THE BRONZE QUOLL, *DASYURUS SPARTACUS* (MARSUPIALIA: DASYURIDAE), A NEW SPECIES FROM THE SAVANNAHS OF PAPUA NEW GUINEA

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Van Dyck, S., 1987. The Bronze Quoll, *Dasyurus spartacus* (Marsupialia: Dasyuridae), a new species from the savannahs of Papua New Guinea. *Aust. Mammal.* **11**: 145-156.

Dasyurus spartacus sp. nov. is described from the low mixed savannahs of southwestern Papua New Guinea. It differs from all other species of *Dasyurus* in the extreme narrowness of the rostrum measured between left and right lachrymal canals. Its hallux and ear lengths are small. *D. spartacus* is a specialised species; its affinities lie with *D. albopunctatus* and possibly *D. dunmalli* (a fossil species).

Key words: *Dasyurus spartacus*, marsupial, Papua New Guinea, phylogeny.

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UNTIL 1979 *Dasyurus albopunctatus* Schlegel, was the only quoll known from Papua New Guinea. In that year J. Waithman published results of a mammal survey undertaken in the Trans-Fly Plains of southwest Papua New Guinea during 1972-3. Part of this collection included 5 specimens of a *Dasyurus* referred to *D. geoffroii* (Waithman 1979) collected at Morehead, Mibini and Mari. Subsequent references to this *Dasyurus* have also been made under the specific title of *geoffroii* (Ziegler 1977, Archer 1979, Archer 1982, Honacki, Kinman and Koeppl 1982, Arnold 1983, Taylor 1984). It is now clear that these specimens represent a new species of *Dasyurus* which is described here as *D. spartacus*.

MATERIALS AND METHODS

Dasyurus systematics follow Kirsch and Calaby (1977); terminology of cranial, external and dental morphology follows Archer (1981); and tooth number follows Archer (1978). Cranial and dental measurements were made with NSK electronic digital calipers after the method shown in Table 1. All specimens compared in diagnosis were adults with fully erupted $P\frac{3}{3}$.

Specimens of *Dasyurus* were examined in each of the following museums: Bernice Bishop Museum, Honolulu (BBM); British Museum (Natural History) London (BM); Rijksmuseum van Natuurlijke Histoire, Leiden (RMNH); American Museum of Natural History, New York (AMNH); Museum National D'Histoire Naturelle, Paris (MNHN). Additional specimens examined and mentioned in this paper have registration numbers prefixed as follows: National Museum and Art Gallery, Papua New Guinea, Boroko (PM); Queensland Museum Brisbane (J, JM or F); Western Australia Museum, Perth (WAM); Australian Museum, Sydney (M).

I have examined the following holotypes: *Dasyurus geoffroii geoffroii* Gould 1841 (BM 41.1213), *D. g. fortis* Thomas 1906 (BM 6.8.1.340), *D. hallucatus hallucatus* Gould 1842 (BM 42.5.26.16), *D. h. exilis* Thomas 1909 (BM 9.4.23.8), *D. h. predator* Thomas 1926 (BM 15.3.5.77) *D. h. nesaeus* Thomas 1926 (BM 26.3.11.25), *D. albopunctatus albopunctatus* Schlegel 1880 (RMNH Specimen a.), *D. a. fuscus* Milne-Edwards 1880 (MNHN 1880-1463), *D. a. daemonellus* Thomas 1904 (BM 3.12.1.24), *D. dunmalli* Bartholomai 1971 (F 6579). The holotypes of *D. viverrinus* (Shaw 1800) and *D. maculatus* (Kerr 1792) are presumably lost.

SYSTEMATICS

Dasyurus spartacus sp. nov. (Fig. 1, Table 1)

Holotype. PM 22000, adult male, dry skin, skull and dentaries, collected 11 April 1973 by J. Waithman.

Type locality. Morehead, Trans-Fly Plains, Papua New Guinea 8°41'S, 141°39'E (Fig. 2).

Paratypes. From Morehead, adult male PM22004 in ethanol with skull extracted, collected 25

Specimen	Sex	Loc	BL	ZW	IO	I^1-M^5	P^{1-2}	M^{2-5}	I_1-cond	I_1-M_5	P_{1-2}	M_{2-5}	RW(l)	HB	TV	HF(su)	E(n)
PM22000	adult M	Morehead	70.2	43.8	9.6	36.9	6.3	17.6	59.6	34.2	7.0	20.5	17.7	345	285	55	30
PM22001	juv M	Morehead	37.3	22.8	9.6	-	4.4	-	31.2	-	4.5	-	12.6	125	100	30	24
PM22002	juv F	Mibini	52.2	31.4	11.1	-	5.8	-	42.3	30.2	5.4	20.2	16.0	230	202	47	33
PM22003	adult F	Mari	66.5	39.0	9.2	35.9	7.3	17.2	55.2	32.6	6.6	19.3	17.8	305	250	54	36
PM22004	adult M	Morehead	74.4	47.3	10.5	38.8	7.1	17.5	63.7	35.6	6.9	20.7	19.5	380	240*	55	41

Table 1. Measurements for holotype and paratypes of *Dasyurus spartacus.* Abbreviations as follows: BL = basicranial lenth, IO = interorbital width (measured dorsally), RW(l) = rostrum width measured between lachrymal canals, ZW = zygomatic width.

November 1973 by H. Parnaby; juvenile male PM22001, puppet skin with skull extracted, collected 17 May 1973 by J. Waithman.

From Mari (oil line No. 1) 9°11'S, 141°42'E, adult female PM22003 skull only, collected 18 July 1973 by J. Tametona.

From Mibini 8°50'S, 141°38'E, juvenile female PM22002 skin with skull extracted, collected 26 June 1973 by J. Waithman.

Diagnosis. *D. spartacus* is a medium sized but thick set *Dasyurus* immediately separable from all other species of *Dasyurus* by the extreme narrowness of the rostrum measured between left and right lachrymal canals (Fig. 3). It also possesses a reduced hallux (Fig. 4) and the pinna is small.

