A *Hystrix* Linnaeus, 1758 incisor (Mammalia, Rodentia) from the Early Pleistocene of Senèze, France

Thomas MÖRS
Department of Palaeobiology,
Swedish Museum of Natural History,
P.O. Box 50007, SE-104 05 Stockholm (Sweden)
thomas.moers@nrm.se

Marguerite HUGUENEY
22 avenue Condorcet,
F-69100 Villeurbanne (France)
marguerite.hugueney@gmail.com

Published on 29 December 2017

urn:lsid:zoobank.org:pub:98B5A339-F61F-4186-8905-4C2B46D67DAC

Mörs T. & Hugueney M. 2017. — A *Hystrix* Linnaeus, 1758 incisor (Mammalia, Rodentia) from the Early Pleistocene of Senèze, France. *Geodiversitas* 39 (4): 797-802. https://doi.org/10.5252/g2017n4a8

ABSTRACT
Excavations carried out between 2001 and 2006 in the Early Pleistocene locality Senèze (Haute-Loire, France) yielded the fragment of a large upper incisor with anteriorly grooved enamel band, documenting a large-bodied rodent in Senèze for the first time. A thorough study of this incisor and particularly of its enamel microstructure led to its assignment to *Hystrix refossa* Gervais, 1852, despite the presence of longitudinal grooves which are usually considered as characteristic of the castorid genus *Trogontherium* Fischer von Waldheim, 1809 and which have not been noticed in *Hystrix* Linnaeus, 1758 so far. The presence of *H. refossa* is in accordance with the partly steppic environment previously documented in the Senèze locality.

KEY WORDS
Hystricidae,
Old World porcupines,
Villafranchian,
tooth morphology,
enamel microstructure,
palaeoenvironment.

RÉSUMÉ
*Une incisive d'*Hystrix *(Mammalia, Rodentia) du Pléistocène inférieur de Senèze, France.*
Les fouilles effectuées entre 2001 et 2006 dans le Pléistocène inférieur de la localité de Senèze (Haute-Loire, France) ont livré un fragment d'une grosse incisive supérieure à bande d'émail antérieure cannelée et mis en évidence, pour la première fois dans ce gisement, la présence d'un rongeur de grande taille. L'étude de cette incisive, et plus particulièrement de la microstructure de son émail, conduit à sa détermination comme *Hystrix refossa* Gervais, 1852, malgré la présence des sillons longitudinaux qui sont généralement considérés comme caractéristique du castoridé *Trogontherium* Fischer von Waldheim, 1809 et qui n'étaient jusqu'à présent pas signalés chez *Hystrix* Linnaeus, 1758. La presence d'*H. refossa* est en accord avec l'environnement en partie steppique déjà reconnu à Senèze.

MOTS CLÉS
Hystricidae,
Porcs-épics de l'Ancien-Monde,
Villafranchien,
morphologie dentaire,
microstructure de l'émail,
paléoenvironment.

