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THE FIRST APPEARANCE OF *HYSTRIX* (RODENTIA, MAMMALIA) IN PORTUGAL, LAST INTERGLACIAL, GRUTA DA FIGUEIRA BRAVA (SETÚBAL)

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ABSTRACT

A fossil remain of porcupine, a large-sized rodent hitherto unknown in Portugal, was identified during the 2010-13 excavation of the Last Interglacial deposit of Figueira Brava cave. The specimen is a left hemimandible retaining the PM/4 to M/2 series but lacking the incisor and the M/3. Based on the analysis of its morphological and odontometric features, we assign the fossil to *Hystrix cristata* (Linnaeus, 1758). Nowadays, *H. cristata* is found in Africa as well as, recently introduced, in Italy. Most Late Pleistocene occurrences of the genus are assigned to the species *Hystrix (Acanthion) vinogradovi* but, as demonstrated by the fossil discovered in Figueira Brava, *H. cristata* once existed in Europe.

Keywords: iberian peninsula, Hystricidae, late Pleistocene

RÉSUMÉ

PREMIÈRE OCCURRENCE DE HYSTRIX (RODENTIA, MAMMALIA) AU PORTUGAL, DERNIÈRE PÉRIODE INTERGLACIAIRE, GRUTA DA FIGUEIRA BRAVA (SETÚBAL)
Un reste fossile de porc-épic, un rongeur de grande taille jusqu'à maintenant inconnu au Portugal, a été identifié lors des fouilles archéologiques de 2010-13 dans un dépôt de la dernière période interglaciaire de la grotte de Figueira Brava. Le spécimen est une hémimandibule gauche conservant les séries PM/4 à M/2 mais dépourvue d'incisive et de M/3. Sur la base de l'analyse de ses caractéristiques morphologiques et odontométriques, nous attribuons le fossile à *Hystrix cristata* (Linnaeus, 1758). Aujourd'hui, *H. cristata* se trouve en Afrique ainsi qu'en Italie (introduction récente). La plupart des occurrences du genre au Pléistocène supérieur ont jusqu'à présent été attribuées à Hystrix *(Acanthion) vinogradovi* mais le fossile découvert à Figueira Brava démontre que *H. cristata* a existé autrefois en Europe.

Mots-clés : péninsule ibérique, Hystricidae, Pléistocène supérieur

1 - INTRODUCTION

Hystricidae (Fischer, 1817), a family of large rodents known as Old World porcupines by contraposition to the New World porcupines of the family Erethizodontidae, The Hystricidae have a line of fossil representatives stretching back to the Early Miocene, *c.* 20 MA (millions of years) ago (Barbière & Marivaux, 2015). Their scarcity in the fossil record is a characteristic of the whole family, represented today by only three genera: *Hystrix*, *Atherurus* and *Trichys*. In Europe, the area of distribution of porcupines declined from the Pliocene to the Pleistocene, probably due to the increasingly colder and unstable climactic conditions (Montoya, 1993). The family's present-day distribution includes all of Africa and tropical and sub-tropical Asia, with a small nucleus in Italy (Rosevear, 1969; Monadjem *et al.,* 2015).

Because of marked intra-specific variability, namely in size and shape, the taxonomy of this family, and especially so that of the *Hystrix* genus, remains a focus of intense debate (Sallari & Sardela, 2009). This is the more so with regards to the family's fossil representatives, despite the phylogenetic studies already undertaken (Rovie-Ryan *et al.,* 2017). Of the three genera recognized among the Hystricidae, the one of relevance here, *Hystrix*, features eight extant species: *H. cristata*, *H. africaeaustralis*, *H. indica*, *H. brachyura*, *H. javanica*, *H. crassispinis*, *H. pumila* and *H. sumatrae* (Wilson & Reeder, 2005).

In Europe, most Pleistocene remains of *Hystrix* have been assigned to *H. primigenia* or *H. major*, the former

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apparently older and smaller than the latter (Koliadimou & Koufos, 1991; Montoya, 1993). However, a large number of other taxa have been named, namely *H. vinogradovi*, a Middle Pleistocene form found in forested contexts and thought to be significantly smaller than *H. cristata* (Gallindo-Pelicenna *et al.,* 2011). In Iberia, all late Middle or Upper Pleistocene fossil remains of *Hystrix* have been assigned to *H. vinogradovi*, *H. brachyura* or even *H. brachyura vinogradovi*. The single exception is a specimen from the Mousterian levels of Devil's Tower (Gibraltar), which Garrod *et al.* (1928) identified as *H. cristata*.

The specimen described here is the first record of *H. cristata* (Linnaeus, 1758), the crested porcupine, in Portugal. It was found at Figueira Brava cave (38°28'14"N, 8°59'10"W; WGS84 datum), in a Middle Palaeolithic archaeological context dated to the later part of the Last Interglacial period (figs. 1 & 2).

Nowadays, *H. cristata* is found mainly in Africa, where it prefers hot and dry climates. It is spread across the northern coasts of Morocco, Algeria, and Tunisia, with a small nucleus in the coast of Libya. It also occurs in shrublands, grasslands and forests along a strip bordering the southern part of the Sahara, from the Atlantic to Ethiopia (Amori & Smet, 2016; Aulagnier *et al.,* 2018). An European population exists in southern Italy and Sicily as a result of human introduction in Late Antiquity or Early Medieval times (Santini, 1980; Riquelme Cantal & Morales Muñiz, 1997; Amori & Angelici, 1999; Masseti *et al.,* 2010; Aulagnier *et al.,* 2018), with a recent expansion to northern Italy having been noted (Mori *et al.,* 2013). Garrod *et al.* (1928) mention earlier reports of the species' presence in southern Spain during the XIXth century but so far no material evidence to that effect (e.g., osteological remains and field reports) has been forthcoming.

