

Systematic notes on Asian birds. 21.
Babbler jungle: a re-evaluation of the ‘*pyrrogenys*’ group of
Asian pelloerneines (Timaliidae)

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The taxonomy of the jungle babblers, Delacour’s tribe Pelloerneini, has long been subject to reversals of opinion, suggestive of a still-poor understanding of natural relationships. At the unstable boundary of genera *Trichastoma* and *Pelloerneum*, groups of taxa usually taken to comprise a continental species *tickelli* and an insular species *pyrrogenys* have shifted from positions in separate genera to being neighbours in first one and then the other of these two. A fresh morphological analysis and newly described vocalizations show them to be one another’s probable closest relative, potentially conspecific but due to limitations on the allowable use of vocalization evidence among allopatric populations, for the time being at least, kept as separate entities. The Sumatran taxon *buettikoferi*, long held to be a subspecies of one or other of these two, has unique songs and a sufficient array of other peculiarities to be treated unequivocally as a full species, perhaps not more closely related than as sister species to the whole of the rest of the cluster.

Introduction

The Afro-Asian jungle babblers are an assemblage of soberly-coloured, unspectacular birds whose status as a tribe Pelloerneini (Delacour, 1946) lost standing with the down-grading of the babbler family category (Sibley & Ahlquist, 1990), and whose acceptance as a natural group has been weakened by confusion over its content. With recognition on anatomical grounds of a genus *Kakamega* Mann, Burton & Lennerstedt, 1978, for species *poliothorax* Reichenow, 1900, some headway has been made among African representatives. Less in Asia, where certain obvious anomalies have persisted unchallenged. This paper examines a particularly troublesome set of taxa on shifting ground between *Pelloerneum* Swainson, 1832, and *Trichastoma* Blyth, 1842, namely those usually identified as forming species *pyrrogenys* Temminck, 1827, and *tickelli* Blyth, 1859 (Temminck’s and buff-breasted babblers). Viewed across the range of geographical variation of this ‘*pyrrogenys* cluster’ (our term), morphology and recent information on vocalizations argue for restoration of perspective by predicating a search for the generic boundary on better understanding of biological species-limits.

Occupying forest-edge and understorey habitats allopatrically from the NE Indian subcontinent (east from Assam and Bangladesh) and SW China (Yunnan province)

south through mainland SE Asia to the Greater Sunda islands, the taxa involved are: on the continent, *t. assamense* Sharpe, 1883; *t. fulvum* Walden, 1875; *t. grisescens* Ticehurst, 1932; *t. annamense* Delacour, 1926 and nominate *t. tickelli* Blyth, 1859; in Borneo, *p. canicapillum* Sharpe, 1887, *p. longstaffi* Harrisson & Hartley, 1934 and *p. erythrota* Sharpe, 1883; and in Java nominate *p. pyrrogenys* Temminck, 1827 (E Javan *besuki* Kloss, 1931, synonymized: Mees, 1996). Described as a full species, Sumatran *buettikoferi* Vorderman, 1892, has long been downgraded to a subspecies either of Temminck's or of buff-breasted babbler. Largely because it fills a gap on the cluster distribution map, alternative options appear not to have been considered.

Chasen (1935) may be said to have signed off early systematic opinion on the cluster by sinking all of its Sunda island forms into a single species '*pyrrhogenys*', of the genus *Aethostoma* Sharpe, 1902 (Sharpe's replacement name for *Trichastoma*, then considered preoccupied). The continental species *tickelli* he returned to its original position in *Pellorneum*, placing it next to Sundaic *P. capistratum* (Temminck, 1823) (black-capped babbler), separated from *Aethostoma* in his linear sequence by another small jungle babbler genus, *Malacocincla* Blyth, 1845. Chasen assigned no cluster-member to *Malacocincla* even though, by then, Harrisson & Hartley (1934) had described *longstaffi* from the spinal range of Sarawak as a form of that genus – presaging a post-war inclination toward broader genera overall.

Delacour (1946) lumped babblers across the board, shrinking the list of generic names applicable to his forest-floor and undergrowth-living pelloerneines globally to just *Malacocincla* and *Pellorneum*. The latter he actually slimmed, by switching species *tickelli* (identified apparently from its rectal bristle length as showing intermediate characters) to the head of his *Malacocincla*. An *M. pyrrogenys* followed it directly, and Delacour is the first reviser to have implied a particular relationship between these two; the first also to have dissociated *pyrrogenys* firmly from another Sundaic species, *rostratum* Blyth, 1842 (white-chested babbler), its long-time neighbour in *Aethostoma*. No separate mention is made of Sumatran *buettikoferi* as a form of *pyrrogenys* since Delacour worked only down to the level of Chasen's species. However, this anomalously pale taxon (see below) is liable to have assisted a decision on the species-sequence.

In his Peters Check-list treatment of babblers, Deignan (1964) re-validated Blyth's name *Trichastoma* which, as an outcome of Delacour's broad-spectrum lumping, then took priority over *Malacocincla*. He also transferred a subspecies *buettikoferi* from *T. pyrrogenys* to *T. tickelli*, unfortunately without explaining why. More recently, Ripley & Beehler (1985) analysed all pelloerneines quantitatively, comparing what they evidently judged to have been representative populations of each then-accepted species across set characters to identify relatedness by the sum of nearest-neighbour linkages. Density of linkages was then mapped to highlight potential generic groupings. Especially interesting in terms of the cluster is their failure to make even one link between species *pyrrogenys* and *tickelli* (a return to the pre-Delacour state of affairs) against a near-maximum possible number between *pyrrogenys* and *capistratum*; and none again between *capistratum* and *tickelli* – internally consistent but in no overall support of any previous arrangement. Notwithstanding, all three, i.e., including *pyrrogenys* because of links found with *capistratum*, were assigned by them to *Pellorneum*.

Finally, van Marle & Voous (1988) accepted Deignan's recognition of a Sumatran taxon *T. tickelli buettikoferi*, and Inskipp et al. (1996) concurred but, following Ripley &

Beehler (1985), diverted this to *Pellorneum* rather than leaving it in *Trichastoma*. Van Marle & Voous's claim of a second Sumatran subspecies of *tickelli*, *concreta* Büttikofer, 1895, on Belitung island, cites Mees (1971) whose actual identification was of a small-island form of *T. (Malacocincla) abbotti* (Blyth, 1845) (Abbott's babbler).

Materials and methods

The working proposition that cluster-members are more closely related to one another than any is to an outsider group was investigated phenetically, by comparing (a) plumage patterns and colour tones, (b) general morphology via six easily-replicated measurements: of wing-length (straightened and flat), tail-length (flattened), tarsus (skeletal), culmen (chord from skull), bill-tip back to front end of narial groove (chord), and longest rictal bristle (= maximum rictus, straightened). Both actions incorporated samples of two other babbler species, *Trichastoma rostratum* and *Pellorneum capistratum*, selected for reasons outlined above as the non-cluster pellorneines liable to test the proposition most rigorously.

