

## On the phylogenetic relationships of trogons (Aves, Trogonidae)

Gerald Mayr

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Although trogons (Aves, Trogonidae) are well characterized by the possession of heterodactyl feet, their phylogenetic relationships to other extant birds still are only poorly understood. Molecular studies did not show conclusive results and there are amazingly few comparative studies of the anatomy of trogons. Virtually the only hypothesis on trogon relationships that was supported with derived morphological characters is a sister group relationship to alcediniform birds (bee-eaters, kingfishers, and allies), which share a derived morphology of the columella (ear-ossicle) with trogons. However, in this study a very similar columella is reported for the oilbird (Steatornithidae) and additional previously unrecognized derived osteological characters are presented, which are shared by trogons and oilbirds. A numerical cladistic analysis of 28 morphological characters also resulted in monophyly of Trogonidae and Steatornithidae, although the corresponding node was not retained in a bootstrap analysis.

G. Mayr, *Forschungsinstitut Senckenberg, Sektion für Ornithologie, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany. E-mail Gerald.Mayr@senckenberg.de*

Concerning their phylogenetic relationships, trogons (Trogonidae) certainly are among the most enigmatic taxa among the “higher landbirds”, i.e. the anomalognathous birds of Garrod (1874) which are characterized by the absence of the musculus ambiens. Trogons are small to medium-sized birds which have a pantropic distribution and feed on insects or fruits. They are distinguished from all other birds by a unique toe arrangement, the so-called heterodactyl foot in which the second toe is permanently retroverted (see Collar 2001 for a survey on the life history and biology of trogons). They are usually classified into a monotypic taxon Trogoniformes and, as noted by Sibley and Ahlquist (1972), unlike “other problem groups [...] have received little attention from systematists. No comprehensive study of the anatomy of trogons has been undertaken with the purpose of making critical comparisons with all key groups”. Consequently, there are very few hypotheses on the phylogenetic relationships of trogons which are supported with derived morphological characters (see reviews in Sibley and Ahlquist 1990, Espinosa de los Monteros 2000).

Feduccia (1977) found that trogons share a derived morphology of the columella with the Alcediniformes, i.e. a clade including bee-eaters (Meropidae), kingfish-

ers (Alcedinidae), todies (Todidae), and motmots (Momotidae). He considered the feature to be a synapomorphy of these taxa, but noted that a virtually identical columella also occurs in suboscine Passeriformes. Maurer and Raikow (1981) proposed a phylogeny of “coraciiform” birds based on appendicular myology and also concluded that their analysis “supports inclusion of the Trogonidae in the Coraciiformes, specifically within the subinfraorder Alcedinides, thus allying the trogons most closely with the assemblage of todies, motmots, bee-eaters, and kingfishers”. However, the two characters they listed in order to support this classification (Maurer and Raikow 1981: tables 1 and 2) are both absent in trogons, and likewise one of the two characters which they listed in order to support monophyly of a clade including hoopoes (Upupidae), wood-hoopoes (Phoeniculidae), trogons, and the Alcediniformes is absent in trogons (the other is absent in todies). Nevertheless, Maurer and Raikow (1981) even tentatively considered trogons to be the sister taxon of bee-eaters and kingfishers (Fig. 1), because these taxa have lost the musculus flexor cruris lateralis pars accessoria.

A numerical cladistic analysis of the phylogenetic relationships between trogons and members of the

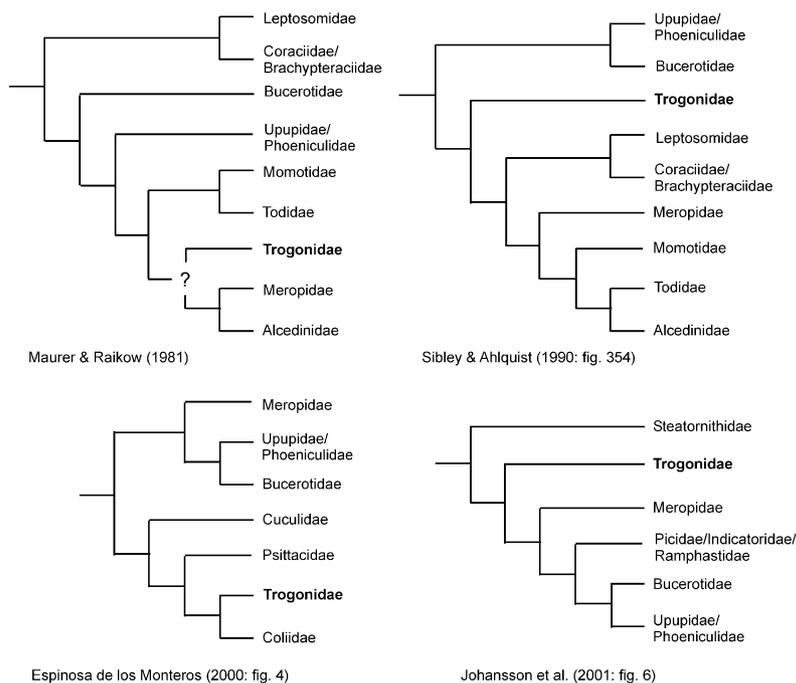


Fig. 1. Some hypotheses on the phylogenetic relationships of trogons in comparison (see text).

“Coraciiformes” (*sensu* Wetmore 1960) by Mayr (1998), which also included the myological data of Maurer and Raikow (1981), did not support monophyly of Trogonidae and Alcediniformes. This analysis resulted in monophyly of Trogonidae and Upupiformes, i.e. a clade including hornbills (Bucerotidae), hoopoes, and wood-hoopoes, but was restricted to “coraciiform” birds only and thus insufficiently comparative.

