COMMENTARY: The correct names of Old World vultures and their sequence.

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"... to affix to each species the specific name to which it is by priority entitled, ... "

"... that order being such as has appeared ... the most conformable to their natural affinities."

(Gurney 1864: v)

"Having the taxonomic hierarchy of names reflects evolutionary history ... "

(Mindell et al. 2018: 3)

Introduction

For very many years I have been interested in, and concerned about, the correct names of vultures (particularly in Latin), and also the sequence of the species in any list. I first delved into this with Mundy (1984), considering at that time that the important works were Brown & Amadon (1968) and Stresemann & Amadon (1979). One of the big arguments back then was whether the Cathartid (New World) vultures were storks (e.g. Rea 1983) or raptors. Four more works have since come on the scene, important in a taxonomic context, being Amadon & Bull (1988), Sibley & Monroe (1990), del Hoyo *et al.* (1994), and Ferguson-Lees & Christie (2001). Indeed, the last one admits that its classification is a "conventional" one (*op. cit.*: 69). Let's unravel that word and say that all previous and early studies relied on morphology, ecology, behaviour, likeness, etc., to express relationships. A *tour de force* back in those days was certainly Jollie's work (1976, 1977 a,b,c) based on anatomy and the skeletal system; his conclusion was that the Falconiformes is a polyphyletic grouping. This echoed in much greater detail his earlier position (Jollie 1953).

"Conventional" classification

But back to the nearly-present day: the names and sequence of species by Ferguson-Lees & Christie (2001: 6 and 7) are shown in their table of contents (only). The nomenclature of the Cathartids has been stable for many years, but note that these authors agree that the "New World vultures [are] actually closely related to the storks" (*op. cit.*: 69), and in this they are on the same side as Amadon & Bull (1988: 297) and del Hoyo *et al.* (1994: 25 and 52). However, whereas Amadon & Bull (*op. cit.*) noted that the New World vultures had "peculiarities",

nevertheless they preferred to keep them in the Falconiformes "for now". But as Sibley & Ahlquist (1990: 484) pithily remarked, how long is that? Confusion is also shown by del Hoyo *et al.* (1994): they maintain the Cathartidae in the Falconiformes (*op. cit.*: 23), but their authors Houston (1994: 25) and Thiollay (1994: 52) accepted its close relationship to the storks. Ferguson-Lees & Christie (2001: 17) even described the New World vultures as "short-necked storks with a hooked bill" and separated them off into the Order Ciconiiformes. At long last, one could say, and not before time. (But wait!, see below).

For the Accipitrid vultures, several changes can be noted. (i) We have stated before (Mundy et al. 1992: 27) that up to that time Amadon & Bull (1988) were the first authors to get all the Latin names correct, except for *rueppellii* (see below). (ii) The name Bearded Vulture is surely to be preferred over Lammergeier, from the French Gypaète barbu and the German Bartgeier, in spite of their opinion (Amadon & Bull 1988: 302) that the Bearded Vulture may not be a vulture at all. See Mundy et al. (1992: Table 44) for comparisons between the Bearded and Egyptian Vultures, suggesting they are closely related. (iii) Both Amadon & Bull (1988: 310) and del Hoyo et al. (1994: 127 and 128) have used "Griffon" for the large cliff-nesting Gyps species, as also did Sibley & Monroe (1990: 271-2) (except inexplicably the [Indian] Long-billed Vulture), with the first two authorities considering the five Gyps species as forming a superspecies (Amadon 1966), rightly in my view (Mundy 2002). Indeed, this opinion was first stated by Sharpe (1874: 5) though he did not use the term, rather saying "five distinguishable species" of the "Griffon Vultures". Then Ferguson-Lees & Christie (2001: 77) discarded the word "Griffon", prompting me to make a case in its defence (Mundy 2002, also Mundy 2017). (iv) In addition, I still maintain my opinion that the two smaller treenesting white-backed vultures should rather be separated in their own genus of *Pseudogyps*, from Sharpe (1873). No recent authority or study agrees with that! (v) More seriously, both del Hoyo et al. (1994: 129) and Ferguson-Lees & Christie (2001: 439) have wrongly used tracheliotus for the Lappet-faced Vulture instead of tracheliotos. We explained this correction (Mundy et al. 1992: 148 and 150, from Rookmaaker 1986); the correct name originated from François Levaillant's baptism as Oricou for the species (Rookmaaker et al. 2004: 213-219). Note that the word for ear in Greek is otos, whereas otus is Latin for owl!

