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Coua cristata maxima—species or subspecies, adult or juvenile, extant or extinct, aberrant or hybrid?

by Nigel J. Collar & Guy M. Kirwan

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Summary.—*Coua cristata maxima*, known by nothing more than a unique specimen taken in south-east Madagascar in 1948, was distinguished by its greater size than other subspecies of Crested Coua *C. cristata* (of which *pyropyga*, sometimes accorded species rank, is the largest) and by its shorter crest, bluer upperparts, wings and tail, fully cinnamon-tawny underparts and mid-sized white tail tips. A separate assessment of the holotype published in 1997 made various refinements to this diagnosis, and our own examination found the facial configuration seemingly inconsistent with that of *pyropyga*, showing a weaker superciliary line and possibly a reduced area of bare skin around the eye, although these features may, like the short crest, simply be indications of immaturity. Even if they are, however, *maxima* appears too distinct to retain subspecific rank: it seems more likely to be either a full species or, as first intimated in 1997, a hybrid. Four of the six *Coua* species around the type locality cannot be possible parents, but seven features of the holotype are consistent with a Blue Coua *C. caerulea* × *C. cristata* pairing. Molecular investigation is urgently needed to determine whether *maxima* is a valid species. If it is, it will either be highly threatened or extinct; little-known hinterland forest from Manafiafy (35 km north-east of Taolagnaro) north at least to Manantenina has been identified for survey.

Three of the world's four main avian checklists, two recent monographs of the Cuculiformes (Payne 2005, Erritzøe *et al.* 2012) and a handbook to the birds of the Malagasy region (Safford & Hawkins 2013) all treat the Crested Coua *Coua cristata* of Madagascar as consisting of four subspecies, arranged anti-clockwise as nominate *cristata* in the east, north and north-west, *dumonti* in the centre-west, *pyropyga* in the south-west and south, and *maxima* in the south-east (Dickinson & Remsen 2013, Clements *et al.* 2023, Gill *et al.* 2024). The fourth list splits *pyropyga* as Chestnut-vented Coua but treats the remaining three subspecies as conspecific (del Hoyo & Collar 2014, HBW & BirdLife International 2024). It is certainly the case that *pyropyga* is well differentiated from nominate *cristata* and subspecies *dumonti* (these two latter being very similar to each other, to the point where we speculate if they might form components of a cline), but it is the taxon *maxima* that in several ways is the most distinctive of the four. However, this last is known from a single specimen, which inevitably reduces the confidence with which a defensible position on its taxonomic status can be taken. Consequently it has been left as an unaddressed issue for many years, with checklists quietly parking it until further light can be shed. Here we attempt to provide a little more context and clarity to this interesting case, prior to and preparatory for the obviously needed step of a molecular analysis.

Three examinations of the holotype

Coua cristata maxima was established by Lt. Col. Philippe Milon based on a male (inexplicably both Erritzøe *et al.* 2012 and Goodman 2013 state the specimen is unsexed)

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which he collected at Fort Dauphin (now Taolagnaro or Tolagnaro), in far south-east Madagascar, on 18 February 1948 (Milon 1950); he later mentioned that he found it in humid forest (Milon 1952). He diagnosed it (in French; all quotations from the original description are our translations) on the basis of both size and colour. As its name indicates, the holotype in the Muséum national d'Histoire naturelle, Paris (MNHN-ZO-1950-392; Figs. 1–5), proved larger than the largest of the known subspecies of Crested Coua *C. c. pyropyga* (in the following sequence of measurements, in millimetres, *maxima* is first vs. *pyropyga*, with the latter's values expressed as means of 14 specimens): bill (from commissure) 30.0

Figure 1. Holotype of *Coua cristata maxima* (MNHN-ZO-1950-392) in ventral view; note the loss of all undertail-coverts (Guy M. Kirwan)

Figure 2. Holotype of *Coua cristata maxima* (MNHN-ZO-1950-392) in lateral view (Guy M. Kirwan)