Externally. Unlike *D. maculatus, D. spartacus* lacks white spots on the tail and lacks striate pads on the fore and hind feet. *D. spartacus* differs from *D. maculatus* in being much smaller (eg. head-body length adult male *D. maculatus* (J8059, in absence of holotype) 605 mm, *D. spartacus* (holotype PM22000) 345 mm, and having much smaller white spots on the body (average diameter of side spots in *D. maculatus* (J8059) 34.4 mm, in *D. spartacus* (holotype PM22000) 5.4 mm.

D. spartacus differs from *D. viverrinus* (Shaw, 1800) in having a hallux.

D. spartacus differs from *D. geoffroii* in having a body colour a deep bronze to tan brown with a black tail and much smaller white body spots (average diameter of side spots in *D. geoffroii* (holotype BM41.1213) 12.1 mm, in *D. spartacus* (holotype PM22000) 5.4 mm. *D. spartacus* possesses a vestigial hallux (Fig. 4) which is approximately 58% smaller than that in *D. geoffroii* (eg. *D. spartacus* (spirit specimen PM22004) 2.1 mm, *D. geoffroii* (spirit specimen JM2057) 4.9 mm. *D. spartacus* has much smaller ears (eg. *D. spartacus* (holotype PM22000) 30.0 mm, *D. geoffroii* (holotype BM41.1213) 60.0 mm.

D. spartacus lacks the striate pads on fore and hind feet present in *D. hallucatus* and *D. albopunctatus. D. spartacus* also differs from *D. hallucatus* and *D. albopunctatus* in being larger (eg. head-body length adult male *D. hallucatus* (JM 5701, in absence of measurements accompanying holotype) 285 mm, *D. albopunctatus* (M14853, in absence of measurements accompanying holotype) 266 mm, *D. spartacus* (holotype PM22000) 380 mm.

Internally. *D. spartacus* differs from *D. maculatus* in being much smaller (adult male basicranial length *D. maculatus* (J8935, in absence of holotype) 96.7

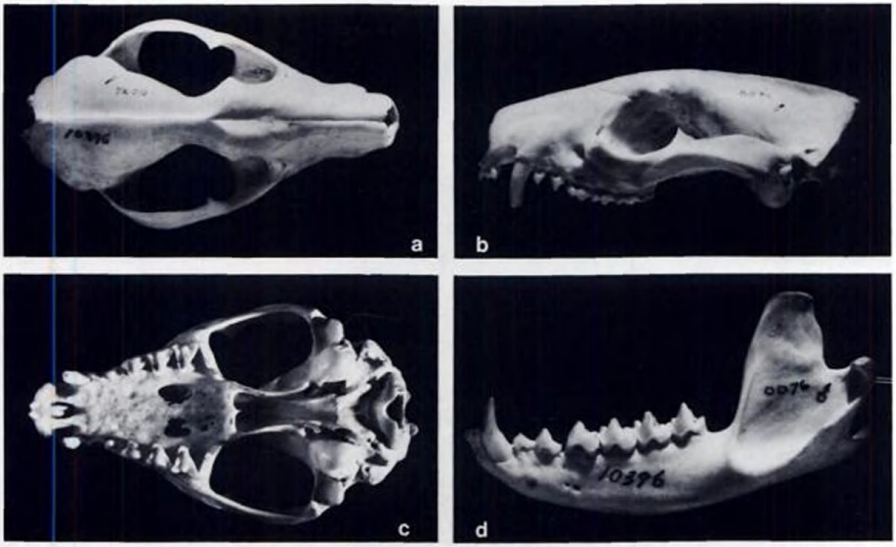

Fig. 1. Dasyurus spartacus, skull and dentary of holotype PM22000; scale, a x 0.80, b x 0.80, c x 0.83, d x 1.12.

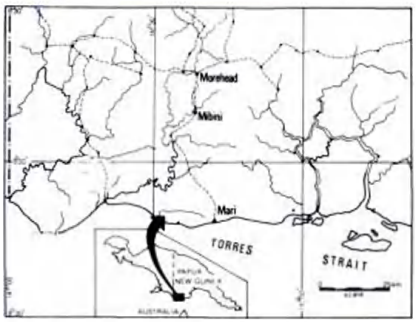

Fig. 2. Map showing collection sites (Morehead, Mibini and Mari) of *Dasyurus spartacus* in Papua New Guinea.

mm, *D. spartacus* (holotype PM22000) 70.2 mm. *D. spartacus* also has a procumbent and separated I^1, a metaconid on M_2 and a short, crushed premolar row.

D. spartacus differs from *D. viverrinus* in having a procumbent and separated I^1, greatly reduced metaconids, and a short and crushed premolar row.

D. spartacus differs from *D. geoffroii* in having a short and crushed premolar row with broad, bulbous premolars.

D. spartacus differs from *D. hallucatus* in being much larger (basicranial length adult male *D. hallucatus* (J16752 as holotype is female) 62.5 mm, *D. spartacus* (holotype PM22000) 70.2 mm, having a 'U' shaped incisor row, having the metacone of M^2 posterior to stylar cusp D, having M^5 reduced with no metacone, having metacrista of M^3 shorter than the metacrista of M^4, having metaconids reduced and having a short and crushed premolar row with bulbous premolars.

D. spartacus differs from *D. albopunctatus* in being larger (adult male basicranial length *D. albopunctatus* (M14854, as holotype is female with smashed skull) 57.0 mm, *D. spartacus* (holotype PM22000) 70.2 mm, and in having less reduced metaconids.

Description. A thick-set, narrow-nosed quoll distinctive for its rich dark, golden-brown tonings, minute white spots, dark golden-bronze feet and dark tan tail.

Pelage. Colour for holotype as follows (colour names after Ridgway 1912); dorsal fur above shoulders 11.2 mm with basal 4.5 mm fine, silky, apical 6.7 mm medially thickened, spinous. Basal 8 mm Clove Brown (dark chocolate), median 1.6 mm Ochraceous-Tawny (orange-brown), apical 1.6 mm Fuscous Black. Fur of back between shoulders appears as dark chocolate flashed with orange.