Pattern and colour comparisons were made across the ten cluster taxa, plus all six currently recognized 'out-group' subspecies: nominate *T. r. rostratum* (Peninsular Malaysia) and *r. macropterum* Salvadori, 1868 (Borneo), and *P. c. nigrocapitatum* (Eyton, 1839) (Thai-Malay Peninsula), *c. capistratoides* Strickland, 1849 and *c. morrelli* Chasen & Kloss, 1929 (Borneo), and nominate *c. capistratum* (Java). Since most jungle babblers are sexually dimorphic by size, in all possible instances sex determinations from specimen labels were cross-checked against wing- and tail-length data, and position in a bi-coordinate scattergram plot of these two measurements. Where outcomes clashed, the independent morphological evidence took precedence. Measurements of males only were then compared across those taxa for which a minimum five individuals could be assembled from all sources, including in some instances live birds measured by one of us in the field (an anticipated non-skeletal shrinkage factor was not detected in the raw data). This forced the exclusion of two cluster-members, *t. griseus*, of which only the type specimen (BMNH 1932.10.20.2) was seen, and *t. annamense*, but none of the 'out-group' taxa. All museum skins handled are listed in the Appendix.

The sound repertoire of some Asian babblers includes alternative vocalizations that can be different enough not to be associated readily without an actual view of the singer. From collective field experience of the vocalizations of cluster-members *fulvum*, *tickelli*, *canicapillum* and *pyrogenys*, we are convinced these reclusive but relatively common, closely approachable birds have no hidden songs that might have supported alternative relationship hypotheses, and that recordings available to us were representative of their normal repertoire. The literature on these and other forms (e.g., *assamense*) supports this conclusion. Known to us from only a single contact in the field, and otherwise undescribed, Sumatran *buettikoferi*'s persistent songs, listened to and recorded at length, were sufficiently striking that equivalents would never have been missed had they occurred in the repertoires of other, more-often observed cluster-members.

For ease of comparison of vocalizations, wide-band-mode sonograms (fig. 2) have been re-drawn to emphasize areas of main sound energy. In the field, tape-recordings were used to conduct preliminary cross-population song-recognition experiments

between actively vocalizing (territorial) Peninsular Malaysian *tickelli* and W Javan *pyrogenys* (both of which responded routinely and strongly to play-back of their own voices), and to test their reaction to songs of *buettikoferi*. Results stand on their own merit, but the exercise should be replicated, and extended to more taxa.

Cluster cohesion

In their 'out-group' role, *T. rostratum* and *P. capistratum* stand for all pelloerneines as the species previous revisers have at one time or another identified most closely with some taxon now treated as a cluster-member. Acting separately, and independent of actual relatedness, as stated, they allow a test of whether cluster-members really are more alike than any is to a non-cluster taxon.

Table 1. Sample-sizes, and ranges and means (mm) of six standard measurements (wing, tail, tarsus, culmen from skull, bill-tip from anterior end of narial groove, longest rictal bristle) taken from eight cluster taxa (excluding only *t. griseescens* and *t. annamense*) and all recognized subspecies of *T. rostratum* and *P. capistratum*.

Taxon	Wing	Tail	Tarsus	Culmen	Bill-tip	Rictus
<i>t. assamense</i> (n = 7)	65-68 (66.8)	53-57 (55.1)	27.8-29.8 (28.6)	15.6-17.1 (16.3)	8.3-9.0 (8.6)	7.5-8.8 (8.2)
<i>t. fulvum</i> (n = 7)	64-70 (65.4)	54-62 (56.7)	25.2-27.1 (26.2)	15.2-18.0 (16.6)	8.3-9.2 (8.8)	7.7-9.7 (8.9)
<i>t. tickelli</i> (n = 18)	64-67 (65.5)	53-59 (56.0)	25.5-28.0 (26.7)	16.0-17.9 (17.0)	8.3-9.5 (9.1)	8.0-10.1 (9.1)
<i>p. canicapillum</i> (n = 6)	66-69 (67.5)	55-60 (57.1)	24.8-27.0 (26.1)	16.5-17.2 (16.9)	8.9-9.5 (9.3)	10.1-11.7 (11.0)
<i>p. longstaffi</i> (n = 13)	67-72 (69.5)	53-60 (57.1)	24.6-28.0 (26.5)	15.3-17.3 (16.5)	8.5-9.5 (9.1)	10.2-15.3 (11.8)
<i>p. erythro</i> (n = 6)	69-74 (70.8)	56-62 (57.9)	26.1-27.3 (26.6)	16.5-17.8 (17.2)	8.9-10.1 (9.4)	9.5-12.5 (11.5)
<i>p. pyrogenys</i> (n = 12)	65-71 (68.5)	52-57 (54.8)	25.8-28.4 (26.8)	16.0-17.7 (17.0)	8.2-10.5 (9.4)	8.6-12.2 (10.0)
<i>buettikoferi</i> (n = 12)	65-70 (67.1)	49-52 (50.2)	26.7-27.8 (27.0)	15.6-18.2 (16.8)	9.0-9.9 (9.4)	9.5-10.7 (10.0)
<i>r. rostratum</i> (n = 10)	73-75 (74.2)	51-55 (53.0)	25.2-27.8 (27.0)	19.6-21.7 (20.6)	10.8-12.9 (11.5)	10.4-13.4 (11.9)
<i>r. macropterum</i> (n = 13)	73-79 (75.2)	48-54 (51.4)	25.8-28.0 (26.7)	17.1-19.3 (17.7)	10.1-11.2 (10.7)	11.2-13.6 (12.4)
<i>c. nigrocapitatum</i> (n = 29)	69-74 (71.3)	55-62 (58.6)	28.7-32.3 (30.0)	16.4-20.8 (18.8)	8.2-10.5 (9.6)	3.7-6.8 (4.9)
<i>c. morrelli</i> (n = 11)	70-74 (72.3)	52-56 (54.0)	28.8-30.9 (30.4)	18.1-18.8 (18.3)	8.8-10.5 (9.5)	4.6-5.6 (5.2)
<i>c. capistratoides</i> (n = 13)	70-75 (72.2)	54-58 (55.4)	29.2-31.6 (30.5)	17.2-19.2 (18.0)	8.5-10.4 (9.4)	5.3-7.3 (6.3)
<i>c. capistratum</i> (n = 5)	69-71 (70)	54-57 (56.3)	30.3-32.3 (31.1)	17.8-19.0 (18.3)	8.7-9.9 (9.5)	3.1-5.3 (4.7)

All measurements of the total 14 taxa are summarized as ranges and means in table 1. To create a basis of visual comparison, means were organized into three bi-coordinate plots (fig. 1): of wing-length against tail-length as a generalized representation of locomotory adaptations; culmen against tarsus-length as a generalized foraging adaptation, measuring, e.g., reach; and bill-tip against maximum rictus-length as a generalized measure of prey-capture and handling adaptations.

