

RESULTS OF THE ARCHBOLD
EXPEDITIONS. NO. 104.
SYSTEMATIC REVISION OF THE
MARSUPIAL DASYURID GENUS
SMINTHOPSIS THOMAS

MICHAEL ARCHER

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CONTENTS

Abstract	65
Introduction	65
Acknowledgments	66
Methods	67
Systematics	74
<i>Sminthopsis</i> Thomas	74
Key to Species of <i>Sminthopsis</i>	77
Subgenus <i>Sminthopsis</i> Thomas	84
<i>Sminthopsis murina murina</i>	94
<i>Sminthopsis leucopus</i> (Gray)	102
<i>Sminthopsis ooldea</i> Troughton	108
<i>Sminthopsis longicaudata</i> Spencer	115
<i>Sminthopsis granulipes</i> Troughton	120
<i>Sminthopsis psammophila</i> Spencer	127
<i>Sminthopsis virginiae</i> (Tarragon)	132
<i>Sminthopsis douglasi</i> Archer	144
<i>Sminthopsis macroura</i> (Gould)	148
<i>Sminthopsis butleri</i> Archer	163
<i>Sminthopsis hirtipes</i> Thomas	169
<i>Sminthopsis crassicaudata</i> (Gould)	176
Subgenus <i>Antechinomys</i> Krefft	187
<i>Antechinomys laniger</i> (Gould)	187
Geographic Character Correlation in <i>Sminthopsis</i>	187
Interspecific Affinity in <i>Sminthopsis</i>	202
Discussion of Interpretation of Character State Polarity	209
Generic Affinity and Origins of <i>Sminthopsis</i>	211
Material Examined	212
Literature Cited	217

ABSTRACT

The history of the systematics of *Sminthopsis* is reviewed. A terminology is defined for the skull, dentition, foot, and other external structures. Important dental characters include the size of the canines, premolar width, width and length of molars, anterior cingula, reduction of the paracone, development of the entoconid and orientation of metacristids and hypocristids.

Two subgenera, *Sminthopsis* and *Antechinomys*, and the following species in each are recognized:

- S. murina* (including *albipes*, *fuliginosa*, and *tatei*)
- S. ooldea*, new rank
- S. leucopus* (including *ferruginifrons*, *mittelli*, and *leucogenys*)
- S. virginiae* (including *nitela*, *rufigenis*, *lumholtzi*, and *rona*)
- S. macroura* (including *froggatti*, *larpinta*, *stalkerii*, and *monticola*)
- S. hirtipes*
- S. granulipes*
- S. psammophila*
- S. butleri*
- S. douglasi*
- S. longicaudata*
- S. crassicaudata* (including *centralis* and *ferruginea*)

Subgenus *Antechinomys*

S. laniger (including *spenceri*)

Other unique populations that may prove to be species are known from the George Gill Range, Northern Territory, and Doomadgee Mission, Queensland.

Most species exhibit geographic variation and this is described as subspecies of each respective species. Some variation appears to be clinal within geographically widespread species, such as *Sminthopsis murina*. Size, tail length, tympanic wing development, brachycephaly, palatal fenestration, interorbital width, crowding of the premolar toothrow, and development of entoconids appear to vary as a function of relative aridity, both within and between species. This variation occurs independently in several different species groups.

Sminthopsis granulipes and *S. ooldea* represent morphological extremes within the genus, the former possessing many structurally ancestral characters and the latter exhibiting the most derived characters—those adapted to arid environments.

The species of *Sminthopsis* are most like those of *Ningau* but also show similarity to species of *Neophascogale* and *Phascosorex*.

INTRODUCTION

I have recently reviewed the systematics of *Sminthopsis* (*Antechinomys*) (Archer, 1977). Previous comprehensive reviews and revisions of *Sminthopsis* (*Sminthopsis*) are those of Waterhouse (1846), Krefft (1871), Thomas (1888), Ogilby (1892), Iredale and Troughton (1934), Tate (1947), and Ride (1970). Thomas (1888, p. 300) noted that "The smaller species of this genus present unusual difficulty in their discrimination. . . ." partly because of "the close resemblance existing between the skulls and teeth of the different species. . . ." His approach was conservative and he recognized only four species. In later works Thomas (1898, 1906, and 1922) named additional taxa, an amplification of his earlier synthetic treatment and not the products of further revision. Tate

(1947) recognized 10 species and 13 subspecies. He made the first attempt to consider interspecific affinities within the genus and allocated species to either a *S. rufigenis* or *S. crassicaudata* Division. Troughton (1965) recognized 12 species; of these, two were polytypic, together having at least seven subspecies. He named one species and two subspecies and suggested (p. 320) that *S. longicaudata* "may represent some annectant generic form. . . ." rather than *Sminthopsis*. His work is comprehensive but incomplete because of the greater attention he paid to specimens from Eastern rather than from Western Australia. Ride (1970) presented a popular work on Australian mammals that contained a complete list of species of Australian mammals together with an index that

listed synonymies. It is based not only on examination of specimens in most major Australian and overseas collections, including type specimens, but also on the results of work by his pupils. Ride (1970) recognized 11 species of *Sminthopsis* and no subspecies.

These earlier studies were based primarily on conspicuous features of the ears, tails, feet, and pelage. Some of these are known to be variable (Ride, 1970), and none of them are useful to paleontologists who want to compare characters of modern and fossil specimens. Although all previously used morphological characters were examined during the present study, I focused on characters of the skull, dentition, and hind feet. To this extent my revision may be regarded as an extension of Bensley (1903), but differs in that it then applies the characters examined in order to review and revise taxonomy.

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METHODS

STRUCTURES USED IN CLASSIFICATION

MORPHOLOGY OF THE HIND FOOT: The features of the plantar surface require a descriptive terminology (fig. 1). The hallux is variously reduced, as is the hallucal pad. The second, third, and fourth interdigital pads are variously fused. The metatarsal and posthallucal pads are usually absent (there are exceptions in two species). The foot pads may have granular or striate apical areas. The distal end of each digit bears a terminal pad that may be completely granular or striate. Relative length of the foot varies with species, as do the hairy areas of the sole. Two regions of interdigital pad structure must be distinguished: the granular pads themselves and the sometimes enlarged and/or striated apical granules of each pad. It has not been clear from earlier studies what relation striae bear to granules. Troughton (1965) suggested that some striated apical areas may develop by fusion through wear of larger apical granules. This interpretation has effected recognition by mammalogists of the specific status of *Sminthopsis leucopus* (Thomas, 1888; Troughton, 1965). In *S. leucopus* and *S. longicaudata* apical striae are clearly not simply the result of fusion by wear of apical granules.

MORPHOLOGY OF TEETH: The terminology used to describe the structure of the teeth is shown in figures 2 and 3. Nomenclature for particular teeth is that used by Thomas (1888), Ride (1964), and Archer (1976b). All systems of homology in current use (except Archer 1978, which was completed after this manuscript was finalized)

are based on the evident misconception that true tooth replacement occurs in postcanine cheekteeth (Archer, 1974c). At least in the dasyurid *Antechinus flavipes*, the tooth called the fourth premolar by Thomas (1888) develops from a position on the dental lamina between the third premolar and the deciduous fourth premolar and is thus not a replacement tooth for the deciduous fourth premolar, and that tooth is the first tooth in the molariform *Zahnreihe*. Tentatively, I use here the serial nomenclature of Thomas, such that the cheekteeth are called: canines (C), first premolars (P1), third premolars (P3), fourth premolars (P4), deciduous premolars (dP4), first molars (M1), second molars (M2), third molars (M3), and fourth molars (M4). I have reviewed the abnormal dental evidence relevant to the justification of this terminology (Archer, 1975c) and proposed a nomenclature of crown morphology elsewhere (Archer, 1975a, 1975b, 1976b). A further updating of dental terminology has been given elsewhere (Archer, 1978). In the present work I denote upper or lower teeth by superscript (P¹) or subscript (P₁) numbers and indicate both upper and lower teeth by lack of super or subscript numbers (P1).

The canine may be caniniform, as in *Sminthopsis granulipes*, or premolariform, as in *S. longicaudata*. In some species, for example, *S. virginiae*, the base of the enamel on C1 may extend only halfway down the exposed crown. Although the unworn enamel crown appears to have a relatively constant size, the root sometimes grows to such an extent that the base of the crown occurs well beyond the edge of the alveolus. This

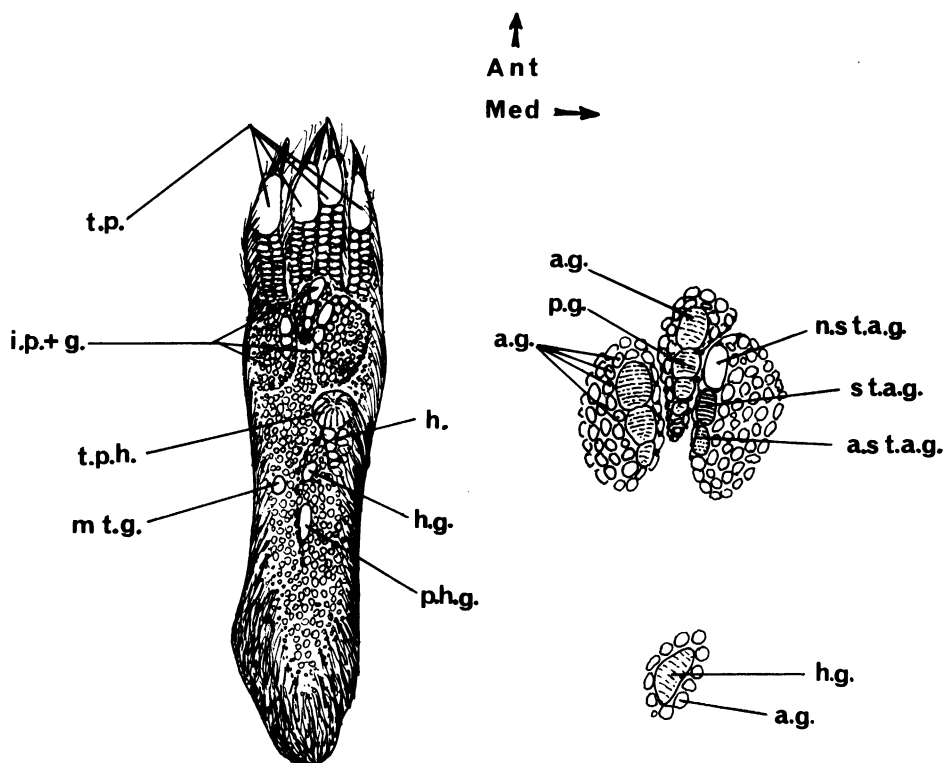


FIG. 1. Right hindfoot of *Smynthopsis* with terminology of pads and granules: a.g., apical granule; a.s.t.a.g., apparently striated apical granule; h., hallux; h.g., hallucal granule; i.p.+g., interdigital pads and granules; m.t.g., metatarsal granule; n.s.t.a.g., non-striated apical granule; p.g., proximal granule; p.h.g., posterior hallucal granule; s.t.a.g., striated apical granule; t.p., terminal pads of digits; t.p.h., terminal pad of hallux.

occurs more frequently in males. Some species show the same condition in P⁴ where the anterior root is more greatly affected than the posterior root, and, as a result, the crown often tilts posteriorly.

Lengths of upper molar crowns differ relative to widths. There may be as many as six or even seven styler cusps on one tooth. Some are uncommon and these I regard as abnormalities (Archer, 1975c). Styler cusps of dasyurids commonly occur in four positions (Archer, 1976b). Styler cusp B (or the stylocone) is at the buccal end of the anterior paracrista. Styler cusp D is the largest, occurs about midway along the buccal side of the crown, and is always present on M² and M³ though it may be small on M³. Between styler cusps D and B, and sometimes lingual

to their buccal position, there is sometimes a very small styler cusp C. The posterobuccal edge of the crown, at the point where the posterior metacrista terminates buccally is called the metastyler corner. A discrete cusp does not usually occur in this position. Between the metastyler corner and styler cusp D there is sometimes a small cusp called styler cusp E. The anterobuccal corner of the crown is the parastyler corner, although there is not usually a discrete styler cusp in this position. A small laterally compressed anteroposterior bladlike crest commonly forms part of the parastyler crest. This generally extends to the anterior corner of the tooth and functions with the posterior blade of P⁴ to enclose an embrasure opposing the protoconid of M₁.

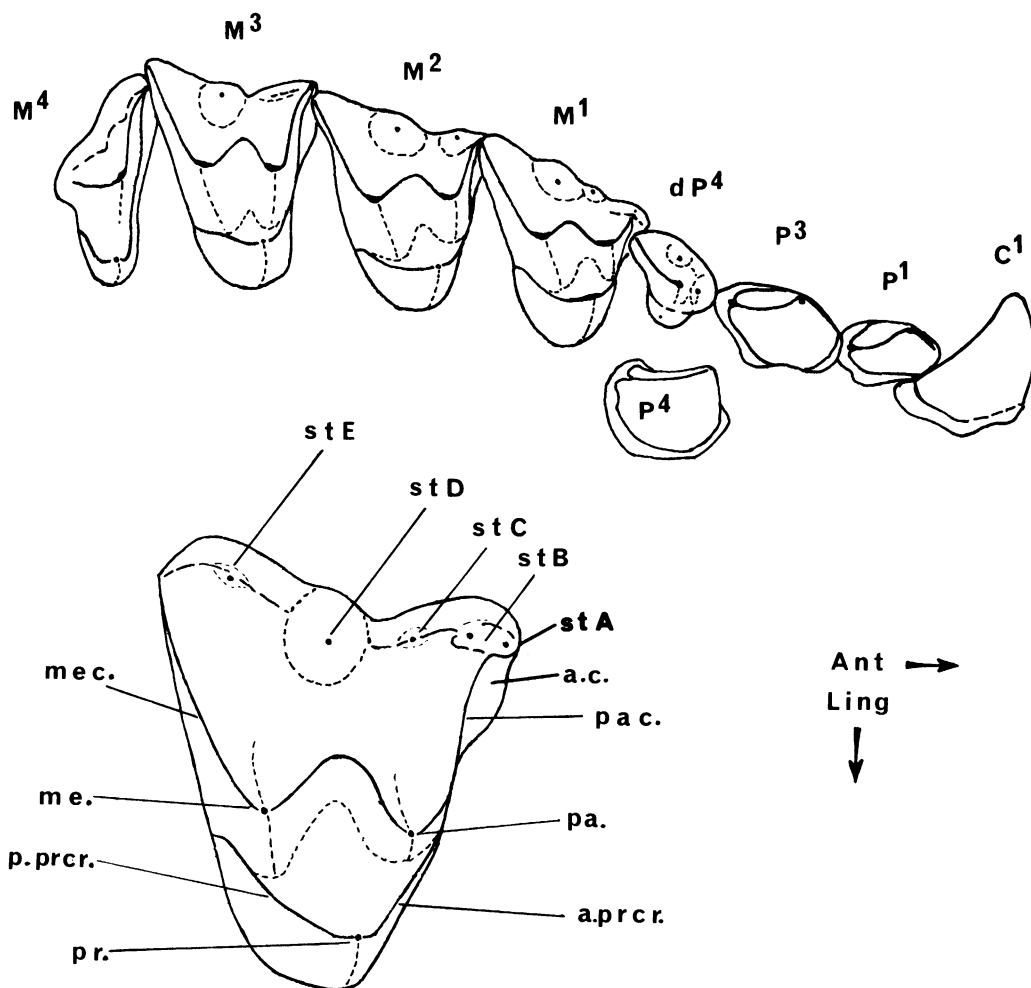


FIG. 2. Upper cheek-teeth of *Sminthopsis* (based on *S. douglasi*). a.c., anterior cingulum (or pre-cingulum); a.p.r.c.r., preprotocrista; me., metacone; mec., metacrista; pa., paracone; p.a.c., paracrista; p.p.r.c.r., post-protocrista; pr., protocone; st A, position of stylar cusp A; st B-E, stylar cusps B, C, D, and E.

The talonid is the most important area of the lower teeth providing information about species' affinities. Generally there are only three cusps on the talonid: hypoconid, hypoconulid and entoconid. Sometimes there is a small metastylid.

MORPHOLOGY OF SKULL AND DENTARY: Cranial structures require a comparative terminology (figs. 4-5). Basicranial terminology follows Archer (1976a). Relative length and width of palatal vacuities, ex-

tent of development of interdental fenestrae, supraorbital processes of the frontal, lacrimal processes, relative length of the rostrum, relative size of the alisphenoid and petrotic tympanic wings, and size and positions of basicranial foramina are, in some cases, species-specific features. Overall shape of the masseteric fossa and development of the angular process of the dentary distinguish some species.

Names of basicranial foramina used here

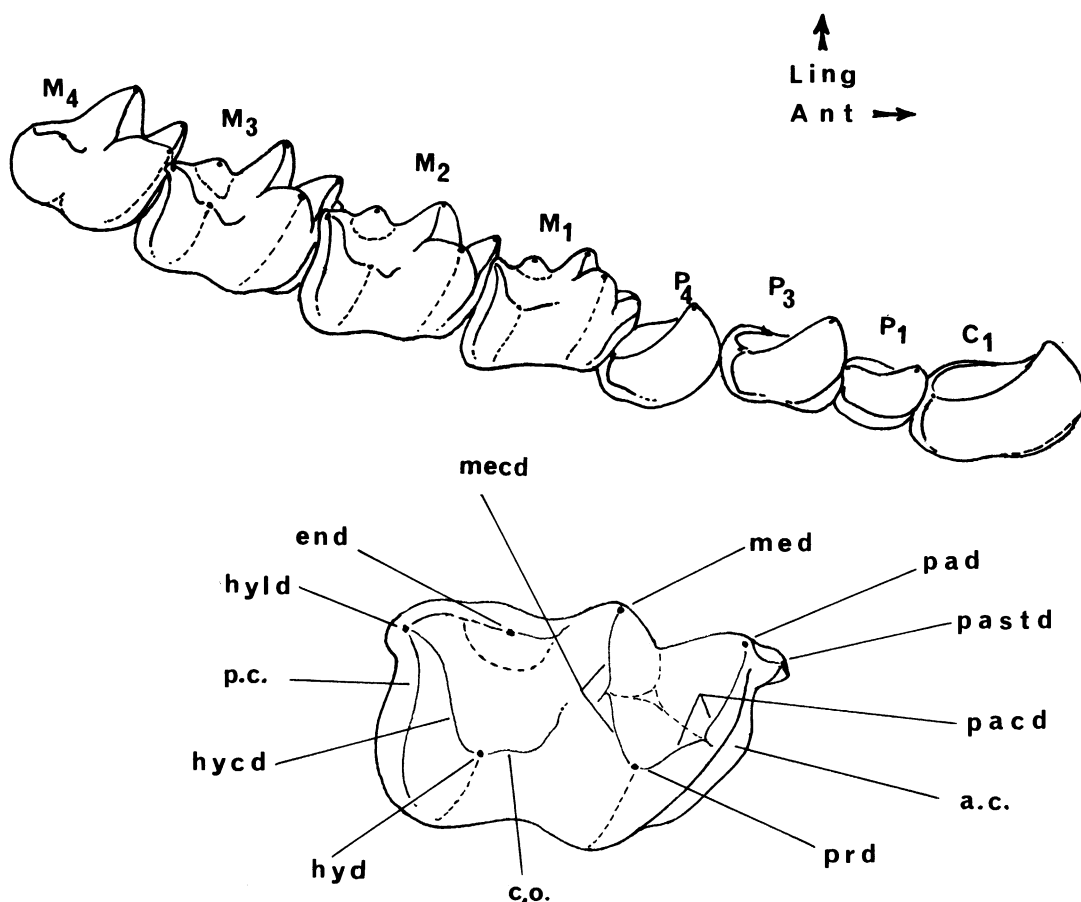


FIG. 3. Lower cheekteeth of *Sminthopsis* (based on *S. douglasi*). a.c., anterior cingulum (or precingulid); c.o., cristid obliqua; end, entoconid; hycd, hypocristid; hyd, hypoconid; hyd, hypoconulid; mecd, metacristid; med, metaconid; pacd, paracristid; pad, paraconid; pastd, parastyloid; p.c., posterior cingulum (or postcingulid); prd, protoconid.

were determined in part by latex injections of the circulatory system of *Sminthopsis murina* (Archer, 1976a). This has necessitated introduction of terms not used by Gregory (1910). In some species the position of a few foramina are variable and do not provide useful means for diagnosing species. An extreme example of variation occurs in the holotype of *Sminthopsis crassicaudata centralis* Thomas which is unique in possessing a very large midventral pituitary foramen. In other species modifications of size of the alisphenoid tympanic wing results in modi-

fication of position of the basicranial foramina. These modified positions are often useful diagnostic features.

MENSURATION AND REFERENCE NUMBERS

Measurements were taken with a Helios dial caliper. Limits of the dimensions I measured are described below and illustrated in figure 6.

- a: basal length (BL).
- b: maximum skull width (ZW).

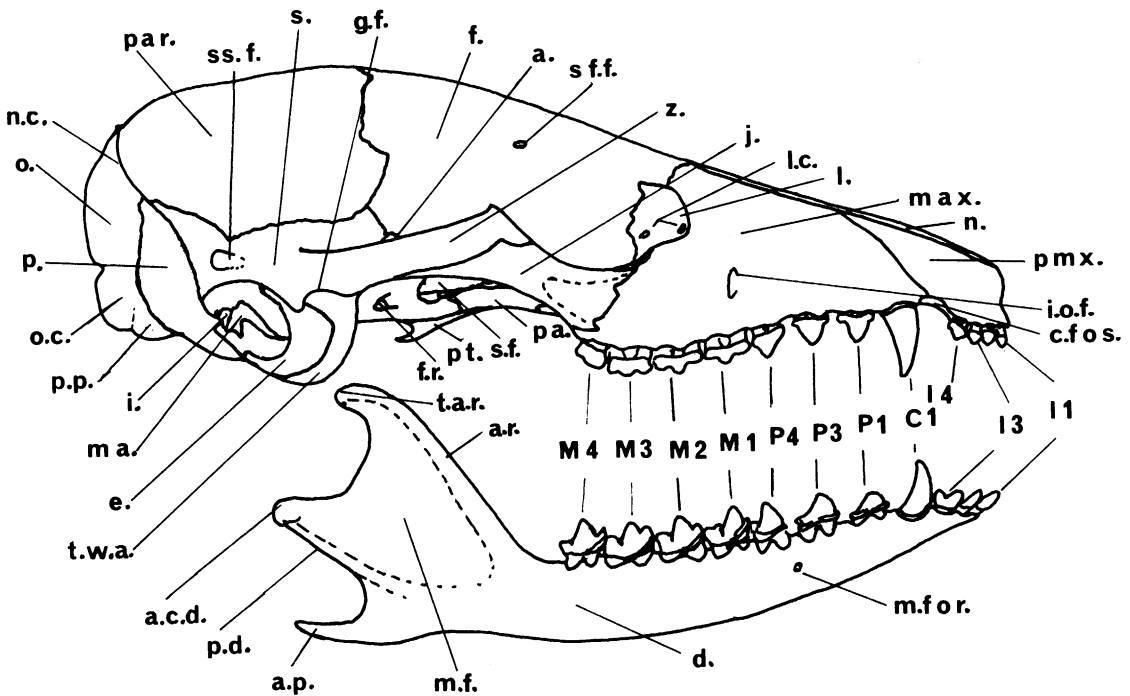


FIG. 4. Lateral view of skull and dentary of *Sminthopsis* (based on *S. granulipes*). a., alisphenoid; a.c.d., articular condyle of dentary; a.p., angular process; a.r., anterior border of ascending ramus; c.fos., canine fossa; d., dentary; e., ectotympanic; f., frontal; f.r., foramen rotundum; g.f., glenoid fossa; i., incus; i.o.f., infraorbital foramen; j., jugal; l., lacrimal; l.c., lacrimal canal; ma., malleus; max., maxilla; m.f., masseteric fossa; m.for., mental foramen; n., nasal; n.c., nuchal crest; o., occipital; o.c., occipital condyle; p., periosteal; pa., palatine; par., parietal; p.d., posterior border of dentary; pmx., premaxilla; p.p., paroccipital process; pt., pterygoid; s., squamosal; s.f., sphenorbital fissure; sf.f., supraorbital foramen; ss.f., subsquamosal foramen; t.a.r., tip of ascending ramus; t.w.a., tympanic wing of alisphenoid; z., zygomatic portion of squamosal.

c: outside bullae width (OBW); caliper points between alisphenoid bulla and mesial edge of postglenoid processes.

d: inside bullae width (IBW); minimum distance between alisphenoid bullae.

e: length of maxillary toothrow (C^1 – M^4); anterior edge of C^1 root to posterior edge of M^4 root.

f: length of upper molar row (M^1 – M^4); from anterior side of M^1 paracone root to posterior side of M^4 posterior root.

g: length of first three upper molars (M^1 – M^3); from M^1 , as described above in f to posterior face of M^3 metacone root.

h: breadth across palate and toothrows (R–LM³); from buccal side of metacone roots.

i: minimum interorbital frontal width (IO).

j: distance between posterior edge of premax-

illary vacuity and anterior edge of maxillary vacuity (IPVD).

k: dentary length (DL); from the posterior edge of articular condyle to anterior edge of the I_1 alveolus.

l: length of lower toothrow (I_1 – M_4); from anterior edge of I_1 alveolus to posterior edge of M_4 talonid root (this may vary fractionally because sometimes the M_4 talonid root was not exposed and in that case the measurement was made to base of the crown).

m: length of lower molar row (M_1 – M_4); measured from anterior face of the anterior root of M_1 to the M_4 posterior root, as described above for l.

n: length of first three lower molars (M_1 – M_3); from M_1 as described above in m to posterior face of the posterior root of M_3 .

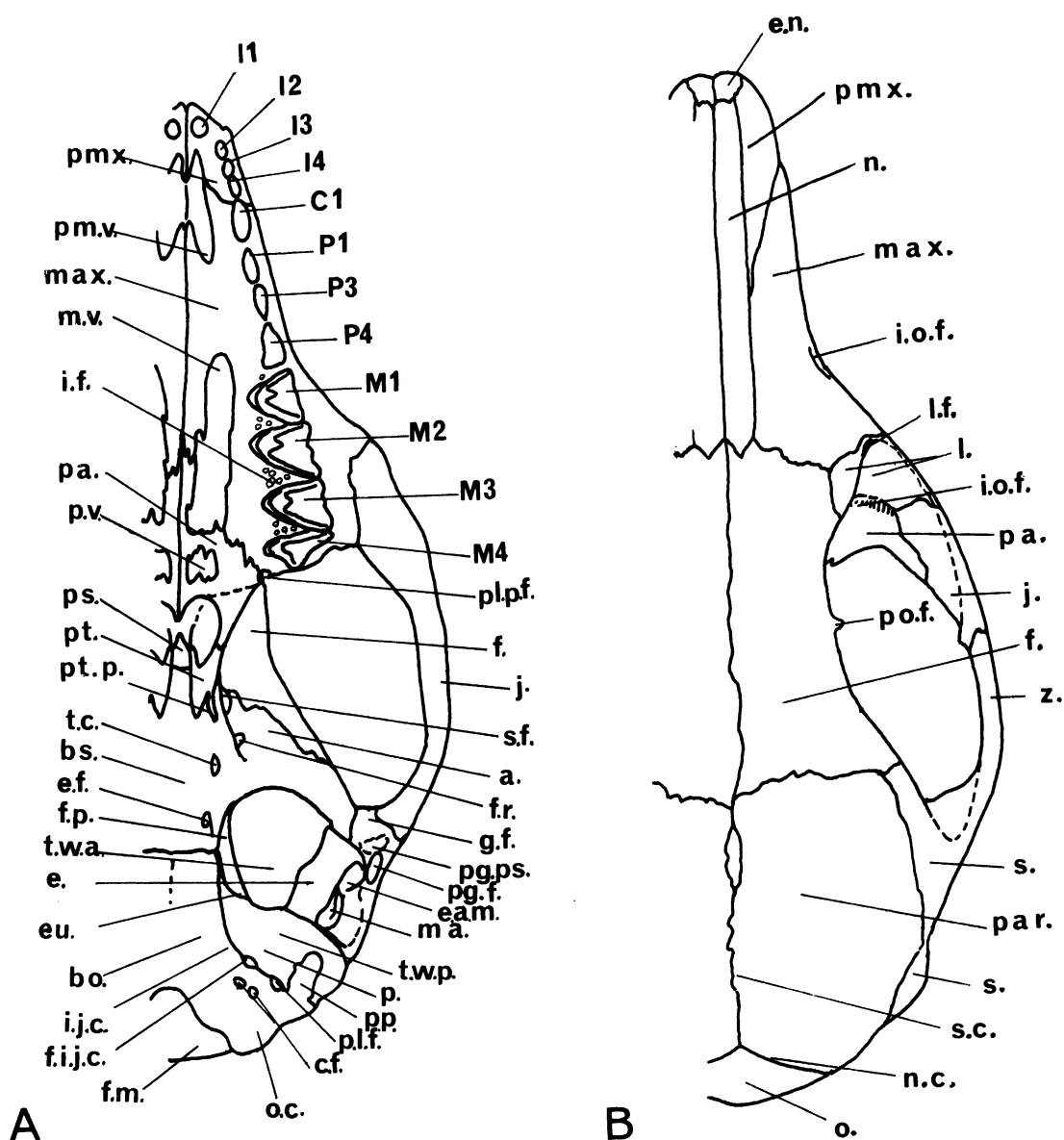


FIG. 5. A. Ventral view of skull of *Sminthopsis* (based on *S. granulipes*). a., alisphenoid; bo., basioccipital; bs., basisphenoid; c.f., condylar (and or hypoglossal) foramen; e., ectotympanic; e.a.m., external auditory meatus; e.f., entocarotid foramen; eu., bony eustachian canal; f., frontal; f.i.j.c., foramen for internal jugular canal; f.m., foramen magnum; f.p., foramen pseudovalve; f.r., foramen rotundum; g.f., glenoid fossa; i.f., interdental fenestrae; i.j.c., internal jugular canal; j., jugal; ma., malleus; max., maxilla; m.v., maxillary vacuity; o.c., occipital condyle; p., periotic; pa., palatine; pg.f., postglenoid fossa; pg.ps., postglenoid process; p.l.f., posterior lacerate foramen; pl.p.f., posterolateral palatal foramen; pm.v., premaxillary vacuity; pmx., premaxilla; p.p., paroccipital process; ps., pre-sphenoid; pt., pterygoid; pt.p., pterygoid process; p.v., palatine vacuity; s.f., sphenorbital fissure; t.c., transverse canal; t.w.a., tympanic wing of alisphenoid; t.w.p., tympanic wing of periotic. B. Dorsal view of skull of *Sminthopsis* (based on *S. granulipes*). e.n., external nares; f., frontal; i.o.f., infraorbital foramen; j., jugal; l., lacrimal; l.f., lacrimal foramen; max., maxilla; n., nasal; n.c., nuchal crest; o., occipital; pa., palatine; par., parietal; pmx., premaxilla; po.f., postorbital foramen; s., squamosal; s.c., sagittal crest; z., zygomatic part of squamosal.

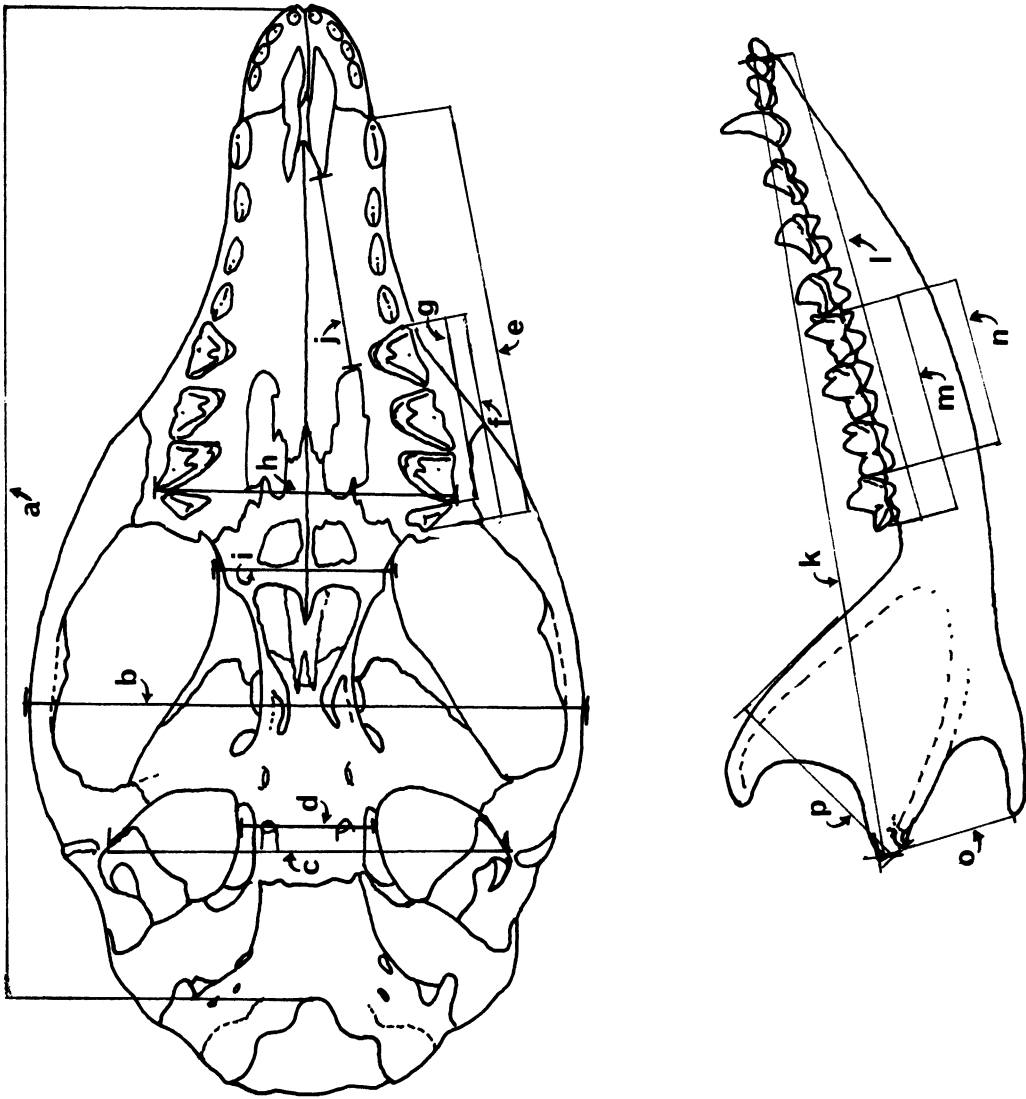


FIG. 6. Measures described in text and the positions from which they were taken in the skull and dentary of *Sminthopsis*.

o: condyle-angular (C-AP); greatest distance between tip of the angular process and buccal tip of the articular condyle.

p: condyle-ramus (C-AR); determined by placing blade of the calipers flat as possible along leading edge of the ascending ramus and measuring to posterior edge of the articular condyle, a measurement that relies on the general condition that the anterior face of the ascending ramus, for most of its dorsal length, is more or less straight.

Certain characters were not measured because of extreme variation within species that overlapped broadly from one species to another and even overlapped with species of other genera. An example of this type of character is dentary depth which varies with age of the animal and sometimes differs within a series of specimens by a factor of three. Other characters were not measured because

they would be repeating an already existing dimension. For example, transverse width of the alisphenoid bulla was indirectly given by other basicranial measurements.

Absolute size of the dentition and its parts are useful in differentiating species. The way in which I took these measurements are shown in figure 6. Generally, the most useful absolute dimensions are lengths of the M1-3. They are not affected by age and are little affected by intraspecific variation. Dimensions affected by age include lengths of tooththrows involving premolars, canines, or incisors. Accordingly, these measurements have been made only on adults. Adults, as defined by Thomas (1888, p. 7), are those in which the fourth premolars have fully erupted.

My attempts to measure crest lengths of molars produced unreliable results. The protocone, paracone, metacone, stylar cusp B, protoconid, and hypoconid do not have vertical lingual edges. They are curved, and as a result, their length is directly dependent on tooth wear.

ABBREVIATIONS OF INSTITUTIONS

A, Tasmanian Museum, Hobart
 AM, Australian Museum, Sydney
 AMNH, American Museum of Natural History, New York
 B, Butler collection in Western Australian Museum, Perth
 BM, British Museum (Natural History), London
 C, National Museum of Victoria, Melbourne
 CM, C.S.I.R.O. collection at Lyneham, Canberra
 D, Victorian Fisheries and Wildlife, Melbourne
 J or JM, Queensland Museum, Brisbane
 MM, Macleay Museum, University of Sydney, Sydney
 MVZ, Museum of Vertebrate Zoology, University of California, Berkeley
 NTM, Northern Territory Museum, Darwin
 PC, Pearson collection of the Tasmanian Museum, Hobart
 QVM, Queen Victoria Museum, Launceston
 SAM, South Australian Museum, Adelaide
 WAM, Western Australian Museum, modern mammals (for example, WAM M2021) and fossil vertebrate collection (for example, 68.5.30)

SYSTEMATICS

SMINTHOPSIS THOMAS

Podabrus Gould, 1845 (*Nec Podabrus* Westwood, 1840).

Sminthopsis Thomas, 1888.

TYPE SPECIES: *Sminthopsis crassicaudata* (Gould, 1844).

REFERRED SPECIES: *Sminthopsis murina* (Waterhouse, 1838); *S. leucopus* (Gray, 1842); *S. crassicaudata* (Gould, 1844), *S. macroura* (Gould, 1845a); *S. virginiae* (De Tarragon, 1847); *S. psammophila* Spencer, 1895; *S. hirtipes* Thomas, 1898; *S. longicaudata* Spencer, 1909; *S. granulipes* Troughton, 1932; *S. ooldea* Troughton, 1965, new rank; *S. butleri*, new species; *S. douglasi*, new species; *S. (Antechinomys) laniger* (Gould, 1856).

DIAGNOSIS: Small dasyurids differing from those of other dasyurid genera by possession of the following combination of characters: The squamosal-frontal bones contact

on the side wall of the braincase; the false palate has openings (the palatine vacuities) within the palatine bones; the nasals are only just expanded posteriorly; upper molars lack posterior cingula; the third premolars are only slightly reduced or subequal in size to P2; the fourth upper incisors are longer-crowned than I²; the metacristids and hypocristids are transverse to the long axis of the lower cheektooth row; the supratragus of the external ear is curled; the hind feet are narrow (with respect to other small dasyurids) with reduced postinterdigital pads. The specific sets of characters which distinguish species of *Sminthopsis* from the comparably sized species of *Ningaui* and *Planigale* have been detailed in Archer (1975b, 1976d). None of the characters noted above is individually unique to species of *Sminthopsis*.

DESCRIPTION: Tail: The tail varies from shorter than, to twice nose-vent length, is variably incrassated, and may have (S.

psammophila only) a small crest or (*S. (Antechinomys) laniger* only) a terminal brush.

EAR: All species have a curled external edge of the supratragus and relatively large ears.

HIND FOOT: Five toes are present on all members of the subgenus *Sminthopsis*, whereas *S. (Antechinomys)* has four hind toes. The hallux is clawless. The postinterdigital pads vary in number but, except in abnormal instances, there is no posthallucal pad. The granules of the interdigital and terminal digital pads may be arranged in rows, and some may develop transverse striae. The extent of hair covering the ventral surface of the hind foot varies from a small corner of the heel to the whole ventral surface of the foot.

TEETH: The crown height of I^1 is equal to or larger than that of I^2 (except *S. granulipes* where it is often smaller than I^2). The crown of I^4 is longer than or equal to that of I^2 . All upper incisors are normally single-cusped (except some I^4) and single-rooted. Diastema occur between I^1 and I^2 . Crowns of I^2 to I^4 are basically triangular with the apex at the occlusal corner. The crown of I^1 is generally taller and less triangular than those of the other incisors. The second lower incisor is generally larger than I_3 (in some *S. virginiae* these are subequal), I_3 is variably bilobed, I_1 to I_3 have spatulate crowns and a lingual shelf but no cusp. A diastema between I_3 and C_1 is variably developed. In forms without this diastema, the posterior face of the I_3 crown is broad transversely and has a posterior notch that fits the canine. The upper canine varies from premolariform in shape and size to caniniform. A basal cingulum is variably developed. Antero- and postero-basal cingular cusps are variable but are most noticeably developed on premolariform canines. Some crowns are erupted well beyond the canine alveolus so that the root forms a significant part of the exposed functional tooth. The lower canine varies from premolariform to caniniform in size and shape, has a basal cingulum linguallly and sometimes buccally, and has the posterior edge of the crown sometimes produced occlusally as a variably developed posterior

cusp (absent or very tiny in *S. virginiae*, *S. douglasi*, *S. crassicaudata*, *S. granulipes*, *S. butleri*, and *S. ooldea*). The posterior upper premolar (P^4) is always larger crowned than any other upper premolar and has a posterolingual cingula; the third upper premolar is either larger than or subequal in height to P^1 . All upper premolars are double-rooted. Lingual and buccal cingula are variably developed. Premolars P^1 and P^3 are widest across their posterior halves, whereas P^4 is widest across the anterior half or middle and has its crown variably erupted beyond the alveoli so that the roots are exposed. The posterior faces P^1 to P^4 are bladelike, whereas the anterior faces are generally rounded.

In the lower premolars the crown height of P_4 is smaller than or subequal to but not generally larger than that of P_3 (except in some *S. granulipes*). Cusps on the buccal and lingual cingula and on the anterior and posterior cingula are variably developed. The posterior edges of the crowns are blade-like as in the upper premolars. The anterior edges are variably bladelike.

In the upper molars, the anterior faces of M^2 and M^3 , from the base of the protocones to the parastylar corners, are transversely oriented with respect to the long axis of the skull. Posterior cingula are absent on upper molars. Anterior cingula are variably developed in M^1 to M^3 . Styler cusp B is distinct on M^1 to M^3 , unfused with the paracone, but reduces in size from M^1 to M^3 . It may be represented in some specimens by a very small cuspule on M^4 . All other styler cusps also reduce in size posteriorly in the tooth-row. The paracone increases in size from M^1 to M^4 . The metacones of M^1 to M^3 remain more or less subequal to each other. A metacone is absent, or reduced to mere bump, on the paracrista of M^4 . The protocones of M^1 to M^3 are subequal, whereas that of M^4 , although clearly present, is smaller. Sometimes small protoconular and metaconular swellings are present on M^1 to M^3 . The paracristae increase in size posteriorly, being largest on M^4 . The metacristae increase posteriorly only as far as M^2 , then decrease again, being smallest or absent on M^4 . The ratio of crown length to crown width decreases posteriorly

from M^1 to M^3 . A metacrista is lacking on M^4 .

The metaconids of M_1 to M_4 are subequal. The protoconids increase in size from M_1 to M_3 but decrease again slightly in M_4 . The hypoconids are subequal on M_1 to M_3 but very reduced on M_4 . The paracristids and metacristids generally increase in length from M_1 to M_3 but decrease on M_4 . The hypocristids increase slightly in length from M_1 to M_2 but decrease from M_2 to M_4 . The width of the talonid of M_1 is greater than the trigonid, generally about equal on M_2 , and generally less than the width of the trigonid on M_3 and M_4 (this gradient varies between species). The paracristid direction changes posteriorly from being roughly anteroposterior in M_1 to being close to transverse on M_4 .

SKULL: The nasals are narrower posteriorly than in most other dasyurid genera, such as *Planigale* and *Antechinus*, but do slightly widen posteriorly in all species. The lacrimal foramina are single or double and are just posterior to, on, or just anterior to the anterior rim of orbit. There is no lacrimonasal contact. On the dorsal rim of the orbit the lacrimal is variously produced into a sharp flange with a posterodorsal spine. The infraorbital canal passes through the maxilla dorsal to the M^1 and M^2 . A small incisivo-maxillary foramen enters the maxilla at or just posterior to the anterior edge of the infraorbital foramen. The sphenopalatine foramen enters the nasal cavity through the orbital wall of the palatine mesial to the maxillary foramen opening into the infraorbital canal. The palatine bone is perforated by a palatine vacuity (referred to here as the palatine vacuity). Another palatal vacuity occurs between the palatine and maxilla (referred to here as maxillary vacuity). A third vacuity in the palate occurs between the premaxilla and maxilla (referred to here as premaxillary vacuity). The posterior edge of the premaxillary vacuity extends posteriorly for a distance that varies between species. An anteroposterior medial depression in the cranium in the region of the frontals varies in development. The postorbital process of the frontal varies in development from being absent to small. The length and

width of the rostrum vary. The palatine bone contacts the maxilla, pterygoid, alisphenoid, basisphenoid, orbitosphenoid, frontal, and lacrimal bones. Bony plates of the ethmoid anterior to the cribiform plate are visible through the orbital wall of the frontal. The alisphenoid contacts the presphenoid, palatine, orbitosphenoid, frontal, squamosal, ectotympanic, and periotic bones, but not the parietal. The squamosal contacts the frontal, parietal, alisphenoid, jugal, ectotympanic, and periotic bones, and comes close to but does not appear to contact the occipital. Nuchal and sagittal crest development varies within and between species. The entocarotid canal is generally reduced. The entocarotid foramen opens vertically through the basiocranium. The elongate pseudovale foramen occurs along almost the full length of the lingual side of the alisphenoid bulla until it contacts the anterolingual edge of the periotic. The internal jugular canal is formed between the contact of the periotic and basioccipital. The posterior lacerate foramen is bounded on one side by the periotic and on the other by the basioccipital, and occurs immediately posterobuccal to the posterior opening of the internal jugular canal. Commonly, two condylar (including hypoglossal) foramina are present on each side, but the number is variable. Some variation occurs in the position of the transverse canal and its foramen with respect to the alisphenoid bulla but generally the canal opens directly anterior to the anterior end of the foramen pseudovale. No bony bar separates the optic foramen from the sphenorbital foramen. The posterolateral palatal foramen is never complete; it lacks a posterior bar. Connective tissues normally extend across this gap to enclose a foramen. The Malleus and incus are not fused. The stapes is columnar and not perforated by a stapedia artery. Bony squamosal and periotic processes which abut against the malleus are generally lacking (although a periotic process is present in *S. hirtipes*). Squamosal, periotic, and mastoid tympanic sinuses are variably developed.

DISCUSSION: *Antechinomys laniger* shares more characters with species of *Sminthopsis* than with any other dasyurid genus.

Thomas (1888) and Ride (1970) noted this similarity. Tate (1947) noted particular similarity between *A. laniger* and *S. crassicaudata*. Most cranial, dental, and even external characters that differentiate *Antechinomys* do so only as a matter of degree. For example, in *Antechinomys* palatal vacuities are larger, molars are wider, alisphenoid inflation is more extensive, the pseudovale foramen is more reduced, limbs are longer, fusion of interdigital pads is more complete, and the hind foot is longer than in any species of *Sminthopsis*. However, *Antechinomys* is distinguished from all *Sminthopsis* because it lacks a fifth toe on the hind foot, a condition unique among small dasyurids. This single character, although a highly derived one, is not a shared derived character and is cladistically useless in determining relationships of *Antechinomys*. For these reasons and others noted below, *Antechinomys* is regarded as a specialized subgenus of *Sminthopsis*.

The *Sminthopsis*-like and those that are not *Sminthopsis*-like characters of *Ningaui* have been discussed elsewhere (Archer, 1975b) and, in terms of cladistics, *Ningaui* represents the sister group of *Sminthopsis* (including *Antechinomys*) and must be accorded separate generic classification.

Other dasyurid genera are more overtly distinct and confusion with species of *Sminthopsis* should not occur.

KEY TO SPECIES OF SMINTHOPSIS

I intend this key to provide a simple means for identifying species. It is in two parts, one based on external characters and one on cranial and dental characters. After an identification is obtained, the specimen should be compared with the appropriate diagnosis, description, and tables of measurements. Alphabetical references refer to figures 7 and 8.

EXTERNAL CHARACTERS

- 1a. Tail with terminal black brush; only four toes on hind foot ... *S. (Antechinomys) laniger* (page 187)

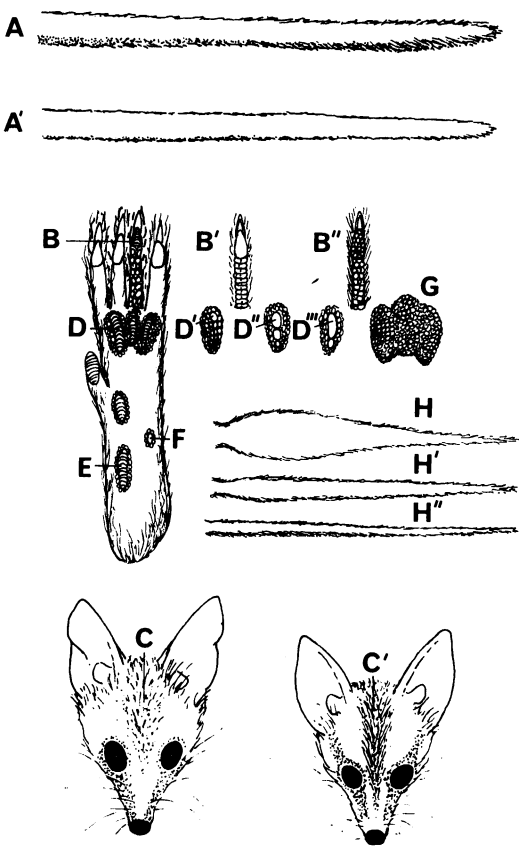


FIG. 7. External characters used in species key.

- b. Tail without terminal black brush; five toes on hind foot 2
- 2a. Tail bicolored with well developed terminal black crest (A) *S. (S.) psammophila* (fig. 35)
- b. Tail unicolored without terminal black crest (A') 3
- 3a. Terminal pads of hind toes granular (B'') 4
- b. Terminal pads of hind toes smooth (B') or striate (B) 5
- 4a. Interdigital pads are only sparsely covered, if at all, with hairs; lacks head stripe (C) *S. (S.) granulipes* (fig. 33)
- b. Interdigital pads densely covered by hairs; has head stripe (C') *S. (S.) hirtipes* (fig. 57)
- 5a. Apical granules of interdigital pads clearly striated (D) 6

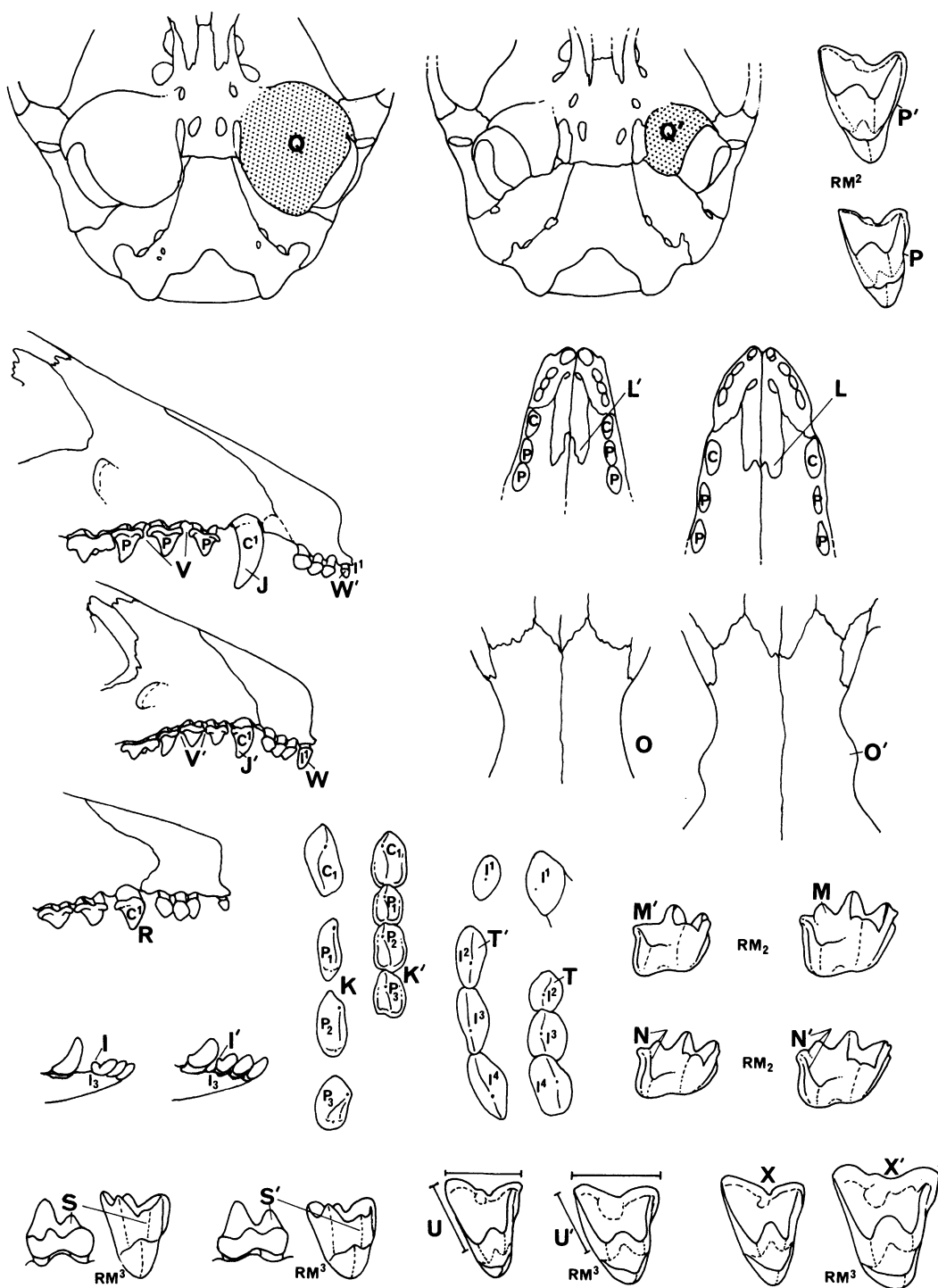


FIG. 8. Skull and dental characters used in species key.

- b. Apical granules of interdigital pads not clearly striated (D'-D'') 7
- 6a. Tail twice nose-vent length; large posthallucal granule present (E)
..... *S. (S.) longicaudata*
- b. Tail less than twice nose-vent length; normally posthallucal pads absent
..... *S. (S.) leucopus* (fig. 13)
- 7a. Rufous cheeks 8
- b. No rufous cheeks 9
- 8a. Tail thin (H''); large animal (mean nose-vent length of adults 100 mm., o.r. 81.1-126.0); metatarsal granule sometimes present (F)
..... *S. (S.) virginiae* (fig. 40)
- b. Tail moderately incrassated (H'); very large animal (one adult female nose-vent length is 88 mm.); no enlarged metatarsal granule *S. (S.) douglasi* (fig. 40)
- 9a. Tail thin (H'') 10
- b. Tail incrassated (H) 12
- 10a. Very small (mean nose-vent 6.7 mm., o.r. 58-72); tail much longer than head and body *S. (S.) ooldea* (fig. 13)
- b. Larger than 10a; tail length variable 11
- 11a. Vague head stripe present and pale; head domed dorsally
..... *S. (S.) butleri* (fig. 53)
- b. Dark patch sometimes present but not stripe (C); head not conspicuously domed
..... *S. (S.) murina* (fig. 13)
- 12a. Head stripe present and clear (C'); enlarged oval or round apical granule on interdigital pads (D'-D'') .. *S. (S.) macroura* (fig. 50)
- b. No head stripe; no markedly enlarged apical granule (D' or G) 13
- 13a. Interdigital pads fused (G); dark head patch (C); buff areas in body pelage; tail shorter than head and body
..... *S. (S.) crassicaudata* (fig. 63)
- b. Interdigital pads not fused or joined only at base; no dark head patch; dark body; tail longer than head and body
..... *S. (S.) ooldea* (fig. 13)

CRANIAL AND DENTAL CHARACTERS

- 1a. I_3 markedly bifid with large posterior lobe (I); I^1 very small (W'); C^1 very large (J); premolars spaced (V) and very narrow (K); anterior palatal vacuities do not extend posterior to C^1 alveolus (L)
..... *S. (S.) granulipes* (fig. 29)
- b. I_3 barely bifid (I'); other characters vary but do not occur in same combination as 1a 2

- 2a. Large entoconids M_{1-3} (M) 3
- b. Tiny to absent entoconids M_{1-3} (M') 6
- 3a. Premaxillary vacuities extend posteriorly well beyond C^1 alveolus (L'); hypocristid contacts entoconid M_3 (N)
..... *S. (S.) crassicaudata* (fig. 60)
- b. Premaxillary vacuities short (L); hypocristid clearly separate from entoconid M_3 (N')
..... 4 (4-5) require confirmation of skin and size characters, see tables 1, 2.
- 4a. Medium-sized species (see tables 1-2 for *S. macroura*); no postorbital processes on frontals (O); C^1 not grossly enlarged (J'); premolars much longer than wide (K); no continuous anterior cingulum on upper molars (P) *S. (S.) macroura* (fig. 45)
- b. Larger than size of *S. macroura* (see tables 1-2); presence of postorbital processes (O') variable; C^1 large (J); premolars broad (K'); presence of anterior cingulum upper molars (P') variable 5
- 5a. Commonly anterior cingulum present on upper molars (P'); commonly postorbital processes present on frontals (O'); smaller than 5b (see tables 1-2)
..... *S. (S.) virginiae* (fig. 37)
- b. No known specimens have postorbital processes (O); none have anterior cingula on upper molars (P); larger than 5a (see tables 1-2)
..... *S. (S.) douglasi* (fig. 35)
- 6a. Premaxillary vacuities extend posterior to level of C^1 alveolus (L') 7
- b. Premaxillary vacuities do not extend posterior to level of C^1 alveolus (L)
..... *S. (S.) hirtipes* (fig. 43)
- 7a. Alisphenoid tympanic wing enlarged (Q) .. 8
- b. Alisphenoid tympanic wing not markedly enlarged (Q') 9
- 8a. Upper molars wide relative to length (U); anterior border of ascending ramus tall and subparallel to posterior border of dentary *S. (Antechinomys) laniger* (Archer, 1977)
- b. Upper molars relatively narrow (U'); anterior border of ascending ramus and posterior border of dentary divergent
.. *Sminthopsis (S.) longicaudata* (fig. 27)
- 9a. Very small species (see tables 1-2 for *S. ooldea*); paracone reduced (S); premolars very wide (K'); I^2 subrounded (T)
..... *S. (S.) ooldea* (fig. 23)
- b. Size larger than *S. ooldea* (see tables 1-2); paracone unreduced (S'); premolars relatively narrow (K); I^2 elongate (T') 9

TABLE 1

Absolute Measurements (in Millimeters) in *Sminthopsis*

Abbreviations: BL, basicranial length; ZW, maximum zygomatic width; OBW, outside bullar width; IBW, inside bullar width; IO, minimum interorbital width; IPVD, interpalatal vacuity distance; DL, dentary length; C-AP, articular condyle of dentary to tip of angular process; C-AR, C to anterior border of ascending ramus; N, sample number; \bar{X} , sample mean; τ , standard error of the mean; OR, observed range; S, standard deviation; CV, coefficient of variation. Locality names abbreviated as follows: Herbert River, Queensland; Virgin Bore Creek, Western Australia; Doomadgee Mission, Queensland. All place names and populations are noted in text.

	N	$\bar{x} \pm \tau$	OR	s	CV		N	$\bar{x} \pm \tau$	OR	s	CV
Sminthopsis murina (total)						S.m., Mt Molloy					
BL	86	23.6 \pm .16	21.0-27.6	1.44	6.12	9	23.7 \pm .75	21.1-27.0	2.24	9.45	
ZW	95	13.7 \pm .10	11.2-17.0	0.98	7.12	8	13.8 \pm .57	12.0-17.0	1.60	11.61	
OBW	88	9.3 \pm .06	8.3-10.6	0.58	6.18	9	9.5 \pm .23	8.7-10.6	0.68	7.18	
IBW	79	3.4 \pm .03	2.8- 4.2	0.30	8.81	9	3.6 \pm .12	3.2- 4.2	0.37	10.25	
C ¹ -M ⁴	114	9.8 \pm .05	8.7-11.3	0.49	5.03	9	10.0 \pm .17	9.5-11.2	0.51	5.10	
M ¹ -4	116	5.2 \pm .02	4.7- 5.8	0.19	3.72	9	5.4 \pm .06	5.2- 5.7	0.19	3.52	
M ¹ -3	121	4.6 \pm .02	4.3- 5.3	0.19	4.12	9	4.8 \pm .05	4.6- 5.0	0.15	3.10	
R-LM ³	120	8.0 \pm .04	7.0- 9.0	0.42	5.27	10	8.3 \pm .13	7.8- 8.8	0.36	4.32	
IO	114	4.9 \pm .03	4.1- 5.8	0.32	6.58	8	4.7 \pm .14	4.2- 5.3	0.41	8.65	
IPVD	71	3.5 \pm .05	2.3- 4.8	0.42	12.01	9	3.5 \pm .15	2.8- 4.2	0.45	12.97	
DL	110	18.7 \pm .11	16.0-20.9	0.14	6.12	9	19.0 \pm .51	17.0-21.6	1.53	8.07	
I ₁ -M ₄	116	11.1 \pm .05	9.7-12.7	0.54	4.87	9	11.5 \pm .17	10.9-12.5	0.50	4.32	
M ₁ -4	120	5.8 \pm .02	5.2- 6.5	0.21	3.54	9	6.0 \pm .06	5.7- 6.4	0.19	3.23	
M ₁ -3	123	4.4 \pm .02	3.9- 4.8	0.20	4.46	10	4.5 \pm .07	4.0- 4.7	0.23	5.18	
C-AP	99	5.2 \pm .03	4.1- 6.1	0.33	6.32	9	5.3 \pm .17	4.7- 6.1	0.51	9.53	
C-AR	109	4.3 \pm .04	3.4- 5.2	0.41	9.60	9	4.3 \pm .16	3.7- 5.2	0.49	11.39	
S.m., SE.Qd						S.m., NSW.					
BL	7	22.1 \pm .24	21.0-23.0	0.64	2.89	10	23.3 \pm .43	21.4-25.4	1.37	5.88	
ZW	6	12.8 \pm .45	12.1-15.0	1.11	8.70	10	13.4 \pm .25	12.0-14.6	0.87	6.48	
OBW	6	8.7 \pm .07	8.5- 9.0	0.17	1.92	11	9.1 \pm .12	8.5-10.0	0.48	4.28	
IBW	6	3.2 \pm .09	3.0- 3.6	0.23	7.13	11	3.5 \pm .10	2.9- 3.6	2.77	7.93	
C ¹ -M ⁴	9	9.3 \pm .12	8.8-10.0	0.37	3.99	10	9.6 \pm .12	9.2-10.2	0.42	4.32	
M ¹ -4	9	5.2 \pm .06	4.9- 5.3	0.17	3.19	10	5.1 \pm .04	5.0- 5.3	0.13	2.61	
M ¹ -3	8	4.5 \pm .05	4.3- 4.7	0.15	3.25	11	4.5 \pm .04	4.3- 4.7	0.12	2.72	
R-LM ³	9	7.1 \pm .23	7.2- 8.7	0.70	9.83	11	7.9 \pm .12	7.3- 8.8	0.42	5.35	
IO	7	4.5 \pm .08	4.1- 4.7	0.22	4.89	11	5.0 \pm .11	4.4- 5.7	0.38	7.69	
IPVD	6	3.2 \pm .12	2.6- 3.4	0.30	9.27	3	3.2 \pm .17	2.5- 3.5	0.58	18.08	
DL	9	17.5 \pm .37	16.0-19.7	1.12	6.38	11	18.4 \pm .37	17.1-20.1	1.11	6.05	
I ₁ -M ₄	9	10.7 \pm .13	10.0-11.2	0.38	3.51	11	11.1 \pm .16	10.4-12.0	0.52	4.64	
M ₁ -4	10	5.7 \pm .05	5.4- 5.9	0.17	2.92	11	5.7 \pm .06	5.5- 6.0	0.20	3.55	
M ₁ -3	10	4.3 \pm .04	4.0- 4.4	0.14	3.20	11	4.3 \pm .07	4.0- 4.5	0.22	5.04	
C-AP	9	5.0 \pm .09	4.7- 5.0	0.27	5.39	10	5.1 \pm .11	4.6- 5.7	0.35	6.85	
C-AR	9	3.9 \pm .11	3.5- 4.7	0.34	8.65	11	4.1 \pm .08	3.7- 4.5	0.27	6.54	
S.m., Vict.						S.m., S.A.					
BL	4	22.1 \pm .48	21.0-23.2	0.96	4.32	6	23.9 \pm .65	22.1-25.7	1.59	6.65	
ZW	4	12.9 \pm .29	12.2-13.5	0.57	4.43	7	14.0 \pm .58	12.2-15.7	1.53	10.96	
OBW	4	8.8 \pm .09	8.6- 9.0	0.17	1.97	6	9.3 \pm .18	8.8- 9.8	0.45	4.78	
IBW	4	3.3 \pm .07	3.0- 3.5	0.14	4.28	5	3.6 \pm .10	3.4- 4.0	0.24	6.51	
C ¹ -M ⁴	5	9.2 \pm .09	9.0- 9.5	0.20	2.17	7	9.5 \pm .11	9.2- 9.8	0.30	3.19	
M ¹ -4	6	5.0 \pm .07	4.7- 5.2	0.18	3.58	8	5.1 \pm .07	4.9- 5.4	0.18	3.58	
M ¹ -3	6	4.4 \pm .03	4.3- 4.5	0.07	1.59	7	4.5 \pm .05	4.4- 4.7	0.14	3.14	
R-LM ³	5	7.9 \pm .07	7.8- 8.2	0.17	2.10	7	8.1 \pm .16	7.3- 8.7	0.43	5.36	
IO	5	4.6 \pm .09	4.3- 4.8	0.20	4.35	7	4.9 \pm .17	4.4- 5.6	0.46	9.36	
IPVD	4	2.9 \pm .20	2.3- 3.2	0.39	13.50	5	3.1 \pm .18	2.6- 3.6	0.40	12.90	
DL	5	17.6 \pm .33	16.5-18.4	0.73	4.16	7	18.8 \pm .46	17.3-20.2	1.22	6.48	
I ₁ -M ₄	5	10.6 \pm .10	10.3-10.9	0.22	2.11	7	10.9 \pm .20	9.9-11.5	0.53	4.91	
M ₁ -4	6	5.5 \pm .04	5.5- 5.7	0.09	1.63	7	5.7 \pm .06	5.5- 5.9	0.16	2.86	
M ₁ -3	7	4.1 \pm .03	4.1- 4.3	0.09	2.23	7	4.3 \pm .05	4.1- 4.5	0.14	3.29	
C-AP	5	5.0 \pm .07	4.8- 5.2	0.16	3.16	6	5.4 \pm .15	4.9- 5.9	0.36	6.68	
C-AR	5	3.9 \pm .15	3.4- 4.2	0.34	8.79	7	4.4 \pm .18	3.9- 5.2	0.49	11.10	
S.m., W.A. (all)						S.m., Albany					
BL	50	23.9 \pm .18	21.0-27.6	1.25	5.23	7	23.7 \pm .52	21.7-24.9	1.38	5.81	
ZW	57	13.9 \pm .11	11.2-15.5	0.83	5.95	10	13.8 \pm .23	12.7-14.7	0.73	5.26	
OBW	54	9.4 \pm .05	8.3-10.1	0.40	4.26	8	9.4 \pm .10	8.9- 9.8	0.27	2.90	
IBW	46	3.4 \pm .04	2.8- 4.3	0.28	8.24	8	3.5 \pm .04	3.3- 3.6	0.12	3.41	
C ¹ -M ⁴	72	10.0 \pm .06	8.7-11.0	0.47	4.71	11	10.1 \pm .13	9.3-10.5	0.43	4.29	
M ¹ -4	72	5.2 \pm .02	4.7- 5.8	0.17	3.35	11	5.2 \pm .04	4.9- 5.4	0.14	2.65	
M ¹ -3	74	4.7 \pm .02	4.3- 5.2	0.17	3.65	11	4.6 \pm .03	4.5- 4.8	0.11	2.48	
R-LM ³	73	8.0 \pm .05	7.0- 9.0	0.42	5.25	11	8.0 \pm .14	7.4- 8.7	0.47	5.82	
IO	72	5.0 \pm .03	4.4- 5.8	0.26	5.17	11	4.9 \pm .06	4.5- 5.2	0.21	4.38	
IPVD	41	3.7 \pm .10	2.4- 4.8	0.67	17.99	3	4.2 \pm .10	4.0- 4.3	0.17	4.12	
DL	69	18.9 \pm .12	16.7-21.7	1.03	5.47	11	18.6 \pm .27	17.0-19.7	0.89	4.76	
I ₁ -M ₄	72	11.2 \pm .06	10.0-12.5	0.50	4.44	11	11.2 \pm .14	10.4-11.7	0.47	4.17	
M ₁ -4	69	5.8 \pm .02	5.4- 6.2	0.18	3.17	11	5.8 \pm .05	5.5- 6.1	0.18	3.13	
M ₁ -3	73	4.4 \pm .02	4.0- 4.7	0.18	4.06	12	4.4 \pm .05	4.0- 4.6	0.16	3.62	
C-AP	62	5.3 \pm .04	4.6- 5.8	0.28	5.27	10	5.3 \pm .07	4.9- 5.6	0.23	4.40	
C-AR	69	4.7 \pm .05	3.6- 5.2	0.44	9.27	11	4.5 \pm .11	3.9- 5.0	0.37	8.19	

TABLE 1—(Continued)

	N	$\bar{x} \pm T$	OR	s	CV		N	$\bar{x} \pm T$	OR	s	CV
S. m., Denmark						S. m., Tambellup					
BL	10	23.8+32	21.6-24.8	1.00	4.20	7	24.6+32	23.2-25.6	0.86	2.49	
ZW	12	14.2+16	13.3-15.5	0.56	3.94	3	14.6+64	13.8-15.9	1.12	7.64	
OBW	11	9.6+08	9.3-10.1	0.25	2.63	5	9.8+15	9.4-10.1	0.34	3.46	
IBW	8	3.6+06	3.3- 3.9	0.18	5.03	6	3.1+30	3.4- 4.3	0.74	-	
C ¹ -M ⁴	12	10.1+13	9.4-10.9	0.45	4.44	8	10.2+13	9.6-10.8	0.35	3.48	
M ¹ -4	12	5.1+04	4.9- 5.3	0.12	2.44	8	5.3+08	5.1- 5.8	0.22	4.10	
M ¹ -3	12	4.6+04	4.4- 4.8	0.13	2.85	9	4.8+07	4.6- 5.2	0.22	4.60	
R-LM ³	12	8.1+09	7.8- 8.9	0.30	3.74	9	8.2+16	7.3- 9.0	0.48	5.82	
IO	12	5.0+07	4.7- 5.4	0.24	4.75	8	5.2+24	4.8- 5.5	0.67	12.82	
IPVD	11	4.3+12	3.9- 4.8	0.35	8.14	4	3.4+17	3.0- 3.8	0.34	9.90	
DL	9	19.1+25	17.5-20.7	0.84	4.40	9	19.3+35	17.2-20.4	1.06	5.48	
I ₁ -M ₄	11	11.4+14	10.5-11.8	0.48	4.21	9	11.4+14	11.0-12.2	0.42	3.72	
M ₁ -4	11	5.8+04	5.5- 6.0	0.14	2.38	9	6.0+05	5.8- 6.2	0.14	2.36	
M ₁ -3	11	4.4+04	4.1- 4.5	0.14	3.13	9	4.5+05	4.3- 4.7	0.15	3.24	
C-AP	11	5.3+07	4.9- 5.7	0.23	4.34	8	5.4+12	4.9- 5.7	0.33	6.18	
C-AR	11	4.6+11	4.1- 5.2	0.37	8.07	9	4.2+13	3.6- 4.8	0.39	9.33	
S. m., Bulong nr Kalgoorlie						S. oldea					
BL	2	23.0+07	22.9-23.0	0.10	0.43	6	19.8+22	19.3-20.4	0.55	2.78	
ZW	3	13.3+12	13.1-13.5	0.21	1.60	6	11.0+28	10.2-12.1	0.68	6.16	
OBW	4	9.1+06	8.9- 9.2	0.13	1.42	6	8.0+08	7.7- 8.3	0.19	2.43	
IBW	3	3.1+15	2.8- 3.3	0.27	8.53	6	2.6+10	2.2- 2.9	0.25	9.54	
C ¹ -M ⁴	4	9.3+10	9.0- 9.4	0.19	2.06	7	8.0+11	7.6- 8.5	0.28	3.53	
M ¹ -4	4	5.0+05	4.9- 5.1	0.10	2.00	7	4.6+05	4.4- 4.7	0.12	2.65	
M ¹ -3	4	4.5+04	4.4- 4.6	0.08	1.81	7	4.1+01	4.0- 4.3	0.03	0.69	
R-LM ³	4	7.4+08	7.3- 7.6	0.15	2.06	7	6.7+67	6.4- 6.9	0.18	2.65	
IO	4	5.0+09	4.8- 5.2	0.18	3.65	7	4.2+07	4.0- 4.5	0.17	4.12	
IPVD	3	3.0+00	3.0- 3.0	0.0	0.0	7	3.7+18	3.2- 4.6	0.47	12.63	
DL	4	18.0+15	17.6-18.3	0.29	1.63	7	15.4+18	14.5-15.9	0.48	3.14	
I ₁ -M ₄	4	10.4+06	10.4-10.6	0.13	1.24	7	9.0+07	8.7- 9.3	0.20	2.17	
M ₁ -4	4	5.6+05	5.5- 5.7	0.10	1.79	8	5.1+05	4.9- 5.3	0.15	2.87	
M ₁ -3	4	4.2+04	4.1- 4.3	0.08	1.93	8	3.8+04	3.6- 4.0	0.13	3.29	
C-AP	4	5.2+04	5.1- 5.3	0.08	1.56	7	4.6+07	4.4- 4.9	0.20	4.25	
C-AR	4	4.4+06	4.3- 4.6	0.13	2.93	7	4.1+09	3.8- 4.3	0.24	5.89	
S. leucopus (total)						S. l., Tasm. and Bass Strait Is					
BL	23	25.3+25	22.7-27.4	1.21	4.80	7	24.6+58	22.7-27.1	1.54	6.27	
ZW	23	14.4+21	12.3-16.3	0.99	6.87	7	13.5+31	12.3-14.7	0.83	6.18	
OBW	21	9.6+03	8.7-10.5	0.14	1.47	6	9.3+20	8.7-10.0	0.48	5.16	
IBW	23	3.7+06	3.1- 4.2	0.28	7.64	7	3.6+09	3.1- 3.8	0.23	6.51	
C ¹ -M ⁴	23	10.6+08	9.6-11.4	0.38	3.59	7	10.4+14	10.0-10.9	0.37	3.53	
M ¹ -4	22	5.4+03	5.0- 5.6	0.14	2.50	7	5.4+05	5.3- 5.6	0.12	2.27	
M ¹ -3	23	4.8+03	4.5- 5.1	0.13	2.71	7	4.8+04	4.7- 5.0	0.10	2.24	
R-LM ³	23	8.6+11	7.3- 9.5	0.53	6.11	7	8.1+21	7.3- 8.8	0.57	7.02	
IO	23	5.5+05	5.0- 6.0	0.24	4.34	7	5.6+08	5.2- 5.9	0.22	3.99	
IPVD	20	4.2+09	3.0- 4.9	0.39	9.20	5	4.0+13	3.5- 4.4	0.33	8.29	
DL	22	20.2+23	17.9-22.3	1.05	5.22	6	19.5+54	17.9-21.0	1.21	6.22	
I ₁ -M ₄	22	11.6+14	11.0-13.0	0.65	5.64	6	12.0+16	11.6-12.6	0.39	3.22	
M ₁ -4	24	6.0+03	5.5- 6.3	0.16	2.64	7	6.1+03	6.0- 6.2	0.09	1.47	
M ₁ -3	23	4.5+03	4.0- 4.9	0.14	3.04	7	4.6+03	4.5- 4.6	0.07	1.52	
C-AP	22	5.4+08	4.6- 6.1	0.37	6.84	6	5.1+14	4.6- 5.6	0.35	6.96	
C-AR	22	4.3+08	3.5- 5.0	0.36	8.33	7	4.1+14	3.5- 4.7	0.37	8.96	
S. l., all Vict.						S. l., fossil Vict.					
BL	15	25.6+20	24.0-27.4	0.78	3.03	-	-	9.8-10.9	-	-	
ZW	15	14.7+23	13.3-16.3	0.90	6.11	-	-	-	-	-	
OBW	15	9.7+11	9.1-10.5	0.44	4.53	-	-	-	-	-	
IBW	15	3.8+07	3.3- 4.2	0.28	7.24	-	-	-	-	-	
C ¹ -M ⁴	15	10.8+08	10.4-11.4	0.30	2.81	18	10.3+04	9.8-10.9	0.18	1.76	
M ¹ -4	15	5.4+03	5.2- 5.6	0.12	2.21	20	5.2+03	4.8- 5.4	0.16	2.99	
M ¹ -3	15	4.8+03	4.6- 5.1	0.13	2.78	20	4.7+03	4.3- 4.9	0.13	2.84	
R-LM ³	14	8.8+11	8.0- 9.5	0.41	4.61	-	-	-	-	-	
IO	15	5.5+06	5.2- 6.0	0.24	4.45	-	-	-	-	-	
IPVD	14	4.5+08	3.9- 4.9	0.29	6.45	-	-	-	-	-	
DL	15	20.7+18	19.2-22.3	0.69	3.33	20	19.7+21	17.5-20.9	0.95	4.82	
I ₁ -M ₄	15	12.3+10	11.6-13.0	0.39	3.15	20	11.5+13	10.8-12.3	0.59	5.10	
M ₁ -4	15	6.1+03	5.9- 6.3	0.12	2.01	20	5.9+03	5.7- 6.1	0.12	2.09	
M ₁ -3	15	4.5+03	4.3- 4.8	0.11	2.46	20	4.4+03	4.3- 4.6	0.12	2.71	
C-AP	15	5.5+09	4.9- 6.1	0.35	6.39	14	5.1+13	3.7- 5.7	0.47	9.37	
C-AR	14	4.4+09	3.8- 4.9	0.34	7.77	20	4.1+07	3.7- 4.7	0.29	7.10	

TABLE 1—(Continued)