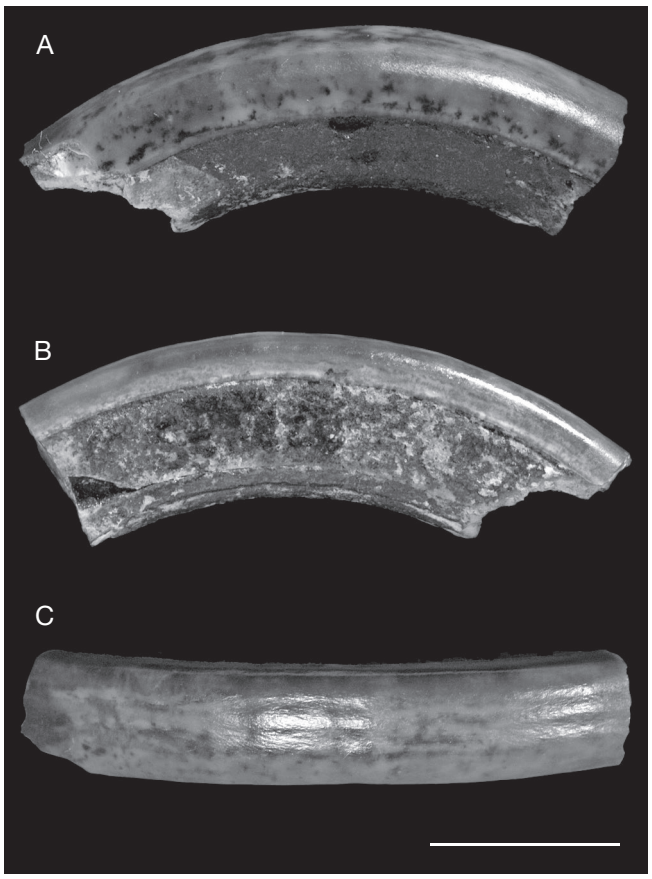


Fig. 1. — *Hystrix refossa* Gervais, 1852 from Senèze, right upper incisor: **A**, buccal side; **B**, medial side; **C**, upper side. Scale bar: 1 cm.

INTRODUCTION

The Early Pleistocene maar deposits of Senèze are famous since the end of the 19th century for their exceptionally preserved mammal assemblage (Delson *et al.* 2006; Nomade *et al.* 2014). Senèze is the reference locality for the Mammal Neogene unit MN 18, and the faunal list comprises more than 40 mammal species (Guérin 1982; Bruijn *et al.* 1992; Pastre *et al.* 2015). Up to now, no large rodent was ever found in the Senèze locality, but the recent excavations yielded the fragment of a large, faintly grooved incisor. This demonstrates that a large-sized rodent was also present in this locality. Two families of large rodents, Castoridae and Hystricidae, could occur in the stratigraphic level of Senèze. They have strict but different habitat requirements: large species of the genus *Hystrix* Linnaeus, 1758 are inhabitants of steppe and savannah environments, where they feed mainly on fruits, grains as well as underground roots and bulbs, and frequently gnaw bones (Niethammer 1982). The precise food requirements of the fossil castorid genus *Trogontherium* Fischer von Waldheim, 1809, characterized by its ornamented upper incisors, are unknown but the extant genus *Castor* Linnaeus, 1758 points to water proximity and to forested environments (Freye 1978). Therefore, the generic attribution of this incisor might help to define more accurately the palaeoenvironment of the Senèze locality, in addition to the data provided by the sedimentological and paleontological studies.

Institutional and collection abbreviations

FSL	Université Claude-Bernard, Lyon 1, Sciences de la Terre, Villeurbanne;
KOE	Koenigswald collection, Steinmann Institute, University of Bonn, Bonn;
NRM-PZ	Palaeozoological collections, Department of Palaeobiology, Swedish Museum of Natural History, Stockholm;
NRM-VE	Vertebrate collections, Department of Zoology, Swedish Museum of Natural History, Stockholm;
SEN	Senèze collection, presently housed at FSL.

SYSTEMATIC PALAEONTOLOGY

Order RODENTIA Bowdich, 1821
Family Hystricidae Burnett, 1830
Genus *Hystrix* Linnaeus, 1758

Hystrix refossa Gervais, 1852
(Fig. 1A-C)

Castoridae indet. – Delson *et al.* 2006: 277, 286.

Material. — The incisor (SEN 04-0139) described here was obtained in the 2004 excavation at "locus P233, couche H moyenne", a site which is characterized by lacustrine near shore sediments with repetitive slope slides (Pastre *et al.* 2015: text-figs 3-4).

Measurements. — Antero-posterior diameter (DAP) = 8.74 mm × transverse diameter (DT) = 6.75 mm.

