65097 from Mundubbera District, southern Queensland.

The first upper incisor is evidently sharply tapered at the tip. In the pouch young its crown width is 4.2; in the slightly older specimens, 4.8, 4.9. This may diminish in adults to 4.5.

The second incisor has the external lamina equal to, or slightly longer than, the inner lamina. Chipping against i^1 takes place very early in life. The length of the outer lamina in the pouch female is 3.9; inner lamina, 3.4; in the male from Atherton, 4.4 and 4.1; in A.M.N.H. No. 65097 (chipped), 4.5 and 4.0.

The crown length of the third incisor reaches a maximum of about 8 mm., that of its external lamina, 4.2 to 4.4. In the pouch female these amounts were much shorter, 5.6 and 3.7 mm.

The third premolar, although small and short, has usually a strong cingulum on which are two stout cuspules. The postero-internal cusp is large. These teeth soon become greatly worn, even in juvenal specimens. The length of p^3 varies from 5.8 to 6.1 (rarely less); its

anterior width is 2.5 to 2.9; its posterior width, 3.3 to 4.2.

The lengths of dp^4 , m^1 , and m^4 are approximately 6.0 to 6.8; 6.7 to 7.6; 8.5 to 9.5 mm.

The permanent premolar is subequal in length to p^3 but is often more compressed. Its length varies from 5.1 to 6.1, its anterior width, 2.3 to 2.5; its posterior width, 2.9 to 3.8 mm. Also subject to rapid abrasion, it is erupted after m^3 . The cingulum is relatively weak. In an unworn state (A.M.N.H. No. 65062, from Glen Ferneigh, New South Wales) even the postero-internal cusp is seen to be obsolescent, although the tooth is markedly thickened at its position. Length, 5.7; anterior width, 2.2; posterior width, 2.7 mm.

THE *Protemnodon rufogrisea-dorsalis* GROUP

This includes two species of wallabies, one large and the other medium in size, in which i^3 is broad and deep, and p^4 is considerably reduced and almost always shorter than m^1 . The lower premolar, p_4 , is short, especially in *rufogrisea*.

Protemnodon rufogrisea is considerably larger than *P. dorsalis* and lacks the conspicuous blackish dorsal line. The posterior palatal foramina are frequently reduced in size by encroachment of filaments of bone. Those of *dorsalis* are widely open. The lacrimal is usually less expanded on the face in *rufogrisea* than in *dorsalis*. There are certain differences in the teeth.

Protemnodon rufogrisea (Desmarest)

This species differs from *bicolor* and *agilis* by the comparatively small size of its premolars. The rostrum is more slender and attenuate; the anteorbital canal is short (7.5 mm.; 8.5 in *bicolor*; ± 13.0 in *agilis*). The posterior part of the palate is extensively fenestrated, although the fenestrae are often crossed by slender webs of bone. In young specimens the external and internal lobes of i^3 are very much deeper than long. The diastema is very long (38 mm.; in *bicolor*, ± 25 mm.). *Protemnodon rufogrisea* is a much larger wallaby than the somewhat similar *dorsalis*.

According to the interpretation of Iredale and Troughton (1934, p. 49), the original

rufogrisea was discovered first on King Island, Bass Strait, between Australia and Tasmania. The mainland race, *banksiana*, was recorded eight years later. The Tasmanian race, *frutica* (= *bennetti*), was the last to be discovered. This is the only large wallaby occurring in Tasmania.

Reduction of p_4^1 in the Tasmanian race, although sufficiently pronounced if those teeth are compared with p_4^1 of either *agilis* or *bicolor*, has not advanced so far as it has in the mainland race. (We have no material from King Island.)

Protemnodon rufogrisea rufogrisea (Desmarest)

Kangurus rufogriseus DESMAREST, 1817, Nouveau dictionnaire d'histoire naturelle, nouv. ed., vol. 17, p. 36.

Kangurus ruficollis DESMAREST, 1817, *op. cit.*, nouv. ed., vol. 17, p. 37.

TYPES: Thomas (1888, p. 33) made no mention of the Desmarest types, and perhaps that of *rufogriseus* no longer existed when he wrote. But earlier Waterhouse (1846, p. 217) recorded "the [type ?] specimen [*ruficollis*] in the Museum at Paris."

Kangurus rufogriseus, which holds only page precedence (valueless under the Rules) over *ruficollis*, was explicitly stated by Desmarest to be from "New Holland." Yet Iredale and Troughton (1934, p. 49) corrected and restricted the locality to King Island. *Kangurus ruficollis* was originally described by Desmarest from King Island. Thomas (1888, p. 33) cited both names from Lesson (1827, p. 222), so probably Iredale and Troughton should be regarded as "first revisers."

Protemnodon rufogrisea banksiana (Quoy and Gaimard)

Kangurus banksianus QUOY AND GAIMARD, 1825, Ann. Sci. Nat., Paris, ser. 1, vol. 5, p. 481, note.

TYPE: Possibly in Paris, but probably lost. Type region: Blue Mountains, New South Wales.

Quoy and Gaimard wrote: "Oaring or Waring is a species . . . smaller than the ordinary [red] kangaroo; it inhabits only the mountains; its color is reddish brown marked with small black lines on the head. Sir J.

Banks owns the only skin of this animal, which has been taken to England. We propose for this species the name . . . *Kangurus banksianus* . . . "The identification of this vague description is obviously open to question, but we may again consider Iredale and Troughton (1934, p. 49) as "first revisers." And, since the description by Quoy and Gaimard was founded upon the work of Barallier, who referred to the Blue Mountains, that area may be regarded as type locality. The range of this mainland race is enormous, from Mount Gambier and the coast of Victoria north at least to southern Queensland, about 1000 miles.

MATERIAL EXAMINED: Two short series taken by Raven in northern New South Wales and in the Mundubbera District of southern Queensland; two specimens from Ebor, New South Wales, in the United States National Museum; one in the Museum of Comparative Zoölogy from the Bunya Mountains.

The biology of this mainland race of *rufogrisea* has been studied by several authors: Jones (1924, p. 245), Finlayson (1930, p. 47; 1931, p. 78), and Troughton (1941, p. 202).

This is the large, red-necked wallaby (as opposed to the small, red-necked wallaby, *Thylogale thetis*). Typically it is grizzled gray with an undertone of reddish or chestnut, which becomes almost clear chestnut on the neck and rump. The tail is gray. The underparts are white, with a suggestion of gray bases in the belly region.

Skull with moderately broad zygomata and rather elongate muzzle, the sides of which are slightly expanded in age. The facial expanse of the lacrimal is very slight (3.5 mm.) in comparison with that of the smaller *dorsalis* (5.5 mm.). The length of the anteorbital canal is ± 7.5 mm.; the anterior palatal foramina are well opened and rather elongate (8.0 mm.).

The form of the teeth is relatively aberrant for *Protemnodon*. The width of i^1 in juvenal, A.M.N.H. No. 65058, is 4.9 to 5.1 mm. This narrows in age to 4.2.

The second incisor is wedge shaped in section in youth, narrowly pointed anteriorly and reaching a thickness of 3.0 mm. posteriorly, with the external lamina (4.7 to 5.0) stronger and deeper than the internal one.

Wear reduces this tooth in section to a rectangular outline; the labial face is narrowed to 3.2 mm. (M.C.Z. No. 29417).

The third incisor is a large tooth not unlike that of *P. agilis*. The unworn crown length measures 7.5 to 9.2 mm.; that of the external lobe, 4.4 to 5.1 mm. Abrasion cuts these amounts to 6.5 to 7.0 and 3.5 to 4.0 mm.

The unworn p^3 is relatively thick, and the cingulum is well developed (in contrast to p^4). The cingulum bears an anterior and a median cusplule inward from which are two basins. The postero-internal cusp is only partly separated from the secant ridge. The outer face of the tooth is deeply scored at about its middle by two vertical grooves. The dimensions of p^3 are: length, ± 5.9 to 6.8; anterior width, 2.5 to 3.2; posterior width, 3.6 to 4.0 mm.

The deciduous fourth premolar usually exceeds p^3 in length: 6.0 to 6.7; the length of m^1 , 7.1 to 7.9; of m^4 , 9.6, with anterior and posterior lophs, 7.4 and 6.7.

The permanent premolar is rather short and so much compressed that the cingulum anteriorly is obsolete. Length, 6.1 to 6.8; anterior width, 2.2 to 2.5; posterior width, 3.5 to 4.0. In proportion to the size of this wallaby p^4 is exceptionally small and the corresponding lower sectorial teeth, p_{3-4} , have crown lengths of only 5.0 to 5.3 and ± 4.7 , respectively.

Protemnodon rufogrisea fruticosa (Ogilby)

Macropus (Halmaturus) fruticosa OGILBY, 1838, Ann. Mag. Nat. Hist., vol. 1, p. 219 (May 1, 1838).

Macropus bennetti WATERHOUSE, 1838, Proc. Zool. Soc. London, for 1837, p. 103 (May 25, 1838, *vide* Iredale and Troughton).

TYPES: Thomas (1888) stated them to be "not traceable."

The type localities of *fruticosa* and *bennetti* were, respectively, "Van Diemens Land" and "Nova Cambria Australi." Iredale and Troughton (1934, p. 49) consider this latter an error.

In the American Museum there are three Tasmanian specimens referable to this form: A.M.N.H. Nos. 892, juvenal male, skin and skull from the Verreaux collection; 6372, juvenal skull only; 69548, juvenal skull only. The United States National Museum has

three Tasmanian specimens. U.S.N.M. No. 124341 is especially instructive, as, besides having p^3 and dp^4 in position, p^4 has been exposed in its alveolus and is measurable. In A.M.N.H. No. 6372, p^4 is developed on one side, p^3 and dp^4 remaining on the other.

The incisors seem generally smaller than those of the mainland *banksiana*. The premolars, as stated earlier, are in some examples less reduced than in the mainland form. Length of p^3 in A.M.N.H. Nos. 892 and 6372 are 6.6 and 6.7 mm., but in U.S.N.M. No. 124341, only 5.8. Length of p^4 in A.M.N.H. Nos. 6372, 69548, U.S.N.M. Nos. 174601, 174747: 7.8, 7.2, 6.9, 7.0. Molars three and four are subequal in length, 9.3 mm. in U.S.N.M. No. 174747, 9.8 and 10.0 in No. 174601. The width of the anterior loph of m^4 is 7.8 to 8.0; of posterior loph, 6.5.

***Protemnodon dorsalis* (Gray)**

Halmaturus dorsalis GRAY, 1837, Mag. Nat. Hist. (Charlesworth), vol. 1, p. 583.

TYPE: "Not traceable" (Thomas, 1888, p. 38).

The type locality may be taken as restricted by Gould to the Namoi Hills (north-west of Tamworth), New South Wales (Iredale and Troughton, 1934, p. 50). The center of distribution appears to be northern New South Wales and southern Queensland. The species extends at least as far north as Rockhampton, central Queensland.

The American Museum collection contains a fine series of 15 specimens obtained by H. C. Raven at Lochaber Station, Mundubbera District, 150 miles northwest of Brisbane, southern Queensland. Raven also procured three skins only and nine skulls without skins. There is a specimen from Bunya Mountains in the Museum of Comparative Zoölogy.

Protemnodon dorsalis resembles *rufogrisea* but is much smaller and has a pronounced black dorsal stripe. No subspecies have been differentiated. Waterhouse (1846b, p. 154) gave the length of p^4 of an adult male as 3 lines (6.3 mm.), which is closely in accord with American Museum material. In females p^4 is usually smaller (5.8 mm.).

The crown length of i^1 varies from 4.5 (A.M.N.H. No. 65080, pouch female) to 5.0.

In greatly worn specimens this is reduced to 3.9 mm.

The external lamina of the wedge-shaped (in section) i^2 is slightly shorter than the internal lamina: 4.2 to 4.6 and 4.5 to 4.5. In A.M.N.H. No. 65075, male, wear has diminished this to 3.4 and in A.M.N.H. No. 65082 to 2.4 (root only).

The third incisor resembles that of *rufogrisea* closely, but the depth of the crown (enamel-bearing portion) is considerably less (5.5:7.0). The crown length varies from 7.5 to 8.5 mm., and the external lamina from 4.3 to 4.6. In the much-eroded A.M.N.H. No. 65082, female, the crown length is only 5.5 and the lamina 3.5.

The third premolar, compared with that of *rufogrisea*, is slightly more compressed, and the cingulum, which likewise bears two cusps with interior basins, is extended farther forward. Its length, from 5.5 to 5.7; anterior width, ± 2.8 ; posterior width, 3.5 to 3.8 (wearing to 3.2).

The deciduous tooth usually slightly exceeds p^3 in length: 5.6 to 5.9 mm.

The lengths of the true molars, m^1 and m^4 , are 6.0 to 7.0 and 8.7 to 9.9 mm.

The fourth premolar, freshly erupted in A.M.N.H. No. 65088, male, has, like *rufogrisea*, a strongly differentiated postero-internal cusp. The cingulum, weak and narrow to the middle of the tooth, is obsolete anteriorly. The length of p^4 is 6.3 to 7.1 mm.; anterior width, ± 2.2 ; posterior width, 3.9 to 4.2, wearing to 3.4 and 3.5. The tooth is usually considerably longer than m^1 .

SETONIX LESSON

Setonix LESSON, 1842, Nouveau tableau du règne animal, mammifères, p. 194.

TYPE: *Kangurus brachyurus*.

The skull of *Setonix* is short-faced and relatively massive, with heavy zygomatics. The incisive foramina are very short (3 mm.). Large posterior palatal openings are present. The outline of the incisors is \cap -shaped, not \wedge -shaped. The dominant incisor is i^1 ; i^2 , which has the rather shallow notch on the side as in *Protemnodon*, is a small tooth not much larger than i^1 . This is different from the condition present in *Thylogale billardieri* with which, on account of the shortness of the tail in both wallabies, *S. brachyurus* has

sometimes been confused. The fourth premolar, thick and massive and provided with a broad cingulum, is longer than m^1 . The mandible is short and heavy, its coronoid process broad, heavy, and non-falcate. The masseteric fossa is broadly open. The short tail of *Setonix* functions as a prop.

Jones (1923-1925, p. 261) places *Setonix* with *Dendrolagus* in his brachyodont section of the Macropodinae, as opposed to his hypsodont section (p. 219, nine genera, from *Lagostrophus* to *Dorcopsis*), but I have not been able to appreciate this distinction in practice.

Setonix appears to be derivative of *Protemnodon*—either the *bicolor* group or the *eugenii* group. The massive p^3 and p^4 are reminiscent of the state of those teeth in *P. bicolor*, particularly as they are significantly longer than dp^4 and m^1 , respectively. But the much reduced size of the otherwise *Protemnodon*-like i^3 favors the *eugenii* group, in which this tooth has not undergone the same degree of enlargement to be observed in the large wallabies and in *Macropus* (*sensu stricto*).

Setonix brachyurus (Quoy and Gaimard)

Kangurus brachyurus QUOY AND GAIMARD, 1830, Voyage de . . . l'Astrolabe, Zoologie (for 1826-1829), vol. 1, p. 114.

Halmaturus (*Thylogale*) *brevicaudatus* GRAY, 1838, Ann. Nat. Hist., vol. 1, p. 108.

TYPE: Perhaps not in existence. Should be at Paris Museum. I have a photograph of a specimen collected at King River by G. Shortridge.

Six specimens, including one juvenal, from Gingin, Western Australia, collected by F. W. Teasdale, and one without locality from the zoological gardens represent this anatomically distinct wallaby in the American Museum. The Museum of Comparative Zoölogy has several specimens collected by G. C. Shortridge. A specimen, No. 6447, of this species from H. A. Ward and Co., marked "New South Wales," is possibly erroneously labeled. A further West Australian series, taken by Allen and Darlington, comes variously from Pemberton, from Margaret River (?), and from Rottnest Island. In the United States National Museum there are seven specimens from Busselton, West Australia, taken by C. M. Hoy.

The incisive crowns are unworn in

A.M.N.H. No. 74493. There is a trace of a vertical groove in the outer half of i^1 , and the tooth tapers, its width greatest (3.6 mm.) in young, least (3.0) in old specimens.