	N	$\bar{x} \pm T$	OR	s	CV		N	$\bar{x} \pm T$	OR	s	CV
S. virginiae (total)						S.v. N., Guinea					
BL	20	26.1 \pm .33	23.0-29.2	1.46	5.59	5	26.0 \pm .79	25.0-29.2	1.78	6.83	
ZW	20	16.1 \pm .25	14.2-18.0	1.13	7.04	5	15.9 \pm .65	14.2-18.0	1.46	9.16	
OBW	19	10.0 \pm .10	9.3-10.9	0.42	4.22	5	9.9 \pm .29	9.3-10.9	0.65	6.60	
IBW	19	3.9 \pm .08	3.4- 4.5	0.34	8.69	5	4.0 \pm .13	3.8- 4.5	0.80	7.40	
C ¹ -M ⁴	21	10.7 \pm .10	9.9-11.8	0.46	4.29	5	10.7 \pm .30	10.0-11.8	0.66	6.18	
M ¹ - ⁴	23	5.8 \pm .05	5.0- 6.0	0.24	4.06	5	5.7 \pm .07	5.5- 5.9	0.16	2.77	
M ¹ - ³	25	5.1 \pm .05	4.5- 5.4	0.23	4.51	6	5.0 \pm .07	4.9- 5.2	0.17	3.34	
R-LM ³	22	9.2 \pm .10	8.3- 9.9	0.45	4.89	5	9.0 \pm .19	8.5- 9.7	0.43	4.81	
IO	22	5.0 \pm .06	4.5- 4.6	0.30	6.03	5	5.0 \pm .18	4.5- 5.5	0.40	8.00	
IPVD	3	4.0 \pm .34	3.5- 4.8	0.59	14.72	-	-	-	-	-	
DL	21	21.1 \pm .25	19.0-23.0	1.14	5.40	5	20.8 \pm .55	20.1-23.0	1.22	5.88	
I ¹ -M ⁴	22	12.2 \pm .10	11.4-13.5	0.49	4.02	5	12.2 \pm .36	11.4-13.5	0.80	6.60	
M ¹ - ⁴	24	6.5 \pm .04	6.0- 6.9	0.20	3.08	6	6.4 \pm .04	6.2- 6.5	0.11	1.70	
M ¹ - ³	26	4.9 \pm .05	4.4- 5.0	0.19	0.91	6	4.7 \pm .01	4.6- 4.8	0.03	0.60	
C-AP	19	6.1 \pm .08	5.5- 6.8	0.34	5.56	4	5.8 \pm .18	5.5- 6.3	0.26	6.21	
C-AR	21	5.6 \pm .10	4.9- 6.3	0.45	8.06	5	5.5 \pm .21	5.0- 6.2	0.47	8.48	
S.v. Australia						S.v. Herbert River					
BL	15	26.1 \pm .36	23.9-28.3	1.41	5.40	7	26.2 \pm .71	23.9-28.3	1.89	7.21	
ZW	15	16.2 \pm .21	14.3-17.9	1.03	6.33	7	16.0 \pm .49	14.3-17.9	1.30	8.11	
OBW	14	10.1 \pm .09	9.3 10.5	0.33	3.25	7	9.8 \pm .12	9.3-10.3	0.31	3.19	
IBW	14	3.9 \pm .10	3.4- 4.4	0.36	9.24	7	4.0 \pm .14	3.6- 4.4	0.38	9.52	
C ¹ -M ⁴	16	10.7 \pm .10	9.9-11.1	0.39	3.66	6	10.7 \pm .13	10.3-11.1	0.31	2.93	
M ¹ - ⁴	18	5.8 \pm .06	5.0- 6.0	0.26	4.40	8	5.9 \pm .03	5.7- 6.0	0.09	1.62	
M ¹ - ³	19	5.1 \pm .06	4.5- 5.4	0.24	4.80	8	5.2 \pm .04	5.1- 5.4	0.10	0.50	
R-LM ³	17	9.2 \pm .11	8.3- 9.9	0.46	4.97	7	9.3 \pm .16	8.8- 9.9	0.43	4.78	
IO	17	5.0 \pm .07	4.6- 5.6	0.28	5.63	7	5.0 \pm .14	4.6- 5.6	0.37	7.30	
IPVD	4	4.3 \pm .29	3.5- 4.0	0.57	13.36	-	-	-	-	-	
DL	16	21.2 \pm .28	19.0-22.8	1.13	5.37	7	20.9 \pm .57	19.0-22.8	1.51	7.23	
I ¹ -M ⁴	17	12.2 \pm .08	11.4-13.0	0.34	2.79	7	12.1 \pm .12	11.7-12.4	0.30	2.52	
M ¹ - ⁴	18	6.5 \pm .05	6.0- 6.9	0.22	3.33	8	6.6 \pm .22	6.3- 6.1	0.61	9.23	
M ¹ - ³	20	4.9 \pm .04	4.4- 5.0	0.19	5.83	8	4.9 \pm .04	4.7- 5.0	0.11	2.18	
C-AP	15	6.2 \pm .08	5.7- 6.8	0.30	4.89	7	6.1 \pm .10	5.7- 6.4	0.26	4.33	
C-AR	16	5.6 \pm .11	4.9- 6.3	0.45	7.96	7	5.5 \pm .23	4.9- 6.3	0.60	10.96	
S.v. (nitela form)						S. douglasi					
BL	4	26.0 \pm .50	25.0-27.0	1.00	3.85	2	28.3 \pm .16	26.7-29.8	2.19	7.75	
ZW	4	16.2 \pm .31	15.5-17.0	0.43	3.87	2	17.3 \pm .36	16.9-17.6	0.50	2.89	
OBW	3	10.1 \pm .23	9.7-10.5	0.40	3.96	2	11.0 \pm .30	10.7-11.3	0.42	3.86	
IBW	3	3.6 \pm .12	3.4- 3.8	0.20	5.56	1	4.0 \pm 0	4.0- -	0	0	
C ¹ -M ⁴	4	10.4 \pm .26	9.9-11.0	0.52	4.99	2	12.4 \pm .60	11.8-13.0	0.85	6.84	
M ¹ - ⁴	4	5.5 \pm .18	5.0- 5.8	0.35	6.44	2	7.0 \pm .16	6.8- 7.1	0.22	3.19	
M ¹ - ³	4	4.8 \pm .11	4.5- 5.0	0.21	4.46	3	6.1 \pm .10	5.9- 6.2	0.17	2.84	
R-LM ³	4	8.7 \pm .18	8.3- 9.1	0.35	4.07	2	10.1 \pm .30	9.8-10.4	0.43	4.20	
IO	4	4.9 \pm .09	4.8- 5.2	0.19	3.86	2	5.2 \pm .07	5.1- 5.2	0.10	1.92	
IPVD	2	4.2 \pm .43	3.5- 4.8	0.60	14.29	1	5.6 \pm 0	5.6- -	0	0	
DL	3	21.4 \pm .49	20.5-22.2	0.85	3.99	2	22.8 \pm .75	22.0-23.5	1.06	4.66	
I ¹ -M ⁴	4	12.0 \pm .19	11.4-12.5	0.38	3.18	2	14.3 \pm .65	13.6-14.9	0.92	6.45	
M ¹ - ⁴	4	6.3 \pm .12	6.0- 6.5	0.24	3.87	3	8.0 \pm .12	7.8- 8.2	0.20	2.50	
M ¹ - ³	4	4.7 \pm .11	4.4- 4.9	0.21	4.55	3	6.1 \pm .04	6.0- 6.1	0.07	1.15	
C-AP	3	6.1 \pm .12	5.9- 6.2	0.21	3.48	2	6.5 \pm .20	6.3- 6.7	0.28	4.35	
C-AR	3	5.4 \pm .12	5.2- 5.6	0.20	3.70	2	5.6 \pm 0	5.6- -	0	0	
S. macroura (total)						S.m. (typical form), Darling Downs					
BL	63	22.3 \pm .17	18.4-25.3	1.38	6.18	3	20.9 \pm .21	20.6-21.3	0.36	1.72	
ZW	67	13.9 \pm .09	12.3-16.2	0.72	5.19	4	13.1 \pm .16	12.8-13.5	0.31	2.37	
OBW	70	9.2 \pm .04	8.5- 9.9	0.37	4.07	3	8.8 \pm .04	8.7- 8.8	0.07	0.80	
IBW	69	3.3 \pm .04	2.2- 3.9	0.29	8.90	3	3.2 \pm .10	3.0- 3.3	0.17	5.41	
C ¹ -M ⁴	85	9.4 \pm .05	7.9-11.3	0.49	5.23	5	9.1 \pm .12	8.7- 9.4	0.26	2.85	
M ¹ - ⁴	84	5.2 \pm .03	4.7- 5.8	0.23	4.48	5	5.0 \pm .09	4.8- 5.3	0.21	4.25	
M ¹ - ³	85	4.6 \pm .02	4.2- 5.1	0.19	4.21	5	4.5 \pm .09	4.4- 4.9	0.21	4.72	
R-LM ³	80	8.1 \pm .05	7.1- 9.7	0.42	5.21	5	7.6 \pm .05	7.5- 7.8	0.11	1.47	
IO	86	4.2 \pm .03	3.4- 4.9	0.32	7.72	5	4.2 \pm .09	3.9- 4.4	0.19	4.61	
IPVD	17	3.7 \pm .10	2.5- 4.4	0.41	11.12	-	-	-	-	-	
DL	84	18.0 \pm .11	15.3-20.2	1.03	5.70	5	16.8 \pm .16	16.4-17.4	0.37	2.18	
I ¹ -M ⁴	83	10.7 \pm .05	9.4-12.0	0.49	4.61	5	10.1 \pm .11	9.8-10.4	0.24	2.37	
M ¹ - ⁴	84	5.9 \pm .03	5.6- 6.4	0.24	4.14	5	5.7 \pm .10	5.5- 6.1	0.23	4.02	
M ¹ - ³	86	4.4 \pm .03	3.9- 4.8	0.32	7.28	5	4.2 \pm .09	4.0- 4.5	0.21	4.91	
C-AP	72	5.4 \pm .04	4.4- 6.1	0.34	6.34	3	5.1 \pm .09	4.9- 5.2	0.16	3.10	
C-AR	82	4.5 \pm .05	3.3- 5.7	0.44	9.85	4	4.1 \pm .10	3.9- 4.3	0.22	5.45	

TABLE 1—(Continued)

	N	$\bar{x} \pm T$	OR	s	CV		N	$\bar{x} \pm T$	OR	s	CV
S. m., Virgin Bore Ck						S. m., cent. N.T.					
BL	5	22.7 \pm .33	21.8–23.4	0.73	3.21	11	22.4 \pm .45	19.7–25.3	1.48	6.62	
ZW	7	13.6 \pm .20	13.0–14.5	0.52	3.81	11	14.0 \pm .18	13.2–15.1	0.58	4.16	
OBW	7	9.3 \pm .09	8.9–9.5	0.23	2.48	12	9.1 \pm .13	8.5–9.8	0.44	4.79	
IBW	7	3.3 \pm .11	3.0–3.7	0.29	8.65	12	3.1 \pm .13	2.2–3.9	0.45	14.43	
C ¹ –M ⁴	8	9.6 \pm .06	9.3–9.8	0.17	1.80	15	9.5 \pm .13	8.2–10.4	0.51	5.34	
M ¹ – ⁴	8	5.2 \pm .06	5.0–5.5	0.16	3.08	15	5.2 \pm .05	4.9–5.4	0.18	3.48	
M ¹ – ³	8	4.7 \pm .07	4.4–5.0	0.20	4.33	15	4.6 \pm .05	4.4–4.9	0.18	3.81	
R–LM ³	8	7.8 \pm .06	7.5–8.0	0.18	2.32	14	8.0 \pm .15	7.6–9.7	0.54	6.78	
IO	8	4.2 \pm .06	3.9–4.4	0.16	3.82	15	4.3 \pm .08	3.8–4.8	0.30	7.03	
IPVD	2	3.7 \pm .20	3.5–3.9	0.28	7.64	2	3.8 \pm .14	3.6–4.0	0.20	5.26	
DL	8	18.2 \pm .21	17.5–18.9	0.61	3.34	14	18.1 \pm .28	15.9–20.0	1.05	5.81	
I ₁ –M ₄	8	10.7 \pm .10	10.4–11.3	0.27	2.52	15	10.8 \pm .14	9.6–11.7	0.53	4.89	
M ₁ – ₄	8	5.8 \pm .05	5.5–6.0	0.15	2.60	15	5.9 \pm .06	5.5–6.3	0.25	4.20	
M ₁ – ₃	8	4.3 \pm .04	4.2–4.5	0.12	2.77	15	4.4 \pm .05	4.2–4.8	0.20	4.46	
C–AP	8	5.3 \pm .04	5.1–5.4	0.10	1.89	11	5.3 \pm .08	5.1–5.7	0.25	4.77	
C–AR	8	4.3 \pm .07	3.9–4.5	0.19	4.39	14	4.3 \pm .09	3.9–4.8	0.33	7.66	
S. m., cent. WA.						S. m., Doonadgee Miss.					
BL	3	21.0 \pm .60	20.3–22.3	1.04	4.97	15	22.2 \pm .49	18.4–24.7	1.92	8.63	
ZW	3	12.9 \pm .47	12.3–13.8	0.82	6.32	17	14.4 \pm .24	12.5–16.2	0.97	6.75	
OBW	3	8.8 \pm .20	8.5–9.2	0.35	4.01	21	9.4 \pm .09	8.6–9.9	0.41	4.35	
IBW	3	3.0 \pm .09	2.8–3.1	0.16	5.27	19	3.4 \pm .04	2.9–3.6	0.15	4.54	
C ¹ –M ⁴	3	8.8 \pm .15	8.5–9.0	0.26	3.00	21	9.2 \pm .11	7.9–9.6	0.51	9.20	
M ¹ – ⁴	3	5.0 \pm .10	4.9–5.2	0.17	3.46	21	5.0 \pm .05	4.7–5.4	0.21	0.41	
M ¹ – ³	3	4.5 \pm .10	4.4–4.7	0.17	3.84	21	4.5 \pm .03	4.2–4.7	0.16	3.48	
R–LM ³	3	7.5 \pm .23	7.1–7.9	0.40	5.33	19	8.3 \pm .08	7.4–8.8	0.36	4.33	
IO	3	4.2 \pm .12	4.0–4.4	0.21	5.05	21	3.9 \pm .06	3.5–4.3	0.25	6.51	
IPVD	–	–	–	–	–	6	3.5 \pm .08	3.3–3.8	0.19	5.42	
DL	3	16.5 \pm .39	15.9–17.2	0.67	4.04	20	18.1 \pm .25	15.3–19.8	1.10	6.09	
I ₁ –M ₄	3	10.1 \pm .15	9.9–10.4	0.26	2.61	19	10.4 \pm .07	9.4–11.0	0.32	3.07	
M ₁ – ₄	3	5.8 \pm .04	5.7–5.8	0.07	1.21	19	5.7 \pm .04	5.3–6.0	0.19	3.28	
M ₁ – ₃	3	4.2 \pm .50	3.9–4.4	0.29	6.93	19	4.2 \pm .03	4.0–4.4	0.12	2.86	
C–AP	3	5.0 \pm .18	4.7–5.3	0.31	6.16	18	5.5 \pm .09	4.5–6.1	0.38	6.97	
C–AR	3	3.9 \pm .23	3.7–4.4	0.41	10.41	19	4.7 \pm .12	3.3–5.7	0.51	10.81	
S. hirtipes						S. butleri					
BL	4	19.8 \pm .10	19.3–20.4	0.20	0.84	6	21.1 \pm .41	20.1–22.8	1.00	4.72	
ZW	3	11.0 \pm .19	10.2–12.1	0.32	2.23	3	13.7 \pm .59	12.6–14.6	1.01	7.40	
OBW	4	8.0 \pm .09	7.7–8.3	0.17	1.66	6	8.9 \pm .12	8.6–9.4	0.30	3.33	
IBW	4	2.6 \pm .10	2.2–2.9	0.21	7.39	6	3.1 \pm .11	2.8–3.5	0.28	9.01	
C ¹ –M ⁴	5	8.0 \pm .10	7.6–8.5	0.22	2.21	5	8.8 \pm .14	8.4–9.2	0.30	3.45	
M ¹ – ⁴	6	4.6 \pm .08	4.4–4.7	0.20	1.06	5	5.0 \pm .09	4.8–5.3	0.19	3.87	
M ¹ – ³	6	4.1 \pm .08	4.0–4.3	0.19	3.94	6	4.6 \pm .08	4.3–4.7	0.17	3.76	
R–LM ³	5	6.7 \pm .12	6.4–6.9	0.26	3.17	6	7.5 \pm .09	7.3–7.8	0.21	2.85	
IO	5	4.2 \pm .05	4.0–4.5	0.12	2.40	6	4.3 \pm .16	4.1–4.5	0.40	9.23	
IPVD	4	3.7 \pm .14	3.2–4.6	0.27	6.00	6	2.5 \pm .11	2.2–2.6	0.27	10.88	
DL	4	15.4 \pm .12	14.5–15.9	0.24	1.29	4	17.2 \pm .48	16.3–18.4	0.96	5.59	
I ₁ –M ₄	5	9.0 \pm .22	8.7–9.3	0.49	4.46	3	10.3 \pm .12	10.1–10.5	0.20	1.94	
M ₁ – ₄	6	5.1 \pm .08	4.9–5.3	0.19	3.15	6	6.1 \pm .10	5.6–6.2	0.24	3.93	
M ₁ – ₃	6	3.8 \pm .06	3.6–4.0	0.15	3.43	6	4.5 \pm .08	4.1–4.6	0.19	4.20	
C–AP	4	4.6 \pm .09	4.4–4.9	0.19	3.20	6	5.1 \pm .12	4.7–5.5	0.30	5.80	
C–AR	4	4.1 \pm .08	3.8–4.3	0.16	3.74	6	4.1 \pm .12	3.7–4.4	0.30	7.32	
S. granulipes						S. psammophila					
BL	4	27.1 \pm .52	26.4–28.6	1.04	3.84	4	30.1 \pm .57	28.4–31.1	1.14	3.79	
ZW	4	15.6 \pm .53	14.7–17.1	1.05	6.73	3	17.4 \pm .17	17.1–17.7	0.30	1.72	
OBW	2	10.1 \pm .07	10.0–10.1	0.10	0.99	4	12.6 \pm .23	12.2–13.0	0.45	3.60	
IBW	2	3.9 \pm .31	3.7–4.1	0.44	11.28	4	3.6 \pm .06	3.5–3.7	0.11	3.17	
C ¹ –M ⁴	5	11.3 \pm .15	10.8–11.6	0.34	3.00	4	13.7 \pm .21	13.2–14.2	0.42	3.09	
M ¹ – ⁴	5	5.5 \pm .07	5.3–5.7	0.16	2.87	4	7.0 \pm .08	6.8–7.2	0.15	1.10	
M ¹ – ³	5	4.9 \pm .06	4.8–5.1	0.14	2.88	4	6.2 \pm .08	6.0–6.3	0.15	2.44	
R–LM ³	5	8.9 \pm .17	8.5–9.6	0.39	4.38	4	10.6 \pm .13	10.4–10.9	0.26	2.49	
IO	4	5.4 \pm .24	5.2–5.8	0.48	8.81	4	6.3 \pm .12	6.0–6.6	0.24	3.87	
IPVD	1	5.2 \pm .00	5.2–5.2	0.00	0.00	1	6.4 \pm .00	6.4–6.4	0.00	0.00	
DL	5	22.2 \pm .53	21.2–24.2	1.18	5.32	4	26.4 \pm .25	24.5–30.0	2.50	9.47	
I ₁ –M ₄	5	13.6 \pm .26	12.8–14.3	0.59	4.33	4	15.9 \pm .23	15.2–16.2	0.45	2.85	
M ₁ – ₄	5	6.1 \pm .07	5.9–6.3	0.16	2.69	4	8.0 \pm .10	7.8–8.3	0.21	2.59	
M ₁ – ₃	6	4.7 \pm .07	4.4–4.8	0.16	3.49	4	6.0 \pm .03	6.0–6.1	0.05	0.90	
C–AP	4	5.9 \pm .19	5.7–6.5	0.39	6.56	4	7.1 \pm .15	6.8–7.5	0.30	4.23	
C–AR	5	5.3 \pm .23	4.5–5.9	0.52	9.83	4	5.4 \pm .13	5.1–5.7	0.25	4.63	

TABLE 1—(Continued)

	N	$\bar{x} \pm T$	OR	s	CV		N	$\bar{x} \pm T$	OR	s	CV
<i>S. longicaudata</i>						<i>S. crassicaudata</i>					
BL	1	25.6 \pm .00	25.6–25.6	0.00	0.00	63	22.4 \pm .13	19.5–25.9	1.00	4.48	
ZW	1	16.6 \pm .00	16.6–16.6	0.00	0.00	52	13.2 \pm .08	11.4–14.6	0.54	4.11	
OBW	2	11.6 \pm .20	11.4–11.8	0.28	2.43	51	9.1 \pm .04	8.4–9.8	0.26	2.86	
IBW	1	2.8 \pm .00	2.8–2.8	0.00	0.00	49	3.1 \pm .04	2.5–3.7	0.27	8.56	
C ¹ –M ⁴	3	11.2 \pm .14	10.9–11.3	0.23	2.09	70	9.3 \pm .04	8.6–10.0	0.30	3.24	
M ¹ –4	3	5.8 \pm .10	5.6–5.9	0.17	2.98	71	5.0 \pm .02	4.7–5.5	0.18	3.60	
M ¹ –3	3	5.1 \pm .07	5.0–5.2	0.12	2.39	73	4.5 \pm .02	4.2–4.9	0.16	3.48	
R–LM ³	3	9.0 \pm .15	8.7–9.2	0.26	2.93	66	7.8 \pm .04	7.0–8.7	0.34	4.32	
IO	2	5.2 \pm .22	5.3–5.6	0.31	5.64	68	4.5 \pm .03	4.0–4.9	0.22	4.97	
IPVD	1	2.0 \pm .00	2.0–2.0	0.00	0.00	21	2.4 \pm .07	1.6–3.0	0.31	13.11	
DL	3	21.2 \pm .27	20.8–21.7	0.47	2.24	68	17.7 \pm .08	15.9–19.7	0.70	3.94	
I ₁ –M ₄	3	12.6 \pm .12	12.3–12.8	0.20	1.59	70	10.6 \pm .04	9.7–11.3	0.33	3.07	
M ₁ –4	3	6.6 \pm .18	6.3–6.9	0.31	4.67	71	5.7 \pm .02	5.1–6.2	0.21	3.60	
M ₁ –3	3	5.0 \pm .15	4.7–5.2	0.26	5.28	87	4.3 \pm .04	3.8–4.7	0.34	7.80	
C–AP	2	6.7 \pm .26	6.4–6.9	0.36	5.31	62	5.3 \pm .03	4.4–5.9	0.27	5.02	
C–AR	2	4.6 \pm .07	4.5–4.6	0.10	2.17	67	3.8 \pm .04	3.1–5.2	0.30	7.78	

- 10 (10–12 require confirmation of size and external characters, see tables 1–2).
- 10a. M³ metacrista clearly subequal to M³ length (U); very tiny entoconids M_{1–3} (smaller than N) *S. (S.) butleri* (fig. 52)
- b. M³ metacrista normally much shorter than M³ length (U'); tiny to small entoconids M_{1–3} (not as in M) 11
- 11a. Premolars widely spaced (V, K); I₃ mildly bilobed (but clearly less so than in *S. granulipes*) 12
- b. Premolars generally contact (V'); I₃ barely or not at all bilobed (I')
 *S. (S.) murina* (fig. 12)
- 12a. Large (largest species, see tables 1–2); cranium domed posterodorsally (see fig. 34); upper molars massive and swollen near base of crown (X')
 *S. (S.) psammophila* (fig. 34)
- b. Medium-sized (see tables 1–2); cranium not domed (see fig. 19); upper molars long but not massive or swollen at base of crowns (X) *S. (S.) leucopus* (fig. 19)

SUBGENUS *SMINTHOPSIS* THOMAS

Sminthopsis Thomas, 1888.

TYPE SPECIES: *Sminthopsis crassicaudata* (Gould, 1844).

REFERRED SPECIES: All species of genus except *Antechinomys laniger* (Gould, 1856).

DIAGNOSIS: Species of *Sminthopsis* differing from those of the subgenus *Antechinomys* in having five toes on the hind foot, no terminal brush on the tail (although a crest develops in *Sminthopsis psammophila*), shorter limbs, and generally non-flared lac-

rimals (although *S. hirtipes* has variably developed crests on the lacrimals).

DESCRIPTION: As for the genus except for the character states restricted to *Antechinomys* noted below.

Sminthopsis murina (Waterhouse)

Phascogale murina Waterhouse, 1838.

Phascogale albipes Waterhouse, 1842.

Antechinus fuliginosa Gould, 1852.

Sminthopsis murina tatei Troughton, 1965.

TYPE SPECIMENS: *Phascogale murina* Waterhouse, 1838. Holotype: BM 55.12.24.95, male, skin and skull. I have examined the holotype. Type locality: Waterhouse (1838, p. 76), "Hab. North of Hunter's River, New South Wales." Thomas (1888, p. 305), "Hunter R., N.S.W." Label on type skin, "Hunter's R. N.S.W." *Phascogale albipes* Waterhouse, 1842. Holotype: BM 1080C, male, skull; BM 95.3.21.12 (skin). I have examined the holotype. Type locality: Waterhouse (1842, p. 48), "Port Adelaide." Thomas (1888, p. 305), locality is South Australia but footnote suggests "The 'South Australia' here referred to appears only to mean the southern part of Australia, i.e. Victoria." Iredale and Troughton (1934, p. 10), Port Adelaide or Port Lincoln as possible type locality. Label attached to holotype states South Australia. *Antechinus fuliginosa* Gould, 1852. Holotype: BM 44.2.15.20, male, skin and skull. I have examined the holotype. Type locality: Gould (1852, letter-

press to plate 41) does not state type locality but notes species very abundant in King Georges Sound and in the vicinity of Perth. Thomas (1888, p. 305), Toodyay, W. A." Tate (1947, p. 121), "River Avon, King Georges Sound, Western Australia" Specimen label (which is not the original label) attached to holotype, "R. Avon, W.A." *Sminthopsis murina tatei* Troughton 1965. Holotype: AM M7157, adult male, skull and carcase in spirit. I have examined the holotype. Type locality: Troughton (1965, p. 316), "from Tolga on the Atherton Tableland, at approximately 2,460 ft, north-eastern Queensland."

DIAGNOSIS: *Sminthopsis murina* differs from *S. granulipes* in having a thin, non-incrassated tail; unfused and hairless interdigital pads of the hind feet; smooth terminal digital pads; and a relatively less bifid I_3 . It differs from *S. hirtipes* in having a thin tail; hairless, unfused interdigital pads of the hind feet; smooth terminal digital pads; lack of a prominent head stripe; the length of the metacrista of M^3 less than the crown length; and a relatively small alisphenoid bulla. It differs from *S. crassicaudata* in having a thin tail; unfused interdigital pads of the hind feet; tiny to absent entoconids; an enlarged row of apical granules on the interdigital pads of the hind foot; the metacrista of M^3 less than the crown length; and the premaxillary vacuity extends posteriorly well beyond the canine alveolus. It differs from *S. leucopus* and *S. longicaudata* in having the interdigital pads without striate apical granules. It also differs from *S. longicaudata* in having the tail-vent length much less than twice the nose-vent length; non-striate terminal pads of the digits; caniniform canine; and relatively small alisphenoid and periotic bullae. It differs from *S. psammophila* in being smaller; in having unfused interdigital pads on the hind feet; small terminal digital pads; and no crest whatsoever on the tail. It differs from *S. butleri* in having no pronounced head stripe; and no conspicuously enlarged apical granules on the interdigital pads of the hind feet. It differs from *S. virginiae* and *S. douglasi* in having small to absent entoconids; no pronounced head stripe; metacrista of M^3

that is much shorter than the crown length; no conspicuously enlarged apical granules on the interdigital pads of the hind feet; and premaxillary vacuities that extend posteriorly well beyond the canine alveolus. It also differs from *S. thomasi* in being smaller and in having a thin tail. It differs from *S. ooldea* in being larger; lacking an incrassated tail; having normally non-premolariform canines; relatively unreduced paracones on M^{1-3} ; and relatively narrow premolars. It differs from *S. macroura* in lacking a pronounced head stripe; lacking a markedly enlarged round to oval apical granule on the interdigital pads, lacking large entoconids, and in having a long premaxillary vacuity that extends posterior to the edge of the C^1 alveolus.

DESCRIPTION: Tail: The tail-vent length is either slightly shorter than, equal to, or longer than the nose-vent length. The tail is invariably thin.

HIND FOOT: The interdigital pads are fused at the bases or slightly up from the bases. Each interdigital pad is covered by granules, not striae (exceptions are noted below), and a medial anteroposterior row of such granules is commonly present. The granules increase slightly in size toward the apex of the pad. Usually a small hallucal pad or enlarged granule is present. A small posterior metatarsal or enlarged granule is rarely present. Very rarely (abnormally) a posthallucal pad or enlarged granule is present. The extent of covering of hair on the ventral surface is sparse, only covering the heel and extending as a wedge anteriorly from heel.

PELAGE MARKINGS: The body is devoid of any distinguishing markings except on the forehead and between the ears where the pelage is darker than elsewhere on the head. The color of the pelage on the back varies geographically.

NIPPLE NUMBER: Eight to 10 nipples are normal but six have been recorded. The number appears to be geographically distinctive.

DENTITION: I^1 is taller-crowned than I^2 , I^2 shorter-crowned in length than I^3 , and I^4 generally longer-crowned than I^3 but sometimes is subequal. C^1 varies from caniniform

TABLE 2

Relative Cranial, Dental, and External Morphology Expressed as Ratios in *Sminthopsis*

Abbreviations: TV, tail-vent length; HB, head-body (nose-vent). Other abbreviations as in table 1. Place name abbreviations as follows: Flinders Naval Depot, Victoria (F.N.D.); Herbert River, Queensland (Herb. R.); Virgin Bore Creek, Western Australia; Doomadgee Mission, Queensland.

	\bar{x}	OR	N	\bar{x}	OR	N	\bar{x}	OR	N	\bar{x}	OR	N
S. murina, all				S. m.,WA,all			S. m.,Albany WA			S. m.,Denmark WA		
M ₁₋₃	4.4	4.0-4.7	91	4.4	4.0-4.7	42	4.4	4.0-4.6	14	4.4	4.1-4.5	11
M ₁₋₄ /I ₁ -M ₄	0.52	0.47-0.59	83	0.52	0.48-0.56	38	0.52	0.50-0.55	11	0.51	0.48-0.56	11
TV/HB	1.03	0.77-1.42	45	1.02	0.54-1.42	31	1.00	0.54-1.12	7	0.94	0.82-1.02	10
BL/ZW	1.71	1.54-1.86	57	1.70	1.61-1.77	23	1.72	1.66-1.77	7	1.68	1.62-1.71	10
BW/ZW	0.42	0.35-0.48	58	0.43	0.40-0.48	23	0.43	0.41-0.47	8	0.43	0.40-0.45	8
IO/ZW	0.36	0.31-0.42	66	0.36	0.33-0.40	29	0.36	0.33-0.38	10	0.35	0.33-0.38	12
M ₁₋₃ /R-LM ³	0.58	0.51-0.65	82	0.58	0.53-0.63	38	0.58	0.54-0.63	11	0.56	0.54-0.60	12
M ₁₋₄ /C ₁ -M ₄	0.53	0.48-0.58	83	0.52	0.49-0.57	38	0.52	0.50-0.54	11	0.51	0.48-0.54	12
IPVD/M ₁₋₃	0.75	0.50-1.02	52	0.83	0.52-1.02	21	0.90	0.87-0.92	3	0.93	0.87-1.02	9
S. m.,Tambellup WA				S. m.,wheatfields WA			S. m.,Kalgoorlie WA			S. m.,S.A.,all		
M ₁₋₃	4.5	4.3-4.7	10	4.2	4.0-4.3	4	4.2	4.1-4.3	4	4.3	4.1-4.5	7
M ₁₋₄ /I ₁ -M ₄	0.52	0.50-0.56	9	0.53	0.52-0.54	3	0.54	0.53-0.55	4	0.53	0.50-0.59	7
TV/HB	0.96	0.80-1.17	7	1.27	1.17-1.42	3	1.13	1.05-1.20	4	1.02	0.86-1.20	11
BL/ZW	1.71	1.61-1.76	3	1.72	1.72-1.72	1	1.71	1.69-1.72	2	1.69	1.57-1.84	6
BW/ZW	0.43	0.40-0.47	4	0.45	0.45-0.45	1	0.46	0.44-0.48	2	0.39	0.35-0.43	5
IO/ZW	0.38	0.37-0.38	2	0.37	0.36-0.38	2	0.38	0.36-0.40	3	0.36	0.32-0.39	7
M ₁₋₃ /R-LM ³	0.58	0.53-0.63	8	0.60	0.59-0.62	3	0.61	0.60-0.62	4	0.56	0.51-0.62	7
M ₁₋₄ /C ₁ -M ₄	0.53	0.49-0.56	8	0.54	0.52-0.56	3	0.54	0.52-0.57	4	0.54	0.50-0.57	7
IPVD/M ₁₋₃	0.72	0.63-0.83	4	0.69	0.68-0.70	2	0.67	0.65-0.68	3	0.68	0.58-0.78	5
S. m.,Vict.				S. m.,N.S.W.,all			S. m.,N.S.W.,coastal			S. m.N.S.W.,inland		
M ₁₋₃	4.2	4.1-4.3	8	4.3	4.0-4.5	11	4.3	4.0-4.5	7	4.2	4.0-4.5	4
M ₁₋₄ /I ₁ -M ₄	0.52	0.50-0.55	6	0.51	0.47-0.54	11	0.51	0.47-0.53	7	0.52	0.50-0.54	4
TV/HB	-	-	-	0.77	0.77-0.77	1	-	-	-	0.77	0.77-0.77	1
BL/ZW	1.72	1.67-1.78	5	1.70	1.63-1.77	9	1.71	1.67-1.77	6	1.67	1.63-1.70	3
BW/ZW	0.42	0.41-0.44	5	0.43	0.39-0.48	10	0.43	0.42-0.45	6	0.42	0.39-0.48	4
IO/ZW	0.35	0.33-0.37	5	0.37	0.34-0.42	10	0.37	0.34-0.42	6	0.36	0.35-0.37	4
M ₁₋₃ /R-LM ³	0.56	0.52-0.57	6	0.57	0.53-0.62	11	0.57	0.53-0.62	7	0.57	0.55-0.61	4
M ₁₋₄ /C ₁ -M ₄	0.54	0.53-0.58	6	0.53	0.50-0.57	10	0.53	0.50-0.54	6	0.54	0.53-0.57	4
IPVD/M ₁₋₃	0.62	0.52-0.67	5	0.72	0.57-0.81	3	0.69	0.57-0.81	2	0.78	0.78-0.78	1
S. m.,Qld, all				S. m.,SE.Qld			S. m.,Mt Molloy Qld			S. ooldea		
M ₁₋₃	4.4	4.0-4.7	22	4.3	4.0-4.7	11	4.4	4.0-4.7	8	3.8	3.6-4.0	8
M ₁₋₄ /I ₁ -M ₄	0.53	0.49-0.56	20	0.53	0.51-0.55	9	0.53	0.50-0.56	8	0.56	0.54-0.57	7
TV/HB	-	-	-	-	-	-	-	-	-	1.22	1.20-1.25	3
BL/ZW	1.72	1.54-1.86	14	1.77	1.71-1.86	5	1.70	1.54-1.77	8	1.80	1.68-1.93	6
BW/ZW	0.43	0.38-0.47	15	0.44	0.40-0.47	5	0.43	0.38-0.46	8	0.50	0.45-0.53	6
IO/ZW	0.35	0.31-0.38	14	0.37	0.36-0.38	4	0.34	0.31-0.36	8	0.38	0.35-0.41	6
M ₁₋₃ /R-LM ³	0.59	0.52-0.65	19	0.60	0.52-0.65	9	0.58	0.52-0.64	7	0.62	0.58-0.66	7
M ₁₋₄ /C ₁ -M ₄	0.54	0.51-0.58	20	0.55	0.52-0.58	9	0.54	0.51-0.57	8	0.57	0.55-0.59	7
IPVD/M ₁₋₃	0.70	0.50-0.89	17	0.69	0.58-0.77	6	0.70	0.58-0.85	8	0.89	0.76-1.15	7
S. leucopus,Tas.&F.N.D.				S. l.,Tas.			S. l.,F.N.D.(Flinders Nav.D)			S. virginiae,N.G.&Herb.R.		
M ₁₋₃	4.6	4.4-4.9	10	4.6	4.4-4.9	10	4.6	4.4-4.8	6	4.8	4.6-5.0	14
M ₁₋₄ /I ₁ -M ₄	0.51	0.48-0.55	14	0.51	0.49-0.55	7	0.50	0.48-0.51	7	0.54	0.48-0.58	12
TV/HB	0.89	0.74-1.02	8	1.02	1.01-1.02	2	0.85	0.74-0.98	6	1.02	1.02-1.02	1
BL/ZW	1.79	1.70-1.90	14	1.82	1.76-1.90	7	1.76	1.70-1.81	7	1.64	1.52-1.78	12
BW/ZW	0.41	0.35-0.44	14	0.42	0.40-0.44	7	0.40	0.35-0.43	7	0.38	0.34-0.42	12
IO/ZW	0.40	0.36-0.43	14	0.41	0.40-0.43	7	0.38	0.36-0.40	7	0.31	0.29-0.33	12
M ₁₋₃ /R-LM ³	0.58	0.48-0.66	14	0.60	0.56-0.66	7	0.55	0.48-0.52	7	0.56	0.52-0.59	12
M ₁₋₄ /C ₁ -M ₄	0.52	0.48-0.56	14	0.53	0.51-0.56	7	0.50	0.48-0.52	7	0.55	0.48-0.57	11
IPVD/M ₁₋₃	0.85	0.70-1.02	11	0.80	0.70-0.90	6	0.91	0.81-1.02	5	0.79	0.79-0.79	1

to premolariform, is conspicuously taller-crowned than P¹, but sometimes is about the same crown height as P⁴. The upper premolars are markedly longer than narrow, P³ is taller and longer-crowned than P¹ and shorter-crowned than P⁴. Premolar size generally increases gradually posteriorly. The anterior

cingular cusp on P¹ is tiny to absent. The same cusp is tiny to small on P³ to P⁴, the posterior cingular cusp is tiny to small, buccal cingula are small to absent, and posterolingual cingula are small. dP⁴ (e.g., J16480, J20431) has three roots and three main cusps; a paracone, a subequal styler cusp D (stD);

TABLE 2—(Continued)

	\bar{x}	OR	N	\bar{x}	OR	N	\bar{x}	OR	N	\bar{x}	OR	N
	S.v., Herbert River, Qld			S.v., New Guinea			S. douglasi			S. macroura, all		
M ₁₋₃	4.9	4.7 -5.0	8	4.7	4.6 -4.8	6	6.1	6.0 -6.1	2	4.4	3.9 -4.9	52
M ₁₋₄ /I ₁ -M ₄	0.54	0.52-0.58	7	0.53	0.48-0.55	5	0.56	0.55-0.57	2	0.55	0.51-0.59	32
TV/HB	-	-	-	1.02	1.02-1.02	1	1.02	1.02-1.02	1	1.17	0.81-1.23	16
BL/ZW	1.64	1.57-1.67	7	1.64	1.52-1.78	5	1.64	1.58-1.69	2	1.60	1.45-1.69	24
BW/ZW	0.38	0.34-0.42	7	0.38	0.36-0.39	5	0.40	0.40-0.40	1	0.42	0.39-0.49	23
IO/ZW	0.31	0.29-0.33	7	0.32	0.30-0.33	5	0.30	0.30-0.30	2	0.29	0.23-0.34	28
M ¹⁻³ /R-LM ³	0.56	0.52-0.59	7	0.56	0.53-0.59	5	0.60	0.60-0.60	2	0.58	0.51-0.65	30
M ¹⁻⁴ /C ¹ -M ⁴	0.55	0.51-0.57	6	0.54	0.48-0.56	5	0.57	0.55-0.59	2	0.55	0.52-0.59	32
IPVD/M ¹⁻³	-	-	-	0.79	0.79-0.79	1	0.95	0.95-0.95	1	0.78	0.57-0.85	10
	S. m., Darling Downs			S. m., Richmond, Qld			S. m., central WA&N.T.			S. m., Virgin Bore Ck		
M ₁₋₃	4.2	4.0 -4.5	6	4.5	4.1 -4.9	21	4.3	3.9 -4.5	6	4.3	4.2 -4.5	8
M ₁₋₄ /I ₁ -M ₄	0.56	0.55-0.59	5	0.55	0.53-0.56	4	0.57	0.56-0.58	4	0.54	0.52-0.56	8
TV/HB	-	-	-	1.14	1.08-1.20	2	1.11	0.89-1.17	5	1.19	1.00-1.23	7
BL/ZW	1.61	1.57-1.66	3	1.60	1.54-1.66	4	1.63	1.61-1.67	4	1.65	1.61-1.69	5
BW/ZW	0.43	0.43-0.43	2	0.42	0.41-0.43	4	0.46	0.45-0.46	4	0.44	0.40-0.49	7
IO/ZW	0.32	0.30-0.34	4	0.31	0.30-0.31	4	0.31	0.28-0.33	4	0.31	0.29-0.33	7
M ¹⁻³ /R-LM ³	0.60	0.58-0.65	5	0.56	0.55-0.58	4	0.60	0.56-0.63	4	0.60	0.55-0.64	8
M ¹⁻⁴ /C ¹ -M ⁴	0.55	0.54-0.58	5	0.53	0.52-0.54	4	0.57	0.54-0.59	4	0.55	0.53-0.56	8
IPVD/M ¹⁻³	-	-	-	0.85	0.85-0.85	1	0.57	0.57-0.57	1	0.81	0.80-0.81	2
	S. m., Doomadgee Miss.			S. hirtipes			S. butleri			S. granulipes		
M ₁₋₃	4.2	4.0 -4.3	11	4.5	4.3 -4.7	6	4.5	4.1 -4.6	6	4.7	4.4 -5.0	6
M ₁₋₄ /I ₁ -M ₄	0.55	0.51-0.59	11	0.55	0.52-0.58	5	0.56	0.56-0.56	1	0.45	0.42-0.47	5
TV/HB	0.85	0.81-0.89	2	1.17	1.02-1.28	4	1.01	1.01-1.01	1	0.64	0.53-0.71	3
BL/ZW	1.55	1.45-1.65	8	1.64	1.60-1.70	4	1.56	1.56-1.56	1	1.75	1.67-1.80	4
BW/ZW	0.41	0.39-0.43	8	0.52	0.50-0.55	4	0.43	0.43-0.43	1	0.41	0.41-0.41	2
IO/ZW	0.26	0.23-0.30	9	0.36	0.34-0.36	4	0.30	0.30-0.30	1	0.35	0.33-0.38	4
M ¹⁻³ /R-LM ³	0.54	0.51-0.58	9	0.59	0.57-0.62	5	0.56	0.56-0.56	1	0.55	0.50-0.58	5
M ¹⁻⁴ /C ¹ -M ⁴	0.55	0.53-0.57	11	0.53	0.52-0.55	5	0.53	0.53-0.53	1	0.49	0.47-0.50	5
IPVD/M ¹⁻³	0.79	0.75-0.83	6	0.92	0.84-0.98	4	0.67	0.67-0.67	1	1.08	1.08-1.08	1
	S. psammophila			S. longicaudata			S. crassicaudata, all			S. c., Tambellup, W.A.		
M ₁₋₃	6.0	6.0 -6.1	4	4.9	4.7 -5.2	5	4.3	3.8 -4.6	36	4.1	3.8 -4.5	10
M ₁₋₄ /I ₁ -M ₄	0.51	0.49-0.55	4	0.53	0.51-0.54	3	0.54	0.49-0.57	23	0.54	0.52-0.56	10
TV/HB	1.27	1.13-1.39	3	2.06	2.06-2.06	1	0.71	0.59-0.80	37	0.66	0.59-0.74	8
BL/ZW	1.71	1.66-1.76	3	-	-	-	1.70	1.60-1.80	14	1.67	1.60-1.74	4
BW/ZW	0.51	0.51-0.52	3	0.54	0.54-0.54	1	0.46	0.42-0.51	12	0.44	0.43-0.46	5
IO/ZW	0.36	0.35-0.37	3	0.32	0.32-0.32	1	0.34	0.30-0.36	17	0.35	0.34-0.36	7
M ¹⁻³ /R-LM ³	0.59	0.55-0.61	4	0.56	0.54-0.58	3	0.57	0.52-0.65	24	0.56	0.52-0.60	12
M ¹⁻⁴ /C ¹ -M ⁴	0.52	0.49-0.55	4	0.51	0.51-0.52	3	0.53	0.50-0.56	25	0.53	0.52-0.56	12
IPVD/M ¹⁻³	1.02	1.02-1.02	1	0.40	0.40-0.40	1	0.51	0.47-0.58	6	-	-	-
	S. c., Innamincka, S.A.			S. c., Victoria			S. c., N.T.					
M ₁₋₃	4.3	4.2 -4.3	4	4.4	4.1 -4.6	15	4.3	4.2 -4.6	7			
M ₁₋₄ /I ₁ -M ₄	0.53	0.51-0.55	4	0.50	0.49-0.51	2	0.54	0.53-0.57	7			
TV/HB	0.79	0.77-0.80	2	-	-	-	-	-	-			
BL/ZW	1.74	1.71-1.80	3	1.69	1.65-1.73	2	1.71	1.68-1.70	5			
BW/ZW	0.46	0.45-0.48	3	0.44	0.42-0.45	2	0.50	0.49-0.51	2			
IO/ZW	0.32	0.30-0.34	3	0.34	0.33-0.34	2	0.34	0.32-0.36	5			
M ¹⁻³ /R-LM ³	0.58	0.55-0.61	4	0.55	0.52-0.57	2	0.60	0.55-0.65	6			
M ¹⁻⁴ /C ¹ -M ⁴	0.53	0.52-0.54	4	0.52	0.50-0.53	2	0.54	0.53-0.55	7			
IPVD/M ¹⁻³	-	-	-	0.57	0.57-0.57	1	0.51	0.47-0.58	6			

and a taller metacone. The very low protocone is rudimentary. stB and stA (see fig. 2 for abbreviations) may be represented by variable swellings on the anterobuccal cingulum. stD is connected to the metacone by a low crest. The anterior cingulum on M¹ to M⁴ is confined to the anterobuccal corner. Styler cusp C is variably developed between stB and stD. The metacrista of M³ is shorter than or subequal to its crown length. The diastema is variously developed around C₁.

The first four lower premolars are generally in contact anteroposteriorly but are sometimes separated by slight spaces. The first lower canine is premolariform and subequal in crown height to P₃, P₃ is taller-crowned than P₄ which is subequal to or larger than P₁. Small posterior cingular cusps are developed on P₁ to P₄ and sometimes on C₁. The posterior lobe of I₃ is small to absent. The lower canine has a narrow lingual cingulum. There is also a very narrow lingual cingulum

TABLE 3
Measurements (in Millimeters) of Unique and Type Specimens

Abbreviations: as in table 1 or else as follows: AM, Australian Museum; AMNH, American Museum of Natural History; BM, British Museum; C, National Museum of Victoria; J, Queensland Museum; LDC, Knowsley Museum (in the Liverpool Museum); SAM, South Australian Museum; WAM, Western Australian Museum.

	BL	ZW	OBW	IBW	C-M ¹	M ¹⁻⁴	M ¹⁻³	R-LM ³	IO	IPVD	DL	I ₁ -M ₄	M ₁₋₄	M ₁₋₃	C-AP	C-AR
<i>Phascogale murina</i> (BM 55.12.24.95)	-	-	-	-	-	4.9	4.4	-	-	-	-	-	5.6	4.2	-	-
<i>Phascogale albipes</i> (BM 1080C)	25.0	15.1	9.9	-	9.9	5.4	4.7	8.2	5.3	3.9	-	11.3	5.9	4.3	-	-
<i>S. murina tatei</i> (AM M7157)	25.4	15.6	10.4	3.9	10.4	5.6	5.0	8.7	5.5	-	20.3	11.8	6.3	4.6	6.2	4.7
<i>Antechinus fuliginosa</i> (BM 44.2.15.20)	-	-	-	-	8.9	4.9	4.4	7.4	4.8	3.1	17.6	10.6	5.4	4.1	5.3	4.0
<i>S. murina</i> Kangaroo Is. (SAM M7936)	-	14.4	-	-	11.2	5.8	5.2	8.6	5.8	4.6	20.8	12.7	6.2	4.7	5.5	4.6
<i>Phascogale leucopus</i> (BM 43.5.31.5)	-	-	-	-	10.0	5.4	4.7	-	5.9	3.8	19.0	11.7	6.0	4.7	-	-
<i>Antechinus ferruginifrons</i> (BM 54.11.19.3)	-	-	-	-	11.4	5.8	5.1	8.7	5.3	4.3	22.4	13.3	6.3	4.8	-	4.9
<i>S. ooldea</i> (AM M7502)	-	-	-	-	8.8	4.8	4.3	7.2	-	-	-	10.3	5.3	4.0	-	-
<i>S. longicaudata</i> (C7803)	-	-	11.4	-	11.3	5.9	5.2	9.1	5.6	-	10.8	12.8	6.9	5.2	6.4	4.6
<i>S. granulipes</i> (AM MC669)	-	14.7	-	-	10.6	5.4	5.0	9.0	5.4	-	21.1	12.8	6.1	4.7	5.5	5.0
<i>S. psammophila</i> (C6203)	31.0	-	13.0	3.5	13.7	6.8	6.0	10.9	6.2	-	25.9	16.1	7.8	6.0	7.5	5.7
<i>Phascogale virginiae</i> (J25890)	24.9	15.2	9.9	3.5	10.5	5.9	5.1	8.7	4.8	-	20.5	12.4	6.6	5.0	5.7	5.0
<i>S. nitela</i> (BM 97.4.12.6)	22.5	14.2	9.4	3.3	9.8	5.0	5.1	8.7	4.3	3.9	18.3	11.4	6.6	5.0	5.5	4.5
<i>S. rufigenis</i> (BM 22.2.2.76)	23.2	14.6	8.9	3.8	9.8	5.7	5.3	8.3	4.4	3.8	19.5	11.8	6.6	5.2	5.5	4.9
<i>Phascogale rona</i> (AMNH 104005)	-	-	-	4.0	10.1	5.9	5.1	9.3	5.4	4.1	20.4	11.8	6.5	4.9	5.8	5.4
<i>S. douglasi</i> (J5173)	26.7	16.9	10.7	4.0	11.8	6.8	5.9	9.8	5.1	5.6	22.0	13.6	7.8	6.0	6.3	5.6
<i>Podabrus macrourus</i> (LDC 275)	-	14.5	-	-	10.4	5.6	5.2	8.5	4.6	3.8	19.8	11.9	6.2	4.5	5.2	4.5
<i>Antechinus</i> (P.) <i>froggatti</i> (AM M8019)	21.3	-	-	-	8.5	4.9	4.4	7.5	4.1	-	16.2	9.4	9.5	4.2	5.3	4.4
<i>S. stalkeri</i> (BM 6.3.9.91)	21.0	13.0	8.8	3.0	9.1	5.3	4.9	8.2	3.8	3.4	16.9	10.4	6.0	4.4	4.9	4.3
<i>S. monticola</i> (AM B9579)	23.1	14.2	9.5	3.7	9.6	5.7	5.2	8.5	4.8	-	18.3	11.1	6.4	4.8	5.0	4.6
<i>S. butleri</i> (WAM M7158)	22.8	14.6	9.4	3.2	9.2	4.9	4.3	7.7	4.4	2.9	18.4	10.1	5.6	4.1	5.5	4.4
<i>S. hirtipes</i> (BM 97.12.17.1)	24.0	15.4	11.2	2.8	9.9	5.2	4.7	9.0	5.2	5.3	19.4	11.0	5.5	4.0	6.1	4.3
<i>Phascogale orassicaudata</i> (BM 44.10.15.4)	-	-	-	-	9.1	5.1	4.6	-	-	-	-	10.7	5.6	4.0	-	-
<i>S. c. centralis</i> (BM 2.9.8.7)	22.5	13.2	9.1	3.2	9.7	5.3	4.8	8.0	4.6	2.8	18.2	10.9	5.9	4.4	5.0	3.8
<i>Phascogale lanigera</i> (BM 47.12.4.5)	-	14.3	10.3	2.8	9.5	4.8	4.4	8.3	5.4	2.4	18.9	10.8	5.4	3.9	5.8	3.5
<i>Antechinomys spenceri</i> (BM 97.11.3.12)	26.3	15.3	11.4	2.2	11.1	5.7	4.9	9.1	5.5	2.1	21.7	12.5	6.5	4.8	6.7	4.0

variably developed but commonly present on P₁ to P₄. The fourth lower deciduous premolar (e.g., J16480, J20431) has two roots and one main cusp, the protoconid. On the posterior flank of protoconid of dP₄, a swelling or minor cusp suggests a metaconid. A posterior cingular cusp connects to the metaconid of dP₄ by a crest. The lower premolars have a continuous lingual and posterior cingulum and a small anterior cingular cusp that may be homologous with the paraconid of the posterior molars. Parastylids are present on M₁ to M₄. Entoconid development is slight to absent on M₁ to M₃. The talonid is wider than the trigonid on M₁ only. Anterior cingula on M₁ to M₄ are generally very reduced or absent and are always absent at the

base of the protoconid. The paraconid varies from smaller than to subequal to the metaconid on M₄.

SKULL AND DENTARY: The rostrum is elongate. The nasals expand only very slightly at the posterior ends. A depression in the midline between the frontals is very shallow or entirely absent. The lacrimal foramina are just on or posterior to the anterior rim of the orbit. A premaxillary vacuity varies in length but generally extends posterior to a point level with the middle of P¹. Dorsolateral expansion of the lacrimal rim over the orbit is minimal to absent. The alisphenoid bulla is small and the ectotympanic ring is broadly exposed. The mastoid process is uninflated. The periotic bulla is small. The foramen

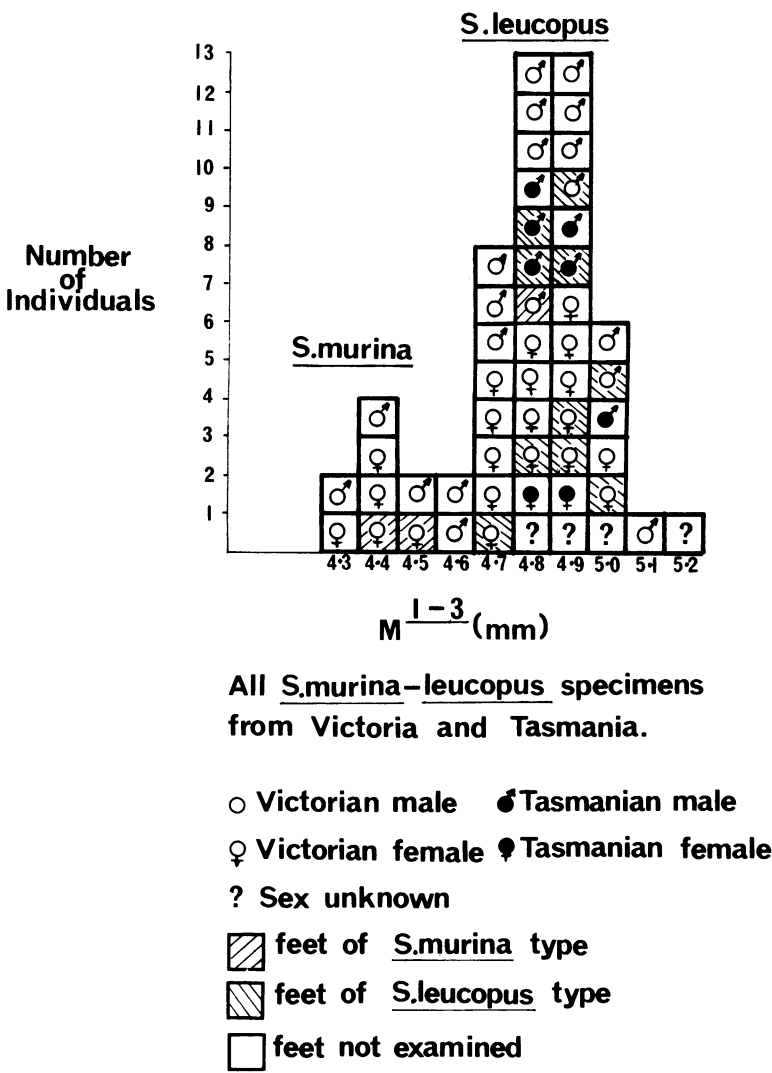
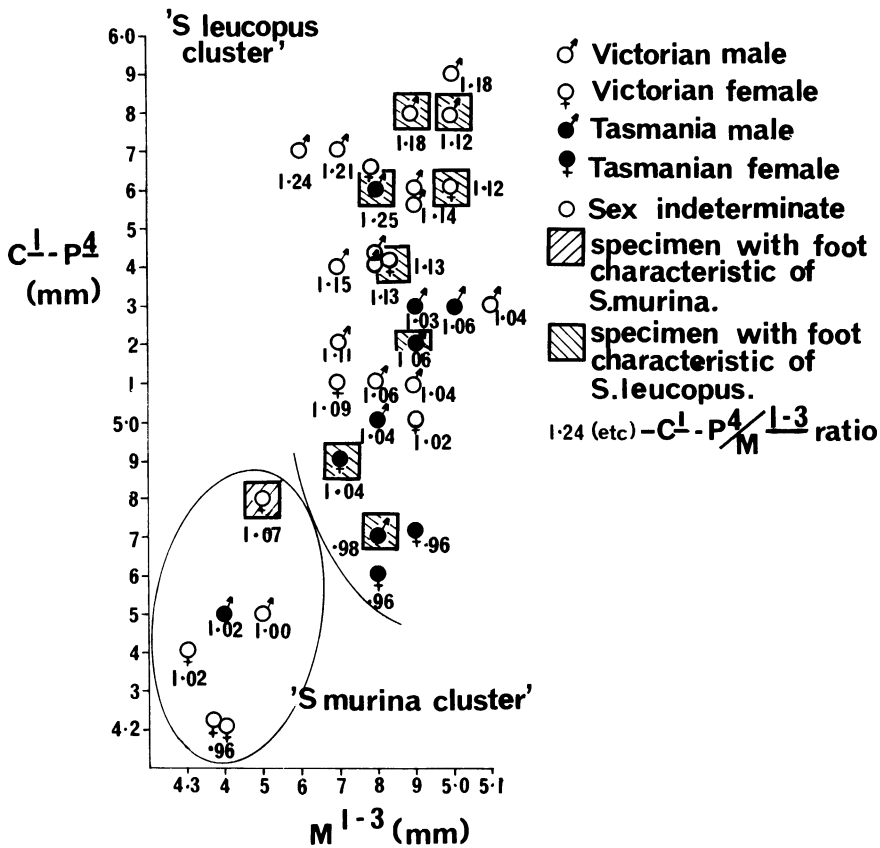


FIG. 9. Separation of *Sminthopsis murina* and *S. leucopus* using molar size.

pseudovale is large. The ventral alisphenoid floor of the foramen rotundum extends laterally and the foramen is, dorsoventrally, relatively small. The alisphenoid bar between the sphenorbital foramen and the foramen rotundum is relatively wide. The masseteric fossa between the anterior and posterior borders of the ascending ramus is large. The anterior border of the ascending ramus and posterior edge of the dentary are

divergent (i.e., clearly not parallel), and the distance between the articular condyle and the tip of the ascending ramus is equal to or slightly shorter than the distance between the articular condyle and the tip of the angular process.

DISCUSSION: Troughton (1965) included *S. leucopus* and *S. ooldea* in the species *S. murina*, and Tate (1947) considered *S. leucopus* to be a subspecies of *S. murina*. In



Adult *S. murina*-*leucopus* from Victoria and Tasmania.

FIG. 10. Separation of *Sminthopsis murina* and *S. leucopus* using molar size and anterior cheek-tooth spacing.

the present study 36 modern specimens of *S. leucopus-murina* from localities in Victoria, Tasmania, and the Bass Strait Islands, and "fossil" remains of at least 20 individuals of *S. leucopus-murina* from the Pyramids Cave in southwestern central Victoria have been examined. I have concluded that *S. leucopus* and *S. murina* are sibling, but distinct species. Initially, all modern specimens of *S. murina* and *S. leucopus* used in this study were treated as one sample and various parameters graphed (figs. 9-11). A distinct bimodality is apparent in M^{1-3} size, a measure unaffected by age. The bimodality is not sexual because each cluster itself appears to be

sexually bimodal (a feature more apparent in the large cluster). The ratio of C^1-P^4 (adult) length to M^{1-3} length (fig. 10) (determined by subtracting M^{1-4} length from C^1-M^4 length and dividing the result by M^{1-3} length) also indicates two different sorts of animals. Those with the highest ratio are also those with the largest M^{1-3} values and vice versa. In general, individuals with larger molars have relatively more spread-out premolar rows such that premolars tend not to contact one another anteroposteriorly. Further, a bivariate plot (fig. 11) of minimum interorbital width value (IO) against M^{1-3} length (using only adult specimens) produces two

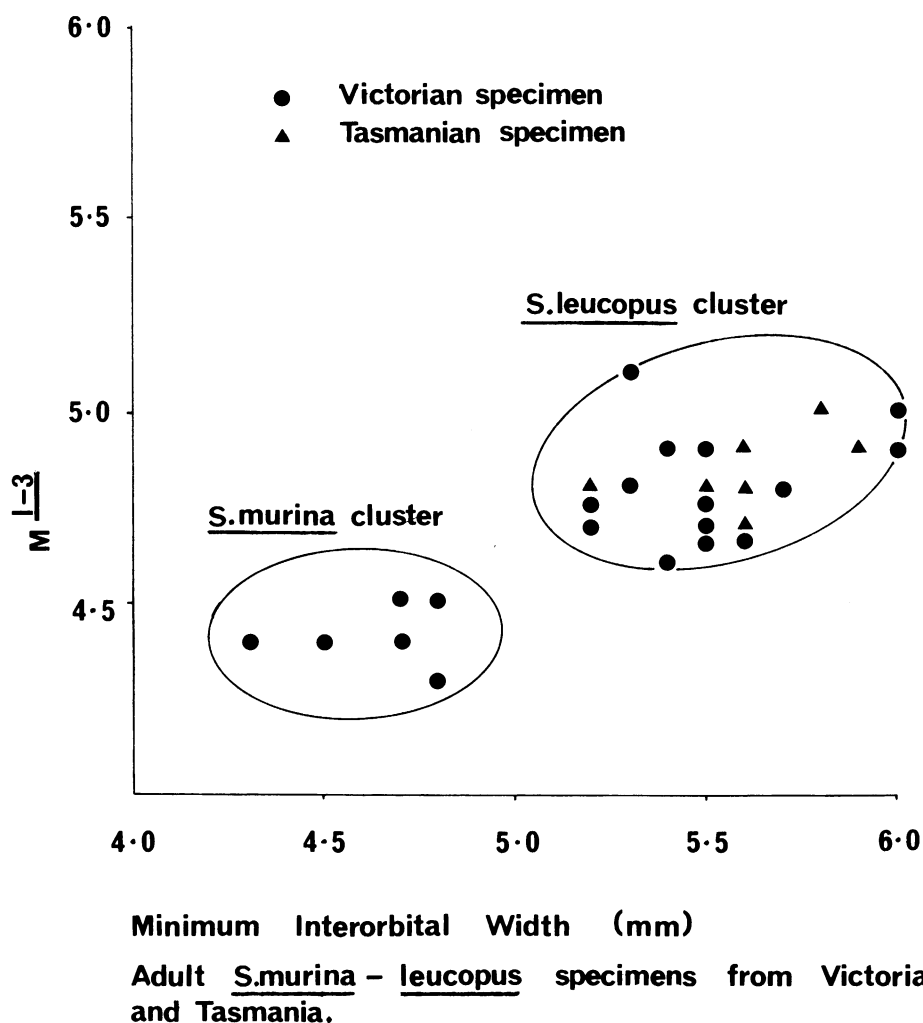


FIG. 11. Separation of *Sminthopsis leucopus* and *S. murina* using molar size and interorbital width.

clusters. When other information is considered, *S. murina*-type feet with non-striated pads occur only once (see below under discussion of *S. leucopus*) among the larger Victorian "*S. murina*" specimen cluster. All Tasmanian specimens I examined have *S. leucopus*-type feet.

Tasmanian specimens have a lower $(C^1-P^4)/(M^{1-3})$ ratio value than Victorian *S. leucopus* specimens (fig. 10). If there are two species of *Sminthopsis* in southern Victoria, both lacking large entoconids and being of similar general size, it would seem likely that

specialization would occur in some way that would enable them to coexist. Specimens of Victorian *S. murina* are in most respects the smallest in Australia. It might be expected that these, the most southern on the continent, should be the largest. In Western Australia, for example, the largest specimens of *S. murina* are clearly those of the south coastal areas. In Victoria, there may be a selective advantage for *S. murina* to be small in order to coexist with the similar but larger *S. leucopus*. There is also a difference in the $(C^1-P^4)/(M^{1-3})$ ratio of most Victorian and

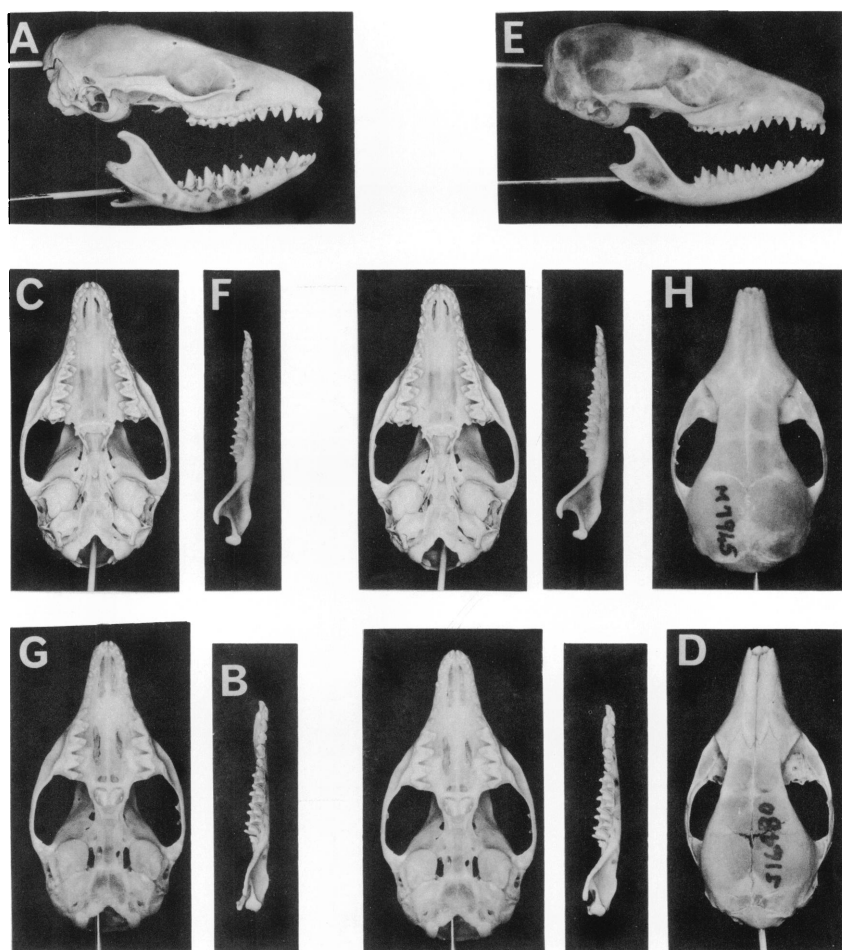


FIG. 12. *Sminthopsis murina*. A–D, J16480, juvenile with dp4, Mt. Molloy, Queensland (*S. m. tatei*). E–H, WAM M7845, adult, from near Augusta, Western Australia (*S. m. fuliginosa*). A–H, $\times 2$.

non-Victorian *S. leucopus*. Small values for Victorian *S. murina* and very large values for Victorian *S. leucopus* may be interpreted as evidence suggesting that character displacement has occurred in response to the sympatric *S. murina*. To test this hypothesis it will be necessary to try breeding individuals of *S. murina* with *S. leucopus* or to establish beyond any reasonable doubt that the two types are in fact truly sympatric. At present, there are too few specimens of Victorian *S. murina*, particularly from south central to coastal areas. The only evidence

for sympatric association occurs in a sample of isolated dentaries representing 20 individuals of *Sminthopsis* spp. from Pyramids Cave, Victoria Range, Victoria. Of these, 19 have the characters of *S. leucopus* and one has the characters of *S. murina*. This sample was made available by Mr. N. Wakefield who knew of no reason for believing the specimens to represent a mixed sample (personal commun.). I have (Archer, 1974a) given reasons for being cautious about assuming contemporaneity of cave fossils.

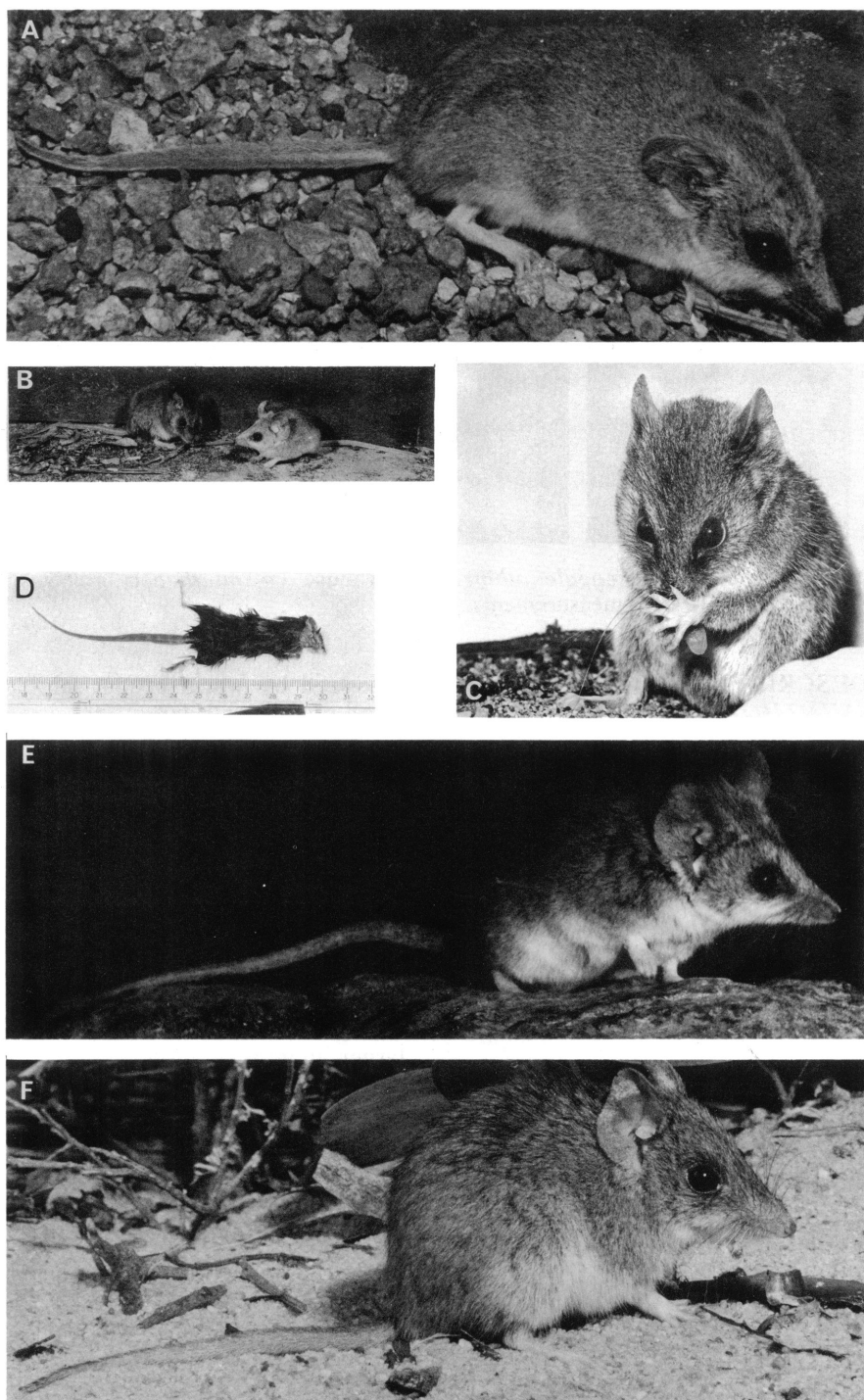


FIG. 13. *Sminthopsis murina*, *S. ooldea*, and *S. leucopus*. A, *S. m. murina*, southeastern Queensland. B, *S. m. fuliginosa*, southwestern Western Australia (left) and *S. m. tatei*, Mt. Molloy, Queensland (right), showing differences in ear length and color. C, *S. m. fuliginosa*, southwestern Western Australia. D, *S. ooldea*, Warburton Range, Western Australia, showing an incrassated tail. E, *S. ooldea*, North Well Station, South Australia (photo by H. Aslin). F, *S. leucopus*, Victoria (photo by P. Woolley).

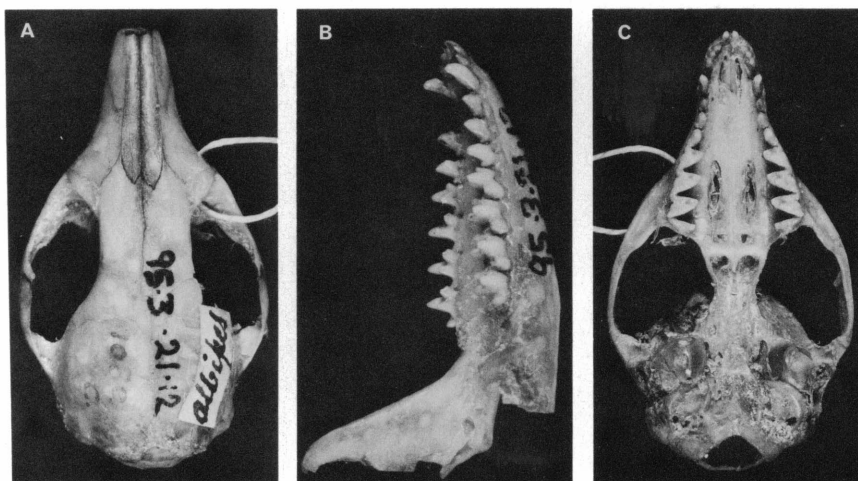


FIG. 14. Holotype of *Phascogale albipes* Waterhouse (= *Sminthopsis murina*), BM1080C (=BM95.321.12). See table 2 for measurements.

DESCRIBED FORMS OF *SMINTHOPSIS MURINA*

Several names have been applied to specimens (the types) here regarded as *S. murina*. Subspecific distinction has a precise taxonomic meaning (e.g., Amadon 1949; Mayr, Linsley, and Usinger, 1953; Ride, 1964; and McNeil, 1972) and I have not attempted here to examine the statistical validity of subspecies. Because some of the named forms are allopatric, I have employed the name to qualify the form of the species occurring in the vicinity of the type locality, or having the particular morphological form. Use of these names is not to be interpreted as recognition of their subspecific status. More information is required before the actual status of these forms can be determined.

Sminthopsis murina murina

GEOGRAPHIC DISTRIBUTION: Range of this form includes southeastern Queensland, eastern New South Wales, and southeastern Australia, as far west as the southeastern half of South Australia. Type specimens from within this range are the holotypes of *Phascogale murina* Waterhouse and *Phascogale albipes* Waterhouse.

RECOGNITION: These animals are char-

acterized by warm brown midback pelage, small cranial and dental measurements, and ten nipples (although rare variations of eight or nine are known).

REMARKS: The status of *albipes* is confused by the dubious locality data of the type specimen. However, I and Krefft (1867), Thomas (1888), and Tate (1947) have concluded that no purpose is served by recognizing *albipes* as a form distinct from the nominate form. Only Waterhouse (1842, p. 48) stated that *albipes* "approaches most nearly to the *P. murina*, but differs in being larger, in general colouring, and especially in having the tail of a dark colour, and not white, as in that species." Color differences of this sort have not been found useful in distinguishing forms other than *fuliginosa*.

VARIATION: Pedal variation in the nominate form is exemplified by J 4269, from the McPherson Range in southeastern Queensland, where the apical granules of two pads are fused with proximal granules on one foot. Apparent striae are visible on the enlarged granules. Nipple variations of eight (C 892) and nine (AM M6579) are known, although Krefft (1869) stated that this form consistently has 10.

HABITAT AND REPRODUCTION: Locality data for the few specimens of Victorian *S.*

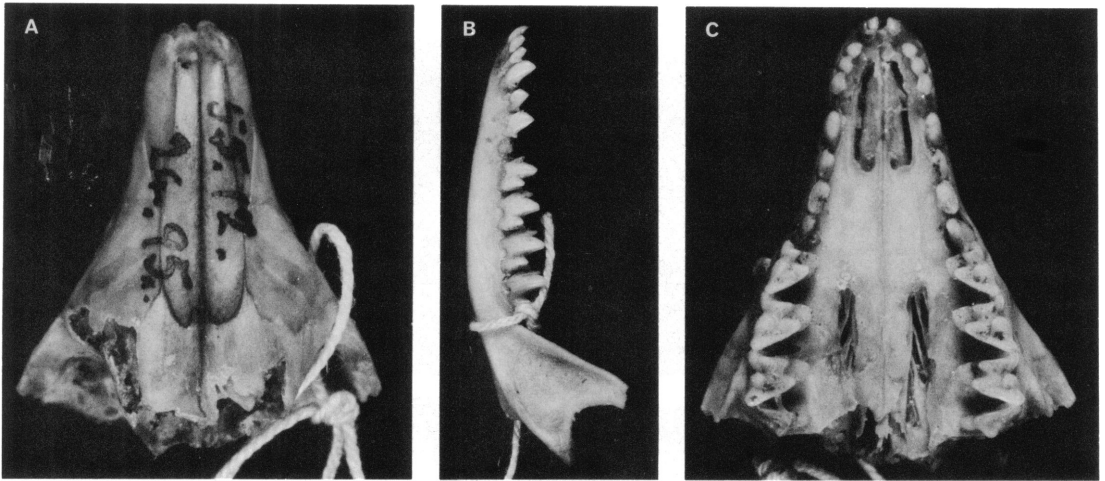


FIG. 15. Holotype of *Phascogale murina* Waterhouse (= *Sminthopsis murina*), BM55.12.24.95. See table 2 for measurements.

murina that I examined indicate that this form prefers non-coastal habitats in contrast to southern Victorian *S. leucopus* which seems abundant in and perhaps confined to coastal or nearby lowland habitats. Brazenor (1950, p. 22) related that *S. murina* in Victoria "is usually found amongst tufty grass on the edge of scrub country and lives upon insects." In New South Wales (Marlow, 1958) it occupies open woodland and sclerophyll forest on both sides of the Great Dividing Range. In the upper Richmond and Clarence rivers area of New South Wales (Calaby, 1966) it occurs in woodland and partly cleared land including wet fringes close to rain forest. Calaby recorded specimens collected from hollow fallen logs, among heaps of old wood, and deserted beehives. Nests in hollow logs were cup-shaped, 7–10 cm. in diameter and made of dried grass, leaves, or a mixture of both. At least some males caught while Calaby was spotlighting in August 1960 had active sperm in the testes. On the Darling Downs (Troughton, 1967) *S. murina* inhabited clumps of grass in scrubby places.

