Apalodermatinae, a new family-group name for the African trogons (Trogonidae), with clarification of the authorship of Harpactini

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ABSTRACT: Phylogenomic analysis provides strong evidence for reciprocal monophyly of African, New World and Asian trogons. The family-group name Trogonini is available for the New World trogons, whereas the clades of African and Asian trogons have been named 'Apaloderminae' Sibley and Ahlquist, 1985, and 'Harpactini' Sibley, Ahlquist and Monroe, 1986, respectively. However, we demonstrate that the latter two names did not meet the requirements of the ICZN Code (1999) and are therefore unavailable. We review past usage of family-group names of the trogons and show that no name is available for the clade of African trogons. To remedy this, we describe this taxon and make a family-group name available. We show that the correct authorship of the family-group name of the Asian trogons is Harpactini S.F. Baird (1851).

KEYWORDS: nomenclatural availability, phylogeny, Trogoniformes, Harpactidae, Harpacticidae, Harpacteinae.

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The trogons (Trogonidae Billberg, 1828) have long been regarded as a 'natural' (i.e., monophyletic) group and subdivisions above the species level have been indicated with genus limits (e.g., Sharpe, 1900; Peters, 1945; Wolters, 1976). Supra-generic relationships among the trogons only began to be documented since the mid-1980s using molecular studies. In this note, we review the evidence for phylogenetic relationships among the major groups of trogons, discuss possible ways to represent this information in a classification, and review the family-group nomenclature.

SYSTEMATICS

Phylogenies based on DNA-DNA hybridisation data placed the African genus *Apaloderma* Swainson, 1833, as the sister taxon of the New World genus *Trogon* Brisson, 1760, and the Asian genus *Harpactes* Swainson, 1833 (Sibley & Ahlquist, 1985; Sibley *et al*., 1988; Sibley & Ahlquist, 1990). These data showed a deep divergence between African, New World and Asian trogons, which led the authors to place these in two subfamilies, one containing the African trogons and the other containing the New World and Asian trogons (Sibley *et al*., 1988; Sibley & Ahlquist, 1990). Reciprocal monophyly of African, New World and Asian trogons could not be investigated because only one to three species per genus were included.

A study of mitochondrial cytochrome-*b* sequence data of 20 trogon species recovered African, New World and Asian trogons as three reciprocally monophyletic groups (Espinosa de los Monteros, 1998). African and Asian trogons formed two well-supported monophyletic groups, whereas support for monophyly of New World trogons was poor and the clade was

not recovered in all analyses. The African clade was sister to the New World and Asian trogons but this, again, was poorly supported.

Johansson and Ericson (2005) analysed a data set comprising both mitochondrial (cytochrome-*b* and 12S rRNA) and nuclear (myoglobin intron 2, beta-fibrinogen intron 7 and G3PDH) DNA sequences of 13 trogon species, plus outgroups. African and Asian trogons formed two well-supported monophyletic groups, whereas support for monophyly of New World trogons was moderate. The clade of African species was sister to a clade comprising New World and Asian trogons, with high bootstrap support.

Analysis of a multi-locus DNA sequence data set, comprising the mitochondrial cytochrome-*b* gene and the nuclear RAG-1 exon of 28 trogon species, plus outgroups, recovered a phylogeny in which African and Asian trogons formed two well-supported monophyletic groups (Moyle, 2005). However, New World trogons did not form a monophyletic group (Moyle, 2005). The phylogeny obtained in this study placed two New World genera (*Euptilotis* Gould, 1858, and *Pharomachrus* de la Llave, 1832) sister to all other trogons, but with poor support. A sister-group relationship of African and Asian trogons was also poorly supported.

Another multi-locus study was based on sequences of two mitochondrial genes (ND2 and ND3) and two nuclear gene regions (G3PDH and TGFb5) of 29 trogon species, plus outgroups (Hosner *et al*., 2010). The African species formed a well-supported clade, but New World and Asian trogons did not form reciprocally monophyletic groups and their relationships were poorly supported. The New World (Caribbean) genus *Priotelus* G.R. Gray, 1840 was sister to all other trogons, but with poor support.