The molecular evidence for a phylogenetic position of the Trogonidae is inconclusive. The DNA–DNA hybridization study of Sibley and Ahlquist (1990) resulted in a sister group relationship between trogons and a clade including rollers (Coraciidae and Brachypteraciidae), cuckoo-rollers (Leptosomidae), and the Alcediniformes (Fig. 1). Although in most of the melting curves underlying their analysis the curves of trogons are not particularly close to the above taxa, Sibley and Ahlquist (1990) concluded that at “this point we have no reason to assume that the owls, nightjars, or turacos are more closely related to trogons than the groups with which they have long been associated, but this possibility must be considered”. Indeed, an analysis of the 12S mitochondrial rDNA by Mindell et al. (1997: Fig. 8.5) supported monophyly of trogons and nightjars (Caprimulgidae) if all characters were equally weighted; if the transversions were given higher weight than the transitions, trogons were the sister taxon of owls. However, a molecular analysis of complete cytochrome b and nearly complete 12S ribosomal RNA sequences by Espinosa de los Monteros (2000) resulted in sister group relationship between trogons and mousebirds (Coliidae) or trogons and a clade including cuckoos

(Cuculidae) and hoopoes, depending on the weighting mode applied to the data (Fig. 1; this analysis yielded some very odd results as, for example, paraphyly of Cuculidae and Alcedinidae respectively). An analysis of DNA sequences of nuclear and mitochondrial ribosomal genes by van Tuinen et al. (2000) even showed trogons and cranes (Gruidae) to be monophyletic. A recent and fairly comprehensive analysis of DNA sequences of two nuclear, protein-coding genes by Johansson et al. (2001) resulted in a sister group relationship between trogons and a clade including bee-eaters, Upupiformes and Piciformes (woodpeckers and allies), with the oilbird (*Steatornithidae*) being the sister taxon of this clade (Fig. 1). Although current molecular methods do not provide unequivocal evidence concerning the systematic relationships of trogons, none of the above mentioned molecular studies supported monophyly of trogons and alcediniform birds.

In this study, previously unrecognized derived osteological characters are presented which are shared by trogons and the oilbird, *Steatornis caripensis*, the sole extant representative of the Neotropical *Steatornithidae*. Oilbirds are nocturnal frugivores which are currently included in the paraphyletic (see Mayr 2002) “Caprimulgiformes” (see Thomas 1999 for a survey on the biology of these birds). Although a closer relationship between trogons and the oilbird was already considered by Fürbringer (1888) and Verheyen (1956), who placed the Trogonidae between nightjars and the oilbird in his linear classification, this has not been supported with derived characters so far.

## Material and methods

Osteological comparisons with representatives of all higher avian taxa are based on skeletons in the ornithological department of Forschungsinstitut Senckenberg, including the following species of trogons: *Harpactes ardens*, *H. oreskios*, *H. reinwardtii*, *Pharomachus mocinno*, *P. patoninus* and *Trogon viridis*. All non-osteological characters were taken from the literature. Anatomical terminology follows Baumel and Witmer (1993) and Vanden Berge and Zweers, (1993). Since monophyly of the “Coraciiformes” *sensu* Wetmore (1960) has not yet been conclusively shown (Burton 1984, Mayr 1998, Johansson et al. 2001), I here use the terms Alcediniformes for the taxon including Meropidae, Alcedinidae, Todidae, and Momotidae, and Upupiformes for the taxon including Bucerotidae, Upupidae, and Phoeniculidae (see Mayr 1998 and below). The term Cypselomorphae is used for the monophyletic (see Mayr 2002) taxon which includes the Caprimulgiformes *sensu stricto* (Caprimulgidae and Nyctibiidae) and the Apodiformes *sensu lato* (Aegothelidae, Apodidae, Hemiprocnidae, and Trochilidae).

A matrix of 28 morphological characters (see Appendices I and II for character descriptions and character matrix) was subjected to a cladistic analysis with the phylogenetic software PAUP, version 3.1 (Swofford 1993). The shortest tree was found with the exhaustive search option and the delayed transformation (DELTRAN) mode. The consistency index (CI), retention index (RI), and rescaled consistency index (RC) were calculated and the robustness of the tree was tested with a bootstrap analysis of 1000 replicates; multistate characters were coded as “polymorphisms”. Outgroup comparisons were made with tinamous (Tinamidae) which are generally considered to be a sister taxon of all neognathous birds (e.g., Cracraft and Clarke 2001).

## Results

### Monophyletic taxa within “higher landbirds”

Monophyly of the Upupiformes (Bucerotidae, Phoeniculidae, and Upupidae) is well supported both with morphological evidence and by most molecular analyses (Burton 1984, Sibley and Ahlquist 1990, Harshman 1994, Mayr 1998, Espinosa de los Monteros 2000, Johansson et al. 2001). Shared derived features are, among others (Mayr 1998): (1) mandible with rectangular cross section in area of pars symphysialis and more or less well developed processus retroarticulares, (2) extremitas omalis of furcula widened and with short processus acromialis, (3) hypotarsus, tendon of musculus flexor hallucis longus enclosed in bony canal, (4) musculus flexor metacarpi ulnaris attached to os metacarpale minus (usually this muscle is attached to

the os metacarpale majus, see Stegmann 1965), (5) musculus pterygoideus with “retractor palatini” slip (Burton 1984), and (6) musculus pectoralis, pars propatagialis longus tendinous (Maurer and Raikow 1981).