(vi) In the nineteenth century, the Rüppell's Griffon was consistently called rueppelli (e.g. Sharpe 1874: 9) whereas in the twentieth century it was just as consistently spelled *rueppellii*, starting with Sclater (1924: 47, actually as rüppellii). The original namer, Alfred Eduard Brehm, used both spellings as Ruppellii (Brehm 1852: 44) and Rüppelli (op. cit.: 47) in his article. I have not been able to discern why one or other of the later authors favoured either *rueppelli* or *rueppellii*, but now it is rueppelli. I have recently told the story (Mundy 2016), which also unnecessarily involves the 'First Reviser'. (vii) Finally, and no doubt following Dean Amadon's lead (Amadon 1977, Stresemann & Amadon 1979: 308-9, Amadon & Bull 1988: 310), Ferguson-Lees & Christie (2001: 7) put the four large dark/black vultures all together in the genus Aegypius. This is a possible if not probable decision: they are solitary (territorial?), treenesting, and rather similar in their ecology especially in their approach to carcasses, and two of them (at least) have the same 'head-twist' (Kopfdrehen, König 1976). But as yet there is still no comparative behavioural study of these four 'king' species, so each should meantime remain in its own genus.

Perhaps the last word in this section could go to Kemp & Crowe (1990) who did a phylogenetic analysis of diurnal raptors, using 37 derived characters from an examination of museum skins and literature. Their main conclusions were: Cathartidae are "most closely related to storks"; within the Accipitridae is a group of eagle-like clades that includes the Old World vultures but with *Gypaetus* included in the "aquilae" and separated from *Neophron* and all the other Old World vultures (here called "aegypii"); and that the primary radiation of diurnal raptors had occurred when the Gondwana continents "were still closely associated" or at least before they became "widely separated" (*op. cit.*: 173). This last conclusion is astounding and wrong! Gondwanaland, the ancient, southern supercontinent, originally comprised Africa, Antarctica, Arabian Peninsula, Australasia, Indian subcontinent, and South America; it started to split up "around 200 million years ago" (Anderson 2001: 8). By the end of the Cretaceous period, about 69 Mya (and before the asteroid), these continents were already very widely separated (Anderson 2001: 37). Birds of prey, and particularly vultures, date back to the Eocene period, "more than 50 million years ago" (Rich 1983). (Only the New World vultures, not the Old World vultures). Meanwhile mention should be made of Holdaway's (1994, but presented at a conference in 1992) phylogenetic (=cladistic) analysis of the Accipitridae, using some or other of a marvelous array of 273 osteological characters. Aegypius, Gyps and Necrosyrtes clustered together as 'core' Aegypiines, but Gypaetus was separated from Neophron.

Be all that as it may, I take the year of 1990 as a key one in the progress of studies on the taxonomy of birds of prey (next section). Hopefully the correct names of vultures can now be laid to rest (barring my insistence (?) on griffon and *Pseudogyps*!); however the sequence of species is still in a state of flux.

Molecular studies with DNA

These began with Sibley & Ahlquist (1990). They wrote a detailed history of the classification of diurnal raptors that started with Linnaeus and his first order of birds, named the Accipitres. This method of DNA-DNA hybridization broke the 'stalemate' of the previous morphological studies, which had "not achieved a consensus" (*op. cit.*: 484). They concluded that the Cathartidae are more closely related to the storks. They also proposed that the Old World vultures, which are "carrion-eating eagles" (*op. cit.*: 485) (meaning they evolved from eagles?), diverged as a clade from typical

accipitrines round 23.4 Mya, a (very) long time after the break-up of Gondwanaland, and when grasslands (food for grazing ungulates) had expanded in the Oligocene epoch, 38-22 Mya. This (late) date of 23.4 Mya is in line with the known fossil history of Old World vultures (Rich 1983: 17, Mundy *et al.* 1992: 54 and Table 12), with the oldest *Arikarornis* being dated to the Lower Miocene (Howard 1966), about 20 Mya (?).

