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Authors

Angelici, Francesco Maria
Colangelo, Paolo
Gippoliti, Spartaco

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Out of Europe: Investigating *Hystrix cristata* (Rodentia: Hystricidae) skull morphometric geographic variability in Africa

FRANCESCO M. ANGELICI[1*], PAOLO COLANGELO[2], SPARTACO GIPPOLITI[3]

[1] *FIZV, Via Marco Aurelio 2, I-00184 Rome (Italy)*
[2] *Consiglio Nazionale delle Ricerche, Istituto di Ricerca sugli Ecosistemi Terrestri, CNR-IRET, Via Salaria km 29.300, I-00015 Montelibretti, Rome (Italy)*
[3] *Società Italiana per la Storia della Fauna 'Giuseppe Altobello', Viale Liegi 48, I-00198 Rome (Italy)*

* corresponding author: francescomariaangelici@gmail.com

SUMMARY

The crested porcupine *Hystrix cristata* is one of the most well-known members of the Family Hystricidae, yet very little is known regarding its geographic variability in Africa. Two alternative hypotheses exist; pre-1940s classical taxonomy supported the existence of a distinct Eastern African species, *Hystrix galeata*, whereas recent molecular data seem to support only a North-South separation inside one single species, with the geographic-ecological barrier represented by the Sahara desert. Our morphometric data support the recognition of *Hystrix cristata senegalica* Cuvier, 1822 as the sub-Saharan representative of the species with a clear morphological difference between the North African and sub-Saharan crested porcupines, which seem re-conductible mostly to size difference. Within *H. c. senegalica*, our analysis seems to support a weak separation between the West African and the East African samples. Owing to considerable qualitative skull differences and overlooked molecular data, the taxonomic status of *H. galeata* remains uncertain as well as the status of porcupines of North-East Africa (Nubia). Our results also highlight the role of North Africa (mainly the Maghreb) as a refuge for the nominal taxon. This suggests that intraspecific variability is presently overlooked and that further integrative studies and more samples are needed to adequately assess the geographic variability of sub-Saharan crested porcupines.

INTRODUCTION

The Crested porcupine *Hystrix cristata* Linnaeus, 1758 is among the most studied species among the Old World family Hystricidae, especially thanks to several studies conducted in the European range of the species i.e. peninsular Italy and Sicily (Santini, 1980; Pigozzi, 1997; Amori & Angelici, 1999; Mori et al., 2016) while the species continues to be incorrectly reported as present also in Greece and Albania (Happold 2013) but has never been present in that area. While in the Italian

peninsula the species is experiencing a well-known northward range expansion (Amori & Angelici, 1992, 1999; Angelici & Amori, 1999; Spada et al., 2008; Mori et al., 2013), basic aspects relating to the taxonomy, distribution, behavioral ecology and population trends of the species in Africa remain unstudied. As currently understood, the monotypic *Hystrix cristata* occurs from desert oasis to 3,550 a.s.l. in Ethiopia (Afework Bekele & Yalden, 2013), along a wide geographic range encompassing several well-known centers of endemism such as the Somali Desert or the Ethiopian Dome (Moodly & Bruford, 2007). It is not clear if this wide distribution range may reflect its well-known ecological adaptability, and thus ability to overcome important biogeographical barriers such as the Nile Basin, the Ethiopian Highlands or the Sahara Desert – including the palaeo Chad Basin (Douady et al., 2003; Lihoreau et al., 2006), or alternatively if a more complex biogeographical history is masked by an oversimplified taxonomy, as is suspected with the African golden wolf, here referred to as the *Canis anthus* complex (Gippoliti, 2020), a taxon occurring over the same wide geographic range of *Hystrix cristata*.

Previous research has focused on the understanding of the origin of the species in Europe, with some authors arguing for a natural presence (Amori & Angelici, 1992) and others for an historic introduction from North Africa (Trucchi & Sbordoni, 2009; Masseti et al., 2010). Morphological data had evidenced that Italian crested porcupines are the smallest ones, and those from North Africa are just a little bigger (Corbet & Jones, 1965). More recent data (Angelici et al., 2003) showed that porcupines from Sicily are smaller than those from the Italian mainland. Molecular studies led some support to the hypothesis of a recent introduction of the Italian population (despite a genetic substructuring that it is not easily in agreement with a recent introduction) revealing a strong affinity between the Italian and Maghreb populations, while also highlighting the existence of a distinct sub-Saharan clade

that apparently extends in coastal Libya (see Trucchi & Sbordoni, 2009).

In the present paper we focus on the morphological diversity of *Hystrix cristata* over the whole range and propose a preliminary taxonomic assessment as basis to strength monitoring and conservation policy (cf. Gippoliti & Groves, 2020). It should be noted that details on the geographic distribution of the species in Africa are not well known and understood (e.g. cf Happold, 2013; Amori & De Smet, 2016). We included, for instance, most of the available materials from Somalia, a country that is excluded from the current range of the species (Amori & De Smet, 2016; Trucchi et al., 2016). Historically, some taxonomists recognized a distinct East African species, *Hystrix galeata* Thomas, 1893, possibly with a disjoint range from that of *H. cristata* (Mohr, 1965) and which would differ from *H. cristata* for larger dimensions and several morphological characters of the skull (Thomas, 1893; Lönnberg 1912; Mohr, 1965), while several subspecies of *Hystrix cristata* were recognized in West and North Africa (Cabrera, 1924; Ellermann, 1940; Mohr, 1965; Rosevear, 1969) based on skull size and shape.

The aim of this study is to assess if morphometrical data of the skull support a mainly North-South divide of *Hystrix cristata* (Corbet & Jones, 1965; Trucchi & Sbordoni, 2009) or a West-East sub-Saharan ones as implied by Mohr (1965) and the more recent paper by Trucchi et al. (2016). We discuss our results also in light of the two available molecular studies so far available, particularly the nuclear DNA study by Trucchi et al. (2016), which added some details regarding phylogeographic patterns of African *Hystrix cristata* that need further analysis.

