

## Revision of the Genus *Dorcopsis* (Macropodidae: Marsupialia)

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Multivariate analysis and morphological studies indicate that there are four species of *Dorcopsis*. *Dorcopsis atrata* and *D. hageni* are monotypic, while *D. luctuosa* includes two distinct subspecies (one newly described here), and *D. muelleri* four (also one newly described here). The three mainland New Guinean species are probably parapatric, but only in one instance are taxa recorded as occurring in close proximity. *Dorcopsis luctuosa* is probably the sister taxon to the remaining taxa, while the autapomorphic *D. atrata* is probably convergent upon the species of *Dorcopsulus*.

### INTRODUCTION

THE forest wallabies of the genus *Dorcopsis* are among the most plesiomorphic of living macropodids (Flannery 1984). Along with the closely related *Dorcopsulus*, they are the only genus of macropodoid presently restricted to the island of New Guinea and its satellite islands. However, fossils of *Dorcopsulus* and the closely related genus *Dorcopsoides* are known from Tertiary sediments in Australia.

A species of *Dorcopsis* was first made known by Quoy and Gaimard (1830); but they described their material under the name *Didelphis brunii*, thinking that it was the species seen by De Bruijn and named *Didelphis brunii* Schreber; which was however, a species of *Thylogale*. Quoy and Gaimard's animal was probably the western species of *Dorcopsis*, to which Owen (1839) was referring under the name *Hypsiprymnus dorsocephalus*, and Gray (1843) as *Halmaturus asiaticus*. This is made more likely by the fact that the latter specifically mentioned Lobo Bay as a locality, and that the British Museum had received a specimen from there via the Leiden Museum some time previously. It was not until 1866 that the first available name was awarded to a New Guinea forest Wallaby: *Macropus muelleri* Schlegel.

Husson (1955) argued that the earliest name for a species of this group is actually *Kangurus veterum* Lesson and Garnot, 1826. George and Schurer (1975), however, maintain that this name actually refers not to a member of this group but to *Dendrolagus inustus*. Lesson and Garnot's description reads as follows (translated by CPG): "... This animal we provisionally name kangaroo of Aru (*Kangurus veterum* N.), is called *Podin* by the Papuans of the port of Dorey, New Guinea. Differs from the Australian kangaroos by the dimensions of its limbs. Size is that of a common Hare: its ears are proportionately shorter than other species. Head rounded, muzzle

more conical, less shortened than the "oualabat". Neck less slender. Forelimbs more elongated, stronger, more robust; hindlimbs less long, bigger. Tail is one-third shorter. Pelage is uniformly brown on upper parts, passing to grey on underside . . ." (Lesson and Garnot 1826, p.164).

Perhaps the most significant part of the vague description (which to judge from the size given must have been of a juvenile) is the limb proportions, which would certainly fit best with a tree-kangaroo as George and Schurer proposed. The short tail and colour, however, do not fit well with any of the Vogelkop tree-kangaroos, and are indeed reminiscent of a species of *Dorcopsis*. Given the vagueness of the description we suggest that it be regarded as a *nomen dubium* and that it be allowed to lapse.

Schlegel and Muller (1845) gave *Didelphis brunii* Quoy and Gaimard, 1830 (*nec* Schreber 1778) generic rank as *Dorcopsis*. Troughton (1937) substituted the name *Conoyces* Lesson, 1842, for the genus, but as shown by Tate (1945) the type of Lesson's name is *Didelphis brunii* Gmelin, 1788, who gives as his primary reference Schreber (1778): not *Didelphis brunii* Quoy and Gaimard, 1830. *Conoyces* is hence a junior synonym of *Thylogale* Gray, 1837.

A second species of *Dorcopsis* was described by d'Albertis (1874) as *Halmaturus luctuosus*; Miklouho-Maclay described (1884) *Dorcopsis chalmersii* and (1885) *D. beccarii*; Heller (1897) described *D. hageni*; Rothschild and Rothschild (1898), *D. rufolateralis*; Jentink (1908), *D. lorentzii*; Thomas (1913), *D. mysoliae*. Thomas (1922) and Troughton (1937) described new taxa as subspecies of *D. hageni* Heller, 1897. Finally in 1957 Van Deusen made known a further new species, *D. atrata*. Of these taxa, *D. mysoliae* was from Misool Island, west of the Cenderawasih

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Peninsula, Irian Jaya; *D. atrata* from Goodenough Island, east of mainland Papua New Guinea; all other putative taxa were from the New Guinea mainland itself.

In the meantime a series of related, smaller species were being made known, beginning with *Dorcopsis macleayi* Miklouho-Maclay (1885). Matschie (1916) placed this species in a new genus, *Dorcopsulus*, about whose validity opinions have differed since then, some putting it into *Dorcopsis*, others leaving it as distinct. The question of the relationships between *Dorcopsis* and *Dorcopsulus* we leave to a future publication, and at this time we deal only with the larger-sized species, *Dorcopsis* in the strict sense.

#### MATERIAL AND METHODS

Between us we have studied material in the following collections: Australian Museum, Sydney (AM M); Macleay Museum, Sydney (MM); Museum of Victoria, Melbourne (NMV); National Wildlife Collection, Canberra (CM); Western Australian Museum (WAM); British Museum (Natural History), London (BM); Museum National d'Historie Naturelle, Paris (MNP); Rijksmuseum van Natuurlijke Historie, Leiden (RML); Instituut voor Taxonomische Zoologie, Amsterdam (ZMA); Zoologisches Museum A. Humboldt, Berlin (ZMB); Landesmuseum für Naturkunde, Karlsruhe (LNK); American Museum of Natural History, New York (AMNH). Some of the specimens in the Australian Museum were collected by one of us (TFF).

We made notes on external and craniodental characters, and took a series of measurements on the skulls and teeth of each specimen. The measurements are listed and described in the Appendix. These measurements were utilized in a series of multivariate analyses (SPSS "Direct" method, Discriminant Functions). Three analyses were performed: Skulls, adults only; Skulls, adults and older juveniles only; Teeth, all ages. Skull and tooth measurements were treated separately because they are different kinds of data: skulls grow, teeth do not, hence skulls are subject to ontogenetic allometry, teeth only to static allometry, reducing correlations between them to a point where it loses biological validity to treat them together except perhaps as a bivariate diagnostic tool.

#### RESULTS

The *Dorcopsis* specimens we have studied fall very neatly into four groups, which are well-defined geographically and differ by colour and colour pattern, pattern of dorsal hair-tracts, body proportions, and skull characters. We rate them as four distinct, probably allopatric, species. The earliest available names are as follows: for the western brown to reddish species, *D. muelleri*

(Schlegel 1866); for the north coastal fawn to blackish brown species with a light dorsal stripe, *D. hageni* Heller, 1897; for the southeastern dark grey species, *D. luctuosa* (D'Albertis 1874); and for the black species from Goodenough Island, *D. atrata* Van Deusen, 1955.

Within two of these four species (*D. muelleri* and *D. luctuosa*) there are quite sharply distinct geographic forms, distinguished from each other by size and other features and are sharply differentiated by multivariate analysis (Figs 1-2). These we rate as subspecies; some are already named, others not; in two cases the evidence is good enough to warrant the description of two new subspecies, but in some other cases we merely point to the probable existence of new subspecies for the evidence is not yet enough to describe and define them.

Within *D. hageni* there is some polymorphism, which appears to have a geographic component, but not sharply enough to warrant the recognition of subspecies. At least one of the subspecies of *D. muelleri* is also polymorphic in an interesting manner.