Monophyly of the Alcediniformes (Meropidae, Alcedinidae, Todidae, and Momotidae) also is well supported with derived morphological characters, including: (1) skull with distinct nasofrontal hinge, (2) columella with large, hollow, bulbous basal and footplate area exhibiting a large fenestra on one side (Feduccia 1977, Fig. 2E–G), (3) scapi clavicularae of furcula very narrow at extremitas sternalis, (4) carpometacarpus with os metacarpale minus distinctly exceeding os metacarpale majus in length, (5) first phalanx of hallux with proximal end greatly widened (Mayr 1998: Fig. 20F), (6) second and third toe coalescent for part of their length, (7) tendon of musculus flexor hallucis longus not supplying hallux (Maurer and Raikow 1981), and (8) musculus abductor digiti II reduced (Maurer and Raikow 1981).

Mayr (2002) further showed that the “Caprimulgiformes” *sensu* Wetmore (1960) are paraphyletic and established monophyly of a clade including nightjars (Caprimulgidae), potoos (Nyctibiidae), owl-nightjars (Aegothelidae), swifts (Apodidae), tree swifts (Hemiprocnidae), and hummingbirds (Trochilidae). The following derived features are shared by members of this clade, which is equivalent to the Cypselomorphae of Huxley (1867): (1) ossa palatina with distinct proces-

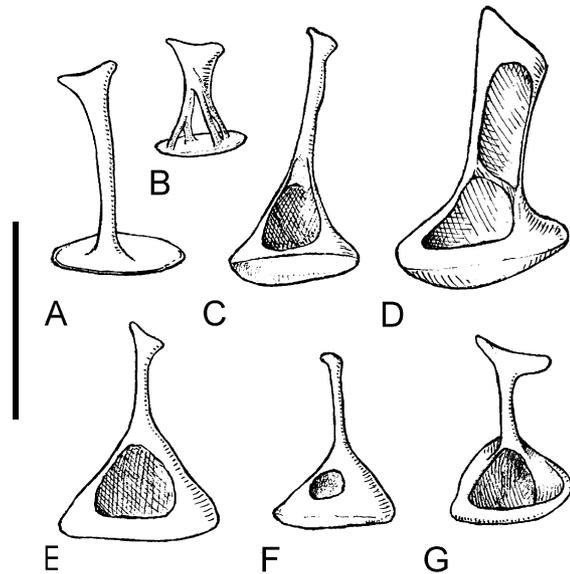


Fig. 2. Columella of A, *Chrysolophus pictus*, Phasianidae (left, primitive morphology which is found in most birds); B, *Colinus colius*, Coliidae (left); C, *Pharomachus pavoninus*, Trogonidae (left); D, *Steatornis caripensis*, Steatornithidae (right); E, *Momotus momota*, Momotidae (right); F, *Merops nubicus*, Meropidae (left); G, *Halcyon chloris*, Alcedinidae (left). The scale bar equals 2 mm.

sus rostrales, (2) processus orbitalis of quadratum strongly reduced, (3) condylus caudalis of quadratum completely reduced, condylus lateralis separated from elongate condylus medialis by a deep but narrow furrow, (4) beak very wide with narial openings large and reaching almost to the tip of the beak; distal part of rami mandibulae very narrow, and (5) fossa dorsalis of phalanx proximalis digiti majoris divided into two depressions by an oblique bulge.

In the analysis of Mayr (2002) the systematic relationships of the Steatornithidae, which are generally included in the “Caprimulgiformes”, remained unresolved.

#### Derived characters shared by Trogonidae and Alcediniformes (numbers in parentheses refer to characters in Appendix I)

1. Columella with large, hollow, bulbous basal and footplate area exhibiting a large fenestra on one side (character 6; Fig. 2C).
2. Skull with distinct naso-frontal hinge (character 1). Although certainly derived within neornithine birds, this feature is also present in many other avian taxa, e.g. Steatornithidae, Podargidae, Strigiformes, and Psittaciformes.
3. Feet syndactyl, i.e. third and fourth toe coalescent for part of their length (character 16). This feature is also found in all Upupiformes except the genus *Bucorvus*, the passeriform genus *Rupicola* (Cotingidae), and at least some Trochilidae. In alcediniform birds, the second toe is further also connected to the third over part of its length (see below).

#### Derived characters shared by Trogonidae and Steatornithidae (numbers in parentheses refer to characters in Appendix I)

1. Columella with large, hollow, bulbous basal and footplate area which exhibits a large fenestra on one side (character 6; Fig. 2D): The columella of *Steatornis* has not been described so far and differs mainly from that of trogons in that the ascending strut is hollow and widened, which probably is an autapomorphic feature of oilbirds that might be functionally related to the unique echolocation of these birds (see Thomas 1999). Because the bulbous footplate also occurs in taxa without an echolocating system (see above), it is more likely to be of phylogenetic rather than functional significance.
2. Skull with distinct naso-frontal hinge (character 1; see above).
3. Distal end of humerus with deep and sharply delimited fossa musculi brachialis (character 11; Fig. 3A, B). I found an equally marked fossa m. brachialis