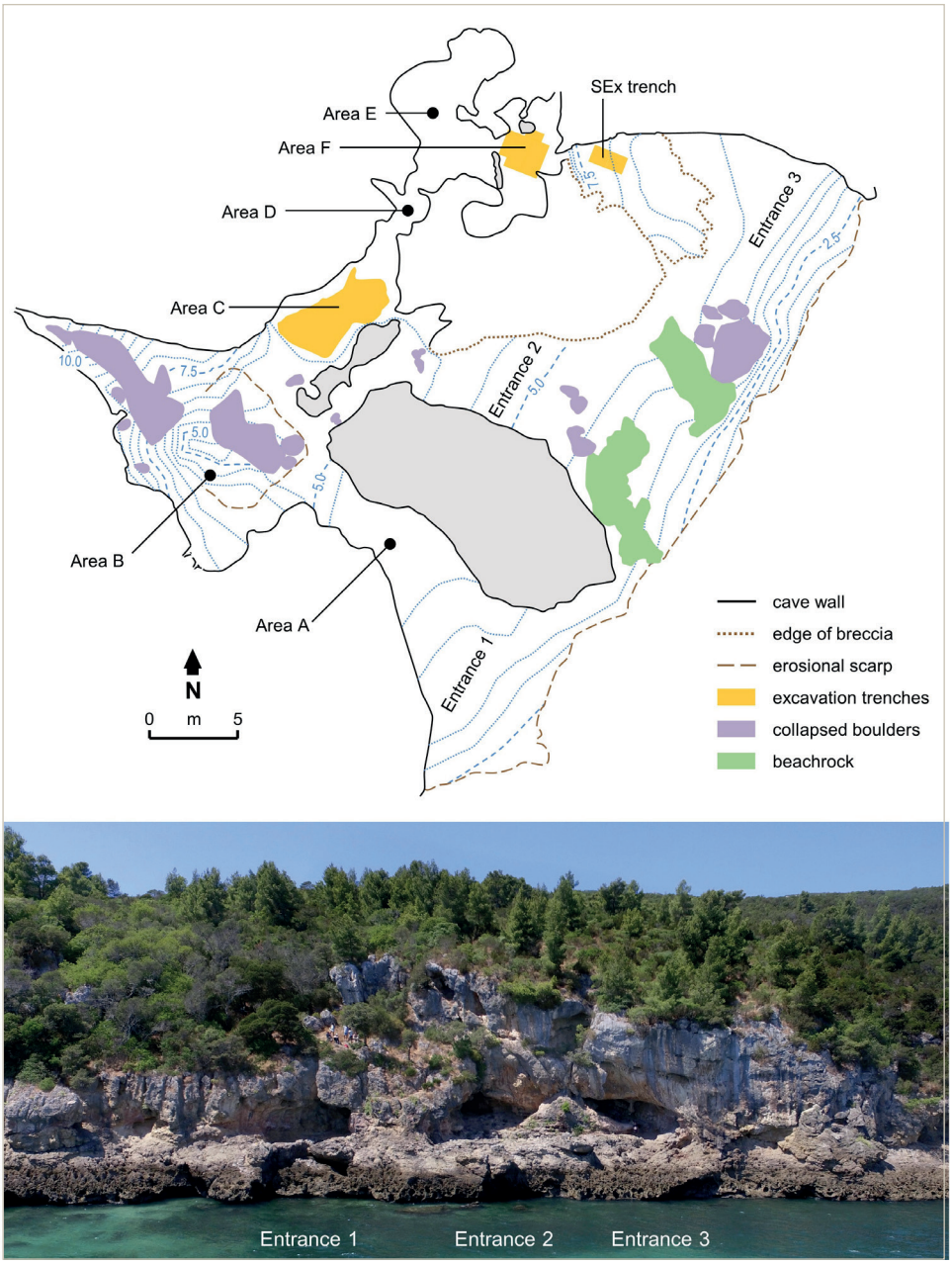

Fig. 1: Figueira Brava cave. Plan with indication of excavated areas (top), and drone overview (bottom). The marine abrasion platform of MIS 5e in front of the extant entrances was originally part of the cave space; it became unroofed as a result of postglacial sea-level rise and associated marine erosion processes. After Zilhão *et al.* (2020).

Fig. 1 : Grotte de Figueira Brava. Plan avec indication des zones fouillées (en haut) et vue d'ensemble par drone (en bas). La plateforme d'abrasion marine du MIS 5e devant les entrées existantes faisait à l'origine partie de l'espace de la grotte ; son toit a disparu à la suite de l'élévation postglaciaire du niveau de la mer et des processus d'érosion marine associés. D'après Zilhão et al. (2020).

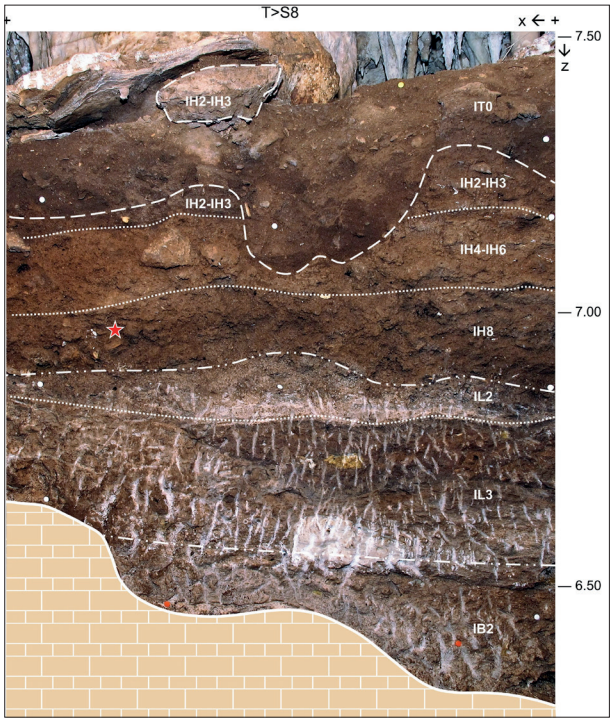

Fig. 2: The Area F stratigraphy.
The FB-2013-838 specimen was retrieved in unit IH8, while straightening the stratigraphic profile for recording. The red star indicates its position. Elevations are in m above modern sea level. After Zilhão *et al.* (2020).
Fig. 2 : Stratigraphie de la zone F. Le spécimen FB-2013-838 a été récupéré dans l'unité IH8, pendant le levé du profil stratigraphique pour l'enregistrement. L'étoile rouge indique sa position. Les altitudes sont au-dessus du niveau actuel de la mer. D'après Zilhão et al. (2020).

2 - MATERIALS AND METHODS

Within all species of the genus *Hystrix*, dental wear introduces much inter-individual variation in tooth morphology, there exists a lack of studies addressing that variation, and enamel patterns have not changed much since the Neogene (van Weers, 2005; Tong, 2008). These factors complicate species differentiation in the fossil record (Sulimski, 1960; Fistani *et al.,* 1996), where osteometrics, and in particular odontometry, are considered to provide the best discriminators (Tong, 2008). For instance, *H. vinogradovi* is defined as significantly smaller than *H. cristata*, and the latter as smaller than *H. primigenia*, with no overlapping (Fistani *et al.,* 1996).