MATERIALS AND METHODS

We analyzed 90 skulls of adult *Hystrix cristata* specimens (Table S1 in supplementary

material) from Peninsular Italy (24), Sicily (11) and Africa (55).

For each specimen, 22 linear measurements were collected on the skull following the same procedure described by Angelici et al. (2003). These 22 measurements (16 from the skull, and 6 from the mandible) are (Fig. 1): Nasal length (NL), Frontal length (FL), Parietal length (PaL), Interorbital maximum width (IW), Zygomatic maximum width (ZW), Zygomatic process minimum width (ZPW), Condylo-basal length (CL), Cranial height (CH), Foramen occipitalis width (FOW), Exoccipitalis height (EOH), Maximum length of upper left alveolar line (AL), Palatal length (PL), Central incisor foramina length (IFL), Bullae tympanicae width (BW), Post-tympanic processes width (PTW), Basi-occipitalis width (BOW), Mandibular length (ML), Mandibular maximum height (MH), Distance length of condylar process to angular appendix (CA), Distance length of condylar process to alveolar beginning (CAB), Maximum length of lower left alveolar line (LL), Distance length of condylar process to dental foramen (CAF). All the measurements are available in the Zenodo database (doi: 10.5281/zenodo.4579441).

All the linear measurements were recorded using a digital caliper (precision 0.01 mm) (Marcus, 1988), except for FOW, which was taken with a manual caliper (precision 0.05 mm). Adult specimens were recognized by the complete eruption of premolars and molars (cf. Mohr, 1965; Angelici & Luiselli, 1999).

Statistical analyses were performed in the R statistical environment v 4.0.2 (R Core Team, 2021). Some missing data, due to damaged or incomplete parts of some skulls, were present for some measurements with a percentage ranging from 1% up to a maximum of 14% (NL = 4.4%, IW = 1.1%, ZW = 14.4%, ZPW = 5.5%, FOW = 3.3%, EOH = 3.3%, BW = 2.2%, PTW = 5.5%, BOW = 5.5%, ML = 3.3%, MH = 1.1%, CA = 6.7%, CAB = 1.1%, CAF = 1.1%). In order to produce a complete analysis with all the specimens and all the measurements, missing data were imputed using the predictive mean matching method implemented in the R package mice v 3.12 (van Buuren & Groothuis-Oudshoorn 2011).

The occurrence of patterns of morphological differentiation across the whole sample was investigated by a Principal Component Analysis (PCA) performed on the covariance matrix, using the R package ADE4 v 1.7-16 (Dray & Dufour, 2007). Prior to perform the PCA all the measures were log transformed. The statistical significance of the observed morphological differences among seven OTUs defined on the basis of geographic location of samples, namely on biogeographical units (West Africa, East Africa, Central Africa, Nubia, North Africa, Sicily, and mainland Italy), were tested using non-parametric MANOVA (npMANOVA) (Anderson, 2001) and pairwise npMANOVA implemented in the R package RVAideMemoire v 0.9-78 (Hervé, 2018) with 999 randomizations. Significance levels for pairwise npMANOVA were corrected using the false discovery rate (FDR) method (Benjamini and Hochberg, 1995). Successively, to highlight possible clinal variation we performed two PCA in the two clades, i.e. Mediterranean and sub-Saharan.

Because the influence of size of skull measurement variation is well demonstrated in mammals, we obtained a size-corrected dataset by regressing the condylobasal length versus all other measurements. Indeed, Mori et al. (2019) demonstrated that in *Hystrix* the condylobasal length is a good proxy of skull volume and body size. The obtained size-corrected dataset was used to replicate the above mentioned analyses (PCA and npMANOVA).

Finally, to visualize phenetic relationships among groups, a cluster was obtained by Euclidean distances among means using the Ward method (Ward, 1963).
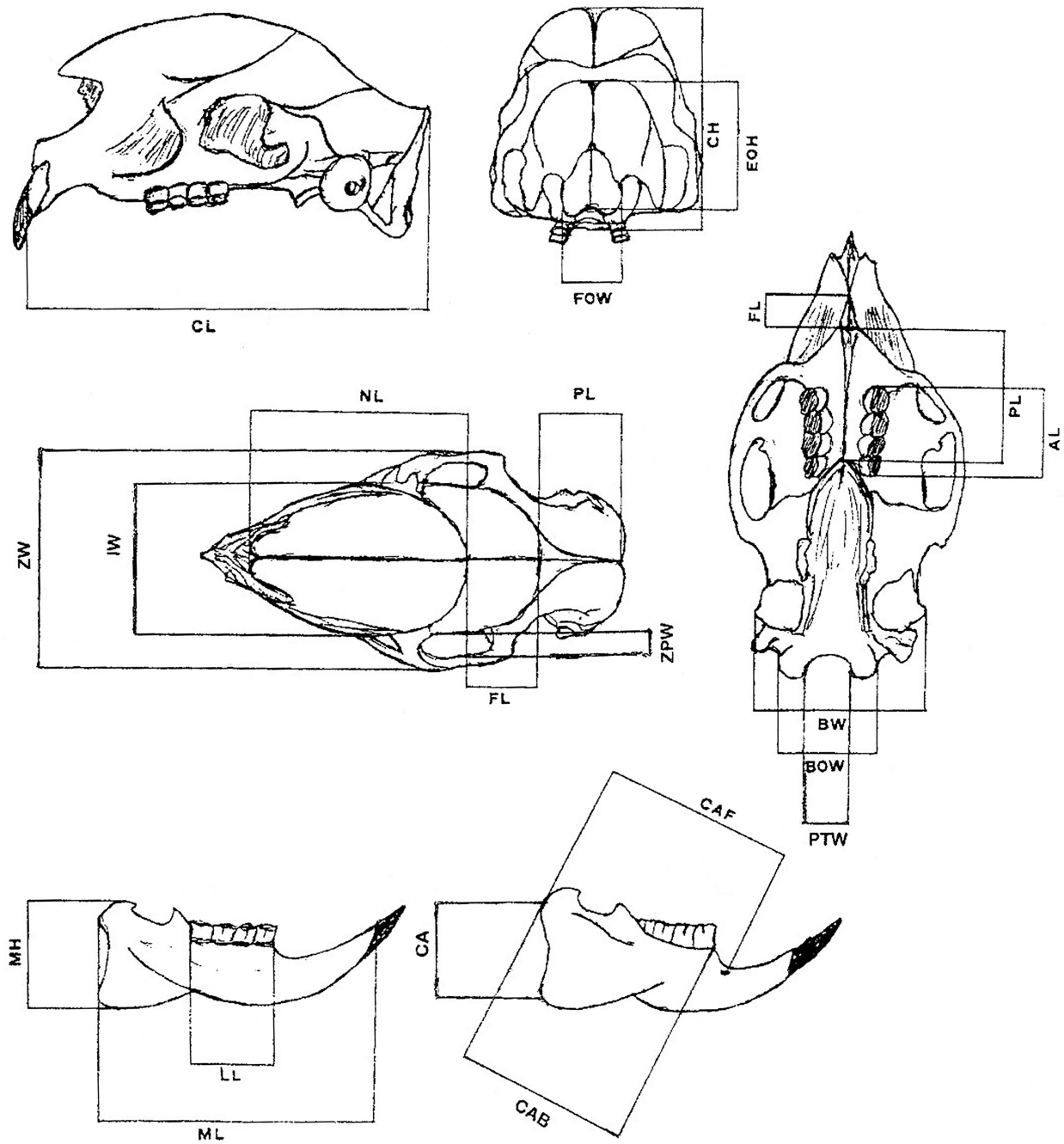
Figure 1. Measurements (n = 22) taken from the skulls and mandibles (n = 90) of *Hystrix cristata*. From Angelici et al. (2003), modified.

