

## Late Quaternary vertebrates from the Bird's Head Peninsula, Irian Jaya, Indonesia, including descriptions of two previously unknown marsupial species

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**Abstract** – A systematic treatment of late Quaternary vertebrate remains from two archaeological cave sites in the Ayamaru Lakes region, central Bird's Head Peninsula, Irian Jaya, documents the occurrence of 41 mammal species, three bird species and an as-yet-undetermined variety of lizards, snakes and frogs. At least nine mammal species are recorded from the Bird's Head for the first time; two of these are described as new and three others are almost certainly extinct on the Bird's Head. The new species are a diminutive striped possum, genus *Dactylopsila*, and an unusual ringtail possum with no close relatives among extant New Guinean pseudocheirids; the latter species is allocated with considerable reservation to the genus *Petauroides*, which otherwise includes only the Australian Greater Glider, *P. volans*. An apparently new species of *Pogonomelomys* is left unnamed pending wider revision of this group.

### INTRODUCTION

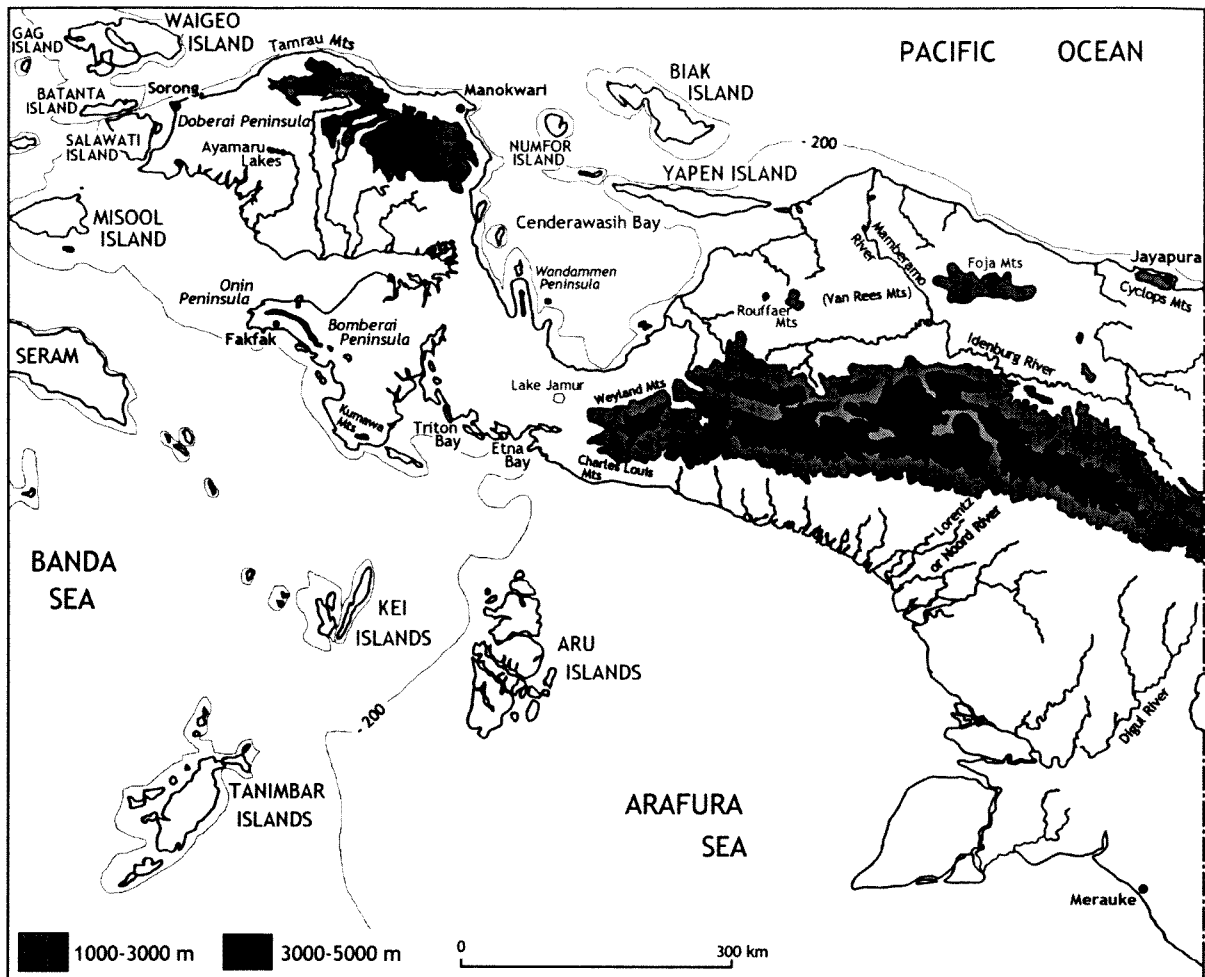
The Bird's Head Peninsula (= Vogelkop) of Irian Jaya, Indonesia, has a relatively long history of European settlement and associated biological investigation (Vink 1965; Frodin and Gressitt 1982), yet its vertebrate fauna ranks among the most poorly known of any region in greater New Guinea. Recent archaeological research in the Ayamaru Lakes area, central Bird's Head, has provided abundant, well-preserved vertebrate faunal remains from two small caves (Kria Cave: Pasveer 1998; Toé Cave: Jelsma 1998). These faunas appear to span the late Pleistocene through to late Holocene and constitute a significant source of information on the nature of late Quaternary environmental change in a lowland New Guinean habitat (Pasveer and Aplin in press).

The purpose of this paper is to present a full systematic account of the terrestrial vertebrate fauna, including descriptions of two previously unknown species of marsupials. Pasveer and Aplin (in press) provide a detailed palaeoecological analysis of the faunas, hence this topic is given only brief attention here. The wider biogeographic implications of the prehistoric and modern fauna of the Bird's Head are also discussed in a separate publication by Aplin (in press). Responsibility for this work is as follows: Boles: identification of bird remains; Aplin and Pasveer: all other identifications; Aplin: description of new species of marsupials.

### THE SITES

The excavated sites are located in the vicinity of the Ayamaru Lakes, central Bird's Head Peninsula (see Figure 1 for localities mentioned in the text). The undulating Ayamaru Plateau lies at c. 350–600 m above sea level and supports low open rainforest, interspersed with native gardens and patches of regrowth vegetation. The area is dotted with numerous, low, beehive-shaped hills, many of which contain caves. Toé Cave (Jelsma 1998) lies on a small peninsula jutting into one of the lakes, while Kria Cave (Pasveer 1998) is situated about 2 km northeast of the lakes and about 12 km from Toé Cave. Both caves are small and contain relatively shallow but archaeologically productive deposits.

In Toé Cave a total of three metre squares was excavated, reaching bedrock at a maximum depth of 140 cm (Jelsma 1998). The sequence is interpreted as consisting of two major strata: an upper unit of mid- to late Holocene age, and a lower unit of probable late Pleistocene age, the two separated by a shallow zone of potentially intermixed sediments (Pasveer and Aplin in press). One radiocarbon date of 2930±65 BP on bone collagen was obtained from within the upper unit. As noted by Jelsma and reported more fully by Pasveer and Aplin (in press), the lower unit contains a distinctive fauna including numerous mammal species characteristic of cooler, montane habitats. This difference is most readily interpreted as a consequence of significant



**Figure 1** Map of Irian Jaya and surrounding islands, showing many of the localities mentioned in the text. The 'Bird's Head' is the region consisting of the Doberai and Bomberai Peninsulas. The distribution of land above each of the 1000 m and 3000 m contours is indicated, as is the 200 m bathymetric contour, representing the approximate extent of land exposed during the last glacial maximum of 22,000–18,000 BP.

environmental change since the time deposition and therefore hints at a late Pleistocene age for these levels. Attempts to date the lower unit using radiocarbon have thus far failed; other methods are currently being explored.

In Kria Cave two metre squares were excavated, reaching maximum depths of 170–195 cm; bedrock lies some 20–40 cm deeper. The Kria Cave deposit appears to be undisturbed and a product of more or less continuous sedimentation. The oldest radiocarbon date on charcoal, at about 35 cm above the bedrock, gave an uncalibrated age of  $6900 \pm 80$  BP (Pasveer 1998). Five stratigraphic units are distinguished on the basis sedimentological characteristics and associated fluctuations in the amounts of various archaeological remains; these are referred to as Units I to V, Unit I being the surficial unit and Unit V the deepest excavated sediments. Deposition of Unit II ended around 4000 BP (Pasveer and Aplin in press). Unit I appears to have accumulated following a hiatus, and contains very little faunal material.

## MATERIAL AND METHODS

Type and figured specimens are lodged in the vertebrate palaeontological collection of the Western Australian Museum, Perth (WAM 98.7.9–98.7.57), pending their transfer to an Indonesian institution. Other specimens are identified by site code (K = Kria; T = Toë) and 'find number', the latter usually corresponding to a sample of material from a single excavation unit or 'level'. Within each such sample, individually-mentioned bones are identified by a decimal serial number after the main find number e.g. T596.1, T596.2, T596.3 etc.

The system of tooth numbering for marsupials follows Lockett (1993). Tooth crown terminology follows Archer (1976) for marsupials in general, Springer (1993) for pseudocheirid possums and Musser (1981) for rodents. For higher level marsupial systematics we follow Aplin and Archer (1987); for mammal species taxonomy we generally follow Flannery (1995a) except for the mosaic-tailed rats where we follow the more recent taxonomy of Menzies (1996). Full citation details for species level

taxa can be found in Laurie and Hill (1954), Walton (1988) or Flannery (1995a) for marsupials and bats, in Musser and Carleton (1993) for rodents and in Mayr (1941) for birds. Citation details for mammalian family-level taxa can be found in Wilson and Reeder (1993). Full references are provided in the bibliography for taxa described more recently than these checklists. All measurements are in millimetres. Reference specimens prefixed with 'AM M', 'WAM M' or 'ANU M' are from the modern mammal collections of the Australian Museum, Sydney, the Western Australian Museum, Perth, or the Department of Prehistory, Research School of Pacific Studies, Australian National University, Canberra, respectively. Modern distributional records of all vertebrates recorded from the Bird's Head region are summarized elsewhere by Aplin (in press).

## SYSTEMATIC PALAEOONTOLOGY

### Class Salientia Laurenti, 1768

#### Order Anura Rafinesque, 1815

Frog remains are present but scarce in both sites. As yet, no attempt has been made to identify this material which includes few ilia, the skeletal element most frequently used for identification of fossil anurans.

### Class Reptilia Laurenti, 1768

#### Order Squamata Oppel, 1811

#### Family Agamidae Gray, 1827

This family is represented by numerous dentaries and maxillae and selected postcranial elements, the majority coming from the lower levels of Kria Cave. No attempt has been made to identify these remains below family level. The genus *Hypsilurus* (formerly *Goniocephalus*) is represented by at least five species on the Bird's Head Peninsula.

#### Family Boidae Gray, 1825

Snake vertebrae occur in almost every level of both sites, with occasional craniodental elements also present. All of the better-preserved material is referable to the family Boidae. No attempt has been made to further identify this material. Four species of pythons are recorded from the region and *Morelia viridis* was taken by hunters during the period of fieldwork in the area.

#### Family Scincidae Gray, 1825

Skink remains are relatively uncommon in both

sites; several craniodental fragments appear to represent the Blue-tongued Skink, *Tiliqua gigas* (Schneider), which is recorded as a living animal from the Bird's Head.

### Family Varanidae Gray, 1827

Varanids are moderately well-represented by vertebrae and a variety of postcranial and tooth-bearing elements. Most of the remains are from quite large monitors; three large *Varanus* species are currently known from the Bird's Head Peninsula.

## Class Aves Linnaeus, 1758

### Order Casuariiformes Sclater, 1880

#### Family Casuariidae Kaup, 1847

#### *Casuarius bennettii* Gould, 1857

Cassowary remains are present in many levels but only eight fragments were adequate for species determination; all represent the Dwarf Cassowary, *Casuarius bennettii*. This species is most commonly associated with montane habitats but it has been recorded locally in the lowlands (Coates 1985). The fossil material is distributed through all major units including both upper and lower levels of Toé Cave.

Cassowary eggshell is present in small quantities through the sites; it is most abundant in the lower units of both caves. Nesting may occur at any time of year (Coates 1985).

### Order Galliformes Temminck, 1820

#### Family Megapodiidae Swainson, 1837

#### Megapodiidae cf. *Aepyodius arfakiensis* (Salvadori, 1877)

Several fragmentary tibiotarsi from the lowermost unit of Kria Cave are referable to a megapodiid. These are a good match morphologically for *Aepyodius arfakiensis* but are slightly smaller. They have not been compared to *A. bruijini* (Oustalet, 1880), a related taxon endemic to Waigeo Island. Thin-walled, large diameter eggshell fragments from several levels in both caves are probably attributable to a megapode.

*Aepyodius arfakiensis* is widely distributed through the mountains of New Guinea, with localities ranging from 750–2700 m elevation. It also occurs on Misool Island, where it occupies unusually low elevations (Mees 1965). Dwyer (1981) reported seeing eggs in the Southern Highlands Province of Papua New Guinea in all months of the year except July, August and November.

**Order Strigiformes Weigler, 1830****Family Tytonidae Ridgway, 1914*****Tyto* sp. cf. *T. tenebricosa* (Gould, 1845)**

This taxon is represented by a range of skeletal elements, all coming from the lower unit of Toé Cave. The Sooty Owl is the only large *Tyto* species recorded from the Bird's Head region and the fossil material is a good match with modern specimens of this species. However, reference material is not available for several, related taxa and the identification is therefore regarded as likely but not certain.

*Tyto tenebricosa* ranges from the lowlands up to at least 3660 m elevation; it is probably most abundant in montane habitats. The species roosts in cavities under tree roots, in stream banks and under rocks, and takes a wide size-range of mammalian prey, from small marsupials and rodents up to young individuals of *Dorcopsulus vanheurni* (Diamond 1972; Majnep and Bulmer 1977).

**Class Mammalia Linnaeus, 1758****Infraclass Prototheria Gill, 1872****Order Monotremata Bonaparte, 1838****Family Tachyglossidae Gill, 1872*****Zaglossus bruijnii* (Peters and Doria, 1876)**

Represented in most levels of both deposits, but especially abundant in the lower unit of Toé Cave. The type locality of *Zaglossus bruijnii* is Hatam, Arfak Mountains in the northeast part of the Bird's Head Peninsula, hence the fossil material probably represents typical *bruijnii*. The species is still occasionally captured on the Ayamaru Plateau (Elimas Kambuaya pers. comm.).

Geographic variation within *Z. bruijnii* is poorly understood (Flannery 1995a). The fossil remains are noticeably larger and more robust than AM M9852, an adult male from Mt Hagen in the Western Highlands Province of Papua New Guinea.

**Supercohort Marsupialia Illiger, 1811****Order Dasyuromorphia Gill, 1872****Family Dasyuridae Goldfuss, 1820*****Dasyurus albopunctatus* Schlegel, 1880**

Poorly represented. The most complete specimens are K1053.1, a right dentary fragment containing all four molars, and T593.1, a left maxillary fragment with alveoli for P<sup>3</sup> and M<sup>1</sup>. These are both slightly larger than AM M30736, an adult male from the

Kwiyawagi area of Irian Jaya. The type locality of *D. albopunctatus* is Hatam, Arfak Mountains in the northeast part of the Bird's Head Peninsula.

***Myoictis melas* (Müller, 1840)**

Represented by a small number of specimens from both older and more recent levels in both caves. The most complete and informative specimen is K1035.1, a maxillary fragment with M<sup>1-3</sup>. This specimen agrees closely in size and morphology with AM M8907 from 4 km SW of Bernhard Camp on the Idenberg River. *Myoictis melas* has been recorded from several localities in the northeast part of the Bird's Head Peninsula.

Relatively fine, irregular tooth-marks are observed on many of the archaeological bones from Kria Cave (and to a lesser extent, from Toé). These marks are usually concentrated around areas of former tendinous muscle attachment and are clearly not made by a rodent, but rather by some creature with small but robust caniniform teeth. Of the various possible agents, *Myoictis melas* is perhaps the most likely, both in terms of its size and dental morphology and also in view of its propensity to frequent areas of human habitation (Flannery 1995a).

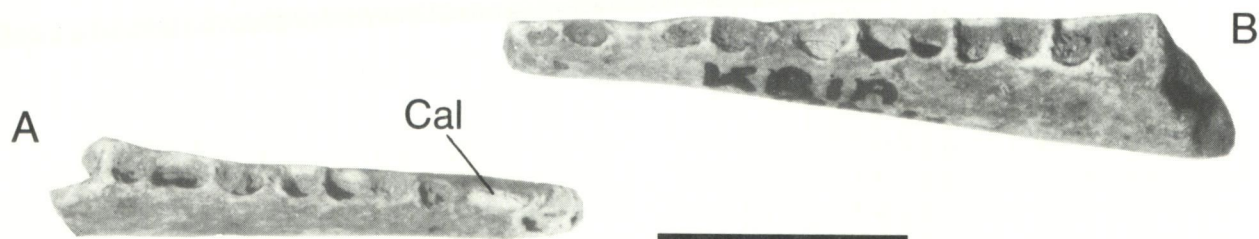
**Order Peramelemorphia Kirsch, 1968****Family Peroryctidae Groves and Flannery, 1990*****Echymipera kalubu* (Lesson, 1828)**

This species is most convincingly represented by several isolated upper molars (e.g. M<sup>3</sup>: K1155.1). These show the characteristic, enlarged metacone (hypocone) and associated posterior cingulum which serves to distinguish *E. kalubu* from each of *E. rufescens* and the recently described *E. echinista* Menzies, 1990a (see also Lidicker and Ziegler 1968). Several edentulous dentaries are also referred to *E. kalubu*, based on the alveolar to ramal proportions and the absence of significant premolar region diastemata (Figure 2A).

*Echymipera kalubu* has been recorded from several localities on both the western and eastern margins of the Bird's Head Peninsula.

***Echymipera rufescens* (Peters and Doria, 1875)**

This species is better represented than the last, with several dentaries bearing teeth (e.g. K1088.1) and others preserving the premolar alveoli with the characteristic long diastemata of the premolar region (Figure 2B). The fossil specimens resemble modern *E. rufescens* from Okiapmin in the West Sepik Province (AM M32583, AM M32592), except



**Figure 2** Fossil mammal specimens from Kria and Toé Caves: A, WAM 98.7.9, *Echymipera kalubu*, right dentary fragment with alveoli for canine,  $P_{1-3}$  and anterior root of  $M_1$ , semiocclusal view; B, WAM 98.7.10, *Echymipera rufescens*, left dentary fragment with alveoli for canine,  $P_{1-3}$  and  $M_1$ , semiocclusal view. Cal = canine alveolus. Scale bar = 10 mm.

that they are somewhat larger. This is also true of the referred postcranial material which includes some truly enormous specimens, presumably representing males.

