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Review

Everything mammal conservation biologists always wanted to know about taxonomy (but were afraid to ask)

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ABSTRACT

Conservation biology and biodiversity are today disciplines that no serious biologist can ignore, yet the practical importance and scientific value of taxonomy is greatly overlooked in today conservation practice. This is particularly true for researchers that have spent most of their time investigating the biology and management of a few species of mammals in a few places. It is here highlighted that the trend to replace taxonomic infraspecific units by ad hoc ecological and 'conservational' units having no universality is based on a misunderstanding of the concept of taxon as being a fixist and essentialist one. In this perspective paper, based on the author's experience, several case-studies are discussed showing how a misunderstanding of taxonomy hampers biodiversity cataloguing and, by consequence, conservation of evolutionary history.

1. Introduction

Most modern biologists have such a disregard of taxonomy and nomenclature that often they use the Linnaean binominals just to comply with norms or better bestow an appropriate sense of 'science' to a manuscript. Gippoliti and Groves (2018) offered a brief historical perspective on the causes and effects of this trend of abandonment of taxonomy and descriptive biology in European mammalogy in favour of such fields as experimental biology and genetics. While taxonomy has been defended by some of the most eminent contemporary biologists (May, 2004; Wilson, 2004), it seems that among conservation biologists, especially those dedicating their life to one or few species of large mammals (the great majority), the simple word 'taxonomy' emanates an outdated flavour of fixism and of museums, of office work, dust, skins and skulls, and even underlying 'racism' in some cases, that is perceived, negatively, as the opposite of field work, open air, behavioural ecology, wildlife, evolutionary biology and, obviously, conservation biology (but see McNeely, 2002). So one always finds a chapter on taxonomy while dealing with a treatise on specific mammal taxa (generally compiled by a 'behavioural ecologist' or 'evolutionary biologist'), typically including old references if not just one basic paper offering very simplified taxonomies that, despite being challenged by modern research (i.e., phylogeographic or behavioral), are given as static and unchanging. One serious consequence is that this last 'authoritative' taxonomic synthesis (assuming one is available) represents for many researchers a starting point for investigating taxonomic issues. If, as has often been the case, the author severely oversimplifies the taxonomy of a living organism, acquiescing to the fashion of "taxonomic inertia" (Gippoliti, Cotterill, Zinner, & Groves, 2018), all previous literature, including much original and detailed taxonomic work, is destined to disappear from global scientific knowledge. Furthermore, in biological circles taxonomy is often seen as a service, not a scientific discipline, with its value being measured by its provision of the simpler and more stable species' lists (Holyński, 2017; see also Dubois, 1998).

It should be emphasized at this point that study collections in modern museums are a direct result of the Darwinian revolution with its emphasis on variability and evolution, yet most biologists hold the pre-Darwinian view that a museum collection should have one 'typical' specimen for each 'species' considered enough for zoological studies to the extent that other specimens – duplicates – were exchanged with other museums. It is no surprise that current genetic research is often in disagreement with the prevailing taxonomic accounts for a given species or genus, but most biologists acknowledge the fact without providing explanations or alternative views – as though taxonomy had negligible relevance to biological variability and his study.

On the other hand, caution is required when dealing with the results of genetic data. In the words of Goldstein, DeSalle, Amato, and Vogler (2000), "There continues to be considerable confusion, however, over the appropriate utilization and relevance of most kinds of genetic data [.….]. We maintain that this confusion revolves around inferring the appropriate biological boundaries to which certain analytical methods can legitimately be applied. Specifically, some studies have confused character data intended for diagnostic purposes with adaptive information geared toward identifying "evolutionary significance" or

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Table 1
Taxonomy of American *Rangifer* in the 20th century. Taxa listed separately in the two groups; Tundra and Forest reindeer.