RESULTS

The PCA performed on the complete dataset (Fig. 2) shows the presence of a remarkable morphological variation along the first PC axis that explains 69.35% of the total variance. According to variable contribute plots (Fig. 2) this axis represents also an allometric axis, with specimens on negative PC1 values (left side of the Fig. 2) being those showing the highest value for all the measurements. The Mediterranean sample is well differentiated by the sub-Saharan sample by PC1. Interestingly the Nubian sample largely overlaps with the Mediterranean clade. The higher dimensions (PC2, PC3 and PC4) seem less correlated with size but do not provide any evident differentiation among potential OTUs (Operational Taxonomic Units).

The non-parametric MANOVA confirms the presence of a statistically significant difference among the seven groups (F = 13.701, p < 0.001). The pairwise non-parametric MANOVA (Tab. 1) shows significant differences between sub-Saharan OTUs with respect to Mediterranean OTUs (Italy, Sicily and North Africa). Within the sub-Saharan sample (with the only exception of Nubia) no significant differences were recognized among OTUs. By contrast, among the Mediterranean OTUs we recognized only a significant difference between Sicily and Italy.

The cluster analysis (Fig. 3) is congruent with PCA and npMANOVA and shows the occurrence of two main clusters: a sub-Saharan and a Mediterranean one. The Nubian sample is phenetically related to the Mediterranean sample. Within each cluster high phenetic similarity among OTUs is present.

Finally all the above mentioned analyses were performed on a size corrected dataset (Supplementary material: Figs. S1, S2, S3, S4, Table S2). Despite the correction for size, the trends described above seem conserved, with the only exception of the difference between Mediterranean and sub Saharan samples that mostly rely on size differences

Table 1: pairwise non-parametric MANOVA. Pairwise F values are reported above the diagonal. Significance level (p-values) is reported below the diagonal. Significant p-values after FDR adjustment are highlighted with **boldface.** CA = Central Africa; EA = East Africa; IT = mainland Italy; SI = Sicily; NA = North Africa; Nubia; WA = West Africa.

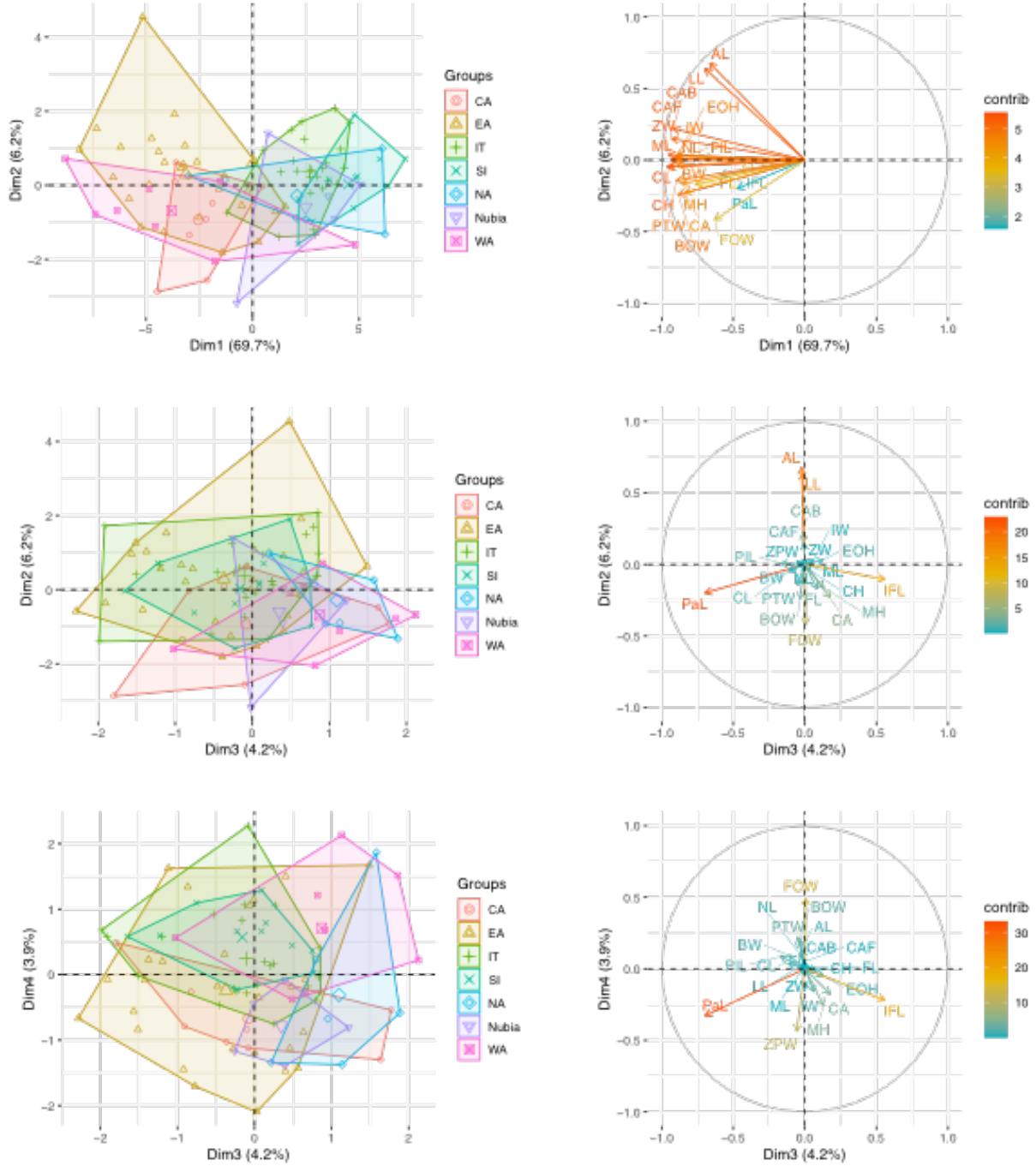|	CA	EA	IT	SI	NA	Nubia	WA
CA		1.5	25.5	31.1	5.9	7.8	1.5
EA	0.1708		42.4	38.6	9.9	10.3	2.2
IT	**0.0001**	**0.0001**		6.3	2.0	1.9	25.2
SI	**0.0002**	**0.0001**	**0.0003**		3.1	3.0	23.7
NA	**0.0063**	**0.0007**	0.0827	0.0432		0.4	5.6
Nubia	**0.0017**	**0.0001**	0.0644	0.0381	0.8114		6.5
WA	0.2017	0.0863	**0.0001**	**0.0002**	**0.0250**	**0.0154**	