Oliveros *et al*. (2020) used 3581 genome-wide ultra-conserved elements (UCEs) to reconstruct phylogenetic relationships among 12 species of trogons, plus outgroups. African, New World and Asian trogons formed three well-supported monophyletic groups, of which the clade with African species was sister to the New World and Asian trogons (with high support). The divergence between African and New World/Asian trogons was estimated at 23 million years ago (mya), whereas the split between the New World and Asian trogons was estimated at 22 mya (Oliveros *et al*., 2020).

TAXONOMY

Taxonomic recognition of higher-level groups is justified now that the African, New World and Asian trogons have been documented, with strong support, as reciprocally monophyletic groups (Oliveros *et al*., 2020). The same three clades had already been found in phylogenetic studies based on mitochondrial DNA data (Espinosa de los Monteros, 1998) and combined mitochondrial and nuclear DNA data (Johansson & Ericson, 2005), but support for the New World clade was poor to moderate. The early divergence of African trogons, followed by a divergence between New World and Asian trogons, is supported by multiple studies (Sibley & Ahlquist, 1990; Espinosa de los Monteros, 1998; Johansson & Ericson, 2005; Oliveros *et al*., 2020), and thus may also be recognized taxonomically.

We maintain the name Trogonidae for the extant (crown-group) trogons and reserve the name Trogoniformes for a more inclusive clade that also includes extinct stem-group representatives, including *Eotrogon* Mayr *et al*., 2023, *Septentrogon* Kristoffersen, 2002, *Masillatrogon* Mayr, 2009 and *Primotrogon* Mayr, 1999 (see Mayr *et al*., 2023). This preserves current usage of the names Trogonidae and Trogoniformes (Mayr, 2017).

African, New World and Asian trogons have been recognized as three subfamilies (Collar, 2001; Gaudin, 2023). An argument in favour of this arrangement is that the divergence (split)

between African and New World/Asian trogons occurred close to that between New World and Asian trogons (Oliveros *et al*., 2020). An alternative arrangement recognizes two subfamilies (one for African trogons and another for the clade comprising New World and Asian trogons) with a further subdivision of the latter subfamily into two tribes (one each for New World and Asian trogons) (Sibley *et al*., 1988; Sibley & Ahlquist, 1990; Espinosa de los Monteros, 1998; Johnsgard, 2000). We prefer the latter arrangement because this is a more explicit representation of current knowledge of relationships (i.e., branching order) than recognition of three subfamilies. However, both taxonomic arrangements are consistent with the evidence, and the choice between these arrangements is arbitrary.

A third arrangement, which places African and Asian trogons in a single subfamily and recognizes two subfamilies for the New World trogons, was proposed by Forshaw (2009). However, this arrangement is inconsistent with current knowledge of phylogenetic relationships among trogons, because African and Asian trogons do not form a clade to the exclusion of New World trogons.

NOMENCLATURE

To be available, every new name published after 1930 must be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon (Article 13.1.1; ICZN, 1999), or be accompanied by a bibliographic reference to such a published statement (Article 13.1.2), or be proposed expressly as a new replacement name (*nomen novum*) for an available name (Article 13.1.3). Family-group names published after 1999 must also be accompanied by an explicit indication that the name is intentionally new (e.g., 'subfam. nov.' or 'new subfamily', Article 16.1; ICZN, 1999), and be accompanied by a citation of the type genus (Article 16.2; ICZN, 1999).

The family-group name Trogoninae is available for the clade formed by New World and Asian trogons, and the name Trogonini is available for the New World trogons. Bock (1994) considered 'Harpactini' Sibley, Ahlquist and Monroe, 1986 as an available name. However, the publication by Sibley *et al*. (1986: 10) lacked a description or definition, and also lacked a bibliographic reference to such a statement, and thus failed to meet Articles 13.1.1 and 13.1.2 (ICZN, 1999). As a result, 'Harpactini' Sibley, Ahlquist and Monroe, 1986 is a *nomen nudum*. However, a much older family-group name is available because S.F. Baird (1851: 323) introduced the name Harpactinae. Thus, the correct authorship of the family-group name of the Asian trogons is:

Harpactini S.F. Baird, 1851: 323.