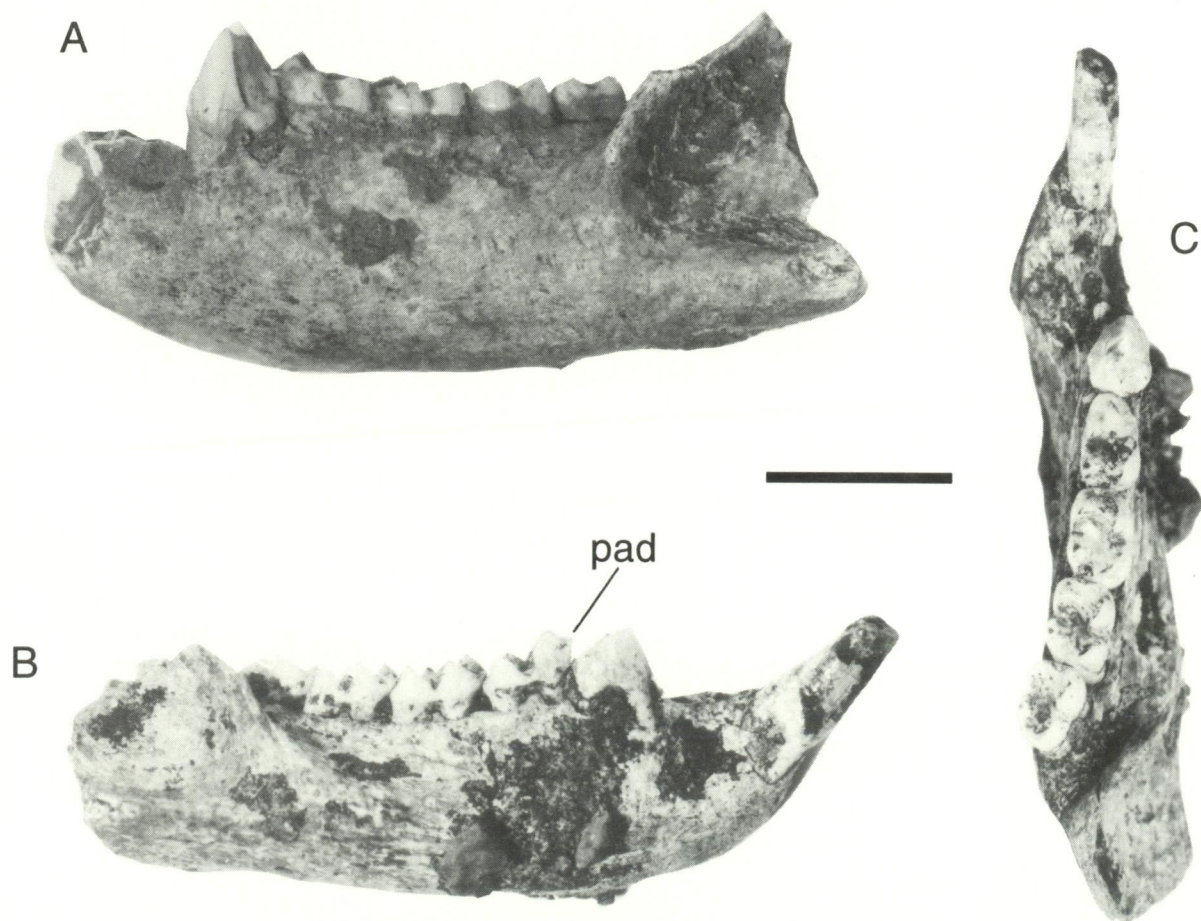
Dollman (1930) referred two specimens from the Arfak Mountains to *E. gargantua* Thomas, 1914, a gigantic form of *E. rufescens* described initially from the Mimika River in southwest Irian Jaya. Flannery (1995a) noted the presence in the Gulf Province of Papua New Guinea of a similarly gigantic form of

*E. rufescens*. The systematics of this group are in need of revision.

*Echymipera rufescens* has been recorded on both the western and eastern periphery of the Bird's Head Peninsula.

*Microperoryctes longicauda* (Peters and Doria, 1875)

A very slender dentary fragment (T572.1) and a



**Figure 3** Fossil mammal specimens from Kria and Toé Caves: A, WAM 98.7.21, partial left dentary of *Phalanger gymnotis* with  $P_3$  and  $M_{1-4}$ , lateral view; B, WAM 98.7.22, partial right dentary of *Phalanger* sp. cf. *P. intercastellanus* with  $I_1$  (tip missing),  $P_3$  and  $M_{1-4}$ , lateral view; C, WAM 98.7.22 in occlusal view. pad = paraconid. Scale bar = 10 mm.

variety of postcranial elements are referred to this small-bodied species. The jaw fragment compares well in size and morphology with AM M30734 from the Kwiyawagi area. The dentary and some of the referred postcranial material comes from the presumed late Pleistocene, lower unit of Toé Cave. However, other postcranial material consistent in size with this taxon comes from various levels through the Kria Cave deposit.

The type locality of *Microperoryctes longicauda* is Hatam, Arfak Range. Flannery (1995a) noted that both the typical race and *M. l. dorsalis* from the western end of the Central Cordillera are quite large-bodied in comparison with the much smaller *M. l. ornatus* of eastern New Guinea. Throughout New Guinea, *M. longicauda* is generally confined to elevations above about 1000 m. Its occurrence through to the upper levels of Kria Cave indicates a possible extension to lower elevations on the Bird's Head.

None of the bandicoot remains is small enough to be referable to the Mouse Bandicoot, *M. murina*, which is known from a distinctive population in the Anggi Lakes region of the Arfak Mountains (Flannery 1995a).

#### Order Diprotodontia Owen, 1866

#### Family Phalangeridae Thomas, 1888

Much of the phalangerid material cannot be identified below generic level. However, sufficient diagnostic material is present to distinguish at least four taxa of *Phalanger* and two of *Spiloglossus*. Three of the four *Phalanger* species can be associated with known extant taxa; the fourth is tentatively referred to an extant species but with little real confidence.

#### *Phalanger gymnotis* (Peters and Doria, 1875)

This species is represented in most levels in both caves. Included are several well-preserved dentaries (Figure 3A) showing the characteristic, high-crowned,  $P_3$  and relatively small molars with finely-punctate enamel. The Ground Cuscus has been recorded from both the western and eastern margins of the Bird's Head Peninsula. It has an extremely broad altitudinal distribution, from sea level to 2700 m (Flannery 1995a). Feiler (1978) and



Figure 4 Fossil mammal specimens from Kria and Toé Caves: WAM 98.7.24, partial right dentary of *Phalanger orientalis* with  $I_1$  and alveoli for two unicuspid teeth,  $P_3$  and  $M_{1-4}$ . A, semiocclusal view; B, lateral view. Scale bar = 10 mm.

George (1987) identified the mainland Ground Cuscuses as a separate taxon, *P. leucippus* Thomas, 1898, distinct from *P. gymnotis* of the Aru Islands. We follow Flannery (1995a) in treating these taxa as a single species.

*Phalanger* sp. cf. *P. intercastellanus* Thomas, 1895

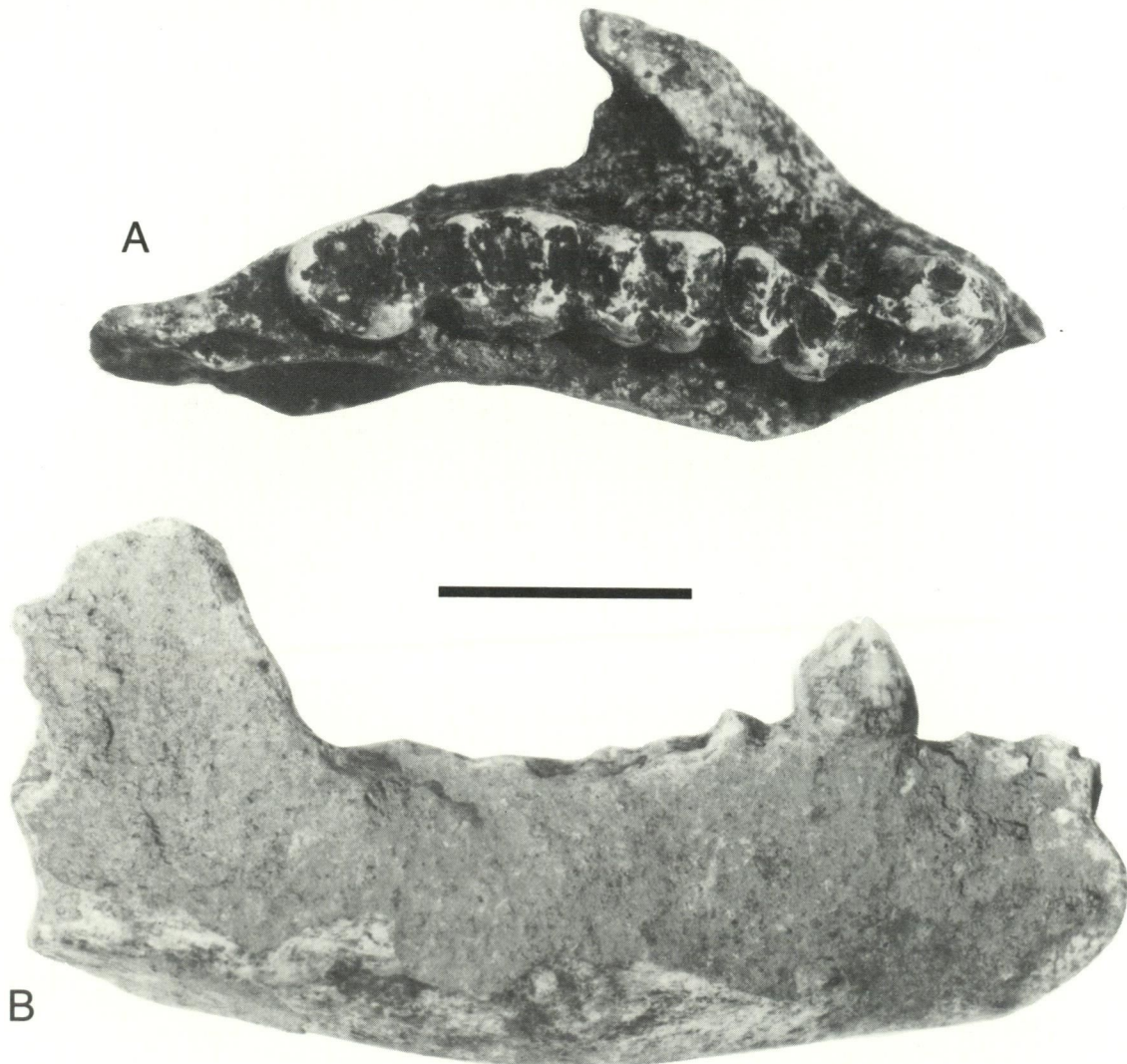
A distinctive, small-toothed cuscus is represented by several well-preserved dentaries from Toé Cave (Figure 3B,C). These are similar in size to a specimen of *P. intercastellanus* from southern New Guinea (AM M30722 from the Timika area of Irian Jaya) but differ from this and other specimens of *P. intercastellanus* in various details of molar structure (e.g. presence of a distinct paraconid on the  $M_1$ , small size of  $M_{2,3}$  paraconids, absence of entostylids on posterior molars). The identity of the small-

toothed Bird's Head cuscus will probably not be settled until such time as a modern specimen becomes available.

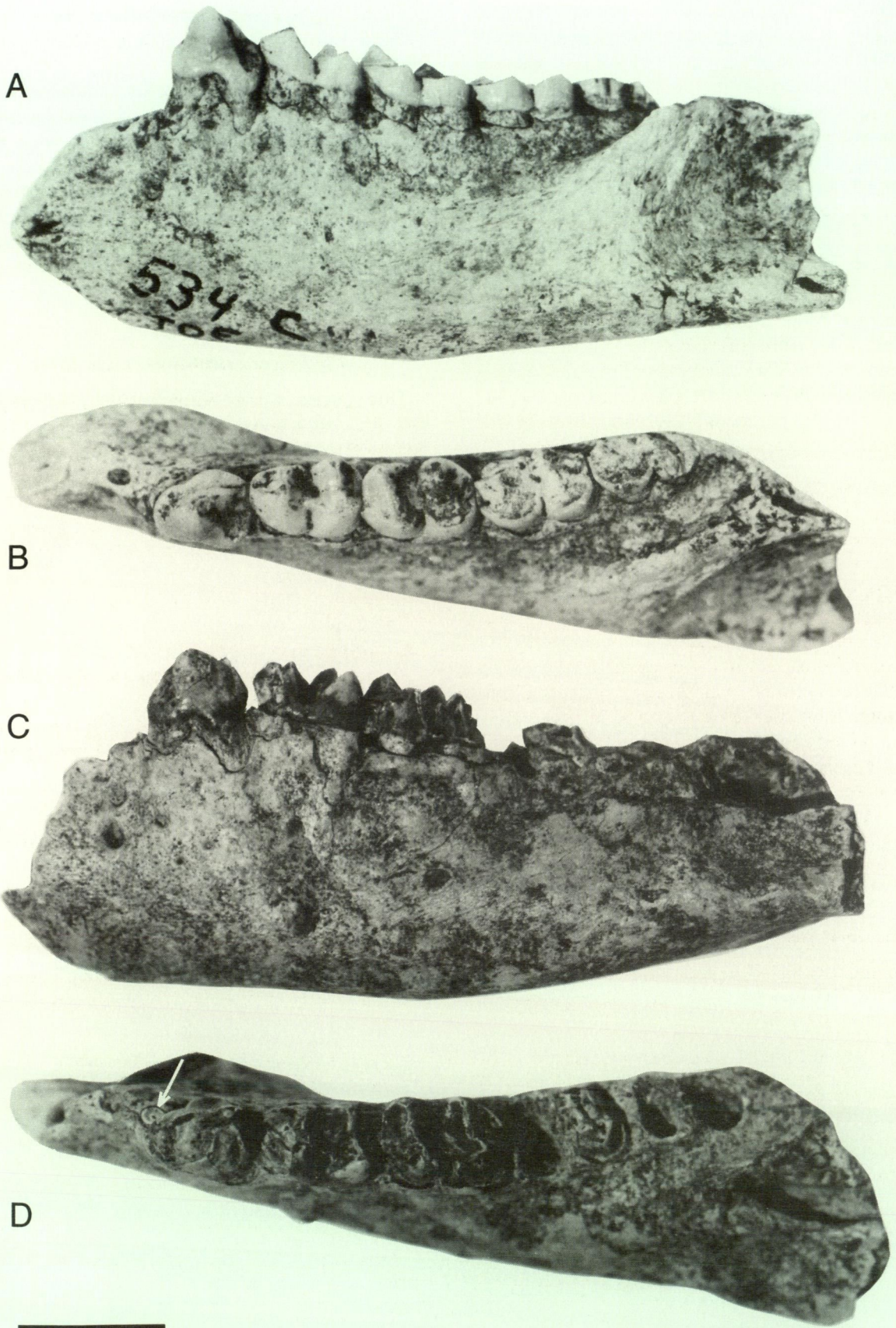
*Phalanger intercastellanus* is the common cuscus of lowland forests of southern New Guinea (Colgan *et al.* 1993; Flannery 1995a), extending west to the Timika area of Irian Jaya and the Aru Islands. It has not been recorded on the Bird's Head. North of the Central Cordillera it is replaced by the closely related *P. orientalis*. The two species are not known to occur sympatrically, although their ranges may abut in the Madang Province.

*Phalanger orientalis* (Pallas, 1766)

This species is more abundant than the preceding two and occurs in all levels of both caves (Figure 4A,B shows a well-preserved jaw lacking



**Figure 5** Fossil mammal specimens from Kria and Toé Caves: A, WAM 98.7.23, partial right maxilla of *Phalanger vestitus* with  $P^3$  and  $M^{1-4}$ , occlusal view; B, WAM 98.7.25, partial right dentary of *P. vestitus* with  $P_3$  and alveoli for all other teeth, lateral view. Scale bar = 10 mm. Note relatively large size and complexity and lateral inflection of the  $P^3$  and relatively short diastema and low-crowned, bulbous  $P_3$ . These are all features that serve to distinguish *P. vestitus* from the similar-sized *P. orientalis*. The  $P_3$  of *P. gymnotis* is higher crowned and bears fewer and less prominent crests (see Figure 3A).



**Figure 6** Fossil mammal specimens from Kria and Toé Caves: A, WAM 98.7.26, partial left dentary of *Spilocus maculatus* with  $P_3$  and  $M_{1-4}$ , lateral view; B, WAM 98.7.26, occlusal view; C, WAM 98.7.27, partial left dentary of *Spilocus rufoniger* with  $P_3$  and  $M_{1-2}$ ,  $M_3$  roots, lateral view; D, WAM 98.7.27, occlusal view. Scale bar = 10 mm. Note root (arrowed) of additional, third unicuspid tooth adjacent to anterior root of  $P_3$  of *S. rufoniger* and its larger, more prominently-crested molars and more robust dentary compared to *S. maculatus*.



cheekteeth). Modern Bird's Head specimens are referred to the nominate subspecies (Menzies and Pernatta 1986) which occurs across northern New Guinea and into the northern Moluccas. The fossil specimens are a close match in both size and morphology with modern specimens from Salawati Island (e.g. AM M28711). However, all of these western New Guinean specimens are considerably larger in both jaw and tooth dimensions than modern specimens from the Sepik District and Torricelli Range of Papua New Guinea. Despite recent systematic treatments of the *Phalanger orientalis* group by Menzies and Pernatta (1986), George (1987) and Colgan *et al.* (1993), the nature of geographic variation within the group remains poorly understood.

#### *Phalanger vestitus* (Milne-Edwards, 1877)

Several partial dentaries from the lower units of Toé and Kria Caves are referable to this species. They are readily distinguished from the more abundant remains of *P. orientalis* by their overall shorter tooththrows and relatively shorter diastemata, and by the lower-crowned, more bulbous  $P_3$  (Figure 5B). A complete maxillary tooththrow was also recovered from Toé Cave (Figure 5A).

*Phalanger vestitus* was first described from a specimen from the Tamrau Range in the northern Bird's Head; more recently, Flannery (1995a) collected the species at 2200 m in the Arfak Mountains. Elsewhere in New Guinea, *P. vestitus* is known from widely scattered localities, the majority falling in a narrow band of oak forest between 1200 and 1600 m elevation (Flannery 1995a).

#### *Spilocuscus maculatus* (Desmarest, 1818)

Remains of this widespread, lowland species are found in all levels of both sites. Better-preserved

dentaries (Figure 6A,B) show alveoli for two single-rooted, unicuspid teeth between the  $P_3$  and the procumbent lower incisor. The lower incisors are more steeply inclined than in *S. rufoniger* and the molars are shorter and relatively broader and have more coarsely crenulate enamel. Flannery and Calaby (1987) and George (1987) noted additional distinguishing characteristics of each species.

Bird's Head populations of *S. maculatus* are referred to the nominate race (Feiler 1978; George 1987). Tate (1945a) restricted the type locality to Manokwari, northeast Bird's Head Peninsula.

#### *Spilocuscus rufoniger* Zimara, 1937

This species is well represented in the lower unit of Toé Cave, and also present in Unit V of Kria Cave (Figure 6C,D). It is readily distinguished from *S. maculatus* by its larger but relatively narrower molars, more robust dentary and less steeply-inclined lower incisors, and by the presence of a third unicuspid tooth, situated lingual to the anterior root of  $P_3$ .

*Spilocuscus rufoniger* is primarily a species of northern New Guinea, although it has also been collected on the Lorentz River, southern Irian Jaya (Flannery 1995a). All records are from below 1200 m elevation. Throughout its range, *S. rufoniger* is restricted to primary forests; it is nearly always found in sympatry with the more widespread and abundant *S. maculatus*.

#### Family Macropodidae Gray, 1821

##### *Dendrolagus* sp. cf. *D. goodfellowi* Thomas, 1908

A member of the *D. goodfellowi* group is represented by a dentary (WAM 98.7.11) with the lower incisor root, the  $P_3$  and the  $M_2$  (Figure 7A,B), and by isolated  $P_3$  (K1159.1) and  $P^3$  (K1137.1). The

**Table 1** Dental measurements (in millimetres) of *Dendrolagus* sp. cf. *D. goodfellowi* subsp. indet. from Kria and Toé Caves. Measurements: L = crown length; AW = crown anterior width; PW = crown posterior width.

	$P_3$ L	$P_3$ PW	$M_2$ L	$M_2$ AW	$M_2$ PW	$P^3$ L	$P^3$ AW	$P^3$ PW
WAM 98.7.11	8.4	3.8	5.8	4.3	4.1	—	—	—
K1137.1	—	—	—	—	—	8.9	4.4	4.0
K1159.1	8.7	3.5	—	—	—	—	—	—

**Table 2** Dental measurements (in millimetres) of *Dendrolagus inustus* from Kria and Toé Caves. Measurements: L = crown length; AW = crown anterior width; PW = crown posterior width.