#### TAXONOMY AND SYSTEMATICS

##### (1) *DORCOPSIS MUELLERI* (Schlegel 1866). Brown *Dorcopsis*.

**Diagnosis.** Colour of dorsal surface some shade of brown (as opposed to grey in *D. luctuosa* and black in *D. atrata*), and lacking the white dorsal stripe of *D. hageni*. Underside grey to white or

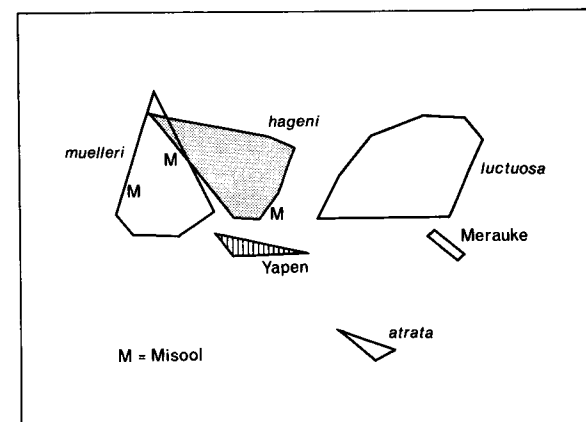


Fig. 1. Graph of First and Second Discriminant Functions for 18 cranio-mandibular measurements of *Dorcopsis* species. As in Fig. 2, individual specimens are not plotted, only distribution polygons. Discriminant Function 1 (61% of total variance), on the horizontal axis, denotes small size with posteriorly broadened nasals, long palatal vacuities and long incisive foramina. Discriminant Function 2 (14% of total variance), on the vertical axis, denotes an elongated skull but short incisive foramina, combined again with posteriorly broad nasals. Note that, as for the dental graph (Fig. 2), *D. l. phyllis* n. ssp. ("Merauke") and *D. m. yapeni* n. ssp. ("Yapen") are separated from conspecifics, but that *D. m. mysoliae* ("Misool") is not.

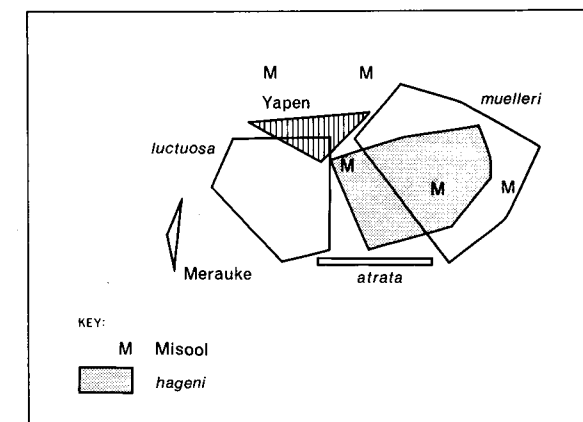


Fig. 2. Graph of First and Second Discriminant Functions for seven dental measurements of the species of *Dorcopsis*. Polygons are constructed by joining up the most outlying specimens from each sample. Discriminant Function 1 (accounting for 72% of total variance) is on the horizontal axis. It is strongly dependent on absolute size, especially total toothrow length. Discriminant Function 2 (19% of the total variance) is on the vertical axis; high scores on this Function denote large-sized secutor, broad  $M^2$  and short incisor row. Note separation of "Merauke" (*D. l. phyllis* n. sp.) from other *D. luctuosa*, and of "Yapen" (*D. m. yapeni* n. sp.), but not "Misool" (*D. m. mysoliae*) from other *D. muelleri*.

creamy (as opposed to blackish brown in *D. atrata*), this tone sharply set off from that of upper side (not sharply set off in *D. luctuosa*); throat whiter than rest of underside; limbs paler than rest of upper side; dorsal hair tracts divided by either a whorl, or pair of whorls, level with scapulae, or by a pair of transverse partings from axillae running towards middle of back (as opposed to the "V" pattern of *D. luctuosa*). Dorsal outline of facial skeleton straight in lateral

view; braincase rounded (except for sagittal crest, usual in adults), falling away abruptly behind, in front of nuchal crest; nasals broad, posteriorly rounded; rostrum broad, rounded; palatine vacuities tend to be short and broad; posterior margin of palate somewhat concave. Toothrows straight, parallel; secators (P3) long (shorter in *D. luctuosa*), equal to two and a quarter to two and a half molar lengths, narrow, mesially pointed.

**Distribution:** Lowlands of Irian Jaya, as far east as Danau (=Lake) Biru in the north, and the Setakwa/Mimika Rivers district in the south; the offshore islands of Misool, Salawatti, and Yapen (Fig. 3).

##### (a) *Dorcopsis muelleri muelleri* (Schlegel 1866)

1830 *Didelphis brunii* Quoy and Gaimard. Dorey (=Manokwari), in the Cenderawasih (formerly Vogelkop) district of Irian Jaya. Not of Schreber, 1778 (a *Thylogale*).

?1839 *Hypsiprymnus dorsocephalus* Owen. New Guinea. *Nomen nudum*.

1843 *Halmaturus asiaticus* Gray. Lobo Bay (see Laurie and Hill 1954, p. 24). *Nomen nudum*.

1866 *Macropus muelleri* Schlegel. Lobo Bay.

1898 *Dorcopsis rufolateralis* Rothschild and Rothschild. "North New Guinea".

**Diagnosis:** Dorsal colour overall reddish brown; hair shafts medium red-brown to clay-brown, bases only slightly paler. Arms creamy-brown; legs also contrastingly lighter than body. Underside creamy with a red tinge, extending up posterior flanks in a broad wedge in front of stifle. One or two scapular whorls. Claws dark. Tail naked for one-sixth of its length. Size large, at

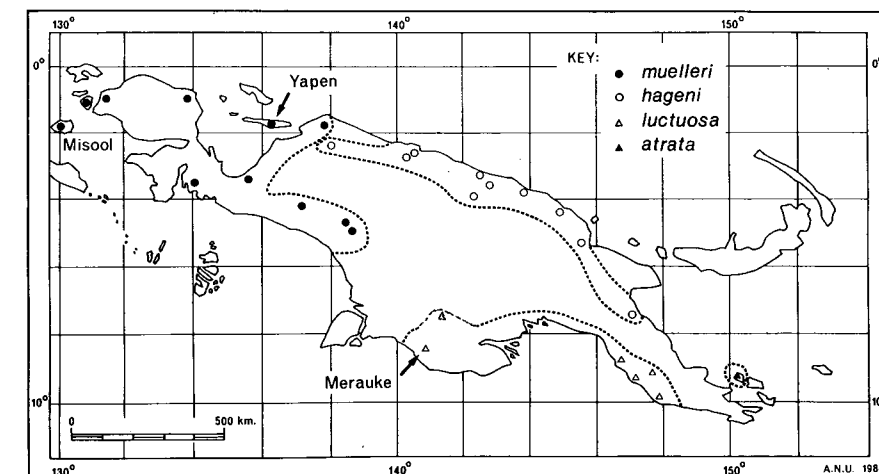


Fig. 3. Distribution of the species of *Dorcopsis*. The labelled localities are as follows: *D. muelleri* - Misool, type locality (and entire distribution) of *D. m. mysoliae*; Yapen, type locality (and entire distribution) of *D. m. yapeni* n. ssp. *Dorcopsis luctuosa* - Merauke, type locality of *D. l. phyllis* n. ssp.; Fly delta localities are in same general area. Other localities for *D. luctuosa* represent nominotypical *D. l. luctuosa*. Other localities for *D. muelleri* represent nominotypical *D. muelleri* or allied (undescribed) taxa, on the Cenderawasih Peninsula; more easterly localities represent *D. m. lorentzii*.

