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SYSTEMATIC NOTES ON MEGAPODIIDAE (AVES, GALLIFORMES), INCLUDING THE DESCRIPTION OF FIVE NEW SUBSPECIES

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INTRODUCTION

Megapodiidae (megapodes, brush-turkeys, scrubfowl, and relatives) form a peculiar family within the Galliformes. They show an unusual incubation strategy which shows resemblance to that practiced by reptilians but which is unknown for other bird families: eggs are laid in burrows or in mounds of leaves or other organic debris gathered by the birds, and heat generated by decaying leaves or, in case of burrow-nesting, heat from geothermal activity or from sun-radiation results in hatching of the chicks, providing that a temperature of c. 33 ºC and a moderate humidity are maintained (Dekker & Jones 1992). Once hatched, the chick struggles to the surface and leaves the hatching-area on the foot or on the wing without its parents paying attention to them. This breeding behaviour has fascinated naturalists and scientist for over a century (e.g., from Wallace 1869, to Booth & Seymour 1984, Immelmann & Böhner 1984, Kloska & Nicolai 1988, and Dekker & Jones 1992). Much of the present-day knowledge of megapodes is gathered in a forthcoming book, The Megapodes (Megapodiidae) (Jones, Dekker, & Roselaar, in press), to be published by the Oxford University Press. While working on this book, we soon became aware that the systematics of various taxa of Megapodiidae were outdated. The last major revisions of the family were those of Gray (1861), Oustalet (1879-1880, 1880, 1881), and Ogilvie-Grant (1893), with partial surveys of some taxa or of some regions by Salvadori (1882), Mayr (1938), and White & Bruce (1986), and a mere listing of all forms by Peters (1934). New research on specimens of Megapodiidae in various zoological collections resulted in conclusions about species and subspecies limits which were in part at variance with those in the earlier literature. Most of these data will be published in the forthcoming book, but part of it needs separate publication.

METHODS

All specimens of Megapodiidae in the bird collections

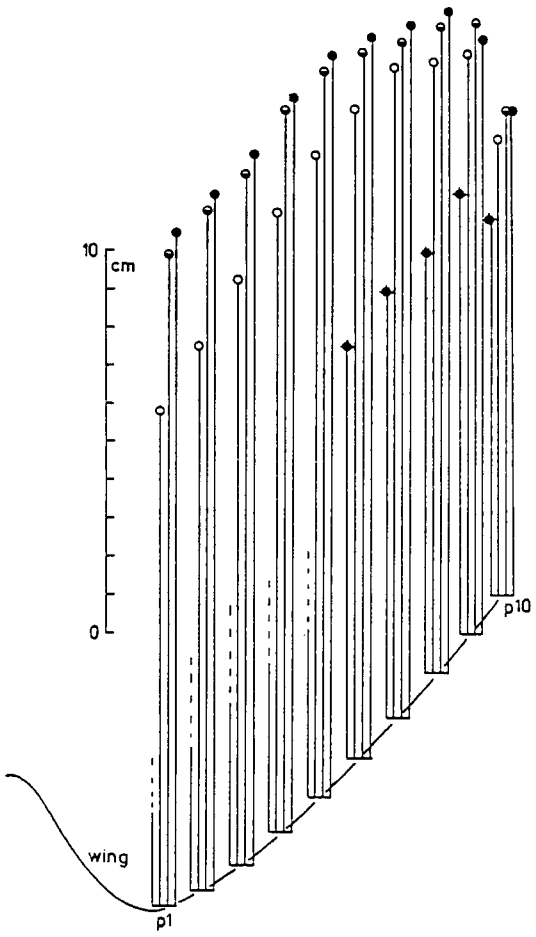

Figure 1. Wing shape and average lengths of full-grown primaries of 4 different feather generations of *Megapodius reinwardt reinwardt* (average adult wing length *c.* 233 mm).
Primary lengths measured from insertion in skin to tip. P1 is innermost primary, p10 is outermost. Black 'star-dot' is 1st (juvenile) generation (innermost 5 not measured because these are often shed in 1st moult before they are full-grown), open dot is 2nd generation, half-black dot is 3rd generation, black dot is definitive (adult) generation.

of the zoological musea of Amsterdam (Zoological Museum Amsterdam, ZMA), Leiden (Nationaal Natuurhistorisch Museum, RMNH), Tring (British Museum of Natural History, BMNH), Bonn (Zoologisches Forschungsinstitut und Museum Alexander Koenig, ZFMK), Dresden (Staatliches Museum für Tierkunde, SMTD), and Berlin (Zoologisches Museum der Humboldt Universität zu Berlin, ZMB) were measured and checked for plumage characters and moults. Some additional birds were examined by R. W. R. J. Dekker in the museum of Bogor, Indonesia (Museum Zoologicum Bogoriensis, MZB). Altogether, data of just over 1000 birds were obtained. Of each bird, about 15 measurements were taken, of which eight later appeared useful, the others being too difficult to standardize. For the method of measuring, see Jones *et al.* (in press). Notes on the colour of the bare parts and other data were taken from the labels.

Special attention was paid to primary flight-feather moult, and in many birds lengths of individual primaries (from point of insertion in the skin to the tip of the feather) were measured. Measuring primary length, assessment of the shape of the outer primary, and inspection of moult appeared to be of utmost importance for the study of size variation in populations of Megapodiidae. Megapodes have 10 functional primary flight-feathers; chicks hatch with the inner eight of these primaries well-developed (Pycraft 1900, Clark 1964; this study) and can fly immediately once the earth surface has been reached. At an age of 14-18 days, the outer two primaries start to grow, and at the same time the innermost primaries and the body start to moult (own data). At an age of about two months, the more or less barred plumage of the chick has been replaced by a plumage similar to that of the adult, and juveniles are inseparable from adults in body-feathering from then on, though the leg bones have attained only *c.* 80% of adult length, the arm bones c. 90 %, and the weigth only *c.* 40% of that of an adult (Sutter 1965; own data). Inclusion of these juvenile birds in a sample of adults would severely blur the morphometric data-set of a population. However, the first generation primaries of a juvenile are distinctly shorter, narrower, and more pointed at the tip than the feathers of an adult, and the outermost feather of this 1st generation, which is the last to be moulted, is present up to an age of 10-18 weeks, facilitating ageing even when the body plumage is similar to that of an adult.

At an age of about five months, all bones of the skeleton have reached their definitive length, but most flight-feathers and often also tail-feathers are of a second generation which is still shorter than adult feathers. Inclusion of measurements based on these second generation feathers renders data on length of wing and tail of a sample untrustworthy. However, the outermost primary of the second generation of feathers is virtually always more pointed at tip than in adult and generally still shorter, though less so than the first

generation (fig. 1), making ageing often still possible. When an immature is older than 7-9 months, the outer primaries are of at least a third generation(and the inner often already of a fourth) and the age can no longer be ascertained; birds like these were included in the adult samples used in this study, even though the wing and tail of a few known-age birds are still up to 5% shorter than in older birds.

A REVISION OF THE GENUS TALEGALLA

The genus *Talegalla* is restricted to the lowlands and hills of New Guinea, the Aru Islands, Japen Island in the Geelvink Bay, and Salawati and Misoöl off northwest New Guinea. In the mountains of New Guinea, Japen, and Misoöl it is replaced by *Aepypodius arfakianus*, on Waigeo by *Aepypodius bruijnii*. The genus consists of three species, which replace each other geographically. They are closely similar in morphology and could easily be considered to form a single species. However, some marginal overlap between some of the taxa occurs locally without evidence of hybridization. See fig. 2. All three undoubtedly derived from a single widespread lowland species which in geologically distant epochs became fragmented in distribution, leading to isolated popultions in west, north-east, and south-east New Guinea, separated by mountain-ranges (Hartert *et al.* 1936, Ripley 1960). All species are rather large, like a small turkey, with long tails and tarsi and an all-black plumage, rather similar to curassows *Crax* of South America which have a similar way of life. The three species differ in colour of bare parts (bare skin of face and throat, iris, bill, and leg), in the structure of the feathers of the crown, and in the length of the bare part of the lower tibia. Juveniles and immatures are hard to separate from adults, differing mainly in more normal-shaped feathering on the crown, less extensive amount of bare skin on the face and throat, and in the presence of some rufous on the lower neck. However, the species differ somewhat in these respects, adults of *T. jobiensis* often retaining some juvenile characters, while some juveniles of *T. fuscirostris* show adult characters. Juveniles and immatures are also smaller than adults, and therefore can not be used in morphometrical comparisons of populations. As shape of crown-feathers and colour of bare parts of juveniles may not be trustworthy for species-recognition either, juveniles should not be used in the study of geographical variation. They have to been omitted from the samples measured with help of the ageing characters given under 'methods'. Sexes are similar in size once adult, as in *Megapodius*, *Leipoa*, and *Eulipoa*, but in contrast to (especially) *Alectura* and *Aepypodius*. During this study, 100 adult skins of *Talegalla* species were examined, resulting in the recognition of the following taxa:

TALEGALLA CUVIERI

Talegalla cuvieri cuvieri

Talegalla Cuvieri Lesson, 1828, *Manuel d'Ornithologie* 2, p. 186. No locality, but based on a bird collected during the voyage of the ship Coquille at Dorei (now Manokwari), Vogelkop Peninsula, Irian Jaya, Indonesia, by Lesson and Garnot; holotype, formerly in Paris Museum, no longer in existence, missing already in the last century (Oustalet 1881).

Diagnosis. A medium-sized *Talegalla;* crown-feathers reduced, mainly consisting of a stiffened shaft with short and scanty lateral barbs, forming glossy bristles closely depressed to the skull. Iris pale yellow, sometimes with orange inner ring or with red tinge. Bare skin of head and neck yellow to yellow-green. Bill reddish-yellow, orange, or red. Leg and foot yellow, orange, or yellow-red. Bare lower tibia 7.5 (3-12) mm long (n=15), measured at side from feathering to tibio-tarsal joint.

Distribution. Vogelkop and (probably) Bombarai peninsula's, as well as Misoöl and Salawati islands, Irian Jaya.

Measurements. See table 1. A single adult bird examined from Salawati is similar in measurements to birds from the Vogelkop Peninsula, four birds from Misoöl are on average slightly smaller and may eventually prove to be a separate race when more specimens are available.

Talegalla cuvieri granti

Talegalla cuvieri granti **subspecies nova.** Holotype:

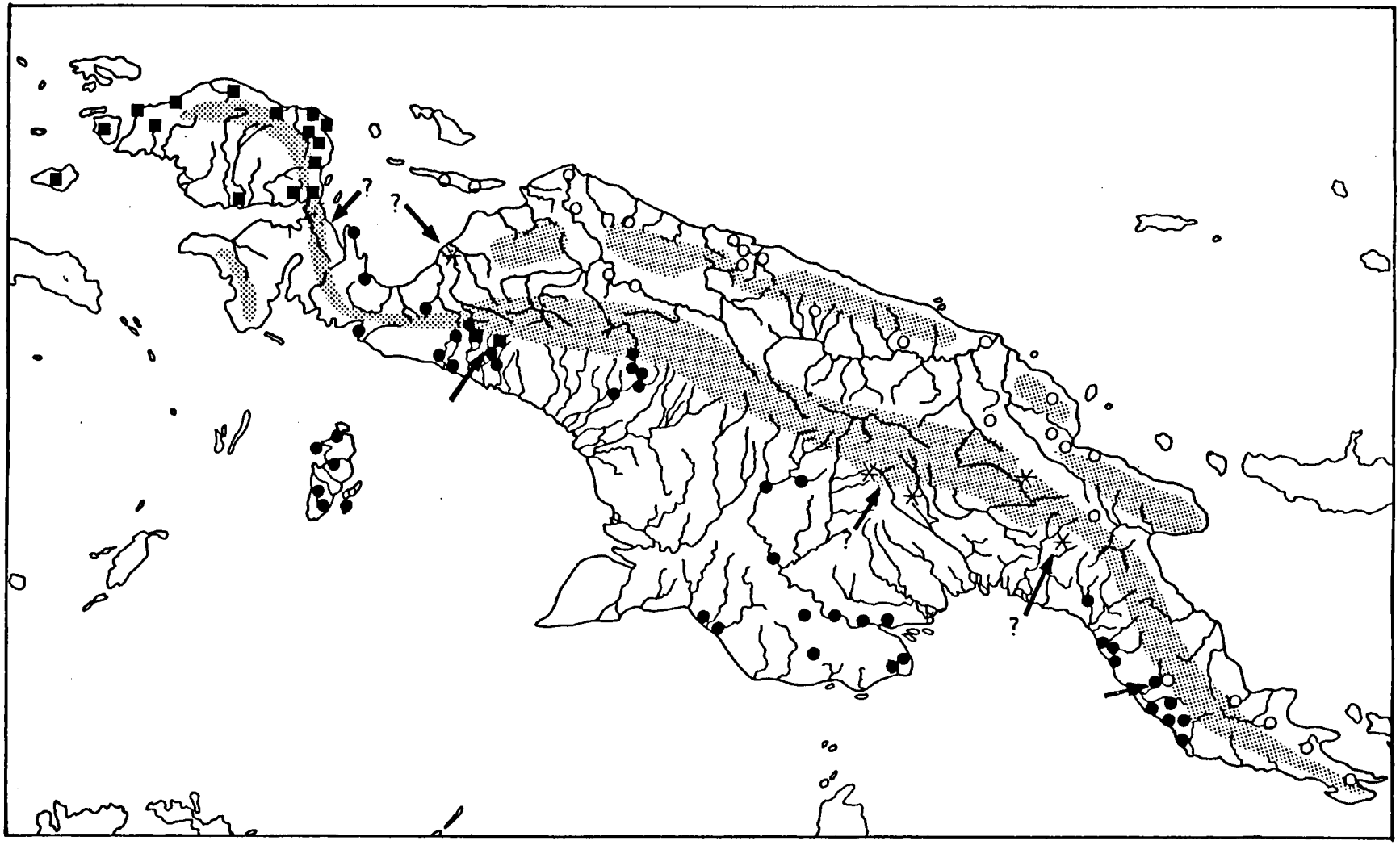

Figure 2. Distribution of *Talegalla*. Each mark represents a locality from where specimen(s) were examined or from which recorded in the literature (see text). Mountains (shaded), not inhabited by the genus, form a barrier.
Black square: *T. cuvieri*. Open circle: *T. jobiensis*. Black dot: *T. fuscirostris*. Star: a *Talegalla* is recorded, but the species is not yet known. Arrow: area of overlap

