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REVIEW

Lorenzo Camerano (1856–1917) and his contribution to large mammal phylogeny and taxonomy, with particular reference to the genera *Capra*, *Rupicapra* and *Rangifer*

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Abstract
In this paper, we commemorate the professional activity of Prof. Lorenzo Camerano 100 years after his death on 22 November 1917, with a special emphasis on his mammalogical studies. Our two aims are to widespread some of his little-known results on the systematic and phylogenetics of ungulates (particularly of the genus *Capra*) and to increase knowledge about that particular period of taxonomic research in Europe before the advent of the New Synthesis. Of particular interest are some of the results concerning the recent evolutionary history of chamois in Western Europe. Camerano, through specimen-based research based on abundant material, was able to design a phylogeographic picture that was confirmed by genetic studies only a few years ago.

Keywords Mammalogy · Species concept · Hybridization · Phylogeography · Specimen-based taxonomy

1 Introduction

Remembering the taxonomic work of Lorenzo Camerano (Fig. 1) 100 years after his death is an occasion to call for a new foundation of systematic comparative mammalian biology in Europe. Perhaps better known for the herpetological contributions and descriptions of new species (i.e. *Pelophylax lessonae*, *Archaeolacerta bedriagae*), the mammalogical work of Camerano cannot be simply dismissed as that of an old-fashioned museum taxonomist (leaving aside any consideration of the negative perception generally given to museum scientists and their contribution to Natural History), considering his internationally known contribution to ecology and his statistical approach to biology (Cohen 1994; McCann 2014). Yet, following a number of circumstances linked to paradigm shifts in science (Gippoliti and Groves 2012, in press) and the predominance of English as scientific language, the papers of Camerano dealing with mammal taxonomy are often simply ignored today by the overall majority of mammalogists (for a complete list of his papers, see Rosa 1918).

Lorenzo Camerano was born in Biella (Piedmont, Italy) and spent all of his scientific career at Turin University. There, in 1894, he became the director of the Zoological Museum, which, under his care, became world-renewed. He had several scientific interests, among them systematics and herpetology, and he was the pre-eminent taxonomic authority on Gordian worms (Nematomorpha) of his time. Of special interest for mammalogists are the several studies he made on skull morphology and the morphometrics of different mammal taxa, which were aimed at improving the scientific method to assess intra- and interspecific morphological variability. Camerano was ahead his time when he discussed the relationship between systematic biology and experimental biology; he highlighted that a finer taxonomic knowledge of living organisms is critical for the utilization of data resulting from experimental biology (cf. Jenner and Wills 2007; Attenborough 2015). He laments that, in his era, only in a very minimal fraction of published papers was one able to clearly understand the identity of the studied species (Camerano 1901b). Regrettably, as stressed already by Rosa (1918), the several technical

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Fig. 1 Portrait of Lorenzo Camerano

contributions of Camerano were easily overlooked by theoretic researchers of evolutionary studies. Although in Camerano's time, biodiversity conservation was still not perceived as a serious scientific issue, it is perhaps not an accident that the Royal decree to ban hunting of the Apennine chamois (*Rupicapra ornata*) on 9 January 1913 was prepared and discussed by Senator Camerano.

The widespread ignorance of Camerano's work among following generations is not easy to accept due to several factors. After all, his papers include primary data and conscientious attempts to compare particular taxa based on a plethora of characters (often on all available evidence), e.g. based on skull, teeth, postcranial and horn/antler measurements, and original methods of analysis of metric data (see also below). Camerano had, in reality, prepared the field for future improvements based on larger sample sizes and new methods. Some of his sample sizes were extraordinary (see below in *Rangifer* and *Rupicapra*), and some were similar to sample sizes of contemporary revisions (sample sizes of some taxa still today remain limited—see Scala and Lovari (1984) in *Rupicapra ornata* and *R. pyrenaica*). As we show below, some of his opinions fit well with current knowledge based on today's much more sophisticated statistical methods and more powerful data sets (i.e. genetic data).