Table 1. Skull measurements of adult *Dorcopsis*.

| (A) MALES                           |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
|-------------------------------------|--------------------|-----------------------|---------------------|--------------|-------------------------|-----------------|----------------|-----------------------------|-------------------------|------------------------------|--|
| Adult                               |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| Specimen                            | Total Skull Length | Condylar Basal Length | Bizygomatic Breadth | Nasal Length | Posterior Nasal Breadth | Rostrum Breadth | Rostrum Height | Maxillary Tooththrow Length | Height Mandibular Ramus | Length of Palatine Vacuities |  |
| <i>D. muelleri</i>                  |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| <i>D. m. muelleri</i> RML13475      | ca.140             | —                     | 58                  | —            | 16                      | —               | —              | 40                          | 14                      | 14.5                         |  |
| <i>D. m. lorentzii</i> RML24235     | 149                | 140                   | 60                  | 56           | 15                      | 20.5            | 22             | 41                          | 15                      | —                            |  |
| <i>D. m. mysoliae</i> BM61.12.11.22 | 121                | 115.3                 | 55                  | 46           | 13                      | 16.5            | 19             | 39                          | 13.5                    | 14                           |  |
| <i>D. m. yapeni</i> BM46.691        | 120                | 114                   | 55                  | 47           | 12.2                    | 17              | 17.2           | 37.2                        | 14                      | ca.17                        |  |
| <i>D. hageni</i>                    |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| RML24256                            | —                  | —                     | —                   | 52           | 14.5                    | 19              | 21             | 40                          | —                       | 17                           |  |
| AM M6211                            | —                  | —                     | 59                  | 55           | 16                      | 20              | 22             | 39                          | —                       | 16                           |  |
| LNK535                              | 134                | 129                   | 57                  | 52           | 14.5                    | 19              | 22.5           | 41.5                        | 14                      | 15.5                         |  |
| AM M13636                           | 133.5              | 130                   | 60                  | 50           | 15                      | 21              | 21             | 38                          | —                       | 16.6                         |  |
| <i>D. luctuosa</i>                  |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| <i>D. l. luctuosa</i>               |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| AM M7385                            | 135                | 125                   | 56                  | 54           | 19                      | 20              | 22             | 36                          | 15.5                    | 13                           |  |
| AM M9139                            | 134.9              | 126.6                 | 59.9                | 58.4         | 16.7                    | 17.3            | 21.8           | 38.8                        | 15.1                    | 16                           |  |
| AMNH108112                          | —                  | —                     | 56.4                | 50.2         | 13.3                    | 23.2            | 21.2           | 37.4                        | 12.9                    | —                            |  |
| <i>D. l. phyllis</i>                |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| AMNH105988                          | —                  | —                     | 51.4                | 39.9         | 14.3                    | 22.0            | 20.4           | 32.7                        | 11.9                    | —                            |  |
| AMNH105981                          | —                  | —                     | 52.8                | 40.8         | 14.8                    | 22.4            | 19.5           | 35.0                        | 11.7                    | —                            |  |
| AMNH105979                          | —                  | —                     | 52.6                | 43.7         | 16.6                    | 22.9            | 19.7           | 34.9                        | 12.3                    | —                            |  |
| NMV C7096                           | ca.111             | 104                   | 50.0                | 46.0         | 12.5                    | 17.0            | 17.8           | 37.0                        | —                       | —                            |  |
| <i>D. atrata</i>                    |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| AMNH157277                          | 112.9              | 109.3                 | 53.6                | 42.5         | 11.1                    | 18.8            | 17.8           | 38.5                        | —                       | 17.0                         |  |
| AMNH157276                          | 117.9              | 111.9                 | 51.0                | 45.2         | 10.2                    | 16.8            | 18.1           | 39.0                        | 13.0                    | 14.8                         |  |
| AM M19461                           | 121                | 116                   | 55.5                | 48.0         | 11.5                    | 19.0            | 20.0           | 41.0                        | 13.5                    | 14.5                         |  |
| Young Adult                         |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| <i>D. muelleri</i>                  |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| <i>D. m. muelleri</i>               |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| RML13481                            | 128                | 126                   | 54.5                | 51           | 14                      | 19              | 22             | 40.5                        | 13.5                    | 14                           |  |
| RML13473                            | 129                | 122                   | 54                  | 51           | 12                      | 19              | 20             | 39                          | 12                      | 12                           |  |
| RML cat.ost.m                       | —                  | —                     | 54                  | 50           | 16.5                    | 19.5            | 21.5           | 42                          | 14                      | 16                           |  |
| <i>D. m. lorentzii</i>              |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| RML24254                            | 131                | 124                   | 57                  | 50           | 13.5                    | 18              | 21             | 41                          | 13                      | 10                           |  |
| RML74268                            | 127                | 119                   | 54                  | 50           | 13                      | 18              | 21             | 40                          | 13.5                    | 12                           |  |
| ZMA17991                            | 123                | 117                   | 55                  | 46           | 13                      | 17              | 19             | 40                          | 13                      | 12                           |  |
| BM13.6.18.97                        | 116.5              | 112.5                 | 56                  | 45           | 14                      | 17              | 18             | 40.5                        | 13                      | 11.5                         |  |
| ZMB91751                            | 117                | 113                   | 54                  | 44           | 12                      | 16              | 18             | 40                          | 12                      | ca.14                        |  |
| <i>D. m. mysoliae</i>               |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| RML cat.ost.f                       | —                  | —                     | 60                  | 55           | 16                      | 18              | 22.5           | 43                          | 14                      | 17                           |  |
| <i>D. hageni</i>                    |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| ZMB22369                            | 134                | 128                   | 57                  | 56           | 14                      | 18              | 23.5           | 42                          | 14                      | 15                           |  |
| AM M13634                           | 129.5              | 122                   | 55                  | 51           | 16                      | 18              | 20             | 40                          | —                       | 15.4                         |  |
| AM M6098                            | 131.7              | 125.5                 | 61.7                | 51.2         | 13.2                    | 17.2            | 19.8           | 39.3                        | 13.8                    | 15.8                         |  |
| BM22.2.2.63                         | 144                | 136                   | 61.0                | 54           | 16                      | 21.5            | 22             | 42.2                        | 15                      | 14                           |  |
| <i>D. luctuosa</i>                  |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| <i>D. l. luctuosa</i>               |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| ZBM22717                            | 120                | 114                   | 52                  | 48           | 13                      | 18              | 19.5           | 38                          | 12.2                    | 15.2                         |  |
| NMV C10784                          | 119                | 111.7                 | 53.8                | 42.4         | 14.6                    | 17.2            | 18.6           | 37.9                        | —                       | —                            |  |
| RML cat.ost.a                       | 121                | 114                   | 54                  | 49           | 14                      | 18              | 20             | 39                          | 12                      | 15                           |  |
| AM M7052                            | 120                | 111                   | 53                  | 47           | 16                      | 17              | 21             | 37                          | 13                      | 15                           |  |
| AM M19464                           | 120                | 111                   | 52.7                | 47.7         | 13                      | 14.8            | 19.5           | 35.5                        | 12.7                    | 13.5                         |  |
| BM8.10.8.37                         | 114                | 109.5                 | 55                  | 45.5         | 14                      | 17.2            | 20             | 36                          | 12                      | 16                           |  |
| <i>D. atrata</i>                    |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| AM M19458                           | 107.5              | 104                   | 51                  | 41           | 10.5                    | 16              | 16.2           | 37                          | 12                      | 11                           |  |
| (B) FEMALES                         |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| Adult                               |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| <i>D. muelleri</i>                  |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| <i>D. m. lorentzii</i>              |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| RML24253                            | 121                | 114                   | 52                  | —            | 11.5                    | 16              | 17             | 39                          | 12                      | 12                           |  |
| ZBM91753                            | 120                | 114                   | 54                  | 46           | 13                      | 17              | 19             | 42                          | 13                      | 14                           |  |
| ZMB91752                            | 121                | 114                   | 50                  | 45           | 13.2                    | 17              | 17             | 38                          | 12.5                    | 14.5                         |  |
| BM11.11.11.109                      | 118.5              | 112.5                 | 55                  | 45           | 14.5                    | 16.5            | 17.5           | 38                          | 13.5                    | 10.5                         |  |
| <i>D. m. mysoliae</i>               |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| BM61.12.11.23                       | 118                | 110.5                 | 51.5                | 40+          | 14                      | 16.5            | 18             | 37                          | 13                      | 10                           |  |
| AMB22402                            | —                  | —                     | 51                  | 41           | 12                      | 12              | 14.5           | 38                          | 13                      | 11                           |  |
| <i>D. m. yapeni</i>                 |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| BM46.693                            | 115                | 108.5                 | 52.3                | 43           | 12.5                    | 15              | 15.2           | 37                          | 13                      | ca.17                        |  |
| <i>D. hageni</i>                    |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| AM13633                             | 117.2              | 109.8                 | 53.6                | 45.9         | 13.3                    | 15.0            | 16.5           | 37.8                        | 12.7                    | 11.5                         |  |
| AM M13632                           | 119.2              | 112.9                 | 51.5                | 45.6         | 11.9                    | 15.1            | 16.8           | 38.3                        | 12.1                    | ca.16.5                      |  |
| <i>D. luctuosa</i>                  |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| <i>D. l. luctuosa</i>               |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| ZMB6035                             | 123                | 114                   | 54                  | 51           | 17                      | 20              | 22.5           | 35                          | 16                      | 14                           |  |
| ZMB11521                            | 124                | 117                   | 58                  | 53           | 16.5                    | 19              | 20             | 36                          | 14.5                    | ca.12                        |  |
| AM M790                             | ca.108+            | —                     | 50                  | 45           | 14                      | 16              | 18             | 36                          | 11                      | 12                           |  |
| AM M3663                            | 108                | 101                   | 52                  | 45           | 15                      | 16              | 17.5           | 35                          | 12                      | 14                           |  |
| <i>D. l. phyllis</i>                |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| AMNH105998                          | —                  | —                     | 46.4                | 37.0         | 12.0                    | 20.0            | 17.5           | 32.8                        | 10.5                    | —                            |  |
| AMNH105982                          | —                  | —                     | 48.5                | 40.9         | 9.0                     | 20.3            | 19.2           | 33.7                        | 11.6                    | —                            |  |
| RML17239                            | 107                | 101                   | 51                  | 41.0         | 16.0                    | 18.0            | 18             | 33.0                        | 12.0                    | 12.5                         |  |
| WAM M2808                           | —                  | —                     | 48.3                | 41.0         | 13.0                    | 14.5            | 15.5           | 32.8                        | 10.4                    | 13.2                         |  |