	Grant (1902)	Miller (1924)	Allen (1942)	Banfield (1961)
Tundra group	*R. arcticus*	*R. arcticus arcticus*	*R. arcticus arcticus*	
	R. groenlandicus	*R. groenlandicus*	*R. arcticus groenlandicus*	*R. t. groenlandicus*
	R. pearyi	*R. pearyi*	*R. arcticus pearyi*	*R. t. pearyi*
	R. granti	*R. granti*	*R. arcticus granti*	*R. t. granti*
		R. arcticus ogilvyensis	*R. arcticus osborni*	*R. t. eogroenlandicus*
		R. excelsifrons		
		R. arcticus caboti	*R. arcticus caboti*	
Forest group		*R. dawsoni*	*R. dawsoni*	*R. t. dawsoni*
	R. caribou	*R. caribou caribou*	*R. caribou caribou*	*R. t. caribou*
		R. caribou sylvestris	*R. caribou sylvestris*	
	R. terraenovae	*R. terraenovae*	*R. terraenovae*	
	R. montanus	*R. montanus*	*R. montanus*	
	R. osborni	*R. osborni*		
	R. stonei	*R. stonei*	*R. arcticus stonei*	
		R. mcguirei		
		R. fortidens		

"evolutionary potential"." Goldstein et al. (2000: 121).

Although it is not always feasible to associate results of new genetic studies with previous taxonomic studies, a cursory examination of all available literature should offer some insight about the existence of overlooked morphological differentiation in the studied taxon. Genetic data can furnish today the first evidence of the uniqueness of a particular population, and should be appropriately considered in conservation strategies even if an integrative approach to taxonomic questions should remain the final goal (Padial, Miralles, De la Riva, & Vences, 2010).

One of the most paradigmatic case studies is offered by the taxonomy of caribou (or reindeer) *Rangifer tarandus*. Here the classic reference is that of Banfield (1961), who, in agreement with the spirit of the time, had lumped all he could into one species and nine (six in America) subspecies (Table 1). Geist (2007) recalled that the paper drew criticism as soon as it appeared, but apparently none was published. In recent decades, there has been a growing body of evidence that the situation is much more complicated (as implied by older taxonomic accounts), yet the solution has been not to revise again the *Rangifer* taxonomy, but to create a radically new infra-specific terminology to accommodate the evident diversity. Accordingly, Canadian wildlife biologists and authorities rely on a list of ecotypes (four or five) (Festa-Bianchet, Ray, Boutin, Côté, & Gunn, 2011) and, below these, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2011) recognises 11 Designatable Units (DUs). These DUs are identified as irreplaceable components of Canada's biodiversity, and constitute evolutionarily significant and discrete populations or collections of populations. Naming conventions do not always correspond, however, between jurisdictions, and ecotype identification can be ambiguous (COSEWIC, 2011; Pond, Brown, Wilson, & Schaefer, 2016). As a result, papers are often incomprehensible for non-specialists (and I suspect also for some specialists), while genetic data are rarely obtained for all described taxa beyond those currently accepted, or for unambiguous 'ecotypes', as they are defined simply by the names of places and herds, etc.

Were it not for the population declines of several caribou 'types', their questionable taxonomy might never again have become a scientific issue. Valerius Geist, although following the Biological Species Concept (BSC) orthodoxy (but see below) and thus not challenging the mono-specificity of *Rangifer*, at least called for greater attention to obviously distinct subspecies, especially among the so-called woodland caribou, *Rangifer tarandus caribou* Gmelin, 1788, which he regarded as a catch-all for larger caribou. Banfield (1961) lumped into this subspecies not only the (a) true woodland caribou, but also (b) the insular endemic Newfoundland caribou (*R. t. terraenovae* Bangs, 1896), the (c) barren-ground form most closely related to true woodland caribou but nevertheless biologically distinct, the Labrador caribou (*R. t. caboti* Allen, 1914), as well as the (d) western Osborn's caribou (*R. t. osborni* Allen, 1902) from British Columbia (Geist, 2007: 25). With a few exceptions, it seems that Geist's call for a revised taxonomy was not met with any substantial reply in the following decade. Concerned with the potential loss of diversity within *Rangifer*, Miller, Barry, Calvert, and Zittlau (2007) concluded that "the use of the subspecies as the basic unit in the conservation of endangered caribou (*Rangifer tarandus*) would produce a 'melting pot' end-product that would mask important genotypic, phenotypic, ecological, and behavioural variations found below the level of the subspecies. Therefore, we examined options for establishing the basic conservation unit for an endangered caribou population: use of subspecies based on taxonomy, subspecies based solely on mtDNA, Evolutionarily Significant Units, and the geographic population. We reject the first three and conclude that the only feasible basic unit for biologically and ecologically sound conservation of endangered caribou in North America is the geographic population" (Miller et al., 2007: 19). Thus, Miller and co-authors thought of Banfield's taxonomy as written in stone and failed to consider the simple possibility that it should be changed and improved through the results of half a century of new scientific evidence, more specimens, and more tools (in two words, through a 'taxonomic revision'). The trend to replace taxonomic infra-specific units (subspecies and 'aggregates of subspecies' as recognised by the International Code of Zoological Nomenclature, Anonymous 1999) by ad hoc ecological and 'conservational' units having no universality is based on a misunderstanding of the concept of taxon as being a fixist and essentialist one (Dubois, 2006a). Much has been written about 'taxonomic stability' and its negative effects (Padial & De la Riva, 2006). Among others, Bremer, Bremler, Karis, and Källersjöm (1990), Dominguez and Wheeler (1997), Dubois (2005) and Gaffney (1977, 1979), insisted that, in taxonomy, "stability is ignorance". It is clear from the *Rangifer* case-study that the abandonment of taxonomy had a serious impact on the conservation and management policies, and that taxonomy must be considered an independent scientific discipline that should be wielded by experts of the sector (Dubois, 2003). The mismatch between proposed subspecific taxonomy of black rhinoceros *Diceros bicornis* and the management units (or 'ecotypes') recognised by conservation managers (Rookmaaker, 2011) demonstrate that this issue deserves more widespread attention.