2 Mammalian subspecies described by Camerano

Camerano described several mammalian subspecies (see Giglio-Tos 1917–1918; Wilson and Reeder 2005). One leopard subspecies, *Felis pardus ruwenzorii* Camerano, 1906, is currently synonymized with *Panthera pardus pardus* following the phylogeographic evaluation carried out by Uphyrkina et al. 2001. The issue of African leopard taxonomy, however, was relatively neglected after Pocock's (1932) paper (see also Anco et al. 2017; Dobroruka 1961, 1962, 1966a, b, c; Dobroruka and van Bree 1965). An additional form of Quagga, *Equus quagga Trouessarti* Camerano, 1908, synonym of *Equus quagga quagga* according to Groves and Bell (2004), is based on a voucher in the Turin Museum, while a plains zebra subspecies from Ethiopia, *Hippotigris Chapmanni Jallae* Camerano, 1902, is evidently a synonym of *Equus burchellii boehmi*. A subspecies of the Spanish ibex from Sierra Morena, *Capra pyrenaica cabrerae* Camerano, 1917, has often been overlooked owing to the scarce knowledge of the paper (cf. Ureña et al. 2018). And finally, a subspecies of Siberian ibex, *Capra sibirica filippii* Camerano, 1911, is generally considered a synonym of *Capra sibirica sakeen* (Groves and Grubb (2011).

Some authors consider Camerano's divisions of Reindeer, "*cilindricornis*" and "*compressicornis*" (Camerano 1902) as proposed taxa (e.g. Banfield 1961), or as something similar to taxa (Jacobi 1931), but both names are actually labels for two antler architecture types (ecotypic variation) in this genus (for detail see below). From a zoological nomenclature point of view, they are probably better considered as available names, although this was not clearly the intention of Camerano, who does not specify type specimens and type localities.

In general, Camerano's taxonomic work that focused on mammals was often devoted to disentangling intraspecific differentiation of groups (e.g. reindeer, caprines), some with speciation well underway (e.g. Geist 1998; Groves and Grubb 2011; Klütsch et al. 2012; Anco et al. 2017).

His work was always aimed at understanding the evolutionary histories of taxa and phylogenetic relationships to arrive at taxonomic conclusions that were in agreement with such history. For instance, in his classic study on *Rupicapra* he not only identified the three major lineages named *rupicapra*, *pyrenaica* and *ornata* (which he accepted as valid species), but on the basis of the rich Alpine materials he speculated that the western Alpine populations still showed traces of introgression between the modern chamois that had arrived from eastern Europe and the older *pyrenaica*/*ornata* inhabitants (Camerano 1915, 1916a). This is a remarkable result that came one century ahead of molecular studies (Rodríguez et al. 2010; Gippoliti 2013). In this and other instances (Iberian ibexes, cf. Camerano 1917/1918a), Camerano deals with hybridization as apparently a normal force of evolutionary history and speciation; in this, he was probably also influenced by a paper by a young Italian zoologist, Alessandro Ghigi, on hybridization in the origin of species (Ghigi 1912) and by the Hologenesis theory of Rosa (1909). The latter represents currently little-known speciation theory that was predated in several aspects of the phylogenetic revolution introduced later by Henning (Luzzatto et al. 2000). Again, Camerano was ahead of his time in this issue, as numerous current molecular studies show that hybridization and reticulation have been significant in the evolution of most mammalian orders (see e.g. Zinner et al. 2011; Groves et al. 2017 and references therein).

3 Genus *Rangifer*

Examining Camerano's contribution to reindeer taxonomy (Camerano 1902), one remains surprised at the amount of material he studied, specifically of the Svalbard/Spitsbergen taxon (49 more or less complete skulls of all ages; Fig. 2). He generously furnished the absolute measures of his samples to facilitate further studies, and he also analyzed his sample through his 'somatometric method' (Camerano 1900, 1901a). His idea was based on the work by Angelo Andres (1897) who had proposed to use the thousandth part of a base length for comparison purposes in zoology ("metodo di millesimi somatici" the method of somatic thousandths). The suggested method, however, stands for nothing other than expressing a relative ratio of two measurements in per mils through the formula L: 1000 = l: x where L is the one length (called as "base length") and l the another length of any body part under study. The use of such fractions seemed to be advantageous for comparative studies in biology.