Figure 2. Principal Component Analysis based on 22 measurements for the whole dataset. Geographic groups (OTUs) are highlighted by different colors and symbols. PC axis 1 to axis 4 and associated variables contributions are reported.
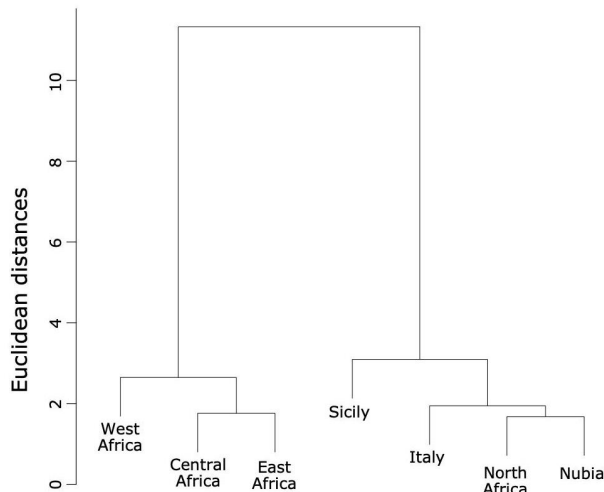
Figure 3. Cluster Dendrogram based on Euclidean distances and obtained using the Ward method. The cluster shows phenetic relationships among the seven geographic groups.

DISCUSSIONS

Taxonomy

Corbet & Jones (1965) were the first to treat the *Hystrix cristata* complex as composed of a single monotypic species, i.e. without considering the existence of subspecies. Previous authors (Ellermann, 1940; Mohr, 1965) treated *H. galeata* (from Eastern Africa) as a good species, and sometimes even *Hystrix aerula* Thomas, 1925 was considered a small sized species endemic of the Air Massif in Northern Niger (Thomas, 1925). According to our results, North African and Sub-Saharan porcupines seem clearly distinct mainly by size. Qualitative differences between skulls of North African and West African porcupines were discussed by Cabrera (1924). We have to evidence that North-East Africa *Hystrix cristata* (North-East Sudan, Eritrea) while morphometrically similar to the North African sample, are genetically linked to sub-Saharan clade by Trucchi & Sbordoni (2009), the latter also present in Western Libya and Southern Tunisia. Owing to poor sampling in Eastern Libya and mtDNA data, the nominate *Hystrix cristata* range should be limited for the moment to the Maghreb, for which the role of a phylogeographical refuge is well established (Huseman et al., 2014).