Figure 3. Holotype of *Coua cristata maxima* (MNHN-ZO-1950-392) in dorsal view (Guy M. Kirwan)

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Figure 4 (left). Holotype of *Coua cristata maxima* (MNHN-ZO-1950-392), view of right side of head (Guy M. Kirwan)

Figure 5 (right). Holotype of *Coua cristata maxima* (MNHN-ZO-1950-392), view of left side of head (Guy M. Kirwan)

vs. 26.7, tarsus 45.0 vs. 41.2, wing 175 vs. 162, tail 232.5 vs. 212.0 (Milon 1950). None of the highest values of the *pyropyga* sample were as high as those for *maxima* (this is also true in the independent sampling of the former undertaken by Benson *et al*. 1976–77); moreover, the width of the central rectrices of *maxima* proved notably greater than those of all three other subspecies (45 vs. <40), and various other, unquantified indications of its greater size involved 'the thickness of the tarsi, the width of the back, etc.' (Milon 1950). In plumage, the holotype was deemed to have four basic points of difference from *C. cristata* (Table 1).

In the field the absence of white on the underparts and the presence of blue in the upperparts was striking, such that when Milon (1950) first saw the bird (when it must have been facing away from him) he thought it was a Blue Coua *C. caerulea*. No other specimen exists, but Milon (1950) mentioned that when the holotype was collected 'other individuals of the same form were seen in the vicinity'.

One or more of the authors of Goodman *et al*. (1997), reconsidering the case of *maxima*, examined the holotype and compared it with other material of *cristata*. This involved plumage descriptions that extended but also slightly modified the diagnosis in Milon (1950), focusing solely on details of the upperparts and underparts (Table 1), and referring to a particularly frustrating feature of the specimen, not mentioned by Milon himself, which is that it had 'lost most of the undertail coverts during preparation'. With this very unusual and unfortunate circumstance, a crucial piece of evidence concerning *maxima*'s relationships to the other taxa in the *C. cristata* complex—chestnut/rufous or white/buffy undertail-coverts—has been lost (witness Fig. 1). Goodman *et al*. (1997) made the ambiguous remark that Milon (1950) had 'noted that the ventrum of the *maxima* specimen was tawny cinnamon with no reddish coloration at the base of the tail', which must be the source of the mistaken assertion in Payne (2005) that the 'under tail coverts lack rufous'. It is true that Milon (1950) described the belly ('*ventre*') of *maxima* as 'cinnamon fawn', but he made no comment about the colour at the base of the (under)tail. However, an illustration in Milon (1952) of all four subspecies of *C. cristata* (Fig. 6) shows the undertail-coverts of *maxima* the same colour as in *pyropyga* (and indeed of the belly of *maxima*). It is tempting to assume that this was based directly on the recently collected holotype, but the loss of the

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TABLE 1

Schematised diagnoses of *Coua cristata maxima* based on three detailed reviews; comparisons throughout are with other *C. cristata* taxa.

	Milon (1950)	**Goodman *et al*. (1997)**	This paper
Size	Larger than largest form of *C. cristata* (=*pyropyga*) with broader rectrices	–	Second largest extant member of *Coua*, with rectrices proportionately broader than in *C. cristata*
Crest	Shorter than in *dumonti* and *pyropyga* and a little shorter than in nominate *cristata* [evidently judged visually]	–	Shorter (based on visual comparisons; no attempt made to quantify)
Head-sides	Like *C. cristata* taxa	–	More feathered area around eye and on ear-coverts, with weaker black fringing line
Upperparts	Distinctly darker and bluer (less green) mantle than other subspecies	Back 'grayish blue' vs. 'gray or greenish gray', uppertail 'intense violet blue' recalling *C. caerulea* vs. 'more subdued iridescent blue with greenish tinge in *pyropyga* and innermost secondaries… blue vs. iridescent green	Greyish-blue vs. greenish-grey crown and upper body, with iridescent deep rich blue inner remiges and tertials vs. iridescent greenish grey, and iridescent violet-blue vs. greenish-blue uppertail
Underparts	Described as 'more pigmented' (i.e. more extensively coloured), lower breast's cinnamon fawn carrying onto belly and flanks, not shading to pale fawn or almost white	Throat 'cold bluish gray' vs. 'gray', upper breast 'tawny brown' vs. 'purplish gray', lower paler 'tawny brown' with no sign of change at vent* vs. 'light tawny brown' shading to 'white with a rufous vent'	Darker grey throat, deeper cinnamon-tawny breast, cinnamon-tawny lower breast, belly and flanks (not shading to white although a few whitish feathers where the undertail-coverts have been lost)
Tail tips	White tail tips (40 mm) larger than in nominate (17–31) but smaller than in *dumonti* and *pyropyga* (43–65)	–	–