The second incisor: outer lamina, 3.1 mm.; inner lamina, 2.8. The crown length is reduced by abrasion and chipping to 2.6.

The crown length of i^3 is 3.7 mm., of the outer lamina (which extends up the tooth for only 1.5 to 2.0 mm.), 2.4. Wear shortens the crown length to 3.2.

The third premolar is ± 4.5 mm. long. Its anterior and posterior widths are almost equal: 2.9 and 3.2. It is considerably longer than dp^4 (4.1).

The first molar varies from 4.0 to 4.6 mm. with anterior and posterior widths, 4.1 to 4.5 and 4.2 to 4.8. The widest tooth is m^3 (anterior loph, 4.9 to 5.0), and m^4 measures 4.8 to 5.1 by 4.3 to 4.8 (anterior) and 3.5 to 3.9 (posterior).

The large p^4 , almost as thick anteriorly as posteriorly, is longer than m^1 . Its length is 6.0 to 7.8 mm.; its anterior width, 2.8 to 3.8; posterior width, 3.1 to 4.0. Its cingulum has two stout cuspules near the middle of the tooth.

THYLOGALE GRAY

Thylogale GRAY, 1837, Mag. Nat. Hist. (Charlesworth), vol. 1, p. 583.

Conoyces LESSON, 1842, Nouveau tableau du règne animal, mammifères, p. 194.

The generic definition of *Thylogale* given by Gray was "hinder fold of the hinder upper cutting tooth [i^3] scarcely larger than the front one, so that the tooth appears only notched behind. Front incisor short, simple."

TYPES: Of *Thylogale*, *Halmaturus thetis* (not *Kangurus eugenii*). Under the name *Conoyces*, Lesson listed "*Macropus brunii*/*Didelphis brunii* Gm." This leads us straight back to *Didelphis brunii* Schreber, the first reference cited by Gmelin, 1788 ("Systema naturae," 13th ed., p. 109). Both Cabrera (1919, p. 155) and Troughton (1937, p. 118) are mistaken in synonymizing *Dorcopsis* with *Conoyces*.

Thomas (1888, p. 52) stated that the animal that Gray indicated as representative of his new concept was not, as stated by Gray, an actual specimen of *eugenii* Desmarest, but an example of the red-necked eastern Aus-

tralian species *thetis* (= *thetidis*). This statement by a "first reviser" signifies that the groove of i^3 of *thetis* really conformed to Gray's definition, something which is not true in the case of the real *eugenii* (a small *Protemnodon*). In *thetis* the crown length of i^3 reaches maximum in proportion to the combined lengths of i^1 and i^2 (as much as 7.2:6.0 mm.), although in some examples wear has already shortened the crown of i^2 . This dental character is particularly noticeable in specimens from New South Wales, rather less so in those from southern Queensland. Further features found in *thetis* (but not in *stigmatica* or *brunii*) are the extremely short anterior palatal foramina (3.5 mm.), the length of p^4 exceeding m^1 , its relatively great thickness front and back, and the ample development of the anterior part of its interior cingulum. In the skin of *thetis* the hairs of the dorsal part of the neck run forward from a whorl at the withers to the crown of the head, much as in *Petrogale*, *Dorcopsis*, and *Dendrolagus*, yet this is not true in either *stigmatica* or *brunii*.

Four species of small wallabies are currently referred to *Thylogale*. In *thetis*, *stigmatica*, and (partly) *brunii*, the condition of the notch of i^3 is substantially as in *thetis*. *Thylogale billardieri* has i^3 slightly aberrant. The small species *eugenii*, *parma*, and *bedfordi*, often treated as *Thylogale*, are in this paper transferred to *Protemnodon*. In them the notch of i^3 appears on the labial face of the unenlarged tooth. Raven and Gregory (1946) have already suggested that *eugenii*, figured by Jones (1924, figs. 169, 170), is "a small member of *Protemnodon*."

Thylogale may be regarded as a distinctly aberrant genus (on account of the unusual features of its third incisors), which has descended from a *Protemnodon*-like ancestor, although *Protemnodon billardieri* of Tasmania provides an intermediate condition of i^3 . In *Thylogale* i^2 and i^3 have distinctive patterns, and p^3 and p^4 are relatively large teeth, while p^4 is commonly retained long after the full development of m^4 . This is contrary to what takes place in true *Macropus*. In both p^3 and p^4 strong internal cingula are present, much as in true *Protemnodon*.

The type species, *thetis*, is the most specialized of the species of *Thylogale*, and the New

Guinea *brunii* is in some ways the least specialized. In *brunii* the teeth are heavier, and the notch is not so near the back of the tooth as in *thetis*. The red-legged *stigmatica* group of Queensland and south New Guinea, with i^3 smaller, has teeth intermediate between *brunii* and *thetis*. The short-tailed *billardieri* of Tasmania may be annectant with *Protemnodon*.

Thylogale thetis (Lesson)

Halmaturus thetis LESSON, 1828, Manuel de mammalogie, p. 229.

Halmaturus thetidis CUVIER, 1829, Histoire naturelle des mammifères, livr. 56 (fig.).

Halmaturus nuchalis WAGNER, 1842, in Schreber, Die Säugethiere, Suppl., vol. 3, p. 128.

TYPES: Of *thetis*, Paris Mus. No. 59 (40A), a mounted specimen, adult male, marked "brought by the Thetys in 1826, died in the zoo, 1833. One of the types of the kangaroo, *thetis* Cuvier." No skull was found in 1937.

The type skin has a hair whorl on the withers, whence the hairs are directed forward to the crown as in *Dorcopsis*. There is a well-marked hip stripe, and the inside of the ear is white. The back in the faded skin is reddish fuscous, becoming more reddish towards the shoulders. Thence forward to the ears is all rufous. The length of the head and body is 680 mm.; of tail, 470; of hind foot (c.u.), 163, (s.u.), 145. There seems to be no way of determining which specimen of *thetis* was studied by Gray when he drew up his diagnosis of *Thylogale*.

Thylogale thetis is becoming rather rare. The American Museum possesses an adult female, A.M.N.H. No. 886, originally from the Verreaux collection. H. C. Raven collected three specimens: A.M.N.H. No. 65130, male, from Glen Ferneigh, New South Wales, and A.M.N.H. Nos. 65131 and 65133 from Mundubbera, southern Queensland. All exhibit the reversed neck pelage, but in the two from Queensland i^3 is less enlarged than I have described above. In the Museum of Comparative Zoölogy are two skins without skulls from Queensland taken by Flood. Hoy collected a series of eight individuals from near Gloucester and one from Dorriggo, New South Wales, for the United States National Museum.

The first incisor is distinctly broader at the

tip in young than in old animals of the United States National Museum series. In the majority of specimens its breadth is 3.2 to 3.4 mm. This may be reduced by wear to 3.1 or rather less.

The second incisor was not found unchipped in a single specimen. In the two youngest examined, U.S.N.M. Nos. 221182-221183, young males with m^3 still unerupted, i^2 was both chipped and much worn. The maximum crown length measured was 4.1, the minimum (in an old male), 2.9 mm.

The third incisor also showed considerable wear, even in rather young animals. The greatest length of the inner lamina was 7.4 (U.S.N.M. No. 221185, male). In most cases the outer lamina ended some 4 mm. in front of the inner one. Thus the groove is not truly at the back of i^3 . Owing to the fact that the crown of the enameled portion of the tooth is not deep and stands on a relatively small root, its crown length is quickly shortened by abrasion to less than 7 mm. In old animals it may reach only 6.1 to 6.3 mm.

Unworn p^{3-5} are from 5.6 to 6.0 mm. in length; the width of the anterior part is 2.5 to 3.1, of the posterior, 3.0 to 4.1. Wear will reduce the posterior width to as little as 2.8 mm.

The largest unworn dp^4 measured is 5.6 mm. in length, or shorter than p^3 ; the shortest (worn, front and back), 4.8. The width across the posterior loph varies from 4.3 to 4.7. The anterior loph is from 0.1 to 0.2 mm. narrower.

The length of unworn m^1 varies from 5.4 to 5.7; its width, from 5.0 to 5.5. It is distinctly shorter than p^4 .

The fourth molar, developed in only three of the United States National Museum specimens, is only slightly longer than m^3 , 7.3 to 8.0 compared with 7.2 to 7.7 mm., and is equally narrow; the anterior and posterior lophs are 5.7 to 6.2 and 5.1 to 5.8. In m^3 , the anterior loph is 5.4 to 6.5; the posterior, 5.1 to 5.8 mm.

The permanent premolar, following the shedding of p^3 and dp^4 , is apparently erupted, as in some *Macropus*, after m^3 is in place and before the appearance of m^4 . In two specimens with the deciduous teeth still present, m^3 is just visible in its alveolus, but in a third specimen at the same stage of molar

development p^4 , although freshly erupted, is fully in place. The length of the unworn tooth is from 6.3 to 6.7 mm. Its width anteriorly is 3.1 to 3.2, becoming reduced by wear to 2.6; its posterior width, 3.5 to 3.9 mm. The internal cingulum is strongly developed to form a pair of confluent basins.

The range of this species is typically New South Wales with extensions into Queensland. Lucas and Forbes-Leith (1884) record it in Victoria, and Jones (1923-1925) states that it is found in the south and east of South Australia.

Thylogale stigmatica Gould

Besides true *stigmatica*, typically from near Rockingham Bay, Queensland, three additional rather weak races of the red-legged padymelon have been recognized, namely, *wilcoxi* from southeastern Queensland and northern New South Wales, *coxenii* from Cape York (of which we have no specimens), and *oriomo* from south New Guinea.

Thylogale stigmatica can be distinguished from the red-necked padymelon, *T. thetis* of New South Wales, by the only moderate development of i^3 , the crown length of which in *thetis* may reach 7 mm., while in *stigmatica* it measures only 5.7 mm. The length of the anterior lobe of i^3 in *thetis* is ± 6.7 mm.; in *stigmatica*, ± 5.0 . In *thetis*, too, the infraorbital foramen has three openings (possibly not constant).

In *stigmatica* p^4 is a comparatively large tooth; the crown lengths of p^4 and m^1 are 7 and 5.4 mm., respectively. The internal cingulum is well developed forward, and the front of the tooth is almost as broad as the back. In juvenals the crown lengths of p^3 and dp^4 are 5.1 and 4.6 mm., respectively.

The foramen internal to the paroccipital process in *stigmatica* is widely open, while in *thetis* it is almost plugged by bone. The ectopterygoid fossae of *stigmatica* are somewhat narrower than those of *thetis*, and the bony connection across the palate behind the posterior vacuities is weaker and slenderer than in *thetis*.

The maxillo-nasal suture in *stigmatica* is much shorter than the premaxillo-nasal suture; in *thetis* these sutures are nearly equal in length. The three incisors in the premaxilla

extend well in front of the nasal notch in *stigmatica*. In *thetis* the root of i^3 stands behind the notch.

In the mandible of *stigmatica* the connection between the masseteric fossa and the internal fossa for passage of the mandibular nerve may be so large that one can see through from side to side. The corresponding opening in *thetis* is very small and well within the masseteric cavity. The lower incisor of *stigmatica* is considerably more attenuate and delicate than that of *thetis*. The tail is much shorter than that of *thetis*, approximately as 3:4.

This is the red-legged padymelon. The hairs of the neck are neither reversed nor red, as are those of *thetis*. The fore and hind legs and sides are more or less russet, the dorsal pelage is mixed gray and brown, and the underparts are dull white with the bases of the hairs gray.

***Thylogale stigmatica stigmatica* Gould**

Thylogale stigmatica GOULD, 1860, Mammals of Australia, pt. 12 (vol. 2), text to pls. 33-34.

TYPE: B.M. No. 60.11.13.1 (1856a), adult male, from Point Cooper, north of Rockingham Bay, near Cardwell, Queensland, collected by McGillivray, voyage of the "Rattlesnake," June, 1848. I have a photograph of the type skull.

The crown length of i^3 of the type is 5.7 mm.; of p^4 , 7.5 (the width of posterior half, 4.0); length of m^1 , 5.3.

Henry C. Raven collected eight specimens from Evelyn, two from Atherton Tableland, and four from Ravenshoe, as well as some 20 skulls without skins from Evelyn and Atherton. G. Neuhäuser took two at Lake Barrine. The above are localities close together and a little to the south of Cairns. They average 60 miles north of the type locality.

I have also studied eight specimens from Atherton and one from the Bellenden Ker Range in the United States National Museum. At the Museum of Comparative Zoölogy are two specimens from Millaa Millaa, one from Mount Spurgeon, one from Mount Carbine, and two from Lake Barrine.

Most of this material is adult and has the teeth considerably worn, but M.C.Z. No. 29293, male, from Lake Barrine, M.C.Z. No.

29310 from Mount Carbine, and A.M.N.H. No. 65139, pouch male, are quite young and serve to show the characters of the unworn incisors and deciduous premolars.

The width of i^1 varies from 3.0 to 3.3 mm. Some initial taper distally is to be noted in the newly cut tooth, but this quickly wears off and the tooth broadens to slightly more than 3 mm.

In i^2 , as in other *Thylogale*, the outer lamina is longer than the inner, the notch between them serving (as is usual in macropods) for the insertion of the anterior point of the blade of i^3 . This tooth narrows rapidly towards the root. The length of the external lamina varies from 3.9 mm. to 4.1 in unworn teeth, that of the inner lamina being ± 0.6 mm. less. Wear reduces this crown length to 3.5, 2.3, 2.1 in old animals.

In i^3 , as in most kangaroos, the inner lamina is the longer. The crown length is 5.5 to 6.0; the outer lamina, 5.0 to 5.6 mm. These become reduced by abrasion to 5.7 and 5.2 or rather less. In very old specimens the two laminae are worn off, leaving stumps that measure 3.4, 3.5, and 3.7 mm. in crown length.

The length of p^3 is from 5.1 to 5.4; its anterior and posterior widths are 2.5 to 2.8 and 3.1 to 3.3. The cingulum and postero-internal cusp are well developed.

The length of dp^4 varies from 4.8 to 5.0, the width of its posterior (broader) loph from 4.0 to 4.2 mm. This tooth is therefore shorter than p^3 .

The first molar has the crown length 5.2 to 5.4 mm., but this may be reduced by wear to 5.0 mm.

The fourth molar varies in length from 6.4 to 7.4, and the width of its anterior loph from 5.3 to 5.7, posterior loph, 4.4 to 5.3. The molars in this wallaby, independently of sex, are unusually variable in size.

The fourth premolar is a large tooth, 6.8 to 7.5 mm. in length. Its anterior width is 3.7 to 4.3; its posterior width, 2.9 to 3.1 (both widths narrowed by wear). The cingulum and postero-internal cusp are well developed.

***Thylogale stigmatica wilcoxi* (M'Coy)**

Halmaturus wilcoxi M'Coy, 1866, Ann. Mag. Nat. Hist., ser. 3, vol. 18, p. 322.

Halmaturus temporalis DE VIS, 1884, Proc. Roy. Soc. Queensland, vol. 1, p. 111.

TYPES: In Melbourne (*vide* Thomas, 1888, p. 49).

M'Coy published no measurements of the skull of the type and compared *wilcoxi* not with *stigmatica* but with the less closely related *parma*, *thetis*, and *eugenii*=*derbiana*. The type locality of *wilcoxi* is Richmond River, New South Wales; that of *temporalis*, Moreton Bay. Both localities are near Brisbane.

One rather young specimen of this apparently rare form was collected by H. C. Raven at Glen Ferneigh, northeastern New South Wales, and two others were taken at Lochaber Station, Mundubbera, southern Queensland. The animal from northern New South Wales is rather more warmly colored than are the two from southern Queensland.

Thylogale stigmatica coxenii (Gray)

Halmaturus coxenii GRAY, 1866, Proc. Zool. Soc. London, p. 220.

Halmaturus gazella DE VIS, 1884, Proc. Roy. Soc. Queensland, vol. 1, p. 110.

COTYPES: Of *coxenii*, B.M. No. 66.4.23.1, adult male shown as "lectotype" (Thomas, 1922, p. 128); and B.M. No. 66.4.23.2, juvenile female, both from Port Albany, Cape York, collected by Coxen. I have photographs of the skulls of the two cotypes. The crown length of i^3 in the male, 4.5 mm.; of p^4 , 6.9 (its posterior width, 3.3); in the female, p^3 , 4.7; dp^4 , 4.3.

