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The taxonomy of *Tanygnathus sumatranus*

by T. Arndt, N. J. Collar & M. Wink

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<http://zoobank.org/urn:lsid:zoobank.org:pub:94C9C8BF-5D8A-46BB-B040-6BF90E80205B>

SUMMARY.—Philippine taxa currently assigned to Blue-backed, Azure-rumped or Müller's Parrot *Tanygnathus sumatranus* are distinctive both morphologically (larger bill, red vs. pale yellow iris, royal blue vs. glossy turquoise-blue rump, paler green head and duller green underparts; and males having darker green mantles and no blue on the carpals and scapulars) and genetically (as distinct from Indonesian *T. sumatranus* as *T. lucionensis* is from *T. megalorhynchus*). We therefore propose *T. everetti* (with subspecies *burbidgii* and *freeri*; race *duponti* synonymised with nominate) to be elevated to species rank with the name Blue-backed Parrot, leaving Indonesian *T. sumatranus* (with subspecies *sangirensis*) as Azure-rumped Parrot. The taxonomic status of *T. e. burbidgii* (Sulu Islands) and *T. s. sangirensis* (Talaud Islands), both notably larger than their respective nominates, deserves study.

Blue-backed, Azure-rumped or Müller's Parrot *Tanygnathus sumatranus* is distributed in five or six subspecies across multiple islands in the Philippines and Sulawesi (plus adjacent archipelagos), Indonesia. These break down as (in the Philippines): *T. s. duponti* on Luzon, *T. s. freeri* on Polillo, *T. s. everetti* on Panay, Negros, Samar, Leyte and Mindanao, *T. s. burbidgii* on the Sulu Islands, and (in Indonesia) *T. s. sangirensis* (Talaud Islands) and *T. s. sumatranus* (Sulawesi and its immediate satellites, the Togian Islands, Banggai Islands and Sula Islands) (Forshaw 1973, Dickinson *et al.* 1991, del Hoyo & Collar 2014, Clements *et al.* 2018); however, some authorities consider *sangirensis* to be a synonym of *sumatranus* (White & Bruce 1986, Dickinson & Remsen 2013, Gill & Donsker 2018).

The distinctiveness of the Philippine taxa from the Indonesian taxa appears to have gone largely unnoticed. Forshaw (1973) illustrated only nominate *sumatranus*, while the portraits of nominate *sumatranus* and *everetti* in Collar (1997) and del Hoyo & Collar (2014) miss some key differences. Those in Juniper & Parr (1997) are rather better but not wholly accurate; the best indication is in Forshaw & Knight (2010). Given that there appears to be a suite of consistent characters separating *duponti*, *freeri*, *everetti* and *burbidgii* from *sangirensis* and *sumatranus*, a more detailed consideration of the evidence is warranted.

Methods

Morphological study.—NJC examined and measured a total of 61 male specimens representing five of the six taxa preserved in the American Museum of Natural History, New York (AMNH), Muséum National d'Histoire Naturelle, Paris (MNHN), Museum für Tierkunde, Dresden (MTD), Natural History Museum, Tring (NHMUK), National Museum of Natural History, Washington DC (USNM) and Zoologisches Museum Berlin (ZMB). The sample involved two *duponti* (both in AMNH), eight *everetti* (four in AMNH, two in NHMUK, one in USNM, one in ZMB), 15 *burbidgii* (four in AMNH, one in MNHN, one in MTD, five in NHMUK, two in USNM, two in ZMB), nine *sangirensis* (two in AMNH, three in MTD, three in NHMUK, one in USNM), 22 *sumatranus* from Sulawesi (all in USNM), plus

four from the Peleng and Banggai Islands (two in AMNH, two in MTD) and four from the Sula Islands (all in AMNH).