Inevitably, outcomes are not entirely straightforward. Bill-tip versus maximum rictus shows the best discrimination, with good separation of cluster, *T. rostratum* and *P. capistratum* groupings. Not all cluster-members are closer to one another than any is to an 'out-group', but end-members of the cluster group (*assamense* and *longstaffi*) connect via a continuous, almost-linear sequence of nearest-neighbour linkages. Continental and Bornean cluster taxa nest at opposite ends of this sequence, with *buettikoferi* almost exactly intermediate and, interestingly, Javan *pyrogenys* displaced slightly towards the continental contingent (after *buettikoferi*, nearest to nominate *tickelli*). *P. capistratum* subspecies all nest closer to one another than any is to an outside taxon, as do the two *T. rostratum* subspecies.

Culmen versus tarsus-length would have provided even better confirmation of predictions had it not been for a large difference in mean bill-size between the two *T. rostratum* subspecies, bringing Bornean *macropterum* much closer to the cluster grouping than to its mainland counterpart. *P. capistratum* taxa nest remotely and tightly, and within the cluster grouping, this time, continental and island taxa show no tendency to segregate. By a modest distance, the cluster outlier here is *assamense*.

Wing- versus tail-length plots show an actual, if only marginal, overlap between *P. capistratum* subspecies and the cluster grouping, involving Bornean *erythrothe* and bringing *longstaffi* closest to nominate *capistratum*. These, therefore, are least supportive of working predictions. *T. rostratum* subspecies nest remotely, nevertheless, and within the cluster grouping Bornean and continental representatives are once again more or less segregated. Once again also, nominate *pyrogenys* aligns marginally closer to continental taxa. The one remarkable difference is in the position of *buettikoferi*, of average cluster wing-length but remotely isolated from all other taxa on account of its disproportionately short tail.

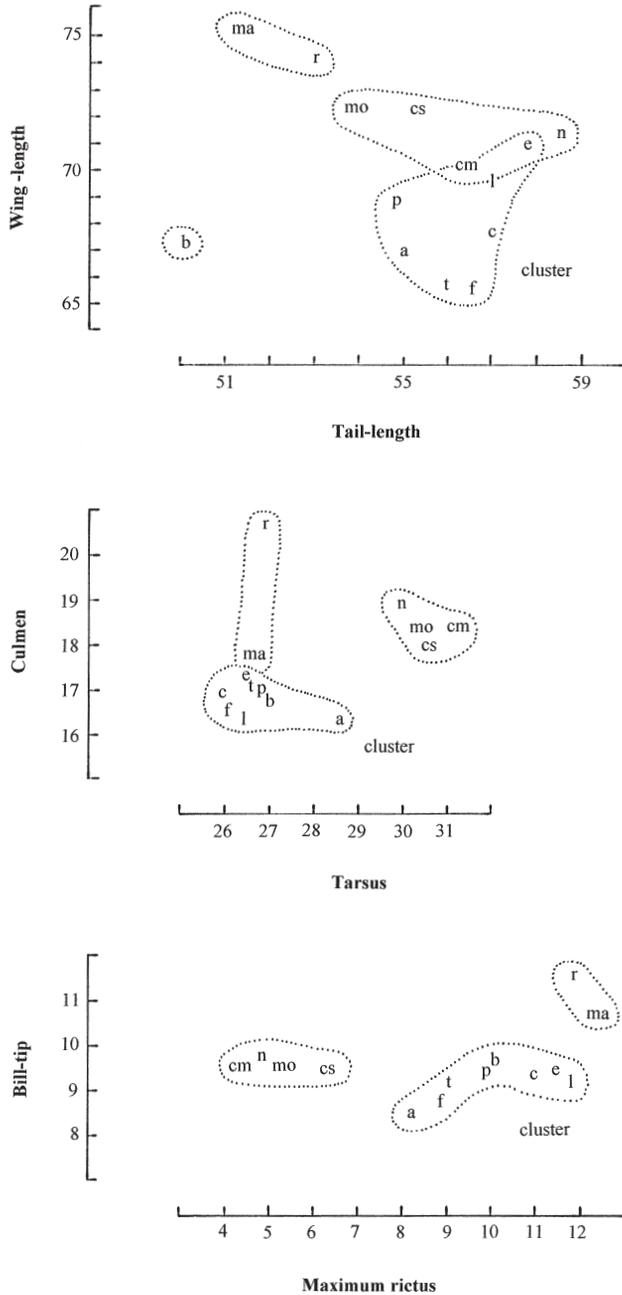


Figure 1. Three bi-coordinate plots of sample means of the measurements set out in table 1: wing-length against tail-length; culmen against tarsus-length; and bill-tip against longest rictal bristle (maximum rictus). Letters identify taxa as follows: a = *assamense*; f = *fulvum*; t = *tickelli*; b = *buettikoferi*; c = *canicapillum*; l = *longstaffi*; e = *erythrota*; p = *pyrrogenys*; r = *rostratum*; ma = *macropterum*; n = *nigrocapitatum*; mo = *morrelli*; cs = *capistratoides*; cm = *capistratum*.

In only three instances (14 percent of chances overall) do individual cluster-member plots emerge as closer to a non-cluster position than to a cluster fellow, hence the proposition that the cluster forms a cohesive whole is at least not rejected by this exercise. Colours and patterns give it general support on the basis that more within-cluster variation seems to be due to level of pigment saturation than to any real qualitative difference. Upperparts are unmarked. On the continent, they range from dark dun brown (far-northwestern *assamense*) to light brown tinged grey (W Burmese *grisescens*) or rufous-brown (*fulvum* and *annamense*, and southern nominate *tickelli*). W Bornean *erythrota* and Javan *pyrrogenys* approach *assamense* but are a shade more chestnut; *canicapillum* (Mt Kinabalu, NW Borneo) is slightly richer than these, and Bornean spinal range *longstaffi* richer still, whereas Sumatran *buettikoferi* is sandy olive brown, wholly non-rufescent like *grisescens*. Cap matches dorsum on the continent and in *buettikoferi*; is duller, darker brown in *pyrrogenys*; a shade more sooty and contrasting in *erythrota* and *canicapillum*; and sooty grey, strongly contrasting, in *longstaffi*. In all three Bornean taxa it is edged laterally by a contrast-heightening, pale grey supercilium – a rare, genuine pattern distinction from other cluster-members.

'Out-group' upperparts rather closely match *longstaffi* except that *T. rostratum* subspecies show no cap-contrast whereas *capistratum* subspecies all possess a uniformly full black cap back to nape level, edged by a long white, pale grey, mixed or, in Java, pale orange-and-white supercilium. Among understorey pectorneines generally, this pattern most closely matches that of W African *Illadopsis cleaveri* (Shelley, 1874), with supercilium much better developed than in any cluster-member.