We have no specimens at the American Museum of Natural History.

Thylogale stigmatica orio
(Tate and Archbold)

Macropus coxenii orio TATE AND ARCHBOLD, 1935, Amer. Mus. Novitates, no. 804, p. 1.

TYPE: A.M.N.H. No. 104429, adult male, from the Oriomo River, southern Papua.

Since the foregoing description of the type and paratypes was published, two additional specimens have been collected by the Third Archbold Expedition at the Wassi Kussa River, south coast of New Guinea.

In *T. s. orio* the total length of the crown of i^3 may attain 6.2 mm., that of the anterior lobe, 6.0.

Thylogale brunii (Schreber)

These dark brown wallabies of the New Guinea region are sharply distinct from *T. thetis* and *T. stigmatica* of Australia, because of their color. Their skulls and teeth, on the contrary, offer few good distinctive characters. In general, the skulls are somewhat larger and the teeth heavier. Other small details are shown beyond under the races of *brunii*.

Although a number of names have been applied to these brown wallabies, there seem, on completion of the present survey, to remain only three valid races. These are: true *brunii* of Aru and southern New Guinea; *brownii* of the Bismarck Archipelago and the lowlands of northern New Guinea, as far west as Hollandia; and the long-haired high mountain race *keysseri* of the Huon mountains and the eastern parts of the great central range in Papua. I find no record of *brunii* in New Guinea, west of longitude 138° E. on the south coast, except on Kei and Aru Islands, or west of Hollandia (longitude 141° E.) on the north coast of New Guinea (although Goldfuss recorded it from Salar, near Timor, in 1819).

Determination of the generic identity of the original *Didelphis brunii* Schreber, 1778—whether a *Thylogale* or a *Dorcopsis*—has long presented difficulties to systematists. Schreber's plate and description were taken directly from the plate (213) and description of Bruijn (1714). The place of origin of Bruijn's wallaby remains unknown. In spite of the slender *Dorcopsis*-like rostrum depicted by Bruijn for his animal, I believe it a *Thylogale*.

Bruijn's plate of "Filander" shows a pouched, kangaroo-like animal with the underparts and under side of the tail white. The hands and feet are dark. A distinct white face stripe, beneath which is a dark stripe, runs from the corner of the mouth to the ear. This last is definitely a character of *Thylogale brunii* (as understood today) and not of *Dorcopsis*.

Schlegel and Müller (1839–1844) cannot be considered the "first revisers," inasmuch as they believed they were dealing with *Dorcopsis*, not *Thylogale*. Their citation of Schreber's name constitutes a misidentification, and their description of "*Dorcopsis*

brunii," founded actually upon Papuan material, is, if anything, a formal naming of a wallaby of the genus *Dorcopsis* without any reference to the entirely different animal *Thylogale* (or *Macropus* or *Didelphis*) *brunii*.

The real "first reviser" is apparently Schlegel (1866). He drew special attention to the Aru Island wallaby, recorded by Wallace as early as 1857 ("The Malay Archipelago," p. 487), and tied it to *Didelphis brunii* Schreber (Bruijn's wallaby). His action amounted to restriction of the type locality of *brunii* to the Aru Islands. Thomas (1888), reviewing the situation, concluded not only that Bruijn's plate truly portrayed the species now known as *Thylogale brunii* but also emphasized the presence of this species on the Aru Islands and the absence therefrom of *Dorcopsis*.

While at Sturt Island Camp on the Fly River in 1936, I was able to compare the external characters of newly killed *Thylogale* and *Dorcopsis* before skinning:

Thylogale brunii

Color above brownish gray, beneath white
A dark cheek stripe from behind eye to corner of mouth, above which is a white area
A white hip stripe
Ears white inside
Hair not reversed from withers to nape
Girth of forearm 40 mm.
Girth of hind foot at metatarsus 55 mm.
Hind foot relatively long and heavy
Tail white beneath
Tip of tail without enlarged tactile scales beneath

In Bruijn's picture the cheek stripe and the white under side of the tail are distinctively like those of *Thylogale*, while the remaining characters cannot be distinguished.

This conclusion regarding the generic position of Bruijn's animal supports that of Thomas (1888, pp. 49-50) and denies relationship to *Dorcopsis* (same reference, p. 87). The question of the spelling of the name, raised by Thomas, is settled under the International Rules by adoption of Schreber's spelling, *brunii*. Restriction of the type locality to the Aru Islands (the Aru Island wallaby of Thomas) is apparently attributable to Schlegel (1866).

Thylogale brunii brunii (Schreber)

Didelphis brunii SCHREBER, 1778, Die Säugethiere, vol. 2, pl. 153.

Macropus jukesii MIKLOUHO-MACLAY, 1884, Proc. Linnean Soc. New South Wales, vol. 9, p. 891.

Macropus gracilis MIKLOUHO-MACLAY, 1884, Proc. Linnean Soc. New South Wales, vol. 9, p. 894.

TYPES: Of *brunii*, none in existence. The type locality, erroneously given by Bruijn as Java (where no marsupials occur), has been restricted to the Aru Islands by Schlegel's (1866) alliance of the Schreber reference with wallaby found on Aru. This restriction was acceded to by Thomas (1888) and by subsequent writers. I have a photograph of a topotype, Genoa Mus. No. 1576. I saw the types (mounted skins) of *jukesii* and *gracilis* in Sydney but can now assert only that they are members of the *brunii* group.

Specimens that I regard as typical *brunii*,

Dorcopsis mülleri

Color above bluish gray, beneath whitish gray
No such cheek stripe. Area around mouth merely pale gray merging with pale gray of chin
No hip stripe
Ears pigmented inside
Hairs reversed from withers to nape
Girth of forearm 30 mm.
Girth of hind foot at metatarsus 45 mm.
Hind foot relatively short and slight
Tail gray beneath
Tip of tail with enlarged tactile scales beneath

seen by me in 1937, include Genoa C.E. No. 10478 (skin only, adult male), C.E. No. 10479 (young female), both collected by Beccari at Wokan, Aru, in April, 1873; C.E. No. 1578 (skin) and C.E. No. 1579 (skull), being parts of a juvenile female, taken by Beccari on Aru Island, May, 1873; C.E. No. 1574 (skin) with C.E. No. 3961 (complete skeleton); and C.E. No. 1575 (adult male skin) with C.E. No. 1576 (skull), these animals also secured by Beccari, March 14, 1873. Besides the material at Genoa, four specimens from Aru were listed by Thomas (1888) in the British Museum.

A single specimen, C.E. No. 1577 (skin),

was collected by Beccari at Grand Kei, August 3, 1873.

There exists in the Brisbane Museum an unnumbered, smoky-colored, adult male from the Herberton Gorge marked "*M. parma* cf." Only the cheek teeth (no incisors) are preserved. The length of p^4 is 7.3 mm., its greatest width 3.4; p^4-m^4 is 32.3 mm. This may possibly represent an extension of the New Guinea *brunii* group into Australia.

The Archbold collection of *T. brunii brunii* comprises the following from south New Guinea: Wuroi River, eight specimens; Mabaduane, south of the mouth of the Fly River, two; Bugi, Wassi Kussa, west of Mabaduane, one; Sturt Island camp, left bank of Fly River below Strickland junction, nine; Lake Daviumbu, right bank of middle Fly River, eight. Some of these specimens were referred in my previous paper (1937) to *lauterbachii*. I now believe all to be identical to true *brunii* of Aru.

We have no specimens from southeast New Guinea. The record by Miklouho-Maclay of *jukesii* = *gracilis* from Port Moresby may indicate a distinct race with relationships analogous to that of *Phalanger maculatus chrysorrhoeus* and *P. m. goldiei*, or it may merely represent an extension of the range of *brunii*. I have seen no Port Moresby specimens.

The most obvious difference between *Thylogale brunii* of south New Guinea and *T. thetis* and *stigmatica* is its wholly different color system. The pelage is predominantly dark brown, varying in forms from gray brown to chocolate brown, in contrast to the red legs or red nape of *stigmatica* or *thetis*. The anterior and posterior palatal foramina, the ectopterygoid fossae, and the posterior palatal connection conform more closely to those of *stigmatica*, but the premaxillary processes separating the anterior foramina are broader and project farther back into the palate than in *stigmatica*. The relationship of the nasals to the premaxillae and maxillae is as in *thetis*. The posterior portion of the jugal, adjoining the glenoid fossa, is shallow and ligulate in *thetis* and *stigmatica*, but deep and relatively massive in *brunii*. The small foramen beneath the anterior face of the condyle is considerably enlarged (not so in *thetis* or *stigmatica*). The teeth and skull gen-

erally are much heavier and stronger than in either species.

The second incisor (unworn in *brunii*, pouch juvenal female, A.M.N.H. No. 108025, from the Fly River) is thicker and more broadly triangular than is the case in either *thetis* or *stigmatica*. On the inner lamina there is a small, inward projection 1.5 mm. from the front of the tooth and an inward projection at the back. The posterior part of the outer lamina (the labial face of the tooth) is bent outward well beyond the face of i^3 , giving the labial face of i^2 a distinctly concave form. This concavity becomes deeper, like a shallow groove, as it is traced upwards to the base of the enamel. The usually broad posterior face of the tooth greatly widens the posterior notch (posterior thickness of unworn tooth, 2.5 mm.). These peculiarities can only be seen in pouch young as abrasion quickly destroys them, reducing the crown (in section) to a rather thick parallelogram. The prominences of the postero-internal and postero-external angles of i^2 usually remain.

The groove in i^3 , which crosses the crown from back to front, is open also at the front. It may become closed when wear has resulted in the coalescence anteriorly of the inner and outer laminae. The front of the tooth is relatively broad and fits snugly into the exceptionally wide groove at the back of i^2 . The inner lamina (A.M.N.H. No. 104436) has the blade minutely rugose, but lacks the deep valley to be seen in the race *tibol* from northeast New Guinea. The crown length in south New Guinea material is ± 7.3 mm.; the outer lamina, ± 6.6 . These become reduced by wear to ± 5.5 and ± 5.2 mm.

The third premolar, relatively broad in south New Guinea *brunii*, measures: length, ± 6.1 ; anterior width, ± 3.0 ; posterior (greatest) width, ± 4.0 .

The length of dp^4 is ± 5.8 mm.; of m^1 , ± 5.5 mm. The fourth molar is ± 8.0 mm. in length; its anterior loph, 6.3; posterior loph, 5.4.

The permanent premolar comes into place after the eruption of m^3 (A.M.N.H. No. 108017). Its postero-internal cusp, otherwise well set off, is connected by a low, narrow ridge with the main blade. The internal cin-gulum, although narrowed anteriorly, is dis-

tinct. The length of the tooth is ± 8.4 mm.; its anterior width, 3.2; its posterior width, 4.1 mm. Its greater length, compared with m^1 , is accentuated by the fact that the anterior and posterior ledges of m^1 are often worn by contact with dp^4 and m^2 before eruption of p^4 .

In the pouch young of *Thylogale brunii*, A.M.N.H. No. 108025, from the Fly River, south New Guinea, I have been able to distinguish vestiges of two "prelacteal" incisors. These minute teeth have been disturbed by the cleaning of the skull to the extent that they seem to lie on their sides. The deciduous second incisor (?) is not entirely structureless but shows indications of a slight blade. Its estimated length and breadth are 0.7 by 0.5 mm. Both the right and the left teeth lie directly behind i^{2-2} on the outer part of the narrow wall of bone separating the alveoli of i^2 and i^3 . Deciduous third incisor (?) is similar to the vestigial di^3 (?) of *Macropus* and is implanted in the undissolved bone of the premaxilla directly beneath the posterior part of the emerging external lamina of i^3 . The tiny, single-rooted tooth of the left side lies, adhering to the bone, just in front of the right one, whither it has apparently been washed when the skull was cleaned. The crown of di^3 (?) is somewhat narrower and more compressed than that of *Macropus*. Its length is ± 0.7 mm.; its width, ± 0.3 mm.

Thylogale b. brunii in our Sturt Island Camp, north bank of the Fly River, seemed to inhabit precisely the same habitat as *Dorcopsis*. Both were moderately common in the rather heavy forest that occupies the several miles of territory between the Fly River and the swampy open plains of the Aramia River basin.

Thylogale brunii brownii Ramsay

Halmaturus brownii RAMSAY, 1877, Proc. Linnean Soc. New South Wales, vol. 1, p. 307.

Macropus lugens ALSTON, 1877, Proc. Zool. Soc. London, p. 126.

Macropus tibol MIKLOUHO-MACLAY, 1885, Proc. Linnean Soc. New South Wales, vol. 10, pts. 1-2, p. 141.

Thylogale lauterbachii MATSCHIE, 1916, Mitt. Zool. Mus. Berlin, vol. 8, pp. 290-292.

Types: Cotypes of *brownii*, Sydney Museum, No. 1033, male; No. 1034, female, both

collected by the Rev. George Brown in New Ireland. Type of *lugens*, B.M. No. 77.7.18.17, juvenal male, collected by the Rev. George Brown, "Duke of York Island or adjoining shores of New Britain or New Ireland." Of *tibol*, probably in Sydney Museum (I did not see it there) from the "Maclay Coast," north of the Finisterre Range and east of Madang. Of *lauterbachii*, Berlin Mus. No. 22362 (skull) and No. 22363 (skin), field no. 681, from Ogeramngang, near the source of the Bulung River, "in forest."

I have photographs of the type skulls of *lugens* and *lauterbachii*.

Two specimens from near Hollandia, an adult male and a juvenal male, are provisionally referred to *tibol*. The younger one is markedly brownish beneath. The adult is distinguished by the very pale gray color of the dorsal surface of the neck, in contrast to the blackish brown of the crown and ears. The length of p^4 in the adult (A.M.N.H. No. 151857) is 7.2 mm., of p^3 in the juvenal (A.M.N.H. No. 152491), 4.9 mm.

I have examined the following material: a specimen (A.M.N.H. No. 99851) from New Britain recorded (Tate and Archbold, 1937) as *brownii*; two specimens from Bubui, Mandated Territory (U.S.N.M. Nos. 35819/20690, male, and 35820/20691, female); one specimen from the Sepik River (C.N.H.M. No. 31864, male).

The dark brown *Thylogale* of northeast New Guinea have consistently smaller teeth than those of south New Guinea. *Thylogale tibol*, like *T. lauterbachii*, had a weakly defined hip stripe. The color of the underparts in juvenal *tibol*, *lauterbachii*, *lanatus*, and A.M.N.H. No. 152498 from near Hollandia is definitely not white, as is generally the case in juvenal *brunii*. It varies from pale brownish to gray brown, with the hair tips washed with pale cinnamon. Apparently the long-haired, mountain-inhabiting form *keysseri* (= *lanatus*) is more closely related to the lowlands animals of the north coast than to *T. brunii* of the south coast of New Guinea.

The foramen magnum is alike in *brunii* and *tibol*. In both it differs somewhat in outline from that of *brownii* of the Bismarck Archipelago.

In i^2 the general form described for true

brunii is adhered to, the posterior parts of the tooth spreading widely inward and outward to embrace the thickened anterior edge of i^3 . But the concave face and, particularly, the shallow vertical groove at the base of the enamel are less pronounced. This is seen to be true not only in the Sepik River specimen, C.N.H.M. No. 31864, but also in A.M.N.H. No. 151857 from the Cyclops Mountains and in A.M.N.H. No. 99851, *brownii*, from New Britain.

The third incisor, like the second, has a prominent rugosity on the inner lamina not far (1.5 mm.) from the front. This is followed by a vertical valley which considerably narrows the tooth. Beyond the valley the internal lamina, roughened by several minute cusps, continues to the back of the outer lamina (e.g., C.N.H.M. No. 31864, juvenal male, from Sepik River). The form of this tooth, as indicated above, is quite sharply different from that of true *brunii* of south New Guinea.

Both p^3 and p^4 in north New Guinea specimens are smaller, shorter teeth than in *brunii*. The length of p^3 is ± 5.5 mm.; its anterior and posterior widths are 2.4 and 2.9 mm. These dimensions in p^4 are 7.0, 3.1, and 3.4 mm. (in the New British specimen, 6.5, 3.1, and 3.8 mm.).