Therefore, to the current state of knowledge, it seems wise to recognize the two groups with a subspecific name; *Hystrix cristata cristata* Linnaeus, 1758 for the Maghrebian population and *Hystrix cristata senegalica* Cuvier, 1822 for the sub-Saharan populations. The taxonomic allocation of our 'Nubian' population needs further investigation, as it is morphologically closer to *H. c. cristata* although the few mtDNA data available associated it to the sub-Saharian clade (Trucchi & Sbordoni, 2009). Although body size is generally considered an unreliable taxonomic character (Demment & Van Soest, 1985), there is evidence from the taxonomically much better-known genus *Papio* (savannah baboons) that body size is phylogenetically informative and not only affected by ecological conditions (Jolly, 2012; Dunn et al., 2013). It is therefore desirable that future studies deal with unraveling the role of genetics and the environment in determining the large differences in size observed between the two clades and the possible taxonomic significance of this.
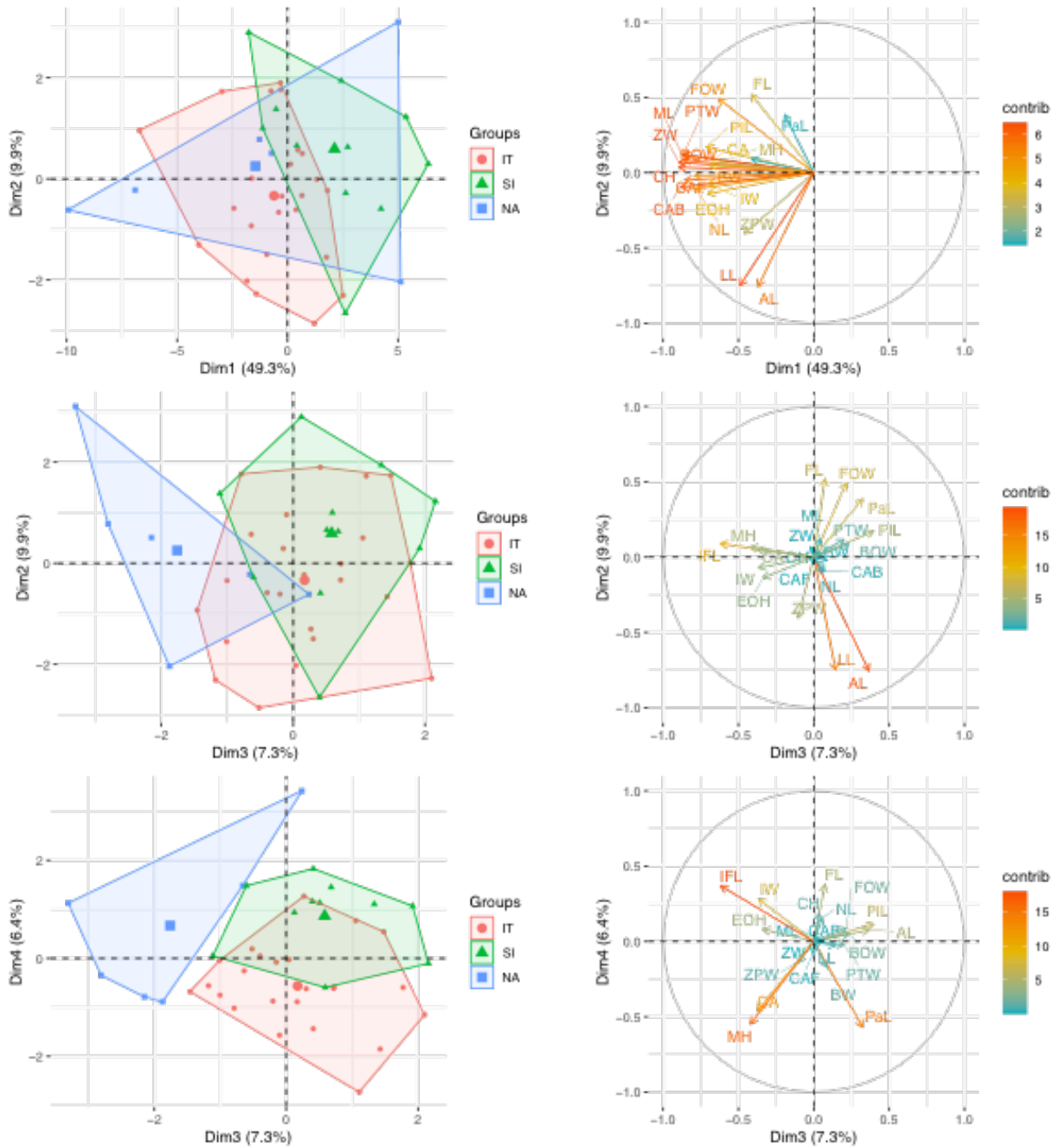
Figure 4. Principal Component Analysis based on 22 measurements for the Mediterranean samples. Geographic groups (OTUs) are highlighted by different colors and symbols. PC axis 1 to axis 4 and associated variables contributions are reported.
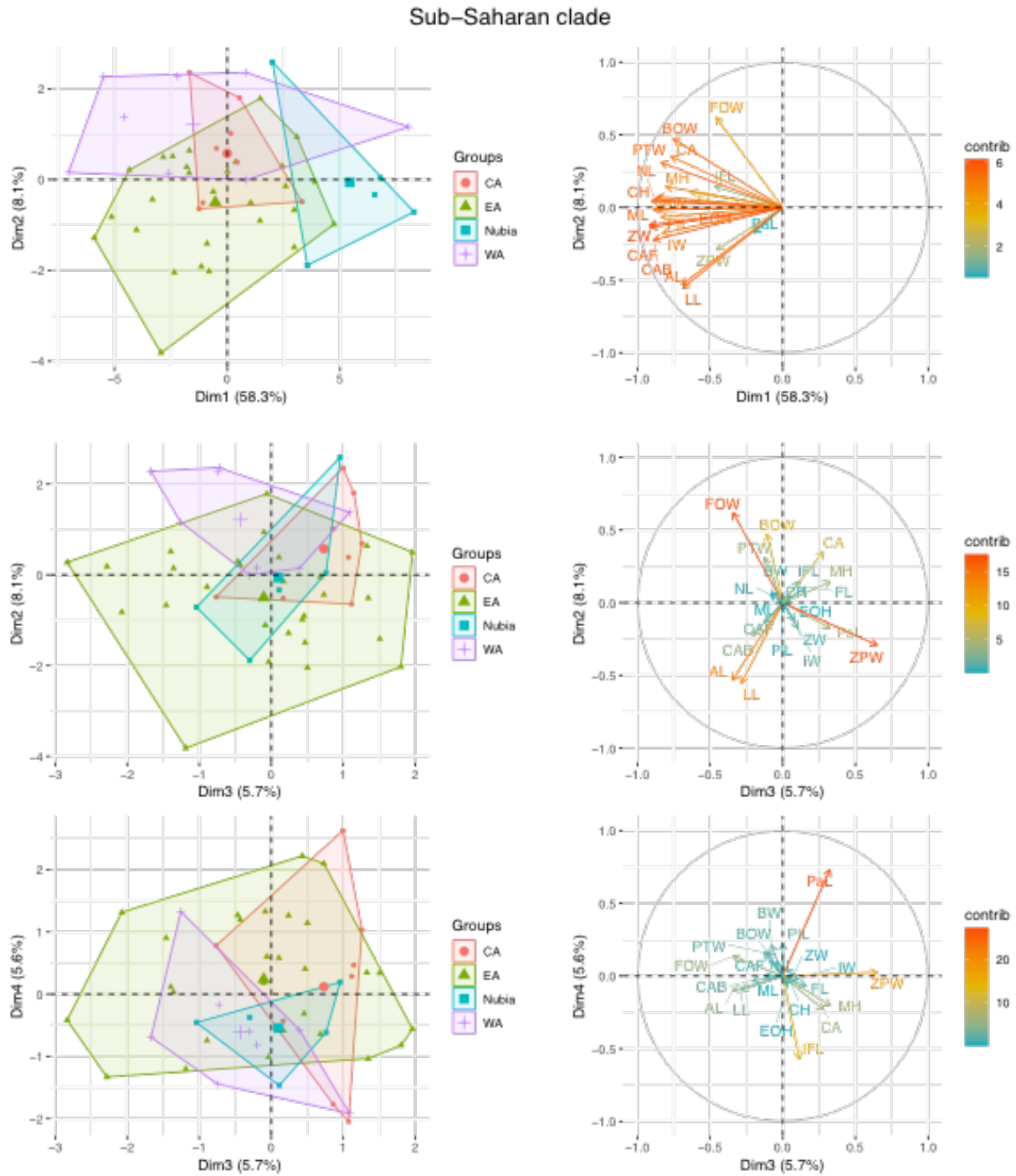
Sub−Saharan clade