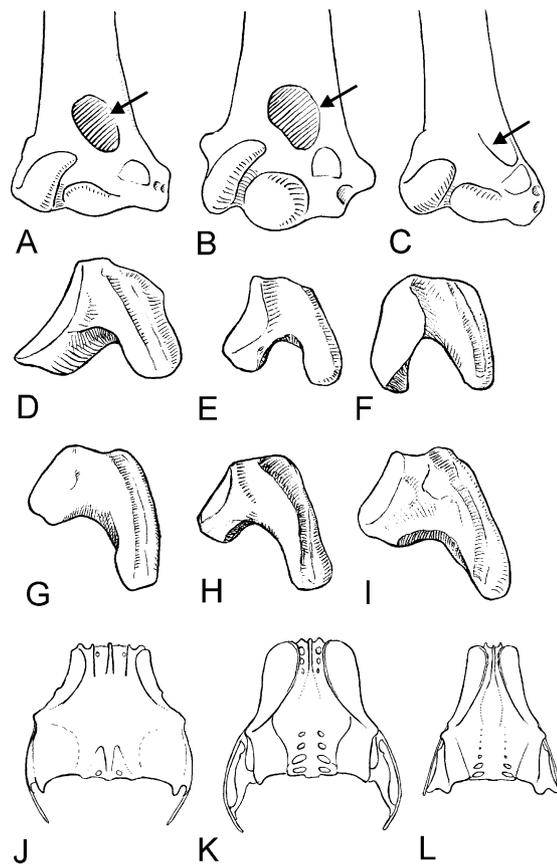


Fig. 3. Distal end of right humerus (A–C), right os carpi ulnare (D–I), and pelvis (J–L) of A, *Harpactes oreskios*, Trogonidae; B, *Steatornis caripensis*, Steatornithidae; C, *Halcyon chloris*, Alcedinidae; D, *Crypturellus cinnamomeus*, Tinamidae (probably represents the primitive morphology within neornithine birds); E, *Chrysolophus pictus*, Phasianidae; F, *Halcyon chloris*, Alcedinidae; G, *Nyctibius griseus*, Nyctibiidae; H, *Steatornis caripensis*, Steatornithidae; I, *Harpactes reinwardtii*, Trogonidae; J, *Steatornis caripensis*, Steatornithidae; K, *Harpactes reinwardtii*, Trogonidae; L, *Halcyon chloris*, Alcedinidae. The arrows indicate the fossa musculi brachialis; slightly schematic and not to scale.

only in *Batrachostomus* (Podargidae), and hornbills (Bucerotidae). The distal end of the humerus of *Steatornis* otherwise strongly differs from that of trogons and virtually all other “higher landbirds”, which might be functionally related to the hovering flight of these birds (see Olson 1987).

4. Os carpi ulnare with crus longum being much longer than crus breve (character 12; Fig. 3H, I). I otherwise found this feature only in the Cypselomorphae, the Barn-Owl *Tyto alba* (Strigiformes), doves (Columbidae), some parrots (Psittacidae) and herons (Ardeidae). It is absent in all putatively basal extant birds, as tinamous (Tinamidae) and Gallanseres (fowl and waterfowl). Because of its occurrence in a number of taxa with completely different flight styles, this feature probably also is of phyloge-

netic rather than functional significance (although it certainly evolved more than once in the above listed birds).

5. Pelvis very wide in mediolateral direction, width across antitrochanters as much or more than length of synsacrum (character 13; Fig. 3J, K). The pelvis of *Steatornis* otherwise exhibits a highly derived morphology and differs from the pelvis of all other extant birds.

The last two characters might be synapomorphies of a more comprehensive clade including Trogonidae, Steatornithidae, and Cypselomorphae (see Fig. 4).

### Results of the phylogenetic analysis with PAUP 3.1

Analysis of the character matrix in Appendix II with PAUP 3.1 resulted in two most parsimonious trees (Length = 68, CI = 0.65, RI = 0.53, RC = 0.34) in both of which trogons are sister taxon of the Steatornithidae (Fig. 4). The corresponding node collapsed, however, in the bootstrap analysis. Two of the above listed derived characters shared by Trogonidae and Steatornithidae, i.e. characters 12 and 13, were optimized as synapomorphies of the taxon (Cypselomorphae + (Trogonidae + Steatornithidae)).

The phylogenetic tree resulting from the analysis with PAUP 3.1 is depicted here mainly to show that monophyly of the taxon (Trogonidae + Steatornithidae) is the most parsimonious hypothesis based on the

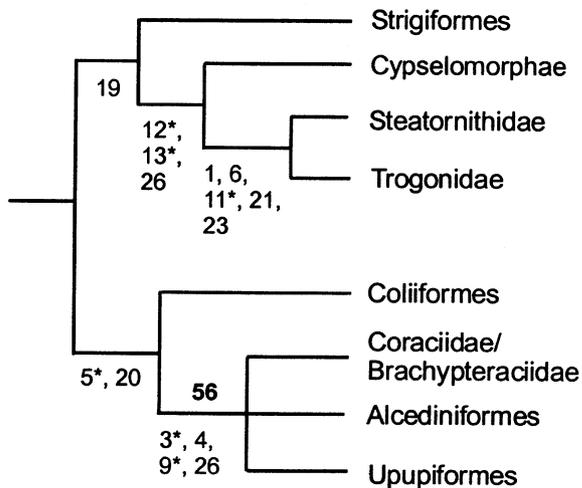


Fig. 4. Strict consensus tree of two most parsimonious trees resulting from a cladistic analysis of the character matrix in Appendix II with PAUP 3.1 (Length = 68, CI = 0.65, RI = 0.53, RC = 0.34). Characters supporting the nodes in both of the resulting trees are indicated (the numbers refer to Appendix I, the asterisked characters have CI = 1.0). The value in boldface indicates bootstrap support of the single node that did not collapse in the bootstrap analysis (1000 replicates)

characters tabulated in Appendix II. It should not be regarded as a definitive phylogeny of all taxa included in the analysis, which would require the inclusion of many additional putatively related taxa.