	$P_3$ L	$P_3$ PW	$M_1$ L	$M_1$ AW	$M_1$ PW	$M_2$ L	$M_2$ AW	$M_2$ PW
K756.1	—	—	—	—	—	—	—	—
K852.1	—	—	—	—	4.4	—	—	—
K1149.1	9.5	4.1	—	4.4	4.3	—	—	—
T515.1	9.5	—	3.9	—	4.1	—	—	—
T516.1	9.4	—	3.9	—	4.1	—	—	—

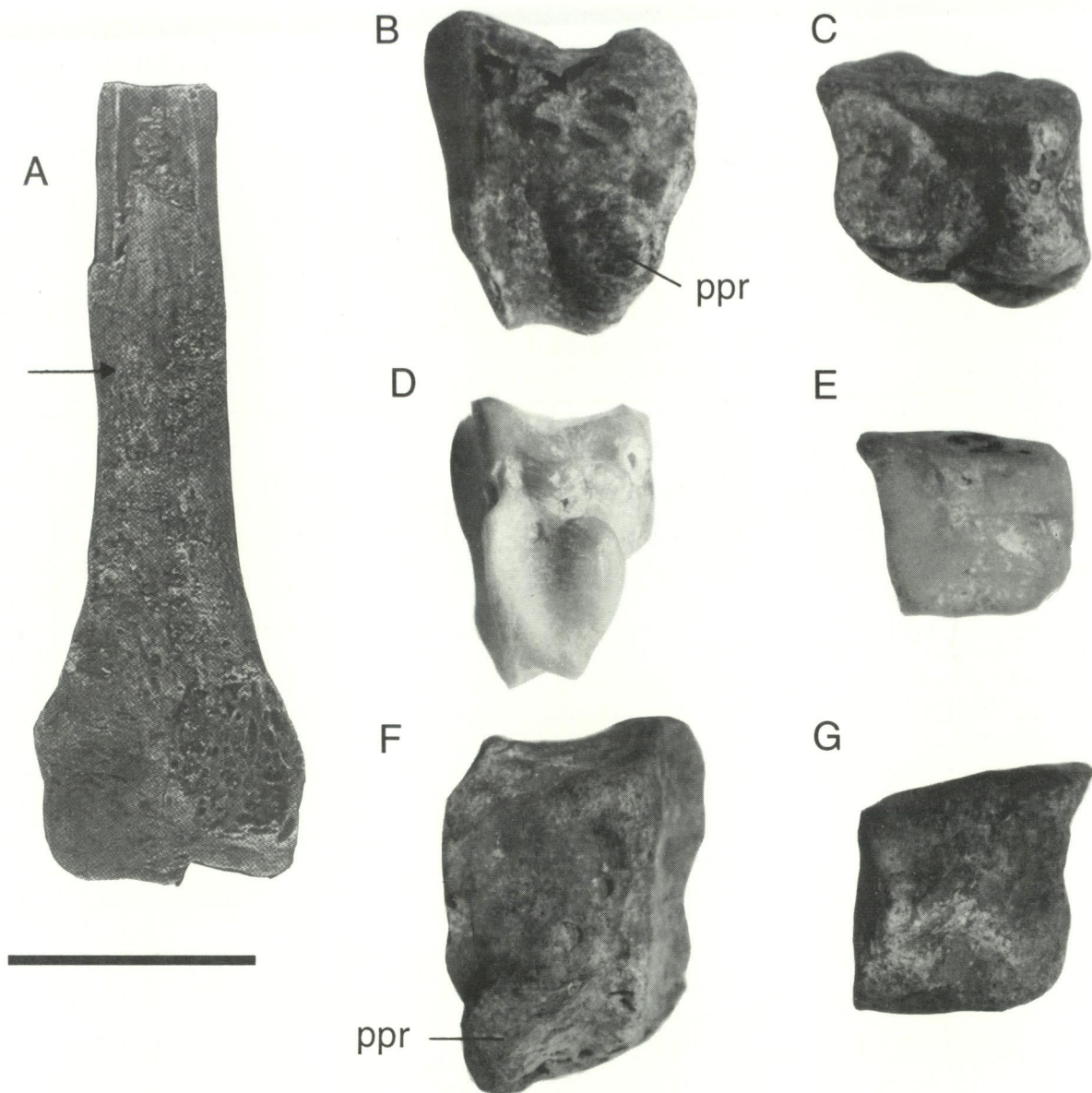
$P_3$  of WAM 98.7.11 has two intermediate cusps and a continuous occlusal crest which produces an even cutting edge, contrasting with the characteristically interrupted occlusal crest of *D. inustus* (Figure 7C). The  $M_2$  has a shorter anterior cingulum than specimens of *D. inustus*. Measurements of dental material of both species of tree-kangaroos are compared in Tables 1 and 2. The Vogelkop Tree-kangaroo, *D. ursinus* Müller, 1840, has much broader molars and a distinctive

premolar morphology. Most records of this latter species come from higher elevations in the Arfak Mountains (Flannery 1995a).

Further evidence of a species of the *D. goodfellowi* group is provided by postcranial remains from the lower unit of Toé Cave. These include a distal fibula (Figure 8A), showing the characteristically short tibio-fibular contact of the *D. goodfellowi* group (*D. inustus* has a longer zone of contact), and a well-preserved cuboid (Figure 8B,C). The latter specimen



**Figure 7** Fossil mammal specimens from Kria and Toé Caves: A, WAM 98.7.11, *Dendrolagus* sp. cf. *D. goodfellowi*, right dentary fragment with  $I_1$  root,  $P_3$ ,  $M_1$  roots and  $M_2$ , lateral view; B/B', WAM 98.7.11 stereoscopic pair, occlusal view; C, WAM 98.7.12 *Dendrolagus inustus*, partial left dentary with  $P_3$ ,  $M_{13}$  and  $M_4$  roots, occlusal view. Scale bars = 10 mm.



**Figure 8** Fossil mammal specimens from Kria and Toé Caves: A, WAM 98.7.57, *Dendrolagus* sp. cf. *D. goodfellowi*, right fibula, distal portion, medial aspect (arrow indicates the proximal extent of the characteristically short tibiofibular contact); B, WAM 98.7.13, right cuboid of *Dendrolagus* sp. cf. *D. goodfellowi*, plantar aspect; C, WAM 98.7.13, medial aspect; D, right cuboid of *D. matschiei* (WAM M21013), plantar aspect; E, WAM M21013, medial aspect; F, WAM 98.7.14, left cuboid of *D. inustus*, plantar aspect; G, WAM 98.7.14, medial aspect. Scale bar = 10 mm. Note smaller size of plantar process (ppr) of cuboid in the two *D. goodfellowi* group species compared with *D. inustus*, in which the process is larger and projects further laterally.

resembles the cuboid (Figure 8D,E) of *D. matschiei* Förster and Rothschild, 1907, a member of the *D. goodfellowi* group, in various features [e.g. small size and medial position of plantar process; posterior (calcaneal) and anterior (metatarsal) facets strongly convergent laterally] and is quite distinct from that of *D. inustus* (Figure 8F,G) from the same levels in the deposit.

The *D. goodfellowi* group has its stronghold in eastern New Guinea, where three species occur (Flannery 1993). Only *D. goodfellowi* itself is known to extend very far west, with a distinct subspecies, *D. g. pulcherrimus* Flannery, 1993, present in the isolated Torricelli Range of northern Papua New

Guinea and Foja Mountains of Irian Jaya. No member of the group has previously been recorded as far west as the Bird's Head.

Special comparisons were made with *D. g. pulcherrimus* and with *D. spadix* Troughton and Le Souef, 1936 of the Papuan Plateau, a large expanse of rugged limestone country north of the Gulf of Papua. Of these taxa, the fossil material more closely resembles *D. g. pulcherrimus* in having a simple upper premolar lacking a posterobuccal cusp, a shorter-crowned lower premolar with evenly spaced cuspules, and a weak anterior cingulum on the  $M_2$ . It is tentatively referred to *D. goodfellowi*, but is left unallocated at subspecies level.

*Dendrolagus inustus* Müller, 1840

This species is identified from numerous craniodental remains (Figure 7C) and diagnostic postcranial elements (e.g. calcaneum, cuboid; Figure 8F,G) and is present in all major stratigraphic units of both caves (see Table 2 for dental measurements). The fossil remains presumably represent typical *D. inustus* (type locality: Triton Bay), however they also compare closely with reference specimens of *D. inustus finschi* Matschie, 1916 from the Torricelli Range (e.g. AM M24437). The species occurs from near sea level up to a maximum elevation of 1400 m (Flannery 1995a).

*Dorcopsis muelleri* (Schlegel, 1866)

The remains of a *Dorcopsis* wallaby are extremely abundant at all levels in the Kria deposit and in the upper levels of Toé Cave. Occasional specimens were also recovered from the lower levels of Toé Cave.

According to Groves and Flannery (1989), all *Dorcopsis* from the western part of Irian Jaya are referable to *D. muelleri*, but with various mainland and insular subspecies distinguished

chiefly on characters of the pelage. The fossil material agrees closely in size and morphology with modern specimens of *D. muelleri muelleri* from the Timika River Area (see Table 3 for dental measurements of two modern specimens and of the large fossil sample from Kria Cave; also Figures 9–11).

All species of *Dorcopsis* are sexually dimorphic in body size, with males attaining greater size than females. This dimorphism is clearly expressed in the fossil sample which shows a bimodality in most dental dimensions, but especially in the posterior molars. Inferred male and female individuals from the fossil sample are contrasted in Figures 9 and 10.

Statistical comparisons of material from each of the major stratigraphic units in the Kria Cave deposit failed to reveal any change in dental dimensions through the deposit. However, variation in the sex ratio between different samples might potentially confound such an analysis, so the results are not regarded as definitive. Too few dental specimens were recovered from the lower unit of Toé Cave to permit statistical comparisons of the presumed late Pleistocene sample with those from Holocene levels.

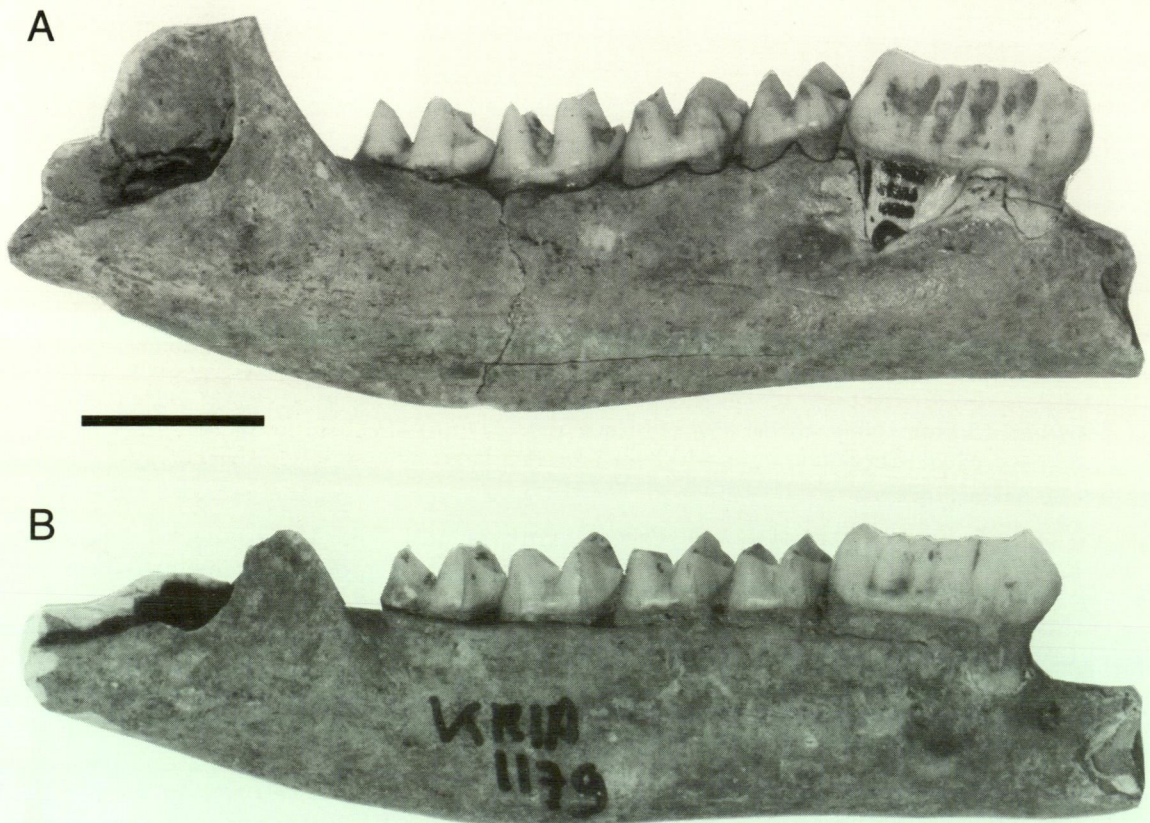
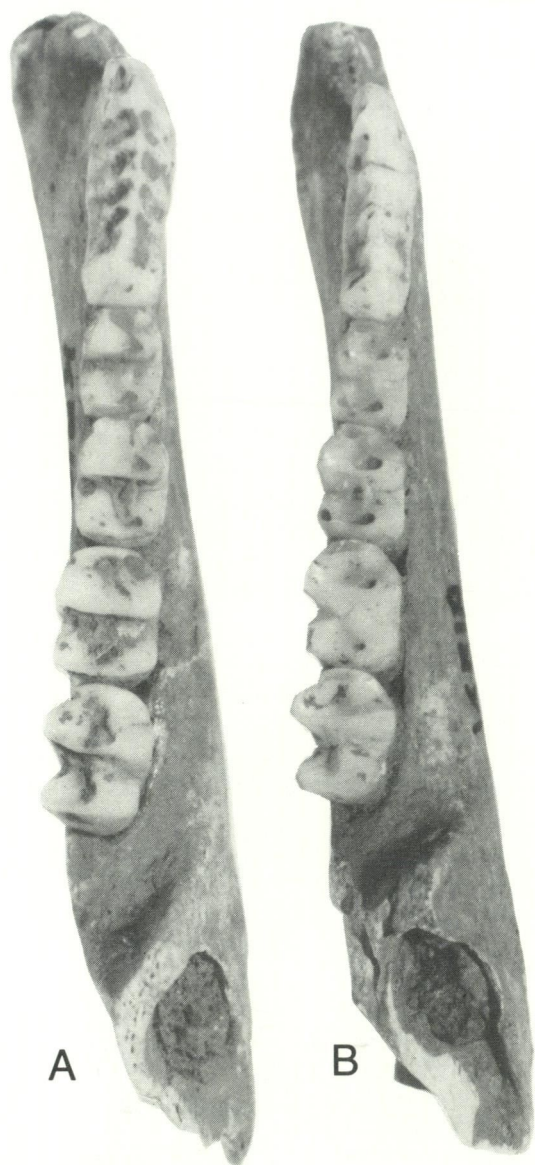


Figure 9 Fossil mammal specimens from Kria and Toé Caves: A, WAM 98.7.15, partial right dentary of *Dorcopsis muelleri*, probable male specimen with  $P_3$  and  $M_{1,4}$ , lateral view; B, WAM 98.7.16, partial right dentary of *Dorcopsis muelleri*, probable female specimen with  $P_3$  and  $M_{1,4}$ , lateral view. Scale bar = 10 mm.



**Figure 10** Fossil mammal specimens from Kria and Toé Caves: A, WAM 98.7.15, partial right dentary of *Dorcopsis muelleri*, probable male specimen with P<sub>3</sub> and M<sub>1-4</sub>, occlusal view; B, WAM 98.7.16, partial right dentary of *Dorcopsis muelleri*, probable female specimen with P<sub>3</sub> and M<sub>1-4</sub>, occlusal view. Scale bar = 10 mm.

*Dorcopsulus vanheurni* (Thomas, 1922) and *Dorcopsulus* sp.

There are no modern records of the genus *Dorcopsulus* from the Bird's Head. The fossil material is derived primarily from the lower levels of Toé Cave and includes both well-preserved dentaries (e.g. WAM 98.7.18, T539.1) and a maxilla (T564.1), as well as a variety of postcranial elements. A single I<sup>3</sup> was recovered from Unit V of Kria Cave. *Dorcopsulus* species today are confined to montane forests above about 800 m altitude.

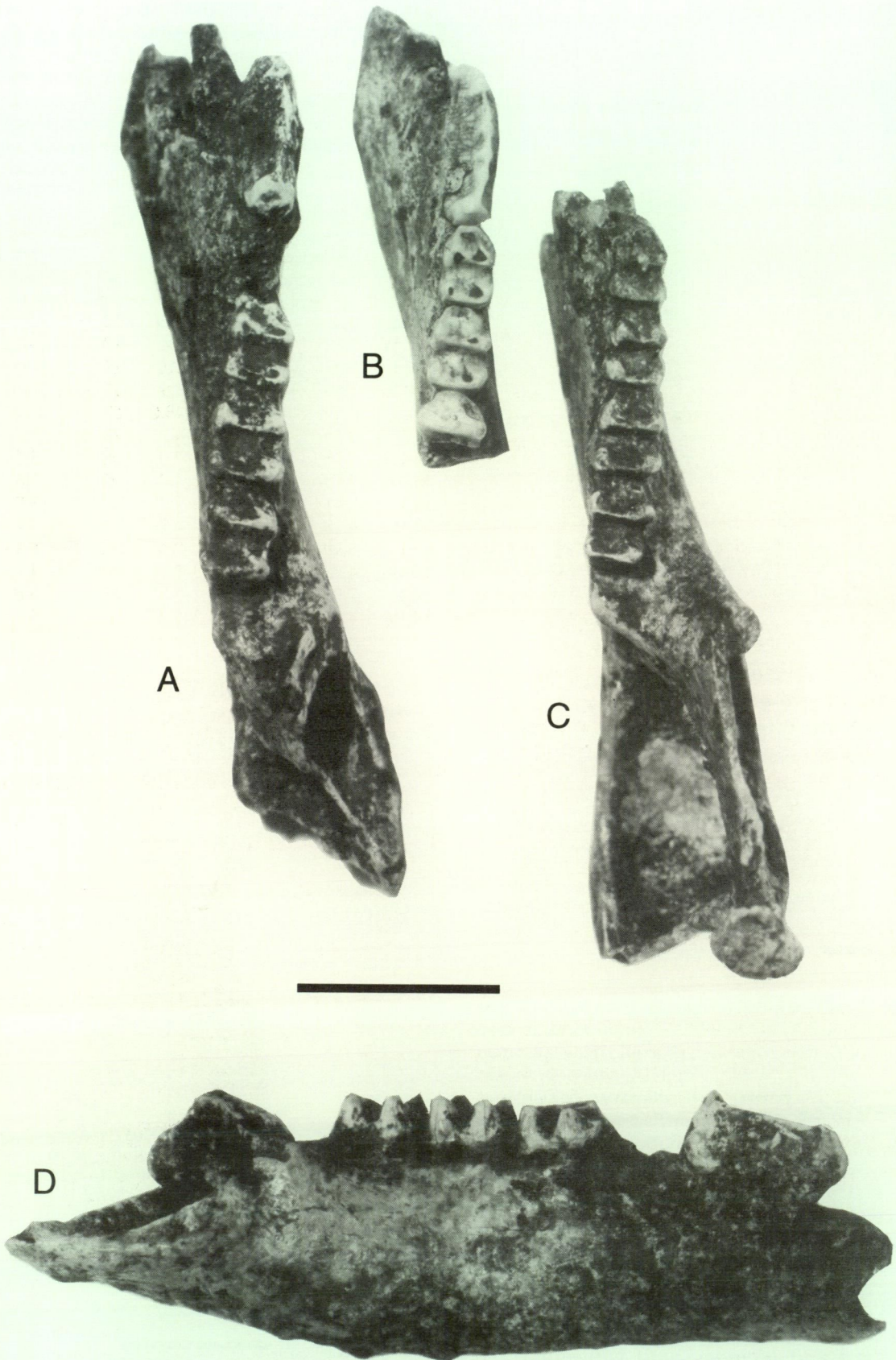
Two distinct forms of *Dorcopsulus* are represented

**Table 3** Summary statistics for lower cheektooth measurements (in millimetres) of *Dorcopsis muelleri* from Kria Cave compared with two modern specimens from Etna Bay: AM M32339 (Female - F) and AM M32341 (Male - M). Measurements: L = crown length; W = crown anterior width. In several measurements (e.g., M<sub>1</sub>W, M<sub>3</sub>W) the modern male specimen falls outside of the range of the archaeological sample.

	Kria Cave Sample			N	Modern	
	Mean	Std-Dev	Range		F	M
DP <sub>2</sub> L	8.22	1.69	7.2-12.9	10	-	-
DP <sub>2</sub> W	3.12	0.19	2.8-3.4	10	-	-
DP <sub>3</sub> L	5.93	0.17	5.6-6.1	11	-	-
DP <sub>3</sub> W	2.60	0.17	2.3-2.9	11	-	-
P <sub>3</sub> L	12.84	0.81	11.1-15.0	67	12.6	14.3
P <sub>3</sub> W	3.46	0.30	2.8-4.1	78	3.7	4.4
M <sub>1</sub> L	5.95	0.37	5.1-7.0	98	5.6	5.6
M <sub>1</sub> W	3.70	0.19	3.2-4.0	97	3.8	4.2
M <sub>2</sub> L	6.41	0.33	5.6-7.2	103	5.9	6.0
M <sub>2</sub> W	4.18	0.22	3.7-4.7	104	4.4	4.8
M <sub>3</sub> L	6.99	0.36	6.1-7.9	102	6.4	7.2
M <sub>3</sub> W	4.73	0.22	4.3-5.3	104	4.9	5.6
M <sub>4</sub> L	7.05	0.32	6.2-7.9	65	6.8	7.5
M <sub>4</sub> W	4.81	0.25	4.3-5.4	67	5.1	5.6



**Figure 11** Fossil mammal specimens from Kria and Toé Caves: WAM 98.7.17, partial left maxilla of *Dorcopsis muelleri*, probable male specimen with P<sub>3</sub> and M<sup>1-3</sup>, occlusal view. Scale bar = 10 mm.