CONDITION OF HOLOTYPE: The holotype of *S. murina* (Waterhouse) (BM 55.12.24.95) represents a juvenile male in which P4 are just erupting. Skull and denta-

ries are badly damaged. The skull consists of a rostrum broken off behind the toothrow. All lower teeth are present, but both dentaries are broken behind M_4 . The skin is incomplete. The right hindlimb and left forelimb are missing, and the tail is broken. Wire in the left foot has caused corrosion of the sole. The feet are shriveled but the left foot still shows the medial row of granules characteristic of *S. murina*. The nose is also distorted, the result of a pinhole. The skin appears faded, being more rufous than recently collected specimens of the nominate form. There are suggestions of paler areas above the eyes and nose and between the ears and posterior part of the eyes.

The skull of the type specimen of *Phascogale albipes* Waterhouse is damaged in the right orbital and left alisphenoid areas. The left and right dentaries are damaged posterior to M_4 . The skin of the holotype (previously thought to have been lost) is flat and has information on attached labels indicating it was presented by J. B. Harvey on December 3, 1841.

Sminthopsis murina fuliginosa

GEOGRAPHIC DISTRIBUTION: Range includes southwestern Western Australia, and

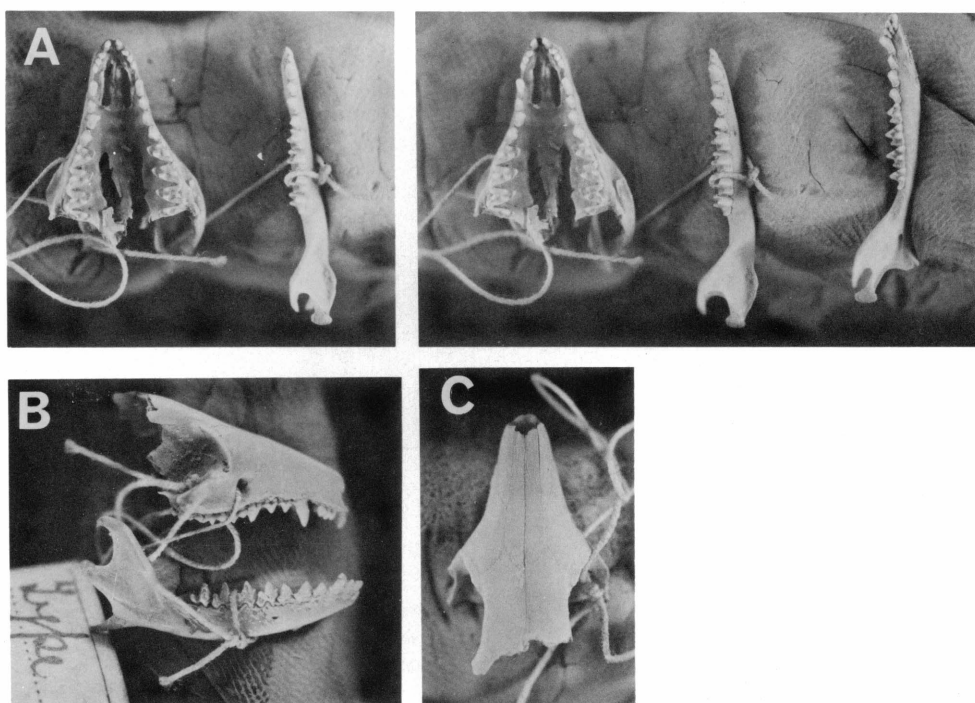


FIG. 16. Holotype of *Antechinus fuliginosa* Gould (= *Sminthopsis murina fuliginosa*), BM44.2.15.20. See table 2 for measurements.

possibly western South Australia. The type locality of *Antechinus fuliginosa* Gould is within this range.

RECOGNITION: Compared with other forms of *S. murina*, these have relatively dark body color, large size, and eight nipples. Dental dimensions are usually larger than those of typical *murina* but generally smaller than those of *tatei*.

REMARKS: Glauert (1933) evidently regarded *albipes* and *fuliginosa* to be synonymous and used the name *albipes* (the older name) for *murina* from southwestern Australia. Troughton (1965) and Krefft (1867) concluded that *fuliginosa* would or should be accorded full specific status. Thomas (1888), Tate (1947), Troughton (1967) and Ride (1970) did not.

Whittell (1954, p. 108–109) presented J. Gilbert's handwritten notes on the "Dtamin" and the "Twoor-dong," both considered

by Whittell to refer to *S. murina*. Gilbert noted that the "Dtamin" occurs in "the grass lands of the Toodyay Valley and in the thick groves of *Xanthorrhoea* surrounding the swamps and lakes of Perth," and that the "Twoor-dong" occurs at King Georges Sound. He believed they are unlike in that the "Twoor-dong" "differs in its mode of making a nest and other habits, but is very much darker, having the cheeks paler, while the under side is not so pure a white." Gould (1852), after receiving this information from Gilbert, identified the "Dtamin" (or "Otam-in") as the form *albipes* and proposed the name *fuliginosus* for the "Twoor-dong." I do not recognize this distinction here, and the characters noted by Gilbert do not separate southwestern *S. murina* into more than one form.

VARIATION: Tail-vent length of specimens of *fuliginosa* varies, being shorter than

nose-vent length in most south coastal individuals (e.g., from Denmark and Albany), approximately equal in many inland areas, and longer than nose-vent length in the northern and northeastern areas of its Western Australian distribution. A specimen (WAM M2262) from Mt. Clarence, Albany has a nose-vent length of 81.0 and a tail-vent length 44.0. Rather than tapering to a distal point, this tail terminates abruptly. There are no marks or other evidence to suggest the tail was damaged during life and it appears to have been born with a small tail.

The color of the dorsal pelage in recently collected specimens of *fuliginosa* is definitely fuliginous with an almost total lack of brown or rufous hairs such as are common in specimens of typical *murina*. Extreme variation of older specimens in the Western Australian Museum resulted from prolonged exposure to light and chemicals. During World War II, the curator was forced to make dry skins of older alcoholic specimens in order to reuse the alcohol. Abnormalities or deviations from the normal pattern of hind foot structure described above occur in at least one foot of a fourth of the *fuliginosa* specimens available for examination during this study. The most common variation is fusion (not by wear) of an apical and proximal granule. This occurs most commonly on the fourth interdigital pad. When fusion occurs, striae may become visible (e.g., WAM M3894) within the fused granules and not, as Troughton (1965) suggested, as striae composed of granules fused by wear. In some specimens, striae with physical surface expression develop, such as occur on the second and fourth pads of both feet of WAM M6878. Because most specimens in the Western Australian Museum are dried skins, it is difficult to be certain that some apparent cases of striae are not artifacts of dehydration; WAM M6878 (a spirit specimen) shows that at least in one instance surface striae are not artifacts of dehydration. Extremes in pedal variation are shown by WAM M1854 and M6998. The right foot of WAM M1854 has a very large striate posthallucal granule, an elongated striate hallucal granule and two enlarged but oval metatarsal granules, an

Antechinus-like situation. The left foot is identical except that the elongate posthallucal granule consists of two elongated striate granules which are themselves incompletely fused. Neither foot is any wider than normal *S. murina* feet and certainly not comparable with the broad feet of species of *Antechinus*. The other unusual specimen, WAM M6998, has an elongate posthallucal granule on the left and right foot, which unlike the corresponding granule in WAM M1854, appears striate without actually being so on the surface of the pad. Other pedal variations include incompletely fused interdigital pad granules (WAM M1564), worn granules with somewhat indistinct boundaries (WAM M5442), lack of clear median granule rows (WAM M1836 and M895), lack of symmetry with fusion on the fourth interdigital pad (WAM M1341) and a slightly enlarged metatarsal granule on the left but not the right foot (WAM M1642). Variation in nipple number in *fuliginosa* is low. Combining observations made here with those of Krefft (1866), 49 out of more than 50 females have eight nipples. The single exception is a specimen (WAM M3393) from Denmark, Western Australia, with six nipples. Gilbert (prior to 1846, see Whittell, 1954, p. 109) noted another female from the south coast that evidently had six nipples.

Extreme variations in entoconid development have been noted elsewhere for specimens of *S. m. fuliginosa* (Archer, 1975); WAM M2472, from Narrikup, Western Australia has large entoconids of a size and position comparable with specimens of *S. macroura*. This specimen has very short premaxillary vacuities (extending only back to the posterior edge of the C¹ alveolus) which is not typical of specimens of *S. murina* but is of specimens of *S. macroura*. The locality data recorded for this specimen are probably incorrect.

CLINAL VARIATION: Morphological variation in *fuliginosa* suggests that clines exist in absolute size, relative tail-vent length, entoconid size, premolar-molar row length, brachycephaly, and other cranial measures. There are discussed below.

UNIQUE SPECIMENS: Specimens within

the range of, and possibly representing extreme cases of variation, in *fuliginosa* include WAM M7495, collected by P. Bridge in 1967 from the doline of Easter Cave near Augusta, Western Australia. The carcass was decomposing and only the skull and skeleton were retained. Although adult, it is smaller in many measurements than any other *S. murina* specimen examined in the present study. Entoconids are absent from the lower molars. This is the normal condition for inland, but not south coastal, individuals of *fuliginosa*. Various attempts have been made, without success, to trap more of these animals. None of the fossil dasyurid specimens from caves in this area represent this type of variant. Some specimens from caves near Augusta, dated at 430 ± 160 years BP (GaK-2949, Archer and Baynes, 1972) show an apparent lack of entoconids but the specimens are worn. Others from the same deposit have tiny to small entoconids.

A specimen, WAM M8222, collected by D. Kitchener in 1971 from Tarin Rock Reserve, approximately 241 km. southeast of Perth is, in several characters, the largest specimen of *S. murina* from Western Australia. Not all the measurements of the small specimen from Easter Cave and the very large specimen from Tarin Rock are the smallest or largest compared with all *fuliginosa* specimens. But Easter Cave is in the south coastal area, where on the average the largest specimens occur, and Tarin Rock is in an inland area where on the average the smallest individuals occur (see above). A specimen, WAM M2595, from Harrismith, Western Australia, registered in 1941, has a skull normal for *S. murina* but a skin normal for *S. macroura*. This may be the result of an error in association of skin and skull. If the locality is correct for the skin, and the skin represents *S. macroura*, this is the southwesternmost occurrence of that species. If, although less likely, the skin comes from the same animal as the skull, the animal was unique.

HABITAT AND REPRODUCTION: Nests are sometimes made of dead Marri leaves (*Eucalyptus calophylla*) (H. Butler, personal commun.) or paperbark (*Melaleuca* sp.)

(WAM M3393, catalogue data) in the center of dead blackboys (*Xanthorrhoea* sp.). Other individuals have been captured from hollow logs (e.g., WAM M7153, catalogue data) sometimes two meters above the ground (e.g., WAM M6998, catalogue data). Two specimens (BM 6.8.354-5) obtained by Shortridge were evidently (label data) trapped in marshy low-lying country among "Ti-Tree" scrub along King River, Albany. Early reports by J. Gilbert (Gould, 1852, text for plate 41, and Whittell, 1954) of capturing four to seven individuals in single nests "which so resembled the nests of small black ants that . . ." he "overlooked hundreds until aboriginals showed them to be nests of the marsupial" are regarded by Calaby (1954) as almost certainly nests of the ant *Iridomyrmex conifer*. Other reports similar to those of Gilbert's have been recorded (Krefft, 1866; F. R. Bradshaw, WAM M676, catalogue data; T. E. Evans and R. Johnstone, WAM M8075, personal commun.). Johnstone and Evans believe the animal they captured had taken over an abandoned nest of ants. In similar situations Johnstone has recovered snakes, lizards, and pigmy possums (*Cercartetus concinnus*). Prince (personal commun.) collected an individual from an abandoned termite mound. These nest sites are found in areas adjacent to swamps (Gilbert, in Whittell, 1954), as well as wet and dry sclerophyll forest. Individuals of *fuliginosa* are likely opportunistic and in areas where blackboys are abundant they make use of natural spaces in decaying stumps, perhaps taking over abandoned nests of pigmy possums (*Cercartetus*). In areas where blackboys are not abundant (and Johnstone and Prince both said blackboys were uncommon in the area in which they recovered animals from insect nests) they may use cavities in abandoned ant or termite nests. In captivity, this form makes nests with tissue paper and as many as three individuals of both sexes nest together. They are more secretive than other species I have observed (including *crassicaudata*, *virginiae*, *ooldea*, and *macroura*) and are the most difficult to maintain in captivity. One male, captured as a subadult, survived a year in captivity. A juvenile female

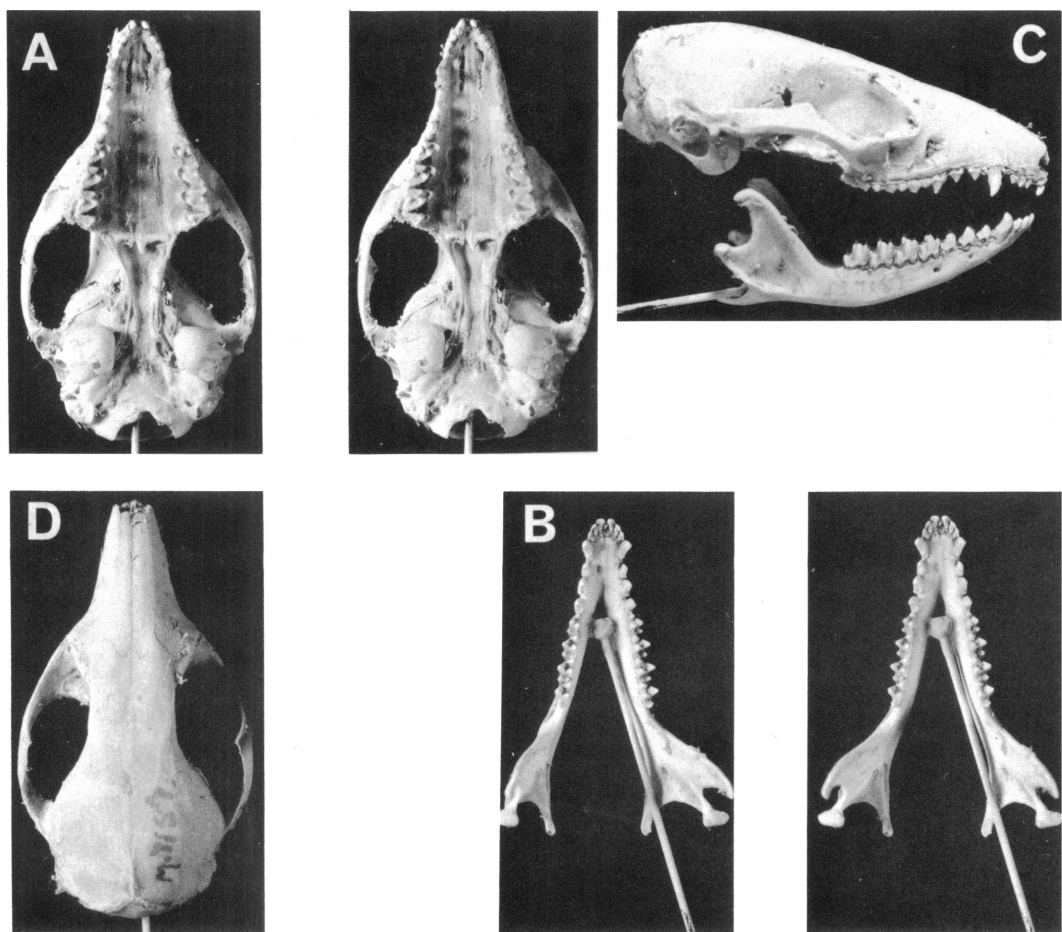


FIG. 17. Holotype of *Sminthopsis murina tatei* Troughton, AM M7157. See table 2 for measurements.

held for two months had several segments of a tapeworm protruding from the cloaca. Foods preferred included insects, cooked chicken, egg, and honey. Small lizards and mammals were ignored. Five out of seven females with young, or evidently lactating, have been caught in October (e.g., WAM M7153), one (WAM M676) may have been collected in November, and the seventh (WAM M6998) was collected in August (from an inland locality about 322 km. north-northeast of Perth). These data suggest that this form normally breeds in September to November.

Sminthopsis murina tatei

GEOGRAPHIC DISTRIBUTION: The range of this form is only northeastern Queensland. The type locality of *Sminthopsis murina tatei* Troughton lies within this range.

RECOGNITION: This form is similar to but lighter than *fuliginosa* and said by Troughton (1965, p. 316) to differ from any geographically intermediate forms in having larger hind feet and longer tails.

REMARKS: A series of 11 specimens (e.g., J16475) from Mt. Molloy, northeastern Queensland, approximately 64 km. north of

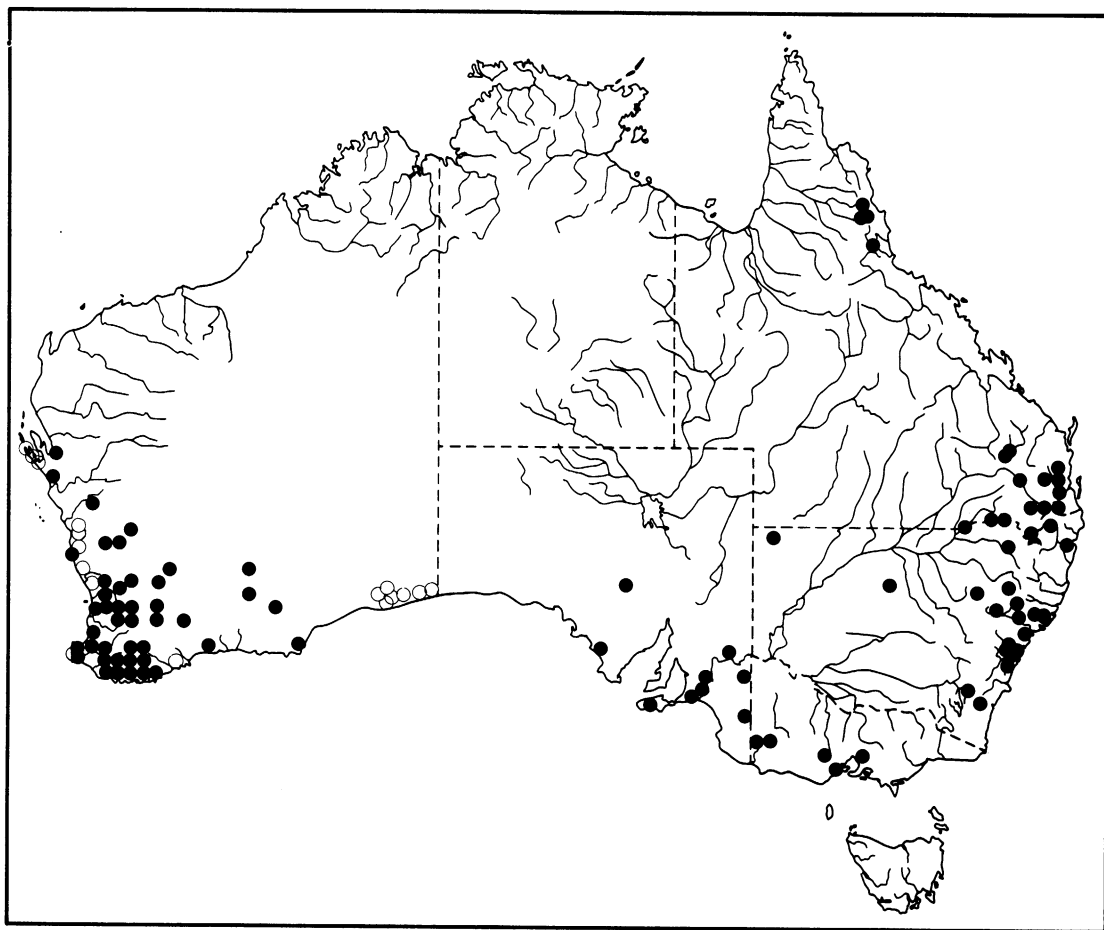


FIG. 18. Geographic distribution of *Sminthopsis murina* (solid dots represent specimens observed, hollow circles represent cave fossils observed).

Tolga) includes individuals that closely resemble specimens mentioned by Tate (1947, pp. 120–121) and described by Troughton (1965, p. 316) as *tatei*. This series provides information about normal variation. No cranial or dental characters are found to consistently separate *tatei* from *fuliginosa*. Ear lengths may differ, those of *tatei* being relatively longer, but this possibility has not been thoroughly examined. Several Mt. Molloy specimens (e.g., J15896) show eight nipples and only one specimen (J21316) from 3.2 km. north of Mt. Molloy may possess less than eight. It has five enlarged nipples but there appear to be suggestions of at least one

other which is undeveloped. Tate (1947) also noted a specimen with six nipples.

REPRODUCTION: In captivity, one Mt. Molloy pair mated on three consecutive nights, the third, fourth, and fifth of October 1974.

THE KANGAROO ISLAND POPULATION

GEOGRAPHIC DISTRIBUTION: These animals are only known from Kangaroo Island, South Australia.

RECOGNITION: They are similar to *fuliginosa* but differ in having a relatively shorter ear length.

REMARKS: Aitken (1972) recorded two specimens from Kangaroo Island which are distinct from adjacent mainland Australian specimens, and are most similar in size, color, and tail length to south coastal Western Australian specimens of *fuliginosa*. Aitken considers they may differ subspecifically from mainland South Australian *S. murina* but possibly be referable to *fuliginosa*.

SMINTHOPSIS MURINA AROUND COASTAL AUSTRALIA

There appear to be three forms of *S. murina* in South Australia which may also be geographically isolated. The first, possibly representing *fuliginosa*, is represented by animals from the Eyre Peninsula (e.g., SAM M3870) and north as far as Wirraminna (e.g., SAM M7537). Color of the midback is not as warm brown as in southeastern Australian animals. The second is the typical form and is recorded from various localities east of the Flinders Range. These animals (e.g., SAM M7536) have a warmer brown midback pelage than those of *fuliginosa*. The third form occurs on Kangaroo Island (e.g., SAM M7936) and is even more fuliginous and less brown than many specimens of *fuliginosa*. There is an apparent tendency for individuals of *fuliginosa* and of those from Kangaroo Island to have tail-vent lengths longer than nose-vent lengths. Although Jones (1923, p. 118) listed three animals from "Adelaide" that have shorter tail than head and body lengths, P. Aitken (*in litt.*) says there are no specimens in the South Australian Museum collections of *S. murina* recorded from Adelaide but they may be among five specimens lacking data. He suggests it is possible that Jones might have listed "Adelaide" as a source rather than a locality. Individuals of the nominate form, east of the Flinders Range, generally have tail-vent lengths shorter than the nose-vent lengths, as do individuals of the typical form in New South Wales and Victoria. The tendency for longer tail-vent lengths is typical of specimens from more inland populations of *fuliginosa* such as those from Hampton Hills. This suggests the possibility that the Flinders Range is a bar-

rier between grayer long-tailed individuals on the west side referable to *fuliginosa*, and browner short-tailed individuals on the east side referable to the nominate form. A specimen Thomas (1888, p. 305) called specimen "h" from South Australia, which has eight nipples and shows "no other differences . . ." from Western Australian specimens, may have come from west of the Flinders. Although their size is larger and their ears are smaller, specimens from Kangaroo Island are most similar to specimens of *fuliginosa*. In turn, specimens from Kangaroo Island and those of *fuliginosa* are similar to those of *tatei*. All three clearly differ from specimens referable to the nominate form. At some time in the past, large fuliginous *S. murina* with eight nipples may have been distributed around southern and eastern Australia, including what is now Kangaroo Island but not Tasmania. Following the isolation of Kangaroo Island from Western Australia and western South Australian populations by Pleistocene changes in sea level, populations in South Australia, Victoria, New South Wales, and southeastern Queensland developed an additional pair of nipples, became less fuliginous and smaller (reasons for their smaller size, as noted above, might be character displacement in relation to *S. leucopus*). At least within Western Australia (and probably South Australia) differentiation also took place in response to rainfall or other climatic gradients that extend inland from coastal areas. I collected specimens (e.g., 72.1.1075) of this species from surface deposits in caves on the Hampton Tableland of the Nullarbor (preliminary notes about the fauna are given in Archer, 1974b). This material has been radiocarbon dated as "modern" (GaK 3471) and suggests that the Nullarbor was until very recently not a barrier to dispersal between South Australian and Western Australian populations of *S. murina*.

FOSSIL RECORDS OF *SMINTHOPSIS MURINA*

Because I have not attempted to allocate fragmentary fossil remains to particular

forms of *S. murina*, these remains are recorded here by geographic area. I have made or checked the Western Australian and South Australian identifications. Unless otherwise noted, only published records are reviewed here. Western Australia: Bremer Bay, 1190 ± 80 yrs. BP (Butler and Merrilees, 1971); Devils Lair, from levels above and below a level dated at $12,175 \pm 275$ yrs. BP (Dortch and Merrilees, 1972); Cave 1 (Au24), dated at 430 ± 160 yrs. BP (Archer and Baynes, 1972); Mammoth Cave, (Archer and Baynes, 1972), dated at greater than 31,500 years BP (Merrilees, 1968) and greater than 37,000 years BP (Lundelius, 1960); Horseshoe Cave (Nullarbor), dated as "modern" (Archer, 1974b). South Australia: Victoria Cave, Pleistocene deposits (Smith, 1972); Fromm's Landing shelter (as *S. cf. S. murina*) (Wakefield, 1964c). Victoria: Wombeyan Caves, Pleistocene deposits (Wakefield, 1972). Victoria Range, uncertain age (Wakefield, 1963c).

Sminthopsis leucopus (Gray)

Phascogale leucopus Gray, 1842.

Antechinus ferruginifrons Gould, 1854.

Podabrus mitchelli Krefft, 1867.

Antechinus leucogenys Higgins and Petterd, 1883.

TYPE SPECIMENS: *Phascogale leucopus* Gray, 1842. Holotype: BM 41.1812 skin and 43.5.315 skull, adult male collected by Leadbeater (according to the specimen label attached to 41.1812). I have examined the holotype. Type locality: Gray (1842, p. 261) "Hab. Australia." Label attached to skin (41.1812) and Thomas (1888) give Tasmania. *Antechinus ferruginifrons* Gould, 1854. Lectotype (selected by Thomas, 1922c, p. 128) BM 54.11.19.3 skin and skull, adult male (according to specimen label of cotype BM 54.11.19.4 and Tate, 1947, p. 121) collected by Mr. Pamplin. Lectotype and cotype have been examined by me. Type locality: Gould (1854, text for plate 36), "apparently of the Sydney district. . . ." Label attached to skin of cotype, "N.S.W." *Podabrus mitchelli* Krefft, 1867. Holotype: No specimen number designated in type description. B. J. Marlow (Curator of Mammals, Australian Mu-

seum) notes (personal commun.) that the holotype is evidently not in the Australian Museum; I have not examined the holotype. Krefft (p. 433) wrote that the specimen had a note attached saying it was obtained by Sir Thomas Mitchell. Type locality: Krefft (1867, p. 434), "Hab. the interior of New South Wales?" *Antechinus leucogenys* Higgins and Petterd, 1883. Holotype: No specimen number designated in type description. Higgins and Petterd (1883) note that a referred specimen (presumably holotype), collected by A. Simpson, is male. I have not examined the holotype. Type locality: Higgins and Petterd (1883, p. 172), "obtained by Mr. A. Simpson, of Launceston, at Ringarooma . . .," Tasmania.

DIAGNOSIS: It differs from the otherwise similar *S. murina* in being generally larger and in having striated elongate apical granules as the normal condition on the interdigital pads of the hind feet; and the premolar row with relatively longer spaces between the premolars. It differs from other species of *Sminthopsis* by the same characters (except the striated apical granules which also occur in *S. longicaudata*) which differentiate *S. murina*.

DESCRIPTION: Tail: The tail-vent length varies, commonly being slightly shorter than, but sometimes slightly longer than the nose-vent length. The tail is invariably thin.

HIND FOOT: The hind feet normally have interdigital pads two, three, and four with striated elongate apical granules, and possess conspicuous enlarged hallucal granules. The terminal pads of the toes, although smooth, often appear striated. Otherwise the feet are as in *S. murina*. Uncommon variations are described in detail below. Thomas (1888, plate 23, fig. 6) and Troughton (1965, fig. 4) illustrated feet of Tasmanian specimens.

PELAGE MARKINGS: As in *S. murina*, except that commonly the pelage of the cheeks, the area of face surrounding the eye, and sometimes (the lectotype of *ferruginifrons*) the crown of the head appears to be suffused with russet hairs.

NIPPLE NUMBER: Ten is normal but seven, eight, and nine have been recorded.

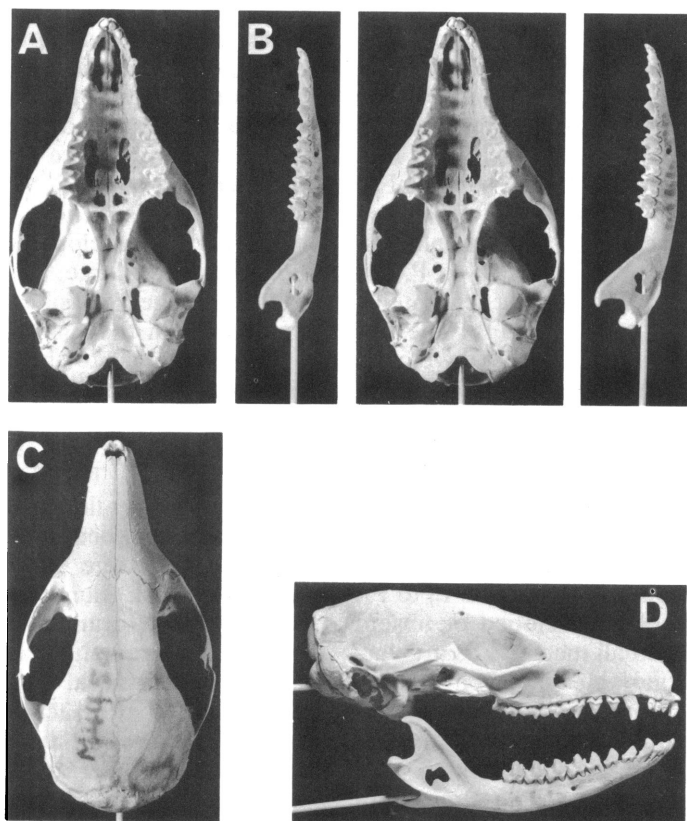


FIG. 19. *Sminthopsis leucopus*. A–D, AM M4459, adult, West Sister Island, Bass Strait. A–D, $\times 2$.

DENTITION: The first upper incisor is taller-crowned and separated by a diastema from I^2 . The crown length and height of I^2 to I^4 are subequal. All the upper incisors lack posterior lobes or buccal cingula. The fourth upper incisor is separated from C^1 by a diastema. The slender, caniniform C^1 is taller than any premolar, its height being increased by the normally over-erupted root which elevates the crown well-above the alveolar rim. Buccal and lingual cingula are present on C^1 but there are no clear posterior or anterior cingular cusps. Diastemata separate C^1 from P^1 and P^1 from P^3 . All premolars are narrow and elongate. P^1 crown is just shorter in length and height than P^3 which is conspicuously shorter than P^4 . Buccal cingula are present on P^1 to P^4 , but lingual cingula

are only variably present on P^1 to P^3 and poorly-developed on P^4 . Small anterior and posterior cingular cusps occur on P^1 to P^4 . The posterior crest of P^4 is concave buccally and the posterior root is much larger than the anterior root. The anterior cingulum is incomplete on M^3 but almost complete on M^1 and M^2 . Styler cusp A (or parastyle) is reasonably distinct on M^1 and M^2 but not on M^3 and M^4 , and styler cusp E is poorly developed but sometimes present on M^1 to M^3 . The metacrista of M^3 is just shorter than or subequal to the crown length of the same tooth. In one specimen (AM M4459), M^4 is abnormally well-developed, possessing small styler cusps C and D, a well-developed crest posterior to the paracone, but no trace of a metacone. The first lower incisor is just tall-

er-crowned than I_2 . The third lower incisor is the shortest lower incisor in height but the longest in crown length, and there is a moderately well-developed posterior lobe on the I_3 crown (which is only just shorter than the same structure in *S. granulipes*). The first lower canine is premolariform, subequal in crown height to P_4 , with poorly developed lingual and buccal cingula, and a small posterior cingular cusp. The teeth C_1 to P_4 are narrow and elongate. Diastemata separate C_1 from P_1 , P_1 from P_3 , and P_3 from P_4 . The first two lower premolars have poorly developed anterior but well-developed posterior cingular cusps. The fourth lower premolar P_4 has a poorly developed anterior but well-developed posterior cingular cusp. All lower premolars have well-developed buccal but poorly developed lingual cingula, and are subequal in crown length although they increase slightly in crown height from P_1 to P_4 . Entoconids are poorly developed or absent on M_1 to M_3 . Very small metastylids are variably present, and variable buccal cingula are poorly developed being generally absent below the protoconid. Parastylids are variably developed on M_3 and M_4 . The talonid is wider than the trigonid on M_1 , sometimes subequal on M_2 , and narrower than the trigonid on M_3 and M_4 .

SKULL AND DENTARY: The following description is based largely on AM M4459 from West Sister Island, Bass Strait. The skull is not brachycephalic and the rostrum is not markedly deep. Only a very slight medial concavity occurs between the anterodorsal corners of each frontal. The interorbital area is very wide with a trace (probably variable) of postorbital processes. The palate is moderately well-fenestrated. The premaxillary vacuity generally extends only as far back as the level of the middle or posterior end of the P^1 alveolus, but may (e.g., D 536) extend as far back as the level of the anterior edge of the P^3 alveolus. The lacrimal canal (with one or two foramina) opens onto the anterior rim of the orbit. There is no development of a sagittal crest. The nuchal crest is low. Lacrimals have not been observed to develop posterodorsal spines. The alisphenoid tympanic wing is poorly developed and has a

very limited contact with the periotic tympanic wing. The ectotympanic is broadly exposed. The periotic tympanic wing is very small and the periotic hypotympanic sinus is tubular. The squamosal epitympanic sinus is small. The transverse foramen is large. The foramen rotundum is variably floored by a shelf of the alisphenoid. The entocarotid canal is poorly developed. The foramen pseudovale is very large. In one specimen (AM M4459) on the right side, a thin bony process extends from the tympanic wing of the alisphenoid almost to the basisphenoid posterior to the transverse canal foramen, thereby almost enclosing a secondary foramen ovale canal such as occurs in some *Sarcophilus* and *Dasyurus*. The foramen rotundum is large and poorly floored ventrally by the alisphenoid. Between the foramen rotundum and the very large sphenorbital fissure, are small foramina (number variable). The posterior lacerate foramen is very large. The stylomastoid foramen lacks any contribution from the squamosal and is variably accompanied by a small accessory foramen. The condylar (including hypoglossal foramen) is variable in number and size. The dentary is relatively shallow below the teeth. The angular process is slender at the tip but widens rapidly toward the body of the dentary. The masseteric fossa is moderately large.

DISCUSSION: Troughton (1965, p. 308) suggested that Thomas (1888, pl. 23) illustrated as *S. leucopus*, the foot of a Cape York specimen of *S. virginiae*. W. D. L. Ride (*in litt.* June 5, 1973) compared specimens in the collections of the British Museum (Nat. Hist.) with plate 23, figure 6 of Thomas's (1888) *Catalogue* and is satisfied that the figure represents the hindfoot of specimen BM 52.1.15.4, a male *S. leucopus* in spirit from Tasmania presented by R. Gunn. The specimen is accompanied by a label bearing measurements and a note that it is 'e' of the *Catalogue* and that the pads are transversely striated. It also bears the words 'Sole Ear.' This label appears to be in the handwriting of Thomas. Ride interprets the latter word to mean that this is the specimen figured in Thomas's plate 23, figures 5 and 6; and with which figured hindfoot it

agrees. Another specimen in the collection, BM 1939.3244, collected in Cape York, north Queensland on June 23, 1898 by A. S. Meek (Rothchild Bequest), bears a note in Troughton's hand "Apparently juvenile of *Sm. lumholtzi* note sole pads E. Le G.T." But this specimen cannot be that figured by Thomas because it was collected and accessed after the *Catalogue* was written. Troughton (1965, p. 308) wrote that a striated foot pad condition may be produced by "wearing down of the apical rows of enlarged granules. . . ." which "tends to produce smooth oblong apical areas with the grooves between the worn granules appearing as transverse striations" thus producing the *leucopus* condition in an *S. murina* foot. In the present study, I have examined many specimens with worn feet and the striated condition commonly seen in *S. leucopus* could not have been produced in this way. Further, it is clear from examination of juvenile *S. leucopus* (e.g., AM M1837, D525, D523, D521) that the striated enlarged apical granules clearly can not be simply an artifact of wear because the striae are clear in juveniles.

DESCRIBED FORMS OF *SMINTHOPSIS LEUCOPUS*: As in the case of *S. murina*, several names have been applied to specimens (the types) that are here all referred to *S. leucopus*. I have not attempted to determine the statistical validity of subspecies. However, it is useful to use formerly proposed names to qualify forms of the species from particular geographic localities.

Sminthopsis leucopus leucopus

DISTRIBUTION: The nominate form occurs in Tasmania and the Bass Strait Islands. Type specimens from within this range are the holotypes of *Phascogale leucopus* Gray and *Antechinus leucogenys* Higgins and Peterd.

RECOGNITION: The nominate form may be distinguished from *S. l. ferruginifrons* by its generally smaller size, and shorter pre-molar row length. Too few specimens of the nominate form have been examined to notice any consistent differences in color from *ferruginifrons*.

REMARKS: In describing *ferruginifrons*, Gould (1854) made no reference to the nominate form. Krefft (1867) suggested that *ferruginifrons* is a variety of *Antechinus flavipes*. It was not until 1888 when Thomas placed *ferruginifrons* in synonymy with *S. leucopus* that the relationship of the two forms became clear.

PEDAL VARIATIONS: Pedal variations in the nominate form include PC568 (illustrated by Troughton 1965, figure 4) which has the apical granule of the third pad of the left foot poorly developed and in its place occurs a row of median granules. On the same foot is a very large elongate striated posthallucal granule clearly comparable with a similar granule on a specimen of *S. murina fuliginosa* (WAM M1854) cited above. On the right foot of PC568, the large posthallucal granule is absent but in its place are two enlarged, separate oval granules. Another Tasmanian specimen, C6343, has the third pad of the left foot minute, and between the second and fourth pads there is a tiny raised hump, but no pad. On the right foot of the same specimen the third pad is normal.

HABITAT: Green (1972, p. 28) noted that in Tasmania "The distribution and diversity of habitat in which *S. leucopus* has been collected suggests that it has little or no preference." Recorded habitats included subalpine rainforest, the edge of a small brackish lagoon near the coast, heavy dry sclerophyll forest, and coastal heathlands. Capture sites included a hole in rotting timber; a site beneath a pile of bulldozed logs and rubbish; a rough nest made of shredded stringy bark in a narrow space in the middle of firewood stacked in the bush; a site beneath rotting timber in beech rainforest; and a nest composed of stringy bark and leaves behind the lining of an abandoned bus. Sharland (1961) noted that the species in Tasmania makes nests in walls of unoccupied huts, in holes among boxes and papers, and even recorded (p. 61) a "substantial nest of shredded bark some 45 feet up the side of a gum tree . . . Bushmen sometimes find nests on the tops of tree ferns (of the *Dicksonia* genus) which are believed to belong to this species."

CONDITION OF TYPE SPECIMENS: The

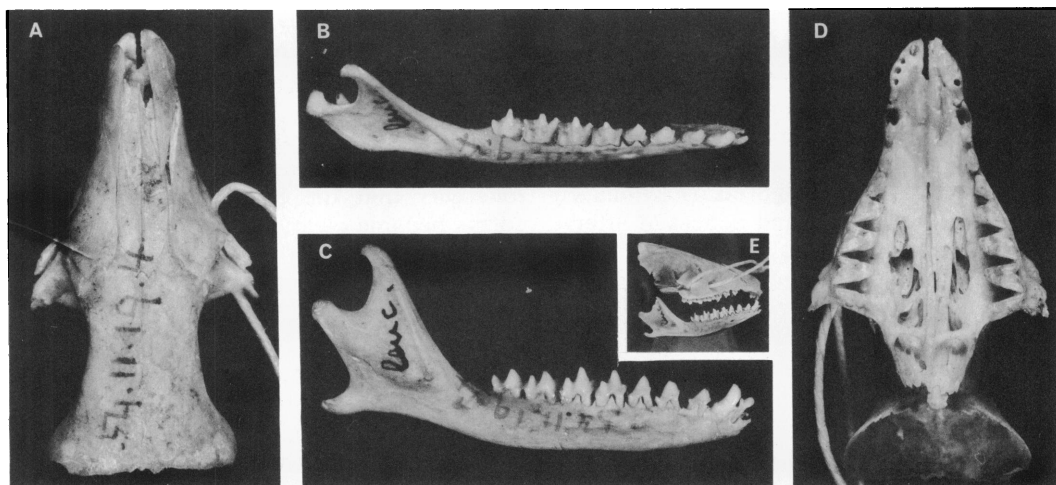


FIG. 20. Cotype of *Antechinus ferruginifrons* Gould (= *Sminthopsis leucopus ferruginifrons*), BM54.11.19.4. See text for remarks about measurements.

skull of the holotype consists of fragments glued to a board. Many of its teeth are loose or missing. The skin is badly damaged, particularly on the ventral side, but the hind feet preserve enough of the interdigital pads to show that the enlarged apical granules are clearly striated. The right and left hind feet are damaged by the corrosion of a wire rod. The left foot has a small hallucal granule. This area on the right foot is destroyed. Compared with the lectotype of *ferruginifrons*, the holotype of *leucopus* has a slightly darker dorsal pelage. The flanks of the two specimens are similar. The face of the holotype of *leucopus* has some rufous hairs in front of the forehead above and behind the eyes but this color on the face is not as conspicuous as it is in the type of *A. ferruginifrons*. I have not examined the type specimen of *Antechinus leucogenys*. However, Higgins and Petterd (1883, p. 172) stated, "hind feet with numerous transversely striated tubercles . . ." and "In its measurements this species approaches to *Albipes* and *Murina*, but differs from both by its exceedingly slender form, the colour of its fur, and the white chin, which is so especially characteristic in this species. . . . The soles of hind feet thickly covered with small tubercles. This species therefore belongs to Gould's

subgenus *Podabrus*." These remarks leave no doubt that this form is referable to the typical form of *Sminthopsis leucopus*.

Sminthopsis leucopus ferruginifrons

DISTRIBUTION: *Ferruginifrons* has only been recorded from southern Victoria and southeastern New South Wales. The type localities of *Antechinus ferruginifrons* Gould and *Podabrus mitchelli* Krefft occur within this range.

RECOGNITION: *Ferruginifrons* may be distinguished from the nominate form by its generally larger size and longer premolar row.

PEDAL VARIATIONS: A Victorian specimen, C925 from Beech Forest, has the second, third, and fourth interdigital pads all bearing median rows of granules, a condition more typical of the feet of *S. murina*. There is some suggestion that in places the median granules are covered or joined by an overlying skin flap. This appears translucent and enables underlying granules to be seen. Another peculiarity of this specimen is its relatively very long tail (92.4 mm., while nose-vent length is 78.3). However, C925 has a C^1-P^4/M^{1-3} ratio of 1.11, indicating a relatively long premolar row, a condition com-

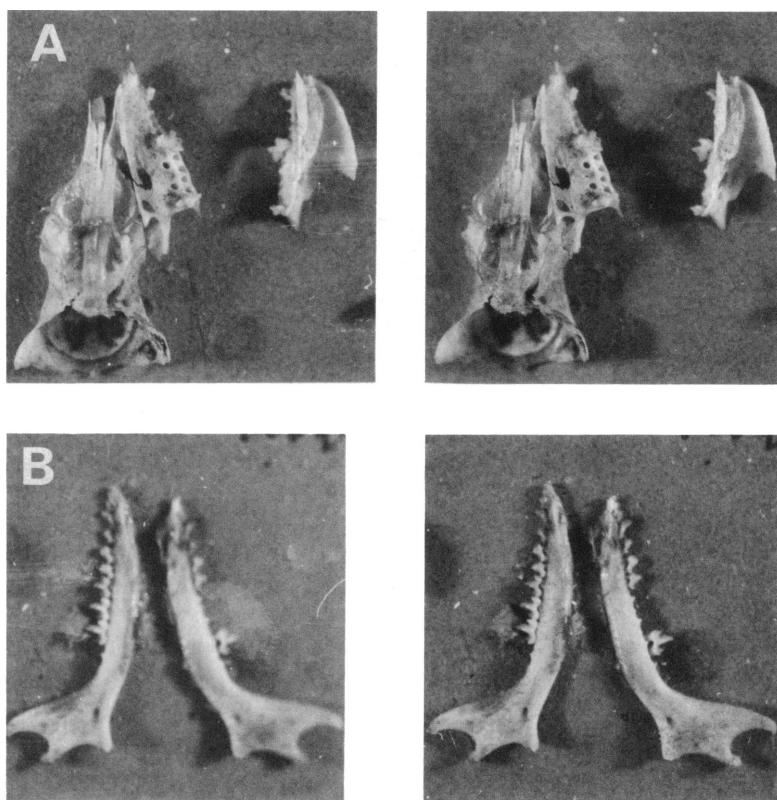


FIG. 21. Holotype of *Phascogale leucopus* Gray (= *Sminthopsis leucopus leucopus*), BM43.5.31.5. See table 1 for measurements.

parable with other Victorian *leucopus* rather than specimens of Victorian *murina*. Other pedal variations are found in three of the six specimens from Waratah Bay, Victoria. Two (D526 and D524) have a second and third interdigital pad that bears a median row of granules rather than an elongate striated apical granule. In both cases however, the fourth pad has a normal (although small in D526) apical granule typical of *S. leucopus*. Both specimens are juveniles collected by F. Baum in January 1964, in the same month and area as two others (D525 and D523) that have feet characteristic of normal *S. leucopus*. Because the specimens are juveniles, the length of the premolar row is not comparable with that of adults. Another juvenile

specimen (D458) from the same locality, but collected a year previously by Mrs. J. Hall, has the right foot normal for *S. leucopus* and the left foot as in D524. Mean M^{1-3} and M_{1-3} measurements for all of these Waratah specimens are respectively, 4.8 and 4.7 and are in accord with Victorian *leucopus*, but not Victorian *murina*. Other pedal variations in Victorian specimens include: incompletely fused median granules present on the third interdigital pad (D804); incompletely fused median granules present on the second interdigital pad (D718); dissimilar left and right feet (D458); a fused apical and lateral granule on the fourth interdigital pad (D521); an elongated hallucal granule (D458); an enlarged but round post-hallucal granule (D804), and

a slightly enlarged metatarsal granule (D7366).

HABITAT: Brazenor (1950) wrote that this species "is now confined to the southwestern part of the State (Victoria), where it lives in scrub, sometimes amongst the roots of small bushes." Ride (1970) claims *S. leucopus* (not distinguishing *ferruginifrons*) lives in sclerophyll forest. Wakefield (1972) wrote that it inhabits dry sclerophyll forest, including areas near wet forest, with a mean annual rainfall between 762 and 1651 mm. Hope and Hope (1972) noted this species caught in pollen traps at Wilson's Promontory.

REPRODUCTION IN ALL *SMINTHOPSIS LEUCOPUS*: In this study, 16 female *leucopus* specimens (Tasmanian and Victorian), have been examined. One (C8928) collected August 20, 1937, from Beech Forest, Victoria, has a developed pouch with unstained pouch hairs but prominent nipples. Another (A868) collected December 9, 1970 from Roland, Tasmania, had eight juveniles. Three specimens (D526, D524 and D523) collected on January 1 and 23, 1964 from Waratah Bay, Victoria, have undeveloped pouch areas typical of juveniles. Two (D734 and D735) collected January 24, 1968, from Heathmore, Victoria have well-developed, stained pouches with enlarged nipples. One (C1024) collected May 29, 1946 from Portland, Victoria, has a well-developed pouch with long stained hairs. Green (1972, p. 34) noted that a specimen in the Queen Victoria Museum, collected October 11, 1970 and kept in captivity for ten days, was found after death to be carrying "a full couplement of eight pouched young of a crown/rump length of 12 mm." These records suggest *leucopus* breeds around August to September.

CONDITION OF TYPE SPECIMENS: The skull and the lectotype (BM 54.11.19.3) is missing the braincase and LI^2 , and the dentaries lack the tips of the angular processes. The skull of the cotype (BM 54.11.19.4) is damaged, having become generally disarticulated. The rear of the left dentary is damaged. Repairs to the skull appear to have been made with some resinous substances and were not successful in restoring the orig-

inal shape. R and LC^1 , LI^3 , RI^{1-4} , RI_{1-2} and LI_{1-3} are missing. $C^1-P^4/(M^{1-3})$ ratio is 1.17 which is also similar to Victorian *S. leucopus*. The skin is faded but in good condition. Gould (1854) gave measurements for *ferruginifrons* but it is not apparent which of the two type specimens the measurements represent. Nose-vent length of the cotype, measured on the dry skin, is 113 mm. and tail-vent length is 76 mm. These measurements, although made on a dry skin, suggest the tail is considerably shorter than the head and body. The hind feet of the cotype show clear elongate striated apical granules on the second, third and fourth interdigital pads, and an elongate striated hallucal granule.

FOSSIL RECORDS OF *SMINTHOPSIS LEUCOPUS*: Quaternary Victorian records of *S. leucopus* are given by Wakefield as follows: Fern Cave (1963b), but noted (p. 40) the "material possibly includes also some *Sminthopsis murina*"; *Sminthopsis* cf. *leucopus* from Victoria Range (1963c), but noted this record may represent *S. murina*; Byaduk and Natural Bridge; Bushfield; and Pyramids Cave deposits (1964a, b, 1967a and 1972); recent and not Pleistocene layers of McEacherns Cave (1967b).

Sminthopsis ooldea Troughton

Sminthopsis murina ooldea Troughton, 1965.

Sminthopsis ooldea: Archer, (1975b).

TYPE SPECIMEN: *Sminthopsis murina ooldea* Troughton, 1965. Holotype: AM M7502, young male, carcase in spirit, and skull, collected by H. E. Green. I have examined the holotype. Type locality: Troughton (1965, p. 316), "Ooldea on the Trans-Continental Railway, South Australia."

DIAGNOSIS: Differs from all other species of *Sminthopsis* in being smaller, in having the paracones reduced on the upper molars, and in P_4 being considerably smaller-crowned than P_3 . It differs from the otherwise similar *S. murina* and *S. leucopus* in having a variably incrassated tail, relatively wider premolars, and relatively wide talonids on the lower molars. It differs from *S. granulipes* in being dark, in having the tail-vent length longer than the nose-vent length, a poorly

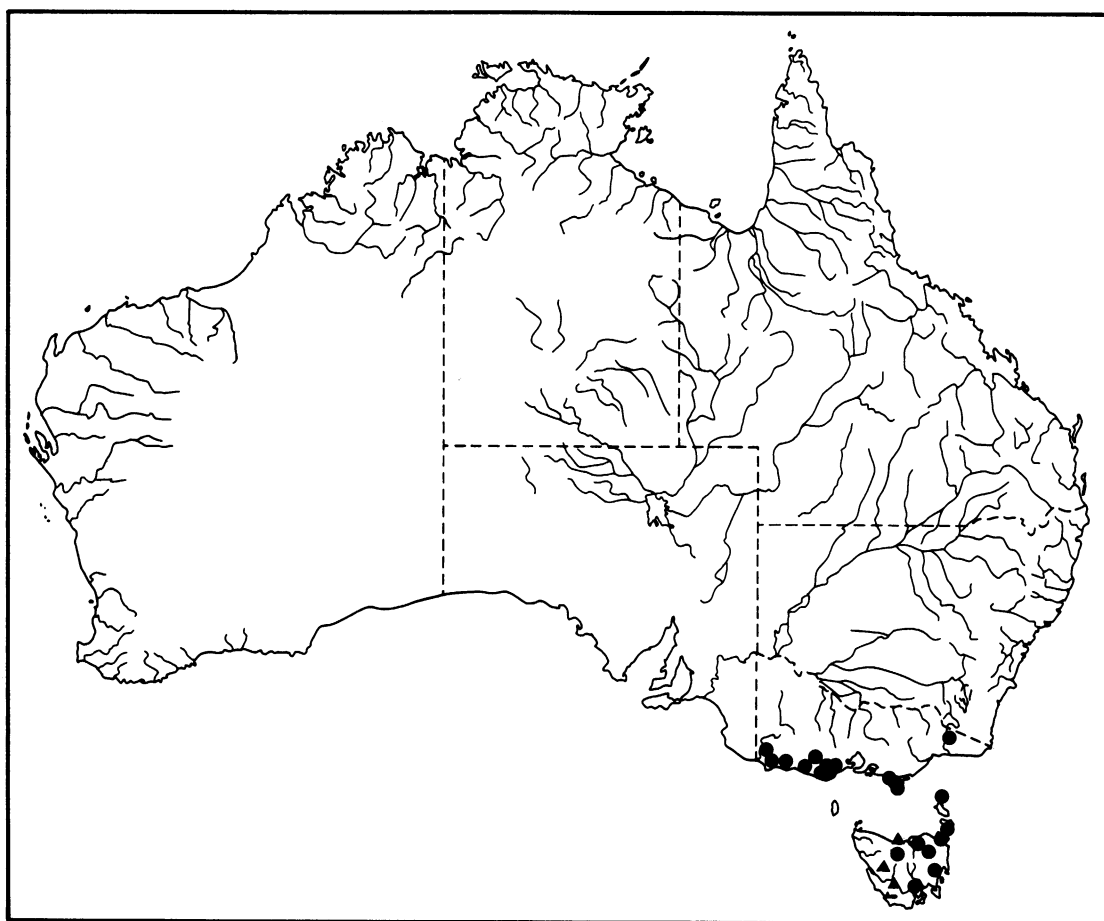


FIG. 22. Geographic distribution of *Sminthopsis leucopus*. Solid dots represent modern specimens examined.

developed posterior lobe on I_3 , wide-crowned premolars, relatively wide and short molars, non-granular terminal pads on the toes, naked interdigital pads, and a medial row of granules on each interdigital pad. It differs from *S. hirtipes* in having non-granular and hairless terminal pads on the toes, hairless interdigital pads on the hind feet, no head stripe, wide premolars, and a relatively slight alisphenoid tympanic wing enlargement. It differs from *S. crassicaudata* in being dark, in having the tail-vent length longer than the nose-vent length, no dark head patch, no entoconids, wide premolars and premaxillary vacuities that do not extend posterior to

a point level with the anterior half of P^1 . It differs from *S. macroura*, *S. virginiae*, and *S. douglasi* in lacking a head stripe; having premolariform canines; lacking entoconids; and lacking conspicuously enlarged oval apical granules on the interdigital pads. It differs from *S. longicaudata* in having the tail-vent length less than twice the nose-vent length, a relatively smaller alisphenoid tympanic wing, premaxillary vacuities that do not extend posterior to a point level with the middle of P^1 , and hind foot pads that lack striated granules. It differs from *S. butleri* in being dark, lacking a dark head stripe or patch, lacking enlarged oval apical granules on the

interdigital pads of the hind feet, having premolariform canines, and in that the premaxillary vacuities do not extend posterior to a point level with the middle of P^1 . It differs from *S. psammophila* in having premolariform canines, wide-crowned premolars, premaxillary vacuities that do not extend posterior to a point level with the middle of P^1 , a tail that lacks a crest of hair, and smooth terminal pads on the toes of the hind feet.

DESCRIPTION: Tail: The tail-vent length invariably exceeds the nose-vent length. The tails of most museum specimens are thin, but all are evidently capable of incrassation (Aslin, 1977, and personal commun.), such as occurs in WAM M5888.

HIND FOOT: The interdigital pads are fused at their common base and each exhibits a median row of slightly enlarged granules. Commonly, there is a single enlarged granule in the position of the hallucal pad and a very slightly enlarged granule in the position of the metatarsal pad (e.g., WAM M5888). The feet are otherwise as in *S. murina*. Troughton (1965, fig. 5C) illustrates a hind foot of the holotype.

PELAGE MARKINGS: Almost no distinguishing markings are present other than a variably developed slightly dark patch between the eyes and the nose. The color of the dorsal pelage varies from Ridgway (1912) Sepia (SAM M7532, dry skin) to Chaetura Black (WAM M8077, spirit specimen).

NIPPLE NUMBER: Eight.

DENTITION: The upper incisors are subrounded in occlusal outline, I^2 being almost round (e.g., WAM M8079), I^4 being only just longer-crowned than I^2 but clearly longer-crowned than I^3 , and I^1 markedly taller-crowned than I^2 . There are normally no posterior lobes on I^1 to I^4 , although rarely (WAM M5782) a tiny posterior cingular cusp may develop on I^4 . A diastema separates I^1 from I^2 , and I^4 from C^1 . A very small depression occurs in the short diastema between I^4 and C^1 and corresponds with the tip of C_1 . C^1 is small, being subequal to or only just exceeding P^4 in height. In lateral view, I^1 , C^1 and P^4 are roughly subequal in height and separated by similar intervals of shorter teeth that are subequal to each other in

height. The first upper canine is subequal to P^4 in height but shorter in length, and its functional height is about twice that of P^1 . The upper premolars are wide but much less so than the lower premolars. No premolar or canine is over-erupted (the condition that develops when the cingulum occurs well above the alveolar level). Both roots of P^4 are subequal and the crown is not markedly tipped posteriorly. P^4 crown height is approximately twice that of P^1 , whereas P^3 crown height is only just larger than that of P^1 . A buccal cingulum is only just visible on C^1 , but better developed on P^1 to P^4 . The lingual cingulum is incomplete on C^1 and P^4 , but complete on P^1 to P^3 . Rarely, the anterobuccal cingulum on P^1 exhibits small swellings such as occur in some specimens of species of *Planigale* and more commonly *Phascogale*. Very small anterior and posterior cingular cusps occur on C^1 to P^4 . No lingual anterior or even posterior cingula occur on M^1 to M^4 . In some specimens (e.g., WAM M5782) the preprotocrista of M^4 extends buccally below the base of the paracone. The paracone of M^1 to M^3 is reduced and approximated to the metacone. Styler cusp A is indistinct on M^2 to M^4 and only just distinct on M^1 of some specimens either as the buccal end of the anterobuccal cingulum (WAM M5782) or as a tiny discrete cusp (WAM M8079). Styler cusp C is rarely developed but sometimes present on M^3 (WAM M8079). Styler cusp E is very small but present on M^1 to M^3 . Marked swellings occur on the crown below the position of the poorly differentiated to absent protoconule. The metacrista of M^3 is subequal to the length of M^3 . I_1 is longer and taller-crowned than the subequal I_2 and I_3 . No clear posterior cusp occurs on I_3 . The C_1 is premolariform, subequal in crown height to P_3 and taller than P_1 , P_4 and I_1 to I_3 . A lingual cingulum on C_1 is well developed but a buccal cingulum is poorly developed or incomplete. The first lower canine is wider than any premolar. The posterobuccal cingulum on C_1 acts with the posterobuccal wall of C_1 to thegose the tip of C^1 . All lower premolars are markedly broad and crowded anteroposteriorly. The first lower premolar is the widest premolar

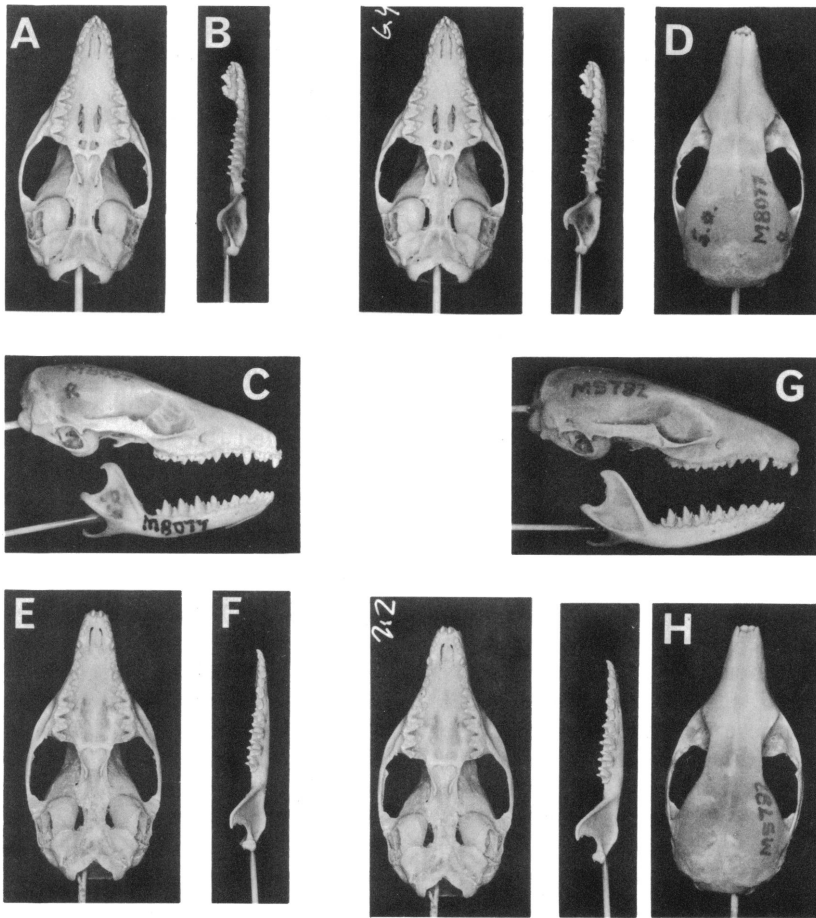


FIG. 23. *Sminthopsis ooldea*. A–D, WAM M8077, adult, Maralinga, South Australia. E–H, WAM M5782, adult, Mt. Boreas, Western Australia. A–H, $\times 2$.

relative to length, having a subrounded occlusal outline. The fourth lower premolar is the narrowest relative to length. Lingual and buccal cingula and well-developed posterior but no anterior cingular cusps occur on P_1 to P_4 . The fourth lower premolar crown height is functionally lower than P_3 and the trigonid of M_1 , although the crown of P_4 is actually only just shorter than P_3 . This functional difference results because P_4 is normally less erupted than P_3 (e.g., WAM M8079). Entoconids are tiny (WAM M8077) or virtually absent (WAM M8079). However, even in specimens with virtually absent entoconids,

a minuscule rise may be detected along the lingual margin of the talonid. In specimens with tiny entoconids, they are larger on M_1 than M_2 to M_4 . In some specimens (WAM M8077) an even tinier metastylid occurs on M_1 . A buccal cingulum is absent, and a parastylid is well developed on M_1 to M_4 . The talonids are reduced and compressed antero-posteriorly on M_1 to M_3 and compressed transversely on M_1 to M_4 . The talonid of M_1 is wider than the trigonid but the remaining talonids are narrower than the trigonids. The ascending ramus of the dentary is wide and the angular process is long and slender.

SKULL AND DENTARY: The skull is not brachycephalic, and the rostrum is shallow vertically. The anterodorsal corner of each frontal is mildly swollen producing a shallow depression in the midline of the skull. The nasals expand just slightly toward the posterior ends. The interorbital area is not narrow and lacks postorbital processes. Premaxillary vacuities sometimes (WAM M8079) extend posteriorly to the level of the middle of the alveolus of P¹. Normally, this vacuity does not extend posterior to the anterior end of P¹ or posterior end of C¹ alveolus. Interdental fenestrae are rare between the molars. The lacrimals never develop posterodorsal spines, although rarely (WAM M8079) a very small crest may develop. The lacrimal canals (one or two on each side) occur on the anterior rim of the orbit. A sagittal crest rarely develops or, if it does, is very low. The normally present nuchal crest is low and extends from the top of the supraoccipital to the posterior edge of the squamosal epitympanic sinus. The alisphenoid tympanic wing is poorly developed and makes only a small contact with the periotic tympanic wing. The ectotympanic is broadly exposed. A poorly developed periotic tympanic wing floors the tubular periotic hypotympanic sinus. The paroccipital hypotympanic sinus is very small. The transverse foramen is small but always present. The foramen rotundum varies in morphology and sometimes has a well-developed ventral alisphenoid floor which obscures direct ventral view into the endocranium (both sides of WAM M8077 and the right side of WAM M8079). On the left side of WAM M8079 a fissure extends anteriorly from the foramen pseudovale, passes anteriorly to the transverse canal foramen, and almost reaches the foramen rotundum. The entocarotid canal is poorly developed and the endocarotid foramen permits direct ventral view into the endocranium. The elongate foramen pseudovale, posterior lacerate foramen, and foramen for the internal jugular canal are well developed. There are two very small condylar (and or hypoglossal) foramina, or rarely (WAM M8079), several tiny foramina present in this position. The dentary

is not markedly deep in adults, with the angular process slender, elongate, not markedly broad at the base, and the masseteric fossa very broad.

DISCUSSION: *Sminthopsis murina* was formerly believed to exist in arid inland as well as coastal areas of Australia. Spencer (1896a, p. 32) recorded *S. murina* (presumably the nominate form) from Oodnadatta and Alice Springs and in addition named *S. murina constricta* on the basis of a specimen found at Oodnadatta. Dixon (1970, p. 107) suggested that the holotype of *constricta* might be C6920, a male from Oodnadatta, South Australia, although Spencer (1896a, p. 32) identified the specimen he described as a female. I have examined specimen C6920 and identified it as *S. crassicaudata*. Specimens Spencer referred to "*S. murina*" (the typical form) are presumed missing. A faded alcoholic specimen (C6921) of *S. ooldea* in the National Museum of Victoria, donated by Spencer in 1916, was collected at Charlotte Waters and bears the identification "*Sminthopsis murina*." Spencer (1896a, p. 32) stated that Mr. Byrne who "has collected a very large number of marsupials, and is thoroughly acquainted with those existing in the Charlotte Waters district . . ." had not collected *S. murina* at Charlotte Waters. I conclude that either Spencer obtained C6921 after 1896 or he did not identify it as "*Sminthopsis murina*." The tail of C6921 is thin and could not have been considered by Spencer to represent *S. murina constricta*. In default of specimens labeled "*Sminthopsis murina*" obtained by Spencer or Byrne from Alice Springs or Oodnadatta, I suggest here that specimens described by Spencer as "*Sminthopsis murina*" (the typical form) probably represent *Sminthopsis ooldea*. It is also possible that *Sminthopsis murina constricta* could be conspecific with *S. ooldea* in which case the name *constricta* would have priority over the name *ooldea*. Body measurements given by Spencer (1896a, p. 33), the evidently distinct incrassated tail of the type, and comments including "the general colouration is closely similar to that of *S. murina*" do not prohibit comparison with

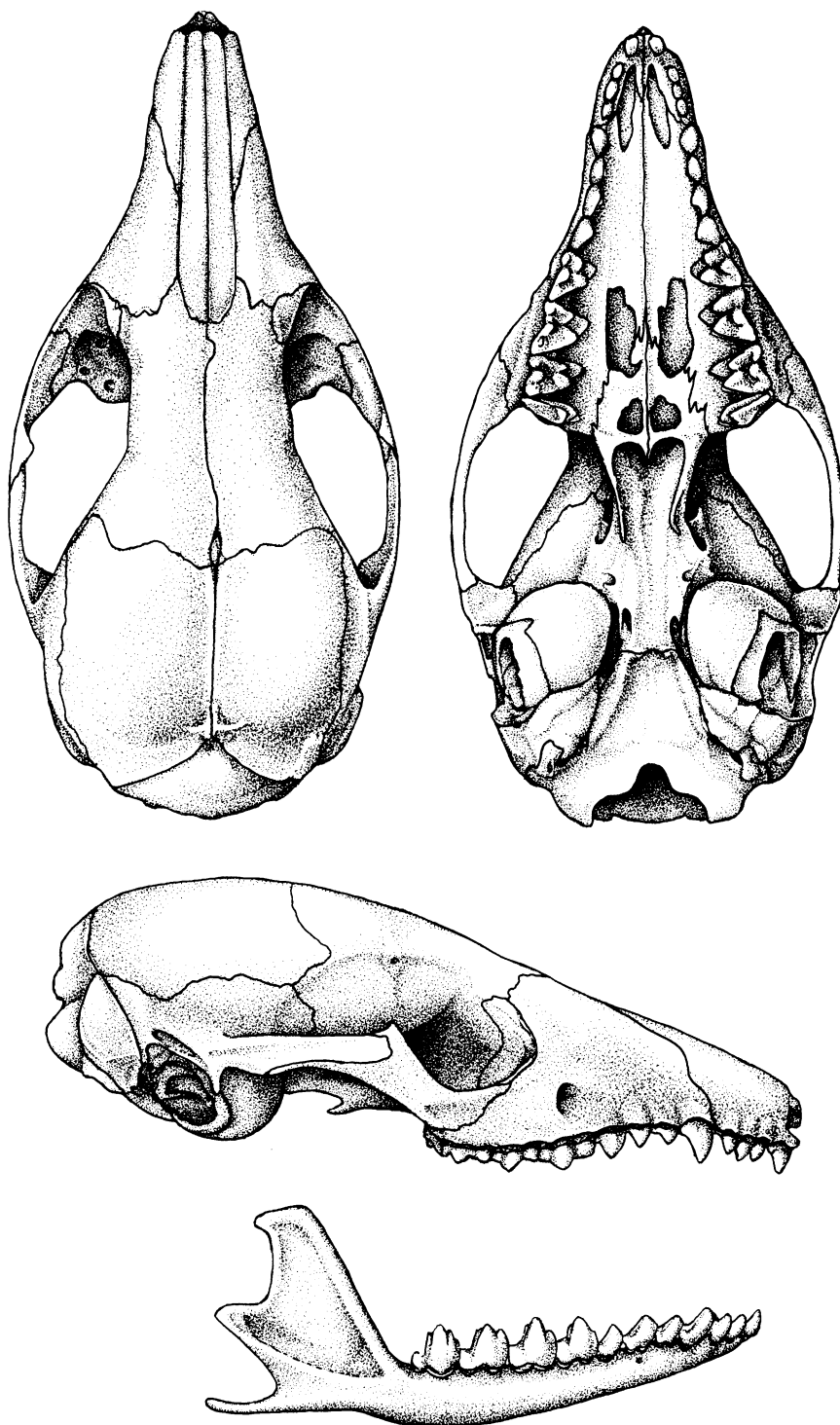


FIG. 24. *Sminthopsis ooldea*, drawings done from photographs, skull and dentary of WAM M8079, adult, near Mt. Olga, Northern Territory. Approx. $\times 4.6$.

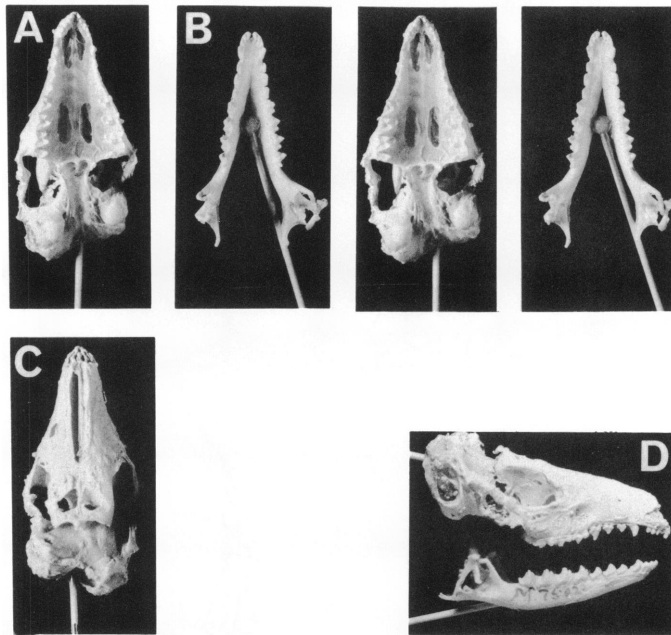


FIG. 25. Holotype of *Smynthopsis ooldea* Troughton, AM M7502. See table 2 for measurements.

S. ooldea. In view of the instability which the name *constricta* introduces into taxonomy, I have applied to the International Commission for Zoological Nomenclature for its suppression (Archer, 1976).

HABITAT AND REPRODUCTION: Very little is known about *S. ooldea*. Specimen WAM M5782, was obtained by G. E. J. Hitchen on July 23, 1963, in a hollow log in an area of red sandy soil with spinifex and mulga (catalogue data); and WAM M8078 obtained January 31, 1967, was found dead near a pool in open mulga country (catalogue data). In the Warburton Range area a lactating female (WAM M6361) was obtained October 28, 1964, and a young female (WAM M5888) was obtained in August 1963. Specimens collected from other areas include a juvenile male (WAM M8078) in January; a young adult male (WAM M8077) in May; a sexually mature adult male (SAM M6366) in July; and a lactating or pregnant female (SAM M7532) in the middle of February 1966. Although most specimens suggest a

breeding period in late winter or early spring, SAM M7532 suggests the species may be polyoestrous or have no fixed breeding season. Burbidge et al. (1976) also noted four individuals (not plotted in fig. 26) collected from the Great Victoria and Gibson Deserts of Western Australia. Two were collected from Queen Victoria Spring in *Eucalyptus gongylocarpa* open-woodland, and in tall open-shrubland including species of *Acacia*. One was caught at Neale Junction in open-woodland of *E. gongylocarpa* over spinifex (*Triodea* sp.), and one was found in the Baker Lake area in a dry creek bed surrounded by tall open-shrubland of *Acacia* spp. and occasional emergent *E. camaldulensis*. Aslin (1977) has summarized information for recently collected South Australian specimens. These localities are not included in figure 26. She noted six specimens collected in December 1974 from near Marla Bore on the Stuart Highway. Five of these were juveniles and the sixth an adult female. A lactating female was obtained near the Garford Out-Station

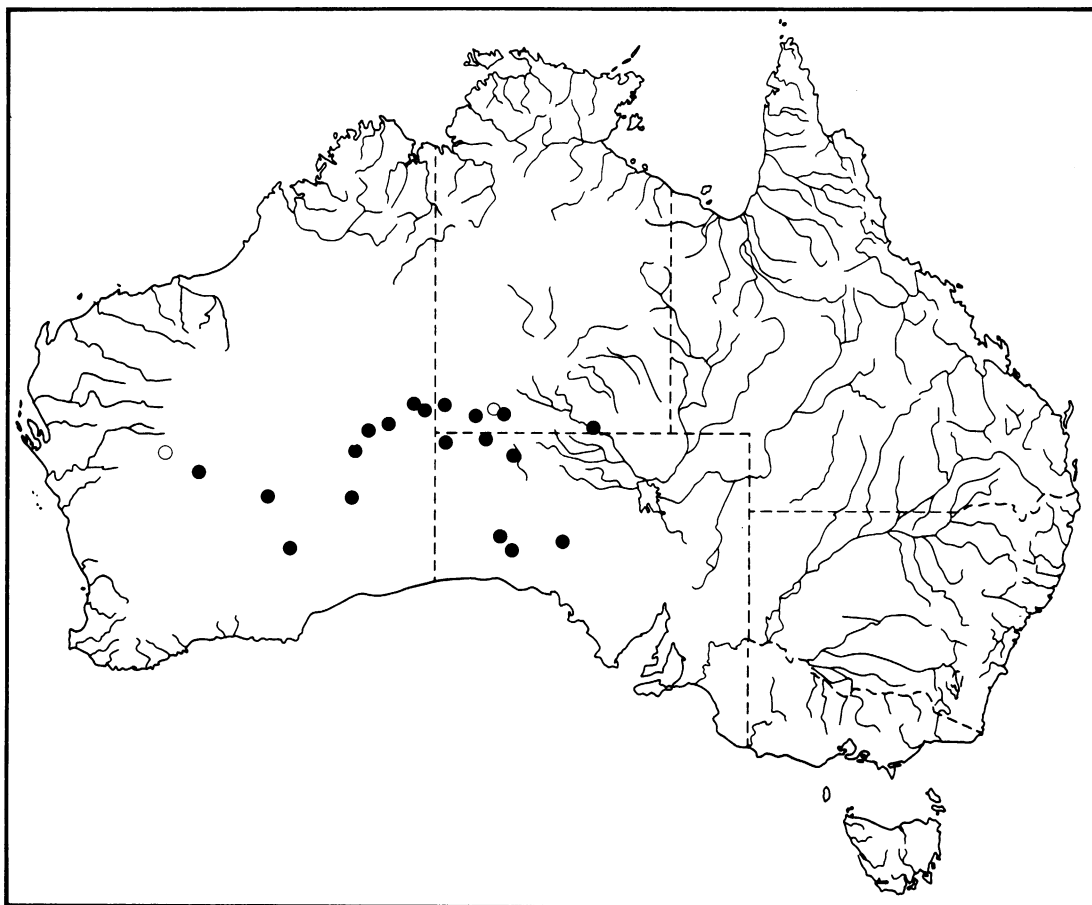


FIG. 26. Distribution of *Sminthopsis ooldea*. Solid dots represent modern specimens observed. Circles represent specimens from the surfaces of caves. See text for additional recent localities.

on Commonwealth Hill Station in December 1974. Another juvenile was obtained northwest of North Wells Homestead in January 1975. Two adult females were collected at Wallatinna in June 1975. Another adult female was caught near Mt. Sarah Homestead north of Oodnadatta in April 1976. In view of all the South Australian localities it appears to occur in a variety of arid habitats but mostly in areas receiving less than 25 cm. of rain per year. Recently collected specimens have come from acacia and eucalypt woodland, mallee scrubland, and sandridge areas with hummock grassland. Aslin notes that one specimen was reported to have been dug from a shallow burrow in a sandridge.

CONDITION OF THE TYPE SPECIMEN: The skull of the holotype is badly affected by some form of corrosion or decalcification (Troughton, 1965, p. 316 says maceration), with the result that the palatal vacuities are artificially enlarged and the skull distorted.

Sminthopsis longicaudata Spencer

Sminthopsis longicaudata Spencer, 1909.

TYPE SPECIMEN: Holotype: C7803, skull and carcase in alcohol, adult male, donated by G. A. Keartland. Type locality: Spencer (1909, p. 451), "West Australia." Troughton (1965, p. 320), "region Pillendinnie (Marble Bar), Western Australia."