The differences by which the subspecies *duponti* was established were not apparent (even though one of the AMNH specimens examined was its type), and we doubt the validity of this taxon; so the two birds from Luzon are lumped in the sample for *everetti*. We were unable to examine specimens representing the insular form *freeri*, but do not regard this as an obstacle to the analysis (four specimens of *freeri* held in the Philippines National Museum, Manila, probably the only museum material available, proved much larger than six specimens of *everetti* but differed only slightly in three plumage characters: Salomonsen 1952). Mensural data were taken from males in mm, using digital callipers accurate to two decimal points for bill from edge of nareal skin to tip, and long rulers for wing (curved) and tail (from point of insertion to tip). The Peleng / Banggai and Sula birds proved mensurally to be mildly untypical and are hence shown independently in Table 2 for interest, but they were included in the sample of *sumatranus* in the analysis of relationships between Indonesian and Philippine taxa.

Iris colour proved to be a significant issue in this case. The potential relevance of this was first noted by TA in 2006 when visiting a private collection of parrots, and he continued to gather evidence both in the field and from photographs and local testimony for as many taxa as possible (*sumatranus*, *sangirensis*, '*duponti*' and *everetti*). For the preparation of this manuscript we put out a call for more photographs from the field (notably for *burbidgii*) and in captivity, and made use of the material supplied in the analysis which follows.

To gauge the degree of difference between taxa in voice, plumage and dimensions we made use of the system of scoring proposed by Tobias *et al.* (2010), in which an exceptional character (radically different coloration, pattern, size or sound) scores 4, a major character (pronounced difference in body part colour or pattern, measurement or sound) 3, medium character (clear difference, e.g. a distinct hue rather than different colour) 2, and minor character (weak difference, e.g. a change in shade) 1; a threshold of 7 is set to allow species status, species status cannot be triggered by minor characters alone, and only three plumage characters, two vocal characters, two biometric characters (assessed for effect size using Cohen's *d* where 0.2–2.0 is minor, 2–5 medium and 5–10 major) and one behavioural or ecological character (allowed 1) may be counted. The notation 'ns' with a score in square brackets equates to 'no score' because of the restriction on the number of characters, but the disallowed score is provided to indicate the further degree of difference.

Molecular study.—Blood samples were obtained from 14 specimens representing three species of *Tanygnathus*, eight from Loro Parque Foundation (LPF; Tenerife, Spain), two from Weltvogelpark Walsrode (Germany), one from Talarak Foundation (Philippines), one from Louisiana State University Museum of Natural Science, Baton Rouge (USA), and one from the Institute of Pharmacy and Molecular Biotechnology, Heidelberg University (Germany), supplemented by a GenBank sample of a specimen held in the Indonesian Institute of Sciences, Bogor. These samples consisted of five *T. lucionensis*, three *T. megalorhynchos* and six *T. sumatranus* (two from the Philippines, four from Indonesia; all origins are indicated in Table 1). Some of these were already available on GenBank, having been obtained from LPF for a thesis (Braun 2014), but they involved no *T. sumatranus* material from the Philippines and were in any case inadequate on their own. For the samples from two living *T. s. everetti* at LPF and the Talarak Foundation respectively we verified their taxonomic identity through photographs and confirmed the former by reference to its CITES documentation.

DNA was isolated from blood samples (stored in a modified EDTA buffer at –20°C, in 80% ethanol, or dried on filter paper). Total DNA was isolated using standard proteinase K (Merck, Darmstadt) and phenol / chloroform procedures (Wink & Sauer-Gürth 2004, Wink

TABLE 1

Samples used in the molecular analysis in this paper, with scientific names, GenBank accession numbers, original voucher numbers and origins (LPF: Loro Parque Foundation, Tenerife, Spain; WVPW: Weltvogelpark Walsrode, Germany; TF: Talarak Foundation, Philippines; LSUMZ: Louisiana State University Museum of Natural Science, Baton Rouge, USA; LIPI: Indonesian Institute of Sciences, Bogor, Indonesia; IPMB: Institute of Pharmacy and Molecular Biotechnology, Department of Biology, Heidelberg Univ., Germany; PH = Philippines; ID = Indonesia; capt., o.u. = captivity, origin unknown). The specimen number in column 3 corresponds to the specimen number in Table 4. ¹ Specimen from Tanahjampea. ² Specimen from Sulawesi. Sample numbers correspond to those in Tables 3 and 4.