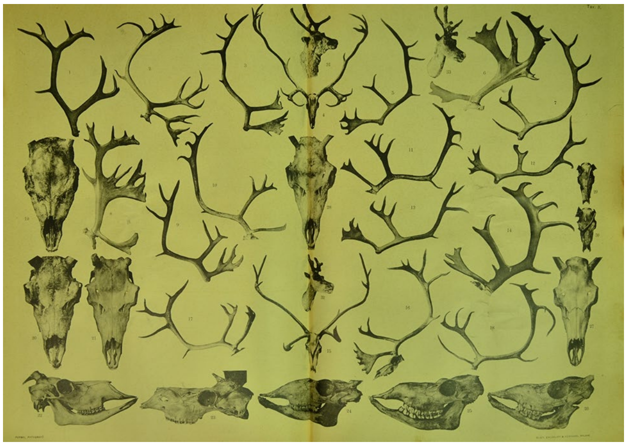

Fig. 2 Part of the *Rangifer* specimens studied by Camerano (1902)

Though Camerano admits that the application of Andres' method gives good results, he argues that computing the relation 1000/L is quite long and tedious. Therefore, he believes that using 360 instead of 1000 as numerator would straightforwardly satisfy the situation and serve the envisaged purpose better. He thus developed the equation $x = 360/L \times l$ and furnished in tabulated form most of the calculated somatic coefficient (Camerano 1900). He (and Andres) developed this method to overcome the problem of allometry in its broadest sense, i.e. the differences in proportions correlated with changes in absolute magnitude of the total organism or of the specific parts under consideration (Gould 1966). Furthermore, Camerano also devoted himself to the quantitative study of organisms using indices of variability, of variation, of the frequency of deviation, and of isolation (Camerano 1901c, d, 1903a).

All this must be seen in the light of the developing art of statistics at the turn of the twentieth century. Thus, in his publications reference is made to the progress achieved by the newly established English and American schools on quantitative studies of animals. The somatic index proposed by Camerano has been only a more or less suitable means for calculating ratios between two measurements at a time when computers were not available. Through this method, Camerano was better able to single out those measures that varied significantly within the sample before the introduction of multivariate analysis. Although Camerano's somatic coefficient is old-fashioned from the current perspective, it was a genuine and pioneering attempt to compare animal populations/species quantitatively and in the correct and comparable way, apparently much appreciated by anthropologists of his time (Neruda 2006). It was, however, ignored by zoologists (cf. Thorpe 1987).

The distinctive small size and very short legs of the Svalbard reindeer are well-appreciated (Jacobi 1931; Klein et al. 1987; Geist 1998). Yet Camerano seems to have been the first to accept *Rangifer spetsbergensis* (Andersén, 1862)—now *R. platyrhynchus* (Vrolik, 1829)—as a clearly valid species distinct from *R. tarandus*, mostly on the basis of skull characters. He found, for instance, qualitative differences in the shape of the orbit cavity, nasals more divergent in the anterior region and posteriorly depressed, and also quantitative differences, for example larger molars. The skull of the Svalbard reindeer overall was shorter and broader in comparison with that of *R. tarandus*.

Lönnberg (1910), Miller (1912) and Flerov (1933) followed him. Lydekker (1915) on the contrary held all reindeer taxa to be subspecies of *Rangifer tarandus*, a view that became the rule in the following decades (see Banfield 1961 and references therein). North American small-bodied arctic reindeer was still unknown in 1902, yet available genetic data confirm the dissimilarity of *Rangifer platyrhynchus* from two other small-bodied taxa *Rangifer pearyi* Allen, 1902 and *R. eogroenlandicus* Degerbøl, 1957 (Gravlund et al. 1998).