Below, cluster-member throats are mainly white, bordered laterally by a thin, black-brown streak at jaw level, except in continental taxa, whose chin and upper throat are invaded from the face by ginger-buff (streak reduced also in some nominate *pyrrogenys*). A broad pectoral band and flanks are ginger-buff on the continent and in *buettikoferi*; richer, more chestnut, in the rest, and at least the upper belly is white in all. Clean white throat and dark jaw-streak also feature in the 'out-group' species, but are characters too frequent among pectorneines generally to be accepted as meaningful at the relationship level desired. Neither 'out-group' shows a pectoral band; remaining underparts of *rostratum* subspecies are white (sides of breast pale grey), and of *capistratum* subspecies solidly orange-chestnut, darkening to brown posteriorly. Among cluster-members, some nominate *tickelli* and *fulvum*, and most *assamense*, of both sexes, are dully brown-streaked from chin to breast; in most just on the breast. Of island birds examined, one among 14 *longstaffi* showed faint streaking on its breast. No such streaking occurs in the 'out-groups'.

Evidence of bare-part colours is equivocal. Adult iris colour (a likely close-range behaviour signal) grades individually from light amber to hazel brown on the continent, apparently also in *buettikoferi*, and from hazel- to red-brown in the rest. In *T. rostratum* it is yellow-brown or brown, and in *P. capistratum* full red. All cluster-member, and *T. rostratum*, feet are some shade of flesh pink, whereas *P. capistratum* feet are grey to purplish brown (but pink in young juveniles).

Among ancillary characters, a little is known about egg types. Nominate *tickelli* and *t. assamense* are stated to lay pale greenish to olive-grey eggs, densely freckled and spotted reddish brown to olive brown, with underlying marks of lavender and purplish grey; size 19.9 x 15.7 mm (mean, n = 60) (Baker, 1927, 1932). Bornean *canicapillum*

eggs are pale blue-green to grey-green, likewise fairly heavily spotted and speckled with brown and, to a lesser extent, purplish grey, in some more densely at the broad end; size 20.1 x 15.0 mm (Gibson-Hill, 1950; ZRCNUS). W Javan *pyrrogenys* eggs are pale blue-grey, finely but densely speckled brown, size 20.5 x 15.0 mm (mean, n = 4) (Hellebrekers & Hoogerwerf, 1967; G.F. Mees). Those of *buettikoferi*, known definitely from only two clutches taken near Medan, NE Sumatra, resemble *pyrrogenys* material; size 19.9 x 15.1 mm (mean, n = 4) (G.F. Mees, C.S. Roselaar, *in litt.*).

Evidently, these eggs are all quite similar. *T. rostratum* eggs, too, are pale greenish, glossless, finely dotted and flecked light chestnut all over (more densely at the broad end), with larger speckles of pale lavender grey. Two measured 21.0 x 15.4 mm and 20.5 x 15.0 mm (ZRCNUS), hence they are also close in size to cluster-member eggs. Apart from occasional variants of *Pellorneum fuscocapillum* (Blyth, 1849) (Sri Lankan brown-capped babbler) (Ali & Ripley, 1971) they are the only other Asian pellorneine eggs of this general colour-type on record, and quite different from those of *P. capistratum* subspecies. The latter lay eggs thickly blotched or clouded inky purple to purple-grey, or densely olive- to deep brown-flecked (flecks coalescing over the broad end) on a glossy stone- to creamy white ground; size 23.0-20.8 x 16.5-14.9 mm (mean 21.9 x 15.8 mm, n = 6), i.e., larger and proportionately slightly longer than among cluster-members (Baker, 1932; Hoogerwerf, 1949; G.C. Madoc, *in litt.*; Oates, 1889; University of Malaya nest record-card scheme; authors' data).

Relatedness

The underlying purpose of these checks of relative similarity was validation of a search for characters interpretable as being derived specifically at cluster level. One in particular is identified. Ripley & Beehler (1985) record *T. tickelli* as lacking a distinctive head-pattern. It certainly is not striking, but the finding here is that all *tickelli* subspecies share facial pattern detail, apparently exclusively, with every other cluster-member, as follows: narrow zone over bill-base, lores and entire anterior face back to around the eye, paler than cap, ginger-rufous other than in *buettikoferi* in which these parts are mostly pale grey (grey also over the eye of Bornean members); all feathers with buff-white centre and darker margin, producing a subtle scaly pattern, and with fine, pale rachial lines from forehead to crown. Laterally, this pattern meets plain (non-scaly) ginger-rufous feathering along the jaw, back from bill-base in continental taxa and *buettikoferi*, from eye level in the rest.

No equivalent detail has been found in any other pellorneine, including the present 'out-group' species. On the assumption that, at close range, even subtle head patterns may aid recognition in nature – hence ought to be conserved by natural selection – we consider this added character makes it acceptable to conclude that cluster-members most probably are a natural, monophyletic group. Estimating how closely knit they might actually be rests on a further layer of recognition-cue evidence.

Song and biological species-limits

For small, cryptically coloured birds tied to dense vegetation cover loud vocalizations could have special importance as recognition signals, acting to maintain contact