### Discussion

Despite opposite statements in some ornithological textbooks (e.g. Eisenmann 1985, Collar 2001), there is no convincing evidence for a closer relationship between trogons and any of the “coraciiform” taxa. For example, the two features that were listed by Maurer and Raikow (1981) in order to support inclusion of trogons into the “Coraciiformes” (loss of musculus ambiens and m. iliofemoralis externus) also occur in Steatornithidae and Cypselomorphae (Hoff 1966), as well as in passeriform and piciform birds (Maurer and Raikow 1981). Apart from the derived morphology of the columella, which in a slightly modified form is reported here also for the oilbird, trogons and alcediniform birds are very different in most aspects of their osteology. Moreover, in all alcediniform birds the second toe, which is retroverted in trogons, is coalescent with the third toe along part of its length. As Maurer and Raikow (1981) noted there is “the irksome question of why heterodactyly should arise in a group situated in the midst of an assemblage of syndactyl forms, as the two conditions are regarded as alternative perching specializations”. In fact, except for jacamars (Galbulidae), there is no other avian taxon in which the second toe is as firmly connected to the third as in the Alcediniformes, and it would be curious if exactly these birds are the sister group of the heterodactyl trogons.

The only diagnostic feature listed by Mayr (1998) in order to support monophyly of Trogonidae and Upupiformes is the tendinous pars propretagialis longus of musculus pectoralis (Maurer and Raikow 1981); this part of m. pectoralis is completely reduced in the Steatornithidae (Hoff 1966). Burton (1984) further mentioned a “retractor palatini” slip of musculus pterygoideus as a derived feature shared by trogons and Upupiformes but stated that “it appears to be of different morphological origin”.

The position of trogons in the melting curves underlying the DNA–DNA hybridization studies of Sibley and Ahlquist (1990) is equivocal. However, in the few figures in which trogons are compared to both alcediniform birds and taxa of the Cypselomorphae, trogons are closer to the latter (Figs. 59 and 73). Unfortunately, the melting curves of trogons and the oilbird are not directly compared in any of the figures.

Although there is a large contrast between the brightly colored trogons and the drab oilbird, plumage coloration of adult birds has little significance concerning higher level relationships, and a similar variation in

plumage coloration is found in various unquestionably closely related taxa, as wrynecks (Jyngidae) and toucans (Ramphastidae), or jacamars (Galbulidae) and puffbirds (Bucconidae). Juvenile trogons exhibit distinct rows of buffy spots on the wing coverts (Collar 2001) which also occur in adults of the Steatornithidae (and several taxa of the Cypselomorphae) but are absent in “coraciiform” birds. Trogons, the oilbird, and all taxa of the Cypselomorphae except swifts and hummingbirds further possess distinct rictal bristles at the base of the beak which are absent in the “Coraciiformes”. Trogons and upupiform birds nest in tree holes, whereas alcediniform birds and ground rollers usually dig burrows in earth banks or cliffs. The oilbirds breed in caves and among the Cypselomorphae only owl night-jars nest in tree holes (Holyoak 1999). However, nesting in tree-holes is found in many unrelated avian taxa, as ducks, woodpeckers and many passeriform birds, and thus probably also is of little phylogenetic value.

Trogons resemble the oilbird in overall morphology of several skeletal elements, e.g. the mandible, the palate and the femur, but there are also some distinct differences between the two taxa. The coracoid of oilbirds, for example, more closely resembles that of certain ciconiiform birds (especially the hamerkop, *Scopus umbretta*) than that of any other extant “higher landbird”. The morphology of the tarsal joint (distal end of tibiotarsus and proximal end of tarsometatarsus) of oilbirds is very different from that of trogons, but differs also from virtually all other extant birds. Oilbirds are further characterized by a unique modification of the syrinx, the so-called “bronchial” syrinx (see Garrod 1873: Fig. 3), which is here considered to be an autapomorphic feature of these birds. A similar type of syrinx occurs in some cuckoos and in frogmouths (King 1989), but according to Griffiths (1994) these traditional categories of syringeal types do not allow to postulate homologies.

Fossil trogons are known already from the early Eocene of England, but the oldest well preserved records are from the early Oligocene of France (Mayr 1999a, 2001a). Except for the somewhat narrower skull, these birds are, however, very similar to their extant relatives and thus do not contribute much to an understanding of the higher systematic relationships of trogons. The Steatornithidae have no certain fossil record, although there are some early Tertiary fossils which show considerable overall similarity to this taxon (the affinities of the putative Lower Eocene oilbird *Prefica nivea* which was described by Olson 1987 are uncertain; see Mayr 1999b, 2001b, Mayr and Daniels 2001).

Summarizing the above, monophyly of Trogonidae and Steatornithidae is at least as well supported by current evidence as monophyly of Trogonidae and Alcediniformes. However, as any other phylogenetic hy-

pothesis, the one presented in this study needs to be strengthened or refuted by complementary data. What is especially needed are detailed studies of the myology of trogons and the oilbird, and molecular studies in which the two taxa are directly compared. It is to be hoped that the present study will stimulate future research in this direction.