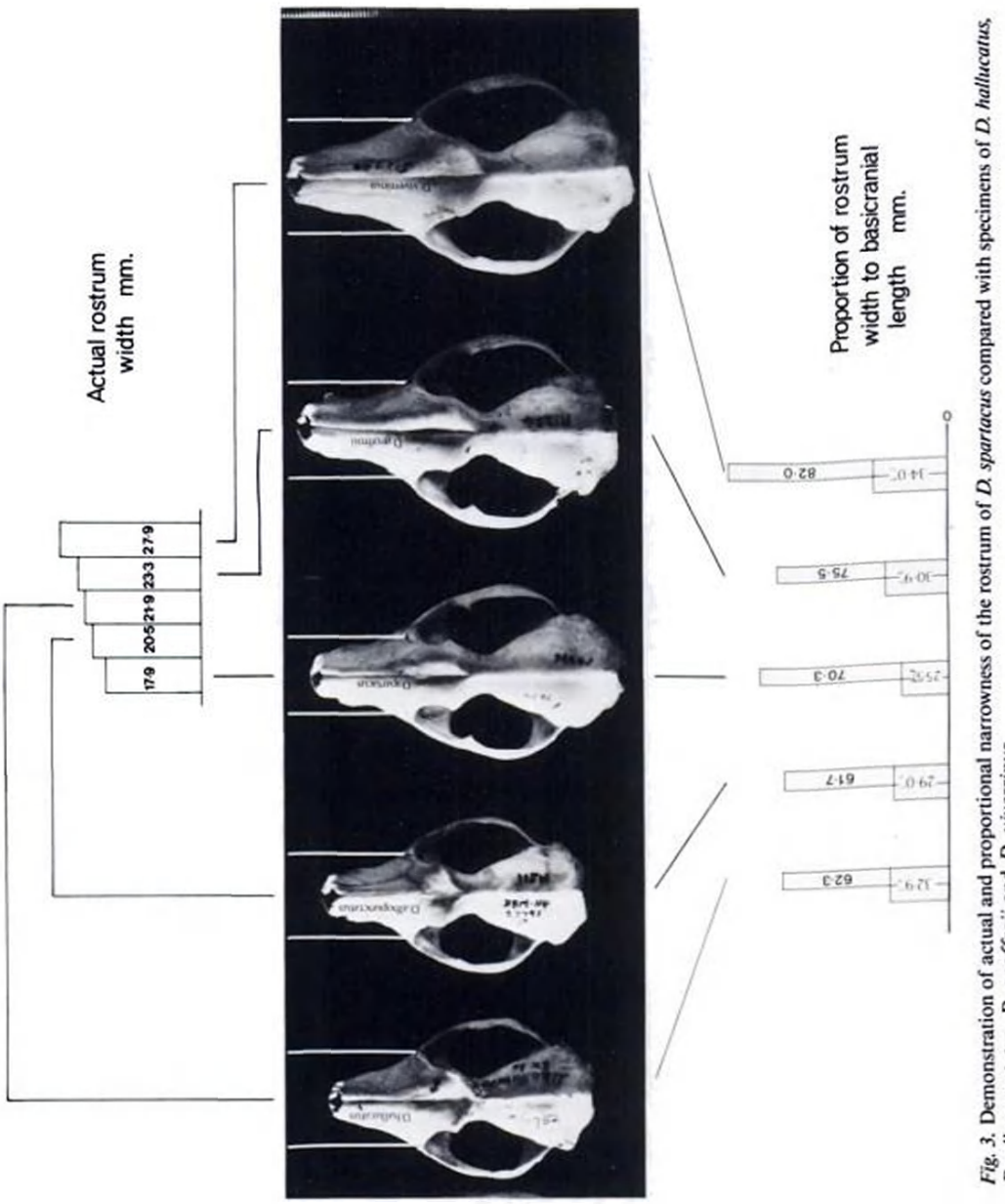

Fig. 3. Demonstration of actual and proportional narrowness of the rostrum of *D. spartacus* compared with specimens of *D. hallucatus*, *D. albopunctatus*, *D. geoffroii* and *D. viverrinus*.

Clove Brown extends anteriorly to tip of nose and posteriorly to tip of tail. On head, relatively long hair (10 mm) lacks tawny band thereby creating very dark (Clove Brown) triangular head patch from nose, above eyes, back to between ears. Hair between eye and ear and for 4 mm above each eye has median band (up to 20 mm long) Chamois (light yellow). Band may increase to 4 mm below eye so that sides of face contrastingly light against dark head-patch.

Hair on rump (to 9 mm long) similar colour to shoulders but median Ochraceous-Tawny band slightly longer (2.5 mm). Sides of body, forearms, thighs characterised by increase in length of median colour band (Yellow Ochre), to 6 mm (on hair of