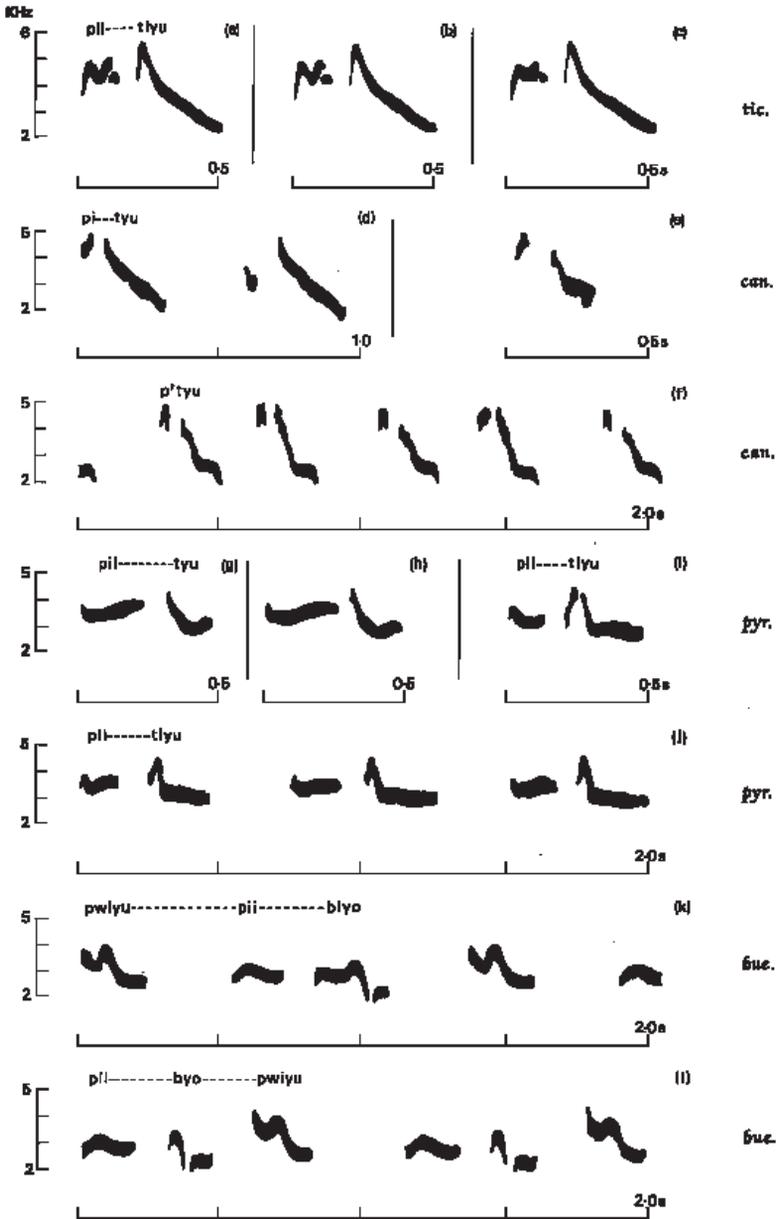


Figure 2. Re-drawn, wide-band-mode sonograms of some advertising/territorial defensive vocalizations of cluster-members: a-c = individual calls of *tickelli* (Peninsular Malaysia); d-e = double call and an isolated half of a double call of *canicapillum* (Mount Kinabalu, Sabah), responding to play-back; f = compressed song of *canicapillum*, responding strongly to play-back; g-h = short-version components of double and triple calls of *pyrrogenys* (SW Java), responding to play-back; i-j = long-version call and triple-call sequence of *pyrrogenys*; k-l = long- and short-version sequences of *buettkoferi* (NE Sumatra), showing extra note re-positioned between versions.

and, in a different context, as the front-line component of spacing and other avoidance mechanisms (Wells, 1982). Understorey pellorneines, including all of the cluster taxa investigated, possess such calls and give them freely. Usually without showing themselves, cluster-members advertise and, because they react to the songs of nearby conspecifics, also to close-range play-back of recordings of their own voice, evidently defend territories vocally. Response, including the shadowing of a loud-speaker sound-source, tends to be strongest during breeding seasons.

On Peninsular Malaysian mountains, nominate *tickelli* gives a not-especially-loud, but arresting "pii-tyu", with slight stress on the first syllable of the second note; duration 0.5 s and the strongly modulated second note pitched mainly between 5.5 and 2.3 KHz (fig. 2a-c). In a tape-recording from Sai Yoke, Kanchanburi province, SW Thailand, the first note is fractionally lengthened and the second shortened, to "pii-tyu", but this variant may have context rather than geographical meaning (see below). Calls of *t. fulvum* heard on Doi Inthanon mountain, Chiang Mai province, NW Thailand, sounded the same as those described in Peninsular Malaysia, and literature descriptions from Burma and NE India, within the ranges of *grisescens* and *assamense* (Ali & Ripley, 1971; Smythies, 1953) are evidently also of this type.

When confronting neighbours or play-back, *tickelli* observed on the Malaysian spinal range shortened their standard call to "pii-tyu", losing the stressed component, and calls were commonly delivered in pairs; sometimes trios. Exchanges can be brisk. At Sai Yoke in June a stimulated bird shadowed the sound-source and was still calling strenuously 40 minutes after play-back ceased. Call or call-burst repeat intervals vary from about one to seven seconds, with means of 2.6 s (n = 62 calls) from Peninsular Malaysia; 2.4 s (n = 18 calls) from SW Thailand.

Reported so far only from Malaysia, nominate *tickelli* has a second call, also given from dense cover. This is a sharply falling cadence of usually five brief squeaks, "pyek", that every so often breaks across a main song sequence. At a range of only a few metres it has been detected as given antiphonally a short distance away from the loud singer, presumably but not definitely by a female partner.

Details of the song of *p. canicapillum* uninfluenced by play-back are not on record but, like *t. tickelli*, Mt Kinabalu birds responded to a recording of their own voice by switching from single to many paired calls. Song components (fig. 2d-e) sound no different from the "pii-tyu" of *tickelli*; duration 0.3-0.4 s, with both notes clipped but the second still strongly modulated, ranging mostly between 5 and 2 KHz. A mean call-burst repeat interval of 2.7 s (n = 36 calls) is close to that of *tickelli*. Birds heavily stimulated by play-back, on the other hand, condensed their calls down to about 0.2 s (rendered "p'tyu"; fig. 2f), delivered at up to 80 per minute.

Kinabalu tapes also include examples of the second vocalization, a sharp "pyek" squeak similar to that of *tickelli*, but in longer cadences (8-15, mean 12, notes) that slightly accelerate towards the end. Careful listening again indicated this was given by a second individual.

Vocalizing nominate *pyrrogenys* were recorded in dense secondary forest at Pelabuanratu, coastal SW Java. Stimulated by play-back, birds gave mostly double, occasionally triple calls, interspersed with only a few singles (two in a run of 37 call-bursts). Components "pii-tyu" (duration about 0.5 s) and subtly-shorter "pii-tyu",

nevertheless, sounded very like their *tickelli* equivalents, even though sonograms (fig. 2j and 2g-i) revealed only a part of the second note is modulated, running between about 4.3 and 2.7 KHz. As shown, versions of the second call differ in presence (i-j) or absence (g-h) of an opening crescendo. A mean call-burst repeat interval of 2.5 s is in line with that of *tickelli* and *canicapillum*. Pelabuanratu tapes included no other call-types, but were made outside the main breeding season for insectivorous birds.

Vocalizations of *buettikoferi* are described from a single encounter in dense secondary forest by the Wampu river near Bukit Lawang, Utara province, Sumatra, during which a bird was tape-recorded and then mist-netted. When first heard, its relatively loud, 3-part calls, "pwiyu-pii-biyo" and "pii-byo-pwiyu" (fig. 2k-l), syllables well-modulated, ranging mainly between 1.8 and 4.4 KHz, were taken to be local variants of *T. rostratum* song (below), but unusually persistent and repeated much faster than normal for that species. Their "pii-biyo" component is not unlike the "pii-tiyu" of other cluster taxa, and is of the right duration, approximately 0.5 s. What sets *buettikoferi* song apart from these is its loudness and the extra "pwiyu" note, conspicuously stressed in both call-versions. Tape-recordings alone do not exclude the possibility that the two versions derived from separate individuals alternating song-bouts antiphonally. Singing took place entirely in dense cover, but during play-backs the whole song crossed and re-crossed the position of the speaker, and after capture of the one individual no more was heard. Observers concluded that it alone gave the whole sequence, alternating between versions simply by compressing "biyo" to "byo" and, without greatly changing the length of the call-interval, advancing or retarding the position of "pwiyu" to make it sound either initial or terminal. No other types of vocalization were detected, which again may indicate that no other birds were near.