Scientific name	GenBank no.	No.	Voucher no.	Source of sample
<i>Tanygnathus lucionensis</i>	MK689343	1	35185	LPF (PH)
<i>Tanygnathus lucionensis</i>	MK689344	2	35188	LPF (PH)
<i>Tanygnathus lucionensis</i>	KM611480	3	36539	LSUMZ (capt., o.u.)
<i>Tanygnathus lucionensis</i>	MK689348	4	53885	WVPW (capt., o.u.)
<i>Tanygnathus lucionensis</i>	MK689349	5	53890	WVPW (capt., o.u.)
<i>Tanygnathus megalorhynchos</i>	KM372555	6	35186	LPF (ID)
<i>Tanygnathus megalorhynchos</i>	KM372556	7	35187	LPF (ID)
<i>Tanygnathus megalorhynchos</i>	MK689351	8	85365	IPMB (ID ¹)
<i>Tanygnathus sumatranus</i>	KM372557	9	35189	LPF (ID)
<i>Tanygnathus sumatranus</i>	MK689345	10	35190	LPF (ID)
<i>Tanygnathus sumatranus</i>	MK689346	11	35191	LPF (ID)
<i>Tanygnathus sumatranus</i>	AB177972	12	—	LIPI (ID ²)
<i>Tanygnathus sumatranus</i>	not yet available	13	78067-20190515n	LPF (PH)
<i>Tanygnathus sumatranus</i>	not yet available	14	96205	TF (PH)

TABLE 2

Measurements of males of four taxa in the *Tanygnathus sumatranus* complex, with the doubtfully valid *duponti* combined with *everetti*. Data for the Banggai and Sula Islands are kept separate simply to illustrate their slightly anomalous measurements, but they were included in the sample for *sumatranus* in the analysis.

	<i>n</i>	bill	wing	tail
<i>everetti</i>	10	33.3 ± 1.24	196.1 ± 6.97	137.3 ± 10.12
<i>burbidgii</i>	14	35.1 ± 2.04	215.6 ± 4.53	154.2 ± 9.46
<i>sangirensis</i>	9	31.8 ± 1.71	213.5 ± 6.64	136.7 ± 2.94
<i>sumatranus</i> (Sulawesi)	22	31.6 ± 1.3	199.4 ± 4.94	123.4 ± 4.19
<i>sumatranus</i> (Peleng / Banggai)	4	31.4 ± 0.98	190.5 ± 5.97	118.5 ± 2.89
<i>sumatranus</i> (Sula Islands)	4	33.1 ± 1.01	194.0 ± 9.76	120.8 ± 6.75

et al. 2009). The mitochondrial cytochrome *b* gene (> 900 nucleotides; nt) was selected and amplified as an informative marker gene. It has been used by MW before for a phylogenetic reconstruction of many other bird taxa, including parrots (Kraus & Wink 2015). The PCR (polymerase chain reaction) amplifications were performed in 50 µl reaction volumes containing 1 × PCR buffer (Bioron, Ludwigshafen), 100 µM dNTPs, 0.2 units of *Taq* DNA polymerase (Bioron, Ludwigshafen), 200 ng of DNA and 5 pmol of primers for cytochrome *b* (as described in Arndt & Wink 2017). Thermal cycling involved five minutes at 94°C, followed by 35 cycles of 40 seconds at 94°C, 40 seconds at 52°C, one minute at 72°C and a final extension at 72°C for ten minutes. Products were precipitated with 4 M NH₄Ac and ethanol and centrifuged for 15 minutes (13,000 rpm). For sequencing, the ABI 3730

automated capillary sequencer (Applied Biosystems, CA, USA) with the ABI Prism Big Dye Terminator Cycle Sequencing Ready Reaction Kit 3.1 (carried out by STARSEQ GmbH, Mainz, Germany) was employed. The same primers were used as for the initial PCR amplifications.