Our identification is based on the morphological comparison of the Figueira Brava specimen with extant *Hystrix* from the reference collection of the Muséum national d'histoire naturelle (Paris). In addition, we measured the teeth of 28 mandibles from that collection identified as *H. cristata* and *H. javanica*, and of 99 mandibles from the Natural History Museum (London) identified as *H. cristata* (60), *H. africaeaustralis* (16), *H. brachyura* (8) and *H. indica* (39). To reduce inter-observer variability, all tooth measurements, including those of the Figueira Brava fossil, were made by the same person. We then compared our data with published measurements of reference and fossil material (Sulimski, 1960; Montoya, 1993; Van Weers, 1994; Cuenca-Bescós *et al.,* 1999; Baryshnikov, 2003; Van Weers, 2005; López-García *et al.,* 2008; Salari & Sardella, 2009).

Using a Mitutoyo Vernier calliper with a precision of 0.01 mm, we took two measurements: length of the mandibular PM4, and length of the mandible's tooth series. The latter was taken from PM/4 to M/3. In the Figueira Brava specimen, however, the M/3 is missing, so in this case our measurement for the series was taken from PM/4 to the limit of the alveolar space. The potential source of error introduced by this resort must be borne in mind when assessing results drawn from the comparison of complete mandibles.

Reference specimens measured for this study are deposited in the following institutions: Muséum National d'Histoire Naturelle (MNHN), Paris, France; Natural History Museum (NHM), London, United Kingdom. The Figueira Brava specimen is currently in storage at UNIARQ – Centro de Arqueologia da Universidade de Lisboa, Portugal.

3 - DESCRIPTION AND CONTEXT

Our specimen bears inventory number FB-2013-838 and is a well preserved left hemimandible with PM/4, M/1, and M/2 (fig. 3). It clearly belongs to a rodent, one bearing hypsodont teeth with roots, as in all Hystricidae. The teeth have buccal and lingual infoldings that,

Fig. 3: Figueira Brava's *Hystrix* mandible.
Lateral and occlusal views (photos: J. P. Ruas). After Zilhão *et al.* (2020).
Fig. 3 : Mandibule Hystrix de Figueira Brava. Vues latérales et occlusales (photos: J. P. Ruas). D'après Zilhão et al. (2020).

with wearing, become infibulate (small enamel islets), producing a particular pattern typical of the genus *Hystrix* (Hillson, 2005).

The fossil was found in unit IH8 of the stratigraphic succession excavated in Area F of Figueira Brava. IH8 is a variably cemented sandy loam at the base of the site's FB4 phase, which is comprised of units IH2-IH8. Bayesian modelling of the U-Th dating results for flowstone and other stratigraphically associated speleothems allows us to constrain the succession with much precision and indicates that the accumulation of FB4 took place during GI (Greenland Interstadial) 22, i.e. 87.6-90.0 ka ago (Rasmussen *et al.,* 2014). This dating is consistent with the paleonvironmental information provided by the remains of land vertebrates (including the tortoise, *Testudo hermanii*) and the plant charcoal assemblage, which is dominated by the stone pine, *Pinus pinea*, and where the Angiosperm component reveals a low-elevation, Mediterranean, limestone bedrock ecosystem with *Olea europaea*, *Quercus* sp., *Prunus* sp., *Rhamnus-Phillyrea*, *Ficus carica*, and *Vitis vinifera*. This evidence suggests climate and environmental conditions largely similar to those extant in the Holocene. For a detailed description of context, see Zilhão *et al.* (2020).

Area F corresponds to the back of the original cave, where the deposit is protected by a speleothem-cum-breccia barrier situated at the interface with the nowadays external parts of the site. Most of the latter's original sedimentary infill has been lost to marine erosion. IH8 accumulated atop flowstone unit IL1, which formed in the early part of a hiatus in sedimentation and in human occupation during which the site was used as a den by carnivores, namely bear and lynx. Porcupines also den in deep burrows and in caves (Amori & De Smet, 2016), where their presence is often revealed, if only indirectly, by the gnawing marks left on bones previously accumulated by carnivores, e.g. hyenas (MacDonald & Barrett, 1993; Diedrich, 2009). Once sedimentation resumed, the skeletal remains produced by the animal activity that took place at Figueira Brava during the hiatus became incorporated in the IH8 deposit, commingled with the stone tools, the charcoal and the anthropogenic faunal remains denoting human repossession of the site.

The stratigraphic context described above implies that the porcupine mandible must have entered the site during the time interval calculated for the boundary between IL1 and IH8. Based on the Bayesian modelling of the sequence of dating results, that interval corresponds to the two millennia between 89.8 and 91.7 ka, towards the end of the ten millennia long GI 23 (90.1-104.0 ka) and at the very beginning of MIS (Marine Isotope Stage) 5b.

4 - RESULTS AND DISCUSSION

Our results are presented in tabs. 1 & 2 and figs. 4 & 5. Fig. 4 shows that the Figueira Brava premolar is significantly larger than the few published measurements