Description

Orientation

This very incomplete incisor is represented only by a 3 cm long fragment which lacks the anterior part as well as the posterior part. Despite the small size of the fragment, a noticeable bending of the tooth can be observed and allows to identify it as an upper incisor. Unfortunately the chisel-shaped anterior tip, which would make it possible to orientate the tooth and which bears several diagnostic characteristics, is not preserved. However, one of the extremities of the fragment is hollow, it represents the growing part of the incisor i.e., the posterior one. Consequently the opposite extremity, completely filled with dentine, is the anterior part. Therefore it is possible to determine this tooth as a right upper incisor.

Shape

The shaft has a DAP larger than the DT, its cross-sectional shape is therefore less than 0.8 (DT/DAP = 0.77; Rybczynski 2007: appendix 48). The shape of the cross-section of the incisor is triangular with rounded angles, the inner side being the more rectilinear.

Enamel band

The enamel cover extends on the inner side for roughly 2 mm, while it ends with a thin longitudinal fold, and a little lower on the more rounded outer side. The anterior face is a little convex and its enamel surface faintly grooved, with three folds separated by two flat furrows.

Enamel microstructure

The incisor enamel is two-layered, with a thick inner layer (portio interna, PI) making up at least 75% of the overall thickness of the enamel band, and with a thin outer layer (portio externa, PE) which forms maximal 25% of the overall thickness (Fig. 3A, C, H). The PI is formed by multiserial Hunter-Schreger bands (HSB) with each band being four to six prisms thick (Fig. 3D, F-G, I). The HSB are inclined with approximately 20°. The orientation of the interprismatic matrix (IPM) is parallel to the prisms. The transition zone between PI and PE is somewhat irregular and not very sharp. The PE is formed by radial enamel with steeply inclined prisms and IPM oriented almost vertically to the prisms.

Comparisons

Castor

The incisor of extant beaver is described by Miller (1912: 951) as follows: "Upper incisor heavy […]; shaft about as deep as wide, the anterior face slightly curved, a little longer as sub-equal outer and inner faces […]; enamel […] essentially smooth but with very obscure longitudinal wrinkles". Rybczynski (2007: appendix 48 = upper incisor enamel) indicates that: "a small number of *Castor canadensis* Kuhl, 1820 individuals exhibit weakly grooved incisal enamel" and upper incisors of Early Pleistocene (MN 17) *Castor fiber* Linnaeus, 1758 from St-Vallier show faint longitudinal wrinkles (Hugueney 2004). Moreover, a *Steneofiber* Geoffroy, 1833 individual from the Early Miocene (MN 2) of St-Gérand-le-Puy (Allier; FSL 98190) shows the same ornamentation as the Senèze incisor whereas the other incisors from St-Gérand-le-Puy are smooth, as all *Steneofiber* incisors from the Early Miocene (MN 5) of Hambach (Mörs & Stefen 2010).

Trogontherium

In the two extinct castorid species *Trogontherium minus* Newton, 1890 and *Trogontherium cuvieri* Fischer von Waldheim, 1809 the upper incisor appears irregularly rounded in transverse section. The incisors of *T. minus* are a little smaller in size than the Senèze incisor and the incisors of *T. cuvieri* are much larger. The enamel cover ends abruptly at the beginning of the inner face but extends obliquely more largely on the outer one. The enamel band displays longitudinal raised and evident striation considered as characteristic of this genus. Schreuder (1929: 165, fig. 15) stated for *T. cuvieri*: "on the granular enamel the older specimens sometimes show distinct longitudinal ridges and grooves". Mörs *et al.* (1998: 143) described incisor fragments of *T. minus* with "finely-wrinkled enamel […] with longitudinal furrows" from the Late Pliocene (MN 16) of Hambach.