For phylogenetic reconstructions, the nucleotide sequences were aligned manually with BioEdit version 7.0.9.0. No internal stop codons or frame-shifts were observed in the sequences, which were translated entirely by using the chicken *Gallus* mitochondrial code. Phylogenetic trees were reconstructed using the Maximum Likelihood (ML) algorithm in MEGA version 7 (Kumar *et al.* 2016) with related parrot species (three *Eclactus* Parrot *Eclactus roratus*, one Western Corella *Cacatua pastinator*, one Yellow-crested Cockatoo *C. sulphurea*) as outgroups. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. A discrete Gamma distribution was used to model evolutionary rate differences among sites (five categories [+G, parameter = 7.5450]). The rate variation model allowed for some sites to be evolutionarily invariable ([+I], 52.49% sites). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 19 nucleotide sequences (14 ingroup and five outgroup taxa). Codon positions included were 1st+2nd+3rd. There were altogether 1,140 positions in the final dataset.

Sequence data have been submitted to GenBank (accession numbers listed in Table 1).

Results

Morphological evidence.—Photographs from the field, including from the Sulu Islands (taxon *burbidgii*) repeatedly confirmed that Philippine birds possess red irides and Indonesian birds yellowish-white irides. We were impressed to note that two engravings made in the 19th century by J. G. Keulemans to illustrate Salvadori (1891)—both currently viewable on the Wikipedia online entry for Blue-backed Parrot—depict *everetti* and *burbidgii* with red eyes, presumably because live specimens were in London Zoo at the time. We were unable, however, to find photographs from the Banggai Islands, from which the subspecies *incognitus* was described by Eck (1976) on the basis of its brown or grey-brown irides. This form was not admitted by White & Bruce (1986) because of the collector's unreliable practices in relation to iris colour annotation.

Accepting that iris colour is a consistent difference, we find that the Philippine forms *everetti* (with '*duponti*') and *burbidgii* differ from Indonesian nominate *sumatranus* and *sangirensis* in at least seven phenotypic characters, which we list here followed by our 'Tobias' score for their perceived degree of difference. In both sexes Philippine forms differ by their larger bills (see Table 2; effect size of *everetti* vs. *sangirensis* 1.62 and vs. *sumatranus* 1.15; effect size of *burbidgii* vs. *sangirensis* 1.75 and vs. *sumatranus* 2.02; as *burbidgii* is here treated as conspecific with *everetti*, the lower values for *everetti* must be considered, hence score 1); blood-red or orange-red vs. yellowish-white irides (3); pale matt royal blue in place of slightly glossy turquoise-blue lower back and rump (2); paler green head (ns[1]); and duller green underparts (ns[1]). Moreover, in males the Philippine forms further differ by their absence of blue in the carpal feathers and scapulars (2); and much darker green mantle (ns[2]). Philippine birds thus reach a total of 8 under the Tobias criteria, and achieve species rank as a consequence.

The difference in wing length between *everetti* and *burbidgii* (Table 2) yields an effect size of 3.32. The difference in tail length between nominate *sumatranus* and *sangirensis* (Table 2) yields an effect size of 3.70. Both these findings point to the distinctness and validity of the