Table 1 continued

| (B) FEMALES            |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
|------------------------|--------------------|-----------------------|---------------------|--------------|-------------------------|-----------------|----------------|-----------------------------|-------------------------|------------------------------|--|
| Adult                  |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| Specimen               | Total Skull Length | Condylar Basal Length | Bizygomatic Breadth | Nasal Length | Posterior Nasal Breadth | Rostrum Breadth | Rostrum Height | Maxillary Tooththrow Length | Height Mandibular Ramus | Length of Palatine Vacuities |  |
| <i>D. atrata</i>       |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| AMNH157275             | 104.0              | 98.3                  | 50.4                | 40.7         | 10.2                    | 17.1            | 15.2           | 36.1                        | —                       | 16.3                         |  |
| AM M19457              | 109                | 105.6                 | 52.4                | 44.2         | 11.3                    | 13.3            | 16.2           | 34.0                        | 13.7                    | 16.6                         |  |
| Young adult            |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| <i>D. muelleri</i>     |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| <i>D. m. lorentzii</i> |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| RML24264               | 121                | 114                   | 51                  | 47           | 11                      | 17              | 18             | 39                          | 12                      | —                            |  |
| BM13.6.18.99           | 118.5              | 111.5                 | 52                  | 46           | 13                      | 16              | 16.5           | 39                          | 12                      | 12                           |  |
| BM13.6.18.98           | 116                | 112                   | 53.3                | 45           | 15                      | 17              | 17             | 40                          | 12                      | 7.5                          |  |
| <i>D. m. mysoliae</i>  |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| BM13.3.6.23            | 107                | 99.5                  | 48                  | 41           | 13                      | 14.5            | 15             | 35                          | 10                      | 6.5                          |  |
| <i>D. m. yapeni</i>    |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| BM46.692               | 109                | 104                   | 52.5                | 42           | 12                      | 15              | 15             | 35                          | 12                      | 13.5                         |  |
| <i>D. hageni</i>       |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| NMV7577                | 121                | 117                   | 53                  | 47           | 14                      | 18              | 20             | 40                          | 12                      | 13                           |  |
| ZMB A.228.10           | 115                | 106                   | 52                  | 44           | 14.5                    | 16              | 18             | 38                          | 12                      | ca.9                         |  |
| ZMB A101.10            | 120                | 113                   | 54                  | 49           | 15                      | 18              | 19             | 39                          | 12                      | 13                           |  |
| ZMB VII.56             | 116                | 109                   | 52                  | 42           | 14                      | 17              | 17             | 40                          | 11.5                    | 11.2                         |  |
| RML12494               | 115                | 108                   | 56                  | 46           | 13                      | 19              | 17             | 37                          | 13                      | 15                           |  |
| ZMB VII41              | 109                | —                     | —                   | 42           | 11                      | 16              | 17             | 36                          | 11                      | ca.11                        |  |
| ZMB[unreg.]            | 116                | 109                   | 52                  | 47           | 12.5                    | 17              | 19             | 37                          | 12                      | 11                           |  |
| ZMB11361               | —                  | —                     | 51                  | 44           | 12                      | 17              | 19             | 38.5                        | 12                      | 14                           |  |
| RML16436               | 113                | 107                   | 51                  | 45           | 14                      | 16              | 18             | 40                          | 12                      | 15                           |  |
| RML16430               | 114                | 108                   | 53                  | 45           | 14                      | 18              | 17             | 38                          | 13                      | 15                           |  |
| <i>D. luctuosa</i>     |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| <i>D. l. luctuosa</i>  |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| BM61.8.23              | 114                | 106                   | 52                  | 42+          | 14.5                    | 17              | 17             | 35                          | 12                      | 13                           |  |
| NMW2981                | 112                | 105                   | 52                  | 45           | 14                      | 18              | 18.5           | 37                          | 11                      | ca.12                        |  |
| AM M7449               | 108                | 102                   | 51                  | 46           | 14                      | 17              | 17             | 36                          | 12                      | 15                           |  |
| <i>D. l. phyllis</i>   |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| ZMA5243                | 100                | 94                    | 49.5                | 46           | 13                      | 16              | 16             | 32                          | 11                      | 6.5                          |  |
| <i>D. atrata</i>       |                    |                       |                     |              |                         |                 |                |                             |                         |                              |  |
| AM M19460              | 119                | 115                   | 54.5                | 48.5         | 11                      | 16.5            | 19             | 37                          | 13.3                    | 14.6                         |  |
| AM M19456              | 100.6              | 95.5                  | 49.3                | 39.8         | 10                      | 12.3            | 14.5           | 35.5                        | 10.3                    | 13.8                         |  |

