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ADAPTIVE BRANCHING OF THE KANGAROO FAMILY IN RELATION TO HABITAT

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INTRODUCTION

The present report is a summary of the principal conclusions of a more detailed, unpublished work by H. C. Raven on the evolution of the kangaroos, containing a revision of the genera and species, both recent and fossil.

The modern classification of the Macropodidae and consequently the materials for the study of the evolution of the family are very largely embodied in Oldfield Thomas' well-known "Catalogue of the Marsupialia and Monotremata of the British Museum" (1888), supplemented by "The mammals of South Australia" by Frederic Wood Jones (pt. 2, 1924), and by Iredale and Troughton (1934). Although Thomas' excellent work does not use the word evolution and begins with the most advanced members of the family, working backward to the most primitive, a careful reading of the text shows that Oldfield Thomas had very definite and, as it seems to us, usually well-founded views concerning the interrelationships of the major divisions of the family. Dollo, following Huxley, was more interested in the major evolutionary features in the marsupials as a whole than in the detailed relationships of the included genera and species. Bensley (1903) in his well-known monograph gave excellent comparative figures of single upper and lower molars and premolars, as well as the soles of the foot in several species of kangaroos.

In 1921 the authors of the present report went together to Australia from the American Museum of Natural History in order to make personal contacts with fellow naturalists in the Australian museums, to gain

field experience and some first-hand knowledge of the habits of the marsupials, and especially to secure a representative collection of Australian marsupials both for exhibition and for our study collections. One of us (H. C. R.) remained in Australia for about two years for the purpose of collecting and studying the habits of these animals in the field. A series of specimens of various marsupials was also injected with preservatives in the field and brought home for comparative anatomical study. Thanks to the kind cooperation of various Australian naturalists, including the late Dr. Charles Anderson of the Australian Museum, Sydney, Mr. Heber Longman of the Queensland Museum, Brisbane, and Prof. Frederic Wood Jones, then of the University of Adelaide, a number of rare and interesting forms, together with considerable fossil material not represented in our own collections, were secured. We have also to thank Dr. Gerrit S. Miller, Jr., of the United States National Museum, and Dr. W. H. Osgood, of the Chicago Natural History Museum, for the loan of valuable specimens for comparison, while our own Department of Mammals, under the chairmanship of Dr. Harold E. Anthony, has been unstinting in its assistance. For the use of figures 6, 17, and 21 we are indebted to Dr. G. H. H. Tate of the Department of Mammals here, who photographed the skulls of these rare marsupials in the collection of the British Museum (Natural History) in 1937. After the untimely death of H. C. Raven, Dr. John Eric Hill, Assistant Curator of the Department of Mammals, rendered invaluable assistance in the final stages of the work. (W.K.G.)

¹ Died April 5, 1944.

It might perhaps be deemed strange and it is certainly unusual to plan a work professing to deal primarily with the evolution of a family of recent mammals instead of the conventional catalogue of the collections secured. But we are convinced that in the case of the marsupials there is a greater need of more studies on evolution where the emphasis is laid upon the structural relationships and genetic affinities rather than solely upon the systematic differences. For the differences between the species and genera of kangaroos have been most thoroughly and judiciously treated by Oldfield Thomas and his successors and are already a matter of record.

We have also examined the literature and specimens of the numerous Pleistocene kangaroos with the view of determining, if possible, their connections with the recent genera.

The kangaroos appear to be a singularly favorable group for the study of evolution for the reason that a relatively large number of "living fossils" plainly perpetuate the chief stages, from the tiny and generalized musk kangaroo (*Hypsiprymnodon*), which, as shown by Oldfield Thomas and Dollo, represents an early stage following the descent of the ancestral phalangerid from the trees, to such specialized giants as the Pleistocene *Palorchestes*.

ADAPTIVE BRANCHING IN RELATION TO HABITAT

In order to collect small mammals successfully, one must naturally know where to set traps and with what sorts of food to bait them. Examination of stomach contents and later of the dried skull and dentition brings out clearly the relations between structure, habits, and habitat without, however, either confirming or disproving the classical saying that changes in habit precede changes in structure. In the case of the kangaroos the ancestral habitat is doubtless the rain forest, and the ancestral foods are leaves, seeds, berries, fruit, and roots lying on or near the ground, together with insects, grubs, and worms. Of this ancestral stage only the tiny musk kangaroo of north Queensland remains as a living witness. But the forest leads out into the gullies and thickets, and here we find the typical rat kangaroos (*Bettongia*) which with their short muzzles and strong jaws tear at the tough woody roots and wear down their teeth, as do bandicoots.

And in other directions the rain forest leads into the open forest, where beneath the thin silvery shade of the eucalypts fine grass grows. From here to the open plains the grass-eating wallabies and kangaroos are met in most abundance, while in the border zone the larger wallabies hide in the forest by day and move out to feed on the grassy plains at night. Some of the Pleistocene kangaroos (the Sthenurinae), acquiring massive jaws and thickly wrinkled molars, may have fed upon the coarser shrubs of the forest. Thus there seem to be discernible relations between the classification and evolution of the kangaroos and their several habitats, which are expressed in the phylogenetic diagram (fig. 1).

We may then proceed to outline our present understanding of the evolution of the group under the subfamilies as recognized by Thomas, with the addition of the Pleistocene Sthenurinae.

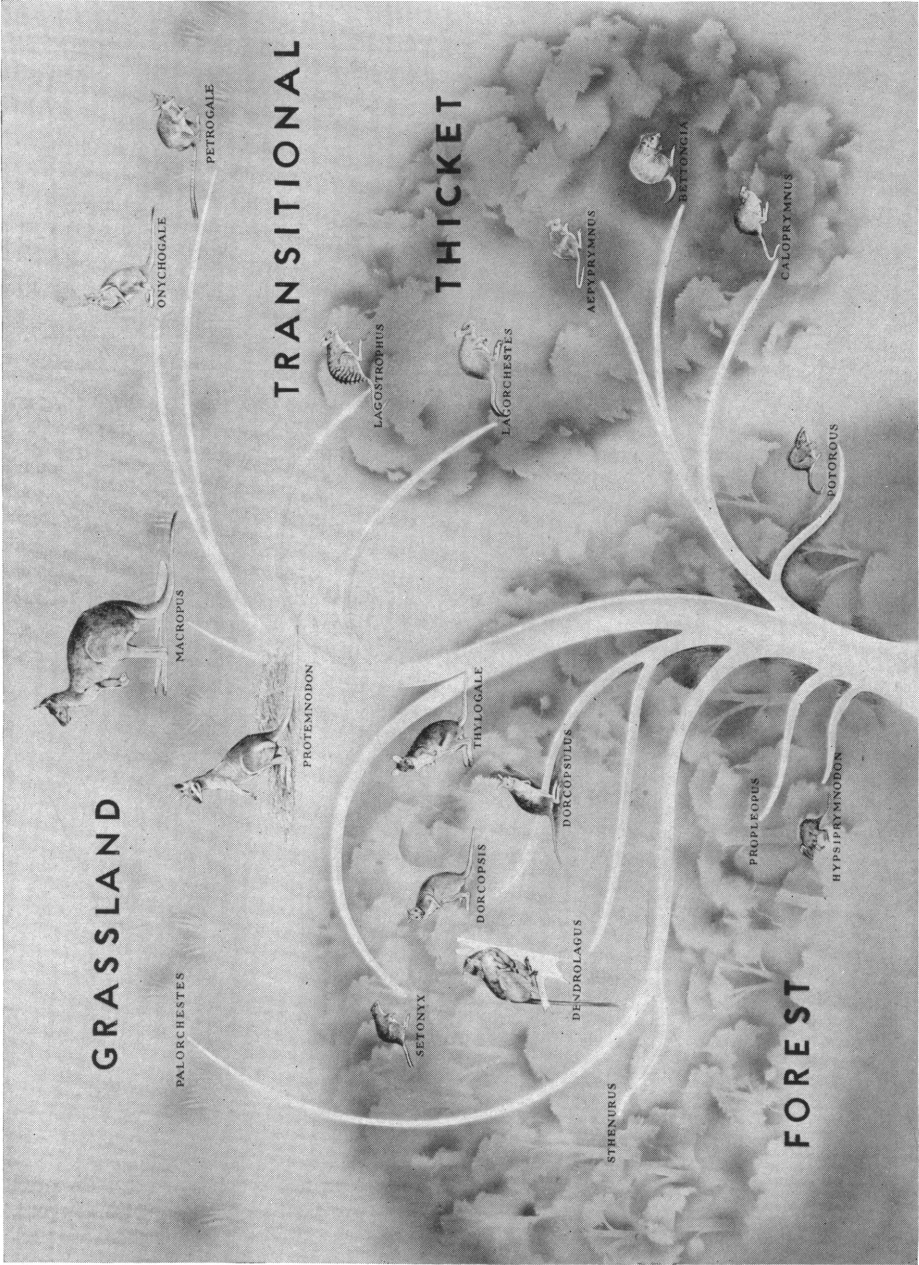


Fig. 1. Adaptive branching of the kangaroos in relation to habitat.

TABLE 1
PRINCIPAL CHARACTERS OF THE SUBFAMILIES

	Nature of Habitat	Canine	I ³ Notch	Post. Upper Premolar	Man- dibular Sym- physis	Upper Molar Crowns		
Hypsiprymnodontinae	Forest	×	0	Diagonally placed, many grooves	Loose	Quadrilateral		
Potoroinae	Thicket	×	0	Elongate, straight, trenchant, grooved	Loose	Quadrilateral		
Sthenurinae (<i>Sthenurus</i> , <i>Palorchestes</i>)	Forest and grass- land	0	0	Roundly triangular crown, grooves reduced, inner lobe complete, no secant edge, no grooves	Anky- losed	Bilophodont		
Macropodinae Brachyodont Section <i>Dorcopsis</i> , <i>Dendrolagus</i>	Forest	×	0	Elongate with se- cant edge, with grooves, postero- internal lobe complete	Loose	Bilophodont		
<i>Thylagale</i> , <i>Setonix</i>	Forest	0	×	Same as above	Loose	Bilophodont		
Hypsodont Section <i>Lagostrophus</i> , <i>Lagor- chestes</i> , <i>Protemnodon</i> , <i>Peradornas</i> , <i>Petro- gale</i> , <i>Onychogalea</i> , <i>Macropus</i>	Grass- land	×	0	×	0	Size variable, crown compressed, pos- tero-internal lobe present	Loose	Bilophodont

THE MUSK KANGAROOS (HYPISIPRYMNODONTINAE)

According to Pierson Ramsay, the describer of *Hypsiprymnodon moschatus* (cited by Oldfield Thomas, 1888, p. 124), this "highly interesting and anomalous marsupial inhabits the dense and damp portions of the scrubs [rain forest] . . . Its habits are chiefly diurnal . . . it progresses in much the same manner as the kangaroo rats (*Hypsiprymnus*), to which it is closely allied, but procures its food by turning over the débris in the scrubs in search of insects, worms, and tuberous roots, frequently eating the palm berries (*Ptychosperma alexandrae*), which it holds in its forepaws after the manner of the phalangers, sitting up on its haunches, or sometimes digging like the bandicoots. . ."

As noted by Oldfield Thomas and later authors, this little kangaroo links the

Macropodidae with the older Phalangeridae, first, because its hind foot retains the hallux and the digital pads, while the second and third digits are strongly syndactylous.