**Figure 12** Fossil mammal specimens from Kria and Toé Caves: A, WAM 98.7.18, partial right dentary of *Dorcopsulus vanheurni* with  $P_3$  and  $M_{2-4}$ , occlusal view; B, WAM 98.7.19, partial right dentary of *Dorcopsulus* sp. (smaller-toothed form) with  $P_3$ ,  $M_{1-2}$  and  $M_3$  protolophid, occlusal view; C, WAM 98.7.20, partial right dentary of *Dorcopsulus* sp. (smaller-toothed form) with  $M_{1-4}$ , occlusal view; D, WAM 98.7.18, partial right dentary of *Dorcopsulus vanheurni* with  $P_3$  and  $M_{2-4}$ , lateral view. Scale bar = 10 mm.

**Table 4** Dental measurements (in millimetres) for *Dorcopsulus vanheurni* and *Dorcopsulus* sp. from Toé Cave. Measurements: L = crown length; AW = crown anterior width; PW = crown posterior width.

	P <sub>3</sub> L	M <sub>1</sub> L	M <sub>1</sub> AW	M <sub>1</sub> PW	M <sub>2</sub> L	M <sub>2</sub> AW	M <sub>2</sub> PW	M <sub>3</sub> L	M <sub>3</sub> AW	M <sub>3</sub> PW	M <sub>4</sub> L	M <sub>4</sub> AW	M <sub>4</sub> PW
<i>Dorcopsulus vanheurni</i>													
WAM 98.7.18	8.0	-	-	-	4.1	3.2	3.3	4.5	3.6	3.7	4.9	3.4	3.2
T539.1	-	-	-	-	-	3.1	-	4.5	3.5	3.6	-	-	-
<i>Dorcopsulus</i> sp.													
WAM 98.7.20	-	3.7	2.5	2.6	3.7	2.8	2.8	3.9	3.1	3.2	4.2	3.1	2.8
WAM 98.7.19	7.6	3.6	2.5	2.6	3.7	2.9	2.9	3.9	3.2	-	4.5	3.3	2.9
T299.2	7.8	3.7	2.5	2.7	-	-	-	-	-	-	-	-	-

among the cranio-dental remains. The more common form (Figure 12A,D) is consistent in size and morphology with the westernmost available specimens of *D. vanheurni*, from the Kwiyawagi area (e.g. AM M17204, M17205). *Dorcopsulus vanheurni* is widespread in montane forests along the central mountain chain of New Guinea, but is absent from the isolated north coastal ranges and all island groups.

Two specimens differ from material referred to *D. vanheurni* in having appreciably narrower molars (Figure 12B,C; Table 4) and a shorter, more cuspidate P<sub>3</sub>. These specimens do not appear to represent *Dorcopsulus macleayi* of southern Papua New Guinea, the only other currently recognized species in the genus, which is larger-toothed than *D. vanheurni* and has a distinctively bulbous, cingulate P<sub>3</sub>. *Dorcopsulus* species are not known to display any sexual dimorphism in tooth size, although this sample may of course represent the exception. The intriguing alternative possibility that these specimens represent a previously unknown species will only be settled with the recovery of further material.

#### Family Pseudocheiridae (Winge, 1893)

The remains of five different ringtail possum species can be distinguished in the collections. Three of these are confidently allocated to known taxa; one is tentatively referred to a modern taxon; while the fifth is a previously unknown species which is here named as new.

#### *Petauroides ayamaruensis* Aplin, sp. nov.

Figure 13

#### Material Examined

##### Holotype

WAM 98.7.39, a fragmentary right dentary preserving M<sub>1</sub>-M<sub>4</sub> and the roots of I<sub>1</sub> and P<sub>3</sub>.

##### Other Material

WAM 98.7.45, a left dentary fragment with alveoli

for M<sub>2,4</sub>, from Unit V of Kria Cave is referred to his species. Tentatively referred postcranial specimens are: WAM 98.7.46, a right femur shaft; WAM 98.7.47, a left proximal femur fragment; WAM 98.7.48, a right proximal tibia fragment; WAM 98.7.49, a distal left femur fragment; all derive from the probably late Pleistocene lower unit of Toé Cave, on the southwestern margin of the Ayamaru Lakes.

#### Type Locality and Age

Unconsolidated cave sediments of early Holocene age in Kria Cave, 3 km east of the village Suwiam/Mapura, northeast of the Ayamaru Lakes, Ayamaru Plateau, central Bird's Head, Irian Jaya, Indonesia. Excavated from Unit V (135-140 cm depth) of Kria Cave square 1N1E, dated to c. 7500-6000 BP (Pasveer 1998).

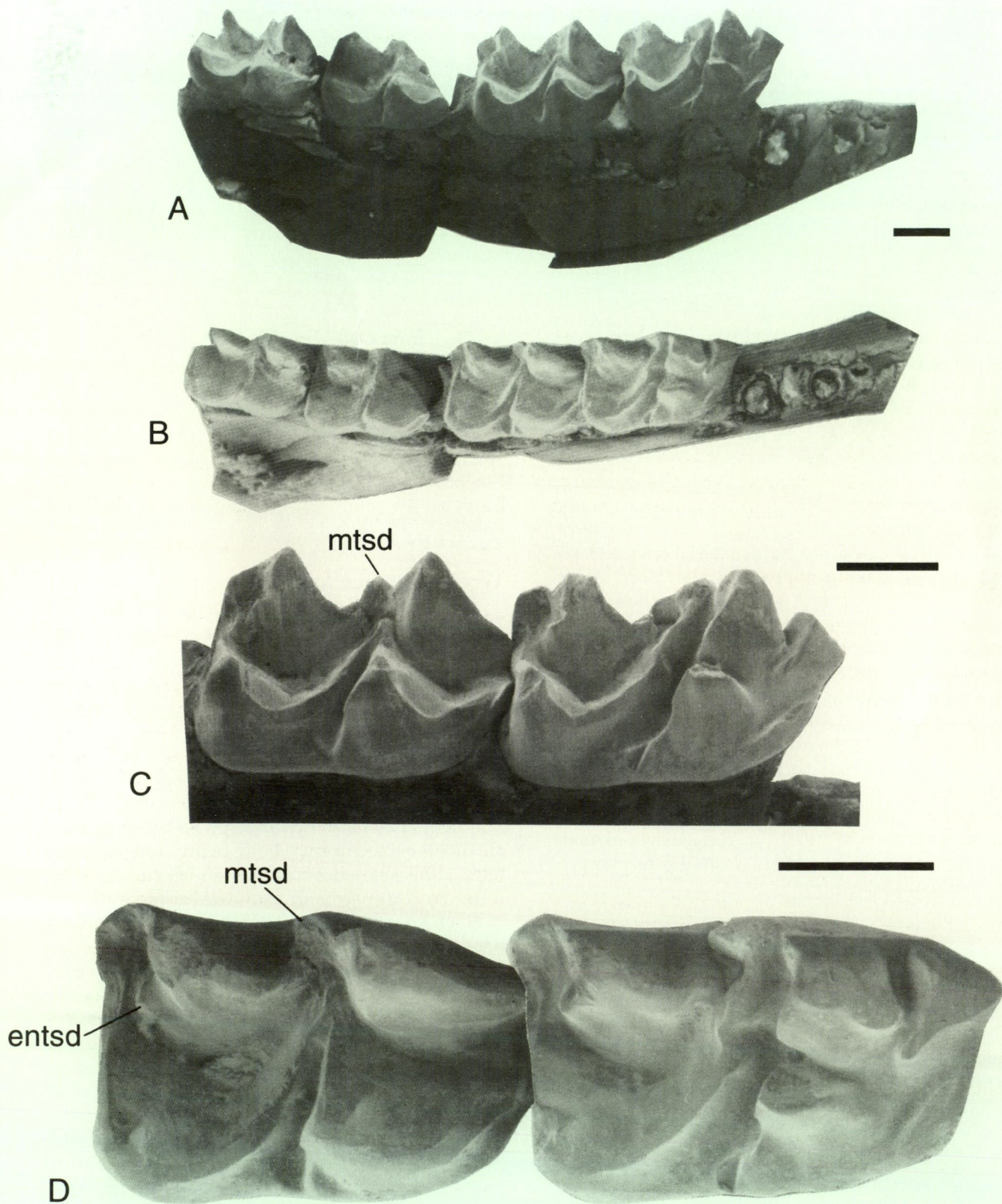
#### Diagnosis

A very small pseudocheirid species differing from all other named forms, both living and fossil, in having the following combination of characters: M<sub>1</sub> with well-developed, isolated paraconid and distinct, crested protostylid but lacking protostylid basin; M<sub>1,2</sub> with isolated entostylid ridge on posterobuccal face of entoconids; M<sub>1,4</sub> pre-entocristids swing lingually to contact metastylids; M<sub>2,4</sub> with distinct metastylids and accessory postprotocristids but lacking posterobuccal trigonid basins and with very weak anterobuccal cingula; diastemal region of dentary with reduced number of minute, unicuspid, teeth.

Differs specifically from the extant Greater Glider, *Petauroides volans*, in being considerably smaller in both tooth and jaw dimensions and having a larger, more discrete paraconid on M<sub>1</sub>, a more strongly developed anterobuccal cingulum on all lower molars and a less well developed posterobuccal metastylid crest on M<sub>1</sub>.

#### Etymology

Named for the Ayamaru Plateau and Lakes of central Irian Jaya, the only known region of occurrence of the species.



**Figure 13** Fossil mammal specimens from Kria and Toé Caves: scanning electron micrographs of WAM 98.7.39, holotype of *Petauroides ayamaruensis* sp. nov., a partial right dentary with roots of  $I_1$  and  $P_3$  and  $M_{1-4}$ . A, semiocclusal view of cheektooth series; B, occlusal view of cheektooth series; C, semiocclusal view of  $M_{1-2}$ ; D, occlusal view of  $M_{1-2}$ . Scale bars = 1 mm. Note isolated entostylid (entsd) ridge on  $M_{1-2}$ ; connection between metastylid (mstd) and pre-entocristids on  $M_{2-4}$ ; and partial enclosure of the buccal hypoflexid embrasures on  $M_{1-2}$  by ridges from the protostylid and protoconid, respectively. These are all potential synapomorphies between the new fossil species and the extant species *Petauroides volans* and *Hemibelideus lemuroides*.



## Description

### Dentary

The holotype preserves the horizontal ramus from the root of  $I_1$  back to the postalveolar shelf. The alveolar rim forward of  $M_1$  is damaged, but it preserves roots of  $P_3$  and calcite-filled vascular channels of diastemal region; ventral border broken away posterior to  $M_2$ . The referred dentary (WAM 98.7.45) has the ventral border intact and also preserves the anteroventral portion of the masseteric fossa.

Dentary of typical pseudocheirid form; mandibular symphysis terminates below anterior root of  $M_2$ ; ventral border of ramus relatively straight; ramal depth below  $M_1$  of holotype 6.0 mm, below  $M_{3,4}$  of holotype and referred specimen 5.8-5.9 mm; primary mandibular foramen positioned below centre of  $M_1$ , smaller accessory foramen below anterior root of  $P_3$ ; anteroventral border of masseteric fossa not deeply excavated; large masseteric foramen in anterior position within masseteric fossa.

### Dentition

*Incisor and Unicuspid Premolars.* Root of procumbent lower incisor 2.3 mm in depth. Alveolar rim damaged in diastemal region but clear from surviving portions that no large, deeply-rooted unicuspid teeth were present.

$P_3$ . Roots of  $P_3$  indicate a relatively short crown; posterior root larger than anterior. Alveolar length 2.1 mm.

$M_1$ . Length 3.1 mm; anterior width 1.5 mm; posterior width 1.5 mm. Protoconid highest and largest cuspid; protostylid slightly higher than metastylid; paraconid slightly lower than metastylid.

Paraconid distinct from preprotocristid; pyramidal, with three distinct crests; apex positioned near lingual margin of tooth. Preparacristid runs forward from cusp apex to form anteriormost point of tooth; lingual postparacristid overlaps preprotocristid *en echelon* to form a prominent 'lingual parastylid' *sensu* Springer (1993); buccal postparacristid less well developed but also overlaps preprotocristid *en echelon* to terminate just forward of the anterior crest of the protostylid. Anterobuccal face of paraconid supports a narrow cingulum.

Protoconid narrow, set slightly obliquely to long axis of tooth; preprotocristid descends to base of paraconid, overlapped by lingual and buccal postparacristids as described above. Postprotocristid runs posterolingually to meet short anterior crest from metastylid. Posterior surface of

protoconid with prominent buttress which is separated at base by fissures from each of the protostylid and the cristid obliqua. Lingual surface of protoconid gently convex with weak buttress leading to apex. Protostylid separated from buccal face of protoconid by deep fissure; laterally compressed, with well-developed anterior crest that runs forward to approach buccal postparacristid and more subdued posterobuccal crest that terminates in a basal cingular cuspule. This cusp expands posteriorly to form a partial buccal shelf across the hypoflexid embrasure, but without contacting the anterior surface of the hypoconid. Anterobuccal cingulum irregular, cusped; forms low but distinct shelf between protostylid and paraconid.

Metastylid distinct from postprotocristid; positioned lingual to line between protoconid and entoconid. With three distinct crests: anterior crest short, forms 90° 'step' with postprotocristid; posterolingual crest more elongate, passes lingual to overlap pre-entocristid *en echelon*; posterobuccal crest also elongate, meets prehypocristid to form composite cristid obliqua.

Tips of hypoconid and entoconid slightly damaged but clear that latter cusp slightly taller than former. Hypoconid approximately level with protostylid. Low hypoconulid forms posterolingual corner of tooth. Hypoconid apex conical, positioned at posterobuccal corner of tooth; with weak, anterolingually directed buttress. Prehypocristid descends anterior surface of hypoconid, then swings anterolingually in gentle curve to meet posterobuccal crest of metastylid. Resultant cristid obliqua clearly composite, the two components separated by a fissure. Posthypocristid runs lingually and slightly posteriorly to terminate at base of hypoconulid.

Entoconid laterally compressed, long axis parallels that of protoconid; apex positioned slightly forward of hypoconid. Pre-entocristid runs anterobuccally, then swings lingually to terminate in v-shaped pocket formed by paired posterior metastylid crests. Low shelf situated lingual to anterior end of pre-entocristid. Entostylid ridge small and isolated from postentocristid and hypoconulid; connected to posterobuccal face of entoconid by vertically-oriented crest. Hypoconulid low, narrow cusp; set oblique to long axis of tooth and forming angle of 110° with postentocristid.

$M_2$ . Length 2.7 mm; anterior width 1.6 mm; posterior width 1.7 mm. Metaconid higher than hypoconid which is subequal to entoconid. Protoconid is slightly lower than hypoconid / entoconid. All primary cuspids higher than metastylid. Protoconid positioned slightly posterior to metaconid, on buccal margin of tooth; apex conical, lingual surface broadly convex.

Preprotocristid runs short distance anteriorly before turning anterolingually; terminates in a distinct, upturned 'paraconid', approximately 0.3 mm buccal to anterior end of premetacristid. Anterior margin of tooth formed by narrow shelf between preprotocristid and premetacristid. Weak anterobuccal cingulum situated below anterolingually-directed portion of preprotocristid. Short postprotocristid runs lingually to meet anterior end of cristid obliqua. Accessory postprotocristid descends into hypoflexid embrasure, terminating in basal cingular cuspule. Metaconid high, narrow; set oblique to long axis of tooth. Buccal and lingual surfaces of metaconid with broad buttresses. Premetacristid runs anterobuccally then swings lingually; weak anterolingual cingulum present below anterior portion of premetacristid. Postmetacristid descends rear of cusp before swinging posterolingually to contact metastylid.

Metastylid positioned as in  $M_1$ , lingual to line drawn between metaconid and entoconid; adpressed against pre-entocristid but separated by distinct fissure from cristid obliqua and postprotocristid. Posterior crest forms low shelf, lingual to pre-entocristid.

Hypoconid as in  $M_1$  except that prehypocristid more evenly curved rather than flexed. Weak basal cuspule on anterobuccal face of hypoconid, partially enclosing the hypoflexid embrasure. Prehypocristid terminates in a small cuspid posterobuccal to metaconid and slightly lingual to the midline of the tooth; same cuspid also aligned with postprotocristid, but separated from the latter by a narrow fissure. Posthypocristid more nearly transverse than on  $M_1$ ; meets short posterobuccal crest from hypoconulid.

Entoconid as in  $M_1$  but lingual buttress more distinct; anterior portion of pre-entocristid swinging lingually to contact metastylid. Entostylid ridge same form and relations as in  $M_1$  but more distinctly divided from entoconid except basally.

$M_3$ . Damaged, lacking metaconid and anterolingual corner of tooth; entoconid chipped. Posterior width 1.7 mm; talonid and trigonid appear subequal in width. Protoconid subequal in height to hypoconid. Relations of metastylid and pre-entocristid as in  $M_{1,2}$ . Remaining portions of trigonid consistent with  $M_2$  trigonid except as follows: lacking anterobuccal cingulum; and accessory postprotocristid terminates on anterior surface of hypoflexid embrasure without associated cingular cuspule or buccal shelf.

Talonid consistent with that of  $M_2$  except as follows: prehypocristid runs further forward before turning lingually (result is more confined hypoflexid embrasure); anterior end of prehypocristid bifurcates, one section contacts

prominent, transversely narrow cuspid in alignment with postprotocristid (these elements separated by a distinct fissure, located at midpoint of tooth), the other section contacts posterobuccal crest from metastylid; entostylid ridge absent but entoconid with vertical ridge in equivalent position; and hypoconulid reduced, posterolingual corner of tooth formed by posthypocristid.

$M_4$ . Slightly damaged in trigonid basin and along anterior margin of tooth. Length 2.7 mm; anterior width 1.5 mm; posterior width 1.4 mm. Whole tooth more elongate and narrower than  $M_{2,3}$ . Metaconid higher than entoconid which in turn is higher than each of protoconid and hypoconid (latter cuspids subequal). All primary cuspids higher than metastylid. Relations of metastylid and pre-entocristid as in  $M_{1,3}$ . Trigonid similar in basic form to that of  $M_2$  but differs in the following ways: preprotocristid runs further forward before turning lingually (results in wider anterior shelf between preprotocristid and premetacristid); terminates in very small, upturned 'paraconid'; lingual buttress of metaconid more prominent; and accessory postprotocristid less distinct, terminates on rear surface of protoconid.

Talonid differs from that of  $M_3$  in the following ways: prehypocristid shifted further buccally, terminates just lingual to longitudinal line of protoconid apex; hypoconid with more distinct anterolingual buttress; entoconid lacks entostylid ridge or equivalent vertical crest and also without postentocristid; hypoconulid absent; posthypocristid transversely oriented, terminates in broad postentoconal shelf.

#### Referred Postcranial Material

The great bulk of the pseudocheirid postcranial material comes from the lower unit of Toé Cave, with only a small number of specimens originating from Kria Cave. The combined sample was initially divided into two groups corresponding to the larger *Pseudochirops* spp. and a second group of smaller ringtail species. Within the latter, each skeletal element was examined carefully for variation in both size and morphology. Some immature postcranial elements from the upper part of the Kria Cave deposit were excavated in association with dental material of *Pseudochirulus* sp. cf. *P. canescens* and are referred to that taxon. Among the remaining material, two subtly different size classes and morphologies were noted. The larger, more abundant form is tentatively identified as *Pseudochirulus schlegelii*, based on the relative abundance of dental remains of this species. The remaining four specimens, all derived from the lower unit of Toé Cave are tentatively referred to *Petauroides ayamaruensis*, despite the absence of associated dental remains of this taxon.

The tentatively referred femora of *Petauroides ayamaruensis* are similar in basic proportions to those of other ringtail possums and do not show any obvious elongation of the shaft of the kind which characterizes the Greater Glider, *Petauroides volans*. However, comparisons with fossil material referred to *P. schlegelii* and with modern reference specimens of *Pseudocheirus peregrinus* indicate some significant differences in morphology, most notably a flattening of the proximal femoral region producing a highly obtuse angle between the femoral head and the greater and lesser trochanters as compared with a less obtuse angle in the *Pseudocheirus* and *Pseudochirulus* spp. Among pseudocheirids available for comparison, a similar flattening of the proximal femur was observed only in *P. volans* (WAM M16197) and its closest living relative, *Hemibelideus lemuroides* (WAM M19228).

## Remarks

### Comparisons

*Petauroides ayamaruensis* is an extremely distinctive pseudocheirid which is only assigned to the extant genus *Petauroides* with considerable reservation. The following comparisons begin with the geographically proximate species of *Pseudochirulus* and then extend to the species of other extant genera of pseudocheirids including *Petauroides*. Brief comparisons are also made to the various pseudocheirid genera recorded from the mid- to late Tertiary of Australia.