least in males; the single available fully adult male skull is considerably larger than the three young adults (i.e., with all molars erupted but sphenoccipital synchondrosis ["basilar suture"] unfused) (Table 1). Nasals somewhat broadened posteriorly, less rounded into frontals than other subspecies. Zygomatic arches bowed outward, Teeth (incisors, canines, cheekteeth) large (Table 2).

Distribution: Apparently the southern peninsula of Cenderawasih.

Specimens seen: RML 13473 (Jentink's cat.b, cat.ost.a), skin, skull and skeleton, from Lobo

Bay 3.51°S, 134.04°E, lectotype of *muelleri* Schlegel; RML 13474 (cat.a

Bay, and probably syntypes of *asiaticus* Gray; BM 41.1109, skin, no locality.

Notes: There are possibly two separate subspecies among these specimens. The two Lobo Bay skins have the hair-shafts more reddish with the bases barely detectably paler, while the two from Andai have darker, more clay-brown shafts with the bases a clearly (but not sharply) lighter version of the same. Without larger series from each locality, preferably backed up by cranial characters, it is impossible to confirm the consistency of these differences.

(b) *Dorcopsis muelleri lorentzii* Jentink, 1908

1908 *Dorcopsis lorentzii* Jentink. Alkmaar, Noord River, Irian Jaya.

Diagnosis: Dorsal colour medium fawn to deep chocolate brown, the dark skins predominating; hairs absolutely unicoloured from base to tip. Arms fawn; legs not contrasting as much with body. Underside grey-white to creamy yellow, forming a wedge in front of stifle. Throat whiter than rest of underside; muzzle white. A single scapular whorl, inconspicuously expressed; often showing a slight tendency to double (Fig. 4a, b). Claws dark, to black. Tail naked for one-tenth to one-sixth of its length, slightly depigmented at tip. Skull apparently as in nominotypical *muellerii*, but palatine vacuities tend to be shorter, more oval, often divided by struts into two or more on one or both sides.

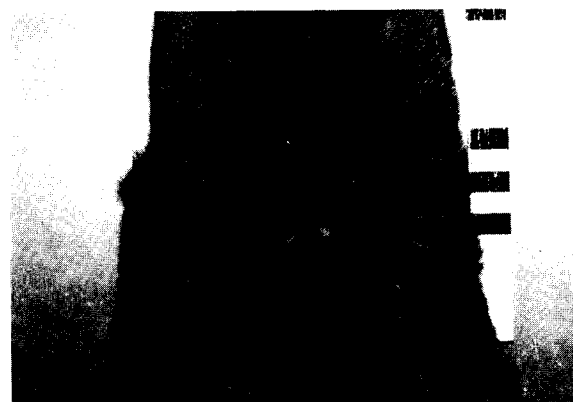
Distribution: Mainland of Irian Jaya, at least south of the main cordillera.

Specimens seen: RML 24254, subadult skull, from Alkmaar (4.40°S, 138.43°E), lectotype of *lorentzii*; RML 24253 and -5, skulls, from Alkmaar, paratypes of *lorentzii*; RML 24235, 24265, -, -7, -9, -70, skins and skulls, from Alkmaar; RML 24268, skull only, Alkmaar; RML unregistered, skin only, Alkmaar; RML 24264, subadult, skull only, Van Weel's Camp (4.51°S, 138.45°E); ZMB 91751, -2, -3, skins and skulls, from Lower Menoo, Weyland Range (3.43°S, 135.24°E); BM 1939.2912, skin and skull, Setakwa River (4.18°S, 137.17°E); BM 13.6.18.96., -7, -8, -9, skins and skulls, Setakwa River; BM 11.11.11.105, -6, -7, -8, -9, -10, skins and skulls (mostly subadult), from Mimika River (4.43°S, 138.28°E); BM 22.3.23.10, skin and skull from Kloof Bivak, Noord River (4.39°S, 138.42°E); ZMA 17.990, -1, skins and skulls, Kloof Bivak.

Notes: This is the best-represented of the subspecies of *D. muelleri*, well distinguished from all others, especially by the unparallelled unicoloured nature of the hairs. The three Weyland Range specimens are rather darker than most others, their undersides more creamy yellow. The adult male skulls are all much larger



(a)



(b)

Fig. 4. Hairwhorl patterns in *D. m. lorentzii* (a) BM 22.3.23.10 Kloof-bivak; (b) BM 11.11.11.109 Mimika River.

than those of adult females or subadults of either sex; evidently sexual dimorphism is established largely by male hypermorphosis. The teeth of the two sexes, with the possible exception of the incisors, are the same size (Table 2).

(c) *Dorcopsis muelleri mysoliae* Thomas, 1913

1913 *Dorcopsis mysoliae* Thomas. Mysol Island (=Pulau Misool).

Diagnosis: Overall tone dull brown; shafts dark brown, bases very pale grey. The limbs, especially the legs, contrast very considerably with the body in their lighter, greyer colour. Underside grey to white, sharply set-off from upper side, without a lateral wedge in front of stifle; throat white; cheeks light, grading into dark colour of head. Claws light in colour. Hair plush; most skins have long conspicuous partings from armpits up to shoulders (Fig. 5), but a few have paired whorls as in nominotypical *muelleri*. Nearly one-fifth of tail is naked, this region being very sharply set-off from haired part; tail-tip is dark. Posterior ends of nasal evenly convex, less rounded than in mainland races; premaxillary/maxillary suture straight, not sinuous like mainland forms; zygomatic straight-sided rather than outbowed; palatine vacuities broad, rounded. Size small; skulls of both sexes equivalent in size, in both



Fig. 5. Hairwhorl of *D. m. mysoliae*. BM 61.12.11.23 Misool.

adults and (apparently) young adults — i.e. no hypermorphosis in male.

Distribution: P. Misool.

Specimens seen: BM 61.12.11.22, skin and skull, type of *mysoliae*; BM 61.12.11.23-4, skins and skulls; BM 13.3.6.23, skin and skull; RML *muelleri* cat.e, f, g, h, i, j, k, l, m, skins, and cat.ost.i, j, k, l, m, skulls; ZMA, unregistered, skin only; ZMB 22402, skull only; ZMZ, unregistered, skin only. (All are from Misool).

Notes: The difference between the skins with the parting and those with the whorls is so striking that we initially considered whether they might represent two species; but no other differences are apparent, so we ascribe it to polymorphism. (There are no intermediate states). RML cat.f, k and m have whorls; all the rest, in all collections, have partings.

(d) *Dorcopsis muelleri yapeni* n.subsp.

Type: BM 46.691, adult male skin and skull, Pulau Yapen (=Japen Island), Irian Jaya, Indonesia.