Hystrix

For living Old World porcupine Miller (1912: 547) stated "Upper incisor robust […] the shaft scarcely compressed, but with antero-posterior diameter perceptibly greater than lateral diameter […] Anterior face slightly oblique, nearly flat though a little rounded off at edges; posterior surface narrow so that the outline of cross-section is nearly an isocele triangle with all angles rounded". Upper incisors are smooth and literature

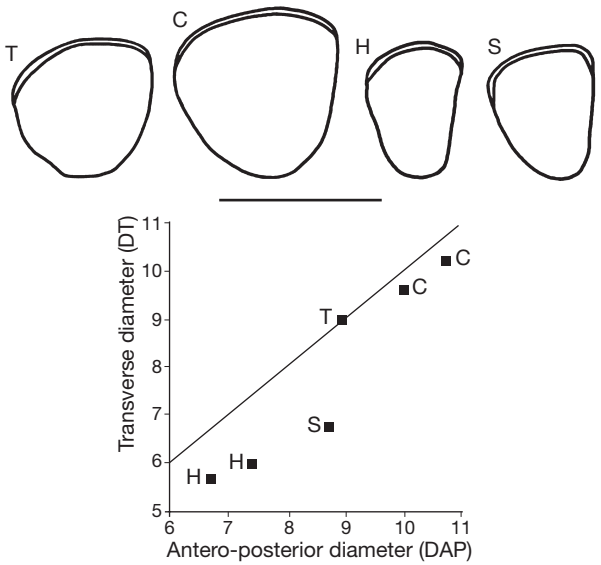


Fig. 2. — Cross-sections and measurements (in mm) of upper incisors of large rodents from Saint-Vallier and Senèze. Abbreviations: **C**, *Castor fiber* Linnaeus, 1758; **H**, *Hystrix refossa* Gervais, 1852; **T**, *Trogontherium cuvieri* Fischer von Waldheim, 1809; **S**, specimen from Senèze. Scale bar: 10 mm.

does not mention furrows on the enamel band. However, some NRM-VE specimens from Africa, labelled either as *Hystrix cristata/galeata* or as *Hystrix africaeaustralis* Peters, 1852 show upper incisors that look very similar to the Senèze incisor. Although this feature is not consistent, a huge adult skull of *H. cristata/galeata* (A60/1143) has clearly grooved upper incisors, whereas most of the large adults do not exhibit this feature (e.g. A59/3984, A64/2071, A64/1450). Juveniles usually do not show grooved upper incisors, but one small juvenile (A59/3982) has clearly grooved upper incisors, and even the lower ones show a medial furrow. In *H. africaeaustralis*, e.g. one adult specimen (A58/3980) possesses clearly grooved upper incisors, as does a juvenile specimen (A59/3982) of similar size but with dp4 and not yet erupted m3. None of the available specimens of *Hystrix indica* Kerr, 1792 has grooved incisors (adult e.g. A59/1902, A59/5436, juvenile A59/3701)

In the Early Pleistocene (MN 17) locality Saint-Vallier all three genera are present and upper incisors documented (Hugueney 2004). These specimens are of particular interest as the stratigraphical age of Senèze is close to that of St-Vallier and the material was available for direct comparison. The size of the Senèze incisor is small compared to the castorids of St-Vallier. But it is worth to notice that ontogenic differences in size in castorids are huge, as beavers grow almost all along their life and can reach 15-17 years old or even older (Freye 1978). The St-Vallier *Hystrix* incisor is small but it corresponds to a young individual; porcupines show like castorids a huge enlargement of their incisors during life time. In contrast to the upper incisors of *Castor* and *Trogontherium* of the same locality, the enamel band of the *Hystrix* upper incisor is smooth. Compared to the fossils from St-Vallier, the cross-sectional ratio of the Senèze incisor is closer to that of *Hystrix* than to *Castor* or *Trogontherium,* in which these ratios approach 1 (Fig. 2; Rybczynski 2007: appendix 47).