hybridization method The was quickly overtaken by sequence data of, in the first instance, the cytochrome b gene in the mitochondria (Wink 2007: 63), then later to include nuclear genes. A spate of studies on DNA molecules has followed which have in effect also made redundant the earlier phylogenetic work on morphological/anatomical characters. First in the field was Ingrid Seibold's study, from Michael Wink's laboratory, of birds of prey, based on "nucleotide sequences of the mitochondrial cytochrome b gene" (Seibold 1994: 168). New World vultures are an "offshoot of the storks", and Old World vultures comprise two different lineages (Seibold et al. 1994). These authors stated that "if the cytochrome b gene tree accurately reflects vulture phylogeny (!, that is the point), then Gypaetus and Neophron together are more ancient than the more recent *Aegypius* and *Gyps*. Interestingly, Seibold et al. (1994) had Aegypius, Torgos, Sarcogyps and Trigonoceps clustered together (in her PhD thesis, Seibold suggested uniting them in a single genus), these four species with Necrosyrtes being what we called the 'dark' or black vultures (Mundy et al. 1992: 21 and 28). The dam had now broken, and molecular phylogenetics became the way to go, with studies abounding up until today.

Eventually a nuclear gene was also used (Lerner & Mindell 2005, Griffiths *et al.* 2007), and by the latest study considered here (Mindell *et al.* 2018) no less than six nuclear genes were so employed (along with four mitochondrial genes). Presumably

absorbing the molecular phylogenetics before them, del Hoyo & Collar (2014) produced a list of New World and Old World vultures. In view of the tremendous achievement and importance of this work, their names and sequences (again, not listed separately) are to be emphasised. It is therefore to be regretted that their (non) listing has retrogressed! Nevertheless, they have usefully indicated those species that have subspecies "currently / tentatively / usually / generally recognised" (del Hoyo & Collar 2014: 516, 522, 526, 528) as well as the IUCN's assessment of endangerment (five categories from critically endangered to least concern), actually done by BirdLife International. In particular they put the New World vultures into their own Order Cathartiformes (following Voous 1985: xii), and they show the two lineages of Old World vultures, viz. Tribes Gypaetini and Gypini, in different Subfamilies. Happily all the Latin names are correct, but ignoring *Pseudogyps*, and for the English names they have disdained "Griffon" for "Vulture", except curiously for the Himalayan Griffon (on large size?). But most seriously they have inserted the two white-backed vultures (numbers 50 and 51) into the larger Gyps group, between number 49 (Himalayan Griffon) and 52 (Indian Vulture), and unforgivably they have separated the four dark/black vultures into two distant pairs, viz. 46 and 47, and 57 and 58. They acknowledge that Sarcogyps, Trigonoceps and Torgos are "often/formerly subsumed within Aegypius" (op. cit.: 526 and 528), but still they have separated them by eight species of Gyps and Necrosyrtes. Very strange!

Finally, we can come to the most recent study considered here, that by Mindell *et al.* (2018). Their names and sequence were shown in their Table 1.1. As noted before, the Cathartid vultures are stable in their nomenclature and in their own Order Cathartiformes. The two lineages of Old World vultures (Gypaetinae and Aegypiinae) are shown. In Table 1.1, all Latin names are correct (though it should be Cape not cape), but in Figure 1.2c the authors have wrongly reverted to *rueppellii* and *tracheliotus*. The order of species is different between Table 1.1 and Figure 1.2c. In particular they have kept the dark/black vultures together, though separating off the Hooded Vulture at the start of the Aegypiinae, and (rightly in my view) maintained each in its own genus. This is surely to be preferred.

Mindell et al. (2018) have introduced a significant and crucial criterion, that of the age of a clade, genus and species - "taxonomic categories [should] reflect approximate ages of named taxa" (op. cit.: 4). Could we then expect that an earlier species would appear in a sequence before a later one? From Figure 1.2c, it seems that africanus is seen first and coprotheres/indicus last; africanus is listed first in Table 1.1 and coprotheres last, but the other Gyps species do not have the same sequence. For their Table 1.1, the authors have based it on Gill and Donsker (2017, version 7.1). I was able to refer to version 10.2 (Gill et al. 2020, accessed 25 July 2020), and while that sequence also begins with africanus, the other Gyps are in a different order. All very confusing if not irritating!