*but then acknowledging the loss of vent feathering.

undertail-coverts *after* preservation in Paris seems less likely than their loss, as Goodman *et al*. (1997) said, during preparation or when the bird was shot. At any rate, this image must be assumed to have given Goodman (2013), in his account of *maxima*'s characters (condensing those in Goodman *et al*. 1997), the confidence to report 'lower breast to vent tawny-brown (not whitish) with increasing colour saturation'.

From our own examinations of the holotype (NJC in 2013, NJC & GMK in 2023)—when we could find *no* undertail-coverts—we confirm the diagnostic characters identified by Milon (1950) and Goodman *et al*. (1997), sometimes with slight modifications (Table 1; we use 'cinnamon-tawny' for the rather beautiful colour of the breast). However, we were and remain struck by the rather different-looking configuration of plumage and pattern around the face of *maxima*. Milon (1950) stated that 'the colours of the … bare skin around the eye' were as in 'the other subspecies', but the holotype itself is hardly supportive: (1) it possesses a relatively weak and diffuse black superciliary line dividing the crested crown from the naked head-sides, and (2) it appears to lack a large area of bare skin around (and especially above) the eye (Figs. 4–5). In *C. cristata* (*s. l.*) the bold superciliary line and wide bare periocular skin are as obvious in museum specimens (see Figs. 7–8) as they are in

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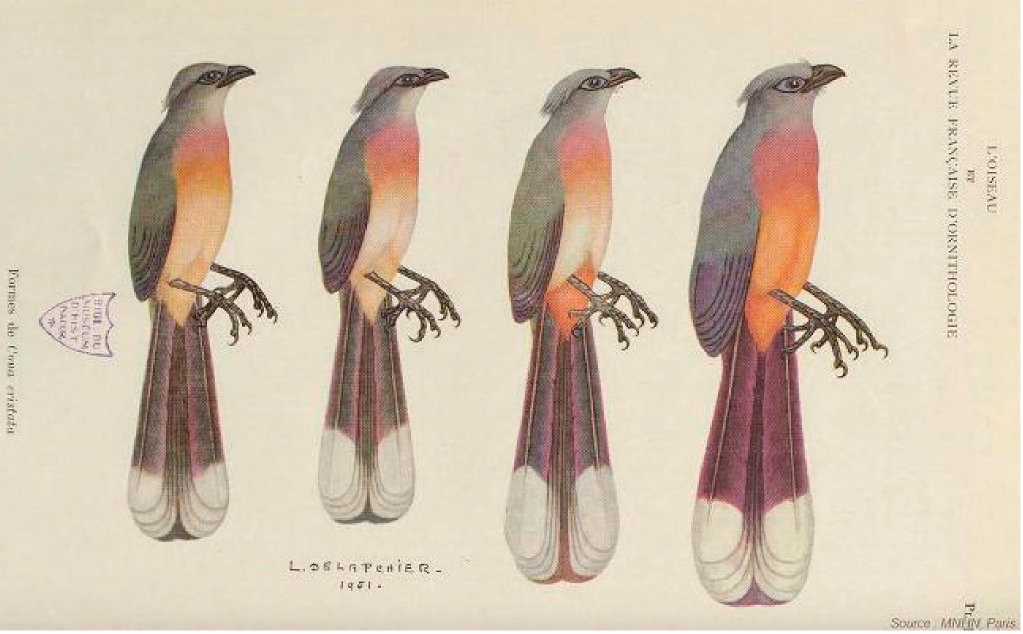

Figure 6. Illustration of the four subspecies of *Coua cristata* (left to right: nominate *cristata*, *dumonti*, *pyropyga* and *maxima*) in Milon (1952, plate IV).

