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Morphological review of the genus *Eupherusa* (Trochilidae) does not support recognition of the monotypic genus *Dicranurania* Sangster *et al.*, 2023

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Summary.—Sangster *et al*. (2023) erected a new genus (*Dicranurania*) for the Mexican Woodnymph [*Thalurania*] *ridgwayi* (Nelson, 1900), which phylogenetic evidence suggests is the most likely sister group of the genus *Eupherusa* Gould, 1857, and distantly related to (and polyphyletic with) the other species of *Thalurania* Gould, 1848. Here, with a representative sample of study skins, I demonstrate that their morphological diagnosis of *Dicranurania* was based on a broad mischaracterisation of *Eupherusa* phenotypes, which improperly exaggerated the distinctiveness of [*T.*] *ridgwayi*. Therefore, I encourage systematists to classify [*T.*] *ridgwayi* as a fifth species of *Eupherusa*, and relegate *Dicranurania* to its synonymy.

Sangster *et al*. (2023) recently examined the taxonomic status of Mexican Woodnymph [*Thalurania*] *ridgwayi* (Nelson, 1900), a hummingbird species endemic to western Mexico, and erected a new monotypic genus (*Dicranurania*) to accommodate it, on phylogenetic and morphological grounds. The revision was prompted by McGuire *et al*. (2014), who found evidence that [*T.*] *ridgwayi* is the phylogenetic sister of the genus *Eupherusa* Gould, 1857, and only distantly related to (and polyphyletic with) other species in the genus *Thalurania* Gould, 1848. Stiles *et al*. (2017: 406) qualitatively compared the morphology of [*T.*] *ridgwayi* and the four *Eupherusa* species, and concluded that 'the available evidence favors the inclusion of *ridgwayi* [as a fifth member of] the genus *Eupherusa*'. Stiles *et al*. (2017: 406) summarised the evidence as follows:

> 'Closest to *ridgwayi* and separated by a short branch is the genus *Eupherusa* Gould, 1857, with four closely related species. Males of *ridgwayi* differ from those of all species of *Eupherusa* in lacking white in the tail and rufous in the remiges. However, the blue crown of male *ridgwayi* is quite similar to that of *E. cyanophrys* [Rowley & Orr, 1964], and the blackish underparts are shared with *E. nigriventris* [Lawrence, 1868], which also has less extensive rufous in the remiges; its shallowly forked tail also resembles more closely those of *Eupherusa* species. Females of *ridgwayi* and *Eupherusa* share gray underparts and differ mainly in tail patterns, although here again *E. nigriventris* has less extensive white in the tail than do those of the other *Eupherusa* species.'

Accordingly, most subsequent authors have placed [*T.*] *ridgwayi* in *Eupherusa* (e.g., Clements *et al*. 2022, Gill *et al*. 2023). However, Sangster *et al*. (2023) challenged this conclusion, arguing based on 'multiple prominent [morphological] differences' that [*T.*] *ridgwayi* should be placed in a monotypic genus (*Dicranurania*). Here, I review the morphological characters used by Sangster *et al*. (2023) in their taxonomic diagnosis of *Dicranurania*, by examining a representative sample of study skins of [*T.*] *ridgwayi* and the four *Eupherusa* species.

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Specimen evidence

Study skins of [*T.*] *ridgwayi* and three of four *Eupherusa* species (all except Stripe-tailed Hummingbird *E. eximia*) are rare in collections because of their restricted geographic ranges and conservation statuses: [*T.*] *ridgwayi* is currently listed as Vulnerable and Blue-capped Hummingbird *E. cyanophrys* as Endangered (BirdLife International 2018a,b). The Delaware Museum of Nature & Science (DMNH, formerly Delaware Museum of Natural History), Wilmington, contains approximately 50% (15/30) of the global total of publicly accessible (databased) study skins of [*T.*] *ridgwayi*, 33% (34/102) of *E. cyanophrys* and 23% (10/44) of White-tailed Hummingbird *E. poliocerca* Elliot, 1871 (Vertnet.org, accessed 19 March 2023). The DMNH collection also contains a sizeable sample (27/602) of available *E. eximia* (Delattre, 1843) specimens and a single male of Black-bellied Hummingbird *E. nigriventris* (1/95). Most of this material was collected in the 20th century and is in excellent condition, making the DMNH collection well suited for a study of this kind.

Morphological criteria for generic classification

Genera defined by morphological characters are typically composed of (1) multiple species that share a suite of 'unique synapomorphies' (i.e., shared derived characters not present in other closely related clades) or, in the case of monotypic genera, (2) one species that possesses a suite of 'unique autapomorphies' (i.e., derived characters not shared by closely related species). Therefore, to demonstrate that [*T.*] *ridgwayi* is sufficiently divergent from all *Eupherusa* species as to warrant the erection of a monotypic genus (*Dicranurania*), one would need to identify a suite of unique autapomorphies in [*T.*] *ridgwayi* not found in the closest relatives of the [*T.*] *ridgwayi* + *Eupherusa* clade (i.e., the genera *Goldmania* Nelson, 1911, and *Microchera* Gould, 1858; see McGuire *et al*. 2014). Here, I applied this standard to scrutinise the diagnostic characters used by Sangster *et al.* (2023) to distinguish *Dicranurania* from *Eupherusa*.