The genus *Pseudochirulus* contains five extant species in New Guinea and one in Australia. Two species are known to occur on the Bird's Head Peninsula, namely *P. schlegelii* and *P. canescens*; the latter taxon and *P. mayeri* (Rothschild and Dollman, 1932) are also similar in molar size to *Petauroides ayamaruensis*. According to Springer's (1993) analysis and our own comparative studies, the lower dentition of species of *Pseudochirulus* is characterized by: marked elongation of the  $P_3$ ; a well-marked separation of the metastylid from the postmetacristid; direct contact between the metastylid and the postprotocristid; buccal convexity of the cristid obliqua; absence of an entostylid ridge on all molars; lack of connection between pre-entocristids and metastylids; moderate to strong development of anterobuccal cingula on lower molars; retention of at least one moderate-sized unicuspid tooth in the diastemal region. *Pseudochirulus canescens* evidently differs from other species of the genus and from *Petauroides ayamaruensis* in having a conical entoconid which lacks a blade-like pre-entocristid. *Pseudochirulus schlegelii* differs from *Petauroides ayamaruensis* in its larger size and in the following, additional morphological features:  $M_1$  protostylid conical, with weak anterior crest;  $M_1$  with stronger anterobuccal

cingulum;  $M_{2,4}$  cristid obliqua lacking lingual inflection, meeting accessory postprotocristids at a more buccal position on rear of trigonid;  $M_{2,4}$  preprotocristids also lack lingual inflection, anterior portions of trigonid basin between preprotocristids and premetacristids are considerably wider; all lower molars relatively broader, especially  $M_4$  which is approximately equal in length and width to  $M_3$ .

*Petauroides ayamaruensis* is similar to the species of *Pseudochirops* in the form and relations of both the preprotocristid and the cristid obliqua on  $M_{2,3}$ , and in the presence of an entostylid ridge. Some *Pseudochirops* species (e.g. *P. cupreus*) also show contact between the pre-entocristid and the metastylid, as observed in *Petauroides ayamaruensis*. *Pseudochirops* species differ from *Petauroides ayamaruensis* in their proportionally larger  $P_3$  and in many details of lower molar morphology including: presence of a protostylid basin on  $M_1$ ; presence of a distinct posterobuccal trigonid basin (incipient only in the Australian *P. dahli*); absence of accessory postprotocristids on all molars; lack of interruption of the entostylid ridge which contacts the postentocristid or hypoconulid on  $M_{1,3}$ , or  $M_{2,3}$  (*P. dahli*); presence of at least one moderately large unicuspid tooth in the diastemal region. All known species of *Pseudochirops* are also much larger than *Petauroides ayamaruensis*.

*Pseudocheirus peregrinus* (including *occidentalis*) is similar to *Petauroides ayamaruensis* in the lack of elongation of  $P_3$ , the form and relations of both the preprotocristid and the cristid obliqua, and the lack of well-developed anterobuccal cingula on  $M_{2,4}$ . In most specimens of *P. peregrinus*, the pre-entocristids are straight and pass clear of the metastylid; in occasional specimens, the anterior end of the pre-entocristid swings lingually to contact the metastylid. *Pseudocheirus peregrinus* also differs from *Petauroides ayamaruensis* in lacking entostylid ridges and having more distinct hypoconulids on all lower molars, and in having a less differentiated paraconid and more strongly crested protostylid on  $M_1$ . Two or three moderately large unicuspid teeth are usually present in the diastemal region.

*Petauroides volans* is considerably larger than *Petauroides ayamaruensis*. Nevertheless, the two species agree in numerous, detailed points of molar morphology including: the very similar position and relations of the  $M_{1,2}$  entostylid ridges; the similar size and relations of the  $M_1$  paraconid and protostylid, and the presence of a posterior protostylid crest leading to a buccal cingular cuspule and hypoflexid shelf; the form and relations of the metastylids and pre-entocristids; the form and relations of the cristid obliqua; and the presence of an accessory postprotocristid on  $M_{2,4}$ . The  $P_3$  is similarly short in both taxa and the diastemal region either lacks unicuspid teeth or supports tiny,

shallow-rooted teeth. *Petauroides volans* differs from the fossil taxon in having the  $M_1$  paraconid more firmly united to the preprotocristid; a less well-developed anterobuccal cingulum (absent from  $M_{2,4}$  in *P. volans*); and a more elongate posterobuccal metastylid crest on  $M_1$ , which makes a greater contribution to the cristid obliqua.

*Hemibelideus lemuroides* is also similar to *Petauroides ayamaruensis* in many of these same features that unite the fossil taxon with *Petauroides volans*. However, *H. lemuroides* differs from each of the other taxa in the following features:  $M_1$  protostylid higher, more strongly crested; entostylid ridges absent from  $M_{1,2}$  (although one or two vertical crests present in same position on the buccal surface of the entoconid); anterobuccal cingula absent from  $M_{2,3}$ ; small anterolingual cingula present on  $M_{2,3}$ ; posthypocristids of  $M_{2,3}$  less transverse and bowed posteriorly; anterior molars with prominent buccal shelf across hypoflexid embrasure; and  $P_3$  more elongate.

*Petauroides ayamaruensis* also warrants comparison with each of *Pseudocheirus stirtoni* Turnbull and Lundelius, 1970 and *Pseudocheirus marshalli* Turnbull and Lundelius, 1970 from the early Pliocene Hamilton Local Fauna of Victoria (Turnbull and Lundelius 1970; Turnbull *et al.* 1987b). The former taxon is very close in dental morphology to *Petauroides volans*, to the extent that Archer (1984) included *stirtoni* in *Petauroides* (see also Springer 1993). [Turnbull *et al.* (1987b), however, remained opposed to this action in the absence of any evidence that *stirtoni* was specialized for gliding.] *Pseudocheirus stirtoni* is slightly larger-toothed than *Petauroides ayamaruensis* and further differs from the recent fossil taxon in having an uninterrupted entostylid ridge on  $M_{1,3}$ , small anterobuccal cingula on all lower molars and straighter pre-entocristids which fail to meet the metastylids. In these features, *P. stirtoni* is less similar to *Petauroides volans*, and *Petauroides ayamaruensis* is more so. However, *P. stirtoni* also shows further, detailed points of similarity to those of *Petauroides volans* in its premolar and upper molar morphology and there can be little doubt of the close relationship between the two.

*Pseudocheirus marshalli* is also slightly larger than *Petauroides ayamaruensis*. The two species are similar in having an isolated entostylid ridge on  $M_{1,2}$  which fails to connect with the postentocristid. However, *P. marshalli* differs from *P. ayamaruensis* in having a more conical, uncrested protostylid on  $M_1$ . Upper molars of *P. marshalli* show fewer points of resemblance to those of *Petauroides volans*.

Geologically-earlier fossil pseudocheirids such as species of *Pildra*, *Paljara* and *Marlu* (Woodburne *et al.* 1987; Pledge 1987) differ from all recent pseudocheirids in having a shorter, simple-crowned  $P_3$ ; poorly developed  $M_1$  para- and

metaconids and protostylid; and generally lower-crowned and less strongly-crested molars. Entostylid ridges are present in some taxa (e.g. *Pildra* spp.), but always with strong connection to the postentocristid or hypoconulid. No special affinity is observed with *Petauroides ayamaruensis*. The Plio-Pleistocene species of *Pseudokoala* (Turnbull and Lundelius 1970; Turnbull *et al.* 1987b; Archer *et al.* 1997) differ from *Petauroides ayamaruensis* in their much greater size, weakly-differentiated metastylids, lack of entostylid ridges, more extensive secondary ornamentation of the trigonid and talonid basins, and foreshortening of the posthypocristid which fails to reach the lingual side of the tooth on  $M_{1,3}$ .

#### Phylogenetic Relationships

*Petauroides ayamaruensis* is clearly distinct from all described recent and fossil pseudocheirid species. The closest similarity in lower molar morphology is observed with *Petauroides volans*, the living Greater Glider of eastern Australia, and with two, potentially related, fossil species from the early Pliocene of Victoria. These similarities include several characters that are arguably apomorphic within the context of the wider pseudocheirid radiation (e.g. presence of interrupted entostylid ridge, elongation of  $M_4$ ).

The observed similarity in femoral head morphology between material tentatively referred to *Petauroides ayamaruensis* and each of *Petauroides volans* and *Hemibelideus lemuroides* may also be significant. The latter taxon possesses a rudimentary plagiopatagium along with specialized dermal musculature (Johnson-Murray 1987), and is reported to make extended leaps of 2–3 m (Walker 1983; Winter and Goudberg 1995), yet it is similar in general limb-bone proportions to other non-gliding pseudocheirid species. The lack of any extremely elongate limb elements among the fossil remains makes it unlikely that *Petauroides ayamaruensis* was a specialist glider like *P. volans*. However, some precursor adaptation such as occurs in *H. lemuroides* cannot be ruled out.

Generic placement of the new fossil species is problematic. Our initial view was that the fossil was generically distinct from all previously known pseudocheirids. However, after more detailed comparisons, we are now of the opinion that the new taxon is most likely monophyletic with *Petauroides volans*; and furthermore, at least in regard to lower molar morphology, that the fossil taxon differs from the living species only in relatively trivial features (e.g. size). Accordingly, we refer *ayamaruensis* to the extant genus *Petauroides*, but not without considerable reservation.

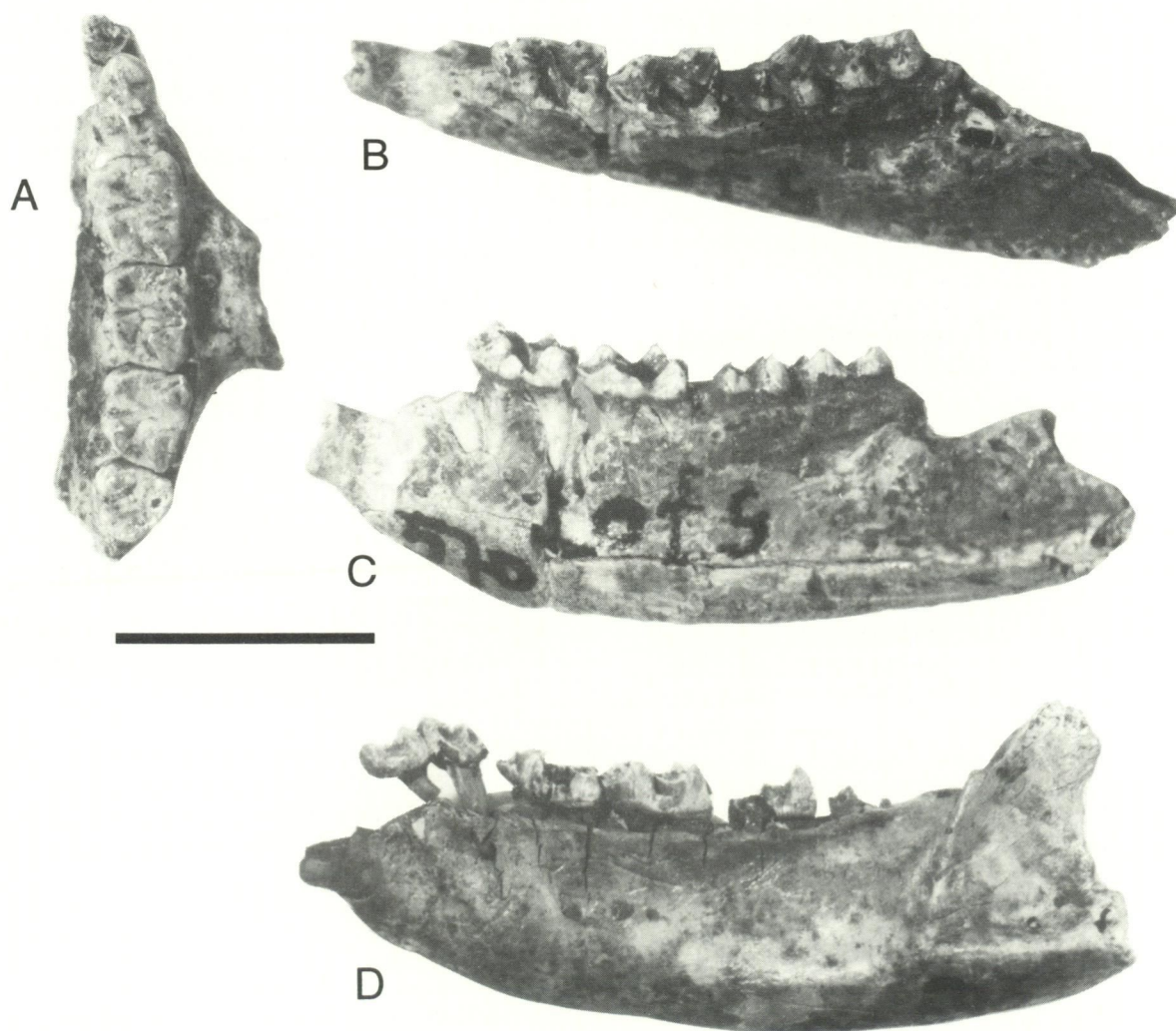
One major cause of concern is that many of the dental characteristics (e.g. entostylid development, metastylid relations) which are used to diagnose

certain pseudocheirid lineages, are also demonstrably variable at an individual or inter-population level. With such limited material of the new taxon, we cannot rule out the possibility that some of the apparent special similarities to *Petauroides volans* represent individual rather than specific features. Discovery of the upper molars of *Petauroides ayamaruensis* might help remove some of this uncertainty through provision of a wider suite of dental characters for analysis. A second reason for concern is that the phyletically distinct and well-established clade comprised of *Petauroides volans* and *Hemibelideus lemuroides* (McQuade 1984; Baverstock *et al.* 1990; Springer *et al.* 1992) is not otherwise represented in the New Guinean mammal fauna. However, it should be noted that several other pseudocheirid genera (*Pseudochirops*, *Pseudochirulus*) have representatives in both Australia and the New Guinea regions [see Aplin *et al.* (1993) for a general discussion of Australian-New Guinean faunal interchange]. And finally,

mirroring the concerns of Turnbull *et al.* (1987b) regarding generic allocation of *P. stirtoni*, the few postcranial elements which might conceivably belong to *Petauroides ayamaruensis* are similar in proportions to those of other pseudocheirids (including the 'leaping' *H. lemuroides*) and lack the extreme elongation seen in the major limb elements of *Petauroides volans*. If this new pseudocheirid is indeed a close relative of *Petauroides volans*, then we predict that it is not a glider, but perhaps a 'leaper' along the lines of *Hemibelideus lemuroides*.

#### Natural History

The remains of *Petauroides ayamaruensis* are confined to the lowermost unit of the Kria Cave deposit, with some tentatively referred postcranial material coming from the lower unit of Toé Cave. The fauna from these levels contains a number of typically montane species and it is possible that *Petauroides ayamaruensis* was also part of this higher-elevation faunal assemblage.



**Figure 14** Fossil mammal specimens from Kria and Toé Caves: A, WAM 98.7.28, partial left maxilla of *Pseudochirops albertisii* with  $P^3$  and  $M^{1-4}$ , occlusal view; B, WAM 98.7.29, partial left dentary of *Pseudochirops albertisii* with roots of  $I_1$  and  $P_3$ , and  $M_{1-4}$ , occlusal view; C, WAM 98.7.29, lateral view; D, WAM 98.7.30, partial left dentary of *Pseudochirops coronatus* with root of  $I_1$ ,  $P_3$  (displaced), and  $M_{1-4}$ , lateral view. Scale bar = 10 mm.

*Pseudochirops albertisii* (Peters, 1874)

This species is identified from several well-preserved maxillae and dentaries from the lower unit in Toé Cave (Figure 14A–C). These compare closely to modern specimens from near the type locality in the Arfak Mountains.

*Pseudochirops albertisii* is found only in montane forest above 1000 m elevation. Flannery (1995a) reported that in the Arfak Mountains, *P. albertisii* currently occupies secondary forest, being displaced in primary forest by its congener *P. coronatus*.

*Pseudochirops coronatus* (Thomas, 1897)

This species was only recently resurrected from synonymy within *P. albertisii* by Flannery (1995a). It is currently restricted to primary forest above 1000 m elevation in the Arfak Mountains.

*Pseudochirops coronatus* can be distinguished from *P. albertisii* by its slightly larger molars and proportionally more elongate third premolars. The fossil material of *P. coronatus* includes one well-preserved dentary with  $P_3$ - $M_3$  (Figure 14D), as well as several less complete specimens.

Fossil remains of both *Pseudochirops* species are most abundant in the lower unit of Toé Cave. We have not attempted to identify postcranial material below the generic level.

*Pseudochirulus* sp. cf. *P. canescens* (Waterhouse, 1846)

Four isolated molar teeth and a variety of postcranial elements, all from the upper levels of Kria Cave, are tentatively referred to a member of the *Pseudochirulus canescens* complex. The teeth represent several individuals at different stages of dental wear. Measurements are given in Table 5.

Members of the *P. canescens* complex are widely distributed through lowland habitats of New Guinea and extend to Salawati and Japen Islands. Tate (1945b) recognized five subspecies of *P. canescens*, including three from Irian Jaya: *canescens* (type locality: Triton Bay), *bernsteini* Schlegel, 1866 (type locality: Salawati Island) and *dammermani* Thomas, 1922 (type locality: "Netherland New Guinea"). The group is in need of comprehensive revision.

The only modern specimen of *P. canescens* from western New Guinea available for comparison has very worn teeth. Specimens from further east in Papua New Guinea (e.g. AM M15365, from Mt Sisa) are similar to the fossil taxon in having relatively narrow upper molars and conical rather than the more typically crested entoconids on the lower molars, but differ in other details of morphology. Direct comparisons with topotypic material of *Pseudochirulus mayeri* at the Museum of Natural History, Leiden, revealed more significant differences in cusp morphology and molar proportions.

*Pseudochirulus schlegelii* (Jentink, 1884)

Recent work by Musser and Sommer (1992) and Flannery (1995a) has done much to clarify the status of this poorly known species. At the present time, it is apparently restricted to the Arfak Mountains, where it has been recorded from elevations between 750 m and 1900 m.

*Pseudochirulus schlegelii* is identified from several well-preserved dentaries from the lower unit of Toé Cave (Figure 15A,B); other, less complete cranial and postcranial material occurs in the same levels. These specimens are indistinguishable in size and

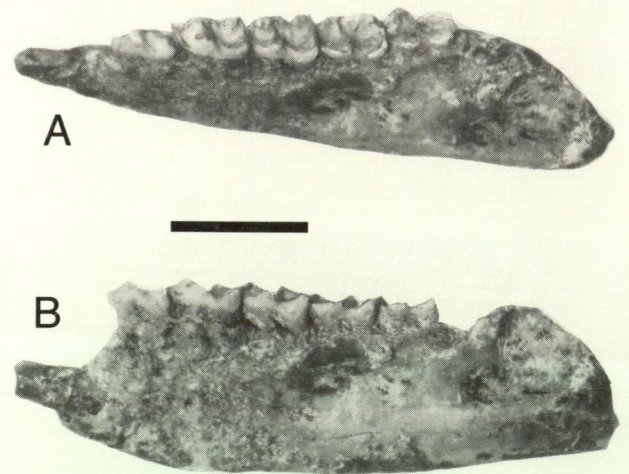


Figure 15 Fossil mammal specimens from Kria and Toé Caves: WAM 98.7.31, partial left dentary of *Pseudochirulus schlegelii* with root of  $I_1$ ,  $P_3$  and  $M_{1-4}$ . A, semiocclusal view; B, lateral view. Scale bar = 10 mm.

Table 5 Dental measurements (in millimetres) for *Pseudochirulus* sp. cf. *P. canescens* from Kria Cave. Measurements: L = crown length; AW = crown anterior width; PW = crown posterior width.

	M <sup>1</sup> L	M <sup>1</sup> AW	M <sup>1</sup> PW	M <sup>2</sup> L	M <sup>2</sup> AW	M <sup>2</sup> PW	M <sup>3</sup> L	M <sup>3</sup> AW	M <sup>3</sup> PW	M <sub>4</sub> L	M <sub>4</sub> AW	M <sub>4</sub> PW
K648.1	2.8	2.2	2.2	–	–	–	–	–	–	–	–	–
K638.1	–	–	–	2.6	2.3	2.1	–	–	–	–	–	–
K648.2	–	–	–	–	–	–	2.6	2.2	2.0	–	–	–
K648.3	–	–	–	–	–	–	–	–	–	3.1	1.7	1.8

morphology from modern 'trophy' jaws collected by Flannery in the Arfak Mountains.