BMNH cat. nr. 1911.12.20.2, adult male, collected during the British Ornithologists' Union Expedition to New Guinea on 11 February 1911 on the upper Iwaka River at the southern foot of the Pegunungan Sudirman (Snow Mountains; *c.* 4º 14' S, 136º 56' E), Irian Jaya, Indonesia; collector C. H. B. Grant. Altitude not given, but 'collected in the mountains around my highest camp on the Iwaka River' (C. H. B. Grant in Ogilvie-Grant 1915), and, as the expedition did not venture to higher grounds than 4000' (Ogilvie-Grant 1915), probably collected somewhat below this level. Wing 285 mm, tail 169 mm, tarsus 101 mm, middle toe 58.6 mm, middle claw 19.8 mm, bill to skull 47.2 mm, bill to nostril 27.5 mm, bill depth at base 21.5 mm. Paratypes: BMNH cat. nrs. 1911.12.20.1 and 1911.12.20.3, males, collected 30 January 1911 and 13 February 1911 on the same locality as the holotype.

Diagnosis. Similar to nominate *cuvieri* from Vogelkop Peninsula, but larger in all measurements, especially those of tarsus, middle toe, bill to skull, and bill depth at base not overlapping with those of nominate *cuvieri*. Iris clear pale yellow or pale dirty yellow, bare skin medium olive-green, bill dull pale tomato-red or orange-red, leg and foot deep or rich orange with pinkish-flesh nails (Ogilvie-Grant 1913 and data from labels); bill brown and yellow, feet orange-yellow (Rothschild & Hartert 1913).

Distribution. Only known from the type locality (see above) and from the nearby upper Setakwa River (*c.* 4º 20' S, 137º 18' E), at an altitude of 2500-3000', two or three days inland from Canoe Camp on the Utakwa River, where three birds (of which only one adult) were collected by A. S. Meek in August 1910 (Rothschild & Hartert 1913). Both these localities are in the foothills on the south side of the central mountain range of New Guinea, while nominate *cuvieri* lives north-west of the central range. Both races are sometimes considered to be connected with each other along the shore of south-west New Guinea (e.g., inland of Kamrau, Triton, Kajumera, and Etna bays: map in Hartert *et al.* 1936), but only *T. fuscirostris* has been collected in part of this area so far. Suitable habitat for *T. cuvieri* is probably available in this hilly area, but as long as no specimens are collected the boundary between nominate *cuvieri* and *granti* remains uncertain.

Measurements. See table 1. The southern foothills of the west part of the central mountain range of New Guinea form the only known locality where *T. cuvieri* and *T. fuscirostris* meet or overlap. In this area, the measurements of the local subspecies *T. c. granti* are on average *c.* 9% larger than elsewhere, while those of the local race *T. f. occidentis* are *c.* 4% smaller than further east. Outside the overlap area, the measurements of *T. fuscirostris* are on average only c. 2% smaller than *T. cuvieri*, but in the south-western foothills the difference is much larger. This is likely due to character displacement.

Etymology. The reason to use the name *granti* for the newly described race of *T. cuvieri* is threefold: (1) in honour of C. H. B. Grant (1878-1958), the collector of the type specimen, who made the British Ornithologists' Union Expedition to New Guinea successful by coming to help when a disaster appeared unevitable due to the untimely death of the expedition's bird collector W. Stalker on the Mimika River in 1910, and who, among others, later made important contributions to Afrotropical ornithology (Mackworth-Praed 1958); (2) in honour of W. R. Ogilvie-Grant (1863-1924), who did the research on the ornithological collection of the British Ornithologists' Union Expedition to New Guinea and who published many articles on all fields of ornithology, including a revision of the Megapodiidae in 1893 (Anonymus 1924); (3) to draw attention to the large size of the bird (Latin *grandis*- large, great), though admittedly *grandis* or *major* would have been a more correct adjective in this respect.

Remarks. Rothschild & Hartert (1913) were the first to note the large size of the birds of the southern foothills. They described them as 'similar to birds from north-west New Guinea, but larger', without atttaching a name to the taxon. Description of a new subspecies based on only three specimens and some additional evidence from the literature seems rather meagre, the more when one considers that the sample of four birds from Misoöl was thought to be too small to use for a description of a new smaller race of *T. cuvieri*. However, of eight different measurements of the Misoöl birds only one (wing) did not show overlap with the data of typical nominate *cuvieri* from the Vo-

	(1) T. cuv. cuvieri			(2) T. cuv. cuvieri			(3) T. cuv. granti			(4) T. fusc. occid.			(5) T. fusc. meyeri		
	mean	Sd	range	mean	Sd	range	mean	Sd	range	mean	Sd	range	mean	Sd	range
wing	273.8	3.10	271 - 278	285.8	4.25	279 - 291	290.3	4.62	285 - 293	267.2	5.57	260 - 281	278.0	8.27	265 - 286
tail	160.2	5.24	155 - 167	164.3	4.78	156 - 172	169.3	3.51	166 - 173	147.3	5.60	137 - 159	160.5	5.09	154 - 167
tarsus	86.8	1.59	85.0-88.5	90.7	2.91	85.1-95.5	99.2	2.05	97.8- 101	88.1	2.33	82.5-92.7	88.8	3.05	86.2-94.2
mid-toe	49.0	1.91	46.9-51.5	49.8	1.47	47.0-52.0	57.3	2.91	54.0-59.4	47.2	1.97	43.0-49.7	49.8	2.55	48.0-53.5
mid-claw	18.1	1.00	17.0-18.4	18.5	1.35	15.6-20.4	19.6	0.40	19.1-19.8	17.5	1.00	16.0-19.8	19.2	0.64	18.3-19.8
bill-skull	39.6	0.86	38.6-40.7	40.8	1.33	38.5-43.1	45.7	1.46	44.3-47.2	38.8	1.57	35.7-41.0	40.2	0.78	39.0-40.6
bill-nostril	22.6	0.90	21.7-23.8	23.6	1.21	21.2-26.1	26.6	0.86	25.8-27.5	22.0	1.52	19.0-24.6	22.2	0.85	21.2-23.2
bill depth	18.4	1.04	17.3-19.5	18.8	0.85	17.3-19.8	20.9	0.74	20.1-21.5	17.0	0.70	15.8-18.0	18.3	0.71	17.4-19.3

	(6) T. fusc. aruensis			(7) T. fusc. fuscir.			(8) T. job. jobiensis			(9) T. job. longic.			(10) T. job. longic.		
	mean	Sd	range	mean	Sd	range	mean	Sd	range	mean	Sd	range	mean	Sd	range
wing	274.6	8.26	265 - 286	284.6	10.6	272 - 299	274.2	6.34	268 - 283	288.0	4.55	282 - 293	295.7	8.34	277 - 306
tail	156.6	10.4	144 - 178	176.4	6.89	168 - 186	157.5	2.38	154 - 160	178.5	8.66	168 - 187	188.8	8.29	171 - 202
tarsus	83.9	2.62	78.0-88.6	90.2	3.26	84.3-94.2	91.3	2.17	88.8-94.2	92.0	4.30	85.3-96.8	93.7	3.52	88.2-99.8
mid-toe	46.8	1.13	44.6-48.0	48.6	2.76	45.0-51.5	49.2	1.31	47.5-50.5	52.8	2.06	51.0-55.5	51.8	2.77	48.2-57.3
mid-claw	17.6	1.64	15.8-20.5	18.5	1.68	16.1-19.8	18.6	1.28	16.8-20.4	18.7	1.16	17.6-20.2	19.6	1.60	16.8-22.8
bill-skull	38.4	1.07	36.7-40.2	38.6	1.23	36.6-40.0	41.4	1.33	40.4-44.0	40.4	0.59	39.7-41.0	43.4	2.38	40.5-49.0
bill-nostril	21.6	0.75	20.5-22.7	21.8	0.79	20.8-22.7	23.3	0.91	22.1-24.8	23.2	1.68	21.5-25.0	24.7	1.63	23.2-29.3
bill depth	16.5	0.73	15.5-17.6	17.1	0.61	16.4-18.0	18.5	0.26	18.3-18.8	18.7	0.31	18.3-19.0	20.3	1.31	18.3-23.0

Table 1. Measurements of wing, tail, tarsus, middle toe without claw, middle claw, bill to skull, bill to nostril, and bill depth at base of adult birds of *Talegalla*. Sexes similar in size, data combined.

(1) *T. cuvieri cuvieri*, Misoõl Island (West Papuan Islands) (n=4), (2) *T. cuvieri cuvieri*, Salawati and Vogelkop Peninsula (north-west New Guinea) (n=19), (3) *T. cuvieri granti*, Iwaka River (south-west New Guinea) (n=3), (4) *T. fuscirostris occidentis*, Kapare to upper Lorentz rivers, including Iwaka River (south-west New Guinea) (n=23), (5) *T. fuscirostris meyeri*, southern shore of Geelvink Bay (north-west New Guinea) (n=7), (6) *T. fuscirostris aruensis*, Aru Islands and Kumbe-Merauke area (southern New Guinea) (n=9), (7) *T. fuscirostris fuscirostris*, south-east New Guinea (n=7), (8) *T. jobiensis jobiensis*, Japen Island (Geelvink Bay) (n=6), (9) *T. jobiensis longicauda*, basins of Mamberamo and Idenburg rivers east to Humboldt Bay area (northern New Guinea) (n=5), (10) *T. jobiensis longicauda*, Astrolabe Bay area east to Milne Bay (north-east New Guinea) (n=15).

gelkop Peninsula, and the averages of the measurements of Misoöl birds were only 1-4% below those of the Vogelkop population. In contrast to this, of eight parameters of Iwaka birds only wing, tail, and middle claw overlapped with those of typical nominate *cuvieri* (the Iwaka birds are on average 2-6% larger for these three), while averages of tarsus, middle toe, bill to skull and to nostril, and bill depth at base were as much as 9-15% larger. The small difference in colour of the bare skin of the head and neck of both subspecies (reported to be yellow to yellow-green in nominate *cuvieri* and medium olive-green in *granti*) may be due to a different interpretation of similar colours by the collectors and probably has no diagnostic value.

TALEGALLA FUSCIROSTRIS

Talegalla fuscirostris fuscirostris

Talegalla fuscirostris Salvadori, 1877, *Ann. Mus. Civ. Storia Nat. Genova* 9, p. 332; 'southern New Guinea and Aru Islands'. The types are two birds from Epo and Hall Sound, north-west of Port Moresby, south-east Papua New Guinea, collected by D'Albertis in April 1875 (Salvadori 1882); not examined.

Diagnosis. Close to *T. cuvieri*, showing a similar reduction of the crown feathers, but the tips of the glossy shafts of the feathers less depressed against the skin of the skull and occasionally slightly curled upwards. Bare parts darker, except for leg and foot: iris brown, bare skin of head and neck cobalt-blue to bluish-black, bill dark horn-brown to black, and leg and foot lemon-yellow or (rarely) orange. Bare part of lower tibia longer, 24 (15-33) mm (n= 15). Size medium, as in *T. cuvieri cuvieri*, but tail proportionally longer and bill more slender at base.

Distribution. South-eastern part of Papua New Guinea, from Rigo area west to at least Kerema area. Further east it is replaced by *T. jobiensis*, with which it also may overlap in the southern foothills of the central mountain range (both species have been collected on the upper Aroa River: Rothschild & Hartert 1901). The species occurs also further west, but the boundary between this race and the others has not yet been established.