Figure 7 (left). Three heads of specimens of *Coua cristata cristata* held in the Natural History Museum, Tring, top to bottom: NHMUK 1931.8.18.515, 1931.8.18.513, 1931.8.18.510 (N. J. Collar, © Trustees of the Natural History Museum, London)

Figure 8 (right). Three heads of specimens of *Coua* [*cristata*] *pyropyga* held in the Natural History Museum, Tring, top to bottom: NHMUK 1931.8.18.536, NHMUK 1931.8.18.541, NHMUK 1931.8.18.542 (N. J. Collar, © Trustees of the Natural History Museum, London)

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Figure 9 (left). Crested Coua *Coua cristata cristata*, Ankarafantsika National Park, October 2019 (detail) (Paul van Giersbergen)

Figure 10 (right). Blue Coua *Coua caerulea*, Ranomafana National Park, November 2019 (detail) (Paul van Giersbergen)

photographs of live individuals (e.g. Fig. 9). They are, by contrast, so little apparent in the holotype of *maxima* that we must query its illustration in Safford & Hawkins (2013) and Hawkins *et al*. (2015) (where, incidentally, the undertail-coverts are shown as rufous).

Options for classification

What, then, are the options for the classification of *Coua cristata maxima*? Del Hoyo & Collar (2014) exposed the issue when they split *pyropyga* from *cristata* and *dumonti* on the basis of its pale chestnut or strong rufous vs. whitish or buffy-white undertail-coverts, paler upperparts (especially tertials), much longer white tail tips and larger size (see Figs. 11–12). This arrangement offered a suite of options for the treatment of *maxima*, arguably the least coherent of which was to leave it, as del Hoyo & Collar (2014) did, as an outlying subspecies of the rather dissimilar *C. cristata*. Three alternatives were suggested, to which we here add a fourth (the first in the following list): a subspecies of the more similar-sized *C. pyropyga*; a taxon requiring species rank of its own; an 'aberrant individual of a known form' (Goodman 2013); or a hybrid (a possibility first raised by Goodman *et al*. 1997). We consider these five options here, dwelling longest on the last, after reviewing the issue of the age of the bird at the time of collection.

Length of crest and degree of feathering around the eye are gauges of age in couas (Benson *et al*. 1976–77, Goodman 2013; R. B. Payne *in litt*. 2024), so it may be that *maxima*'s comparatively short crest and apparently largely feathered periocular area are signs of its immaturity. However, Milon (1950) explicitly indicated that the 'colour of… the bare skin around the eye' of *maxima* was 'as in the other races', and indeed it was illustrated as such in Milon (1952; see Fig. 6). The current condition of the head-sides in *maxima* may therefore simply be attributable to shrinkage of the skin over time (H. van Grouw and R. B. Payne *in litt*. 2024). So is the holotype of *maxima* adult or immature? Bare skin was visible when the feathers on the head-sides were moved aside, but the extent of it was extremely hard to gauge. We are therefore frankly unsure, as we have examined many specimens in which such a contraction has not occurred over comparable or longer periods of time: every one

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Figure 11. Ventral view of three *Coua* [*cristata*] *pyropyga* and three *C. c. cristata* specimens in the Natural History Museum, Tring, top to bottom: NHMUK 1931.8.18.542, NHMUK 1931.8.18.541, NHMUK 1931.8.18.536, NHMUK 1931.8.18.510, NHMUK 1931.8.18.513, NHMUK 1931.8.18.515 (N. J. Collar, © Trustees of the Natural History Museum, London)

of the 21 specimens of nominate *cristata*, ten full-grown *dumonti* and 11 *pyropyga* held in the Natural History Museum, Tring, UK (NHMUK), was taken years before the holotype of *maxima* but has unreduced bare periocular skin (examples in Figs. 7–8).