On the basis of a much smaller number of specimens for comparison, he could affirm the lack of notable differentiation between reindeers from Europe, Greenland and Siberia. Camerano, as we have seen, was also the first to establish the two general types of antler architecture in *Rangifer*, which he named varietà *cilindricornis* (occupying typically open habitats) and varietà *compressicornis* (occupying forest habitats). Camerano does not consider antlers to be a reliable taxonomic character (*contra* Bubenik, 1975) so these two names, even if italicised, should not be considered taxonomic entities, as explained in details in Camerano (1901b). It seems that while Camerano's paper was greatly neglected, paternity of his antler classification was given to Jacobi (1931) (e.g. Banfield 1961). Jacobi (1931) and Banfield (1961) followed early descriptions in grouping subspecies as either "tundra" reindeer/caribou (*cylindricornis*) or "forest" reindeer/caribou (*compressicornis*), based on the horizontal plain cross-sectional shape of the antler's main beam. It is interesting to note that molecular research has confirmed that the same 'ecotype' evolved in different evolutionary lineages, confirming Camerano's choice to direct attention to the basal part of the skull for phylogenetic/taxonomic studies.

Here, it is useful remember that, as Camerano had explained in a previous work (Camerano 1901b), he dislikes the term 'subspecies' and preferred 'varietà geografica', while he used the term 'varietà' itself to indicate morphological trends that have no taxonomic basis, such as antler shapes in reindeer. Although Camerano (1902) did not study American specimens, while discussing the photos of *Rangifer montanus* Seton-Thompson 1899 (Allen 1900) he reported that the skulls seemed to belong to the same group as Siberian reindeer, while the antlers appeared somewhat intermediate between those of *caribou* and *arcticus* (Camerano 1902:167).

Camerano was aware that subspecies are often designated with subjective and arbitrary criteria (see also Wilson and Brown 1953; Futuyma 1986; Geist 1991; Cronin 1997; Zink 2004). With his somatometric method, he wished to assess geographical variation in an objective way. In his criticism regarding Lydekker's approach to polytypic species (Lydekker 1915), Camerano also emphasized the importance of an 'equipollenza' criteria (equivalent value) among the recognized subspecies. A century later, the same problem was raised concerning below-species conservation plans within polytypic species (Gippoliti and Amori 2002, 2007).

Although some authors acknowledge that the environment affects skull and antler size and shape, using metric skull characters has persisted in *Rangifer* taxonomy (e.g. Manning 1960; Banfield 1961; Thomas and Everson 1982; Hakala et al. 1985; Gunn and Fournier 1996). The *negative* effects of an excessively morphometric-based taxonomy—which lumped together different taxa with similar skull and antler measurements—have been discussed by Geist for the 'woodland' caribou (2007), but it is a more widespread concern for several ungulate taxa (cf. Gippoliti et al. 2018).

Although there is a need for revision of the whole genus *Rangifer* based on morphological and genetic evidence, the peculiarity of Svalbard reindeer seems to be well supported already using morphological parameters and genetic evidence (e.g. Geist 1998; Groves and Grubb 2011; Kvie et al. 2016a, b), which accords perfectly with Camerano's evaluation.

Camerano produced another little-known paper on *Rangifer* where he analyzed a complete and a partial antler, and a right metatarsus collected on Franz Joseph Land (Camerano 1903b). After a detailed comparative study of metatarsus loaned from American museums, he concluded that such remains were probably carried by the sea to Franz Joseph Land after the death of the reindeer and that these animals do not belong to the Svalbard species, but to arctic representatives of *Rangifer tarandus*.

4 Genera *Rupicapra* and *Capra*

Camerano produced some of the best-documented studies on *Rupicapra* and *Capra* so far published (see references in this section). In contrast to some contemporaneous colleagues (e.g. Richard Lydekker), Camerano (1912) concurred with Miller's (1912) recognition of several *Rupicapra* species, but based on numerous dataset and detailed comparisons. Specifically, Miller (1912) recognized four *Rupicapra* species (*R. rupicapra, R. ornata, R. pyrenaica*, and *R. parva*), while Camerano (1916a, b) accepted three species (*R. rupicapra, R. pyrenaica and R. ornata)*—again in perfect accord with the current evidence derived from complex genetic studies (e.g. Rodríguez et al. 2010; Peréz et al. 2017). Thanks to the richness of the materials at his hand he also refuted the claim of the existence of five species of chamois from different Alpine regions that Matschie had proposed (but not named) in 1906. Regarding *Rupicapra* from the Alps, the Turin Museum had over 100 skins, over 300 skulls of all ages and over 70 horn pairs (Camerano 1914) and much more was measured and studied in private collections. This vast material allowed Camerano also to study the morphological variability of the species. Differences between forest and glacier chamois had been already reported by many researchers and hunters. Camerano evidenced the presence of two main color forms in the Alps, which he named varietà *fuscescens* and varietà *clarescens* (Camerano 1914: 31). The first one, darker, was more common in the north-eastern Alps, while the second one, lighter and with a wider throat patch, appeared to be more common in the south-western sectors of the Alps. Camerano argued this could be evidence of former introgression between a darker species from Eastern Europe and the older *pyrenaica*-like species.