Measurements. See table 1.

Talegalla fuscirostris occidentis

Talegalla fuscirostris occidentis White, 1938, *Ibis* (14)2, p. 763. Holotype: adult male, collected by the Wollaston Expedition at Canoe Camp on the Setakwa River, just south of central range in south-west Irian Jaya, Indonesia, on 24 October 1912 (thus, close to the type locality of *T. cuvieri granti;* see above). According to White (1938), type in BMNH, but, though a large series was present from the type locality and surroundings in this collection, the type was neither found among them nor in the cabinet of type specimens.

Diagnosis. Similar to nominate *fuscirostris*, but wing shorter, tail much shorter, and tarsus, middle toe, and claws slightly shorter. Bill measurements as in nominate *fuscirostris*. The smallest subspecies of the genus, with tail proportionally and absolutely shorter than in other taxa.

Distribution. Examined from lowlands and hills just south of the central mountain range of western New Guinea, between the Kapare and upper Lorentz rivers, or between about 136º and 139º E and 4º 30' and 5º S. Known to occur west to Etna Bay and east to the Oriomo River (Mayr 1938, 1941; Rand & Gilliard 1967), but birds from the latter locality are more likely to belong to the next subspecies. Probably intergrades with the previous race further east and with the next race further south.

Measurements. See table 1.

Talegalla fuscirostris aruensis

Talegalla fuscirostris aruensis **subspecies nova**. Holotype: RMNH '*T. cuvieri*' cat. nr. 12, adult female, collected at Wanumbai, Aru Islands, Indonesia, on 16 May 1865 by Von Rosenberg. Wing 271 mm, tail 145 mm, tarsus 81 mm, middle toe 47.0 mm, middle claw 16.4 mm, bill to skull *c.* 38.5 mm, bill to nostril *c.* 20.5 mm, bill depth at base 16.5 mm. Paratypes: RMNH 'T. cuvieri" cat. nr. 13, a male collected at Trangan, Aru, on 9 July 1865 by Von Rosenberg; SMTD nr. C7298, a male from Gomo, Aru, collected in or before1883 by Riedel; ZMB 51178, a female from Wanggar, Aru, collected on 25 July 1931 by Stein.

Diagnosis. Similar to *T. fuscirostris fuscirostris* and

T. f. occidentis in plumage. Size about intermediate between these or slightly nearer to *occidentis*, but tarsus markedly shorter than both, generally 85 mm or less, against usually 86 mm and over in the other subspecies of *T. fuscirostris*. The bare part colours are apparently less constant than in *occidentis* and nominate *fuscirostris*, as a yellow iris and olive-green leg and foot are occasionally reported (labels in RMNH; Salvadori 1882), but most birds do not deviate from the standard of *T. fuscirostris*.

Distribution. Examined from Aru Islands (see holotype and paratypes) and from Kumbe and Merauke in southern Irian Jaya (see Mees 1982). On the Aru Islands, also recorded from Wokam, Sungei Barkai, and Giabu-Lengan (Salvadori 1882, Berlepsch 1911). Probably this race in the lower Fly River area, where the species was recorded from 'Fly River', Oriomo River, Tarara, Gaima, Sturt Island Camp, and Lake Daviumbu (Salvadori 1882, Mayr 1938, Rand 1942), but, as the authors do not supply tarsus lengths, the subspecies involved remains uncertain. Birds reported from the upper Fly River (e.g., Palmer Junction Camp and Black River Camp: Rand 1942) are either *aruensis*, *occidentis*, nominate *fuscirostris*, or intermediates between some of these.

Measurements. See table 1. No difference in size between four birds from Aru Islands and five from the Kumbe-Merauke area.

Etymology. Named after the type-locality, Aru Islands, Indonesia.

Remarks. The occurrence of this race on the Aru Islands and in the southern lowlands of New Guinea is a further indication that both areas were connected during the ice ages when sea-levels had dropped considerably. On the other hand, the populations of the southern foot of the central mountain range may have been long isolated from those of the southern lowlands, as both differ in proportions: *occidentis* has a proportionally shorter tail than the other populations of *T. fuscirostris*, and *aruensis* has proportionally shorter legs than others. In a sample of birds of *aruensis*, 78% has a tarsus length of 85 mm and less (n=9), while 91% of *occidentis* (n=22) and 86% of nominate *fuscirostris* (n=7) have a tarsus length equal to or longer than 86 mm.

Talegalla fuscirostris meyeri

Talegalla fuscirostris meyeri **subspecies nova.** Holotype: SMTD cat. nr. C 772, adult female, collected May 1873 at Rubi (3º 16' S, 134º 51' E), south shore of Geelvink Bay, Irian Jaya, Indonesia, by A. B. Meyer. Wing 284 mm, tail 167 mm, tarsus 86 mm, middle toe 48.2 mm, middle claw 19.4 mm, bill to skull 39.0 mm, bill to nostril 22.8 mm, bill depth at base 17.4 mm. Paratypes: a series in SMTD, collected by Meyer in May 1873, cat nrs. C767 (a male from 'Napan'; for locality, see below), C769 (a male from Rubi), and C923 (a male from Rubi); also ZMB 9409, collected by Meyer, original label lost, but undoubtedly also collected at head of the Geelvink Bay as Meyer did not pay a visit to other localities within the known range of *T. fuscirostris*.

Diagnosis. A rather large subspecies, almost similar in size to nominate *fuscirostris* from south-east New Guinea, but tail shorter and bill longer and thicker at base; plumage characters and length of bare tibia as in nominate *fuscirostris*. Larger than *occidentis* from south of central mountain range, especially in tail length, less so in wing, toe, claw, and bill lengths and in bill depth; rather close in size to *aruensis* but tarsus and middle toe lengths as well as bill depth markedly greater. Bare parts of two birds from Ta River (see below): iris brown, bill and bare skin blue or black, and leg and foot once red, once yellow (from labels at skins in MZB), thus as in nominate *fuscirostris* except for the red leg and foot of one bird. Bare parts of birds from Napan and Rubi are not clear; according to Meyer (1874), who included the birds he collected on these localities in *cuvieri*, all birds had yellow bare parts, but probably this refers to true *cuvieri* from Vogelkop Peninsula only. In skins from Napan and Rubi examined, bill and bare skin of head and neck appeared dark, as in nominate *fuscirostris* and *occidentis*, not yellow as in *T. cuvieri*, but the colour may eventually have been dusky-red, as in *T. jobiensis*; leg and foot appeared reddish-yellow, similar to nominate *fuscirostris* and *occidentis*, not as pale as in *T. cuvieri*, but perhaps similar to *T. jobiensis*.

Distribution. The only race of *T. fuscirostris* occurring north of the central mountain range of New Guinea; restricted to lowlands and hills at the head of

Geelvink Bay, where examined from Rubi (see above), Napan (either one of two localities with that name, one at 2º 54' S, 134º 48' E, the other at 3º 08' S, 136º 02' E; as Meyer clearly states that his 'Napan' is on the western shore of Geelvink Bay, and moreover old maps do only mention the first locality, it is highly likely to be the first-mentioned one), and Ta River (a tributary of the upper Siriwo River at the northern foot of the Weyland Mountains, at c. 30 m altitude; see also Van Bemmel 1947).

Measurements. See table 1.

Etymology. Named in honour of A. B. Meyer (1840-1911), the collector of the type specimen, one of the first scientific bird collectors in New Guinea, and in his time one of the best specialists of the avifauna of the area. He was Director of the Zoologisches-Anthropologisches-Ethnographisches Museum in Dresden (now the SMTD), and, with his assistant L. W. Wiglesworth, wrote the book 'The Birds of Celebes', published in 1898 (Gebhardt 1964).

Remarks. Of the three originally disjunct species of *Talegalla* surrounding the central mountain range of New Guinea (see intro of *Talegalla*), the north-eastern species *T. jobiensis* has crossed the main range in the eastern tip of New Guinea towards the upper Aroa river (Rothschild & Hartert 1901), and probably it did likewise further west in Papua New Guinea (Jones *et al.* in press), showing some overlap with *T. fuscirostris* at the southern foot of the central range. The race of each species involved, *T. jobiensis longicauda* and *T. fuscirostris fuscirostris*, differ in size, especially in bill dimensions, thus possibly avoiding competition by specializing on different food. *T. cuvieri* from north-west New Guinea has penetrated south of the central range in the west of New Guinea, showing some overlap with *T. fuscirostris*, again, the races involved (*T. cuvieri granti* and *T. fuscirostris occidentis*) differ markedly in size. On the other hand, *T. fuscirostris* has penetrated north of the central range at the head of the Geelvink Bay, but in this area the race involved (*T. f. meyeri*) is not known to overlap with *T. cuvieri cuvieri* (occurring further west) or *T. jobiensis jobiensis* (occurring further east), nor do the measurements differ from these northern species. In fact, the measurements of *meyeri* are markedly similar to those of *T. cuvieri* and to *T. jobiensis*, more so than to the other races of *T. fuscirostris*. Thus, for instance, while the other three races of *T. fuscirostris* are characterized by a slender bill, *T. f. meyeri* has a heavy bill similar to that of the two northern species. As the seven specimens of *T. f. meyeri* examined do not show much individual variation in morphological characters, some people may suggest that the form is a stabilized hybrid between *T. fuscirostris* and *T. cuvieri* or *T. jobiensis*. However, the length of the bare tibia is typical for *T. fuscirostris* (on average, 26.0 mm bare), and in the feathering of the crown *meyeri* also resembles the other races of *T. fuscirostris* (though the crown of *T. cuvieri* is rather similar). As the collector of the Rubi and Napan birds made no remarks on the colour of the bare parts on the label, we are not absolutely certain about these, though in skins they appear to be similar to those of the other races of *T. fuscirostris* and certainly not to those of *T. cuvieri* (see Diagnosis, above). The bare parts of one of the two birds from Ta River are similar to *T. fuscirostris*, but leg colour of the other bird (red) fits *T. jobiensis*, while the tail length of the latter bird (191 mm, omitted from table 1) is also markedly longer than in other *T. f. meyeri* but valid for *T. jobiensis*. Thus, *T. fuscirostris meyeri* may grade into *T. jobiensis jobiensis* in the Ta River area, though crown feathering, length of bare tibia, and bill colour of the two known birds from this locality fully conform to those of *T. fuscirostris*.

TALEGALLA JOBIENSIS

Talegalla jobiensis jobiensis

Talegallus jobiensis A. B. Meyer, 1874, *Sitzungsber. Math.-Naturwiss. Cl. Kaiserl. Akad. Wissenschaften, Wien,* 69(1-5), p. 87. Based on a type series of two males, two females, and one juvenile, collected in April 1873 on Japen Island, Geelvink Bay, Irian Jaya, Indonesia, by A. B. Meyer, then in SMTD. At present, only one bird of this series remains in the SMTD, an adult male, labelled 'type', cat. nr. C 3135, collected Ansus, Japen. Another bird of the type series, an adult female, is in RMNH, cat. nr. 1. Measurements of SMTD C 3135 and RMNH 1, respectively: wing 283,

272 mm, tail 159, 154 mm, tarsus 89.5, 88.8 mm, middle toe 48.2, 47.5 mm, middle claw 16.8, 20.4 mm, bill to skull 41.3, 40.7 mm, bill to nostril 22.7, 23.5 mm, bill depth at base 18.8, 18.3 mm.

Diagnosis. A *Talegalla* of medium size, close in size to *T. cuvieri cuvieri*, differing from *T. cuvieri* (and *T. fuscirostris*) in feathering of crown: feathers lanceolate (webs not reduced), forming a dense bushy crest extending to the nape, with the tips of feathers often slightly curled upwards, not closely depressed to the skull. A small part of the lower tibia unfeathered, 7.9 (3-13) mm (n=15), as in *T. cuvieri*. Colour of bare parts different from both other species: iris and bill brown, red-brown, or red, bare skin of head red-brown to dark red, of neck pink to cherry-red; leg and foot salmon, pink-red, orange-red, or vermilion-red.

Distribution. Examined from Japen Island only. Probably occurs opposite Japen Island on the eastern coast of Geelvink Bay, west of the basin of the Mamberamo River, but though a *Talegalla* is recorded from Mt. Elephant and Talandjang in this area (Meyer 1874, Rothschild & Hartert 1901), even the species here is not known. Birds occurring from the Mamberamo basin east to the border between Irian Jaya and Papua New Guinea are sometimes considered to be nominate *jobiensis*, but are better included into the next subspecies (see below).

Measurements. See table 1.