DIAGNOSIS: Medium-sized species of *Sminthopsis* differing from all species in having the tail-vent length approximately twice the nose-vent length, and in having pronounced striae as ridges on the terminal pads of the digits. It also differs from *S. murina*, *S. leucopus* and *S. ooldea* in having a posthallucal or metatarsal enlarged striate granule, extreme premolarization of C1, and a well-developed alisphenoid tympanic wing. It also differs from *S. granulipes* in having enlarged striate granules on the interdigital pads, having a thin tail, lacking hair on the interdigital pads, in having relatively long premaxillary vacuities which extend posterior to a point level with posterior edge of the C1, and in having a well-developed alisphenoid tympanic wing. It also differs from *S. psammophila* in being smaller, in lacking a tail crest, in having striate enlarged apical granules on the interdigital pads, in having a posthallucal or metatarsal enlarged granule, in having relatively long premaxillary vacuities, and relatively longer and narrower upper molars. It also differs from *S. macroura* and *S. douglasi* in having a thin tail; lacking a head stripe, having enlarged posthallucal or metatarsal granules, striate apical granules on interdigital pads, premolariform C1, relatively long premaxillary vacuities, tiny to absent entoconids on M₁ to M₃ relatively longer and narrower upper molars and a well-developed alisphenoid tympanic wing. It also differs from *S. virginiae* in lacking a head stripe, having striate apical granules on the interdigital pads, lacking rufous cheeks, in having premolariform C1, relatively long premaxillary vacuities, relatively longer and narrower upper molars and a well-developed alisphenoid tympanic wing. It also differs from *S. crassicaudata* in having a thin tail, unfused interdigital pads, enlarged hallucal and posthallucal or metatarsal granules, striate apical granules on the interdigital pads, small to absent entoconids on M₁ to M₃; relatively longer and narrower upper molars; and a well-developed alisphenoid tympanic wing. It also differs from *S. butleri* in having enlarged posthallucal or metatarsal granule, striate enlarged apical granules on the interdigital pads; a well-developed ali-

sphenoid tympanic wing, and relatively longer and narrower upper molars.

DESCRIPTION: Tail: The thin tail is greater than twice the head and body length (TN/NV ratio of holotype is 2.02).

HIND FOOT: The hind foot has elongate striated apical granules on the hallucal and interdigital pads. There is also a smaller elongate, striated metatarsal or posthallucal granule. The position of this pad is not clear in any specimen examined, but it is particularly obscure in the dried feet of WAM M2394. The terminal pads of the toes are striate. The hind foot of the holotype has been illustrated by Troughton (1965, fig. 7), and the hind foot of C9970 is shown in figure 27 which is from a drawing kindly made by Ms. D. White (National Museum of Victoria).

NIPPLE NUMBER: C9970 has six juveniles in the pouch but it has not been possible to determine if there are more than six nipples.

PELAGE: Spencer (1909) noted the presence of a dark line in the holotype running along each side of the face through the eye, a white forearm and white dorsal surfaces on the front and hind feet, chin, and lips, and a general gray body color with a rufous tinge. I have not seen any distinctive markings on the specimens examined during the present study.

DENTITION: I² to I⁴ are nearly subequal in size but the crown of I⁴ is slightly longer than the crown of I². There is no posterior lobe on I⁴. Diastemata separate I⁴ from C¹ and C¹ from P¹. C¹ to P⁴ have small anterior and posterior cingular cusps. C¹ has anterior and posterior cingula, lacks cingula on the lingual and buccal bases of the paracone, is premolariform, and shorter-crowned than P⁴ but taller-crowned than P¹ to P³. P¹ to P⁴ have complete cingula except for immediately below the paraconid on the lingual and buccal sides. Styler cusp A on the upper molars is indistinguishable from the anterobuccal end of the anterior cingula. Styler cusp B is present on M¹ and connected to the paracone by a paracrista. Styler cusp C is absent. Styler cusp D is largest on M¹, smaller on M², very reduced on M³, and absent on M⁴. Styler cusp

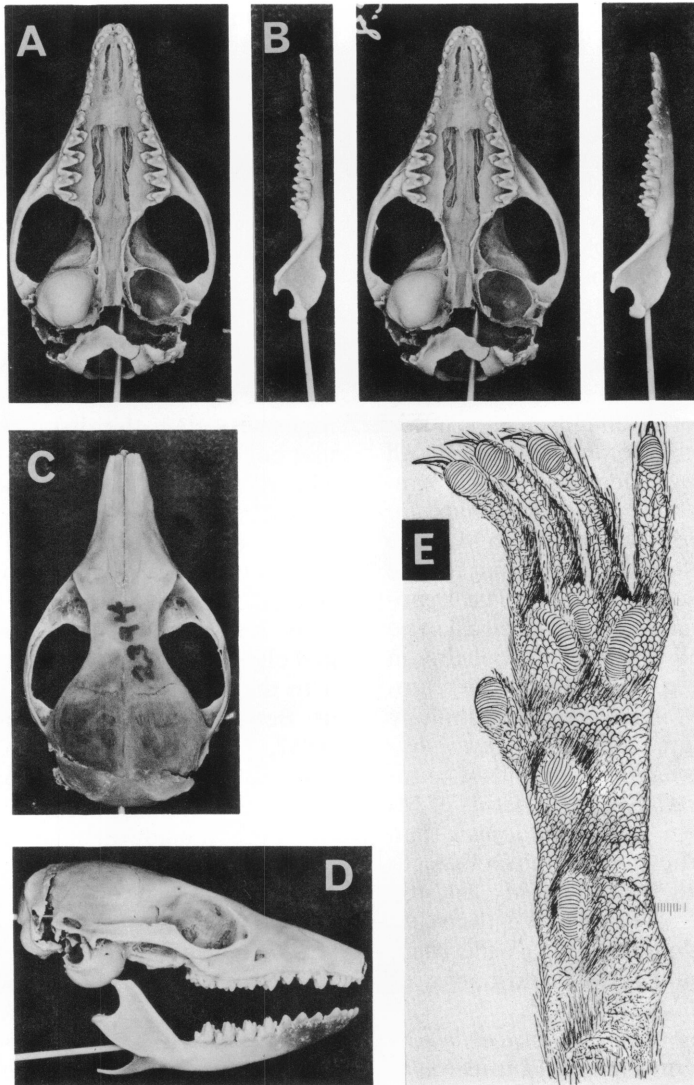


FIG. 27. *Sminthopsis longicaudata*. A–D, WAM M2394, adult, Marble Bar, Western Australia. E, left hind foot of C9970, adult, central Australia, (drawing by Ms. D. White, National Museum of Victoria) to show the pronounced transverse striations on the pads, and the well-developed posthallucal pad.

E is possibly distinguishable on M^2 to M^3 connected to the metastylar corner of the tooth by a low buccal enamel ridge. Protoconules are prominent on M^1 to M^3 . The paracones increase in size from M^1 to M^4 . The metacones of M^1 to M^3 are subequal in height whereas the metacone of M^4 is very

small. The protocones of M^1 and M^3 are subequal, larger than the protocone of M^4 , and smaller than the protocone of M^2 . The anterior cingulum is continuous on M^4 but not on M^1 to M^3 . The length of the paracrista increases from M^1 to M^4 . The metacristae of M^1 and M^3 are subequal and shorter than the

metacrista of M^2 . I_1 is taller-crowned than I_2 which is subequal to or just larger than I_3 . I_3 has a small posterior lobe. A small diastema may occur between I_3 and C_1 (66.3.105) or be lacking (WAM M2394). C_1 is premolariform, subequal in crown height to P_3 , smaller than P_4 , larger than P_1 , and has complete buccal and lingual cingula (the specimens examined are worn and determination of the extent of the cingular development is uncertain). C_1 also has a pronounced posterior cingular, but no anterior cingular cusp. P_1 is shorter-crowned than P_2 which is shorter-crowned than P_3 . Complete lingual and buccal cingula appear to be present on P_1 to P_4 . Small but clear anterior cingular cusps occur on P_1 to P_3 , but only sometimes on P_4 . All lower premolars have clear posterior cingular cusps. Protoconids and paraconids increase in size posteriorly from M_1 to M_4 . The metaconids of M_2 to M_3 are subequal in size and larger than that cusp on M_1 . The hypoconids of the lower molars are subequal. The entoconids are small on M_1 to M_3 but tiny in some specimens (e.g., 66.3.105). The entoconids have the *S. macroura* morphology and are not connected to the posterior hypocristid. No trace has been found of entostylids or metastylids. The paracristids of M_2 to M_4 are subequal in length and longer than that crest in M_1 . The metacristids of M_1 to M_3 increase in length from M_1 to M_3 , and the metacristid of M_4 is subequal in length to that crest in M_2 . The talonid of M_1 is wider than the trigonid, subequal in M_2 , and narrower than the trigonid in M_3 to M_4 .

SKULL AND DENTARIES (BASED ON WAM M2394): A mild mid-frontal, mid-nasal depression exists. The lacrimal foramina are variably single or double and on the rim of the orbit. Nuchal crests may develop on the occipital-parietal bone boundary. The transverse and sphenorbital foramina are moderate in size. The foramen rotundum has a well-developed ventral bony shelf. The foramen pseudovalve is narrow. The entocarotid canal is well developed and obscures direct ventral view into the cranium through the basisphenoid. The basisphenoid has a pronounced mid-ventral longitudinal depression. The alisphenoid tympanic wing is en-

larged so as to almost completely enclose the ectotympanic. A fragment of the periotic adhering to the alisphenoid tympanic wing of WAM M2394 suggests that the periotic tympanic wing is also well developed. The paroccipital process is well developed. Palatal vacuities are large with the premaxillary vacuity extending posteriorly to the level of the anterior end of the posterior half of P^4 . Interdental fenestrae between consecutive molars are prominent, almost reducing the palate in these areas to a bony lattice. In the dentary (based on WAM M2394 and 66.3.105), the distance from the articular condyle to the tip of the ascending ramus is much less than the distance from the articular condyle to the tip of the angular process. The masseteric fossa is moderate and the symphysis extends back to the level of the posterior end of P_3 .

DISCUSSION: Troughton (1965, p. 320) suggested that this "species may represent some annectant generic form, based on cranial characters, but it seems difficult to relate it to the genera referred to within the scope of Bensley's phylogenetic review." Tate (1947, p. 120) said "it apparently represents a special, long-tailed development of the division of *Sminthopsis* having striated pads." Although Troughton may have examined the cranial and dental characters, Tate did not. It seems apparent on the basis of the present study, that *S. longicaudata* cannot be referred to any described modern genus other than *Sminthopsis*. This is shown by the common possession of large palatine vacuities, narrow nasals, *Sminthopsis*-like upper and lower molars, elongated hind-foot, incisor gradient in which I^4 is longer-crowned than I^2 , and squamosal-frontal contact on the side of the braincase. The features which make it unusual are the extremely long tail, the striated apical granules and the presence of a metatarsal granule. However, elongate striated apical granules are also present in *S. leucopus*, metatarsal granules are not uncommon in *S. virginiae* (although smaller), and large striated metatarsal granules occur as abnormalities in specimens of *S. murina* and Tasmanian *S. leucopus*. The proportionately long tail of *longicaudata* is unequaled

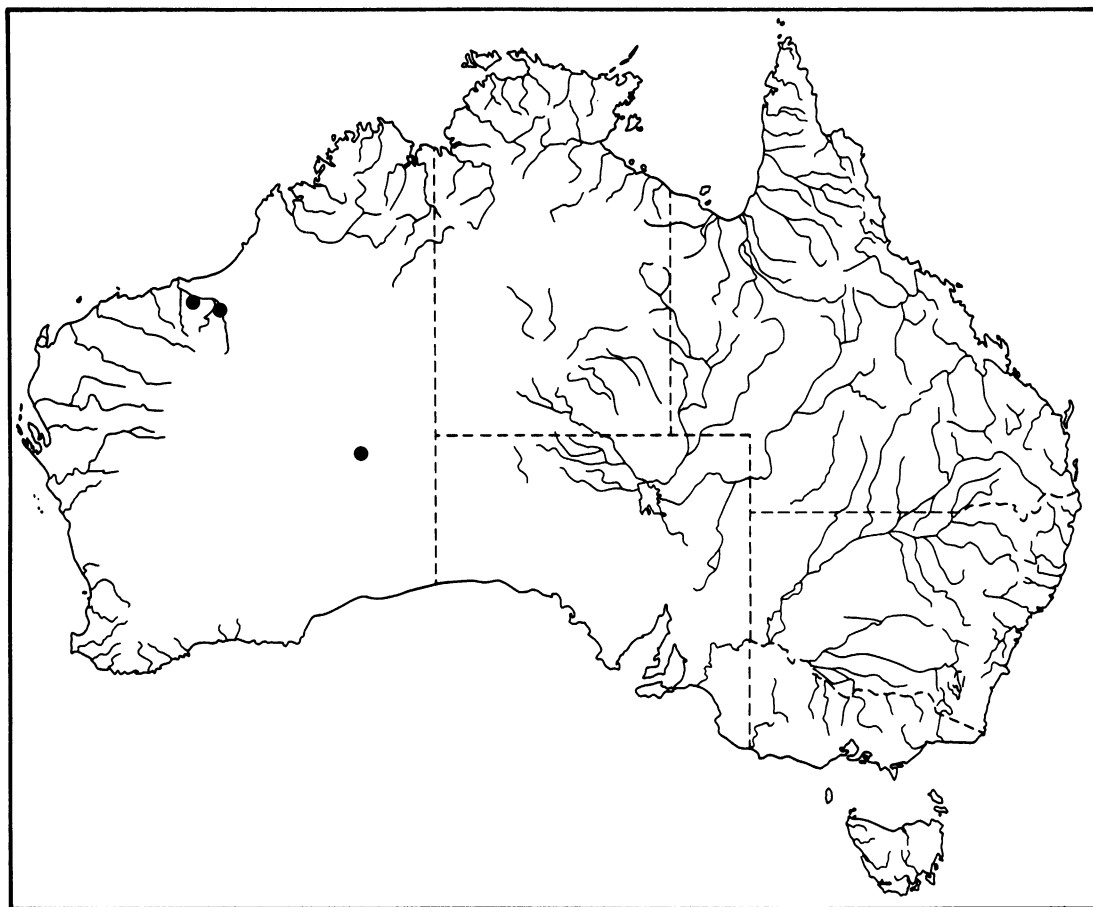


FIG. 28. Distribution of *Sminthopsis longicaudata*. Solid dots represent modern specimens observed. The circle in the northwest, on Cape Range, represents specimens from the surfaces of caves (see text). The circle in east central Western Australia represents a modern specimen obtained by Burbidge et al. in 1975 (see Burbidge et al., 1976).

and only approximated by *Antechinomys* where, nevertheless, it is not as long. As a result of the present study, it is evident that the dental and foot characters of *longicaudata* represent a species of *Sminthopsis*. It is unfortunate that no opportunity has been available to examine the intact basicranium of C9970 for perhaps here a possible generic distinction of *longicaudata* might be evident.

Troughton's (1965) difficulty in accepting *longicaudata* as a species of *Sminthopsis* is probably the result of its possession of striated apical granules. He (1965, p. 307–308) did not accept the view, held in the present

study, that *leucopus* has striate apical granules and considers that *longicaudata* is, in this respect, a unique species in the genus. On the other hand, it would probably be a mistake to suggest that *leucopus* and *longicaudata* form a natural group in opposition to other species of *Sminthopsis*, solely because both possess striated granules. At least in the case of two species, *S. leucopus* and *S. murina*, it is clear that there can be intra-specific variation in this character.

Some characters of the skull and teeth of *S. longicaudata* resemble those of *S. crassicaudata* and *Antechinomys* and include the

gross reduction of C1, the very large palatal vacuities, and the enlarged tympanic wings of the alisphenoid and periotic. They also appear to be characters which reflect arid-adaptation and could have been convergently developed. The upper molars of *longicaudata* are clearly much narrower than those of *crassicaudata* and species of *Antechinomys* and, in this respect, resemble *granulipes*, *psammophila* and *murina*. The small to tiny entoconids are also clearly unlike those of *crassicaudata*.

Overall, there can be little doubt that *longicaudata* is a *Sminthopsis*. However, it also represents a side branch of that genus which has apparently developed arid-adapted specializations independent of other arid-adapted species such as *S. hirtipes*.

HABITAT AND REPRODUCTION: The habitat of the type specimen collected by Keartland is unknown. Troughton (1965, p. 30) noted that L. Glauert (no reference specified) concluded that the type came from the "region Pillendinnie (Marble Bar), Western Australia." The basis for Glauert's opinion is not clear. It is possible that it was based on the fact that the only other specimen known to Glauert at the time was WAM M2394 obtained by R. N. W. Bligh, around 1940, from Marble Bar. In 1954 A. M. Douglas obtained another specimen (66.3.105) from a pile of broken bones beneath a roost of the Ghost Bat (*Macroderma gigas*) in a breakaway cave near Ripon Hills, about 97 km. east of Marble Bar, Western Australia. It seemed apparent to Douglas that the material in the bone pile represented the remains of prey of the Ghost Bat. Douglas (personal commun.) was informed by residents in the Marble Bar area that they had seen animals fitting the description of *S. longicaudata* climbing trees. The fourth known modern specimen (C9970) was possibly collected for Spencer and bears the locality description "Central Australia."

Specimen C9970 is a female with six attached pouched young. Unfortunately, it is not known in what month of the year the specimen was obtained.

FOSSIL RECORDS: Quaternary specimens (age unknown but probably Recent) have

been identified in this study from material (e.g., 67.4.417) collected from caves on North West Cape, Western Australia. These "fossils" are associated with similarly preserved specimens of *Antechinus rosamondae* and *A. macdonnellensis*, all three previously unknown from North West Cape. These identifications were reported in Kendrick and Porter (1974).

Sminthopsis granulipes Troughton

Sminthopsis granulipes Troughton, 1932.

TYPE SPECIMEN: Holotype: Masters Collection, Palmer's register no. 669 in the "old collection" of the Australian Museum, skull and carcase in alcohol, adult female. Troughton (1932, p. 352) noted that the earliest Australian Museum register states "Coll. George Masters 1869?" I have examined the holotype. Type locality: Troughton (1932, p. 352), "King George's Sound, south Western Australia."

DIAGNOSIS: Medium-sized species of *Sminthopsis* differing from all other species in having a strongly bilobed I_3 (*S. psammophila* and *S. leucopus* sometimes have a mildly bilobed I_3). It differs from *S. murina*, *S. leucopus* and *S. ooldea* in invariably having an incrassated tail, granular terminal pads on the digits; haired and fused interdigital pads; very large canines; and relatively short premaxillary vacuities which do not extend posteriorly beyond a point level with the rear of C^1 alveoli. It differs from *S. psammophila* in being smaller; having an incrassated tail; lacking a crest on the tail; and in having hair on the interdigital pads. It differs from *S. hirtipes* in having a very reduced alisphenoid tympanic wing, large canines, and very narrow and spaced premolars. It differs from *S. macroura* and *S. douglasi* in having granular terminal pads on the digits, haired interdigital pads without enlarged apical granules, in lacking a head stripe, in having small to absent entoconids on M_1 to M_3 , and in having narrow and spaced premolars. It differs from *S. virginiae* in having an incrassated tail, granular terminal pads on the digits, fused and haired interdigital pads, narrow and spaced premolars, small to absent

entoconids on M_1 to M_3 , a lack of a head stripe, and a lack of enlarged apical granules on the interdigital pads. It differs from *S. crassicaudata* in being larger, in having granular terminal toe pads, haired interdigital pads, short premaxillary vacuities, large canines, and conspicuously longer upper molars (the metacrista of M^3 being shorter than or equal to the length of M^3), and in lacking large entoconids. It differs from *S. longicaudata* in having an incrassated tail shorter than twice the nose-vent length, granular terminal pads on the digits, hair on the interdigital pads, a lack of striated apical granules, relatively short premaxillary vacuities, and a relatively more poorly developed alisphenoid tympanic wing. It differs from *S. butleri* in having an incrassated tail, fused and haired interdigital pads, granular terminal pads on the toes, a lack of enlarged apical granules on the interdigital pads, small entoconids, relatively short premaxillary vacuities, and narrow widely spaced premolars.

DESCRIPTION: Tail: The tail is much shorter than the nose-vent length and is always incrassated.

HIND FOOT: The hind foot is haired over all of the sole except for a small area proximal to the interdigital pads. Sparsely distributed hairs are present sometimes on the interdigital pads themselves (e.g., WAM M2371). All the pads of the hind and fore feet, including the terminal digital pads, are covered with well-defined small granules. No enlarged or striated granules occur on the foot pads.

NIPPLE NUMBER: Specimen WAM M711 has 12 young and presumably at least as many nipples. Specimen WAM M10206 has 12 nipples.

PELAGE: A head stripe is lacking. A dark ring occurs around the eye but it does not extend to the nose. The tail is creamy white in color. There are no other consistent and conspicuous body markings. One specimen (WAM M711) shows a poorly defined saddle of darker color extending across the middle of the back. Photographs taken by W. D. L. Ride of a live individual suggest there is a vague stripe between the rear of the eye and ear and possibly a short distance in front of

the eye, as well as a very vague and diffuse dark patch on the forehead and between the ears. The nose appears to be quite dark. The head in profile shows a narrow long rostrum in front of a deep and large cranium. Dry (not previously described) and wet pelage colors (Ridgway, 1912), are as follows: Middle of back Olive Brown to Clove Brown (WAM M2333, dry), Cinnamon Brown to Proutt's Brown (WAM M711, dry), and ?Blackish Brown (3) (WAM M6812, wet); flank Light Buff to Pale Ochraceous-Buff (M2333), Light Ochraceous-Buff to Warm Buff (M711 and M6812); Belly paler than Cream color (M2333), paler than Pale Yellow Chalcidony to Massicot Yellow (M711), and much paler than Cream color, almost white (M6812).

DENTITION: I^1 is reduced and subequal in crown height to I^2 . Upper incisor crown lengths increase posteriorly from I^1 to I^4 . I^4 has a small posterior lobe. A large diastema occurs between I^4 and C^1 with a deep depression corresponding to the tip of C^1 . C^1 is narrow, caniniform, very tall-crowned being twice the crown height of P^1 , and lacks lingual and buccal cingula and anterior and posterior cingular cusps. Crown height and length increase posteriorly from P^1 to P^4 . Diastemata occur between C^1 and P^1 , and all premolars. P^1 to P^4 have anterior and posterior cingular cusps, are very narrow and long, and lack lingual and buccal cingula. The three-rooted dP^4 (B1830) has only two principal subequal (height) cusps, the paracone and the metacone. It lacks any trace of stylar cusp D, but has other minuscule swellings which may be homologous with stylar cusp E, stylar cusp A, and the protocone. Stylar cusp A is distinct on M^1 and M^2 when unworn (B1830), but is otherwise indistinguishable from the buccal end of the anterior cingulum. Stylar cusp B is relatively small on M^1 . Stylar cusp C is variably present on the flank of stylar cusp D (e.g., WAM M6062). Stylar cusp D decreases in size posteriorly from M^1 to M^3 and is small when present on M^4 (WAM M6062). Stylar cusp E is often developed as a minute buccal crest extending anteriorly from the metastylar corner of the molar crown. A possible homo-

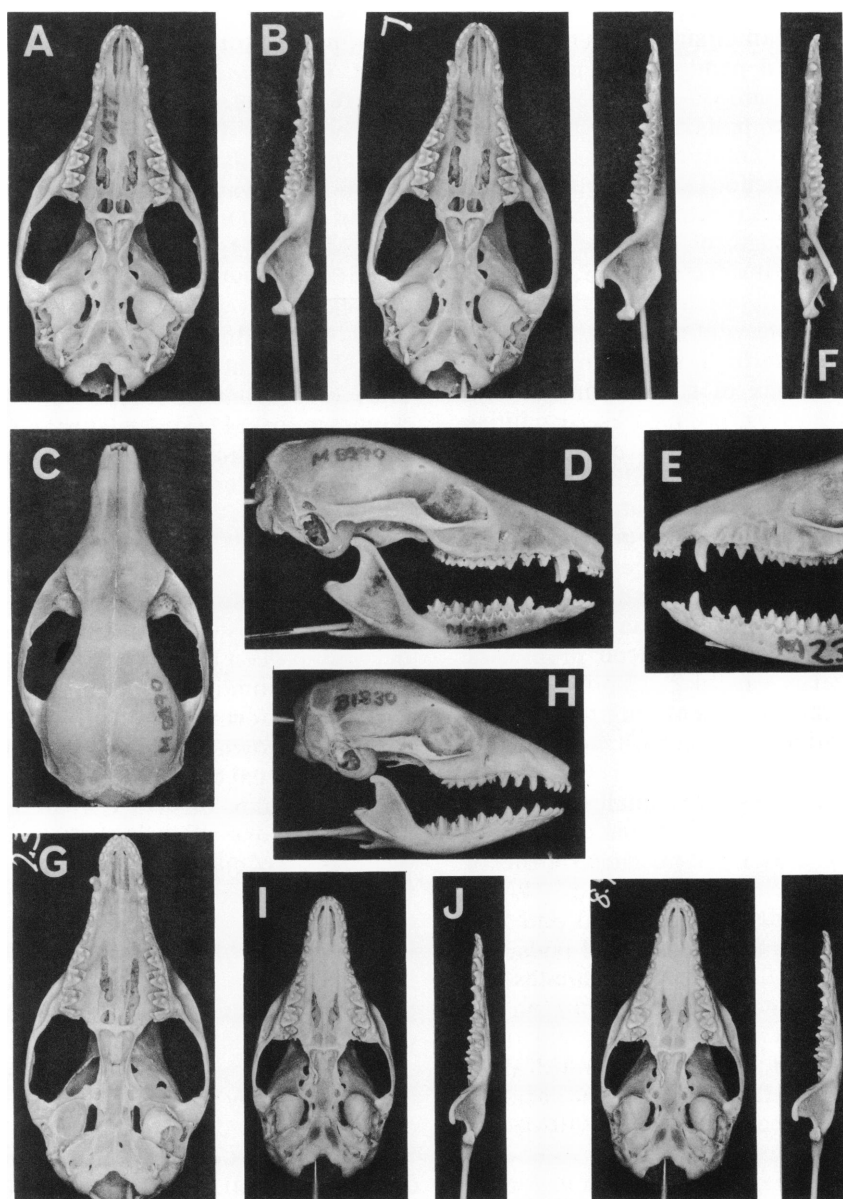


FIG. 29. *Sminthopsis granulipes*. A-D, WAM M8090, adult, from near Three Springs, Western Australia. E-G, WAM M2333, adult, Marvel Loch, Western Australia. H-J, WAM B1830, juvenile, Gingin, Western Australia. A-J, $\times 2$.

logue of this cusp occurs on dP^4 as an isolated cusp on the buccal edge of the crown without connection to the metastylar corner of the tooth. The paracones increase in

height from M^1 to M^4 . The metacones of M^1 to M^8 are subequal. The protocones of M^1 and M^3 are subequal in height, smaller than that cusp on M^2 , and larger than that cusp

on M^4 . An anterior cingulum is incomplete on M^1 to M^4 . A paracrista is absent on dP^4 , M^1 (in the unworn condition), and may be poorly developed on M^2 (e.g., B1830). Paracristae increase in length from M^1 (in worn teeth) to M^4 . The metacrista increases in length from dP^4 to M^2 . The metacrista of M^3 is subequal to that crest on M^1 . The outline of the upper molars is relatively very narrow and long, being more like that of *Antechinus* than most *Sminthopsis*. For the same reason, the metacrista of M^3 is much shorter than the crown length. I_1 is the tallest lower incisor crown. I_3 has a marked bifid crown with the posterior lobe being equivalent to almost half the length of the anterior lobe. Diastemata separate I_3 from C_1 , C_1 from P_1 , and all premolars from each other. Lingual and buccal cingula are absent on C_1 to P_4 . C_1 crown height is approximately twice that of P_1 . Generally there are no clear posterior or anterior cusps on C_1 although a small posterior cusp sometimes occurs (e.g., WAM M6812). Posterior cingular cusps and commonly small anterior cingular cusps (P_4 is the only tooth in which the appearance of an anterior cingular cusp is variable) are present on P_1 to P_4 . DP_4 is two-rooted with a prominent protoconid, smaller hypoconid, very small paraconid, and rudiments of a buccal cingulum. The paraconids of M_1 to M_3 increase in height posteriorly. The paraconid of M_4 is subequal to that cusp on M_3 . The metaconids of M_2 to M_4 are subequal in height and larger than that cusp on M_1 . The protoconids increase slightly in height from M_1 to M_4 . The hypoconids of M_1 and M_3 are subequal and taller than that cusp on M_4 and shorter than that cusp on M_2 . The entoconids are small when present and are not contacted by the hypocristid. They increase in height posteriorly from M_1 to M_3 . One specimen (B1830) shows a small metastylid on M_1 . The paracristid of M_1 is shorter than that crest on M_2 to M_4 where it is subequal in length. The relative lengths of the metacristae are similar to that of paracristae. The trigonid is narrower than the talonid on M_1 and M_2 , wider than or subequal to the talonid in M_3 , and wider than the talonid in M_4 .

SKULL AND DENTARY: The skull is dol-

ichocephalic with a narrow rostrum. Sagittal and nuchal crests develop with age. A longitudinal medial depression occurs across the frontal-nasal suture. The lacrimal canal is double and on the edge of the orbit. The lacrimal bone in older individuals (e.g., WAM M1668) may develop posterodorsal lacrimal spines which extend out over the orbit. The sphenorbital fissure, the posterior lacerate foramen, the foramen rotundum, the entocarotid foramen, and the opening to the eustachian canal are very large. The internal jugular vein canal is pronounced, short, and has a large posterior foramen. The periotic tympanic wing and the alisphenoid tympanic wing are relatively little developed and leave the ectotympanic broadly exposed. The paroccipital process is large but lacks auditory sinus development. The premaxillary vacuity commonly extends as far back as the level of the posterior edge of C^1 alveolus and only once (WAM M6012) as far back as the level of the anterior alveolus of P^1 . The maxillary vacuity extends anteriorly as far forward as the level of the protocone root of M^1 . The dentary is very elongate and shallow. The masseteric fossa is large with the anterior border of the ascending ramus and the posterior margin of the dentary widely divergent. The symphysis extends posteriorly to the level of the posterior end of P_3 . The distance between the articular condyle and the tip of the ascending ramus is not markedly shorter than the distance between the articular condyle and the tip of the angular process.

DISCUSSION: This very distinctive species was not recognized until 1932 probably because little attention had been paid to cranial and dental characters in the species of *Sminthopsis*. Using only external characters, specimens of *S. granulipes* might, as Troughton (1932) suggested, be mistaken for *Sminthopsis crassicaudata*.

It is likely that common possession of haired and fused interdigital pads and granular terminal digital pads in *Sminthopsis hirtipes* and *S. granulipes* are convergently developed characters related to the relatively arid situations inhabited by these species rather than indications of close relationship.

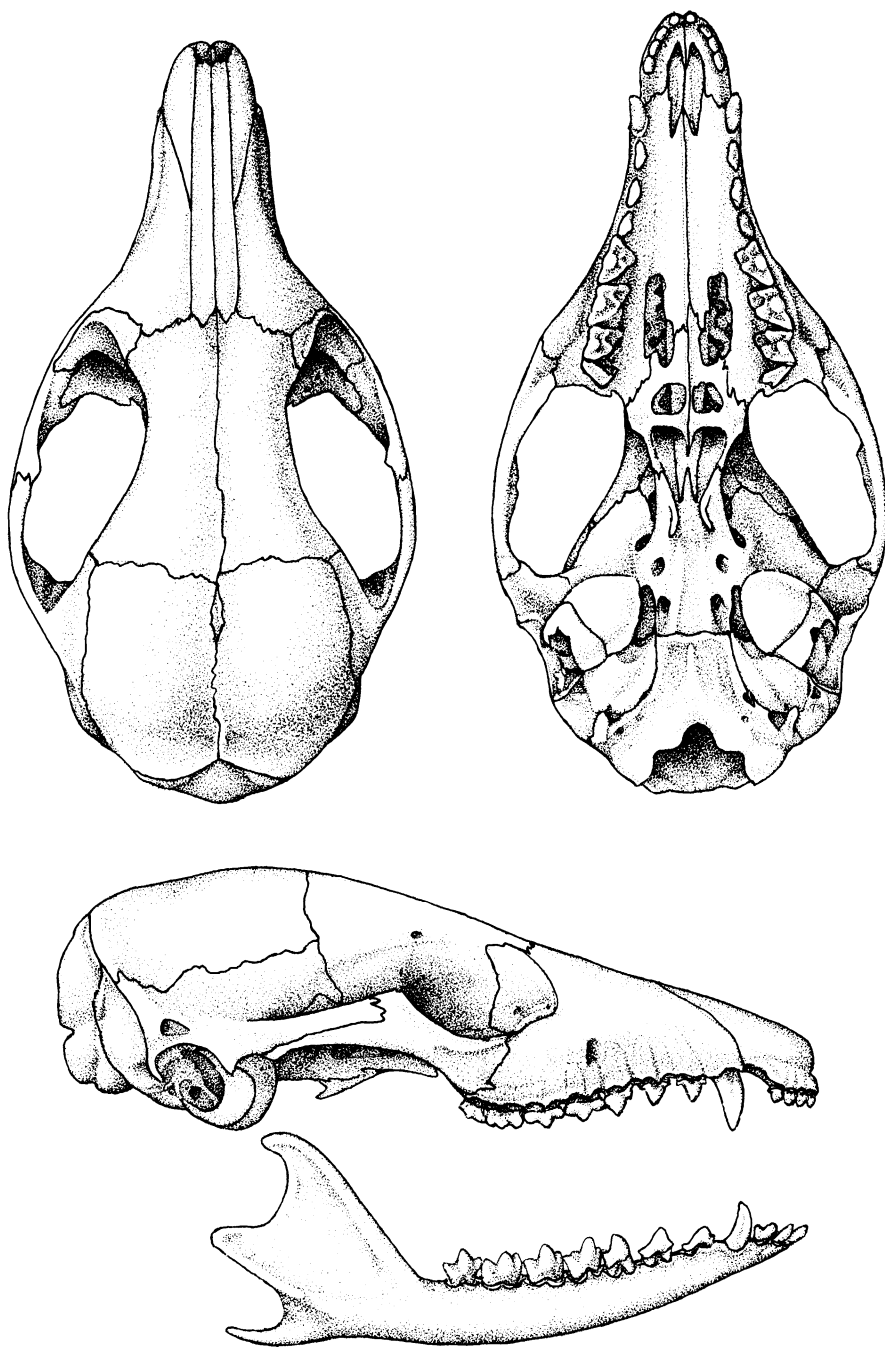


FIG. 30. *Sminthopsis granulipes*. Drawings based on photographs and specimen WAM M8090, adult, near Three Springs, Western Australia.

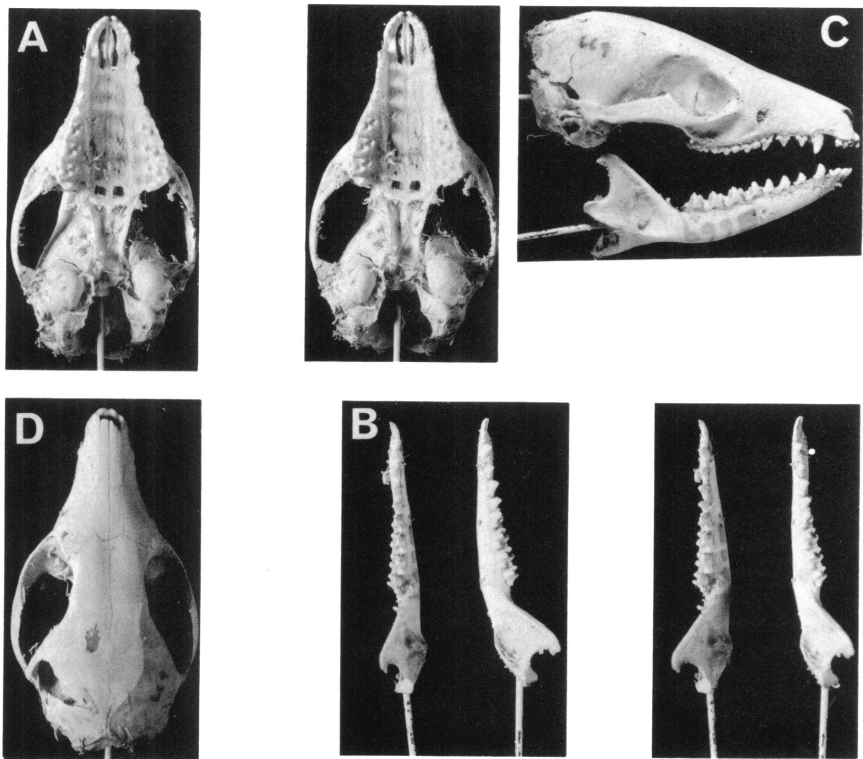


FIG. 31. Holotype of *Sminthopsis granulipes* Troughton, Palmer Register (Australian Museum) no. 669. See table 2 for measurements.

Cranial and dental characters do not indicate any close resemblance between these species and demonstrate the unique character of *S. granulipes*. It may be related to *S. psammophila* in that both share reduced entocoinids, spaced premolars, long skulls, small bullae, narrow molars, and, to some extent, a bilobed I_3 .

Neophascogale lorentzii, one of the endemic dasyurids of New Guinea, is similar in many cranial and dental characters to *S. granulipes*. For example, both possess a markedly bifid I_3 , long bladelike and widely spaced premolars, very long and narrow upper molars, palatine vacuities, and very reduced alisphenoid bullae (an otherwise unexpected character in *S. granulipes*

considering its relatively arid situation). Further, the *Sminthopsis* character of contact between the squamosal and frontal bones also occurs in some *Neophascogale* specimens. The significance of these similarities is not clear. There are many dental differences including the relative reduction of P4, presence of a posterior cingulum in *Neophascogale*, and the fact that *Neophascogale* commonly has a stylar cusp C combined with a relatively reduced stylar cusp D. The similarities suggest that *S. granulipes* may be, in some ways, a primitive species and cast some doubt on the closer affinities previously proposed by me (Archer, 1975b) between *S. ooldea* and species of *Ningau*, or my idea that *Sminthopsis* is the sister group

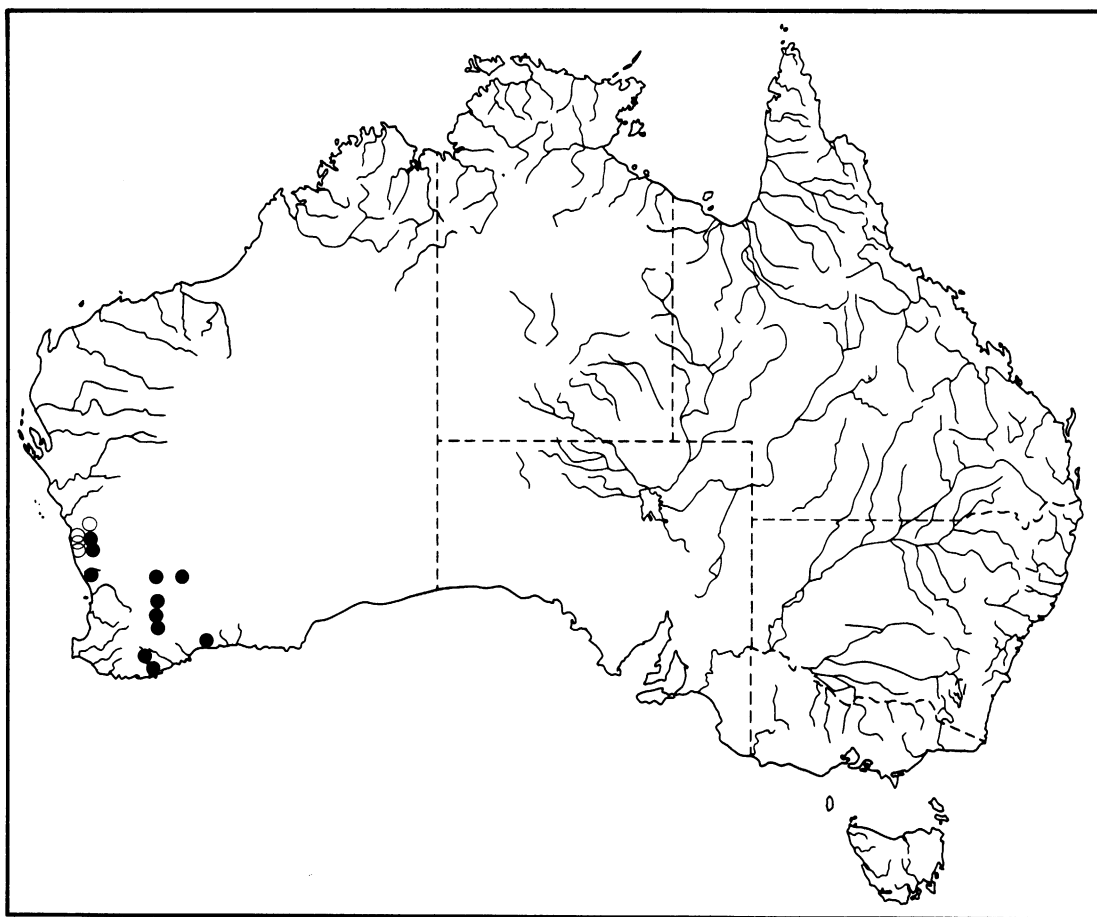


FIG. 32. Geographic distribution of *Sminthopsis granulipes*. Solid dots represent modern specimens. Circles represent fossil specimens. See text for additional recent localities from the Great Victoria and Gibson desert areas of Western Australia.

of *Ningaui*. This is discussed below in the sections dealing with species and generic affinity.

HABITAT AND REPRODUCTION: A. Chapman (Western Australian Museum) records habitat notes (*in litt.* June 21, 1973, via D. Kitchener) for specimens (WAM M10101 and M10209) collected in March 1973, from Bendering Fisheries and Fauna Reserve in southwestern Western Australia. Chapman notes of this area: "In general terms the vegetation of this reserve is mallee and wodjil (*Casuarina* sp. and *Acacia* sp.) scrub—with *Eucalyptus salmonpholoia* and blue mallet, *Eucalyptus falcata*. There is also

some low heath." *Sminthopsis granulipes* was trapped at two sites which were markedly different. Site 1: Medium height open scrub—with upper layer of *Grevillea eriostachya*, *G. pterosperma*, and *Eucalyptus burracoppinensis* to about 3 m. There was a low strata composed of several species of shrubs. Little ground cover was noted. It was found on loamy sand with a laterite subsoil. Site 2: A uniformly low open heath assemblage (to 60 cm.) of predominantly *Acacia* sp. and *Isoopogon* sp. There were occasional emergents of *Acacia sclerophylla* and *Gastrolobrium spinosum*. Ground cover and leaf litter were almost absent except under

small bushes. Specimen WAM M6812 was obtained in December 1964 near Moora, Western Australia, by H. A. Waters who noted that the animal was ploughed up in an area of yellow soil and *Banksia*. Specimens WAM M10205 and M10206 were collected in March 1973 from Lake Grace South, Western Australia, by Messrs. N. McKenzie and K. Youngson. They note the trapsite was in tall open shrubland with deep white sand, *Banksia prionotes* and *B. attenuata*, and sparse to deep leaf litter. Specimen WAM M10205 had insect remains, sand, and *Me-laleuca* needles in its stomach. It has also been recorded from Cockleshell Gully Reserve (Chapman and Kitchener, 1977).

One female (WAM M711) obtained 48.3 km. east of Ravensthorpe had 12 young in the pouch. The label records August 1925, which may have been either the collection date or the date of accession. D. Kitchener (*in litt.* June 21, 1973) has kindly provided the following comments on WAM M10205 and M10206. WAM M10205, collected March 15, 1973, shows no pouch development or obvious nipples. WAM M10206, obtained March 10, 1973, has a pouch with an opening 6.5 mm. in diameter. On the right side there are six nipples, spatulate-shaped, 1.1 mm. long, and apparently unused. On the left side there are also six nipples, one of which is elongate, being 2.4 mm. in length. These records seem inadequate to determine the normal breeding period(s) of the species.

REMARKS ABOUT DISTRIBUTION RECORDS: Records of a large *Sminthopsis* from Hastings Cave (=Drovers Cave, see Merliees, 1968) given by Lundelius (1960) are attributable to *S. granulipes* (Archer and Baynes, 1972). Modern distribution records have been given by Glauert (1933) as Nun-garin, and 48 km. east of Ravensthorpe. Bannister (1969) also recorded the species from Gingin, Western Australia. Cave specimens have been identified in the present study from several caves on the coastal plain of Australia (e.g., 68.6.85 from Stockyard Gully Cave, 69.4.140 from Hastings Cave, and 69.6.161 from Facts of Life Cave). The type specimen was part of a collection made by G. Masters at "King Georges Sound and Salt

River" (see Ride, 1970, p. 201). Because of the more inland distribution of specimens other than the type, it is possible that the locality of the type was not actually the King George's Sound area. Another specimen (WAM M1968) is recorded as having been collected 11.3 km. from the west end of the Stirling Ranges. This locality datum may have been confused with that of a specimen (WAM M1668) of *Myrmecobius fasciatus*. It also seems probable that a specimen, regarded by Tate (1947) to be a topotype of *S. granulipes* from Albany, is either not that species or bears incorrect locality data. Tate (1947) stated that the specimen was only represented by a skin originally identified as "*murina fuliginosa*." It is likely that many early collectors, such as Masters, based their activities in Albany (on King George's Sound) but also collected farther inland.

Sminthopsis psammophila Spencer

Sminthopsis psammophila Spencer, 1895.

TYPE SPECIMEN: Holotype: National Museum of Victoria specimen no. C6203, skull and carcass in alcohol, adult male, obtained by the Horn Expedition June 18, 1894. Spencer (1895, p. 224) noted the specimen was first seen by "Mounted Trooper Cowle. . . ." I have examined the holotype. Type locality: Spencer (1895, p. 224), "Central Australia, near Lake Amadeus." Parker (1973, p. 6), "between Kurtitina Well and Ayers Rock . . .," Northern Territory.

DIAGNOSIS: This species is the largest *Sminthopsis*. It differs from all other species by having a short terminal crest of black hairs on the tail. It differs from *S. murina*, *S. leucopus*, and *S. ooldea* in having granular terminal pads on the digits. It differs from *S. granulipes* in having a thin tail, hairless interdigital pads, a median row of slightly enlarged apical granules on each interdigital pad, small entoconids on M_1 to M_3 , and premaxillary vacuities which extend posteriorly beyond a point level with the alveolus of C^1 . It differs from *S. hirtipes* in having a thin tail, small entoconids on M_1 to M_3 , relatively longer premaxillary vacuities, relatively small alisphenoid tympanic wings, in-

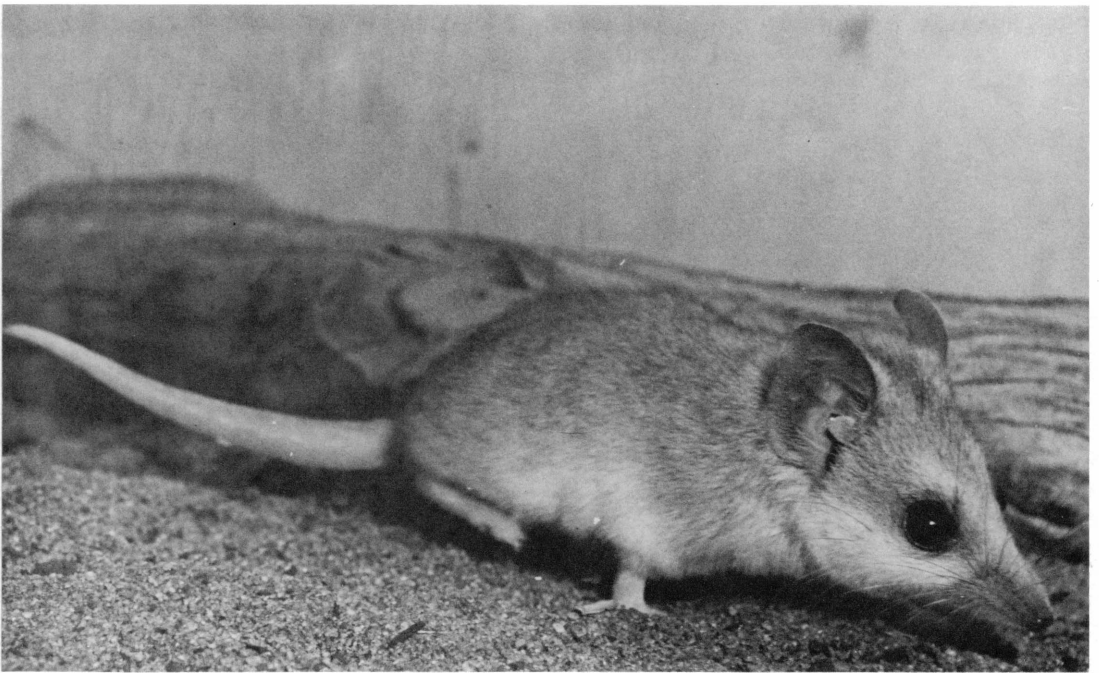


FIG. 33. Live *Sminthopsis granulipes*, southwestern Western Australia, showing the characteristic long head and light incrassated tail.

flated relatively longer and narrower upper molars and wider premolars, and in a lack of hair on the interdigital pads. It differs from *S. macroura* and *S. douglasi* in having a thin tail, granular terminal pads on the digits, no enlarged single apical granule, small rather than large entoconids on M_1 to M_3 , relatively longer premaxillary vacuities, and no conspicuous head stripe. It differs from *S. virginiae* in lacking a head stripe, in lacking a single enlarged apical granule on the interdigital pad, in having granular terminal toe pads, relatively longer premaxillary vacuities, small rather than large entoconids on M_1 to M_3 , and no anterior cingulum on M^1 to M^3 . It differs from *S. crassicaudata* in having a thin tail, relatively shorter premaxillary vacuities (though both extend posterior to the level of C^1 alveolus), granular terminal pads on the digits, small rather than large entoconids on M_1 to M_3 ; and relatively longer and narrower premolars. It differs from *S. longicaudata* in lacking striated apical granules on the hind feet, in lacking striate ter-

minal pads on the digits, in having a tail which is less than twice as long as the nose-vent length, and in having relatively short premaxillary vacuities (although both extend posterior to the level of the alveolus of C^1). It differs from *S. butleri* in lacking conspicuously enlarged apical granules on the interdigital pads of the hind feet, in having granular terminal pads on the digits, relatively longer and narrower upper molars, and relatively larger entoconids.

DESCRIPTION: Tail: The tail is long and thin and has a "laterally thin, dorso-ventral, feather-like crest of stiff hairs on the distal quarter of the tail . . ." (Aitken, 1971, p. 105).

FEET: As described by Spencer (1895) and Aitken (1971), the hind foot has hair on the ventral surfaces except the pads and a median strip that extends from about 3 mm. posterior to the hallux to the base of the interdigital pads. The interdigital pads have slightly enlarged median rows of granules but without any suggestion of a large apical gran-

ule. Aitken (1971) noted that the fourth pad of the front foot is horseshoe shaped. There is evidently no hallucal pad on the hind foot. The terminal pads of the digits are granular.

NIPPLE NUMBER: The number has never been recorded.

PELAGE: The mid-dorsal region has a drab, brindled appearance that continues onto the forehead between the ears, producing a dark patch similar to that of *S. crassicaudata* which ends between the eyes. A dark ring is present around the eye (not white as Spencer 1895, records). The crest on the tail is generally fuscous black.

DENTITION (BASED ON SAM M7662 AND WAM M6217): I^1 is tall and small, and separated from I^2 by a diastema. The I^4 is considerably longer-crowned than I^3 which is slightly longer-crowned than I^2 . The I^4 has no conspicuous posterior lobe. The diastema between I^4 and C^1 has a fossa which corresponds to the tip of C_1 . C^1 is caniniform, considerably taller-crowned than P^4 , lacks cingula, and has no conspicuous posterior cingular cusp. P^1 is shorter-crowned than P^3 which is shorter-crowned than P^4 . Premolars appear to lack continuous lingual and buccal cingula, although cingula do occur on the anterior and posterior margins of the teeth leading away from anterior and posterior cingular cusps. Upper premolars are narrow-crowned and do not contact each other anteroposteriorly. Styler cusp A is vaguely distinguishable on M^1 only, being indistinguishable from the anterobuccal corner of the anterior cingulum on M^2 to M^4 . Styler cusp B is present on M^1 to M^4 and is connected to the paracone via a paracrista except on M^1 which has no paracrista. Styler cusp D is largest on M^1 , slightly smaller on M^2 , smallest on M^3 , and absent on M^4 . Styler cusp E is present and subequal in size on M^1 to M^3 . The paracones of M^1 to M^4 increase in size posteriorly. The metacones of M^1 to M^3 are subequal in size. M^4 lacks a metacone. The protocones of M^1 to M^3 are subequal in size and larger than the protocone of M^4 . The anterior cingula of M^2 to M^4 are short and narrow. The anterior cingulum of M^1 is long and narrow and does not contact the preprotocrista. There are no protoconules or metaconules. The paracristae of

M^2 to M^4 increase in length posteriorly. The metacristae of M^1 and M^3 are subequal and shorter than the metacrista of M^2 . The I_1 is the tallest lower incisor crown but I_3 is the longest. I_3 has a moderate posterior lobe. No diastema separates P_1 and C_1 . C_1 to P_1 lack buccal cingula. C_1 has a lingual cingulum, a posterior cingular cusp, and is taller-crowned than P_3 or P_4 . P_1 is shorter-crowned than P_3 which is subequal to P_4 . Lingual cingula occur on P_1 to P_4 but are incomplete beneath the protoconid. Anterior cingular cusps are present on P_1 to P_4 , being largest on P_1 and smallest on P_4 . Posterior cingular cusps are present on P_1 to P_4 , being smallest on P_1 and largest on P_4 . The lower premolars generally do not contact each other anteroposteriorly. The paraconids increase in height posteriorly from M_1 to M_4 . The metaconids of M_2 to M_4 are subequal and larger than the metaconid of M_1 . The protoconid of M_1 is subequal to that cusp in M_4 and shorter in height than that cusp in M_2 and M_3 . The hypoconids of M_1 to M_3 are subequal in height. The entoconids are very small on M_1 to M_4 , being smallest on M_4 . They increase in size posteriorly from M_1 to M_3 . The entoconids are situated close to the hypoconulids and the lingual end of the hypocristid (a condition which approximates that seen in *S. crassicaudata*). The paracristids on M_1 to M_3 increase in length posteriorly. The paracristid of M_4 is subequal to the paracristid of M_2 . The metacristids of M_1 to M_3 increase in length posteriorly and the metacristid of M_4 is subequal in length to the metacristid of M_3 . The talonid of M_1 is wider than the trigonid, subequal to it in M_2 , and wider than the talonid in M_3 to M_4 .

SKULL AND DENTARY (BASED ON SAM M7662): The cranium is gently but clearly domed with maximum convexity occurring in the parietals posterior to a point above the ventral tip of the tympanic wing of the alisphenoid. Nuchal and sagittal crests are developed. A longitudinal depression occurs in the region of the naso-frontal suture. No postorbital processes occur on the frontals. The lacrimal foramina occur on the rim of the orbit. The transverse canal foramina are very large and equal to or larger than the size

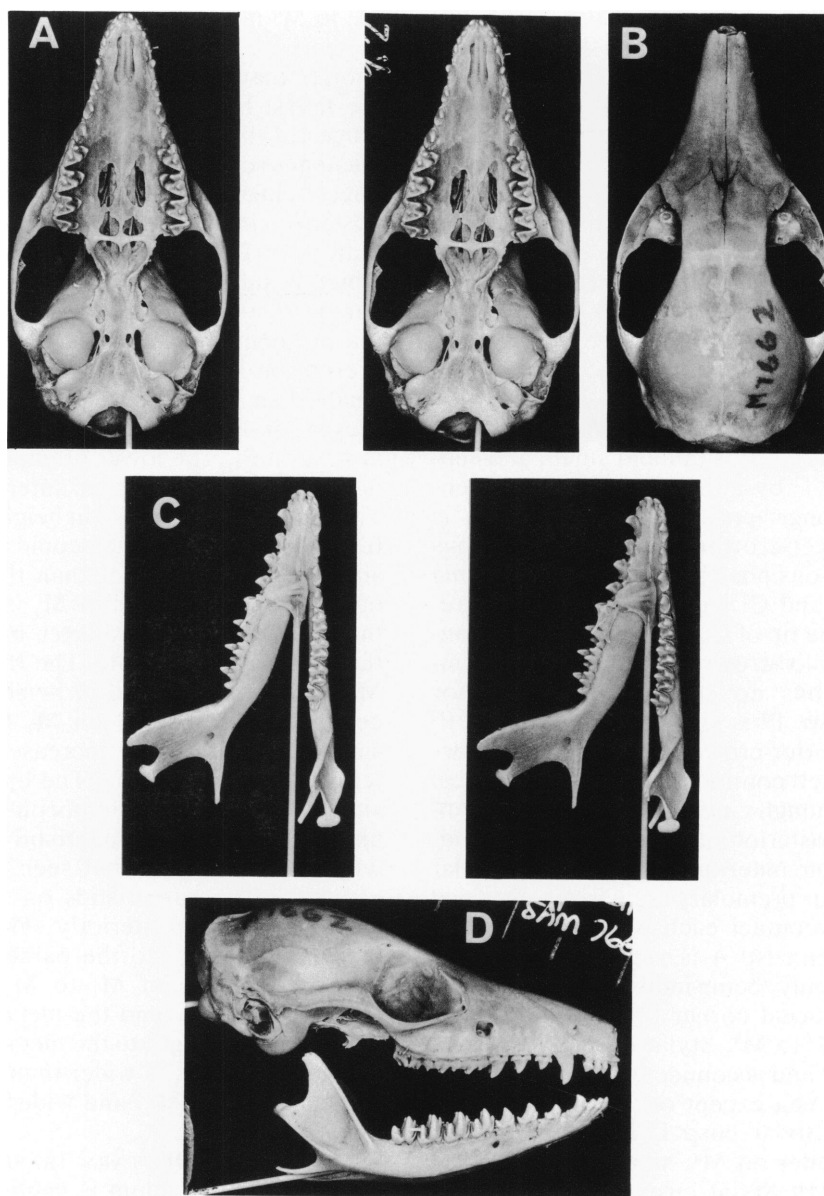


FIG. 34. *Sminthopsis psammophila*, SAM M7662, adult, South Australia. A-D, $\times 2$.

of the foramen rotundum. Small basicranial openings appear to extend from the foramina of the transverse canal into the alisphenoid hypotympanic sinus. Openings also extend posteriorly to link up with the endocranial space, as well as mesially to cross the basi-

sphenoid. The foramen rotundum has a well-developed ventral bony shelf. The entocarotid canal opens posteriorly and allows an unimpeded ventral view through the basisphenoid. The foramen pseudovale is elongate, and the posterior lacerate foramen

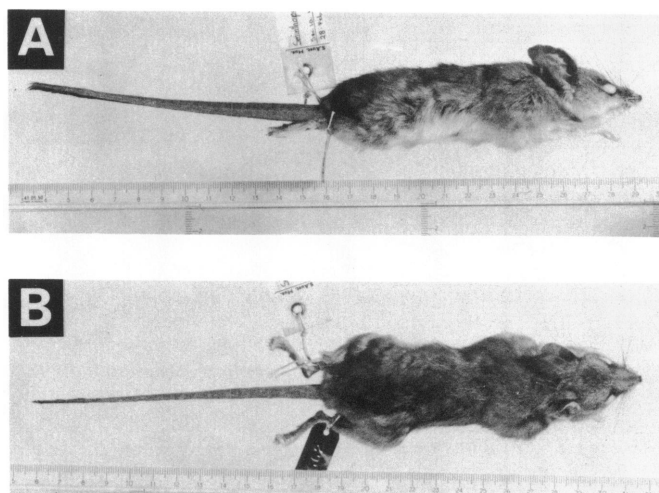


FIG. 35. *Sminthopsis psammophila*, SAM M7662, adult, South Australia. Numbers on scale are centimeters.

large. The basioccipital has an anteroventral median keel. The basisphenoid is only mildly convex in the ventral midline. The hamular process of the pterygoid lacks distal enlargements. The alisphenoid and periotic tympanic wings are moderately enlarged but leave the ectotympanic relatively well exposed. Palatal vacuities are relatively small with the premaxillary vacuity extending posteriorly to the level of the anterior end of P^1 , and the maxillary vacuity extending anteriorly to the level of the metacone of M^1 . Posterolateral palatine vacuities are well formed but not closed posteriorly. The masseteric fossa of the dentary is moderate in size. The angular process is elongate. The symphysis extends posteriorly to the level of the middle of P_3 .

DISCUSSION: Tate (1947) regarded this species to be a race of *S. macroura* (as *lapinta psammophila*). This synonymy was unjustifiable as Troughton (1967) pointed out. With the recent discovery of this species on the Eyre Peninsula of South Australia, Aitken (1971) has published an excellent description of its color, general morphology and habitat data.

Sminthopsis psammophila has much in common with *S. granulipes* including the almost *Antechinus*-like upper molars (in outline), the long head, spaced and narrow pre-

molars, relatively poor development of the alisphenoid and periotic tympanic wings, small entoconids, and well-haired granulated hind feet and toe tips. There are of course differences such as the lack of pronounced bifidity of I_3 , the seemingly very different tail and pelage, and the very large ears of *S. psammophila*. Aitken (1971) suggested that *S. psammophila* was similar to *S. murina* but considered that statements regarding phylogenetic position were premature until all species of *Sminthopsis* had been examined.

HABITAT AND REPRODUCTION: Aitken (1971) concluded that the preferred habitat in South Australia is sand dune and interdune areas with mallee-broombrush (*Melaleuca uncinata*), and spinifex (*Triodia*). Parker (1972) suggested that the holotype from the Northern Territory was collected in sandhill country with spinifex (*Triodia*) and groves of desert oak (*Casuarina decaisneana*) in the swales. I have also identified remains of the species (see Parker 1973, p. 6, and WAM M6217) from owl pellets collected in 1959 and 1962 at Ayers Rock. Because all of these collection areas are dissimilar in one way or another, precise assessment of basic habitat requirements cannot yet be made other than to say it is a dry country

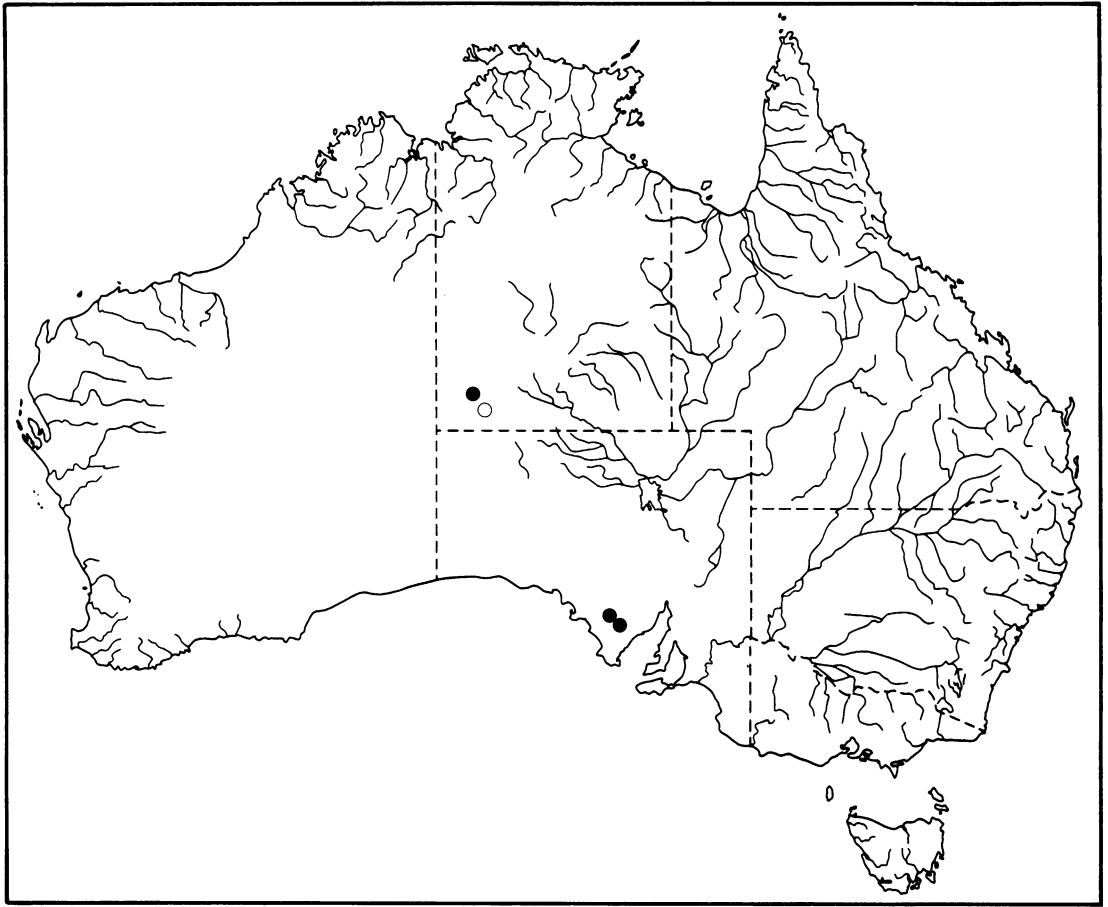


FIG. 36. Geographic distribution of *Sminthopsis psammophila*. Solid dots represent modern specimens observed. Circles represent specimens from the surfaces of cave floors.

animal that is found in some areas where sand dunes and spinifex occur.

No breeding data has been recorded. Aitken (1971 and *in litt.*) did not record nipple number.

REMARKS ABOUT THE TYPE SPECIMEN: In most respects the holotype is somewhat smaller than South Australian individuals. This may indicate a cline such as occurs in *S. murina* in which smaller dental dimensions appear to characterize more inland populations.

Sminthopsis virginiae (Tarragon)

Phascogale virginiae Tarragon, 1847.

Sminthopsis nitela Collett, 1897.

Sminthopsis rufigenis Thomas, 1922.

Sminthopsis lumholtzi Iredale and Troughton, 1934.

Phascogale rona Tate and Archbold, 1936.

TYPE SPECIMENS: *Phascogale virginiae* Tarragon, 1847. Holotype: Original type specimen is lost (Collett, 1887b, p. 579). Neotype: J15890, skull, carcase in alcohol, adult male. Collector is unknown. I have examined the neotype. Type locality: Type locality of the lost holotype is unknown (Tarragon, 1847, pp. 177–178). Type locality of the neotype is Herbert Vale (on the Herbert River, approximate lat. 18° 30', long. 145° 50'), northeastern Queensland, elevation 42.6 m. above sea level. *Sminthopsis nitela*

Collett, 1897. Cotypes: Male and female plus two other specimens (according to Collett 1897, pp. 334–335) one of which is BM 97.4.12.6 (by exchange with the Christiania Museum), skull and alcoholic carcase, adult female, collected by K. Dahl, July–October 1894. I have examined BM 97.4.12.6. Type locality: Collett (1897, p. 335), “Daly River, Northern Australia . . .” Dahl (1897, p. 208) noted that specimens were brought to him by Aborigines “on the Daly River, about sixty miles from the coast.” *Sminthopsis rufigenis* Thomas, 1922. Holotype: BM 22.2.2.76 (originally from the Buitenzorg Zoological Museum, Java), skull, and alcoholic carcase, adult female. I have examined the holotype. Type locality: Thomas (1922a), Aru Islands. *Sminthopsis lumholtzi* Iredale and Troughton, 1934. Holotype: University Museum of Zoology, Oslo, no. 2063, adult male, collected by C. Lumholtz, 1883. I have examined photographs and casts of the skull of the holotype. Type locality: Lumholtz (1889), Herbert Vale. This is along the Herbert River valley, northeastern Queensland (see discussion below). *Phascogale rona* Tate and Archbold, 1936. Holotype: AMNH 104005, skin and skull, adult female, collected by R. Archbold and A. L. Rand, March 14, 1933. I have examined the holotype. Type locality: Tate and Archbold (1936), Rona Falls, Laloki River, Astrolabe Range, Papua.

DIAGNOSIS: Large species of *Sminthopsis* comparable with *Antechinus flavipes* in size and similar to *S. douglasi* but differing from *S. douglasi* in being smaller, having a thin tail, and commonly a continuous anterior cingulum on the upper molars. It differs from *S. murina*, *S. ooldea* and *S. leucopus* in having large entoconids on M_1 to M_3 , a pronounced dark stripe on the forehead; and a premaxillary vacuity that does not extend posteriorly beyond a point level with the rear of the alveolus of C^1 . It differs from *S. granulipes* and *S. hirtipes* in being larger, in having a thin tail, rufous cheeks, large entoconids on M_1 to M_3 , enlarged apical granules on the hairless interdigital pads, and non-granular terminal pads on the toes. It differs from *S. psammophila* in being smaller, hav-

ing no crest on the tail, having rufous cheeks, large entoconids on M_1 to M_3 , smooth non-granular terminal pads on the toes; and a distinct mid-forehead stripe. It differs from *S. crassicaudata* in being larger, in having a thin tail, enlarged apical granules on the interdigital pads, entoconids on M_1 to M_3 that are clearly not contacted by the hypocristid, a premaxillary vacuity that extends no farther posteriorly than a point level with the rear of the alveolus of C^1 , and a P4 that is conspicuously larger than P3. It differs from *S. macroura* in being larger, in having a thin tail, rufous coloring on the cheeks, and commonly a continuous anterior cingulum on the upper molars. It differs from *S. longicaudata* in having a tail-vent length that is less than twice the nose-vent length, non-striated to barely striated terminal pads on the digits and the apical granules of the interdigital pads, large entoconids on M_1 to M_3 , canini-form canines; and a premaxillary vacuity that does not extend posteriorly beyond a point level with the rear of the alveolus of C^1 . It differs from *S. butleri* in being larger, having large entoconids on M_1 to M_3 , and in having rufous cheeks.

DESCRIPTION: Tail: The tail-vent length always exceeds the nose-vent length. The tail is always thin.

HIND FOOT: The very large oval apical granule is three to six times the size of the much smaller lateral granules (e.g., AM M7568), and the apical granule is commonly smooth without physical striae on its surface although it often appears to be striated (e.g., WAM M4056). Interdigital pads are separated to their base, and a small hallucal pad and isolated apical granule are present. The hind foot is relatively wide for *Sminthopsis* (but this condition varies intraspecifically in *S. murina* and to some extent *S. leucopus*). Commonly a small but conspicuous metatarsal granule is present (e.g., MM M1185). Pedal variations are described in detail below.

NOSE: The nose color and shape are variable but in some populations (e.g., Herbert River, Queensland) it is light colored, has a shallow medial groove which does not extend to the top of the nose, has a virtually

hairless narrow surrounding rim around the ventrolateral area, and nostrils whose mesial edge is less than half way between the lateral edge of the nose and the medial groove.

NIPPLE NUMBER: Two specimens from mainland Australia (C222 and MM M1180) have eight nipples, whereas six nipples have consistently been reported (Thomas, 1922 and Tate, 1952) for animals from New Guinea.

PELAGE MARKINGS: The face has a distinctive rufous patch on each side of the head extending from the nose, usually surrounding the eye, on the cheek and back as far as the anterior portion of the ear (e.g., B1841), and even beneath the ear. In some specimens it even continues posteriorly beyond the ear, merging with the lighter rufous flanks (e.g., WAM M2811). A dark mid-dorsal stripe is present on the head and clearly contrasts with the rufous areas on the sides of the head. The head stripe passes back between the ears and merges with the general dorsal body color. The color of the pelage of the back varies from Ridgeway (1912) Chaetura Black to Blackish Mouse Gray. Skins appear "flecked" or hispid because of lightly coloured tips on the guard hairs.

DENTITION: I^1 is taller-crowned than or subequal to I^2 . I^4 is always longer-crowned than I^2 and larger than or subequal to I^3 . The upper incisors lack posterior lobes. Diastemata separate I^1 from I^2 and I^4 from C^1 . A depression in the premaxilla posterior to I^4 corresponds with the position of C_1 tip. C^1 is large and exceeds P^4 in height but not length. C^1 functional height (i.e., the amount of crown and root extending beyond the alveolus of C^1) is between two and four times the crown height of P^1 . P^1 size is commonly reduced in direct proportion to the increase in size of C^1 . P^4 and C^1 are commonly erupted such that their crown bases are higher above the level of the palate than is the crown base of P^3 . The anterior root of P^4 is commonly longer than the posterior root. Combined with a posterior recurving of the P^4 crown, this commonly results in a tall, posteroventrally inclined tooth. Some specimens (e.g., AMNH 105817) exhibit only a slightly recurved P^4 . The crown height of P^4

is approximately twice that of P^1 , and the crown height of P^3 is intermediate or closer to that of P^1 . The buccal cingulum of C^1 is slight to absent. Buccal cingula on P^1 to P^4 and lingual cingula on P^3 to P^4 are constant. Lingual cingula on P^1 and C^1 are variably developed. Anterior and posterior cuspules on C^1 are absent or tiny, but present on P^1 to P^4 although the anterior cusps may be very small. Anterior cingula on M^1 to M^4 may be a normal feature but this was not checked in all specimens. It is at least a constant feature of Queensland Museum Cape York specimens, AMNH New Guinean specimens, and the type specimens of *rufigenis* and *rona*. However, the type of *nitela* and NTM4340, a specimen of *nitela*, lack a continuous anterior cingulum. Styler cusp A is barely distinct on M^1 but indistinct on M^2 to M^4 . Styler cusp E is variably present (e.g., J15890). The metacrista is shorter than or subequal to the length of M^3 . The alveolar area of the molar row is frequently elevated above the palate causing the tooth crowns to appear high above the palate (e.g., WAM M2811). The crown of I_1 is subequal to or longer than that of I_2 . I_3 is the longest lower incisor. A small posterior cusp is present on I_3 . Buccal and lingual cingula are commonly, but not invariably, present on C_1 . Thegotic wear (see Every, 1970 and 1972) is frequently evident on C^1 . C_1 is taller than P_4 . The premolars are broad and often so spaced that they do not contact one another (e.g., MM M1180). P_1 is reduced in size, being considerably smaller than P_3 (e.g., MM M1180). P_4 is often taller than or equal in height to the protoconids of the lower molars (e.g., WAM M2811). P_3 and P_4 crown heights are subequal, or P_4 slightly exceeds P_3 . Buccal cingula are present on P_1 to P_4 . The shape of the cingular margin of P_3 and P_4 is variable but occasionally the posterobuccal corner of the tooth is depressed ventrally producing a marked anterodorsal slope in the buccal cingulum. P_4 crown shape above the cingulum is variable. It is sometimes compressed anteroposteriorly producing a tall slender crown (e.g., AMNH 105582). Entoconids are well developed on M_1 to M_3 and are not near the hypocristids. Buccal cingula are commonly developed on

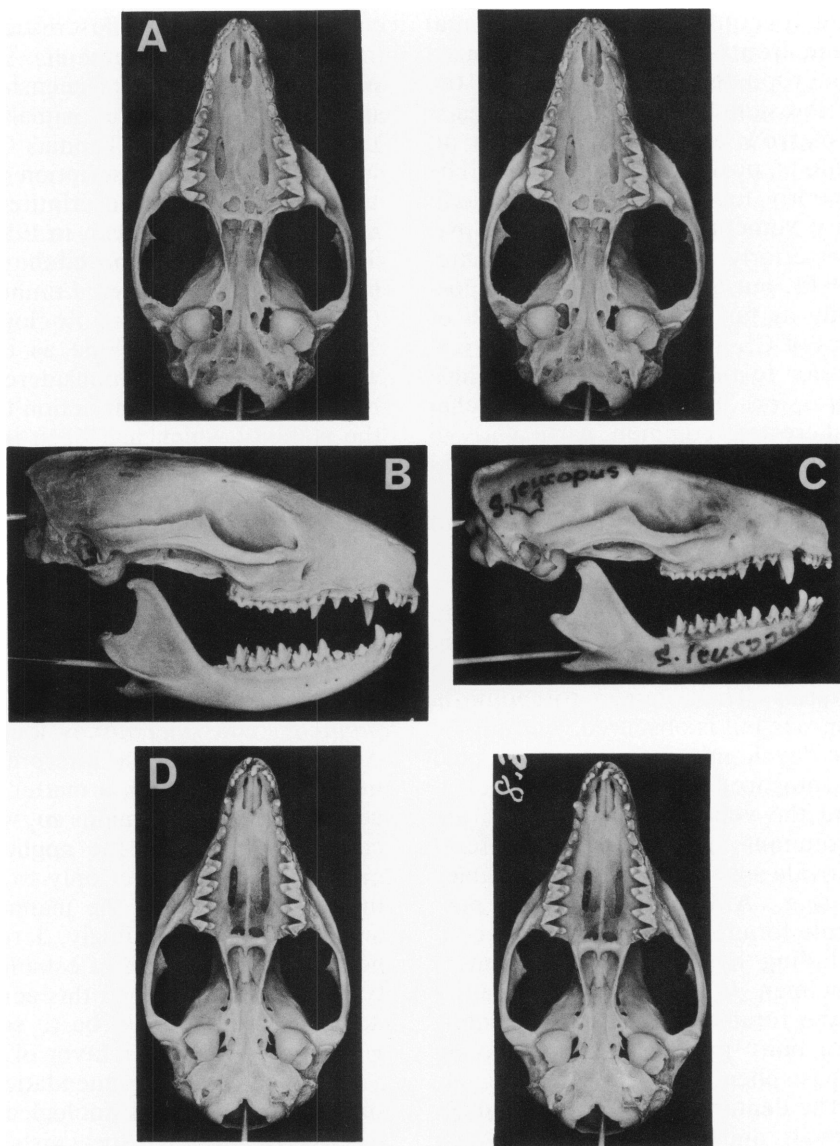


FIG. 37. *Sminthopsis virginiae*. A–B, AMNH 105796, adult, Lake Daviumbu, Papua (*rufigenis*). C–D, J3237, adult, Cooktown, Queensland (n nominate form). A–D, $\times 2$.

M_1 to M_3 but are generally incomplete beneath the protoconid and hypoconid (an exception is M_1 of WAM M2811). Parastylids are well developed on M_2 to M_4 . The talonid is wider than the trigonid on M_1 to M_2 but subequal to or narrower than the trigonid of M_3 . The ascending ramus is wide. The an-

terior margin of the ascending ramus and the posterior margin of the dentary are sharply divergent. The angular process is very broad at its base, tapers quickly, and is relatively short.