Red tertials and secondaries.—Sangster *et al*. (2023) wrote that the 'Secondaries and tertials lack red [in *Dicranurania*, whereas the red coloration is] present in *Eupherusa*'. However, *Goldmania bella* (Nelson, 1912), a member of the likely sister group of the [*T.*] *ridgwayi* + *Eupherusa* clade (McGuire *et al*. 2014), also has red tertials and secondaries (Nelson 1912, Schulenberg & Sedgwick 2021). Therefore, this character is not *uniquely* synapomorphic to *Eupherusa*, as Sangster *et al*. (2023) claimed when they wrote that '*Eupherusa* can be distinguished from all other emeralds [tribe Trochilini] by the presence of red on the tertials.' Red tertials were either ancestral to the *Goldmania* + *Eupherusa* (*sensu lato*) clade (i.e., not derived in the [*T.*] *ridgwayi* + *Eupherusa* clade, and therefore unfit for use in diagnosing genera) or evolved independently more than once (i.e., also unfit to be diagnostic characters). Sangster *et al*. (2023) were adamant that any character that 'has evidently evolved multiple times independently in emerald hummingbirds carries little weight in grouping taxa into genera.' Therefore, by their own criteria, since red tertials are also lacking in Violet-capped Hummingbird *Goldmania violiceps* Nelson, 1911, Snowcap *Microchera albocoronata* (Lawrence, 1855), Coppery-headed Emerald *M. cupreiceps* (Lawrence, 1866), White-tailed Emerald *M. chionura* (Gould, 1851), and apparently all other emerald species, the *absence* of red tertials in *Dicranurania* must also be ancestral, or else it evolved multiple times independently. It is not a 'unique autapomorphy' of [*T.*] *ridgwayi*, as defined above, and therefore not valuable for diagnosing genera.

Tail shape.—Sangster *et al*. (2023) claimed that all four *Eupherusa* species have 'square' tails, and this formed the basis of their argument that the 'forked' tail of [*T.*] *ridgwayi* is a unique autapomorphy that supports its placement in a monotypic genus. However, they

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Figure 1. Plate 54 from the supplemental volume of *A monograph of the Trochilidae, or family of humming-birds* (Gould & Sharpe 1887), showing '*Callipharus nigriventris*' (= Black-bellied Hummingbird *Eupherusa nigriventris*). Note the bronzy-green colour and rounded shape of the tails (*contra* Sangster *et al*. 2023). The annotations at the bottom of the plate read: '*Callipharus nigriventris* / J. Gould & W. Hart del et lith. / Mintern Bros. imp.' Courtesy of Smithsonian Institution Libraries and Biodiversity Heritage Library.

apparently overlooked that *E. nigriventris* has a 'more strongly rounded' tail than other *Eupherusa* species (Ridgway 1911: 399)—decidedly not square—as demonstrated by Gould & Sharpe's (1887) original plate (Fig. 1), the lone *E. nigriventris* study skin in my sample (Fig. 2, DMNH 59857) and photos of live birds taken from an appropriate angle (e.g.., Macaulay Library, ML 449382291). Furthermore, within the clade containing *Eupherusa* and its nearest relatives, the forked tail is not unique to [*T.*] *ridgwayi*—both Pirre Hummingbird *Goldmania bella* and *G. violiceps* have forked tails—and forked tails also occur in other clades of emeralds, as well as in more distant clades within Trochilidae. Therefore, this homoplastic character ought to '[carry] little weight in grouping taxa into genera' (Sangster *et al*. 2023: 63).

Uppertail colour.—Sangster *et al*. (2023) claimed that all *Eupherusa* species have 'black' tails, evidently referring to the dorsal surface of the central rectrices, because the outer rectrices are mostly white in *Eupherusa*. On this basis, Sangster *et al*. (2023) argued that the 'mostly blue' tail of [*T.*] *ridgwayi* is a unique autapomorphy that distinguishes it from all *Eupherusa* species and supports the erection of a monotypic genus. This argument was apparently based on a misunderstanding because no *Eupherusa* species has a black tail.