Subspecies of C. cristata.—This is the status quo, whether *C. pyropyga* is accepted as a separate species or not. Because the elevation of *C. pyropyga* to species rank isolates *maxima* from the remaining subspecies of *C. cristata*, del Hoyo & Collar (2014) judged that the case for also treating *maxima* as a species was compelling. However, this was to miss the consideration raised by R. B. Payne (*in litt*. 2024) that in its darker upperparts and mid-sized white tail tips *maxima* is taxonomically closer to nominate *cristata* than it is to *pyropyga*, and that nominate *cristata*, known to occur 200 km north of Taolagnaro (R. J. Safford *in litt*. 2024), might extend in undetected pockets of secondary habitat south throughout Madagascar's eastern humid forests (as vaguely speculated in Rand 1936, Milon 1952), making it as close geographically to *maxima* as *pyropyga* seems to be. Nevertheless, we are sceptical, for at least three reasons: (1) the size difference of *maxima* vs. nominate *cristata* is greater than it is vs. *pyropyga* (Benson *et al*. 1976–77 offer independent means: nominate *cristata* wing 136, tail 185 and *pyropyga* 162, 207 vs. *maxima*'s 172, 224—C. W. Benson's own measurements); (2) the likelihood that *maxima* shared rufous undertail-coverts with *pyropyga* appears rather greater

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Figure 12. Dorsal view of the same three *Coua* [*cristata*] *pyropyga* and three *C. c. cristata* specimens, as in Fig. 11, in the Natural History Museum, Tring, top to bottom: NHMUK 1931.8.18.542, NHMUK 1931.8.18.541, NHMUK 1931.8.18.536, NHMUK 1931.8.18.510, NHMUK 1931.8.18.513, NHMUK 1931.8.18.515 (N. J. Collar, © Trustees of the Natural History Museum, London)

than that it shared white ones with nominate *cristata*; and (3) the *known* distance between the type locality of *maxima* and the easternmost occurrence of *pyropyga* is *far* smaller.

Subspecies of C. pyropyga.—The last three points—relatively close in size, probably identical in colour of the undertail-coverts, and known geographical proximity—make a fair case for treating *maxima* as a form of *pyropyga*, if the latter is treated specifically and despite its overall paler coloration.

Species.—The possibility than *maxima* could be a 'distinct species' was glancingly mentioned by Goodman *et al*. (1997), rather strongly endorsed ('may well represent a separate species') by Goodman & Wilmé (2003), and echoed by Goodman (2013) and Safford *et al*. (2022). Under the Tobias criteria (Tobias *et al*. 2010), where a cumulative score of 7 is required for species rank, we allow the larger size (always conceding $n = 1$) a score of 2, the cinnamon-fawn lower breast and belly 3, and the blue vs. green inner remiges and tertials 2, thus a total of 7. If the shorter crest (allow 2) and more feathered head-sides/weaker superciliary line (allow 2) are not discounted as signs of immaturity, the total score could rise to 11.

Aberrant.—The concept of the 'aberrant' specimen rose to prominence with the steady trawl of described taxa by the Peters (1931–87) checklist, whenever a plausible treatment

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of forms known only by one or two specimens was needed. Over time, a few such taxa have been shown to be based on genuinely 'aberrant' specimens, e.g. Hooded Seedeater *Sporophila melanops* (Areta *et al*. 2016), but the majority of cases remain unresolved. However, the ascription of 'aberrant' to a taxon almost invariably involves colour variation and rarely if ever size; even the phenomenon of 'runt' (small, seemingly malformed) birds has rarely if ever been invoked as a confident explanation of an anomalous taxon. Certainly the circumstance of an aberrant bird that is *larger* than the form to which it is judged to belong, as well as differently coloured, appears simply to be undocumented in wild birds. The fact that its discoverer saw at least one other similar bird only diminishes the aberration hypothesis further, to the point where we elect to discard it.