Enamel microstructure

The incisor enamel in both Hystricidae and Castoridae is two-layered with a PI made of HSB and a PE made of radial enamel. The main difference in the schmelzmuster of these two rodent families is the thickness of the HSB. In Hystricognathi the HSB are multiserial, with each band containing four to seven prisms (Martin 1992). In contrast, Castorimorpha have uniserial, one prism thick HSB (Mörs *et al.* 2016). Therefore porcupines and beavers are easy to identify and keep apart by their incisor enamel microstructure (Koenigswald & Mörs 2001). Additional discriminating features described by Koenigswald & Mörs (2001) are the inclination of the HSB and the PI/PE ratio. Castoridae, especially large forms like *Anchitheriomys* Roger, 1898, *Castoroides* Foster, 1838, and *Trogontherium* show less inclined HSB, and a significantly thicker PE than Hystricidae. The longitudinal and transverse sections of the enamel of the Senèze incisor (Fig. 3) demonstrate clearly that it belongs to a hystricid. For comparison, we have additionally figured longitudinal sections of *Hystrix primigenia* (Wagner, 1848) from the Late Miocene (Turolian, MN 13) of Polgárdi, Hungary, which show an almost identical schmelzmuster (Fig. 3B, E).

DISCUSSION AND CONCLUSIONS

According to the whole faunal record and to new $^{40}Ar/^{39}Ar$ datings, the locality Senèze has a numerical age range between 2.09 and 2.21 Ma, i.e., slightly younger than St-Vallier (Guérin 1982; Nomade *et al.* 2014; Pastre *et al.* 2015). Both localities have been recently assigned to the Pleistocene epoch (Gibbard & Head 2009). The *Hystrix* material from St-Vallier was assigned to *Hystrix refossa*, a large and hypsodont Eurasian/African species with a stratigraphic range from Late Pliocene to Late Pleistocene (Weers 1994, 2005; Weers & Rook 2003; Rook & Sardella 2005). The relatively low-crowned species *Hystrix primigenia* and *Hystrix depereti* Sen, 2001 have about the same size as *H. refossa,* but are not reported after MN 15 (Sen 1999; Weers & Rook 2003). From the Late Pliocene/Early Pleistocene, there are only two species known according to Weers (1994): *H. refossa* and *Hystrix vinogradovi* Argyropulo, 1941. The latter is a minute species and if the St-Vallier material represents *H. refossa*, the larger Senèze incisor could well represent the same species. The type-locality of *H. refossa* is Perrier-Etouaires (Puy-de-Dôme), a locality geographically very close to Senèze (less than 50 km), but assigned to a slightly older stratigraphic level (MN 16; Bruijn *et al.* 1992; Nomade *et al.* 2014). The presence of a large, hypsodont porcupine in Senèze, as well as in St-Vallier, is in accordance with the partly steppic environment of the two localities which is also documented by other elements of the faunas (Heintz *et al.* 1974; Nomade *et al.* 2014); moreover some pollen morphotaxa found in Senèze could correspond to plants suitable for *Hystrix* diet like underground parts of *Rumex* L., *Plantago* L. and Cichorioideae Chevall., as well as bark of trees like *Fraxinus* L. (Niethammer 1982); gnawed bones have not been reported from Senèze so far.

The study of enamel microstructure of the incisor fragment from Senèze clearly indicates the presence of *Hystrix* and points to the fact that, at least regarding to the families considered here (Hystricidae and Castoridae), the shape and, particularly, the cross-sectional shape of incisors is of taxonomic value and that we have to be cautious with assignments based on ornamentation of the enamel band.

Acknowledgements

Many thanks are due to Eric Delson (New York), Martine Faure and the late Claude Guérin (Lyon), the organizers of the excavations. We thank Daniela C. Kalthoff (Stockholm) for assistance with the specimen preparation, SEM work and discussions, Olavi Grönwall (Stockholm) for access to the collection of recent porcupines, Arlette Armand and Robert Hugueney (Lyon) for photographs. The artwork was kindly made by Javier Herbozo (Stockholm). Last but not least, we acknowledge Sevket Sen (Paris), Jerome Prieto (Munich) and an anonymous reviewer for their valuable remarks on a previous version of the manuscript.

