

**PROMEROPS AS A THRUSH,
AND ITS IMPLICATIONS FOR THE EVOLUTION OF NECTARIVORY IN BIRDS**

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SUMMARY

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The familial relationships of the South African sugarbirds (*Promerops*) have never been firmly established, although an alliance with the Meliphagidae or the Sturnidae has been suggested on rather equivocal grounds. The syrinx in *Promerops* is now shown to have the derived "turdine thumb" configuration that is characteristic of the true Old World flycatchers and the thrushes (Muscicapini auct. and Turdinae), to which group *Promerops* should now be moved. *Promerops* shows that the highly specialized morphology and behaviour associated with nectarivory can evolve in a "saltational" manner, leaving no intermediate forms and few clues to the identity of the ancestral taxon. Nectarivorous feeding adaptations are a very poor indication of relationships. The closest relatives of other nectarivorous groups of birds are probably best sought among taxa that lack morphological specializations for nectar feeding.

INTRODUCTION

To those familiar with the South African Cape and Gurney's Sugarbirds *Promerops cafer* and *P. gurneyi*, either in the field or the museum, the title of this paper at first may seem unlikely, for it is difficult to reconcile the appearance and behaviour of *Pomerops* with that of the thrushes, chats, and flycatchers of the family Muscicapidae. Yet we have discovered that the morphology of the syrinx makes this the most reasonable hypothesis of relationship of *Promerops*; indeed, it is now seen to be the only one for which any really sound evidence exists.

The sugarbirds are adapted for feeding on the nectar of Proteaceae and consequently have a long, slightly decurved bill and a nectar-adapted tongue with a fringed tip. Both species have greenish-yellow rumps and conspicuous yellow undertail coverts and sides of the rump. The tail is elongate in both sexes of *Promerops gurneyi* and is spectacularly so in adult males of *P. cafer*, which, with the elaborate displays of the latter, make it a highly distinctive bird. As Skead (1967: 232) has remarked, the sugarbirds "are not close relatives of the sunbirds [Nectariniidae, which are also nectar-

adapted], and nothing else in Africa is really like them."

Sibley & Ahlquist (1974) have outlined the taxonomic history of *Promerops* in detail. In brief, except for Sibley and Ahlquist themselves, virtually all previous authors have allied *Promerops* with other nectar-feeding birds, either the Nectariniidae or the Australasian honeyeaters of the family Meliphagidae. There has never been much sustained support for a nectariniid relationship for *Promerops*, but the genus has frequently been placed in or near the Meliphagidae. The more recent systematic studies of *Promerops* have dwelt on the differences between this genus and the Meliphagidae, whereas no cogent morphological similarities between *Promerops* and any other group have been identified. It is now generally conceded that the feeding adaptations of *Promerops* and the Meliphagidae are only convergently similar. This, coupled with the zoogeographical difficulties inherent in a relationship with the Meliphagidae, has caused some authors to place *Promerops* in its own family, Promeropidae.

Sibley & Ahlquist (1974) on the other hand used the electrophoretic pattern of egg white proteins to show that *Promerops* was a nectar-adapted deriva-

tive of the starlings (Sturnidae), and they suggested several external and behavioural characters supporting this. The unreliability of the egg white protein techniques (see Brush 1979) has at least in some instances resulted in what Sibley & Ahlquist (1980) have noted may have been erroneous conclusions that may be viewed as compromising their data concerning *Promerops*. More importantly, their paper (Sibley & Ahlquist 1974) makes no comparisons between *Promerops* and the Muscicapidae, so their data cannot be evaluated in light of our findings.

THE SYRINX AND RELATIONSHIPS OF *PROMEROPS*

The syrinx in the Muscicapidae (including Turdidae) is highly distinctive in having the dorsolateral musculature protruding as an elongated thumb-like structure, the "turdine thumb", first recognized by Ames (1975). This is characteristic of the true muscicapid flycatchers and the thrushes and has not yet been found in any genus thought to be unrelated to this group, with the exception of the Bornean genus *Chlamydochaera*, previously placed in the Campephagidae but now removed to the Muscicapidae (e.g. Ames 1975; Ahlquist *et al.* 1984; Olson MS). Certain genera thought to be related to the Muscicapidae have been found to lack the "turdine thumb" and either have been, or should be, removed to other families (Ames 1975; Harrison 1976; Olson *et al.* 1983; Olson 1984). The relationships of most of these had been disputed in any case. The "turdine thumb" of the syrinx defines a natural, monophyletic group the interrelationships of which have long been recognized on the basis of more traditional, though not always consistent, external systematic characters.