SKULL AND DENTARY: The skull is domed anteroposteriorly such that the out-

line of the anteroposterior dorsal midline is conspicuously convex. The anterodorsal part of each frontal is bulged producing a narrow anteroposterior depression in the midline of the skull. The interorbital area is relatively narrow and sometimes (not always) exhibits postorbital processes. The palate is poorly fenestrated. The premaxillary vacuity sometimes (e.g., MM M1182) extends posteriorly to the level of the anterior end of P¹, but generally it extends posteriorly only as far as the posterior end of the alveolus of C¹. The lacrimal canal is just on or anterior to the rim of the orbit, in a slight depression. Development of nuchal and sagittal crests is common, particularly in older individuals. The lacrimal sometimes (e.g., WAM M2811) develops a posterodorsal spine. The interorbital area is narrow and tubular. The basicranium is broad. The alisphenoid tympanic wing is very poorly developed and leaves the ectotympanic broadly exposed. The ventral periotic tympanic wing is relatively small. The size of the transverse foramina varies. The foramen rotundum is moderate in size but is obscured ventrally by an anterior development of the alisphenoid floor. The entocarotid canal varies in development and the ventral opening of the entocarotid foramina varies in size. The foramen pseudovale size varies but is sometimes very large (e.g., AMNH 105796). The posterior lacerate foramen is large, and the condylar (including hypoglossal) foramen is small. Specimen J3237 shows basicranial variation: the foramen pseudovale is interrupted by a bony posterolateral projection from the basisphenoid portion of the alisphenoid. The dentary tends to be very deep in adult animals, and makes the lower molars seem short by comparison (e.g., WAM M2811). The angular process is very broad at its base (e.g., WAM M2811), not slender as in most other species. The masseteric fossa is very broad.

DISCUSSION: The name *Sminthopsis virginiae* (Tarragon) was in common use from 1847 to 1934 and during that time, no one doubted how the name should be applied. During that time, Collett (1887a, p. 549) noted that the type of *S. virginiae* was evidently

lost and described another specimen which matched Tarragon's description but which was collected by Lumholtz from Herbert Vale in northeastern Queensland (remarks on the collection of the animal are provided by Lumholtz, 1889). Thomas (1888, p. 302) accepted Collett's description as Collett intended, an amplified description of *S. virginiae* (Tarragon). However, in 1934 Iredale and Troughton (p. 11) proposed the name *S. lumholtzi* for the specimen Lumholtz obtained (University Museum of Zoology, Oslo, no. 2063) from Herbert Vale as the holotype. Tarragon's name was considered by them to be inquiring and their action thereby upset the stability which had been introduced by Collett (1887a) and Thomas (1888). The name *lumholtzi* has been used in the literature mostly by Troughton but has not been used to qualify any new zoological observations largely because Tate (1947) suggested that *S. lumholtzi* should be a synonym of *S. rufigenis*. The synonymy introduced in the present paper involves the name *S. nitela* Thomas which would take priority over both *lumholtzi* and *rufigenis* as the valid name. As is shown here, the interpretation of the name *nitela* has been a matter of some uncertainty, and still remains so, whereas there can be no doubt of the application of the name *virginiae* subject only to our continuing to interpret it in the manner of Collett and Thomas. Accordingly, I reintroduce it here by the expedient of establishing a neotype. The alternative to this action (which I do not support) would be to suppress both *virginiae* and *nitela* in favor of *rufigenis*. In accordance with recommendation 75A of the International Code of Zoological Nomenclature I have consulted specialists (namely Mr. B. J. Marlow, the late Mr. H. Van Deusen, Dr. D. Kitchener, and Dr. W. D. L. Ride). None has raised objections to this solution to the problem. Dr. Francis Petter of the National Museum of Natural History in Paris informs me (*in litt.* September 18, 1973) that the holotype of *Phascogale virginiae* is not in that Museum. Queensland Museum J15890, from Herbert Vale, northeast Queensland (collector unknown), is selected as the neotype of *Sminthopsis virginiae* (Tar-

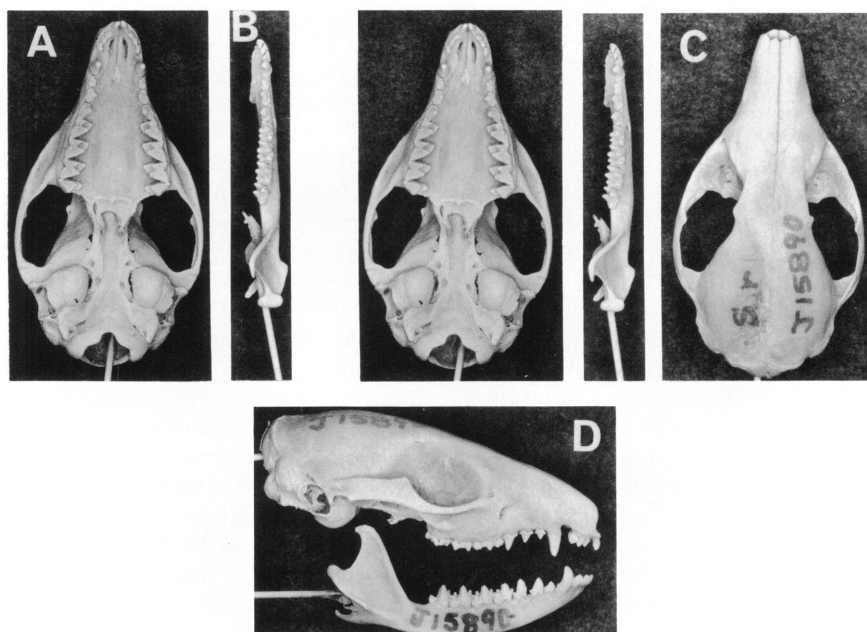


FIG. 38. Neotype of *Phascogale virginiae* Tarragon (= *Sminthopsis virginiae virginiae*), J15890, adult, Herbert Vale, Queensland. A-D, $\times 2$.

ragon) rather than the specimen used by Collett and Thomas to define the characters of *S. virginiae*. The decision not to use this specimen (the only one Lumholtz collected) as a neotype is based on the fact that Lumholtz's specimen is badly preserved, being a mounted specimen with badly damaged feet, skull, and dentaries. The original type locality is unknown and the specimen now chosen is from the same locality as the specimen which Collett and Thomas used to fix the morphological concept of *S. virginiae*. There is, in addition, a large series of specimens from the Herbert River in the Macleay Museum.

Tate and Archbold (1941) recognized the synonymy of *S. rona* (Tate and Archbold) and *S. rufigenis* Thomas. Troughton (1965) discussed the similarity of *S. nitela* Collett and *S. virginiae* (as *lumholtzi*). Ride (1970, p. 247) recognized the synonymy of *S. virginiae* (as *S. lumholtzi*) and *S. rufigenis*. The oldest name is *S. virginiae* (Tarragon).

FORMS OF *SMINTHOPSIS VIRGINIAE*: Five

names have been proposed for specimens (holotypes) considered in this study to be referable to *S. virginiae*. No attempt has been made to determine the statistical validity of these as subspecies. However, some of these names are useful to describe geographically isolated forms which are also morphologically unique. In addition, other possibly unique forms are noted which have no formal names.

Sminthopsis virginiae virginiae

DISTRIBUTION: Range of this form is only northeastern Queensland. Type specimens from within this range are the holotype of *S. lumholtzi* Iredale and Troughton and the neotype of *S. virginiae* Tarragon.

RECOGNITION: This form differs from *rona* in being larger, having a relatively larger alisphenoid tympanic wing, and a nipple number of eight. It is not clear how the typical form may consistently be distinguished from the *nitela* form, other than by its larger size.

PEDAL VARIATIONS: Pedal variation in the nominate form is illustrated in a series of 10 alcohol specimens (MM M1178–87) collected at or near the type locality (Herbert River) by an unknown person at an unknown time. Four out of eight have enlarged metatarsal granules; all eight have hallucal granules; seven out of eight have apparent striae on the apical granules (without any actual surface expression on the granule); one has no striae at all; three out of eight exhibit some adjacent granule fusion between the apical and surrounding granules, and in one case (MM M1181) fusion or wear has obliterated the granule boundaries over most of the surface of interdigital pads two to four on the left foot only. In another case (MM M1186) the skin of the foot has slipped, the smooth cover of the apical granules has been raised, and beneath this surface cover the apical granules are clearly striated.

NIPPLE NUMBER: Tate (1952) examined over 60 New Guinean individuals of *rona* and suggested that nipple number and body color served to distinguish the nominate form from *rona*. Specimens of *rona* have (Tate, 1952, p. 580) "distinctly darker pelage and tail and more markedly russet hands and feet," specimens of the nominate form being definitely grayer. He also notes that although specimens of *rona* he examined were dried skins, the nipple number is consistently six thereby differing from the nominate form which has eight.

HABITAT AND REPRODUCTION: The specimen obtained by Lumholtz was presumably given to him by aborigines. Lumholtz (1889, p. 252) noted that "It burrows in the earth and is dug up by the natives, who are fond of its flesh." This observation led Collett (1887a) to assume the species was not arboreal. Tate (1952, p. 579) discussed the habitat of the typical form in northeastern Queensland. He said that it "favours open rocky forest and brushy places in full sunlight." Later he added that it "inhabited the grassy, well-illuminated environment . . ." of *Melomys lutillus* and even, he suspected, was responsible for eating parts of specimens of *M. lutillus* caught in traps.

Tate (1952) recorded that the only female

of this form he examined had eight nipples. Two other specimens (C222 and MM M1180) I have examined had eight nipples. Nothing is recorded about the breeding period for this form.

Modern records of *S. v. virginiae*: Troughton (1965, p. 318) referred specimens (e.g., J5173) to this form from Julia Creek, north central Queensland. These specimens are described below as a new species, *S. douglasi*. Troughton also referred a specimen (AM M4403) from 145 km. northwest of Anthonys Lagoon, en route to Newcastle Waters, Northern Territory, to the nominate form. On the basis of the present study, this specimen is referred to *macroura* (see below). Bannister (1969) referred (and I agree in the identification) a specimen obtained by Mr. H. Butler in 1965 at Kalumburu, Western Australia, to this form.

CONDITION OF TYPE SPECIMENS AND COMMENTS: The undamaged skull and dentaries of the neotype of *virginiae* represent a young adult male. The alcohol carcass has distinctly rufous cheeks, and a darker brown dorsal head coloration that extends down the back and flanks. A hairless rim surrounds the lateral and ventral sides of the rhinarium. The median groove of the rhinarium does not extend to the top of the nose. The apical granules of the interdigital pads are large, oval and appear faintly striated although these striations do not exist physically on the surface of the pads. There is a large hallucal granule on a slightly enlarged hallucal pad. There is no clear indication of a metatarsal pad or enlarged granule. The interdigital pads are separated to their bases. Hair covering on the ventral surface of the foot extends diagonally across the foot from the proximomesial corner of the heel to the distolateral corner of the foot at the base of the fifth toe. Alcohol measurements are as follows: nose-vent (without skull in head), 86.4; tail-vent, 98.7; hind foot (su), 20.7; ear (n), 18.9. The holotype of *lumholtzi* has not been examined. However, photographs of the skull have been kindly provided by Dr. W. D. L. Ride and a cast of the dorsal side of the cranium has been examined. The label with the holotype says "*Sminthopsis virgin-*

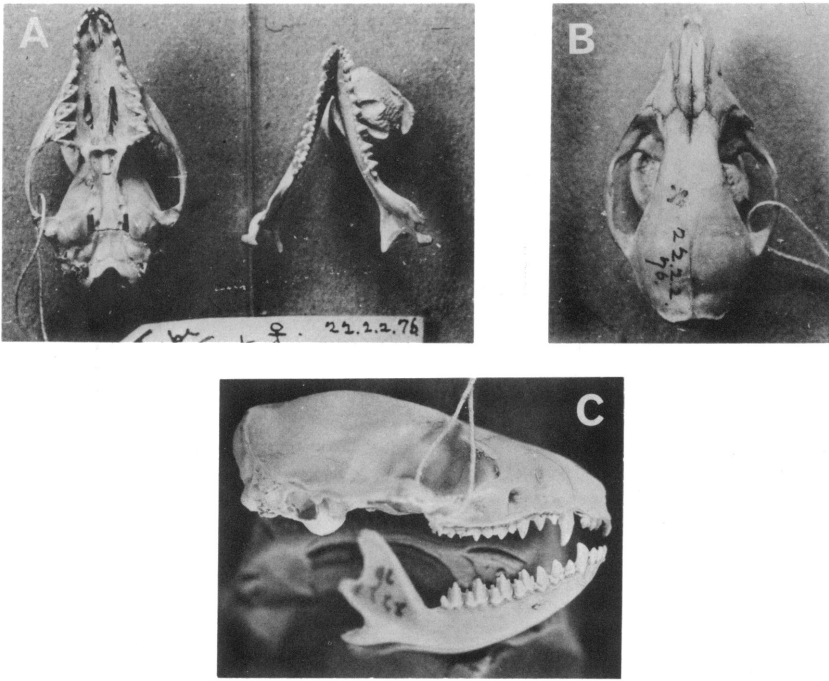


FIG. 39. Holotype of *Sminthopsis rufigenis* Thomas, BM 22.2.2.76. See table 2 for measurements.

iae, de Tarrag, Herbert River Queensland J. 83 Ltz." Lumholtz (1889) stated that the specimen of *S. virginiae* he obtained came from Herbert Vale in the Herbert River valley, in the last days of his stay. He also recorded (p. 253) that "Near the end of February . . ." he left for the Valley of Lagoons west of the Herbert River valley. However, the date of collection of January on the label is the same as that given by Collett (1887b). Thomas (1888) mistakenly described the locality of Lumholtz's specimen of *S. virginiae* as "Herbert Vale, Central Queensland." In view of Lumholtz's own remarks (1889) and map it is clear that the Herbert Vale Lumholtz refers to is the one in northeastern Queensland. Parker (1973) commented on this possible confusion in localities. Photographs of the skull of the holotype indicate that the teeth are worn, the posterior portion of the palate is missing, the right alisphenoid tympanic wing is broken, the left angular

process is broken and the right dentary is missing posterior to M_4 . RC_1 and P_1 also appear to be missing. Collett (1887b) gave a description and measurements of the body and skull.

Sminthopsis virginiae rufigenis

DISTRIBUTION: Range includes Papua, and the Aru Islands. The type localities of *Phascogale rona* Tate and Archbold and *Sminthopsis rufigenis* Thomas are within this range.

RECOGNITION: *Rufigenis* may be distinguished from the nominate form by its smaller size, smaller alisphenoid tympanic wing, and lower nipple number (six). It is not yet clear how this form may consistently be distinguished from *nitela*.

REMARKS ABOUT EXTERNAL MORPHOLOGY: Both alcohol specimens (the type of *rufigenis* and AM M7568, Port Moresby, Pa-

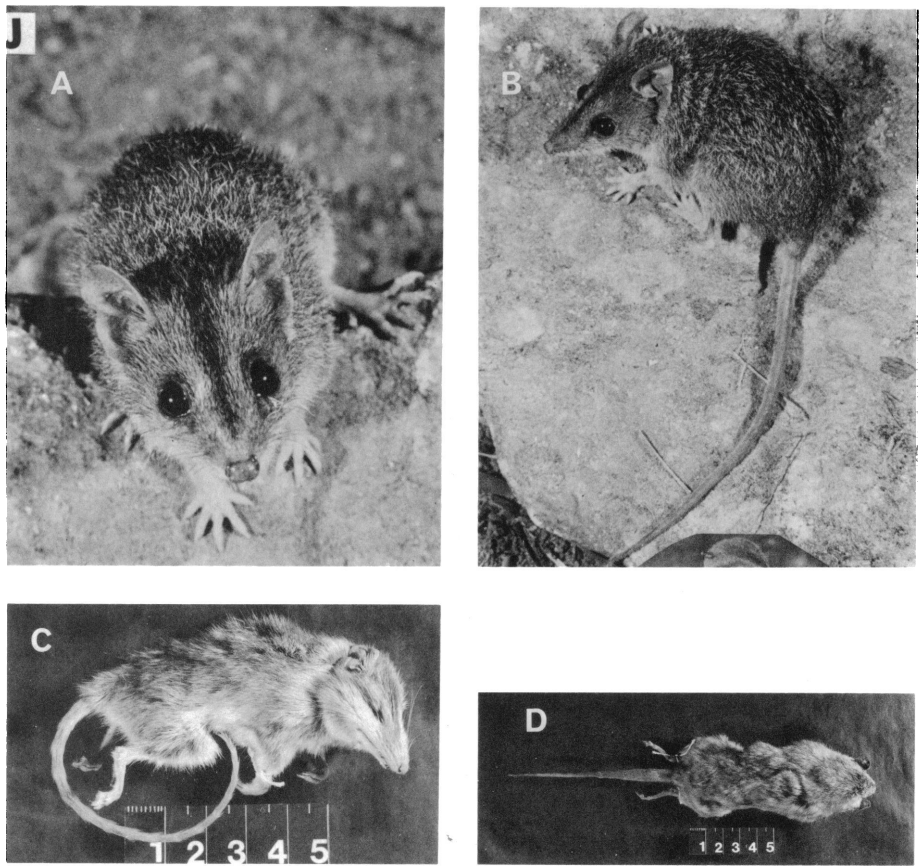


FIG. 40. *Sminthopsis virginiae* and *S. douglasi*. A–B, adult, Iron Range, Queensland. C, Neotype, J15890, adult, scale units are centimeters. D, *Sminthopsis douglasi*, paratype, AM M2172, scale units are in centimeters.

pua) of *rufigenis* seen in this study have no enlarged metatarsal granules on the hind foot. The noses of the holotype of *rufigenis* and AM M7568 are similar to the nose of the neotype of *S. virginiae* in being light colored, having a shallow medial groove which does not extend to the top, and a relatively hairless rim around the ventrolateral corners. There are no known females of *rufigenis* with more than six nipples. A dry skin of *rufigenis* examined in this study (WAM M2811 from the middle Fly River, Lake Daviumbu, Papua) has darker upper fore foot and hind foot pelage, and a more ochraceous belly color than two dry skins of *nitela* (NTM 4340, B 1841).

HABITAT: Tate (Tate and Archbold,

1941) trapped over 60 individuals of *rufigenis* from the Lake Daviumbu area in the savanna country of the middle Fly River where they were found to inhabit low grass-savanna with swamps and flooded extensions of the lake.

CONDITION OF TYPE SPECIMENS: The skull of the holotype of *Sminthopsis rufigenis* is in good condition except for some damage to the nasals. The dentaries are warped buccally, a condition not uncommon in decalcified spirit specimens. Thomas (1922a and 1922b) gave a description of the skull and externals, noting that the type is a female with two juveniles, and six nipples. The apical granules of the interdigital pads are elongated, striate, and surrounded by much smaller granules. Only the third inter-

digital pad suggests the apical granule is part of a median row of granules. The hallucal pad has a small oval apical granule with apparent rather than actual striae. The skull of the holotype of *Phascogale rona* is broken with most damage occurring to the cranium. Tate and Archbold (1936, p. 2) noted that the holotype had a broken occipital region. It should be pointed out that the label gives "Tail vert: 98" indicating a possible source of confusion in tail length measurements. Presumably TV could mean either "tail vertebrae" or "Tail-vent," the latter being the measure I have used (following Thomas, 1888) and as more appropriate for marsupials than the former.

Sminthopsis virginiae nitela

DISTRIBUTION: Range includes the northern Kimberleys, Arnhemland, and possibly Melville Island. The type locality for *Sminthopsis nitela* Collett occurs within this range.

RECOGNITION: *Nitela* may be distinguished from the nominate form by its smaller size, and from the nominate form and *rufigenis* by its lack of an anterior cingulum on the upper molars.

REMARKS: Specimens referred to *nitela* in this study are all somewhat diverse and may represent more than one form. Areas involved include the type locality; Kalumburu Mission in Western Australia (lat. 14° 15', long. 126° 40'); Oenpelli Mission (lat. 12° 20', long. 133° 04'); East Alligator River; Four-mile Billabong on the Wildman River (lat. 12° 38', long. 132° 02') in the Northern Territory; and Melville Island off the coast of the Northern Territory.

Specimen WAM M5056 from Oenpelli Mission: The carcase in alcohol of this specimen has enlarged apical granules on the interdigital pads that clearly resemble those of the nominate form, but it has a smaller hallucal pad and granule. Its teeth are smaller than any other specimen of this species. Another specimen from this locality recorded by Johnson (1964, pp. 442–443) is larger and more closely approximates other specimens of *S. virginiae* from north-central Aus-

tralia and New Guinea. Johnson's description suggests close similarity with the characters of WAM M4056. He considered his specimen to represent *nitela* because it agrees closely with Collett's (1897) original description.

Specimen B1841 from Kalumburu Mission: This specimen (obtained by W. H. Butler in 1965) is a juvenile (M^3 is erupting) and the feet are dessicated. However, the apical granules of the interdigital pads, as well as the external body coloring, are clearly representative of *S. virginiae*. This is the only known specimen of this species from Western Australia.

Specimen C6344 from the East Alligator River: In terms of dental size, this specimen is referable to the *nitela* form rather than the nominate form of the species.

Specimen NTM4340 from the Four-mile Billabong, Wildman River: This specimen (obtained by F. Pocock in 1968) has unusual hind feet with very long and apparently striated apical granules. The length and narrow width of these granules are unmatched by any other specimens of *S. virginiae* I have seen and more closely resemble those of *S. leucopus*. The skull is badly damaged, evidently having been burned during preparation.

Specimen AM M4403 from 145 km. northwest of Anthonys Lagoon: This specimen (obtained by T. G. Campbell) was referred by Troughton (1965) to *S. virginiae* (as *lumloltzi*). It is abnormal dentally (Archer, 1975) and it may represent *S. macroura*. The tail is mildly incrassated and reminiscent of *S. macroura*, but the external coloration and feet suggest *S. virginiae*. It may represent a hybrid between *S. virginiae* and the adjacent Barkly Tableland *S. macroura*.

Specimen SAM M4072 from Melville Island: The hind feet of SAM M4072 (collected by W. Dodd in 1913) have interdigital pads with medial rows of slightly enlarged granules, a few of which appear faintly striated without having actual physical ridges on the surface. This morphology is closer to *S. murina* or *S. macroura* than *S. virginiae*. There is no hallucal pad or enlarged granule. However, the external body coloration and size

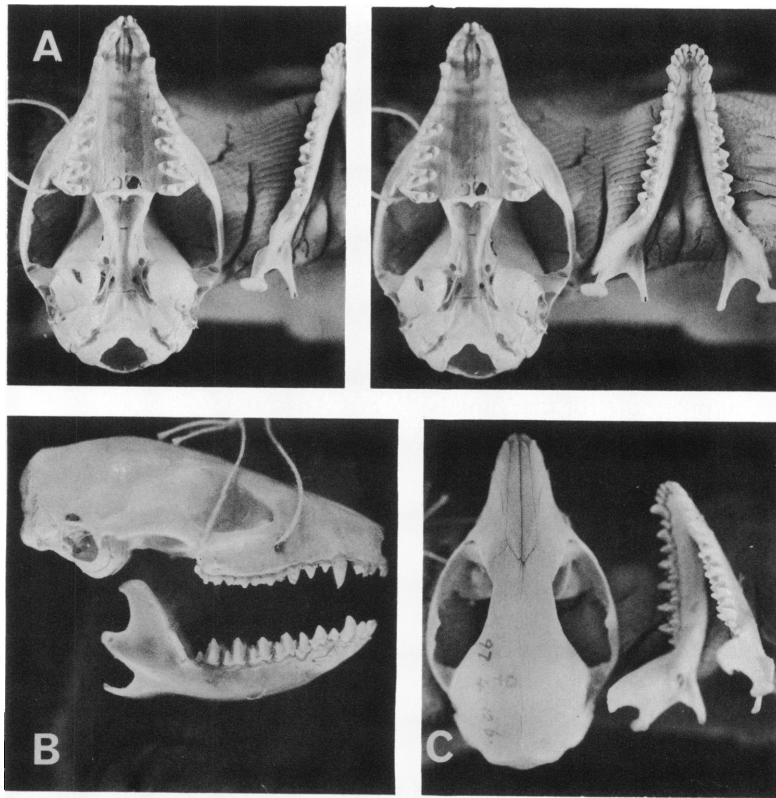


FIG. 41. Cotype *Sminthopsis nitela* Collett, BM 97.4.12.6. For measurements see table 2.

of the teeth are consistent with *S. virginiae* and closest to *rufigenis*. This animal may represent a distinct Melville Island form.

Cotype BM 97.4.12.6 from the Daly River: The hind feet of the alcoholic cotype have elongate and apparently striate apical granules, distinct enlarged and apparently striate hallucal granules, rufous cheeks, and a pronounced head stripe. Contrary to the original description, the tail is not incrassated, but is robust (see key characters of *Sminthopsis*), a character condition indicative of *S. virginiae*, not *S. macroura*.

VARIATION IN NOSES: The noses of some of these central northern Australian specimens (e.g., WAM M4056, SAM M4072, and the cotype of *nitela*) are comparable with those of specimens of the nominate form and the single alcoholic specimen of *rufigenis* ex-

amined in the present study. However, some are not. NTM 4340 and B1841 appear to have bicolored noses (in contrast to the common caramel color) being light-colored at the base but darker toward the top. In NTM4340 the nose is damaged and it is not clear whether there is a hairless ventrolateral rim around the corners. In B1841 it is clear that there is such a rim. This hairless rim is typical (but not diagnostic) of *S. virginiae*.

HABITAT: Collett (1897) stated that the type specimens of *nitela* were collected in July and October 1894, by aborigines who dug them out of gardens. Dahl (1897) noted that according to the evidence of the aborigines who collected the specimens, they were found sleeping in holes in the ground. There is therefore an apparent similarity in burrowing habits between *nitela* and the nominate

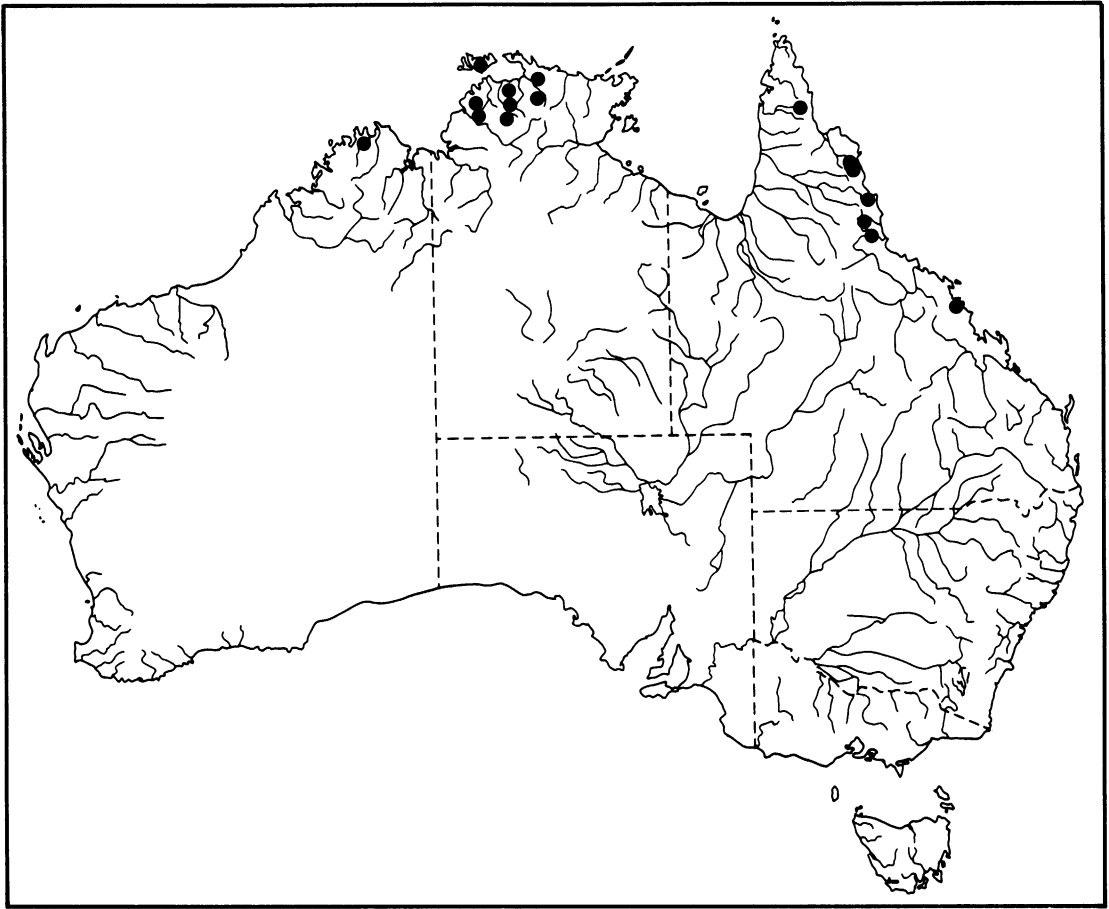


FIG. 42. Geographic distribution of *Sminthopsis virginiae* in Australia. The distribution in New Guinea is not shown, but discussed in text.

form (see above for comments by Lumholtz on collection of the specimen from Herbert Vale).

REMARKS ABOUT THE COTYPE OF NITELA: Collett (1897, p. 334) stated that the tail is incrassated and that on the foot there are "smooth (not striated) pads." He also noted the rufous cheeks and head stripe. His comparisons are made with *S. leucopus*. Thomas (1906) regarded *nitela* to be a synonym of *larapinta* Spencer (which is regarded here as a form of *S. macroura*) and suggested Collett was muddled about its distinction from *larapinta* by Spencer's (1896a and b) failure to mention the existence of a head stripe in *larapinta*. Thomas (1906),

however, failed to comment on Collett's observation of the rufous cheeks, size, and body color of *nitela* which are clearly not comparable with the corresponding features of *larapinta*. Tate (1947, p. 124) similarly treated *nitela* as a form of *larapinta* even though the rufous color of the cheeks and his photographs of the skull clearly indicated to him affinity with *rufigenis*. Iredale and Troughton (1934) followed convention and treated *nitela* as a form (in this case a synonym) of *larapinta*, and Johnson (1964) followed Tate (1947) even though he expressed the opinion that his specimen showed conspicuous differences from Spencer's (1896a) illustration of *larapinta*. Troughton (1965)

disagreed with Tate's arrangement and regarded *nitela* to be closely allied with the typical form of *S. virginiae* (as *lumpholtzi*). Ride (1970, p. 122) referred specimens from the Kimberley region of Western Australia to *nitela*. These specimens are described below as a new species, *Sminthopsis douglasi*.

None of the specimens (except the problematical AM M4403) of *S. virginiae* I have examined from northern central Australia have the "incrassated" tail Collett (1897) claimed occurred in the type of *nitela*. Johnson (1964, p. 443) noted of the specimen he referred to *nitela*, that the "tail is rather thick at the base, but is not conspicuously incrassated." The actual condition of the cotype of *nitela* is similar and Collett's description is misleading. The question of incrassation is often open to opinion. It is clear, for example, that the tails of *Sminthopsis macroura* are incrassated. They commonly have short narrow bases near the body which expand abruptly then gradually taper off in diameter towards the tip. This is a "spindle-shape." Another similar sort of incrassation is clearly exhibited by most *S. crassicaudata*. If, however, the tail does not have a grossly enlarged region but does have a base which is narrower than anywhere along the tail except the distal end, the question of incrassation may become a matter of opinion. The tails of some species do have narrow bases but not conspicuously swollen posterior parts. *Sminthopsis virginiae* is an example of such a species.

Collett (1897) also said of the cotype of *nitela* that the pads of the soles were "smooth" not striated. In fact, the apical granules have apparent striations, which is in keeping with the general appearance of the feet of most *S. virginiae*.

The diversity of hind-foot morphology in specimens from central northern Australia suggests that there may be more than one form of *S. virginiae* from this region of Australia. In particular the Melville Island specimen and the Wildman River specimen are both very distinctive. Some of these are evidently referable to *nitela*, whereas others may represent unnamed taxa.

Sminthopsis douglasi Archer

Sminthopsis douglasi Archer, 1979.

HOLOTYPE: Queensland Museum J5173, skull and carcass in alcohol, juvenile female, obtained by M. Browne, registered in the Queensland Museum July 24, 1931. Type locality: Archer (1979) "Julia Creek (lat. 20° 40' S, long. 141° 40' E) north central Queensland, in the watershed of the Cloncurry River."

DIAGNOSIS (Archer, 1980): Very large species of *Sminthopsis*, larger than all species except *S. psammophila*. Morphologically, it is similar to the smaller *S. virginiae* but differs from the latter in being much larger, having a very stout to incrassated tail, and in lacking a continuous anterior cingulum on the upper molars (some *S. virginiae* also appear to lack a continuous anterior cingulum, see above). It differs from all other species of *Sminthopsis* by the same characters which differentiate *S. virginiae*.

DESCRIPTION (after Archer, 1979): Tail: The tail is approximately equal to, or slightly longer than, the nose-vent length. Incrassation varies from being stout (paratype) to conspicuously swollen (holotype).

EAR: The ear is relatively large, with a markedly curled external edge on the supratragus, and with rufous hairs on the posterior-internal and ventral margins of the pinna of the holotype.

VIBRISSAE (see Jones, 1923, for terminology): The mystacial vibrissae are in seven to eight poorly defined rows with two to seven vibrissae in each row. Three submental vibrissae, one to two supraorbital vibrissae, and two to three genal vibrissae are present on each side.

HIND FOOT: The interdigital pads are fused near their bases. The apical granules are enlarged, elongate, and striate. The second and fourth pads appear in the holotype to have slight physical ridges on the surface of the granules although this may be an artifact of alcoholic dehydration. All interdigital pads of the paratype have striate apical granules with physical ridges on the surface of granule. The apical granule of the left third

interdigital pad of the holotype is not clearly striate. There is no enlarged hallucal granule in the holotype although a slightly enlarged hallucal granule occurs in the paratype. Metatarsal granules are not present. Hair on the feet covers the heel and extends diagonally across the foot to the anterodistal corner. The terminal pads of the digits are not clearly striate in the holotype but suggestions of striae occur on the terminal pads of the paratype.

PELAGE MARKINGS: The general color is as in *S. virginiae*, with rufous coloring on the cheeks and surrounding the eyes (except around the anterior margin). In the holotype the rufous coloring extends anteriorly just beyond the eye but in the paratype rufous coloring extends to the rhinarium. A dark brown head stripe extends in the holotype as far anteriorly as the rufous coloration. In the paratype the head stripe extends to the rhinarium. Although both specimens are alcoholic carcasses, there is an appearance of rufous hairs throughout the postcranial pelage, behind the ears, forearm, beneath the base of tail, and around the ankle.

NOSE: The hairless rim is restricted to the extreme ventral margins of the rhinarium. The medial groove in the holotype extends to (or stops just short of) the top of the rhinarium. The nose is bicolored, being caramel at the base to dark reddish brown at the top. The nose of the paratype is damaged but does not conflict with this description.

NIPPLE NUMBER: The holotype has eight relatively undeveloped nipples. The paratype has seven enlarged and elongate nipples, but one appears to be missing from the right side.

DENTITION: I^1 is conspicuously larger than I^2 and set off from that tooth by a diastema. I^4 is slightly larger than I^2 , and a slight increase in incisor crown size occurs from I^2 to I^4 . Between I^4 and C^1 is a fossa corresponding with the crown tip of C_1 . C^1 is considerably less than twice the height of P^4 , and subequal to twice the height of P^1 . There is an increase in premolar size from P^1 to P^4 . Buccal cingula on P^1 to P^4 are continuous, and poorly developed to absent on C^1 . Lin-

gual cingula are present on P^1 to P^4 , except beneath the paracone, and poor to absent on C^1 . Anterior and posterior cingula are present on C^1 to P^4 with small anterior cusps occurring on C^1 to P^4 and small posterior cusps on P^1 to P^4 . dP^4 has a large metacone, small and approximated paracone, basal poorly differentiated protocone, stylar cusp D (present on the LdP^4 but not RdP^4), prominent metacrista, no paracrista, possibly (RdP^4) a minuscule continuous anterior cingulum, and three roots. Continuous anterior cingula are absent on M^1 to M^3 (although the RM^1 of the paratype may have a minuscule continuous anterior cingulum) and present on M^4 . There are vague suggestions of stylar cusp C on M^2 and M^3 . The abnormal nature of stylar cusp C on RM^1 of the holotype and the compressed M^3 of the paratype I have described elsewhere (Archer, 1975). The metacrista of M^3 in the holotype is shorter than the crown length. I_1 is the largest lower incisor. I_2 is larger than I_3 . I_3 has a very small posterior cusp. C_1 is larger than P_4 . Premolars increase in size from P_1 to P_4 . Continuous buccal cingula occur on P_1 to P_4 . Anterolingual cingula are absent or tiny on P_1 to P_4 . The buccal and lingual cingula of C_1 are entire in the paratype but poorly developed in the holotype. The tip of the crown of P_4 of the holotype is visible beneath dP_4 . dP_4 is two-rooted with a protoconid, a topographic homologue of the hypoconulid, and a minuscule anterior cingulum. The entoconids on M_1 to M_3 are large but not in contact with the hypocristids. The talonids of M_1 and M_2 of the paratype are wider than the trigonids, but on M_3 the two are subequal as they are on M_2 of the holotype. An abnormal bifid entoconid occurs on RM_3 of the paratype (Archer, 1975).

SKULL AND DENTARIES: The lacrimal foramina are single or double, and on or just posterior to the edge of the orbit. The lacrimal has a variably developed posterodorsal spine. Postorbital processes are not present in the holotype or paratype. A dorsal antero-posterior depression is notable between the frontals. The skulls are mildly domed dorsally (but apparently less so than in *S. vir-*

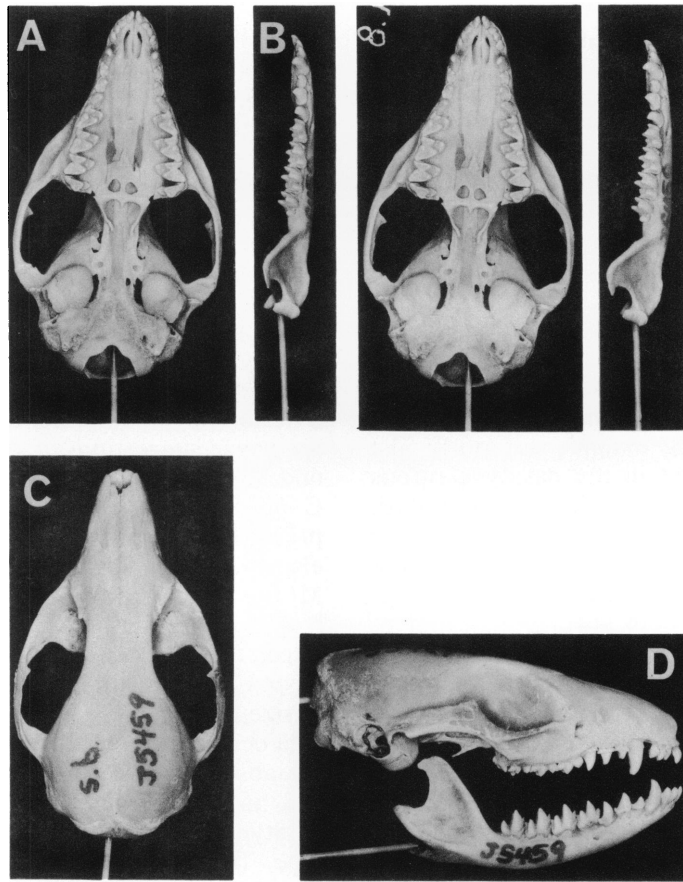


FIG. 43. *Sminthopsis douglasi*, Holotype, J5459. A-D, $\times 2$.

giniae). The premaxillary vacuities are short, not reaching a point level with the posterior edge of the canine alveolus. An indentation in the palate of the paratype suggests an incipient posterolateral palatal foramen. The alisphenoid and periotic tympanic wings are poorly developed and broadly expose the ectotympanic. The transverse foramina is small. The foramen rotundum is exposed ventrally in the paratype but is partially obscured by a ventral bony shelf in the holotype. The foramen pseudovalle is large with posterolateral projections extending out from the basisphenoid portion of the alisphenoid. The entocarotid canal varies in development from short in the paratype to

relatively long in the holotype. On the right side of the holotype, entocarotid canal development is such that the entocarotid foramen permits direct dorsoventral observation into the cranial cavity. The basioccipital walls of the internal jugal canal are not vertical. The masseteric fossa of the ascending ramus is broad with the anterior border of the ascending ramus and the posterior margin of the dentary widely divergent. The angular process of the dentary is stout, short, and abruptly tapered.

DISCUSSION: Troughton (1965) referred J5173 and J5459 to *S. virginiae* (as *lumholtzi*) without giving reasons. He did not mention the mildly incrassated tails or very large size

of these specimens. He also referred another north-central Australian specimen, AM M2172 from Myangarie Station, Richmond, with a markedly incrassated tail, to *S. virginiae*. Parker (1973) suggested that these specimens should be reexamined in view of the locality and habitat data. Subsequently, all of these specimens were named *S. douglasi* by Archer (1979). All three are much larger than *S. virginiae* and have mildly to conspicuously incrassated tails.

Sminthopsis douglasi appears to be most closely related to *S. virginiae*. Its large size may be a response to the presence of the sympatric and also distantly related *S. macroura* (e.g., J7680 from Richmond and J11463 from Julia Creek). Both species share many cranial, dental, and external characters such as the large and morphologically similar entoconids, small alisphenoid tympanic wings, short premaxillary palatal vacuities, relatively large canines, similar foot pad structure, and caudal incrassation. If competition occurred at some time in the past it might be expected that some form of character displacement would develop, such as the much larger size of *S. douglasi* (from a structurally smaller ancestral form similar to ancestral *S. virginiae*) (Archer, 1979).

HABITAT AND REPRODUCTION (Archer, 1979): The type locality and Richmond are ecologically different than areas inhabited by *S. virginiae*. Berney (1905:15) described the Richmond district as "this district, which lies within a radius of 70 miles of the township of Richmond, is situated 250 miles south of the Gulf of Carpentaria and a like distance from the east coast. Through the middle of it passes the Flinders River, which, like all the western waterways, only runs during the wet season. Its southern half consists of open, practically treeless, downs, well-watered by bore streams (artesian), along which beds of bulrushes (*Typha angustifolia*) have formed, making excellent shelter for many semiaquatic birds. The northern portion may be again divided into half downs and open timbered country, and half rough, low basalt ranges, more or less covered with gidea (acacia) and boree scrub. Along the river grow tall white-barked gums, while

coolibahs (both eucalypts) take their place on the creeks." The lower rainfall of the Julia Creek and Richmond areas (444–459 mm. per year) contrasts with the higher rainfall of areas containing *S. virginiae* (1135 mm. or more per year). The relatively more arid habitat of *S. douglasi* is probably responsible for selection for incrassated tails. Paratype J5459 had six juveniles attached to its nipples. These were removed for determination of the nipple number. The juveniles are shrivelled through alcohol dehydration. The lengths of the heads from nose to posterior edge of the occipital range from 6.0–6.4 mm.

MENSURATION: Measurements given by Archer (1979) for the holotype are (in mm.): HB 95.0; T, 97.0; HF, 21.0; E, 16.0. The tail measurement was probably made from the dorsal side and not as recommended by Thomas (1888, p. viii) from the vent. The former method is convenient for placental mammals which have a clear cut external boundary between the tail and body, but not for marsupials whose body and tail commonly have no such external boundary.

DETAILS OF THE PARATYPE: Paratype J5459 consists of a skull and damaged carcass in alcohol, collected by M. Browne at Garomna, Julia Creek. This is possibly the same locality as that of the holotype, although Garomna is not listed in the Queensland Museum catalogue in regard to the holotype. The registration date given in the Queensland Museum catalogue for J5459 is May 24, 1933. This date may roughly correspond with the collection date, but of this there can be no certainty. Although J5459 is technically an adult, having P4 erupted, it is a young adult with relatively unworn teeth. Both the holotype and paratype are females and may be expected to be smaller on the average than males. AM M2172 is a male and has a larger skull, although the teeth are subequal in size.

DETAILS OF THE REFERRED SPECIMEN: AM M2172, a young adult male, skin and skull, from Wyangarie Station, Richmond, north Queensland. It was presented by F. L. Berney to the Australian Museum. An old label attached to the skin says "*Sminthopsis* sp. nov. allied to *virginiae*. Central Queens-

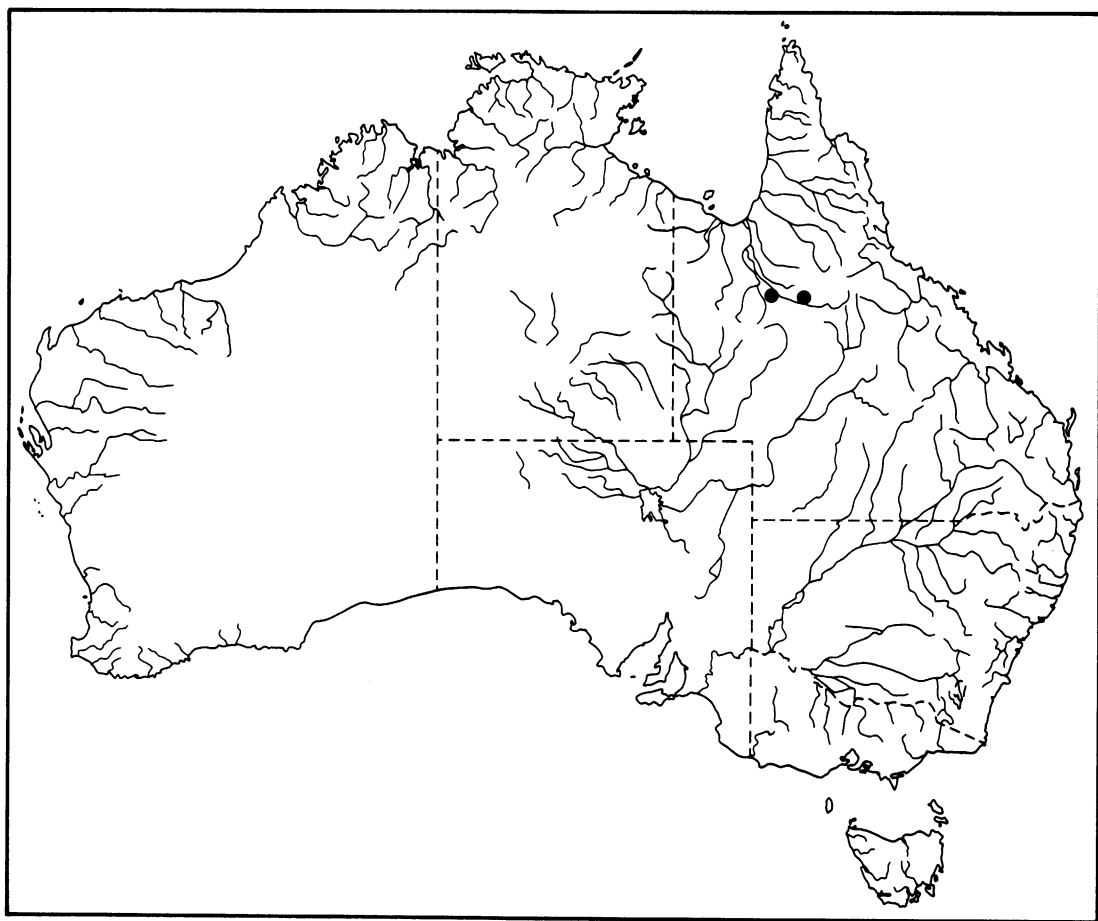


FIG. 44. Geographic distribution of *Sminthopsis douglasi*.

land." A note on the same label in E. Le G. Troughton's hand says "original label proving that A. A. McCulloch observed distinction, in association with 'virginiae.' E. LeG. T. 5/11/1963." The skin, even in the dehydrated state, shows a pronounced incrassated tail.

Sminthopsis macroura (Gould)

Podabrus macrourus Gould, 1845.

Antechinus (Podabrus) frogatti Ramsay, 1887.

Sminthopsis larapinta Spencer, 1896b.

Sminthopsis stalkerii Thomas, 1906.

Sminthopsis monticola Troughton, 1965.

TYPE SPECIMENS: *Podabrus macrourus* Gould, 1845. Holotype: No holotype was

originally designated. Lectotype: Designated here as no. 275 in Lord Derby's Catalogue of the Mammals in the Knowsley Museum in the Liverpool Museum, skin and skull, adult male, collected by J. Gilbert. I have examined the lectotype and paratypes BM 44.4.4.62 and BM 87.5.4.1. Type locality: Gould (1845a, p. 79), "Hab. Open plains, Darling Downs, New South Wales." Tate (1947, p. 122), "Darling Downs, south Queensland" Label with lectotype (John Gilbert's label, *in litt.* J. I. Harris, March 20, 1974), "Open Plains Darling Downs New South Wales." *Antechinus (Podabrus) frogatti* Ramsay, 1887. Holotype: AM M8019, skull and carcase in alcohol, adult

female, collected by W. W. Froggatt. I have examined the holotype. Type locality: Ramsay (1887, p. 551), "the neighborhood of Derby . . ." Western Australia. Troughton (1932, p. 353), "under debris near a beach, in the 'dindan' [*sic*] scrub bordering King Sound." *Sminthopsis larapinta* Spencer, 1896b. Lectotype: Dixon (1970) chose C6270, skull in carcase in alcohol, adult male, collected by P. M. Byrne, as the lectotype (a holotype not originally designated by number in the type description). I have examined the lectotype. Type locality: Spencer (1896b), Charlotte Waters (lat. 25° 55' S, long. 134° 54' E), Central Australia. *Sminthopsis stalker* Thomas, 1906. Holotype: BM 6.3.9.91, skull and skin, adult male, collected by W. Stalker, August 1, 1905. I have examined the holotype and paratype BM 6.3.9.90. Type locality: Thomas (1906, p. 543), South west of Alroy (lat. 19° 17' S, long. 136° 03' E), Barkly Tableland, Northern Territory. *Sminthopsis monticola* Troughton, 1965. Holotype: B 9579 (in the Australian Museum; this has nothing to do with the Butler collections), skull and carcase in alcohol, young adult female, donated in 1885 by E. H. Palmer. I have examined the holotype. Type locality: Troughton (1965, p. 311), Lawson (lat. 33° 43' S, long. 150° 26' E), altitude 732 m., on the Dividing Range.

DIAGNOSIS: A medium-sized *Sminthopsis* differing from *S. murina*, *S. ooldea*, and *S. leucopus* in having an incrassated tail, a pronounced head stripe, enlarged round to oval apical granules on the interdigital pads of the hind feet, large entoconids on M_1 to M_3 , and short premaxillary vacuities not extending posteriorly beyond a point level with the posterior edge of C^1 alveoli. It also differs from *S. murina* and *S. leucopus* in having an incrassated tail. It differs from *S. granulipes* and *S. hirtipes* in lacking granulated toe pads, lacking hair on the interdigital pads, in having a single enlarged round to oval apical granule on each interdigital pad, and large entoconids on M_1 to M_3 . It differs from *S. psammophila* in being smaller, having an incrassated tail, large entoconids on M_1 to M_3 , and in lacking a tail crest or granulated toe

pads. It differs from *S. crassicaudata* in having enlarged round to oval apical granules on the interdigital pads, a distinct stripe as opposed to a dark patch on the forehead, short premaxillary vacuities which do not extend posteriorly beyond a point level with the posterior margin of C^1 alveoli; and entoconids which are not close to or in contact with the hypocristids on M_1 to M_3 . It differs from *S. longicaudata* in having a head stripe, an incrassated tail, that is less than twice the nose-vent length, non-striated apical granules on the interdigital pads and terminal pads of digits, short premaxillary vacuities which do not extend posterior to a point level with the posterior margin of C^1 alveoli; and large entoconids on M_1 to M_3 . It differs from *S. butleri* in having an incrassated tail, and large entoconids on M_1 to M_3 . It differs from *S. virginiae* and *S. douglasi* in lacking conspicuous rufous cheeks, and in having a proportionally smaller apical granule on the interdigital pads. It also differs from *S. virginiae* in being smaller, in having an incrassated tail and in lacking an anterior cingulum on M^1 to M^4 (although this last character is not present in all *S. virginiae*, see above). It differs from *S. butleri* in having a distinct (as opposed to indistinct) stripe on the forehead, an incrassated tail, and distinct entoconids on M_{1-3} .

DESCRIPTION: Tail: The tail length varies according to geographic area but ranges from being shorter to longer than the nose-vent length. It is invariably incrassated.

HIND FOOT: Often apical granules appear to be oriented into medial rows (as in *S. murina*) of two to four granules, with the largest distal granule referred to as the apical granule. The apical granule is round to oval, enlarged, and normally twice, but less than three times, the size of the adjacent proximal granule in the medial row. The three interdigital pads are normally fused more than halfway up their height. Normally, there are no metatarsal pads or granules or hallucal pads or enlarged hallucal granules, although slightly enlarged hallucal granules are known. Apical granules may appear smooth or apparently (not actually) striated.

PELAGE MARKINGS: Color is variable ac-

cording to geographic area, being black-speckled gray in individuals from the Darling Downs to uniform rufous in central Australian individuals. A head stripe is always present.

NOSE: Generally the median groove of the rhinarium extends to the top of the rhinarium. If a rim is present ventrolateral to the rhinarium, it is generally haired. The nose is commonly dark, rarely caramel-colored although some exceptions are noted below.

NIPPLE NUMBER: Seven to eight nipples have been noted, the former being uncommon and presumably an aberration.

DENTITION: I^1 is the tallest upper incisor (although the crown height of I^1 may not exceed the crown height of the other upper incisors). A diastema separates I^1 from I^2 . The crown heights of I^2 to I^4 are subequal, and the crown lengths increase in size from I^2 to I^4 . A posterior lobe may be tiny or absent in I^4 . A diastema separates I^4 from C^1 . C^1 is caniniform and taller-crowned than P^4 . In short-headed forms (such as those from Doomadgee Mission, see below), C^1 to P^4 may lack spaces between consecutive teeth while in longer-headed animals (e.g., J11463) spaces may exist between C^1 and P^1 and between P^1 and P^3 . C^1 lacks lingual and buccal cingula but may have very small anterior and posterior cingular cusps. P^1 is slightly shorter-crowned than P^3 , whereas P^3 is considerably shorter-crowned than P^4 . Small anterior and posterior cingular cusps are present on P^1 to P^4 . Narrow lingual and buccal cingula are generally present on P^1 to P^4 . dP^4 is three-rooted with two principal cusps, a paracone and a metacone, which may either be subequal in height (e.g., J7685) or the metacone may be taller than the paracone (e.g., J7685). A minor cusp homologous with the protocone, and a minor cusp possibly homologous with stylar cusp A are present. The anterior cingulum of dP^4 is generally incomplete but there are some exceptions (e.g., J7683). Stylar cusp A is not distinguishable from the buccal edge of the anterior cingulum of the upper molars. Stylar cusp B is variably connected to the paracone by the paracrista (e.g., it is not connected in J7685 and the

paracrista is extremely reduced; it is connected in J7696 and the paracrista is reasonably well developed). The position of stylar cusp B also varies being directly buccal to the paracone (e.g., J7696) or anterobuccal to the paracone (e.g., J7685). Stylar cusp D decreases in height from M^1 to M^3 and is absent on M^4 . Stylar cusp E is poorly developed, but if present (e.g., J12282) occurs as an isolated minuscule cusp. The paracones increase in height posteriorly from M^1 to M^4 . The metacones of M^1 and M^3 are subequal in height and smaller than the metacone of M^2 . The paracrista of M^1 is variably present (see above). The paracristae increase in length posteriorly from M^1 to M^4 . The metacristae of M^1 and M^3 are subequal in length and shorter than that crest in M^2 . I_1 is the tallest lower incisor crown. A small posterior lobe on I_3 is variably present. The C_1 is caniniform, taller-crowned than P_4 , has a conspicuous lingual cingulum but poorly developed to absent buccal cingulum, and a small posterior cingular cusp which is variably present. A diastema occurs between C_1 and P_1 in older individuals, but not between I_3 and C_1 . Buccal cingula are developed on P_1 to P_4 , P_3 and P_4 and sometimes P_1 have lingual cingula. P_1 is markedly shorter in crown height and length than P_3 . P_3 is shorter-crowned in length and height than P_4 but the difference is not as great between P_3 and P_4 as it is between P_1 and P_3 . All lower premolars have small to absent anterior cingular cusps, but well-developed posterior cingular cusps. dP_4 has one principal cusp, the protoconid, as well as a large cusp posterobuccal to the protoconid, and homologous with the hypoconid. Lingual and anterobuccal cingula are present on dP_4 , as is a small posterior cusp possibly homologous with the hypoconulid. The paraconids increase in size posteriorly from M_1 to M_4 . The metaconids increase in size posteriorly from M_1 to M_3 . The metaconid of M_4 is subequal to that of M_3 . The protoconids increase slightly in height from M_1 to M_3 , and the protoconid of M_4 is subequal in height to that cusp on M_2 . The hypoconids of M_1 to M_3 are subequal in height. The entoconids are large on M_1 to M_3 , and increase in height posteriorly from

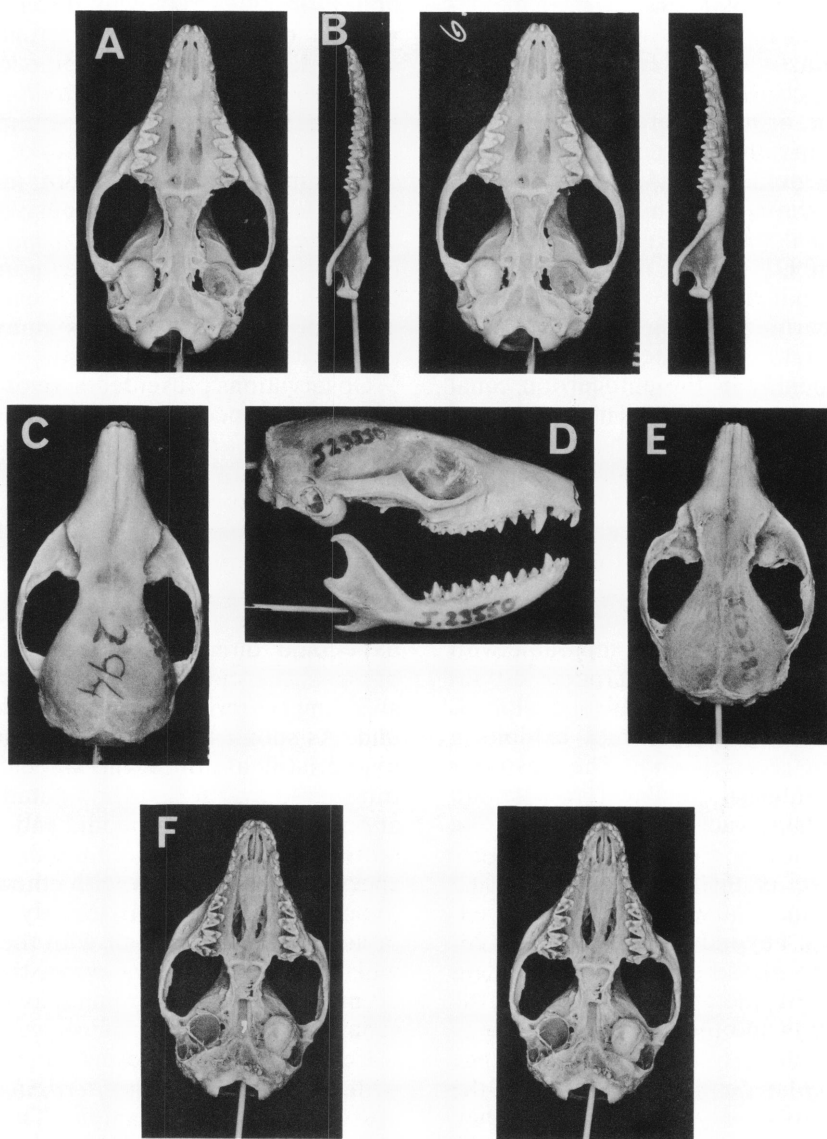


FIG. 45. *Sminthopsis macroura*. A–D, J23550, adult, Darling Downs, Queensland (n nominate form). E–F, J12283, adult, Doomadgee Mission, Queensland (Doomadgee form). A–F, $\times 2$.

M_1 to M_3 . An entoconid is variably present on M_4 as a small talonid crest connected to the cristid oblique. The paracristids of M_1 to M_3 increase in size posteriorly. The paracristid of M_4 is subequal to that crest in M_2 . The metacristids of M_2 to M_3 are subequal and longer than that crest in M_4 which is

longer than that crest in M_1 . The trigonid of M_1 is narrower than the talonid, subequal to it on M_2 , and wider than the talonid on M_3 and M_4 . Occasionally (e.g., J11436) the talonid of M_2 is wider than the trigonid and the talonid and trigonid of M_3 are subequal in width.

SKULL AND DENTARIES: A median longitudinal depression in the region of the nasofrontal contact varies from mildly concave to flat. The lacrimal foramina are single or double and on, or just anterior to, the rim of orbit. The foramen rotundum has a broad ventral alisphenoid shelf which obscures direct ventral view into the cranium. The transverse canal foramina vary in size from small (e.g., J10991) to large (e.g., J7698). The entocarotid canal similarly varies but is generally short permitting a direct ventral view into the cranium. In some specimens the basicranial opening of the entocarotid canal is very large (e.g., J11133). The number of condylar foramina (including the hypoglossal foramen) is variable. The foramen pseudovale is very long and wide, more so in individuals with a smaller alisphenoid tympanic wing. A short keel occurs on the anteroventral midline of the basioccipital. The alisphenoid tympanic wing development varies geographically, but is never comparable with forms such as *S. hirtipes*. The periotic tympanic wing is similarly variably developed. The mastoid process sometimes exhibits a slight inflation (e.g., J7698). The posterior lacerate and internal jugular foramina are large. The palatal vacuities are small. The premaxillary vacuity does not extend posterior to the level of the posterior edge of C¹ alveolus. The maxillary vacuities do not extend anteriorly beyond the level of the M¹ protocone. The masseteric fossa of the dentary is large with the anterior border of the ascending ramus and the posterior border of the dentary widely divergent. The distance from the articular condyle to the tip of the ascending ramus is only slightly shorter than the distance from the articular condyle to the tip of the angular process.

DISCUSSION: Classification of *S. macroura* has often been confused by use of external characters alone. For example, using external characters, Thomas (1888) synonymized *S. crassicaudata* with *S. macroura*, and Troughton (1965) suggested that the form *stalker*i Thomas (regarded in the present study as a synonym of *S. macroura*) might be synonymous with *S. crassicaudata*. Most early workers (except Kreff, 1867

and Ramsay, 1887) who discussed one or another of the geographic forms of *S. macroura* tend to have been preoccupied with comparison with *S. crassicaudata*. As a result, there has been little comparison between different populations of *S. macroura*. For example, Spencer (1896b), in naming *S. larapinta*, compared it extensively with *S. crassicaudata*, briefly, *S. murina* and earlier (1896a) *S. leucopus*. It appears unlikely that he considered affinity with *S. macroura* because of Thomas's (1888) synonymy of the latter with *S. crassicaudata*.

Observations presented here of cranial and dental differences between *S. macroura* and *S. crassicaudata* make it apparent that the two species are at best only distantly related and confusion of the two should not occur. The talonid morphology is notably different in the two forms despite the fact that both have well-developed entoconids. In *S. crassicaudata* the hypocristid passes from the hypoconid directly across the talonid and passes very close to the entoconid before swinging posteriorly to contact the hypoconulid. As soon as the tooth sustains wear, the hypocristid assumes the appearance of a transverse wall across the talonid buttressed at one end by the hypoconid and at the other by the entoconid. In *S. macroura* (and other species of *Sminthopsis* with entoconids), the hypocristid swings posteriorly before approaching the entoconid, with the result that when the tooth sustains wear, the hypocristid and the entoconid remain as integral and separate structures.

Confusion of the forms of *S. macroura* with species other than *S. crassicaudata* has also occurred. For example, Thomas (1906) synonymized *nitela* (see above under *S. virginiae*) with *larapinta* (a form of *macroura*). He was followed in this by Iredale and Troughton (1934), Tate (1947), and Johnson (1964). However, Thomas (1906) also named *S. stalker*i (considered here to be a form of *S. macroura*), differentiating it from *S. larapinta* on the basis of a shorter tail and more buffy color. It is interesting to note that previously (1888) he synonymized the form *froggatti* (considered here to be a form of *S. macroura*), the holotype of which also has a

shorter tail than body length and a dark head stripe (see Troughton, 1932), with *S. crassicaudata*. Tate (1947) even placed the much larger and distinctive *S. psammophila* in synonymy with *S. macroura*.

Geographic variation in *S. macroura*, with few exceptions, involves only slight differences in size, tail length, and body color. In the present study no consistent cranial or dental characters were found that separated the nominate form (*macroura*) from other forms (e.g., *froggatti*) and this is the basis for the synonymy employed here. It is true that the body color of the animals from the Darling Downs black soil areas (the nominate form of *macroura*) is much darker than other forms and this is presumably the basis for Ride's (1970) specific separation of the typical form. In the present study color differences of this sort were not considered sufficient reason for specific distinction. Finlayson (1933, p. 199), in regard to Australian small mammals, said "it would be regrettable if an over-free use of specific names were allowed to obscure the fact that several adaptable marsupials have successfully colonized huge tracts presenting a wide range of ecological conditions, without undergoing important structural changes in so doing." The teeth and skulls of specimens referred to *S. macroura* in this study are closely similar. Further, there are no known examples of sympatry of any of the forms. On the contrary, in intermediate areas there are often specimens which are not clearly one form or the other. Finally, it is apparent that if features such as tail length and body color are good indicators of distinction, nearly every population of *S. macroura* may in some minor way be differentiated from every other. Single specimens (such as WAM M6075, see below, or the holotype of *S. monticola*) often present unusual character combinations of the sort which have been said to characterize subspecies and even species.

One form, so far known only from Doomadgee Mission, is characterized by relative brachycephaly, commonly anteroposteriorly compressed molars, and maloccluded premolars. Some of the animals caught as adults show this tendency. A colony of these ani-

mals was raised and studied in captivity (e.g., Godfrey, 1969b). The tendency toward brachycephaly is much more apparent in individuals born in captivity (e.g., WAM M6903). This same phenomenon has been noted in an inbred colony of *Dasyuroides byrnei* (study in preparation). The phenomenon of anteroposteriorly compressed molars has also been found to be an abnormality in other dasyurid species (Archer, 1975c). The significance of this is the caution it should provide in using these characters alone to distinguish taxa, since they may well be poor indicators of taxonomic uniqueness. Accordingly, although the Doomadgee animals are discussed below as a separate form, more work is required with non-inbred individuals to test the case for taxonomic separation. It should be noted here that Kirsch (1967) used a Doomadgee specimen of *S. macroura* to obtain serological data for the species, because there is a possibility that the cranial and dental abnormalities common in this form (and they are very apparent in the individual, WAM M6903, used by Kirsch) are related to abnormalities in other tissues, such as blood.

FORMS OF *SMINTHOPSIS MACROURA*: Five names have been applied to individuals from populations in different localities. No attempt has been made here to test the statistical validity of these as subspecies and the names are used here only because they are useful in qualifying a particular form of the species which occurs at or near the type locality. Additional unnamed forms are noted where these are at least as distinctive as the named forms.

Sminthopsis macroura macroura

DISTRIBUTION: The range of this form includes the Darling Downs of south central and southeastern Queensland and north central New South Wales. The type locality of *Podabrus macrourus* Gould lies within this range.

RECOGNITION: These animals may be distinguished from other forms of *S. macroura* by their overall dark coloration, with dark-tipped guard hairs on the dorsal sur-

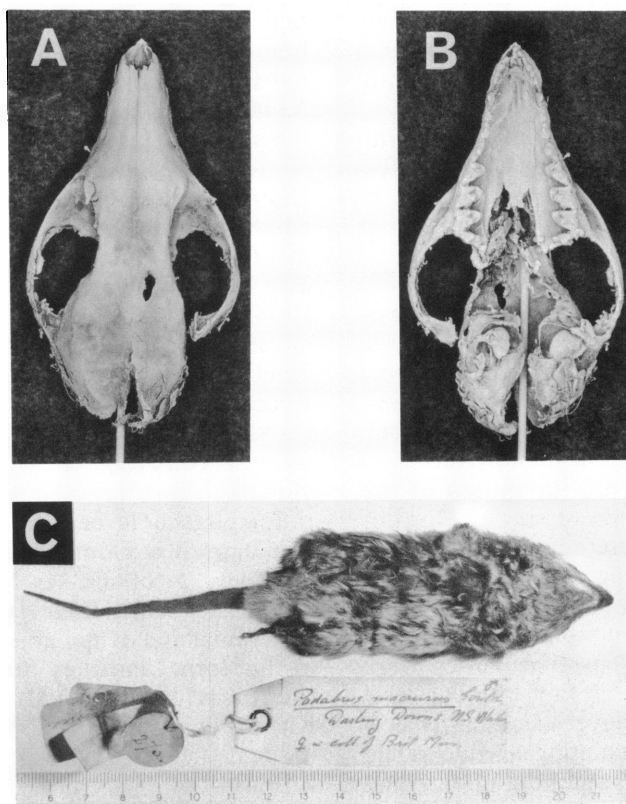


FIG. 46. Lectotype, *Podabrus macrourus* Gould, no. 275 in the Liverpool Museum (see the text). For measurements see table 2. Units on the scale in C are in centimeters.

face, and very little to no rufous hairs. The overall appearance is of black-speckling on a medium gray background.

REMARKS: In terms of most cranial and dental ratios, specimens of the nominate form most closely resemble those from Richmond in north-central Queensland, but they are also similar to those from central Northern Territory, northern South Australia and some from central and northwestern Western Australia. They are least similar to Doomadgee specimens from northwestern Queensland but are also clearly different from south Kimberley and Barkly Tableland specimens. In terms of absolute skull and dental size, they are most similar to central Australian specimens and most unlike

Doomadgee specimens and the single specimen (the holotype) of *monticola*.

Ride (1970) excluded all the named forms considered here to represent *S. macroura* except *monticola* from *S. macroura*. Troughton's (1965) description of the color of the holotype of *monticola* and dental and cranial size and proportions suggest *monticola* is more similar to the central Australian *froggatti* form than the nominate form.

Troughton's (1965) effort to demonstrate the specific distinctness of *S. macroura* from *S. crassicaudata* precluded his giving sufficient attention to differences between *froggatti* and the nominate form. However, he suggested that the granules of the feet in specimens of the *froggatti* form (as *larapin-*

ta) have "small and smoothly rounded apical summits to the sole pads as figured by Spencer . . ." which "are diagnostic of the species," whereas he says in specimens of the nominate form of *macroura* there is an "enlarged apical 'bead' on the pads" In view of the sorts of variation found in the present study (see below) this difference would not necessarily indicate specific distinction. Troughton (1967), although adamant about Tate's (1947) supposed error in regarding the *froggatti* form as a subspecies of *S. macroura*, does not give a satisfactory reason for why this should not be so, particularly on the basis of hind-foot structure. Although large alcohol series of specimens of the typical form of *macroura* have not been examined in this study, specimens that have been seen of all forms of *macroura* appear similar.

OTHER CHARACTERS OF THE NOMINATE FORM: No information is available about nipple number, pedal variation, reproduction or habitat.

REMARKS ABOUT THE TYPE SPECIMEN: The lectotype skin lacks the right fore and hind limbs, the left fore foot is present but separate from the skin, and the left hind foot is attached to the skin but badly damaged. The tail was clearly incrassated and, as preserved, is slightly shorter than the body. The skull is also damaged in that the basioccipital, basisphenoid and part of the palate are missing. Other lesser damage occurs in the basicranial region. The whole skull and both dentaries appear to have been subjected to minor chemical corrosion which has removed or partly decalcified some parts of the teeth. However, there can be no doubt that this skull and dentary preserves the characters (e.g., premaxillary vacuity length, entonoid size and morphology, size of the alisphenoid tympanic wing) used here to diagnose *S. macroura*. The dentaries (still joined by tissue) are relatively undamaged except for the left ascending ramus.

The reasons for nominating this specimen as the lectotype include the fact that the two paratypes BM 87.5.4.1 and BM 44.4.4.62 are also damaged, the former having a badly damaged skull and skin, and the latter lack-

ing a skin. Further, there appears to have been an impression held by Oldfield Thomas that the Liverpool specimen was the type specimen. On the label of BM 87.5.4.1 (evidently in Thomas's handwriting) is the note "No - in Liverpool is mentioned as type."

There are four labels associated with the lectotype. Label 1: (front) "*Mus. Derbianum Liverpool Type* Des. by Gould. P.Z.S. 1845-6 p. 79" (back), "*Podabrus Macrourus* Gould o. Darling Downs. N.S. Wales ♀ in coll of Brit Mus." Label 2: (front) "*Podabrus Macrourus* male" (back), "No 25"; Label 3: (front) "J. Gould July 1845 length 7 In"; Label 4: (front) "Old Male. then something illegible. Open Plains, Darling Downs. New South Wales." Label 4 is evidently Gilbert's label (personal commun. J. I. Harris, March 20, 1974). Measurements of the lectotype (not included in table 1) are as follows: ZW:14.5; C¹-M⁴:10.4; M¹-4:5.6; M¹⁻³:5.2; R-LM³:8.5; IO:4.6; IPVD:3.8; DL:19.8; I₁-M₄:11.9; M₁₋₄:6.2; M₁₋₃:4.5; C-AP: 5.2; C-AR:4.5; Measurements on the dry skin: TV:79.4; HB:84.0; HF(su):16.7.

Sminthopsis macroura froggatti

DISTRIBUTION: Range of this form includes most of arid Australia in all states except Victoria and Tasmania. The type localities of *Antechinus (Podabrus) froggatti* Ramsay, *Sminthopsis larapinta* Spencer and *Sminthopsis stalkerii* Thomas lies within this range.

RECOGNITION: This form, although diverse in color, does not show the dark, dusky color of the typical form, is smaller than *monticola*, and has a longer head than Doomadgee Mission animals.

REMARKS: Within the range of *froggatti*, three populations have been named. The holotype of *Antechinus (Podabrus) froggatti* Ramsay was collected from pindan (*Acacia*) scrub near Derby. No other specimens from this locality have been examined in the present study, although some (e.g., from Virgin Bore Creek) may have come from pindan scrub. The lectotype of *Sminthopsis larapinta* Spencer comes from Charlotte Waters. According to Spencer (1896a, p. 34) these

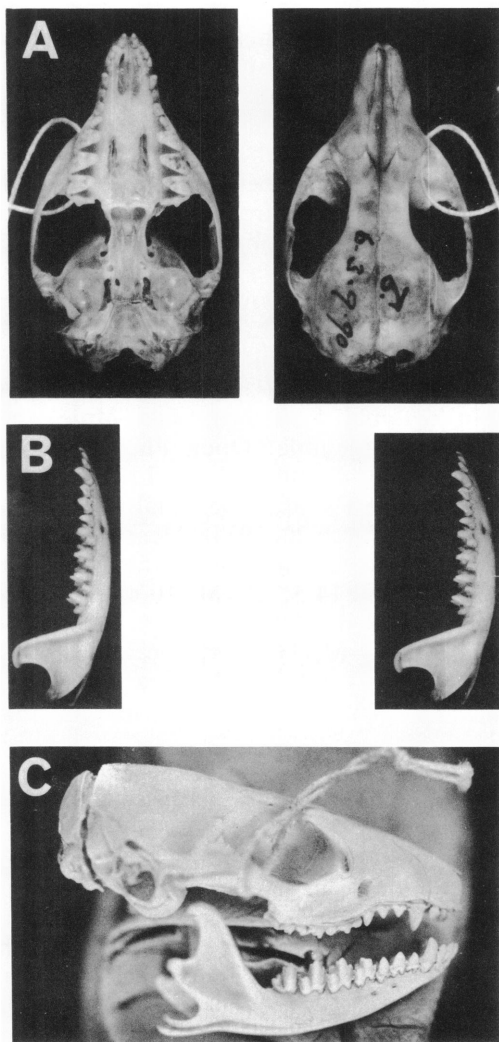


FIG. 47. Cotypes of *Sminthopsis stalker* Thomas (= *Sminthopsis macroura froggatti*). A–B, cotype BM 6.3.9.90, $\times 2$. C, cotype BM 6.3.9.91, $\times 2.4$. See table 2 for measurements.

central Australian animals (as *larapinta*) are characterized by “(1) the remarkably long, stout and strongly-incrassated tail, and (2) the relative length and width of the hind-foot.” The color he described as mouse-gray, suffused on the dorsal surface with rufous. In specimens I have examined, tail length was found to be variable but not un-

commonly shorter than the nose-vent length. The width of the hind foot does not appear to distinguish this form. The rufous color is more characteristic of central Australian individuals than those of the northern Australian grasslands including the Barkly Tableland. The holotype of *Sminthopsis stalker* Thomas comes from southwest of Alroy, on the Barkly Tableland. No consistent way of separating all Barkly Tableland *S. macroura* from other north and central Australian *S. macroura* has been found in this study. Thomas’s (1906) description of *stalker* suggests it differs in several minor ways from *froggatti*. Thomas evidently had a specimen (BM 97.11.3.11, collected in 1887 at Charlotte Waters and presented to the British Museum by Spencer) of central Australian *S. macroura* at hand when he described *stalker* (1906), but he (1906, p. 542) described *larapinta* as “drab-gray” and noted that the holotype of *stalker* is “colored like *S. larapinta*” He continues, however, to say “General color above more buffy than in *S. larapinta*, the light rings on the hairs dull cream-buff, their fine tips dark brown.” I have noted a prevalence of dark brown tips on the mid-back hairs in central Australian specimens in contrast to specimens from the northern grasslands and Barkly Tableland. The holotype of *stalker* may now be faded but it does appear slightly browner than other Barkly Tableland specimens examined by me. This may therefore represent color variation within the Barkly Tableland populations.

Other features that Thomas (1906) suggested differentiated *stalker* from *froggatti* (as *larapinta*) included the feet of the holotype of *stalker* that (in his opinion) were more hairy than those of *larapinta*. Having examined the holotype of *stalker*, I consider that the vague appearance of this hairy condition is largely due to the fact that the foot is shriveled, bringing the haired regions of both sides closer together so that the protruding hairs from both sides overlap each other. The holotype of *stalker* has a tail length of 65 mm. and a head and body length of 70 mm. (Thomas, 1906). The paratype (BM 6.3.9.90) has for the same measure-

ments 70 and 72 mm., respectively. This contrasts with the longer tails of most other northern Australian *S. macroura*. It might be argued that the somewhat short tails of the types are indications of their juvenile condition. However, Finlayson (1933) stated that in five specimens of central Australian *froggatti* (as *larapinta*), the tail exceeded the head and body by 25–30 percent at all stages of growth. In any case, the holotype of *stalker* is not a juvenile, P⁴ having just erupted. It seems likely that these tail lengths are good indications of what would have been the fully adult condition, and hence again variation within the Barkly Tableland population. The holotype of *stalker* is intermediate in some respects, such as tail length, between specimens of *froggatti* from central Australia and other specimens from the Barkly Tableland. The type locality of the holotype of *stalker* is near the southwestern edge of the Barkly Tableland. The paratype, which has a shorter tail than the holotype, is described as coming from Alexandria, which may be more centrally located on the Barkly Tableland (Parker, 1973, comments about the former location of Alexandria).