The teeth of the woolly-haired, mountain-inhabiting race *lanatus* agree far more closely with the above than with the form found in south New Guinea.

Thylogale brunii keysseri
(Förster and Rothschild)

Macropus keysseri FÖRSTER AND ROTHSCHILD, 1914, Novitates Zool., vol. 21, p. 261.

Macropus keysseri lanatus THOMAS, 1922, Ann. Mag. Nat. Hist., ser. 9, vol. 9, p. 670.

TYPES: Of *keysseri*, B.M. No. 28.10.23.1, adult male, from Ogeramnang, Huon Gulf, 1800 to 2000 meters, collected by Keysser ("probably in the grass plains of the Munggi"). Of *lanatus*, B.M. No. 28.10.1.4, old male, from Saruwaged Mountains, 3600 meters, collected by Keysser, August, 1914. I have photographs of both types.

Additional material includes C.N.H.M. No. 34207 and U.S.N.M. No. 268751, both from Saruwaged; A.M.N.H. No. 79788, female, Sevia, Huon Peninsula; and two from

Murray Pass in the Wharton Range, 2850 meters (recorded by Tate and Archbold, 1937, p. 416).

Reduction of tooth size, initiated in the lowlands race of northeast New Guinea, seems to have been carried slightly farther in these mountain forms. Otherwise their only outstandingly distinctive character is their long, woolly pelage. The length of p^3 is reduced to 5.3 mm. in A.M.N.H. No. 79788, to 4.8 in A.M.N.H. No. 104145 from Murray Pass; of p^4 , to 6.5 in A.M.N.H. No. 79788, to 6.7 in A.M.N.H. No. 104075, to 6.6 in C.N.H.M. No. 34207.

***Thylogale billardierii* (Desmarest)**

Kangurus billardierii DESMAREST, 1822, Mammalogie ou description des espèces de mammifères, suppl., vol. 2, p. 542.

Halmaturus (Thylogale) tasmanei GRAY, 1838, Ann. Nat. Hist., vol. 1, p. 108.

Macropus (Halmaturus) rufiventer OGILBY, 1838, Ann. Nat. Hist., vol. 1, p. 220; 1838, Proc. Zool. Soc. London, p. 23.

TYPE: Of *billardierii*, Paris Mus. No. 76 (51), a juvenal of undetermined sex, collected by Labillardière. "Patrie. La terre de Van-Diemen."

The type is a mounted skin with the skull still inside. The color, faded, is fuscous brown above, buffy beneath. The crowns of the upper incisors measure: i^1 , 4.3; i^2 , 4.3; i^3 , 6.1. A strongly developed notch is developed on the labial face of i^3 , two-fifths of the distance from the back of the tooth. The length of the head and body is 520 mm.; tail, 270; hind foot (c.u.), 138, (s.u.), 125.

Henry C. Raven obtained a series of this isolated species at Arthur River, Tasmania. At the United States National Museum are one from Arthur River, one from Gladstone, and three from Perkins Island, Tasmania.

In this species both i^2 and i^3 are considerably larger than in *parma*, and their structure suggests intergradation with *Thylogale*, in which genus the species *billardierii* is now placed. There is a small canine, and p^3 and p^4 are much narrower anteriorly than posteriorly and are considerably longer than the molariform dp^4 and m^1 , which stand immediately behind each. This short-tailed Tasmanian wallaby has been confused repeatedly with *Setonix brachyurus* of south Western Australia.

The dental dimensions in *billardieri* are: first incisor, width of crown 4.0 to 4.1 mm., wearing at base of enamel to 3.5. This tooth is thin at its inner edge and very thick where it touches i^2 .

The crown length of i^2 , external lamina, is 5.0 to 5.3 mm.; its internal lamina, bent strongly inward, 4.9. At 1.2 mm. from the back of the external lamina a transverse ridge crosses almost to the internal lamina. The posterior sulcus between the inner and outer laminae is rather wide.

The third incisor, although its groove does not nearly reach the back of the tooth, is quite suggestive of i^3 of *Thylogale*, as its internal lamina extends almost to the front of the blade and the groove traverses the occlusal surface for almost its entire width. The crown length is 5.4 to 6.1 mm., the external lamina measuring 4.7 to 4.9. These wear to 5.1 and 4.2, or less.

The canine, soon deciduous, lies appressed to the bone. The length of the enamel-covered portion is 1.5; its antero-posterior width is 1.1 mm. A minute cuspule appears behind its base (A.M.N.H. No. 65216, female).

The third premolar, narrow anteriorly, has little anterior cingulum. The strongly developed postero-internal cusp is joined by a thin low enamel ridge to the secutor cusp. Length, 4.8 to 5.1 mm.; anterior width, 2.0 to 2.3; posterior width, 2.9 to 3.3.

The maximum length for dp^4 is 4.8 mm. The lengths of m^{1-4} are 4.7 to 5.5, 5.6 to 6.0, 6.0 to 6.5, and 6.5 to 6.7.

The fourth premolar: length, 6.7 to 7.0; anterior width, 2.0 to 2.2; posterior width, 3.6 to 4.2.

Thylogale billardieri, shaggy coated and short tailed, is probably the least specialized of the species of *Thylogale*. Its likeness to *Setonix brachyurus* is illusory, as the characters of the teeth deny any very close relationship.

MACROPUS SHAW AND NODDER

Macropus SHAW AND NODDER, 1790, The naturalist's miscellany, vol. 1, text to pl. 33.

Gigantomys LINK, 1794, Beiträge zur Naturgeschichte, vol. 1 (1), p. 70.

Kangurus GEOFFROY AND CUVIER, 1795, Mag. Encyclopédique, vol. 2, no. 6, p. 188.

Halmaturus ILLIGER, 1811, Prodromus sys-

tematis mammalium et avium, p. 80. (New name for *Kangurus*.)

TYPES: Of *Macropus*, *Macropus giganteus* Shaw and Nodder (by monotypy) = *Mus canguru* Müller.¹ Of *Gigantomys* and *Kangurus* unknown but presumed also to be "Captain Cook's kangaroo" (*canguru*).

Macropus as a generic concept was first proposed by Shaw and Nodder (1790) and was accompanied by a plate (33). The text, although cast in more technical language than that of Hawkesworth (1773), nevertheless contains allusions to the "Captain Cook's kangaroo," and in it the works of "Cook" (Hawkesworth), Zimmermann, and Pennant are cited. Shaw and Nodder, apparently unacquainted with Müller's name *canguru* of a year earlier, employed the specific name *giganteus* of Zimmermann. They described their novelties first in Latin, accompanied by technical names (in the present instance *Macropus giganteus*), and afterwards in English. Their work consisted of unpaginated text accompanying numbered, dated plates. The plate, number 33, was dated June 1, 1790. The specimen figured on plate 33 conforms well in appearance with the kangaroo today called the great gray kangaroo, the color being brownish gray and the face devoid of any such white line as is found in *Macropus parryi*. It is probably the same species as Müller's *Mus canguru*, although it is drawn in a different attitude.

The genus *Macropus* can be distinguished from *Protemnodon* (= *Wallabia*) by relatively few characters. The occasional early loss of p^3 and dp^4 (following the eruption of m^2) and the relatively early loss also of p^4 (after eruption of m^3) are characters not found in the typical wallabies, *bicolor* and *agilis*, although possibly less distinctive for species of wallabies such as *P. dorsalis* and *P. rufogrisea*, which have small premolars. The precocious shedding not only of p^4 but also of m^1 and sometimes m^2 , accompanied by forward movement of the molars in the toothrows in *Macropus*, is an important character. In one old specimen of *M. rufus* only m^4 remains. The tendency towards extreme enlargement

¹ *Macropus major* Shaw was not proposed until 1800 and so, contrary to the views of Iredale and Troughton (1934), cannot displace either *giganteus* or *canguru*.

of i^3 (less developed in *Megaleia*) is a further characteristic, as is possibly the presence still of "prelacteal" teeth in *robustus erubescens* of Queensland and *canguru major* also of Queensland (southern). A final character may be added—that of extremely large size.

INTERRELATIONSHIPS OF THE "LARGE KANGAROOS," GENUS *Macropus*

It is relatively immaterial whether *Osphranter*, *Megaleia*, and *Macropus* (*sensu stricto*) are treated as species, subgenera, or genera. Their relations to one another and their combined position with regard to other macropod genera remain constant in any case. Probably they can be considered to best advantage as subgenera, since if treated as full genera each genus becomes virtually monotypic. Schwarz (1910a) published on the genus.

When adults of *Osphranter*, *Megaleia*, and *Macropus* are compared with one another various specializations become apparent, few of which are sufficiently striking to indicate either marked conservatism or marked progressiveness. The anteorbital canal in *Osphranter* is moderately long (10 mm.), in *Megaleia* very long (16 mm.), in *Macropus* very short (7 mm.). The rostrum anterior to p^4 in *Osphranter* is moderately deep (38 mm.), in *Megaleia* very deep (45 mm.), in *Macropus* moderately deep (36 mm.). The maxillo-nasal suture in *Osphranter* is short (19 mm.), in *Megaleia* moderate (27 mm.), in *Macropus* long (32 mm.). The interlacrima breadth in *Osphranter* is moderate (39 mm.), in *Megaleia* moderate (37 mm.), in *Macropus* very wide (50 mm.). The anterior end of the floor of the anterior nares (premaxillary) is scarcely grooved in *Osphranter*, profoundly grooved in *Megaleia*, ungrooved in *Macropus*. The anterior palatal foramina are elongate in *Osphranter* (17 to 18 mm.), elongate in *Megaleia* (17 to 19 mm.), short in *Macropus* (7 to 8 mm.). Lateral swelling of the nasals in age is most pronounced in *Osphranter*, slight in *Megaleia*, moderately pronounced in *Macropus*. The interpterygoid width in *Osphranter* is moderate (26 mm.), in *Megaleia* much greater (32 mm.), in *Macropus* moderate (28 mm.). The basioccipital in *Osphranter* is deeply keeled, in *Megaleia* and *Macropus* weakly keeled. The diastema in *Osphranter* is short

(42 mm.), in *Megaleia* rather long (50 mm.), in *Macropus* rather long (53 mm.). In the mandibles the connection between the masseteric and nerve canals lies deep in *Osphranter* and *Megaleia* but is well exposed in *Macropus*. The diastema corresponds with that of the maxilla.

Study of the measurements in table 5 reveals but two significant facts; that m^4 in *Megaleia* is extremely large, and that p^3 and p^4 have subequal dimensions in *Megaleia* and *Macropus* but not in *Osphranter*. In general, low measurements indicate much worn teeth.

The premolars in *Osphranter*, *Megaleia*, and *Macropus* show slight but distinct features. In *Osphranter* p^3 and p^4 though short are both relatively massive. The third upper premolar is slightly smaller than p^4 . Both are only slightly narrower in front than behind (the point of measurement of width), and both have a relatively heavy postero-internal cusp from which a low cingulum extends almost to the front of the tooth.

In *Megaleia*, although a general resemblance of p^4 to p^3 exists, the postero-internal cusp is much more distinctly separated from the main secant ridge in both teeth, and in p^4 a well-defined antero-internal cusp is present at the front of the internal cingulum. Furthermore, a marked groove separates the smaller, anterior portion from the larger, posterior portion of the secant ridge.

In *Macropus* (*sensu stricto*) p^3 and p^4 are divergent morphologically. The third upper premolar becomes hourglass shaped by compression of its two sides slightly anterior to the middle of the tooth, the posterior part of the hourglass being considerably wider than the anterior. The postero-internal cusp, although separate and distinct, is much smaller than that in *Megaleia*. The fourth upper premolar in *Macropus* is very much narrower in front than at the back, and the internal cingulum barely reaches the middle of the tooth. The secant ridge is cleft less deeply than that of *Megaleia*, and the postero-internal cusp is less prominent.

On the basis of the sum of their characteristics, *Osphranter* may be considered slightly the more generalized, with *Macropus* (*sensu stricto*), in which i^3 is a complex *Osphranter*-type tooth, closer to it than to

Megaleia. This last, with its still small i^3 , thickened p^3 and p^4 , cranial peculiarities (detailed elsewhere), and peculiarly woolly pelage, diverged early from a combined *Osphranter-Macropus* type of kangaroo.

THE SPECIFIC IDENTIFY OF "CAPTAIN
COOK'S KANGAROO"

The diversity of opinions as to the specific identity of Captain Cook's kangaroo (Troughton, 1941; Raven, 1939; Iredale and

Hawkesworth (1773). An unidentifiable kangaroo (or wallaby) was first glimpsed but not captured at Endeavour River on June 22, 1770 (*op. cit.*, p. 560). A macropod subsequently caught was said (*op. cit.*, p. 578) to resemble a jerboa and when full grown to be as large as a sheep. But "this animal was a young one, much under its full growth, weighing only 38 pounds . . . The forelegs were only eight inches long, and the hind legs two and twenty . . . the skin is covered with a

TABLE 5
COMPARISON OF CHEEK TEETH OF *Osphranter*, *Megaleia*, AND
Macropus (SENSU STRICTO)

| | <i>Osphranter</i> | <i>Megaleia</i> | <i>Macropus</i> |
|----------------|-------------------|-----------------|------------------------|
| p^3 | | | |
| Length | 6.5- 7.6 | 6.6- 8.0 | 6.7- 8.0 |
| Greatest width | 3.8- 4.6 | 4.0- 5.9 | 4.2- 6.3 |
| dp^4 | | | |
| Length | 7.1- 9.0 | 7.5- 8.9 | 6.7- 9.5 |
| Greatest width | 5.7- 7.5 | 6.2- 7.1 | 6.0- 7.5 |
| m^1 | | | |
| Length | 8.0-10.0 | 9.3-11.0 | 8.5-11.0 |
| Greatest width | 7.0- 8.5 | 7.4- 9.6 | 7.1- 9.4 |
| m^4 | | | |
| Length | 12.2-13.8 | 13.5-15.0 | 11.7-12.8 ^a |
| Greatest width | 9.3-10.3 | 10.0-11.0 | 9.1-10.1 |
| p^4 | | | |
| Length | 7.3- 9.9 | 6.9- 8.5 | 6.0- 7.2 ^a |
| Greatest width | 4.0- 5.2 | 3.8- 4.7 | 3.6- 4.5 |

^a The teeth are often larger in *M. c. fuliginosus*.

Troughton, 1925, 1934) has led me to review once again the evidence bearing upon this difficult subject. I am particularly fortunate to have been able to examine all the original literature and illustrations at first hand. The problem consists of two parts: the establishment, in terms of modern species and subspecies, of the correct scientific name of the Cook's kangaroo and its identity, disputed by Iredale and Troughton (1925 and 1937), Raven (1939), and Troughton (1941); and, after that, the establishment of this species as the type of *Macropus*.

The earliest account and drawing of Captain Cook's kangaroo are contained in

short fur, of a dark mouse or grey color except the head and ears which bear a slight resemblance to those of a hare."

A few days later (*op. cit.*, p. 586) a larger kangaroo, also with juvenal dentition, weighing 84 pounds was reported shot. There is no way to know whether these two animals were of the same species. Both were taken at Endeavour River near Cooktown, northern Queensland.

The plate (20 of Hawkesworth), which probably depicts the adult, is in my opinion a quite good reproduction of one of the larger species of *Macropus*. No trace of hip stripe or face stripe can be detected, and this fact,

together with the recorded color, seems to rule out all *Thylogale* and the whiptail, *Protemnodon parryi* (advocated by Iredale and Troughton, 1937). The only really large species of Macropodidae that conceivably could have been found near Cooktown are the great gray, the red, and one of the antelope group, *M. robustus reginae* Schwarz. Specimens of all three are contained in the collections of this museum. Juveniles of the red kangaroo (race *pallidus*) are light gray with russet hair bases and *M. reginae* is dark brownish gray, but the short-haired great gray kangaroo of northern Queensland (A.M.N.H. No. 107375 from Mt. Carbine) fits both the brief description and the picture of Hawkesworth most closely.

Müller (1776) applied the name *Mus canguru* to the two specimens mentioned in Hawkesworth, using the Hawkesworth language almost word for word. His illustration (pl. 3, fig. 3) is almost identical to that of Hawkesworth (pl. 20).