In *E. cyanophrys* and *E. poliocerca*, adults have 'bright metallic bronze-green' tails (Fig. 3; Ridgway 1911: 398). In *E. eximia*, the tails are 'very dark greenish-bronze' (Elliot 1879: 213), 'dark bronze-green or greenish bronze' (Ridgway 1911: 394), and, in the subspecies *E. e.*

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Figure 2. Ventral view of the closed tail of an adult male Black-bellied Hummingbird *Eupherusa nigriventris* (DMNH 59857), showing the rounded tail shape (i.e., outer rectrices are progressively shorter than inner rectrices) (Matthew R. Halley)

Figure 3. Dorsal view of adult male hummingbirds in the genus *Eupherusa*, demonstrating variation in tail colour (left to right): Blue-capped Hummingbird *E. cyanophrys* (DMNH 25003); White-tailed Hummingbird *E. poliocerca* (DMNH25021); Black-bellied Hummingbird *E. nigriventris* (DMNH 59857); Stripe-tailed Hummingbird *E. eximia* (DMNH 24959); and Mexican Woodnymph [*Thalurania*] *ridgwayi* (DMNH 25029) (Matthew R. Halley)

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nelsoni Ridgway, 1910, 'dark dull bronzy, sometimes more dusky terminally' (Ridgway 1911: 396). In some specimens of *E. eximia* (e.g., DMNH 24959), there is even a dark bluish-green hue that resembles the tail of [*T.*] *ridgwayi* (Fig. 3). The tail of *E. nigriventris* has been described as 'dusky bronze or dull blackish glossed with bronze' (Ridgway 1911: 400) and 'purplish-black' (Elliot 1879: 211), but the adult male in my sample (DMNH 59857) has a dark greenish-bronze tail—certainly not 'black' (Fig. 3)—and the birds depicted by Gould & Sharpe (1887, Pl. 54) also had bronzy-green tails (Fig. 1).

By reducing the colourful variation in *Eupherusa* tails to 'black', Sangster *et al.* (2023) gave the false impression that the 'mostly blue' tail of [*T.*] *ridgwayi* was a unique autapomorphy that supported the erection of a monotypic genus. This error cannot be attributed solely to a lack of access to study skins of the relevant taxa, because the correct range of tail colour variation in *Eupherusa* was available in literature (e.g., Elliot 1879, Ridgway 1911), which Sangster *et al*. (2023) did not cite.

Undertail pattern.—Sangster *et al.* (2023: 64) stated that 'females of [*T.*] *ridgwayi* do not differ mainly in tail pattern from *Eupherusa*'. This seems to have been a typographical error (i.e., the word 'not' was mistakenly inserted). However, their assertion that the absence of white on the outer rectrices of [*T.*] *ridgwayi* males is a unique autapomorphy, which supports the erection of a monotypic genus, does not withstand scrutiny. Males of *Goldmania bella* and *G. violiceps* also lack white in the tail, and they do not form a clade with [*T.*] *ridgwayi* to the exclusion of *Eupherusa* (McGuire *et al*. 2014, Stiles *et al*. 2017). Therefore, the absence of white is either ancestral (i.e., not derived and therefore unfit for diagnosis) or independently evolved more than once, in which case it is not appropriate for diagnosing genera (Sangster *et al*. 2023: 63).

The lessons of *Callipharus* Elliot, 1879

Sangster *et al*. (2023) neglected to mention that, until Peters (1945: 76–77) placed *E. nigriventris* in *Eupherusa*, it was formerly classified in the monotypic genus *Callipharus* Elliot, 1879, because of its considerable divergence from *E. poliocerca* and *E. eximia*. Ridgway (1911: 400) was so convinced of the need to separate *E. nigriventris* from *Eupherusa*, that he wrote: 'Considering all its peculiarities, I feel sure that *Callipharus* should stand alone in any arrangement of the family that does not involve a very great reduction in the number of genera.' In addition to the diminutive size of 'the miniature *Eupherusa*' (Elliot 1879: 211), the tail of *E. nigriventris* is 'more strongly rounded [than other *Eupherusa* species, and] … [the] underparts [are] velvety black' (Ridgway 1911: 399). However, phylogenetic data suggest that *E. nigriventris* is nested within a clade of other *Eupherusa* species (McGuire *et al*. 2014), rendering the monotypic *Callipharus* unnecessary, and thereby expanding the morphological heterogeneity of *Eupherusa*.

Sangster *et al*.'s (2023) omission of this literature is notable because *Callipharus* set the precedent for the degree of morphological divergence that would be expected, if one were to attempt to carve out a monotypic genus for any species in the *Eupherusa* (*sensu lato*) clade. On morphological grounds, the case for recognising *Callipharus* (for *E. nigriventris*) is arguably stronger than the case for recognising *Dicranurania* (for [*T.*] *ridgwayi*).

Conclusion

The purportedly diagnostic characters used to distinguish *Dicranurania* from the genus *Eupherusa* (*sensu stricto*) were based on a mischaracterisation (homogenisation) of *Eupherusa* phenotypes, which made the characters of [*T.*] *ridgwayi* appear to be exaggerated. Sangster *et al*. (2023) also overlooked the precedent of the monotypic genus *Callipharus* Elliot, 1879,

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which further weakens their argument. Therefore, I propose that [*T.*] *ridgwayi* be included in a morphologically heterogenous *Eupherusa*, following Stiles *et al*. (2017), and that *Dicranurania* be demoted to the synonymy of *Eupherusa*.

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