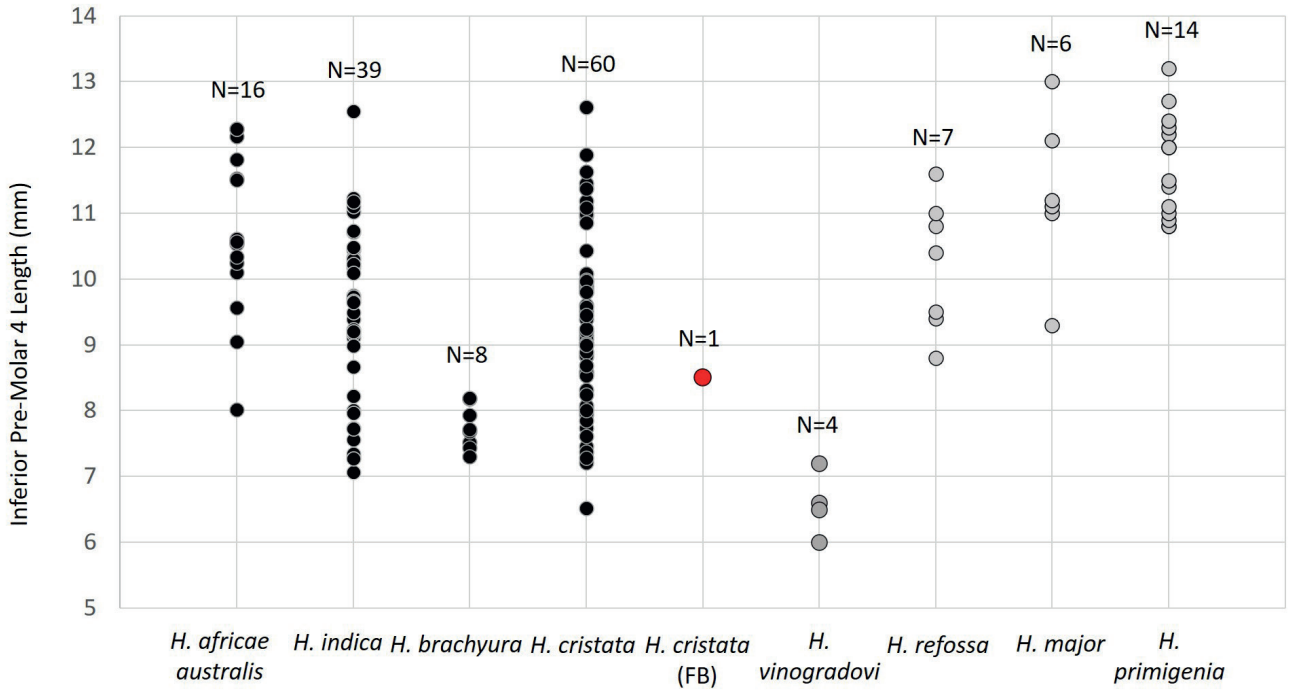

Fig. 4: *Hystrix* lower PM/4 length (mm).

Measurements for extant species and the Figueira Brava specimen (FB): this paper. Measurements for fossil taxa are as follows: Montoya (1993), Van Weers (1994) and Sulimski (1960) for *H. primigenia*; Montoya (1993) for *H. major*; Van Weers (1994) for *H. refossa*; Cuenca-Bescós *et al.* (1999), López-García *et al.* (2008) and Salari & Sardella (2009) for *H. vinogradovi.*

Fig. 4 : Longueur (mm) PM/4 inférieure de Hystrix. Mesures pour les espèces encore existantes et le spécimen de Figueira Brava (FB) : cet article. Les mesures pour les taxons fossiles sont issues des références suivantes : Montoya (1993), Van Weers (1994) et Sulimski (1960) pour H. primigenia; Montoya (1993) pour H. major; Van Weers (1994) pour H. refossa; Cuenca-Bescós et al. (1999), López-García et al. (2008) et Salari & Sardella (2009) pour H. vinogradovi.

for *H. vinogradovi* (= *H. brachyura vinogradovi*) and is consistent with *H. cristata*. It also shows that the variation in lower premolar size documented among extant *H. cristata* encompasses the corresponding *H. vinogradovi* range even though both have premolars that, on average, are smaller than those of *H. primigenia* and *H. major*.

One female *H. cristata* from Senegal curated at the NHM has a lower premolar (6.52 mm) smaller than most *H. vinogradovi* specimens (with a single exception, a 6.0 mm tooth found among the latter). These results suggest a wider range of variation in the cranial size of *H. cristata* than hitherto assumed. Indeed, most values for the extant and almost all values for the fossil lower premolars that we measured fall within the interval bracketed by the minimum and maximum values for *H. cristata* given in fig. 4.

In fig. 5, we compare the size of the tooth series in extant species with four fossil specimens: two *H. vinogradovi* and two *H. cristata*, one from Figueira Brava (30.23 mm), the other from Devil's Tower (30.0 mm). The two fossil *H. cristata* are in the range of extant *H. cristata, H. africaeaustralis* and *H. indica*. The two *H. vinogradovi* fall just below the range of extant *H. cristata* (tab. 2).

Based on these comparisons, we conclude that the Figueira Brava mandible belongs in *H. cristata*. We further suggest that, on the grounds of odontometrics alone, little reason exists to go on accepting that the specimens so far assigned to *H. vinogradovi* represent a distinct taxon; in all likelihood, they are but small *H. cristata*.

Even though attempts to phylogenetically differentiate the several *Hystrix* species have been made, the only exemplar of *H. africaeaustralis* studied by Rovie-Ryan *et al.* (2017) does not separate completely from *H. cristata*. These two species hybridize in captivity, but they do not breed in the wild, not even when they are sympatric (Barthelmess, 2006). Nevertheless, it remains possible that all recognized extant species of *Hystrix* are in fact but different populations of a single species, or at least very close species that diverged not long ago. With time, the rise of geographic or ecological barriers may have led to divergence, but the variation in size seen across both time and space could well be largely explained by adaptation to climate.

According to Cuenca-Bescós *et al.* (1999), *H. cristata* is an indicator of warmer phases because of its current African distribution. Therefore, the presence of the genus in Middle and Upper Pleistocene contexts of Europe could stem from warm-phase immigration. During the coldest phases, porcupines would have persisted in Iberia only, because of its more southerly latitude and comparatively milder climate.