Diagnosis: Most closely resembles *D. m. mysoliae*, but with the following differences: overall colour browner; hair bases pure white; arms

more contrasting in tone. Transverse partings present as in most *mysoliae*, but fail to reach mid-line of shoulders (Fig. 6). Claws pale brown. Fur still thicker, more plush. Compared to mainland subspecies (but *mysoliae* is unknown in this respect), the extremities (tail, hindfoot, ears) are relatively shorter (Table 3); this is not a purely paedomorphic (progenetic) phenomenon, as extremities cease growth earlier than the body as a whole, so that in mainland taxa, and other species of the genus, the ratios of various extremities to head plus body length are higher in young than in adults. Premaxillary-maxillary suture strongly angled in middle. Posterior nasal margin straight, less convex than in any other subspecies. Size apparently as in *mysoliae*, with perhaps greater increase between young and full adult stages, in both sexes. Midlinks on molars more strongly developed than other subspecies. The incisor row is shorter than in other subspecies, and the secutor averages smaller especially compared to the molar row (Table 2).

Distribution: Pulau Yapen (formerly spelt Japen).

Specimens seen: BM 46.691 (the type), -2, -3, skins and skulls, all from P. Yapen.

Notes: Although there are only three specimens in collections, this subspecies seems so distinctive in so many characters that we have no qualms about naming and describing it. Other characters, less clearly discernable on univariate analysis (Table 1), are shown by the Discriminant Function analysis, on both cranial and dental characters (Figs 1-2). All three skulls show a feature which is very rare, though not unknown, in other taxa: the palatine vacuities are open behind, reflecting failure of ossification of the post-palatine bars.

A photograph of a living *D. muelleri* from Danau Biru, in the Mamberamo River district of Irian Jaya, kindly sent to us by Dr Ron Petocz, shows an animal resembling *D. m. yapeni* in its short, straight transverse partings, but seemingly much greyer in tone. Museum specimens from this region are entirely lacking.

Table 3. External measurements of *Dorcopsis*.

|                        | (Adults and subadults only) |                              |                         |
|------------------------|-----------------------------|------------------------------|-------------------------|
|                        | Tail as % head plus body    | Hindfoot as % head plus body | Ear as % head plus body |
| <i>D. muelleri</i>     |                             |                              |                         |
| <i>D. m. lorentzii</i> | 60.2-70.6(11)               | 20.7-23.6(10)                | 7.1- 9.7(8)             |
| <i>D. m. salawatti</i> | 71.3 (1)                    | 23.0 (1)                     | 9.4 (1)                 |
| <i>D. m. yapeni</i>    | 57.8-59.2(2)                | 18.3-18.9(2)                 | 5.5- 6.1(2)             |
| <i>D. hageni</i>       | 68.8-75.0(4)                | 22.3-26.7(3)                 | 8.3- 8.7(3)             |
| <i>D. luctuosa</i>     |                             |                              |                         |
| <i>D. l. luctuosa</i>  | 59.0-67.9(5)                | 21.1-24.5(4)                 | 8.0-10.9(4)             |
| <i>D. l. phyllis</i>   | 57.0-58.8(2)                | 20.9-21.4(2)                 | 10.1-10.3(2)            |
| <i>D. atrata</i>       | 51.3-56.9(6)                | 16.3-18.2(5)                 | 4.0- 6.0(5)             |



Fig. 6. Hairwhorl of *D. m. yapeni*. BM 46.692 Yapen.



Fig. 7. Hairwhorl of *D. muelleri*. BM 33.11.4.4 Salawatti.

(e) *Dorcopsis muelleri* subsp. from Salawatti.

Specimens seen: BM 33.11.4.4, skin and skull; RML 13477 (cat.n.), skin only; RML 13478 (cat.o, cat.ost.i), 13479 (cat.p, cat.ost.j), skins and skulls; RML 13480 (cat.ost.e), skull only. All these specimens are juveniles.

We are fairly sure that the P. Salawatti *Dorcopsis* will prove to be a distinct subspecies of *D. muelleri*, but it cannot be adequately defined at present because all museum specimens are juvenile. The skins all have transverse partings, as long as those of (most skins of) *mysoliae* (Fig. 7). They are medium to dark brown, the hair-bases nearly white (not as pure white as in *yapeni*); there is a white wedge from the underside in front of the stifle, the limbs are contrastingly paler than the body; the tail-tip is depigmented; the claws are an off-white colour. The scaptor is curved inward anteriorly (one specimen only). Other characters resemble nominotypical *muelleri*, as far as can be made out.

(2) *DORCOPSIS LUCTUOSA* (D'Alberty, 1874). Grey Dorcopsis.

Diagnosis: Colour very dark, greyish ("olive-silvery-brown" is an apt description of many specimens) (as opposed to brown as in *D. hageni* and *D. muelleri* and black in *D. atrata*); hair-bases pale brown or grey. Limbs not contrastingly lighter than body; hands and feet blackish. Underside drab greyish to creamy orange, not sharply set-off from upperside (sharply set-off in *D. muelleri*, and blackish brown in *D. atrata*); chest nearly black; throat pale grey-brown, contrasting with head which is nearly black. Claws dark. A whorl just behind each axilla is prolonged into a back-curving hair-part; the hair-stream anterior to this does not run forward, but merely somewhat more medially than that posterior, so that the whole effect is of a V-pattern running back from axillae to just behind scapula, which is unique in the genus (Fig. 8). Cranially, the rostrum is very narrow (broader in *D. muelleri*

and *D. hageni*); the premaxillary-maxillary suture is angled; the nasals are straight-sided; the naso-frontal suture is flared but does not wedge far backward into the frontals; the postorbital processes are less produced, more shelflike, than in *D. muelleri*; the palatine vacuities are long, with very thin (sometimes unossified) bars behind; the basicranium is constricted in the middle. Tooth-rows are curved in at the back, not straight and parallel (as in *D. muelleri* and *D. hageni*). Secators are short, and more sexually dimorphic in relative size than in *D. muelleri*. The midlinks on the molars are poorly developed.

Distribution: The south-east coastal lowlands of New Guinea, from Merauke to Milne Bay (Fig. 3).

Notes: Except for George and Schurer (1978), George (1979) and Archer, Flannery and Grigg (1985), this taxon has not been distinguished, in recent years, even subspecifically, from *D. muelleri*. We find it to be a highly distinctive species, cranially and dentally perhaps the most distinctive of all in the genus.



Fig. 8. Hairwhorl of *Dorcopsis luctuosa* holotype BM75.4.16.1 south-east New Guinea.

(a) *Dorcopsis luctuosa luctuosa* (D'Alberty 1874).

1874 *Halmaturus luctuosus* D'Alberty. "South-east New Guinea".

1884 *Dorcopsis chalmersii* Miklouho-Maclay. South coast of New Guinea, opposite Samarai Island.

1885 *Dorcopsis beccarii* Miklouho-Maclay. Hills around Port Moresby.

Diagnosis: Size large; strongly sexually dimorphic; teeth relatively large; tail, hindfoot, ears relatively long; colour medium to dark grey or fawn-grey.