Hybrid.—The possibility that the holotype of *maxima* is a hybrid, first suggested by Goodman *et al*. (1997), then repeated by Payne (2005) and Erritzøe *et al*. (2012), needs exploration. The position of the type locality, Taolagnaro (25°01′S, 46°59′E; elevation 0–40 m), allows for the following members of the genus *Coua*, having ranges which are known or thought to approach the city within several tens of kilometres, to be considered as potential parents: Crested Coua *C*. [*cristata*] *pyropyga*, Blue Coua *C. caerulea*, Red-fronted Coua *C. reynaudii*, Olive-capped Coua *C*. [*ruficeps*] *olivaceiceps* (also split in del Hoyo & Collar 2014), Running Coua *C. cursor* and Giant Coua *C. gigas*. (Even *C. cristata cristata* might be considered—see above under 'Subspecies of *C. cristata*'.) Goodman *et al*. (1997) took the view that *C*. [*cristata*] *pyropyga* had to be one parent, given the overall resemblance of *maxima* to the phenotypes represented within the *cristata* complex that led Milon to treat it trinomially; and they suggested that the other might be *C. caerulea* or *C. reynaudii*. These two are certainly stronger candidates than the other three on the list, mainly because they are, like *C. cristata* (*s. l.*), arboreal rather than terrestrial couas: the prospect of a successful interbreeding of two species with such different ecological adaptations seems remote.

Judging hybrid status involves the scrutiny of organisms for morphological intermediacy. Such intermediacy is not necessarily exact, but it is typically present in certain characters such that a diagnosis can be made with some confidence (Wilson 1990, Estabrook *et al*. 1996, Hennache *et al*. 2003, Gholamhosseini *et al*. 2023). In this respect plumage considerations further reduce the chances of a terrestrial coua being involved in the pedigree of *maxima*: all three species have heavy facial markings like *cristata* (*s. l.*), so would hardly be likely to produce an offspring without them, and *olivaceiceps* has a creamy throat and lilac-grey breast while *cursor* has a buffy-rufous throat and a grey breast. Size is another consideration: assuming the intermediacy of the male *maxima* between the smaller *pyropyga* and a larger other parent, and using wing length (no difference between the sexes) as an index (mean male data in mm from Goodman 2013), we have 135 for *cursor*, 137 for *reynaudii*, 162 for *pyropyga*, 169 for *olivaceiceps*, 175 for *maxima*, 194 for *caerulea* and 215 for *gigas*. Clearly all three terrestrial birds fail this test, *cursor* and *olivaceiceps* by being far too small and *gigas* far too large.

Of the two arboreal options, however, *reynaudii* can be rapidly eliminated on the basis of characters that find no evidence of expression or intermediacy in *maxima*, namely its overall dark green plumage, rufous crown, heavy black supercilium and relatively short bill and wings. This then leaves *C. caerulea* as the only plausible candidate to be the second parent of *maxima*. Blue Coua is coloured throughout a rather deep, soft blue, muted by the slightest suffusion of grey on the head and breast, while the wings and tail are somewhat glossy, the former with a violet tinge that can appear greenish at some angles, the latter shaded rich violet and lacking white tips; the skin above, below and behind the dark eye is a paler, brighter blue, circumscribed by a feathered black line. The notion that such a uniform bird, much larger than any extant congener except Giant Coua, could be one parent

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of *maxima* might seem outlandish at first. Nevertheless, it bears mention that molecular analysis has found Blue and Crested Couas more closely related to each other (except perhaps the unsampled Verreaux's: see genus account in Goodman 2013) than to other couas (Johnson *et al*. 2000), and the list of (six) characters in *maxima* which are consistent with *caerulea* as a progenitor is striking:

- it is 13 mm longer-winged than *pyropyga* and 19 mm shorter-winged than *caerulea* (see above)
- the crest is short (*caerulea* has fairly long crown feathers but nothing amounting to what is typically regarded as a crest)
- like *caerulea*, it possesses a smaller area of bare skin round the eye than *pyropyga*, only detectable by parting the head-side feathering (Figs. 4–5 and 10)
- it appears to show a relatively diffuse (less sharply defined) blackish superciliary line (more like *caerulea*; Figs. 4–5 and 10)
- the upperparts, wings and particularly tail are bluer than in any other coua taxon except *caerulea*, although only slightly more so (not easily shown in photographs) than *cristata*
- the rectrices are intermediate in width (45 mm *fide* Milon) between those of *pyropyga* (32.4 mm) and *caerulea* (58.2 mm), mid-point 45.3 mm, based on means of five normally prepared male specimens of each species randomly selected in NHMUK).

The retention of white tail tips in *maxima* and the fact that these tips are intermediate in size between *pyropyga* and *dumonti* is beyond our capacity to explain.

Extant, extinct, illusion?

If *Coua* [*cristata/pyropyga*] *maxima* is a valid taxon, the question arises whether a population representing it might still be extant. Goodman *et al*. (1997) ominously reported that 'Most of the natural lowland forest in the immediate vicinity of Tolagnaro has been destroyed', without inferring a consequence. Six years later Goodman & Wilmé (2003) were more categorical, even while conceding that some forest still stood: 'The remaining forest blocks surrounding Tolagnaro are ornithologically well known, and it is certain that this form is extinct'. Even so, after another ten years Goodman (2013), who attributed the bird's disappearance from Tolagnaro to hunting (because, after all, 'seemingly appropriate forested habitat remains in this region'), reflected that the form *might* still be found in forest stretching 200 km to the north: 'The [hinterland] forest from N of Manafiafy [35 km north-east of Taolagnaro north] to at least the Manantenina area or perhaps even Vangaindrano, which is ornithologically poorly known, holds potential for finding a remnant population of *maxima* and such exploration should be given high priority'. If that possibility is to be seriously entertained—and we are unaware that anyone has yet done so, or anywhere repeated the idea—our own inclination would be to consider the population as representing a full species, which would increase the urgency with which a new search should be undertaken.

For reasons stated above, we find the option that *Coua cristata maxima* is based on an aberrant individual unconvincing. On the other hand, the possibility that it is a hybrid *C. cristata* × *C. caerulea* appears plausible to us, but we emphatically do not consider the idea to be incontrovertible. One objection is that Milon (1950) saw other birds in the vicinity similar to the one he collected; a possible counter is that he simply saw a second bird that made more than one appearance while he was stalking the first, in which case (Crested Couas laying two eggs: Goodman 2013) he might have been in the presence of two full-grown offspring (a possibility consistent with the feathered head-sides) of an unseen pair

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(not necessarily mixed: avian hybrids are commonly the product of heterospecific rape by the larger-bodied male parent, which plays no part in rearing the offspring: Rohwer *et al*. 2014). Another objection is that Milon found *maxima* in 'humid forest' (Milon 1952), a habitat that *pyropyga*, at least, tends to shun (Goodman 2013): a possible counter here is that niche overlap between *C. caerulea* and *C. cristata* (*s. l.*) is greater than expected (Chiatante 2022), and that the two species approach each other in south-eastern Madagascar to 'a ground distance of less than 2 km' (Goodman *et al*. 1997: 49), which surely suggests a circumstance for at least occasional direct encounters between them.

Even so, the only realistic position to take in this interesting case is to urge a molecular study of the holotype of *Coua cristata maxima* and its putative parents and relatives. The possibility that it does, after all, represent a genuine taxon—and therefore in our assessment a distinct species, inevitably highly threatened (unless already extinct)—demands that the matter be resolved as soon as possible. It is disappointing that one attempt to extract DNA from the specimen failed (R. Davion *in* Goodman 2013), but perhaps modern techniques (e.g. Tsai *et al*. 2020) can now be applied to satisfactory effect.

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