Incidentally, he does not accept as valid the subspecies *caucasica* Lydekker, of which he studied 11 skulls, and the subspecies *asiatica* Lydekker, of which he could only examine the photos of the skull and skin of one of the syntypes (Camerano 1915). Regrettably, most of the considerable work undertook by Camerano would be overlooked by the forthcoming generations of European mammalogists (Gippoliti and Groves 2012, in press).

While his taxonomic conclusions on *Rupicapra* taxonomy are relatively well-known, much less seems to be known about his studies on the genus *Capra*, published during the First World War and just before his death. Specifically, Camerano produced two papers on phylogenetic relationship among members of the genus *Capra* (Camerano 1915/1916; 1916/1917) which apparently have never been cited in relevant literature (e.g. in otherwise exhaustive monographs—Heptner et al. 1966; Danilkin 2005), possibly as result of the state of war at the time and low circulation of the journal). In his first paper, Camerano extends an early observation of Forsyth Major (1879) regarding the position of palatine foramina to all members of the genus *Capra*. In particular, he notes that in *Capra ibex*, *Capra pyrenaica*, *Capra nubiana* and *Capra walia* the palatine foramina open well behind the maxillo-palatine suture, while in *Capra aegagrus*, *Capra caucasica* and *Capra sibirica* the palatine foramina are situated either in the correspondence of the maxilla-palatine suture or anteriorly to it (Camerano 1915/1916). Camerano proposes the name *Euibex* as subgenus for the first group, and *Eucapra* (= *Capra*) for the second. In the second paper, comparing the horns of *Capra ibex* and *Capra sibirica*, he concluded that the forms of knots differ notably, with those of *C. ibex* being compressed internally toward the horn while in *C. sibirica* the knots are equally developed both toward the horn and externally. What is more interesting is that the same differences exist among all members of *Euibex* and *Eucapra* that he was able to study (Camerano 1916/1917). Camerano noted that in *Euibex* the lacrimo-maxillary suture (which he called *fontanella fronto-naso-maxilla-lacrimale*) is quite large dorsally and has a grossly triangular shape. In this subgenus, the contact between the lacrimal and maxillary bones extends more than in *C. sibirica* and *C. caucasica* (Camerano 1915/1916: 569). The different extension of the lacrimal bones affects the shape of the suture, which in the subgenus is a narrow line, while in *C. aegagrus* and *C. hircus* it is much larger and grossly rectangular in shape (Fig. 3). Finally, Camerano (1916/1917) remarks as well that the coloration of *Capra sibirica*, as noted by von Liburnau (1906) and Lydekker too (1913), shows a closer affinity with *Capra aegagrus* (especially in the case of *C. sibirica hagenbecki* and *C. s. sibirica*—see Matschei 2012; Damm