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## References

- Baumel, J. J. and Witmer, L. M. 1993. Osteologia. – In: Baumel, J. J., King, A. S., Breazile, J. E., Evans, H. E. and Vanden Berge, J. C. (eds). Handbook of avian anatomy: Nomina Anatomica Avium. – Publ. Nuttall Ornithol. Club 23: 45–132.
- Beddard, F. E. 1898. The structure and classification of birds. – Longmans, Green and Co., London.
- Berman, S. L. and Raikow, R. J. 1982. The hindlimb musculature of the mousebirds (Coliiformes). – Auk 99: 41–57.
- Burton, P. J. K. 1984. Anatomy and evolution of the feeding apparatus in the avian orders Coraciiformes and Piciformes. – Bull. Br. Mus. (Nat. Hist.) Zool. 47: 331–443.
- Collar, N. J. 2001. Family Trogonidae (Trogons). – In: del Hoyo, J., Elliott, A. and Sargatal, J. (eds). Handbook of the Birds of the World, Vol. 6. Lynx Edicions, Barcelona, pp. 80–127.
- Cracraft, J. and Clarke, J. 2001. The basal clades of modern birds. – In: Gauthier, J. and band Gall, L. F. (eds). New Perspectives on the Origin and Early Evolution of Birds. Peabody Museum of Natural History, Connecticut, New Haven, pp. 143–156.
- Eisenmann, E. S. B. 1985. Trogon. – In: Campbell, B. and Lack, E. (eds). A Dictionary of Birds. Poyser, Calton, pp. 609–610.
- Espinosa de los Monteros, A. 2000. Higher-level phylogeny of Trogoniformes. – Mol. Phyl. Evol. 14: 20–34.
- Feduccia, A. 1977. A model for the evolution of perching birds. – Syst. Zool. 26: 19–31.
- Fürbringer, M. 1888. Untersuchungen zur Morphologie und Systematik der Vögel, zugleich ein Beitrag zur Anatomie der Stütz- und Bewegungsorgane, Vol. 2. – Van Holkema, Amsterdam.
- Gadow, H. 1893. Vögel. II. – Systematischer Theil. – In: Bronn, H. G. (ed.). Klassen und Ordnungen des Thier-Reichs, Vol. 6. C. F. Winter, Leipzig.
- Garrod, A. H. 1873. On some points in the anatomy of *Steatornis*. – Proc. Zool. Soc. Lond. 1873: 526–535.
- Garrod, A. H. 1874. On certain muscles of the thigh of birds and on their value in classification. Part II. – Proc. Zool. Soc. Lond.: 111–123.
- Griffiths, C. S. 1994. Monophyly of the Falconiformes based on syringeal morphology. – Auk 111: 787–805.
- Harshman, J. 1994. Reweaving the tapestry: What can we learn from Sibley and Ahlquist (1990)? – Auk 111: 377–388.
- Hoff, K. M. 1966. A comparative study of the appendicular muscles of Strigiformes and Caprimulgiformes. Unpubl. PhD thesis, Washington State University.
- Holyoak, D. T. 1999. Family Aegotheidae (Owlet-nightjars). – In: del Hoyo, J., Elliott, A. and Sargatal, J. (eds). Handbook of the Birds of the World, Vol. 5. Lynx Edicions, Barcelona, pp. 252–265.
- Hudson, G. E., Schreiweis, D. O., Wang, S. Y. C. and Lancaster, D. A. 1972. A numerical study of the wing and leg muscles of Tinamous (Tinamidae). – Northwest Science 46: 207–255.

- Huxley, T. H. 1867. On the classification of birds; and on the taxonomic value of the modifications of certain of the cranial bones observable in that class. – Proc. Zool. Soc. Lond. 1867: 415–472.
- King, A. S. 1989. Functional anatomy of the syrinx. – In: King, A. S. and McLelland, J. (eds). Form and function in birds, Vol. 4. Academic Press, London, pp. 105–192.
- Johansson, U. S., Parsons, T. J., Irestedt, M. and Ericson, P. G. P. 2001. Clades within the ‘higher land birds’, evaluated by nuclear DNA sequences. – J. Zool. Syst. Evol. Res. 39: 37–51.
- Johnston, D. W. 1988. A morphological atlas of the avian uropygial gland. – Bull. Br. Mus. (Nat. Hist.) Zool. 54: 199–259.
- Maurer, D. and Raikow, R. J. 1981. Appendicular myology, phylogeny, and classification of the avian order Coraciiformes (including Trogoniformes). – Ann. Carnegie Mus. Natur. Hist. 50: 417–434.
- Mayr, G. 1998. “Coraciiforme” und “piciforme” Kleinvögel aus dem Mittel-Eozän der Grube Messel (Hessen, Deutschland). – Courier Forsch.-Inst. Senckenberg 205: 1–101.
- Mayr, G. 1999a. A new trogon from the Middle Oligocene of Céreste, France. – Auk 116: 427–434.
- Mayr, G. 1999b. Caprimulgiform birds from the Middle Eocene of Messel (Hessen, Germany). – J. Vert. Paleontol. 19: 521–532.
- Mayr, G. 2001a. A second skeleton of the early Oligocene trogon *Primitrogon wintersteini* Mayr 1999 (Aves: Trogoniformes: Trogonidae) in an unusual state of preservation. – Senckenbergiana lethaea 81 (2): 335–338.
- Mayr, G. 2001b. Comments on the osteology of *Masillapodargus longipes* Mayr 1999 and *Paraprefica major* Mayr 1999, caprimulgiform birds from the Middle Eocene of Messel (Hessen, Germany). – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 2001 (2): 65–76.
- Mayr, G. 2002. Osteological evidence for paraphyly of the avian order Caprimulgiformes (nightjars and allies). – J. Ornithol. 143 (1): 82–97.
- Mayr, G. and Daniels, M. 2001. A new short-legged landbird from the early Eocene of Wyoming and contemporaneous European sites. – Acta Palaeontologica Polonica 46 (3): 393–402.
- McKittrick, M. C. 1991. Phylogenetic analysis of avian hindlimb musculature. Univ. Michigan Mus. – Zool. Misc. Publ. 179: 1–85.
- Mindell, D. P., Dorenson, M. D., Huddleston, C. J., Miranda Jr., H. C., Knight, A., Sawchuk, S. J. and Yuri, T. 1997. Phylogenetic relationships among and within select avian orders based on mitochondrial DNA. – In: Mindell, D. P. (ed.). Avian Molecular Evolution and Systematics. Academic Press, Ann Arbor, pp. 213–247.
- Olson, S. L. 1987. An early Eocene oilbird from the Green River Formation of Wyoming (Caprimulgiformes: Steatornithidae). – Documents des Laboratoires de Géologie de Lyon 99: 57–69.
- Sibley, C. G. and Ahlquist, J. E. 1972. A comparative study of the egg white proteins of non-passerine birds. – Bulletin of the Peabody Museum of Natural History 39: 1–276.
- Sibley, C. G. and Ahlquist, J. E. 1990. Phylogeny and classification of birds: a study in molecular evolution. – Yale University Press, New Haven and London.
- Stegmann, B. 1965. Funktionell bedingte Eigenheiten am Metacarpus des Vogelflügels. – J. Ornithol. 106 (2): 179–189.
- Stresemann, E. 1927–34. Aves. – In: Kükenthal, W. and Krumbach, T. (eds.). Handbuch der Zoologie. – de Gruyter, Berlin and Leipzig.
- Swofford, D. L. 1993. PAUP: Phylogenetic analysis using parsimony, version 3.1. – Illinois Natural History Survey, Champaign.
- Thomas, B. T. 1999. Family Steatornithidae (Oilbird). – In: del Hoyo, J., Elliott, A. and Sargatal, J. (eds). Handbook of the Birds of the World, Vol. 5. Lynx Edicions, Barcelona, pp. 244–251.
- Vanden Berge, J. C. and Zweers, G. A. 1993. Myologia. – In: Baumel, J. J., King, A. S., Breazile, J. E., Evans, H. E. and Vanden Berge, J. C. (eds) Handbook of avian anatomy: Nomina Anatomica Avium. – Publ. Nuttall Ornithol. Club 23: 189–247.
- van Tuinen, M., Sibley, C. G. and Hedges, B. S. 2000. The early history of modern birds inferred from DNA sequences of nuclear and mitochondrial ribosomal genes. – Mol. Biol. Evol. 17: 451–457.
- Verheyen, R. 1956. Les Striges, les Trogones et les Caprimulgi dans la systématique moderne. – Institut royal des Sciences naturelles de Belgique 32 (3): 1–31.
- Wetmore, A. 1960. A classification for the birds of the world. – Smithsonian Miscellaneous Collections 139 (11): 1–37.
- Zusi, R. L. and Bentz, G. D. 1984. Myology of the purple-throated carib (*Eulampis jugularis*) and other hummingbirds (Aves: Trochilidae). – Smithsonian. Contrib. Zool. 385: 1–70.