REFERENCES

Bruijn H. de, Daams R., Daxner-Höck G., Fahlbusch V., Ginsburg L., Mein P. & Morales J. 1992. — Report on the RCMNS working group on fossil mammals, Reisenburg 1990. *Newsletters on Stratigraphy* 26 (2/3): 65-118.

Delson E., Faure M., Guérin C., Aprile L., Argant J., Blackwell B. A. B., Debard E., Harcourt-Smith W., Martin-Suarez E., Monguillon A., Parenti F., Pastre J.-F., Sen S., Skinner A. R., Swisher III C. C. & Valli A. M. F. 2006. — Franco-American renewed research at the Late Villafranchian locality of Senèze (Haute-Loire, France). *Courier Forschungsinstitut Senckenberg* 256: 275-290.

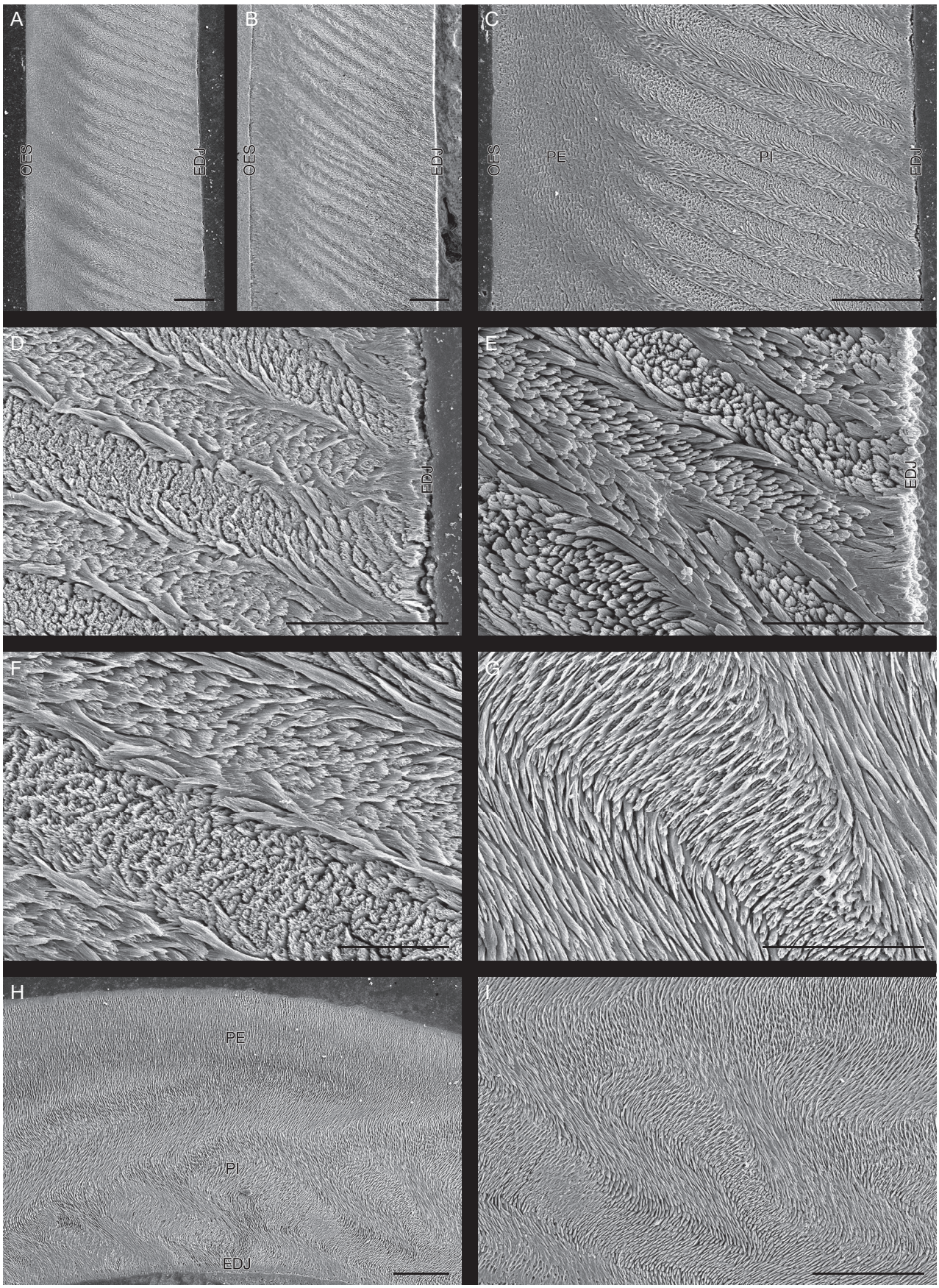
Freye H.-A. 1978. — Familie Castoridae Gray, 1872 – Biber, *in* Niethammer J. & Krapp F. (eds), *Handbuch der Säugetiere Europas.* Akademie Verlagsgesellschaft, Wiesbaden: 182-200.