On 11 July 1984, while examining the syringes of various Meliphagidae and some of their presumed relatives, we discovered that the syrinx in *Promerops* has the "turdine thumb" and is in every respect typically thrush-like (Fig. 1). We examined the syrinx in one specimen of *Promerops gurneyi* (AMNH 2765), and three specimens of *Promerops cafer* (USNM 558752-53, AMNH no number), and found the "turdine thumb" extremely pronounced in all of them.

Olson had collected two of the specimens of *P. cafer* in 1983 and prepared them as skeletons, at which time he saved the syringes and tongues in

fluid. Although he routinely examined the syrinx in the various muscicapids and presumed muscicapids that he collected (see Olson 1984), the syringes of *Promerops* were kept mainly because the taxonomic position of the genus had so long been in doubt, but Olson did not scrutinize these specimens for muscicapid affinities. Thus the "turdine thumb" was overlooked.

Because Ames (1971) had previously examined the syrinx in *Promerops* and briefly reported on its condition in Sibley & Ahlquist (1974), a word of explanation for his also having overlooked the "turdine thumb" is in order. The syringeal character by which the Meliphagidae may be recognized occurs in the *ventral* musculature and consists of a distinctive posterior gap between the two halves of the ventral muscle mass. It is not necessary to expose and examine the dorsal musculature that makes up the "turdine thumb" to check the meliphagid condition, which is lacking in *Promerops*. Indeed, when we made our discovery, each of us had been looking at a syrinx of *Promerops* under a dissecting microscope for some time before Olson chanced to clear away the tissue overlying the dorsal musculature to expose the obvious "turdine thumb". When Ames (1975) conducted his original survey of the distribution of this character, he looked for it among the various groups of "Old World Insect Eaters" with which the Muscicapidae are usually associated, but there was no reason at that time to examine *Promerops* in this connection. In the present study, Ames re-examined the specimen that he described originally and found the "turdine thumb" to be present and well developed.

The tarsus is not booted nor are the young spotted in *Promerops*. These features are characteristic of many of the Muscicapidae but are neither restricted to them nor invariably present. Particularly in some of the chats, the tarsus may be scutellate and the young unspotted (Ripley 1952). The yellow in the plumage and the elongated tail of *Promerops* that Sibley & Ahlquist (1974) cite as being similar to those of some starlings, also occur in the Muscicapidae (e.g. *Pogonocichla*, the adults of which are mostly yellow, and *Enicurus*, in which the tail is greatly elongated). The peculiarly shaped primaries, particularly the fifth, of adult males of *Promerops*, which are not so much notched as they are greatly expanded in the basal