As stated, mainstream understanding of the systematics of the *pyrogenys* cluster accepts a continental species, *tickelli*, and island species *pyrogenys*, and the notion that *buettikoferi* can only belong with one or other of these two. Findings in this section, backed by an admittedly still rudimentary set of cross-taxon voice recognition experiments, ought now to force a revision. The fact that W Javan *pyrogenys* reacted to tapes of both Thai and Malaysian *tickelli* apparently exactly as they did to close-range play-backs of their own voice suggests to us that, were these remotely allopatric populations to meet, voice might fail them as an isolating mechanism. Not so with *p. pyrogenys*'s nearest geographical neighbour, *buettikoferi*, play-back of whose songs to the same Pelabuanratu group at the same time of year – also to *tickelli* in Peninsular Malaysia – elicited no obvious responses at all. With no interruption of singing or investigation of the sound-source, apparently, it went unrecognised, at least by territorial males.

Consequences for taxonomy

General colour-tone differences between continental and Bornean/Javan cluster members alone may be considered sufficient for an assumption of reproductive isolation and the continued recognition of two full species. An alternative case could be made for rejecting the significance of the small differences that tend to nest most continental taxa slightly apart from most Sunda island taxa in some, but not all, measurement analyses, and for reducing continental taxa to the status of subspecies of a sin-

gle, expanded species *pyrrogenys*. Beyond reasonable doubt, all of the taxa involved are closely related, but much hangs on treatment of the vocal evidence (cf. Payne, 1986). A precautionary principle accepts only divergence of an important signal in allopatry as directly supportive of a split. Non-divergence eliminates voice as a potential isolating mechanism but says nothing about potential alternative, second-line mechanisms, hence its taxonomic implications must be seen to be neutral. While this runs counter to the approach of assuming no speciation event has occurred until positive reasons can be found for judging otherwise, by default, the two-species arrangement has to be maintained. In addition, of course, the voices of some cluster taxa have still to be described.

Arguments for the sinking, or otherwise, of *tickelli* into *pyrrogenys*, on the other hand, do not hinder recognition of a fully separate *buettikoferi* – status it has not enjoyed since well before the emergence of the biological species concept. Shape peculiarities, notably its short tail relative to all other investigated cluster-members, may not add much to vocal evidence, but *buettikoferi* is odd in other ways as well. Its general paleness (extreme for the cluster, including even *t. grisescens*) runs counter to a well-authenticated trend among SE Asian forest birds, of increasing colour saturation towards the ever-humid equatorial zone. The expectation is that an equatorial representative of a latitudinally more widely distributed species would occupy the rich end of the latter's tone spectrum and that, were this species *pyrrogenys*, Sumatran populations would parallel conspecifics in Borneo – whereas *buettikoferi* clearly does not. There is also an issue of habitats occupied. South through the Thai-Malay Peninsula, *tickelli* follows a not-uncommon tendency of retreating up slopes (Medway & Wells, 1976) so that, on Malaysian mountains, few have been found below 700 m elevation and most of the population lives above the montane forest ecotone. Bornean taxa are all mostly montane birds (none recorded below 500 m) (F.H. Sheldon, pers. comm.; Smythies, 1999), whereas south of the equatorial zone the trend reverses. Javan populations occur down to sea level, indeed, have not definitely been identified above approximately 900 m, hence they may not even enter montane forest. Records of *buettikoferi* are dispersed over most of the length of Sumatra, i.e., across the equator, yet everywhere they are largely from below the steep-land boundary (Wells, 1999). Van Marle & Voous (1988) cite altitude records of 800 and 900 m elevation, but the latter at least is from the Padang Highlands, a major plateau system. Once more, therefore, *buettikoferi* bucks the trend set by continental and Bornean relatives at equivalent latitudes.

One taxonomic option considered is that *buettikoferi* is only convergently similar to other taxa and not a cluster-member at all. Details of head pattern, elements of its song, egg-type, etc., make this unlikely. As a member, however, it is perhaps not more than the sister taxon of the rest of the cluster, possibly even a relict of some earlier radiation of this group (compare the locally endemic lowland Sumatran blue flycatcher *Cyornis ruecki* (Oustalet), 1881, recorded in some of the same areas). It is even possible to speculate that Sumatra might have been double-invaded and that a population of true *pyrrogenys* (or *tickelli*) awaits discovery there in typical mountain habitat – or at least that one did exist in Sumatra long enough to have caused *buettikoferi*'s isolating mechanisms to be reinforced by character displacement.

Though specifically not in the brief of this paper, the issue of assigning cluster-

members to a genus remains. Songs of the sympatric, locally syntopic, 'out-group' taxa would not be expected to contain much evolutionary evidence of relevance. It is, nevertheless, curious that while those of *T. rostratum*: rather loud, slurred three- and four-part whistles, "chiri-biri-bee"; "chirer-bir-chio"; or "chiri-biri-bee-riu", well-stressed and inflected on the terminal note (cf. Lekagul & Round, 1991) are of the same superficial type as, e.g., those of *buettikoferi*, *P. capistratum* song is quite different from all. The latter's loud call over most, probably all, of its southern range is a single, incisive but strongly modulated "hu-eet", which in Peninsular Thailand (within the range of subspecies *nigrocapitatum*) and northernmost Borneo (range of subspecies *morrelli*) inverts to "hee-uut" or "pi-uu". Play-back elicits no obvious response from conspecifics, implying some functional difference between this call and the loud calls of cluster-members, whereas a second vocalization, a low chatter or chuckle of 5-9 squeaky notes incorporating several strong harmonics (BLNSA), invokes quite a vigorous response (Stuebing, 1986). Lekagul & Round (1991) describe the chuckle as introduced by an explosive "pretty-too". This may perhaps be thought of as cluster-like, but the loud call definitely is not, lending modest support to our uncoupling of this bird from the cluster on other grounds. *P. capistratum* also has different behaviour, living mostly, and foraging probably exclusively, on the ground. There, it walks sedately with head bobbing forward like a rail-babbler (*Eupetes*) or miniature galliform – as does the type species of the genus, *P. ruficeps* Swainson, 1832 (puff-throated babbler). Some cluster-members also move on the ground, (reported in continental representatives and Bornean *longstaffi*) but without this distinctive comportment. They forage as well in understorey vegetation, and within suitable cover some sing from perches up to 4 m above ground, behaviour unknown to us in any *capistratum* population.