Gibbard P. L. & Head M. J. 2009. — IUGS ratification of the Quaternary System/Period and the Pleistocene Series/Epoch with a base at 2.58 MA. *Quaternaire* 20 (44): 411-412. https://doi.org/10.4000/quaternaire.5289

Guérin C. 1982. — Première biozonation du Pléistocène européen, principal résultat biostratigraphique de l'étude des Rhinocerotidae (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur d'Europe occidentale. *Geobios* 15 (4): 593-598. https://doi.org/10.1016/S0016-6995(82)80076-4

Heintz E., Guérin C., Martin R. & Prat F. 1974. — Principaux gisements villafranchiens de France. *Mémoires du Bureau de Recherches géologiques et minières, Paris* 78 (1): 169-182.

Fig. 3. — Longitudinal (**A**, **C**, **D**, **F**) and transversal (**G**-**I**) sections of incisor enamel in *Hystrix refossa* Gervais, 1852 from the Early Pleistocene (MN 18) of Senèze, France (NRM-PZ M. 7981) and in *Hystrix primigenia* (Wagner, 1848) from the Late Miocene (Turolian, MN 13) of Polgárdi, Hungary: **A**-**C**: overviews of the whole enamel band from the enamel dentine junction (**EDJ**) to the outer enamel surface (**OES**), showing thick portio interna (**PI**) with inclined, multiserial Hunter-Schreger bands (**HSB**) and thin portio externa (**PE**) with radial enamel; **D**-**F**: close ups showing the inclined, multiserial HSB close to the EDJ (**D**, **E**) and in the center of the tooth (**F**); **G**, detail of **I** showing three neighbouring bands; **H**, overview over the whole enamel band from the enamel dentine junction (**EDJ**) to the outer enamel



surface (**OES**), showing thick portio interna (**PI**) with multiserial Hunter-Schreger bands (**HSB**) and thin portio externa (**PE**) with radial enamel; **I**, close up of the PI showing the multiserial HSB. **B**, **E**, KOE 1849B. Scale bars: A-C, H, I, 100 µm; D, E, G, 50 µm; F, 25 µm.

HUGUENEY M. 2004. — Les grands rongeurs du Pliocène supérieur de Saint-Vallier (Drôme, France): Castoridae, Hystricidae (Mammalia, Rodentia). *Geobios* 37: S126-S132. https://doi.org/10.1016/S0016-6995(04)80012-3

KOENIGSWALD W. VON & MÖRS T. 2001. — The enamel microstructure of *Anchitheriomys* (Rodentia, Mammalia) in comparison with that of other beavers and of porcupines. *Paläontologische Zeitschrift* 74 (4): 601-612. https://doi.org/10.1007/BF02988167

MARTIN T. 1992. — Schmelzmikrostruktur in den Inzisiven alt- und neuweltlicher hystricognather Nagetiere. *Palaeovertebrata, Mémoire extraordinaire*: 1-168.