### Family Petauridae Gill, 1872

#### *Dactylopsila* Gray, 1858

Remains of *Dactylopsila* are not especially abundant in either deposit but they are nonetheless of great interest. Three taxa are clearly recognizable among the material. Two of these can be referred to the extant species *D. palpator* and *D. trivirgata*. The third is represented in the Kria fauna by a selection of fragmentary dentaries and isolated incisors which are substantially smaller than the associated specimens of *D. trivirgata* and smaller than any previously named member of the genus. They are here described as a new species.

#### *Dactylopsila palpator* Milne-Edwards, 1888

An edentulous but otherwise fairly well preserved dentary (Figure 16A) from the lower unit of Toé Cave is confidently referred to this species. It is readily distinguished from the more abundant remains of *D. trivirgata* from Kria Cave by the more forward extension and greater depth of the masseteric fossa and by the shorter, more steeply sloping diastema between the cheektooth row and the massive  $I_1$  alveolus. Several postcranial elements from the lower unit of Toé Cave are also referred to this species.

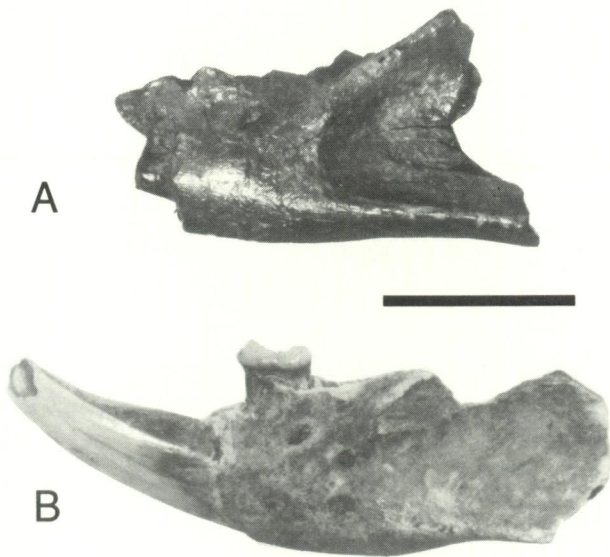


Figure 16 Fossil mammal specimens from Kria and Toé Caves: A, WAM 98.7.32, partial left dentary of *Dactylopsila palpator* with root of  $I_1$  but otherwise edentulous, lateral view; B, WAM 98.7.33, partial left dentary of *Dactylopsila trivirgata* with  $I_1$  (missing tip) and  $M_1$ , lateral view. Scale bar = 10 mm.

*Dactylopsila palpator* is most common in upper montane habitats but may occur as low as 1200 m elevation (Ziegler 1982). A modern specimen collected by Flannery in the Arfak Mountains (AM M29254) agrees with the fossil specimen in all particulars.

#### *Dactylopsila trivirgata* Gray, 1858

This species is represented by a fairly well preserved dentary with  $I_1$  and  $M_1$  (Figure 16B), as well as several other edentulous dentaries and a small number of isolated molars and lower incisors. These specimens agree in all details with reference material of *D. trivirgata* (including topotypic material: WAM M42624 from the Aru Islands) and are readily distinguishable from both *D. palpator* and *D. megalura* Rothschild and Dollman, 1932, the latter of which is confined to montane forests along the central cordillera of western New Guinea (Flannery 1995a). Further points of comparison among these species are noted below, following the description of a new, diminutive striped possum.

*Dactylopsila trivirgata* is widespread in lowland and lower montane habitats of New Guinea and is known from several localities on the Bird's Head. It is present at several levels within the Kria Cave deposit but is represented by only a single postcranial element in Toé Cave.

#### *Dactylopsila kambuayai* Aplin, sp. nov.

Figure 17

#### Material Examined

##### Holotype

WAM 98.7.40, a fragmentary right dentary preserving  $I_1$ ,  $M_2$  and the roots of  $M_1$  and  $M_3$ - $M_4$ .

##### Paratypes

WAM 98.7.50, fragmentary left dentary with  $I_1$  and alveoli for  $M_1$ - $M_4$ ; WAM 98.7.51, fragmentary right dentary with  $I_1$  and alveoli for  $P_3$ - $M_4$ ; WAM 98.7.52, fragmentary right dentary with  $I_1$  and alveoli for  $M_1$ - $M_4$ ; WAM 98.7.53, fragmentary left dentary with alveoli for  $M_1$ - $M_4$ ; and WAM 98.7.54, isolated  $I_1$ ; all paratypes from Kria Cave, levels IV1 (85-90 cm depth square 1N1E) to V5 (145-150 cm depth square 0N0E).

##### Other Material

WAM 98.7.55, a right distal humeral fragment, and WAM 98.7.56, a left ilium fragment, are tentatively referred to this species.

#### Type Locality and Age

Unconsolidated cave sediments of mid-Holocene age in Kria Cave, 3 km east of the village Suwiam/

Mapura, northeast of the Ayamaru Lakes, Ayamaru Plateau, central Bird's Head, Irian Jaya, Indonesia. Holotype recovered from Unit V (135–140 cm depth) of Kria Cave square 0N0E. Unit V is dated to c. 7500–6000 BP (Pasveer 1998).

### Diagnosis

A diminutive, small-toothed species of *Dactylopsila*, with deeply-excavated masseteric fossa and anteriorly-positioned ascending ramus. Length of  $M_2$  less than  $2/3$  that of stratigraphically-associated specimen of *D. trivirgata*.  $M_2$  further differs from *D. trivirgata* in lack of well-differentiated 'paraconid', lack of continuity between premetacristid and anterior margin of tooth and more lingual position of the protoconid and hypoconid. Differs from *D. palpator* in smaller size of jaw and teeth, and  $M_2$  with less bulbous lingual cusps. Differs from *D. megalura* in smaller size, more anterior placement of masseteric fossa and ascending ramus and more steeply upturned distal third of  $I_1$ . Differs from *D. tatei* Laurie, 1952 in smaller size of lower jaw and teeth and lesser development of pre- and post-metacristids on  $M_2$ .

### Etymology

Named after Elimas Kambuaya, SMP1

schoolteacher at Mefkajim/Ayamaru, in recognition of his assistance with all aspects of the archaeological excavations in Toé and Kria Caves and for his continued interest in the modern fauna and archaeology of the Ayamaru region.

### Description

#### Dentary

Dentary basically similar in form to other members of genus, but extremely small (Figure 17A; Table 6). Masseteric fossa deeply excavated, extending forward to below the posterior root of  $M_3$ . Leading edge of ascending ramus level with anterior root of  $M_3$ . Mental foramen positioned below anterior root of  $M_2$ , opening forwards.

Number of teeth forward of  $M_1$  uncertain because of damage to all specimens. All molars with undivided anterior and posterior roots. Combined length of alveoli  $M_1$ – $M_4$  8.3 mm in WAM 98.7.50; alveolar lengths  $M_1 > M_2 = M_3 > M_4$ .

#### Dentition

$I_1$ . With typical *Dactylopsila* form but root relatively slender, crown relatively short with distal third strongly upturned, enamel relatively thin and does not extend as far down root as in *D. palpator*.

**Table 6** Dental and jaw measurements (in millimetres) for *Dactylopsila kambuayai* sp. nov. compared with specimens of *D. trivirgata* from Kria Cave, *D. palpator* from Toé Cave, and modern specimens of *D. trivirgata*, *D. palpator*, *D. tatei* and *D. megalura*. The modern specimen of *D. trivirgata* is from Wokam, Aru Islands and is therefore topotypic. Measurements: C = crown; D = depth; L = length; aL = alveolar length; AW = crown anterior width; PW = crown posterior width; Dent D = dentary depth below  $M_2$ .  $I_1$  crown depth is measured at the base of the enamel;  $I_1$  crown length is measured from the incisor tip to the base of the enamel cap, on the ventral border of the tooth.

	$I_1$ CD	$I_1$ CL	$M_1$ aL	$M_2$ aL	$M_1$ L	$M_1$ PW	$M_2$ L	$M_2$ AW	$M_2$ PW	Dent D
<i>D. kambuayai</i>										
WAM 98.7.40	4.0	–	–	–	–	–	2.3	1.7	1.8	6.8
WAM 98.7.51	4.2	–	2.5	2.1	–	–	–	–	–	–
WAM 98.7.52	4.1	13.7	–	2.1	–	–	–	–	–	–
WAM 98.7.53	–	–	2.6	2.3	–	–	–	–	–	–
WAM 98.7.54	4.1	12.7	–	–	–	–	–	–	–	–
WAM 98.7.50	4.1	12.6	–	2.2	–	–	–	–	–	6.7
<i>D. trivirgata</i>										
WAM 98.7.33	4.8	–	–	2.9	3.8	2.4	–	–	–	9.3
K766.1	4.8	17.2	2.8	2.6	–	–	–	–	–	–
K1008.2	–	–	–	2.8	–	–	–	–	–	–
WAM M42624	4.9	17.1	–	–	3.4	2.2	2.6	2.0	2.1	9.3
<i>D. palpator</i>										
WAM 98.7.32	–	–	3.6	2.8	–	–	–	–	–	8.5
ANU M170	5.8	17.5	3.5	2.6	3.5	2.5	2.6	2.3	2.3	9.9
<i>D. tatei</i>										
AM M27900	–	–	–	–	–	–	2.7	2.3	2.2	–
<i>D. megalura</i>										
AM M32374	–	–	–	–	–	–	3.2	2.3	2.2	–



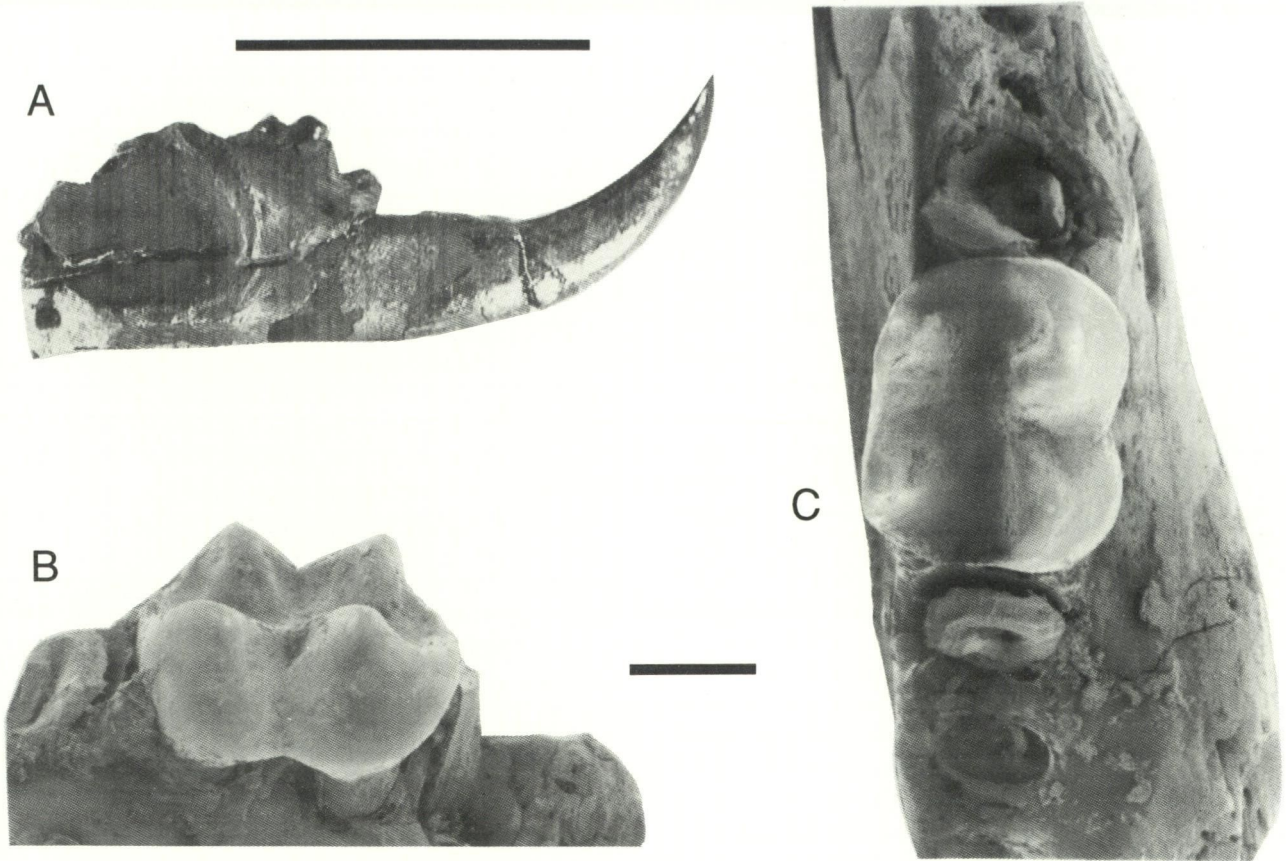


Figure 17 Fossil mammal specimens from Kria and Toé Caves: WAM 98.7.40, holotype of *Dactylopsila kambuayai* sp. nov., a partial right dentary retaining  $I_1$  and  $M_2$ . A, lateral view; B,  $M_2$  in semiocclusal view; C,  $M_2$  in occlusal view. Scale bars = 10 mm for A and 1 mm for B-C.

$M_2$ . Occlusal outline rectangular, talonid slightly wider than trigonid (Figure 17B,C). Overall crown morphology bunodont, with four principal cusps positioned in each of four major quadrants and enclosing central longitudinal valley. Lingual cusps (metaconid and entoconid) are slightly higher than those on the buccal side of the tooth (protoconid and hypoconid). Protoconid positioned approximately 2/5 of the way across tooth from buccal margin, buccal face steeply inclined and bearing faint basal cingulum. Cusp apex conical; lingual surface with broad buttress. Preprotocristid runs forward to base of cusp then swings anterolingually to terminate approximately half way across front of tooth. No trace of 'paraconid' at anterobuccal corner of tooth. Talonid basin opens onto anterior margin of tooth. Postprotocristid very short, runs posterolingually to meet prehypocristid (cristid obliqua). Metaconid positioned on lingual margin of crown, slightly forward of protoconid. Cusp apex conical, lingual surface vertical, buccal surface flattened. Three distinct crests originate from just below cusp apex: premetacristid passes straight forward to terminate at anterolingual

corner of tooth; accessory premetacristid runs in anterobuccal direction to terminate in the trigonid basin; postmetacristid runs back along lingual margin of tooth to meet pre-entocristid. Postmetacristid longest of three crests. Hypoconid positioned approximately 1/3 of way across tooth from buccal margin, slightly buccal to protoconid, buccal face steeply inclined and encircled by faint basal cingulum. Cusp apex conical, lingual surface flattened. Prehypocristid (cristid obliqua) straight, runs anterolingually to meet postprotocristid; union of the two crests producing a small buccal fossette at hypoflexid. Posthypocristid swings lingually to merge smoothly with posterior margin of talonid basin. Entoconid positioned on lingual margin of tooth, slightly forward of hypoconid. Cusp apex conical, lingual surface vertical, buccal surface convex but lacking buttress. Pre- and postentocristids of equal length. Pre-entocristid straight, runs forward along lingual margin of tooth to meet postmetacristid. Postentocristid runs posteriorly to terminate at posterolingual corner of tooth. Talonid basin opens onto posterior margin of tooth.

## Remarks

### Comparisons

The relatively great depth of the lower jaw and massiveness of the lower incisor of *Dactylopsila kambuayai* serve to associate the fossil species with the striped possums, and to distinguish it from all other described diprotodontians, including the similar-sized *Petaurus abidi* Ziegler, 1981 of the Torricelli Mountains. A total of 13 species-level taxa has been proposed within *Dactylopsila* (including *Dactylonax*). Tate and Archbold (1937) provided measurements of the type material of most named forms, and Tate (1945c) later commented on type material not examined during the earlier study. Laurie (1952) subsequently described *D. tatei* from West Fergusson Island off the eastern end of Papua New Guinea. Recent accounts of the genus (Flannery 1995a, 1995b) list four species, namely *D. megalura*, *D. palpator*, *D. tatei* and *D. trivirgata*. The last species has several weakly differentiated geographic races (Tate 1945c; Laurie and Hill 1954). The genus has not been subject to critical review since Tate (1945c), and a major revision is long overdue.

A summary of the available external body and dental measurements of various type specimens is given in Table 7, along with data on several topotypic specimens. These data indicate a general uniformity in body size across the majority of named forms, with the exception of *D. tatei* which is significantly smaller-bodied and smaller-toothed. Two taxa have been described from the Bird's Head region, namely *D. albertisii* Peters and Doria, 1875 (= *D. angustivittis* Peters and Doria, 1880; proposed as a potential replacement name) and *D. arfakensis* Matschie, 1916. Tate (1945c) recognized these

western forms as a distinct subspecies, *D. trivirgata albertisii*, but Laurie and Hill (1954) listed them under the typical form. Dental measurements of the holotype of *arfakensis* demonstrate that it is a large-toothed form, equivalent in molar size to nominotypical *trivirgata* from the Aru Islands. Unfortunately, dental measurements are not available for the holotype of *D. albertisii*; however in all external measurements this form is evidently within the size range of *trivirgata*.

The fragmentary dentaries and few available teeth of *D. kambuayai* indicate that it is considerably smaller than any other named member of the genus (Table 6). In addition, morphological differences in the jaws and teeth provide some useful characters by which to distinguish the various currently recognized forms.

**Dentary.** The dentary of *D. kambuayai* is most similar to that of *D. palpator* and *D. tatei* (AM M27900), most notably in the forward placement and degree of excavation of the masseteric fossa, and in the form of the mental foramen which opens forward in each case. The dentary of *D. trivirgata* generally has a less deeply excavated masseteric fossa and the mental foramen opens vertically. The dentary of *D. megalura* is quite distinctive, with a posteriorly positioned and lower-angled ascending ramus.

**Lower Incisor.** The  $I_1$  of *D. kambuayai* is most similar to that of *D. trivirgata* and *D. tatei* but is substantially smaller. The  $I_1$  of *D. palpator* is more heavily enamelled and has a more robust root. *Dactylopsila megalura* has a less strongly curved  $I_1$ . The robust, upwardly curving  $I_1$  of all *Dactylopsila* species differs markedly from the more gracile and gently inclined

**Table 7** Selected measurements (in millimetres) on holotypes or topotypic material for all named taxa within *Dactylopsila* (including *Dactylonax*). The majority of the data are drawn from Tate and Archbold (1937). The hindfoot measurement for the holotype of *D. albertisii* comes from van der Feen (1962). Data for *D. tatei* and *D. palpator* are from Laurie (1952). Data for topotypic *D. trivirgata* are for WAM M42624, an adult female from Wokam, Aru Islands. Measurements: HB = head + body length; TL = tail length; Pes (s.u.) = pes length, without claw; CBL = cranium condylobasal length;  $M^{1-3}$  = length of  $M^{1-3}$ .

Taxon	Material	HB	TL	Pes (s.u.)	CBL	$M^{1-3}$
<i>trivirgata</i>	Topotypic	200	290	41	51.6	8.5
<i>albertisii</i>	Holotype	260	325	40	—	—
<i>arfakensis</i>	Holotype	320	330	45	55.7	9.0
<i>biedermanni</i>	Holotype	240	310	45	50.2	8.7
<i>hindenburgi</i>	Holotype	—	—	—	50	—
<i>infumata</i>	Holotype	273	347	46	55.5	—
<i>kataui</i>	Topotypic	213–259	260–302	45–47	—	9.0–9.3
<i>melampus</i>	Topotypic	220–327	243–398	44–52	—	—
<i>occidentalis</i>	Holotype	250	320	50	49.7	8.6
<i>pictata</i>	Holotype	275	320	44	—	9.6
<i>tatei</i>	Type series	173–213	262–286	42–46	43.6–48.8	8.0–8.5
<i>palpator</i>	Topotypic	196–255	194–236	43–50	45.5–57.9	8.2–9.3
<i>ernstmayeri</i>	Topotypic	215	190	51	54.1	9.1
<i>megalura</i>	Co-types	200–215	280–285	43–45	—	—

lower incisors present in all *Petaurus* species and in *Gymnobelideus leadbeateri* McCoy, 1867.

$M_2$ . The  $M_2$  of *D. trivirgata* differs from that of *D. kambuayai* in several significant respects, viz the protoconid and hypoconid are positioned closer to the buccal margin of the tooth, resulting in a less steeply inclined buccal surface; the anterobuccal corner of the tooth bears a distinct 'paraconid' (probably a neomorphic parastylid) separated from the protoconid by a fissure; the premetacristid is more strongly developed, while the accessory premetacristid is indistinct; the cristid obliqua runs anteriorly to meet the postprotocristid, hence the buccal hypoflexid pocket is weakly developed; and the postentocristid is far stronger, swinging buccally to meet the posthypocristid at a point about midway across the rear of the tooth.