Its dentition also has advanced but little toward the kangaroo type (fig. 4). Thus its posterior upper premolars inherit the prominent, vertically high and compressed crowns, with the cutting edge and prominent vertical grooves, which are characteristic of the phalangers. Likewise these opposite secant premolars are directed sharply outward as in the phalangers, while in the mandible the secant premolars could be derived in a general way from the type illustrated by the Pleistocene phalanger *Burramys* of Broom (1896), which it also somewhat resembles in its

TABLE 1 (continued)

Longitudinal Connecting Ridges Be- tween Loph- s of Upper Molars	Relative Lengths (ap.) m ¹ and m ⁴	Elevation of Mandibular Condyle Above Level of Tooth Row	Inclina- tion of Ant. Border Ascend- ing Ramus to Tooth Row	Ears	Tail: Head and Body Length ¹	Foot: Head and Body Length ¹
Absent	m ¹ > m ⁴	Low	About 45°	Short	Medium (64-66%)	Medium to long (23-24%)
Absent	m ¹ > m ⁴	Low	Slightly more	Moderate	Very short to medium (43-81%)	Short to very long (18-37%)
Present	m ¹ < m ⁴	High	Steep	—	—	—
Present	m ¹ < m ⁴	Intermediate	Less steep	Short to very short	Short (60%) to very long (111%) (<i>Dendrola- gus</i>)	Short to moder- ate (19-23%)
Present	m ¹ < m ⁴	High	Nearly at right angle	Short	Very short (43-56%)	Very short (16-18%)
Present	m ¹ < m ⁴	High	Nearly at right angle	Usually long (except in <i>Lagostro- phus</i> , <i>Lagor- chestes</i>)	Medium to long (62-100%)	Medium to long (21-29%)

very long procumbent lower incisors. It is even more primitive than *Burramys*, however, in retaining vestiges of the second lower incisors, which are minute teeth, the crowns of which rest largely on those of the enlarged first incisors. The small upper molars are remarkably primitive for a kangaroo in that they are brachyodont, virtually quadritubercular, and diminish in size from m¹ to m⁴ as in certain phalang-ers; also the opposite tooth rows converge posteriorly instead of being more nearly parallel as in the kangaroos. All this is ap-arently reminiscent of a time when the secant premolars were the dominant teeth of the dentition, whereas in the typical kangaroos the premolars finally become

much reduced as the molars gain in size and importance.

The tail is slender in contrast with that of typical kangaroos. On the other hand, the little musk kangaroo is a true kangaroo in the hopping adaptations of its hind feet, a singularly constant character in the en-tire family. Also the two halves of its mandible are slightly movable at the sym-physis, as in the kangaroos, due to the ligamentous connection there, while the general shape of the skull with its elon-gate muzzle and simple ungrooved upper incisors approaches that of *Potorous tridac-tylus* of the rat kangaroos. As in *Potorous tridactylus*, the "alisphenoid bullae" are relatively small and but little inflated.

¹ Percentages based mostly on measurements given by Oldfield Thomas (1888).

THE RAT KANGAROOS (POTOROINAE)

From such a type as *Hypsiprymnodon*, described above, the steps to *Potorous tridactylus* (fig. 5) are not many. The muzzle in this species, however, is even more elongate than that of *Hypsiprymnodon*, while its secant upper premolar (p^4 of Thomas) has become extremely elongated anteroposteriorly and lacks an inner basal cusp. In passing we may note that after comparing the skulls and teeth we can hardly agree with Bensley (1903, p. 143) in referring *Hypsiprymnodon* to the same subfamily with *Aepyprymnus*, while separating *Potorous* and *Caloprymnus*, apparently on the basis solely of the number of grooves on the fourth upper premolar, because the number of grooves on the outer side of this tooth varies in the different species of *Potorous* from four to two.

In all the Potoroinae (as defined by Thomas) the fourth premolars are the dominant cheek teeth in both the upper and lower jaws, in the sense that they are the most conspicuous single pair of teeth and that they stoutly maintain their place below the front end of the zygomatic arch instead of being pushed forward by the oncoming molars, as they are in the typical kangaroos. These forms, all living in thickets, evidently give their teeth very hard usage, grinding them down on the tough woody tissue of roots mixed with more or less sand, grass, and seeds. The molars, quadritubercular in *Potorous* and *Bettongia*, become almost bilophodont in *Aepyprymnus*. While, as noted above, the muzzle of *Potorous tridactylus* is elongate, that of *P. platyops* is markedly shorter and could give rise to the still shorter face of *Bettongia* and *Aepyprymnus*. The auditory bullae are small in *Potorous*

tridactylus in spite of its small body size, but they become very large and inflated in *Bettongia lesueuri*, possibly indicating life in more open country.

The hind feet, rather primitively short in *Potorous* and retaining the primitive friction pads, are long and slender in *Bettongia* and *Aepyprymnus*. All lack the hallux. The fore claws are large and are used for digging. Of these genera *Potorous* is the most primitive in retaining the friction pads on the pes, the elongate muzzle, narrow cranium, low mandibular condyle, very oblique coronoid process, markedly procumbent slender lower incisors, slender malar with small masseteric tubercle, slight inflation of auditory bulla. All these habitus features go with its forest habitat and its heritage from *Hypsiprymnodon*. *Caloprymnus* (fig. 6) is highly specialized in its extremely wide short muzzle, wide cranium, reduced grooves on its premolars, and relatively very long hind feet. These features go with its semi-arid habitat in South Australia.

Of the remaining genera, *Bettongia* (fig. 7) inherits from *Hypsiprymnodon* the narrow grooves on its secant premolars, as well as most features of its dentition. The bullae range from medium to very large. A picture by Harry Burrell (Le Souef and Burrell, 1926, fig. 54, p. 235) shows *Bettongia* using its tail in a prehensile way to carry nesting material—a heritage of its arboreal phalangerine ancestry. *Aepyprymnus* (fig. 8) has developed a heavier dentition throughout, with shorter face, very short diastema, more heavily braced skull. *Bettongia* and *Aepyprymnus* live in grass country, hiding in thickets.

THE HEAVY-JAWED PLEISTOCENE KANGAROOS (STHENURINAE)

The Pleistocene *Sthenurus* (fig. 9) has a remarkably robust, wide, short, and deep skull, with extremely short face, massive jaws ankylosed at the symphysis, great vertically deep zygomatic arches with long downwardly produced masseteric malar processes on the anterior ends of the malars; the posterior lower premolars (fig. 1) are

short, bunodont, with prominent postero-external swelling and double longitudinal crest, with four or more grooves on the lingual side. The primitive crest points obliquely outward in unworn teeth. The upper premolars when unworn approach a tricuspid type, which could be derived from a *Dendrolagus*-like form through

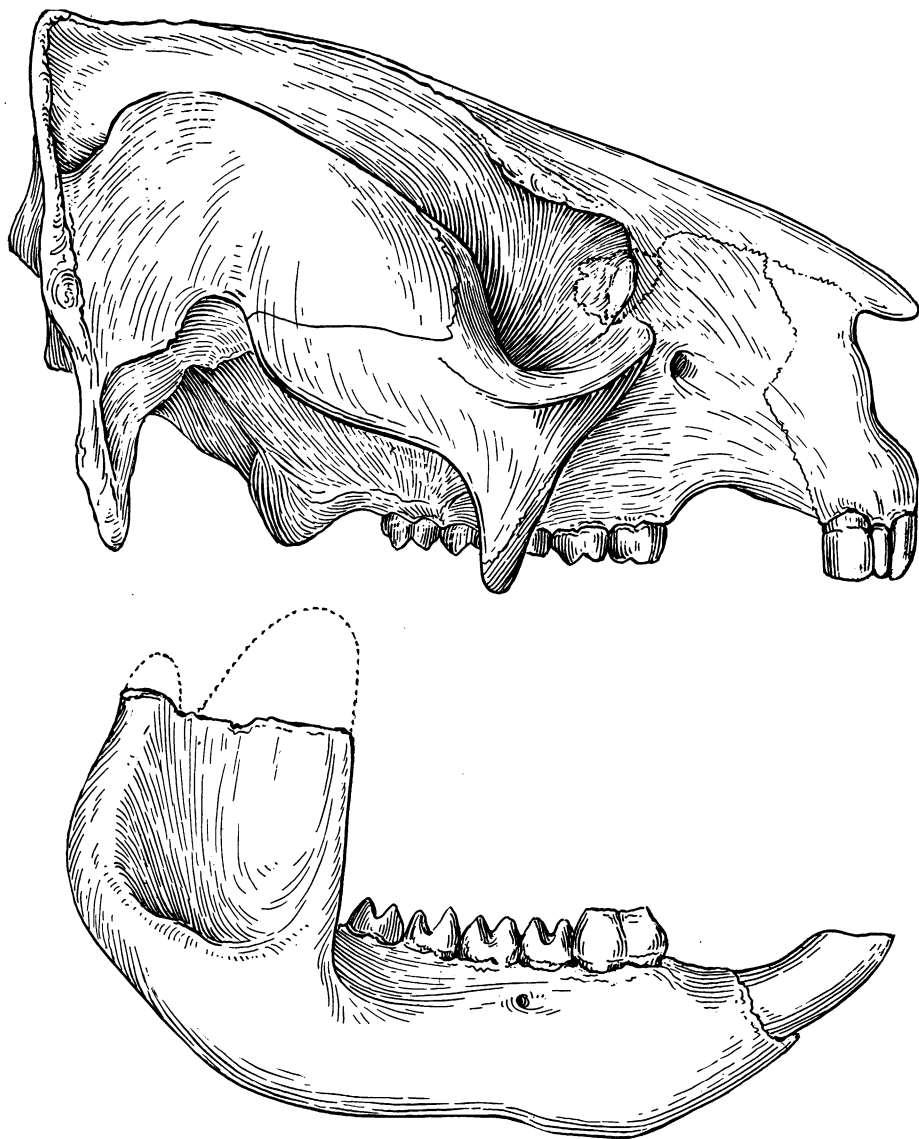


Fig. 2. *Sthenurus occidentalis* Glauert. Skull and lower jaw from model by Glauert and photographs of the type. $\times \frac{2}{3}$.

marked anteroposterior shortening, which is evident in all other parts of the skull. The molars are massive, with thick longitudinal connecting crests and many prominent grooves and plications, in wide contrast to the smooth, sharp ridges of typical kangaroos.

Possibly the Sthenurinae may be survivors of the more primitive forms that

gave rise to the tree kangaroos, from which, however, they differ in the characters of their premolars, but on the whole it seems easier to derive the *Sthenurus* premolars from a forerunner of the *Dendrolagus* type than from those of either the typical *Macropus* or the *Hypsiprymnodontinae* and *Potoroinae*. The genus *Sthenurus* includes six or more species described

by Owen (1839, 1873, 1874), De Vis (1896), and Glauert (1910), all of the stout-jawed type.

The Pleistocene *Palorchestes* (including two species described by Owen, 1873, 1874a, and one by De Vis, 1896) belonging to this subfamily had a skull 16 inches in length, which was proportioned more as in normal kangaroos (fig. 10). Its premolars

and mandible, however, are related to those of *Sthenurus* (figs. 2, 9). It may be, therefore, that we are dealing with dolichocephalic and brachycephalic related genera within the same subfamily, as in certain groups of ungulates, and as in the genera *Potorous* and *Dorcopsis*, each of which has a dolichocephalic and a brachycephalic species.

THE WALLABIES, TREE KANGAROOS, AND KANGAROOS (MACROPODINAE)

Passing to the Macropodinae, or true kangaroos (*Macropus*), wallabies (*Protemnodon*), pademelons (*Thylogale*), and allied forms, we enter a group containing the majority of the species of the family and ranging from the tiny banded wallaby (*Lagostrophus*) to the gigantic *Macropus titan* of the Pleistocene and including even the highly specialized tree kangaroo (*Dendrolagus*). The brachyodont members of this subfamily (*Dorcopsis*, *Dendrolagus*, and *Thylogale*) are predominantly forest-living forms, some of which extend their range into more open country, but the majority, including the hypsodont section (cf. table 1), inhabit the grasslands and even invade the areas cleared by man.

The most conspicuous evolutionary tendency in the dentition is the assumption of sharply bilophodont and progressively hypsodont molars, which adapt these animals to the grasslands, together with the gradual reduction of p_4^* in size and functional importance, culminating in their complete elimination in old individuals of certain species of *Macropus*. With the pushing out of the p_4^* at the front end of the tooth row, the molars gradually move forward in the jaw and in turn fall out in front, so that in extremely old, great gray kangaroos only the fourth molar may be retained, but in a marked forward position in the jaw.