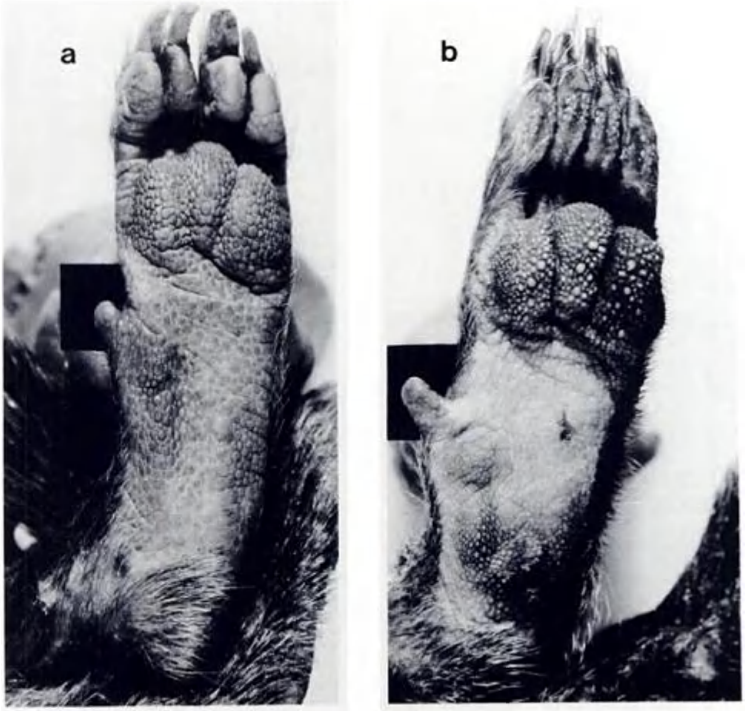

Fig. 4. Left hind foot of a. *Dasyurus spartacus* (PM22004) and b. *D. geoffroii* (JM2057) showing the reduced hallux in *D. spartacus.*

11 mm) so overall colour of sides is bright golden-bronze. Belly fur soft, to 21 mm between hindlegs, Cream Colour (almost colourless).

Tail short-haired for basal ⅓, more distally hair lengthens to 37 mm at tip and darkens to Fuscous Black (black) at tip. Tail shorter haired and lighter coloured ventrally. Hair on upper surface hind and forefoot, a shiny Sepia.

Small white spots (maximum diameter 6.5 mm) occur randomly from forehead to rump. No white spots on ventral surface or on tail, fore or hindfeet.

Vibrissae. Approx. 25 mystacial vibrissae (up to 35 mm) each side in 5 distinct horizontal rows. More dorsal vibrissae Fuscous Black, more ventral colourless; supra-orbital vibrissae (Fuscous Black) number 2 left, 3 right; genals (Fuscous Black and colourless) 6 left, 5 right; ulna-carpals (colourless) 3 right, 6 left; submentals (colourless) 6.

Tail. Tail shorter (by approx. 20%) than nose-vent length, non-incrassated, bushy toward tip.

Hindfoot. Interdigital pads raised, joined, minutely granulated. Apical granules only slightly larger than surrounding granules. Slightly enlarged granule may represent hallucal granule on both feet. Metatarsal granules not present in holotype. Hair on foot covers heel. Terminal pads of digits weakly striate (Fig. 4).

Ear. Pinna very small, curled external edge on large supratagus. Fawn hairs on postero-internal and ventral margins of pinna.

Dentition (Fig. 1). Upper incisors: I^1 narrow, peg-like, procumbent, slightly curved, taller-crowned than all upper incisors; I^1 separated by large diastema from I^2. Left and right I^1 widely separated. Crown height, length subequal in I^2 and I^3. I^4 slightly greater crown height and length than

I^2 and I^3. All upper incisors lack buccal cingula yet no lack of differentiation between root and crown. I^4 with no anterior or posterior cusp. Root of I^4 narrow.

Upper canines: C^1 long, slender, caniniform with indistinct boundary between root and crown. No buccal or lingual cingula. No anterior or posterior cusp.

Upper premolars: Small diastema between crowns C^1 and P^1, P^1 and P^2, P^2 and M^3. P^1 shorter crown height than P^2. Minute anterior, posterior cingula cusps P^1 and P^2. P^2 broad postero-lingually.

Upper molars: Posterior tip P^2 not contacting parastylar corner M^2. Anterior cingulum below combined stylar cusp B-paracone short, broad, complete to prominent paraconule at base of paracone-stylar cusp B apex. Paracone-stylar cusp B of M^2 approx. half height of metacone. Stylar cusp C, E not visible on L or RM^2. Trigon basin plunges steeply from prominent metaconule down to weak posterior cingulum.

M^3, stylar cusp B and paracone separate. Broad anterior cingulum contacts metastylar corner M^2, tapers down along base of paracrista, rises steeply to base of paracone apex at prominent paraconule. M^3 lacks stylar cusps A, C and E. Stylar cusp D prominent and broad. No posterior cingulum; prominent metaconule as in M^2.

M^4, anterior cingulum complete, broader, much longer than M^3. Paraconule, metaconule prominent. Stylar cusp D reduced but broad. Stylar cusps C, E absent. Posterior cingulum absent.

M^5, broad at anterior cingulum terminates quickly away from metastylar corner M^4, posterior cingulum absent. Protocone reduced, narrow. Metastylar corner reduced.

Lower incisors: I_1 much taller crown height than I_1. I_1, I_2, I_3 oval in anterolateral view. I_1 and I_2 gouge-like in occlusal. I_2 subequal crown height I_3. All lower incisors with prominent lingual cusp. I_3 with most conspicuous posterolingual cusp almost as tall as primary incisive cusp. Lower canine rests between posterior cusp and primary incisive cusp I_3.

Lower canines: C_1 large, broad, caniniform, characterised by upward, forward projection and sickle-like curvature root to crown tip. No buccal, very weak lingual cingulation, no posterior cusp.

Lower premolars: Premolar row very short, P_1, P_2 crushed together, overlapping, separate from M_2 by small diastema. Lack buccal, lingual cingulation. Crown height P_2 much taller P_1. Premolars relatively broad, bulbous, both with weak posterior cusp, P_2 with very weak anterior cusp. Bulk of each premolar mass concentrated posterior to line drawn transversely through middle of the two premolar roots.

Lower molars: All molars broad, bulbous, tightly crushed together. M_2 talonid wider than trigonid, anterior cingulum absent. No buccal or lingual cingulum. Paraconid absent. Metaconid reduced to small bulge of enamel subequal height to minute entoconid. Metacristid greatly reduced, oblique to long axis of dentary; hypocristid more perpendicular. Cristid obliqua very short, extends from hypoconid to posterior wall of trigonid intersecting at point well lingual to point directly below tip of protoconid. Hypocristid terminates midway between hypoconid, metastylid. Long, low entoconid. From base of metaconid posteriorly entoconid forms prominent semicircular bulge of enamel (occlusal view) on endoloph. Indistinct posterior cingulum.