Talegalla jobiensis longicauda

Talegallus longicaudus A. B. Meyer, 1891, *Abh. Ber. Königl. Zool. Anthrop.-Ethnogr. Mus. Dresden* 4, p. 15. Holotype: SMTD cat. nr. C 10432, an adult of unknown sex, collected January 1891 at Stephansort (head of Astrolabe Bay) by B. and H. Geisler. Type examined: wing *c.* 305 mm, tail 196 mm, tarsus 95 mm, middle toe 49.5 mm, middle claw 22,8 mm, bill to skull 45.5 mm, bill to nostril 24.8 mm, bill depth at base 21.4 mm.

Diagnosis. Similar to nominate *jobiensis*, but wing and (especially) tail longer. The largest-sized taxon of *Talegalla*.

Distribution. Northern New Guinea, north of central mountain range, from the basins of the Mamberamo and Idenburg rivers east through the Sepik and Huon areas to Milne Bay in the south-eastern tip of New Guinea. Locally also in foothills just south of central range: east of Rigo in the south-eastern tip and on the upper Aroa River in the Port Moresby district (where occurring together with *T. fuscirostris*: Rothschild & Hartert 1901). A *Talegalla* recorded at Lake Kutubu and Mount Sisa in the southern Highland Province and in the Karimui area of Chimu province of Papua New Guinea (Diamond 1972, Dwyer 1981, Coates 1985), close to the range of *T. fuscirostris*, is (based on voice and egg size) presumed to be *T. jobiensis* (Dwyer 1981).

Measurements. *T. j. longicauda* is the largest member of the genus *Talegalla*, as far as the populations near the type locality are concerned. Further west, in north-eastern Irian Jaya, the populations are on average smaller and birds from here are sometimes united with the even smaller ones from Japen Island into nominate *jobiensis* (Mayr 1941). However, though the size may indeed clinally become smaller from north-east New Guinea westward, the birds from the Mamberamo basin in Irian Jaya are still considerably larger than birds from Japen, and therefore all populations occurring east from the Mamberamo basin are included in *longicauda*. See table 1.

SPECIES LIMITS WITHIN THE GENUS MEGAPODIUS

Ogilvie-Grant, revising the family in 1893 before the polytypic species-concept became into general usage, recognized 15 species of *Megapodius*. Peters (1934) reduced this number to nine, Mayr (1938) further reduced this to three, including all taxa in *Megapodius freycinet* except for *M. pritchardii* and *M. laperouse*, which live on remote islands in Polynesia and Micronesia, respectively. Some authors increased the number by one due to inclusion of the taxon *wallacei* in *Megapodius*, following Ripley (1964). For reasons partly given below but mainly in Jones *et al.* (in press), the monotypic *wallacei* is here considered to belong to a separate genus, *Eulipoa*. Mayr's reason to combine most forms into a single species is obvious: all have complementary distributions (the few cases of overlap reported were considered to be doubtful by Mayr), and all have superficially similar plumages, being

generally clad in olive or brown on the upperparts and grey on the underparts, without contrasting tinges except sometimes on the rump. Only the leg, bill, and bare facial skin show bright colours. In some taxa, the brown of the upperparts extends to the underparts (e.g., in *bernsteinii* and *decollatus*), in others the grey of the underparts reaches the upperparts (e.g., in *laperouse*); in some, the general colours are dark and saturated (deep rufous-brown in *tabon* and *castanonotus*, black in *freycinet* and *layardi*), in others they are pale and diluted (e.g., in *cumingii* and *nicobariensis*), partly even lacking pigments as in *pritchardii* which shows some albinistic patches.

The taxa *laperouse* and *pritchardii* are not markedly more saturated or diluted in colour than the others, and their remoteness from the core distribution of *Megapodius* does not seem to be a good reason to split them from the remaining taxa, *contra* the opinion of Mayr (1938). In fact, the breeding area of *nicobariensis* is more distant from that of its neighbour *cumingii* of Labuan Island (2500 km) or from *reinwardt* of Kangean Island (3000 km) than is that of *laperouse* of the Mariana Islands from *decollatus* of New Guinea (2000 km), or that of *pritchardii* of Niuafo'ou from *layardi* of Vanuatu (1700 km). Thus, as an extension of Mayr's opinion, one may suggest that the whole genus *Megapodius* consists of a single species, with a highly fragmented range resulting in a large number of subspecies.

However, when looking in detail to the geographical variation shown by *Megapodius*, two different types of variation between populations of neighbouring islands become apparent:

(1) A slight and very gradual variation in colour of plumage and in absolute size. Between some populations, the difference is perhaps large enough to recognize subspecies, but even within these subspecies no changes in colour of bare parts or in relative proportions of tail, bill length, tarsus length, or other parts of bill and leg occur.

(2) A considerable variation in colour of bare parts (facial skin, bill, leg) and in relative proportions of tail, bill, tarsus, toes, etc., often combined with a difference in plumage colour and in absolute size. This variation is considered here to be that between species.

Thus, *M. forstenii* on Gorong Island in the Moluccas is abruptly replaced by *M. reinwardt* on Kasiui Island only *c.* 25 km to the south-east. Both species differ markedly in bare part colours (dull in *M. forstenii*, bright red in *M. reinwardt*) and in relative proportions of tail, tarsus, toes, and claws (e.g., the tail/tarsus ratio is markedly different), and also in absolute size and general plumage colour. In this case, both are considered to be separate species. Within *M. reinwardt*, some variation in general colour occurs, as well as a more marked variation in absolute size, lending support to the recognition of some races, but none of these differs from the others in colours of bare parts or in relative proportions of body extremities. Even within *M. cumingii*, where the races as recognized here differ markedly in general colour and in absolute size, bare part colours are similar and proportions do not differ.

The reasons for giving different values to a number of variable characters are twofold:

(1) Bare part colours have an important function in display, while body colour is generally subdued and cryptic. Bare parts are thus apparently more important for recognition of conspecifics than body colour, not only in the brush-turkeys *Aepypodius* and *Alectura* and in *Macrocephalon* which all have greatly enlarged and boldly coloured bare parts with conspicuous bare wattles or knobs, but also in *Talegalla* and *Megapodius*. *Leipoa* and *Eulipoa*, which have boldly patterned body plumage but inconspicuously coloured bare parts, are probably an exception.

(2) Differences in proportions of tail, bill, bill depth, tarsus, toes, claws, etc. in relation to body mass are likely to reflect differences in locomotion, foraging technique, incubation strategy (burrow diggers may have differently proportioned feet than leaf gatherers), or (in case of relative tail length) display, in contrast to variation in general size without change in proportions.

Voice is another important character for mutual recognition in these sombre-tinged birds living pair-wise in dense undergrowth. Though data on voice are not yet available for all taxa, those which are known tend to support the delimitation of species advocated here, showing minor differences between the races and sometimes marked ones between species (R. W. R. J. Dekker *pers. comm.*).

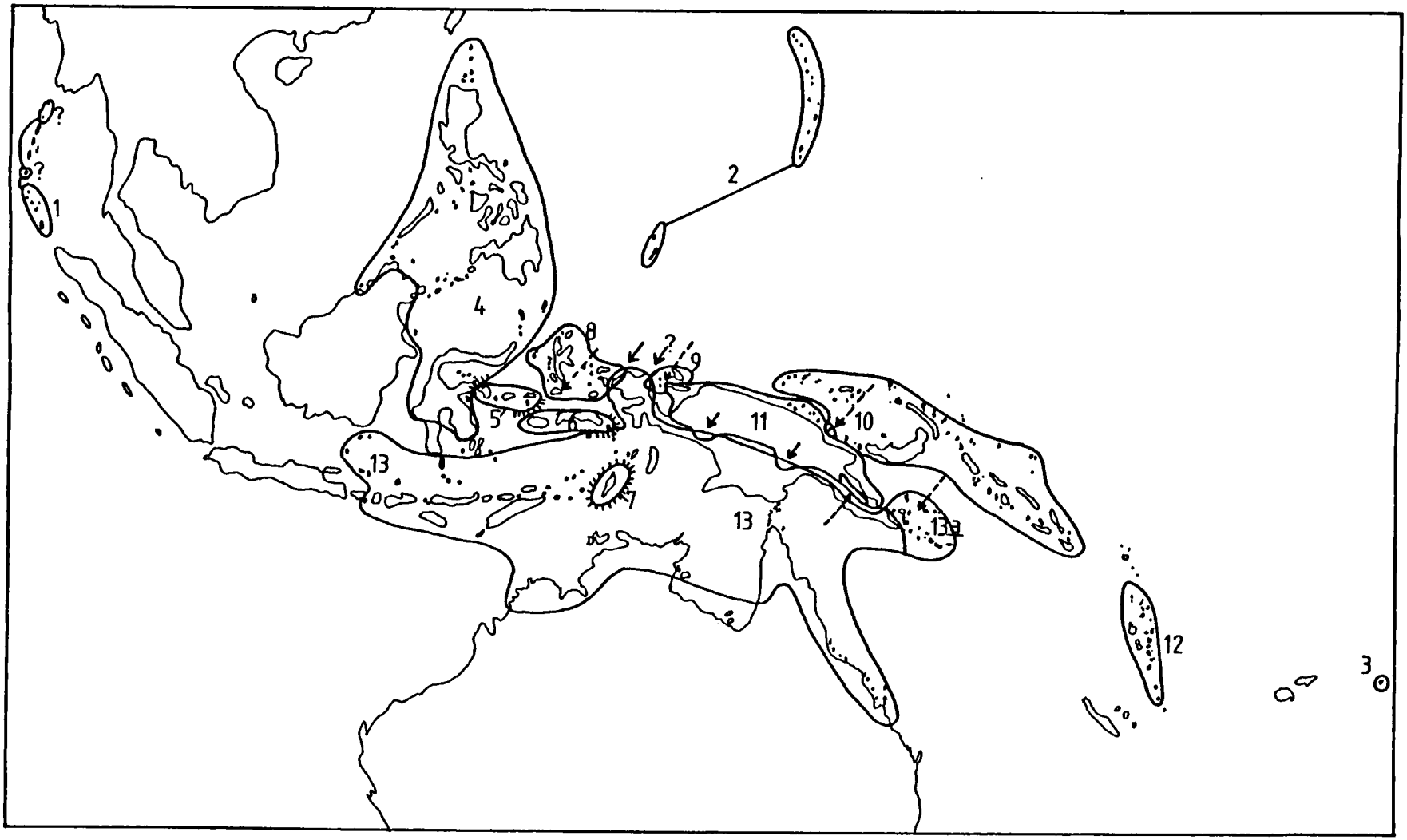

Figure 3. Areas of contact of *Megapodius* species.
Solid arrow: area of marginal overlap without hybridization or with limited hybridization only. Broken arrow: areas with apparent secondary hybridization, or with some gene-flow
Hatched border between species' ranges: apparent competitive exclusion, ranges virtually touching but no evidence of gene-flow. See text.
(1) *M. nicobariensis*, (2) *M. laperouse*, (3) *M. pritchardii*, (4) *M. cumingii*, (5) *M. bernsteinii*, (6) *M. forstenii*, (7) *M. tenimberensis*, (8) *M. freycinet*, (9) *M. geelvinkianus*, (10) *M. eremita*, (11) *M. decollatus*, (12) *M. layardi*, (13) *M. reinwardt* (13a: hybrid zone between *M. reinwardt* and *M. eremita* - *M. 'macgillivrayii*').

The abrupt replacement in space of one taxon by a related one without sign of introgression of genes among them is another reason to consider the genus *Megapodius* to consist of more than one species: such a distribution points to competitive exclusion, which should not exist between subspecies (Mayr 1963). See fig. 3 for areas of overlap, hybridization, and possible competitive exclusion.

We assume that competitive exclusion within *Megapodius* prevents coexistence of more than one species of the genus in a single locality: the specialized incubation strategy may render a species highly vulnerable should another megapode with a similar breeding strategy and similar habitat requirements invade within its range. The larger species might usurp the incubation mounds or nesting-grounds of the smaller one once the breeding ranges overlap, thus preventing the smaller species to reproduce and leading to rapid extinction of the latter. The present-day distribution of *Megapodius* with only a single species on each group of islands is apparently not due to fragmentation of the range of a once widespread species, but is more likely the result of a long history of colonizations and extinctions by a number of species. In a wider context, this may not pertain only to *Megapodius*, but to all Megapodiidae: when more megapodes co-exist (notwithstanding the undoubtedly old history of the family, rarely more than two), they either should have different breeding strategies or have different habitat requirements. The small *Megapodius cumingii gilbertii* on Sulawesi would probably not have survived in the presence of the large *Macrocephalon maleo* when both would have been mound builders, and the small *Eulipoa wallacei* in the Moluccan islands can survive next to the larger species of *Megapodius* on these islands only by reproducing on coastal beaches and outlying islands, some of which are reached by long nocturnal flights during which the pair-bond is apparently maintained with use of flashing white under wing-coverts and vent (Jones *et al.*, in press). However, a few species with similar breeding strategy but of different genera are reported to overlap and occasionally even lay in the same mound (R. W. R. J. Dekker *pers. comm.*).