Specimens seen: BM 75.4.16.1, juvenile skin and skull, "south-east New Guinea", type of *luctuosa*; RML cat.ost.a, skull only; BM 8.10.8.3, skin and skull, Epa (8.44°S, 146.43°E); ZMB 22717, skull only, Epa; BM 76.10.28.3, -4, -5, juvenile skins and skulls, Aleya; AM 7385 and 7449, skins and skulls, Laloki district, Port Moresby; AM 8665, 7052, 3663, skins and skulls, Port Moresby; AM 15288, skin and skull, Taronga Zoo, of stock from Brown River area, Port Moresby; AM M19464, skin and skull, Vaimuri logging area, near Port Moresby; NMV 2981, skull only, Port Moresby; Macleay, M383, skin only, Port Moresby, type of *beccarii*; Macleay, M399, skin only, Port Moresby; ZMB 6035, skull only, Laloki; AM 790, skin and skull, Astrolabe Range (9.33°S, 147.26°E); ZMB 11521, Astrolabe Range; BM 6.1.8.23, skull only, Upper Gira River (7.59°S, 147.59°E); AM S1863, skull only, Mt. Lamington; NMV C26610, 23027, 16188, 18536, 18513, 18599, 18600, skins and skulls, mostly juvenile, all from Healesville Sanctuary, ex Port Moresby; NMV C10784,

11300, skins and skulls, Melbourne Zoo, ex Port Moresby.

Notes: All these specimens are remarkably homogenous, varying only in the tone of the body colour. AM 790, however, has an elongated whorl in the midline of the back as well as the typical V pattern.

(b) *Dorcopsis luctuosa phyllis* n.subsp.

Type: ZMA 5243, adult female skin and skull, Merauke (8.27°S, 140.22°E) (Fig. 10).

Diagnosis: Much smaller than nominotypical *D. l. luctuosa*, with little sexual dimorphism; teeth relatively smaller; extremities shorter (Table 3); colour darker, nearly black.

Notes: This highly distinctive subspecies is, in some respects, analogous to *D. muelleri yapeni*; in particular the shortened tail, feet and ear, in combination with the smaller size, are the same in both. The type has an anomalous hair-tract pattern: the right side of the V is present, but on the left this is replaced by two small, partly connected, whorls near the midline of the back.

Specimens seen: the type; RML 17239, skin and skull, Kali Koembe, Kaisa village, west of Merauke; NMV C7096, coll. A. Goldie, 1881 (and so probably from Fly Delta); WAM M2808 (received in exchange from American Museum, formerly AMNH 108012), skull only, L. Daviumbu, Middle Fly River. Tate and Archbold (1936) give additional data on specimens in the AMNH from the Fly River.

Etymology: For Phyllis R. Groves, in recognition of her invaluable assistance to us in studying specimens, in discussion and (in the case of CPG) in general support.

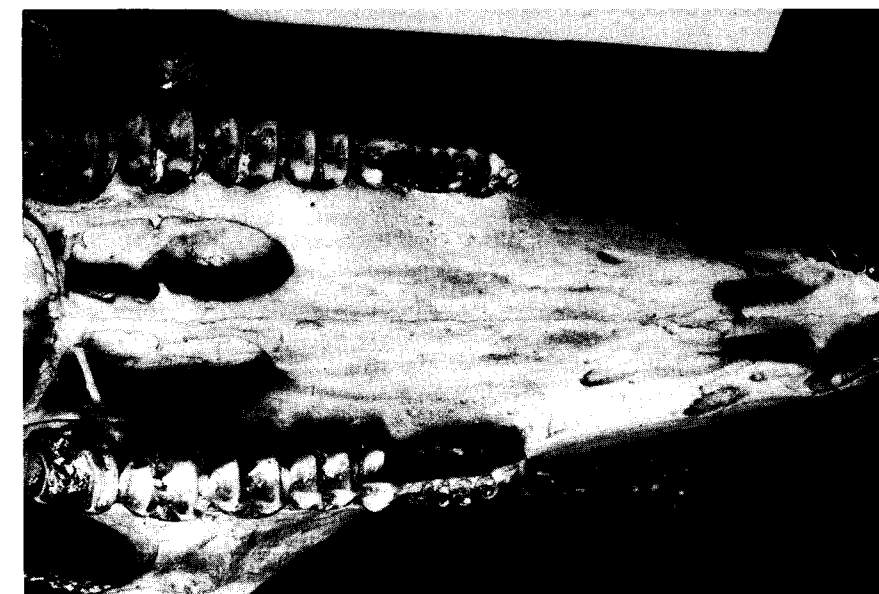


Fig. 9. *Dorcopsis luctuosa luctuosa* RML cat.ost. a, palatal view.



Fig. 10. Dorsal views of study skins of (from left to right) ZMA 5243, holotype of *Dorcopsis luctuosa phyllis* n. ssp.; ZMA 17991 and 17990, *Dorcopsis muelleri lorentzi*, Kloof Bivak, Irian Jaya.

(3) *DORCOPSIS HAGENI* Heller, 1897. White-striped *Dorcopsis*.

1897 *Dorcopsis hageni* Heller. Stefansort, Astrolabe Bay.

1922 *Dorcopsis hageni caurina* Thomas. Pionierbivak, Mamberamo River.

1937 *Conoyces hageni eitape* Troughton. Eitape (=Aitape).

Diagnosis: Fawn-brown, sometimes with a greyish cast, to nearly blackish-brown; a white or very pale fawn dorsal stripe from nape to root of tail (which is unique in the genus). Hair bases white. Underside grey-white. Claws light brown. Limbs contrastingly pale, fawn. Tail fawn, with a brown crest along dorsal midline of its proximal third; often a hairless callus on dorsum of root. Whorls behind axillae, but not extended into partings like *D. luctuosa*. Tail averaging longer than other species; hindfoot long. Size very large. Naso-frontal suture flared laterally, not wedging much into frontals; premaxillary-maxillary suture straight; secator (P3) broad, mesially blunt not pointed as in other taxa, and short, not more than two molar lengths (see also Table 2). Palatine vacuities tend to be short; posterior margin of palate V-shaped.

Distribution: Lowlands of northern New Guinea, from the region of the Mamberamo River in the west to the Morobe Coast (Fig. 3).

Specimens seen: LNK 535, skin and skull, Stephansort, type of *hageni*; ZMB 22369, skin and skull, Stephansort; AM M6211, skin and

skull, Aitape, type of *eitape*; AM M6 098, juvenile, skull only, Aitape; BM 1939.2911, skin and skull, Hol; RML 16430, skin and skull, Humboldt's Bay; BM 22.2.2.63, skin and skull, young adult, Pionierbivak, type of *caurina*; ZMB VII.41 and an unregistered specimen, skins and skulls, Momofolag, Lower Sepik River; ZMB A.101.10, skin and skull, Berlinhafen; ZMB VII.56, skin and skull, Malu, Lower Sepik; RML 24256, skin and skull, Tami River (2.41°S, 140.51°E); ZMB A.228.10, skin and skull; RML 12494, skin and skull, Tami River; RML 16436, skin and skull, Lake Sentani; NMV 7576, skin and skull, juvenile, Ramu River (Arim); ZMB 11861, skin and skull, Ramu River; NMV 7577, skin and skull, Potsdamhafen; AM13633-4, 17202-3 skin and skull, AM13636, skull only, Yapsiei area, Lower August River; AM19062, skin and skull, Wara Bruk, Madang Province.

Notes: Despite its strongly divergent external appearance, this species is cranially and dentally very close to *D. muelleri*. There is considerable individual variation, which to some extent is geographically circumscribed. A blackish morph, in which the dorsal stripe is relatively inconspicuous, occurs at Pionierbivak, Malu and Monofolag; a grey-fawn-brown type with a white dorsal stripe occurs at Hol, Berlinhafen, Queen Augusta River, Tami River, and Aitape; while a dull brown form with fawn-toned stripe is from Astrolabe Bay. The series from Yapsiei in the Australian Museum range from fawn to dark brown. The type of *caurina*, though far from mature, is the largest specimen of the whole genus seen in the present study.