M_3, talonid slightly wider than trigonid. Anterior cingulum very poorly developed originating lingually in weak parastylid notch into which hypoconulid M_2 tucked. No buccal cingulum. Narrow, weak posterior cingulum almost obliterated by crushing anterior cingulum of M_4. Paraconid well developed, smallest trigonid cusp. Entoconid well developed, subequal in height to paraconid. Cristid obliqua extends from hypoconulid to posterior wall of trigonid intersecting trigonid at point directly below tip of protoconid but well buccal to metacristid fissure. From base metaconid posteriorly, endoloph follows line oblique and lingual to dentary axis.

M_4, trigonid wider than talonid. Prominent parastylid wraps around hypoconulid M_3, weak anterior cingulum on M_4. No buccal or posterior cingula. Reduced cristid obliqua intersects trigonid at point well lingual to longitudinal vertical midline drawn through tip of protoconid but buccal to metacristid fissure. Entoconid M_4 worn but was obviously large, making prominent bulge of enamel on endolph. Rest of morphology as in M_3 except that metaconid is more reduced.

M_5, trigonid much wider than talonid. Anterior cingulum as in M_3. Posterior cingulum absent. Of three main trigonid cusps metaconid slightly taller than paraconid but both dwarfed by protoconid. Hypoconid M_5 talonid much smaller than M_4. Between hypoconid and base of metacristid, cristid obliqua forms low, very weak crest, which contacts trigonid wall directly below metacristid fissure. Evidence of small entoconid.

Skull (Fig. 1). *D. spartacus* is unique amongst *Dasyurus* species in having a high skull and extremely narrow rostrum between the lachrymal canals. Sagittal and nuchal crests are highly developed. Dorsally the rostrum is gently grooved longitudinally by a depression running along the nasal sutures. One lachrymal foramen occurs on each side of the orbital rim. The left and right alisphenoid tympanic bullae are widely separated and relatively small. The foramen pseudovale is small and bisected by a thin bridge of the alisphenoid. The foramina of the transverse canal are large and obvious, whereas the entocarotid foramina are small and obscure. The internal jugular canal foramina are large; the canals are raised and prominent. The posterior lacerate foramina are large and exposed as are the carotid foramina. The premaxillary vacuities extend from the level of the I^4 root back to the level of the middle of the C^1 root. The very small maxillary vacuities extend from the level of the protocone root of M^2 back to a level slightly posterior to the protocone root of M^4. Minute palatine vacuities extend from the level of stylar cusp B on M^5.

Variation in paratypes. Dental and cranial. In adult female PM22003 palatine vacuities are large and more numerous than in the holotype. All teeth are very worn. The anterior cingulation of M^5 is broad and complete to the trigon basin. A very wide diastema separates P_2 and M_2. In juvenile female PM22002 R and LM^4 are partially erupted, R and LM^5 are unformed. RM^2 shows large stylar cusp C. LM_2 shows bifid entoconid while L and RM_5 are partially erupted. The unworn dentition of this paratype clearly demonstrates the very reduced metaconids of R and LM_2 and the strong development of entoconids on M_{2-5}.

In juvenile male PM22001 $M^{4\&5}$ are unformed. All other teeth are partially erupted. Stylar cusp C is present on both R and LM^2 but not M^3. The crown tip of RP^2 is bifid and a minute, single-rooted, splinter-like M^1 occurs between RP^2 and RM^2. On the dentary all teeth are partially erupted, M_5 is unformed. The entoconids of R and LM_2 are bifid.

In adult male PM22004 all teeth are so worn that RP^2 is represented by two blunt roots, the tooth crown (presumably) having worn away.

External characters. In juvenile paratype female PM22002 (Fig. 5) both hind feet and the left forearm are missing. Colour closely matches holotype except that black guard hairs appear much more prominently over the back and sides. Juvenile paratype male PM22001 is very young and newly furred and appears more golden in colour than the holotype or paratypes. The tail is short-furred, but demonstrates the golden base which is replaced by black fur one third of the way down the tail toward the tip. In spirit paratype adult male PM22004 Fuscous black hairs appear slightly bleached to dark reddish brown. The partly everted penis shows the penis appendage observed and mentioned by Woolley and Webb (1977).

Reproduction. Waithman (field notes) recorded 7 nipples for PM22003. Assuming growth rates similar to those recorded for *Dasyurus viverrinus* (Fleay 1935), juveniles PM22001 and PM22002, collected 17 May 1972 and 26 June 1973 respectively, may have both been born in February.

Habitat. Specimens of *D. spartacus* were collected in low mixed savannah at three localities: three from Morehead 8°41'S, 141°39'E (Fig. 6); one from Mibini 8°50'S, 141°38'E; and one from Mari 9°11'S, 141°42'E. PM22001 was 'brought in by school children from a road pit' (field notes J. Waithman) and PM10400 was killed while raiding a fowl house. Collection details for the other specimens are not available. Collection areas experience a monsoonal climate where 75% of annual rainfall (1682 mm for Morehead) falls during a wet season lasting from December to May (Paijmans, Blake, Blecker and McAlpine 1971).

The habitat type, low-mixed savannah (Paijmans et al. Plate 16, Fig. 2, 1971) occurs in Indorodo, Goe and Mibini land systems where the habitat is inundated and waterlogged during the wet season and burned during the dry season. Trees average approximately 15 m in height but some grow as tall as 28 m. Most common species include *Tristania suaveolans, Melaleuca symphocarpa, Xanthostemon crenulatus, Grevillia glauca* and *Banksia dentata.* Less common species include *Deplanchea tetraphylla, M. viridiflora, E.*

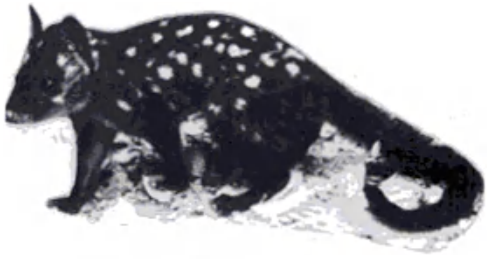

Fig. 5. Juvenile female *Dasyurus spartacus* (PM22002). Photo: J. Waithman.