TABLE 3

Tanygnathus parrots: informative sites in the nucleotide dataset. Dots indicate that the base is identical to that in the first line. This table only includes the sites which were sequenced in all individuals; six informative sites were excluded here, because of missing data in a few sequences.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
# <i>Tanygnathus lucionensis</i> _35185_MK689343_CAPT	-	0.002	-	-	-	-	-	-	-	-	-	-	-	-
# <i>Tanygnathus lucionensis</i> _35188_MK689344_CAPT	0.005	0.003	-	-	-	-	-	-	-	-	-	-	-	-
# <i>Tanygnathus lucionensis</i> _36539_KM611480_CAPT	0.005	0.003	-	-	-	-	-	-	-	-	-	-	-	-
# <i>Tanygnathus lucionensis</i> _53885_MK689348_CAPT	0.005	0.003	0.003	-	-	-	-	-	-	-	-	-	-	-
# <i>Tanygnathus lucionensis</i> _53890_MK689349_CAPT	0.005	0.003	0.003	0.000	-	-	-	-	-	-	-	-	-	-
# <i>Tanygnathus megalorhynchus</i> _35186_KM372555_CAPT	0.033	0.031	0.031	0.031	0.031	-	-	-	-	-	-	-	-	-
# <i>Tanygnathus megalorhynchus</i> _35187_KM372556_CAPT	0.033	0.031	0.031	0.031	0.031	0.000	-	-	-	-	-	-	-	-
# <i>Tanygnathus megalorhynchus</i> _85365_MK689351_TAN_IND	0.033	0.031	0.031	0.031	0.031	0.000	0.000	-	-	-	-	-	-	-
# <i>Tanygnathus sumatranus</i> _35189_KM372557_CAPT	0.058	0.057	0.057	0.057	0.055	0.053	0.053	0.055	-	-	-	-	-	-
# <i>Tanygnathus sumatranus</i> _35190_MK689345_CAPT	0.058	0.057	0.057	0.057	0.055	0.053	0.053	0.055	0.055	0.000	-	-	-	-
# <i>Tanygnathus sumatranus</i> _35191_MK689346_CAPT	0.058	0.057	0.057	0.057	0.055	0.053	0.053	0.055	0.055	0.000	0.002	-	-	-
# <i>Tanygnathus sumatranus</i> _AB177962_SUL_IND	0.074	0.072	0.072	0.072	0.072	0.067	0.067	0.067	0.067	0.015	0.015	-	-	-
# <i>Tanygnathus sumatranus</i> _78067-20190515n	0.060	0.058	0.058	0.058	0.058	0.062	0.062	0.062	0.062	0.039	0.041	0.057	-	-
# <i>Tanygnathus sumatranus</i> _96205	0.062	0.060	0.060	0.060	0.060	0.063	0.063	0.063	0.063	0.041	0.043	0.058	0.002	-

TABLE 4

Tanygnathus parrots: estimates of evolutionary divergence (p distance) between sequences. The number of base differences per site from between sequences are shown. The analysis involved 14 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. All ambiguous positions were removed for each sequence pair. There were a total of 1,140 positions in the final dataset. Specimen number (across top and left column) corresponds to specimen number in Table 3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
[1] # <i>Tanygnathus lucionensis</i> _35185_MK689343_CAPT	-	-	-	-	-	-	-	-	-	-	-	-	-	-
[2] # <i>Tanygnathus lucionensis</i> _35188_MK689344_CAPT	0.002	-	-	-	-	-	-	-	-	-	-	-	-	-
[3] # <i>Tanygnathus lucionensis</i> _36539_KM611480_CAPT	0.005	0.003	-	-	-	-	-	-	-	-	-	-	-	-
[4] # <i>Tanygnathus lucionensis</i> _53885_MK689348_CAPT	0.005	0.003	0.003	-	-	-	-	-	-	-	-	-	-	-
[5] # <i>Tanygnathus lucionensis</i> _53890_MK689349_CAPT	0.005	0.003	0.003	0.000	-	-	-	-	-	-	-	-	-	-
[6] # <i>Tanygnathus megalorhynchus</i> _35186_KM372555_CAPT	0.033	0.031	0.031	0.031	0.031	-	-	-	-	-	-	-	-	-
[7] # <i>Tanygnathus megalorhynchus</i> _35187_KM372556_CAPT	0.033	0.031	0.031	0.031	0.031	0.000	-	-	-	-	-	-	-	-
[8] # <i>Tanygnathus megalorhynchus</i> _85365_MK689351_TAN_IND	0.033	0.031	0.031	0.031	0.031	0.000	0.000	-	-	-	-	-	-	-
[9] # <i>Tanygnathus sumatranus</i> _35189_KM372557_CAPT	0.058	0.057	0.057	0.057	0.055	0.053	0.053	0.055	-	-	-	-	-	-
[10] # <i>Tanygnathus sumatranus</i> _35190_MK689345_CAPT	0.058	0.057	0.057	0.057	0.055	0.053	0.053	0.055	0.055	0.000	-	-	-	-
[11] # <i>Tanygnathus sumatranus</i> _35191_MK689346_CAPT	0.058	0.057	0.057	0.057	0.055	0.053	0.053	0.055	0.055	0.000	0.002	-	-	-
[12] # <i>Tanygnathus sumatranus</i> _AB177962_SUL_IND	0.074	0.072	0.072	0.072	0.072	0.067	0.067	0.067	0.067	0.015	0.015	-	-	-
[13] # <i>Tanygnathus sumatranus</i> _78067-20190515n	0.060	0.058	0.058	0.058	0.058	0.062	0.062	0.062	0.062	0.039	0.041	0.057	-	-
[14] # <i>Tanygnathus sumatranus</i> _96205	0.062	0.060	0.060	0.060	0.060	0.063	0.063	0.063	0.063	0.041	0.043	0.058	0.002	-