Diagnosis: The species in this clade differ from those in *Apaloderma* and Trogonini by a combination of (*i*) upper mandible (maxilla) notched but non-serrated; (*ii*) nostrils oval, lacking opercula, and largely hidden by anteriorly oriented bristles; (*iii*) tarsus partially feathered; (*iv*) rectrices long and broad; (*v*) central rectrices with distinctly truncated tips in adults; and (*vi*) outer three pairs of rectrices graduated in length and extensively white to (rarely) pinkish or yellowish (Johnsgard, 2000).

Type genus: *Harpactes* Swainson, 1833.

Contents: two genera, *Apalharpactes* Bonaparte, 1854 (two species) and *Harpactes* (ten species) (e.g., Dickinson & Remsen, 2013; Gill *et al*., 2023). *Apalharpactes* is sometimes included in *Harpactes* (e.g., Espinosa de los Monteros, 1998; Johnsgard, 2000; Forshaw, 2009).

ZooBank LSID for Harpactinae: 3186D482-12E9-478C-BA04-F75CCF496146

The name of the African trogons is more problematic. Bock (1994) considered 'Apalloderminae' Sibley and Ahlquist, 1985 as an available name, and emended its spelling to 'Apalodermatidae'. However, Sibley and Ahlquist (1985: 115, 133) included neither a description nor diagnosis that would satisfy Article 13.1.1 (ICZN, 1999), nor any reference to a source that included such a description or diagnosis (Article 13.1.2; ICZN, 1999). In a preliminary classification of birds based on the results of DNA-DNA hybridisation, Sibley *et al*. (1986: 10) used the name 'Apalloderminae' but again this name lacked a description or definition, and lacked a bibliographic reference to such a statement, and thus failed to meet Articles 13.1.1 and 13.1.2 (ICZN, 1999). Sibley *et al*. (1988: 416) and Sibley and Ahlquist (1990: 351) also used the name 'Apalloderminae' for African trogons, and similarly lacked a description or definition, and a bibliographic reference to such a statement, for the two groups.

Espinosa de los Monteros (1998: 951) presented a classification of the trogons, which included the name 'Apalloderminae'. His paper includes a figure in which the character states of trogon species were coded, but not presented in words (p. 949), which fails to meet Article 13.1.1 (ICZN, 1999). The paper includes the statement that "The plesiomorphic state for these two regions [head, rump] is brown in the Asian trogons and green in the African and New World trogons" (p. 950). This statement did not validate the name 'Apalloderminae' because the relevant phrase referred to character states (green head and green rump) that are shared between African and New World trogons and thus are not characters that are purported to differentiate the African trogons.

Johnsgard (2000: 27) used the family-group names 'Apalloderminae' and 'Apalodermini' for the African trogons; Collar (2001: 80) recognized the family-group name 'Apalodermatinae' for African trogons; and Forshaw (2009: 37) used the family-group names 'Apalodermatinae' for African and Asian trogons, and 'Apalodermatini' for African trogons. All three authors included a description of the distinctive character states of the African trogons that satisfied Article 13.1.1 (ICZN, 1999). However, all three publications lacked an explicit indication that these names were intentionally new. Thus, these publications did not satisfy Article 16.1 (ICZN, 1999). The family-group names used in these works for the African trogons were therefore *nomina nuda*.

We conclude that no family-group name is available for the African trogons. To remedy this, we propose:

Apalodermatinae new subfamily

Diagnosis: The species in this clade differ from those in Trogonini and Harpactini by the presence of a sulcus rather than a canal for the tendon of musculus flexor hallucis longus (Mayr, 2016; Mayr *et al*., 2023), and by the combination of (*i*) strongly coloured bare facial lappets; (*ii*) two anterior toes not fused basally; (*iii*) serrations on the cutting edges of the upper mandible (maxilla) weak or vestigial; (*iv*) central tail feathers without black tip (Johnsgard, 2000; Forshaw, 2009); (*v*) absence of a white pectoral line dividing chest and belly colour; (*vi*) red belly; (*vii*) presence of white spots on the secondary feathers; (*viii*) mantle and back green; (*ix*) colour of the head same as mantle and back; and (*x*) colour of the rump same as back (Espinosa de los Monteros, 1998).