The next year, 1777, several other names, now in synonymy, appeared: *Jerboa gigantea* Zimmermann, *Jaculus giganteus* Erxleben, *Didelphis gigantea* Schreber. Still other synonyms appeared during succeeding years.

When the attempt is made to synonymize *Mus canguru* Müller from Endeavour River, at Cooktown, Queensland (Müller wrote "South America") with *Macropus giganteus* Shaw and Nodder, some slight difficulty is met. Müller states of *canguru*: "The kangaroo—*Mus canguru*—Lieut. Cook discovered on his journey around the world at the Endeavour River in South America [*sic*] an animal very rare and much like *Mus jaculus* No. 20, but which when grown is as large as a sheep. Probably that was the example which Mr. Gore obtained, young, long not grown, and only 38 pounds. The head, neck, and shoulders were very small in comparison with the other part. The tail was only as long as the body, thick at the rump and thin at the end. The front feet, serving only to scratch, were short, only 8 inches long, and were held against the breast of the animal which sat always upright like a rabbit. The hind foot had a length of 22 inches. The skin had dark mouse-colored hair. Head and ears were colored like a hare The meat was palatable."

The measurements in the foregoing account were quoted from Hawkesworth (1773, p. 578).

Shaw and Nodder (1790), basing their information on two sources, Pennant (1781, p. 306) and Hawkesworth (1773, pp. 677, 578, pl. 20), omitted the name of the collector, the place of origin, and the dimensions, but gave instead more anatomical information. They added, "The kangaroo is by far the largest animal of its genus; being as large as full grown sheep."

Pennant naturally omitted the kangaroo from his earliest work ("Synopsis of quadrupeds," 1771). In his 1781 edition (the first of the "History of quadrupeds" p. 306), referring to Hawkesworth and to Zimmermann (1777, p. 526), he provided various facts not given by Shaw and Nodder, such as the immaturity of Cook's animals: "weight of the largest shot was eighty-four pounds; but this, on examination of the grinding teeth, had not attained its full growth." Pennant's plate 35 represents a kangaroo in the same attitude as that in Hawkesworth but reversed, apparently by use of a translucent tracing material.

Zimmermann (1777), citing Hawkesworth, described Cook's kangaroo as *Jerboa gigantea*. Although no illustration was published, the word "Kangaroo" appears on the map at the end of his work at approximately the position of Cooktown.

Thus, the works of Müller, Pennant, and Zimmermann are all based upon the material shot at Cooktown, and all illustrations are founded upon the Hawkesworth plate. Shaw and Nodder (1790, pl. 33) published a basically new drawing but even that drawing is sufficiently like the original (Hawkesworth) to be considered to represent the same species.

Any one of the three drawings, as stated, could conceivably represent either the great gray kangaroo, the red kangaroo (which is grayish in youth), or a member of the *robustus* group, although the first is the most likely. In my opinion, it could not represent *parryi*, as maintained by Iredale and Troughton. *Macropus parryi* has a prominent white face mark and very long tail, and it is doubtful whether one would weigh as much as 84 pounds while still young.

Iredale and Troughton (1934) were possibly mistaken in stating that the type locality of *M. major* Shaw was Sydney, New South Wales. A perusal of Shaw's words shows that he believed Endeavour River to be in New South Wales. Apparently "New South Wales" was used up to the early part of the eighteenth century to signify any part of the east coast of Australia (Shaw, 1800, p. 506); also, Shaw's discussion relates mainly (pp. 505-508) to Captain Cook's kangaroo of Endeavour River. But he also gives details (pp. 509-510) of a specimen weighing 150 pounds taken some years later at Botany Bay [Sydney], New South Wales. It is the last to which Iredale and Troughton would restrict the name *major*. Since the two forms, *canguru* Müller and *major* (of Iredale and Troughton) Shaw are in any event conspecific, it is understandable that Shaw (1800, p. 505) placed his own *giganteus* Shaw and Nodder, 1790, in the synonymy of *major*. In this single connection Iredale and Troughton may be considered as first revisers, and *major* may stand for the eastern race of *canguru*, south of Cape York.

SUBGENUS *OSPHRANTER* GOULD

Osphranter GOULD, 1842, Proc. Zool. Soc. London, for 1841, p. 80.

Phascolagus OWEN, 1874, Phil. Trans. Roy. Soc., London, vol. 164, p. 262.

Dendrodorcopsis ROTHSCHILD, 1903, Novitates Zool., vol. 10, p. 414.

TYPES: Of *Osphranter*, *antilopinus* Gould (by monotypy). Of *Phascolagus*, *Macropus erubescens* Sclater (by subsequent designation, Iredale and Troughton, 1934). Of *Dendrodorcopsis*, *D. bernardus* Rothschild.

This subgenus is composed of large, powerfully built kangaroos such as the antilopine, the euro, and the wallaroo, which have relatively short, massive skulls showing neither such elongation of the rostrum as appears in *Macropus* (*sensu stricto*) nor such slenderness of the mandibular ramus as in *Megaleia* and *Macropus*.

Typically, *Osphranter* has the outline of the three upper incisors more or less \cap -shaped (not \wedge -shaped as in *Macropus*). The third upper incisor, although much longer than that tooth in *Megaleia*, is shorter than in *Macropus*, and its labial surface bears only

one groove. The permanent p_4 are somewhat more massive than the same teeth in *Macropus* and *Megaleia*.

The paired processes of the premaxillae that separate the anterior palatal foramina are considerably stouter and broader than in *Macropus* and *Megaleia*. The sides of the rostrum are considerably inflated in adults of both sexes (rarely slightly so in the other subgenera). The anteorbital canal, although moderately lengthened, is shorter than in *Megaleia*. (In *Macropus* the canal is so short as to be almost beneath the lacrimal foramen.) The palate is nearly entire, with the exception of a pair of small openings at the level of the descending processes of the maxilla. The squamosal root of the zygoma is greatly deepened, in males being about twice as deep as the jugal. The two squamosals tend to approach each other over the surface of the parietals. There is no postglenoid foramen (present both in *Macropus* and in *Megaleia*).

The sizes of the sexes are markedly dissimilar, the females being relatively small. The varied size of p_4 , considerably smaller in females than in males, seems to be an attribute of *Osphranter* generally. Although the dark gray color and rough winter pelage of *robustus* form a marked contrast to the usually short, crisp, red coat of typical *antilopinus*, this contrast is weakened when *erubescens*, sometimes regarded as a race of the latter, is considered. In *erubescens* the body color is nearer gray than brown and the hind limbs and tail in females are whitish or very pale tan. In old males the limbs are gray. Juvenals of *erubescens* are darker gray than adults. Further exceptions are found. In A.M.N.H. No. 35758, without skull, a "zoo" specimen of unknown origin labeled *robustus cervinus*, the pelage though bright rufescent is fully as long as that of *robustus*.

Iredale and Troughton (1934) treated *antilopinus*, *isabellinus*, *erubescens*, *reginae*, *robustus*, and *bernardus* (= *woodwardi* Rothschild) as full species. It is more probable that all are subspecies of a single species, especially as there seems to be no case of geographical overlap of the "species." The name *robustus*, dating from 1841 (1840), supersedes all others and is here employed as the specific name for all races of *robustus* and

antilopinus. Le Souef (1928) reviewed the group.

The geographical distribution of *Osphranter* apparently covers the greater part of the continent, with the possible exception of the "sandy ridge desert" (Australia Official Handbook, 1941, p. 8). Most of the races are evidently markedly tolerant of water deficiency, in contrast to *Macropus* (*sensu stricto*). Where more than 40 inches of rain a year occur, races with much darker pelage are found: e.g., *bernardus* in Arnhemland, *reginae* in northeastern Queensland, *robustus* in New South Wales. Red is present in the coats of almost all races, the only exceptions being *bernardus* and *robustus*, in which, if red is present at all, it is almost wholly obscured. Maximum red coloration is found in the race *cervinus* of the southern half of Western Australia.

Probably the central race, from both the ecological and the morphological viewpoints, is *erubescens*. This inhabitant of arid to semi-arid country occupies the immense area of the Great Basin from the Gulf of Carpentaria to the Southern Ocean. To the eastward it reaches the eastern uplands; to the southwest it extends to the Eucla Basin (Glauert); in Central Australia it is present as far as the "western end of the MacDonell Ranges" (Spencer); to the northwest (beyond Alexandria) it probably grades imperceptibly into *antilopinus*.

***Macropus (Osphranter) robustus* Gould**
Macropus (Osphranter) robustus robustus
 Gould

Macropus (Petrogale) robustus GOULD, 1841, Proc. Zool. Soc. London, for 1840, p. 92.

Types: Cotypes in the British Museum. Male and female were listed by Thomas (1888, p. 24), and subsequently (1922, p. 128) the same male (B.M. No. 41.1099) was indicated as "lectotype."

TYPE LOCALITY: Mountain tops (Blue Mountains, 80 miles west of Sydney) in New South Wales.

Its heavy build and relatively short limbs serve to distinguish *robustus* proper from the other large, gray brown kangaroo of New South Wales, *Macropus kanguru major*. The skull and teeth have been compared in pre-

vious pages with those of *Macropus* and *Megaleia*.

Although the American Museum has three specimens of the "wallaroo" procured in the wild by H. C. Raven in New South Wales and a considerable number of "zoo" animals, wild-caught material representing this race in this country is decidedly meager. One of the "zoo" specimens (No. 70323) is melanistic.

Unfortunately, an adequate analysis of the dental features of *M. robustus robustus* of New South Wales has not been possible owing to paucity of material. The youngest wild-caught specimen I have been able to examine is A.M.N.H. No. 65025, juvenal male, in which m_2^2 are present and the third premolars, although still present in the upper and lower jaws, are already badly ground down. A.M.N.H. No. 65026, a young adult female with m_3^3 nearly in place, has abraded p^3 and dp^4 on the left side, p^4 newly erupted on the right. Both p_{4-4} are in place and virtually unworn. No. 65027, a much older female, has m_4^4 almost in place and p_4^4 already much worn. All three are from Glen Ferneigh, northern New South Wales. These animals are by no means topotypical.

The first incisor of the youngest specimen, male, has the crown width 5.3 mm.; in A.M.N.H. No. 65026, 5.5; in No. 65027, also 5.5 mm. In the last the enamelless root is already extruded through the alveolus.

The second incisor, anteriorly chipped against i^1 , has no true labial groove but instead is very slightly concave at its center. Its measurable crown length is 4.9 (probably 5.5 in the unworn tooth). In the next larger specimen (the front chipped) the crown length is 4.5; and in the oldest, in which this tooth is considerably worn, it is 4.9. The height of the enamel-bearing part of the tooth is 6.3 in the youngest, 5.2 in the oldest of the three. In the unworn "zoo" specimen, A.M.N.H. No. 80088, the posterior groove is not quite at the back but opens slightly towards the labial face. The length of the inner lamina is 5.4; of the outer lamina, 5.1 mm.

The third incisor in *Osphranter robustus*, one of the diagnostic organs when comparing this subgenus with typical *Macropus* or with *Megaleia*, has the elongate cutting edge of

Macropus (both much longer than that of *Megaleia*) but possesses one groove on the labial face instead of two. The crown of the juvenal male, slightly chipped and scarcely worn, has the measurable length 9.9 mm. (in unchipped state probably ± 10.2), the labial groove is placed 4.1 (± 4.4) mm. from the front of the tooth. The posterior angle of the crown is sharply angular, not rounded as in *Megaleia*.

The third premolar, badly abraded, cannot be adequately described in any of the three examples. Its inner surface is so completely worn down that no trace remains of the postero-internal cusp. Its length in the young male and female is 6.5–6.6 mm. The width of the anterior part is 3.7 and 3.5, that of the posterior portion (probably reduced by abrasion) is 4.0 and 4.2 mm. In a younger "zoo" specimen (locality unknown), A.M.N.H. No. 80088, p^3 is scarcely worn. There are a low postero-internal cusp and a large cingulum. The length is 7.4; the anterior width, 4.0; the posterior width, 4.6 mm.

The deciduous premolar, like p^3 , is strongly worn. Its length and anterior and posterior widths are 7.1 and 7.4, 6.2 and 5.8, 6.4 and 6.0 mm. The length might well reach 7.5, were the tooth unworn. In the unworn specimen, No. 80088, the length of this tooth is 8.8 mm.

In A.M.N.H. No. 65027, female, the fourth molar is 12.2 mm. long. The width of its anterior loph is 9.6; posterior loph, ± 9.0 mm.

The permanent fourth premolar (right) is newly erupted (while m^3 is not fully in position) in A.M.N.H. No. 65026. The main blade, 8.4 mm. in length, is deeply fissured at 2.9 mm. from the front, the anterior portion pointed and cusp like, the posterior portion more rounded in profile. The postero-internal cusp, although well set off by a valley from the sectorial blade, is rather small and is at least 1.5 mm. lower than the main blade. Anterior to this cusp the well-developed cingulum bows inward and bears one elongate cuspsule. It narrows again at the anterior half of the tooth, where it carries two more small cuspsules. The posterior width of the tooth, greatest at the cingulum cuspsule, is 4.4 mm.; the anterior width, 3.5 mm.

The lower third premolar in *robustus* (A.M.N.H. No. 65025) is blade like in its anterior portion (width, 2.4 mm.). At the very back it broadens, probably to form a postero-internal cusp, but no separating valley develops. The width at this cusp level, the maximum of the tooth, is 3.1 mm. The crown length of p_3 is 5.7 mm.

The condition of unworn p_4 can be determined from A.M.N.H. No. 65026. Only slightly larger than p_3 , the tooth is less contrastingly broadened at the back; the sectorial edge is sinuate and bends inward, making contact with the inner front of m_1 , instead of becoming transversely broadened as in p_3 . The anterior and posterior widths are, respectively, 2.6 and 3.0 mm.

In the three specimens just discussed the progressive inflation (with age) of the lateral walls of the rostrum, typical to some extent of all the large kangaroos but carried to its extreme in *antilopinus*, can be observed: rostral width, level with the back of the rostral processes of the premaxilla, in No. 65025, 29.3; in No. 65026, 30.5; in No. 65027, 36.9 mm.

Macropus (Osphranter) robustus *erubescens* Sclater

Macropus erubescens SCLATER, 1870, Proc. Zool. Soc. London, p. 126.

Macropus argentatus ROTHSCILD, 1905, Novitates Zool., vol. 12, p. 509.

Macropus robustus alexandriae SCHWARZ, 1910, Novitates Zool., vol. 17, p. 102.

Types: Not seen. Of *erubescens*, from Lake Hope, 200 miles interior from Port Augusta, South Australia. Of *argentatus*, from Northern Territory. Of *alexandriae*, from Alexandria, Northern Territory.

The Archbold collection contains nine specimens taken by G. Neuhäuser at Pentland, Mount Carbine, and Quamby in Queensland. Raven secured a dozen more at Kaban, Atherton Tableland, and near-by places. Twelve others were taken for the Museum of Comparative Zoölogy by W. E. Schevill in the Hughendon and Richmond areas. I have seen no wild-caught specimens from the south of Australia.

It is improbable that *erubescens* remains racially constant over such an enormous

north-south range as results from the above synonymy, especially as it may be desirable to include the brownish gray *alligatoris* here instead of in the synonymy of the red *antilopinus*. Nevertheless it seems likely that the wallaroos of Queensland west of the divide must be merged with *erubescens* (or its northern representative, which would carry the name *alexandriae*), leaving *reginae* for the darker, strictly coastal race.

It is worthy of note that the males of this inland race in the northern parts of its range have short, reddish gray pelage and blackish ears, while the females, which are very much smaller, have the ears colored gray and the general color pale drab gray, grayer in young, more drab brown in older specimens.

In i^2 of northern examples of *erubescens* there is a tendency to develop an ample though not extensive (up the enamel) median labial cleft and for the second (almost posterior) groove to be moved farther forward on the labial face of the tooth. This is especially noticeable in A.M.N.H. No. 65033, juvenal female, from Kaban. In it the median groove extends (in very shallow form) upward almost to the base of the enamel. This is far less apparent in No. 65029, however. The crown length in No. 65033 (inner lamina) is 5.4 mm. The anterior groove is 2.7 mm. from the front of the tooth, the posterior groove 5.0 from the front.