Troughton (1962, 1965 and 1967) has been uncertain about the taxonomic status of the name *stalker* Thomas. In 1934 Iredale and Troughton listed *stalker* as a full species. However, in 1962 Troughton referred to it as “a northern race (*stalker*) from Alroy and Alexandria Downs (N.T.)” of *S. macroura* (as *larapinta*). In 1965 he treated it as a full species but suggested it may be referable to *S. crassicaudata centralis*. In 1967 he considered *stalker* to be synonymous with *S. c. centralis*. Tate (1947) referred to this form as *S. larapinta stalker*. He also considered that Thomas (1906) used, as a basis for comparison, the type of *S. nitela* Collett which Thomas (1888) had previously placed in the synonymy of *S. macroura* (as *S. larapinta*). This seems unlikely because Thomas also had specimens (e.g., BM6.3.9.112) of *froggatti* (which he regarded as *larapinta*) collected by Stalker.

VARIATION: Variation in hind foot structure is exemplified by eight specimens (C8775–C8782) from Brunette Downs Sta-

tion collected 0.8 km. from the Homestead, June 13, 1968. The hind foot of C8776 has no clear median row of interdigital pad granules posterior to the apical granule. Specimen C8781 has the covering skin missing from the apical granule of the right fourth pad revealing underlying transverse ridges. Specimens C8775 and C8780 have apparent striate apical granules on the surface of the pads (there are no striae visible on other specimens in this series such as C8779). Seven out of eight specimens have tiny to small hallucal granules. Specimen C8781 has no hallucal granule. Complete fusion of an apical granule with an adjacent granule occurs in none of the specimens although there is partial fusion in C8775 and C8779.

Variation in tail incassation (maximum tail diameter) is provided by the same series and ranges from 5.2 to 9.2 mm. The two largest diameters (9.2 and 9.1) are males as are the two smallest (5.2 and 6.2). The three females have intermediate tail diameters (6.8, 7.6, 8.9).

NIPPLE NUMBER: Three females from Brunette Downs Station (e.g., C8778) and all other specimens of this species I have examined have eight nipples. Woolley (1973) also reported eight nipples.

HABITAT AND REPRODUCTION: Spencer (1896a) stated that P. M. Byrne informed him that this form in central Australia (including the type locality) “seems to prefer stony tablelands, whilst *S. crassicaudata* prefers the softer ground near the creeks and amongst the sand-hills.” Spencer regarded *froggatti* (as *larapinta*) to be a burrowing form. Specimen WAM M4512 was found by an aboriginal girl at Jiggalong Mission from a small burrow near Jiggalong Creek. Specimen WAM M4513 was obtained late in May 1959 by A. M. Douglas, from rocks near Green Pool on the Little De Grey River, northeast of Bamboo Creek. Specimen B3060 was obtained by W. H. Butler from the North Kintore Range, Northern Territory, where it was trapped in an open creek bed. Finlayson (1933) noted that this form was less common than *S. crassicaudata* around the Lake Eyre Basin in South Australia, and (1961, p. 156) that like *S. crassicaudata centralis*, it “is

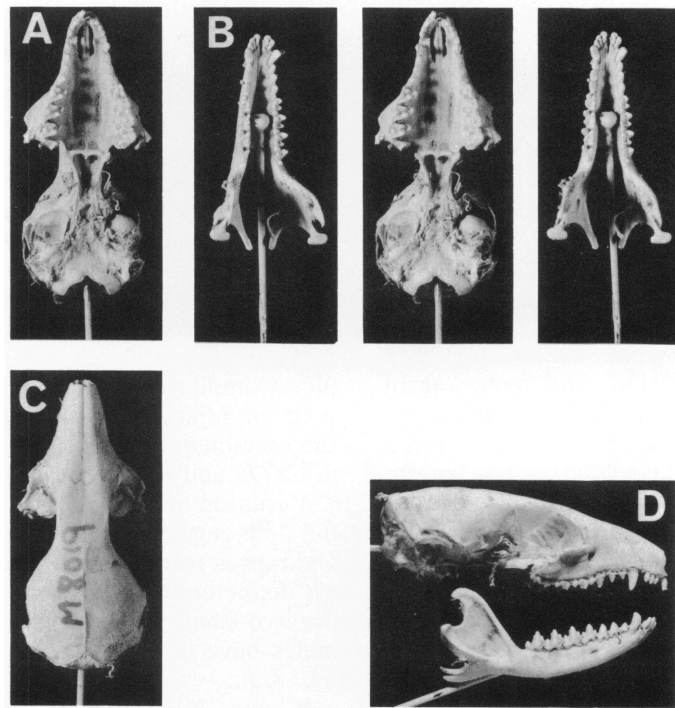


FIG. 48. Holotype of *Antechinus (Podabrus) froggatti* Ramsay (= *Sminthopsis macrourus froggatti*), AM M8019. See table 2 for measurements.

periodically very plentiful in the eastern part of the Lake Eyre Basin, but is very sparse elsewhere . . ." in the center of Australia. On the Barkly Tableland, most specimens appear to have been caught on open treeless grassed and cracked black soil plains (Parker, 1973). A large sample (Northern Territory Museum) of skeletal remains was obtained from Owl and Letter-winged Kite pellets collected on Brunette Downs on the Barkly Tableland in 1970. Some of these pellets included as many as five individuals of *froggatti* and suggest that this animal is at times very abundant on the black soil plains. From the same pellets, specimens of *Planigale ingrami*, *Pseudomys forresti*, and *Rattus villosissimus* were recovered. Specimens in the British Museum collected by W. Stalker from Alexandria have several comments on the labels as follows: "tail too fat to skin" (BM 6.3.9.83); "caught in among dead tim-

ber on the plain" (BM 6.3.9.86); "Native name Baraga" (BM 6.3.9.89); "redbrown (?) sand and spinifex (BM 6.3.9.112). K. G. Buller (Western Australian Museum) stated (personal commun.) that he collected *froggatti* on two separate occasions from grassed black-soil plains along Virgin Bore Creek, Gogo Station, Western Australia. Virgin Bore Creek flows through a broad valley of black-soil. According to Buller, the animals were abundant on his first trip in July 1963. After he left, floods completely filled the black-soil valley of Virgin Creek and remained at high water levels for many days. When he returned less than one year later, he found the animals again plentiful in the cracks along the creek bank. Evidently, some individuals maintain themselves in the hillsides adjacent to the black-soil valley. When floods recede, these individuals spread out across the valley rapidly building up pop-

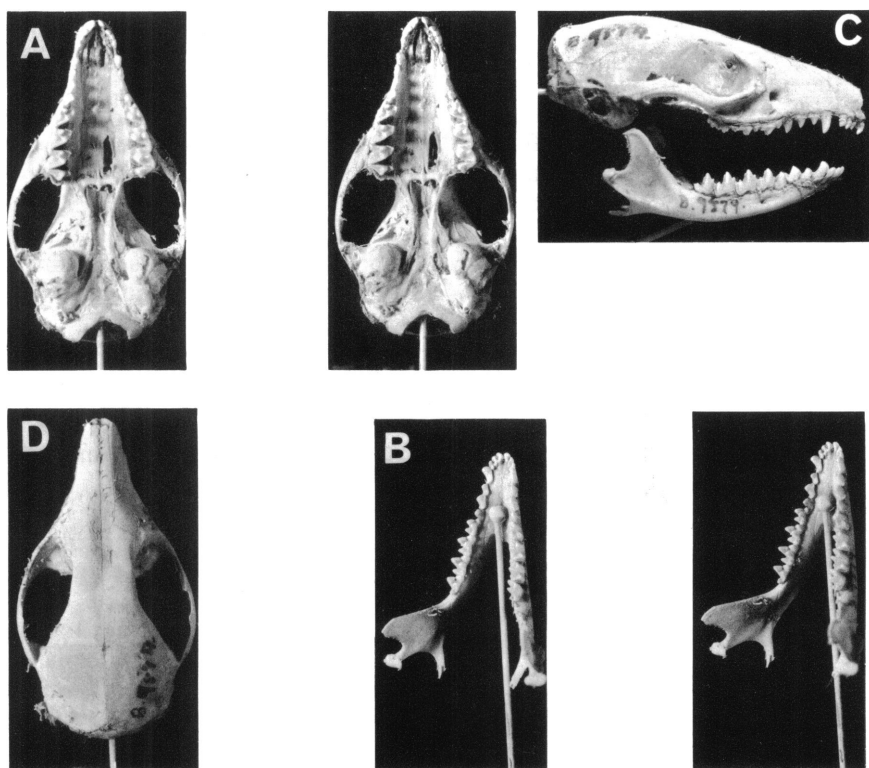


FIG. 49. Holotype of *Sminthopsis monticola* Troughton (= *Sminthopsis macroura monticola*), AM B9579 (in the Australian Museum with nothing to do with the Butler Collection of the Western Australian Museum). See table 2 for measurements.

ulation numbers. It seems reasonable to suppose that since the rainy season in this area is predictable, the animals will have a breeding season which corresponds in some way to the time of year when recolonization of the rich black-soil habitat is again possible.

Specimen WAM M5411 from New Mundiwindi, Western Australia, has five of the eight nipples swollen and supporting juveniles. It was obtained by G. M. Storr on March 5, 1962. Woolley (1973) summarized field and laboratory studies that show that births in this form occur between July to February followed by a lactation period of greater than 62 days.

REMARKS ABOUT TYPE SPECIMENS: The holotype of *Antechinus (Podabrus) froggatti* Ramsay, described by Ramsay (1887) and

Troughton (1932), has a shorter tail than nose-vent length. The color of the back (perhaps faded) is described by Troughton (1932, p. 352) as "reminiscent of *Mus musculus*, the tone about dark grizzled olive brown, being a mixture of the warm buff and dark mummy brown tips; basal fur of back deep neutral grey. Dark pencilling of back continuing over the crown and down the centre of the snout." The body, hind- and fore-foot, skull and dentition of the lectotype of *Sminthopsis larapinta* Spencer are figured by Spencer (1896a, plates 2-3). The lectotype itself confirms Spencer's (1896a) illustration of a small hallucal granule but in addition possesses an enlarged small post-hallucal granule. The skull has not been removed from the alcohol carcase. The skull of the

holotype of *Sminthopsis stalkerii* Thomas is comparable with other Barkly Tableland specimens of *S. macroura*. I¹ is broken on both sides, the interdigital pads have one slightly enlarged oval apical granule, there is a slight suggestion of apparent striae (but without actual ridges) on the apical granules of the right foot, the pads of the left foot are damaged, the interdigital pads appear to be virtually free of hair, the pelage is reddish brown and probably faded, and the head stripe, although present, is not clear. The paratype of *stalkerii* (BM 6.3.9.90) is a skin and skull of a young male (P⁴ is almost completely erupted). The tail is distinctly incrassated (as stuffed it is 5.6 mm. in diameter), the head stripe is clearly present, the interdigital pads are free of hair, there are enlarged median rows of granules on the interdigital pads, and pin holes have damaged the feet.

Sminthopsis macroura monticola

DISTRIBUTION: This form is known only from the type locality. The holotype of *Sminthopsis monticola* Troughton is the only type that has been collected from this locality.

RECOGNITION: The mid-back hair color (although possibly faded) of the holotype is similar to central Australian specimens of *froggatti* in being more rufous than specimens of the nominate form, but the absolute size of M¹⁻³ (5.2 mm.) is very large (equaled by only one other specimen) and the IO/ZW ratio (0.34) and (M¹⁻⁴)/(C¹-M⁴) ratio (0.61) are also very large for the species.

REMARKS: The reasons for the decision by Ride (1970) to refer *monticola* to the nominate form of *macroura* rather than *froggatti* (which he accords full specific status) seem questionable because the color of the holotype, as described by Troughton (1965), does not recall specimens of the nominate form. The only similar features are the tail length and the relatively less arid habitat. But in fact the TV/HB ratio of the holotype of *monticola* (0.99) is more similar to the mean for central Australian *froggatti* than Darling Downs *macroura* individuals used in this study.

HABITAT: The characteristics of the type locality are unusual for *S. macroura*. If the locality data of the holotype of *monticola* are reliable (and I am inclined to doubt that they are), this animal was collected from an area 732 m. above sea level in an area which was naturally dominated by wet sclerophyll forest. This sort of habitat is otherwise unknown for *S. macroura*. If the data are not in error, it is perhaps surprising that specimens in addition to the holotype have not been collected since 1885.

DOOMADGEE MISSION FORM

DISTRIBUTION: This form is known only from Doomadgee Mission, northwestern Queensland.

RECOGNITION: The tail is proportionately shorter than any other form of *macroura*, and the color is generally lighter than specimens of the nominate form or central Australian *froggatti* but similar to Barkly Tableland and Kimberley specimens of *froggatti*. The skulls are brachycephalic, extreme examples (e.g., SAM M8325) having the (M¹⁻³)/(R-LM³) ratio as low as 0.51 and the IO/ZW ratio as low as 0.23. Many of these specimens (e.g., WAM M6903) shows abnormalities that may be the result of captivity (Archer, 1975). However, 12 specimens in the South Australian Museum (including SAM M8293 and M8325), caught in the field at various times by L. Fawcett and children from Doomadgee Mission, and P. Crowcroft, suggest that brachycephaly may also be a normal feature of the wild populations.

REMARKS: This form of *S. macroura* has no formal name and until more research is done that establishes the normal presence of its unusual characters in wild-caught animals from this area, the form should remain unnamed. The results of the present study are only suggestive of the morphological distinctness of this form within *S. macroura*. Its affinities are not clear. In color and dental ratios specimens of this form are more similar to Barkly Tableland specimens of *froggatti*, although the very short tail more closely resembles central Australian specimens of *froggatti*. Recognition of the poten-

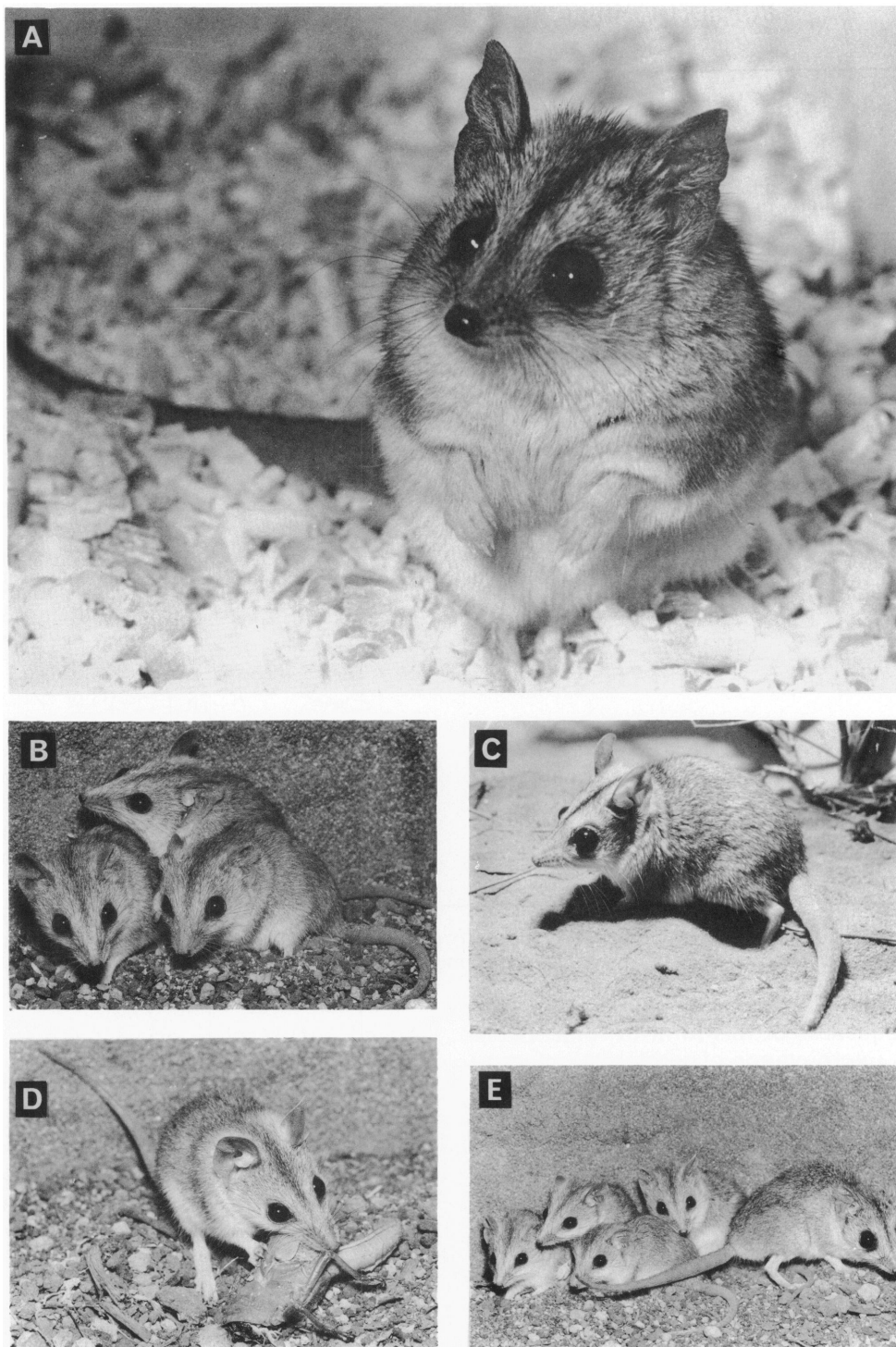


FIG. 50. *Sminthopsis macroura*. A, Western Australia (photograph by W. D. L. Ride). B, D–E, Doomadgee Mission, Queensland (photographs by the Queensland Museum). C, Doomadgee Mission (photograph by H. Aslin).

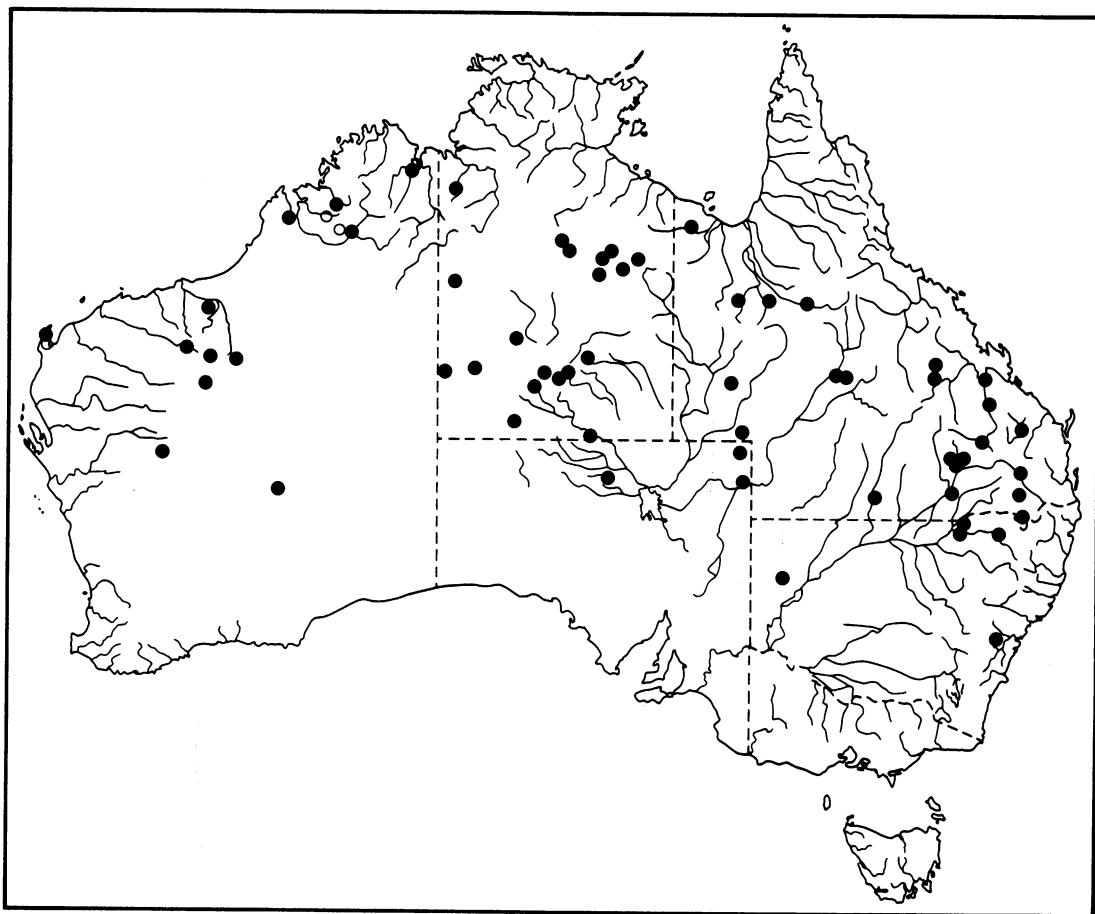


FIG. 51. Geographic distribution of *Sminthopsis macroura*. Solid dots represent modern specimens observed, and hollow circles represent cave specimens observed.

tial uniqueness of this form to some extent effects interpretation of serological information obtained by Kirsch (1967) because the specimen used by Kirsch to represent "*Sminthopsis larapinta*" was WAM M6903, a particularly brachycephalic and dentally abnormal individual. Doomadgee *macroura* has also been the subject of studies in torpor (Godfrey, 1966 and 1968) and reproduction (Godfrey, 1969b).

NIPPLE NUMBER: Godfrey (1969b) reported that this form had eight nipples.

HABITAT AND REPRODUCTION: Doomadgee Mission occurs in an area dominated by tropical layered woodland and leached podzolic soils, which differs from the Barkly Ta-

bleland habitat of semiarid tussock grassland, low tree savannah and brown soils of heavy textures (Stephens, 1963 and Williams, 1955). Doomadgee also occurs in an area whose drainage systems empty into the Gulf of Carpentaria. These coastal drainage systems in northern Australia are generally the habitat for the forms of *S. virginiae* while *S. macroura* tends to dominate the internally drained areas.

Godfrey (1969b) noted that in the laboratory this form is polyoestrous with a gestation period of 12.5 days. Birth occurred between July to February, followed by a lactation period of 70 days.

OTHER POSSIBLY UNIQUE FORMS OF SMIN-

THOPSIS MACROURA: Specimens from intermediate regions in Australia are difficult to assign to one or another of the forms of *S. macroura*. Specimen WAM M6075 from Cosmo Newberry Mission, central Western Australia is referred here to *froggatti* but in all its cranial proportions and its longer tail length (TV 93.0, HB 90.0) it is unlike other central Western Australian specimens. Although caught on August 10, 1963, this specimen was maintained in captivity until it died on March 21, 1964 at which time it weighed 31.5 gms. The tail is heavily incrassated and in that character resembles the holotype of *monticola*. It is possible that captivity had something to do with its unusually large size.

Specimen AM M4403, from 145 km. northwest of Anthonys Lagoon, en route to Newcastle Waters, Northern Territory may represent a hybrid between *S. macroura* and *S. virginiae* (see above under *S. virginiae*).

Other unique specimens include AM M5237 from Wyndham, Western Australia, which is the largest specimen of *macroura* examined in this study. The alcohol skin is damaged. Specimen WAM M7768 from Kildurk Station, Northern Territory, is browner than South Kimberley animals and in this respect resembles central Australian specimens of *froggatti*. Specimen WAM M6842 from Mt. Hart Station, Western Australia, also appears to be browner than the south Kimberley specimens from Virgin Bore Creek.

Modern and fossil records of all *S. macroura*: Other modern records of *S. macroura* which I have checked include those given by Glauert (1933) as Alexandria, and Tanami, both Northern Territory localities. Bannister (1969) recorded a specimen obtained by H. Butler on Northwest Cape, Western Australia. I have identified fossil specimens representing this species: Specimen 72.9.56 from "Napier Range No. 4 Cave," Windjana Gorge, Western Kimberley Region, collected by A. M. Douglas and G. W. Kendrick in 1966; and 67.10.5 from a cave 5 km. south of "former Virgin Bore," Gogo Station, western Kimberley Region collected by K. G. Buller and G. W. Kendrick in 1967.

Sminthopsis butleri Archer

Sminthopsis butleri Archer, 1979.

TYPE SPECIMEN: Holotype: WAM M7158, skull and carcase in alcohol, adult female, collected by W. H. Butler, December 14, 1965. I have examined the holotype. Type locality: Archer (1979), "Kalumburu (Lat. 14° 15', Long. 126° 40'), northern Western Australia."

DIAGNOSIS (Archer, 1979): A medium-sized species of *Sminthopsis* that differs from most *S. murina*, *S. leucopus* and *S. ooldea* in having a vague head stripe, and conspicuously enlarged and unstriated apical granules on the interdigital pads, non-granular terminal toe pads, and relatively long premaxillary vacuities. It differs from *S. psammophila* in being smaller, in lacking a crest on the tail; and in having non-granular terminal pads on the digits. It differs from *S. macroura* and *S. douglasi* in having a thin tail, in lacking entoconids on M_1 to M_3 , and in having relatively short premaxillary vacuities. It differs from *S. virginiae* in being smaller, lacking rufous cheeks, lacking entoconids on M_1 to M_3 , and in having relatively short premaxillary vacuities. It differs from *S. crassicaudata* in having a thin tail, a lack of entoconids on M_1 to M_3 , and an enlarged apical granule on the interdigital pads. It differs from *S. longicaudata* in having a tail that is less than twice the nose-vent length, a relatively small alisphenoid tympanic wing, a lack of elongate striated apical granules on the interdigital pads, and a lack of striations on the terminal pads on the digits. It differs from *S. hirtipes* in having a thin tail, relatively long premaxillary vacuities, non-granular terminal pads of the digits, a relatively small alisphenoid tympanic wing, and in lacking hair on the interdigital pads of the hind-feet.

DESCRIPTION: Tail: The tail is invariably thin and about equal in length to the nose-vent length.

HIND FOOT: The hind foot has three interdigital pads that are united at their com-

mon base. Each interdigital pad has a median row of granules which become progressively larger toward the distal end of each pad and culminates in a large apical granule. Of five alcohol specimens, only one (B1937) exhibits fusion of an apical granule with the proximal granules (on the left and right fourth interdigital pads, the apical granule is fused with a proximal granule and there is also an imperfect fusion involving apical and proximal granules of the left and right second interdigital pads). On some interdigital pads (e.g., the fourth of WAM M7158 and B1941), the apical rows are not as long and do not involve as many granules as in other specimens (e.g., the third of B1943 and WAM M7158). A hallucal granule is variably present, being clearly differentiated for example in B1943, B1941, and B1937 but virtually absent on the right foot of B1937 and both feet of WAM M7158. No granules exhibit actual ridges on the surface of the pads but some apical and proximal granules (e.g., B1941) have apparent striae. The hallux does not extend forward far enough to touch the second interdigital pad.

NOSE: The nose has a medial groove which does not extend to the top of the naked rhinarium. A narrow, hairless, ventrolateral rim is present.

NIPPLE NUMBER: Specimen WAM M7158 has eight distinct nipples.

PELAGE: A relatively dark mid-dorsal head stripe is present which extends from an area about midway between the nose and the anterior edge of the eye, to between the ears, behind which it merges with the color of the back. A dark ring occurs around each eye but these do not form part of the lateral face stripes. The very light color of the belly extends onto the flanks between the fore and hind legs and along the base of the cheeks beneath the ear. Ridgway (1912) colors for a dry skin (WAM M7156) and an alcohol carcase (WAM M7158) are as follows: Above the eye, Vinaceous-Buff to Avellaneous (M7156) or Pale Ochraceous-Buff (mixed) (M7158); middle of the back, Buffy brown to Drab Mouse Gray (former as tips of hairs) (M7156) or Blackish Brown (M7158); flank, Pale Ochraceous salmon to Vinaceous-Buff

(M7156) or Light Buff (M7158); belly, white to Ivory yellow (M7156) or paler than Masticot yellow (M7158).

DENTITION: I^1 is the tallest upper incisor and is set off from I^2 by a diastema. Upper incisor crown heights increase posteriorly from I^2 to I^4 . I^4 has a small (B1995) or absent (WAM M7156) posterior lobe. A diastema occurs between I^4 and C^1 . C^1 has postero-buccal and posterolingual cingula, a small posterior circular cusp, and is caniniform although its crown height is shorter than that of P^4 . The P^1 is slightly shorter in crown height than P^3 and P^3 is conspicuously shorter in crown height than P^4 . Lingual and buccal cingula on P^1 to P^4 are incomplete at the base of the paraconid. Posterobuccal cingula on P^1 to P^3 are variably rugose with small irregular cusps. dP^4 (e.g., B1995) is three-rooted with three principal cusps, the paracone, metacone, and stylar cusp D. There is also a very reduced protocone and possibly the homologue of stylar cusp B on the anterobuccal cingulum. A complete anterior cingulum is present from the preprotocrista to the parastylar corner of dP^4 . dP^4 metacrista is large but the paracrista is not a prominent crest. The paracones of M^1 to M^4 increase in height posteriorly. The protocones of M^1 to M^3 are subequal in height to each other, as are the metacones. The protocone of M^4 is the smallest of the upper molars. Stylar cusp D is largest on M^1 and decreases in size posteriorly being minuscule or absent on M^4 . Stylar cusp A is indistinct on M^1 to M^4 but may be distinguishable on M^1 (e.g., WAM M7156). Stylar cusp A is defined by the intersection of an anterior crest from stylar cusp B and the anterior molar cingulum. Stylar cusp C is not present. An anterior cingulum is incomplete except on M^1 where it is sometimes complete (e.g., B1995). Rarely, an anterior cingulum is complete on M^2 (e.g., B1939). The paracrista of M^1 is well-formed and either extends buccally (e.g., B1995) or anterobuccally (e.g., WAM M7156) to the paracone. The paracrista length increases posteriorly from M^1 to M^4 . The metacristae of M^1 and M^3 are subequal in length and shorter than the metacrista of M^2 . The I_1 is taller-crowned than I_2 . The I_3 has a small

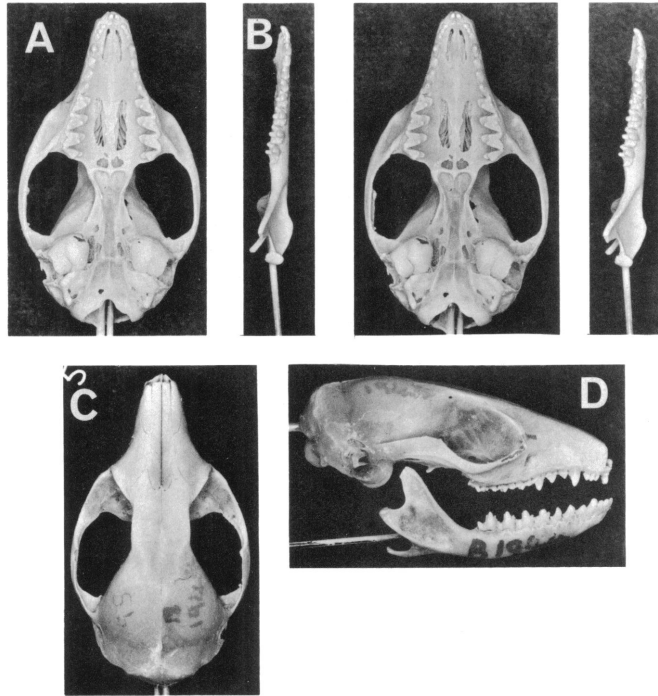


FIG. 52. Holotype *Sminthopsis butleri* Archer, WAM M7158, adult, Kalumburu, Western Australia. A–D, $\times 2$.

posterior lobe. C_1 is caniniform, subequal in crown height to P_4 , has a small posterior cingular cusp, a complete lingual cingulum, and an incomplete buccal cingulum. P_1 is shorter-crowned than P_3 which is shorter-crowned than P_4 . Lingual and buccal cingula of P_1 to P_3 are small and generally incomplete. P_4 lacks a buccal cingulum but has a lingual cingulum. dP_4 (e.g., B1995) is two-rooted with the protoconid as the only main cusp. There is also a small anterior cusp homologous either with the paraconid of M_1 or the anterior cingular cusp of the anterior premolars, and a small posterior cusp homologous either with the hypoconulid of M_1 or the posterior cingular cusp of the anterior premolars. A swelling between the posterior cusp and the protoconid may be homologous with a hypoconid. The paraconids of M_1 to M_4 increase in height posteriorly. The metaconids of M_1 to M_4 are subequal in height. The pro-

toconids increase in height from M_1 to M_4 . The hypoconids of M_1 to M_3 are subequal in height and taller than the hypoconid of M_4 . The entoconids are tiny on M_1 to M_3 and absent on M_4 . On one specimen (B1995) a tiny metastylid appears on M_1 . The paracristids of M_2 to M_4 are subequal in length and longer than the paracristid of M_1 . The metacristids of M_1 to M_3 increase in length posteriorly from M_1 to M_3 . The metacristid of M_4 is subequal to that crest in M_2 . The trigonid is narrower than the talonid on M_1 , subequal in width on M_2 , and wider than the talonid on M_3 and M_4 .

SKULL AND DENTARY: The skull is relatively brachycephalic with a short deep rostrum and broad zygomatic arches. It is domed posteriorly and has (in older individuals) well-developed sagittal and nuchal crests. A longitudinal median depression occurs in the region of the naso-frontal suture.

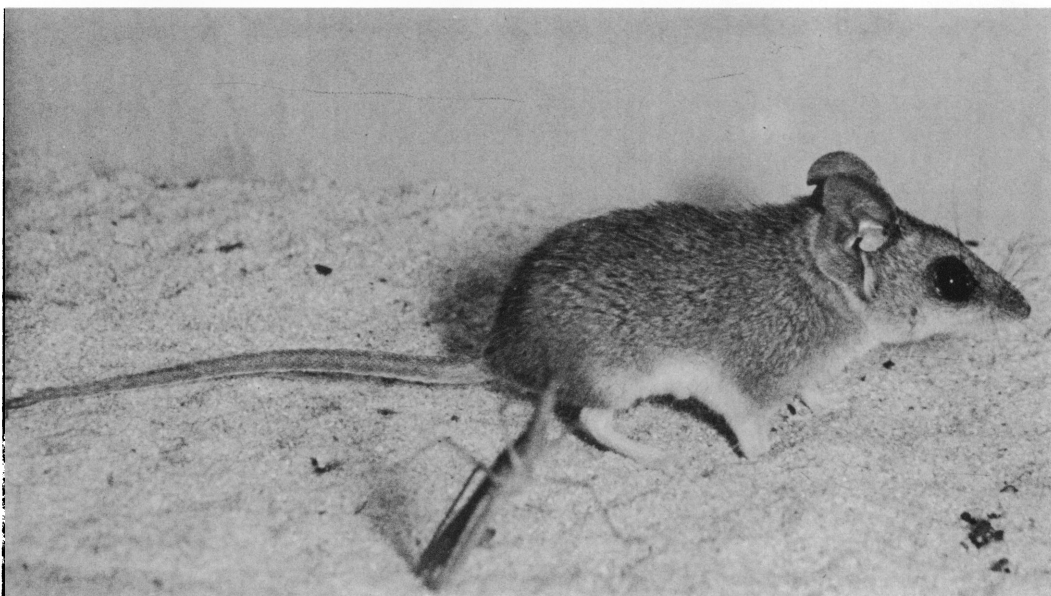


FIG. 53. *Sminthopsis butleri*, holotype in life, WAM M7158 (photograph by W. D. L. Ride).

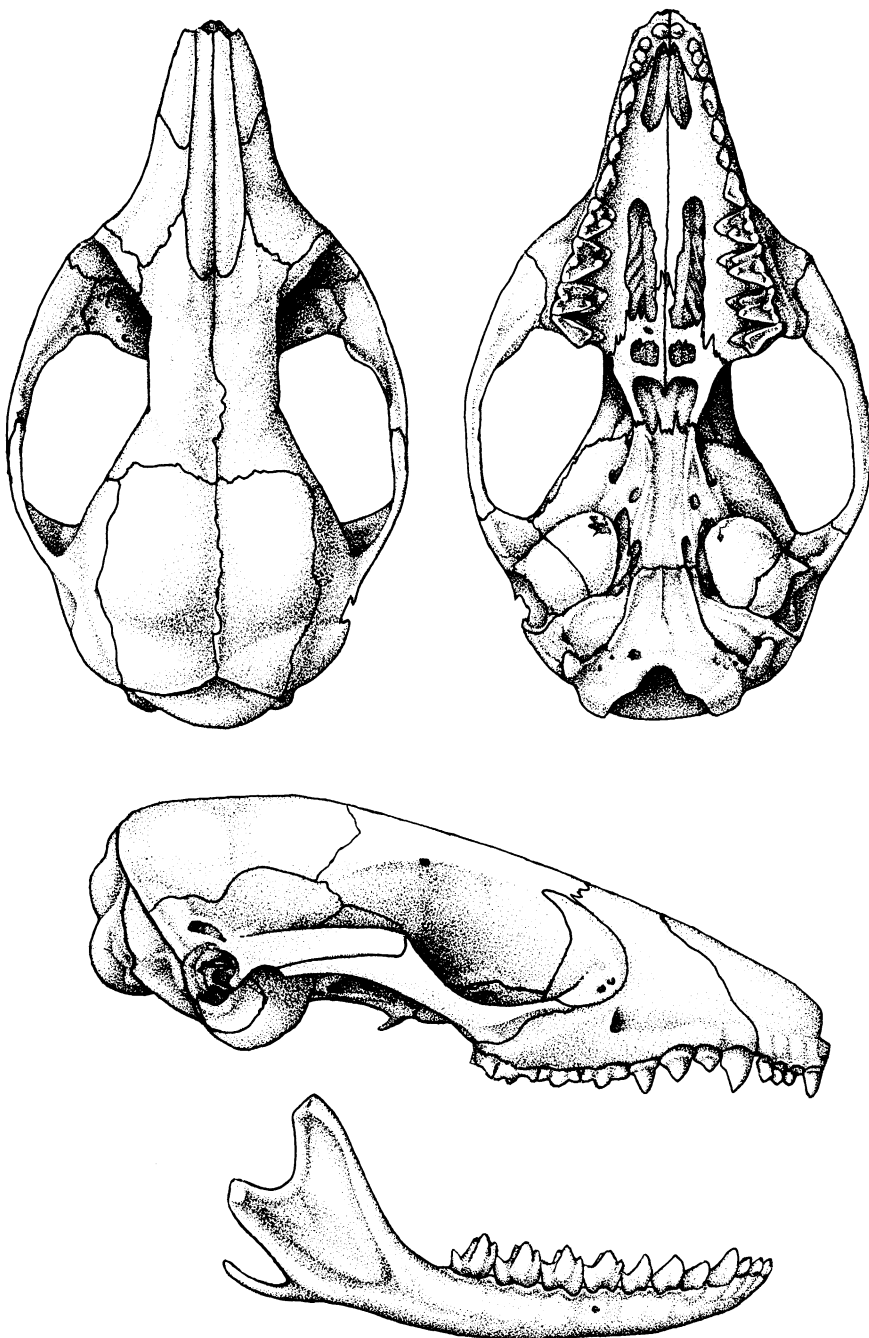


FIG. 54. Drawing of holotype WAM M7158 of *Sminthopsis butleri* based on photographs, the skull and the dentary.

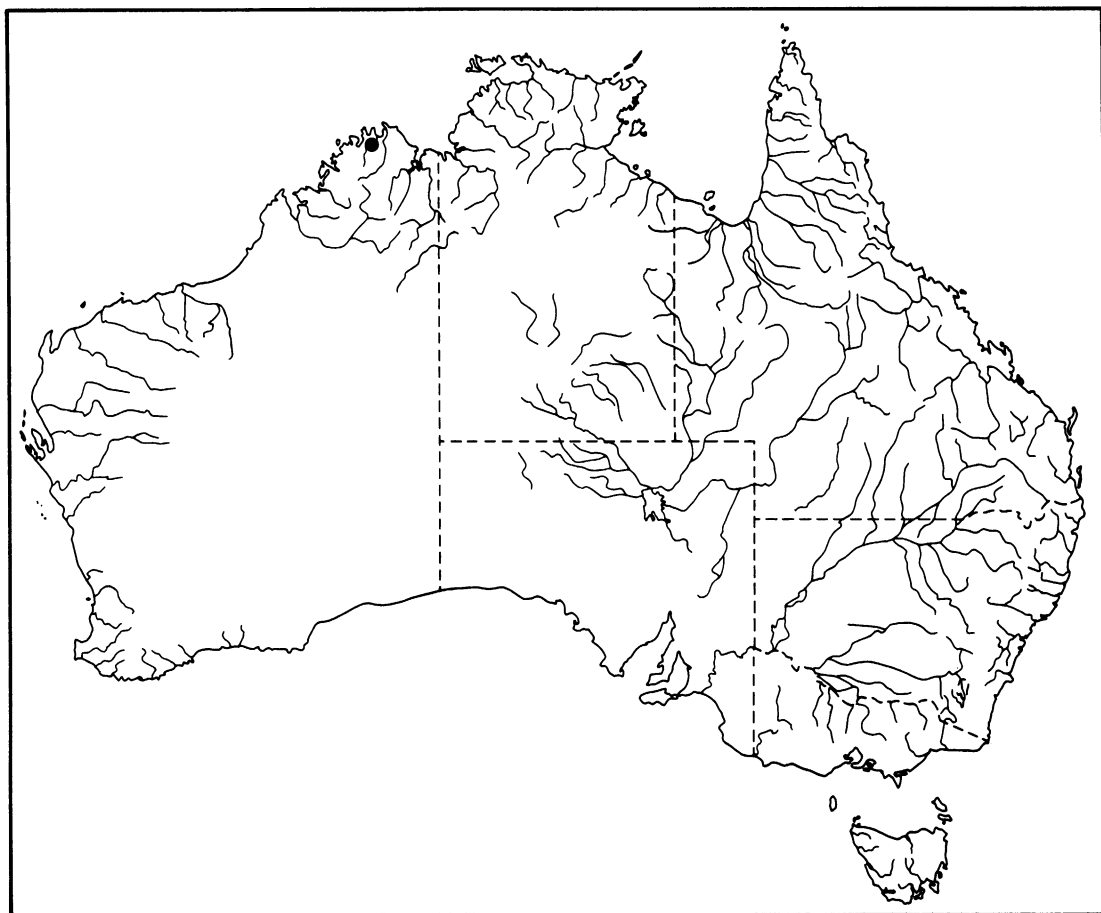


FIG. 55. Geographic distribution of *Sminthopsis butleri*.

The interorbital region has pronounced postorbital swellings but no postorbital processes. There are two lacrimal foramina on each side (except on one side of WAM M2155, where there is only one normally on the edge of the orbit). The alisphenoid tympanic wing is only slightly enlarged leaving the ectotympanic broadly exposed. The periotic tympanic wing is relatively little developed. The foramen pseudovale is large. The transverse canal foramina are relatively large but smaller than the foramen rotundum. The opening to the eustachian canal is large, as is the internal jugular vein and the posterior lacerate foramina. The entocarotid canal is open ventrally but well developed. The condylar fo-

ramina (including the hypoglossal foramen) is single or multiple. The premaxillary vacuity extends posteriorly usually to the level of the anterior root of P^1 (e.g., B1995) or the posterior root of P^1 (e.g., WAM M7156). Usually (e.g., B1995) several small interdental fenestrae occur between adjacent upper molars. The maxillary vacuity extends forward to the level of the anterior end of M^1 . The distance between the articular condyle of the dentary and the tip of the ascending ramus is slightly shorter than the distance from the articular condyle to the tip of the angular process. The masseteric fossa is large. The symphysis extends posteriorly to the level of the posterior edge of P_3 .

DISCUSSION: This species has been the subject of serological analysis by Kirsch (1967, as *S. nitela*, and 1977, as *S. butleri*) who also examined sera of the following species: *S. macroura* from Doomadgee Mission, Queensland; *S. murina* from Busselton, and Scott River, Western Australia; *S. granulipes* from Western Australia (including a specimen from Gingin); and *S. crassicaudata* from Wongan Hills, Western Australia. He considered all the species to be serologically differentiable at the species level. Ride (1970) considered the Kalumburu specimens to possibly represent *S. virginiae* (as *nitela*). However, the virtual absence of entoconids, rufous cheeks or comparable foot structure serve to distinguish *S. butleri* from *S. nitela*. Archer (1979) suggested that the affinities of *S. butleri* probably lie with *S. macroura*.

HABITAT AND REPRODUCTION (Archer, 1979): W. H. Butler's field notes (in the Western Australian Museum Library) state that he collected "north of the King Edward River about 4 miles from the Longini landing for cargo." Specimens include one male and two females. One was "caught on blacksoil sand plain junction at bottom of airstrip . . ." and two were removed from "flood debris at back of Mission." The black-soil plain and sand plain were "heavily vegetated with eucalypt and grass." The specimens were collected on December 12, 1965 and January 20, 1966. At the time of collection there were heavy rains in the area, producing as much as 711 points in two days.

Specimen WAM M7158 had seven pouch young (including WAM M7155-7) at the time of collection, December 12, 1965.

Remarks about the holotype: Archer (1979) notes that the holotype consists of a well-preserved carcase and relatively little-damaged (fig. 52) skull and dentaries. External measurements (mm.) as follows: HB, 88; TV, 89; HF (su), 16; E (n), 17.

Sminthopsis hirtipes Thomas

Sminthopsis hirtipes Thomas, 1898.

TYPE SPECIMEN: *Sminthopsis hirtipes* Thomas, 1898. Holotype: BM 97.12.17.1,

adult male, skull, and carcase in alcohol. Details of collector and date were not given in the original description, but label indicates, and Tate (1947, p. 124) stated "purchased from Gerrard . . ." I have examined the holotype. Type locality: Thomas (1898, p. 4), Station Point, Charlotte Waters (whose modern position is Lat. 25° 55' S, Long. 134° 54' E, see Parker, 1973, p. 49) interior of South Australia (actually Northern Territory).

DIAGNOSIS: Medium-sized species of *Sminthopsis* that differs from *S. murina* and *S. leucopus* in having an incrassated tail, and from these species and *S. ooldea* in having a pronounced head stripe, fused and haired interdigital pads without median rows of enlarged granules, granular terminal pads of the digits, enlarged alisphenoid and periotic tympanic wings, lacrimals with laterally produced rims and often posterodorsal spines, short premaxillary vacuities that generally do not extend posteriorly beyond a point level with the posterior edge of the C¹ alveolus, and an *angular process-articular condyle* distance which considerably exceeds the *articular condyle-tip of ascending ramus* distance. It differs from *S. granulipes* in being smaller, in having a pronounced head stripe, a non-bifid I₃ crown, almost total absence of entoconids on M₁ to M₃, relatively wide premolars and short canines. It differs from *S. psammophila* in being smaller, in having an incrassated and non-crested tail; and an almost total absence of entoconids on M₁ to M₃. It differs from *S. virginiae* in having an incrassated tail, and from *S. virginiae* and *S. thomasi* in being smaller, in having hair on the interdigital pads, in having granulated terminal toe pads, in absence of entoconids on M₁ to M₃, and in having relatively small canines. It differs from *S. crassicaudata* in having hair on the interdigital pads, in having granulated terminal pads of the digits, relatively short premaxillary vacuities, and in the absence of entoconids on M₁ to M₃. It differs from *S. longicaudata* in having an incrassated tail which is also less than twice the length of the head and body length, relatively short premaxillary vacuities, no metatarsal pad development on the hind

foot, non-striated granules on the haired interdigital pads, and granular terminal pads on the toes. It differs from *S. butleri* in having an incrassated tail, haired and fused interdigital pads, granular terminal pads of the digits; and relatively short premaxillary vacuities.

DESCRIPTION: Tail: The tail length is approximately equal to nose-vent length (but commonly exceeds it slightly, e.g., WAM M1577) and is clearly incrassated. In only one instance does the tail appear to be only slightly incrassated (WAM M1547) and this is a dried skin.

EAR: The ear is notable for the extensive covering of hairs on the inside of the pinna.

HIND FOOT: The hind foot has the entire plantar surface covered with hair. The interdigital pads are fused to the top and stand up as a single large trilobed pad. All surfaces of the foot are granulated, including the terminal pads of the digits. The fore feet have similar granular pads and the palmar pads are fused and well-haired. Ventral surfaces of the digits of the fore foot are not as well-haired as those of the hind foot.

NIPPLE NUMBER: In three females examined, the nipple number was six.

PELAGE MARKINGS: The head has a dark area between the ears and on the forehead. In two specimens (both alcoholic carcasses, WAM M5783 and M8083) there is a distinct mid-dorsal stripe running posteriorly from a point about midway between the nose and the anterior corner of the eye. This stripe merges into a dark patch on the forehead. The eye is surrounded by a ring of dark hairs and there is some suggestion from the alcoholic specimens that the dark area around the eye is part of the dark stripe that runs for a short distance in front of each eye back to each ear. Two dried skins (WAM M1577 and M1547), although possibly faded, do not show facial features as clearly as the alcoholic specimens. Photographs taken by W. D. L. Ride in 1967 of an animal (WAM M8943) which had just died at Neale Junction, Western Australia, show a distinct dark head patch and a ring around the eye which extends for a short distance toward the nose and ear.

DENTITION (this description is based on specimens other than NTM1899): I^1 is the tallest upper incisor. I^2 to I^4 increase in crown length posteriorly, and I^4 crown is commonly shorter in height than that of I^3 . No posterior lobe occurs on I^4 . I^4 and C^1 are separated by a diastema. C^1 is short-crowned, almost premolariform, and subequal in height to P^4 . C^1 has a tiny to absent anterior cingular cusp, a distinct posterior cingular cusp, no buccal and only a poorly developed lingual cingulum. Diastemata separate C^1 , P^1 , and P^3 from adjacent teeth. P^1 is slightly smaller-crowned in length and height than P^3 , and P^3 is markedly smaller-crowned in length and height than P^4 . Anterior and posterior cingular cusps are present on P^1 to P^4 , but generally are very small on the anterior end of P^4 . Lingual and buccal cingula are poorly developed on P^1 to P^4 . Paracones on M^1 to M^4 increase in height posteriorly from the metacones of M^1 and M^3 and are subequal in height and shorter than the metacone of M^2 . Styler cusp A is indistinguishable from the buccal end of the anterior cingulum on the upper molars. Styler cusp B is connected by a low paracrista to the paracone. Styler cusp C is variably present (e.g., present on M^3 of WAM M8083) on the posterior flank of styler cusp B. Styler cusp D is largest on M^1 , smallest on M^3 and unknown on M^4 . Styler cusp E commonly occurs as a minuscule buccal crest between the metastyler corner of the tooth and styler cusp D. Paracristae increase in length from M^1 to M^4 . The metacristae of M^1 and M^3 are subequal and shorter than the metacrista of M^2 . The anterior cingula on the upper molars are incomplete (one known exception is M^1 of WAM M1577). I_1 is the tallest lower incisor crown, and has a very small posterior lobe. I_3 and C_1 are not separated by a diastema, unlike C_1 and P_1 . P_1 is separated from P_3 by a diastema, and generally (not invariably) P_3 is separated from P_4 by a diastema. Anterior cingular cusps are tiny or absent on P_1 to P_4 but posterior cingular cusps are prominent. P_1 is shorter-crowned in length and height than P_4 which is shorter-crowned than P_3 . The paraconids increase in size posteriorly from M_1 to M_4 . The metaconids of M_1

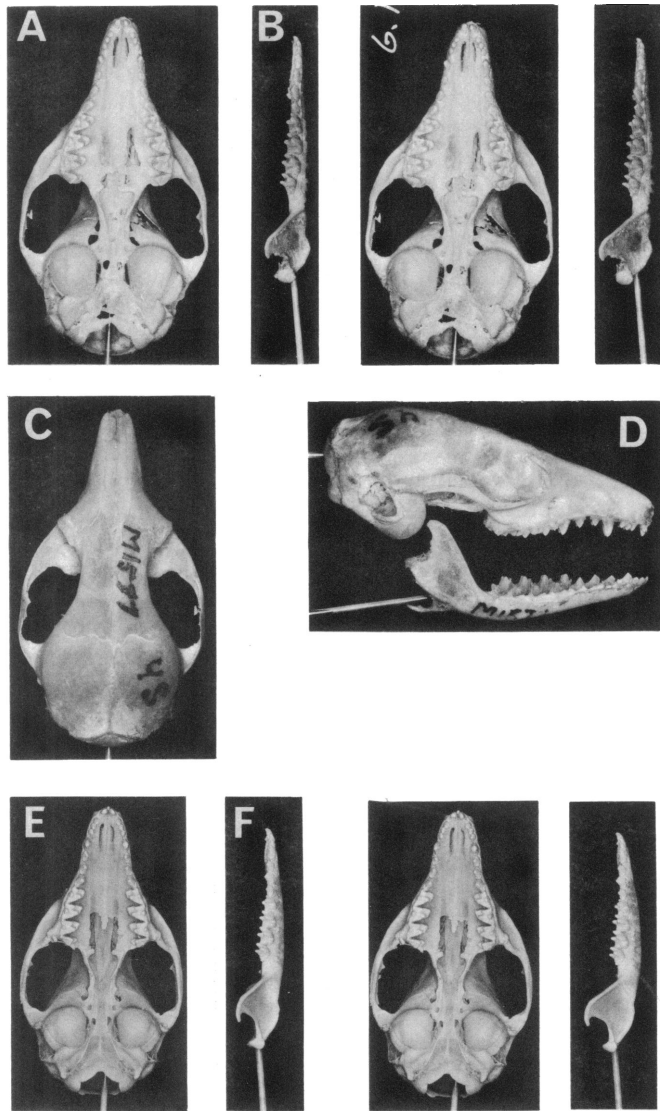


FIG. 56. *Sminthopsis hirtipes*. A-D, WAM M1577, adult, Winduldarra, Western Australia. E-F, NTM 1899, adult, George Gill Range, Northern Territory. A-F, $\times 2$.

to M_3 are subequal in height and just taller than the metaconid of M_4 . The protoconids of M_1 to M_3 increase in height posteriorly. The protoconid of M_4 is subequal in height to that cusp on M_2 . The hypoconids of M_1 to M_3 are subequal in height. Lingual talonid cusps are tiny to absent, and when present

(e.g., M_3 of WAM M1577) it is not clear if the cusp is an entoconid or a metastylid because it contacts the base of the metaconid and is crestlike. The paracristids increase in length posteriorly from M_1 to M_3 , but the paracristid of M_4 is subequal in length to that crest in M_2 . The metacristids increase in

length posteriorly from M_1 to M_3 , but the metacristid of M_4 is subequal in length to that crest on M_2 . The trigonid of M_1 is narrower than the talonid, subequal on M_2 , and talonid on M_3 and M_4 .

SKULL AND DENTARIES (this description is based on specimens other than NTM1899): The palatal vacuities are small. The premaxillary vacuity sometimes extends as far posteriorly as the level of the anterior end of P^1 alveolus (e.g., WAM M1547), but generally does not reach posterior to a point level with the posterior end of C^1 alveolus (e.g., WAM M1577). Interdental fenestrae are present between molars but very small in size. The maxillary vacuities do not extend anterior to a point level with the protocone of M^1 . The anterodorsal portion of the frontals is swollen, producing a mid-dorsal depression. Lateral lacrimal rims are developed in some individuals (e.g., WAM M1547 and M1577) such that they continue the curve of the frontal bone as part of the anterior rim of the orbit. This lacrimal "flaring" is not as conspicuously developed in other individuals (e.g., WAM M8083 and M5783). The extent of development may have a sexual basis because it is better developed in males than females. In two individuals (WAM M1577 and M5783), the dorsal edge of the lacrimal is produced as a spur near the anterodorsal edge of the orbit and may serve as a base for soft tissue attachment. Generally, two lacrimal foramina occur on the anterior rim of the orbit. The basicranium of some specimens is substantially modified as a result of the enlarged tympanic wings. The alisphenoid tympanic wing is greatly enlarged and obscures most of the ectotympanic. The ventral periotic tympanic wing and the mastoid tympanic wing are also enlarged. The periotic hypotympanic sinus is somewhat better developed than is common in other species. The dorsal roof of the alisphenoid hypotympanic sinus is markedly convex dorsally and as a result, the whole of the alisphenoid hypotympanic sinus forms an oblate sphere. Enlargement of the periotic hypotympanic sinus causes the basioccipital walls of the internal jugular canal to be vertical. The transverse canal is enlarged. Ali-

sphenoid tympanic wing development extends anteromesially to such an extent that the foramen of the transverse canal is just at the anteromesial corner of the alisphenoid tympanic wing. The posterior half of the dentary of the nominate form exhibits a structural modification which reflects the relatively enlarged alisphenoid hypotympanic sinus of that form: the distance between the tip of the angular process and the dorsal surface of the articular condyle is much longer (almost one-and-a-half times longer) than the distance between the dorsal surface of the articular condyle and the dorsal tip of the ascending ramus. This modification enables the angular process to clear the surface of the alisphenoid tympanic wing when the dentary is depressed. This adaptation is better developed in some individuals (e.g., WAM M1577) than others (e.g., WAM M8083), depending on the degree of development of the alisphenoid hypotympanic sinus.

DISCUSSION: On the basis of external characters alone, *Sminthopsis hirtipes* is unmistakably distinct from all other *Sminthopsis*. However, Thomas (1906), in describing the form *stalkerii*, stated that it was intermediate in some respects between *S. hirtipes* and *S. larapinta* (the latter considered here to be a form of *S. macroura*). I have examined the type specimens of *stalkerii* (BM 6.3.9.90 and BM 6.3.9.91) and placed them within *S. macroura* (see above). The terminal pads of the toes of the type specimens of *stalkerii* are not granular, a feature which at once distinguishes them from *S. hirtipes*. Troughton (1965, p. 314) claimed that the tail in *S. hirtipes* is "without definite incrassation," an observation with which I cannot agree.

HABITAT AND REPRODUCTION: Specimen WAM M5783 was obtained in July to August 1963 by M. DeGraaf and others from a burrow on the edge of a claypan, on alluvial flats below the limestone cap supporting Warburton Mission. DeGraaf noted that nearby Glenegan Station had had 50 to 75 mm. of rain during the previous week. Specimen WAM M8943, collected by W. D. L. Ride and A. M. Douglas August 11, 1967, was obtained at Neale Junction, Western Australia

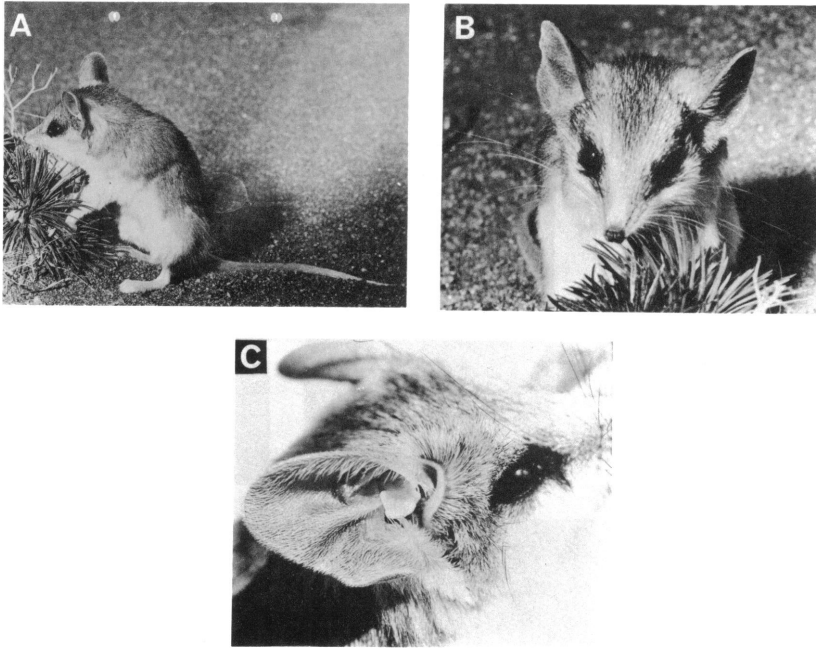


FIG. 57. *Sminthopsis hirtipes*, photographed (by W. D. L. Ride) shortly after it died, Neale Junction, Western Australia.

in a sandy area containing spinifex and eucalypts. All except one specimen of this species are known from arid central Australia. Specimen WAM M10208 was collected in 1973 from a coastal area along the Kalbarri Road about 500 km. north of Perth. This area is semiarid with an average annual rainfall of between 250 and 380 mm., and is characterized by sandy soils and scrubby vegetation. More recent specimens (not plotted in fig. 59) have been noted by Burbidge et al. (1976) coming from the Great Victoria and Gibson desert areas of Western Australia. They obtained four individuals from Queen Victoria Spring. Two were in open-woodland of *Eucalyptus gongylocarpa*. One was in a patch of *Helichsytum apiculatum*. The third was found dead on a track. The fourth was in an area of sparse regenerating mallee and *Casuarina* sp., 0.5 m. high growing on gravelly sand. Three were collected from the Neale Junction area. One of these came from a crest and the other two from the slope of a sandhill. In both areas of the sandhill there

was an open-woodland of *E. gongylocarpa* although the individual from the top of the sandhill was obtained in a patch of bare red sand.

Three females from Western Australia (WAM M1548, M5783 and M8083) have six nipples but show different stages of pouch development. Specimen WAM M8083, collected May 15, 1968, has the pouch very poorly developed and the nipples mere depressions around the circumference of the pouch area. The lack of wear on the teeth, and the fact that P^4 and M^4 have erupted indicate the animal is a young adult. Specimen WAM M5783, obtained July to August 1963, has the pouch well-developed with six prominent but not elongate nipples, and unstained pouch hairs. The animal may have been approaching breeding condition. The teeth are worn and suggest a completely mature individual. Specimen WAM M1548, collected by O. Lipfert at Well 29 on the Canning Stock Route in 1931, probably in mid- or late-August (on the basis of other dates for Lipfert's

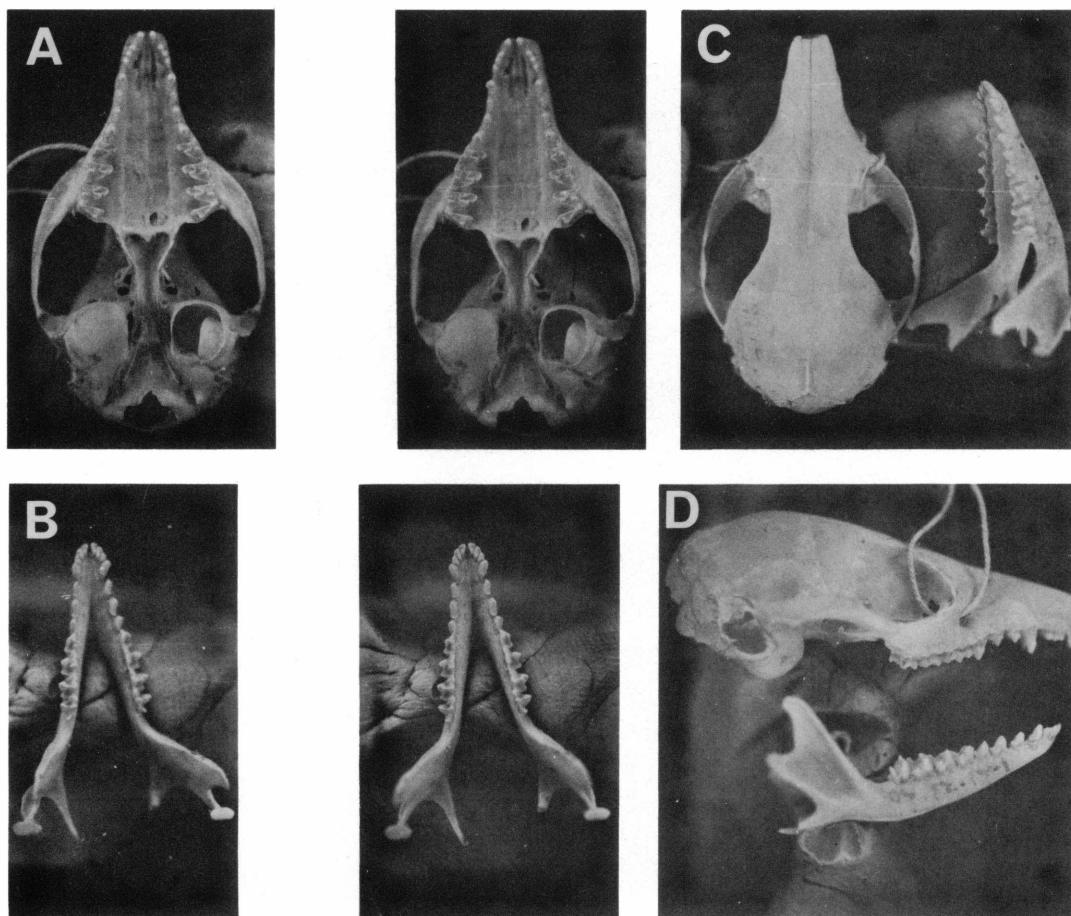


FIG. 58. Holotype of *Smynthopsis hirtipes* Thomas, BM 97.12.17.1, adult, Station Point, Charlotte Waters, Northern Territory. See table 2 for measurements.

Canning Stock Route bird and mammal collection, G. M. Storr, *in litt.*, June 20, 1972) is a female with six equal-sized and probably non-lactating nipples. A juvenile was obtained at the same time as WAM M1548. This limited information suggests *S. hirtipes* breeds around July and August.

CONDITION OF THE HOLOTYPE: The skull which is in good condition indicates the animal is an adult, and to judge from the extremely worn teeth, a very old adult. The carcase (in alcohol), which is also in good condition, has a clearly incrassated tail but

a scrotum which is only half the size of scrotums in other adults. Possibly, it represents a post-breeding condition.

A NON-TYPICAL FORM OF *SMYNTHOPSIS HIRTIPES*: Two distinct and allopatric forms of *S. hirtipes* have been recognized. The first is the nominate form (and includes all known specimens except NTM1899), the holotype of which comes from Charlotte Waters, Northern Territory. The second form is represented by only one specimen (NTM1899) from Reedy Creek, George Gill Range, Northern Territory. It has not been named

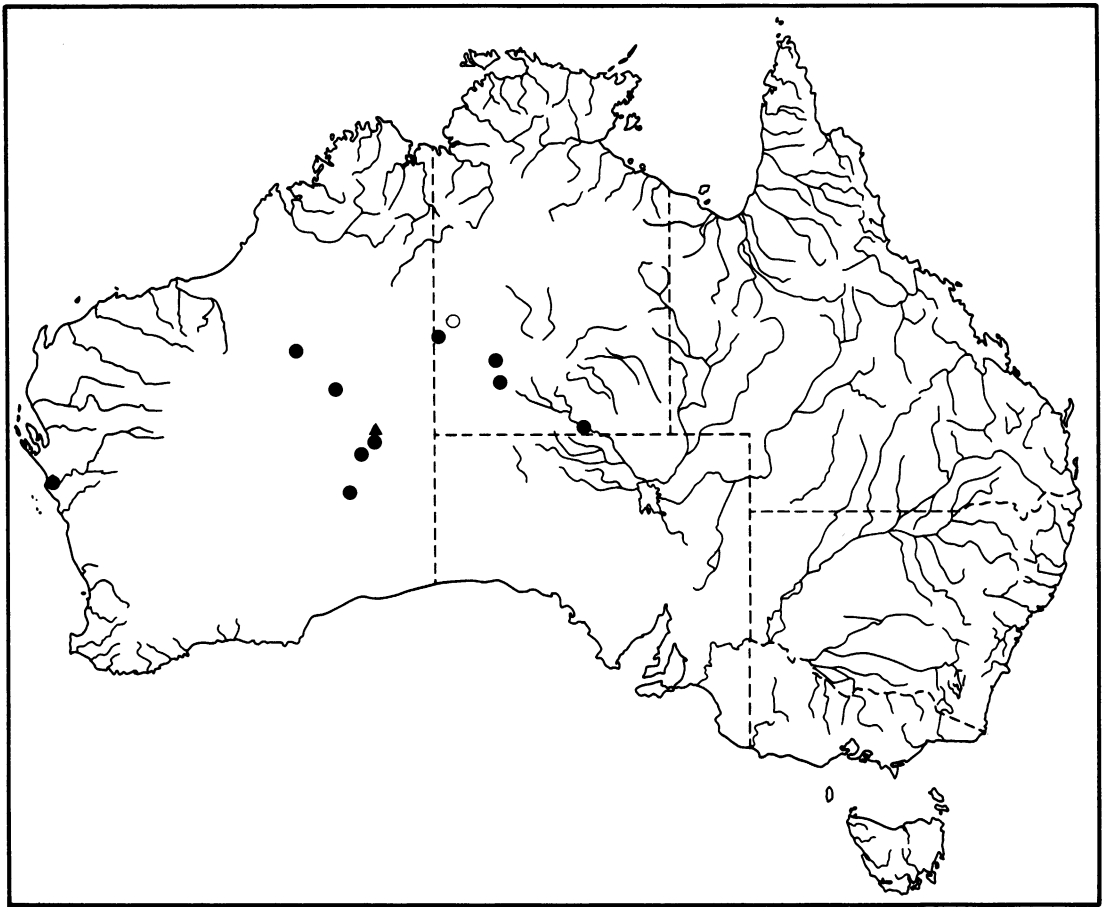


FIG. 59. Geographic distribution of *Sminthopsis hirtipes*. Specimens from the Great Victoria and Gibson desert areas of Western Australia reported by Burbidge et al. (1976) are not included on this map but are discussed in the text.

and should remain unnamed pending the discovery of more specimens. In all characters except those discussed below, the Reedy Creek form resembles specimens of the typical race. It may be differentiated from specimens representing the typical form by the following combination of characters: its overall small body measurements; the tail-vent length which is about equal to, rather than much longer than, the nose-vent length; and the hind foot which has relatively much smaller hairs on the interdigital pads (the average length of several measured hairs on the interdigital pads of the hind foot of NTM1899 is 0.3 mm., and of several of the larger hairs

on the ventral surface of the hind foot near the interdigital pads, 1.3 mm., whereas in a foot of a specimen (WAM M8083) of the typical form, the average hair length on the interdigital pads is 0.4 mm. as opposed to 2.5 mm. on the areas adjacent to the interdigital pad); the hind foot of the Reedy Creek form does not have the "gerbille-like" appearance of specimens of the typical form as described by Thomas (1898); all cranial and dental measurements, except one, of NTM1899 are absolutely smaller than corresponding measurements of the typical form (the exception is the distance between the posterior edge of the articular condyle of the dentary and the

anterodorsal edge of the ascending ramus, which is larger in NTM1899 than the mean of the same measurement in specimens of the typical form, a difference apparent in the more widely flaring masseteric fossa of the dentary of NTM1899; and alisphenoid tympanic wing development which is relatively smaller in the Reedy Creek form.

The holotype of *S. hirtipes* is described by Thomas (1898) as having "feet quite different to those of any other species and more recalling those of some of the African Gerbilles." He gave, with other dimensions, 4.7 mm. for the combined lengths of M^1 to M^3 , 5.1 mm. for interorbital breadth and a basal length of 24 mm. All of these characters clearly compare with the specimens treated in this study as members of the nominate form and are in contrast to those of NTM1899. Thomas (1906, p. 543) described *S. stalker* as "an interesting link between the hairy-soled *S. hirtipes* Thos., described from Charlotte Waters, and the ordinary naked-soled species of the genus. Its shorter tail and more buffy color will also distinguish it from *S. larapinta*." Some of the smaller measurements given by Thomas for the holotype of *stalker* (e.g., basal length 21.4, zygomatic breadth 13.0) suggest comparison with NTM1899 but M^{1-3} measurement of the holotype of *stalker* Thomas (4.9; Thomas, 1906, gave 4.7) is much larger than the corresponding measurement of NTM1899. The holotype of *stalker* and the cotype (BM 6.3.9.90) from the same locality are considered here to represent a form of *S. macroura* (see above). Among other differences, the type of *stalker* has normal *macroura*-like entoconids whereas NTM1899 has no entoconids.

The type locality of *Sminthopsis hirtipes* is only about 400 km. from Reedy Creek where NTM1899 was collected, and neither population appears to be confined by any particular geographic barrier. Therefore, it seems possible that future work will demonstrate the full specific status of the Reedy Creek form. However, because actual sympatry has not been demonstrated, and because NTM1899 is the only specimen of this

form, I have made no attempt to name this form.

Unfortunately, virtually nothing is known about the natural history of the Reedy Creek form. Reedy Creek or its near vicinity has been visited by various zoologists including members of the Horn Expedition in 1894, Finlayson who in the early 1930s collected at Quadajunta and Yaringa which are west and southwest of King's Canyon, and an Australian Museum party that collected at Reedy Creek in 1965 (S. Parker, personal commun.). Evidently no specimens of *Sminthopsis* were collected from these localities.

Supposed fossil records of *S. hirtipes*: Records of *S. hirtipes* based on fossil remains from caves on the west coastal plain of Western Australia are given by Lundelius (1957). Archer and Baynes (1972) concluded that the specimens on which these identifications were based represent *S. murina* and *S. granulipes*.

Sminthopsis crassicaudata (Gould)

Phascogale crassicaudata Gould, 1844.

Sminthopsis crassicaudata centralis Thomas, 1902.

Sminthopsis crassicaudata ferruginea Finlayson, 1933.

TYPE SPECIMENS: *Phascogale crassicaudata* Gould, 1844. Holotype: BM 44.7.9.10 (dry skin) and BM 44.10.15.4 (skull), adult male, collected by J. Gilbert. I have examined the holotype. Type locality: Gould (1844, p. 105) "*Hab.* Western Australia." Gould (1845, text for pl. 47 of vol. 1) stated that the type was sent "by Mr. Gilbert, who procured it at the Military Station on William's River. . . ." Western Australia. *Sminthopsis crassicaudata centralis* Thomas, 1902. Holotype: BM 2.9.8.7 skin and skull, adult male, collected by Hillier June 21, 1902. I have examined the holotype.

TYPE LOCALITY: Thomas (1902, p. 492) "*Hab.* Killalpanima, Lake Eyre East, desert region of South Australia." *Sminthopsis crassicaudata ferruginea* Finlayson, 1933. Holotype: No holotype was designated because the description was considered by Fin-

layson (1933, p. 199) to be provisional. He stated "a detailed diagnosis is deferred pending further investigation." Type locality: Finlayson (1933, p. 199) noted that this form occurs in the Macdonnell Range, Northern Australia.

DIAGNOSIS: A small species of *Sminthopsis* differing from other species in having large entoconids that contact the lingual end of the hypocristid so that with wear, a transverse crest develops involving the entoconid and hypoconid as buttressing ends. It also differs from *S. murina* and *S. leucopus* in lacking enlarged apical granules on the interdigital pads, and in having an incrassated tail, a pronounced dark head patch (not a stripe), and large entoconids. It also differs from *S. ooldea* in having narrow premolars, longer palatal vacuities, relatively unreduced paracones on the upper molars, large entoconids, longer ears, and shorter tail. It also differs from *S. virginiae* in being smaller, in having an incrassated tail, in lacking enlarged hallucal granules, in lacking enlarged apical granules on the fused interdigital pads, in lacking a head stripe (although it has a dark head patch), in having long premaxillary vacuities which extend posteriorly to a point posterior to the alveolus of C¹, and in having relatively reduced C1. It also differs from *S. macroura* and *S. douglasi* in being smaller, in having a dark head patch rather than a head stripe, relatively long premaxillary vacuities, relatively reduced C1, in lacking enlarged hallucal granules, in having fused interdigital pads on the hind feet, and in lacking enlarged apical granules on the interdigital pads. It also differs from *S. granulipes* in being smaller, in having a dark tail, hairless interdigital pads on the hind foot, non-granular terminal pads on the digits, relatively shorter and wider upper molars, in lacking an enlarged posterior lobe on I₃, in having large entoconids, and relatively wider less-spaced premolars. It also differs from *S. psammophila* in being smaller, in lacking a crest on the incrassated tail, in lacking granular terminal pads on the digits, in having relatively reduced C1, relatively shorter and wider upper molars, and large entoconids. It

also differs from *S. longicaudata* in having a relatively short incrassated tail, non-striated granules on the terminal toe and interdigital pads, in lacking hallucal, posthallucal or metatarsal enlarged granules in having a relatively less-developed alisphenoid tympanic wing, in having relatively shorter and wider upper molars, and in having large entoconids. It also differs from *S. hirtipes* in lacking hair on the fused interdigital pads, in lacking granular terminal pads on the digits, in having relatively long premaxillary vacuities, relatively less-developed alisphenoid tympanic wing, and large entoconids. It also differs from *S. butleri* in having an incrassated tail, no enlarged apical granules on the interdigital pads, entoconids on M₂ to M₄, and long premaxillary vacuities.

DESCRIPTION: Tail: The tail is almost always incrassated. Several specimens examined in this study, although obviously referable to *crassicaudata* on cranial, dental and pedal characters, do not have obviously incrassated tails (e.g., WAM M690, M1275). In total, six out of 65 skins of *crassicaudata* examined in the Western Australian Museum collection have tails which are not clearly incrassated. In these specimens, although the tails are not obviously swollen, they are spindle-shaped. Tail length varies geographically, being longer in inland forms and shorter in coastal forms, but no specimen examined in this study has a tail length which equals or exceeds the nose-vent length. Tails of some dried specimens may not be representative of the condition in the living animal. Gilbert (in Wittell, 1954, p. 107) noted that "The most striking and singular character in this species, is the extraordinary form of the tail, the size of which in the dried skin is nearly a third less than nature, from its peculiar form it was quite impossible to skin it without making an incision nearly its full length, the middle or largest part was a lump of white oily fat."

EAR: The ear is large and prominent. Krefft (1867, p. 11) said "they carry their ears folded down, never erect, when alive. . . ." This is not substantiated by live

animals of this or any other dasyurid species I have kept in captivity. The folded condition is only characteristic of an intimidated individual. A similar reaction is the fluffing of brushed tails (as in *Phascogale* and *Dasyurus*) which in the relaxed state are much less conspicuous. Recent renditions of dasyurids with fluffed tails (e.g., Ride, 1970) are often given because while animals are observed by people they are likely to be excited or intimidated.

HIND FOOT: The interdigital pads two to four are fused well up from their base, and near their apex. No single enlarged apical granule exists although in some individuals from inland localities, a moderately well-defined row of apical granules is sometimes apparent (Troughton, 1965, p. 309). Presence of a hallual granule is variable (absence being regarded as a diagnostic feature by Jones, 1923). Among 65 Western Australian specimens, clear development of a hallual granule occurs in 12 specimens (e.g., WAM M2281 and M772). No hair occurs on the interdigital pads. The terminal pads of the digits are smooth and lack striae or granules.

NIPPLE NUMBER: Spencer (1896a) recorded only one (possibly abnormal) individual with six. Spencer (1896a), Krefft (1867) and Troughton (1965) all recorded 10, presumably the normal number. Finlayson (1933) recorded eight and 10.