Figure 5. Principal Component Analysis based on 22 measurements for the sub-Saharan samples. Geographic groups (OTUs) are highlighted by different colors and symbols. PC axis 1 to axis 4 and associated variables contributions are reported.

For what concerns the origin of the two putative subspecies, it is interesting to note that Trucchi & Sbordoni (2009), on the basis of mtDNA, recognize the reciprocal monophyly of the two clades, compatible with a long isolation, but also suggest the possible past connection between the two clades along a putative corridor between East and North Africa. However, in Trucchi et al. (2016), nuclear DNA data seem to suggest a different scenario with a sister group relationship between the East African crested porcupines (*H. galeata*) and the other porcupines, and an origin of the Northern African clade from West Africa. The reduced sample numbers of both studies do not allow any firm conclusions. Our data, if we assume that size differences also reflect phylogenetic relatedness, seem more in agreement with the mtDNA-based scenario. However, we think that the issue clearly deserves further investigations.

Geographic range and conservation status

The conservation of the nominal subspecies in North Africa is cause of concern, as factual records appear quite limited, and the geographic expansion of the porcupine in Peninsular Italy is somewhat obscuring its grim status elsewhere. In Morocco, according to Aulagnier & Thevenot (1986), *H. cristata* is widespread in the Eastern part of the country, whereas conservation problems are reported by Cuzin (2003), who considers the species in decline starting in 1950. The species is present in Algeria in various locations, and also in Tunisia, albeit being scarce in this latter country (Le Berre, 1990). *H. cristata* was considered rare already in the last century in Cyrenaica, Eastern Libya (Hartert, 1923), whereas was present in Tripolitania (Toschi, 1954). According to Ranck (1968), the species was present only in mountainous Libyan coastal areas; more recently it was recorded near Misurata by Walid (2011) even if it would be not so common. In Egypt it is now probably extinct (Happold, 2013). Furthermore, *Hystrix* from Sinai were genetically assigned to *H. cristata* by Trucchi et al. (2016) but morphologically they are more similar to *Hystrix indica* Kerr, 1792 (Saleh & Basuony, 1998), a point that needs clarification. Small isolated populations of *H. cristata* may survive in Mauritania, Mali, and Niger (Happold, 2013). Regarding *H. c. senegalica*, we noted that the geographic range of sub-Saharan porcupine is still not well understood (see Fig. 4). The exclusion of Somalia and North Kenya (Amori & De Smet, 2016) from the known range appears without basis (see Mohr, 1965: 151), as there lies the type locality of *H. galeata*.

The current presence of *H. cristata* in Southern Somalia was confirmed by Gedow Amir (email to SG on January 2019); the current presence in Central Kenya is reported by Butynski & De Jong (2017) in Lolldaiga Hills Ranch, and the species is usually reported from Darfur, Western Sudan, as well (Happold, 1967; Wilson, 1979). Therefore we are inclined to explain the mismatch between geographic origin of historical museum specimens and the last available distribution map of the species not to recent extirpation events (cfr. Mori et al., 2019) but to a general lack of knowledge especially in the Horn of Africa (cfr. Gippoliti, 2020). However, uncertainty remains regarding many areas of the *Hystrix cristata* African range, in particular in the Central Africa region, as it can be seen in the maps of Fig. 6. Biogeographical and systematic interpretations are clearly dependent on a better understanding of the presence and identity of porcupines in central Africa.
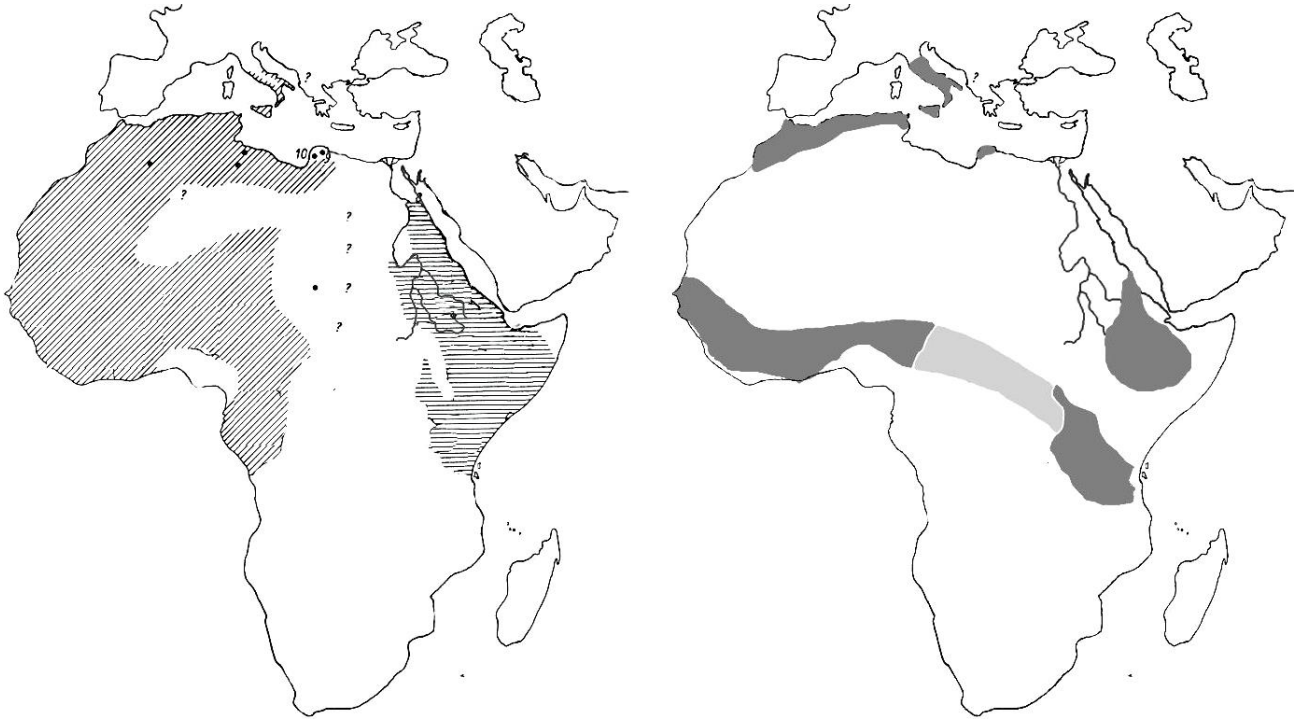
Figure 6. Range of the *Hystrix cristata* complex according to different authors: on the left from Mohr (1965) modified, who recognized *H. galeata* (horizontal lines) as a distinct species; on the right from Amori & De Smet (2016), modified.