The  $M_2$  of *D. palpator* is more similar to that of *D. kambuayai* but differs in being slightly broader anteriorly and in having more bulbous lingual surfaces to the metaconid and entoconid. *Dactylopsila palpator* has significantly larger teeth than the fossil taxon.

The  $M_2$  of *D. tatei* is similar to that of *D. kambuayai* in having lingually-placed protoconid and hypoconid and a distinct buccal hypoflexid pocket, but differs in having a better developed 'paraconid' and stronger pre- and postmetacristids.

The only specimen of *D. megalura* available for comparison has extremely worn teeth and no meaningful comparisons can be made.

The  $M_2$  is relatively narrower in all species of *Petaurus* species and further differs from those of all *Dactylopsila* species, including *D. kambuayai*, in having more prominent transverse crests originating from each of the four principal cusps. Based on measurements provided by Turnbull *et al.* (1987a), *Dactylopsila kambuayai* is similar to *P. norfolkensis* in  $M_2$  width but closer to *P. breviceps* in  $M_2$  length.

*Postcranial Elements.* The referred humeral fragment is more similar to that of *D. palpator* than *D. trivirgata*, most notably in the greater elongation of the humeral shaft between the origin of the lateral process and the expansion of the deltoid crest. The width of the shaft at this point is 3.0 mm, compared with 3.25 mm in *D. palpator* and 3.8 mm in *D. trivirgata*. The referred, partial ilium is likewise closest to that of *D. palpator* in morphology, these species together sharing a short ilial shaft compared with the long shaft of *D. trivirgata*.

#### Phylogenetic Relationships

*Dactylopsila kambuayai* is most similar in its known craniodental and postcranial morphology to *D. palpator* and *D. tatei*, and less so to either *D. trivirgata* or *D. megalura*. The polarity of the

postcranial features is difficult to determine on account of the highly specialized nature of the postcranial skeleton in members of the Petaurinae, the immediate sister-taxon of Dactylopsilinae. However, meaningful comparisons can be made in the case of the craniodental features.

Of the various species of *Dactylopsila*, *D. trivirgata* is perhaps closest in  $M_2$  morphology to species of *Petaurus*. Particular points of similarity include the buccal placement of the protoconid and hypoconid, and corresponding poor development of the buccal hypoflexid fossette; the presence of a distinct 'paraconid' (albeit somewhat less isolated from the protoconid in *Petaurus*); and the strongly developed premetacristid which swings anterobuccally to form the anterior margin of the trigonid basin. These numerous points of similarity with *Petaurus* spp. suggest that *D. trivirgata* has diverged relatively little in molar morphology from an ancestral petaurine condition. In contrast, *D. kambuayai* and *D. palpator* share a suite of apparently derived conditions including lingual displacement of the protoconid and hypoconid, resulting in formation of a buccal hypoflexid fossette, reduction or loss of the 'paraconid', and reduction of the premetacristid. Several of these features are apparently also present in *D. tatei*. *Dactylopsila kambuayai*, *D. palpator* and *D. tatei* also share an undeniably derived shortening of the diastemal region and forward placement of the ascending ramus of the dentary, associated with an overall shorter, broader facial skeleton.

These limited comparisons point to a possible close relationship between *D. kambuayai* and each of *D. tatei* of Fergusson Island and the highly specialized *D. palpator* of montane New Guinea. Flannery (1995b) has previously noted similarities in body proportions and coloration between *D. tatei* and *D. palpator*. *Dactylopsila tatei* is restricted to primary forest above 600 m elevation on Fergusson Island.

#### Natural History

The remains of *Dactylopsila kambuayai* occur together with those of *D. trivirgata* in several units of the Kria Cave deposit and it is likely that the two species occurred sympatrically in lowland rainforest around the site. *Dactylopsila kambuayai* is absent from the lower unit of Toé Cave which contains the remains of *D. palpator* and *D. trivirgata* (rare), along with a wide variety of characteristic elements of the present day montane fauna. Given the possible special relationship between *D. kambuayai* and *D. palpator*, it is tempting to interpret their stratigraphic distributions as a manifestation of altitudinal sibling replacement, *D. kambuayai* displacing *D. palpator* as the 'second' striped possum in the Ayamaru region following the environmental change from 'montane' to 'lowland' habitats during the early to mid Holocene. Many

examples of altitudinal sibling replacement are documented in the modern vertebrate fauna of New Guinea (Taylor *et al.* 1982; Donnellan and Aplin 1989; Flannery 1995a).

Measurements of the lower jaw and  $M_2$  of *D. kambuayai* are between 66% and 82% of the equivalent dimensions in *D. palpator*, while the width of the humeral shaft is 85% that of *D. palpator*. These linear differences probably translate into a difference in body weight of around 60-70% (i.e. a body weight of around 200-250 g might be anticipated for *D. kambuayai*).

The absence of remains of *D. kambuayai* above Unit IV in Kria Cave suggests that it may have become locally extinct in the immediate vicinity of the Ayamaru Lakes, perhaps as a consequence of human activities. However, other parts of the Bird's Head are less heavily disturbed and there is no reason why it should not persist somewhere in the region. The fact that *D. kambuayai* has not been collected in the more intensively surveyed Lorentz (Noord) and Mamberano River basins and the Weyland Range to the east in Irian Jaya (Frodin and Gressitt 1982), makes it unlikely that *D. kambuayai* will be found as a living animal outside of the Bird's Head region.

#### *Petaurus breviceps* Waterhouse, 1838

This species is represented by two isolated lower incisors from Kria Cave (K756.1, K1035.2), and a partial humerus from a core sample of uncertain stratigraphic provenance in Toé Cave. The incisors are a good match with the lower incisor of West Sepik Province *P. breviceps* and are considerably smaller than the equivalent tooth of *P. abidi*.

*Petaurus breviceps* occurs throughout the New Guinea region, from sea level to the limit of tree growth (Flannery 1995a, 1995b); it is known from several localities on the Bird's Head Peninsula. *Petaurus abidi* is still known only from the Torricelli Range where it is most abundant in disturbed forest at around 1000 m elevation (Flannery 1995a). On zoogeographic grounds, *P. abidi* might be expected to occur on the Bird's Head, mirroring the distributions of *Dendrolagus inustus* and *Pseudochirops albertisii*. However, the fossil assemblages provide no evidence of the past or present occurrence of *P. abidi* in the Ayamaru region.

#### Supercohort Placentalia Owen, 1837

#### Order Rodentia Bowdich, 1821

#### Family Muridae Illiger, 1815

#### *Hydromys chrysogaster* Geoffroy, 1804

The Common Water-rat is represented by a

partial dentary from Kria Cave (K702.1) retaining the  $M_2$  ( $L = 3.7$ ;  $W = 2.6$ ) and the lower incisor root. This specimen is comparable in morphology but slightly larger than AM M17734 from the Thurnwald Range, West Sepik Province. The  $M_2$  of *H. chrysogaster* is much narrower for its length than the  $M_2$  of *Parahydromys asper* and also lacks the anterobuccal expansion seen in the latter species. Other New Guinean species of *Hydromys* are considerably smaller-bodied and smaller-toothed than *H. chrysogaster* (Musser and Piik 1982; Flannery 1995a).

*Hydromys chrysogaster* is widely distributed throughout the New Guinea region from sea level to 1900 m elevation and is also found on islands to the west of New Guinea (Flannery 1995a, 1995b). It has not previously been recorded from the western part of Irian Jaya, probably as a consequence of limited collecting effort in suitable habitats.

#### *Mallomys* sp. cf. *M. aroensis* (De Vis, 1907)

A species of *Mallomys* is represented by several well-preserved dentaries containing teeth (Figure 18), as well as various postcranial elements. The dental material agrees closely with a modern specimen obtained recently by Flannery (1995a) in the Arfak Mountains and referred by him to *M. aroensis*. However, the modern Arfak specimen differs in some respects from typical *aroensis* (Flannery *et al.* 1989) and we therefore remain uncertain as to the specific identity of the Bird's Head *Mallomys*.

All *Mallomys* species are restricted to montane habitats (Flannery 1995a). The fossil specimens all come from the lower unit of Toé Cave.

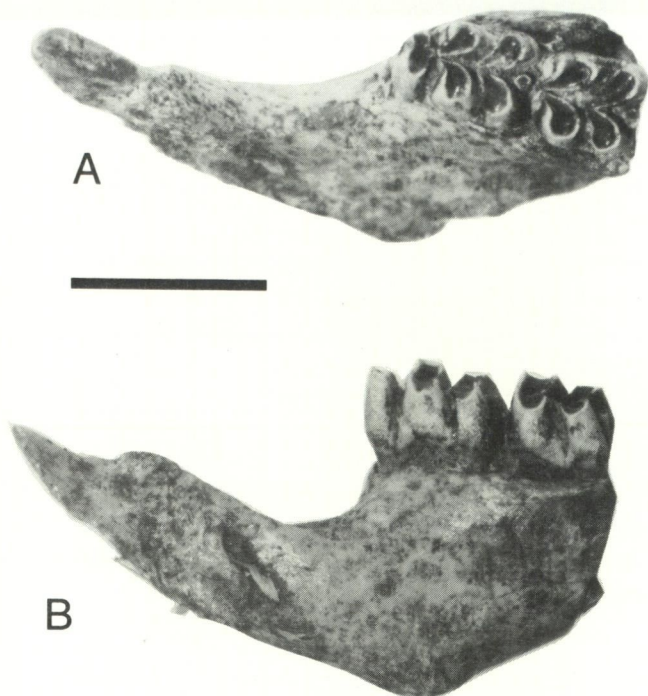
#### *Parahydromys asper* (Thomas, 1906)

An edentulous, but otherwise well-preserved, dentary from Kria Cave represents this species. The  $M_{1,2}$  alveolar length of 9.8 mm is slightly larger than in specimens from the Southern Highlands Province of Papua New Guinea (e.g. AM M18563).

*Parahydromys asper* is widely distributed in lower to mid-montane habitats throughout New Guinea and has recently been recorded from the Arfak Mountains [P.A. Woolley pers. comm. to Flannery (1995a)].

#### *Paramelomys* Rümmler, 1936

*Paramelomys* (formerly part of *Melomys*) is a complex genus with several taxa still in need of revision (Menzies 1996). Nevertheless, identification of fragmentary fossil material may be attempted on the basis of tooth size and known geographic distributions. *Paramelomys* species can be



**Figure 18** Fossil mammal specimens from Kria and Toé Caves: WAM 98.7.34, partial right dentary of *Mallomys* sp. cf. *M. aroaensis* with  $I_1$  and  $M_{1,2}$ ; A, occlusal view; B, medial view. Scale bar = 10 mm.

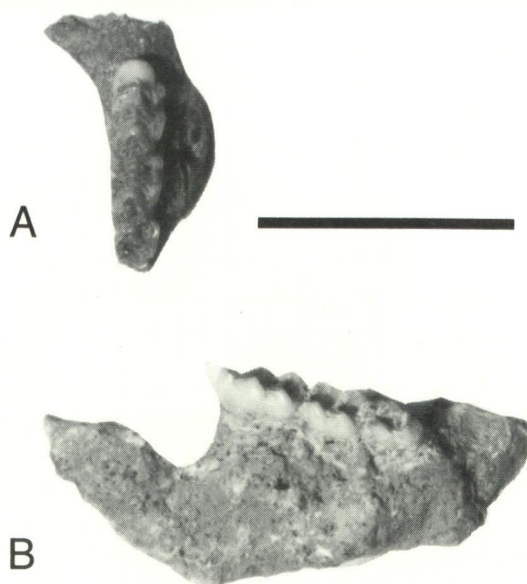
distinguished on details of molar morphology from members of the other, related genera of mosaic-tailed rats (*Abeomelomys*, *Chrotomys*, *Melomys*, *Mammomys*, *Pogonomelomys*; Menzies 1990b, 1996).

The limited sample of fossil *Paramelomys* falls into two groups on the basis of size. Two specimens represent a large-toothed form, the  $M_1$  measuring 2.9–3.0 mm in length with a constant width of 1.9 mm (K723.1, K675.1). An isolated  $M_1$  of a smaller taxon measures 2.6 x 1.7 mm (K630.1).

The larger-toothed form is a close match in size and morphology with specimens of *Paramelomys platyops* (Thomas, 1906) from Mt Banggiki, near Kobakma, Irian Jaya (e.g. AM M27307, M27308). This species is widely distributed in lowland habitats, from sea level to 900 m elevation, and is recorded from one locality in the northeast Bird's Head (Flannery 1995a).

The second fossil taxon is smaller than all but a few species of mosaic-tailed rats. It agrees closely in size and morphology with modern specimens of *P. rubex* (Thomas, 1922) from the Arfak Mountains (e.g. AM M28752). Unfortunately, it has not been possible to compare the fossil taxon with another small-toothed member of this group, *P. steini* (Rümmler, 1935), which is still known only from 2000–2600 m in the Weyland Range (Menzies 1996).

*Paramelomys rubex* is probably most abundant in montane habitats (Flannery 1995a), but it also



**Figure 19** Fossil mammal specimens from Kria and Toé Caves: A, WAM 98.7.35, partial right maxilla of *Pogonomelomys bruijni* with  $M_{1,3}$ , occlusal view; B, WAM 98.7.36, partial right dentary of *Pogonomelomys bruijni* with root of  $I_1$  and  $M_{1,3}$ , medial view. Scale bar = 10 mm.

extends down into hill forest at 800 m elevation on the Papuan Plateau (Aplin, unpublished observations). Several species are probably still included within this taxon, despite the considerable progress represented by Menzies' (1996) revision.

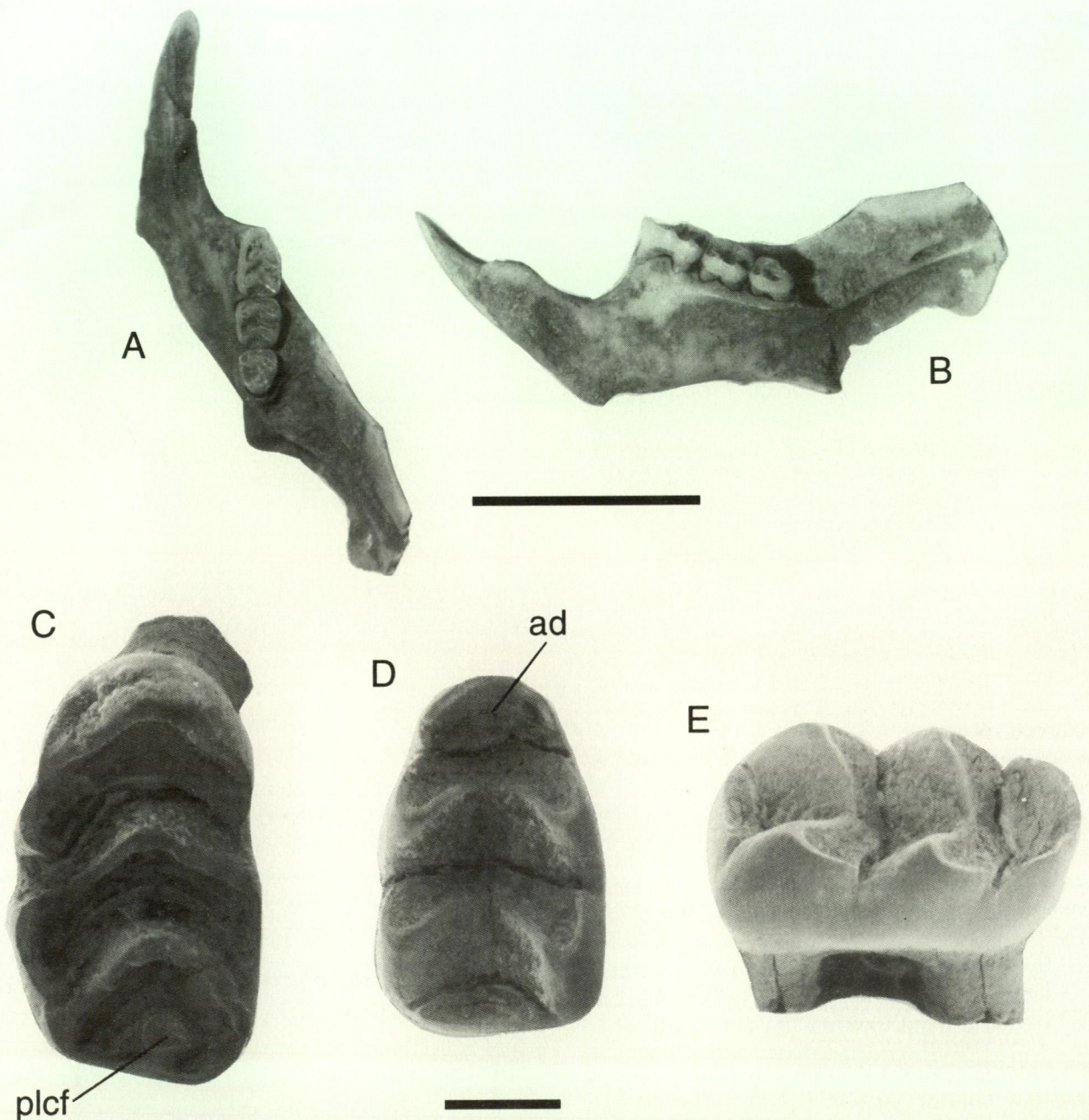
#### *Pogonomelomys bruijni* (Peters and Doria, 1876)

*Pogonomelomys bruijni* is represented in both Toé and Kria Caves and occurs in all major units (Figure 19). The molar row measures 8.2–8.3 mm in three well-preserved dentaries (T294.1, T557.2, T564.2) and 8.0 mm in a partial maxilla (WAM 98.7.35). The first upper molar of WAM 98.7.35 measures 3.8 x 2.0 mm. The specimens are very close in morphology to, but slightly larger in tooth dimensions than, AM M2372, a specimen of *P. bruijni brassi* from the lower Strickland River.

Nominotypical *P. bruijni* is recorded from Salawati Island and the central Bird's Head. The species is apparently confined to lowland and hill forest habitats.

#### *Pogonomelomys* sp.

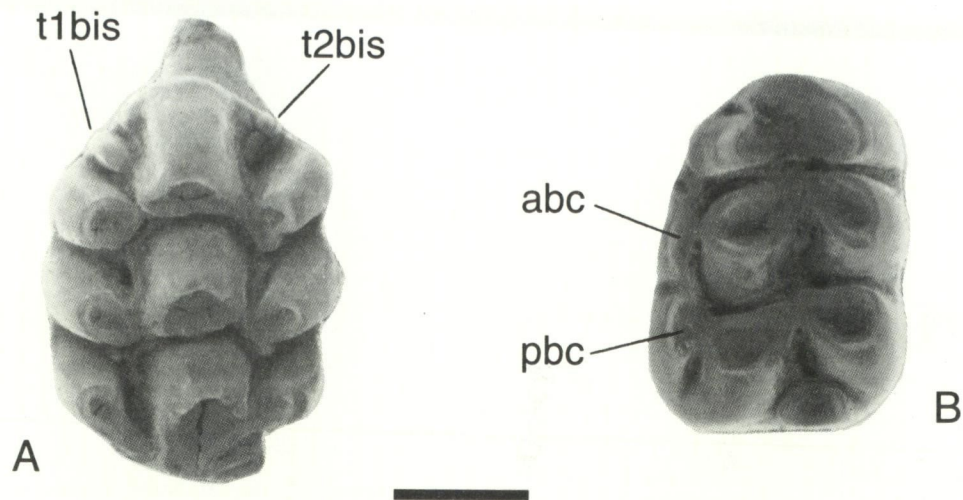
A probable second species of *Pogonomelomys* is represented by three well-preserved dentaries (Figure 20A,B), and several isolated  $M$ 's (Figure 20C) and  $M_1$ s (Figure 20D,E), derived from various levels in Kria Cave and the upper unit in Toé Cave.



**Figure 20** Fossil mammal specimens from Kria and Toé Caves: A, WAM 98.7.38, almost complete right dentary with  $I_1$  and  $M_{1-3}$ , representing an apparently unnamed species of *Pogonomelomys*, occlusal view; B, WAM 98.7.38, medial view; C, WAM 98.7.43, isolated left  $M^1$  of *Pogonomelomys* sp., probably same species as WAM 98.7.38, occlusal view; D, WAM 98.7.44, isolated left  $M^1$  of *Pogonomelomys* sp., probably same species as WAM 98.7.38, occlusal view; E, WAM 98.7.44, semiocclusal view. Scale bars = 10 mm for A–B and 1 mm for C–E. Referral of this material to *Pogonomelomys* is supported by the relatively unreduced posterior lower molars, the presence of a posterolingual cingular fossette (plcf) on  $M^1$ , and the relatively strong separation of the anteroconid (ad) from the medial lamina on  $M^1$ .