Fig. 6. Dasyurus spartacus habitat, low-mixed savannah at Morehead, Papua New Guinea. Photo: H. Parnaby.

polycarpa, T. longivalvis, Acacia spp., *Dillenia alata, Parinari nonda* and *Xanthostemon barassii.* A patchy open shrub layer 1.0-3.3 m in height contains *Acacia leptocarpa, Choriceras tricorne, Melastoma polyanthum, Rhodamnia, Acacia simsii, Timonius Glochidion, Sinoga lysicephala* and low *Pandanus.* The ground layer (with a cover of 80-100%) contains *Imperata cylindrica, Pseedopogonotherum irritans, Germainia capitata, Eriachre squarrosa, Schoenus* spp., *Schleria* and *Rhynchospora rubra. Nepenthes* and *Danella* are always present and *Utricularia, Drosera* and *Eriocaulon* occur in areas of very poor drainage (Paijmans et al. 1971).

Etymology. The name *spartacus* embodies many features shared by this dasyurid with the notorious Thracian gladiator — strength, a tenacious fighting spirit, and the capacity to draw blood.

DISCUSSION

Past reference to this new dasyurid as *D. geoffroii* has resulted from not only its strong superficial resemblance to *D. geoffroii* but also from a reasonable expectation that *D. geoffroii* with its extensive pre-European distribution throughout Australia (Ride 1968, Archer 1979, Johnson and Roff 1982) could occur in New Guinea. One notable feature, however, differentiates quolls north and south of Torres Strait; the condition of the premolar row. In Australia the genus *Dasyurus* is characterised by a long premolar row with premolars generously spaced. In New Guinea these premolars are crowded and crushed together in a short row.

Uncrowded premolars have long been considered the primitive condition in didelphoids and hence Dasyuroids (Thomas 1887, Bensley 1903, Tate 1947, Archer 1976). But although premolars in the genus *Dasyurus* are generally widely spaced, the loss of P3 indicates considerable prelusive specialisation. It could well be that the relaxed condition of the two-premolared row is a further derivation in the dasyurid pattern of premolar crushing and single-rooting of P3 prior to its ultimate expulsion from the row. This pattern is demonstrated in Table 2, where in the more primitive condition eg. *Murexia longicaudata*, the lower premolar row may occupy up to 32% of the entire lower tooth row. In *Phascogale tapoatafa,* a slightly more specialised dasyurid exhibiting a trend toward loss of P_3, the value decreases to approximately 25%. In *Sarcophilus harrisii* where P_3 has been lost from both upper and lower tooth rows, the percentage of lower premolar row drops to approximately 17%.

In *D. hallucatus, D. viverrinus, D. maculatus* and *D. geoffroii* this value ranges from approximately 22-23% and suggests a trend of premolar loss then subsequent rostrum and dentary lengthening — a reversal of the trend exhibited by *Sarcophilus.* The greatly reduced premolar rows of *D. spartacus* and *D. albopunctatus* (19-20%) appear to demonstrate the premolar condition just subsequent to the loss of P3 and would suggest that these two species were in fact more primitive than all the others.

The possibly Pliocene *Dasyurus dunmalli* from the Chinchilla Sand, with its single rooted P_3 could lend support to this argument. With a crushed and only slightly greater proportion of premolar row (22%), *D. dunmalli* could represent the species ancestral to *D. spartacus* and *D. albopunctatus.* However, the same constraints that Bartholomai (1971) and Archer (1982) applied to the interpretation of the significance of *D. dunmalli* in *Dasyurus* phylogeny must be applied simultaneously to *D. spartacus* and *D. albopunctatus.* In these two species a consideration of character states apart from the premolar row indicates specialisation of a highly derived nature eg. disproportionate C^1, V-shaped upper incisor row, metacone M^2 perpendicular to stylar cusp D, M^2 reduced without entoconid, specialised penis, metacrista M^3 shorter than in M^4, greater reduction of paracones, metaconids reduced and upper premolars bulbous (see Table 3).

These features clearly make *D. spartacus* and *D. albopunctatus* (along with *D. dunmalli* for fewer

reasons) ineligible for consideration as the most plesiomorphic members of the genus when the morphologically primitive *D. hallucatus* is considered. If *D. dunmalli* was considered the sister species of *D. spartacus* and *D. albopunctatus*, then loss of P3 must have occurred once in *D. hallucatus* and then reversal of the premolar character state occurred once in the *D. dunmalli* lineage whereupon the persistent *Dasyurus* 2-premolar trend reemerged in *D. albopunctatus* and *D. spartacus* (Fig. 7A). While this is a tempting and parsimonious approach it assumes many synapomorphies from *D. dunmalli* of which so little material (a few incomplete dentaries) is available.

Archer (1982) has suggested that loss of P_3 may have occurred twice within the genus, once from the primitive *hallucatus-albopunctatus* stock (I do not accept the association of *albopunctatus* with *hallucatus* as ancestral in *Dasyurus*) and then once again from the common ancestor (*dunmalli*-like) of the species *viverrinus*, *geoffroii* and *maculatus*. However, two synapomorphies (more reduced metaconids and broad, oval premolars) of *dunmalli* and the *spartacus-albopunctatus-maculatus* group suggest that *D. dunmalli* is more closely related to these three species than to *viverrinus* and *geoffroii*. In this case loss of P_3 may have occurred once in the *hallucatus-viverrinus-geoffroii* line and then once again in the ancestor (*D. dunmalli?*) of *D. spartacus* and *D. albopunctatus*.