PELAGE: Descriptions have been given by Gould (1844), Spencer (1896a), Finlayson (1961), and Troughton (1965). Thomas's (1888) description is confused because of his synonymy of *S. macroura* with *S. crassicaudata*. Because no Ridgway colors have previously been given, two dry skins are described here. NTM3610 is from Hamilton Downs, Northern Territory, and J11437 is from Millmerran, Queensland. Middle of back, Buffy Brown (NTM3610) Cinnamon Brown to Bister (J11437); belly, almost white (NTM3610, J11437); patch behind ear, Pinkish Buff (NTM3610, J11437); forehead patch, Dark Olive (NTM3610), Buffy Brown (J11437). Typical dorsal underfur, such as that of WAM M7942, from Kokardin, Western Australia, is between Slate-Gray and Slate Color. WAM M7942 shows a very pale

saddle of short hairs which extends across the face in front of the eyes and is in this respect abnormal. In most specimens, the dark patch on the forehead and between the ears is generally wider than the head stripes of other species. A dark area encircles the eye and sometimes extends to the nose. A dark patch also occurs on the anterodorsal area of the ear.

DENTITION: I^1 is the tallest upper incisor and is separated from I^2 by a diastema. I^2 to I^4 crown lengths increase posteriorly. I^4 has a conspicuous but small posterior lobe. I^1 is separated from C^1 by a diastema in which occurs a fossa corresponding with the tip of C_1 . C^1 has a variably developed small anterior cingular cusp, a larger posterior cingular cusp (present on WAM M7746, absent in B2950), and lacks buccal and lingual cingula. Crown heights and lengths of P^1 to P^4 increase posteriorly. All upper premolars have anterior and posterior cingular cusps although the anterior cusp on P^4 may be very small (e.g., J7654), and lingual and buccal cingula are variably developed but generally absent below the tip of the paracone. The dp^4 (e.g., WAM M2421) is three-rooted with two principal cusps, a paracone and a slightly larger metacone. A minor cusp on the anterobuccal edge of the crown may be homologous with styler cusp A, and another minor cusp may be homologous with the protocone. No rudiment exists of styler cusp D. The paracones of M^1 to M^4 increase in height posteriorly. The metacones of M^1 to M^3 are subequal, as are the protocones. The protocone of M^4 is smaller than that cusp on M^1 to M^3 . Styler cusp A, even on unworn teeth, is not clearly distinguishable from the buccal edge of the anterior cingulum. Styler cusp D is subequal on M^1 and M^2 and taller than that cusp on M^3 . Styler cusp D, when present on M^4 (e.g., WAM M7746), is very small. Styler cusp C is variably present and tiny. In one specimen (WAM M7746) the position of styler cusp C varies. In M^1 it may be recognized as a minor cusp on the posterior flank of styler cusp B, and in M^3 it may be recognized as a minor cusp or ridge isolated between styler cusps D and B. Styler cusp E is also variably developed such that in one speci-

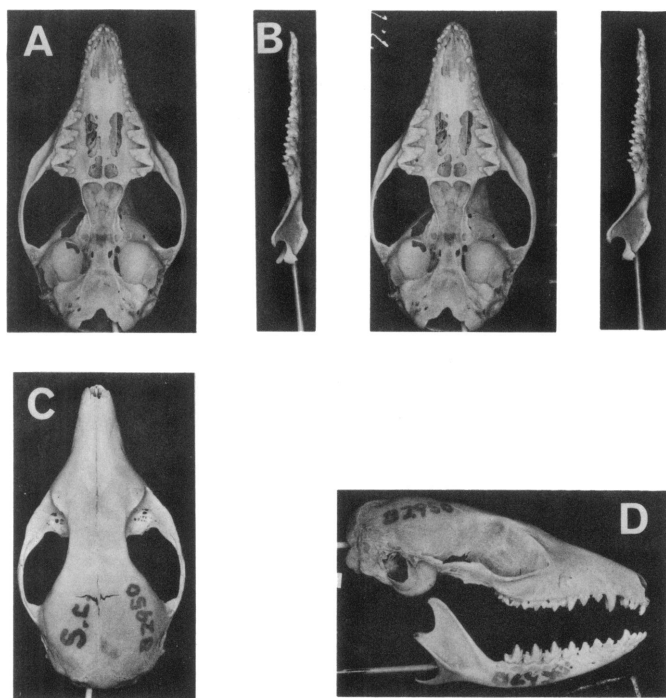


FIG. 60. *Sminthopsis crassicaudata*, WAM B2950, adult, Curtin Springs, Northern Territory. A–D, $\times 2$.

men (WAM M7746) there are two minor stylar cusps present in this position on M^1 to M^3 . The paracristae increase in length from M^1 to M^4 . The metacristae of M^1 and M^3 are subequal in length and shorter than that crest in M^2 . Anterior cingula are incomplete on the upper molars. I_1 is the tallest lower incisor crown. I_3 has a small posterior lobe. A diastema between I_3 and C_1 is not always present. C_1 is premolariform with a small posterior cingular cusp and an incomplete buccal and lingual cingulum. C_1 crown is slightly taller than the crown of P_4 . P_1 crown is the shortest in length and height of the lower premolars. P_3 and P_4 are subequal in crown height. P_3 crown length is longer than the crown length of P_4 . Lower premolars have very small anterior and posterior cingular cusps, and variable cingula, being sometimes continuous on the buccal side (e.g., WAM M2421) but generally poorly developed on the lingual side. dP_4 is two-rooted with one

principal cusp, the protoconid. There are also small anterior and posterior cingular cusps, possibly homologous with a paraconid and hypoconulid, and a minor cusp or swelling that may represent a hypoconid between the posterior cingular cusp and the protoconid. dP_4 has a lingual but no buccal cingulum. The paraconids and protoconids of M_1 to M_3 increase in size posteriorly. The metaconid of M_4 is subequal to that cusp in M_3 . The hypoconids of M_1 to M_3 are subequal in height. The entoconids are present and large on M_1 to M_3 , increase in size posteriorly from M_1 to M_3 , and are variably present and tiny on M_4 . On M_1 to M_3 the posterior hypocristid extends from the hypoconid to a position immediately behind or on the flank of the entoconid. Because of this proximity to the entoconid, as soon as (or even before) the tooth sustains wear from the metacone of an upper molar, a continuous cristid is produced, bound by the entoconid

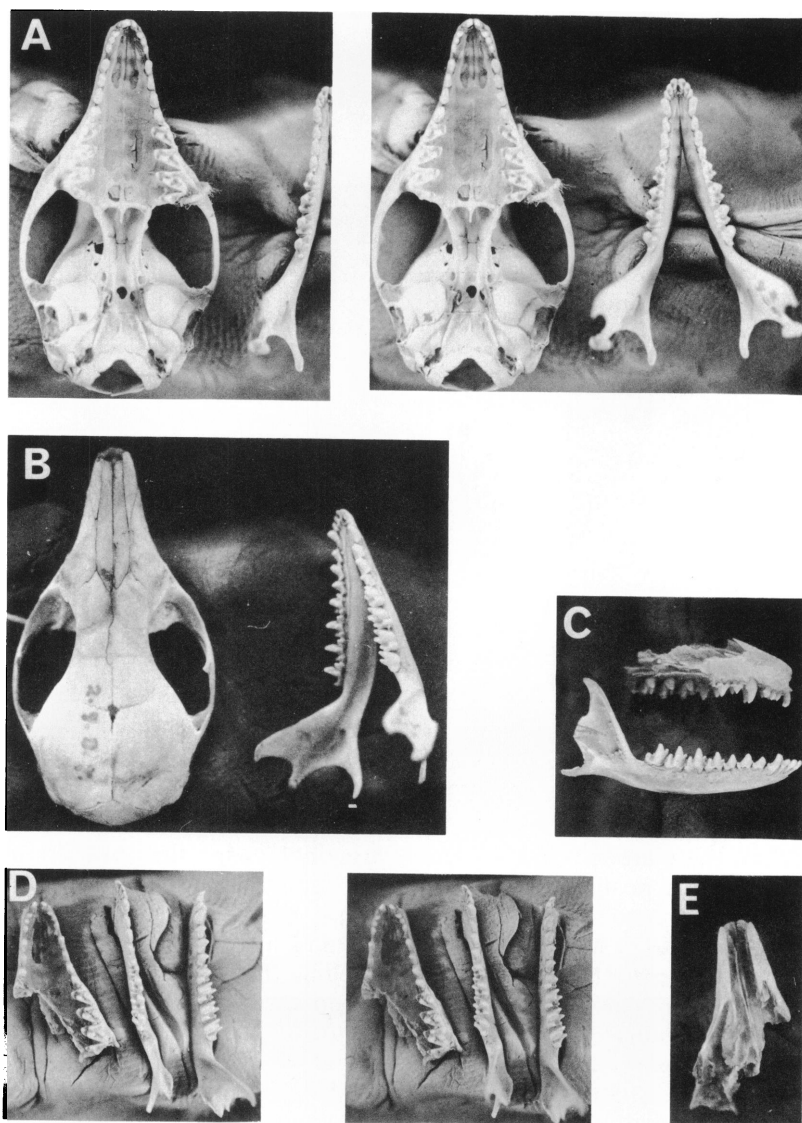


FIG. 61. A–B, Holotype of *Sminthopsis crassicaudata centralis* Thomas, BM 2.9.8.7, Killalpaninna, South Australia. C–E, Holotype of *Phascogale crassicaudata* Gould, BM 44.7.9.10, Western Australia. See table 1 for measurements.

on one end and the hypoconid on the other. The paracristids increase in length from M_1 to M_3 . The paracristid of M_4 is subequal to that of M_2 . The metacristids of M_1 to M_3 increase in length posteriorly from M_1 to M_3 . The metacristid of M_4 is subequal in length

to that of M_3 . The trigonids of M_1 and M_2 are narrower than the talonids, subequal in width on M_3 , and wider than the talonid on M_4 .

SKULL AND DENTARY: The frontals are swollen anterodorsally by the expanded eth-

moid (and or presphenoid) sinuses which produce a distinct concavity on the dorsal surface of the skull between the anterior parts of the two frontals. The lacrimal foramen is single or double and on or just outside the edge of the orbit. The foramen for the entocarotid canal is large and permits direct ventral view into the endocranium. The basisphenoid has only a shallow mid-ventral concavity. The foramen pseudovalle is long and wide. The condylar foramen (including the hypoglossal foramen) is large and variable in number. The basioccipital has a short mid-ventral anterior keel. The alisphenoid tympanic wing is moderately well-developed but still leaves the ectotympanic exposed. Alisphenoid and periotic tympanic wing development is somewhat variable, with larger wings occurring in central Australian specimens. The paroccipital process shows slight enlargement in some specimens (e.g., B2950). The premaxillary, maxillary, and palatine vacuities are very large, with premaxillary vacuities extending posteriorly to the level of the rear of P^1 or even the anterior root of P^3 . Interdental fenestrae are numerous between the upper molars. The anterior border of the ascending ramus and the posterior border of the dentary are subparallel but less so than in *Antechinomys*. The distance between the articular condyle and the tip of the ascending ramus is variable, being sometimes longer than the distance from the articular condyle to the tip of the angular process, depending on the degree of tympanic wing enlargement. The masseteric fossa is relatively small and elongate. The symphysis extends posteriorly to the level of the middle or posterior end of P_3 .

DISCUSSION: *Sminthopsis crassicaudata* has sometimes been the subject of misunderstanding. Thomas (1888) synonymized *macroura* with *crassicaudata*. Spencer (1896a) described *constricta* as a subspecies of *murina*. Tate (1947) considered *constricta* as well as *centralis* to be subspecies of *macroura*. Finlayson (1933) considered the possible synonymy of *larapinta* with *centralis*. These synonymies reflect an underestimation of the distinctness of *crassicaudata*. In fact, the talonid structure immediately sets

crassicaudata apart from all other dasyurid species.

The skull of the possible holotype (see Dixon, 1970) of *Sminthopsis murina* var. *constricta* Spencer (C6920) was removed for examination and confirms the characters of the carcass which indicate that it is a specimen of *crassicaudata*. Dixon (1970) noted that neither the sex nor the measurements of this possible holotype (C6920) correspond with those given by Spencer (1896a). In view of the reference here of C6920 to *crassicaudata*, acceptance of C6920 as the holotype threatens stability of *Sminthopsis crassicaudata centralis* Thomas, 1902. For this reason, an application has been made to the International Commission on Zoological Nomenclature for the suppression of the name *Sminthopsis murina* var. *constricta* Spencer, 1896a (Archer, 1976e).

FORMS OF *SMINTHOPSIS CRASSICAUDATA*: Two names have been applied to specimens regarded here as representing *S. crassicaudata*. The statistical validity of these as subspecies has not been tested but one of these names is useful in qualifying a form which occurs in central Australia. Morton (1978a, p. 153) has stated that "Analysis of morphological variation within *S. crassicaudata* indicates that characters vary clinally (Morton, unpubl. data), and it is impossible to define the two subspecies satisfactorily. Nevertheless, it is sometimes convenient to refer to the long-tailed, sandier-coloured, inland representative of the species as *S. crassicaudata centralis*."

Sminthopsis crassicaudata *crassicaudata*

DISTRIBUTION: The range of this form includes the less arid areas of Western Australia, South Australia, Victoria, New South Wales and Queensland. There is no clear boundary between the range of this and the *centralis* form. The type locality of *Phascogale crassicaudata* Gould occurs within this range.

RECOGNITION: This form may be distinguished from *centralis* by its relatively shorter tail, darker, duller coloration, subequal P^3

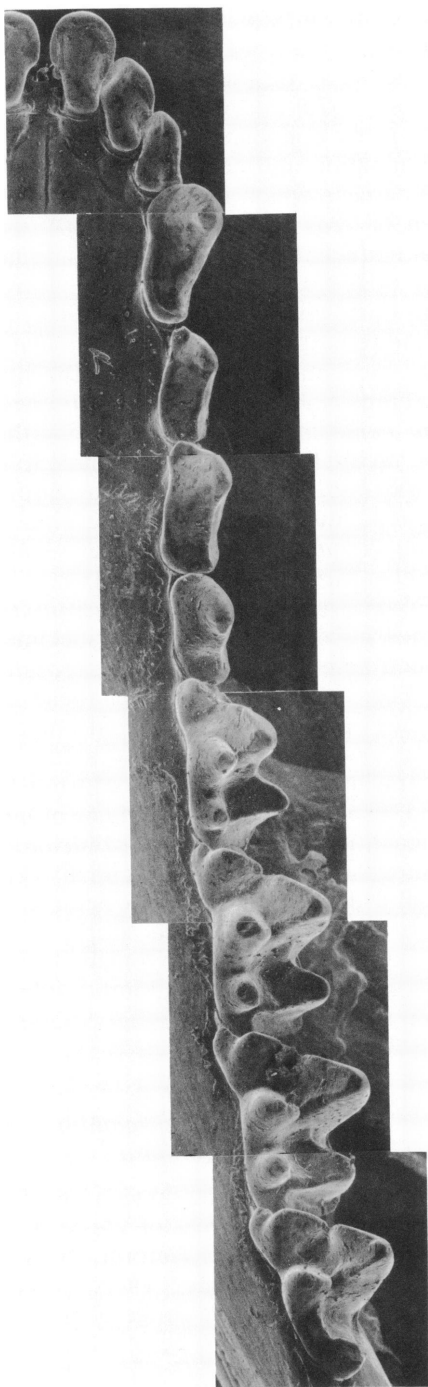


FIG. 62. *Sminthopsis crassicaudata*. Scanning electron microscope photographs of RI₁–M₄.

and P⁴ although this character is not constant, and possibly also by differences in the morphology of the interdigital pads. Finlayson (1933, pp. 197–199) and Troughton (1965, p. 309) both noted that the nominate form has less coarsely granulated interdigital pads.

REMARKS: The collector of the type specimen, Gilbert (in Wittell, 1954, p. 108), said “I take this to be a rare animal or at least a very rare local species, for no person to whom I have shown the only specimen I ever obtained at all recognizes the species, not even any of the natives could remember to have seen it.” Similarly, Shortridge (1910) said of the form in Western Australia that it is apparently rare, the Western Australian Museum having only two specimens from Day Dawn and Dongara. Glauert (1933) stated that the species was common, and later (1954, p. 130) noted that although only one specimen was received at the Western Australian Museum in 1952–1954, “there were 10 in 1942–44; 14 in 1932–34; and four in 1922–24. This may not be a true picture of this useful little animal’s status as official propaganda has been conducted on its behalf.” I have examined 113 Western Australian specimens of *crassicaudata*. Although it is difficult to be certain how much of a discrepancy exists between registration dates and the actual dates of collection for older Western Australian Museum specimens, the vast majority of specimens of this species were registered between 1920 and 1940. This roughly corresponds with a period of general land-clearing activities in the southwestern part of the state. Furthermore, the most frequently recorded method of collection is the process of mallee-root pulling which follows land clearing. This suggests the interesting possibility that initial clearing of land (before stump removal) may favor the establishment of *crassicaudata*.

HABITAT: Gilbert (in Gould, 1845) noted that the type specimen was brought into the Military Station on William’s River by a domestic cat. Krefft (1867) remarked on their ferociousness in captivity and their ability to kill rodents. This often quoted attribute has

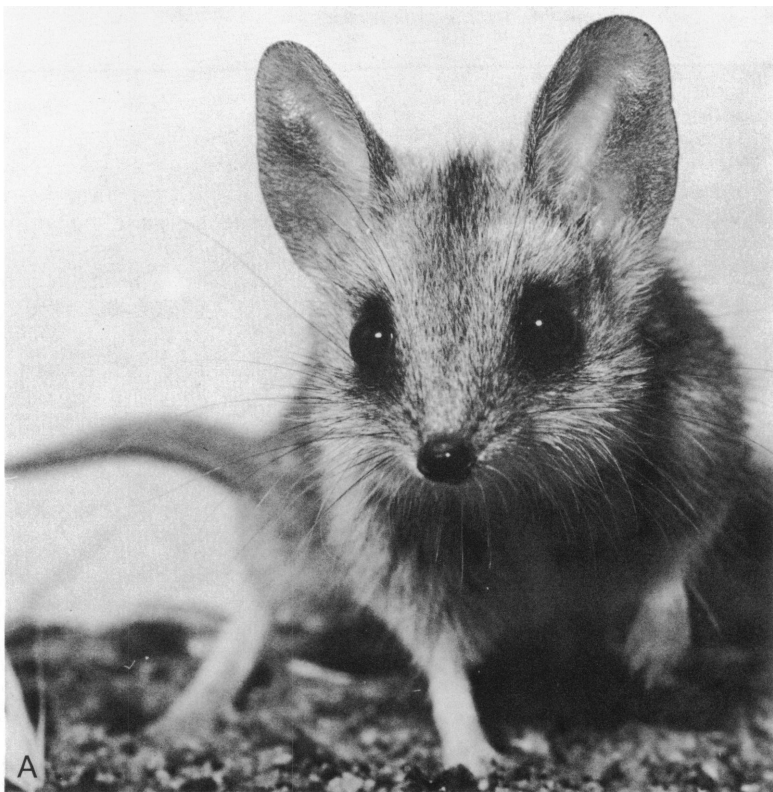


FIG. 63. *Sminthopsis crassicaudata*. A, individual from southwestern Western Australia. B, individual from eastern Australia.

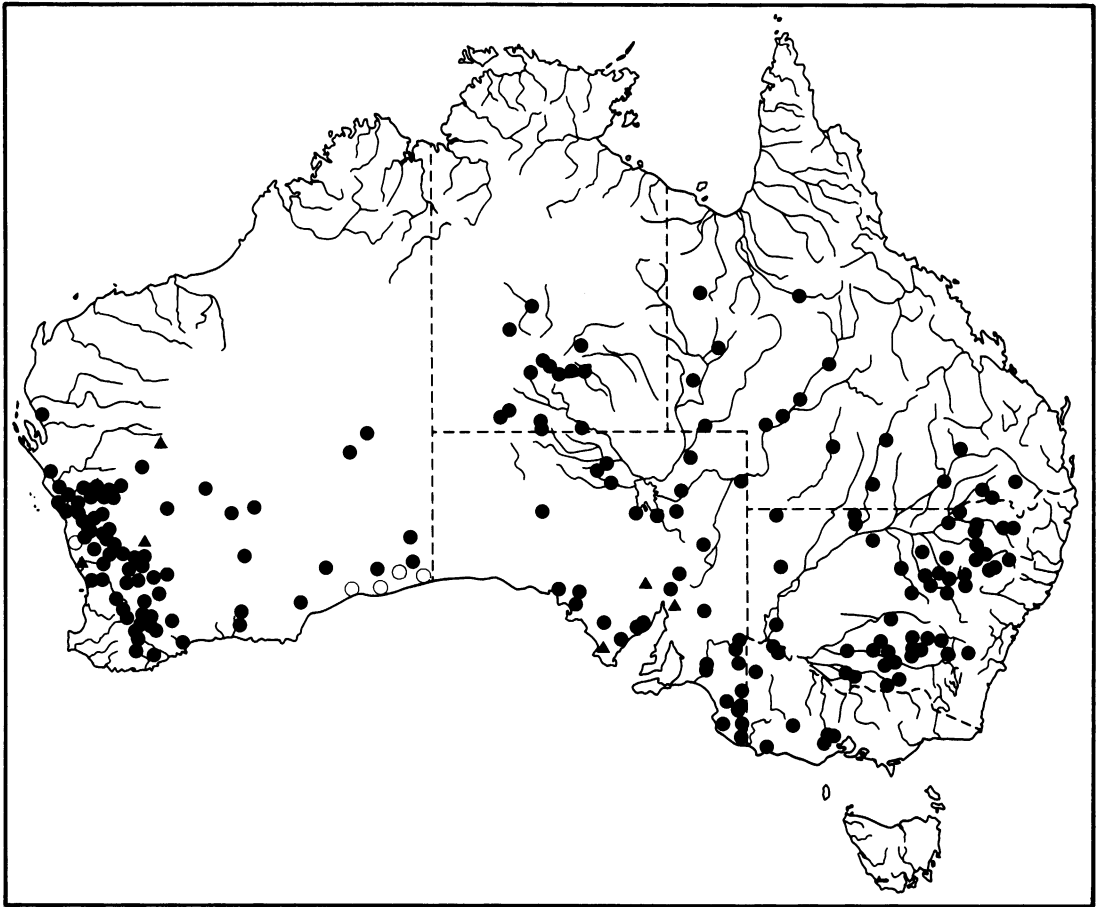


FIG. 64. Geographic distribution of *Smynthopsis crassicaudata*. Solid dots represent modern specimens and hollow dots represent cave specimens examined.

not been my experience which is that this species is reluctant to consume hairless baby mice let alone to kill adult mice. Shortridge (1910) recorded that the species frequents dry sandy and often treeless districts in Western Australia. Marlow (1958) said that in New South Wales they inhabit open plains and woodland and are widely distributed west of the Great Dividing Range. Ride (1970) concluded that the species inhabits woodland heaths, grasslands, and stony places throughout its range. Morton (1978a) concluded that the species predominantly inhabits open grassland and shrubland.

REMARKS ABOUT DISTRIBUTION RECORDS: I have not been able to locate the

specimens noted by Shortridge (1910) and Glauert (1933) from Day Dawn and Dongara. Further, with the exception of WAM M1122 and M1123 from Yanchep, there are no modern specimens from the southern part of the Swan Coastal Plain (Archer and Baynes, 1972). For this reason, the locality data of the two specimens from Yanchep (both collected at the same time) are suspect. The then Curator, L. Glauert frequently recorded the locality of the donor rather than the specimen in the register (Mees, 1963, p. 169, and A. M. Douglas, personal commun.). It is also possible that the two specimens were transported on Wanneroo with mallee roots which are commonly used for firewood. Distribu-

tion records given by Krefft (1864) are Gall Creek along the lower Murray River; by Wakefield (1966a) Mildura, Karawinna, Werimull, Carwarp, Swan Hill, Rainbow, Birchip, Warrnacknabeal, the northern edge of the Little Desert near Kiata, and Goroke, Victoria; by Wakefield (1966b), Mondellundellun, Victoria; by Bannister (1969), Bolgart, Wubin, Yere Yere Farm, and Caron, Western Australia; and by Hampton and Seebeck (1970), Clarkfield, Victoria. The record given by Finlayson (1931) of *Sminthopsis crassicaudatus macrourus* from 45 km. northeast of Rockhampton, Queensland, may not represent *S. crassicaudata*. Late Quaternary records were given by Lundelius (1957, p. 178) "Remains were found in all the caves along the Eyre Highway from Murrae-llellan Cave to Abrakurrie Cave"; by Cook (1960) from caves near Margaret River (these specimens have been re-identified as *S. murina*, Archer and Baynes, 1972); by Lundelius (1963), Cocklebidy, Murrae-llellan, and Madura caves on the Western Australian side of the Hampton Tableland and the Roe Plain; by Wakefield (1963a, 1963b, and 1964a), Mt. Hamilton, Fern Cave, Byaduk Caves, and Natural Bridge in Victoria; by Wakefield (1967b), McEachern's Cave, Victoria (in the recent layers only); by Smith (1972), Victoria Cave, South Australia; and by Archer (1974), Horseshoe Cave on the Western Australian side of the Hampton Tableland. Other specimens of late Quaternary age include 68.6.92, from the Stockyard Gully cave system (the only fossil record from the Swan Coastal Plain).

OTHER STUDIES INVOLVING THE NOMINATE FORM: Alexander (1922), Ewer, (1968), White (1951), Crowcroft and Godfrey (1968), and Morton (1978b) have reported aspects of behavior and social organization. Hope and Godfrey (1968), Cooper and Hope (1971), and Breckon and Hulse (1972) reported on aspects of physiology and chemical polymorphism. Godfrey (1968), and Dawson and Hulbert (1970) reported studies of body-temperatures and torpor, and Godfrey (1969b) and Smith, Bennet, and Chesson, (1978) reported the effects of varying photoperiods on reproduction. Martin (1965),

Godfrey and Crowcroft (1971), and Breckon and Hulse (1972) discussed aspects of raising this species in the laboratory. Tyndale-Biscoe (1973) noted behavioral characteristics which relate to the animal's inability to become torpid; Morton (1978a and c) has reported aspects of this species distribution, reproduction and life history. He has also noted (his figure 1) some localities not recorded in my figure 64.

REMARKS ABOUT THE HOLOTYPE: The holotype consists of a skin and skull, the specimen having at one time been mounted. The skull is badly damaged consisting of a rostrum which is missing RP^4-M^4 . The left and right dentaries are both broken. The skin is in reasonable condition.

Sminthopsis crassicaudata centralis

DISTRIBUTION: Range of this form includes northern South Australia, central Western Australia, southern Northern Territory, and possibly southwestern Queensland and western New South Wales. There are no obvious breaks or barriers which separate *centralis* from the nominate form. The type locality of *Sminthopsis crassicaudata centralis* Thomas and (if it exists) *Sminthopsis crassicaudata ferruginea* Finlayson occur within this range.

RECOGNITION: The *centralis* form may be differentiated from the nominate form by its longer tail, longer ear, more rufous color, and differentiable median row of granules on the interdigital pads. Finlayson (1933) also noted that *centralis* differed in being lighter in build with longer limbs, having a relatively broader, longer and more pointed ear, larger hind feet, canine which may be slightly longer, premolars which are less disproportionate in size relative to each other, and posterior margins of the nasals which are more sharply angulated. Troughton (1965, p. 309) stated that *centralis* has interdigital pads that are "more coarsely granulate, with the outer interdigital pads less inflated, and the three pads with a single row of enlarged granules down the midline, compared with the overall fine granulation in the typical form."

REMARKS: Finlayson (1933) examined a

large number of specimens (approximately 50) extending from the Macdonnell Range in the Northern Territory to southeastern South Australia and concluded (p. 198) that while "there is a considerable individual variation which is responsible for the occasional appearance of similar individuals at widely sundered places, the chief result of this analysis has been to reveal a steady change in colouration, and in length of tail and ear, as one proceeds from south to north, together with the retention, almost unmodified, of skull characters, foot structure and pattern of markings." He also noted (p. 197) of specimens referable to *centralis* that the "ground colour of the dorsum, in the present series of 22, is remarkably inconstant, and varies. . . . The differences do not appear altogether capriciously, however, but represent to some extent at least, adaptations to the prevailing colour of the environment during periods when the *Sminthopsis* population is stationary. The paler forms appear in the bleached sandhill-claypan country near the channels, and the richer pink forms in the red gibber plains." Although Finlayson (1933) recognized this intraspecific and clinal variation, he provisionally named another form, *ferruginea*, for the northern end members of the cline, in contrast to *centralis* which he reserved for the pallid individuals in this area. This seems unjustified and even Finlayson (1961) did not continue to use *ferruginea*.

HABITAT: Spencer (1896a, p. 30) said that in central Australia *centralis* is "a burrowing (?), nocturnal animal, and hence . . . not easy to catch." Specimens were caught on sandy plains at Charlotte Waters, Northern Territory. P. M. Byrne informed Spencer (1896a) that *centralis* preferred softer ground near the creeks and amongst the sandhills rather than the stony tablelands preferred by *S. macroura* (as *larapinta*) around Charlotte Waters. Finlayson (1933) noted that although this form apparently is normally uncommon, it was very common in 1930–1932, at the time of a mouse (*Mus musculus*) plague. Local residents regarded *centralis* to be a predator of mice. Finlayson was

told by Aiston that in the early part of 1932, at Mulka, while the *centralis* were breeding it was found in nests on the surface. At other times during 1930–1932, it was found in shallow burrows in all types of country. After the mouse plague subsided, the *centralis* disappeared. The following winter, specimens were taken from holes (p. 197) "in a sluggish condition very different from its usual vivacity" which suggested "a partial hibernation in this and allied species, in captivity, have met with no success." Parker (1973, p. 5) noted that the Northern Territory *centralis* (I identified the specimens) "Prefers more densely vegetated areas and softer soils . . . (sandhills, seasonal swamps, bore overflows and creeks)," and that following good seasons it was locally common. Morton (1978a, also reviewing work by Martin Denny on populations in western New South Wales) has concluded that although Spencer (1896) and Parker (1973) have claimed the species prefers more densely vegetated areas than the closely related *S. macroura*, the reverse is true. This conflicting claim may be due to the fact that Spencer and Parker were reporting observations based on more inland populations than the ones studied by Morton and Denny. I have collected *centralis* from Etadunna (alternative spelling is Etudanna) Station, 16.9 km. south of Killalpaninna, South Australia. They were spotlighted and hand-caught at night on gibber plain (sparsely vegetated sheets of silcrete cobbles and clay soils) in November 1972. Two individuals were kept in captivity at Etadunna Station where they thrived on honey, moths, and centipedes.

REMARKS ABOUT THE HOLOTYPE AND TYPE LOCALITY: The skull of the holotype is grossly abnormal. The L and RI⁴ have partially divided roots and crowns, there are two accessory palatine vacuities anterior to the normal pair, and there is a large "pituitary vacuity" in the midline of the basisphenoid between the foramina pseudovale. There is also an abnormal fontanelle between the posterodorsal corner of the petrotic and

the paroccipital bones. Some of these abnormalities have been previously noted (Archer, 1975c).

Thomas (1902) listed Killalpanima, Lake Eyre East, desert region of South Australia, as the type locality for *centralis*. This would appear to be a mistaken rendition of Killalpaninna, a now-abandoned Mission along the Cooper Creek once run by Lutherans (Bonthon, 1971).

REPRODUCTION IN ALL *SMINTHOPSIS CRASSICAUDA*: Spencer (1896a) noted that although females with young were secured in November and December, one was secured with 10 pouch young in July which suggests *centralis* may be polyoestrous. Woolley (1973) reviewed information about reproduction in the laboratory which indicated that the species is polyoestrous, with a gestation period of approximately 13–16 days, births occurring in most months of the year, lactation lasting 60–70 days, and females maturing up to 44 days before males.

SUBGENUS *ANTECHINOMYS* KREFFT

Antechinomys Krefft, 1967.

TYPE AND ONLY SPECIES: *Antechinomys laniger* (Gould, 1856).

DIAGNOSIS: The species of *Antechinomys* differs from all species of the subgenus *Sminthopsis* in possessing only four hind toes, a terminal brush on the tail, relatively longer limbs, and widely flared lacrimal bones.

DESCRIPTION: A revision of *Antechinomys* has been given elsewhere (Archer, 1977).

DISCUSSION: Tate (1948) suggested that *Antechinomys* was most similar to *Smin-*

thopsis, and in particular to *S. crassicaudata*. I agree and have reviewed this matter elsewhere (Archer, 1977). In terms of cladistics *Antechinomys* must be regarded as a taxon subordinate to *Sminthopsis*. The single species, *A. laniger* shares most apomorphic character states with *S. crassicaudata*. *S. crassicaudata* has a suite of character states (all individually present in one or another of the other species of the subgenus *Sminthopsis*) which are homologous with the same but better developed states in *Antechinomys* such as the very large palatal vacuities, very wide molars, fused interdigital pads on the hind foot, and very large ears. However, it also has a few apomorphic characters that separate it from *A. laniger* and at least superficially ally it with other *Sminthopsis*, such as the incrassated tail, and autapomorphic character states including the unique talonid morphology.

Antechinomys laniger (Gould)

Phascogale laniger Gould, 1856.

Antechinomys spenceri Thomas, 1906.

REMARKS: The systematics of *Antechinomys* have recently been reviewed by Lidicker and Marlow (1970) who regarded the genus to contain two species. In my revision of *Antechinomys* (Archer, 1977), I concluded the genus was monotypic. I also gave details of the type material, subspecies, and proposed a hypothesis for the origin and radiation of *Antechinomys*. In that earlier work, *Antechinomys* was treated as a full genus, although a sister group of *Sminthopsis* with distinct affinities to *S. crassicaudata*.

GEOGRAPHIC CHARACTER CORRELATION IN *SMINTHOPSIS*

Species of *Sminthopsis* range in habitat from tropical closed forest to the most arid inland areas of Australia. Species considered restricted to inland or relatively arid locali-

ties are *S. hirtipes*, *S. longicaudata*, *S. ooldea*, *S. psammophila*, and *S. douglasi*. Species occurring in continentally peripheral localities are *S. leucopus*, *S. murina*, *S. vir-*

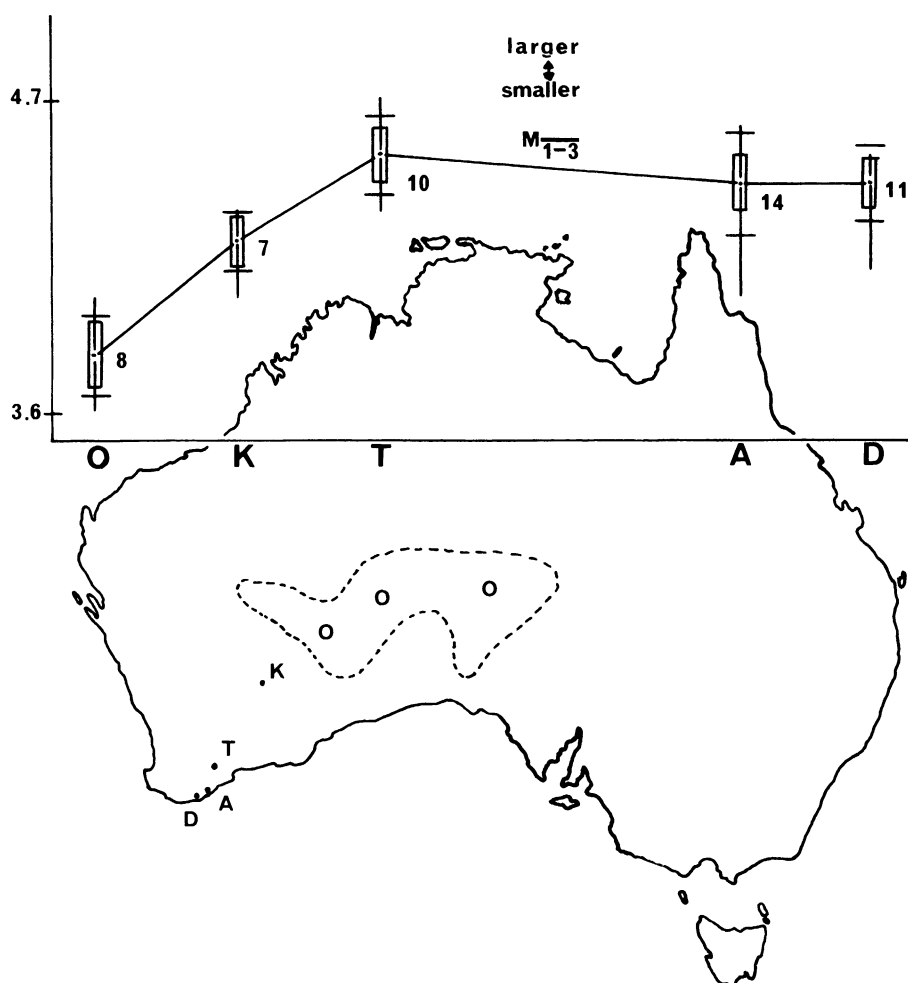


FIG. 65. Absolute size (mm.) of M_{1-3} as a function of locality. K, "Kalgoorlie" population from the area around Kalgoorlie (av. annual rainfall 260 mm.); T, Tambellup population (460 mm./yr.); A, Albany population (960 mm./yr.); D, Denmark population (1140 mm./yr.); O represents *Sminthopsis ooldea* (from areas where the average rainfall is 60 mm. or less per year). Horizontal line connects the means. Vertical lines represent the observed range. Short horizontal lines represent one standard deviation. Rectangles represent 95 percent confidence intervals for the mean. Number represents the sample size. BL, basicranial length; BW, bullar width (combined widths of both bullae); HB, head-body (nose-vent) length; IO, interorbital width (minimum); IPVD, interpalatal vacuity distance; TV, tail-vent length; ZW, zygomatic width (maximum).

giniae, and *S. butleri*. Three species have broader ranges and do not occupy exclusively arid or non-arid habitats: *S. crassicaudata*, *S. granulipes*, and *S. macroura*. All are adapted to arid habitats, some populations of which have secondarily spread into areas of less aridity.

Some species have broad habitat ranges. *Sminthopsis murina*, for example, in Western Australia, ranges from the very wet areas of the extreme southwest, to the arid areas northeast of Kalgoorlie. Pressure to adapt to these different habitats might result in differences in morphology. *Sminthopsis murina*

with its relatively wide distribution and reasonable representation in museum collections, lends itself to an examination of this kind.

I examined five samples of Western Australian *Sminthopsis murina fuliginosa*: Twelve specimens from Denmark (e.g., WAM M1005); 14 from Albany (e.g., WAM M825); 10 from Tambellup (e.g., WAM M626); seven from Hampton Hills Station (e.g., WAM M1341); and two from the eastern wheatfields area (e.g., WAM M2401) such as Merredin. I chose these populations of *S. m. fuliginosa* because they represent geographically widespread localities and because they are the largest samples available from single localities. Nevertheless, sample size from each locality is small and more specimens and more information about climates and localities will be required before statistical confidence can be given to the correlations I suggest below.

Cranial and dental characters were plotted against average annual rainfall for the following localities: Denmark, 1140 mm.; Albany, 960 mm.; Tambellup, 460 mm.; Kalgoorlie and other east central wheatfield localities, 260 mm. Consideration of effective rainfall (which includes evaporation rates), rainfall regularity, and other variables would be desirable, but requires some unavailable information about collection sites.

Sminthopsis ooldea is plotted with the above samples in the figures because in most measurements it has values at one extreme of those present in *S. murina fuliginosa*; it is regarded as a derivative of an *S. murina*-like ancestor; and it occupies areas that are more arid than those occupied by *S. murina*. Characters considered here are: (1) absolute size; (2) size of the alisphenoid bullae or tympanic wings; (3) spacing of teeth anterior to the molars; (4) size of the palatal vacuities; (5) width of the posterior part of the palate; (6) interorbital width; (7) tail length; (8) head length (brachycephaly versus dolichocephaly); and (9) entoconid size. Absolute size (as measured by M_{1-3}) indicates an overall, but not consistent, drop in size toward the center of Australia (fig. 65). As a result, ratios have been used in an attempt to portray relative

differences in development of particular characters. As an example, bullar width divided by zygomatic width produces a ratio expressing bullar width as a proportion of zygomatic width. Simpson, Roe and Lewontin (1960) considered use of ratios for this purpose and pointed out that with no other information, it is not clear which variable is responsible for differences in ratio values. For this reason, absolute values for both variables involved have been plotted along with ratio values in figures 65–73. Ratio values are plotted with the sample mean (the mean of the value for each individual), observed range, standard deviation, and 95 percent confidence limits.

ABSOLUTE SIZE OF M_{1-3} : M_{1-3} length is a general indication of overall size and appears (fig. 65) to demonstrate that south coastal individuals of *Sminthopsis murina fuliginosa* are on the average larger than inland animals.

Although some inland species of *Sminthopsis*, such as *S. ooldea* (M_{1-3} length, 3.8 mm.) and the George Gill Range form of *S. hirtipes* (3.7) are small, others, such as *S. douglasi* (6.1), *S. psammophila* (6.0), *S. longicaudata* (5.0), and *S. granulipes* (4.7), are large. Therefore, the trend suggested by *S. murina fuliginosa* is not apparent within the genus as a whole.

In cases where inland animals are relatively smaller, the reason may simply be temperature regulation. Smaller body size results in an increase of the ratio of surface area to body volume. Species of *Sminthopsis* in arid areas, although basically nocturnal, are subject to physiological stresses of aridity. In the first place they are not strictly nocturnal but rather should be regarded as crepuscular, remaining active as long as conditions are tolerable. Secondly, although nocturnal activity in arid areas certainly reduces stress due to high temperatures and water loss, arid area inhabitants will still have less total water available than crepuscular species in non-arid areas.

In at least two cases, absolute size may be the result of character displacement. *Sminthopsis virginiae* and *S. douglasi* are both large species. *Sminthopsis douglasi* is also

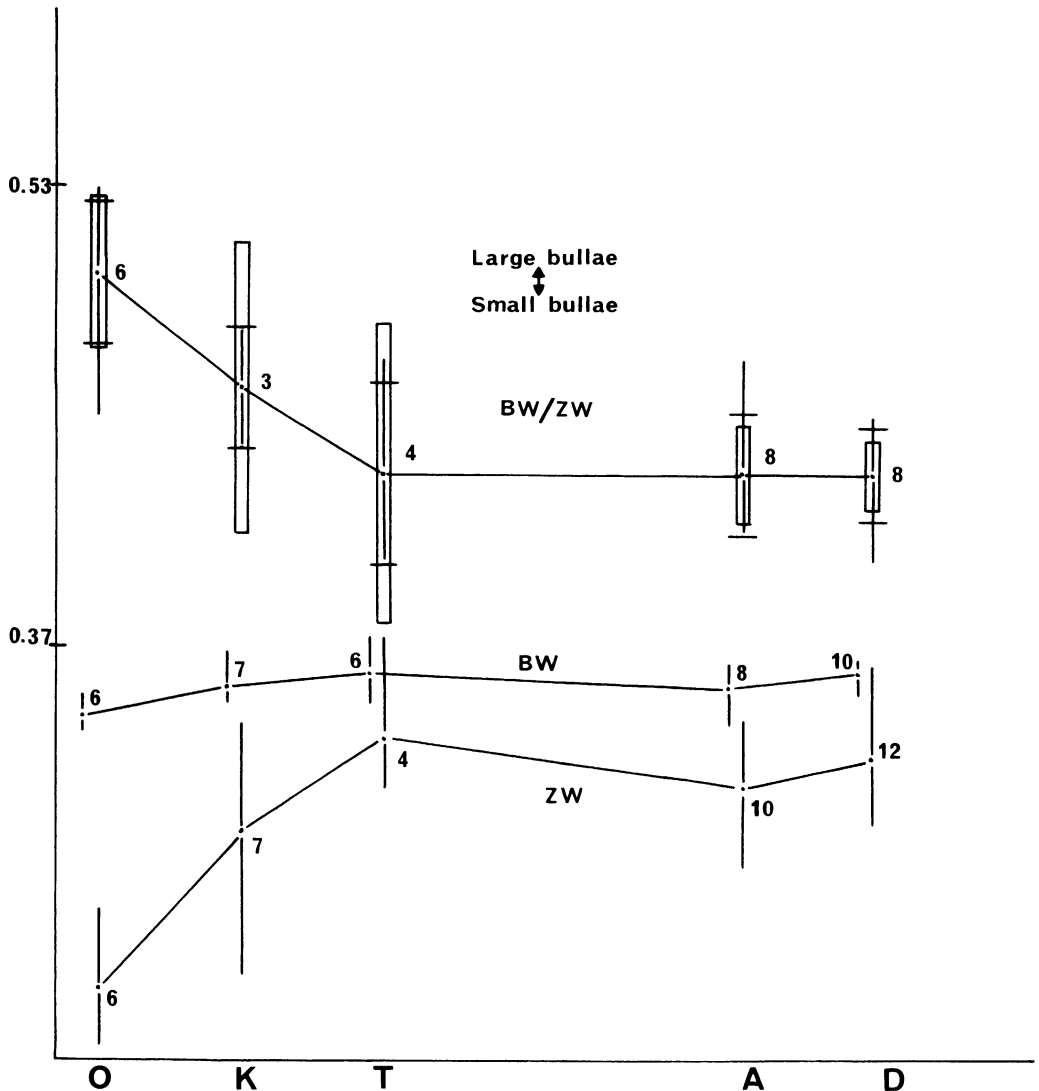


FIG. 66. Relative size of the alisphenoid tympanic wings (bullae) as a function of locality. Upper graph is the ratio of BW (bullar width) to ZW (zygomatic width) which are also portrayed separately in the lower two graphs. Higher ratio values indicate relatively larger bullae. Numbers on the ordinate axis are the highest and lowest ratio values. Values for BW and ZW are not shown but are given in tables. Other symbols are as in figure 65.

sympatric with a morphologically similar species, *S. macroura*, whereas *S. virginiae* is not sympatric with any similar species except *S. butleri* at Kalumburu, Western Australia. *Sminthopsis douglasi* and *S. macroura* are similar in tooth and cranial morphology. The much larger size of *S. douglasi* may be an example of character dis-

placement in response to the smaller and sympatric species *S. macroura*. *Sminthopsis leucopus* in Victoria is about the same size as Tasmanian *S. leucopus* (although it differs in other respects). Victorian *S. murina* are on the average smaller than other *S. murina*. It might be expected that Victorian individuals, which are the farthest south in Australia,

lia, should be the largest. The fact that they are the smallest suggests that their size may be the result of character displacement in response to the sympatric and larger *S. leucopus*.

WIDTH OF THE ALISPHENOID TYMPANIC WINGS OR BULLAE: Width of the alisphenoid bullae was determined by subtracting the distance between the bullae from the outside width across both bullae. This gives a value for the combined widths of both alisphenoid bullae. When bullae width is divided by zygomatic width, the ratio expresses the proportion of skull width occupied by alisphenoid bullae. Comparing values of this ratio for different populations of *Sminthopsis murina fuliginosa* (fig. 56), relative bullae size increases toward more inland areas. In contrast, the absolute bullae size is essentially similar in all *S. m. fuliginosa*, with only a small drop in animals from the Kalgoorlie area (a general term to describe animals from Hampton Hills and central eastern wheat-fields areas). The absolute size of the zygomatic arch width is also essentially constant (fig. 56) inland to Tambellup but a sharp drop occurs in size in animals from the Kalgoorlie area, so that the bullae widths of these inland animals represent a proportionally larger amount of the zygomatic width.

The fact that absolute size of the bullae remains almost constant in all populations of *S. m. fuliginosa* suggests there is an optimum bullae size for this form which is independent of body size.

Relatively large bullae characterize inland species of *Sminthopsis*. The largest mean ratio values (BW/ZW) are those of *S. longicaudata*, 0.54; *S. hirtipes*, 0.52; *S. psammophila*, 0.51; *S. ooldea*, 0.50; and Northern Territory *S. crassicaudata*, 0.50. The smallest values include those of *S. virginiae*, 0.38; Victorian *S. leucopus*, 0.40; Doomadgee Mission *S. macroura*, 0.41 and *S. granulipes*, 0.41.

Enlarged bullae are also typical of other inland dasyurids such as species of *Antechinomys*, *Antechinus*, *Phascogale*, *Dasyercus*, and *Dasyuroides*. In many of these the squamosal and paroccipital bones, as well as the alisphenoid, have well-developed tym-

panic wings. Tate (1947) suggested that in dasyurids larger bullae correspond with a better developed ability to perceive sound. Reig and Simpson (1972) suggested that development of tympanic sinuses in dasyurids and other carnivorous animals may have occurred either to aid intraspecific communication or to aid in finding prey, rather than to evade predators. In view of the massive numbers of dasyurids found in owl pellets in caves around Australia, evasion of predators cannot be dismissed as a significant reason for large bullae in these carnivores. Webster (1961, 1962), Petter (1953), Lay (1972), and others have produced ample evidence for a direct correlation between larger bullae size and increasing aridity in various nonmarsupial groups. Webster and Webster (1975) concluded that larger bullae enhance sensitivity to low frequency sounds such as are produced by the attack flight of owls and the strike of snakes. Nel and Holte (1965) have produced field evidence for a selective advantage in predator avoidance for prey species with large bullae. In view of the fact that the principal predators on small dasyurids are probably owls, it seems highly likely that larger bullae in dasyurids may similarly serve to detect owls striking. This ability would become most critical in open, sparsely vegetated areas where there was need to forage farther from points of safety.

PROPORTIONS OF MOLAR ROW TO ANTE-MOLAR ROW LENGTHS: The length of the upper molar row in *Sminthopsis murina fuliginosa* was divided by the length of the whole cheektooth row. The resulting ratio expresses the proportion of the cheektooth row taken up by the canine and the premolars. This ratio was smaller in south coastal than inland populations, indicating that coastal animals have a relatively larger amount of the tooth row taken up by the canine and premolars. Absolute values for both measurements in *fuliginosa* decrease toward inland Western Australia, with a marked decrease in animals from the Kalgoorlie area. The rise in the ratio value at this point results briefly from the great decrease in size in the value of C¹-M⁴.

Except for *Sminthopsis longicaudata*, *S.*

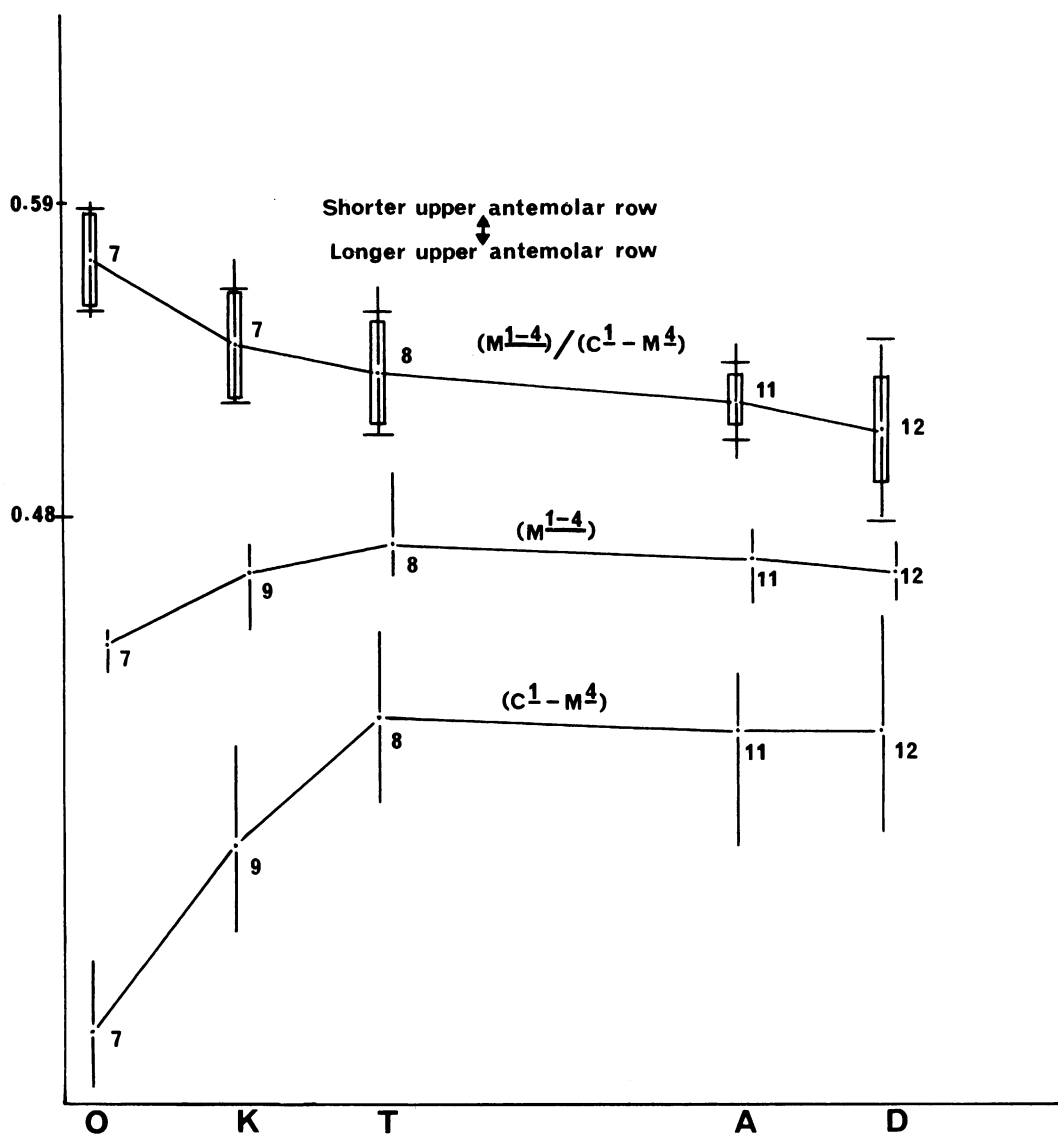


FIG. 67. Relative length of the upper antemolar toothrow as a function of locality. High ratio values indicate relatively shorter antemolar toothrows. Abbreviations and symbols are as in figure 65.

granulipes, and *S. psammophila*, relatively short antemolar cheektooth rows occur in inland species of *Sminthopsis*. Relatively long canine and premolar rows occur in *S. granulipes*, 0.49 (M^{1-4}/C^1-M^4); *S. psammophila*, 0.52; Victorian *S. crassicaudata*, 0.52; *S. leucopus*, 0.50 and 0.53; south coastal populations of *fuliginosa*, 0.51 and 0.52; *S. virginiae*, 0.54 and 0.55; and *S. longicaudata*,

0.51. Relatively short antemolar toothrows occur in central Western Australian populations of *froggatti* (*S. macroura*), 0.57; *S. ooldea*, 0.57; and *S. douglasi*, 0.57.

The same trends are apparent in the lower antemolar cheektooth row (fig. 68).

Observations I have made on captive individuals of *Sminthopsis* (*S. murina*, *S. crassicaudata*, *S. virginiae*, and *S. ma-*

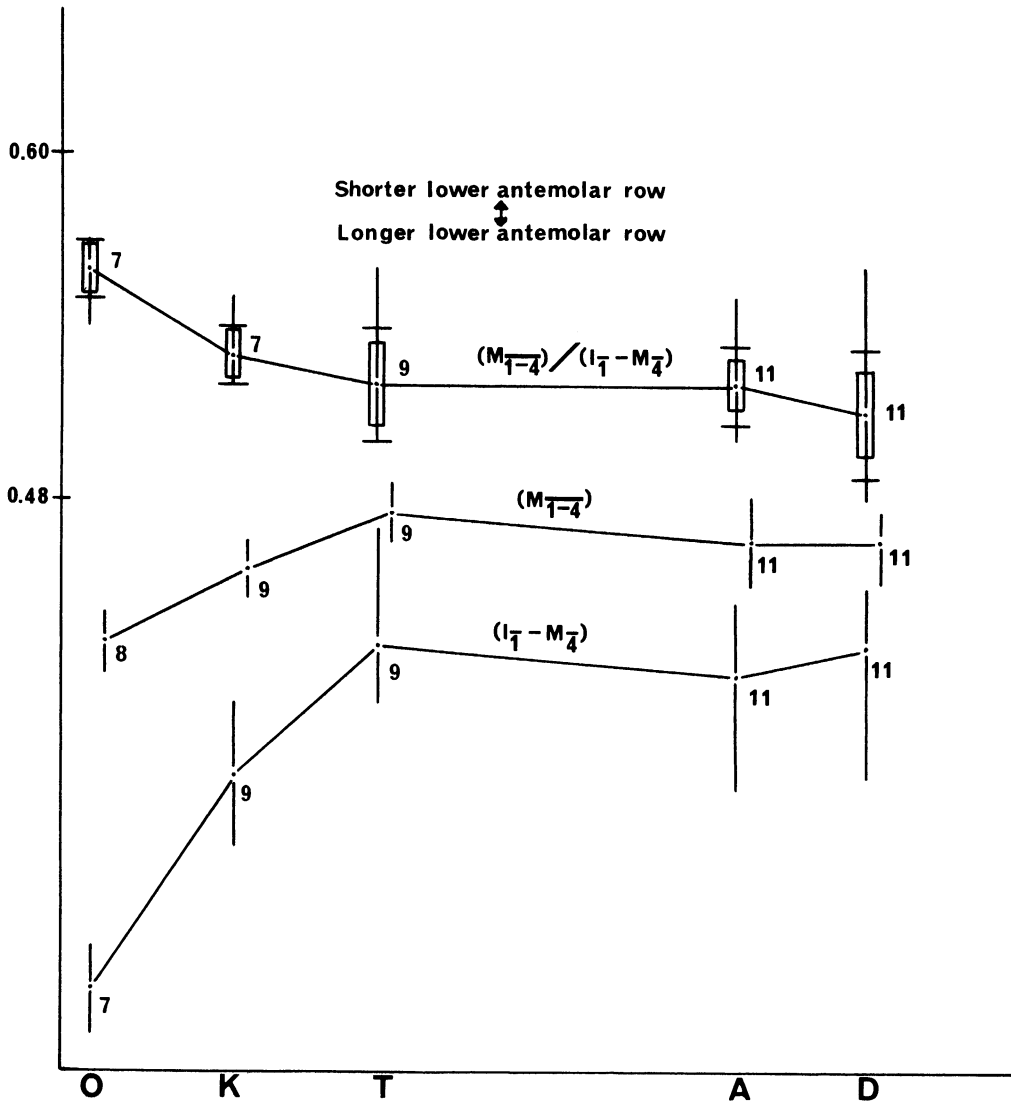


FIG. 68. Relative length of the lower anteromolar tooththrow as a function of locality. Higher ratio values indicate relatively shorter anteromolar tooththrows. Abbreviations and symbols are as in figure 65. The same relationships are evident in the lower dentition as in the upper (fig. 67).

croua) suggest that relatively longer anteromolar cheektooth rows correlate directly with more strictly insectivorous, rather than carnivorous habits. Shorter anteromolar cheektooth rows of inland animals may reflect the need to deal either with vertebrate prey such as lizards or more heavily sclerotized insect cuticles.

In some of the species with the longest an-

temolar cheektooth rows, such as *Sminthopsis granulipes*, there is an interesting specialization that maintains occlusion. The lower third incisor is strongly bilobed so that the posterior face of I^4 opposes or shears past the anterior facet of the posterior lobe of I_3 . Thereby I_3 acts as two teeth against which the shorter-crowned I^4 shears or occludes. In other species with shorter ante-

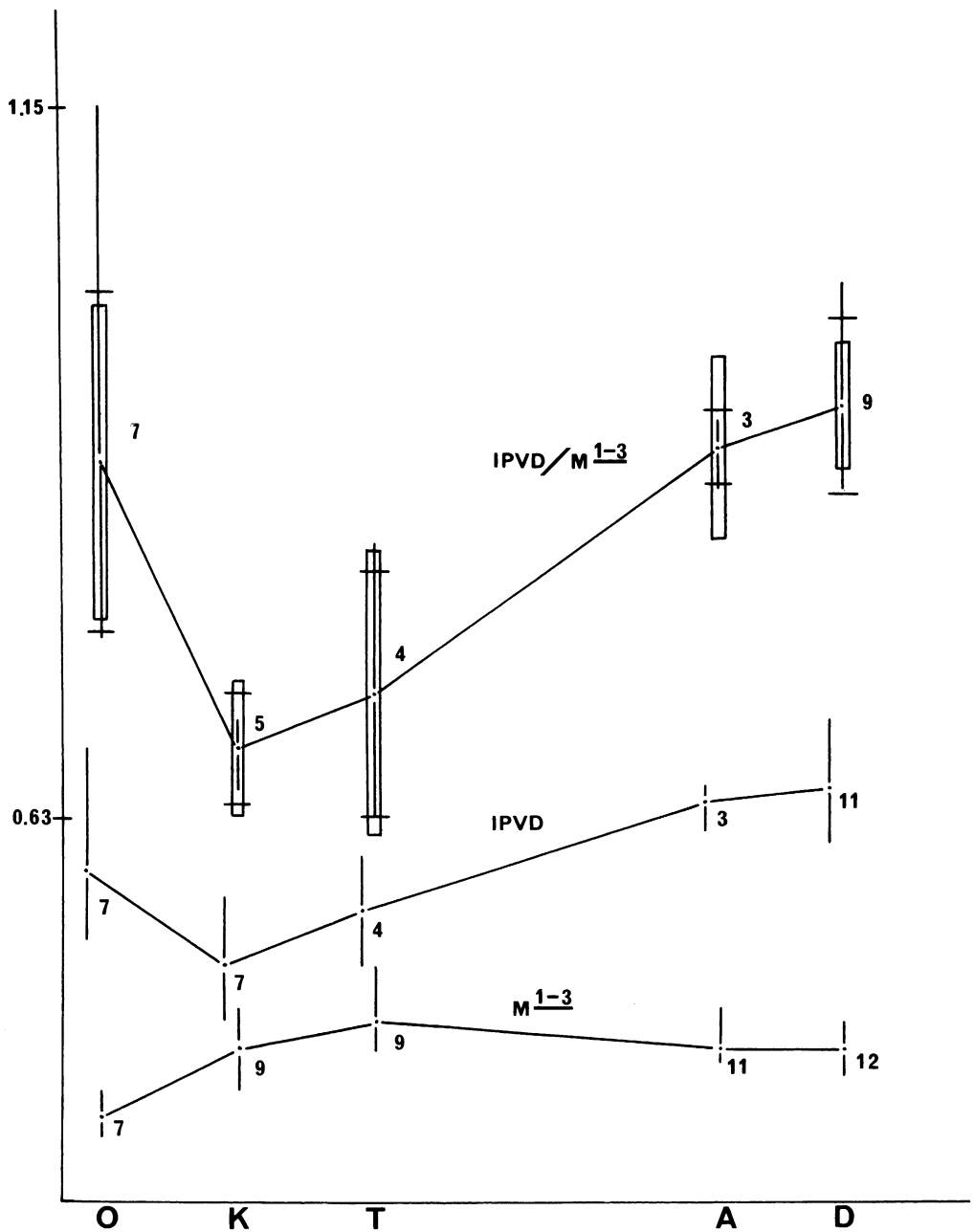


FIG. 69. Relative size of the palatal vacuities as a function of locality. IPVD is the distance between the palatal vacuities and hence is inversely proportional to the size of the palatal vacuities. Lower ratio values indicate relatively larger palatal vacuities. Abbreviations and symbols are as in figure 65.

molar cheektooth rows, I_3 abuts C_1 and the posterior face of I^4 opposes the anterior face of C_1 . In *S. leucopus* the only other species

with a comparably long cheektooth row, I_3 is again somewhat more bilobed than in other species. This adaptation occurs in species of

Neophascogale, and to a lesser extent in those of *Phascolosorex*.

There also appears to be a clear correlation between length of antemolar cheektooth row and premolar width. Premolars tend to be narrow in longer antemolar dentitions, and broad in shorter, often crowded antemolar dentitions. This correlation extends throughout the dasyurids and suggests that animals eating harder-to-crush prey have broader and therefore stronger premolars. The thin premolars of *Sminthopsis granulipes* would hardly stand the stress of mauling or cutting small mammal or lizard carcasses. Some *Sminthopsis*, such as *S. ooldea* and the Doomadgee Mission *S. macroura*, have premolars as broad as those of *Antechinus flavipes*. These forms also have short antemolar cheektooth rows and may be more generally carnivorous or adapted to crushing particularly hard insects.

SIZE OF PALATAL VACUITIES: A measure of the degree of palatal fenestration is obtained by dividing the distance between the adjacent ends of the maxillary and premaxillary vacuities (IPVD) by M^{1-3} length. Figure 69 clearly indicates a trend in *Sminthopsis murina fuliginosa* for increased palatal fenestration in more inland populations. Absolute IPVD values show a pronounced drop from coastal to inland populations, indicating an absolute increase in size of palatal vacuities toward central Australia. Values for *Sminthopsis ooldea* are in distinct contrast to this trend and represent one of the ways in which *S. ooldea* clearly and consistently differs from *S. murina*.

Considering all species of *Sminthopsis*, the smallest ratio (IPVD/ M^{1-3}) values (indicating the largest palatal vacuities) occur in inland populations of *S. murina fuliginosa*, 0.69 and 0.67; *S. butleri*, 0.67; *S. crassicaudata*, all populations, 0.51 and 0.57; and *S. longicaudata*, 0.40. The largest ratio values (i.e., the smallest vacuities) occur in Victorian *S. leucopus*, 0.91; south coastal populations of *S. m. fuliginosa*, 0.90 and 0.93; *S. granulipes*, 1.08; *S. psammophila*, 1.02; *S. ooldea*, 0.89; *S. hirtipes*, 0.92; and *S. douglasi*, 0.95. Although this distribution does not consistently demonstrate the same trend

shown by *S. m. fuliginosa*, the largest vacuities are in fact found in some of the inland populations but only one of the peripheral populations (*S. butleri*), and small vacuities occur in all coastal forms (except *S. butleri*) but also some inland forms.

Gregory (1910) noted on the basis of earlier ontogenetic work, that the palate in some marsupials, complete in young animals, appears to fenestrate as development proceeds. A series of skulls of *Dasyurus geoffroii* (e.g., WAM M6366, WAM M6376) show clearly that posterior palatal vacuities are almost totally lacking in juvenile animals, developing in very young individuals, and well developed in adults. Palatal vacuities in marsupials cannot be merely an example of primitive incompletely developed palates. Fenestration, at least in the posterior region, appears to be secondary. Risks in having fenestrated palates are clear. In a specimen of *Sminthopsis virginiae* (MM M1178) an insect leg passes through the maxillary vacuity into the nasal passage where it is wedged among the turbinal bones and caused necrosis of adjacent bones. Such risks are clearly increased by enlarging palatal vacuities and it seems reasonable to conclude that there must be a strong selective advantage to palatal fenestration that outweighs these risks. The apparent trend for greater fenestration in inland forms suggests the advantage may be correlated with aridity. This is generally supported by examination of other arid-adapted dasyurid and non-dasyurid genera. The peramelids, *Macrotis* and *Chaeropus*, of the five Australian genera, are typical of inland or relatively arid habitats and in both, but particularly *Chaeropus*, palatal vacuities are very large. Two other genera, *Echymipera* and *Isoodon*, are more typical of coastal or less arid habitats and in both of these the palatal vacuities are smaller. Within the genus *Dasyurus* (in the sense of Thomas, 1888) only two species, *D. geoffroii* and *D. hallucatus*, occupy relatively arid habitats and in both palatal vacuities are larger than in the other three east coastal and New Guinean forms. It is possible that fenestration facilitates heat exchange between incoming air in the nasal passage and the moister air of the

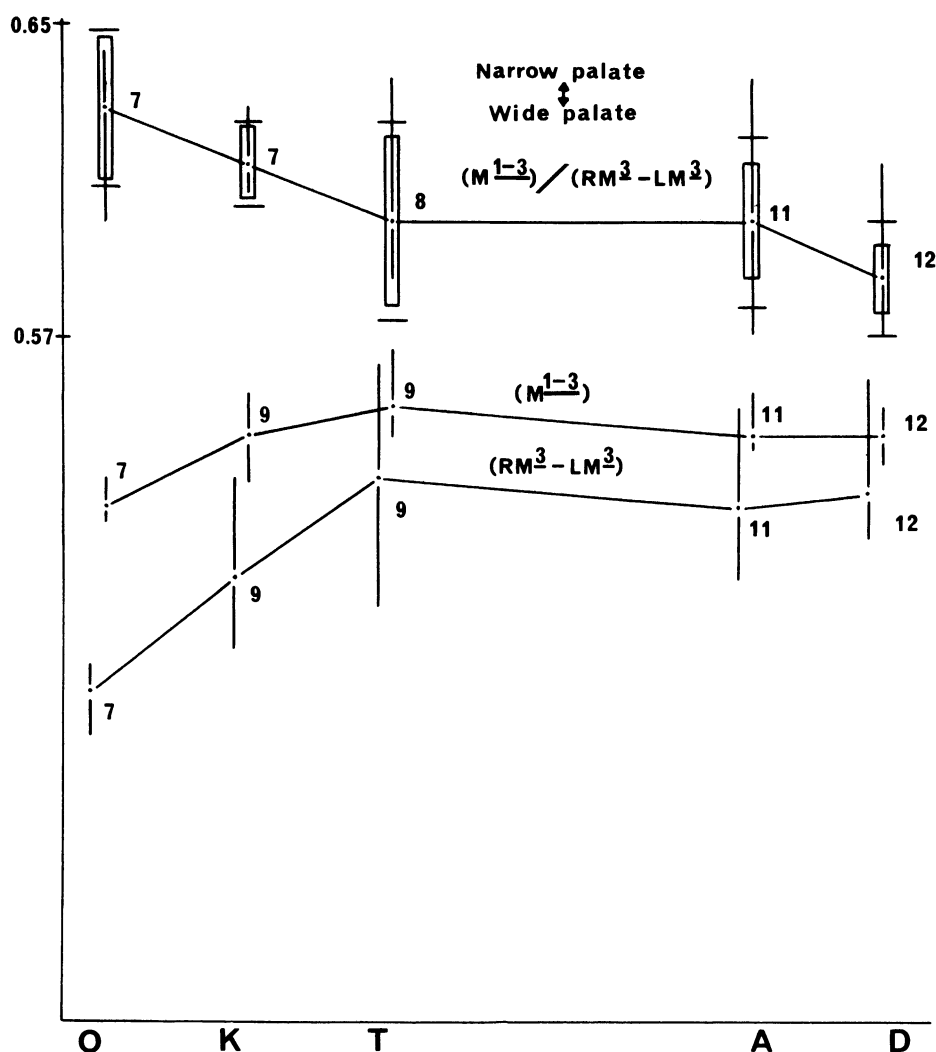


FIG. 70. Relative width of the posterior part of the palate as a function of locality. Higher ratio values indicate relatively narrower palates. Abbreviations and symbols are as in figure 65.

buccal cavity. If the animal occasionally breathes through its mouth, evaporation would lower the temperature of the air in that area and the membranes covering the palate. Air passing over the nasal side of these membranes in the regions of the vacuities would be cooled. This would be an advantage only if temperature were a controlling factor on the animal's activity and this is likely to be significant to crepuscular forms in arid areas. Other less plausible reasons for fenestration

could be the need to conserve calcium, or to lighten the skull.

POSTERIOR PALATE WIDTH: The ratio of $(M^{1-3}) / (R-LM^3)$ gives a measure of relative palatal width in the molar area. The apparent trend (fig. 70) is for narrower palates to occur in more inland populations of *S. murina fuliginosa*. Absolute values of $R-LM^3$ in *S. m. fuliginosa* show a reasonably constant size from coastal areas to Tambellup, but appear to drop sharply in the Kalgoorlie area. This

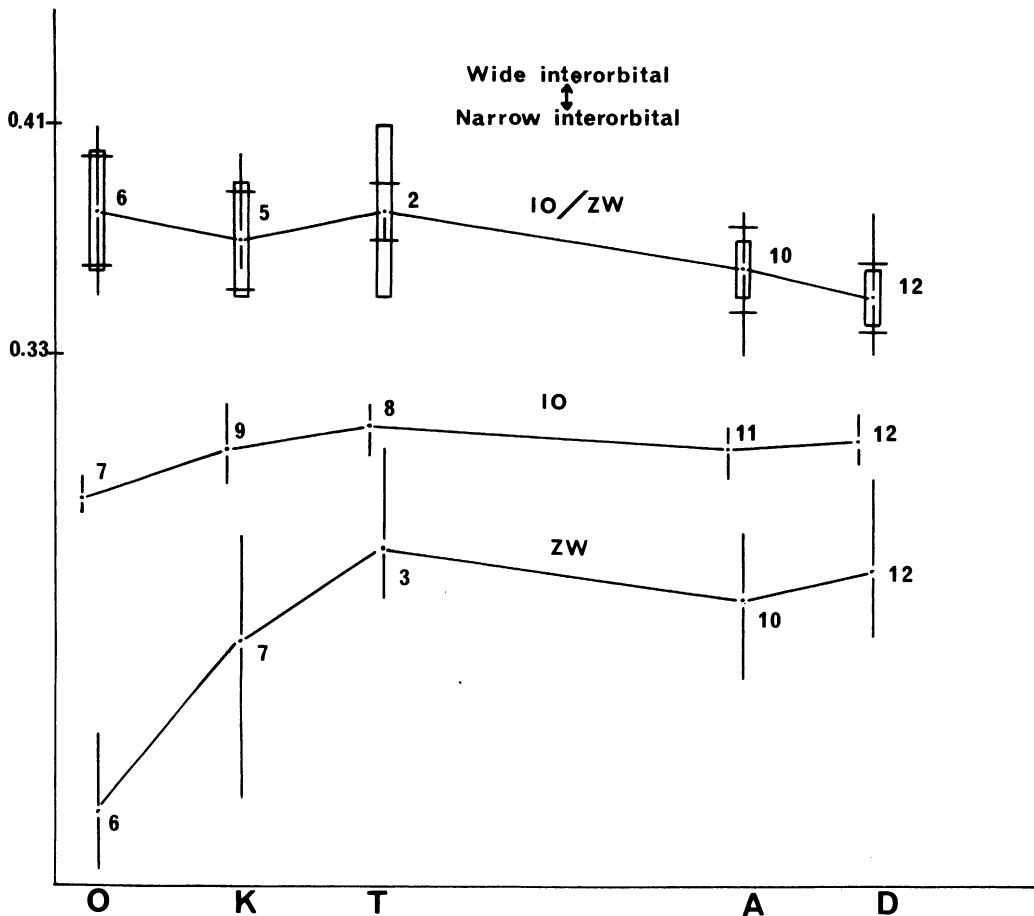


FIG. 71. Relative width of the interorbital region of the skull as a function of locality. Higher ratio values indicate relatively wider interorbital regions. Other symbols and abbreviations are as in figure 65.

is more marked than the drop in M^{1-3} size and results in the higher ratio values for the sample from the Kalgoorlie area.

Considering interspecific distribution of this character, the narrowest palates are those of *Sminthopsis ooldea*, 0.62 ($M^{1-3}/R-LM^3$); Tasmanian *S. leucopus*, 0.60; Hampton Hills *S. murina*, 0.61; *S. thomasi*, 0.60; central populations of *S. macroura froggatti*, 0.60; Northern Territory populations of *S. crassicaudata centralis*, 0.60; *S. hirtipes*, 0.59; and *S. psammophila*, 0.59. The widest palates are those of Victorian *S. leucopus*, 0.55; Doomadgee Mission *S. macroura*, 0.54; *S. granulipes*, 0.55; south coastal pop-

ulations of *S. murina fuliginosa*, 0.56; *S. virginiae*, 0.56; Richmond *S. macroura*, 0.56; and the nominate form of *S. crassicaudata* from southwestern Western Australia, 0.56; and Victoria, 0.55. As can be seen, narrow palates appear, with the exception of Tasmanian *S. leucopus*, to be more typical of inland species. I do not know what particular adaptive advantage narrow palates would have for inland animals. Perhaps it is pleiotropically related to other characters.

RELATIVE WIDTH OF THE INTERORBITAL AREA: Relative interorbital width is expressed as a function of zygomatic width.

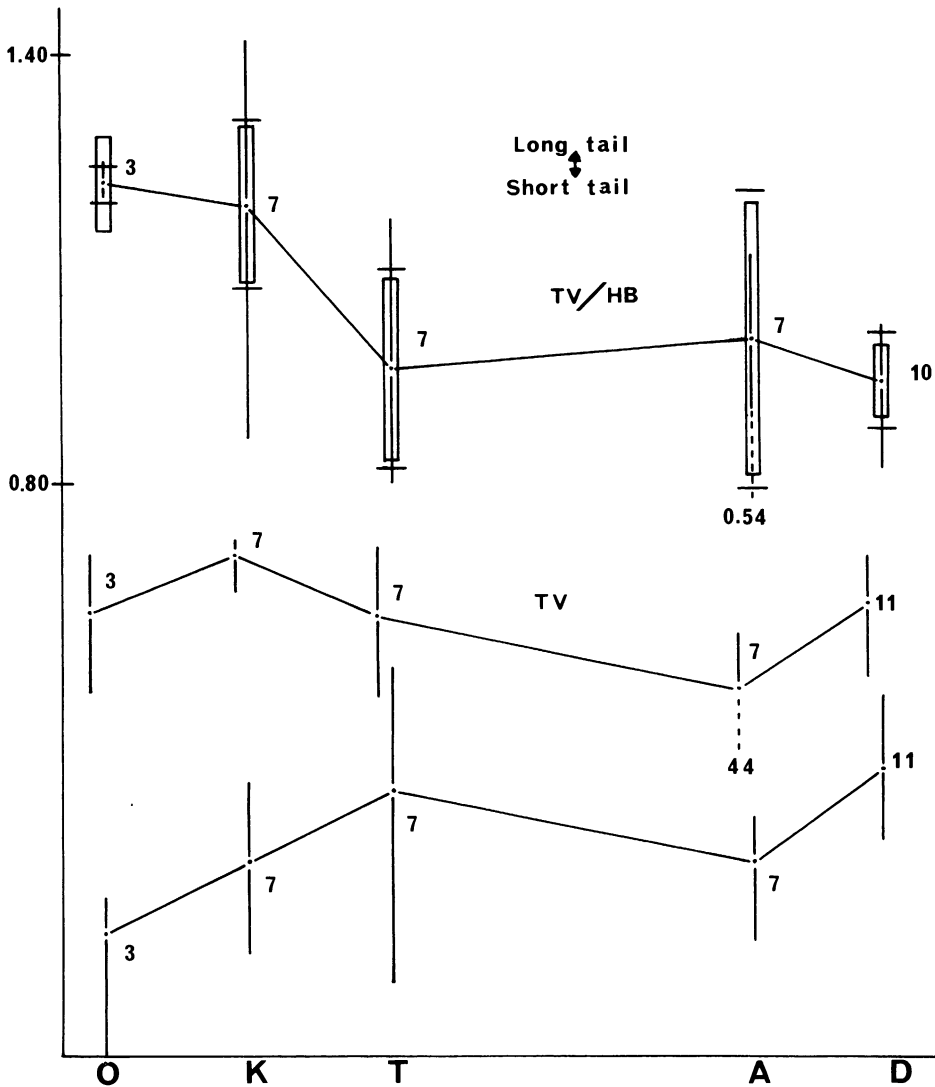


FIG. 72. Relative tail length as a function of locality. Higher ratio values indicate relatively longer tails. TV, tail-vent length. HB, nose-vent length. Other abbreviations and symbols as in figure 72.