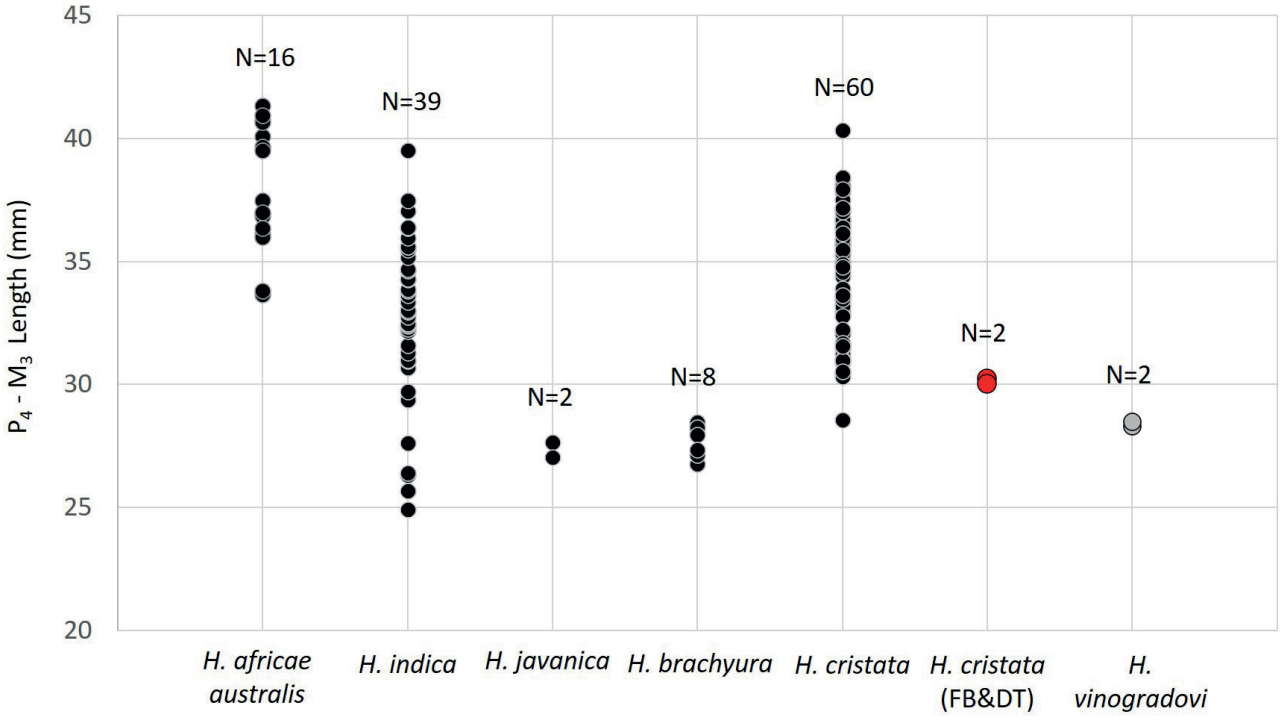

Fig. 5: *Hystrix* lower PM/4-M/3 length (mm).
Measurements for extant species and the Figueira Brava specimen (FB): this paper. Measurements for Devil's Tower (30 mm) after Garrod *et al.* (1928) and for *H. vinogradovi* after Baryshnikov (2003) and Van Weers (2005).
Fig. 5 : Longueur (mm) de PM/4-M/3 inférieure de l'Hystrix. Mesures pour les espèces encore existantes et le spécimen de Figueira Brava (FB) : cet article. Mesures pour Devil's Tower (30 mm) d'après Garrod et al. (1928) et pour H. vinogradovi d'après Baryshnikov (2003) et Van Weers (2005).

	N	Mean	Standard Deviation	Maximum	Minimum
H. cristata	60	9.33	1.30	12.61	6.52
H. africaeaustralis	16	10.70	1.74	12.28	8.01
H. brachyura	8	8.90	0.33	8.19	7.06
H. indica	39	7.74	0.33	9.75	7.06
H. vinogradovi	4	6.58	0.49	7.20	6.00
H. refossa	7	10.21	1.01	11.60	8.80
H. major	6	11.28	1.24	13.00	9.30
H. primigenia	14	11.74	0.77	13.20	10.80

Tab. 1: Descriptive statistics for the length of the lower PM/4 of *Hystrix* in fig. 4.
The length of the Figueira Brava cave specimen is 8.50. All measurements are in mm.
Tab. 1 : Statistiques descriptives de la longueur des PM/4 inférieures d'Hystrix de la fig. 4. La longueur du spécimen de la grotte de Figueira Brava est de 8,50. Toutes les mesures sont en mm.

	N	Mean	Standard Deviation	Maximum	Minimum
H. cristata	60	34.41	2.60	38.32	28.55
H. africaeaustralis	16	37.94	5.85	41.34	33.65
H. brachyura	8	27.58	0.67	28.45	26.76
H. indica	39	32.72	3.34	39.51	24.90
H. javanica	2	27.34	0.43	27.03	27.64
H. vinogradovi	2	28.40	0.14	28.50	28.30
H. cristata (FB, DT)	2	30.12	0.16	30.23	30.00

Tab. 2: Descriptive statistics for the length of the lower PM/4 to M/3 tooth series of *Hystrix* in fig. 5.
"*H. cristata* (FB, DT)" denotes the specimens from Figueira Brava (FB) and Devil's Tower (DT). All measurements are in mm.
Tab. 2 : Statistiques descriptives de la longueur de la série de dents PM/4 à M/3 inférieures d'Hystrix de la fig. 5. « H. cristata (FB, DT) » désigne les spécimens de Figueira Brava (FB) et de Devil's Tower (DT). Toutes les mesures sont en mm.

No confirmed record of *H. cristata* exists in the Holocene of Iberia. The taxon is also entirely absent from archaeological and paleontological contexts of the peninsula's Pleistocene that securely post-date the end of the Last Interglacial. In this respect, the porcupine contrasts with other warm-adapted taxa that would seem to have persisted well into MIS 3 and have natural, non-reintroduced extant populations — namely, the tortoise, *Testudo hermanii* (Jiménez-Fuentes *et al.,* 1998; Nabais & Zilhão, 2019). Unlike cave lion, leopard, hyena, and other taxa that, nowadays, only exist in Africa but persisted in Europe until the end of the Ice Age (Cardoso, 1993; Davis, 2002), porcupines would therefore seem to have become extinct in Iberia with the onset of the first glacial maximum of the Upper Pleistocene, ca. 72 ka ago.

5 - CONCLUSION

The morphology of teeth and mandible, as well as the size of the lower PM/4 and the length of the mandible's tooth series place the Figueira Brava specimen well within the variation of extant and paleontological specimens of *Hystrix cristata*. It is therefore to this taxon, not to *H. vinogradovi*, the other species hitherto recognized in the Upper Pleistocene of Iberia, that we have assigned our fossil. Available *H. vinogradovi* measurements, however, fall within the lower range of extant *H. cristata*, and so the possibility must be entertained that the corresponding material represents smaller-sized individuals, or populations, of *H. cristata*; previously found in Gibraltar (at Devil's Tower), this taxon's Upper Pleistocene existence in Iberia is now

corroborated in Portugal (at Figueira Brava). The secure and precise dating of the Figueira Brava specimen to the 89.8-91.7 ka ago interval shows that *Hystrix* persisted in the area until the end of the Last Interglacial. No reliably dated fossil occurrences are known thereafter, and so porcupines probably became regionally extinct with the onset of last Ice Age. Human reintroduction in Late Antiquity explains the extant Italian population as well as, in all likelihood, the unconfirmed reports that porcupines were present in southern Spain during the XIXth century.

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AUTHORS CONTRIBUTIONS

João Luís Cardoso classified the specimen to *H. cristata* based on morphological comparison with material from the Paris reference collection. Cleia Detry took all the tooth measurements and produced the associated odontometric comparisons. João Zilhão directed the excavation of Figueira Brava; he collected the FB-2013-838 mandible, and identified it as porcupine, on May 24, 2013, while straightening the East profile of square T8.