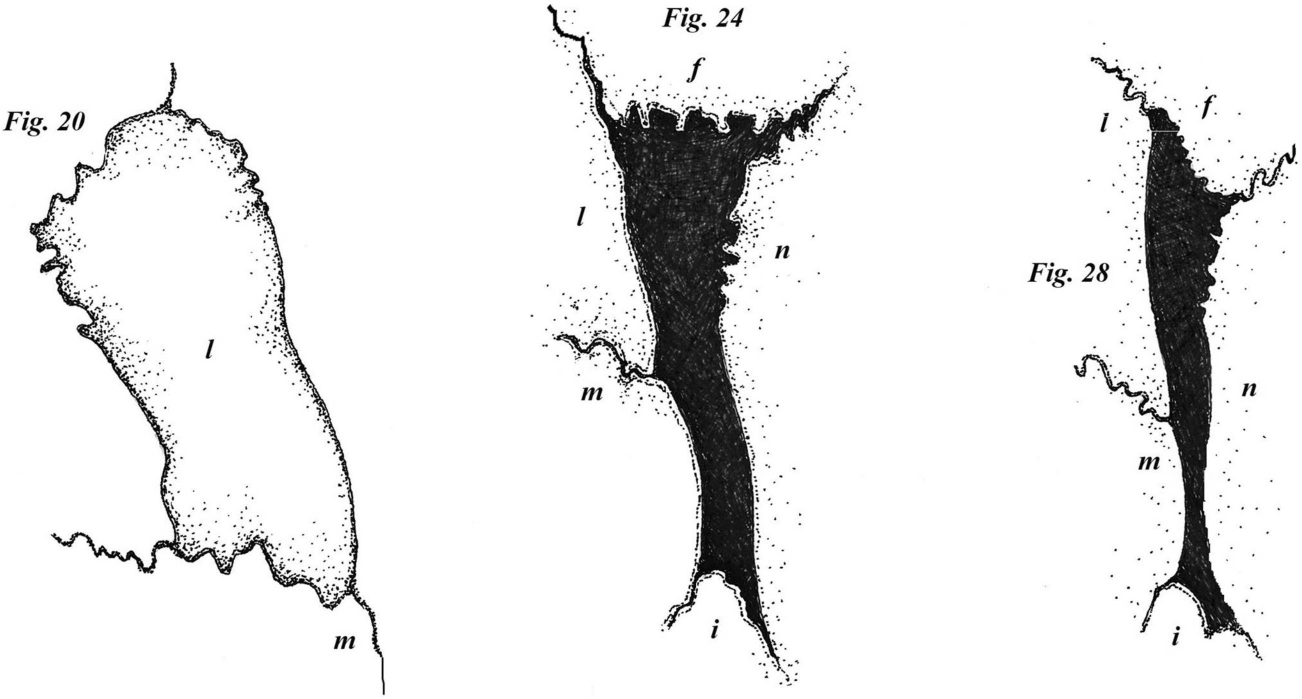

Fig. 3 Lacrimo-maxillari suture of *Capra sibirica* (n. 20), *Capra aegagrus* (n. 24) and *Capra nubiana* (n. 28). Redrawn from Camerano (1915/1916), courtesy Tommaso De Francesco

and Franco 2014), while nothing similar is known for *C. ibex*, *C. nubiana*, and *C. walia*, further supporting his subgeneric classification. This proposed and somewhat unorthodox view may have some phylogenetic legitimacy—see Zvychaynaya (2010).

Working out phylogenetic relationships among caprines is a challenge to mammalogists. Much work has been done to expose basic relationships (reviewed e.g. by Groves and Grubb 2011). It is also known that some species and lineages have undergone natural introgressions or could have an entirely hybrid origin (e.g. Pidancier et al. 2006; Ropiquet and Hassanin 2006; Zvychaynaya 2010; Groves and Grubb 2011). We reconstructed the distribution of *Euibex* and *Eucapra* character states (see above) using two published phylogenies, those of Zvychaynaya (2010) and Bibi et al. (2012), based on different datasets, specifically on mitochondrial and nuclear and on mitochondrial and morphological characters (Fig. 4a, b). In both cases, *Euibex* condition is restricted to two successive lineages, one comprising *Capra ibex* + *C. pyrenaica* (a bond Camerano was the first to support) and the second *C. nubiana* + *C. walie*. Regardless of whether *Capra falconeri* and *C. aegagrus* form the most basal lineage or lineage related to *C. caucasica* + *C. cylindricornis*, both reconstructions are ambiguous, as they require two evolutionary changes: two independent origins of *Euibex* condition or one origin of *Euibex*-condition and the subsequent reversal to *Eucapra*-condition.

In summary, *Euibex* and *Eucapra* conditions are not restricted to particular monophyletic groups, which make them inapplicable taxonomically, but they are certainly beneficial for reconstructing and understanding morphological evolution in caprines.