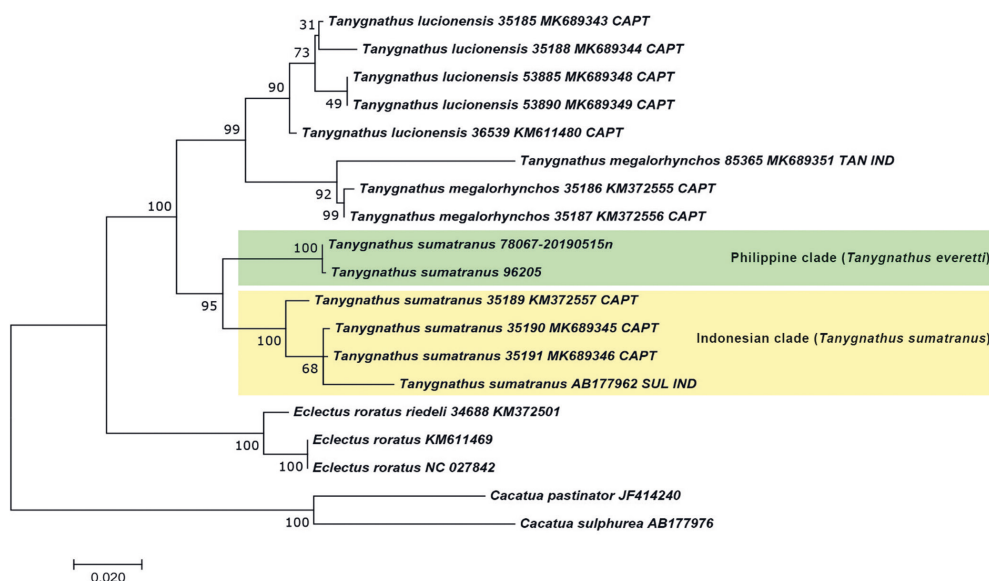


Figure 1. *Tanygnathus* parrots phylogenetic tree. CAPT = captive live bird. IND = Indonesia as the known source. TAN = Tanahjampea. SUL = Sulawesi. Evolutionary history was inferred by using the Maximum Likelihood method based on the General Time Reversible model (Nei & Kumar 2000). The tree with the highest log likelihood (−3897.11) is shown. The percentage of trees in which the associated taxa clustered together is shown next to the branches. Numbers at the branches are bootstrap values (in %) from 500 replications.

forms *burbidgii* and *sangirensis*; *burbidgii* is larger in all dimensions than any other taxon except the little-known *freeri* (see below), while *sangirensis* almost matches it for wing length and almost matches *everetti* for tail length while exactly matching nominate *sumatranus* for bill length. It is also worth noting that the four Peleng and Banggai birds proved to have shorter wings and tails than any other taxa, and that the four Sula birds had larger bills than either *sumatranus* or *sangirensis* (Table 2).