SUPPLEMENTARY MATERIALS

Measurements of extant *Hystrix* can be found in the reference collections of the *Muséum national d'Histoire naturelle*, Paris (France) and Natural History Museum, London (UK) (tabs. S1 & S2). *H. galeata*, *H. somaliensi*, *H. cuvieri* and *H. senegalica* are non-valid synonyms of *H. cristata* that are no longer used. *H. ambigua* is synonym for *H. africaeaustralis*. Nowadays, *H. leucura* and *H. hodgsoni* are classified as *H. indica*. We used the geographic location of the species described by IUCN (Amori & Smet, 2016) to assign a valid taxonomic identification to all the measured specimens.

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Species	Institutional Prefix	Registration Number	Additional Registration Number	Collector Numbers or other	Location	Sex	Length P4-M3	Length P4	Width P4	Length M3	Width M3
Hystrix africa australis	NHMUK ZD	1966,509			Rukusi Dam, Fort Jameson Dist. N. Rodhesia. Zambia	Female	36.12	11.53	8.94	10.50	8.44
*Hystrix hodgsoni**	NHMUK ZD	1973,1735			Unknown	Female	24.90	7.06	6.34	6.86	6.36
Hystrix cristata	NHMUK ZD	GERM 507b			Xanthus. Turkey	Unknown	36.70	10.85	8.26	9.00	7.31
Hystrix africa australis	NHMUK ZD	1939,2273			Unknown	Unknown	33.65	10.10	7.80	7.97	7.27
Hystrix leucura	NHMUK ZD	1946,223			Ceylon	Unknown	36.39	10.44	8.08	9.66	7.05
Hystrix leucura	NHMUK ZD	1946,224			Ceylon	Unknown	32.25	7.96	6.55	8.41	6.20
Hystrix brachyurus	NHMUK ZD	1948,12			Karbour Gat. W. Sumatra	Male	27.35	7.30	6.41	6.71	5.71
Hystrix brachyura	NHMUK ZD	1948,14			Karbour Gat. W. Sumatra	Female	26.76	7.68	5.72	6.73	5.68
Hystrix brachyurus	NHMUK ZD	1948,15			W. Sumatra	Male	26.77	7.44	6.33	6.67	5.58
Hystrix africae australis	NHMUK ZD	1949,395		746	Ezelfontein. Near Lebifontein. Namaqualand	Male	33.79	8.01	6.16	8.69	6.58
Hystrix brachyura brachyura	NHMUK ZD	1955,3204		4	Malasya	Female	28.25	7.71	5.42	6.79	6.28
Hystrix brachyura brachyura	NHMUK ZD	1955,3205		128/14	Salak. Malasya	Male	28.00	7.93	6.11	7.58	5.86
Hystrix galeata	NHMUK ZD	1962,151		225	Kangaita. Kerugoya. Kenya	Unknown	37.50	9.45	7.99	9.51	8.10
Hystrix cristata	NHMUK ZD	1962,152		257	Kengoya, S. of Mt. Kenya	Male	35.22	10.43	8.76	8.75	8.46
Hystrix cristata senegalica	NHMUK ZD	1962,461		271	Musaia. Koinadugu Dist. Sierra Leone	Unknown	37.10	9.02	6.21	9.45	7.43
*Acanthion L. leucurus**	NHMUK ZD	1966,1177			Gonagama Kilialgale. Ceylon	Female	29.37	7.72	4.67	7.56	6.02
Acanthion L. leucurus	NHMUK ZD	1966,1178			Ceylon	Male	33.63	10.09	7.43	8.59	6.98
Hystrix cristata	NHMUK ZD	1966,5991		469	Dinder National Park. Dinder River. Blue Nile. Sudan	Unknown	31.69	7.28	4.72	7.30	5.54
Hystrix africae-australis	NHMUK ZD	1966,862		765	N.R. Rodhesia. C. Africa	Female	36.35	9.05	6.19	9.51	8.05
Hystrix cristata	NHMUK ZD	1973,173			Brussels Zoo (possibly from Italy or North Africa)	Unknown	35.32	7.37	5.87	8.94	6.80
Hystrix cristata	NHMUK ZD	1973,1732			Kenya	Male	37.19	11.08	8.85	19.17	7.98
Hystrix africa australis	NHMUK ZD	1973,1733			Unknown	Male	41.34	12.17	9.36	10.6	8.20
Hystrix hodgsoni	NHMUK ZD	1973,1736			Unknown	Male	25.67	7.73	5.88	6.01	5.61
Hystrix indica leucurus	NHMUK ZD	1977,405			Sri Lanka	Unknown	30.95	8.00	5.65	7.27	6.06
Hystrix indica leucura	NHMUK ZD	1977,407		R43	Sri Lanka	Unknown	33.03	8.66	6.84	8.01	6.17
Hystrix galeata	NHMUK ZD	1977,408		291	Kenya	Unknown	37.03	11.63	8.18	11.24	8.09
Hystrix leucura	NHMUK ZD	1845.1.8.8.	GERM 887a		Nepal	Unknown	26.40	7.27	6.01	6.66	5.69
Hystrix leucurus	NHMUK ZD	GERM 508a			Nepal	Unknown	33.81	10.22	6.99	8.08	6.93
Hystrix senegalica	NHMUK ZD	1847.12.4.2	GERM 748b		Unknown	Unknown	34.77	8.31	6.05	9.36	7.16
Hystrix leucura	NHMUK ZD	1847.7.22.8	GERM 508c		Nepal	Unknown	32.47	9.65	7.80	7.52	7.86
Hystrix cuvieri (africa australis)	NHMUK ZD	1851.3.17.1	GERM 748d		Portugal?	Unknown	38.41	9.80	8.05	9.23	8.18
Hystrix leucura	NHMUK ZD	1856.5.6.24	GERM 507c		Unknown	Unknown	34.28	9.75	8.19	9.35	6.94
Hystrix leucura (malabaricus)	NHMUK ZD	1865.1.30.10	GERM 1479a		S. India	Unknown	35.17	12.55	8.68	10.26	7.11
Hystrix africae australis	NHMUK ZD	1867.2.24.7	GERM 748h		Natal. S. Africa	Unknown	40.68	12.28	8.66	10.11	9.66
Hystrix brachyurus	NHMUK ZD	1879.11.21.199			Province Wellerley. India	Female	27.94	8.19	6.25	5.87	5.76
Hystrix hodgsoni	NHMUK ZD	1879.11.21.637			Nepal	Unknown	26.32	7.29	5.77	6.62	5.52
Hystrix leucura	NHMUK ZD	1888.2.5.25			Nilghiris	Female	32.95	8.99	7.07	8.49	6.74
Hystrix leucura	NHMUK ZD	1888.2.5.24			India	Male	31.29	9.20	7.68	7.89	6.24
*Hystrix leucura**	NHMUK ZD	1888.4.12.5	GERM 508j		Ceylon	Unknown	30.68	9.11	6.55	7.00	5.81
Hystrix leucura	NHMUK ZD	1888.4.12.6	GERM 508k		Ceylon	Unknown	30.98	9.49	6.62	8.49	6.47
Hystrix leucura	NHMUK ZD	1895.6.1.89			Haithathum. Aden. Arabia	Male	33.86	9.39	7.01	7.76	5.77
Hystrix leucura	NHMUK ZD	1899.11.6.82			Unknown	Unknown	32.73	9.67	6.89	7.89	6.44
Hystrix brachyura	NHMUK ZD	1903.2.6.73			Malek. Malasya	Male	28.45	7.52	6.46	6.37	5.93
Hystrix leucura	NHMUK ZD	1903.4.12.1			Datta Khel. Torhi Valley Dist. Punjab.	Unknown	34.69	10.21	7.00	8.27	7.58
Hystrix cristata	NHMUK ZD	1903.4.21.1			Vizzini. Sicily	Unknown	30.99	8.08	7.44	7.88	6.35
Hystrix africae australis	NHMUK ZD	1907.1.11.79			Zambia	Unknown	37.47	10.34	8.34	9.41	7.98
Hystrix ambigua	NHMUK ZD	1907.11.12.1			Malawi	Unknown	40.08	10.56	8.04	10.8	9.72
Hystrix cuvieri	NHMUK ZD	1904.11.3.86			Hakheila. Upper Egypt	Unknown	31.55	9.00	6.76	7.72	8.46
Hystrix galeata	NHMUK ZD	1904.2.5.7			Fort Hall	Male	36.13	9.97	8.58	9.54	8.13
Hystrix	NHMUK ZD	1904.7.5.25			Morroco	Unknown	32.77	7.61	5.87	8.41	6.73
Hystrix cuvieri	NHMUK ZD	1904.8.2.31			Avakin. Sudan	Unknown	35.46	8.53	7.68	8.91	7.96
Hystrix	NHMUK ZD	1904.8.2.32			Suakin. Sudan	Unknown	30.97	7.85	5.57	8.08	7.07
*Hystrix galeata**	NHMUK ZD	1905.5.10.12			Unknown	Unknown	30.54	8.24	6.41	8.16	6.37
Hystrix africa australis	NHMUK ZD	1905.8.13.2			Zomba. Nyasa	Unknown	39.66	10.53	8.26	9.14	8.33
Hystrix brachyurus	NHMUK ZD	1905.9.27.1			Singapore	Unknown	26.77	7.44	6.33	6.67	5.58
Hystrix galeata	NHMUK ZD	1906.11.1.48			N.E. Africa	Unknown	34.79	9.80	8.45	7.89	7.47
Hystrix somaliensi	NHMUK ZD	1906.5.4.9			Somaliland	Male	32.23	9.96	8.20	9.82	7.75
Hystrix leucura	NHMUK ZD	1910.12.2.40		136	Sehore. Central India	Male	37.48	10.33	7.37	9.00	7.79
Hystrix leucura	NHMUK ZD	1910.12.2.41			Central India	Female	33.34	10.73	7.86	10.11	6.85
*Hystrix**	NHMUK ZD	1912.12.28.24			Somali	Unknown	32.03	7.21	4.93	8.39	7.08
Hystrix africa australis (H. galeata)	NHMUK ZD	1913.10.18.188			Unknown	Female	39.51	11.82	8.73	11.10	7.12
Hystrix	NHMUK ZD	1914.3.8.50			Kania. Dinda. Sudan	Unknown	33.50	9.02	6.78	8.62	7.12
Hystrix	NHMUK ZD	1914.4.29.6			Mlaugi. Nyasaland	Unknown	38.08	9.24	6.21	9.70	7.40
Hystrix leucura	NHMUK ZD	1915.11.1.125			Mirwah. Karipur State	Male	32.96	9.23	7.07	8.16	7.00
Hystrix leucura	NHMUK ZD	1915.11.1.127			Mirpur Sukkur	Unknown	32.45	10.48	8.36	8.99	6.50