A history of invasions and extinctions by various species of *Megapodius* may explain some of the peculiarities in their present-day distribution. For instance, *M. reinwardt reinwardt* occupies a huge range from Nusa Penida (off Bali) and Salombo Besar (in the eastern Java Sea) east to Milne Bay on the eastern tip of New Guinea and north to the Vogelkop Peninsula of New Guinea and to many islands in the Banda and Flores seas such as Banda, the Tukangbesi Group, and Salajar (see fig. 3). Within this range, variation is markedly small (further division in races as advocated by Mayr in 1938 appears to be unfounded: Jones *et al.* in press), indicating that either the present-day distribution is recent or that gene-flow between the islands occurs due to inter-island exchanges by the birds. In the latter case, the distribution must be recent too, otherwise the species would have colonized the islands further north, which are at present inhabited by a number of smaller species which differ greatly fom *M. reinwardt* in, e.g., tail/tarsus ratio. On the Tanimber Islands, within the range of *M. reinwardt*, the large *M. tenimberensis* occurs, completely surrounded by the smaller *M. reinwardt* on other islands. In tail/tarsus ratio and in other characters, *M. tenimberensis* seems closely related to the small-sized *M. cumingii gilbertii* from Sulawesi, to *M. bernsteinii* from the Banggai and Sula islands, and to *M. forstenii* on the southern Moluccas. It is tempting to suggest that small-sized relatives of this group formed by *M. tenimberensis*, *M. cumingii*, *M. bernsteinii*, and *M. forstenii* once occurred on the Lesser Sunda Islands and on islands in the Banda, Flores, and Java seas, where they were exterminated by invading large-sized *M. reinwardt*. Only the even larger *M. tenimberensis* had been able to cope with the intruders. The same may have happened on the Vogelkop Peninsula, where small-sized relatives of *M. freycinet* or *M. geelvinkianus* may have been replaced by large *M. reinwardt reinwardt*. Where an original species was more matched in size to the invading *M. reinwardt*, a zone of secondary hybridization could be the result, as seems to be the case on the islands off south-east New Guinea, where variable intermediates between *M. reinwardt* and *M. eremita* occur (*'M. macgillivrayi'*). The present-day boundaries of the range of *M. reinwardt* are not likely to be fixed yet.

When one considers *M. reinwardt* to be a recent successfully spreading species, characterized by a

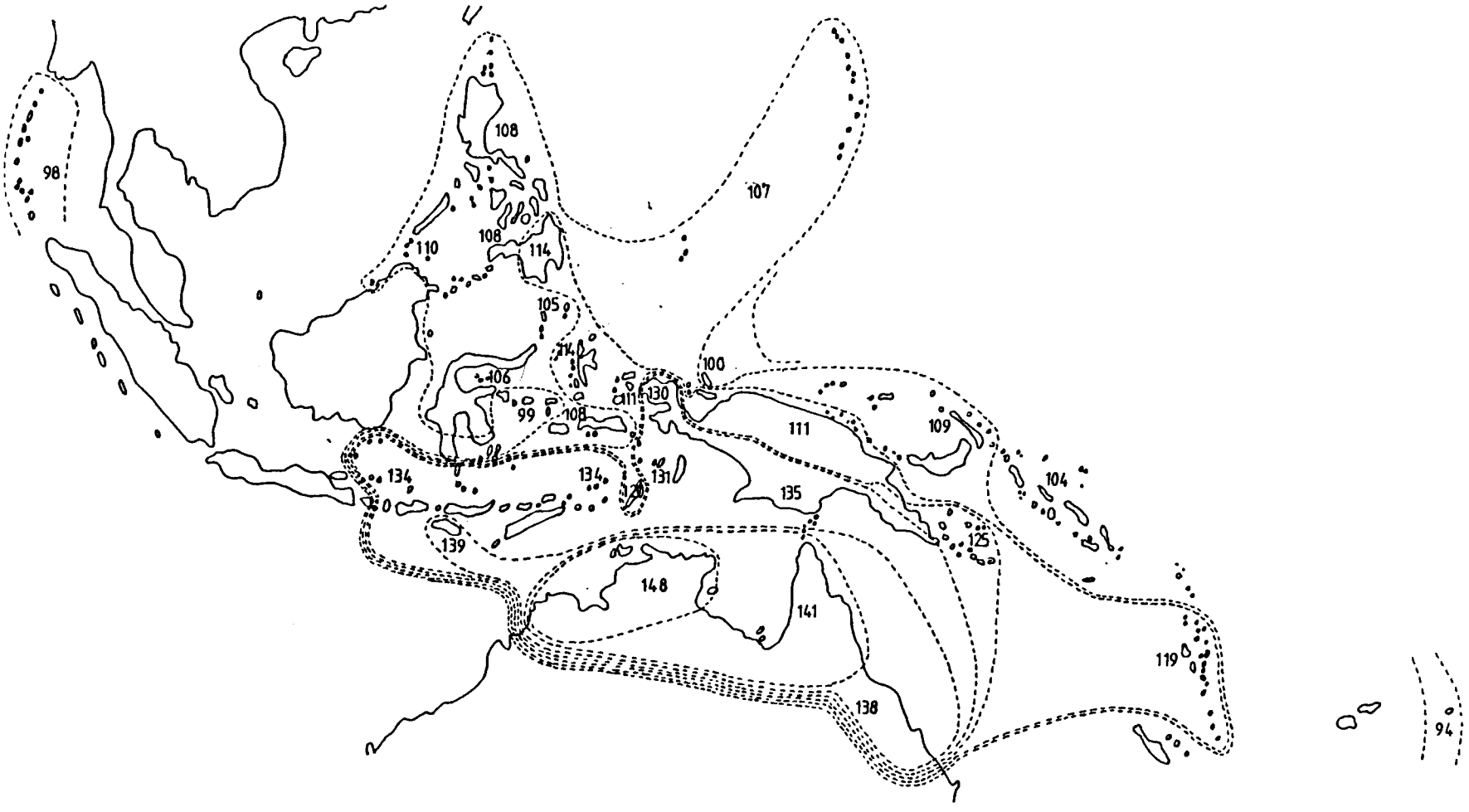

Figure 4. Average tail/tarsus ratio x100 of populations of *Megapodius*.

high tail/tarsus ratio, it is interesting to compare this ratio with that of other species of *Megapodius* (fig. 4): the ratio of *M. reinwardt* is much higher than in the other species (only hybrid populations on the islands of south-east New Guinea and in the Astrolabe Mountains of eastern New Guinea are intermediate). The remaining species show a trend of decreasing ratio towards west, north, and east, as if the Indo-Pacific was colonized by successive waves of *Megapodius* out from a centre in southern New Guinea or northern Australia, in which the older radiations had a longer tarsus or a shorter tail.

GEOGRAPHICAL VARIATION IN SOME SPECIES OF MEGAPODIUS

MEGAPODIUS CUMINGII

The Philippine Megapode *Megapodius cumingii* is widespread in the Philippines, on the islands off northern Borneo, in Sulawesi, and on many islands in between. Many taxa have been described, but most have sunk into synonymy. Study of *c.* 110 adult specimens of *M. cumingii* revealed that most of the races described are valid, however. Only the situation on the Sulu Islands and on Maratua (off eastern Borneo) is still unclear due to lack of specimens. Thus, whether *balukensis* Oberholser, 1924, from Balukbaluk (off western Basilan in the northern Sulus) or *tolutilis* Bangs & Peters, 1927, from Maratua can be maintained is yet to be settled. Both names are based on a single specimen only, perhaps not yet full-grown, and not available during this study. The populations inhabiting the Talaud and Sangihe islands, between eastern Mindanao (where *tabon* occurs) and northern Sulawesi (where *gilbertii* occurs) are usually attributed to a single taxon, *sanghirensis* Schlegel, 1880. A study of a larger number of specimens than available to earlier authors on megapodes revealed that two separate races are involved, differing in size and (slightly) in colour.

Megapodius cumingii sanghirensis

Megapodius sanghirensis Schlegel, 1880, *Notes Leyden Museum* 2, p. 91. Based on a type series from Sangihe (Great Sangi) and Siau islands in RMNH: *M. sanghirensis* cat. nr. 1, 2, 3 & 6, collected in or before 1866 on Siau by Van Duyvenbode and cat. nrs. 4 & 5, collected on Sangihe on 29 November 1865 and on 23 January 1866 by Hoedt. Type series examined, measurements included in table 2.

Diagnosis. A medium-sized megapode, smaller than *M. cumingii tabon* from eastern Mindanao, but larger than *M. cumingii gilbertii* from Sulawesi, differing from these and other races of *M. cumingii* by distinctly darker and more saturated body colour. The upperparts are dark chestnut-brown, less bright rufous than in some other dark-coloured taxa of *Megapodius*, often with a maroon or purplish tinge. The underparts are deep grey with some olive tinge on the belly.

Distribution. Examined from Sangihe, Siau, Tahulandang, and Ruang ('Gunung Api'), all in the Sangihe Group. Not yet reported from any of the other (smaller) islands in the group.

Measurements. See table 2. No obvious differences in size between populations of the various islands.

Remarks. A single bird of a series of three examined from Ruang, the southernmost island of the Sangihe Group and the one closest to Sulawesi, is paler than the other two on the upperparts, almost matching the colour of the darkest specimens of *gilbertii* from Sulawesi. The colour of the other two birds is similar to those from Sangihe, Siau, and Tahulandang. In size, all three are larger than *gilbertii*. Perhaps some gene-flow exists between *gilbertii* of Sulawesi and *sanghirensis* from the Sangihe Islands.

Megapodius cumingii talautensis

Megapodius cumingii talautensis **subspecies nova.** Holotype: SMTD cat. nr. C 13098, adult male, collected 10 November 1893 by Cursham on Kaburuang, Talaud Islands. Wing 244 mm, tail 78 mm, tarsus 72.5 mm, and bill to skull 26.6 mm. Paratypes, all collected by Cursham: SMTD C13099, adult female, 10 November 1893, BMNH 98.4.29.24, unsexed adult, 16 November 1893 (both from Kaburuang), BMNH 1930.2.15.1, subadult female, 26 August 1896, as well as BMNH 97.5.12.22, BMNH 97.5.12.23, SMTD C15419, SMTD C15421, SMTD C15422, and ZMB

	(1) gilbertii			(2) sanghirensis			(3) talautensis			(4) pusillus			(5) tabon		
	mean	Sd	range	mean	Sd	range	mean	Sd	range	mean	Sd	range	mean	Sd	range
wing	205.1	5.04	196 - 213	231.4	5.19	224 - 240	244.3	3.97	240 - 254	245.4	5.48	239 - 254	257.2	2.63	255 - 261
tail	64.9	2.65	60 - 69	71.7	3.31	66 - 76	75.1	2.33	72 - 79	76.4	3.10	73 - 82	84.2	2.90	81 - 87
tarsus	61.2	2.92	55.5-66.4	66.7	3.18	62.0-71.7	72.7	2.77	69.6-78.3	70.7	2.04	67.6-73.3	73.8	2.21	71.0-76.4
claw	17.6	1.15	15.3-19.8	20.4	1.47	18.7-22.2	23.5	1.40	21.7-25.2	21.6	0.98	20.5-23.1	22.6	1.27	21.3-24.1
bill	27.2	1.25	25.0-29.5	28.3	1.27	26.2-29.8	29.0	1.52	27.0-31.4	28.8	1.47	27.6-30.7	31.0	1.83	28.6-32.5

Table 2. Measurements of wing, tail, tarsus, middle claw, and bill to skull of adult birds of various populations of *Megapodius cumingii*. Sexes similar in size, data combined.
(1) *gilbertii* from Sulawesi, Lembeh, and Togian islands (n=24), (2) *sanghirensis* from Sangihe Islands (n=12), (3) *talautensis* from Talaud Islands (n=10), (4) *pusillus* from Masbate, Basilan, and Zamboanga Peninsula (western Mindanao), Philippines (n=8), (5) *tabon* from eastern Mindanao (n=4).

	(1) Waigeo			(2) Misoöl			(3) Salawati			(4) Numfor			(5) Biak		
	mean	Sd	range	mean	Sd	range	mean	Sd	range	mean	Sd	range	mean	Sd	range
wing	229.4	3.83	222 - 236	224.8	6.10	214 - 232	214.9	7.19	207 - 223	197.3	4.85	190 - 210	189.4	5.37	178 - 197
tail	77.5	1.87	73 - 81	75.9	2.76	72 - 80	71.6	1.59	69 - 74	66.9	2.46	64 - 70	61.2	1.85	58 - 64
tarsus	70.4	2.35	68.0-74.0	67.5	3.59	63.8-71.5	64.6	3.11	61.0-69.3	61.3	1.99	60.0-64.2	61.5	2.14	59.3-64.9
claw	20.5	0.80	19.4-21.8	20.0	1.52	17.8-22.8	18.4	0.86	17.4-19.8	17.1	0.60	16.5-17.7	16.9	0.83	15.5-18.0
bill	31.4	1.65	27.4-32.4	29.8	1.74	27.4-32.0	29.7	1.59	27.2-32.6	25.9	1.66	24.7-27.8	26.2	1.13	24.2-29.7

Table 3. Measurements of wing, tail, tarsus, middle claw, and bill to skull of adult birds of various populations of *Megapodius freycinet* and *Megapodius geelvinkianus*. Sexes similar in size, data combined.
(1) *M. freycinet freycinet* from Waigeo, Gebe, and Gag islands (n=11), (2) *M. freycinet freycinet* from Misoöl Island (n=12), (3) *M. freycinet oustaleti* from Salawati and Sorong islands (n=6), (4) *M. geelvinkianus* from Numfor Island (n=4), (5) *M. geelvinkianus* from Biak, Supiori, and Aifundi islands (n=11).