If consideration is given to Bartholomai's (1971) warning regarding the dubious nature of speculating on the relationships of *D. dunmalli* then another approach (free from the influence of *D. dunmalli*) is represented in Fig. 7B. To opt for the most parsimonious approach the assumption in this case is made that the crushing of the premolar row in *D. spartacus* and *D. albopunctatus* is a highly derived condition associated with the shortening of the rostrum. Archer (1976) notes that the reduction of P3 and widening of the premolar tooth row are derived states within the dasyurids as a whole. Bensley (1903) related the tendency of simultaneous premolar reduction and canine enlargement to a need for increased killing efficiency in more carnivorous forms. Tate (1947) noted that short muzzles and short palates accompany short, crowded tooth rows in vertebrate-killing dasyurids and Thomas (1887) related premolar reduction to specialisation in dasyurids. In this interpretation, *D. spartacus* and *D. albopunctatus* are sister species more closely related to one another than either is to *D. geoffroii*.

The upshot of these considerations is twofold. Firstly that regardless of a preferred phylogeny, *D.*

		Length lower premolar row (P)				Length lower tooth row (T)				Relative lower premolar row P/T%			
	N	$\bar{x} \pm R$	OR	SD	CV	$\bar{x} \pm R$	OR	SD	CV	$\bar{x} \pm R$	OR	SD	CV
M. longicaudata	10	7.04 ± 0.28	5.5-8.4	0.89	12.64	21.57 ± 0.72	18.2-25.8	2.28	10.57	32.57 ± 0.41	29.73-34.50	1.31	4.41
P. tapoatafa	10	5.09 ± 0.05	4.8-5.4	0.16	3.14	20.22 ± 0.18	19.3-20.9	0.58	2.87	25.19 ± 0.28	24.27-26.94	0.89	3.53
D. byrnei	10	4.02 ± 0.06	3.7-4.3	0.20	4.98	18.19 ± 0.16	17.6-19.2	0.49	2.69	22.09 ± 0.25	20.78-23.36	0.80	3.62
P. macdonnellensis	10	2.34 ± 0.08	2.0-2.7	0.26	11.11	11.76 ± 0.16	10.9-12.4	0.52	4.42	19.90 ± 0.65	16.26-22.69	2.04	10.25
D. hallucatus	10	6.64 ± 0.16	5.9-7.2	0.50	7.53	28.61 ± 0.49	26.5-31.1	1.55	5.42	23.20 ± 0.30	21.86-25.00	0.95	4.09
D. maculatus	10	10.54 ± 0.25	8.8-12.2	0.80	7.59	47.06 ± 0.77	41.9-50.0	2.44	5.18	22.40 ± 0.41	21.00-25.68	1.29	5.76
D. viverrinus	10	7.67 ± 0.14	6.8-8.4	0.45	5.87	34.93 ± 0.80	30.6-39.3	2.52	7.21	22.00 ± 0.23	20.85-23.17	0.72	3.27
D. geoffroii	10	8.02 ± 0.10	7.3-8.4	0.32	3.99	37.06 ± 0.62	34.5-40.2	1.97	5.32	21.67 ± 0.25	20.40-22.90	0.80	3.69
D. spartacus	10	6.83 ± 0.05	6.6-7.0	0.17	2.49	34.13 ± 0.39	32.6-35.6	1.23	3.60	20.03 ± 0.15	19.38-20.47	0.47	2.35
D. albopunctatus	10	5.16 ± 0.16	4.1-5.8	0.52	10.08	26.81 ± 0.43	24.5-28.8	1.35	5.04	19.22 ± 0.44	16.27-21.48	1.40	7.28
S. harrisii	10	11.23 ± 0.15	10.5-11.9	0.46	4.10	66.61 ± 0.86	62.7-70.9	2.73	4.10	16.87 ± 0.20	15.95-18.18	0.63	3.73
D. dunmalli	1	7.83				35.7				22.00			

Table 2. Pattern of relative length of dasyuroid premolar row reducing with increasing specialisation.