The third upper incisors develop a postero-external groove, which appears in an incipient stage (fig. 3, A) in *Thylogale*, reaches its climax in the large wallabies (*Protemnodon*), where it has shifted to the middle of the labial surface and then passes forward to near the front end of the labial face in some of the large kangaroos

(fig. 3, C). This groove wears off with age and may disappear entirely in very old skulls.

Dorcopsis (*sensu lato*), inhabiting the forests of New Guinea, includes small wallabies with a very long secant p^4 with conspicuous internal cusp. The p^4 is relatively larger than in the higher kangaroos. The molars are brachyodont; the upper canines, although small, are present. The tail and ears are relatively short; the feet are of moderate length.

The genus *Dorcopsis* Schlegel and Müller, 1842 (type, *Didelphys brunii* Schreber, 1777) includes many species. Matschie (1916) divides the group into two genera, *Dorcopsis* (fig. 11) and *Dorcopsulus* (type, *D. macleayi*, our fig. 12), the latter being small with a short muzzle, less elongate "secator" (compressed upper premolar), and more extended and abrupt nakedness of the tail. Some of the species of *Dorcopsulus*, which vary in minor characters, may almost include the survivors of the ancestral stock leading to *Thylogale* and the higher kangaroos, while *Dorcopsis* (*sensu stricto*) is a specialized dolichocephalic side branch (fig. 11).

One species (*D. macleayi*), according to Thomas (1888, p. 92), is in many ways intermediate between "*Dorcopsis*" (= *Dorcopsulus*) and "*Macropus*" (= *Thylogale*) *brownii*, while the type *D. brunii* bears a strong superficial resemblance to "*Macropus brunii*" of Aru (Thomas, 1888, p. 89). In the other direction, Garrod (1875) and Thomas (1888, p. 87) have pointed out that *Dorcopsis* (= *Dorcopsulus*) is connected with the tree kangaroo, *Dendrolagus*. Bensley (1903, pp. 153, 178, 201) even concluded that *Dorcopsis* was derived from *Dendrolagus*, but we think that the

evidence can be better interpreted in the opposite way.

Dendrolagus (fig. 13) inhabits the rain forests of New Guinea and north Australia, browsing in the trees and on the ground; when climbing, the powerful arms are used in alternation with the broad-soled hind feet, which move in unison and thus retain the typical kangaroo type of locomotion.

In spite of the marked superficial difference in appearance from normal kangaroos, it would be quite unjustifiable to separate the tree kangaroos as a distinct subfamily, because, as noted above, they are closely related to *Dorcopsulus*. In its dentition *Dendrolagus* closely resembles that genus, though its p^4 is somewhat less secant. The skull is broader in the facial region. The most significant difference is to be found in the arboreal adaptations of *Dendrolagus*, namely, its comparatively broad short pes with wide plantar pad, proportionately heavy fore limbs, and strong curved claws. Its tail is long, slender, and evenly haired above and below, and its ears are shorter than in any other member of the family. Here again *Dorcopsulus* seems to be in every way closely related to *Dendrolagus* and an ideal structural ancestor for it, as well as for the higher kangaroos.

The closure of the palatine fenestrae in several species of widely separated genera of macropods, such as *Aepyprymnus*, *Dendrolagus*, *Palorchestes*, and *Macropus*, is considered to be purely secondary.

The three species of hare wallabies, *Lagorchestes*, inhabit dry country from the interior of New South Wales to islands off the northwest coast. This genus has advanced far beyond the Potoroinae in its more bilophodont molars and its more abruptly constricted face as seen from above (see fig. 14). Also its fourth upper premolar is smaller than that of the Potoroinae and has a pronounced anterior cusp and strong internal cingulum with a basal cusp at the postero-internal end. A strongly developed process of the maxilla juts down from the lower border of the zygomatic arch as in typical kangaroos. The groove on the labial surface of the upper third incisor is pronounced and well

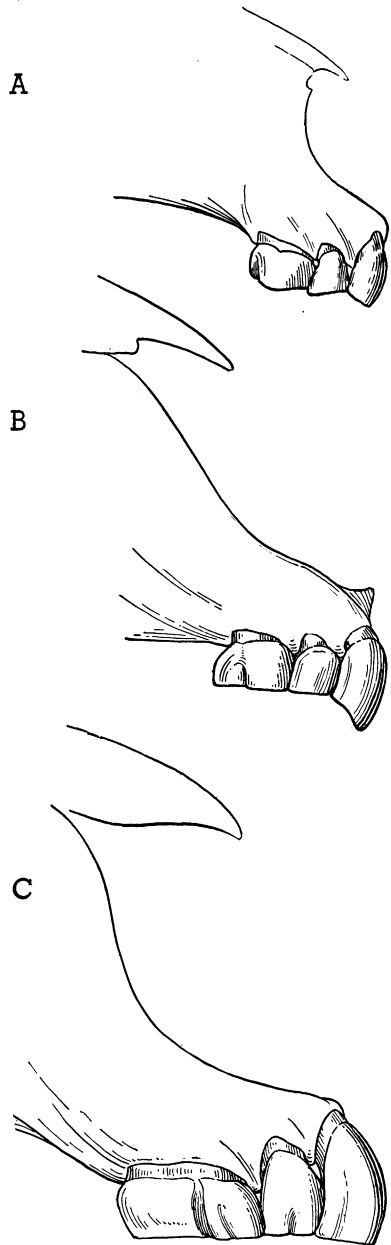


Fig. 3. Outlines of upper incisors: A, *Thylogale*; B, *Proteimnodon*; C, *Macropus*. $\times 1\frac{1}{2}$.

forward in position. On the other hand, in common with the Potoroinae, *Lagorchestes* retains the upper canines (although small). The body is small and the head

deep and broad, the muzzle short; the tail and foot are comparatively long. It may have been derived as a dwarf from the stem of the typical wallabies (*Protemnodon*), which has secondarily sought the cover of thickets.

Lagostrophus, the banded wallaby of Western Australia and some of the islands of Sharks Bay, Western Australia, is a diminutive kangaroo with a very narrow short muzzle and fairly wide skull; it has lost the upper canine (fig. 15). In conjunction with its compressed muzzle, the second and third incisors are nearly parallel with those of the opposite side. In most respects it is a typical kangaroo, although living in thickets, to which it is adapted by its small size. Its nearest living relatives are *Thylogale* and *Petrogale*. Like *Lagorchestes* it may have been derived from the hypsodont, grass-living stem of the higher kangaroos, which has secondarily invaded the thickets.

Thylogale,¹ the pademelon wallabies (fig. 16), are a compact group of about nine species, all small brachyodont wallabies with short tails, short feet and ears, and a groove near the posterior margin of the third upper incisor; the nasals are very broad posteriorly. They inhabit the forest from New Guinea and the New Britain group of islands to Tasmania. They are not found far from the coast of Australia. The upper premolar retains its position even in old skulls, and in general these are primitive forerunners of the larger wallabies and true kangaroos of the grasslands.

Setonix of southwestern Australia, as noted by Oldfield Thomas (1888, p. 62), convergently resembles externally the rat kangaroos (*Potorous gilberti* and *P. platyops*) of the same region, but its nearest relatives belong to the genus *Thylogale*. It resembles *Thylogale stigmatica* in having a peculiar upward central projection of the top of the rhinarium (fig. 17). Its secant premolar is greatly elongated with many

grooves (another convergence toward the Potoroinae), and its skull is broadly and strongly built with enlarged zygomatic arches, all indicating coarse tough food. Its third upper incisor differs from that of *Thylogale* in being very small, its notch about at the center instead of at the back (Oldfield Thomas, 1888, p. 61).

Protemnodon (fig. 18) contains mainly the "large wallabies" of Thomas, but includes certain forms (*eugenii*, *bedfordi*, and *parma*, and perhaps one or two others) which Thomas referred to his group of "small wallabies." The *protemnodons* are widely distributed over the whole of Australia and Tasmania and even reach New Guinea. We also include here a number of Pleistocene forms, mainly described by Owen, Lydekker, and De Vis, some of which were larger than the largest living kangaroo (see below).

In most of the recent large wallabies the secant p_4 is somewhat less conspicuous than in the type of "*Macropus*" *anak* Owen but is always retained throughout life. The muzzle is shorter than in *Macropus*. The molar teeth are not so brachyodont as in *Thylogale* but are less hypsodont than in typical *Macropus*. The third upper incisor has usually a well-developed groove about the middle of the labial surface. Palatal vacuities are conspicuous.

The ears are larger than in *Thylogale*, the feet are longer, and the tail is longer and tapering.

These forms all feed on the grassland, though some of them spend the day hiding in the forest or thickets. In general their color is not so dark as it is in the forest-living forms. A cheek stripe and a hip stripe are frequently present. The most conspicuous feature of the fossil *protemnodons* was the elongated, highly secant p_4 in the lower jaw, to which the name refers.

The connections between the recent large and small wallabies and the Pleistocene forms were badly confused in the nomenclature. Thomas (1888) divided the genus *Macropus* into three groups, using size as his principal criterion: first, *Macropus (sensu stricto)*, including only the largest living kangaroos (*M. giganteus*,

¹ We are accepting Oldfield Thomas's designation (1888, p. 10) of the type of *Thylogale* Gray as *Macropus thetidis* [thetis] Lesson (1827, p. 129). We regard "*Thylogale eugenii* (Desmarest, 1817)," Wood Jones (1924, p. 235) as an aberrant member of the *Protemnodon* group (see p. 11).

antelopinus, *robustus*, *isabellinus*, *rufus*, *magnus*); second, the "large wallabies" (*M. ualabatus*, *ruficollis*, *greyi*, *dorsalis*, *parryi*, *irma*, *agilis*); third, the "small wallabies" (*M. coeneti*, *stigmaticus*, *wilcoxi*, *brunii*, *browni*, *thetidis*, *eugenii*, *parma*, *billardieri*, *brachyurus*). Since 1888 a number of forms have been added to each of these groups. As noted above, *eugenii*, *parma*, and *bedfordi* are here included with the "large wallabies" named above in *Protemnodon*, for the following reasons:

1. The type of *Protemnodon* Owen is the Pleistocene form *Macropus anak* Owen, based on "a portion of a left mandibular ramus, including the molar series . . .," which was figured by him in his memoir of 1874 (pl. 25, figs. 1, 2). This was a very good type, and it compares closely in almost every feature, except its greater size, with the corresponding parts of a modern wallaby, such as *Protemnodon bicolor* or *P. agilis* (fig. 18).

2. He later referred to the same species several maxillary tooth rows which were shown by Lydekker (1887) to belong to different genera. Nevertheless this did not invalidate the use of the name *Protemnodon* for members of the genus to which the type of *Protemnodon anak* belonged.

3. *Wallabia* Trouessart, 1905, which was chosen by Iredale and Troughton (1934, p. 47) as the generic name of this group, is clearly antedated by *Protemnodon* Owen.

4. De Vis (1896, p. 104) referred to "*Protemnodon anak* Owen (*partim*)" several other named Pleistocene forms but in turn grouped them all under *Halmaturus*, a synonym of *Macropus*.

Another difficult problem has been the proper limitation of the genus *Thylogale* Gray, 1837. Gray's definition of this subgenus of "*Halmaturus*" (*Macropus*) was: "The hinder fold of the hinder upper cutting tooth scarcely larger than the front one, so that the tooth appears only notched behind. Front incisor short, simple." The type and only species cited by Gray was *eugenii*, which Thomas (1888, p. 10) synonymized with *Macropus thetidis*, probably because Gray's definition applies perfectly to *thetidis* but not to *eugenii* in Thomas' sense (*op. cit.*, p. 54). The ex-

cellent descriptions and figures of "*Thylogale eugenii*" by Wood Jones (1924, pp. 235, 239) prove that he is dealing with a small member of *Protemnodon*, not *Thylogale*, as these terms are understood above. Apparently no true *Thylogale* exists in South Australia at the present time.