MILLER G. S. 1912. — *Catalogue of the Mammals of Western Europe in the Collection of the British Museum.* British Museum (Natural History), London, 1019 p. https://doi.org/10.5962/bhl.title.8830

MÖRS T., KOENIGSWALD W. VON & HOCHT F. VON DER 1998. — Rodents (Mammalia) from the late Pliocene Reuver Clay of Hambach (Lower Rhine Embayment, Germany). *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO* 60: 135-160.

MÖRS T. & STEFEN C. 2010. — The castorid *Steneofiber* from NW Germany and its implications for the taxonomy of Miocene beavers. *Acta Palaeontologica Polonica* 55: 189-198. https://doi.org/10.4202/app.2009.0013

MÖRS T., TOMIDA Y. & KALTHOFF D. C. 2016. — A new large beaver (Mammalia, Castoridae) from the Early Miocene of Japan. *Journal of Vertebrate Paleontology* 36 (2): e1080720. https://doi.org/10.1080/02724634.2016.1080720

NIETHAMMER J. 1982. — Familie Hystricidae Burnett, 1830, *in* NIETHAMMER J. & KRAPP F. (eds), *Handbuch der Säugetiere Europas.* Akademie Verlagsgesellschaft, Wiesbaden: 385-605.

NOMADE S., PASTRE J. F., GUILLOU H., FAURE M., GUÉRIN C., DELSON E. DEBARD E., VOINCHET P. & MESSAGER E. 2014. — $^{40}Ar/^{39}Ar$ constraints on some French landmark Late Pliocene to Early Pleistocene large mammalian paleofaunas: Paleoenvironmental and paleoecological implications. *Quaternary Geochronology* 21: 2-15. https://doi.org/10.1016/j.quageo.2012.12.006

PASTRE J.-F., DEBARD É., NOMADE S., GUILLOU H., FAURE M., GUÉRIN C. & DELSON E. 2015. — Nouvelles données géologiques et téphrochronologiques sur le gisement paléontologique du maar de Senèze (Pléistocène inférieur, Massif Central, France). *Quaternaire* 26 (3): 225-244. https://doi.org/10.4000/quaternaire.7368

ROOK L. & SARDELLA R. 2005. — *Hystrix refossa* Gervais, 1852 from Pirro Nord (Early Pleistocene, Southern Italy). *Rivista Italiana di Palaeontologia e Stratigrafia* 111 (3): 489-496. https://doi.org/10.13130/2039-4942/6333

RYBCZYNSKI N. 2007. — Castorid phylogenetics: implications for the evolution of swimming and tree-exploitation in beavers. *Journal of Mammal Evolution* 14: 1-35. https://doi.org/10.1007/s10914-006-9017-3

SCHREUDER A. 1929. — *Conodontes* (*Trogontherium*) and *Castor* from the Teglian Clay compared with Castoridae from other localities. *Archives du Museum Teyler* 6: 99-321.

SEN S. 1999. — Family Hystricidae, *in* RÖSSNER G. E. & HEISSIG K. (eds), *The Miocene Land Mammals of Europe*. Friedrich Pfeil, Munich: 427-434.

WEERS D. J. VAN 1994. — The porcupine *Hystrix refossa* Gervais, 1852 from the Plio-Pleistocene of Europe, with notes on other fossil and extant species of the genus *Hystrix*. *Scripta Geologica* 106: 35-52.

WEERS D. J. VAN 2005. — A taxonomic revision of the Pleistocene *Hystrix* (Hystricidae, Rodentia) from Eurasia with notes on the evolution of the family. *Contributions to Zoology* 74: 301-312.

WEERS D. J. VAN & ROOK L. 2003. — Turolian and Ruscinian porcupines (genus *Hystrix*, Rodentia) from Europe, Asia and North Africa. *Paläontologische Zeitschrift* 77 (1): 95-113. https://doi.org/10.1007/BF03004562

Submitted on 21st October 2016;
accepted on 6 March 2017;
published on 29 December 2017.