Without exploring further, or considering the real position of *capistratum* itself, we find little support for the recent transfer of cluster species to *Pellorneum*. Provisionally, our preference instead is to retain them in *Trichastoma*. As others have pointed out, of course, ultimately, such boundaries will be tested at molecular level.

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Appendix

Inventory of museum specimens handled, with collection locality. Use of a dash indicates no registration mark available. Acronyms are as per Acknowledgements.

T. t. assamense (Sharpe, 1883)

Males: BMNH 1882.1.20.231 (Dollah, Arunchal Pradesh); 1949.Whi.1.13720 (Margherita, Assam); 1969.41.491 (Margherita); 1938.4.14.26 (Gora, N Burma); 1938.4.14.27 (Gora); 1939.12.8.167 (Luushkang Gu, N Burma); 1941.12.1.564 (Myitkyina-Putao road, N Burma).

Females: BMNH 1949.Whi.1.13721 (Margherita, Assam).

Undetermined: BMNH 1886.10.1.5312 (Sadiya, Assam); 1969.41.490 (Margherita, Assam); 1949.Whi.1.13719 (Charduar, Assam); 1895.7.14.1257 (Chaka, Manipur).

T. t. fulvum (Walden, 1875)

Males: BMNH 1924.12.21.175 (Bao Ha, Tonkin); 1924.12.31.178 (Thai-Nien, Tonkin); 1927.6.5.974 (Bac Kau, Tonkin); 1935.10.23.483 (Sontay mountain, Tonkin); 1928.6.26.1419 (Nape, Laos); 1928.6.26.1423 (Nam Teun, Laos); 1928.6.26.1424 (Nam Teun).

Females: none.

Undetermined: BMNH 1924.12.21.144 (Bao Ha, Tonkin); 1935.10.23.485 (Sontay mountain, Tonkin); 1935.10.23.486 (Phutho, Tonkin).

T. t. grisescens (Ticehurst, 1932)

Males: BMNH 1932.10.20.2 (S Arakan Yoma, Burma; Type).

Females: none.

Undetermined: none.

T. t. annamense (Delacour, 1926)

Males: BMNH 1928.6.26.1425 (Phuqui, N Annam); 1928.6.26.1426 (Phuqui); 1928.6.26.1427 (Phuqui).

Females: none.

Undetermined: BMNH 1927.6.5.970 (Thua-luu, N Annam); 1927.6.5.1414 (An-Bien, Cochinchina).

T. t. tickelli (Blyth, 1859)

Males: BMNH 1916.12.27.871 (Ban Salui, Chumphon, S Thailand); 1955.1.5896 (Khao Ram, Nakhon Si Thammarat, S Thailand); 1910.12.27.307 (Chong, Trang, S Thailand); 1936.4.12.1447 (Chong); 1936.4.12.1450 (Ulu Bertam, Pahang, Peninsular Malaysia); 1936.4.12.1451 (Ulu Bertam); 1936.4.12.1456 (Genting Semangkok, Main Range, Peninsular Malaysia); 1941.5.30.4136 (Genting Semangkok); 1908.12.15.108 (Genting Bidai, Main Range, Peninsular Malaysia); 1936.4.12.1453 (Genting Bidai); 1936.4.12.1455 (Genting Semangkok); ZRCNUS -(Ban Tapli, Ranong, S Thailand).

Females: BMNH 1916.12.27.873 (Ban Map Ammarit, Chumphon, S Thailand); 1936.4.12.1458 (Ban Tha San, Chumphon, S Thailand); 1936.4.12.1457 (Ban Tapli, Ranong, S Thailand); 1886.10.1.5329 (Pakchan, S Tenasserim); 1936.4.12.1449 (Khao

Nong, Surat Thani, S Thailand); 1955.1.5893 (Khao Nong); 1936.4.12.1495 (Khao Ram, Nakhon Si Thammarat, S Thailand); 1036.4.12.1446 (Bukit Kutu, Selangor, Peninsular Malaysia).

Undetermined: ZRCNUS - (Ranong river, Ranong, S Thailand); BMNH 1936.4.12.1448 (Khao Nong, Surat Thani, S Thailand); 1941.5.30.4137 (Khao Nong); 1955.1.5894 (Khao Nong); 1936.4.12.1213 (Khao Luang, Nakhon Si Thammarat, S Thailand); 1955.1.5895 (Khao Ram, Nakhon Si Thammarat, S Thailand); 1955.1.5897 (Khao Ram); 1936.4.12.1452 (Korbu, Main Range, Peninsular Malaysia).

***T. p. canicapillum* (Sharpe, 1887)**

Males: BMNH 1898.9.12.53 (Mount Kinabalu, Sabah, Borneo); 1908.12.9.44 (Mount Kinabalu); 1969.29.245 (Mount Kinabalu); ZRCNUS - (three from Kiau, Mount Kinabalu).

Females: BMNH 1895.11.19.25 (Mount Kinabalu, Sabah, Borneo); 1898.9.12.54 (Mount Kinabalu).

Undetermined: none.

***T. p. longstaffi* (Harrisson & Hartley, 1934)**

Males: BMNH 1893.7.2.56 (Mount Kalulong, Sarawak, Borneo); 1927.4.18.912 (Mount Dulit, Sarawak); 1935.10.22.427 (Mount Dulit); 1935.4.27.429 (Mount Dulit); 1935.10.22.430 (Mount Dulit); 1935.10.22.431 (Mount Dulit); 1996.16.22 (Mount Mulu, Sarawak).

Females: BMNH 1955.6.119.21 (Mount Mulu, Sarawak).

Undetermined: BMNH 1892.4.29.33 (Mount Dulit, Sarawak, Borneo); 1927.4.18.913 (Mount Dulit); 1935.10.22.428 (Mount Dulit).

***T. p. erythro* (Sharpe, 1883)**

Males: BMNH 1890.6.14.26 (Mount Penrissen, Sarawak, Borneo); 1935.12.27.3 (Mount Penrissen); 1893.7.4.11 (Mount Poi, Sarawak); 1969.29.2.247 (Mount Poi); ZRCNUS - (two from Mount Penrissen).

Females: none.

Undetermined: none.

***T. p. pyrogenys* (Temminck, 1827)**

Males: RMNH 16.5.1903 (Djampang Tengah, Preanger, W Java); 52389 (Djampang Tengah); 52393 (Djampang Tengah); 52395 (Preanger, W Java); - (two from Preanger); 52399 (Pangrango, W Java); 52403 (Pangrango); 52404 (Pangrango); 52408 (Tjibarenno, Preanger); 52410 (Pangrango); 52414 (Besuki, E Java).

Females: BMNH 1927.4.18.914 (Tamansari, E Java); RMNH 52397 (Preanger).

Undetermined: ZRCNUS - (Pelabuanratu bay, W Java).