Compared with that of the juvenal U.S.N.M. No. 237607 (*antilopinus*) from south of Port Darwin, Western Australia, i^2 of the Kaban specimen has a much more definite posterior notch, and p^3 is narrower at the back and of more uniform width. In general, however, the two forms match very closely. Bearing in mind the occasional variability of p^3 and p^4 within a race, no more than racial distinction should be accorded them.

The tendency to carry the labial groove forward appears also in i^3 , e.g., in A.M.N.H. No. 65033, the groove being only 2.4 mm. from the front of the tooth.

In a pouch specimen, U.S.N.M. No. 238324, female (Hoy No. 1338), collected October 18 (young of female, No. 238323, collected same date), of *robustus erubescens* from Atherton Tableland, a pair of minute,

single-rooted teeth stand in the premaxillae slightly exterior to where the posterior portion of the main cutting blades of i^{2-3} is erupting. Their form is narrowly oval, their size 1.7 by 0.8. Are these remarkable teeth remnants of a "prelacteal" or a milk incisive dentition? They are not caniniform. Attention is drawn elsewhere to similar milk third incisors in *Macropus canguru major* and in *Thylogale*.

**Macropus (Osphranter) robustus
bernardus Rothschild**

Macropus robustus DAHL, 1897, Zoologist, ser. 4, vol. 1, p. 212.

Dendrodorcopsis woodwardi ROTHSCILD, 1903, Novitates Zool., vol. 10, p. 414.

Macropus bernardus ROTHSCILD, 1904, Novitates Zool., vol. 10, p. 543.

TYPE: Not seen. From the sandstone ranges of the Central Tableland in Arnhemland (Dahl).

This race, first discovered by Dahl and later collected by Tunney about the headwaters of the South Alligator River, is apparently a local, somewhat melanistic derivative of the *erubescens-alligatoris* (= *antilopinus*) type of *Osphranter*. Rothschild reports that *bernardus* and "*alligatoris*" occur together and that their skulls are "practically indistinguishable." The uplands of Arnhemland are probably somewhat more humid than the surrounding lower country and consequently carry more vegetation, which may account for the darker hues of *bernardus*. The color above and below, according to Rothschild, is "sooty brownish black."

**Macropus (Osphranter) robustus reginae
Schwarz**

Macropus robustus reginae SCHWARZ, 1910, Novitates Zool., vol. 17, p. 103.

TYPE: Not seen. From Mount Abbott, southeast of Townsville, northern Queensland.

As the type locality was very close to the sea and on the east side of the main ranges, it may be expected that *reginae* represents the darkest, most saturate of the color forms. Whether the race of *robustus* from the top of the divide should be named *reginae* is somewhat open to question. It is treated here

under *erubescens*. If shown to be truly distinct from southern *erubescens* it will probably take the name *alexandriae* Schwarz.

Macropus (Osphranter) robustus antilopinus
(Gould)

Osphranter antilopinus GOULD, 1842, Proc. Zool. Soc. London, for 1841, p. 80.

Macropus robustus woodwardi THOMAS, 1901, Novitates Zool., vol. 8, p. 395.

Macropus robustus alligatoris THOMAS, 1904, Novitates Zool., vol. 11, p. 224.

Macropus robustus rubens SCHWARZ, 1910, Novitates Zool., vol. 17, p. 99.

Macropus robustus bracteator THOMAS, 1911, Ann. Mag. Nat. Hist., ser. 8, vol. 7, p. 609.

TYPES: Thomas (1888, p. 22) referred to two (male and female) cotypes and later (1922, p. 128) indicated the male (B.M. No. 42.5.26.5) as lectotype; from Port Essington, North Australia. Of *woodwardi*, from Grant Range, Fitzroy River. Of *alligatoris*, from South Alligator River, Arnhemland. Of *rubens*, from Box Soak, Shaw River, Western Australia. Of *bracteator*, from McClintock Range, east Kimberly District, north Western Australia.

The cotypes of *antilopinus* were strongly reddish. The type of *alligatoris* as well as a series in the United States National Museum taken by Hoy is brownish gray with little red. Hoy's specimens of *alligatoris* were obtained in the same general area as his series of wide-muzzled *antilopinus*, about 100 miles south of Port Darwin. Therefore the two are either full species or the one (*antilopinus*) is a somatic specialization of the other.

The character of the greatly inflated rostrum, combined with short, broad nasals, has long been used to separate *antilopinus* from other types of *robustus*, and particularly from *alligatoris*. Both of these occur in the same general region and their dentitions are identical. It is suggested that some modifying factor—some parasitic or enzyme-producing agent, operating in the same way as galls modify the growth of plants—may be responsible for the exceptional degree of enlargement and shortening of the rostrum of *robustus alligatoris* (the unmodified) to produce *robustus antilopinus* (the modified). Instead, is this perhaps a dimorphic race pro-

ducing two distinct strains (with some intergrades) based upon genetic factors? If either of the above is true, the effect as far as the skull is concerned is strictly local. Characters modified (in *antilopinus*) include width of anterior palate, depth of buccal depression, width of anterior nares, width of nasals, length of nasals (?), lacrimal width, and width of the nasal process of the premaxilla. Unmodified characters (*alligatoris*) include dentition, anterior palatine foramina, maxillo-premaxillary suture in the palate, lacrimal contact with frontal, anteorbital canal, posterior portion of palate, and posterior (cerebral, optic, otic) portions of cranium.

In the pouch young (female) in Hoy's series, U.S.N.M. No. 237607, the crown of i^2 , wholly unworn, attains a length of 6.4 mm. along the internal lamina and 5.0 on the labial lamina. It may thus be thought of as a slightly larger tooth than in typical *robustus*. In a young male, U.S.N.M. No. 237614, the tooth, although chipped and slightly worn, still measures a total of 5.7 mm., but in the many older specimens this length is reduced to as little as 4.2 mm. The same is not true for i^3 , the maximum crown length of which is 10.7, with the labial groove varying in position from 2.9 to 4.1 mm. from the anterior edge.

The third premolar is also larger than that of our measured juvenal *robustus erubescens*: the length is 7.4 mm., the anterior and posterior widths are 3.6 and 4.5.

The fourth (permanent) premolar tends also to be slightly larger. Even in some worn specimens the length may reach 9 mm., although it may be as little as 7.8. The anterior width varies from 4.2 to 4.5 in little worn specimens and the posterior width from 4.5 to 4.9. These figures are based mainly upon Hoy's material.

Macropus (Osphranter) robustus isabellinus
(Gould)

Osphranter (?) isabellinus GOULD, 1842, Proc. Zool. Soc. London, for 1841, p. 81.

TYPE: Not seen. A skin without skull from Barrow Island, off the coast of northwestern division, Western Australia.

I have seen no specimens of this island form, which was re-collected by Tunney in

1900 (Troughton, 1941, p. 228). Waite (1901) gave a quite detailed description of the race, showing it to be somewhat smaller than the form occurring on the mainland (*rubens*). The skull depicted in his illustrations is unquestionably that of an *Osphranter*.

Macropus (Osphranter) robustus cervinus
Thomas

Macropus robustus cervinus THOMAS, 1900, Proc. Zool. Soc. London, p. 113.

TYPE: Not seen. From Yalgoo, Murchison District, middle Western Australia.

The Museum of Comparative Zoölogy has a short, wild-taken series of this race: three from Nannekine (labeled "topotypes"); three from Meekathera; and one from Mullewa. There is one specimen at the United States National Museum (No. 155369).

In all these the coat is deeply red, with little or no gray or black hairs, and the pelage is relatively long and soft, certainly much longer and softer than that of the tropical races previously treated.

The patchy geographical distribution has been shown by Shortridge (1909, p. 808), although it is here suggested that the material from north of the Ashburton River, being short haired, may be better thought of as representing the tropical form *antilopinus* (locally, *rubens*).

The third premolar, unworn in M.C.Z. No. 29311, is 6.5 mm. in length, 3.5 wide anteriorly, and 4.0 posteriorly. This is well within the dimensional range of *robustus robustus*. The fourth molar is unerupted but visible in three of the specimens listed. In those three p^4 is in place (unworn in one of them). In the unworn specimen, M.C.Z. No. 28035, female, the length of p^4 is 8.7 mm.: its greatest (posterior) width, 4.7; its anterior width, 4.0 mm. This suggests a tooth somewhat smaller than that of true *robustus* but may not be relied on because founded upon a single individual.

SUBGENUS **MACROPUS** SHAW AND NODDER
(SENSU STRICTO)

Macropus (Macropus) canguru (Müller)

The status of this, the great gray or Captain Cook's kangaroo, has already been discussed. *Macropus canguru*, which comprises

several geographical races, is distinguished subgenerically from the equally large red kangaroos and antilopine kangaroos by characters of the skull and teeth. The unworn crown of the unusually elongate third upper incisor in *canguru* is twice as long as are the combined crowns of i^{1-2} . It has two external grooves that divide the labial face of the tooth into three lobes, the posterior of which is as large as the middle and anterior ones combined. The outer margin of the ectopterygoid fossa is smoothly rounded instead of sharply ridged as in *Osphranter robustus*. Additional skull characters of this kangaroo were set forth when comparing it with *Osphranter* and *Megaleia*.

There is a hair whorl at the middle of the back, anterior to which the hair slopes forward to between the ears. The complete hair covering of the internarial septum has long been employed as a diagnostic skin character.

The black-faced kangaroo, which has received the name *Macropus melanops* Gould, is regarded today by some Australian zoologists as a variation prone to occur in the more densely shrubby portions of the ranges of both the east Australian *canguru major* and the Western Australian *c. ocydromus*. Thus it perhaps represents merely a somatic variant. The Western Australian *melanops* has frequently a white mark on the forehead (Le Souef). Otherwise, the several large kangaroos possessing two folds in the labial face of i^3 related to *canguru*, namely, *major*, *ocydromus*, *fuliginosus*, and *tasmaniensis*, are in this paper given the ranks of geographical races only.

The kangaroos of this subgenus were discussed by Le Souef (1923).

Macropus (Macropus) canguru canguru
(Müller)

Mus canguru MÜLLER, 1776, Linné . . . vollständiges Natursystem . . . swölfter Lateinischen Ausgabe, p. 62.

Jerboa gigantea ZIMMERMANN, 1777, Specimen zoologiae geographicae quadrupedum, p. 526.

Jaculus giganteus ERXLEBEN, 1777, Systema animalium, p. 409.

Didelphis gigantea SCHREBER, 1777, Die Säugethiere, vol. 3, p. 552 (pl. 154, published later).

Macropus giganteus SHAW AND NODDER, 1790, The naturalists miscellany, vol. 1, text for pl. 33.

Macropus major SHAW, 1800, General zoology, vol. 1, pt. 2, p. 505, pl. 105 (part).

Types: Not in existence (Thomas, 1888).

The type locality of this race is close to Cooktown, Endeavour River, northern Queensland. Although there are probably no topotypes in existence, Raven (1939) has pointed out that specimens have been recorded only 40 miles from the type locality. The nearest approach to topotypical material at this museum comprises A.M.N.H. No. 107375, old male, skin and skull collected by Gabriele Neuhäuser at Mount Carbine, 1200 feet, and a skull, A.M.N.H. No. 153071, by the same collector, from an unknown locality also in northern Queensland. Dental features of these specimens are:

| | A.M.N.H. No. 107375 | A.M.N.H. No. 153071 |
|-----------------|------------------------|------------------------|
| | ADULT MALE | ADULT |
| p ³ | Shed | Shed |
| dp ⁴ | Shed | Shed |
| m ¹ | Shed | 10.0 × 7.9 |
| m ⁴ | 12.2 × 10.0 | 12.6 × 10.1 |
| p ⁴ | Shed | Shed |

Compared with skins attributed to the South Australian race *major* from the Cairns area (Atherton Tableland) and from southern Queensland, that taken by Neuhäuser at Mount Carbine is significant for the shortness of the pelage and for its pallid coloration. It was collected in mid-December. The length of the dorsal pelage is only 10–12 mm., compared with 25 (Kaban in April), 20–25 (Ravenshoe in January), 40–50 (New South Wales from July to August). It appears probable that this race with extremely short thin hair, exemplified by our specimen from Mount Carbine, may be the real "Captain Cook's kangaroo."

***Macropus (Macropus) canguru major* Shaw**

Macropus major SHAW, 1800, General zoology, vol. 1, pt. 2, p. 505, pl. 115.

TYPE: Probably not in existence. The type locality was restricted to "Botany Bay" = Sydney, New South Wales, by Iredale and Troughton (1934).

This race is regarded as the principal and

most widely distributed (as opposed to the typical race, *M. c. canguru*, of the extreme north of Queensland) race of the great gray kangaroo. It is held to extend from the Atherton area of north Queensland south to northern Victoria and South Australia. If we may believe McCoy (1867), the Kangaroo Island race *fuliginosus* replaces or formerly replaced it on the mainland in the extreme south of South Australia.

The American Museum collection includes a considerable number of skulls and a few skins of this race, taken by H. C. Raven in two areas: the Atherton region (about 15 specimens), near Cairns, in the southern part of northern Queensland, and the Mundubera District (five specimens), some 150 miles northwest of Brisbane. In addition, we have random specimens (mostly zoological garden material without locality), at least two of which are from New South Wales.

The first incisor, wholly unworn in the pouch female, A.M.N.H. No. 65017, has the crown width 6.5 mm. The same width shows in A.M.N.H. No. 66180, female, in which m¹ are in place.

The second incisor, unworn in A.M.N.H. No. 66180, young female, has a labial groove and a narrow, posterior groove. The crown length is 6.0 mm., and the labial groove is 3.2 mm. from the front of the tooth. The inner and outer sides of the posterior groove are of equal length. Neither of these grooves is deep, so they are soon worn away.

The third incisor, as is typical in *canguru*, bears two labial grooves, both of which penetrate the body of the tooth more deeply than those of i² and the posterior of which is deeper than the anterior. The crown length in A.M.N.H. No. 66180 is 10.2 mm. The anterior groove commences 3.0 mm. from the front of the tooth, and the posterior groove 4.6 mm. from the front.

The third premolar, unworn in A.M.N.H. No. 65017 and very slightly worn in A.M.N.H. No. 66180, is typically hourglass shaped, with the anterior portion (width 3.7 mm.) separated from the posterior portion (width 4.8) by deep internal and external grooves. The postero-internal cusp is large and is functionally continuous with the two internal cusps of dp⁴. The anterior part of the internal

cingulum is much reduced and bears a single low cusp. The length of p^3 is 7.3 mm.

The length of the deciduous fourth premolar varies from 9.4 to 8.4 mm. The width of the anterior loph is from 7.0 to 6.0; of the posterior loph, 7.5 to 6.5. In older specimens the tooth may become as short as 7.5 mm. through abrasion.

The first molar, first erupted of the molars and retained until p^4 has been shed, is much subject to abrasion. The length of the newly erupted tooth varies from 8.5 to 10.7 mm.; the width of the anterior loph is ± 7.0 ; that of the posterior loph, ± 7.5 . In old specimens wear has often reduced the length of the tooth by 1 mm.

The fourth molar is found fully erupted in only one of our wild-caught individuals. It is seen to be partly through in five of them. This tooth never attains the large size seen in *M. rufus*. It varies in length from 11.7 to 12.8 mm. The width of its anterior loph varies from 8.6 to 9.1; that of its posterior loph is ± 8.0 mm.

The permanent fourth premolar erupts only slightly ahead of m^4 ; in A.M.N.H. No. 65020 from southern Queensland the left premolar is in place, and the right is coming through synchronously with m^{4-4} . In A.M.N.H. No. 65022 from the same region, virtually equal in age, this premolar is definitely somewhat more advanced than m^4 , that of the right side being much worn and the tooth of the left side already shed. In an aged male with m^{4-4} fully in place, A.M.N.H. No. 65023, all four permanent premolars have been shed.¹

¹ I draw attention here to an anomalous premolar in U.S.N.M. No. 236686, a male (labeled *melanops*), one of two specimens (the female is U.S.N.M. No. 236687) taken by Hoy at Port Lincoln, near the tip of the Eyre Peninsula, 100 miles northwest of Kangaroo Island. The outline of the premolar is subtriangular through the great enlargement of the postero-internal cusp, which is set off from the main blade by a deep valley. The tooth is thus shaped almost like a trefoil. Its length is 10.5 mm.; the width of the (normal) anterior portion, 4.5 mm.; the width of the (anomalous) posterior portion, 8.7 mm. The deciduous p^4 is still present on that side, its length 10.5 and greatest width 9.5. But on the opposite side of the jaw permanent p^4 is already in position, its length 9.0, anterior width 4.7, posterior width 5.6. The permanent premolars of the female are normal, but smaller. The third molars are in position, with the fourth molars visible in the alveoli.