32283, all unsexed adults and all collected 'autumn 1896' (the latter seven from Karakelong).

Diagnosis. Rather similar in coloration to *sanghirensis*, and thus markedly darker than the remaining races of *M. cumingii*. Distinctly larger than *sanghirensis*, about intermediate between *tabon* from the mountains of eastern Mindanao and *sanghirensis*. When series of *sanghirensis* and *talautensis* are compared, *talautensis* differs on average in even darker colour, showing black-brown upperparts with a more pronounced maroon tinge and plumbeous-black underparts.

Distribution. Examined from Karakelong and Kaburuang in the Talaud Group. Also occurs on Salebabu, between Karakelong and Kaburuang.

Measurements. Intermediate between *tabon* and *sanghirensis* in all measurements, especially wing and tail hardly overlapping in length with either of these. See table 2. More or less similar in size to *M. cumingii pusillus* from Masbate, Cebu, Zamboanga peninsula (western Mindanao) and Basilan, but differing markedly in colour. No obvious difference in size between birds from Karakelong and Kaburuang.

Etymology. Named after the group of islands on which the species occurs.

Remarks. Meyer & Wiglesworth (1894) already pointed to the possibility that Sangihe and Talaud birds differed, but considered the number of specimens then available to be insufficient to describe a new race.

MEGAPODIUS FREYCINET

The Dusky Megapode *M. freycinet* is restricted to the northern Moluccas, the West Papuan Islands, and to the swampy coast of north-west Vogelkop Peninsula, Irian Jaya, where it may come in contact with the Orange-footed Megapode *M. reinwardt* which generally occurs further inland. It has been collected on the islands of Tifore and Batang Kecil (Salvadori 1876, 1882), halfway Halmahera and northern Sulawesi, but its status on these islands is unknown. Though marked geographical variation in size within *M. freycinet* has been known for over 100 years (Schlegel 1866, Oustalet 1880), no subspecies have formally been described (e.g., see revisions of *Megapodius* in Ogilvie-Grant 1893 and Mayr 1938). After examination of 120 specimens of *M. freycinet* in the collections of the BMNH, RMNH, SMTD, ZMA, and ZMB, three races appear to be valid, differing in size and in relative length of tail and claws. Minor variation in colour may occur too (Schlegel 1866, Oustalet 1880, Salvadori 1882, De Schauensee 1940), but the effect of bleaching and wear on the colour of live specimens and colour change with age in skins is considerable, and this makes assessment of slight colour differences impossible. The following races are recognized:

Megapodius freycinet freycinet

Megapodius freycinet Quoy & Gaimard, 1823, Voyage de l'Uranie, Zool., p. 125, pl. 32, Waigeo and Gebe islands. Holotype from Waigeo (Oustalet 1880), in Paris museum, not examined. Synonym: *Alecthelia Urvillii* Lesson & Garnot, 1826, *Bull. Sci. Nat.* VIII, p. 115, Gebe Island; based on a pullus flown aboard a ship at over two miles from the coast of Gebe (Oustalet 1880).

Diagnosis. A rather small all-black *Megapodius* with dull red to dark vinous-red bare facial skin and dark olive to black legs and feet. Tail and claws are short in relation to body size, more so than in other races of the species.

Distribution. Birds examined from Waigeo, Gag, Gebe, and Misoöl, off western New Guinea, Irian Jaya. Data from literature (identification to race in part supported by measurements supplied) from Boni Island (just off Waigeo) (Gray 1861), Saonek Island (just off Waigeo) (De Beaufort 1914), Kofiau (Salvadori 1882, Ripley 1957, 1959), and Kamuai (Schildpad Islands) (De Schauensee 1940). For a distribution map, see fig. 5.

Measurements. See data in table 3. Birds from Misoöl are on average smaller than typical birds from Waigeo, Gag, and Gebe, with bill and tarsus lengths intermediate between those of the populations of Waigeo and Salawati, but wing, tail, and claw lengths are much closer to Waigeo birds than to Salawati and the population from Misoöl is therefore included in nominate *freycinet*. Alternatively, the sample from Misoöl may have been a mixture of the larger nomi-

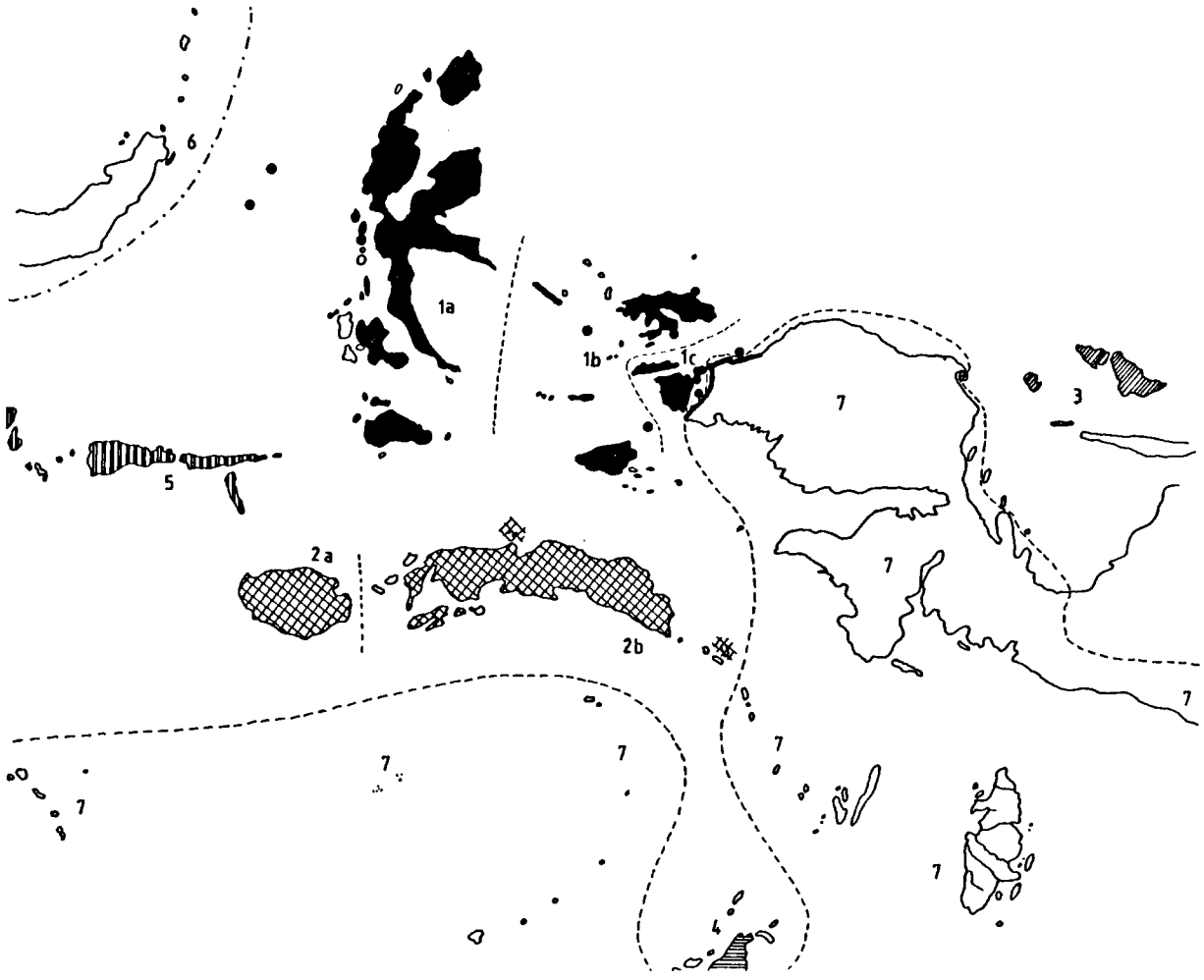

Figure 5. Distribution of subspecies of *Megapodius freycinet* and *Megapodius forstenii* and of some other species of *Megapodius*.
(1) *M. freycinet* (a - *quoyii*, b - nominate *freycinet*, c - *oustaleti*), (2) *M. forstenii* (a - *buruensis*, b - nominate *forstenii*), (3) *M. geelvinkianus*, (4) *M. tenimberensis*, (5) *M. bernsteinii*, (6) *M. cumingii*, (7) *M. reinwardt* (broken line: northern boundary of species).

nate *freycinet* occurring on Misoöl proper and of a smaller subspecies occurring on the many small islands offshore of Misoöl, but this is not supported by the data on the labels of the specimens, most of which had localities from Misoöl itself (see Mees 1965, 1980), with only a few showing a generalized locality 'Misoöl'. Wing measurements of two birds from Kamuai (Schildpad Islands, between Misoöl and Salawati), supplied by Mayr & de Schauensee (1939), agree best with those of Misoöl; the larger bird (wing 229 mm) is too large to belong to the small race described as new below, the smaller one (wing 212 mm) is too small for nominate *freycinet*, but may have been a not full-grown immature, like other birds of nominate *freycinet* from the literature with wing below 222 mm.

Megapodius freycinet oustaleti

Megapodius freycinet oustaleti **subspecies nova.** Holotype: RMNH *M. freycinet* cat. nr. 50, adult male, collected on Sorong Island by Bernstein on 28 November 1864. Wing 207 mm, tail 72 mm, tarsus 63 mm, claw of middle toe 18.5 mm, bill to skull 29.8 mm. Paratypes: RMNH cat. nr. 53, subadult male, collected on Sorong Island by Bernstein on 11 September 1864; RMNH cat. nr. 49, adult male, collected on Salawati in January 1877 by Bruijn; RMNH cat. nr. 48, aduit female, collected 1 March 1865 on Salawati by Bernstein; BMNH 81.5.1.5666, adult male, collected on Sakamun Island off Salawati on 11 July 1868 by D. S. Hoedt, ex Gould collection.

Diagnosis. Similar to nominate *freycinet* from Waigeo in colour and in proportions of tail, tarsus, claw, and bill lengths as compared to wing length, but distinctly smaller in all measurements, especially wing.

Distribution. Birds examined from Salawati, Sakamun Island (off Salawati), Sorong Island, mainland New Guinea opposite Sorong Island, and 'Pulau Penang off north-west New Guinea' (not located). Data from literature (identification supported by measurements) from Tsiof and Jef Maän islands (Sele Strait, between Salawati and New Guinea) (De Schauensee 1940), Arar Island (Sele Strait) (Ripley 1964), Batanta (Salvadori 1882, Ripley 1964), Pulau Hum (off north-west Vogelkop), and Ramoi and Dore Hum (coast of northern Vogelkop) (Salvadori 1882). For a distribution map, see fig. 5.

Measurements. See table 3 and fig. 6. The wing is generally 221 mm or less, against 222 mm and over in typical nominate *freycinet*. Of six birds of *oustaleti* examined and of seven specimens from the literature (Oustalet 1880, De Schauensee 1940), only one had wing over 221 mm (viz., once 223) and 11 of the 13 had wing below 215 mm; of 11 nominate *freycinet* examined and of 15 from the literature (Rothschild *et al.* 1932, Mayr & De Schauensee 1939, De Schauensee 1940, Gyldenstolpe 1955) all had wing 222 mm and over (this sample excluding Misoöl birds).

Etymology. Named in honour of J.-F. É. Oustalet (1844-1905), professor of the Muséum Nationale d'Histoire Naturelle in Paris, president of the International Ornithological Congress of 1900, author of many books on birds, among which was the first revision published on the family Megapodiidae, and one of the first to note the small size of the Salawati birds. See Anonymus (1906).