Onychogalea unguifer, the nail-tailed wallaby of the northwest coast of Australia, is virtually a small, specialized *Protemnodon* with a delicate dentition and slender limbs (see fig. 19). Its name refers to the possession of a "peculiar horny excrescence at the tip of the tail" (Thomas). The upper premolars are greatly reduced and bilobate. The skull is moderately broad and the muzzle compressed. The molars are hypsodont in accordance with its habitat of open dry country. The tail is very long in *O. unguifer* but only moderately long in *O. lunata*.

The rock wallabies, *Petrogale*, are widely distributed over the whole of Australia, but not Tasmania (Thomas, 1888, p. 62), in suitable localities where there are rocky hillsides and caves offering shelter. All the incisors are delicate, the third laterally spatulate with a slight groove on its lateral face. The muzzle is narrow, the skull moderately broad (see fig. 20). The foot is very long, narrow, with a short claw on the main digit. The tail is very long.

The single species of *Peradorcas*, *P. concinna* Gould, the little rock wallaby, is a remarkably specialized animal from the northwest coast of Australia (cf. fig. 21). "General characters as in *Petrogale*, but the molars on each side increased in number, seven at least on each side and probably more, falling out in front and renewed behind as in the Manatee (*Trichechus*)"—a remarkable case of sudden departure from the ancestral type. The skull, as described by Thomas (1888, p. 71), is very small and quite different in shape from that of the other species of rock wallabies. Facial portion comparatively short and braincase large. Muzzle short, narrow, and pointed, not inflated. Nasals very narrow in front and enormously broadened behind. Both the tail and the foot are moderately long.

In the true kangaroo, *Macropus*, as

noted above (p. 8), the dentition reaches a new evolutionary plane, in which the reduced upper and lower fourth premolars lose their importance and are shoved out of the dentition shortly after the eruption of the fourth molar. The molars meanwhile have acquired a fore-and-aft sequence, the front ones being shed as the hinder ones push forward. In connection with the grazing habits the muzzle becomes elongated, producing a long, compressed, lingual channel in the mandible. The groove on the third upper incisor varies in the different species, as does the length

of the crown of this tooth (see fig. 22). As noted above, the true kangaroos are confined to the grassy regions of Australia and Tasmania. Some of the recent ones reach a standing height of 7 feet, which must have been greatly exceeded by some of the Pleistocene species of *Protemnodon*.

The foot structure in the subfamily is remarkably uniform in essentials, but there is gradual lengthening of the foot from *Thylogale* to the great kangaroos.

The principal species of *Macropus* are listed above.

CONCLUSIONS

1. The general concept of the origin and evolution of the kangaroos from small, arboreal, forest-living phalangers, as developed by Huxley, Dollo, and Bensley, seems entirely in harmony with the field and museum studies herein summarized. These new studies also strongly support the thorough taxonomic work of Oldfield Thomas.

2. Many "living fossils" still survive to indicate the several lines of adaptive branching, starting from the ancestral forest-living *Hypsiprymnodon*: in one direction leading into the thickets (Potorinae); in another direction from the forest out into the grasslands (*Thylogale*, *Protemnodon*, *Macropus*); in a third direction, probably derived from *Dorcopsulus* and ending up in the trees (*Dendrolagus*); a fourth line, including the thick-jawed giants (Sthenurinae) of the Pleisto-

cene, may have started not far from *Dorcopsulus*.

3. The true wallabies (*Protemnodon*) are here separated from the true kangaroos (*Macropus*) because of the persistence of their large fourth premolars. The evidence for their close relationship to the Pleistocene *Protemnodon* is set forth.

4. Notwithstanding the great differences between the primitive *Hypsiprymnodon* and such highly specialized genera as *Macropus*, *Dendrolagus*, and *Sthenurus*, the survival in the existing and Pleistocene faunas of so many living fossils, together with the failure of any of the kangaroos to spread from the New Guinea region into Malaysia, suggests a relatively late geological date (middle to late Tertiary) for the origin of the family from phalangers akin perhaps to the Pleistocene *Burramys*.

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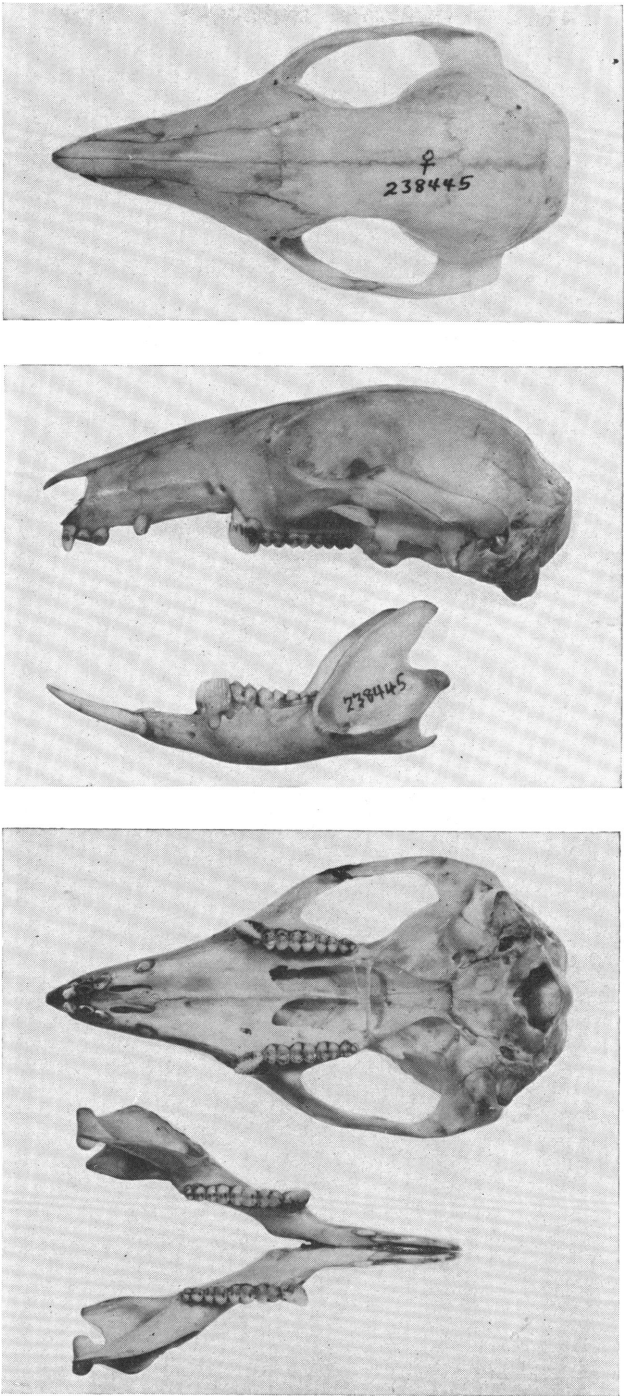


Fig. 4. *Hypsiprymnodon moschatus* Ramsey. U.S.N.M. No. 238445.

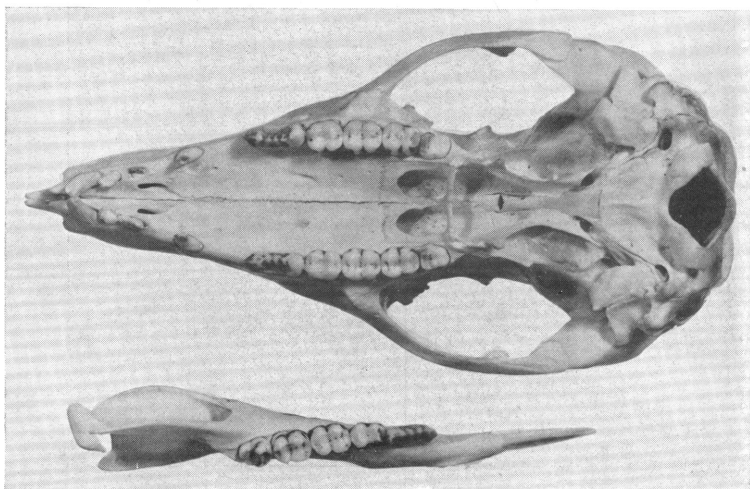
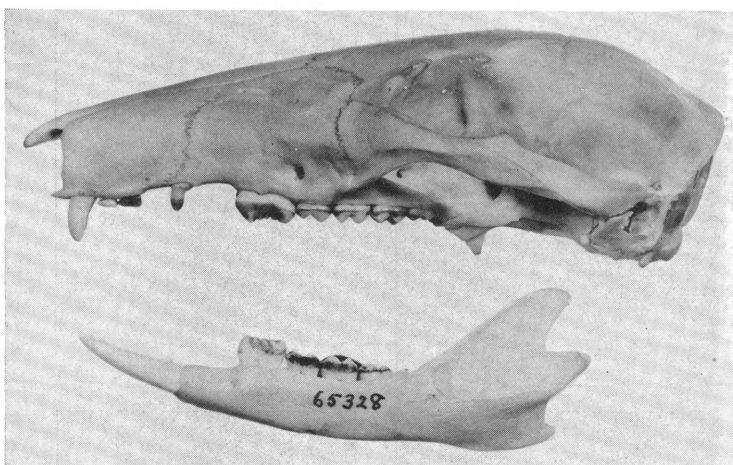
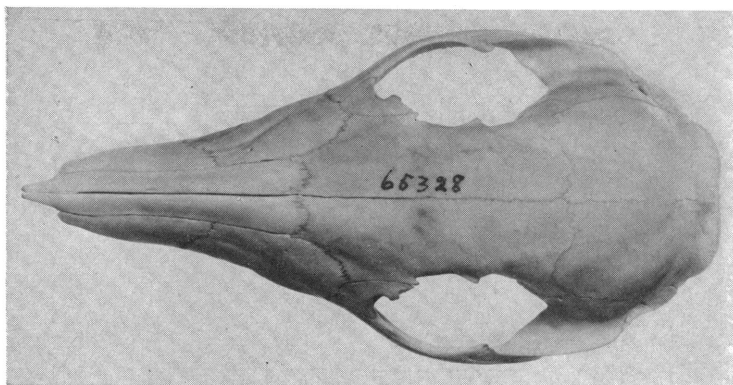


Fig. 5. *Potorous tridactylus* Kerr. A.M.N.H. No. 65328.