Hystrix leucura	NHMUK ZD	1915.11.1.128			Gambat. Airpur state	Female	29.72	9.71	7.61	8.41	7.30
Hystrix leucura	NHMUK ZD	1919.11.8.34		363	Khojdan. Baluchistan	Unknown	37.04	11.02	7.60	9.34	8.07
Hystrix	NHMUK ZD	1919.7.7.3657			Tangiers	Unknown	34.99	9.39	7.43	9.03	8.34
Hystrix senegalica	NHMUK ZD	1919.7.7.3695			Bakel. Senegal	Unknown	33.89	9.89	7.62	8.65	7.04
Hystrix leucura	NHMUK ZD	1919.8.21.1		343	Mervil. NW Persia	Female	35.97	11.02	8.63	9.33	7.29
*Hystrix leucura**	NHMUK ZD	1920.2.8.14			St George Matugarna. Ceylon	Male	35.61	10.30	7.13	10.17	6.99
Acanthion hodgsoni	NHMUK ZD	1921.10.4.35			Hatiban. Nepal	Male	27.60	7.34	5.73	6.51	5.16
Hystrix cristata	NHMUK ZD	1921.10.5.2			Montalto di Castro. Rome	Female	33.62	9.02	7.43	9.04	7.47
Hystrix africae-australis	NHMUK ZD	1923.5.9.168			Louisvale, Upington District, Orange River.	Unknown	37.00	10.57	8.44	9.19	7.43
*Hystrix galeata**	NHMUK ZD	1924.2.25.8		358	Sagayo	Male	36.40	9.82	8.38	8.48	7.14
*Hystrix galeata (cristata)**	NHMUK ZD	1924.2.25.9		358a	Sagayo. Tanganyika territory	Female	40.32	12.61	8.86	8.87	8.13
Hystrix africae australis	NHMUK ZD	1925.1.2.266			Karibib. S. W. Africa	Unknown	36.94	10.25	8.42	9.20	8.30
Hystrix	NHMUK ZD	1925.12.5.2			Ashkote. Kashmir	Unknown	37.82	9.85	6.48	9.24	7.51
*Hystrix senegalica**	NHMUK ZD	1925.5.12.87		60	Farak. Damergon	Female	30.90	6.52	5.16	8.29	6.8
Hystrix leucura	NHMUK ZD	1926.10.8.68			Saharumpur. Siwaliks	Male	35.46	10.17	7.77	8.33	7.58
Hystrix leucura	NHMUK ZD	1926.10.8.69			Unknown	Unknown	36.35	10.71	7.98	9.01	7.34
Hystrix leucura	NHMUK ZD	1926.10.8.70			Bijvar	Unknown	35.60	11.23	7.99	8.90	7.82
Hystrix africae australis	NHMUK ZD	1926.12.7.301		2342	Sandfontein. S.W. Africa	Unknown	40.72	11.51	8.87	9.56	8.23
Hystrix africae australis	NHMUK ZD	1926.12.7.302		2185	Sandfontein. S.W. Africa	Female	36.00	12.28	8.36	10.72	7.81
Hystrix	NHMUK ZD	1928.6.3.15			Gombe. Nigeria. W. Africa	Unknown	33.67	10.08	7.93	9.71	7.35
Hystrix leucura	NHMUK ZD	1929.10.19.6			Morai. Kumaon	Unknown	32.16	11.10	7.77	8.39	6.79
Hystrix africae australis	NHMUK ZD	1928.9.11.394		2774	Kovares. S. Kaokoveld. S.W. Africa	Male	36.85	10.61	8.34	8.88	7.85
Hystrix leucura	NHMUK ZD	1931.1.10.10			Hoshangabad. India	Unknown	39.51	11.18	8.03	9.66	7.94
Hystrix africae-australis	NHMUK ZD	1934.8.10.18			M. Mgahirga/S.W. Uganda	Male	40.95	9.56	**	9.07	8.03
Hystrix leucura	NHMUK ZD	1936.1.22.11			Ceylon	Male	34.27	9.17	6.85	8.73	6.37
Hystrix leucura	NHMUK ZD	1937.10.8.5			Summaduwa. Ceylon	Unknown	32.39	8.22	5.96	7.89	6.27
Hystrix leucura	NHMUK ZD	1937.10.8.6			Ceylon	Unknown	31.60	7.56	5.08	8.17	6.95
Hystrix galeata	NHMUK ZD	1937.2.24.97		7227	Dangra. Abyssinia	Female	34.91	8.00	6.00	8.68	8.56
Hystrix leucura	NHMUK ZD	1933.7.29.14		19	Shambaganux. S. India	Female	34.63	9.73	7.43	9.22	6.62
Hystrix	NHMUK ZD	1906.5.4.10			Somaliland	Unknown	33.46	9.99	8.68	8.40	7.13
Hystrix galeata	NHMUK ZD	1907.1.6.5			Fort Hall, British East Africa	Unknown	37.92	11.37	8.28	10.47	9.28
Hystrix galeata	NHMUK ZD	1901.7.6.10			Saqualla. Havash. Abyssinia	Unknown	34.55	8.69	7.40	9.17	7.17