Remarks. The occurrence of a small form of *M. freycinet* on localities where it may come into contact with the large *M. reinwardt* of western and southern New Guinea may by some be explained as character displacement, with only smaller-than-average birds of *M. freycinet* surviving in the overlap area due to competition with the large *M. reinwardt*. However, it is more likely that *M. reinwardt* has recently arrived in the Vogelkop Peninsula from the south (see the chapter on species limits within *Megapodius*). In a geologically recent past, the Vogelkop may have been inhabited by a small *Megapodius* related to the *M. freycinet/M. geelvinkianus* group, thus linking the present-day ranges of *M. freycinet* on the West Papuan Islands and of *M. geelvinkianus* on the islands in the Geelvink Bay. The small size of *M. freycinet oustaleti* then perfectly fits into a cline of decreasing size running from Ternate through Halmahera, Waigeo, Salawati, and Numfor to Supiori-Biak (fig. 6). However, *M. freycinet* and *M. geelvinkianus* differ in general colour, in colour of bare parts, and in relative length of tarsus, reason to consider them to be separate species. *M. reinwardt* is probably still extending its range and may be in the process of swamping *M. freycinet oustaleti*. Three birds examined in the

	(1) Ternate			(2) Halmahera etc.			(3) Obi group			(4) Buru			(5) Ceram		
	mean	Sd	range	mean	Sd	range	mean	Sd	range	mean	Sd	range	mean	Sd	range
wing	241.1	5.65	231 - 252	231.5	5.77	219 - 241	224.4	6.83	215 - 237	226.8	6.66	215 - 235	210.0	5.38	201 - 225
tail	86.6	3.53	82 - 93	82.7	2.55	78 - 87	78.9	2.58	75 - 83	77.4	4.53	72 - 83	70.3	2.69	65 - 74
tarsus	72.6	3.31	68.0-77.0	72.0	3.25	66.0-78.5	69.4	2.66	66.2-72.2	71.0	3.92	67.4-75.5	66.3	2.91	61.0-70.7
claw	23.3	1.60	21.3-26.2	23.1	1.48	19.6-26.0	21.4	2.13	19.5-25.0	23.6	1.78	21.3-26.9	19.7	0.92	17.9-21.4
bill	32.1	1.63	29.8-34.1	30.9	1.20	28.2-33.8	29.4	1.96	27.3-31.8	30.2	1.17	28.8-32.2	29.8	1.15	27.6-32.5

Table 4. Measurements of wing, tail, tarsus, middle claw, and bill to skull of adult birds of various populations of *Megapodius freycinet* and *Megapodius forstenii*. Sexes similar in size, data combined.
(1) *M. freycinet quoyii* from Ternate Island (n=13), (2) *M. freycinet quoyii* from Tidore, Mare, Kajoa, Morotai, Rau, Halmahera, and Bacan islands (n=46), (3) *M. freycinet quoyii* from Obi Group (n=7), (4) *M. forstenii buruensis* from Buru (n=9), (5) *M. forstenii forstenii* from Ceram, Tudju Islands, Ambon, and Haruku (n=25).F

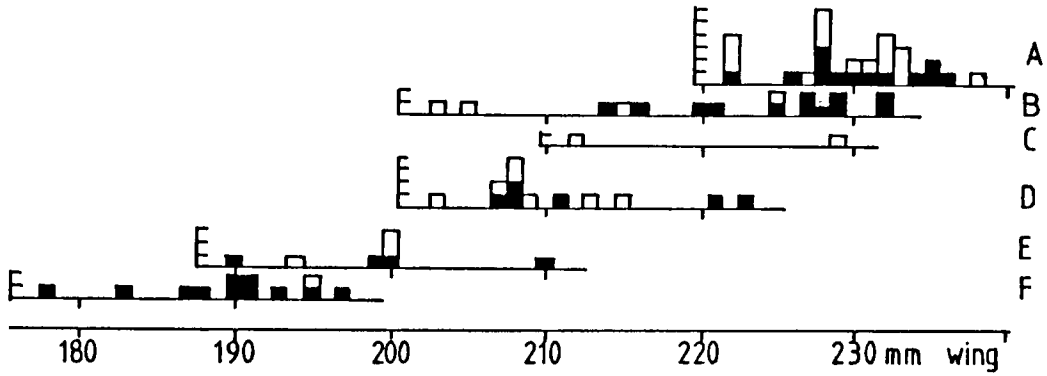

Figure 6. Frequency histogram of wing length of *Megapodius freycinet* (A-D) and *M. geelvinkianus* (E-F) to show apparent decrease of size eastward.
Black squares: specimens examined, all adult. Open squares: data from the literature, in part probably including not full-grown non-juvenile birds (see text).
(A) Waigeo, Gebe, and Gag islands, (B) Misoöl Island, (C) Schildpad Islands, (D) Salawati and Sorong islands, (E) 'Dorei' and Numfor Island, (F) Supiori, Biak, and Aifundi islands.

RMNH from 'Sorong' (unknown whether island proper or opposite mainland) are hybrids between both species (RMNH cat. nrs. 51, 52, and 54, collected 1864 by Bernstein). These hybrids are superficially similar in colour to *M. decollatus* from northern New Guinea (eastern shore of Geelvink Bay to Mambare River), and one may suppose that *M. decollatus* could be a stabilized hybrid between *M. reinwardt* and *M. geelvinkianus* or *M. eremita*, but, while the three hybrids are perfectly intermediate between their parents in colour, size, and relative proportions of extremities, *M. decollatus* neither resembles the three hybrids nor *M. geelvinkianus* or *M. eremita* in relative proportions.

Most birds examined from Dorei or nearby Manokwari in the eastern Vogelkop Peninsula are *M. reinwardt*, but a single bird labelled 'Dorei' in the RMNH was *M. geelvinkianus,* with size and measurements similar to the birds from Numfor (which differ somewhat from typical *M. geelvinkianus* from Supiori-Biak). *M. geelvinkianus* may either breed on the small islands off the eastern Vogelkop, like Pulau Manasbari off Dorei, parallel to the situation of *M. freycinet* in the west, or the bird, collected by Von Rosenberg on 12 January 1869, was imported from Numfor by native traders.

Megapodius freycinet quoyii

Megapodius quoyii G. R. Gray, 1861, *Proc. Zool. Soc.* p. 289, pl. 32, southern Halmahera. Based on a pullus collected by A. R. Wallace, now in the BMNH, cat. nr. 60.9.5.38, examined. No further details on collection date or locality on the label.

Diagnosis. Similar in general size (wing, tarsus, bill, mass) to nominate *freycinet* from Waigeo, but tail and claw markedly longer. See table 3 and fig. 7.

Distribution. Examined from Morotai, Rau, Halmahera, Ternate, Tidore, Mare, Kajoa, Bacan, Obi Major, and Obi Latu. Data from literature from Obi Bisa (Rothschild & Hartert 1901). For a distribution map, see fig. 5.

Measurements. Birds from Morotai, Rau, Tidore, Mare, and Bacan are similar in size to those from the type locality Halmahera, but birds from Ternate are on average larger (table 4, fig. 8). The difference is not large enough to consider Ternate to be inhabited by a separate race. Birds from the isolated islands Tifore and Batang Kecil (halfway Halmahera and Sulawesi) are small: average wing of three birds is 210 mm (Salvadori 1882). The small size is perhaps due to immaturity or to influence of nearby *M. cumingii gilbertii* from Sulawesi, which has an average wing of 205.1 mm (range 196-213, n=24); the plumage is similar to *M. freycinet*, however, with wing even less brown-olive (Salvadori 1882), not largely brown-olive as in *M. c. gilbertii*. None of the three birds was examined.

Remarks. The name *M. quoyii* is usually considered to be a synonym of *M. freycinet*, but the birds from all northern Molucca Islands differ constantly from those of the West Papuan Islands in proportionally longer tail and claws. Though the type of *M. quoyii*, a pullus, can not be assigned to a race on size or plumage characters, its Halmaheran origin justifies the correctness of the use of the name *quoyii* for the northern Moluccan populations.

The birds from the Obi Group of islands are problematical. Four of the seven adults from Obi Major are inseparable in size and colour from *M. freycinet quoyii* from further north, but the other three show a slight olive-green tinge on the upperparts rather than being all black, and the measurements are somewhat smaller. Perhaps a slight introgression of genes of *M. forstenii buruensis* from Buru occurs.

MEGAPODIUS FORSTENII

Forsten's Megapode *M. forstenii* is a small megapode from the southern Molucca Islands with a largely dusky olive-brown plumage, except for a plumbeous-grey hindneck and underparts; the bare facial skin is dull red to dark grey, leg and foot are dull olive-green to blackish. Opinions differ whether the birds from Buru can be recognized as a separate subspecies from those of Ceram and surrounding islands: Stresemann (1914a, b), Toxopeus (1922), Siebers (1930), and Van Bemmel (1948) are among those who consider size and colour differences to be large enough to separate Buru birds from those of Ceram, but in much of the more recent literature all populations are

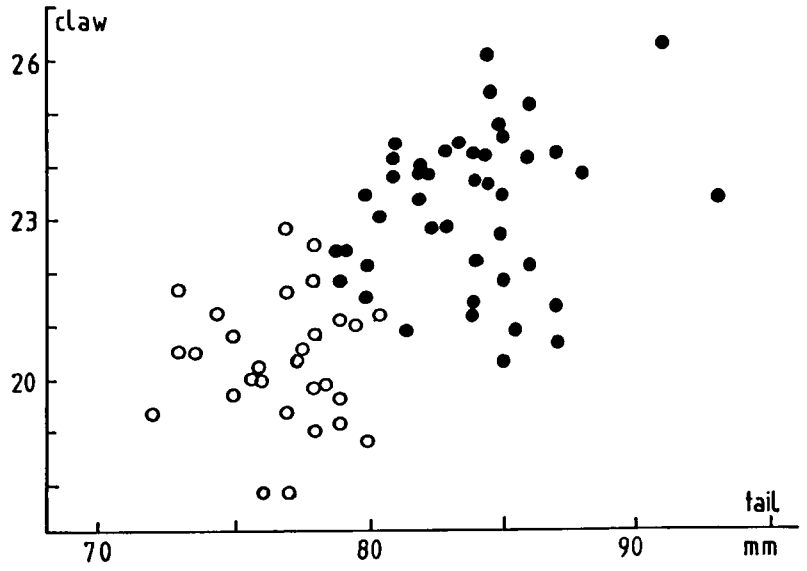

Figure 7. Difference in length of tail and middle claw between two subspecies of *Megapodius freycinet*. Open circles: nominate *freycinet* (Waigeo, Misoöl, etc.). Black dots: *quoyii* (northern Molucca Islands).

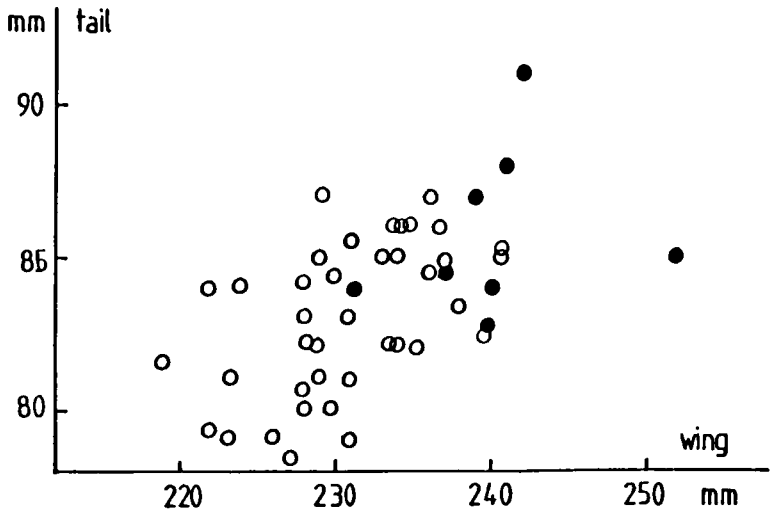

Figure 8. Difference in lenght of wing and tail between some populations of *Megapodius freycinet quoyii*. Open circles: Halmahera. Black dots: Ternate.

considered to form a single taxon, probably because the series available to most authors was small and contained some not full-grown birds. For our study, 35 adult birds were examined, and the recognition of two races seems well-founded.

Megapodius forstenii forstenii

Megapodius Forstenii G. R. Gray, 1847, *The Genera of Birds*, 3, p. 491, pl. 124. No type or type locality given, but undoubtedly based on the single existing specimen of *Megapodius* collected by Forsten in the southern Moluccas, now in the RMNH. This bird is here designated to be the holotype: cat. nr. 15, adult female, collected in 1840 by Forsten on Ceram; wing 210 mm, tail 71 mm, tarsus 69.5 mm, claw of middle toe 20.8 mm, bill from skull 30.3 mm.

Diagnosis. Characters as for the species; small in all measurements, wing generally 215 mm or less, tail generally 73 mm or less, middle claw generally 21 mm or less.

Distribution. Examined from Ceram, Nusa Tulun and Pulau Aleï (Tudju Islands, off northern Ceram), Ambon, Haruku, and Gorong (Ceramlaut Islands). Occurs also Pulau Pombo (off Ambon) and on Saparua (R. W. R. J. Dekker pers. comm.).

Measurements. See table 4 and fig. 9.

Remarks. Ambon and Haruku birds were stated to be darker olive-brown than those of Ceram (Oustalet 1880), but no constant difference in size or measurements was found between the populations of any of the localities examined.