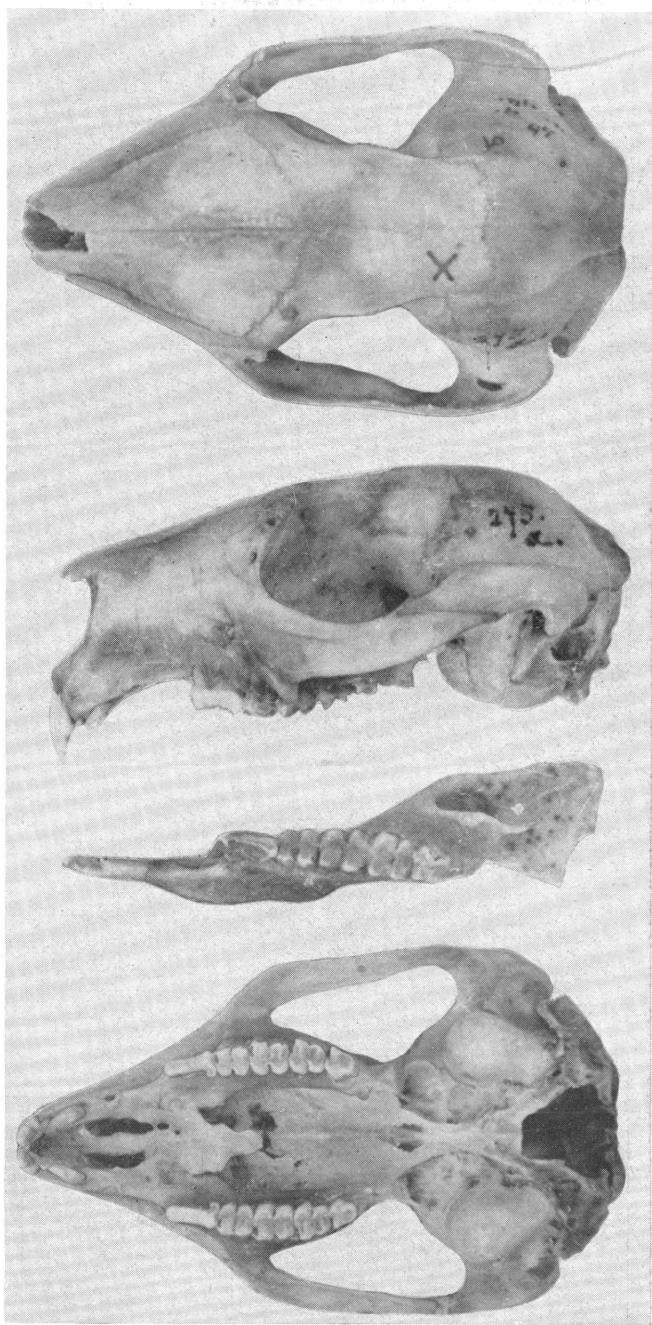


Fig. 6. *Caloprymnus campestris* Gould. Type, B.M.N.H. No. 46.4.4.44.

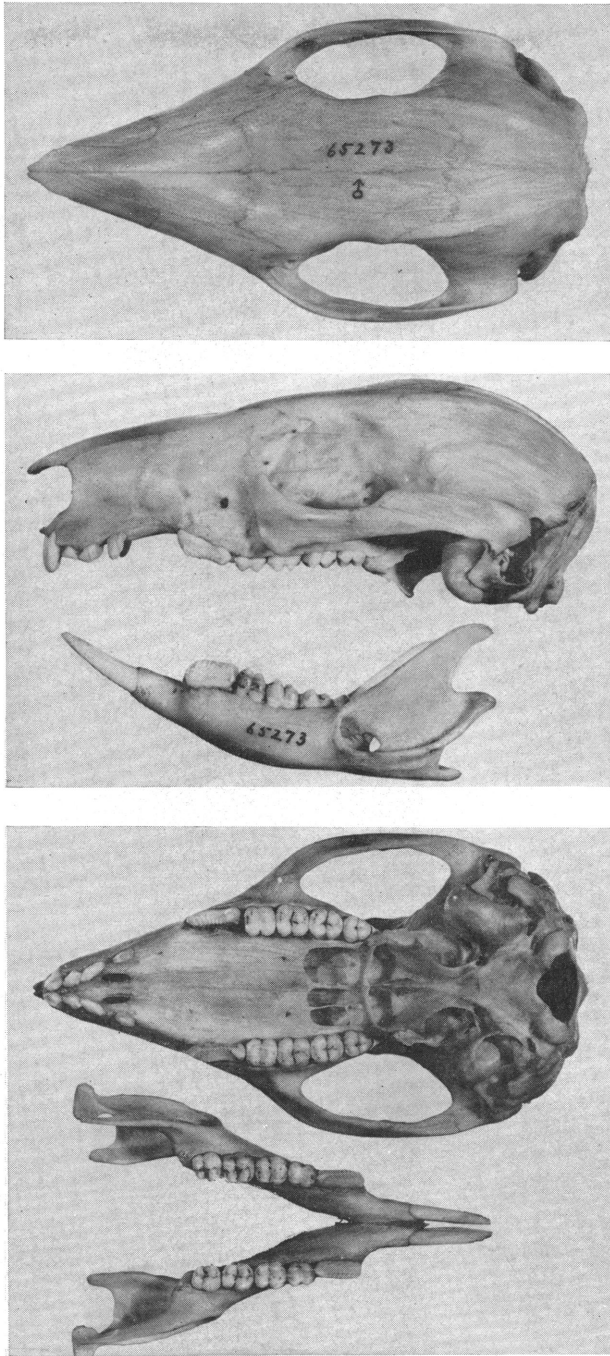


Fig. 7. *Bettongia cuniculus* Ogilby. A.M.N.H. No. 65273.

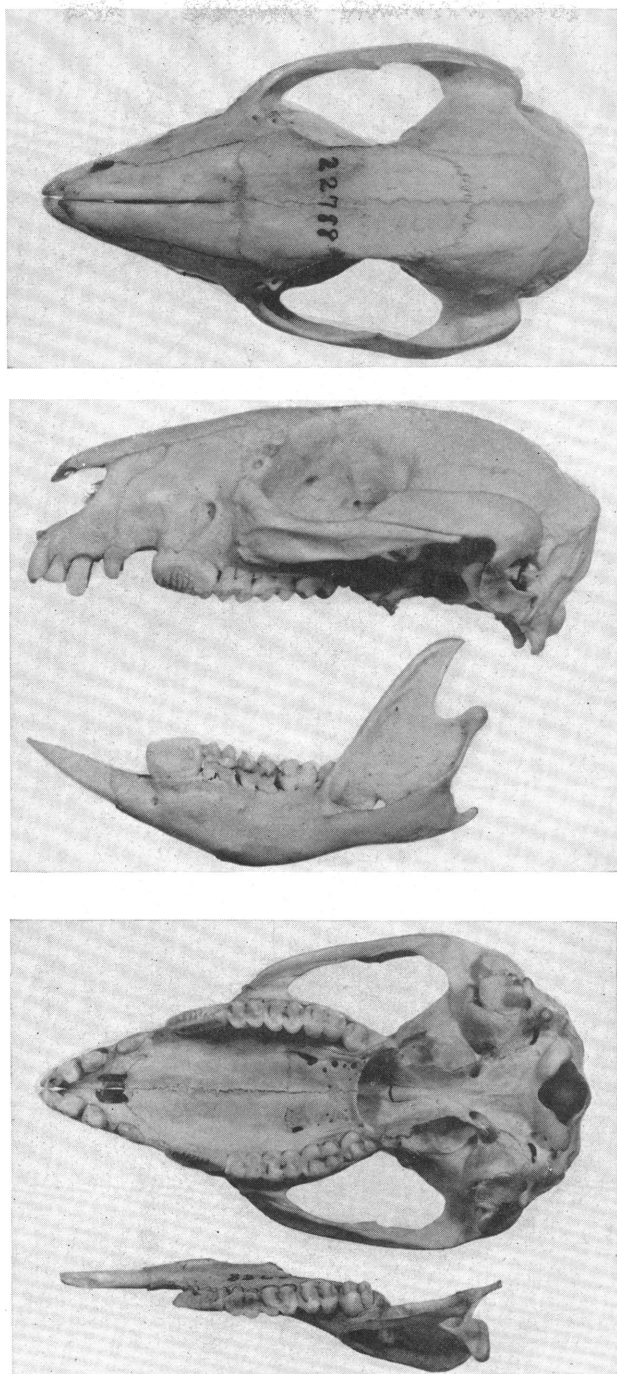


Fig. 8. *Aepyprymnus rufescens* Gray. A.M.N.H. No. 22788.

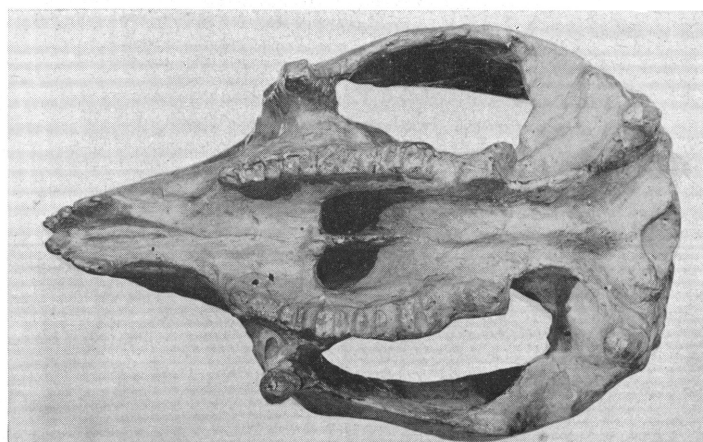
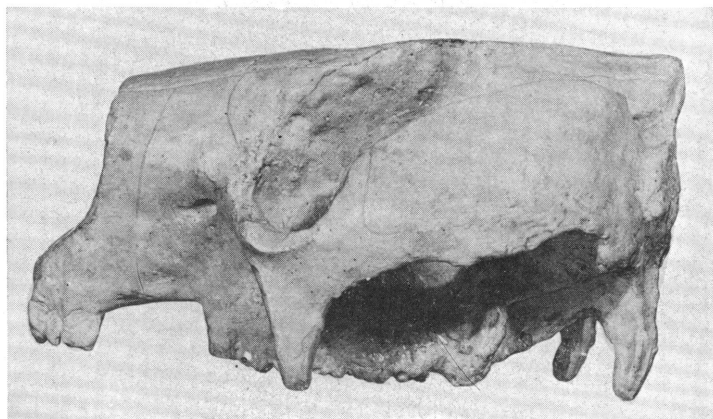


Fig. 9. *Sthenurus occidentalis* Glauert. Cast.

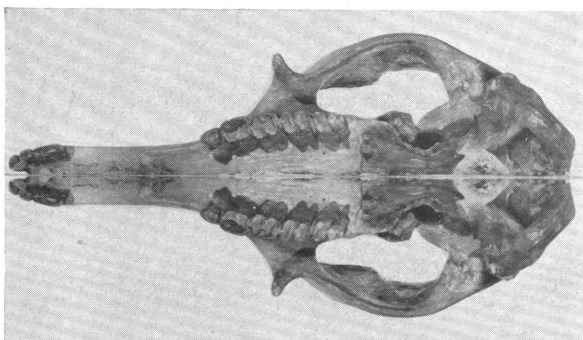
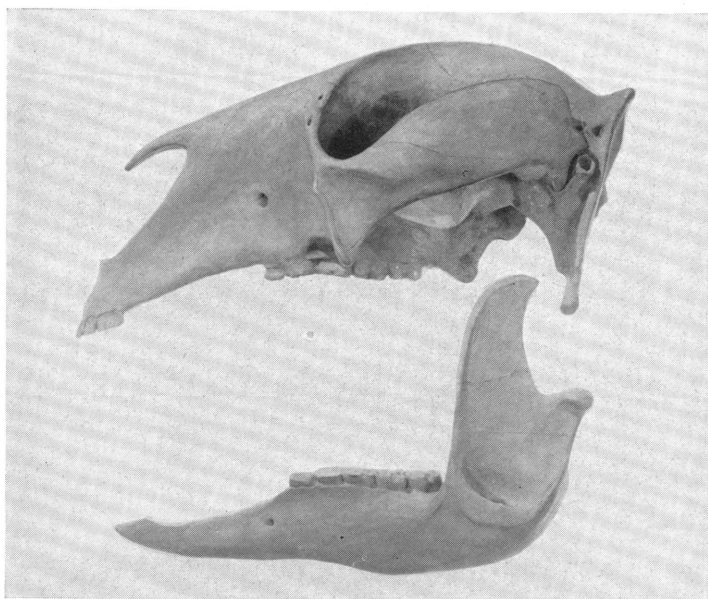
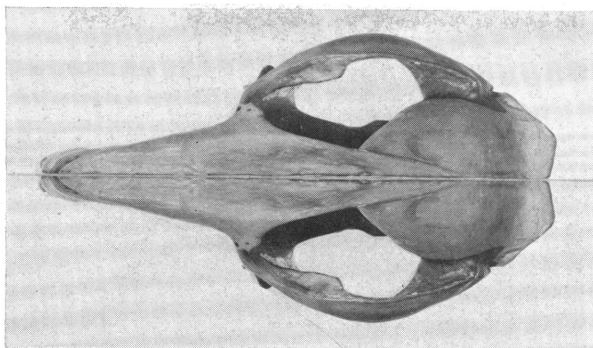


Fig. 10. *Palorchestes*. Model restoration by H. C. Raven.