Molecular evidence.—The dataset consisting of all 14 samples of the genus *Tanygnathus* had 224 variable and 106 phylogenetically informative sites (all latter in Table 3). Genetic distances (*p* distance) are tabulated in Table 4. The phylogeny was reconstructed using Maximum Likelihood (Fig. 1). Birds identified as *T. lucionensis*, *T. megalorhynchos* and Indonesian *T. sumatranus* formed separate clusters within a monophyletic *Tanygnathus* clade (bootstrap support 99% and 95%). The position of the two Philippine birds within the *T. sumatranus* cluster clearly indicates their genetic distinctiveness (as great as that between *T. lucionensis* and *T. megalorhynchos*) and is consistent with evidence above that populations representing *T. sumatranus* in the Philippines in reality constitute a distinct species.

Discussion

On the basis of these results, in which phenotypic and genetic evidence point independently to the same conclusion, we judge that Philippine taxa group together as one species under the name *T. everetti* and Indonesian taxa as another under the name *T. sumatranus* (Fig. 2). Because ‘Azure-rumped Parrot’ *roughly* reflects the colour of

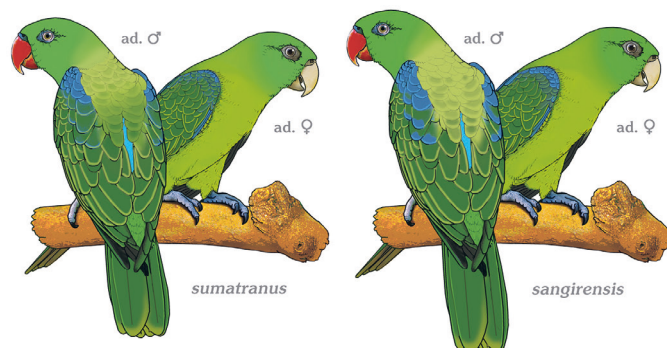
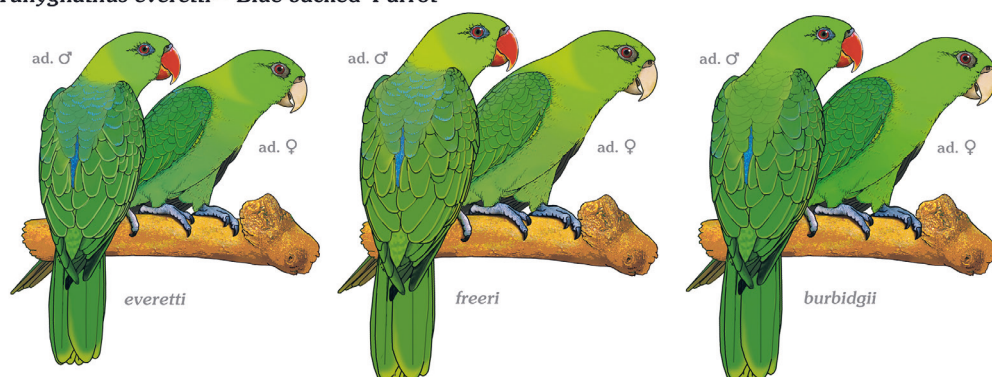
Tanygnathus sumatranus* – Azure-rumped Parrot**Tanygnathus everetti* – Blue-backed Parrot**

Figure 2. Overview of the plumage patterns of all taxa of the *Tanygnathus sumatranus* and *Tanygnathus everetti* complex (Thomas Arndt)

the Sulawesi populations and ‘Blue-backed Parrot’ *roughly* reflects that of those in the Philippines, we suggest that these two names, which hitherto have been used as alternatives for the broader species, be exclusively assigned henceforth to *T. everetti* (Blue-backed Parrot) and *T. sumatranus* (Azure-rumped Parrot).