In A.M.N.H. No. 65017 a pair of minute rounded teeth, deciduous or "prelacteal" incisors homologous to those described in *robustus reginae*, can be perceived. These teeth, however, are less elongate, more rounded. Their dimensions are ± 1.5 mm. by 1.2 mm.

Macropus (Macropus) canguru ocydromus
Gould

Macropus ocydromus GOULD, 1842, Ann. Mag. Nat. Hist., vol. 10, p. 1.

TYPES: In the British Museum. Thomas (1922) indicated B.M. No. 44.7.2.1 as "lectotype" (male, specimen k of his 1888 "Catalogue"). Originally two cotypes, the above mentioned and specimen 1, a female, were indicated. Both were from the Swan River, Western Australia.

Thomas (1888, pp. 18-19) had an extensive series of this south Western Australian *canguru*. The principal collection in America is the small series, including most age stages, in the Museum of Comparative Zoölogy. Specimens are from Pemberton and Pindawa Well, Western Australia. The distribution of this race has been indicated by Shortridge (1909) and by Glauert (1934).

The first incisor is not tapered towards the tip, even in pouch young. Its width in a pouch female (M.C.Z. No. 28028) is 6.2 mm.; in an old female, 5.1; in a second, unsexed juvenal, 5.6.

The crown of i^2 in the unworn state is provided with two labial grooves: one at the middle, the other almost at the back of the tooth. In the above-mentioned pouch female the total length of the blade of i^2 is 6.1 mm.; in the young specimen, M.C.Z. No. 28070, this is reduced by attrition of the shortening crown to 5.5; and in the old M.C.Z. No. 28029 to 4.1. The tooth is chipped both anteriorly and posteriorly and badly worn.

The third incisor was not erupted in M.C.Z. No. 28028. It has been lost in M.C.Z. No. 28070 (the alveolus, 7.2 mm.) and in the old female, M.C.Z. No. 28029, was chipped and much worn, leaving a total crown length of only 8.4 mm. However, it could be observed that this tooth bears the twin labial grooves that characterize i^3 in *canguru*.

The third premolar in a juvenal male, M.C.Z. No. 28071, is 7.4 mm. in length by

5.4 in posterior width and 4.2 in anterior width. In a second, probably female, specimen these measurements are 6.6, 6.0, 3.8—wider behind and more compressed in front. This tooth has the hourglass shape seen in *canguru major*.

The first molar has an original length of about 10.5 mm., which is often reduced by abrasion to 10.0 or less. Its width (posterior loph) varies from 8.0 to 8.5 mm.

The fourth molar, found in two female specimens, M.C.Z. Nos. 28018 and 28029, varies from 13.5 to 13.6 in length, from 9.3 to 9.5 in the width of its anterior loph, and from 8.9 to 9.3 in the width of its posterior loph. In both of these specimens p^4 has already been shed.

The deciduous premolar in both M.C.Z. Nos. 28070 and 28071 is 8.8 mm. in length; its greatest (posterior) width varies from 7.1 to 7.4 mm.

The lacrimal processes in *ocydromus* are rather prominent; the anteorbital canal is very short (± 4.8 mm.); the meatal width, ± 4.0 . The length of the anterior palatal foramina is ± 7.5 . The posterior part of the palate is but slightly fenestrated.

Macropus (Macropus) canguru fuliginosus
(Desmarest)

Kangurus fuliginosus DESMAREST, 1817, Nouveau dictionnaire d'histoire naturelle, nouv. ed., vol. 17, p. 35, pl. 22.

TYPE LOCALITY: Kangaroo Island, South Australia.

This museum possesses a young adult (A.M.N.H. No. 74140) from Kangaroo Island presented by Prof. F. Wood Jones. A male "zoo" specimen, A.M.N.H. No. 90356, only slightly older is reputed to represent this race. In addition there are five topotypical specimens in the United States National Museum, two of them juvenals and one an adult with p^4 and m^4 in place. The third and fourth premolars of *fuliginosus* appear to be considerably larger than those of mainland *M. canguru major*.

The first incisor in U.S.N.M. No. 236682, juvenal male, has the crown length 6.7 mm. That of a slightly older female is 6.1; those of two other young females (somewhat worn) are less. It appears then that the erupting tip

of the crown may be slightly broader than the part which follows.

The second incisor is provided with two labial grooves, a faint anterior and a strongly marked posterior one. The back of the tooth is also notched. The maximum crown length (in juvenal male U.S.N.M. No. 236682) is 7.2 mm. The shallow anterior groove stands 3.0 mm. behind the front edge of the tooth and the deep posterior groove 6.0 mm. from the same edge. Abrasion and chipping quickly reduce this to 6.6 mm. long, with grooves 2.8 and 5.1 from the front. In U.S.N.M. No. 236699, young female, and in U.S.N.M. No. 236683, female (with m^3 present), the grooves are worn away and the crown length is cut down to ± 4.7 mm.

The third incisor, unworn in U.S.N.M. No. 236682, has the crown length 12.0 mm. Its two distinct labial grooves are at 2.7 and 4.0 from the anterior edge of the tooth. This tooth is also speedily worn down; the same measurements in No. 236683, female (with the tooth chipped against i^2), are 11.5, 1.8, and 3.9 mm. This tooth thus appears to be slightly larger than in *major*.

The third premolar is also rather large. Its length in the young, unworn male is 8.3 mm. Its anterior width is 4.6 mm. and posterior width 5.0. In a scarcely older female the same dimensions are 7.3, 4.2, and 4.8 mm. This tooth and dp^4 are usually shed between the eruption of m^2 and m^3 .

The deciduous premolar may reach a length of as much as 10.4 mm., and the anterior and posterior widths range from 6.5 to 8.1 and 7.1 to 9.0. The usual size is length 9.0, anterior and posterior widths 7.0 and 8.0 mm.

The measurements of the first molar in unworn condition are highly variable: length from 9.9 to 12.2 mm.; width of anterior loph from 8.0 to 8.8; width of posterior loph from 7.9 to 9.7.

The fourth molar, present in only one specimen (U.S.N.M. No. 236681, male), has the length 14.2 mm., the width of the anterior loph 11.8 (the posterior part of this incompletely erupted tooth could not be measured).

The permanent fourth premolar, present in the same specimen, is 10.3 mm. long. The anterior width is 4.0; the posterior width, 5.7.

It is thus substantially larger than the same tooth in *major*.

In *M. c. fuliginosus* of Kangaroo Island the skull, the braincase, and the zygomata are broad in contrast to the relatively narrow rostrum. The frons is low and nearly flat. Jones (1923-1925, fig. 181; 1924) has illustrated other characters.

Macropus (Macropus) canguru tasmaniensis
Le Souef

Macropus giganteus tasmaniensis LE SOUEF, 1923, Australian Zool., vol. 3, p. 145.

The single specimen in our collection attributed to the race *tasmaniensis* is a "zoo" animal, A.M.N.H. No. 70115, male. Judging by the state of the bones of the skull, it was in poor health; p^3 , dp^4 , m^1 , and m^2 are in place; p^4 and m^{3-4} are not yet developed. Compared with that of mainland *major* and King Island *fuliginosus*, dp^4 of this animal is very small.

The first incisor, somewhat worn, has the crown breadth 5.8 mm. The second incisor, scarcely worn, has two labial grooves and no posterior groove. Its crown length is 5.9 mm. The anterior groove is 3.0 from the front of the tooth; the posterior one, 5.4. The latter corresponds to the posterior notch of other *Macropus*.

The third incisor, with crown length 10.6 mm., is quite unworn. Its first groove is 2.5 from the front of the tooth, its second groove 4.5 from the front.

The third premolar is 6.7 mm. in length. Its anterior and posterior widths are 4.1 and 5.1.

The length of dp^4 is 8.6 mm.; the width of the anterior loph, 6.4, of the posterior loph, 7.0. The same dimensions for m^1 are 10.5, 7.7, and 8.2.

The incisive foramina are only 4.5 mm. in length, the anteorbital canal but 5.5. The skull seems to resemble that of *fuliginosus* most closely.

SUBGENUS MEGALEIA GISTEL

Megaleia GISTEL, 1848, Naturgeschichte Thierreichs höhere Schulen, Stuttgart, p. ix [copy in library, Academy of Natural Sciences of Philadelphia].

Gerboidea GERVAIS, 1855, Histoire naturelle des mammifères, vol. 2, p. 271.

Boriogale OWEN, 1874, Phil. Trans. Roy. Soc., London, vol. 164, p. 247.

TYPES: Of *Megaleia*, *Halmaturus laniger* Gaimard = *rufus* Desmarest. Of *Gerboidea*, *Kangurus rufus* Desmarest (by original designation). Of *Boriogale*, *Macropus (Boriogale) magnus* Owen (by monotypy).

In a long list of generic and subgeneric names, Gistel (above) proposed *Megaleia* as a subgenus of *Halmaturus*, indicating *H. laniger* as its representative species. Palmer (1904) has shown the type of *Megaleia* to be *laniger* Gaimard [by original designation and by monotypy]. No word of description accompanied the proposal of either *Megaleia* or *Gerboidea*. Owen, erecting *Boriogale*, briefly compared its premolars with those of *Osphranter robustus*. The present group was reviewed by Schwarz (1910a) and in part by Finlayson (1936).

Megaleia possesses a number of characteristics not shared by *Macropus* (*sensu stricto*) or *Osphranter*. These characteristics include the unusually large size of m^4 ; the shortness of the crown of i^3 , in which (A.M.N.H. No. 6418/8061) a trace of a shallow groove is visible, 2.2 mm. from the front; the slenderness of the incisive roots; the deeply and abruptly excavated median depression in the base of the rostrum immediately behind i^{1-2} ; the usually very elongate anterior palatal foramina; the considerable depth of the rostrum (in contrast to that of *M. canguru*); the long anteorbital canal; the enlarged facial portion of the lacrimal; the enlarged outer opening of the auditory meatus; and the broad \cap -shape of the pterygoid fossa, when viewed from behind.

Certain characters are shared with one of the above-mentioned subgenera and not with the other. With *Osphranter*, the considerable depth and shortness of the rostrum, the deep median keel on the basioccipital; with *Macropus*, the presence of a postglenoid foramen, and the shallowness of the mandibular ramus in comparison with that structure in *Osphranter*.

Externally *Megaleia* is normally dichromatic; the males are rufous, the females bluish gray. Young males are gray with rufous hair bases. *Megaleia* contains only the species *rufus*.

Macropus (Megaleia) rufus (Desmarest)

The red kangaroo or (in the female) the blue flyer is a single species weakly divisible into three races. Typically it occurs as a red race in the southeastern portion of Australia. A second normally red race, *dissimulatus*, of which this museum has no specimen, is found in south Western Australia and a third, very short-haired, russet gray race, *pallidus*, in north Western Australia and the interior of northern Queensland.

The three races of *rufus* are so closely allied and information on their dentition at all ages is so meager that I have preferred to discuss the dental characters of the races together in one place and to point out any contrasting characters that can be observed.

The characters of the incisor teeth in an unabraded state have been observed in only a few specimens of the Queensland race *pallidus*. The first incisor is tapered; its width in pouch young (M.C.Z. No. 29394) is only 5.4 mm. This increases gradually to 6.5 mm. in old males.

The second incisor in unworn, unchipped specimens (pouch young) has the length of the cutting edge varying from 5.2 (M.C.Z. No. 29419, female) to 5.8 (M.C.Z. No. 29394, female). In a juvenal male (M.C.Z. No. 29384) this tooth blade, already slightly chipped in front, still measures 5.7 mm. In subadults the tooth blade becomes shortened to 5.0, 4.8, by chipping of its front and rear against i^1 and i^3 . The blade shows no labial groove, but a posterior one into which i^3 is notched. The blade of the third incisor is initially from 7.9 to 8.0 mm. in length, the single labial groove being placed from 2.3 to 2.8 mm. from the anterior end. Chipping of the front of the tooth against i^2 and abrasion of the entire tooth crown against the lower incisor soon reduce its length to 7.0 or less.

The third premolar, a relatively little-compressed tooth, when newly erupted is 8.0 mm. in length by 5.0 (posterior) and 4.0 (anterior). In a young male *dissimulatus* from Western Australia (M.C.Z. No. 28027), p^3 is 7.3 mm. in length, 5.9 in posterior width, and 4.5 in anterior width. This tooth becomes greatly crowded in older specimens so that its maximum dimensions may be reduced to

6.8 by 4.3 (posterior), 3.9 (anterior). The tooth is shed with or slightly before dp^4 .

The molariform dp^4 in *pallidus* of Queensland may have an original length of 8.6 mm. and greatest width of 6.8 (M.C.Z. No. 29381, juvenal female), but its length is speedily reduced, first by wear against p^3 and later against m^1 . In M.C.Z. No. 29384, juvenal male, the length of this tooth, unworn, is only 7.5. Its greatest width varies from 6.2 to 6.8 mm. So, too, with m^1 ; in the newly erupted state its length may be 10.4, but longitudinal wear reduces it substantially. The large (and very late-erupted) m^4 varies from 14 to 15 mm. by 10.0 to 10.7 mm.

The permanent p^4 in *rufus* is usually slightly smaller and narrower than p^3 . In M.C.Z. No. 29368, young adult male from Richmond, Queensland, it replaced dp^4 before m^1 was in place, but more usually m^3 is in place before p^4 appears. In *pallidus* (A.M.N.H. No. 107694), having $m^{4\frac{1}{2}}$ in place, one p^4 has already been shed. The permanent fourth premolar in true *rufus* of South Australia (A.M.N.H. No. 65037, adult male) measures 7.2 by 4.1 (posterior width); in young adult male from Queensland, *pallidus* (M.C.Z. No. 29368), 8.0 by 4.7 (posterior), 3.5 (anterior).

Macropus (Megaleia) rufus rufus (Desmarest)

Kangurus rufus DESMAREST, 1822, Mammalogie ou description des espèces de mammifères, suppl., vol. 2, p. 541.

Kangurus laniger GAIMARD, 1823, Bull. Soc. Philom., Paris, p. 138.

Macropus (Boriogale) magnus OWEN, 1874, Phil. Trans. Roy. Soc., London, vol. 164, p. 247.

TYPES: If in existence, the types of *rufus* and *laniger* should be in the Paris Museum, that of *magnus* in the British Museum among the Owen paleontological collection. Localities are: of *rufus*, Blue Mountains; of *laniger*, Port Macquarie; of *magnus*, "northern" parts of South Australia.

This kangaroo is poorly represented in American collections. Besides a number of "zoo" specimens, the American Museum has but two wild-caught individuals, Nos. 65037 and 65038, adult males from Halet, between Adelaide and Terawi, South Australia, obtained by H. C. Raven in 1921. Both have the

characteristic woolly, orange brown fur of southeastern males. The United States National Museum has two wild specimens from Coombie, northern New South Wales (Nos. 38529, male, and 38858, female) and one from Farina, north of Lake Torrens, south Australia (No. 236689, male).

McCoy (1867) wrote of *rufus*: "only found towards the warm northern boundary of the colony [Victoria], where it occurs in immense numbers . . ."

Macropus (Megaleia) rufus dissimulatus
Rothschild

Macropus rufus dissimulatus ROTHSCILD, 1905, *Novitates Zool.*, vol. 12, p. 508.

Macropus rufus occidentalis CAHN, 1906, *Zool. Beob.*, vol. 47, p. 361.

TYPES: Of *dissimulatus*, presumably at Tring. Of *occidentalis*, at the Senckenberg Museum, Frankfurt. According to Glauert (1934) the type locality of *dissimulatus* is probably the Gascoyne River. That of *occidentalis* is the Murchison River, a few miles to the south of the Gascoyne River.