2. Descent versus adaptation

Geist, O'Gara, and Hoffmann (2000) demonstrated the presence of this conflict in systematic biology. The formal and informal taxonomies of the caribou represent an extreme step toward classification by appearance and ecological adaptation rather than phyletic relationships. In a little-known paper centred on the Svalbard reindeer, the Italian zoologist Lorenzo Camerano identified some of the problems associated with a classification of *Rangifer* regarding the criteria of phylogenetic relationship and diagnosability, aside from simple size differences (allometry) (Camerano, 1902; Gippoliti & Robovský, 2018). Accordingly, based on a large collection of Svalbard skulls as well as some Eurasian and American specimens, Camerano remarked that the most informative part of the skull for taxonomic research was the inferior part (including dentition), while the superior part of the cranium was influenced by the form of the antlers, the latter aspect being linked to the environments where the reindeer live. He thus coined the term 'Cylindricornis' for the large and rounded antlers typical of open habitats, and 'Compressicornis' for the smaller antlers typical of forest-living reindeer. He was well aware this was not a taxonomic distinction, yet Banfield (1961) largely used antler size and shape for his taxonomic revision, and separated the seven subspecies he recognized in the two groups Cylindricornis and Compressicornis (Banfield, 1961).

Genetic assessments using mitochondrial DNA (mtDNA) have attributed the most pronounced intraspecific split (first formally described as subspecies by Banfield in 1961) to two distinct phylogeographical lineages that originated south of the American/Laurentide ice sheets (North American lineage; NAL) and north of the ice sheets (Beringian–Eurasian lineage; BEL) (Cronin, MacNeil, & Patton, 2005; Flagstad & Røed, 2003; Klütsch, Manseau, & Wilson, 2012; McDevitt et al., 2009; Weckworth, Musiani, McDevitt, Hebblewhite, & Mariani, 2012; Yannic et al., 2014). Polfus et al. (2016) demonstrated that independent evolutionary trajectories can converge on a similar phenotype and, for the first time, showed that the boreal ecotype of caribou in North America contained two phylogeographical assemblages (confirming the earlier findings of Camerano).