The distinction between the two species would be more clear-cut were it not for the fact that the two forms with the largest ranges, *T. e. everetti* and *T. s. sumatranus*, each have considerably larger subspecies on small outlying island groups. Consequently the longer wing of *T. s. sangirensis* comes close to matching that of *T. e. burbidgii*, while its longer tail is almost exactly the same as that of *T. e. everetti*. The greater size of *sangirensis* than nominate *sumatranus* (which should ensure its reinstatement as a valid taxon by those who have synonymised it—see Introduction, and Table 2) and of *burbidgii* than nominate *everetti* even raises the issue of whether they might qualify for species rank themselves. However, in plumage *sangirensis* is very close to *sumatranus*, and its classification as a species would seem only to be likely under a fairly extreme application of the phylogenetic species concept. On the other hand, *burbidgii* differs, as noted in its original description, by its slightly yellower green head (Tobias score 1) and lack of blue edges to the mantle feathers (1) (Sharpe 1879), plus a rather weaker pale yellowish edging to the wing-coverts, which thus appear less ‘scaled’ (perhaps 1; greater sample needed); with an effect size of 3.32 for wing length (score 2) these characters accumulate a Tobias score of 5, which indicates a

considerable degree of differentiation. It is also worth noting that the form *freeri* appears to be even larger than *burbidgii*, with Salomonsen (1952) reporting two males and two females having wing 227, 237, 217, 228 mm and tail 157, 174, 159, 165 mm (means 227.3 and 163.8 mm respectively vs. 215.6 and 154.2 mm in *burbidgii* in Table 2). Certainly all three small-island forms merit further taxonomic study—tissue sampling from museum material for additional genetic work is clearly called for—and conservation in their own right; and the differences between *burbidgii* and *everetti* particularly need to be remembered if, as seems likely, *ex situ* endeavours commence in the light of growing evidence, being gathered and reviewed elsewhere, of the newly split species' extreme rarity.

The sample of Peleng / Banggai and Sula birds is far too small for interpretation, but the relatively short wings and tails of the former and the relatively large bills of the latter are worth recalling if the opportunity ever arises to review their taxonomic status. However, any move to reinstate *incognitus* for Peleng / Banggai birds would need to take into account the improbability of the leapfrog pattern in which Sula birds remain with nominate *sumatranus*. Some individuals from all these islands and from Sangihe had the turquoise rump showing touches of the blue found in Philippine taxa, but in other respects their plumages aligned with Sulawesi birds.

The biogeographic affinities between the Philippines and Sulawesi (with or without varying parts of western Wallacea) are indicated in ornithology by the genus *Prioniturus* (involving two dispersal events: Schweizer *et al.* 2012) and by the species Purple Needletail *Hirundapus celebensis* and Citrine Canary-flycatcher *Culicicapa helianthea*. More broadly, Philippine Scrubfowl *Megapodius cumingii* also reaches the islands off northern Borneo while Barred Rail *Hypotaenidia torquata* leapfrogs the Moluccas to the West Papuan islands and north-west New Guinea. Further such correspondence is found in the species pairs Pink-bellied *Ducula poliocephala* and White-bellied Imperial Pigeons *D. forsteni* and the recently split Philippine *Pernis steerei* and Sulawesi Honey-buzzards *P. celebensis* (differences under the Tobias criteria scored in del Hoyo & Collar 2014). The split here of *Tanygnathus sumatranus everetti* may suggest that a fresh consideration of the taxonomic standing of the needletail (usually regarded as monotypic), scrubfowl, rail and canary-flycatcher might result in new arrangements.

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