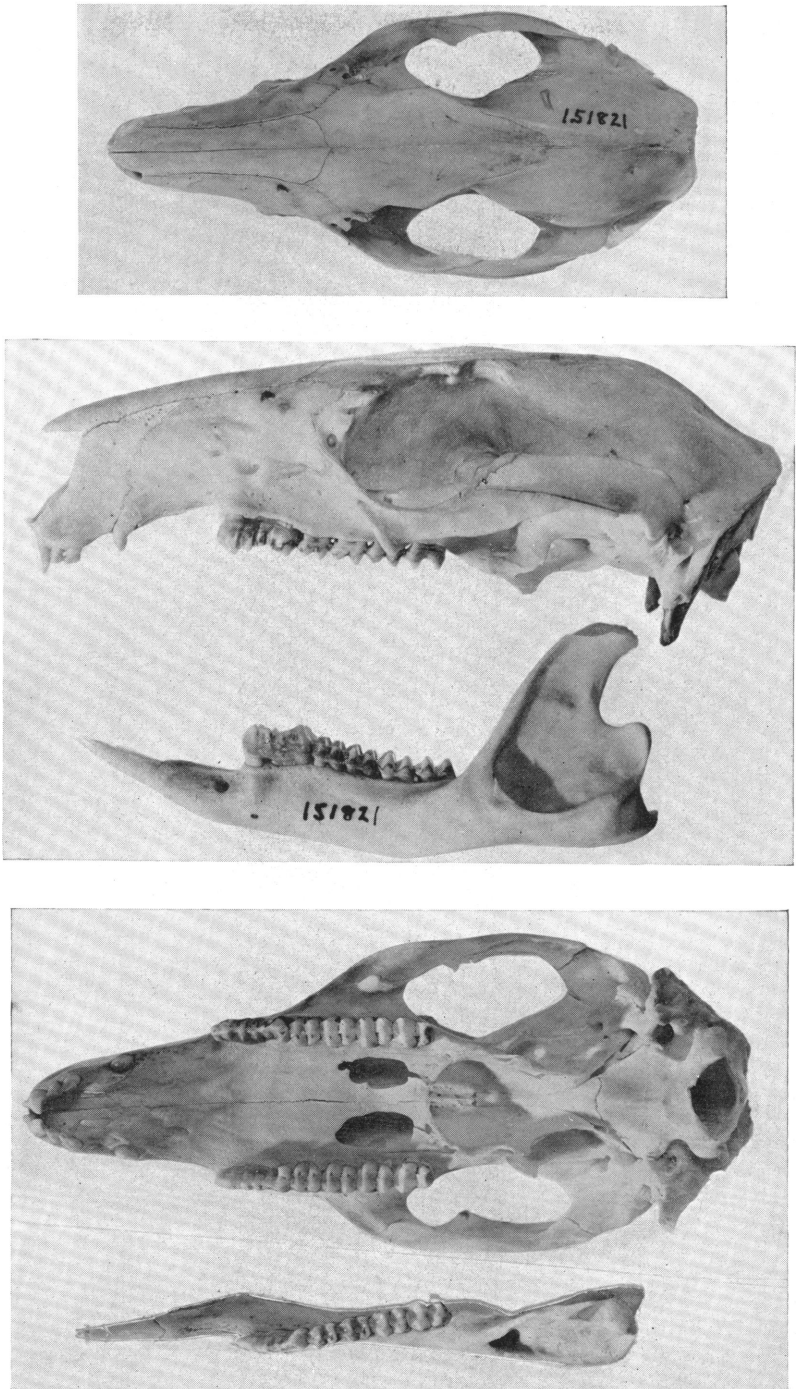


Fig. 11. *Dorcopsis (Dorcopsis) luctuosa* D'Albertis. A.M.N.H. No. 151821.

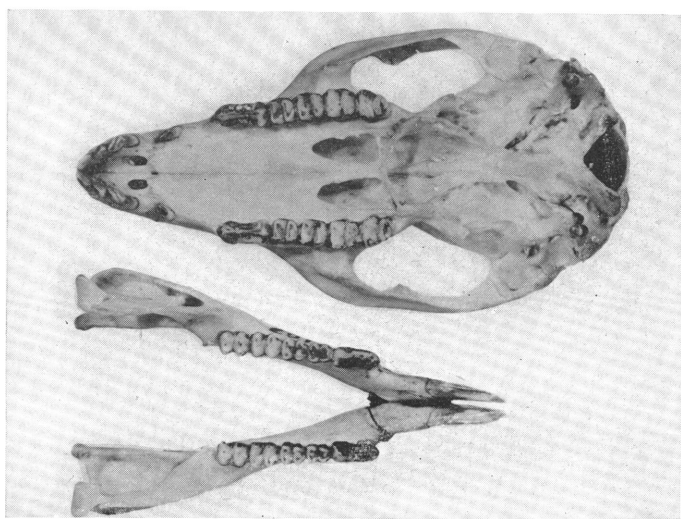
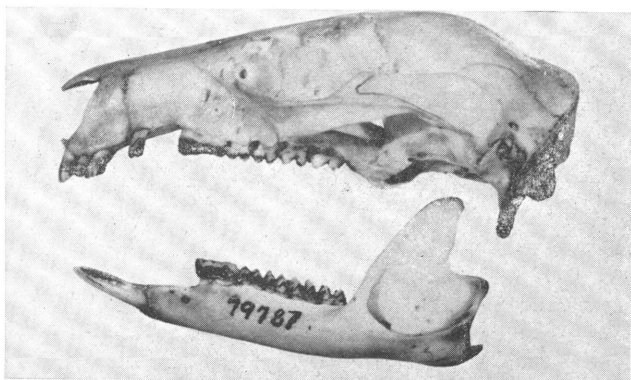
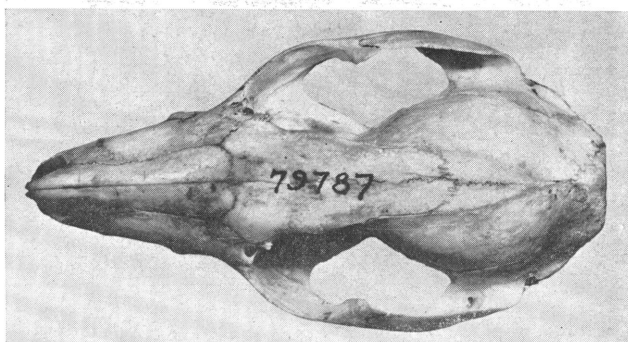


Fig. 12. *Dorcopsis (Dorcopsulus) macleayi* Miklouho-Maclay. A.M.N.H. No. 79787.

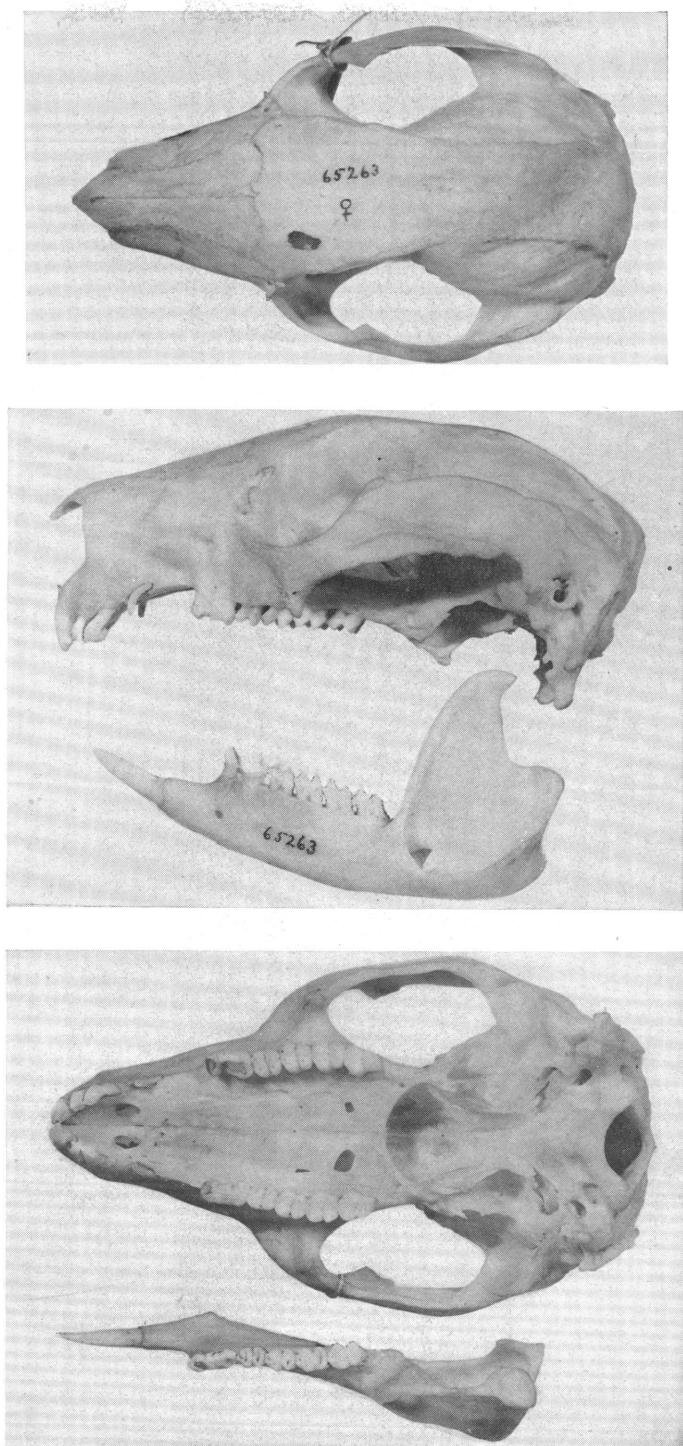


Fig. 13. *Dendrolagus lumholtzi* Collett. A.M.N.H. No. 65263.

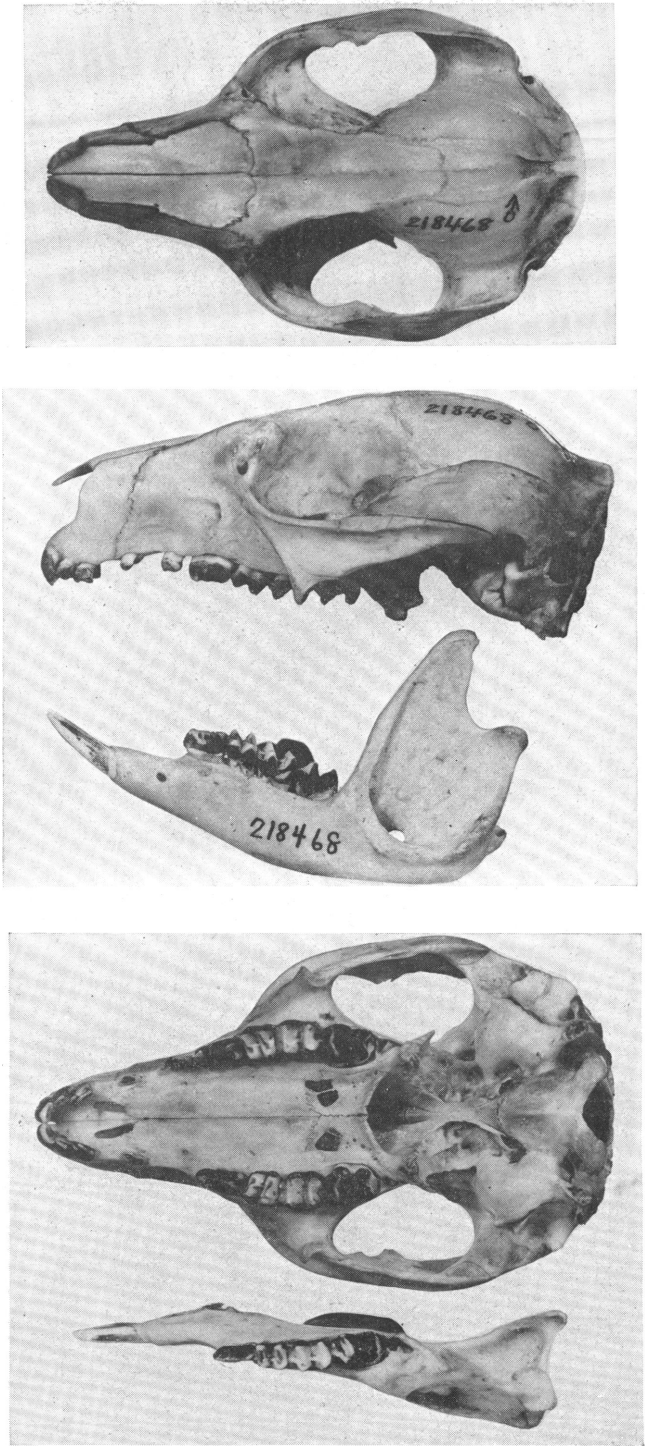


Fig. 14. *Lagorchestes conspicillatus* Gould. U.S.N.M. No. 218468.