In brief then, and in spite of the number of studies that deal with the taxonomy of diurnal raptors, both morphologically (the conventional classification) and in terms of DNA in genes, from perhaps Sharpe (1874) to Mindell *et al.* (2018), no one classification has got the names and sequence of vultures in an agreeable fashion (to me). Probably we should be surprised at that situation. Notwithstanding, I would here like to propose my own version, particularly for the Old World vultures, in Table 1. In this regard, there are seven questions that need to be answered:

 (i) As an Order with several Families, is the Falconiformes (or currently the Accipitriformes) monophyletic or polyphyletic?

- (ii) Are the New World vultures (Cathartidae) closer to the storks than to the diurnal birds of prey?
- (iii) Are the Old World vultures themselves (now 16 species) monophyletic or polyphyletic?
- (iv) Are *Gyps* species, i.e. the true griffons, recognised as comprising a superspecies, and if so what should their names and sequence be?
- (v) Is *Pseudogyps* recognised as the genus for the two smaller, tree-nesting white-backed vultures?
- (vi) How are the dark/black vultures (five species) to be treated?
- (vii) Finally, what should be a nomenclature and sequence for the Old World vultures?

Answers are as follows:

- (i) Earlier called the Falconiformes (e.g. by del Hoyo *et al.* 1994: 23) but now the Accipitriformes (from Ferguson-Lees & Christie 2001 onwards), the Order has included the Families Accipitridae and Pandionidae, and sometimes others, viz. Sagittariidae, Cathartidae and Falconidae. No modern study supports the monophyly of the Order (Griffiths *et al.* 2007: 594, Mindell *et al.* 2018: 12), which harks back to Jollie's (1976: 285) opinion.
- (ii) Whereas for years the similarities between New World vultures and storks were emphasised (up to Sibley & Monroe 1990: xii) such that Cathartidae were placed in the Order Ciconiiformes (Ferguson-Lees & Christie 2001: 6), today these vultures have their own Order Cathartiformes. This is now considered to be "sister to ... Accipitriformes" (Mindell *et al.* 2018: 5). Indeed these authors put the same age on these two Orders, arising about 60 Mya.

- (iii) The Old World vultures are now generally seen as a polyphyletic group. In particular, Gypaetus, Neophron and Gypohierax all sit comfortably with each other and with the harrier-hawks (gymnogenes) Polyboroides spp., and as a different lineage or clade to the core-vultures. Note that the Subfamily for this latter group is Accipitrinae, Tribe Gypini (del Hoyo & Collar 2014) or back to original name of (Subfamily) an Aegypiinae (Mindell et al. 2018).
- Five large vultures in the genus Gyps, viz. (iv) fulvus (1783), indicus (1786), coprotheres (1798), rueppelli (1852) and himalayensis (1869) (with their dates of scientific naming) share so many characteristics (Mundy 2002), and are just about allopatric to each other (Mundy et al. 1992: 20), as clearly to form a superspecies (Amadon 1966). This has been recognised by other authorities, e.g. Ferguson-Lees & Christie (2001: 7) and del Hoyo & Collar (2014: 526, but called a "species-group" by them). In my terminology these five species are griffons, which is a special kind of vulture, even a super-vulture. The newly accepted Slender-billed Vulture Gyps tenuirostris is not a griffon, rather so far an unusual kind of vulture (Mundy in press), though still a Gyps of some sort. What sequence should these five species have? _ by history/naming above), (as or on distribution perhaps? Note that *fulvus* and rueppelli have the largest ranges and coprotheres the smallest (Mundy et al. 1992: Table 2). Objectively, they should have the order dictated by the appearance of each taxon in the phylogenetic record. This puts the listing by Mindell et al. (2018: Figure 1.2c), as the 'front-runner', viz. himalayensis first, then rueppelli, fulvus,

[*tenuirostris*], *indicus* and *coprotheres* last. In fact these species are clustered tightly together, so one wonders how they differentiated them (not explained by these authors)? For example, the Himalayan Griffon is larger than all the others (Bergmann's rule?), was it really the first one to appear? Never mind, their list has something approaching an objective basis, and can be accepted for the time being.