The morphology of the dentary and teeth is very close to that of *P. bruijnii*, but the cheekteeth are smaller (the lower molar row in this taxon measures 7.2–7.3 mm and the  $M^1$  3.6 x 1.9 mm). The  $M^1$  differs from that of *P. bruijnii* in having cusp t4 subequal to, rather than larger than, cusp t1. *Pogonomelomys mayeri* (Rothschild and Dollman, 1932) is smaller toothed with a  $M^{1-3}$  length of 6.6–6.8 (N=3) and  $M^1$  of 3.2 x 1.8–1.9 (Tate 1951).

This taxon has also been compared with reference material of the following medium to large-bodied taxa of mosaic-tailed rats, without finding any special similarity: *Abeomelomys sevia* (Tate and Archbold, 1935), *Mammelomys lanosus* (Thomas, 1922), *Mammelomys rattoides* (Thomas, 1922), *Melomys leucogaster* (Jentink, 1908), *Paramelomys lorentzii* (Jentink, 1908), *Paramelomys mollis* (Thomas, 1913), and *Paramelomys moncktoni* (Thomas, 1904). The fossil



**Figure 21** Fossil mammal specimens from Kria and Toé Caves: A, WAM 98.7.41, isolated left  $M_1$  of *Pogonomys* sp. cf. *P. loriae*, occlusal view; B, WAM 98.7.42, isolated left  $M_1$  of *Pogonomys* sp. cf. *P. loriae*, occlusal view. Scale bar = 1 mm. Note presence of anterior accessory cusps t1bis and t2bis on  $M_1$  and the strong connection between the posterobuccal (pbc) and anterobuccal (abc) cusplets on  $M_1$ , both of which suggest affinities to *P. loriae*.

taxon is consistent only with species of *Pogonomelomys* in combining a fully-enclosed posterior cingular fossette on the upper molars with relatively unreduced third molars (Menzies 1990b). We conclude that it probably represents a previously unknown species of *Pogonomelomys*. Its presence in the uppermost level of Toé Cave suggests that the species may still occur in the Ayamaru region.

#### *Pogonomys* sp. cf. *P. loriae* Thomas, 1897

Isolated upper  $M_1$  (WAM 98.7.41) and lower  $M_1$  (WM 98.7.42) of a *Pogonomys* species were retrieved from fine-sieved soil samples from Units II and V of Kria Cave (Figure 21). The two specimens are derived from an equivalent-sized taxon and most likely represent a single species.

Flannery (1995a) listed four species of *Pogonomys*, but noted that one of them, *P. loriae*, "encompasses at least two biological species". Three of the species are recorded from the Bird's Head Peninsula, namely *Pogonomys macrourus* (Milne-Edwards, 1877), *P. loriae* and *P. sylvestris* Thomas, 1920, although Flannery (1988) expressed doubt regarding Dollman's (1930) record of *P. sylvestris* from the Arfak Mountains.

The fossils are closest in morphology to specimens of *P. loriae*, including both large-toothed, white-bellied (e.g. AM M16140; Mt Sisa, Southern Highlands Province) and small-toothed, grey-bellied (e.g. AM M15423; Mt Elimbari, Eastern Highlands District) forms of this undoubtedly composite taxon. They are larger than each of *P. macrourus* (e.g. AM M24972, M24977; both Mt Karimui) and *P. sylvestris* (e.g. AM M15451, M16239; both Mt Elimbari) and further differ from each of these taxa in details of

morphology. In particular, the fossil  $M_1$  is consistent with *P. loriae* and differs from each of *P. sylvestris* and *P. macrourus* in lacking both an oblique crest between t1 and t5, and a basal, anterior cingular pocket between t2 and t3. Of the two distinct forms of *P. loriae*, the fossil  $M_1$  is closest in size to the smaller, grey-bellied form but is more similar in details of morphology (e.g. presence of distinct t1bis and t2bis; more anterior placement of t9) to the larger, white-bellied form. The fossil  $M_1$  differs from both forms of *P. loriae* in lacking a cingular ridge between the posterobuccal cusplet and the base of the hypoconid, and in the greater size of the posterobuccal cusplet which directly abuts the anterobuccal cusplet (in *P. loriae* the two are discrete, but linked by a short narrow crest).

#### *Rattus praetor* (Thomas, 1888)

A moderately large-bodied species of *Rattus* is represented by numerous fragmentary remains from the upper levels of both sites (e.g. K628.2, K712.1). The more complete specimens compare favourably with reference material of *R. praetor coenorum* Thomas, 1922 from Salawati Island (e.g. AM M29374).

*Rattus praetor* is a common garden pest of northern New Guinea (Flannery 1995a); its recorded distribution includes the Bird's Head Peninsula (Taylor *et al.* 1982; Flannery 1995a).

#### *Rattus* sp. indet.

An isolated lower molar (K1155.2) from Unit V in Kria Cave appears to represent a second species of *Rattus*. This tooth measures 3.1 x 2.0 mm, compared

with 3.5–3.6 x 2.3 mm in the specimens identified as *R. praetor*.

The fossil tooth differs from the  $M_1$  of the introduced Pacific Rat, *Rattus exulans browni* (Alston, 1877), in having a broader anterior lamina. It differs from specimens of the widely distributed montane species *R. niobe* (Thomas, 1906) in having more smoothly rounded rather than angular posterior surfaces on the protoconid and hypoconid. The closest match is to specimens of *R. verecundus* (Thomas, 1904) from mid-elevations in Papua New Guinea; however we stop short of making this allocation based on such limited material. *Rattus verecundus unicolor* (Rümmler, 1935) and *R. niobe arrogans* (Thomas, 1922) are both recorded from montane habitats on the Bird's Head Peninsula.

#### *Uromys caudimaculatus* (Kreffft, 1867)

A partial dentary retaining  $M_2$  (T596.3), recovered from the lower unit of Toé Cave is clearly referable to a species of *Uromys*. The  $M_2$  measures 3.7 x 3.1 mm and has relatively straight anterior and posterior lophids, the latter without a deeply concave posterior surface. A partial  $M^1$  from Unit V of Kria Cave (K1183) is also referred to this species.

Groves and Flannery (1994) recorded *Uromys caudimaculatus multiplicatus* (Jentink, 1907) from the western half of Irian Jaya, although it does not appear to have been collected on the Bird's Head. *Uromys caudimaculatus* has a wide geographic and altitudinal range within New Guinea, extending from sea level to nearly 2000 m elevation.

Two additional species of *Uromys* are found on islands in Cenderawasih (Geelvinck) Bay, east of the Bird's Head. These are: *U. emmae* Groves and Flannery, 1994, a small form related to *U. caudimaculatus*, from Owi Island; and *U. boeadii* Groves and Flannery, 1994, a probable member of the *U. anak* – *U. neobritannicus* group, from Biak. The fossil material has not been compared with western *caudimaculatus* but is very similar to specimens of *U. caudimaculatus papuanus* Meyer, 1876 from Papua New Guinea; it is less similar in molar morphology to *U. emmae*.

#### *Xenuromys barbatus* (Milne-Edwards, 1900)

This species is represented by a well-preserved maxilla with  $M^{1-3}$  (Figure 22), derived from the lower unit of Toé Cave. The  $M^1$  of *X. barbatus* differs from that of *Uromys* spp. in having cusps t1 and t4 positioned farther posteriorly relative to the central cusps of the respective lophs. The molar row of the fossil specimen measures 11.8 mm; measurements of the individual teeth are as follows:  $M^1 = 6.2 \times 3.2$  mm;  $M^2 = 3.6 \times 3.2$  mm;  $M^3 = 2.7 \times 2.5$  mm. These



Figure 22 Fossil mammal specimens from Kria and Toé Caves: WAM 98.7.37, partial left maxilla of *Xenuromys barbatus* with  $M^{1-3}$ , occlusal view. Scale bar = 10 mm.

measurements are consistent with previously recorded specimens of this rarely collected rodent (Tate 1951; Flannery *et al.* 1985).

Previous records of *X. barbatus* are widely scattered, from Mt Dayman in far southeastern Papua, to the Torricelli Mountains and the Idenburg River in Irian Jaya (Flannery 1995a). The species has not previously been recorded on the Bird's Head Peninsula.

### Order Chiroptera Blumenbach, 1779

#### Family Pteropodidae Gray, 1821

##### *Dobsonia* sp. cf. *D. magna* Thomas, 1905

A large pteropodid is represented by occasional remains in both cave deposits. Several well-preserved but edentulous dentaries from the lower unit of Toé Cave and an isolated lower molar from the lowermost unit of Kria Cave provide the most diagnostic remains. These are larger than *D. minor* (Dobson, 1879; type locality Amberbaki, Bird's Head Peninsula) and are generally consistent with reference material of *Dobsonia magna* from further east in New Guinea; however, in the absence of critical comparisons with other species in the region, most notably *D. moluccensis* (Quoy and Gaimard, 1830), we hesitate to make a definite determination. *Dobsonia magna* is recorded from the Arfak Mountains.

#### Family Hipposideridae Miller, 1907

##### *Hipposideros diadema* (Geoffroy, 1813)

Remains of a moderately large microchiropteran bat are present in many levels through the Kria Cave deposit. Only one species, a large



hipposiderid, appears to be represented. A precise match was obtained against reference material of *Hipposideros diadema* from the Ok Menga valley, near Tabubil in western Papua New Guinea (e.g. AM M29377). As *H. diadema* commonly roosts in caves, it seems likely that at least some of the bat remains represent natural deaths.

*Hipposideros diadema* occurs throughout the New Guinea region and west into southeast Asia. It has not previously been recorded from the Bird's Head Peninsula, but neither have many other widespread and common bat species. Medium-sized bats observed coming and going during the archaeological excavation in Kria Cave may well have been the modern descendants of this prehistoric colony.

### Order Artiodactyla Owen, 1848

#### Family Suidae Gray, 1821

##### *Sus scrofa vittatus* (Boie, 1828) X *Sus celebensis* Müller and Sclegel, 1845

Groves (1981) argued that the New Guinea domestic and feral pigs are derived from hybridization between two southeast Asian wild pigs, both of which may have been brought into domestication by early agriculturalists. This interesting possibility requires further testing using molecular markers; however, in the absence of a plausible alternative taxonomy, we have followed Groves' concept. The date of introduction of pig into the New Guinea region is still unknown, but recent work suggests that it may have occurred in the late Holocene (Flannery 1995a).

The New Guinea Pig is represented by a small number of diagnostic elements from the upper levels of both Toé and Kria Cave. These include the angular process of a right dentary (T104.1) and a femoral shaft (T104.2), both from an immature animal. Other, large, nondiagnostic bone fragments from upper levels of both Toé and Kria Caves may also be from this taxon.

### DISCUSSION

Kria and Toé Caves together have yielded the remains of 41 species of mammals, at least three species of birds and an as yet undetermined number of squamates and frogs (see Table 8). The prehistoric mammal fauna includes approximately half of the mammal species currently known to occur on the Bird's Head Peninsula, and provides the first record for a further 9–10 species (the uncertainty being due to the possible presence of two species of *Dorcopsulus*). All of the species are representative of either lowland forest or montane forest habitats, with no indication of drier or more open vegetation types.

Of the 28 mammal species recorded only in the modern fauna, the great majority are either small insectivorous or nectarivorous bats or small to medium-sized marsupials [e.g. '*Antechinus*' spp.; *Distoechurus pennatus* (Peters, 1874); *Cercartetus caudatus* (Milne-Edwards, 1877)] and rodents [e.g. *Leptomys elegans* Thomas, 1897, *Paramelomys mollis* (Thomas, 1913)]. These groups are poorly represented in the prehistoric faunas and specific absences might well be attributable to sampling bias. Two more noteworthy absences from the cave faunas are Raffray's Bandicoot, *Peroryctes raffrayana* (Milne-Edwards, 1878) and the Vogelkop Tree-kangaroo, *Dendrolagus ursinus*. The latter species is often stated to occur down to sea level, based on a record at Cape Oransbari by Rappard (Husson and Rappard 1958); however, other data suggest that, at least in the Arfak Mountains, the species is confined to higher elevation forests. Its absence from the lower unit of Toé Cave, where many other higher elevation species are represented, is perhaps related to the presence in these levels of two other *Dendrolagus* species, namely *D. inustus* and an as yet undetermined member of the *D. goodfellowi* group. The absence of *P. raffrayana* cannot be readily explained, but may be a consequence of the overall poor representation of bandicoots in the older levels of both sites.

Among the mammal species recorded from the Bird's Head Peninsula for the first time, several are present in the upper levels of one or other of the sites and are thus likely to persist in the area today. Included in this category are the Water Rat, *Hydromys chrysogaster*, the Diadem Horseshoe Bat, *Hipposideros diadema*, and an apparently undescribed species of *Pogonomelomys*. The newly described *Dactylopsila kambuayai* is not represented in deposits younger than 5000 BP and so may no longer occur in the immediate vicinity of the sites; however, there seems a reasonable chance that it survives somewhere on the Bird's Head.

Six of the newly-recorded mammal species are represented exclusively in the lowermost unit of Kria Cave (dating to the mid- to early Holocene) and/or the lower unit of Toé Cave (probably of late Pleistocene age). Several of these species (*Dendrolagus* sp. *D. goodfellowi* group; *Dorcopsulus vanheurni* and *Dorcopsulus* sp.; *Spilocuscus rufoniger*) are conspicuous, large-bodied taxa of the kind favoured by native hunters; their absence from the list of modern Bird's Head mammals is presumed to be genuine. Each of these taxa thus appears to have become regionally extinct on the Bird's Head over the last 5–6000 years. In the case of the *Dendrolagus* and *Dorcopsulus* species, both of which are associated with montane habitats, local extinction has probably occurred largely as a consequence of environmental change since the end of last glaciation, perhaps exacerbated by hunting pressure. *Spilocuscus*

**Table 8** List of mammal species recorded from the Bird's Head of Irian Jaya, Indonesia, drawing upon the archaeological faunas from Kria and Toé Caves as well as modern records based on literature reports and museum holdings (data from Flannery 1995a and Aplin in press). An \* indicates that the taxon is restricted to the basal levels in each of the archaeological deposits. A ? after a record indicates a tentative identification.

	KRIA	TOÉ	MODERN		KRIA	TOÉ	MODERN
MONOTREMATA				<i>Dactylopsila trivirgata</i>	+	+	+
Tachyglossidae				<i>Petaurus breviceps</i>	+	+	+
<i>Zaglossus bruijnii</i>	+	+	+	Acrobatidae			
DASYUROMORPHIA				<i>Distoechurus pennatus</i>	-	-	+
Dasyuridae				RODENTIA			
' <i>Antechinus</i> ' <i>melanurus</i>	-	-	+	Muridae			
' <i>Antechinus</i> ' <i>naso</i>	-	-	+	<i>Hydromys chrysogaster</i>	+	-	+
<i>Dasyurus albopunctatus</i>	+*	+*	+	<i>Hyomys dammermani</i>	-	-	+
<i>Myoictis melas</i>	+	+	+	<i>Leptomys elegans</i>	-	-	+
<i>Phascosorex doriae</i>	-	-	+	<i>Mallomys</i> sp. cf. <i>M. aroensis</i>	-	+*	+
<i>Phascosorex dorsalis</i>	-	-	+	<i>Melomys rufescens</i>	-	-	+
PERAMELEMORPHIA				<i>Parahydromys asper</i>	+	-	+
Peroryctidae				<i>Paramelomys mollis</i>	-	-	+
<i>Echymipera kalubu</i>	+	+	+	<i>Paramelomys platypops</i>	+	-	+
<i>Echymipera rufescens</i>	+	+	+	<i>Paramelomys rubex</i>	+?	-	+
<i>Microperoryctes longicauda</i>	+?	+*	+	<i>Pogonomelomys bruijnii</i>	+	+	+
<i>Microperoryctes murina</i>	-	-	+	<i>Pogonomelomys</i> sp.	+	+	-
<i>Peroryctes raffrayana</i>	-	-	+	<i>Pogonomys loriae</i>	+?	-	+
DIPROTODONTIA				<i>Pogonomys macrourus</i>	-	-	+
Phalangeridae				<i>Pogonomys sylvestris</i>	-	-	+
<i>Phalanger gymnotis</i>	+	+	+	<i>Rattus niobe arrogans</i>	-	-	+
<i>Phalanger</i> sp. cf.				<i>Rattus praetor</i>	+	+	+
<i>P. intercastellanus</i>	-	+*	-	<i>Rattus</i> sp. cf. <i>R. verecundus</i>	+?*	-	+
<i>Phalanger orientalis</i>	+*	+*	+	<i>Uromys caudimaculatus</i>	+	+	-
<i>Phalanger vestitus</i>	+*	+*	+	<i>Xenuromys barbatus</i>	-	+*	-
<i>Spilocuscus maculatus</i>	+	+	+	CHIROPTERA			
<i>Spilocuscus rufoniger</i>	+*	+*	-	Pteropodidae			
Macropodidae				<i>Dobsonia magna</i>	+?	+?	+
<i>Dendrolagus</i> sp. cf.				<i>Dobsonia minor</i>	-	-	+
<i>D. goodfellowi</i>	+*	+*	-	<i>Macroglossus minimus</i>	-	-	+
<i>Dendrolagus inustus</i>	+	+	+	<i>Nyctimene albiventer</i>	-	-	+
<i>Dendrolagus ursinus</i>	-	-	+	<i>Nyctimene cyclotis</i>	-	-	+
<i>Dorcopsis muelleri</i>	+	+	+	<i>Paranyctimene albiventer</i>	-	-	+
<i>Dorcopsulus vanheurni</i>	+?*	+*	-	<i>Pteropus conspicillatus</i>	-	-	+
<i>Dorcopsulus</i> sp.	-	+*	-	<i>Pteropus neohibernicus</i>	-	-	+
Burramyidae				<i>Rousettus amplexicaudatus</i>	-	-	+
<i>Cercartetus caudatus</i>	-	-	+	<i>Syconycteris australis</i>	-	-	+
Pseudocheiridae				Hipposideridae			
<i>Petauroides ayamaruensis</i>				<i>Hipposideros calcaratus</i>	-	-	+
sp. nov.	+*	+?*	-	<i>Hipposideros diadema</i>	+	-	-
<i>Pseudocheirops albertisii</i>	-	+*	+	<i>Hipposideros papua</i>	-	-	+
<i>Pseudocheirops coronatus</i>	-	+*	+	<i>Rhinolophus euryotis</i>	-	-	+
<i>Pseudochirulus</i> sp. cf.				Vespertilionidae			
<i>P. canescens</i>	+	-	+	<i>Nyctophilus microtis</i>	-	-	+
<i>Pseudochirulus schlegelii</i>	+*	+*	+	ARTIODACTYLA			
Petauridae				Suidae			
<i>Dactylopsila kambuayai</i> sp. nov.	+	-	-	<i>Sus scrofa</i> X <i>Sus celebensis</i>	+	+	+
<i>Dactylopsila palpator</i>	-	+*	+				

*rufoniger* is a species of lowland and hill forests and there is no obvious environmental reason for its disappearance. However, the species is evidently rare and in decline over much of its former range along the north coast of New Guinea (Flannery and Calaby 1987; Flannery 1995a), presumably as a

consequence of habitat disturbance and direct hunting pressure; its disappearance from the Bird's Head may also be a direct consequence of human agency.

The absence of *Xenuromys barbatus* from both the upper levels of the cave deposits and from the

recorded modern fauna is probably explained by the apparent scarcity of this species. As summarized by Flannery (1995a), *X. barbatus* is recorded over a wide geographic and altitudinal range, yet appears to be nowhere common.

The cuscus identified as *Phalanger* sp. cf. *P. intercastellanus* is represented by a few specimens from the lower levels of Toé Cave. Its apparent association with a largely montane fauna in these levels is at odds with the general impression of *P. intercastellanus* as a denizen of lowland and hill forests. Until such time as this identification can be clarified, no conclusions can be drawn regarding the past and present status of this taxon on the Bird's Head Peninsula.

The newly described *Petauroides ayamaruensis* is known with certainty only from the lower unit of Kria Cave, although some postcranial specimens from the lower unit of Toé Cave are also tentatively referred to this taxon. The stratigraphic distribution of this distinctive species suggests that it may have been associated with the 'montane' fauna which evidently spread across the Ayamaru Plateau during late Pleistocene through to mid-Holocene times (Pasveer and Aplin in press). If this enigmatic marsupial survives today anywhere on the Bird's Head Peninsula, then it is probably in the montane forests of the Arfak or Tamrau Mountains.

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