In addition, Hosner *et al*. (2010) identified two synapomorphic insertions or deletions (of 14 bp and 1 bp) for *Apaloderma* (and hence Apalodermatinae) among their nuclear DNA sequences but provided no further details. Our alignments, using MUSCLE (Edgar, 2004) as implemented in MEGA7 (Kumar *et al*., 2016), of the G3PDH and TGFb5 data sets of Hosner *et al*. (2010), as made available on GenBank, show that in the G3PDH locus there is a 14 bp deletion (at position 103 of the *A. aequatoriale* sequence, GenBank accession number HQ379971) and a

1 bp insertion (at position 161) that are synapomorphic for the three species of *Apaloderma* (and hence Apalodermatinae).

Determination of stem: the correct stem is found by deleting the case ending from the genitive singular, classical Greek *derma* n. (skin) giving *dermat-os*; Article 29.3.1 (ICZN, 1999).

Type genus: *Apaloderma* Swainson, 1833.

Contents: one genus (*Apaloderma*) with three species: *A. narina* (Stephens, 1815); *A. aequatoriale* Sharpe, 1901; and *A. vittatum* Shelley, 1882 (e.g., Dickinson & Remsen, 2013; Gill *et al*., 2023). The latter species is sometimes placed in the genus *Heterotrogon* Richmond, 1895 (e.g., Peters, 1945; Gaudin, 2023).

ZooBank LSID for new subfamily: D8A06EC1-D7BB-428C-BB45-3FD6373B480A

Taking these changes into account, the higher-level classification of the trogons becomes as follows:

Trogonidae Billberg, 1828
- Apalodermatinae Sangster, Gregory & Dickinson **subfam. nov.**
- Trogoninae Billberg, 1828
  - Harpactini S.F. Baird, 1851
  - Trogonini Billberg, 1828

DISCUSSION

The family-group name Harpactini S.F. Baird, 1851, would appear to represent a junior homonym of the crustacean name 'Harpactidae' Dana, 1846: 152. However, the latter name was misspelled because the type genus of this name was *Harpacticus* H. Milne-Edwards, 1840 (Dana, 1846: 152). According to Article 35.4.1 (ICZN 1999), such misspellings must be corrected. Indeed, the family-group name of the crustacean taxon has been corrected to Harpacticidae Dana, 1846 (e.g., Walter & Boxschall, 2023). As a result, Harpactini S.F. Baird, 1851, is not pre-occupied by 'Harpactidae' Dana, 1846. Unfortunately, the erroneous name 'Harpactidae' is sometimes still used for the crustacean taxon (e.g., Bao *et al*., 2008; Kim *et al*., 2013; Jørgensen *et al*., 2019).

Cooke (1965) introduced the family-group name 'Harpactini' for a group of spiders (Arachnida) based on *Harpactes* Templeton, 1835. However, the generic name *Harpactes* Templeton, 1835, is preoccupied by *Harpactes* Swainson, 1833 (Aves) and has been replaced by *Harpactea* Bristowe, 1939. Thus, the family-group name 'Harpactini' Cooke, 1965, was based on a genus that is a junior homonym and is therefore invalid (Article 39; ICZN, 1999). In addition, Cooke (1965) lacked a description or definition for the name 'Harpactini', and also lacked a bibliographic reference to such a statement, rendering the name 'Harpactini' Cooke, 1965, a *nomen nudum* (Article 13.1.1; ICZN, 1999). *Harpactea* is currently classified in the subfamily Harpacteinae Deeleman-Reinhold and Deeleman, 1988 (e.g., Chatzaki & Arnedo, 2006; Platania *et al*., 2020). The latter name is not preoccupied by Harpactini S.F. Baird, 1851, due to a one-letter difference in the stem of the two names (i.e., Harpacte- and Harpact-) (Article 55.4; ICZN, 1999).

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