In his last published contributions, Camerano (1917/1918b, c) revised *Capra sibirica.* After analyzing all that was known at the time about skulls, horns and color patterns, he reached the conclusion that, mainly based on the presence or absence of a lighter saddle in adult male coats, two geographically separated species could be proposed: *Capra sibirica,* occurring in the north-east of the Altai Region, and *Capra sakeen,* with light saddle, occurring in the south-west. He also provisionally accepted *hagenbecki* as a valid subspecies of *Capra sibirica* and *wardi* as a valid subspecies of *Capra sakeen*. So far, only one species has been generally accepted, and the taxon *wardi* is now synonymized with *Capra sibirica sakeen* in the latest monographs (e.g. Groves and Grubb 2011; Damm and Franco 2014). Genetic and morphological data (Zvychainaya and Puzachenko 2009; Zvychaynaya 2010) seem to support recognition of two species among '*Capra sibirica*', with more or less the same geographical range outlined by Camerano.

5 Conclusions

We could summarize that, despite some ignorance of his work by numerous generations of zoologists, Camerano certainly had an extraordinary taxonomic perception. His scientific (mammalogical) contribution is a great one. Unorthodox in some views, it remains nonetheless predominantly correct, even in some tangled topics, and even when examining the up-to-date evidence obtained from independent data sets (e.g. DNA data), which is more than admirable.

As Rosa (1918) emphasized, Lorenzo Camerano was, among the other things, a systematic zoologist and a

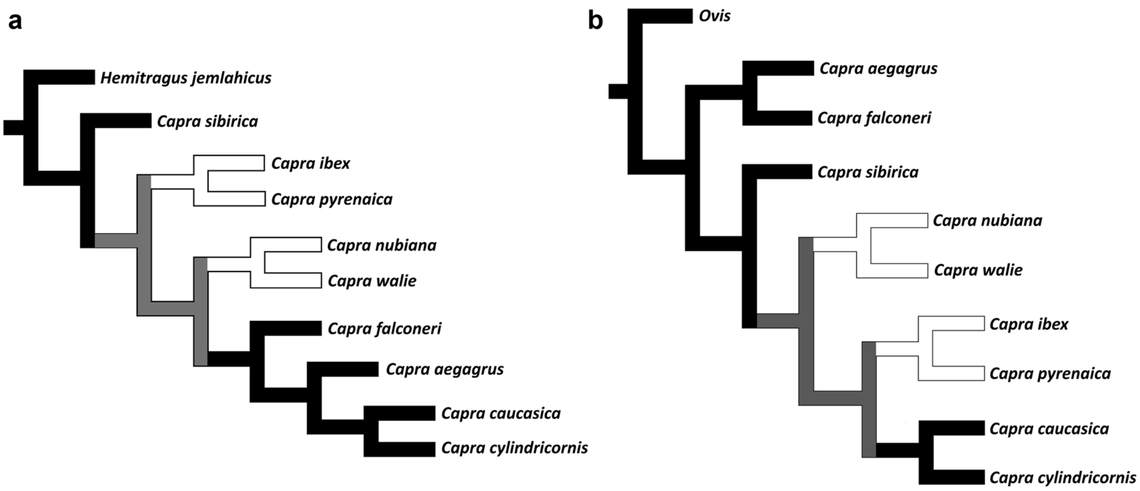

Fig. 4 **a** Reconstruction of *Euibex* (white) × *Eucapra* (black) character states using the phylogeny produced by Zvychaynaya (2010) based on mitochondrial cyt *b* and nuclear SRY genes. **b** Reconstruction of *Euibex* × *Eucapra* character states using the phylogeny produced by Bibi et al. (2012) based on mitochondrial cytochrome *b* and 52 morphological characters. The grey colour indicates an ambiguous reconstruction

Museum director, which negatively influenced the consideration that academic colleagues gave him. Further, he was a systematic zoologist of "banal" reptiles and amphibians, of invertebrates (a work that was and remains left largely to amateurs) and, we may add, of large mammals too! On his death a considerable gap opened up between mammalian collections, systematics and the research world in Italy, and it has not been yet filled (Gippoliti et al. 2014). Now that a certain amount of turmoil has been created by a taxonomic revision of the world's ungulates, doubling the number of recognized species (Groves and Grubb 2011), Lorenzo Camerano stands up as a giant, reminding us by his example that scientists must never be afraid to test new scientific hypotheses.

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