Material in America representative of this race includes M.C.Z. No. 28027, male, from Yandil, in which the pelage, entirely in agreement with Schwarz's (1910a, p. 90) remarks, is very red and densely velvety.

According to Schwarz (1910) the original *dissimulatus* was a specimen of south Western Australian *rufus* "in gray pelage." Just how common such a variant is cannot now be ascertained, but Glauert states that "blue" males are not rare about the Gascoyne. The usual color of the south Western Australian race, deep russet in males and also in the majority of the females, conforms to the description given by Cahn for *occidentalis*. Shortridge (1909, p. 810) shows *rufus* to be absent from the extreme southwestern corner of the continent. He writes, "the females, although normally blue, are frequently of the same sandy-red color as the males; the males themselves being very rarely but occasionally, blue." This probably explains the color of Rothschild's type of *dissimulatus*.

Macropus (Megaleia) rufus pallidus Schwarz

Macropus rufus pallidus SCHWARZ, 1910, *Novitates Zool.*, vol. 17, p. 89.

TYPE: Not seen. From Shaw River, a

tributary of De Grey River, approximately latitude 21° S., north Western Australia.

Material from the typical area is still very scarce in collections. One specimen (U.S.N.M. No. 155371) from Woodstock, north Western Australia, is in the United States National Museum. From the environs of Richmond and Hughendon, along the Flinders River, northern Queensland, a very fine series taken by P. J. Darlington and W. E. Schevill can be seen at the Museum of Comparative Zoölogy. In the American Museum of Natural History is a specimen taken by Neuhäuser at Malbon, near the southwest corner of northern Queensland. Darlington also records it from near Coen.

In view of the known climatic shift towards extreme aridity of the central and western parts of Australia during Quaternary time, I see no objection to the view that the short-haired pallid form of *rufus* formerly extended from the northwestern division of Western Australia across the continent to western Queensland. The very short (but nevertheless woolly), pale, sandy red hair of the males of this race seems to be uniform, whether Queensland specimens or Western Australian specimens are considered.

It has been customary for some time to place *pallidus* in the synonymy of *dissimulatus*. In point of fact, the latter may well be closer to typical *rufus*, the more humid climate of the immediate past having permitted former contact between those two races of similar southern latitudes. All the specimens of *pallidus* seen by me are strikingly different in color from either *rufus* or *dissimulatus*.

SUBFAMILY STHENURINAE

Raven and Gregory (1946) placed the two extinct genera *Sthenurus* and *Palorchestes* apart from other Macropodinae in the subfamily Sthenurinae. I find it impossible to reconcile the gigantic, long-snouted *Palorchestes* satisfactorily with the broad-headed, short-faced *Sthenurus*, even on so broad a basis as the subfamily. Although parts of the skull of *Palorchestes* (*azael* only) and several rather complete skulls of *Sthenurus* are known, little is known of their skeletons. The only known structures common to the two genera are the forms of the permanent premolars, p_3^s and p_4 . It is questionable whether

these isolated resemblances are sufficiently cogent to warrant bringing the two so close to one another, especially when the molars and upper fourth premolars are considered. Accordingly, I have separated *Palorchestes* from *Sthenurus*, and have introduced for the accommodation of the former the subfamily Palorchestinae.

When Owen prepared his manuscripts on fossil Macropodidae (1874 to 1880) he possessed comparatively little material representing *Palorchestes*. His published texts are made difficult of interpretation today by his system of dental nomenclature. (He designated the last molars of marsupials as m_3^2 instead of m_4^1 .) Lydekker (1887) rectified the dental nomenclature of Owen. It remained for De Vis (1896) to sum up the scattered information on *Sthenurus*, *Palorchestes*, and the Macropodinae. In spite of the greater quantity of material then before him, De Vis failed to illustrate or describe the form of dp_4^1 in *Palorchestes*. (They are clearly molariform in *Sthenurus*, as shown in Owen's drawing, 1874, pl. 22, figs. 3, 4.) De Vis' illustration (*ibid.*, pl. 14, fig. 1), though marked "lower deciduous premolar," is not molariform.

Lydekker (1887, p. 231) pointed out the completeness of the internal crest of the premolars of *Sthenurus*, *Procoptodon* (p. 232), and *Palorchestes* (p. 237) in comparison with the rudimentary state of that crest in modern Macropodinae. De Vis (1896, p. 80) emphasized further the distinctness of both *Palorchestes* and *Sthenurus* from his "*Halmaturus*" (which included modern *Protemnodon* and *Thylagale*).

STHENURUS OWEN

Sthenurus, together with *Procoptodon* and its synonym *Pachysiagon*, demonstrates the development among the Macropodidae of extreme shortening, deepening, and increased massiveness of the skull and jaws. The diastemata are much shortened, and the roots of the lower incisors are set sharply upward at a decided angle to the molar tooth line.

De Vis, in his treatment of the genus (1896, pp. 88-89), concluded that *Sthenurus* and *Procoptodon* were congeneric. A valuable and extensive series of figures accompanied that treatment. It is clear from these figures that the upper permanent premolar is much

larger than the lower. This reduced size of the lower premolar conforms with the condition to be seen in most other Australian marsupial families.

Procoptodon appears to be an offshoot of *Sthenurus*, distinguished from it by accentuation of the shortening and deepening of the mandibles and by development of more sculpturing, "a series of vertical folds" (Lydekker), in the enamel of the molars. This latter distinction can be readily appreciated from figures. I conclude provisionally that *Procoptodon* may be subgenerically distinct from *Sthenurus*.

The very great depth of the mandible (taken beneath m_1 , 49 mm.) in *rapha* (Owen, 1874, pl. 78, fig. 1) is evident, in proportion to the length of the ramus from the front of the symphysis to the back of the angle (160 mm. in same figure), as is also the fact that the back of the symphysis lies beneath the anterior loph of m_1 . In one respect, namely, the size of p_4^1 in proportion to the size of m_1^1 , *Procoptodon* is less specialized than typical *Sthenurus atlas*; this is apparent in *P. rapha* (Owen, 1874, pl. 77, figs. 8, 10).

SUBGENUS STHENURUS OWEN

Sthenurus OWEN, 1873, Proc. Roy. Soc., London, vol. 21, no. 141, p. 128; 1874, Phil. Trans. Roy. Soc., London, vol. 164, pt. 1, pp. 265-274.

TYPE: *Macropus atlas* Owen.

Sthenurus has relatively unornamented molars; their lophs are high, sharp, and rectilinear.

Sthenurus atlas (Owen)

Macropus atlas OWEN, in Mitchell, 1838, Three expeditions into the interior of eastern Australia, vol. 2, p. 359, pl. 29, fig. 1.

In the figure of the type specimen from Wellington Valley the very large unerupted p_4 is shown still inside the cut-away mandible, with the small bilophodont dp_4 still in place above it. The molars (m_{1-2}) are high-cusped bilophodont structures. The crown lengths of dp_4 , p_4 , and m_1 measure, respectively, ± 11 , 19, and 13 mm. The outer faces of the molars are but little fluted. The depth of the ramus beneath m_1 is ± 23 mm.

In Anderson's specimen b from Mammoth Cave, Western Australia (1932, pl. 45, fig. 1), there are present a premolar and five molari-

form teeth, which must be interpreted as p^3 , dp^4 , and m^{1-4} . His specimen a (a cast), also from Mammoth Cave, exhibits the very large p_4 characteristic of typical *Sthenurus*. The normally projecting nasals (for example, in pl. 46, fig. 1) do not show in this specimen. Specimen c from King Island, Tasmania, is also an adult with p^4 , m^{1-4} in place. Anderson drew attention to the unusual depth of the jugal posteriorly. This material appears to be specifically identical to the Tasmanian specimen which Scott (1906) discussed under the name "*Procoptodon rapha*."

The restoration of *Sthenurus* depicted by Raven and Gregory (1946, fig. 9) appears to be founded upon the work of Glauert, Scott, and Anderson.

SUBGENUS PROCOPTODON OWEN

Procoptodon OWEN, 1873, Proc. Roy. Soc., London, vol. 21, no. 145, p. 387; 1874, Phil. Trans. Roy. Soc., London, vol. 164, pt. 2, pp. 786-797.

Pachysiagon and *Leptosiagon* OWEN, 1874, Phil. Trans. Roy. Soc., London, vol. 164, pt. 2, pp. 784-785.

TYPES: Of *Procoptodon*, *Macropus goliah* Waterhouse. Of *Pachysiagon*, *P. otuel* Owen. Of *Leptosiagon*, *L. gracilis* Owen.

In view of the great depth of its ramus, its extremely short massive symphysis, and its very short diastema, "*Palorchestes*" *crassus* Owen may belong here (see my remarks under that genus).

Lydekker (1891), discussing the mandibles of two specimens of *Procoptodon*, from northern New South Wales, pointed out among other things the extreme height of the outer wall of the masseteric fossa, the summit of which reaches the level of the molar series, and depicted the aperture of the fossa (pl. 21, fig. 2a).

Sthenurus (*Procoptodon*) *goliah* (Waterhouse)

Macropus goliah WATERHOUSE, 1846, A natural history of the Mammalia, vol. 1, p. 59.

Waterhouse's brief remarks serve little beyond establishing authorship of the name *goliah*. The type, from Darling Downs, was said to be a part of a "right" maxilla containing two molar teeth, "the two molars measuring together in the longitudinal direction one inch and a half [± 38 mm.], and the width of one of the molars being $7\frac{1}{2}$ lines [± 16

mm.]. The only right maxilla indicated in Lydekker's "Catalogue" (1887), of which he remarked, "This specimen is the type," contained "the last three true molar teeth" instead of two as stated by Waterhouse. It was figured by Owen (1874, pl. 79, fig. 1). It is difficult to reconcile these two statements, especially as Waterhouse cites Owen's manuscript. One wonders whether the specimen depicted on the same plate (fig. 8) may be the original *goliah*. It is a right maxillary (not a left mandibular as stated) fragment containing two molars. The length of these two molars is 48 mm. and the width of the largest 18 mm. The degree of enlargement, if any, of Owen's figures is not given.

De Vis (1896, pp. 89-93 and pl. 15) furnished further information on this species and published pictures of individual teeth.

PALORCHESTINAE, NEW SUBFAMILY

PALORCHESTES OWEN

Palorchestes OWEN, 1874, Phil. Trans. Roy. Soc., London, vol. 164, pt. 2, pp. 797-800.

TYPE: *Palorchestes azael*.

A second species, *P. parvus* De Vis, has been described.

Large to very large, extinct, kangaroo-like marsupials having the rostrum elongate, the posterior palate entire, the anterior palatal foramina united and placed halfway between the canines and the premolars. In the dentition i^3 is the largest tooth and has no external fold (*parvus* De Vis, 1896, pl. 14, fig. 10). There is a rather large upper canine (type of *azael*); the lower cheek teeth are narrower than the upper (a common macropod character); the premolars are subtriangular to oval (Owen's and De Vis' plates); p_3^3 simple, p_4^4 complex, dp_4^4 not depicted (but known as mp^4 to De Vis; 1896, p. 84); the molars relatively complex and, with the exception of the posterior loph of m_4^4 , becoming progressively broader posteriorly. This last condition is in agreement with the progressively enlarging but very differently constructed molars of *Macropus*, *Osphranter*, and *Megaleia*.

In *Palorchestes* the somewhat oval p_3^3 and p_4^4 bear some resemblance to the same teeth in *Sthenurus*. The p^4 is a large, highly peculiar tooth having a large external cone, weakly grooved on the buccal side, and a smaller in-

ternal cone. This tooth is a totally different tooth from p^4 of *Sthenurus* and *Procoptodon*, which (De Vis, 1896, pl. 16, figs. 3, 7) were larger but not very different from the corresponding lower p_4 of those genera.

Palorchestes crassus Owen (1880) from Queensland was based upon a part of a mandible containing three molariform teeth, designated by Owen m_{1-3} . Some of his conclusions regarding this specimen may be erroneous, because Lydekker (1887, p. 238) reached the conclusion that the same teeth had probably been transposed.

De Vis (1883) described the generally oval lower premolar of a "young" *Palorchestes* and stated that its dimensions were "eight lines \times 3 lines." It has an internal loop of dentine that gave it a reniform outline. He recorded p_3 , m_1 , and m_2 in place. It is not certain whether the premolar described was p_4 or dp_4 —probably the former, as dp_4 would in all likelihood have been molariform. The lower incisor was stated to be exceptionally broad and the mandibular symphysis much more firmly ankylosed than in *Macropus*. De Vis suggested relationship of *Palorchestes* to *Sthenurus*. The American Museum has a cast of a palate collected by Raven (A.M.N.H. No. 18363, Dept. Geol. and Paleont.) in which the large external and the smaller internal cone-shaped cusps are unworn and admirably clear.

De Vis (1896, pp. 81–88) reviewed *Palorchestes*. Just as Lydekker had done he considered the deep-jawed *crassus* (which seems to me nearer *Sthenurus*) a synonym of *azael*. He proposed a new, smaller species, *parvus*. He showed (1896, pl. 14, fig. 10) the very broadly arched incisive tooththrows of *P. parvus* as well as those characters of p^4 which he believed linked *Palorchestes* with the otherwise very different *Sthenurus*.

Scott (1916) put on record a mandibular tooththrow of *Palorchestes* from Tasmania. He interpreted four molariform teeth as the posterior half of p^4 , m^1 , m^2 , and the anterior half of m^3 , respectively.

Palorchestes azael Owen

Palorchestes azael OWEN, 1874, Phil. Trans. Roy. Soc., London, vol. 164, pt. 2, p. 798; 1874, *ibid.*, vol. 166, pp. 197–204 (important skeletal evidence).

Palorchestes crassus OWEN, 1885, Trans. Zool. Soc. London, vol. 11, pp. 7–10. (This synonymy is questionable.)

TYPES: Of *azael*, the anterior part of a skull, from Victoria, showing alveoli of three incisors, the canine, and five cheek teeth. Of *crassus*, the greater part of the mandibles, except incisive portion, of a specimen from Queensland.

Lydekker (1887, p. 238) and De Vis (1896, p. 81) believed that the molars of *crassus*, by the relatively different sizes of which Owen had distinguished *crassus* from *azael*, had been transposed. They therefore placed it in synonymy. The former recorded two additional specimens, one from Darling Downs, the other from Wellington Valley, New South Wales. De Vis recorded nine specimens or fragments of *P. azael*.

I am not satisfied that *crassus* is related to *azael*. If tracings of the lateral views of the skull of *azael* and of the mandible of *crassus* are matched together so that approximately correct occlusion of the cheek teeth is accomplished, a remarkable degree of disparity at once becomes apparent in the region of the rostrum, the upper and lower diastemata, and the symphysis. The elongate muzzle (with worn alveoli for a large canine and three incisors) and the elongate rostral diastema (103 mm. from the back of the alveolus of i^3 to the front of the premolar) of *azael* contrast in an extraordinary manner with the abbreviated diastema of the mandible of *crassus* (± 33 mm. from the rear of the upper side of the symphysis to the anterior edge of the alveolus of the premolar). The long muzzle of *azael* also contrasts with the great massiveness of the symphysis and the extraordinarily deep mandible (depth beneath the anteriormost molar, ± 70 mm.) of *crassus*.

Instead, *crassus* appears to be a thick-jawed kangaroo quite distinct from *Palorchestes*. Nor is it very close to *Sthenurus*, which has wholly different molar patterns. All three, however, have premolars which agree with one another in being suboval or subtriangular in section and subconical in profile, and in possessing few cusps, in contrast to the strongly secant premolar teeth of the Macropodinae and Potoroinae.

In the restoration of *Palorchestes* made by Raven (Raven and Gregory, 1946, fig. 10) the

type mandible of *crassus* was obviously disregarded. The lower diastema (restored) is shown by Raven as equally elongate with the upper one.

***Palorchestes parvus* De Vis**

Palorchestes parvus DE VIS, 1896, Proc. Linnean Soc. New South Wales, ser. 2, vol. 10, p. 84.

This was a smaller species than *P. azael*, and its teeth differed in a number of ways set forth by its author. One specimen figured (by De Vis, 1896, pl. 14, fig. 10) demonstrates the very wide upper incisive arch of *Palorchestes*, wholly unlike that of any modern genus. De Vis dealt with 26 specimens, chiefly fragments.

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