3. Conservation implications

Cotterill, Taylor, Gippoliti, Bishop, and Groves (2014), Groves and Grubb (2011), Groves et al. (2017) and Gippoliti, Cotterill, Zinner et al. (2018) were not the first to advocate for the superiority of the Evolutionary Species Concept in the framework of conservation practice. Geist et al. (2000) argued that: "For conservation purposes, the classification of species as adaptive radiations, the 'evolutionary species concept', is superior to any guesswork about 'biological species' based on conjectures about what might, or might not, happen to hybrids in nature should the different forms ever meet. In short, while the biological species concept is theoretically elegant, it is in practice so difficult to apply to large mammals as to be virtually useless. Classification and nomenclature based on the evolutionary species concept is more consistent with phylogeny and thus scientifically more significant than an unnatural misapplication of the biological species concept." (Geist et al., 2000: 6). Goldstein et al. (2000) were among the few to discuss the overlooked delimitation of conservation units at the species/subspecies boundary in a phylogenetic framework. The critical fact is that units recognised by taxonomic revisions should be recognised as units for conservation, whatever their taxonomic level (and taxonomists should be freed from political oversight to make those decisions). A taxonomic splitting approach is superior because it draws attention towards otherwise overlooked populations (Diniz-Filho, Loyola, Raia, Mooers, & Bini, 2013; Thakur, Wullschleger, Schättin, & McShea, 2018). Discovery or rediscovery of narrow endemics and their recognition as species lineages is a powerful tool to direct more scientific attention toward critical habitats and regions (cf. Taylor, Denys, & Cotterill, 2019). After its rediscovery and its classification as a separate species, the uniquely forest-adapted Bale grivet monkey *Chlorocebus djamdjamensis* (Carpaneto & Gippoliti, 1994; Groves, 2001) has become an effective umbrella species for montane forest conservation and tourism in southern Ethiopia (Mekonnen, Bekele, Fashing, Hemson, & Atickem, 2010; Mekonnen, Bekele, Hemson, Teshome, & Atickem, 2010). It is interesting to note that if *C. djamdjamensis* had been considered a subspecies, the scientific interest would have remained low mainly because it would have 'disappeared' in a country so particularly rich in endemism as Ethiopia. This is clearly demonstrated by the minimal attention given to the classically accepted but never taxonomically revised subspecies of *Colobus guereza*, such as *C. g. gallarum* (but see Zinner et al., 2019). Interestingly, it is possible that in absence of a clear demarcation between taxonomic entities, some studies of *Colobus guereza gallarum* had in fact failed to study the true members of this highly distinctive and threatened taxon (Gippoliti, pers. obs.).

4. Importance of taxonomy for comparative biology

Discussing the relevance of taxonomic studies, Camerano (1901) explained clearly how the exact knowledge of the taxonomy of 'model' species in experimental biology was a basic requirement for a correct analysis and comparison of the results. Philip Herskhovitz had to highlight the same concept while dealing with the growing interest for primatological research in the US (Herskhovitz, 1965). The problem here lies not so much in the rank accorded to the studied taxa, but primarily in their recognition. If I consider the olive baboon *Papio anubis* a subspecies or a species, the use of a Latin name (binominal or trinominal) – perhaps coupled with the geographic origin of the study material – allows other researchers to make full use of previous data for their meta-analysis. However, it should be stressed that an overly synthetic approach at the species level is followed generally by a similar synthetic approach even at the intraspecific level. How can one deal taxonomically with the different forms of olive baboon found on the Ethiopian highlands (*P. doguera*) and the Sudan lowlands (*P. heuglini*) if *P.anubis* is treated as a subspecies? This was possibly one reason that had led some systematists to adopt the concepts of 'superspecies' and 'semispecies' (Amadon, 1966). Dandelot (1971) adopted it for African primates and in some way opened the way to a more analysis-based taxonomy. Interestingly some animals such as the brown bear *Ursus arctos*, that clearly accommodates "populations that have acquired some, but not yet all, attributes of species' rank; borderline cases between species and subspecies" (Mayr, 1963: 671) have never been subjected to such an approach. Consequences are long-lived even today with a strong opposition to test the conspecificity of the several taxa presently subsumed under *Ursus arctos* (Gippoliti, 2016), as we have also seen with caribou. The result is that much 'intraspecific' variability among commonly recognised mammal species continue to be overlooked in both field studies and in conservation concerns (Robuchon et al., 2019; Thakur et al., 2018). This is particularly true – dangerously so - for restricted range taxa in little-known geographic areas. Neglect of taxonomic issues is often accompanied by a total disregard for literature older than twenty-thirty years. Here the cost is evident especially in those regions where there has been scant scientific activities in recent decades. Interestingly, some currently 'difficult' regions, such as Sudan and Eritrea, were among the first to be penetrated by western explorers, explaining why the old literature is not always easily replaced by modern texts. In their classic synthesis on Ethiopian mammals, Yalden, Largen, and Kock (1977) often used the argument that "too many subspecies have been recognized for a restricted Region" to justify a very simplified taxonomy at both species and subspecies level, thus completely ignoring environmental complexity as a speciation force. Before Carpaneto and Gippoliti (1994) 'rediscovered' *Chlorocebus djamdjamensis* and subsequent researchers confirmed their taxonomic distinctiveness (Groves, 2001; Haus et al., 2013; Mekonnen et al., 2018) some strange-looking grivet monkeys from Ethiopia had reached some laboratories in eastern Europe and some – luckily – found their way to Jilhava Zoo in the Czech Republic, which undertook a quest for their identity. If inexperienced biologists use as a starting point oversimplified references, there is a high risk that poorly based assumptions are maintained, which, with time and repetition, become credible, but no more scientific. A case in point, again from the Horn of Africa, is the continuing neglect surrounding the existence and conservation status of the Nubian wild ass *Equus africanus africanus* (cf. Moehlman, Kebede, & Yohann, 2015), whose phylogenetic distinctiveness from the Somali wild ass *Equus africanus somaliensis* has been confirmed by molecular data (Kimura et al., 2011).