Available materials and the present analysis do not allow any further discrimination within *H. c. senegalica* , due to the high overlap of the Western and Eastern groups. Interestingly, specimens from Eastern Democratic Republic of Congo (here included in the Central Africa OTU) seem phenotypically closer to the Eastern group, confirming previous identification by Hatt (1940). Thomas described a distinctive species, *Hystrix galeata*, from East Africa (type locality: Lamu, Kenya coast) as compared with *H. cristata* from West Africa; nasals and frontals narrow, especially in the interorbital region of the skull, nasals wide anteriorly; premaxillae broad; height of the skull at M^1 very great (Thomas, 1893). On the basis of a morphometric study, Corbet & Jones (1969) found considerable overlap in the mean differences between West and East African porcupines, so not only they did not accept *H. galeata* as a distinct species, but also claimed that 'these skull characters provide any justification for the recognition of a subspecific

difference' (Corbet & Jones 1969: 296). With this move that it is typical of the second half of the XX Century (cf. Gippoliti, 2019), the complex taxonomic history of *Hystrix cristata* fell in oblivion with severe consequences for our understanding of the genus diversity in Africa and conservation of some components as the Maghrebian taxon. On the other hand, the distinct difference in both shape and size between the skulls of *H. c. cristata* from Italy, typical *H. c. senegalica* and putative *H. galeata* from Somalia can be clearly appreciated in Fig. 7, to our knowledge the first graphical illustration comparing the skull of *H. galeata* with those of the other main members of the *H. cristata* group. Availability of additional specimens from the whole range could be crucial to increase our understanding of the species' variability in Africa. This is also urgent given that the crested porcupine is a valuable species for local communities providing both meat and quills for traditional medicine (Assogbadjo et al., 2005**;** Mouzoun et al., 2018).
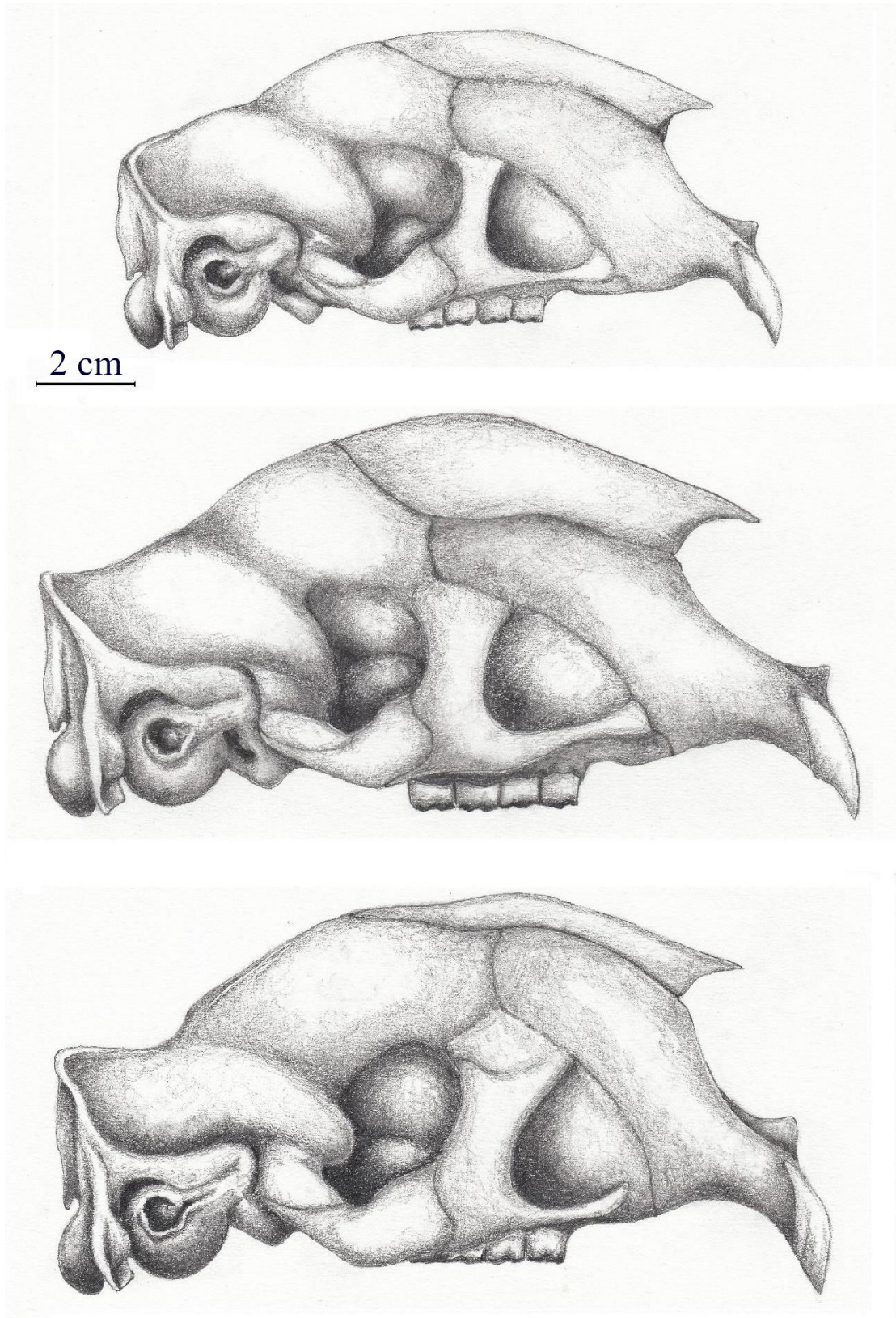
Figure 7. From top to bottom, skulls of*: Hystrix cristata cristata* - n. 78, Vigna Taglianti collection from Nazzano, near Rome, Museo Zoologico 'Sapienza' University of Rome; redraw from Amori et al., (2008: 698); *Hystrix cristata senegalica* NHM 62.461, redraw from Rosevear (1969); putative *H. galeata* from Mogadishu - C.E. 32735, Museo di Storia Naturale Giacomo Doria in Genoa; redraw from a photo courtesy of G. Doria.