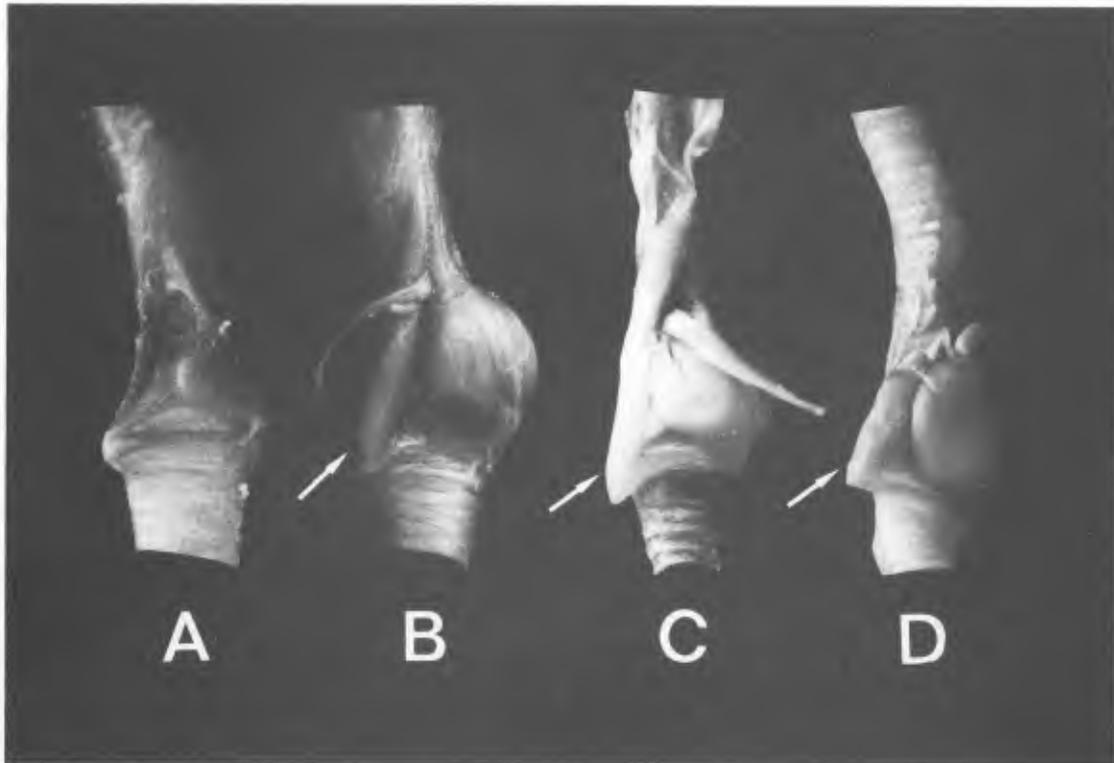


FIGURE 1

Syringes in lateral view. A, Greater Blue-eared Starling, *Lamprotornis chalybeus* (Sturnidae), showing the generalized oscine configuration; B, Whitecrowned Cliffchat *Thamnolaea coronata* showing the typical "turdine" configuration; C, Gurney's Sugarbird *Promerops gurneyi*; D, Cape Sugarbird *P. cafer*. The "turdine thumb" that defines the Muscicapidae, including *Promerops*, is indicated by arrows.

two-thirds of the inner web, are not really similar to the notched condition in the starlings of the genus *Lamprotornis*. The primaries may be modified in the Muscicapidae as well (e.g. *Cercomela sinuata*), but again are not similar to the condition in *Promerops*. Because the primaries are much less modified in *P. gurneyi* and it displays correspondingly simpler (Skead 1967), this species appears to be the more primitive. The extreme specialization of the primaries very likely arose within *Promerops*, as probably did the yellow in the plumage and the elongated tail, in which case these characters are not likely to be useful indicators of relationship.

The open, cup-shaped nest of *Promerops* is more like that in the Muscicapidae than in the Sturnidae, which typically, but not always, nest in cavities or crevices or build domed nests. Many other birds build cup-like nests, however, so this has little significance other than slightly favouring a muscicapid relationship over a sturnid one. The same holds for the eggs, which have a buffy ground colour and are heavily spotted and scrawled in *Promerops*, whereas in starlings the eggs are usually blue (rarely white) and usually spotted with red. The eggs in the Muscicapidae are variable in colour, sometimes being buffy and often being spotted, although to judge from the descrip-

tions of South African species in McLachlan & Liversidge (1978), none seems to be as heavily marked and scrawled as in *Promerops*.

One factor favouring a muscicapid rather than a meliphagid relationship for *Promerops* is geography, for the Muscicapidae have speciated and diversified extensively in southern Africa. In the area covered by McLachlan & Liversidge (1978) there are about 43 resident species of Muscicapidae in 15 genera (*Erithacus*, *Pogonocichla*, *Erythropgyia*, *Cossypha*, *Saxicola*, *Myrmecocichla*, *Thamnolaea*, *Cercomela*, *Oenanthe*, *Monticola*, *Zoothera*, *Turdus*, *Melaenornis*, *Namibornis*, and *Muscicapa*). Some of these are among the most characteristic birds of drier, unforested areas such as frequented by *Promerops*. In all fairness, however, it should be noted that none of the above genera bears the slightest resemblance to *Promerops*.

There is no evidence to suggest that the distinctive "turdine" syrinx has evolved more than once. Apart from *Promerops*, this condition is present only in birds that had already been considered allied on traditional morphological characters and that can reasonably be assumed to constitute a monophyletic group. With the protein data mooted, the only evidence to be advanced in the attempt to determine the relationships of *Promerops* is in the morphology of the feeding apparatus and the syrinx. Nectarivorous specializations have evidently evolved independently in "at least 12 oscine groups" (Sibley & Ahlquist 1974: 24), so convergence in feeding adaptations seems much more likely than in syringeal morphology. Furthermore, it had already been largely agreed upon that the feeding adaptations of *Promerops* probably evolved independently of those in other nectarivorous birds. Any argument that the similarities in syringeal morphology between *Promerops* and the Muscicapidae are the result of convergence would be unconvincing for the simple reason that there are no other characters of *Promerops* that strongly suggest a closer association between it and some other group.