(4) *DORCOPSIS ATRATA* Van Deusen, 1955. Black *Dorcopsis*.

Diagnosis: Colour black dorsally (unique in the genus), venter blackish brown (also unique), both with white underfur. Ears and tail relatively shorter than in other *Dorcopsis*. Pelage long and luxuriant relative to all other *Dorcopsis* species. Dorsal hair tracts divided by a single whorl at the level of the scapulae. Skull and particularly nasals narrower than in other *Dorcopsis* species. Premolars hypsodont and short. On average smaller than any mainland *Dorcopsis* species.

Distribution: Montane rainforests between 1 000 and 1 800 m on Goodenough Island, D'Entrecasteaux Group, Papua New Guinea (Fig. 3).

Specimens seen: AM M19456 female skin and skull; AM M19260 male in spirit; AM M19459 female skin and skull; AM M19461 male skin, skull, skeleton; AM M19458 male skin and skull; AM M19460 female skin and skull; AM M19457 female skin and skull; AM M19462 skeleton.

#### DISCUSSION

Distribution: All *Dorcopsis* species except *D. atrata* are confined to lowlands (below 400 m). *D. atrata* differs markedly in habitat needs from the others in that it inhabits mid-montane rainforest on very steep terrain (pers. obs. TFF). In the experience of TFF in West Sepik Province is that *Dorcopsis hageni* is never found in even the lowest foothill forest, but can be abundant on the river floodplains. Present understanding of the distribution of the species of *Dorcopsis* suggest that the three mainland taxa recognized by us are parapatric. Unfortunately, collections of *Dorcopsis* from regions where the species are likely to abut are few (Fig. 3). Only in northern Irian Jaya have we records of two taxa in close proximity, where *hageni* and *muelleri* have been recorded on the lower Mamberamo River. No intergradation is evident in this case, and the Mamberamo may form a boundary between these two taxa.

Relationships: A number of features suggest that *Dorcopsis luctuosa* may be the sister taxon to all other species of *Dorcopsis*. Apparently derived features shared by all taxa except *D. luctuosa* include: posterior nasal narrowing, straight toothrows, concave post palatal margins, relatively short nasals, and a relatively broad basi-cranium. Within the clade containing the three remaining species, *D. atrata* is the most autapomorphic, and may be the sister taxon to a *muelleri-hageni* clade. Its short ears and tail are reminiscent of *Dorcopsulus* spp. from montane New Guinea, but this may be convergence due to habitat similarities.

#### SUMMARY

There are four species of *Dorcopsis*. *Dorcopsis atrata* and *D. hageni* and monotypic, while *D. luctuosa* includes two subspecies and *D. muelleri* four. *Dorcopsis luctuosa* may be the sister taxon to the remaining species.

#### ACKNOWLEDGEMENTS

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#### APPENDIX

Measurements used in discriminate function analysis: greatest skull length; condylobasal length; basilar length; bimastoid breadth; braincase breadth; interorbital breadth; nasal length; least nasal breadth; greatest nasal breadth; snout breadth; snout height; upper cheektooth length; upper

incisor row length; total upper toothrow length; molar row length; palate breadth; incisive foramen length; P<sup>3</sup> length; P<sup>3</sup> breadth; M<sup>2</sup> length; M<sup>2</sup> breadth; Dentary height; palatal fenestra maximum length.

## Diets of macropodoid marsupials: General patterns and environmental influences

TERENCE J. DAWSON<sup>1</sup>

Information available on the diets of the Australian macropodoids has been reviewed. The characteristics of the vegetation have also been considered in terms of digestibility by enzymic or fermentative means. Rough or fibrous plant material requires extended fermentative digestion and is consequently not a reasonable diet option for most small species.

Diet variation shows some basic patterns, with body size being the most important. The small species, such as rat-kangaroos, tend to be specialized, feeding on high quality but scattered foods. Intake of underground fungi is especially significant to some species. The "medium" size macropodoids tend to be more generalist feeders and a wide variety of vegetation appears in their diet, the more common components varying with species and environment. Characteristic of their intakes is a relatively low fibre content. Even when browse is taken, on close observation, it is apparent that the animals are selecting the lower fibre parts of the plants. The large macropodoids, especially the kangaroos, are specialist grass eaters. The Red Kangaroo may be less selective than the other species, perhaps by necessity.

When communities of macropodoids are examined, resource partitioning appears evident. However, the basis of this is unclear and we cannot yet assess the role of competition in diet selection or community structure. A similar picture is seen when the interaction between macropodoids and domestic stock is considered. Diet overlap can occur between the kangaroos and sheep and cattle, notably with grass, but the fine detail of such overlap has yet to be examined. Competition among these species is a very complex issue. While it is suspected to occur in some situations, firm evidence is sparse.

#### INTRODUCTION

THE macropodoids are the dominant native mammalian herbivores of the Australian continent. Numerous herbivorous, quadrupedal marsupials also existed until the late Pleistocene megafaunal extinctions some 20 000-40 000 years ago (Archer 1984), but whether it was Aboriginal man, climatic change or both that led to these extinctions, the macropodoids survived with considerable diversity. Currently, there is concern for the survival of these unusual herbivores, but also worry about competition with domestic herbivores. My interest in the diets of the macropodoids is related to both of these concerns. However, this review will examine only the general patterns in the diets of macropodoids because other papers in this volume will deal with specific aspects e.g., kangaroo-sheep competition (Edwards, this volume).

Insights gained from this examination of diets may form a basis to help answer a series of important questions. What habitats do the macropodoids require for continued food and shelter? What vegetation do they consume that might have been available for animal production? Does the combined impact of wild and domestic herbivores result in pasture degradation to the disadvantage of all? Pasture degradation seems to have occurred in the early days of the grazing industry in our arid and semi-arid rangelands (Williams and Oxley 1979) and associated with this there was a marked decline in the species richness of native mammalian herbivores.

The earliest of the macropodoids probably arose in the mid-Tertiary, 15-20 MYBP (Archer 1984). These were inhabitants of the floor of the temperate forests that then covered Australia (Truswell and Harris 1982). The Musky Rat-kangaroo, *Hypsiprymnodon moschatus*, of the northern Queensland rainforests is considered a modern example of this body-form and life-style. It feeds on invertebrates, fruit, seeds and leaves. The stomach is relatively simple but, as pointed out by Highway (1939, cited in Hume 1982a), it is partly compartmentalised (Fig. 1) and therefore is intermediate between the simple stomachs of the possums and the complex forms of the wallabies and kangaroos.

Complex stomachs are the hallmark of the macropodoids and the basis of their success as herbivores (Hume 1982a). The expanded forestomach is basically a large vat in which plant material is partially digested by micro-organisms. The role of these micro-organisms is very complex. They provide a macropodoid with many necessary products but it is their part in the extraction of energy from complex plant carbohydrates that is most important. These carbohydrates are largely the structural components of cell walls, often referred to as fibre, and they can be broken down only by fermentation.

The fermentation by micro-organisms, mainly bacteria, is carried out in an oxygen-free (anaerobic) environment. Because oxygen is not available the micro-organisms are able to extract only a small amount of energy from the

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