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## Appendices

### Appendix I: Character descriptions.

1. Skull, distinct naso-frontal hinge: absent (0), present (1).
2. Skull, largely or completely ossified septum nasale: absent (0); present (1).
3. Conchae nasales in proximal area of narial openings more or less strongly ossified: no (0), yes (1).
4. Palate directly desmognathous, i.e. processus maxillopalatini to a greater or lesser extent fused along their midline: no (0), yes (1).
5. Skull, functional processus basipterygoidei: present (0), absent (1). Within the Cypselomorphae, this feature is absent in Aegothelidae, Hemiprocnidae, Apodidae, and Trochilidae which is here considered to be a synapomorphy of these taxa (see Mayr 2002).
6. Columella with large, hollow, bulbous basal and footplate area which exhibits a large fenestra on one side: no (0), yes (1). This character was listed by Feduccia (1977) in order to support monophyly of trogons and alcediniform birds. Due to the absence of adequate material, the columella of the Nyctibiidae was not investigated.
7. Atlas, incisura fossae: open (0), closed (1). Within the Cypselomorphae, the incisura fossae is closed in swifts and hummingbirds which is here, based on the phylogeny of Mayr (2002), considered synapomorphic for these taxa; accordingly the character has been coded as “0” for the Cypselomorphae.
8. Scapula, acromion distinctly bifurcate: no (0), yes (1). In the Upupidae and Phoeniculidae (Upupiformes), the acromion is weakly bifurcated which is here considered synapomorphic for these birds (the character is absent in the Bucerotidae).
9. Sternum with well developed, blade-like, dorso-ventrally high spina externa the dorsal margin of which is continuous with a crest on the cranial surface of the carina sterni: no (0), yes (1). The spina externa of trogons also is well developed but rather low in dorso-ventral direction and exhibits a more or less distinctly bifurcate tip.
10. Humerus, proximal end, sulcus transversus very deep, long, and rectangular-shaped: no (0), yes (1).
11. Humerus, distal end, fossa musculi brachialis deep and sharply delimited: no (0), yes (1). Within the Upupiformes this feature occurs in the Bucerotidae.
12. Os carpi ulnare with crus longum being much longer than crus breve: no (0), yes (1).
13. Pelvis very wide in mediolateral direction, width across antitrochanters as much or more than length of synsacrum: no (0), yes (1).