On the basis of the available evidence, we would place *Promerops* in the Muscicapidae, as defined by the syrinx. Within this group the relationships of *Promerops* are otherwise obscure, but because it is clearly one of the most highly derived members of this radiation, *Promerops* can conveniently

be placed at the end of any listing of the species of Muscicapidae.

THE IMPLICATIONS OF *PROMEROPS* FOR THE EVOLUTION AND SYSTEMATICS OF NECTARIVOROUS BIRDS

Many birds feed on nectar, even though not especially adapted for it. In South Africa alone, Oatley & Skead (1972) have reported 73 species that are not primarily nectarivorous as feeding on nectar, including seven non-passerine families: doves (Columbidae), parrots (Psittacidae), louries (Muscophagidae), colies (Coliidae), woodhoopoes (Phoeniculidae), barbets (Capitonidae), and honeyguides (Indicatoridae). Among passerines they record drongos (Dicuridae), orioles (Oriolidae), crows (Corvidae), tits (Paridae), babblers (Timaliidae), bulbuls (Pycnonotidae), warblers (Sylviidae), starlings (Sturnidae), and various finch-like birds (Ploceidae, Estrildidae, Carduelinae), among others, as feeding on nectar. Of interest in connection with *Promerops*, they list five genera and seven species of Muscicapidae as feeding on nectar (Cape Rock Thrush *Monticola rupestris*, Mocking Chat *Thamnolaea cinnamomeiventris*, Buffstreaked Chat *Oenanthe bifasciata*, Whitebrowed Robin *Erythropgyia leucophrys*, Pallid Flycatcher *Melaenornis pallidus*, Black Flycatcher *M. pammelaina*, and Fiscal Flycatcher *M. silens*). To these may be added Sentinel Rock Thrush *Monticola explorer* (T. B. Oatley, pers. comm.).

Selection pressure to evolve morphological specializations that enhance the ability to feed on nectar must be fairly intense, with some such adaptations having evolved more than a dozen times within the oscine passerines (Sibley & Ahlquist 1974). The case of *Promerops* is particularly instructive in that it illustrates the fact that a high degree of specialization for nectarivory can appear in a "saltational" manner, leaving no intermediate forms and obliterating most traces of the ancestry of the newly evolved taxon.

Non-nectar-adapted relatives have been identified for some of the specialized nectarivores such as the Drepanidini, which are cardueline finches (Raikow 1976). Many of the Drepanidini, however, are still finchlike and not nectarivorous. The various members of the "Coerebidae" are derived from the New World nine-primaried oscines

(Fringillidae *sensu lato*), mostly from the Thraupinae. *Chloropsis*, sometimes placed in its own family or in the "Irenidae" is almost certainly a nectarivorous bulbul (Pycnonotidae) (Olson, in prep.). The closest relatives of the Nectariniidae have not been identified, but if plumage similarities may be taken as suggestive, then it may be the sunbirds rather than *Promerops* that are derived from starlings (Sturnidae).

Once specialized adaptations for nectarivory have evolved, the transformed species may then give rise to a radiation of numerous similarly adapted species. This has not taken place with *Promerops*, but it certainly has in such groups as the Nectariniidae, Meliphagidae, and the Drepanidini. The many instances and apparent ease with which specializations for nectarivory have appeared suggest abundant opportunities for parallel evolution. Thus a single family or even a single genus might give rise to specialized nectarivores on more than one occasion. This appears to have happened in the Drepanidini, where the tubular tongue has almost certainly evolved more than once (Olson & James, in prep.). The "Coerebidae" is without doubt an artificial collection including several independently evolved nectar-adapted derivatives of tanagers (Olson *in Wetmore et al.* 1984). Given the differences in tongue structure within the Nectariniidae (see Gill 1971, and references therein), it might be questioned whether this family is strictly monophyletic, that is, whether the closest common ancestor of all species of Nectariniidae was also specialized for nectar feeding.

In summary, we should recognize (a) that extreme specialization for nectarivory may appear essentially *de novo* in a group that otherwise shows no such morphological tendencies, (b) that these specializations may effectively mask the affinities of specialized nectarivores, but (c) should not be used to exclude nectarivorous taxa from the family-level group from which they were derived once their relationships can be established and (d) that the strong possibility of parallel evolution may call into doubt the strict monophyly even of closely similar groups of species of nectarivores. As a thrush, *Promerops* demonstrates with unparalleled force and clarity the fact that nectarivorous feeding adaptations are extremely unreliable for determining affinities within the Passeriformes.

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