At a certain point during the 20th century, ethologists assumed a key role in resolving taxonomic details among mammals, with apparently poor results if we look at the state of knowledge of the canids, one of the most studied mammal group, in Africa (cf. Gaubert et al., 2012; Saleh & Basuony, 2014). Poor taxonomy exerted its costs on several scientific disciplines, including behavioural ecology itself. Lacking vouchers and provenance, it is not uncommon today to have problems with the determination of the exact identity of a species being observed and studied in captivity (see Gippoliti, 2017 for discussion regarding research on patas monkeys of the genus *Erythrocebus*). Likewise in karyological research it is often difficult to know exactly to which species the described chromosomes had belonged. It is also possible that behavioural and personality differences reported in some species (i.e. chimpanzee) are an artefact of ignorance of the taxonomic identity of the individuals observed in zoos and laboratories (Gippoliti, pers. obs.).

5. Importance of types, vouchers and history

At least in mammalogy, often very little importance is given to type specimens and, more generally, to historical facts linked to the early scientific study of a taxon. I have shown that an historical approach is crucial to understand the geographical gaps (often enormous) in our museum materials and general knowledge of the Ethiopian endemic monkeys of the genus *Theropithecus* (Gippoliti, 2010). In the same paper it was discovered that some specimens in the Chicago's Field Museum of Natural History evidenced the historical presence of geladas in Gojjam, where the species appears extirpated today (Zinner et al., 2018). Despite the rich documentation surrounding the Field Museum expedition to Ethiopia (Fuertes & Osgood, 1936), some primatologists maintain that these are disputed records, denying objectivity to vouchers that form the basis of our knowledge of the biological world (see also Gippoliti, 2018). There are however interesting examples of better integration between museums data and biodiversity conservation planning in some lesser-known African countries such as Mozambique and Togo (Amori et al., 2016; Neves, Da Luz Mathias, & Bastos-Silveira, 2018).

The lack of images of a described taxon or the disappearance of its type or type series can cause a proposed name to be treated as a synonym. An exemplary case was recalled to me by the staff of a medium-sized Italian museum. An international expert on African mammals asked to examine the few specimens of hyrax, Procaviidae, in the museum's collection. During the visit, he noted that the labels of two specimens reported a wrong (or outdated) designation. Neither he, nor the curatorial staff had any suspicion that the person who labelled the specimens was author of this 'wrong' species name and that they were actually looking at the type series! This is just one of the consequences of indolence in taxonomic science and natural history museums, pervasive particularly in some western European countries during the 20th century (Andreone et al., 2014; Gippoliti, Amori, Castiglia, Colangelo, & Capanna, 2014). It should be added that often overlooked is that critical specimens may be in museums other than those that are (currently) most important in Europe and America. As a consequence some taxa and geographic regions can be overlooked in prominent phylogeographic studies. To provide just one example, it was discovered that the four specimens of *Alcelaphus tora* used by Flagstad, Syvertsen, Stenseth, and Jakobsen (2001) to study the evolution of hartebeests did not include any topotypical specimen but the type series of *Alcelaphus tora rahatensis* Neumann, 1906 plus an additional Sudan specimen not referable to *tora* (Gippoliti, pers. data). Clearly this situation could be rectified by looking for specimens from Eritrea that are certainly stored in some Italian museums.