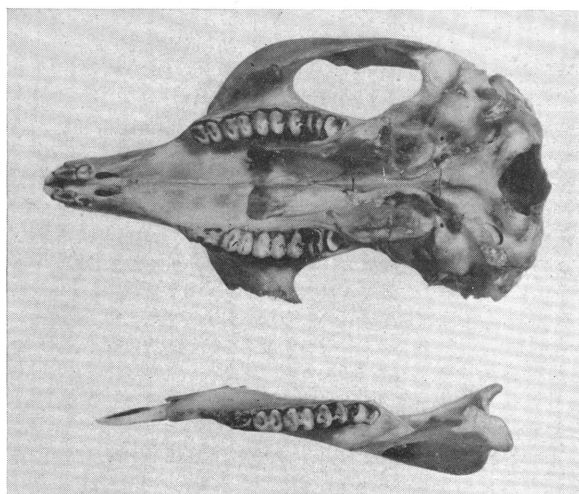
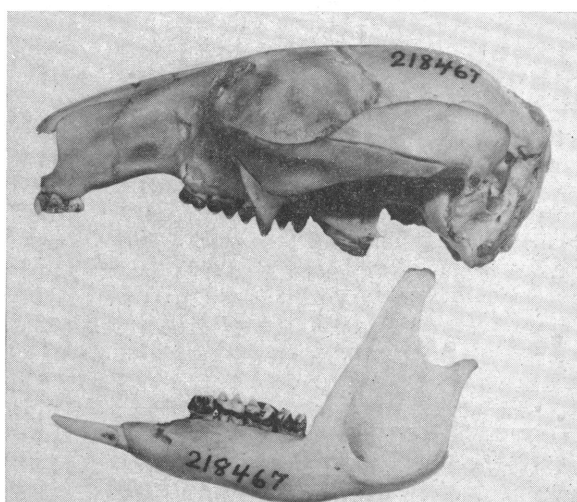
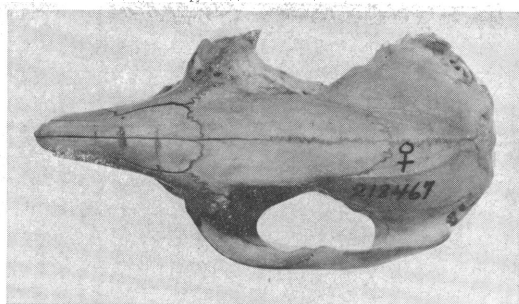


Fig. 15. *Lagostrophus fasciatus* Peron and Lesueur. U.S.N.M. No. 218467.

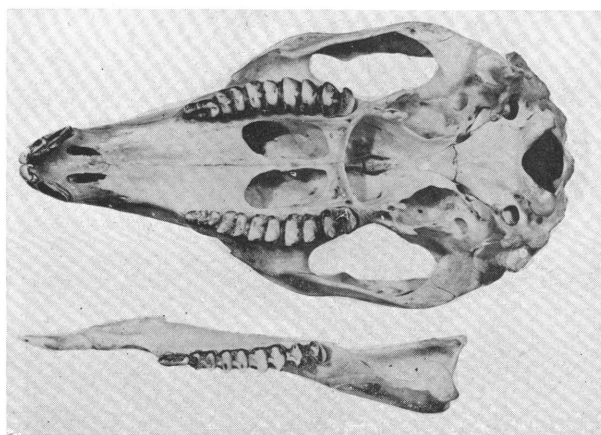
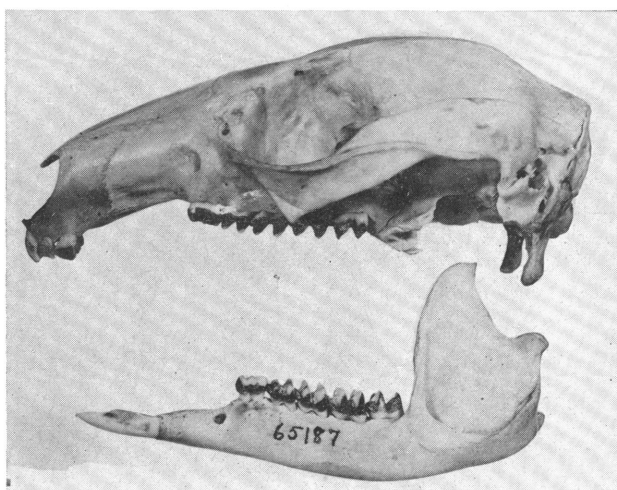
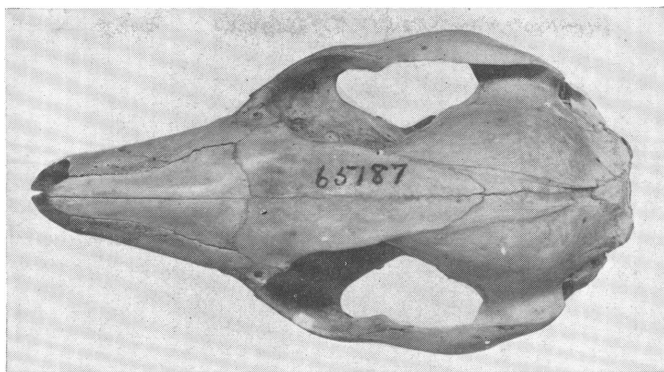


Fig. 16. *Thylogale stigmatica* Gould. A.M.N.H. No. 65187.

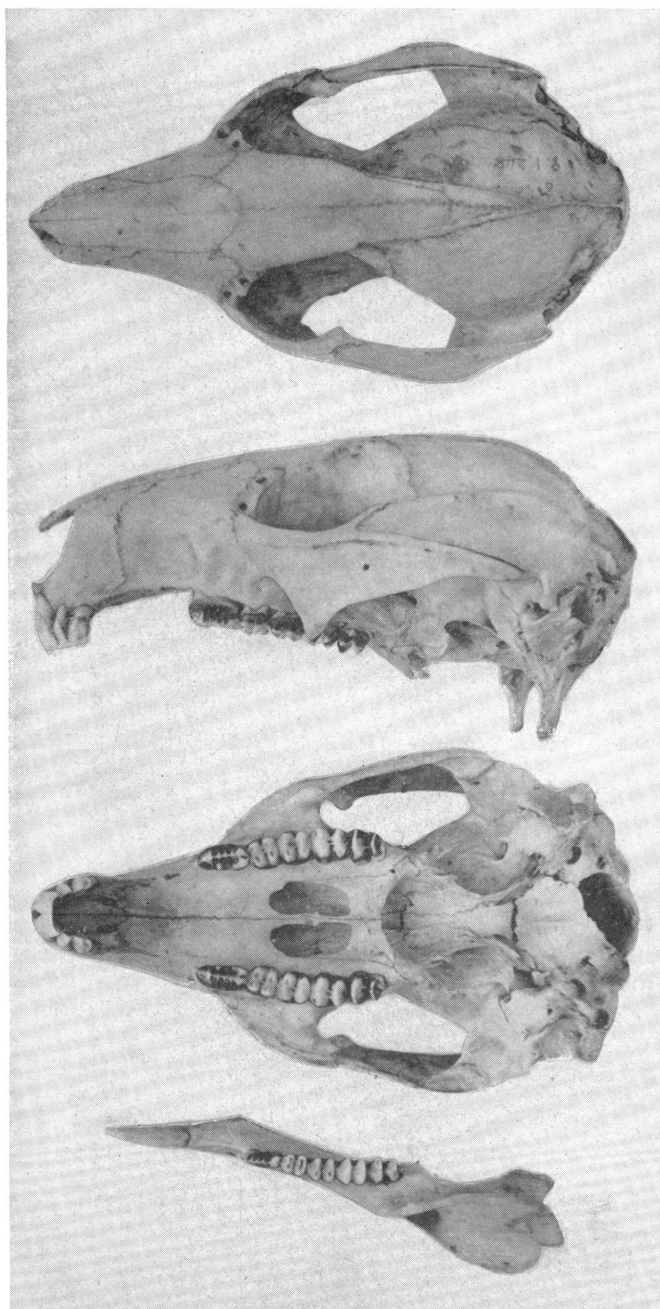


Fig. 17. *Setonix brachyurus* Quoy and Gaimard. Topotype. E.M.N.H. No. 6.8.1.248.

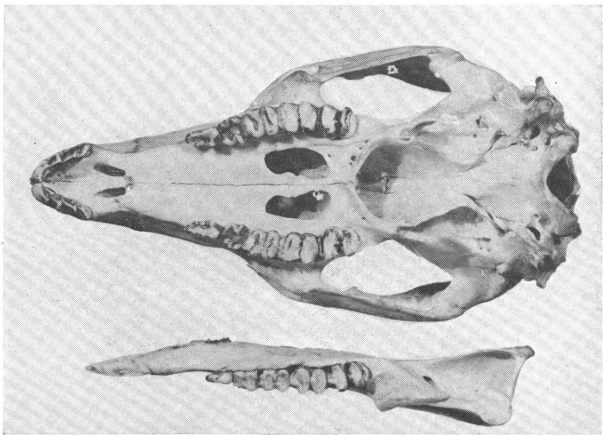
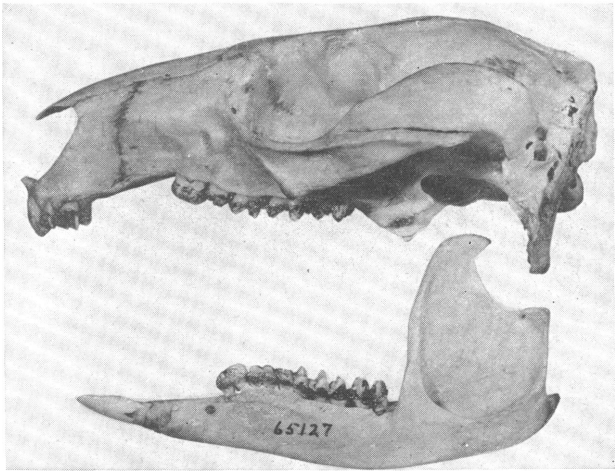
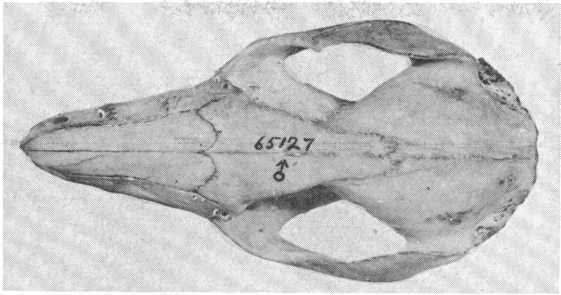


Fig. 18. *Protemnodon bicolor* Desmarest. A.M.N.H. No. 65127.