***T. buettikoferi* Vorderman, 1892**

Males: RMNH 15969 (E Sumatra); 5145 (Medan, Utara, Sumatra); 68129 (Medan); - (Padang Highlands, Barat, Sumatra); ZRCNUS 3.221.64 (Tuntungan, Medan); 3.221.66 (Serdang, Utara, Sumatra); 3.221.68 (Serdang); 3.221.69 (Galang, Utara, Sumatra); 3.221.70 (Galang); 3.221.71 (Karsan, Utara, Sumatra).

Females: none.

Undetermined: RMNH 25556 (Medan, Utara, Sumatra); ZMA 6604 (Medan).

***T. r. rostratum* Blyth, 1842**

Males: BMNH 1936.4.12.1119 (Kuala Lipis, Pahang, Peninsular Malaysia); 1936.4.12.1120 (Kuala Lipis); 1936.4.12.1121 (Kuala Teku, Pahang, Peninsular Malaysia); 1936.4.12.1123 (Pintu Gedong island, Selangor, Peninsular Malaysia); 1886.10.1.5410 (Jaffaria, Johor, Peninsular Malaysia); 1886.10.1.5411 (Jaffaria).

Females: BMNH 1882.1.20.248 (Maliwun, Tenasserim); 1886.10.1.5553 (Lumut, Perak, Peninsular Malaysia); 1886.10.1.5409 (Kelang, Selangor, Peninsular Malaysia); 1996.16.19 (Kelang); 1936.4.12.1122 (Tanjung Malim, Selangor, Peninsular Malaysia); 1969.27.385 (Tahan, Pahang, Peninsular Malaysia).

Undetermined: BMNH 1886.10.1.5407 (Kossoom, Phangnga, S Thailand); 1886.10.1.5408 (Kelang, Selangor, Peninsular Malaysia); 1936.4.12.1118 (Kuala Teku, Pahang, Peninsular Malaysia); 1936.4.12.1124 (Pasir Bantang, Barat, Sumatra).

***T. r. macropterum* (Salvadori, 1868)**

Males: ZRCNUS 3.220.83 (Kota Kinabalu, Sabah, Borneo); 3.220.87 (Betottan, Sabah); 3.220.89 (Bettotan). [Sexed relative to a larger sample of live handlings].

Females: none.

Undetermined: none.

***P. c. nigrocapitatum* (Eyton, 1839)**

Males: BMNH 1886.10.1.5274 (Maliwun, Tenasserim); 1936.4.12.1390 (Ban Tha San, Chumphon, S Thailand); 1936.4.12.1391 (Ban Tha San); 1910.12.27.299 (Chong, Trang, S Thailand); 1955.1.5886 (Narathiwat, S Thailand); 1955.1.5887 (Narathiwat); 1955.1.5888 (Narathiwat); 1955.1.5889 (Narathiwat); 1955.1.5891 (Narathiwat); 1955.1.5892 (Narathiwat); 1936.4.12.1403 (Pelarit, Perlis, Peninsular Malaysia); 1936.4.12.1392 (Gurun, Kedah, Peninsular Malaysia); 1936.4.12.1395 (Taiping, Perak, Peninsular Malaysia); 1906.7.23.176 (Kuala Teku, Pahang, Peninsular Malaysia); 1941.5.30.4138 (Bentong, Pahang); 1936.4.12.1402 (Gunung Senyum, Pahang); 1886.10.1.5276 (Kelang, Selangor, Peninsular Malaysia); 1886.10.1.5278 (Kelang); 1886.10.1.5281 (Kelang); 1886.10.1.5285 (Kelang); 1936.4.12.1393 (Cheras, Selangor, Peninsular Malaysia); 1936.4.12.1398 (Genting Bidai, Main Range, Peninsular Malaysia); 1886.10.1.5297 (Pulai, Johor, Peninsular Malaysia); 1886.10.1.5298 (Pulai); 1886.10.1.5299 (Pulai); 1886.10.1.5301 (Pulai); 1886.10.1.5302 (Pulai); 1886.10.1.5303 (Pulai); 1886.10.1.5304 (Pulai).

Females: BMNH 1886.10.1.5279 (Kossoom, Phangnga, S Thailand); 1936.4.12.1388 (Khao Ram, Nakhon Si Thammarat, S Thailand); 1955.1.5884 (Khao Ram); 1910.12.27.300 (Ban Lam Phila, Trang, S Thailand); 1936.4.12.1389 (Ban Lam Phila); 1936.4.12.1396 (Temengor, Perak, Peninsular Malaysia); 1908.12.15.125 (Tanjung Malim, Selangor, Peninsular Malaysia); 1886.10.1.5184 (Selangor); 1886.10.1.5277 (Kelang, Selangor); 1886.10.1.5283 (Kelang); 1886.10.1.5286 (Kelang); 1936.4.12.1394 (Kelang); 1941.5.30.4139 (Bukit Tampin, Negeri Sembilan, Peninsular Malaysia); 1886.10.1.5300 (Pulai, Johor, Peninsular Malaysia); 1886.10.1.5305 (Pulai).

Undetermined: BMNH 1886.10.1.5273 (Ban Kachon, Tenasserim); 1886.10.1.5275

(Kossoom, Phangnga, S Thailand); 1936.4.12.1400 (Ban Na, Surat Thani, S Thailand); 1955.1.5885 (Bandon, Surat Thani, S Thailand); 1910.12.27.301 (Ban Lam Phila, Trang, S Thailand); 1955.1.5890 (Narathiwat, S Thailand); 1936.4.12.1404 (Pelarit, Perlis, Peninsular Malaysia); 1936.4.12.1396 (Changkat Mentri, Perak, Peninsular Malaysia).

***P. c. morrelli* Chasen & Kloss, 1929**

Males: BMNH 6.5.2.33 (NW Borneo); 1956.60.347 (Mount Magdalena, E Sabah, Borneo). [Sexed relative to a larger sample of live handlings].

Females: BMNH 1956.60.348 (Mount Magdalena, E Sabah); 1996.16.46 (Danum valley, E Sabah); 1901.1.31.15 (Lawas, N Sarawak, Borneo).

Undetermined: None.

***P. c. capistratoides* (Strickland, 1849)**

Males: BMNH 1935.10.32.437 (Mount Dulit, Sarawak, Borneo); 1935.10.32.438 (Mount Dulit); 1876.7.28.96 (Bintulu, Sarawak); 1876.7.28.50 (Sibu, Sarawak, Borneo); 1927.4.18.807 (Samarahan, Sarawak); 1922.11.29.97 (Sarawak). [Sexed relative to a larger sample of live handlings].

Females: none.

Undetermined: none.

***P. c. capistratum* (Temminck, 1823)**

Males: BMNH 1969.41.1356 (Java); 1969.41.1357 (Java); 1927.4.18.814 (Pelabuanratu bay, W Java); 1927.4.18.810 (Karangbolang, central Java); 1969.41.1360 (Mojokerto, E Java). [Sexed from label data only].

Females: none.

Undetermined: none.