There appears to be a trend in *Sminthopsis murina fuliginosa* for relatively narrower interorbital widths to occur in inland areas (fig. 71). Absolute values show what appears to be a discrepancy in the Tambellup sample. This is probably caused by the small number of specimens (two). It is possible that if more specimens had intact zygomatic arches, a lower mean figure would result.

Considering *Sminthopsis* as a whole, the

highest values, representing least differences between the two dimensions and therefore relatively wider interorbital widths, are those of Tasmanian *S. leucopus*, 0.41 (IO/ZW); *S. ooldea*, 0.38; and the Hampton Hills population of *S. murina fuliginosa*, 0.38. Lowest values are those of Doomadgee Mission *S. macroura*, 0.26; *S. douglasi*, 0.30; and *S. butleri*, 0.30. This character does not appear to show the same gradient as *S. m. fuligi-*

nosa. The tendency for larger values to occur in inland species is apparent but not the rule.

Possibly this measure is correlated in a non-linear but geometric way with absolute size. In many large carnivorous marsupials such as *Dasyurus* and *Sarcophilus*, the IO/ZW ratio is very small. In these forms the area of attachment for the temporalis muscle is large, often resulting in the development of a sagittal crest to provide additional area for attachment. However, in smaller animals, as skull width and hence width of the chewing muscles decreases, the volume of chewing muscles decreases at an even faster rate because volume could be a function almost of the cube of the radius of the muscle diameter. It may be that the volume of muscle necessary to deal with hard foods is disproportionately small in small animals. If so, larger size of relative interorbital width in small inland animals needs to be considered simultaneously with absolute size before the significance of this character can be understood.

RELATIVE TAIL LENGTH: The apparent trend (fig. 72) is for inland individuals of *Sminthopsis murina fuliginosa* to have relatively longer tails than south coastal animals. Specimens from Hampton Hills Station have on the average the longest tails. Absolute values show a surprising difference in mean body length between animals from Denmark and Albany. Mean body length of animals from the Kalgoorlie area is as small as that of Albany animals but the tail is proportionally much longer.

Among all species of *Sminthopsis*, the highest TV/HB values are those of *S. ooldea*, 1.22; *S. longicaudata*, greater than 2.00; Kimberley *S. macroura*, 1.32; inland populations of *S. murina fuliginosa*, 1.13 and 1.27; *S. psammophila*, 1.27; and the nominate form of *S. hirtipes*, 1.17. The lowest values are those of Doomadgee Mission *S. macroura*, 0.89; southwestern Western Australian nominate *S. crassicaudata*, 0.66; *S. granulipes*, 0.67; all *S. leucopus*, 0.85 and 0.97; south coastal populations of *S. m. fuliginosa*, 0.93 and 1.00; and the nominate form of *S. murina* from New South Wales,

0.77. This appears to present a clear trend, with longer tails occurring in more inland or arid areas. The short-tailed *S. crassicaudata* shows an intraspecific trend of the same sort as *S. murina*, even though on an overall basis it does not appear to support the inter-specific trend.

Tail length probably serves as a temperature regulating mechanism by changing the ratio of surface area to body volume. Another reason for increasing tail length in animals making fast and long journeys across relatively exposed areas of ground could be its use as a counter weight or rudder for directional shifts. Ride (1970, p. 126) suggested such a use for the tail in *Antechinomys*.

RELATIVE SKULL LENGTH: The ratio of basicranial length to zygomatic width (BL/ZW) is a good index of brachycephaly. Mean differences in populations of *Sminthopsis murina fuliginosa* are not great. Nevertheless, a trend is suggested for relatively longer heads to occur in inland areas (fig. 73). Absolute values suggest the mean ratio value of the Tambellup animals is in error, a result of the small number (three) of intact specimens. Overall, both dimensions appear to undergo reduction toward inland areas.

Considering *Sminthopsis* as a whole, the two most brachycephalic forms are *S. butleri*, 1.56; and Doomadgee Mission *S. macroura*, 1.55. The most dolichocephalic forms are the nominate form of *S. leucopus*, 1.82; *S. ooldea*, 1.80; *S. crassicaudata*, Northern Territory and South Australian populations, 1.71, 1.74; *S. granulipes*, 1.75; inland populations of *S. murina fuliginosa*, 1.71 and 1.72; and southeastern Queensland *S. murina*, 1.77. This suggests (the only marked exception being *S. leucopus*) that long-headedness is not characteristic of coastal species of *Sminthopsis*, but may be characteristic of inland species.

A possible reason for long heads in inland areas could be its value in temperature regulation, but this advantage would seem to be countered by the advantages of shorter heads to animals killing active or harder-to-crush prey, an advantage hypothesized above in regard to crowded tooththrows. In dasyurids in general, shorter heads charac-

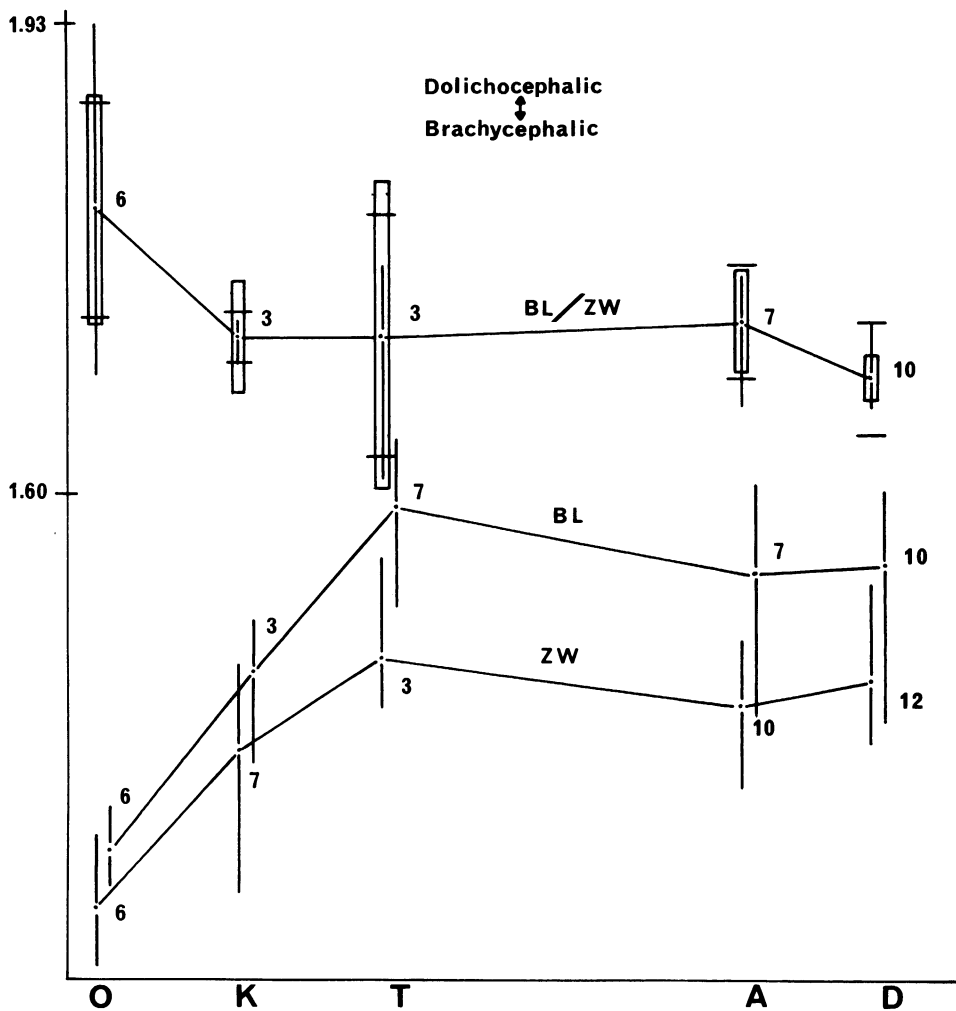


FIG. 73. Relative skull length as a function of locality. Higher ratio values indicate relatively longer (dolichocephalic) skulls. BL, basicranial length. Other abbreviations and symbols as in figure 65.

terize more inland forms (e.g., *Dasyercus*, *Dasyuroides*, all arid-adapted *Antechinus*, *Ningau*, and *Planigale*) and longer heads more coastal forms (e.g., coastal *Antechinus* such as *A. swainsonii*, *A. minimus*, *A. flavipes*, *Neophascogale*, *Phascosorex*, and *Murexia*). The reasons for the apparent exception of *Sminthopsis* are not understood.

ENTOCONID SIZE: Size of the entoconid

in *Sminthopsis murina fuliginosa* varies regionally. Along the south coast and up the west coast of Western Australia, very small entoconids are usually present. Inland populations have smaller entoconids and in the Hampton Hills specimens they are gone altogether. Similarly, north of Perth they become very small and north of the Jurien Bay area on the west coast entoconids disappear.

There is little variation in entoconid size within populations of *S. m. fuliginosa*. Only one Tambellup specimen (WAM M626) has very small entoconids, whereas the other 12 lack entoconids and only one Hampton Hills specimen (WAM M2180) in nine has entoconids. In the Albany and King Georges Sound samples, only one (WAM M2046) out of 14 has no entoconid development.

Considering interspecific distribution of this character, species with large entoconids are *Sminthopsis crassicaudata*, *S. macroura*, *S. douglasi*, and *S. virginiae*. Species, or forms, with tiny or no entoconids are *S. hirtipes*, *S. ooldea*, inland populations of *S. murina fuliginosa*, *S. butleri*, and *S. leucopus*. Species with tiny to small entoconids are *S. granulipes*, *S. psammophila*, *S. longicaudata*, and coastal populations of *S. murina*. The apparent trend is for entoconids to be absent in inland forms. It also appears that large entoconids are not common in south or east coastal forms. These areas are generally occupied by animals with tiny to small entoconids. Considering other dasyurid genera, the same pattern emerges with large entoconids being rare in inland forms. For example, the inland species of *Dasycercus*, *Dasyuroides*, *Antechinus*, *Ningaui*, and *Planigale* all have very tiny or, more commonly, no entoconids at all, and most species of *Antechinus*, *Phascogale*, *Plascogale*, and the four endemic New Guinea dasyurid genera, which occur in areas with higher rainfall, have small to large entoconids.

Apparently no clear relationship exists between the type of food eaten and the presence or absence of entoconids in dasyurids. The entoconid encloses the lingual side of the talonid basin and occludes against the posterolingual corner of the protocone of the corresponding upper molar. The advantage of this arrangement would be the closure of the talonid basin. In species lacking the entoconid, the tongue must provide this function. I do not know why or how these differences in structure should relate to geographic locality. Presence or absence of small cusps in this position have been noted in specimens

of *Vulpes vulpes* (the Red Fox) by Kurten (1967) and Hager (1972). Kurten (1967) suggested some connection between the appearance of this cusp and changing climatic conditions, possibly due to a pleiotropic gene effect. Hager (1972) found the two conditions to alternate up through a stratified Quaternary deposit in Colorado.

REMARKS: The nine characters discussed above suggest correlation between morphology and aspect(s) of habitat. Some characters are more tightly correlated than others showing intraspecific as well as interspecific correlation. Several of these characters may be related to one another and result from a single broad adaptation. For example, predation upon relatively harder invertebrate or vertebrate prey may effect length of tooth-row, interorbital width, and palatal width. Similarly, the need to regulate body temperature and water loss may effect total size, tail length size of palatal vacuities, and possibly even head length. Before any of these suggestions can be substantiated, aspects of the ecology of species of *Sminthopsis* must be examined in the field.

The suggestion that these apparent character clines can be interpreted as a function of relative aridity may seem unjustified because these animals are commonly regarded as strictly nocturnal. Those *Sminthopsis* I kept in captivity could better be described as crepuscular, commonly taking advantage of twilight and early morning, sometimes even remaining active until mid-morning. The recovery of abundant *S. macroura* from pellets of *Elanus scriptus* on the Barkly Tableland (Parker, 1973) also suggests diurnal activity. Even if they are largely nocturnal, food supplies, available water, extremes in temperature and other aspects of the environment in inland areas will differ from those in coastal areas. It is these overall habitat differences that are important in interpreting the possible significance of distribution of particular morphological characters noted here. Only field studies will elucidate the relative importance of particular aspects of the habitat in determining morphology.

INTERSPECIFIC AFFINITY IN *SMINTHOPSIS*

I have attempted here to examine affinities between species of *Sminthopsis* using a cladistic approach. Polarity of character states within *Sminthopsis* have been determined as set out below. Some of the characters are elaborated more fully elsewhere (Archer, 1976a, 1976b, and 1976c). The result of this analysis is shown in figure 74 where groupings have been based on interpreted shared derived (synapomorphic) character states.

CHARACTER ANALYSIS

1. EXTERNAL CHARACTERS

Interdigital and terminal toe pads of the hind feet—striated or granulated (unstriated): The striated condition is regarded to be primitive among dasyurids because it is the almost universal condition among dasyurids living in non-arid areas of Australia and New Guinea (aridity being regarded as a relatively recent development in Australian climatic history, see below), and because it is similarly almost universal among living didelphids, the living sistergroup of the dasyuroids. Although it is probable that the states of this character are also correlated with way of life, such that arboreal or semi-arboreal species have striations and strictly terrestrial species have granulations, the correlation is not clear. For example, *Sminthopsis leucopus* (with interdigital pad stations) is not clearly any more arboreal in habit than *Sminthopsis murina* (with interdigital pad granulations). Similarly, although it is possible that *S. longicaudata* (with pronounced striations) climbs, the only observations of a live individual occurred in an open terrestrial situation.

Metatarsal pads or enlarged granules—present or absent: These are present in almost all didelphids and in other non-arid-adapted and even some arid-adapted dasyurids. Absence is therefore regarded to be a derived state within dasyuroids.

It presumably correlates with a reduction

in climbing efficiency but an increase in efficiency in rapid terrestrial locomotion. Presence of these pads in both an arid-adapted form (e.g., *S. longicaudata*) and a non-arid-adapted form (*S. leucopus*) suggests the states of this character are not correlated with climate.

Hallux—present or absent: Primitive dasyuroids and didelphids have five hind toes although the hallux, or fifth toe, is commonly smaller than the rest. Loss of the hallux within the dasyuroids has occurred within a few genera (e.g., *Dasyurus*, *Dasyuroides*, *Myrmecobius*) and appears to be the derived state. Within *Sminthopsis* it only occurs in *S. (Antechinomys) laniger* which is overall the most highly derived (apomorphic) species of the genus. Loss of the hallux in this form is similarly regarded here to be the derived state within *Sminthopsis*. The hallux is small in some other *Sminthopsis* such as *S. crassicaudata* and reduction to loss may be a corollary of foot elongation (see below).

Height of interdigital pads—low or elevated: Didelphids and the vast majority of dasyuroids have relatively low interdigital pads. The raised condition is only found in a few arid-adapted species such as *Sminthopsis crassicaudata* and *S. (Antechinomys) laniger*. The raised condition is therefore regarded to be derived. The function may be to provide a more efficient buffer between the feet and substrate in habitats where temperature extremes are common.

Enlarged apical granule(s) on interdigital pads—present or absent: As noted above, granular interdigital pads represent a derived dasyuroid condition. Enlargement of one or more apical granules occurs only in some species of *Sminthopsis*. For this reason, it is interpreted here to be a further derived condition. The possible functions of enlarged granules are unclear.

Conspicuous covering of hair on the interdigital pads—present or absent: The soles of the hindfeet of didelphids and the vast majority of dasyuroids are almost entirely devoid of hair. A covering of hair on the in-

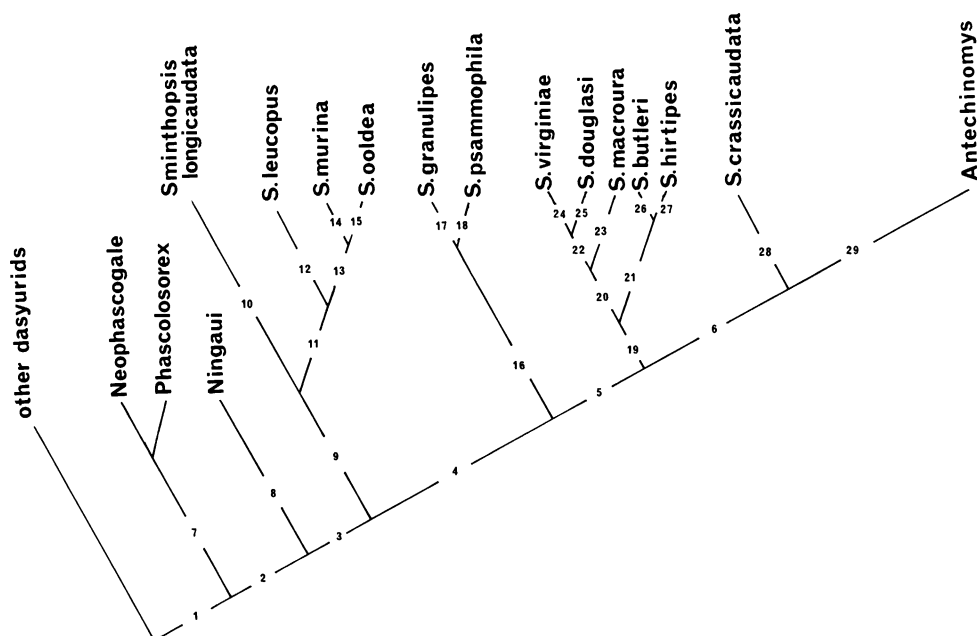


FIG. 74. Cladogram illustrating cladistic relationships of *Sminthopsis* based on shared derived (synapomorphic) characters. Numbers 1–29 refer to synapomorphic character sets as follows: 1, I^4 generally longer-crowned than I^2 ; 2, loss of posterior cingula on upper molars, narrow hind feet, narrow nasals; 3, narrow hind feet, squamosal-frontal contact, reduced metatarsal granules, transverse metacristids and hypocristids; 4, loss of all metatarsal granules, interdigital pads granular rather than striate; 5, large conical entoconids, wide molars; 6, reduced size, long limbs, large palatal vacuities, very wide molars, large interdental fenestrae, fused and high interdigital pads, large pinnae; 7, reduced P4, bilobed I_3 , narrow premolars, variable squamosal-frontal contact; 8, reduced size, loss of entoconids, reduced paracone, wide premolars; 9, reduced size, reduced entoconids, reduced canines; 10, elongate tail, large tympanic wings, fenestrate palate, very reduced C1; 11, loss of metatarsal pads; 12, mildly bifid I_3 , sometimes rufous cheeks, premolars separate; 13, non-striated interdigital pads, premolars contact; 14, relatively large size, premolars only just contact; 15, small size, large tympanic wings, elongate tail, reduced paracones, reduced talonids, broad crowded premolars; 16, reduced entoconids, granular terminal toe pads, bilobed I_3 ; 17, incrassated tail, markedly bilobed I_3 , very narrow premolars; 18, very large size, tail crest, reduction of I_3 bilobed condition; 19, head stripe, very short premaxillary vacuity, deep head, tendency for one apical granule to enlarge on the hind foot interdigital pads; 20, pronounced head stripe, large isolated apical granule on the interdigital pads; 21, reduced size, reduced or absent entoconids, reduction of enlarged apical granules on the interdigital pads; 22, rufous cheeks, hispid fur, large oval to elongate apical granules that are often apparently striate, very large canine; 23, reduced size, incrassated tail, round enlarged apical granule, large bullae; 24, cingulum on anterior face of the upper first molar; 25, stout tail, larger size; 26, markedly domed head, short head; 27, incrassated tail, hairy interdigital pads and soles, large bullae; 28, incrassated tail, unique entoconids; 29, loss of hallux, loss of entoconids, elongate limbs, tail brush, large tympanic wings.

terdigital pads occurs on the hindfeet of only a few arid-adapted dasyuroids, notably some species of *Sminthopsis*. For these reasons, it is considered to be a derived state. It probably functions as insulation between the foot and the substrate.

Tail—long or short: In the present study I have suggested that long tails may be an adaptation to arid habitats in allowing better heat exchange and in facilitating rapid directional shifts when moving across open areas. The longest tails in small Australian mam-

imals are found in arid-adapted species (e.g., *Sminthopsis longicaudata*, *S. (Antechinomys) laniger*, and *Notomys longicaudata*), and as a result long tails are regarded to be the derived condition. Some species, such as *S. crassicaudata* exhibit clines in length, with the individuals that occupy less arid habitats having shorter tails.

Tail width—incrassated or thin: In species of *Sminthopsis* as in all dasyuroids, there is a good correlation with the ability to store fat in tails and occupation of habitats in which availability of food is either seasonal or unpredictable. For this reason, tail incrassation is concluded to be a derived state in *Sminthopsis*.

Tail brush or crest—present or absent: There is no absolute correlation between the occurrence of tail brushes or crests and habitat among Australian mammals in general. However, among dasyuroids, the majority of tail crest or brush-bearers occupy arid habitats. The only exceptions include the essentially non-arid *Phascogale tapoatafa*, some species of *Dasyurus*, and to a lesser extent some species of *Antechinus* such as *A. flavipes*. I do not know the taxonomic distribution of tail crests or brushes in didelphids but suspect the primitive didelphid state is for lack of a crest or brush. This also appears to be the plesiomorphic state for dasyuroids. It is possible that crests and brushes are more useful to animals in open arid areas because they are generally more visible and also might help facilitate rapid directional shifts in open areas.

Hindfoot length—proportionally “normal” or elongate: The vast majority of didelphids and dasyuroids have hind feet in which the length is less than four times the width of the sole. In some *Sminthopsis*, sole length is proportionally much longer sometimes exceeding six times the width. Proportional elongation within *Sminthopsis* is therefore regarded here to be a derived state. The most elongate feet occur in arid-adapted species such as *S. (Antechinomys) laniger*. Perhaps it is an adaptation to rapid cursorial movement because it effectively produces a longer leg. These animals run on the inter-

digital pads of the hindfoot. A longer foot would therefore result in a longer stride.

Limb length—“normal” or elongate: As above for foot length, elongate limbs would presumably be an advantage to a small cursorial dasyuroid in an open arid habitat. Not surprisingly, the longest limbs in *Sminthopsis* occur in *S. (Antechinomys) laniger spenceri* a highly arid-adapted form. Proportionally shorter limbs are the basic primitive character state in didelphids and dasyuroids.

Pinna size—“standard” or elongate: As in the case of tail length, longer pinnae are evidently adaptive as temperature regulating devices. They are also adaptive in the primary function of collecting sounds. Both of these functions are particularly required in the open areas of central Australia. Didelphids and most non-arid-adapted dasyuroids have small pinnae, presumably the primitive character state. One arid-adapted dasyuroid is a peculiar exception to this. *Antechinus rosamondae* has such a reduced pinna that externally it is almost invisible. This extreme reduction however may reflect the fact that it lives among *Spinifex (Triodia)* bushes which could be a pointed problem to a large-eared dasyuroid.

Head stripes—absent or present: Occurrence of head stripes among marsupials in general varies. Although it is tempting to suggest head stripes are a derived state within the Marsupialia, no clear evidence is available to support this suggestion. However, within *Sminthopsis*, head stripes occur most commonly (but not invariably) among arid-adapted species. For this reason, they are regarded here to be the derived state within *Sminthopsis*. Their function, unless it is disruptive coloration, is not clear. The most vivid head stripes occur in *S. macroura* and *S. virginiae*, species which frequently occupy grasslands. The dark head stripes may have the effect of breaking the appearance of the head into two vertically narrow halves which would make them more difficult to see amongst clumps of grass.

Cheek color—same as the body or rufous: Rufous cheeks occur in some species of *Antechinus* (some *A. flavipes*) and *Smin-*

thopsis (*S. virginiae*, *S. douglasi*, and *S. leucopus*). The infrequency of this color is the basis for assuming here that rufous cheeks are the derived character state. There does not appear to be an environmental correlation for this state, and its function is not clear unless it is also adaptive as disruptive coloration.

Absolute size—large or small: The average dasyuroid and didelphid is small, being about the size of *Antechinus flavipes*. However, most *Sminthopsis* are even smaller with only about three species overlapping the lower size range of *Antechinus*. Small size is physiologically adaptive in arid habitats in facilitating heat loss. The smallest *Sminthopsis* species occupy arid habitats and it is possible that their small size is a secondary adaptation to this arid environment. This hypothesis is supported by the fact that the vast majority of other dasyuroids are larger. Against this interpretation of polarity is the fact that two of the largest *Sminthopsis* species (e.g., *S. psammophila*) also occupy arid habitats and *Ningau*, the interpreted sister group of *Sminthopsis*, contains two very small species. Nevertheless, I have concluded here that large size is primitive in *Sminthopsis* and that small size is a secondary derived state achieved independently within *Sminthopsis* and *Ningau* in response to common problems of survival in arid habitats.

2. CRANIAL CHARACTERS

Skull length—"standard" or brachycephalic: Within the Dasyuroidea there is much variation exhibited in the degree of brachycephaly. However, there can be little doubt that the most brachycephalic forms such as species of *Dasyurus*, *Sarcophilus*, *Planigale*, *Myoictis*, and some *Antechinus* are exhibiting a derived condition often associated with reduced premolar number (Archer, 1975c, 1976b). Dasyuroids and didelphids interpreted to be primitive are not brachycephalic. Similarly, within *Sminthopsis* the brachycephalic forms (e.g., some *S. macroura*) are often those with crowded

toothrows and brachycephaly therefore appears to be a derived condition. In other dasyuroids it has been suggested (Archer, 1976b) that brachycephaly, associated with a shortened cheektooth row, correlates with a better developed ability to kill larger, more active prey.

Skull depth—"standard" or deep: Within *Sminthopsis* only species in the *S. macroura* species group exhibit deep heads (dorsoventral skull depth anterior to the bullae). In the extreme, such as occurs in *S. virginiae*, this contributes to the powerful appearance of the skulls and suggests a more massive temporal musculature. The greater skull depth is also apparent in the rostrum. This condition is rare in small dasyuroids most of which tend to widen rather than deepen the skulls with increasing size. For these reasons, deep skulls in *Sminthopsis* are regarded here to be derived.

Domed skull—dorsally convex, flat, or concave in longitudinal section: Markedly domed skulls occur in *Sminthopsis butleri* and to a lesser extent in some *S. virginiae*. The doming occurs in the region of the nasal-frontal sutures and is rare among other dasyuroids. The function is unknown. It is presumed here to be a derived state because of its rare occurrence in dasyuroids.

Alisphenoid tympanic wings (bullae)—enlarged or small: Elsewhere in this paper I have demonstrated that, with rare exception, bullae size in *Sminthopsis* is correlated with type of habitat, larger bullae occurring in more arid areas. This leads to the conclusion that an enlarged tympanic wing is a derived condition in *Sminthopsis*. Similar considerations of dasyuroids in general lead to the same conclusion that enlarged alisphenoid tympanic wings are a specialized condition. This is further supported by noting that with very few exceptions, didelphids have small or even absent alisphenoid tympanic wings (Archer, 1976a). Notable didelphoid exceptions include *Dromiciops* and *Sparassocynus* but these are universally regarded to be specialized in this regard.

Length of the premaxillary vacuity—extending anterior or posterior to the level of

the canine alveolus: This feature varies within *Sminthopsis* as well as other dasyuroids and didelphids, and the polarity of premaxillary vacuity length is not clear. It is very short only in the *S. macroura* species group and consequently a short premaxillary vacuity is tentatively regarded here to be the derived state. However, a very long premaxillary vacuity such as occurs in *S. crassicaudata* and *S. (Antechinomys) laniger* is regarded to be an alternative derived state (see below under size of the palatal vacuities). The primitive state is interpreted to be intermediate (extending posteriorly to about the level of the canine) such as occurs in *S. granulipes* or *S. ooldea*. Possible function for enlarged palatal vacuities is discussed below.

Maxillary vacuity length—long or short: Elsewhere in this paper I have suggested that a direct correlation appears to exist between the degree of aridity and length of palatal vacuities (of which the maxillary vacuity is the largest component) in at least some groups of Australian marsupials, including the various species of *Sminthopsis*. From an assumption that Australian aridity is a relatively recent development, it could be concluded that a well-fenestrated palate is a derived condition. This hypothesis is supported by the fact that most didelphids have poorly fenestrated palates, and because they are the living sister group of the dasyuroids, this suggests that poor palatal fenestration is the primitive character state for dasyuroids. The same conclusion applies to *Sminthopsis* such that enlarged palatal vacuities are regarded here to be the derived state. As elaborated elsewhere in this paper, I propose that palatal vacuities might be involved in heat exchange between the nasal passage and the wet oral cavity with larger vacuities therefore being expected in more arid habitats.

Interdental fenestrae—absent or present: Abundant small perforations occur in the palate in areas between the adjacent molars in some arid-adapted species such as *Sminthopsis crassicaudata* and *S. (Antechinomys) laniger*. They almost never occur in

non-arid adapted species, and are extremely rare in all other dasyuroids and didelphids. For these reasons, their presence is considered to be a derived state. Their function may be as noted above for general palatal fenestration which could contribute to a nasal-oral heat exchange mechanism.

3. DENTAL CHARACTERS

Third lower incisor—simple or bilobed crown: A markedly bilobed I_3 occurs in *Sminthopsis granulipes*. A less-bilobed I_3 occurs in *S. leucopus* and *S. psammophila*. A bilobed I_3 is a rare condition among dasyuroids occurring elsewhere only in *Neophascogale* and *Phascolosorex*. To the best of my knowledge it does not occur at all in didelphids and is therefore a highly unique derived state. The possible function of this adaptation is discussed elsewhere (Archer, 1976b). It provides a longer incisiform tooth-row. In the discussion of *S. granulipes* (above) I suggested that the distribution of this feature would prohibit some of the sister group hypotheses proposed in this study if it were assumed to be a shared derived state within the Dasyuroidea. The doubt this raises is reinforced by noting that *Neophascogale* and *Phascolosorex* also have a variable squamosal-frontal contact, a character state rare in dasyuroids but universal among *Sminthopsis*. Against the hypothesis of a *Sminthopsis*-*Neophascogale* (and *Phascolosorex*) sister group is the hypothesis of the *Sminthopsis*-*Ningaui* (which lacks a squamosal-frontal contact) sister group which involves the apparently shared derived features of loss of posterior cingula on the upper molars and secondary narrowing of the posterior end of the nasals. At present I favor a *Sminthopsis*-*Ningaui* sister group, but it will be necessary to have more neontological data to test these alternative hypotheses.

Canine size—large or small: Caniniform canines characterize most didelphids and dasyuroids; premolariform canines are clearly a derived state. However, although some *Sminthopsis* species such as *S. crassicaudata*

data have premolariform canines, others such as *S. virginiae* have evidently enlarged the canine from a more "normal" primitive size. Larger canines appear to be adaptations for killing thicker or more difficult to hold prey such as small vertebrates. Premolariform canines occur in *Sminthopsis* species evidently adapted only for killing smaller insect prey. These intimations are supported by observations of feeding preferences noted above.

Premolar width and toothrow length—narrow and uncrowded or wide and crowded: With few exceptions (such as *Sparassocynus* and *Didelphodon*), didelphids have narrow premolars in uncrowded premolar rows. This is presumably the primitive condition. Among primitive (Archer, 1976b) dasyuroids, such as *Murexia*, the same condition occurs as it also does in most *Sminthopsis*. In other less primitive dasyuroids, such as *Dasyurus*, *Myoictis*, *Sarcophilus*, and *Dasycercus*, the premolar row is crowded, the premolars are often very wide, and the posterior premolar is either lost or reduced in size. This secondary reduction has occurred at least twice within the dasyuroids (within some *Antechinus* and some *Planigale*). It also seems to have been independently operating within *Sminthopsis* such that *S. ooldea* has similarly developed a crowded premolar toothrow and wide premolars, although P3 is not yet significantly reduced. Clearly reduction of P3, widening of the premolars, and crowding of the premolar tooth row are derived states within *Sminthopsis* as well as within dasyuroids as a whole. The most crowded toothrows and widest premolars occur in dasyuroids such as *S. ooldea* adapted to arid habitats (*Sarcophilus* is also arid-adapted because, although it now occupies Tasmania, it recently occurred across most of Australia including the Nullarbor and Arnhemland). Elsewhere (Archer, 1976b) I suggested that these dental features might reflect an adaptation to eating harder less easily commutated prey. This sort of prey might be expected to represent a greater proportion of the available food in arid areas than in less arid areas because

there is overall a greater need to protect against dessication which would result in thicker cuticles and other sorts of dermal protection.

Upper molar shape—elongate and narrow or short and wide: Elsewhere (Archer, 1976b) I have concluded that the primitive dasyuroid upper molar was evidently didelphid-like in being, among other things, elongate and narrow. Among dasyuroids, markedly short and wide upper molars occur only in some species of *Sminthopsis* (and *Antechinomys*), and notably among (but not including all) species occupying arid inland areas. This suggests that short and wide upper molars represent the derived character state. The function of this adaptation is not clear. In effect it results in long transversely oriented preparacristae and postmetacristae which are the principal shearing crests of the upper molars. In larger dasyuroid lineages undergoing evolution to greater carnivory, it is common for the postmetacristae to enlarge, but longitudinally not transversely. In any case, the extreme dasyuroid example of transversely elongated postmetacristae (*S. (Antechinomys) laniger*) appears not to relish small vertebrates and evidently prefers a strictly invertebrate diet (Archer, 1976). Some understanding of the functional significance of transversely oriented elongate postmetacristae may come from a study of the chewing mechanics of the highly arid-adapted *Notoryctes* which exhibits the extreme marsupial condition of this derived state and is evidently a strict invertebrate eater.

Paracone size—unreduced or reduced: Paracone height relative to metacone height varies within didelphids but in the vast majority of dasyuroids the paracone is lower than the metacone. In some genera, the paracone is even further reduced such that it becomes a small cusp near the flank of the metacone. This has occurred in *Sminthopsis*, *Ningau*, *Planigale*, and in the extreme (with paracone loss) in *Notoryctes*. In *Sminthopsis* this reduction has occurred only in the tiny arid-adapted *S. ooldea*. Comparable reduction in *Ningau* and *Planigale* is also oc-

curing in very small to tiny dasyuroids. Because *P. maculata* is evidently not arid-adapted and yet has very reduced paracones, the significant common denominator here may be small size. In fact there are no dasyuroids as small as these that do not also exhibit extreme paracone reduction. Conversely, no large dasyuroids exhibit this type of reduction. *Sarcophilus* exhibits a small paracone but this is the result of progressive fusion with or lack of differentiation from the metacone rather than direct reduction in size. The function of reduced paracones presumably is subordination of the preparacristae to enlarging postmetacristae. Perhaps these teeth are too small relative to the prey to usefully involve more than one principal shearing crest.

Anterior cingula on upper first molar—incomplete or complete: These are complete on the anterior molars of some *Sminthopsis virginiae*. They are incomplete in other species of this genus. Within the Dasyuroidea in general, a complete cingula on M¹ appears to be primitive (Archer, 1976b) although it is not common. Absence of this structure in species of *Sminthopsis* other than *S. virginiae* would presumably indicate loss within this genus. But because the weight of evidence presented above suggests that *S. virginiae* is not otherwise the most plesiomorphic species, I have concluded that either the anterior cingulum in *S. virginiae* is secondarily acquired or the absence of a complete cingulum has been achieved polyphyletically within *Sminthopsis*. The function of this cingulum is to shear against the opposing metacristid of the lower first molar. An increase in its size would increase shear as well as more effectively increase the area of the molar crown.

Entoconids—large, reduced or absent: As indicated elsewhere (Archer, 1976b), entoconids are present in almost all didelphids. Among dasyurids, species occupying higher rainfall habitats such as those of highland New Guinea have well-developed entoconids. Whereas among those occupying arid inland areas of Australia, many (but not all) lack entoconids. Because central Australian

aridity appears to be a relatively recent development, and because the primitive didelphoid condition appears to be possession of entoconids, I have concluded that an absence of entoconids in Australian dasyurids is a derived condition. This means the derived reduced condition was evidently achieved independently in the *Sminthopsis murina* and *S. psammophila* groups, as well as probably *Ningaui*. The possible functions of large entoconids are discussed in Archer (1976b). Essentially they enclose the talonid basin and probably thereby increase the efficiency of crushing resulting from protocone-talonid occlusion. It is not clear however why this should be less important to arid-adapted species of *Sminthopsis*.

Talonids—unreduced or reduced: This character state appears to vary in the same way as paracone size. It is large in primitive didelphids and dasyuroids and only notably reduced in tiny generally arid-adapted dasyuroids such as one species of *Sminthopsis* (*S. ooldea*), and all species of *Ningaui* and *Planigale*. Tiny size is the outstanding common denominator of these forms. In fact, there are no tiny dasyurids whose talonids are not also disproportionately reduced. It is perhaps relevant here to note that the small and highly desert-adapted *Notoryctes* has effectively lost its talonids altogether. The function of the talonids is to provide an occlusal surface to oppose the protocone of an upper molar. This part of the molar is involved in the crushing of bits of food cut by the crests of the trigonid. Suppression of this phase of mastication suggests that it is functionally less important to tiny dasyurids, perhaps because they are simply too small. The spaces occurring between the trigonids of these tiny teeth may be too small to permit efficient use of protocone-talonid occlusion. In fact, at this diminutive size, it is probable that a significant amount of crushing rather than only cutting will occur between the trigonids and the upper molars. In terms of insect cuticle, there must be a lower limit to the size of an efficient tribosphenic sectorial tooth.

DISCUSSION OF INTERPRETATION OF CHARACTER STATE POLARITY

Basic to many of the foregoing interpretations of character state polarity are the two assumptions that widespread aridity in central Australia is a relatively recent event and that the ancestral species of *Sminthopsis* was not arid-adapted. The first assumption, that of late-developing aridity, is supported by a growing body of palynological (e.g., Callen and Tedford, 1976; Galloway and Kemp, in press) and vertebrate paleontological (e.g., Stirton, Tedford, and Woodburne, 1968; Archer, 1978) data. Galloway and Kemp (in press) have most recently reviewed the development of late Cainozoic environments in Australia. In the early Miocene the climate of most of Australia was wet and *Nothofagus*-dominated forests covered much of the continent. Since the middle Miocene (about 15 My BP), Australia has gradually (with fluctuations) become drier, evidently culminating about 17,000 years ago with extreme aridity.

The second assumption is less easily justified. As yet, there are no actual fossils referable to *Sminthopsis* from Tertiary deposits and all known fossils of *Sminthopsis* are referable to modern species. Therefore, nothing precludes the possibility that the first *Sminthopsis* evolved as an arid-adapted derivative of some other type of dasyurid and subsequently gave rise to species only secondarily adapted to non-arid habitats. If this were the case, my interpretation of polarity based on the concept of secondary arid-adaptations would be wrong and the cladogram (fig. 64) upside down. As it is, I consider that it is more probable that the ancestral *Sminthopsis* was not arid-adapted for the following reasons: (1) The morphological diversity within *Sminthopsis* is high and this suggests that the radiation was older than the Pleistocene (when the really extensive development of aridity occurred) and quite probably had its beginnings during the Miocene. Some species of fossil dasyurids from the middle Miocene Kutjamarpu fauna are evidently

very similar to modern species of *Antechinus* (C. Campbell, personal commun.) suggesting that phyletic lineages in at least some small dasyurids may be traceable well back into the Tertiary. (2) Species of *Sminthopsis* I regard here to be primitive (e.g., *S. leucopus*) are almost invariably occupying non-arid coastal areas, habitats that presumably have been available throughout the Cainozoic, whereas the species I regard here to be highly derived (e.g., *S. ooldea* and *S. (Antechinomys) laniger*) are occupying extensive continental arid habitats that have evidently only been developed since the middle Miocene. Although this is a weaker point, it implies that there has certainly been much more time in non-arid areas to develop a radiation in *Sminthopsis* than there has been in arid areas. (3) Perhaps most persuasively, species exhibiting the greatest number of plesiomorphic dasyurid rather than just *Sminthopsis* character states are occupying relatively non-arid habitats (e.g., *S. murina* and *S. leucopus*), whereas species exhibiting the least are occupying arid habitats (e.g., *S. (Antechinomys) laniger* and *S. crassicaudata*).

SPECIES GROUPS

I have recognized five species groups: (1) the *Sminthopsis murina* species group, containing *S. murina*, *S. ooldea*, *S. leucopus*, and *S. longicaudata*; (2) the *S. psammophila* species group, containing *S. psammophila* and *S. granulipes*; (3) the *S. macroura* species group, containing *S. macroura*, *S. virginiae*, *S. douglasi*, *S. butleri*, and *S. hirtipes*; (4) *S. crassicaudata*; and (5) *S. (Antechinomys) laniger*.

The *Sminthopsis murina* species group: The most derived species in this group is *Sminthopsis ooldea*. It is convergent on species in other groups of *Sminthopsis* in the derived characters of tail incassation, entonid loss, canine reduction and wider mo-

lars and even on species of other genera such as *Planigale* and *Ningaui* in premolar width, and paracone and talonid reduction. Although it shares most derived characters with species of the *S. murina* group, it clearly represents a very highly derived member of this group, sharing almost none of the plesiomorphic characters of the other three species. Within this group, *S. ooldea* and *S. longicaudata* appear to have undergone independent arid-adaptation.

THE *SMINTHOPSIS PSAMMOPHILA* SPECIES GROUP: Both species in this group have conspicuous unique derived characters and could represent monotypic groups of their own. However, they are closer morphologically to each other than either is to any other species. They share the derived characters of reduced entoconids and granular terminal pads of the digits, as well as primitive characters such as small bullae and narrow molars. Retention of small bullae in these otherwise arid-adapted species is puzzling because as noted above in the character analysis, small bullae normally correlate in dasyuroids with non-arid habitats.

Sminthopsis granulipes has either independently developed some of the characters of species of *Phascolosorex* and *Neophascogale* or else is incorrectly placed in the cladogram. Previously (Archer, 1976b), I suggested it might represent a structural intermediary between *Sminthopsis* and *Neophascogale-Phascolosorex* but I now consider that at least some of the characters they share are plesiomorphic such as the large canines and narrow molars. Although the common possession in both taxa of a bilobed I_3 and widely spaced premolars might be regarded as indicative of common ancestry, recognition of these forms as a phyletic group requires convergence in loss of posterior cingula on the upper molars, in premolar reduction, basic structure of the hind foot, as well as aspects of the skull in *S. granulipes* and other species of *Sminthopsis*. I cannot dismiss this possibility but regard it as highly improbable.

Sminthopsis granulipes and *S. psammophila* both show different arid-adaptations,

such as tail structure, and suggest the probability that both have independently adapted to arid conditions.

THE *SMINTHOPSIS MACROURA* SPECIES GROUP: The species included in this group are more similar to one another than are the members of any other polytypic group. Nevertheless, subgroups within this group are indicated. *S. douglasi* and *S. virginiae* are very similar, sharing many derived characters of the foot, pelage, skull, and dentition. They probably represent sibling species. The large size of *S. douglasi* may indicate character displacement resulting from its sympatric relationship with the related but smaller species, *S. macroura*.

Sminthopsis macroura is more similar to *S. virginiae* and *S. douglasi* than it is to the other members of the *S. macroura* group. It shares the derived characters of the isolated and enlarged apical granule and the head stripe. It also retains many more primitive characters in common with these two species than it does with *S. butleri* or *S. hirtipes*.

Sminthopsis butleri is placed with *S. hirtipes* because they share the derived characters of reduction of head stripe, entoconid reduction, and possibly the secondary reduction of an enlarged apical granule. Direct evidence for secondary reduction of the apical granule is lacking. Its interpretation as a derived condition is hypothetical and based on the interpretation of loss of *S. macroura*-like characters in *S. butleri* including the vestigial condition of the head stripe and the presence of minuscule entoconids.

Sminthopsis hirtipes has several unique derived characters such as the haired interdigital pads and very large bullae. Both *S. hirtipes* and *S. douglasi* appear to have converged in at least one arid-adaptation, incrassated tails, and both are evidently convergent on arid-adapted species of other groups.

Sminthopsis crassicaudata: Characters that might be regarded as shared derived, such as interdigital pad construction, size of palatal vacuities, and the incrassated tail are probably adaptations to arid habitats and likely to be convergent. Although it does

have several possibly shared derived characters with *S. (Antechinomys) laniger*, most are of the same potentially arid-adapted kind and hence presumably subject to convergence. If convergence has not occurred in the development of these characters, *Sminthopsis crassicaudata* would be more similar to *S. (Antechinomys) laniger* than to any other species of *Sminthopsis* and accordingly classifiable as a member of the subgenus *Antechinomys*. I do not think this is appropriate for the following reasons: The entoconid remnants of *Antechinomys* are not similar in topography to the large entoconids of *S. crassicaudata*; the tails of both species are arid-adapted, but in completely different ways. In both regards *S. crassicaudata* resembles other arid-adapted members of the subgenus *Sminthopsis*, and it seems preferable to regard *S. crassicaudata* as a highly derived and arid-adapted member of the sub-

genus *Sminthopsis*, with some characters that foreshadow those of *Antechinomys*. If they had an immediate common ancestor, it probably would have lacked most of the derived arid adaptations, and in so doing probably would have been referable to the subgenus *Sminthopsis*.

Sminthopsis (Antechinomys) laniger: The reasons for the decision to include *Antechinomys* within *Sminthopsis* are noted above in the systematic section. Although it has shared derived characters only with *Sminthopsis*, its unique derived characters are so unlike other *Sminthopsis* that it has been given subgeneric distinction. Previously (Archer, 1977), I suggested that *Antechinomys laniger* was in the process of active speciation, with less arid-adapted populations isolated from, but surrounding, the highly arid-adapted central Australian populations.

GENERIC AFFINITY AND ORIGINS OF *SMINTHOPSIS*

Ningaui shares many derived character states with *Sminthopsis*, but so does the *Neophascogale-Phascosorex* group and it is not immediately clear which is the sister group of *Sminthopsis*. *Ningaui* lacks the squamosal-frontal contact of *Sminthopsis* and some *Neophascogale* (and *Phascosorex*), but *Ningaui* shares many of the derived characters of *Sminthopsis* that are absent in *Neophascogale* and *Phascosorex* such as wide molars, narrow nasals, and absent posterior cingula on the upper molars. In order to conclude, as I do, that *Ningaui* is the sister group of *Sminthopsis*, it is necessary to postulate either polyphyletic achievement of the squamosal-frontal contact in *Sminthopsis* and the *Neophascogale-Phascosorex* group, or else loss of this character in *Ningaui*.

Planigale is unlike *Sminthopsis* in so many ways (Archer, 1976d) that it cannot be regarded as closely related. It is convergent on the highly arid-adapted *S. ooldea* in the

derived characters of very small size, very wide premolars, reduced paracones, and loss of entoconids.

The interpretation developed above of polytypic origins for arid adaptations within the genus *Sminthopsis* presumes a non-arid-adapted common ancestor. Further, because many of the arid adaptations within the genus appear to have been independently developed there was probably a "pre-arid" *Sminthopsis* radiation some products of which subsequently, and independently, underwent arid adaptation. This radiation must have paralleled what appear to have been similar radiations in macropodids (e.g., Bartholomai, 1972). Other arid-adapted dasyurid species such as *Dasyurus cristicauda*, *Dasyuroides byrnei*, *Dasyurus geoffroyi*, *Phascogale calura*, *Ningaui ridei*, and *Planigale gilesi* probably evolved their arid adaptations, in the same way in response to the same pressures.

MATERIAL EXAMINED

Sminthopsis murina murina

SOUTH AUSTRALIA: Unspecified locality (BM1080c, 95.3.21.12, 43.8.12.35); Chauncey's Line (SAM M7533, M7538); Sedan (SAM M6469); Victor Harbour (SAM M7536, M8355); 38 km. NNE Overland Corner (SAM M7941); Bordertown (SAM M3870); between Mt. Barker and Murray Bridge (WAM M4502); Ferries McDonald National Park (SAM M7534); NW Billiatt National Park, (SAM M8636); Big Heath National Park (SAM M7682).

VICTORIA: Brimboal Scrub 24 km. N of Casterton (D681-2); 22 km. NNW Coleraine (C4510); Bannockburn (D554); approx. 2 km. SW Mt. Buninyong (D532); Christmas Hills (D779, D771).

NEW SOUTH WALES: Hunter's River (BM55.12.24.95); Mt. Brown, Richmond Rn. (CM382); north shore, Sydney (MM M836, AM M6583); Waterfall, S of Sydney (AM M7651); Paterson R., Eccleston (AM M7461); Lake George, nr. Canberra (WAM M4690); Con. Ck., Bendilhera (CM1420); Wallaby Ck., Tooloom (CM142); Tamworth (AM M1513); Warialda (AM M4993); nr. Deepwater (AM M9130, M8993, M9050); El Trune Stn. (AM M8611, MVZ 133184-6); Sugarloaf Mt. (AM M8206); Severn R. (BM53.10.22.24, BM53.10.22.27); Darling Downs (BM53.10.22.23); Mungindi (AM M9835); Wyee (AM M9172); Merriwa 48 km. NW Muswellbrook (AM M9137); Weetaliba, via Coolah (AM M7880); Lake Macquarie (AM M7673); Cranebrook (AM M9736-7); Bungwahl, Myall Lake (AM M9713) Smiths Lakes, Bulahdelah (AM M9936, M9902), Cox's Valley (AM M4845); E Kurrajong (AM M6639, M6753); Whiteman Ck., Grafton (AM M7444); Marleytrack, Roy. Nat. Park (AM M9147-8) between Redhead and Newcastle (AM M6952); Chariot Hills, Drake (AM M10223-4); Smithfield, Sydney (AM M6579).

QUEENSLAND: Walston, Via Ipswich (J19681); Hazeldene (J5913, J5914); Mt. Nebo Rd. (J5708); Warra (J7019); Dalveen area (J12670); Dalby (J7845); Glasshouse Mtns. (J10990); Esk (J8132); Swanfels, nr. Warwick (J10367); McPherson Rn. (J4269); Black Gin Ck. (J1742); Wonga Hills via Chinchilla (AM M7664-6); Mt. Glorious, 32 km. W Brisbane (AM M8565).

Sminthopsis murina fuliginosa

WESTERN AUSTRALIA: River Avon (BM44.2.15.20); Hampton Hills Stn., Bulong (WAM M2179-83, M1341, M1836, M2193, M1674); 1.6 km. SSW Walyamoning Rock (WAM M8738);

Merredin (WAM M2401); Minnivale (WAM M2534); Aldersyde (WAM M1169); Narrogin (WAM M1564); Gracefield (BM7.7.18.15); Tambellup (WAM M625-7, M677-8, M709, M740, M748-9, M852, M854, M1102, AM M4581); King George's Sound (BM46.4.4.59-61; MM M824-9); King River, Albany (WAM M951, BM6.8.1.354-5); Albany (WAM M2046, M2312, BM44.10.30.2, 96.7.1.2, 7.9.1.46-7); Mt. Clarence, Albany (WAM M2262-3); 1.6 km. S King Creek, nr. Albany (WAM M7100); Lake McKail, Albany (WAM M11379); Denmark area (WAM M1005-6, M1126, M1156, M1231, M1295, M1840-1, M1849, M1835, M1969, M2702, MVZ13342); Chorkerup (WAM M1714, M1758, M1317); Newlands (WAM M901, M981, M1177, M1313-4); Bridgetown (WAM M1960, M8037, M2047); Tralee, Lowden (WAM M1874); Forest Grove, nr. Busselton (WAM M1171, M1642, M8122, M10232, M2059); Caves district nr. Margaret River (WAM M206); Armadale (WAM M423); Cannington (WAM M1333); Wooroloo (WAM M81); 8 km. S Fields Find (WAM M6998); Caron (WAM M2345); Long Island, Jurien Bay (WAM M5424); 48 km. N Murchison House (WAM M7153); Overlander Service Stn. (WAM M10217); Fitzgerald Reserve, E side of Dempster Inlet (WAM M8170); Mt. Bland lowlands of Fitzgerald River area (WAM M8075); Ravensthorpe (WAM M1646); approx. 4 km. WSW Israelite Bay (WAM M8652); 77 km. E Norseman (WAM M3894); Cranbrook (WAM M2453); Gracefield, Kojonup (WAM M7384); Gracefield (WAM M9034); Eleker, G.S.R. (WAM M1223-4); Ferndale, Tackalarup via Mt. Barker (WAM M1945, M1988); Tarin Rock Reserve (WAM M8222); Bolgart (WAM M7145-50); Harvey (WAM 4983a); Balingup (WAM M1179); Gnowangerup (WAM M1211); Warren Bend, via Manjimup (WAM M1392); Margetup, Salt River (WAM M4); Karragullen (WAM M2839); Brunswick Jctn. (WAM M2854); Narrikup (WAM M4538); Bindoon (WAM M5084); Higginsville (WAM M5440, M5442, M5463); Talling Stn. (WAM M6386); Bolgart (WAM M7145-50); 6.4 km. E of 61 mile peg, Great Northern Highway (WAM M7152); Fish Creek, W of Broke Inlet (WAM M7668); Yallingup (WAM M7767); G. O'Shea's property, Scott River (WAM M6886); Bendering Sandlewood Res. (WAM M9565); Dragon Rocks Res. (WAM M9938); Perup and Tone rivers (WAM M9972); nr. Pemberton (WAM M10231); Buntine Res. (WAM M10283-5); Easter Cave, Augusta (WAM M7945); Toodyay (BM53.10.22.25); Perth (BM53.10.22.24,

BM58.10.22.24); Oyster Harbour (nr. Albany) (BM6.10.25.3); 19.3 km. E Albany (BM27.12.15.17, 27.12.15.19); Wundowie (WAM M6604); Dryandra Forest (WAM M9074); Wilson's Inlet (WAM M9001); Boyagin Reserve (WAM M9034-44). Boro R. (AM M 5434).

Fossil specimens (not all plotted on distribution map) from W.A. caves have been identified as follows: Doline approx. 37 km. W Eucla (67.10.62); Horseshoe Cave (N59) (e.g., 72.1.5); N149, nr. Mundrabilla (e.g., 67.10.214); Weebubie Cave (67.3.102); Chowilla Sinkhole (65.9.140); Nannup Cave (e.g., 65.10.150); Deepdene Cave (e.g., 71.11.204); Mammoth Cave (e.g., in 65.12.220); Devils Lair (in 69.4.185); Strong's Cave (65.9.32); Windy Harbour Cave (e.g., 65.12.118); Harleys Cave (e.g., 66.2.73); Golgotha Cave (63.7.107); Lake Cave (65.12.38); Yallingup Cave (e.g., 63.6.46); Skull Cave (e.g., 71.10.23); Wedges Cave (in 65.12.395); Hastings Cave (e.g., 69.4.143); Smithys Cave (e.g., 67.9.50); Drovers Cave (e.g., 69.4.190); Darch, coast S Lancelin (in 62.3.5); cave in Boomerang Gorge, Yanchep (e.g., 68.6.34); Weelawadji Cave (e.g., 65.4.21); Super Cave (68.5.45); Facts of Life Cave (e.g., 69.6.160); Rifle Barrel Cave (e.g., 69.6.279); cave (E31), N. Stockyard Gully (70.6.184); Pussy Cat Cave (WAM, assoc. with 69.6.10); Pretty Cave (65.12.388); Brown Bone Cave (e.g., 68.5.22); Army Cave (65.12.389); Gooseberry Cave (WAM, assoc. with 68.6.111); Cave in Mt. Many peaks district (63.2.25); Baba Head (71.7.49); False Entrance Well (71.7.85); Many Peaks area (63.2.25); Mouth of Donnelly R. (71.3.77).

SOUTH AUSTRALIA: 100 of Blessing, 34 km. WSW Lock (SAM M7535); Wirraminna (SAM M7537).

THE KANGAROO ISLAND FORM

SOUTH AUSTRALIA: 100 of Cassini, Kangaroo I. (SAM M7664, M7936); Kangaroo I. (SAM M8997-8).

Sminthopsis murina tatei

QUEENSLAND: Mt. Molloy (J16475-6, J16478-80, J15895-6, J20431, J16647-8); 3.2 km. N Mt. Molloy (J19995); Tolga (AM M7157); Blencoe Ck. (JM993).

Sminthopsis ooldea

WESTERN AUSTRALIA: 8 km. N Mt. Boreas which is 80 km. NW Laverton (WAM M5782); Elder Creek, Warburton Range (WAM M5888, M6361); Queen Victoria Spring Wildlife Sanctuary (WAM); Neale Junction area (WAM); Baker

Lake area (WAM); Altona Stn. North Well (WAM M8078); shelter excavation, Wilgie Mia, Weld Ra. (WAM, fossil); Mt. Davies (in B1724); 3 km. N Giles Weather Stn. (AM M9700).

NORTHERN TERRITORY: 40 km. NW Mt. Olga (WAM M8079); Charlotte Waters (C6921); Curtin Springs (NTM5495).

SOUTH AUSTRALIA: Fregon, approx. 48 km. S Ernabella (SAM M6366); Maralinga (WAM M8077); Musgrave Park (SAM M7532); Ooldea (AM M7502); 24 km. NW Mulgathing (SAM M8999); 48 km. S Mt. Davies (SAM M9207).

Sminthopsis leucopus leucopus

TASMANIA (AND BASS STRAIT): Tas., unspecified local. (BM43.5.31.5, BM41.1812, BM52.1.13.3); Tas., unspecified local. (Pearson Coll. in AM, no. 568); Hobart (AM M1837); NW Mt. Barrow (1965.1.158); Binnalong Bay (1963.1.149); Tas., unspecified local. (C6343, C7363); Orford (A825); Lilydale (C1009); Roland (A868); Eddystone Point (A886); West Sister I. (C9566, AM M4459); Clarke I. (AM M4343).

Sminthopsis leucopus ferruginifrons

VICTORIA: Gippsland (BM86.5.15.9); 18 km. S Colac (D518, D520-1, D522, D535-6); Airey's Inlet (D5343); Mt. Clay Rifle Rn. (D826); Jackson's Crossing, Rodger R. (D498); Bats Ridge (D427); South Portland (AM M7425); Flinders Naval Depot, Sandy Point (D803, D804-7, D793); Waratah Bay (D523-7, D458, D741); Wilson's Promontory (C8818, C10019); 2.4 km. N Forrest (D710); Beech Forrest (C891-2). Heathmere (D734-5); Apollo Bay Rd., Forrest (D5278); 2.4 km. E Forrest (D874); Gorae West, nr. Portland (D425); Stoney River (C9470); Mirrabooka, via Tambour (C7366); Gillibrand R. (C7270).

NEW SOUTH WALES: Locality unspecified (BM54.11.193, BM54.11.19.4).

Sminthopsis virginiae virginiae

QUEENSLAND: Herbert Vale (J15890); Herbert R. (MM M1178-87); Cape York (BM1939.3244, Palmer no. 656, in AM); Hampden, nr. Mackay (J3109); Cairns (C221-2); 6.4 km. up Rocky R., nr. Coen (AM M8420); Cooktown (AM M878, J3237); Home Rule (Qd. Museum); Marrey Ck. scrub, via Coen (CM 739); Shipton's Flat, north Queensland (AMNH 196634, 155166).

Sminthopsis virginiae rufigenis

NEW GUINEA: Aru Islands (BM22.2.2.76-8); Central Division, Rona (AMNH 104005); Papua, Middle Fly R. (WAM M2811, AMNH 105817,

AMNH 105824, AMNH 105827, AMNH 105852); Laloki Nursery, Bomana, Port Moresby (AM M7445, M7568); Port Moresby (C6751).

Sminthopsis virginiae nitela

WESTERN AUSTRALIA: Kalumburu (B1841).

NORTHERN TERRITORY: Melville I. (SAM M4072); East Alligator R. (C6344); Four-mile Billabong, Wildman R. (NTM 4340b); Oenpelli Mission (WAM M4056); Daly R. (BM97.4.12.6); Mt. Tolmer (DCM 10021, CSIRO Lyneham); Mary R., 11 km. NE Moline (MVZ 133339–40); S Alligator R., 81 km. NE Pine Ck. (MVZ 133338).

Sminthopsis douglasi

QUEENSLAND: Julia Ck. (J5173, J5459); Wyangarie Stn., nr. Richmond (AM M2172).

Sminthopsis macroura macroura

QUEENSLAND: Mundubbera (J14380); Milmeran (J9156); Texas (J7407); Dalby (J9155); Willumbilla (J7806); Banana (J8179); between Chinchilla and Mundubbera (AM M7615); Capello (J7697–8); Oberina, nr. Roma (J5746).

NEW SOUTH WALES: Darling Downs (No. 275 in Lord Derby's Catalogue of the mammals in the Knowsley Museum, Liverpool Museum); Darling Downs (BM 87.5.4.1, BM46.4.4.62); between Moree and Warialda district (AM M7402); approx. 16 km. N Mungindi (AM "A. female").

Sminthopsis macroura froggatti

WESTERN AUSTRALIA: King Sound, nr. Derby (AM M8019); Wyndham (AM M5237); Mt. Hart Stn. (WAM M6842); Virgin Bore Ck., Gogo Stn. (WAM M5691–4, M5698–9, M5701, M7748–9); Exmouth Townsite (WAM); Neds Well, NW Cape (WAM M7159); Ningaloo Cave, NW Cape (WAM M7960); Cosmo Newberry Mission (WAM M6075); Mt. Egerton, via Meekatharra (WAM M2584); Jiggalong Ck., Jiggalong Mission (WAM M4512); New Mundiwindi (WAM M5411); 27 km. NE Marillana (WAM M5086); Old Talawana (WAM M8405); Yardia H.S., NW Cape (B160); Green Pool, Little De Grey R., 13 km. NE Bamboo Ck. (WAM M4513); Cave (Napier Range "No. 4"), Windjana Gorge (with 72.9.65.6); Cave 5 km. S former Virgin Bore, Gogo Stn. (67.10.5).

NEW SOUTH WALES: Mootwingie (SAM M9522); 2 km. Milparinka (AM M10228).

SOUTH AUSTRALIA: Johnson's No. 3 Bore (SAM M7931); Innamincka (AM M8294).

NORTHERN TERRITORY: Alexandria (BM 6.3.9.81–90, 6.3.9.112; WAM M512); Alroy (BM

6.3.9.91); Charlotte Waters (BM97.11.3.11, 15.2.22.4, AM M1142, C6207); Kildurk Stn., nr. Wyndham (WAM M7768); Ehrenberg Ra. (WAM M5411); N Kintore Ra. (B3060); Cadny (B21–2, C.S.I.R.O., Lyneham); Hamilton Downs Stn. (C.S.I.R.O., Lyneham); Mitchell Bore (NTM1084); Brunette Downs Stn. (NTM5418, NTM5422B, C8775–82); Yeundumu (SAM M8321–2); Simpson's Gap, nr. Alice Springs (NTM2503); 24 km. NNE Alice Springs, Bond Springs Stn. (NTM 4389); Banka Banka Hstd. (NTM3313); Limestone Bore, Amburton Stn. (NTM296); central Australia (WAM M8791); unspecified locality in N.T. (NTM1587); Helen Springs, via Powell Ck. (AM M3786); Tanami Gold Field (WAM M10348, AM M7699); Newcastle Waters (AM M4403); Hermannsburg (BM10.6.21.16); Tennant Ck. (MVZ 133188–96, 134305); Mt. Doreen Stn., 254 km. W Alice Springs.

QUEENSLAND: Richmond (AM M2173, J7647–9, J7650, J7652–3, J7665, J7680–6, J7689–91, J7693–6); Currane, Dartmouth (J9154); Barcarolle, nr. Longreach (AM M3926–M3929, J4986, J4989–90); Belcong; Capello (J7697–8, J10988); Westwood, via Rockhampton (J3689); ?Bellmore Stn., nr. Collinvale (WAM M4511); Muriweh Stn. (J1942–3); Diamantina R. (AM M2749); Julia Ck. (J5174, J11463); Emerald (J10296); Cloncurry (J10880); Old Cashmere nr. St. George (J6479); Gayndah (J11133); Wondoon (J9113); Qld, locality unspecified (J10477); Cunnamulla (AM M6955–6); Mt. Isa (AM M9168, M9169); Miles (J10477).

Sminthopsis macroura monticola

NEW SOUTH WALES: Blue Mtns. (AM B9579).

THE DOOMADGEE MISSION FORM

QUEENSLAND: Doomadgee Mission (WAM M6903, J12283, J11656, J11620, J11436, J10991, J11663, J12282, SAM M8291–7, M8303, M8309, M8315, M8321–35, M8337–8, M8341–2).

Sminthopsis hirtipes hirtipes

WESTERN AUSTRALIA: Well 29 Canning Stock Route (WAM M1547–8, SAM M3152–3); Winduldarra (WAM M1577); Djindirana Claypan, 85 km. N Everard Jctn. (WAM M8083); Elder Ck., Warburton Ra. (WAM M5783); Neale Jctn. (WAM M8943); ESE Gunga Dam, 26 mile peg, Kalbarri Rd. (WAM M10208).

NORTHERN TERRITORY: Charlotte Waters (BM97.12.17.1), bet. Maast's Bluff and Mt. Liebig (AM M6477).

THE GEORGE GILL RANGE FORM

NORTHERN TERRITORY: Reedy Creek, George Gill Ra. (NTM 1899).

Sminthopsis butleri

WESTERN AUSTRALIA: Kalumburu (WAM M7155-8; B1939, B1943, B1995).

Sminthopsis granulipes

WESTERN AUSTRALIA: King Georges Sound (No. 669, Masters Coll. in AM); Nungarin (WAM M1397); 11 km. Stirling Ra. (WAM M1668); Kon-dinin (WAM M6062); Tenterden (WAM M1968); 24 km. W Three Springs (WAM M8090); Marvel Loch (WAM M2333); Kulin (WAM M2371); Gingin (B1830); 26 km. NW Moora (WAM M6812); 48 km. E Ravensthorpe (WAM M711). Additional modern specimens not examined but unmistakably identified by D. Kitchenier include: Lake Grace (WAM M10205-6); Bending Fisheries and Fauna Reserve (WAM M10101, M10209). Fossils from caves include: Stockyard Gully (68.6.85); Hastings Cave (e.g., 69.4.140); Drovers Cave (68.6.126); Facts of Life Cave (69.6.161).

Sminthopsis psammophila

SOUTH AUSTRALIA: Section 10, 100 of Mam-blyn (SAM M7662), Section 45, 100 of Boonerdo (SAM M7971-2).

NORTHERN TERRITORY: Lake Amadeus (C6203); Ayers Rock (WAM M6217).

Sminthopsis longicauda

WESTERN AUSTRALIA: Unspecified locality but probably W.A. (C7803, C9970); Marble Bar, nr. Port Hedland (WAM M2394); Ripon Hills nr. Bamboo Ck. (66.3.105). Approx. 6 km. E Miss Gipson Hill, Baker Lake area, boundary of Gibson and Great Victoria deserts (WAM). Fossils from caves include: Owl's Roost Cave (CR4) (69.7.4176); Cape Range (66.4.64).

Sminthopsis crassicauda

No attempt has been made here to distinguish specimens of the typical from the *centralis* form since, as Finlayson (1933) notes, the two clearly grade into one another and many specimens are not assignable to a particular form.

WESTERN AUSTRALIA: Williams R. (BM44. 10.15.4, 44.7.9.10); 59 km. S Balladonia (WAM M3133); Rippleton, Tambellup (WAM M1832); Woodlands, Tambellup (WAM M797, M872,

M1011, M1031); Tambellup (WAM M670, M549, M5964, M772, M733, M2277, AM M4597-601, M5471, M5472, M5837, M5944, M5974, M5995; Kurrajong, Tambellup (WAM M1055-6); Kalbarri National Park (WAM M7896); Lake Biddy (WAM M7733); locality unknown (WAM M7511, M5435, BM56.12.29.11); Cranbrook (WAM M1138-9, M429); Gnarlabing, Katanning (WAM M1307); Benalla, via Kojanup (WAM M373); 24 km. SW Loongana (B3233); Reid (WAM M3039); 13 km. W Naretha (WAM M7746); Warburton Ra. area (WAM M7736); Hampton Hills, Bulong (WAM M1204-5, M1570, M1837, M1342, M1676-7); Wy-alkatchem (WAM M1329); Spring Valley, Keller-berin (WAM M2438); Merredin (WAM M1174); Pithara (WAM M1966); Cunderdin (WAM M2281); Marloo Stn., Murchison (WAM M1157-8); Rhy-zanthella, Corrigin (WAM M1845-6); Pingelly (WAM M2596); Nokaning, nr. Merredin (WAM M1394); Maya, Wongon Hills (WAM M1080); Carnamah (WAM M2421); Kukerin (WAM M2561); Nalkain (WAM M671); Greenough (WAM M2452); Tammin (WAM M1565); 7 km. E Forrest (AM M9171); Koolanooka (WAM M1764); Kukerin (WAM M2560); Lilyvale, Cranbrook (WAM M1138-9); Buniche, Lake Biddy (WAM M1387); Narembeen (WAM M1965); Wubin (WAM M1753, M1735); nr. Caron (WAM M912); Yanchep (WAM M1122-3); Buntine (WAM M690); Coomberdale (WAM M1275); Bencubbin (WAM M2713); Benalla, via Kojonup (WAM M373); Mingenew (WAM M873); Badgebup, Katanning (WAM M1194); Morawa (WAM M2283); Doubtful I. Bay, Gairdner River (WAM M564); central Australia (WAM M8792); Cranbrook (WAM M429); Bunjil (WAM M911, M2280); N Korrelocking (WAM M2286); Dalwallinu (WAM M2214); Lomas, via Brookton (WAM M1140); Yandanooka (WAM M2290); Wepowie, Ogilvie (WAM M2334); Kokardin (WAM M7942); East Pingelly (WAM M2624); Walkwalkin, Koorda (WAM M995); Balladonia (WAM M125, AM M4565); Wedin, via Narrogin (WAM M2621); Dumbleyung (WAM M1766); Ballidu (WAM M2215); Lake Grace (WAM M2436); Bencubbin (WAM M2413); Koorda (WAM M696); Nyabing (WAM M3895, M2275); Coorow (WAM M1374); Calingiri (WAM M7795); Talling Stn. (WAM M6385); Yalgoo (WAM M1073); Tenindewa, Geraldton (WAM M6160); Binnu (WAM M6618); Yo-gangarra (WAM M3238); Caron (WAM M6228-9, M6331); Wongan Hills (WAM M7536); Corrigin (WAM M3896); Bruce Rock (WAM M2995); Newdegate (WAM M2930); Bolgart (WAM M6694); Bencubbin (WAM M1251-2); Kukerin (WAM M2287); Talling Stn., via Mullewa

(WAM M6548); 10 km. NE Katanning (WAM M6895); Mt. Morgans, 51 km. E Leonora (WAM M4510); Buckley's Chance, Bonjil (WAM M2726); Bodallin (WAM M6608); Trayning (WAM M2729); 39 km. S Tambellup (WAM M6332); Salmon Gums (WAM M2698); Kariotdale, Coomberdale (WAM M875); East Katanning (WAM M2499); Latham, Wongan Hills (WAM M1300); Yuna (WAM M2723); Cue (WAM M6617). Cave fossils as follows: Murra-el-elevyn Cave (68.3.62); Doline approx. 37 km. W Eucla (e.g., 67.10.337); Firestick Cave (e.g., 67.10.50); Thylacine Hole (70.11.27); Cocklebidy Cave (e.g., 68.2.240); Cave 10 km. S Madura (68.3.31); Skink Hole (67.10.488); Abrakurrie Cave (67.3.147); Stockyard Gully (68.6.92).

SOUTH AUSTRALIA: Kilalpaninna (BM 2.9.8.7); Oodnadatta (C6920, SAM M7547, M7590-3, BM 56.83); Naracoorte (WAM M4488, SAM M5680, M7648); Streaky Bay (WAM M4494, M4497); Port Macdonnell (C7788, C7882); Strelzecki Rd., 13 km. S Innamincka (AM M8320); Innamincka (SAM M7647, AM M8321-2); 16 km. S Innamincka (AM M8204, M8295); 26 km. S Innamincka (AM M8574); 102 km. S Innamincka (AM M8323); foot of McDonnell Ra. (AM M3288); Mulka, via Maree (C6347, SAM M3365, M3367); Dulkaninna (WAM M4504, MVZ 129259); Wirrula (WAM M4503); Cowell (WAM M4491, M4507); west coast (WAM M8082); Glen Roy (SAM M4709); Caliph, via Loxton (SAM M5480); Etadunna Stn. (SAM M6134); Loxton (SAM M5544); Frances (SAM M2674); McDonnell Ra. (SAM M3479); Gurrui (SAM M2988); Ceduna (SAM M3573); Mitchelville (SAM M6203); Peake (SAM M3193); Merna Merna, via Quorn (SAM M5683); Lock 2, River Murray (SAM M7539); Macumba (SAM M7543-6); Lake Eyre (SAM M7548-9, M7550-3, M7638-9); Warrambo (SAM M7160-1, M7167, M7562-6, M7613-5, M7627, M8255, M8257); Partacoona (SAM M7569-75, M7577-83, M7588, M7600, M7633, M7636-7, M7653); Wharminda (SAM M7556-9, M7632); Woakurie Ra., nr. Beachport (SAM M7542); Talaranga Well (SAM M7619); Mt. Gambier (SAM M8253, M7605); Glen Lesley Stn. (SAM M7617); Mungala Stn. (SAM M7933-4); 14 km. S Wellington (SAM M8252); Manum (SAM M8254, M8258); Strangways R.S. (SAM M9510-1); Goyders Lagoon (SAM M8441); Woollana Stn. (SAM M7649); Pitcairn Stn. (SAM M9532); Renmark (SAM M6321); Yeeland (SAM M8256); Mypolonga, nr. Murray R. (MVZ 121610); locality unspecified (BM45.11.3.2).

NORTHERN TERRITORY: Curtin Springs (B2950); Charlotte Waters (AM M1142); Kunoth

Well, Hamilton Downs Stn. (NTM 1083); Cadney Bore, Hamilton Downs Stn. (NTM 3611); 32 km. N Alice Springs (SAM M7643); 8 km. E Kulgera (WAM M4475).

VICTORIA: Cowangie (SAM M8654); Ararat (WAM M4505, M8084); Mt. Mercer (C9562-3, C9491); Mt. Egerton (C9082); Myrniong (C9655-6); Toorambarry (C4509); Carwarp (C4265, C4842); Beaufort (C2996-7); Mildura (C2473, C7883); S Portland (AM M7426).

NEW SOUTH WALES: Widgiewa Stn. (AM M2589-90, M2618-9, M2653-4, M2755); Dunedoo (AM M2622); Mangaloo, nr. Coolamon (AM M5030); 32 km. S Mungindi (AM M8383); Mungindi (AM M8056, M9795, M8244); Deniliquin (C7517); nr. Deniliquin (C2044); Glenelg, via Gilgandra (AM M8384); Gilgandra (AM M8297); Narrabri (AM M6749); 11 km. Cobram (C4841); Coonbilly Hmst., 32 km. SE Yantabulla (AM M9162); Ravensworth, 58 km. W Hay (CM 1426); Tirlta (Woodstock Bore), approx. 137 km. NE Broken Hill; Darling R. (BM46.8.3.37, 46.5.14.41); Mongardie (BM26.3.11.267); 18 km. NW Trangie (BM70.814); Bellata (AM M7314, M7317); Warral, via Tamworth (AM M5213); Tamworth (AM M2898); Mungindi (AM M9825-7, M6367, M6368); Quirindi (AM M7308); Coonamble (AM M6881, M6929, M9729, M7821); Tottenham (AM M6877); Nyngan (AM M7035, M7224); Coolamon (AM M8057); Currobubula (AM M6968); Girilambone (AM M7026); Delungera (AM M7400); Crookwell (AM M7396); Quandary (AM M9728); Dubbo (19 km. from) (AM M6869); Breeza (AM M6835); Wilbury via Nyngan (AM M6841); Inverell (AM M6744, M7051, M6697); Gunningbar (AM M3744); 24 km. NW Dunnedoo (AM M4346, M5124); Pilligawarrina (AM M3743); Weerona Wee Waa (AM M4347); Millvale (AM M7483); Widgiewa Stn. (AM M2589-90, M2618-9, M2653-4, M2755); Garmain (AM M7336, M7377-9, M7337); Curlew via Gunnedah (AM M9821); Carramar (Gilgandra) (AM M9287); Redbank Stn. (40 km. NNE Coonamble) (AM M9288); Barmedman (AM M5999); Walbundrie (AM M7169); Bringagee (AM M7271, M7296); Collarenebri (AM M9703); Evbelong (AM M4539); Temora dist. (AM M7549); Caldwell (AM M7672); West Wyalong (AM M7850); Binnaway (AM M9031); Curraweena (Moree) (AM M1557); 69 km. N Bourke (AM M1760); Boggabri (AM M3136); Moree (AM M3899); 48 km. Corowa (AM M5301); Quandialla, nr. Grenfell (AM M7032, M7311); Narrandera (AM M7156); Yanco (AM M9037); 40 km. SE Narrabri (AM M8990, M8992); Lake Cawndilla via Menindee (AM M8991); Bendick Murrell (AM M7267); Binalong (AM M7272); Galgol (AM

M9272); Mt. Wood, Tibooburra (AM M10194); Warrawidgie 29 km. W Griffith (AM 10229); Armatree via Gilgandra (AM M10316).

QUEENSLAND: Barcarolle, nr. Longreach (J4984, J4987–8, J4991, AM M3927); Marion Downs Stn., 64 km. Boulia (AM M8503); 18 mile yard, Marion Downs Stn. (AM M8501); Boombah Stn., nr. St. George (J4778); Richmond (J7654); Millmerran (J11388, J11437); Goondiwindi (J8760); Inglewood (J11342); Cunnamulla (AM); Gilruth Plains, Cunnamulla (J14388, AM M9836); Kyaba

Ck., Thylungra, 97 km. NW Quilpie (AM M8243, M9794, M9828, M9822–4, M8296); Quilpie (J16775); Braidwood, via Jundah (J14376); Walumbilla (J7405); Sandringham Stn. (SAM M7645); Birdsville (SAM M7589, M7594–8, M7604, M7611, M7616, M7640, M9225); Charleville (MVZ 135244); Dickaree, nr. Birdsville (AMNH 153413); Tanbar Stn. (AMNH 198639); Mt. Isa (AM M9284); 5 km. N Birdsville (AM M9677); Munkonnie Stn. NW Birdsville (Qd. Mus.); Windorah (AM M10195); Davies Ck. nr. Mareeba (AM M8905).

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