6. Breeding for *ex situ* conservation

Taxonomy is particularly important regarding *ex situ* conservation endeavours. Recognition of this resulted in the development of the Evolutionary Significant Unit (ESU) concept (Ryder, 1986) as a means to recognize and deal with conservation units below the species level. The determination of infraspecific units of conservation has since become a prominent field of research (Coates, Byrne, & Moritz, 2018).

The current emphasis to increase genetic variation 'at all costs' is destined to have a considerable impact on *ex situ* populations. Mixing different subspecies of Dama gazelle (*Nanger dama*) (Senn et al., 2014; but see Schreiber, Moreno, Groves, & Robovský, 2018) has been suggested as a way to combat the small number of founders in the *Nanger dama mhorr* population, a taxon already extinct in the wild. Is this step really necessary at this time? Scientific studies have repeatedly reported instances of outbreeding depression observed in long-term managed, apparently monotypic species such as *Oryx leucoryx* (Marshall & Spalton, 2000) or those species exhibiting high karyotypic variability as *Nanger soemmerringi* (Benirschke, Kumamoto, Olsen, Williams, & Oosterhuis, 1984). Analysis of population demographic values between pure and introgressed captive populations of wisent *Bos bonasus* and the Mongolian wild horse *Equus przewalskii* show that the introgressed individuals have not fewer health problems than non-introgressed ones (Gippoliti, Cotterill, Groves, & Zinner, 2018). This should logically call for a cautious approach and the maintenance of non-introgressed stocks as benchmarks for future reference (Groves, 1995). Even captive stocks of relatively secure species may regain a conservation role if populations *in situ* are declining or in trouble. Recently there has been increasing concern regarding introgression between *Connochaetes gnou* and other, introduced gnu species in South African game reserves — the zoo stocks could become crucial for the maintenance of a pure population (Grobler et al., 2011). However, traditional taxonomy is instead often dismissed by *ex situ* managers who fail to understand that phenotypic differentiation is often indirect evidence of a history of lineage sorting and regional adaptation (cf. Steiner et al., 2016).

Ex situ resources are certainly limited but there are other solutions rather than lumping and promoting an old-style, BSC-based taxonomy just for the sake of convenience. There should be more attention to phylogenetically diverse or species-poor lineages (Cadotte & Davies, 2010). There should be an increased emphasis on breeding programmes and collaboration with other bodies/institutions and the private sector, so as to increase space availability and population size of *ex situ* populations. It should be noted that, if the international conservation community (including zoos) raise the profile of an endemic taxon, be it the Javan leopard or the Apennine brown bear (Gippoliti, 2004) it can possibly lead to increased attention by the national and local communities *in situ*, so that zoos can help save species in the wild, even without reintroductions. It is difficult, after all, to care for something that is perceived as dispensable (Gippoliti, 2019).

7. Conclusions

'Annihilation' of vertebrate population diversity has been clearly demonstrated by *ad hoc* meta analysis (Ceballos, Ehrlich, & Dirzo, 2017). Regrettably, the failure of conservation biologists and other stakeholders to appreciate that taxonomic research elucidates the evolutionary history of taxa must be considered a further factor limiting the effectiveness of the conservation community to fight biodiversity loss. Study of biological diversity and evolutionary processes represents the most crucial challenge for the present and future generations. In absence of a basic understanding of phylogenetic data, conservation cannot be informed by a simple remedy such as the so-called 'genetic rescue' without provoking a further loss of the planet's evolutionary history (Dubois, 2006b; Gippoliti, Cotterill, Groves et al., 2018; Leech, Jelinski, DeGroot, & Kuzyk, 2017). A clearer understanding among all practitioners of the value of taxonomy and of the differences between the disciplines of population genetics and systematics is required, as designation of conservation units is often encountered at the interface of population genetics and systematics (DeSalle & Amato, 2004). A better understanding of the taxonomy of some of the most iconic organisms of the Earth, such as 'brown bears', 'caribous', 'giraffes' and 'African golden jackals' represent a decisive step not only for conserving the evolutionary history of these species-complexes, but to identify overlooked biodiversity hotspots that urgently need more attention.

Declaration of Competing Interest

I declare that there are no conflicts of interest in relation with this paper.

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