Tab. S1: Measurements from the reference collection of the Natural History Museum in London.
* Measurements from the right mandible, the remaining measurements come from left mandibles.
** The measurement was not possible to take due to incomplete broken tooth.

Tab. S1: Mesures de la collection de référence du Natural History Museum de Londres.
** Les mesures proviennent de la mandibule droite, les autres mesures proviennent de la mandibule gauche.*
*** La mesure n'a pas pu être prise en raison d'une dent cassée incomplète..*

Species	Registration Number	Additional Registration Number	Location	Sex	Length P4-M3	Length P4	Width P4	Length M3	Width M3
H. cristata	MNHN-ZM-AC-1883-1971		Unknown	Unknown	30.46	9.09	7.23	7.71	6.00
H. cristata	MNHN-ZM-AC-1890-2002	S1 RC - t111	Captive specimen from MNHN zoo	Unknown	28.55	9.14	6.98	9.13	7.38
H. cristata	MNHN-ZM-MO-1921-147		Senegal, and then captive specimen from MNHN zoo	Unknown	35.00	7.74	5.55	9.00	6.88
H. cristata	MNHN-ZM-AC-1922-382	St RC. - tIII	Unknown	Unknown	31.45	8.55	7.27	8.10	6.86
H. javanica	MNHN-ZM-AC-1922-387	S1.RC - t76	Unknown	Unknown	27.03	7.21	6.22	7.08	5.56
H. cristata	MNHN-ZM-AC-1923-1025	S1-RC-t112	Unknown	Unknown	31.54	8.82	7.49	8.23	6.21
H. cristata	MNHN-ZM-AC-1925-13		Captive specimen from MNHN zoo	Unknown	30.30	8.57	7.30	7.10	6.78
H. cristata	MNHN-ZM-AC-1928-286		Unknown	Unknown	35.69	10.99	8.65	10.62	8.15
H. cristata	MNHN-ZM-AC-1930-162		Captive specimen from MNHN zoo	Female	38.32	11.89	8.03	9.68	8.52
H. cristata	MNHN-ZM-AC-1933-35		Captive specimen from MNHN zoo	Female	33.29	9.60	7.99	8.74	8.28
H. cristata	MNHN-ZM-AC-1936-556		Captive specimen from MNHN zoo	Unknown	33.16	9.57	7.18	7.27	6.59
H. cristata	MNHN-ZM-MO-1933-35		Algeria, Alger	Female	31.22	8.05	6.42	8.32	6.63
H. cristata	MNHN-ZM-MO-1959-259		Captive specimen from MNHN zoo	Female	32.98	8.89	7.53	8.28	7.70
H. cristata	MNHN-ZM-MO-1962-2222		Algeria, from Alger zoo	Unknown	36.57	11.19	7.42	9.57	7.61
H. cristata	MNHN-ZM-MO-1962-2223		Fouta, Djaloun, Guinée	Unknown	38.07	11.45	8.65	9.48	8.52
H. cristata	MNHN-ZM-AC-1971-202		Unknown	Unknown	36.78	9.95	6.80	8.97	7.48
H. cristata	MNHN-ZM-AC-1978-6		Unknown	Female	35.71	11.38	8.36	8.79	7.72
H. cristata	MNHN-ZM-MO-1990-662		Captive specimen from MNHN zoo	Female	34.38	10.96	7.75	8.30	6.99
H. cristata	MNHN-ZM-MO-1995-3133		Senegal, Bandia	Unknown	32.13	7.46	5.12	8.39	6.99

Tab. S2: Measurements from the reference collection of the *Muséum national d'Histoire naturelle* in Paris.
*Measurements from the right mandible, the remaining measurements come from left mandibles.
Tab. S2: Mesures de la collection de référence du Muséum national d'Histoire naturelle de Paris.
**Mesures effectuées sur la mandibule droite, les autres mesures proviennent de la mandibule gauche.*