Megapodius forstenii buruensis

Megapodius duperreyii buruensis Stresemann, 1914, *Novit. Zool.* 21, p. 41. Holotype: an adult male from Gunung Fogha (Mount Mada), Buru, collected by A. Dumas in August 1898, then in the Rothschild collection, now in the American Museum of Natural History; not examined.

Diagnosis. Similar to nominate *forstenii*, but larger in all measurements, with values generally over those cited under nominate *forstenii*. See table 4 and fig. 9.

Distribution. Restricted to Buru island, southern Moluccas. For collection localities and altitudes inhabited, see Stresemann (1914b) and Siebers (1930).

Measurements. Of all 26 birds measured from Ceram and surrounding islands, only three have wings of over 215 mm, while nine examined from Buru as well as 11 others from the literature (Stresemann 1914a) all had wing 215 mm and over. These three larger birds were all from Ambon, and one may suggest that, seeing the importance of Ambon as a trade centre for the Moluccan area, they may have been imported from Buru. However, the data on the labels do not support this: one was collected on Ambon by Hoedt (a reliable collector) on 18 February 1868, another had been obtained at 'Ajamatan, Ambon-Hitu' on 2 January 1923 by Kopstein, and only the third was a trade skin obtained from Teysmann in 1877 with no other details on the label than 'Ambon 1876', which does not seem reliable, but Teysmann's sample contained also three megapodes which did not deviate from other Ambon birds in size.

Remarks. As a few birds can not properly be identified by measurements, one may doubt the validity of *buruensis*. However, over 90% of the birds from the southern Molucca Islands can be racially identified, and thus recognition of *buruensis* seems well grounded. Moreover, both races differ, though slightly, in colour also: when series of both are compared, *buruensis* shows paler and greener mantle and scapulars, not as dark and brownish-olive as in nominate *forstenii*, and rump and upper tail-coverts are more olive-brown, less umber-brown.

A NOTE ON ETYMOLOGY OF MEGAPODIIDAE

Part of the races described as new in this paper are eponyms (named after a person) rather than pointing to characters of the new race or being derived from the collecting locality. One may deplore this, but it is in tradition with the naming of Megapodiidae: of 63 specific names in use or formerly in use, almost half (46%) is derived from persons (*abbotti, andersoni, bernsteinii, brazieri, brenchleyi, bruijnii, burnabyi, cumingii, cuvieri, dillwyni, duper-*

reyii, forstenii, freycinet, gilbertii, gouldii, hueskeri, laperouse, lathami, layardi, lowii, macgillivrayi, pritchardii, quoyii, reinwardt, robinsoni, rosinae, stairii, urvillii, and *wallacei*), 27% are based on a character (*affinis, assimilis, brunneiventris, castanonotus, decollatus, fuscirostris, longicauda, ocellata, perrufus, purpureicollis, pusillus, pyrrhopygius, rubrifrons, rubripes, senex, tolutilis,* and *tumulus*), 24% are toponyms (*arfakianus, aruensis, balukensis, buruensis, eremita, huonensis, geelvinkianus, jobiensis, misoliensis, nicobariensis, occidentis, sanghirensis, tenimberensis, trinkutensis,* and *yorki*), and 3% is derived from a local name (*maleo* and *tabon*); if looked at species and subspecies names considered valid at present, these values are 44%, 23%, 28%, and 5%, respectively.

CHECK-LIST OF EXTANT SPECIES OF MEGAPODIIDAE

This list is mainly given here to show how the newly described races of Megapodiidae fit in the other known taxa of the group. Deviations of traditional systematics shown below but not given in this article are explained in Jones *et al.* (in press).

Alectura lathami

Polytypic:	lathami	(eastern Australia north to just south of Cooktown, Queensland)
	purpureicollis	(northern Queensland south to Cooktown)

Aepypodius arfakianus

Polytypic:	arfakianus	(mainland New Guinea)
	misoliensis	(Misoöl Island)
	(incertae sedis)	(Japen Island; apparently different in bare part colours but only a single specimen available)

Aepypodius bruijnii

Monotypic		(Waigeo)

Talegalla cuvieri

Polytypic:	cuvieri	(Vogelkop Peninsula and Misoöl)
	granti	(southern foothills of Snow Mountains)

Talegalla fuscirostris

Polytypic:	fuscirostris	(eastern New Guinea south of main range)
	aruensis	(Aru Islands and southern New Guinea from Kolepom Island to lower Fly River)
	occidentis	(southern New Guinea between Triton Bay and upper Lorentz River)
	meyeri	(head of Geelvink Bay, north of central range)

Talegalla jobiensis

Polytypic:	jobiensis	(Japen Island and eastern shore of Geelvink Bay)
	longicauda	(northern New Guinea from Mamberamo Basin eastward)

Leipoa ocellata

Monotypic	(interior western and southern Australia)

Macrocephalon maleo

Monotypic	(Sulawesi and Butung Island)

Eulipoa wallacei

Monotypic	(Moluccan Islands and Misoöl)

Megapodius pritchardii

Monotypic	(Niuafo'ou, Polynesia)

Megapodius laperouse

Polytypic:	senex	(Palau Islands, Micronesia)
	laperouse	(Mariana Islands, Micronesia)
Megapodius nicobariensis		
Polytypic:	nicobariensis	(Middle Nicobar Islands)
	abbotti	(Little and Great Nicobar, southern Nicobar Islands)
Megapodius cumingii		
Polytypic:	gilbertii	(Sulawesi and Togian islands)
	cumingii	(small islands off Saba; Balabac and Palawan)
	dillwyni	(Luzon, Mindoro, Marinduque, and islands off northern Luzon north to Batan)
	pusillus	(central Philippines, western Mindanao, and Basilan)
	tabon	(eastern Mindanao)
	talautensis	(Talaud Islands)
	sanghirensis	(Sangihe Islands)
	(incertae sedis)	(Sulu Islands and Maratua Island off eastern Borneo; perhaps one or more smaller races involved, for which names *balukensis* and *tolutilis* may be available, but too few specimens known to decide on validity)
Megapodius bernsteinii		
Monotypic		(Sula and Banggai islands)
Megapodius tenimberensis		
Monotypic		(Tanimbar Islands)
Megapodius freycinet		
Polytypic:	quoyii	(northern Moluccan Islands)
	freycinet	(Waigeo, Gag, Gebe, Kofiau, and Misoöl islands, off north-west New Guinea)
	oustaleti	(Batanta, Salawati, and coast of and small islands off Vogelkop Peninsula)
	(incertae sedis)	(Batang Kecil and Tifore islands, between Sulawesi and Halmahera; described as small, and perhaps a valid small race of *M. freycinet* or *M. cumingii* or a hybrid between these, or the few specimens available were not full-grown immatures of *M. freycinet*)
Megapodius geelvinkianus		
Monotypic (?):	geelvinkianus	(Biak, Supiori, and Aifundi islands)
	(incertae sedis)	(Numfor and Mios Num islands; perhaps a larger race, but an insufficient number of specimens available)
Megapodius forstenii		
Polytypic:	forstenii	(Ceram, Ambon, Haruku, Saparua, Tudju, and Gorong islands, southern Moluccas)
	buruensis	(Buru Island, southern Moluccas)
Megapodius eremita		
Monotypic (?):	eremita	(Melanesia from Wuvulu and Ninigo Islands through Bismarck Archipelago to Guadalcanal and Malaita in Solomon Islands)
	(incertae sedis)	(San Cristobal, eastern Solomon Islands; perhaps a larger race, but an insufficient number of specimens available)
Megapodius layardi		
Monotypic (?):	layardi	(New Hebrides, Vanuatu)
	(incertae sedis)	(Banks Islands, Vanuatu; perhaps a larger race but an insufficient

number of specimens available)

Megapodius decollatus

Monotypic (?):	decollatus	(northern New Guinea from eastern shore of Geelvink Bay to Mambare River; small islands off coast from Tendanye to Manam)
	(incertae sedis)	(Japen Island; perhaps a smaller race but an insufficient number of specimens available)

Megapodius reinwardt

Polytypic:	reinwardt	(Vogelkop Peninsula south along southern New Guinea to Milne Bay and on north-east coast west to Mambare River, islands in northern Torres Strait, and on many islands in Banda and Flores seas, from Aru, Kai, and Watubela groups in east through Banda, Tukangbesi, and Lesser Sunda islands to Salajar, Djampea, and Nusa Penida islands, but excepting Tanimbar Group of islands)
	tumulus	(north-west Australia east to Groote Eylandt)
	yorki	(eastern Australia from Cape York Peninsula south to about Cooktown, including offshore islands and islands in southern Torres Strait)
	castanonotus	(eastern Australia from Cape Tribulation to Yeppoon, including many offshore islands)
	macgillivrayi	(D'Entrecasteaux, Trobriand, and Louisiade archipelago's off eastern New Guinea; a hybrid swarm between *M. reinwardt reinwardt* and *M. eremita*)
	(incertae sedis)	(mountains of eastern New Guinea inland from Huon Gulf to Astrolabe Mountains; a separate race or species, or hybrids between *M. reinwardt reinwardt* and an unknown species)
	(incertae sedis)	(Melville and Bathurst islands, northern Australia; name *melvillensis* available, but either based on immature birds of *tumulus* or a valid smaller race)
	(incertae sedis)	(Kangean, Salembu Besar, Karamian, and Matasiri islands in eastern Java Sea; considered racially separable by Meise 1941 due to the small size but not formally described, and sample may have consisted of not full-grown immatures of *M. reinwardt reinwardt*)

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ERRATUM

Inadvertently, the following figure was omitted from Bull. Zool. Mus. Univ. Amsterdam, 14 (2): 31

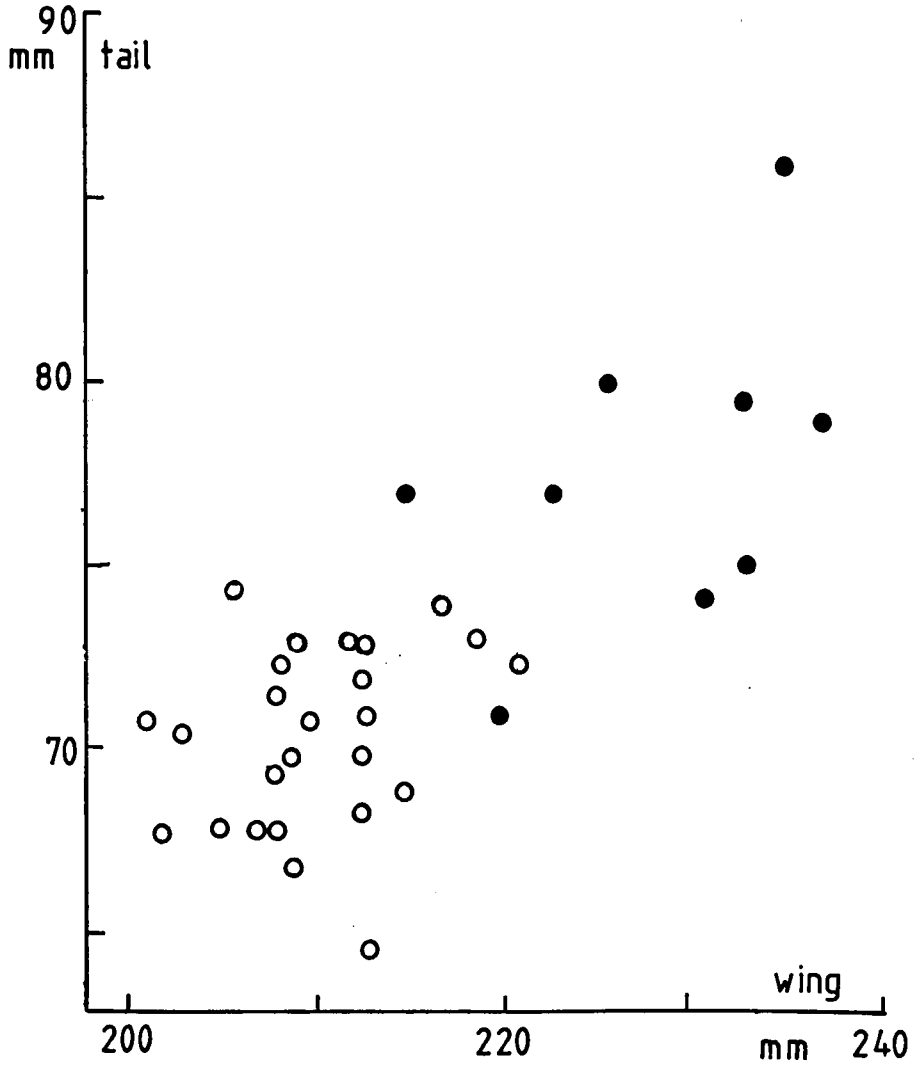

Fig. 9. Differences in length of wing and tail between both subspecies of *Magapodius forstenii*. Opencircles: nominate *forstenii*. Black dots: *buruensis*.