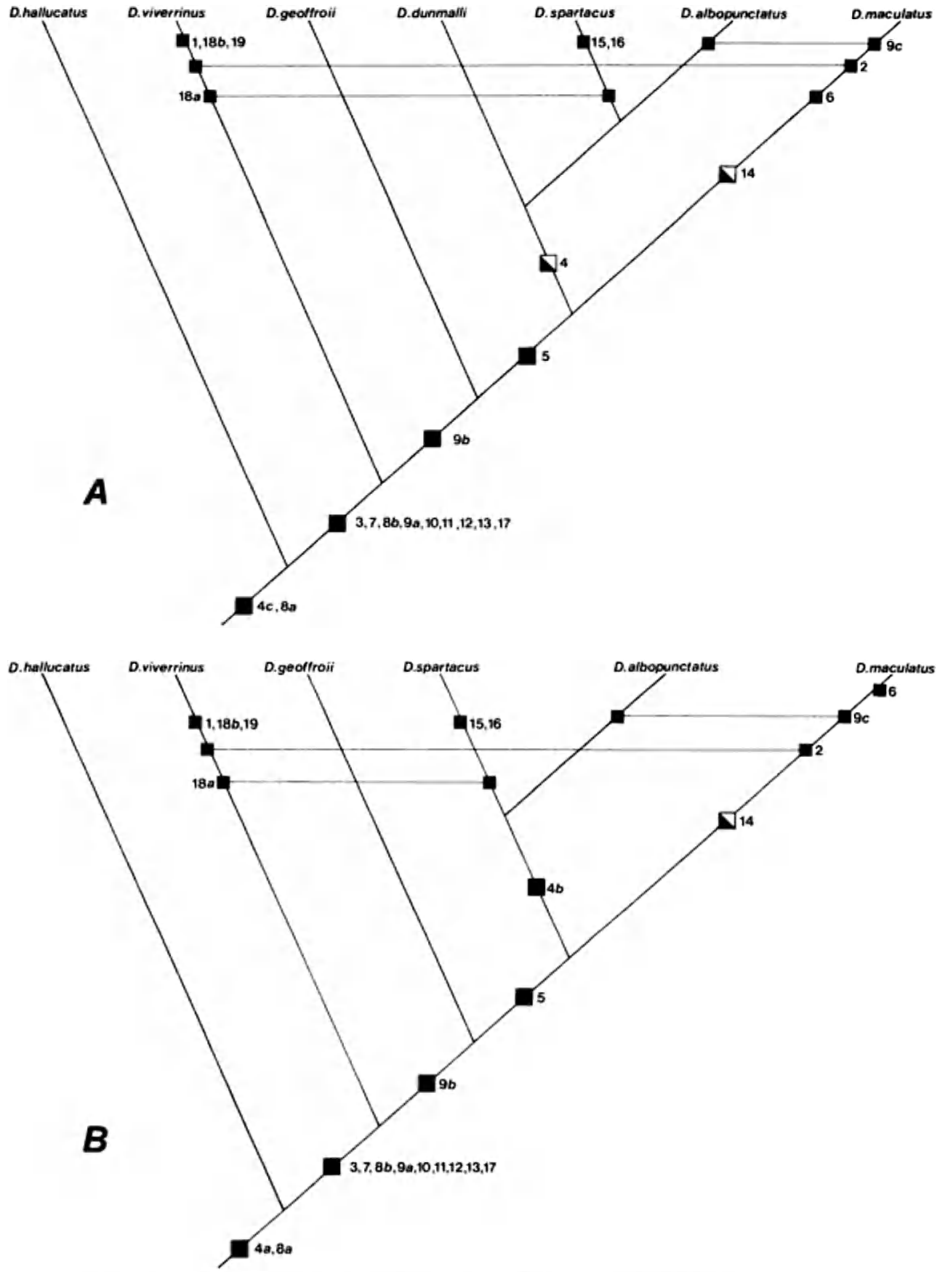

Fig. 7. Two cladograms of the hypothetical relationships of *Dasyurus spartacus*. Cladogram A includes the Pliocene species *D. dunmalli* and reflects interpretation 4A of Table 3. Cladogram B includes only extant members of the genus and reflects interpretation 4B of Table 3. See Table 3 for reference to all other apomorphies depicted in the cladograms.

Character (in pleisiomorphic state)		*Dasyurus hallucatus*	*Dasyurus geoffroii*	*Dasyurus viverrinus*	*Dasyurus spartacus*	*Dasyurus albopunctatus*	*Dasyurus maculatus*	*Dasyurus dunmalli*
1. $I\frac{1}{-}$ narrow, peglike		P	P	A	P	P	P	-
2. $I\frac{1}{-}$ procumbent, separate		P	P	A	P	P	A	-
3. $C\frac{1}{-}$ proportionate		P	A	A	A	A	A	A
4. Premolar row long, premolars spaced	a	A3	A3	A3	A2	A2	A3	A1
	b	A1	A1	A1	A2	A2	A1	
5. Premolars narrow, small		P	P	P	A	A	A	A
6. Molars non-bulbous		P	P	P	P	P	A	P
7. Incisor row V-shaped		P	A	A	A	A	A	-
8. Paracones reduced		A1	A2	A2	A2	A2	A2	-
9. Metaconids unreduced		P	A2	A1	A2	A3	A3	A2
10. Metacone $M\frac{2}{-}$ perp. to St. cusp D		P	A	A	A	A	A	-
11. Metacrista $M\frac{3}{-}$ equal to or longer $M\frac{4}{-}$		P	A	A	A	A	A	-
12. $M\frac{5}{-}$ unreduced		P	A	A	A	A	A	-
13. $M\frac{5}{-}$ with metacone		P	A	A	A	A	A	-
14. M_5 with entoconid		A	A	A	A	A	P	-
15. Skull height low		P	P	P	A	P	P	-
16. Broad rostrum width between lachrymals		P	P	P	A	P	P	-
17. Penis simple		P	A	A	A	A	A	-
18. Possession of hallux		P	P	A2	A1	P	P	-
19. Hind foot short and broad		P	P	A	P	P	P	-

Table 3. Character states of features thought to be useful in phylogenetic interpretation of quoll evolution. Character 4 presents two interpretations (see discussion). a. that the premolar state in *D. dunmalli* represents the least derived of all conditions and b. that excluding *D. dunmalli*, the crushed premolar state in *D. spartacus* and *D. albopunctatus* represents the most derived premolar condition seen in the genus.

spartacus is a highly specialised species, more derived than *D. geoffroii* but not as specialised as *D. maculatus*. Its greatest affinities are with *D. albopunctatus*. Secondly that *D. albopunctatus*, far from being the traditionally accepted primitive species so frequently associated with *D. hallucatus* is one of the more highly derived members of the genus.

One could have hoped for a more comfortable phylogenetic scenario from the tropical rainforests of New Guinea out of which such a parade of primitive taxa has emerged in the past.

ACKNOWLEDGEMENTS

The examination of type material held in overseas institutions was made possible through the financial support of the Royal Zoological Society of New South Wales, the Linnean Society of New South Wales and the Queensland Museum Board of Trustees. I gratefully acknowledge the help of the following for allowing me to examine specimens in their care: J. Menzies (National Museum and Art Gallery, Papua New Guinea), L. Gibson (Australian Museum), D. Kitchener (Western Australian Museum), C. Kemper (South Australian Museum),

A. Allison and C. Kishinami (Bernice Bishop Museum, Hawaii), M. Tranier (Museum National D'Histoire Naturelle, Paris), C. Smeenk (Rijksmuseum van Natuurlijke Histoire, Leiden), P. Jenkins (British Museum, Natural History, London), R. Angermann (Museum fur Naturkunde de Humboldt-Universititat zu Berlin) and G. Musser (American Museum of Natural History, New York). I also thank H. Parnaby (University of New South Wales) and J. Waithman (Conservation Commission of The Northern Territory) for collection details and photos of specimens, and particularly M. Archer (University of New South Wales) and R. Raven (Queensland Museum) for their helpful discussions with me. B. Cowell (Queensland Museum) produced the photographs.

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