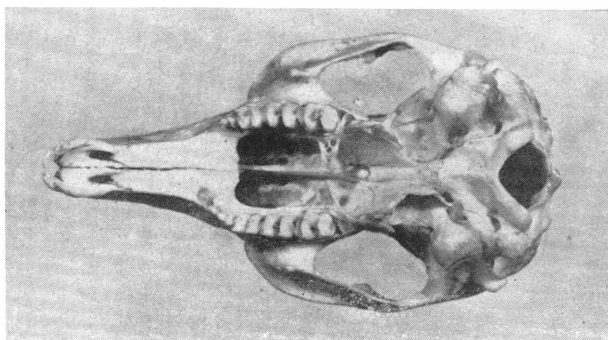
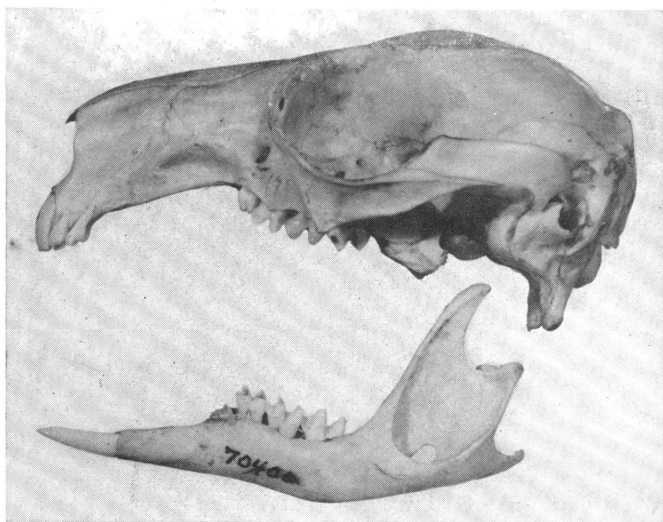
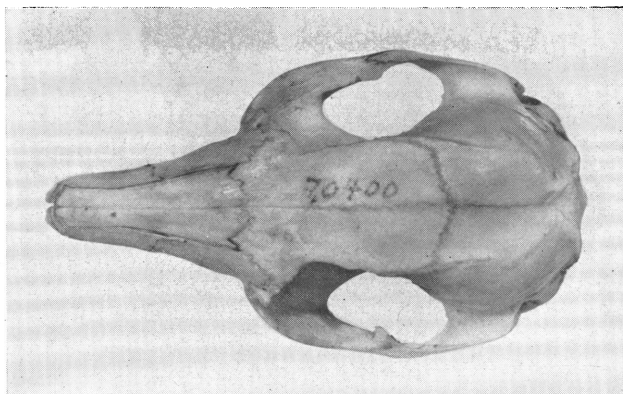


Fig. 19. *Onychogalea unguifer* Gould. A.M.N.H. No. 70400.

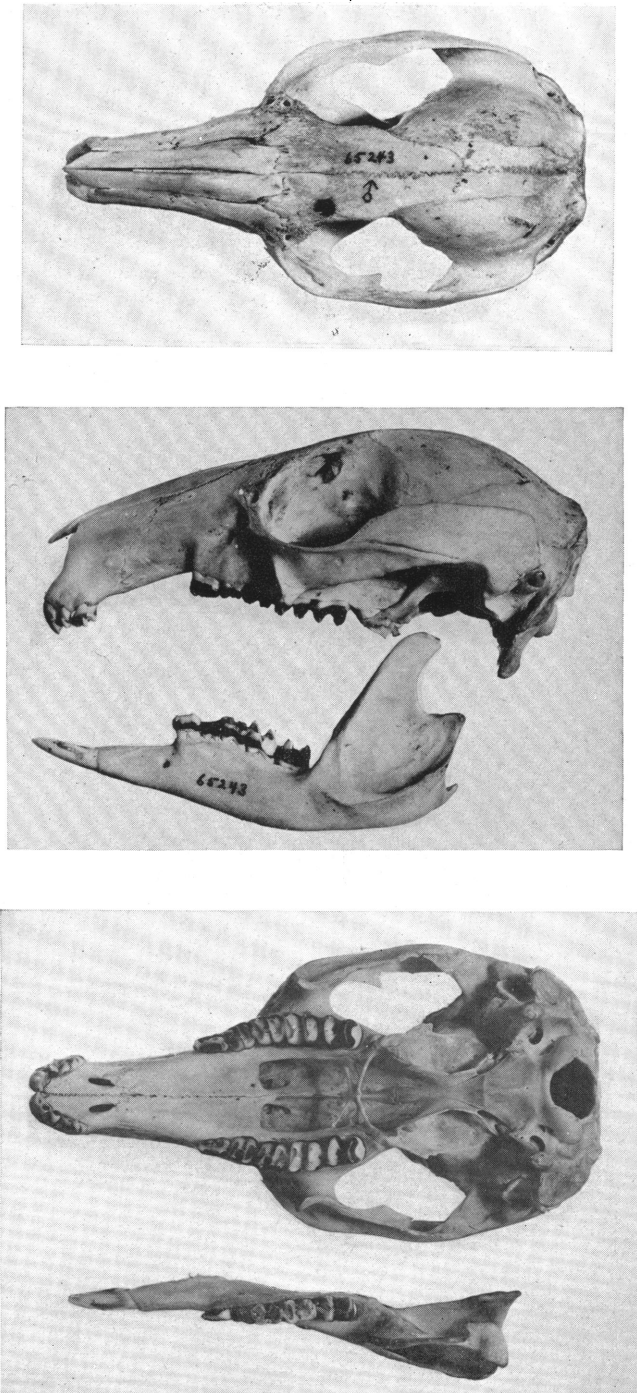


Fig. 20. *Petrogale penicillata* Griffith. A.M.N.H. No. 65243.

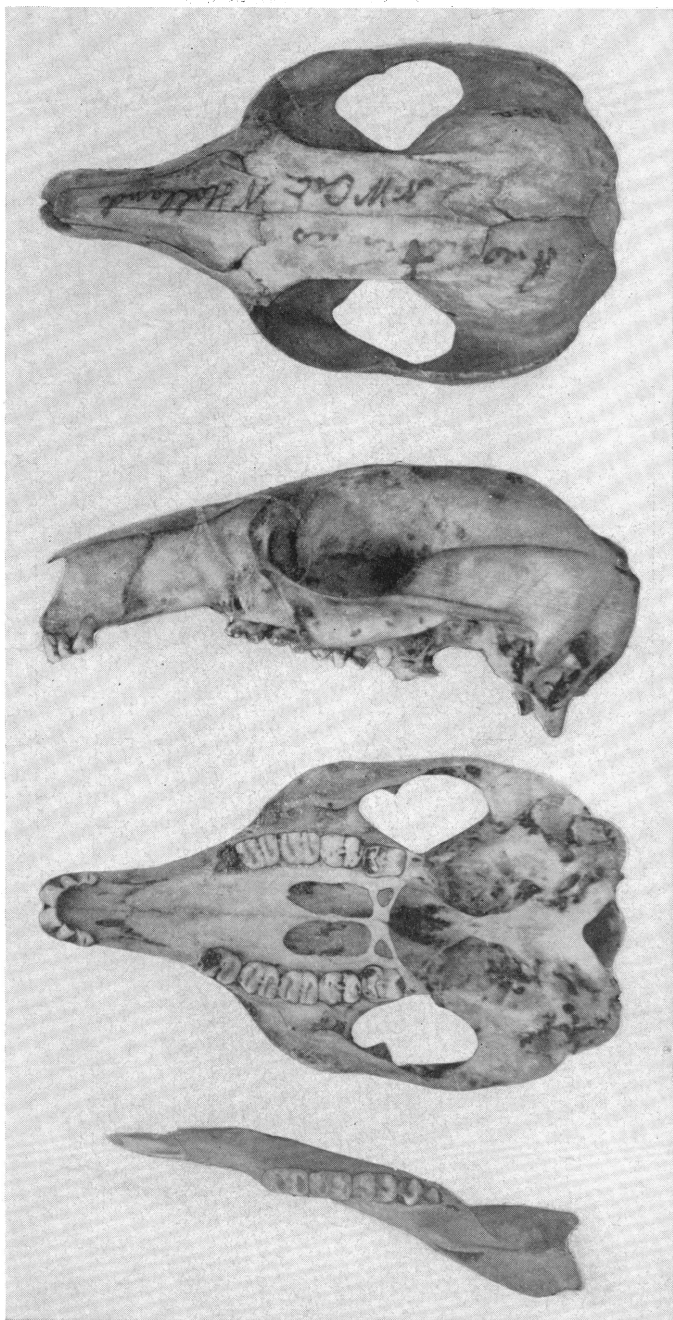


Fig. 21. *Peradorcas concinna* Gould. Type, B.M.N.H. No. 42.5.26.20.

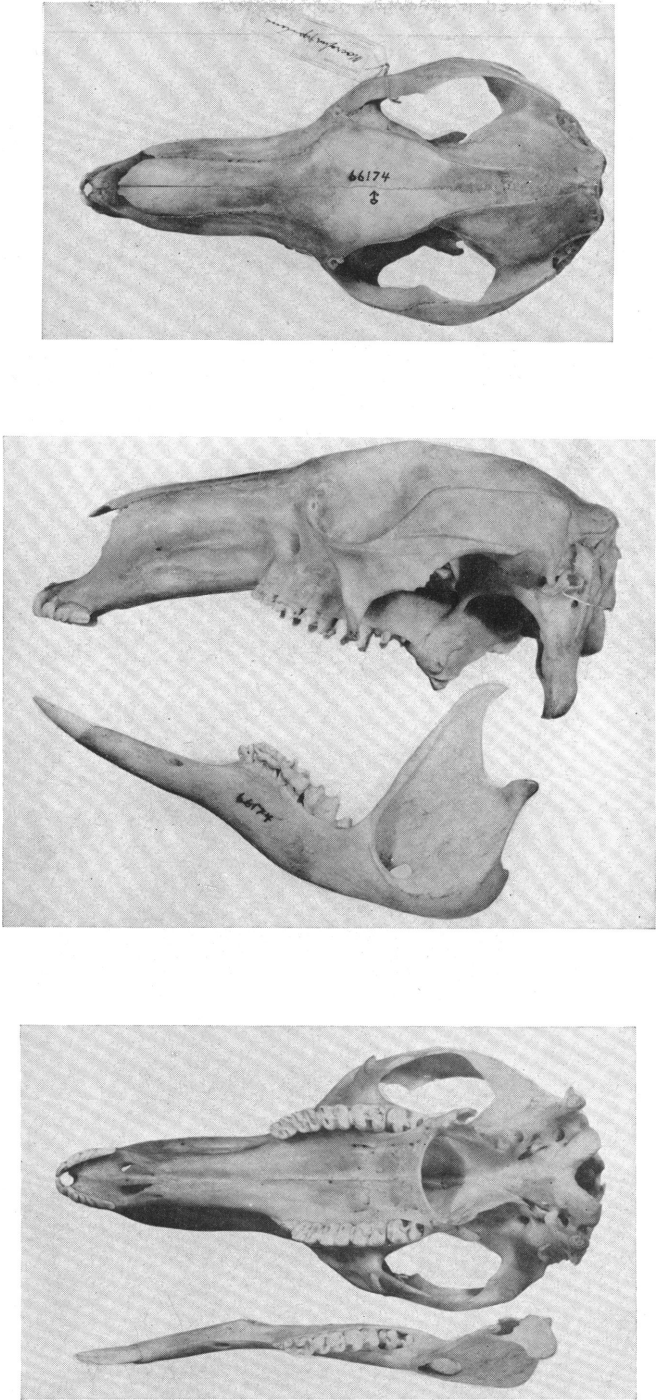


Fig. 22. *Macropus giganteus* Zimmerman. A.M.N.H. No. 66174.