Morphometric variation

The observed morphological variation seems largely traceable to size (as deduced by loading plot) in *Hystrix cristata*, particularly when the North African and sub-Saharan samples are compared. Size differences have been generally explained as generated by a response to the productivity of the regions of provenance (Corbet & Jones, 1965). Two described taxa, *H. c. aerula* Thomas, 1925 and *H. c. somalensis* Lönnberg, 1912, were based on specimens of small size originating from semi-desert regions. Therefore, the available evidence seems to support a role for ecology and local environmental conditions for body size variation in Africa, discarding general theories such as Bergman rule (Mori et al. 2019).

Cardini et al. (2013) found that the largest sized individuals among some Primate species groups are generally found in Central Africa around the Central forest block, with size decreasing towards both West and East. However, the fact that in the genus *Chlorocebus* size is greater in West Africa was interpreted as a result of genetic inheritance, as a distinct taxon, *C. sabaeus* (Linnaeus, 1766), occurs there. Contrary to the primate studies, *Hystrix* originating from near the central forest block are relatively smaller than those in East and West Africa. Further, while both arboreal and semi-terrestrial monkey genera always showed reduced size towards the Eastern African coast, no such pattern is visible in *Hystrix*. Unfortunately, the several geographic gaps in the museum's collection (see also Ferguson, 2020) do not allow a clear understanding of geographic variation in sub-Saharan crested porcupines. The issue deserves further studies as the possible role of the former Mega Chad Basin as a biogeographic factor responsible for separating Western and Eastern mammal faunas (Granjon & Dobigny, 2003), a pattern our analysis does not fully support in *Hystrix* although the meaning of size decrease in Central Africa should deserves further studies.

CONCLUSIONS

Our results support a North African/sub-Saharan divide inside *Hystrix cristata* while we could determine only a moderate phenotypic distinctiveness between Western and Eastern sub-Saharan populations. North-East Africa ('Nubia') is inhabited by a small-sized form that according to mtDNA belongs to the sub-Saharan clade. From a conservation perspective, more data on the status of the species from North Africa seem an urgent task.

It should be stressed that most African specimens found in museum collections originated from pre-Second World War years. Several gaps in our knowledge of *Hystrix* distribution, diversity and biology in Africa could be eliminated if more researchers collaborated in increasing the amount of materials stored in world's museums of Natural History. An increase in field research to better determine the distribution of the species in many areas is also desirable, using both capture records and camera trapping sessions.

Furthermore, from the results obtained by us and a review of the literature including published molecular research, it seems evident that the taxonomy and nomenclature of sub-Saharan *Hystrix cristata* (here referred as *H. c. senegalica*) needs a thorough an integrated revision, based on consistent data both of a biomolecular and morphometric nature, filling as many as possible biogeographical gaps now existing in current databases.

Vomero and G. Marangoni (Zoological Museum of Rome), L. Lapini (Natural History Museum of Udine), D. Scaravelli (Natural History Museum of Cesena), R. Villa and S. Biscardi (Rome), P. Iacopelli (Museum of Terrasini, Palermo), M. Sarà (University of Palermo), M. Bon (Natural History Museum of Venezia), S. Dolce (Natural History Museum of Trieste), E. Gavetti (Natural History Museum of Torino), G. Doria and the late G. Truffi (Natural History Museum of Genova), J. Barreiro (Natural History Museum of Madrid), J. Cuisin (Natural History Museum of Paris), P.D. Jenkins and M. Sheridan (Natural History Museum of London), F. Spitzenberger (Natural History Museum of Vienna), G. Storch (Forschungsinstitut Senckenberg, Frankfurt am Main), K.H. Fuchs (American Museum of Natural History, New York), R.W. Thorington and H.L. Kafka (Smithsonian Institution, Washington). We are also indebted to the late M. Corti, and to E. Mori for useful suggestions on some previous drafts of the manuscript. Special thanks to G. Milana for the reworking of Fig. 6, and to T. De Francesco for the drawing of Fig. 7. K. Kawata kindly reviewed the English style. Two reviewers and D. Fontaneto provided valuable criticism to our MS.

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