The two white-backed vultures, bengalensis (v) and africanus, are not griffons but a different kind of bird though with some strong similarities; I have always thought of them as a 'compromise' vulture (Mundy 1982: 282) or perhaps a 'generalist'. Surely they have evolved away from the Gyps group which are specialists; how then can they have appeared before this group (Mindell et al. 2018: Figure 1.2c)? However, these authors are right to separate them off from the Gyps clade. They are similarly separated by Johnson et al. (2006: 6). Therefore, I have always appreciated Sharpe's (1873) viewpoint that they deserve their own genus *Pseudogyps*, though he did that distinction only on the number of tail feathers (12 in distinction to 14). Regretfully this distinction of *Pseudogyps* has always been scorned (e.g. Sibley & Monroe 1990: 271, Seibold & Helbig 1995: 163, Johnson et al. 2006: 1), or "subsumed into Gyps" (Griffiths et al. 2007: 598). The white-backed vultures are different from their local griffons, and I don't expect one gene (cytochrome b?) to be able to tell them apart. Arshad et al. (2009) used both the cytochrome b and a nuclear gene, and did not even mention *Pseudogyps*; the Indian White-rumped Vulture bengalensis showed the "earliest divergence" (op. cit.: 419). Mindell et al. (2018: 12) used ten genes and

also failed to mention *Pseudogyps*. Was their earliest divergence of *africanus* followed by *bengalensis*, about two million years ago (*op. cit.* : Figure 1.2c)? I wonder how many genes need to be examined before my adherence to *Pseudogyps* can be justified?

- (vi) All five species of dark/black vultures are each placed in their own monotypic genus by Mindell et al. (2018: Figure 1.2c). The same is done in version 10.2 of the IOC World Bird List. I think this is the correct treatment so far. But as regards the sequence of species, that shown by Mindell et al. (2018: Figure 1.2c) is preferable over that shown in their Table 1.1, in that Necrosyrtes monachus should be the link between this group of four black species and the larger Gyps clade. We previously thought of Necrosyrtes as an "excellent link" (Mundy et al. 1992: 28) between the two 'super-groups' of vultures, but without specifying our reasons. Lerner & Mindell (2005: 340) stated that Necrosyrtes is "more closely related to ... Gyps than to the other four [black] monotypic ... genera", though behaviourally and ecologically it is more similar to the latter group. Either way it should follow Gyps (actually the whitebacked vultures) and link them to the dark/black group. Curiously, Aegypius monachus is named the Cinereous Vulture (Amadon & Bull 1988: 310), Eurasian Black Vulture (del Hoyo et al. 1994: 128) and Monk Vulture (Ferguson-Lees & Christie 2001: 7 and 437). The name Cinereous, meaning ashy/ashy-grey, fits the adult bird the best.
- (vii) In summary, and considering all the above points, I have shown my preferred nomenclature and sequence for the Old World vultures in Table 1.

Table 1: Names and sequence of Old World vultures as preferred by me (P.J.Mundy).

Order Accipitriformes		
Family Accipitridae		
Subfamily Gypaetinae		
Palm-nut Vulture	Gypohierax angolensis	
Bearded Vulture	Gypaetus barbatus	
Egyptian Vulture	Neophron percnopterus	
Subfamily Accipitrinae		
Himalayan Griffon	Gyps himalayensis *	
Rüppell's Griffon	Gyps rueppelli *	
Eurasian Griffon	Gyps fulvus *	
Indian Griffon	Gyps indicus *	
Cape Griffon	Gyps coprotheres *	
Slender-billed Vulture	Gyps tenuirostris	
African White-backed Vulture	Pseudogyps africanus	
Indian White-rumped Vulture	Pseudogyps bengalensis	
Hooded Vulture	Necrosyrtes monachus	
Cinereous Vulture	Aegypius monachus	
Lappet-faced Vulture	Torgos tracheliotos	
White-headed Vulture	Trigonoceps occipitalis	
Red-headed Vulture	Sarcogyps calvus	

Note: those Gyps species marked with an asterisk (*) comprise a superspecies.

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