14. Tarsometatarsus, hypotarsus, tendon for musculus flexor hallucis longus enclosed in bony canal: no (0), yes (1). The presence of this character in the Nyctibiidae (Cypselomorphae) is here considered to be autapomorphic; accordingly it has been coded as "0" for the Cypselomorphae.
15. Tarsometatarsus with very marked fossa parahypotarsalis medialis, margo medialis at proximal end of shaft forming a sharp ridge: no (0), yes (1). Within the Upupiformes, this character is absent in *Bucorvus* (Bucerotidae). Since *Bucorvus* is generally considered to be the sister taxon of the other Bucerotidae (e.g. Sibley and Ahlquist 1990), it is uncertain whether this represents the primitive condition or a reversal into the primitive condition; accordingly the character was coded as "01" for the Upupiformes.
16. Third and fourth toe coalescent for part of their length: no (0), yes (1). Within the Upupiformes, this character is absent in *Bucorvus* (Bucerotidae, see comments above).
17. Aftershaft: well developed (0), small or absent (1) (after Gadow 1893, Stresemann 1927-34, Sibley and Ahlquist 1990).
18. Right arteria carotis: present (0), absent (1) (after Beddard 1898, Stresemann 1927-34, Verheyen 1956, Sibley and Ahlquist 1990). Within the Cypselomorphae, the right arteria carotis is absent in the Nyctibiidae, Trochilidae and most swifts; underlying the phylogeny of Mayr (2002) it is most parsimonious to assume that it was present in the last common ancestor of these taxa.
19. Oil gland: tufted (0), naked (1) (after Johnston 1988). Within the Alcediniformes a minutely tufted or naked oil gland occurs in the Momotidae and Meropidae.
20. Young at hatching: feathered (0), naked (1) (after Stresemann 1927-34, Sibley and Ahlquist 1990).
21. Musculus pectoralis, pars propretagialis longus: fleshy (0), tendinous or completely reduced (1) (after Hoff 1966, Hudson et al. 1972, Maurer and Raikow 1981, Zusi and Bentz 1984). This character was listed by Mayr (1998) in order to support monophyly of trogons and upupiform birds.
22. Musculus scapulotriceps, humeral anchor: present (0), absent (1) (after Hoff 1966, Hudson et al. 1972, Maurer and Raikow 1981). Hoff (1966) states that in *Bubo* (Strigiformes) there is a "narrow tendinous connection to the posterior surface" of the caput humeri which I assume to be homologous to the "humeral anchor" of Maurer and Raikow (1981). In the Caprimulgiformes "insertion is always similar to that of *Bubo*" (Hoff 1966). According to the description in Zusi and Bentz (1984), the humeral anchor seems to be absent in the Trochilidae which, based on the phylogeny of Mayr (2002), is here considered to be autapomorphic for this taxon. Within the Upupiformes, this feature is absent in the Bucerotidae (Maurer and Raikow 1981).
23. Musculus extensor longus digiti majoris, pars distalis: present (0), absent (1) (after Hoff 1966, Hudson et al. 1972, Maurer and Raikow 1981, Zusi and Bentz 1984). Within the Tinamidae the pars distalis is absent in *Eudromia* and *Tinamotis* (Hudson et al. 1972) which is here considered an autapomorphy of these taxa. Within the Cypselomorphae this feature is absent in Aegothelidae (Hoff 1966) and Trochilidae (Zusi and Bentz 1984) but present in Caprimulgidae and Nyctibiidae; the condition in swifts is unknown and based on the phylogeny of Mayr (2002) it is assumed that it was present in stem group representatives of the Cypselomorphae.
24. Musculus iliobtibialis lateralis, acetabular part: present (0), absent (1) (after Hoff 1966, Maurer and Raikow 1981, Berman and Raikow 1982, Zusi and Bentz 1984, McKittrick 1991).
25. Musculus iliobtibialis lateralis, postacetabular part: present (0), absent (1) (after Hoff 1966, Maurer and Raikow 1981, Berman and Raikow 1982, Zusi and Bentz 1984, McKittrick 1991).
26. Musculus iliofemoralis externus: present (0), absent or fused to m. iliobtibialis caudalis (1) (after Hoff 1966, Hudson et al. 1972, Maurer and Raikow 1981, Berman and Raikow 1982, McKittrick 1991).
27. Musculus popliteus: present (0), absent (1) (after Hoff 1966, Hudson et al. 1972, Maurer and Raikow 1981, McKittrick 1991). Within the Cypselomorphae, this muscle is absent in Aegothelidae, Hemiprocnidae, Apodidae, and Trochilidae which is here considered to be a synapomorphy of these taxa.
28. Tendons of Musculus flexor hallucis longus and m. flexor digitorum longus extensively fused: absent (0), present (1) (after Hoff 1966, Hudson et al. 1972, Maurer and Raikow 1981, Berman and Raikow 1982).

Appendix II. Character matrix of 28 morphological characters for Trogonidae, Coliiformes, Strigiformes, Cypselomorphae, Alcediniformes, Upupiformes, and Coraciidae/Brachypteraciidae (see Appendix I for character definitions). Outgroup comparisons were made with Tinamidae, unknown character states are indicated by "?".

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Tinamidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coraciidae/Brachypt.	0	1	1	1	1	0	01	1	1	0	0	0	0	0
Alcediniformes	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Steatornithidae	1	1	0	1	0	1	0	0	0	1	1	1	1	0
Coliiformes	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Cypselomorphae	0	0	0	0	0	0	0	0	0	1	0	1	1	0
Upupiformes	0	1	1	1	1	0	1	0	1	0	01	0	0	1
Strigiformes	1	1	0	0	0	0	0	0	0	0	0	01	0	0
Trogonidae	1	1	0	0	0	1	1	0	0	0	1	1	1	1
	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Tinamidae	0	0	01	0	0	0	0	0	0	0	0	0	0	0
Coraciidae/Brachypt.	1	0	1	0	1	1	0	1	0	0	0	1	0	1
Alcediniformes	1	1	1	01	01	1	0	1	1	1	1	1	1	1
Steatornithidae	0	0	1	0	1	0	1	0	1	0	1	1	0	1
Coliiformes	0	0	0	1	0	1	?	?	?	1	1	0	1	1
Cypselomorphae	0	0	01	0	1	01	01	0	0	01	01	1	0	1
Upupiformes	01	01	1	1	0	01	1	01	1	1	1	1	1	1
Strigiformes	0	0	1	0	1	0	0	0	0	0	1	0	0	01
Trogonidae	0	1	0	1	1	1	1	0	1	1	1	1	1	0